



Fouling bryozoans in Argentine harbours (Southwest Atlantic): new records and the description of a new species

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Abstract

Non-indigenous bryozoans are frequent components of biofouling assemblages in harbour environments worldwide. We performed a survey of artificial hard substrates in six harbours spanning 16 degrees of latitude along the coast of Argentina, from Ingeniero White (38°47' S) to Ushuaia (54°48' S). *Microeciella argentina* n. sp., distributed in warm-temperate waters of northern Patagonia and Buenos Aires Province, is described. The non-indigenous species (NIS) *Callopora dumerilii*, *Smittoidea spinigera* and *Stephanollona boreopacifica* are recorded here for the first time in the Southwest Atlantic. Their occurrence in fouling assemblages of warm-temperate harbours and their previous absence in these areas suggest that they probably arrived in Argentina by international shipping traffic. *Callopora dumerilii* is native to Europe and the northeast Atlantic. *Smittoidea spinigera* and *Stephanollona boreopacifica* are native to China and Korea, respectively. The morphological differences between *S. spinigera* and the Californian species *S. prolifera*, which is invading European harbours in the North Sea, are discussed. *Bugula neritina*, *Bugulina flabellata*, *Cryptosula pallasiana* and *Fenestrulina delicia*, common in harbours of Buenos Aires Province, are here recorded in Patagonia, highlighting the importance of regional shipping traffic to secondary spread of NIS. *Arachnidium fibrosum*, *Buskia socialis*, *Anguinella palmata*, *Aetea cultrata*, *Bicellariella edentata* and *Exochella moyanoi*, previously known from Brazil, and *Hippothoa divaricata*, are here recorded in Argentina. This study shows that warm-temperate harbours in Buenos Aires Province and northern Patagonia are particularly prone to the introduction of non-indigenous bryozoans.

Key words: Bryozoa, non-indigenous species, *Microeciella argentina* n. sp., Argentina, Patagonia

Introduction

The rate of documented invasions of marine non-indigenous species (NIS) in coastal communities has greatly increased in the last decades (Bailey *et al.* 2020). Hull fouling is well-known as a vector for the transport and introduction of marine organisms (Carlton & Hodder 1995; Gollasch 2002). Among several groups of benthic invertebrates composing the fouling assemblages, bryozoans frequently have a relatively high biodiversity and the ability to exploit a great variety of substrates (Watts *et al.* 1998). They are usually associated with artificial habitats as main mechanisms of dispersal (Miranda *et al.* 2018; Xavier *et al.* 2021). A high proportion of non-indigenous bryozoan species has been found in harbours and marinas worldwide (e.g., Ryland 1965; Gordon & Mawatari 1992;

Harmelin 2014). The complexity of the group often requires a considerable level of taxonomic expertise to discover the appearance of a NIS, particularly in regions where native species of the same genera are already present (Ryland *et al.* 2014; Ferrario *et al.* 2015).

The occurrence of non-indigenous bryozoans in the fouling assemblages of harbours along the coast of Argentina has been known for several decades (Lichtschein de Bastida & Bastida 1980; reviewed in Orensanz *et al.* 2002; Schwindt *et al.* 2020). Recent studies have reported the high abundance of a previously unreported species of *Fenestrulina* (López-Gappa & Liuzzi 2016), as well as the importance of domestic shipping traffic for the regional spread of NIS (Meloni *et al.* 2021). A large scale study performed in Patagonian harbours (Schwindt *et al.* 2014) and a survey of artificial substrates in a brackish harbour environment of Buenos Aires Province (López-Gappa & Liuzzi 2018) added new records to the list of non-indigenous bryozoans known in the southern Southwest Atlantic.

The aim of this study is to report the appearance of new bryozoan NIS in harbours spanning 16 degrees of latitude along the coast of Argentina, and to expand the southern limit of distribution of several warm-temperate species previously known from Brazil.

Materials and methods

Bryozoan colonies were sampled between 2005 and 2019 from artificial substrates (recruitment panels, pier pilings) in six harbours spanning 16 degrees of latitude along the coast of Argentina (Fig. 1; Table 1). Some species (*Callopora dumerilii*, *Hippothoa divaricata*, *Cryptosula pallasiana*) were found on mytilid bivalves attached to pier pilings. No new records or NIS bryozoans were found in Ushuaia harbour. The material examined was deposited in the National Collection of Invertebrates at the Museo Argentino de Ciencias Naturales (MACN-In). Additional material of the species analysed in this study was found in 23 samples stored in the MACN-In collection. Except for three dry samples (MACN-In 11771, 19538, 20570), all the remaining material at the MACN-In collection was stored in 70% ethanol.

TABLE 1. Location of the harbours sampled in this study.

Harbour	Province	Latitude (S)	Longitude (W)
Ingeniero White	Buenos Aires	38°47'33.7"	62°16'18.37"
San Antonio Este	Río Negro	40°47'42.34"	64°53'19.12"
Puerto Madryn (Storni pier)	Chubut	42°44'19.33"	65°00'53.65"
Comodoro Rivadavia	Chubut	45°51'36.1"	67°27'34.21"
Puerto Deseado	Santa Cruz	47°45'21.31"	65°54'34.58"
Ushuaia ¹	Tierra del Fuego	54°48'43.37"	68°18'19.57"

¹No new records or NIS bryozoans were found in Ushuaia harbour.

Some colonies were coated with gold/palladium and images were obtained using a Philips XL-30 scanning electron microscope (SEM) at the Museo Argentino de Ciencias Naturales (MACN). Digital photographs were also obtained with an AxioCam MRc camera mounted on a Zeiss Stemi 2000-C stereomicroscope using the software AxioVision SE64. Measurements were made using ImageJ on the SEM and stereomicroscope images.

The synonymic lists are not intended to be complete. They comprise mainly the original description, modern records of the species usually including SEM illustrations, reports from neighbouring localities and harbour environments. The descriptions are based on the material examined. In a few cases (*Bugula neritina*, *Bugulina flabellata*, *Fenestrulina delicia*, *Cryptosula pallasiana*), however, we omitted the descriptions since the species had been already described based on material from neighbouring Argentine harbours (see Lichtschein de Bastida & Bastida 1980; López-Gappa & Liuzzi 2016).

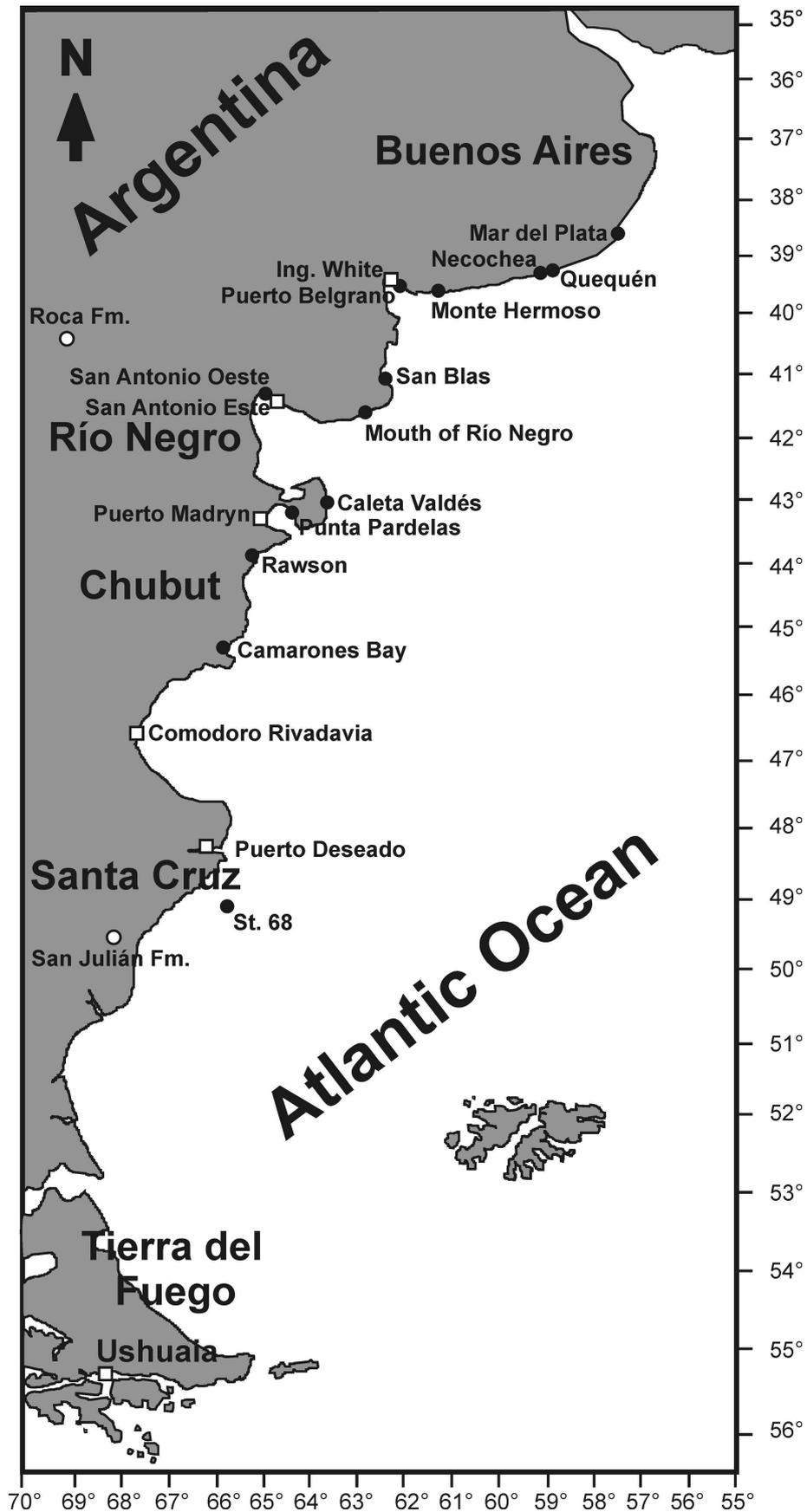


FIGURE 1. Map of the study area. Hollow squares: harbours sampled in this study. Hollow circles: fossil localities. Solid circles: other localities mentioned in the text.

Systematic account

Phylum Bryozoa Ehrenberg, 1831

Class Gymnolaemata Allman, 1856

Order Ctenostomatida Busk, 1852b

Family Arachnidiidae Hincks, 1880

Genus *Arachnidium* Hincks, 1859

Arachnidium fibrosum Hincks, 1880

(Fig. 2)

Arachnidium fibrosum Hincks 1880: 511, pl. 71, figs 6, 7; Marcus 1938: 51, pl. 12, fig. 29A, pl. 11, fig. 29B; Marcus 1941: 27; Prenant & Bobin 1956: 226, fig. 99; Hayward 1985: 82, fig. 24; Vieira *et al.* 2008: 10; De Blauwe 2009: 60, figs 35–37.

Material examined. MACN-In 32532, Monte Hermoso, September 23, 1981, collected by Claudia Bremec. MACN-In 42251, Ingeniero White harbour, September 4, 1984, 5 m, collected by Daniel Martínez. MACN-In 43869, Ingeniero White harbour, June 22, 2016, collected by Sandra Fiori.

Description. Colony uniserial, adnate, branching, forming a dense network on the substrate. Autozooids expanded distally, irregular in outline, with a slender, tubular, proximal portion, producing up to eight buds. Orifice subterminal, on a papillate peristome. Buds consist of long, bifurcating cylindrical stolons which anastomose irregularly to form a network, sometimes giving rise to stellate bodies that seem to be aborted autozooids. Short, characteristic tapering filaments are common around the margins and on the frontal surface of the autozooids.

Remarks. Due to its disjunct geographic distribution (see below), this species could be regarded as cryptogenic, i.e. a species that is not demonstrably native or exotic (Carlton 1996) in Argentina. This study expands its geographic range southwards by about 13 degrees of latitude, from Parana State (Brazil) to Monte Hermoso (Buenos Aires Province).

Distribution. Europe (Hincks 1880; Prenant & Bobin 1956; Hayward 1985; De Blauwe 2009), Atlantic coast of United States (Maturó 1968), Brazil (Marcus 1938, 1941; Vieira *et al.* 2008), Buenos Aires Province (this study).

Family Buskiidae Hincks, 1880

Genus *Buskia* Alder, 1856

Buskia socialis Hincks, 1887

(Figs 3–5)

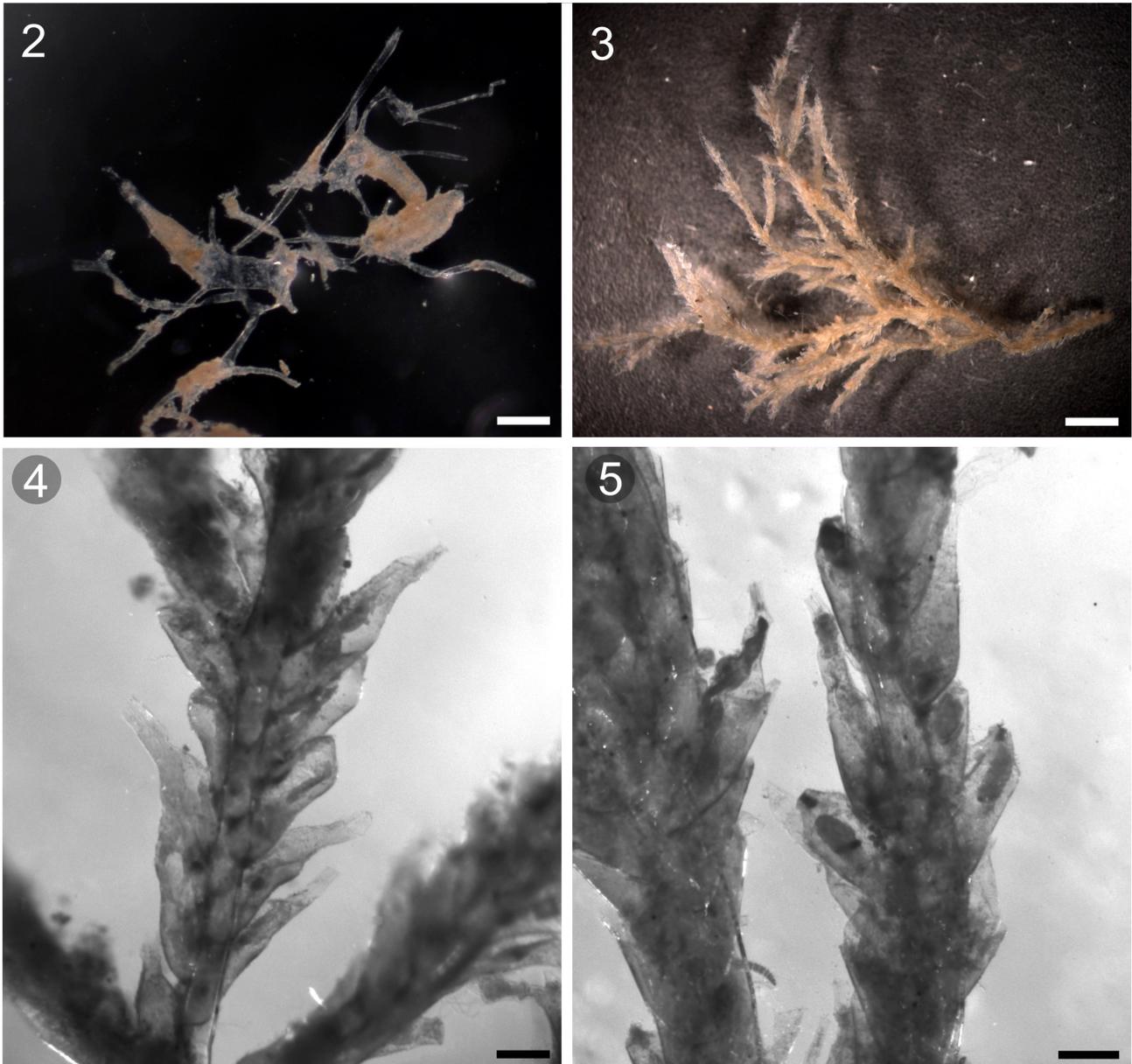
Buskia socialis Hincks 1887: 310, pl. 9, fig. 7; Marcus 1937: 143, pl. 28, fig. 77B, pl. 29, fig. 77A; Prenant & Bobin 1956: 310, fig. 141; Gordon & Mawatari 1992: 14, fig. 2G; Vieira *et al.* 2008: 9; Schwindt *et al.* 2020: 15.

Material examined. MACN-In 35765. April, 1968, Mar del Plata harbour, collected by Ricardo Bastida, identified by Analía Amor. MACN-In 43871, San Antonio Este harbour, December 6, 2016, collected by Karen Castro.

Description. Colony erect, flexible, yellowish, up to 3 cm long. Branching opposite or alternate. Stolon diameter about 104 µm near the apex of the branches, to about 237 µm in older parts of the colony. Retracted zooids flask-shaped, disposed in two longitudinal series along the stolon, about 521–778 µm long and 176–212 µm wide, with proximal end widened and recumbent on the stolon, and anterior end narrower and raised. Insertion point of the zooid on the stolon near the base. The lateral edges near the proximal end of the zooid may be produced into one or two projections adjacent to the stolon.

Remarks. Although Mar del Plata harbour has been intensively sampled, *B. socialis* was not found again there

after 1968. The species was not mentioned in a comprehensive study of the bryozoans of three harbours of Buenos Aires Province (Lichtschein de Bastida & Bastida 1980). *Buskia socialis* is a widespread species and was previously found in Rio de Janeiro (Marcus 1937) and São Sebastião (Brazil), where it has been regarded as non-indigenous (Xavier *et al.* 2021). It should also be regarded as a NIS in Argentina, due to its global disjunct distribution and its restricted geographic range in the Southwest Atlantic. This record, together with the mention in Schwindt *et al.* (2020), confirms the establishment of *B. socialis* in Argentina.



FIGURES 2–5. **FIGURE 2.** *Arachnidium fibrosum* (MACN-In 43869), zooids and stolons. **FIGURES 3–5.** *Buskia socialis* (MACN-In 35765); **3**, general aspect; **4–5**, close-up of branches and zooids. Scale bars. **2, 4, 5:** 200 μm ; **3:** 1000 μm .

Distribution. Mediterranean Sea (Hincks 1887), Portugal (Reverter-Gil *et al.* 2014), Red Sea (Hastings 1927), Atlantic coast of the United States (Maturó 1968), Brazil (Marcus 1937; Xavier *et al.* 2021), Buenos Aires and Río Negro provinces (this study). Gordon & Mawatari (1992) suggest that its presence in New Zealand could be due to transport by recreational vessels.

Family Nolellidae Harmer, 1915

Genus *Anguinella* van Beneden, 1845

Anguinella palmata van Beneden, 1845

(Figs 6–8)

Anguinella palmata van Beneden 1845: 34, pl. 4, figs 18–24; Marcus 1937: 133, pl. 26, fig. 71a, b; 1941: 28, fig. 28; Hayward 1985: 92, fig. 29; Gordon & Mawatari 1992: 11, pl. 5A; Winston & Hayward 2012: 22, fig. 11; Vieira *et al.* 2014: 501, figs 46–48.

Material examined. MACN-In 43872, Ingeniero White harbour, June 22, 2016, collected by Sandra Fiori.

Description. Colony erect, about 4–5 cm high, flexible, forming grey-brown tufts, consisting of primary and secondary axes giving rise to tubular zooids that are slightly incurved towards the colony axis. Zooids elongate, about 748–1150 μm long and 131–174 μm diameter, cylindrical, opaque, merging without external differentiation into the branch axis; surface with a muddy texture due to the accretion of silt particles; internal anatomical details not visible.

Remarks. This supposed globally distributed species probably comprises a cryptic species complex (Waeschenbach *et al.* 2015). *Anguinella palmata* has been regarded as cryptogenic in Brazil, where its main dispersal mechanism is by hull fouling (Miranda *et al.* 2018; Xavier *et al.* 2021). This is the first record of *A. palmata* for Argentina, where it should also be regarded as cryptogenic.

Distribution. Europe (Hayward 1985), Atlantic coast of Africa (Cook 1985) and United States (Winston & Hayward 2012), New Zealand, Australia (Gordon & Mawatari 1992), Brazil (Marcus 1937; Vieira *et al.* 2014; Xavier *et al.* 2021) and Buenos Aires Province (this study). Gordon & Mawatari (1992) suggest that *A. palmata* was introduced in New Zealand by maritime traffic.

Order Cheilostomatida Busk, 1852b

Family Aeteidae Smitt, 1868

Genus *Aetea* Lamouroux, 1812

Aetea cultrata Vieira, Almeida & Winston, 2016

(Figs 9–11)

Aetea sica: Vieira *et al.* 2008: 12 (in part).

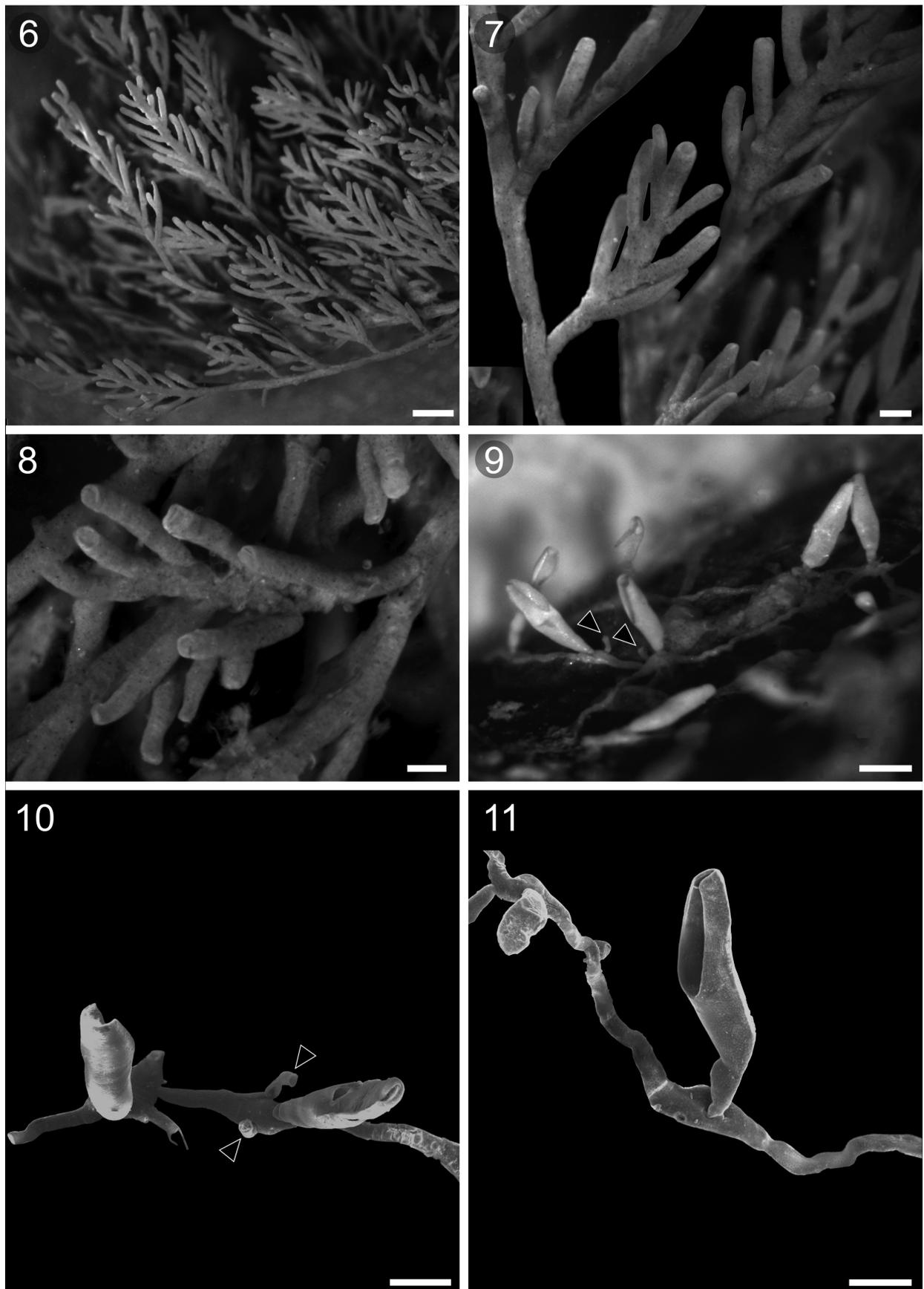
Aetea cultrata Vieira *et al.*, 2016: 64, figs 6–11.

Material examined. MACN-In 43873, Storni pier, Puerto Madryn, October 27, 2016, collected by Karen Castro.

Description. Colony creeping, uniserial, branching, delicate, consisting of an adnate basal portion and erect, distal, tubular stalks. Basal portion slightly punctate, about 269–438 μm long by 70–79 μm wide, expanded distally and tapering proximally. Erect stems about 395 μm long by 91 μm wide, with proximal cylindrical punctate portion. Frontal membrane occupying one side of the upper half of the stalk, with parallel lateral margins, about 175 μm long, with U-shaped proximal margin and straight distal end. One or two tubular, semi-erect zoeciules (kenozooids) may be present, arising from the lateral edges of the distal part of the attached creeping portion.

Remarks. *Aetea cultrata* has been regarded as cryptogenic in Brazil (Xavier *et al.* 2021). This is its first record for Argentina, where it should also be considered cryptogenic based on its presence in fouling communities and its biogeographical and taxonomic history (see Carlton 1996). Its southern limit of distribution is here expanded by more than 21 degrees of latitude. The records of *A. sica* for Argentina (Amor & Pallares 1965; Schwindt *et al.* 2020) should be re-examined, as they could actually belong to *A. cultrata* (see Vieira *et al.* 2016).

Distribution. Brazil (Vieira *et al.* 2008, 2016; Xavier *et al.* 2021), Florida, USA (Winston 1982), Chubut Province (this study).



FIGURES 6–11. **FIGURES 6–8.** *Anguinella palmata* (MACN-In 43872); **6**, general aspect; **7–8**, close-up of branches and zooids. **FIGURES 9–11.** *Aetea cultrata* (MACN-In 43873); **9**, general aspect of zooids, stolons and zoeciules (arrowheads); **10**, close-up of zoeciules (arrowheads); **11**, close-up of one zooid. Scale bars. **6**: 1000 µm; **7–9**: 200 µm; **10**, **11**: 100 µm.

Family Calloporidae Norman, 1903

Genus *Callopora* Gray, 1848

Callopora dumerilii (Audouin, 1826)

(Figs 12–14)

Flustra dumerilii Audouin, 1826: 240.

Callopora dumerilii: Ryland 1965: 33, fig. 15b; Hayward & Ryland 1998: 160, figs 40, 42a; De Blauwe 2009: 194, figs 180, 181.

Material examined. MACN-In 43874, Storni pier, Puerto Madryn, October 27, 2016, collected by Karen Castro.

Description. Colony encrusting, unilaminar. Autozooids oval, separated by deep grooves. Gymnocyte smooth, reduced, visible only on the proximo-lateral corners of the autozoid. Cryptocyst developed as a narrow and beaded raised border encircling the oval opesia. Four pointed and erect oral spines at the distal end of the autozoid. The proximal pair usually present, the distal pair absent or occluded in ovicelled zooids. Avicularia adventitious, sometimes absent, located proximo-laterally to the opesia, small, mounted on the gymnocyte, with a triangular pointed rostrum directed proximally or distally. Kenozooids scattered among the autozooids, with a peripheral, smooth gymnocyte and a well-developed beaded cryptocyst. Communication between autozooids by dietellae. Ovicell globular, spherical, ectooecium almost completely membranous, except for a narrow peripheral band; entooecium coarsely granular, with a reticulate appearance. Ancestrula tatiform, with ten delicate, erect spines.

Remarks. *Callopora dumerilii* was found on the ribbed mussel, *Aulacomya atra* (Molina, 1782). It was included by Ryland (1965) in his study of fouling bryozoans from European harbours. This is the first record of *C. dumerilii* for South America. Its disjoint geographic distribution and the appearance in the fouling assemblage of a Patagonian harbour suggests that it should be regarded as a NIS that probably arrived in Argentina by maritime traffic.

Distribution. From Norway to Morocco and Madeira, the Mediterranean Sea (Hayward & Ryland 1998), Holland and Belgium (De Blauwe 2009) and Chubut Province (this study). Its presence in the Atlantic coast of North America is based on the records of Whiteaves (1901) for the Gulf of St. Lawrence, Osburn (1933) for Maine, and Maturo (1968) for the Atlantic coast of the United States, although the species was not included in the comprehensive study by Winston & Hayward (2012) on the bryozoans from Maine to Virginia. *Callopora dumerilii* has also been cited for remote archipelagos in the Southern Hemisphere, such as Tristan da Cunha (Waters 1888) and Amsterdam Island (Balavoine 1958), in both cases without descriptions or illustrations.

Family Bugulidae Gray, 1848

Genus *Bugula* Oken, 1815

Bugula neritina (Linnaeus, 1758)

(Fig. 15)

Sertularia neritina Linnaeus, 1758: 815.

Bugula neritina: Lichtschein de Bastida & Bastida 1980: 380, fig. 6; Gordon & Mawatari 1992: 21, pl. 2G, 5F; Hayward & Ryland, 1998: 220, fig. 68; Giachetti *et al.* 2020: Table S1.

Material examined. MACN-In 43875, Comodoro Rivadavia harbour, April 25, 2019, collected by Mariana Abelando.

Description. See Lichtschein de Bastida & Bastida (1980).

Remarks. Molecular studies have found that *B. neritina* is a complex of cryptic species (McGovern & Hellberg 2003; Fehlauer-Ale *et al.* 2013) which still have not been assigned species names (McCann *et al.* 2019).

Distribution. One of the commonest members of fouling assemblages throughout the world, except in polar and subpolar regions (Gordon & Mawatari 1992). Widely recorded in harbours and marinas of Brazil, where it has been regarded as a non-indigenous species (Xavier *et al.* 2021). Its local distribution includes Mar del Plata,

Belgrano (Lichtschein de Bastida & Bastida 1980), Puerto Madryn (Giachetti *et al.* 2020) and Comodoro Rivadavia (this study) harbours, as well as the Malvinas/Falkland Islands (Hastings 1943), where it is also regarded as a NIS (Schwindt *et al.* 2020).

Genus *Bugulina* Gray, 1848

Bugulina flabellata (Thompson in Gray, 1848)

(Fig. 16)

Bugulina flabellata: Ryland, 1960: 82, figs 2A, B, 9A–C, pl. 2 A, D; Lichtschein de Bastida & Bastida 1980: 381, fig. 7; Gordon & Mawatari, 1992: 21, pl. 5E; Hayward & Ryland, 1998: 216, fig. 66; De Blauwe 2009: 220, figs 218–220.

Material examined. MACN-In 43876, Comodoro Rivadavia harbour, April 25, 2019, collected by Mariana Abelando.

Description. See Lichtschein de Bastida & Bastida (1980).

Distribution. Widely distributed in warm and temperate waters of both hemispheres (Gordon & Mawatari 1992). Its presence in Brazil, however, has been regarded as doubtful (Vieira *et al.* 2008). Its local distribution includes Mar del Plata, Belgrano (Lichtschein de Bastida & Bastida 1980) and Comodoro Rivadavia (this study) harbours.

Genus *Bicellariella* Levinsen, 1909

Bicellariella edentata Marcus, 1955

(Figs 17–20)

Bicellariella ciliata: Marcus 1937: 65, pl. 14, fig. 33.

Bicellariella sp.: Hastings 1943: 396, fig. 27A.

Bicellariella ciliata f. *edentata* Marcus 1955: 292, fig. 45.

Bicellariella edentata: Vieira *et al.* 2008: 16.

Material examined. MACN-In 11771, Belgrano harbour, 1920. MACN-In 32310, Rawson, February 8, 1977. MACN-In 32367, Mar del Plata, February, 1983. MACN-In 43870, Ingeniero White harbour, June 22, 2016, collected by Sandra Fiori.

Description. Colony erect, branching, flexible, attached to the substratum by rhizoids which issue from the basal surface of the autozooids. Branches biserial, bending frontally towards their extremity. Autozooids alternating, long, with contiguous proximal regions; distal regions flaring and curving outwards. Autozoid base forked, separated from the middle portion by a constriction; middle portion slender, in turn separated from the flaring distal portion by a second constriction. Frontal membrane oval, oblique, occupying the terminal third of the autozoid, with a distal, C-shaped operculum, bearing a single median proximal spine, and a row of usually four long, curved oral spines along the distal margin. Median zooid at a branch bifurcation bearing three spines, one median distal, and one on each side of the proximal end of the opesia. Axillary zooid bearing only one distal and one inner spine. Avicularia pedunculate, shaped like a bird's head, attached to the outer side of the autozoid, proximal to the frontal membrane; rostrum with a sharply curved tip, distal outer margin concave, inner margin straight to slightly undulating; mandible triangular, with a pointed, downcurved tip. Ovicell subglobular, prominent, at right angle to the branch axis, attached to the inner edge of the opesia by a short peduncle, with the opening facing the frontal membrane. Ancestrula and first autozooids erect, funnel-shaped, with a terminal circular membrane surrounded by delicate, curved spines.

Remarks. As noticed by Marcus (1955), *B. edentata* differs from *B. ciliata* in the shape of the bird's-head avicularium. While in the European *B. ciliata* the rostral margin is heavily serrated (see De Blauwe 2009, fig. 239), it was described as smooth in the Brazilian species *B. edentata* (Marcus 1955), and has just a slight undulating margin in the present material (Fig. 20). The smooth beak of the avicularium was also recognized by Hastings (1943) in her R.S.S. 'William Scoresby' material from Station WS776 (46°18'15" S, 65°02'15" W, off San Jorge Gulf).

Distribution. Brazil (Marcus 1937, 1955; Vieira *et al.* 2008), Buenos Aires and Chubut provinces (this study). Its presence in several localities off Buenos Aires and Chubut provinces suggests that this is a warm-temperate native species that reaches its southern limit of distribution in Patagonia (Hastings 1943).

Family Romancheinidae Jullien, 1888

Genus *Exochella* Jullien, 1888

Exochella moyanoi Ramalho & Calliari, 2015

(Figs 21–23)

Exochella longirostris: Canu, 1908: 300, pl. VI, fig. 13; Marcus 1937: 82, fig. 43; 1941: 22, fig. 16; 1949: 1 (non *E. longirostris* Jullien, 1888).

Exochella moyanoi Ramalho & Calliari, 2015: 578, fig. 6A–C.

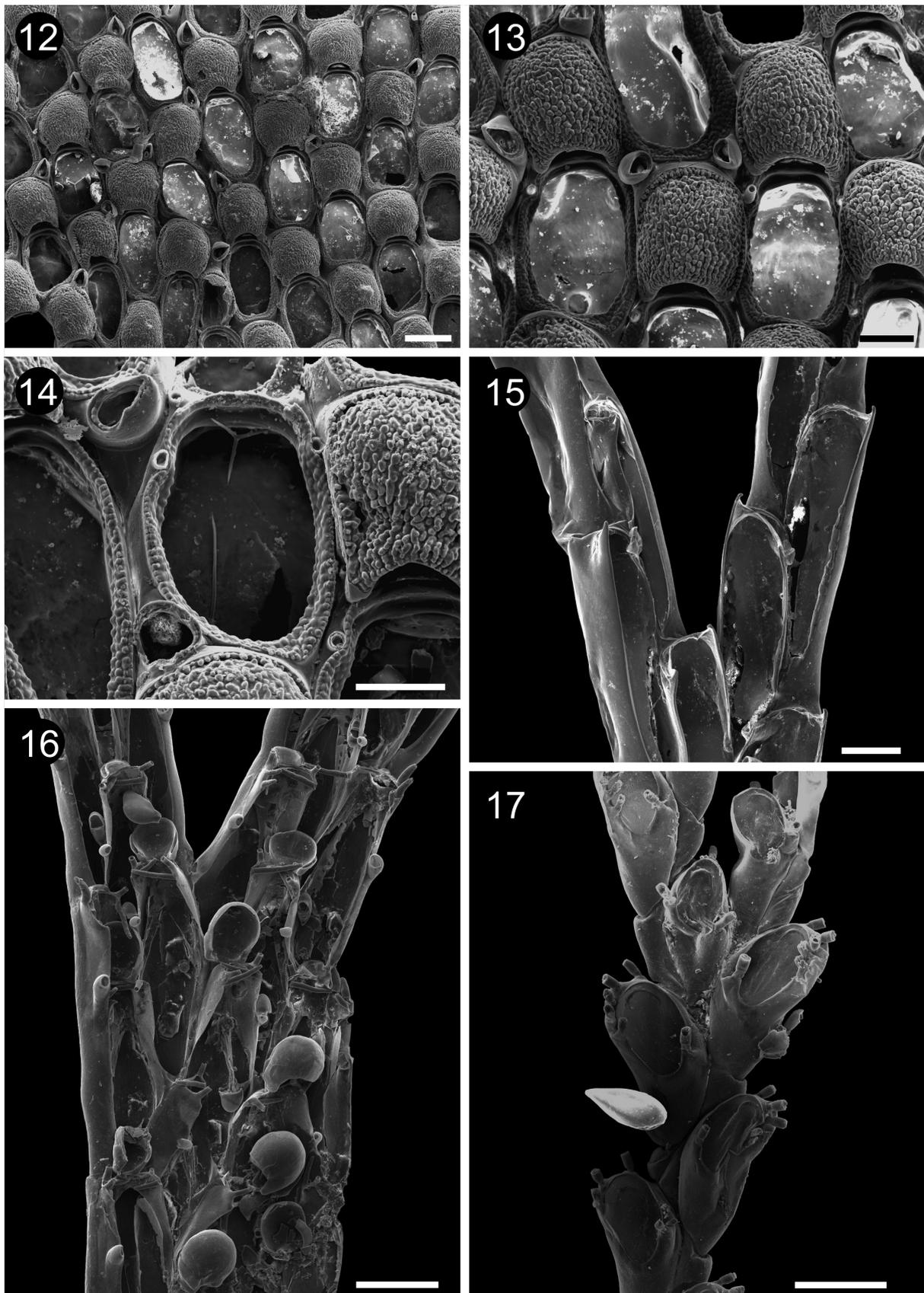
Material examined. MACN-Pi 1920, Holocene material identified by Canu (1908) as *Exochella longirostris* Jullien, Belgrano harbour ('Puerto Militar' in Canu 1908). MACN-In 32304, *Mytilus* bank, off Mar del Plata. MACN-In 32531, *Mytilus* bank, off Mar del Plata, January 15, 1971. MACN-In 43877, Storni pier, Puerto Madryn, October 27, 2016, collected by Karen Castro.

Description. Colony encrusting, unilaminar, multiserial, usually closely adnate on hard substrates. Autozooids irregularly hexagonal, $335\text{--}431 \times 246\text{--}373 \mu\text{m}$, disposed quincuncially, separated by distinct sutures. Frontal shield slightly convex, smooth, with 11–13 marginal areolae separated by ridges converging towards the center; areolae initially rounded and conspicuous, then becoming more slit-like, their size restricted by increasing frontal calcification. Primary orifice D-shaped, with indistinct proximo-lateral condyles; proximal border slightly concave, without denticle. Oral spines 2–4, delicate, cylindrical, articulated, mostly absent, even in marginal autozooids. Peristome well-developed, with a medio-proximal prominent mucro flanked by two proximo-lateral concave spaces; bluntly triangular processes project from the lateral borders but do not fuse with the median mucro; secondary orifice barely longer than wide, $92\text{--}131 \times 100\text{--}119 \mu\text{m}$. Adventitious avicularia usually single, sometimes paired, developing from one of the marginal areolae, located mid-laterally, sometimes proximally; rostrum triangular, protruding, pointing towards the orifice of the neighbouring lateral or proximal autozoid; crossbar complete. Ovicell rounded, endozooidal, budding from the distal peristomial margin over the proximal frontal shield of the following zooid, visible only during early ontogeny, then completely covered by frontal calcification. Ancestrula tatiform, with ovoid opesia, gymnocyst granular, more developed proximally and ten delicate spines. Early astogeny with a first pair of zooids budded distolaterally.

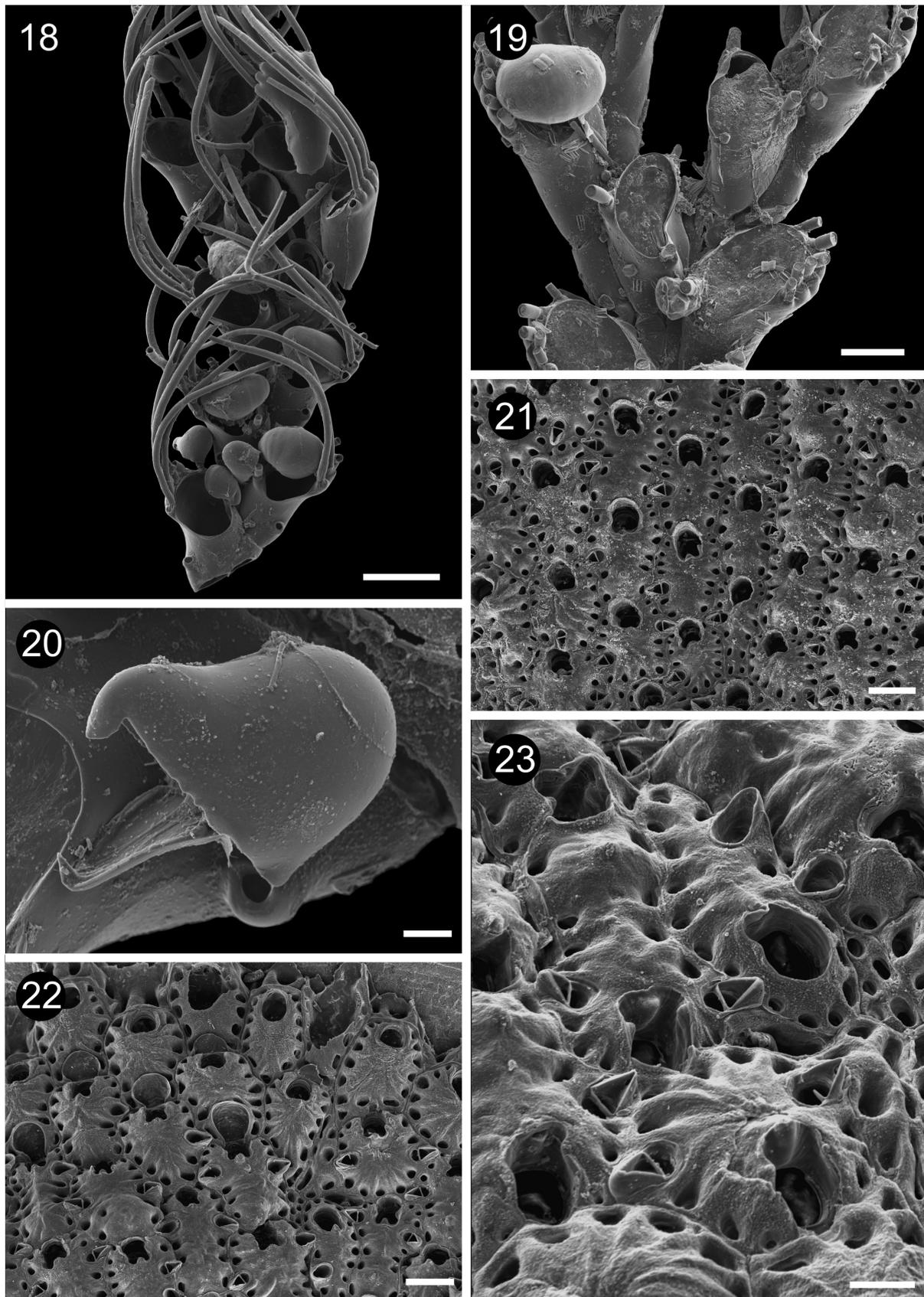
Remarks. *Exochella longirostris* Jullien, 1888, a common species in the Magellanic Region, differs from *E. moyanoi* in its slightly larger zooids, coarsely nodular frontal shield and more slender adventitious avicularia (see Hayward 1991).

The examination of Holocene ('Postpampéen') material from Puerto Belgrano identified as *E. longirostris* shows that it is identical with Recent material of *E. moyanoi*. In the Bahía Blanca estuary, the marine transgression occurred during the middle-late Holocene, after 7,500 yr B.P. (Aliotta & Farinati 1990). Its presence in Argentina before the arrival of European maritime traffic shows that *E. moyanoi* is a warm-temperate native species reaching its southern limit of distribution at Chubut province, Argentina. This study expands its geographic distribution southwards by about 5 degrees of latitude.

Distribution. Brazil, from Espírito Santo to Rio Grande do Sul (Vieira *et al.* 2008, as *E. longirostris*; Ramalho & Calliari 2015), Buenos Aires and Chubut provinces (this study); Holocene of Belgrano harbour, Buenos Aires Province (Canu, 1908).



FIGURES 12–17. **FIGURES 12–14.** *Callopora dumerilii* (MACN-In 43874); **12**, general aspect; **13**, ovicelled zooids; **14**, detail of zooid and avicularium. **FIGURE 15.** *Bugula neritina*, general aspect (MACN-In 43875). **FIGURE 16.** *Bugulina flabellata*, general aspect (MACN-In 43876). **FIGURE 17.** *Bicellariella edentata*, general aspect (MACN-In 32310). Scale bars. **12, 15, 17:** 200 μm ; **13, 14:** 100 μm ; **16:** 300 μm .



FIGURES 18–23. **FIGURES 18–20.** *Bicellariella edentata* (MACN-In 32310); **18**, general aspect; **19**, branch bifurcation and ovicelled zooid; **20**, close-up of avicularium. **FIGURES 21–23.** *Exochella moyanoi* (MACN-In 43877); **21**, general aspect; **22**, growing margin, showing ovicells in different stages of development; **23**, close-up of peristomes and avicularia. Scale bars. **18**, **21**, **22**: 200 μm ; **19**, **23**: 100 μm ; **20**: 20 μm .

Family Hippothoidae Busk, 1859

Genus Hippothoa Lamouroux, 1821

Hippothoa divaricata Lamouroux, 1821

(Figs 24–27)

Hippothoa divaricata Lamouroux, 1821: 82, pl. 80, figs 15, 16; Moyano, 1986: 101, pl. 1; Hayward & Ryland, 1999: 86, figs 16, 17A, B.

Material examined. MACN-In 43878, R/V *Shinkai Maru*, Campaign XI, Station 68, 48°27' S, 65°27' W, 103 m, March 5, 1979. MACN-In 43888, Storni pier, Puerto Madryn, October 27, 2016, collected by Karen Castro.

Description. Colony encrusting, uniserial, branching, delicate. Each zooid usually gives rise to one distal and two disto-lateral zooids, the latter diverging from the parent zooid at oblique angles; sometimes there may also be two proximo-lateral branches. Zooids of three types: autozooids, female zooids and zoeciules. Autozooid length 522–765 µm, widest in the region of the disto-lateral buds, tapering distally and proximally, with a proximal slender cauda of variable length. Two distal septula give rise to the next autozooid in line. Three pairs of rounded pore chambers in the base of the lateral walls, two of them associated with buds. Autozooids and female zooids bearing a median longitudinal keel, which is the highest point of the frontal shield. Orifice longer than wide, placed beyond the highest point of the autozooid, slanted downwards towards the cauda of the next zooid; anter rounded, sinus U-shaped, condyles well-developed. Female zooids about the same size of autozooids, but with a shorter cauda; ovicell globular, bimucronate, with a pair of pseudopores in non-eroded specimens. Zoeciules small, narrow, elongated, arising from the usual budding sites of autozooids or female zooids; orifice ovate, distal. Ancestrula schizoporelloid, with smooth frontal shield, budding one distal, symmetric zooid.

Remarks. The delicate colonies of *H. divaricata* were growing on the shells of the ribbed mussel, *Aulacomya atra*. The species was previously unknown in fouling assemblages (Ryland 1965; Gordon & Mawatari 1992; Harmelin 2014) and has not been found in Brazilian harbours and marinas (Miranda *et al.* 2018; Xavier *et al.* 2021).

H. divaricata was recorded by Waters (1904) for Navarino Island in the Cape Horn region of southern Chile, but the specimen figured by him was collected in an Antarctic station. His Chilean material could actually belong to *Neothoa patagonica* (Busk, 1852a) or *N. chilensis* (Moyano, 1982), two common uniserial Magellanic hippothoids.

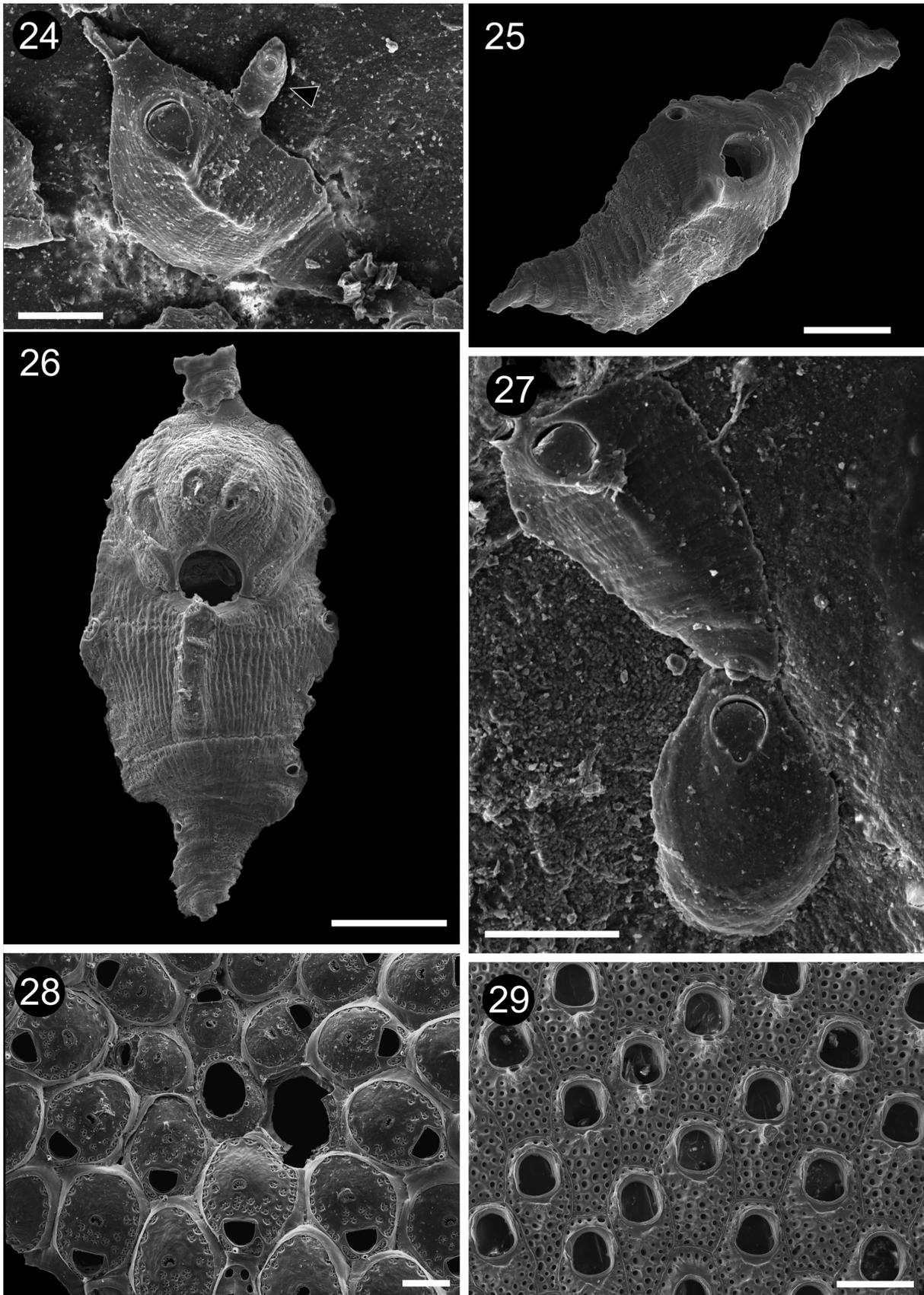
The material from Pernambuco, Brazil, identified as *H. divaricata* by Marcus (1939), was later regarded by Morris (1980) as belonging to a different species, *H. brasiliensis*, which lacks zoeciules and keeled autozooids.

Despite extensive sampling in the Magellan region, Moyano (1986) only found *H. divaricata* in northern Chile. López Gappa (1985) also did not find this species in his study of the Hippothoidae from Ría Deseado, Santa Cruz Province. Our material seems identical to Moyano's Chilean specimens, both having a schizoporelloid ancestrula which buds only one mid-distal autozooid. We agree with Moyano's (1986) view in that Viviani (1977) may have dealt with more than one species in his records of *H. divaricata* for the whole Chilean coast.

The New Zealand subspecies *H. divaricata pacifica* Gordon, 1984, was recently raised to full species rank by Gordon (2020). It is characterized by a kenozooidal ancestrula, which gives rise to one distal ecaudate and two proximo-lateral long-caudate autozooids.

The presence of *H. divaricata* in a sample collected on the Patagonian shelf off Santa Cruz Province, at a depth of 103 m, suggests that this is a native species in Argentina. The morphology of the Southwest Atlantic material closely agrees with European descriptions of the species (e.g., Ryland & Gordon 1977; Hayward & Ryland 1999). However, its identification as *H. divaricata* is still not completely certain, as the ancestrula of the European material is unknown.

Distribution. Chubut and Santa Cruz provinces, Patagonia (this study). Widely distributed in the North Atlantic and the Mediterranean (Hayward & Ryland 1999). Records beyond this region are doubtful due to taxonomic uncertainties.



FIGURES 24–27. **FIGURES 24–27.** *Hippothoa divaricata*; **24**, zoeciule (arrowhead) (MACN-In 43873). **25**, autozooid (MACN-In 43878); **26**, ovicelled zooid (MACN-In 43878); **27**, ancestrula and first zooid (MACN-In 43873). **FIGURE 28.** *Fenestulina delicia*, ancestrula and early astogeny (MACN-In 43879). **FIGURE 29.** *Cryptosula pallasiana*, general aspect (MACN-In 43880). Scale bars. **24–27:** 100 μ m; **28:** 200 μ m; **29:** 400 μ m.

Family Fenestrolinidae Jullien, 1888

Genus *Fenestrolina* Jullien, 1888

Fenestrolina delicia Winston, Hayward & Craig, 2000

(Fig. 28)

Fenestrolina delicia Winston, Hayward & Craig, 2000: 417, figs 13–15; De Blauwe 2009: 386, figs 415–417. Wasson & De Blauwe 2014: 2, figs 2, 3; López-Gappa & Liuzzi 2016: 510, fig. 2a-d.

Material examined. MACN-In 43879, Storni pier, Puerto Madryn, October 27, 2016, collected by Karen Castro.

Description. See Winston *et al.* (2000) and López-Gappa & Liuzzi (2016).

Remarks. The dispersion of *F. delicia* from Quequén to other Argentine harbours was predicted by López-Gappa & Liuzzi (2016). In Puerto Madryn the species has not yet attained the high frequency that it had in Quequén harbour in 2012–2013.

Distribution. Atlantic and Pacific coasts of North America (Winston *et al.* 2000; Dick *et al.* 2005), Europe (De Blauwe 2009; Wasson & De Blauwe 2014), Quequén harbour (López-Gappa & Liuzzi 2016) and Chubut Province, Argentina (this study).

Family Cryptosulidae Vigneaux, 1949

Genus *Cryptosula* Canu & Bassler, 1925

Cryptosula pallasiana (Moll, 1803)

(Fig. 29)

Eschara pallasiana Moll, 1803: 64, pl. 3, fig. 13.

Cryptosula pallasiana: Ryland 1965: 72, fig. 34b; Lichtschein de Bastida & Bastida 1980: 384, figs 18–23; Gordon & Mawatari, 1992: 29, pl. 1A–C, pl. 3C, pl. 8C; Hayward & Ryland 1999: 194, figs 74C, 76; López-Gappa & Liuzzi 2018: 1164; Castro *et al.* 2020: 70.

Material examined. MACN-In 18244, Quequén harbour. MACN-In 32387, Punta Pardelas. MACN-In 37995/38084, Necochea. MACN-In 19538, Quequén harbour, March 1931. MACN-In 8575, Puerto Belgrano, April 11, 1956. MACN-In 35506/7, Mar del Plata, November 1, 1963. MACN-In 35397, Riacho Jabalí, San Blas, October 6, 1968. MACN-In 32270, Mar del Plata, 1976. MACN-In 32307, San Antonio Oeste, February 7, 1977. MACN-In 32311, Camarones Bay, February 10, 1977. MACN-In 32312, Caleta Valdés, February 14, 1977. MACN-In 43881, Storni pier, Puerto Madryn, October 27, 2016, collected by Karen Castro. MACN-In 43880, Puerto Deseado harbour, April 24, 2019, collected by Jessica Chiarandini Fiore.

Description. See Lichtschein de Bastida & Bastida (1980), Gordon & Mawatari (1992) and Hayward & Ryland (1999).

Remarks. Colonies of *C. pallasiana* were found on shells of the ribbed mussel, *Aulacomya atra*. This common bryozoan fouler had been previously recorded in the fouling assemblages of Mar del Plata, Quequén and Belgrano harbours (Lichtschein de Bastida & Bastida 1980; López-Gappa & Liuzzi 2018), and Nuevo Gulf (Castro *et al.* 2020). It is also common in coastal areas of Argentina, from Mar del Plata to Valdés Peninsula, but was not found in Puerto Deseado harbour by Schwindt *et al.* (2014). Hence, its appearance in this harbour seems to be relatively recent. According to the sample stored in MACN-In 19538, the species is present in Argentina at least since 1931.

Distribution. Widespread around the world, particularly in ports and harbours (Gordon & Mawatari 1992). First recorded for Patagonia by Castro *et al.* (2020).

Family Smittinidae Levinsen, 1909

Genus *Smittoidea* Osburn, 1952

Smittoidea spinigera (Liu, 1990)

(Figs 30–32)

Smittina spinigera Liu, 1990: 122, fig. 2a–d.

Smittoidea spinigera: Liu, Yin & Ma 2001: 614, pl. 53, figs 1–3; McCuller & Carlton 2018: 155, fig. S23; Liuzzi *et al.* 2018: 218; Schwindt *et al.* 2020: 15.

Smittoidea sp.: Schwindt *et al.* 2014: Table S1.

Material examined. MACN-In 43883, San Antonio Este harbour, October 10, 2005, collected by Evangelina Schwindt. MACN-In 43882, Ingeniero White harbour, June 22, 2016, collected by Sandra Fiori.

Description. Colony encrusting, unilaminar, multiserial, whitish. Autozooids subhexagonal, $232\text{--}368 \times 171\text{--}277$ μm , disposed quincuncially, separated by distinct sutures. Frontal shield convex, rugose, rising to a high peristome and a suboral avicularian umbo, with one series of 9–14 large marginal areolae separated by ridges. Primary orifice deep, obscured by the peristome, with 2–3 distal oral spines, only their bases persisting in ovicelled zooids; a pair of conspicuous, acute condyles pointing proximally and a lyrule ending laterally in two sharp points. Peristome with raised ridges and a proximal U-shaped sinus. A suboral avicularium directed proximally and obliquely upwards on the distal side of the umbo; rostrum blunt, crossbar complete, with a conspicuous ligula. A small rounded pore on each side of the suboral avicularium connects with the avicularian chamber. Ovicell hyperstomial, spherical, wider than long ($144\text{--}175 \times 166\text{--}198$ μm), somewhat flattened frontally, not closed by the operculum, with a peripheral band of smooth ectooecium; entoecium pierced by 26–32 rounded or irregular pores with raised edges. Ancestrula tatiform, with proximal cryptocyst and nine delicate spines. Embryos orange.

Remarks. Several authors have recorded *Smittoidea prolifica* Osburn (see original description in Osburn 1952) as introduced in The Netherlands (De Blauwe & Faasse 2004) and the German North Sea (Markert *et al.* 2016; Kind & Kühlenkamp 2018). Thanks to the courtesy of Hans De Blauwe, we were able to compare our material with SEM images of *S. prolifica* from the Netherlands. Our material differs from *S. prolifica* in the ligula of the suboral avicularium (present in *S. spinigera*, absent in *S. prolifica*), in the orientation of the suboral avicularium (perpendicular to the frontal shield in *S. prolifica*, oblique in *S. spinigera*), and also in the pores of the ovicell (with raised margins in *S. spinigera*, with smooth margins in *S. prolifica*).

Smittoidea sp. of Schwindt *et al.* (2014) is the specimen of San Antonio Este stored at MACN-In 43883. *Smittoidea spinigera* was not found again at this harbour in 2018, whose pilings are now heavily populated by the introduced solitary ascidian *Styela clava* (Herdman) (Pereyra *et al.* 2017; Castro *et al.* 2021).

Distribution. China (Liu 1990; Liu *et al.* 2001 and references therein), Buenos Aires and Río Negro provinces (this study, and previous reports in Schwindt *et al.* 2014, 2020; Liuzzi *et al.* 2018). Although it was found on marine debris transported to the Hawaiian Islands and the NE Pacific by the 2011 tsunami that was generated by the Great East Japan Earthquake (McCuller & Carlton 2018), this is the first record of *S. spinigera* established in coastal areas beyond its area of origin.

Family Phidoloporidae Gabb & Horn, 1862

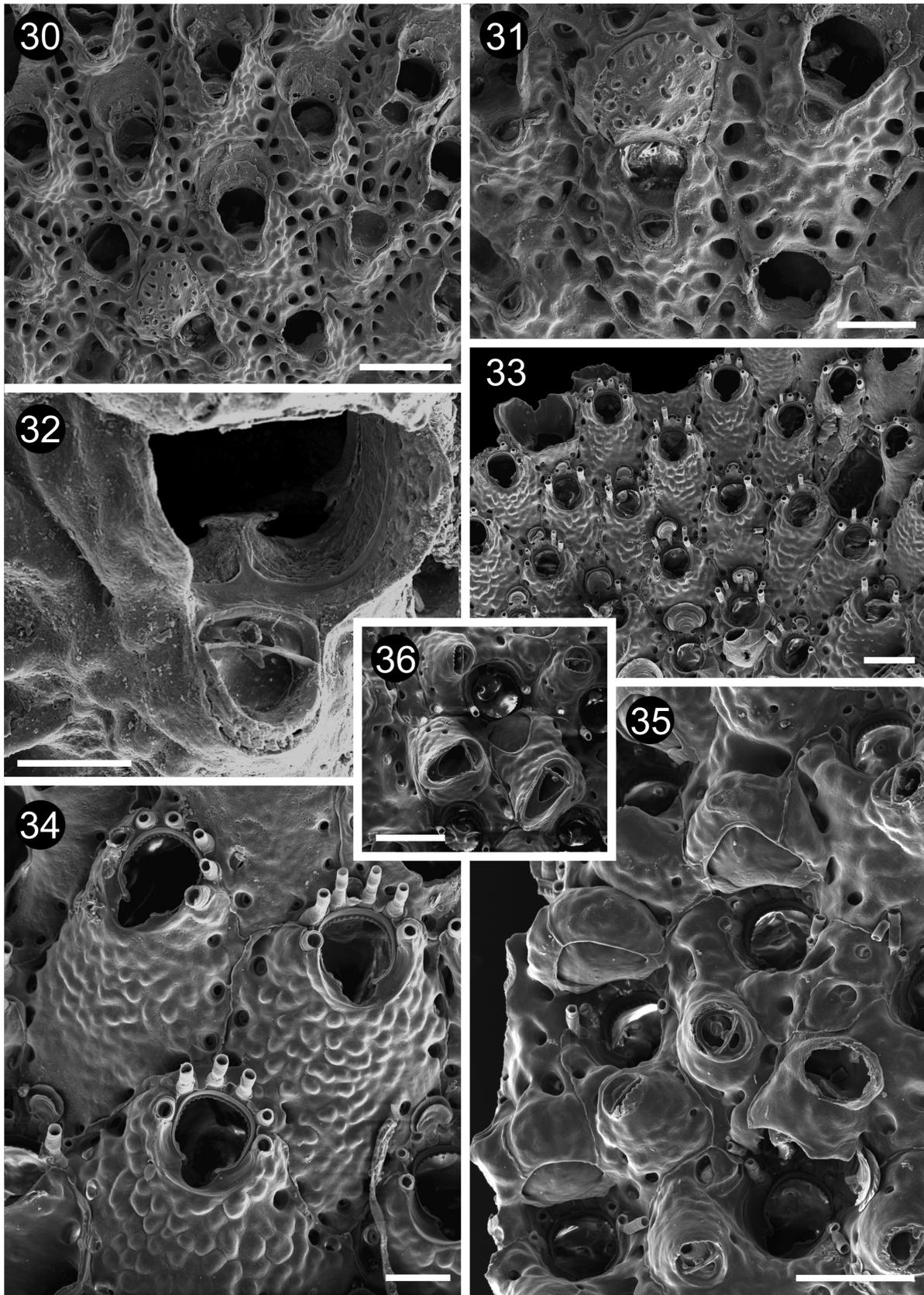
Genus *Stephanollona* Duvergier, 1921

Stephanollona boreopacifica Yang, Seo & Gordon, 2018

(Figs 33–36)

Stephanollona boreopacifica Yang *et al.* 2018: 510, figs 32–34.

Material examined. MACN-In 43884, San Antonio Este harbour, November 29, 2018, collected by Evangelina Schwindt.



FIGURES 30–36. **FIGURES 30–32.** *Smittoidea spinigera* (MACN-In 43883); **30**, general aspect; **31**, ovicelled zooid; **32**, close-up of primary orifice and suboral avicularium. **FIGURES 33–36.** *Stephanollona boreopacifica* (MACN-In 43884); **33**, growing margin; **34**, three zooids with oral spines; **35**, ovicells and smaller oval avicularia; **36**, close-up of larger triangular avicularia. Scale bars. **30, 33, 35, 36:** 200 μm ; **31, 34:** 100 μm ; **32:** 50 μm .

Description. Colony encrusting, multiserial, mostly unilaminar, but frontal budding may occur in central areas of large colonies. Autozooids with clear boundaries and regularly oriented only near the growing edge; with indistinct limits and unordered in central areas of mature colonies. Frontal shield nodular, surrounded by 7–14 marginal areolar pores. Orifice cleithriate; distal and lateral rims of anter beaded; sinus broadly U-shaped; condyles on sloping proximolateral shoulders of anter. Oral spines 5–6, long, cylindrical, only their basis remaining in ovicellate zooids. Avicularia adventitious, dimorphic, 1–2 per zooid, absent near the growing edge; avicularian cystid swollen, protruding. Smaller avicularia oval, obliquely orientated, with serrated rostral rim, thin crossbar, and ligula on rostral side of crossbar. Larger avicularia directed disto-laterally, rostrum elongate-triangular with rounded tip and extensive palatal shelf; opesia foramen semicircular; rostral foramen triangular, bordered by smooth cryptocyst, with a relatively long ligula projecting from the crossbar. Ooecium initially recumbent on distal zooid, its shape later obscured by secondary calcification, with rounded triangular frontal tabula and very short labellum; associated avicularia may occur on the ooecium in central parts of mature colonies. Ancestrula not seen.

Remarks. *Stephanollona boreopacifica* was previously known only from its original description. The disjunct geographic distribution and the appearance in a fouling assemblage of a Patagonian harbour suggests that this species should be regarded as a NIS that probably arrived in Argentina by maritime traffic.

Distribution. South Korea (Yang *et al.* 2018), Río Negro Province, Argentina (this study). This is the first record of the species for the Southern Hemisphere and the Atlantic Ocean.

Class Stenolaemata Borg, 1926

Order Cyclostomatida Busk, 1852b

Family Oncosoeciidae Canu, 1918

Genus *Microeciella* Taylor & Sequeiros, 1982

Microeciella argentina López-Gappa and Liuzzi n. sp.

(Figs 37–40)

Holotype. MACN-In 43885, sublittoral *Mytilus* bank off Mar del Plata, depth unknown (35–50 m according to Penchaszadeh 1974), January 15, 1971.

Paratypes. MACN-In 43886, Punta Pardelas, Chubut, on *Aulacomya atra*, collected by SCUBA diving by J. Callebaut, September 13, 1978.

Additional material. MACN-In 20570, mouth of Río Negro, A.R.A. “San Luis”, July 6, 1932. MACN-In 43887, Storni pier, Puerto Madryn, October 27, 2016, collected by Karen Castro.

Description. Colony encrusting, multiserial, thin, flat, initially fan-shaped, soon expanding by peripheral budding around its margin to attain an irregularly subcircular shape, maximum observed diameter 8 mm. Colour white when dried. Growing margin narrow, usually one generation of zooids visible at budding zone. Ancestrula only visible in young colonies, usually completely overgrown during astogeny; protoecium rounded, about 102 µm in diameter, with sparse, scattered pseudopores; distal tube elongate, strongly curved, about 344 µm long by 82 µm wide, aperture longitudinally elliptical, 83 by 48 µm, tilted to one side. Two distal zooids strongly curved to right and left budded from the ancestrula. Autozooids elongate, proximally indistinct; pseudopores scattered, teardrop-shaped, pointed distally, 5–6 µm wide. Apertures circular to longitudinally elliptical, 84–124 µm long by 65–80 µm wide, sometimes closed by pseudoporous diaphragms; peristomes low. One or more gonozooids near or at a certain distance from the margin of each colony; brood-chamber ovoidal to subcircular, elongate to wider than long (L/W 0.70–2.5), outline indented (but roof not crossed) by apertures of neighbouring autozooids; roof densely pseudoporous, with parallel wrinkles on its surface. Ooeciopore terminal, smaller than an autozooidal aperture, subcircular to transversely elliptical, 58 × 87 µm, erect or curved proximally.

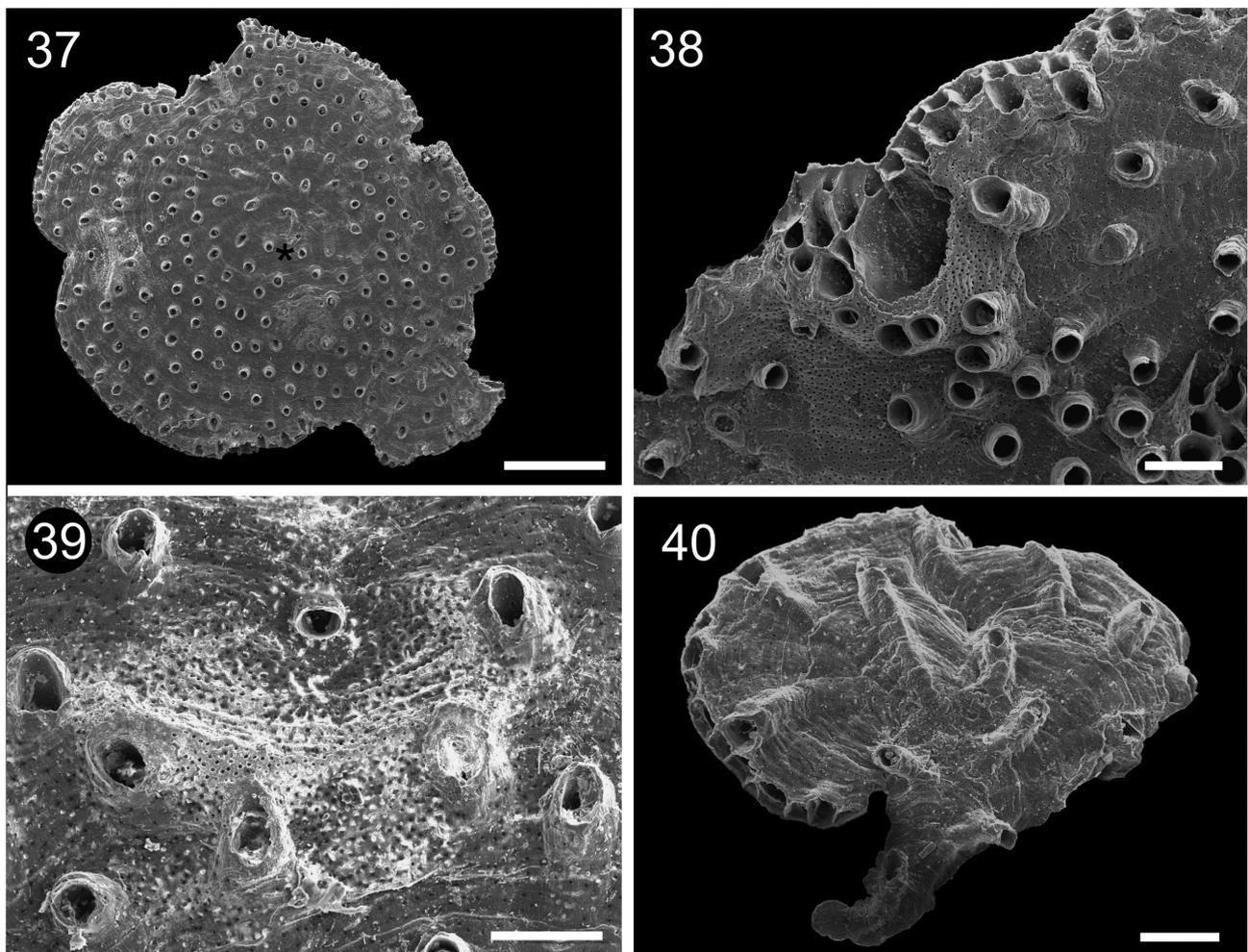
Remarks. A closely related species, *M. suborbicularis* (Hincks, 1880), has been recorded as a cenozoic fossil in Argentina. It has been mentioned for the early Paleocene (Danian, Roca Formation, Río Negro Province; Canu 1911), the late Oligocene (San Julián Formation, Santa Cruz Province; Canu 1904), and the early Miocene (Punta

Borja, Comodoro Rivadavia, Chenque Formation, Chubut Province; Canu 1908) of Patagonia. The examination of the material from the Roca Formation identified by Canu (1911) as *Diastopora (Berenicea) suborbicularis* (MACN-Pi 1885), however, shows that it is not conspecific with *M. suborbicularis*. One of the two colonies deposited in the MACN-Pi collection was reproductive. Its gonozooid differs from that of the Recent *M. suborbicularis* by being twice as wide as long, with its roof penetrated by autozooidal peristomes, as has been recently described for *Platonea* sp. from the Roca Formation (Brezina *et al.* 2021). A re-examination of the Oligocene and Miocene materials (Canu 1904, 1908) from Patagonia would be necessary to confirm their identity.

Microeciella argentina n. sp. differs from *M. suborbicularis*, a well-known European species (see Harmelin 1976, as *Microecia suborbicularis*; Hayward & Ryland 1985a, b; De Blauwe 2009, as *Eurystrotos compacta*; Taylor & Zaton 2008), in the L/W ratio of the gonozooid (longer than wide in *M. suborbicularis*, longer than wide to wider than long in *M. argentina* n. sp.), in the shape of the brood chamber roof (draped back over the proximal frontal wall in *M. suborbicularis*, crossed by wrinkles in *M. argentina* n. sp.), and in the shape of the ancestrula (distal tube of the ancestrula straight in *M. suborbicularis*, strongly curved in *M. argentina* n. sp.). Genetic studies would help to better distinguish the two species.

According to the material examined, *M. argentina* n. sp. is present in coastal localities of Río Negro and Chubut provinces at least since 1932, and in a sublittoral mussel bank off Buenos Aires Province since 1971.

Distribution. Buenos Aires, Río Negro and Chubut provinces, Argentina (this study).



FIGURES 37–40. *Microeciella argentina* n. sp.; **37**, general aspect (Holotype, MACN-In 43885). The likely location of the overgrown ancestrula is marked with an asterisk; **38**, colony margin and developing gonozooid (Paratype, MACN-In 43886); **39**, close-up of gonozooid (Holotype, MACN-In 43885); **40**, ancestrula and early astogeny (Paratype, MACN-In 43886). Scale bars. **37**: 1000 µm; **38–40**: 200 µm.

Discussion

Many species arriving in a new region may have small and restricted populations (Carlton 2009), persisting as minor components of ecological assemblages without ever becoming invasive (Williamson & Fitter 1996; Coutts *et al.* 2018). Some NIS may explode quickly, others undergo a prolonged lag between arrival and population outbreak (Crooks & Soulé 1999; Rilov *et al.* 2004). None of the bryozoan species found in harbours surveyed in this study has yet become abundant in Patagonia. *Fenestulina delicia*, however, has been reported as a highly invasive fouler along the Atlantic coasts of Europe (De Blauwe *et al.* 2014), and reached densities of almost 5,000 colonies.m⁻² in Quequén harbour (Buenos Aires Province) in 2013 (López-Gappa & Liuzzi 2016). *Bugula neritina*, *Bugulina flabellata* and *Cryptosula pallasiana* are among the most commonly encountered marine fouling bryozoans in ports and marinas around the world (Gordon & Mawatari 1992), but have not yet achieved high abundances in Patagonian harbours. These three species, plus *Fenestulina delicia*, were previously reported in harbours of Buenos Aires province (Lichtschein de Bastida & Bastida 1980; López-Gappa & Liuzzi, 2016), and are now present in Patagonian harbours. *Bugula neritina*, *Bugulina flabellata* and *Fenestulina delicia* have so far only been found within Argentine harbours but not in natural intermediate areas, supporting the hypothesis that domestic traffic has the potential for regional spread of NIS, as has been highlighted in a recent study of hull fouling in an oceanographic vessel serving routes in the southwest Atlantic (Meloni *et al.* 2021).

Detecting the presence of NIS may be challenging, particularly for little known taxa, requiring comprehensive field surveys and rigorous taxonomic analyses (Wasson *et al.* 2000). The fouling assemblages of Mar del Plata harbour were thoroughly sampled during the 1960's and 1970's (Lichtschein de Bastida & Bastida 1980, and references therein). The presence of *Buskia socialis* in Mar del Plata, however, remained unnoticed, but is now confirmed by the finding of material obtained in 1968 and stored in a museum collection. The species was not detected again in Mar del Plata, but now appears almost 50 years later in San Antonio Este, a northern Patagonian harbour. The inconspicuous appearance of *B. socialis*, its low abundance, and the similarity of their colonies with those of *Amathia* spp. (as *Bowerbankia* spp. in Lichtschein de Bastida & Bastida 1980, see Waeschenbach *et al.* 2015) may explain the spatial and temporal inconsistency of its records in Argentina. Likewise, *Smittoidea spinigera* was found in two north Patagonian harbours over a time interval of eleven years. In this case, its population in San Antonio Este may have disappeared or dropped below detection level due to the outbreak of the invasive ascidian *Styela clava* during the 2010's (Pereyra *et al.* 2015, 2017; Castro *et al.* 2021).

It is known that the ability to detect and evaluate invasion risks is compromised by a deficit in taxonomic expertise (Ricciardi *et al.* 2021) and that taxonomic errors may cause cascade-like processes affecting hypotheses and management decisions (Bortolus 2008). For example, the invasion of the northern Californian coast by the European blue mussel, *Mytilus galloprovincialis* Lamarck, 1819, was masked during decades due to its morphological similarity with a native sibling species, *M. trossulus* A. Gould, 1850 (Geller 1999). Detailed morphometric analyses were necessary to distinguish *Schizoporella japonica* Ortmann, 1890, introduced from Japan to the Pacific coast of North America and Europe, from several native *Schizoporella* species (Ryland *et al.* 2014). Identification errors may also be caused by the incorrect assignation of voucher material in museum collections. Despite the advantages of molecular barcoding, Viard *et al.* (2019) showed that COI sequences of the introduced compound ascidian *Botrylloides diegensis* Ritter & Forsyth, 1917 were deposited in a public database and erroneously assigned as belonging to the native species *B. leachii* (Savigny, 1816).

The identification of the *Smittoidea* that appeared in San Antonio Este and Ingeniero White harbours was challenging and highlights the importance of taxonomy in invasion studies. It was known that the Californian species *S. prolifica* had invaded harbours in the Netherlands and the German North Sea since at least 1998 (De Blauwe & Faase 2004; Markert *et al.* 2016; Kind & Kuhlenkamp 2018), so we suspected that the same species was present in northern Patagonia. Only after the comparison of our material with SEM images of *S. prolifica* from the Netherlands it was possible to ascertain that the Patagonian colonies did not belong to *S. prolifica*, but to the Chinese species *S. spinigera*. Both the presence of *S. spinigera* and *Stephanollona boreopacifica* in San Antonio Este harbour suggest that overseas maritime traffic from East Asia may have been responsible for these invasions.

The present study showed a relatively higher number of non-indigenous and cryptogenic bryozoans in warm-temperate Buenos Aires Province and Patagonian harbours such as Ingeniero White, San Antonio Este and Puerto Madryn than in those located in cold-temperate waters such as Puerto Deseado and Ushuaia. While comparing marine fouling invasions in ports of Patagonia, Schwindt *et al.* (2014) found that San Antonio Este showed the highest

number of non-indigenous and cryptogenic species among the ports they studied, although its maritime activity was not the highest among the ports compared. In addition to water temperature, another possible explanation for this fact is that San Antonio Este is a major regional node for exporting goods, often receiving vessels laden with ballast water.

Vessel activity is a key driver determining the presence of NIS in coastal waters (Lindegren *et al.* 2022), but is not the only factor affecting the number of non-indigenous and cryptogenic species. Rumbold *et al.* (2020) examined the number of non-indigenous peracarid species in Mar del Plata and Puerto Madryn harbours. They found a higher number of NIS peracarids in Mar del Plata, which has higher levels of organic matter, organic carbon, hydrocarbons and tributyltin than Puerto Madryn, in spite of the more international maritime traffic in the latter (Schwindt *et al.* 2010).

Together with the first detection of NIS bryozoans, we also found some cases that, according with the available literature, may be interpreted as warm-temperate species reaching their southern distribution limits in northern Patagonia. As stressed by Lonhart (2009), collecting new range data is not a trivial matter, and often new range records may be the result of monitoring programs or surveys designed for other purposes. The warm-temperate bryozoan assemblage inhabiting Buenos Aires and Río Negro provinces is relatively undersampled compared with the Magellanic fauna living in southern Patagonia and the fjord region of southern Chile (López-Gappa 2000). This survey of fouling bryozoans in Patagonian harbours has coincidentally contributed to increase our knowledge of the still-understudied fauna of bryozoans inhabiting the warm-temperate coast of Argentina.

Acknowledgments

We are grateful to Hans De Blauwe for sending us SEM images of *Smittoidea prolifica* from The Netherlands. Fabián Tricárico operated the SEM at MACN. Claudia del Río allowed us access to Canu's material stored in the MACN-Pi collection. We thank Dennis Gordon and Kamil Zágóršek for improving the original version of our manuscript. Financial support by CONICET (PIP 2017–2019 No. 0254CO to JLG and MGL, PIP 508 to ES) and FONCYT (PICT 2016-1083 to ES) is acknowledged. Thanks to Sandra Fiori and Eder dos Santos for the Ingeniero White sampling in 2016 and to the SCUBA diving Team of Prefectura Naval Argentina for the sampling carried out at San Antonio Este, Comodoro Rivadavia and Puerto Deseado under the project GCP/ARG/023/GF.

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