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Barremian bryozoans from Serre de Bleyton (Drôme, SE France)

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(With 13 figures)

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Abstract

A newly discovered bryozoan fauna from Serre de Bleyton in the Vocontian Basin is described for the first time. The fauna is dominated volumetrically by small nodular cyclostomes. In total, 20 species are recognized, comprising 19 stenolaemates and one cheilostome. Among the stenolaemates is a new eleid cyclostome, *Elea periallos* nov. spec., notable for being the earliest species of this genus, the oldest eleid to possess mandibulate polymorphs (eleozoids), and the only eleid with a complex brood chamber extending distally of the ooeciopore. A stenolaemate with lunaria may be a cystoporate, either derived from older sediments or considerably younger than any previously known cystoporates, or a cyclostome homeomorph of a cystoporate.

Keywords: Bryozoa, Cretaceous, Barremian, France, taxonomy.

Zusammenfassung

Eine neu entdeckte Moostierchenfauna von Serre de Bleyton im Vocont Becken wird zum ersten Mal beschrieben. Die Fauna wird von kleinen, knolligen Cyclostomata dominiert. Insgesamt konnten 20 Arten nachgewiesen werden, darunter 19 Stenolaematen und eine Form der Cheilostomata. Unter den Stenolaematen ist eine neue eleide cyclostome Form bemerkenswert: *Elea periallos* nov. spec. Diese neue Art ist der älteste Vertreter der Gattung *Elea* und die älteste Eleidae mit mandibulaten Polymorphen (Eleozoiden). Weiters stellt sie die einzige Eleidae mit komplexem Brutraum dar, der sich distal der Ooeciopore erstreckt. Ein stenolaemate Form mit Lunaria könnte ein umgelagerte cystoporate Bryozoen darstellen oder das jüngste Mitglied der Cystoporata sein. Möglicherweise handelt es sich aber auch um eine cyclostomate Form mit einer zu den Cystoporata homeomorphen Morphologie.

Schlüsselwörter: Bryozoen, Kreide, Barremium, Frankreich, Taxonomie.

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Introduction

Bryozoans were slow to recover from the mass extinction event (or events) of the Late Permian. Although the first significant post-Palaeozoic evolutionary radiation occurred in the Middle Jurassic, this was short-lived and it was not until the Early Cretaceous that a more sustained radiation of the phylum commenced (TAYLOR & LARWOOD 1990). Diversification was initially limited to the order Cyclostomata. The richest Early Cretaceous (Neocomian) cyclostome faunas come from southeastern France and adjoining parts of Switzerland. These bryozoans formed the subject of a long succession of papers written or coauthored by Bernard WALTER (DELAMETTE & WALTER 1984; WALTER 1972, 1977, 1983, 1985, 1986a, 1986b, 1987, 1989, 1991, 1993, 1995; WALTER & BUSNARDO 1971; WALTER & CLAVEL 1979; WALTER *et al.* 1975). Despite the comprehensive research of WALTER and his collaborators, fresh discoveries can still yield new and important additions to the Neocomian bryofauna, as evidenced by the material from Serre de Bleyton in Drôme that is described in this paper. Of particular importance is the discovery of an eleid (meliceritid) cyclostome that is not only the oldest example of this group of operculate cyclostomes to possess mandibulate polymorphs (eleozoids) but also has crescent-shaped gonozooids unlike other the ovate gonozooids of other eleids.

Serre de Bleyton is situated in the Vocontian Basin (Fig. 1). The Barremian turbiditic sediments deposited here comprise bioclastic grainstones containing both autochthonous and allochthonous fossils, including ammonoid steinkerns, belemnites, bivalves, brachiopods, crinoids, corals and sponges, in addition to the bryozoans. Ammonoid (LUKENDER 2010) and belemnite (JANSSEN 2010) evidence suggests a late Early to Late Barremian age, although diagnostic zonal species are unfortunately lacking. Other macrofossil species are typical of Mediterranean Barremian faunas.

Material and methods

The locality at Serre de Bleyton comprises three small outcrops along a forest road. Bryozoans were collected from Locality 1 (N44°28'55", E5°18'00") and Locality 2 (N44°28'54", E5°17'58") by Gero MOOSLEITNER.

All of the studied material is deposited in the collections of the Naturhistorisches Museum, Vienna, abbreviated NHMW. Specimens were cleaned ultrasonically before sorting with the aid of a binocular microscope. Well-preserved and/or fertile examples of each species were selected for study using a low-vacuum scanning electron microscope (LEO 1455VP) at the Natural History Museum, London. This instrument allowed back-scattered electron images to be obtained of uncoated specimens temporarily mounted to stubs using adhesive carbon tabs, or affixed to stage mounts with Blu-Tack.

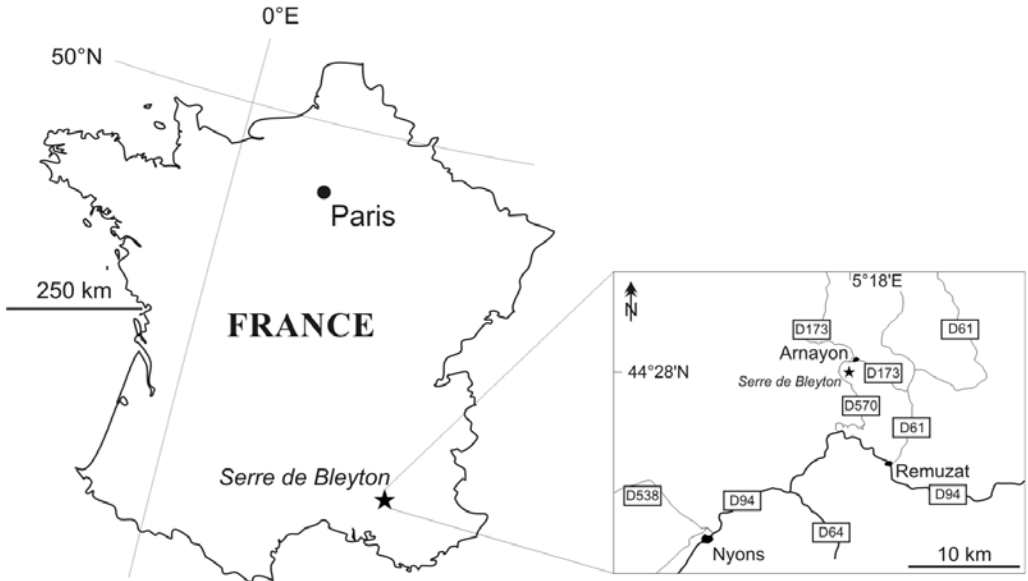


Fig. 1: Locality map of Serre de Bleyton (from LUKENEDER 2010).

Systematic palaeontology

Apart from one cheilostome colony, all of the bryozoans are cyclostomes. While most Mesozoic cyclostome bryozoans can be identified using external morphological features, especially if fertile colonies with larval brood chambers (gonozooids) are available, this is not always the case for free-walled cyclostomes (mostly cerioporines) in which thin sectioning to reveal internal morphology is important. Preparation of the large number of thin sections required to characterise the cerioporines adequately was not possible for the current study. Silicification of many cerioporine colonies introduces a further difficulty. Therefore, the cerioporines are given only a cursory treatment. While a full taxonomic description is presented for the single new species introduced in this paper, only brief synonymies and remarks, as well as figures, are provided for the other species.

Unless otherwise stated, all cited material is from Locality 2 at Serre de Bleyton.

Class Stenolaemata BORG, 1926

Order Cyclostomata BUSK, 1852

Suborder Tubuliporina MILNE-EDWARDS, 1838

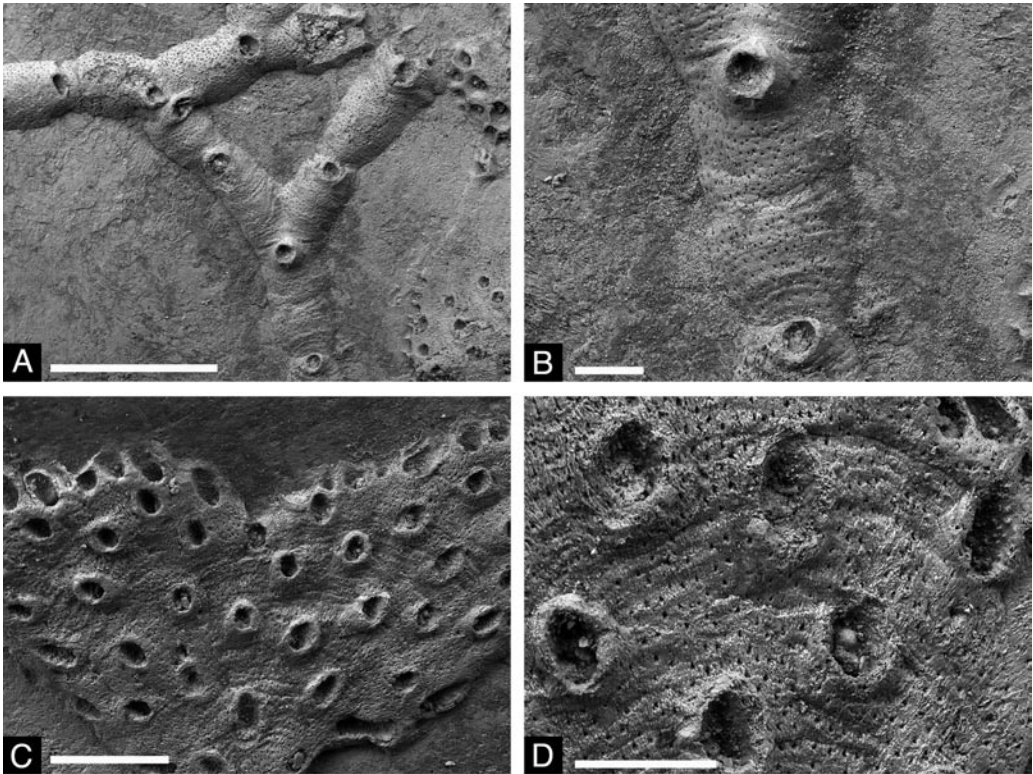


Fig. 2: Encrusting tubuliporine cyclostome bryozoans from the Barremian of Serre de Bleyton. A-B: *Stomatopora* cf. *melvillei* PITT & TAYLOR, 1990; NHMW 2009z0154/0001(a). A: bifurcating branches. B: zooid. C-D: *Oncousoecia* sp.: NHMW 2009z0154/0002. C: flabellate branches. D: autozooids with elongate apertures and pseudopores. Scale bars: A = 1 mm; B, D = 200 μ m; C = 500 μ m.

Family Stomatoporidae PERGENS & MEUNIER, 1886

Genus *Stomatopora* BRONN, 1825

***Stomatopora* cf. *melvillei* PITT & TAYLOR, 1990**

(Fig. 2A-B)

cf. 1990 ‘*Stomatopora*’ *melvillei* PITT & TAYLOR: 68, figs 3-6.

Material: NHMW 2009z0154/0001(a) (colony encrusting a small bivalve fragment together with a colony of *Reptoclausa* aff. *neocomiensis* D’ORBIGNY, 1853), 2009z0154/0032 (7 colonies).

Remarks: *Stomatopora*, as broadly interpreted, is the commonest runner-like encrusting cyclostome in the Mesozoic. Numerous species have been described, all characterized by uniserial colonies with bifurcating branches. Species-level taxonomy is hampered by the lack of basal gonozooids in fossil *Stomatopora*. Alternative characters offering promise for distinguishing species in this simple genus include zoecial budding pattern (e.g. ILLIES 1973), early astogeny and pseudopore morphology (ZATON & TAYLOR 2009), but these have yet to be studied adequately in the great majority of nominal species.

A fragmentary, scanned colony of *Stomatopora* preserving 10 zooids resembles *S. melvillei* PITT & TAYLOR from the Aptian Faringdon Sponge Gravel of Oxfordshire, England. The Serre de Bleyton colony has zooids measuring about 0.48-0.81 mm long by 0.43 mm wide, with apertures 0.10-0.11 mm wide, dimensions falling within the range observed for *S. melvillei*. However, important early astogenetic stages are lacking in the scanned specimen.

Family Oncousoeciidae CANU, 1918

Genus *Oncousoecia* CANU, 1918

***Oncousoecia* sp.**

(Fig. 2C-D)

Material: NHMW 2009z0154/0002.

Remarks: *Oncousoecia*, an extant genus with ribbon-like encrusting colonies and simple gonozooids, was recently revised by TAYLOR & ZATON (2008). The scanned specimen from Serre de Bleyton has flabellate branches and longitudinally elongate autozooidal apertures about 0.10-0.14 mm long by 0.07-0.08 mm wide. There are no gonozooids. Colony-form resembles *O. coarctata* (CANU & BASSLER, 1926), as redescribed by PITT & TAYLOR (1990) from the Aptian Faringdon Sponge Gravel, but the apertures are more closely-spaced and elongate in the Serre de Bleyton colony. A species from the Upper Barremian of Ardèche figured by WALTER *et al.* (1975, pl. 10, fig. 15) as *Proboscina riordeauana* D'ORBIGNY, 1852 is similar to the Serre de Bleyton species but appears to have branches that are more convex.

Family Multisparsidae BASSLER, 1935

Genus *Reptoclausia* D'ORBIGNY, 1853

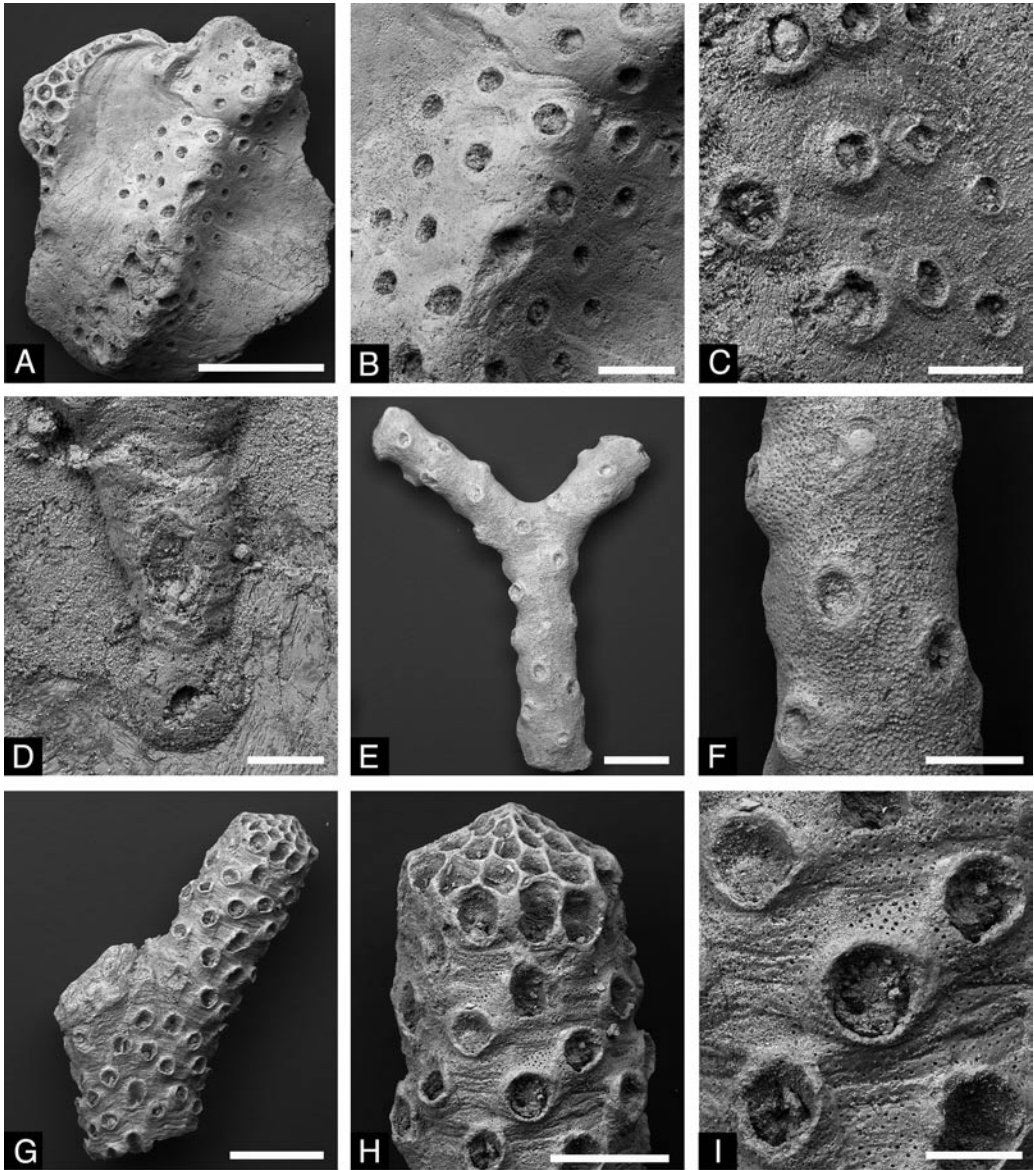


Fig. 3: Tubuliporine cyclostome bryozoans from the Barremian of Serre de Bleyton. A-D: *Reptoclausa* aff. *neocomiensis* D'ORBIGNY, 1853; A-B, NHMW 2009z0154/0003. A: small colony showing ridge of autozooids between troughs occupied by kenozooids without apertures. B: detail of autozooids. C-D: NHMW 2009z0154/0001(b). C: pronounced gradient of decreasing autozooidal aperture diameter from ridge crest (left) towards kenozooidal furrow (right). D: ancestrula. E-F: *Mecynoecia* cf. *icaunensis* (D'ORBIGNY, 1850); NHMW 2009z0154/0004. E: bifurcating branch. F: autozooids. G-I: *Cardioecia neocomiensis* (D'ORBIGNY, 1853); NHMW 2009z0154/0005. G: broken bifurcating branch. H: growth tip. I: autozooids. Scale bars: A, E, G = 1 mm; B, C, D, I = 200 μ m; F, H = 500 μ m.

***Reptoclausia* aff. *neocomiensis* D'ORBIGNY, 1853**
(Fig. 3A-D)

aff. 1853 *Reptoclausia neocomiensis* D'ORBIGNY: 888, pl. 765, figs 1-2.

aff. 1972 *Idmonea neocomiensis* (D'ORBIGNY, 1853) – WALTER: 296.

Material: NHMW 2009z0154/0003, 2009z0154/0001(b) (young colony encrusting a small bivalve fragment together with a colony of *Stomatopora* cf. *melvillei* PITT & TAYLOR, 1990), 2009z0154/0033 (4 colonies).

Remarks: Autozooids of *Reptoclausia* are arranged in longitudinal ridges between which are areas of low relief occupied by featureless kenozooids lacking apertures. In the type species, *R. neocomiensis*, originally described from the Neocomian [Upper Valanginian] of Ste Croix, Switzerland, these ridges are lens-shaped and relatively short, tapering and pinching out with growth. In contrast, the Serre de Bleyton colonies of *Reptoclausia* usually have more prolonged ridges reminiscent of those found in the Aptian species *R. hagenowi* (SHARPE, 1854) (see PITT & TAYLOR 1990: 82).

A marked gradient of decreasing autozooid size is developed from ridge crests, down ridge flanks and towards kenozooidal regions (Fig. 3C). In the scanned Serre de Bleyton colonies apertural diameter grades from about 0.11 mm to 0.07 mm along this transect. One of the Serre de Bleyton colonies preserves early astogenetic stages, including the ancestrula (Fig. 3D) with a protoecium measuring 0.26 mm in diameter. The ancestrula appears not to have been described in *R. neocomiensis* but in *R. hagenowi* the protoecium is large, 0.35 mm in diameter (PITT & TAYLOR 1990). This presumably reflects a larger larva at settlement in *R. hagenowi* than *R. aff. neocomiensis*.

Family Mecynoeciidae CANU, 1918

Genus *Mecynoecia* D'ORBIGNY, 1853

***Mecynoecia* cf. *icaunensis* (D'ORBIGNY, 1850)**
(Fig. 3E-F)

cf. 1850 *Entalophora icaunensis* D'ORBIGNY: 37.

cf. 1987 *Mecynoecia icaunensis* (D'ORBIGNY, 1850) – WALTER: 38, figs 2, 7, pl. 1, figs 22-29, pl. 5, figs 1-16.

cf. 1995 *Mecynoecia icaunensis* (D'ORBIGNY, 1850) – WALTER: 419, pl. 56, fig. 8.

Material: NHMW 2009z0154/0004, 2009z0154/0034 (3 branch fragments).

Remarks: Infertile fragments of an erect, narrow-branched (vinculariiform) tubuliporine are identified as *Mecynoecia* cf. *icaunensis* (D'ORBIGNY, 1850) on the basis of the large autozooids, which have frontal walls about 0.28 mm in width and apertures

0.17-0.20 mm by 0.15 mm in the scanned specimen. If the species really is *M. icaunensis* this would extend the range of a typically Valanginian-Hauterivian species upwards into the Barremian.

Family Plagioeciidae CANU, 1918

Genus *Cardioecia* CANU & BASSLER, 1922

***Cardioecia neocomiensis* (D'ORBIGNY, 1853)**

(Fig. 3G-I)

1850 *Bidiastopora neocomiensis* D'ORBIGNY: 800, pl. 784, figs 9-11.

1922 *Cardioecia (Bidiastopora) neocomiensis* (D'ORBIGNY, 1850) – CANU & BASSLER: 19, pl. 4, fig. 3.

p.p. 1985 *Mesenteripora sanctacrucensis* WALTER: 16, pl. 5, figs 1-7, pl. 6, figs 3-7 only, pl. 9, fig. 12 only.

1990 *Cardioecia neocomiensis* (D'ORBIGNY, 1850) – PITT & TAYLOR: 99, figs 63-68.

Material: NHMW 2009z0154/0005.

Remarks: This Valanginian-Aptian species has cylindrical branches that, when viewed in transverse section or at the growth tip, can be seen to possess a median budding lamina. Branch diameter and other aspects of morphology may vary between populations (PITT & TAYLOR 1990): the scanned Serre de Bleyton colony, which is infertile, has relatively narrow branches (1.09-1.27 mm) and small autozooids, with frontal walls about 0.24 mm wide and apertures 0.17-0.19 mm long by 0.13-0.18 mm wide.

Genus *Wassypora* WALTER, 1993

***Wassypora claveli* (WALTER, 1993)**

(Fig. 4A-D)

1993 *Wassypora claveli* WALTER: 64, text-fig. 6, pl. 1, figs 5-7, pl. 2, figs 9-13.

Material: NHMW 2009z0154/0006, 2009z0154/0007, 2009z0154/0035 (16 branch fragments).

Remarks: WALTER (1993) introduced *Wassypora* for narrow-branched (vinculariiform) tubuliporines with gonozooids having the general shape of a V. The type species was designated as *Entalophora vassiacensis* D'ORBIGNY, 1853, originally described from the Lower Aptian (or Upper Barremian) of France. Two other species have been placed in the genus: *W. claveli* WALTER, 1993, and provisionally *Clinopora quadripartita* CANU & BASSLER, 1926 (redescribed as *Entalophoroecia quadripartita* by PITT & TAYLOR 1990:

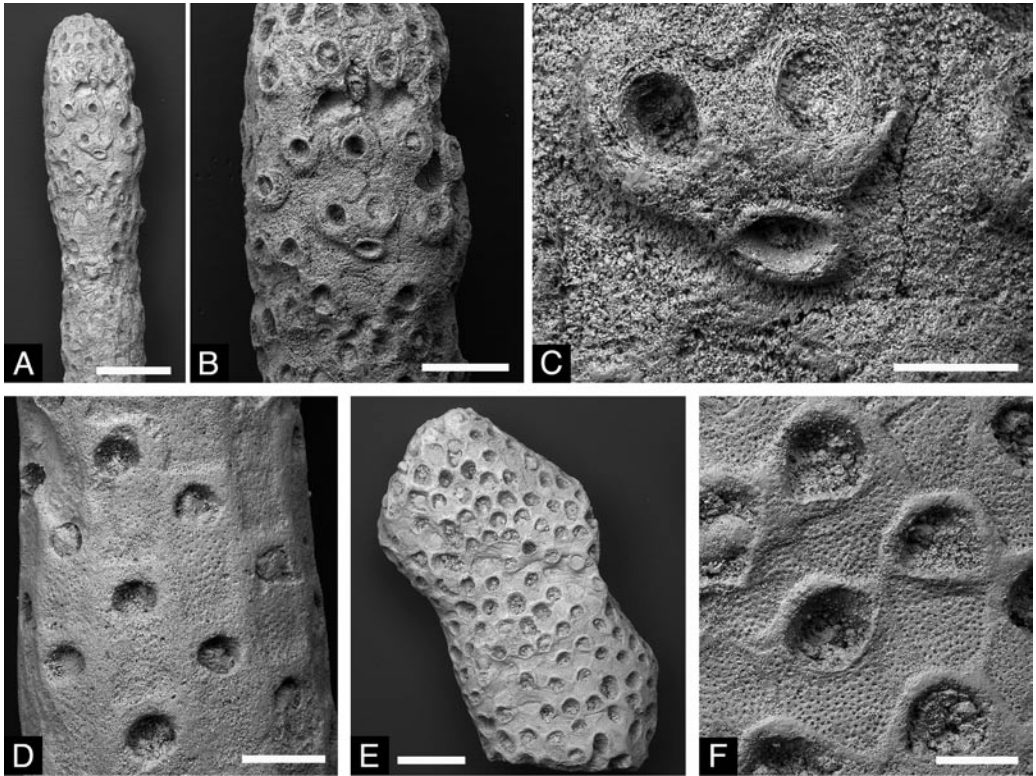


Fig. 4: Erect tubuliporine cyclostome bryozoans from the Barremian of Serre de Bleyton. A-D: *Wassypora claveli* (WALTER, 1993). A-C: NHMW 2009z0154/0006. A: fertile branch. B: gonozooid. C: oeciopore with two autozooidal apertures above. D: NHMW 2009z0154/0007; autozooids arranged in longitudinal files. E-F: *Ceata* sp.; NHMW 2009z0154/0008. E: broken branch. F: autozooids. Scale bars: A, E = 1 mm; B = 500 μ m; C, D, F = 200 μ m.

103) which is unusual in having large numbers of kenozooids interspersed between the autozooids.

Branches of *Wassypora* from Serre de Bleyton possess autozooids arranged in longitudinal files (Fig. 4D). Branches vary from about 0.7 to 1.4 mm in diameter. Autozooids are small, with frontal walls measuring about 0.31-0.38 mm long by 0.19-0.20 mm wide, and apertures 0.08-0.09 mm long by 0.09-0.10 mm wide. The oeciopore is strongly compressed, 0.09 x 0.15 mm in the single example measured (Fig. 4C). These dimensions most closely match *W. claveli* among the recognized species of *Wassypora*, although the gonozooid seems more complex than is typical for this species (WALTER 1993: text-fig. 6) and is more like that of *W. vassiacensis* (WALTER 1993: text-fig. 5).

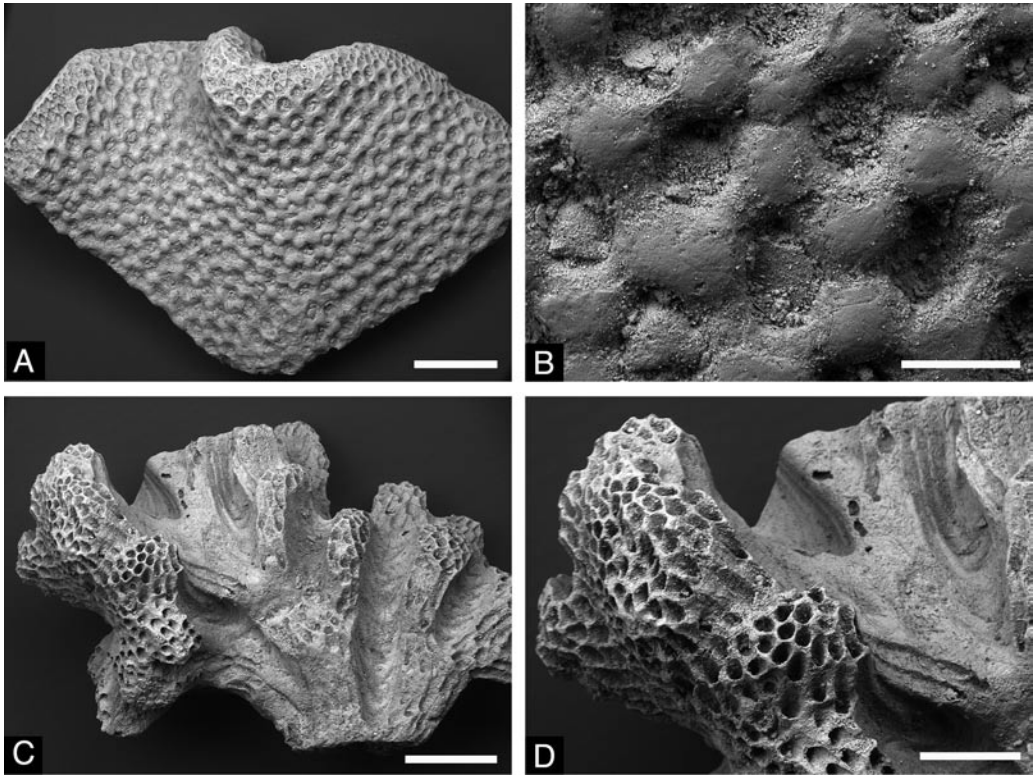


Fig. 5: Cyclostome bryozoans from the Barremian of Serre de Bleyton. A-B: *Poriceata ardescensis* WALTER, 1983; NHMW 2009z0154/0009. A: folded, bifoliate frond. B: autozooidal apertures with stout tubercles at their corners. C-D: *Apsendesia neocomiensis* D'ORBIGNY, 1850; NHMW 2009z0154/0010. C: colony fragment. D: detail showing autozooidal apertures clustered into fascicles. Scale bars: A, C = 1 mm; B = 200 μm ; D = 500 μm .

Family Semiceidae BUGÉ, 1952

Genus *Ceata* STRAND, 1928

Ceata sp. (Fig. 4E-F)

Material: NHMW 2009z0154/0008, 2009z0154/0036 (4 branch fragments).

Remarks: With the 'Senonian' type species of *Cea rustica* D'ORBIGNY, 1854, *Ceata* has strap-like, bifoliate branches and characteristically thin frontal walls that are often either undeveloped or eroded away. In the Lower Cretaceous species *Ceata granulata* (CANU & BASSLER, 1926) the gonozooid has two digitate lateral lobes extending well

distally of the ooeciopore. No gonozooids have been seen in the material from Serre de Bleyton, and the autozooids are larger than those in Faringdon Sponge Gravel populations of *C. granulata* (see PITT & TAYLOR 1990: 100), averaging about 0.4 mm long by 0.35 mm wide with apertures 0.18 mm long by 0.20 mm wide. Kenozooids are present, as are pseudoporous terminal diaphragms.

Genus *Poriceata* WALTER, 1983

***Poriceata ardescensis* WALTER, 1983**

(Fig. 5A-B)

1983 *Poriceata ardescensis* WALTER: 252, fig. 1, pl. 1, figs 3-9.

Material: NHMW 2009z0154/0009, 2009z0154/0037 (sample).

Remarks: This very distinctive species has been recorded previously from the Upper Hauterivian and Lower Barremian of Vaud, Switzerland, and from the Lower Barremian and Upper Barremian of Drôme and Ardèche in France respectively. Colonies possess gently folded bifoliate fronds. Well-preserved specimens have stout tubercles (Fig. 5B) at each of the corners of the generally six-sided autozooids. These tubercles are sometimes replaced by pores but it is unclear whether this reflects ontogeny or poor preservation. The gonozooids, observed in some of the Serre de Bleyton specimens, are very broad and were well figured by WALTER (1983).

Family Fasciculiporidae WALTER, 1970

Genus *Apsendesia* LAMOUROUX, 1821

***Apsendesia neocomiensis* D'ORBIGNY, 1850**

(Fig. 5C-D)

1850 *Apsendesia neocomiensis* D'ORBIGNY: 87.

1986a *Apsendesia neocomiensis* D'ORBIGNY, 1850 – WALTER: 83, pl. 10, figs 5-6.

Material: NHMW 2009z0154/0010, 2009z0154/0038, 2009z0154/0039 (2 fragments from Locality 1).

Remarks: Fragments of a fasciculate tubuliporine with autozooidal apertures in irregular bundles are tentatively identified as *Apsendesia neocomiensis* D'ORBIGNY, 1850. This species was originally described from the Upper Valanginian of Fontenoy, Yonne, France, and later recorded from deposits of the same age at Ste Croix, Vaud, Switzerland (WALTER 1972).

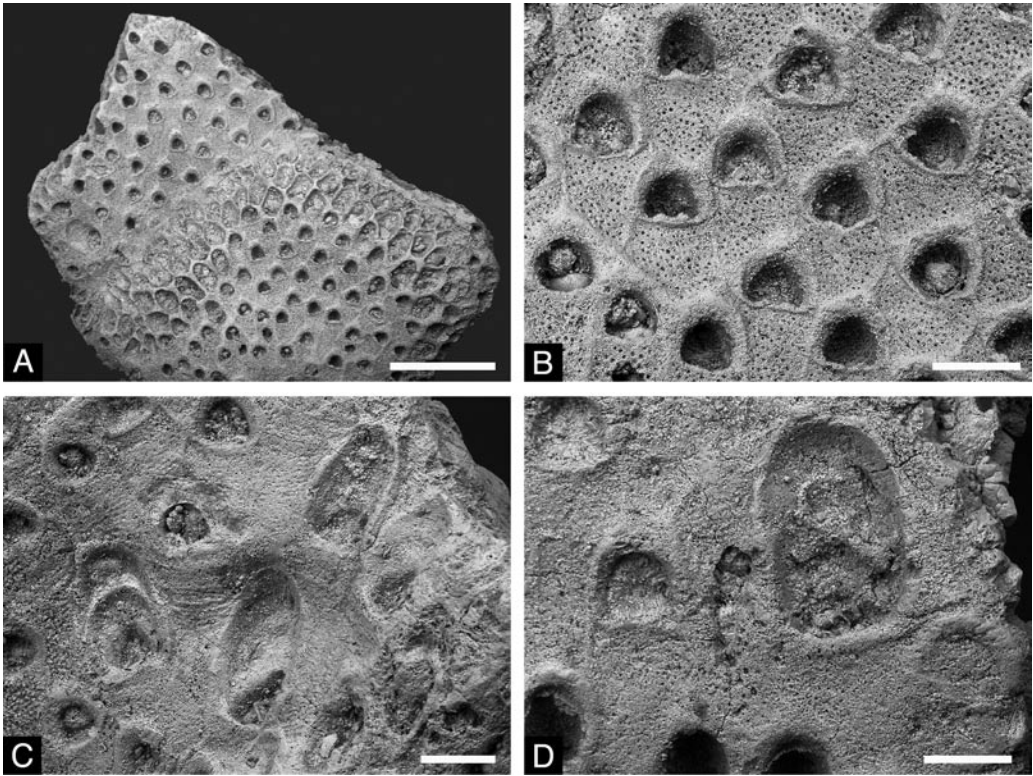


Fig. 6: *Elea periallos* nov. spec. from the Barremian of Serre de Bleyton. A-B: paratype, NHMW 2009z0154/0017. A: bilfoliate branch with an overgrowth. B: detail of autozooids from overgrowth. C: paratype, NHMW 2009z0154/0016; group of eleozooids, some with intramural buds. D: paratype, NHMW 2009z0154/0018; eleozooid (right) and several autozooids. Scale bars: A = 1 mm; B-D = 200 μ m.

Family Eleidae D'ORBIGNY, 1853

Genus *Elea* D'ORBIGNY, 1853

Elea periallos nov. spec.

(Figs 6-7)

Diagnosis: *Elea* having autozooids with prominent hinge teeth; operculum rarely preserved in-situ, ?non-porous; mural tubercles sometimes developed just within apertural shelf; gonozooids with crescent-shaped brood chamber, lateral lobes extending well distally of subcircular oocciopore; eleozooids with rounded apertures about three times longer than an autozooidal aperture, mandibles not observed.

Etymology: Gr. periallos, before all others, in reference to this species being the oldest eleid cyclostome known to have mandibulate polymorphs (eleozooids).

Material: Holotype – NHMW 2009z0154/0011. Paratypes – NHMW 2009z0154/0012-0018. Non-type material – NHMW 2009z0154/0040 (sample).

Type locality and horizon: Serre de Bleyton, near Rumuzat, Drôme Provencal, France; Barremian.

Description: Colony initially encrusting, often extensive, sometimes growing freely with transversely folded basal lamina, unilamellar or with overgrowths (Fig. 6A), becoming erect bifoliate with broad fronds and occasional overgrowths; frond thickness about 0.7 mm.

Autozooids small, subhexagonal (Figs 6B, 7G) with pseudoporous frontal walls, pseudopores simple, circular; boundary walls salient. Aperture semielliptical, equidimensional or slightly wider than long, rounded distally, hingeline with two prominent teeth (Fig. 7A), apertural rim particularly thick distally, apertural shelf sloping, sometimes with mural tubercles (Fig. 7D); opercula seldom preserved in-situ, putative examples seemingly non-pseudoporous, slightly convex and sunken (Fig. 7B); terminal diaphragms planar, sunken, evenly pseudoporous, the pseudopores smaller than those of frontal wall (Fig. 7C). Intramural buds sometimes present (Fig. 7D).

Gonozooids moderately common; brood chamber crescent-shaped (Fig. 7E, H) with lateral lobes extending well distally of ooeciopore, frontal wall densely pseudoporous, floor locally pustulose, occluding polygonal, aborted autozooids (Fig. 7E). Ooeciopore sub-circular (Fig. 7F), smaller than an autozooidal aperture, located terminally along median axis of gonozooid; atrial ring subdued.

Eleozooids moderately common, sometimes in clusters (Fig. 6C), variable in size but always larger than autozooids (Fig. 6D). Aperture semielliptical, longer than wide, rounded distally, about three times as long as an autozooidal aperture, hingeline plain, without teeth; mandibles not observed; rostral platform deep; terminal diaphragms observed. Intramural buds common, mostly eleozooidal but sometimes autozooidal.

Measurements:

Autozooids

| | |
|-----------------|----------------------|
| Frontal length | 0.38-0.48 mm, n = 10 |
| Frontal width | 0.21-0.27 mm, n = 10 |
| Aperture length | 0.11-0.14 mm, n = 10 |
| Aperture width | 0.12-0.15 mm, n = 10 |

Gonozooids

| | |
|------------------------|---------------------|
| Median frontal length | 0.57-0.74 mm, n = 3 |
| Maximum frontal length | 1.43-1.80 mm, n = 2 |
| Frontal width | 1.2 mm, n = 1 |

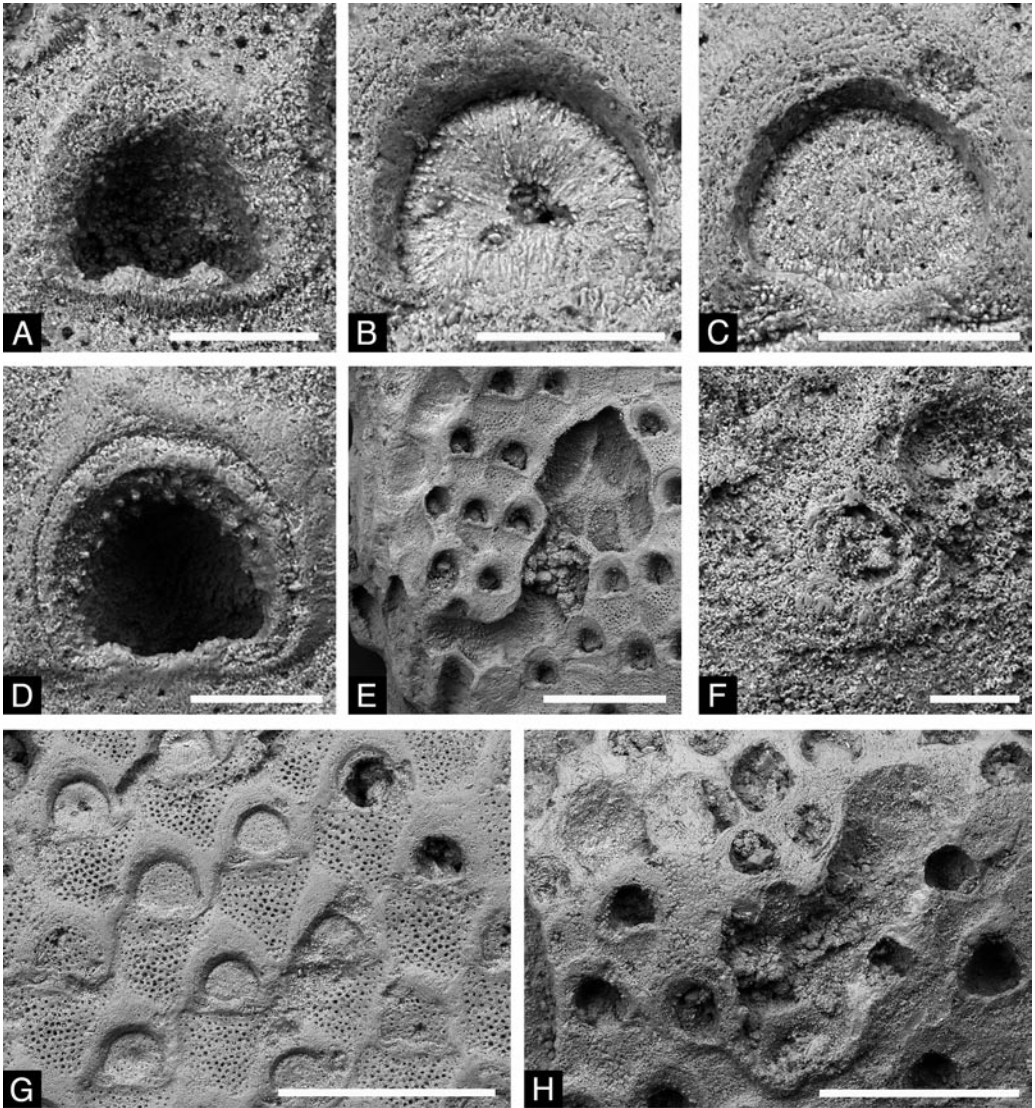


Fig. 7: *Elea periallos* nov. spec. from the Barremian of Serre de Bleyton. A: paratype, NHMW 2009z0154/0017; autozooidal aperture showing prominent hingeteeth. B-D, G: paratype NHMW 2009z0154/0012; B: apparent *in situ* operculum (damaged). C: terminal diaphragm with pseudopores. D: autozooidal aperture with intramural bud and mural tubercles. G: group of autozooids. E: holotype, NHMW 2009z0154/0011; deroofed gonozooid, the left side of which is largely missing. F: paratype, NHMW 2009z0154/0015; oocypore. H: paratype, NHMW 2009z0154/0013; broken gonozooid. Scale bars: A-D, F = 100 μm ; E, G, H = 500 μm .

| | |
|-------------------|----------------|
| Ooeciopore length | 0.08 mm, n = 1 |
| Ooeciopore width | 0.08 mm, n = 1 |

Eleozoids

| | |
|-----------------|---------------------|
| Frontal length | 0.48-0.83 mm, n = 3 |
| Frontal width | 0.30-0.44 mm, n = 3 |
| Aperture length | 0.27-0.45 mm, n = 3 |
| Aperture width | 0.17-0.27 mm, n = 3 |

Remarks: This new species is remarkable for three reasons. First, it is the oldest known eleid cyclostome to possess mandibulate polymorphs termed eleozoids (Fig. 6C-D). These are analogues of cheilostome avicularia in the sense of having hypertrophied opercula and which likely functioned in defence. In a review of polymorphism in eleids, TAYLOR (1985) remarked that no Barremian or Aptian species of this family were known to possess eleozoids, although PITT & TAYLOR (1990: 107) subsequently noted the occurrence of eleozoids in an Aptian colony of *Meliceritites dendroidea* (KEEPING, 1883). The finding of eleozoids in *E. periallos* suggests that these polymorphs evolved soon after the origin of eleids, which first appear in the fossil record in the Early Barremian (TAYLOR 1993: 477), although it is not until the Cenomanian that eleozoids are found in the majority of species (TAYLOR 1985: fig. 4). The eleozoids of *E. periallos* are of the rostrozoid type, having a rostrum-like aperture. Mandibles have not been found *in situ*, as is true for many other eleid species. The shape of the aperture resembles that found in such eleids as *E. viskova* TAYLOR, 1994, *Reptomulteia filiozati* (LEVINSEN, 1912) and *R. oceani* (D'ORBIGNY, 1850).

A second unusual, indeed apparently unique, feature of the new species is the shape of the gonozoid. In all previously described eleids in which these larval brooding polymorphs have been described they have a simple shape, typically longitudinally ovate but occasionally rounded subtriangular (TAYLOR 1985, 1994; TAYLOR & WEEDON 1996). The gonozoids of *E. periallos*, however, have a basically crescentic shape (Fig. 7E, H), with long lateral lobes extending well distally of the ooeciopore. This unexpected morphology recalls gonozoids found in cyclostome families such as Plagioeciidae and Mecynoeciidae rather than Eleidae or their putative ancestors Multisparsidae (TAYLOR & WEEDON 1996).

Thirdly, *E. periallos* is the oldest known species of *Elea*. This genus was revised in its entirety by TAYLOR (1994) who described 11 species, ranging from Lower Albian to Upper Campanian. No Barremian or Aptian species of *Elea* were previously known.

Compared to the described species of *Elea*, *E. periallos* is distinguished by its crescent-shaped brood chamber. The broad, rounded aperture of the eleozoids is most similar to those of *E. viskova* TAYLOR, 1994 but this Turonian species has narrow, strap-like branches.

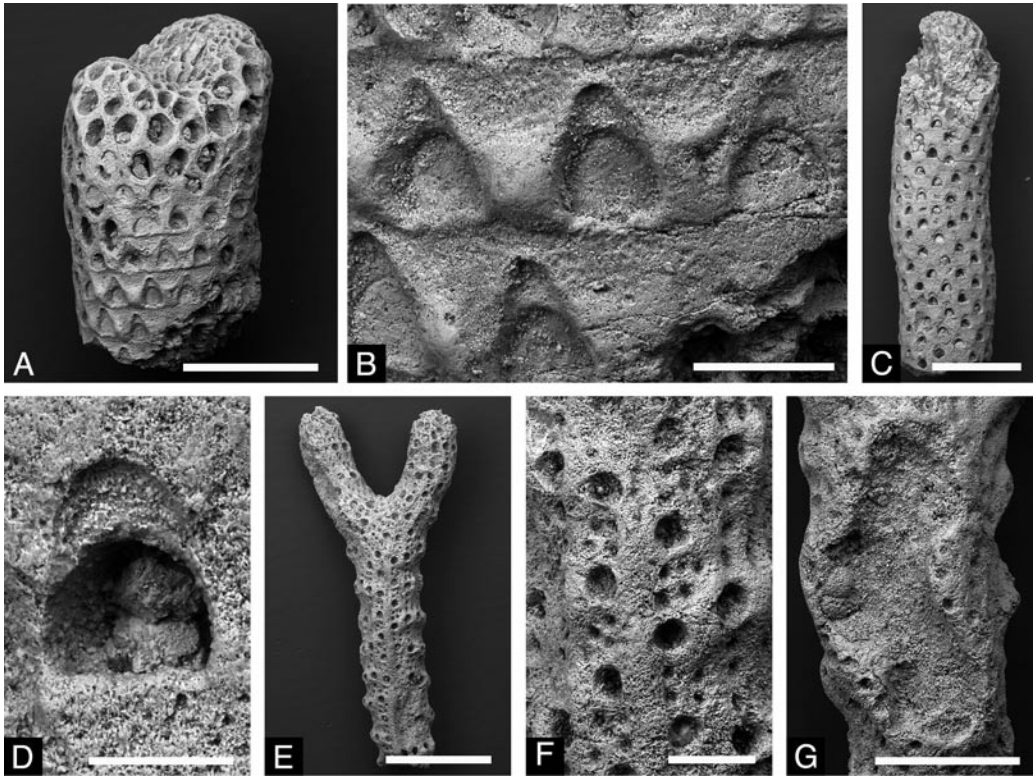


Fig. 8: Erect cyclostome bryozoans from the Barremian of Serre de Bleyton. A-B: *Meliceritites gracilis* (GOLDFUSS, 1827); NHMW 2009z0154/0019. A: damaged branch. B: autozooids closed by terminal diaphragms. C-D: *Meliceritites* aff. *gracilis* (GOLDFUSS, 1827); NHMW 2009z0154/0020. C: slender branch. D: autozooidal aperture with deep shelf. E-G: *Siphodictyum gracile* LONSDALE, 1849. E-F: NHMW 2009z0154/0021. E: obverse side of bifurcating branch. F: detail showing autozooids and cancelli. G: NHMW 2009z0154/0022; reverse surface of branch with deroofed gonozooid. Scale bars: A, C, E = 1 mm; B, F = 200 μ m; D = 100 μ m; G = 500 μ m.

Genus *Meliceritites* ROEMER, 1840

Meliceritites gracilis (GOLDFUSS, 1827)

(Fig. 8A-B)

- 1827 *Ceriopora gracilis* GOLDFUSS: 35, pl. 10, fig. 11a-c.
 1975 *Meliceritites semiclausa* (MICHELIN, 1846) – WALTER et al.: 109, fig. 8, pl. 10, figs 5-6.
 1990 *Meliceritites gracilis* (GOLDFUSS, 1827) – PITT & TAYLOR: 104, figs 81-84.

Material: NHMW 2009z0154/0019.

Remarks: This is the type species of *Meliceritites*, an eleid genus characterized by its narrow cylindrical branches. *M. gracilis* was originally described from the Cenomanian of Essen, Germany, but has also been recorded from the Barremian and Aptian (PITT & TAYLOR 1990). It is distinguished from other members of the genus by the high arch-like apertures that occupy a large proportion of the frontal surfaces of the autozooids and have deep distal shelves (Fig. 8B). In the scanned specimen from Serre de Bleyton, the branch is about 1.4 mm in diameter and the zooidal apertures 0.19 mm long by 0.15 mm wide. No *in situ* opercula are present but many of the apertures are closed by a terminal diaphragm located proximally of the apertural rim. Tubercles may be developed at the proximolateral corners of adjacent apertures aligned in transverse rows.

***Meliceritites* aff. *gracilis* (GOLDFUSS, 1827)**

(Fig. 8C-D)

Material: NHMW 2009z0154/0020.

Remarks: A second species of *Meliceritites* has more slender branches (c. 1.1 mm diameter) than *M. gracilis* and smaller autozooidal apertures (0.14 long by 0.12 mm wide), less crowded on the branch surface and arranged in quincunx rather than transverse rows. To judge from the deep distal apertural shelf (Fig. 8D), however, this un-named species is closely related to *M. gracilis*.

Suborder Cancellata GREGORY, 1896

Family Horneridae GREGORY, 1899

Genus *Siphodictyum* LONSDALE, 1849

***Siphodictyum gracile* LONSDALE, 1849**

(Fig. 8E-G)

1849 *Siphodictyum gracile* LONSDALE: 94, pl. 5, figs 16-23.

1990 *Siphodictyum gracile* (LONSDALE, 1849) – PITT & TAYLOR: 134, figs 150-153.

Material: Locality 1 – NHMW 2009z0154/0021, 2009z0154/0022, 2009z0154/0041 (5 branch fragments). Locality 2 – NHMW 2009z0154/0042 (6 branch fragments).

Remarks: This narrow-branched species is known from the Barremian to the Aptian, including localities in south-east France (e.g. WALTER & BUSNARDI 1971; WALTER et al. 1975; WALTER 1977; WALTER & CLAVEL 1979; DELAMETTE & WALTER 1984). It is distinguished by having differentiated obverse (frontal) and reverse surfaces, the former bearing longitudinal rows of autozooidal apertures separated by cancelli (kenozooids)

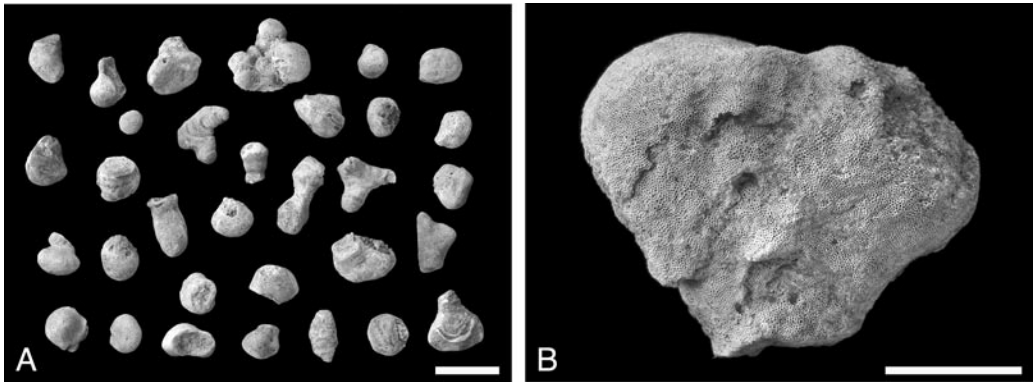


Fig. 9: Cerioporine cyclostome bryozoans from the Barremian of Serre de Bleyton. A: selection of nodular colonies that dominate the bryozoan fauna; NHMW 2009z0154/0023. B: Colony of *?Ceriopora* sp., the largest specimen in the collection; NHMW 2009z0154/0024. Scale bars = 10 mm.

(Fig. 8E-F), and the latter covered entirely by cancelli. When present, gonozooids occur on the reverse surface and are typically preserved minus their cancellate roofs (Fig. 8G). The Serre de Bleyton colonies have very thin branches, 0.5-0.7 mm wide, and tiny autozooidal apertures measuring about 0.06-0.08 mm in diameter.

Suborder Cerioporina VON HAGENOW, 1851

Family Cerioporidae BUSK, 1859

?Genus *Ceriopora* GOLDFUSS, 1826

?*Ceriopora* sp. (Figs 9B, 10A-B)

Material: NHMW 2009z0154/0024, Locality 1.

Remarks: In terms of biomass, nodular bryozoans are dominant at Serre de Bleyton (Fig. 9A). These are free-walled cyclostomes, and occur along with likely sclerosponges having the same general shape. As mentioned earlier, thin sectioning is needed for precise taxonomy.

The largest bryozoan in the collection has an expanded head on a narrower, broken base and measures almost 30 mm across (Fig. 9B). A multilayered internal construction is evident from abraded areas of the colony. The best-preserved patches on the colony surface show monomorphic apertures about 0.12-0.14 mm in diameter, with thick zoecial walls averaging 0.06 mm wide (Fig. 10A-B). This colony is tentatively assigned to *Ceriopora* pending thin section study.

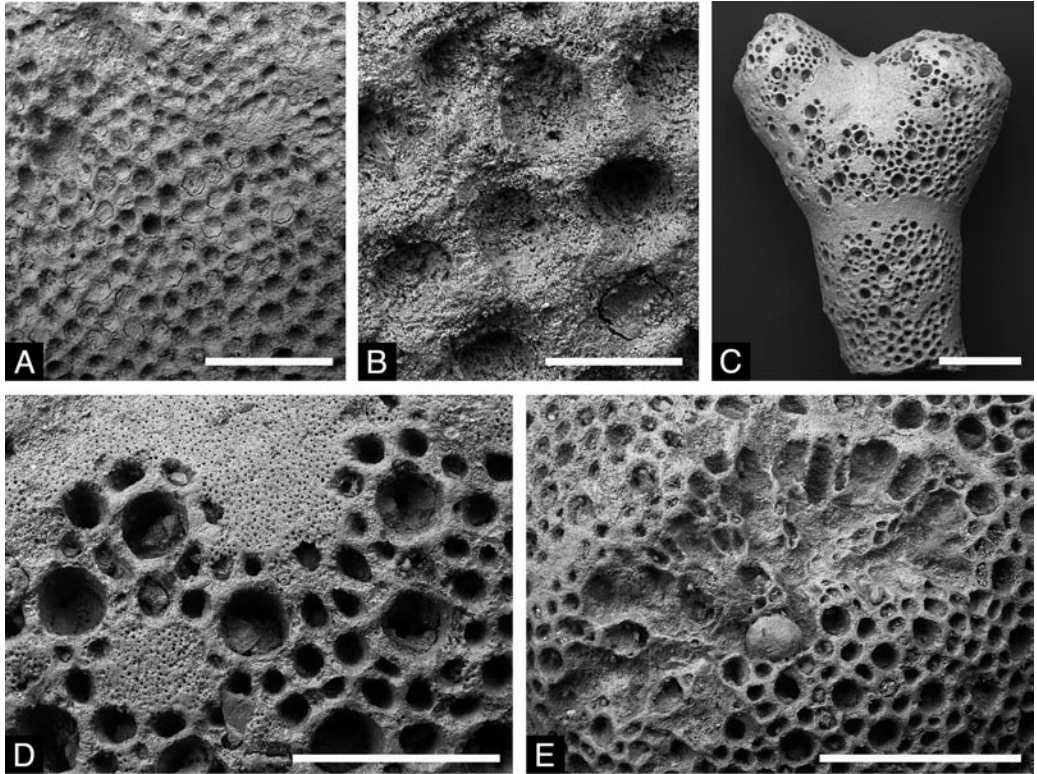


Fig. 10: Cerioporine cyclostome bryozoans from the Barremian of Serre de Bleyton. A-B: ?*Ceriopora* sp.; NHMW 2009z0154/0024. A: well-preserved colony surface. B: apertures and thick interzooidal walls. C-E: *Clausia* sp. C-D: NHMW 2009z0154/0025; C: bifurcating branch. D: large autozooidal apertures surrounded by smaller kenozooidal apertures, many closed by terminal diaphragms. E: NHMW 2009z0154/0026; gonozooid lacking roof. Scale bars: A, C, E = 1 mm; B = 200 μ m; D = 500 μ m.

Genus *Clausia* D'ORBIGNY, 1853

***Clausia* sp.**
(Fig. 10C-E)

Material: NHMW 2009z0154/0025, 2009z0154/0026.

Remarks: The scanned specimens of this dendroid cyclostome have branches up to 2 mm in width (Fig. 10C). Autozooidal apertures are large, about 0.15 mm in diameter, and surrounded by smaller, more angular kenozooids, some of which are closed by a pseudoporous terminal diaphragm (Fig. 10D). A de-roofed gonozooid (Fig. 10E) has

radial septa connecting some worn autozooids presumed to have supported a pseudoporous roof.

The Serre de Bleyton species resembles both *Heteropora arborea* KOCH & DUNKER, 1837, as redescribed by WALTER (1972: 336), and *Clausa zonifera* CANU & BASSLER, 1926, as revised by PITT & TAYLOR (1990). In view of problems over the generic concept of *Heteropora* (see NYE 1976), the type species of which lacks the clear zooidal dimorphism seen in most other species assigned to the genus, *Clausa* is preferred. Apertural diameter is slightly smaller than in *C. zonifera* CANU & BASSLER, 1926 from the Aptian of Faringdon, England.

?Genus *Diplocava* CANU & BASSLER, 1926

?*Diplocava* sp.
(Fig. 11A-C)

Material: NHMW 2009z0154/0027.

Remarks: A robust cerioporine is questionably assigned to *Diplocava*, a genus requiring thin sections for confirmation. The scanned colony is fertile, with irregular-shaped gonozooids roofed by pseudoporous exterior walls and a subcircular oeciopore 0.11 mm in diameter (Fig. 11C). Groups of autozooids around the gonozooids form low hummocks (Fig. 11A). Elsewhere, the colony surface is flatter, with polygonal autozooidal apertures averaging 0.10 mm in diameter and showing indications of beading along their rims (Fig. 11B).

Genera indet.
(Fig. 11D-F)

Material: NHMW 2009z0154/0028, 2009z0154/0029.

Remarks: Two examples are illustrated of free-walled cyclostomes, probably cerioporines, with lamellar colonies. In one colony (Fig. 11E-F) there is clear zooidal dimorphism, apertures of the smaller kenozooids sometimes being closed by exterior walls. The second colony has slightly larger, monomorphic zooids and no exterior walls (Fig. 11D).

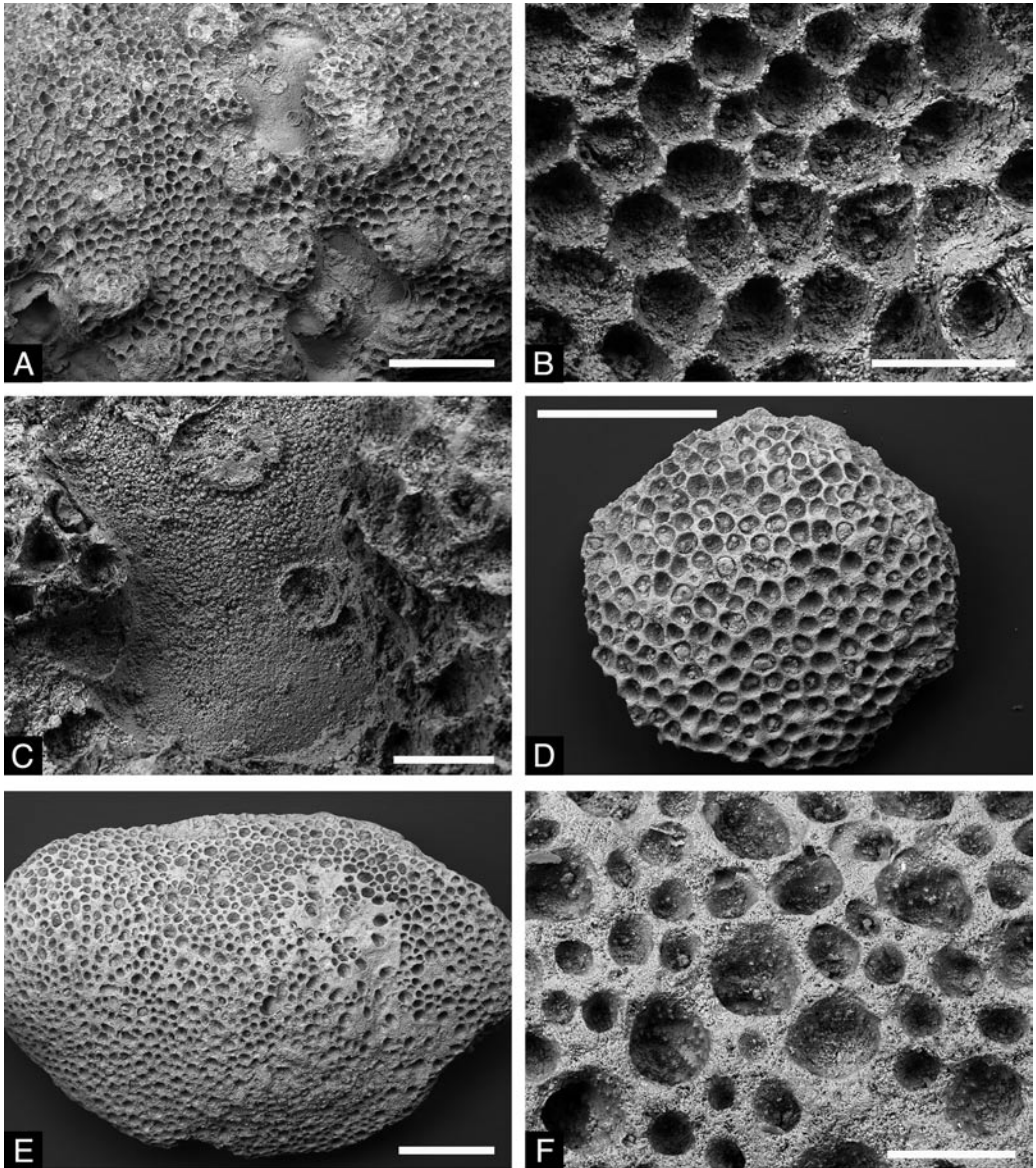


Fig. 11: Cerioporine cyclostome bryozoans from the Barremian of Serre de Bleyton. A-C: *?Diplocava* sp.; NHMW 2009z0154/0027. A: colony surface showing autozooids and gonozooids. B: autozooidal apertures. C: gonozooid with oeciopore right of centre. D-F: indeterminate cerioporines with small, disc-shaped colonies. D: species with monomorphic apertures; NHMW 2009z0154/0029. E-F: species with dimorphic apertures; NHMW 2009z0154/0028. Scale bars: A, D, E = 1 mm; B, C, F = 200 μ m.

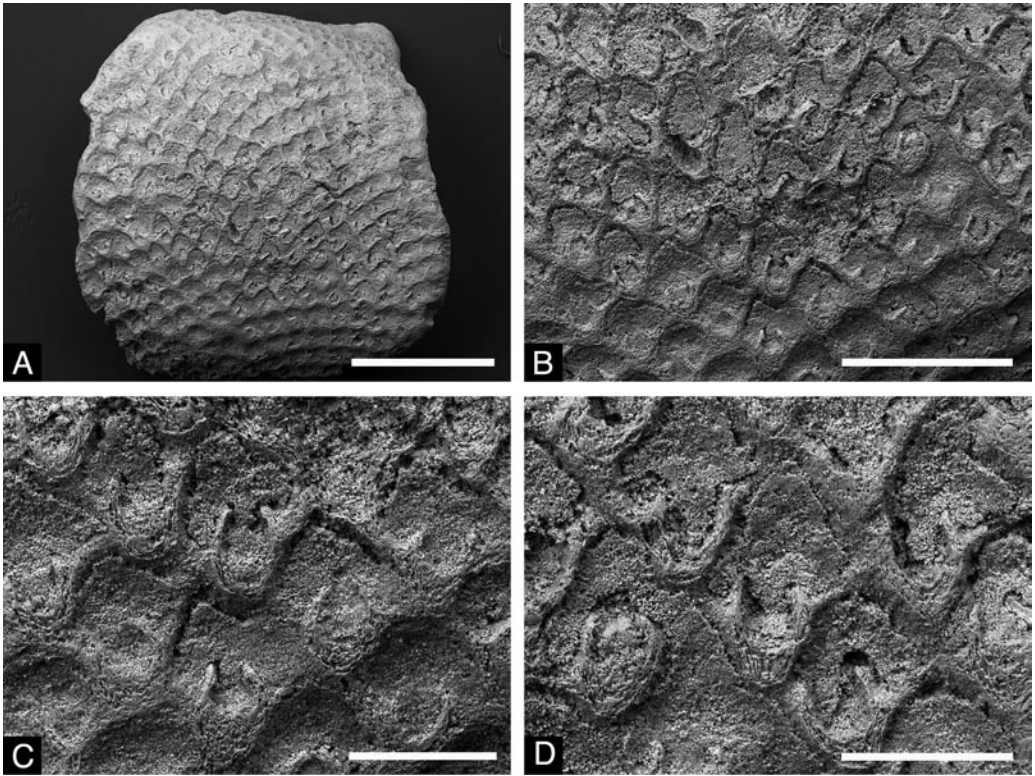


Fig. 12: Unidentified stenolaemate bryozoan with lunaria from the Barremian of Serre de Bleyton; NHMW 2009z0154/030. A: entire preserved colony. B: variable preservation of zooids on colony surface. C-D: sediment-filled apertures with horseshoe-shaped lunaria. Scale bars: A = 1 mm; B = 500 μ m; C-D = 200 μ m.

Order Incertae sedis

(Fig. 12)

Material: NHMW 2009z0154/0030.

Remarks: An abraded fragment of a thin lamellar colony is remarkable in showing diamond-shaped apertures (0.17-0.24 mm long by 0.14-0.17 mm wide) with well-developed, horseshoe-shaped lunaria (Fig. 12C-D). Lunaria are structures normally associated with bryozoans of the Order Cystoporata, a group that is generally believed to have become extinct in the Triassic. However, lunaria have been described in an Upper Cretaceous stenolaemate, *Lunariopsis cava* VOIGT, 1993, a putative cyclostome of uncertain familial affinity from the Cenomanian of Wesfalia, Germany. Unlike the Serre de Bleyton specimen, colonies of *L. cava* are ramose erect and have extremely thick walls between the subcircular apertures.

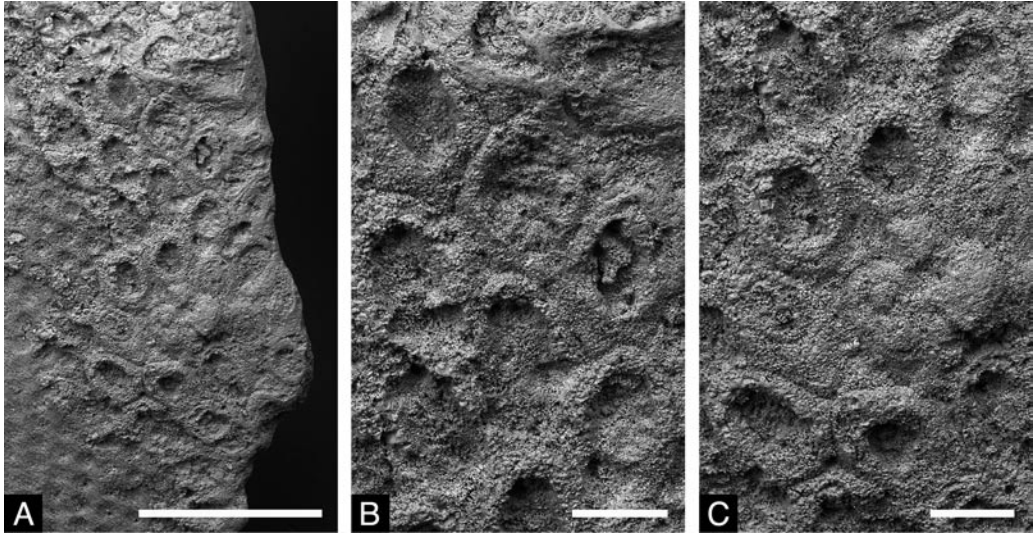


Fig. 13: Cheilostome bryozoan ?*Charixa* sp. from the Barremian of Serre de Bleyton; NHMW 2009z0154/031. A: poorly-preserved colony encrusting a shell fragment. B: autozooids. C: zooids from early astogeny, some apparently with closure plates. Scale bars: A = 1 mm; B, C = 200 μ m.

Thin sectioning is needed to establish the true identity of this specimen, although this would be difficult to accomplish in a single, thin colony. The specimen could be: (1) an indigenous cystoporate considerably younger than any previously described; (2) a cystoporate derived from Palaeozoic rocks and redeposited with undoubted Barremian bryozoans; or (3) an indigenous cyclostome homeomorph of a cystoporate. Study of the sediment infilling the zooids could be useful as microfossils diagnostic of the age may be present.

Class Gymnolaemata ALLMANN, 1856

Order Cheilostomata BUSK, 1852

Suborder Malacostegina LEVINSEN, 1902

Family Electridae STACH, 1937

?Genus *Charixa* LANG, 1915

?*Charixa* sp.
(Fig. 13)

Material: NHMW 2009z0154/0031.

Remarks: Only one cheilostome bryozoan has been observed in the collection from Serre de Bleyton. This is a poorly-preserved, multiserial colony encrusting a shell fragment with about 25 zooids visible (Fig. 13A). Measuring about 0.35-0.42 mm long by 0.28-0.31 mm wide, the zooids have ovoidal opesia and moderately well-developed proximal gymnocysts (Fig. 13B). Some of the older zooids appear to possess closure plates and/or intramural buds (Fig. 13C). Ovicells, avicularia and spines are not evident. In view of its early stratigraphical age and general morphology, this cheilostome is almost certainly an electrid, and can be identified provisionally as a species of *Charixa*, a genus recorded recently from the Barremian of Argentina (TAYLOR et al. 2009).

Conclusions

The Serre de Bleyton bryozoan fauna is dominated by small nodular cerioporine cyclostomes (Fig. 9A). Preservation of surface features varies from moderate to poor. Some specimens are strongly abraded and silicification may further destroy surface details, although this appears to be more intense in colony interiors. There is evidence of breakage of colonies and rounding-off of broken edges. Some of the bryozoans are attached to other bryozoans, sponges, shell fragments or, in one instance, a crinoid stem.

At least 20 bryozoan species occur in the Barremian of Serre de Bleyton, comprising 19 stenolaemates and one cheilostome. This figure is an underestimate of the true diversity as there are sure to be additional species of free-walled cyclostomes that would require thin sectioning to be recognized and characterized. Considerable scope remains for further study. Most of the Serre de Bleyton species and genera are typical for the Neocomian of southeastern France and many have been described previously from the Barremian. However, there are a few unexpected finds. These include *Elea periallos* nov. spec., the earliest known species of *Elea* and the oldest eleid cyclostome with mandibulate polymorphs (eleozooids). The single specimen of a stenolaemate with pronounced lunaria is also noteworthy as these structures are generally associated with the Ordovician-Triassic order Cystoporata. Finally, the cheilostome ?*Charixa* sp. is the first species of this order to have been noted in the bryozoan-rich sediments of the Barremian of southeastern France.

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