



Systematics of the Miocene–Recent bryozoan genus *Pentapora* (Cheilostomata)

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The four existing species of the ascophoran bryozoan *Pentapora* Fisher, 1807 are revised, and two new fossil species are introduced: *Pentapora lacryma* sp. nov. from the Pliocene Coralline Crag Formation of Suffolk, and *Pentapora clipeus* sp. nov. from the Pliocene of Emilia, Italy. The Arctic species *Pentapora boreale* Kuklinski & Hayward possesses a lyrula, does not belong in *Pentapora*, and is a junior synonym of *Raymondia rigida* (Lorenz). The morphology of the autozooids is relatively uniform within the genus, and the main distinguishing characters are those of the ovicells and, particularly, the giant avicularia that are developed sporadically in all species apart from *Pentapora foliacea*, popularly known as ‘Ross coral’. A phylogenetic analysis based on skeletal characters returned a single shortest tree in which the three species of *Pentapora* from the North Atlantic (*P. foliacea*, *Pentapora pertusa*, and *P. lacryma* sp. nov.) form a clade crownward of the three basal species from the Mediterranean (*Pentapora ottomulleriana*, *Pentapora fascialis*, and *P. clipeus* sp. nov.).

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ADDITIONAL KEYWORDS: evolution – morphology – new species – phylogeny – zooidal polymorphism.

INTRODUCTION

Among the first genera of bryozoans to be named was *Pentapora*, introduced by G. Fischer in 1807. For many years *Pentapora* remained neglected: most of the species now referred to it were assigned to *Eschara*, a ‘catch-all’ genus once used to accommodate diverse cheilostome bryozoans with erect, bifoliate colonies, or to the unrecognizable genus *Lepralia*. Despite problems over the taxonomies of both *Eschara* and *Lepralia*, *Pentapora* was not revived until 1968, when Hastings & Ryland chose a type species – *Millepora foliacea* Ellis & Solander, 1786 – and provided a diagnosis of the genus along with a comprehensive description of *Pentapora foliacea*.

Four recent and one fossil species have been assigned to *Pentapora*. They include *P. foliacea*, men-

tioned above, which is known colloquially as ‘Ross Coral’, and is the largest bryozoan in British waters, with colonies commonly reaching 40 cm in diameter. Johnston (1847: 351) even mentioned a colony seen by Mr Couch that measured seven feet, four inches (= 224 cm) in circumference. Colonies of another nominal species of *Pentapora*, *Pentapora fascialis* (Pallas, 1766), from the Mediterranean can attain a similar size, 70 cm in diameter (Cocito & Ferdeghini, 2001) in the Ligurian Sea, and up to 100 cm diameter in the Adriatic Sea (Cocito, Novosel & Novosel, 2004), and are significant bioconstructing organisms supporting a diverse associated biota (Cocito, 2004). There has been disagreement about whether *P. foliacea* and *P. fascialis* are separate species, with newer works (e.g. Hayward & Ryland, 1999) tending to regard *P. foliacea* as a junior synonym of *P. fascialis*. The geographical distribution of the *P. foliacea*–*P. fascialis* species complex at the present day extends

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discontinuously along the west coast of Britain, from the Hebrides in the north to the English Channel in the east, and thence southwards across the Bay of Biscay and along the Portuguese coast to Morocco, and on into the Mediterranean at least as far east as the Adriatic Sea (Gautier, 1962; Zabala, 1986; Hayward & Ryland, 1999). Another recent species of *Pentapora*, *Pentapora ottomulleriana* (Moll, 1803), also lives in the Mediterranean Sea. The fourth extant species assigned to *Pentapora* is *Pentapora boreale* Kuklinski & Hayward (2004), from Spitsbergen. Fossil examples of *Pentapora*, mostly referred to the extinct species *Pentapora pertusa* (Milne-Edwards, 1836), have been described from Europe and North Africa.

Pentapora is classified in the Bitectiporidae, a family of cheilostome bryozoans comprising 16 genera and ranging from the Eocene to recent times (Bock, 2006). Bitectiporids have autozooidal orifices with a narrow to broad sinus, and sometimes possess condyles and/or oral spines. The frontal shield is lepralioid with marginal areolar pores (Banta, 1977), and with or without pseudopores inwards of the margins of the zooids. Adventitious avicularia of normal size are occasionally replaced by giant avicularia (Hincks, 1880; Hayward & Ryland, 1999). Both layers of the ovicells are calcified but remain unfused (Carson, 1978), and the ectoecium contains one or more pores.

The purpose of this paper is to provide taxonomic redescriptions of all previously described species of *Pentapora*, and to introduce two new fossil species. As is customary for cheilostome bryozoans, the descriptions are based on skeletal morphology. This has the advantage of allowing the same characters to be used for both recent and fossil species. Phylogenetic relationships between the six recognized species of *Pentapora* are inferred.

MATERIAL AND METHODS

Recent specimens are housed in the zoological collections of the Natural History Museum, London (NHM). These include historical collections, plus material collected in the north-east Atlantic and Mediterranean by means of scuba diving during the past 6 years. The fossil *Pentapora* used for this study are housed in the palaeontological collections of the NHM. Some are from older collections but others were obtained from localities of the Pliocene Coralline Crag of Suffolk during August 2007, and the Pliocene of Monte Padova in Italy during May 2008. We have also examined material from Gallina, Reggio Calabria, collected by F. Toscano (Naples), and Monte Apa, Catania (A. Rosso Collection, Catania).

Soft parts of selected recent specimens were removed by bleaching with a hydrogen peroxide solution 40% m/v in water (130 volumes) and sodium hypochlorite (domestic bleach), according to the method advocated by Toscano (2008). Fragments of some of the fossils were soaked in liquid sodium hypochlorite to remove modern organic contaminants, and were then washed thoroughly in water. Both fossil and recent samples were air-dried and examined uncoated in a LEO 1455-VP low-vacuum SEM at the NHM.

Measurements of zooidal skeletal characters were made from SEM images using Image.Net® (Hesp Technology Software). Lengths and widths of autozooids and their primary orifices were measured, and, when present, ovicells and normal and giant avicularia were also measured, including crossbar and avicularium orifice sizes. For each dimension, the range, mean \pm standard deviation, and number of measurements are given.

Phylogenetic analysis was undertaken using PAUP 4.0 software, as described below.

SYSTEMATICS

FAMILY BITECTIPORIDAE MACGILLIVRAY, 1895

GENUS *PENTAPORA* FISCHER, 1807

Type species: Millepora foliacea Ellis & Solander, 1786. Subsequent designation by Hastings & Ryland (1968).

Revised diagnosis: Colony multiserial, encrusting unilamellar or multilamellar, or more often attached by an encrusting base, but developing erect bifoliate branches to form a domed meandriiform structure comprising anastomosed and folded laminae (eschariform), or a bushy colony with strap-like bifurcating branches (adeoniform). Colour white or pale orange in encrusting species, deep orange in erect species, fading to pale after death; embryos and larvae pale in colour.

Autozooids oval to rectangular or rounded hexagonal, arranged quincuncially. Frontal shield lepralioid, flat or slightly convex, initially finely granular but becoming rugose, wrinkled, or knobbly as a result of secondary calcification; evenly porous, with marginal areolar pores and central pseudopores of similar size, deepening and often becoming obscured by secondary calcification. Interzooidal boundary walls salient in young zooids, often covered by secondary calcification in older zooids. Orifice longer than wide, rectangular to semi-elliptical with the proximal margin straight, slightly concave, or convex, and bearing a small mucro; oral spines absent or present, typically lost or overgrown during late ontogeny; lappets (lateral pro-

longations of the orificial rim) variably developed, when pronounced producing trifoliate secondary orifice. Condyles present, typically small and downwardly curved, dividing the primary orifice into a large anter and a smaller poster. Operculum pale brown, translucent, with marginal sclerites. Short median septum developed on basal walls at proximal ends of zooids in all but one species. Multiporous septula present in lateral and transverse vertical walls. Ovicell hyperstomial, as wide as long, usually globose or flat; closed by the operculum; porous, either a single central pore or multiple pores scattered over surface of oecium, or arranged in an arc above orifice, enveloped by secondary calcification in most species; lappets generally better developed in fertile zooids, occasionally forming a complete bridge above the orifice.

Avicularia adventitious, suboral, not present on all zooids; placed on the umbo, directed proximally, varying from acute to almost normal to the frontal plane; rostrum rounded, crossbar calcified. Normal-sized avicularia occasionally replaced by giant avicularia with spatulate or subtriangular rostrum, crossbar uncalcified or calcified with or without a columella, occasionally covered by closure plate.

Remarks: *Pentapora* was introduced by Fisher (1807) to replace *Eschara sensu* Lamarck, 1801 non Linnaeus, 1758. Fisher included four species in his new genus: *Millepora foliacea* Ellis & Solander, 1786, *Millepora taenialis* Ellis & Solander, 1786, *Millepora cervicornis* Ellis & Solander, 1786, and *Pentapora tubulata* sp. nov. The genus was then neglected for more than 150 years. For example, *Pentapora* is not mentioned in three standard compilations of bryozoan names (Jelly, 1889; Bassler, 1935, 1953). It was left to Hastings & Ryland (1968) to revive *Pentapora*, and to

select *M. foliacea* as the type species. According to these authors, *M. taenialis* is a variety of the type species, *P. tubulata* is unrecognizable, and *M. cervicornis* belongs in either *Porella* or *Smittina*.

PENTAPORA FOLIACEA (ELLIS & SOLANDER, 1786)
(FIGS 1A, 2, 3)

Millepora foliacea: Ellis & Solander, 1786: 133.

Pentapora foliacea: Fischer, 1807: 307; Hastings & Ryland, 1968: 506 (part), Figure 1A–D, F–M; Hayward & Ryland, 1979: 94 (part), figs 32, 33A; ?Bishop, 1987: 13, figs 22–25.

Eschara foliacea Lamarck, 1801: 375; Milne-Edwards, 1836: 34–38, pl. 3, fig. 1; Busk, 1854: 89.

?*Eschara bidentata* Milne-Edwards, 1836: 38, pl. 3, figs 2, 2a.

Eschara foliacea: Johnston, 1847: 350, pl. 67, figs 1–5.

Lepralia foliacea: Hincks, 1879: 159; Hincks, 1880: 300, pl. 31, fig. 3, pl. 47, figs 1–4; Waters, 1879: 124, pl. 15, fig. 8; Jelly, 1889: 127; Waters, 1891: 273, pl. 29, figs 1–3; Calvet, 1900: pl. 13, fig. 20; Waters, 1925: 657, pl. 36, fig. 5.

Hippodiplosia foliacea: ?Canu & Bassler, 1925: 31, pl. 7, figs 8–9; ?Canu & Bassler, 1928: 34, pl. 3, fig. 11; Canu & Bassler, 1930: 50, pl. 6, figs 1–2; Balavoine, 1956: 35, pl. 1, figs 1–6, pls 2, 3.

?*Hippodiplosia otto-mulleriana*: Lagaaij, 1952: 80, pl. 7, figs 5, 6.

Pentapora fascialis: Hayward & Ryland, 1999: 200 (part), figs 79, 80A, 81A–B.

Material examined: NHM 1897.5.1.813, Portugal, Bracebridge Wilson Collection. NHM 1897.5.1.812, 1897.5.1.815, Hastings, Kent. 99.5.1.808, Isle of Man, Hincks Collection. NHM 99.7.1.1415, Lisbon, Busk

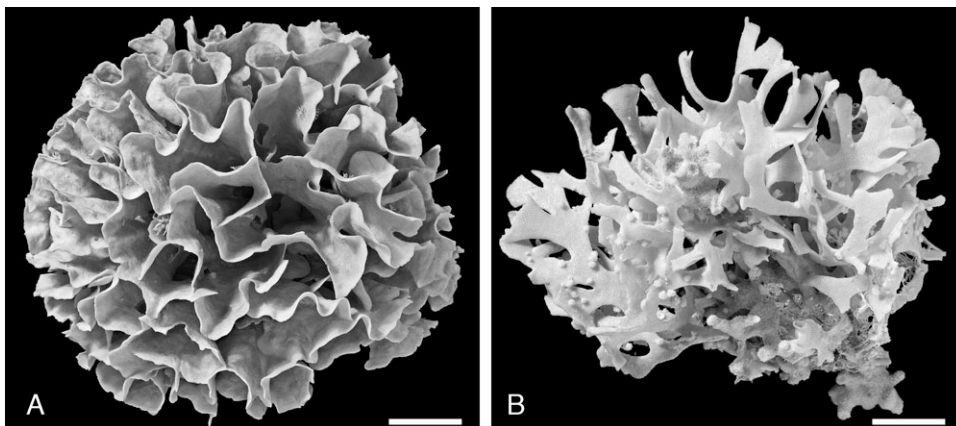


Figure 1. Large colonies of the cheilostome bryozoan *Pentapora*. A, eschariform colony of *Pentapora foliacea* (Ellis & Solander, 1786), British waters, NHM 2009.1.28.3. B, adeoniform colony of *Pentapora fascialis* (Pallas, 1766), NHM 2001.1.25.4, near Marseille. Scale bars: A = 4 cm; B = 2 cm.

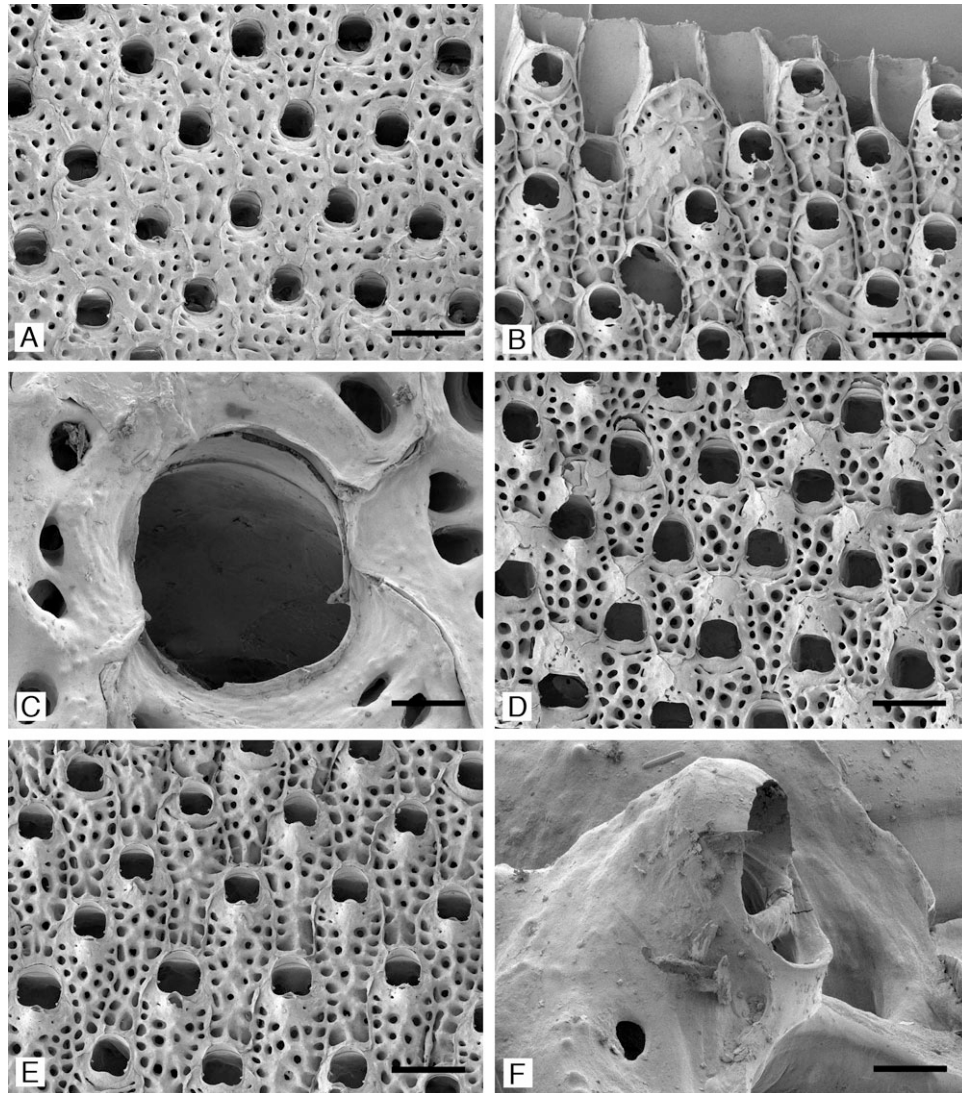


Figure 2. *Pentapora foliacea* (Ellis & Solander, 1786), Skomer Nature Reserve, Watwick, Dyfed, Wales, NHM 2007.9.14.5; scanning electron micrographs of coated specimens imaged using secondary electrons. A, old autozooids. B, growing edge and a kenozooid (left of centre). C, primary orifice. D, ovicellate zooids. E, autozooids, many with small suboral avicularia. F, oblique profile of suboral avicularium. Scale bars: A, B = 0.4 mm; C = 150 μ m; D, E = 0.4 mm; F = 40 μ m.

Collection. NHM 99.7.1.4903, Weymouth, Busk Collection. NHM 99.7.1.1418, Dartmouth, Busk ex Forbes Collection. NHM 11.10.1.1566, Guernsey, 1865. NHM 11.10.1.1561, Cornwall. NHM 11.10.1.1566, Guernsey, Norman Collection, 1865. NHM 11.10.1.1560, The Minch, Hebrides, Norman Collection, 1866. NHM 19.6.25.93, Guernsey, Norman Collection. NHM 25.4.21.2, cable 10 miles north-west of Scilly Island, 40 fathoms, Wilson Collection. NHM 1964.4.8.1, 2 miles off Gull Rock, Portscatho, Cornwall, 20 fathoms, Nicholas & Lane Collection. NHM 1965.8.20.20, La Chapelle Bank. NHM 1967.8.5.1, Martin's Haven, Pembrokeshire, illustrated by Hastings & Ryland

(1968, Fig. 1A–D, F–M). NHM 1967.8.5.1, Martin's Haven, Pembrokeshire, 18 m, 1958. NHM 1975.7.18.2, Herm, Channel Islands, Lagaaij Collection, 1973. NHM 1985.1.10.54, Boreray, St Kilda, Hayward Collection, July 1979. NHM 1997.9.24.2, off Eddystone Light, 60 m, Tilbrook Collection, May 1994. NHM 2009.1.28.1, growing on French Atlantic Cable, 60 miles west of Brest, 60–70 fathoms, Manger Collection. NHM 2009.1.28.2, ~8 miles south of Littlehampton, Sussex, 20 m, Mitchell Collection, November 2001. NHM 2007.9.14.2, Persier Reef, Devon, 50°17.107'N, 3°58.056'W, 24 m, Lombardi & Hiscock Collection, August 2005. NHM 2007.9.14.4, Skomer Nature

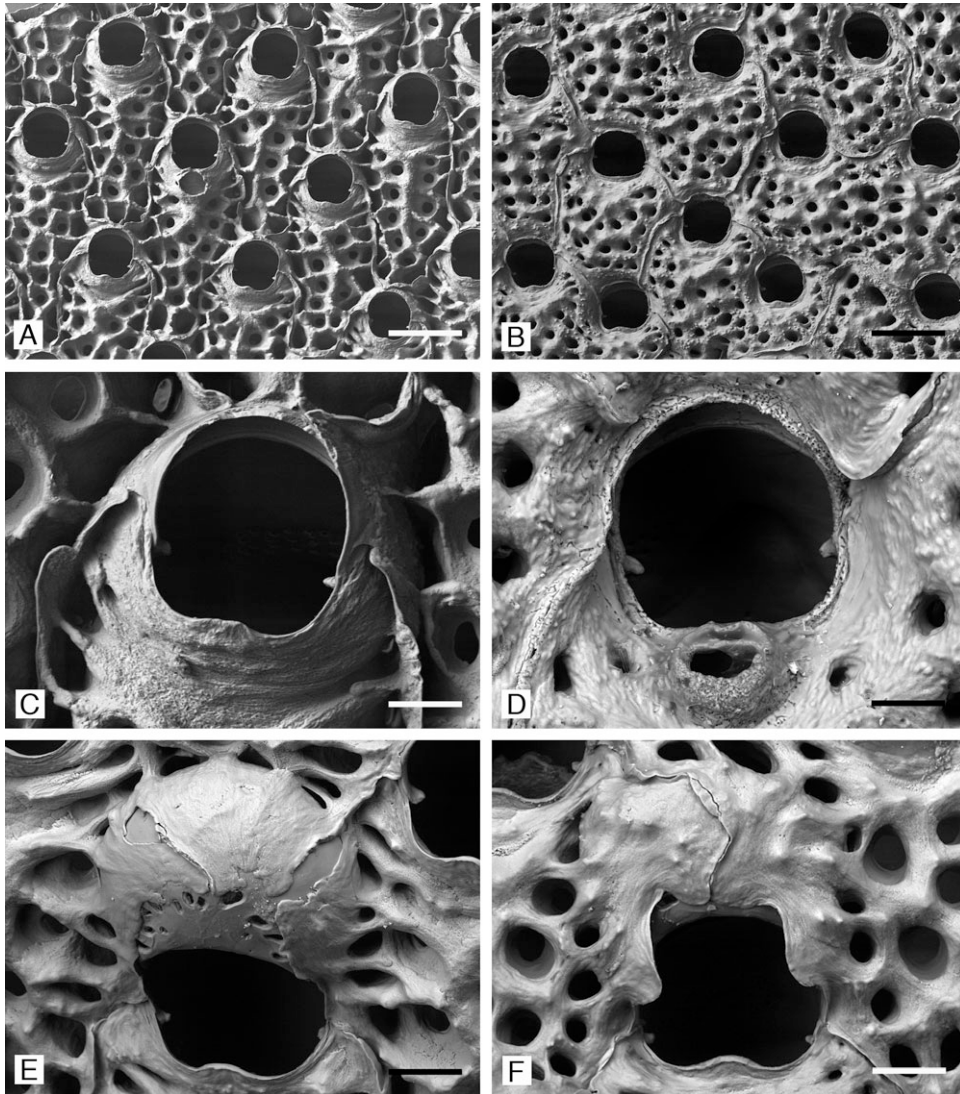


Figure 3. *Pentapora foliacea* (Ellis & Solander, 1786); scanning electron micrographs of uncoated specimens imaged using back-scattered electrons. A–C, NHM 2009.1.28.2, Littlehampton, Sussex, England. A, young autozooids close to growing edge. B, older autozooids. C, primary orifice of a young autozooid. D, primary orifice, Boreray, St Kilda, Scotland, NHM 1985.1.10.54. E–F, Persier Reef, Plymouth, Devon, England, NHM 2007.9.14.2. E, young ovicell. F, older ovicell embedded in secondary calcification. Scale bars: A = 290 µm; B = 180 µm; C, D = 60 µm; E, F = 100 µm.

Reserve, Watwick, Dyfed, Wales, 51°41.736'N, 5°8.989'W, Lombardi Collection, August 2006. NHM 2007.9.14.5, Bardsey Island, North Wales, 54°45.095'N, 4°47.260'W, Tompsett Collection. NHM 2007.9.14.13, Flat Ledges, Scilly Islands, 49°58.035'N, 6°15.215'W, Porter Collection, May 2007. NHM 2009.1.28.1, British waters, no details.

Revised diagnosis: *Pentapora* with foliaceous, box-like colonies; autozooids large, averaging 0.81-mm long by 0.36-mm wide; avicularia monomorphic, small; ovicell with pores in a band close to orifice.

Description: Colonies developing three-dimensional, box-like growths comprising folded and anastomosing bilamellar plates from an extensive encrusting base. Early astogeny unknown.

Autozooids longer than wide, 0.67–0.93 mm long (mean 0.81 ± 0.09 mm; $N = 20$) by 0.28–0.44 mm wide (mean 0.36 ± 0.04 mm; $N = 20$), roughly rectangular in shape, initially elongate, but becoming more equidimensional during ontogeny (Hayward & Ryland, 1999); arranged quincuncially; zooidal boundary walls salient. Frontal shield lepralioid, granular, with areolar pores and pseudopores, both becoming less

distinct through wall thickening during ontogeny, which also obscures zooidal boundaries. Primary orifice 0.11–0.20 mm long (mean 0.18 ± 0.02 mm; $N = 15$) by 0.16–0.19 mm wide (mean 0.18 ± 0.01 mm; $N = 15$), a pair of downturned condyles between anter and poster; secondary orifice slightly oval to trifoliate because of the development of lappets. Operculum brown, lustrous. No oral spines. Basal walls with short median septum extending distally from transverse wall (Fig. 2B, marginal zooids). Multiporous septula in lateral and transverse vertical walls near their bases; circular to ovoidal shallow muscle impressions may be visible close to septula. Ovicell elliptical, wider than long, 0.21–0.25 mm long (mean 0.23 ± 0.01 mm; $N = 20$) by 0.27–0.35 mm wide (mean 0.31 ± 0.02 mm; $N = 20$), a few scattered pores arranged in a band proximally above orifice, becoming overgrown by secondary calcification.

Avicularia monomorphic, adventitious, suboral, usually placed on an umbo, inconspicuous, small, longer than wide, 0.09–0.11 mm long (mean 0.100 ± 0.005 mm; $N = 10$) by 0.08–0.10 mm wide (0.090 ± 0.007 mm; $N = 10$); rostrum semielliptical; orifice 0.050 ± 0.005 mm long by 0.030 ± 0.004 mm wide; crossbar averaging 0.060 ± 0.008 mm long. Giant avicularia not observed, presumed lacking.

Remarks: The neotype specimen of *M. foliacea* Ellis & Solander, 1786, reputedly present in the NHM collections, was actually destroyed at the Royal College of Surgeons during World War II (M. Spencer Jones, pers. comm.). Neither an illustration of *M. foliacea* nor a type locality were given by Ellis & Solander, but they reported that the species was distributed commonly around the British coast, citing Ellis (1755) and Linnaeus (1758). Ellis (1755, pl. 30, figs a, A–C) illustrated the species from the Isle of Wight, prompting Hastings & Ryland (1968) to choose this illustration as the lectotype of *P. foliacea*.

The large and striking colonies of *P. foliacea* have long attracted the attention of naturalists, and are a familiar sight to divers around the west and south coasts of Britain today (Fig. 1A). As noted above, the relationships between this Atlantic species and the Mediterranean *P. fascialis* are uncertain: some authors have regarded them as distinct species, whereas others have considered them to be synonyms. The final answer may depend on molecular analysis. For the purpose of the present paper, *P. foliacea* and *P. fascialis* are described separately. Apart from their provenance, the typically bifurcating branches of *P. fascialis* and the presence of giant avicularia are the best means of differentiating between the two species. In addition, the secondary thickening of the frontal shield is generally greater in *P. fascialis* than in *P. foliacea* (Figs 2A, 3B). As pointed out by Hayward &

Ryland (1979), *Eschara bidentata* Milne-Edwards, 1836, is an ontogenetic variety of *P. foliacea* in which the lappets are particularly well developed.

Pliocene fossils from the Scaldisian (late Zanclean to Piacenzian) of Wilmarsdonk, Belgium, lacking giant avicularia, and assigned by Lagaaij (1952) to *Hippodiplosia ottomulleriana* (Moll) (see below), were reidentified as *P. foliacea* by Bishop (1987). This identification is provisionally accepted here, although it should be noted that the small fragments available for study raise the possibility of giant avicularia being present but remaining undetected in this population of *Pentapora*.

Distribution: Recent: north-eastern Atlantic from St Kilda in the north to the coast of Morocco in the south, including the English Channel as far east as Hastings; Mediterranean occurrences, which are seldom adequately described in the literature, require reassessment in view of the close similarities between *P. foliacea* and *P. fascialis*. Fossil: questionably, Pliocene (late Zanclean–Piacenzian), Belgium (Bishop, 1987).

PENTAPORA FASCIALIS (PALLAS, 1766)
(FIGS 1B, 4–6)

Eschara fascialis: Pallas, 1766: 42.

Eschara foliacea Milne-Edwards, 1836: 34, pl. 3, fig. 1; Manzoni, 1870: 18, pl. 4, fig. 4; Manzoni, 1876, pl. 5, fig. 6.

Lepralia foliacea Hincks, 1879: 159; Hincks, 1880: 300, pl. 47, figs 1–4; Waters, 1879: 124, pl. 15, fig. 8; Waters, 1891: 273, pl. 19, figs 1–3; Calvet, 1900: pl. 13, fig. 20; Waters, 1925: 657, pl. 36, fig. 5.

Hippoporina foliacea Neviani, 1939: 51.

'*Hippodiplosia*' *fascialis* Gautier, 1952: 164.

Pentapora foliacea Hastings & Ryland, 1968: 506 (part), fig. 1E only; Hayward & Ryland, 1979: fig. 33B.

Pentapora fascialis Zabala, 1986: 401, fig. 132; Zabala & Maluquer, 1988: 115, figs 238–239, pl. 8, fig. E; Hayward & Ryland, 1999: 200 (part), fig. 80B only; Hayward & McKinney, 2002: 53, fig. 25A–E.

Pentapora fascialis fascialis Chimenz, Rosso & Balduzzi, 2005: 5.

Material: Recent: NHM 34.2.20.15, Port Western, South Australia, Busk Collection. NHM 1879.4.25.2, Naples, Italy, Waters Collection. NHM 79.4.25.53, 97.5.1.864, Naples, Waters Collection. NHM 96.12.2.2, Marseille, Vayssière Collection. NHM 99.7.1.1417, 99.7.1.4907, coast of Spain, Busk Collection. NHM 99.7.1.29, Mediterranean, Busk Collection. NHM 1963.9.4.8, Oran, Algeria, 54 fathoms, Waters-O'Donoghue Collection. NHM 1965.9.2.21, Station 228, Mediterranean, Gautier Collection. NHM

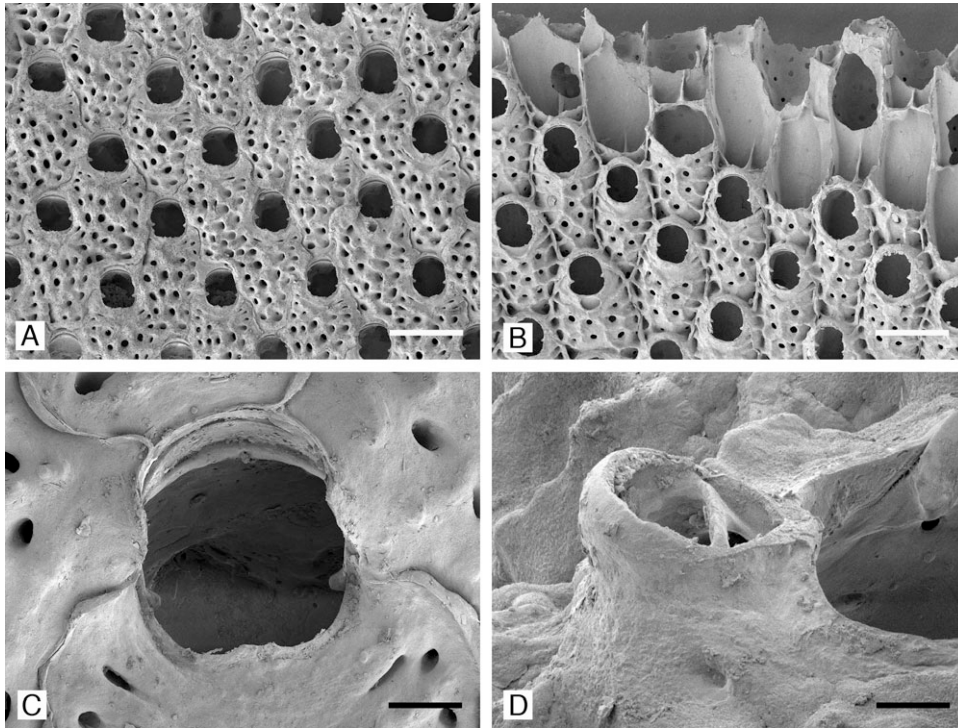


Figure 4. *Pentapora fascialis* (Pallas, 1766), Tino Island, Italy, NHM 2007.9.14.14; scanning electron micrographs of coated specimens imaged using secondary electrons. A, autozooids. B, growing edge. C, primary orifice. D, oblique profile of normal suboral avicularium. Scale bars: A = 0.5 mm; B = 0.4 mm; C = 100 μ m; D = 0.5 mm.

2001.1.25.4, near Marseille, Warren Collection, 1975. NHM 1975.1.12.384, Emborios Cave, Chios, Greece, 50 feet, Hayward Collection, August 1967. NHM 2007.9.14.14, Tino Island, Italy, 44°17.68'N, 9°50.88'E, Lombardi & Cocito Collection, July 2007.

Fossil: NHM BZ 5664-8, Pliocene, Emilian, Gillima, Calabria, Italy, Toscano Collection. NHM BZ 5672-4, Middle Pliocene, Castell'Arquato, Piacenza, Emilia, Italy, Pizzaferrri Collection. NHM BZ 5669-71, Lower Pleistocene, Arda stream, Castell'Arquato, Piacenza, Emilia, Italy, Pizzaferrri Collection.

As far as can be ascertained (e.g. Kuklinski & Taylor, 2008), the type material of bryozoans described by Pallas (1766), including *Eschara fascialis*, has been lost.

Revised diagnosis: *Pentapora* with colonies of narrow, bifurcating branches; autozooids large, averaging 0.88 mm long by 0.42 mm wide, frontal shield thickly calcified; avicularia dimorphic, the giant avicularia spatulate; ovicell with a few scattered pores.

Description: Colonies developing erect, narrow, strap-like, bifurcating branches from an encrusting base. Early astogeny unknown.

Autozooids longer than wide, 0.68–1.28 mm long (mean 0.88 ± 0.13 mm; $N = 20$) by 0.32–0.54 mm wide

(mean 0.42 ± 0.05 mm; $N = 20$) in recent samples, 0.73–0.79 mm long (mean 0.75 ± 0.03 mm; $N = 20$) by 0.44–0.48 mm wide (mean 0.46 ± 0.02 mm; $N = 20$) in Pliocene fossils, roughly rectangular in shape, arranged quincuncially with distinct boundaries becoming obscured during later ontogeny. Frontal shield lepralioid, granular, with areolar pores and pseudopores, developing knobs as thickening increases during ontogeny. Primary orifice 0.17–0.25 mm long (mean 0.21 ± 0.02 mm; $N = 20$) by 0.14–0.21 mm wide (mean 0.18 ± 0.01 mm; $N = 20$) in recent material, 0.13–0.19 mm long (mean 0.17 ± 0.02 mm; $N = 20$) by 0.11–0.17 mm wide (mean 0.15 ± 0.02 mm; $N = 20$) in Pliocene fossils, a pair of downturned condyles between anter and poster; secondary orifice slightly oval to trifoliate, following the development of lappets. Operculum brown, lustrous. Oral spines lacking in recent material, but very occasionally observed lateral to the orifice in Pliocene fossils. Basal walls with short median septum extending distally from transverse wall. Multiporous septula present in lateral and transverse vertical walls. Ovicells globular or elliptical, wider than long, 0.19–0.25 mm long (mean 0.22 ± 0.01 mm; $N = 20$) by 0.24–0.35 mm wide (mean 0.32 ± 0.03 mm; $N = 20$) wide, pores few, scattered, becoming occluded by secondary calcification.

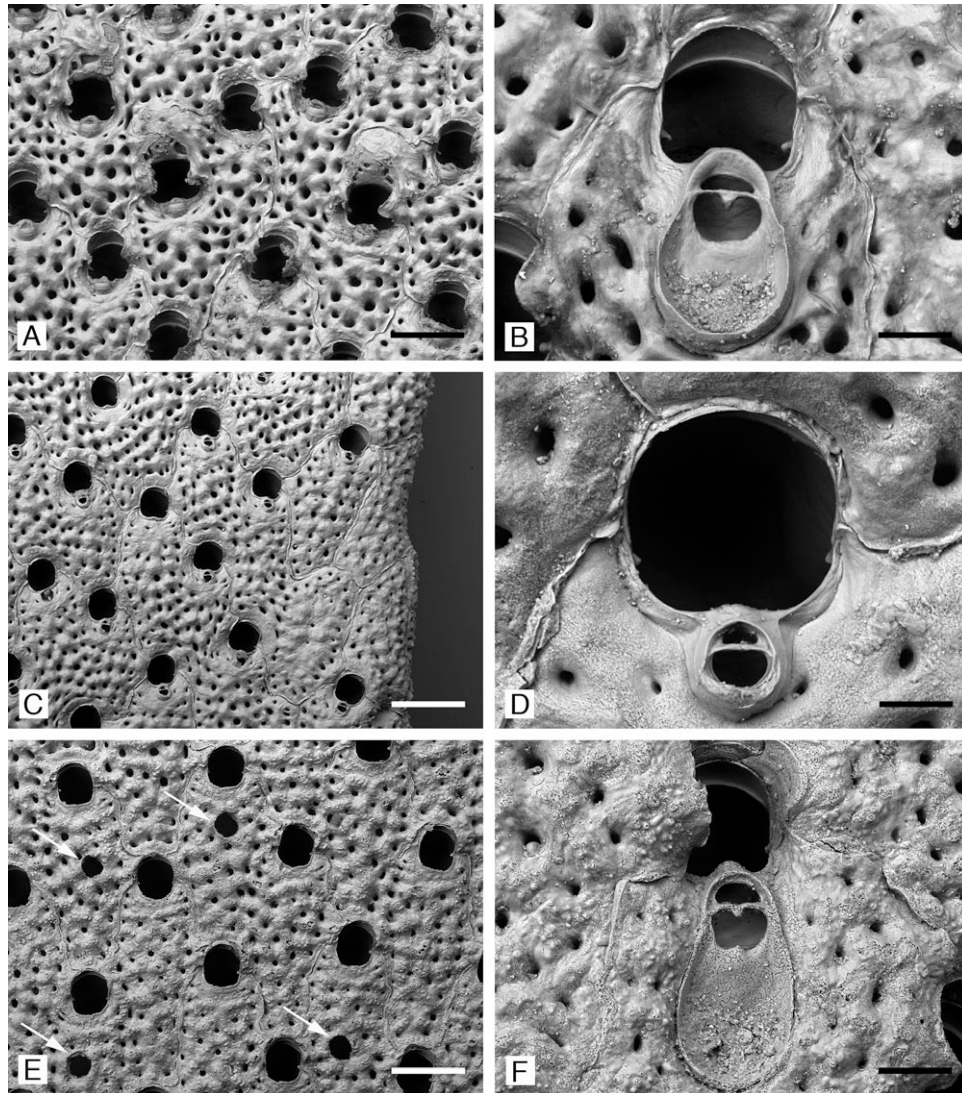


Figure 5. *Pentapora fascialis* (Pallas, 1766), scanning electron micrographs of uncoated recent specimens imaged using back-scattered electrons. A, B, Tino Island, Italy, NHM 2007.9.14.14. A, group of autozooids, some with ovicells. B, autozooidal orifice and giant suboral avicularium. C, D, Oran, Algeria, NHM 1963.9.4.8. C, edge of branch showing autozooids (most with normal suboral avicularia) and marginal kenozooids. D, orifice and normal suboral avicularium. E, F, reputedly from Port Western, South Australia, NHM 34.2.20.15. E, inferred predator boreholes (arrowed) in frontal shields. F, giant suboral avicularia. Scale bars: A = 280 μ m; B = 100 μ m; C = 470 μ m; D = 60 μ m; E = 300 μ m; F = 100 μ m.

Avicularia dimorphic, adventitious, suboral, proximally directed. Normal avicularia small, inclined at a high angle to frontal surface, longer than wide, 0.08–0.12 mm long (mean 0.09 ± 0.01 mm; $N = 10$) by 0.07–0.09 mm wide (mean 0.08 ± 0.003 mm; $N = 10$) in recent material, 0.08–0.11 mm long (mean 0.09 ± 0.01 mm; $N = 10$) by 0.07–0.09 mm wide (mean 0.08 ± 0.01 mm; $N = 10$) in Pliocene fossils; rostrum short, semielliptical; orifice 0.050 ± 0.005 mm long ($N = 10$) by 0.030 ± 0.007 mm wide ($N = 10$); crossbar

averaging 0.050 ± 0.004 mm long ($N = 10$). Giant avicularia occasionally replacing normal avicularia; longer than wide, 0.29–0.42 mm long (mean 0.34 ± 0.07 mm; $N = 5$) by 0.17–0.20 mm wide (mean 0.11 ± 0.01 mm; $N = 5$) in recent material, 0.26–0.41 mm long (mean 0.32 ± 0.05 mm; $N = 5$) by 0.13–0.23 mm wide (mean 0.18 ± 0.05 mm; $N = 5$) in Pliocene fossils; rostrum spatulate, palate deep; orifice 0.13 ± 0.04 mm long by 0.070 ± 0.001 mm wide ($N = 5$); crossbar averaging 0.110 ± 0.001 mm long ($N = 5$).

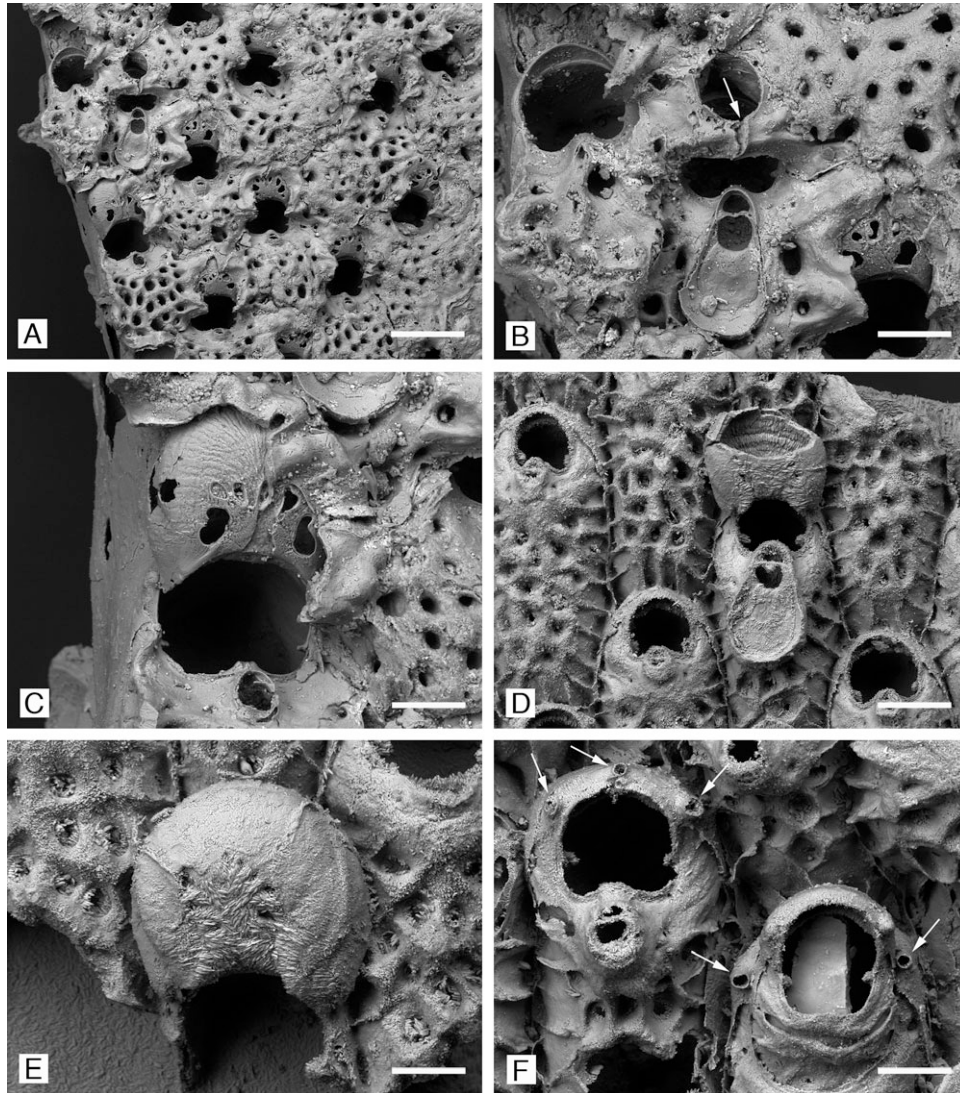


Figure 6. *Pentapora fascialis* (Pallas, 1766), scanning electron micrographs of uncoated fossil specimens imaged using backscattered electrons. A–C, Lower Pleistocene, Arda stream, Castell’Arquato, Piacenza, Emilia, Italy, NHM BZ 5669. A, colony fragment showing zooids with normal and giant avicularia, and ovicells overgrown by secondary calcification. B, giant avicularium in autozooid having primary orifice almost obscured by lappets forming a bridge. C, ovicell. D–F, Pliocene, Emilian, Gillina, Calabria, Italy. D, E, NHM BZ 5664. D, autozooids, showing normal avicularia and a giant avicularium, and a broken ovicell. E, ovicell. F, NHM BZ 5667. bases of oral spines (arrows). Scale bars: A = 300 μm ; B = 150 μm ; C, E = 120 μm ; D = 200 μm ; F = 110 μm .

Remarks: Autozooid morphology in the Mediterranean species *P. fascialis* is identical to the North Atlantic species *P. foliacea*, although frontal shield thickness can be greater in the former species. This has led many authors to regard them as synonyms. Although *P. foliacea* always constructs foliaceous colonies composed of broad fronds (eschariform) (Fig. 1A), colonies of *P. fascialis* typically comprise narrow, bifurcating, strap-like branches (adeoniform) (Fig. 1B). However, some populations of *P. fascialis* may also develop foliaceous colonies. Foliaceous and

strap-like branches are even occasionally present within single colonies (Cocito & Ferdeghini, 2000), suggesting ecophenotypic control of colony form. Indeed, Cocito & Ferdeghini (2000) studied a population from the Gulf of Spezia, in the Ligurian Sea, in which colonies growing in unidirectional flow regimes were foliaceous, whereas those in more turbulent habitats had broad laminae in the upstream parts of colonies, but narrow strap-like branches in downstream parts. On the other hand, giant avicularia have only ever been found in Mediterranean *P. fas-*

cialis (e.g. Fig. 5B); they are unreported from *P. foliacea* in the North Atlantic. Although the development of giant avicularia in *Pentapora* may also be under ecophenotypic control, such avicularia can be useful in discriminating between closely related cheilostome species (Lombardi *et al.*, 2008). Therefore, we here treat *P. fascialis* and *P. foliacea* as separate species pending the availability of molecular data. The cladistic analysis below offers some support for the distinction of *P. fascialis* and *P. foliacea*, in that they are separated by the Pliocene *Pentapora lacryma* sp. nov. in our phylogenetic analysis.

Hayward & McKinney (2002: 54) described the lophophores of Adriatic *P. fascialis* thus: 'Tentacles light orange, 17–19; lophophore bell-shaped, radially symmetrical away from colony edge, obliquely truncate along colony margins and locally (at chimneys?) on colony surface.'

Distribution: Recent: Mediterranean Sea, from the Strait of Gibraltar in the west to the Aegean in the east. Specimens (NHM 34.2.20.15) reputedly from South Australia exactly match the Mediterranean *P. fascialis* (Fig. 5E–F). If the provenance is correct, this represents a distant geographical outlier, likely to have resulted from an anthropogenic introduction of the species. Perhaps significantly, the South Australian material contains tiny inferred predator borings of a type not observed in Mediterranean populations, but like those known from Australian bryozoans belonging to other species (*P. Bock*, unpubl. data). Fossil: Middle Pliocene–Lower Pleistocene, Emilia and Calabria, Italy (Fig. 6A–F).

PENTAPORA OTTOMULLERIANA (MOLL, 1803) (FIG. 7)

Eschara otto-mulleriana: Moll, 1803: 60.

Lepralia pallasiana var. *projecta* Waters, 1878: pl. 1, fig. 17; Waters, 1879: 42, pl. 18, fig. 3; Jelly, 1889: 131; Calvet, 1902: 25.

Hippodiplosella spinosissima: Barroso, 1920: 7, text-fig.

Lepralia Otto Mulleriana Waters, 1923: 548, pl. 17, figs 1–2, 5–7; Waters, 1925: 539, pl. 29, fig. 20; Waters, 1926: 428, pl. 18, fig. 8.

Hippodiplosia granulosa: Canu & Bassler, 1925: 31, pl. 3, figs 2–3, pl. 7, figs 6–7.

Hippodiplosia otto-mulleriana Canu & Bassler, 1927: 35; Canu & Bassler, 1930: 49, pl. 6, figs 8–9.

Lepralia otto-mulleriana Calvet, 1927: 30.

Hippodiplosia ottomulleriana Gautier, 1962: 66.

Pentapora ottomulleriana Zabala, 1986: 403, fig. 133; Zabala & Maluquer, 1988: 115, fig. 237, pl. 8, figs F–G.

Material examined: NHM 99.7.1.1749, Mediterranean, Busk Collection. NHM 2007.9.14.16, on rhizomes of *Posidonia oceanica*, Monterosso al Mare,

Ligurian Sea, Italy, 44°08.30'N, 9°38.00'E, 10 m, 2001, Lombardi & Cocito Collection, 2001. Attempts to locate Moll's type material have been unsuccessful.

Revised diagnosis: *Pentapora* with encrusting colonies; autozooids moderately large, averaging 0.75 mm long by 0.48 mm wide, frontal shield knobby; avicularia monomorphic, large, spatulate; ovicell with numerous, evenly distributed pores.

Description: Colony encrusting, unilamellar. Early astogeny unknown.

Autozooids longer than wide, 0.58–0.97 mm long (mean 0.75 ± 0.05 mm; $N = 10$) by 0.37–0.61 mm wide (mean 0.48 ± 0.05 mm; $N = 10$), roughly rectangular in shape, arranged quincuncially with distinct zooidal boundaries, surface knobby. Primary orifice 0.24–0.29 mm long (mean 0.27 ± 0.01 mm; $N = 10$) by 0.17–0.22 mm wide (mean 0.2 ± 0.01 mm; $N = 10$); condyles present; oral spines numbering 4–9, placed all around the anter. Basal walls lacking median septum. Multiporous septula present in lateral and transverse vertical walls. Ovicells averaging 0.28–0.44 mm long (mean 0.34 ± 0.03 mm; $N = 10$) by 0.32–0.48 mm wide (mean 0.41 ± 0.03 mm; $N = 10$), periphery knobby, resembling a frontal shield; pores numerous, distributed more or less evenly, some elongate and aligned radially.

Avicularia adventitious, normally suboral, directed proximally, large (giant), 0.21–0.26 mm long (mean 0.24 ± 0.01 mm; $N = 5$) by 0.13–0.17 mm wide (mean 0.14 ± 0.01 mm; $N = 5$); rostrum spatulate; orifice 0.11 ± 0.01 mm long by 0.08 ± 0.01 mm wide ($N = 5$); crossbar calcified, averaging 0.09 ± 0.01 mm long ($N = 5$). Sporadic lateral avicularia, acute to the frontal plane, observed in some colonies from Croatia (M. Novosel Collection, Zagreb).

Remarks: Apart from having an exclusively encrusting colony form, *P. ottomulleriana* can be distinguished from the other species of the genus by the knobby frontal shield calcification and the numerous, basally articulated oral spines (Fig. 7A, D–F). Avicularia are monomorphic, and, judging by their large size and overall morphology (Fig. 7D, F), they are more likely to be homologous with the giant avicularia of other species of *Pentapora* than with the normal-sized avicularia.

Distribution: Mediterranean Sea, including Spain, France, Algeria, Tunisia, and Italy (Zabala, 1986); Croatia (M. Novosel, pers. comm., 2008).

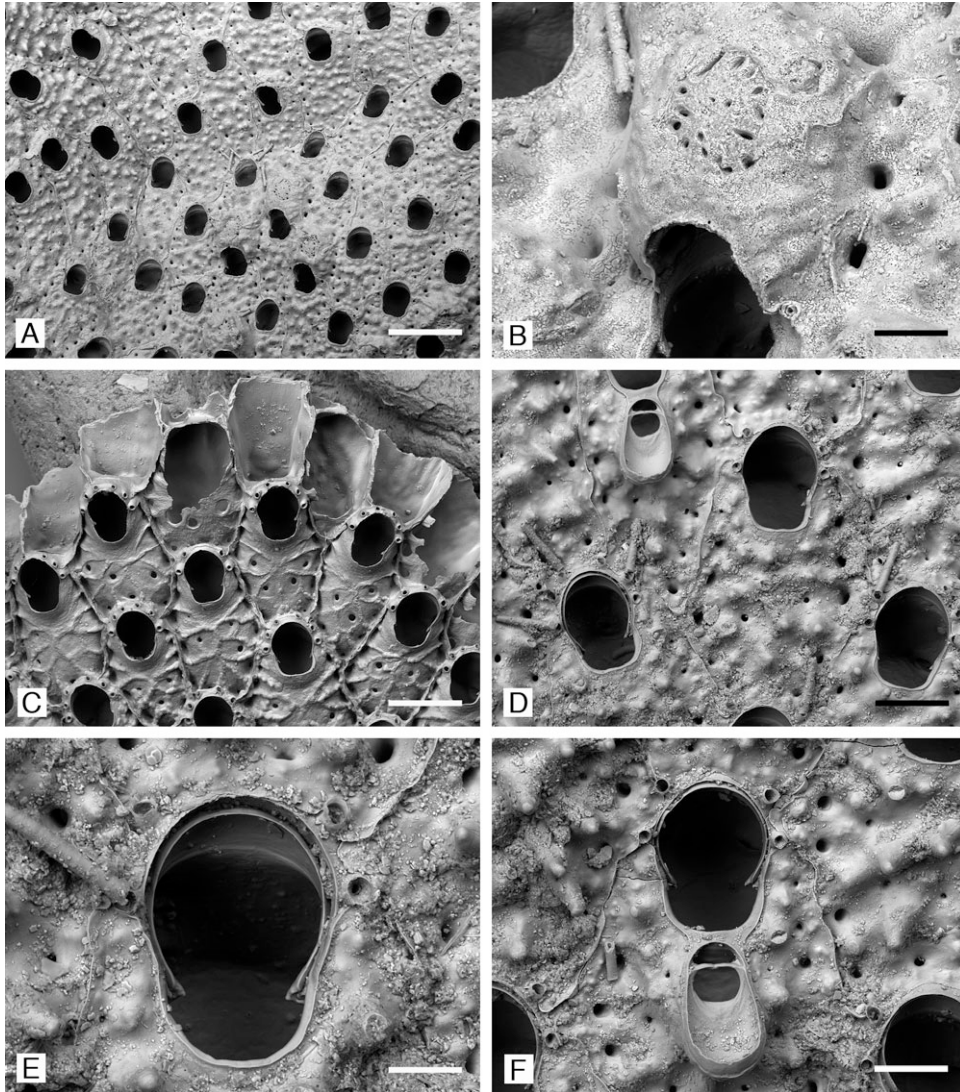


Figure 7. *Pentapora ottomulleriana* (Moll, 1803), Monterosso al Mare, Liguria, Italy, NHM 2007.9.14.16; scanning electron micrographs of uncoated specimens imaged using back-scattered electrons. A, autozooids. B, ovicell. C, young zooids at the growing edge. D, autozooids and an avicularium. E, primary orifice. F, avicularium. Scale bars: A = 600 μm ; B = 100 μm ; C = 350 μm ; D = 200 μm ; E = 75 μm ; F = 130 μm .

PENTAPORA PERTUSA (MILNE EDWARDS, 1836)
(FIG. 8)

Eschara pertusa: Milne Edwards, 1836: 9, pl. 10, figs 3, 3^o, 3b, 3c; Busk, 1859: 65 (part), pl. 10, figs 2a, 2a' only.

non *Eschara pertusa* Michelin, 1840: 330, pl. 79, fig. 2.

Material examined: NHM B1651, D37800-5, D55498, Pliocene, Coralline Crag Formation, Suffolk. NHM D34873-4, Coralline Crag Formation, Broom Pit, Reid Collection. NHM D51059, Coralline Crag Formation, Crag Pit Nursery (NGR 458580), Aldeburgh, Suffolk, Pitt Collection, 1967. NHM D50182, Coralline Crag

Formation, Broom Pit, Gedgrave, Suffolk, Burrows Collection. NHM BZ 5643, Coralline Crag Formation, Aldeburgh Mbr, Aldeburgh Hall, Suffolk, Wilson & Taylor Collection. NHM BZ 5644, Coralline Crag Formation, Broom Pit, Gedgrave, Suffolk, Wilson & Taylor Collection. NHM BZ 5645 (sample), Coralline Crag Formation, Sudbourne, Suffolk, Whiteley Collection. NHM BZ 5646 (sample), BZ 5647, Coralline Crag Formation, Crag Farm, Sudbourne, Suffolk, Whiteley Collection. NHM BZ 5676, Coralline Crag Formation, ?Ramsholt Member, Broom Pit, Gedgrave, Suffolk, Lombardi Collection, August 2007.

D'Hondt (2006: 29) listed the type of this species (as *Hippopleurifera pertusa*) as no. 4553 in the Milne

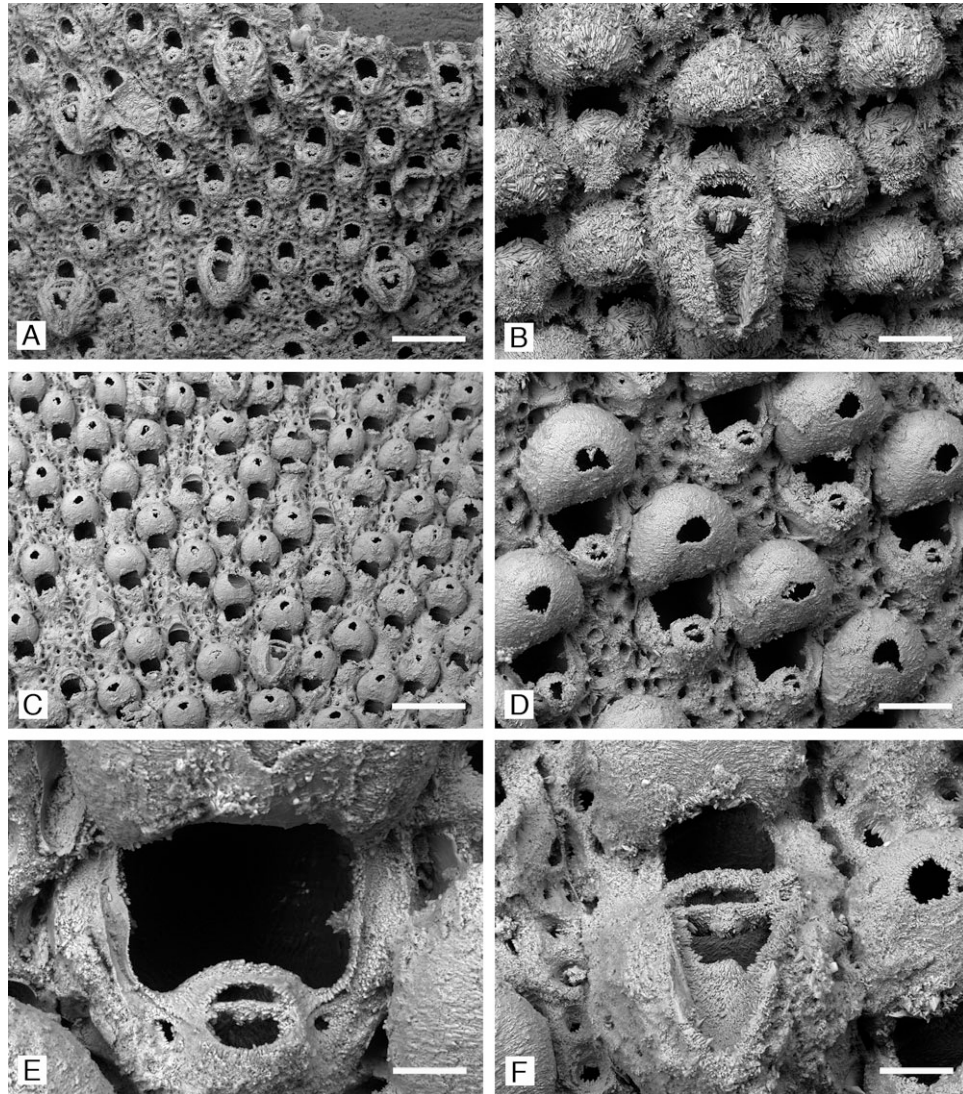


Figure 8. *Pentapora pertusa* (Milne Edwards, 1836), scanning electron micrographs of uncoated specimens from the Pliocene Coralline Crag Formation of Suffolk, England, imaged using back-scattered electrons. A, autozooids and several giant avicularia, Broom Pit, NHM D50182. B, ovicellate zooids and giant suboral avicularium with details obscured by diagenetic cement, Aldeburgh Member, Aldeburgh Hall, NHM BZ 5643. C–F, NHM BZ 5676, ?Ramsholt Member, Broom Pit. C, patch of colony dominated by ovicellate zooids. D, ovicells and normal suboral avicularia. E, orifice and normal suboral avicularium. F, giant triangular suboral avicularium. Scale bars: A = 280 μm ; B = 190 μm ; C = 520 μm ; D = 220 μm ; E = 60 μm ; F = 100 μm .

Edwards Collection of the Museum National d'Histoire Naturelle, Paris.

Revised diagnosis: *Pentapora* with erect, foliaceous colonies; autozooids large, averaging 0.81 mm long by 0.31 mm wide; avicularia dimorphic, the giant avicularia very large with triangular rostra; ovicell with a single central pore.

Description: Colonies developing three-dimensional, box-like growth comprising folded and anastomosing

bilamellar plates from an extensive encrusting base.

Autozooids longer than wide, 0.75–0.92 mm long (mean 0.81 ± 0.06 mm; $N = 10$) by 0.24–0.31 mm wide (mean 0.27 ± 0.03 mm; $N = 10$), roughly rectangular in shape. Frontal shield lepralioid, slightly convex, granular, with areolar pores and pseudopores. Primary orifice longer than wide, 0.11–0.21 mm long (mean 0.17 ± 0.03 mm; $N = 10$) by 0.11–0.19 mm wide (mean 0.16 ± 0.03 mm; $N = 10$); condyles present. No oral spines. Basal walls with short median septum

extending distally from transverse wall. Ovicells globular, slightly wider than long, averaging 0.24 ± 0.01 mm long by 0.31 ± 0.02 mm wide ($N = 10$), with one large central pore; not enveloped by secondary calcification.

Avicularia dimorphic, adventitious, suboral, proximally directed. Normal avicularia small, as long as wide, mean length and width 0.09 ± 0.01 mm ($N = 10$), located on a suboral umbo; crossbar calcified. Giant avicularia occasionally replacing normal avicularia, very large, 0.34–0.51-mm long (mean 0.42 ± 0.07 mm; $N = 10$) by 0.18–0.24-mm wide (mean 0.25 ± 0.04 mm; $N = 10$) wide, prominent, occupying more than half of the frontal shield; rostrum triangular, acute to the frontal plane, raised at distal end; palate long; crossbar with columella.

Remarks: Milne Edwards (1836, pl. 10, fig. 3C) depicted an example of one of the large and pointed giant avicularia that are characteristic of this species in his material from the [Coralline] Crag of Sudbourne, Suffolk. Thus it is clear that his description refers to *P. pertusa* rather than the sympatric *P. lacryma* sp. nov. (described below), in which the giant avicularia are smaller and spatulate. The uniporous ovicells (Fig. 8D) are another feature of *P. pertusa* enabling its distinction from *P. lacryma* sp. nov., and indeed all other species of *Pentapora*. References to this species without illustrations (e.g. Buge, 1957) are impossible to evaluate, as are putative examples lacking the diagnostic giant avicularia or uniporous ovicells (e.g. El Hajjaji, 1992; Pouyet & Moissette, 1992; Haddadi-Hamdane, 1996).

Most specimens of *P. pertusa* and the co-occurring *P. lacryma* sp. nov. from the Coralline Crag Formation of Suffolk come from shell limestones leached of aragonite (see Balson, 1983). Given that the frontal shields of recent *P. foliacea* and *P. fascialis* have a thick outer coating of aragonite that is added during late ontogeny (Taylor, Kudryavtsev & Schopf, 2008), the loss of this diagenetically unstable layer may have altered the appearance of the fossil colonies, as compared with the pristine skeleton. In particular, any lappets or secondary overgrowths of ovicells may not be preserved in aragonite-leached fossils of *Pentapora*.

Distribution: Pliocene, Late Zanclean–Early Piacenzian, Coralline Crag Formation, Aldeburgh, and Sudbourne members, questionably Ramsholt Member, Suffolk, UK.

***PENTAPORA LACRYMA* SP. NOV. (FIGS 9, 10)**

Eschara pertusa Milne-Edwards, 1836: Busk, 1859: 65 (part), pl. 10, figs 2a', 2b only.

Material examined: Holotype: NHM D50716, Coralline Crag Formation, Broom Hill, Suffolk, Burrows Collection. Paratypes: NHM BZ 5648-9, Pliocene, Coralline Crag Formation, Aldeburgh Member, Crag Pit Nursery, Aldeburgh, Suffolk, Bishop & Taylor Collection. NHM BZ 5677, Coralline Crag Formation, Aldeburgh Member, Aldeburgh Hall, Suffolk, Lombardi Collection, August 2007. NHM D50989, Coralline Crag Formation, Sudbourne Hall, Suffolk, Burrows Collection. NHM D50173-5, Coralline Crag Formation, Sudbourne Church, Suffolk, Burrows Collection. NHM D51060, Coralline Crag Formation, Crag Pit Nursery (NGR 458580), Aldeburgh, Suffolk, Pitt Collection, 1967. NHM D55497, Coralline Crag Fm., Sudbourne Park Gates, Suffolk, Vallentin Collection. Other material: NHM BZ 5240, Coralline Crag Formation, Sudbourne Member, Crag Farm Yard, Suffolk, Tilbrook Collection, presented 1997. NHM BZ 5650-1, Coralline Crag Formation, Aldeburgh Member, Aldeburgh Hall, Suffolk, Tilbrook Collection, May 1994. NHM BZ 5652, Coralline Crag Formation, Crag Pit Farm, Suffolk, Tilbrook Collection, presented 1997. NHM BZ 5653, Coralline Crag Formation, Aldeburgh Member, Aldeburgh, Suffolk, Taylor Collection. NHM BZ 5654-6 (samples), Coralline Crag Formation, Crag Farm, Sudbourne, Suffolk, Whiteley Collection. NHM BZ 5657, Coralline Crag Formation, Sudbourne Member, Sudbourne, Suffolk, Taylor Collection, 1999. NHM BZ 5658, Coralline Crag Formation, Crag Farm, Sudbourne, Suffolk, Pitt Collection. NHM BZ 5659, Coralline Crag Formation, Richmond Farm, Gedgrave, Suffolk, Pitt Collection. NHM D34979, two specimens (Fig. 10) questionably assigned to *P. lacryma* sp. nov., Pliocene, Red Crag Formation, Walton-on-Naze, Essex, Harmer Collection.

Diagnosis: *Pentapora* with erect foliaceous colonies; autozooids small, averaging 0.51-mm long by 0.27-mm wide; giant avicularia teardrop-shaped; ovicells with pores distributed over entire surface.

Description: Colonies developing three-dimensional, box-like growths comprising folded and anastomosing bilamellar plates from an extensive encrusting base that is often multilamellar. Diameter up to 12 cm (NHM BZ 5240). Early astogenetic stages with small-sized zooids; ancestrula not clearly identifiable.

Autozooids longer than wide, 0.37–0.69 mm long (mean 0.53 ± 0.03 mm; $N = 10$), 0.13–0.41 mm wide (mean 0.27 ± 0.02 mm; $N = 10$), roughly rectangular in shape. Frontal shield lepralioid, slightly convex, granular, with areolar pores and pseudopores. Primary orifice longer than wide, 0.14 ± 0.18 mm long (mean 0.15 ± 0.02 mm; $N = 5$) by 0.11 ± 0.18 mm wide (mean 0.13 ± 0.03 mm; $N = 5$); condyles present;

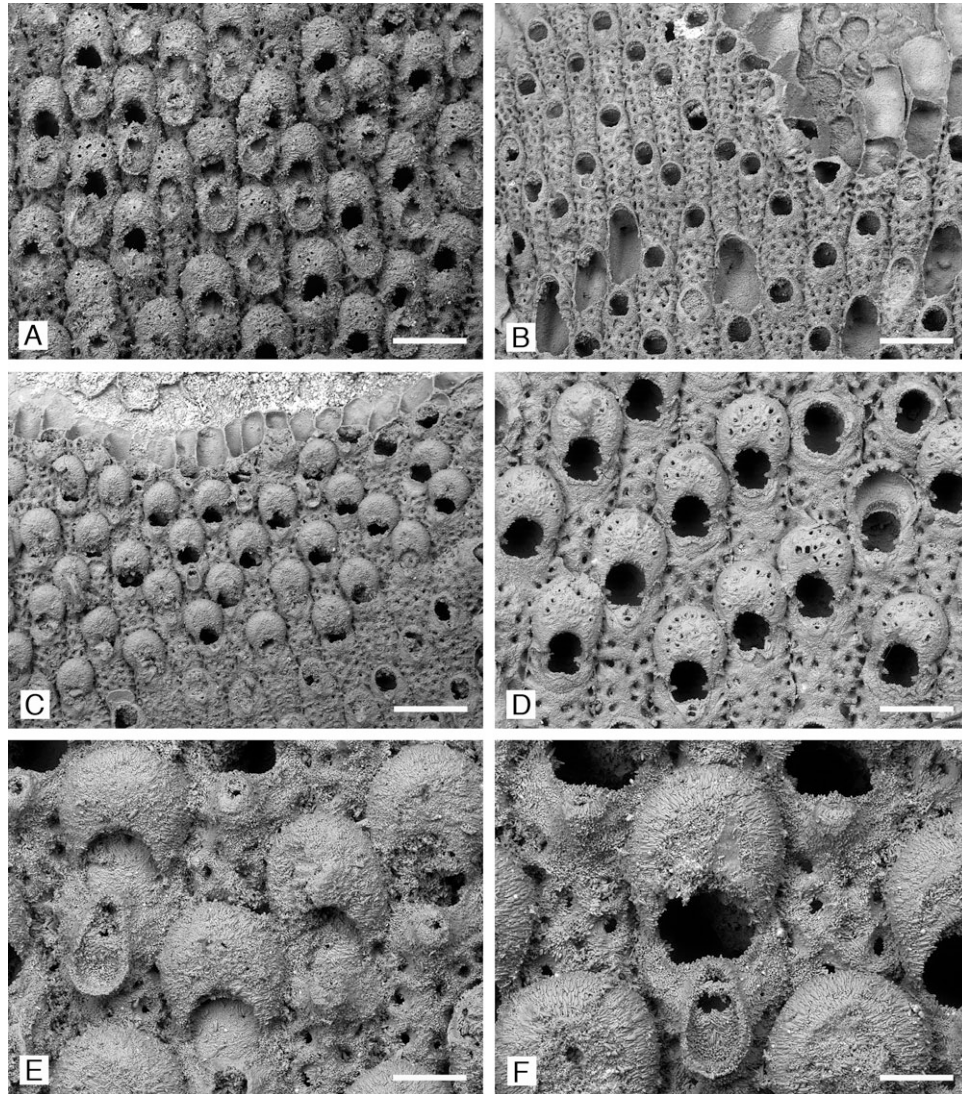


Figure 9. *Pentapora lacryma* sp. nov., scanning electron micrographs of uncoated specimens from the Pliocene Coralline Crag Formation of Suffolk, England, imaged using back-scattered electrons. A, ovicellate autozooids and giant avicularia partly obscured by diagenetic cement, Aldeburgh Member, Aldeburgh Hall, NHM BZ 5677. B, C, E, F, Aldeburgh Member, Crag Pit Nursery, Aldeburgh, NHM BZ 5648. B, autozooids from encrusting base. C, growing edge of encrusting base showing ovicellate zooids and a few giant avicularia. E, ovicellate zooids with closure plates and a giant avicularium (left). F, ovicell (pores obscured by diagenetic cement) and giant avicularium. D, holotype with ovicellate zooids showing evenly porous oecia, Broom Hill, NHM D50716. Scale bars: A = 55 μ m; B = 240 μ m; C = 520 μ m; D = 230 μ m; E = 150 μ m; F = 130 μ m.

lappets present; closure plates occasionally developed (Fig. 9E). Oral spines seemingly lacking (although spine bases may have been obscured by epitaxial cement). Basal walls with short median septum extending distally from transverse wall. Ovicells wider than long, 0.16–0.24 mm long (mean 0.19 ± 0.02 mm; $N = 20$) by 0.19–0.28 mm wide (mean 0.24 ± 0.02 mm; $N = 20$), not embedded in the frontal shield of the distal zooid or overgrown; pores numerous, scattered over entire surface.

Avicularia dimorphic, adventitious, suboral, proximally directed; crossbar calcified. Normal avicularia small, 0.07–0.11 mm long (mean 0.09 ± 0.02 mm; $N = 5$), 0.05–0.08 mm wide (mean 0.07 ± 0.01 mm; $N = 5$), placed on an umbo normal to the frontal plane. Giant avicularia sporadically replacing normal avicularia, 0.20–0.27 mm long (mean 0.24 ± 0.02 mm; $N = 15$), 0.11–0.18 mm wide (mean 0.16 ± 0.02 mm; $N = 15$); rostrum spatulate, teardrop shaped; palate deep, broad; crossbar with columella.

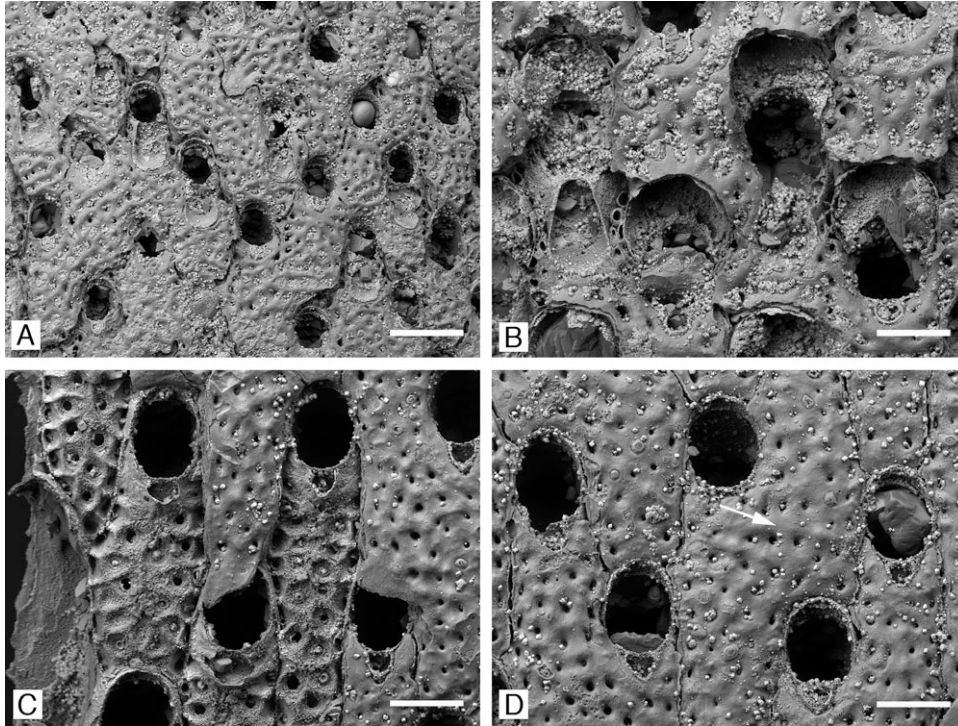


Figure 10. *?Pentapora lacryma* sp. nov., scanning electron micrographs of uncoated specimens from the Pliocene Red Crag Formation of Walton-on-Naze, Essex, England, imaged using back-scattered electrons. A, B, NHM D34979(a). A, autozooids and giant avicularia. B, broken ovicells and a giant avicularium (left). C, D, NHM D34979(b). C, autozooids with and without the outer aragonitic layer of the frontal shield. D, autozooid preserving the aragonite layer, sometimes merging across zooidal boundaries (arrow). Scale bars: A = 430 μ m; B = 210 μ m; C = 170 μ m; D = 160 μ m.

Etymology: The species name (Latin, *lacryma*, tear) alludes to the shape of the giant avicularia.

Remarks: Some of the specimens assigned by Busk (1859) to *Pentapora* [as *Eschara*] *pertusa* from the Coralline Crag Formation in fact belong to *P. lacryma* sp. nov. It differs from *P. pertusa* in having numerous small pores scattered over the entire surface of the ovicell (Fig. 9D), whereas *P. pertusa* has a single large medial pore (Fig. 8D). A second striking difference is evident in specimens possessing giant avicularia. These are relatively small and teardrop shaped in *P. lacryma* sp. nov. (Fig. 9A, D), but are large, prominent, and triangular in *P. pertusa* (Fig. 8B, F). Although fragments of *P. pertusa* and *P. lacryma* sp. nov. can be found together in the same pieces of limestone matrix, suggesting that the two species lived in close sympatry, individual colony fragments always seen to have ovicells and giant avicularia characteristic of one species or the other – transitional forms are lacking. The identification of non-ovicellate fragments without giant avicularia is, however, difficult, as noted above in the remarks for *P. pertusa*.

Distribution: Pliocene, Late Zanclean–Early Piacenzian, Coralline Crag Formation, Aldeburgh and Sudbourne members, questionably Ramsholt Member, Suffolk, UK and Red Crag Formation, Essex (note that many of the erect bryozoans in the Red Crag were derived and transported from the older Coralline Crag, which may be true of the specimens of *?P. lacryma* sp. nov. recorded here).

PENTAPORA CLIPEUS SP. NOV. (FIG. 11)

Material examined: Holotype: NHM BZ 5662, Middle Pliocene, Monte Padova (level 90), Castell'Arquato, Piacenza, Emilia, Italy, Pizzaferrri Collection. Paratype: NHM BZ 5663, details as for holotype.

Diagnosis: *Pentapora* with erect bifoliate colonies; autozooids small, averaging 0.55-mm long by 0.37-mm wide; giant avicularia spatulate, often with closure plate containing two pores, crossbar uncalcified; ovicell with pores in a band close to orifice.

Description: Colonies erect, bilamellar, represented only by small fragments. Base and early astogeny unknown.

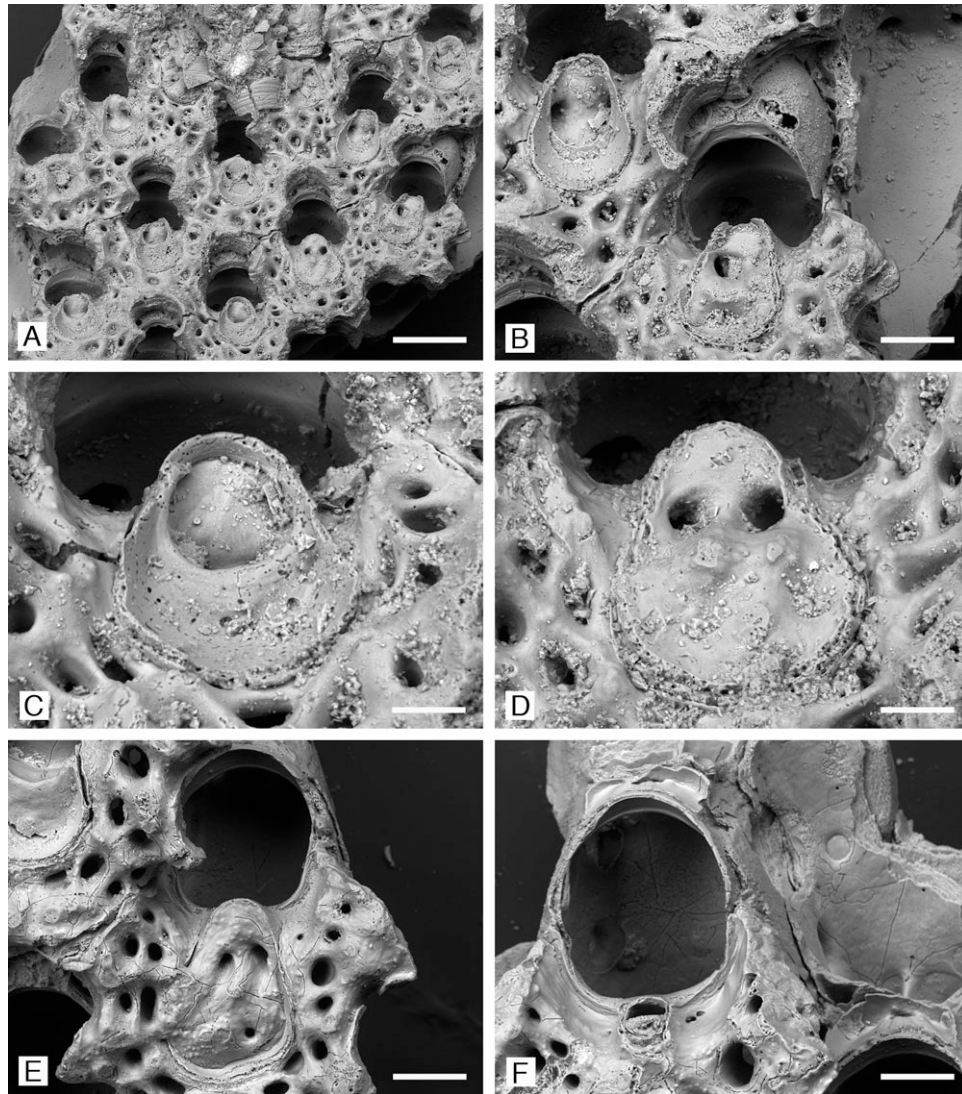


Figure 11. *Pentapora clipeus* sp. nov., scanning electron micrographs of uncoated specimens from the Middle Pliocene of Monte Padova, Castell'Arquato, Piacenza, Emilia, Italy, imaged using back-scattered electrons. A–D, holotype, NHM BZ 5662. A, colony fragment with zooids bearing giant avicularia. B, partly overgrown ovicell and two giant avicularia. C, giant avicularium; note the lack of a calcified crossbar. D, giant avicularium with closure plate containing two pores. E, paratype, NHM BZ 5663. E, orifice with left lappet preserved and giant avicularium with closure plate. F, primary orifice, normal suboral avicularium, and median septum and circular muscle impression visible on the basal wall of the broken zooid at the top left. Scale bars: A = 280 μ m; B = 100 μ m; D = 60 μ m; E = 50 μ m; F = 100 μ m.

Autozooids small, longer than wide, 0.48–0.60 mm long (mean 0.55 ± 0.06 mm; $N = 5$), 0.33–0.42 mm wide (mean 0.37 ± 0.04 mm; $N = 5$). Frontal shield lepralioid, slightly convex, granular, with areolar pores and pseudopores; zooidal boundaries becoming less distinct during ontogeny. Primary orifice slightly longer than wide, 0.18–0.25 mm long (mean 0.22 ± 0.03 mm; $N = 5$), 0.17–0.22 mm wide (mean 0.20 ± 0.02 mm; $N = 5$); condyles present; lappets sometimes developed. Oral spines often present but few in number. Basal walls with short median septum

extending distally from transverse wall. Ovicells globular, becoming completely embedded by calcification of the frontal shield of the distal zooid; pores present in a band close to the primary orifice.

Avicularia dimorphic, adventitious, suboral, proximally directed. Normal avicularia small, 0.07–0.08 mm long (mean 0.080 ± 0.005 mm; $N = 5$), 0.06–0.07 mm wide (mean 0.070 ± 0.006 mm; $N = 5$). Giant avicularia often substituting for normal avicularia, 0.17–0.27 mm long (mean 0.21 ± 0.03 mm; $N = 15$), 0.15–0.20 mm wide (0.17 ± 0.02 mm; $N = 15$), occupy-

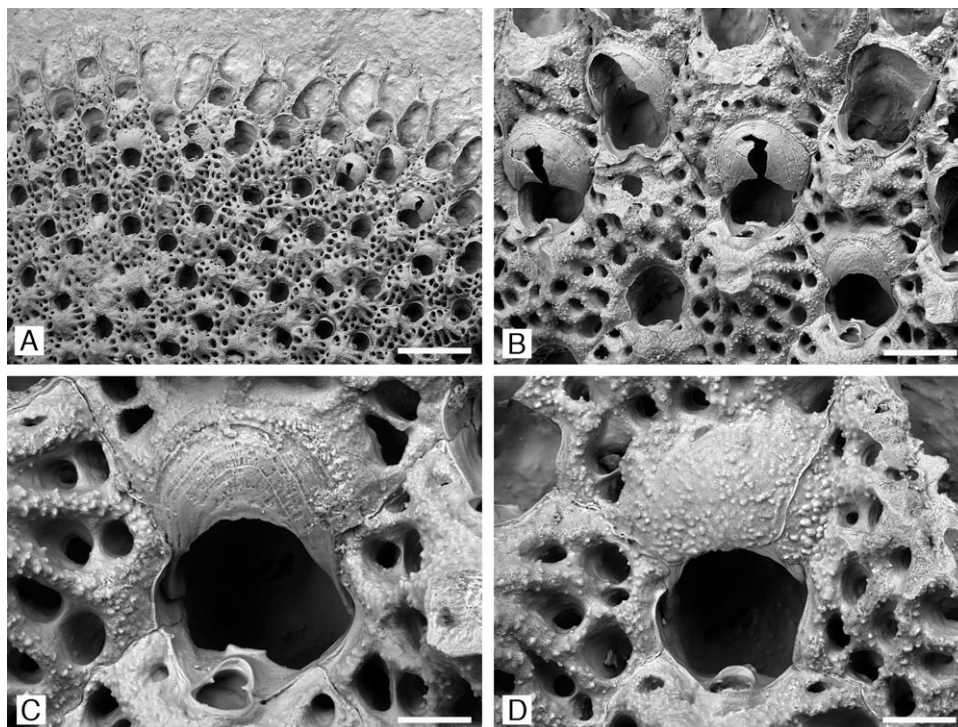


Figure 12. *Raymondcia rigida* (Lorenz, 1886), holotype of *Pentapora boreale* Kuklinski & Hayward (2004), Kingsfjorden, Spitsbergen, NHM 2003.3.10.1; scanning electron micrographs of uncoated specimen imaged using back-scattered electrons. A, zooids and growing edge. B, zooids with ovicells and suboral avicularia. C, primary orifice, nonporous ovicell, suboral avicularium and lyrula. D, primary orifice, suboral avicularium and ovicell overgrown by granular calcification. Scale bars: A = 600 μm ; B = 200 μm ; C = 80 μm ; D = 100 μm .

ing less than half of the length of the autozooid, lying normal to the frontal plane partially within the primary orifice; rostrum spatulate; crossbar uncalcified; closure plates often present, containing two or occasionally three pores.

Etymology: The species name (Latin, *clipeus*, shield) alludes to the distinctive closure plates that occlude many of the giant avicularia.

Remarks: This new species is most easily recognized by the closure plates of the giant avicularia (Fig. 11A–E), structures that are not present in other species of *Pentapora*, except occasionally in *P. lacryma* sp. nov., where they lack the pores seen in *P. clipeus* sp. nov. The absence of a calcified crossbar in the giant avicularia is another distinctive feature (Fig. 11C): this does not seem to be simply the result of breakages, in view of the good condition of the material. Material of *P. clipeus* sp. nov. comes from a locality preserving aragonite, in contrast to most of the *P. pertusa* and *P. lacryma* sp. nov. specimens described above, where aragonite has been leached. This may account for the preservation of orificial lappets and secondary calcification overgrowing the ovicells (Fig. 11B). The new

species shares with *P. lacryma* sp. nov. the possession of small autozooids. However, unlike the other fossil species of *Pentapora*, *P. pertusa* and *P. lacryma* sp. nov., ovicell pores are arranged in a band close to the primary orifice in *P. clipeus* sp. nov. (Fig. 11A, B); *P. pertusa* has single large ovicell pore (Fig. 8A), whereas numerous pores are scattered across the entire ovicell surface in *P. lacryma* sp. nov. (Fig. 9D).

Distribution: Pliocene, Piacenzian, Monte Padova, Emilia, Italy.

FAMILY SMITTINIDAE LEVINSSEN, 1909
GENUS *RAYMONDCIA* SOULE, SOULE &
CHANEY, 1995

RAYMONDCIA RIGIDA (LORENZ, 1886) (FIG. 12)

Smittina rigida: Lorenz, 1886: 91, figs 8, 8a.

Pentapora boreale: Kuklinski & Hayward, 2004: 81, fig. 1a, c.

Raymondcia rigida: Grischenko, Dick & Mawatari, 2007: 1108, fig. 24.

Material: NHM 2003.3.10.1, holotype of *P. boreale*, Kongsfjorden, Spitsbergen, 79°03.51'N, 11°34.4'E, Kuklinski Collection. NHM 2003.3.10.2–6, paratypes

of *P. boreale*, Kongsfjorden, Spitsbergen, 79°01.8'N, 11°49.8'E, Kuklinski Collection.

Brief description: Colony encrusting, unilaminar.

Autozooids hexagonal, boundaries well defined, averaging 0.58 ± 0.03 mm long by 0.41 ± 0.04 mm wide (Kuklinski & Hayward, 2004). Frontal shield convex, granular, a pronounced conical umbo proximal of the orifice; areolar pores and pseudopores large. Primary orifice as wide as long, 0.15 ± 0.02 mm long by 0.16 ± 0.01 mm wide; condyles and oral spines lacking; lyrula broad. Ovicells hyperstomial, imperforate, slightly wider than long, averaging 0.18 ± 0.02 mm long by 0.25 ± 0.03 mm wide, becoming overgrown by granular calcification extending proximally from distal zooid (Kuklinski & Hayward, 2004). Lateral and transverse walls bearing multiporous septula. Median septum lacking on basal wall.

Avicularia monomorphic, suboral, lying below the lyrula, proximally directed, small; rostrum rounded, spatulate; crossbar uncalcified apart from short condyles.

Remarks: Restudy of the holotype and paratypes of *P. boreale* from Kongsfjorden, West Spitsbergen, show this species to belong to another genus, *Raymondcia*, and to be a junior synonym of *R. rigida* (Lorenz, 1886), which was comprehensibly redescribed recently by Grischenko *et al.* (2007). The most important feature of '*P. boreale*' that enables it to be excluded from *Pentapora* is the presence of a lyrula (Fig. 12C, D). Because of its location deep within the orifice, the lyrula was apparently missed by Kuklinski & Hayward (2004) when they originally described the species. Furthermore, the species lacks two features found in *Pentapora*: a porous ectooecium and orificial condyles (the 'minute and rounded condyles' noted by Kuklinski & Hayward were not evident when the material was restudied using SEM).

PHYLOGENETIC ANALYSIS

The phylogenetic analysis was undertaken using the program PAUP 4.0. A matrix of 20 characters, nine qualitative and 11 quantitative, was assembled for the six species of *Pentapora* that we have accepted (see the Appendix). Five of these characters are multistate, the remainder are binary. Gap analysis was used to determine character states for quantitative characters. Among the quantitative characters, three are ratios similar to those successfully used for bryozoan phylogenetics (e.g. Cheetham *et al.*, 2006).

Out-group selection is problematical in *Pentapora* because there is no phylogenetic analysis available for the family (Bitectoporidae) to which the genus belongs, and the genera assigned to this family are

too morphologically variable to provide a clear indication of character polarization. Similar variability is evident in the closely related Smittinidae, making this also difficult to use as an out-group. Therefore, we have reluctantly chosen to root the tree on an in-group taxon: *P. ottomulleriana*. This species was selected because it exhibits character states considered to be primitive for *Pentapora*, including an entirely encrusting colony form, lack of median septa, monomorphic avicularia, and oral spine bases.

The exhaustive search algorithm of PAUP yielded a single most parsimonious tree of 29 steps; the next shortest trees (three) had 31 steps. Of the 20 characters employed, 11 were found to be parsimony informative. The shortest tree (Fig. 13) had a consistency index (*CI*) of 0.862, a retention index (*RI*) of 0.667, and a rescaled consistency index (*RC*) of 0.575.

Three species, the extant *P. foliacea* plus the Pliocene species *P. pertusa* and *P. lacryma* sp. nov., form a clade in which *P. foliacea* and *P. pertusa* are sister species. Outside this essentially Atlantic clade are the Mediterranean species: the Pliocene-recent *P. fascialis* and the Pliocene *P. clipeus* sp. nov. Bootstrap support values for the clades range from 69 to 86, based on a heuristic search of 1000 replicates.

Although the phylogeny is concordant with the biogeography, with the more basal species living in the Mediterranean and the crownward species in the Atlantic, many of the synapomorphies supporting the major clades are quantitative characters that may be suspect in view of the known plasticity of such characters in bryozoans related to factors such as seawater temperature and nutrient levels (e.g. Okamura, 1987; Lombardi *et al.*, 2006).

The oldest fossil occurrence of *Pentapora* appears to be from the Upper Miocene (Messinian) of Morocco. Material from Morocco was identified by El Hajjaji (1992) as *P. pertusa*, but the lack of giant avicularia or uniporous ovicells means that El Hajjaji's specimens must be left in open nomenclature as *Pentapora* sp. From a stratigraphical standpoint, the relatively short range of *Pentapora* (less than 4 million years for the identifiable species) means that testing the phylogeny against the fossil record is of doubtful value.

The separation of *P. fascialis* and *P. foliacea* on the cladogram by the Pliocene *P. lacryma* sp. nov. is notable, in view of the debate about whether these two extant species are synonyms. If synonymous, they would be expected to come out as sister species. Indeed, the sister species of *P. foliacea* is inferred to be the Pliocene *P. pertusa* that, although similar in autozooidal morphology, has uniquely uniporous ovicells and an enormous triangular giant avicularium. The only species of *Pentapora* to have lost the giant avicularia is *P. foliacea*, assuming that the monomorphic avicularia of *P. ottomulleriana* are correctly clas-

sified as giant avicularia, as suggested by their size and horizontal inclination. Dimorphism of avicularia into normal and giant types apparently occurred immediately crownward of *P. ottomulleriana*, with all subsequent species retaining dimorphic avicularia, apart from *P. foliacea*.

DISCUSSION AND CONCLUSIONS

Colonies of *Pentapora* are among the most striking and largest bryozoans in the Atlantic and Mediterranean at the present day, and are represented in the fossil record from the Miocene to Pleistocene in Europe and North Africa. The taxonomy of the genus presents difficulties because of the comparative uniformity in the skeletal morphology of the autozooids and the normal-sized suboral avicularia. Indeed, ontogenetic variations in the autozooidal skeletons within single colonies may be greater than the differences between species. In the case of fossil colonies, additional variability that has no taxonomic significance can result from the preservation or non-preservation of the aragonite layer on the frontal surfaces of colonies (Fig. 10C).

Two characters that are critical in discriminating between species of *Pentapora* are the giant avicularia and ovicells. Giant avicularia are hypertrophied avicularia that sporadically replace the normal-sized avicularia in *Pentapora*, as well as in some other cheilostome genera (e.g. Soule, 1973). They are distinct polymorphs in the sense that no intermediates

exist between normal-sized and giant avicularia in *Pentapora*: within a colony it is always possible to categorize individual avicularia as either normal or giant. Four of the six species of *Pentapora* show dimorphism of the avicularia, possessing both normal-sized and giant avicularia. A problem arises with *P. ottomulleriana*, where there is only one type of avicularium (Fig. 7F) that in size and shape is closer to a giant avicularium in species having dimorphic avicularia (e.g. Fig. 5B) than it is to a normal-sized avicularium (e.g. Fig. 5D). In the cladistic analysis, the avicularia of *P. ottomulleriana* were therefore coded as giant avicularia. Apart from *P. ottomulleriana*, avicularia also appear to be monomorphic in *P. foliacea*, but in this case they clearly correspond to the normal-sized avicularia seen in other species of the genus. The absence of giant avicularia in *P. foliacea* seems to be an important taxonomic character, although it may be that giant avicularia are extremely rare in this species and are yet to be discovered. It is not known why normal-sized avicularia are sometimes replaced by giant avicularia in cheilostomes. If an environmental trigger is involved (e.g. presence of predators), the absence of giant avicularia in species such as *P. foliacea* may be without taxonomic significance.

Ovicell porosity is another useful character in *Pentapora* taxonomy. All species belonging to the genus have pores in the ectooecium, although these may be overgrown by secondary cryptocystal calcification (Fig. 3F). The Pliocene species *P. pertusa* is unique in

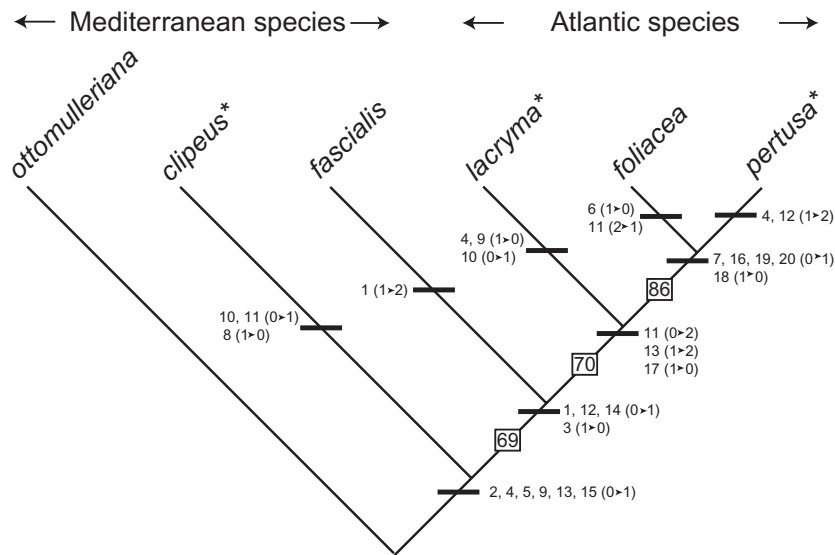


Figure 13. Cladogram showing the inferred phylogenetic relationships between species of *Pentapora* based on an analysis rooted on *Pentapora ottomulleriana*. The numbers in the squares are bootstrap support values for clades along the spine of the tree. Smaller figures are character numbers (see the Appendix), with state changes given in brackets. Extinct species are indicated with asterisks. Note that the Atlantic species form a clade crownward of the Mediterranean species in this analysis.

having only one large and central pore (Fig. 8D); other species have multiple pores, either arranged in a crescent just above the autozooidal orifice (Fig. 3E) or distributed across the entire surface of the ooecium (Fig. 9D). Nothing is known about the function of these pores in *Pentapora*. However, within the *Celleporella hyalina* (L.) species complex along the Chilean coast, the number of pores is a plastic character modulated by water temperature, and is negatively correlated with latitude, and therefore temperature and oxygen level in the water (Navarrete *et al.*, 2004). Further investigations are needed to see whether the variability in pore number between species of *Pentapora* has any environmental significance. The fact that the greatest difference in pore number occurs between two sympatric species (*P. pertusa* and *P. lacryma* sp. nov.) suggests high levels of biological control within the genus, if not within species.

The phylogenetic tree, based entirely on skeletal morphological characters, and rooted on *P. ottomulleriana*, separates the recent and fossil North Atlantic species from the Mediterranean species (Fig. 13). This interpretation places the three Mediterranean species *P. ottomulleriana*, *P. clipeus* sp. nov., and *P. fascialis* basal to a clade consisting of the three North Atlantic species *P. lacryma* sp. nov., *P. foliacea*, and *P. pertusa*. It should be noted, however, that the three characters supporting the North Atlantic clade are all metric, and may potentially reflect the different environmental conditions, such as low mean annual temperature and annual range of temperature, experienced by Atlantic species relative to Mediterranean species (Lombardi *et al.*, 2006). Characters defining the Atlantic clade do not include the two characters (giant avicularia and ovicell porosity) that are of most value in discriminating between species of *Pentapora*. Further studies are needed to test the proposed phylogeny, as well as molecular data to support or falsify the separate identity of the living species *P. fascialis* and *P. foliacea*. Investigations of fossil faunas will also be worthwhile in view of the large number of bilamellar ascophoran cheilostomes described during the long period (1807–1968) when *Pentapora* was effectively forgotten by bryozoan taxonomists.

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APPENDIX

PHYLOGENETIC DATA

Character list

1. Colony form: encrusting unilaminar (0); erect bilamellar foliaceous (1); erect bilamellar dichotomous (2).
2. Median septum: absent (0); present (1).
3. Oral spines: absent (0); present (1).
4. Ovicell porosity: evenly porous (0); proximally porous (1); single pore (2)
5. Small avicularia: absent (0); present (1).
6. Giant avicularia: absent (0); present (1).
7. Giant avicularium rostrum: spatulate (0); triangular (1).
8. Giant avicularium crossbar: uncalcified (0); calcified (1)
9. Giant avicularium crossbar ligulation: nonligulate (1); ligulate (1).
10. Mean autozooid length: > 600 µm (0); < 600 µm (1).
11. Mean autozooid width: > 400 µm (0); 300–400 µm (1); 200–300 µm (2).
12. Ratio of mean autozooid length/width: < 2 (0); 2–2.9 (1); > 3 (2).
13. Mean autozooid orifice length: > 250 µm (0); 200–250 µm (1); < 200 µm (2).
14. Mean autozooid orifice width: > 190 µm (0); < 190 µm (1).
15. Ratio of mean autozooid orifice length/width: > 1.3 (0); < 1.3 (1).
16. Ratio of mean autozooid length/orifice length: > 4 (0); < 4 (1).
17. Small avicularium length: > 90 µm (0); < 90 µm (1).
18. Small avicularium width: > 80 µm (0); < 80 µm (1).
19. Giant avicularium length: < 300 µm (0); > 300 µm (1).
20. Giant avicularium width: < 200 µm (0); > 200 µm (1).

Matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>P. ottomulleriana</i>	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	?	?	0	0
<i>P. foliacea</i>	1	1	0	1	1	0	?	?	?	0	1	1	2	1	1	1	0	0	?	?
<i>P. fascialis</i>	2	1	0	1	1	1	0	1	1	0	0	1	1	1	1	0	1	1	0	0
<i>P. pertusa</i>	1	1	0	2	1	1	1	1	1	0	2	2	2	1	1	1	0	0	1	1
<i>P. lacryma</i> sp. nov.	1	1	0	0	1	1	0	1	0	1	2	1	2	1	1	0	0	1	0	0
<i>P. clipeus</i> sp. nov.	?	1	1	1	1	1	0	0	1	1	1	0	1	0	1	0	1	1	0	0