

The operculate cyclostome bryozoans: a chronicle of convergence, controversy and classification

Paul D. Taylor

Department of Earth Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK. e-mail: p.taylor@nhm.ac.uk

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1. Introduction

Evolutionary convergence among bryozoans is rife (see Taylor 2020a, chapter 9.11), and the application of molecular phylogenetics is revealing increasingly more cases. One of the earliest recognized examples of the independent acquisition of similar traits in two independent bryozoan clades concerns the evolution of cheilostome-like traits in the Cretaceous–Paleocene cyclostome family Eleidae (‘melicerititids’), which has been known for over one hundred years (e.g., Gregory 1899, p. 288). Uniquely for cyclostomes, eleids possess hinged opercula closing the autozooidal apertures, and most species also have avicularia-like polymorphs with modified opercula. So great is their similarity to cheilostomes that some 19th century bryozoologists (Waters 1891) considered eleids to be closer to cheilostomes than to cyclostomes. Their indisputable recognition as cyclostomes – or at least as stenolaemates – did not come until the seminal study of Levinsen (1912). Controversy remains about the phylogenetic position of eleids within the class Stenolaemata.

This essay discusses past and present research on eleid cyclostomes to show how opinions have changed about this distinctive bryozoan family. Important historical misinterpretations have included the belief that eleid opercula were immovable terminal diaphragms rather than hinged structures, and the avicularia-like zooids represented reproductive zooids. Contemporary debate has focussed on the phylogeny and classification of eleids: are they cyclostomes belonging to the suborder Tubuliporina Milne Edwards, 1838, or should they be regarded as non-cyclostome stenolaemates constituting the independent order Melicerititida Viskova, 1992? First, however, I will briefly outline the

key features of eleid morphology.

Specimen repository abbreviations. BSM: Seminary Museum, Barcelona, Spain; MM: Manchester Museum, UK; MNHN: Museum Nationale d'Histoire Naturelle, Paris, France; NHMUK: Natural History Museum, London, UK; NHMW: Naturhistorisches Museum, Vienna, Austria; PINM: Paleontological Institute, Moscow.

2. Eleid morphology

The defining apomorphy of the family Eleidae is the presence in all nine genera of a hinged operculum closing the zooidal aperture. In most species, examples of opercula have been found in-situ and, contrasting with the majority of cheilostome opercula, they are calcified structures, although the possibility cannot be entirely discounted that some species had unmineralized autozooidal opercula. Like the apertures into which they fit, eleid opercula vary from semi-circular to gothic arch, rounded pentagonal or triangular in shape, according to species (Figs 2A, F and 3A, E). Some have a slight proximomedial indentation on the outer surface which tends to be very slightly convex. The operculum is hinged on the proximal edge of the aperture. This hingeline is almost straight and often has a short condyle close to each corner, the two condyles sometimes linked by a low ridge. Therefore, in adequately specimens the former presence of opercula can be inferred on the basis of the morphology of the aperture and hinge line even when no opercula remain in-situ.

Eleid opercula are exterior walls. A thin layer of strip-like units of calcification constitutes the outer surface of the operculum, underlain by a thicker layer of transverse fibres (Taylor & Weedon 1996). Opercula often have a 'recrystallized' appearance, perhaps suggesting diagenetic alteration from originally high-Mg calcite. This would be consistent with rapid biomineralization (cf. Ma et al. 2014) given the requirement for the operculum to grow quickly once the aperture was completely formed and the zooid became functional. When well-preserved, pseudopores are visible on the outer surfaces of opercula. These are sometimes evenly spaced across the entire surface but are more often arranged in a crescent parallel to the distolateral edge. A pair of inclined ridge-like sclerites may be visible on the inner surfaces of opercula dissected out from colonies (Taylor 1994, fig. 12). In many species the operculum closed against a narrow shelf along the distolateral edge of the aperture (Fig. 1C–F).

Boardman (1983, fig. 38) offered a hypothetical reconstruction of the soft tissues of eleids in the vicinity of the aperture. He depicted occlusor muscles anchored on the distal interior surface of the operculum and passing into the zooidal chamber, but did not show any muscles involved in the opening of the operculum. Possibly the everting lophophore simply pushed open the operculum without the need for specific muscles. Less likely is the use of an elastic ligament to open the operculum as this would have led to post-mortem loss of opercula following decay of the occlusor muscles that held them closed, which is inconsistent with the large number of opercula that have been found preserved in-situ.

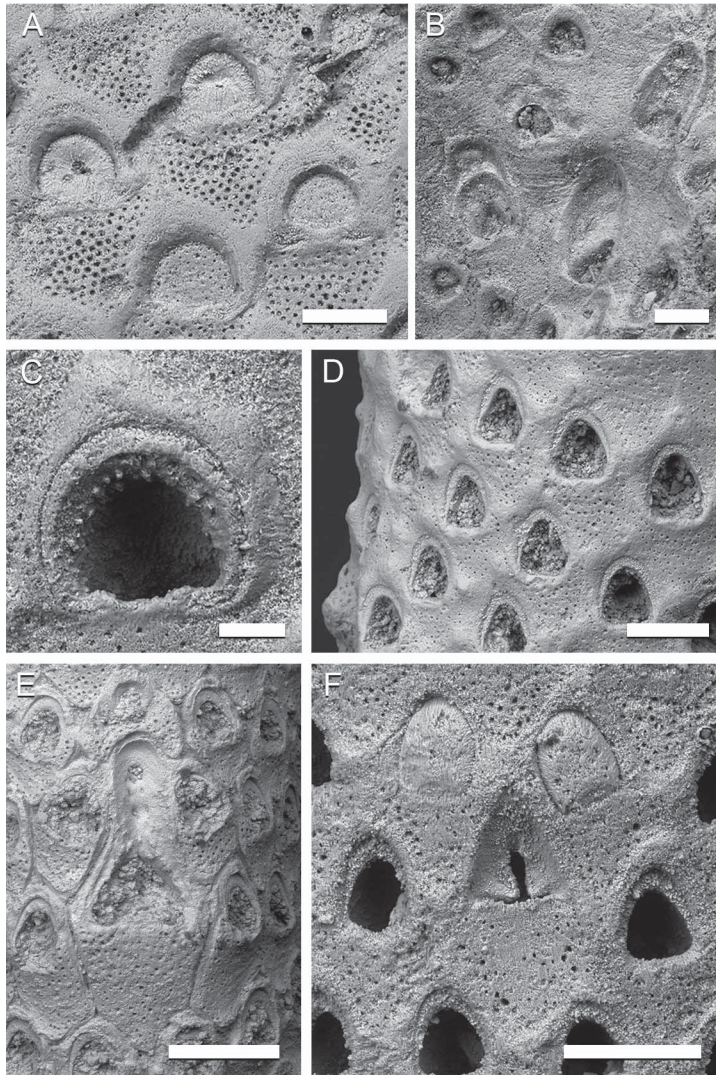


Figure 1. *Eleid* external morphology. A–C, *Elea periallos* Taylor, 2010 (Barremian, Serre de Bleyton, France) ; A, four autozooids, the two in the upper left with in-situ opercula, the two in the lower right with terminal diaphragms (NHMW 2009z0154/0012); B, autozooids and three elozooids with enlarged apertures (NHMW 2009z0154/0016); C, autozooidal aperture (NHMW 2009z0154/0016). D, *Meliceritites ornata* (d’Orbigny, 1852), edge of branch showing tubercles at the corners of the zooids and opercular shelves (NHMUK BZ 8555; Campanian, Talmont, France). E, *Meliceritites* sp., rostrozooid with torqued autozooids adjacent to the rostrum (BSM 26748; Upper Cretaceous, Salas, Spain). F, *Meliceritites royana* Waters, 1891, large trifolizoid and two distal autozooids with in-situ opercula (NHMUK BZ 8516; Campanian, Archiac, France). Scale bars: A, B, D, F = 200 μm ; C = 50 μm ; E = 500 μm .

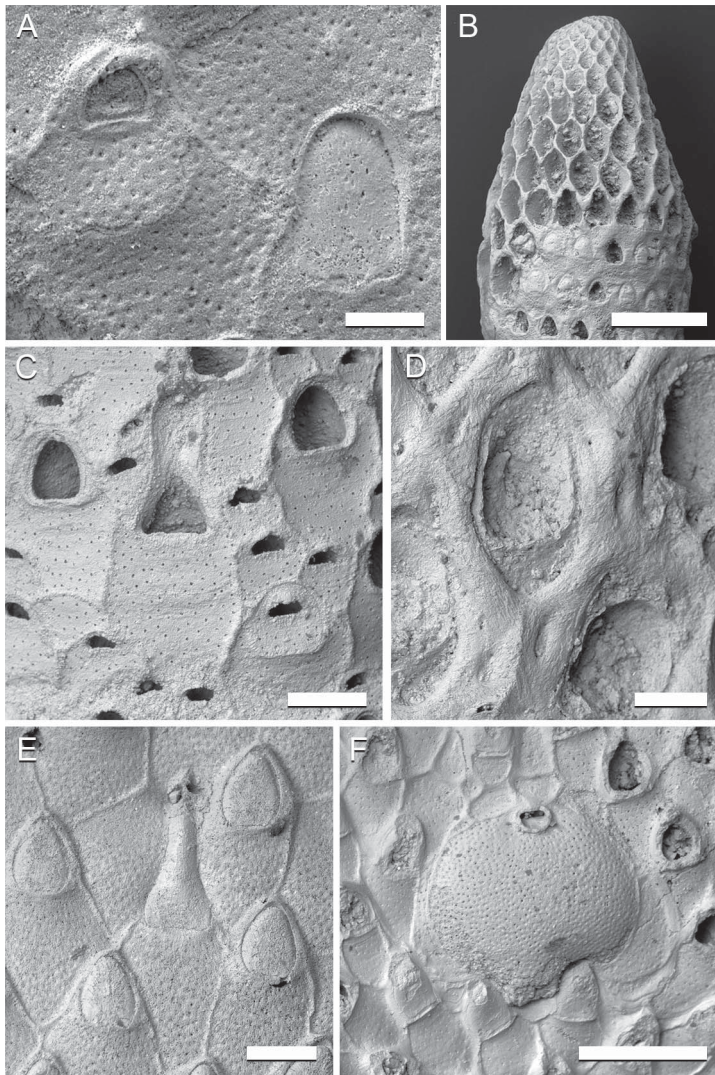


Figure 2. *Eleid* external morphology. A, *Elea pseudolamellosa* Taylor, 1994, autozoooid with in-situ operculum (lower right) and intramurally budded small eleozoooid with operculum (upper left) (NHMUK BZ 8805; Campanian, Aubeterre-sur-Dronne, France). B, *Meliceritites ornata* (d'Orbigny, 1852), growing tip (NHMUK BZ 8555; Campanian, Talmont, France). C, *Atagma* sp. with a rostruzoooid, numerous eleozoooids and a few autozoooids, one of which (lower right) contains an intramural demizoooid (NHMUK D53448; Vesterival, France). D, *Biforicula collinsi* Taylor, 2020, a free-walled eleid showing an autozoooid with a reduced frontal wall (centre) surrounded by kenozooids with thick walls and small openings (NHMUK BZ 8889; Albian, Paddlesworth, England). E, *Reptomulitea levinseni* Taylor, 1994, four autozoooids and a rostruzoooid, each with intact opercula, and a kenozoooid to the left of the rostrum (NHMUK D58930; Coniacian or Santonian, Vattetot, France). F, *Reptomulitea oceani* (d'Orbigny, 1852), gonozoooid (NHMUK D4387; Cenomanian, Cap de la Hève, France). Scale bars: A = 100 μm ; B, F = 500 μm ; C–E = 200 μm .

Eleid autozooids differ from those of other cyclostomes in lacking significant peristomes. Thin sections reveal the very long, narrow proximal parts of the autozooids forming a well-defined and wide endozone in ramose species (Fig. 3). Rapid broadening of the trumpet-shaped zooidal tubes occurs in the exozone where they bend through approximately 90° to meet the colony surface (Fig. 3A). Autozooids in most eleids are elongate hexagons in frontal outline. In conventional fixed-walled species they have a flat, facet-like, pseudoporous frontal wall covering the bulk of the frontal surface (Fig. 1A, C). Eleid pseudopores are always circular and do not exhibit the shape variety seen in many other cyclostomes (cf. Zaton & Taylor 2009). In eleid species with a dominantly free-walled skeletal organization, frontal walls are greatly reduced in size (Fig. 2D) or non-existent. Tubercles are sometimes developed at the corners of the zooids, and terminal diaphragms may seal apertures (Fig. 1D). Terminal diaphragms are usually recessed from the edge of the aperture, occasionally beneath the level of the opercular shelf (e.g., Taylor 1994, fig. 294), allowing their distinction to be made from opercula even when poorly preserved. They may contain pseudopores or have a single central pore.

Polymorphic zooids – eleozooids – with modified apertures and opercula are present in the majority of eleid species. The oldest examples date from the Barremian (Taylor 2010; Fig. 1B), and by the Cenomanian the majority of species possessed eleozooids (Taylor 1985, fig. 4). Three main types of eleozooids can be recognized: rostrozooids, trifoliozooids and demizooids (Taylor 1985). Rostrozooids are invariably larger than autozooids (Figs 1E, 2C, E) as they possess an enlarged (hypertrophied), mandible-like operculum. The orientations of the autozooids adjacent to rostrozooids may be torqued towards the elongated rostrum (Fig. 1E). The large size of rostrozooids makes it possible that they had a functional lophophore and, in this respect, are analogous to the B-zooids of the cheilostome *Steginoporella* (e.g., Banta 1973). Trifoliozooids are usually, but not always, smaller than the autozooids, and are distinguished by having the aperture constricted internally to leave an inverted T-shaped opening (Fig. 1F). In-situ opercula are seldom preserved and the narrow opening into the zooidal chamber would seem to preclude the presence of a feeding lophophore, even in the larger examples of these polymorphs. Trifoliozooids equal in size to the autozooids are abundant in two Late Cretaceous species: *Meliceritites magnifica* (d'Orbigny, 1852) and *M. royana* Waters, 1891 (Fig. 1F). In the first of these species they are distributed in regular transverse rows alternating with two rows of autozooids (Taylor 1985, fig. 2D), thus making up about one-third of the zooids in the colony. Demizooids are small polymorphs with semicircular apertures, often with the operculum preserved in-situ. Too tiny for a feeding lophophore, demizooids are especially abundant in *Atagma* Lonsdale, 1850, where they may totally surround the autozooids (Fig. 2C). Sometimes more than one type of eleozooid is present in a single species, as in some species of *Atagma* where sporadic rostrozooids (Fig. 2C) occur in addition to the numerous demizooids.

Like other cyclostomes, eleids possess gonozooids. The gonozooids of eleids have brood chambers which are entire (i.e., not pierced by autozooids), bulbous, and densely pseudoporous. They are usually longitudinally ovoidal to pyriform in shape but can be

almost circular (Fig. 2F), and have a terminal ooeciopore that is typically transversely elliptical in shape and lacks an operculum. *Elea periallos* Taylor, 2010 is exceptional in having crescent-shaped brood chambers with lateral lobes extending distally of the ooeciopore. An 'atrial ring' is present just inside the ooeciopore in many eleid species (e.g., Taylor 1994, fig. 25). The inflated brood chamber part of the gonozooid typically appears to emerge from the aperture of what looks otherwise like a normal autozooid, sometimes initially in the form of a narrow tube (Taylor 1985, fig. 2I). Distally, gonozooids take up space on the colony surface that would have been occupied by other autozooids, which are overgrown by the floor of the brood chamber (e.g., Taylor 1985, fig. 3; Pitt & Taylor 1990, fig. 94). This growth pattern suggests that the destiny of the immature zooid as a gonozooid may have been determined at a relatively late stage. Indeed, it cannot be ruled out that gonozooids possessed opercula that were subsequently shed before the brood chamber developed.

Many eleids contain kenozooids sealed by pseudoporous frontal walls, especially species of the encrusting genus *Reptomultealea* where they can be moderately common (Fig. 2E). They are also found adjacent to brood chambers where there is insufficient space for an autozooid. In addition, small, open kenozooids (Fig. 2D) occupy the spaces between the autozooids and other polymorphs in free-walled eleids, functionally replacing frontal walls in providing gaps between the apertures and therefore the lophophores.

Intramural buds are very common in eleids. New autozooids may be budded into defunct autozooids or rostrozooids, while small eleozooids (demizooids and trifoliozooids) are often found budded into defunct autozooids (Fig. 2A, C) and rostrozooids.

Early astogenetic stages have been described from only a few eleids because colony bases are known in only a few erect species and early zooids tend to be overgrown in encrusting species. Ancestrulae have a large protoecium, a short or very short distal tube (Taylor 1994, fig. 288), and an aperture with a hingeline suggesting that they were operculate like the later zooids in the colony, although in-situ opercula have yet to be recorded in eleid ancestrulae.

Colony-form varies largely according to genus in eleids (Taylor 1994, table 2). The most speciose genus, *Meliceritites*, has delicate ramose colonies, as does *Atagma*, the free-walled genus *Foricula*, and most species of *Meliceritella*. In *Meliceritella* autozooids open only along one side of the branches, with kenozooids or eleozooids forming the 'dorsal' side. A single species of *Meliceritella* has fenestrate colonies (Taylor 1987). Tubular ramose (cavariiform) colonies distinguish *Semielea*, while bifoliate colonies (foliose or palmate) are found in *Elea* and the free-walled genus *Biforicula*. Encrusting eleids, which are invariably multilamellar, characterize *Reptomultealea* and the free-walled genus *Reptoformicula*. In these two genera, as well as many erect eleids (Fig. 3B), overgrowths are common and originate through 'intraoecial fission' (*sensu* Hillmer et al. 1975). An autozooidal chamber becomes subdivided by a central ring linked to the inner edge of the aperture by 5 or 6 radial walls (e.g., Taylor 1994, fig. 272). The central ring circumscribes a pseudoancestrula and the other walls demarcate 5 or 6 additional zooids, all of which grow upwards to form the locus of a radially spreading overgrowth.

Budding zones are often proportionally broader in eleids than in other cyclostomes. In ramose colonies of *Meliceritites* this can be reflected in the tall conical growing tips of the branches (Fig. 2B), contrasting with the low, dome-shaped growing tips typical of other cyclostomes.

3. Early studies

The prolific French taxonomist Alcide d'Orbigny is credited for being the first scientist to recognise the operculate cyclostomes as a distinct taxonomic group when proposing the family Eleidae d'Orbigny, 1852. His diagnosis of Eleidae noted that the zooidal apertures protrude little (i.e., lack appreciable peristomes), are closed by an operculum, and have a 'triangular semilunar' shape. Furthermore, 'intermediate or special' zooids (i.e., open kenozooids) are absent but accessory zooids (i.e., eleozooids) may be present, although in smaller numbers. He also observed the mass of small, immature zooids at the centres of the branches in erect species (cf. Fig. 3B).

One existing genus, *Meliceritites* Roemer, 1840, and ten new genera of his own were assigned by d'Orbigny (1852) to Eleidae. In the sequence they were described in his text, d'Orbigny's (1852) new eleid genera are: *Nodelea*, *Multinodelea*, *Elea*, *Retelea*, *Semielea*, *Reptelea*, *Multealea* (Fig. 6), *Semimultealea*, *Reptomultealea* and *Clausimultealea*. As was his custom, these genera were distinguished largely by differences in colony-form, reflected in the first part of the name, appended with *-elea*. For example, *Reptomultealea* was used for eleids with reptant (encrusting), multi-layered colonies. Levinsen (1912) was unconvinced by the validity of d'Orbigny's genera and placed all species into the oldest

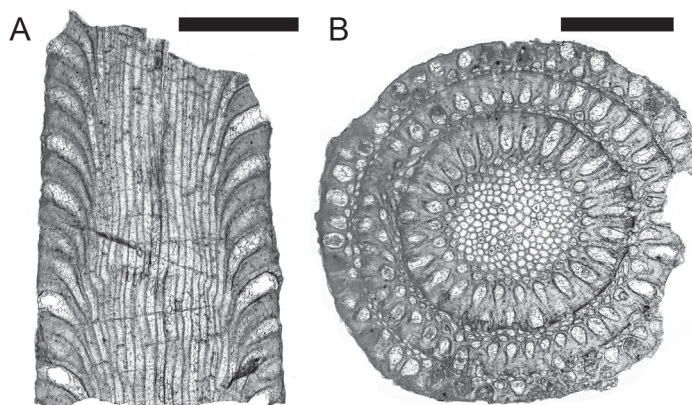


Figure 3. Longitudinal (A) and transverse (B) thin sections of *Meliceritites royana* Waters, 1891. The trumpet-shaped zooids are evident in (A), and the endozone in both (A) and (B). Two layers of intracolony overgrowth can be seen in (B). MM 9055 (A) and MM 9054 (B). Scale bars = 1 mm.

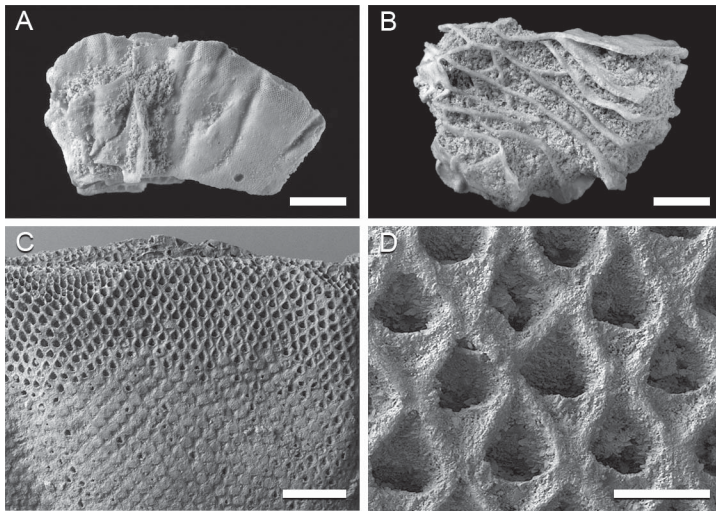


Figure 4. *Retelea pulchella* d'Orbigny, 1852, MNHN.F.A24679, Turonian, Troo, Loir-et-Cher, France. Originally described by d'Orbigny (1852) as an eleid, this genus does not belong to Eleidae. A, lateral view of reticuliporiform colony with growing edge at top. B, underside of the colony. C, growing edge (top) followed by a narrow zone of zooids with open apertures, and proximal zooids with closed apertures. D, open apertures. Scale bars: A, B = 5 mm; C = 1 mm; D = 200 μ m.

genus *Meliceritites*. However, subsequent researchers (e.g., Taylor 1994) have tended to maintain *Elea*, *Semielea*, *Reptomulteala* and *Meliceritites*, respectively for species with bifoliate, tubular, encrusting and ramose colonies. D'Orbigny's genus *Retelea* has reticuliporiform colonies (see Taylor 2020a, p. 124) and is not an eleid: the triangular autozooidal apertures lack distinct hingelines, notwithstanding d'Orbigny's stylized figure of the type species (see Taylor & Gordon 2002, fig. 5A, C; Fig. 4 herein), while in-situ opercula and eleozooids have not been recorded in this genus.

D'Orbigny (1852) grouped Eleidae together with another new family, Myriozoumidae d'Orbigny, 1852, in his 'Division Centrifuginés Operculinés. The name of this division serves to underline the fact that he interpreted eleids as bryozoans with opercula. Two genera were placed by him in Myriozoumidae: the extant cheilostome *Myriozoum* Donati, 1750 and *Foricula* d'Orbigny, 1852, a free-walled operculate cyclostome transferred by later bryozoologists (e.g., Voigt 1973) to Eleidae. According to Sidney F. Harmer's notes (<http://www.bryozoa.net/library/harmernotes/myriozoon.html>), *Myriozoum* is a mis-spelling of 'Miriozoon'; the genus is now usually called *Myriapora* Blainville, 1830 and is the type genus of the ascophoran family Myriaporidae Gray, 1841.

The earliest genus of an undoubted eleid to have been named is *Meliceritites*, introduced by Roemer (1840, p. 18) for three species: *Ceriopora gracilis* Goldfuss, 1827, *Ceriopora roemeri* Hagenow, 1839, and *Meliceritites porosa* Roemer, 1840. There is no evidence that Roemer observed the opercula or eleozooids now known to be key features of *Meliceritites*. Instead, Roemer's description emphasised the distally pointed, six-sided

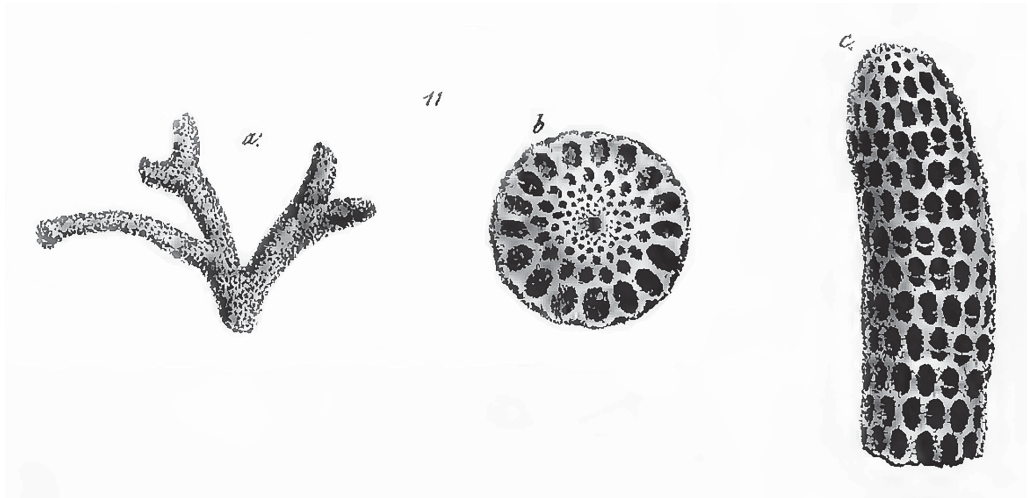


Figure 5. The original illustrations of *Ceriopora gracilis* Goldfuss, 1826, the first eleid species to have been formally described.

zooids resembling those of the cheilostome *Melicerita* Milne Edwards, 1836, from which he derived the genus name *Meliceritites*. The type species of *Meliceritites* was chosen by Gregory (1899, p. 323) who selected *Ceriopora gracilis* Goldfuss, 1827 as it was not only the first species to be described but also the first listed by Roemer (1840). Unfortunately, Goldfuss's figure (reproduced here as Fig. 5) of *Meliceritites gracilis* from the Cenomanian of Essen in Germany depicts a heavily worn bryozoan. Only traces of the reinforced hingelines dividing the openings of some zooids into two parts point to the identity of this species as an eleid. Note that *Meliceritites* has been often incorrectly spelled '*Meliceritites*' (e.g., Marsson 1887; Waters 1891). The same mistake has led to the incorrect spelling of some higher taxa based on this genus, notably the family Melicerititidae of Pergens (1890).

The 'order' Salpingina was established by Hagenow (1851) for two genera: *Escharites* Roemer, 1840 (subsequently regarded as synonymous with *Meliceritites*, and in any case pre-occupied by *Escharites* Guettard, 1770) and a new genus *Inversaria* Hagenow, 1851. The latter is now known to be an onychocellid cheilostome (Voigt & Williams 1973; Taylor et al. 2018). Hagenow diagnosed Salpingina on the basis of both the trumpet-shaped zooids widening rapidly near the colony surface, and the unusually shaped apertures provided with an operculum that could be found in-situ in some species. No mention was made by Hagenow of the avicularia-like polymorphs.

In his thesis on cyclostomes from Maastricht, Hamm (1881) recognized a 'typus Stigmatoporina'. This heterogeneous group that includes *Meliceritites*, *Cyrtopora* and *Stigmatopora* was subsequently criticized by both Gregory (1899, pp. 285–286) and Levinsen (1912, pp. 5–6). Hamm believed the calcified coverings of the apertures not to be hinged structures analogous to cheilostome opercula but instead closure plates of the kind that are present in many cyclostome genera and which are not a justification for recognising Eleidae as a distinct taxon.

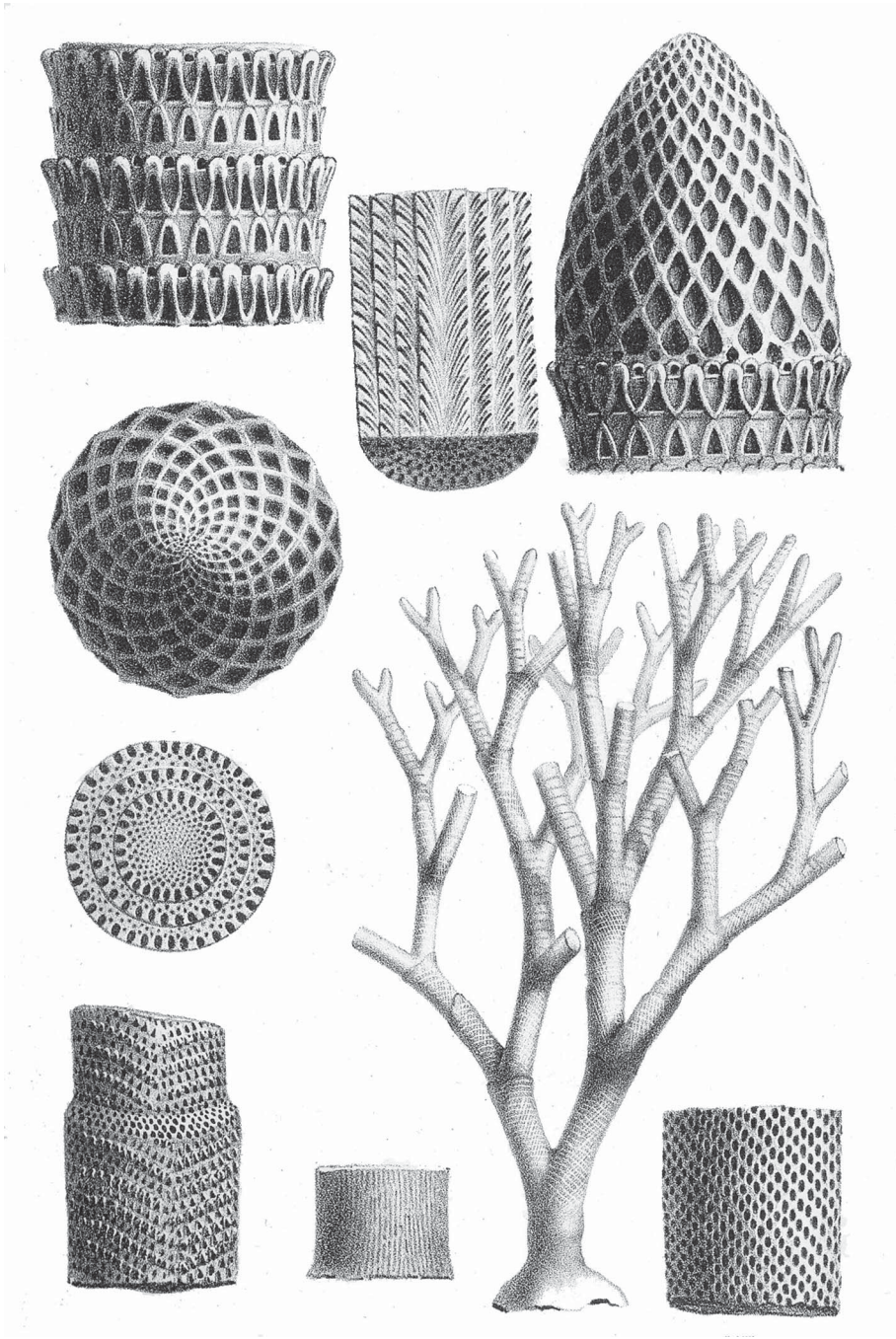


Figure 6. *The beautiful, yet very stylized figures of Muletea [Melicerites] magna d'Orbigny, 1852, plate 740.*

Marsson (1887) introduced another higher taxon, 'Typus Metoporina'. This was founded on the trumpet-shaped zooids, enlarging towards the colony surface where a rhombic-hexagonal frontal wall contained a small aperture. He included two families – Ceidea [sic] and Eleidea [sic] – in Metoporina. A three-sided aperture was said by Marsson to be present in eleids but according to Levinsen (1912) he appeared to have viewed the operculum as a transitory covering which later disappeared.

Pergens (1890, p. 391) proposed the superfluous family Meliceritidae [sic] into which he placed *Elea*, *Meliceritites* (as *Melicerites*) and the other genera that had been attributed to Eleidae by d'Orbigny (1852). He mentioned neither opercula nor avicularia-like polymorphs, but described the aperture as usually triangular and surrounded by a protruding peristome. Perhaps the latter is explicable because a new species he described in this paper, *Meliceritites dollfussi*, has the tallest peristomes found among eleids. The structures used by d'Orbigny (1852) to demarcate *Nodelea* and *Multinodelea* were described by Pergens as 'ovicelles saillantes', thus supporting the notion that they had a reproductive role. Eleidae was placed by Pergens in a new higher taxon he called Meliceritina.

In a paper evocatively entitled 'On Chilostomatous Characters in Meliceritidae and other Fossil Bryozoa', Waters (1891) was in no doubt that eleids possessed avicularia. However, he did not recognise the presence of calcified opercula in the autozooids, and believed that the mandibles of the avicularia-like zooids may have been chitinous. This may be because Waters described in this paper a new species – *Meliceritites royana* Waters, 1891 – in which calcified mandibles have yet to be recorded in the large trifolizoooids and were possibly lacking.

The discovery of true reproductive polymorphs in eleids can be attributed to Canu (1897a, pl. 5, fig. 10) who depicted a clear example of a gonozooid in a species identified by him as *Semielea sarthacensis* d'Orbigny, 1852. In the same paper Canu introduced the term 'eléocellaires' for the distinctive avicularium-like polymorphs of eleids. Additional examples of eleid gonozooids were figured by Canu in another paper published in 1897 (Canu 1897b, pl. 22, figs 1, 2, 6, 13), while in one of his later papers concerning cyclostome gonozooids he described further examples of gonozooids from five species of eleids (Canu 1918).

Gregory (1899) gave a lengthy account of Eleidae in the first part of his catalogue of the Cretaceous Bryozoa in the British Museum (Natural History). This consisted of an historical review followed by illustrated descriptions of species represented in the BM(NH) collections. Gregory introduced the genus *Reptoceritites* (Gregory 1899, p. 319), which "differs from *Reptelea* by the presence of avicularia", with the new species *R. rowei* Gregory, 1899 as the type species. He accepted Waters' (1891) interpretation that the 'cellules accessoires' of d'Orbigny (1852) represent avicularia. However, he misinterpreted some of these polymorphs as gonozooids ('gonoecia'), for example in *Meliceritites semiluna* (d'Orbigny, 1852) (Gregory 1899, fig. 34). He believed that while opercula may have existed in eleids they were chitinous and not fossilized, the calcified structures visible in the apertures of many colonies instead represented closure plates (i.e.

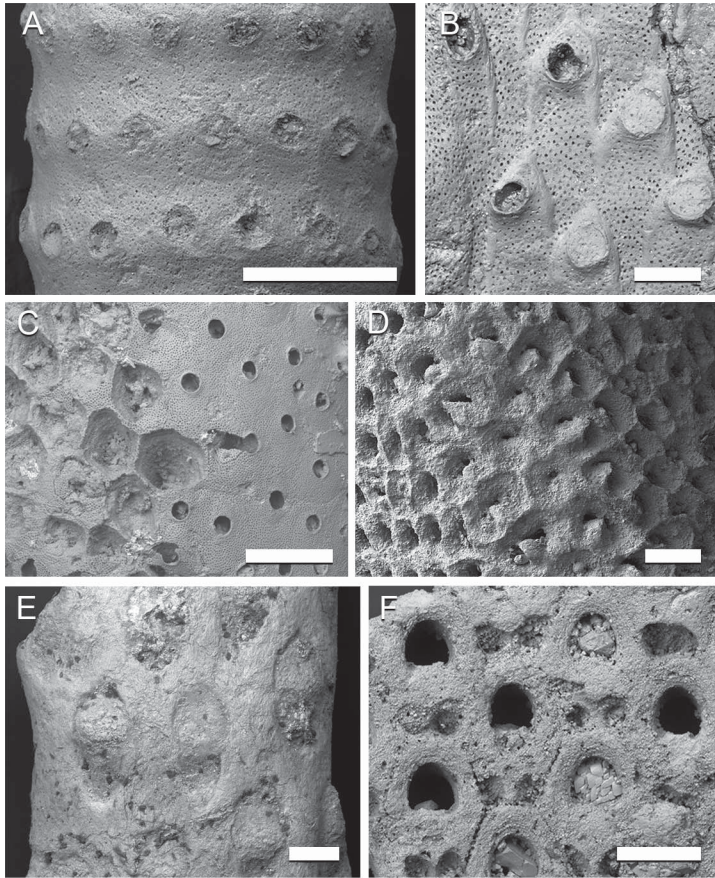


Figure 7. Some relevant non-eleid bryozoans. A, *Collapora straminea* (Phillips, 1829), a tubuliporine cyclostome with facet-like frontal walls (NHMUK; Jurassic, Bajocian, Yorkshire coast, England). B, *Multisparsa* sp. showing raised boundary walls reminiscent of eleids, the three zooids in the lower right closed by terminal diaphragms (NHMUK; Jurassic, Bathonian, East Cranmore, England). C, *Cyclocites primogenitum* Canu & Bassler, 1922, a species with thin, facet-like frontal walls (right) attributed by its authors to Eleidae despite the lack of diagnostic operculate autozooids (NHMUK D58985; Bathonian, Blainville, France). D, *Semicea tubulosa* d'Orbigny, 1854, a syntyne of the type species of this genus on which Semiceidae is founded, a family sometimes incorrectly believed to be closely related to Eleidae (MNHN.F.A24701; 'Senonian', Tours, France). E, *Elea taylori* Viskova, 2011, a Jurassic bryozoan that shows no certain eleid traits (PINM 5038/50; Callovian, Troshkovo–Rechitsy, Russia). F, *Biforicula ligitima* Viskova, 2011, note the crenulate boundaries between the zooids in the lower left of this cheilostome (PINM 2922/104; Campanian, Amyrosievka, Russia). Scale bars: A, C = 500 μm ; B, D–F = 200 μm .

terminal diaphragms) that sealed inactive zooids. Gregory postulated that eleids evolved from the Jurassic–Cretaceous genus *Haplooeicia* Gregory, 1896 (= *Collapora* Quenstedt, 1881) which resembles *Meliceritites* in having externally hexagonal zooids with facet-

like frontal walls containing subterminal apertures (Fig. 7A). This view was reiterated by Gregory (1909, p. 299) who remarked about *Haplooeicia*: “This genus has been discovered in the Cretaceous by M. Filliozat, who places it among the Eleidae; and that it is intermediate between the Entalophorids and Eleids appears most probable”.

Eleids were described by Lang (1906, p. 60) as “a very natural family [i.e. monophyletic] remarkable for exhibiting characters relative to both the groups Cyclostomata and Cheilostomata”. Lang recognised the presence of ‘avicularia’ but not opercula, although he did note the occurrence of closed zooids which can now be identified as zooids with in-situ opercula. The shape of the apertures was accorded particular taxonomic significance in Lang’s study that dealt only with encrusting species of eleids.

A detailed study of the operculate cyclostomes was published by G.M.R. Levinsen in 1912. Levinsen (1912, p. 19) went as far as to propose dividing cyclostomes into ‘two suborders’ – Cyclostomata inoperculata and Cyclostomata operculata – the latter consisting entirely of the Eleidae, which he referred to as Meliceritidae Pergens, 1890 (even though d’Orbigny’s family name of 1852 has priority). Levinsen clearly had a deep knowledge and understanding of eleids. He was in doubt about the presence of hinged opercula in these cyclostomes, nor of the similarity between the mandibulate heterozooids and the avicularia of cheilostomes which he believed to be analogous rather than homologous. Another eleid feature having analogues among cheilostomes are ‘regenerations’ (i.e. intramural buds), recognised by Levinsen for the first time. As for the gonozooids, Levinsen described a low ring-shaped ridge (= atrial ring) in the interior of the brood chambers a little inwards of the ooeciopore, comparing it with similar structures found in some living species of the articulate cyclostome *Crisia*.

As mentioned earlier, all of the eleid species described by Levinsen (1912) were placed by him in the genus *Meliceritites*. In a subsequent publication (Levinsen 1925), however, he created a new genus – *Meliceritella* – for ramose species in which autozooids opened only along one side of the branches.

4. Later studies

Here, I review research published after the pivotal work of Levinsen (1912). Canu & Bassler (1922) somewhat surprisingly placed Eleidae in the ‘subdivision’ Rectangulata Waters, 1887 (i.e. lichenoporidae and their kin). Reflecting the high value these two authors placed on gonozooids in cyclostome taxonomy, they diagnosed Eleidae thus (pp. 81–82): “The ovicell [gonozooid] is a large, pyriform, globular sack, with well-defined outlines. It is formed on the completely consolidated distal tubes. The oeciostome [sic] is terminal. The tubes are closed by a perforated facette”. Note that no mention is made in this diagnosis of either the eleozooids or the calcified opercula. Species belonging to three genera were attributed to Eleidae by Canu & Bassler (1922): *Meliceritites*, *Semimultelea* and the new genus *Cyclocites*. The last of these, which is monospecific for the Jurassic species *Cyclocites primogenitum* Canu & Bassler, 1922 (Fig. 7C), is not an eleid; Walter

(1970) placed it in synonymy with the cerioporine genus *Ceriocava* d'Orbigny, 1852. *Foricula* was considered by Canu & Bassler (1922) to be a subgenus of *Meliceritites*. Avicularia-like polymorphs as 'eleocellaria' were noted as being present in eleids but putative opercula were dismissed as calcareous laminae (i.e. terminal diaphragms) of the type commonly found closing the dead or aborted zooids of cyclostomes. Four years later, however, these authors had accepted the existence of opercula in eleids (Canu & Bassler 1926). The family was retained within Rectangulata in this later paper.

Through the lengthy period during which Ehrhard Voigt studied Cretaceous bryozoans, several of his publications include descriptions or mentions of eleids. Voigt (1924) introduced *Elea nodulifera* and *Semimultealea polytaxis*. His descriptions of these two new species are mute with regard to opercula and eleozoids. *Elea nodulifera* was later transferred to *Foricula* by Voigt (1973) but would now be placed in *Biforicula*, a genus introduced by Voigt (1989) for *Foricula*-like species with bifoliate colonies. Voigt (1951) described two eleid species from the Maastrichtian of Ilten near Hannover: *Meliceritites hagenowi*, a nom. nov. for the *Escharites gracilis* (Goldfuss, 1826) of Hagenow (1851), and *Foricula filicosa* (Brydone, 1929), a species originally placed in the cheilostome genus *Biflustra* d'Orbigny, 1852. Voigt observed the presence of walls dividing the apertures of many zooids of *M. hagenowi* without understanding their significance in the formation of overgrowths by intrazoecial budding (see above). He also observed small eleozoids 'regenerating' within autozooids. The pits or pores (kenozooids) between the autozooids of the free-walled *F. filicosa* were regarded by him as small heterozooids. Voigt (1964, p. 434) redescribed *Meliceritella steenstrupi* (Pergens & Meunier, 1886) in a study of Dano-Montian bryozoans from Poland. Again, no mention was made of the opercula and he made the incorrect statement that Levinsen had believed eleids to be cheilostomes which, he added, is disproven by "...the sac-like gonozooids and by the nature of the long tube-like cells perforated by pseudopores". Within a few years, however, Voigt had acknowledged the presence of opercula in eleids (e.g., Voigt 1971, p. 89).

The attribution of Eleidae, together with nine other cyclostome families, to a superfamily Crisiacea was published without explanation by Vigneaux (1949). Subsequent taxonomic studies of cyclostomes have ignored this superfamily.

In the bryozoan part of the *Treatise on invertebrate paleontology* (Bassler 1953, p. 75), the diagnosis of Eleidae noted the common presence of avicularia but made no mention of the calcified opercula. Bassler included Eleidae, along with Semiceidae Buge, 1952 (=Ceidae d'Orbigny, 1854) and Lobosoeciidae Canu & Bassler, 1922, in the cyclostome suborder Salpingina Hagenow, 1851. The shared characters between these families were given as the tubular shape of the zooids and the presence in some taxa of facet-like frontal walls. Branch surface morphology (Fig. 7D) in the type species of *Semicea*, *Semicea tubulosa* d'Orbigny, 1854, is quite unlike that of any known eleid. *Lobosoecia* Canu & Bassler, 1922 is based on the misidentification as *Meliceritites semiclausa* Michelin, 1846 of a *Collapora*-like species.

Brood's (1972) major monograph of the Late Cretaceous cyclostomes of Scandinavia perhaps surprisingly described only one eleid species: *Meliceritella verticillata* (d'Orbigny,

1853). Eleidae was placed by Brood in the suborder Salpingina. His diagnosis of this suborder stated: “Avicularia-resembling kenozoocia (eleocellaria) are present” (Brood 1972, p. 357). Brood believed that salpingines probably evolved from a tubuliporine ancestor during the Jurassic. Elsewhere in his monograph (p. 67), Brood remarked that the calcified opercula reported by Levinsen (1912) in eleids were probably terminal diaphragms.

Disagreement over the subordinal placement of Eleidae has continued in papers published during the past 50 years. Following Bassler (1953), Salpingina was retained as a cyclostome suborder that included Eleidae in studies of Early Cretaceous bryozoan faunas published by Bernard Walter and his coauthors (e.g., Masse & Walter 1974; Walter et al. 1975). However, four eleid species described by Zagorsek & Vodrazka (2006) from the Czech Republic were placed in the suborder Cerioporina Hagenow, 1851. Martha et al. (2019, p. 237), in a revision of bryozoans in the collection of Ehrhard Voigt, placed Eleidae in the suborder Melicerititida Pergens, 1890, while Ernst (2021) referred the family to the suborder Tubuliporina Milne Edwards, 1838.

In 1965 Viskova began publishing papers describing species from Russia attributed by her to *Meliceritites* or other eleid genera (Viskova 1965, 1972, 2011). She has also contributed an important review of the morphology and classification of these bryozoans (Viskova 2016), and a revised diagnosis of stenolaemates incorporating characters of eleids (Viskova 2020). Importantly, her earlier monograph on post-Palaeozoic marine bryozoans (Viskova 1992) introduced the Order Melicerititida, thus removing eleids from the cyclostomes into a separate order having the same taxonomic rank. This taxonomic change is critically evaluated below.

Some of the species considered by Viskova to be eleids do not belong to this family. These include three species from the Callovian stage of the Jurassic (Viskova 2011) which considerably antedate the oldest incontestable eleids from the Barremian stage of the Cretaceous. All three Jurassic species lack convincing evidence of opercula, hingelines or eleozooids. Both *Elea lyapini* Viskova, 2011 and *Elea troshkovensis* Viskova, 2011 can be reinterpreted as fixed-walled tubuliporines, while *Elea taylori* Viskova, 2011 is poorly preserved externally (Fig. 7E) and has unusually thick walls; its affinities are unclear. Another species described in the same paper as *Biforicula ligitima* Viskova, 2011 is a cheilostome. The crenulate zooidal boundaries marking the position of a cuticular layer betray the cheilostome identity of this Campanian species (Fig. 7F).

With the assistance of Ehrhard Voigt, who made his large collection available to me, I began studying eleids some forty years ago with the ultimate goal of monographing the entire family. Only one part of the monograph, covering the genera *Elea*, *Semielea* and *Reptomultelea*, has been published (Taylor 1994). This described 36 species, 20 of which were new, and summarized eleid morphology. Earlier papers focussed on predatory borings in species of *Meliceritites*, which were found to be more common in the autozooids than the heterozooids (Taylor 1982), and polymorphism in eleids (Taylor 1985). The latter paper proposed the term ‘eleozoid’ to replace Canu’s (1897a) ‘eleocellaria’, and distinguished three main types of eleozooids: rostrozooids, trifoliozooids and demizooids. Miscellaneous eleid species were described from the Campanian of

Germany (Taylor 1987), the Aptian (Pitt & Taylor 1990) and Albian (Taylor 2020b) of southern England, the Barremian of SE France (Taylor 2010), and the Cenomanian–Turonian of the Czech Republic (Taylor & Zagorsek 2011). The palaeogeographical range of eleids was extended southwards into the continent of Gondwana with the record of an unnamed species of *Reptomultealea* from the Albian of Tamil Nadu, India (Taylor 2019, fig. 3C). This paper also briefly mentioned an undescribed eleid from Texas, the only species belonging to the family known from the Americas. The species concerned belongs to *Reptomultealea*, comes from the late Albian Main Street Formation of Denton County, and is represented by two specimens in the NHMUK collections (BZ 2365 and BZ 2368). It lacks eleozooids but preserves a few in-situ autozooidal opercula.

5. Phylogeny, classification and evolution

After their phylogenetic affinity with cheilostomes had been discounted, eleids became almost universally acknowledged as an aberrant family of cyclostomes. Lena Viskova, however, proposed their removal from the order Cyclostomata and inclusion in a separate order, the Melicerititida Viskova, 1992. The reasons for making this important taxonomic change were fully explained by Viskova (2016). She argued that a combination of unique characters – funnel-shaped zooids, facettes, semicircular apertures with a straight proximal edge, calcified opercula, and various types of eleozooids – serve to differentiate eleids from cyclostomes in both a morphological and an evolutionary sense, taking the group to “... a new evolutionary level, quite different from that of the other orders of the Stenolaemata.” (Viskova 2016, p. 154). On the other hand, Viskova did not deny a close relationship between eleids and cyclostomes, suggesting that eleids “branched off” from cyclostomes (which she referred to as Tubuliporida) in the Jurassic (Viskova 2016, p. 158). Therefore, the justification for placing these bryozoans in their own order becomes one of morphological distance and not phylogeny. If Melicerititida is accepted, then the crown-group Cyclostomata (i.e. post-Palaeozoic cyclostomes with gonozooids and regular interzooidal pores) would become paraphyletic, some species being more closely related to eleids than they are to other cyclostomes.

Gregory (1899) was the first to suggest a close phylogenetic relationship between eleids and the Jurassic cyclostome genus *Haplooeicia* (= *Collapora*). This hypothesis was corroborated by Taylor & Weedon (1996) who pointed to several characters shared by multisparisids such as *Collapora* and the eleid *Meliceritites*: (1) very short peristomes; (2) erect branches arising from sheet-like, multiseriate encrusting bases (cf. the oligoseriate encrusting bases of many erect cyclostomes); (3) overgrowths originating through intrazooecial fission; (4) longitudinally elongate gonozooids with an atrial ring just inside the ooeciopore; and (5) a transversely fibrous layer within the skeletal walls. In addition, the pseudoporous frontal walls of *Collapora* and some other multisparisids can have a facet-like appearance if they are surrounded by raised boundary walls (Fig. 7B), probably reflecting proximal retraction of the secretory epithelium before calcification.

A cladistic analysis of cyclostome phylogeny based on 46 morphological characters in 28 post-Palaeozoic cyclostome genera (Taylor & Weedon 2000) corroborated the close relationship between *Collapora* and the eleids *Meliceritites* and *Foricula*. This analysis was criticised by Viskova (2016) on the grounds that it did not specify which characters were of more or less phylogenetic significance. However, the analysis made no a priori assumptions about the relative values of the characters employed. Although molecular data has since challenged the relationships of the extant taxa in this tree (Waeschenbach et al. 2009), it is mute about the integrity of the extinct *Collapora+Meliceritites+Foricula* clade. A future challenge will be to use morphological characters to identify the closest living relative of eleids in order to estimate the position of this extinct family within the framework of a cyclostome molecular tree.

The description of three species assigned to *Elea* from the Callovian of the Moscow region prompted Viskova (2016, p. 154) to suggest that eleids evolved in the Middle Jurassic basins of the East European Platform and from there migrated into western Europe. The dubious identity of these Jurassic species as eleids casts doubt on this scenario. Instead, the oldest unequivocal eleids occur in the Barremian of SE France (Walter et al. 1975; Taylor 2010), although to suppose that the clade actually originated here would be unwarranted. Indeed, the presence of two genera – *Meliceritites* and *Elea* – the latter possessing eleozoids, points to a prehistory unrepresented in the known fossil record. Free-walled eleids enter the fossil record in the Albian with the appearance of both *Foricula* and *Biforicula* (Taylor 2020b); although Voigt (1981) claimed that *Foricula* is present in the Aptian, this requires confirmation. The encrusting genera *Reptomultealea* and *Reptoforicula* are first known in the Albian (Taylor 1984) and the Cenomanian (Taylor & Zagorsek 2011), respectively. *Semielea* appeared in the Turonian (Taylor 1994), *Atagma* in the Coniacian, and *Meliceritella* in the Santonian. Of these nine genera, only *Biforicula*, *Meliceritites* and *Meliceritella* survived into the final Maastrichtian stage of the Cretaceous, and only *Meliceritella* crossed the KPg boundary into the Danian.

The Chalk Sea covering much of northern Europe during the Late Cretaceous, including its sandy marginal facies, together with the carbonate platform of the Aquitaine Basin, host the great majority of eleids, probably in excess of 100 species. The only eleids recorded from outside Europe are the undescribed species of *Reptomultealea* from the Albian of the southeastern USA and from southern India mentioned above. Interestingly, eleids have not been found among the diverse bryozoan faunas of Campanian–Maastrichtian age present in these two regions (Guha & Nathan 1996; McKinney & Taylor 2006), nor are they known from coeval bryofaunas in South Africa (Taylor 2019) or Western Australia (E. Håkansson, D.P. Gordon & P.D. Taylor in preparation).

6. Conclusions

Uniquely among non-cheilostome bryozoans, eleids have autozooidal apertures closed by calcified, hinged opercula. In addition, many species possess polymorphic zooids resembling cheilostome avicularia. These two traits were not always recognized

by bryozoologists working in the 19th century. For example, d'Orbigny (1852) acknowledged the presence of opercula but considered the avicularia-like polymorphs to be reproductive zooids, whereas Waters (1891) and Gregory (1899) denied the existence of calcified opercula while identifying the polymorphs as analogues of cheilostome avicularia. Even as late as the 1970s, the presence of calcified opercula in eleids was being questioned by the cyclostome specialist Krister Brood (Brood 1972).

For two reasons eleids offer the best opportunities for studying patterns of morphological evolution among extinct cyclostomes. First, they are a monophyletic group, easy to distinguish from other bryozoans when adequately preserved. Secondly, they possess supplementary morphological characters to those normally present in cyclostomes, viz. opercula and associated apertural structures, and a variety of eleozooids. The fact that eleids could be confidently interpreted as a monophyletic group provided an early indication of the evolutionary plasticity in cyclostome skeletal organization as both fixed- and free-walled species occur in this family (Taylor 2000).

Aside from their intrinsic interest, eleids offer an important insight into the evolution of polymorphism in bryozoans, corroborating the notion that the possession of an operculum is essential for the evolution of a myriad of avicularia and avicularia-like polymorphs (see Schack et al. 2018). Opercula represent a 'pre-adaptation' for the evolution of polymorphs based on modifications of this hinged structure (Schopf 1973; Taylor 1985). This is at least part of the explanation for why higher levels of polymorphism occur in cheilostomes and eleid cyclostomes than in other cyclostomes, ctenostomes and phylactolaemate bryozoans.

The role played by eleids in the dramatic evolutionary turnover during the Late Cretaceous from cyclostome- to cheilostome-dominance deserves future study. Did cheilostomes come to occupy and progressively outcompete eleids in ecological niches that favoured bryozoans equipped with opercula and defensive polymorphs? Could emerging micropredators have had a greater impact on eleids than they did on cheilostomes?

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