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Pyrisinellidae, a new family of anascan cheilostome bryozoans

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Abstract

A new family of anascan-grade cheilostome bryozoans, Pyrisinellidae **n. fam.**, is introduced, together with two new genera, *Pyrisinella* **n. gen.** and *Spinisinella* **n. gen.** Containing species previously assigned either to the large, paraphyletic Calloporidae, or Microporidae, pyrisinellids are characterized by having small autozooids with a conspicuous pear-shaped ridge formed by the mural rim and distal rim of the opesia, articulated oral spines, and hyperstomial ovicells recumbent on the distal zooid and indenting its mural rim. Five species of pyrisinellids are described, two of which are new: *Spinisinella zagorseki* **n. gen. et sp.**, from the Cenomanian or Turonian (Upper Cretaceous) of the Czech Republic, and *Setosinella perfluxa* **n. sp.**, from the Langhian (Middle Miocene) of Kalimantan, Indonesia. A Recent species, *Megapora ringens* (Busk), is redescribed and questionably assigned to Pyrisinellidae. Important evolutionary changes within Pyrisinellidae having parallels elsewhere among anascan cheilostomes include: (1) the development of opesiules for passage of the parietal muscles which correlates with a change from a trifoliate to a semielliptical opesia; and (2) the transition from an open spinose ovicell in the oldest species (*Spinisinella zagorseki*) to a conventional ovicell with a solid hood-like ooecium that characterizes all other species belonging to the family.

Key words: Bryozoa, Cheilostomata, new taxa, fossil, Recent

Introduction

Calloporidae Norman, 1903 is one of the largest families of bryozoans with respect to generic diversity: D.P. Gordon placed no fewer than 76 genera in this anascan-grade neocheilostome family in his provisional listing of genera for the *Treatise on Invertebrate Paleontology* (http://www.bryozoa.net/treat_family_2011.pdf). The type genus of Calloporidae, *Callopora* Gray, 1848, has: (1) multiserial encrusting colonies; (2) autozooids with extensive ovoidal opesia, a circumopesial ring of articulated spines, a slight frontal wall comprising cryptocystal and gymnocystal elements, pore chambers, and ovicells containing an ectooecial window through which the entooecium is visible; and (3) small avicularia borne generally on the gymnocystal of the autozooids. Other genera placed in Calloporidae, however, differ considerably from *Callopora*. Ryland & Hayward (1977, p. 87) remarked: "The genera assembled in this family are a somewhat heterogeneous group". More recently, Reverter-Gil *et al.* (2011, p. 13) described Calloporidae as "disproportionately large and a little heterogeneous, with morphological characters that overlap with those of other (including segregate) families". Indeed, some calloporids are uniserial encrusters, others grow erect, many have an extensive frontal wall composed of gymnocystal and/or cryptocystal components, while some lack spines or have oral spines at the distal end of the autozooid only, a hyperstomial ovicell with a fully calcified ectooecium, and do not develop avicularia or have avicularia varying widely in morphology and location.

While large families can be justified if they are monophyletic, Calloporidae as currently applied is almost certainly paraphyletic. Taking the family as a whole, no unique apomorphies are evident: calloporid characters are either primitive and were inherited from their malacostegan ancestor (e.g. articulated spines and pore chambers), or are advanced relative to malacostegans but shared with other neocheilostome families (e.g. ovicells and avicularia). Calloporidae is the oldest known family of neocheilostomes, first recorded in the Albian stage of the mid-

Cretaceous (e.g. Ostrovsky *et al.* 2008), and as currently constituted represents a waste-bin for basal, paraphyletic neocheilostomes (i.e. cheilostomes with brooded larvae). The dismantling of Calloporidae into monophyletic groups (clades) of genera is clearly necessary and has already begun. For example, Grischenko *et al.* (2004) introduced a new family, Doryporellidae, for 'calloporids' with a distinctive suite of characters including an extensive cryptocystal frontal wall ornamented by a reticulate pattern of polygonal ridges. Similarly, Gordon & Winston (in Winston 2005) made the new family Foveolariidae and Tilbrook (1998) resurrected Antroporidae Vigneaux, 1949 for various genera formerly placed in Calloporidae.

Canu & Bassler's (1933) monograph of the bryozoan fauna from the Vincentown Limesand (Paleocene) of New Jersey introduced a new monospecific genus *Setosinella*, with *S. prolifica* Canu & Bassler, 1933 as the type species. *Setosinella* was assigned by Canu & Bassler (1933) to Setosellidae Levinsen, 1909. While *Setosinella* does indeed possess autozooids resembling those of the type genus of Setosellidae, *Setosella* Hincks, 1877, the latter genus has characteristically small colonies with spirally budded zooids and a setiform avicularium located distally of each autozooid (see Silén 1942; Rosso 2008), features not seen in *Setosinella*. Placement of *Setosinella* in Setosellidae is therefore inappropriate. The description of a second, Cretaceous species assigned to *Setosinella* prompted Taylor & McKinney (2006) to transfer the genus to Calloporidae, which, as noted above, is a paraphyletic waste-bin. An alternative assignment to Microporidae Gray, 1848 (Gordon 2011) is equally unsatisfactory given the immersed ovicells and lack of a gymnocyst in this family compared with the hyperstomial ovicells and gymnocyst of *Setosinella*.

The aim of the current paper is to describe two new genera (*Pyrisinella* and *Spinisinella*) which are considered to be closely related to *Setosinella*, to unite these two genera with *Setosinella* in a new family (Pyrisinellidae), and to describe all known species of the new family, two of which are new (*Spinisinella zagorseki* and *Setosinella perfluxa*).

Material and methods

Material from museum collections, including type specimens, as well as specimens of a new species of *Setosinella* collected in East Kalimantan, Borneo (Indonesia), have been used for this study. The Indonesian fossils were found during the second field season of the Marie Curie Throughflow Project in June 2011. They came from a thin floatstone of platy corals in a marly matrix at the top of a patch reef exposed in a road-cutting in the Indominco Mine near the village of Bontang. This section (0.151300°N; 117.304380°E) has been designated TF126 and is known colloquially as the '3D Reef' (Novak *et al.* submitted). Based on larger benthic foraminifera in combination with calcareous nannoplankton, it is dated as Langhian (Middle Miocene), early Tf2 age in the East Indian letter classification (Novak *et al.* submitted). A total of 18 colonies of the new Miocene species of *Setosinella* were obtained from three bulk samples. They encrust the bases of various platy scleractinian corals such as agaricidas, *Cyathoseris, Echinopora, Podabacia* and *Porites.* All specimens of this new species have been catalogued and deposited in the fossil collections of the Natural History Museum, London (abbreviated NHML). In order to remove clay particles, the bryozoans were variously cleaned, including scrubbing under running water with a soft toothbrush, soaking in a dilute solution of the detergent Quaternary-O and treatment in an ultrasonic bath.

Through the kindness of JoAnn Sanner (Smithsonian Institution, Washington DC) we have been able to obtain new SEM images of the type material of *Setosinella prolifica* Canu & Bassler, 1933 and *Amphiblestrum orbiculatum* Canu & Bassler, 1920. For further comparison with the new Miocene species from Kalimantan, studies were also made of topotype specimens of *S. prolifica* and *A. orbiculatum*, plus the type material of *S. meniscacantha* Taylor & McKinney, 2006, all held in the palaeontological collections of the NHML, as well as material of the Recent species *Megapora ringens* (Busk, 1856) from the zoological collections of the NHML. Finally, SEM images taken at the NHML by Kamil Zágoršek, were used to describe a new taxon from the Cretaceous of Bohemia. The only known specimen of this rare species is in the collection of the Národní Museum, Prague (abbreviated, NMP) and comes from Kaňk, in the vicinity of the city of Kutná Hora, where Late Cenomanian to Early Turonian rocks outcrop (Taylor & Zágoršek 2011). The tiny colony fouls a larger colony of the cyclostome *Stomatopora divaricata* (Reuss) figured by Počta (1892) who appears to have overlooked its presence.

Scanning electron microscopy (SEM) was undertaken on uncoated specimens using a low-vacuum scanning electron microscope (LEO VP-1455) at the NHML, using a back-scattered electron detector. Zooidal measurements were made from SEM images with the image processing program ImageJ. Measurements are given as the mean in microns plus or minus standard deviation, observed range and number of specimens used and total number of measurements made.

Systematic account

Family Pyrisinellidae fam. nov.

Diagnosis. Colony encrusting and multiserial. Autozooids distinct, oval, separated by deep furrows. Gymnocyst narrow, visible around entire circumference of zooid, often enlarged proximally. Cryptocyst extensively developed, depressed, flat and granular. Frontal surface of autozooids marked by pear-shaped ridge formed proximally and laterally by mural rim and distally by distal rim of opesia. Opesiules absent or present but few in number and small. Orifice trifoliate or semielliptical. Oral spines present, closely spaced, forming an arch distally around the orifice. Cryptocystal closure plates often developed. Ovicell hyperstomial, resting on distal zooid and indenting its mural rim. Growing edge stepped, revealing windows of pore chambers, that of the distal pore chamber the largest, ovoidal and facing frontally. Avicularia absent or present and variously adventitious, interzooidal or vicarious; rostrum acuminate or rounded; pivotal bar entirely calcified or represented by two condyles.

Type genus. Pyrisinella gen. nov.

Remarks. This new family is erected to accommodate two new genera (*Pyrisinella* and *Spinisinella*) plus an existing genus (*Setosinella*) which share a sufficient numbers of skeletal morphological characters to suggest that they represent a clade of anascan-grade neocheilostomes distinguishable from other 'calloporids'. In all three genera, the small autozooids have a salient mural rim extending to the proximolateral corners of the opesia and joining with the opesial rim to form a pear-shaped ridge around the cryptocyst and opesia, an arch of oral spines over the orifice, and a prominent hyperstomial ovicell. A fourth genus, *Megapora*, is tentatively referred to Pyrisinellidae, although it differs from the other three genera in that the proximal part of the pear-shaped ridge is located within the cryptocyst rather than representing a true mural rim marking the boundary between the cryptocystal and gymnocystal components of the frontal wall. Although a few genera of Microporidae Gray, 1848 possess a similar pear-shaped ridge, they differ from pyrisinellids in one or more of the following characters: immersed ovicells, lack of gymnocyst, and presence of connecting tubes between the zooids (as in *Mollia* Lamouroux, 1816).

Pyrisinella is chosen as the type genus of the new family for the following reasons: (1) *Spinisinella* is represented by only a single small colony whereas *Pyrisinella* is abundant; (2) using *Setosinella* as the type genus would result in a family name confusingly similar to Setosellidae Levinsen, 1909; and (3) *Megapora* is only provisionally assigned to the new family.

Stratigraphical distribution. Cretaceous (Cenomanian or Turonian) to Miocene (Langhian), ?Recent.

Key to the species of Pyrisinellidae

1.	Opesia trifoliate; opesiules lacking
	Opesia semielliptical; opesiules present
2.	Ovicell ooecium constructed of spines
-	Ovicell ooecium conventional, hood-like
3.	Ridge on frontal wall coincident with mural rim; ovicell not associated with a small distal kenozooid
	Pyrisinella meniscacantha
-	Ridge on frontal wall located within cryptocyst; ovicell associated with a small distal kenozooid Megapora ringens
4.	Avicularia present; oral spines located close to rim of opesia
-	Avicularia lacking; significant gap between oral spines and rim of opesia
5.	Interzooidal avicularia numerous, long and narrow; vicarious avicularia rare
-	Interzooidal avicularia rare, triangular and small

Genus Pyrisinella n. gen.

Diagnosis. Colony encrusting, multiserial, unilaminar. Autozooids small, distinct, rounded polygonal, longer than broad, separated by deep furrows. Gymnocyst convex, narrow, best developed proximally. Cryptocyst extensively developed, depressed, flat and densely granular, bounded by pear-shaped ridge comprising mural rim and distal rim of opesia. Opesia trifoliate. Oral spines present. Ovicell hyperstomial, globular, prominent, smooth with a dumbbell-shaped opening, resting on proximal gymnocyst of distal zooid and indented its mural rim. Intramural buds common. Closure plates depressed beneath level of cryptocyst. Avicularia interzooidal or more commonly adventitious. Distal pore chamber larger than distolateral pore chambers; pore windows oval. Ancestrula having the appearance of a small astogenetically mature autozooid with an indeterminate number of spine bases, budding a single distal zooid.

Type species. Setosinella meniscacantha Taylor & McKinney, 2006.

Etymology. From the Latin *pirum*, meaning pear, in reference to the pear-shaped ridge formed by the mural rim and distal rim of the opesia.

Remarks. Important differences between this monospecific genus and the Paleocene type species of *Setosinella, S. prolifica* Canu & Bassler, 1933, are the trifoliate shape of the opesia and lack of opesiules.

Distribution. Upper Cretaceous (Maastrichtian) of Alabama, Mississippi and North Carolina, USA.

Pyrisinella meniscacantha (Taylor & McKinney, 2006) n. comb.

(Figs 1-8; Table 1)

Setosinella meniscacantha Taylor & McKinney, 2006: 110-112, pls. 75-76.

Material examined. *Holotype*: NHM BZ 4796(1a), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama, USA. *Paratypes*: BZ 4796(1b), encrusting same shell as holotype; BZ 4810(2), BZ 5042, Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama, USA; BZ 5182, Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina, USA.

Description. Colony encrusting, multiserial, unilaminar, usually irregular in outline shape. Growing edge stepped, implying intrazooidal budding, some incomplete buds present comprising basal wall and stumps of vertical walls (Figs. 7, 8). Distal pore chamber larger than distolateral pore chambers; pore windows oval (mean L = 33 μ m, mean W = 16 μ m) surrounded by a mural ring. Ancestrula having the appearance of a small astogenetically mature autozooid (mean $L = 165 \mu m$, mean $W = 140 \mu m$) with an indeterminate number of spine bases; budding a single periancestrular zooid distally (Fig. 2). Autozooids in zone of primary astogenetic change transitional in size between ancestrula and later autozooids. Autozooids small, rhomboidal, longer than broad (mean L/W = 1.20), separated by deep furrows and arranged in well-defined rows. Gymnocyst narrow, usually broadest proximally. Cryptocyst depressed, forming an extensive flat shelf, finely and densely granular, with granules immediately proximally of orifice tending to be aligned in weak radial rows. Mural rim salient, together with distal rim of opesia forming pear-shaped ridge enclosing cryptocyst and opesia. Opesia trifoliate, the larger, distal semielliptical part divided from the shallower proximal part by an indentation in the mural rim (Fig. 5). Six to eight oral spine bases, large and closely spaced, arranged in a prominent crescentic arch around distal rim of orifice; distalmost pair of oral spines hidden by ovicell in ovicellate zooids. Ovicell hyperstomial, globose, prominent, with a dumbbell-shaped opening, resting on proximal gymnocyst of distal zooid and indenting its mural rim (Fig. 6). Intramural buds observed especially in damaged zooids. Closure plates depressed beneath level of cryptocyst, with a sunken pore located almost centrally. Avicularia interzooidal or more commonly adventitious, confined to furrows between autozooids and budded onto autozooidal gymnocyst, most orientated obliquely distally; gymnocyst variably developed, more extensive in interzooidal than adventitious avicularia; cryptocyst granular and broadest proximally; opesia a uniformly tapering teardrop shape; rostrum acuminate, longer than wide; pivotal bar calcified.

Remarks. Taylor & McKinney (2006) originally assigned this species from the Late Cretaceous of the Atlantic and Gulf Coast plains of the USA to *Setosinella* Canu & Bassler, 1933, having questioned the presence of opesiules in the type species of this genus, *S. prolifica*. However, new SEM studies have shown that opesiules are present in *S. prolifica* (see below), whereas they are clearly lacking in *Pyrisinella*.



FIGURES 1–8. *Pyrisinella meniscacantha* (Taylor & McKinney, 2006) **n. comb**, Cretaceous, Maastrichtian, Prairie Bluff Chalk, Livingston, Alabama, USA **1.** view of colony, NHM BZ 4796 (1a), holotype, scale bar = 500 μ m; **2.** same, ancestrula and early astogeny showing overgrowth of some early zooids at centre, scale bar = 100 μ m; **3.** same, close-up of a nonovicellate autozooid, scale bar = 100 μ m; **4.** same, ovicellate autozooids and avicularia, scale bar = 100 μ m; **5.** close-up of two autozooids and interzooidal avicularium, showing the trifoliate opesia and six orificial spine bases, NHM BZ 4796 (1b), paratype, scale bar = 100 μ m; **6.** close-up of ovicell and avicularium, NHM BZ 4796 (1a), holotype, scale bar = 100 μ m; **7.** same, stepped edge of colony with some incomplete buds, pore windows and closure plates visible along the margin, scale bar = 200 μ m; **8.** same, intramural bud, scale bar = 100 μ m.

Small, fan-like outgrowths observed in some of the larger colonies of *Pyrisinella meniscacantha* from the Prairie Bluff Chalk were considered by Taylor & McKinney (2006) to be peripheral subcolonies budded from the larger colony but new SEM observations show this not to be the case. Instead, they represent new colonies founded by larvae that settled close to the edge of a dormant or dead colony, in some instances within a partly formed zooid at the growing edge.

Distribution. Maastrichtian (Upper Cretaceous) of Alabama, Mississippi and North Carolina, USA.

	N (colonies, zooids)	Mean	SD	Range
Zooid length	3, 30	361	29	295–405
Zooid width	3, 30	304	33	243–374
Orifice length	3, 30	83	17	47–123
Orifice width	3, 30	98	17	57–132
Ovicell length	3, 25	133	21	78–167
Ovicell width	3, 25	154	19	126–191
Avicularia length	3, 12	139	28	87–133
Avicularia width	3, 12	77	12	50–90

TABLE 1. Measurements (in µm) of Pyrisinella meniscacantha (Taylor & McKinney, 2006) n. comb.

N, Number of colonies and number of zooids measured; SD, standard deviation.

Genus Spinisinella gen. nov.

Diagnosis. Colony encrusting, multiserial, unilaminar. Autozooids small, distinct, oval, slightly longer than broad, separated by deep furrows. Gymnocyst narrow. Cryptocyst extensively developed, depressed, flat and granular; mural rim salient, together with distal rim of opesia forming pear-shaped border around the cryptocyst and opesia; opesiules lacking. Opesia trifoliate, longer than wide, a pair of rounded indentations present in the proximal third. Oral spines present. Ovicell cribrate, ooecium represented by a pair of spine bases arranged parallel to the long axis of the zooid and bordering a depression on the proximal gymnocyst of the distal zooid. Avicularia and ancestrula not observed.

Type species. Spinisinella zagorseki n. sp.

Etymology. *Spini-*, in reference to the ovicell ooecium constructed of spines, combined with *-sinella*, the suffix used for other genera belonging to this family.

Remarks. The spinose ovicell of this new genus is unique for Pyrisinellidae. Ostrovsky & Taylor's (2005) review of spinose ovicells in cheilostome bryozoans found these primitive ovicells to be present in ten genera belonging to five families of anascan-grade cheilostomes. Of these genera, the zooidal characters of *Spinisinella* most closely resemble the Cretaceous (and ?Paleocene) monoporellid genus *Stichomicropora* Voigt, 1949 (see also Taylor & McKinney 2002, 2006), especially *Stichomicropora* sp. 3 of Ostrovsky & Taylor (2005, pp. 329, 331, fig. 8A-C) from the Coniacian of Kent. However, the ovicell spine bases of species of *Stichomicropora* are aligned transversely to the long axis of the zooids, forming either a straight line or a gently curved arch, whereas those of *Spinisinella* are arranged parallel to the long axis. In addition, *Spinisinella* has trifoliate opesia and lacks opesiules, compared with *Stichomicropora* in which the opesia is semielliptical and opesiules are present in the cryptocyst.

Distribution. Cenomanian or Turonian (Upper Cretaceous).

Spinisinella zagorseki n. sp.

(Figs 9–12; Table 2)

Material examined. *Holotype*: NMP O-6751, Cretaceous, Cenomanian or Turonian, Kaňk, Bohemian Basin, Czech Republic.

Etymology. Named for Kamil Zágoršek (Národní Museum, Prague) in recognition of his significant contribution to the study of bryozoans.



FIGURES 9–12. *Spinisinella zagorseki* **n. sp.**, NMP O-6751, holotype, Cretaceous, Cenomanian or Turonian, Kaňk, Czech Republic. **9.** view of colony, scale bar = $200 \mu m$; **10.** ovicellate and non-ovicellate autozooids, scale bar = $100 \mu m$; **11.** close-up of two autozooids, scale bar = $100 \mu m$; **12.** close-up of spinose ovicell, scale bar = $20 \mu m$.

Description. Colony encrusting, multiserial, unilaminar. Autozooids small, distinct, separated by deep furrows, oval, slightly longer than wide (mean L/W = 1.14). Gymnocyst narrow, separated from the extensive cryptocyst by a thin salient mural rim forming together with distal rim of opesia a pear-shaped border around the cryptocyst and opesia, highest distally. Cryptocyst deep, shelf-like, flat and finely granular. Opesia trifoliate, longer than wide, a pair of rounded downwards directed denticles separating the larger, distal semielliptical part from the shallower proximal part with a straight or barely convex edge (Fig. 12). Four oral spine bases located distolaterally of the opesia (mean D = 10 μ m). Ovicell spinose, ooecium represented by two pairs of spine bases (mean D = 15 μ m) arranged in a line parallel to the proximal-distal axis of the zooids, the proximal pair positioned close to the distal oral spine bases of the maternal zooid; a depression on the proximal gymnocyst of the distal zooid (Fig. 12). Avicularia and ancestrula not observed.

Remarks. This species is immediately distinguishable from other species of pyrisinellids in having a spinose ovicell represented by two pairs of spine bases. The spine bases in living colonies are inferred to have borne basally articulated spines bent towards the median axis of the ovicell to form a cage-like structure. The embryo would have been accommodated in the space between the depression on the proximal gymnocyst of the distal zooid and the overarching spines. Given their close proximity to the ovicell, it is possible that the distalmost pair of oral spines of the maternal zooid also contributed to the ovicell roof. If so, the brood chamber was constructed, unusually, by spines from both the maternal and distal zooids.

Distribution. Cenomanian or Turonian? (Late Cretaceous) of the Bohemian Basin, Czech Republic.

	N (colonies, zooids)	Mean	SD	Range
Zooid length	1, 8	201	22	159–230
Zooid width	1, 8	176	15	154–197
Orifice length	1, 8	65	4	55–69
Orifice width	1, 8	57	8	51–63
Cryptocyst length	1, 8	83	12	61–96
Cryptocyst width	1, 8	130	10	113–143

TABLE 2. Measurements (in µm) of Spinisinella zagorseki n. sp.

N, Number of colonies and number of zooids measured; SD, standard deviation.

Genus Setosinella Canu & Bassler, 1933

Revised diagnosis. Colony encrusting, multiserial, unilaminar. Autozooids small, distinct, rounded polygonal or oval, longer than broad, separated by deep furrows. Gymnocyst convex, narrow, best developed proximally. Cryptocyst extensively developed, depressed and flat, finely granular, bounded by a salient mural rim, forming pear-shaped ridge together with distal rim of opesia, perforated by two small circular or reniform lateral opesiules situated about midway along cryptocyst. Opesia semicircular. Oral spines present, variable in number. Ovicell hyperstomial, globular, prominent and smooth, resting on proximal gymnocyst of distal zooid and indented its mural rim. Avicularia interzooidal, vicarious or absent. Pore chambers placed distally and distolaterally; pore windows oval. Ancestrula having the appearance of a small astogenetically mature autozooid but with a different number of spines, budding a single autozooid in a distal location. First generation of zooids transitional in size between ancestrula and astogenetically mature zooids.

Type species. Setosinella prolifica Canu & Bassler, 1933, by monotypy.

Remarks. This genus was founded by Canu & Bassler (1933, p. 41) for a rare new species from the Paleocene Vincentown Limesand of New Jersey. Canu & Bassler (1933), and subsequently Bassler (1953), placed *Setosinella* in the family Setosellidae on account of its similarity to *Setosella* Hincks, 1877, particularly with respect to the morphology of the autozooidal frontal wall, while noting the existence of some important differences between the two genera. First, the ovicell of *Setosinella* seems not to be closed by the operculum as in *Setosella* where it is also smaller and subimmersed. Furthermore, *Setosinella* does not exhibit a spiral pattern of zooidal budding and lacks the small setiferous avicularia located distally of each autozooid that is characteristic of *Setosella*. Finally, *Setosinella* has conspicuous oral spines represented by stout spine bases in fossil material.

In his provisional listing of genera for the revision of *Treatise on Invertebrate Paleontology*, Gordon (2011) reassigned *Setosinella* to Microporidae. Canu & Bassler (1933) had earlier mentioned in their description of the genus its affinity to Microporidae, commenting that the zooidal structure of *Setosinella* was exactly that of *Micropora* but differing in the ovicell, which is hyperstomial and not closed by the operculum in *Setosinella* but endozoecial and closed by the zooidal operculum in *Micropora*. Microporidae, unlike *Setosinella*, also lacks a gymnocyst and the oral spines are usually replaced by a short pair of tubular processes, except in the Antarctic species *Micropora notialis* Hayward & Ryland, 1993, which has articulated oral spines on the marginal zooids, and in *Andreella* Jullien, 1888. Furthermore, the Cretaceous-Paleocene genus *Hoplitaechmella* Voigt, 1949, placed in Microporidae because of its endozoecial ovicell by Voigt (1949), shows up to eight oral spines and also resembles *Setosinella* in the extensive granular cryptocyst entirely surrounded by a prominent mural rim, and the semicircular to trifoliate orifice. It differs, however, in the type of ovicell and greater prominence and convexity of the cryptocyst contrasting with the deep, flat cryptocyst of *Setosinella*.

Based on the similarities between their Maastrichtian species *Setosinella* [now *Pyrisinella*] *meniscacantha* and the genus *Amphiblestrum* Gray, 1848, as well as the apparent lack of opesiules, Taylor & McKinney (2006) suggested that *Setosinella* belonged to Calloporidae in the broad sense of this family currently prevailing. SEM study of well-preserved material of *S. meniscacantha* showed clearly that opesiules were lacking in this species. Regarding opesiules in *S. prolifica*, Canu & Bassler (1933, p. 42) stated: "We have not observed true perforating opesiules; the place of some of these is, however, sufficiently indicated to prove that they must occur. They must have been very small, which explains their disappearance in fossilization". Canu & Bassler's figures of *S. prolifica*

do not provide any evidence that opesiules are actually present in *Setosinella*. However, SEM studies of an NHML topotype of *S. prolifica*, identified and donated by R.S. Bassler, reveal the presence of two small circular lateral opesiules (Fig. 22) in a few zooids; diagenetic cementation and/or infilling sediment probably explains the inability to observe opesiules in all zooids. Additionally, opesiules are clearly visible in all of the 18 specimens of the new species of *Setosinella*, *S. perfluxa*, described here from the Miocene of East Kalimantan (see below). These structures, defined as open foramina in the cryptocyst for the passage of parietal muscles, are here considered to be a generic character that is also correlated with the shape of the opesia, the main opening through which the tentacle crown is extruded. A trifoliate opesia with notches at the proximolateral corners to accommodate the parietal muscles but without opesiules is interpreted to be the primitive state in Pyrisinellidae, whereas a smaller semicircular opesia accompanied by opesiules for the parietal muscles is inferred to be the advanced state (see Discussion below).

Distribution. Paleocene (Thanetian)–Miocene (Langhian).

Setosinella prolifica Canu & Bassler, 1933

(Figs 13-22; Table 3)

Setosinella prolifica Canu & Bassler, 1933: 41-42, pl. 9, figs 7-8.

Material examined. *Holotype*: USNM 73903, Paleocene, Vincentown, New Jersey, USA; NHML D33347 (encrusting another bryozoan), details as for holotype.

Description. Colony encrusting, multiserial, unilaminar. Growing edge stepped, budding pattern apparently intrazooidal. Pore windows (mean L = $26 \mu m$, mean W = $13 \mu m$) visible in transverse vertical walls at colony growing edge, oval, facing frontally. Ancestrula small (L = $125 \ \mu m$, W = $100 \ \mu m$), resembling later autozooids with two solid oral spines. Autozooids small, distinct, separated by deep furrows, rounded hexagonal or oval, longer than wide (mean L/W = 1.46). Gymnocyst narrow, better developed proximally to the opesia, separated from cryptocyst by salient mural rim together with distal rim of opesia forming a pear-shaped outline. Cryptocyst extensive, deep, shelf-like, generally flat except for a very slight median convexity, finely granular and perforated by two small circular opesiules (D = $10 \mu m$) (Fig. 22) usually obscured by sediment or cement. Opesia semielliptical, limited distally by the mural rim and proximally by a transverse salient trabeculum attached to the mural rim. Oral spine bases numbering seven or eight in non-ovicellate zooids, six in ovicellate autozooids, closely spaced in an arch around the distal margin of the opesia; spine diameters ranging from 10 to 20 µm, variability independent of their position in the arch. Ovicells numerous, hyperstomial, globular, prominent, slightly broader than long, smooth, the ectooecium completely calcified, resting on proximal gymnocyst of distal zooid and indenting its mural rim. Avicularia interzooidal numerous, long and narrow, confined to furrows between autozooids, orientated obliquely distally. Gymnocyst variably developed, narrower laterally, more extensive proximally and distally. Cryptocyst generally narrow, broadest proximally. Opesia teardrop shaped. Rostrum longer than wide, truncated distally, the tip open or channeled. Two small sharp condyles present. Vicarious avicularia rare (Fig. 15), triangular, distally orientated, generally observed at the margin of the colony. Gymnocyst narrow, more extensive laterally. Cryptocyst broadest proximally. Rostrum long and narrow, truncated distally, the tip open or channeled.

Remarks. Canu & Bassler (1933) described small, perforated distal kenozooids surmounting some of the autozooids in this species. These structures are reinterpreted here as oval pore windows visible at the growing edge of a colony fouling an older colony in the type specimen. They also reported four oral spines but a greater number (6-8) is clearly evident in SEM images of the holotype and the NHML topotype specimen. The latter specimen also provides evidence that the opesiules hypothesized to exist by Canu & Bassler (1933), but not actually observed by them, are indeed present in *Setosinella prolifica*.

Distribution. Thanetian (Paleocene), Vincentown Limesand of New Jersey, USA.



FIGURES 13–18. *Setosinella prolifica* Canu & Bassler, 1933, USNM 73903, holotype, Paleocene, Vincentown Limesand, Vincentown, New Jersey, USA. **13.** ovicellate and non-ovicellate autozooids, scale bar = 200μ m; **14.** ovicellate autozooids and interzooidal avicularia, scale bar = 100μ m; **15.** ancestrula, early astogeny and vicarious avicularium visible at the colony growing edge (centre lower right), scale bar = 200μ m; **16.** growing edge of colony fouling an older colony, scale bar = 200μ m; **17.** close-up of an ovicellate autozooid and two interzooidal avicularia, scale bar = 100μ m; **18.** detail of colony growing edge showing a distal pore window, scale bar = 100μ m.



FIGURES 19–22. Setosinella prolifica Canu & Bassler, 1933, NHML D33347, Paleocene, Vincentown Limesand, Vincentown, New Jersey, USA. **19.** view of colony encrusting another bryozoan, scale bar = $100 \mu m$; **20.** ovicellate and non-ovicellate autozooids, scale bar = $100 \mu m$; **21.** close-up of an interzooidal avicularium, scale bar = $20 \mu m$; **22.** close-up of a zooid showing two small circular opesiules, scale bar = $20 \mu m$.

	N (colonies, zooids)	Mean	SD	Range
Zooid length	2, 20	302	41	221–349
Zooid width	2, 20	206	22	177–238
Orifice length	2, 20	75	10	54–92
Orifice width	2, 20	79	10	66–96
Ovicell length	2, 10	120	4	116–126
Ovicell width	2, 10	146	15	126–165
Cryptocyst length	2, 20	148	23	125–167
Cryptocyst width	2, 20	178	25	131–219
Avicularia length	2, 20	227	14	211–244
Avicularia width	2, 20	70	9	57–77

TABLE 3. Measurements (in µm) of Setosinella prolifica Canu & Bassler, 1933

N, Number of colonies and number of zooids measured; SD, standard deviation.

Setosinella orbiculata (Canu & Bassler, 1920) n. comb.

(Figs 23-30; Table 4)

Amphiblestrum orbiculatum Canu & Bassler, 1920, pp. 161-162, pl. 30, fig. 4.



FIGURES 23–26. Setosinella orbiculata (Canu & Bassler, 1920) **n. comb.**, USNM 63932, holotype, Eocene, Priabonian, Ocala Limestone, Bainbridge, Georgia, USA. **23.** view of part of the colony with putative ancestrula (bottom centre), scale bar = 200μ m; **24.** part of the colony showing distal pore windows at the colony growing edge, scale bar = 200μ m; **25.** close-up of two autozooids and interzooidal avicularium; autozooid on right shows possible pores in the cryptocyst obscured by epitaxial cement; scale bar = 100μ m; **26.** close-up of an ovicellate autozooid, scale bar = 100μ m.

Material examined. *Holotype*: USNM 63932, Eocene (Upper Jacksonian = Priabonian), Ocala Limestone, Old Factory, 1.5 miles above Bainbridge, Georgia, USA; NHML D34666, details as for holotype.

Description. Colony encrusting, multiserial, unilaminar. Growing edge stepped implying intrazooidal budding. Pore windows (mean $L = 45 \mu m$, mean $W = 15 \mu m$) visible in transverse vertical walls at colony growing edge, oval, facing frontally and laterally. Ancestrula not observed intact; apparent ancestrula in holotype represented by basal walls only, approximately 260 μm long and 240 μm wide, budding a distal and two distolateral zooids. Autozooids small, distinct, rounded hexagonal or oval, little elongated (mean L/W = 1.38), separated by deep furrows. Gymnocyst slight, broadest proximally. Mural rim thin, salient, together with distal rim of opesia forming a pear-shaped wall around cryptocyst and opesia. Cryptocyst shelf-like, deep, flat, granular. Opesia semicircular, limited distally by the mural rim and proximally by a transverse salient trabeculum attached to the mural rim. An indeterminate number of spine bases in non-ovicellate zooids, six in ovicellate autozooids, forming an arch close to the distal rim of the opesia. Ovicell hyperstomial, globular, prominent, slightly broader than long, smooth, the ectooecium completely calcified, resting on proximal gymnocyst of distal zooid and indenting its mural rim, opening dumbbell-shaped. Avicularia rare, interzooidal, small and triangular.

Remarks. Compared with the type species of the genus, *Setosinella prolifica* from the Paleocene, this Late Eocene species has larger autozooids and smaller and less frequent avicularia. Unequivocal opesiules and pores were not observed during SEM study of both holotype and topotype but the coarse preservation of the cryptocyst may account for this absence. Canu & Bassler's solitary photograph of this species (Canu & Bassler, 1920, pl. 30, fig. 4) shows up to about 10 pores ('tremopores') distributed more or less evenly over the cryptocyst, and scanning

electron micrographs hint at the possible existence of pores in a few zooids (Fig. 25). Like the opesia and oral spines, these structures have been inked in on top of Canu & Bassler's photograph. Canu & Bassler (1920) noted the similarity between *Amphiblestrum orbiculatum* and *Micropora* but remarked on the difference in the ovicells, which are hyperstomial in *A. orbiculatum* but endozooecial in *Micropora*.

Canu & Bassler (1920, p. 161) assigned this species to *Amphiblestrum* on the grounds of the 'interopesial avicularia', oral spines and hyperstomial ovicell explaining that this species is a very divergent type of *Amphiblestrum* where the opesia is transformed into a real aperture with an operculum. We here reassign the species to *Setosinella* because of the combination of the following characters: zooids with a narrow gymnocyst separated from the extensive and flat cryptocyst by a thin, salient mural rim that, together with the rim of the opesia forms a pear-shaped wall, hyperstomial ovicell, and semielliptical opesia with a distal arch of oral spines. There are other species assigned to *Amphiblestrum* (e.g., *A. willetti* Brown, 1952) which resemble *Setosinella* but have an ovoidal rather pear-shaped mural rim.

Distribution. Priabonian (Late Eocene), Upper Jacksonian of Georgia, USA.

	N (colonies, zooids)	Mean	SD	Range
Zooid length	1, 10	391	41	327–443
Zooid width	1, 10	283	45	246-356
Orifice length	1, 10	68	4	62–73
Orifice width	1, 10	89	5	79–95
Ovicell length	1,5	140	10	126–155
Ovicell width	1,5	152	8	147–167
Cryptocyst length	1, 10	255	34	192–286
Cryptocyst width	1, 10	255	43	206–308
Avicularia length	1, 2	180	16	168–192
Avicularia width	1, 2	79	3	77–81

TABLE 4. Measurements (in µm) of Setosinella orbiculata (Canu & Bassler, 1920) n. comb.

N, Number of colonies and number of zooids measured; SD, standard deviation.

Setosinella perfluxa n. sp.

(Figs 31-38; Table 5)

Material examined. *Holotype*: NHML BZ 5849, Langhian (Middle Miocene), Indominco Mine, Bontang, East Kalimantan, Indonesia; *Paratype*: BZ 5850, details as for holotype.

Etymology. From the Latin *per*, through, and *fluxus*, flow, in reference to the name of the Marie Curie Project 'Throughflow' funding this research.

Description. Colony encrusting, multiserial, unilaminar, usually irregular in outline shape. Growing edge stepped implying intrazooidal budding. Oval pore windows (mean 38 μ m by 16 μ m) exposed along distal, distolateral and proximolateral vertical walls at the colony growing edge. Ancestrula resembling a very small autozooid (mean L = 140 μ m, mean W = 120 μ m), with up to ten spine bases visible around the entire mural rim, possibly with additional spine bases hidden by surrounding autozooids (Fig. 33); budding a single periancestrular zooid distally. Autozooids small, rounded hexagonal, longer than broad (mean L/W = 1.24), separated by deep furrows. Gymnocyst narrow, more developed proximally and laterally of the orifice, separated from the extensive cryptocyst by a thin, salient mural rim which together with distal rim of opesia forms a pear-shaped wall around cryptocyst and opesia. Cryptocyst shelf-like, deep, flat and finely granular, perforated by two small reniform opesiules. Opesia semicircular, limited distally by the mural rim and proximally by a transverse salient trabeculum attached to the mural rim. Nine oral spine bases in non-ovicellate zooids, six in ovicellate autozooids, forming an arch around but somewhat distant (mean D = 28 μ m) from the distal edge of the opesia (Fig. 38); spine diameters ranging from 10 to 20 μ m independently of their position. Ovicell hyperstomial, globular, prominent, slightly broader than long, smooth, the ectooecium completely calcified, resting on proximal gymnocyst of distal zooid and indenting its mural rim (Fig. 34). Avicularia lacking.



FIGURES 27–30. *Setosinella orbiculata* (Canu & Bassler, 1920) **n. comb.**, NHML D34666, Eocene, Priabonian, Ocala Limestone, Bainbridge, Georgia, USA. **27.** view of part of the colony, scale bar = 200 μ m; **28.** ovicellate autozooids and interzooidal avicularia, scale bar = 100 μ m; **29.** close-up of two ovicellate autozooids and interzooidal avicularium, scale bar = 100 μ m; **30.** poorly preserved early astogenetic stages, scale bar = 100 μ m.

Remarks. Compared with the Paleocene type species of *Setosinella*, this new Miocene species has slightly more oral spines (9 vs 7–8) which are placed significantly more distantly from the distal rim of the opesia and larger autozooids. Furthermore, it lacks avicularia, which also differentiates *S. perfluxa* from *S. orbiculata*.

Distribution. Langhian (Middle Miocene) of East Kalimantan, Indonesian Borneo.

	N (colonies, zooids)	Mean	SD	Range
Zooid length	3, 40	374	39	330–451
Zooid width	3, 40	300	45	223–382
Orifice length	3, 40	57	8	45–69
Orifice width	3, 40	84	10	57–132
Ovicell length	3, 9	159	12	145–187
Ovicell width	3, 9	172	15	147–189
Cryptocyst length	3, 40	199	20	125–167
Cryptocyst width	3, 40	222	30	131–219

TABLE 5. Measurements (in µm) of Setosinella perfluxa n. sp.

N, Number of colonies and number of zooids measured; SD, standard deviation.



FIGURES 31–38. Setosinella perfluxa **n. sp.,** Miocene, Langhian, Indominco Mine, Bontang, East Kalimantan, Indonesia. **31.** view of colony NHML BZ 5849, holotype, scale bar = 500 μ m; **32.** same, several autozooids, scale bar = 200 μ m; **33.** same, close-up of an ovicellate autozooid, scale bar = 100 μ m; **35.** view of colony NHML BZ 5850, paratype, scale bar = 500 μ m; **36.** same, early astogeny, scale bar = 200 μ m; **37.** same, close-up of a zooid showing two small reniform opesiules, scale bar = 100 μ m; **38.** same, close-up of a zooid at the colony growing edge, showing oral spine bases and distal pore window, scale bar = 100 μ m.

Genus Megapora Hincks, 1877

Revised diagnosis. Colony encrusting, multiserial, unilaminar. Autozooids small, distinct, rounded polygonal or oval, longer than broad, separated by deep furrows. Gymnocyst narrow. Cryptocyst well developed, granular, depressed except for a rounded submarginal ridge. Opesia strongly trifoliate. Oral spines present. Distal pore chamber larger than distolateral pore chambers; pore windows oval. Ancestrula smaller than astogenetically mature autozooids, with gymnocyst absent (or overgrown), an extensive granular cryptocyst, trifoliate opesia and oral spines. Ovicell hyperstomial, prominent; ectooecium with a narrow, median triangular window; distal zooid reduced to small kenozooid. Avicularia absent. Kenozooids often developed around edge of colony.

Type species. Lepralia ringens Busk, 1856.

Remarks. This cold-water monospecific genus is tentatively assigned to Pyrisinellidae. Although the morphology of the autozooids is closely similar to both *Pyrisinella* and *Spinisinella*, the pear-shaped ridge characteristic of pyrisinellids is located inwardly of the mural rim and is formed by a cryptocystal elevation (plus the distal rim of the opesia) rather than being coincident with the mural rim at the boundary between the gymnocyst and the cryptocyst. The taxonomic importance of this difference is unclear. The mural rim in anascans is typically located at the highest point of the frontal wall and is the line along which the frontal membrane is attached to the skeleton. It is conceivable that this attachment migrated outwards during the evolution of *Megapora* from a conventional pyrisinellid ancestor, causing it to lie outwardly of the highest point on the frontal wall.

Distribution. Recent.

Megapora ringens (Busk, 1856)

(Figs 39–44; Table 6)

Lepralia ringens Busk, 1856: 308.

Megapora ringens: Hincks, 1880: 172, pl. 22, fig. 1; Prenant & Bobin, 1966: 273; Ryland & Hayward, 1977: 107, fig. 47; Hayward & Ryland, 1998: 196–199, fig. 58B–59.

Material examined. NHML 1911.10.1.629, Recent (specimen figured by Hincks, 1880, pl. 22, fig. 1), Shetland (Barlee), 80–170 fathoms. NHML 1911.10.1.631, Recent, Porcupine Bight, several encrusting three small pebbles.

Description. Colony encrusting, multiserial, unilaminar, developing small rounded patches. Pore chambers present, distal pore chamber slightly larger than distolateral pore chambers; pore windows oval (mean $L = 37 \mu m$, mean $W = 10 \mu m$), surrounded by a mural ring, that of the distal pore chamber facing frontally. Ancestrula oval and smaller than astogenetically mature autozooids ($L = 223 \,\mu m$, mean $W = 166 \,\mu m$); gymnocyst absent or hidden by later zooids, cryptocyst densely granular, occupying half of the frontal area, opesia trifoliate with two small oral spines (D = 12 μ m) placed distally (Fig. 44). Autozooids in zone of early astogeny transitional in size and morphology between ancestrula and later autozooids (Fig. 43). Autozooids small, rounded hexagonal or oval, longer than broad (mean L/W = 1.27), separated by deep furrows. Gymnocyst narrow, slightly broader proximally. Cryptocyst extensive, coarsely and densely granular, depressed centrally, submarginally raised to form a rounded ridge which together with distal rim of the opesia forms a pear-shaped outline on the frontal wall and around the opesia. Opesia strongly trifoliate, the proximal edge gently convex with rounded indentations at the proximolateral corners; a pair of rounded thick lateral denticles directed downwardly divide the larger, distal semicircular part of the opesia from the smaller but broader proximal part (Fig. 41). Oral spines numbering six, arranged in an arch around the distal edge of the opesia, the most proximal pair almost level with the denticles; distalmost pair of oral spines spaced more widely in ovicellate than non-ovicellate zooids. Complete ovicell not observed but that figured by Hayward & Ryland (1998, p. 197, fig. 58B) is hyperstomial, prominent, rounded and elongated, with a narrow, median triangular ectooecial window with thickened edges; a small rounded triangular kenozooid with a cryptocystal frontal area and a tiny central lacuna is present immediately distally of each ovicell (Fig. 41). Closure plates developed in some autozooids as distal extensions of the cryptocyst, with a small tuberculum located medially level with the proximal edge of the opesia, which is completely occluded (Fig. 40). Kenozooids of irregular shape frequently present along lateral margins of lobate colonies, slightly smaller (L = $258-291 \mu m$, W = 195–218 µm) than autozooids; gymnocyst narrow but wider than in autozooids; cryptocyst coarsely and densely granular, continuous over the entire frontal area except for a small, round, lacuna (mean $D = 25 \mu m$) near the centre (Fig. 42). Avicularia absent.



FIGURES 39–44. *Megapora ringens* (Busk, 1856), NHML 1911.10.1.631, Recent, Porcupine Bight. **39.** view of several autozooids and kenozooids, scale bar = $200 \,\mu\text{m}$; **40.** group of autozooids showing a closure plate and lateral, distolateral and distal pore windows, scale bar = $200 \,\mu\text{m}$; **41.** detail of the strongly trifoliate orifice with six oral spine bases and inner view of a broken ovicell with associated distal kenozooid, scale bar = $100 \,\mu\text{m}$; **42.** zooid and kenozooid at the colony growing edge, scale bar = $100 \,\mu\text{m}$; **43.** early astogeny, scale bar = $200 \,\mu\text{m}$; **44.** close-up of ancestrula, scale bar = $20 \,\mu\text{m}$.

Remarks. None of the material examined of this species had an intact ovicell; in all instances the roof of the ovicell was broken, revealing a floor consisting of an exterior skeletal wall with planar spherulitic microstructure delineating two lobes on either side of a median depression (Fig. 41). The presence of a small kenozooid distal of each ovicell, which is unique among the species described in this paper, recalls various other cheilostomes (e.g. Bishop & Househam 1987; Ostrovsky *et al.* 2008), and may signify evolutionary reduction of the zooid distal of the maternal zooid from an autozooid to a kenozooid.

Hayward & Ryland (1993) introduced the new genus *Apiophragma* for *M. hyalina* Waters, 1904, referring to the shape of the mural rim from the Greek *apios*, a pear and *phragma*, a wall. *Apiophragma* resembles *Megapora* in its depressed cryptocyst, thick mural rim and distal arc of spines but differs in having only a weakly trifoliate

opesia which is much smaller and narrowly bell-shaped, and the presence of opesiules. The inclusion of *Apiophragma* in the new family Pyrisinellidae should be considered after restudy of the type material of *A. hyalina*.

Distribution. Recent of boreal and arctic areas, widely distributed in the northeast Atlantic, extending southwards, in deep waters, as far as the Shetland Isles and Bergen, Norway (Hayward & Ryland 1998).

	N (colonies, zooids)	Mean	SD	Range
Zooid length	3, 30	414	39	367–489
Zooid width	3, 30	333	32	294–384
Orifice length	3, 15	100	13	82–116
Orifice width	3, 15	93	3	90–95
Ovicell length	2, 3	180	3	177–182
Ovicell width	2, 3	219	11	206-228

TABLE 6. Measurements (in µm) of Megapora ringens (Busk, 1856)

N, Number of colonies and number of zooids measured; SD, standard deviation.

Discussion

The species united here were previously assigned either to the large, paraphyletic, 'waste-bin' family Calloporidae, or doubtfully to Microporidae. Recognition of the new family Pyrisinellidae allows these species to be placed for the first time in a putative clade distinguished from other anascans by a combination of characters including: a frontal wall consisting of an extensive, depressed cryptocyst and a narrow marginal gymnocyst with a pear-shaped ridge (usually the mural rim) outlining the cryptocyst and opesia; a crescent of spine bases around the distal edge of the trifoliate or semicircular opesia; small zooid size; pore chambers, of which the distal one has a frontally facing window; an intrazooidal mode of budding; and hyperstomial ovicells resting on the gymnocyst of the distal zooid. Other characters present or absent include opesiules, avicularia, kenozooids, closure plates and intramural reparative buds. Assessing which of these characters are primitive and which are advanced awaits a phylogenetic analysis incorporating related taxa, a task beyond the scope of the current paper.

Evolutionary changes within Pyrisinellidae can be suggested based on the different geological ages of the five or six included species, along with comparisons with other anascans. The pyrisinellid species are distributed in time as follows: *Spinisinella zagorseki* (c. 93 Ma), *Pyrisinella meniscacantha* (c. 67 Ma), *Setosinella prolifica* (c. 57 Ma), *Setosinella orbiculata* (c. 35 Ma), *Setosinella perfluxa* (c. 14 Ma), and the questionably assigned Recent species *Megapora ringens*. Character suites of particular interest are the frontal wall/opesia complex and ovicells.

The two Cretaceous species (*Spinisinella zagorseki* and *Pyrisinella meniscacantha*), as well as the Recent *Megapora ringens*, have trifoliate opesia and lack opesiules. Parietal muscles that pull on the frontal membrane to raise hydrostatic pressure and extend the tentacles presumably pass through the rounded indentations at the proximolateral corners of the opesia. The three species of *Setosinella* from the Cenozoic have semielliptical opesia and opesiules, which can be interpreted as a more derived condition in which the parietal muscles pass through the separate openings provided by the opesiules. Other groups of anascans appear to have independently acquired opesiules, for example lunulitiforms such as *Discoporella* and *Selenaria* (Cook 1965; Cook & Chimonides 1985). Ristedt (1991) and Moyano (1994) described the evolution of more complete calcified coverings of the frontal surface of anascan zooids through development of the cryptocyst in a distal direction and the formation of opesiules, a morphoseries leading from taxa with a minor cryptocyst (as in *Amphiblestrum*), to the increasingly more protected condition seen in such opesiulate genera as *Micropora* and *Andreella*.

All pyrisinellids have hyperstomial ovicells resting on the proximal gymnocyst of the distal zooid and indenting its mural rim. In the oldest species, *Spinisinella zagorseki*, the ovicell has a primitive, spinose morphology. The ooecium of *S. zagorseki* was apparently constructed from two pairs of spines borne on the proximal gymnocyst of the distal zooid, possibly supplemented by the distalmost pair of oral spines of the maternal zooid (the spines themselves are broken-off). The ooecium would have been a loose, cage-like structure (cf. Ostrovsky & Taylor 2004, text-fig. 2B). Similar ovicells constructed of separated, basally articulated spines are known in the 'calloporid' *Distelopora* and the monoporellid *Stichomicropora*, both from the Late Cretaceous. The

frontal wall and opesial morphologies of the second of these genera are sufficiently similar to those of *Spinisinella* to suggest a close relationship. Younger pyrisinellids have more conventional ovicells with non-spinose ooecia. Evolutionary change from spinose to non-spinose ooecia appears to have occurred independently in 'calloporids', monoporellids and cribrimorphs (see Ostrovsky & Taylor 2005). Pyrisinellids provide a further example of this trend. The change from a spinose ooecium of the type found in *Spinisinella* to a non-spinose ooecium like that of *Pyrisinella* and younger pyrisinellids would have entailed: (1) reduction in spine number from four to two; (2) fusion of the basal articulations; (3) flattening of the two spines; and (4) lateral coalescence of the spines along the midline of the ooecium to form a hood-like structure. Subsequent changes in pyrisinellid ovicell morphology were comparatively minor. However, in the questionable pyrisinellid *Megapora ringens* the ovicell has an incompletely calcified ectooecium containing a triangular window (Hayward & Ryland 1998), and there is a small kenozooid distally of the ooecium which can be interpreted as the vestige of distal autozooid.

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