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Journal of Paleontology / Volume 89 / Issue 06 / November 2015, pp 956 - 965
DOI: 10.1017/jpa.2015.64, Published online: 09 May 2016

Link to this article: http://journals.cambridge.org/abstract_S0022336015000645

How to cite this article:
Leandro M. Pérez, Juan López-Gappa and Miguel Griffin (2015). New and little-known bryozoans from Monte León Formation (early Miocene, Argentina) and their paleobiogeographic relationships. Journal of Paleontology, 89, pp 956-965 doi:10.1017/jpa.2015.64

Journal of Paleontology, 89(6), 2015, p. 956–965
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0022-3360/16/0088-0906
doi: 10.1017/jpa.2015.64

Journal of
PALEONTOLOGY
A JOURNAL OF THE PALEONTOLOGICAL SOCIETY

New and little-known bryozoans from Monte León Formation (early Miocene, Argentina) and their paleobiogeographic relationships

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Abstract.—The bryozoan fauna from the South American Cenozoic is poorly known. The study of new material collected in the Monte León Formation (early Miocene), gave us the opportunity to describe four new species: *Valdemunitella canui* n. sp., *Foveolaria praecursor* n. sp., *Neothoa reptans* n. sp., and *Calyptotheca santacruzana* n. sp. Two of them (*V. canui* and *C. santacruzana*) were first recorded by F. Canu and interpreted as recent species from the Australian bryozoan fauna, but are herein described as new species. The stratigraphic range of *Otionella parvula* (Canu, 1904) is extended to the early Miocene. The present study emphasizes the close relationships between the South American Neogene bryozoan faunas and those of other Gondwanan sub-continents such as New Zealand and Australia.

Introduction

Cenozoic invertebrate faunas from southern South America may provide different kinds of evidence potentially useful when studying the paleogeographic evolution of this region. Such faunas have been known since the early work of d'Orbigny (1842) and Darwin (1846)—with Sowerby (1846) describing the invertebrates collected by the latter—who assembled large collections of mollusks during their famous trips of scientific exploration around the world. While mollusks are by far the most common and best known group of megafossils in Cenozoic rocks from this region of Patagonia (del Río, 2004a, 2004b; Parras and Griffin, 2009; Parras et al., 2008; Parras, Dix, and Griffin, 2012; Griffin and Pastorino, 2012), the bryozoans also exhibit a considerably diverse taxonomic composition, and are represented in many units such as the Monte León Formation (Parras et al., 2012; Casadío, Campbell et al., 2010). Although first reported from Cenozoic rocks in South America in the first half of the nineteenth century, this group is still poorly known in this region, and consequently their paleobiogeographic affinities remain poorly understood.

Pioneering contributions toward the knowledge of the Patagonian bryozoans (Ortmann, 1900, 1902; Canu, 1904, 1908, 1911; Pallaroni, 1920; Frenguelli, 1920, 1927; Conti, 1949; Leanza, 1956) included descriptions of Cenozoic assemblages recorded in different places of southern Argentina. More recently, Muravchik, Griffin, and Pérez (2004) and Pérez et al., (2013) furthered the knowledge on this group identifying Neogene taxa from Entre Ríos (east-central Argentina). Casadío et al. (2010) suggested a Pan-Gondwanan connection revealed in the geographic distribution of fossil bryozoans. They based such connection on the presence of the Family Cinctiporidae in the Monte León Formation (early Miocene, Aquitanian to early Burdigalian; Parras et al., 2012). This taxon has been considered distinctive of the New Zealand Cenozoic record, thus eliciting interest in the paleobiogeographic relations among the southern hemisphere bryozoans and their connection with paleogeographic and paleoceanographic events occurring during the Cenozoic. Important among these are the opening of Drake Passage (34 Ma; Lagabrielle et al., 2009) and the establishment of the Antarctic Circumpolar Current.

The species reported by Ortmann (1900, 1902) are the only ones so far known from early Miocene beds from Argentina and were collected by that author in beds now included in the Monte León Formation (Mouth of the Santa Cruz River and further south along the Atlantic coast), El Chacay (Upper Río Chalia, Río Chico, Arroyo Gío), and San Julián Formation (San Julián). Of the six species mentioned by Ortmann, only three were new, i.e. *Melicerita triforis* Ortmann, 1900; *Reticulipora patagonica* Ortmann, 1900; and *Tennysonia subcylindrica* Ortmann, 1900. The former came from the Upper Río Chalia, and the other two from Santa Cruz River mouth. The other three species mentioned by Ortmann, i.e. *Cellaria fistulosa* (Linnaeus, 1758), *Aspidostoma giganteum* (Busk, 1854), and *Heteropora pelliculata* (Waters, 1879), came from Río Chico, Santa Cruz, and Arroyo Gío.

The main goal of this paper is to describe five taxa identified in the Monte León Formation exposed in coastal ravines of the Monte León National Park (Santa Cruz Province, Argentina). The probable paleobiogeographic and temporal relationships of these taxa in connection with the well-known fossil record of bryozoans from other regions at equivalent latitude are also discussed.

Geological setting

Several Patagonian Neogene units lie exposed along the Atlantic coast from northern Río Negro Province to Tierra del Fuego. The marine units harbor a diverse fauna of macroinvertebrates. One of the most fossil-rich units is the Monte León Formation, which is especially well exposed along the coastal cliffs in the Monte León National Park and along the southern margin of the Santa Cruz River mouth (Parras and Griffin, 2009), all in Santa Cruz Province. Bryozoans are a common component of the fossil assemblages in this unit. Specimens are well preserved and the colony fragments examined suggest that bryozoan biodiversity was very high. Early work on the paleontology of this unit includes Sowerby (1846), Ihering (1897, 1907, 1914), Cossmann (1899), Ortmann (1900, 1902), and Ameghino (1906).

All the material analyzed comes from the section at Cabeza de León (Fig. 1.1). At this locality, the section includes almost ~47 m of silicoclastic rocks in medium to fine sandy to silty beds. The lower part of the section includes mainly siltstone and fine-grained sandstone with abundant trace fossils such as *Thalassinoides* isp. and *Ophiomorpha* isp. The lower part of the section carries an abundant fauna of decapods and bivalves preserved in life position. Overlying these beds there are sparse corals, serpulids, and the bryozoan assemblage analyzed herein (Parras et al., 2012).

The overlying 11 m are very bioturbated medium- to fine-grained sandstones with bioclastic lenses within the fine-grained layers. The fossil assemblage in these lenses mostly includes bivalves and gastropods, and to a lower extent echinoderms, barnacles, scaphopods, and bryozoans. A few of the bivalves are preserved in life position, while most of the association is of sedimentological origin.

The upper part of the section includes about 19 m of siltstones, tuff, fine sandstone, and heterolithic beds lacking fossils (Fig. 1.2; see also Parras et al., 2012).

Most of the Monte León Formation seems to have been deposited in a relatively low-energy shelf setting, with a gradual upward shallowing trend and an abundant supply of volcanic ash (Malumián, 1999).

Isotopic studies by Parras et al. (2012) render Sr^{87}/Sr^{86} ages of 22.12 Ma at the base and 17.91 Ma at the top, which appears to be consistently early Neogene (Aquitanian to early Burdigalian).

Material and methods

The material studied was collected by Pastorino and Griffin in the year 1995 and it comes from the same locality and bed, i.e. Cabeza de León [50°21′32″S, 68°52′58″W], Monte León

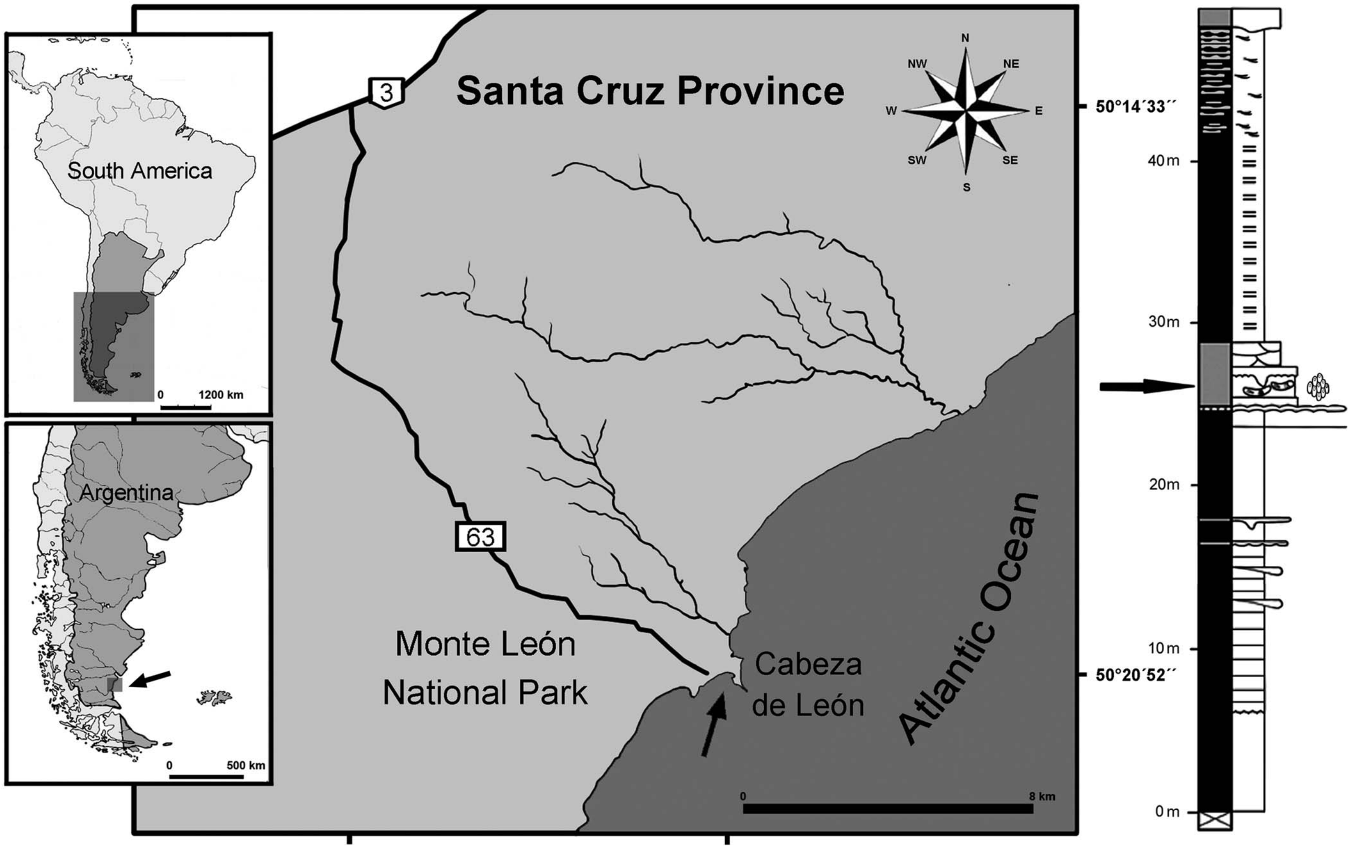

Figure 1. (**1**) Map of the study area. (**2**) Schematic section of the Monte León Formation at Cabeza de León, deposited during the early Neogene (Aquitanian to early Burdigalian). The section includes almost ~47 m of silicoclastic rocks in medium to fine sandy to silty beds. Arrow shows the bed containing the described bryozoans.

Formation, in Santa Cruz Province, Argentina (Fig. 1.1). Specimens were recovered by washing (ultrasound) and sieving the loose sediment and then picking the material under a binocular microscope. Colonies were analyzed and photographed using a scanning electron microscope (SEM) at the Servicio de Microscopía Electrónica de Barrido y Microanálisis of LIMF (Departamento de Mecánica, Facultad de Ingeniería – UNLP) and at the Museo Argentino de Ciencias Naturales (MACN). Specimens are housed in the collection of the División Paleozoología Invertebrados - Museo de La Plata (MLP).

Systematic paleontology

Order Cheilostomata Busk, 1852
Suborder Neocheilostomina d'Hondt, 1985
Infraorder Flustrina Smitt, 1868
Superfamily Calloporoidea Norman, 1903
Family Calloporidae Norman, 1903
Genus *Valdemunitella* Canu, 1900
Valdemunitella canui new species
Figure 2.1, 2.2

1908 *Membranipora pyrula* Hincks, 1881; Canu, p. 257–258, pl. 1, fig. 10. *Non Membranipora pyrula* Hincks, 1881, p. 3, pl. 1, fig. 2.

Diagnosis.—*Valdemunitella* with large vicarious avicularia and without tubercles on the proximal gymnocyst. Six pairs of lateral, plus one or two smaller proximal spines, curved over the opesia.

Description.—Unilaminar encrusting colony. Zooids elongated-oval, 0.48–0.60 × 0.18–0.24 mm, more slender proximally. Opesia encompassing 70% of zooidal length. Gymnocyst moderately developed, without tubercles. Cryptocyst narrow, granular, laterally and proximally encircling the opesia. Most zooids with six pairs of lateral spines curving over the opesia, plus one or two smaller proximal spines. Vicarious avicularia elongated, 0.60 × 0.24 mm, with a pair of short sharp condyles located closer to the proximal than to the distal end of the avicularia. Ovicell hyperstomial, rounded, bifenestrate, with a median suture.

Etymology.—Honoring Ferdinand Canu, who identified the Cenozoic fossil bryozoans from Patagonia between 1904 and 1911.

Type.—Holotype MLP 34536. Encrusting a bilaminar erect bryozoan. Early Miocene, Monte León Formation, Cabeza de León, Santa Cruz Province, Argentina.

Occurrence.—Punta Borja, Comodoro Rivadavia (Canu, 1908). Cabeza de León, Santa Cruz Province, Argentina (this study).

Remarks.—*Membranipora pyrula* was originally described by Hincks (1881) from Recent material collected in Bass Strait, Australia. Recent material from Australia was later recorded by MacGillivray (1886) and Uttley (1951). A neotype was later chosen by Brown (1952) from among specimens coming from the original locality. Brown (1952) also recorded the species from the Middle Miocene of New Zealand. Gordon (1986) published the first SEM illustrations of New Zealand specimens. Hincks' species, whose synonymy was listed by Uttley (1951) and Brown (1952), is now regarded as belonging to the calloporid genus *Valdemunitella* Canu, 1900, because it possesses spines bordering the opesiae of autozooids, bifenestrated ovicells, and avicularia lacking a pivot bar (Uttley, 1951; Gordon, 1986).

The specimen from Monte León seems to be conspecific with material from the Patagoniano of Punta Borja (Comodoro Rivadavia, Chubut Province) described as *Membranipora pyrula* by Canu (1908). It should be included in *Valdemunitella* because it shows spines curved around the opesia, a bifenestrated ovicell, and lacks an avicularian pivot bar. However, the Miocene fossil from Argentina differs from Hincks' species by lacking the conspicuous tubercles on the proximal gymnocyst and by having a somewhat longer vicarious avicularium (cf. plate 6F in Gordon, 1986).

Family Foveolariidae Gordon and Winston, 2005 in Winston, 2005
Genus *Foveolaria* Busk, 1884
Foveolaria praecursor new species
Figure 2.3, 2.4

Diagnosis.—Erect *Foveolaria* with relatively short zooids and gymnocyst. The only pair of pores is located halfway between the distal margin of the opesia of the preceding zooid and the proximal margin of the avicularia. Suboral avicularia located within a depressed area of gymnocyst proximal to the opesia.

Description.—Colony erect, dichotomously branching. Branches measuring approximately 1.4 mm in diameter. Zooids 0.44–0.61 × 0.26–0.42 mm, arranged quincuncially in around 10 longitudinal series. Opesia 0.15–0.19 × 0.16–0.24 mm, oval, occupying roughly one-third of zooidal length. Cryptocyst encircling the opesia, steeply descending, faintly granular. Gymnocyst reduced, smooth, slightly convex, bearing a pair of proximal pores located halfway between the distal margin of the opesia of the preceding zooid and the proximal margin of the avicularia. Oral spines lacking. Avicularia single, pointing latero-proximally, located within a depressed area of gymnocyst proximal to the opesia. Rostrum elongated, with a pair of small condyles, but without a pivot bar. Ovicells unknown.

Etymology.—From the Latin *praecursum* ± *or* masculine suffix, meaning preceding, foregoing, because this species could be the forerunner of the species currently living in South America and New Zealand.

Types.—Holotype MLP 34537. A small fragment of an erect branch. Paratypes MLP 34538-34544. Early Miocene, Monte León Formation, Cabeza de León, Santa Cruz Province, Argentina.

Occurrence.—Only known from the type locality.

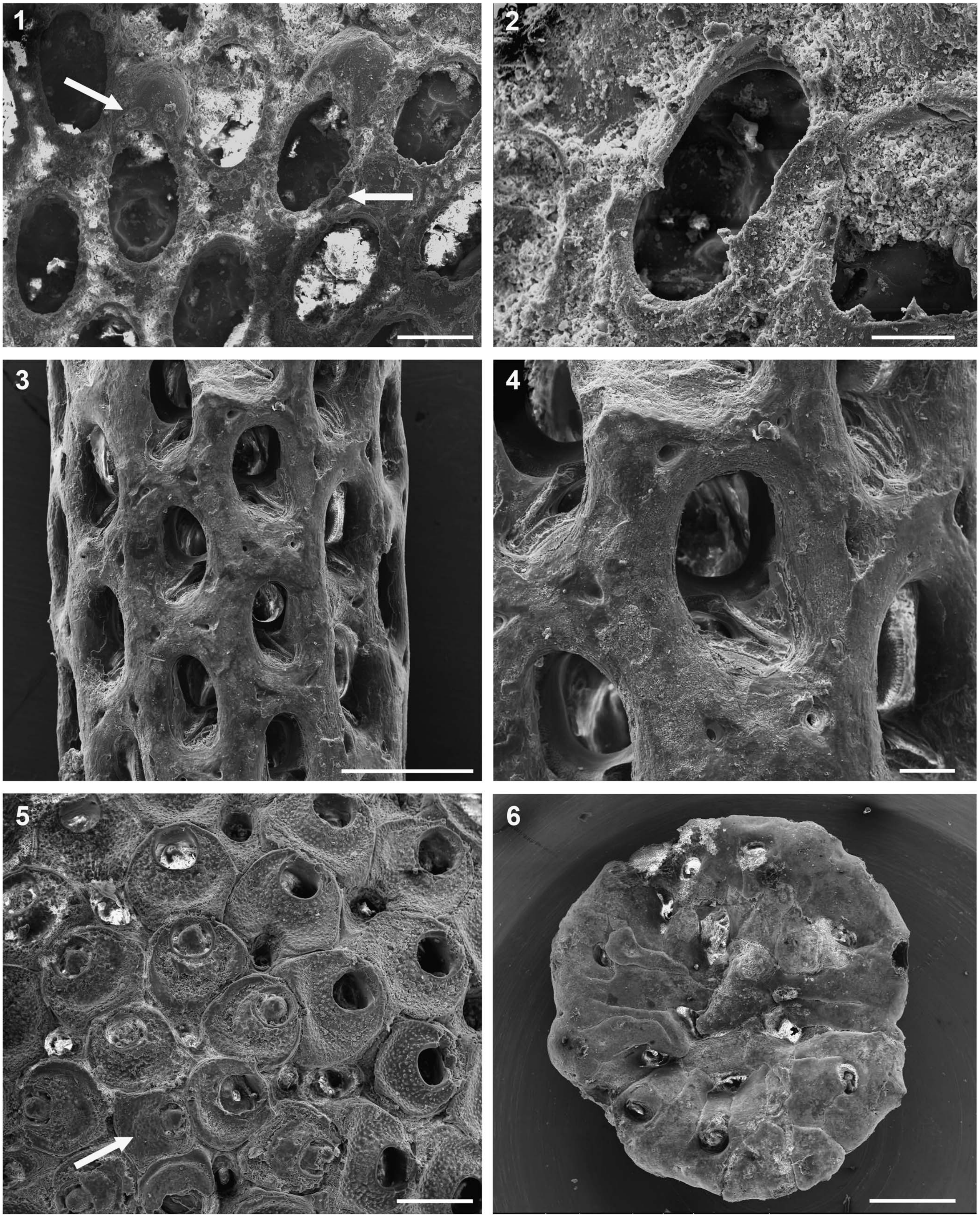

Figure 2. *Valdemunitella canui* n. sp. Holotype (MLP 34536); (**1**) general view of autozooids and ovicells. Left arrow shows one of the fenestrae, right arrow indicates a spine basis; (**2**) vicarious avicularia. *Foveolaria praecursor* n. sp. Holotype (MLP 34537); (**3**) general aspect of a branch; (**4**) detail of an autozooid. *Otionella parvula* (MLP 34545); (**5**) frontal view, ancestrula (arrow) and early astogeny; (**6**) basal surface of the colony, showing basal avicularia. Scale bars represent (**1**) and (**5**), 200 μm; (**2**) and (**4**), 100 μm; (**3**) and (**6**), 500 μm.

Remarks.—The type species of *Foveolaria* chosen by Canu (1900) is *F. elliptica* Busk, 1884. The genus is represented by four fossil species (Uttley, 1951; Brown, 1952, 1958), i.e. (1) *Foveolaria everettensis* (Uttley, 1951), from the Lower Oligocene of New Zealand; (2) *Foveolaria curdiensis* Brown, 1952, from the Middle Miocene of Southwestern Victoria; (3) *Foveolaria marwicki* Brown, 1952, from the Lower Oligocene of New Zealand; and (4) *Foveolaria thomasi* Brown, 1958, from the Miocene of Southwestern Victoria.

Among the recent species of *Foveolaria*, the original description of *F. elliptica* Busk, 1884, included specimens from two widely distant geographic areas: Bass Strait (Australia) and the continental slope off Argentina/Uruguay (H.M.S. Challenger station 320, 1097 m). Waters (1888) and Moyano (1974) recorded the presence of *F. elliptica* in the Magellan region and López Gappa and Lichtschein (1990) published a SEM illustration of a colony from the Patagonian shelf. Gordon (1986) published the first SEM photograph of New Zealand material showing two pairs of pores and transversal avicularia not located in a gymnocystal depression.

The fossil specimens from the Monte León Formation differ clearly from the four Cenozoic species from Australia and New Zealand (see Uttley, 1951; Brown, 1952, 1958) but bear a strong resemblance to *F. elliptica*. The new species differs from *F. elliptica*, however, because its zooids and gymnocyst are shorter, and in the location of the pores with regard to the distal margin of the opesia of the preceding zooid.

Superfamily Microporoidea Gray, 1848
Family Otionellidae Bock and Cook, 1998
Genus *Otionella* Canu and Bassler, 1917
Otionella parvula (Canu, 1904)
Figure 2.5, 2.6

1904 Lunulites parvula *n. sp.*; Canu, p. 8, pl. 1, figs. 10, 11.

1946 Reptolunulites parvula Canu 1904; Buge, p. 207.

1985 *Otionella parvula* (Canu); Cook and Chimonides, p. 581–583, figs. 3, 4, 6, 7.

Description.—Colony minute, circular, diameter 2.2 mm, basal surface thickly calcified, composed of irregular sectors separated by sutures. Ancestrula small, wider than long, 0.20 × 0.23 mm, with an almost straight proximal border and two pointed proximo-lateral expansions. Early astogeny consists of one distal, two lateral and two proximal zooids. Autozooids wider than long, 0.23–0.28 × 0.29–0.31 mm, rounded distally and concave proximally, separated by prominent margins. Opesia small, subcircular, encircled by a prominent rim. Cryptocyst thickly nodular. Peripheral zooids with enlarged opesiae. Avicularia interzooidal, frequent, much smaller than autozooids, with proximal cryptocyst and rounded opesia. Basal avicularia with short, nodular cryptocyst and subcircular opesia.

Material.—MLP 34545. Early Miocene, Monte León Formation, Cabeza de León, Santa Cruz Province, Argentina.

Occurrence.—Cabo Curioso, Santa Cruz Province (Canu, 1904). Cabeza de León, Santa Cruz Province, Argentina (this study).

Remarks.—This is the first time that fossil specimens of *O. parvula* are found after its original description by Canu. The material herein examined extends its fossil record from the Oligocene (Cabo Curioso, San Julián Formation; Canu, 1904) to the early Miocene.

Suborder Ascophora Levinsen, 1909
Infraorder Hippothoomorpha Gordon, 1989
Superfamily Hippothooidea Fischer, 1866
Family Hippothoidae Busk, 1859
Genus *Neothoa* Moyano, 1986
Neothoa reptans new species
Figure 3.1–3.3

Diagnosis.—*Neothoa* with autozooids having a relatively elongated and narrow cauda and 2–4 blunt median umbos in their midline. Female zooids wedge-shaped, smaller than autozooids. Ovicell perforated by 1–2 small pores.

Description.—Uniserial encrusting colony, each autozooid budding one distal and one or two disto-lateral zooids. Autozooids 0.43–0.46 × 0.17–0.19 mm, elongate-pyriform, tapering proximally into a narrow and relatively long cauda. Marginal pores occasionally present in the cauda and always replacing the lateral buds in non-ramifying autozooids. Frontal wall smooth, faintly striated, with 2–4 blunt umbos along the midline. Orifice subcircular, encircled by a faint rim; sinus U-shaped, wide and shallow, flanked by a pair of blunt condyles. Female zooids laterally budded, 0.15 × 0.14 mm, subtriangular or wedge-shaped, with an unconspicuous suboral umbo; orifice D-shaped, with a very wide and shallow sinus. Ovicell rounded, occasionally perforated by 1–2 small pores. Male zooids or zoeciules apparently absent. Ancestrula unknown.

Etymology.—From the Latin *reptans*, due to the crawling growth habit of the species.

Type.—Holotype. MLP 34546. Encrusting uniserial colony. Early Miocene, Monte León Formation, Cabeza de León, Santa Cruz Province, Argentina.

Occurrence.—Only known from the type locality.

Remarks.—Within the family Hippothoidae, two genera with uniserial, branching zoaria could accomodate this new species: *Hippothoa* Lamouroux, 1821, and *Neothoa* Moyano, 1986. The main morphological feature separating the two genera is the ancestrula, which is schizoporelloid in *Hippothoa* and tatiform in *Neothoa*. Because no ancestrulae were found in the fossil material herein examined, the generic assignment proposed in this study is tentative and was based on morphological features of the autozooids, ovicelled zooids, and the ovicell.

The fossil material agrees with *Hippothoa patagonica* Busk, 1852, type species of *Neothoa*, in possesing a wedge-shaped

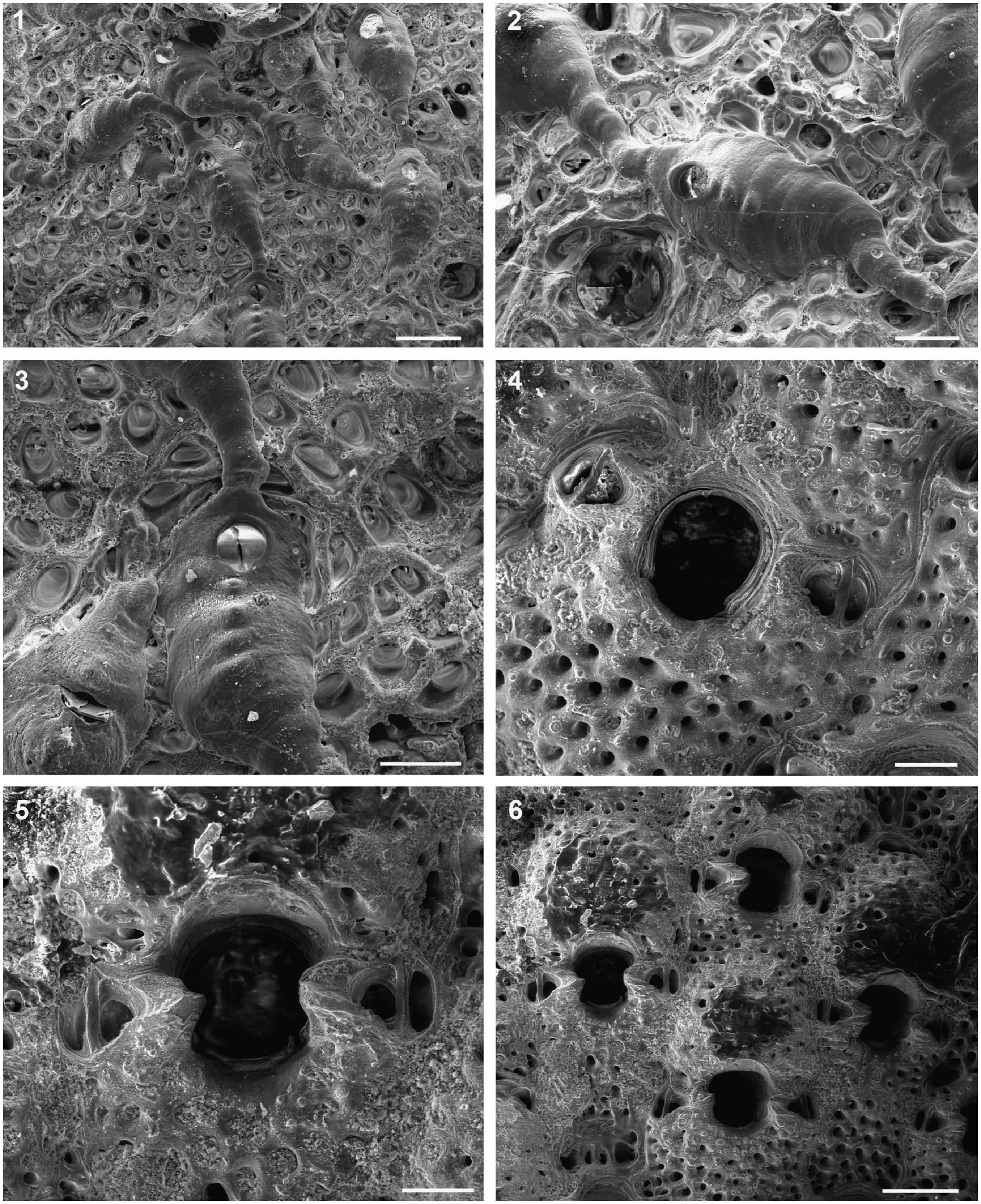

Figure 3. *Neothoa reptans* n. sp. Holotype (MLP 34546); (**1**) general aspect of the uniserial colony growing on a bilaminar bryozoan; (**2**) detail of an autozooid showing the tapering proximal cauda; (**3**) autozooid and ovicelled zooid. *Calyptotheca santacruzana* n. sp. Holotype (MLP 34547); (**4**) autozooid, showing details of the lateral notches, condyles and lunula; (**5**) adventitious avicularia projecting over the orifice; (**6**) ovicelled zooids. Scale bars represent (**2–5**), 100 μm; (**1, 6**), 200 μm.

ovicelled zooid and a scarcely perforated ovicell. It differs from the type species of *Hippothoa*, *H. divaricata* Lamouroux, 1821, by the absence of zoeciules and by having a non-filiform autozooidal cauda. It should also be pointed out that the three species of *Neothoa* described so far (*N. patagonica* [Busk, 1852], *N. chiloensis* [Moyano, 1982], and *N. vivianii* [Moyano, 1986]), have only been recorded around the southern tip of South America. *N. reptans* n. sp. differs from the three living species of *Neothoa* by having a more elongated and narrower cauda and 2–4 blunt median umbos in the autozooids. *Neothoa* is not represented in the fossil record, whereas *Hippothoa* has been found in European Tertiary deposits (Canu and Lecointre, 1928). If the generic assignment herein proposed proves to be valid, this would be the first fossil occurrence of the genus *Neothoa*.

Infraorder Lepraliomorpha Gordon, 1989
Superfamily Smittinoidea Levinsen, 1909
Family Lanceoporidae Harmer, 1957
Genus *Calyptotheca* Harmer, 1957
Calyptotheca santacruzana new species
Figure 3.4–3.6

1908 Schizoporella biturrita Hincks, 1884; Canu, p. 288, pl. 9, fig. 1. Non *Schizoporella biturrita* Hincks (1884; p. 280).

Diagnosis.—*Calyptotheca* with a concave, wide and shallow sinus in the orifice. Avicularia usually paired, protruding, pointing toward the orifice. Ovicell immersed in the frontal wall of the distal autozooid, not crossed by suture lines.

Description.—Unilaminar encrusting or bilaminar erect colony. Irregularly polygonal and convex autozooids measuring 0.75–1.03 × 0.54–0.67 mm. Frontal shield perforated by numerous rounded pseudopores. Orifice subcircular, longer than wide, 0.22–0.26 × 0.16–0.20 mm, with a pair of lateral notches, two robust condyles and a concave, wide and shallow sinus. A narrow ledge of calcification (lunula) surrounds the internal margin of the orifice, appearing to be continuous with the condyles. Avicularia sutural, usually paired, rarely unique, pointing toward the orifice or disto-medially; rostrum triangular, protruding, pivot bar complete. Ovicell immersed in the frontal wall of the distal autozooid, with pseudopores of similar size to those of frontal shield. Orifice dimorphism, ovicellated orifice slightly larger than autozooid orifice. Basal pore-chambers present in the distal half of the zooid. Ancestrula unknown.

Etymology.—Refering to Santa Cruz Province.

Types.—Holotype. MLP 34547. Encrusting colony. Paratypes MLP 34548-34556. Early Miocene, Monte León Formation, Cabeza de León, Santa Cruz Province, Argentina.

Occurrence.—Punta Borja, Comodoro Rivadavia (Canu, 1908). Cabeza de León, Santa Cruz Province, Argentina (this study).

Remarks.—This species was first recorded and described as *Schizoporella biturrita* Hincks by Canu (1908) from the Patagoniano of Comodoro Rivadavia. *S. biturrita* was originally described by Hincks (1884) on the basis of Recent material from Port Phillip Heads, Australia. His original description shows an orifice with a narrow U-shaped sinus and avicularia associated with tower shaped processes. Bock (1982) recorded this species as *Gigantopora biturrita* and published its first SEM illustration, showing the raised processes on each side of the orifice, a large and prominent ovicell, and proximo-laterally oriented avicularia. Gordon and Parker (1991), based on a personal communication by P. Bock, clarified the synonymy of the species, showing that *S. biturrita* is a junior synonym of *Cellepora variolosa* MacGillivray, 1869, whose valid name is now *Calyptotheca variolosa* (see also Bock, 2001). Other junior synonyms of the recent Australian species are *Schizoporella baccata* Maplestone, 1913, and *Eschara* (?) *huttoni* Tate in Hutton, 1878. *Schizoporella tuberosa* var. *angustata* Waters, from the Tertiary of New Zealand, was included by Canu (1908) in the synonymy of *S. biturrita*, but the original illustration in Waters (1887) shows a narrow U-shaped sinus. The fossil material from Monte León, regarded herein as a new species, differs from *Calyptotheca variolosa* by the absence of raised processes on each side of the orifice, the orientation of its avicularia and the characteristics of its unconspicuous ovicell, which lacks the central umbo and is immersed in the frontal wall of the distal autozooid. It also differs from *Schizoporella tuberosa* var. *angustata* by its wide and shallow sinus.

The generic assignment of this new species is controversial, as it shares characters in common with the genera *Calyptotheca* (Lanceoporidae) and *Cosciniopsis* (Gigantoporidae). The type species of *Cosciniopsis*, *C. coelatus* Canu and Bassler, 1927, has been recently redescribed by Tilbrook (2006). It resembles the Patagonian species in the characteristics of its frontal shield and ovicell, but differs from it by the absence of avicularia and the striking dimorphism of the orifice in the ovicelled zooids, which have a straight or slightly convex poster. The material under study is remarkably similar to another species assigned to *Cosciniopsis*, *C. lonchaea* (Busk, 1884), due to the pair of latero-oral avicularia directed towards the orifice. On the other hand, the fossil species from Monte León, resembles *Calyptotheca wasinensis* (Waters, 1913), type species of *Calyptotheca*, in the characteristics of its primary orifice, particularly by the presence of a lunula. The new species herein described is assigned to the genus *Calyptotheca* because of the presence of a lunula continuous with the lateral condyles in the primary orifice. Although the new species lacks cormidial ovicells as those in *C. wasinensis*, this is not an excluding character. For instance, *C. tenuata* Harmer, 1957, has ovicells not crossed by suture lines and it has been recently regarded as a member of *Calyptotheca* by Cumming and Tilbrook (2014).

Discussion

Several extant taxa of bryozoans shared by the austral regions—such as the southernmost tip of South America, Australia and New Zealand—point toward paleobiogeographic relations among these areas. The affinities among the bryozoan faunas of these regions were discussed by Moyano (1982, 1997). Recent taxonomic advances in this group of invertebrates and the use of SEM to study them allow the recognition of vicariant species in cases previously believed to be disjunct distributions. Such is the case of *Chiastosella ettorina*, recently described from the

Burwood Bank (Ragazzola et al., 2014) and previously considered conspecific with *C. watersi* from New Zealand (see Hayward, 1980).

There are several fossil and living species of *Hippomenella* in New Zealand (Brown, 1952; Gordon, 1984) and Australia (Brown, 1958). *H. ramula* from the slope off Cape Horn was previously considered by Moyano (1982, 1983, 1991) as conspecific with the New Zealand species *H. vellicata*. It was recently described as a new species by Hayward and Winston (2011) based on material coming also from the slope off Cape Horn. Contrarily, extant species such as *Escharella spinosissima* and *Villicharixa strigosa* are still considered to be taxa shared by the Magellanic and Australasian regions (Moyano, 1997).

Paleobiogeographic relations among the faunas of the austral regions have been recently studied from different perspectives. The hypothesis that shelf areas around South America, Antarctica and Australasia could be colonized by organisms originating in either one of these continents during the Neogene has been strengthened by evidence based on the fossil record.

A Miocene trans-Antarctic seaway has been postulated as a dispersal route for marine shelf fauna (Casadío et al., 2010), but the driving force connecting all sectors of the southern ocean was the establishment of the Circum Antarctic Current (Nelson and Cooke, 2001; Lawver and Gahagan, 2003). The varying ocean circulation patterns and climate conditions (and the ensuing changes in global sea-level) at different moments of the Cenozoic (Zachos et al., 2001) surely played different roles in the dispersion of organisms throughout the southern hemisphere. The taxa and their different ecological requirements and their kind of larval development are important when considering dispersal routes, whether in extant or their related fossil groups. Several mechanisms of dispersal have been proposed for marine invertebrates, such as transport by birds (Green and Figuerola, 2005 and references therein), planktotrophic larvae transported by currents (Levin, 2006 and references therein), rafting of juveniles or adults by marine algae such as kelp (Helmuth et al., 1994; Thiel and Haye, 2006), or even pumice adrift on the ocean surface (Coombs and Landis, 1966; Bryan et al., 2012). Intentional or unintentional anthropochory should not be discarded for extant taxa.

In the case of bryozoans, the presence of the Family Cinctiporidae in New Zealand and South America—previously recorded only in New Zealand—suggests that shelf areas in these regions were somehow connected either physically or by different ocean currents active at that time. The material referred to this family from Patagonia (Casadío et al., 2010) comes from the same unit as the specimens described herein.

Three of the five species dealt with in this work (*V. canui*, *F. praecursor*, and *C. santacruzana*) are closely related taxonomically to others currently living in the southwestern Pacific Ocean. Similarly, Beu et al. (1997) gave a list of 22 mollusk genera shared between South America and New Zealand during the late Oligocene-Miocene. Changes in landmass distribution throughout the Cenozoic are well documented, and South America was isolated from other regions during most of this period. However, the southern tip of the continent was relatively close to Antarctica during the early part of the Cenozoic. Antarctica—or the shelf areas surrounding it or separating West Antarctica from East Antarctica—thus provided a connecting path between Australasia and South America, at least before the definite configuration of the southern continents was finally established (Fig. 4). Sub-Antarctic islands (e.g., Kerguelen, Campbell, Macquarie) also provided shelf environments that could be easily colonized by a diverse array of invertebrates, among them bryozoans. The configuration of landmasses and seaways during the early Miocene—when the bryozoan fauna of the Monte León Formation thrived—were surely favorable for the dispersion of benthic faunas along shallow shelf areas or crossing deep-water stretches driven by currents.

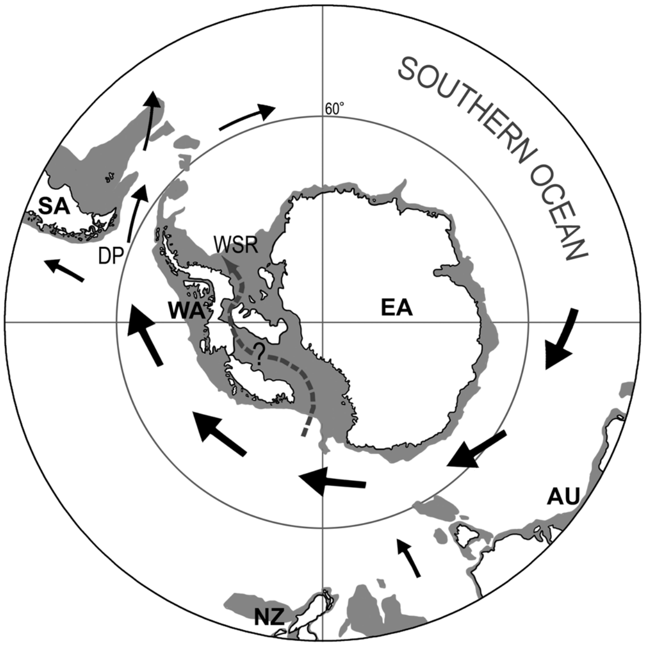

Figure 4. Polar stereographic projections to 45°S of the southern ocean at the early Miocene (modified from Lawver and Gahagan, 2003). The arrows indicate possible seaways between the Australasian and Magellanic regions. AU, Australia; DP, Drake Passage; EA, East Antarctica; NZ, New Zealand; SA, South America; WA, West Antarctica; WSR, Weddell Sea region.

Conclusions

Five bryozoan species were identified in the Monte León Formation. Four of them were new to science (*Valdemunitella canui* n. sp., *Foveolaria praecursor* n. sp., *Neothoa reptans* n. sp., and *Calyptotheca santacruzana* n. sp.), and the temporary registration of the fifth, *Otionella parvula*, is extended to the early Miocene.

The record of the genera *Valdemunitella*, *Foveolaria*, and *Calyptotheca* in Santa Cruz Formation (early Miocene), supports the idea of a common paleobiogeographic distribution with regions of the southern hemisphere such as New Zealand and Australia.

The development of the Circum-Antarctic Current and the opening of the Drake Passage was of paramount importance in the paleobiogeography of South America during the early Miocene. There are close relationships between the South

American Neogene bryozoan faunas and those of other Gondwanan sub-continents.

Acknowledgments

G. Pastorino collected the materials from Monte León Formation. We are grateful to P. Taylor for help with the literature, to K. Tilbrook for comments on the generical affinities of *C. santacruzana*, and A. Parras and D. Urteaga for the stratigraphic information raised in Cabeza de León. CONICET funded a postdoctoral fellowship to L.M.P. and additional support was granted by the Agencia Nacional de Promoción Científica y Técnica (grants PICT-2012-1726 to M.G. and PICT-2012-1403 to J.L.G.) and CONICET (PIP 2013-0247 to J.L.G.).

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Accepted 28 April 2015