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ORIGINAL PAPER

New insigths into the diversity of rissoids from sub-antarctic and antarctic waters (Gastropoda: Rissooidea)

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Abstract Molluscs have been regarded as one of the most extensively studied and better known marine invertebrates groups in sub-Antarctic and Antarctic benthic communities. In order to test this statement we address here the study of some species of the caenogastropod family Rissoidae, collected during several expeditions to Tierra del Fuego and the Scotia Arc. Currently, the local diversity of this family accounts for a total of 30 species, which were thoroughly revised mostly as part of two monographs. The present study provides new information on shell morphology, radulae and distribution for four of these species: *Onoba fuegoensis* (Strebel, 1908), *O. delecta* Ponder, 1983, *O. klausgrohi* Engl, 2011 and *Haurakia averni* Ponder and Worsfold, 1994; also contributes to a better understanding of the intraspecific variability of two other species: *Onoba schythei* (Philippi, 1868) and *O. algida* Ponder and Worsfold, 1994; and seven new species are described: *Onoba clara, O. sandwichensis, O. verrucosa, O. antleri, O. caribu, O. oligochordata*, and *O. ernestoi*. These new findings increase the number of species currently known from the studied area, and provide the first record of a species with multispiral protoconch, and the first record of a bathyal species from southern South America. Furthermore, as part of this study the presence of "antler-like" marginal teeth is reported for two species, a condition thus far not reported for any other Rissoidae. This study highlights that, even being one of the most intensively studied marine invertebrate groups, molluscs from the Sub-Antarctic and Antarctic waters still remain scarcely known.

Keywords Antarctica · Southwestern Atlantic · Rissoidae · Mollusca · Southern Ocean

Introduction

Molluscs are one of the most abundant and diversified groups of marine invertebrates in sub-Antarctic and Antarctic benthic communities (Jazdzewski et al. 1986; Mühlenhart-Siegel 1988; Thatje and Mutschke 1999; Gray 2001; Brandt et al. 2007). The group was intensively studied in the area since the early expeditions to Antarctica, by the end of the nineteenth and early twentieth centuries. According to Clarke et al. (2007), this is one of the best known groups of marine benthic invertebrates. However, and despite the numerous species described, few molluscan families from this area were thoroughly revised. Among them are the Rissoidae, a family that before the 1980s, in Tierra del Fuego, Malvinas/Falkland Islands and the Scotia Arc, was represented by a reduced number of species described isolatedly (e.g.: Martens and Pfeffer 1886; Strebel 1908; Melvill and Standen 1912). At the 1980s/1990s, two monographs greatly enlarged the local knowledge of the group: Ponder (1983) compiled all available information on the sub-Antarctic and Antarctic species, provided new characters for already known species, suggested several synonymies and described numerous new species. This study was subsequently enlarged in a second monograph dealing with the Southwestern

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South American species (Ponder and Worsfold 1994). After that, only two additional species present in the Scotia Arc (and none from southern South America) were described (Engl 2011). The information arising from the above-mentioned studies resulted in the fact that Rissoidae appears at present as one of the most diversified gastropod families, with a total of 25 species of *Onoba*, 4 of *Powellisetia* and one *Haurakia* currently recognized from the southeastern tip of South America (i.e., Tierra del Fuego and Malvinas/Falkland Islands) and the Scotia Arc.

The aim of this study is to provide new information on Rissoidae gastropods, one of the "most intensively studied" groups from the Southern Ocean, with view to contributing to a better understanding of the local diversification of this group, and the morphological radiation of shell and radular characters.

Materials and methods

The studied material comes from several sampling trips along the Magellan Strait, the Beagle Channel (south of Tierra del Fuego) and Isla de los Estados, aboard the A.R.A. *Alférez Sobral*; and from the expeditions of the R/V *Polarstern* "LAMPOS 2002" to the Scotia Arc islands and the B.O. *Puerto Deseado* "BBB Abril 2016" to the Area Marina Protegida Namuncurá—Banco Burdwood (Fig. 1). Bottom fauna was obtained with a benthic dredge (2 mm mesh-size). Molluscs were sorted from the sediment under

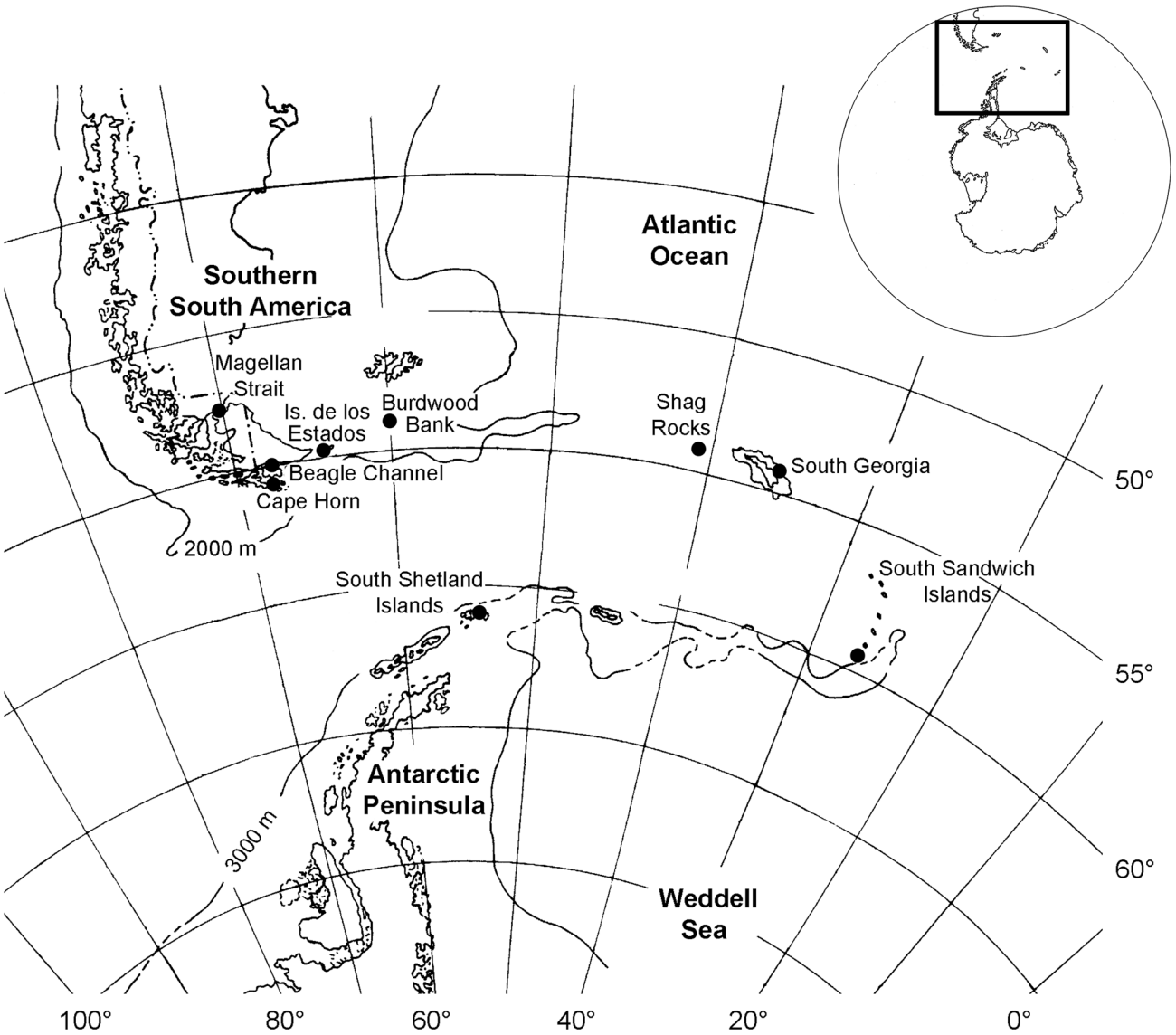

Fig. 1 Location map, showing the sampled sites

a stereoscopic microscope and fixed in a 5% sea-water formalin solution. The material was deposited in the collections at Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires, and Museo de La Plata (MLP), La Plata. Additional material from the collection at the Museum für Naturkunde (ZMB), Berlin, was studied. The number of specimens (sp.) and shells (sh.) in each studied lot is indicated in the Material examined sections.

Radulae were dissected under stereoscopic microscope and both radulae and shells were cleaned in a 2% hypochlorite solution before mounting for scanning electron microscopy (SEM) study. Shell measurements were taken with micrometer eyepiece mounted on a stereoscopic microscope, and correspond to: maximum shell length (*L*) and maximum shell width (*W*), perpendicular to *L*. The *L*/*W* ratio is given, along with its standard deviation (SD) and number of measured specimens (*n*). Protoconch length (*L*) and diameter were measured on SEM photographs.

Illustrations of the types of the species previously known from the studied area are given in Ponder (1983) and Ponder and Worsfold (1994).

Systematics

Rissoidae Gray, 1847.

Onoba H. and A. Adams, 1852.

Type species: *Turbo striatus* J. Adams, 1797 (by monotypy).

Onoba clara new species, Fig. 2a–c

"Rissooidea species 2" - Engl 2012: 119, pl. 39, Fig. 5.

Type locality: 61°23′27.0″S 55°26′49.2″W, Elephant Island, South Shetland Islands, 285 m.

Type material: Holotype (MLP-Ma 14313) and 20 paratypes (MLP-Ma 14314; MACN-In 41100) from the type locality.

Known distribution: South Shetland Islands and Bransfield Strait (Antarctic Peninsula); 94–285 m depth (Engl 2012; herein).

Etymology: The species name makes reference to its bright appearance (= "clara" in Spanish).

Diagnosis: Shell small, elongate-conic. Protoconch with spirally arranged pustules. Teleoconch with 2 prominent spiral keels per whorl, thin spiral threads and weak axial riblets. Aperture markedly digitated by spiral keels.

Description: *Shell* (Fig. 2a, b): Small (max. *L* observed = 3.35 mm), elongate-conic ($L/W = 1.5 \pm 0.2$, $n = 10$), delicate, white, translucent. Protoconch of 1 ½ globose whorls, high ($L = 370$ µm), about 450 µm in diameter; shiny, microscopically sculptured with small, dense, spirally arranged pustules (Fig. 2b). Teleoconch of up to 3 ¾ whorls, outline markedly gradated; primary sculpture consisting of 2 prominent spiral keels per whorl at the spire, and 6–7 on last whorl, reducing in solidness towards the base, and a weaker additional sub-sutural cord, increasing in solidness towards last whorl (Fig. 2a). Secondary spiral sculpture comprising numerous, closely and regularly distributed, extremely thin spiral threads; and weak, widely spaced axial riblets, which pass over the spiral sculpture (Fig. 2a, b). Sutures covered by a weak, additional spiral cord. Aperture subcircular; outer lip thin to slightly thickened, opisthocline, markedly digitated by primary spiral sculpture (keels); sometimes mimicking internally the outer primary spiral sculpture; inner lip posteriorly attached to base (Fig. 2a). Umbilical chink represented by a short groove (Fig. 2a).

Radula (Fig. 2c): Central tooth with wide, trapezoidal base, having one pair of strong basal denticles; cusp widely triangular, with 5–6 denticles at each side of median denticle. Median denticle wide, sharply pointed; lateral denticles elongated, gradually shortening outwards. Lateral teeth with triangular, asymmetric cusp: main denticle distally rounded, with obscure basal bifurcation on inner side; and 8 narrow, pointed lateral denticles on each side, the outer ones wider. Cusp of inner marginal teeth with about 15–18 narrow denticles restricted to outer and distal margins.

Operculum: Ovate, with excentric nucleus; paucispiral, of about 2 ½ whorls. Yellowish, translucent.

Remarks: *Onoba clara* n. sp. is sharply different from any other *Onoba* from sub-Antarctic and Antarctic waters. The elongate shell outline somewhat resembles that of *O. fuegoensis*, but the prominent spiral keels and digitated outer lip of the aperture, characteristic of this species, clearly differentiate it.

The few, prominent spiral keels present in *Onoba clara* n. sp. are also present in members of *Lironoba* Iredale, 1915 and *Cingula* Fleming, 1818. *Lironoba* however, is characterized by the presence of a weak keel and/or spiral lirae on the last whorl of the protoconch which, in addition, is sculptured with extremely minute pits (Ponder 1985: 75, Fig. 126). On the other hand, members of *Cingula* show the protoconch bearing spiral striae or spiral striae with micro-lamellae between, which is also different from the conspicuous pustules present in *Onoba clara* n. sp.

Onoba clara n. sp. is also similar to "*Lironoba" australis* (Tenison-Woods, 1877) from Australia, in general shell outline. However, the latter species has a ridge-like structure on the inner surface of the operculum, and the aperture is not digitated by the spiral ribs, as it is in *O. clara* n. sp.

Onoba clara n. sp. was referred by Engl (2012: 119) as "Rissooidea species 2" (sic).

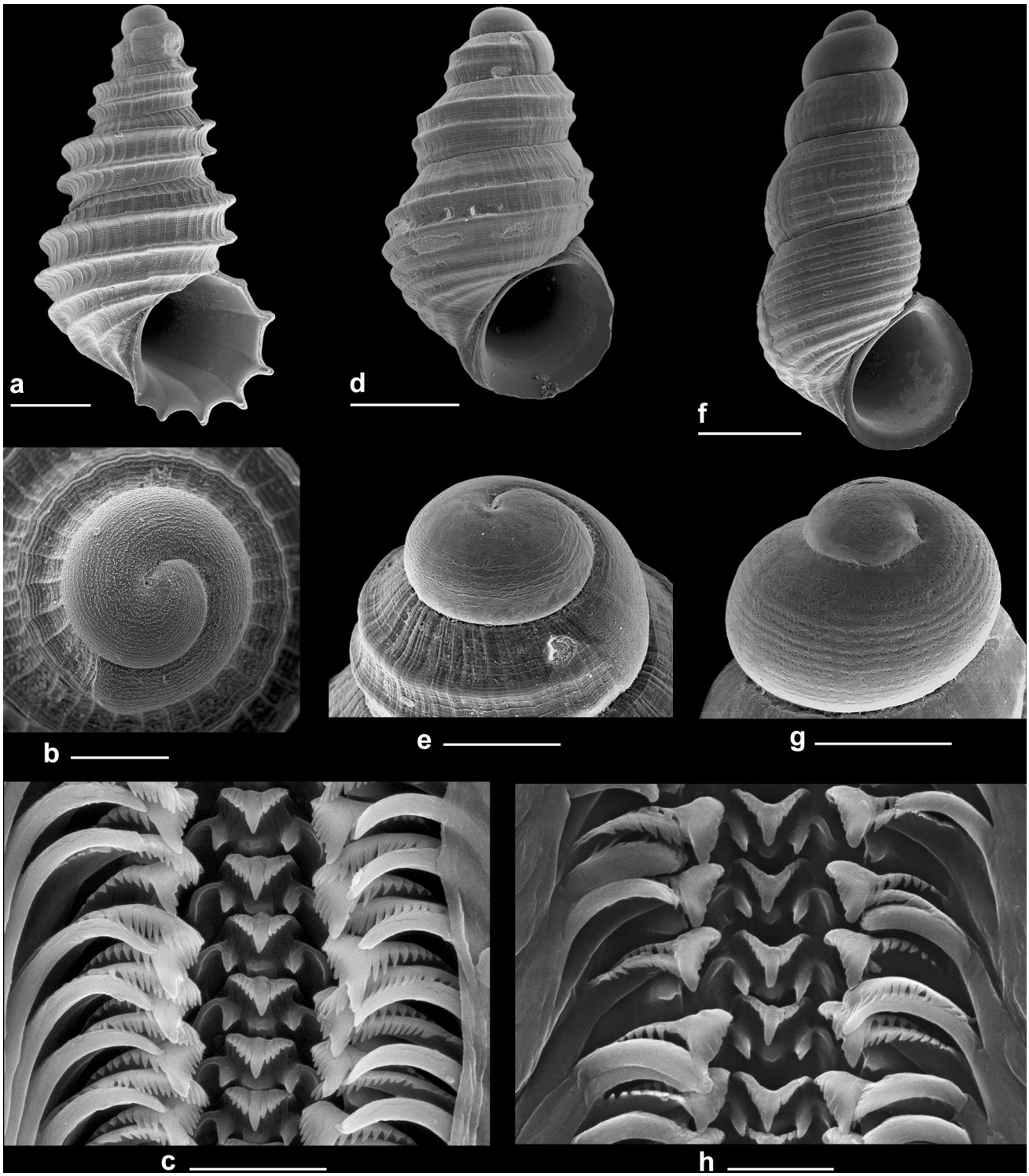

Fig. 2 **a–c** *Onoba clara* new species, **a** holotype (MLP-Ma 14313), **b, c** paratypes (MLP-Ma 14314). **d, e** *Onoba sandwichensis* new species, holotype (MLP-Ma 14315). **f–h** *Onoba klausgrohi*, **f–h** specimens from South Sandwich Islands (MLP-Ma 14317, MLP-Ma 14318). **a, d, f** apertural view, **b, e, g** detail of protoconch, **c, h** radula. *Scale bars* **a, d, f** 500 µm, **b, e, g** 200 µm, **c, h** 10 µm

Onoba sandwichensis new species, Fig. 2d, e

Type locality: 59°54′58.8″S 32°28′19.8″W, South Sandwich Islands, 521 m.

Type material: Holotype (MLP-Ma 14315) and 1 paratype (MLP-Ma 14316) from the type locality.

Known distribution: Only known from the type locality.

Etymology: The name refers to the provenance of the species.

Diagnosis: Shell small, ovate-conic, with 2 strong but low spiral cords per whorl, thin spiral threads and well-discernible axial growth lines. Aperture subovate, weakly subangled posteriorly, with prominent external varix. Protoconch with low, irregular spiral cords.

Description: *Shell* (Fig. 2d, e): Small (max. *L* observed = 2.05 mm), ovate-conic ($L/W = 1.79 \pm 0.09$, $n = 3$), moderately solid, white, dull. Protoconch of 1½ whorls, low and wide, of about 300 µm *L* and 400 µm in diameter; microscopically sculptured with low, irregular spiral threads (although slightly worn in the available specimens) (Fig. 2e). Teleoconch of up to 3 whorls, outline convex although indented by primary spiral sculpture; primary sculpture consisting of 2 strong but low, spiral cords at the spire, and 7–8 on last whorl and base; a weaker additional sub-sutural cord on penultimate whorl, present (Fig. 2d). Secondary sculpture comprising few, wavy spiral threads; and well-discernible growth lines. Sutures impressed, simple. Aperture subovate, weakly subangled posteriorly; outer lip orthocline, evenly arcuated, with prominent external varix; inner lip attached to base (Fig. 2d).

Radula and operculum: unknown.

Remarks: The species resembles *Onoba paucilirata* (Melvill and Standen, 1916) and *O. paucicarinata* Ponder, 1983, from which it differs by being considerably narrower ($L/W = 1.79$ vs. 1.41–1.40 in *O. paucilirata* and *O. paucicarinata*, respectively). Moreover, *O. sandwichensis* n. sp. has well-discernible growth lines, stronger than in *O. paucilirata*, but less evident than the distinct axial lamellae present in *O. paucicarinata*. Furthermore, *O. paucicarinata* has a protoconch with irregularly arranged, raised pustules (instead of low, irregular spiral cords).

The strong spiral cords present in the teleoconch of *Onoba sandwichensis* n. sp. also resemble those of *Lironoba* species. However, *O. sandwichensis* n. sp. lacks the characteristic duplicated peristome and micropitted protoconch reported for members of *Lironoba* (Ponder 1985).

Onoba klausgrohi Engl, 2011, Fig. 2f–h

Onoba klausgrohi Engl, 2011: 54, Fig. 3; Engl 2012: 114, pl. 37, Fig. 4.

Type locality: 59°42.55′S 27°57.02′W to 59°42.62′S 27°57.68′W, off Southern Thule, South Sandwich Islands, 332–340 m.

Material examined: South Sandwich Islands: 59°42.55′S 27°57.02′W, 332 m (MLP-Ma 14317: 3 sp., 12 sh.; MACN-In 41101: 3 sp., 12 sh.); 59°54.98′S 32°28.33′W, 521 m (MLP-Ma 14318: 4 sp., 5 sh.).

Known distribution: Only known from South Sandwich Islands; 332–521 m depth (Engl 2011; herein).

Description: The general shell morphology was properly described by Engl (2011).

Protoconch of 1 ¾ globose whorls, about 380 µm *L* and 400 µm in diameter; translucent, glossy, sculptured with spiral elements (Fig. 2g).

Operculum: Ovate, paucispiral. Yellowish, translucent.

Radula (Fig. 2h): Central tooth with wide, trapezoidal base, having one pair of strong basal denticles; cusp with 5 denticles at each side of median denticle. Median denticle long, narrow, distally rounded. Lateral teeth with triangular, asymmetric cusp: main denticle somewhat blunt; with 6–7 wide, short inner denticles and 6–7 narrow, sharply pointed outer denticles. Cusp of inner marginal teeth with 13–15 narrow denticles, restricted to outer and distal margins. Cusp of outer marginal teeth with several narrow denticles.

Remarks: *Onoba klausgrohi* was previously known only from empty shells, which according to Engl's descriptions, had worn protoconchs. The material here studied (Fig. 2f–h) provides information on the protoconch sculpture, operculum and radular morphology.

Onoba verrucosa new species, Fig. 3a–c

Type locality: 59°42′33.0″S 27°57′12″W, South Sandwich Islands, 332 m.

Type material: Holotype (MLP-Ma 14319) and seven paratypes (MLP-Ma 14320; MACN-In 41102) from the type locality.

Known distribution: Only known from the type locality.

Etymology: The name refers to the wart-like pustules of the protoconch.

Diagnosis: Shell minute, inflated. Teleoconch sculptured with five strong spiral cords per whorl, interspaces wider than cords. Protoconch with large, low, spirally arranged pustules.

Description: *Shell* (Fig. 3a–c): Minute (max. *L* observed = 1.9 mm), low-spired, inflated ($L/W = 1.24 \pm 0.05$, $n = 6$), delicate, white. Protoconch of 1 ½ inflated whorls, about 375 µm *L*, and 470 µm in diameter; translucent, shiny, sculptured with large, irregular, spirally arranged pustules (Fig. 3b, c). Teleoconch of up to 2 convex whorls; sculptured with 5 strong spiral cords per whorl, and 11–12 on last whorl and base; interspaces

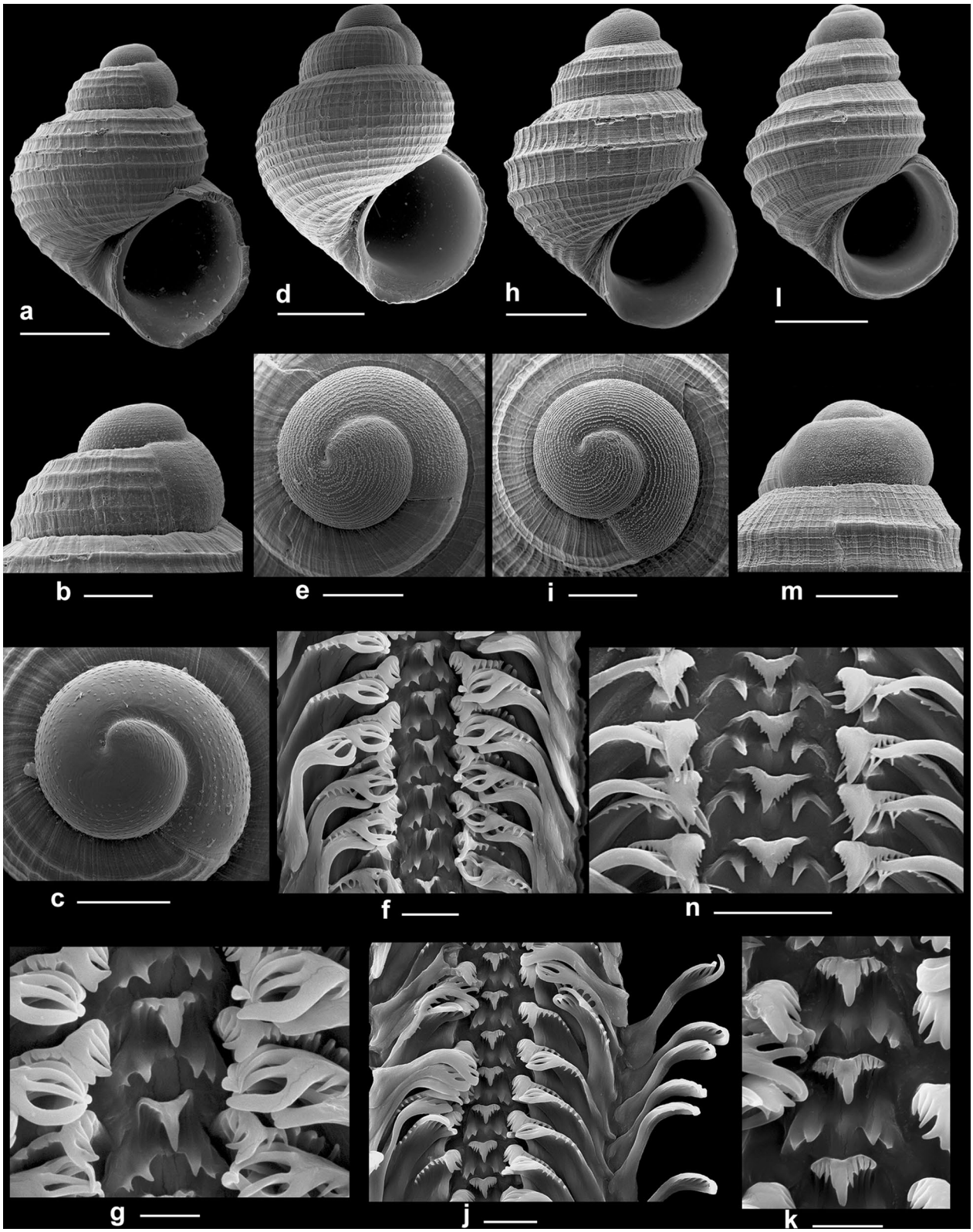

Fig. 3 **a–c** *Onoba verrucosa* new species, **a, b** holotype (MLP-Ma 14319), **c** paratype (MLP-Ma 14320). **d–g** *Onoba antleri* new species, **d** holotype (MLP-Ma 14321), **e–g** paratypes (MLP-Ma 14322). **h–k** *Onoba caribu* new species, **h** holotype (MLP-Ma 14323), **i–k** paratypes (MLP-Ma 14324). **l-n** *Onoba oligochordata* new species, **l, m** holotype (MLP-Ma 14325), **n** paratype (MLP-Ma 14326). **a, d, h, l** apertural view, **b, c, e, i, m** detail of protoconch, **f, j, n** radulae, **g, k** detail of central tooth. *Scale bars* **a, d, h, l** 500 µm, **b, c, e, i, m** 200 µm, **f, j, n** 10 µm, **g, k** 5 µm

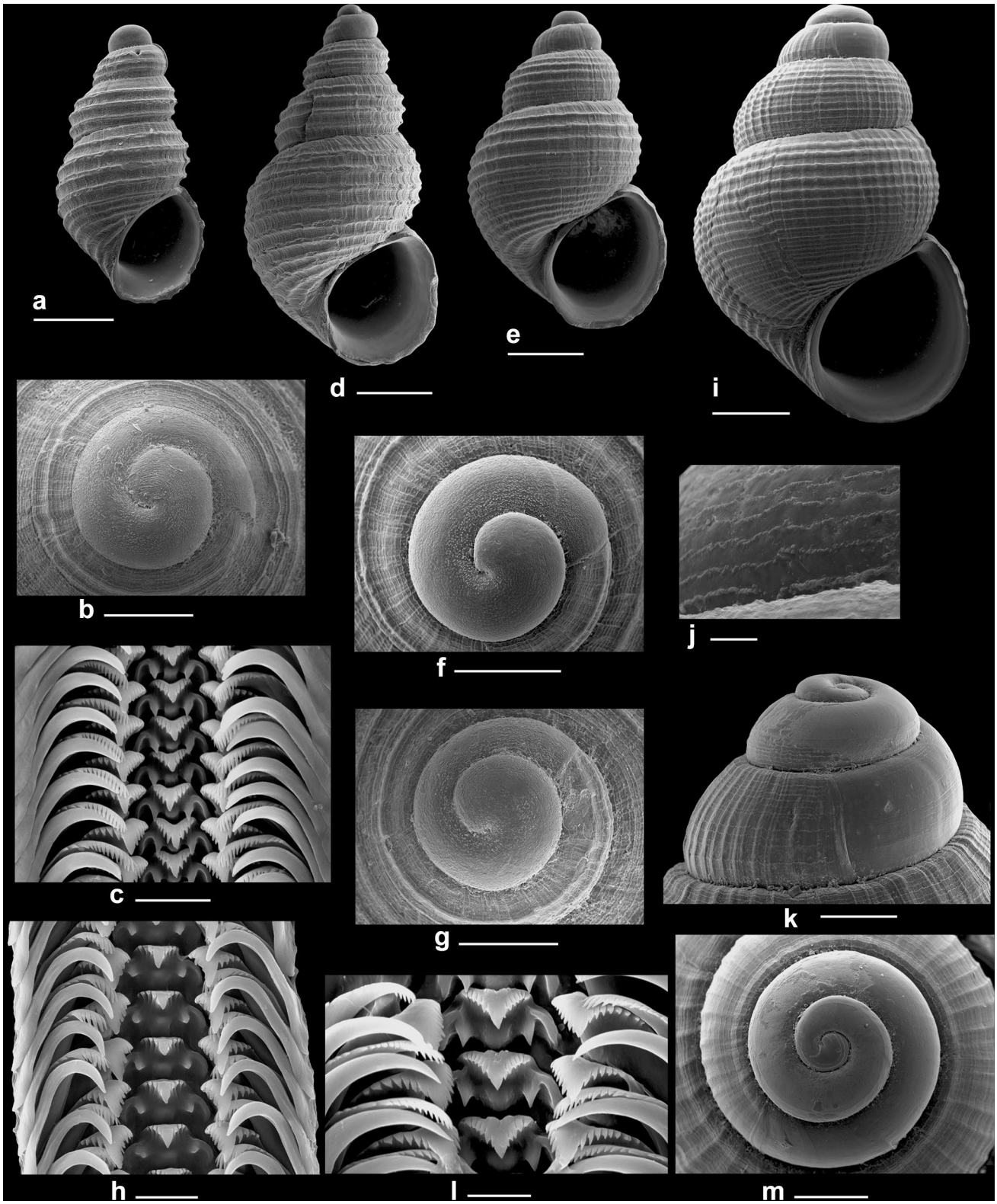

Fig. 4 **a–c** *Onoba fuegoensis*, **a** specimen from Cabo San Pío (MLP-Ma 14327), **b, c** specimen from Puerto Parry (MLP-Ma 14328). **d–h** *Onoba schythei*, **d, f** specimens from San Juan del Salvamento (MLP-Ma 14334), **e** specimen from Punta Moat (MLP-Ma 14332), **g, h** specimen from Puerto Parry (MLP-Ma 14333). **i–m** *Onoba ernestoi* new species, **i–k** holotype (ZMB 103.638-a), **l, m** paratypes (ZMB 103.638-b). **a, d, e, i** apertural view, **b, f, g, k, m** detail of protoconch, **j** detail of protoconch sculpture, **c, h, i** radulae. *Scale bars* **a, d, e, i** 500 µm, **b, f, g, k, m** 200 µm, **j** 20 µm, **c, h, l** 10 µm

wider than cords (Fig. 3a). Secondary sculpture consisting of closely-set, obscure spiral threads and weak axial growth lines. Sutures impressed, simple. Aperture subovate, somewhat expanded; outer lip evenly arcuated, without external varix; inner lip posteriorly attached to base. Umbilicus wide, deep (Fig. 3a).

Operculum: paucispiral, thin, yellowish.

Radula: unknown.

Remarks: *Onoba verrucosa* n. sp. resembles, in its inflated shell outline, *O. inflatella* (Thiele, 1912) from *Gauss* station (Davis Sea, east Antarctica). However, the new species here described has a lower incremental rate of whorls, which results in a smaller shell at similar number of whorls. Moreover, *O. inflatella* has a markedly wider umbilicus.

Onoba antleri new species, Fig. 3d–g

Type locality: 54°01′21.6″S 62°01′19.8″W, Burdwood Bank, 272 m.

Type material: Holotype (MLP-Ma 14321) and 52 paratypes (MLP-Ma 14322; MACN-In 41103) from the type locality.

Known distribution: Only known from the type locality.

Etymology: The name refers to the peculiar morphology of the marginal teeth of the radula, which reminds of the antlers of a deer.

Diagnosis: Shell small, inflated. Teleoconch sculptured with numerous, narrow spiral cords and thin axial riblets. Protoconch sculptured with dense, small granules joined in branching spiral arrangement. Radula: Central teeth with two pairs of basal denticles; cusp with 2–4 denticles on each side of median denticle. Cusps of marginal teeth "antler-like".

Description: *Shell* (Fig. 3d, e): Small (max. *L* observed = 2.6 mm), inflated ($L/W = 1.38 \pm 0.07$, $n = 11$), delicate, white, dull. Protoconch of 1 ½ convex whorls, about 350 µm *L*, and 470 µm in diameter; translucent, shiny, sculptured with small, irregular, granules joined in dense branching, spiral rows (Fig. 3e). Teleoconch of up to 2¼ convex whorls; sculpture cancellate: spiral cords narrow, low, flat, regularly distributed, in number of 6–8 per spire whorl, and 13–14 on last whorl and base, separated by interspaces wider than cords width; axial sculpture consisting of extremely thin riblets, which pass over the spirals (Fig. 3d). Secondary spiral sculpture hardly visible. Sutures impressed. Aperture subovate, somewhat angled posteriorly, slightly expanded anteriorly; outer lip thin, regularly curved, without external varix; inner lip posteriorly attached to base. Umbilicus represented by a narrow groove (Fig. 3d).

Operculum: Thin, paucispiral; yellowish.

Radula (Fig. 3f, g): Central tooth with triangular base, having two pairs of acute basal denticles; cusp with 2 denticles on each side of median denticle. Median denticle long, narrow, sharply pointed. Lateral teeth with asymmetric cusp: main denticle wide, bifid; with 4 narrow, elongated denticles at the inner margin and 5–9 pointed denticles at the outer margin, shorter than the inner ones. Cusps of marginal teeth "antler-like", with about 7, long and narrow distal denticles; inner marginals with 4–5 additional, shorter and sharp denticles at the outer margin.

Remarks: *Onoba antleri* n. sp. resembles *O. verrucosa* n. sp. in general shell outline. However, the former has a larger number of narrower spiral cords and stronger axial sculpture, determining a cancellate pattern. Moreover, the umbilicus of *O. antleri* n. sp. is considerably narrower, and its protoconch has a distinct branching arrangement of joined granules, which clearly differs from the spirally aligned large pustules of *O. verrucosa* n. sp.

Onoba caribu new species, Fig. 3h–k

Type locality: 61°23′27″S 55°26′49.2″W, Elephant Island, South Shetland Islands, 285 m.

Type material: Holotype (MLP-Ma 14323) and 17 paratypes (MLP-Ma 14324; MACN-In 41104) from the type locality.

Known distribution: The species is only known from the type locality.

Etymology: The name refers to the morphology of the marginal teeth of the radula, which resembles the shape of caribou (="caribú" in Spanish) antlers.

Diagnosis: Shell small, inflated, with 3–4 prominent spiral cords per spire whorl, and about 9 at the base, crossed by raised axial riblets. Protoconch sculptured with beaded spiral rows of pustules. Radula: Central teeth with two pairs of basal denticles; cusp with 5–6 denticles on each side of median denticle. Cusps of marginal teeth "antler-like".

Description: *Shell* (Fig. 3h, i): Small (max. *L* observed = 2.1 mm), inflated ($L/W = 1.28 \pm 0.08$, $n = 10$), delicate, white, dull. Protoconch of 1½ bulbous whorls, about 370 µm *L*, and 450 µm in diameter; shiny, sculptured with beaded spiral rows of small, dense pustules (Fig. 3i). Teleoconch of up to 3¾ convex whorls. Primary sculpture consisting of prominent, widely-spaced spiral cords, in number of 3–4 per spire whorl and 11–12 on last whorl and base; those on the base, more delicate (Fig. 3h). Axial sculpture composed of raised riblets, which undulate when passing over the spiral cords. Secondary sculpture consisting of close, extremely thin spiral threads. Sutures impressed. Aperture subovate, somewhat angled posteriorly, slightly expanded anteriorly; outer lip orthocline, slightly to markedly undulated by primary spiral sculpture, without external varix; inner lip almost completely attached

to base (Fig. 3h). Umbilical chink represented by a short groove (Fig. 3h).

Operculum: Thin, of about 3 whorls, with long growing edge, yellowish.

Radula (Fig. 3j, k): Central tooth with triangular base, having two pairs of strong basal denticles; cusp with 5–6 denticles on each side of median denticle. Median denticle long, narrow, distally rounded. Lateral teeth with asymmetric cusp: main denticle wide, bifid; with 4–6 narrow, pointed denticles at the inner margin and 7–8 widely triangular denticles at the outer margin, shorter than the inner ones. Cusps of marginal teeth "antler-like", with 5–7 long and narrow, distal denticles; inner marginals with 4–6 additional, shorter and sharp denticles at the outer margin.

Remarks: *Onoba caribu* n. sp. resembles *O. paucilirata* by having low, broadly-conical shells sculptured with a low number of strong spiral cords. However, the shell of *O. caribu* n. sp. is lower (*L*/*W* 1.28 vs. 1.40 in the holotype of *O. paucilirata*), has 11–12 (instead of 6 + 1) spiral cords in the last whorl, and shows distinct axial riblets. In shell sculpture *O. caribu* n. sp. resembles *O. delecta* Ponder, 1983 (see below), which however has a narrower and higher spire (*L*/*W* 1.59 vs. 1.28, respectively), and bears disperse granules in the protoconch (instead of spiral rows of pustules). *Onoba paucicarinata* is also similar in having few spiral cords and distinct axial lamellae, but *O. caribu* n. sp. has a larger and wider shell (*L*/*W* 1.40 vs. 1.28, respectively).

The radula of *O. caribu* n. sp. closely resembles that of *O. antleri* n. sp., by having "antler-like" marginal teeth, although the number of denticles in the central teeth is different. These two species also clearly differ in the number and solidness of spiral cords, which generate a cancellate pattern with square interspaces in *O. antleri* n. sp., instead of the rectangular interspaces present in *O. caribu*. Both species also differ in protoconch sculpture.

Onoba oligochordata new species, Fig. 3l–n

Type locality: 61°23′27.0″S 55°26′49.2″W, Elephant Island, South Shetland Islands, 285 m.

Type material: Holotype (MLP-Ma 14325) and two paratypes (MLP-Ma 14326; MACN-In 41105) from the type locality.

Known distribution: Only known from its type locality.

Etymology: The name refers to the few spiral cords present in the teleoconch.

Diagnosis: Shell minute, inflated; teleoconch with 2–3 strong spiral cords per whorl, raised axial riblets and thin spiral threads. Protoconch with irregularly distributed pustules. Radula: Central teeth with a pair of sharp basal denticles and 4–5 short denticles at each side of median denticle; lateral teeth with narrow denticles.

Description: *Shell* (Fig. 3l, m): Minute (max. *L* observed = 1.58 mm), inflated (*L*/*W* = 1.2 ± 0.2, *n* = 2), solid, white. Protoconch of 1½ globose whorls, low (L about 200 µm), sculptured with small, prominent, irregularly distributed pustules (Fig. 3m). Teleoconch of up to 2½ convex whorls. Primary sculpture consisting of strong, rounded spiral cords, in number of 2 in the first whorl, increasing to 8 in last whorl and base (Fig. 3l). Axial sculpture composed of numerous riblets which pass over the spiral cords. Secondary sculpture consisting of delicate spiral threads. Sutures impressed. Aperture subovate, weakly angled posteriorly, somewhat expanded anteriorly; outer lip orthocline, without distinct varix; inner lip posteriorly attached to base (Fig. 3l). Umbilical chink represented by a small groove (Fig. 3l).

Operculum: Thin, paucispiral, yellowish.

Radula (Fig. 3n): Central tooth with wide, trapezoidal base, having one pair of sharp basal denticles; cusp with 4–5 denticles at each side of median denticle. Median denticle wide; lateral denticles shorter and narrower. Lateral teeth with triangular, asymmetric cusp: main denticle wide; with 8 inner and 6 outer narrow denticles at the sides, the outer more widely separated. Inner marginal teeth with 4–5 long, narrow distal denticles and several additional smaller denticles at the outer margin.

Remarks: *Onoba oligochordata* n. sp. resembles *O. paucicarinata* in shell sculpture. However, the former has somewhat weaker and more densely arranged axial riblets, the aperture sub-ovate and weakly angled posteriorly, and somewhat expanded anteriorly (vs. regularly ovate in *O. paucicarinata*); furthermore, the external varix present in the latter species, is lacking in *O. oligochordata* n. sp.

Onoba oligochordata n. sp. is also similar to *O. paucilirata* in general shell outline, but it is much smaller (when comparing specimens of equal number of whorls) and it is sculptured with well-marked axial riblets (which are absent in *O. paucilirata*).

Another morphologically similar species is *O. caribu* n. sp., which however strikingly differs in radular morphology (particularly by the presence of antler-like marginal teeth) and in protoconch sculpture (spirally aligned vs. irregularly distributed).

Onoba fuegoensis (Strebel, 1908), Fig. 4a–c

Rissoia (?Cingula) fuegoensis Strebel, 1908: 56, pl. 6, Figs. 90 a–b.

Onoba fuegoensis (Strebel, 1908): Ponder and Worsfold 1994: 43, Figs. 23 e, f, 24 a–c, 30.

Type locality: 54°43′S 64°08′W, [Isla de los Estados], Tierra del Fuego, 36 m.

Material examined: Beagle Channel: 55º06′S 66º29′W, Cabo San Pío, 65–80 m (MLP-Ma 14327: 1 sh.). Isla de

los Estados: 54°42′48.0″S 63°50′36.0″W, San Juan del Salvamento, 38–60 m (MACN-In 41107: 30 sh.); 54°46′S 64°22′W, Puerto Parry, 35 m (MLP-Ma 14328: 10 sp., 30 sh.). Burdwood Bank: Área Marina Protegida Namuncurá – Banco Burdwood: 54°30′23.4″S 59°48′39.24″W, 105 m (MACN-In 41106: 2 sh.).

Remarks: *Onoba fuegoensis* was properly redescribed and figured by Ponder and Worsfold (1994), who also discussed the intraspecific variability of the species and its great similarity with *O. schythei* (Philippi, 1868). The identity of the material studied herein was confirmed by studying the radula, shell and protoconch (Fig. 5a–c). This material provides an additional difference to separate *O. fuegoensis* from *O. schythei*: in the former, the interspaces between the primary spiral cords show beaded spiral threads, whereas in the latter, threads are smooth. The species was previously reported from Isla de los Estados, Burdwood Bank and Cape Horn; the material studied herein provides the first record of the species for the Beagle Channel.

Onoba schythei (Philippi, 1868), Fig. 4d-h

Rissoa Schythei (sic) Philippi, 1868: 225.

Onoba scythei (sic) (Philippi, 1868): Ponder and Worsfold 1994: 39, Figs. 23a, c, 24d, h, 28, 29.

Type locality: Freto Magellanico [=Magellan Strait].

Material examined: Magellan Strait: 53°48′37.9″S 71°37′27.6″W, Cabo Holland, 15–25 m (MACN-In 41108: 2 sp.). Beagle Channel: 54°50′S 68°20′W, Bahía Golondrina, 5 m (MLP-Ma 14329: 3 sh.); 54°50′S 68°19′W, Bahía Golondrina, 5 m (MLP-Ma 14330: 3 sh.); 54°50′53″S 68°14′40″W, 16 m (MLP-Ma 14331: 6 sh.); 55°01′30.0″S 66°41′42.0″W, Punta Moat, 15–18 m (MLP-Ma 14332: 4 sh.). Isla de los Estados: 54°46′S 64°22′W, Puerto Parry, 35 m (MLP-Ma 14333: 1 sp.); 54°42′48.0″S 63°50′36.0″W, San Juan del Salvamento, 38–60 m (MLP-Ma 14334: 15 sh.; MACN-In 41109: 15 sh.).

Remarks: Ponder and Worsfold (1994) redescribed *O. schythei*, pointing out the great morphological variability between the "shallow" (mainly intertidal) and the "deep-water" (15–36 m) specimens they studied. The former was described as having shorter and broader shells, with more flattened spiral sculpture, than the latter. The authors also commented that these two forms "intergrade". As part of this study, we found both morphological extremes (Fig. 5d–g), as well as intermediate forms that resemble Ponder and Worsfold's (1994) Fig. 28c (not figured herein). However, the specimens here studied do not show a clear correspondence between shell morphology and depth: both extremes of the shell variation were found coexisting subtidally, between 15 and 18 m depth; and specimens with intermediate morphologies were found between 5 and 35 m.

Ponder and Worsfold (1994: 43) mentioned that they had "only been able to examine a radula from a shallow-water specimen". Nevertheless, the caption of their Fig. 23a, c (assigned to radulae of *O. schythei*) refers to two specimens: one coming from East Malvinas/Falkland Islands, intertidal (Fig. 23a: "Sta. TW3") and the other from the Magellan Strait, 111 m (Fig. 23c: "Sta. 75-49"); the latter, however, was not included in their list of material examined. The authors described the main denticle of the central tooth as "blunt", which agrees with their Fig. 23c. However, their Fig. 23a shows a sharply triangular main denticle, which is in agreement with the material examined herein (Fig. 5h). The latter seems to be the normal condition of the species.

The material here studied provides the first record of the species from the Beagle Channel. Previously, the species was known from Southern Chile, Magellan Strait, Cape Horn; East of Tierra del Fuego, Isla de los Estados and Malvinas/Falkland Islands (Ponder and Worsfold 1994); it had been improperly referred as *O. scythei*, being its actual spelling *O. schythei*.

Onoba ernestoi new species, Fig. 4i–m

Type locality: 55°28′48.0″S 66°03′24.0″W, Cape Horn, 1279 m.

Type material: Holotype (ZMB 103.638-a) and four paratypes (ZMB 103.638-b; MACN-In 41110) from the type locality.

Known distribution: Only known from the type locality.

Etymology: The species is named after Ernesto Güller, for supplying our sampling gears.

Diagnosis: Shell small, widely-conic; teleoconch with numerous spiral cords per whorl, microscopic wavy spiral threads in the interspaces, and weak axial riblets; protoconch multispiral, sculptured with very thin spiral treads.

Description: *Shell* (Fig. 4i–k, m): Small (max. *L* observed = 2.95 mm), widely-conic ($L/W = 1.4 \pm 0.1$, $n = 4$), translucent, whorls convex. Protoconch multispiral, of 2 ¾ whorls, about 540 µm *L* and 600 µm in diameter, somewhat sunken in the first whorl; translucent, sculptured with thin, densely set spiral threads (Fig. 4j, k, m). Teleoconch of up to 2¾ whorls, sculptured with 10 low, rounded spiral cords on penultimate whorl, and 21 spiral cords on last whorl and base; with extremely fine, microscopic wavy spiral threads and weak axial riblets that give a wavy appearance to spiral elements; interspaces as wide as cords (Fig. 4i). Aperture subovate, weakly channelled posteriorly; widely rounded anteriorly. Inner lip posteriorly attached to base (Fig. 4i). Umbilical chink represented by a shallow, narrow groove (Fig. 4i). Colour white.

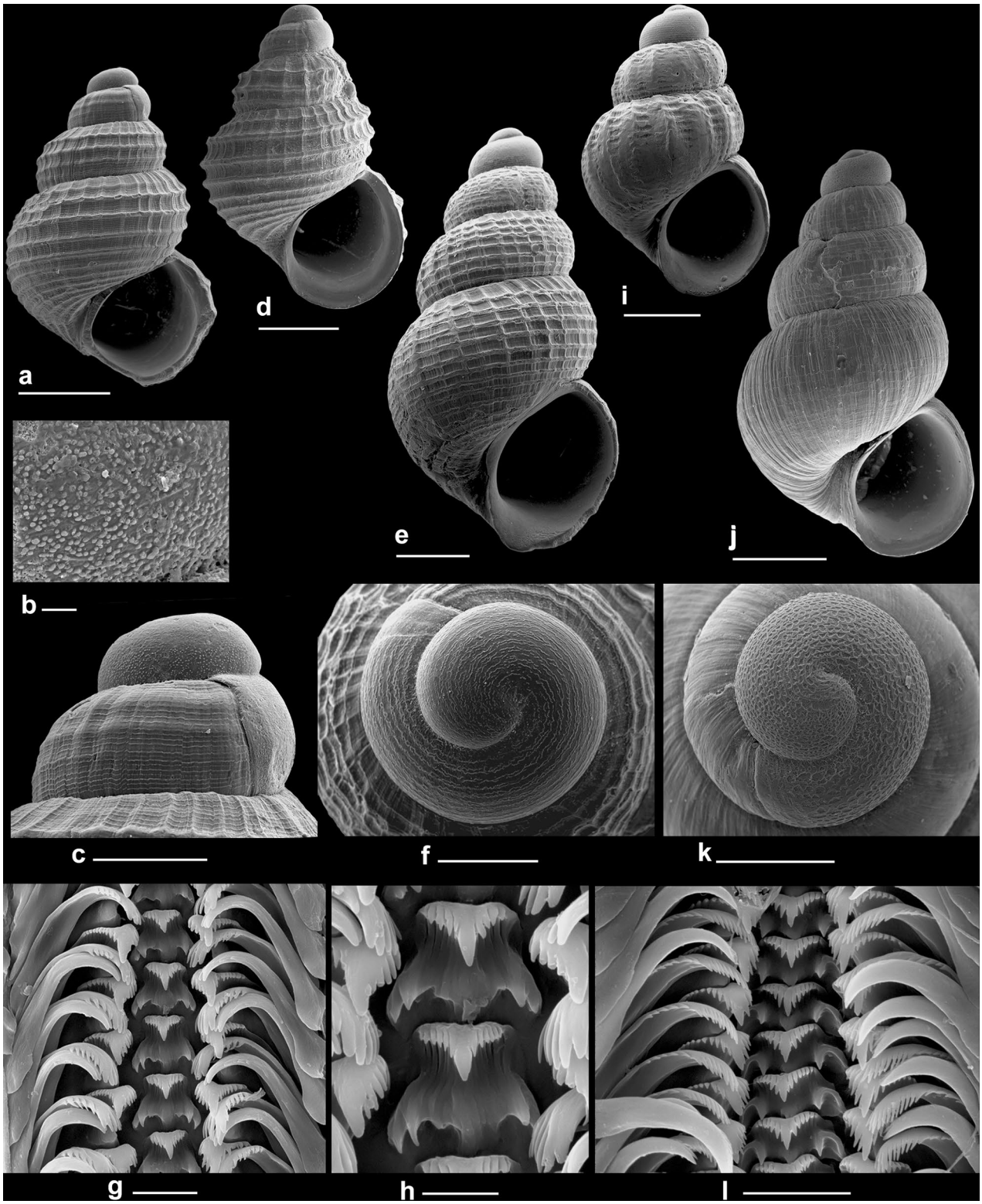

Fig. 5 **a–d** *Onoba delecta*, **a–c** specimen from Shag Rocks (MLP-Ma 14335), **d** specimen from South Georgia (MACN-In 36283, same specimen figured in Zelaya 2005). **e–h** *Onoba* cf. *algida*, **e** specimen from San Juan del Salvamento (MLP-Ma 14337), **f–h** specimens from Cabo San Pío (MLP-Ma 14336). **i** *Onoba algida*, specimen from San Juan del Salvamento (MLP-Ma 14337). **j–l** *Haurakia averni*, specimens from Bahía Cánepa (MLP-Ma 14338). **a, d, e, i, j** apertural view, **b** detail of protoconch sculpture, **c, f, k** detail of protoconch, **g, l** radulae, **h** detail of central tooth. *Scale bars* **a, d, e, i, j** 500 µm, **b** 20 µm, **c, f, k** 200 µm, **g, l** 10 µm, **h** 5 µm

Operculum: Subovate, posteriorly angled, with excentric nucleus; of about 2 ¼ whorls; yellowish-brown.

Radula (Fig. 4l): Central tooth with wide, trapezoidal base, having one pair of strong basal denticles; cusp with 4–6 denticles at each side of median denticle. Median denticle wide, sharply pointed. Lateral teeth with triangular, asymmetric cusp: main denticle wide, with obscure basal bifurcation on inner side; with 6–7 inner and 6–9 outer, pointed denticles at the sides. Cusp of inner marginal teeth with about 12–14 narrow denticles, restricted to outer and distal margins.

Remarks: *Onoba ernestoi* n. sp. closely resembles *O. emiliorolani* Engl, 2011 by having a translucent, inflated shell, sculptured with numerous spiral cords. However, both species are clearly different in protoconch morphology: the new species here described has a multispiral protoconch of about 2¾ whorls, sculptured with thin, densely arranged spiral threads, whereas the protoconch of *O. emiliorolani* is paucispiral, of about 1½ whorls, and sculptured with numerous fine granules. In addition, *O. ernestoi* n. sp. has a somewhat less triangular shell outline, with wider spiral cords and a narrower umbilical chink.

Onoba ernestoi n. sp. also resembles in general shell morphology *O. subantarctica* (Thiele, 1912) from Kerguelen Islands. However, the former has a less conical outline, with more convex whorls, and the teleoconch sculptured with fewer (10 on penultimate whorl) and stronger spiral cords (vs. the 14 thin spiral lines that constitute the microsculpture of *O. subantarctica*), and well-discernible axial riblets. Moreover, the protoconch of *O. ernestoi* strongly differs from that of *O. subantarctica* by being multispiral and by lacking the weak axial threads that are present in the latter species.

Onoba delecta (Ponder, 1983), Fig. 5a–d

Rissoia grisea (Strebel, 1908: 53) (*non* von Martens, 1885).

Onoba delecta Ponder, 1983: 20, Fig. 15f; Zelaya 2005: 116, Fig. 15.

Type locality: 53°51′S 37°38′W, South Georgia, 97–101 m.

Material examined: Shag Rocks: 53°23′48.0″S 42°42′18.0″W, 313 m (MLP-Ma 14335: 1 sh.). South Georgia: 54°30′S 35°50′W, 94 m (MLP-Ma 7304: 6 sp.; MACN-In 36283: 6 sp.); 53°58′S 37°09′W, 138 m (MACN-In 36284: 2 sp.).

Known distribution: Shag Rocks (herein); Malvinas/Falkland Islands, South Georgia (Ponder 1983; Zelaya 2005).

Remarks: The original description is good enough for recognizing the species, although the material on which Ponder (1983) based his description had worn protoconchs; this fact led him to describe it as "apparently smooth". The material studied herein (Fig. 5a–d) reveals that the protoconch of this species is actually sculptured with microscopic, irregular granules (Fig. 5c, d).

The figure provided by Zelaya (2005: Fig. 15) was taken from a markedly tilt specimen, suggesting another species; the same specimen is here refigured (Fig. 5d) thus confirming its identity. This study allows including the Shag Rocks to the known distribution of the species.

Onoba cf. *algida* Ponder and Worsfold, 1994, Fig. 5e–h

Material examined: Beagle Channel: 55°05′36″S 66°28′48.0″W, Cabo San Pío, 65–80 m (MLP-Ma 14336: 20 sp., 13 sh.). Isla de los Estados: 54°42′48.0″S 63°50′36.0″W, San Juan del Salvamento, 38–60 m (MLP-Ma 14337: 15 sh.); 54°51′S 64°30′W, Bahía Cánepa, 60 m (MACN-In 41111: 21 sp., 34 sh.).

Description: *Shell* (Fig. 5e, f): Small (max. L observed = 2.91 mm), elongate-conic ($L/W = 1.7 \pm 0.1$, $n = 11$), translucent, whorls convex. Protoconch paucispiral, of 1 ½ whorls, about 350 µm L and 500 µm in diameter; translucent, sculptured with microscopic ridges arranged in somewhat irregular spiral lines (Fig. 5f). Teleoconch of up to 3½ whorls, sculptured with well-developed axial and spiral elements, which originate a cancellate pattern (Fig. 5e). Primary axial sculpture consisting of numerous, low, narrow axial ribs, 15–19 in the last whorl; primary spiral sculpture composed of 7 low spiral cords on penultimate whorl, and about 13 on last whorl and base; secondary sculpture consisting of prominent axial lamellae and microscopic spiral threads, of variable width. Aperture ovate, weakly angled posteriorly; expanded anteriorly. Inner lip posteriorly attached to base (Fig. 5e). Umbilical chink represented by a narrow groove (Fig. 5e). Colour white.

Operculum: Subovate, posteriorly angled, with eccentric nucleus; yellowish-brown, translucent.

Radula (Fig. 5g, h): Central tooth with triangular base, having two pairs of prominent basal denticles; cusp with 4–6 denticles at each side of median denticle. Median denticle long, rounded at the tip. Lateral teeth with triangular, asymmetric cusp: main denticle wide, distally rounded; with 5 inner and 7–9 outer narrow lateral denticles. Cusp of inner marginal teeth with about 12 denticles, restricted to outer and distal margins; distal denticles longer and wider. Cusp of outer marginal teeth with few, broad distal denticles; outer margin with few, minute denticles.

Remarks: *Onoba algida* was properly described by Ponder and Worsfold (1994), although based solely on empty shells coming from Bahía Cánepa, Isla de los Estados. We collected specimens at Isla de los Estados that clearly agree with the description of this species (MLP-Ma 14337: Fig. 5i), except in having a greater number of axial ribs in the last whorl: 10–15 axial ribs instead of the 7–9 described

by Ponder and Worsfold (1994). However, it should be noted that the number of ribs reported by these authors seems to correspond to those seen in apertural view (such as evidenced by their Fig. 27a), and not to the entire whorl. We found coexisting with the above referred specimens, other live-collected specimens and well-preserved shells that show narrower, lower and more numerous axial ribs in the last whorl: 15–19. Whether this variation in the number and solidness of the axial sculpture is related to the preservation of the shells, or corresponds to different species, remains an open question. Curiously, the protoconch morphology and sculpture of these two forms are not different (compare Fig. 5f herein with Ponder and Worsfold 1994: Fig. 20g).

Haurakia Iredale, 1915.

Type: *Rissoa hamiltoni* Suter, 1898 (by original designation).

Haurakia averni Ponder and Worsfold, 1994, Fig. 5j–l

Pusillina (Haurakia) averni Ponder and Worsfold, 1994: 23, Fig. 16A, B.

Type locality: 54°47.2′S 64°18.4′W, NW arm Bahía York, Isla de los Estados, Tierra del Fuego, 38 m.

Material examined: Isla de los Estados: 54°51′S 64°30′W, Bahía Cánepa, 60 m (MLP-Ma 14338: 12 sp., 4 sh.).

Known distribution: Isla de los Estados, Tierra del Fuego, and Southern Chile; 40–900 m (Ponder and Worsfold 1994).

Description: The shell was properly described by Ponder and Worsfold (1994).

Operculum: Ovate with subcentral nucleus; of about 2 ½ whorls; with long growing edge.

Radula (Fig. 5l): Central tooth with wide trapezoidal base, having one pair of sharply pointed basal denticles, and a "tongue-like" central expansion; cusp with 6–7 denticles at each side of median denticle. Median denticle elongated, pointed. Lateral teeth with triangular, asymmetric cusp: main denticle wide, sometimes bifid; with 5 inner and 8–10 outer narrow lateral denticles. Cusp of inner marginal teeth with about 14 denticles at the outer and distal margins: the 5 more basal, shorter and wider. Cusp of outer marginal teeth with a large main denticle and 5–7 shorter denticles on inner margin.

Remarks: *Haurakia averni* was described based on empty shells and was originally tentatively included in *Pusillina (Haurakia)*, "pending examination of the radula" (Ponder and Worsfold 1994: 25). The almost smooth shell surface and the aperture with a broad anterior expansion and a distinct posterior sinus (Fig. 5j, k) agree with other *Haurakia* species. The radula of this species (studied herein by first), like other species of *Haurakia*, shows the "tongue-like" central expansion of the base of central tooth and the absence of marginal denticles (Fig. 5l). However, the number of denticles in the cusp of central and lateral teeth of the material here examined is greater than that mentioned by Ponder (1985) as diagnostic for *Haurakia*, which is currently regarded as a full genus (Criscione et al. 2016).

Discussion

In their study of the distributional pattern of the Rissoidae, Ávila et al. (2012) recognized the southeast coast of South America (including the Burdwood Bank and South Georgia) and Antarctica as some of the most diverse sites of *Onoba*. The material studied herein reveals that the diversity of these areas is higher than previously thought; in fact, seven new species are recognized and described herein: one of them (*O. ernestoi*) from Cape Horn, another from the Burdwood Bank (*O. antleri*), two from South Sandwich Islands (*O. sandwichensis* and *O. verrucosa*) and three from South Shetland Islands (*O. clara, O. caribu* and *O. oligochordata*). Most of these new species were found from 272 to 332 m depth, with one species (*O. sandwichensis*) occurring at 521 m and another (*O. ernestoi*) at bathyal waters. The latter provides the first record of a bathyal species from southern South America. The new findings arising from this study raise the total number of species of *Onoba* known from Tierra del Fuego, Malvinas/Falkland Islands and the Scotia Arc, from 25 to 32 species. Ávila et al. (2012) described the endemicity of rissoids in southeastern South America, as relatively high (66.7%), and that of the Antarctica as "significant" (37.5%). The addition of the two species described by Engl (2011) and the seven new species described herein would result in an increase of those values to 69.0 and 66.7%, respectively. Ponder (1983), on the basis of protoconch morphology, suggested that the high endemicity of this family in the sub-Antarctic area could be related to the fact that most species are direct developers.

The present study not only increases the number of species currently known from Tierra del Fuego, Malvinas/Falkland Islands and the Scotia Arc, but also provides new information on the protoconch morphology of *O. delecta* and *O klausgrohi*, the radular morphology of *O. schythei, O. klausgrohi* and *Haurakia averni*, new distributional records for *O. fuegoensis, O. schythei* and *O. delecta*, and contributes to a better understanding of the intraspecific variability of *Onoba schythei* and *Onoba algida*.

As part of this study, the first species of *Onoba* with multispiral protoconch is reported from sub-Antarctic and Antarctic waters: *O. ernestoi*. This condition is rare among species of *Onoba* (Ponder 1985); in fact, in the

Atlantic Ocean it has been previously mentioned for only five species, all of them from the northern hemisphere (Ávila et al. 2012). The presence of multispiral protoconchs has been associated by Ponder (1985) and Ávila et al. (2012) with planktotrophic developmental mode.

Out of the nine species for which the radula was studied herein, six species show the typical rissoid radula, with a wide central tooth having a single pair of basal denticles, and with the marginal teeth having similar, small denticles. However, in *Onoba* cf. *algida* and two of the new species here described (*O. antleri* and *O. caribu*) the central tooth is highly triangular, having two pairs of basal denticles. Although unusual for *Onoba*, the presence of two pairs of basal denticles had been previously described for *O. crassicordata*. This condition also agrees with that present in some species of *Alvania*, a genus that also includes taxa with similar shell morphology (Ponder 1985). Ponder (1985) differentiated *Alvania* and *Onoba* based on some anatomical characters. The available material herein does not allow for anatomic studies. Despite that, and even considering such characters, recently performed molecular studies have revealed that both *Onoba* and *Alvania*, as traditionally regarded, are polyphyletic: morphological, radular and anatomical characters seem to be similar among very distant groups, explained by convergence and plesiomorphy (Criscione et al. 2016). None of the rissoid species from our study area were included in molecular phylogenies. These facts determine the need for revising the identity of the species of *Onoba* from the study area, by using molecular information.

To date, only the rissoid genera *Onoba, Powellisetia* and *Haurakia* have been reported from our study area (Ponder 1983; Ponder and Worsfold 1994); furthermore, the genus *Alvania* has been formally considered as "distributed world-wide except Antarctic and Subantarctic regions" (Ponder 1985). Taking into account this zoogeographic information, and the morphological similarities with other sub-Antarctic and Antarctic species, *O.* cf. *algida, O. antleri* and *O. caribu* are tentatively assigned to the genus *Onoba*. However, the particular "antler-like" morphology of the marginal teeth of *O. antleri* and *O. caribu*, which has not been reported before for any other member of Rissoidae, could justify the proposal of a new genus for accommodating them.

The results arising from this study make evident that, even when molluscs are one of the best known groups of benthic marine invertebrates in sub-Antarctic and Antarctic waters (as stated by Clarke et al. 2007), the current knowledge of the group is far from being complete, even in the case of the Rissoidae, a group that has been carefully monographed in recent times.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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