

## Lower Cretaceous bryozoans from Argentina: a 'by-catch' fauna from the Agrio Formation (Neuquén Basin)

Paul D. Taylor<sup>a,\*</sup>, Darío G. Lazo<sup>b</sup>, M. Beatriz Aguirre-Urreta<sup>b</sup>

<sup>a</sup> Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD, UK

<sup>b</sup> Department of Geological Sciences, University of Buenos Aires, Buenos Aires 1428, CONICET, Argentina

### ARTICLE INFO

#### Article history:

Received 5 September 2007

Accepted in revised form 7 July 2008

Available online 16 July 2008

#### Keywords:

Bryozoans

Taxonomy

Agrio Formation

Cretaceous

Neuquén Basin

Argentina

### ABSTRACT

Mesozoic bryozoans are uncommon in the Southern Hemisphere and none have yet been described from the Lower Cretaceous of Argentina. This paper describes six taxa from the lower Valanginian to the upper Hauterivian–?lower Barremian Agrio Formation of the Neuquén Basin. New species are *Charixa burdonaria* sp. nov., notable for being the oldest known spine-bearing cheilostome and for constructing multilayered colonies intergrown with serpulid worms, and an unusual cyclostome described as *Neuquenopora carrerai* gen. et sp. nov. The poor preservation and/or lack of diagnostic gonozooids makes taxonomic assignment of the remaining bryozoans, all cyclostomes, uncertain. Apart from *Multizonopora* sp., a cerioporine cyclostome with bushy, ramose colonies, all of the Agrio Formation bryozoans are encrusters. In general, the Agrio Formation bryozoan fauna resembles faunas from the Neocomian and Aptian of north-west Europe. The relatively low diversity may be an artefact of collecting effort, although environmental factors may also be important, with the intergrowths between *C. burdonaria* and serpulids from the top of the Agrio Formation being reminiscent of some present day occurrences of primitive cheilostomes in lagoons with fluctuating salinities.

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### 1. Introduction

Bryozoans have a global fossil record extending from the Lower Ordovician to the present-day. However, while both Palaeozoic and Cenozoic bryozoans have been widely described from all continents around the world, including Argentina in South America (e.g., Carrera, 2003; Muravchik et al., 2004; Sabbatini, 2002; and references therein), records of Mesozoic bryozoans are strongly centred on Europe. Southern Hemisphere examples of Mesozoic bryozoan faunas are especially rare. The extent to which this pattern reflects a heterogeneous biogeographical distribution at the time versus inadequate collecting effort or lack of suitable facies is not yet resolved. However, Taylor and Ernst (2008) have argued that this is a true pattern of biological distribution, at least as far as bryozoans in the Jurassic are concerned. There are indications that by the Late Cretaceous bryozoan communities had attained a wider global distribution, with diverse faunas known from peninsular India, southern Africa and Australasia (e.g. Brood, 1977; Guha and Nathan, 1996; Taylor and Gordon, 2007).

Lower Cretaceous bryozoans from Argentina have attracted little attention compared to other benthic biota. Although they are moderately common in the fossil record (see e.g. Lazo et al., 2005),

there is no modern data on their taxonomy, diversity, palaeoecology or palaeobiogeography. Hitherto, there have been only brief mentions of Early Cretaceous bryozoans from Argentina (see Weaver, 1931, p. 172). Therefore, the description of newly collected bryozoans from the Agrio Formation of the Neuquén Basin is significant. This material is effectively a 'by-catch' obtained during sampling for molluscs and other macrofossils. It may not therefore be representative of the true diversity of species present. Nevertheless, and despite the variable quality of preservation of the bryozoans, it has been possible to recognise a moderate diversity of taxa, including one new genus and two new species. This paper describes the taxonomy of the Agrio Formation bryozoans and comments on their biogeographical, environmental and evolutionary significance.

### 2. Geological setting

The Neuquén Basin was a retro-arc depocentre during Late Jurassic–Early Cretaceous times, located near the present international Argentine–Chilean boundary along the Andes, between 32° and 40° S (Fig. 1). The northern part of the basin forms a narrow belt with a trend parallel to the present Principal Cordillera, while in the south the basin expands to the east to form the Neuquén Embayment. The Agrio Formation, defined by Weaver (1931) in the Río Agrio section within the Neuquén Embayment, is the upper unit of

\* Corresponding author.

E-mail address: [p.taylor@nhm.ac.uk](mailto:p.taylor@nhm.ac.uk) (P.D. Taylor).

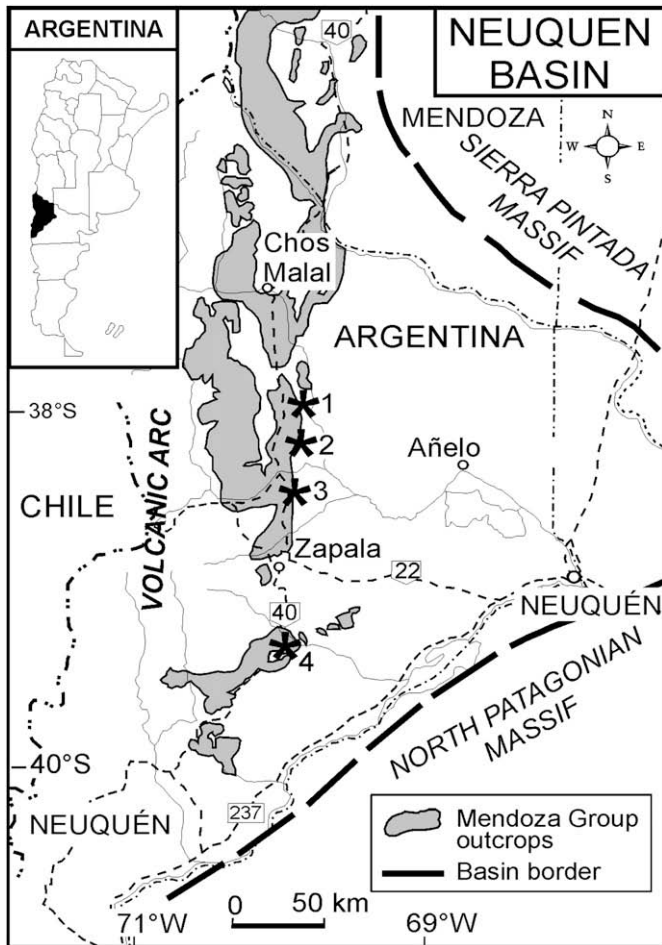


Fig. 1. Map of the Neuquén Basin showing the outcrop of the Mendoza Group and bryozoan localities (1–4) in the Agrio Formation.

the Mendoza Group (Groeber, 1953) (Fig. 1). In the type area the section reaches a thickness of 1178 m where its three members are very well developed. The lower or Pilmatué Member (Leanza and Hugo, 2001) is mainly composed of massive clay shales interbedded with thin layers of packstones and wackestones. Towards the top of the lower member the clay shales are dominant. The middle or Avilé Member is represented by yellowish brown coarse sandstones, often cross-bedded, and lacks marine fossils. The upper or Agua de La Mula Member (Leanza and Hugo, 2001) is composed largely of massive clay shales in the lower part and grey calcareous shales interbedded with sandy limestones and sandstones in the upper part (Fig. 2). The unit has a rich and abundant fossil biota composed mainly of invertebrates. Studies on ammonoids combined with nannoplankton and palynology have provided an excellent biostratigraphy for the Agrio Formation (Aguirre-Urreta et al., 2005, 2007). Nautilids, bivalves and echinoids are also relatively well-known (Cichowolski, 2003; Lazo, 2007a; Rodríguez, 2007). Comprehensive accounts of the lithofacies, palaeoecology and palaeoenvironments of the Agrio Formation can be found in Lazo et al. (2005) and Lazo (2007b).

The studied bryozoans were collected at four localities in the Agrio Formation (Fig. 1). From north to south these are:

(1) Mina La Continental: access from national road 40, 60 km south of Chos Malal, about 8 km east of the junction of road 40 with a gravel road that leads to the old Mina La Continental. The upper part of the Agua de la Mula Member of the Agrio Formation is well exposed here.

- (2) Agua de la Mula: access from national road 40, 80 km south of Chos Malal, along a gravel road that leads to a dry oil well. The entire Agrio Formation is well exposed. This is the type locality of the upper member of the formation.
- (3) Bajada del Agrio: the Agrio Formation forms the hills south of Bajada del Agrio. It is well exposed in the slopes adjacent to gravel road 10, some 5 km southwest of Bajada del Agrio.
- (4) Cerro Birrete: located immediately east of national road 40, 50 km south of Zapala near the junction with a gravel road to Paso Aguerre. The lower part of the Pilmatué Member of the Agrio Formation is exposed on the hillside of Cerro Birrete.

### 3. Systematic palaeontology

All material has been lodged in the Colección Paleontología, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires (CPBA), Buenos Aires, Argentina. Each catalogue number refers to a sample of specimens from a given section and stratigraphical level. Suffix numbers indicate the number of specimens with a given catalogue number.

After initial optical microscopy, uncoated specimens were studied at higher magnifications using a low-vacuum LEO 1455-VP scanning electron microscope at the Natural History Museum in London. The images obtained with this instrument are back-scattered electron images. Specimens lightly coated in ammonium chloride were also photographed optically.

Order: Cheilostomata Busk, 1852

Suborder: Malacostegina Levensen, 1902

Family: Electridae Stach, 1937

Genus *Charixa* Lang, 1915

*Type species.* *Charixa vennensis* Lang, 1915, Upper Albian, Dorset, England. Revised by Taylor (1986).

*Charixa burdonaria* sp. nov.

Figs. 3–4

*Derivation of name.* From the type locality Agua de la Mula, water of the mule, *L burdo*, mule.

*Material.* Holotype: CPBA 20129.1, Agua de la Mula Member, Agrio Formation, upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Agua de la Mula, encrusting potamidid gastropods assigned to *Cerithium* cf. *C. heeri* Pictet and Renévier by Weaver (1931, p. 385, pl. 42, Fig. 284). Paratypes: CPBA 20129.2–5, details as for holotype; CPBA 20130.1–3, as for holotype but encrusting the bivalve *Steinmanella vacaensis* (Weaver). Other material (too poorly preserved to be assigned with absolute certainty to *C. burdonaria*): CPBA 20131.2–3, 20132, details as for holotype but locality is Mina La Continental, also encrusting gastropods.

*Description.* Colony encrusting, pluriserial, zooids arranged irregularly, spaces between uniserial chains becoming infilled by later zooids. Multilamellar growth frequent, origin unknown (intracolony or intercolony?), producing massive colonies up to 10 mm thick. Pore chambers not observed but likely present based on occurrence of pore windows. Early astogeny unknown.

Autozooids variable in size and shape, about 0.31–0.58 mm long by 0.19–0.29 mm wide, pyriform or longitudinally ovoidal. Proximal gymnocyst slight in ovoidal autozooids, moderately long in pyriform zooids some developing a median longitudinal fissure (rhamma). Cryptocyst forming a narrow, inwardly-sloping ledge diminishing in width distally, not shelf-like, pustulose. Spine bases

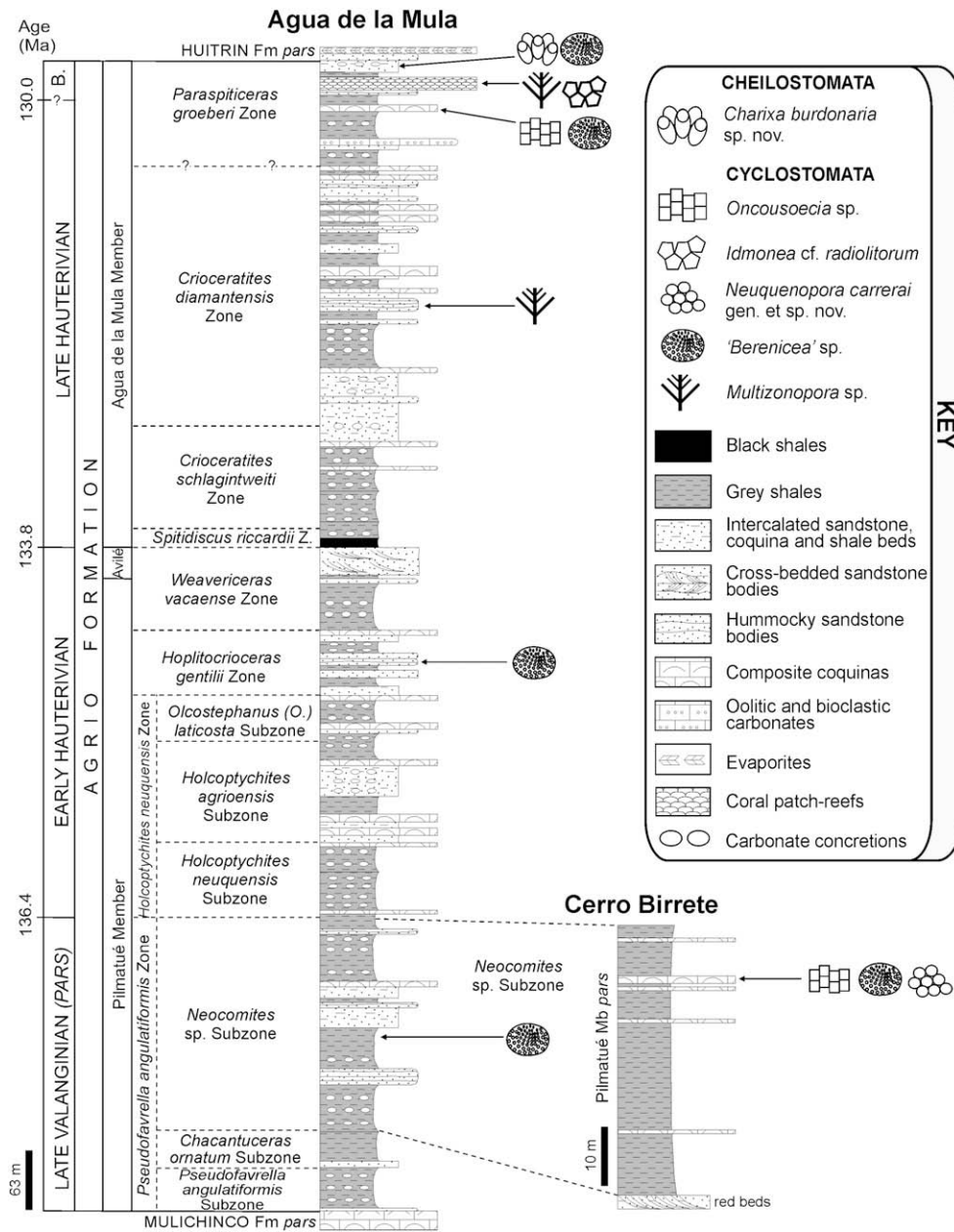


Fig. 2. Stratigraphical sections of the Agrio Formation at two localities in the Neuquén Basin showing sedimentary facies variations and fossil distributions. Ammonoid zonation from Aguirre-Urreta et al. (2005, 2007); ages from Ogg et al. (2004). B = Barremian.

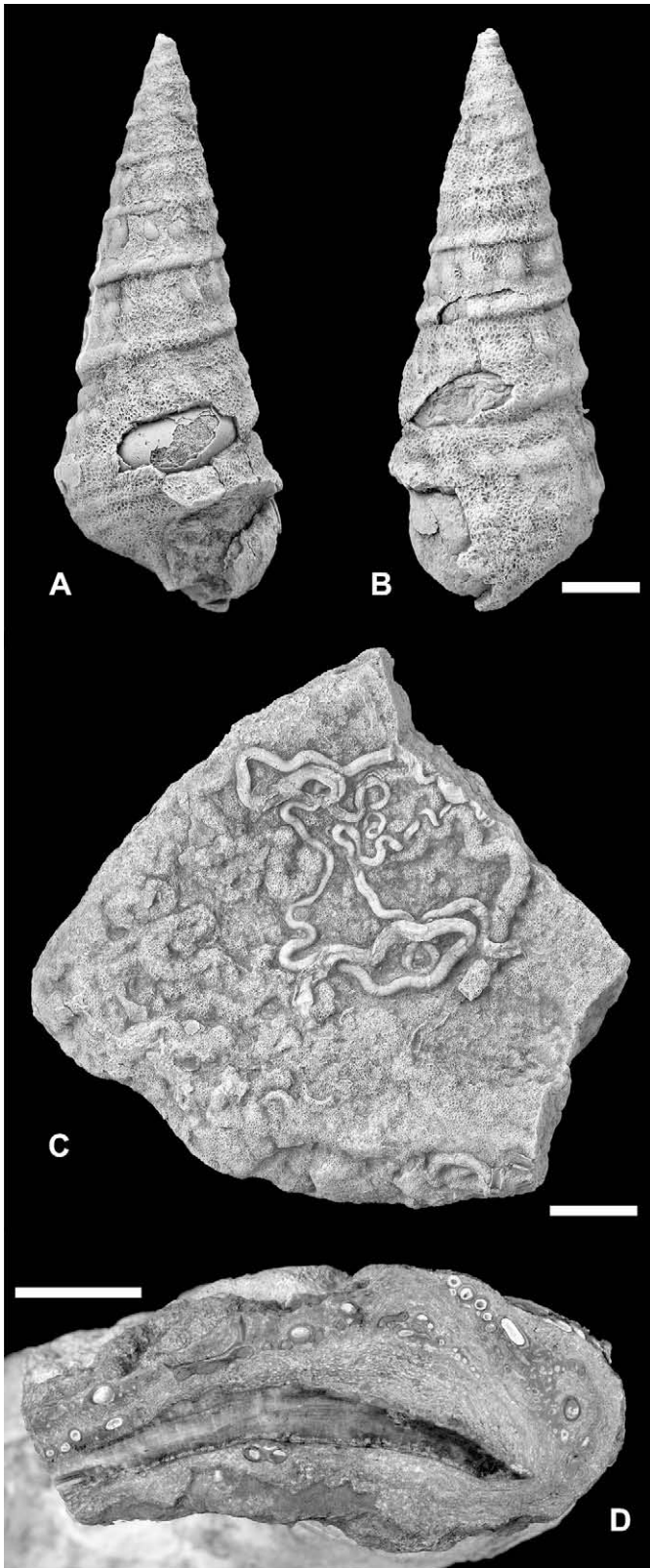
absent or restricted to a single oral pair at the distolateral corners of the zooid, about 20 μm in diameter. Opesia longitudinally ovoidal, occupying most of frontal surface of zooids, about 0.20–0.36 mm long by 0.11–0.19 mm wide. Intramural buds infrequent. Closure plates not observed. No ovicells. Presumed kenozooids intercalated in normal budding pattern and overgrowing proximal gymnocysts of autozooids, smaller than autozooids and more irregular in shape but otherwise similar. Avicularia lacking.

Remarks. Taylor (1986) assigned to the primitive cheilostome genus *Charixa* Lang four named species from the Aptian and Albian, and in addition, questionably, an un-named species from the Barremian. No further species have since been added to *Charixa*. Colonies in *Charixa* are characteristically irregular and pluriserial, but fusion to form a regular colony with zooids arranged in quincunx does not occur, unlike most other sheet-like cheilostome bryozoans, and colony growth resembles the composite multiserial pattern

described by Silén (1987). Zooids are either non-spinose or have only a single pair of articulated spines preserved as two oral spine bases located at the distolateral corners of the opesia. The only cheilostome from the Agrio Formation clearly fits within the concept of the genus *Charixa*. It is the oldest known species of this genus and represents the earliest record of spines in a cheilostome bryozoan.

In possessing oral spine bases, *C. burdonaria* resembles *C. lindiensis* Taylor, 1986 from the Aptian of Tanzania but *C. burdonaria* has zooids of slightly larger average size and buds zooids onto the gymnocysts of older zooids, a feature not observed in *C. lindiensis*. This form of budding does occur in another species of *Charixa*, *C. cryptocauda* from the Albian of South Africa in which, however, the buds are well differentiated kenozooids rather than the poorly-differentiated ?kenozooids of *C. burdonaria*. Furthermore, spine bases are lacking in *C. cryptocauda*, as they are in the two English species of *Charixa*, *C. vennensis* Lang, 1915, from the Albian and *C. lhuydi* (Pitt, 1976) from the Aptian.





**Fig. 3.** *Charixa burdonaria* sp. nov., Agua de la Mula Member, Agrio Formation, upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Agua de la Mula. A–B, holotype encrusting a potamidid gastropod, CPBA 20129.1, scale bar 5 mm. C–D, paratypes intergrown with serpulids encrusting the bivalve *Steinmanella vaccaensis* (Weaver). C, external view, CPBA 20130.1, scale bar 10 mm. D, section showing bivalve shell covered by a thick overgrowth of bryozoans and serpulids on both sides, CPBA 20130.2, scale bar 10 mm.

**Occurrence.** Upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Agrio Formation, Agua de la Mula Member, Neuquén Basin.

Order: Cyclostomata Busk, 1852  
 Suborder: Tubuliporina Milne Edwards, 1838  
 Family: Oncousoeciidae Canu, 1918  
 Genus: *Oncousoecia* Canu, 1918

**Type species.** *Oncousoecia lobulata* Canu, 1918, Recent, Britain.

*Oncousoecia* sp.  
 Figs. 5B, 6A–B

**Material.** CPBA 20090.1, Agua de la Mula Member, Agrio Formation, upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Agua de la Mula, encrusting the bivalve *Isognomon ricordeanus* (d'Orbigny). CPBA 20125.1 (infertile specimen), Pilmatué Member, Agrio Formation, upper Valanginian, *Neocomites* sp. Subzone, Cerro Birrete, encrusting the bivalve *Hinnites* sp.

**Description.** Colony encrusting, oligoserial, bifurcating, branches of low profile, infertile branches narrow, about 0.35 mm wide, fertile branches lobate, up to 2.5 mm wide. Early astogeny unknown. Autozooids elongate, frontal wall 0.60–1.00 mm long by 0.20–0.24 mm wide. Aperture subcircular, 0.14–0.15 mm in diameter, a short peristome sometimes preserved. Frontal walls too worn to reveal details of pseudopore morphology. Gonozooids pyriform, undilated proximal part of about equal length to dilated distal part, the transition between them gradual, total length 1.36–1.40 mm and maximum width 0.20–0.24 mm. Ooeciopore smaller than an autozoid aperture, slightly transversely elliptical, about 0.08 mm long by 0.09 mm wide. Kenozooids developed along branch margins.

**Remarks.** Distinguishing between species of *Oncousoecia* is difficult even in well preserved fossils. Although gonozooids are present in the Neuquén species, both available specimens are very heavily worn, making comparisons with European and North American Cretaceous species problematical. The pyriform gonozooid resembles that of *O. depressa* (d'Orbigny, 1850) as interpreted by Canu and Bassler (1926) but this European species has considerably larger zooids (see Pitt and Taylor, 1990).

**Occurrence.** Upper Valanginian, *Neocomites* sp. Subzone, Agrio Formation, Pilmatué Member; and upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Agrio Formation, Agua de la Mula Member, Neuquén Basin.

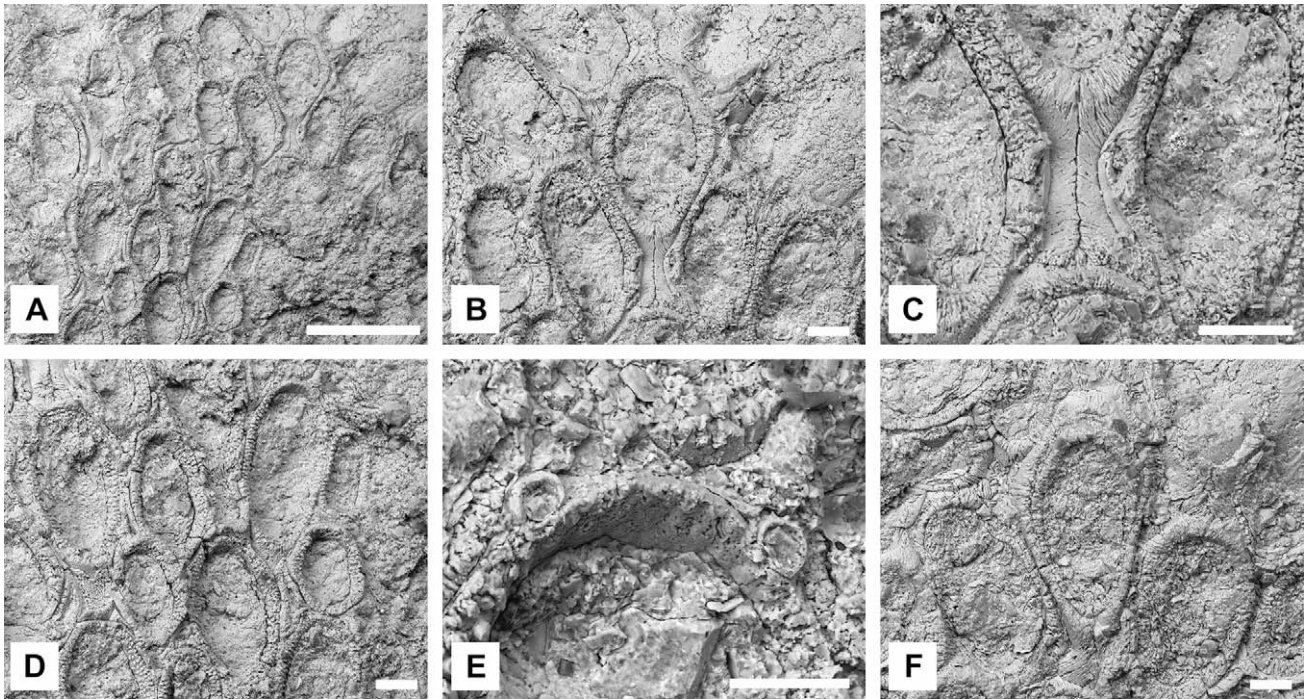
Family: Multisparsidae Bassler, 1935  
 Genus *Idmonea* Lamouroux, 1821

**Type species.** *Idmonea triquetra* Lamouroux, 1821, Bathonian, France.

*Idmonea* cf. *radiolitorum* d'Orbigny, 1850  
 Figs. 5A, 6C–D

**Material.** CPBA 20297.1, encrusting the bivalve *Isognomon* sp. CPBA 20090.1 (infertile), encrusting the bivalve *Isognomon ricordeanus* (d'Orbigny). Agua de la Mula Member, Agrio Formation, upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Agua de la Mula.

**Description.** Colony encrusting, oligoserial, branches about six autozooids wide, bifurcating, moderately high in profile, crests



**Fig. 4.** *Charixa burdonaria* sp. nov., scanning electron micrographs of holotype, CPBA 20129.1, Agua de la Mula Member, Agrio Formation, upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Agua de la Mula. A, irregular, pluriserial zooids, scale bar 500 µm. B, zooid with long proximal gymnocyst (cauda) forming part of an initial uniserial chain, scale bar 100 µm. C, detail of gymnocyst with median crack, scale bar 100 µm. D, zooids of widely varying size, the smallest probably being kenozooids, scale bar 100 µm. E, detail of the distal end of a zooid showing a pair of spine bases, scale bar 50 µm. F, zooid (centre) containing intramural bud, scale bar 100 µm.

rounded, branch width 1–1.3 mm. Early astogeny unknown. Autozooids rounded rhombic, longer than wide, frontal wall 0.28–0.39 mm long by 0.15–0.19 mm wide, a gradient of decreasing zooid size evident from branch crests to margins. Aperture transversely elliptical, 0.07–0.09 mm long by 0.08–0.12 mm wide, distal rim thickened. Worn frontal walls with large, closely spaced circular pseudopores. Terminal diaphragms closing apertures of some zooids apparently present a little beneath level of aperture. Gonozooids all preserved without their frontal walls, represented by inverted pear-shaped depressions along branch midlines, 0.91 mm long by 0.62 mm width in one measured example. Ooeciopores not preserved. Kenozooids developed along branch margins, similar to the outermost autozooids but still smaller and lacking apertures.

**Remarks.** This species has more robust branches than *Oncousoecia* sp. and the autozooids are stouter. It resembles *I. radiolitorum* d'Orbigny, 1850 (see Pitt and Taylor, 1990), a long-ranging European Cretaceous species, although the autozooids are somewhat smaller than those of putative *I. radiolitorum* from the British Aptian.

**Occurrence.** Upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Agrio Formation, Agua de la Mula Member, Neuquén Basin.

?Family: Plagioeciidae Canu, 1918  
Genus *Neuquenopora* gen. nov.

**Derivation of name.** From its occurrence in the Neuquén Basin.

**Type species.** *Neuquenopora carrerai* sp. nov., lower Hauterivian, Pilmatué Member, Agrio Formation, Cerro Birrete, Neuquén Basin.

**Diagnosis.** Colony encrusting, thick, multiple generations of buds visible at growing edge, radial fascicles developed locally in late

astogeny. Autozooids partly fixed-, partly free-walled, opening on frontal surface and at growing edges. Gonozooid fixed-walled, transverse, much wider than long, roofed by pseudoporous exterior wall not penetrated by autozooidal peristomes; ooeciopore transversely elliptical, slightly smaller than adjacent autozooidal apertures.

**Remarks.** This distinctive cyclostome has a 'flabellotrypiform' morphology with a marginal growing edge where most of autozooidal openings appear to occur. The genus *Flabellotrypa* Bassler, 1952 itself has an Ordovician–Devonian range and is either a cyclostome (Brood, 1975) or a ceramoporid cystoporate (Dzik, 1981). Mesozoic bryozoans with similar colony-forms include a 'variety' of *Ceriocava corymbosa* (Lamouroux, 1821) from the Middle Jurassic of France described by Walter (1970), and *Hyporosopora larwoodi* Pitt and Taylor, 1990 from the Aptian of England. *Neuquenopora* differs from all of these species in developing radial fascicles in colonies reaching late astogeny. These fascicles appear as a series of proximal prolongations of the growing edge with grooved areas between.

The strongly transverse fixed-walled gonozooid of *Neuquenopora* set among free-walled autozooids recalls that found in *Amphimarssoniella klaumanni* Voigt, 1974 from the Cenomanian of Germany. Referred by Voigt to Corymboporidae on account of its fungiform (mushroom-shaped) colonies, *A. klaumanni* further resembles *Neuquenopora* in having autozooids opening predominantly around the growing edge, although the German species also has polygonal apertures of free-walled zooids and elliptical apertures of fixed-walled zooids on the upper surface of the colony. The question of whether there is a close phylogenetic relationship between *Neuquenopora* and *Amphimarssoniella* cannot be answered without the discovery of more material for detailed comparative study. For the present, the new genus is questionably placed in Plagioeciidae on account of its similarities to the plagioeciid species *Hyporosopora larwoodi*.



*Neuquenopora carrerai* sp. nov.

Figs. 5B, 7

**Derivation of name.** Named for Dr Marcelo G. Carrera (Universidad Nacional de Córdoba) in recognition of his research on Argentinian fossil bryozoans.

**Material.** Holotype: CPBA 20125.1, Pilmatué Member, Agrio Formation, upper Valanginian, *Neocomites* sp. Subzone, Cerro Birrete, encrusting the bivalve *Hinnites* sp. Paratypes: three small colonies on the same substrate as the holotype. Other material: CPBA 20125.2, several heavily worn colonies probably of this species.

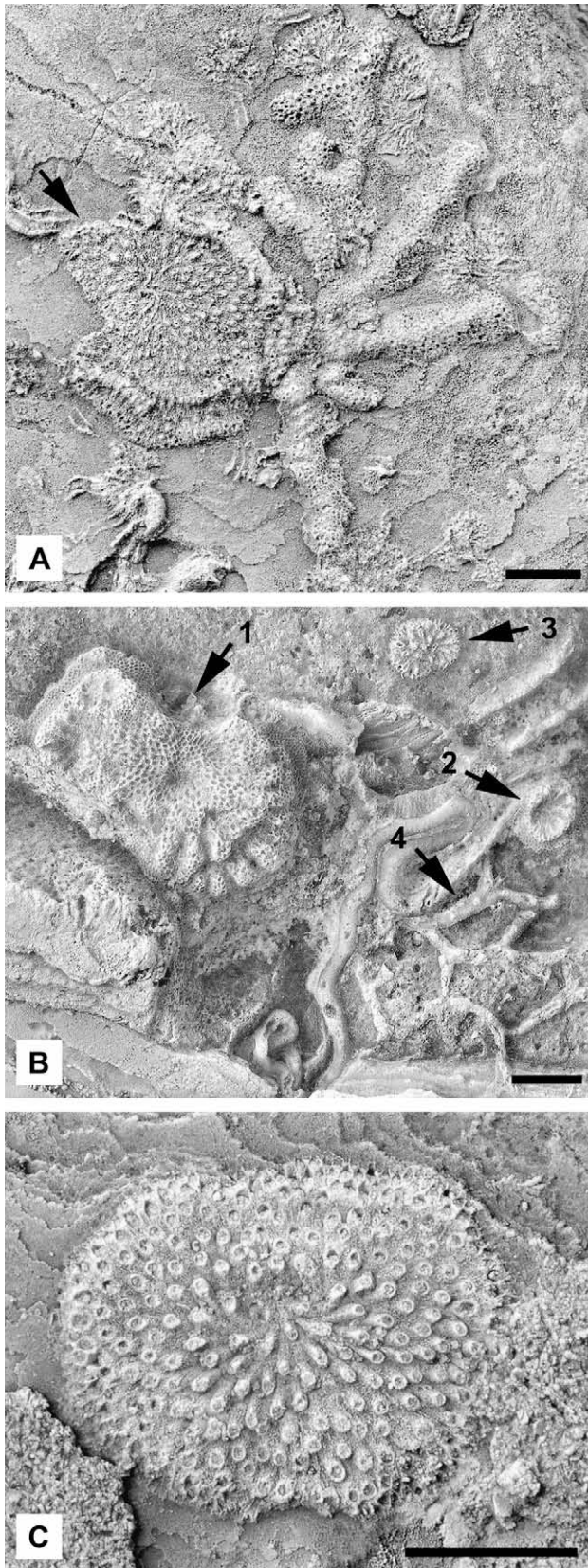
**Description.** Colony encrusting, multiserial, unilamellar, thick, initially subcircular, becoming more irregular in outline shape during growth. Growing edge steep, exposing many generations of polygonal, usually hexagonal, free-walled zooidal apertures/buds; no preserved fringe of basal lamina extending beyond budding zone. Frontal colony surface in early astogeny composed of apparent exterior wall calcification, corroded examples revealing elongate, slightly convex autozooidal frontal walls; in late astogeny at least in part covered by polygonal openings representing either free-walled autozooidal apertures or zooids from which capping exterior walls have been lost through abrasion. Fascicles developed in latest astogeny, radial, multiserial, two to four zooids wide, separated by depressions.

Autozooids free- or fixed-walled, most (?all) opening at colony growing edge and in fascicles as typically hexagonal apertures about 0.08–0.09 mm in diameter. Frontal walls in early astogeny elongate, at least 0.6 mm long and about 0.11 mm in maximum width.

Gonozooid fixed-walled, densely pseudoporous, considerably wider than long, 0.21 mm long by 1.03 mm wide, somewhat crescent-shaped, not penetrated by autozooids, located close to growing edge and inclined distofrontally in the single known example. Apparent oocypore positioned at extreme distomedial edge of gonozooid, transversely elliptical, slightly shorter than adjacent autozooidal apertures, about 0.06 mm long by 0.09 mm wide.

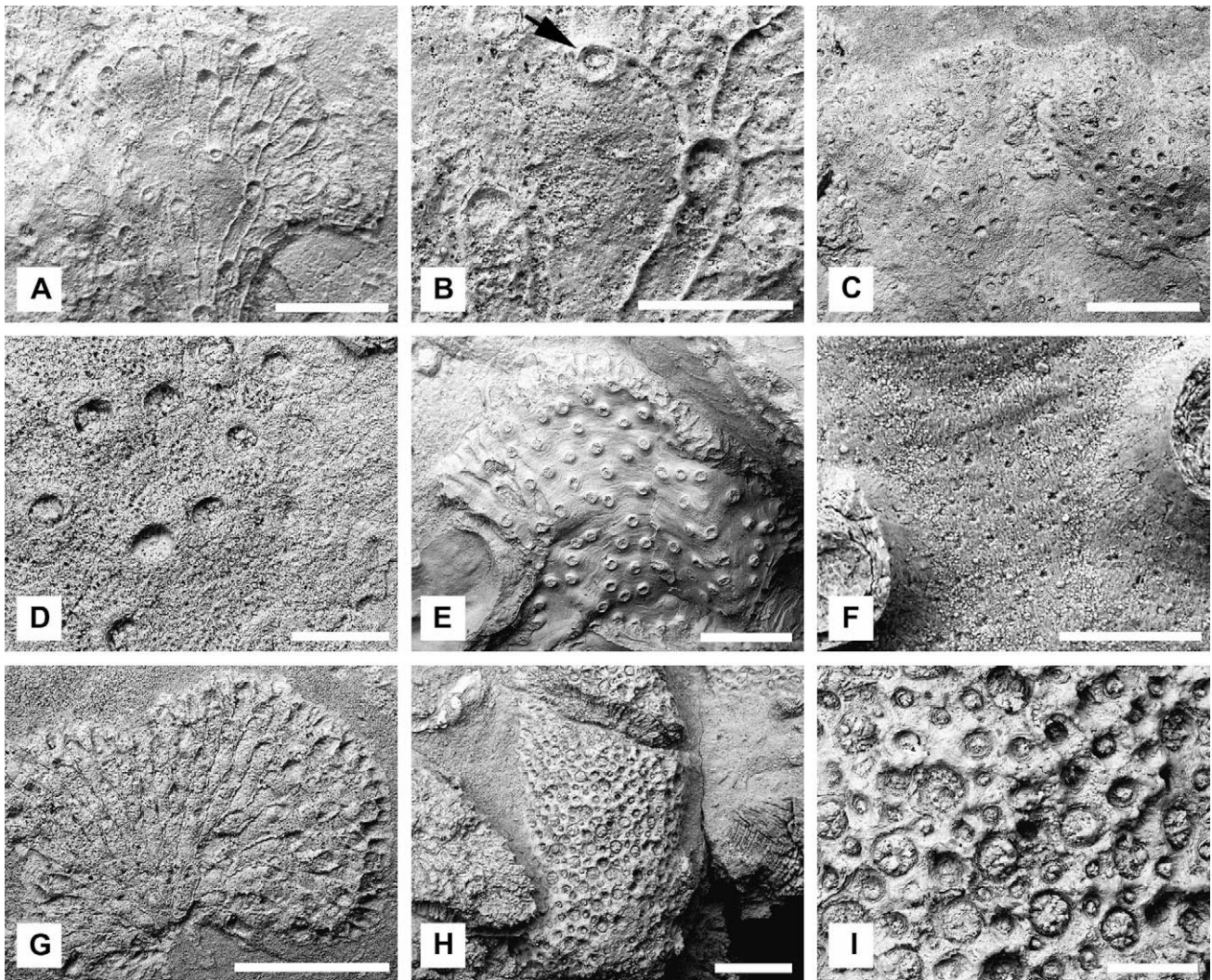
**Remarks.** Although indifferently preserved, material of this bryozoan is sufficiently distinct from other described cyclostomes to warrant its recognition as a new genus and species. Neither the flabellotrypiform colonies of supposed *Cerriocava corymbosa* from the Jurassic nor *Hyporosopora larwoodi* from the Aptian are known to develop fascicles like those present in *N. carrerai*. The transverse gonozooids of *N. carrerai* differ from the longitudinally elongate gonozooids present in the Jurassic species *C. corymbosa*. While *H. larwoodi* does share with *N. carrerai* transverse gonozooids and a similar oocypore, the gonozooids are somewhat less elongate in the species from the English Aptian. Colonies of *H. larwoodi* are always small, typically less than 3 mm in diameter and less than half the size of *N. carrerai*.

**Occurrence.** Upper Valanginian, *Neocomites* sp. Subzone, Agrio Formation, Pilmatué Member, Neuquén Basin.



**Fig. 5.** Encrusting cyclostome bryozoans from the Agrio Formation. A, CPBA 20090.1, Agua de la Mula Member, Agrio Formation, upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Agua de la Mula; worn colonies of the branching *Idmonea* cf. *radiolitorum* d'Orbigny, 1850 and spot-like '*Berenicea*' sp. (arrowed). B, CPBA 20125, Pilmatué Member, Agrio Formation, upper Valanginian, *Neocomites* sp. Subzone, Cerro Birrete; holotype (1) and a paratype (2) of *Neuquenopora carrerai* sp. nov., along with colonies of '*Berenicea*' sp. (3) and *Oncousoecia* sp. (4). C, CPBA 19748.13, Pilmatué Member, Agrio Formation, lower Hauterivian, *Hoplitocrioceras gentilii* Zone, Bajada del Agrio; infertile colony of '*Berenicea*' sp. Scale bars 2 mm.





**Fig. 6.** Scanning electron micrographs of cyclostomes from the Agrio Formation. A–B, *Oncousoecia* sp., CPBA 20090.1, Agua de la Mula Member, Agrio Formation, upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Agua de la Mula; A, fertile lobe, scale bar 1 mm; B, gonozooid with oeciopore arrowed, scale bar 500  $\mu$ m. C–D, *Idmonea* cf. *radiolitorum* d’Orbigny, 1850, CPBA 20297.1, Agua de la Mula Member, Agrio Formation, upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Agua de la Mula; C, closely spaced branches, scale bar 1 mm; D, autozooids (left) and kenozooids (right) at the edge of a Branco, scale bar 250  $\mu$ m. E–F, ‘*Berenicea*’ sp., CPBA 20126.1, Pilmatu  Member, Agrio Formation, upper Valanginian, *Neocomites* Subzone, Bajada del Agrio; E, well preserved colony encrusting the worm *Parsimonia antiquata* (Sowerby), scale bar 1 mm; F, detail of frontal wall showing tiny pseudopores, scale bar 10  $\mu$ m. G, ‘*Berenicea*’ sp., Agua de la Mula Member, Agrio Formation, upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Agua de la Mula; typical preservation with frontal walls mostly worn to expose chamber-filling cement and the vertical walls between the zooids, scale bar 1 mm. H–I, *Multizonopora* sp., CPBA 20127, Agua de la Mula Member, Agrio Formation, upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Agua de la Mula; H, weathered branch, scale bar 1 mm; I, detail showing large autozooidal apertures surrounded by smaller kenozooids, scale bar 250  $\mu$ m.

#### Incertae familiae

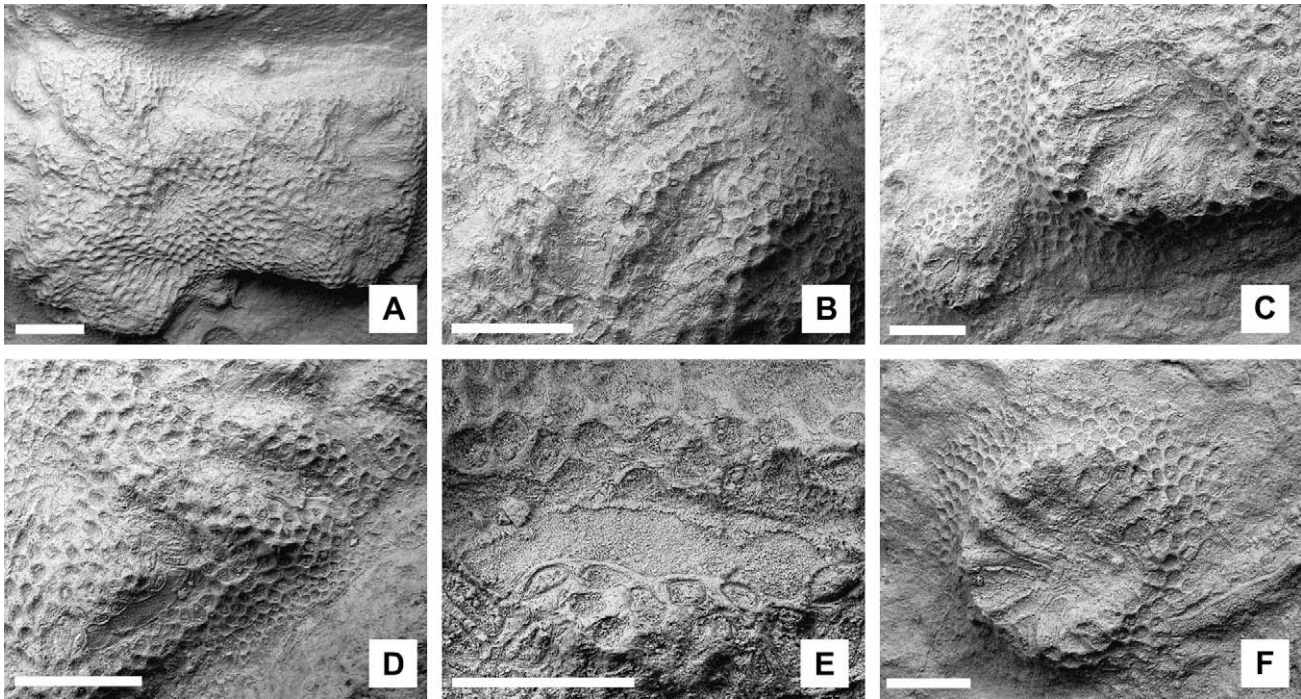
‘*Berenicea*’ spp.  
Figs. 5, 6E–G

**Material.** CPBA 20126.1, Pilmatu  Member, Agrio Formation, upper Valanginian, *Neocomites* Subzone, Bajada del Agrio, encrusting tubes of the worm *Parsimonia antiquata* (Sowerby). CPBA 20090.1, Agua de la Mula Member, Agrio Formation, upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Agua de la Mula; encrusting the bivalve *Isognomon ricordeanus* (d’Orbigny). CPBA 20131.1, Agua de la Mula Member, Agrio Formation, upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Mina La Continental; two species encrusting a potamidid gastropod. CPBA 20125.1–2, Pilmatu  Member, Agrio Formation, upper Valanginian, *Neocomites* sp. Subzone, Cerro Birrete, encrusting the bivalve *Hinnites* sp. CPBA 20087, Agrio Formation, lower Valanginian–upper Hauterivian, unknown locality, encrusting the

bivalve *Mimachlamys robinaldina* (d’Orbigny). CPBA 19748.13, 19748.30, Pilmatu  Member, Agrio Formation, lower Hauterivian, *Hoplitocrioceras gentilii* Zone, Bajada del Agrio; encrusting the bivalve *Gervillella aviculoides* (Sowerby). CPBA 20297.2, Agua de la Mula Member, Agrio Formation, upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Agua de la Mula.

**Remarks.** Encrusting tubuliporine cyclostomes with small, sub-circular, sheet-like colonies are among the commonest bryozoans throughout the Jurassic and Lower Cretaceous. Apart from species having distinctive features such as apertures aggregated into fascicles, these have historically been assigned to *Berenicea* Lamouroux, 1821. However, this genus is unrecognizable following destruction of the type material of the type species. Species formerly placed in *Berenicea* are now redistributed among a number of other genera which are distinguishable principally using characters of the gonozooid. A problem, however, is that gonozooids are typically present in only a small minority of colonies within populations, meaning that





**Fig. 7.** *Neuquenopora carrerai* sp. nov., scanning electron micrographs of the holotype (A–E) and a paratype (F) from the same substrate, CPBA 20125.1, Pilmatué Member, Agrio Formation, upper Valanginian, *Neocomites* sp. Subzone, Cerro Birrete. A, colony surface, scale bar 1 mm. B, colony margin showing apertures arranged in radial fascicles, scale bar 1 mm. C, thick growing edge meeting a small conspecific colony, scale bar 500 µm. D, margin with gonozooid (lower left), scale bar 1 mm. E, gonozooid, scale bar 500 µm. F, small flabellotrypiform colony, scale bar 500 µm.

many forms cannot be assigned to a genus. This is true of the colonies from the Neuquén Basin, none of which have gonozooids. They are therefore assigned to the form-genus ‘*Berenicea*’, as advocated by Taylor and Sequeiros (1982).

Based on autozooid size differences, a minimum of three species of ‘*Berenicea*’ can be estimated to be present in the Neuquén Basin. Only one of these is preserved well enough to show another character of systematic value, the morphology of the pseudopores (Fig. 4F). This species, which encrusts tubes of the worm *Parsimonia antiquata* (Sowerby) from Bajada del Agrio, has subcircular pseudopores which are small (ca 5 µm) and spaced about 20 µm apart. Two species differing conspicuously in autozooid size occur together with *Charixa burdonaria* on a potamidid gastropod from Mina La Continental.

Suborder: Cerioporina von Hagenow, 1851

Family: Cerioporidae Busk, 1859

Genus *Multizonopora* d’Orbigny, 1853

*Type species.* *Heteropora arborea* Koch and Dunker, 1837, Lower Cretaceous, Germany.

*Multizonopora* sp.  
Figs. 6H–I, 8

*Material.* CPBA 20127, Agua de la Mula Member, Agrio Formation, upper Hauterivian–?lower Barremian, *Paraspiticeras groeberi* Zone, Agua de la Mula. CPBA 20128, Agua de la Mula Member, Agrio Formation, upper Hauterivian, *Crioceratites diamantensis* Zone, Bajada del Agrio.

*Description.* Colony erect, ramose, bushy, up at least 11.5 cm in diameter, comprising regularly bifurcating cylindrical branches about 2.5 mm in diameter, thickening to 4.5 mm at colony base. Intracolony overgrowths uncommon. Maculae not observed.

Autozooids free-walled, long curved tubes opening on colony surface as subcircular apertures averaging 0.09 mm in diameter, separated by smaller kenozooids. Kenozooids numerous, smaller and with more angular apertures than autozooids, about 0.06 mm in diameter. Gonozooids not observed.

*Remarks.* This species is a typical ramose cerioporine cyclostome. Unfortunately, gonozooids are not visible, casting some doubt over its correct generic identity. Walter (1989) considered *Multizonopora* to be a junior synonym of *Heteropora* Blainville, 1830 but because of problems over the identity of *Heteropora*, as based on the characters of the Maastrichtian type species (see Nye, 1976), we favour placing the Agrio Formation species into *Multizonopora*. The Lower Cretaceous type species of *Multizonopora*, *M. arborea* (Koch and Dunker), was comprehensively redescribed by Hillmer (1968) and Walter (1989). One of the available Agrio Formation specimens (Fig. 8A) is a large, air-weathered colony measuring 11.5 cm across, preserving some basal branches but not the colony origin or substrate which are both eroded away. The second specimen (Fig. 8B) is a piece of limestone full of broken branches and interpreted as a reworked shell bed.

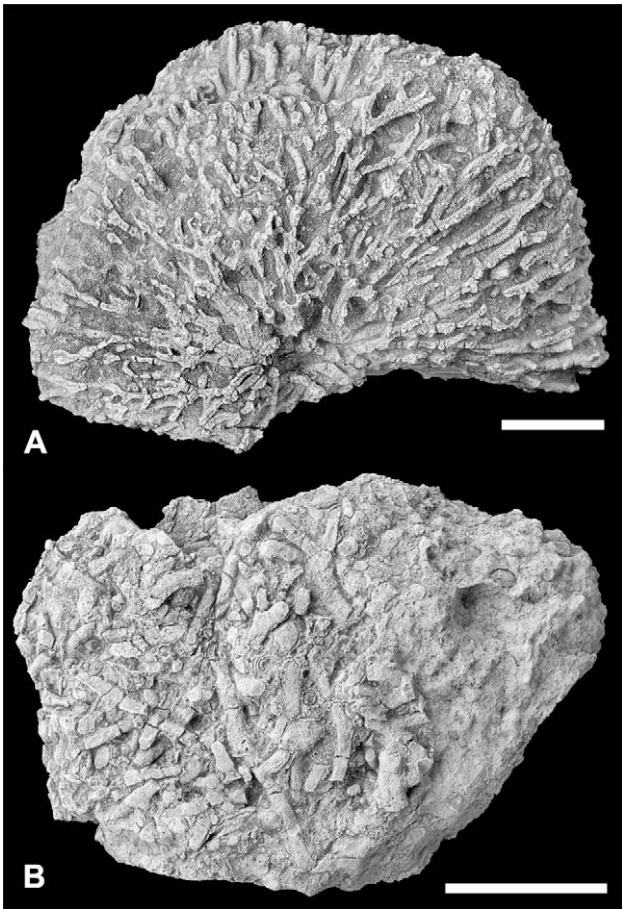
#### 4. Discussion

The bryozoans described here from the Agrio Formation of the Neuquén Basin provide a first glimpse of bryozoans that inhabited the region now represented by South America during the Early Cretaceous and allow a tentative assessment of their palaeobiogeographical, palaeoecological and evolutionary significance.

##### 4.1. Palaeobiogeography

The Agrio Formation fauna resembles bryozoan faunas from the Lower Cretaceous of Europe (England, France and Germany) in terms





**Fig. 8.** *Multizonopora* sp. A, relatively intact ramose colony, CPBA 20128, Agua de la Mula Member, Agrio Formation, upper Hauterivian, *Crioceratites diamantensis* Zone, Bajada del Agrio. B, broken branches in a small slab of limestone, CPBA 20127, Agua de la Mula Member, Agrio Formation, upper Hauterivian–?lower Barremian, *Paraspiticerus groeberi* Zone, Agua de la Mula. Scale bars 20 mm.

of the taxa present: most of the species present belong to genera ubiquitous in coeval deposits in Europe. Only the genus *Neuquenopora* gen. nov. may be considered a possible endemic. Remarkably, ammonoids and bivalves from the Agrio Formation also show Tethyan affinities, although some are endemic or Andean taxa. Thus different faunal elements in this unit point to open exchange during the Early Cretaceous between Europe and the southeastern Pacific, suggesting that similar high water temperatures pertained (Aguirre-Urreta et al., 2007; Lazo, 2007a).

#### 4.2. Palaeoecology and environments

Among the bryozoans in the Agrio Formation, encrusting forms dominate, the only erect species being a large cerioporine cyclostome (*Multizonopora* sp.; Fig. 8). However, it is possible that narrow-branched erect species are present but were not collected as they are inconspicuous in the field and often require processing of bulk sediment samples.

In common with other Lower Cretaceous bryozoan faunas (e.g. Pitt and Taylor, 1990), cyclostomes greatly outnumber cheilostomes in diversity. However, the single cheilostome found in the Agrio Formation is notable for its large size compared with cheilostomes recorded elsewhere in the Lower Cretaceous. The thick, multilayered masses of *C. burdonaria* sp. nov. have no parallel among contemporaneous cheilostomes, all of which form small, single-layered colonies (see Taylor, 1986). Colonies of *C. burdonaria* have been found encrusting two substrates, potamidid gastropods

(Fig. 3A–B), and the bivalve *Steinmanella vacaensis* (Fig. 3C–D) from near the top of the Agua de la Mula Member. Both occurrences come from a single shell pavement within shales that contain carbonate nodules hosting a diverse association, including decapods and bivalves. Colonies of *C. burdonaria* sp. nov. encrusting the gastropod substrates are occasionally associated with the cyclostome ‘*Berenicea*’. Some of the *C. burdonaria* sp. nov. colonies are multilamellar and recall bryozoans living in symbiosis with hermit crabs (e.g. Taylor, 1994), although the poor preservation makes this idea difficult to substantiate.

Large multilamellar masses of *C. burdonaria* sp. nov. intergrown with the serpulid worm *Parsimonia antiquata* (Sowerby) encrust disarticulated bivalve substrates, covering both the inner and outer surfaces (Fig. 3C–D). The outer ornamentation of the bivalve is roughly replicated by the bryozoans. These large masses are probably aggregations of numerous colonies rather than single colonies. The intergrowths are reminiscent of some occurrences of related malacostegan cheilostomes at the present-day. In the Coorong Lagoon of South Australia, buildups of *Conopeum aciculata* (MacGillivray) can be found intergrown with serpulids (Bone and Wass, 1990). Most of the growth in these build-ups occurred about 700 years BP but a new population explosion in 1989 was related to increased freshwater run-off and lowering of the salinity in this lagoon where salinities normally reach up to 70 ppt (Bone, 1991). Freitas et al. (1994) reported an unusual co-occurrence of the serpulid *Ficopomatus enigmaticus* (Fauvel) and a bryozoan identified as *Membranipora savarti* (Audouin) (= *Acanthodesia savartii*) in the Albufeira Coastal Lagoon, near Lisbon, Portugal. This happened after heavy rainfall reduced the salinity in the lagoon from a normal marine value to about 6.5–9 ppt. Taking these two examples together, it seems that abnormal salinities are able to trigger population flushes in co-occurring malacostegan bryozoans and serpulids, which may have implications for inference of palaeosalinities in the Neuquén Basin during the Early Cretaceous. The presence of trigoniid bivalves along with potamidid gastropods in the same bed points to variations in salinity. While trigoniids strongly suggest euhaline conditions, potamidids suggest brackish to euhaline waters. Recent Potamididae are common intertidal gastropods with an amphibious existence in muddy habitats, especially brackish water mangroves, confined to tropical and subtropical regions (Bandel and Kowalke, 1999; Kowalke, 2002). In addition, unpublished isotopic analyses and faunal evidence suggest salinity changes during the deposition of the Agrio Formation (see Lazo, 2007a). Those related to bryozoans are briefly described below.

In the *Neocomites* sp. Subzone there are monospecific mass aggregations of *Parsimonia antiquata* (Sowerby) within shales. These aggregations form lenses that reach 2 m in maximum thickness near Bajada del Agrio. The serpulid tubes are encrusted by small-sized oysters, plicatulids and the bryozoan ‘*Berenicea*’. Similar mass aggregations of serpulids occur in stressed modern environments such as lagoons, bays and fiords. They can acquire a gregarious life habit under a range of salinities, from brachyhaline to hyperhaline (Ten Hove and van den Hurk, 1993).

Coral patch-reef facies occur at a number of levels in the *Paraspiticerus groeberi* Zone (Fig. 2; Lazo et al., 2005). These facies contain a combination of flat, globose, conical, and ramose coral colonies that may reach approximately 1 m in maximum height. Scleractinian corals are the main component, although sponges, bryozoans (*Multizonopora* sp. and *Idmonea* cf. *radiolitorum*), regular echinoids, bivalves, and gastropods are also recorded. The lack of coalescence of corals and the limited lateral extension of the facies, which is restricted mainly to Agua de la Mula and Bajada del Agrio, suggests that the corals constituted a patch-reef and that salinity ranged from brachyhaline to euhaline (James and Bourque, 1992).

#### 4.3. Evolution of cheilostome spines

Spines known or presumed to have defensive roles are found in many cheilostome bryozoans. Some are unmineralized, others consist of solid calcium carbonate, but the majority are hollow and basally articulated (see Silén, 1977). Spines of this latter type are often considered to be polymorphic zooids (spinozooids). In fossil cheilostomes such spines are invariably lost following decay of their basal organic articulations. However, their former presence is marked by characteristic spine bases (Fig. 4E), usually either arranged in a ring around the opesia, or forming one or a few pairs of oral spines near the distolateral corners of the opesia. Neither of the two earliest cheilostome genera, *Pyrporopsis* Pohowsky, 1973 (?Oxfordian, ?Kimmeridgian – Berriasian) and *Wawalia* Dzik, 1975 (Valanginian–Aptian), show any evidence of having possessed spines (see Ostrovsky et al., 2008). Prior to the discovery of *C. burdonaria*, in which many zooids have a single pair of oral spine bases (Fig. 4E), the oldest spines known were from Aptian species belonging to *Charixa* and *Spinicharixa* (Taylor, 1986). The fossil record of cheilostome spines can now be pushed back to the upper Hauterivian.

Onset of major radiation in cheilostome bryozoans was delayed until the late Albian–early Cenomanian and coincided with the first appearance in the fossil record of ovicells for brooding embryos prior to their release as non-planktotrophic larvae (Taylor, 1988). All pre-Albian cheilostomes, including *C. burdonaria*, lack ovicells. They are inferred to be like modern malacostegines in releasing non-brooded, planktotrophic larvae called cyphonautes. Brooding in ovicells has been interpreted as a key evolutionary innovation. The most primitive cheilostome ovicells consist of rings of basally-articulated spines, borne by the zooid distal to the maternal zooid, modified to form open cages for embryonic brooding (Ostrovsky and Taylor, 2004, 2005). Therefore, the origin of spines represents a crucial step in cheilostome evolution. The discovery of spines in *C. burdonaria* allows spine origin to be dated as late Hauterivian or before. Furthermore, evidence from this species suggests that oral spines were the first to evolve. Subsequently it seems that spines spread proximally around the entire circumference of the opesia, as is first seen in *Spinicharixa* in the Aptian. This proliferation into proximal regions was essential for spines to be located close enough to the orifice of the preceding zooid to be ‘co-opted’ for protection of the embryos of this maternal zooid.

#### 5. Conclusion

Much focused collecting and research remains to be done before we can obtain a satisfactory understanding of the evolutionary palaeobiogeography of Mesozoic bryozoans. However, the bryozoan fauna described here from the Agrio Formation of the Neuquén Basin adds significant new data on the global distribution of genera during the Early Cretaceous and on the time of origin of a critical morphological feature – spines – in cheilostome bryozoans.

#### Acknowledgments

Phil Crabb (NHM) expertly undertook the macrophotography. Débora Rodríguez (UBA) provided the Cerro Birrete section. D. Rodríguez, Diana Fernández and Cecilia Cataldo (UBA) are thanked for their help during fieldwork. Miguel Griffin (MLP) is acknowledged for his help in the identification of the gastropods. This research was supported by grants PICT 14143, CONICET PIP 5960 and UBACYT x084 to Aguirre-Urreta.

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