



A new genus and species of cheilostome bryozoan associated with hermit crabs in the subantarctic Southwest Atlantic

Juan López-Gappa^{1,3} · María G. Liuzzi^{1,3} · Diego G. Zelaya^{2,3}

Received: 10 August 2017 / Revised: 7 December 2017 / Accepted: 16 December 2017
© Springer-Verlag GmbH Germany, part of Springer Nature 2017

Abstract

Some bryozoan species occur on gastropod shells occupied by hermit crabs, often dominating the shell surface to the exclusion of other encrusters. Symbioses between bryozoans and pagurid crabs are known from a wide latitudinal range, including tropical, warm- and cold-temperate regions. Here we describe *Burdwoodipora paguricola* gen. et sp. nov., a cheilostome bryozoan associated with pagurized shells occupied by the hermit crab *Pagurus comptus* White in subantarctic waters of the Southwest Atlantic. The association seems to be obligate, as the bryozoan was always found enlarging the last whorl of its gastropod substrate. The new species, however, is not species specific with regard to its shell substrate, as it was found to be associated with 31 species of gastropods with helicoidal coiling. Well-developed colonies may project up to 360° from the outer lip of the shell. The chamber built by the bryozoan is usually larger than the whorl that would have been generated by the gastropod. This is one of the few known cases of an obligate association between a bryozoan and a pagurid crab outside the ascophoran family Hippoporidridae and is also the first bryozoan/hermit crab symbiosis documented in the subantarctic region. The inclusion of *Burdwoodipora* in the Pacificincolidae, a family currently represented by just four species from the Northern Hemisphere, is discussed.

Keywords Bryozoa · Symbiosis · Pagurid crabs · *Pagurus comptus* · Burdwood Bank

Introduction

Bryozoans are sessile, filter-feeding organisms showing a wide range of substrate preferences, from generalists to highly specific (Ryland 1974). It has been shown experimentally that bryozoan larvae actively select the substrate where the adult colony is usually found (Ryland 1959). Some representatives of the phylum may develop massive colonies on gastropod shells occupied by hermit crabs, often dominating the shell surface to the exclusion of other encrusters (Taylor 1994). In this regard, species of the bryozoan genus *Hippoporidra* Canu and Bassler often show obligate

associations with pagurids, building multilayered colonies around gastropod shells inhabited by the crabs (Cook 1968a). The colony often enlarges the shell space to accommodate the crab, following the same helicospiral shape of the snail (Pérez et al. 2015). In some cases, all what is left of the gastropod is a tiny shell of a few mm in size near the apex (Taylor 1994).

The evolutionary history of these associations may be traced back to the Middle Jurassic and they became common in the Neogene (Taylor 1994). The symbioses between bryozoans and pagurid crabs range in depth from the intertidal to almost 500 m. They are known to occur along a wide latitudinal range, including tropical, warm- and cold-temperate regions (Taylor 1994; Williams and McDermott 2004), with some cases also reported in subarctic and Arctic waters (Tilbrook and Grischenko 2004; Kuklinski et al. 2008). The associations between bryozoans and pagurid crabs may also be facultative. In these cases, bryozoan colonies may be found both on pagurized shells and also on other substrates. For instance, just 4 of 13 bryozoan species associated with hermit crabs off the Otago Peninsula, New Zealand, were regarded as obligate symbionts (Taylor et al. 1989).

✉ Juan López-Gappa
lgappa@macn.gov.ar

¹ Museo Argentino de Ciencias Naturales, Angel Gallardo 470, Ciudad Autónoma de Buenos Aires C1405DJR, Argentina

² Departamento Biodiversidad y Biología Experimental, FCEN – UBA, Ciudad de Buenos Aires, Argentina

³ Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina

Pagurus comptus white is a small hermit crab (carapace length up to 12.5 mm) which inhabits shells of five gastropod species in the intertidal of central-southern Chile (Soto and George-Nascimento 1991). It is distributed in cold-temperate waters around the southern tip of South America, including Chile, the Magellan Strait, the Malvinas/Falkland islands and the continental shelf from Cape Horn to Uruguay (Boschi et al. 1992).

The aim of this study is to describe a new genus and species of cheilostome bryozoan showing an obligate association with the hermit crab *P. comptus* in subantarctic waters, to discuss its taxonomic affinities at the family level and to analyse its relationship with the pagurized gastropods used as substrates.

Materials and methods

The material for this study came mainly from the benthic surveys of RV *Shinkai Maru* (July–August 1978, see Cousseau et al. 1979), GC-189 *Prefecto García* (December 2015), FV *Erin Bruce* (February 2016) and RV *Puerto Deseado* (March–April 2016). Additional material was found while examining samples of pagurid crabs housed at the collection of invertebrates of the Museo Argentino de Ciencias Naturales (MACN–In) (Table 1).

Bryozoan colonies were cleaned in diluted domestic bleach (NaClO solution) and coated with gold–palladium (40–60%). Digital images were obtained using a conventional SEM (Phillips XL–30) at MACN. The length and width of zooids and polymorphs were measured using a stereomicroscope with a micrometer eyepiece. The ancestrula and early astogeny were photographed with a Leica DFC7000 T camera mounted on a Leica DM2500 optical microscope.

Voucher specimens were deposited in MACN–In.

Results

Family Pacificincolidae Liu and Liu 1999

Burdwoodipora gen. nov.

Description

Colony unilaminar, enlarging the last whorl of pagurized gastropod shells, frontal budding absent. Frontal shield uniformly perforated by pseudopores. Orifice with a pair of robust smooth condyles and a proximal sinus. Oral spines absent. Adventitious avicularia latero-oral or placed on a suboral umbo. Ovicells imperforate, not closed by the operculum, immersed below the frontal wall of the succeeding

zooid. Multiporous pore plates in lateral walls. Uncalcified areas in basal walls. Ancestrula tatiform.

Type species

Burdwoodipora paguricola sp. nov., by monotypy.

Etymology

The word *Burdwoodipora* was formed combining the name of the bank where the type species was found, and *-pora*, a commonly used suffix in bryozoan taxonomy. The gender is feminine.

Remarks

Burdwoodipora gen. nov. shares with the ascophoran family Hippoporidridae Vigneaux its association with hermit crabs, a cleithriate orifice and the absence of oral spines. However, in *Burdwoodipora* there is no frontal budding, which is characteristic of many species of *Hippoporidra*. In addition, since new zooids originate only along the margin, the colony lacks the mammillae or monticules serving as excurrent water outlets (see Banta et al. 1974) that characterize *Hippoporidra* (see Ryland 2001). Furthermore, skeletal dimorphism is seemingly absent in *B. paguricola*, while in the monticules of *Hippoporidra* there are raised groups of large, male zooids having greatly reduced lophophores composed of non-ciliated tentacles (Cook 1977). Other polymorphs in *Hippoporidra* are the cortical zooids, which form the bases of branches and have reduced orifices without polypides (Cook 1964, 1968a). Although we did not observe the feeding behaviour in living colonies of *B. paguricola*, zooids do not show morphological or size differences suggesting the existence of sexual dimorphism or reduced polymorphs. Zooidal dimorphism is not reflected in the skeleton of the hippoporidrid *Odontoporella* either (see Carter and Gordon 2007), but in this genus the frontal wall is perforated by a single row of marginal areolae. The abovementioned characters suggest that *B. paguricola* is not a member of the Hippoporidridae.

The new genus also bears some resemblance to the lanceoporid *Calypotheca* Harmer (see Harmer 1957; Cumming and Tilbrook 2014; Sebastian and Cumming 2016), with which it shares the presence of a perforated frontal shield, adventitious avicularia originated from marginal pores, a pair of condyles and a proximal sinus in the orifice. The most obvious distinguishing character between *Burdwoodipora* and the Lanceoporididae, however, is the ovicell, which is sunken beneath the frontal shield of the succeeding zooid in the former, instead of being large, perforated and cor-midial such as in *Calypotheca*.

Table 1 List of the non-type material of *Burdwoodipora paguricola* examined as part of this study

Cruise	Station	Locality	Date	Latitude (S)	Longitude (W)	Depth (m)	MACN-In
EB	L57	Off Chubut Province	19 Feb 2016	43°37.888'	60°04.841'	110	41326
EB	L58	Off Chubut Province	19 Feb 2016	43°39.778'	60°03.851'	107	41327
SM IV	111	E of Tierra del Fuego Province	12 Aug 1978	52°29'	64°35'	183	41122
SM IV	119	E of Tierra del Fuego Province	10 Aug 1978	53°31'	66°27'	95	41123
SM IV	128	Isla de los Estados	09 Aug 1978	54°30'	64°25'	111	41124
PD	27	Burdwood Bank	28 Mar 2016	54°11.543'	58°19.876'	90	41125
PD	28	Burdwood Bank	30 Mar 2016	54°28.834'	59°11.674'	122	41126
PD	30	Burdwood Bank	10 Apr 2016	54°16.672'	59°57.790'	96	41127
PD	17 (haul 283)	Burdwood Bank	15 Apr 2016	54°36.270'	61°05.506'	195	41131
PD	17 (haul 284)	Burdwood Bank	15 Apr 2016	54°35.836'	61°06.860'	168	41132
PD	23	Burdwood Bank	13 Apr 2016	54°45.556'	59°53.197'	187	41133
PD	29	Burdwood Bank	30 Mar 2016	54°23.315'	59°41.182'	65	41134
PD	31	Burdwood Bank	10 Apr 2016	54°30.390'	59°48.654'	105	41135
PD	32	Burdwood Bank	30 Mar 2016	54°32.358'	60°07.895'	92	41136
PD	33	Burdwood Bank	08 Apr 2016	54°25.225'	60°37.576'	100	41137
PD	36	Burdwood Bank	19 Apr 2016	53°56.003'	61°33.661'	199	41138
PD	9	E of Tierra del Fuego Province	17 Apr 2016	54°14.615'	65°58.379'	74	41128
PD	5	S of Tierra del Fuego Province	06 Apr 2016	55°02.287'	65°46.121'	118	41129
PD	11	Isla de los Estados	22 Apr 2016	54°30.113'	64°08.429'	99	41130
GG	4	S of Tierra del Fuego Province	Dec 2015	55°03.926'	66°40.971'	38-44	41141
GG	5	S of Tierra del Fuego Province	Dec 2015	55°02.480'	66°04.465'	86	41142
GG	6	S of Isla de los Estados	Dec 2015	55°00.406'	65°49.680'	103	41143
GG	6B	S of Tierra del Fuego Province	Dec 2015	54°57.376'	65°27.432'	56	41144
GG	14	Burdwood Bank	Dec 2015	54°26.368'	60°39.133'	99	41145
GG	17	Burdwood Bank	Dec 2015	54°29.064'	59°04.873'	138	41146
–	–	Bayly Island, Cape Horn	Aug 1959	55°38.400'	67°37.800'	–	26545
BB	19	Off Cape San Pío, Beagle Channel	19 Apr 1939	55°04'	66°33'	58	23895
BB	–	Isla de los Estados	13 Mar 1941	54°26.5'	64°53.0'	102	24998
SL	–	Isla de los Estados	12 Feb 1934	54°45.675'	63°49.114'	–	21963
SL	–	Isla de los Estados	Dec 1934	54°45.761'	64°16.288'	28	22554
SL	–	Isla de los Estados	Dec 1934	54°41.583'	64°01.617'	50	22609
SL	–	Zeballos Island, Isla de los Estados	Dec 1933	54°39.453'	64°08.074'	50	22307
SL	–	Colnett Harbour, Isla de los Estados	Jul 1935	54°43.800'	64°18.600'	31	22554
SL	–	Le Maire Strait	30 Apr 1935	54°48'	64°55'	94	22705

References of the cruises: EB: FV *Erin Bruce*, SM IV: RV *Shinkai Maru*, PD: RV *Puerto Deseado*, GG: *Guardacostas Prefecto García*, BB: ARA *Bahía Blanca*, SL: ARA *San Luis*. See also Fig. 3

The family Pacificincolidae was established by Liu and Liu (1999) to include just the type genus *Pacificincola*. De Blauwe (2006) later introduced the genus *Primavelans* based on characters of the early astogeny. Currently, the family includes four species distributed in the Northern Hemisphere. A singular feature of all pacificincolids is an opening located in the distal part of the suboral umbo. It was regarded as an ascus by Liu and Liu (1999), but Nielsen (1981) had previously shown that in fact it was the aperture of a small heterozoid. The location and structure of the avicularia associated with the suboral umbones in

B. paguricola suggest a homology with the suboral heterozoids of the Pacificincolidae. In addition, the ovi-cells and the perforated frontal walls of *B. paguricola* strongly resemble those found in this family. Therefore, the Pacificincolidae seems to be the most adequate place for *Burdwoodipora* at the family level.

***Burdwoodipora paguricola* sp. nov.**

(Figures 1, 2, 3; Tables 1, 2, 3).

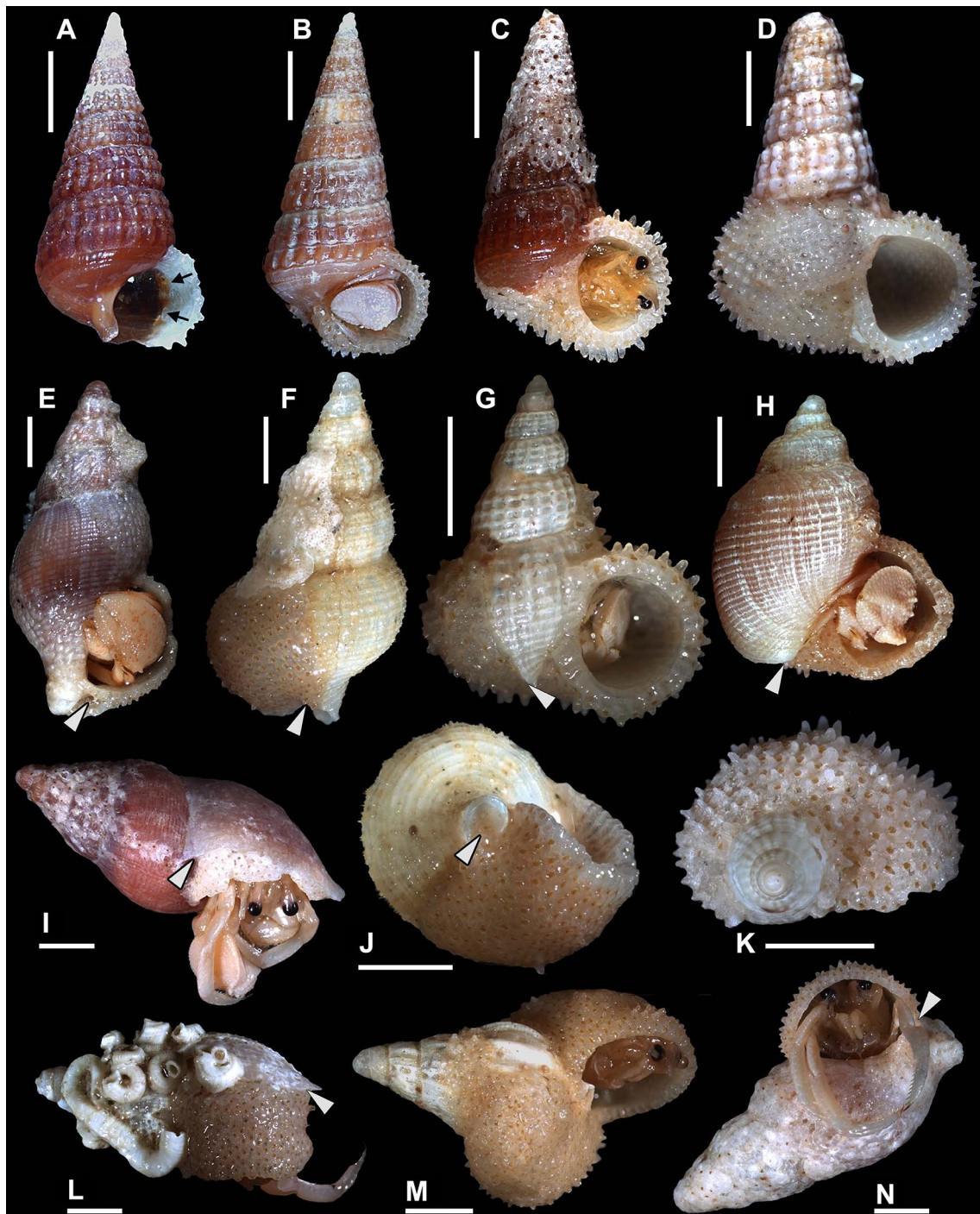
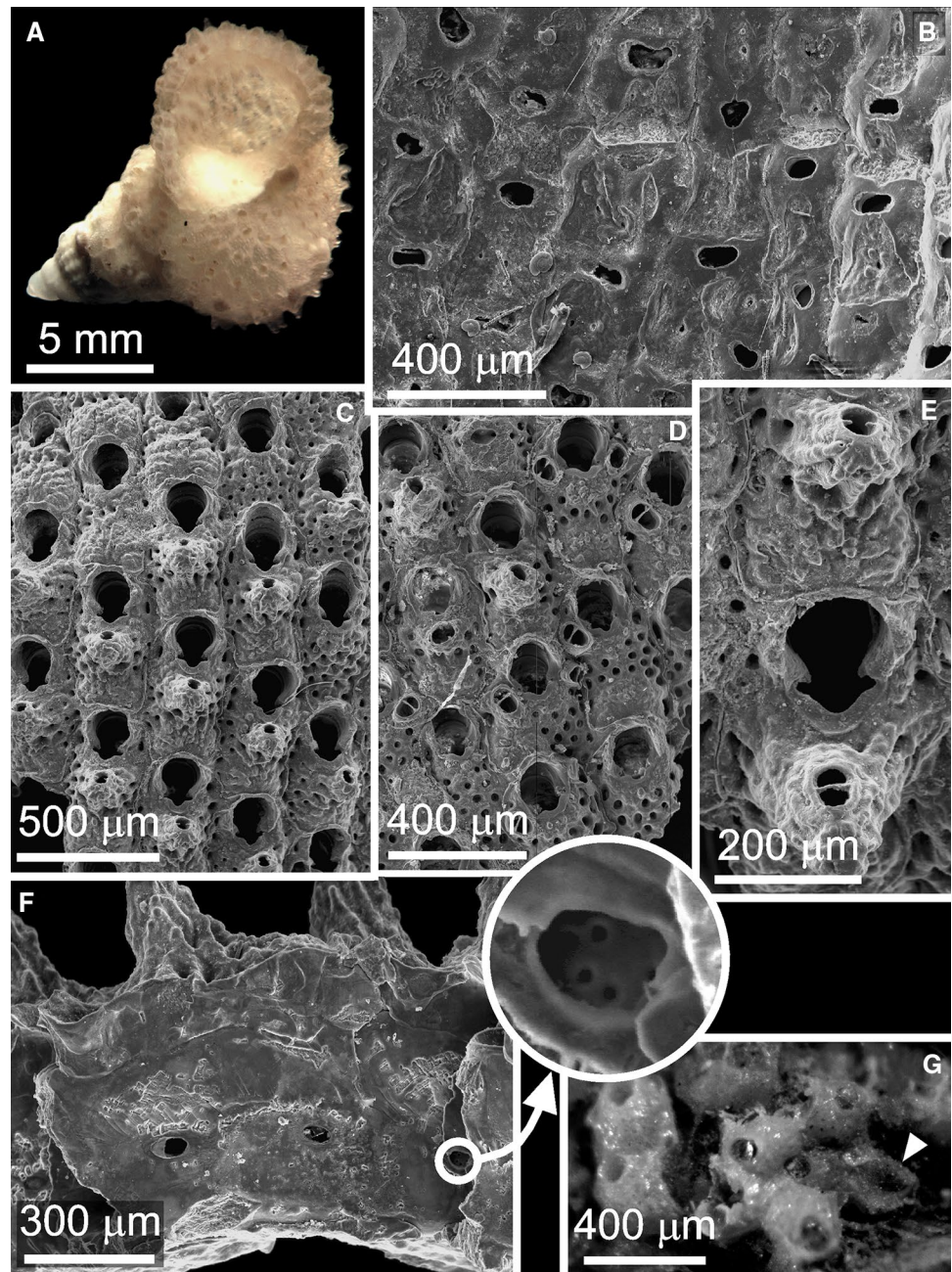


Fig. 1 *Burdwoodipora paguricola* gen. et sp. nov. on pagurized shells. **a–d** Successive growth stages of the bryozoan colony; black arrows in **a** show the outer lip of the shell aperture. **e–j, l, n**: changes in form and size of the gastropod aperture caused by colony growth; white arrowheads show alterations in the siphonal area (**e–h, j, l, n**) and at the junction of the aperture with the last whorl (**i**). **k, m**

Final appearance of the colony. Gastropod species used as substrate: *Cerithiopsis caelatum* (**a–d**), *Pareuthria atrata* (**e, i, l–n**), *Met euthria batialis* (**f, j, k**), Buccinnidae indet. 1 (**g**) and *Admete magellanica* (**h**). Note the occurrence of other bryozoans (**c, e, f, i**) and tubicolous polychaetes (**l**) growing on the same shell used as a substrate by *B. paguricola*. All scales represent 2 mm

Fig. 2 *Burdwoodipora paguricola* gen. et sp. nov. **a** Holotype (MACN-In 41120). **b** Uncalcified areas in basal walls (MACN-In 41127). **c** General aspect showing orifices, ovicells and adventitious avicularia on the suboral umbones (MACN-In 41126). **d** Several zooids with latero-oral avicularia (MACN-In 41127). **e** Detail of a zooid (MACN-In 41128). **f** Pore plates on lateral walls (MACN-In 41126). *Inset:* detail of a multiporous pore plate. **g** Tatiform ancestrula and early astogeny (MACN-In 41127). The arrowhead points to the ancestrula



Type locality

54°31.679'S, 61°27.979'W, 137 m, PD station 35, 31 Mar 2016.

Type material

Holotype (MACN-In 41120, Fig. 2a). *Paratypes* (MACN-In 41121): 24 colonies from the type locality.

Other material examined

See Table 1.

Description

Young colonies encrusting gastropod shells inhabited by pagurid crabs but soon building a unilaminar layer with the frontal surfaces of the zooids facing outwards (Fig. 1). The helicospiral growth of the bryozoan colony enlarges the last

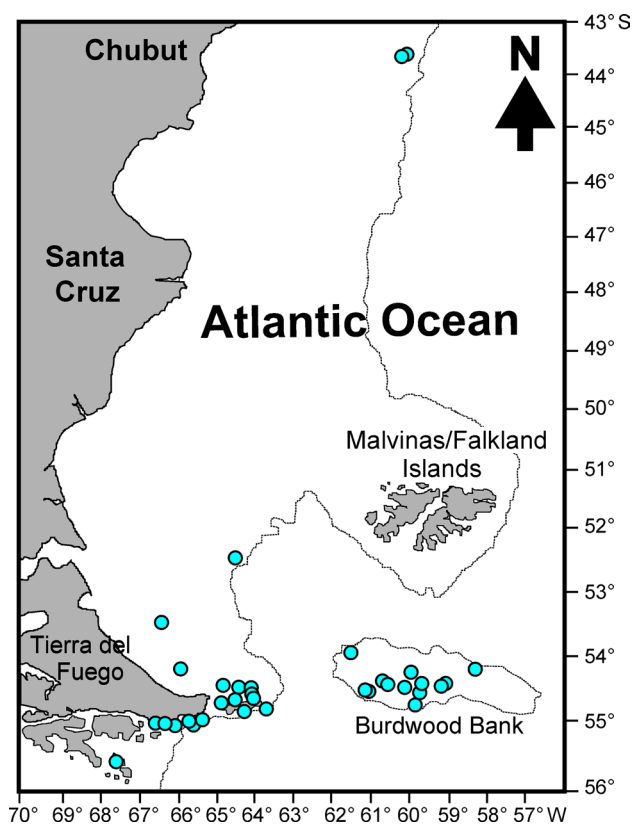


Fig. 3 Study area and stations where *Burdwoodipora paguricola* gen. et sp. nov. was collected (see Table 1 for further details). Line shows the 200 m isobath

Table 2 Measurements (mm) of *Burdwoodipora paguricola* gen. et sp. nov.

	Mean	SD	Range	N
Zooid length	0.45	0.107	0.36–0.67	10
Zooid width	0.27	0.058	0.20–0.36	10
Ovicell length	0.12	0.020	0.09–0.15	10
Ovicell width	0.23	0.026	0.17–0.26	10
Orifice length	0.18	0.018	0.16–0.22	10
Orifice width	0.15	0.015	0.12–0.17	10
Avicularium length	0.084	0.008	0.069–0.095	10
Avicularium width	0.060	0.005	0.053–0.070	10

SD standard deviation

whorl of the shell, not forming nodules or conical processes on its surface. Basal wall with a characteristic elliptical or irregularly shaped uncalcified area of variable size (Fig. 2b). Frontal budding absent. Zooids 0.45×0.27 mm, quincuncially arranged, regularly oriented (Fig. 2c). Frontal shield tuberculate, perforated by large pseudopores (Fig. 2c, d). Slightly larger marginal pores may in fact be areolae. Orifice cleithriate, 0.18×0.15 mm, with a robust pair of smooth

Table 3 Gastropods serving as a substrate for *Burdwoodipora paguricola* gen. et sp. nov.

Species	Family
<i>Admete magellanica</i> (Strebel)	Cancellariidae
<i>Argeneuthria cerealis</i> (Rochebrune & Mabile)	Buccinidae
Buccinidae indet. 1	Buccinidae
Buccinidae indet. 2	Buccinidae
<i>Calliostoma</i> sp. 1	Calliostomatidae
<i>Calliostoma</i> sp. 2	Calliostomatidae
<i>Cerithiopsis caelatum</i> (Gould, 1849)	Cerithiopsidae
<i>Epitonium</i> cf. <i>strebli</i> Zelaya & Güller	Epitoniidae
<i>Fuegotrophon pallidus</i> (Broderip)	Muricidae
<i>Glypteuthria meridionalis</i> (Smith)	Buccinidae
<i>Homalopoma cunninghami</i> (Smith)	Colloniidae
<i>Mangelia hyemalis</i> (Mabile & Rochebrune)	Turridae
<i>Margarella violacea</i> (King)	Calliostomatidae
<i>Mathilda argentina</i> Castellanos	Mathildidae
<i>Met euthria batialis</i> Pastorino	Buccinidae
<i>Met euthria martensi</i> (Strebel)	Buccinidae
<i>Microdeuthria michaelsoni</i> (Strebel)	Buccinidae
<i>Neactaeonina argentina</i> Zelaya, Schejter & Ituarte	Acteonidae
<i>Parabuccinum bisculptum</i> (Dell)	Buccinidae
<i>Parabuccinum rauscherti</i> Harasewych, Kantor & Linse	Buccinidae
<i>Pareuthria atrata</i> (Smith)	Buccinidae
<i>Pareuthria fuscata</i> (Bruguère)	Buccinidae
<i>Pareuthria venustula</i> Powell	Buccinidae
<i>Savateria</i> sp.	Buccinidae
<i>Solariella</i> sp.	Solariellidae
<i>Tectonatica impervia</i> (Philippi)	Naticidae
<i>Thesbia</i> sp.	Raphitomidae
<i>Toledonia vagabunda</i> (Mabile)	Acteonidae
<i>Trophon ohlini</i> Strebel	Muricidae
<i>Trophon plicatus</i> (Lightfoot)	Muricidae
<i>Xymenopsis buccineus</i> (Lamarck)	Muricidae

lateral condyles and a wide, arrow-shaped sinus (Fig. 2c–e). A peristome reinforces the distal part of the orifice. Oral spines absent. An umbo usually present immediately below the sinus, often becoming columnar and attaining a huge size (Fig. 2c–f). An avicularium pointing upwards (i.e. perpendicular to the frontal surface) located on the distal surface of the umbo; rostrum elliptical, crossbar complete, without columella (Fig. 2e). One or sometimes two latero-oral avicularia of similar shape pointing towards the centre of the frontal shield may develop from marginal pores (Fig. 2D). Ovicells 0.12×0.23 mm, imperforate, not closed by the operculum (i.e. acleithral sensu Ostrovsky 2008), with radial rows of tubercles and a central smooth area, immersed below the frontal wall of the succeeding zooid (Fig. 2c–e). Lateral walls punctured by multiporous pore plates located at a

certain distance from the basal wall (Fig. 2f). Ancestrula tatiform, with several delicate spines around the opesia, etching a shallow depression on the shell (Fig. 2g). Early astogeny producing a single medio-distal zooid, which in turn buds two proximo-lateral and two distal zooids (Fig. 2g).

Etymology

The name of the species alludes to the association with gastropod shells inhabited by pagurid crabs.

Remarks

Burdwoodipora paguricola gen. et sp. nov. shares some morphological features with apparently unrelated bryozoan species. Its cleithriate orifice and arrow-shaped sinus are identical to those found in the cleidochasmatid cheilostome *Characodoma protrusum* (Thornely) (see Soule et al. 1991). A similar suboral umbo has been found in the lanceopodid *Calyptotheca churro* Sebastian and Cumming, a species from tropical Australia (Sebastian and Cumming 2016).

The new species was always found growing on and expanding the last whorl of gastropod shells inhabited by the hermit crab *Pagurus comptus*. No species-specific relationship between bryozoans and gastropods was detected. In fact, among the studied material, 31 gastropod species belonging to the subclasses Vetigastropoda, Caenogastropoda and Heterobranchia served as the substrate for *B. paguricola* (Table 3). In all cases, bryozoans were observed on gastropods with helicoidal coiling. This is consistent with the fact that only those shells were found to be pagurized.

In all cases when the early astogeny could be observed, it took place at the junction of the aperture to the last whorl, in the siphonal canal, or nearby. This suggests that the bryozoan recruits on shells after the death of the gastropod, as these locations are occupied or swept by soft tissues when the snail is alive. In holostomate shells such as in *Margarella*, *Calliostoma* and *Tectonatica*, the colony then extends all along the outer lip of the aperture until reaching the columellar lip. In siphonate shells (such as those of *Cerithiopsis caelatum* and buccinids), the colony also extends anteriorly, along the outer lip of the aperture, until reaching the siphonal area. At this point, the colony separates from the outer lip and crosses over the siphonal area of the shell, reaching the columellar lip (Fig. 1a–c, e–g, j, l, n). This pattern of growth originates a smaller-sized shell aperture, of holostomatous appearance. Sometimes, the alteration in the shape and reduction in the size of the original shell aperture were also observed in the posterior part (Fig. 1i). Once it reaches the columellar lip, the bryozoan colony extends along the parietal/umbilical area of the shell (Fig. 1c, d). Simultaneously, the zooids from the outer lip of the aperture grow outwards, increasing the size of the chamber occupied by

the crab, whose growth follows the same helicospiral as that described by the shell whorls (Fig. 1d, g, h, j, k–m). However, the new chamber built by the growing bryozoan colony gradually increases the radius of the helicoid, more than expected for the gastropod shell (Fig. 1d, g, h, k, m). The colony may project up to 360° from the outer lip of the shell (Fig. 2m), mostly preserving the shell-like morphology, although the “whorl” originated by the bryozoan is larger than the whorl that would have been generated by the gastropod itself.

Distribution

Currently known from the Burdwood Bank and the continental shelf off Tierra del Fuego and Chubut provinces (Fig. 3), from 28 to 199 m (Table 1).

Discussion

The new species here described was always found living on dead gastropod shells colonized or with signals of having been occupied by the hermit crab *Pagurus comptus*. In this regard, Cook (1968b, 1985) observed that larvae of *Hippoporidra senegambiensis* (Carter) were found near the aperture of the shell and settled only on *Turritella* shells inhabited by hermit crabs and not on living gastropod specimens that were offered to them as alternatives. No colonies of *B. paguricola* were found either on living specimens of gastropods or on other biological or non-biological substrates. Healthy colonies, however, were sometimes found on empty gastropod shells. The presence of this species and also of other cheilostome and cyclostome bryozoans on these substrates suggests that the epibionts may continue living on shells temporarily lying on the seafloor that may serve as a surplus available for pagurids seeking more attractive refuges.

The growth of the colony occurs always as if continuing the direction of growth of the shell, forming a single layer of zooids facing outwards and, with the exception of the early astogeny, etching no scars on the gastropod shell. Thus, the colony is restricted to the anterior part of the shell, leaving the rest of it as a suitable substrate for other bryozoans, serpulid and spirorbid polychaetes, hydrozoans, folliculinid ciliates and other sessile invertebrates (see Fig. 1c, e, f, i, l). Among other bryozoans regarded as symbionts of pagurids, only the New Zealand hippoporidrid *Odontoporella bishopi* Carter and Gordon builds a tube formed by a single layer of zooids (Carter and Gordon 2007).

The association between *B. paguricola* and *P. comptus* resembles the symbiotic relationship observed between the zoanthid cnidarian *Epizoanthus paguricola* (Roule) and the hermit crab *Sympagurus dimorphus* (Studer). Such

association was found in scallop beds located between 85 and 131 m depths in the northern part of the Atlantic sector of the Magellanic Region, i.e. in the same biogeographical province as in the present study. In this case, the crab lives within the soft spiral cavity built by the zoanthid (Schejter and Mantelatto 2011).

Judging from the material here studied, *B. paguricola* seems to be a common species in the southern Southwest Atlantic. It is noteworthy that such a frequent species was never found during repeated scientific surveys collecting benthos along the southern Patagonian shelf during the 19th and 20th centuries. This may be due to the fact that the material may have been deposited in the crustacean or mollusc collections (i.e. directed to other taxonomists) during separation. This was indeed the case in the Museo Argentino de Ciencias Naturales, where we found nine samples containing *B. paguricola* on gastropod shells occupied by *P. comptus* collected between 1933 and 1959 (Table 1) that had been stored in the carcinological collection. The species is likely to be present in gastropod and hermit crab collections obtained in Chilean localities of the Southeastern Pacific south of Chiloe Island, the Magellan Strait and the Cape Horn area.

Taylor et al. (1989) recorded four non-hippoporidrid species that were found only in association with hermit crabs in New Zealand, and were possibly obligate pagurid symbionts. They stated, however, that this may reflect more an incomplete knowledge of the New Zealand bryozoan fauna than obligatory symbiosis. As *B. paguricola* was never found on other kind of substrates among abundant material collected during intensive recent surveys in the Burdwood Bank (Schejter et al. 2016), it can be assumed with a reasonable degree of certainty that this non-hippoporidrid bryozoan is an obligate symbiont of pagurid crabs.

From a biogeographical point of view, bryozoan–hermit crab symbioses are more common in tropical and warm-temperate areas (Taylor 1994), but are also known to occur at northern hemisphere high latitudes, including subarctic (Tilbrook and Grischenko 2004), Arctic (Kuklinski et al. 2008) and cold-temperate environments (Taylor et al. 1989). A symbiosis between a bryozoan and a hermit crab has been recorded in the Cretaceous of Antarctica (Aguirre-Urreta and Olivero 1992). The present finding is the first documented case, however, of such an association in the subantarctic region.

Acknowledgements We are grateful to Dennis Gordon for advice about the taxonomic affinities of *Burdwoodipora*, and to Ricardo Bastida and Laura Schejter for the material collected during the RV *Shinkai Maru* and FV *Erin Bruce* cruises, respectively. We also thank the crews of the RV *Puerto Deseado* and the coastguard GC-189 *Prefecto García*, and particularly Marina Güller, for their help to obtain the samples. Matías Urcola, Carla Minghetti and María del Mar Eivers helped us to sort the material from the sediment in the laboratory. L. Schejter and

Mariana Abelando coordinated the cruises of the *Puerto Deseado* and *Prefecto García*, respectively. D. Gordon and Paul Taylor made useful comments on an earlier version of the manuscript. Financial support by Consejo Nacional de Investigaciones Científicas y Técnicas (PIP 2013–2015 No. 0247 to JLG), Agencia Nacional de Promoción Científica y Tecnológica (PICT 2012–1043 to JLG and PICT 2016–2983 to DGZ) and Universidad de Buenos Aires (UBACyT 20020150100195BA to DGZ) is acknowledged.

References

- Aguirre-Urreta MB, Olivero EB (1992) A Cretaceous hermit crab from Antarctica: predatory activities and bryozoan symbiosis. *Antarct Sci* 4:207–214
- Banta WC, McKinney FK, Zimmer RL (1974) Bryozoan monticules: excurrent water outlets? *Science* 185:783–784
- Boschi EE, Fischbach CE, Iorio MI (1992) Catálogo ilustrado de los crustáceos estomatópodos y decápodos marinos de Argentina. *Frente Marít* 10:7–94
- Carter MC, Gordon DP (2007) Substratum and morphometric relationships in the bryozoan genus *Odontoporella*, with a description of a new paguridean-symbiont species from New Zealand. *Zool Sci* 24:47–56
- Cook PL (1964) Polyzoa from West Africa. Notes on the genera *Hippoporina* Neviani, *Hippoporella* Canu, *Cleidochasma* Harmer and *Hippoporidra* Canu & Bassler (Cheilostomata, Ascophora). *Bull Br Mus (Nat Hist) Zool* 12:1–35
- Cook PL (1968a) Bryozoa (Polyzoa) from the coasts of tropical West Africa. *Atlantide Rep No* 10:115–262
- Cook PL (1968b) Observations on living Bryozoa. *Atti Soc Ital Sci Nat Mus Civ Storia Nat Milano* 108:155–160
- Cook PL (1977) Colony-wide water currents in living bryozoa. *Cah Biol Mar* 18:31–47
- Cook PL (1985) Bryozoa from Ghana. A preliminary survey. *Ann Mus R Afr Centrale, Sci Zool, Tervuren* 238:1–315
- Cousseau MB, Hansen JE, Gru DL (1979) Campañas realizadas por el buque de investigación “Shinkai Maru” en el Mar Argentino, desde abril de 1978 hasta abril de 1979. Organización y reseña de datos básicos obtenidos. *Inst Nac Investig Desarro Pesq, Ser Contrib* 373:1–625
- Cumming RL, Tilbrook KJ (2014) Six species of *Calyptotheca* (Bryozoa, Cheilostomata, Lanceoporididae) from the Gulf of Carpentaria and northern Australia, with description of a new species. *Zootaxa* 3827:147–169
- De Blauwe H (2006) On the taxonomy and distribution of the family Pacificincolidae Liu & Liu, 1999 (Bryozoa, Cheilostomata), with the description of a new genus. *Bull Inst R Sci Nat Belg, Biol* 76:139–145
- Harmer SF (1957) The Polyzoa of the Siboga Expedition. Part 4. Cheilostomata Ascophora II. *Siboga Exped* 28d: 641–1147
- Kuklinski P, Barnes DKA, Wlodarska-Kowalczyk M (2008) Gastropod shells, hermit crabs and Arctic bryozoan richness. In: Hageman SJ, Key Jr MM, Winston JE (eds) *Bryozoan studies 2007*, Va Mus Nat Hist Spec Publ No. 15, Martinsville, VA, pp 93–100
- Liu XX, Liu HL (1999) Systematic position of *Mucronella perforata* Okada et Mawatari 1937. *Chin J Oceanol Limnol* 17:338–342
- Nielsen C (1981) On morphology and reproduction of ‘*Hippodiplosia*’ *insculpta* and *Fenestulina malusii* (Bryozoa, Cheilostomata). *Ophelia* 20:91–125
- Ostrovsky AN (2008) Brood chambers in cheilostome Bryozoa: diversity and revised terminology. In: Hageman SJ, Key Jr MM, Winston JE (eds) *Bryozoan studies 2007*, Va Mus Nat Hist Spec Publ No. 15, Martinsville, VA, pp 195–203

- Pérez LM, Griffin M, Pastorino G, López-Gappa J, Manceñido MO (2015) Redescription and palaeoecological significance of the bryozoan *Hippoporidra patagonica* (Pallaroni, 1920) in the San Julián Formation (late Oligocene) of Santa Cruz province, Argentina. *Alcheringa* 39:1–7
- Ryland JS (1959) Experiments on the selection of algal substrates by polyzoan larvae. *J Exp Biol* 36:613–631
- Ryland JS (1974) Behaviour, settlement and metamorphosis of bryozoan larvae: a review. *Thalass Jugosl* 10:239–262
- Ryland JS (2001) Convergent colonial organization and reproductive function in two bryozoan species epizoic on gastropod shells. *J Nat Hist* 35:1085–1101
- Schejter L, Mantelatto FL (2011) Shelter association between the hermit crab *Sympagurus dimorphus* and the zoanthid *Epizoanthus paguricola* in the southwestern Atlantic Ocean. *Acta Zool (Stockholm)* 92:141–149
- Schejter L, Rimondino C, Chiesa I, Díaz de Astarloa J, Doti B, Elías R, Escolar M, Genzano G, López Gappa J, Tatián M, Zelaya D, Bremec CS (2016) Namuncurá marine protected area: an oceanic hotspot of benthic biodiversity at Burdwood Bank, Argentina. *Polar Biol* 39:2373–2386
- Sebastian P, Cumming RL (2016) Three new species of *Calypthotheca* (Bryozoa: Lanceoporidae) from the great barrier reef, tropical Australia. *Zootaxa* 4079:467–479
- Soto RE, George-Nascimento M (1991) Uso de conchas de gastrópodos por el cangrejo ermitaño *Pagurus comptus* White, 1847 (Crustacea: Paguridae) en el intermareal rocoso de Chile Centro-Sur. *Rev Biol Mar, Valpo* 26:281–294
- Soule JD, Soule DF, Chaney HW (1991) New tropical Pacific and Indian Ocean Cleidochasmatidae (Cheilostomata: Ascophora). In: Bigey FP (ed) *Bryozoaires Actuels et Fossiles: Bryozoa Living and Fossil*. *Bull Soc Sci Nat l'Ouest-Fr, Mém HS* 1:465–486
- Taylor PD (1994) Evolutionary palaeoecology of symbioses between bryozoans and hermit crabs. *Hist Biol* 9:157–205
- Taylor PD, Schembri PJ, Cook PL (1989) Symbiotic associations between hermit crabs and bryozoans from the Otago region, southeastern New Zealand. *J Nat Hist* 23:1059–1085
- Tilbrook KJ, Grischenko AV (2004) New sub-Arctic species of the tropical genus *Antropora* (Bryozoa: Cheilostomata): a gastropod–pagurid crab associate. *J Mar Biol Assoc UK* 84:1001–1004
- Williams JD, McDermott JJ (2004) Hermit crab biocoenoses: a worldwide review of the diversity and natural history of hermit crab associates. *J Exp Mar Biol Ecol* 305:1–128