Redescription and palaeoecological significance of the bryozoan *Hippoporidra patagonica* (Pallaroni, 1920) in the San Julián Formation (late Oligocene) of Santa Cruz province, Argentina

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Hippoporidra is a cheilostome bryozoan that predominantly encrusts gastropod shells inhabited by hermit crabs. The genus has a Pan-Atlantic distribution and its fossil record ranges from the Eocene to Holocene. *Cellepora patagonica* Pallaroni is here transferred to *Hippoporidra* and its autozooids and avicularia are described for the first time based on scanning electron microscopy. *Hippoporidra patagonica* can be distinguished from the remaining species of the genus by the peculiar shape of its interzooidal avicularia and the morphology of its orifice, which is semicircular, with a straight proximal border. In addition, many specimens have adventitious avicularia located on a suboral umbo. The record of *Hippoporidra patagonica* (Pallaroni) in the Gran Bajo Member of the San Julián Formation (late Oligocene) in Patagonia confirms the presence of this genus at the southern tip of South America and indicates a Pan-Atlantic distribution during the Cenozoic.

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THE INVERTEBRATES found in Cenozoic deposits of southern South America are valuable tools for reconstructing the palaeogeographic and palaeoenvironmental evolution of this region. Cenozoic faunas have been known from the region since the work of d'Orbigny (1842) and Sowerby (1846), who described many of the molluscs. Other invertebrates have received relatively less attention, although some, such as the bryozoans, are conspicuous and highly diverse. Following those pioneering contributions, large collections of Patagonian fossil invertebrates were assembled by others (such as Carlos Ameghino, John Hatcher, Gaetano Rovereto), who sent the specimens to various foreign researchers for formal description and illustration. Ortmann (1900, 1902), Canu (1904, 1908, 1911), Pallaroni (1920) and Conti (1949) published early descriptions of Cenozic bryozoan assemblages from Patagonia. Later, Frenguelli (1920, 1927) recorded the presence of several species in Entre Ríos and Chubut. Subsequently, Leanza (1956) analyzed ecological and biological aspects of the relationship between a fossil bryozoan and a hermit crab in Patagonian Cenozoic deposits, and Brood (1981) described new and little-known species from the Miocene of Chilean Patagonia.

As with other metazoan taxa (Williams & McDermott 2004), several bryozoan species are associated with pagurid crabs inhabiting gastropods shells (Morris *et al*. 1989, Taylor *et al*. 1989, Taylor 1994, Kuklinski *et al*. 2008). These crabs colonize empty shells lying dispersed on the sea bottom and use them as temporary shelter. Upon lying on the bottom, the shells become available for the settlement of bryozoan larvae, which later develop an encrusting colony. The bryozoan may completely cover the gastropod shell inhabited by the hermit crab (Pallaroni 1920, Roger & Buge 1948, Leanza 1956, Cook 1964, Taylor & Cook 1981, McKinney & Jackson 1989, Walker 1992, Taylor & Schindler 2004). The association between these invertebrates has been recorded in fossil assemblages as old as the Early Jurassic (see Walker 1992, Taylor 1994). Pagurized shells encrusted by bryozoans preserved in the lower beds of the San Julián Formation

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(late Oligocene) in Santa Cruz Province are abundant enough that a representative number of specimens can be analyzed. The relationship between bryozoans and pagurids takes place when the bryozoan begins to bud an encrusting colony on a gastropod shell. The gastropod host may belong to various taxa providing a suitable benthic island (Carter 1972, Hoffmann & Krobicki 1989) substrate of biogenic origin for larval settlement. *Hippoporidra* Canu & Bassler, 1927 is an Eocene–Holocene cheilostome bryozoan genus predominantly encrusting gastropod shells inhabited by hermit crabs (Taylor 1994, Taylor & Schindler 2004). This paper aims to record the presence of *Hippoporidra* in the Gran Bajo Member of the San Julián Formation and to describe the morphology of its autozooids and polymorphs based on scanning electron microscopy for the first time. The faunal context of *Hippoporidra* and its palaeobiogeographic distribution in the Southern Hemisphere are also discussed.

Geological setting

The specimens were recorded at the locality known as 'Conito Colmena' in Santa Cruz Province, Argentina (Fig. 1A). Erdmann *et al*. (2008) recorded exposures of the Gran Bajo Member of the San Julián Formation (Bertels 1970, 1979) at this site. The Gran Bajo Member is restricted to exposures at the base of the cliffs surrounding the depression known as Gran Bajo de San Julián and a few scattered localities along the coast in the vicinity of Puerto San Julián. The San Julián Formation includes a maximum of 80 m of siliciclastic sediments represented by yellow and brownish sandstones, greenish-grey limestones, shell beds and thin conglomerates (Erdmann *et al*. 2008; Fig. 1B). It also hosts tuffaceous beds with a few coal-bearing layers (Panza *et al*. 1995). The depositional environment was a coastal plain to a sandy shallow platform (Náñez *et al*. 2009).

The San Julián Formation has been variously attributed an early Eocene to early Miocene (Panza *et al*. 1995, Parras & Casadío 2005), or late Eocene to early Oligocene age based on the microfossil fauna (Bertels 1970, 1975, 1979, Náñez 1990, Náñez *et al*. 2009, Malumián *et al*. 1998, Malumián 1999). Recently, ^{87}Sr/^{86}Sr isotopic dating yielded a late Oligocene age (Parras & Casadío 2002, Parras *et al*. 2012).

Material and methods

All material collected comes from the same locality and bed, i.e., 'Conito Colmena' (49°24′33.03″S, 67°57′56.20″W; Fig. 1A). Colonies were analyzed and photographed using a Leica MZ95 binocular microscope with a Leica IC 80 HD camera and a Philips series XL model 30 SEM at the Museo Argentino de Ciencias Naturales (MACN). The megascopic material was examined under direct light with a hand lens and photographed using a Nikon D100 digital camera, and is housed in División Paleozoología Invertebrados, Museo de La Plata (MLP).

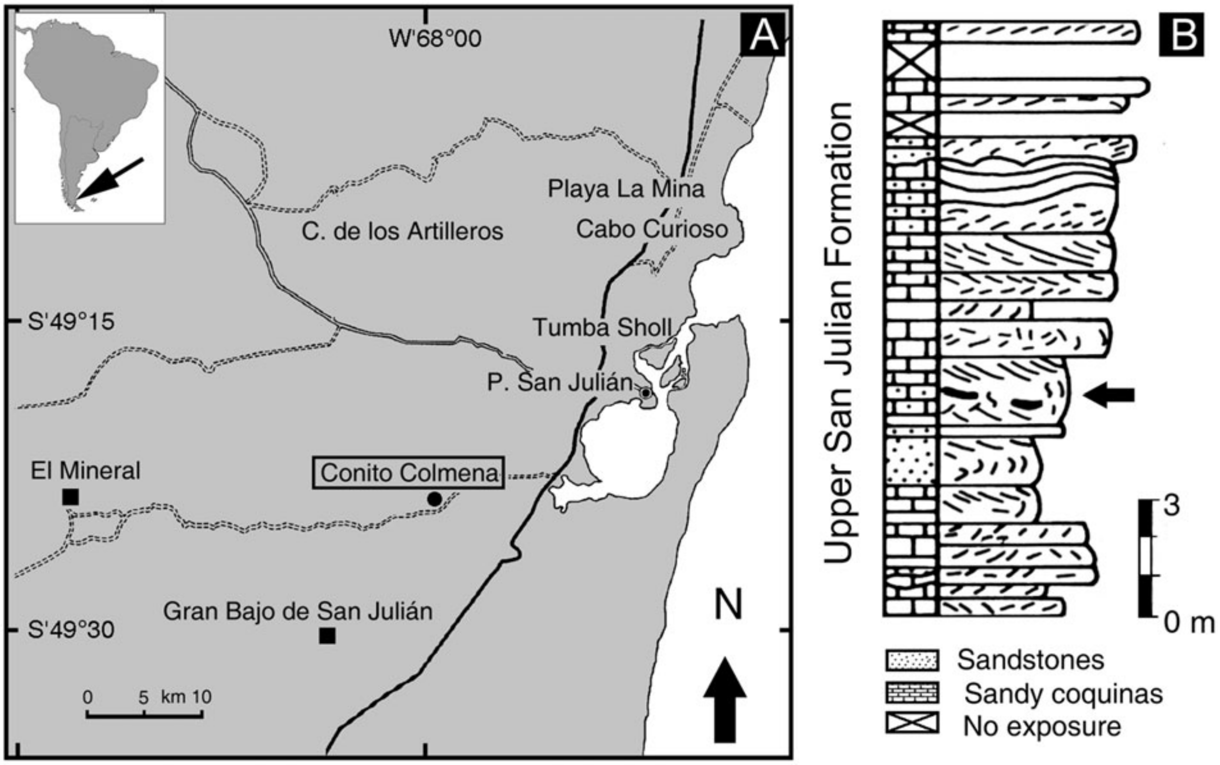

Fig. 1. **A**, Map of the study area. **B**, Measured section from the San Julián Fomation at the "Conito Colmena" quarry in Santa Cruz province; the arrow indicates the fossiliferous level.

Type specimens are housed in the collection of Dipartimento di Scienze della Terra dell'Ambiente e della Vita (DISTAV), Università degli Studi di Genova, Italy. Supplementary materials are housed in Universidad de Buenos Aires (UBA), Facultad de Ciencias Exactas y Naturales, Colección Ciencias Geológicas CPBA, Argentina.

Systematic palaeontology

Order CHEILOSTOMATA Busk, 1852
Suborder ASCOPHORA Levinsen, 1909
Infraorder LEPRALIOMORPHA Gordon, 1989
Family HIPPOPORIDRIDAE Vigneaux, 1949

Hippoporidra Canu & Bassler, 1927

Type species. *Cellepora edax* Busk, 1859 [revised by Taylor & Cook, 1981], Pliocene (Coralline Crag), Suffolk, UK.

Hippoporidra patagonica (Pallaroni, 1920) comb. nov. (Figs 2, 3)

* 1920 *Cellepora patagonica* Pallaroni, p. 22, figs 1–4.
v. 1956 *Cellepora parasitica* Mich.; Leanza, p. 146, figs 1–3.
1994 *Celleporaria patagonica* (Pallaroni); Taylor, p. 174, fig 10E.

Diagnosis. Colony robust, multilamellar, very thick, covering the whole external surface of gastropod shells. Autozooids chaotically arranged, without distinguishable boundaries, their convex frontal wall pierced by areolae only. Orifice semicircular, with straight proximal border. A pair of small condyles separating the small poster from the anter. Monticules scattered over the colony surface in a quincuncial pattern, composed of several cortical zooids with protruding frontal walls and orifices slightly smaller than those of autozooids. Peristomial avicularia small, ovate, with complete pivotal bar, close to the proximal margin of the orifice, usually on a peristomial suboral umbo. Interzooidal avicularia large, protruding, ovate, with blunt, triangular rostrum and a complete pivotal bar. Ovicells unknown.

Types. The syntypes are four specimens examined by Pallaroni (1920) (the two lower ones of fig. 1, and two sectioned specimens illustrated in fig. 2) DISTAV: N. 3079/ROV 1. Collected by Prof. Gaetano Rovereto in San Julián (locality not precisely stated) [Patagoniano

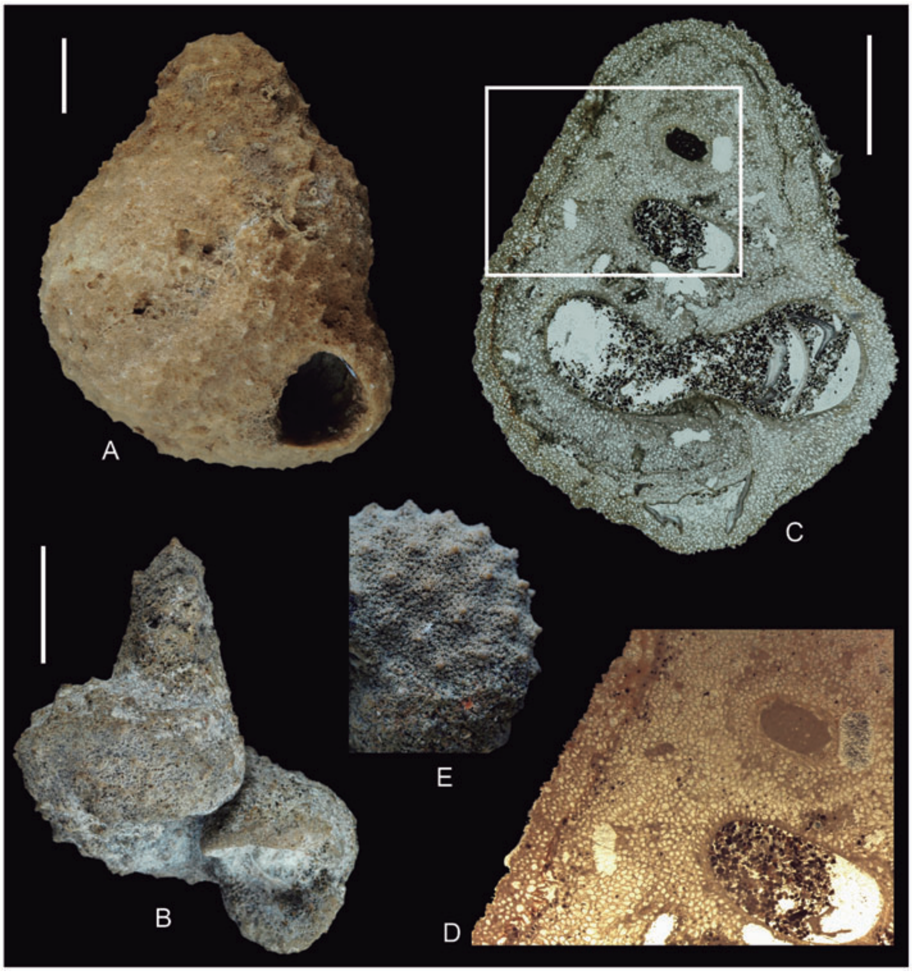

Fig. 2. Gastropod-like colonies of *Hippoporidra patagonica*. **A**, Exterior of colony [MLP34490]; **B**, another colony showing a protruding last whorl disrupting the original pattern produced by the gastropod shell [MLP33773]; **C**, longitudinal section showing successive cross-sections of the helicospiral tubular cavity constructed by the bryozoan colony [MLP33778]; **D**, detailed view of the longitudinal section of the colony (boxed area as marked in fig. 2C); **E**, monticules showing a quincuncial pattern [MLP33768]. Scale bars = 10 mm.

inf. (Eocene); *sensu* Ameghino 1906]. The lower-left specimen illustrated in Pallaroni's (1920, fig. 1) is here designated the lectotype.

Material. There are 13 new colonies registered under the numbers MLP 33768–33778, 34490, 34491. This new material consists of gastropod-shaped bryoliths of variable dimensions (Table 1). UBA, Facultad de Ciencias Exactas y Naturales, Colección Ciencias Geológicas CPBA No. 6605, three figured specimens examined by Leanza (1956, fig. 1), from Puerto San Julián [not 'San Juan' as stated by Leanza (1956, p. 146) owing to a typist's mistake], Santa Cruz.

Locality. 'Conito Colmena' Santa Cruz Province, Argentina (Fig. 1A).

Occurrence. Gran Bajo Member, San Julián Formation, late Oligocene (Parras & Casadío 2002, Parras *et al*. 2012).

Description. The encrusting and monticulated colony entirely covers the gastropod shell used as the substrate for the initial settlement of a larva. The colony shape may be irregular but usually attains a gastropod-like morphology (Fig. 2A, B). Colony dimensions are 23–59 mm in length × 20–47 mm in width (Table 1). It forms a multilamellar structure that becomes very thick internally (Fig. 2C, D). The colony continues growing beyond the shell aperture and commonly rectifies or changes orientation with respect to the shell axis. The aperture that the bryozoan leaves for the crab becomes subcircular (Fig. 2A) with a maximum diameter of 8–13 mm. The external surface of the colony develops conspicuous monticules showing a quincuncial pattern, having a centre-to-centre spacing of 2.85 mm (Fig. 3A). The cortical zooids that make up these structures are considerably modified with respect to autozooids, with a massive and compact protuberance in the centre of their frontal walls (Fig. 3B).

The autozooids are arranged chaotically and are difficult to discriminate from each other. Their frontal walls are pierced by a single row of large marginal areolae (Fig. 3C). The orifice is semicircular, with a straight or slightly concave proximal border, 0.08–0.10 mm long × 0.12–0.14 mm wide, with small, rounded condyles separating a larger anter from a smaller poster (Fig. 3D). The marginal areolae are scarce and very large; they are located around the orifice and along the borders between zooids, and are separated from each other by nodular septa. Interzooidal avicularia are larger than autozooids, randomly directed, scattered across intermonticular areas, 0.34–0.36 mm long × 0.24–0.30 mm wide, globular and protruding, with a subtriangular, blunt rostrum and a complete pivotal bar (Fig. 3E). Suboral, adventitious avicularia are small, elliptical, with a complete pivotal bar, commonly associated with a suboral umbo (Fig. 3F). Ovicells unknown.

Specimen no.	Maximum length (mm)	Maximum width (mm)
MLP 33768	33	21
MLP 33769	33	24
MLP 33770	23	20
MLP 33771	51	36
MLP 33772	51	37
MLP 33773	34	29
MLP 33774	34	28
MLP 33775	–	33
MLP 33776	46	44
MLP 33777	56	39
MLP 33778	44	35
MLP 34490	59	47
MLP 34491	58	43
CPBA 6605	44	38

Table 1. Lengths and widths (mm) of colonies of *Hippoporidra patagonica* in the collection of the Museo de La Plata and Facultad de Ciencias Exactas y Naturales, UBA.

Occurrence. Patagonia San Julián, in beds referred to the '*Patagoniano inferior*' (Eocene; *sensu* Ameghino 1906, Pallaroni 1920). The specimens were preserved in the bioclastic bed from the San Julián Formation exposed at 'Conito Colmena'. The gastropod-like colonies were found together with a rich fauna of shallow-water oyster banks (Parras & Casadío 2002, Náñez *et al*. 2009).

Remarks. The presence of *Hippoporidra* in the San Julián Formation expands the range of biotic interactions known for the late Oligocene fauna and represents the first record of the genus from South America and the southernmost record known to date. It extends the southern distributional boundary of the genus by 15° of latitude.

Hippoporidra patagonica is abundant in the San Julián Formation. The colonies cover the external surfaces of gastropods and project beyond the aperture of the shell, maintaining a residence for the hermit crab. The colony continues developing the normal shape of the gastropod shell (Taylor & Cook 1981, Walker 1992), although in some specimens the helicoid pattern may be altered.

In addition to *H. patagonica*, other extant and fossil species are assigned to *Hippoporidra*: *H. edax* (Busk, 1859), Miocene to Pliocene of W Europe and E USA, up to Holocene of the east coast of the USA and circum-Caribbean; *H. senegambiensis* (Carter, 1882), Holocene, West Africa; *H. picardi* (Gautier, 1962), Holocene, Aegean Sea and South Africa; *H. littoralis* Cook, 1964, Holocene, West Africa; *H. lusitania* Taylor & Cook, 1981, Holocene, North Sea; *H. dictyota* Ryland, 2001, Holocene, Atlantic Coast of North America; *H. portelli* Taylor & Schindler, 2004, Eocene, North America.

Hippoporidra patagonica can be distinguished from the other species in the genus by the peculiar shape of its interzooidal avicularia and the morphology of its orifice, which is semicircular with a straight proximal border, instead of cleithridiate. The adventitious avicularia are commonly located on a suboral umbo, a feature that is absent in other species of *Hippoporidra*. In addition,

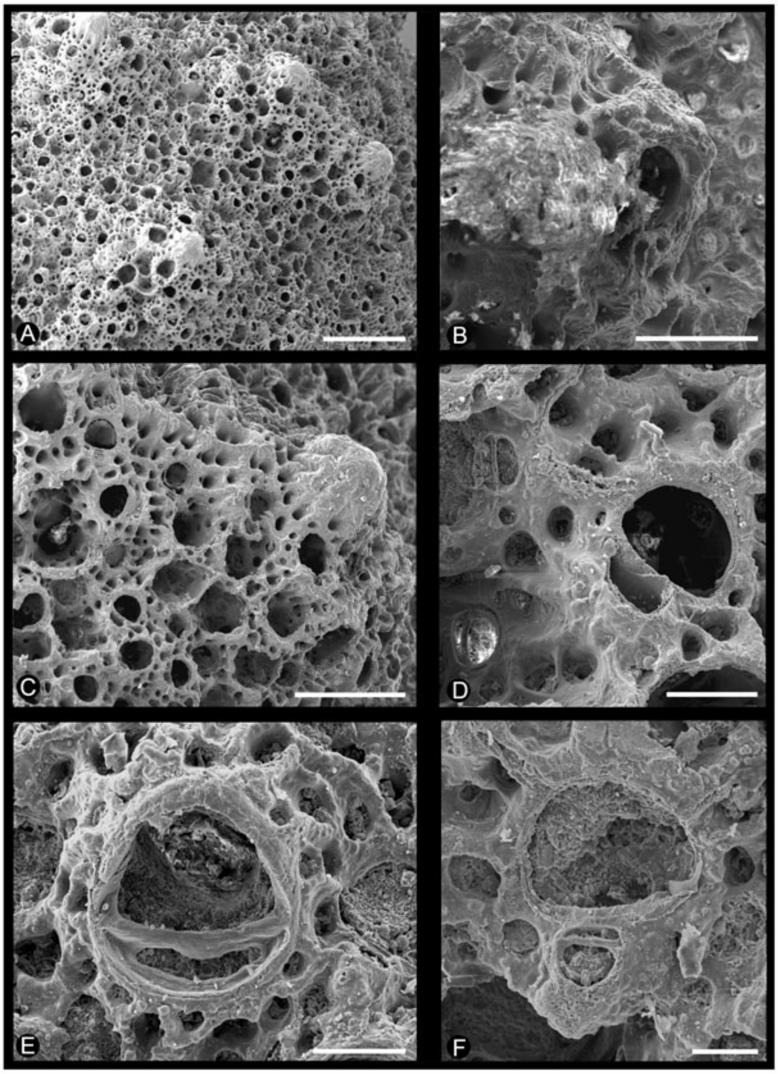

Fig. 3. Details of *Hippoporidra patagonica* colonies illustrated by SEM. **A**, Monticules (scale bar = 1000 µm); **B**, general aspect of a cortical zooid (scale bar = 250 µm) [MLP33768]; **C**, autozooids, monticule and orifices (scale bar = 500 µm); **D**, detail of orifice (scale bar = 100 µm); **E**, Interzooidal avicularium (scale bar = 100 µm); **F**, suboral adventitious avicularium (scale bar = 50 µm). [A, C, D, E, F: MLP33769]

the zoaria of *H. patagonica* do not produce the thick, bifurcating branches characteristic of other species of the genus (e.g., Taylor & Schindler 2004). No ovicells were observed by Pallaroni (1920) and none is present in the available material. Concerning the species name applied by Leanza (1956) to his Argentinean specimens, it may be recalled that French material from the Faluns de Touraine referred to '*Cellepora parasitica* Michelin' (e.g., Roger & Buge 1948) was subsequently placed in *Hippoporidra*, according to Taylor (1994, see also Taylor & Cook 1981). On the other hand, the Patagonian record by Taylor (1994, fig. 10E) is tentatively included in *H. patagonica* pending confirmation, since that specimen (BMNH D 52745) has not been examined by us, and its zooidal morphology has not been illustrated.

Discussion

Bryozoans are well represented in Paleogene and Neogene deposits of Argentina (Ortmann 1900, 1902, Canu 1904, 1908, 1911, Pallaroni 1920, Conti 1949, Muravchik *et al*. 2004). They are abundant and diverse in association with the rich molluscan fauna represented in the Cenozoic marine strata of Patagonia.

Palaeoecological and palaeobiogeographical significance

Leanza (1956) described the morphology of gastropod-like specimens heavily encrusted by bryozoans available to him. Endorsing Pallaroni's ideas, he interpreted the process generating the structures and also analyzed palaeoecological aspects of a colony he regarded as belonging to *Cellepora*, which was found surrounding a pagurized shell of *Turritella ambulacrum* Sowerby, 1846 (see Leanza 1956, fig. 3). That author considered the relationship to be a case of mutualism in which the bryozoan begins to bud a colony on the gastropod shell and later builds a conical tube in which the hermit crab lives. As the crab grows, instead of abandoning the shell to find a new one, as is usual in non-bryozoan-colonized shells (with the risks entailed in this process), it induces the colony to keep growing along the widening rim of the tube in which it lives, while thickening the wall. This explains why the gastropod-like tubular structure formed by the colony remains open, i.e., the living hermit crab avoids occlusion of the aperture by the continually growing colony, and at the same time benefits from such a relationship (Taylor 1994, Williams & McDermott 2004, Klicpera *et al*. 2013). Structures formed under this peculiar growth relationship differ markedly from those bryoliths generated by circumrotatory encrustation of empty non-pagurized gastropod shells—or other bioclastic nuclei—as revealed in longitudinally sectioned specimens (cf. Kidwell & Gyllenhaal 1998).

Ryland (2001) showed that the monticules of the living colonies of *Hippoporidra dictyota* are composed of male zooids bearing reduced, non-feeding lophophores, which are involved in the formation of excurrent outlets (Banta *et al*. 1974).

The record of *Hippoporidra patagonica* in the Gran Bajo Member of the San Julián Formation in Patagonia confirms the presence of this genus at the southern tip of South America and supports a Pan-Atlantic distribution for the genus during the Cenozoic (Taylor & Cook 1981). This new, southernmost, record shows that the genus was more widespread during the Oligocene than at present, since *Hippoporidra* seems to be absent from the cold-temperate seas of the southwestern Atlantic (see López Gappa 2000). Variations in the seawater conditions along the Atlantic coast of southern Patagonia may be better understood by analyzing the tectonic and oceanographic history of southern South America and Antarctica. After the Drake Passage opened to deep water circulation during the Eocene–Oligocene transition (*ca* 31–32 Ma; Lawver & Gahagan 2003, and references therein), thus allowing the development of the cold Malvinas/Falkland Current, a progressive northwards shift of thermally sensitive brachiopods (from Antarctica to Uruguay and Brazil) took place (Manceñido & Griffin 1988). Moreover, according to a biogeographical analysis of the Miocene molluscan faunas of Argentina and Uruguay by Martínez & del Río (2002), several dominant Caribbean bivalves and gastropods have likewise moved northwards, or become extinct locally. Analyses of the bryozoan faunas from these regions could be usefully employed to test the consistency of these biogeographic trends.

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