

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

Guido Pastorino¹ and Miguel Griffin²

¹Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Av. Ángel Gallardo 470, C1405DJR, Ciudad Autónoma de Buenos Aires, Argentina <gpastorino@macn.gov.ar>

²División Paleozoología Invertebrados, Museo de La Plata. Paseo del Bosque s/n, B1900FWA, La Plata, Argentina <patagonianoyster@gmail.com>

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 brasiliiana* 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*)

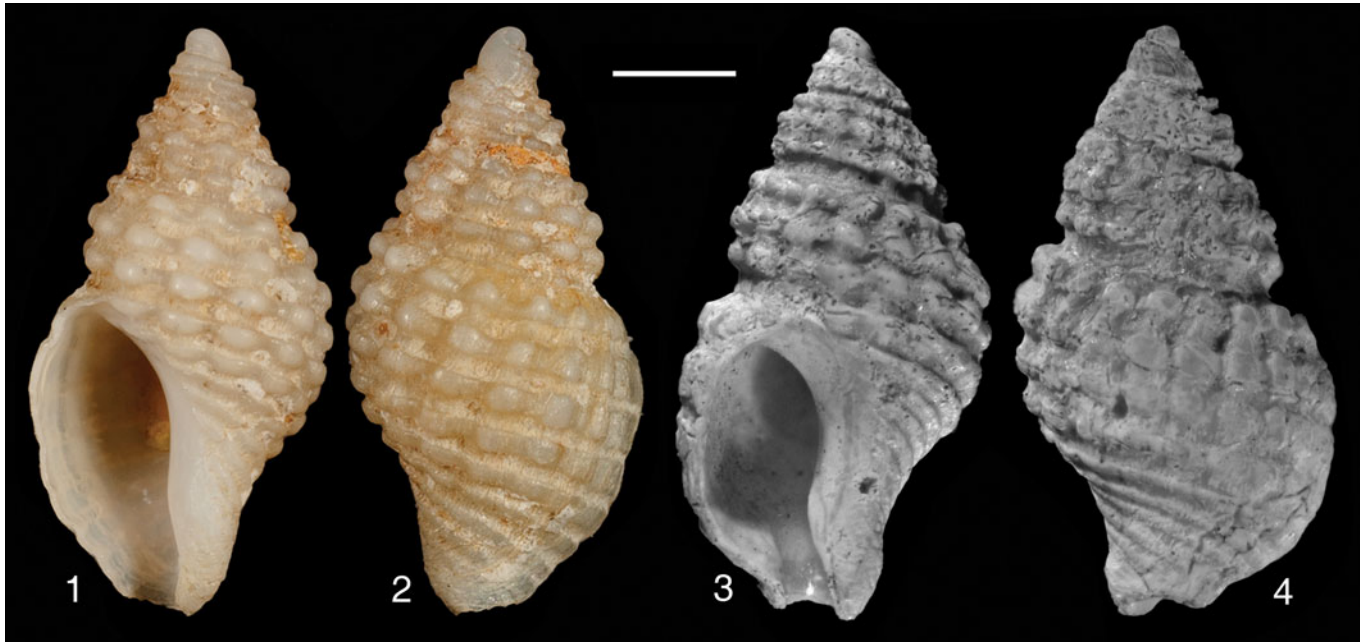


Figure 1. *Antistreptus magellanicus* Dall, 1902. (1, 2) Holotype (USNM 96190); (3, 4) holotype of *Euthria (Glypteuthria) contraria* Strebel, 1902 (NHR Type-1051). Scale bar = 1 mm.

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

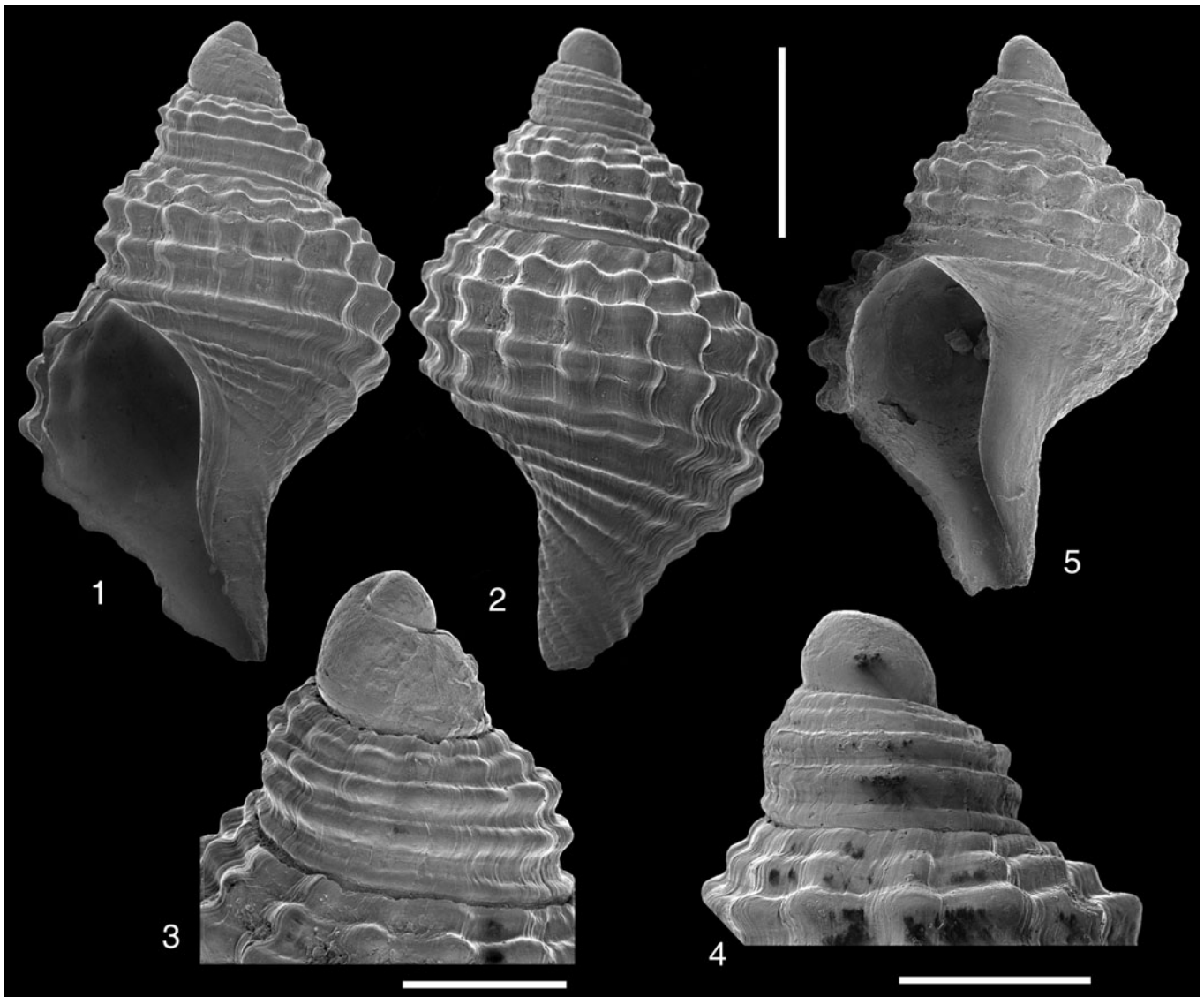


Figure 2. *Antistreptus magellanicus* Dall, 1902. (1, 2) Uncoated SEM views of a probable syntype of *Antistreptus rolani* Castellanos, 1986 (MLP-Ma 4692); (3, 4) uncoated SEM views of the protoconch of specimen in (1, 2); (5) uncoated SEM apertural view of another probable syntype of *Antistreptus rolani*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

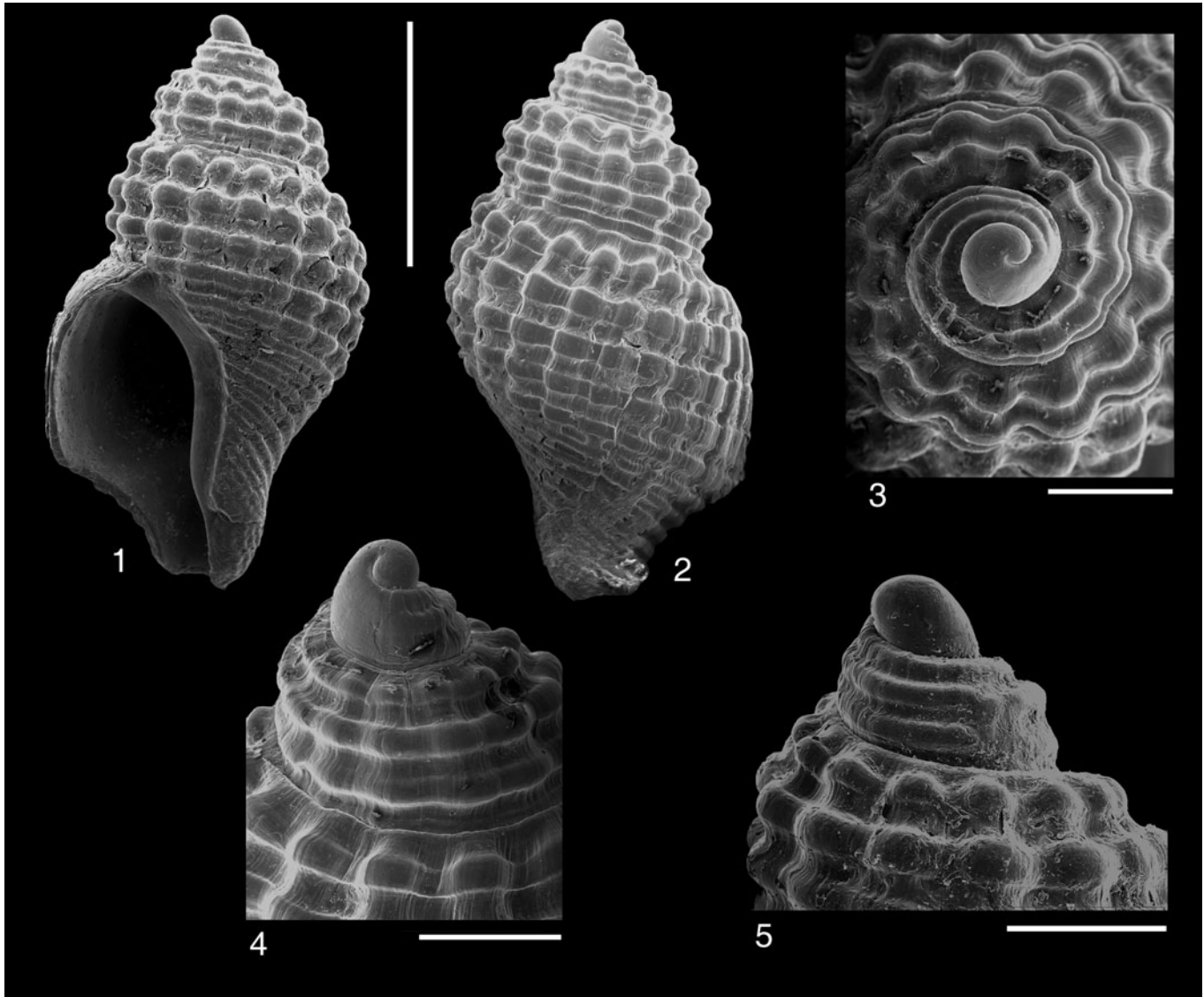


Figure 3. *Antistreptus magellanicus* Dall, 1902. (1, 2) MACN-In 16244-1 SEM coated; (3–5) three views of the protoconch. Scale bars = 2 mm (1, 2); 500 μ m (3–5).

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

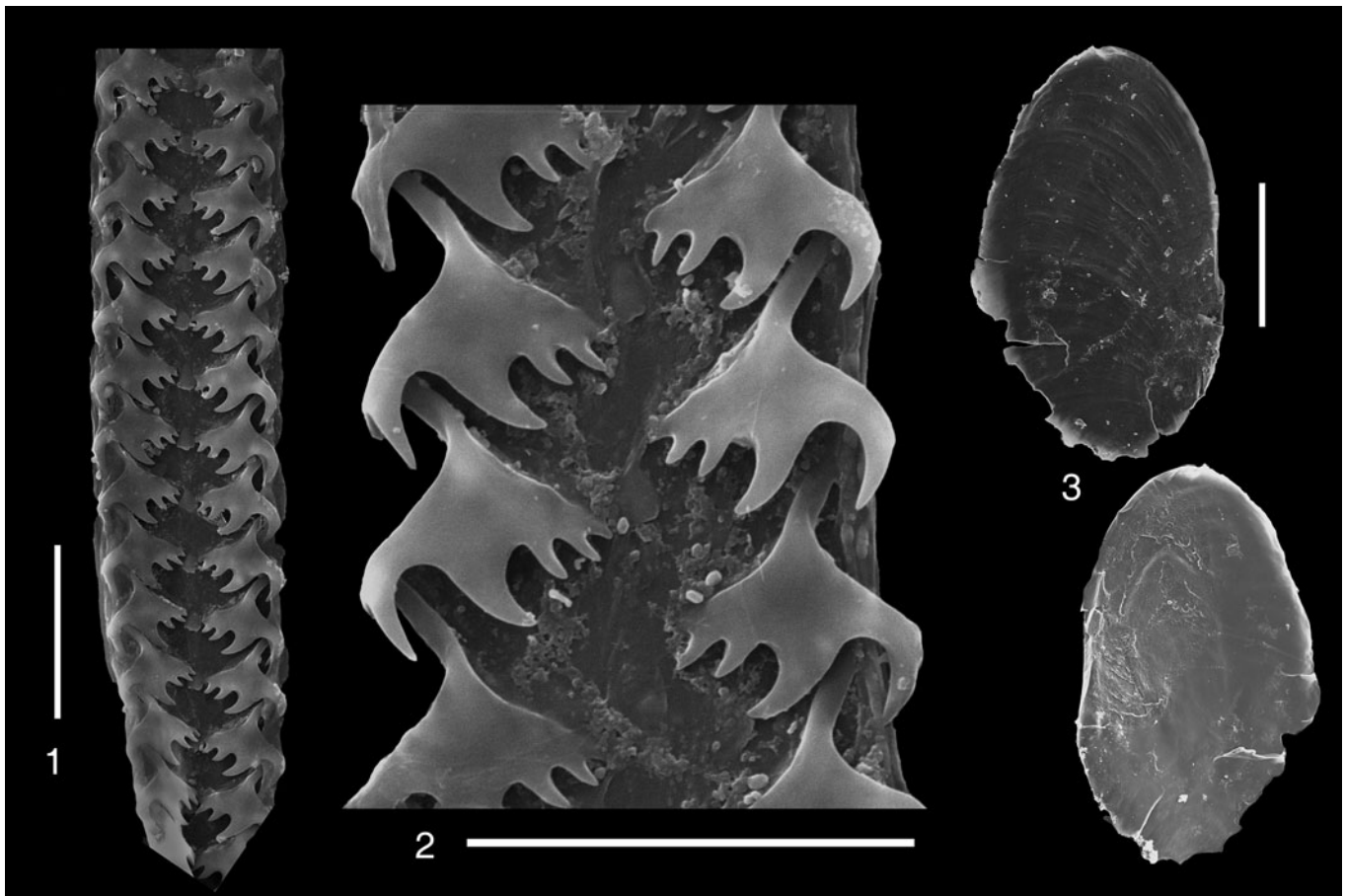


Figure 4. *Antistreptus magellanicus* Dall, 1902, MACN-In 16244-1. (1) Dorsal view of radula; (2) detail of the radula; (3) external and internal view of the operculum. Scale bars = 25 µm (1); 20 µm (2); 500 µm (3).

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 *Meteuthria 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 Martignell, 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

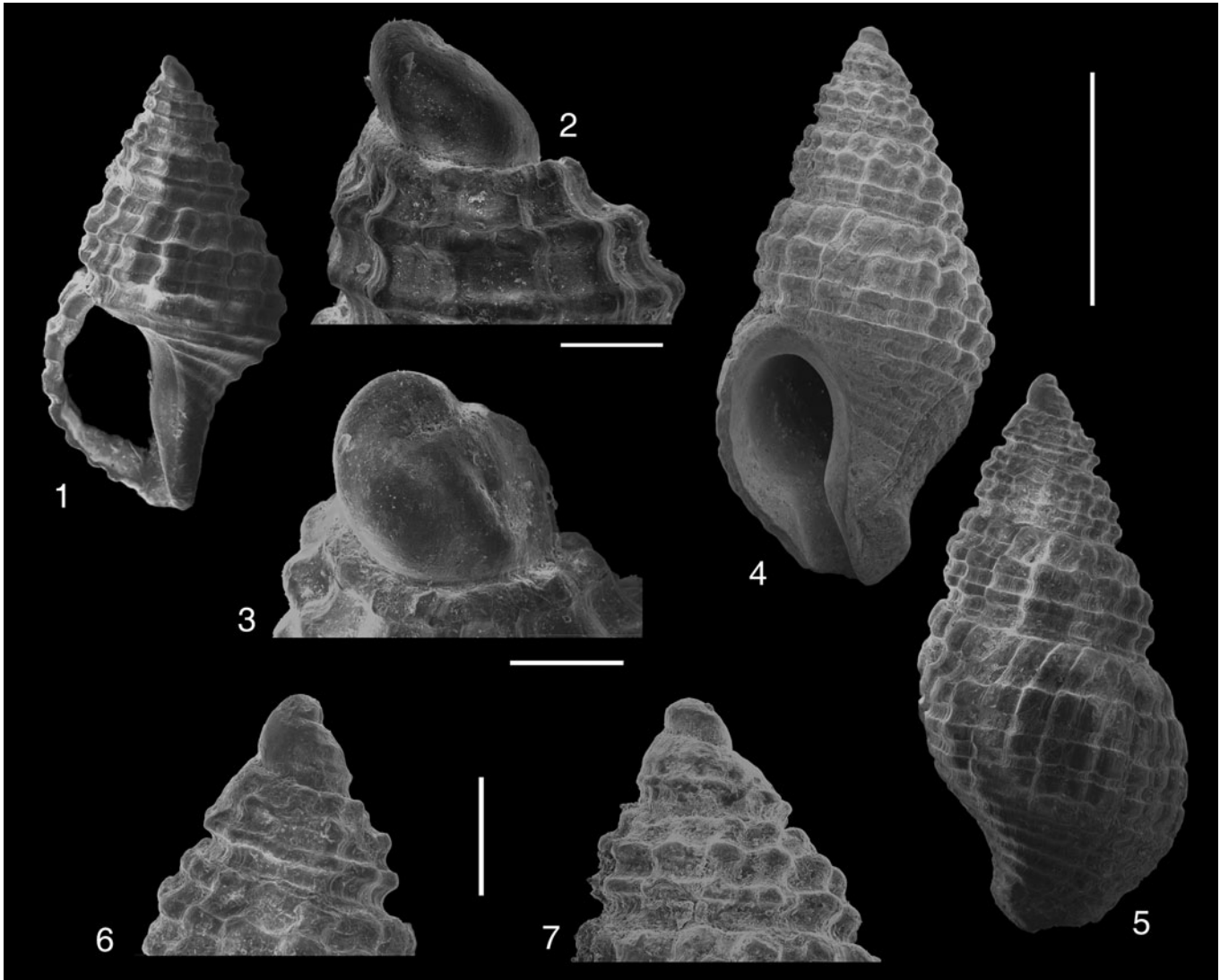


Figure 5. *Antistreptus magellanicus* Dall, 1902, MACN-Pi 6450 from the Punta Entrada Member of the Monte León Formation, 50°21'25.4"S, 68°53'05.9"W. (1) Apertural view, SEM coated; (2, 3) two views of the protoconch; (4, 5) another specimen, apertural and abapertural views, MACN-Pi 6450; (6, 7) two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

Acknowledgments

The following persons generously sent material or pictures of types from the collections under their care: A. Tablado (MACN); M. Forshage (NHR); E. Strong (USNM) and C. Damborenea and G. Darrigran (MLP). R. Bieler (Field Museum, Chicago) generously helped with books and German translations of some Thiele's descriptions. S. Nielsen (Universidad Austral, Chile) and an anonymous reviewer considerably improved the manuscript with helpful suggestions.

This work was supported by PICT 2016/1309 from Agencia Nacional de Promoción Científica y Tecnológica. We acknowledge funding by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) of Argentina, to which G.P. and M.G. belong as members of the Carrera del Investigador Científico.

References

- Barreda, V., and Palamarczuk, S., 2000, Estudio palinoestratigráfico del Oligoceno tardío–Mioceno en secciones de la costa patagónica y plataforma continental Argentina: INSUGEO, Serie Correlación Geológica, v. 14, p. 103–138.
- Bastida, R., Roux, A., and Martínez, D.E., 1992, Benthic communities of the Argentine continental shelf: *Oceanologica Acta*, v. 15, p. 687–698.
- Bertels, A., 1970, Sobre el “Piso Patagónico” y la representación de la época del Oligoceno en Patagonia austral, República Argentina: *Revista de la Asociación Geológica Argentina*, v. 25, p. 495–450.
- Bertels, A., 1975, Bioestratigrafía del Paleógeno en la República Argentina: *Revista Española de Micropaleontología*, v. 7, p. 429–450.
- Bertels, A., 1980, Estratigrafía y foraminíferos (Protozoa) bentónicos de la Formación Monte León (Oligoceno) en su área tipo, provincia de Santa Cruz, República Argentina: 2° Congreso Argentino de Paleontología y Bioestratigrafía y 1er Congreso Latinoamericano de Paleontología (Buenos Aires, 1978), *Actas*, v. 2, p. 213–273.
- Beu, A.G., and Maxwell, P.A., 1990, Cenozoic mollusca of New Zealand: *New Zealand Geological Survey Paleontological Bulletin*, v. 58, p. 1–518.
- Blainville, H.M.D. de, 1828, Vers et Zoophytes, in *Dictionnaire des sciences naturelles*: Strasbourg, F. G. Levrault, v. 55, 566 p.
- Blisniuk, P.M., Stern, L.A., Chamberlain, C.P., Idelman, B., and Zeitler, P.K., 2005, Climate and ecologic changes during Miocene surface uplift in the southern Patagonian Andes: *Earth and Planetary Science Letters*, v. 230, p. 125–142.
- Boss, K.J., Rosewater, J., and Ruhoff, F.A., 1968, The zoological taxa of William Healey Dall: *United States National Museum Bulletin*, v. 287, p. 1–427.
- Carcelles, A., 1944, Nota sobre algunos moluscos magallánicos obtenidos frente al Río de la Plata: *Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo*, v. 1, p. 1–11.
- Carcelles, A., 1950, Catálogo de los moluscos marinos de Patagonia: *Anales del Museo Nahuel Huapi*, v. 2 extra nueva serie 8, p. 41–100.
- Carcelles, A., and Williamson, S., 1951, Catálogo de los moluscos marinos de la provincia magallánica: *Revista del Instituto Nacional de Investigación de las Ciencias Naturales*, v. 2, *Ciencias Zoológicas*, p. 225–383.
- Casadio, S., Pastorino, G., and Griffin, M., 2009, Early Miocene sea pens (Cnidaria: Anthozoa) and the taphonomic history of an unconventional hard substrate community. Reunión Anual de Comunicaciones de la Asociación Paleontológica Argentina: *Ameghiniana*, v. 46, p. 68R Suplemento.
- Castellanos, Z.J.A. de, 1970, Catálogo de los moluscos marinos bonaerenses: *Anales de la Comisión de Investigaciones Científicas de la provincia de Buenos Aires*, v. 8, p. 93–365.
- Castellanos, Z.J.A. de, 1986, Sobre una nueva especie de *Antistreptus* Dall, 1902 (Moll. Buccinulidae): *Neotropica*, v. 31, p. 132 [printed 1985, published 1986].
- Castellanos, Z.J.A. de, 1989, Novedades sobre micromoluscos subantárticos (Mollusca, Gastropoda): *Neotropica*, v. 36, p. 89–92 [printed 1988, published 1989].
- Castellanos, Z.J.A. de, 1992, Catálogo descriptivo de la malacofauna marina magallánica 7. Neogastropoda: Columbellidae = Pyrenidae, Cominellidae y Fasciolaridae: La Plata, Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, 41 p.
- Cooper, R.A., Sadler, P.M., Munnecke, A., and Crampton, J.S., 2010, Graptoloid evolutionary rates track Ordovician–Silurian global climate change: *Geological Magazine*, v. 151, p. 349–364.
- Crampton, J.S., Cooper, R.A., Beu, A.G., Foote, M., and Marshall, B.A., 2010, Biotic influences on species duration: interactions between traits in marine molluscs: *Paleobiology*, v. 36, p. 204–223.
- Cuvier, G., 1795, Second mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la Société d'Histoire Naturelle de Paris, le 11 prairial an troisième: *Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts*, 1795 [1. année] v. 2, p. 433–449.
- Dall, W.H., 1902, Illustrations and descriptions of new, unfigured, or imperfectly known shells, chiefly American, in the U. S. National Museum: *Proceedings of the United States National Museum*, v. 24, p. 499–566.
- Dall, W.H., 1908, Reports on the Mollusca and Brachiopoda: *Bulletin of the Museum of Comparative Zoology, Harvard College*, v. 43, p. 205–487.
- Del Río, C.J., 2004a, Revision of the large Neogene pectinids (Mollusca Bivalvia) of eastern Santa Cruz and Chubut provinces (Patagonia Argentina): *Journal of Paleontology*, v. 78, p. 690–699.
- Del Río, C.J., 2004b, Neogene marine molluscan assemblages of Eastern Patagonia (Argentina): a biostratigraphic analysis: *Journal of Paleontology*, v. 78, p. 1097–1122.
- Del Río, C.J., and Camacho, H.H., 1998, Tertiary nucleolids and arcoids of eastern Patagonia (Argentina): *Palaeontographica (A)*, v. 250, p. 47–88.
- Del Río, C.J., and Martínez, S.A., 2006, The family Volutidae in the Tertiary of Argentina (Mollusca Gastropoda): *Journal of Paleontology*, v. 80, p. 919–945.
- Dell, R.K., 1990, Antarctic mollusca with special reference to the fauna of the Ross Sea: *Bulletin of the Royal Society of New Zealand*, v. 27, p. 1–311.
- DeVries, T., 1985, *Architectonica (Architectonica) karsteni* (Rutsh, 1934): a Neogene and Recent offshore contemporary of *A. (Architectonica) nobilis* Röding, 1798 (Gastropoda, Mesogastropoda): *The Veliger*, v. 27, p. 282–290.
- Doello-Jurado, M., 1918, Nota preliminar sobre la presencia de algunas especies de la fauna magallánica frente a Mar del Plata: *Physis*, v. 4, p. 119–125.
- Engl, W., 2012, *Shells of Antarctica*: London, ConchBooks, 402 p.
- Finlay, H.J., 1926, A further commentary on New Zealand molluscan systematics: *Transactions of the New Zealand Institute*, v. 57, p. 320–485.
- Forcelli, D.O., 2000, Moluscos magallánicos, guía de moluscos de Patagonia y sur de Chile: Buenos Aires, Vázquez Mazzini, 200 p.
- Forcelli, D.O., Narosky, T., and Zaffaroni, J.C., 2015, Moluscos marinos de Argentina, Uruguay y Brasil: Buenos Aires, Vázquez Mazzini Editores, 272 p.
- Gili, C., and Martinell, J., 1994, Relationship between species longevity and larval ecology in nassariid gastropods: *Lethaia*, v. 27, p. 291–299.
- Griffin, M., and Pastorino, G., 2005, The genus *Trophon* Montfort, 1810 (Gastropoda: Muricidae) in the Tertiary of Patagonia: *Journal of Paleontology*, v. 79, p. 296–311.
- Griffin, M., and Pastorino, G., 2006, *Madrynomys bruneti* n. gen. and sp. (Bivalvia: Modiomorphae): a Mesozoic survivor in the Tertiary of Patagonia?: *Journal of Paleontology*, v. 80, p. 272–282.
- Griffin, M., and Pastorino, G., 2012, Microbivalves from the Monte Leon Formation (early Miocene), Patagonia, Argentina: *Revue de Paleobiologie Volume Spécial*, v. 11, p. 447–455.

- Griffin, M., and Pastorino, G., 2013, Cenozoic Ampullinidae and Naticidae (Mollusca, Gastropoda) from Patagonia, Argentina: *Journal of Paleontology*, v. 87, p. 502–525.
- Hain, S., 1990, The benthic seashells (Gastropoda and Bivalvia) of the Weddell Sea, Antarctica: *Reports on Polar Research*, v. 70, p. 1–181.
- Hallam, A., 1987, Radiations and extinctions in relation to environmental change in the marine Lower Jurassic of northwest Europe: *Paleobiology*, v. 13, p. 152–168.
- Hansen, T., 1980, Influence of larval dispersal and geographic distribution on species longevity in neogastropods: *Paleobiology*, v. 6, p. 193–207.
- Hoffman, A., and Szubsda-Studencka, B., 1982, Bivalve species duration and ecologic characteristics in the Badenian (Miocene) marine sandy facies of Poland: *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, v. 163, p. 122–135.
- Ihering, H. von, 1907, Les Mollusques fossiles du Tertiaire et du Crétacé supérieur de l'Argentine: *Anales del Museo Nacional de Buenos Aires, Serie III*, v. 7, p. 1–611.
- Jablonski, D., 1994, Extinctions in the fossil record: Philosophical Transaction of the Royal Society of London B, v. 344, p. 11–17.
- Jablonski, D., and Hunt, G., 2006, Larval ecology, geographic range, and species survivorship in Cretaceous mollusks: organismic versus species-level explanations: *The American Naturalist*, v. 168, p. 556–564.
- Kennedy, W. J., 1977, Chapter 8 Ammonite Evolution, in Hallam, A., ed., *Developments in Palaeontology and Stratigraphy*, v. 5, p. 251–304. [https://doi.org/10.1016/S0920-5446\(08\)70328-5](https://doi.org/10.1016/S0920-5446(08)70328-5)
- Kiel, S., and Nielsen, S.N., 2010, Quaternary origin of the inverse latitudinal diversity gradient among southern Chilean mollusks: *Geology*, v. 38, p. 955–958.
- Lawver, L.A., and Gahagan, L.M., 2003, Evolution of Cenozoic seaways in the circum-Antarctic region: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 198, p. 11–37.
- Le Roux, J.P., 2012, A review of Tertiary climate changes in southern South America and the Antarctic Peninsula, part 1: oceanic conditions: *Sedimentary Geology*, v. 247–248, p. 1–20.
- Linnaeus, C., 1771, *Mantissa plantarum altera Generum editionis VI., & Specierum editionis II: Holmiae [Stockholm], Laurentii Salvii*, p. 143–587.
- Linse, K., 2002, The shelled Magellanic Mollusca: with special reference to biogeographic relations in the Southern Ocean: *Theses Zoologicae*, v. 34, 252 p.
- Liow, L.H., Skaug, H.J., Ergon, T., and Schweder, T., 2010, Global occurrence trajectories of microfossils: environmental volatility and the rise and fall of individual species: *Paleobiology*, v. 36, p. 224–252.
- Lyle, M., Gibbs, S., Moore, T.C., and Rea, D.K., 2007, Late Oligocene initiation of the Antarctic Circumpolar Current: evidence from the South Pacific: *Geology*, v. 35, p. 691–694.
- Martín, S.M., and César, I.I., 2004, *Catálogo de los tipos de Moluscos Gastropoda-Bivalvia-Cephalopoda del Museo de La Plata: La Plata, Fundación Museo de La Plata "Francisco Pascasio Moreno," 74 p.*
- Martins, A.M.F., 1996, Anatomy and systematics of the western Atlantic Ellobiidae (Gastropoda: Pulmonata): *Malacologia*, v. 37, p. 163–332.
- Melville, J.C., and Standen, R., 1912, The marine mollusca of the Scottish National Antarctic Expedition. Part 2: *Transactions of the Royal Society of Edinburgh*, v. 48, p. 333–366.
- Náñez, C., 1988, Foraminíferos y bioestratigrafía del Terciario medio de Santa Cruz oriental: *Revista de la Asociación Geológica Argentina*, v. 43, p. 493–517.
- Nielsen, S.N., and Frassinetti, D., 2007, The Miocene Architectonicidae (Gastropoda) of Chile: *Paläontologische Zeitschrift*, v. 81, p. 291–303.
- Orbigny, A.D. d', 1834–1847, *Mollusques*, in Bertrand, C.P., ed., *Voyage dans l'Amérique Méridionale (Le Brésil, La République Orientale de l'Uruguay, La République Argentine, La Patagonie, La République du Chili, La République de Bolivie, La République du Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833: Paris, Chez Ve, Levrault, vol. 5, 758 p.*
- Parras, A., Dix, G.R., and Griffin, M., 2012, Sr-Isotope chronostratigraphy of Paleogene–Neogene marine deposits: Austral Basin, southern Patagonia (Argentina): *Journal of South American Earth Sciences*, v. 37, p. 122–135.
- Pastorino, G., 2016, Revision of the genera *Pareuthria* Strebel, 1905, *Glyptothria* Strebel, 1905 and *Met euthria* Thiele, 1912 (Gastropoda: Buccinulidae) with the description of three new genera and two new species from south-western Atlantic waters: *Zootaxa*, v. 4179, p. 301–344.
- Pastorino, G., and Griffin, M., 2018, A new Patagonian long-lived species of *Cycloclamys* Finlay, 1926 (Bivalvia: Pectinoidea): *Alcheringa*, v. 42, p. 447–456. DOI: 10.1080/03115518.2018.1440005.
- Pérez, L.M., Griffin, M., Pastorino, G., López-Gappa, J.J., and Manceñido, M.O., 2015, Redescription and palaeoecological significance of the bryozoan *Hippoporidra patagonica* (Pallaroni, 1920) in the San Julián Formation (late Oligocene) of Santa Cruz Province, Argentina: *Alcheringa*, v. 39, p. 1–7.
- Philippi, R.A., 1893, Descripción de algunos fósiles Terciarios de la República Argentina: *Anales del Museo Nacional de Chile*, v. 10, p. 1–15.
- Powell, A.W.B., 1951, Antarctic and subantarctic mollusca: Pelecypoda and Gastropoda: *Discovery Reports*, v. 26, p. 47–196.
- Powell, A.W.B., 1958, Mollusca from the Victoria-Ross Quadrants of Antarctica, British, Australian and New Zealand Antarctic Research Expedition, 1929–1931 under the command of Sir Douglas Mawson: *Reports—Series B (Zoology and Botany)*: Canberra, B.A.N.Z.A.R. expedition committee, v. 6, p. 167–210.
- Prothero, D.R., 2014, Species longevity in North American fossil mammals: *Integrative Zoology*, v. 9, p. 383–393.
- Rafinesque, C.S., 1815, *Analyse de la nature ou tableau de l'univers et des corps organisés*: Palermo, Barravecchia, 224 p.
- Raup, D., 1990, A kill curve for Phanerozoic marine species: *Paleobiology*, v. 17, p. 37–48.
- Rickards, R.B., 1977, Chapter 10, Patterns of evolution in the graptolites, in Hallam, A., ed., *Developments in Palaeontology and Stratigraphy*, v. 5, p. 333–358.
- Rios, E., 2009, *Compendium of Brazilian sea shells: Rio Grande, RS, Evagraf*, 676 p.
- Rutsch, R., 1934, Die Gastropoden aus dem Neogen der Punta Gavilán in Nord-Venezuela: *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, v. 54, p. 1–88.
- Scarabino, F., and Ortega, L., 2004, Registros uruguayos de *Aulacomya atra atra* (Bivalvia: Mytilidae): Rol de condiciones oceanográficas anómalas y de dispersión por feofitas flotantes: *Comunicaciones de la Sociedad Malacológica del Uruguay*, v. 8, p. 299–304.
- Shuttleworth, R.J., 1854, Diagnosen neuer Mollusken: *Mitteilungen der Naturforschende Gessellschaft in Bern*, v. 1852, p. 125–148.
- Shuto, T., 1974, Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology: *Lethaia*, v. 7, p. 239–256.
- Signorelli, J.H., Urteaga, D., and Teso, V., 2015, *Zulma Ageitos de Castellanos: publications and status of described taxa: Zootaxa*, v. 4034, p. 45–69.
- Stanley, S.M., 1979, *Macroevolution: Pattern and Process*: San Francisco, W. H. Freeman and Company, 332 p.
- Strebel, H., 1905, Beiträge zur Kenntnis der Molluskenfauna der Magalhaens-Provinz. 3: *Zoologischen Jahrbücher, Abteilung für Systematik, Geographie, und Biologie der Tiere*, v. 22, p. 575–666.
- Strebel, H., 1908, Die Gastropoden (mit Ausnahme der nackten Opisthobranchier): *Wissenschaftliche Ergebnisse der Schwedischen Südpolar Expedition 1901–1903*, v. 6, p. 1–111.
- Swainson, W., 1840, *A Treatise on Malacology or Shell and Shell Fish: Lardner's Cabinet Cyclopaedia*: London, Longman, Orme, Brown, Green, Longmans, and John Taylor, 384 p.
- Thiele, J., 1912, Die Antarktischen Schnecken und Muscheln, in *Deutsche Südpolar-Expedition (1901–1903) Im Auftrage des Reichsamtes des Innern herausgegeben von Erich von Drygalski Leiter der Expedition*: Berlin, Druck und Verlag von Georg Reimer, v. 13, *Zoologie*, v. 2, p. 183–286.
- Thiele, J., 1929, *Handbuch der systematischen Weichtierkunde. [Loricata; Gastropoda: Prosobranchia]*: Jena, Gustav Fischer, v. 1, 376 p.
- Tippet, D., 1983, A new sinistral Turrid from Brazil (Gastropoda: Turridae): *The Nautilus*, v. 97, p. 135–138.
- Trovant, B., Márquez, F., Del Río, C., Ruzzante, D.E., Martínez, S., and Orensanz, J.M., 2018, Insights on the history of the scorched mussel *Brachidontes rodriguezii* (Bivalvia: Mytilidae) in the southwest Atlantic: a geometric morphometrics perspective: *Historical Biology*, v. 30, p. 564–572.
- Valentine, J.W., 2009, Overview of marine biodiversity, in Witman, J.D., and Roy, K., eds., *Marine Macroecology*: Chicago, University of Chicago Press, p. 3–24.
- Valentine, J.W., and Moores, E.M., 1970, Plate tectonic regulation of faunal diversity and sea level: a model: *Nature*, v. 228, p. 657–659.
- Wallace, C.C., and Bosellini, F.R., 2015, *Acropora* (Scleractinia) from the Oligocene and Miocene of Europe: species longevity, origination and turnover following the Eocene–Oligocene transition: *Journal of Systematic Palaeontology*, v. 13, p. 447–469.
- Wenz, W., 1938, *Gastropoda, Teil und Prosobranchia, Handbuch der Paläozoologie*: Berlin, Verlag von Gebrüder Borntraeger, v. 6, p. 1–480.

Accepted: 21 January 2019