



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*

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Abstract

Among benthic mollusc samples from the deep Southern Atlantic Ocean collected during various expeditions of the German Research Vessel *Polarstern* were several representatives of the genus *Brookula*, of which four new deep water records are presented herein. Two of the species, *B. bohni* sp. nov. and *B. charleenae* sp. nov. are described and differences to congeners are given. For *Brookula argentina* (Zelaya, Absalão & Pimenta, 2006) and *B. exquisita* Clarke, 1961 range extensions are provided. The problematic use of the genus *Benthobrookula* instead of the genus *Brookula* is discussed and the use of the genus name *Benthobrookula* is discouraged until more detailed data on morphology and anatomy are available. For the first time the soft part gross morphology of *Brookula pfefferi* Powell, 1951 has been investigated and illustrated. *Brookula decussata* (Pelseneer, 1903) has to be regarded as a potential senior synonym of *B. pfefferi*. Examination of the type material has shown that *B. antarctica* Dell, 1990 does not differ from *B. strebeli* Powell, 1951 and the former becomes a junior synonym of *B. strebeli*. Morphometric data for all *Brookula* species from the Subantarctic and Antarctic waters of the Southern Atlantic Ocean are also provided, allowing a total of nine species to be included in this sector.

Key words: Vetigastropoda, Trochoidea, *Brookula*, Antarctica, deep-sea, taxonomy

Introduction

Among Antarctic deep-water gastropods (Schwabe *et al.* 2007) species of the genus *Brookula* belong to the more minute forms (up to 2.5 mm). Their small size may be the reason why the older literature contains few records (e.g., Thiele 1925, Powell 1951). With optimized sampling technologies (e.g., Agassiz Trawl with an inlet of 500 µm mesh size), a more detailed study of deep sea bottom communities, including organisms of all sizes, is possible. The new material permitted the study of the minute species in *Brookula* and the newly established genus *Benthobrookula* (see Zelaya *et al.* 2006), including the comparison of several new species described during the last few decades (Clarke 1961, Dell 1990, Numanami & Okutani 1991, Numanami 1996, Absalão *et al.* 2001, Absalão & Pimenta 2005, Zelaya *et al.* 2006). Absalão *et al.* (2001) and Zelaya *et al.* (2006) illustrated and described all primary types of the species of *Brookula* from the Southern Atlantic Ocean. However, despite their efforts to clarify the taxonomic status of the described species of *Brookula*, there is no agreement about the systematic position of the genus within the Vetigastropoda.

The genus was originally introduced with the characters of its type species *Brookula stibarochila* Iredale, 1912 (pp. 219–220) as follow: “Shell minute, globosely turbinate, perforate, glassy, transparent... First whorl

and a half unsculptured, the succeeding whorls bearing sloping axial laminae, the interstices crossed with fine regular striae...Aperture circular, continuous. Umbilicus narrow and deep". The lack of iridescence of the inner shell layer has never been mentioned. This character is unusual for trochids (Hickman & McLean 1990, as nacreous layer) and could be interpreted as a skeneid shell character. However, the absence of iridescence does not necessarily mean that a nacreous layer is lacking and some skeneid gastropods do have such a layer (Marshall 1988). Absalão *et al.* (2001) and Absalão & Pimenta (2005) followed Warén (1992), who provisionally placed the genus *Brookula* in the trochid subfamily Eucyclinae; other authors placed the genus in the families Skeneidae (= "Cyclostrematidae" of authors, *non* P. Fischer, 1885) (e.g., Iredale 1912, Thiele 1925, Clarke 1961, 1962, Kay 1979, Hickman & McLean 1990, Dell 1990, Numanami & Okutani 1991, Numanami 1996, Tsuchida & Hori 1996, Lindner 1999, de Barros *et al.* 2001, Zelaya 2005) or in the family Liotiidae (e.g., Finlay 1924, Powell 1937, 1951, 1960; but see Powell 1979). To highlight the unresolved systematic status of the genus Zelaya *et al.* (2006) placed the taxon under Trochoidea. Surprisingly, they transferred all so far known Antarctic *Brookula* species to *Benthobrookula* Iredale, 1912 only due to differences in protoconch diameter and ornamentation in both genera. Iredale (1912) already used differences in protoconch diameters to place *Cyclostrema conicum* Watson, 1886 in *Brookula*.

Bouchet & Rocroi (2005) classified both Skeneidae (as Skeneinae) and the Liotiidae (= Cyclostrematidae) under the superfamily Turbinoidea.

The examination of the shell morphology alone will not solve the problem of the family membership of *Brookula* s.l. Zelaya *et al.* (2006) provided the first SEM (scanning electron microscope) images of radulae, after Thiele (1925) illustrated the first radula of a potential *Brookula* species, of select southern Atlantic *Benthobrookula* species (but see remarks under *Brookula argentina*, and also Dell 1990 for generic assignment of species). However, shell and radula characteristics alone were insufficient to determine the classification of the genus. Anatomical and genetic work is needed.

In the context of an inventory of Antarctic molluscs, the authors encountered several brookulid species. The following species were identified: *Brookula argentina* (Zelaya, Absalão & Pimenta, 2006), *B. calypso* (Melvill & Standen, 1912), *B. exquisita* Clarke, 1961, *B. pfefferi* Powell, 1951, and *B. strebeli* Powell, 1951. The aim of the present paper is to describe two additional new species, illustrate the soft part anatomy of *Brookula pfefferi*, and giving range extensions for *B. argentina* (Zelaya, Absalão & Pimenta, 2006) and *B. exquisita* Clarke, 1961. Moreover, a comparative table of characters for all Antarctic and Subantarctic *Brookula* species is given. For information on the remaining species considered herein we refer to the works of Absalão *et al.* (2001) and Zelaya *et al.* (2006).

Material and methods

This study was based on specimens collected by the German RV *Polarstern* during various expeditions (EASIZ III, ANDEEP I, II) in Antarctica. All herein reported specimens were sorted either from Agassiz Trawl or epibenthic sledge samples, which were carefully examined under a stereoscopic microscope and preserved either in 75% or in 96% pre-cooled ethanol. All material is deposited in the mollusc section of the Bavarian State Collection of Zoology, Munich, Germany (ZSM Mol).

For the examination of the external anatomy of the soft parts, a shell was broken and the animal body carefully removed. The soft part was then dehydrated by using the AXA method of Kees van Achterberg (Leiden, The Netherlands). His method is based on the alcohol-ethyl acetate method used for the preparation of Syrphidae (Vockeroth 1966). In van Achterberg's modified version the ethyl acetate was replaced by amyl acetate. The soft part was placed in a bowl with a 40 : 60 mixture of xylene and 96% ethanol for 24 hours. Then the liquid was poured off and replaced by 100% amyl acetate, which was permitted to evaporate for at least 24 hours.

Due to the low number of sufficiently preserved specimens of the new species we performed a study of the soft parts only and radulae were not prepared.

For scanning electron microscopy (SEM), the objects were mounted on stubs using double sided adhesive tabs. After sputter coating for 135 seconds (POLARON Equipment Ltd., Watford, United Kingdom) they were examined with a LEO 1430VP SEM (Electron Microscopy Ltd., Cambridge, United Kingdom). Images were digitally processed using Corel Photo Paint software. They were oriented in the standard views as in Zelaya *et al.* (2006) to allow a better comparison. Hickman & McLean's (1990) terms for describing shells and soft parts are used.

Sediment data (obtained from a multicorer) are available for the following stations:

PS 61/041, 59°22.24'S 60°04.06'W to 59°22.55'S 60°04.01'W, 2359–2375 m: This station lies in the Shackleton Fracture zone. The sediment consisted of silty-clay to coarse sand, with pebbles and rocks. The surface bioturbation at this station was less than 25%. Lonestones and phytodetritus were not present in this area.

PS 61/043, 60°27.12'S 56°05.10'W to 60°27.18'S 56°04.80'W, 3959–3961 m: The station lies within the island arc of the Elephant Islands. The sediment was silty-clay to cobble. Its surface bioturbation was in excess of 75%.

PS 61/131, 65°19.19'S 51°32.54'W to 65°19.99'S 51°31.23'W, 3050–3055 m: The sediment was described as green-grey mud, with grains ranging from silty-clay to pebble-cobble (range of grain size 7–31 µm). The covering by lonestones is about <5–25%, while phytodetritus amounted to <25–75%. The sediment showed a surface bioturbation of <25–>75%.

PS 61/140, 58°15.98'S 24°53.72'W to 58°16.13'S 24°53.87'W, 2947–2970 m: The sediment consisted of a mixture of silty-clay to sandy-silt, grey-brown sandy mud, that had pebbles mixed in. The grain size ranged from 35–235 µm. A small amount (<5%, each) of lonestones and phytodetritus was found in this area, the surface bioturbation, however, ranged from <25–>75%.

Abbreviations

AL – aperture length (in mm)

SL – shell length (in mm)

SW – shell width (in mm)

OD – original designation.

MCZ – Museum of Comparative Zoology, Cambridge, United States of America.

MLP – Museo de La Plata, La Plata, Argentina.

NHM – Natural History Museum, London, United Kingdom.

ZMB – Natural History Museum Berlin (formerly Zoologisches Museum Berlin), Germany.

ZSM – Bavarian State collection of Zoology, Munich, Germany.

Systematics

Brookula Iredale, 1912

Type species: Brookula stibarochila Iredale, 1912, OD.

Distribution: Mainly in the oceans of the southern hemisphere, northern hemisphere records from the Indian and Pacific Oceans only. Shallow water to abyssal depth (Gage & Taylor 1991). Miocene to Recent (Finlay 1924).

Diagnosis: Shell 1.2–2.5 mm, trochoid globose, thin, orthostrophic, paucispiral, dextral, with up to 4 rounded whorls. Periostracum absent. Umbilicus ranges from closed to widely open. Protoconch with smooth or anastomosing ribbed sculpture, up to 400 µm in diameter. Shell sculpture consists of axial ribs; spiral sculpture well defined, but weaker, sometimes overriding and forming beads at intersections with axial ribs; fine growth lines present. Suture deeply constricted. Aperture rounded, with a slightly thickened lip and complete peritreme, nacreous layer absent. Operculum circular, multispiral, with central nucleus.

Radula rhipidoglossate, formula 5-2-1-2-5; rhachidian stout, higher than wide, with cusped edge well serrated. Outer lateral and marginal teeth similar, except for smaller cusps in the latter.

Cephalic tentacles with a dense fringe of sensory papillae at the distal end; foot anterior with two wide, posterior with two shorter lappets, laterally with short, elongate epipodial tentacles without epipodial sensory organs but a fringe of slender hair-like cilia.

***Brookula argentina* (Zelaya, Absalão & Pimenta, 2006)**

(Figs 1–2)

Benthobrookula argentina Zelaya, Absalão & Pimenta, 2006: 79–80, fig. 4.

Holotype (MLP: 11977), not examined, SEM images available in Zelaya *et al.* (2006).

Type locality: Atlantic Ocean, South Georgia (54°18'S 35°30'W), 94 m (OD).

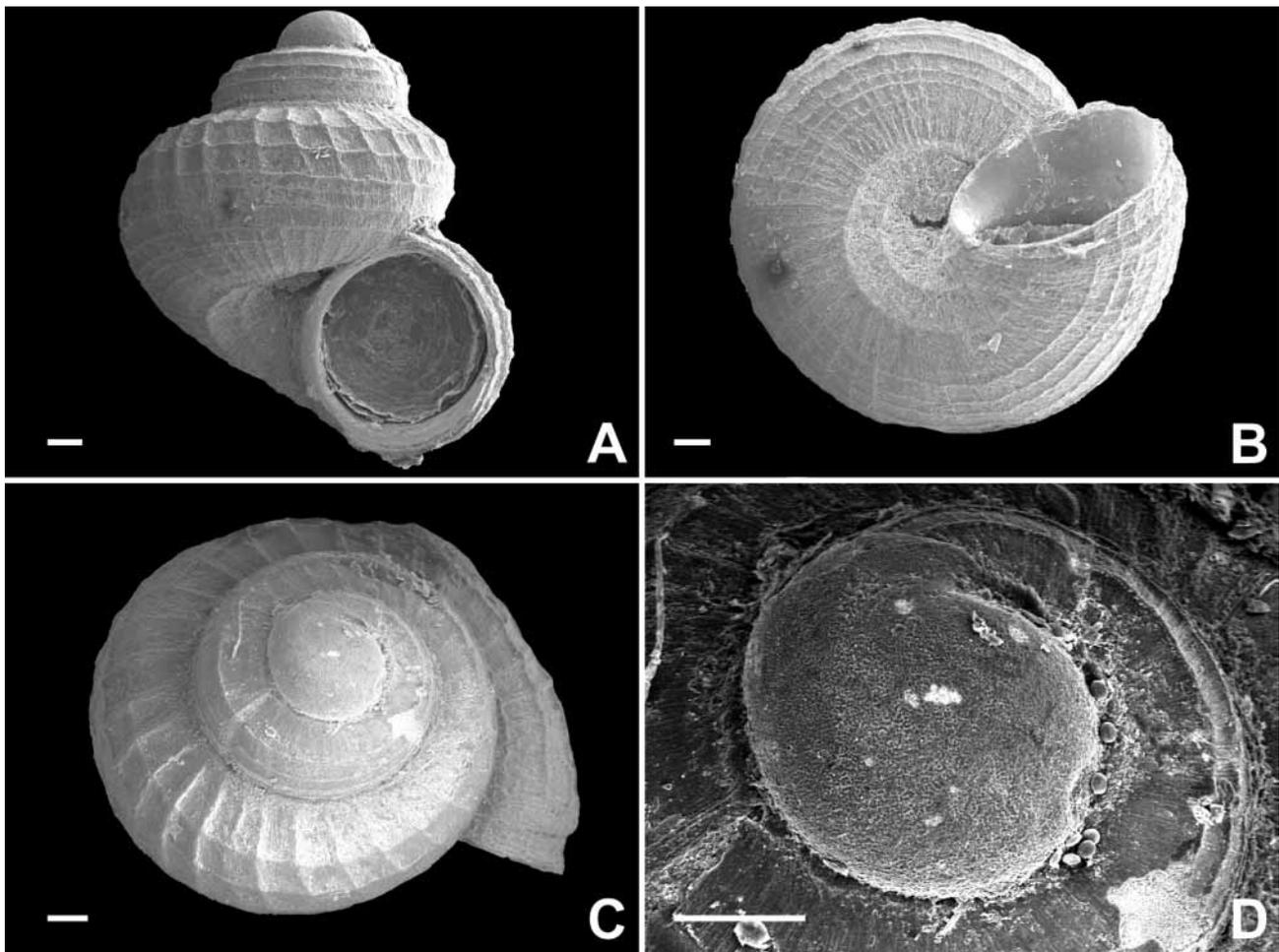


FIGURE 1: A–D, *Brookula argentina* (Zelaya, Absalão & Pimenta, 2006) (ZSM Mol 20020184) from Antarctica, Bransfield Strait, St. PS 56/149–01 (62°30.00'S 56°55.80'W to 62°30.10'S 56°56.10'W), 909–911 m. **A**, Ventral view of the complete shell. **B**, View of the shell base showing the strong spiral cords around the umbilicus. **C**, Apical view. **D**, Detail of fig. C to show the fine protoconch ornamentation. Scale bars: 100 µm.

Material examined: Five specimens (ZSM Mol 20070902) from Antarctica, Bransfield Strait, St. PS 56/174–01 (63°01.10'S 61°09.10'W to 63°01.30'S 61°08.60'W), 311–365 m, collected during the ANT XVII/3 (EASIZ III) expedition. One specimen (ZSM Mol 20020184) from Antarctica, Bransfield Strait, St. PS 56/149–01 (62°30.00'S 56°55.80'W to 62°30.10'S 56°56.10'W), 909–911 m, collected during the ANT XVII/3 (EASIZ III) expedition, leg. Michael Schrödl.

Remarks: The new material considerably extends the geographic and bathymetric range of this species that formerly was known from its type locality only (Fig. 2).

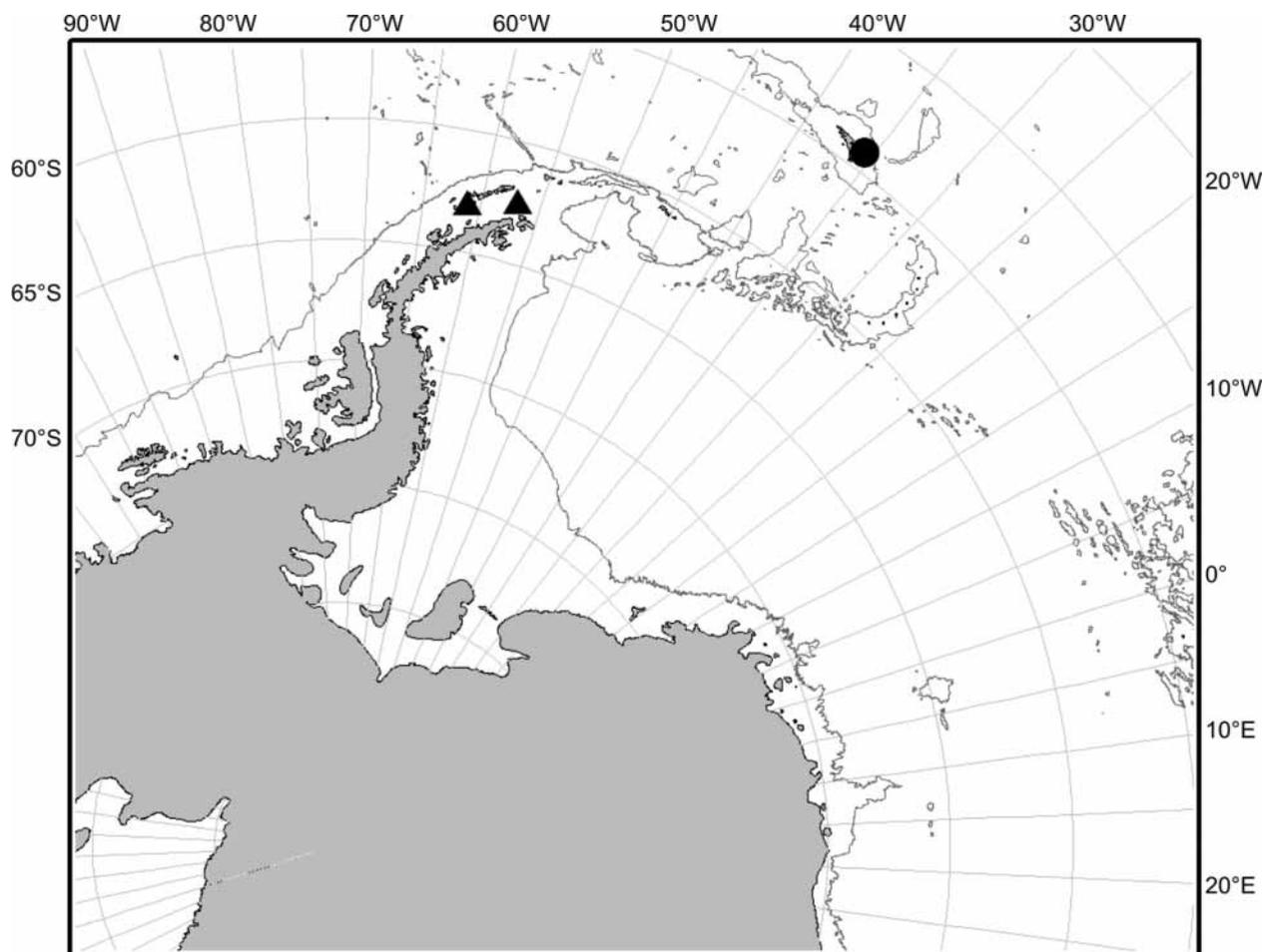


FIGURE 2: The geographic distribution of *Brookula argentina* (Zelaya, Absalão & Pimenta, 2006). The circle marks the literature data (type locality only), while the triangles show the new records. A 2500 m depth contour in light grey.

***Brookula exquisita* Clarke, 1961**

(Figs 3–4)

Brookula (Benthobrookula) exquisita Clarke 1961: 356–357, pl. 3, fig. 8, pl. 4, fig. 2.

Holotype (MCZ: 225964), not examined, SEM images available in Absalão *et al.* (2001) and Zelaya *et al.* (2006).

Type locality: Antarctica, South Georgia (55°29'S 37°57'W), 3758 m. OD.

Material examined: Four specimens (ZSM Mol 20070892–20070894), Antarctica, South Sandwich Islands, St. PS 61/140–08 (58°15.98'S 24°53.72'W to 58°16.13'S 24°53.87'W), 2947–2970 m, leg. Michael Schrödl, March 22 2002, ANT XIX/4 (ANDEEP II) expedition. One specimen fixed and preserved in 75%

ethanol (ZSM Mol 20070892); remainder dry shells only including SEM-mounted specimen (ZSM Mol 20070894). One specimen (ZSM Mol 20021582), Antarctica, South Sandwich Islands, St. PS 61/140–07 (58°16.00'S 24°53.78'W to 58°16.39'S 24°54.85'W), 2941–2945 m, leg. Michael Schrödl, March 21 2002, ANT XIX/4 (ANDEEP II) expedition, fixed and preserved in 96% ethanol. One dry specimen (ZSM Mol 20070901), Antarctica, Northwest Weddell Sea, St. PS 61/131–03 (65°19.19'S 51°32.54'W to 65°19.99'S 51°31.23'W), 3050–3055 m, leg. Michael Schrödl, March 5 2002, ANT XIX/4 (ANDEEP II) expedition. Five specimens (ZSM Mol 20021216; 20021170), Antarctica, Drake Passage, St. PS 61/041–03 (59°22.24'S 60°04.06'W to 59°22.55'S 60°04.01'W), 2359–2375 m, leg. Katrin Linse, January 26–27 2002, ANT XIX/3 (ANDEEP I) expedition, fixed and preserved in 96% ethanol.

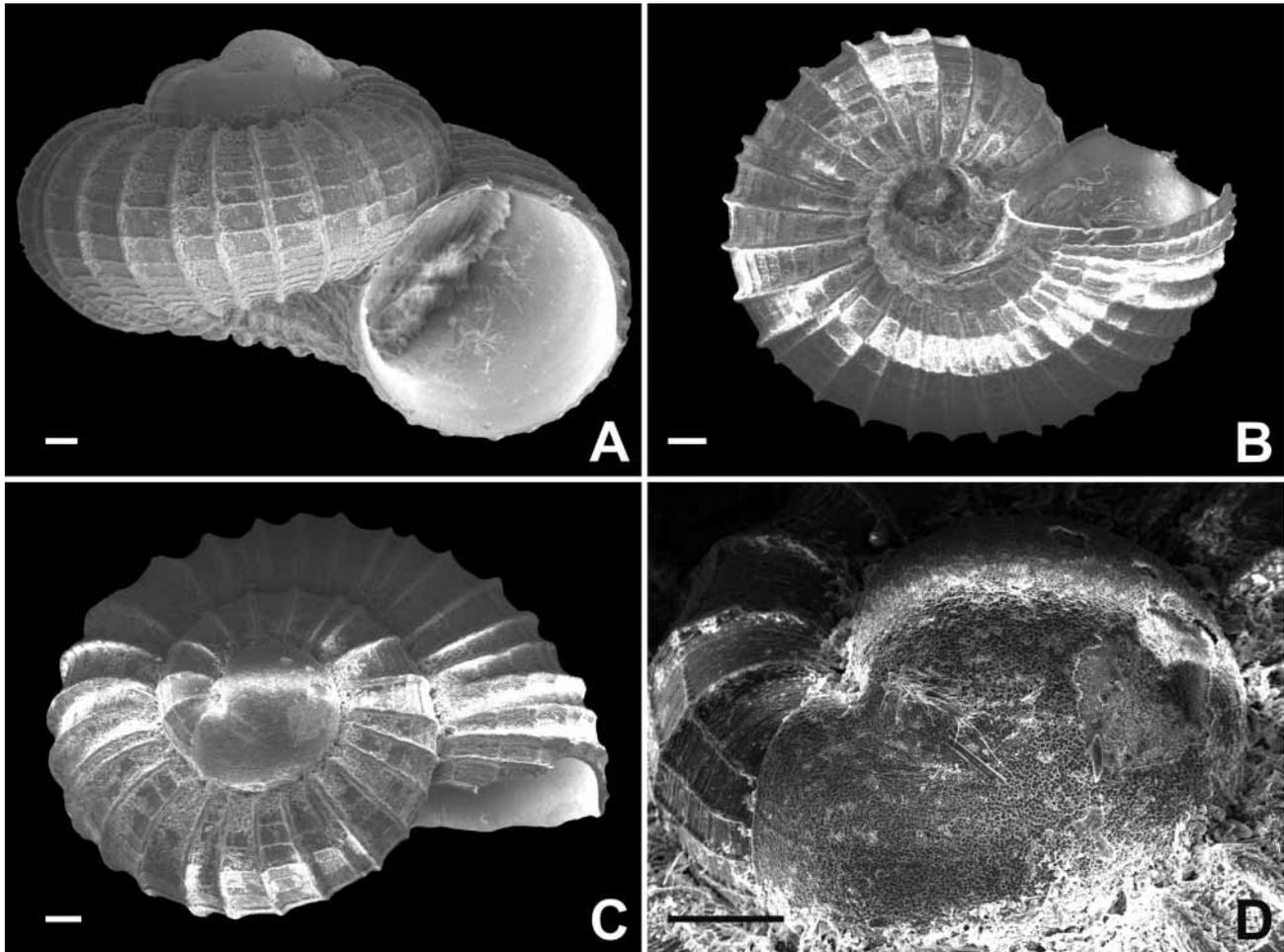


FIGURE 3: A–D. *Brookula exquisita* Clarke, 1961 (ZSM Mol 20070894) from Antarctica, South Sandwich Islands (58°15.98'S 24°53.72'W to 58°16.13'S 24°53.87'W), 2947–2970 m depth. **A.** Ventral view of the complete shell. **B.** View of the shell base showing the wide opening of the umbilicus. **C.** Apical view. **D.** Detail of fig. C to show the fine protoconch ornamentation. Scale bars: 100 μ m.

Description of a specimen examined by SEM (ZSM Mol 20070894)

Shell minute, 1.11 mm long, 1.67 mm wide (Fig. 3A), SL/SW ratio 0.66, depressed, fragile, white in color, with roundly inflated whorls, clearly expanded laterally, low spired, spire angle 126°. Protoconch (Fig. 3D) of one whorl, 320 μ m in diameter, 116 μ m long, globose, sculptured with fine anastomosing threads, forming reticulate pattern. Teleoconch (Figs 3A, C) of up to 1.75 whorls with convex profile. Whorls connected only for a short distance, more or less at periphery of preceding one. Suture consequently deep and

channeled. Last whorl clearly increasing in diameter and laterally expanded. Aperture circular, 0.68 mm high (SL/AL ratio 1.63), peritreme holostomate, with thin lip. Shell base roundly inflated. Umbilicus (Fig. 3B) phaneromphalous, circular, wide, surrounded by four slightly elevated spiral cords, two of them entering umbilicus. Shell surface cancellate. Axial sculpture of narrow ribs, 29 on last whorl in the holotype, deeply entering the umbilicus. Ribs regularly spaced, rounded, interspaces about four times rib width. Spiral sculpture of numerous flat threads, five on first teleoconch whorl, about 14 on the last adult whorl, distinctly narrower than axial ribs, partly overlaying axial ribs. Operculum circular, multispiral, with centric nucleus.

Remarks: This is the first record of this species from outside the type locality and the new material considerably extends the geographic and bathymetric range of this species (Fig. 4).

There are minor differences to the description of the holotype presented by Zelaya *et al.* (2006). Although somewhat smaller (1.11 mm vs 1.5 mm) our specimen has a slightly larger protoconch (320 μm vs 300 μm). The spire angle in our specimen is greater (126° vs 105°) and although the teleoconch whorl number is smaller (1.75 vs 2.25), the number of axial ribs on the last body whorl is similar (29 vs 28). However, too little is known about the intraspecific variation of this species to warrant the description of a new species on these differences alone.

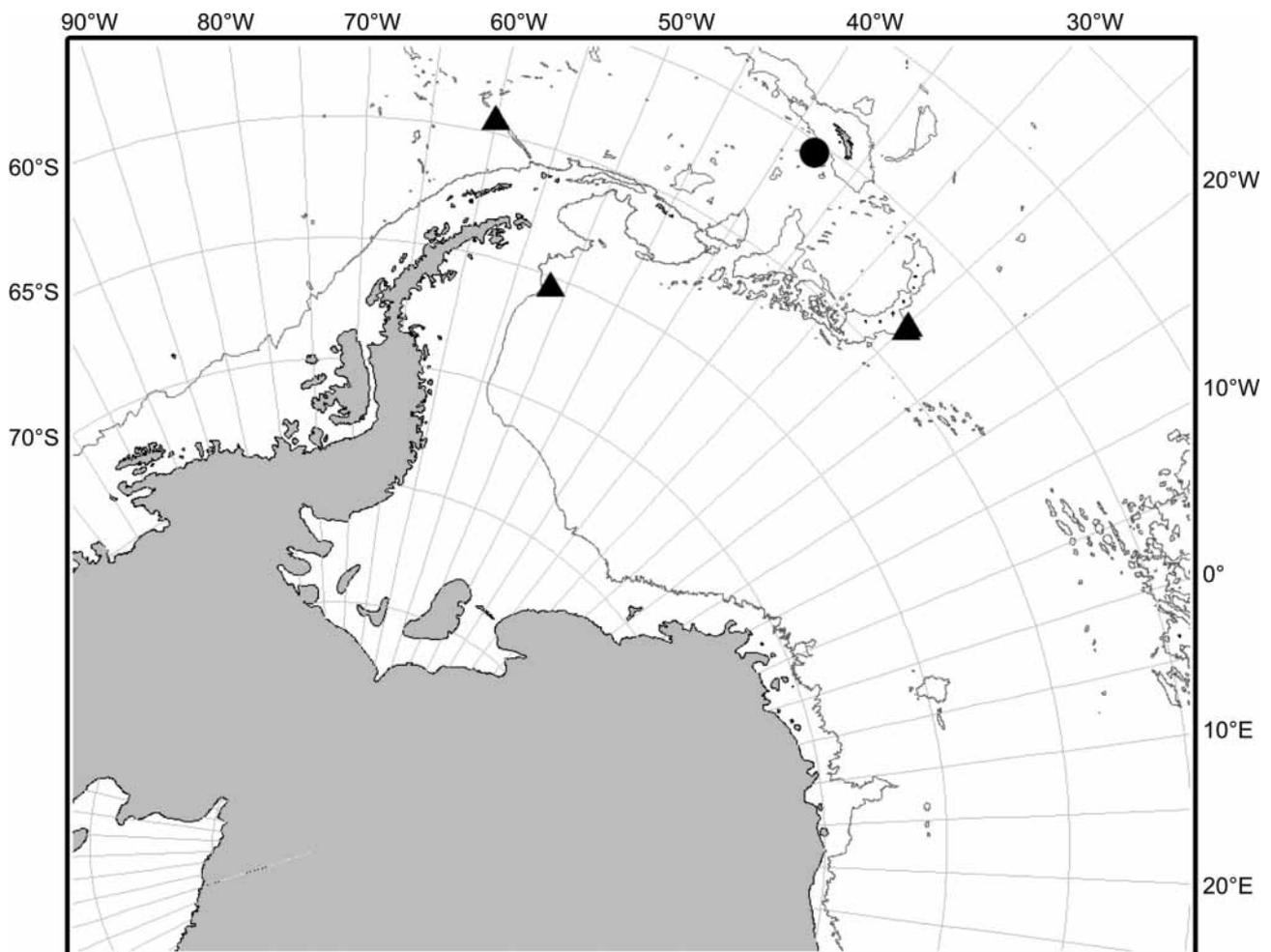


Figure 4: The geographic distribution of *Brookula exquisita* Clarke, 1961. The circle marks the literature data (type locality only), while the triangles show the new records. A 2500 m depth contour in light grey.

***Brookula charleenae* sp. nov.**

(Figs 5–6)

Type material

Holotype (ZSM Mol 20070879), leg. Michael Schrödl, March 22 2002, during the ANT XIX/4 (ANDEEP II) expedition.

Two **paratypes** (ZSM Mol 20070880) from type locality, all specimens were fixed and preserved in 75% ethanol except for the SEM-mounted holotype.

Type locality: Antarctica, South Sandwich Islands, St. PS 61/140–08 (58°15.98'S 24°53.72'W to 58°16.13'S 24°53.87'W), 2947–2970 m (Fig. 6).

Etymology: The species is named after the first author's daughter Charleen Schwabe.

Description: Shell minute, reaching 1.42 mm long and 1.25 mm wide (Fig. 5A), globosely turbinate, fragile, white in color, with roundly inflated whorls, slightly expanded laterally, low spired, spire angle ranges from 70° (holotype) to 81° (larger paratype). Protoconch (Figs 5C, D) of 1.5 whorls, 278 µm in diameter, 220 µm high, globose, sculptured with fine anastomosing threads, forming reticulate pattern. Teleoconch (Fig. 5A) of up to 2.75 whorls with convex profile. Suture deeply constricted. Last adult whorl globose, slightly expanded laterally. Aperture circular, peritreme holostomate, with thin lip. Shell base roundly inflated. Umbilicus (Fig. 5B) narrow, circular, deep. Axial sculpture of narrow ribs, 28 on last whorl in the holotype, 27 on the penultimate whorl, deeply entering the umbilicus. Ribs regularly spaced, rounded, nearly lamellous, interspaces between them about three times rib width. Spiral sculpture of numerous flat threads, twelve on first teleoconch whorl, about 42 on last adult whorl, narrower than axial ribs, partly double-spaced, not overlaying axial ribs distally. Operculum circular, multispiral, with centric nucleus.

TABLE 1: Shell morphometric data of *Brookula charleenae* sp. nov.

| Specimen | SL | SW | SL/SW ratio | Spire angle (°) | AL | SL/AL ratio |
|----------|------|------|-------------|-----------------|------|-------------|
| holotype | 1.42 | 1.25 | 1.14 | 70 | 0.61 | 2.33 |
| paratype | 0.80 | 0.82 | 0.98 | 80 | 0.42 | 1.90 |
| paratype | 1.00 | 1.00 | 1.0 | 81 | 0.51 | 1.96 |

Comparisons: *Brookula pfefferi* Powell, 1951: despite nearly the same shell proportions, the new species can be easily separated from *B. pfefferi* by 1) the absence of spiral cords on the shell base, 2) the higher number of spiral threads on the last adult whorl (42 vs 20–26), 3) the smaller protoconch (278 vs 330–400 µm).

Brookula strebeli Powell, 1951: this species has nearly the same size but has 1) a higher SL/SW ratio (1.20 vs 1.14), 2) a larger protoconch (300 vs 278 µm), 3) by nearly the same teleoconch whorl number (2 vs 2.75) a lower number of axial ribs (20 vs 28), 4) a much lower number of spiral threads (14 vs 42), 5) a nearly-closed umbilicus, 6) three to four spiral cords on the shell base.

Brookula calypso (Melvill & Standen, 1912): in contrast to the new species this species has 1) a higher spire angle (90 vs 81°), 2) a larger sized protoconch (295 vs 275 µm) with only one whorl vs 1.5 whorls, 3) only 14–17 vs 28 spiral ribs on the last whorl, 4) two vs no spiral cords around the umbilicus.

Brookula conica (Watson, 1886): the only other South Atlantic deep water species that does not have spiral cords around the umbilicus differs in 1) its larger size (up to 1.8 vs 1.42 mm), 2) the wider umbilicus (130 vs 105 µm [data from Absalão *et al.* 2001, fig. 2 b]), 3) the lower number of the wider spaced axial ribs (19 vs 28), 4) having very fine axial lines between the spiral threads, 5) its much smaller protoconch (145 vs 278 µm [data from Absalão *et al.* 2001, figs 2 f, d]).

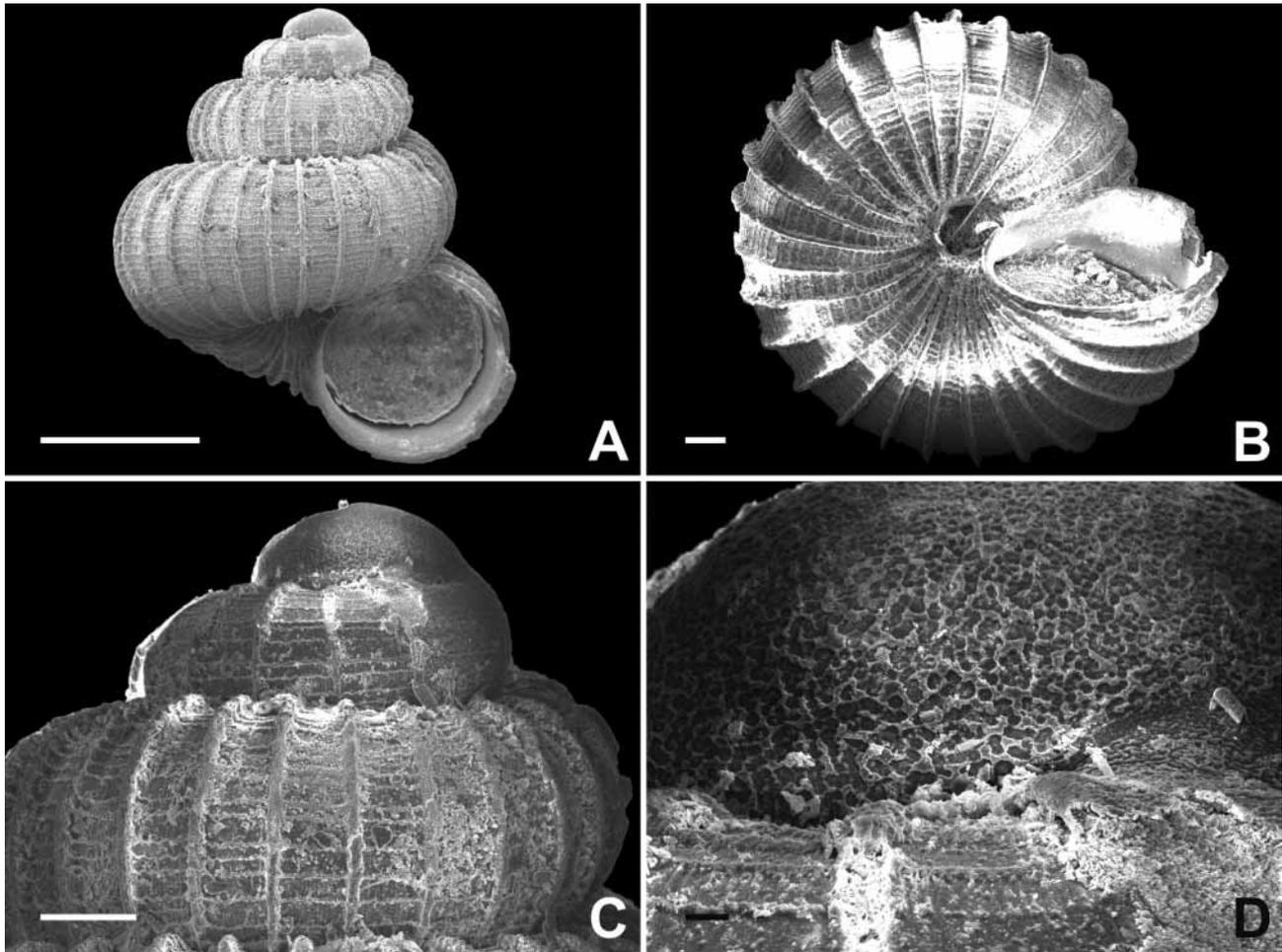


FIGURE 5: A–D, Holotype of *Brookula charleenae* sp. nov. (ZSM Mol 20070879) from Antarctica, South Sandwich Islands (58°15.98'S 24°53.72'W to 58°16.13'S 24°53.87'W), 2947–2970 m depth. **A**, Ventral view of the complete shell. **B**, View of the shell base showing the circular, deep opening of the umbilicus. **C**, Detail of fig. A, showing the protoconch and the first 1.5 teleoconch whorls. **D**, Detail of fig. C to show the fine protoconch ornamentation. Scale bars: A 500 μ m, B, C 100 μ m, D 10 μ m.

Brookula paranaensis (Zelaya, Absalão & Pimenta, 2006): this species differs from the new species in having 1) different shell proportions (compare table in original description), 2) a similar sized protoconch (270 vs 278 μ m) with only one whorl, 3) a larger spire angle, 4) a higher number (42 vs 28) of closer set axial ribs, 5) a smaller number of spiral threads on last adult whorl (20–21 vs 42), 6) three to four vs no spiral cords around the umbilicus.

Brookula kerguelensis Thiele, 1925 is the most similar species. It differs, however, in 1) its larger size (1.6 x 1.35 mm with the same whorl number), 2) the lower spire angle (c. 68°, taken from the illustration), 3) the smaller number of less closely set and flatter axial ribs on the penultimate whorl (c. 20 vs 27) on last whorl, 4) having an oval aperture. This species is known from a single slightly worn specimen (holotype, ZMB/Moll-64050) from the Kerguelen Islands (49°S 70°44'E) only.

None of the comparable congeners was ever reported from such depths.

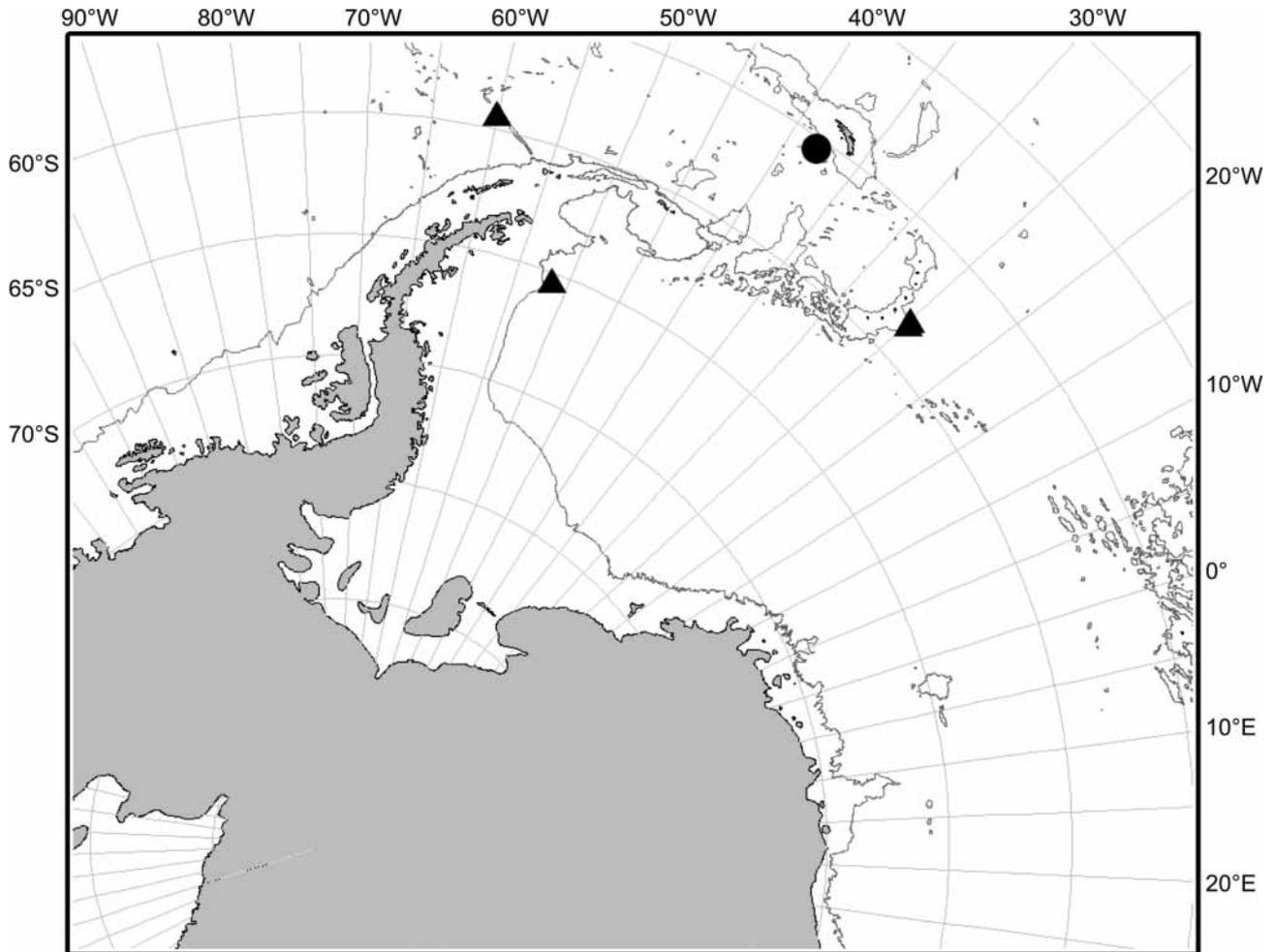


FIGURE 6: The geographic distribution of *Brookula charleenae* sp. nov. with a 2500 m depth contour in light grey.

***Brookula bohni* sp. nov.**

(Figs 7–8)

Type material

Holotype (ZSM Mol 20070895), leg. Katrin Linse, February 4 2002, ANT XIX/3 (ANDEEP I).

Paratypes, one from type locality (ZSM Mol 20021185). Two paratypes (ZSM Mol 20021177) Antarctica, Drake Passage, St. PS 61/042–02 (59°40.29'S 57°35.43'W to 59°40.42'S 57°35.27'W), 3680–3683 m, Katrin Linse, January 27 2002, ANT XIX/3 (ANDEEP I). Besides the SEM-mounted holotype, all other specimens are fixed and preserved in 96% ethanol.

Type locality: Antarctica, South Shetlands, St. PS 61/043–08 (60°27.12'S 56°05.10'W to 60°27.18'S 56°04.80'W), 3959–3961 m (Fig. 8).

Etymology: The species is named after our friend Jens Michael Bohn (ZSM), a holothurian specialist and participant of the relevant expeditions. We selected his surname because his nickname is “Bohni”.

Description: Shell minute, up to 1.30 mm long, 1.28 mm wide (Fig. 7A), globose turbate, fragile, translucent white in color, with inflated whorls slightly depressed at the shoulder, slightly expanded laterally, low spired, spire angle ranging from 80° (smallest paratype) to 85° (holotype). Protoconch (Fig. 7D) of 1.25 whorls, 280 µm in diameter, 100 µm high, globose, sculptured with fine anastomosing threads, forming

microscopic pits of irregular arrangement. Teleoconch (Figs 7A, C) of up to 2.75 whorls with convex profile. Suture incised. Last adult whorl globose, slightly depressed at shoulder. Aperture oval, peritreme holostomate, although very weak at periphery of preceding whorl; with thick inner, thin outer lip. Shell base roundly inflated. Umbilicus (Fig. 7B) tightly open, circular, deep. Axial sculpture of narrow ribs, ranging from 29 (largest paratype) to 31 on last whorl in holotype, 25 on penultimate whorl. Ribs regularly spaced, rounded, low, interspaces about three times rib width. Spiral sculpture of numerous flat threads, seven on first teleoconch whorl, about 12 on last adult whorl, narrower than axial ribs, crowded in upper and lower half of whorl, centrally absent (in the two small paratypes) or interrupted by distinctly separated slightly higher spirals, not overlaying the axial ribs distally. Nine flat spirals, two spiral cords (with inner being largest), which surround umbilicus, at shell base. Operculum circular, multispiral, with centric nucleus.

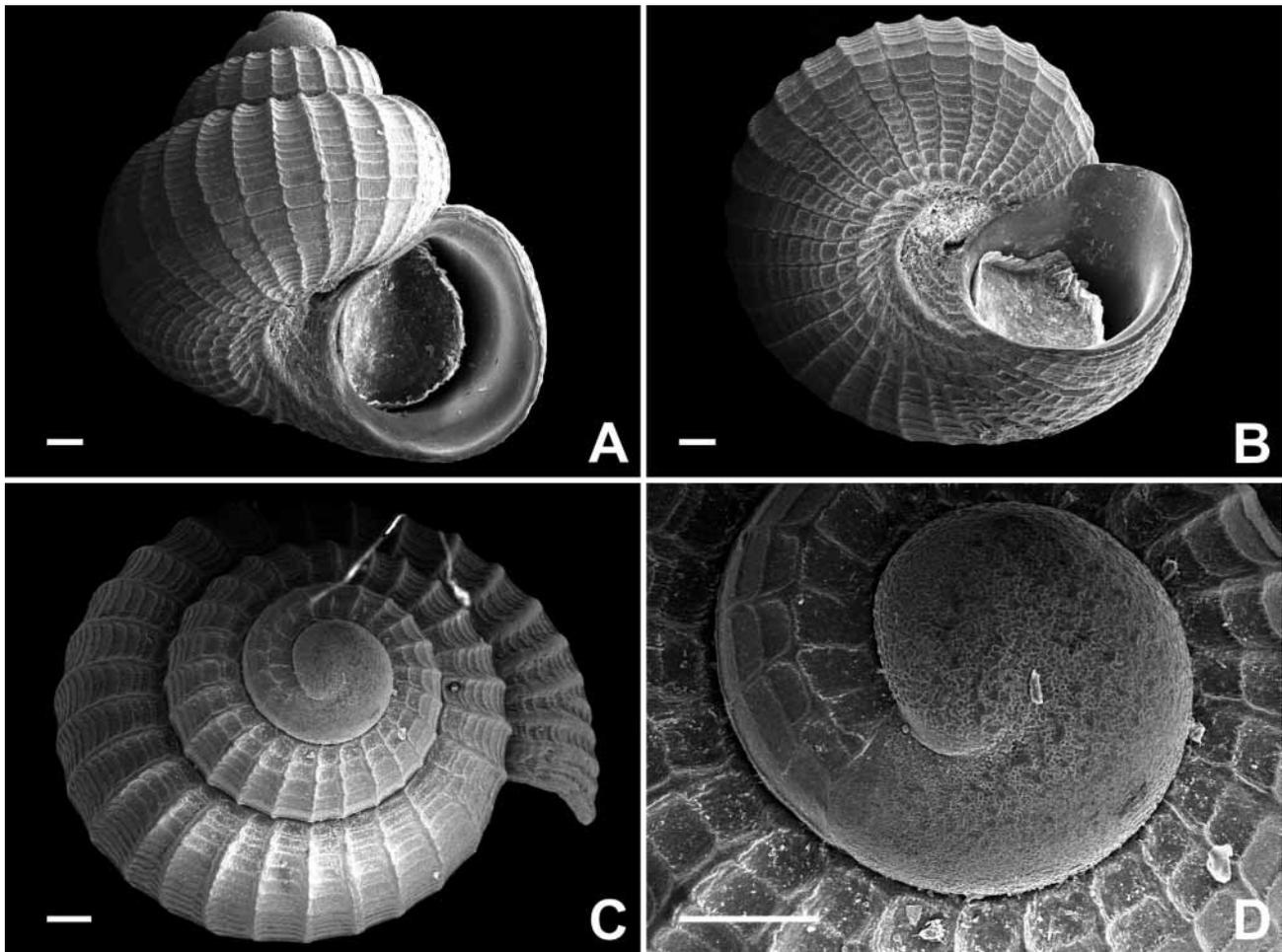


FIGURE 7: A–D, Holotype of *Brookula bohni* sp. nov. (ZSM Mol 20070895) Antarctica, South Shetlands, St. PS 61/043–08 (60°27.12'S 56°05.10'W to 60°27.18'S 56°04.80'W), 3959–3961 m. **A**, Ventral view of the complete shell. **B**, View of the shell base showing the narrow opening of the umbilicus. **C**, Apical view to show the protoconch and the teleoconch whorls. **D**, Detail of fig. C to show the fine protoconch ornamentation. Scale bars: 100 μ m.

Comparisons: *Brookula spinulata* Absalão, Miyaji & Pimenta, 2001 differs in 1) its coarse sculpture with spinulate projections at the axial ribs, 2) the presence of fine axial lines between the spiral threads, 3) the lower number (6 vs 12) of spirals on the last body whorl, despite the general larger size, 4) the lower number (20 vs 29–31) of axial ribs.

TABLE 2: Shell morphometric data of *Brookula bohni* sp. nov.

| Specimen | SL | SW | SL/SW ratio | Spire angle (°) | AL | SL/AL ratio |
|----------|------|------|-------------|-----------------|------|-------------|
| holotype | 1.30 | 1.28 | 1.02 | 85 | 0.73 | 1.78 |
| paratype | 1.30 | 1.25 | 1.04 | 81 | 0.74 | 1.76 |
| paratype | 1.00 | 0.90 | 1.11 | 84 | 0.48 | 2.08 |
| paratype | 0.95 | 1.05 | 0.91 | 80 | 0.63 | 1.51 |

Brookula calypso (Melvill & Standen, 1912) differs in 1) having cancellate sculpture, built up by regularly arranged axial ribs and spiral threads, 2) the presence of small axial threads between the axial ribs, 3) having a slightly larger protoconch (295 vs 280 μm) although it has only one whorl, 4) having a larger spire angle (90 vs 85°), 5) having a shallow suture.

Brookula powelli Clarke, 1961 differs in 1) shell proportions (0.81–0.93 vs 0.91–1.11, SL/SW ratio), 2) the lesser acute spire angle (min. 93.5 vs max. 85°), 3) the wider umbilicus (440 vs 135 μm), 4) the larger protoconch (one whorl of c. 350 μm vs 1.25 whorl of 280 μm), 5) the higher number of axial ribs at last whorl (37 vs 29–31), 6) the round vs oval aperture.

The oval aperture and the characteristic sculpture make the species easily separable from the remaining Antarctic congeners.

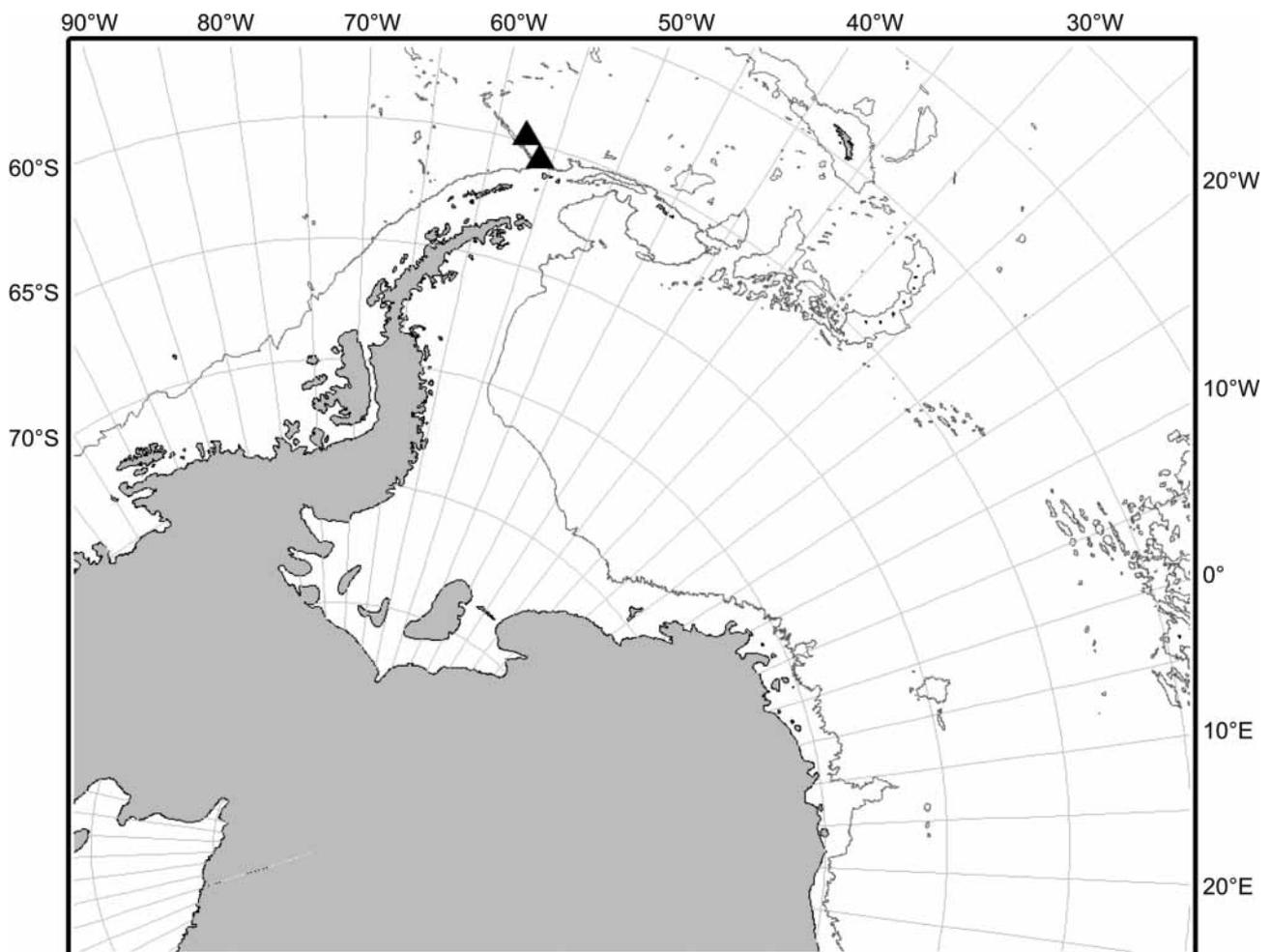


FIGURE 8: The geographic distribution of *Brookula bohni* sp. nov. with a 2500 m depth contour in light grey.

***Brookula pfefferi* Powell, 1951**

(Fig. 9)

? *Cyclostrema decussatum* Pelseneer, 1903: 19, pl. 5, fig. 48.

Brookula pfefferi Powell, 1951: 104, pl. 5, fig. 8.

Brookula rossiana Dell, 1990: 102, fig. 169.

Brookula sinusbreidensis Numanami & Okutani, 1991: 38, figs 2–6.

Brookula delli Numanami, 1996: 55, figs 30A–E.

Holotype of *B. pfefferi* (NHM 1961.368).

Type locality: Atlantic Ocean, South Georgia, off mouth of Stromness Harbour (54°04'S 36°27'W – 53°58'S 36°26'W), 155–178 m. OD.

Material examined: 40 specimens (ZSM Mol 20021687), Weddell Sea sector of the Antarctic Peninsula (63°01.10'S 61°09.10'W), 311–365 m, ANT XVII/3 (EASIZ 3).

Remarks: This is the only species for which numerous specimens were available. The shell morphology of *B. pfefferi* is sufficiently described in Absalão *et al.* (2001) and Zelaya *et al.* (2006) but at least a first preliminary (excluding the ctenidia) overview of the external bauplan of the species may be given here (Fig. 9). Radula data were provided by Zelaya *et al.* (2006). A detailed histological examination is being undertaken by Thomas Kunze (Ludwig-Maximilians University, Munich, Germany).

The cylindrical head has a cloven, obtusely pointed snout. There is a pair of long, thick cephalic tentacles that show in their anterior half laterally dense fringes of sensory papillae. It is likely that the short rudiment on the base of the cephalic tentacle (Fig. 9C) belongs to the eye stalk (eyes are not visible in the examined specimen), but this has to be confirmed by the histological data. The foot is fleshy and elongate, anteriorly with two wide, conical foot lappets and posteriorly, under the horny, circular, multispiral operculum (Fig. 9D) with two shorter ones. Laterally between the anterior and posterior foot lappets a fringe of about 12 short, smooth, elongate epipodial tentacles is situated; at least on the dried animal, the tentacles do not show epipodial sense organs. There is a dense fringe of slender, hair-like cilia on the lateral foot margins. Immediately behind the right cephalic tentacle (Figs 9A, C, E; marked with “*”) we detected a structure, which could be a penis, but also requires confirmation by histology.

Examination of the shell by SEM showed that the inner shell layer of the aperture does not consist of a prismatic nacreous layer as typical for iridescence (see Fuchigami & Sasaki 2005).

Absalão *et al.* (2001) failed to locate the holotype of *Cyclostrema decussatum* Pelseneer, 1903, and Zelaya *et al.* (2006) did not take that species into account. The holotype of this species should be together with the other Pelseneer types in the Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium, but according to Yves Terryn (Scientific Associate), who searched the collection for it on the authors' request, the type is not to be found. Based on the species' original descriptions and figures we can not see differences between *Brookula decussata* (Pelseneer, 1903) and *B. pfefferi* Powell, 1951, and consider the latter merely a junior synonym of the former. It is important to point out that *Brookula decussata* (Pelseneer, 1903) does not “clearly differ from *Benthobrookula pfefferi* in having a smaller shell, with fewer, more separated, spiral threads” (Zelaya *et al.* 2006, p. 80) but is instead really similar (see also Powell 1951, p. 104). A direct comparison of Pelseneer's illustration (1903, pl. 5, fig. 48) with the photo of the holotype of *Brookula pfefferi* Powell, 1951, available from Zelaya *et al.* (2006, fig. 5A), does not only show the close similarity but also give the impression that the spiral threads are not “more separated”. In addition, while Zelaya *et al.* (2006) gave a maximum size of 1.83 mm for *Brookula pfefferi* Powell, 1951 (2 mm in the original description!), the maximum shell size for *B. decussata* (Pelseneer, 1903) is originally given as 2.5 mm and can thus under no circumstances be defined as “smaller”.

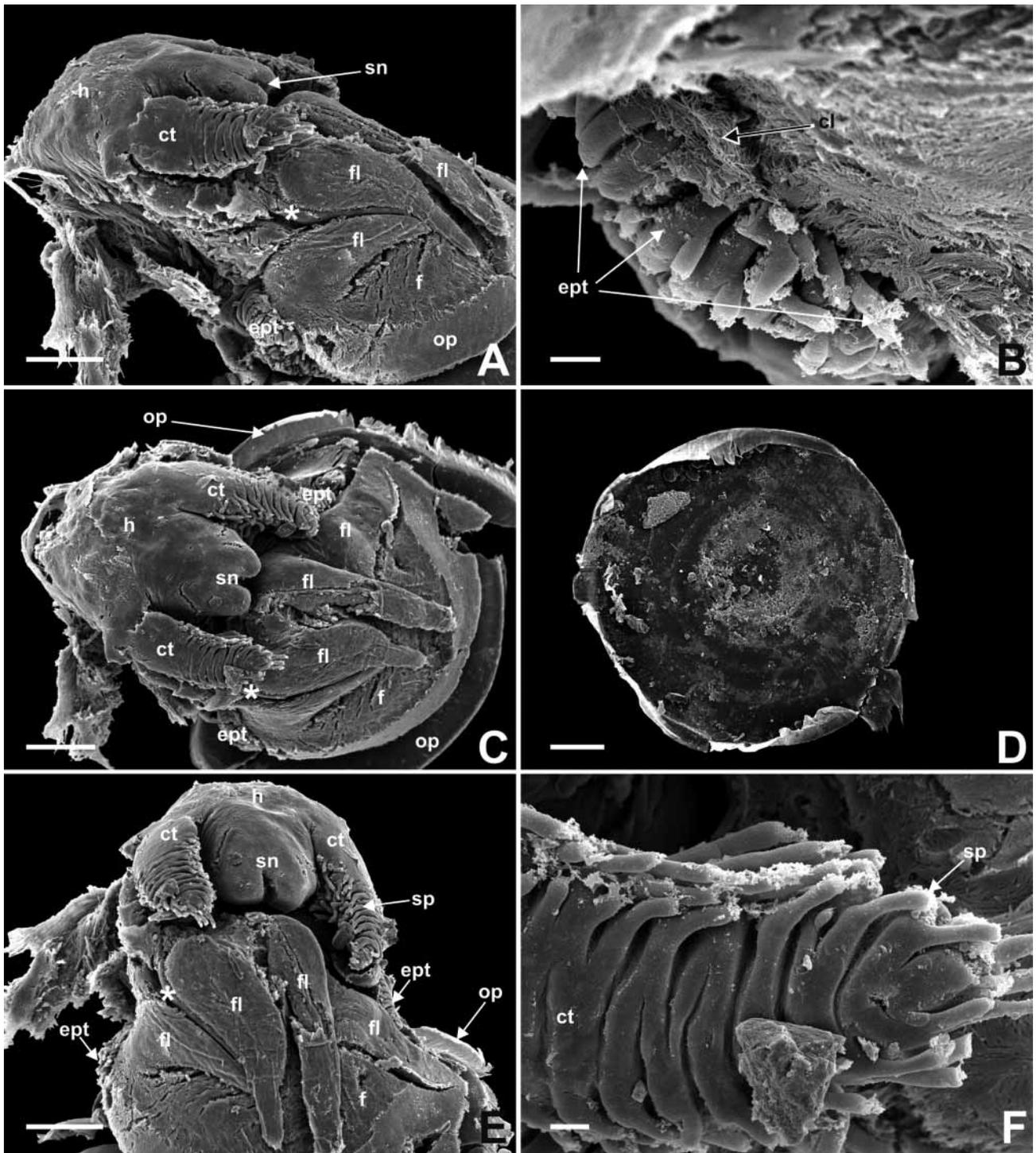


FIGURE 9: External anatomy of a dried specimen of *Brookula pfefferi* Powell, 1951 (ZSM Mol 20021687). **A**, right anterior-lateral view. **B**, detail of the right part of the foot, showing the epipodial tentacles and ciliar fringe. **C**, dorso-frontal view. **D**, multispiral operculum. **E**, frontal view. **F**, detail of figure 1C, showing the right cephalic tentacle with the numerous sensory papillae. Scale bars A, C–E 100 μ m, B, F 10 μ m. **cl** – cilia; **ct** – cephalic tentacle; **ept** – epipodial tentacle; **f** – foot; **fl** – foot lappet; **h** – head; **op** – operculum; **sn** – snout; **sp** – sensory papillae; * – most probable the penis.

Revised List of Southern Atlantic Ocean species of *Brookula*

The Subantarctic and Antarctic sector of the Atlantic Ocean is seemingly the most diverse region for the genus *Brookula*, represented by the following species: *B. argentina*, *B. bohni* sp. nov., *B. calypso*, *B. charlee-*

nae sp. nov., *B. exquisita*, *B. pfefferi*, *B. powelli*, and *B. strebeli*. A ninth species, *B. lamonti* Clarke, 1961, was described from the Scotia Sea but unfortunately neither the shell fragments of the holotype nor the insufficient description permit a definitive assessment of taxonomic status (see Zelaya *et al.* 2006). All other species were well (re)described and may be distinguished with our comparisons tool (Table 3). Some additional described species like *B. sinusbreidensis* Numanami & Okutani, 1991, *B. delli* Numanami, 1996, *B. rossiana* Dell, 1990, and *B. antarctica* Dell, 1990 could not be separated from the above listed species and must be considered merely junior synonyms of them as partly already pointed out by Absalão *et al.* (2001). The first three species are undoubtedly conspecific with *B. pfefferi* Powell, 1951, while a comparison of the type material shows that *B. antarctica* Dell, 1990 does not differ from *B. strebeli* Powell, 1951 and thus becomes a junior synonym of the latter.

TABLE 3: Comparison of *Brookula* species from the Subantarctic and Antarctic waters of the Southern Atlantic Ocean. Data for species not treated in the present work are extracted from Zelaya *et al.* (2006). + stands for “yes”, – stands for “no”, ± stands for “moderate”. * The maximum shell length is established by the SL/SW ratio of the holotype multiplied by the maximum shell width given in the original description. ** includes the maximum shell size of *B. decussata* (see remarks under *B. pfefferi*).

| Species | max. shell length in mm | SL/SW ratio > 1 | Umbilicus with spirals | Suture deep | Aperture circular | Umbilicus wide | Protoconch = 300 µm | Axial ribs shallow | Spire angle ≥ 90° | Axial ribs on last whorl (max.) |
|--------------------------|-------------------------|------------------|------------------------|-------------|-------------------|----------------|---------------------|--------------------|-------------------|---------------------------------|
| <i>B. argentina</i> [17] | 1.22 | + [1.00–1.15] | + | + | + | + | – [270–300 µm] | + | – [85–88°] | 30 [24–30] |
| <i>B. bohni</i> [4] | 1.30 | + [0.91–1.11] | + | + | – | – | – [270–280 µm] | + | – [80–85°] | 31 [29–31] |
| <i>B. calypso</i> [1] | 1.29 | + [1.07] | + | – | – | – | – [295 µm] | + | + [90°] | 38 |
| <i>B. charleena</i> [3] | 1.42 | + [0.98–1.14] | – | + | + | – | – [270–278 µm] | – | – [0.42–0.61] | 28 [26–28] |
| <i>B. lamonti</i> [1] | 1.61* | + [1.12] | + | + | – | – | ? | – | – | 25 |
| <i>B. pfefferi</i> [54] | 2.50** | + [1.00–1.08] | + | + | + | – | + [330–400 µm] | + | – [86°] | 38 |
| <i>B. strebeli</i> [15] | 1.34 | + [1.16–1.24] | + | – | – | – | + [about 300 µm] | + | – [79.8–82°] | 20 |
| <i>B. powelli</i> [6] | 1.50 | – [0.81–0.93] | + | + | + | + | + [about 350 µm] | + | + [93.5–103°] | 37 |
| <i>B. exquisita</i> [13] | 1.33 | – [0.66–0.85] | + | + | + | + | + [300–320 µm] | ± | + [105–126°] | 29 [28–29] |

Conclusions

We present here the description of two new species of *Brookula*, namely *Brookula charleenae* and *Brookula bohni*. Shell characteristics permit distinguishing them from the other southern Atlantic congeners (see Table 3). With the new species, the number of Southern Atlantic *Brookula* species increases to nine.

In addition, range extensions are given for *Brookula argentina* (Zelaya, Absalão & Pimenta, 2006) and *B. exquisita* Clarke, 1961. The former was known from South Georgia from 94 m depth only but was collected in the Antarctic Bransfield Strait at 911 m depth. The abyssal *B. exquisita* Clarke, 1961 was also known from South Georgia only, here we add records from the Drake Passage, the South Sandwich Islands, and also from the Northwestern Weddell Sea.

The scarcity of the deep water material does not permit a detailed anatomical study but the large number of specimens of *Brookula pfefferi* enabled us to provide the first account on the soft part morphology of a representative of this genus. However, the observed characteristics are still insufficient to clarify the affiliation of the genus *Brookula* to a family. *Brookula* is a trochiform gastropod of still uncertain systematic placement, though membership in Eucyclinae is rejected based on the uninterrupted peristome in *Brookula* (compare Hickman & McLean 1990).

The argumentation why Zelaya *et al.* (2006) grouped all the Antarctic and Subantarctic species of *Brookula* into the genus *Benthobrookula* Clarke, 1961 is weak. They wrote that the protoconch in *Brookula* compared to *Benthobrookula* is 1) smooth vs fine anastomosing, 2) not inflated vs globose, and 3) smaller (245 vs 300–400 µm). This reasoning based upon the single available SEM picture of a topotype of *Brookula stibarochila* (the type species), available from Warén (1992, fig. 23B). Firstly, this image was taken under a lower magnification than the protoconch examinations of the authors, so it remains unclear whether the surface is smooth or ornamented in the sense of Zelaya *et al.* (2006). The protoconch structure alone is insufficient to separate both taxa (see also Warén 1992, figs 15 & 19), especially as only a part of the involved species were examined (see also Dell 1990) and the fossil records of *Brookula* were not discussed at all. Secondly, the protoconch is inflated but vague. And third, Zelaya *et al.* (2006) grouped species under *Benthobrookula*, which do not have such a large protoconch: e.g., *B. paranaensis* Zelaya, Absalão & Pimenta, 2006 (about 275 µm, p. 82), *B. calypso* (Melvill & Standen, 1912) (about 295 µm, p. 83) and others with about 300 µm wide protoconches. In addition, Zelaya *et al.* (2006) also stated that the genus *Benthobrookula* is restricted to “the South Atlantic Ocean...from Antarctic to Brazilian waters” but obviously they did not take into account species like, e.g., *Brookula iki* Kay, 1979 from Hawaii, *B. tanseimaruae* Tsuchida & Hori, 1996 from Japan (both Pacific Ocean), *B. kerguelensis* Thiele, 1925, *B. sinusbreidensis* Numanami & Okutani, 1991 (= *B. pfefferi* Powell, 1951) (both Southern Indian Ocean), *B. aethiopica* Thiele, 1925 and *B. denseplicata* Thiele, 1925 (both tropical Indian Ocean), which show strong similarities to or belong to their representatives of *Benthobrookula*. In conclusion it may be said that none of the criteria used by Zelaya *et al.* (2006) to separate *Brookula* from *Benthobrookula* is sufficiently well-founded to justify this separation into two genera.

A detailed (including anatomy) study of more material, including the type species, would be necessary to solve the problem. Meanwhile we recommend maintaining the traditional use of the genus *Brookula*.

To disentangle the systematic and taxonomic bedevilment of the genus *Brookula*, further revisers will hopefully also take the Indo-Pacific species into account and provide morphologic or anatomic studies.

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