

Gastropods of the genus *Antistreptus* as examples of persistent molluscan lineages in the Neogene of the southwestern Atlantic

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Abstract.—Gastropods of the southwestern Atlantic genus *Antistreptus* Dall, 1902 from extant and Neogene deposits are reviewed. Fossil specimens come from the Punta Entrada Member of the Monte León Formation (50°21′25.4″S, 68°53′05.9″W). Extant samples are from museum collections and two expeditions on board the R/V “Puerto Deseado” to Burdwood Bank (54°13.934′S, 66°30.997′W) and surroundings. Dissection of soft parts and study of the type material of *A. magellanicus* Dall, 1902, *Euthria* (*Glypteuthria*) *contraria* Strebel, 1908, and *A. rolani* Castellanos, 1986 reveal that the latter two nominal species are synonymous. Neogene material assigned to the same genus could not be distinguished as a different species. According to the stratigraphic occurrence of the fossil material, the life-span of the genus *Antistreptus* Dall, 1902 and the species *A. magellanicus* Dall, 1902 is ~22 Myr, similar to that of the bivalve *Cyclochlamys argentina* Pastorino and Griffin, 2018.

Introduction

The life-span of a clade of any organism through the ages is difficult to calculate. Most living beings leave no record of their presence on earth. However, some animals produced hard parts that persist as a witness of the evolution of the whole group. Mollusks and corals are probably among the best known animals regarding the duration of their lineages, based on the records of hard parts they leave behind. The ages based on the survival of a clade are very variable depending on the author and taxa considered. Wallace and Bosellini (2015) found several Eocene species of *Acropora* corals living as long as 28 Myr. Raup (1990) cited different authors and groups as examples of the average duration of species in the fossil record (e.g., ammonoids 1–2 Myr, according to Kennedy, 1977; Cenozoic bivalves 10 Myr, sensu Stanley, 1979) among mollusk groups. Prothero (2014) cited 3.21 Myr for large mammals.

Different from other groups of invertebrates, gastropods show the larval life in the morphology of the protoconch. This feature was explored by several authors (Shuto, 1974; Hansen, 1980; Jablonski, 1994; Jablonski and Hunt, 2006, etc.) as a tool that, when linked to geographic distributions, could eventually lead to some conclusions on speciation and lineage duration. In this way, Jablonski (1994) pointed out that molluscan species durations are positively correlated with geographic ranges. Gili and Martinell (1994), in a thorough study on nassarids from Europe, agreed with results of previous authors that species with planktotrophic larvae have a longer life-span than those with non-planktotrophic larvae. These authors indicated that the main factor influencing duration of a species is the larval ecology that modified its dispersion capacity. Valentine and

Moores (1970) and Valentine (2009) mentioned environmental stability among factors that regulate species diversity.

Sinistral gastropods are unusual in the southwestern Atlantic malacofauna, where only 14 species belonging to different groups have been reported so far. The genus *Triphora* Blainville, 1828 is well represented by eight species in Brazil, of which only one reaches Uruguayan waters (Rios, 2009). Also from Brazil is a sinistral Conoidean represented by the Borsoninae *Borsonia brasiliana* Tippet, 1983. The genus *Blauneria* Shuttleworth, 1854, a sinistral Ellobidae, is represented by only one species in the western Atlantic (Martins, 1996). Three sinistral species were described from truly Antarctic waters under the genus *Prosipho*. The remaining forms belong in *Antistreptus* Dall, 1902, including two nominal species described from Patagonia, mostly from shallow waters (e.g., *A. magellanicus* Dall, 1902, and *A. rolani* Castellanos, 1986).

In this paper we review the gastropod genus *Antistreptus* Dall, 1902 that, together with a recent study of bivalves of the genus *Cyclochlamys* Finlay, 1926, has species with morphologically indistinguishable specimens spanning the unusually long time range of ~20 Myr (i.e., early Miocene–Recent).

Materials and methods

The fossil specimens described herein come from shell-beds at the top of the Punta Entrada Member of the Monte León Formation (Bertels, 1970, 1980). The locality (50°21′25.4″S, 68°53′05.9″W) lies within the boundaries of the Monte León National Park. The shell-beds are included within a loose or very poorly cemented sandstone exposed along the cliff just south of the Monte León beach, which is interpreted as part of

the generally regressive sedimentation represented by the Monte León Formation. These sedimentological concentrations are parautochthonous and contain a rich, abundant, and well-preserved megafauna (Ihering, 1907; del Río and Camacho, 1998; del Río, 2004a, b; Griffin and Pastorino, 2005, 2006; del Río and Martínez, 2006, and references therein). A schematic section of the locality is given in Griffin and Pastorino (2012).

According to Bertels (1970, 1975), the Monte León Formation ranges between Chattian and Rupelian, based on its foraminifera content. Also based on foraminifera, Nández (1988) suggested a late Oligocene–early Miocene age for the Monte León Formation. Barreda and Palamarczuk (2000) considered it early Miocene based on palynological data. We agree with Parras et al. (2012), who indicated an entirely early Miocene (Aquitania–early Burdigalian) age for the Monte León Formation based on $^{87}\text{Sr}/^{86}\text{Sr}$ ages drawn from shells of oysters, pectinids, and brachiopods; the recorded ages ranging from 22.12 Ma (+0.46, –0.54) at the base to 17.91 Ma (+0.38, –0.4) at the top.

The fossil samples were washed with diluted H_2O_2 and sieved following the usual procedure for foraminifera and small mollusks, as described in Beu and Maxwell (1990). Specimens were also analyzed and photographed under SEM at the MACN.

New material from extant populations was collected mainly during two expeditions aimed at studying the biodiversity in Burdwood Bank, located ~150 km east of Isla de los Estados (Staten Island, off the eastern tip of Tierra del Fuego) and 200 km south of the Malvinas (Falkland) Islands and from stations in the area by ships en route to the Campaña Antártica de Verano (CAV, Antarctic Summer Fieldwork). The samples were obtained with a Rauschert sledge on board the Argentine R/V Puerto Deseado. The sledge has a 55 x 15 cm mouth-opening, equipped with a 1 x 1 mm mesh-size nylon net. Radulae were taken from preserved specimens, cleaned with commercial bleach (sodium hypochlorite), coated with gold-palladium, and examined using a Philips XL30 SEM at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN).

Repositories and institutional abbreviations.—The fossil and extant material is housed in MACN Invertebrate Paleontology collection (MACN-Pi) and Invertebrate collection (MACN-In), respectively. Additional collections studied were those housed in the MACN (Buenos Aires, Argentina) and the Museo de La Plata, Malacology collection (MLP-Ma), in La Plata, Argentina. Type material used in this research is housed in the MLP; United States National Museum, Smithsonian Institution, Washington, D.C. (USNM), USA, and the Naturhistoriska Riksmuseet, Stockholm (NHR), Sweden.

Systematic paleontology

Class Gastropoda Cuvier, 1795
 Order Neogastropoda Wenz, 1938
 Family Buccinidae Rafinesque, 1815
 Genus *Antistreptus* Dall, 1902

Type species.—*Antistreptus magellanicus* Dall, 1902 from Magellan Strait, Chile, 52°38'00"S, 70°10'30"W, in 19.75 fathoms, by original designation.

Other species.—Only one species was described in this genus.

Remarks.—In the original description of the genus, Dall (1902, p. 532) wrote: “...sinistral with a dextral nucleus;” yet the illustration of the protoconch of the holotype of *A. magellanicus* showed that, while its axis is slightly inclined with respect to the teleoconch axis, it is always sinistral. When described by Dall (1902), the type species was known to occur in the southwestern Atlantic, and no fossil representatives were then recorded.

Antistreptus magellanicus Dall, 1902 Figures 1–5

- 1902 *Antistreptus magellanicus* Dall, p. 532.
 1908 ?*Euthria* (*Glypteuthria*) *contraria* Strebel, p. 29, pl. 1, figs. 4a–c.
 1908 *Antistreptus magellanicus* Dall, pl. 15, fig. 14.
 1912 *Antistreptus magellanicus*; Melville and Standen, p. 354.
 1918 *Antistreptus magellanicus*; Doello-Jurado, p. 123.
 1944 *Antistreptus magellanicus*; Carcelles, p. 7, fig. 5.
 1950 *Antistreptus magellanicus*; Carcelles, p. 62, pl. 2, fig. 39.
 1951 *Antistreptus magellanicus*; Carcelles and Williamson, p. 298.
 1951 *Antistreptus magellanicus*; Powell, p. 148.
 1968 *Antistreptus magellanicus*; Boss et al., p. 196.
 1970 *Antistreptus magellanicus*; Castellanos, p. 103, pl. 9, fig. 9.
 1986 *Antistreptus rolani* Castellanos, p. 132 (dated 1985, published 1986).
 1989 *Antistreptus rolani*; Castellanos, p. 90, fig. 3 (dated 1 December 1988, published September 1989).
 1992 *Antistreptus rolani*; Castellanos, p. 26, pl. 3, fig. 30.
 1992 *Antistreptus magellanicus*; Castellanos, p. 25, pl. 3, fig. 29.
 1992 *Antistreptus magellanicus*; Bastida et al., p. 294.
 2000 *Antistreptus magellanicus*; Forcelli, p. 91, fig. 241.
 2002 *Antistreptus magellanicus*; Linse, p. 100, pl. 12, figs. 9.1.1, 9.1.2.
 2004 *Antistreptus rolani*; Martín and César, p. 17.
 2015 *Antistreptus magellanicus*; Forcelli et al., p. 66, fig. 164.
 2015 *Antistreptus rolani*; Signorelli et al., p. 53, pl. 1, figs. G, H.

Holotype.—*Antistreptus magellanicus* (USNM 96190) from R/V Albatross sta. 2777, 52°38'00"S, 70°10'30"W, Magellan Strait, Chile, 19.75 fathoms [36.1 m] (Dall, 1908, pl. 15, fig. 14). In 1908 Dall added sta. 2773, 52°23'S, 68°11'W, in 10 fathoms [18.3 m]; *Euthria* (*Glypteuthria*) *contraria*, northern Argentina, 37°50'S, 56°11'W in 100 m; *Antistreptus rolani*, apparently 37°35'S, 56°25'W, 40 fathoms [73.1 m], off Buenos Aires Province, Argentina, but see below.

The holotype (USNM 96190) is photographed for the first time here (Fig. 1.1, 1.2). The material of *Euthria* (*Glypteuthria*)

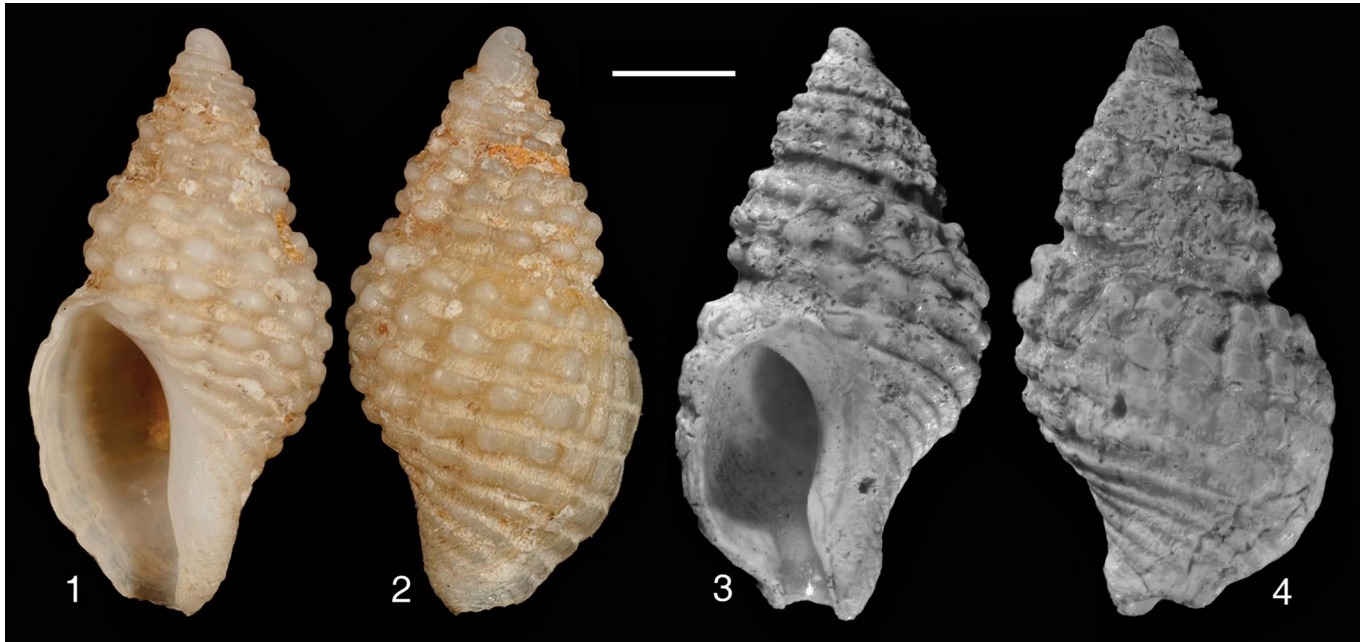


Figure 1. *Antistreptus magellanicus* Dall, 1902. (1, 2) Holotype (USNM 96190); (3, 4) holotype of *Euthria (Glypteuthria) contraria* Strebel, 1902 (NHR Type-1051). Scale bar = 1 mm.

contraria from the Swedish Antarctic Expedition is a specimen represented only by the shell housed in the NHR collection as Type-1051; it is illustrated here (Fig. 1.3, 1.4). The type material of *A. rolani* (MLP-Ma 4692) consists of two specimens, the measurements of which differ from those indicated by the author. After careful reading of the original description, it appears that Castellanos had at least three specimens from three different expeditions: (1) from the research vessel *Undine*, 37°35'S, 56°25'W, at 40 fathoms depth, of 3.8 x 2.6 mm height and width, respectively, and 2.1 x 0.9 mm of aperture dimensions; (2) from the Spanish fishing vessel *Puente Gondomar*, 46°S, 60°W, 3.9 x 2.2 mm and aperture 2.1 x 0.9; and (3) “another specimen” 3.2 x 2 mm and aperture 2 x 0.7 mm, perhaps from the research vessel *Shinkai Maru* from 43°30'S, 59°50'W at 116 m depth. In 1992 Castellanos, in a re-description of *A. rolani*, mentioned only two specimens: “tipo,” a supposed holotype of 3.8 x 2.6 mm and aperture of 2.1 x 0.9 mm and “paratipo,” a supposed paratype of 3.0 x 2.2 and the same aperture size. She mentioned the type locality as 46°S, 60°W at 600 m depth, which is different from the locality given in the original description. Signorelli et al. (2015) mentioned that both specimens housed under MLP-Ma 4692 are apparently syntypes collected by the Japanese vessel *Shinkai Maru*, although none of the specimens agrees with the original measurements published by the author (Castellanos, 1986). In any event, these specimens were identified by the author. Both are illustrated here in Figure 2.1–2.5, with 3.45 and 3 mm of maximum height. Thus, regardless of the uncertain identification of the type material, we can safely assume that they represent accurately the idea that she had of *A. rolani*. Whichever specimen is finally considered holotype or lectotype, or whether they are deemed to be syntypes, they can all easily be identified as juveniles of *A. magellanicus*. All the specimens identified as *A. rolani* have the last whorl undeveloped showing a smaller aperture and an

apparently longer siphonal canal than the rest. Adult specimens have a thicker shell, smaller aperture, and the siphonal canal appears somewhat deeper.

Occurrence.—Fossil material comes from the Punta Entrada Member of the Monte León Formation (Bertels, 1970, 1980). Extant specimens are from off Buenos Aires Province (~37°S) to Ushuaia, including Malvinas Is. and Burdwood Bank, in 20–262 m. Bastida et al. (1992) studied material from R/V *Shinkai Maru*, reportedly from a depth range of 56–169 m.

Description.—Shell small, up to 4.9 mm high, sinistral, fusiform, with four slightly convex whorls; protoconch sinistral, with coiling axis sloping ~40–45° with respect to teleoconch coiling axis, of ~1.5 convex, smooth, whorls; transition to teleoconch well defined; suture impressed; aperture oval, elliptic, labrum sharp; siphonal canal rather deep, oblique, and long, inclined ~30° from shell axis; parietal callus thin; growth lines closely spaced all over shell surface; spiral ornamentation of three cords, anterior weaker, all starting right after protoconch end; sometimes a flat cord running over suture line; 12 cords in last whorl, the basal seven whorls narrower and less marked; axial ornamentation of low ribs after the first whorl, 7–8 in the second whorl, 15 in the third, 20 in the last; axial ribs forming nodes at the intersection with spiral cords; periostracum translucent, scaly between axial ribs; color off whitish.

Operculum, pale yellowish, ovate-elliptical, nucleus subterminal, attachment area small, somewhat indefinite.

Radulae rachi glossated with very small rachidian teeth, subrectangular with a very thin base, with three very short, blunt, obsolete cusps. Laterals triangular, fan-shaped, basal plate with long, narrow *Prosipho*-like “handle,” with three short, slightly curved cusps pointing towards the center of the

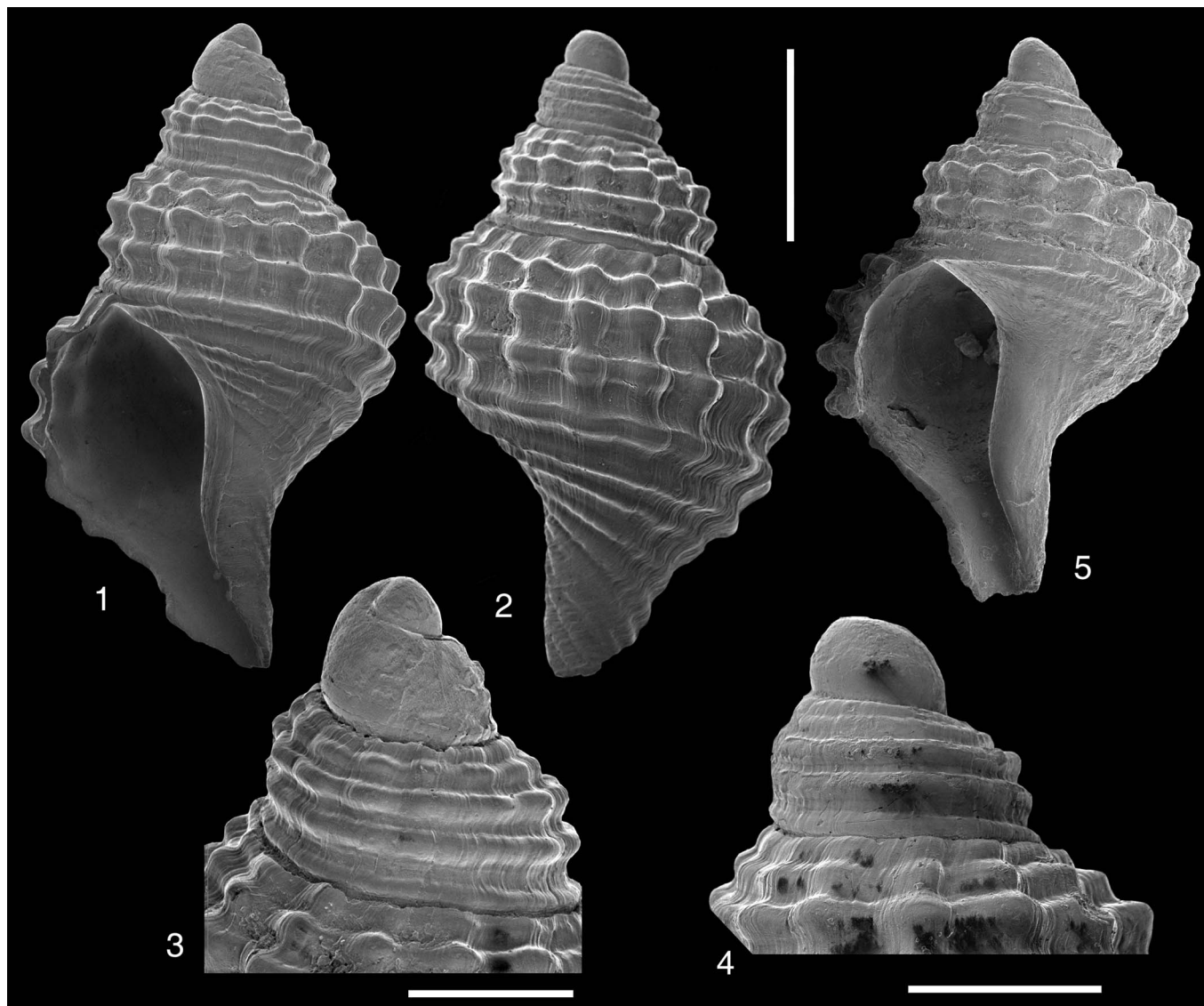


Figure 2. *Antistreptus magellanicus* Dall, 1902. (1, 2) Uncoated SEM views of a probable syntype of *Antistreptus rolandi* Castellanos, 1986 (MLP-Ma 4692); (3, 4) uncoated SEM views of the protoconch of specimen in (1, 2); (5) uncoated SEM apertural view of another probable syntype of *Antistreptus rolandi* Castellanos, 1986 (MLP-Ma 4692). Scale bars = 1 mm (1, 2, 5); 500 μ m (3, 4).

ribbon and two larger curved cusps, the outer one bifid. Eyes present.

Materials.—One specimen, MACN-In 16244-1, 37°35'S, 56°25'W in 40 fathoms [73.1 m]; one shell, MACN-In 25779, 54°57'S, 64°42'5"W in 20 fathoms [36.5 m]; one shell, MACN-In 25780, 54°46'S, 64°36'8"W in 20 fathoms [36.5 m]; one sp., MACN-In 16158, 37°31'S, 56°23'W in 70 m; one shell, MACN-In 22087, Puerto Cook, Isla de los Estados in 20 fathoms; one sp. MACN-In 42257, Burdwood Bank Expedition, collected on April, 2017, St. 39 Cr. 79, 54°13.934'S, 66°30.997W in 53 m, bottom net trawl; two shells, MACN-In 42258, Campaña Antartica de Verano CAV2014, St. 8, Cr. 26, collected 30 March 2014, 55°4.297'S, 66°1.857'W in 207 m; two shells, MACN-In 42259, Burdwood Bank Expedition, collected April 2017, St. 26, Cr. 316, 54°5.501'S, 60°41.978'W in 122 m, modified Agassiz dredge;

four shells, MACN-In 42260, R/V "Aldebaran" St. 9506, Cr. 56, 13 June 1995, 37°46.42'S, 55°03.07'W, 253 m to 37°44.2'S, 55°01.34'W, in 262 m, collected from the root of kelp *Macrocystis pyrifera* (Linnaeus, 1771) (described in Scarabino and Ortega, 2004); 14 shells, MLP-Ma 14697, Ushuaia ?, Tierra del Fuego, Argentina.

Fossil material.—Five shells, MACN-Pi 6450, shell-beds at the top of the Punta Entrada Member of the Monte León Formation, 50°21'25.4"S, 68°53'05.9"W.

Remarks.—Dall described the new genus and new species in 1902 without illustrating it, which he did in 1908 (Dall, 1908, pl. 15, fig. 14). In this same year, Strebel (1908) described *Euthria* (*Glypteuthria*) *contraria*, making no reference to Dall's species, of which he had no knowledge at that time. However, Dall included the locality of Strebel in his 1908

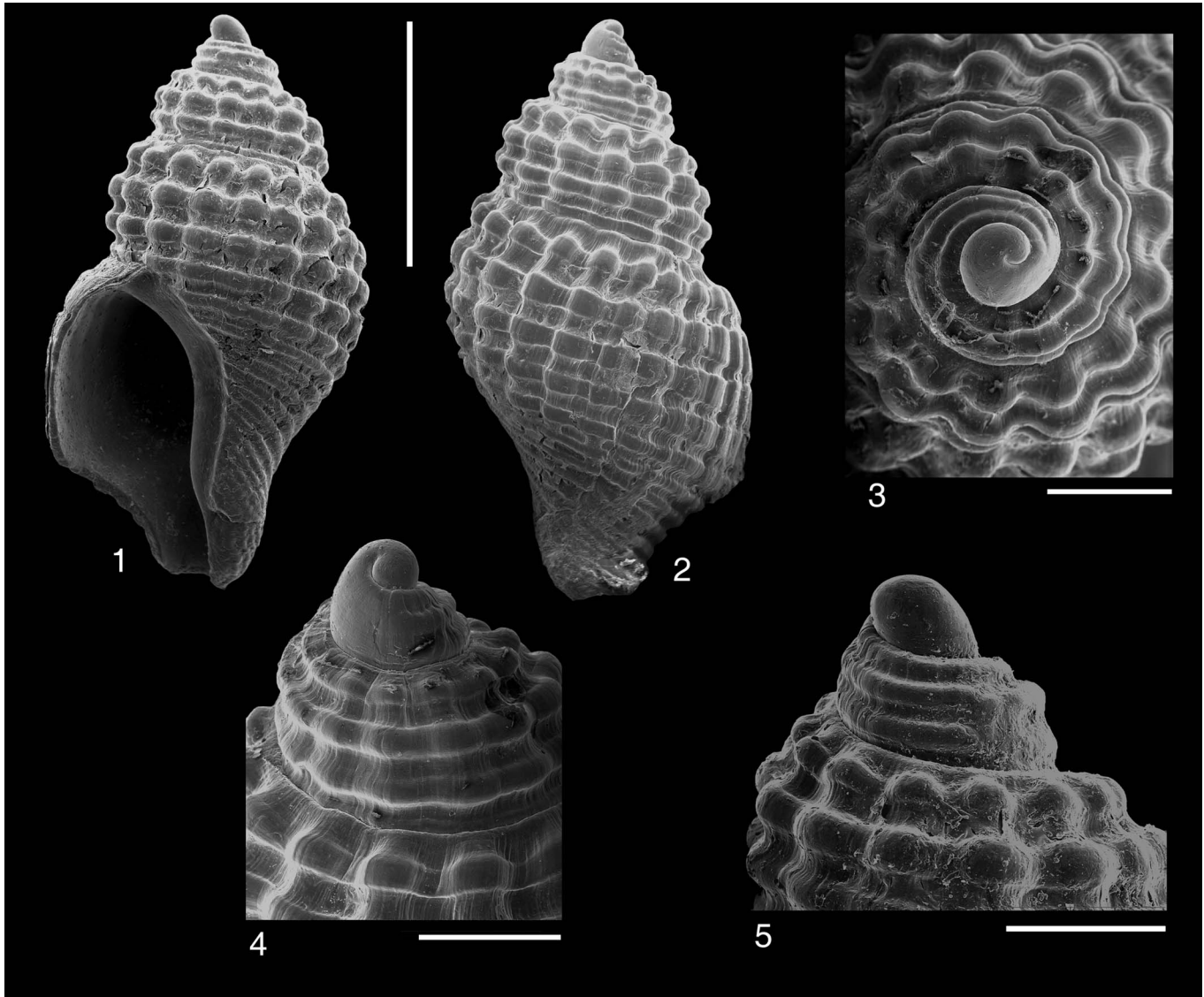


Figure 3. *Antistreptus magellanicus* Dall, 1902. (1, 2) MACN-In 16244-1 SEM coated; (3–5) three views of the protoconch. Scale bars = 2 mm (1, 2); 500 μ m (3–5).

paper. The illustration and the holotype of *E. contraria*, illustrated here for the first time (Fig. 1.3, 1.4), clearly suggest they are synonyms.

Thiele (1929) acknowledged a shell similarity between his *Anomacme smithi* Strebel, 1905 and *Antistreptus magellanicus*, including both species in *Antistreptus*, with two sections: *Antistreptus* s. s. and *Anomacme*, in which shell coiling direction (dextral in *Anomacme* and sinistral in *Antistreptus*) was the sole difference. He also described the radula of his *Antistreptus* s. l. based on the radula of *Anomacme smithi*, illustrated previously (Thiele, 1912, pl. 16, fig. 14), which was the only one known at that time. However, Powell (1951, p. 148) disagreed with this combination of both genera because the radula of *A. magellanicus* was unknown.

Hain (1990) discussed three sinistral species as belonging in the genus *Prosipho* (e.g., *P. contrarius* Thiele, 1912; *P. perversus* Powell, 1951; *P. reversa* Powell, 1958), considering *contrarius* and *perversus* as synonyms. He illustrated the radula of

P. contrarius. This radula with absent rachidian and only two lateral teeth with similar-sized cusps is completely different from that of *A. magellanicus*. This rules out *Antistreptus* or *Prosipho* for these species with the sinistral shell as a unique similarity. Unaware of this radular difference, Hain (1990, p. 59) compared the rachidian-less radula of *Prosipho contrarius* with *Antistreptus* (sensu Thiele, 1929); however he was actually comparing *Anomacme* instead, which does have a central tooth as well.

Engl (2012) justified the inclusion of all sinistral Antarctic *Prosipho* species in *Antistreptus* because Hain (1990) stated that the missing central tooth in the radula of *Prosipho contrarius* also was a feature of *Antistreptus*. Hain (1990) showed that the radula of *P. contrarius* is different from the other known species of *Prosipho* and suggested that all Antarctic sinistral species belong in a genus different from *Prosipho*. However, he mentioned the radula of *Antistreptus*, which had not been actually described or illustrated at that time. It seems that he understood

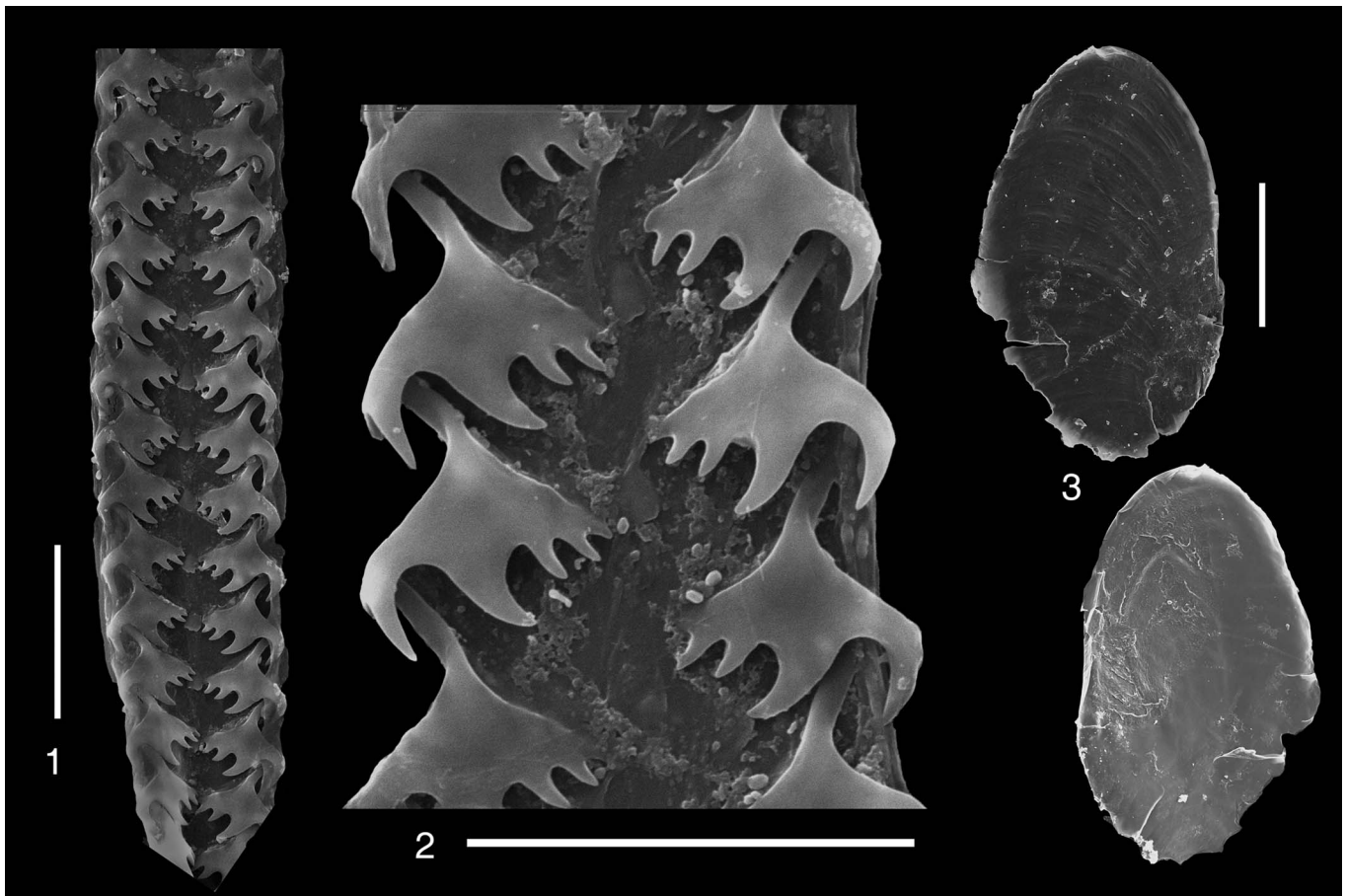


Figure 4. *Antistreptus magellanicus* Dall, 1902, MACN-In 16244-1. (1) Dorsal view of radula; (2) detail of the radula; (3) external and internal view of the operculum. Scale bars = 25 µm (1); 20 µm (2); 500 µm (3).

Thiele's inclusion of *Anomacme smithi* and *Antistreptus magellanicus* in *Antistreptus* as an indication of similar radular features. The radula, shown here for the first time (Fig. 4.1, 4.2, dissected from the specimen in Fig. 3), is clearly different and suggests that *Antistreptus* is a valid genus different from *Anomacme* and *Prosipho*. Nevertheless, it should probably be treated as a genus of Prosiphinae. Dell (1990) considered all three Antarctic sinistral species of *Prosipho* as valid and he did not compare them with the Magellanic genus *Antistreptus*.

Linse (2002) described a new genus and species, *Crenatosiphio beaglensis*, and illustrated a radula extremely similar to the one we described here for *A. magellanicus* Dall, 1902. In addition, the shell of *C. beaglensis* Linse, 2002 is puzzling, similar to *Met euthria martensi* (Strebel, 1905), despite the fact that the radula of the latter species points towards a different genus (Thiele, 1912; Pastorino, 2016).

Discussion

Together with the recently described pectinoid bivalve *Cyclochlams argentinus* Pastorino and Griffin, 2018, *Antistreptus magellanicus* Dall, 1902 represents long-lasting lineages of mollusks showing no changes (at least in shell morphology, see Fig. 5) since at least the early Miocene from the same deposits. These two species are unrelated, but share three features in

common: (1) their small size (<5 mm), (2) their preference for shelf or upper slope environments, and (3) their habit of living (if not exclusively) in association with the southern kelp *Macrocystis pirifera*. Such association with *Macrocystis* could well be a factor contributing to their distribution because *Cyclochlams* Finlay, 1926 species are byssate during some period of their lifespan and *A. magellanicus* Dall, 1902 has been documented living among the “roots” of drifting masses of *M. pirifera* (Scarabino and Ortega, 2004) as far north as the Uruguayan coast.

Yet none of these factors appears to explain such a long duration for these species (~17–20 Myr). The duration or life of a species has been dealt with on many occasions and for different groups of organisms such as, among others, microfossils (Liow et al., 2010), graptolites (Rickards, 1977; Cooper et al., 2010), bivalves (Stanley, 1979; Hoffman and Szubda-Studencka, 1982), gastropods (Hansen, 1980; Gili and Martiniell, 1994), ammonites and bivalves (Kennedy, 1977; Hallam, 1987), and mammals (Prothero, 2014). Longevity of species varies and could be correlated to factors such as environmental differences, taxonomic lineage, geographic range, larval type, or other causes (Crampton et al., 2010).

Architectonica karsteni Rutsch, 1934, an architectonicid gastropod reported by DeVries (1985) and Nielsen and Frassinetti (2007) from Miocene–Pliocene deposits in Central and South American Pacific coast (Peru and Chile) and extant

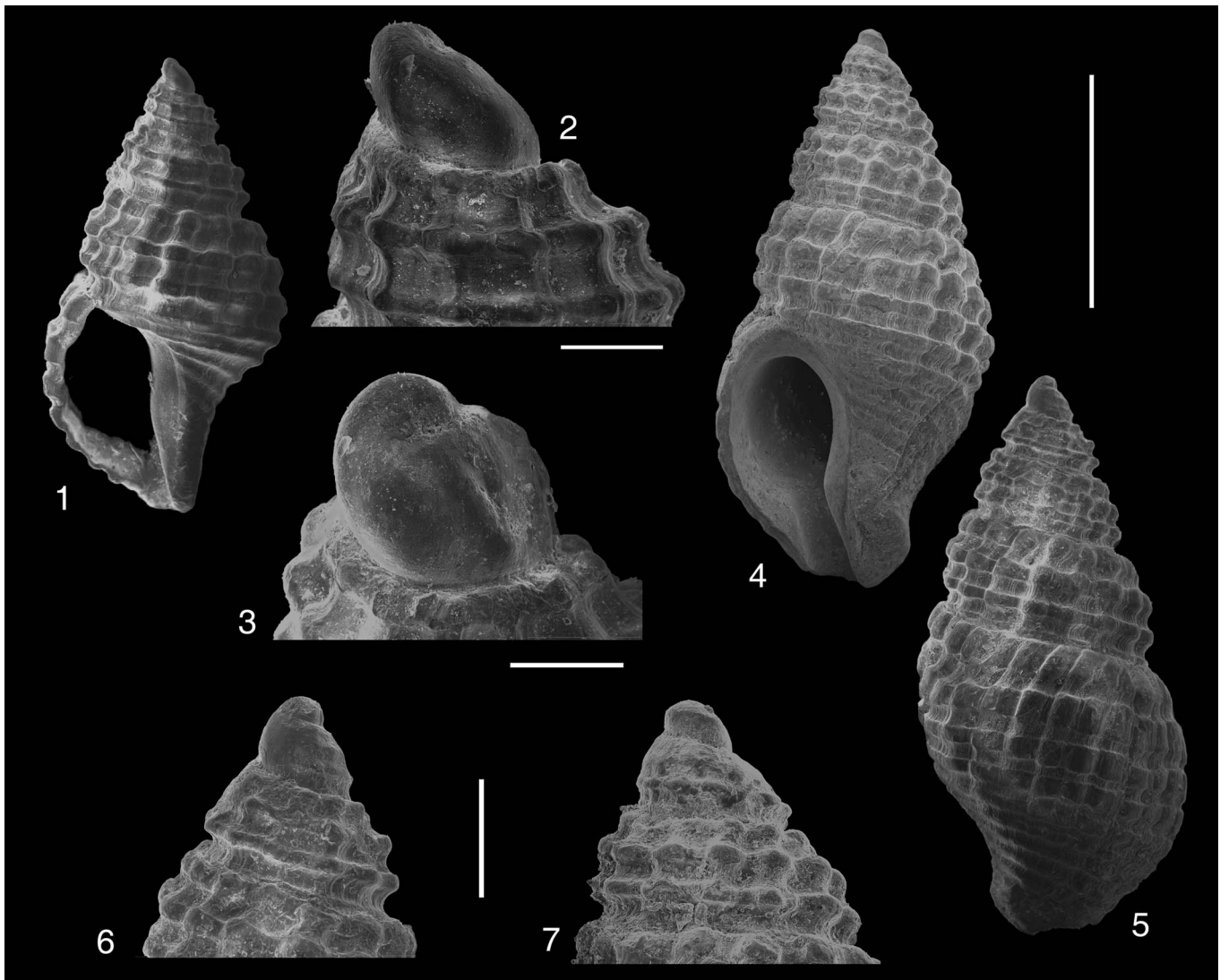


Figure 5. *Antistreptus magellanicus* Dall, 1902, MACN-Pi 6450 from the Punta Entrada Member of the Monte León Formation, 50°21'25.4"S, 68°53'05.9"W. (1) Apertural view, SEM coated; (2, 3) two views of the protoconch; (4, 5) another specimen, apertural and abapertural views, MACN-Pi 6450; (6, 7) two views of the protoconch of specimen in (4, 5). Scale bars = 2 mm (1, 4, 5); 200 µm (2, 3); 500 µm (6, 7).

from Central America Pacific coast, is another example of a similar lifespan for a Neogene mollusk. In addition, in a recent work on the southwestern Atlantic scorched mussels of the genus *Brachidontes* Swainson, 1840, Trovant et al. (2018) showed that *B. lepida* (Philippi, 1893) from North Argentine deposits of the Paraná Formation of Miocene age is morphologically closer to the extant species *B. rodriguezii* (d'Orbigny, 1846) than to the other extant and fossil species of the same genus. However, in both cases, the sizes of the specimens are considerably larger than those described here.

The reasons for the temporal persistence of *Antistreptus* Dall, 1902 and eventually other species nowadays living on the wide shelf along the Atlantic coast of southernmost South America and found fossil in Neogene stratigraphic units in the area remain obscure. However, the fact that the paleoceanographic, tectonic, and paleogeographic conditions on the shelf have remained fairly stable throughout the Neogene (with the obvious paleoclimatic changes affecting adjacent

land environments being much more pronounced) may have potentially favored relatively long-lived ecological structures of the different communities inhabiting the shelf and consequently relatively slow evolutionary rates in at least some of the lineages of marine invertebrates that formed them.

It should be noted that while examples of large mollusk species, such as muricids and naticids (Griffin and Pastorino 2005, 2013), appear to have a short stratigraphic records in the area (with very few species or none in common with the recent faunas), some small species seem to have survived for longer—since at least the early Miocene (Pastorino and Griffin, 2018). A comprehensive revision of the fossil fauna is still wanting, but a similar pattern can be observed at a generic rank, with many genera of small species found in Neogene units surviving nowadays on the shelf (Casadio et al., 2009; Griffin and Pastorino, 2012; Pérez et al., 2015). The significance of size is not clear, but may be related to the relatively stable paleoecological conditions.

The Atlantic coast of Patagonia lies along a passive continental margin, which has remained relatively stable throughout the Cenozoic, as opposed to the Pacific (Kiel and Nielsen, 2010). While the final opening of the Drake Passage and the ensuing definitive separation of Antarctica—and the subsequent establishment of the circum-Antarctic Current—produced paleoceanographic and paleoclimatic changes that, together with the uplift of the Andes along the eastern margin of the South American plate, strongly affected the continental environments in this part of the continent, the effects on marine environments along the shelf were probably less marked (Lawver and Gahagan, 2003; Lyle et al., 2007; Le Roux, 2012). Contrarily, marine environments along the western seaboard of the South American plate were strongly affected by tectonic activity. Consequently, the diversity in habitats was bound to increase significantly. At the same time, the ongoing tectonic activity entails highly unstable physical environments, with the consequent changes in paleoecological structure of the communities living there (Blisniuk et al., 2005).

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