



This work is licensed under a Creative Commons Attribution License (CC BY 4.0).

Monograph

[urn:lsid:zoobank.org/pub:AD68CEDD-2F2D-4010-BE7A-1B1AE9E4A0F3](https://zoobank.org/pub/AD68CEDD-2F2D-4010-BE7A-1B1AE9E4A0F3)

The Vetigastropoda (Mollusca) of Walters Shoal, with descriptions of two new genera and thirty new species

David G. HERBERT 

Department of Natural Sciences, National Museum Wales,
Cathays Park, Cardiff, CF10 3NP, UK.

Institute of Systematics, Evolution, Biodiversity (ISYEB),
Muséum national d'histoire naturelle, CNRS, SU, EPHE,
UA, CP 51, 57 rue Cuvier, 75005 Paris, France.

Email: phasianella@gmail.com

[urn:lsid:zoobank.org/author:0C09EE45-6198-482E-857A-EF690C2A016F](https://zoobank.org/author/0C09EE45-6198-482E-857A-EF690C2A016F)

Abstract. The vetigastropod material collected on Walters Shoal during Cruise MD208 of the Tropical Deep-Sea Benthos programme is documented. In total, 50 species were obtained, 30 of which are new and apparently endemic to the seamount. Of the other 20 species, eight are regionally endemic to the south-western Indian Ocean, 11 are more widely distributed in the Indo-West Pacific and one is possibly of deep-water Atlantic origin. The primary affinities of the fauna are with warm temperate South Africa and the tropical western Indian Ocean, but one species is potentially a seamount endemic of southern affinity. A new pseudococculinid genus living on decomposing bird feathers is described, a biogenic substrate association previously unknown in the Mollusca. The following new genera are described: *Imbricoscelis* gen. nov. and *Pterodacna* gen. nov. The following new species are described: *Akritogyra crenulata* sp. nov., *Bathymophila williamsae* sp. nov., *Benthobrookula araneum* sp. nov., *Be. galeneae* sp. nov., *Be. laticostata* sp. nov., *Be. scalaroides* sp. nov., *Be. semisculpta* sp. nov., *Bruceina areneformis* sp. nov., *Calliostoma pantopunctatum* sp. nov., *Cantrainea herosae* sp. nov., *Carinastele achrosta* sp. nov., *Cornisepta marshalli* sp. nov., *Emarginula lentiginosa* sp. nov., *E. nodulicostata* sp. nov., *E. retrogyra* sp. nov., *E. salebrosa* sp. nov., *Fluxinella dufresneae* sp. nov., *Gibbula roseosticta* sp. nov., *Hadroconus scobina* sp. nov., *Kaiparathina monticola* sp. nov., *Lissotesta wareni* sp. nov., *Microcollonia miniata* sp. nov., *Mikro crassus* sp. nov., *Parviturbo cicatricosus* sp. nov., *Phragmomphalina candida* sp. nov., *Pterodacna boucheti* gen. et sp. nov., *Solariella asaphea* sp. nov., *Spinicalliotropis lepidota* sp. nov., *Stomatella multilirata* sp. nov. and *Trenchia mcleani* sp. nov. The following new combinations are proposed: *Brookula coronis* Barnard, 1963 is transferred to *Imbricoscelis* gen. nov., *Cantharidus nolfi* Poppe, Tagaro & H. Dekker, 2006 is transferred to *Kaiparathina* Laws, 1941 and *Solariella incisura* Melvill, 1909 is transferred to *Phragmomphalina* Herbert & Williams, 2020. The following new synonyms are proposed: *Carinastele wareni* Vilvens, 2014 is a synonym of *Bruceina cognata* (Marshall, 1988); *Fluxinella stellaris* Bozzetti, 2008 is a synonym of *Agagus stellamaris* Herbert, 1991.

Keywords. Gastropoda, south-western Indian Ocean, new genera, new species.

Herbert D.G. 2024. The Vetigastropoda (Mollusca) of Walters Shoal, with descriptions of two new genera and thirty new species. *European Journal of Taxonomy* 923: 1–119. <https://doi.org/10.5852/ejt.2024.923.2445>

Introduction

The vetigastropod fauna of much of the south-western Indian Ocean has been relatively well documented (Herbert 2015, and references therein; Williams *et al.* 2020; Vilvens 2021, 2022). However, these studies included few samples from the deeper water regions and geographically isolated seamounts to the south of Madagascar and east of southern Africa. The only records of vetigastropod molluscs from this region are those reported by Barnard (1963a) who recorded nine species (seven newly described) from two widely separated dredge hauls taken in 1961 by the *Africana II* on the Madagascar Plateau and on the Sapmer Bank Seamount (on the edge of the Southwest Indian Ridge), both more than 600 km distant from Walters Shoal. A third such haul at 1300 m on the Mozambique Ridge contained no vetigastropods. More recently, samples collected on the Almirante Leite Knolls, an off-shelf seamount 250 km east of Maputo (MNHN, MAINBAZA Expedition, 2009), have yielded additional material, including previously unknown vetigastropods (Alf *et al.* 2010; Herbert 2012). Two species, a calliostomatid and a colloniid were also recorded in association with wood and bone substrata respectively on seamounts on the Southwest Indian Ridge (Amon *et al.* 2017). No prior records of vetigastropods exist for Walters Shoal itself.

The purpose of this paper is to document the vetigastropod material collected during the MNHN expedition to Walters Shoal in April–May 2017 (Cruise MD208 of the Tropical Deep-Sea Benthos programme). In total, 50 species were obtained, 30 of which are new species described herein. The primary affinities of the fauna are with warm-temperate South Africa and the tropical western Indian Ocean, but some, primarily deeper water taxa, are shared with the south-western Pacific.

Material and methods

All Walters Shoal samples were collected during Cruise MD208 of the Tropical Deep-Sea Benthos programme and are deposited in the Muséum national d’histoire naturelle in Paris, France.

Shells were photographed using a Leica Z16 APO apochromatic zoom macroscope and image stacks were then combined using Helicon Focus Pro (Helicon Soft Ltd) to provide extended depth of field. For SEM study specimens were coated with gold and examined at low accelerating voltage (5–10 kV) using a Jeol Neoscope JCM-5000 or JCM-7000 Benchtop SEM. Radulae were extracted by maceration of the buccal mass in dilute NaOH, rinsed in distilled water and subsequently dehydrated in ethanol, mounted and air-dried on stubs before coating. Following Bouchet *et al.* (2008: 15) the bathymetric range of species is given as the ‘inner values’ of the depth range of individual samples to provide the most conservative estimate (excepting instances where only a single sample is available). Where possible, holotypes of new species were selected from amongst those specimens for which tissue snips preserved for molecular analysis were available. As a result, the holotype may not be the most mature and well-preserved shell. In such cases a mature, well-preserved paratype is illustrated in addition to the holotype (e.g., *Calliostoma pantopunctatum* sp. nov.).

Institutional abbreviations

MNHN = Muséum national d’histoire naturelle, Paris, France
NMSA = KwaZulu-Natal Museum, Pietermaritzburg, South Africa
SAMC = South African Museum, Cape Town, South Africa

Results

Class Gastropoda Cuvier, 1797
Subclass Vetigastropoda Salvini-Plawen, 1980
Order Lepetellida Moskalev, 1971
Superfamily Fissurelloidea J. Fleming, 1822
Family Fissurellidae J. Fleming, 1822
Subfamily Emarginulinae Children, 1834

Genus *Agariste* Monterosato, 1892

Type species

Emarginula compressa Cantraine, 1835[†] (original designation), Pleistocene, Italy.

Agariste phrygium (Herbert & Kilburn, 1986)
Fig. 1

Emarginula phrygium Herbert & Kilburn, 1986: 10, figs 30–34. Type loc.: off Qora River (32°34.0' S, 28°49.7' E), E Cape, South Africa, depth 400–420 m.

Agariste phrygium – Landau *et al.* 2003: 24.

Emarginula phrygium – Herbert 2015: 22. — Muratov & Heyns-Veale 2020: 59, fig. 8 (of holotype).

Material examined

WALTERS SHOAL – slopes • 1 empty shell; stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; MNHN.

Distribution

Walters Shoal and the eastern seaboard of South Africa; dredged on coarse sandy substrata at depths of 420–599 m; living specimens unknown.

Remarks

This highly distinctive species was previously known only from the holotype. This second specimen from Walters Shoal is considerably larger than the holotype (base 9.0 × 6.1 mm, height 8.3 mm vs base 5.8 × 4.7 mm, height 3.7 mm) and proportionately taller, suggesting that height increases more rapidly than length as the shell grows. The shell is also proportionately narrower, but this is almost certainly simply a reflection of the width of the object on which it was living.

Landau *et al.* (2003) drew attention to the similarity between this species and *Emarginula compressa* Cantraine, 1835 from the Pleistocene of Italy, type species of *Agariste* Monterosato, 1892. They considered the strongly convex base and markedly recurved apex with the protoconch off-set to the right, shared by these species to be distinctive features distinguishing *Agariste* from *Emarginula*. Sculpturally, *A. phrygium* differs from *A. compressa* in having a relatively coarse sculpture of radial ribs and uneven concentric ridges, whereas *A. compressa* has a much finer sculpture of close-set radial ribs and irregular concentric growth-lines (Palazzi & Villari 1996: pl. 2 figs 78–79; Vazzana 1996: pl. 2 fig. 8). *Agariste juliencilisi* Landau, Marquet & Grigis, 2003, from the Pliocene of Spain, is sculpturally more similar to *A. phrygium*, but the shell is more laterally compressed and has a much lower profile.

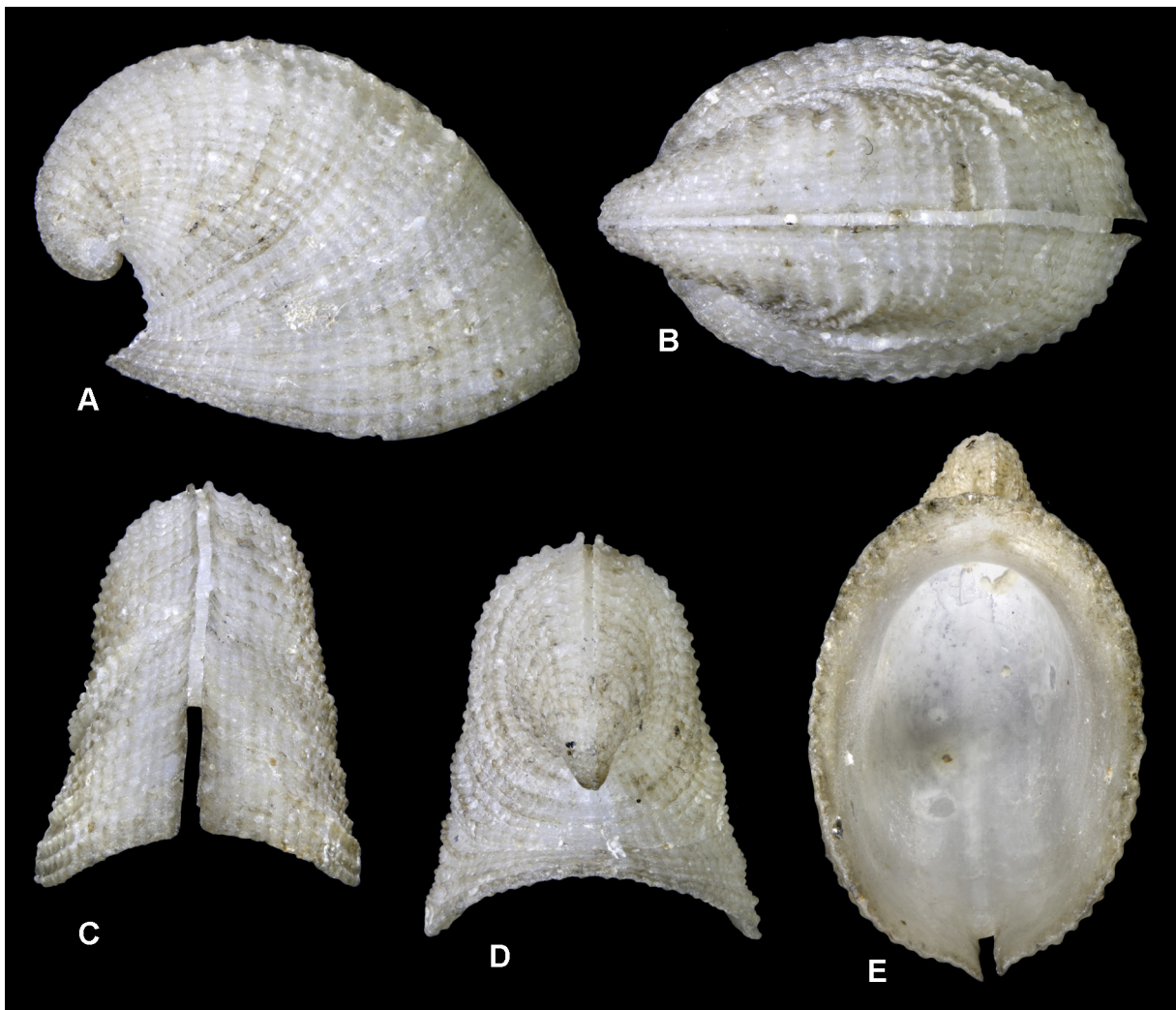


Fig. 1. *Agariste phrygium* (Herbert & Kilburn, 1986), Walters Shoal, stn DW4887, base 9.0×6.1 mm, height 8.3 mm (MNHN). A–B. Lateral and dorsal views. C–D. Anterior and posterior views. E. Basal view.

Genus *Emarginula* Lamarck, 1801

Type species

Emarginula conica Lamarck, 1801 (monotypy) [= *Emarginula fissura* (Linnaeus, 1758)], Recent, north-eastern Atlantic.

Emarginula lentiginosa sp. nov.

[urn:lsid:zoobank.org:act:BDBEBCEE-044B-405A-B4FB-78CCB37B4E7D](https://zoobank.org/urn:lsid:zoobank.org:act:BDBEBCEE-044B-405A-B4FB-78CCB37B4E7D)

Fig. 2

Diagnosis

Shell small, apex strongly recurved, extending well beyond posterior margin of base; slit approx. 0.25–0.33 length of anterior slope; selenizone at most weakly sunken with elevated margins and regular,

moderately coarse lunulae; sculpture finely and crisply cancellate, interstices simple; radial ribs with rounded nodules where crossed by concentric ridges; pale buffish-white with small brownish spots on radial ribs; no broad blotches of colour on anterior face.

Etymology

From the Latin "*lenticula*" – "a freckle"; in reference to the colour pattern of small brown spots.

Material examined

Holotype

WALTERS SHOAL • empty shell; slopes, stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017; MNHN-IM-2000-38246.

Paratypes

WALTERS SHOAL – **slopes** • 2 empty shells; stn DW4880; 33°17' S, 43°51' E; depth 275–318 m; 1 May 2017; MNHN-IM-2000-38247 • 7 empty shells; same collection data as for holotype; MNHN-IM-2000-38248 • 1 empty shell; stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; MNHN-IM-2000-38249 • 2 empty shells; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; MNHN-IM-2000-38250 • 5 empty shells; stn DW4893; 33°16' S, 43°58' E; depth 623–629 m; 4 May 2017; MNHN-IM-2000-38251.

Other material

WALTERS SHOAL – **slopes** • 3 empty shells; stn DW4877; 33°10' S, 43°49' E; depth 217–256 m; 1 May 2017; MNHN • 6 empty shells; stn DW4879; 33°17' S, 43°52' E; depth 288–300 m; 1 May 2017; MNHN • 7 empty shells; stn DW4880; 33°17' S, 43°51' E; depth 275–318 m; 1 May 2017; MNHN • 50+ empty shells; same collection data as for holotype; MNHN • 12 empty shells; stn DW4885; 33°17' S, 43°55' E; depth 272–380 m; 3 May 2017; MNHN • 20+ empty shells; stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN • 13 empty shells; stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; MNHN • 9 empty shells; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; MNHN • 8 empty shells; stn DW4892; 33°12' S, 44°01' E; depth 624–646 m; 4 May 2017; MNHN • 10 empty shells; stn DW4893; 33°16' S, 43°58' E; depth 623–629 m; 4 May 2017; MNHN • 1 empty shell; stn DW4894; 33°09' S, 43°50' E; depth 199–261 m; 5 May 2017; MNHN • 7 empty shells; stn DW4897; 33°09' S, 43°59' E; depth 490–584 m; 5 May 2017; MNHN • 6 empty shells; stn DW4898; 33°09' S, 44°01' E; depth 652–668 m; 6 May 2017; MNHN • 3 empty shells; stn DW4899; 33°09' S, 44°02' E; depth 707–720 m; 6 May 2017; MNHN • 6 empty shells; stn DW4900; 33°10' S, 44°01' E; depth 660–670 m; 6 May 2017; MNHN • 2 empty shells; stn CP4902; 33°08' S, 44°02' E; depth 700–711 m; 7 May 2017; MNHN.

Description

SHELL. Small (basal length up to 6.0 mm), strongly recurved, apex extending well beyond posterior margin of base; basal outline broadly ovate ($L/W \pm 1.45$), slightly concave in side view; height moderate ($H/L 0.51–0.57$); anterior slope strongly convex; posterior slope concave. Anterior slit moderately deep, 0.25–0.33 length of anterior slope; selenizone initially forming a low mid-line rib with scarcely raised margins, but margins becoming more elevated with growth, though frequently damaged; lunulae of selenizone moderately coarse and regular; final part of selenizone at most weakly sunken; remaining sculpture cancellate, comprising ± 16 primary radial ribs with further secondary and tertiary ribs between them; radial sculpture crossed by concentric ridges, similar to secondary ribs in strength; ribs with rounded nodules where crossed by concentric ridges; interstices between ribs and ridges almost square, forming a crisp reticulation, each interstice with a pair of radially elongate intritacal pits; pits often joined apically and diverging basally; basal margin unevenly crenulated by ends of radial ribs; interior

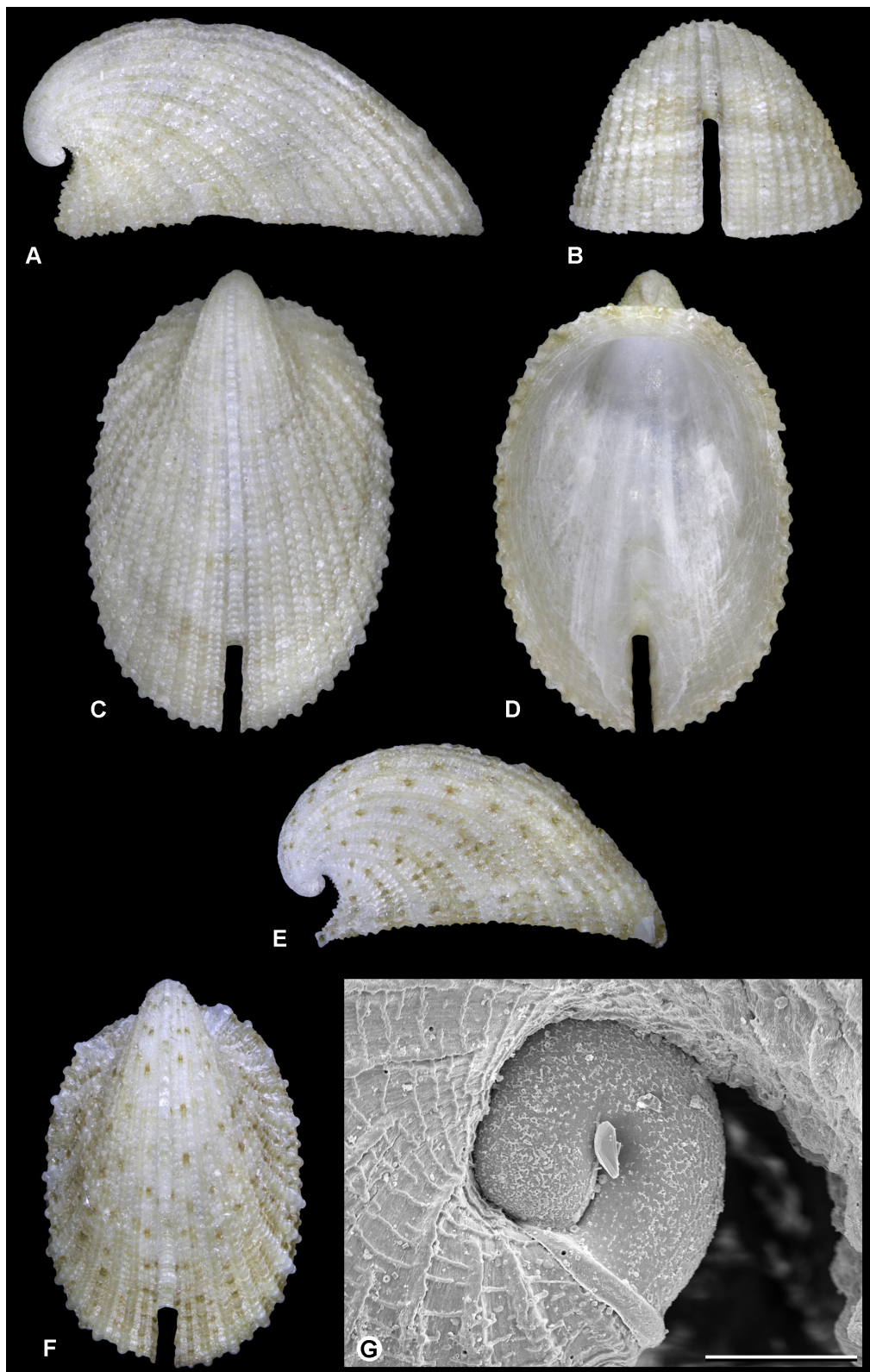


Fig. 2. *Emarginula lentiginosa* sp. nov. A–D. Holotype, base 8.4×5.8 mm, height 4.3 mm (MNHN-IM-2000-38246). E–F. Fresh specimen retaining colour pattern, stn DW4893, basal length 5.9 mm (paratype, MNHN-IM-2000-38251). G. Protoconch, stn DW4893, scale bar=100 µm (paratype, MNHN-IM-2000-38251).

with thickened rim surrounding anterior slit, extending apically as a broad, low mid-line ridge, of similar length to the slit itself; interior of recurved apex scarcely visible or not visible in largest specimens.

PROTOCONCH (Fig. 2G). Typically emarginuliform; single whorl with a thickened terminal varix; sculpture with flocculated superficial granulation; maximum diameter \pm 165 μ m.

COLOUR. Fresh specimens pale buffish-white, recurved apex generally whiter; radial ribs with small brown or olive-brown spots (Fig. 2E–F); spotted ribs usually, but not always alternating with unspotted ribs. No broad blotches of colour on anterior face. The holotype is not fresh and its colour pattern has faded.

DIMENSIONS. Holotype, base 8.4 \times 5.8 mm, height 4.3 mm (= largest specimen).

Distribution

Common as empty shells on the slopes of Walters Shoal, at depths of 256–707 m; dredged and trawled on a variety of sandy substrata; living specimens unknown.

Remarks

In terms of its general shape and sculpture, *Emarginula lentiginosa* sp. nov. is allied to a number of species. The most geographically proximate of these is *E. natalensis* Barnard, 1963, a common species off the eastern seaboard of southern Africa (Herbert 2015). That species, however, is generally less strongly recurved, its selenizone is noticeably sunken and the shell has a greenish colour with darker blotches on the anterior slope (Herbert & Kilburn 1986). The material recorded as *E. natalensis* by Barnard (1963a) from *Africana* stn A1248 on the Sapmer Bank Seamount adjacent to the Southwest Indian Ridge may well in fact be *E. lentiginosa* [cf. *Imbricoscelis coronis* (Barnard, 1963) which also occurs at both localities (see below)]. Also similar is *E. harmilensis* Sturany, 1903 from the Red Sea, the holotype of which was recently illustrated by Albano *et al.* (2017). This too is less strongly recurved and has a sunken selenizone, and its colour pattern includes bold brown blotches on the anterior face (see also Singer 1998). I cannot agree with the conclusion of Geiger (in Albano *et al.* 2017) that this species is a synonym of *E. costulata* Deshayes, 1863 from the south-western Indian Ocean. That species is less strongly recurved, has coarser sculpture with compound interstices and is of an olive-green colour (Kilburn 1978 (as *E. tenuicostata*); Drivas & Jay 1985; Herbert & Kilburn 1986 (as *E. tenuicostata*); Herbert 1987a) [illustrations of lectotype available from <https://science.mnhn.fr/institution/mnhn/collection/im/item/2000-4750>]. *Emarginula maculata* A. Adams, 1863 from southern Japan and the Philippines (Sasaki 2000a; Poppe & Tagaro 2020) is another similar species, but this too has a mottled rather than a finely spotted colour pattern and has bold blotches on the anterior face. *Emarginula curvata* Schepman, 1908 from the Sulu Archipelago has finer radial sculpture, a sunken selenizone and lacks the freckled colour pattern.

Emarginula nodulicostata sp. nov.

[urn:lsid:zoobank.org:act:DA82AFE9-2C80-4ED8-AEF2-6945D3329814](https://zoobank.org/urn:lsid:zoobank.org:act:DA82AFE9-2C80-4ED8-AEF2-6945D3329814)

Fig. 3

Diagnosis

Shell very small, stout, uniformly milky white; apex strongly recurved, extending well beyond posterior margin; dorsal profile strongly convex, anterior slit narrow and deep; sculpture coarsely cancellate, radial and concentric elements of similar strength; radial ribs nodular where crossed by concentric ridges; sculptural interstices simple; basal margin broader at posterior, distinctly crenulated at ends of radial ribs.

Etymology

From the Latin “*nodus*” – “a knot or swelling”, dim. “*nodulus*”, and “*costa*” – “rib”, “*costatus*” “ribbed”; in reference to the nodose sculpture of the radial ribs.

Material examined

Holotype

WALTERS SHOAL • empty shell; summit area south-west, stn WS04; 33°12.2' S, 43°50.8' E; depth 40 m; 30 Apr. 2017; MNHN-IM-2000-38252.

Paratypes

WALTERS SHOAL • 6 empty shells; summit area, south-west, stn WS03; 33°12.2S, 43°50.8' E; depth 40 m; 30 Apr. 2017; MNHN-IM-2000-38253 • 11 empty shells; summit area south-west, stn WS04; 33°12.2' S, 43°50.8' E; depth 40 m; 30 Apr. 2017; MNHN-IM-2000-38254 • 1 empty shell; summit area, south, stn WS06; 33°15.1S, 43°54.5' E; depth 26 m; 1 May 2017; MNHN-IM-2000-38255 • 10 empty shells; summit area, south, stn WS07; 33°15.4S, 43°52.2' E; depth 30–33 m; 2 May 2017; MNHN-IM-2000-38256 • 3 empty shells; summit area, south-east, stn WS08; 33°13.7S, 43°55.9' E; depth 30–33 m; 3 May 2017; MNHN-IM-2000-3824657.

Description

SHELL. Very small (basal length up to 3.45 mm), but relatively thick; apex strongly recurved, extending well beyond posterior margin of base; basal outline evenly ovate ($L/W=1.37-1.40$), slightly concave in side view; height moderate ($H/L=0.52-0.65$); dorsal profile strongly convex in side view, posterior slope comprising only one-third height of shell in adult; anterior face slightly flattened either side of slit; posterior slope almost vertical in largest specimens, much less so in smaller ones; protoconch tucked under recurved apex, slightly twisted to right. Anterior slit narrow and deep, approx. one-third of anterior slope; selenizone initially forming a broad mid-line rib (margins scarcely raised) with coarse lunulae that project above its margins (Fig. 3E arrow), but selenizone becoming somewhat sunken nearer to slit in largest specimens; remaining sculpture relatively coarsely cancellate, comprising ± 16 primary radial ribs with narrower secondary ribs between them; secondaries stronger laterally, those between anterior ribs more slender; radial sculpture crossed by coarse concentric ridges; radial and concentric sculpture of similar strength; radial ribs roundly nodular where crossed by concentric ridges; interstices between ribs and ridges simple, square to concentrically elongate-rectangular, with paired intritacalx pits; basal margin distinctly crenulated at ends of radial ribs and noticeably broader posteriorly (Fig. 3C). Interior with broad, low ridge underlying selenizone posterior to anterior slit, approx. $\frac{2}{3}$ length of slit; ridge itself with shallow central furrow; with interior of apex only just visible in basal view.

PROTOCONCH (Fig. 3F). Typically emarginuliform; single whorl with sharp, flared terminal lip; surface with finely flocculated superficial granulation, maximum diameter $\pm 140 \mu\text{m}$.

COLOUR. Uniformly milky white, somewhat translucent when fresh.

DIMENSIONS. Holotype, base 3.45×2.50 mm, height 2.25 mm (= largest specimen).

Distribution

A shallow-water species known only from the summit area of Walters Shoal, at depths of 26–40 m; living specimens unknown.

Remarks

Other strongly recurved species in which the apex lies beyond the posterior margin of the base include *Emarginula adamsiana* Sowerby II, 1863 from Japan, *E. convexa* Hedley, 1907 from Queensland, *E. dahli* Thiele, 1913 from the Bismarck Archipelago, and *E. circumalbum* Poppe & Tagaro, 2020 and *E. galericulata* A. Adams 1852 from the Philippines. All except *E. convexa* attain a larger size

than *E. nodulicostata* sp. nov. (basal length >4.5 mm); in addition *E. adamsiana* is pale pink, and *E. galericulata* has finer sculpture. *Emarginula convexa* has an indistinct concentric colour pattern of pale green and grey zones, more numerous radial ribs and finer concentric sculpture. *Emarginula circumalbum* is a deeper-water species (250–500 m) and has a proportionately broader basal outline and a much shorter slit. The poorly known *E. dahli* is perhaps the most similar species, but this also occurs in much deeper water (160–180 m).

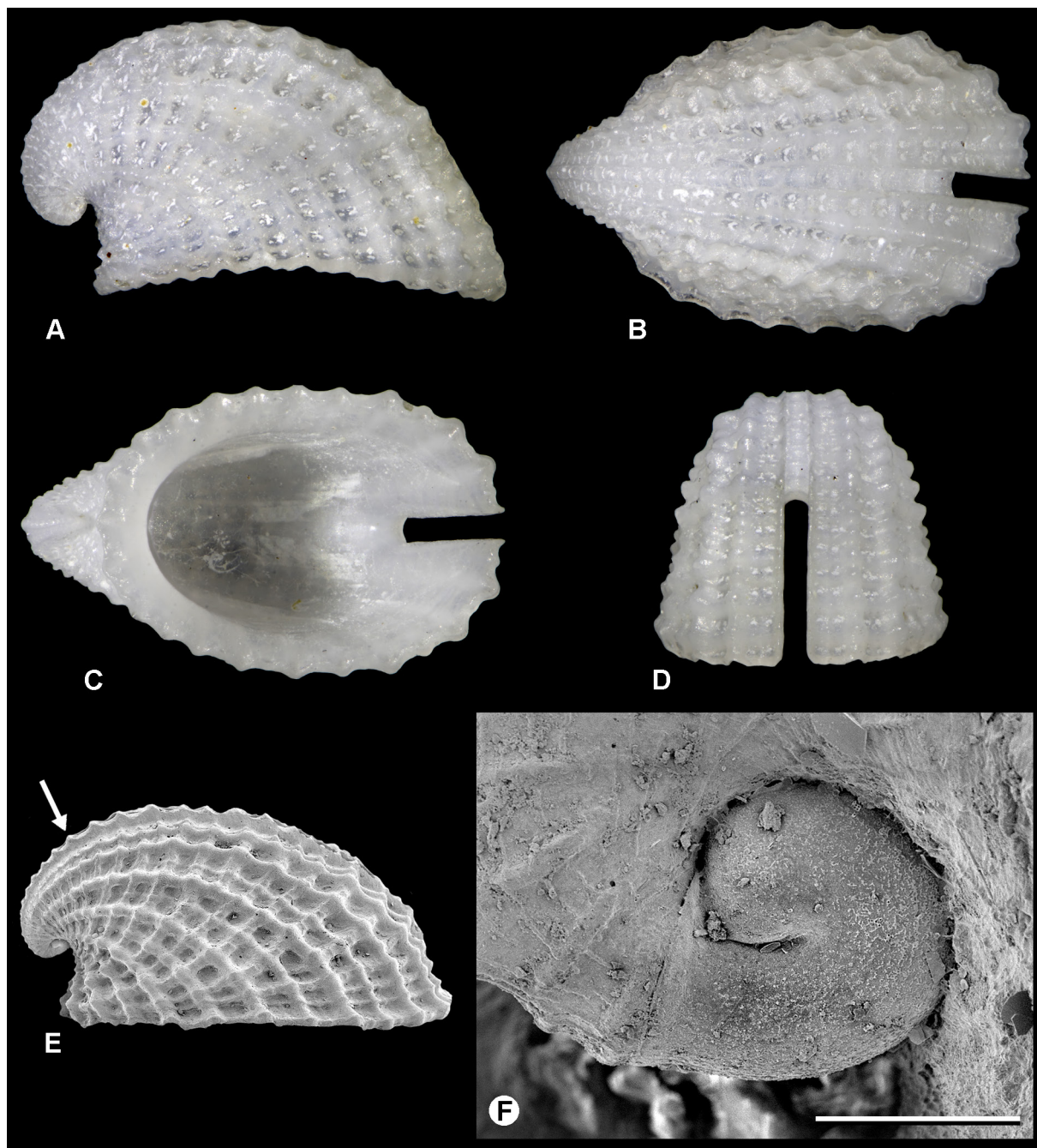


Fig. 3. *Emarginula nodulicostata* sp. nov. **A–D.** Holotype, base 3.45×2.5 mm, height 2.25 mm (MNHN-IM-2000-38252). **E.** SEM of subadult specimen to show detail of sculpture, projecting lunulae of early selenizone arrowed, stn WS07, basal length 3.15 mm (paratype, MNHN-IM-2000-38256). **F.** Protoconch, stn WS07, scale bar = 100 μ m (paratype, MNHN-IM-2000-38256).

Emarginula retrogyra sp. nov.

urn:lsid:zoobank.org:act:AA5A658F-0F58-485C-9786-AE7C6CCACE17

Fig. 4

Diagnosis

Shell thin, relatively high and with apex strongly recurved such that its interior scarcely visible in basal view; apex not overhanging posterior margin of base; protoconch tucked under recurved apex, but largely remaining free of teleoconch due to strong apical recurvature; margins of selenizone distinctly elevated, but thin; sculpture fine and relatively uniform, comprising close-set, finely nodular radial ribs crossed by weaker, less elevated, concentric ridges; interstices quadrate and simple; pale straw brown with darker concentric bands.

Etymology

From the Latin “*retro*” – “backwards” and “*gyro*” – “to turn around”; in reference to the strongly recurved apex.

Material examined

Holotype

WALTERS SHOAL • empty shell; slopes; stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017; MNHN-IM-2000-38258.

Paratypes

WALTERS SHOAL – **slopes** • 1 empty shell; same collection data as for holotype; MNHN-IM-2000-38259 • 1 empty shell, juvenile; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; MNHN-IM-2000-38260 • 2 empty shells, juvenile; stn DW4897; 33°09' S, 43°59' E; depth 490–584 m; 5 May 2017; MNHN-IM-2000-38261.

Other material

WALTERS SHOAL – **slopes** • 1 empty shell, juvenile (broken); stn DW4879; 33°17' S, 43°52' E; depth 288–300 m; 1 May 2017; MNHN • 1 empty shell, juvenile; stn DW4885; 33°17' S, 43°55' E; depth 272–380 m; 3 May 2017; MNHN.

Description

SHELL. Small and thin (basal length up to 10.5 mm); relatively high ($H/L \pm 0.64$); anterior slope convex, but not strongly so and apex not extending over posterior margin of base; tip of apex nonetheless strongly recurved; basal outline evenly ovate ($L/D \pm 1.3$), slightly concave in side view; anterior face not flattened; posterior slope for the most part straight, becoming strongly concave beneath recurved apex; protoconch tucked under recurved apex, but largely remaining free of ascending posterior face of teleoconch due to strong apical recurvature. Anterior slit moderately deep, approx. one-third of anterior slope; margins of selenizone distinctly elevated, but thin and mostly broken away in holotype, but partially remaining in paratypes; selenizone itself not raised, bearing coarse, evenly-spaced lunulae, these becoming more numerous and more close-set nearer to slit; remaining sculpture of fine, close-set radial ribs, of which approx. 22 primary with secondary and tertiary intermediaries between them; primary and secondary ribs of more or less equal size at shell margin, tertiaries usually slightly weaker; intervals between ribs narrow, but well defined; concentric sculpture of fine, close-set ridges; these weaker and not as markedly raised as radial ribs; ridges cross ribs rendering latter crisply nodular (Fig. 4E); interstices between ribs and ridges deep, quadrate, simple, with one or a pair of intritacalx pits; basal margin mostly damaged in holotype, but evidently finely crenulated at ends of radial ribs with shallow grooves on interior, underlying radial ribs, longer and more evident in juveniles. Interior with

broad ridge underlying selenizone, approx. twice length of slit; ridge itself with shallow central furrow; interior of apex scarcely visible due to extent of recurvature.

PROTOCONCH (Fig. 4F). Typically emarginuliform; single whorl with thickened terminal varix; rotated 90° further with regard to teleoconch such that varix is parallel with plane of shell aperture; surface with sparse superficial granulation; maximum diameter $\pm 180 \mu\text{m}$.

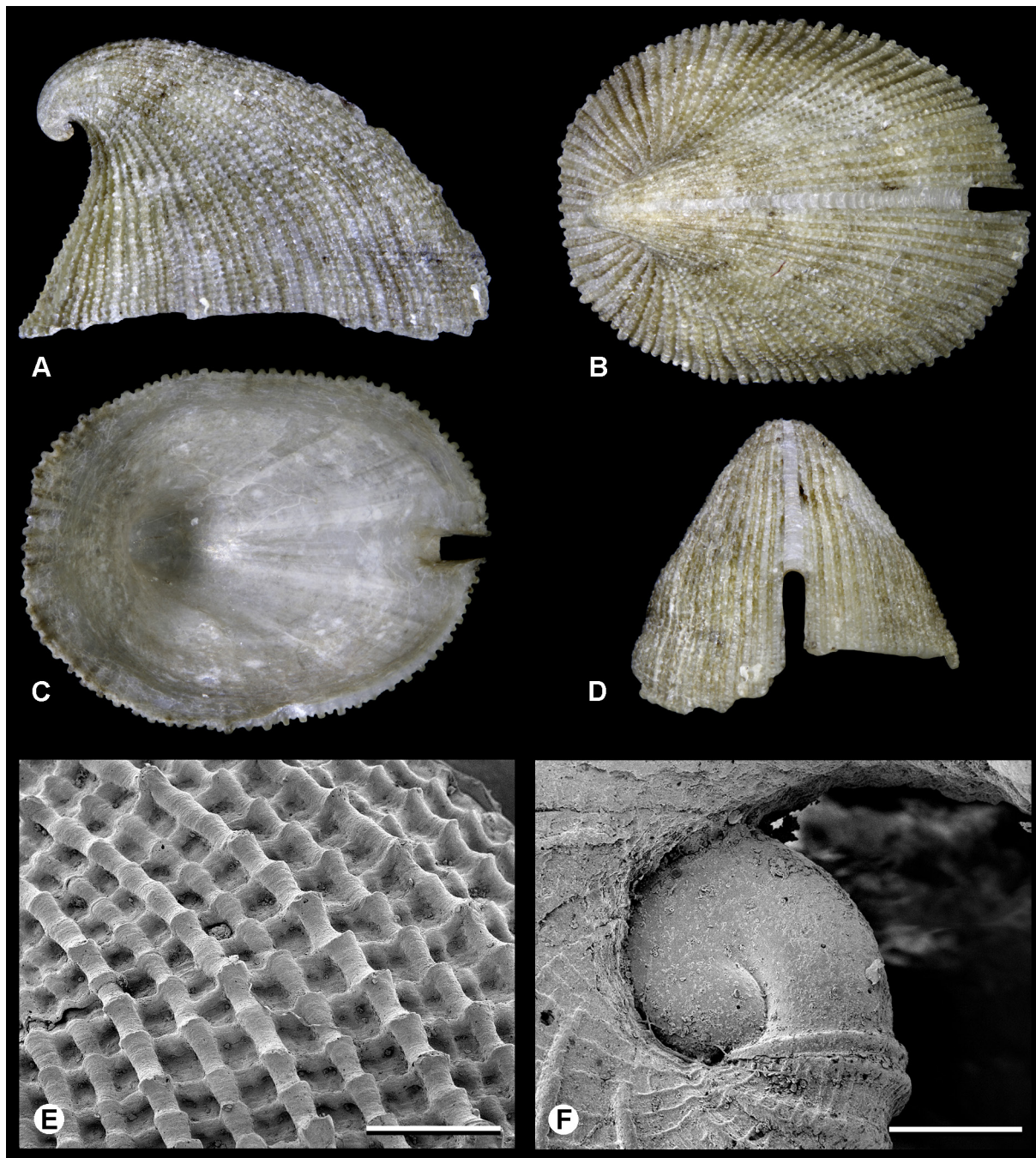


Fig. 4. *Emarginula retrogyra* sp. nov. **A–D.** Holotype, base 10.5×8.1 mm, height 6.7 mm (MNHN-IM-2000-38258). **E.** SEM showing detail of sculpture, stn DW4890, scale bar=0.5 mm (paratype, MNHN-IM-2000-38260). **F.** Protoconch, stn DW4890, scale bar=100 μm (paratype, MNHN-IM-2000-38260).

COLOUR. Holotype rather dirty pale olive-brown, but fresher specimens with broad, darker greenish-brown concentric bands and occasional greenish-brown spots.

DIMENSIONS. Holotype, base 10.5 × 8.1 mm, height 6.7 mm (= largest specimen).

Distribution

Known only from the slopes of Walters Shoal, at depths of 300–492 m; living specimens unknown.

Remarks

The moderately high, finely sculptured shell of *E. retrogyra* sp. nov., with its strongly recurved apex, is distinctive. The Philippines specimen, illustrated by Poppe & Tagaro (2020: pl. 23 fig. 4a-c) as *Emarginula choristes* Dall, 1925, closely resembles the new species, though its apex is not as strongly recurved and it has a more distinctly greenish hue. Japanese *E. choristes* has a more elevated shell (H/L=0.85–0.95) with a shorter slit and a less strongly recurved but more posteriorly positioned apex (level with the posterior margin of the base). In addition, it has a distinct sculpture in which the major radial ribs are fewer (± 16) and remain more prominent (Dall 1925; Habe 1955; Hasegawa 2018). *Emarginula annielangleitae* Poppe & Tagaro, 2020 from the Philippines has a similar lateral profile to that of *E. retrogyra*, but again it is not as strongly recurved. It also attains a considerably larger size (length up to 18 mm) and has more dominant primary radial ribs that remain prominent at the basal margin. *Emarginula dubia* Schepman, 1908 from Indonesia and the Philippines has a similar fine sculpture, but is neither as elevated nor as recurved as *E. retrogyra*. Of the South African species, *E. viridicana* Herbert & Kilburn, 1986 has a similar shape, but its apex is less strongly recurved and the shell is more robust with much coarser sculpture, whereas in *E. connelli* Kilburn, 1978, the shell is taller, the apex overhangs the posterior basal margin and the primary radial ribs remain significantly stronger than the secondaries at the shell margin.

Emarginula salebrosa sp. nov.

[urn:lsid:zoobank.org:act:CAA337F8-D068-4E4D-BECB-300A2A848FB8](https://zoobank.org/act:CAA337F8-D068-4E4D-BECB-300A2A848FB8)

Fig. 5

Diagnosis

Shell small and thick, uniformly whitish; apex strongly recurved, close to or just beyond posterior margin of base; anterior face slightly flattened either side of slit; anterior slit narrow and deep; sculpture coarsely cancellate, comprising 14–16 primary radial ribs with narrower secondary ribs in intervals; ribs with strong nodules where crossed by coarse concentric ridges; interstices between ribs and ridges simple, roundly quadrate depressions with single or paired intritacalx pits.

Etymology

From the Latin “*salebra, salebrosus*” – “roughness, rough”; in reference to the coarse sculpture.

Material examined

Holotype

WALTERS SHOAL • empty shell; slopes, stn DW4898; 33°09' S, 44.01' E; depth 652–668 m; 6 May 2017; MNHN-IM-2000-38262.

Paratypes

WALTERS SHOAL – **slopes** • 2 empty shells; same collection data as for holotype; MNHN-2000-38263 • 5 empty shells; stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017; MNHN-2000-38264 • 6 empty shells; stn DW4883; 33°14' S, 43°51' E; depth 290–326 m; 2 May 2017; MNHN-2000-38265 •

8 empty shells; stn DW4892; 33°12' S, 44°01' E; depth 624–646 m; 4 May 2017; MNHN-2000-38266 •
6 empty shells; stn DW4899; 33°09' S, 44°02' E; depth 707–720 m; 6 May 2017; MNHN-2000-38267 •
4 empty shells; stn DW4900; 33°10' S, 44°01' E; depth 660–670 m; 6 May 2017; MNHN-2000-38268.

Other material

WALTERS SHOAL – slopes • 1 empty shell; stn DW4880; 33°17' S, 43°51' E; depth 275–318 m; 1 May 2017; MNHN • 1 empty shell; stn DW4885; 33°17' S, 43°55' E; depth 272–380 m; 3 May 2017; MNHN • 1 empty shell; stn DW4888; 33°10' S, 43°57' E; depth 299–311 m; 3 May 2017; MNHN • 1 empty shell, juvenile; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; MNHN.

Description

SHELL. Small (basal length up to 8.4 mm) and thick; apex strongly recurved, extending slightly beyond posterior margin of base in some specimens, not quite reaching it in others; dorsal profile strongly convex, basal outline broadly ovate (L/W=1.3–1.4), flat or slightly concave in side view; height moderate (H/L 0.56–0.63); anterior slope humped in side view, anterior face slightly flattened either side of slit; posterior slope almost straight and steeply inclined in largest specimens, less so in smaller ones; protoconch tightly tucked beneath apex, missing in many specimens. Anterior slit narrow and moderately deep, approx. one-third of anterior slope; selenizone initially forming a low mid-line rib (margins scarcely raised) with coarse lunulae, but selenizone becoming proportionately less prominent with growth, its margins weaker than neighbouring primary ribs, but not sunken; remaining sculpture coarsely cancellate, comprising 14–16 primary radial ribs with narrower secondary ribs between them; occasional tertiary ribs laterally near basal margin; radial sculpture crossed by coarse concentric ridges, equal in strength to secondary ribs; radial ribs with strong nodules where crossed by concentric ridges; interstices between ribs and ridges simple, roundly quadrate depressions rather than crisp reticulations, with single or paired intritacalx pits; basal margin coarsely crenulated by ends of radial ribs; interior with broad, low thickened ridge underlying selenizone, interior of apex clearly visible.

PROTOCONCH (Fig. 5F). Somewhat eroded in material available, but typically emarginuliform; a single whorl sculptured with traces of irregular superficial granulation; a thickened terminal lip not evident; maximum diameter ± 140 µm.

COLOUR. Fresher juvenile specimens uniformly white, larger shells dirty white.

DIMENSIONS. Holotype, base 7.0 × 5.4 mm, height 4.4 mm; largest specimen, base 8.4 × 6.0 mm, height 4.7 mm.

Distribution

Known only from the slopes of Walters Shoal, at depths of 311–707 m; living specimens unknown. The species may in fact be extinct (see below).

Remarks

The coarse sculpture of *Emarginula salebrosa* sp. nov. resembles that of *E. nodulicostata* sp. nov., but the present species attains a much larger size (basal length 8.4 mm vs < 3.5 mm), has a less recurved apex and lives at significantly greater depths (>300 m vs < 50 m). Another sculpturally similar species is *E. circumalbum* Poppe & Tagaro, 2020 from the Philippines, but that species has a somewhat broader shell, finer radial ribs, a much shorter slit and the lunulae of the selenizone protrude well above the shell surface in side view. *Emarginula dahli* Thiele, 1913 from the Bismark Archipelago has a more strongly recurved apex and a keel-like selenizone with raised edges and protruding lunulae.

None of the available specimens of *Emarginula salebrosa* sp. nov. are in fresh condition. All, even the juvenile individuals, appear to be old and some are filled with consolidated sediment suggesting that they are subfossil. It is thus quite possible that the species is no longer extant.

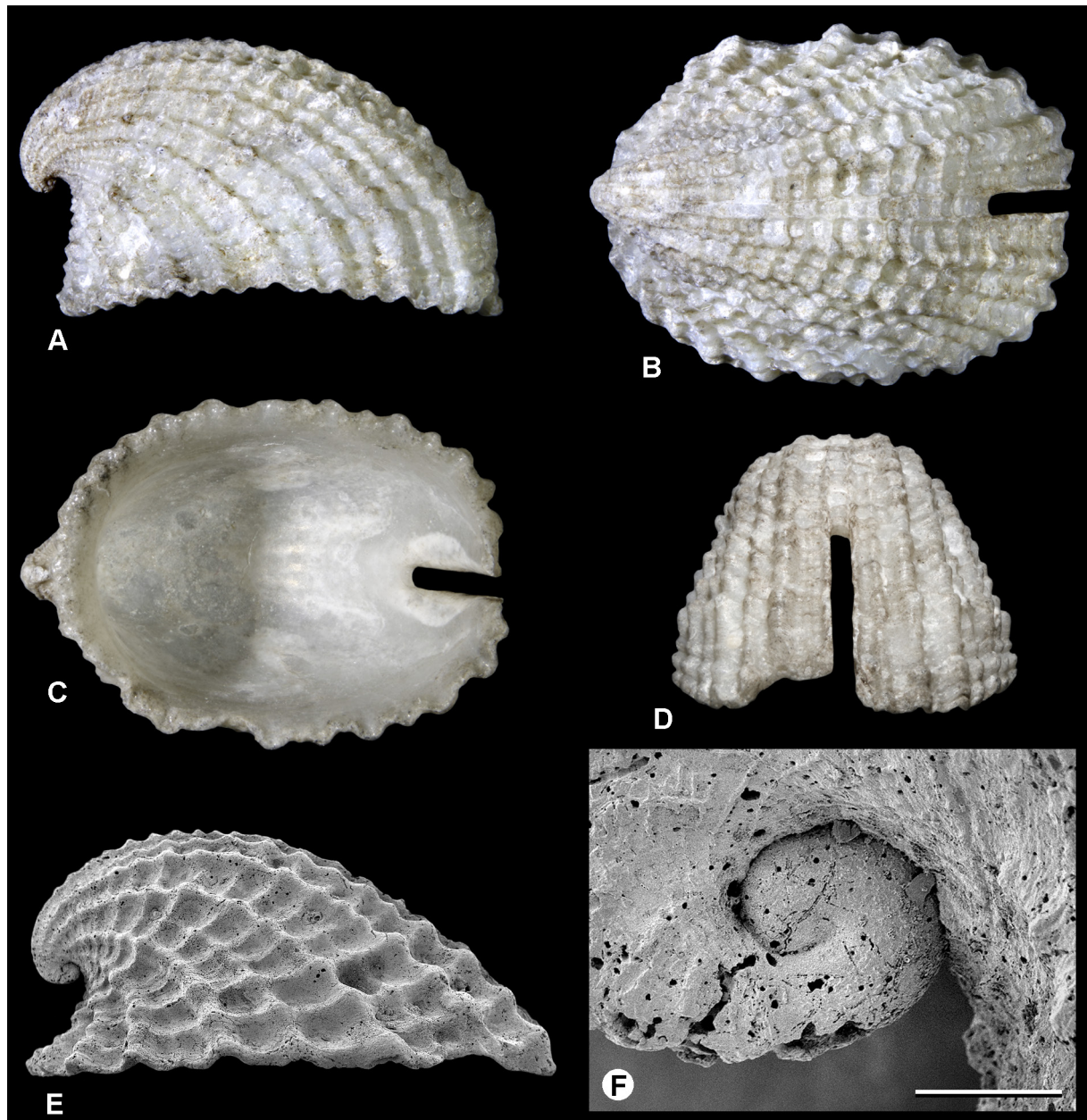


Fig. 5. *Emarginula salebrosa* sp. nov. **A–D.** Holotype, base 7.0×5.4 mm, height 4.4 mm (MNHN-IM-2000-38262). **E.** SEM of juvenile specimen showing detail of sculpture, stn DW4899, basal length 4.1 mm (paratype, MNHN-IM-2000-38267). **F.** Protoconch, stn DW4899, scale bar = 100 μ m (paratype, MNHN-IM-2000-38267).

Emarginula sublaevis Schepman, 1908

Fig. 6

Emarginula sublaevis Schepman, 1908: 91, pl. 7 fig. 9. Type loc.: *Siboga* stn 280, 8°17.4' S, 127°30.7' E (off eastern tip of Timor Island), depth 1224 m.

Emarginula sublaevis – Thiele 1913 in 1912–1919: 64, pl. 7. figs 16–17. — Hasegawa 2018: 143, figs 14g–j.

Material examined

WALTERS SHOAL – **slopes** • 2 empty shells, juvenile; stn DW4899; 33°09' S, 44°02' E; depth 707–720 m; 6 May 2017; MNHN • 1 empty shell; stn DW4900; 33°10' S, 44°01' E; depth 660–670 m; 6 May 2017; MNHN • 1 living specimen; stn CP4901; 33°09' S, 44°01' E; depth 647–672 m; 6 May 2017; DNA tissue sample; MNHN-IM-2013-67271 • 1 living specimen; stn CP4902; 33°08' S, 44°02' E; depth 700–711 m; 7 May 2017; DNA tissue sample; MNHN-IM-2013-67272.

Distribution

Japan and the central Indo-West Pacific to the south-western Indian Ocean. Collected on the slopes of Walters Shoal at depths of 670–707 m; trawled alive at depths of 672–700 m, on coarse substrata with abundant solitary corals, decapods and empty pteropod shells.

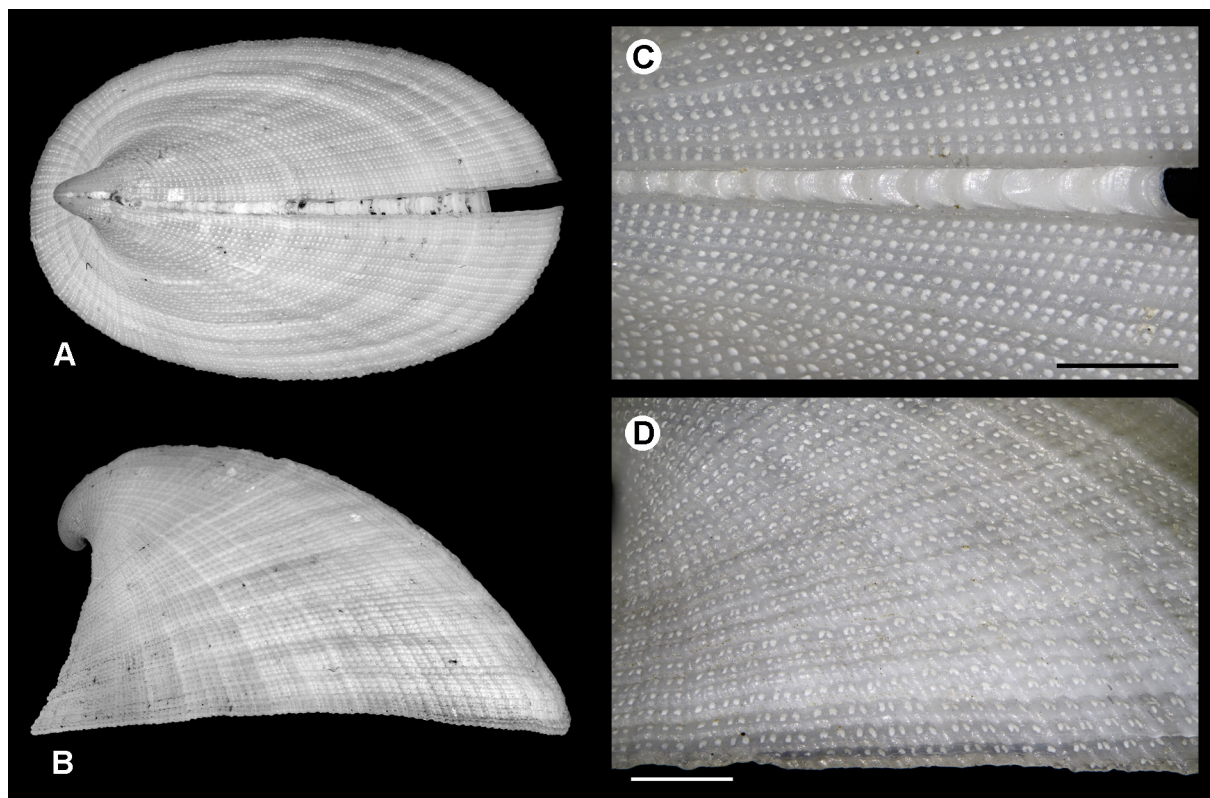


Fig. 6. *Emarginula sublaevis* Schepman, 1908. **A–B.** Dorsal and side views, Walters Shoal, stn CP4901, base 15.6 × 10.1 mm, height 8.3 mm (MNHN-IM-2013-67271). **C–D.** Detail of selenizone morphology and shell sculpture, Walters Shoal, stn DW4900 (MNHN). Scale bars = 1.0 mm.

Remarks

This is the first record of *Emarginula sublaevis* from the Indian Ocean. Recently recorded from the Ogasawara Islands and Japan (Hasegawa 2018), the species was previously known only from the holotype dredged off East Timor. The shell is distinctive on account of its relatively large size, coarsely lunulate selenizone with keeled lateral margins (Fig. 6C) and extremely fine sculpture (Fig. 6D). The original figure of the holotype provided by Schepman (1908) rather exaggerates the strength of the radial sculpture, but the photograph of the same specimen provided by Hasegawa (2018) gives a more realistic depiction. The intritacalx pits are small and simple, dividing progressively with growth as intermediary radial ribs (secondary to quaternary) arise by intercalation between the primary ribs, though there is little difference in rib strength at the shell margin.

The specimens from the Walters Shoal have a slightly narrower basal profile than the holotype (L/W 1.48–1.54 vs 1.37 in holotype) and the apex lies somewhat closer to the posterior margin, but such differences are trivial when considered in terms of the extent of intraspecific variation shown in some other species of *Emarginula*. Though geographically distant from the central Indo-West Pacific records, I can find no grounds to consider the Walters Shoal material a distinct species.

Emarginula poppeorum Romani & Crocetta, 2017 [= *E. gigantea* Poppe, 2008, non Coquand, 1859, nec Seguenza, 1863] is evidently a related species of even larger size, attaining a length of up to 55 mm (Poppe & Tagaro 2020). Hasegawa (2018) considered *E. hosoyai* Habe, 1953 to be a synonym of *E. sublaevis*, but more recently, Poppe & Tagaro (2020) treated it as distinct.

Emarginula undulata Melvill & Standen, 1903

Fig. 7

Emarginula undulata Melvill & Standen, 1903: 290, pl. 20 fig. 1. Type loc.: Gulf of Oman (25°58' N 56°54' E), depth 285 m.

Emarginula vadum Barnard, 1963b: 297, figs 23d, 24b. Type loc.: off Cape Vidal, KwaZulu-Natal, South Africa, depth 146–183 m.

Emarginula undulata – Thiele 1915 in 1912–1919: 75, pl. 9 figs 10–11. — Herbert & Kilburn 1986: 12, figs 2–3, 39–44. — Bosch *et al.* 1995: 30. — Singer 1998: 7. — Herbert 2015: 22. — Poppe & Tagaro 2020: 44, pl. 37 figs 3–4.

Emarginula vadum – Kilburn 1978: 444, pl. 4a, e.



Fig. 7. *Emarginula undulata* Melvill & Standen, 1903, Walters Shoal, stn DW4878, base 6.8 × 4.6 mm, height 3.8 mm (MNHN).

Material examined

WALTERS SHOAL – slopes • 1 empty shell; stn DW4877; 33°10' S, 43°49' E; depth 217–256 m; 1 May 2017; MNHN • 2 empty shells; stn DW4878; 33°09' S, 43°50' E; depth 221–256 m; 1 May 2017; MNHN • 1 empty shell; stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017; MNHN • 2 empty shells; stn DW4885; 33°17' S, 43°55' E; depth 272–380 m; 3 May 2017; MNHN • 1 empty shell; stn DW4897; 33°09' S, 43°59' E; depth 490–584 m; 5 May 2017; MNHN.

Distribution

Widely distributed along the continental margin of the western Indian Ocean, from the Gulf of Oman southwards to eastern South Africa, at depths of 50–400 m (living 75–120 m) (Herbert 2015) and recently recorded from the Philippines (Poppe & Tagaro 2020). Found on the slopes of Walters Shoal, at depths of 256–490 m (none collected alive).

Remarks

Emarginula undulata is a distinctive species on account of its thin shell with numerous fine, concentrically elongate intritacal pits, raised selenizone and relatively few, broad, radial ridges with widely-spaced, conical bumps.

Subfamily Zeidorinae Naef, 1913

Genus *Cornisepta* McLean & Geiger, 1998

Type species

Fissurisepta antarctica Egorova, 1972 (original designation), Recent, Antarctica.

Cornisepta marshalli sp. nov.

[urn:lsid:zoobank.org:act:1D805ECB-2850-4290-9696-E9A5E8867488](https://zoobank.org/urn:lsid:zoobank.org:act:1D805ECB-2850-4290-9696-E9A5E8867488)

Fig. 8

Diagnosis

Shell asymmetrically conical, anterior slope longer, straight or lightly convex; posterior slope distinctly concave; protoconch missing; apical foramen at summit of anterior slope, internal transverse septum well developed; shell lacking raised pustules; sculpture primarily of thin, irregularly-spaced, co-marginal ridges; microsculpture extremely fine, comprising concentric ripples and radial threads; translucent white.

Etymology

Named for Dr Bruce Marshall (National Museum of New Zealand – Te Papa Tongarewa), in recognition of his invaluable contribution to vetigastropod taxonomy and systematics, and of his friendship and support during my early career.

Material examined

Holotype

WALTERS SHOAL • empty shell; slopes, stn DW4898; 33°09' S, 44°01' E; depth 652–668 m; 6 May 2017; MNHN-IM-2000-38269.

Paratypes

WALTERS SHOAL – slopes • 3 empty shells; stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN-IM-2000-38270 • 1 empty shell; stn DW4892; 33°12' S, 44°01' E; depth 624–646 m; 4 May 2017; MNHN-IM-2000-38271 • 1 empty shell; same collection data as for holotype; MNHN-IM-2000-38272 • 1 empty shell; stn DW4900; 33°10' S, 44°01' E; depth 660–670 m; 6 May 2017; MNHN-IM-2000-38273.

Description

SHELL. Basal outline evenly elliptical ($L/W=1.33\text{--}1.36$), flat in side view; height moderate ($H/L=0.56\text{--}0.72$); lateral profile asymmetrically conical; anterior slope longer, straight or slightly convex; posterior slope shorter, distinctly concave; apical foramen at summit of anterior slope, its posterior border higher than anterior one and lateral profile of apex thus somewhat notched (Fig. 8A); internal transverse septum well developed, straight, extending ventrally for about half shell height, its ventral margin shallowly concave; sculpture primarily of thin, irregularly-spaced, co-marginal ridges of uneven strength and sometimes discontinuous; shell lacking raised pustules, but with a rather uneven microsculpture of extremely fine, close-set, concentric ripples crossed by similarly fine radial threads.

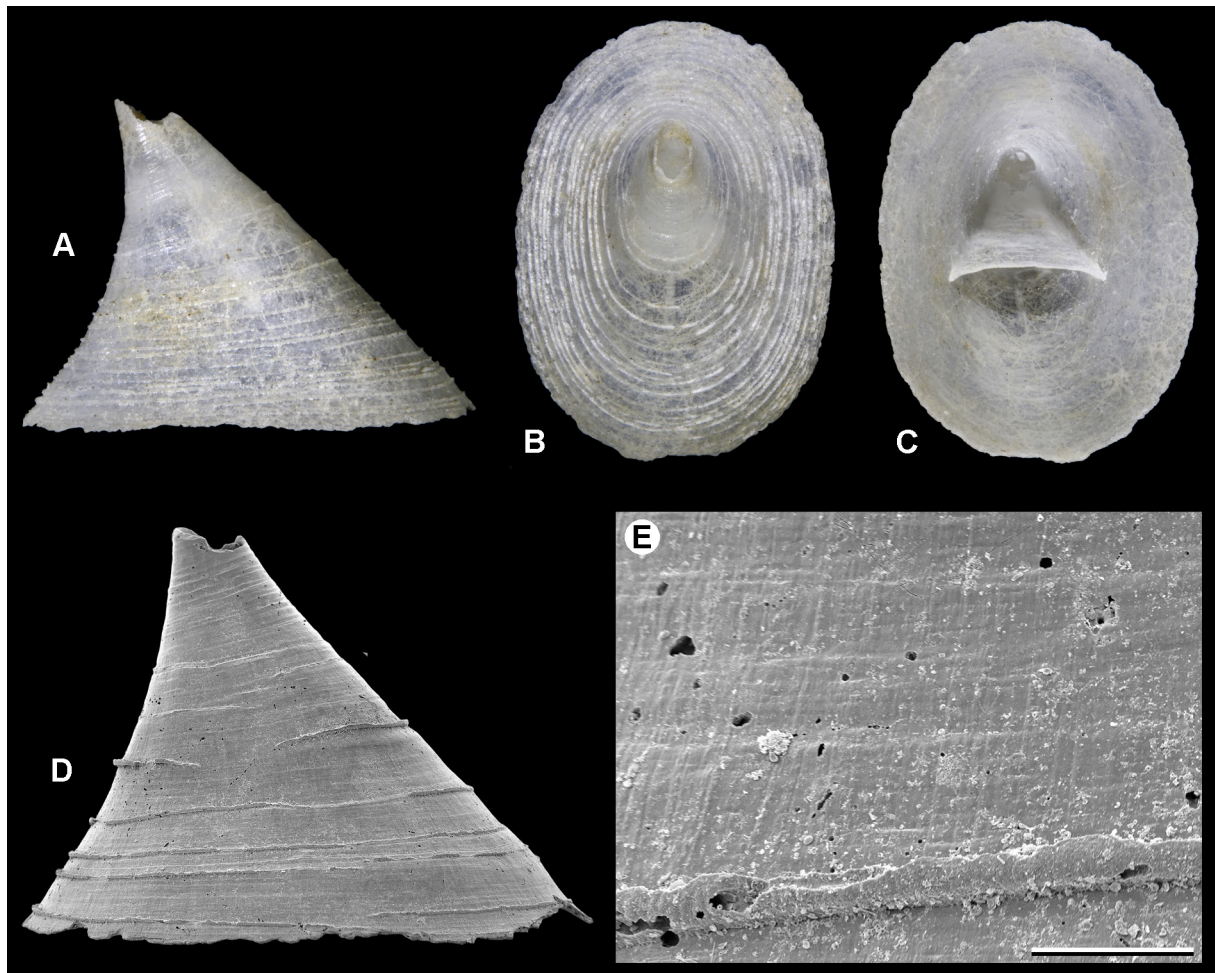


Fig. 8. *Cornisepta marshalli* sp. nov. **A–C.** Holotype, base 4.5×3.3 mm, height 3.25 mm (MNHN-IM-2000-38269). **D.** SEM showing raised concentric ridges, stn DW4886, height 2.7 mm (paratype, MNHN-IM-2000-38270). **E.** Microsculpture, stn DW4886, scale bar = 100 μm (paratype, MNHN-IM-2000-38270).

PROTOCONCH. Missing.

COLOUR. Translucent white, co-marginal ridges more opaque.

DIMENSIONS. Holotype, base 4.50×3.30 mm, height 3.25 mm; largest specimen, base 6.0×4.5 mm, height 3.35 mm.

Distribution

Known only from sandy substrata on the slopes of Walters Shoal, at depths of 582–660 m; living specimens unknown.

Remarks

The loss of the protoconch, elevated-conical profile of the shell and strong internal septum clearly ally this species with *Cornisepta* McLean & Geiger, 1998. However, it differs from other members of this genus in having a sculpture of concentric ridges rather than raised pustules. In terms of its concentric sculpture, *C. marshalli* sp. nov. somewhat resembles *Profundisepta denudata* Simone & Cunha, 2014 from Brazil, but that species retains its protoconch and has radial rows of fine pustules.

Superfamily Lepetelloidea Dall, 1882
Family Pseudococculinidae Hickman, 1983

Genus *Pterodacna* gen. nov.

[urn:lsid:zoobank.org:act:E9BE7547-02C0-4F83-8157-FB4F14BA186C](https://doi.org/10.21203/rs.3.rs-1111111/v1)

Type species

Pterodacna boucheti gen. et sp. nov.

Diagnosis

Shell very small (length < 2.0 mm), thin and fragile, base evenly elliptical, basal profile flat; apex at ±0.2 of length from posterior end; anterior slope convex; posterior slope almost straight; interior lacking apical septum. Protoconch elliptical, apical portion long and slender, fused to terminal lip; microsculpture of close-set, irregular, minute pits. Teleoconch with irregular collabral growth-lines and close-set, microscopic, concentric ripples; radial sculpture mostly absent, but anterior third with shallow radial undulation. Radula with rachidian tapering to a narrow cusplike point, innermost lateral broadly trigonal with a blunt vestigial cusp at antero-medial corner; laterals 2–4 with bluntly rounded cusps; fifth lateral large, its cusp with three strong trigonal denticles; inner marginals with simple recurved cusps lacking denticles, middle marginals more slender, their cusps with fine lateral denticles, outer marginals distally spatulate with finely denticulate margins. Animal lacking pigmented eyes, cephalic tentacles well developed, oral disk large; posterior of foot with two small epipodial tentacles.

Etymology

From the Greek “*pteron*” (πτερό) – “a feather” and “*dakno*” (δάκνω) – “to bite”; in reference to the feeding habits of the animal. Not the fossil *Pteradacna* Andrusov, 1907 (Bivalvia: Cardiidae).

Remarks

The morphology of the protoconch and radula of *Pterodacna* gen. nov. is typical of taxa referable to the Pseudococculinidae (Hickman 1983; Marshall 1986). Within this family, the most similar genus is *Tentaoculus* Moskalev, 1976, the shell of which is very similar to that of *Pterodacna* gen. nov., in terms of its shape, sculpture and protoconch morphology. Based on these characters alone, *Pterodacna*

gen. nov. would key out as *Tentaoculus* using the key to pseudococculinid genera provided by Marshall (1986). However, the radula of *Pterodacna* gen. nov. differs significantly from that of *Tentaoculus*. Whereas the rachidian tooth in the radula of *Pterodacna* gen. nov. tapers to a point and lacks a cusp, that of *Tentaoculus* retains a finely serrate cusp. Similarly, the cusp of the large innermost lateral tooth has a broad, serrate cutting edge in *Tentaoculus* and the cusps of laterals 2–4 are also serrate (Marshall 1986, 1996; Warén & Bouchet 2009), whilst in *Pterodacna* gen. nov. the innermost lateral has at most a blunt vestigial cusp on its antero-medial corner and the cusps of laterals 2–4 are bluntly rounded and not serrate. Furthermore, the fifth lateral of *Pterodacna* gen. nov. has a cusp with three strong denticles, in contrast to the more finely serrate fifth lateral cusp found in species of *Tentaoculus*. Broader comparison shows that some of the features of the radula of *Pterodacna* gen. nov. are shared with other pseudococculinid taxa; notably the robust tricuspid fifth lateral is shared with *Notocrater ponderi* Marshall, 1986 and a pointed cusplless rachidian is present in *Mesopelex zelandica* Marshall, 1986. The most characteristic features of the radula of *Pterodacna* gen. nov. include the posterior mid-region dip in the transverse rows of teeth, the very broad, essentially cusplless first lateral tooth and the bluntly rounded cusps on laterals 2–4.

Pterodacna gen. nov., like many small bathyal and abyssal limpets, is associated with a biogenic substrate. Commonly within the Pseudococculinidae this substrate is water-logged decaying wood (Marshall 1986), but those species of *Tentaoculus* for which habitat data are available exhibit associations with more unusual substrates, including the carapaces of living stone crabs (Lithodidae) and decaying algal holdfasts (Marshall 1986), as well as chondrichthyan egg cases (Marshall 1996). The association of *Pterodacna* gen. nov. with decaying bird feathers represents the first record of a deep-sea limpet living and feeding on such a substrate. In fact, it is the first record of any gastropod subsisting on a substrate of this nature (Ponder & Lindberg 2020).

Pterodacna boucheti gen. et sp. nov.

[urn:lsid:zoobank.org:act:CDBAC4BE-2727-48F8-85BA-D9326A23B322](https://doi.org/10.21203/rs.3.rs-3123232/v1)

Figs 9–11

Diagnosis

See generic diagnosis.

Etymology

Named for Prof. Philippe Bouchet (MNHN) in recognition of the numerous expeditions he has organised, which have led to the discovery of so many fascinating creatures, including this minute limpet.

Material examined

Holotype

WALTERS SHOAL • living specimen; slopes, stn CP4906; 33°26' S, 44°00' E; depth 799–837 m; 9 May 2017; alive on decomposing bird feather, DNA tissue sample; MNHN-IM-2013-67323.

Paratypes

WALTERS SHOAL • 12 specimens, living; same collection data as for holotype; MNHN-IM-2000-38245.

Description

SHELL. Very small (length up to 1.9 mm), thin and fragile, basal outline more or less evenly elliptical, broadest medially, anterior and posterior ends of similar shape, basal profile flat; L/D = 1.47–1.55, H/L \pm 0.5; apex at \pm 0.2 of length from posterior end; anterior slope convex; posterior slope for the most part straight, sometimes slightly bulging in mid-region; interior lacking apical septum. Teleoconch

sculptured with occasional irregular collabral growth-lines and faint, close-set, microscopic, concentric ripples; radial sculpture mostly absent, but anterior third with shallow, radial undulations (Fig. 10C).

PROTOCONCH (Fig. 10D–E). Elliptical, length $\pm 185 \mu\text{m}$, width $\pm 130 \mu\text{m}$, apical portion long and slender, fused to terminal lip, separated from subsequent part of protoconch by a shallowly curved groove; microsculpture comprising a crisp and irregular pattern of close-set, minute pits, most evident apically; terminal lip gently convex, not thickened.

COLOUR. Uniformly translucent milky white, with yellowish colour of body showing through apically.

DIMENSIONS. Holotype, length 1.90 mm, diameter 1.25 mm, height 1.00 mm (= largest specimen).

EXTERNAL ANATOMY (Fig. 10F). Animal mostly whitish except for apical part of visceral hump which is tinged yellowish-brown; head with well-developed, distally expanded snout, with roundly D-shaped oral disc with rounded rim; cephalic tentacles stout; pigmented eyes lacking; foot broadly ovate, somewhat truncated anteriorly; two small epipodial tentacles present at rear of foot; mantle edge simple.

RADULA (Fig. 11). Formula $\infty+5+1+5+\infty$, with up to 32 transverse rows of teeth, rows of asplayed M-shape, lateral 5 is most anterior tooth; rachidian with trigonal base-plate, anterior shaft tapering to rounded tip, lacking cusp; innermost lateral large, its outer anterior margin broadly expanded, antero-medial corner with small irregularly shaped cusp, usually bluntly rounded; laterals 2–4 progressively smaller and less triangular, cusp of lateral 2 an oblique blunt ridge, cusp of lateral 4 small and bluntly rounded, that of lateral 3 of intermediate shape; lateral 5 much larger, its cusp with three robust trigonal denticles, anterior face of cusp base angular. Inner four marginals relatively stout with recurved non-denticulate cusps. Thereafter marginals progressively more slender, their recurved cusps with pectinate margins; cusps of outermost marginals less strongly recurved, broader and more spatulate. Latero-marginal structures not evident. In folded state, laterals 2–4 lie behind lateral 1 and central field is overlain by lateral 5 and marginals.

Distribution

Known only from the slopes of Walters Shoal, at depths of 799–837 m. Living on decomposing bird feather.

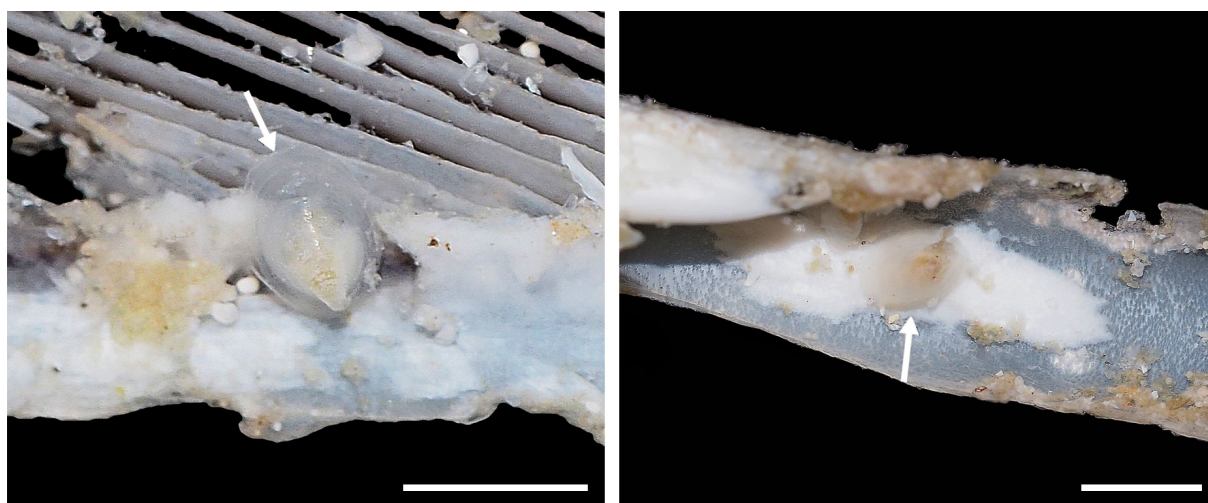


Fig. 9. *Pterodacna boucheti* gen. et sp. nov., specimens in situ (arrows) on the barbs and rachis of decomposing bird feather. Scale bars = 2.0 mm. Images courtesy of Alain Barrère/MNHN.

Remarks

See remarks under genus description.

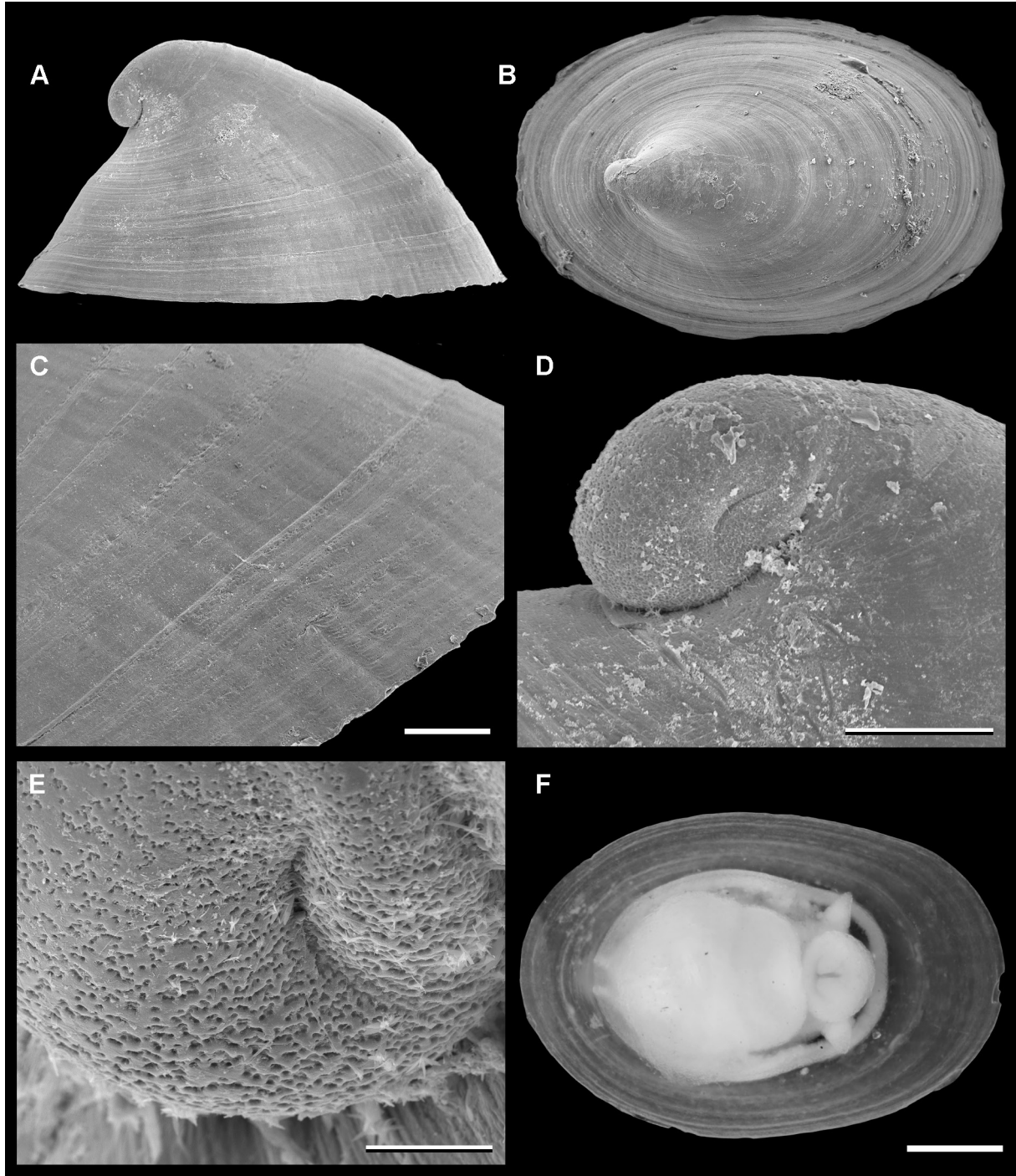


Fig. 10. *Pterodacna boucheti* gen. et sp. nov. **A.** Holotype, side view, basal length 1.9 mm (MNHN-IM-2013-67323). **B.** Dorsal view, length 1.7 mm (paratype, MNHN-IM-2000-38245). **C.** Sculptural detail of holotype, scale bar=100 μ m. **D.** Protoconch of holotype, scale bar=100 μ m. **E.** Pitted microsculpture of protoconch, scale bar=25 μ m (paratype, MNHN-IM-2000-38245). **F.** Ventral view of preserved specimen, scale bar=250 μ m (paratype, MNHN-IM-2000-38245).

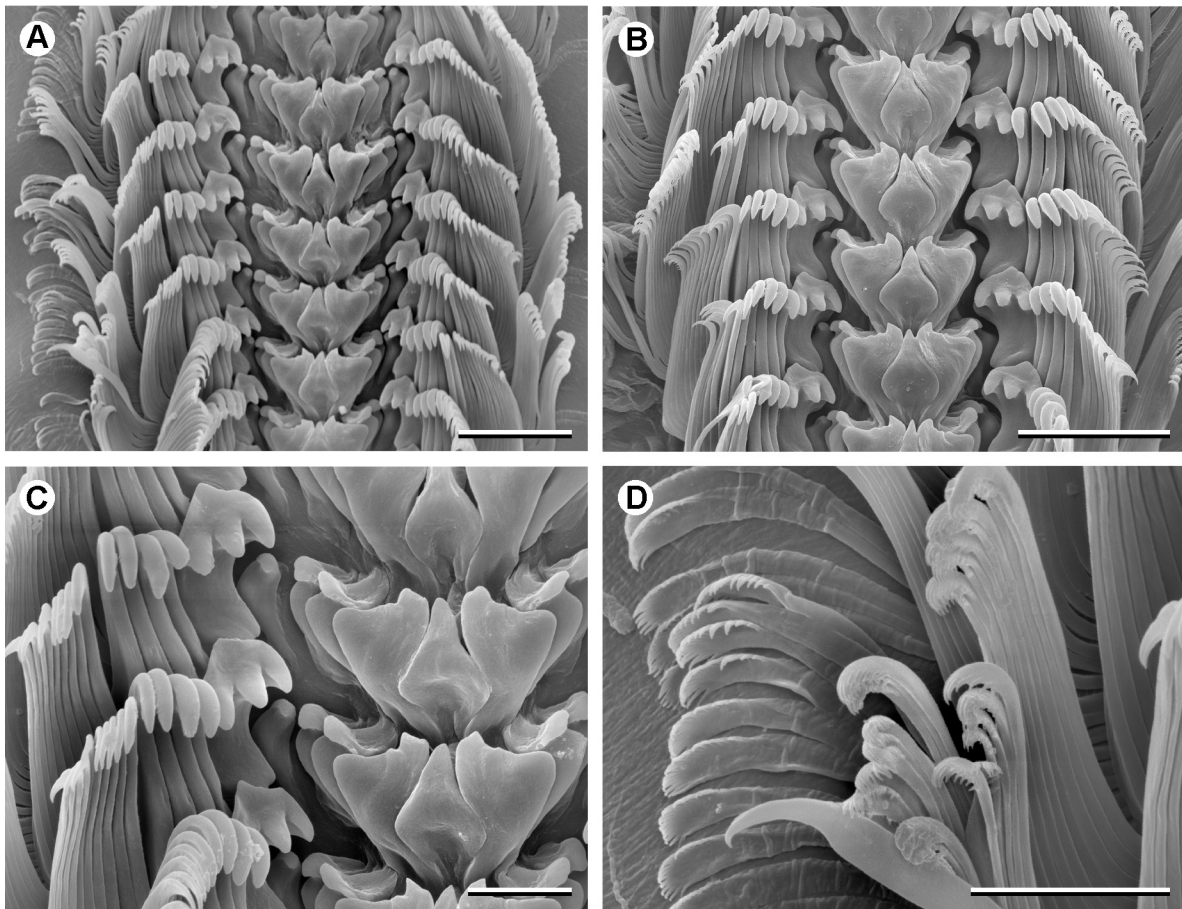


Fig. 11. *Pterodacna boucheti* gen. et sp. nov., radula (paratype, MNHN-IM-2000-38245). **A.** Entire width of radula, anterior third, scale bar=25 μ m. **B.** Entire width of radula, posterior third, laterals 2–4 folded behind lateral 1, scale bar=25 μ m. **C.** Detail of rachidian, lateral and inner marginal teeth, scale bar=10 μ m. **D.** Details of marginal teeth, scale bar=10 μ m.

Superfamily Scissurelloidea Gray, 1847
Family Scissurellidae Gray, 1847

Genus *Sinezona* Finlay, 1926

Type species

Schismope brevis Hedley, 1904 (original designation), Recent, New Zealand.

Sinezona insignis (Smith, 1910)

Fig. 12

Schismope insignis Smith, 1910: 208, pl. 8 figs 4, 4a. Type loc.: four miles south of Port Elizabeth, South Africa.

Sinezona insignis – Herbert 1986: 626, figs 10, 32–35; 2015: 13. — Geiger 2012: 468, figs 347–351.



Fig. 12. *Sinezona insignis* (Smith, 1910), Walters Shoal, stn WB09, shell diameter 0.65 mm (MNHN-IM-2013-67306).

Material examined

WALTERS SHOAL • 1 living specimen; summit area, south, stn WB05; 33°15.1S, 43°54.5' E; depth 26–30 m; 1 May 2017; DNA tissue sample; MNHN-2013-67305 • 1 living specimen; summit area, north-west, stn WB09; 33°13.8S, 43°55.8' E; depth 27–30 m; 4 May 2017; DNA tissue sample; MNHN-2013-67306.

Distribution

A shallow-water species known from the south-eastern coast of South Africa and several islands in the south-eastern Atlantic. The present records from the summit area of Walters Shoal represent an eastern extension of the known range.

Remarks

Evidently a species prone to dispersal to isolated shallow-water localities by rafting on kelp holdfasts. Return eddies of the eastward flowing Agulhas Return Current may extend in the direction of Walters Shoal (Lutjeharms & Ansoerge 2001), facilitating colonisation.

Order Seguenziida Haszprunar, 1986
Superfamily Seguenzioidea Verrill, 1884
Family Calliotropidae Hickman & McLean, 1990

Genus *Calliotropis* Seguenza, 1903

Type species

Trochus otto Philippi, 1844 (original designation), Pliocene, Italy and Recent, N Atlantic.

Calliotropis eucheloides Marshall, 1979
Fig. 13A–C, G

Calliotropis eucheloides Marshall, 1979: 527, fig. 3a–c. Type loc.: east of Chanter Islets, Raoul Island, Kermadec Islands, 366–402 m.

Calliotropis eucheloides – Vilvens 2006: 62, figs 24–27; 2007: 46, figs 138–155, 160, 161; 2020: 39, figs 17a–o, 18a–o; 2021: 108, fig. 7j–n. — Herbert 2015: 29.

Material examined

WALTERS SHOAL – **slopes** • 7 empty shells; stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017; MNHN • 1 living specimen; stn DW4885; 33°17' S, 43°55' E; depth 272–380 m; 3 May 2017; DNA tissue sample; MNHN-IM-2013-67238 • 10+ empty shells; stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN • 10+ empty shells; stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; MNHN • 1 living specimen; stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; DNA tissue sample; MNHN-IM-2013-67239 • 1 living specimen; stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; DNA tissue sample, photographed alive; MNHN-IM-2013-67240 • 1 empty shell, juvenile; stn DW4889; 33°09' S, 43°58' E; depth 353–465 m; 3 May 2017; MNHN • 10+ specimens, some living; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; MNHN • 1 empty shell; stn DW4891; 33°12' S, 44°01' E; depth 650–653 m; 4 May 2017; MNHN • 12 specimens, some living; stn DW4892; 33°12' S, 44°01' E; depth 624–646 m; 4 May 2017; MNHN • 1 empty shell, juvenile; stn DW4893; 33°16' S, 43°58' E; depth 623–629 m; 4 May 2017; MNHN • 1 empty shell; stn DW4896; 33°07' S, 43°51' E; depth 325–357 m; 5 May 2017; MNHN • 1 empty shell, juvenile; stn DW4898; 33°09' S, 44°01' E; depth 652–668 m; 6 May 2017; MNHN • 1 empty shell; stn CP4901; 33°09' S, 44°01' E; depth 647–672 m; 6 May 2017; MNHN • 2 empty shells; stn CP4903; 33°11' S, 44°01' E; depth 620–642 m; 7 May 2017; MNHN • 1 living specimen; stn DW4904; 33°11' S, 44°01' E; depth 652 m; 7 May 2017; DNA tissue sample; MNHN-IM-2013-67241 • 1 empty shell; stn DW4904; 33°11' S, 44°01' E; depth 652 m; 7 May 2017; MNHN.

Distribution

Widespread in the Indo-West Pacific (Vilvens 2007, 2021). In the south-western Indian Ocean, it has been recorded from north-western and southern Madagascar (Vilvens 2006, 2021) and the east coast of South Africa (Herbert 2015). On Walters Shoal it is known only from the slopes at depths of 357–652 m (live-collected material 380–652 m); dredged on substrata of coarse sand.

Remarks

As currently interpreted, this species is widespread and variable (Vilvens 2006, 2007, 2021). With records from off eastern South Africa and off western Madagascar, its occurrence on Walters Shoal is unsurprising. Vilvens (2006) noted that Madagascan shells were somewhat larger than south-western Pacific specimens and differed slightly in sculptural detail, but observed that South African specimens were more typical in size. Material from Walters Shoal appears to be intermediate (diameter up to 12.0 mm). I should also point out that whereas the columella denticle in south-western Pacific specimens is a single rounded entity (see figures in Marshall 1979; Vilvens 2007), in specimens from the south-western Indian Ocean this denticle is apically notched in mature specimens (Fig. 13A herein; Vilvens 2006: fig. 26; Herbert 2015: fig. 5d), sometimes appearing as two separate, but basally fused denticles. Molecular sequence data will be required in order to establish whether one or more species is involved.

The external anatomy of a living specimen photographed on board ship (Fig. 13G) was similar to that described for *Calliotropis* by Hickman & McLean (1990). The head-foot is mostly whitish, but the oral area and foot sole are pale apricot. The tip of the snout is greatly expanded laterally, forming trigonal, palp-like extensions. The cephalic lappets are small, the cephalic tentacles well developed and micropapillate, and the eyes large and black on stout stalks. The neck lobes are digitate, although the right one is smooth posteriorly. There are 4–5 well-developed micropapillate epipodial tentacles on each side, with smaller intermediaries, all of which have apricot-tinged epipodial sense organs at the base. A rehydrated specimen had what appeared to be a large post-ocular peduncle behind the right eyestalk (obscured in the living specimen).

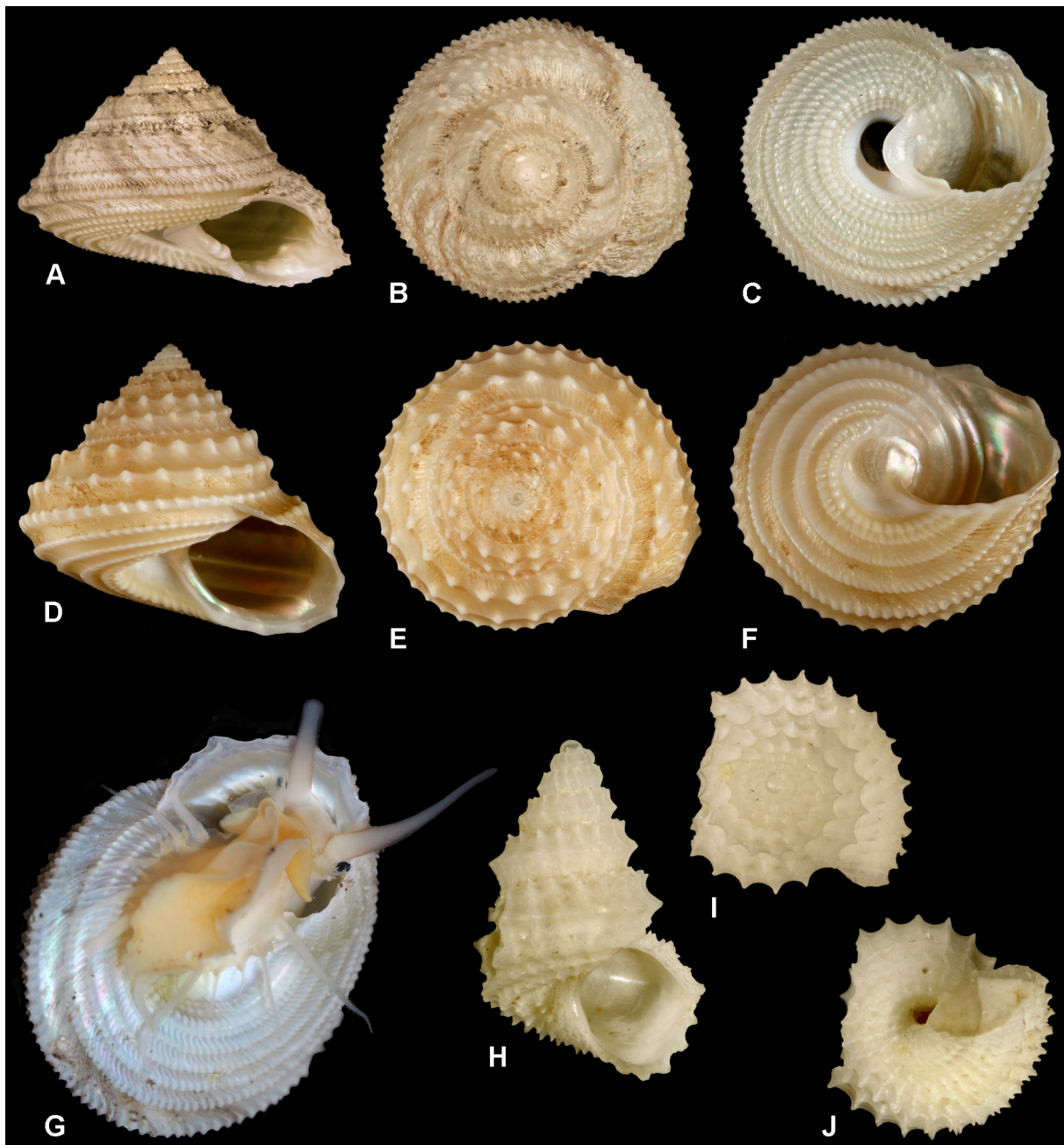


Fig. 13. A–C. *Calliotropis eucheloides* Marshall, 1979. A. Apertural view showing duplex tooth at base of columella, Walters Shoal, stn DW4904, diameter 12.0 mm (MNHN-IM-2013-67241). B–C. Apical and basal views, Walters Shoal, stn DW4892, diameter 10.6 mm (MNHN). D–F. *Calliotropis velata* Vilvens, 2006, Walters Shoal, stn CP4910, diameter 15.9 mm (MNHN-IM-2013-67242). G. *Calliotropis eucheloides*, living animal, shell diameter 12.2 mm (MNHN-IM-2013-67240), image courtesy of Alain Barrère/MNHN. H–J. *Spinicalliotropis lepidota* sp. nov., holotype, height 2.9 mm (MNHN-IM-2000-36293).

Calliotropis velata Vilvens, 2006
Figs 13D–F, 14A–B

Calliotropis velata Vilvens, 2006: 57, figs 1–7. Type loc.: off north-western Madagascar, 15°18.3' S, 46°10.3' E [off Mahajanga], depth 500–550 m.

Calliotropis sp. 2. cfr. *concovospira* (Schepman, 1908) – Nolf & Verstraeten 2003: 16, text-fig.

Calliotropis velata – Vilvens 2021: 102, fig. 4a–h.

Material examined

MADAGASCAR • 1 empty shell; SW of Nosy Be; 13.833°S, 47.617°E; depth 850–1125 m; Feb. 1975; ORSTOM leg.; dredged; NMSA J1961 • 1 empty shell; off Toliara; depth 400–800 m; Jan. 2001; W. Massier don.; trawled; NMSA L5555.

WALTERS SHOAL – **slopes** • 1 empty shell; stn CP4905; 33°32' S, 44°00' E; depth 1000–1052 m; 9 May 2017; MNHN • 1 living specimen; stn CP4910; 32°5' S, 44°06' E; depth 986–988 m; 10 May 2017; DNA tissue sample; MNHN-IM-2013-67242 • 1 living specimen; stn CP4910; 32°5' S, 44°06' E; depth 986–988 m; 10 May 2017; DNA tissue sample; MNHN-IM-2013-67243 • 1 empty shell; stn CP4910; 32°5' S, 44°06' E; depth 986–988 m; 10 May 2017; MNHN • 6 empty shells; stn CP4911; 32°46' S, 44°18' E; depth 964–965 m; 10 May 2017; MNHN • 4 specimens, some living; stn CP4912; 32°49' S, 44°23' E; depth 961–966 m; 10 May 2017; MNHN.

Distribution

West coast of Madagascar, from the Nosy Be area south to the Taolagnaro (Fort Dauphin) region, at depths of 425–986 m and the east coast of Mozambique (Vilvens 2021); extending south to Walters Shoal where it has been trawled on the surrounding slopes at depths of 965–1000 m (live-taken material 966–986 m), on substrata of coarse sand, solitary coral rubble and pteropod shell debris, with diverse sponges, cnidarians, decapods and echinoids.

Remarks

Specimens from Walters Shoal typically have four spiral cords on the base, the strength of the beading of which varies between individuals. The innermost basal cord, which is usually the most coarsely beaded, and also often the strongest, may occasionally be duplex. The observation of Vilvens (2006) regarding the absence of a correlation between specimen size and the closure of the umbilicus by the overarching septum applies equally to material from Walters Shoal.

The shell microsculpture is typical of *Calliotropis*, comprising well-defined, tightly packed, slash-like marks (Fig. 14A). The protoconch is large and globose, strongly exsert, comprising approx. 1.25 whorls, diameter 500–510 µm (Fig. 14B); apex rounded, terminal lip very slightly convex, not thickened; surface smooth, no superficial microsculpture evident.

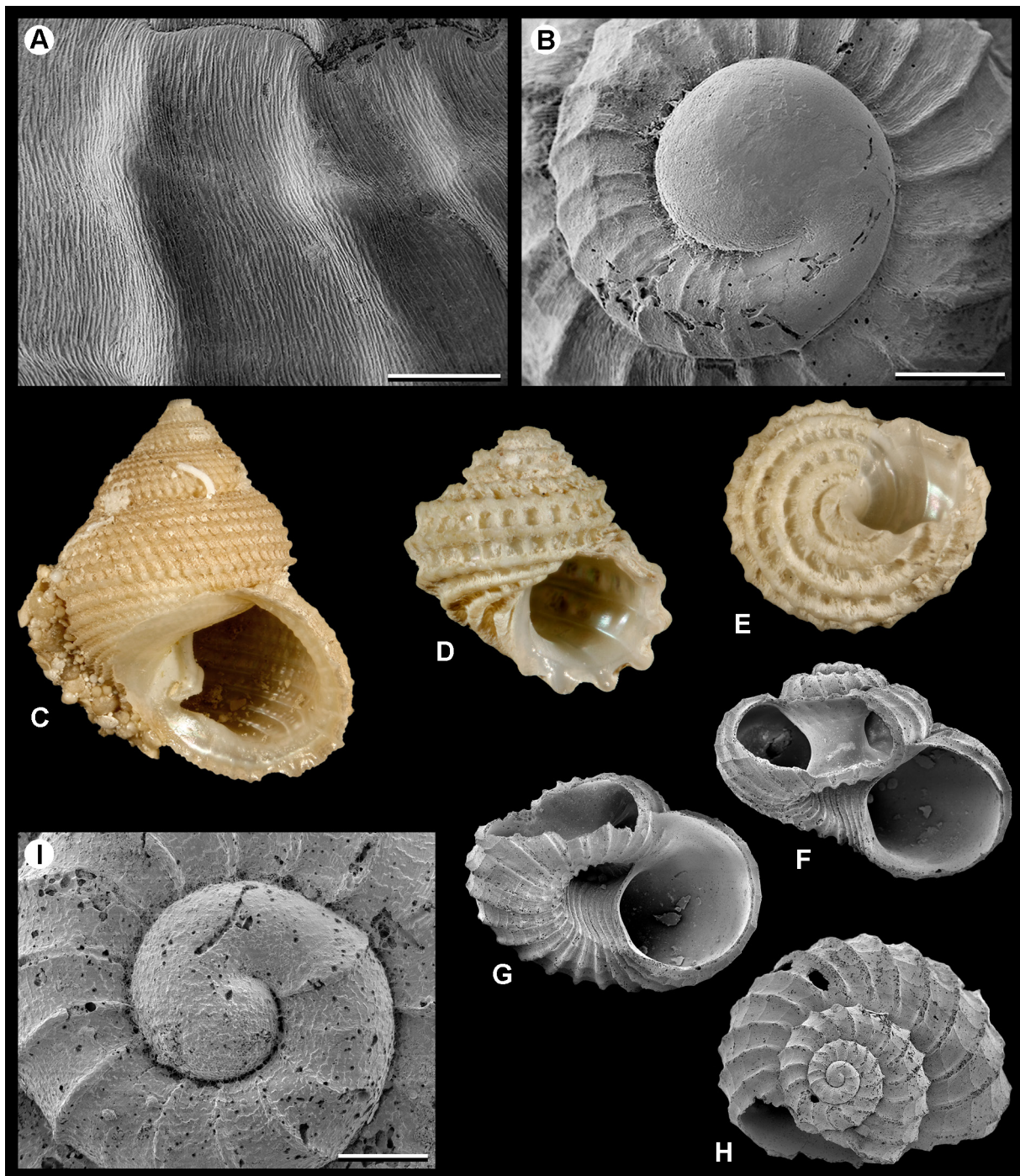


Fig. 14. **A–B.** *Calliotropis velata* Vilvens, 2006, Walters Shoal, stn CP4911 (MNHN), scale bars=200 µm. **A.** Microsculpture, third whorl. **B.** Protoconch. **C.** *Danilia textilis* Herbert, 2012, Walters Shoal, stn DW4887, height 11.7 mm (MNHN-IM-2013-67256). **D–E.** *Vaceuchelus gemmula* (Turton, 1932), Walters Shoal, stn WB05, height 3.4 mm (MNHN-IM-2013-67254). **F–H.** *Vetulonia parajeffreysi* Absalão & Pimenta, 2005, Walters Shoal, stn CP4913, diameter 2.5 mm (MNHN). **I.** *Vetulonia parajeffreysi*, protoconch, Walters Shoal, stn CP4913, scale bar=100 µm (MNHN).

Genus *Spinicalliotropis* Poppe, Tagaro & Dekker, 2006**Type species**

Calliotropis (*Spinicalliotropis*) *spinosa* Poppe, Tagaro & Dekker, 2006 (original designation), Recent, Philippines.

Remarks

On the grounds of morphological and molecular evidence, Kano *et al.* (2009) demonstrated that *Spinicalliotropis*, originally proposed as a subgenus of *Calliotropis*, should be treated as a distinct genus. However, due to its unresolved position in their molecular analysis, Kano *et al.* (2009) considered it a taxon incertae sedis within the Seguenzioidea. Zhang & Zhang (2018) similarly found *Calliotropis* to be paraphyletic when species of *Spinicalliotropis* were included within it. For the present, since it is conchologically more similar to *Calliotropis* than to any of the varied assemblage of genera currently treated as unassigned seguenzioids, I maintain it in the Calliotropidae, but I follow Kano *et al.* (2009) in treating it as an entity distinct from *Calliotropis*.

In the original description of *Spinicalliotropis*, Poppe *et al.* (2006) indicated that the Caribbean *Calliotropis clavata* (Watson, 1879) was also referable to their new taxon and Kano *et al.* (2009) similarly included this species in their list of taxa that they considered to belong in *Spinicalliotropis*. If this proves to be the case, then *Spinicalliotropis* becomes a junior synonym of *Echinogurges* Quinn, 1979, of which *Trochus* (*Margarita*) *clavatus* Watson, 1879 is the type species. Pending molecular evidence that the Caribbean and Indo-West Pacific species concerned are congeneric, I employ *Spinicalliotropis* for taxa from the latter region.

***Spinicalliotropis lepidota* sp. nov.**

[urn:lsid:zoobank.org:act:D5DFC0BB-04A2-455D-B28D-E84E01333B93](https://zoobank.org/act:D5DFC0BB-04A2-455D-B28D-E84E01333B93)

Fig. 13H–J

Diagnosis

Shell small, elevated-trochiform ($H/D \pm 1.20$), apical angle 56° , uniformly whitish; protoconch globose, exsert; teleoconch sculptured by angular spiral cords, crossed and rendered spinose by crisp axial ribs; spire whorls with only two spiral cords (P1 and P2); ribs raised to form scale-like spines where they cross cords on later whorls; base with three conspicuously spinose spiral cords below P3, which emerges at insertion of outer lip; umbilicus of moderate width with two weak cords within; aperture subquadrate.

Etymology

From the Greek “*lepis*” (*λεπις*) – “a scale”, and “*lepidotos*” (*λεπιδωτος*) – “scaly”; with reference to the scale-like spines on the spiral cords.

Material examined**Holotype**

WALTERS SHOAL • empty shell; slopes, stn DW4893; $33^\circ 16' S$, $43^\circ 58' E$; depth 623–629 m; 4 May 2017; MNHN-IM-2000-36293.

Description

SHELL. Small (height 2.9 mm), elevated-trochiform, higher than wide ($H/D \pm 1.2$), apical angle 56° ; spire whorls with two strong, angular spiral cords, crossed and rendered spinose by crisp axial ribs; suture strongly indented and periphery slightly above mid-whorl; base rounded and umbilicate; teleoconch

Table 1. Species of *Spinicalliotropis* Poppe, Tagaro & H. Dekker, 2006, holotype height, teleoconch whorl number and apical angle.

Species	Height (mm)	Teleoconch whorls	Apical angle
<i>Spinicalliotropis chalkeie</i> (Vilvens, 2007)	6.5	6.2	62°
<i>Spinicalliotropis ericius</i> (Vilvens, 2006)	4.7	5.5	70°
<i>Spinicalliotropis lamellifera</i> (Jansen, 1994)	4.8	5.7	68°
<i>Spinicalliotropis lepidota</i> sp. nov.	2.9	5.25	56°
<i>Spinicalliotropis solariellaformis</i> (Vilvens, 2006)	6.0	5.5	69°
<i>Spinicalliotropis spinosa</i> (Poppe, Tagaro & Dekker, 2006)	4.2	5.5	66°
<i>Spinicalliotropis stephanos</i> Vilvens, 2021	4.2	5.0	69°

of 5.25 whorls; part of last adult whorl missing in single specimen available. First teleoconch whorl evenly rounded and with 13–14 smooth axial ribs; two spiral cords develop during second whorl, P1 below adapical suture, P2 at periphery; cords nodular at intersections with axial ribs; cords and ribs strengthening during third and fourth whorls, ribs becoming more crisp and raised to form scale-like spines where they cross cords; those on P1 angled adapically; two weaker secondary spiral cords develop near end of fourth whorl, S1 between P1 and adapical suture and S3 below P2; secondary cords also spinose; P3 emerges level with suture on last adult whorl, below periphery; a further, weak secondary cord S2 arises between P1 and P2 in final quarter whorl, resulting in total of six spiral cords above and including P3 just prior to outer lip; axial ribs somewhat thinner and more numerous in this region. Base with 3 strong spiral cords below P3 and slightly weaker fourth at edge of umbilicus; basal cords conspicuously spinose and somewhat more close-set than those above periphery; umbilicus of moderate width, its interior with additional faint cord. Aperture subquadrate; peristome interrupted in parietal region; inner lip strongly concave below insertion of columella onto paries; edge of outer lip thin, somewhat damaged in specimen available; interior chalky white, retaining traces of nacre.

PROTOCONCH. Translucent pale greyish-white; globose, strongly exsert, comprising approx. 1.25 whorls, diameter 260 µm.

COLOUR. Uniformly whitish with traces of underlying nacre visible in places.

DIMENSIONS. Holotype, height 2.9 mm, diameter 2.5 mm (estimated by extension of evenly conical spire profile).

Distribution

Known only from the slopes of Walters Shoal, at a depth of 623–629 m; living specimens unknown.

Remarks

Spinicalliotropis lepidota sp. nov. has a more acute spire than all other species currently referred to the genus (Table 1). In addition, although the holotype has only slightly fewer teleoconch whorls, it is substantially smaller than the other species. Three species of *Spinicalliotropis* have been recorded from the south-western Indian Ocean: *S. ericius* (Vilvens, 2006), *S. solariellaformis* (Vilvens, 2006) and *S. stephanos* Vilvens, 2021, but besides being larger and broader, all have three primary spiral cords on the middle spire whorls (only two in *S. lepidota*). The spiral cords on the base of *S. lepidota* are also more conspicuously and sharply spinose. *S. stephanos* has a much narrower umbilicus. *Calliotropis acherontis* Marshall, 1979, which also occurs in the south-western Indian Ocean (Vilvens 2006, 2021; Herbert 2015) and has a narrowly conical shell, is larger (height up to 5.0 mm) and lacks the spinose sculpture typical of species of *Spinicalliotropis*.

Whilst I hesitate to describe a new species based on a single somewhat damaged specimen, the shell is for the most part in good condition and evinces characters that clearly set it apart from others in the genus, as detailed above.

Family Chilodontaidae Wenz, 1938

Genus *Danilia* Brusina, 1865

Type species

Monodonta limbata Philippi, 1844 (monotypy) [= *Danilia tinei* Calcara, 1839)], Recent, Mediterranean.

Danilia textilis Herbert, 2012

Fig. 14C

Danilia textilis Herbert, 2012: 415, figs 4e, 6c, 13, 15–17. Type loc.: off Rame Head, E Cape, South Africa, depth 150–160 m.

Danilia textilis – Herbert 2015: 32.

Material examined

WALTERS SHOAL – **slopes** • 6 empty shells; stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN • 1 living specimen; stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; DNA tissue sample; MNHN-IM-2013-67255 • 1 living specimen; stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; DNA tissue sample; MNHN-IM-2013-67256 • 6 empty shells; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; MNHN • 1 living specimen; stn DW4897; 33°09' S, 43°59' E; depth 490–584 m; 5 May 2017; DNA tissue sample; MNHN-IM-2013-67257 • 2 empty shells; stn DW4897; 33°09' S, 43°59' E; depth 490–584 m; 5 May 2017; MNHN.

Distribution

East coast of South Africa to central Mozambique, in 110–500 m (Herbert 2012) and Walters Shoal where it occurs on the slopes at depths of 582–599 m (live-taken material 584–599 m); dredged on coarse sand and rocks with diverse sponges, cnidarians, crustaceans and ophiuroids.

Remarks

In most respects, specimens from Walters Shoal are identical to those occurring off continental south-east Africa. The only consistent morphological difference is that the shells from Walters Shoal are all uniformly white or pale buff, whereas continental shells are commonly mottled or blotched with brown and even the palest specimens have some brown markings associated with the outer lip varix. This difference may relate to the fact that on Walters Shoal the species occurs at somewhat greater depths (live-taken specimens 584–599 m vs 150–250 m). The illustrated specimen was live-taken and has a tube of cemented sediment particles attached to the shell opposite the outer lip and opening near the base of the columella. It is probable that this was made by a polychaete worm and may be indicative of a commensal relationship. The remains of similarly positioned tubes are evident on additional dead-collected specimens.

Genus *Imbricoscelis* gen. nov.

urn:lsid:zoobank.org:act:F5D489A2-3CBD-4ACB-97E1-B0B7BECE60A8

Type species

Brookula coronis Barnard, 1963.

Diagnosis

Shell small, globose-turbiniiform; whorls evenly rounded; apical sculpture of collabral ribs, developing into broad forwardly sloping lamellae on later whorls, frequently overlapping; microsculpture of slash-like marks; base rounded and umbilicate; exterior of outer lip with a strong subterminal varix. Radula formula $\infty+3+1+3+\infty$, rachidian weakly hooded; teeth in central field with complex interlocking of tooth bases and shafts, their cusps coarsely dentate; latero-marginal plate absent; marginal teeth slender with pectinate outer margin. Operculum corneous, broadly multispiral.

Etymology

From the Latin “*imbrex*” – “a roofing-tile”, “*imbricatus*” – “overlapping” and the Greek “*skelis*” (σκελίς) – “a rib”; with reference to the close-set, overlapping, lamellate axial sculpture. Gender feminine.

Remarks

Many features of the shell, including the microsculpture and protoconch form, as well as the radula and operculum indicate that *Imbricoscelis* gen. nov. has affinity with chilodontaid and calliotropid seguenzioids, but it is unlike any of the existing genera known therein. The type species was originally referred to *Brookula* Iredale, 1912 (unassigned Seguenzioidea), but it shows only limited similarity to the type species *Brookula stibarochila* Iredale, 1912, a minute, shallow-water, subtropical species which has coarsely cancellate spire whorls (topotype illustrated by Warén 1992). Species of the deeper-water genera *Benthobrookula* Clarke, 1961 and *Vetulonia* Dall, 1913 are perhaps more similar, but they have far fewer axial ribs, much more distinct spiral sculpture and lack a strong collabral varix behind the outer lip. The recently described genus *Toroidia* Hoffman & Freiwald, 2018 from the NE Atlantic likewise has lamellate axial ribs, but they are much narrower than those of *Imbricoscelis* and do not overlap. In addition, the shells are more elevated, have a narrower umbilicus, a more globose protoconch and the outer lip lacks a subterminal varix (Hoffman & Freiwald 2018).

The form of the protoconch and the morphology of the radula, in particular the relatively coarsely dentate teeth in the central field and the lack of any latero-marginal structures, leads me to believe that *Imbricoscelis* gen. nov. has more affinity with the Chilodontaidae than with the Calliotropidae. The protoconch is neither bulbous nor strongly exsert as it is in many extant calliotropids (compare Figs 14B and 16B).

Imbricoscelis coronis (Barnard, 1963) gen. et comb. nov.

Figs 15–16

Brookula coronis Barnard, 1963a: 12, pl. 2 figs 5–6. Type loc.: *Africana II*, Station A1248 (approx. 36°48' S, 52°08' E) [Sapmer Bank Seamount], depth 400 m.

Brookula coronis – Kensley 1973: 44, fig. 114. — Giles & Gosliner 1983: 8.

Type material

Syntypes

SAPMER SEAMOUNT, SOUTHWEST INDIAN RIDGE • 9 empty shells; stn A1248; approx., 36°48' S, 52°08' E; depth 400 m; 9 Jul. 1961; R.S. *Africana II* leg.; SAMC A29928 (not seen). Although Barnard (1963a) mentioned 11 dead specimens, Giles & Gosliner (1983) recorded only nine. Repeated attempts to obtain photographs from the SAMC of a representative specimen from this syntype series have proved fruitless.

Material examined

WALTERS SHOAL – **slopes** • 3 empty shells; stn DW4877; 33°10' S, 43°49' E; depth 217–256 m; 1 May 2017; MNHN • 5 empty shells; stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017; MNHN • 6 empty shells; stn DW4885; 33°17' S, 43°54' E; depth 272–380 m; 3 May 2017; MNHN • 21 empty shells; stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN • 13 specimens, some living; stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; MNHN • 3 empty shells; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; MNHN • 6 empty shells; stn DW4892; 33°12' S, 44°01' E; depth 624–646 m; 4 May 2017; MNHN • 4 empty shells; stn DW4893; 33°16' S, 43°58' E; depth 623–629 m; 4 May 2017; MNHN • 90+ empty shells; stn DW4898; 33°09' S, 44°01' E; depth 652–668 m; 6 May 2017; MNHN • 30+ specimens, some living; stn DW4899; 33°09' S, 44°02' E; depth 707–720 m; 6 May 2017; MNHN • 50+ empty shells; stn DW4900; 33°10' S, 44°01' E; depth 660–670 m; 6 May 2017; MNHN • 9 empty shells; stn CP4901; 33°09' S, 44°01' E; depth 647–672 m; 6 May 2017; MNHN • 11 specimens, some living; stn CP4902; 33°08' S, 44°02' E; depth 700–711 m; 7 May 2017; MNHN • 2 empty shells; stn CP4903; 33°11' S, 44°01' E; depth 620–642 m; 7 May 2017; MNHN • 1 empty shell; stn CP4908; 33°29' S, 44°00' E; depth 900–950 m; 9 May 2017; MNHN • 3 empty shells; stn CP4911; 32°46' S, 44°18' E; depth 964–965 m; 10 May 2017; MNHN.

Description

SHELL. Small (height up to 3.1 mm), globose-turbiniform, proportions variable but always somewhat wider than high ($H/D=0.76-0.89$); whorls evenly rounded, spire relatively low; suture strongly indented, inserted close to periphery (mid-whorl) on spire whorls, descending slightly below this on last adult whorl; sculpture predominantly axial; base rounded and umbilicate; teleoconch of up to 3.5 whorls, the last adult whorl with a strong subterminal varix. First teleoconch whorl evenly rounded, initial

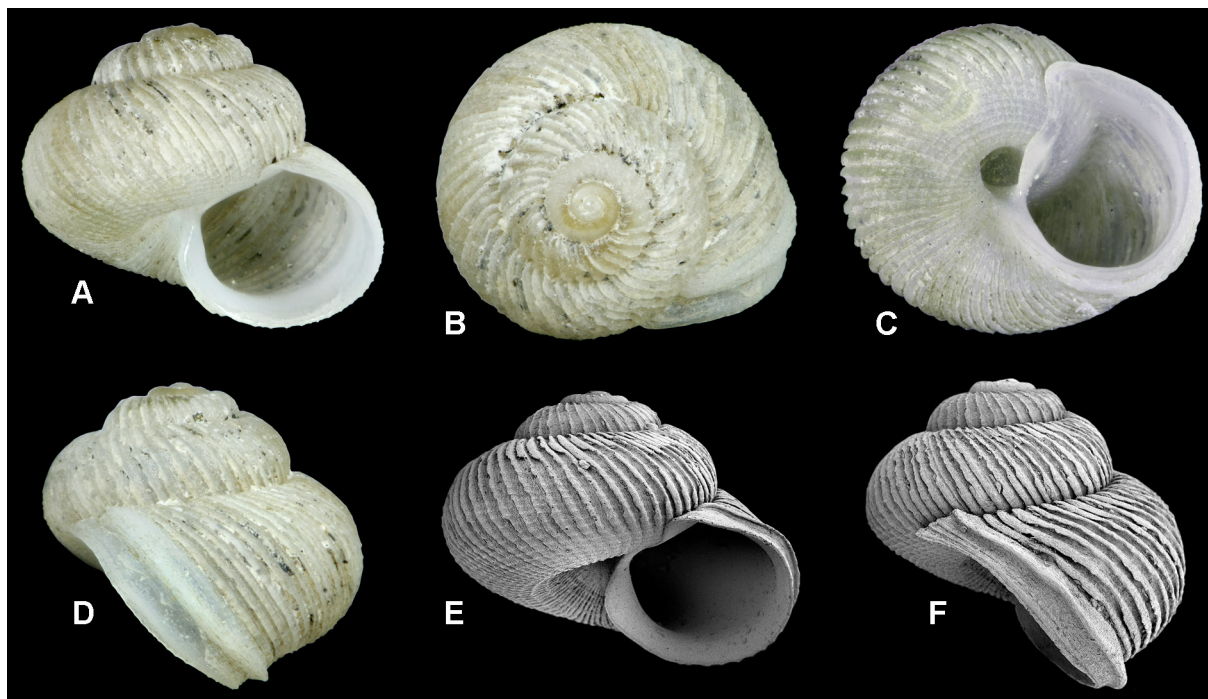


Fig. 15. *Imbricoscelis coronis* (Barnard, 1963) gen. et comb. nov. **A–D.** Apertural, apical, basal and lateral views of typical specimen, height 2.8 mm, Walters Shoal stn DW4899 (MNHN). **E.** SEM of depressed specimen, rib crests mostly damaged at whorl periphery, DW4898, height 2.4 mm. **F.** Lateral view SEM to show detail of subterminal external varix, DW4898, height 2.9 mm.

half smooth, sculptured only by microscopic granules; second half of first whorl with 11–14 rather ill-defined collabral ribs (Fig. 16A); rib intervals with traces of vermiform microsculpture caused by fusion of microgranules; ribs strengthen during second whorl, becoming forwardly sloping lamellae, almost overlapping base of rib in front by end of whorl; lamellae becoming tightly packed and overlapping during third and subsequent whorls, their crests frequently damaged; exposed portion of lamellae with indistinct spiral threads (Figs 15E, 16C); lamellae with microsculpture of fine close-set scratch-like axial marks (Fig. 16D), in places overlain with a chalky intritacalx-like deposit (Fig. 16E); final lamella behind outer lip greatly enlarged, forming strong, angular subterminal varix (Fig. 15D, F); lamellae continue around periphery, becoming progressively weaker on base and into umbilicus; spiral threads more distinct on base, close-set and numerous, present also in umbilicus; base evenly rounded; umbilicus of moderate width, lacking a distinct margin, but sometimes with a low, indistinct funicle spiralling into it from mid-point of columella. Aperture subcircular, strongly prosocline, almost tangential; peristome interrupted in parietal region; inner lip strongly concave below insertion of columella onto paries, thin and somewhat reflected over umbilicus in this region; inner lip thickened and somewhat flaring below mid-point of columella; basal and outer lips evenly rounded, edge beyond subterminal varix thin; interior smooth, lacking obvious nacre even in live-collected specimens.

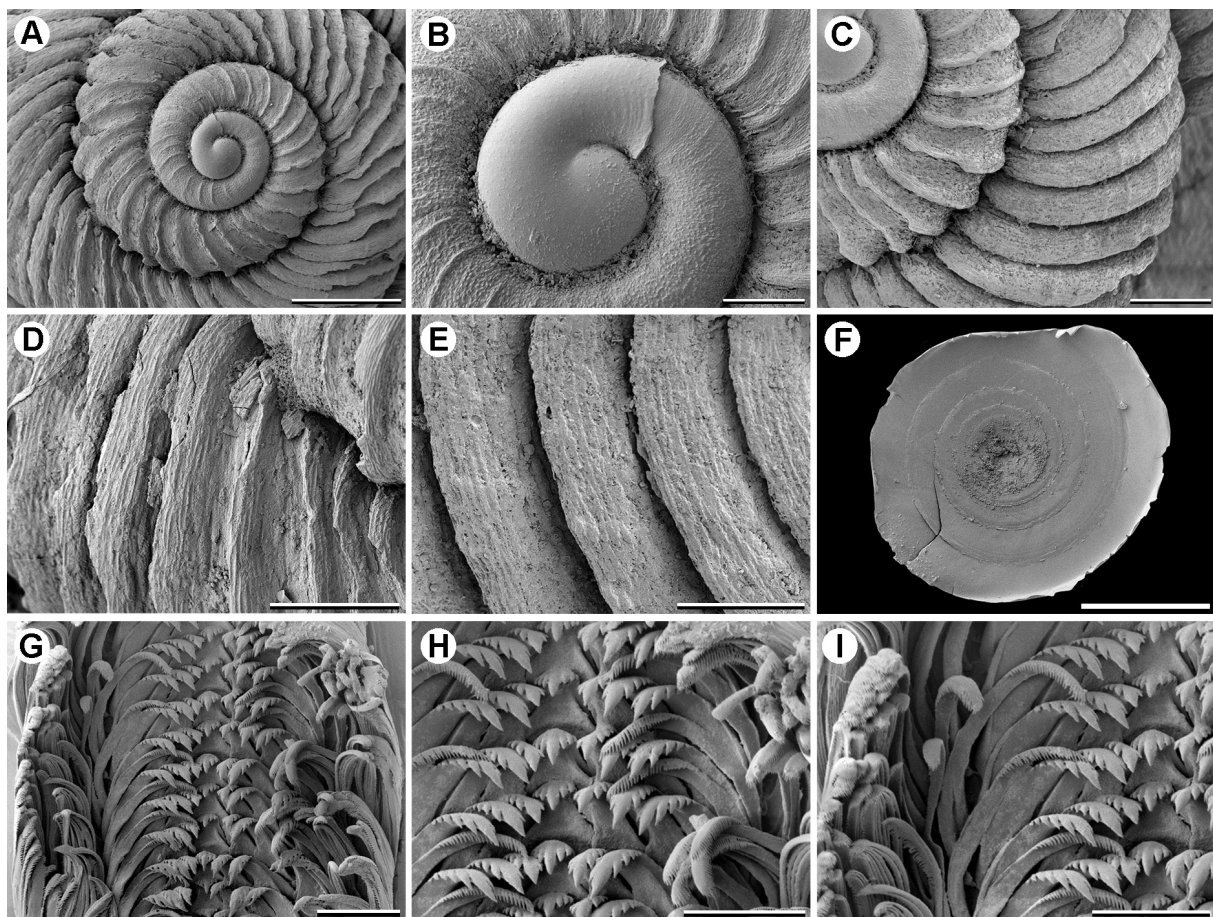


Fig. 16. *Imbricoscelis coronis* (Barnard, 1963) gen. et comb. nov., SEM, Walters Shoal, stn CP4902 (MNHN). **A.** shell apex. **B.** Protoconch. **C.** Sculpture of overlapping lamellate ribs with fine spiral lirae. **D.** Microsculpture of slash-like axial marks. **E.** Microsculpture overlain by intritacalx layer. **F.** Operculum. **G–I.** Radula. **G.** Full width of radula. **H.** Rachidian and lateral teeth in central field. **I.** Latero-marginal area. Scale bars: A, F = 500 μ m; B, E = 100 μ m; C–D = 200 μ m; G = 25 μ m; H–I = 20 μ m.

PROTOCONCH (Fig. 16B). Translucent, pale greyish-white; comprising approx. 1.25 whorls, diameter approx. 290 μ m; apical bulb rounded; surface for the most part smooth, but with traces of irregular granulation where unworn; terminal lip straight, slightly flaring, not thickened.

COLOUR. Uniformly dirty white.

DIMENSIONS. Height 3.0 mm, diameter 3.0 mm (fide Barnard 1963a); largest specimen, height 3.1 mm, diameter 3.5 mm.

OPERCULUM (Fig. 16F). Corneous; initially tightly multispiral, but whorls broadening with growth and becoming more openly multispiral.

RADULA (Fig. 16G–I). Formula $\infty+3+1+3+\infty$, with ± 50 transverse rows of teeth. Rachidian with lateral flanges of shaft slightly expanded creating a relatively weak hood; central cusp well developed, lanceolate and with two smaller lateral cusps on each side. Lateral teeth overlapping extensively, their cusps asymmetrically trigonal; central denticle largest, lateral denticles well developed on outer margin, progressively decreasing in size toward tooth shaft; inner margin with fewer denticles. Marginal teeth numerous and slender; cusps of inner ones recurved, narrowly and asymmetrically spatulate, inner margin straight and smooth, outer margin curved and finely pectinate for a considerable distance; outer marginals similar, but with pectinate outer margin extending further down shaft; outermost marginals somewhat broader.

EXTERNAL ANATOMY. Only dried bodies available, rehydration of which revealed limited detail; cephalic tentacles prominent; eyestalks with well-developed, pigmented eyes; right post-ocular peduncle present; left neck lobe digitate, right one entire; 3–4 epipodial tentacles evident on each side, perhaps more.

Distribution

Previously known only from the Sapmer Bank Seamount, adjacent to the Gallieni Fracture Zone of the Southwest Indian Ridge [± 900 km SE of Walters Shoal]. Here recorded from the slopes of Walters Shoal at depths of 256–964 m (live-taken material 640–707 m); dredged and trawled on coarse sandy substrata with abundant cnidarians, ophiuroids and bivalves.

Remarks

Although Barnard had 11 specimens of this species, his description of it is brief and inadequate; hence I have chosen to provide a more detailed description above. There can be little doubt, however, that the material from Walters Shoal belongs to the same species. It is evidently associated with seamounts in the vicinity of the Southwest Indian Ridge and appears to be a species with southern rather than tropical affinity.

The Pliocene *Vetulonia philippinensis* Kiel, Aguilar & Kase, 2020 is superficially similar, but it has fewer, more rounded, non-overlapping axial ribs, a narrower umbilicus and lacks a subterminal varix behind the outer lip.

Genus *Vaceuchelus* Iredale, 1929

Type species

Euchelus angulatus Pease, 1868 (original designation) [= *Vaceuchelus foveolatus* (A. Adams, 1853)], Recent, south Pacific.

Vaceuchelus gemmula (Turton, 1932)

Fig. 14D–E

Euchelus gemmula Turton, 1932: 194, pl. 49, no. 1347. Type loc.: Port Alfred, E Cape, South Africa.

Vaceuchelus gemmula – Herbert 2012: 452, figs 42–44; 2015: 34 (further references).

Material examined

WALTERS SHOAL – **summit area** • 1 empty shell; south-west, stn WS03; 33°12.2' S, 43°50.8' E; depth 40 m; 30 Apr. 2017; MNHN • 13 empty shells; south, stn WS06; 33°15.1' S, 43°54.5' E; depth 26 m; 1 May 2017; MNHN • 17 empty shells; south, stn WS07; 33°15.4' S, 43°52.2' E; depth 30–33 m; 2 May 2017; MNHN • 17 empty shells; south-east, stn WS08; 33°13.7' S, 43°55.9' E; depth 30–33 m; 3 May 2017; MNHN • 1 living specimen; south, stn WB05; 33°15.1' S, 43°54.5' E; depth 26–30 m; 1 May 2017; DNA tissue sample; MNHN IM-2013-67254 • 1 empty shell; south, stn WB05; 33°15.1' S, 43°54.5' E; depth 26–30 m; 1 May 2017; MNHN • 4 empty shells; north-west, stn WB09; 33°13.8' S, 43°55.8' E; depth 27–30 m; 4 May 2017; MNHN • 1 empty shell; north-west, stn WB10; 33°09.1' S, 43°51.8' E; depth 30 m; 6 May 2017; MNHN. – **slopes** • 1 empty shell; stn DW4885; 33°17' S, 43°55' E; depth 272–380 m; 3 May 2017; MNHN • 1 empty shell; stn DW4892; 33°12' S, 44°01' E; depth 624–646 m; 4 May 2017; MNHN • 1 empty shell; stn CP4901; 33°09' S, 44°01' E; depth 647–672 m; 6 May 2017; MNHN.

Distribution

Eastern South Africa, here extended eastwards to Walters Shoal, where it has been collected primarily on the summit area by brushing and suction sampling at depths of 26–40 m (live-taken material 26–30 m); occasional dead specimens extending down to 647 m.

Remarks

Previously thought to be endemic to the eastern coast of South Africa, at latitudes between 31° S and 34° S, but specimens from Walters Shoal from 33° S are indistinguishable from South African ones. As in South Africa, the Walters Shoal material spans a considerable bathymetric range, living specimens having been collected in water as shallow as 26 m and dead shells at depths up to 647 m (to 500 m in South Africa).

Genus *Vetulonia* Dall, 1913

Type species

Vetulonia galapagana Dall, 1913 (original designation), Recent, eastern Pacific.

Remarks

Vetulonia was tentatively referred to the Calliotropinae by Warén & Bouchet (1993), but no further progress has been made in clarifying the affinity of the genus. Kano *et al.* (2009) noted some anatomical similarity with calliotropids and chilodontoids, but in the absence of molecular data, chose to treat *Vetulonia* as a skeneimorph seguenzioid of uncertain affinity. More recently Kiel *et al.* (2020) placed the genus in the Seguenziidae.

Adult and juvenile radulae of *V. jeffreysi* Dall, 1913 [= *V. paucivaricosa* (Dautzenberg, 1889)] were figured by Warén & Bouchet (1993) and a re-evaluation of these images in the light of more recent studies on seguenzioid taxa indicates considerable similarity with radulae of species now referred to the Chilodontidae (Herbert 2012). The juvenile radula, apart from its reduced number of lateral teeth,

is very similar to that of species of *Herpetopoma* Pilsbry, 1890 and *Vaceuchelus*, whereas the adult radula is much like that of species of *Granata* Cotton, 1957, all of which belong to the Chilodontidae. Furthermore, the strong axial ribs on the first teleoconch whorl and its vermiform microsculpture (see below) are features common in chilodontids, as are the relatively low, non-globose protoconch with granular microsculpture, and the claviform eyestalks with large eyes (Herbert 2012). I believe these similarities are sufficient to indicate that *Vetulonia* is also referable to the Chilodontidae.

Vetulonia parajeffreysi Absalão & Pimenta, 2005
Fig. 14F–I

Vetulonia parajeffreysi Absalão & Pimenta, 2005: 194, figs 3–8. Type loc.: Campos Basin, off Rio de Janeiro State, Brazil, 1290 m.

Material examined

WALTERS SHOAL • 1 empty shell; south plain, stn CP4913; 33°52' S, 44°05' E; depth 1539–1615 m; 11 May 2017; MNHN.

Remarks

A single damaged specimen referable to *Vetulonia* was collected, height 1.85 mm, diameter 2.5 mm (H/D=0.74). Despite its poor quality, I record the occurrence of this material on Walters Shoal as it represents the first record of the genus from the Indian Ocean. The specimen closely resembles *V. parajeffreysi* from similar depths in the south-western Atlantic. The shell is more depressed than the holotype of that species, but is closer to the less elevated specimen illustrated (Absalão & Pimenta 2005: fig. 8). Since the specimen from Walters Shoal is damaged, it is difficult to be certain of its identity, but I can find no features that might serve to clearly differentiate it from *V. parajeffreysi*. The protoconch (diameter 270 µm) is slightly tilted, but not conspicuously raised above the first teleoconch whorl. Its apical region is rounded, but not bulbous, the surface coarsely granular and the terminal lip convex, with a slight step down to the first teleoconch whorl (Fig. 14I). The latter possesses a distinct vermiform microsculpture between the axial ribs.

Family Choristellidae Bouchet & Warén, 1979

Genus *Bichoristes* McLean, 1992

Type species

Bichoristes wareni McLean, 1992 (original designation), Recent, Norfolk Ridge.

Remarks

Bichoristes is a monotypic genus and is the only choristellid in which the shell is planispiral rather than helically coiled. However, the jaw and radula closely resemble those of other choristellid genera (McLean 1992) and thus like them, *B. wareni* is assumed to live within spent elasmobranch egg cases and to feed on decomposing bacteria growing on the inner egg case wall.

Bichoristes wareni McLean, 1992
Fig. 17A–D

Bichoristes wareni McLean, 1992: 287, figs 46–53. Type loc.: Norfolk Ridge (24°55' S, 168°22' E) [not 162°22' E as given], depth 505–515 m.

Material examined

WALTERS SHOAL – **slopes** • 1 empty shell; stn DW4879; 33°17' S, 43°52' E; depth 288–300 m; 1 May 2017; MNHN • 1 living specimen; stn DW4880; 33°17' S, 43°51' E; depth 275–318 m; 1 May 2017; MNHN • 4 empty shells; stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017; MNHN • 17 empty shells; stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN • 7 empty shells; stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; MNHN • 1 empty shell, fresh; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; MNHN • 10 empty shells, some fresh juveniles; stn DW4893; 33°16' S, 43°58' E; depth 623–629 m; 4 May 2017; MNHN • 1 empty shell; stn DW4897; 33°09' S, 43°59' E; depth 490–584 m; 5 May 2017; MNHN • 1 empty shell; stn DW4898; 33°09' S, 44°01' E; depth 652–668 m; 6 May 2017; MNHN • 1 empty shell; stn DW4899; 33°09' S, 44°02' E; depth 707–720 m; 6 May 2017; MNHN.

Distribution

Until now known only from the type material from the Norfolk Ridge, south-east of New Caledonia. Here recorded for the first time in the Indian Ocean; from the slopes of Walters Shoal, at depths of 300–707 m; dredged on substrata of coarse sand; one live-taken specimen 275–318 m.

Remarks

Although geographically distant from the original sample discussed by McLean (1992), I can find no consistent differences by which to separate the Walters Shoal specimens from the original Norfolk Ridge material. The holotype (diameter 3.2 mm) is somewhat larger than the specimens from Walters Shoal (diameter of largest specimen 2.5 mm), but this is likely simply a reflection of the number of teleoconch whorls (respectively 3.2 vs 2.7 whorls). Like the holotype, the specimens from Walters Shoal have a smooth protoconch with a relatively small apical bulb (rounded or somewhat ovate) which

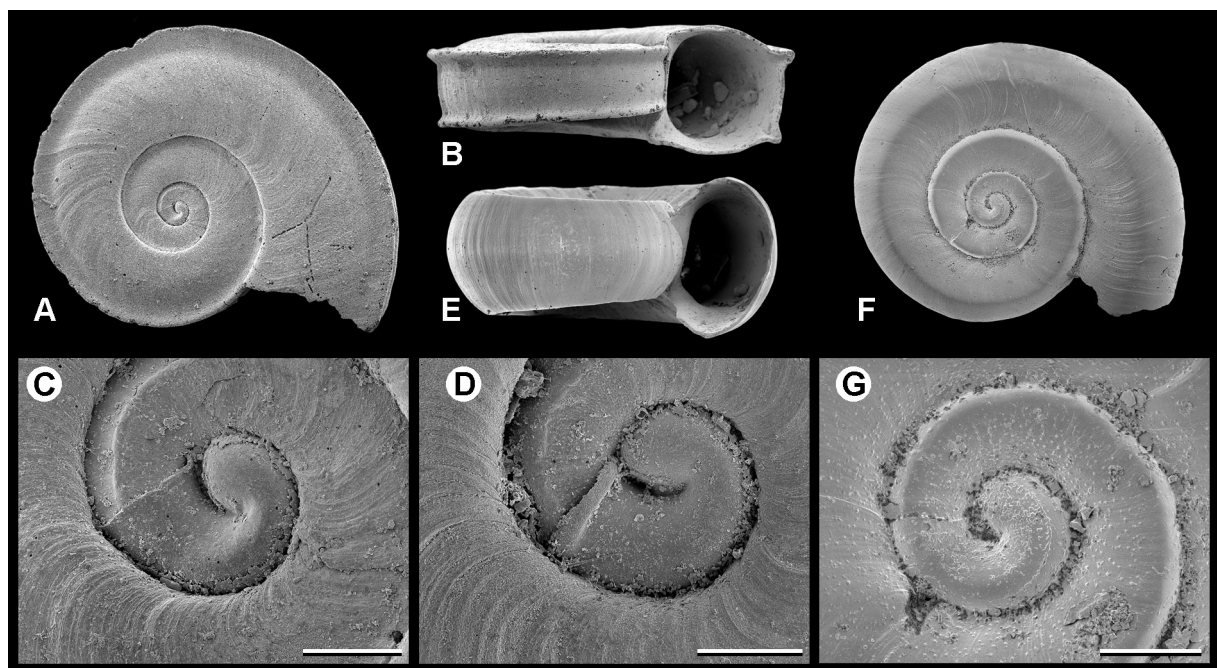


Fig. 17. A–D. *Bichoristes wareni* McLean, 1992. A–B. Apical and apertural views, diameter 2.4 mm, stn DW4886 (MNHN). C. Protoconch of A. D. Protoconch of juvenile with thickened terminal lip, stn DW4893 (MNHN). E–G. *Eudaronia ?biconcava* (Thiele, 1925), stn CP4913 (MNHN). E–F. Apertural and apical views, diameter 1.4 mm. G. Protoconch. Scale bars = 100 µm.

is followed by an expanding terminal tube, from which it is separated by a relatively deep suture-like groove (Fig. 17C–D). The protoconch of species of *Choristella* is of the same form (McLean 1992). In several fresh juvenile shells from Walters Shoal, the protoconch has a distinct, rounded terminal varix (Fig. 17D), but this appears to be a delicate, superficial structure and is partly or completely eroded in adult specimens.

The holotype was collected alive, but McLean (1992) did not state whether the specimen was found in a spent elasmobranch egg case. However, since he stated that no choristellids were “known to be free living and unassociated with the spent egg cases of elasmobranchs”, it is clear that he considered this to be the habitat of *Bichoristes wareni*, the planispiral shell of which he believed would facilitate access to the narrower terminal parts of such egg cases. There is no information to indicate whether or not the single live-taken specimen collected on Walters Shoal was living in an elasmobranch egg case. All specimens from Walters Shoal were sorted from sieved samples of dredged substratum.

Zerotula nummaria Powell, 1940 from northern New Zealand (Family: Zeratulidae) has a superficially similar keeled, planispiral shell, but is smaller (diameter < 1.5 mm) and has less distinct, shallowly undulant keels and a rougher surface (Warén & Hain 1996).

Family Eudaroniidae Gründel, 2004

Genus *Eudaronia* Cotton, 1945

Type species

Cyclostrema (Daronia) jaffaensis Verco, 1909 (original designation), Recent, South Australia.

Remarks

Kano *et al.* (2009) refrained from employing Gründel’s suprageneric taxon pending more anatomical and molecular data. More recently, Bouchet *et al.* (2017), Fukumori *et al.* (2019), Hoffman *et al.* (2020) and Rubio & Rolán (2021) have chosen to use the name at family level.

Eudaronia ?biconcava (Thiele, 1925)

Fig. 17E–G

Lyocyclus(?) biconcavus Thiele, 1925: 117[83], pl. 9 figs 18–19. Type loc.: off Mogadishu, Somalia, *Valdivia* stn 256 (1°49' N, 45°29.5' E), depth 1134 m.

Eudaronia biconcavus [sic] – Warén 1991: 77.

Eudaronia biconcava – Warén 1991: fig. 8A [radula]. — Kano *et al.* 2009: 401. — Rubio & Rolán 2021: 90, fig. 36a–c [syntype].

Material examined

WALTERS SHOAL • 1 empty shell; south plain, stn CP4913; 33°52' S, 44°05' E; depth 1539–1615 m; 11 May 2017; MNHN.

Distribution

Recorded from deep water off Somalia (1134 m) (Thiele 1925), Réunion (1155–1200 m) (Warén 1991) and on the plain surrounding Walters Shoal (1539–1615 m); living specimens unknown.

Remarks

Rubio & Rolán (2021) illustrated a syntype of *Lyocyclus biconcavus* (Museum für Naturkunde, Berlin – ZMB/Moll-109251). When compared to the specimen from Walters Shoal, this syntype, albeit smaller and thus probably subadult (diameter 1.0 mm vs 1.4 mm), has stronger apical and basal keels, and an aperture that is markedly flared where these keels meet the outer lip. My referral of the present material to *E. biconcava* is thus tentative and is influenced by the shared western Indian Ocean provenance. With only one specimen available and with no data concerning intraspecific variation in species of *Eudaronia*, I refrain from describing the Walters Shoal specimen as a new species. More western Indian Ocean specimens will need to be examined before a definitive conclusion can be drawn.

With the exception of *Eudaronia mikra* Hoffman, Gofas & Freiwald, 2020, Recent species of *Eudaronia* exhibit only small differences in shell morphology. Judging from the original figures (Verco 1909) and those provided by Cotton (1959) and Warén (1991), the south Australian *E. jaffaensis* has a deeper shell with more rapidly expanding whorls than *E. biconcava*. In *E. spirata* Hoffman, Gofas & Freiwald, 2020, from seamounts south of the Azores, the apical and basal insertions of the outer lip are level with the apical and basal keels respectively, whereas in the present material and the Berlin syntype these insertions lie some distance below and above these respective keels (Fig. 17E), and the interruption of the peristome thus spans a narrower portion of the penultimate whorl. *Eudaronia aperta* (Sykes, 1925) from off Portugal is similar in the latter respect, but it is difficult to assess since the published images of the species differ considerably in the relative depth of the whorls and the convexity of the periphery (Warén 1991: fig. 14c, e; Hoffman *et al.* 2020: fig. 11). Like *E. spirata*, the apical part of the protoconch of the Walters Shoal specimen bears distinct spiral threads (Fig. 17G). *Eudaronia mikra* has axially costate early whorls and is more similar to species of *Adeuomphalus* Seguenza, 1876.

Family Seguenziidae Verrill, 1884
Subfamily Seguenziinae Verrill, 1884

Genus *Fluxinella* Marshall, 1983

Type species

Fluxinella lepida Marshall, 1983 (original designation), Recent, New Zealand.

Fluxinella dufresneae sp. nov.

[urn:lsid:zoobank.org:act:E5F47BCC-5949-43E3-A122-646CA683873F](https://zoobank.org/urn:lsid:zoobank.org:act:E5F47BCC-5949-43E3-A122-646CA683873F)

Figs 18A–C, 19A–B

Diagnosis

Shell depressed-trochiform, whitish, periphery angular, base flattened and broadly umbilicate; first teleoconch whorl with two strong spiral cords and evenly spaced axial riblets, sinuous above shoulder cord, opisthocline below it; third nodular cord subsequently arising below suture; shoulder cord weakens with growth and lies closer to periphery; whorl profile becomes convex above this core and concave below it; base with 1–2 subperipheral spiral lirae, mid-portion smooth, inner portion with 3–4 spiral lirae; umbilical margin angular, interior of umbilicus with an additional cord spiralling inward; aperture obliquely quadrate; outer lip with broad posterior sinus, protracted below this; inner lip concave either side of a central bulge.

Etymology

Named after the vessel *Marion Dufresne* II, aboard which the Walters Shoal survey (MD208) was conducted. Although the ship was named after the French explorer Marc-Joseph Marion du Fresne (1724–

1772), a man, the species is named after the ship. Since the Latin “*navis*” – “a ship”, is feminine, I employ the name in that gender.

Material examined

Holotype

WALTERS SHOAL • living specimen; south plain, stn CP4913; 33°52' S, 44°05' E; depth 1539–1615 m; 11 May 2017; DNA tissue sample; MNHN-IM-2013-67291.

Paratypes

WALTERS SHOAL • 6 empty shells; same collection data as for holotype; SEM shell; MNHN-IM-2000-38058 • 1 empty shell; slopes, stn CP4918; 32°58' S, 43°27' E; depth 1295–1356 m; 14 May 2017; MNHN-IM-2000-38059.

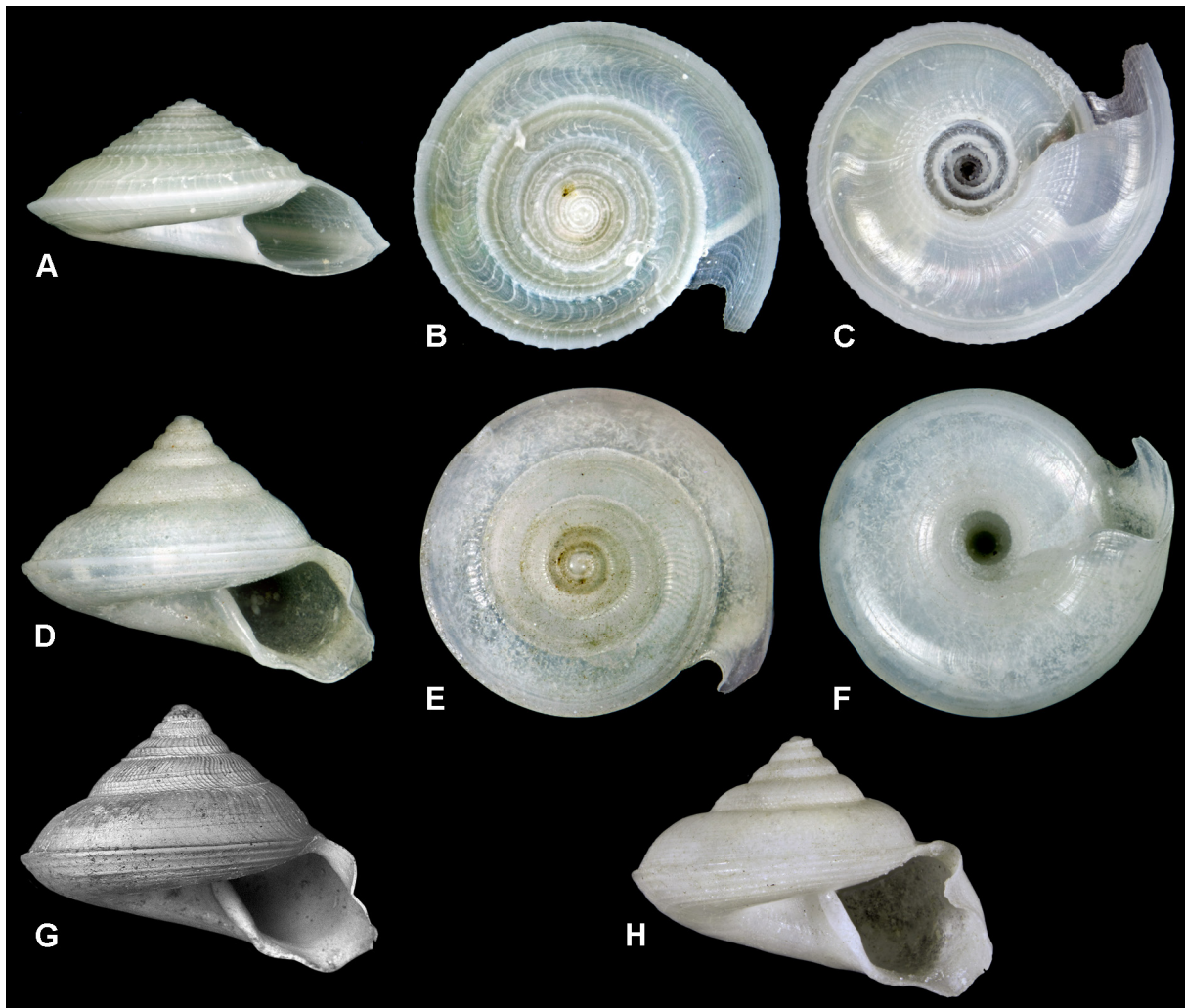


Fig. 18. A–C. *Fluxinella dufresneae* sp. nov., holotype, diameter 6.0 mm (MNHN-IM-2013-67291). D–F. *Hadroconus scobina* sp. nov., holotype, diameter 3.7 mm (MNHN-IM-2000-38060). G. *Hadroconus scobina* sp. nov., holotype, SEM (uncoated) to show detail of sculpture. H. *Hadroconus scobina* sp. nov., specimen with shouldered whorls, diameter 4.0 mm, stn DW4898 (paratype, MNHN-IM-2000-38063).

Description

SHELL. Of moderate size (diameter up to 6.0 mm), depressed-trochiform, width almost twice height ($H/D \pm 0.52$); whorls weakly convex, spire profile shallowly stepped by spiral sculpture; periphery angular; base somewhat flattened, broadly umbilicate; teleoconch of up to 5.5 whorls. First teleoconch whorl initially with two strong spiral cords, one midway between sutures (P1, shoulder cord), the second (P2) at whorl periphery, level with abapical suture (Fig. 19B); distinct axial sculpture of evenly spaced riblets (25–30) extending from suture to suture; riblets sinuous above shoulder cord, opisthocline below it; a third rounded cord (S1) develops below adapical suture toward end of whorl; sculpture of whorls 2–3 similar to that on first whorl, with S1 increasingly prominent and becoming nodular where crossed by axial riblets (Fig. 19A); whorls concave above and below P1; on fourth whorl P1 proportionally weaker and somewhat closer to periphery, with fine spiral thread arising above it; axial riblets becoming more strongly concave above P1 and almost orthocline below it; spiral cords on fifth whorl weakly nodular where crossed by axial riblets and peripheral cord shallowly scalloped; whorl profile becomes convex above P1, but remains concave below it; P1 scarcely evident on second half of last adult whorl, accompanied by numerous additional fine, supra-peripheral spiral lirae; periphery angular, somewhat flange-like. Base with 1–2 subperipheral spiral lirae, axial pliculae extend around periphery, reaching outermost lira but no further; mid-portion of base smooth, sculptured only by fine sinuous growth-lines; inner portion of base with 3–4 spiral lirae, progressively stronger toward umbilicus; umbilical margin angular, bordered by strong spiral cord that becomes raised as it spirals into umbilicus; growth-lines of base strengthen toward umbilical margin, becoming peri-umbilical pliculae and rendering the inner spirals weakly nodular; interior of umbilicus steep-sided with additional cord spiralling inward at mid-columella level. Aperture obliquely quadrate; outer lip with broad, U-shaped posterior sinus, and then protracted toward periphery and notched at peripheral keel; basal lip damaged in holotype (the only mature specimen available), but profile of growth-lines indicates shallow subperipheral sinus; columella lip oblique and slightly thickened, concave where it meets basal lip, projecting somewhat above this, but followed adapically by deeper concavity before its insertion on paries; no thickening of interior of outer lip evident.

PROTOCONCH (Fig. 19B). White; diameter 335–345 μm , comprising ca 1.25 whorls, apical cap evenly rounded; mostly smooth, but with traces of superficial granulation near apex; terminal lip weakly convex, not conspicuously thickened.

COLOUR. Uniformly milky-white, somewhat translucent; interior faintly nacreous.

DIMENSIONS. Holotype, height 3.1 mm, diameter 6.0 mm (= largest specimen).

Distribution

Known only from the slopes and surrounding plain of Walters Shoal, at depths of 1356–1539 m (live-taken specimen 1539–1615 m); obtained by beam trawl on fine sand with abundant echinoids and ophiuroids.

Remarks

Fluxina solarium Barnard, 1963, from 300 km south of Madagascar (depth 875 m), which Marshall (1983) referred to *Fluxinella*, has reference here. Although Barnard (1963a) considered it extremely close to *Fluxina marginata* Schepman, 1909, from Maluku, Indonesia, which is undoubtedly a species of *Fluxinella*, his description of *F. solarium* lacks precision and the figure provided is poor, illustrating only the apical surface. Since the type locality for the species lies only 650 km to the north-east of Walters Shoal, it is clearly important to compare this enigmatic taxon with the specimens from Walters Shoal. Unfortunately, it has not been possible to obtain photographs of the holotype in the South African Museum (Iziko) and comparison can only be based on the inadequate original description and figure, and the drawing provided by Kensley (1973: fig. 250). Nonetheless, neither Barnard's description of

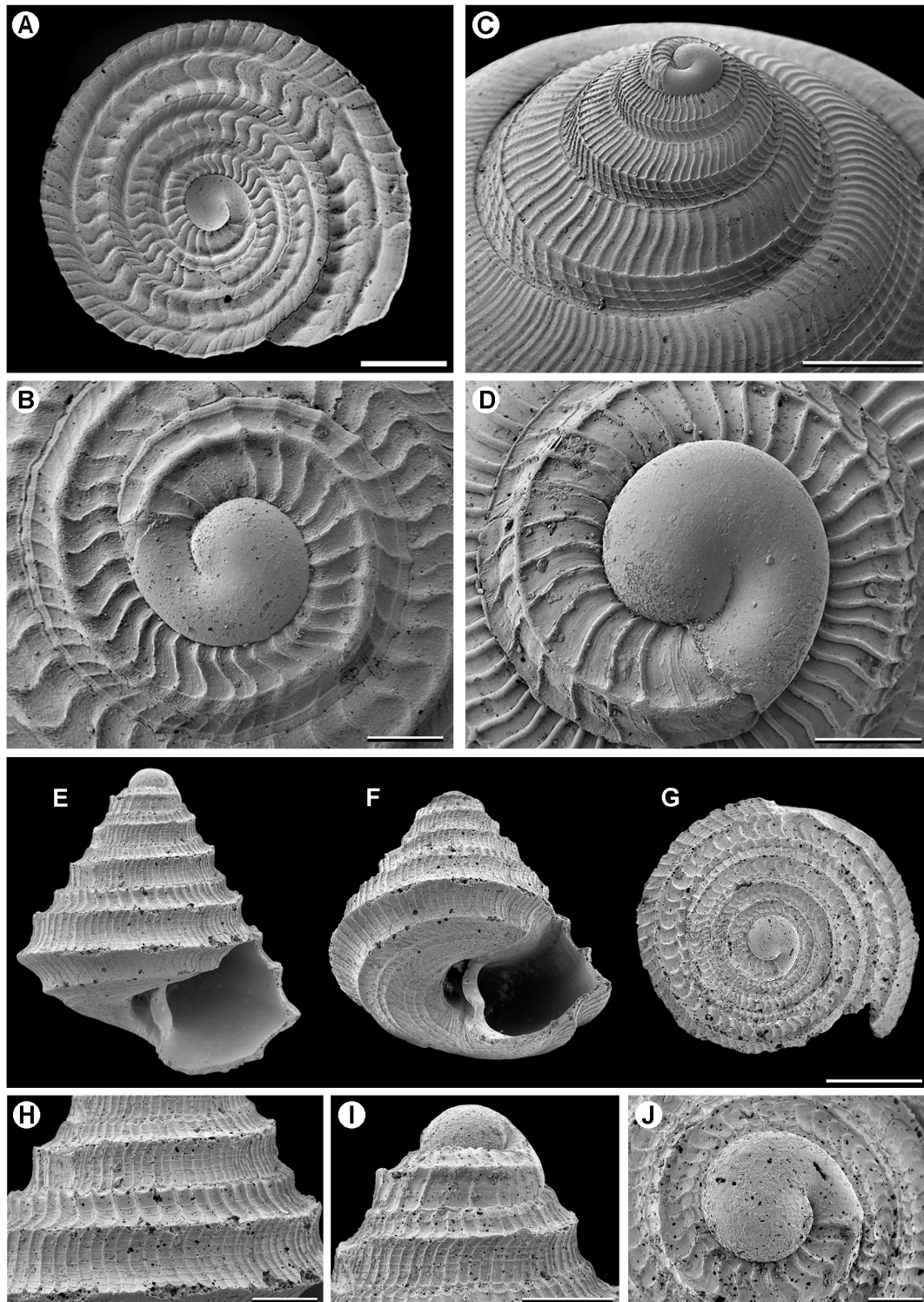


Fig. 19. A–B. *Fluxinella dufresneae* sp. nov., juvenile paratype (MNHN-IM-2000-38058). A. Spire whorls. B. Protoconch. C–D. *Hadroconus scobina* sp. nov., paratype (MNHN-IM-2000-38065). C. Oblique view of spire whorls. D. Protoconch. E–J. *Seguenzia* cf. *S. emmeles* Marshall, 1991, Walters Shoal, stn CP4913, height 1.63 mm, diameter 1.50 mm (MNHN). E–G. Apertural, oblique basal and apical views of shell. H. Detail of sculpture showing more numerous axial riblets below shoulder keel. I. Side view of apex. J. Protoconch. Scale bars: A, C = 0.5 mm; B, D, J = 100 μ m; E–G = 1.0 mm; H–I = 200 μ m.

the ontogeny of the spiral sculpture, nor his statement that the profile of the whorls is biconvex, is compatible with the present material. Likewise, his figure suggests that spiral P1 on the first teleoconch whorl persists as the subsutural cord on subsequent whorls. On this evidence, therefore, I conclude that the Walters Shoal specimens are not conspecific with Barnard's species.

Fluxinella dufresneae sp. nov. resembles some of the other low-spired and relatively strongly sculptured species of *Fluxinella* such as *F. acesta*, *F. euphanes*, *F. megalomphala*, *F. stirophora* and *F. tenera*, all described by Marshall (1991) from the New Caledonian region. It differs from these, however, in that the shoulder spiral of the first teleoconch whorl does not disappear on subsequent spire whorls, but instead persists, albeit weaker and coming to lie progressively lower down the whorl, thus no longer forming a shoulder, but instead becoming a supra-peripheral cord that evanesces only during the latter part of the final whorl. In *Fluxinella marginata* the last adult whorl has a much less convex profile. Furthermore, none of the above species exhibits the nodular subsutural cord on the spire whorls evident in *F. dufresneae*. The southern African *Fluxinella gelida* (Barnard, 1963), from a depth of over 2250 m, north-west of Cape Town, has an almost totally smooth shell.

Fluxinella stellaris Bozzetti, 2008, described from beach-drift samples collected in southern Madagascar (Bozzetti 2008), is not a seguenziid and the name is in fact a junior synonym of *Agagus stellamaris* Herbert, 1991.

Genus *Hadroconus* Quinn, 1987

Type species

Basilissa alta Watson, 1879 (original designation), Recent, Caribbean.

Hadroconus scobina sp. nov.

[urn:lsid:zoobank.org:act:D5D500E3-1B96-4A37-BCA4-70D5544D363F](https://doi.org/10.21203/rs.3.rs-3848885/v1)

Figs 18D–H, 19C–D

Diagnosis

Shell trochiform, spire weakly coeloconoid, periphery with flange-like keel; early sculpture of distinct, evenly spaced, sinuous axial riblets, with a strong spiral cord at shoulder; additional finer spiral cords and lirae developing below shoulder cord; sculpture generally weak on last adult whorl; base with 2–5 distinct subperipheral spiral cords; umbilicus moderately broad; outer lip with a deep U-shaped posterior sinus, a distinct labral projection, a second shallower sinus below periphery, and a third small sinus at base of columella; interior with low collabral thickening extending from insertion of outer lip.

Etymology

From the Latin “*scobina*” – “a file” (noun in apposition); in reference to the file-like sculpture of the spire whorls.

Material examined

Holotype

WALTERS SHOAL • empty shell; slopes, stn DW4885; 33°17' S, 43°55' E; depth 272–380 m; 3 May 2017; MNHN-IM-2000-38060.

Paratypes

WALTERS SHOAL – **slopes** • 3 empty shells; same collection data as for holotype; MNHN-IM-2000-38061 • 5 empty shells; stn DW4892; 33°12' S, 44°01' E; depth 624–646 m; 4 May 2017;

MNHN-IM-2000-38062 • 12 empty shells; stn DW4898; 33°09' S, 44°01' E; depth 652–668 m; 6 May 2017; MNHN-IM-2000-38063 • 3 empty shells; stn DW4899; 33°09' S, 44°02' E; depth 707–720 m; 6 May 2017; MNHN-IM-2000-38064 • 9 empty shells; stn DW4900; 33°10' S, 44°01' E; depth 660–670 m; 6 May 2017; SEM shell; MNHN-IM-2000-38065.

Other material

WALTERS SHOAL – **slopes** • 2 empty shells; stn CP4901; 33°09' S, 44°01' E; depth 647–672 m; 6 May 2017; MNHN • 2 empty shells; stn CP4902; 33°08' S, 44°02' E; depth 700–711 m; 7 May 2017; MNHN • 1 empty shell, juvenile; stn CP4906; 33°26' S, 44°00' E; depth 799–837 m; 9 May 2017; MNHN • 8 empty shells; stn DW4877; 33°10' S, 43°49' E; depth 217–256 m; 1 May 2017; MNHN • 3 empty shells; stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN • 12 empty shells; stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; MNHN • 1 empty shell; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; MNHN • 14 empty shells; stn DW4892; 33°12' S, 44°01' E; depth 624–646 m; 4 May 2017; MNHN • 50+ empty shells; stn DW4898; 33°09' S, 44°01' E; depth 652–668 m; 6 May 2017; MNHN • 16 empty shells; stn DW4899; 33°09' S, 44°02' E; depth 707–720 m; 6 May 2017; MNHN • 27 empty shells; stn DW4900; 33°10' S, 44°01' E; depth 660–670 m; 6 May 2017; MNHN.

Description

SHELL. Small, trochiform (diameter up to 4.3 mm), wider than high ($H/D=0.67-0.75$); spire weakly coeloconoid, whorls convex, suture shallowly to moderately indented, periphery angular with flange-like keel; spire whorls strongly sculptured, last adult whorl weakly so; base somewhat flattened, with moderately wide umbilicus; teleoconch of up to 5.5 whorls. First teleoconch whorl with a strong spiral cord midway between sutures (P1, shoulder cord), another (P2) at whorl periphery, level with or just above abapical suture (Fig. 19D); distinct axial sculpture of evenly spaced riblets (30–32) extending from suture to suture; riblets initially collabral, becoming sinuous above P1 toward end of whorl; sculpture of whorls 2–4 similar to that on first whorl, but with 2–3 additional finer spiral cords developing below P1 (Fig. 19C); P2 strengthening and becoming keel-like; P1 no longer prominent on fifth whorl, additional fine spiral lirae develop above periphery; axial sculpture weakens toward end of fifth whorl, sometimes evident only as faint growth-lines; spiral sculpture variable on latter part of final whorl, scarcely visible in some individuals but fine, close-set lirae present in others; periphery angular, delineated by flange-like keel. Base with 2–5 distinct subperipheral spiral cords, but basal spiral sculpture weakening toward umbilicus and appearing as fine incised lirae; umbilicus with steep sides; umbilical margin a low rounded cord, rather indistinct. Aperture obliquely quadrate; outer lip with a deep U-shaped posterior sinus, its edge flaring outward; below this a distinct labral projection (corresponding with a shallow indentation in whorl profile in some individuals); a second shallower sinus below periphery, its edge flaring; a third small sinus at base of columella; columella more or less straight, distinctly oblique and with a somewhat thickened and reflected margin; angle between columella and paries acute; interior of outer lip with low prosocline thickening extending from its insertion on penultimate whorl, lip thin and fragile beyond this.

PROTOCONCH (Fig. 19D). White; diameter 235–250 μm , comprising ca 1.25 whorls, apical bulb evenly rounded; mostly smooth, but with traces of superficial granulation near apex; terminal lip almost straight or weakly convex, not conspicuously thickened.

COLOUR. Uniformly milky-white, somewhat translucent; interior faintly nacreous.

DIMENSIONS. Holotype, height 2.8 mm, diameter 3.7 mm; largest specimen, height 2.9 mm, diameter 4.3 mm.

Distribution

Known only from the slopes of Walters Shoal, at depths of 256–799 m; on coarse sandy substrata with diverse cnidarians, molluscs, crustaceans and ophiuroids; living specimens unknown.

Remarks

Hadroconus scobina sp. nov. is smaller and comprises fewer whorls than its congeners. Many of the more than 100 specimens available exhibit a mature outer lip profile indicating cessation of growth, but none exceeds a diameter of 4.3 mm or has more than 5.5 whorls. In addition, the protoconch is substantially smaller than in the other species for which this is known (diameter $\leq 250 \mu\text{m}$ vs $\geq 375 \mu\text{m}$). It also differs from other species of *Hadroconus* in having more convex whorls, a more distinctly coeloconoid profile, finer sculpture and a much less clearly demarcated umbilical margin.

Hadroconus sibogae (Schepman, 1908) from Indonesia has coarser axial riblets which crenulate the peripheral keel, and the umbilicus is bordered by a strongly beaded rib. *Hadroconus diadematus* Marshall, 1988 from New Zealand has a distinct angular suprasutural cord above which are numerous fine spiral threads and it retains well-defined sculpture on the last adult whorl. *Hadroconus grandiosus* Marshall, 1991 from south of New Caledonia has flatter whorls without any sutural indentation and also has an angular suprasutural cord, though not as strong as that of *H. diadematus*. *Hadroconus altus* (Watson, 1879) from the Caribbean has an evenly trochoid profile and the peripheral carina is rendered crenate by the relatively coarse axial riblets.

As in *H. altus* (cf. Quinn 1987), intraspecific variation in shell morphology in *H. scobina* sp. nov. is considerable, both in terms of shell shape and strength of sculpture. In some specimens the last adult whorl becomes progressively more flattened below the adapical suture (Fig. 18H), resulting in an almost tabulate shoulder region in the final half-whorl. Likewise, although the axial riblets of the spire whorls are weak or scarcely evident on the final whorl in nearly all specimens, the strength of the spiral sculpture on the last adult whorl varies considerably, being confined to the supra-peripheral region in some individuals, but covering much of the adapical surface in others. The extent of intraspecific variation in the remaining species of *Hadroconus* is unknown since they are known from very few specimens.

Genus *Seguenzia* Jeffreys, 1876

Type species

Seguenzia formosa Jeffreys, 1876 (subsequent designation, Harris 1897: 266), Recent, N Atlantic.

Seguenzia cf. *S. emmeles* Marshall, 1991

Fig. 19E–J

Seguenzia emmeles Marshall, 1991: 93, figs 213–217. Type loc.: off southern New Caledonia, 2100–2650 m.

Material examined

WALTERS SHOAL • 1 empty shell; south plain, stn CP4913; 33°52' S, 44°05' E; depth 1539–1615 m; 11 May 2017; MNHN.

Remarks

A single juvenile shell in poor condition exhibits considerable similarity to *Seguenzia emmeles* from New Caledonia. It differs from that species in having more numerous, but weaker spiral cords on the base and a narrower umbilicus with a less strongly angled margin. In addition, whereas the inner lip of *S. emmeles* is toothless, the specimen from Walters Shoal, even though juvenile, has a distinct rounded columella bulge. *Seguenzia mirabilis* Okutani, 1964 from Japan is also similar to the present specimen, but it has a closed or at most chink-like umbilicus and a strong basal columella tooth (Okutani 2000;

Sasaki 2008). Although it is possible that the differences between the specimen from Walters Shoal and *S. mirabilis* reflect the former's juvenile condition, it also possesses finer and more numerous axial riblets. Unusually, on the fourth whorl these are more close-set below the shoulder keel than above it (9 vs 12 per 0.5 mm). The condition of the specimen is inadequate to meaningfully evaluate its identity and thus I merely note the occurrence of a species resembling *S. emmeles* on the plain surrounding Walters Shoal.

Genus *Visayaseguenzia* Poppe, Tagaro & Dekker, 2006

Type species

Visayaseguenzia maestratii Poppe, Tagaro & Dekker, 2006 (original designation), Recent, Philippines.

Visayaseguenzia compsa (Melvill, 1904)

Fig. 20

Basilissa (*Ancistrobasis*) *compsa* Melvill, 1904: 160, pl. 10 fig. 4. Type loc.: Gulf of Oman, 24°58' N, 56°54' E, depth 156 fathoms [285 m].

Visayaseguenzia compsa – Herbert 2015: 35, figs 3i–j, 4m.

Material examined

WALTERS SHOAL – slopes • 1 empty shell; stn DW4877; 33°10' S, 43°49' E; depth 217–256 m; 1 May 2017; MNHN • 14 empty shells; stn DW4879; 33°17' S, 43°52' E; depth 288–300 m; 1 May 2017; MNHN • 60+ specimens, some living; stn DW4880; 33°17' S, 43°51' E; depth 275–318 m; 1 May 2017; MNHN • 80+ empty shells; stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017; MNHN • 7 empty shells; stn DW4885; 33°17' S, 43°55' E; depth 272–380 m; 3 May 2017; MNHN • 60+ empty shells; stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN • 19 empty shells; stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; MNHN • 36 empty shells; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; MNHN • 1 empty shell; stn DW4892; 33°12' S, 44°01' E; depth 624–646 m; 4 May 2017; MNHN • 80+ empty shells; stn DW4893; 33°16' S, 43°58' E; depth 623–629 m; 4 May 2017; MNHN • 11 empty shells; stn DW4897; 33°09' S, 43°59' E; depth 490–584 m; 5 May 2017; MNHN • 1 empty shell; stn DW4899; 33°09' S, 44°02' E; depth 707–720 m; 6 May 2017; MNHN • 1 empty shell; stn DW4900; 33°10' S, 44°01' E; depth 660–670 m; 6 May 2017; MNHN • 1 empty shell; stn CP4902; 33°08' S, 44°02' E; depth 700–711 m; 7 May 2017; MNHN.

Distribution

Western Indian Ocean, from the Gulf of Oman to north-eastern South Africa; also on the slopes of Walters Shoal, at depths of 256–707 m (live-taken material 275–318 m); dredged on coarse sandy substrata.

Remarks

The abundant material from Walters Shoal of this species is somewhat variable in shell height, strength of sculpture and the relative width of the umbilicus. It is extremely similar to material dredged off northern South Africa that I have referred to *Visayaseguenzia compsa* (Herbert 2015), originally described from the Gulf of Oman. In South African material the labral projection is more elongate in fully mature specimens and, in the single live-collected specimen of *V. compsa* from Walters Shoal, the protoconch and first teleoconch whorl are orange-brown and the following two spire whorls have a faint lime-green wash that appears to originate from the underlying dried viscera. This has not been seen in South African specimens, the apex of which is uniformly whitish in live-collected specimens. This spire coloration of live-collected material from Walters Shoal is not evident in empty shells. South African material also

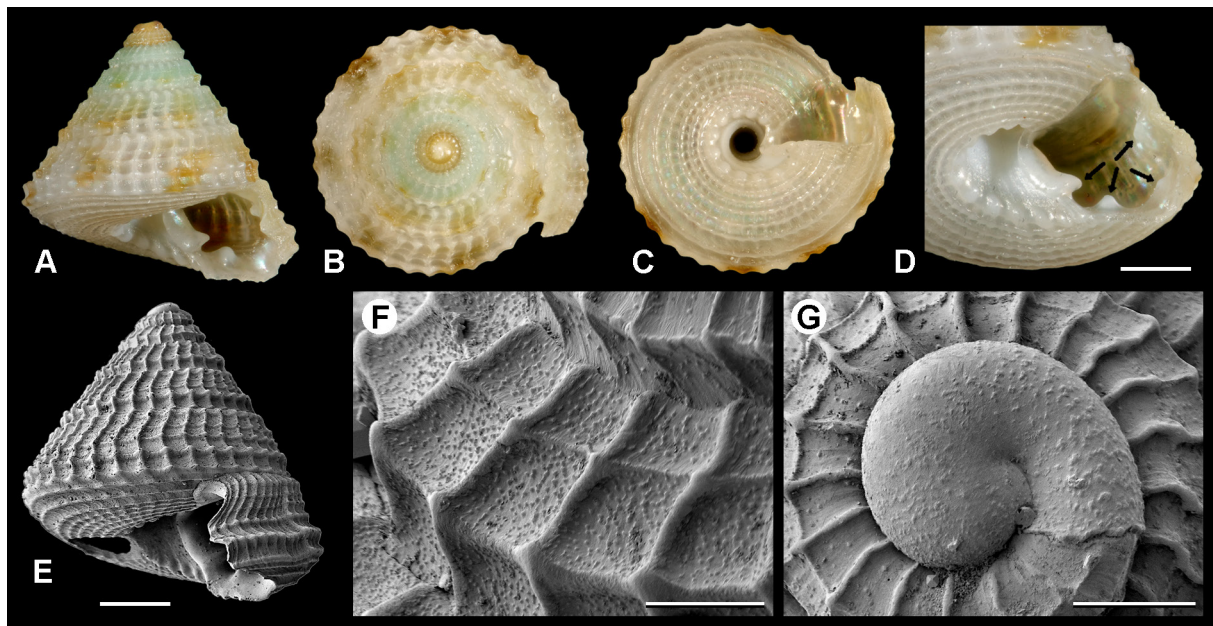


Fig. 20. *Visayaseguenzia compsa* (Melvill, 1904). **A–C.** Apertural, apical and basal views, Walters Shoal, stn DW4880, height 2.85 mm, diameter 2.71 mm (MNHN). **D.** Oblique view of aperture of the same specimen, apertural teeth arrowed. **E–G.** Walters Shoal, stn DW4893, SEM. **E.** Side view of shell showing profile of outer lip. **F.** Microsculpture of crisp granules on early part of second teleoconch whorl. **G.** Protoconch. Scale bars: D–E=0.5 mm; F–G=100 μ m.

occurs in somewhat shallower water (mostly < 100 m) than the samples from Walters Shoal, but the depth at which the holotype was dredged in the Gulf of Oman falls within the depth range of the records from Walters Shoal.

Visayaseguenzia compsa closely resembles *V. cumingi* Poppe, Tagaro & Dekker, 2006 from the Philippines, as well as unidentified material from the Ogasawara Islands (Hasegawa 2018). All are very similar in shape and sculpture, and such differences as may be evident between individuals from these different localities are small and difficult to evaluate, given the distances involved. Resolution of these issues will require more detailed morphological study including additional topotypic samples of *V. compsa*, as well as molecular data.

Visayaseguenzia is clearly closely related to *Calliobasis* Marshall, 1991 and the differences between them are essentially a matter of degree. They are unusual amongst seguenziids in that fresh shells exhibit a distinct colour pattern, usually of pale yellowish-green to brown blotches or axial bands. Marshall (1991) reported that the radula of *Calliobasis* differed from that of other seguenziids in having latero-marginal plates. To date, no information is available concerning the radula of *Visayaseguenzia*. The crisply granular microsculpture of *V. compsa* (Fig. 20F) is similar to that illustrated for *Calliobasis* by Marshall (1991), as is the morphology of the protoconch and the early teleoconch sculpture (Fig. 20G).

Family Trochaclididae Thiele, 1928

Genus *Acremodontina* Marshall, 1995

Type species

Conjectura carinata Powell, 1940 (original designation), Recent, northern New Zealand.

Acremodontina carinata (Powell, 1940)

Fig. 21

Conjectura carinata Powell, 1940: 223, pl. 28 fig. 8. Type loc.: between Spirits Bay and Three Kings Islands, northern New Zealand.

Conjectura carinata – Powell 1979: 74, pl. 20 fig. 22.

Acremodontina carinata – Marshall 1995: 102, figs 20–22, 29–30, 56–59.

Acremodontina aff. *carinata* – Herbert 2015: 84, fig. 9j–k.

Material examined

SOUTH AFRICA – **Eastern Cape** • 3 living specimens; off Mbashe River; stn Q1; 32°18.2' S, 29°4.1' E; depth 200–220 m; 18 Jul. 1982; Natal Museum Dredging Programme, R.V. *Meiring Naudé* leg.; sponge rubble; NMSA V908.

WALTERS SHOAL – **slopes** • 1 empty shell; stn DW4893; 33°16' S, 43°58' E; depth 623–629 m; 4 May 2017; MNHM.

Distribution

Recorded from off northern New Zealand, 27–805 m (living, 88–221 m) (Marshall 1995) and the east coast of South Africa (200–220 m, living in sponge dominated communities) (Herbert 2015). Here recorded also from the slopes of Walters Shoal, at a depth of 623–629 m.

Remarks

I have previously drawn attention to the occurrence of this genus in the south-western Indian Ocean (Herbert 2015). A single specimen belonging to the same species was obtained on Walters Shoal. I can find no features by which south-western Indian Ocean specimens can be convincingly distinguished from those from New Zealand and thus consider them to be conspecific.

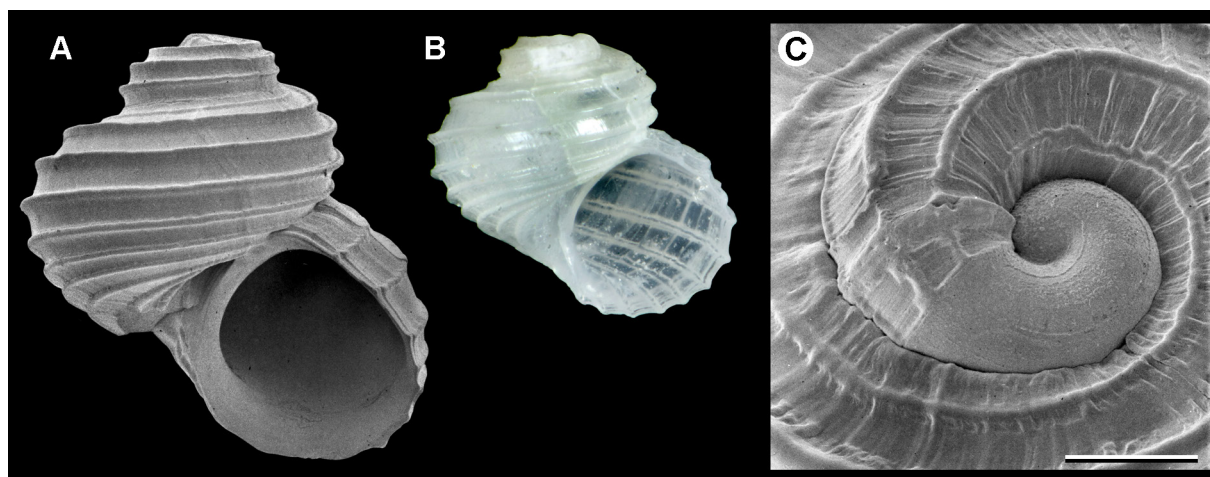


Fig. 21. *Acremodontina carinata* (Powell, 1940). **A.** Off Mbashe River, E Cape, South Africa, height 2.13 mm (NMSA V908). **B.** Subadult specimen, Walters Shoal, stn DW4893, height 1.42 mm (MNHN). **C.** Protoconch of A, scale bar = 100 μ m.

Genus *Trochaclis* Thiele, 1912

Type species

Trochaclis antarctica Thiele, 1912 (monotypy), Recent, Antarctica.

Trochaclis regalis Marshall, 1995

Fig. 22

Trochaclis regalis Marshall, 1995: 97, figs 11–12, 15. Type loc.: off Three Kings Islands, northern New Zealand.

Material examined

WALTERS SHOAL – slopes • 2 empty shells; stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017 • 3 empty shells; stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017.

Distribution

Recorded from the vicinity of the Three Kings Islands, off northern New Zealand (310–710 m) and the slopes of Walters Shoal (382–573 m); dredged on sandy substrata; living specimens unknown.

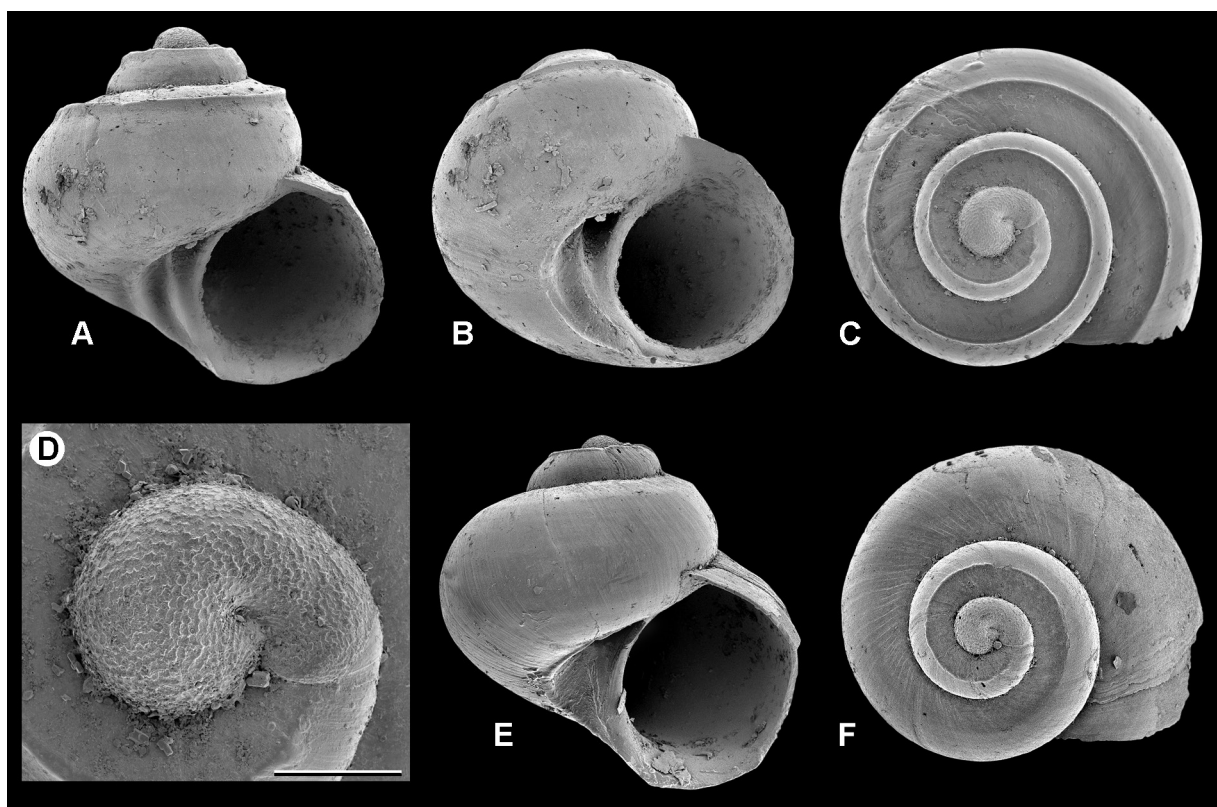


Fig. 22. *Trochaclis regalis* Marshall, 1995, Walters Shoal, stn DW4881 (MNHN). **A–C.** Apertural, oblique and apical views of specimen with persistent shoulder cord, diameter 1.1 mm. **D.** Protoconch of A, scale bar = 100 µm. **E–F.** Apertural and apical views of specimen with shoulder cord evanescent after first whorl, diameter 1.1 mm.

Remarks

When describing *Trochaclis regalis*, Marshall (1995) noted that it was ‘exceedingly similar’ to *T. versiliensis* Warén, Carrozza & Rocchini, 1992 from the western Mediterranean and adjacent Atlantic, the only difference being the degree of persistence of the spiral rib on the early teleoconch whorls. Given the absence of shared species in the vetigastropod faunas of the NE Atlantic and New Zealand, Marshall considered the New Zealand material to be specifically distinct and believed that further differences would be found when the soft parts became available for comparison. The material from Walters Shoal is likewise ‘exceedingly similar’ to *T. regalis* and *T. versiliensis*. In this instance, however, the vetigastropod faunas of the upper bathyal (archibenthic) zone of the south-western Indian Ocean and the region north of New Zealand not uncommonly contain shared, widely distributed species, including four species discussed herein, *Acremodontina carinata*, *Bichoristes wareni*, *Bolma recens* and *Calliotropis eucheloides*, as well as *Calliotropis acherontis* Marshall, 1979. The five specimens available from Walters Shoal show considerable variability in the strength and persistence of the spiral rib. It is distinct and delineates a shoulder-like angulation on the first teleoconch whorl in all specimens, but extends only to 1.25 whorls in some (Fig. 22F), to 1.75 whorls in others and even to the outer lip at 2.25 whorls in one (Fig. 22C). Since I can find no diagnostic characters by which to separate the specimens from Walters Shoal from *T. regalis*, I regard them as conspecific.

Moelleriopsis gritta Hoffman, 2020 from the Azorean region is superficially similar to specimens of the present species in which the spiral rib persists to the aperture, but that species is larger (diameter up to 2.8 mm) and its protoconch bears spiral threads and does not project above the first teleoconch whorl.

Seguenzioidea: family unassigned

Genus *Akritogyra* Warén, 1992

Type species

Akritogyra curvilineata Warén, 1992 (original designation), Recent, north-eastern Atlantic.

Akritogyra crenulata sp. nov.

[urn:lsid:zoobank.org:act:8D95E498-B092-4E51-B2D9-86170462B027](https://zoobank.org/act:8D95E498-B092-4E51-B2D9-86170462B027)

Fig. 23

Diagnosis

Shell very small, turbiniform, slightly wider than high, whorls evenly rounded, base umbilicate; subsutural region crenulated by short, broad riblets; intervals between riblets with close-set, microscopic spiral threads; riblets much weaker peripherally; microsculpture comprising numerous close-set microscopic axial threads; riblets reappear on base crenulating umbilical margin; peristome complete, circular, slightly disjunct; interior non-nacreous.

Etymology

From the Latin “*crena, crenatus*” – “a notch, notched”, dim. “*crenula, crenulatus*”; with reference to the subsutural sculpture.

Material examined**Holotype**

WALTERS SHOAL • empty shell; slopes, stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN-IM-2000-38217.

Paratypes

WALTERS SHOAL • 4 empty shells; same collection data as for holotype; MNHN-IM-2000-38218.

Description

SHELL. Minute (diameter up to 1.1 mm), turbiniform, slightly wider than high ($H/D=0.81-0.93$) whorls evenly rounded; periphery at mid-whorl; base umbilicate; teleoconch of up to 2.25 whorls. Early sculpture of short, broad riblets which crenulate subsutural region; intervals between riblets with close-set, microscopic spiral threads (Fig. 23E); riblets weaken considerably in peripheral region, but reappear on base crenulating umbilical margin; peripheral region rendered weakly undulant by remaining traces

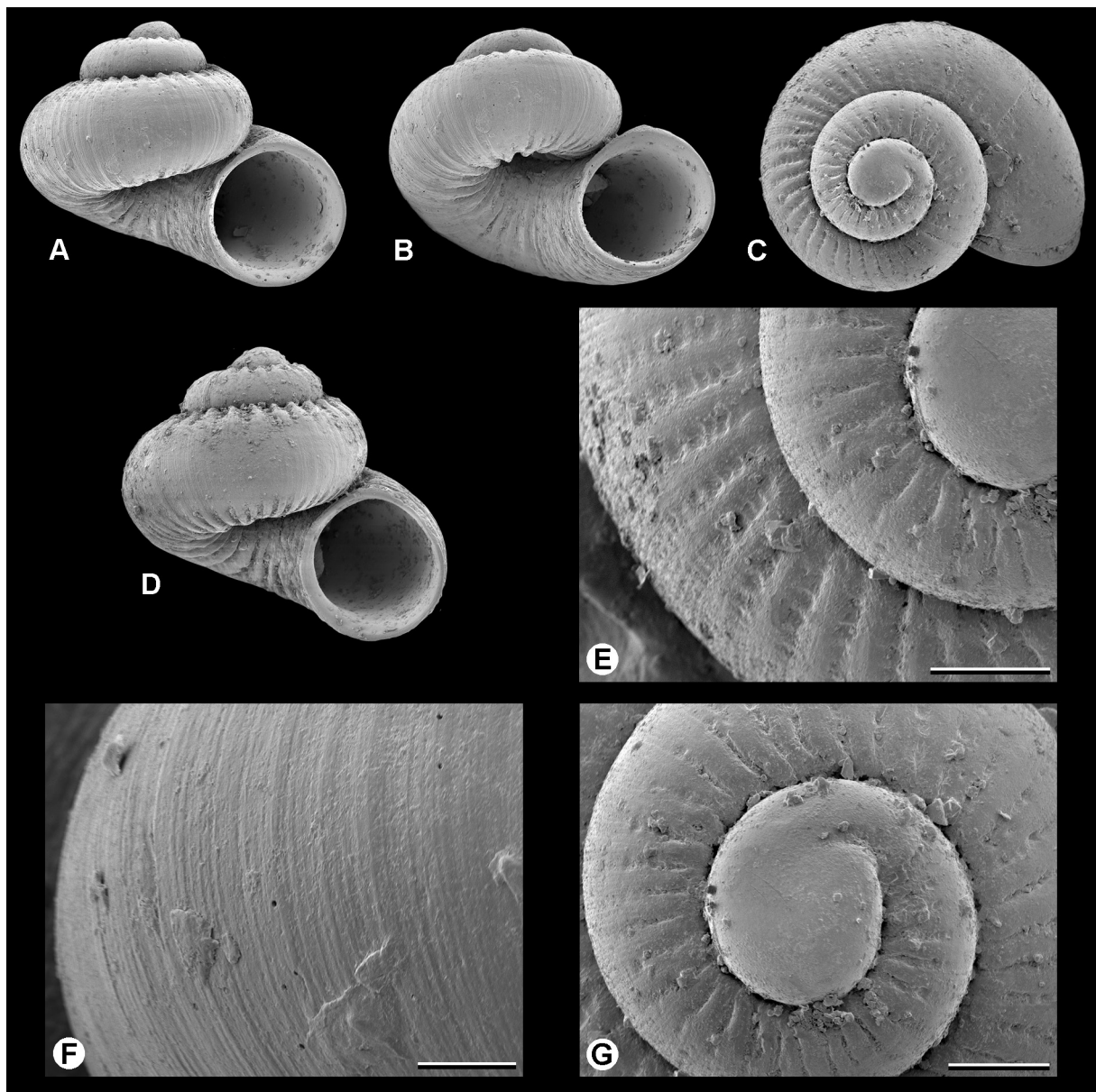


Fig. 23. *Akritogyra crenulata* sp. nov. **A–B.** Apertural and oblique basal views of holotype, height 0.85 mm (MNHN-IM-2000-38217). **C.** Apical view, diameter 0.95 mm (paratype, MNHN-IM-2000-38218). **D.** Strongly sculptured specimen, height 0.93 mm (paratype, MNHN-IM-2000-38218). **E.** Detail of subsutural sculpture, scale bar=100 μ m (paratype, MNHN-IM-2000-38218). **F.** Microsculpture of holotype, scale bar=50 μ m. **G.** Protoconch of C, scale bar=100 μ m.

of axial riblets, but also with numerous close-set microscopic axial threads (Fig. 23F); latter quarter of last adult whorl usually lacking axial riblets below suture; umbilicus of moderate width, its rim rounded and crenulate, its interior with traces of low spiral lirae. Aperture circular, weakly prosocline, peristome complete and a little disjunct from penultimate whorl; outer lip simple; interior smooth, lacking obvious nacre.

PROTOCONCH (Fig. 23G). Globose, moderately exsert, comprising approx. 1.25 whorls, diameter $\pm 245 \mu\text{m}$; with fine superficial granulation where unworn; terminal lip convex, not thickened.

COLOUR. Uniformly translucent milky-white.

DIMENSIONS. Holotype, height 0.85 mm, diameter 1.05 mm; largest specimen, height 1.03 mm, diameter 1.13 mm.

Distribution

Known only from the slopes of Walters Shoal, at a depth of 573–582 m; dredged on coarse sandy substrata; living specimens unknown.

Remarks

I refer this unusual species to *Akritogyra* simply because it shows some similarity to *A. helicella* Warén, 1993 from Iceland (Warén 1993). Quite possibly, this similarity is merely superficial, but I know of no other genus to which the species might belong, and choose to place it in *Akritogyra* rather than create a new genus based on shell characters alone. *Akritogyra helicella* has similar subsutural crenulation and microscopic, wrinkle-like axial microsculpture, but the shell is much more depressed and the umbilicus is wider. Warén (1993) likewise expressed reservations regarding his referral of *A. helicella* to *Akritogyra*, but opted for a conservative approach given the plethora of generic names available for skeneimorph gastropods.

Genus *Benthobrookula* Clarke, 1961

Type species

Brookula (*Benthobrookula*) *exquisita* Clarke, 1961 (original designation), Recent, South Georgia.

Remarks

There is uncertainty regarding the status of *Benthobrookula*. Some authors have chosen to rank it as a full genus, distinct from *Brookula* Iredale, 1912 (Zelaya *et al.* 2006), based on the shape and sculpture of the protoconch (exsert and globose with a microscopically pitted surface), whereas others (Schwabe & Engl 2008) considered such differences inconclusive and discouraged the use of *Benthobrookula* at generic level, pending clarification through further morphological or molecular studies. Accepting that this matter remains unresolved, I believe the illustrations of the shell and protoconch of the type species of *Brookula* (*B. stibarochila* Iredale, 1912) provided by Warén (1992) exhibit features sufficiently distinct from those of *Benthobrookula* to justify their provisional separation. Such features include the much less globose, less exsert and apparently smooth protoconch in *Brookula*, and the absence of fine spiral lirae on the early portion of the first teleoconch whorl.

Brookula stibarochila is a shallow-water, subtropical species with a characteristic coarsely cancellate sculpture on the early teleoconch whorls, comprising subequal axial and spiral elements. In contrast, species of *Benthobrookula* occur in deeper water, mostly at higher latitudes and in general the axial sculpture on the apical whorls is much stronger than the spiral sculpture.

Table 2. Species of *Benthobrookula* Clarke, 1961 from Walters Shoal, summary of characters relating to shell dimensions and sculpture.

Species	Max height [mm]	H/D	Ribs on first whorl	Ribs on last adult whorl	Rib slope	Protoconch diameter [µm]
<i>Be. araneum</i> sp. nov.	1.23	0.83–1.0	23–24	20–23	prosocline	220
<i>Be. galeneae</i> sp. nov.	1.5	1.0–1.1	±30	35–40	ortho-/opisthocline	220–230
<i>Be. laticostata</i> sp. nov.	1.0	1.0	13–16	14–18	prosocline	210
<i>Be. scalaroides</i> sp. nov.	1.3	1.1–1.2	±17	20+	orthocline	200–210
<i>Be. semisculpta</i> sp. nov.	1.35	0.81–0.93	24–27	< 15	prosocline	220

The above notwithstanding, *Benthobrookula* as interpreted by Zelaya *et al.* (2006) includes a range of species, which despite sharing a similar protoconch morphology, exhibit considerable diversity in shell shape and sculpture. Some, such as *Be. pfefferi* (Powell, 1951), closely resemble material from Walters Shoal, yet the type species is somewhat distinct in having a much more depressed, more coarsely sculptured shell, with a wide umbilicus (holotype illustrated by Zelaya *et al.* 2006: fig. 2). *Benthobrookula* itself may thus ultimately prove to be composite. The genus *Aequispirella* Finlay, 1924 is also relevant in this context. This New Zealand taxon has been poorly illustrated in most modern literature, but a good scanning electron micrograph of the type species *A. corula* (Hutton, 1885) was provided by Kaim (2004), showing a shell with a distinctly elevated profile and a much narrower umbilicus. Resolution of the status and relationships of these taxa, and the species referable to each, will require more in-depth study involving molecular data.

Species of *Benthobrookula* from Walters Shoal occur primarily on the slopes of the seamount, but two also range into deeper water on the surrounding plain. The material available was mostly associated with sandy substrata, but no specimens were collected alive. The different species can be relatively easily distinguished based on characters associated with shell proportions, rib number and rib slope, as detailed in Table 2.

***Benthobrookula araneum* sp. nov.**

[urn:lsid:zoobank.org:act:51E19EE6-CE0C-4554-BE8A-10311EAE3267](https://zoobank.org/act:51E19EE6-CE0C-4554-BE8A-10311EAE3267)

Figs 24A–C, 25A, F

Diagnosis

Shell turbiniform, H/D=0.83–1.0, whorls evenly rounded, broadly umbilicate; teleoconch sculptured with axial ribs, 23–24 on first whorl, 20–23 ribs on last adult whorl, never crowded behind outer lip; ribs prosocline, their intervals substantially wider than ribs and sculptured by fine, close-set, spiral threads; ribs less elevated with more rounded crests on base, continuing into umbilicus in some specimens; umbilical margin evenly rounded, its interior with indistinct spiral lirae; protoconch globose and exsert.

Etymology

From the Latin “*araneum*” – “a cobweb” (noun in apposition); in reference to the web-like interaction of axial cords and spiral threads.

Material examined

Holotype

WALTERS SHOAL • empty shell; slopes, stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; MNHN-IM-2000-38068.

Paratypes

WALTERS SHOAL – **slopes** • 7 empty shells; same collection data as for holotype; MNHN-IM-2000-38069 • 1 empty shell; stn DW4898; 33°09' S, 44°01' E; depth 652–668 m; 6 May 2017; MNHN-IM-2000-38070 • 8 empty shells; stn DW4899; 33°09' S, 44°02' E; depth 707–720 m; 6 May 2017; MNHN-IM-2000-38071 • 2 empty shells; stn DW4900; 33°10' S, 44°01' E; depth 660–670 m; 6 May 2017; MNHN-IM-2000-38072 • 1 empty shell; stn CP4902; 33°08' S, 44°02' E; depth 700–711 m; 7 May 2017; MNHN-IM-2000-38073 • 2 empty shells; stn CP4906; 33°26' S, 44°00' E; depth 799–837 m; 9 May 2017; MNHN-IM-2000-38074.

Other material

WALTERS SHOAL – **slopes** • 4 empty shells; stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN • 2 empty shells; stn CP4907; 33°27' S, 44°00' E; depth 880 m; 9 May 2017; MNHN.

Description

SHELL. Very small (height up to 1.23 mm), turbiniform; diameter \geq height ($H/D=0.83-1.0$); whorls rounded and suture distinctly indented; periphery evenly rounded, close to mid-whorl; base rounded, broadly umbilicate; teleoconch of 2.75–3.0 whorls. First teleoconch whorl with 23–24 axial ribs of similar strength, first one short, not extending to abapical suture; ribs more elevated and more prosocline on subsequent whorls, but not increasing in number, narrow and blade-like, their intervals progressively wider; 20–23 ribs on last adult whorl, persisting to end of whorl in most specimens (though last few rather indistinct), but cease up to one quarter-whorl behind outer lip in others; never crowded behind outer lip; intervals between ribs substantially wider than ribs, particularly on final two whorls; intervals sculptured by fine, close-set, spiral threads (Fig. 25F), and even finer and more close-set axial threads (visible only under SEM); ribs continue on to base, but become less elevated, their crests rounded or even flattened, rather than sharp; ribs continue into umbilicus in some specimens, but evanesce at its margin in others; umbilicus relatively wide, margin evenly rounded; interior of umbilicus variably sculptured with fine, rather indistinct spiral lirae. Aperture circular; peristome complete, its edge simple; interior not nacreous.

PROTOCONCH (Fig. 25A). Globose and exsert; diameter ± 220 μm , ca 1.25 whorls; sculptured with fine, anastomosing threads creating an irregular pattern of microscopic pits; terminal lip straight or weakly convex, not thickened.

COLOUR. Uniformly white; freshest specimens somewhat translucent.

DIMENSIONS. Holotype, height 1.23 mm, diameter 1.38 mm (= largest specimen).

Distribution

Known only from the slopes of Walters Shoal, at depths of 582–880 m; on coarse sandy substrata with abundant crustaceans, echinoderms and solitary corals; living specimens unknown.

Remarks

Benthobrookula aethiopica (Thiele, 1925) from 1134 m off Somalia, is of similar size and proportions ($H/D \pm 1.0$), but has 28 axial ribs on the last adult whorl and reportedly lacks spiral sculpture. *Benthobrookula valdiviae* (Thiele, 1925) from a depth of 693 m off the Kenya-Somalia border and *Be. kerguelensis* (Thiele, 1925) from an unspecified depth in the Southern Ocean, both have a similar number of axial ribs to *Be. araneum* sp. nov., but both are proportionately taller ($H/D \pm 1.17-1.19$), have a narrower umbilicus and reach a larger size (height 2.1 mm and 1.6 mm respectively). In *Be. kerguelensis*, the holotype of which was recently figured by Engl (2012: pl. 25 fig. 1), the axial ribs are more robust than in *Be. araneum*.

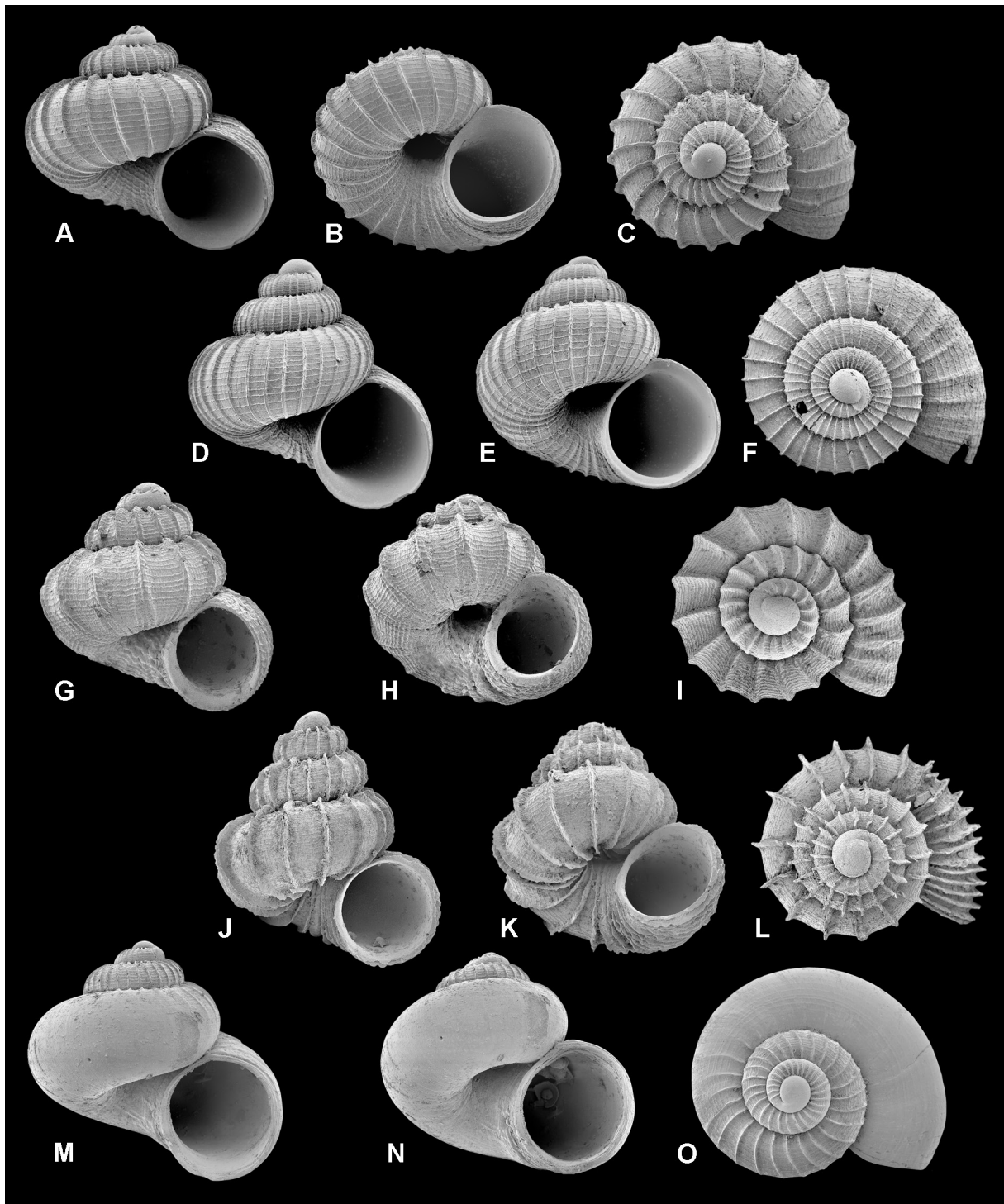


Fig. 24. A–C. *Benthobrookula araneum* sp. nov. A–B. Holotype, height 1.2 mm (MNHN-IM-2000-38068). C. Paratype, diameter 1.1 mm (MNHN-IM-2000-38069). D–F. *Benthobrookula galeneae* sp. nov. D–E. Holotype, height 1.25 mm (MNHN-IM-2000-38075). F. Paratype, diameter 1.2 mm (MNHN-IM-2000-38076). G–I. *Benthobrookula laticostata* sp. nov. G–H. Holotype, diameter 1.0 mm (MNHN-IM-2000-38080). I. Paratype, diameter 1.0 mm (MNHN-IM-2000-38082). J–L. *Benthobrookula scalaroides* sp. nov. J–K. Holotype, height 1.14 mm (MNHN-IM-2000-38084). L. Paratype, diameter 1.0 mm (MNHN-IM-2000-38085). M–O. *Benthobrookula semisculpta* sp. nov. M–N. Holotype, height 1.4 mm (MNHN-IM-2000-38088). O. Paratype, diameter 1.4 mm (MNHN-IM-2000-38090).

Benthobrookula pfefferi (Powell, 1951) from South Georgia is also somewhat similar, but it has a more elevated shell with more numerous axial ribs (36–38 on last adult whorl), and attains a larger size (height 1.83 mm) (Zelaya *et al.* 2006). In terms of overall shell shape and proportions, and the number of axial ribs, perhaps the most similar species is *Be. conica* (Watson, 1886) from off Brazil (Absalão *et al.* 2001), but that species has more robust axial ribs which remain strong in the umbilicus and the umbilical margin lacks spiral cords.

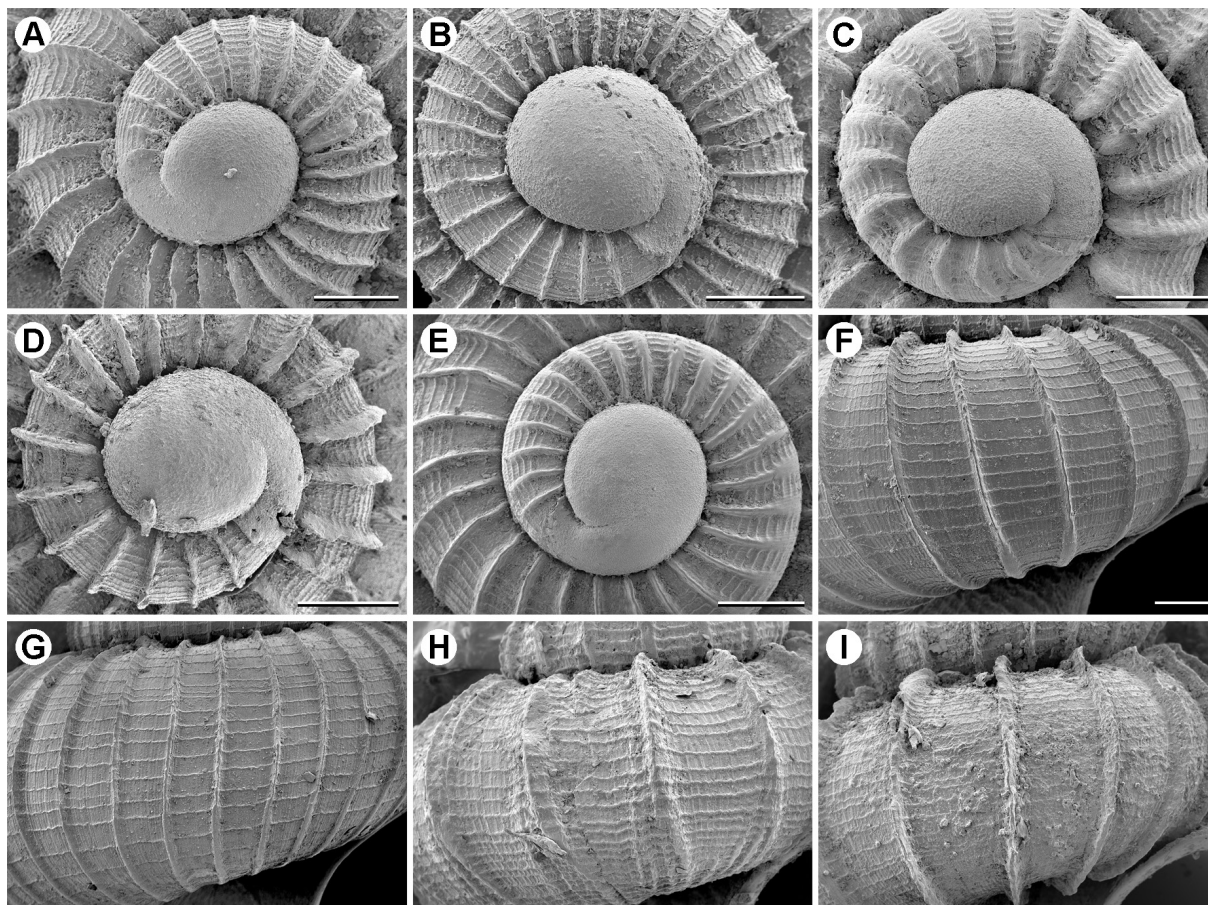


Fig. 25. A, F. *Benthobrookula araneum* sp. nov. A. Protoconch (paratype, MNHN-IM-2000-38069). F. Sculptural detail at start of last adult whorl, holotype. B, G. *Benthobrookula galeneae* sp. nov. B. Protoconch (paratype, MNHN-IM-2000-38076). G. Sculptural detail at start of last adult whorl, holotype. C, H. *Benthobrookula laticostata* sp. nov. C. Protoconch, DW4899 (paratype, MNHN-IM-2000-38082). H. Sculptural detail at start of last adult whorl, holotype. D, I. *Benthobrookula scalaroides* sp. nov. D. Protoconch (paratype, MNHN-IM-2000-38085). I. Sculptural detail at start of last adult whorl, holotype. E. *Benthobrookula semisculpta* sp. nov., protoconch CP4911 (paratype, MNHN-IM-2000-38090). Scale bars = 100 μ m.

Benthobrookula galeneae sp. nov.

urn:lsid:zoobank.org:act:C64B5682-EAAA-4492-8ADB-3B422EA69100

Figs 24D–F, 25B, G

Diagnosis

Shell elevated-turbiniform, H/D=1.0–1.11, whorls evenly rounded, base umbilicate; teleoconch sculptured with axial ribs, ± 30 on first whorl, 35–40 on last adult whorl; ribs narrow, not strongly raised, orthocline or slightly opisthocline; intervals between ribs substantially wider than ribs and sculptured by fine, close-set, spiral threads; axial ribs continue to umbilical margin, but evanesce within; umbilicus of moderate width with evenly rounded margin, its interior with indistinct spiral lirae; protoconch globose and exsert.

Etymology

Named after the Galene, the Nereid of calm seas from Greek mythology.

Material examined

Holotype

WALTERS SHOAL • empty shell; slopes, stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; MNHN-IM-2000-38075.

Paratypes

WALTERS SHOAL • 5 empty shells; same collection data as for holotype; MNHN-IM-2000-38076 • 3 empty shells; slopes, stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017; MNHN-IM-2000-38077 • 40 empty shells; slopes, stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN-IM-2000-38078 • 6 empty shells; south plain, stn CP4913; 33°52' S, 44°05' E; depth 1539–1615 m; 11 May 2017; MNHN-IM-2000-38079.

Description

SHELL. Very small (height up to 1.5 mm), elevated-turbiniform, height \geq diameter (H/D=1.0–1.11) whorls rounded and suture deeply indented; periphery evenly rounded, close to mid-whorl; base evenly rounded and umbilicate; teleoconch of up to 3.25 whorls. First teleoconch whorl with ± 30 close-set, axial ribs; subsequent whorls with similar ribs, becoming more widely spaced on subsequent whorls, orthocline or slightly opisthocline; last adult whorl usually with 35–40 ribs, but weak or obsolete in some specimens; ribs narrow, but not strongly raised, and thus less blade-like; intervals between ribs substantially wider than ribs; intervals sculptured by close-set microscopic spiral threads (Fig. 25G) and even finer and more close-set axial threads (visible only under SEM); basal sculpture similar; axial ribs continue to umbilical margin, but evanesce within; umbilicus of moderate width and deep, its margin evenly rounded; interior of umbilicus sculptured primarily by indistinct spiral lirae. Aperture subcircular, slightly flattened in parietal region; peristome complete, its edge simple; interior not nacreous.

PROTOCONCH (Fig. 25B). Globose and exsert; diameter ± 220 –230 μm , ca 1.25 whorls; with sculpture of fine anastomosing threads producing a network of close-set, irregularly-shaped pits; terminal lip straight, not thickened.

COLOUR. Uniformly translucent milky-white when fresh.

DIMENSIONS. Holotype, height 1.35 mm, diameter 1.23 mm; largest specimen, height 1.50 mm, diameter 1.3 mm.

Distribution

Known only from the slopes and surrounding plain of Walters Shoal, at depths of 382–1539 m; on sandy substrata with cnidarians, crustaceans and echinoderms; living specimens unknown.

Remarks

In comparison with the other species of *Benthobrookula* from Walters Shoal, this material has more numerous, more close-set axial ribs, ca 30 on the first whorl and 35–40 on the last adult whorl. However, there is considerable variation in the strength of the ribs on the last adult whorl, some specimens appearing to have only spiral lirae at this stage. Such specimens may thus resemble *Be. semisculpta* sp. nov., but that species has a deeper final whorl, a less prominent spire and the axial ribs on the spire are prosocline and distinctly curved, rather than orthocline.

Benthobrookula pfefferi (Powell, 1951) from South Georgia is perhaps the most similar species, but that species has a larger protoconch (diameter 330–400 vs 220–230 μm) and a narrower umbilicus with stronger peri-umbilical spiral sculpture (Zelaya *et al.* 2006). *Benthobrookula gemmula* (Turton, 1932), a rather variable but poorly known species widespread off the east coast of South Africa (Kilburn 1977; Herbert 2015), has similar sculpture, but the original photograph provided by Turton shows a shell with a much more prominent spire.

Benthobrookula laticostata sp. nov.

[urn:lsid:zoobank.org:act:032568BA-403D-46F9-AD78-4D1249A81AD5](https://doi.org/10.3896/BI.2017.403D-46F9-AD78-4D1249A81AD5)

Figs 24G–I, 25C, H

Diagnosis

Shell turbiniform, H/D \pm 1.0, whorls evenly rounded, broadly umbilicate; teleoconch sculptured with axial ribs, 13–16 on first whorl, penultimate and last adult whorls each with 14–18; ribs broad and robust, weakly prosocline, their intervals with fine, close-set, spiral threads which ascend and cross ribs; ribs weakening and appearing to split into 3–4 finer riblets below periphery, evanescent prior to umbilicus; umbilicus sculptured with uneven, undulant spiral cords; protoconch globose and exsert.

Etymology

From the Latin “*latus*” – “broad, wide” and “*costa, costata*” – “a rib, ribbed”; in reference to the sculpture of strong, stout ribs.

Material examined**Holotype**

WALTERS SHOAL • empty shell; slopes, stn CP4907; 33°27' S, 44°00' E; depth 880 m; 9 May 2017; MNHN-IM-2000-38080.

Paratypes

WALTERS SHOAL • 2 empty shells; same collection data as for holotype; MNHN-IM-2000-38081 • 3 empty shells; slopes, stn DW4899; 33°09' S, 44°02' E; depth 707–720 m; 6 May 2017; MNHN-IM-2000-38082 • 1 empty shell; south plain, stn CP4913; 33°52' S, 44°05' E; depth 1539–1615 m; 11 May 2017; MNHN-IM-2000-38083.

Description

SHELL. Minute (height up to 1.0 mm), turbiniform; height and diameter more or less equal; whorls rounded, suture strongly indented; periphery evenly rounded, close to mid-whorl; base rounded, broadly umbilicate;

teleoconch of up to 2.5 whorls. First teleoconch whorl with 13–16 broad axial ribs, increasing in strength toward end of whorl; subsequent whorls with similar ribs, progressively more widely spaced; penultimate and last adult whorls each with 14–18 ribs; ribs weakly prosocline, broad and robust, but often weakening prior to outer lip; intervals between ribs 2–3 times wider than ribs, sculptured by fine, close-set, spiral threads (Fig. 25H); threads ascend and cross ribs (though often worn on rib crest); rib intervals also with even finer, more close-set axial threads (visible only under SEM); ribs weakening and appearing to split in to 3–4 finer riblets below periphery, evanescent prior to umbilicus; umbilicus relatively broad with evenly rounded margin, its interior sculptured only with uneven, undulant spiral cords. Aperture circular; peristome complete, almost radial, its edge simple; interior not obviously nacreous.

PROTOCONCH (Fig. 25C). Globose and exsert; diameter $\pm 210 \mu\text{m}$, ca 1.25 whorls; with sculpture of fine anastomosing threads producing network of close-set, irregularly-shaped pits; terminal lip more or less straight, not thickened.

COLOUR. Uniformly white; freshest specimens somewhat translucent.

DIMENSIONS. Holotype, height 1.0 mm, diameter 1.0 mm (= largest specimen).

Distribution

Known only from the slopes and surrounding plain of Walters Shoal, at depths of 720–1539 m, on sandy substrata; living specimens unknown.

Remarks

Benthobrookula laticostata sp. nov. resembles *Be. valdiviae* (Thiele, 1925), from a depth of 693 m off the Kenya-Somalia border, but the latter is larger, proportionately more elevated (height 2.1 mm, diameter 1.8 mm), has a more cyrtocoenoid profile and possesses more numerous, more close-set axial ribs (20 on the last adult whorl). *Benthobrookula conica* (Watson, 1886) from off Brazil is similar, but has narrower ribs that remain strong on the base and continue into the umbilicus (Absalão *et al.* 2001; Absalão & Pimenta 2005). Like *Be. laticostata*, *Be. olearia* (Absalão & Pimenta, 2005) from off southern Brazil has robust axial ribs, but they are more numerous (23 on last adult whorl) and more distinctly prosocline, its spire is less elevated and it has coarser peri-umbilical spiral cords.

Benthobrookula scalaroides sp. nov.

[urn:lsid:zoobank.org:act:8261B816-4DC9-4D46-A58F-D4F056DE1951](https://zoobank.org/act:8261B816-4DC9-4D46-A58F-D4F056DE1951)

Figs 24J–L, 25D, I

Diagnosis

Shell elevated-turbiniiform, H/D=1.1–1.2, whorls evenly rounded, suture deeply indented, base umbilicate; teleoconch sculptured with widely-spaced, sharp, orthocline, axial ribs; first whorl with ± 17 ribs, penultimate whorl with ± 20 ribs; ribs sometimes more close-set in last quarter whorl; rib intervals with microscopic spiral threads; basal sculpture similar, ribs continuing into umbilicus; peristome complete; protoconch globose and exsert.

Etymology

From the Latin “*scala*” – “a flight of stairs”; in reference to the strongly ribbed sculpture.

Material examined

Holotype

WALTERS SHOAL • empty shell; slopes, stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN-IM-2000-38084.

Paratypes

WALTERS SHOAL – slopes • 16 empty shells; same collection data as for holotype; MNHN-IM-2000-38085 • 3 empty shells; stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; MNHN-IM-2000-38086 • 1 empty shell; stn DW4899; 33°09' S, 44°02' E; depth 707–720 m; 6 May 2017; MNHN-IM-2000-38087.

Description

SHELL. Very small (height up to 1.3 mm), elevated-turbiniform; higher than wide (H/D=1.1–1.2); whorls strongly rounded and suture deeply indented; periphery evenly rounded, close to mid-whorl; base rounded, deeply umbilicate; teleoconch of up to 3.25 whorls. First teleoconch whorl with ± 17 axial ribs, increasing in strength toward end of whorl; subsequent whorls with similar ribs, orthocline and progressively more widely spaced until final quarter of last adult whorl where they usually (but not always) become more close-set; penultimate whorl with ± 20 ribs; ribs narrow and blade-like, sometimes appearing weakly alate below adapical suture; intervals between ribs substantially wider than ribs, particularly on final two whorls; intervals sculptured by close-set, microscopic spiral threads (Fig. 25I) and even finer and more close-set axial threads (visible only under SEM); basal sculpture similar, continuing into umbilicus; umbilicus relatively narrow and deep, its margin evenly rounded. Aperture circular; peristome complete, its edge simple; interior not nacreous.

PROTOCONCH (Fig. 25D). Globose and exsert; diameter 200–210 μm , ca 1.25 whorls; where unworn sculptured by fine anastomosing threads producing a network of close-set, irregularly-shaped pits; terminal lip more or less straight, not thickened.

COLOUR. Uniformly white; freshest specimens somewhat translucent.

DIMENSIONS. Holotype, height 1.14 mm, diameter 0.98 mm; largest specimen, height 1.3 mm.

Distribution

Known only from the slopes of Walters Shoal, at depths of 582–707 m; dredged on substrata of coarse sand; living specimens unknown.

Remarks

Other somewhat elevated species of *Benthobrookula* include *Be. charleenae* (Schwabe & Engl, 2008), *Be. kerguelensis* (Thiele, 1925), *Be. nepeanensis* (Gatliff, 1906) and *Be. strebeli* (Powell, 1951). *Benthobrookula charleenae*, from over 2900 m off the South Sandwich Islands, differs in having more close-set axial ribs (27 vs 20 on penultimate whorl) and a larger protoconch (diameter 280 vs 200–210 μm). In *Be. kerguelensis* the shell is larger (height 1.6 mm) and, judging from the original figure, the last adult whorl is deeper and the spire less elevated. *Benthobrookula nepeanensis* from southern Australia has an even more elevated spire and a much narrower umbilicus, whereas in *Be. strebeli* from South Georgia the axial ribs are more prosocline and less blade-like, and the base is imperforate with more conspicuous spiral sculpture (holotype figured by Zelaya *et al.* 2006: fig. 6a).

Benthobrookula semisculpta sp. nov.

[urn:lsid:zoobank.org:act:4FA6CCE8-FA2E-4B11-BCAF-F37EDC68D677](https://zoobank.org/act:4FA6CCE8-FA2E-4B11-BCAF-F37EDC68D677)

Figs 24M–O, 25E

Diagnosis

Shell relatively thick, turbiniform, H/D=0.81–0.93, whorls strongly rounded and suture deeply indented, base umbilicate; first two teleoconch whorls with 24–27 curved axial ribs, their intervals with fine,

close-set, spiral threads; sculpture evanescent during first half of third whorl, but traces of spiral threads may remain; base smooth, with only traces of microscopic growth-lines; umbilicus relatively wide with rounded margin, its interior with indistinct spiral lirae; peristome complete; protoconch globose and exsert.

Etymology

From the Latin “*semis*” – “half” and “*sculptus*” – “carved”; in reference to the sculptured spire whorls and smooth final whorl.

Material examined

Holotype

WALTERS SHOAL • empty shell; slopes, stn CP4906; 33°26' S, 44°00' E; depth 799–837 m; 9 May 2017; MNHN-IM-2000-38088.

Paratypes

WALTERS SHOAL – **slopes** • 1 empty shell; stn DW4898; 33°09' S, 44°01' E; depth 652–668 m; 6 May 2017; MNHN-IM-2000-38089 • 4 empty shells; stn CP4911; 32°46' S, 44°18' E; depth 964–965 m; 10 May 2017; MNHN-IM-2000-38090.

Description

SHELL. Very small (height up to 1.35 mm), relatively thick, turbiniform; wider than high ($H/D=0.81–0.93$); spire whorls strongly rounded and suture deeply indented; periphery evenly rounded, close to mid-whorl; base rounded and umbilicate; teleoconch of up to 2.75–3.0 whorls. First two teleoconch whorls with 24–27 curved axial ribs, progressively more widely spaced; ribs evanescent during first half of third whorl; intervals between ribs with fine, relatively close-set spiral threads on first two teleoconch whorls; threads buttressing ribs but seeming not to cross rib crests (Fig. 25E); additional weaker axial threads cross spiral threads in rib intervals, most noticeable toward whorl periphery (visible only under SEM); this microsculpture also evanescent on third whorl, but traces of spiral threads may remain; base evenly rounded, smooth, with only traces of microscopic growth-lines; umbilicus relatively wide, its margin rounded; interior of umbilicus with fine, indistinct spiral lirae and traces of axial ribs of spire whorls deep within. Aperture circular; peristome complete, its edge simple; upper part of outer lip gently convex; interior not nacreous.

PROTOCONCH (Fig. 25E). Globose and exsert; diameter $\pm 220 \mu\text{m}$, ca 1.25 whorls; with fine anastomosing sculpture creating network of minute, irregularly-shaped pits; terminal lip prosocline, weakly convex, not thickened.

COLOUR. Uniformly white, somewhat glossy.

DIMENSIONS. Holotype, height 1.35 mm, diameter 1.45 mm (= largest specimen).

Distribution

Known only from the slopes of Walters Shoal, at depths of 668–964 m; dredged on coarse sandy substrata; living specimens unknown.

Remarks

I have chosen to refer this species to *Benthobrookula* on account of the coarse ribs and fine spiral threads on the spire whorls. However, within this genus *Be. semisculpta* sp. nov. is rendered distinctive on account of its evanescent sculpture on the latter half of the last adult whorl and the collabral curvature of the axial ribs

on the spire whorls. Although some individuals of other species show reduced or obsolete axial sculpture prior to the outer lip, it is not as extensive as in the present species and the spiral sculpture remains distinct.

Genus *Lissotesta* Iredale, 1915

Type species

Cyclostrema micra Tenison Woods, 1877 (original designation), Recent, Tasmania.

Remarks

In his discussion of *Lissotesta*, Warén (1992) listed *Submargarita impervia* (Strebel, 1908) as a member of this genus. However, *S. impervia* is also the type species of *Photinula (Submargarita)* Strebel, 1908. Therefore, if this referral is correct, *Lissotesta* is in fact a junior synonym of *Submargarita*. However, contemporaneously Dell (1990) treated *Submargarita* and *Lissotesta* as distinct genera and refigured the holotype of *Photinula (Submargarita) impervia* Strebel, 1908. In the original description of *impervia*, Strebel (1908) stated “ein Nabel fehlt” (an umbilicus lacking), a fact confirmed in Dell’s illustration of the holotype. This is not consistent with the diagnosis of *Lissotesta* given by Warén (1992: 169), in which the umbilicus is open and deep. I consequently choose to follow Dell (1990) in treating *Submargarita* and *Lissotesta* as separate entities.

Lissotesta wareni sp. nov.

[urn:lsid:zoobank.org:act:931D472C-26CD-4777-9176-A580973E38BB](https://doi.org/10.3896/urn:lsid:zoobank.org:act:931D472C-26CD-4777-9176-A580973E38BB)

Fig. 26A–C, G

Diagnosis

Shell minute, elevated-turbiniform, H/D=0.98–1.2, whorls rounded, base umbilicate; smooth, sculptured only by very fine, widely spaced, spiral threads; threads often more close-set near periphery of base and coarser around and within umbilicus; aperture subcircular, almost radial; outer lip simple; interior not nacreous; protoconch globose and exsert, its suture scarcely evident, surface finely granular.

Etymology

Named for Dr Anders Warén (Swedish Museum of Natural History), in recognition of his enormous contribution to the discovery and documentation of micro-mollusc diversity.

Material examined

Holotype

WALTERS SHOAL • empty shell; slopes, stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN-IM-2000-38091.

Paratypes

WALTERS SHOAL • 5 empty shells; same collection data as for holotype; MNHN-IM-2000-38092.

Description

SHELL. Minute (height up to 1.0 mm), elevated-turbiniform, H/D=0.98–1.2; whorls rounded and suture strongly indented; periphery evenly rounded, close to mid-whorl; base rounded and umbilicate; teleoconch of up to 2.25 whorls. Sculpture comprising only very fine, narrow, raised, spiral threads; threads mostly relatively widely spaced, but spacing somewhat variable and threads often more close-set near periphery of base; threads somewhat coarser around and within umbilicus; umbilicus of moderate width. Aperture subcircular, almost radial, orthocone or weakly prosocline, peristome briefly interrupted in parietal region, its edge simple; interior not nacreous.

PROTOCONCH (Fig. 26G). Typical of genus; globose and exsert, suture between apical bulb and terminal tube scarcely evident; diameter $\pm 285 \mu\text{m}$; sculpture of fine anastomosing granules.

COLOUR. Uniformly translucent milky-white.

DIMENSIONS. Holotype, height 1.00 mm, diameter 0.85 mm (= largest specimen).

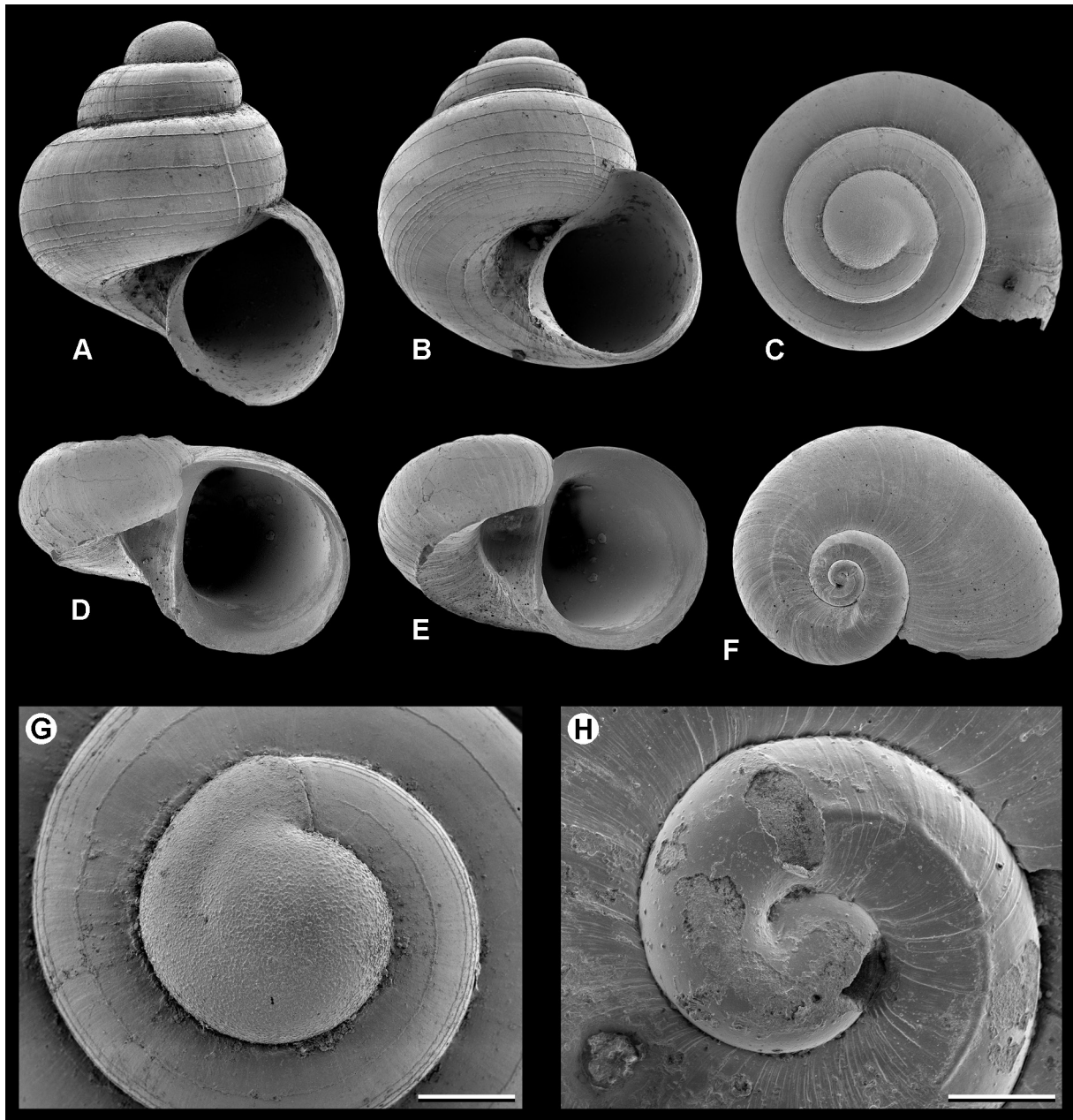


Fig. 26. A–C, G. *Lissotesta wareni* sp. nov. A–B. Apertural and oblique basal views of holotype, height 1.0 mm (MNHN-IM-2000-38091). C. Apical view, diameter 0.86 mm (paratype, MNHN-IM-2000-38092). G. Protoconch (paratype, MNHN-IM-2000-38092). D–F, H. *Trenchia mcleani* sp. nov., holotype (MNHN-IM-2000-38093). D–F. Apertural, oblique and apical basal views, diameter 2.9 mm. H. Protoconch. Scale bars = 100 μm .

Distribution

Known only from the slopes of Walters Shoal, at depths of 573–582 m; dredged on coarse sandy substrata; living specimens unknown.

Remarks

Lissotesta wareni sp. nov. closely resembles *L. mammillata* (Thiele, 1912) from the Davis Sea, East Antarctica. That species, however, is larger (height at two teleoconch whorls 1.6 mm vs 1.0 mm) and has more crowded spiral threads on the base. Thiele mentioned no spiral threads above the periphery, although these are evident in the illustration provided by Dell (1990). *Lissotesta gittenbergeri* (van Aartsen & Bogi, 1988) from the upper bathyal in the NE Atlantic, is another similar species, but it has stronger spiral cordlets (Oliver *et al.* 2023).

Genus *Trenchia* Knudsen, 1964

Type species

Trenchia wolffi Knudsen, 1964 (original designation), Recent, Kermadec Trench.

Remarks

Species of *Trenchia* closely resemble those of *Xyloskenea* Marshall, 1988, but the latter differ in having distinct spiral sculpture on the initial part of the protoconch. In *Trenchia* the protoconch is smooth (Warén & Bouchet 1993; Hoffman *et al.* 2020). Although the protoconch of the material discussed below is somewhat eroded, no spiral sculpture is evident and for this reason I refer the new species to *Trenchia*. This appears to be the first record of the genus from the Indian Ocean.

Trenchia mcleani sp. nov.

[urn:lsid:zoobank.org:act:15A3EF83-0D84-40E8-A2E3-69A4CA507FE3](https://zoobank.org/act:15A3EF83-0D84-40E8-A2E3-69A4CA507FE3)

Fig. 26D–F, H

Diagnosis

Shell small, wider than high, whorls rapidly expanding; spire flattened; spire whorls with low but distinct spiral rib at whorl summit, evanescent on second half of last adult whorl; base with a strong carina emerging from point of insertion of columella lip; a stronger, flange-like carina bordering and spiralling into umbilicus; aperture large, distinctly flattened in columella region; columella lip almost vertical; umbilicus wide. Protoconch evidently lacking spiral sculpture.

Etymology

Named for the late Dr James H. McLean (Natural History Museum, Los Angeles County), in recognition of his very considerable contribution to vetigastropod taxonomy and systematics, and of his friendship and support during my early career.

Material examined**Holotype**

WALTERS SHOAL • empty shell; south plain, stn CP4913; 33°52' S, 44°05' E; depth 1539–1615 m; 11 May 2017; MNHN-IM-2000-38093.

Paratypes

WALTERS SHOAL • 3 empty shells; same collection data as for holotype; MNHN-IM-2000-38094.

Description

SHELL. Small (diameter up to 2.9 mm), wider than high ($H/D \pm 0.69$); teleoconch of up to 2.25 rapidly expanding whorls; spire flattened and slightly tilted, scarcely protruding above penultimate whorl; spire whorls with low but distinct spiral rib at whorl summit, prior to descent toward indented adapical suture; angulation begins as rounded ridge immediately after terminal lip of protoconch, subsequently weakening and evanescent on second half of last adult whorl; periphery evenly rounded; base with strong carina emerging from point of insertion of columella; a similar but stronger, flange-like carina marks border of umbilicus, ending at junction of basal and columella lips and spiralling steeply into umbilicus; inner portion of base between keels more or less flat, but flaring out to form umbilical keel; sculpture of close-set, microscopic, collabral threads and stronger, uneven growth-lines; no spiral microsculpture evident. Aperture weakly prosocline, roundly D-shaped, columella region distinctly flattened; peristome complete; inner lip mostly straight and almost vertical (slightly angled toward base of shell axis); thickened and flaring where umbilical keel meets basal lip; parietal lip short; outer lip and interior smooth.

PROTOCONCH (Fig. 26H). Diameter $\pm 275 \mu\text{m}$, comprising ca 1.25 whorls; apical bulb rounded, but not globose or exsert; suture between apical bulb and terminal tube distinct; surface somewhat eroded but seemingly smooth, no spiral sculpture evident; terminal lip convex, not thickened.

COLOUR. Uniformly cream-white, opaque.

DIMENSIONS. Holotype, height 2.0 mm, diameter 2.9 mm (= largest specimen).

Distribution

Known only from the plain surrounding Walters Shoal, at depths of 1539–1615 m; trawled on coarse sandy substrata; living specimens unknown.

Remarks

Trenchia mcleani sp. nov. has a lower spire and more rapidly expanding last adult whorl than any other species of *Trenchia*. The most geographically proximate species, *T. agulhasae* (Clarke, 1961), from abyssal depths in the Cape Basin, 1600 km SW of Cape Town, has a much more prominent spire and less auriform shape (holotype illustrated by McLean 1992: fig. 58). Perhaps the most similar species is *T. biangulata* Rubio & Rolán, 2013 from the NE Atlantic, which also has a relatively low spire and strong peri-umbilical carina, but that species has a stronger shoulder carina, narrower umbilicus and a shorter, more oblique columella lip, as well as a less auriform shape (Hoffman *et al.* 2020).

Order Trochida Rafinesque, 1815
Superfamily Trochoidea Rafinesque, 1815
Family Calliostomatidae Thiele, 1924 (1847)
Subfamily Calliostomatinae Thiele, 1924 (1847)

Genus *Calliostoma* Swainson, 1840

Type species

Trochus conulus Linnaeus, 1758 (subsequent designation, Herrmannsen 1846: 154), Recent, NE Atlantic and Mediterranean.

Calliostoma pantopunctatum sp. nov.

[urn:lsid:zoobank.org:act:C7DB30D9-F86E-4F8F-8289-4AF393799C34](https://zoobank.org/urn:lsid:zoobank.org:act:C7DB30D9-F86E-4F8F-8289-4AF393799C34)

Figs 27, 28A–B, 38A–B

Diagnosis

Shell height up to 9.8 mm; spire with flat sides and angular periphery; suture not indented; base flattened, anomphalous in adult; sculpture dominated by granular spiral cords; penultimate whorl with five spiral cords of more or less equal size, above and including periphery; base with 9–10 more or less equally spaced, weakly granular spiral cords; apex milky-white, remainder of shell with numerous ginger-brown spots on a milky-white to pale fawn ground; spots present only on spiral cords, usually on alternate granules and more or less axially aligned.

Etymology

From the Greek “*pas, pant-*” (παντ-) – “all, universal, all over” and the Latin “*punctum, punctatum*” – “a spot, spotted”; in reference to the uniformly spotted colour pattern on the shell.

Material examined

Holotype

WALTERS SHOAL • living specimen; slopes, stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017; DNA tissue sample; MNHN-IM-2013-67275.

Paratypes

WALTERS SHOAL – **slopes** • 1 empty shell; stn DW4879; 33°17' S, 43°52' E; depth 288–300 m; 1 May 2017; MNHN-IM-2000-34924 • 1 living specimen; stn DW4885; 33°17' S, 43°55' E; depth 272–380 m; 3 May 2017; DNA tissue sample; MNHN-IM-2013-67276 • 3 empty shells; stn DW4885; 33°17' S, 43°55' E; depth 272–380 m; 3 May 2017; MNHN-IM-2000-34925 • 1 empty shell; stn DW4888; 33°10' S, 43°57' E; depth 299–311 m; 3 May 2017; MNHN-IM-2000-34926 • 10 empty shells; stn DW4896; 3°07' S, 43°51' E; depth 325–357 m; 5 May 2017; MNHN-IM-2000-34927 • 1 living specimen; stn DW4897; 33°09' S, 43°59' E; depth 490–584 m; 5 May 2017; DNA tissue sample; MNHN-IM-2013-67277.

Other material

WALTERS SHOAL – **slopes** • 39 empty shells; stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017; MNHN • 1 empty shell; stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN • 2 empty shells; stn DW4889; 33°09' S, 43°58' E; depth 353–465 m; 3 May 2017; MNHN • 1 empty shell; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; MNHN • 1 empty shell; stn DW4898; 33°09' S, 44°01' E; depth 652–668 m; 6 May 2017; MNHN.

Description

SHELL. Of small to moderate size (height up to 9.8 mm); spire conical with flat sides and angular periphery, adult height slightly greater than diameter; sculpture dominated by granular spiral cords; suture not indented, no deeper than intervals between spiral cords; base flattened, anomphalous in adult; teleoconch of up to 7.0 whorls. First teleoconch whorl rounded (Fig. 28A–B), initially with up to five spiral threads, soon resolving into three primary spiral cords (P1–P3), a fourth (P4) level with abapical suture; P3 strongest; cords crossed by axial ribs and rendered nodular at intersections; P4 rises above suture during third or fourth whorl and secondary spiral (S2) arises during fourth whorl, between P2 and P3; subsequent whorls with five spiral cords, of more or less equal size, above and including periphery; cords bearing rounded granules; cord intervals somewhat wider than cords themselves, particularly that between P1 and P2; cord intervals with fine, close-set, collabral growth-lines. Base with 9–10 more or

less equally spaced spiral cords; subperipheral cord level with suture; cords at most weakly granular, almost smooth; intervals wider than cords, sculptured by fine, close-set growth-lines. Aperture roundly rhomboidal; columella oblique to shell axis, somewhat thickened and reflected over umbilical region; outer lip lacking denticles; interior nacreous.

PROTOCONCH (Fig. 28B). Somewhat exsert, comprising approx. 1.25 whorls, diameter $\pm 375 \mu\text{m}$; surface sculptured with hexagonal network of interconnected ridges on a smooth background; terminal lip with collabral rib resembling axial ribs on early teleoconch.

COLOUR. Protoconch and first teleoconch whorl milky-white, remainder of shell with milky-white to pale fawn ground, maculated with numerous ginger-brown spots; spots present only on spiral cords, usually on alternate granules and with a more or less axial alignment. Basal colour pattern similar; columella and umbilical region whitish.

DIMENSIONS. Holotype, height 5.8 mm, diameter 5.8 mm; largest specimen, height 9.8 mm, diameter 9.1 mm.

EXTERNAL ANATOMY (Fig. 38A–B). Photographs of the living holotype show its external anatomy to conform with that described for *Calliostoma* by Hickman & McLean (1990). Like the shell, the snout, epipodium and sides of the foot are pigmented with numerous brown spots, although these are a darker reddish-brown compared to the ginger-brown maculations on the shell. The cephalic tentacles are faintly and uniformly tinged with a similar brownish colour.

Distribution

Known only from the slopes of Walters Shoal, at depths of 300–652 m (live-taken material 380–490 m); dredged on substrata of coarse sand and fine gravel, with ophiuroids, octocorals and solitary corals.

Remarks

Calliostoma pantopunctatum sp. nov. is highly distinctive amongst species of Calliostomatinae from the south-western Indian Ocean (cf. Lussi 2014; Vilvens 2014). Characteristic features include its pale apex, finely spotted colour pattern, evenly conical spire profile with no whorl convexity or sutural indentation, and relatively coarse spiral sculpture on the last adult whorl, comprising only five spiral cords above and including the peripheral cord. The presence of only one secondary spiral cord (S2) is also unusual. *Calliostoma variegatum* Carpenter, 1864, from the north-east Pacific has a similar spotted colour pattern, but it is considerably larger (height up to 29 mm), has more convex whorls, a more indented suture, and the last adult whorl has a more rounded periphery and more numerous secondary spiral cords (McLean 1996; Tuskes 2019).

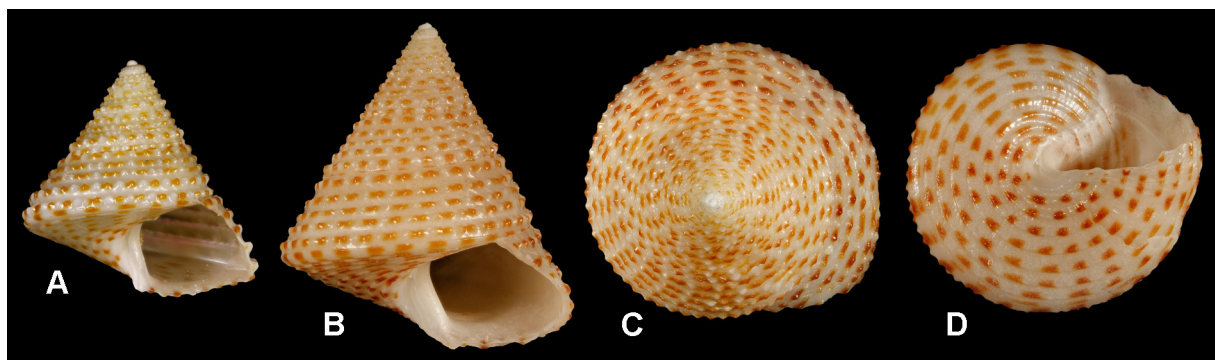


Fig. 27. *Calliostoma pantopunctatum* sp. nov. **A.** Holotype, height 5.8 mm (MNHN-IM-2013-67275). **B–D.** Paratype, height 9.8 mm (MNHN-IM-2000-34924).

In view of the fact that the supraspecific classification of *Calliostoma* sensu lato remains far from resolved, I have chosen not to speculate on the affinities of this new species in relation to others. Molecular data suggests some geographically congruent clustering of calliostomatine species (Williams *et al.* 2010; Marshall 2016), but as yet no Indian Ocean or southern African species have been included in such studies. *Calliostoma pantopunctatum* sp. nov. shows some similarity with *Fautor* Iredale, 1924, but Marshall (2016) has suggested that this is a tropical south-west Pacific taxon.

Thysanodontinae Marshall, 1988

Genus *Bruceina* Özdikmen, 2013

Type species

Herbertina eos Marshall, 1988 (type by typification of replaced name), Recent, south-western Indian Ocean.

Bruceina areneformis sp. nov.

[urn:lsid:zoobank.org:act:63AE5EA2-1B6D-4D73-A783-86AB41A26F83](https://doi.org/10.3896/ab.63AE5EA2-1B6D-4D73-A783-86AB41A26F83)

Figs 28C–F, 29A–C, G

Diagnosis

Shell turbiniform, height up to 5.4 mm; height \approx diameter; base narrowly umbilicate; protoconch hexagonally reticulate; teleoconch sculpture of strong spiral cords, nodular on spire whorls; P3 forms carina-like shoulder cord on spire whorls with S3 present below P3; start of last adult whorl with four strong rounded spiral cords above and including peripheral one, final half-whorl with additional intermediaries, shoulder cord no longer prominent, upper two cords remaining nodular; base with 5–6 rounded spiral cords; aperture subcircular, peristome somewhat flaring at base of columella; shell uniformly whitish.

Etymology

From *Arene* H. Adams & A. Adams, 1854 and the Latin “*forma*” – “shape”; in reference to the superficial resemblance of the species to some members of the areneid genus *Arene*.

Material examined

Holotype

WALTERS SHOAL • empty shell; slopes, stn DW4893; 33°16' S, 43°58' E; depth 623–629 m; 4 May 2017; MNHN-IM-2000-35699.

Paratypes

WALTERS SHOAL – **slopes** • 3 empty shells; stn DW4879; 33°17' S, 43°52' E; depth 288–300 m; 1 May 2017; MNHN-IM-2000-35700 • 1 living specimen, juvenile; stn DW4880; 33°17' S, 43°51' E; depth 275–318 m; 1 May 2017; MNHN-IM-2000-35701 • 19 empty shells; stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017; MNHN-IM-2000-35702 • 14 empty shells; same collection data as for holotype; MNHN-IM-2000-35703 • 7 empty shells; stn DW4897; 33°09' S, 43°59' E; depth 490–584 m; 5 May 2017; MNHN-IM-2000-35704.

Other material

WALTERS SHOAL – **slopes** • 1 empty shell; stn DW4877; 33°10' S, 43°49' E; depth 217–256 m; 1 May 2017; MNHN • 50+ empty shells; stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017; MNHN • 10+ empty shells; stn DW4885; 33°17' S, 43°55' E; depth 272–380 m; 3 May 2017; MNHN •

30+ empty shells; stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN • 3 empty shells; stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; MNHN • 30+ empty shells; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; MNHN • 2 empty shells; stn DW4892; 33°12' S, 44°01' E; depth 624–646 m; 4 May 2017; MNHN • 1 empty shell; stn DW4894; 33°09' S, 43°50' E; depth 199–261 m; 5 May 2017; MNHN • 1 empty shell; stn DW4895; 33°09' S, 43°49' E; depth 238–283 m; 5 May 2017; MNHN • 1 empty shell; stn DW4898; 33°09' S, 44°01' E; depth 652–668 m; 6 May 2017; MNHN.

Description

SHELL. Small (height up to 5.4 mm), turbiniform; height and diameter approximately equal or slightly higher than wide; spire prominent (height approximately equal to that of aperture), with indented suture; whorls evenly rounded, sculptured by strong spiral cords, nodular on spire whorls; umbilicus present, deep and rather narrow; teleoconch of up to 4.0 whorls. First teleoconch whorl with an axial growth flaw shortly after terminal protoconch varix (at 0.1–0.2 whorl); initially sculptured only with fine, close-set spiral lirae, weak uneven growth-lines and occasional irregular, ill-defined, subsutural riblets (Fig. 28F); a single strong spiral cord soon develops midway between sutures, creating distinct, somewhat undulant shoulder; shoulder cord stronger and carina-like on second whorl (= P3 of Marshall 1988), with undulant coronations linked to broad, low, axial riblets (Fig. 28E); near end of first whorl a second cord develops between P3 and abapical suture (= S3 of Marshall 1988), followed during second whorl by a third cord (P1) on shoulder slope, just below adapical suture (Fig. 29G); fine spiral liration of first whorl evanesces near end of second whorl; a fourth cord (P4) also evident at whorl periphery, level with abapical suture; cords rendered nodular where crossed by axial riblets; start of last adult whorl with four strong rounded spiral cords above and including peripheral one (P1, P3, S3, P4); equivalent of P2 not present; in final half-

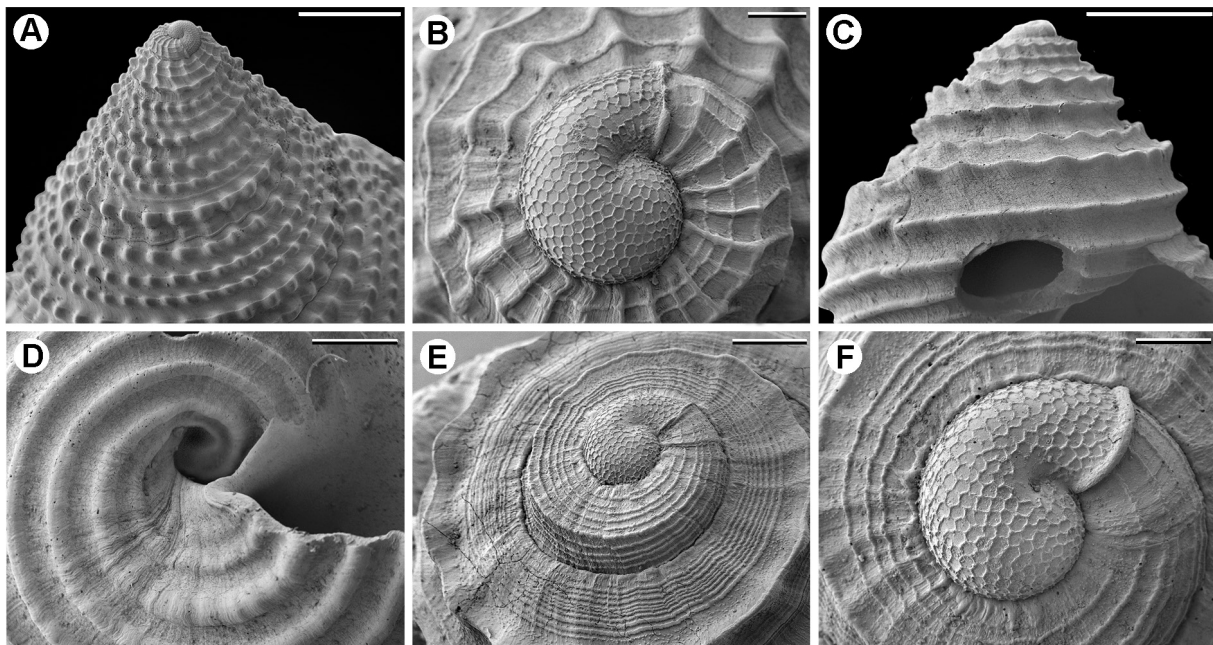


Fig. 28. A–B. *Calliostoma pantopunctatum* sp. nov., holotype (MNHN-IM-2013-67275). A. Oblique view of apex showing development of spiral sculpture. B. Sculptural detail of protoconch and early teleoconch. C–F. *Bruceina areniformis* sp. nov., paratypes C. Side view of spire. D. Umbilical region showing funicle-like cord within. E. Oblique view of apex showing development of spiral sculpture. F. Sculptural detail of protoconch and early teleoconch (C–D=MNHN-IM-2000-35700, E–F=MNHN-IM-2000-35704). Scale bars: A, C=1.0 mm; B, F=100 µm; D=500 µm; E=200 µm.

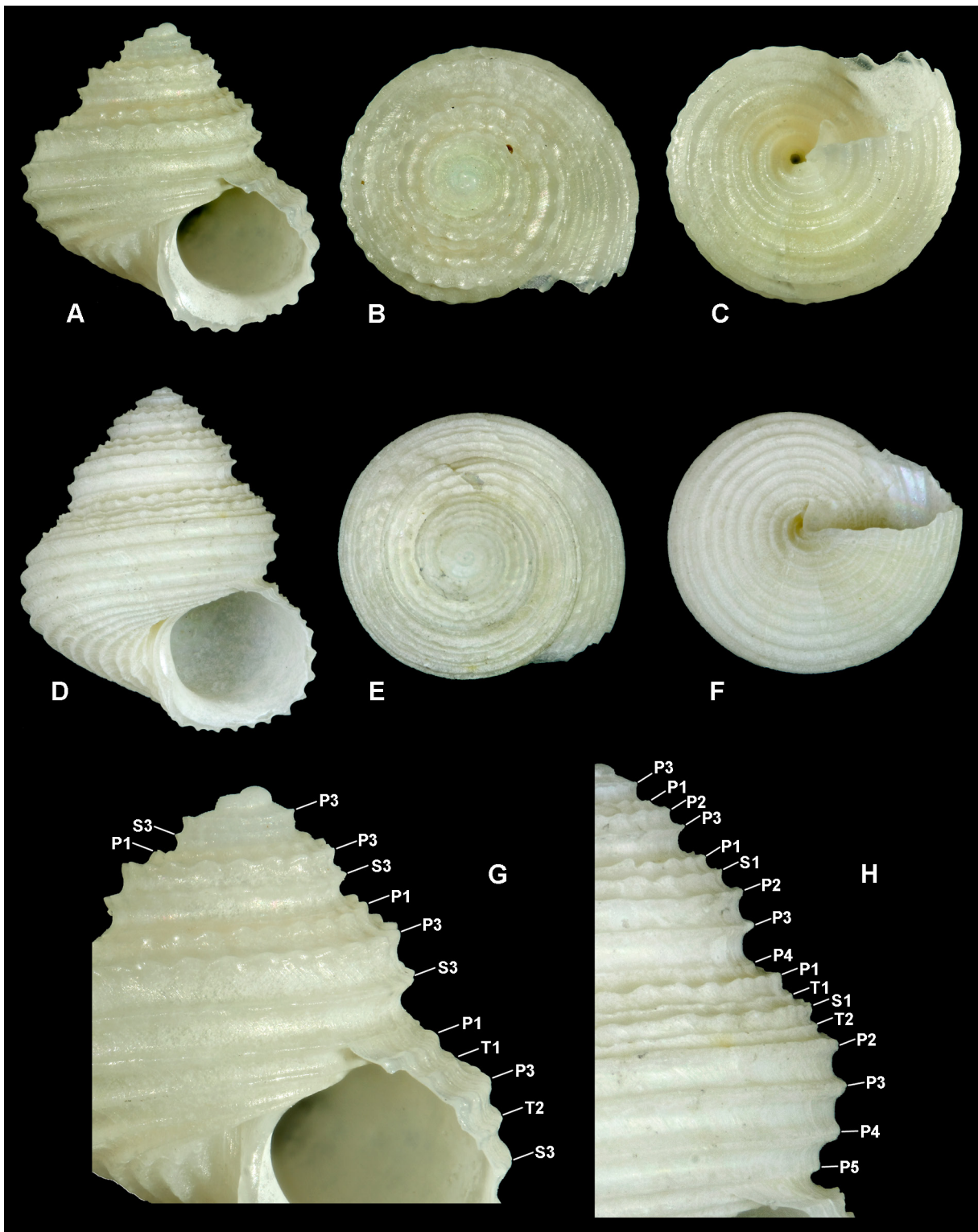


Fig. 29. A–C. *Bruceina areneformis* sp. nov., holotype, height 4.3 mm (MNHN-IM-2000-35699). D–F. *Carinastele achrosta* sp. nov., holotype, height 8.7 mm (MNHN-IM-2000-35705). G–H. Portions of the above holotypes to illustrate numbering of spiral cords, following Marshall (1988). G. *Bruceina areneformis* sp. nov. H. *Carinastele achrosta* sp. nov. The equivalent of P2 is not present in *B. areneformis* sp. nov.

whorl, second and third intervals with finer intermediary cord arising (T1 and T2 respectively); adapical cord slightly weaker than others, shoulder cord no longer as prominent; upper two cords remaining nodular, but axial riblets no longer evident; third and fourth cords shallowly undulant or almost smooth; cord intervals with close-set, microscopic collabral threads. Base typically with 5–6 rounded spiral cords, their intervals slightly narrower toward umbilicus; in some specimens cords in mid-region of base reduced or obsolete, rarely basal cords almost completely lacking; umbilicus narrow and deep, with funicle-like cord spiralling into it at mid-columella level (Fig. 28D); peri-umbilical region sometimes with fine close-set spiral lirae, most obvious in juveniles. Aperture subcircular, peristome incomplete; columella lip concave, basal half somewhat reflected, flaring at junction with basal lip; outer lip thin, crenulated by spiral cords; interior nacreous.

PROTOCONCH (Fig. 28F). Diameter 330–340 μm ; surface sculptured with hexagonal network of interconnected ridges; terminal varix well developed, rib-like.

COLOUR. Uniformly milky-white to pale buff, cord intervals with a faint pink/green iridescence in the freshest specimens.

DIMENSIONS. Holotype, height 4.3 mm, diameter 4.2 mm; largest specimen, height 5.4 mm, diameter 5.3 mm.

OPERCULUM. Corneous, pale golden-brown; whorls narrow and numerous.

RADULA AND EXTERNAL ANATOMY. Unknown.

Distribution

Known only from the slopes of Walters Shoal, at depths of 256–652 m (live-taken specimen 275–318 m); dredged on coarse sandy substrata with octocorals and solitary corals.

Remarks

Although this species might at first glance appear referable to the Areneidae, its operculum lacks the characteristic calcareous granules of the areneid operculum and the hexagonal protoconch microsculpture clearly places it in the Calliostomatidae. Within this family, the overall shell facies, in particular the turbiniform profile and the ontogeny of the spiral sculpture, notably the relatively high position of the primary spiral cord on the first two teleoconch whorls (P3 of Marshall 1988), ally the species to the thysanodontine genus *Bruceina*, a taxon to date known only from the continental shelf and upper slope (50–500 m) off south-eastern Africa (four species). *Bruceina areneformis* sp. nov. has a broader, less elevated spire when compared with *B. cognata* (Marshall, 1988), *B. eos* (Marshall, 1988) and *B. meimiaoae* Huang, 2020, and all three of these species have more numerous spiral cords and are typically of bright pinkish colour (occasional specimens of *B. eos* may be uniformly whitish). *Bruceina chenoderma* (Barnard, 1963) has a more similar shape, but it too is usually pinkish in colour and it has more numerous spiral cords (5 vs 3 above periphery at the start of the last adult whorl) (Herbert 1995). In addition, the granules on the adapical cords of the spire whorls are more angular in *B. chenoderma*. All four South African species attain a larger size (height 7–9 mm) than *B. areneformis*.

Another thysanodontine species, *Carinastele wareni* Vilvens, 2014 from off southern Madagascar, is of relevance here. When describing this species, Vilvens (2014) used a different system for numbering the spiral cords compared to that of Marshall (1988). Thus, the prominent keel-like shoulder cord on the first whorl is P2 for Vilvens and P3 for Marshall. In turn P3 for Vilvens corresponds with S3 for Marshall. Since Marshall defined *Carinastele* as lacking S3, I consider *Carinastele wareni*, which possesses an S3 (sensu Marshall), to be referable to *Bruceina* rather than to *Carinastele*. It was based on a single small specimen (height 2.5 mm), which I believe to be a juvenile specimen of *B. cognata*. It differs from *B. areneformis* sp. nov. in lacking nodules on the two adapical spiral cords on the spire.

Bruceina areneformis sp. nov. exhibits considerable variation with respect to the strength and number of spiral cords on the base. Typically, there are 5–6 basal cords, plus an additional funicle-like cord spiralling into the umbilicus. In some specimens, however, the cords in the mid-region of the base are absent and in such specimens the fine peri-umbilical spiral lirae are often more evident, particularly in juveniles. Above the periphery the cording is usually more consistent, but the adapical cord may become weak or obsolete on the last adult whorl. There is also variation in the strength of the nodules on the cords on the apical surface. Whereas these are usually distinct on the two adapical cords on the spire whorls (Fig. 28C), they often become weak or obsolete on the last adult whorl.

Calliostoma cyrtoida Gofas & Hoffman, 2020 from upper bathyal depths on the South Azorean Seamount Chain is remarkably similar to *Bruceina areneformis* sp. nov. in its general facies. It differs from the latter in having a narrower umbilicus, and the first teleoconch whorl lacks fine spiral lirae and is distinctly bicarinate with more numerous, stronger axial ribs.

Genus *Carinastele* Marshall, 1988

Type species

Carinastele kristelleae Marshall, 1988 (original designation), Recent, New Zealand.

Remarks

Carinastele has been recorded previously from the south-western Indian Ocean (Vilvens 2014), but as noted above under *Bruceina areneformis* sp. nov., the material concerned is in fact referable to *Bruceina*. The present material thus represents the first record of the genus from this region. The above notwithstanding, it remains to be established whether generic differentiation based on patterns of spiral cord ontogeny is supported by molecular data. The overall similarity between *Carinastele achrosta* sp. nov. and the type species of *Bruceina*, as well as the geographic proximity of their distributions, is noteworthy.

Carinastele achrosta sp. nov.

[urn:lsid:zoobank.org:act:80AE5B57-5CCA-4EDF-9BAC-47766274BE71](https://doi.org/10.21203/rs.3.rs-1234567/v1)

Fig. 29D–F, H

Diagnosis

Shell elevated-turbiniform, height up to 8.7 mm; height > diameter; base narrowly umbilicate; protoconch hexagonally reticulate; teleoconch sculpture of strong spiral cords, nodular on spire whorls; P3 forms carina-like shoulder cord on apical whorls, but subsequently migrates downward and becomes peripheral cord, a strong S3 not present below P3; additional secondary and tertiary cords develop on later whorls, only 2–3 uppermost ones nodular; crests of lower cords with shallow median furrow; base with 10 rounded spiral cords; shell uniformly whitish.

Etymology

From the Greek “*achrostos*” (αχρόστος) – “uncoloured”; in reference to the unpigmented shell.

Material examined

Holotype

WALTERS SHOAL • empty shell; slopes, stn DW4899; 33°09' S, 44°02' E; depth 707–720 m; 6 May 2017; MNHN-IM-2000-35705.

Description

SHELL. Relatively small for the genus (height 8.7 mm), elevated-turbiniform ($H/D=1.18$); spire prominent ($1.35 \times$ height of aperture), with indented suture; whorls evenly rounded, sculptured by strong spiral cords, the adapical ones nodular; umbilicus narrow; teleoconch of nearly 5.0 whorls. First teleoconch whorl with an axial growth flaw shortly after terminal protoconch varix (at 0.1–0.2 whorl), soon developing a prominent spiral cord midway between sutures, creating a distinct shoulder; two finer spiral lirae between this and adapical suture; shoulder cord becomes carina-like during second whorl (= P3 of Marshall 1988), and lirae above it strengthen to become cords (P1 and P2) (Fig. 29H); all spiral cords with low, undulant coronations, those above shoulder linked by broad, low, axial riblets; interval between shoulder carina and abapical suture relatively wide and deeply concave; an additional spiral cord (S1) intercalates between subsutural cords (P1 and P2) during third whorl and P3 becomes less carina-like, migrating down whorl to become peripheral cord; start of fourth whorl with four distinct spiral cords (P1, S1, P2, P3), increasing slightly in size from subsutural one to peripheral one and also becoming less obviously nodular; abapical suture level with and concealing a fifth cord (P4); P4 emerges above suture during fourth whorl, revealing a sixth cord (P5) level with abapical suture; two additional intermediary spiral lirae (T1 and T2) arise during fourth whorl, T1 between P1 and S1 and T2 between S1 and P2; P5 emerges above suture just prior to start of last whorl; at this point adapical part of shell has four strong spiral cords above and including periphery (P1, S1, P2, P3) and two below periphery (P4 and P5), with a further two weaker cords (T1 and T2) in intervals 2 and 3; uppermost cord on last whorl (P1) retaining nodules, but nodules weaker and more uneven on cords below this, those near periphery smooth; profile of cords more rounded on fourth and fifth whorls, their crests with traces of shallow median furrow; cord intervals roundly concave, slightly wider than cords themselves; axial sculpture beyond third whorl comprising only close-set, microscopic, collabral growth-lines, most obvious in cord intervals. Base with 10 evenly-spaced, spiral cords, eight of which originate below insertion of outer lip, the last narrower and spiralling steeply into umbilicus; umbilicus very narrow and deep, partly obscured by reflected upper part of columella lip. Aperture subcircular, roundly quadrate in parieto-columellar region; peristome incomplete; columella somewhat flaring at junction with basal lip; outer lip thin, partly damaged but evidently crenulated by spiral cords; interior somewhat calcined, but retaining traces of nacre.

PROTOCONCH. Surface evidently sculptured with hexagonal network of interconnected ridges, but not examined under SEM as the holotype is the only specimen available.

COLOUR. Uniformly milky-white, cord intervals retaining faint iridescence.

DIMENSIONS. Holotype, height 8.7 mm, diameter 7.4 mm.

OPERCULUM, RADULA AND EXTERNAL ANATOMY. Unknown.

Distribution

Known only from the slopes of Walters Shoal, at a depth of 707–720 m; dredged on coarse sand with solitary corals; living specimens unknown.

Remarks

The single available specimen of *Carinastele achrosta* sp. nov. is considerably larger and proportionately taller than any of the more than 175 specimens of *Bruceina areneformis* sp. nov. (height 8.7 mm vs max. 5.4 mm) and it was obtained at a somewhat greater depth. It differs from *B. areneformis* not only in size and relative height, but also in having more numerous spiral cords that are more rounded in profile and possess a faint median furrow, and it has a narrower umbilicus. In size and shape *C. achrosta* is closer to the South African *Bruceina eos* and might be considered an example of the occasional uniformly white specimens of that species (normally bright pink). However, *C. achrosta* differs fundamentally from species

of *Bruceina* in the ontogeny of the spiral cords (compare Figs 29G and 29H). In species of *Bruceina* the shoulder cord of the early whorls (P3) remains more or less at the shoulder and an additional cord (S3) arises beneath this during the second whorl. Such a cord is absent in *C. achrosta* and with growth P3 changes from being the shoulder cord to become the peripheral cord. Marshall (1988) considered the lack of cord S3 to be an important character separating his genera *Carinastele* and *Bruceina* (as *Herbertina*) and for this reason I refer the present material to *Carinastele*. In its overall shape *C. achrosta* resembles the type species, *C. kristelleae*, from New Zealand, but in that species the base is flatter and all the supra-peripheral spiral cords are strongly and sharply nodular. *Carinastele niceterium* (Hedley & May, 1908) and *C. jugosa* Marshall, 1988, from Tasmania and south of New Zealand respectively, both have a more conical spire profile and fewer, stronger spiral cords above the periphery that lack nodules. *Carinastele jugosa* shares with *C. achrosta* the presence of a narrow median furrow on the crest of the spiral cords.

Family Colloniidae Cossmann, 1917
Subfamily Colloniinae Cossmann, 1917

Genus *Microcollonia* Poppe, Tagaro & Huang, 2023

Type species

Leptothyra carminea Bartsch, 1915 (original designation), Recent, South Africa.

Remarks

The small size and thick, anomphalous shell of the following species, with its strong spiral cords, un-beaded on the early teleoconch, suggests that it is referable to *Microcollonia*.

Microcollonia miniata sp. nov.

[urn:lsid:zoobank.org:act:C2937537-9556-4126-A1F7-2F42FEECA6C5](https://zoobank.org/urn:lsid:zoobank.org:act:C2937537-9556-4126-A1F7-2F42FEECA6C5)

Figs 30, 32C–F

Diagnosis

Shell small, turbiniform, very thick, diameter up to 3.0 mm; anomphalous in adult; sculpture dominated by strong spiral cords; early teleoconch whorls with three un-beaded spiral cords, a fourth cord arises below adapical suture on third whorl, bearing bead-like nodules toward end of whorl; suture descending toward insertion of outer lip; base with three spiral cords; adult umbilicus glazed over by columella callus; exterior of outer lip with subterminal swelling; early whorls milky-white, subsequent whorls uniformly vermilion; umbilical region white.

Etymology

From the Latin “*minium*” – “cinnabar”, “*miniatus*” – “painted red with cinnabar”; in reference to the vermilion colour of the shell.

Material examined

Holotype

WALTERS SHOAL • living specimen; summit area, south-west, stn WS03; 33°12.2' S, 43°50.8' E; depth 40 m; 30 Apr. 2017; DNA tissue sample; MNHN-IM-2013-67278.

Paratypes

WALTERS SHOAL • 1 living specimen; same collection data as for holotype; DNA tissue sample; MNHN-IM-2013-67279 • 1 living specimen; summit area, south, stn WB05; 33°15.1' S, 43°54.5' E;

depth 26–30 m; 1 May 2017; DNA tissue sample; MNHN-IM-2013-67280 • 1 living specimen; summit area, south, stn WB05; 33°15.1' S, 43°54.5' E; depth 26–30 m; 1 May 2017; DNA tissue sample; MNHN-IM-2013-67281 • 1 living specimen, juvenile; summit area, south, stn WB05; 33°15.1' S, 43°54.5' E; depth 26–30 m; 1 May 2017; SEM of protoconch; MNHN-IM-2000-35709 • 16 specimens, some living; summit area, north-west, stn WB10; 33°09.1' S, 43°51.8' E; depth 30 m; 6 May 2017; SEM of operculum; MNHN-IM-2000-35708.

Other material

WALTERS SHOAL – **summit area, north-west** • 19 empty shells; stn WB09; 33°13.8' S, 43°55.8' E; depth 27–30 m; 4 May 2017; MNHN. – **summit area, south-west** • 50+ empty shells; stn WS03; 33°12.2' S, 43°50.8' E; depth 40 m; 30 Apr. 2017; MNHN • 40+ specimens, some living; stn WS04; 33°12.2' S, 43°50.8' E; depth 40 m; 30 Apr. 2017; MNHN • 2 empty shells; stn WR01; 33°12.2' S, 43°50.8' E; depth 36 m; 30 Apr. 2017; MNHN. – **summit area, south-east** • 50+ specimens, some living; stn WS08; 33°13.7' S, 43°55.9' E; depth 30–33 m; 3 May 2017; MNHN. – **summit area, south** • 8 specimens, some living; stn WS06; 33°15.1' S, 43°54.5' E; depth 26 m; 1 May 2017; MNHN • 50+ specimens, some living; stn WS07; 33°15.4' S, 43°52.2' E; depth 30–33 m; 2 May 2017; MNHN • 10 empty shells; stn WB05; 33°15.1' S, 43°54.5' E; depth 26–30 m; 1 May 2017; MNHN.

Description

SHELL. Small (diameter up to 3.0 mm) and very thick; profile turbiniform, spire of moderate height; diameter slightly greater than height; sculpture dominated by strong spiral cords; anomphalous in adult; teleoconch of up to 3.0 whorls. First two teleoconch whorls with three spiral cords, the lowest one level with or just above abapical suture; cords smooth, lacking granules or beads; a fourth spiral cord arises below adapical suture on third whorl; this shoulder cord initially with low undulations which strengthen and become almost bead-like toward outer lip; abapical suture level with peripheral cord on last adult whorl, descending distinctly immediately prior to insertion of outer lip; cords on last adult whorl have

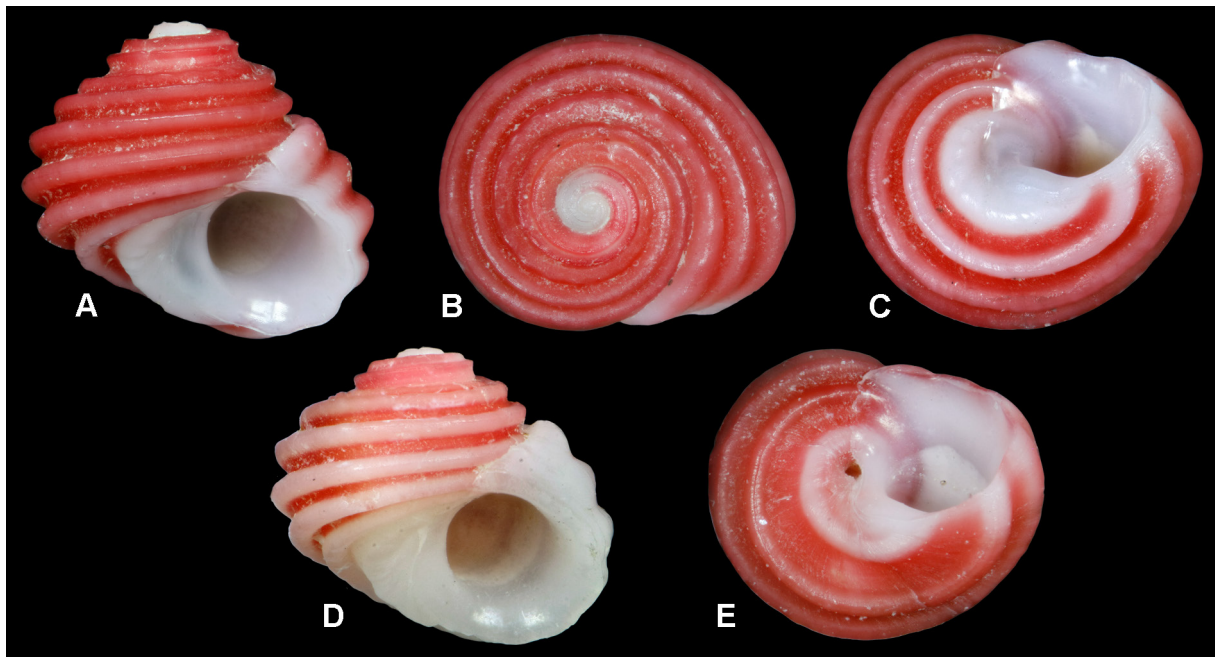


Fig. 30. *Microcollonia miniata* sp. nov. **A–C.** Holotype, diameter 3.0 mm (MNHN-IM-2013-67278). **D.** Faded shell, diameter 2.7 mm, stn WS07 (MNHN). **E.** Umbilicate subadult specimen with only two basal spiral cords, diameter 2.9 mm (paratype, MNHN-IM-2013-67279).

an indistinct spiral thread on their crest; intervals between cords deep, their width equal to or slightly narrower than cords; no significant axial sculpture evident, only microscopic collabral growth striae. Base usually with three spiral cords; outer two cords like those above periphery, inner one broader and with low, ill-defined beads; middle basal spiral cord missing in one specimen (Fig. 30E); umbilicus narrowly patent in juveniles and subadults, but usually glazed over by columella callus in adult, though still remaining somewhat sunken. Aperture subcircular, peristome almost complete, glazed with smooth, glossy callus; columella lip concave, with a very slight swelling at its base; outer lip thick, lacking internal ornamentation, but its edge rendered undulant by spiral cords; exterior of outer lip strengthened by low, broad, subterminal swelling (Fig. 30C); interior not obviously nacreous.

PROTOCONCH (Fig. 32C). Translucent milky-white; diameter $\pm 280 \mu\text{m}$, ca 1.25 whorls, apical bulb rounded; sculptured by three relatively strong subspiral threads, one close to abapical suture, with additional somewhat irregular subspiral thread-like features in their intervals; terminal lip straight, slightly flaring; step-like junction with teleoconch clearly demarcated.

COLOUR. First whorl of teleoconch translucent milky-white like protoconch, becoming progressively more pinkish-red toward end of whorl; subsequent whorls more or less uniformly vermilion; above periphery no colour difference between spiral cords and their intervals except in faded post-mortem specimens (Fig. 30D); basal coloration similar, but cords sometimes paler than their intervals, sometimes not; innermost basal cord uniformly white; peristome and interior of aperture white; vermilion colour of exterior subsequent to subterminal swelling fading to white at lip edge.

DIMENSIONS. Holotype, height 2.7 mm, diameter 3.0 mm (= largest specimen).

OPERCULUM (Fig. 32D). White, paucispiral and thickly calcified; nuclear region slightly domed, but extensively pitted particularly near its centre; nuclear region bounded by a broad raised ring sculptured by a fine anastomosing network of ridges; this ring terminating in a pointed tongue-like extension in the parieto-columellar region; peripheral region adjacent to basal and outer lips of aperture bounded by a narrow flattened ledge.

RADULA (Fig. 32E–F). Formula $\infty+5+1+5+\infty$, length ca 1.0 mm, with 40–45 transverse rows of teeth; rows with a shallow central posterior indentation. Rachidian tooth with angular kite-shaped base-plate leading to small trigonal shaft with no cusp, behind which hood-like secondary flap; wings of kite joined by curved thickening of base-plate, close to anterior margin. Innermost lateral teeth with trigonal expansion of shaft, expansion progressively diminishing toward evenly curved shaft of fifth lateral; tooth overlap extensive; lateral tooth cusps asymmetrically trigonal, increasing in size from first to fifth, outer edge curved and blade-like with 2–4 smaller denticles at outer base. Marginal teeth progressively smaller toward edge of ribbon, their cusps narrow and strongly recurved, with denticulate edges.

Distribution

Known only from the summit area of Walters Shoal, at depths of 26–40 m (living); habitat dominated by coralline algae encrusting the rocky summit; collected by brushing and suction sampling.

Remarks

Microcollonia miniata sp. nov. resembles *M. rubricinctum* (Mighels, 1845) from Hawaii, Japan and the Philippines, but that species has more numerous spiral cords (± 10 vs 7 on last adult whorl), and the cords are paler than their intervals, resulting in a spirally striped colour pattern (Sasaki 2000b; Hasegawa 2018, Poppe *et al.* 2023). Such a colour pattern is evident in *C. miniata* only in older post-mortem specimens in which the intensity of the colour on the spiral cords has begun to fade (Fig. 30D). Similar, more geographically proximate species include *Circumcollonia purpurata* (Deshayes, 1863)

from Réunion and *Microcollonia carminea* (Bartsch, 1915) from South Africa. The former is smaller (diameter 2.0 mm), has ± 12 spiral cords on the last adult whorl, and the base is largely white, with only a narrow deep red band midway between the periphery and the umbilicus. The latter, though of similar size, has more numerous spiral cords (up to 20 on last adult whorl) and the cords are also generally paler than their intervals.

There are additional colloniine samples from deeper water (256–660 m) on the slopes of Walters Shoal, but this material is all in poor condition. One or more species may be involved, and though undoubtedly similar to *M. miniata* sp. nov., I suspect that they represent different species rather than old material of *M. miniata* that has been displaced downslope.

Subfamily Thermocolloniinae Poppe, Tagaro & Huang, 2023

Genus *Cantrainea* Jeffreys, 1883

Type species

Turbo peloritanus Cantraine, 1835 (monotypy), Miocene to Recent, Europe.

Cantrainea herosae sp. nov.

[urn:lsid:zoobank.org:act:78AC55FB-2B32-4C73-A868-8F491E1F85B3](https://zoobank.org/act:78AC55FB-2B32-4C73-A868-8F491E1F85B3)

Figs 31, 32A

Diagnosis

Shell thick, trochoid-turbiniform, spire prominent; height up to 7.4 mm; periphery below mid-whorl; base flattened, anomphalous in adult; sculpture of strong spiral cords, three above periphery, one at periphery; subsutural and shoulder cords distinctly beaded; shell surface with silken sheen; base with indistinct spiral lirae; umbilical region covered with glossy extension of parietal callus; aperture roundly quadrate; columella with a low rounded nodule just below its mid-point; interior highly nacreous; shell uniformly milky-white, with pale straw-coloured periostracum.

Etymology

Named for Virginie Héros (MNHN), in recognition of her stalwart contribution to the institution's Mollusca collection and the Tropical Deep-Sea Benthos programme, over many years.

Material examined

Holotype

WALTERS SHOAL • living specimen; slopes, stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; DNA tissue sample; MNHN-IM-2013-67292.

Paratypes

WALTERS SHOAL – **slopes** • 1 living specimen, juvenile; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; SEM protoconch; MNHN-IM-2000-35706 • 1 empty shell; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; MNHN-IM-2000-35707.

Other material

WALTERS SHOAL – **slopes** • 1 empty shell, subfossil; stn DW4898; 33°09' S, 44.01' E; depth 652–668 m; 6 May 2017; MNHN • 1 empty shell, juvenile; stn DW4900; 33°10' S, 44°01' E; depth 660–670 m; 6 May 2017; MNHN.

Description

SHELL. Thick, relatively small for the genus (height up to 7.4 mm), trochoid-turbiniform, with prominent spire; height slightly greater than diameter ($H/D \pm 1.03$); whorls with strong spiral cords; suture indented, periphery below mid-whorl; base flattened, anomphalous in adult; teleoconch of up to 4.75 whorls. First teleoconch whorl initially with 3 low spiral lirae, but these soon becoming obsolete; early part of second whorl lacking spiral sculpture and bearing only weak, irregular growth-lines; toward end of second whorl a weak angulation develops at mid-whorl, progressively strengthening and becoming distinct shoulder cord during third whorl; two further cords develop toward end of third whorl, one immediately below adapical suture and one between shoulder and abapical suture, these strengthening during fourth whorl, the lower one equal to shoulder cord in strength; a fourth cord at whorl periphery emerges from suture just prior to insertion of outer lip; last adult whorl with low intermediary cord in intervals either side of shoulder cord; axial sculpture indistinct on first two teleoconch whorls, but distinct prosocline pliculae develop on shoulder slope during third whorl; pliculae strengthen during fourth whorl producing distinct beads on subsutural and shoulder cords; pliculae not evident in interval below shoulder, but cord below shoulder evincing weak beading; entire surface of shell with microscopic axial threads giving surface silken sheen. Base flattened, with indistinct spiral lirae; umbilicus narrowly patent in juveniles, but adult specimens with umbilical region covered by glossy extension of parietal

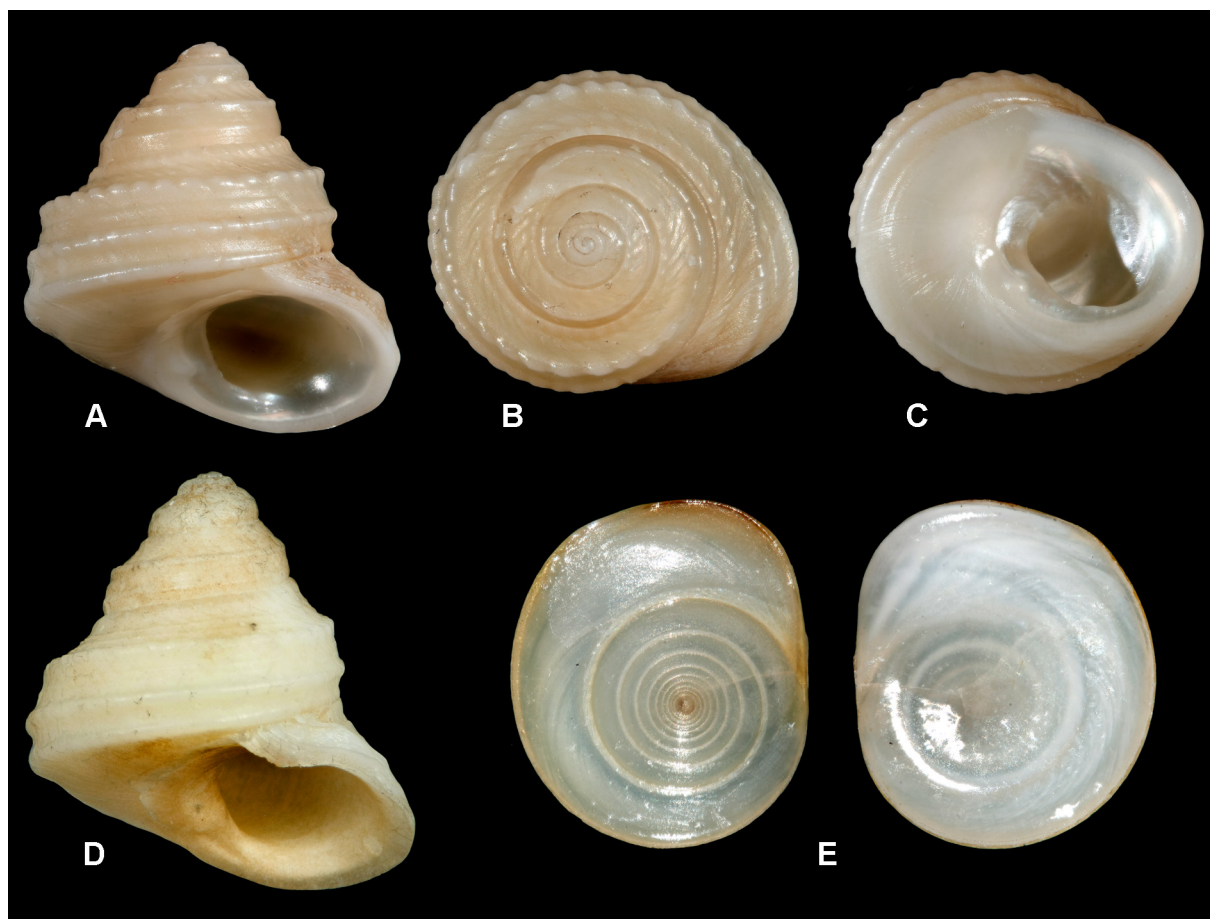


Fig. 31. *Cantrainea herosae* sp. nov. A–C. Holotype, height 7.2 mm (MNHN-IM-2013-67292). D. Paratype with weakly beaded sculpture, periostracum missing, height 7.4 mm (MNHN-IM-2000-35707). E. Interior (left) and exterior (right) of operculum of holotype, greatest diameter 2.45 mm.

callus. Aperture roundly quadrate; peristome interrupted in parietal region; columella oblique to shell axis; outer lip thick, lacking ornamentation; interior highly nacreous, nacre extending over columella and parietal lips; columella with a low rounded nodule just below its mid-point, set back from the edge, mostly in non-nacreous region.

PROTOCONCH (Fig. 32A). Large, translucent milky-white; diameter 360–400 μm , ca 1.25 whorls, apical bulb evenly rounded; sculpture somewhat worn, but retaining microscopic superficial granulation and traces of fine, widely-spaced, subspiral lirae; terminal lip weakly convex and very slightly flaring, not thickened.

COLOUR. Shell uniformly milky-white, covered with a thin pale straw-coloured periostracum; spiral cords paler where periostracum worn away.

DIMENSIONS. Holotype, height 7.2 mm, diameter 6.9 mm; largest specimen, height 7.4 mm, diameter 7.2 mm.

OPERCULUM (Fig. 31E). White, thickly calcified, somewhat translucent; external surface smooth and glossy, that part adjacent to upper columella and paries thicker and curving slightly outward, no evidence of granulation; inner surface weakly convex, showing tightly multispiral nucleus, but becoming paucispiral toward periphery with final two whorls more rapidly expanding; growing edge broad, tinged with brown.

RADULA AND EXTERNAL ANATOMY. Unknown.

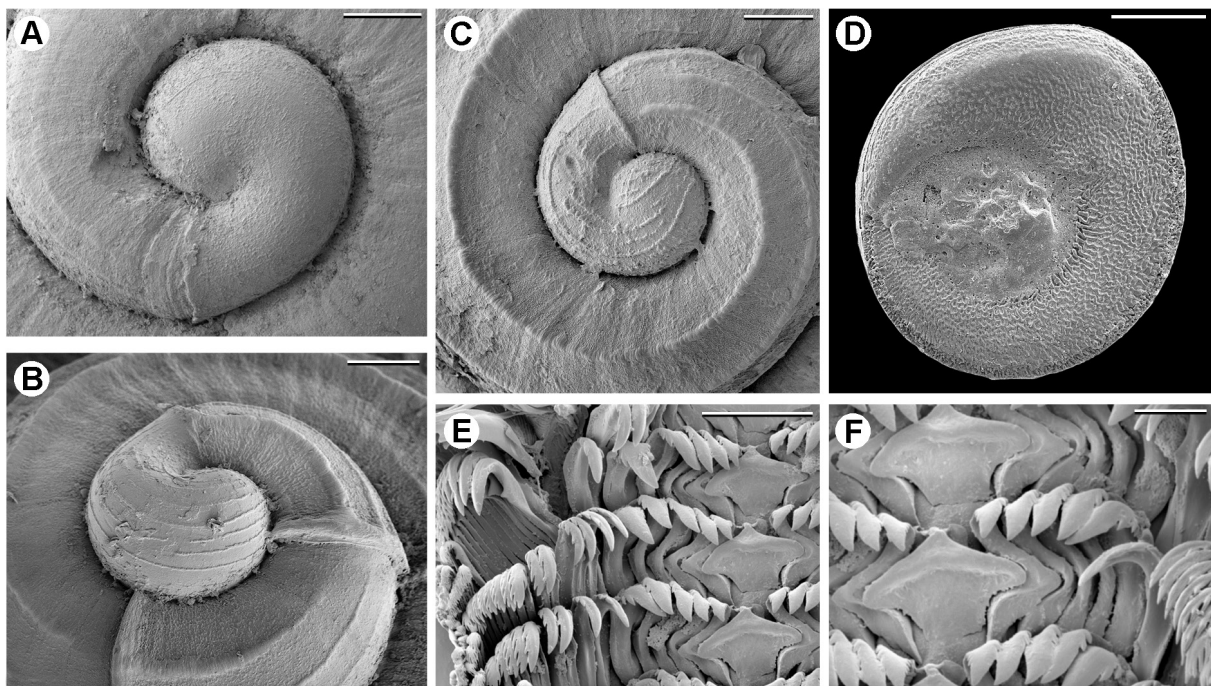


Fig. 32. A. *Cantrainea herosae* sp. nov., protoconch (paratype, MNHN-IM-2000-35706). B. *Parviturbo cicatricosus* sp. nov., holotype, protoconch and axial varices on early teleoconch. C–F. *Microcollonia miniata* sp. nov. C. Protoconch and early teleoconch (paratype, MNHN-IM-2000-35709). D. Operculum, maximum diameter 1.0 mm (paratype, MNHN-IM-2000-35708). E. Radula, half row (ex stn WS07). F. Radula, rachidian and right lateral teeth (ex stn WS07). Scale bars: A–C=100 μm ; D=250 μm ; E=25 μm ; F=10 μm .

Distribution

Known only from the slopes of Walters Shoal; dredged alive in 492–588 m, on coarse sand with abundant ophiuroids and diverse Cnidaria.

Remarks

Cantrainea herosae sp. nov. is rendered distinctive on account of its prominent spire, shouldered whorls and beaded spiral cords. *Cantrainea boswellae* (Barnard, 1969) from a depth of 365 m off Cape Point, *C. indica* (Smith, 1894) from a depth of 1090 m off Sri Lanka, and *C. inexpectata* Marshall, 1979 from ca 800 m on the Kermadec Ridge, are all larger (height 17.5 mm, 26 mm and 11.5 mm, respectively), have a proportionately less elevated spire with less strongly shouldered whorls and have weaker spiral cords that lack beads. *Cantrainea gibbula* (Thiele, 1925) from the Agulhas Bank is of a more similar size (height 8.0 mm), but has more rounded whorls, with more numerous, evenly spaced spiral cords, and the suture descends more strongly prior to the aperture. Perhaps the most similar species is the type species *C. peloritana* (Cantraine, 1835) from the NE Atlantic and Mediterranean, particularly with regard to its prominent spire and shouldered whorls (Smiriglio *et al.* 1992). However, in that species the spiral cords are not as strong and are not beaded.

Some intraspecific variation in sculpture is evident in this species, particularly with regard to the strength of the axial sculpture and the beading on the spiral cords. The single adult paratype (Fig. 31D) has weaker subsutural pliculae than the holotype and the beading of the spiral cords is less conspicuous. In addition, it has two low intermediary spiral cords in the interval above the shoulder cord on the last two whorls, instead of one.

Family Skeneidae Clark, 1851

Genus *Mikro* Warén, 1996

Type species

Mikro globulus Warén, 1996 (original designation), Recent, NE Atlantic.

Remarks

The generic affinity of the new species described below is not clear. I have chosen to refer it to *Mikro* largely on account of its smooth protoconch, distinct spiral rib on the early teleoconch whorls and intra-umbilical keels. It represents the first record of the genus from the Indian Ocean. Although I do not feel confident in this generic referral, I can find no other described genus that appears more appropriate and opt to refrain from describing yet another new skeneimorph genus based solely on shell morphology. I had initially considered it to belong to *Trochaclis*, but species in that genus have a distinct protoconch sculpture of anastomosing threads enclosing irregularly polygonal spaces (cf. *Trochaclis regalis* above and Marshall 1995).

Mikro crassus sp. nov.

[urn:lsid:zoobank.org:act:3CE83169-0B5E-4678-85EA-1150A6EA8C60](https://zoobank.org/act:3CE83169-0B5E-4678-85EA-1150A6EA8C60)

Fig. 33

Diagnosis

Shell globose-turbiniform, white, thick, H/D \pm 1.0, whorls rounded with distinct shoulder delineated by rounded spiral cord, beginning immediately after protoconch, becoming less prominent on last adult whorl; umbilicus narrow, bordered by two well-defined spiral cords, with two finer spiral cords within it; whorls otherwise smooth and glossy; aperture subcircular; basal lip weakly notched by cords bordering umbilicus; outer lip shallowly concave between suture and shoulder; interior of aperture somewhat thickened with opaque, chalky layer (?nacre); protoconch smooth.

Etymology

From the Latin “*crassus*” – “thick”; in reference to the thickness of the shell.

Material examined

Holotype

WALTERS SHOAL • empty shell; south plain, stn CP4913; 33°52' S, 44°05' E; depth 1539–1615 m; 11 May 2017; MNHN-IM-2000-38066.

Paratypes

WALTERS SHOAL • 14 empty shells; same collection data as for holotype; SEM shell; MNHN-IM-2000-38067.

Description

SHELL. Small (diameter up to 3.5 mm), relatively thick, globose-turbiniform, height and width similar (apex missing in most specimens); whorls rounded with distinct shoulder delineated by a rounded spiral cord, middle of shoulder shallowly sunken; teleoconch of up to 3.5 whorls; shoulder cord begins immediately after protoconch as low, broad rib and persists throughout, but becomes broader and less prominent on last adult whorl; periphery and base evenly rounded, periphery at mid-whorl; umbilicus narrow, bordered by two well-defined spiral cords, inner of which forms umbilical rim and ends at junction of columella and basal lips; outer one peri-umbilical, ending at lowest point of basal lip; interval between these cords distinctly concave; two additional, finer spiral cords descending steeply within umbilicus, ending on columella lip, inner one weaker; whorls otherwise smooth and glossy, sculptured only by extremely fine collabral growth-lines. Aperture subcircular, prosocline, peristome interrupted in parietal region; columella lip duplex, with thin outer layer protruding slightly beyond thicker inner layer; basal lip thickened and weakly notched at termination of outer two cords bordering umbilicus; outer lip simple, notched at end of shoulder cord and shallowly concave between this and its insertion on penultimate whorl; interior somewhat thickened, inner layer opaque and chalky.

PROTOCONCH (Fig. 33F). Comprising just less than one whorl, globose and slightly exsert, diameter $\pm 330 \mu\text{m}$; smooth save for an extremely fine superficial granulation; terminal lip straight, slightly flared.

COLOUR. Uniformly milky-white; inner shell layer opaque and chalky. Some individuals partly or almost completely covered with lustreless dark brown coating (Fig. 33D–E).

DIMENSIONS. Holotype, height 2.6 mm (apex missing), diameter 2.9 mm; largest specimen, diameter 3.5 mm.

Distribution

Known only from the plain surrounding Walters Shoal, at a depth of 1539–1615 m; dredged on coarse sandy substrata; living specimens unknown.

Remarks

Mikro crassus sp. nov. is considerably larger than any of the other species currently referred to the genus (most with height < 1.5 mm). The most similar species is *M. hattonensis* Hoffman, Van Heugten & Lavaleye, 2010 from the north Atlantic, but that species has deeper spire whorls and thus a more elevated spire, and it has an unusual pitted (shagreened) micro-sculpture on the shoulder and in the umbilicus. There is also some resemblance to an unidentified species of *Moelleriopsis* Bush, 1897 from Réunion figured by Warén (1992: fig. 31a), but that has a less exsert protoconch with distinct spiral sculpture and a strongly channelled suture (Warén 1992: fig. 26c).

The 15 shells of *Mikro crassus* sp. nov. available are all damaged to some extent and most are juvenile. They all came from a single station and many evince the remains of a dark brown periostracum-like superficial deposit (Fig. 33D–E), possibly of a ferruginous nature, suggesting that the species may live in an unusual and highly specialised microhabitat associated with anoxic conditions (Warén & Bouchet 1989; Warén 1991). A similar superficial layer is evident in the Antarctic *Lacuna abyssicola* Melvill &

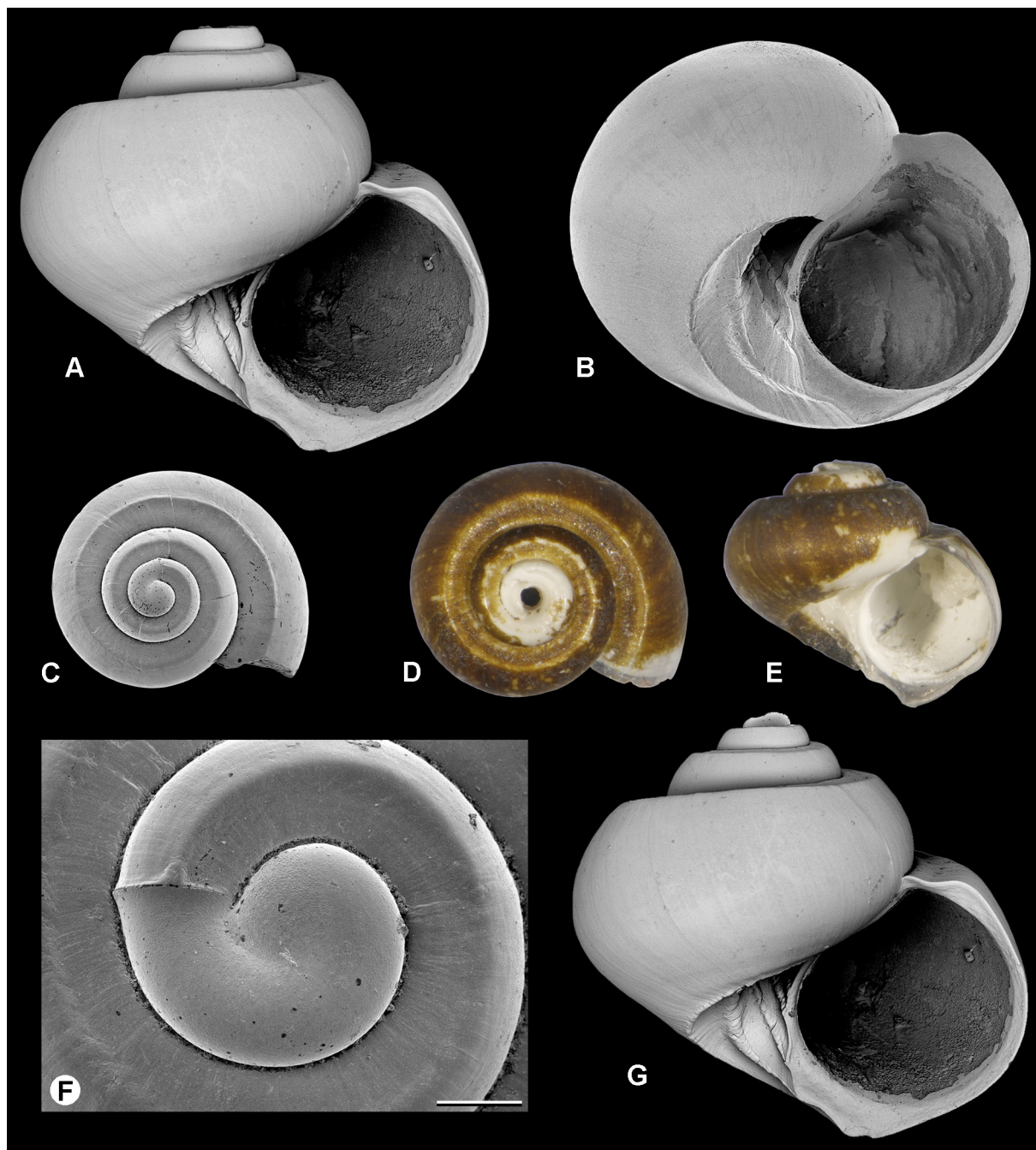


Fig. 33. *Mikro crassus* sp. nov. A–B. Holotype, apertural and oblique basal views (apex missing), diameter 2.9 mm (MNHN-IM-2000-38066). C. Apical view of juvenile specimen with intact apex, diameter 1.5 mm (paratype, MNHN-IM-2000-38067). D–E. Specimen with brown superficial deposit, diameter 1.7 mm (paratype, MNHN-IM-2000-38067). F. Protoconch of C, scale bar=100 µm. G. Composite image of holotype superimposed on apex of C, diameter 2.9 mm.

Standen, 1912, a species which Engl (2012) referred to *Moelleriopsis* on account of “the shape and sculpture of the shell”, at the same time renaming it *Moelleriopsis poppei* Engl, 2012 on account of secondary homonymy with the type species of the genus. However, details of protoconch morphology were not provided and so a comparison with the characteristic protoconch of *Moelleriopsis* detailed by Warén (1992) is not possible. Further confirmation of this generic transfer is needed. The protoconch of *Mikro crassus* sp. nov. does not exhibit the spiral ribs and channelled suture distinctive of that of *Moelleriopsis*.

Genus *Parviturbo* Pilsbry & McGinty, 1945

Type species

Parviturbo rehderi Pilsbry & McGinty, 1945 (original designation), Recent, W Atlantic.

Parviturbo cicatricosus sp. nov.

[urn:lsid:zoobank.org:act:9128AAA8-ECB0-4E9B-8BD1-C6579D59DB86](https://zoobank.org/act:9128AAA8-ECB0-4E9B-8BD1-C6579D59DB86)

Figs 32B, 34

Diagnosis

Shell small, turbiniform, diameter up to 2.8 mm, whorls rounded; umbilicus moderately wide; sculpture of strong angular spiral cords (± 11 on final whorl) and distinct axial varices or growth scars; growth scars becoming more numerous in final quarter whorl; subperipheral cord level with insertion of outer lip; outer lip notched at ends of spiral cords; uniformly milky-white.

Etymology

From the Latin “*cicatrix*” – “a scar”, “*cicatricosus*” – “full of scars”; in reference to the frequent axial varices and growth flaws.

Material examined

Holotype

WALTERS SHOAL • empty shell; slopes, stn DW4879; 33°17' S, 43°52' E; depth 288–300 m; 1 May 2017; MNHN-IM-2000-35710.

Paratypes

WALTERS SHOAL – **slopes** • 1 empty shell; same collection data as for holotype; MNHN-IM-2000-35711 • 1 empty shell; stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN-IM-2000-35712 • 1 empty shell; stn DW4893; 33°16' S, 43°58' E; depth 623–629 m; 4 May 2017; MNHN-IM-2000-35713 • 1 empty shell; stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017; MNHN-IM-2000-35714.

Other material

WALTERS SHOAL – **slopes** • 2 empty shells; stn DW4880; 33°17' S, 43°51' E; depth 275–318 m; 1 May 2017; MNHN • 2 empty shells; stn DW4885; 33°17' S, 43°55' E; depth 272–380 m; 3 May 2017; MNHN • 1 empty shell; stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; MNHN.

Description

SHELL. Small (diameter up to 2.8 mm), turbiniform, wider than high, with rounded whorls and indented suture; periphery evenly rounded, close to mid-whorl; base rounded, with moderately wide umbilicus; teleoconch of up to 2.25 whorls. First teleoconch whorl initially with 3 spiral lirae and strong axial varix at about 0.25 whorls (Fig. 32B); lirae strengthen with growth to form angular cords; further axial varices

or scars occur, often at intervals of approx. 0.25 whorls, becoming more numerous in final quarter of last whorl (Fig. 34C); additional cord arises below adapical suture during second whorl, and a fifth emerges from abapical suture just prior to aperture, at whorl periphery; intervals between spiral cords with weak, close-set axial threads; base similarly sculptured with six cords, subperipheral one level with insertion of outer lip; umbilicus of moderate width, its margin evenly rounded, but narrowing rapidly and with steep sides after innermost basal cord. Aperture subcircular; peristome complete, somewhat flattened in parietal region; columella concave, at most slightly reflected; outer lip notched at ends of spiral cords; interior lacking conspicuous nacre.

PROTOCONCH (Fig. 32B). Glassy with faint corneous tinge; diameter $\pm 350 \mu\text{m}$, ca 1.25 whorls, apical bulb rounded; sculptured with distinct subspiral threads; terminal lip straight, slightly flaring.

COLOUR. Apical whorls translucent, becoming less so with growth; last adult whorl uniformly milky-white.

DIMENSIONS. Holotype, height 2.2 mm, diameter 2.7 mm; largest specimen, height 2.4 mm, diameter 2.8 mm.

OPERCULUM, RADULA AND EXTERNAL ANATOMY. Unknown.

Distribution

Known only from the slopes of Walters Shoal, at depths of 300–623 m; dredged on substrata of coarse sand with octocorals and solitary corals; living specimens unknown.

Remarks

Herbert (2015) referred three South African species to *Parviturbo* and two of these somewhat resemble *Parviturbo cicatricosus* sp. nov., namely *P. agulhasensis* (Thiele, 1925) and *P. alfredensis* (Bartsch, 1915), but both have fewer spiral cords than *P. cicatricosus* and are respectively smaller (diameter 1.8 mm) and larger (diameter 4.8 mm) than *P. cicatricosus*. The third species, *P. sola* (Barnard, 1963), has a much stronger axial sculpture.

In their global revision the genus, Rubio *et al.* (2015) recorded no species of *Parviturbo* from the tropical Indian Ocean, but described four new species from the tropical south-west Pacific. Of these, *P. pombali* Rubio, Rolán & Fernández-Garcés, 2015 from Vanuatu is perhaps the most similar to *P. cicatricosus* sp. nov., but *P. pombali* is smaller (diameter 1.08 mm), and has fewer spiral cords with stronger axial sculpture in their intervals. With respect to their sharp spiral cords and distinct protoconch sculpture, species of the *Parviturbo rehderi* Pilsbry & McGinty, 1945 group from the Caribbean also somewhat resemble *P. cicatricosus*, but these too are smaller and have fewer spiral cords. None of the described species of *Parviturbo* has the distinctive growth scars exhibited by *P. cicatricosus*.

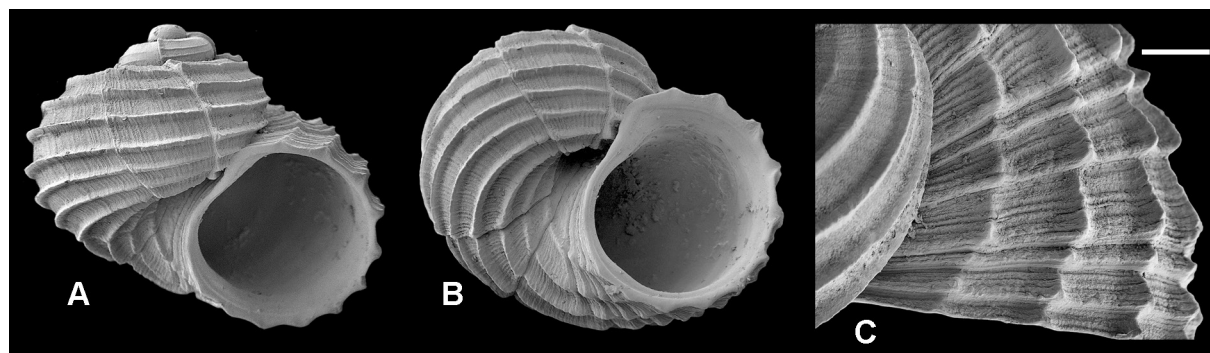


Fig. 34. *Parviturbo cicatricosus* sp. nov., holotype, diameter 2.7 mm (MNHN-IM-2000-35710). **A.** Apertural view. **B.** Oblique basal view. **C.** Strong axial growth flaps behind outer lip, scale bar = 200 μm .

Family Solariellidae Powell, 1951

Genus *Bathymophila* Dall, 1881

Type species

Margarita euspira var. *nitens* Dall, 1881 (monotypy), Recent, Atlantic.

Bathymophila williamsae sp. nov.

[urn:lsid:zoobank.org:act:8EA9EED9-2F46-4B59-BA24-3D8F24B511CC](https://doi.org/10.21203/rs.3.rs-3811111/v1)

Figs 35A–D, 36D–E

Diagnosis

Shell conispiral, wider than high, diameter up to 8.8 mm; spire prominent with shouldered whorls; periphery rounded, below mid-whorl; shell smooth except for coronations at shoulder angulation and spiral lirae on apical whorls; columella reflected and much thickened by deposition of callus, occluding umbilicus; callus lustreless and microscopically granular, lacking discrete swellings or bosses; shell greyish-white with translucent collabral bands.

Etymology

Named for Dr Suzanne T. Williams of the Natural History Museum, London, in recognition of her insightful contributions concerning vetigastropod systematics.

Material examined

Holotype

WALTERS SHOAL • living specimen; slopes, stn CP4918; 32°58' S, 43°27' E; depth 1295–1356 m; 14 May 2017; DNA tissue sample; MNHN-IM-2013-67177.

Paratypes

WALTERS SHOAL • 1 living specimen; south plain, stn CP4913; 33°52' S, 44°05' E; depth 1539–1615 m; 11 May 2017; DNA tissue sample; MNHN-IM-2013-67175 • 1 living specimen; same collection data as for preceding; DNA tissue sample; MNHN-IM-2013-6717 • 1 living specimen; slopes, stn CP4918; 32°58' S, 43°27' E; depth 1295–1356 m; 14 May 2017; DNA tissue sample; MNHN-IM-2013-67178 • 10 empty shells; slopes, stn CP4920; 32°52' S, 43°31' E; depth 1210–1293 m; 14 May 2017; MNHN-IM-2000-35715.

Other material

WALTERS SHOAL • 9 empty shells, juvenile; south plain, stn CP4913; 33°52' S, 44°05' E; depth 1539–1615 m; 11 May 2017; MNHN • 1 empty shell; slopes, stn CP4917; 32°55' S, 43°27' E; depth 1296–1375 m; 13 May 2017; MNHN.

Description

SHELL. Of moderate size for genus (diameter up to 8.8 mm), conispiral, wider than high ($H/D=0.81-0.85$); spire prominent, its whorls convex, but not strongly so, suture relatively shallowly indented; spire whorls shouldered, last adult whorl not so; periphery rounded, below mid-whorl; sculpture weak, shell essentially smooth and glossy save for coronations at shoulder angulation and spiral lirae on apical whorls; base weakly convex, umbilicus occluded by callus deposit; teleoconch of up to 4.75 whorls. First two teleoconch whorls with 6–7 relatively strong spiral lirae with close-set, microscopic axial pliculae in their intervals (Fig. 36D); uppermost lira delimiting distinct shoulder; spiral lirae weaken and become obsolete during third whorl (sometimes quite abruptly so), the shell becoming smooth

and glossy; shoulder angle remains, usually developing into raised subsutural cord with numerous low coronations; strength of cord and its coronations somewhat variable between specimens, very weak in some; cord wanes with growth and coronations usually absent on last adult whorl; the latter with only indistinct growth-lines that extend onto base, strengthening somewhat near umbilical callus; base otherwise smooth save for traces of indistinct spiral lirae; umbilicus lacking, occluded by columella callus even in subadults. Aperture subquadrate to roundly D-shaped; peristome interrupted in parietal region; columella concave, reflected and much thickened by deposition of callus so as to occlude umbilicus; callus lustreless and microscopically granular, lacking discrete swellings or bosses; outer lip thin and simple; interior nacreous, lacking labral ornamentation.

PROTOCONCH (Fig. 36E). Whitish, somewhat translucent; diameter $\pm 400 \mu\text{m}$, ca 1.25 whorls, apical beak lacking; surface texture finely granular with traces of widely spaced spiral threads; terminal lip straight, not thickened.

COLOUR. Greyish-white with translucent collabral bands when fresh, traces of pink/green iridescence evident; older, post-mortem specimens more opaque.

DIMENSIONS. Holotype, height 6.9 mm, diameter 8.5 mm; largest specimen, height 7.5 mm, diameter 8.8 mm.

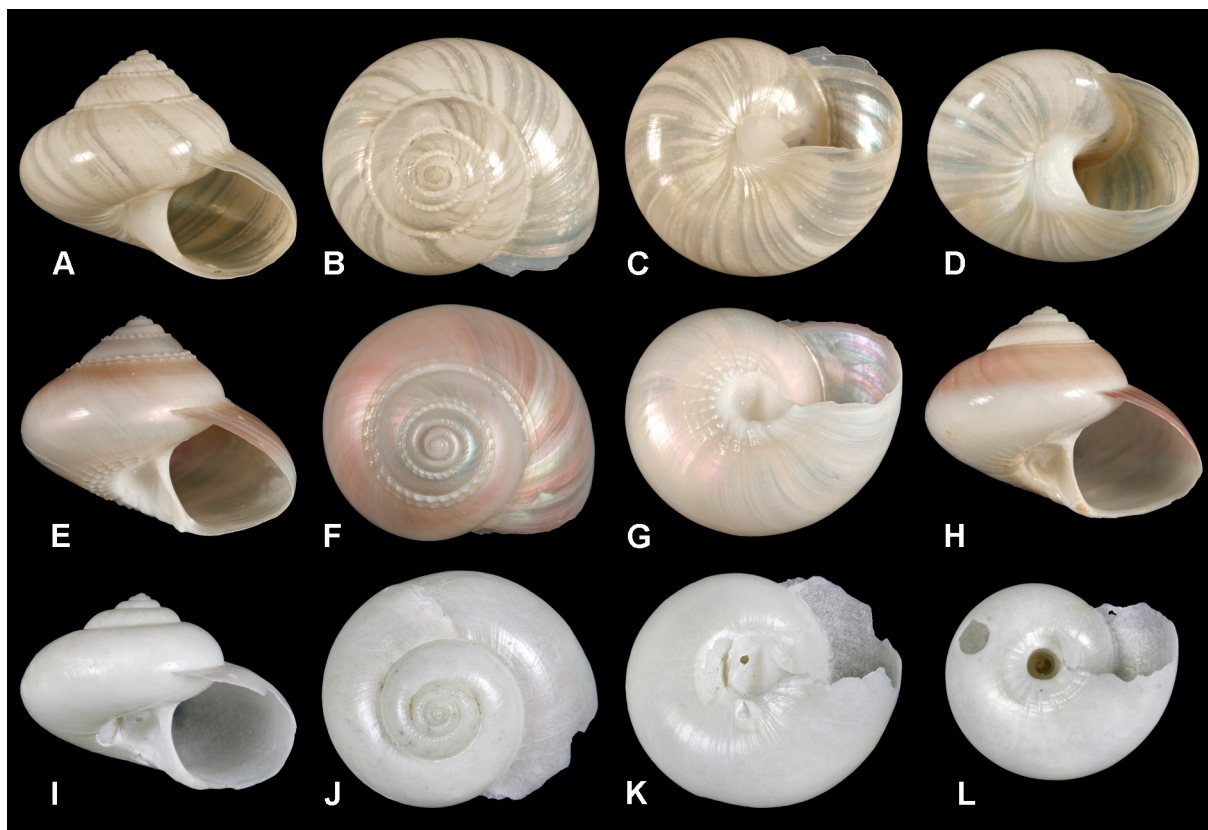


Fig. 35. A–D. *Bathymophila williamsae* sp. nov., holotype, diameter 8.5 mm (MNHN-IM-2013-67177). E–H. *Phragmomphalina vilvensi* Herbert & Williams, 2020. E–G. Walters Shoal, stn CP4907, diameter 14.7 mm (MNHN-IM-2013-67173). H. Large specimen with weak subsutural sculpture, Walters Shoal, stn CP4907, diameter 15.3 mm (MNHN). I–L. *Phragmomphalina candida* sp. nov. I–K. Holotype, diameter 12.8 mm (MNHN-IM-2000-35716). L. Subadult lacking umbilical septum, diameter 9.0 mm (paratype, MNHN-IM-2000-35718).

OPERCULUM. Corneous, pale straw-brown, multispiral with short growing edge.

RADULA AND EXTERNAL ANATOMY. Unknown.

Distribution

Known only from the slopes and surrounding plain of Walters Shoal, at depths of 1293–1539 m (live-taken material 1356–1539 m); obtained by beam trawl on fine sand with diverse echinoderms, cnidarians and crustaceans.

Remarks

The umbilicus is consistently occluded by callus in all adult and subadult specimens. A single juvenile of 3.5 teleoconch whorls retains a patent umbilicus, but this is already narrowed and partially occluded by the progressively thickened columella base.

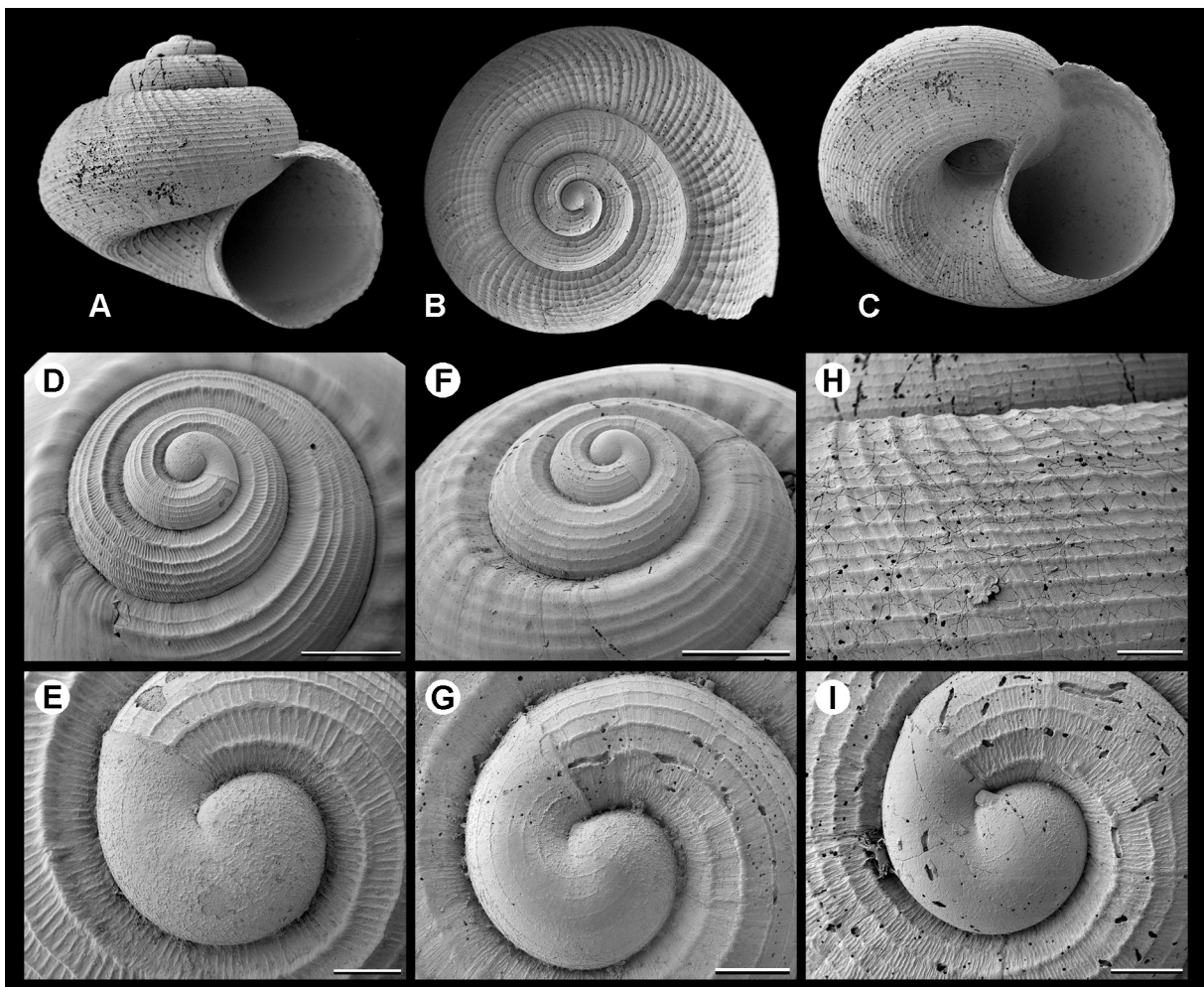


Fig. 36. A–C, H–I. *Solariella asaphea* sp. nov. A, C. Apertural and oblique basal views of holotype, diameter 4.1 mm (MNHN-IM-2000-35719). B. Apical view of paratype, diameter 3.3 mm (MNHN-IM-2000-35720). H. Subsutural sculpture, holotype. I. Protoconch (paratype, MNHN-IM-2000-35720). D–E. *Bathymophila williamsae* sp. nov., paratype (MNHN-IM-2013-67176). D. Oblique view of spire showing detail of apical sculpture. E. Sculptural detail of protoconch. F–G. *Phragmomphalina candida* sp. nov., paratype (MNHN-IM-2000-35718). F. Oblique view of spire showing sunken suture and detail of apical sculpture. G. Sculptural detail of protoconch. Scale bars: D, F=500 µm; E, G, I=100 µm; H=200 µm.

When compared with other Indo-West Pacific species of *Bathymophila*, *B. williamsae* sp. nov. is unusual in lacking one or more swellings or bosses on the basal portion of the columella callus. Most also have more flat-sided whorls. Some specimens of *B. gravida* Marshall, 1999, from off northern New Zealand, also have convex whorls, but that species attains a larger size (diameter up to 16 mm) and has nodular spiral cords around the umbilicus. The only other species of *Bathymophila* recorded from the south-western Indian Ocean, *B. stephanephoros* Vilvens, 2022 from the northern Mozambique Channel, is somewhat smaller (diameter < 6.3 mm), has a strongly coronated subsutural cord and bears two nodules on the umbilical callus. Preliminary analysis of CO1 sequence data indicates that samples of *B. williamsae* cluster as a well-defined monophyletic clade amongst other *Bathymophila* species (S.T. Williams pers. com. 2021).

Genus *Phragmomphalina* Herbert & Williams, 2020

Type species

Phragmomphalina vilvensi Herbert & Williams, 2020 (original designation), Recent, south-western Indian Ocean.

Phragmomphalina vilvensi Herbert & Williams, 2020

Fig. 35E–H

Phragmomphalina vilvensi Herbert & Williams in Williams *et al.*, 2020: 19, fig. 7a, d–f. Type loc.: east of Leven Bank (12°26' S, 48°13' E), off NW Madagascar, northern Mozambique Channel, depth 580 m.

Phragmomphalina vilvensi – Vilvens 2022: 56, fig. 8a–n.

Material examined

WALTERS SHOAL – slopes • 1 empty shell; stn DW4892; 33°12' S, 44°01' E; depth 624–646 m; 4 May 2017; MNHN • 1 empty shell; stn CP4901; 33°09' S, 44°01' E; depth 647–672 m; 6 May 2017; MNHN • 1 living specimen; stn CP4902; 33°08' S, 44°02' E; depth 700–711 m; 7 May 2017; DNA tissue sample; MNHN-IM-2013-67169 • 1 living specimen; stn CP4905; 33°32' S, 44°00' E; depth 1000–1052 m; 9 May 2017; DNA tissue sample; MNHN-IM-2013-67170 • 1 living specimen; stn CP4905; 33°32' S, 44°00' E; depth 1000–1052 m; 9 May 2017; DNA tissue sample; MNHN-IM-2013-67171 • 5 empty shells; stn CP4905; 33°32' S, 44°00' E; depth 1000–1052 m; 9 May 2017; MNHN • 1 living specimen; stn CP4906; 33°26' S, 44°00' E; depth 799–837 m; 9 May 2017; DNA tissue sample; MNHN-IM-2013-67172 • 16 empty shells; stn CP4906; 33°26' S, 44°00' E; depth 799–837 m; 9 May 2017; MNHN • 1 living specimen; stn CP4907; 33°27' S, 44°00' E; depth 880 m; 9 May 2017; DNA tissue sample; MNHN-IM-2013-67173 • 1 living specimen; stn CP4907; 33°27' S, 44°00' E; depth 880 m; 9 May 2017; DNA tissue sample; MNHN-IM-2013-67174 • 16 specimens, some living; stn CP4907; 33°27' S, 44°00' E; depth 880 m; 9 May 2017; MNHN • 20+ specimens, some living; stn CP4908; 33°29' S, 44°00' E; depth 900–950 m; 9 May 2017; MNHN • 2 specimens, living; stn CP4909; 32°45' S, 44°03' E; depth 987–989 m; 10 May 2017; MNHN • 20+ specimens, some living; stn CP4911; 32°46' S, 44°18' E; depth 964–965 m; 10 May 2017; MNHN • 8 specimens, some living; stn CP4912; 32°49' S, 44°23' E; depth 961–966 m; 10 May 2017; MNHN.

Distribution

Known from the northern Mozambique Channel, southern Madagascar and Walters Shoal. On Walters Shoal it has been found on the slopes at depths of 646–1000 m (live-taken material 711–1000 m); obtained mostly by beam trawl on substrata of coarse sand, solitary coral rubble and pteropod shell debris, with living hexacorals, octocorals, decapods, bivalves and echinoids.

Remarks

Specimens of *Phragmomphalina vilvensi* from Walters Shoal closely resemble those from off NW Madagascar. They differ in that the sculpture is somewhat weaker on the mid-spire whorls, particularly on the third whorl where the spiral lirae are finer and the subsutural pliculae not as strongly developed. Additionally, the whorl periphery is generally more rounded in material from Walters Shoal and there are fewer, coarser axial pliculae radiating around the umbilicus. However, these differences are slight and, since preliminary analysis of CO1 sequence data indicates that samples from Walters Shoal cluster amongst those from off NW Madagascar (S.T. Williams pers. com. 2021), evidently reflect geographic variation within a single species.

Virtually every stage in the development of the septum and closure of the umbilicus is present in this material, but there seems to be limited correlation between septum development and shell size, except that juveniles never have a septum. Large specimens of 4.5 whorls may retain a patent umbilicus with minimal septum development. It is unlikely that the species is sexually dimorphic in this regard since the great majority of adult and subadult specimens evince a degree of septum development. Similarly, there is no evidence that the umbilical cavity is used as a brooding chamber for developing embryos. The umbilicus itself is of more or less uniform size in all individuals, unlike the umbilically brooding species of *Cinysca* Kilburn, 1970 (Areneidae) in which the umbilicus of females is broader than that of males (pers. obs.). Furthermore, at full development the septum in species of *Phragmomphalina* completely closes the umbilicus and would need to be resorbed in order to release fully developed embryos.

Phragmomphalina candida sp. nov.

[urn:lsid:zoobank.org:act:B355BF8F-2C1E-4A84-888A-15FF66F50B88](https://zoobank.org/act:B355BF8F-2C1E-4A84-888A-15FF66F50B88)

Figs 35I–L, 36F–G

Diagnosis

Shell elevated-lenticular to subglobose, diameter up to 12.8 mm; whorls convex, lacking shoulder; suture somewhat sunken on second and third whorls; spire whorls with fine spiral lirae and third whorl with weak subsutural pliculae, but remainder of shell smooth and glossy; base umbilicate in juveniles and subadults, covered with thin septum in adults; columella with lustreless granular callus deposit; shell uniformly whitish, often with very faint pinkish wash on adapical surface.

Etymology

From the Latin “*candidus*” – “white”; in reference to the colour of the shell.

Material examined

Holotype

WALTERS SHOAL • empty shell; slopes, stn CP4902; 33°08' S, 44°02' E; depth 700–711 m; 7 May 2017; MNHN-IM-2000-35716.

Paratypes

WALTERS SHOAL – slopes • 1 empty shell; same collection data as for holotype; MNHN-IM-2000-35717 • 5 empty shells; stn DW4898; 33°09' S, 44°01' E; depth 652–668 m; 6 May 2017; MNHN-IM-2000-35718.

Other material

WALTERS SHOAL – slopes • 5 empty shells, juvenile; stn DW4898; 33°09' S, 44°01' E; depth 652–668 m; 6 May 2017; MNHN • 6 empty shells, juvenile; stn DW4899; 33°09' S, 44°02' E; depth 707–720 m; 6 May 2017; MNHN • 4 empty shells, juvenile; stn DW4900; 33°10' S, 44°01' E; depth 660–670 m; 6 May 2017; MNHN.

Description

SHELL. Moderate to relatively large (diameter up to 12.8 mm), elevated-lenticular to subglobose, diameter greater than height; spire prominent, with convex whorls and strongly indented suture; spire whorls lacking an obvious shoulder, but suture somewhat sunken (channelled), distinctly so on second and third whorls (Fig. 36F), less so with subsequent growth and not so on last adult whorl; periphery below mid-whorl, very slightly angled; sculpture weak, shell essentially smooth and glossy save for fine spiral lirae on early spire whorls and very weak subsutural pliculae on third whorl; base less convex, umbilicus closed by thin septum at maturity; teleoconch of up to 5.0 whorls. First teleoconch whorl with 5–7 low spiral lirae, increasing to 8–10 on third whorl through intercalation; no obvious shoulder present, but adapical region of whorl strongly convex and suture thus sunken; uppermost lira may lie atop subsutural convexity and appear as low subsutural cord; axial sculpture on these early whorls indistinct (at most close-set, microscopic threads), but low subsutural pliculae develop during third whorl resulting in weak beading below suture (Fig. 36F); spiral lirae evanesce toward end of third whorl and subsutural pliculae likewise weaken and become obsolete during fourth whorl; last adult whorl smooth and glossy with only microscopic growth-lines and indistinct traces of uneven spiral sculpture; base similarly smooth in adult, but with growth-lines strengthening somewhat toward and into umbilicus, juveniles usually with fine spiral lirae on base; umbilicus patent in juvenile and subadult specimens, steep-sided, with strong cord defining its margin; in large specimens this cord not rendered obviously plicate by growth-lines and base lacking additional peri-umbilical spiral cords; however, in some juveniles the peri-umbilical cord is beaded and there may be weak pliculae radiating from umbilicus with some additional indistinct peri-umbilical spiral sculpture. Aperture subquadrate to roundly D-shaped; peristome interrupted in parietal region; columella slightly oblique to shell axis, shallowly concave and covered with lustreless, granular callus deposit; in holotype callus spreading as thin septum over umbilicus (somewhat damaged or deformed); septum lustreless, but not obviously granular; junction of columella and basal lips rendered angular by peri-umbilical cord; outer lip thin and simple; interior nacreous, lacking labral ornamentation.

PROTOCONCH (Fig. 36G). Translucent milky-white; diameter 340–350 μm , ca 1.25 whorls, apical beak lacking; sculptured by 6–7 fine spiral threads; terminal lip straight, not thickened.

COLOUR. Shell uniformly whitish, often with very faint pinkish wash on adapical surface of last whorl of larger specimens. No living or freshly dead specimens available and any translucence or iridescence lost in samples examined.

DIMENSIONS. Holotype, height 9.2 mm, diameter 12.8 mm (= largest specimen).

OPERCULUM, RADULA AND EXTERNAL ANATOMY. Unknown.

Distribution

Known only from the slopes of Walters Shoal, at depths of 670–707 m; dredged on sandy substrata with solitary corals; living specimens unknown.

Remarks

The overall shell facies and the thin calcareous septum closing the adult umbilicus ally this species with *Phragmomphalina*. Although no undamaged adult specimens are available, the material examined clearly evinces consistent conchological characters that differentiate it from other species of *Phragmomphalina*. The co-occurring *P. vilvensi* differs in having well-developed, coronate subsutural sculpture and strongly plicate spiral cords around the umbilicus. In addition, *P. candida* sp. nov. has a less conical profile and more convex spire whorls with a slightly sunken suture.

In comparison with species of *Phragmomphalina* from elsewhere, *P. diadema* (Marshall, 1999), a species widespread in the south-western Pacific (Williams *et al.* 2013), possesses a distinctly nodular subsutural spiral cord and strong peri-umbilical spiral and axial sculpture, whereas *P. alabida* (Marshall, 1999), from off northern New Zealand, is smaller relative to the number of whorls (10.7 mm at 5 teleoconch whorls vs 12.8 mm at 5 teleoconch whorls) and more elevated. *Phragmomphalina tenuiseptum* (Marshall, 1999) from the Three Kings Rise, has a more similar shape and shares a sunken suture on the spire whorls, but it has rounded collabral axial folds on the spire whorls, as well as spiral threads and axial folds on the inner third of the base.

Solariella incisura Melvill, 1909 from the Saya de Malha Banks (265 m) has much stronger, more well-defined spiral lirae on the first two teleoconch whorls, its suture is not channelled on the mid-spire whorls, the umbilical rim is strongly angled and delineated by a beaded cord with strong radiating pliculae and the interior of the umbilicus bears distinct spiral lirae. The two syntypes (NHMUK 1910.3.17.8–9) are almost certainly juvenile, but specimens of *P. candida* sp. nov. of the same size have a weaker umbilical angle, lack radiating pliculae and the spiral sculpture within the umbilicus is scarcely evident. However, the similarity of the two species is sufficient to indicate that Melvill's taxon is also referable to *Phragmomphalina* rather than to *Solariella*.

Genus *Solariella* Wood, 1842

Type species

Solariella maculata Wood, 1842 (monotypy), Pliocene, England.

Remarks

This species belongs to the southern African radiation previously referred to the genus *Spectamen* Iredale, 1924. However, recent molecular data indicate that other species from this southern African radiation do not cluster with the Australian *Spectamen*, but cluster instead with *Solariella* (S.T. Williams pers. com. 2023). Thus, for the present, I refer this new species to *Solariella*.

Solariella asaphea sp. nov.

[urn:lsid:zoobank.org:act:BB1FF786-D3D4-4B52-9CB3-9E928D81A0ED](https://zoobank.org/act:BB1FF786-D3D4-4B52-9CB3-9E928D81A0ED)

Fig. 36A–C, H–I

Diagnosis

Shell thin, turbiniform, wider than high, diameter up to 4.1 mm; last adult whorl weakly angled at shoulder; base rounded with wide umbilicus; sculpture of fine, close-set, spiral lirae, ± 15 at end of penultimate whorl; first 1.5 whorls with fine, close-set, axial threads with close-set, collabral pliculae developing thereafter; base with similar spiral lirae; uniformly whitish.

Etymology

From the Greek “*asaphes*” (ασαφες) – “indistinct, unclear”; in reference to the rather nondescript features of the shell.

Material examined

Holotype

WALTERS SHOAL • empty shell; slopes, stn DW4900; 33°10' S, 44°01' E; depth 660–670 m; 6 May 2017; MNHN-IM-2000-35719.

Paratypes

WALTERS SHOAL – **slopes** • 1 empty shell; same collection data as for holotype; MNHN-IM-2000-35720 • 4 empty shells; stn DW4898; 33°09' S, 44°01' E; depth 652–668 m; 6 May 2017; MNHN-IM-2000-35721.

Other material

WALTERS SHOAL – **slopes** • 2 empty shells; stn DW4899; 33°09' S, 44°02' E; depth 707–720 m; 6 May 2017; MNHN.

Description

SHELL. Small (diameter up to 4.1 mm), thin, turbiniform, wider than high; spire whorls rounded and suture strongly indented; last adult whorl weakly angled at shoulder and periphery; periphery below mid-whorl; base rounded, with wide umbilicus; teleoconch of up to 3.5 whorls. First teleoconch whorl with ± 7 spiral lirae, increasing to ± 15 at end of penultimate whorl; lirae remain fine and close-set; axial sculpture comprising numerous fine, close-set threads on first 1.5 whorls, with fine regular, collabral pliculae developing thereafter; pliculae and lirae subequal, rendering adapical sculpture finely reticulate (Fig. 36B, H); base with similar spiral lirae, though somewhat finer and more close-set, except near umbilicus; pliculae weaken below periphery, becoming little more than fine growth-lines; margin of umbilicus evenly rounded, but spiral lirae slightly stronger and more widely spaced around and into umbilicus. Aperture subcircular; peristome interrupted in parietal region; columella concave, not thickened or reflected; outer lip thin; interior lacking conspicuous nacre, but no fresh specimens available.

PROTOCONCH (Fig. 36I). Translucent white; diameter ± 360 μm , ca 1.25 whorls, apical beak lacking; mostly smooth, but with traces of fine granulation and widely spaced spiral threads; terminal lip straight, not thickened.

COLOUR. Shell uniformly white to cream-white throughout.

DIMENSIONS. Holotype, height 3.4 mm, diameter 4.1 mm (= largest specimen).

OPERCULUM, RADULA AND EXTERNAL ANATOMY. Unknown.

Distribution

Known only from the slopes of Walters Shoal, at depths of 668–707 m; dredged on substrata of coarse sand with solitary corals; living specimens unknown.

Remarks

Solariella asaphea sp. nov. is superficially similar to three South African species, namely '*Spectamen*' *martensi* Herbert, 2015, '*Sp.*' *multistriatum* (Thiele, 1925) and '*Sp.*' *sulculiferum* Herbert, 1987. However, both '*Sp.*' *martensi* and '*Sp.*' *multistriatum* have a much larger protoconch (diameter > 600 μm) and '*Sp.*' *sulculiferum* is considerably larger (diameter 6.4 mm), has more strongly shouldered whorls and a distinct peri-umbilical angle delineated by a beaded cord (Herbert 1987b).

Two poorly known taxa from 400 m on the Sapmer Bank Seamount, namely '*Solariella*' *dowi* Barnard, 1963 and '*Solariella*' *palirrous* Barnard, 1963, also resemble the present species, but both attain a larger size (diameter 8.5 mm and 6.0 mm respectively). In addition, '*S.*' *dowi* develops two stronger lirae at the end of the third whorl, one below the suture and the other at the shoulder, the former nodular. '*S.*' *palirrous* has less numerous spiral lirae, a tabulate subsutural zone with retractive pliculae and a narrow umbilicus.

Family Trochidae Rafinesque, 1815
Subfamily Cantharidinae Gray, 1857

Genus *Gibbula* Risso, 1826

Type species

Trochus magus Linnaeus, 1758 (subsequent designation, Herrmannsen 1847: 473), Recent, NE Atlantic and Mediterranean.

Remarks

Gibbula s. lat. has been shown to be a paraphyletic taxon (Uribe *et al.* 2016; Affenzeller *et al.* 2017) and it is unlikely that the species described below and the South African species of ‘*Gibbula*’, to which it is undoubtedly related, in fact belong to *Gibbula* s. str. This is a matter undergoing further investigation and the referral of this new taxon to *Gibbula* is a temporary measure.

‘*Gibbula*’ *roseosticta* sp. nov.

[urn:lsid:zoobank.org:act:CE42EB1E-A3B2-4E3A-A4BE-134C435E2E51](https://zoobank.org/urn:lsid:zoobank.org:act:CE42EB1E-A3B2-4E3A-A4BE-134C435E2E51)

Fig. 37

Diagnosis

Shell trochoid-turbiniform, diameter up to 3.7 mm, height \approx diameter; spire conical with angular periphery; base narrowly umbilicate; penultimate and last whorls with three spiral cords, the uppermost weakest, peripheral one strongest; cord intervals with fine, close-set, axial pliculae; apex whitish, spiral cords on second whorl deep rose-pink, colour pattern subsequently fragmented into dashes and blotches of deep rose-pink on whitish ground; cord intervals washed with pale orange-brown.

Etymology

From the Latin “*roseus*” – “rose-coloured” and the Greek “*stiktos*” (*στικτος*) – “spotted”; in reference to the pattern of deep pink spots on the shell.

Material examined

Holotype

WALTERS SHOAL • empty shell; summit area, south-west, stn WS03; 33°12.2' S, 43°50.8' E; depth 40 m; 30 Apr. 2017; MNHN-IM-2000-35722.

Paratypes

WALTERS SHOAL • 3 empty shells; same collection data as for holotype; MNHN-IM-2000-35723 • 7 empty shells; summit area, south, stn WS06; 33°15.1' S, 43°54.5' E; depth 26 m; 1 May 2017; MNHN-IM-2000-35724 • 12 empty shells; summit area, south-east, stn WS08; 33°13.7' S, 43°55.9' E; depth 30–33 m; 3 May 2017; MNHN-IM-2000-35725.

Other material

WALTERS SHOAL • 6 empty shells; summit area, south-west, stn WS03; 33°12.2' S, 43°50.8' E; depth 40 m; 30 Apr. 2017; MNHN • 3 empty shells; summit area, south-west, stn WS04; 33°12.2' S, 43°50.8' E; depth 40 m; 30 Apr. 2017; MNHN • 8 empty shells; summit area, south, stn WS07; 33°15.4' S, 43°52.2' E; depth 30–33 m; 2 May 2017; MNHN • 1 empty shell; summit area, south, stn WB05; 33°15.1' S, 43°54.5' E; depth 26–30 m; 1 May 2017; MNHN • 1 empty shell; summit area, north-west, stn WB09; 33°13.8' S, 43°55.8' E; depth 27–30 m; 4 May 2017; MNHN.

Description

SHELL. Small (diameter up to 3.7 mm), trochoid-turbiniform, height and diameter more or less equal; spire conical with angular periphery; suture shallowly indented; sculpture dominated by strong spiral cords; base narrowly umbilicate; teleoconch of up to 4.5 whorls. First teleoconch whorl with three spiral cords, one peripheral, level with or just above abapical suture, another below adapical suture, and third midway between these; cords strengthen during second and subsequent whorls, particularly middle and peripheral cords; occasional specimens with a fourth, weaker spiral cord above peripheral one on second whorl, but this subsequently evanescent; penultimate and last whorls with three spiral cords, uppermost weakest, sometimes noticeably so, peripheral one strongest; slight thickening immediately below suture may appear as fourth spiral, often enhanced by colour pattern. Microsculpture comprising extremely fine, close-set, axial pliculae, first appearing near beginning of third whorl (Fig. 37E); pliculae most obvious in cord intervals, but also cross cords when unworn; peripheral cord usually with a number of finer spiral lirae, traces of such lirae occasionally also on mid-whorl cord. Base with 5–8 low spiral cords, progressively finer and more close-set toward umbilicus; microsculpture as above; umbilicus open, but relatively narrow and steep-sided, partly obscured by upper part of columella, more so when adult. Aperture roundly quadrate, columella slightly oblique to shell axis, somewhat thickened and reflected; outer lip lacking denticles; interior nacreous.

PROTOCONCH (Fig. 37F). Somewhat worn in all available specimens; comprising approx. 1.25 whorls, diameter 240–280 μm ; apex weakly beaked; terminal lip more or less straight, lacking varix; surface smooth, no superficial microsculpture evident even in freshest juveniles.

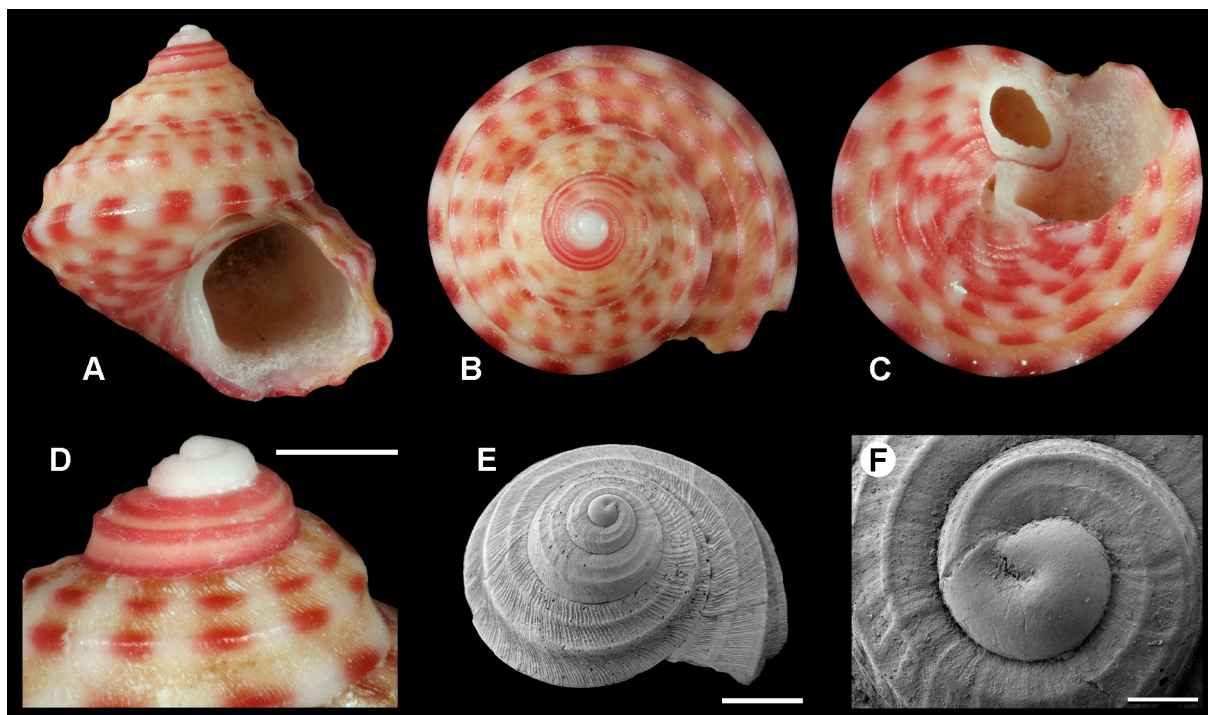


Fig. 37. *Gibbula roseosticta* sp. nov. A–C. Holotype, diameter 3.7 mm (MNHN-IM-2000-35722). D. Spire whorls showing white apex and deep rose-pink spiral cords on second whorl (paratype, MNHN-IM-2000-35724). E. Oblique apical view showing spirally corded early whorls with fine axial pliculae developing near start of third teleoconch whorl (paratype, MNHN-IM-2000-35723). F. Protoconch, sculptural details, if any, eroded (paratype, MNHN-IM-2000-35723). Scale bars: D–E=0.5 mm; F=100 μm .

COLOUR. Protoconch and early part of first teleoconch whorl milky-white; spiral cords subsequently becoming deep rose-pink, conspicuous on second whorl; on third whorl spiral colour pattern becomes fragmented into dashes and subsequently blotches of deep rose-pink on whitish ground; line of such blotches also present below adapical suture, seeming to delineate weak subsutural cord; cord intervals washed with pale orange-brown when fresh. Base with similar colour pattern, blotches tending to merge into axial bands around umbilicus in adults; umbilicus itself white.

DIMENSIONS. Holotype, height 3.7 mm, diameter 3.7 mm (= largest specimen).

OPERCULUM, RADULA AND EXTERNAL ANATOMY. Unknown.

Distribution

Known only from the summit area of Walters Shoal, at depths of 26–40 m; habitat dominated by encrusting coralline algae; collected by brushing and suction sampling; living specimens unknown.

Remarks

This species is clearly allied to the South African ‘*Gibbula*’ radiation, in particular to ‘*Gibbula*’ *multicolor* (Krauss, 1848), which it resembles in both shape and sculpture. That species, however, has a less conical profile, attains a considerably larger size (diameter up to 8.0 mm) and has fine spiral lirae in the cord intervals. It also commonly has blue/green dots and the colour pattern on the apical surface comprises zig-zag axial bands or flames rather than spots aligned in spiral rows. The present species also has a more consistent colour pattern on the second teleoconch whorl, comprising distinctive deep rose-pink spiral lines. In this respect it resembles ‘*G.*’ *zonata* (Wood, 1828) from the west coast of South Africa, but in that species the spiral lines are greyish-purple and do not become fragmented on later whorls. ‘*Gibbula*’ *zonata* also has a less angular periphery, more distinct spiral microsculpture and lacks an umbilicus in the adult.

The occurrence of the South African species *Sinezona insignis* and *Vaceuchelus gemmula* on Walters Shoal are further examples demonstrating an affinity between the summit area fauna of Walters Shoal and the shallow, warm-temperate South African marine fauna. Further examples are evident in the Columbelloidea and Muricidae (respectively Monsecour and Houart pers. com. 2021).

Subfamily Kaiparathininae Marshall, 1993

Genus *Kaiparathina* Laws, 1941

Type species

Kaiparathina praecellens Laws, 1941 (original designation), Miocene, New Zealand.

Kaiparathina monticola sp. nov.

[urn:lsid:zoobank.org:act:C4A503AD-4E0D-4DF7-8A82-ECF326086C36](https://doi.org/10.21203/rs.3.rs-3811111/v1)

Figs 38C–E, 39–40

Diagnosis

Shell elevated-turbiniform, height up to 8.0 mm; whorls strongly convex, periphery often weakly angular, well below mid-whorl; early teleoconch whorls with fine, close-set, spiral threads, but shell smooth and glossy thereafter; anomphalous; 1–3 indistinct spiral cords adjacent to umbilical region; columella noticeably thickened, reflected over umbilical region; shell pale corneous brown, variously marked with white blotches often in two spiral bands, occasionally merging into zig-zag axial flames; protoconch white, its tip sometimes tinged maroon.

Etymology

From the Latin “*mons*” – “a mountain” and “*-cola*” – “a dweller”; reflecting the seamount habitat of the species.

Material examined**Holotype**

WALTERS SHOAL • living specimen; slopes, stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017; DNA tissue sample, photo alive (Fig. 38C–E); MNHN-IM-2013-67168.

Paratypes

WALTERS SHOAL – **slopes** • 1 living specimen; same collection data as for holotype; DNA tissue sample; MNHN-IM-2013-67167 • 4 specimens, living; same collection data as for holotype; MNHN-IM-2000-35726 • 1 living specimen; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; DNA tissue sample; MNHN-IM-2013-67258 • 1 living specimen; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; DNA tissue sample; MNHN-IM-2013-67259 • 1 living specimen; stn DW4897; 33°09' S, 43°59' E; depth 490–584 m; 5 May 2017; DNA tissue sample; MNHN-IM-2013-67260 • 5 specimens, living; stn DW4897; 33°09' S, 43°59' E; depth 490–584 m; 5 May 2017; radula SEM prep.; MNHN-IM-2000-35727 • 2 specimens, living; stn DW4898; 33°09' S, 44°01' E; depth 652–668 m; 6 May 2017; MNHN-IM-2000-35728.

Other material

WALTERS SHOAL – **slopes** • 40+ empty shells; same collection data as for holotype; MNHN • 1 empty shell; stn DW4885; 33°17' S, 43°55' E; depth 272–380 m; 3 May 2017; MNHN • 6 empty shells; stn DW4886; 33°17' S, 43°56' E; depth 573–582 m; 3 May 2017; MNHN • 2 empty shells; stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; MNHN • 11 empty shells; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; MNHN • 15 empty shells; stn DW4897; 33°09' S, 43°59' E; depth 490–584 m; 5 May 2017; MNHN.

Description

SHELL. Relatively large for the genus (height up to 8.0 mm), elevated-turbiniiform, slightly higher than wide; spire prominent with strongly convex whorls; periphery often weakly angular, well below mid-whorl; suture distinctly indented; sculpture weak, shell essentially smooth and glossy; base less strongly convex, umbilicus lacking; teleoconch of up to 5.0 whorls. First two teleoconch whorls with pair of fine, close-set, spiral threads midway between sutures (Fig. 40A), second weaker pair below this, lower one of which close to or level with abapical suture; upper pair each developing shallow adapical groove during second whorl; spiral sculpture evanescent near start of third whorl and later whorls with at most traces of spiral sculpture, though in live-taken specimens spiral patterning in underlying nacre visible by transparency; axial sculpture of weak growth-lines and close-set, microscopic, collabral threads; juvenile and subadult shells with more angular periphery, delineated by low spiral cord; insertion of suture level with cord; cord weak or absent on much of last whorl in adult specimens; base sculptured as above, often with 1–3 indistinct spiral cords adjacent to umbilical region; growth-lines sigmoidal below periphery and somewhat stronger medially; umbilicus lacking. Aperture subcircular; columella noticeably thickened, reflected over umbilical region; outer lip thin, concave below periphery, convex near columella, basal lip thus sinuous; interior nacreous, lacking labral ornamentation.

PROTOCONCH (Fig. 40A–B). Globose, somewhat elevated, comprising approx. 1.25 whorls, diameter 350–375 µm; tip of apex roundly angled, terminal lip convex, lacking terminal or subterminal varix; surface smooth save for three fine, widely spaced, subspiral threads, lowest one close to abapical suture, a fourth one delineating tip of apex.

COLOUR. Protoconch white, its tip sometimes tinged maroon; teleoconch with pale corneous brown ground colour, translucent in live-taken specimens, with pink/green iridescence of underlying nacre showing through. Colour pattern variable; commonly with two spiral rows of white blotches (Fig. 39C), one at periphery, the other between this and adapical suture, sometimes a third row near middle of base;

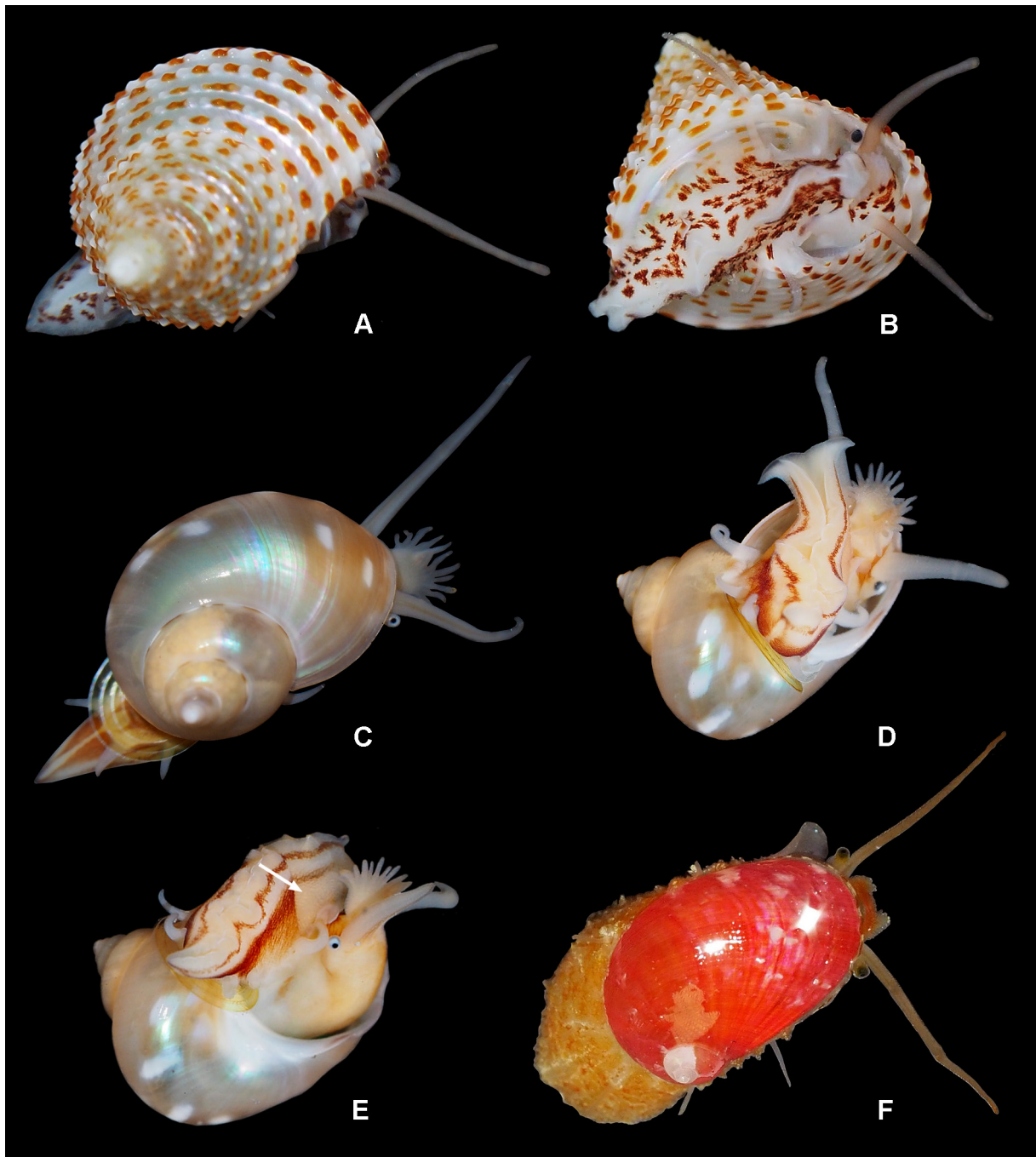


Fig. 38. A–B. *Calliostoma pantopunctatum* sp. nov., holotype, living animal, shell diameter 5.8 mm (MNHN-IM-2013-67275). C–E. *Kaiparathina monticola* sp. nov., holotype, living animal, anterolateral structure arrowed, shell diameter 6.8 mm (MNHN-IM-2013-67168). F. *Stomatella multilirata* sp. nov., Walters Shoal, stn WS03, greatest shell dimension 6.0 mm (MNHN). Images courtesy of Alain Barrère/MNHN.

intervals between white blotches somewhat darker brown, particularly at periphery, on spire whorls this creates a thin supra-sutural line of alternating white/brown dashes; often also with thin subsutural white line; columella and medial area of base white; variation in white and brown markings considerable, the latter sometimes merging into zig-zag axial flames (Fig. 39B); some specimens with broad whitish subsutural band, others with only alternating light and dark peripheral blotches or with blotches absent on spire whorls or present only on spire whorls.

DIMENSIONS. Holotype, height 6.9 mm, diameter 6.8 mm; largest specimen, height 8.0 mm, diameter 7.6 mm.

OPERCULUM. Corneous, thin, light yellowish-brown, tightly multispiral with a short growing margin.

JAW (Fig. 40D–E). Oval-quadrate, lateral portions rounded and dipping anteriorly, posterior edge thus weakly convex and anterior edge weakly concave; surface composed of minute, elongate hexagonal units (occasionally pentagonal).

RADULA (Fig. 40F–G). Formula $\infty+7+1+7+\infty$, with ± 35 transverse rows of teeth; rachidian tooth very large and robust, its cusp basally trigonal but with convex sides; cutting edge dominated by large, narrowly pointed central denticle; basal part of cusp with finer lateral denticles; anterior margin of cusp concave, abutting convex posterior edge of base-plate of next anterior tooth. Lateral teeth slender, scythe-like, cusp elongate and slightly curved, its outer base flanged and bearing small denticles; shaft

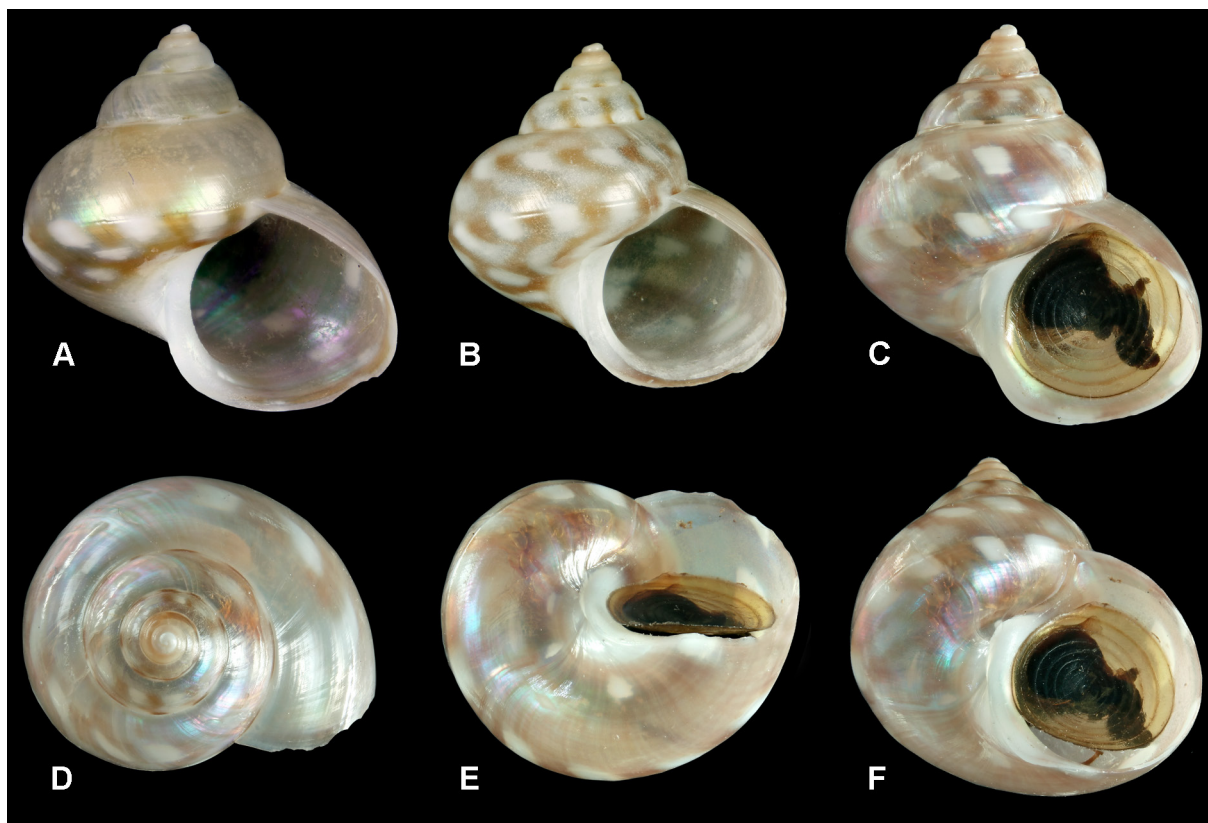


Fig. 39. *Kaiparathina monticola* sp. nov. **A.** Holotype, diameter 6.8 mm (MNHN-IM-2013-67168). **B.** Specimen with zig-zag colour pattern, diameter 6.0 mm (paratype, MNHN-IM-2000-35726). **C–F.** Live-taken specimen with blotched colour pattern, diameter 6.4 mm (paratype, MNHN-IM-2000-35727).

face with thickened pilaster; laterals 3–5 largest. Marginal teeth numerous, progressively reducing in size toward edge of radula, shafts of all but innermost one seemingly fused; cusps of inner marginals narrowly spatulate, outer edge minutely denticulate.

EXTERNAL ANATOMY (Fig. 38C–E). As described for *Kaiparathina boucheti* (Marshall 1993). Animal for the most part milky-white; head and neck tinged with pale apricot-orange; cephalic tentacles well developed, micro-papillate and with a faint orange-brown mid-dorsal line; eyes prominent, pigmented and with open aperture; anterolateral structures pale, coarsely pustulose (arrowed in Fig. 38E), lying beneath non-digitate neck lobes; three unpigmented, micro-papillate epipodial tentacles on each side, each with basal epipodial sense organ; sides of foot beneath epipodium orange-brown, colour progressively deepening ventrally, but then ceasing abruptly, lower portion comprising uniformly pale band, encircled by thinner orange-brown band (evanescent prior to propodial horns) and finally pale

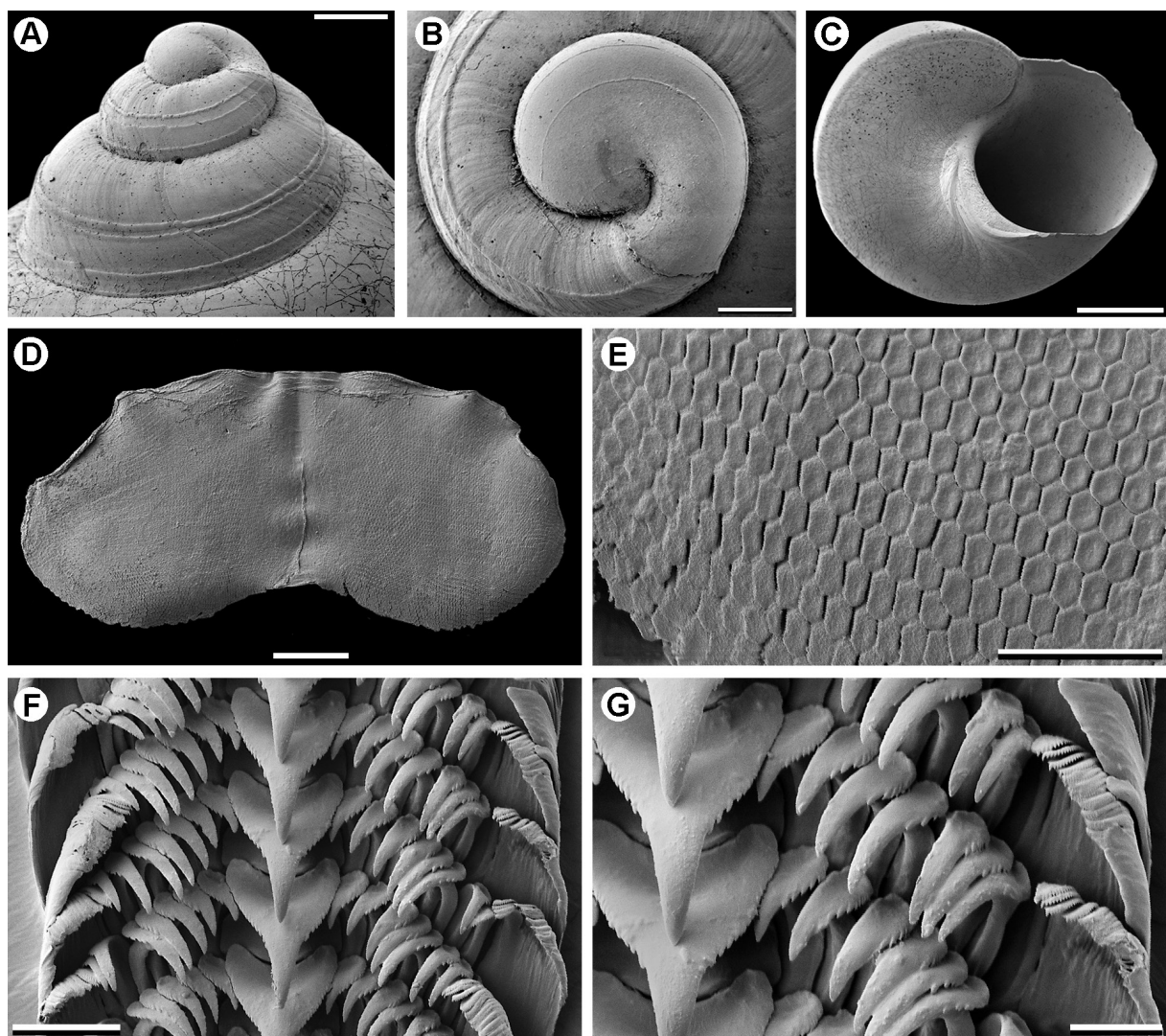


Fig. 40. *Kaiparathina monticola* sp. nov. A–C. Paratypes (MNHN-IM-2000-35726). A. Oblique view of apex. B. Sculptural detail of protoconch. C. Basal view of juvenile showing lack of spiral lirae. D–G. Jaw and radula (paratype, MNHN-IM-2013-67260). D. Ventral (inner) surface of jaw, anterior edge below. E. Detail of jaw structure. F. Radula, entire width. G. Radula, detail of rachidian, lateral and inner marginal teeth. Scale bars: A, D=200 μ m; B, F=100 μ m; C=1.0 mm; E, G=50 μ m.

peripodial fringe; colour pattern continues onto metapodium, which has white mid-line band at extreme posterior (Fig. 38C).

Distribution

Known only from the slopes of Walters Shoal, at depths of 380–652 m (live-taken material 382–652 m); dredged on substrata of coarse sand and fine gravel, with ophiuroids and solitary corals.

Remarks

In terms of its relatively large size, *Kaiparathina monticola* sp. nov. resembles *K. coriolis* Marshall, 1993 and *K. boucheti* Marshall, 1993, both from the New Caledonian region. *Kaiparathina coriolis* has more strongly convex spire whorls, retains an umbilical chink at maturity and has a different coloration. In addition, the terminal cusp of the rachidian tooth is proportionately much smaller than it is in *K. monticola*. *Kaiparathina boucheti* has stronger spiral sculpture on the apical whorls, is more uniform in colour and has a reddish-brown protoconch; the rachidian tooth also has a more distinctly triangular cusp. Perhaps the most similar species is *K. daedala* Marshall, 1993 from off Réunion and this is also the species most geographically proximate to Walters Shoal. Like the present species, *K. daedala* has a narrow supra-sutural band of reddish-brown marks (also present in *K. coriolis*) and a narrow white subsutural line. Elsewhere, the colour pattern in the only two available specimens is variable (Marshall 1993), but neither exhibit the spiral lines of white spots or zig-zag brown axial flames commonly seen in *K. monticola*. In addition, a distinctive feature of *K. daedala* is the presence of numerous spiral threads on the inner two-thirds of the base. Specimens of *K. monticola* of a similar size (4–5 mm) may have 1–2 such spiral threads, but in most individuals they are absent (Fig. 40C). The radula described for *K. daedala* has only five pairs of lateral teeth in each row (vs seven in *K. monticola*), but this difference is undoubtedly size-related and reflects the fact that the type material of *K. daedala* was probably subadult, the number of lateral teeth increasing progressively through in-column transformation of marginal teeth during ontogeny (Marshall 1993). There are, nonetheless, differences in the shape of the radula teeth, the terminal denticle of the rachidian and lateral teeth being proportionately longer in *K. monticola*, whereas the subterminal denticles on these teeth are coarser and more distinct in *K. daedala*. Furthermore, in *K. monticola* the cusp of the rachidian is laterally more convex at its base than the more evenly trigonal rachidian cusp of *K. daedala*. Although likely to be closely related to *K. daedala*, these differences in coloration, basal sculpture and radula tooth morphology justify the separation of the present material as a distinct species.

The shell of *K. monticola* sp. nov. superficially resembles that of some brown-spotted species of *Bathymophila* (Williams *et al.* 2020: fig. 7g), which Williams *et al.* (2022) have shown belong to an undescribed *Bathymophila*-like genus. These differ from *K. monticola* in having a patent umbilicus with a heavy flange around the umbilicus, and a less acutely pointed apex.

Mention should also be made of *Cantharidus nolfi* Poppe, Tagaro & Dekker, 2006 from the Philippines. Although not known anatomically, I believe the shell of this species exhibits all the features characteristic of *Kaiparathina* and I propose that it be transferred thereto. It is of similar size as *K. monticola* sp. nov., but differs in having a colour pattern that typically includes fine, close-set and strongly oblique gold or brown lines.

Subfamily Stomatellinae Gray, 1840

Genus *Stomatella* Lamarck, 1816

Type species

Stomatella auricula Lamarck, 1816 (subsequent designation, Anton 1838: 32), Recent, Indo-West Pacific.

Stomatella auricula Lamarck, 1816

Fig. 41A–C

Stomatella auricula Lamarck, 1816: pl. 450 fig. 1a–b. Type loc.: not originally cited, but later given as “l’Océan des Moluques et de la Nouvelle-Hollande” (Lamarck 1822: 210).

Stomatella auricula – Herbert 2015: 61 (further synonymy and chresonymy).

Material examined

WALTERS SHOAL • 1 empty shell; slopes, stn DW4887; 33°17' S, 43°57' E; depth 599–640 m; 3 May 2017; MNHN.

Remarks

This specimen is quite distinct from the material described below. The rate of expansion of the generating curve is less rapid and the profile of the shell in apical view is thus less elongate and the spire is proportionately larger. It differs further in that the spiral sculpture is much weaker, comprising only relatively widely-spaced, microscopic, incised striae on the apical surface, though these are stronger at the periphery and on the base. It is much closer to *Stomatella auricula*, a shallow-water species common in the tropical south-western Indian Ocean (Herbert 2015), and I identify it as such. It is, however, difficult to explain the occurrence of a single, relatively fresh, shell in comparatively deep water on Walters Shoal, when it is evidently absent on the summit region. It seems likely to stem from stochastic colonisation by isolated individuals, this shell having been transported post-mortem down-slope.

Stomatella multilirata sp. nov.

[urn:lsid:zoobank.org:act:C53FAA23-F8D5-4AFC-853A-4C7CCD3D453E](https://doi.org/10.3896/BI.2024.923.1.1)

Figs 38F, 41D–I, 42–43

Diagnosis

Shell depressed auriform, maximum dimension up to 11 mm; last adult whorl expanding very rapidly and aperture greatly enlarged; sculpture of numerous fine, close-set, spiral lirae, alternating in strength as intermediaries arise; axial sculpture of weak collabral growth-lines, stronger on last half-whorl rendering sculpture weakly and irregularly decussate; apex whitish, remaining shell predominantly crimson, sometimes with an orange tint, variously patterned with paler axial flames or whitish flecks and tent-like markings.

Etymology

From the Latin “*multus*” – “much or many” and “*lira, lirata*” – “a ridge, ridged”; in reference to the sculpture of many fine spiral ridges.

Material examined**Holotype**

WALTERS SHOAL • living specimen; summit area, south-west, stn WS03; 33°12.2' S, 43°50.8' E; depth 40 m; 30 Apr. 2017; DNA tissue sample; MNHN-IM-2013-67246.

Paratypes

WALTERS SHOAL • 1 living specimen; same collection data as for holotype; DNA tissue sample; MNHN-IM-2013-67245 • 1 living specimen; same collection data as for holotype; DNA tissue sample; MNHN-IM-2013-67293 • 1 living specimen; summit area, south-west, stn WR01; 33°12.2' S, 43°50.8' E; depth 36 m; 30 Apr. 2017; DNA tissue sample; MNHN-IM-2013-67244 • 12 specimens, some living; summit area, south, stn WB05; 33°15.1' S, 43°54.5' E; depth 26–30 m; 1 May 2017; radula SEM prep.; MNHN-IM-2000-35729 • 4 specimens, living; summit area, south-east, stn WS08; 33°13.7' S, 43°55.9' E; depth 30–33 m; 3 May 2017; MNHN-IM-2000-35730 • 1 living specimen; summit area, north-west, stn WB10; 33°09.1' S, 43°51.8' E; depth 30 m; 6 May 2017; DNA tissue sample; MNHN-IM-2013-67247.

Other material

WALTERS SHOAL • 30+ specimens, some living; same collection data as for holotype; photographed alive; MNHN • 1 living specimen; summit area, south-west, stn WR02; 33°12.2' S, 43°50.8' E; depth 40 m; 30 Apr. 2017; MNHN • 30+ specimens, some living; summit area, south-west, stn WS04; 33°12.2' S, 43°50.8' E; depth 40 m; 30 Apr. 2017; MNHN • 50+ empty shells; summit area, south, stn WS06; 33°15.1' S, 43°54.5' E; depth 26 m; 1 May 2017; MNHN • 50+ empty shells; summit area, south, stn WS07; 33°15.4' S, 43°52.2' E; depth 30–33 m; 2 May 2017; MNHN • 30+ empty shells;

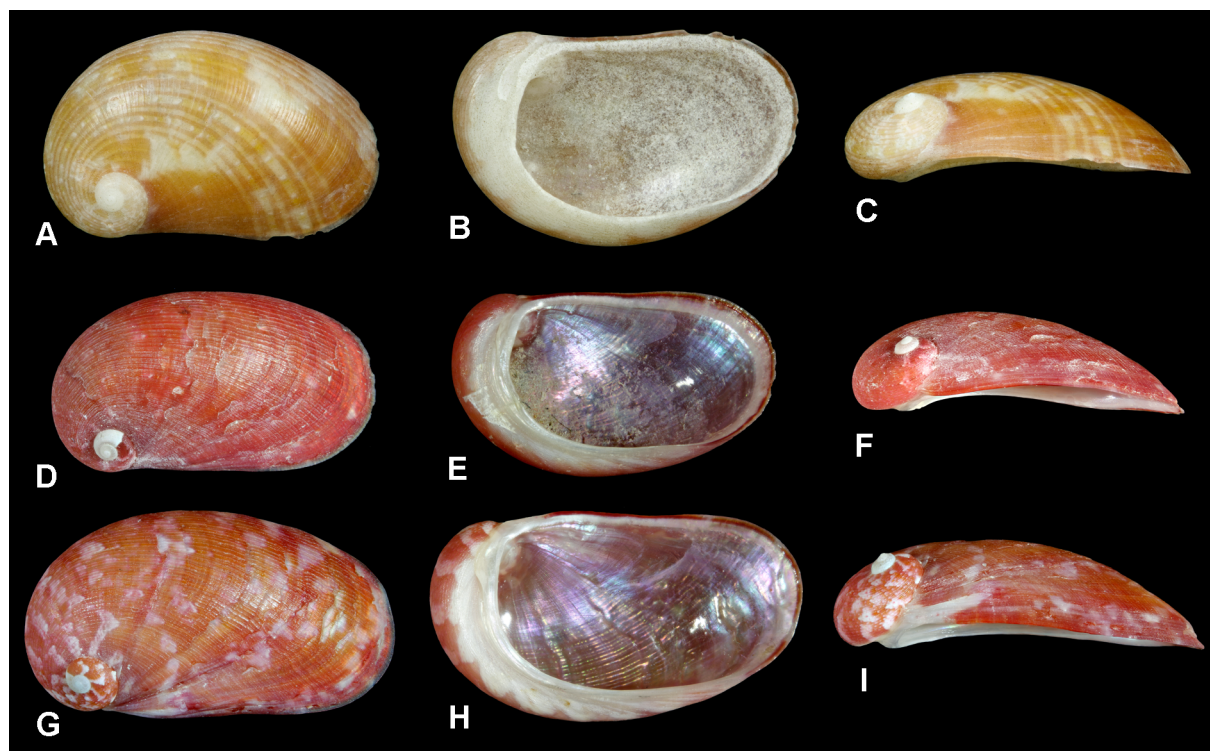


Fig. 41. A–C. *Stomatella auricula* Lamarck, 1816, Walters Shoal, stn DW4887, maximum dimension 6.8 mm (MNHN). D–I. *Stomatella multilirata* sp. nov. D–F. Holotype, maximum dimension 8.3 mm (MNHN-IM-2013-67246). G–I. Paratype with more orange coloration and tented pattern of whitish markings, maximum dimension 9.5 mm (MNHN-IM-2000-35729).

summit area, south-east, stn WS08; 33°13.7' S, 43°55.9' E; depth 30–33 m; 3 May 2017; MNHN • 14 specimens, some living; summit area, north-west, stn WB09; 33°13.8' S, 43°55.8' E; depth 27–30 m; 4 May 2017; MNHN • 10 specimens, some living; summit area, north-west, stn WB10; 33°09.1' S, 43°51.8' E; depth 30 m; 6 May 2017; MNHN.

Description

SHELL. Small (maximum dimension up to 11 mm), thin, depressed-auriform; last adult whorl expanding very rapidly; spire small, but prominent, its whorls rounded with indented suture; periphery rounded, slightly below mid-whorl; base flattened, anomphalous; teleoconch of up to 3.0 whorls; aperture greatly enlarged, often distinctly arched relative to substratum. First teleoconch whorl with 3 spiral lirae, one at shoulder slightly larger, increasing to 4 by end of whorl; additional lirae arise by intercalation reaching ± 8 by end of second whorl; lirae remaining distinct and very numerous on final whorl (Fig. 42B), usually alternating in strength as intermediaries arise; axial sculpture of weak collabral growth-lines, often somewhat stronger on last half-whorl and rendering sculpture weakly and irregularly decussate; stronger growth scars common on last quarter-whorl; base with similar spiral sculpture, but lirae finer and less distinct toward columella. Aperture elongate, roundly rectangular; peristome complete or nearly so; columella strongly concave, curving smoothly into outer lip; outer lip thin; paries and upper columella somewhat thickened by nacreous callus; interior highly nacreous when fresh, underlying spiral sculpture evident by transparency.

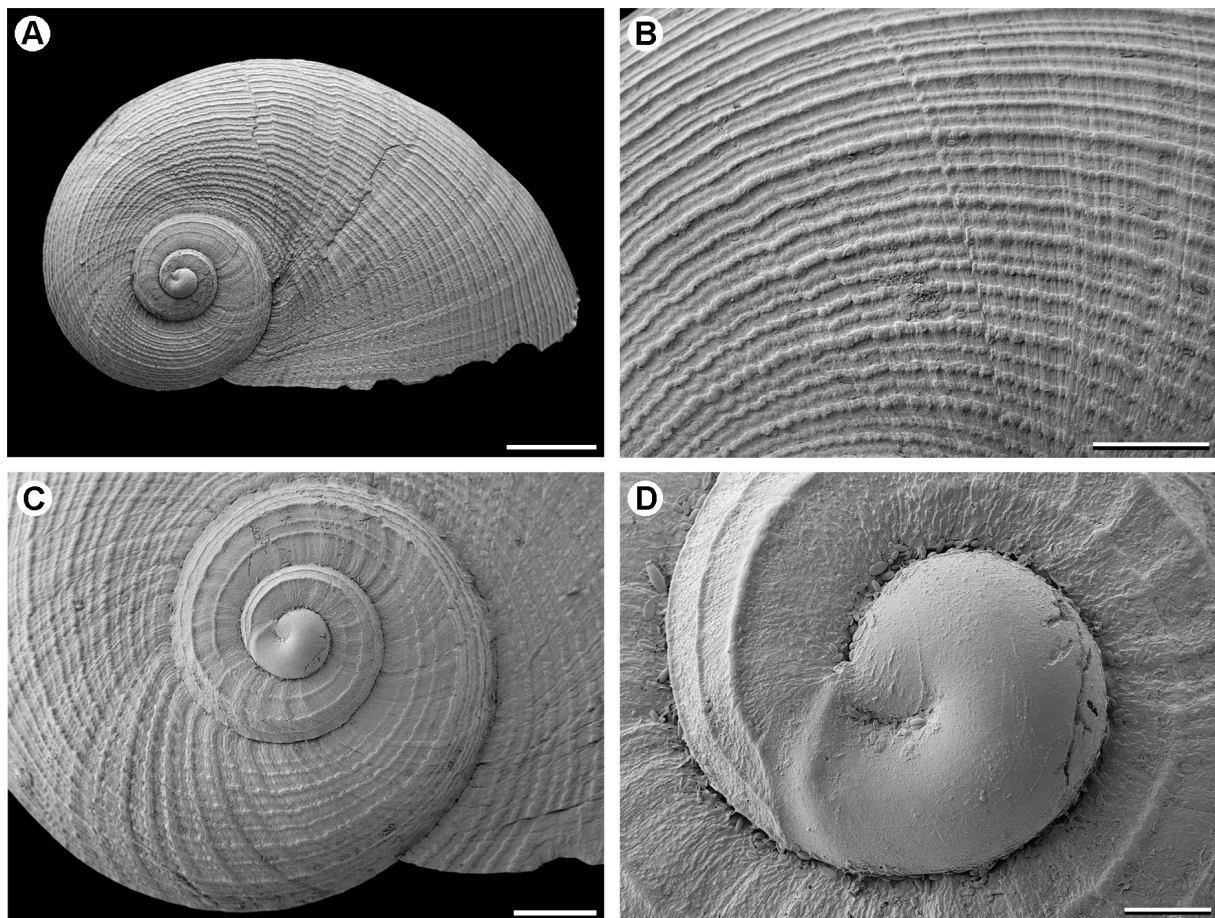


Fig. 42. *Stomatella multilirata* sp. nov., paratypes, subadult (MNHN-IM-2000-35730). **A–C.** Detail of teleoconch sculpture. **D.** Protoconch morphology. Scale bars: A=0.5 mm; B–C=200 µm; D=50 µm.

PROTOCONCH (Fig. 42D). Translucent white; diameter 200–225 μm , ca 1.25 whorls, apical beak weak or absent; sculpture indistinct, most specimens somewhat worn, but traces of fine, widely spaced, spiral threads occasionally evident; terminal lip convex with low subterminal varix.

COLOUR. Apical 1.0–1.5 whorls usually whitish, occasionally translucent corneous with whitish axial bands; second whorl often with brown blotches, becoming progressively more pinkish-red; final whorl predominantly crimson, sometimes with an orange tint, variously patterned with paler axial flames or whitish flecks and tent-like markings; early part of final whorl commonly with pattern of fine alternating crimson and pinkish-brown spiral lines; this pattern congruent with spiral lirae and tending to exaggerate them; columella and inner base white, subperipheral interface between white and crimson zone distinct and frequently scalloped (Fig. 41H).

DIMENSIONS. Holotype, maximum dimension 8.3 mm; largest specimen, maximum dimension 11.0 mm.

OPERCULUM. Absent.

RADULA (Fig. 43). Formula $\infty+5+1+5+\infty$, with ± 30 evenly arcuate, transverse rows of teeth. Rachidian tooth with trigonal base, narrow frontal shaft element and reduced cusp, buttressed on each side by alate flange giving cusp hooded appearance. Lateral teeth with shafts and base-plates overlapping extensively, medial portion of each hidden behind its inner neighbour; cusps comprising larger central denticle with two smaller denticles on each side at cusp base; cusps progressively larger from first to fifth lateral, inner ones hastate, outer ones bluntly spatulate. Cusps of inner marginals elongate-spatulate with well-

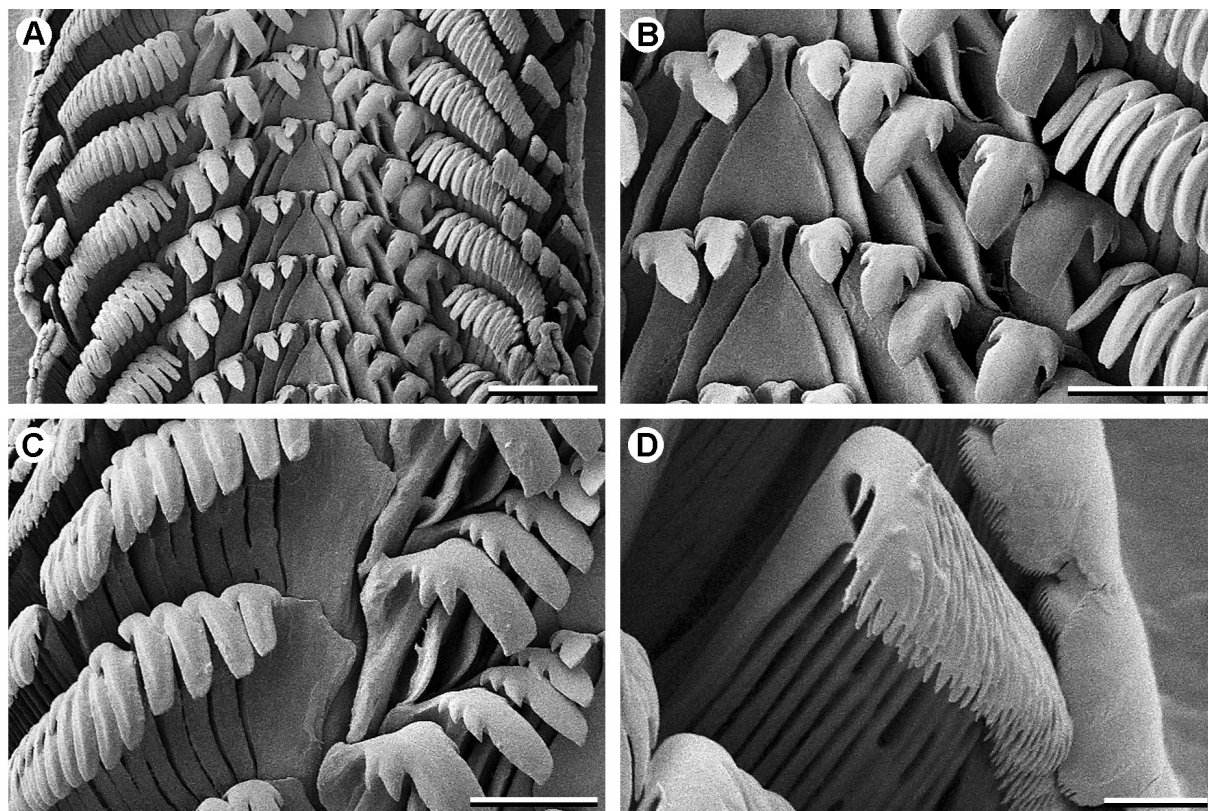


Fig. 43. *Stomatella multilirata* sp. nov., radula (paratype, MNHN-IM-2000-35729). **A.** Entire width of radula. **B.** Detail of rachidian and lateral teeth. **C.** Outer lateral and inner marginal transition zone. **D.** Outer marginal teeth. Scale bars: A=100 μm ; B–C=50 μm ; D=10 μm .

developed basal denticle on outer margin (another also present on inner margin, but usually hidden); shaft of innermost marginal with broad alate medial extension that interlocks with deep socket on outer edge of fifth lateral (Fig 43C); cusps of marginal teeth with progressively finer and more numerous denticles toward edge of radula (Fig. 43D); cusps of outermost marginals roundly spatulate with pectinate fringe.

EXTERNAL ANATOMY. Based on rehydrated specimens and one individual photographed alive (Fig. 38F): as described for Stomatellinae by Hickman & McLean (1990). Head-foot pale fawn-yellow, extensively mottled with darker shades of yellowish-orange. Cephalic lappets present, their margins shallowly scalloped; neck lobes well developed with margins entire; epipodium with three whitish epipodial tentacles on each side and small branched lobes that lie closely applied to ventral shell margin; sides of foot with numerous small tubercles; metapodium enlarged and extending well beyond posterior margin of shell.

Distribution

Known only from the summit area of Walters Shoal, at depths of 26–40 m (living); habitat dominated by encrusting coralline algae; collected by hand, and by brushing and suction sampling.

Remarks

I have already commented on the confused taxonomy of stomatelline trochids (Herbert 2015: 61) and it is thus not without some reservation that I describe a new species while so many of those already proposed remain taxa inquirenda. Amongst stomatelline genera, the depressed, haliotiform shape and relatively fine sculpture of the present species clearly ally it with *Stomatella*, of which the only species currently recognised as occurring in the south-western Indian Ocean is *Stomatella auricula* Lamarck, 1816 (Herbert 2015). That species differs from *S. multilirata* sp. nov. in attaining a larger size (diameter >20 mm) and appearing smoother, the spiral sculpture comprising only fine incised spiral striae (rather than raised spiral lirae), separated by broad, flat-topped intervals (see above and Mermod & Binder 1963). Indeed, in many of the described species of *Stomatella* the sculpture is incised rather than raised, and those described as having a sculpture of raised lirae or threads have frequently proven to belong to *Synaptocochlea* Pilsbry, 1890 (Trochidae: Fossarininae). The depressed, elongate shell and highly nacreous interior of the present species, together with its protoconch and radula morphology and lack of an operculum, clearly demonstrate that it is not referable to *Synaptocochlea*. *Stomatella stellata* Souverbie in Souverbie & Montrouzier, 1863 from New Caledonia is of similar size and sculpture, but the shell is more domed and much less elongate (Herbert 1996). The radula of *S. multilirata* is similar to that of *S. auricula*, but the cusp of the rachidian in that species is considerably larger, almost the same size as that of the innermost lateral (Hickman & McLean 1990: fig. 67c and pers. obs.).

Family Turbinidae Rafinesque, 1815
Subfamily Turbininae Rafinesque, 1815

Genus *Bolma* Risso, 1826

Type species

Turbo rugosus Linnaeus, 1767 (monotypy), Miocene to Recent, NE Atlantic and Mediterranean.

Remarks

Specimens of *Bolma* from Walters Shoal are being studied by Magalie Castelin (MNHN) as part of an on-going molecular phylogenetic investigation of the genus across the Indo-West Pacific, building upon work already published (Castelin *et al.* 2017). Analysis of CO1 sequence data for specimens of both species discussed below confirms that they cluster with other western Indian Ocean samples of the species to which they are here assigned (Castelin unpublished data).

Bolma mainbaza Alf, Maestrati & Bouchet, 2010
Figs 44A–D, 45

Bolma mainbaza Alf, Maestrati & Bouchet, 2010: 95, figs 21–24. Type loc.: Almirante Leite Bank, 26.2° S, 35.03° E, off southern Mozambique, depth 228–230 m.

Bolma mainbaza – Alf & Kreipl 2011: 29, pl. 133 figs 2–3. — Castelin *et al.* 2017 (molecular sequence data).

Material examined

WALTERS SHOAL – **slopes** • 1 living specimen; stn DW4877; 33°10' S, 43°49' E; depth 217–256 m; 1 May 2017; DNA tissue sample; MNHN-IM-2013-64407 • 1 living specimen; same collection data as for preceding; DNA tissue sample; MNHN-IM-2013-64408 • 2 empty shells; same collection data as for preceding; MNHN • 2 empty shells; stn DW4878; 33°09' S, 43°50' E; depth 221–256 m; 1 May 2017; MNHN • 1 living specimen; stn DW4879; 33°17' S, 43°52' E; depth 288–300 m; 1 May 2017; DNA tissue sample; MNHN-IM-2013-64406 • 5 empty shells; same collection data as for preceding; MNHN • 1 living specimen; stn DW4880; 33°17' S, 43°51' E; depth 275–318 m; 1 May 2017; DNA tissue sample; MNHN-IM-2013-64416 • 1 living specimen; same collection data as for preceding; DNA tissue sample; MNHN-IM-2013-64417 • 1 living specimen; same collection data as for preceding; DNA tissue sample; MNHN-IM-2013-64418 • 9 specimens, some living; same collection data as for preceding; MNHN • 10 specimens, some living; stn DW4881; 33°16' S, 43°50' E; depth 377–382 m; 2 May 2017; radula SEM prep.; MNHN • 1 living specimen; stn DW4885; 33°17' S, 43°55' E; depth 272–380 m; 3 May 2017; DNA tissue sample; MNHN-IM-2013-64413 • 1 living specimen; same collection data as for preceding; DNA tissue sample; MNHN-IM-2013-64414 • 1 living specimen; same collection data as for preceding; DNA tissue sample; MNHN-IM-2013-64415 • 5 specimens, some living; same collection data as for preceding; MNHN • 3 empty shells; stn DW4888; 33°10' S, 43°57' E; depth 299–311 m; 3 May 2017; MNHN • 2 specimens, living; stn DW4889; 33°09' S, 43°58' E; depth 353–465 m; 3 May 2017; MNHN • 1 living specimen; stn DW4894; 33°09' S, 43°50' E; depth 199–261 m; 5 May 2017; DNA tissue sample; MNHN-IM-2013-64403 • 1 living specimen; same collection data as for preceding; DNA tissue sample; MNHN-IM-2013-64404 • 1 living specimen; same collection data as for preceding; DNA tissue sample; MNHN-IM-2013-64405 • 1 living specimen; same collection data as for preceding; DNA tissue sample; MNHN-IM-2013-64410 • 5 specimens, some living; same collection data as for preceding; MNHN • 3 specimens, living; stn DW4895; 33°09' S, 43°49' E; depth 238–283 m; 5 May 2017; MNHN.

Description

SHELL (Fig. 44A–C). See original description.

PROTOCONCH (Fig. 45B). Milky-white; diameter \pm 330 μ m, ca 1.25 whorls; apical bulb rounded; sculptured by irregular superficial granulation with traces of widely-spaced, subspiral threads, particularly near terminal lip; terminal lip shallowly convex and slightly flaring; junction with teleoconch clearly demarcated.

OPERCULUM (Fig. 44D). Subcircular, but with portion abutting columella slightly flattened; central bulge weakly pustular, with irregular concentric sculpture peripherally; uniformly white.

RADULA (Fig. 45C–F). Formula $\infty+5+1+5+\infty$, length ca 8.0 mm, with 55–60 transverse rows of teeth; rows with shallow central posterior indentation. Rachidian tooth with broadly ovate base-plate and almost no cusp. Lateral teeth with base-plates broadly and roundly expanded laterally, their cusps relatively small, inner ones bluntly truncate (perhaps worn), outer ones more pointed; extensive basal

overlap of rachidian and lateral teeth; lateral cusps with buttress on outer margin that extends behind shaft of outer neighbour (Fig. 45E). Inner marginal small, appearing to be a sixth lateral, but its shaft similar to and aligned with those of other marginals; second marginal much larger, with strong, elongate-triangular cusp, edges of cusp smooth; remaining marginals progressively smaller, their cusps becoming more slender and developing finely toothed inner margin; outermost marginals with shorter, roundly spatulate cusps.

Distribution

Known from central and southern Mozambique, southern Madagascar and Walters Shoal. On Walters Shoal it has been found on the slopes at depths of 256–377 m (live-taken material 261–377 m); dredged on substrata of coarse sand and fine gravel, with ophiuroids, octocorals and solitary corals.

Remarks

Originally described from the Almirante Leite Bank, a seamount 250 km due east of Maputo, southern Mozambique, *Bolma mainbaza* has subsequently been recorded from off central Mozambique and southern Madagascar at 180–282 m (supplementary data in Castelin *et al.* 2017). The material from Walters Shoal here referred to this species is clearly morphologically very close to that from the type locality, but differs consistently in having fewer beaded spiral cords above the periphery on the penultimate whorl (usually only four, compared to six in the typical specimens). However, Castelin *et al.* (2017) found *B. mainbaza* to be a morphologically variable species and observed that in the genus *Bolma* as a whole, emphasis on traditional criteria such as shell morphology and geographic isolation can lead to inaccurate conclusions regarding species diversity. Clusters of supposedly distinct, range-restricted species may in reality be found to belong to a smaller number of more wide-ranging species when molecular data are taken into consideration. Preliminary comparison of such data indicates that

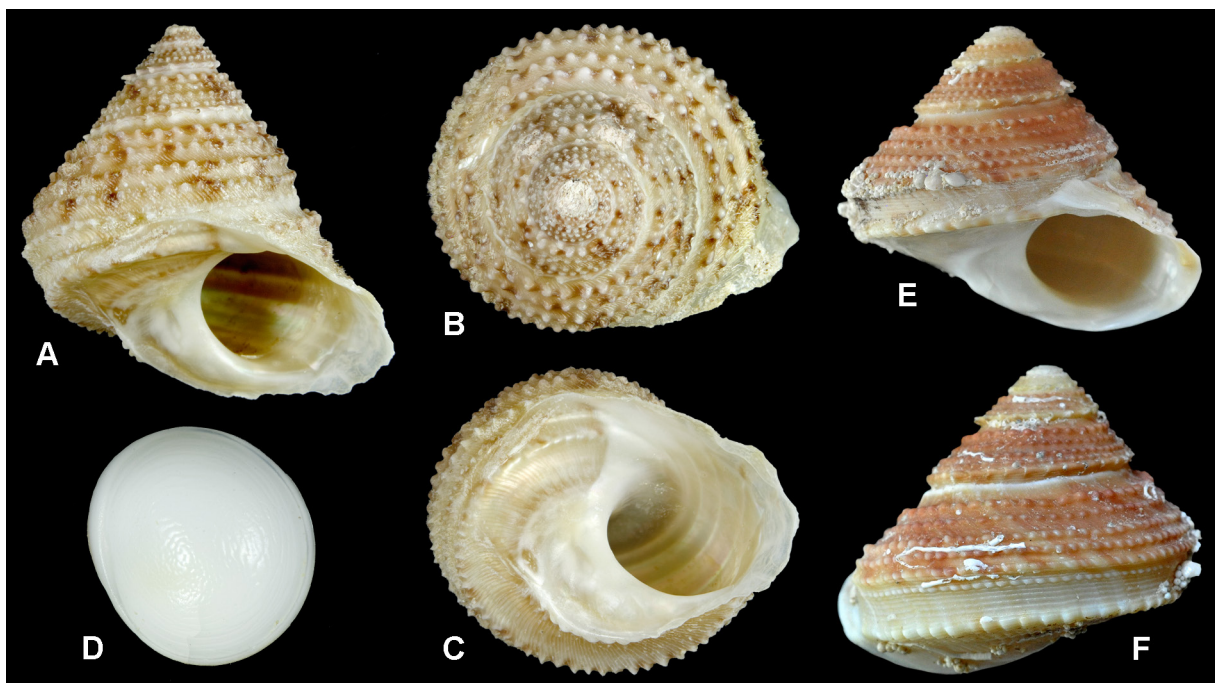


Fig. 44. A–D. *Bolma mainbaza* Alf, Maestrati & Bouchet, 2010, Walters Shoal, stn DW4881, shell (height 23.0 mm) and operculum (maximum diameter 8.5 mm) (MNHN). E–F. *Bolma recens* (Dell, 1967), Walters Shoal, stn DW4890, height 19.1 mm (MNHN-IM-2013-64411, images courtesy of P. Maestrati).

Walters Shoal specimens cluster together with *B. mainbaza* from the type locality, southern Madagascar and the northern Mozambique Channel (Castelin pers. com. 2023). The lower spiral cord number in Walters Shoal specimens is thus likely a reflection of regional intra-specific variation.

The relationship between *B. mainbaza* and the likewise variable *B. bathyraphis* (Smith, 1899) with its spinose synonym *B. gilchristi* (Sowerby III, 1903) remains to be established. No western Indian Ocean material identified as *B. bathyraphis* was included in the molecular analysis of Castelin *et al.* (2017). *Bolma sabiniae* Alf & Kreipl, 2004 from off south-western Madagascar has a much lower spire and a dark purple-red stain on the basal callus.

Bolma recens (Dell, 1967)

Fig. 44E–F

Incilaster recens Dell, 1967: 305, figs 6–7, text-fig. 8. Type loc.: Kiwi Seamount, 30.75° S, 173.25° E, ca 500 km north of New Zealand, 358–677 m.

Bolma clemenceae Bozzetti, 2010: 11. Type loc.: Lavanono, southern Madagascar.

Bolma recens – Beu & Ponder 1979: 32, fig. 11h–i. — Marshall 1979: 549. — Alf & Kreipl 2011: 37, pls 152–154. — Castelin *et al.* 2017 (molecular sequence data). — Araya, Alf & Aliaga 2023: 427, fig. 1e–h.

Material examined

WALTERS SHOAL – **slopes** • 1 living specimen; stn DW4890; 33°09' S, 43°59' E; depth 492–588 m; 4 May 2017; DNA tissue sample; MNHN-IM-2013-64409 • 1 living specimen; same collection data as for preceding; DNA tissue sample; MNHN-IM-2013-64411 • 1 living specimen; same collection data

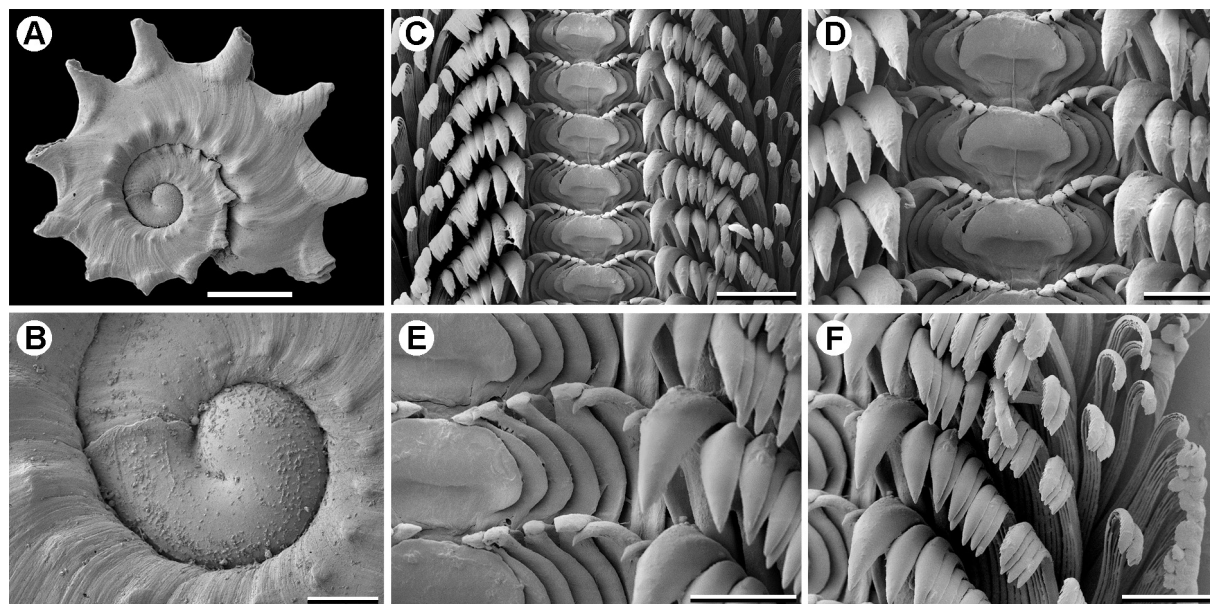


Fig. 45. *Bolma mainbaza* Alf, Maestrati & Bouchet, 2010. **A.** Spinose juvenile shell, Walters Shoal, stn DW4880 (MNHN). **B.** Protoconch of the same. **C–F.** Radula, Walters Shoal, stn DW4881 (MNHN). **C.** Entire width of radula. **D.** Central field and inner marginals. **E.** Detail of lateral and inner marginal teeth. **F.** Marginal teeth. Scale bars: A=500 µm; B, D–F=100 µm; C=200 µm.

as for preceding; DNA tissue sample; MNHN-IM-2013-64412 • 2 empty shells, juvenile; stn DW4898; 33°09' S, 44°01' E; depth 652–668 m; 6 May 2017; MNHN.

Distribution

Widely distributed in the Indo-West Pacific; recorded from the northern Mozambique Channel, southern Madagascar, the Philippines (Araya, Alf & Aliaga 2023) and the south-western Pacific (Castelin *et al.* 2017). On Walters Shoal it was found alive at only one station (492–588 m), dredged on coarse sand with rocks.

Remarks

Bolma recens is easily separated from *B. mainbaza* on account of its strongly bicarinate whorl periphery, with fine spiral cords between the peripheral carinae. The spire angle is also usually broader. Of the two species, *B. recens* is evidently considerably less abundant on Walters Shoal and the limited data available suggest that it occurs at somewhat greater depths (living specimens > 400 m).

Discussion

The vetigastropod fauna of Walters Shoal is not diverse. The total of 50 species is substantially lower than might occur at a locality at a similar latitude (33° S) on the east coast of South Africa (circa East London), which may perhaps contain ± 100 vetigastropod species (although ± 20% of these would likely be exclusively intertidal species for which suitable habitats are not present on Walters Shoal). Groups conspicuously absent on the summit area of Walters Shoal include diodorine fissurellids, haliotids, phasianellids, turbinids, Trochinae and Umboniinae, with anatomids absent at greater depths. Other groups exhibiting generally low diversity include *Calliostoma* species and solariellids.

Of the 50 vetigastropods on Walters Shoal, 30 (60%) are new species apparently endemic to the seamount. Since vetigastropods have non-planktotropic larvae, such a high level of narrow-range endemism might be expected on an isolated seamount. However, given the paucity of our knowledge concerning molluscan seamount communities in the south-western Indian Ocean, this endemism may be more apparent than real, and some connectivity with other seamounts in the region is evident. Of the other 20 species, eight are regionally endemic to the south-western Indian Ocean, a further 11 are more widely distributed in the Indo-West Pacific and one is possibly of deep-water Atlantic affinity. The primary affinities of the fauna are with warm-temperate South Africa and the tropical western Indian Ocean, but some, primarily deeper water taxa, are shared with the south-western Pacific.

The fauna of the summit area comprises species that live only in shallow water and do not extend down the slopes except as empty shells. Such shallow-water forms include regional endemics shared with warm-temperate South Africa, e.g., *Sinezona insignis* and *Vaceuchelus gemmula*, as well as ‘*Gibbula*’ *roseosticta* sp. nov. which, though known only from Walters Shoal, is clearly derived from the endemic southern African ‘*Gibbula*’ radiation. In contrast, *Stomatella multilirata* sp. nov. is likely a peripheral isolate of tropical western Indian Ocean origin. The affinities of *Microcollonia miniata* sp. nov., another common summit area species, are not currently clear.

At greater depths, species such as *Agariste phrygium* and *Danilia textilis* are shared with the eastern seaboard of South Africa, while *Bolma mainbaza*, *Calliotropis velata* and *Phragmomphalina vilvensi* are regionally endemic species of more widespread occurrence in the south-western Indian Ocean. *Bruceina areneformis* sp. nov. likewise belongs to a genus known only from the south-western Indian Ocean. Mostly these regionally endemic species are likely to derive from Indo-West Pacific stock, but the ultimate origin of *Agariste phrygium* is puzzling, as the genus is otherwise known only from the Plio-Pleistocene of the central and western Mediterranean (Landau *et al.* 2003). Another regional endemic

of differing biogeographic affinity is *Imbricoscelis coronis*, which appears to be a species of southern origin associated with seamounts along the Southwest Indian Ridge.

The 11 more widespread Indo-West Pacific species were mostly collected on the slopes and surrounding plains of Walters Shoal. They include both relatively large species such as *Bolma recens*, *Calliotropis eucheloides* and *Emarginula sublaevis*, as well as small to minute taxa such as *Acremodontina carinata*, *Bichoristes wareni*, *Eudaronia ?biconcava*, *Trochaclis regalis* and *Visayaseguenzia compsa*. Significantly, four of these are also recorded from the seas north of New Zealand, suggesting either disjunct distributions or wide-ranging species-level connectivity at upper bathyal depths between the south-western Indian Ocean and the New Zealand-New Caledonia-Fiji triangle. *Calliotropis acherontis* Marshall, 1979 is another such example (Vilvens 2007; Herbert 2015) and *C. bucina* Vilvens, 2006, *C. hataii* Rehder & Ladd, 1973 and *C. metallica* (Wood-Mason & Alcock, 1891) are likewise widely distributed in the Indo-West Pacific (Vilvens 2007). Hickman (2016) postulated that these may represent relictual occurrences of species and lineages with ranges that have now become fragmented and reduced. Molecular data will be needed to test whether these distributions are indeed disjunct or merely a reflection of limited sampling with some connectivity remaining. The molecular data presented by Castelin *et al.* (2017) for *Bolma recens* indicate that populations in the south-western Indian Ocean and those in the south-western Pacific remain conspecific.

Also amongst the widespread Indo-West Pacific species is *Stomatella auricula*, typically a shallow-water species, but one not found on the summit area of Walters Shoal and represented on the shoal only by a single dead shell collected at 599–640 m. Most probably, this results from the stochastic dispersal of isolated individuals from more northerly populations that has not resulted in colonisation, the shell of this individual having been transported down-slope after death.

The new species discovered include summit area species and slope/plains species, and belong to a spectrum of genera, some recorded for the first time in the Indian Ocean (*Akritogyra*, *Carinastele*, *Hadroconus*, *Lissotesta*, *Mikro* and *Trenchia*). Also recorded from the Indian Ocean for the first time are species of *Bichoristes* and *Vetulonia*. The latter is unusual since the species concerned appears to be a south Atlantic one, rather than one from the Indo-West Pacific. However, confirmation of its identity is required. Both of the new genera proposed are currently monotypic and one, *Pterodacna* gen. nov., is to date known only from Walters Shoal. The second, *Imbricoscelis* gen. nov., as discussed above, is a regional seamount endemic. The discovery of the pseudococculinid *Pterodacna* gen. nov. living on decomposing bird feathers, a biogenic substrate association previously unknown in the Mollusca, provides another demonstration of the remarkable capacity of deep-sea limpets to exploit unusual food resources.

Acknowledgements

I thank Prof. Philippe Bouchet (MNHN) for inviting me to study the vetigastropod material collected during the MNHN Walters Shoal expedition. I also thank Virginie Héros and Philippe Maestrati (MNHN) for facilitating the loan of samples, answering numerous queries, providing catalogue numbers for type material and forwarding images of living specimens. In addition, I thank Suzanne Williams (Natural History Museum, London) for comparing CO1 sequence data for Walters Shoal solariellids with her global solariellid molecular dataset, Magalie Castelin (MNHN) for sharing her unpublished molecular data on species of *Bolma* in the south-western Indian Ocean, including Walters Shoal material, and Alain Barrère for images of living animals taken on board ship. Comments on the manuscript provided by Leon Hoffman and an anonymous reviewer were valuable and much appreciated. I am most grateful to the National Museum of Wales and in particular Ben Rowson for access to and assistance with their photomicroscope and SEM facilities.

References

- Absalão R.S. & Pimenta A.D. 2005. New records and new species of *Vetulonia* Dall, 1913 and *Brookula* Iredale, 1912 from Brazil (Gastropoda: Trochidae). *The Veliger* 47 (3): 193–201.
Available from <https://www.biodiversitylibrary.org/page/42497121> [accessed 10 Feb. 2024].
- Absalão R.S., Miyaji C. & Pimenta A.D. 2001. The genus *Brookula* Iredale, 1912 (Gastropoda, Trochidae) from Brazil: description of a new species, with notes on other South American species. *Zoosystema* 23 (4): 675–687.
- Affenzeller S., Haar N. & Steiner G. 2017. Revision of the genus complex *Gibbula*: an integrative approach to delineating the Eastern Mediterranean genera *Gibbula* Risso, 1826, *Steromphala* Gray, 1847, and *Phorcus* Risso, 1826 using DNA tissue sample-barcoding and geometric morphometrics (Vetigastropoda, Trochoidea). *Organisms Diversity & Evolution* 17 (4): 789–812.
<https://doi.org/10.1007/s13127-017-0343-5>
- Albano P.G., Bakker P.A.J., Janssen R. & Eschner A. 2017. An illustrated catalogue of Rudolf Sturany's type specimens in the Naturhistorisches Museum Wien, Austria (NHMW): Red Sea gastropods. *Zoosystematics and Evolution* 93 (1): 45–94. <https://doi.org/10.3897/zse.96.54707>
- Alf A. & Kreipl K. 2011. The family Turbinidae. Subfamilies Turbininae Rafinesque, 1815 and Prisogasterinae Hickman & McLean, 1990. In: Poppe G.T. & Groh K. (eds) *A Conchological Iconography*: 1–82. Conchbooks, Hackenheim, Germany.
- Alf A., Maestrati P. & Bouchet P. 2010. New species of *Bolma* (Mollusca: Vetigastropoda: Turbinidae) from the tropical deep sea. *The Nautilus* 124 (2): 93–99.
Available from <https://www.biodiversitylibrary.org/page/50437713> [accessed 11 Feb. 2024].
- Amon D.J., Copley J.T., Dahlgren T.G., Horton T., Kemp K.M., Rogers A.D. & Glover A.G. 2017. Observations of fauna attending wood and bone deployments from two seamounts on the Southwest Indian Ridge. *Deep-Sea Research II* 136: 122–132. <https://doi.org/10.1016/j.dsr2.2015.07.003>
- Anton H.E. 1838. *Verzeichniss der Conchylien welche sich in der Sammlung von Hermann Eduard Anton befinden*. Eduard Anton, Halle, Germany. <https://doi.org/10.5962/bhl.title.11509>
- Araya J.F., Alf A. & Aliaga J.A. 2023. New records for *Bolma girgyllus* (Reeve, 1861) and *Bolma recens* (Dell, 1967) (Gastropoda: Turbinidae) extend their geographical distributions in the Philippines and Australia. *Journal of Conchology* 44 (5): 425–429.
- Barnard K.H. 1963a. *Deep-sea Mollusca from the Region South of Madagascar*. South African Division of Sea Fisheries, Investigational Reports No. 44.
- Barnard K.H. 1963b. Contributions to the knowledge of South African marine Mollusca. Part IV. Gastropoda: Prosobranchiata: Rhipidoglossa, Docoglossa. Tectibranchiata. Polyplacophora. Solenogastres. Scaphopoda. *Annals of the South African Museum* 47 (2): 201–360.
- Beu A.G. & Ponder W.F. 1979. A revision of the species of *Bolma* Risso, 1826 (Gastropoda: Turbinidae). *Records of the Australian Museum* 32 (1): 1–68. <https://doi.org/10.3853/j.0067-1975.32.1979.201>
- Bosch D.T., Dance S.P., Moolenbeek R.G. & Oliver P.G. 1995. *Seashells of Eastern Arabia*. Motivate Publishing, Abu Dhabi, Dubai and London.
- Bouchet P., Héros V., Lozouet P. & Maestrati P. 2008. A quarter-century of deep-sea malacological exploration in the South and West Pacific: Where do we stand? How far to go? In: Héros V., Cowie R.H. & Bouchet P. (eds) *Tropical Deep-Sea Benthos 25. Mémoires du Muséum national d'histoire naturelle* 196: 9–40.

- Bouchet P., Rocroi J.P., Hausdorf B., Kaim A., Kano Y., Nützel A., Parkhaev P., Schrödl M. & Strong E.E. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia* 61 (1–2): 1–526. <https://doi.org/10.4002/040.061.0201>
- Bozzetti L. 2008. *Fluxinella stellaris* (Gastropoda: Vetigastropoda: Seguenziidae) nuova specie dal Madagascar meridionale. *Malacologia Mostra Mondiale* 61: 15–16.
- Bozzetti L. 2010. *Bolma clemenceae* (Gastropoda: Vetigastropoda: Turbinidae: Astraeinae) dal Madagascar meridionale. *Malacologia Mostra Mondiale* 69: 11–12.
- Castelin M., Williams S.T., Buge B., Maestrati P., Lambourdière J., Ozawa T., Utge J., Couloux A., Alf A. & Samadi S. 2017. Untangling species identity in gastropods with polymorphic shells in the genus *Bolma* Risso, 1826 (Mollusca, Vetigastropoda). *European Journal of Taxonomy* 288: 1–21. <https://doi.org/10.5852/ejt.2017.288>
- Cotton B.C. 1959. *South Australian Mollusca: Archaeogastropoda*. Handbook of the Flora and Fauna of South Australia, Government Printer, Adelaide.
- Dall W.H. 1925. Illustrations of unfigured types of shells in the collection of the United States National Museum. *Proceedings of the United States National Museum* 66 (2554): 1–41. <https://doi.org/10.5479/si.00963801.66-2554.1>
- Dell R.K. 1967. Some Mollusca from deep water to the north of New Zealand, collected by the *Tui*, 1962. *Records of the Dominion Museum* 5: 305–315.
- Dell R.K. 1990. Antarctic Mollusca, with special reference to the fauna of the Ross Sea. *Bulletin of the Royal Society of New Zealand* 27: 1–311.
- Drivas J. & Jay M. 1985. Shells of Réunion. 3. Family Fissurellidae. Subfamily Emarginulinae. *La Conchiglia* 17 (194–195): 3–6.
- Engl W. 2012. *Shells of Antarctica*. Conchbooks, Hackenheim, Germany.
- Fukumori H., Takano T., Hasegawa K. & Kano Y. 2019. Deepest known gastropod fauna: species composition and distribution in the Kuril–Kamchatka Trench. *Progress in Oceanography* 178: e102176. <https://doi.org/10.1016/j.pocean.2019.102176>
- Geiger D.L. 2012. *Monograph of the Little Slit Shells. Volume 1. Introduction, Scissurellidae: 1–728. Volume 2. Anatomidae, Larocheidae, Depressizonidae, Sutilizonidae, Temnocinclidae: 729–1291*. Santa Barbara Museum of Natural History Monographs 7.
- Giles E. & Gosliner T. 1983. Primary type specimens of marine Mollusca (excluding Cephalopoda) in the South African Museum. *Annals of the South African Museum* 92 (1): 1–52.
- Habe T. 1955. *Illustrated Catalogue of Japanese Shells, Series B, No 3, Emarginula choristes Dall*.
- Harris G.F. 1897. *Catalogue of Tertiary Mollusca in the Department of Geology, British Museum (Natural History). Part I. The Australasian Tertiary Mollusca*. British Museum (Natural History), London.
- Hasegawa K. 2018. Sublittoral and upper bathyal vetigastropods (Mollusca: Gastropoda) dredged from the Ogasawara Islands. *Memoirs of the National Museum of Natural Science, Tokyo* 52: 105–152.
- Herbert D.G. 1986. A revision of the southern African Scissurellidae (Mollusca: Gastropoda: Prosobranchia). *Annals of the Natal Museum* 27 (2): 601–632. Available from https://hdl.handle.net/10520/AJA03040798_432 [accessed 11 Feb. 2024].

- Herbert D.G. 1987a. Taxonomic studies on the Emarginulinae (Mollusca: Gastropoda: Fissurellidae) of southern Africa and Mozambique. *Hemitoma, Clypidina, Tugali, Scutus, Zeidora* and two species of *Emarginula*. *South African Journal of Zoology* 22 (1): 1–13.
<https://doi.org/10.1080/02541858.1987.11448013>
- Herbert D.G. 1987b. Revision of the Solariellinae (Mollusca: Prosobranchia: Trochidae) in southern Africa. *Annals of the Natal Museum* 28 (2): 283–382.
Available from https://hdl.handle.net/10520/AJA03040798_405 [accessed 11 Feb. 2024].
- Herbert D.G. 1995. A new species of Thysanodontinae from South Africa (Mollusca: Trochoidea). *Annals of the Natal Museum* 36: 255–259.
Available from https://hdl.handle.net/10520/AJA03040798_201 [accessed 11 Feb. 2024].
- Herbert D.G. 1996. A critical review of the trochoidean types in the Muséum d’Histoire Naturelle, Bordeaux (Mollusca: Gastropoda). *Bulletin du Muséum national d’histoire naturelle, Paris, 4th Series, 18, section A* 3–4: 409–445. <https://doi.org/10.5962/p.290340>
- Herbert D.G. 2012. A revision of the Chilodontidae (Gastropoda: Vetigastropoda: Seguenzioidea) of southern Africa and the south-western Indian Ocean. *African Invertebrates* 53 (2): 381–502.
<https://doi.org/10.5733/afin.053.0209>
- Herbert D.G. 2015. An annotated catalogue and bibliography of the taxonomy, synonymy and distribution of the Recent Vetigastropoda of South Africa (Mollusca). *Zootaxa* 4049 (1): 1–98.
<https://doi.org/10.11646/zootaxa.4049.1.1>
- Herbert D.G. & Kilburn R.N. 1986. Taxonomic studies on the Emarginulinae (Mollusca: Gastropoda: Fissurellidae) of southern Africa and Mozambique. *Emarginula, Emarginella, Puncturella, Fissurisepta* and *Rimula*. *South African Journal of Zoology* 21 (1): 1–27.
<https://doi.org/10.1080/02541858.1986.11447951>
- Herrmannsen A.N. 1846–1847. *Indices Generum Malacozoorum Primordia*. T. Fischer, Cassell. Vol. 1: Part 1: 1–104 [1846]; Part 2: 105–232 [1846]; Part 3: 233–360 [1847]; Part 4: 361–488 [1847]; Part 5: 489–637 [1847]. Theodor Fischer, Kassel, Germany.
Available from <https://www.biodiversitylibrary.org/page/10695423> [accessed 7 Feb. 2024].
- Hickman C.S. 1983. Radular patterns, systematics, diversity and the ecology of deep-sea limpets. *The Veliger* 26 (2): 73–92.
Available from <https://www.biodiversitylibrary.org/page/42412783> [accessed 10 Feb. 2024].
- Hickman C.S. 2016. New species of deep-sea gastropods from the Indo-West Pacific region (Gastropoda: Vetigastropoda: Seguenzioidea: Calliotropidae) with a geologic and biogeographic perspective. *The Nautilus* 130 (3): 83–100.
Available from <https://www.biodiversitylibrary.org/page/59589743> [accessed 10 Feb. 2024].
- Hickman C.S. & McLean J.H. 1990. Systematic revision and suprageneric classification of trochacean gastropods. *Science Series, Natural History Museum of Los Angeles County* 35: 1–169.
- Hoffman L. & Freiwald A. 2018. A new genus and two new species in Calliotropidae (Mollusca: Gastropoda) from NE Atlantic cold-water coral habitats. *Miscellanea Malacologica* 7 (5): 89–96.
- Hoffman L., Gofas S. & Freiwald A. 2020. A large biodiversity of “skeneimorph” (Gastropoda: Vetigastropoda) species from the South Azorean Seamount Chain, with the description of seventeen new species. *Iberus* 38 (supplement 9): 1–82.
- Kaim A. 2004. The evolution of conch ontogeny in Mesozoic open sea gastropods. *Palaeontologia Polonica* 62: 3–183.

- Kano Y., Chikyu E. & Warén A. 2009. Morphological, ecological and molecular characterization of the enigmatic planispiral snail genus *Adeuomphalus* (Vetigastropoda: Seguenzioidea). *Journal of Molluscan Studies* 75: 397–418. <https://doi.org/10.1093/mollus/eyp037>
- Kensley B. 1973. *Sea-shells of Southern Africa. Gastropods*. Maskew Miller, Cape Town.
- Kiel S., Aguilar Y.M. & Kase T. 2020. Mollusks from Pliocene and Pleistocene seep deposits in Leyte, Philippines. *Acta Palaeontologica Polonica* 65 (3): 589–627. <https://doi.org/10.4202/app.00756.2020>
- Kilburn R.N. 1977. Taxonomic studies on the marine Mollusca of southern Africa and Mozambique. Part 1. *Annals of the Natal Museum* 23 (1): 173–214.
Available from https://hdl.handle.net/10520/AJA03040798_574 [accessed 11 Feb. 2024].
- Kilburn R.N. 1978. The Emarginulinae (Mollusca: Gastropoda: Fissurellidae) of southern Africa and Mozambique. *Annals of the Natal Museum* 23 (2): 431–453.
- Lamarck J.B.P.A. 1816. *Tableau encyclopédique et méthodique des trois règnes de la nature*. V. Agasse, Paris, Part 23 [Livraison 84], pls 391–488, et liste des objets représentés dans les planches de cette livraison, 16 pp.
- Lamarck J.B.P.A. 1822. *Histoire naturelle des animaux sans vertèbres*. Verdière, Paris, 6 (2): 1–232.
- Landau B., Marquet R. & Grigis M. 2003. The Early Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 1: Vetigastropoda. *Palaeontos* 3: 1–87.
- Lussi M. 2014. Description of a new species of *Calliostoma* from eastern South Africa with notes on the genus – (Gastropoda: Vetigastropoda: Trochidae). *Malacologia Mostra Mondiale* 85: 14–19.
- Lutjeharms J.R.E. & Anson I.J. 2001. The Agulhas Return Current. *Journal of Marine Systems* 30: 115–138. [https://doi.org/10.1016/S0924-7963\(01\)00041-0](https://doi.org/10.1016/S0924-7963(01)00041-0)
- Marshall B.A. 1979. The Trochidae and Turbinidae of the Kermadec Ridge (Mollusca: Gastropoda). *New Zealand Journal of Zoology* 6 (4): 521–552. <https://doi.org/10.1080/03014223.1979.10428396>
- Marshall B.A. 1983. Recent and Tertiary Seguenziidae (Mollusca: Gastropoda) from the New Zealand region. *New Zealand Journal of Zoology* 10 (3): 235–262.
<https://doi.org/10.1080/03014223.1983.10423911>
- Marshall B.A. 1986. Recent and Tertiary Cocculinidae and Pseudococculinidae (Mollusca: Gastropoda) from New Zealand and New South Wales. *New Zealand Journal of Zoology* 12 (4): 505–546.
<https://doi.org/10.1080/03014223.1985.10428301>
- Marshall B.A. 1988. Thysanodontinae: a new subfamily of the Trochidae (Gastropoda). *Journal of Molluscan Studies* 54 (2): 215–229. <https://doi.org/10.1093/mollus/54.2.215>
- Marshall B.A. 1991. Mollusca Gastropoda: Seguenziidae from New Caledonia and the Loyalty Islands. In: Crosnier A. & Bouchet P. (eds) *Résultats des Campagnes MUSORSTOM, Vol. 7*: 41–109. Mémoires du Muséum National d'Histoire Naturelle, Paris (A) 150.
- Marshall B.A. 1993. A review of the genus *Kaiparathina* Laws, 1941 (Mollusca: Gastropoda: Trochidae). *The Veliger* 36 (2): 185–198.
Available from <https://www.biodiversitylibrary.org/page/42465795> [accessed 10 Feb. 2024].
- Marshall B.A. 1995. Recent and Tertiary Trochaclididae from the southwest Pacific (Mollusca: Gastropoda: Trochidae). *The Veliger* 38 (2): 92–115.
Available from <https://www.biodiversitylibrary.org/page/42466754> [accessed 10 Feb. 2024].

- Marshall B.A. 1996. A new subfamily of the Addisoniidae associated with cephalopod beaks from the tropical southwest Pacific, and a new pseudococculinid associated with chondrichthyan egg cases from New Zealand (Mollusca: Lepetelloidea). *The Veliger* 39 (3): 250–259.
Available from <https://www.biodiversitylibrary.org/page/42501381> [accessed 10 Feb. 2024].
- Marshall B.A. 2016. New species of *Venustatrochus* Powell, 1951 from New Zealand, and new species of *Falsimargarita* Powell, 1951 and a new genus of the Calliostomatidae from the southwest Pacific, with comments on some other calliostomatid genera (Mollusca: Gastropoda). *Molluscan Research* 36: 119–141. <https://doi.org/10.1080/13235818.2015.1128586>
- McLean J.H. 1992. Systematic review of the family Choristellidae (Archaeogastropoda: Lepetellacea) with description of new species. *The Veliger* 35 (4): 273–294.
Available from <https://www.biodiversitylibrary.org/page/42467347> [accessed 10 Feb. 2024].
- McLean J.H. 1996. The Prosobranchia. In: Scott P.H., Blake J.A. & Lissner A.L. (eds) *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. The Mollusca Part 2 – The Gastropoda*. Santa Barbara Museum of Natural History, Volume 9.
- McLean J.H. & Geiger D.L. 1998. New genera and species having the *Fissurisepta* shell form, with a generic-level phylogenetic analysis (Gastropoda: Fissurellidae). *Contributions in Science, Los Angeles County Museum* 475: 1–32. <https://doi.org/10.5962/p.208103>
- Melvill J.C. 1904. Descriptions of twenty-eight species of Gastropoda from the Persian Gulf, Gulf of Oman and Arabian Sea, dredged by Mr F.W. Townsend, of the Indo-European Telegraph Service, 1900–1904. *Proceedings of the Malacological Society of London* 6: 159–169.
<https://doi.org/10.1093/oxfordjournals.mollus.a066056>
- Melvill J.C. & Standen R. 1903. Descriptions of sixty-eight new Gastropoda from the Persian Gulf, Gulf of Oman, and north Arabian Sea, dredged by Mr F.W. Townsend, of the Indo-European Telegraph Service, 1901–1903. *Annals and Magazine of Natural History* 7 (12): 289–324.
<https://doi.org/10.1080/00222930308678859>
- Mermod G. & Binder E. 1963. Les types de la collection Lamarck au Muséum de Genève. Mollusques vivants. Part 5. *Revue suisse de Zoologie* 70 (7): 127–172.
- Muratov I.V. & Heyns-Veale E. 2020. Primary types in the collection of molluscs in the KwaZulu-Natal Museum: Patellogastropoda and Lepetellida. *African Invertebrates* 61 (1): 49–81.
<https://doi.org/10.3897/afrinvertebr.61.51989>
- Nolf F. & Verstraeten J. 2003. Deep-water species of Mollusca in the Mozambique Channel. Part 1. *Neptunea* 2 (3): 1–27.
- Okutani T. 2000. Family Seguenziidae. In: Okutani T. (ed.) *Marine Mollusks in Japan*: 86–87. Tokai University Press, Tokyo.
- Oliver J.D., Hoffman L., Urgorri V. & Templado J. 2023. Seguenzioidean gastropods from the continental shelf and slope off Galicia (NW Iberian Peninsula). *Iberus* 41 (2): 199–249.
- Palazzi S. & Villari A. 1996. Malacofaune batiali plio-pleistoceniche del Messinese, 2: Capo Milazzo. *Naturalista Siciliana* IV, 20 (3–4): 237–279.
- Ponder W.F. & Lindberg D.R. 2020. Chapter 18. Gastropoda 1. In: Ponder W.F., Lindberg D.R. & Ponder J.M. (eds) *Biology and Evolution of the Mollusca, Vol. 2*: 289–364. CRC Press, Boca Raton, LA.
<https://doi.org/10.1201/9781351115254>
- Poppe G.T. & Tagaro S.P. 2020. The Fissurellidae from the Philippines with description of 26 new species. *Visaya Supplement* 13: 1–131.

- Poppe G.T., Tagaro S.P. & Dekker H. 2006. The Seguenziidae, Chilodontidae, Trochidae, Calliostomatidae and Solariellidae of the Philippine Islands. *Visaya*, Supplement 2: 1–228.
- Poppe G.T., Tagaro S.P. & Huang S.-I. 2023. *The Recent Colloniidae with a Study of the Colloniidae Collected by Various Expeditions of the Muséum National d'Histoire Naturelle, Paris*. ConchBooks, Harxheim, Germany.
- Powell A.W.B. 1940. Marine Mollusca of the Aupourian Province, New Zealand. *Transactions of the Royal Society of New Zealand* 70: 205–248.
- Powell A.W.B. 1979. *New Zealand Mollusca: Marine, Land and Freshwater Shells*. Collins, Auckland.
- Quinn J.F. 1987. A revision of the Seguenziacea Verill, 1884 (Gastropoda: Prosobranchia). II. The new genera *Hadroconus*, *Rotellenzia* and *Asthelys*. *The Nautilus* 101 (2): 59–68.
<https://doi.org/10.5962/bhl.part.17407>
- Rubio F. & Rolán E. 2021. A review of Lyocyclidae Thiele, 1925 (Gastropoda: Caenogastropoda) from the Indo-Pacific, with the description of one new genus and twenty-eight new species. *Iberus* 39 (1): 33–96.
- Rubio F., Rolán E. & Fernández-Garcés R. 2015. Revision of the genera *Parviturbo* and *Pseudorbis* (Gastropoda, Skeneidae). *Iberus* 33 (2): 167–259.
- Sasaki T. 2000a. Family Fissurellidae. In: Okutani T. (ed.) *Marine Mollusks in Japan*: 44–53. Tokai University Press, Tokyo.
- Sasaki T. 2000b. Family Turbinidae. In: Okutani, T. (ed.) *Marine Mollusks in Japan*: 88–101. Tokai University Press, Tokyo.
- Sasaki T. 2008. Micromolluscs in Japan: taxonomic composition, habitats, and future topics. *Zoosymposia* 1: 147–232. <https://doi.org/10.11646/zoosymposia.1.1.12>
- Schepman M.M. 1908. The Prosobranchia of the “*Siboga*” Expedition. Part 1. Rhipidoglossa and Docoglossa, with an appendix by Prof. R. Bergh. *Siboga Expeditie 1899–1900, Vol. 49, 1a, Part 1*: 1–107. E.J. Brill, Leiden.
- Schwabe E. & Engl W. 2008. Description of two new deep-water species of the genus *Brookula* Iredale, 1912 (Mollusca, Gastropoda, Trochoidea), with a revision of the genus for the Subantarctic and Arctic Sector of the Atlantic Ocean. *Zootaxa* 1866 (1): 187–204. <https://doi.org/10.11646/zootaxa.1866.1.9>
- Singer B.S. 1998. Summary of the slit and keyhole limpets of the Red Sea (Superfamily: Fissurelloidea) with the accent on the Gulf of Aqaba. *Levantina* 83: 1–12, plus un-numbered plates.
- Smiriglio C., Mariottini P. & Gravina F. 1992. On *Cantrainea peloritana* (Cantraine, 1835) from the Mediterranean Sea (Gastropoda, Prosobranchia: Colloniidae). *Basteria* 56: 83–90.
- Smith E.A. 1910. On South African marine Mollusca with descriptions of new species. *Annals of the Natal Museum* 2 (2): 175–220.
- Strebel H. 1908. Die Gastropoden. *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901–1903 unter Leitung von Dr. Otto Nordenskjöld* 6 (1): 1–111.
Available from <https://www.biodiversitylibrary.org/page/6227399> [accessed 11 Feb. 2024].
- Thiele J. 1912–1919. Scissurelliden und Fissurelliden. In: Martini F.H.W. & Chemnitz J.H. (eds) *Systematisches Conchylien-Cabinet*. Second edition, Küster H.C. (ed.). Bauer & Raspe, Nürnberg. 2(4a): 1–168, pls 1–20 [pp. 1–36, pls 1–4 = 1912; pp. 37–68, pls 5–8 = 1913; pp. 69–104, pls 9–12 = 1915; pp. 105–144, pls 13–16 = 1916; pp. 145–168, pls 17–20 = 1919].
Available from <https://www.biodiversitylibrary.org/page/34338157> [accessed 11 Feb. 2024].

- Thiele J. 1925. Gastropoda der deutschen Tiefsee-Expedition, II. *Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia", 1898–1899*, 17(2): 35–382 [dual pagination; also numbered 1–348]. Gustav Fischer, Jena.
- Turton W.H. 1932. *The Marine Shells of Port Alfred, South Africa*. Oxford University Press, London.
- Tuskes P.M. 2019. Calliostomatidae of the northeast Pacific. *Zoosymposia* 13: 83–96.
<https://doi.org/10.11646/zoosymposia.13.1.9>
- Uribe J.E., Williams S.T., Templado J., Buge B. & Zardoya R. 2016. Phylogenetic relationships of Mediterranean and North-East Atlantic Cantharidinae and notes on Stomatellinae (Vetigastropoda: Trochidae). *Molecular Phylogenetics and Evolution* 107: 64–79.
<https://doi.org/10.1016/j.ympev.2016.10.009>
- Vazzana A. 1996. Malacofauna batiale del Pleistocene inferiore del Vallone Catrica (Reggio Calabria, Italia). *Bolletino Malacologico* 31 (5–8): 143–162.
- Verco J.C. 1909. Notes on South Australian marine Mollusca, with descriptions of new species. Part X. *Transactions of the Royal Society of South Australia* 33: 270–276.
- Vilvens C. 2006. New records and new species of *Calliotropis* (Gastropoda: Chilodontidae: Calliotropinae) from Madagascar, Mayotte Island and Reunion Island. *Novapex* 7 (2–3): 55–71.
Available from <https://www.biodiversitylibrary.org/page/42351233> [accessed 11 Feb. 2024].
- Vilvens C. 2007. New species and new records of *Calliotropis* (Gastropoda: Chilodontidae: Calliotropinae) from Indo-Pacific. *Novapex* 8 (hors série): 1–72.
Available from <https://www.biodiversitylibrary.org/page/42353573> [accessed 7 Feb. 2024].
- Vilvens C. 2014. New species and new records of Calliostomatidae (Gastropoda: Trochoidea) from Madagascar. *Novapex* 15 (HS 9): 1–29.
Available from <https://www.biodiversitylibrary.org/page/53186549> [accessed 10 Feb. 2024].
- Vilvens C. 2020. New species and new records of *Calliotropis* (Gastropoda: Vetigastropoda: Seguenzioidea: Eucyclidae) from the western Pacific. *Novapex Hors Série* 13: 1–79.
- Vilvens C. 2021. New species and new records of *Calliotropis*, *Spinicalliotropis* and *Tibatrochus* (Gastropoda: Vetigastropoda: Seguenzioidea: Eucyclidae) from Madagascar and Mozambique Channel. *Novapex* 22 (4): 97–118.
- Vilvens C. 2022. New records and new species of Solariellidae (Gastropoda: Vetigastropoda: Trochoidea) from south-western Indian Ocean. *Novapex* 23 (2): 45–67.
- Warén A. 1991. New and little known Mollusca from Iceland and Scandinavia. *Sarsia* 76: 53–124.
<https://doi.org/10.1080/00364827.1991.10413466>
- Warén A. 1992. New and little known “skeneimorph” gastropods from the Mediterranean Sea and the adjacent Atlantic Ocean. *Bollettino Malacologico* 27 (10–12): 149–248.
- Warén A. 1993. New and little known Mollusca from Iceland and Scandinavia. Part 2. *Sarsia* 78: 159–201. <https://doi.org/10.1080/00364827.1993.10413534>
- Warén A. & Bouchet P. 1989. New gastropods from East Pacific hydrothermal vents. *Zoologica Scripta* 18 (1): 67–102. <https://doi.org/10.1111/j.1463-6409.1989.tb00124.x>
- Warén A. & Bouchet P. 1993. New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. *Zoologica Scripta* 22 (1): 1–90.
<https://doi.org/10.1111/j.1463-6409.1993.tb00342.x>

- Warén A. & Bouchet P. 2009. New gastropods from deep-sea hydrocarbon seeps off West Africa. *Deep Sea Research Part II: Topical Studies in Oceanography* 56 (23): 2326–2349. <https://doi.org/10.1016/j.dsr2.2009.04.013>
- Warén A. & Hain S. 1996. Description of Zeratulidae fam. nov. (Littorinoidea), with comments on an Antarctic littorinid gastropod. *The Veliger* 39 (4): 277–334. Available from <https://www.biodiversitylibrary.org/page/42501412> [accessed 10 Feb. 2024].
- Williams S.T., Donald K.M., Spencer H.G. & Nakano T. 2010. Molecular systematics of the marine gastropod families Trochidae and Calliostomatidae (Mollusca: Superfamily Trochoidea). *Molecular Phylogenetics and Evolution* 54: 783–809. <https://doi.org/10.1016/j.ympev.2009.11.008>
- Williams S.T., Smith L.M., Herbert D.G., Marshall B.A., Warén A., Kiel S., Dyal P., Linse K., Vilvens C. & Kano Y. 2013. Cenozoic climate change and diversification on the continental shelf and slope: evolution of gastropod diversity in the family Solariellidae (Trochoidea). *Ecology and Evolution* 3 (4): 887–917. <https://doi.org/10.1002/ece3.513>
- Williams S.T., Kano Y., Warén A. & Herbert D.G. 2020. Marrying molecules and morphology: first steps towards a reevaluation of solariellid genera (Gastropoda: Trochoidea) in the light of molecular phylogenetic studies. *Journal of Molluscan Studies* 86 (1): 1–26. <https://doi.org/10.1093/mollus/eyz038>
- Williams S.T., Noone E.S., Smith L.M. & Sumner-Rooney L. 2022. Evolutionary loss of shell pigmentation, pattern, and eye structure in deep-sea snails in the dysphotic zone. *Evolution* 76 (12): 3026–3040. <https://doi.org/10.1111/evo.14647>
- Zelaya D.G., Absalão R.S. & Pimenta A.D. 2006. A revision of *Benthobrookula* Clarke, 1961 (Gastropoda, Trochoidea) in the southwestern Atlantic Ocean. *Journal of Molluscan Studies* 72 (1): 77–87. <https://doi.org/10.1093/mollus/eyi050>
- Zhang Sh. & Zhang Su. 2018. Two deep-sea *Calliotropis* species (Gastropoda: Calliotropidae) from the western Pacific, with the description of a new species. *The Nautilus* 132 (1): 13–18. Available from <https://www.biodiversitylibrary.org/page/62413781> [accessed 10 Feb. 2024].

Manuscript received: 26 August 2023

Manuscript accepted: 31 October 2023

Published on: 28 February 2024

Topic editor: Magalie Castelin

Desk editor: Kristiaan Hoedemakers

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