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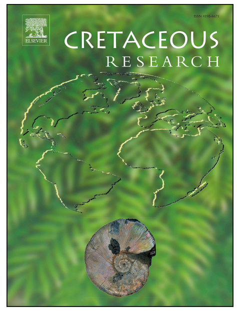

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Author statement

The authors S. Brezina, P. Taylor, M. Romero, E. Palópolo and S. Casadío, certify that all of us have seen and approved the final version of the manuscript, which is being submitted.

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Upper Maastrichtian and Danian bryozoans from Northern Patagonia, Argentina

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ABSTRACT

The specimen-rich and diverse bryozoan fauna encrusting oyster shells from the Maastrichtian and Danian Jagüel and Roca formations in the Neuquén Basin (Patagonia, Argentina) is described. Thirteen cyclostome species are recorded, along with 18 cheilostomes. We introduce two new species: *Akatopora kaufmanni* sp. nov. and *Eoporella lunata* gen. et sp. nov. The latter is a homeomorph of the common Miocene–Recent genus *Microporella*. Ten of the cyclostomes and ten of the cheilostomes could not be identified at species-level because of preservational limitations or lack of diagnostic characters in the available specimens. The most common bryozoans present are sheet-like colonies, among which the ascophoran cheilostome *Balantiostoma* is particularly well represented. Results show that in northern Patagonia the diversity of encrusting bryozoans associated with oyster shells exhibits no major changes across the K/Pg boundary. However, an important increase in the diversity is recorded during the upper Danian.

Keywords:
Taxonomy
Cyclostomata
Cheilostomata
Maastrichtian
Danian
Neuquén Basin
Patagonia

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1. Introduction

The fossil record of bryozoans is rich and extends back to the Ordovician. Bryozoans radiated rapidly during the Late Cretaceous and were diverse and abundant in many marine environments, peaking for both cheilostomes and cyclostomes in the Maastrichtian prior to the K/Pg boundary (Taylor and Waeschenbach, 2015). Late Cretaceous bryozoans are best known from northern Europe thanks largely to the works of the prolific taxonomist Ehrhard Voigt (1905–2004). Rich bryozoan faunas also occur in the Late Cretaceous of central Asia and Europe (Voigt, 1967; Favorskaya, 1985, 1987, 1988, 1992; Koromyslova et al., 2018a, b, c; Koromyslova et al., 2019a, b; Koromyslova and Seltser, 2020), southeastern North America (Taylor and McKinney, 2006; Sogot et al., 2013; 2014), Madagascar (Di Martino et al., 2018) and India (Guha and Nathan, 1996; Taylor and Di Martino, 2018). Bryozoan assemblages reported from tropical environments of Late Cretaceous age are scarce (Di Martino and Taylor, 2013). Late Cretaceous and Paleocene bryozoans are poorly known from South America, where knowledge is largely limited to the work by Canu (1911). Many of the species described by Canu have never been revised and are difficult to interpret from his figures which are retouched photographs. Furthermore, several specimens in his collection housed at the Museo Argentino de Ciencias Naturales Bernardino Rivadavia are missing. This hampers identification of species, which is a strong impediment for comparisons with coeval associations and for studies that could reveal how bryozoans responded to changes associated with the Cretaceous-Paleogene boundary events in South America.

Bryozoans commonly occur as encrustations on hard substrates that include rocks, clasts and the skeletons of living and dead organisms (Taylor and Wilson, 2003). Prominent among skeletal substrates are oysters, which have a high preservation potential in the fossil record. Oysters from the Late Cretaceous–early Paleogene marine successions in Patagonia are abundant and quite well-preserved (Casadío, 1998). They support a rich variety of boring and encrusting sclerobionts, including sponges, polychaetes, bivalves, fungi, algae, barnacles and bryozoans (Brezina et al., 2014, 2017). The aim of our work here is to describe the Maastrichtian and Danian bryozoan faunas encrusting oyster shells from the Jagüel and Roca formations of the Neuquén Basin (Patagonia, Argentina). Aside from its regional significance, this study adds to our limited knowledge of Southern Hemisphere fossil bryozoan faunas from the Late Cretaceous (Taylor, 2019), and to extinction and survival of bryozoans across the K/Pg boundary (e.g. Stilwell and Håkansson, 2012).

2. Geological setting

The Neuquén Basin in west-central Argentina covers parts of the provinces of Río Negro, Neuquén, La Pampa and Mendoza (Fig. 1). Rocks exposed in the basin range in age from Late Triassic to Paleogene. A major transgression from the South Atlantic into the basin occurred during the Maastrichtian to Danian, a time of relative tectonic quiescence and low volcanic activity (Malumián and Náñez, 2011). This transgression reduced the southern tip of South America (Patagonia) to an archipelago during the K/Pg boundary (Aguirre-Urreta et al., 2008). In the

Neuquén Basin, the sediments deposited by this transgression are represented by the Jagüel and Roca formations.

In the deeper parts of the basin mudstones dominate the Maastrichtian and lower Danian deposits (Jagüel Formation). They are massive and presumably intensely bioturbated, indicating a well-oxygenated seafloor (Scasso et al., 2005). The lithology and fossils indicate deposition at mid-shelf depths (Brezina et al., 2014). Shallower proximal areas mainly consist of limestones of the Roca Formation. This formation, which comprises bioclastic packstones and grainstones deposited in subtidal to intertidal settings, shows a regressive character, and has been dated as Maastrichtian in the northern part of the basin (north of 36ºS) but is Danian in age for outcrops in the central and southern parts.

Circulation within the Neuquén Basin was slightly restricted during the upper Maastrichtian and lower Danian (Scasso et al., 2005). Evaporites and mixed carbonate-siliciclastic lithologies in the northernmost part of the Neuquén Basin suggest semi-arid and hypersaline conditions in that part of the basin (Kiessling et al., 2006). The occurrence of salinity stratification in the northwestern part of the Neuquén Basin during the upper Maastrichtian is indicated by high percentages of prasinophytes that suggest stratified and saline waters (Prámparo et al., 2014). Foraminiferal and nannofossil analyses in the central part of the basin indicate that sedimentation during the upper Maastrichtian took place in relatively shallow middle neritic depths (Keller et al., 2007) and normal marine conditions, evidenced by the presence of relatively few terrestrial palynomorphs (Woelders et al., 2017; Guler et al., 2019).

The TEX_{86} based sea surface temperatures obtained by Woelders et al. (2017) in the Jagüel and Roca formations show that the last two million years of the Cretaceous were characterized by multiple warming and cooling phases, with average sea surface temperatures varying between 23°C and 29°C. Within the K/Pg boundary layer, sea surface temperature dropped to <19°C, followed by a rapid warming to 31.6°C. de Winter et al. (2018), based on stable oxygen isotope thermometry of Maastrichtian oyster shells, retrieved water temperatures of 11°C. Discrepancy with TEX_{86}

palaeothermometry was attributed to seasonal bias in the growth of the oysters, while TEX_{86} data appear to be biased towards warmer sea surface water temperatures (de Winter et al., 2018).

3. Material and methods

All of the bryozoans described here are encrusting species. The oyster shells to which they are cemented were collected in the field by bulk sampling from eight localities (Figs. 2). Cleaning methods included scrubbing under running water with a soft toothbrush and brief ultrasonic cleaning. The bryozoans were sorted and preliminary identifications made with the aid of binocular microscopes. The best-preserved specimens were selected for uncoated scanning electron microscopy (SEM) using a LEO 1455VP operating in low vacuum mode at the Natural History Museum, London. Back-scattered images were captured digitally.

Existing material in museum and other collections, as well as specimens newly collected in the field or described in a recent paper (Taylor and Brezina, 2018), were utilized for this study. Repository abbreviations for material in museum collections are as follows: GHUNLPam, Cátedra de Geología Histórica de la Universidad Nacional de La Pampa, Santa Rosa, Argentina; MACN, Museo Argentino de Ciencias Naturales, Ciudad Autónoma de Buenos Aires, Argentina; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; NHMUK, Natural History Museum, London, UK.

Except where noted, measurements were made from zones of astogenetic repetition. All zooidal measurements were taken from digital SEM images. Each measurement is given in the text as mean +/- standard deviation, with the number of specimens used and total number of measurements or counts made enclosed in parenthesis.

Measurements of the cheilostomes use the following abbreviations: AL, avicularium length; AW, avicularium width; OL, orifice length; OW, orifice width; OOW, ovicellate zooid orifice width (where different from normal orifice width); OpL, opesia length; OpW, opesia width; OvL, ovicell length, OvW, ovicell width; ZL, autozooid length (as seen on colony surface); ZW, autozooid width (as seen on colony surface).

Measurements of cyclostomes are identified by some of the same abbreviations as for cheilostomes but with the addition of the following: AD, diameter of equidimensional apertures; AS, distance between midpoints of adjacent apertures; ASW distance between midpoints of adjacent apertures within a row or fascicle; BCL, brood chamber length; BCW, brood chamber width; BrD, ADmn, minimum diameter of apertures; ADmx, maximum diameter of apertures; FS, Distance between centres of successive fascicles; branch diameter or width; FWL, frontal wall length of single zooid; FWW, maximum frontal wall width of single zooid; Gap, distance between edges of adjacent fascicles; GL, gonozooid length including proximal portion and brood chamber; GW, gonozooid width; NAD, nanozooid aperture diameter; OD, ooeciopore diameter.

4. Systematic palaeontology

All the bryozoans described in this work encrust oyster shells from the upper Maastrichtian to the upper Danian of Northern Patagonia, and are listed in Table 1.

Order: Cyclostomata Busk, 1852

Suborder: Tubuliporina Milne Edwards, 1838

Family: Stomatoporidae Pergens and Meunier, 1886

Genus *Voigtopora* Bassler, 1952

Type species. *Alecto calypso* d’Orbigny, 1850, ‘Senonian’ [probably Santonian], Saintes, Charente Maritime, France (see Illies, 1976).

Voigtopora sp.

Fig. 3A─C

Material. MPEF-PI 6132.4, encrusting colony on a valve of *Cubitostrea ameghinoi* Ihering, 1902; upper Danian, Roca Formation, Cerros Bayos, La Pampa.

Description. Colony encrusting, uniserial (Fig. 3A, B), branches originating solely by lateral budding at 70°–90° to the parent branch (Fig. 3C); up to at least 6 autozooids between successive lateral branches. Autozooids broad, parallel-sided, their frontal walls containing abundant circular pseudopores; preserved peristomes short, apertures circular. Ancestrula not observed.

Measurements. AS 231±69.15 µm (2, 13); AD 107±13.34 µm (1, 3).

Remarks. This species somewhat resembles *Voigtopora maconensis* Taylor and McKinney, 2006 from the Late Cretaceous of the southeastern USA, but has shorter, stouter autozooids. Another North American species, *V. thurni* Taylor and McKinney, 2006, possesses autozooids of similar length to those of the Roca *Voigtopora* but ramifications occur both dichotomously and by lateral branching (as in *V. calypso*, the type species of *Voigtopora*), whereas the Roca species shows only lateral ramifications. The lack of an ancestrula and early astogenetic stages in available material discourages the introduction of a new species for the Roca material.

Family: Oncousoeciidae Canu, 1918

Genus *Oncousoecia* Canu, 1918

Type species. *Tubulipora lobulata* Canu, 1918, Recent, British Isles (see Taylor and Zatoń, 2008).

?*Oncousoecia* sp. 1

Fig. 3D–E

Material. MPEF-PI 6132.25, encrusting colony on a valve of *Pycnodonte (Phygraea) sarmientoi* Casadío, 1998; upper Danian, Roca Formation, Casa de Piedra, La Pampa.

Description. Colony encrusting, oligoserial, branches smoothly lobate. Autozooids elongate, the flat frontal walls perforated by subcircular to drop-shaped pseudopores 10 µm in diameter (Fig. 3D); zooidal boundaries not clearly defined; preserved peristomes short, tapering distally; apertures 50 µm in diameter (Fig. 3E). Kenozooids probably present along lateral edges of branches where autozooidal apertures are lacking. Gonozooids and early astogenetic stages not observed.

Measurements. AS 196±48.70 µm (1, 18); AD 54±12.54 µm (1, 19).

Remarks. Although this species is consistent with *Oncousoecia* in colony-form and autozooidal morphology, gonozooids have not been observed and its assignment to this genus must remain tentative. It also resembles, as does ?*Oncousoecia* sp. 2 described below, some species of the Cretaceous stomatoporid *Proboscinopora* Pitt and Taylor, 1990, a genus lacking basal gonozooids.

?*Oncousoecia* sp. 2

Fig. 3F–H

Material. MPEF-PI 6132.9, colony encrusting a valve of *Pycnodonte (Phygraea) sarmientoi*; upper Danian, Roca Formation, Casa de Piedra, La Pampa.

Description. Colony encrusting, oligoserial with bifurcating branches; branch surface marked by fine transverse rugae (Fig. 3F–G). Autozooids elongate with slightly convex frontal walls perforated by subcircular pseudopores 10 µm in diameter (Fig. 3H). Zooidal boundaries moderately well defined; preserved peristomes short, thick; apertures circular. Gonozooids and early astogenetic stages not observed.

Measurements. AS 387±101.16 µm (1, 19); AD 83±11.97 µm (1, 16); FWL 403±43.17 µm (1, 8); FWW 160±28.02 µm (1, 13).

Remarks. Despite the absence of gonozooids, the oligoserial colony-form allows tentative assignment of this species to *Oncousoecia*. The autozooids of ?*Oncousoecia* sp. 2 are appreciably larger than those of ?*O*. sp. 1 (*c*. 80 µm vs. *c*. 55 µm) and zooidal boundaries are more distinct because of the greater convexity of the frontal walls.

?*Oncousoecia* cf. *striata* Canu, 1911

Fig. 4A–F

cf. 1911 *Proboscina striata* Canu, p. 267, pl. 9, figs 8, 9.

Material. MPEF-PI 6132.26, colony encrusting a valve of *Pycnodonte (Phygraea) sarmientoi*; lower Danian, Roca Formation, Casa de Piedra, La Pampa.

Description. Colonies encrusting, oligoserial with bifurcating branches 2–4 zooids wide (Fig. 4A). Ancestrula long, protoecium a flattened hemisphere with a concentric ridge inwards of the margin, without visible pseudopores. Two budded autozooids before the high-angled first branch bifurcation (Fig. 4B–C). Autozooids slightly convex with narrow salient boundary walls; apertures isolated or irregularly clustered into groupings of 2–5 (Fig. 4D, F). Preserved peristomes short to moderate in length. Possible base of an erect stem observed at distal end of an encrusting branch (Fig. 4E).

Measurements. AS 160±76.78 µm (2, 16); AD 96±11.11 µm (1, 9).

Remarks. Specimens studied here have somewhat higher branches than those of the material of ?*O. striata* (MACN-PI 1880) described by Canu (1911) and may represent a distinct species. The lack of gonozooids makes generic attribution difficult but colony-form suggests that this species, as well as the species of Canu (1911), most likely belongs to *Oncousoecia*. However, it may alternatively be the encrusting base of a genus that normally grows erect, such as *Entalophoroecia* Harmelin, 1976.

Genus *Axilosoecia* Taylor and Brezina, 2018

Type species. *Axilosoecia giselae* Taylor and Brezina, 2018, upper Danian, Roca Formation, La Pampa, Argentina.

Axilosoecia giselae Taylor and Brezina, 2018

Fig. 5A–E

2018 *Axilosoecia giselae* Taylor and Brezina, p. 442, fig. 1A–D.

Material. MPEF-PI 6132.28, 6132.31 (holotype), MPEF-PI 6132.28, 6132.33 (paratype) encrusting valves of the oyster *Cubitostrea ameghinoi*, upper Danian, Roca Formation, Cerros Bayos, La Pampa.

Description. Colony encrusting, uniserial, with branches bifurcating at about 90°(Fig. 5A), each internode consisting of one or occasionally two or three zooids (Fig. 5B). Early astogenetic stages with autozooids, about 200 µm long and higher angled bifurcations. Autozooids small, elongate, about 290–400 µm long by 90 µm wide in the zone of astogenetic repetition; apertures tiny, subcircular, about 0.04–0.05 mm wide, preserved peristomes short. Gonozooids positioned in axils of branch bifurcations, long proximal part indistinguishable from an autozooid, distal bulbous part seeming to originate from the peristome and descending onto the substrate (Fig. 5C−D), usually longitudinally elliptical, 230–400 µm long by 200–400 µm wide; ooeciopore subterminal, small, transversely elliptical or subcircular, minute, about 20–30 µm wide (Fig. 5E).

Measurements. BrD 91±15 µm (1, 5); GL 269±27 µm (1, 2); GW 250 µm (1,2).

Remarks. This was one of two new species of *Axilosoecia* described when the genus was introduced by Taylor and Brezina (2018). Both species are characterized by uniserial, runner-like colonies with gonozooids located in the axils of the branch bifurcations. The second species, *A. mediorubiensis* Taylor and Brezina, 2018 from the early Miocene of New Zealand, has longer autozooids, usually more zooids per internode, and gonozooids lacking an autozooid-like proximal part. Since the paper introducing *Axilosoecia* was published, an undescribed species referable to this genus has been found in collections from the Coon Creek Member (Ripley Formation) of New Albany, Union County, Mississippi (PDT unpublished). This Maastrichtian species more strongly resembles *A. giselae* than it does *A. mediorubiensis*.

Family: Tubuliporidae Johnston, 1838

Genus *Platonea* Canu and Bassler, 1920

Type species. *Reptotubigera phillipsae* Harmer, 1915, Recent, Loyalty Island, Australia.

Platonea sp.

Fig. 6A–B

Material. MPEF-PI 6132.5, colony encrusting a valve of *Pycnodonte (Phygraea) sarmientoi*; upper Danian, Roca Formation, Casa de Piedra, La Pampa.

Description. Colony encrusting, comprising a single, curved lobate branch (Fig. 6A) with a wide crescentic growing edge. Ancestrula short, protoecium hemispherical, 95 µm in diameter, smooth surfaced, apparently lacking pseudopores, giving rise to a short distal tube (Fig. 6B). Autozooids in closely spaced, curved transverse rows on either side of branch midline, each row typically with 3 or 4 connate apertures rounded rectangular in shape. Frontal walls convex, the furrows between them delineating clearly the zooidal boundaries. A possible gonozooid with broken roof visible.

Measurements. ADmx 93±5 (1,8); ADmn 82±4 (1,6); FS 219±13 µm (1, 4).*Remarks.* This small colony may perhaps be the species incorrectly attributed by Canu (1911, p. 275) to *Idmonea carinata* Römer, 1840. It is also similar to *Platonea adnata* Taylor and McKinney, 2006 from the Maastrichtian Peedee Formation of North Carolina, which, however, has larger autozooids and a protoecium of substantially greater diameter (165–196 µm vs. 95 µm in the Roca specimen). Introduction of a new species for the Roca cyclostome is deferred pending the discovery of an intact gonozooid complete with ooeciopore.

Family: Plagioeciidae Canu, 1918

Genus *Plagioecia* Canu, 1918

Type species. *Tubulipora patina* Lamarck, 1816, Recent, Europe.

Plagioecia sp.

Fig. 6C–F

Material. MPEF-PI 6132.18. Colony encrusting a valve of *Ostrea wilckensi*; upper Danian, Roca Formation, General Roca, Río Negro.

Description. Colony encrusting, multiserial, reniform in overall shape due to the non-preservation of one side (Fig. 6C), probably originally subcircular. Gonozooids with conspicuously inflated brood chamber (Fig. 6D–E), two times wider than long, oval to rounded triangular with straight distal edge; roof penetrated by numerous autozooidal peristomes; ooeciopore located centrally, slightly smaller than an autozooidal aperture and somewhat transversely elongate. Narrow budding zone exposing one or two generations of autozooids. Protoecium and ancestrula not seen. Autozooids arranged in a roughly quincuncial pattern; frontal walls elongate, becoming more convex distally, zooidal boundaries generally distinct; pseudopores conspicuous (Fig. 6F), longitudinally oval; apertures subcircular, isolated; preserved peristomes short, inclined distally.

Measurements. AS 285±35 µm (1, 11); AD 58±7 µm (1, 10); BCL 750 µm (1, 1); BCW 1475±177 µm (1, 2).

Remarks. The transversely elongate brood chamber pierced by autozooids is typical of the genus *Plagioecia* among cyclostomes of the '*Berenicea*' type (Taylor and Sequeiros, 1982). We defer introducing a new name for this species because a large number of closely similar bereniciform species have been described from the Late Cretaceous to Danian but in very few cases are these well enough known (e.g. gonozooids are often not described) to be accurately compared with the Roca species. It is beyond the scope of the present paper to revise these species in order to establish that the Roca species is new.

Plagioecia aff. *cristata* Taylor and McKinney, 2006

Fig. 7A–E

Plagioecia aff. 2006 *Plagioecia cristata*; Taylor and McKinney, p. 31, pl. 13.

Material. MPEF-PI 6132.18. Colony encrusting a valve of *Ostrea wilckensi*; upper Danian, Roca Formation, General Roca, Río Negro.

Description. Colony encrusting, multiserial, subcircular in outline. Budding zone moderately broad, exposing two to three generations of autozooidal buds. Peripheral subcolonies developed at budding zone, subcircular, partly overgrowing parent colony (Fig. 7A, upper right). Ancestrula not visible: earliest astogenetic stages fouled by a small oyster in the single specimen studied. Autozooids arranged quincuncially, about three or four times longer than wide (Fig. 7B); frontal wall convex with a prominent median keel (Fig. 7C), autozooidal boundaries generally distinct; pseudopores conspicuous, longitudinally oval; apertures circular or longitudinally elongate, isolated, never connate; peristomes inclined distally, preserved length short. Gonozooids with conspicuously inflated brood chambers (Fig. 7D–E), transversely elongate, at least twice wider than long, penetrated by autozooidal peristomes around the edge and occasionally more centrally. Ooeciopore terminal, smaller than an autozooidal aperture, transversely elongated, about half the diameter of an autozooidal aperture.

Measurements. AS 285±35 µm (1, 11); AD 58±7 µm (1,10); BCL 750 µm (1, 2); BCW 1475±177 µm (1, 2).

Remarks. This species shows a close similarity to *Plagioecia cristata* Taylor and McKinney, 2006 from the Maastrichtian of the southeastern USA. However, the gonozooids are broader in specimens from the Roca Formation. The Roca species is also similar to *Plagioecia parvipora* (Canu, 1922), *'P'*. *formosa* (Canu, 1922) and *'Plagioecia' antanihodiensis* Di Martino, Martha and Taylor, 2018 from the Maastrichtian of Madagascar. *P. parvipora* differs from *P.* aff. *cristata* in having a budding zone exposing only 1–2 generations of autozooids and in the flat frontal walls of the autozooids. *'Plagioecia' formosa* is the most similar of the Madagascan species to *P.* aff. *cristata*, but has a central, circular ooeciopore. Finally, *'Plagioecia' antanihodiensis* colonies have autozooids with convex frontal walls and small circular pseudopores.

Genus *Mesenteripora* de Blainville, 1830

Type species. *Mesenteripora michelinii* de Blainville, 1830, Bathonian, Calvados, Normandy, France (see Walter, 1970).

Mesenteripora sp.

Fig. 8A–E

Material. MPEF-PI 6132.28, encrusting base of a colony on a valve of *Pycnodonte (Phygraea) sarmientoi*; upper Danian, Roca Formation, Casa de Piedra, La Pampa.

Description. Colony base encrusting, multiserial, subcircular in outline, somewhat lobate, with six broken erect bifoliate fronds arranged radially (Fig. 8A). Early astogenetic stages present, ancestrula overgrown (Fig. 8B). Autozooids elongate, boundaries marked by a narrow ridge; frontal walls becoming more convex distally; preserved peristomes short, inclined distally; apertures arranged quincuncially, circular to longitudinally elongate, isolated, never connate (Fig. 8C). Gonozooid with inflated brood chamber (Fig. 8D), slightly wider than long, oval to semicircular with straight distal edge, incorporating peristomial bases of some neighbouring autozooids (Fig. 8E); ooeciopore located on distal edge of brood chamber, minute, subcircular. Secondary nanozooids evident as autozooids capped by terminal diaphragms with a tiny central aperture on a short peristome (Fig. 7D–E)

Measurements. AS 240±32 µm (1, 13); AD 77±20 µm (1, 13), OD 56 µm (1, 1), NAD 60±4 µm (1, 3).

Remarks. *Mesenteripora* has erect colonies with bifoliate branches, either broad and frondose or less often narrow and palmate. Only the bases of the branches are preserved in the Roca specimen which resembles *Mesenteripora lirella* Taylor and McKinney, 2006 from the Campanian of Delaware, USA, but differs in having secondary nanozooids and autozooids lacking a prominent median keel on their frontal walls.

Genus *Actinopora* d'Orbigny, 1853

Type species. *Actinopora regularis* d'Orbigny, 1853 (= *Ceriopora stellata* Koch & Dunker, 1837), Valanginian, Sainte-Croix, Switzerland.

Actinopora robertsoniana Canu, 1911

Fig. 9A–E

1911 *Actinopora robertsoniana* Canu, p. 276, pl. 12, fig. 3.

Material. MPEF-PI 6132.17, colony encrusting a valve of *Ostrea wilckensi*; upper Danian, Roca Formation, General Roca, Río Negro.

Description. Colony encrusting, discoidal, unilaminar (Fig. 9A). Autozooidal apertures arranged in radial fascicles separated by areas of exterior wall containing circular pseudopores; fascicles initially uniserial, becoming bi- or triserial (Fig. 9B); new fascicles intercalated between existing fascicles (Fig. 9C). Gonozooid (Fig. 9D) large, transversely elongate, narrow, distal edge almost straight, interrupting fascicles; brood chamber pierced by a single autozooidal peristome in figured example (Fig. 9E); ooeciopore terminal, obliquely transversely elongate, slightly larger than an autozooidal aperture.

Measurements. ASW 130±29 μm (1, 22); Gap 245±53 μm (1, 25); BCW 2933 μm (1, 1); BCL 533 μm (1, 1); OD 63 μm (1, 1).

Remarks. Encrusting cyclostomes attributed to *Actinopora* are very common in the Valanginian–Maastrichtian of Europe (e.g., Gregory, 1909), and the genus has also been recorded living at the present-day (Canu and Bassler, 1929). Colonies are discoidal, often develop peripheral subcolonies (Taylor et al., 2018, fig. 4f), have autozooidal apertures arranged in radial fascicles beyond the zone of astogenetic change, and possess gonozooids with transversely elongate brood chambers. In the absence of a modern revision of *Actinopora*, the relationships between the Roca species, which was named *A. robertsoniana* by Canu (1911), and other nominal species are unclear.

Family: incertae sedis

'*Berenicea*' sp.

Fig. 9F

Material. MPEF-PI 6132.13, colony encrusting a valve of *Ostrea wilckensi*; upper Danian, Roca Formation, General Roca, Río Negro.

Measurements. ZL 143±40 µm (1, 5); ZW 90±10 µm (1, 5).

Description. Colony encrusting, multiserial, unilaminar, immature, fan-shaped, measuring up to 500 µm in diameter, infertile; two generations of buds visible at growing edge. Autozooids about 100 µm long by 90 µm wide (Fig. 9F). Frontal wall convex. Peristomes broken. Ancestrula preserved, not overgrown, protoecium 100 µm in width.

Remarks. The species is left in open nomenclature, following the recommendations of Taylor and Sequeiros (1982) for infertile tubuliporines with 'bereniciform' colonies which, depending on the morphology of the gonozooid, may belong to *Microeciella* Taylor and Sequeiros, 1982, *Reptomultisparsa* d'Orbigny, 1853, *Hyporosopora* Canu and Bassler 1929, *Mesonopora* Canu and Bassler, 1929 or *Plagioecia*.

Suborder: Rectangulata Waters, 1887

Family: Lichenoporidae Smitt, 1866

Genus *Disporella* d'Orbigny, 1853

Type species. *Discopora hispida* Fleming, 1828, Recent, British Isles.

?*Disporella discoidea* (Canu, 1911)

Fig. 9G–H

1911 *Reptocavea discoidea* Canu, p. 278, pl. 12, figs 1–2.

Material. MPEF-PI 6132.63, colony encrusting a valve of *Pycnodonte* (*Phygraea*) *sarmientoi*, upper Danian, Roca Formation, Casa de Piedra, La Pampa.

Description. Colony encrusting, macula at centre slightly depressed (Fig. 9G). Autozooidal apertures longitudinally oval, arranged quincuncially. Alveoli small, located between autozooids and filling macula (Fig. 9H). Gonozooid not seen.

Measurements. OL 82±7 µm (1, 7); OW 52±4 µm (1, 7).

Remarks. The taxonomy of rectangulate cyclostomes is difficult and generic definitions are vague. Therefore, the assignment of Canu's (1911) species to *Disporella* is very tentative, made more so by the lack of a gonozooid.

Suborder: Cerioporina von Hagenow, 1851

Family: Cerioporidae Busk, 1859

Genus *Ceriopora* Goldfuss, 1826

Type species. *Ceriopora micropora* Goldfuss, 1826, Maastrichtian, Maastricht, Netherlands (see Nye, 1976).

Ceriopora sp.

Fig. 10A–C

Material. MPEF-PI 6132.2, colony encrusting a valve of *Cubitostrea ameghinoi*; upper Danian, Roca Formation, Bajada de Jagüel, Neuquén.

Description. Colony encrusting, massive, compound, multilayered (Fig. 10A). Zooidal apertures polygonal, variable in size, lacking any clear dimorphism between autozooids and kenozooids (Fig. 10B–C). Gonozooid not seen.

Measurements. AS 109±13 µm (1, 35); AD 76±20 µm (1, 35).

Remarks. The genus *Ceriopora* has been used in a broad sense to include erect and massive encrusting species in which a clear distinction between larger autozooids and smaller kenozooids is typically lacking, as in the species described here from the Roca Fm. The type species of *Ceriopora*, *Ceriopora micropora*, was redescribed by Nye (1976), with emphasis on internal morphological characters (Hara, 2001).

Order: Cheilostomata Busk, 1852

Suborder: Membraniporina Ortmann, 1890

Superfamily: Membraniporoidea Busk, 1854

Family: Electridae Stach, 1937

Genus *Electra* Lamouroux, 1816.

Type species. *Flustra verticillata* Ellis and Solander, 1786, Recent, North Atlantic Ocean (see Nikulina et al., 2012).

Electra sp.

Fig. 10D–E

Material. MPEF-PI 6132.1, colony encrusting a valve of *Cubitostrea ameghinoi*; upper Danian, Roca Formation, General Roca, Río Negro.

Description. Colony encrusting, multiserial, forming irregular patches on the substrate. Autozooids elongate pyriform in frontal outline shape (Fig. 10D). Gymnocyst well-developed, in some zooids bearing a short spine on the median proximal border of the opesia (Fig. 10E). Cryptocyst narrow. Opesia longitudinally elliptical.

Measurements. ZL 314±22 µm (1, 9); ZW 200.00±22 µm (1, 11); OpL 210±24 µm (1, 10); OpW 163±13 µm (1, 7).

Remarks. The studied specimen resembles *Electra everretti* Taylor and McKinney, 2006 from the Maastrichtian of North Carolina, USA. However, *E. everretti* has a wider cryptocyst and more elongate autozooids. The fragmentary colony from Roca Fm. consists of only 18 to 20 poorly preserved zooids. While the Roca Fm. species, along with *E. everretti*, may be closer to *Einhornia*

Nikulina, 2007, the original diagnosis of *Ellinorina* stipulates the presence of calcified opercula, for which there is no evidence. It is therefore assigned to *Electra* in the broad sense of the genus.Nevertheless, the presence of a spine on the medioproximal edge of the opesia of some of these zooids allows it to be assigned to Electra *sensu lato*.

Genus *Conopeum* Gray, 1848

Type species. Millepora reticulum Linnaeus, 1767, Recent, North Atlantic Ocean.

Conopeum okaiana (Canu, 1911)

Fig. 10F–H

1911 *Membranipora okaiana* Canu, p. 224, pl. 2, fig. 10.

Material. GHUNLPam 17423, colony encrusting a valve of *Turkostrea argentina* Griffin, Casadío and Parras, 2005; lower Danian, Roca Formation, Liu Malal, Mendoza.

Description. Colony encrusting, multiserial, unilamellar (Fig. 10F). Autozooids arranged in well-defined longitudinal rows; broad and rounded hexagonal in frontal outline shape, usually longer than wide; gymnocyst lacking; cryptocyst broadest proximally, narrowing distally, not forming a distinct shelf; opesia oval or inverted pear-shaped, mural rim crenulated; imperforate closure plates present in some autozooids (Fig. 10H). Ancestrula and early astogeny unknown.

Measurements. ZL 235±88 µm (1, 28); ZW 175±67 µm (1, 27); OpL 302±21 µm (1, 6); OpW 205±32 µm (1, 6).

Remarks. *Conopeum spissamentum* Taylor and McKinney, 2006, from the Late Cretaceous of the southeastern USA, differs from *Conopeum okaiana* in normally having small kenozooids at the proximolateral corners of the autozooids which are more rectangular in outline shape. The closure plates of *C. spissamentum* and of two other species from the Late Cretaceous of the southeastern USA – *Conopeum nelsoni* Canu and Bassler, 1926 and *Conopeum paranelsoni* Taylor and McKinney, 2006 – are porous, unlike those of *C. okaiana*.

Suborder: Flustrina Smitt, 1868

Superfamily: Calloporoidea Norman, 1903

Family: Calloporidae Norman, 1903

Genus *Flustrellaria* d'Orbigny, 1853

Type species. *Flustrellaria fragilis* d'Orbigny, 1853, Cenomanian. Le Mans, France.

Flustrellaria sp.

Fig. 11A–C

Material. MPEF-PI 6132.21, colony encrusting a valve of *Pycnodonte (Phygraea) vesicularis* Lamarck, 1806; upper Maastrichtian, Jagüel Formation, Bajada del Jagüel, Neuquén.

Description. Colony encrusting, multiserial, unilaminar. Autozooids rounded rhomboidal in frontal outline, arranged more-or-less quincuncially (Fig. 11A); gymnocyst poorly developed; spine bases numbering about 8–10 (Fig. 11B), distributed circumopesially; cryptocyst finely pustulose, narrowing slightly distally; opesia longitudinally elliptical to pear-shaped. Ovicells broken and crushed (Fig. 10B). Interzooidal avicularia about half the size of autozooids, oval or inverted pear-shaped, rostrum apparently short and rounded (Fig. 11C). Ancestrula and early astogeny not observed.

Measurements. ZL 395±26 μm (1, 10); ZW 263±21 μm (1, 10); AL 327 μm (1, 1); AW 145 μm (1, 1); OpL 250±26 μm (1, 10); OpW 165±24 μm,15 (1, 10).

Remarks. *Flustrellaria* sp. differs from the US Late Cretaceous species *F. anatina* Canu and Bassler, 1926, which has large, spatulate interzooidal avicularia. However, the number of spines can be the same in both species (8–10), although these often include a larger mid distolateral pair in *F. anatina* (see Taylor and McKinney, 2006, pl. 50, fig. 1C).

Genus *Pyriporella* Canu, 1911

Type species. *Pyriporella ameghinoi* Canu, 1911, Danian, Argentina.

Pyriporella ameghinoi Canu, 1911

Fig. 11D–G

1911 *Pyriporella ameghinoi* Canu, p. 235, pl. 4, figs 8–9.

1911 *Pyriporella confluens* Canu, p. 236, pl. 4, figs 10–11.

Material. MPEF-PI 6132.18, colony encrusting a valve of *Ostrea wilckensi*; upper Danian, Roca Formation, General Roca, Río Negro.

Description. Colony encrusting, multiserial, unilaminate. Autozooids arranged more-or-less quincuncially, elongate pear-shaped (Fig. 11D); gymnocyst moderately developed proximally, narrowing laterally and absent distally, spine bases lacking; cryptocyst broad, proximally decreasing in width distally, sloping gently inwards; opesia oval, occupying approximately half of frontal surface area. Ancestrula subcircular, budding a distal and two distolateral zooids, no or few avicularia in early astogeny (Fig. 11E). Intramural buds present in a few zooids (Fig. 11F). Closure plates not seen. Ovicell hyperstomial, large, ectooecium usually completely calcified, a median fissure often evident (Fig. 11G). Avicularia interzooidal, small, numerous, located at corners of autozooids, oriented distolaterally, rounded, pivotal bar not calcified (Fig. 11G).

Measurements. ZL 329±88 µm (1, 15); ZW 257±98 µm (1, 15); AL 140±140 µm (1, 12); AW 70±18 µm (1, 12); OvL 206±14 µm (1, 6); OvW 253±18 µm (1, 5).

Remarks. The paratype of *Pyriporella confluens* Canu, 1911 (MACN-Pi 1844) has the same features as *P. ameghinoi* and is considered to be a junior synonym.

Family: Antroporidae Vigneaux, 1949

Genus *Akatopora* Davis, 1934

Type species. *Akatopora clausentina* Davis, 1934, Eocene, Hampshire, England (see Gordon 1986, plate 7E).

?*Akatopora* sp. 1

Fig. 12A–B

Material. MPEF-PI 6132.20, colony on a valve of *Amphidonte mendozana* Ihering, 1907; upper Maastrichtian, Roca Formation, Huantraico, Neuquén.

Description. Colony encrusting, multiserial, unilaminar (Fig. 12A). Autozooids quincuncially arranged and surrounded by smaller polymorphs that overlap their edges; longitudinally elongate; gymnocyst and cryptocyst not visible due to poor preservation and presence of polymorphs; opesia occupying most of frontal surface, oval. Ovicells not observed. Polymorphs, presumed to be avicularia, numbering about 2–4 per autozooid, directed distally or laterally (Fig. 12B).

Measurements. OpL 325±34 µm (1, 6); OpW 15±22 µm (1, 6); AL 77±11 µm (1, 11); AW 61±13 µm (1, 11).

Remarks. This specimen shows similarities with *Akatopora granulata* (Canu, 1911), but the poor preservation does not allow either the generic or specific identity to be confirmed.

Akatopora kaufmanni sp. nov.

Fig. 12C–E

Etymology. Named for the collector of the holotype, W. Kaufmann.

Diagnosis. *Akatopora* with very small autozooids; cryptocyst moderately wide, granular; opesia pear shaped.

Type horizon. Roca Fm. (Paleocene, upper Danian).

Material. Holotype: NHMUK D32352a, Danian, Roca Formation, General Roca, Rio Negro; collected by W. Kaufmann and purchased May 1927.

Description. Colony encrusting, multiserial, unilaminar (Fig. 12C). Autozooids surrounded by smaller polymorphs that overlap their edges (Fig. 12D); longitudinally elongate; gymnocyst reduced, broadest proximally and tapering distally along the margins of the zooids; cryptocyst moderately wide, tapering distally, inwardly sloping, granular; opesia occupying most of frontal surface, oval or pear-shaped. Intramural buds present but closure plates not observed. Ovicells hyperstomial, ectooecium fully calcified, sometimes with a medial suture, wider than long, *c*. 70µm long by 110 µm wide. Polymorphic zooids, which may be a mixture of avicularia and kenozooids, infilling most of the spaces between the autozooidal opesiae, variable in orientation and size, typically 80–130 µm long by 50–90 µm wide (Fig. 12E).

Measurements. ZL 284±44 µm (1, 7); ZW 160±27 µm (1, 7); OpL 187±8 µm (1, 7); OpW 121±18 µm (1, 7).

Remarks. This new species differs from both the US Maastrichtian species *Akatopora sulcata* (Canu and Bassler, 1926) (see Taylor and McKinney 2006, p. 88) and the New Zealand Recent species *Akatopora circumsaepta* (Uttley, 1951) (see Gordon 1986, p. 35) in its smaller autozooids with proportionally wider cryptocysts. Compared with the Maastrichtian species ?*Akatopora* sp. 1 described above, this Danian species also has smaller zooids. Together with *Cianotremella gigantea* Canu 1911, the holotype encrusts a Roca Formation oyster shell that was purchased by the NHMUK in 1927. Because the two species are so well preserved, they are described here even though the exact locality and stratigraphical horizon from which they were collected is uncertain.

Superfamily: Microporoidea Gray, 1848

Family: incertae sedis

Genus *Cianotremella* Canu, 1911

Type species. *Cianotremella gigantea* Canu, 1911, Danian, Roca Formation, Argentina.

Cianotremella gigantea Canu, 1911

Fig. 12F–H

1911 *Cianotremella gigantea* Canu, p. 257, pl. 7, fig. 14.

Material. NHMUK D32352b, Danian, Roca Formation, General Roca, Rio Negro; collected by W. Kaufmann and purchased May 1927.

Description. Colony encrusting, multiserial, unilaminar (Fig. 12F). Autozooids rectangular to elongate rhomboidal in shape, separated by thin, raised boundary walls; gymnocyst lacking; frontal wall an extensive cryptocyst occupying most of the frontal surface, convex, coarsely granular, apparently imperforate; opesia semicircular, proximal edge slightly bowed, a narrow distal oral shelf visible in some zooids; oral spines lacking. Ovicells absent in the studied specimen. One example of a vicarious kenozooid observed, a little narrower than the autozooids but about the same length; opesia longitudinally elliptical, slightly more than half of the length of the zooid; no associated avicularium. Avicularia present distally of most, possibly all, autozooids, transversely oriented, located within the boundary wall of the associated autozooid (Fig. 12G); rostrum with a rounded or subrounded tip, slightly curved to parallel the distal margin of the autozooidal opesia; a constriction dividing the avicularian opesia from the rostrum but no complete pivotal bars observed (Fig. 12H).

Measurements. ZL 550±62 µm (1, 10); ZW 370±44 µm (1, 10); OpL 123±8 µm (1, 10); OpW 178 ±14 µm (1, 10).

Remarks. Although *Cianotremella* is a distinctive genus, its family-level classification is uncertain. When introducing this monospecific genus, Canu (1911) believed it to be an ascophoran cheilostome. This opinion was followed by Bassler (1953) in the bryozoan *Treatise*. However, *Cianotremella* is clearly an anascan-grade cheilostome with an extensive cryptocystal frontal wall. It may be closely related to *Stictostega* (see Taylor and McKinney, 2006), with which it shares the presence of a small avicularium distal to the autozooid, although the perforations seen in the frontal walls of *Stictostega* Shaw, 1967 cannot be observed in *Cianotremella*. The specimen described here appears to be infertile. Canu (1911, p. 258) described the ovicell thus: “Ovicelle cachée dans la partie supérieure de la zoécie, s'ouvrant, par une fente saillante et transverse, au-dessus de l'aperture"; i.e., immersed and opening via a transverse slit.

Family: Aspidostomatidae Jullien, 1888

Genus *Aspidostoma* Hincks, 1881

Type species. Aspidostoma crassum Hincks, 1881 = *Eschara gigantea* Busk, 1854, Recent, South Atlantic.

Aspidostoma onychocelliferum Canu, 1911

Fig. 13A–D

1911 *Aspidostoma onychocelliferum* Canu, p. 254, pl. 6, fig. 12.

Material. MPEF-PI 6132.68, encrusting colony on a valve of *Pycnodonte (Phygraea) burckhardti* (Böhm, 1903)*;* lower Danian, Roca Formation, General Roca, Río Negro.

Description. Colony encrusting, multiserial, unilaminar. Autozooids rounded hexagonal, separated by deep grooves (Fig. 13A); cryptocystal frontal wall slightly convex, distally sloping inwards towards the opesia, granular (Fig. 13B); opesia wider than long, semi-elliptical. Ovicells hyperstomial, with a cryptocyst-like, non-porous surface. Ancestrula surrounded by six zooids, including a distal and two distolateral zooids budded directly from the ancestrula (Fig. 13C). Interzooidal avicularia small, elliptical, oriented parallel to the edges of the autozooids, pivotal bar not calcified (Fig. 13D).

Measurements. ZL 435±39 (1, 9); ZW 324±37 (1, 9); OpL 87±11 (1, 9); OpW 148±28 (1, 9); OvL 93±10 (1, 2); OvW 129±20 (1, 2); AL 133±38 (1, 3); AW 83±7 (1, 3).

Remarks. Aspidostoma is endemic to the Southern Hemisphere; Cretaceous species assigned to this genus from France belong elsewhere (Taylor, 2019). *Aspidostoma onycocelliferum* Canu, 1911 resembles the Eocene species, *Aspidostoma pyriformis* Hara, 2001, from the La Meseta Formation of the Antarctic Peninsula, but the autozooids of *A. pyriformis* are smaller, the opesiae have anvil-shaped processes, and the interzooidal avicularia are pyriform.

Superfamily: Monoporelloidea Hincks, 1882

Family: Monoporellidae Hincks, 1882

Genus *Monoporella* Hincks, 1881

Type species. Haploporella nodulifera Hincks, 1881, Recent, SE Australia (Cook et al., 2018, p. 129).

Monoporella convexa (Canu, 1911)

Fig. 13E–H

1911 *Micropora convexa* Canu, p. 250, pl. 7, figs 1–3.

Material. MPEF-PI 6132.15 and MPEF-PI 6132.16, colonies encrusting valves of *Ostrea wilckensi*; upper Danian, Roca Formation, General Roca, Río Negro.

Description. Colony encrusting multiserial, unilaminar. Autozooids subhexagonal (Fig. 13E); opesia semielliptical, small, with low rim, lacking oral spine bases in zooids from zone of astogenetic repetition; frontal wall cryptocystal, slightly convex, finely granulated, penetrated evenly by about 8–10 opesiules. Ancestrula similar to later budded zooids but smaller and with four oral spine bases (Fig. 13F). Ovicells broken, the spinose roofs missing exposing the gymnocystal floor (Fig. 13G-H).

Measurements. ZL 504±166 µm (3, 42): ZW 310.5±83. µm (3, 38); OpL 76±13 µm (3, 63); OpW 98±15 µm (3, 62).

Remarks. The observed characters of our material match those of the paratype of *M. convexa* (MACN-Pi 1859). *Monoporella chubuti* (Canu, 1911), also from the Roca Formation, has larger opesia. Revision of both *M. convexa* and *M. chubuti*, including scanning electron microscopy of type material, will be needed to calify the identity of these two species.

Superfamily: ?Thalamoporelloidea Levinsen, 1902

Family: ?Steginoporellidae Hincks, 1884

Genus ?*Labioporella* Harmer, 1926

Type species. Labiopora crenulata Levinsen, 1909, Recent, ?Torres Strait.

?*Labioporella* sp.

Fig. 14A–D

Material. MPEF-PI 6132.8, encrusting colony on a valve of *Pycnodonte (Phygraea) sarmientoi*; upper Danian, Formación Roca, Casa de Piedra, La Pampa.

Description. Colony encrusting, multiserial, unilaminar (Fig. 14A). Autozooids arranged in well-defined rows (Fig. 14B), rounded rectangular in outline shape, proximal edge concave, distal edge convex, variable in width (Fig. 14C), separated by grooves; gymnocyst lacking; cryptocyst well developed, shelf-like, occupying about half of the length of the zooid, granular, sloping inwards at its distal end, narrow proximally; opesia semi-elliptical, longer than wide (Fig. 14D). Ovicells, avicularia and early astogeny not observed.

Measurements. ZL 259±33 (1, 21); ZW 187±27 (1, 25); OL 79±10 (1, 23); OW 124±33 (1, 23).

Remarks. This species is referred to *Labioporella* very tentatively. Although the form and arrangement of the autozooids, their granular cryptocystal frontal walls and opesiae that are longer than wide matches *Labioporella*, the species from the Roca Fm. lacks a prominent median process along the proximal edge of the opesia, and there is no indication of a polypide tube or tiny perforations in the cryptocyst, although these absences may be due to preservation. Should better evidence be found for placing the Roca species in *Labioporella*, it would represent the oldest known example of this genus, which at the present-day occurs in the Pacific, Indian and Atlantic oceans.

Superfamily: Cribrilinoidea Hincks, 1879

Family: Cribrilinidae Hincks, 1879

Genus *Tricephalopora* Lang, 1916

Type species. *Cribrilina triceps* Marsson, 1887, Maastrichtian, Rügen, Germany.

Tricephalopora sp. 1

Fig. 15A–C

Material. MPEF-PI 6132.19, colony encrusting a valve of *Gryphaeostrea callophyla* Ihering, 1903; lower Danian, Roca Formation, General Roca, Río Negro.

Description. Colony encrusting, multiserial, sheet-like. Autozooids elongate hexagonal; orifice round, gymnocyst restricted to narrow band around perimeter of autozooid (Fig. 14A); frontal shield with small costal field comprising 6–7 costae meeting and fusing along the midline of the zooid (Fig. 14B), no lateral intercostal fusions or pelmata visible; worn costae reveal the lumen. Adventitious avicularia paired, located at proximolateral orificial margin, directed proximolaterally inwards (Fig. 14C); rostrum triangular, blunt tipped; crossbar calcified. Ovicell smoothly inflated, lacking porous. Ancestrula and kenozooids not observed.

Measurements. ZL 447±41 µm (1, 13); ZW 298±26 µm (1, 13); OL 129±10 µm (1, 14); OW 139±12 µm (1, 17); AL 46±12 µm (1, 17); AW 59±9 µm (1, 17).

Remarks. This specimen is similar to *T. vibraculata* Turner, 1979 from the Late Cretaceous of New Jersey, USA. However, the specimen from Roca Fm. has fewer costae forming the frontal shield of the autozooids and lacks columnar ?kenozooids. The corroded costae mean that pelmata cannot be observed, and argues against introducing a new species for the Roca material.

?*Tricephalopora* sp.

Fig. 15D–E

Material. MPEF-PI 6132.3, colony encrusting a valve of *Cubitostrea ameghinoi*, upper Danian, Roca Formation, Cerros Bayos, La Pampa.

Description. Colony encrusting, multiserial, sheet-like. Autozooids elongate hexagonal (Fig. 14D); frontal shield with 12–18 costae meeting in a line along the midline of the zooid, no lateral intercostal fusions or pelmata. Scattered avicularia in various positions, poorly preserved. Ovicells gently inflated, lacking pores (Fig. 14E). Ancestrula not observed.

Measurements. ZL 545±42 (1, 13) µm; ZW 223±29 µm (1, 24); OL 137±11 µm (1, 13); OW 215±23 µm (1, 13); OvL 169±16 µm (1, 13); OvW 222±23 µm (1, 11).

Remarks. Specimens are poorly preserved, and typical features of the genus, such as paired avicularia on each autozooidal orifice seem to be lacking, hence assignment to *Tricephalopora* is tentative, even though this seems to be the most appropriate genus.

Infraorder: Umbonulomorpha Gordon, 1989

Superfamily: Arachnopusioidea Jullien, 1888

Family: Arachnopusiidae Jullien, 1888

Genus *Poricella* Canu, 1904

Type species. *Poricella maconnica* Canu, 1904, Eocene, Tunisia.

Poricella tripora (Canu, 1911)

Fig. 16A–C

1911 *Hiantopora tripora* Canu, p. 256, pl. 7, fig. 4.

Material. MPEF-PI 6132.67, colony encrusting a valve of *Pycnodonte (Phygraea) sarmientoi*; upper Danian, Roca Formation, Bajada del Jagüel, Neuquén.

Description. Colony encrusting, multiserial, unilaminar. Autozooids elongate oval (Fig. 16A); frontal shield slightly convex (Fig. 16B), perforated by 3 foramina, often reniform due to the presence of a tongue-like process (Fig. 16C), orifice D-shaped, with a low peristome. Ovicells poorly preserved, apparently semicircular, wider than long. Adventitious avicularia present.

Measurements. ZL 384±34 µm (1, 16); ZW 226±28 µm (1, 15); OL 101±20 µm (1, 21); OW 137±19 µm (1, 21).

Remarks. This specimen has been compared with the paratype of *P. tripora* (MACN-Pi 1845) described by Canu (1911) with which it is deemed conspecific. Along with the following species, it may represent the oldest known record of the genus.

Poricella sp.

Fig. 16D–G

Material. MPEF-PI 6132.23, colony encrusting a valve of *Pycnodonte (Phygraea) sarmientoi*. Upper Danian, Roca Formation, Casa de Piedra, La Pampa.

Description. Colony encrusting, multiserial, unilaminar (Fig. 16D); large distal pore chamber visible at growing edge. Zooids oval, convex; frontal shield perforated by 6–9 foramina, each with a tongue of calcification extending into the opening (Fig. 16E). Orifice D-shaped, slightly elongated, sometimes with a peristome. Adventitious avicularia oval or rounded rectangular, oriented proximally or somewhat proximolaterally, rostrum rounded, crossbar uncalcified (Fig. 16F−G). Early astogenetic stages preserved but not the ancestrula (Fig. 16F).

Measurements. ZL 317±41 µm (1, 17); ZW 223±34 µm (1, 18); OL 67±15 µm (1, 17); OW 70±12 µm (1, 17); AL 78±18 µm (1, 16); AW 80±18 µm (1, 16).

Remarks. Canu (1911, pl. 7, figs 12–13) illustrated material assigned to *Tremogasterina problematica*, which is similar to *Poricella* sp. According to curators at MACN, and as personally ascertained by one of us (S.S. Brezina), the type material of *T. problematica* is missing from the collection.

Genus *Tremogasterina* Canu, 1911

Type species. *Tremogasterina problematica* Canu, 1911. Danian, Roca Formation, General Roca, Argentina.

Tremogasterina problematica Canu, 1911

Fig. 17A–C

1911 *Tremogasterina problematica* Canu, p. 256, pl. 7, figs 12–13.

?1977 *Tremogasterina problematica* Canu, Cook, p. 127, pl. 3A–B.

Material. MPEF-PI 6132.11, colony encrusting a valve of *Pycnodonte (Phygraea) sarmientoi*; upper Danian, Roca Formation, Casa de Piedra, La Pampa.

Description. Colony encrusting, multiserial (Fig. 17A). Autozooids nearly equidimensional, frontal shield flat, pierced by 1-5 foramina (Fig. 17B−C), raised distally as a thickened bar proximal to the orifice. Orifice large, semicircular, rounded distally with an almost straight proximal edge. Ovicells subdued, ectooecium imperforate. Interzooidal avicularia numerous, oval (Fig. 17B), situated distolaterally of ovicells and laterally of autozooids, oriented distally or somewhat distolaterally, rostrum rounded, pivotal bar not calcified (Fig. 17D–E).

Measurements. ZL 281±30 µm (1, 4); ZW 219±22 µm (1, 4); OL 50±9 µm (1, 5); OW 78±10 µm (1, 5); AL 90 µm ±17 µm (1, 6); AW 94±19 µm (1, 6).

Remarks. Following the revision of Cook (1977), this is the only species now assigned to *Tremogasterina*, the others having been transferred to *Poricella*. The validity of *Tremogasterina* needs to be evaluated through a comparative study of *T. problematica* with the type species of *Poricella*, *P. maconnica* Canu, 1904, which is beyond the scope of the current study.

Genus *Trichinopolia* Guha and Nathan, 1996

Type species. *Trichinopolia crescentica* Guha and Nathan, 1996, Maastrichtian, Tamil Nadu, India.

?*Trichinopolia* sp.

Fig. 17F

Material. MPEF-PI 6132.20, colony encrusting a valve of *Amphidonte mendozana*; upper Maastrichtian, Roca Formation, Huantraico, Neuquén.

Description. Colony encrusting, multiserial. Autozooids hexagonal, slightly elongated, uniform in size and shape; frontal shield coarsely preserved, planar, apparently containing at least three foramina; orifice bell-shaped, the rim slightly raised. Adventitious avicularia paired laterally of the orifice which they indent slightly (Fig. 17F). Ovicells and ancestrula not observed.

Measurements. OL 94±11 µm (1, 8); OW 103±21 µm (1, 8); AL 80±10 µm (1, 7); AW 71±6 µm (1,7).

Remarks. The studied specimen is of Maastrichtian age and resembles *Trichinopolia*, a genus first described from the Late Cretaceous of India and subsequently recorded from the Campanian–Maastrichtian of the southeastern USA and California (Taylor, 2008). In particular, the species from the Roca Fm. has an orifice of similar shape to *T. californica* Taylor, 2008 but seemingly lacks the prominent distal spine base seen in the North American species. Unfortunately, the preservation is too poor to be trustworthy about its generic identity. Nevertheless,*Trichinopolia* is the closest fit.

Superfamily: Lepralielloidea Vigneaux, 1949

Family: Romancheinidae Jullien, 1888

Genus *Balantiostoma* Marsson, 1887

Type species. Cellepora marsupium von Hagenow, 1839, Maastrichtian, Rügen, Germany.

Balantiostoma spectabilis (Canu, 1911)

Fig. 17G–H

1911 *Hoplocheilina spectabilis* Canu, p. 262, pl. 8, figs. 1–4.

Material. MPEF-PI 6132.15 and MPEF-PI 6132.66, colonies encrusting valves of *Ostrea wilkensi* Ihering, 1907; upper Danian, Roca Formation, General Roca, Río Negro.

Description. Colony encrusting, multiserial, unilaminar (Fig. 17G). Autozooids elongate hexagonal, frontal shield gently convex, granular, with large marginal areolar pores. Adventitious avicularia with rounded rostra, located singly or paired distolaterally of autozooidal orifice (Fig. 17H), pivotal bar calcified. Early astogeny and ovicells unknown.

Measurements. ZL 322±41 µm (2, 16); ZW 196±31 µm (2, 17); OL 94±31 µm (2, 13); OW 92±21 µm (2, 13); AL 36±0 µm (1, 4); AW 41±5 µm (1, 6).

Remarks. According to curators at MACN, and as personally ascertained by one of us (S.S. Brezina), the holotype of *Balantiostoma spectabilis* is unfortunately missing from the collection.

Balantiostoma elongata (Canu, 1911)

Fig. 18A–D

1911 *Exochella elongata* Canu, p. 264, pl. 9, figs. 1–3.

Material. MPEF-PI 6132.6, colony encrusting a valve of *Pycnodonte (Phygraea) sarmientoi*; upper Danian, Roca Formation, Casa de Piedra, La Pampa. MPEF-PI 6132.12, colony encrusting a valve of *Ostrea wilkensi*; upper Danian, Roca Formation, General Roca, Río Negro.

Description. Colony encrusting, multiserial, unilaminar. Early astogeny preserved; ancestrula ascophoran, small, circular, budding a distal and two distolateral zooids (Fig. 18A). Autozooids elongate, zooidal boundaries marked by grooves and areolar pores (Fig. 18B); frontal shield convex, primary orifice mucronate; without oral spines (Fig. 18B). Ovicell hyperstomial, small, globose, present in the majority of zooids (Fig. 18C). Adventitious avicularia sparse and scattered, located close to autozooidal orifices, directed laterally, small, transversely elliptical, pivotal bar not calcified (Fig. 18D).

Measurements. ZL 283±27 µm (2, 20); ZW 202±29. µm (2, 22); OL 101±11 µm (2, 16); OW 111±14 µm (2, 16); AL 39±48 µm (1, 2); AW 69±31 µm (1, 2); OvL 103±16 (1, 6) µm; OvW 115±56 µm (1, 6).

Remarks. This species is similar to *Balantiostoma nomas* (Shaw, 1967) in having elongate autozooids delineated by prominent grooved boundaries and a mucronate orifice. However, it lacks the oral spines seen in this Late Cretaceous species from North America (see Taylor and McKinney, 2006).

Balantiostoma sp.

Fig. 18E–H

Material. MPEF-PI 6132.7, colony encrusting a valve of *Pycnodonte (Phygraea) sarmientoi*; upper Danian, Roca Formation, Bajada del Jagüel, Neuquén. MPEF-PI 6132.13 and MPEF-PI 6132.14, colonies encrusting valves of *Ostrea wilkensi*; Danian, Roca Formation, General Roca, Río Negro.

Description. Colony encrusting, multiserial, unilaminar (Fig. 18E). Early astogeny preserved, ancestrula tatiform with ?8 spines, apparently budding a distal and two distolateral zooids (Fig. 18F). Autozooids elongate, rhomboidal; frontal shield granular; orifice usually mucronate; 4-6 oral spine bases, generally equal-sized (Fig. 18G−H). Ovicells only observed in MPEF-PI 6132.7, globose. Avicularia present in some autozooids, mostly those with ovicells (Fig. 18H); adventitious, located proximolaterally of opesia, unpaired, cystid chamber bulbous, rostral plane steeply inclined to colony surface.

Measurements. ZL 238±37 µm (3, 28); ZW 190±31 µm (3, 24); OL 54±19 µm (3, 23); OW 63±21 µm (3, 22); OvL 109±22 µm (1, 11); OvW 135±8 µm (1, 11); AL 111±16 µm (1, 13); AW 98±14 µm (1, 14).

Remarks. The studied specimens are moderately well-preserved and share some features with *Balantiostoma octospinigera* Taylor and McKinney, 2006 from the North American Cretaceous. However, the Roca Fm. species differs in having fewer oral spine bases (4–6 vs. 8) and a granular frontal shield.

Family: incertae sedis

Genus *Eoporella* gen. nov.

Type species. *Eoporella lunata* sp. nov., upper Danian, Roca Formation, Casa de Piedra, La Pampa, Argentina.

Etymology. Eos (Gr.) for dawn, in reference to its similarity with the geologically older genus *Microporella*.

Diagnosis. As for type and only species.

Remarks. This new genus is introduced for a distinctive species from the Roca Fm. that strongly resembles the early Miocene–Recent genus *Microporella* but differs in several important morphological details and antedates the oldest known species of *Microporella* by about 40 million years. Condyles in *Eoporella* are situated distally of the proximolateral corners, a little way along the edges of the orifice, whereas when present in *Microporella* they are in the proximolateral corners. The ovicell of *Eoporella* has a coarsely porous, smooth-surfaced entooecium separated from the frontal shield of the distal zooid by a narrow crescent of ectooecium. In contrast, the ovicell of *Microporella* comprises a granular, cryptocyst-like calcified wall that is continuous with the frontal shield of the distal zooid and can be imperforate or pierced by relatively small pores. Furthermore, most – though not all – species of *Microporella* have adventitious avicularia and oral spines, both lacking in *Eoporella*.

Eoporella lunata sp. nov.

Fig. 19 A–F

Etymology. Referring to the lunate shape of the ascopore.

Diagnosis. Lepralioid cheilostome with crescentic ascopore set in an extensive, non-porous concavity on the distal frontal shield bounded by a proximal continuation of the peristome. Orifice with lateral condyles. Ovicell hyperstomial, ectooecium uncalcified except for a narrow rim, entooecium smooth with scattered large, irregular pores. Pore chambers lacking. No avicularia.

Type horizon. Roca Fm. (Paleocene, upper Danian).

Material. Holotype: MPEF-PI 6132.6; paratype: MPEF-PI 6132.10, encrusting colonies on valves of *Pycnodonte (Phygraea) sarmientoi*, upper Danian, Roca Formation, Casa de Piedra, La Pampa, Argentina.

Description. Colony encrusting, multiserial, unilaminar; pore chambers lacking. Autozooids rhomboidal; boundary walls well raised (Fig. 19A–B); frontal shield convex, pseudoporous, pseudopores large, numbering about 40 per zooid; distinct areolar pores not discernible; orifice bell shaped, longer than wide, lateral condyles dividing an horseshoe-shaped anter from a broad, shallow sinus; no oral spines; peristome prominent and flared (Fig. 19C−D); ascopore large, crescentic, set in an extensive, non-porous, apron-like concavity on the frontal shield bounded by a proximal continuation of the peristome (Fig. 19D). Ovicell hyperstomial (Fig. 19E); ectooecium uncalcified except for a narrow, crescentic, smooth rim; entooecium smoothly calcified, with large but sparse (*c*. 10) pores irregularly oval in shape (Fig. 19F). Avicularia not observed.

Measurements. ZL 544±107 µm (2, 13); ZW 386±74 µm (2, 13); OL 103±39 µm (2, 15); OW 100±18 µm (2, 15); OpL 29±8 µm (2, 6); OpW 49±14 µm (2, 6); OvL 256±32 µm (2, 1); OvW 254±24 µm (2, 1); OOW 150 µm (1, 1).

Remarks. This is the only cheilostome in the Roca Fm. with a lepralioid frontal shield pierced by pseudopores. Indeed, *E. lunata* is believed to be the oldest lepraliomorph-grade cheilostome, which is the most speciose group of cheilostomes living in modern seas.

4. Conclusions

Our findings show that in northern Patagonia the diversity of encrusting bryozoans associated with oyster shells exhibits no major change across the K/Pg boundary (table 1), in common with the pattern reported for northern Europe and the southeastern United States by Sogot et al. (2013, 2014). However, an important increase in the diversity is recorded during the upper Danian: at this time 13 cyclostome and 11 cheilostome species are documented on oyster shells contrasting with just four cheilostomes (i.e. *Flustrellaria* sp., ?*Akatopora* sp. 1,, *Poricella tripora* and ?*Trichinopolia* sp.) on Maastrichtian oysters and three (i.e. *Conopeum okalana*, *Aspidostoma onychocelliferum* and *Tricephalopora* sp. 1) on lower Danian shells. There are no records of Maastrichtian encrusting cyclostomes in the studied area, although the relationship between cyclostome and cheilostome species number in the Danian is congruent with information from the Northern Hemisphere (i.e. there are more species of cheilostomes after the K-Pg boundary). It is intriguing that cyclostomes slightly dominated over cheilostomes during upper Danian even though the record is limited. The lower relative abundance of cheilostomes during the upper Danian in the Neuquén Basin is coincident with the decline recorded at the end of the Danian in the Northern Hemisphere (Taylor and Waeschenbach, 2015).

The change in bryozoan biodiversity after the lower Danian correlates with an increase in the number of species of corals, molluscs, echinoids and crabs derived from low latitudes, reflecting higher seawater temperatures spreading south (Kiessling et al., 2005; Casadio et al., 2005; Aguirre-Urreta et al., 2008; Carrera and Casadio, 2016) coincident with sea surface temperatures obtained by Woelders et al. (2017) that show a warming phase after the K/Pg boundary in the Neuquén Basin.

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Figure captions

Fig. 1. Map of fossiliferous localities from which the material comes from.. BdJ: Bajada del Jagüel; CBa: Cerros Bayos; CBu: Cerro Butaló; CdP: Casa de Piedra; GR: General Roca; Hu: Huantraico; LM: Liu Malal; RC: Ranquil-Có.

Fig. 2. Selected stratigraphic sections, illustrating lithology and marking beds that yielded oysters with bryozoans. Dashed line indicates K-Pg boundary.

Fig. 3. A—C, *Voigtopora* sp., MPEF-PI 6132.4, upper Danian, Roca formation, Cerros Bayos, La Pampa. **A, B**, general view of two colonies (scale bars: 400 µm). **C**, lateral branching (scale bar: 200 µm). **D–E**, ?*Oncousoecia* sp. 1., MPEF-PI 6132.25, upper Danian, Roca Formation, Casa de Piedra, La Pampa. **D**, Cylindrical peristomes with thin and elevated edges; the colony is overgrown by *Disporella* sp. to the left (scale bar: 200 µm). **E**, autozooids walls perforated by subcircular to drop-shaped pseudopores (scale bar: 100 µm). **F–H**, ?*Oncousoecia* sp. 2, MPEF-PI 6132.9, upper Danian, Roca Formation, Casa de Piedra, La Pampa. **F**, general view of the colony (scale bar: 600 µm). **G**, surface with fine concentric rugae parallel to the growing margin (scale bar: 400 µm). **H**, frontal walls perforated by approximately subcircular pseudopores (scale bar: 200 µm).

Fig. 4. ?*Oncousoecia* cf. *striata* (Canu, 1911), MPEF-PI 6132.26, lower Danian, Roca Formation, Casa de Piedra, La Pampa. **A**, general view of a colony (scale bar: 1 mm). **B**, ancestrula and three early generations of autozooids (scale bar: 300 µm). **C**, detail of ancestrula and protoecium (scale bar: 100 µm). D, autozooids clustered into groupings of two or three (scale bar: 200 µm). **E**, possible broken erect branch (scale bar: 300 µm). **F**, second colony with autozooidal apertures in groups of two or three (scale bar: 400 µm).

Fig. 5. *Axilosoecia giselae* Taylor and Brezina, 2018, MPEF-PI 6132.28, upper Danian, Roca Formation, Cerros Bayos, La Pampa. **A**, overview of a ramifying colony (scale bar: 1 mm). **B**,

branch bifurcations, autozooids and two gonozooids (scale bar: 400 µm). **C**, two gonozooids showing bulbous brood chambers extending into the branch axils (scale bar: 200 µm). **D**, a pair of gonozooids (scale bar: 100 µm). **E**, gonozooid brood chamber and subterminal ooeciopore (scale bar: 100 µm).

Fig. 6. A–B. *Platonea* sp., MPEF-PI 6132.5, NP4 Biozone, upper Danian, Roca Formation, Casa de Piedra, La Pampa. **A**, general view of a colony with V-shaped fascicles, possible gonozooid indicated by an arrow (scale bar: 500 µm). **B**, detail of ancestrula and its hemispherical protoecium (scale bar: 100 µm). **C–F**. *Plagioecia* sp., MPEF-PI 6132.18, NP4 Biozone, upper Danian, Roca Formation, General Roca, Río Negro. **C**, general view of the colony (scale bar: 500 µm). **D–E**, two gonozooids from the same colony, with the ooeciopore indicated by an arrow in **E** (scale bars: 500µm). **F**, detail of peristomes and pseudopores (scale bar: 100 µm).

Fig. 7. *Plagioecia* aff. *cristata* Taylor and McKinney, 2006, MPEF-PI 6132.18, Biozone NP4, upper Danian, Roca Formation, General Roca, Río Negro (all scale bars: 300 µm). **A**, general view of the colony. **B**, detail of the edge of the colony. **C**, autozooids with prominent median keels. **D–E**, two gonozooids from the same colony, with the ooeciopore arrowed in **E**.

Fig. 8. *Mesenteripora* sp., MPEF-PI 6132.28, NP4 Biozone, upper Danian, Roca Formation, Casa de Piedra, La Pampa. **A**, general view of the colony (scale bar: 1 mm). **B**, early astogeny (scale bar: 200 µm). **C**, broken base of an erect branch (scale bar: 400 µm). **D**. secondary nanozooids (scale bar: 100 µm). **E**, gonozooid (ooeciopore arrowed) surrounded mostly by secondary nanozooids (scale bar: 400 µm).

Fig. 9. A–E. *Actinopora robertsoniana* Canu, 1911, MPEF-PI 6132.17, NP4 Biozone, upper Danian, Roca Formation, General Roca, Río Negro. **A**, general view of colony (scale bar: 1 mm). **B**,

detail (scale bar: 40μm). **C**, fascicle and growing edge (scale bar: 200 μm). **D**, gonozooid of a second colony (scale bar: 400μm). **E**, detail showing probable ooeciopore (arrowed) (scale bar: 200 μm). **F.** *´Berenicea´* sp., MPEF-PI 6132.13, NP4 Biozone, upper Danian, Roca Formation, General Roca, Río Negro (scale bar: 200 µm). **G–H**. *Disporella*? *discoidea* (Canu, 1911), MPEF-PI 6132.65, NP4 Biozone, upper Danian, Roca Formation, Casa de Piedra, La Pampa. **G**, general view (scale bar: 400 µm). **H**, detail showing kenozooids (alveoli) separating autozooidal apertures (scale bar: 100 µm).

Fig. 10. A–C. *Ceriopora* sp., MPEF-PI 6132.2, NP4 Biozone, upper Danian, Roca Formation, Bajada de Jagüel, Neuquén. **A**, general view of the colony (scale bar: 1 mm). **B**, undifferentiated autozooids and kenozooids (scale bar: 200 µm). **C**, detail of zooidal apertures (scale bar: 100 µm). **D–E**. *Electra* sp.,. MPEF-PI 6132.1, NP4 Biozone, upper Danian, Roca Formation, General Roca, Río Negro. **D**, general view. **E**, group of autozooids with gymnocystal frontal walls. (scale bars: 200 µm). **F–H**. *Conopeum okaiana* Canu, 1911, GHUNLPam 17423, NP1-NP2 Biozone, lower Danian, Roca Formation, Liu Malal, Mendoza. **F**, autozooids (scale bar: 400 µm). **G**, hexagonal zooids (scale bar: 200 µm). **H**, autozooids, one with a closure plate (scale bar: 200 µm).

Fig. 11. A–C. *Flustrellaria* sp., MPEF-PI 6132.21, upper Maastrichtian, Jagüel Formation, Bajada del Jagüel, Neuquén. **A**, general view (scale bar: 400 µm). **B**, detail of zooids with small circumopesial spine bases and damaged ovicells (scale bar: 200 µm). **C**, interzooidal avicularium (lower centre) (scale bar: 200 µm). **D–G**. *Pyriporella ameghinoi* Canu, 1911, MPEF-PI 6132.18, NP4 Biozone, upper Danian, Roca Formation, General Roca, Río Negro. **D**, general view of the colony (scale bar: 1 mm). **E**, early astogeny, the ancestrula and first buds missing (scale bar: 100µm). **F**, autozooids, most ovicellate (scale bar: 200 µm). **G**, ovicellate autozooids and small avicularia (scale bar: 200 µm).

Fig. 12. A–B ?*Akatopora* sp. 1, MPEF-PI 6132.20, upper Maastrichtian, Roca Formation, Huantraico, Neuquén. **A**, general view of the colony (scale bar: 600 µm). **B**, avicularia (scale bar: 200 µm). **C–E**. *Akatopora kaufmanni* sp. nov., NHMUK D32352a. Danian, Roca Formation, General Roca, Rio Negro. **C**, general view of the colony with an overgrowing colony of *Cianotremella gigantea* to the right (scale bar: 600 µm). **D**, autozooids surrounded by small polymorphs (scale bar: 200 µm). **E**, detail showing some autozooids with ovicells (200 µm). **F–H**. *Cianotremella gigantea* Canu, 1911, NHMUK D32352b, Danian, Roca Formation, General Roca, Rio Negro. **F**, general view of the colony fouled by a small *Poricella* and a worn spirorbid (lower right) (scale bar: 600 µm). **G**, autozooids and avicularia (scale bar: 300 µm). **H**, autozooids, avicularia and kenozooid (middle left) (scale bar: 400 mm).

Fig. 13. A–D. *Aspidostoma onychocelliferum* Canu, 1911,. MPEF-PI 6132.68, lower Danian, Roca Formation, General Roca, Río Negro. **A–B**, general views of the colony (scale bars: A=400 µm; B=200 µm). **C**, early astogeny with first generations of zooids. **D**, ovicells and avicularia (scale bars: 200 µm).
E–H. *Monoporella convexa* Canu, 1911, MPEF-PI 6132.15 , upper Danian, Roca Formation, General Roca, Río Negro. **E**, general view of autozooids (scale bar: 200 µm). **F**, ancestrula (scale bar: 100 µm). **G**, broken ovicell (scale bar: 100 µm). **H**, early astogeny (scale bar: 200µm).

Fig. 14. ?*Labioporella* sp., MPEF-PI 6132.8, NP4 Biozone, Danian, Formación Roca, Casa de Piedra, La Pampa. **A**, general view of the colony (scale bar: 400 µm). **B–D**, autozooids with semi-elliptical opesiae and shelf-like proximal cryptocysts arranged in longitudinal rows (scale bars: 200 µm).

Fig. 15. A–C. *Tricephalopora* sp. 1. MPEF-PI 6132.19, lower Danian, Roca Formation, General Roca, Río Negro. **A**, general view of zooids (scale bar: 400 µm). **B**, autozooids and adventitious

avicularia located at proximolateral orificial margins (scale bar: 200 µm). **C**, detail of costate frontal shield (scale bar: 100 µm). **D–E**. ?*Tricephalopora* sp., MPEF-PI 6132.3, upper Danian, Roca Formation, Cerros Bayos, La Pampa. **D**, general view of the colony. **E**, ovicellate zooids (scale bars: 200 µm).

Fig. 16. A–C. *Poricella tripora* Canu, 1911, MPEF-PI 6132.67, upper Maastrichtian, Jagüel Formation, Bajada del Jagüel, Neuquén. **A**, general view of oval zooids, with broad orifice (scale bar: 200 µm). **B**, adventitious avicularia (scale bar: 200 µm). **C**, detail of frontal shield perforated by three foramina (scale bar: 60 µm). **D–G**. *Poricella* sp., MPEF-PI 6132.23, upper Danian, Roca Formation, Casa de Piedra, La Pampa. **D**, general view of a colony (scale bar: 400 µm). **E**, growth rim at the upper section. **F**, early astogenetic stages with small zooids (lower center). **G**, group of autozooids, some with peristomes, and avicularia. (scale bars: 200 µm).

Fig. 17. A–E. *Tremogasterina problematica* Canu, 1911, MPEF-PI 6132.11, upper Danian, Roca Formation, Casa de Piedra, La Pampa. **A**, general view of the colony (scale bar: 400 µm). **B**, oval interzooidal avicularia near the orifices (scale bar: 200 µm). **C**, frontal shields with five foramina, highly abraded (scale bar: 100 µm). **D**, zooids near growing edge, some with broken ovicells (scale bar: 200 µm). **E**, growing edge with large distal pore chamber visible in upper centre (scale bar: 200 µm). **F,** ?*Trichinopolia* sp., MPEF-PI 6132.20, upper Maastrichtian, Roca Formation, Huantraico, Neuquén. Detail of frontal shield with poorly preserved lateroproximal adventitious avicularia (scale bar: 100 µm). **G–H**. *Balantiostoma spectabilis* Canu, 1911, MPEF-PI 6132.15, upper Danian, Roca Formation, General Roca, Río Negro. **G**, general view of a small colony (scale bar: 400 µm). **H**, detail of autozooids with areolae; avicularia proximolateral to the orifice (scale bar: 200 µm).

Fig. 18. A–D. *Balantiostoma elongata* Canu, 1911, MPEF-PI 6132.6, upper Danian, Roca Formation, Casa de Piedra, La Pampa.upper Danian. **A**, early astogeny with putative ancestrula

marked by an asterisk (scale bar: 200 µm). **B**, detail of mucro in autozooidal orifice (scale bar: 100 µm). **C**, elongate autozooids and areolar pores (scale bar: 200 µm). **D**, small adventitious avicularia (scale bar: 100 µm). **E–H**. *Balantiostoma* sp., MPEF-PI 6132.7, upper Danian, Roca Formation, Bajada del Jagüel, Neuquén. MPEF-PI 6132.13 and MPEF-PI 6132.14, upper Danian, Roca Formation, General Roca, Río Negro. **E**, general view of a colony (scale bar: 1 mm). **F**, early astogeny with ancestrula (marked by an asterisk) preserving long spines (scale bar: 100µm). **G**, zooids with mucro in proximal edge of the orifice (scale bar: 100 µm). **H**, ovicellate zooids with avicularia proximolaterally of the orifice (scale bar: 200 µm).

Fig. 19. *Eoporella lunata* gen. et sp. nov., MPEF-PI 6132.6, upper Danian, Roca Formation, Casa de Piedra, La Pampa. **A**, general view of a colony (scale bar: 600 µm). **B**, group of zooids (scale bar: 500 µm). **C**, zooids showing pseudoporous frontal shields (scale bar: 200 µm). **D**, orifice and crescent-shaped ascopore (scale bar: 200 µm). **E**, autozooids, some with broken ovicells (scale bar: 300 µm). **F**, ovicell with irregular pores in the entooecium (scale bar: 100 µm).

Table 1. List of encrusting bryozoan species associated with oysters recorded across the K/Pg boundary.

Bryozoan species	Colony form	Collection number
Cheilostomata		
Flustrellaria sp.	encrusting, multiserial	MPEF-PI 6132.21
?*Akatopora* sp. 1	encrusting, multiserial	MPEF-PI 6132.20
Poricella tripora	encrusting, multiserial	MPEF-PI 6132.67
?Trichinopolia sp.	encrusting, multiserial	MPEF-PI 6132.20
early Danian		
Cheilostomata		
Conopeum okaiana	encrusting, multiserial	GHUNLPam 17423
Aspidostoma onychocelliferum	encrusting, multiserial	MPEF-PI 6132.68
Tricephalopora sp. 1	encrusting, multiserial	MPEF-PI 6132.19
late Danian		
Cyclostomata		
Voigtopora sp.	encrusting, uniserial	MPEF-PI 6132.4
Oncousoecia? sp.1	encrusting, oligoserial	MPEF-PI 6132.25
Oncousoecia? sp. 2	encrusting, oligoserial	MPEF-PI 6132.9
Oncousoecia? cf. *striata*	encrusting, oligoserial	MPEF-PI 6132.26
Axilosoecia giselae	encrusting, uniserial	MPEF-PI 6132.28
Platonea sp.	encrusting, oligoserial	MPEF-PI 6132.5
Plagioecia aff. *Cristata*	encrusting, multiserial	MPEF-PI 6132.18
Mesenteripora sp.	encrusting, multiserial	MPEF-PI 6132.28
Actinopora robertsoniana	encrusting, multiserial	MPEF-PI 6132.17
'*Berenicea*' sp.	encrusting, multiserial	MPEF-PI 6132.13
Disporella? *discoidea*	encrusting, multiserial	MPEF-PI 6132.65
Ceriopora sp.	encrusting, multiserial	MPEF-PI 6132.2
Cheilostomata		
Electra sp.	encrusting, multiserial	MPEF-PI 6132.1
?Labioporella sp.	encrusting, multiserial	MPEF-PI 6132.8
Pyriporella ameghinoi	encrusting, multiserial	MPEF-PI 6132.18
Akatopora kaufmanni sp. nov.	encrusting, multiserial	NHMUK D32352a
Cianotremella gigantea	encrusting, multiserial	NHMUK D32352b
Monoporella convexa	encrusting, multiserial	MPEF-PI 6132.15-16
Tricephalopora? sp.	encrusting, multiserial	MPEF-PI 6132.3
Poricella sp.	encrusting, multiserial	MPEF-PI 6132.23
Tremogasterina problematica	encrusting, multiserial	MPEF-PI 6132.11
Balantiostoma spectabilis	encrusting, multiserial	MPEF-PI 6132.15-66
Balantiostoma elongate	encrusting, multiserial	MPEF-PI 6132.6-12
Balantiostoma sp.	encrusting, multiserial	MPEF-PI 6132.7-13-14
Eoporella lunata gen. et sp. nov.	encrusting, multiserial	MPEF-PI 6132.6

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: