Biogeographical relationship of the South America–Antarctic Cenozoic bryozoan biota: The example of austral genus *Aspidostoma*

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Summary Insight into the Cenozoic geologic history of the austral genus *Aspidostoma* is important for the reconstruction of the biogeographical links between South America and Antarctica. *Aspidostoma,* is commonly widespread throughout the Tertiary in the triangle of Antarctica-South America-Australia-New Zealand, reaches its maximum diversity in the late early Eocene of the La Meseta Formation on Seymour Island (West Antarctica) and has its earliest fossil record in the lower Danian (Roca Formation) of Patagonia (South America). The recently studied Canu collection provides valuable data on the taxonomy and the closest biogeographical Magellanic-Antarctic connection. As with *Aspidostoma*, other early Paleocene (Danian) bryozoans from Patagonia, including *Micropora, Figularia, Exochella* and C*elleporaria*, are remarkable for the evolutionary importance and the recognition of migration routes during the early Cenozoic. In this context, the origin of the Recent Antarctic and the Magellan bryozoans should be traced back to the early Paleogene and Neogene bryozoans from Patagonia.

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Introduction

The Paleogene, along with Neogene, represents a transitional time in the Cenozoic evolutionary history of bryozoans, coming between the Cretaceous with the K-T boundary which hampers the extinction and survival of many bryozoan taxa, and the cheilostome-dominated bryozoan faunas of the Eocene-Miocene to Recent.

Aspidostoma Hincks, 1881, - an austral genus with a few living representatives recorded from the Cenozoic of the Southern Hemisphere, is characterized by its endemism, high level of polymorphism, specific diversity, as well as many cases the gigantism in the colonial forms. Most of the occurrences of the genus *Aspidostoma* in the fossil record are from Paleogene and the Neogene strata of the Antarctica-South America-Australia-New Zealand region.

In Antarctica, the anascan microporoideans represented by genus *Aspidostoma* form an important element in the late early Eocene biota on Seymour Island (Hara, 2001). *Aspidostoma* has been also recorded from the younger Cape Melville Formation (lower Miocene) of King George Island, South Shetland Islands (Hara andCrame, 2004). The occurrence of *Aspidostoma,* represented by two new species which predates the Antarctic ones, were recorded from the latest Paleocene to earliest Eocene of the Chatham Island of the New Zealand (Gordon and Taylor, 1999).

The early Cenozoic collection from South America, is made by Argentinian geologist C. Ameghino, who in the early of 19th Century collected in Patagonia. This material was studied and described by Canu in 1908-1911, and more than half of specimens are presently stored at the Museo Argentino Ciencias Naturales "Bernardino Rivadavia" in Buenos Aires. Recent investigations of Canu's collection from the earliest fossil record of this genus of the Southern Hemisphere derived from the shallow–water Roca Formation (lower Danian) of Patagonia (South America). *Aspidostoma* is also well-documented in the younger (lower and upper Miocene) strata of this part of South America. Patagonia should therefore be considered as an important place for the origin and radiation of this genus. According to Moyano (1983), the origin and evolution of the Recent Antarctic and the Magellanic southern American faunas should be traced back to the Paleogene and Neogene Patagonian bryozoans (Hayward, 1995). In this context, the South American bryozoan faunas should be reconsidered as very important in evolutionary studies of southern hemisphere bryozoans.

The geologic history of the genus *Aspidostoma* is essential in addressing the origin of the southern hemisphere faunas both from the Magellanic and Antarctic provinces. It is believed that the origin of the present day Antarctic and the Magellanic bryozoan faunas may lie far back as the Early Cretaceous (approximately 130 Ma), the probable time for the origin of the Weddellian Province (Crame, 1999).

Aspidostoma in the fossil record

The microporoideans, represented by the family Aspidostomatidae and the austral genus *Aspidostoma*, are well-represented in the Cenozoic fossil record of the Southern Hemisphere.

The zoarial diversity of *Aspidostoma* is defined by two different colony growth-forms. These vary between the erect, branching bilamellar zoarium, forming irregular sheet-like plates and lobes; much rarer cylindrical form, as well as those exhibiting the extensive, encrusting, unilamellar bodies. *Aspidostoma* build rather heavily calcified colonies with large autozooids, possessing a granular cryptocyst, small opesia, presence of the interzooidal avicularia and usually a

spectacular, globular ovicell. A very important feature of *Aspidostoma* is the plasticity of the colonial growth pattern, regarded as being related directly to its paleoenvironmental setting.

A rich occurrence of *Aspidostoma* has been documented from late early Eocene clastic sediments of the La Meseta Formation on Seymour Island, Antarctic Peninsula. Here, many bryozoan taxa have proven to be of considerable evolutionary interest, and include the oldest stratigraphical records of many genera (Hara, 2001, 2002). This fauna displays a spectacular diversification of cheilostomes and cyclostomes, including higher taxonomic levels (18 families and 24 genera), a number of new species Hara (2001, 2002), and is of value in deciphering austral biogeographical connections. Most significant in the taxonomic composition of the bryofauna studied, are cyclostomes belonging to the suborder Cerioporina, reminiscent of the Cretaceous in the Northern Hemisphere, and cheilostomes, represented by the families Cellariidae, Lepraliellidae, Smittinidae, Celleporidae, and Philodoporoidae, which originated in and started to radiate during the Eocene. *Aspidostoma* and other bryozoan genera such as *Neofungella*, *Borgella, Macropora* and *Cellarinella* never moved toward the equator, and only occur south of the Antarctic Convergence. The La Meseta bryofauna is highly endemic, within the paleoaustral province, and exhibits biogeographical links and a marked faunal affinity with Tertiary bryozoans from southern South America, New Zealand and Australia.

As with the Seymour Island bryofauna, the latest Paleocene or earliest Eocene Chatham Island Bryozoa contain new species of *Aspidostoma* and also include a number of genera reminiscent of the Cretaceous of the Northern Hemisphere and families common in the Neogene and Recent Southern Hemisphere bryofauna (Gordon and Taylor, 1999).

Fragmentary preserved *Aspidostoma* and *Cellaria* Hara (1994; Pirrie et al.,1997) also highlight an affinity between the Miocene bryozoan assemblage of the Cape Melville Formation on King George Island and the Seymour Island (Hara and Crame, 2004).

The spectacular abundance of bryozoans among which *Aspidostoma* is well-represented is also evident in Oligocene-Miocene strata of the South America, New Zealand and Australia region (MacGillivray,1895; Canu 1904, 1908, 1911; and Brown, 1952, 1958).

The occurrence of Recent *Aspidostoma* with one long-lived species of *Aspidostoma giganteum* (Busk) extends back to the early Neogene or may be even earlier, and nowdays is geographically distributed along the southern Patagonian Shelf, Falkland Islands as far as the South Shetland Islands. A few other minor Recent occurrences of *Aspidostoma* species are known from western South Africa and the western South Island of New Zealand.

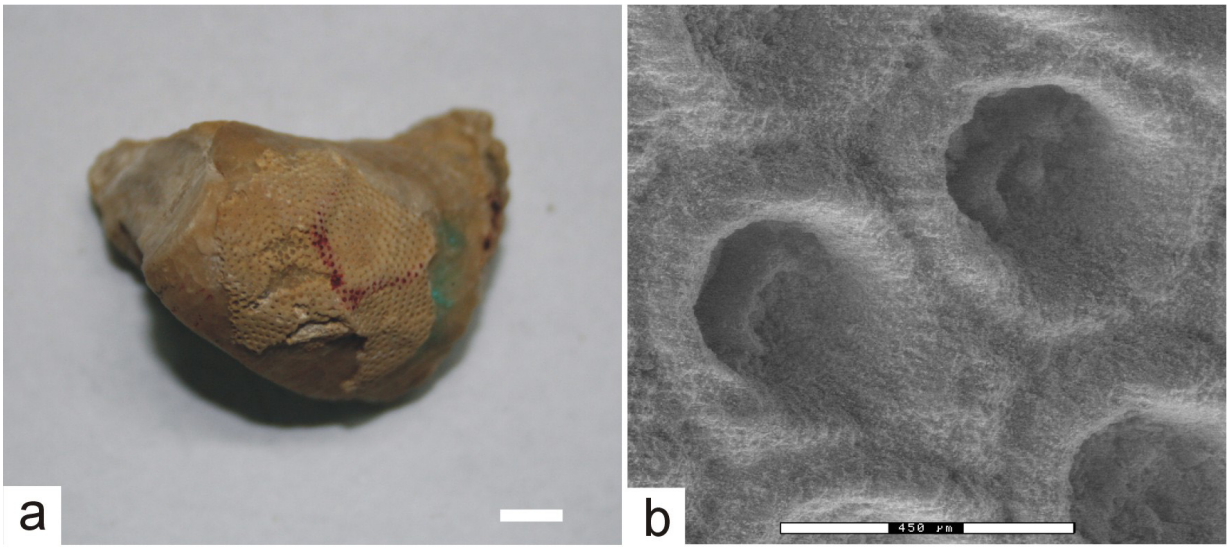

Figure 1. a. general view of the *Aspidostoma onychocelliferum* (Canu, 1911), MACN-Pi no. 1862. Scale bar is 0.4 cm. b. SEM image of *Aspidostoma onychocelliferum* (Canu, 1911), showing the zooecia, MACN Pi no. 1862. Scale bar is 450 µm, a,b. Roca Formation, Paleocene (Danian), Argentina.

Significance of the Magellanic South America bryozoan fauna

Knowledge of the Tertiary fossil bryozoans from southern South America is scarce. Moyano (1983) and Hayward (1995) emphasized that the origins and evolutionary history of the Bryozoa of both Antarctica and Magellanic South America could not be understood without reference to the still poorly known but very extensive Tertiary fossil faunas of Patagonia. The paucity of Paleocene bryozoans globally, in comparison with their spectacular diversification in the early Eocene is of considerable importance in evolutionary studies.

Studies by Hastings (1943) on Recent material noted the faunal similarities between the deep outer Patagonian Shelf and the Antarctic Peninsula; however, the distribution pattern of 195 species from Chile, including the Juan Fernandez Islands, highlighted the faunal dissimilarity between the Magellanic province and Antarctica (Moyano, 1982), and emphasized the sharp discontinuity between the bryozoan faunas of the Patagonian Shelf and the Scotia Arc (Hayward, 1995).

Study of the Canu's collection

Preliminary taxonomic studies of the Canu collection of more than 110 bryozoan specimens of the early Paleocene (Danian) and lower Miocene of southern South America (curated at the Museo Argentino Ciencias Naturales "Bernardino Rivadavia"), have revealed that cyclostome and cheilostome bryozoans have taxonomical counterparts among the late early Eocene faunas of Seymour Island. SEM-based morphological examination of the Caun bryozoan material, which includes *Aspidostoma onychocelliferum* described by Canu in 1911 from the early Paleocene of the shallow-water Roca Formation, shows that *A. onychocelliferum* of South America is closely related to *Aspidostoma* species described from the La Meseta Formation (Seymour Island). However, further detailed taxonomical studies are required, using better preserved and more extensive bryozoan material.

The other faunistic component of the early Paleocene bryozoan genera such as *Figularia, Micropora, Exocella* and *Celleporaria* should be mentioned as very important for the further taxonomical and biogeographical studies. Cheilostomes such as Cribrilinidae Hincks, Microporidae Gray and Romancheinidae Jullien, attain their high species diversity in the Late Cretaceous, and they are well-represented in the Neogene and Recent of the southern hemisphere bryofaunas.

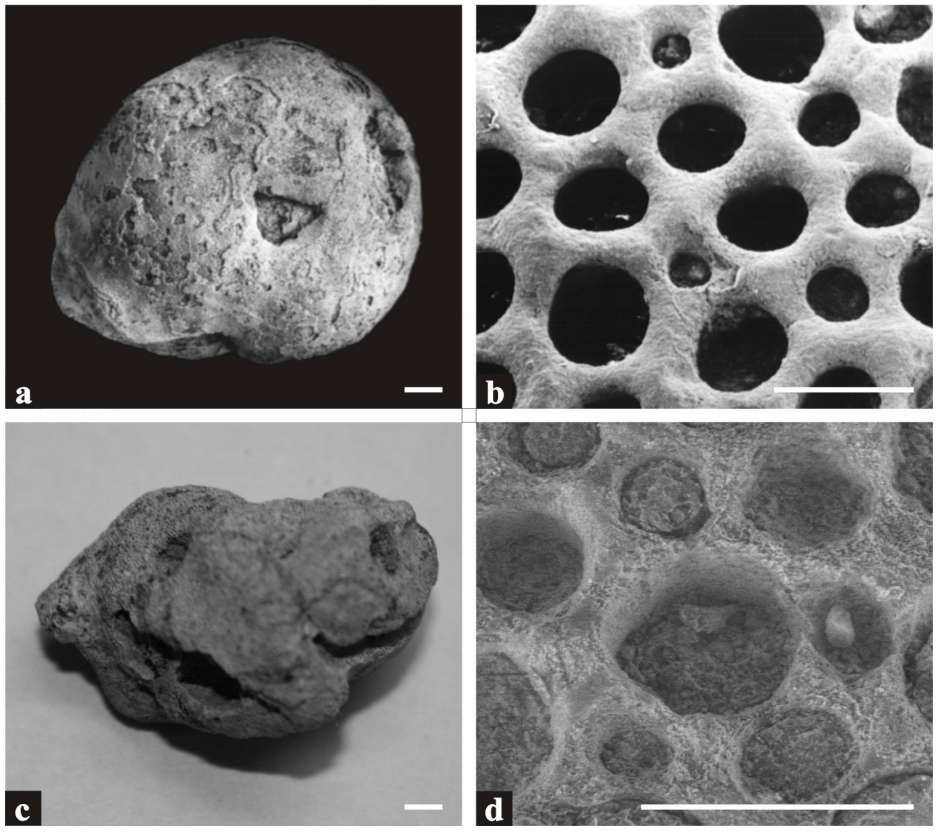

Figure 2. a. *Ceriopora hemispherica* (Hara, 2001) complete hemispherical colony, upper view and ZPAL Br.VIII/108. Scale bar is 0.5 cm; b. SEM image of the autozooecial apertures and ZPAL Br.VIII/108. Scale bar is 0.25 mm; c. *Reptomulticava australis* (Canu, 1908), upper view and MACN-Pi no. 1944. Scale bar is 0.5 cm; d. *Reptomulticava australis* (Canu, 1908), SEM image of the autozooecial apertures and MACN-Pi no. 1944. Scale bar is 250 µm. a, b. ZPAL 1, Telm1, La Meseta Formation (Eocene), Seymour Island, Antarctic Peninsula, c, d. lower Miocene, Patagonia, Argentina.

The Canu collection (Canu, 1908) from the lower Miocene of Patagonia has important taxonomical value. The collection includes cyclostome bryozoan genus described by Canu as *Reptomulticava australis* (Canu, 1908), characterized by massive, globular-shaped colonies, of the same external morphology as *Ceriopora* genus, previously described from latest Paleocene to earliest Eocene of Chathem Island, New Zealand, as well as from the late early Eocene of Seymour Island (La Meseta Formation), Antarctic Peninsula. The reticulate colonies described for the first time from Seymour Island as *Reticrescis* (Hara, 2001) are also present among the Canu's collection of 1908 under the name of *Reticulipora patagonica* (Ortmann, 1900). The detailed paleontological studies of the type material of *Reticulipora dianthus* (Blainville) allowed to include the reticuliporiform colony to a new genus (Hara, 2001). Other bryozoans such as lepraliellids represented by the genus *Celleporaria,* which documented the oldest stratigraphical occurrence in the late early Eocene of the La Meseta Formation (Seymour Island), occurs also in the lower Miocene of Patagonia and is described under the name of *Heteropora crassa* (Canu, 1908).

Biogeography

The studies of the early Paleocene and the lower Miocene bryozoan fauna of South America emphasize the close biogeographical links existing between southern South America (Patagonia), Antarctic Peninsula, New Zealand and Australia, which were associated during the Tertiary with the zoogeographical Weddellian Province (Zinsmeister, 1982; Case, 1989). Undoubtedly, the detailed taxonomical studies of the early Cenozoic bryozoans of the Magellanic and Antarctic provinces suggest their closest connections as was shown by the cyclostome and cheilostome bryozan faunas (Moyano, 1996).

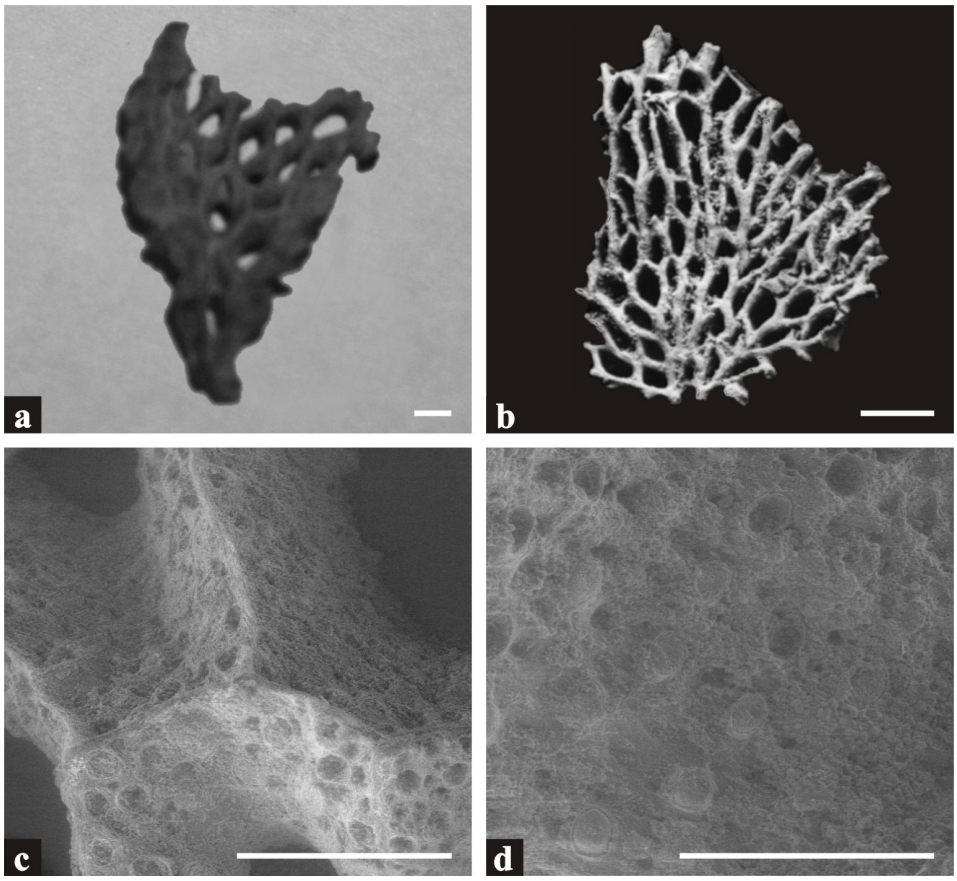

Figure 3. a. *Reticulipora patagonica* (Ortmann), a. Fragment of the reticulate colony, dorsal view and MACN-Pi no. 1955. Scale bar is 1.5 cm; b. *Reticrescis plicatus* (Hara, 2001), fragment of the reliculate colony, dorsal view, ZPAL Br.VIII/A12, La Meseta Formation (Eocene), Seymour Island. Scale bar is 1.5 cm; c. SEM image of the frontal side of a bilamellar branch of *Reticulipora patagonica* (Ortmann) showing budding laminae surrounded by zooecia, MACN-Pi no. 1955. Scale bar is 500 μm; d. SEM image of the external surface of the free-wall of *Reticulipora patagonica* (Ortmann) showing the tubular zooecia, prominent peristomes encircled by the adjacent kenozooecia, MACN-Pi no. 1955, Scale bar is 450 μm. a, c, d, lower Miocene, Patagonia, Argentina.

The preliminary taxonomic analyses of the early Tertiary bryozoan material of southern South America provides the possibility for the faunistic comparision with the early Eocene Antarctic, La Meseta bryozoan fauna, as well as with the Paleocene-Eocene New Zealand bryozoans. These data help up decipher the origins of the Southern Hemisphere fauna.

The occurrence of several genera, such as cyclostome *Ceriopora*, *Reticrescis* and chilostome *Aspidostoma, Celleporaria* and *Osthimosia* which are found in the Eocene of Antarctica, and Paleocene-Miocene of South America, indicates close biogeographical links between South America during the early Paleocene up to the lower Miocene.

The general migration routes of many bryozoan taxa were directed northwards from the Antarctic Peninsula to New Zealand and Australia but also along the western coast of South America throughout the region of Central America to the North Atlantic (Hara, 2001). The majority of temperate-warm genera present in the La Meseta assemblage may have moved toward the equator. This included *Hornera, Cellaria, Reptadeonella, Escharoides*, *Melicerita, Rhynchozoon, Osthimosia, Reteporella,* as well as cosmopolitan genera such as *Crisia*, *Celleporaria, Smittina* and *Smittoidea* (Hara, 2001).

Biogeographical comparision of the southern South America bryozoan fauna of Danian age is interesting because fauna studied by Canu a hundred years ago contain important information. Some representative fauna may have their earliest fossil records in the shallow-water Roca Formation, which predate the New Zealand and the Antarctic bryozoan faunas range between the latest Paleocene and the early Eocene.

However, the evolution and origin of most Antarctic taxa remain unclear, it is necessary for future biogeographical studies to refer the bryozoan material of the early Paleocene and Miocene from South America to the other described bryofaunas from the Southern Hemisphere, to reconstruct the possible migration routes, during the Tertiary. In this context, the evolution of the whole early Cenozoic bryozoans, should be referred to the earlier known, probably Cretaceous bryofauna from Antarctica.

Summary

The bryozoan fauna from the early Cenozoic of South America shows their importance in the reconstruction of the Tertiary ecosystem, and the paleobiogeography of the Southern Hemisphere.

The austral genus *Aspidostoma* is a good example for the reconstruction of the Cenozoic evolutionary history of the bryozoan fauna within the Southern Hemisphere. The genus *Aspidostoma* is also essential in addressing questions concerning the origin of the southern hemisphere faunas both from Magellanic and the Antarctic provinces.

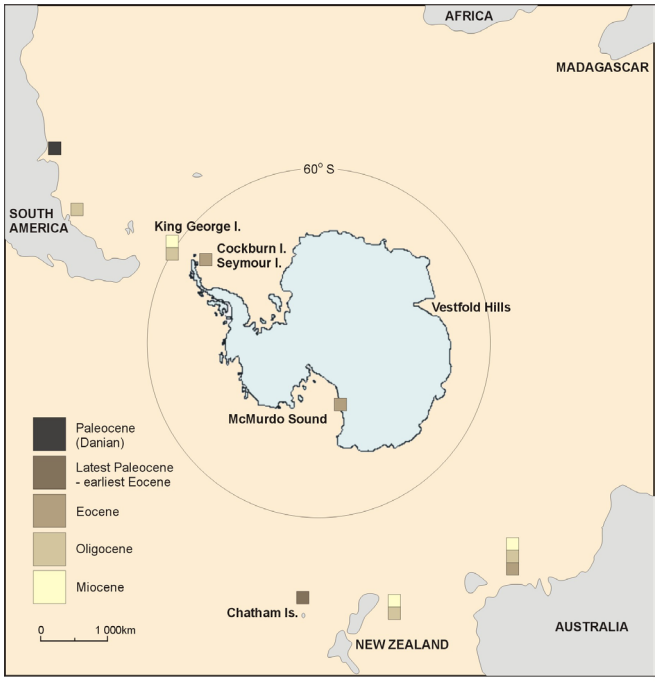

Figure 4. Distribution of the Paleocene-Holocene bryozoan biota in the Antarctic and adjacent areas.

The origin of the present day benthic marine faunas both from the Magellan and Antarctic provinces may lie as far back as the Early Cretaceous – approx. 130 Ma (Crame, 1999), therefore further questions concerning the evolution of the Southern Hemisphere bryozoan fauna should refer to the Antarctic fauna, possibly of the Cretaceous age. This is consistent with the overall evolutionary trend of this group of fossils, which show a decline in diversity of cyclostomes and the origin of many cheilostomes in the Late Cretaceous to early Paleogene (cf. Lidgard et al., 1993; Taylor, 1996; Sepkoski et al., 2000). The biogeographical relationship of the bryozoan fauna in the Southern Hemisphere should be considered and referred to the younger (Oligocene-Pliocene), rich Antarctic bryozoan assemblages, as well as to the Cretaceous or Paleogene bryozoan fauna. The widespread diversity pattern of the Antarctic faunas, is similar to the present day data, which evidently was established by the end of the Paleogene (Bottjer and Jablonski,1988).

The similarity between the La Meseta bryozoans and those living in New Zealand, South America, Africa or Australia may suggest that the Recent bryozoan fauna may be of considerable antiquity and that evolutionary processes at high latitudes are every bit as complex as those elsewhere (Clarke and Crame, 1989). The Southern Ocean bryozoan fauna seems to be the product of a long period of evolution in situ, perhaps expanding back to the Late Cretaceous.

It is noteworthy that the great diversity of new cheilostome bryozoans which occur on Seymour Island is connected with a major Paleocene-Eocene turnover, followed by a rapid increase in generic richness. Eocene bryozoans of the La Meseta Formation, Seymour Island, Antarctic Peninsula are among of the most prolific known from the Tertiary of the Southern Hemisphere, which prove significant in understanding their origin and biogeographic links. Generally, the La Meseta bryofauna is highly endemic, but it also includes bryozoan genera which accentuate the circum-temperate southern distribution, and show the strong biostratigraphical links with the southern South America and a New Zealand-Australian realm.

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