

A REVISION OF *BENTHOBROOKULA* CLARKE, 1961 (GASTROPODA, TROCHOIDEA) IN THE SOUTHWESTERN ATLANTIC OCEAN

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ABSTRACT

A systematic revision of the species of *Benthobrookula* Clarke, 1961 from the Southwestern Atlantic Ocean was carried out. The globose protoconch, sculptured with a reticulate pattern, is recognized as a diagnostic character for the genus. *Benthobrookula exquisita* Clarke, 1961 and *B. powelli* Clarke, 1961 are redescribed and *Cyclostrema calypso* Melvill & Standen, 1912, *Brookula pfefferi* Powell, 1951 and *Brookula strebeli* Powell, 1951 are redescribed and allocated to *Benthobrookula*. *Benthobrookula strebeli* is validated on the basis of the study of topotypical specimens. Two new species are described: *Benthobrookula argentina* from South Georgia and *Benthobrookula paranaensis* from off Brazil. A new allocation of *Scalaria brevis* d'Orbigny, 1840 to *Benthobrookula* is proposed.

INTRODUCTION

Benthobrookula was proposed by Clarke (1961) as a subgenus of *Brookula* including three deep water species from the South Atlantic Ocean: *Brookula (Benthobrookula) exquisita* (type species), *Brookula (Benthobrookula) powelli* and *Brookula (Benthobrookula) lamonti*. With the one exception of Warén (1992), *Benthobrookula* was not reported after the original description, most probably due to the lack of clear diagnostic characters to separate *Benthobrookula* from *Brookula s.s.* In addition to the species described by Clarke (1961), three other species of *Brookula (s.l.)* were described from southernmost South America: *Brookula calypso* (Melvill & Standen, 1912) from Burdwood Bank and *Brookula pfefferi* Powell, 1951 and *Brookula strebeli* Powell, 1951 from shallow waters at South Georgia (the two latter were considered synonymous by Absalão, Miyaji & Pimenta, 2001). Carcelles & Williamson (1951) listed *Cyclostrema gaudens* Melvill & Standen, 1912 and *C. crassicostata* Strebel, 1907 as *Brookula*, but actually these species do not belong to the genus.

In the present paper, a systematic revision of the species of *Brookula (s.l.)* previously reported from the Southwestern Atlantic Ocean is undertaken, and all of them are placed in *Benthobrookula*. Two new species are described and arguments confirming the generic status of *Benthobrookula* are given.

MATERIAL AND METHODS

This study was primarily based on specimens collected by the R/V *Eduardo L. Holmberg* during the 1996 summer expedition to South Georgia and the R/V *Polarstern* during the 'Latin American Polarstern Studies' (LAMPOS, 2002) to the Scotia Sea (Fig. 1). Samples were taken with a dredge and fixed in 10% formalin solution. Molluscs were sorted from the sediments under a stereoscopic microscope and preserved in ethanol 70%. Voucher specimens are housed in Museo de La Plata, La Plata (MLP) and Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN). The specimens from Brazil, previously reported as *Brookula pfefferi* by Absalão *et al.* (2001) (housed in

Museu de Zoologia da Universidade de São Paulo, MZSP), were re-studied and described as a new species. Type specimens housed in the collections of the Natural History Museum, London (BMNH), Museum of Comparative Zoology, Cambridge (MCZ), Canadian Museum of Nature, Ottawa (CMNML) and National Museum of Scotland, Edinburgh (RSM), were used for comparative purposes.

Each species was redescribed and illustrated by scanning electron microscopy (SEM). Radulae were dissected and cleaned with sodium hypochloritic solution. The following shell measurements were recorded: shell width (W = maximum shell diameter) and shell length (L = maximum antero-posterior distance, perpendicular to W). The ratio L/W was calculated, the number of specimens (*n*) counted, and means and standard deviations are given.

SYSTEMATIC DESCRIPTIONS

Genus *Benthobrookula* Clarke, 1961

Type species by original designation: *Brookula (Benthobrookula) exquisita* Clarke, 1961

Benthobrookula exquisita Clarke, 1961

(Figure 2)

Brookula (Benthobrookula) exquisita Clarke, 1961: 356–357, pl. 3, Fig. 8 and pl. 4, Fig. 2 (55°29' S 37°57' W, South Georgia, 3758 m; holotype MCZ 225964 and one paratype CMNML 004742).

Material examined: Holotype and one paratype.

Description: Shell trochiform, somewhat depressed, solid, white, reaching 1.5 mm length and 1.8 mm width (Fig. 2A). Protoconch globose with one whorl, 300 µm diameter (holotype), sculptured with fine anastomosing threads, forming reticulate pattern (Fig. 2C). Teleoconch up to 2.25 whorls, rapidly increasing. Spire low, with wide spire angle (105°); last adult whorl widely expanded. Aperture nearly circular, holostomate, with

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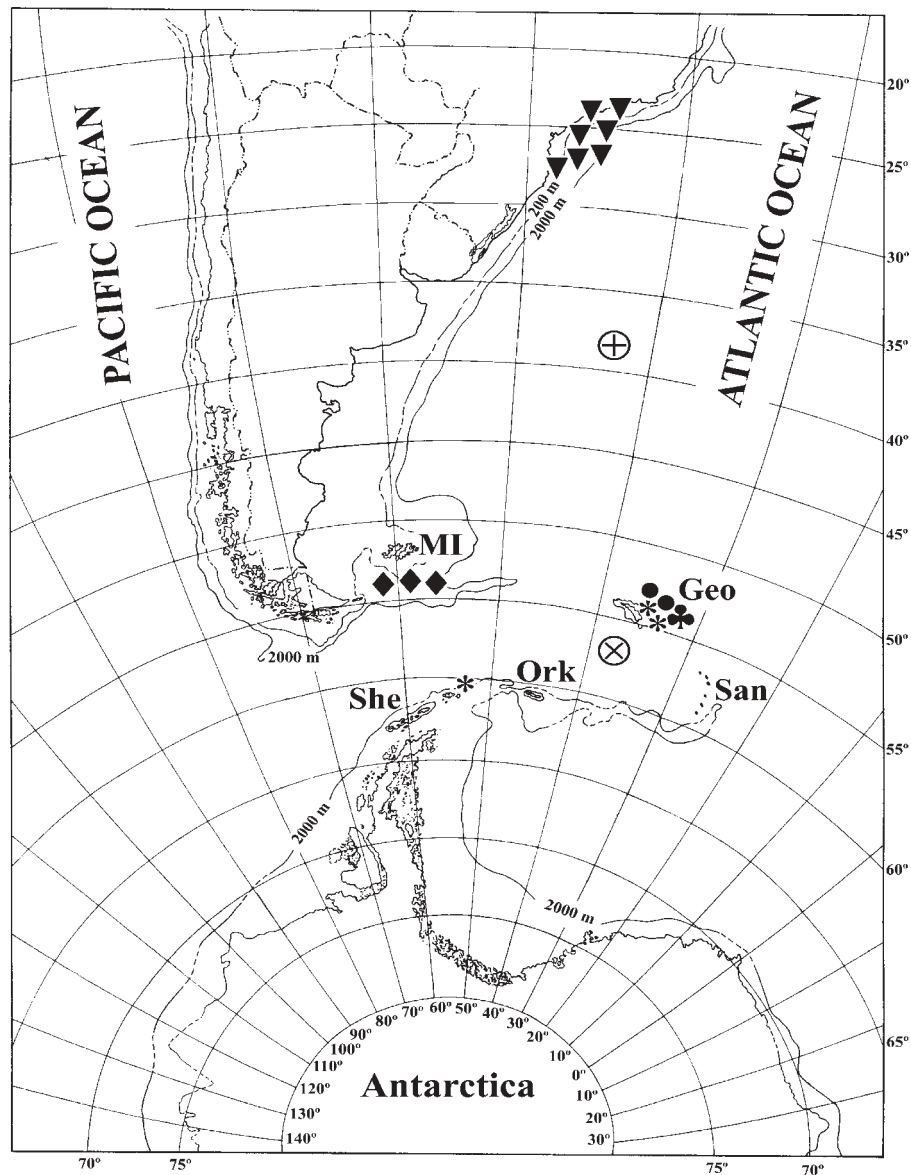


Figure 1. Location map: ♣, *Benthobrookula argentina*; ◆, *Benthobrookula calypso*; ⊗, *Benthobrookula exquisita*; *, *Benthobrookula pfefferi*; ⊕, *Benthobrookula powelli*; ●, *Benthobrookula strebeli*; ▼, *Benthobrookula paranaensis*. MI, Malvinas (Falkland) Islands; Geo, South Georgia; San, South Sandwich Islands; Ork, South Orkney Islands; She, South Shetland Islands.

thin outer lip. Shell surface strongly sculptured; axial sculpture of regularly distributed, rounded ribs, 28 on last adult whorl, separated by interspaces of about four times rib width. Spiral sculpture of few strong threads, five on early whorls, 14–17 on last adult whorl, forming small nodules at intersection with axial ribs (Fig. 2A). Umbilicus open, circular, wide, deep, surrounded by three somewhat elevated spiral cords, one of them entering the umbilicus (Fig. 2B).

Remarks: *Benthobrookula exquisita* is characterized by an expanded last adult whorl, which results in a wide spire angle (Table 1). The wide umbilicus and the heavy ornamentation of the shell are additional diagnostic features of *B. exquisita*.

Benthobrookula exquisita is most similar to *B. powelli* (Fig. 3) from which it differs in having a more laterally expanded last adult whorl (Table 1) with fewer stronger spiral threads and axial ribs.

Benthobrookula powelli Clarke, 1961

(Figure 3)

Brookula (*Benthobrookula*) *powelli* Clarke, 1961: 355–356, pl. 3, Fig. 7 and pl. 4, Figs 1, 9 (38°38.5' S 41°45' W, mid Argentine Basin, 5132 m; holotype MCZ 224960).

Material examined: holotype and seven paratypes from southwest of Cape of the Good Hope, 4586 m (CMNML 020047).

Description: Shell trochiform, somewhat depressed, solid, white, reaching 1.9 mm length and 2.3 mm width (Fig. 3A). Protoconch globose with one whorl, about 350 µm diameter, sculptured with fine anastomosing threads, forming reticulate pattern (Fig. 3C). Teleoconch of up to 2.5 rounded whorls, rapidly increasing. Spire low; spire angle $98.2 \pm 4.7^\circ$ ($n = 6$). Last adult whorl widely laterally expanded. Aperture

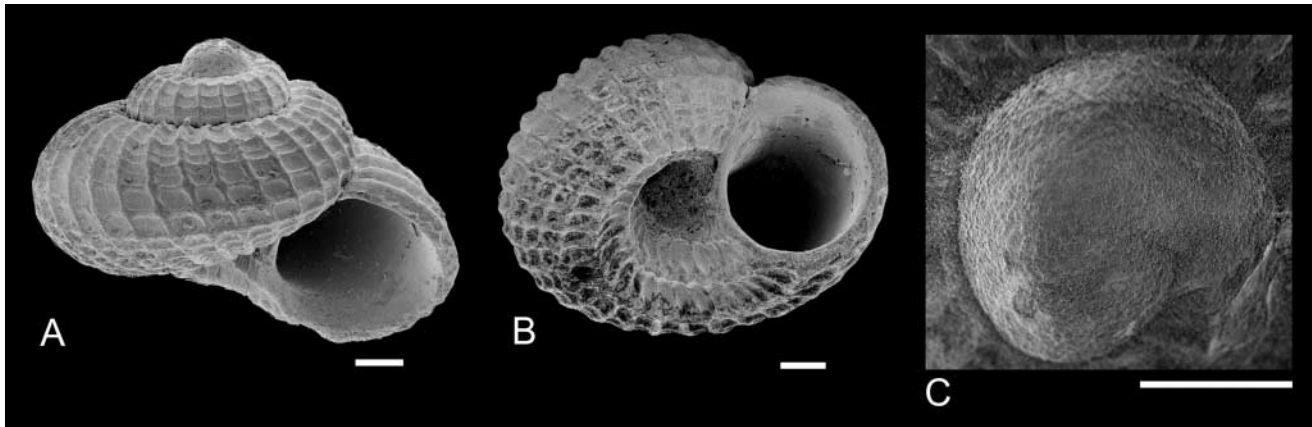


Figure 2. *Benthobrookula exquisita* Clarke, 1961, holotype (MCZ 225964). **A.** Apertural view. **B.** Umbilical view. **C.** Protoconch. Scale bars = 200 μ m.

holostomate, nearly circular, with thin outer lip. Shell surface cancellated; axial sculpture of rounded, regularly spaced ribs, 37 on the last adult whorl; interspaces between ribs three times rib width. Spiral sculpture of numerous flat threads, eight on early whorls, 35 on last adult whorl, narrower than axial ribs; small nodules are formed at the intersection of spiral threads and axial ribs (Fig. 3A). Umbilicus open, circular, wide, deep, surrounded by six elevated spiral cords, three of them entering the umbilicus (Fig. 3B).

Remarks: *Benthobrookula powelli* resembles *B. exquisita* (Fig. 2) in shell shape, differing in the larger number of more closely arranged spiral threads and axial ribs on the last whorl. The last adult whorl is less laterally expanded and the spire angle is lower in *B. powelli* than in *B. exquisita* (Table 1). *Benthobrookula powelli* and *B. exquisita* clearly differ from the remaining Southwestern Atlantic species in having a more laterally expanded last whorl (Table 1) and stronger spiral threads surrounding a very wide umbilicus.

Clarke (1961) reported *B. powelli* as occurring on both sides of the Atlantic Ocean; however such a wide geographical distribution seems strange. The analysis of the conspecificity of these specimens must await additional material from both areas. Clarke (1961) also reported the species from South Georgia (1902 fathoms), but the paratype from this locality could not be located in collections of the CMNML or MCZ (R. Baird & A. Baldinger, personal communication), where other material studied by Clarke was deposited.

Table 1. Shell measurements of the species of *Benthobrookula* here studied.

Species	Shell length (mm)	Shell width (mm)	Ratio L/W	Spire angle (°)
<i>B. argentina</i> (n = 14)	1.22 ± 0.11	1.18 ± 0.09	1.03 ± 0.03	86.6 ± 1.5
<i>B. calypso</i> (n = 1)	1.29	1.2	1.07	90
<i>B. exquisita</i> (n = 2)	1.33 ± 0.24	1.59 ± 0.30	0.84 ± 0.01	105
<i>B. paranaensis</i> (n = 6)	1.46 ± 0.14	1.51 ± 0.17	0.96 ± 0.03	91.2 ± 5.5
<i>B. pfefferi</i> (n = 14)	1.52 ± 0.08	1.46 ± 0.08	1.04 ± 0.02	87.5 ± 3.9
<i>B. powelli</i> (n = 6)	1.50 ± 0.33	1.74 ± 0.37	0.87 ± 0.06	98.2 ± 4.7
<i>B. strebeli</i> (n = 15)	1.34 ± 0.07	1.12 ± 0.04	1.20 ± 0.04	80.9 ± 1.1

***Benthobrookula argentina* new species**

(Figure 4)

Type material: Holotype (MLP 11977) and 10 paratypes from type locality (five in MLP 11978, five in MACN-In 36379).

Type locality: 54°18' S 35°30' W, South Georgia, 94 m.

Etymology: The species name refers to the Argentine Republic.

Other material examined: 95 specimens from type locality (MLP 11979, MACN-In 36380).

Description: Shell trochiform, globose, solid, white, reaching 1.40 mm length and 1.29 mm width (Fig. 4A, B). Protoconch of one whorl, globose, about 300 μ m diameter, sculptured with fine anastomosing threads, forming reticulate pattern (Fig. 4D, E). Teleoconch up to 2.5 rounded whorls. Spire low; spire angle $86.6 \pm 1.5^\circ$ (n = 14). Last adult whorl globose, only slightly expanded laterally. Aperture nearly circular, holostomate, with thin outer lip. Shell surface heavily cancellated; axial sculpture of solid rounded ribs, 24–30 on last adult whorl; interspaces between ribs four times rib width (Fig. 4A, B); secondary intercalated axial ribs are present at base of last adult whorl (Fig. 4C); spiral sculpture consisting of a few cords, four to five on first whorls, six to eight on last adult whorl, only slightly narrower than axial ribs (Fig. 4A, B). Umbilicus open, circular, deep, surrounded by two to three wide, flat spiral cords, well-separated from remaining spiral threads (Fig. 4C). Operculum circular, with central nucleus (Fig. 4F).

Radula: 5–2–1–2–5 (Fig. 4H). Rachidian tooth stout, rather higher than wide, basal plate with a trapezoidal outline; cutting edge wide; main cusp triangular, sometimes bifid, and 9–11 narrower and sharper (reduced in size outwards) secondary cusps on each side (Fig. 4I). Innermost lateral tooth plate-like, triangular in outline, narrower than rachidian tooth, weakly cusped; outer lateral tooth large, claw-shaped, solid, with a prominent main cusp and serrated outer and inner margins (Fig. 4I). Marginal teeth similar to outer lateral tooth, but narrower and with smaller cusps (Fig. 4H). Jaws subquadrangular, thin, paved with rows of juxtaposed rectangular pieces; the anterior margin of each piece is toothed while the posterior one is smooth (Fig. 4G).

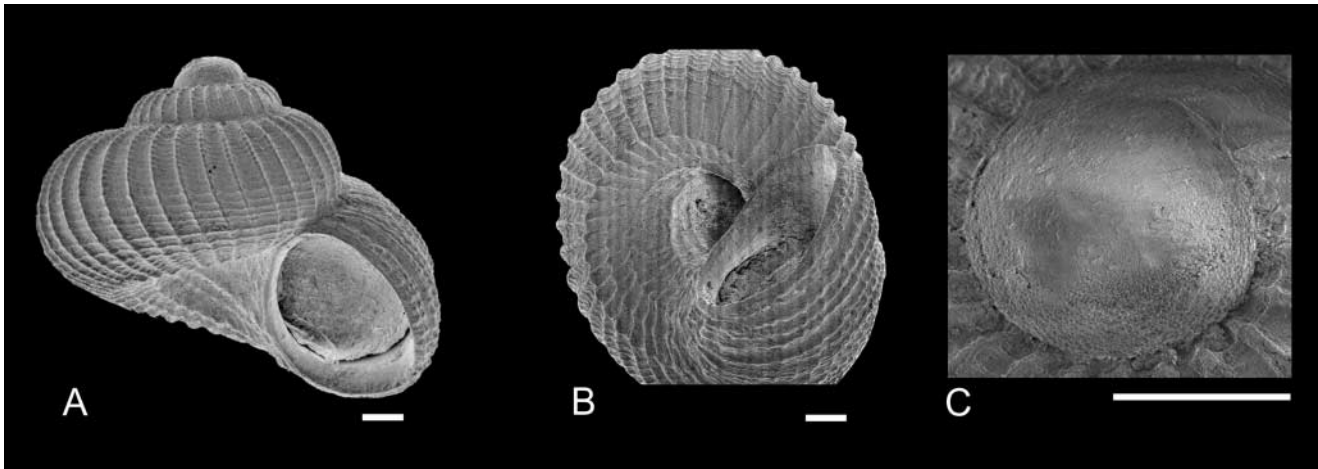


Figure 3. *Benthobrookula powelli* Clarke, 1961, holotype (MCZ 224960). **A.** Apertural view. **B.** Umbilical view. **C.** Protoconch. Scale bars = 200 μm .

Remarks: *Benthobrookula argentina* is well defined by its reduced number of spiral cords on the last whorl. It resembles *B. exquisita* (Fig. 2) and *B. powelli* (Fig. 3) in shell shape but differs from both in having a smaller shell with less laterally expanded last whorl and smaller spire angle (Table 1). *Benthobrookula argentina* also differs from *B. exquisita* and *B. powelli* by its narrower umbilicus with more delicate spiral cords surrounding it. It differs from *B. pfefferi* (Fig. 5), *B. strebeli* (Fig. 6) and *B. calypso* (Fig. 8) in having a stronger shell ornamentation, with a fewer spiral threads on the last whorl. The lower L/W ratio and the greater spire angle in *B. argentina* are additional characters separating it from *B. strebeli*.

***Benthobrookula pfefferi* (Powell, 1951) new comb.**

(Figure 5)

Brookula pfefferi Powell, 1951: 104, pl. 5, fig. 8 (54°04' S 36°27' W to 53°58' S 36°26' W, off mouth of Stromness Harbour, South Georgia, 155–178 m; holotype BMNH 1961368). Zelaya, 2005: 115, fig. 13.

Material examined: holotype (photographs); two specimens, 54°30' S 35°50' W, South Georgia, 94 m (MACN-In 36280; MLP 6847); 18 specimens and 10 shells, 61°23' S 55°27' W, Elephant Islands, 126–155 m (MLP 6846).

Description: Shell trochiform, globose, only slightly expanded laterally, solid, translucent, white, reaching 1.83 mm length and 1.74 mm width (Fig. 5A–C). Protoconch of one whorl, globose, 330–400 μm diameter, sculptured with fine anastomosing threads, forming reticulate pattern (Fig. 5E). Spire low; spire angle $87.5 \pm 3.9^\circ$ ($n = 14$). Teleoconch up to 2.5 rounded whorls. Aperture nearly circular, holostomate, with thin outer lip. Shell surface cancellated; axial sculpture of fine, low, rounded and regularly distributed ribs, 36–38 on last adult whorl, separated by wide interspaces; spiral sculpture of numerous flat threads, 5–12 on first whorls, 20–26 on last adult whorl (Fig. 5A–C). Umbilicus open, circular and deep, surrounded by three to four wide, flat, spiral cords (Fig. 5D). Operculum, radula (Fig. 5F, G) and jaw plates (Fig. 5H, I) as in *B. argentina*.

Remarks: *Benthobrookula pfefferi* is most similar to *B. powelli* (Fig. 3), differing in having a less laterally expanded last whorl and a lower spire angle (Table 1). The number of spiral

threads is lower in *B. pfefferi* than in *B. powelli*, and the spiral cords surrounding the umbilicus more delicate in the former. *Brookula decussata* Pelseneer, 1903 (type locality: 70° S 80°48' W, 500 m), another similar species, clearly differs from *Benthobrookula pfefferi* in having a smaller shell, with fewer, more separated, spiral threads.

Benthobrookula pfefferi differs from *B. strebeli* (Fig. 6) and *B. calypso* (Fig. 8) in having a more laterally expanded last adult whorl with more spiral threads (Table 1). In addition, the umbilicus in *B. pfefferi* is wider than in *B. strebeli*. The more delicate shell sculpture and a large number of spiral threads on the last whorl clearly distinguish *B. pfefferi* from *B. exquisita* (Fig. 2) and *B. argentina* (Fig. 4). *Benthobrookula pfefferi* also differs from *B. exquisita* in having a less laterally expanded last whorl, and from *B. argentina* in the shape of the rachidian tooth, with a larger main cusp.

Most of the examined specimens of *B. pfefferi*, as well as the holotype, showed two distinctive series of spiral threads on the last whorl: the upper one with about 10 well-separated threads, and the lower one with about 15 more closely arranged threads (Fig. 5A, B); however, two specimens from South Georgia showed regularly distributed spiral threads on the entire surface of the last whorl (Fig. 5C).

***Benthobrookula strebeli* (Powell, 1951) new comb.**

(Figure 6)

Brookula strebeli Powell, 1951: 104, pl. 5, fig. 7 (54°04' S 36°27' W to 53°58' S 36°26' W, off mouth of Stromness Harbour, South Georgia, 155–178 m; holotype BMNH 1961369).

Material examined: holotype (photographs); 146 specimens and 27 shells, 54°30' S 35°50' W, South Georgia, 94 m (MLP 6848, MACN 36280-1).

Description: Shell trochiform, globose, solid, white, reaching 1.54 mm length and 1.20 mm width (Fig. 6A, B). Protoconch of one whorl, globose, about 300 μm diameter, sculptured with fine anastomosing threads, forming reticulate pattern (Fig. 6D, E). Teleoconch of up to two rounded whorls. Spire low; spire angle $80.9 \pm 1.1^\circ$ ($n = 15$). Last adult whorl globose. Aperture sub-circular, holostomate, with thin outer lip. Shell surface ornamentated with cancellated sculpture; axial sculpture of rounded, regularly distributed ribs, 20 on last whorl, separated by interspaces four times wider than ribs (Fig. 6A, B); additional secondary axial ribs present at base

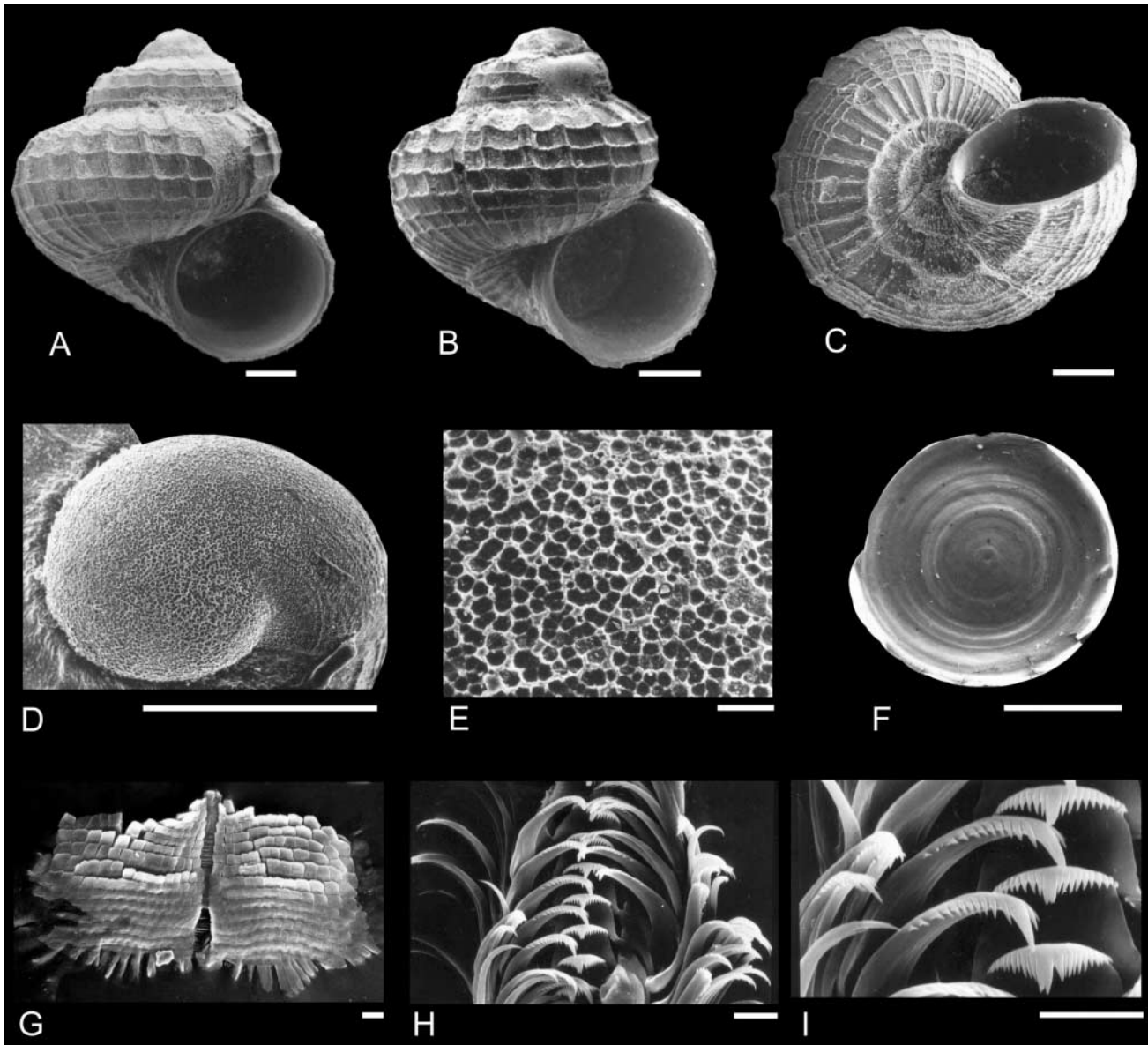


Figure 4. *Benthobrookula argentina* new species. **A.** Holotype (MLP 11977). **B–E.** Other material (MLP 11979). **B.** Apertural view. **C.** Umbilical view. **D.** Protoconch. **E.** Detail of protoconch sculpture. **F.** Operculum. **G.** Internal view of jaws. **H.** Radula. **I.** Details of central and lateral teeth. Scale bars: **A–D, F** = 200 μm ; **E, G–I** = 10 μm .

(Fig. 6C). Spiral sculpture of few narrow threads: six on early whorls, 14 on last adult whorl, more closely arranged towards base (Fig. 6A, B). Umbilicus closed, surrounded by three to four flat spiral cords well separated from remaining spiral threads (Fig. 6C).

Radula (Fig. 6F, G) and jaw plates (Fig. 6H, I) as in *B. argentina*.

Remarks: *Benthobrookula strebeli* can be easily identified by its closed umbilicus, a globose, not laterally expanded, last whorl ($L/W = 1.20 \pm 0.04$), an acute spire angle and a reduced number of axial ribs (Table 1). *Benthobrookula strebeli* is most similar to *B. calypso* (Fig. 8), differing in having a smaller number of spiral threads on the last whorl and a closed umbilicus.

Absalão *et al.* (2001) considered *Benthobrookula strebeli* a synonym of *B. pfefferi*. The present study of additional specimens

from South Georgia make it clear that these are different species; while the last whorl is globose in *B. strebeli* (Fig. 6A, B), it is laterally expanded in *B. pfefferi* (Fig. 5A–C); the umbilicus is open and deep in *B. pfefferi* (Fig. 5D) and closed in *B. strebeli* (Fig. 6C); the number of spiral threads and axial ribs is lower in *B. strebeli* than in *B. pfefferi*, and the spiral threads are stronger in *B. strebeli*.

***Benthobrookula paranaensis* new species**
(Figure 7)

Brookula pfefferi—Absalão *et al.*, 2001: 681–685, Fig. 3C–F (not Powell, 1951).

Type material: Holotype (MZSP 47251) and four paratypes from type locality (MZSP 32506).

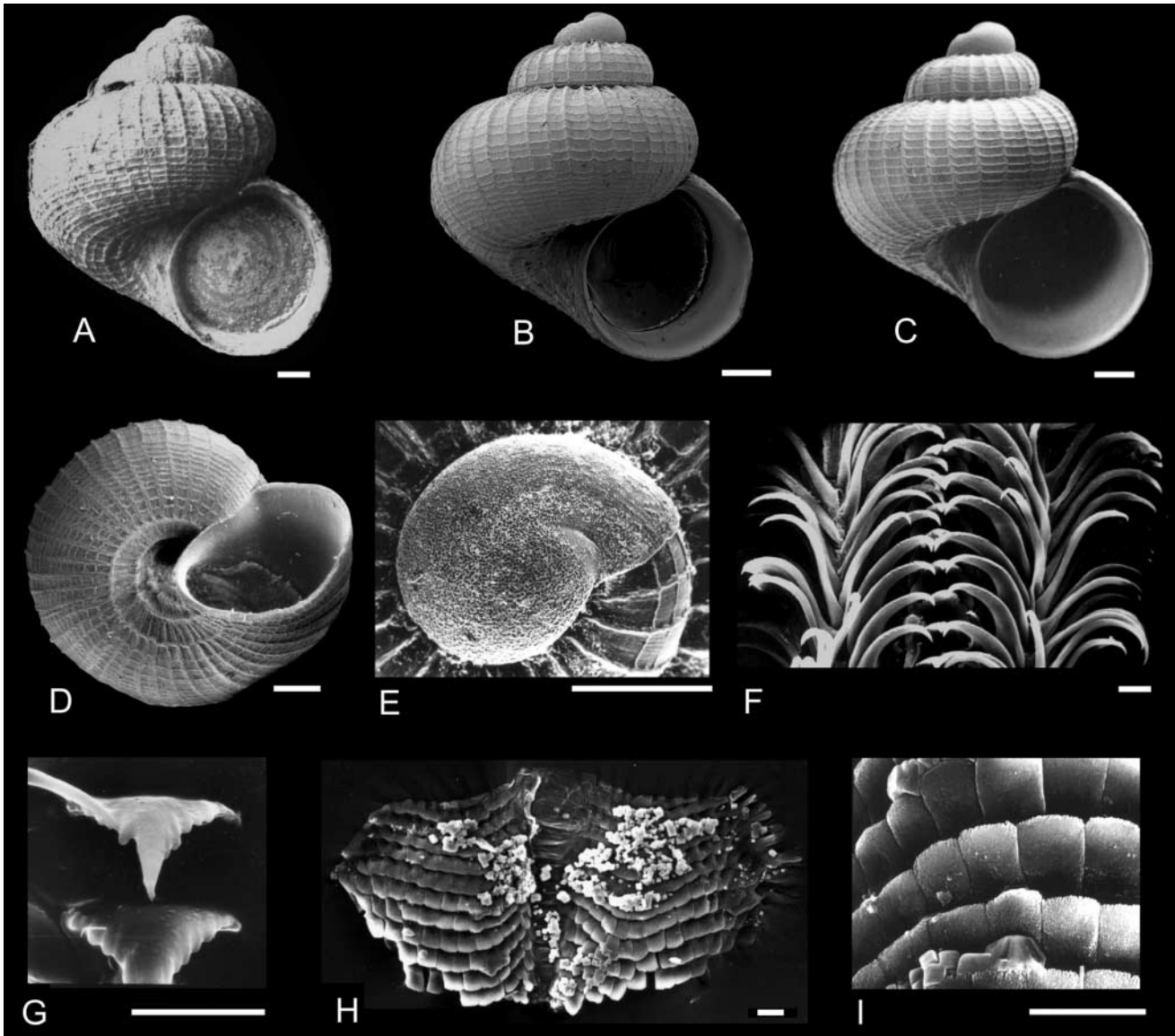


Figure 5. *Benthobrookula pfefferi* (Powell, 1951). **A–C.** Apertural view. **A.** Holotype (BMNH 1961.368). **B,D,I.** Specimens from Elephant Island (MLP 6846). **C.** Specimen from South Georgia (MACN-In 36280). **D.** Umbilical view. **E.** Protoconch. **F.** Radula. **G.** Detail of central tooth. **H.** Internal view of jaws. **I.** Detail of jaw. Scale bars: **A–E** = 200 μm ; **F–I** = 10 μm .

Type locality: 25°53.58' S 45°42.13' W, off Paraná State, Brazil, 256 m.

Etymology: The species name refers to the state of Paraná, Brazil, where the species was collected.

Other material examined: One shell, 24°49.70' S 44°44.97' W, 153 m (MZSP 32510); two shells, 24°0.95' S 43°55.54' W, 135 m (MZSP 32509); five shells, 27°48.07' S 47°24.04' W, 175 m (MZSP 32504); one shell, 27°18.28' S 47°08.77' W, 228 m (MZSP 32503); one shell, 25°51.04' S 45°47.3' W, 206 m (MZSP 32507); one shell, 26°30.99' S 46°15.27' W, 474 m (MZSP 32505).

Description: Shell trochiform, globose, white, reaching 1.62 mm length and 1.76 mm width (Fig. 7A, B). Protoconch of one whorl, globose, about 270 μm diameter, sculptured with fine anastomosing threads, forming a reticulate (Fig. 7E, F).

Teloconch of up to 2.75 rounded whorls, with convex profile. Spire low; spire angle $91.2 \pm 5.5^\circ$ ($n = 6$). Last adult whorl globose, only slightly expanded laterally. Aperture circular, holostomate, with thin outer lip. Axial sculpture of narrow ribs, 42 on last whorl in the holotype, becoming more delicate towards base. Interspaces between ribs twice rib width (Fig. 7D). Spiral sculpture consisting of very thin threads: four on first whorls; 20–21 on last adult whorl (Fig. 7A–D); sometimes upper part of last whorl shows fewer, more widely spaced spiral threads (Absalão *et al.*, 2001: figs 3E, F). Umbilicus open, circular, deep, surrounded by three to four thin spiral cords, well separated from remaining spirals threads (Fig. 7C).

Remarks: *Benthobrookula paranaensis* is based on the material reported by Absalão *et al.* (2001) as *Brookula pfefferi* Powell, 1951. Absalão *et al.* (2001) indicated their doubts about the identification of the Brazilian material. The examination of additional specimens of *Benthobrookula pfefferi* from South

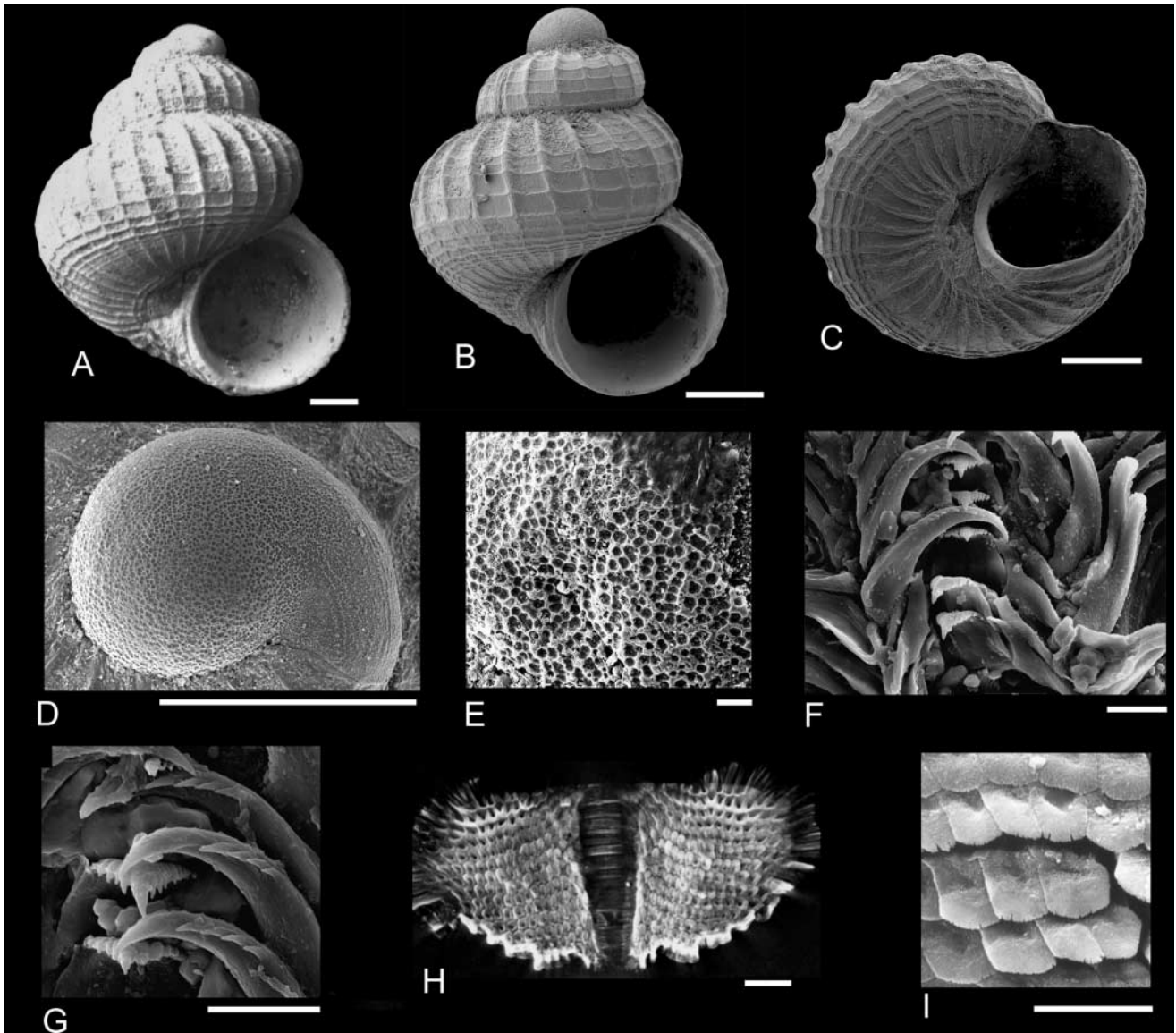


Figure 6. *Benthobrookula strebeli* (Powell, 1951). **A, B.** Apertural view. **A.** Holotype (BMNH 1961.369). **B–I.** Specimens from South Georgia (MLP 6848). **C.** Umbilical view. **D.** Protoconch. **E.** Detail of protoconch sculpture. **F.** Radula. **G.** Detail of central and lateral teeth. **H.** External view of jaws. **I.** Detail of internal view of jaw. Scale bars: **A–D** = 200 μm ; **E–I**: 10 μm .

Georgia allowed us to confirm that the material from Brazil belongs to a new species. *Benthobrookula paranaensis* is most similar to *B. pfefferi*, from which it differs in having a lower spire with greater spire angle (Table 1), and weaker sculpture, particularly at the base of the last whorl. These two species are allopatric.

***Benthobrookula calypso* (Melvill & Standen, 1912)
new comb.**

(Figure 8)

Cyclostrema calypso Melvill & Standen, 1912: 345, fig. 3 (54°25' S 57°32' W, Burdwood Bank, 102 m; holotype RSM 143599).

Material examined: Holotype; one specimen, 54°01' S 62°01' W, Burdwood Bank, 272 m (MLP 11980); one specimen, 54°30' S 56°08' W, Burdwood Bank, 286–290 m (MLP 11981).

Description: Shell trochiform, globose, solid, white, reaching 1.29 mm length and 1.2 mm width (Fig. 8A, B). Protoconch of one whorl, globose, about 295 μm diameter, sculptured with fine anastomosing threads, in reticulate pattern (Fig. 8C, F). Teleoconch of up to 2.5 rounded whorls. Spire low; spire angle 90° ($n = 1$). Last whorl globose. Aperture nearly circular, holostomate, with thin outer lip. Shell surface densely cancellated; axial sculpture of fine, very low, rounded and regularly distributed ribs, 38 on last adult whorl; interspaces between ribs three times rib width; secondary intercalated axial ribs are present on base. Spiral sculpture: 14–17 flat, regularly spaced threads on last adult whorl (Fig. 8A, B). Umbilicus open, circular, narrow, deep, surrounded by two flat spiral cords (Fig. 8D, E).

Remarks: *Benthobrookula calypso* is most similar to *B. pfefferi* from which it differs in being smaller and having a less expanded last whorl with fewer spiral threads. *Benthobrookula calypso*

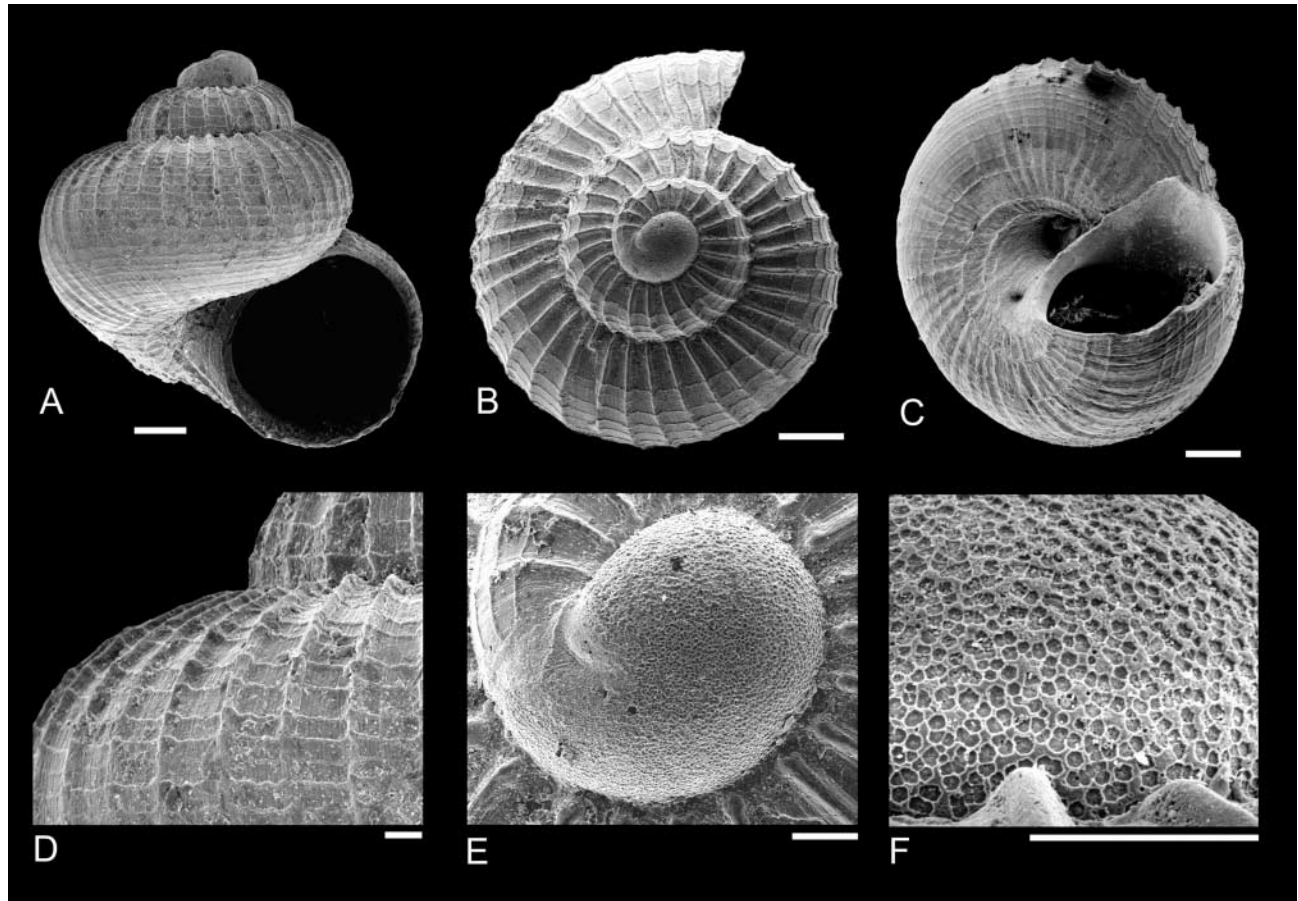


Figure 7. *Benthobrookula paranaensis* new species. **A, C–F.** Holotype (MZSP 47251). **B.** Paratype (MZSP 32506). **A.** Apertural view. **B.** Apical view. **C.** Umbilical view. **D.** Detail of shell sculpture on the last whorl. **E.** Protoconch. **F.** Detail of protoconch sculpture. Scale bars: **A–C:** 200 μm ; **D–F:** 50 μm .

differs from *B. strebeli* (Fig. 6) in having more spiral threads and axial ribs on the last whorl, and an open umbilicus. The globose last whorl and the delicate shell ornamentation of *B. calypso* separate the species from *B. exquisita* (Fig. 2), *B. powelli* (Fig. 3) and *B. argentina* (Fig. 4).

DISCUSSION

Other species of *Benthobrookula*

Benthobrookula lamonti Clarke, 1961 (Fig. 9) was described on the basis of a single specimen collected at 55°29' S 37°57' W, South Georgia, 3758 m depth, and the species has not been reported again. In the original description, Clarke (1961) placed *B. lamonti* in *Benthobrookula* based on the 'apparent bulbouse' protoconch, pointing out the narrow umbilicus, the acute spire and the prominent axial ribs as diagnostic characters for the species. However, this character combination is not exclusive of *B. lamonti*. As the holotype of *B. lamonti* (MCZ 225963) is presently severely damaged, and taking into consideration the rather poor original description and the lack of additional material, the redescription and discussion of the similarities with other species of *Benthobrookula* remains pending.

The Antarctic species *Benthobrookula delli* (Numanami, 1996) and the Brazilian species *Benthobrookula conica* (Watson, 1886), *Benthobrookula spinulata* (Absalão et al., 2001), *Benthobrookula megaumbilicata* (Absalão & Pimenta, 2005), *Benthobrookula proseila*

(Absalão & Pimenta, 2005) and *Benthobrookula olearia* (Absalão & Pimenta, 2005) share the same general morphology and sculpture of the protoconch described here for the Southwestern Atlantic species of *Benthobrookula* (all of them were previously referred to as *Brookula*).

Scalaria brevis d'Orbigny, 1840 (Fig. 10) was described on the basis of a single specimen from Malvinas (Falkland) Islands and has not been reported again. The type material housed in BMNH is now completely disintegrated (K. Way, personal communication). Judging from the original description and figure the species is not a member of the genus *Scalaria*, but most probably a *Benthobrookula* species; however, the protoconch ornamentation could not be examined to confirm the generic placement. *Benthobrookula* (?) *brevis* resembles *B. strebeli* and *B. calypso*, differing from the former in having an open umbilicus and more spiral threads on the last whorl, and from *B. calypso* by the more delicate axial ribs. The slightly angulated last whorl also separates *B. (?) brevis* from other Southwestern Atlantic Ocean species.

Geographic distribution of *Benthobrookula*

Species of *Benthobrookula* are found in the South Atlantic Ocean, distributed from Antarctic (Clarke, 1961; this study) to Brazilian waters (see above). Eight species are reported here from southernmost South America and six species are known from

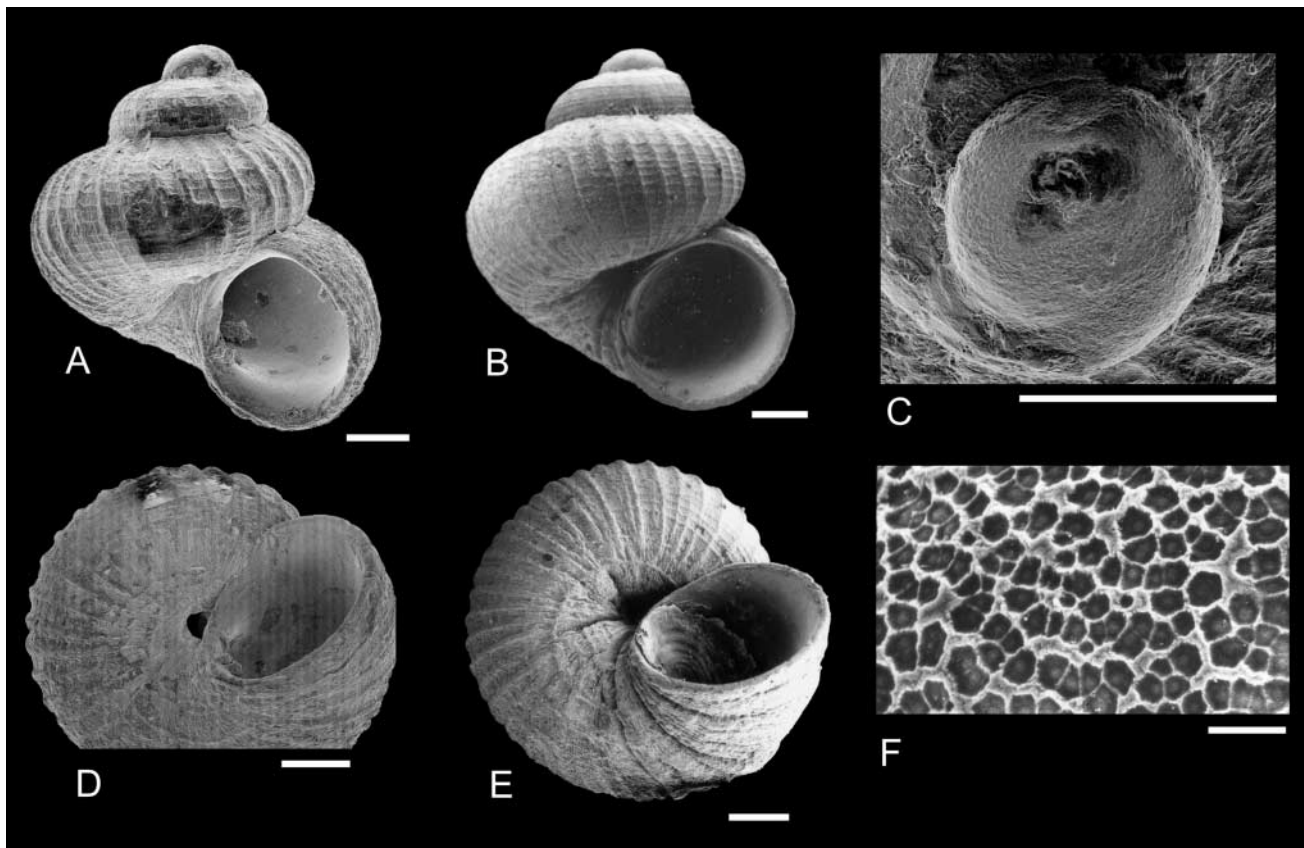


Figure 8. *Benthobrookula calypso* (Melvill & Standen, 1912). **A, B.** Apertural view. **C.** Protoconch. **D, E.** Umbilical view. **F.** Detail of protoconch sculpture. **A, C, D.** Holotype (RSM 153599). **B, E, F.** Specimen from Burdwood Bank (MLP 11980). Scale bars: **A–E** = 200 μm ; **F** = 10 μm .

Brazil. In addition, two species (*B. capensis* (Clarke, 1961) and *B. powelli*) were reported as occurring in the Southeast Atlantic Ocean (Clarke, 1961).

Although *Benthobrookula* was originally described by Clarke (1961) as a deep-water genus (*B. exquisita*, *B. powelli* and *B. lamonti* were collected between 3758 and 4586 m depth) the present study reveals that there are some species of the genus (*B. strebeli*, *B. pfefferi*, *B. calypso* and *B. argentina*) living in waters of only 100 m depth.

Taxonomic status of *Benthobrookula*

The species examined here are characterized by a small trochiform shell, up to 3.5 rounded whorls, with a relatively low spire; the protoconch is globose, sculptured with delicate anastomosing threads, forming a reticulate pattern; the last whorl is globose, sometimes laterally expanded; the shell surface is cancellated. The umbilicus is variably developed, ranging from widely open as in *Benthobrookula exquisita* (Fig. 2B) and *B. powelli* (Fig. 3B) to closed in *B. strebeli* (Fig. 6C).

Benthobrookula was originally proposed as a subgenus of *Brookula*, a criterion also followed by Vaught (1989). However, the evidence on protoconch morphology and ornamentation reported here supports the separation of *Benthobrookula* and *Brookula*, as previously suggested by Warén (1992). Summarizing, the protoconch is globose and densely sculptured with a reticulate pattern (also referred to as ‘alveolar pattern’) in *Benthobrookula*; on the contrary, in *Brookula* the protoconch is not inflated and the surface is smooth. In addition, Clarke (1961) stated that the protoconch in *Benthobrookula* is larger

than in *Brookula* in agreement with data reported here: in *Benthobrookula* protoconchs range from 300 to 400 μm wide while it is 245 μm in diameter in *Brookula stibarochila* (Warén, 1992).

The protoconch sculpture of *Benthobrookula* has been previously erroneously interpreted by several authors. It was described as smooth in *B. calypso*, *B. exquisita*, *B. powelli* and *B. lamonti* (Melvill & Standen, 1912; Clarke, 1961). Absalão *et al.* (2001) redescribed the protoconch of *B. exquisita*, *B. calypso* and *B. powelli* as having ‘a surface covered by very low, irregular wart-like concretions’. A re-examination of the holotype and paratypes of *B. powelli* (Fig. 3) and *B. exquisita* (Fig. 2) under SEM revealed (in better preserved areas) the presence of the above mentioned reticulate pattern (Figs 2C, 3C). The same characteristics were also found in topotypic specimens of *B. calypso* (Fig. 8F). Discrepancies among descriptions are clearly a consequence either of different observational techniques used or the quality of the material examined. The reticulate pattern is only visible through SEM in well preserved specimens; when the protoconch is eroded this pattern disappears and the ‘wart-like concretions pattern’ (reported by Absalão *et al.*, 2001, in the holotypes of *B. exquisita*, *B. powelli* and *B. calypso*) appears.

On the suprageneric placement of *Benthobrookula*

Benthobrookula is currently placed in the Trochoidea, either in Cyclostrematidae (Clarke, 1961) or Skeneidae (Warén, 1992; Numami, 1996). Absalão *et al.* (2001) reported *Benthobrookula lamonti*, *B. calypso*, *B. powelli*, *B. exquisita*, *B. conica*, *B. pfefferi* and *B. spinulata* under *Brookula* in the trochid subfamily Eucyclinae,

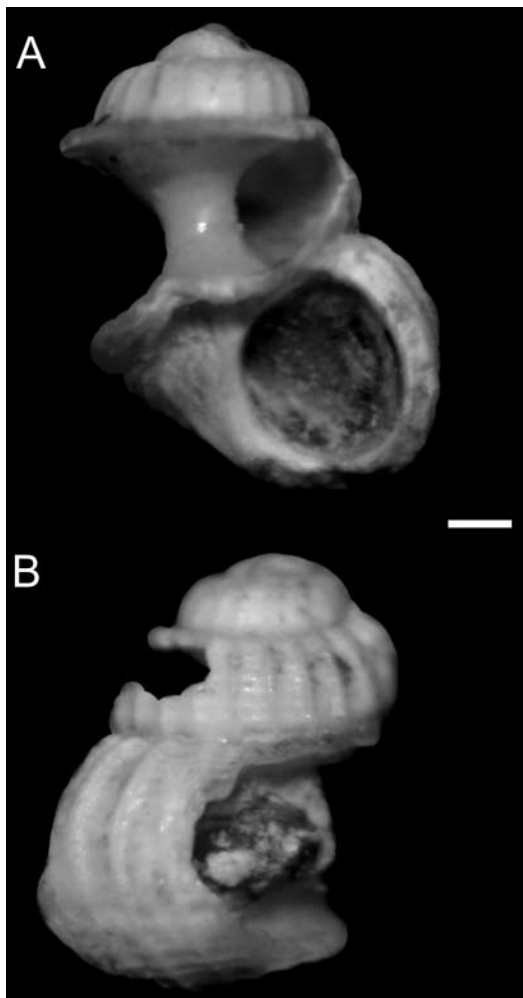


Figure 9. *Benthobrookula lamonti* (Clarke, 1961), holotype (MCZ 225953). Scale bar = 200 μm .

following the suprageneric placement proposed by Warén (1992). According to the criteria of Hickman & McLean (1990) and Warén (1992), the general shell morphology of *Benthobrookula* clearly corresponds to Skeneidae, and not to Trochidae or Cyclostrematidae. Furthermore, Hickman & McLean (1990) and Hickman (1998) reported that Skeneidae are not a monophyletic group. Due to this fact and the confusing definition of Skeneidae, the decision about the suprageneric placement of *Benthobrookula* is postponed. In the meantime the genus is retained in Trochoidea, as previously proposed.

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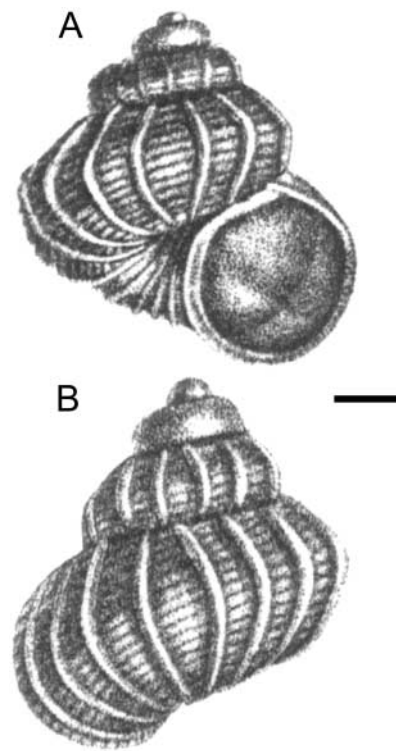


Figure 10. *Benthobrookula* (?) *brevis* (d'Orbigny, 1840). Reproduction of the original figure (d'Orbigny, 1840: pl. 75, Figures 22, 24). Scale bar = 200 μm .

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