

BRYOZOANS ASSOCIATED WITH GASTROPOD SHELLS IN THE EARLY MIOCENE OF PATAGONIA (ARGENTINA)

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New morphological evidence supports that the internal carotid passed directly into the endocranium via the piriform fenestra, rather than coursing through the middle ear.

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NEW BRYOZOANS FROM THE MIOCENE OF PATAGONIA

Two new species of cheilostomes associated with gastropod shells are described from the Monte León Formation.

BRYOZOANS ASSOCIATED WITH GASTROPOD SHELLS IN THE EARLY MIOCENE OF PATAGONIA (ARGENTINA)

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Abstract. This study describes two new species of cheilostome bryozoans associated with gastropod shells from the Monte León Formation (Burdigalian, early Miocene), Argentine Patagonia. *Burdwoodipora griffini* sp. nov. is the second known species and the first fossil representative of the genus, whose geographic distribution is so far restricted to the Magellan region in the southern Southwest Atlantic. It differs from the type species, *B. paguricola*, in lacking suboral adventitious avicularia in most autozooids. *Odontoporella miocenica* sp. nov. is morphologically very close to the type species, the Recent *O. adpressa*, from which it differs in having smaller zooids with fewer areolae and relatively wider orifices. The stratigraphic range of *Odontoporella* is here extended from the Pleistocene to the early Miocene. Its geographic distribution includes southern South America, New Zealand, and New Caledonia, suggesting an austral origin of the genus in the Paleogene of former Gondwana. The possible association of these two species with paguroid crabs is discussed.

Key words. *Burdwoodipora*. *Odontoporella*. Cheilostomata. Hermit crabs. Neogene. Monte León Formation.

Resumen. BRIOZOOS ASOCIADOS A CONCHAS DE GASTERÓPODOS EN EL MIOCENO TEMPRANO DE PATAGONIA (ARGENTINA). En este estudio se describen dos nuevas especies de briozoos queilostomados asociadas a conchas de gasterópodos de la Formación Monte León (Burdigaliano, Mioceno temprano), Patagonia argentina. *Burdwoodipora griffini* sp. nov. es la segunda especie conocida y el primer representante fósil del género, cuya distribución geográfica hasta ahora está restringida a la Región Magallánica, en el Atlántico Sudoccidental austral. Difiere de la especie tipo, *B. paguricola*, por carecer de avicularias adventicias suborales en la mayoría de los autozooides. *Odontoporella miocenica* sp. nov. es morfológicamente muy similar a la especie tipo reciente, *O. adpressa*, de la cual difiere por poseer zooides más pequeños, con menos aréolas, y orificios relativamente más anchos. El rango estratigráfico de *Odontoporella* se extiende aquí desde el Pleistoceno hasta el Mioceno temprano. Su distribución geográfica comprende América del Sur, Nueva Zelanda y Nueva Caledonia, lo que sugiere un origen austral del género en el Paleógeno de Gondwana. Se discute la probable asociación de estas dos especies con crustáceos paguroideos.

Palabras clave. *Burdwoodipora*. *Odontoporella*. Cheilostomata. Cangrejos ermitaños. Neógeno. Formación Monte León.

HERMIT CRABS usually protect themselves from predators by inhabiting empty gastropod shells (Williams & McDermott, 2004). Bryozoans are one of the most frequent invertebrates encrusting the surface of pagurized shells, sometimes even enlarging the size of the chamber occupied by the crab (Taylor, 1994). The association between bryozoans and hermit crabs may be traced back to the Middle Jurassic (Buge & Fischer, 1970), but they became common in the Neogene (Taylor, 1994). A hermit crab with a bryozoan symbiont was found in the late Campanian (Cretaceous) of Antarctica (Aguirre-Urreta & Olivero, 1992).

Obligate relationships between bryozoans and paguroid crabs are known in many species of *Hippoporidra* (Cook, 1964, 1985). *Hippoporidra patagonica*, from the late Oligocene of San Julián Formation, built multilayered colonies around gastropod shells and was so far the only known example of a bryozoan

associated with pagurized gastropods in the Cenozoic of Patagonia (Leanza, 1956; Taylor, 1994; Pérez *et al.*, 2015a).

In the southern Southwest Atlantic, the Magellanic cheilostome *Burdwoodipora paguricola* is an obligate symbiont of *Pagurus comptus*, with its colonies enlarging the last whorl of gastropod shells to accommodate the crab (López-Gappa *et al.*, 2018; López-Gappa & Zelaya, 2021).

Facultative (*i.e.*, non-obligate) associations, in which the bryozoan may also encrust other living or inorganic substrates, are also frequent. Taylor *et al.* (1989) reported that just four out of 13 bryozoan species encrusting pagurized shells in New Zealand are obligate symbionts. Two species of the hippoporidrid genus *Odontoporella* mainly occur in association with gastropod shells but may also be found on other living hosts or on inorganic substrates (López Gappa & Lichtschein, 1990; Carter & Gordon, 2007).

As the fossil record is non-existent for *Burdwoodipora* and slight for *Odontoporella*, this study aims to describe two early Miocene representatives of these genera collected in the Monte León Formation, Santa Cruz Province, Argentina, and to discuss their likely association with paguroid crabs.

GEOLOGICAL SETTING

The Neogene marine sedimentary record is very extended in the Atlantic margin of Argentine Patagonia. In this time segment, the Monte León Formation is one of the geological units with the richest macroinvertebrate fossil remains. It is exposed in the Monte León National Park, Santa Cruz Province (e.g., Parras *et al.*, 2012; Pérez *et al.*, 2015b), where the type location of the unit was defined. The analyzed material was collected at a stratigraphic section called Cabeza de León, which has a bioclastic level with abundant bryozoans at ~27 m from the base (Pérez *et al.*, 2015b). The Monte León Formation originated from the accumulation of siliciclastic sediments with interspersed bioclastic material, deposited in a shallow marine environment with low energy and an abundant supply of volcanic sediments (Malumián, 1999). Bryozoans are among the most abundant, diverse, and best-preserved phyla among the rich association of macroinvertebrates occurring in this stratigraphic unit. Isotopic analysis of Sr⁸⁷/Sr⁸⁶ carried out on fossil shells yielded an absolute age of 17.91 Ma in the upper part of the sequence (early Burdigalian; Parras *et al.*,

2012), from which the fossil bryozoan material was obtained.

Geographic and stratigraphic occurrence

The two new species were found at Cabeza de León (50° 21.423' S; 68° 53.098' W; Fig. 1), within the Monte León National Park (Santa Cruz Province). The material comes from the Punta Entrada Member (upper level of the stratigraphic column), Monte León Formation (early Miocene).

Institutional abbreviations. MACN, Museo Argentino de Ciencias Naturales, Ciudad Autónoma de Buenos Aires, Argentina. MACN-In, Colección Nacional de Invertebrados at MACN. MLP, Museo de La Plata "Francisco P. Moreno", La Plata, Argentina. UNLP, Universidad Nacional de La Plata, La Plata, Argentina.

METHODS

The specimens were coated with gold/palladium and images obtained using a FEI ESEM Quanta 200 SEM at the Laboratorio de Investigaciones en Metalúrgica Física (LIMF), Facultad de Ingeniería, UNLP, and a Phillips XL-30 SEM at MACN. Part of the material was photographed with an AxioCam MRc camera mounted on a Zeiss Stemi 2000-C stereoscopic microscope using the software AxioVision SE64. Morphological measurements were taken from Scanning Electron Microscope (SEM) photos with ImageJ.

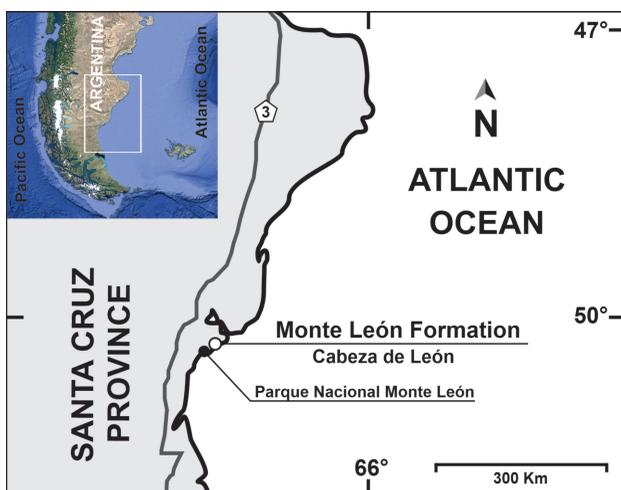


Figure 1. Map of the study area showing the type locality Cabeza de León. Inset image: modified from Google Earth© 2021, Image Landsat / Copernicus, Data SIO, NOAA, U.S. Navy, NGA, GEBCO.

SYSTEMATIC PALEONTOLOGY

Phylum BRYOZOA Ehrenberg, 1831
 Class GYMNOAEMATA Allman, 1856
 Order CHEILOSTOMATA Busk, 1852
 Family HIPPOPORIDRIDAE Vigneaux, 1949

Genus *Odontoporella* Héjjas, 1894

Type species. *Lepralia adpressa* Busk, 1854, selected by Gordon (1989).

Odontoporella miocenica sp. nov.

Figure 2.1– 2.3, Table 1

LSID urn:lsid:zoobank.org:act:BADCA180-E63C-420A-A313-FBDA3121B346

Type material. Holotype, one colony on an indeterminate gastropod shell, MLP 36479. Paratypes, two colonies on *Turritella patagonica* G.B. Sowerby, 1846, MLP 36480, Monte León Formation.

Other material examined. *Odontoporella adpressa* (Busk, 1854), MACN-In 43854, collected at station ZE10 onboard the ship *Lenga*, on December 3, 2011, 53° 11.191' S; 67° 17.918' W, 89 m (see Liuzzi *et al.*, 2018).

Derivation of name. The specific epithet of the new species refers to the Miocene, *i.e.*, the geological epoch of the stratigraphic unit from which the type material was obtained.

Diagnosis. *Odontoporella* with relatively small zooids. Keyhole-shaped orifice bearing a straight to slightly convex proximal margin. Frontal shield surrounded by about 10–14 large areolar pores. Adventitious avicularia latero-proximal to the orifice, 0–1 per zooid, directed outwards, usually absent.

Description. Colony encrusting the surface and also enlarging the last whorl of gastropod shells (Fig. 2.1), closely adnate to the substratum, unilamellar to multilamellar, multiserial. Zooids 274–368 μm long \times 211–267 μm wide. Interzooidal boundaries often hardly visible, marked by thin sutures between adjacent zooids. Frontal shield flat to slightly convex, with radial ridges separated by about 10–14 sulci; each sulcus leading to a conspicuous marginal areolar pore (Fig. 2.2). Orifice keyhole-shaped, 103–119 μm long \times 85–102 μm wide; distal margin formed by the next distal zooid, poster as wide as the anter, proximal margin straight to slightly convex; condyles well-developed, pointing proximally (Fig. 2.3). Adventitious avicularia 0–1 per zooid, usually absent, latero-proximal to the orifice, replacing one of the areolar pores, with a semi-elliptical rostrum pointing towards the orifice of a neighbouring zooid (Fig. 2.3) and a pair

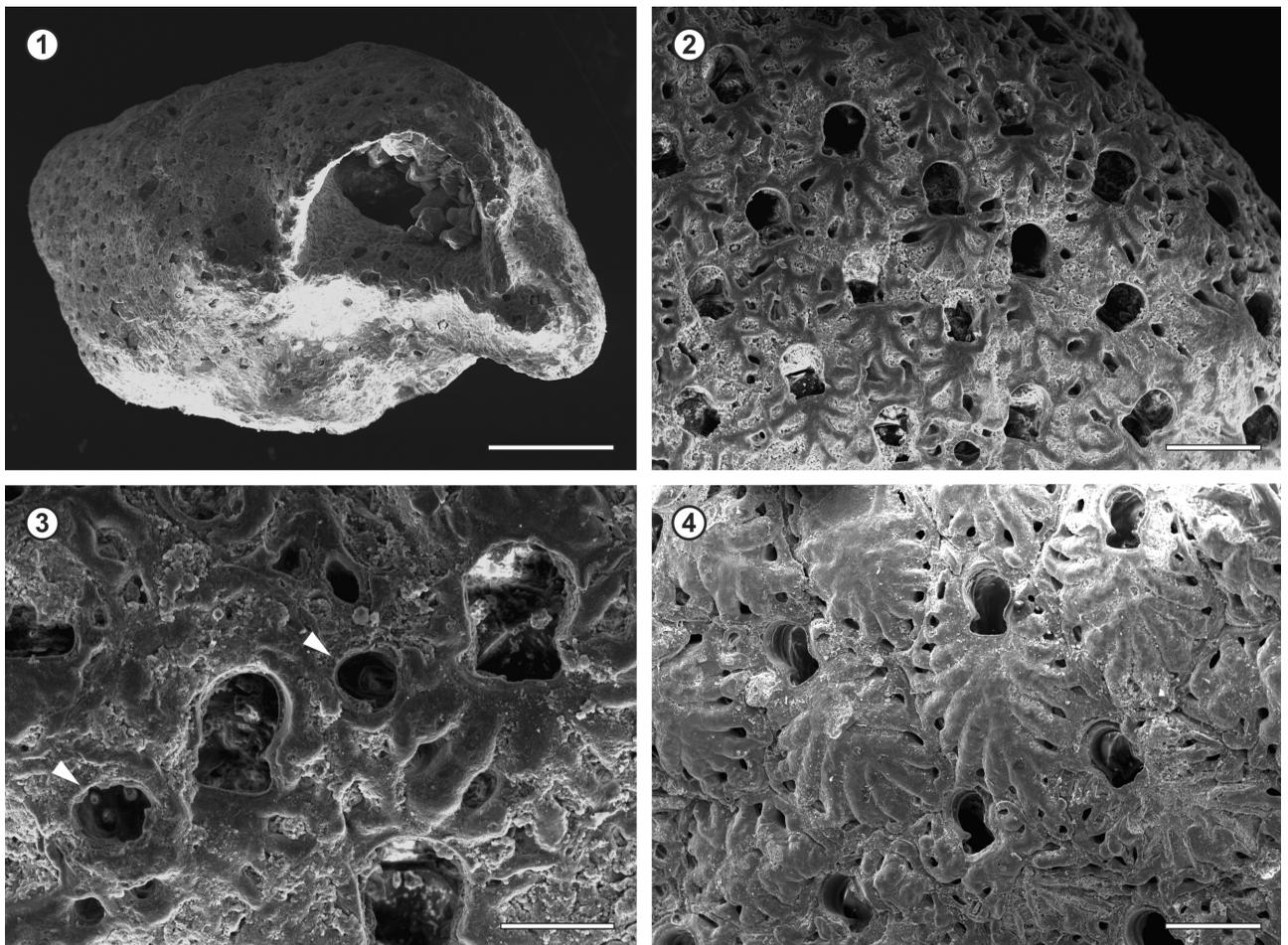


Figure 2. 1–3, *Odontoporella miocenica* sp. nov., holotype (MLP 36479); 1, general aspect of the colony on a gastropod shell; 2, several zooids; 3, detail of the adventitious avicularia (arrows). 4, *Odontoporella adpressa*, several zooids (MACN-In 43854). Scale bars equal 1 mm (1), 0.2 mm (2, 4), and 0.1 mm (3).

TABLE 1 – Measurements (μm) of *Odontoporella miocenica* sp. nov.

	Zooid length	Zooid width	Orifice length	Orifice width
N	10	10	10	10
Mean	317	234	113	94
Minimum	274	211	103	85
Maximum	368	267	119	102
Standard Deviation	27	20	5	5

N: number of measurements.

of small lateral condyles. Interzooidal communications by basal pore chambers. Ancestrula not seen.

Remarks. Four species have so far been included in *Odontoporella*, or its objective junior synonym *Hippopodinella* Barroso, 1924 (see Gordon, 1989), to date.

The Pliocene *Odontoporella venezuelana* (Weisbord, 1967) has two vibracula per zooid and seems unrelated to the remaining species included in this genus. The Pleistocene-to-Recent *Odontoporella bishopi* Carter & Gordon, 2007 clearly differs from *O. miocenica* in having an orifice with distinctly rounded poster and, consequently, concave proximal margin.

Odontoporella adpressa (Busk, 1854) (Fig. 2.4), the type species of the genus, is morphologically very close to *O. miocenica* sp. nov., but differs from the latter in having much larger zooids ($453\text{--}600 \times 351\text{--}425 \mu\text{m}$ in *O. adpressa* vs. $274\text{--}368 \times 211\text{--}267 \mu\text{m}$ in *O. miocenica* sp. nov.), a higher number of areolar pores (14–19 in *O. adpressa* vs. 10–14 in *O. miocenica* sp. nov.) and a proportionally narrower orifice. The southern Chilean taxon *Lepralia appresa* [sic] var. *vinosa* Ridley, 1881, with its narrow sinus and tuberculate frontal shield, seems completely unrelated to *O. adpressa*. Carter & Gordon (2007) also mentioned the existence of an undescribed species of *Odontoporella* in New Caledonia.

The three colonies examined here encrusted the surface of helicospiral gastropod shells. The specimen chosen as holotype was also enlarging the last whorl of the shell, a feature that has been observed in *O. bishopi* (see Carter & Gordon, 2007) but not in *O. adpressa*.

Family ?PACIFICINCOLIDAE Liu & Liu, 1999

Genus *Burdwoodipora* López-Gappa, Liuzzi & Zelaya, 2018

Type species. *Burdwoodipora paguricola* López-Gappa, Liuzzi & Zelaya, 2018, by monotypy.

Burdwoodipora griffini sp. nov.

Figure 3, Table 2

LSID urn:lsid:zoobank.org:act:3A528794-D2BB-4A20-8F5C-6AB2CB610C79

Type material. Holotype, one colony on an indeterminate gastropod shell, MLP 36481. Paratypes, several fragments from two colonies on *Turritella patagonica*, MLP 36482, Monte León Formation.

Derivation of name. The name of the new species honours the palaeontologist Miguel Griffin for his contribution to the knowledge of Argentine Cenozoic marine macroinvertebrates.

Diagnosis. Colony unilamellar, covering the surface and also enlarging the last whorl of gastropod shells. Frontal shield perforated by rounded pseudopores. Orifice cleithriate. Oral spines absent. Adventitious avicularia oval, usually latero-oral, pointing proximally, 0–2 per zooid. Some zooids with a suboral avicularium on the distal side of an umbo. Ovicell with small marginal perforations, tuberculate. A layer of tuberculate and perforate kenozooids partially covering the inner surface of the gastropod shell.

Description. The colony consists of an extremely thick unilamellar layer of autozooids encrusting the surface and enlarging the last whorl of gastropod shells. Monticules and frontal budding absent. Autozooids subhexagonal, $333\text{--}436 \times 216\text{--}313 \mu\text{m}$, arranged quincuncially, separated by thin sutures. Frontal shield convex, uniformly perforated by large rounded pseudopores (Fig. 3.1). Slightly larger marginal pores may, in fact, be areolae. Orifice cleithriate, longer than wide, reinforced by a short peristome more developed distally and laterally, horseshoe-shaped anter separated from the arrow-shaped sinus by a pair of robust pointed triangular condyles (Fig. 3.2). Oral spines absent. Adventitious avicularia usually latero-oral, 0–2 per zooid, oval, often lodged on a raised cystid, pointing proximally; cross-bar complete, without ligula (Fig. 3.2). Additional oval avicularia may occur on the proximal frontal shield. In certain

areas of the colony, some autozooids may bear a blunt suboral umbo immediately below the sinus, with an oval avicularium, pointing diagonally upwards, located on its distal

side (Fig. 3.3). Ovicell subspherical, $198 \times 204 \mu\text{m}$, with small marginal perforations and a tuberculate surface, not closed by the operculum (Fig. 3.4). Interzooidal communica-

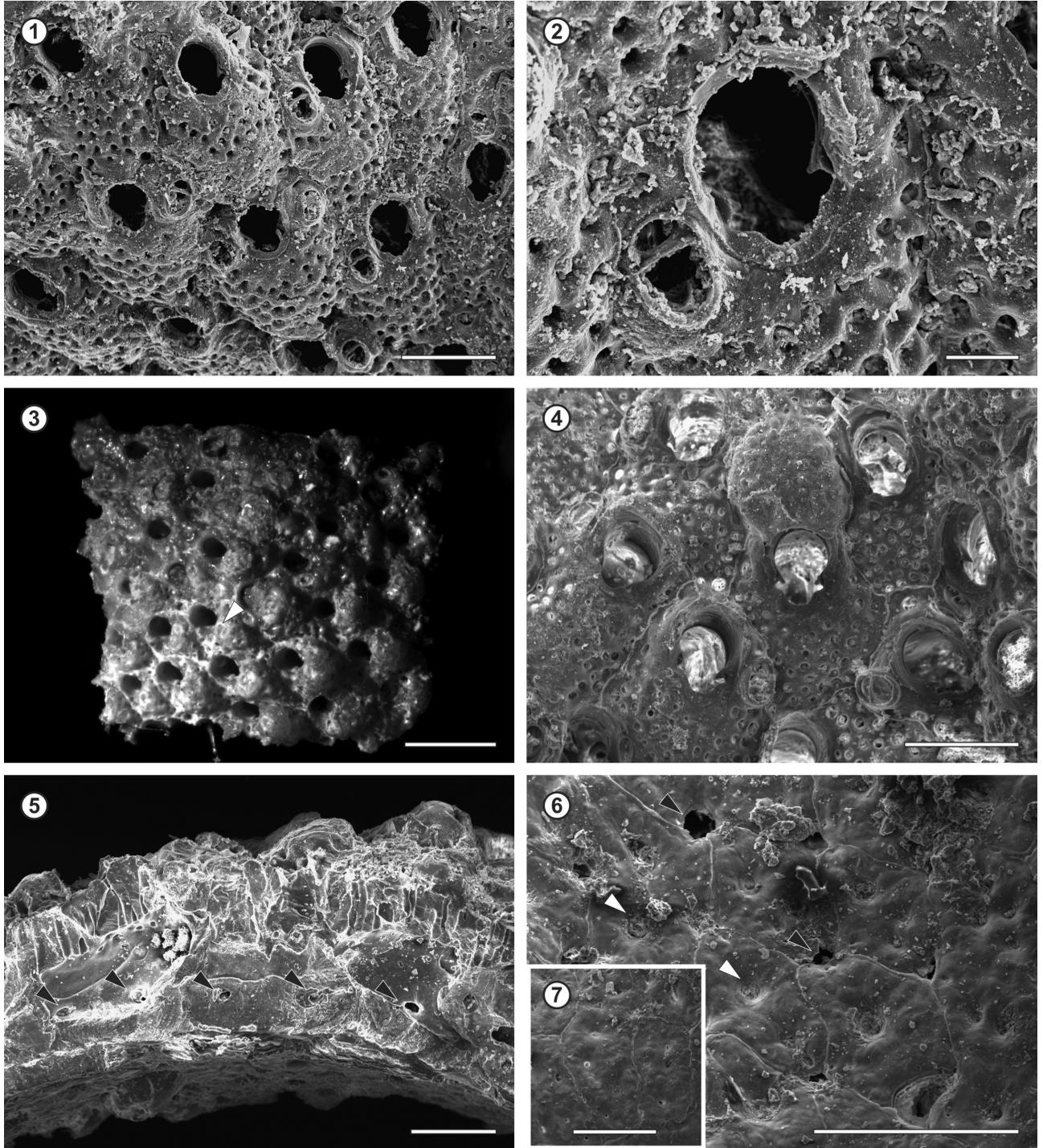


Figure 3. 1–7, *Burdwoodipora griffini* sp. nov.; 1, holotype, general aspect (MLP 36481); 2, holotype, detail of the orifice and adventitious avicularium (MLP 36481); 3, paratype, zooids with suboral umbones and avicularia (arrowed) (MLP 36482); 4, paratype, ovicelled zooid (MLP 36482); 5, paratype, lateral walls with pore plates (arrows) (MLP 36482); 6, paratype, basal walls showing central depressions (white arrows) and uncalcified areas (black arrows) (MLP 36482); 7, paratype, kenozooids (MLP 36482). Scale bars equal 0.2 mm (1, 5), 0.05 mm (2), 0.5 mm (3), 0.3 mm (4), 0.4 mm (6), and 0.25 mm (7).

TABLE 2 – Measurements (μm) of *Burdwoodipora griffini* sp. nov.

	Zooid length	Zooid width	Orifice length	Orifice width
N	10	10	10	10
Mean	398	266	126	104
Minimum	333	216	117	94
Maximum	436	313	138	115
Standard Deviation	31	30	6	8

N: number of measurements.

tions by pore plates located at a certain distance from the basal wall (Fig. 3.5). Basal surface showing a quincuncial arrangement of rhomboidal sutures; the silhouette of each zooid in the basal wall bears a central depression; there is also an uncalcified area between two successive zooids in a longitudinal series (Fig. 3.6). A layer of kenozooids of quadrangular, rectangular, or irregular shape, separated by thin sutures, may partially cover the inner surface of the gastropod shell's last whorl; kenozooid surface tuberculate and perforated by large rounded pseudopores (Fig. 3.7). Ancestrula not seen.

Remarks. *Burdwoodipora griffini* sp. nov. is the second known species of this genus. It differs from the Recent *B. paguricola* in lacking the huge suboral umbo bearing the suboral adventitious avicularium in most autozooids. While the latero-oral avicularia are sometimes present and directed inwards in *B. paguricola*, they are almost constant (unilateral or paired) and directed proximally in *B. griffini* sp. nov. The ovicell is more rounded and less immersed in the fossil than in the Recent species. Although there are slight differences in the orientation of the condyles and the shape of the sinus, the orifices are remarkably similar in both species. The zooids are proportionally longer and more slender in *B. paguricola* than in *B. griffini* sp. nov. In addition, the colony of *B. griffini* sp. nov. also covers the surface of the gastropod shell, instead of just enlarging the last whorl of the shell as in *B. paguricola*. The layer of non-feeding kenozooids growing into the interior of the gastropod shell observed in *B. griffini* sp. nov., but not in *B. paguricola*, agrees with the pattern of tube growth termed tangential accretion by Taylor (1994).

DISCUSSION

Hermit crabs are weakly-mineralized; therefore, they are rarely preserved as body fossils (Taylor, 1994). However, the occupation of gastropod shells by paguroids can be revealed by indirect but unequivocal morphological features, such as the enlargement of the shell last whorl produced by associated bryozoan species, e.g., *Odontoporella miocenica* sp. nov. and *Burdwoodipora griffini* sp. nov. The association of *B. griffini* sp. nov. with hermit crabs is congruent with the growth habit of its only congeneric species, *B. paguricola*, which was found on 52 species of gastropods occupied by *Pagurus comptus* (López-Gappa & Zelaya, 2021).

The type locality of *B. griffini* sp. nov. is close to the known geographic distribution of *B. paguricola*, the depth range of the latter species (38–199 m; López-Gappa & Zelaya, 2021) suggesting the continental shelf off southern Patagonia as the habitat of *B. griffini* sp. nov.

López-Gappa *et al.* (2018) discussed the affinities of *Burdwoodipora* at the family level. They tentatively assigned this genus to the Pacificincolidae due to the absence of oral spines and the presence of a uniformly pseudoporous frontal shield and a suboral umbo bearing an adventitious avicularium that seemed to be homologous to the suboral heterozooids of *Pacificincola*. However, a noticeable feature of both species of *Burdwoodipora* is the cleithridiate orifice, which is not present in any of the Pacificincolidae, but characteristic of the cleidochasmatid genus *Characodoma*, (see Cook & Bock, 1996). Their distribution in the southern hemisphere also argues against the affinities with a boreal family such as the Pacificincolidae. More studies, including phylogenetic analysis, will be necessary to confirm or rectify the position of *Burdwoodipora* within the lepraliomorph Bryozoa.

A dubious species of *Odontoporella* was recorded for the Eocene of Hungary (Zágoršek & Kázmér, 2001), and probable species of this genus are known, but not yet described, for the Pleistocene Setana Formation of Japan, the Lower Miocene (Otaian) of New Zealand, and the Pliocene San Diego Formation of California (P.D. Taylor, personal communication, January 2022). The only previous certain fossil record of *Odontoporella* is the presence of *O. bishopi* in the Pleistocene of the Wanganui Basin, New Zealand (Rust & Gordon, 2011). Therefore, the discovery of *O. miocenica* in

the Monte León Formation extends its stratigraphic range from the Pleistocene to the early Miocene.

The Recent species *O. adpressa* can be easily recognized from other Magellanic cheilostomes by its conspicuous dark brown opercula. Its geographic distribution includes southern Chile (Busk, 1854; Moyano, 1982, 1983, 1991, 1992), the Malvinas/Falkland Islands (Pratt, 1898) and the Burdwood Bank (Schejter *et al.*, 2016), the Patagonian shelf and upper slope (López Gappa & Lichtschein, 1988, 1990; Schejter *et al.*, 2014), and deeper shelf areas off Buenos Aires Province, Argentina (Roux *et al.*, 1988). Its female zooids lack ovicells, brooding embryos of lecithotrophic larvae internally (Carter & Gordon, 2007). The figure of an ovicell in López Gappa & Lichtschein (1990) is erroneous and should be disregarded.

An interesting case of zooidal dimorphism was found in live specimens of *O. bishopi* (Gordon, 1968 as *Hippopodinella adpressa*). The male zooids of this New Zealand species have fewer tentacles than the feeding autozooids, without showing any morphological difference in the zooidal skeleton. It is not known whether zooidal dimorphism also occurs in *O. adpressa*. Former records of *H. adpressa* for the Pacific coast of Mexico and the Galápagos Islands (Osburn, 1952; Soule & Duff, 1957; Soule, 1961; Soule & Soule, 1964) were recently reassigned to two new species of *Abditoporella* (Sosa-Yañez *et al.*, 2015). Embryos are brooded in female zooids with dimorphic orifices in the Mexican species *A. dimorpha* (Sosa-Yañez *et al.*, 2015).

The existence of vicariant Recent species of *Odontoporella* in South America (*O. adpressa*) and New Zealand (*O. bishopi*), as well as the finding of *O. miocenica* sp. nov. in the early Neogene of Patagonia, adds further support to the hypothesis of a trans-Antarctic seaway serving as a dispersal route for marine shelf fauna during the Cenozoic (Casadío *et al.*, 2010).

As proposed by Carter and Gordon (2007), the present distribution of *Odontoporella* in southern South America, New Zealand and New Caledonia suggests that its ancestry is probably to be sought in the austral Paleogene of former Gondwana.

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