

Brood chambers constructed from spines in fossil and Recent cheilostome bryozoans

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Most cheilostome bryozoans brood their larvae in skeletal structures called ovicells which, in evolutionary terms, were derived from spines. Ovicells in the great majority of fossil and Recent cheilostomes, however, have lost all or most traces of their spinose origin. Here we review the occurrence of spinose (including costate) brood chambers in cheilostomes, investigating in detail 32 species belonging to ten genera among five families (Calloporidae, Monoporellidae, Macroporidae, Cribrilinidae and Tendridae). Spinose ovicells are moderately common in the Upper Cretaceous, where they are recorded in 28 species, and also occur in one Palaeocene, seven Eocene-Miocene and 11 Recent species. The most primitive cheilostome ovicells occur in mid-Cretaceous calloporids in which a group of mural spines belonging to the distal zooid were apparently bent towards the maternal zooid to form a cage-like structure for reception of the embryo. The bases of these spines were initially aligned in a distally concave row that later became straight, distally convex and finally horseshoe-shaped, affording progressively better protection for the developing embryo. We suggest that primitive monoporellids inherited from calloporid ancestors a distally concave arrangement of ovicell spine bases, while cribrilinids inherited a horseshoe-shaped arrangement. Important trends that can be recognized in early ovicell evolution include: (1) loss of basal spine articulation; (2) spine flattening; (3) closure of the gaps between spines; (4) reduction in spine number (through loss or fusion), and (5) development of a concave ovicell floor. The conventional ‘unipartite’ ovicells found in the majority of cheilostomes may have originated either by spine fusion, as seems likely in some cribrilinids, or through a progressive loss of spines via an intermediate stage, seen in some calloporids and in two monoporellids, where the ovicell comprises a large pair of flattened spines. The spinose ovicells of some monoporellids and macroporids subsequently evolved investments of hypostegal coelom that allowed secretion of a surface layer of cryptocystal calcification. Acanthostegous brood chambers characteristic of Tendridae apparently provide an example of independent evolution of spinose brooding structures. © 2005 The Natural History Museum, London, *Zoological Journal of the Linnean Society*, 2005, **144**, 317–361.

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INTRODUCTION

Represented by more than 1000 nominal genera (Gordon, 2002), the Cheilostomata are the largest order of bryozoans and are the dominant group in some benthic marine habitats. The oldest cheilostomes date from the Late Jurassic (Pohowsky, 1973; Taylor, 1994) and are related to extant taxa which possess long-living planktotrophic larvae that are not brooded. However, most living cheilostomes brood short-lived,

nonplanktotrophic larvae in skeletal chambers called ovicells. The importance of ovicells to the evolutionary success of cheilostomes is implied by the fact that cheilostomes were of low diversity and limited disparity throughout the Late Jurassic and for most of the Early Cretaceous before undergoing an explosive radiation which was coincident with the appearance of the first ovicells in the calloporid *Wilbertopora mutabilis* Cheetham, 1954 (see also Cheetham *et al.*, in press) during the Late Albian. Acquisition of a new larval type has been postulated as the key evolutionary innovation responsible for this radiation event

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(Taylor, 1988; Taylor & Larwood, 1990). The evolution of short-lived, nonplanktotrophic larvae may have led to greater genetic heterogeneity both within and between populations, promoting allopatric speciation and triggering major radiation. The great majority of Recent and post-Early Cretaceous fossil cheilostomes are brooders, and it is likely that brooding, probably along with certain other evolutionary innovations (Gordon & Voigt, 1996), was instrumental in their rise to dominance among marine bryozoans.

Although cheilostomes exhibit a variety of brooding patterns, ranging from external to intracoelomic (for reviews, see Hyman, 1959; Ström, 1977; Reed, 1991), most species accommodate developing embryos within ovicells. Typically, an ovicell is a two-walled hemispherical outfolding (ooecium) that encloses a coelomic lumen between the walls and forms a roof over the cavity in which the embryo is brooded. This lumen communicates with the visceral coelom of the zooid (either maternal or distal) that constructs the outfold. The ooecium encloses a brooding space with an exit for the larvae through an opening that is generally plugged by either the zooidal operculum or the distal wall of the maternal zooid (for further discussion, see Ostrovsky, 1998; Ostrovsky & Schäfer, 2003; Ostrovsky, Schäfer & Gordon, 2003).

There are three main hypotheses of the origin of brooding in cheilostomes. According to Silén (1944), within the 'Cheilo-Ctenostomatous stem' the first brooders kept their embryos inside an invagination of the zooidal body wall called an embryo sac. This hypothesis was justifiably criticized by Santagata & Banta (1996: 178), who suggested instead that 'vestibular brooding preceded evolution of ovicells among cheilostomes' (discussed in Ostrovsky, 1998). It has been shown, however, that Santagata & Banta's hypothesis is based on some incorrect assumptions and should itself be rejected (Ostrovsky, 2002; Taylor & McKinney, 2002). The third hypothesis, that the first brooders employed external protective receptacles (e.g. Hughes, 1987), is favoured here.

It appears likely that ovicells for brooding embryos evolved from modified spines which may themselves represent polymorphic zooids. This idea dates back to the works of Harmer (1902) and Levinsen (1902) (see Ostrovsky, 1998) and receives support from the fossil record. Lang (1921) described a number of Cretaceous cribrimorph cheilostomes with ovicells constructed of costal spines (see also Larwood, 1962; Ostrovsky, 2002), while remnants of spinose ovicells in the monoporellid genus *Stichomicropora* have been illustrated (but not always described) in several papers (Canu & Bassler, 1926; Voigt, 1930, 1949, 1967, 1981, 1989; Brydone, 1936; Favorskaya, 1987; Taylor, 1987). Recently published descriptions of spinose ovicells in Upper Cretaceous monoporellids (Taylor & McKinney,

2002) and calloporids (Ostrovsky & Taylor, 2004) have interpreted their morphology as primitive. Among Recent cheilostomes the acanthostegous brood chamber known only in the genera *Tendra* and *Heteroecium* (Nordmann, 1839; Repiachoff, 1875; Hincks, 1881, 1892; Ostroumoff, 1886; Levinsen, 1909) represents another kind of spinose brood chamber which is not homologous with an ovicell (see below).

Further questions relevant to ovicell origins and early evolution are: (1) Which zooid constructed the ovicell, maternal or its distal neighbour? (2) How many spines were involved in ovicell formation? (3) What was the distributional pattern of these spines? (4) How did the transition occur between spinose and conventional unipartite ovicells?

Only the first question has been satisfactorily resolved. Harmer's (1902) hypothesis that ovicells originated from two oral spines of the maternal zooid, further advocated by Silén (1977) (see also Silén, 1945; Ryland, 1982), has been rejected (Nielsen, 1981, 1985; Ostrovsky, 1998, 2002; Taylor & McKinney, 2002; Ostrovsky & Schäfer, 2003; Ostrovsky & Taylor, 2004) in favour of their originating from modified mural spines of the distal daughter zooid. Regarding the second question, both Harmer's (1902) hypothesis and the double nature of the ooecial rudiment (earliest stage of ovicell floor calcification, see Ostrovsky *et al.*, 2003; Ostrovsky & Taylor, in press) has led to the supposition that ovicells evolved from a pair of proximal spines (Santagata & Banta, 1996; see also Ryland, 1979). However, the most primitive ovicells known are multi-spinose, as described in this paper. In relation to the third question, Ostrovsky (2002) extended the hypothesis, first proposed by Reingard (1875; see also Braiko, 1967) that brooding in the space between the frontal membrane and a frontal shield of spines (epistegite), as found in the living cheilostome *Tendra zostericola*, could provide an analogue of an early stage in ovicell evolution. Santagata & Banta (1996: 178) suggested that '...the acanthostegous ovicells... might represent a primitive stage in the development of ovicell complexes like those in [the cribrimorph] *Figularia*'. Studying the Recent cribrimorph *Puellina*, Ostrovsky (2002) found a closed horizontal slit in the ovicells which he interpreted as the rudiment of a connection between the brooding cavity and epistegite. However, in the light of recent findings of spinose ovicells in several Cretaceous anascans (Taylor & McKinney, 2002; Ostrovsky & Taylor, 2004), this suggestion seems unlikely to be correct. Instead, spines constructing the most primitive ovicells arose only on the proximal mural rim of the distal zooid, with the proximal gymnocyst of this zooid forming the ovicell floor.

Taylor & McKinney (2002) and Ostrovsky & Taylor (2004) have proposed some basic hypothetical steps in the evolution from simple spinose to costate, and

thence to bivalved and unipartite ovicells. Nonetheless, many questions remain unanswered. Here we present a review of fossil and Recent cheilostomes with brood chambers constructed of spines, including costae which are basally fused spines bent into a parallel orientation with the frontal surface of the zooid. Based on the results obtained, we suggest probable stages in the early evolution of the ovicells in the Cheilostomata, and subsequently in three major clades – Calloporoidea (Calloporidae), Microporoidea (Monoporellidae, Macroporidae) and Cribriolinidea (Cribriolinidae) – where some species have retained primitive spinose ovicells.

MATERIAL AND METHODS

Most of the material used comes from existing museum collections; the following abbreviations are used:

BSS	Bass Strait Survey
CM	Canterbury Museum, Christchurch, New Zealand
GSUH	Graduate School of Science, University of Hokkaido, Sapporo, Japan
MNHN	Muséum National d'Histoire Naturelle, Paris
NHM	The Natural History Museum, London
NIWA	National Institute for Water and Atmospheric Research, Wellington, New Zealand
NMV	National Museum, Victoria, Melbourne
USNM	United States National Museum, Washington
VC	Voigt Collection, Naturmuseum Senckenberg, Frankfurt

Bryozoans were studied in an uncoated condition at the NHM using ISI ABT-55 and LEO 1455VP low vacuum SEMs, both of which produced back-scattered electron images, and in a coated condition at the Universität Wien using a Jeol JSM-6400 SEM with secondary electron imaging. A Leica-M420 binocular microscope was used to image wet specimens of *Monoporella nodulifera*.

Some colonies of *Macropora levinseni* were fixed in 70% alcohol and decalcified using 2 N solution of HCl. For light microscopy, decalcified specimens were embedded in plastic (epoxy resin type TAAB 812), sectioned (2.5–4 µm thick) with a glass knife, and stained with Richardson's stain using standard methods.

OVICELL DESCRIPTIONS

The descriptions given below are based on our own observations, most of them new. In the 'Remarks' sections we consider previous work on the same species. Sections headed 'Additional data from the literature'

concern related species that we have not studied personally.

FAMILY TENDRIDAE VIGNEAUX, 1949

GENUS *TENDRA* NORDMANN, 1839

TENDRA ZOSTERICOLA NORDMANN, 1839

(FIGS 1A–D, 21A)

Material: NHM 11.10.1.489, Recent, Sebastopol Bay, Black Sea, collected by A. Ostroumoff.

Description: Non-brooding autozooids possess two oral and sometimes one or two, occasionally more, proximal mural spines that are more slender and shorter than the oral spines (Fig. 1A, D). Oral spines are truncated, their tips probably having a terminal membranous window (cf. Ostrovsky, 1998). Mural spines are acute.

In addition to the oral spines, the left and right sides of the mural rim in brooding autozooids have a row of horizontally inclined, basally flattened spines (Fig. 1A, B, D). These are long and acute, overarching the frontal membrane to give a brooding cavity between this membrane and the undersides of the spines (Fig. 21A). Each row consists of 10–15 spines (up to 17, according to Repiachoff, 1875 and Levinsen, 1909; 13–18, according to Occhipinti Ambrogi & d'Hondt, 1981), growing towards the opposite row. The proximal part of the opesia is devoid of spines, leaving a gap for oviposition of the eggs and for release of the larvae. This entrance to the brooding cavity may be open but in most instances it is plugged by the operculum of the maternal zooid (Fig. 1A), similarly to the so-called cleithral ovicells found in neocheilostomes. The brood chamber has two openings, proximal and distal.

During development of the brood chamber, the proximal spines evidently commence growth before the distal spines (Fig. 1A, C). They meet the spines growing towards them from the opposite side along the midline of the zooidal frontal surface. In some instances spine growth immediately ceases at this point, but in other cases the spines overgrow one another, sometimes even reaching the opposite side of the mural rim (Fig. 1B). Spine arrangement varies, from rather regular to chaotic, and from very tight (though not fused laterally) to loose with slits between adjacent spines (Fig. 1D). Within the same brood chamber, spines can also be very variable in shape: wide or narrow, flat or more cylindrical, unbranched or bifid (Fig. 1C), straight or curved, and growing along or above the spine lattice. In rare examples only one spine row is developed, either on the left or right side of the zooid (Fig. 1C). In addition, some zooids have up to nine thin mural spines of different length which are not in contact with the spines from either the same or

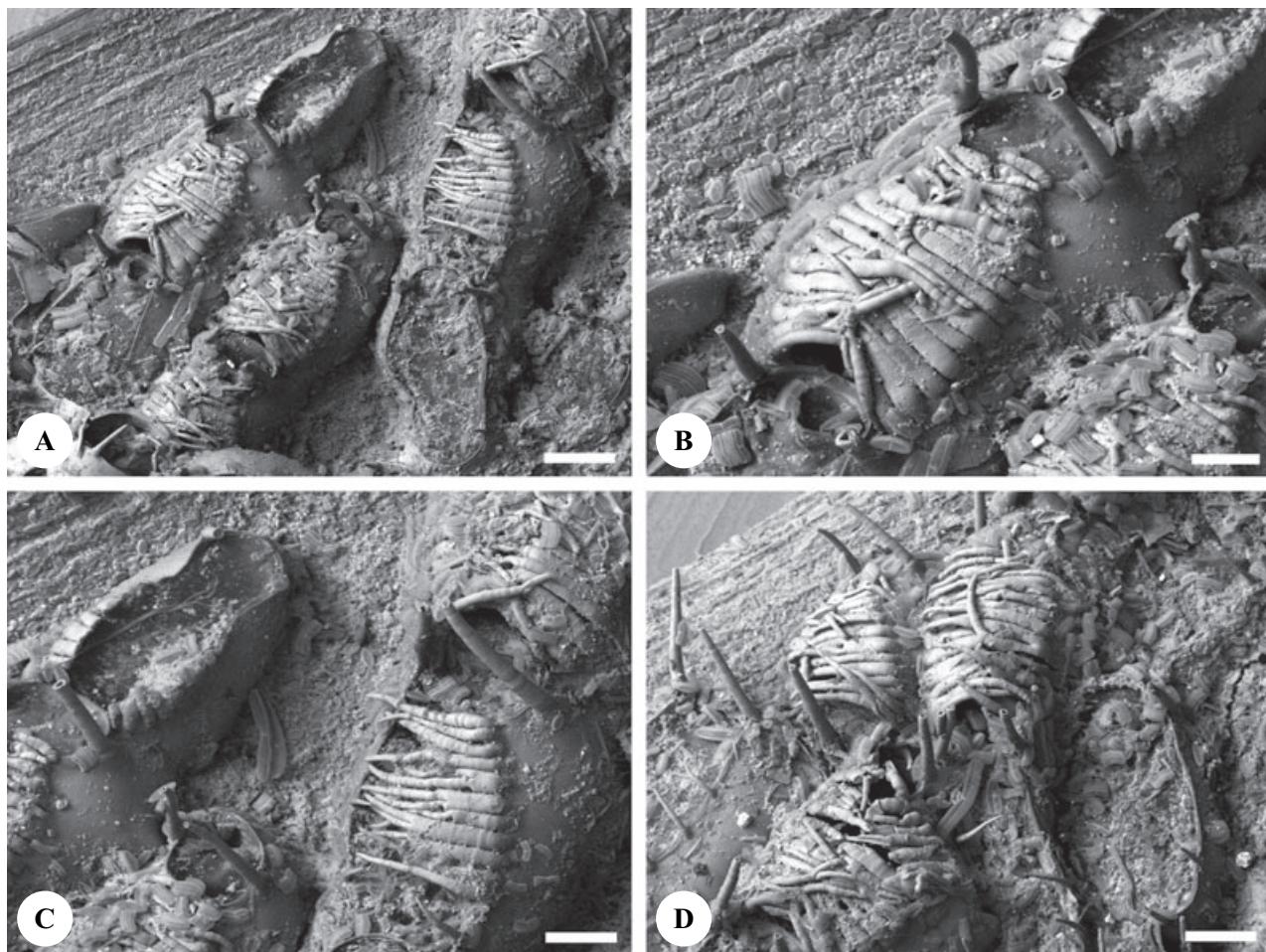


Figure 1. *Tendra zostericola* Nordmann, NHM 11.10.1.489, Recent, Black Sea. A, part of a colony with both brooding and nonbrooding zooids. B, brooding zooid with overlapping frontal spines. C, partially formed brood chamber (left) and brooding zooid with spines developed only on one side (right). D, sparse mural spines in nonbrooding zooid (lower right) and three brooding zooids with different variants of the frontal spine arrangement. Scale bars: A = 250 µm; B = 100 µm; C = 125 µm; D = 150 µm.

the opposite side of the zooid (Fig. 1D) (see also Levinsen, 1909). It is difficult to envisage such a loose construction serving as an effective brood chamber.

All of the oral and mural spines are articulated, as indicated by the presence of a ring furrow at the base of each spine. In contrast, brood-chamber spines appear not to be articulated; unlike oral and mural spines, none are broken off basally. However, sections of decalcified material are required to confirm this supposition. The cavities of all spine types are apparently confluent with the visceral coelom of the zooid distal of the maternal zooid.

Brood chambers are formed near the distal margins of colonies, often being located at the growing edge. In many instances several brooding zooids are found in the same longitudinal row, one following the other (Fig. 1D).

Remarks: The term ‘acanthostegal’ or ‘acanthostegous ooecia’ was introduced by Levinsen (1902, 1909) for the unusual brood chambers constructed of spines in *Tendra zostericola* and *Heteroecium amplectens* (Hincks, 1881). The first superficial description of the ‘cellule treillissées’ and developing embryos inside these brood chambers was given by Nordmann (1839: 191) for *Tendra*. Repiachoff (1875: 132) remarked that these zooids ‘play a role of the ovicells’ known in a majority of the Cheilostomata. Following Repiachoff, Reingard (1875) thought that embryos developed inside the body cavity of specialized zooids in this species. However, he believed that they could not be compared with ovicells since they possess a polypide and an ovary.

Ostroumoff (1886) was the first to recognize the actual position of the developing embryos in the space

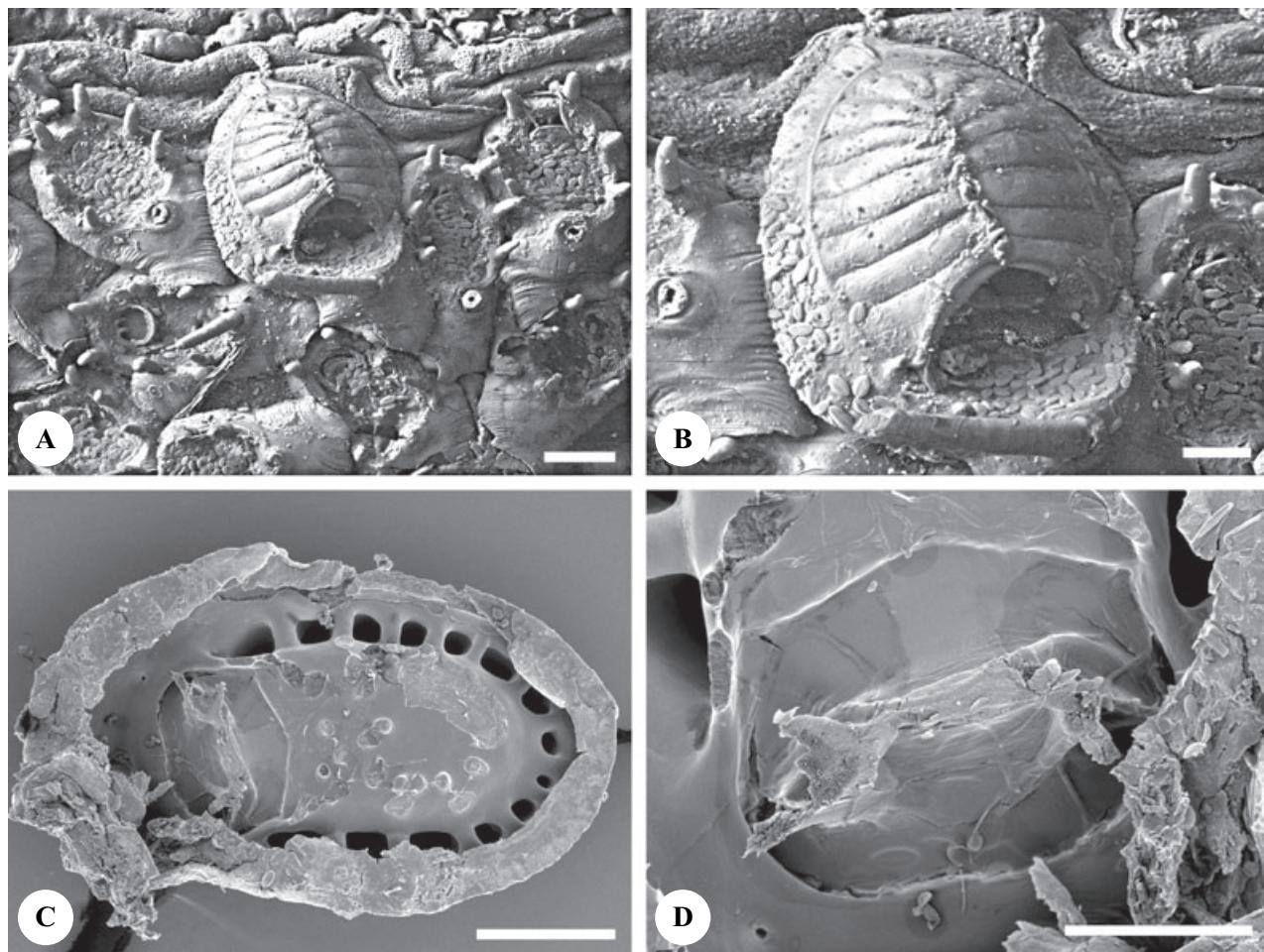


Figure 2. *Heteroecium amplexens* Hincks, NHM 99.5.1.702, Recent, Western Australia. A, part of a colony with several nonbrooding zooids and one brooding zooidal complex. B, brooding zooidal complex. C, brooding zooidal complex from below (distal to the right); openings of the costae surround the floor of brood chamber. D, membranous area with two appendages in the brood-chamber floor; a communication pore in the transverse wall between the maternal zooid and distal kenozoooid can be seen in the left lower corner. Scale bars: A, C = 100 µm; B, D = 50 µm.

between the frontal membrane and the overarching spines. Paltschikowa-Ostroumowa (1926) and Braiko (1967) further studied different aspects of reproduction in *Tendra zostericola* (see also Occhipinti Ambrogi & d'Hondt, 1981, and references therein), which is known from the Mediterranean as well as the Black Sea.

Where several brooding zooids are present successively within the same longitudinal row, all of these zooids (possibly excepting the most distal one) will have produced their own eggs as well as brooding the embryos of the proximal neighbouring zooid. As in cheilostomes with ovicells, formation of the brood chamber by any particular zooid is presumably triggered by the development of an ovary in its proximal neighbour.

GENUS *HETEROECIUM* HINCKS, 1892

HETEROECIUM AMPLECTENS (HINCKS, 1881) (FIGS 2A–D, 21B)

Material: NHM 99.5.1.702, Recent, Western Australia, T. Hincks Collection.

Description: Non-brooding autozooids possess seven mural spines surrounding the frontal membrane. Six of these spines are short, with blunt roundish tips. The seventh spine is several times longer than the others, though approximately equal in width, and is placed on the proximal gymnacyst just behind the frontal membrane. In contrast with the other mural spines, it is basally articulated.

So-called brooding zooids are actually complexes of two zooids, a proximal (maternal) autozooid (probably

an autozooidal polymorph) and a distal kenozooid (Fig. 21B). Laterally juxtaposed and flattened spines overarch the frontal wall of the kenozooid to form the brooding cavity (Figs 2A, B, 21B). The nonarticulated spines, numbering 15–17, start their growth on the mural rim of the kenozooid and meet along the midline above the calcified frontal wall, forming a sort of medial keel. Cavities of the spines are confluent with the visceral coelom of the kenozooid (Fig. 2C). The brood chamber has the shape of an elongated hemisphere, opening proximally where it is plugged by the operculum of the maternal zooid. Brood chambers are always formed in the axils of branch bifurcations, and there is never a zooid distal of the brood chamber. Communication between the maternal autozooidal polymorph and the distal kenozooid is via simple pores (Figs 2D, 21B). The floor of the brood chamber is calcified, except for a peculiar area in its proximal part which is membranous with two lateral appendages (Figs 2C, D, 21B).

Remarks: The first description of this species was given by Hincks (1881) who correctly recognized the spinose structures as brood chambers. However, he believed them to be single zooids with ‘the upper portion of the zooecial aperture . . . much extended’ and ‘roofed in by a number of (soldered) marginal spines’. Hincks also wrote that ‘the zooecium . . . is divided into two chambers – one for the polypide, the other for the embryo’ (1881: 130). In a later work, Hincks (1892) introduced the genus *Heteroecium* and repeated the description mentioned above. Levinsen (1909: 148) described a second species, *H. brevispina* (as ‘Var. *brevispina* n.’), with some clear differences (larger size, more mural spines, shorter proximal spine, etc.) but a brood chamber having the same structure. Not surprisingly, Levinsen (1909: 148) did ‘not understand the significance of the situation of the aperture behind the area formed by the spines’, since he thought that the brood chamber consisted of a single zooid. Nevertheless, he correctly understood the structure of the brooding cavity, and, following Ostroumoff (1886), wrote that ‘the acanthostegal ooecia . . . are cavities internally limited by the covering membrane of the zooecium and externally by a cover made up of two rows of hollow spines’ (Levinsen, 1902: 17). Images of *H. brevispina* recently placed by Dr P. E. Bock on the Bryozoa Home Page website (<http://www.civgeo.rmit.edu.au/bryozoa/cheilostomata/tendridae/heteamp.html>) show the brood chamber to be constructed of 12–13 flattened, nonarticulated spines. Closure of the brood-chamber opening by the zooidal operculum is also clearly seen.

The unusual membranous area in the floor of the brood chamber is interpreted as a rudiment of the frontal membrane to which are attached the parietal

muscles involved in tentacle crown eversion in the autozooids. Sections of decalcified material would help to resolve this issue.

FAMILY CALLOPORIDAE NORMAN, 1903

Remarks: Spinose ovicells were first described by Ostrovsky & Taylor (2004) in three Cretaceous calloporid genera. Here we present a more detailed description of the structure of their ovicells.

GENUS *DISTELOPORA* LANG, 1915

DISTELOPORA BIPILATA LANG, 1915

(FIGS 3A–D, 21C, 24I, L)

Material: NHM D21876, D21879–21883, D23019, Cretaceous, Lower Cenomanian, 10 ft (3.05 m) from the base of the Chalk Marl, Cambridge, England, F. Möckler Collection. NHM BZ4958, Lower Cenomanian (?*carcitanense* Subzone), Porcellaneous Beds (= Chalk Marl), Barrington Chalk Pit, Cambridgeshire, England, A. N. Ostrovsky & P. D. Taylor Collection.

Description: Non-brooding autozooids (i.e. those that have no brood chamber on their proximal gymnacyst) possess 6–8 mural spine bases that indent the mural rim. These are usually paired, with the most proximal pair having the largest diameter and the distalmost pair (the oral spine bases) the smallest. The proximal part of the mural rim is usually devoid of spines (Fig. 3A).

Brooding autozooids positioned distally of maternal (egg-producing) zooids usually have six, sometimes seven, mural spine bases plus an additional 5–10 (usually 6–7) spines that constructed the ovicell. As with the mural spines, only the bases of the ovicell spines are preserved, the spines themselves always being broken off at their basal articulations and lost in these fossils. Ovicell spine bases are aligned in a distally convex arch on the proximal gymnacyst of the distal (brooding) autozooid (Figs 3A–D, 24I, L). This arch is normally gently curved (Figs 3A, C, D, 24I), but is occasionally more convex (Fig. 3B, left ovicell), and a near semicircle of spine bases was found in one example (Fig. 3B, right ovicell, 24 L). As a rule, the median ovicell spine bases are adjacent to the proximal edge of the mural rim of the distal zooid, and may slightly indent it (Fig. 3D). However, they can be also be positioned further from the mural rim (Fig. 3C). The outermost spine bases are always well-separated from the distal edge of the maternal zooid. The distance between adjacent ovicell spine bases is equal to or greater than their diameters. They have either approximately the same diameter as the most distal oral spines or are smaller. The floor of the ovicell, formed by the proximal gymnacyst of the distal zooid, is slightly concave.

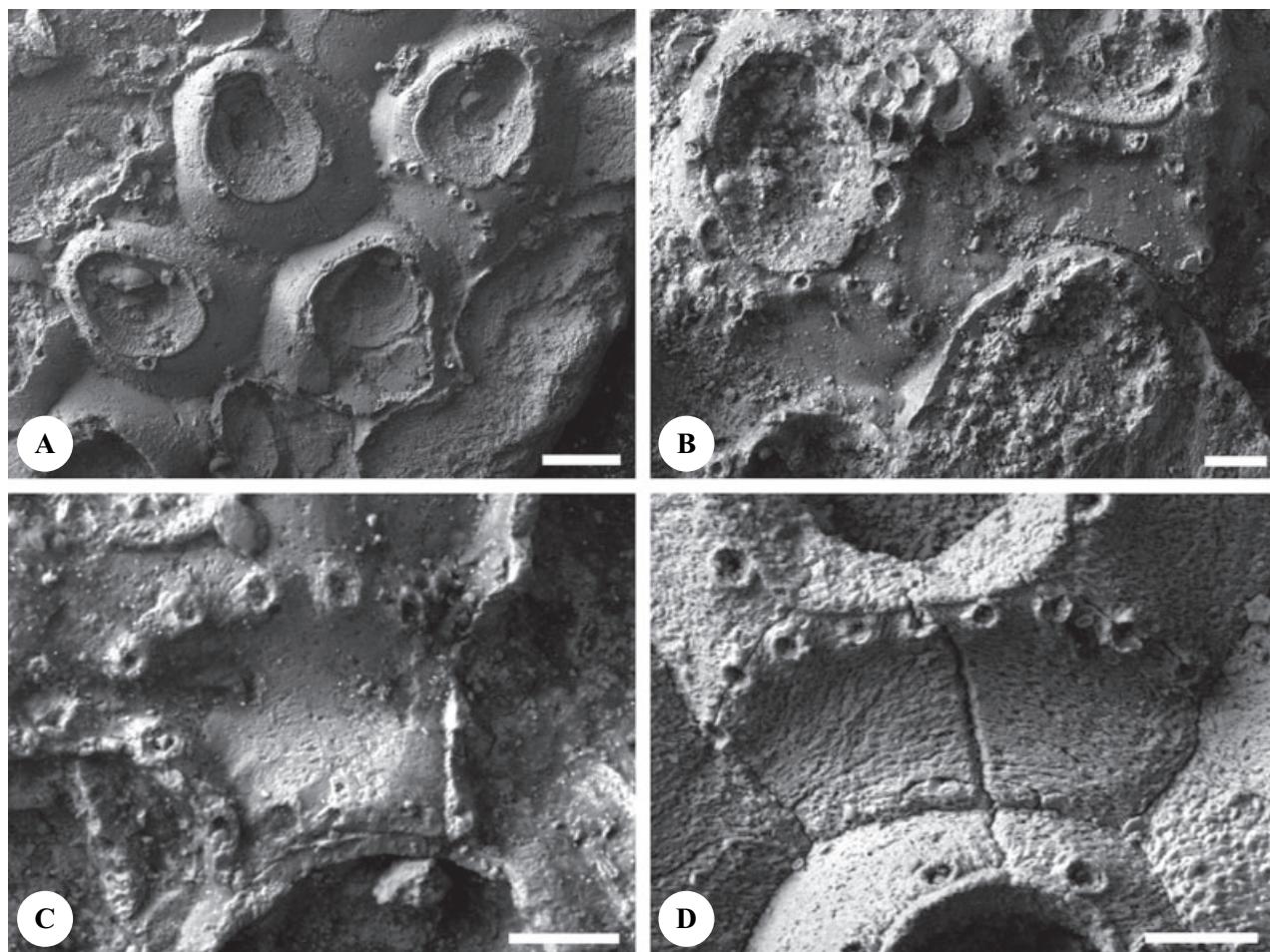


Figure 3. *Distelopora bipilata* Lang, Lower Cenomanian, Cambridge, England. A, part of a colony with several non-vicellate autozooids and one broken ovicell, NHM D21883. B, ovicell spine bases forming a semicircle, NHM D21881. C, ovicell spine bases at some distance from the mural rim, NHM D21881. D, ovicell spine bases forming a gentle arch. Medial spines are adjacent to the proximal edge of the mural rim of the distal zooid, NHM BZ4958. Scale bars: A = 100 µm; B–D = 50 µm.

DISTELOPORA LANGI OSTROVSKY & TAYLOR, 2004
(FIGS 4A, 21C, 24I)

Material: NHM D21873–21875, D21878, D23059, D23111, BZ4961, BZ4962, Cretaceous, Lower Cenomanian, 10 ft (3.05 m) from the base of the Chalk Marl, Cambridge, England, F. Möckler Collection.

Description: Non-brooding autozooids possess 9–11 (up to 16) mural spine bases, including usually four oral mural spines, though as many as six can be present. Proximal spine bases are typically slightly larger than distal spine bases. However, this character varies, and the largest spine bases can be any except for the most distal.

There are 10–12 mural spines in brooding (ooecium-bearing) zooids. Ovicell roofs were constructed of 7–8 spines borne on the proximal gymnocyst of the distal zooid (Figs 4A, 21C, 24I). The bases of these articulated spines typically have the same diameter as distal oral spines but can be somewhat smaller or larger. They are arranged in a gently curved, distally convex arch. The median spines are normally adjacent to the proximal edge of the mural rim of the distal zooid (Fig. 4A) but are sometimes separated from it by a narrow strip of gymnocyst. The outermost spine bases are always located far from the distal edge of the maternal zooid, and the distance between neighbouring ovicell spine bases is equal to or smaller than their diameter. The ovicell floor is slightly concave.

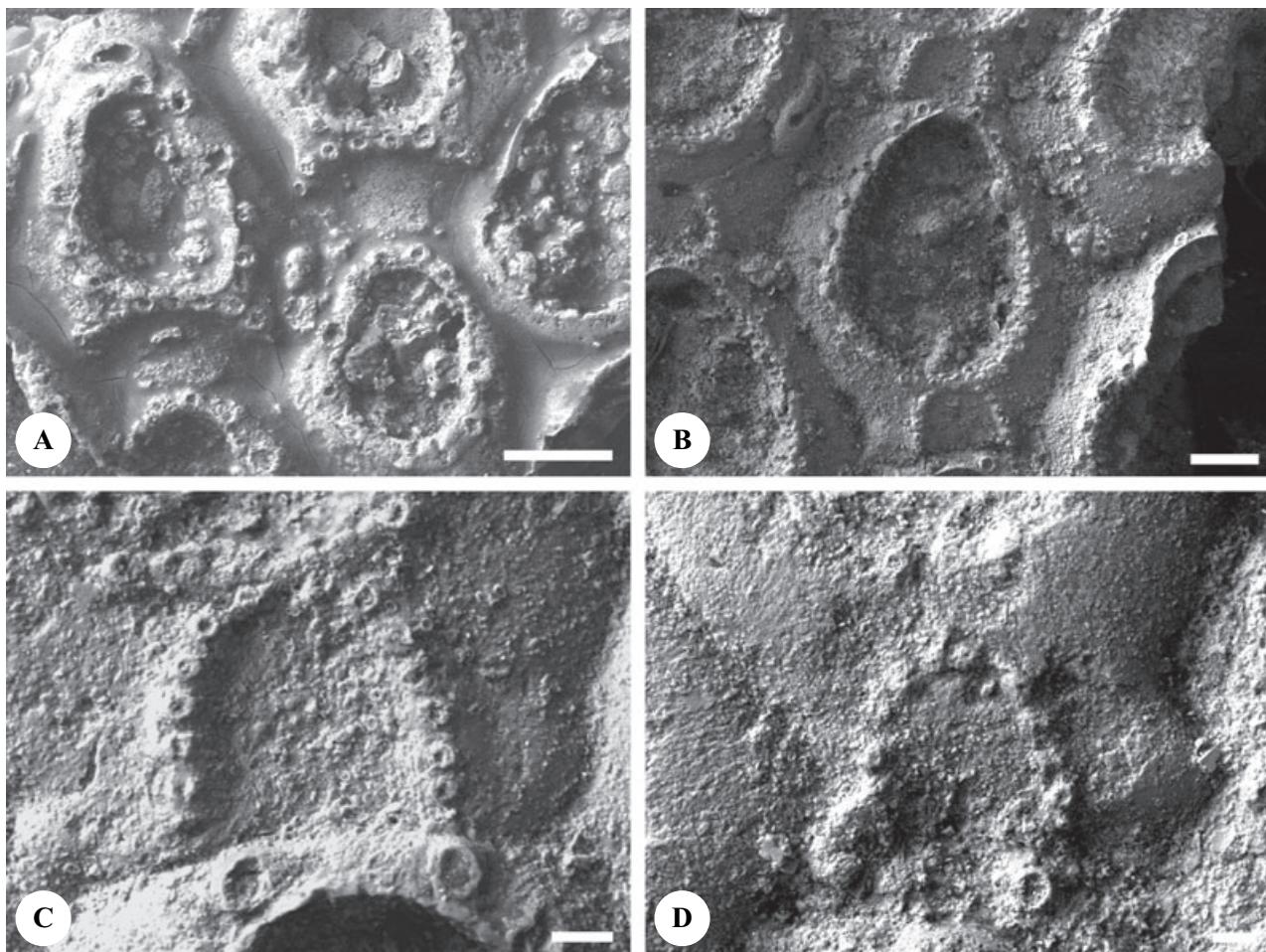


Figure 4. A, *Distelopora langi* Ostrovsky & Taylor, fragment of a colony, with two broken ovicells showing ovicell spine bases in a gently curved arch; medial spine bases are adjacent to the proximal edge of the mural rim of the distal zooid. Lower Cenomanian, Cambridge, England, NHM D23111. B–D, *Distelopora spinifera* Ostrovsky & Taylor; Lower Cenomanian, Cambridge, England. B, part of a colony, showing spine bases of three ovicells; NHM D21651. C, ovicell spine bases arranged in a semicircle, the medial spines adjacent to the proximal edge of the mural rim of the distal zooid; NHM D21667. D, poorly preserved ovicell in which the medial spine bases are some distance from the mural rim of the distal zooid; NHM D21897. Scale bars: A, B = 100 µm; C, D = 25 µm.

DISTELOPORA SPINIFERA OSTROVSKY & TAYLOR, 2004
(FIGS 4B–D, 21D, 24P)

Material: NHM D21651–21653, D21667, D21894, D21897–D21899, D21901, D23308, Cretaceous, Lower Cenomanian, Chalk Marl, Cambridge, England, F. Möckler Collection.

Description: Non-brooding autozooids have 14–24 (usually 18–21) mural spines distributed all around the zooidal aperture. These include two distal and two distolateral oral spines that have largest diameters.

Brooding zooids possess 15–20 mural spines. Ovicell roofs were constructed of 11–15 (often 14) spines positioned on the proximal gymnocyst of the distal, brood-

ing autozooid (Figs 4B–D, 21D, 24P). The ovicell floor is slightly depressed. Ovicell spine bases are of approximately the same diameter or a little smaller than the proximal mural spine bases, and are markedly smaller than the oral mural spines. They are arranged in a semicircular (horseshoe) pattern on a slight ridge (Figs 4B–D, 24P). Median spines are located very close to the mural rim of the distal zooid (Fig. 4B, C) where mural spines of this zooid are often absent. However, there is sometimes a distinct intervening area of gymnocyst between the mural rim and the ovicell spine bases (Fig. 4D). The two most proximal ovicell spines are located close to the distal boundary wall of the maternal zooid. The distance between

adjacent spine bases is approximately equal to their diameter or smaller, although a greater separation is often found in the distal part of the ovicell.

GENUS *UNIDISTELOPORA* OSTROVSKY & TAYLOR, 2004

UNIDISTELOPORA KRAUSEAE
(VOIGT & SCHNEEMILCH, 1986)
(FIGS 5A, B, 21D, 24P)

Material: VC 11025, Cretaceous, Lower Campanian, Grube Allemania, Höver, near Hannover, Germany. VC T10580, Lower Campanian, Grube Alsen, Lägerdorf, near Hamburg, Germany. VC T10581, Lower Campanian, Grube Breitenburg, Germany.

Description: Non-brooding zooids of this uniserial species have 24–25 mural spine bases, compared with 20–21 in ovicellate zooids. Distal spine bases, particularly the four ‘oral’ spine bases, are slightly larger than the others.

Ovicell roofs were constructed of 18–19 spines whose bases are arranged atop a low semicircular ridge and raised above the concave ovicell floor formed by the proximal gymnacyst of the distal brooding zooid (Figs 5A, B, 21D, 24P). The diameter of ovicell spine bases is markedly smaller than that of mural spine bases, especially the nearby oral spine bases of the maternal zooid. In all cases observed, the distal, median ovicell spine bases are located on the mural rim of the distal zooid where mural spines were absent. The two most proximal spine bases are placed very close to the distal edge of the maternal zooid. Ovicell spine bases are closely spaced, with the distance between adjacent bases usually less than spine base diameter, except in the distal part of the ovicell where the spine bases are sparser and spaced further apart.

Remarks: All spines in the species of *Distelopora* and *Unidistelopora* described above were basally articulated, as indicated by the double ring structure seen in some of the spine bases (Figs 4C, 5B; Ostrovsky & Taylor, 2004). This is also supported by the fact that no spines are preserved *in situ*. In the majority of the ovicellate zooids of *Distelopora* spp. and *Unidistelopora krauseae*, the proximal part of the mural rim of the distal zooid lacks mural spines in the zone where ovicell spine bases adjoin it. Thus, the mural spine bases and distalmost, median ovicell spine bases often (always in the case of *U. krauseae*) form a continuous line, and the distalmost ovicell spine bases are positioned where the most proximal mural spine bases are normally located in the nonbrooding zooids (Figs 4A, C, 5A, B, 24P). However, the ‘missing’ proximal mural spines do develop when the ovicell spine bases are separated from the mural rim, and also in intramural reparative buds formed within the distal zooid.

GENUS *GILBERTOPORA* OSTROVSKY & TAYLOR, 2004

GILBERTOPORA LARWOODI OSTROVSKY & TAYLOR,
2004
(FIGS 5C–F, 21E, 24K)

Material: NHM D23297–23298, Cretaceous, Lower Cenomanian, 10 ft (3.05 m) from the base of the Chalk Marl, Cambridge, England, F. Möckler Collection. NHM BZ4954–4957, same details but 20 ft (6.1 m) from the base of the Chalk Marl.

Description: Two small, knob-like oral spines occur in some of the nonbrooding autozooids. They have closed ends and were probably not basally articulated.

The ovicell roof is bipartite, constructed of two claw-like, arched, flattened spines (Figs 5C–F, 21E, 24K). These spines, which are not basally articulated, originate on the proximal gymnacyst of the distal (brooding) zooid which also forms the slightly concave floor of the ovicell. Basally, the spines are rather narrow and separate (similar to *Wilbertopora mutabilis*; Ostrovsky & Taylor, in press) (Fig. 24K), but they broaden to become juxtaposed along the median line of the ovicell where a suture is developed (Figs 5C, E, F, 21E). The internal cavities of the two hollow spines seem not to be confluent, judging from an example in which the ovicell is broken along an apparent calcified wall between the juxtaposed spines. The ovicell has four openings: a distal opening is present between the bases of the two spines and has a teardrop-, oval or subcircular shape (Fig. 5C, F); two elliptical lateral openings (foramina) occur on each side of the ovicell between the arched spines and the floor of the ovicell (Fig. 5D); and the main, proximal opening of the ovicell is a wide, very low arch (Fig. 5E).

FAMILY MONOPORELLIDAE HINCKS, 1882

GENUS *STICHOMICROPORA* VOIGT, 1949

Remarks. Species belonging to this genus can be divided into two groups depending on whether the ovicell spines were basally articulated or basally fused (Taylor & McKinney, 2002). After dealing with each of these groups in turn based on our own studies, we discuss additional data from the literature.

1. SPECIES WITH ARTICULATED OVICELL SPINES

STICHOMICROPORA OCEANI (D'ORBIGNY, 1852)
(FIGS 6A–D, 22A, 24B, E)

Material: NHM D55549, Cretaceous, Lower Cenomanian, *saxbii-orbignyi* Zones, Sables et Gres de Lamnay (lumachelle), Lamnay, Sarthe, France, P. D. Taylor Collection.

Description: All autozooids have two distal oral spines. Non-brooding zooids in addition often possess one

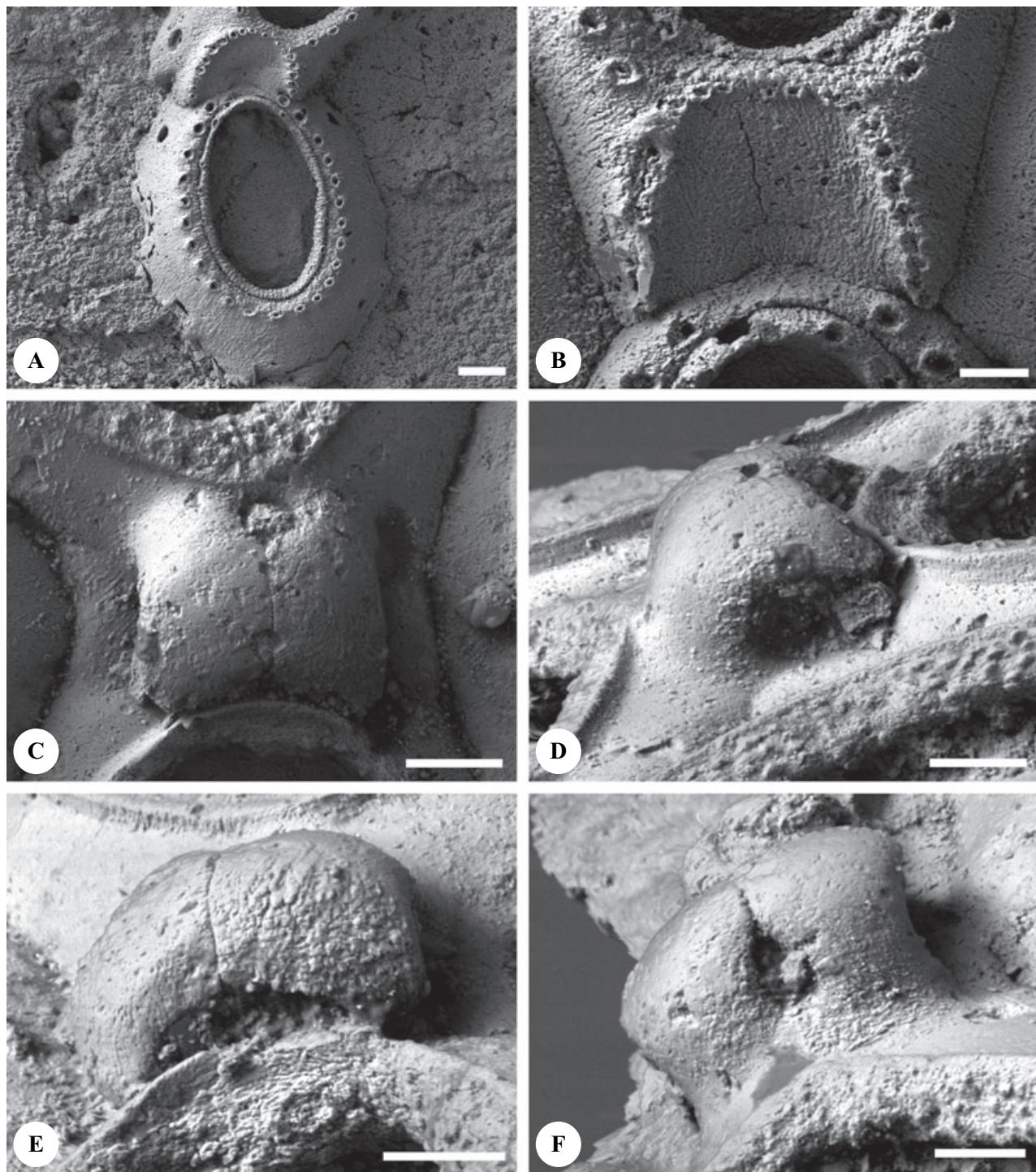


Figure 5. A, B, *Unidistelopora krauseae* (Voigt & Schneemilch), Lower Campanian, northern Germany, VC T10580. A, maternal zooid with ovicell and intramural bud. B, ovicell spine bases arranged in a semicircle along a ridge on the proximal gymnocyst of the distal zooid. C–F, *Gilbertopora larwoodi* Ostrovsky & Taylor, Lower Cenomanian, Cambridge, England. C, complete ovicell of two flattened spines; NHM D23297. D, complete ovicell viewed from the side, showing a lateral foramen; NHM D23298. E, complete ovicell in proximal view, showing the main opening of the ovicell; NHM D23298. F, complete ovicell in distal view, showing the distal opening; NHM D23298. Scale bars: A = 100 µm; B–F = 50 µm.

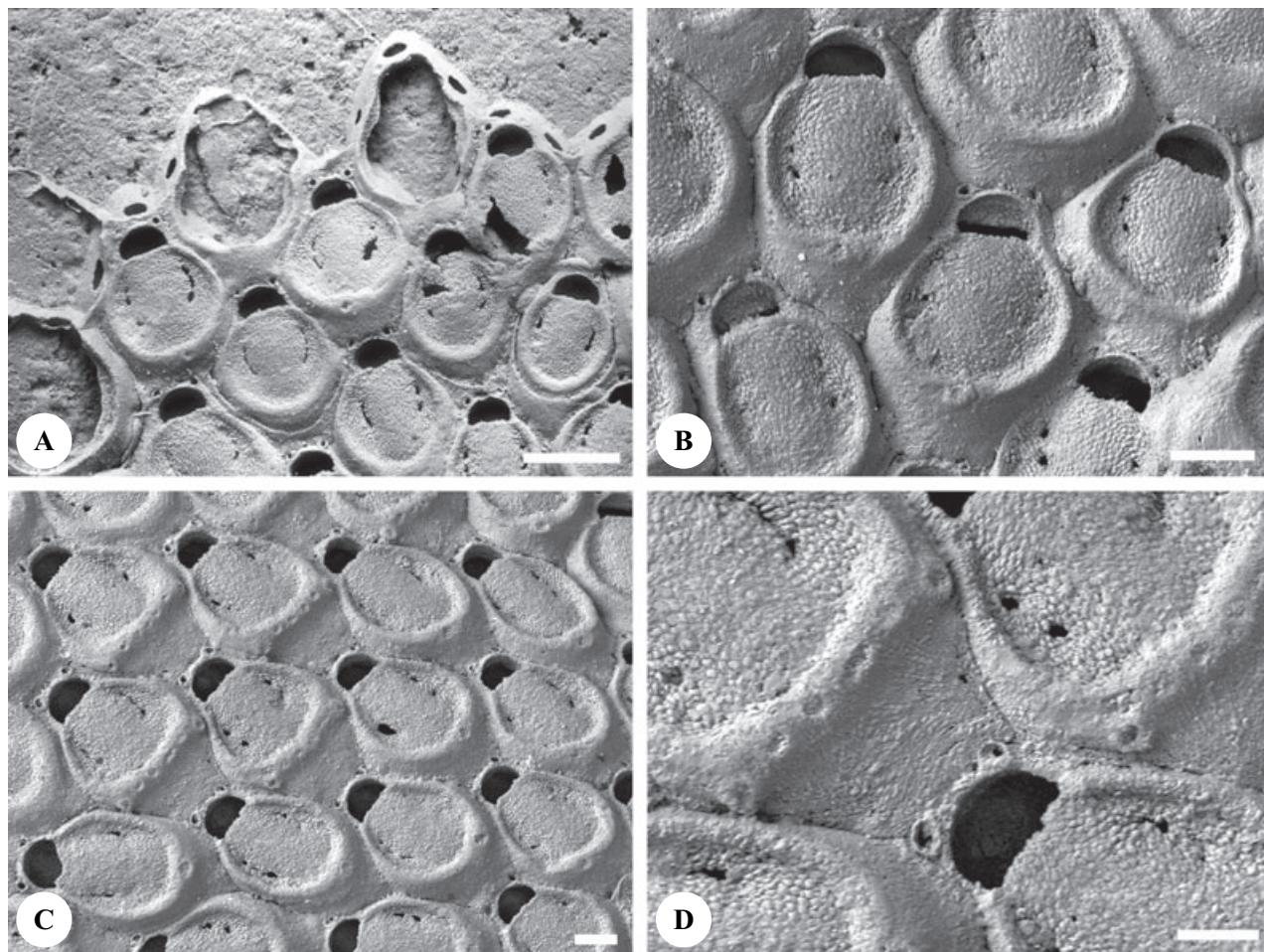


Figure 6. *Stichomicropora oceanii* (d'Orbigny), Lower Cenomanian, Sarthe, France, NHM D55549. A, growing edge of a colony, showing pore chambers and intrazonal budding style. B, nonbrooding zooids, with oral and proximal mural spines. C, oblique view of the colony, with brooding and nonbrooding zooids. D, orifice of maternal zooid and ovicell spine bases arranged in a distally concave arch along the mural rim of the distal zooid, apart from the outermost spine bases which are slightly separated from the mural rim. Scale bars: A = 250 µm; B, C = 100 µm; D = 50 µm.

proximal mural spine, situated medially on the proximal gymnecyst, indenting the mural rim, and having a diameter noticeably greater than the oral spines (Fig. 6A–C).

Distal zooids constructing ovicells are characterized by a transverse row of 5–7 ovicell spine bases (Figs 6C, D, 24B, E). With the exception of the two outermost spines, these spines are positioned on the proximal slope of the mural rim and follow the outline of this rim which varies from gently concave distally to almost straight (Figs 6C, 24B, E). Ovicell spine bases partition the proximal, slightly concave part of the gymnecyst that forms the ovicell floor, from the more distal part of the gymnecyst and the cryptocyst. The outermost spine bases are often slightly offset from the others, being positioned more proximally and distant from the mural rim, and have a larger diameter

(Figs 6D, 24B, E). The distance between adjacent ovicell spine bases is approximately equal to spine base diameter but can be larger or smaller. The gymnecyst forming the ovicell floor has a trapezoidal shape and is enlarged relative to that of zooids not bearing ovicells.

Remarks: Brooding zooids in type material of *S. oceanii* from the d'Orbigny collection were figured by Voigt (1981: fig. 4g), while examples from non-type material was illustrated and briefly described by Taylor & McKinney (2002: fig. 1D).

STICHOMICROPORA MARGINULA (BRYDONE, 1914) (FIGS 7A, B, 22A, 24H)

Material: NHM D44609, Cretaceous, Coniacian, Upper Chalk, Dover, Kent, England.

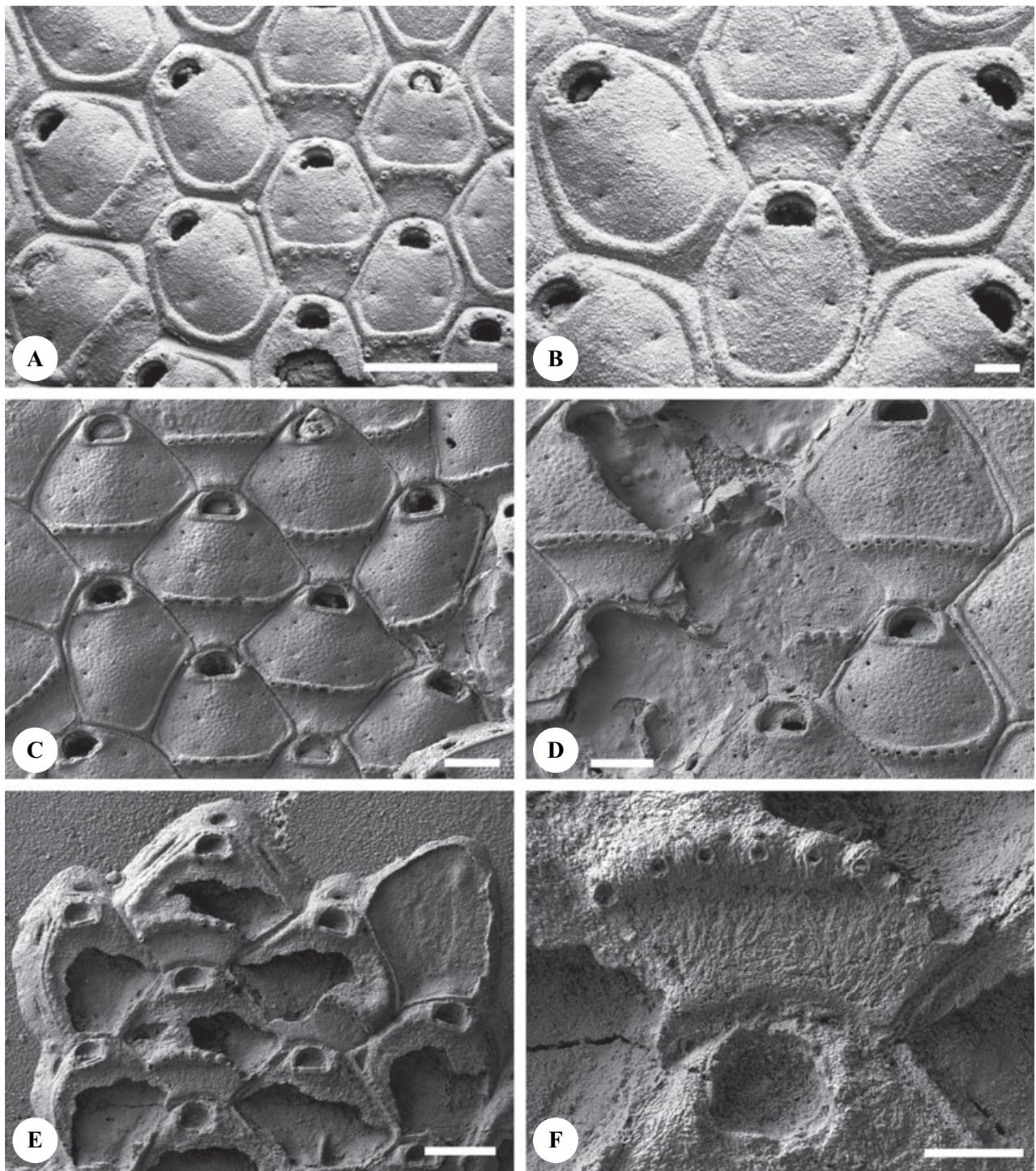


Figure 7. A, B, *Stichomicropora marginula* (Brydone), Coniacian, Kent, England, NHM D44609. A, part of colony with ovicellate and nonovicellate zooids. B, maternal zooid with ovicell preserved as a gently curved, distally convex arch of spine bases. C, D, *Stichomicropora* sp. 1, Campanian, Norwich, England, NHM D42263. C, several fertile zooids with ovicells represented by spine bases arranged in distally concave or distally convex gentle arches, or in a straight line. D, view centred on a damaged part of a colony with distally convex rows of ovicell spine bases (upper left and upper right) and a distally concave row (bottom right). E, F, *Stichomicropora* sp. 2, Campanian, Clarendon, England, NHM D46004. E, edge of colony, showing three ovicells, represented by gently curved, distally convex arches of spine bases, in zooids with broken frontal shields. F, ovicell spine bases and floor. Scale bars: A = 500 µm; B, F = 100 µm; C, E = 250 µm; D = 200 µm.

Description: All autozooids possess six oral spines of which the four distalmost are articulated; the two proximal spines are knob-like with closed ends and probably lacked basal articulations (Fig. 7A, B). In distal brooding zooids there are 7–10 ovicell spine bases arranged in a distally convex arch on the proximal gymnacyst, indenting the broad, elevated mural rim (Figs 7A, B, 24H). The outermost spine bases are slightly offset from the others, being positioned more proximally. These two spines are set well apart from the mural rim, and are always distant from the distal edge of the maternal zooid. The gymnacyst forming the ovicell floor is concave and enlarged relative to that of zooids not bearing ovicells. The distance between neighbouring ovicell spine bases is equal to or less than spine base diameter.

Remarks: Brooding zooids in *S. marginula* were illustrated by Voigt (1967: pl. 20, figs 1, 3; 1989: pl. 17, fig. 8) and Taylor (1987: pl. 9, fig. 8; 2002: pl. 9, fig. 8). These authors described specimens, respectively, from the Upper Santonian of Chodsha Kasian Mountain (near Schaartus), Tadschikistan, and the Coniacian of Dover, England. The ovicells were neither described nor illustrated by Brydone (1914: 98, pl. 4, figs 8, 9) when he first erected this species as *Homalostega marginula*.

STICHOMICROPORA SP. 1
(FIGS 7C, D, 22A, 24A, D, G)

Material: NHM D42263, Cretaceous, Campanian, *mucronata* Zone, Upper Chalk, Earlham Lime Works, Norwich, England. A.W. Rowe Collection.

Description: Autozooids possess two, rarely one, distal oral spines. Those constructing ovicells have a transverse row of 5–10 ovicell spine bases which are located on the proximal edge of the narrow elevated mural rim (Figs 7C, D, 22A, 24A, D, G). This row of spines separates the proximal, slightly concave gymnacyst, forming the ovicell floor, from the distal cryptocyst forming the bulk of the frontal shield. The gymnacyst of the ovicell floor has a trapezoidal shape and may be wider than long or vice versa, depending on the shape of the proximal part of the autozooid. In contrast, nonbrooding zooids possess a very narrow strip of proximal gymnacyst.

The row of ovicell spine bases essentially parallels the proximal edge of the mural rim. This may vary from distinctly or gently concave distally, to straight or almost straight with lateral parts slightly curved distally, to gently convex distally (Figs 7C, D, 24A, D, G). Depending on the curvature of the spine row, the two most lateral spine bases are either closest to or farthest from the distal edge of the maternal zooid. The distance between adjacent ovicell spine bases usually equals spine base diameter but can be larger or

smaller. The diameter of ovicell spine bases increases towards the middle of the row, the outermost lateral spine bases having diameters similar to those of the oral spine bases.

Remarks: Material of this undescribed species in the NHM collections bears the manuscript name *Homalostega cribraria* Rowe. Brooding zooids were illustrated by Taylor & McKinney (2002: fig. 1A, B).

STICHOMICROPORA SP. 2
(FIGS 7E, F, 22A, 24G)

Material: NHM D46004, Cretaceous, Campanian, *mucronata* Zone, Upper Chalk, Clarendon, Wiltshire, England. A.W. Rowe Collection.

Description: All autozooids have 4–6 oral spines of which the distal pair are the smallest. Ovicell-bearing zooids possess a transverse row of eight ovicell spine bases placed on the salient mural rim that separates the proximal, slightly concave gymnacyst, forming the ovicell floor, from the extensive distal cryptocyst (Fig. 7E, F). The ovicell spine bases are arranged in a gently curved, distally convex arch (Figs 7E, F, 24G), with the outermost spine bases always distant from the distal edge of the maternal zooid. The spacing between adjacent ovicell spine bases is greater than their diameter, which is approximately the same as that of the oral spine bases.

STICHOMICROPORA SP. 3
(FIGS 8A–C, 22A, 24E, H)

Material: NHM D4125, Cretaceous, Coniacian, *cortestudinarium* Zone, Upper Chalk, Chatham, Kent, England. W. Gamble Collection.

Description: The tiny autozooids in this species possess four oral spines of which the distal pair are the smallest (Fig. 8A–C). The ovicell roof was apparently constructed of 5–6 spines surrounding the slightly concave ovicell floor formed by the proximal gymnacyst of the brooding zooid (Figs 8A–C, 22A, 24E, H) which is enlarged relative to that of zooids not bearing ovicells. Ovicell spine bases are arranged either in a gently curved, distally convex arch (Figs 8B, 24H), or sometimes in an almost straight line (Figs 8A, C, 24E) with the two outermost spine bases well away from the mural rim of the zooid and from the distal edge of the maternal zooid. Medial ovicell spine bases often slightly indent the mural rim (Fig. 8B). Ovicell spine bases have approximately the same diameter as distal oral spines or are larger. The distance between neighbouring ovicell spine bases is up to two times greater than their diameter.

Remarks: Many of the autozooids in this species are sealed by closure plates, convex laminae covering the

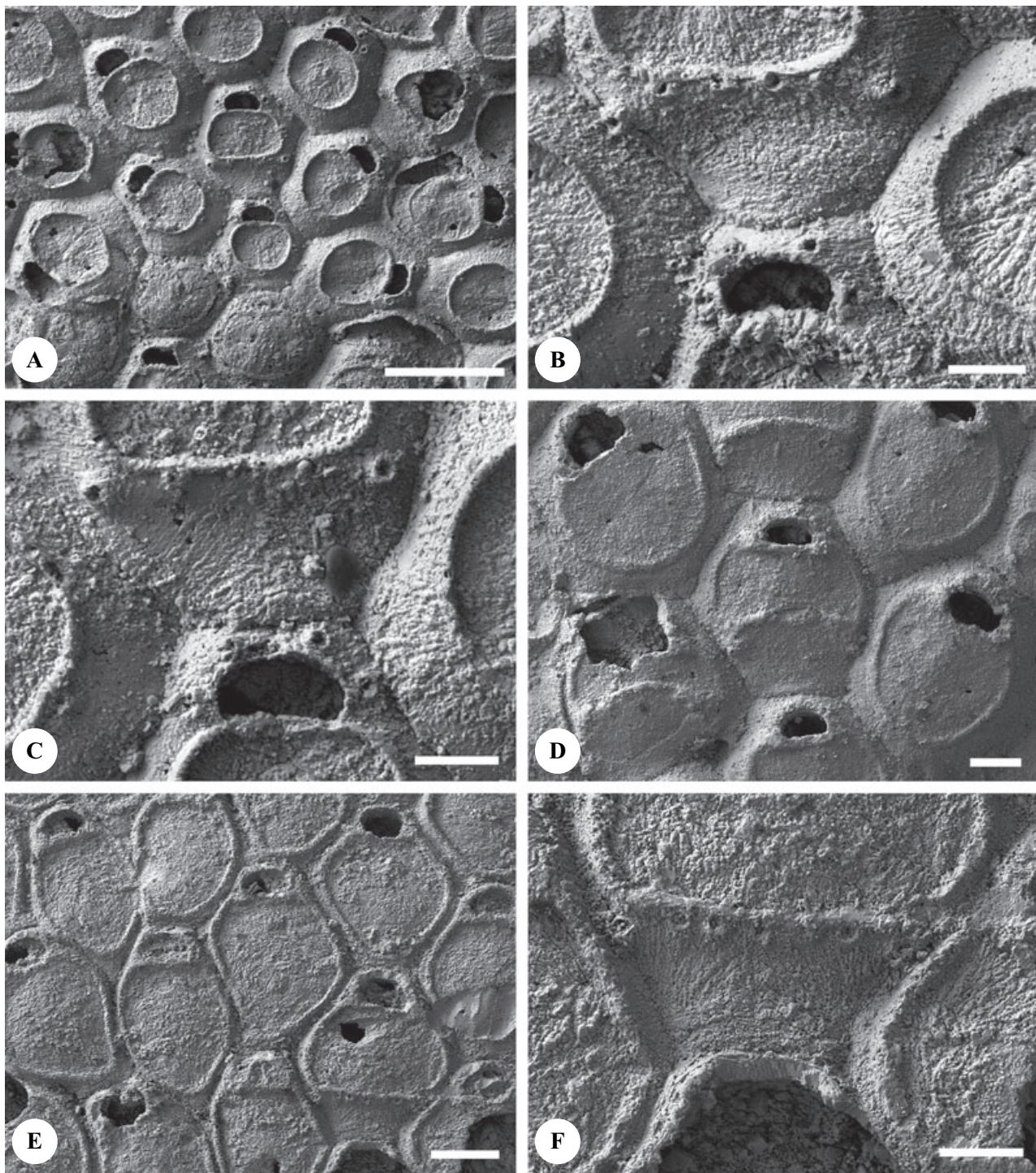


Figure 8. A–C, *Stichomicropora* sp. 3, Coniacian, Kent, England, NHM D4125. A, group of ovicellate and nonovicellate zooids; note closure plates sealing zooids in bottom left. B, ovicell represented by a gently convex line of spine bases of which the innermost are aligned along the mural rim of the distal zooid. C, another ovicell with spine bases arranged in a straighter line. D, *Stichomicropora* sp. 4, worn specimen with distally convex arches of two broken ovicells (centre and top centre); Coniacian, Luton, England, NHM D8185. E, F, *Stichomicropora* sp. 5, Cenomanian, Devon, England, NHM D55618. E, group of zooids with an ovicell (bottom right). F, ovicell spine bases arranged in a straight line along the mural rim of the distal zooid, except for the two most lateral spine bases which are more proximally placed and separated from the mural rim. Scale bars: A, E = 250 µm; B, C = 50 µm; D, F = 100 µm.

cryptocyst and opesia (Fig. 8A). Brydone (1936: 85, pl. 41, fig. 3) described what may be conspecific material as *Homalostega sussexiensis*.

STICHOMICROPORA SP. 4
(FIGS 8D, 22A, 24G)

Material: NHM D8185, Cretaceous, Coniacian or Santonian (upper third of *cortestudinarium* Zone), Upper Chalk, Luton, near Chatham, Kent, England, W. Gamble Collection.

Description: Poor preservation makes it impossible to ascertain the exact number of oral as well as ovicell spine bases in this species. However, the ovicell roof was clearly constructed of several spines (possibly seven or eight), with bases arranged in a gently curved, distally convex arch on the proximal mural rim (Figs 8D, 24G). The slightly depressed gymnocyst forming the ovicell floor is enlarged relative to that of zooids not bearing ovicells.

STICHOMICROPORA SP. 5
(FIGS 8E, F, 22A, 24E)

Material: NHM D55618, Cretaceous, Lower Cenomanian, Wilmington Sands, Wilmington, Devon, England.

Description: Ovicell spine bases number six or seven and are arranged in a straight line or a very gently curved arch on the proximal gymnocyst of the distal zooid. The outermost pair of spine bases are slightly offset from the others, being positioned more proximally (Figs 8E, F, 22A, 24E). The distance between neighbouring ovicell spine bases is equal to or greater than spine diameter.

Remarks: The ovicell of this species was illustrated by Taylor & McKinney (2002: fig. 1C).

2. SPECIES WITH BASALLY FUSED OVICELL SPINES

STICHOMICROPORA BACCATA (CANU & BASSLER, 1926)
(FIGS 9A, B, 22B, 24F, J)

Material: USNM 69954 (syntype suite), Cretaceous, Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee, USA.

Description: Autozooids have 0–4 oral spines of equal diameter, in most instances two. Examples of intact ovicells show them to be constructed of 3–5 flattened spines of variable width. These spines originate on the salient border between the concave trapezoidal proximal gymnocyst (ovicell floor) and the distal cryptocyst. They are arranged in a gently curved, distally convex arch or in a straight line (Figs 9A, B, 24F, J). The spines are directed proximally towards the orifice of the maternal autozooid, their edges closely juxtaposed (Figs 9A, 22B). Each spine has a relatively narrow

base (Fig. 9B), broadens rapidly in its middle part and narrows again towards the tip. Ovicell spine bases are oval, roundish or subquadrate in cross-section, and draped with cryptocystal calcification (Fig. 9B). The tips of the spines form a narrow arch-like opening for the ovicell, placed just above the orifice of the maternal zooid (Fig. 9A). Depressions (facets) occur on the cryptocystal frontal shields of the two zooids laterally adjacent to the ovicell (Fig. 9A, B). Each ovicell possesses three openings: the main proximal opening and two lateral foramina above the cryptocystal facets of the lateral zooids. However, cryptocystal facets are not always developed, and in this case the lateral foramina are probably reduced in size. Communication pores connecting the internal coelomic cavities of the spines with the distal zooidal chamber are clearly seen in broken ovicells. It is likely that the lumens of the juxtaposed spines are not confluent.

Remarks: The first description of the ovicells of *Stichomicropora baccata* (as *Micropora baccata* sp. nov.) was given by Canu & Bassler (1926: 36, pl. 6, figs 4–6) based on material from the Maastrichtian Ripley Formation of Tennessee, USA. Later, Voigt (1930: 473, pl. 22, fig. 5) depicted broken ovicells in specimens from the Campanian (*mucronata* Zone) of Rügen, Germany which are likely to belong to a different species. Taylor & McKinney (2002: fig. 1e, f only) restudied the ovicells of the type material.

STICHOMICROPORA SP. 6
(FIGS 9C–E, 24C, F, J)

Material: NHM BZ4859, Cretaceous, Maastrichtian, PeeDee Formation, Rocky Point Member, Martin Marietta Ideal Quarry, Wilmington, North Carolina, USA, P. D. Taylor Collection. NHM BZ4796, Cretaceous, Maastrichtian, Prairie Bluff Chalk, adjacent to Lake Ridge Apartments, Livingston, Sumter County, Alabama, USA, P. D. Taylor Collection.

Description: Most autozooids possess four oral spines, although some have five, with the distal spines being the smallest. Ovicells are formed by the distal autozooids. In some colonies all of the zooids over large areas possess ovicells (Fig. 9C), with specific zooids being both maternal and constructing brood chambers for their proximal neighbours. Intact ovicells are constructed of four flattened spines of unequal width. These originate along the elevated border between the concave trapezoidal proximal gymnocyst (ovicell floor) and distal cryptocyst. Ovicell spine bases are arranged in a gently curved arch, either distally convex or concave, or in a straight line (Figs 9D, E, 24C, F, J). They are directed proximally towards the orifice of the maternal autozooid. Each spine has a relatively narrow base but broadens distally to become closely juxtaposed, possibly even fused, with the adjacent spines.

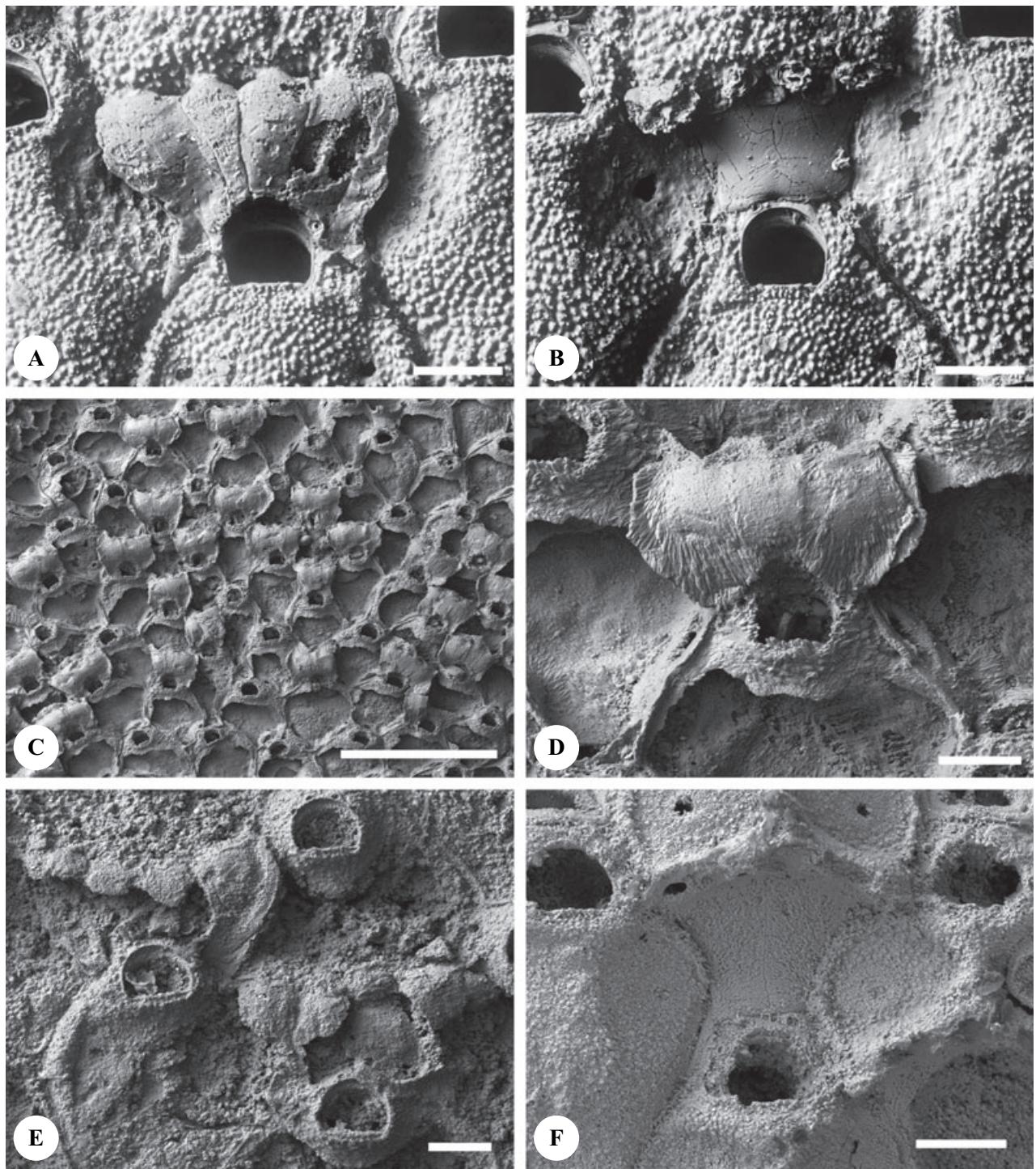


Figure 9. A, B, *Stichomicropora baccata* (Canu & Bassler), Maastrichtian, Tennessee, USA, USNM 69954. A, ovicell with spines intact; note lateral foramina opening above facets in cryptocysts of the two neighbouring autozooids. B, ovicell with spines broken off to reveal gymnocystal floor. C–E, *Stichomicropora* sp. 6. C, D, Maastrichtian, North Carolina, USA, NHM BZ4859. C, part of colony with numerous ovicells. D, ovicell with spines intact. E, two damaged ovicells; Maastrichtian, Alabama, USA, NHM BZ4796. F, *Stichomicropora* sp. 7, broken ovicell showing the floor and lateral facets; Maastrichtian, North Carolina, USA, NHM BZ4186. Scale bars: A, B, D–F = 100 µm; C = 1 mm.

The narrow tips of the spines form the arch-like proximal opening of the ovicell, placed just above the maternal zooid orifice. The outermost ovicell spines are widest, with their outer edges moderately curved (Fig. 9D, E). These edges are positioned just above depressed cryptocystal facets in the frontal walls of the two zooids laterally adjacent to the ovicell. As in *S. baccata*, lateral foramina are present, forming supplementary openings to the main proximal opening of the ovicell. Broken ovicells clearly expose oval communication pores connecting the cavities of the spines with the chamber of the distal zooid. The broken tips of some ovicell spines show that each has an independent cavity at this level, suggesting that, even though the walls of adjacent spines may perhaps be fused, the lumens of the juxtaposed spines are not confluent.

Remarks: This species was initially regarded as *S. baccata* by Taylor & McKinney (2002: fig. 1g), but it evidently differs in the flatter shape of the ovicell spines, greater outward curvature of the lateral ovicell spines, and oral spines averaging four rather than two in number.

STICHOMICROPORA SP. 7
(FIGS 9F, 24J)

Material: NHM BZ4186, Maastrichtian, Peedee Formation, Martin Marietta Ideal Quarry, nr Wilmington, North Carolina, USA, P. D. Taylor Collection.

Description: Autozooids have 5–7, usually six, oral spines. There are no major differences in the morphology of ovicells from that seen in *Stichomicropora* sp. 6 described above.

Remarks: This species resembles *S. baccata* but has ovicells with outwardly bowed lateral spines and generally six rather than two oral spines.

3. ADDITIONAL DATA FROM THE LITERATURE

The type species of *Stichomicropora*, *S. sicksi*, was described by Voigt (1949: 34–35, pl. 7, figs 1–3) from the Campanian (*quadrata* and *mucronata* Zones) of Lägerdorf, Germany. In this species the ovicell is represented by 5–6 bases of evidently articulated spines. These are arranged either in a gentle distally convex arch or in a straight line transverse to the long axis of the zooid (Fig. 24D, G). The trapezoidal proximal gymnocyst of brooding zooids that forms the ovicell floor appears to be almost flat or only slightly concave. The two outermost ovicell spine bases are always distant from the distal edge of the maternal zooid. The distance between neighbouring ovicell spine bases is larger than or sometimes equal to spine diameter.

Plate 7, figure 2 of Voigt's (1949) paper was redrawn by Bassler (1953; fig. 130, 2) for the bryozoan part of the *Treatise on Invertebrate Paleontology*.

Described by Voigt in the same paper (1949: 35–36, pl. 7, figs 4–8) is a second species, *Stichomicropora cf. clathrata* (Reuss, 1872) from the Campanian (*quadrata* and *mucronata* Zones) of Lägerdorf, Oberg and Misburg (near Hannover), Germany. This possesses 6–8 ovicell spine bases arranged in a gently curved, distally convex arch (Fig. 24G). The ovicell floor is trapezoidal and slightly depressed. The distance between neighbouring ovicell spine bases equals their diameter. Ovicells were neither mentioned nor illustrated in the paper of Voigt (1989: pl. 18, fig. 4, pl. 19, figs 5, 6) describing specimens of this species from the Upper Maastrichtian of Curfs Quarry near Maastricht in the Netherlands. Brooding zooids have yet to be described in *Stichomicropora clathrata* (Reuss, 1872), a species recorded from the Upper Cenomanian of Dresden-Plauen, Germany (Voigt, 1989: pl. 18, figs 1–3), the Lower Turonian (*plenus* Zone) of Saxony, Germany (Reuss, 1872: 102, pl. 24, fig. 8), and the Cenomanian-Maastrichtian of England (Brydone, 1936: 85, pl. 41, figs 4, 5).

Homalostega punctilla Brydone, 1936 (p. 85, pl. 41, figs 1, 2) was first described from the Campanian-Maastrichtian of Norfolk, England, and later transferred to *Stichomicropora* by Voigt (1949). Although Brydone stated that no 'ooecia' (ovicells) were observed, he described the 'lower part of frontal walls often sagging in', which undoubtedly refers to the depressed floor of the ovicell, as is evident from his accompanying figures (Fig. 24G).

Stichomicropora erecta (von Hagenow, 1839), variously referred to *Cellepora*, *Homalostega* and *Micropora* (see von Hagenow, 1839, 1846; Marsson, 1887; Levinsen, 1925; Voigt, 1930, 1959), has been recorded from the Maastrichtian of Rügen in Germany, and the Campanian or Maastrichtian of Møen, Aalborg, Faxe and Stevns Klint in Denmark. The only illustration of the ovicell is in the paper of Voigt (1967: pl. 19, fig. 5). However, the figured specimen is poorly preserved, revealing only the distally convex arch of ovicell spine bases, probably numbering six (Fig. 24G).

Ovicells in *Stichomicropora biconstricta* (von Hagenow, 1839) have never been described (see Canu, 1911; Levinsen, 1925; Voigt, 1930, 1959, 1962). However, the gently curved, distally convex arch of what are obviously ovicell spine bases is illustrated in the papers of Canu (1911: pl. 7, fig. 1, as *Micropora convexa* Canu, 1911), Voigt (1930: pl. 22, fig. 6, as *Micropora convexa* Canu, 1911), and Voigt (1959: pl. 6, fig. 3) (see also Fig. 24G). This species has been recorded from the Campanian (*mucronata* Zone) of Rügen in Germany, and Møen, Aalborg, Faxe and Stevns in Denmark, the Lower Maastrichtian of Volsk, Saratov's area, Russia,

and the Roca Formation (which ranges from Maastrichtian to Danian) of Argentina.

Brooding zooids in *Stichomicropora sulcata* (Reuss, 1846) were first figured by Voigt (1967: pl. 20, figs 6, 7) and later described and illustrated by Voigt (1989: 45, pl. 17, figs 1–7, pl. 18, figs 5, 6). Ovicell spine bases, numbering ten, are arranged on the proximal gymnacyst of the distal brooding zooid, either in a gently curved, distally convex arch or in a straight line, slightly indenting the mural rim (Fig. 24D, G). Their diameter is equal to or greater than the oral spine bases, and the distance between neighbouring spine bases is less than their diameter. The gymnacyst of the ovicell floor is enlarged relative to that of zooids not bearing ovicells. Material of this species has been recorded from the Upper Cenomanian-Lower Turonian (*plenus* Zone) of Dresden-Plauen and elsewhere in Saxony, Germany.

Ovicells in *Stichomicropora subquadrata* Favorskaya, 1987 (Cretaceous, Upper Maastrichtian, Scheikaryk range, eastern Turkmenistan) were constructed of six obviously nonarticulated, juxtaposed spines belonging to the distal zooid. The bases of these spines are arranged in a gently curved, distally convex arch, with the distance between bases being less than their diameter (Fig. 24J). The trapezoidal ovicell floor is slightly concave (Favorskaya, 1987: pl. 3, fig. 1a, b). Overall, the morphology of this species is reminiscent of *S. baccata*.

Other species assigned to *Stichomicropora* in which ovicells have yet to be described are: *S. membranacea* (von Hagenow, 1839) from the Lower Maastrichtian of Rügen, Germany (see also von Hagenow, 1846; Voigt, 1930, 1957); *S. glabra* (Voigt, 1924) from the Campanian (*granulata* Zone) of Grube Bütten, near Hannover, Germany (see also Voigt, 1989); and *S. sussexiensis* (Brydone, 1936) from the Coniacian of Sussex, England.

Canu & Bassler (1926) believed that the spines covered the ovicell in *Stichomicropora*, whereas Voigt (1985, 1989) stated that they supported it, calling the ovicells acanthostegous. Both statements are incorrect: the spines themselves constituted the roof of the ovicell (Taylor & McKinney, 2002).

GENUS MONOPORELLA HINCKS (1881)

MONOPORELLA MULTILAMELOSA (CANU & BASSLER, 1920) (FIGS 10A, B, 22C, 24M)

Material: NHM BZ4860, Eocene, Castle Hayne Limestone Formation, Rocky Point Quarry, near Wilmington, North Carolina, USA.

Description: The ovicell roof is bilobate, consisting of two large, flat, nonarticulated spines belonging to the

distal zooid (Figs 10A, 22C, 24M). Each spine resembles an inverted diamond-shaped kite orientated at about 45 degrees to the long axis of the zooid. The bases of the spines form a straight line between the concave trapezoidal proximal gymnacyst, constituting the ovicell floor, and the distal cryptocyst (Fig. 10B). Cryptocryst fabric, sometimes with small pores, is evident around the spine bases, which are separated by a large medial gap (Fig. 10B), but the bulk of the spine surface has a smooth surface texture indicative of gymnacyst (Fig. 10A). The spines are directed proximally towards the orifice of the maternal autozooid. Their internal edges, except basally, are closely juxtaposed. The tips of the spines form a narrow arch-like opening for the ovicell, placed just above the maternal zooid orifice. Outer edges of the spines are positioned above depressed cryptocyst facets in the frontal walls of two zooids laterally adjacent to the ovicell (Figs 10A, 22C). These facets correspond to the two lateral foramina. Thus, each ovicell possesses four openings: distal, proximal and two lateral. Communication pores between the cavities of the spines and the distal zooidal chamber have not been observed. Two juxtaposed calcified walls, upper and lower, can be seen in each spine in broken ovicells.

Remarks: Originally assigned to *Macropora*, this species is here provisionally placed in *Monoporella* although it undoubtedly needs a new genus in view of the contrast shown in ovicell morphology between it and other species of *Monoporella*. Broken ovicells in *Monoporella multilamellosa* from the Eocene of the North and South Carolina were depicted by Canu & Bassler (1920: pl. 41, fig. 2) who apparently did not understand their nature. A brief description and illustration of intact ovicells in this species was given by Taylor & McKinney (2002: 311, fig. 1H).

Ovicells consisting of two flattened spines are also characteristic of *Monoporella vincentownensis* (Ulrich & Bassler, 1907) from the Upper Palaeocene Vincentown Limesand of New Jersey, USA. When redescribing this species Canu & Bassler (1933: 39) mentioned that the zooids are ‘frequently ornamented with two transverse lamellar expansions’, and figured complete and broken ovicells in their pl. 20, figs 5–7, with lateral foramina being visible in Figure 5 (see also Fig. 24M).

MONOPORELLA SP. 1 (FIGS 11A–C, 23A, 24J)

Material: GSUH, Recent, Okinawa Island, Middle Ryukyu Islands, Japan, Pacific Ocean.

Description: Zooids possess 2–6 small oral spines which are apparently articulated. Brooding (distal) autozooids have large, hemispherical hyperstomial ovicells that occupy two-thirds of the zooidal frontal

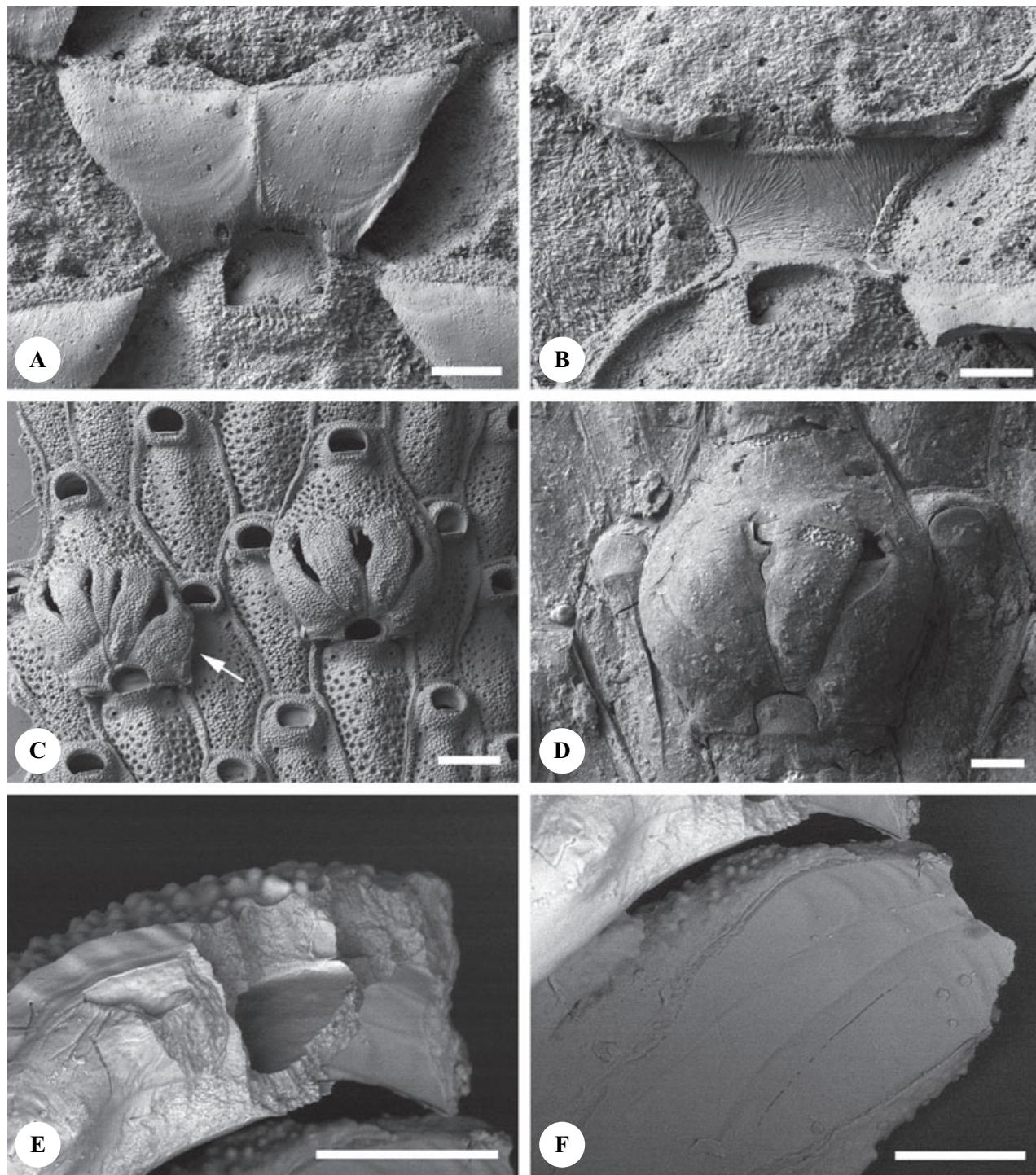


Figure 10. A, B, *Monoporella multilamellosa* (Canu & Bassler), Eocene, North Carolina, USA, NHM BZ4860. A, complete ovicell consisting of two flattened and expanded spines overgrown distally by a narrow fringe of cryptocyst; note lateral foramina. B, broken ovicell exposing gymnocystal floor and showing the medial gap between the bases of the two ovicell spines. C–F, *Monoporella* sp. 2, Recent, Alaska. C, bleached colony fragment with two complete ovicells and lateral foramen arrowed; MNHN 2856–7(b). D, unbleached ovicell; MNHN 2856–7(a). E, broken costa showing coelomic lumen; MNHN 2856–7(b). F, oblique view showing gymnocystal internal surface of ovicell; note limit of the cryptocystal expansion from the outer ovicell surface, and longitudinal grooves; MNHN 2856–7(b). Scale bars: A, B, F = 100 µm; C = 500 µm; D = 200 µm.

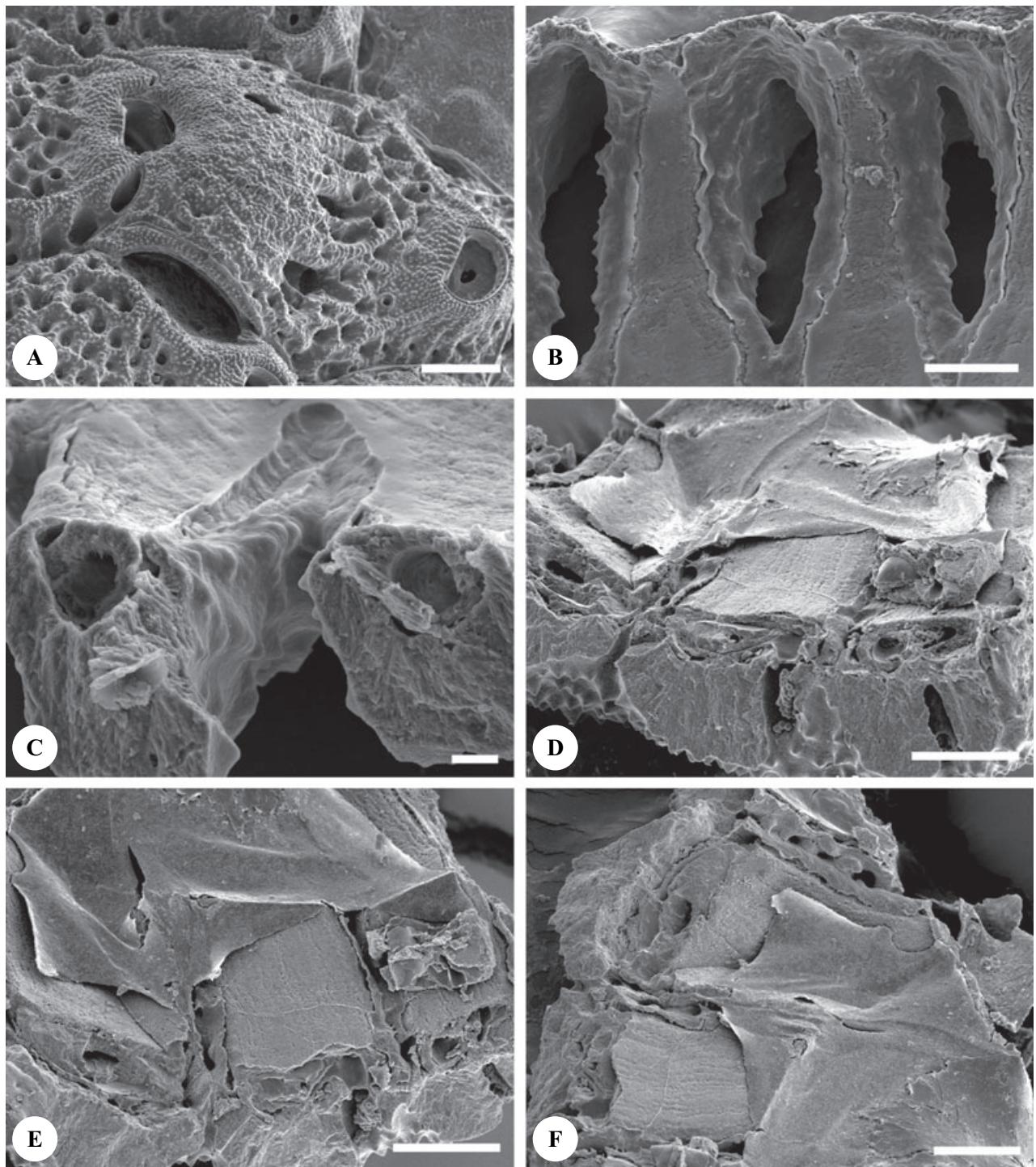


Figure 11. A–C, *Monoporella* sp. 1, Recent, Japan, Pacific Ocean, GSUH. A, oblique lateral view of bleached colony fragment with an ovicell; note distal fissures and large foramina. B, internal ooecial wall, showing fused costae and slits between their bases covered with cryptocyst. C, broken costal bases embedded in cryptocyst. D–F, *Monoporella nodulifera* (Hincks), Recent, Australia; unbleached broken ovicell roof upside down; membranous walls are seen on both sides, as well as three flattened costae covered by cryptocyst which is pierced by canals; cryptocystal insertions with pores are seen between the costae. Scale bars: A = 200 µm; B, D, E, F = 50 µm; C = 10 µm.

surface (Figs 11A, 23A). The arch-like opening of the ovicell is placed just above the maternal zooid orifice, and is closed by the zooidal operculum (cleithral type) (see description of *M. nodulifera* below). Externally, the calcified ovicell roof has a granular appearance similar to the cryptocyst forming the frontal shields of the zooids but with fewer pits and pores. It is enveloped by an external membrane with a hypostegal coelom beneath. This hypostegal coelom is apparently confluent with the hypostegal coelom of the distal brooding zooid (Figs 11A, 23A). It is unknown whether the pores lead to the intracostal coelomic cavities (see below). An arch of six irregular fissures is present around the distal edge of the ovicell roof (Fig. 11A, B). Broken ovicells show that the skeletal wall actually consists of several hollow costae overgrown entirely by cryptocyst (Figs 11C, 23A), apart from the undersides facing into the brooding cavity. The fissures mark borders between the basal parts of the costae which subsequently become fused. It is unclear if the intracostal coeloms become confluent. Edges of ovicells have foramina positioned above the cryptocystal facets in the frontal shields of the two zooids laterally adjacent to the ovicell (Fig. 11A). Each ovicell therefore possesses three openings: the main proximal opening and two lateral foramina.

MONOPORELLA SP. 2
(FIGS 10C–F, 23C, 24J)

Material: MNHN 2856–7, Recent, Alaska, F. Canu Collection.

Description: The hyperstomial ovicells are large, swollen, hemispherical chambers, occupying two-thirds of the frontal surface of the distal (brooding) zooid (Figs 10C, D, 23C). The four or five large costae that form the ovicell are borne on the distal zooid and directed proximally towards the orifice of the maternal autozooid. Ovicell costal bases are arranged in a gently curved, distally convex arch at the boundary between the distinctly concave, elongate, trapezoidal proximal gymnecyst, constituting the ovicell floor, and the distal cryptocyst (Figs 10C, D, 24J). The spine bases are separated from each other by radial fissures, whereas the spine tips are juxtaposed, together forming the arch-like opening of the ovicell which is placed just above the maternal zooid orifice and is closed by the zooidal operculum (cleithral type) (Figs 10D, 23C). Externally, ovicell spines possess a granular cryptocystal fabric, sometimes with small pores leading to the costal coeloms which are confluent with the coelom of the brooding zooid, as is clearly seen in broken ovicells (Fig. 10E). The external skeletal surface of the ovicell is covered by a common (except at the costal tips) membranous wall (Figs 10E, 23C), with a hypostegal coelom beneath that is confluent with the hypostegal

coelom of the brooding zooid. Whereas frontal surfaces of costae are cryptocystal, costal surfaces facing into the brooding cavity have a gymnocystal fabric (Figs 10F, 23C). The edges of the fissures between costal bases show the limits of the extent of the external ooecial hypostegal coelom. Longitudinal grooves on the internal gymnocystal surface of the ooecium could be the remnants of initially independent spines (Fig. 10F). If so, each costa may be a compound structure constructed of two or three fused spines.

Oval-shaped lateral foramina are present (Fig. 10C), positioned above cryptocystal facets in the frontal shields of two zooids laterally adjacent to the ovicell (Fig. 23C). Thus, each ovicell possesses three openings: the main proximal opening plus two lateral foramina.

Remarks: Brief notes and illustrations of the intact as well as broken ovicells in this species were given by Taylor & McKinney (2002: 311, fig. 1I, J). Material in the MNHN, Paris bears Ferdinand Canu's unpublished manuscript name *Macropora elongata*.

MONOPORELLA NODULIFERA (HINCKS, 1881)
(FIGS 11D–F, 12A–D, 13A–D, 23D, 24J)

Material: NHM 1975.1.12.405pt, Recent, Chios, Greece, collected 14 August 1967 (note, this Mediterranean material may not be *M. nodulifera* *sensu stricto* – see Remarks below). BSS160, Tangaroa 81-T-1, sample 160, depth 59 m, 39°43.7'S, 147°19.6'E, Australia, collected 13 November 1981.

Description: All zooids possess 5–6 small, articulated oral spines. The bases of the two most proximal oral spines are often swollen, having the shape of knobs. Brooding (distal) zooids have large, hemispherical hyperstomial ovicells that occupy two-thirds of the zooidal frontal surface. The ovicell can apparently be formed by either an autozooid or a kenozooid. Its arch-like opening is placed just above the maternal zooid orifice and is closed by the zooidal operculum (cleithral type) (Fig. 12) (see also Remarks below). The external part of the calcified ovicell roof has a typically cryptocystal texture, with pits and pores, similar to the cryptocyst of the zooidal frontal shields (Fig. 13A, B, D). It is enveloped on both sides by an external membranous wall enclosing a hypostegal coelom that is confluent with the hypostegal coelom of the brooding zooid (Figs 11D–F, 23D). Broken ovicells show that the skeletal wall actually consists of several flattened, hollow costae overgrown by cryptocyst (Figs 11D–F, 23D, 24J). The 4–6 irregular fissures in an arch along the distal edge of the ovicell represent gaps between the bases of these costae. The costae are not fused but separated by cryptocystal insertions (Figs 11D–F, 23D). Cryptocystal pores on the upward-facing surface of the

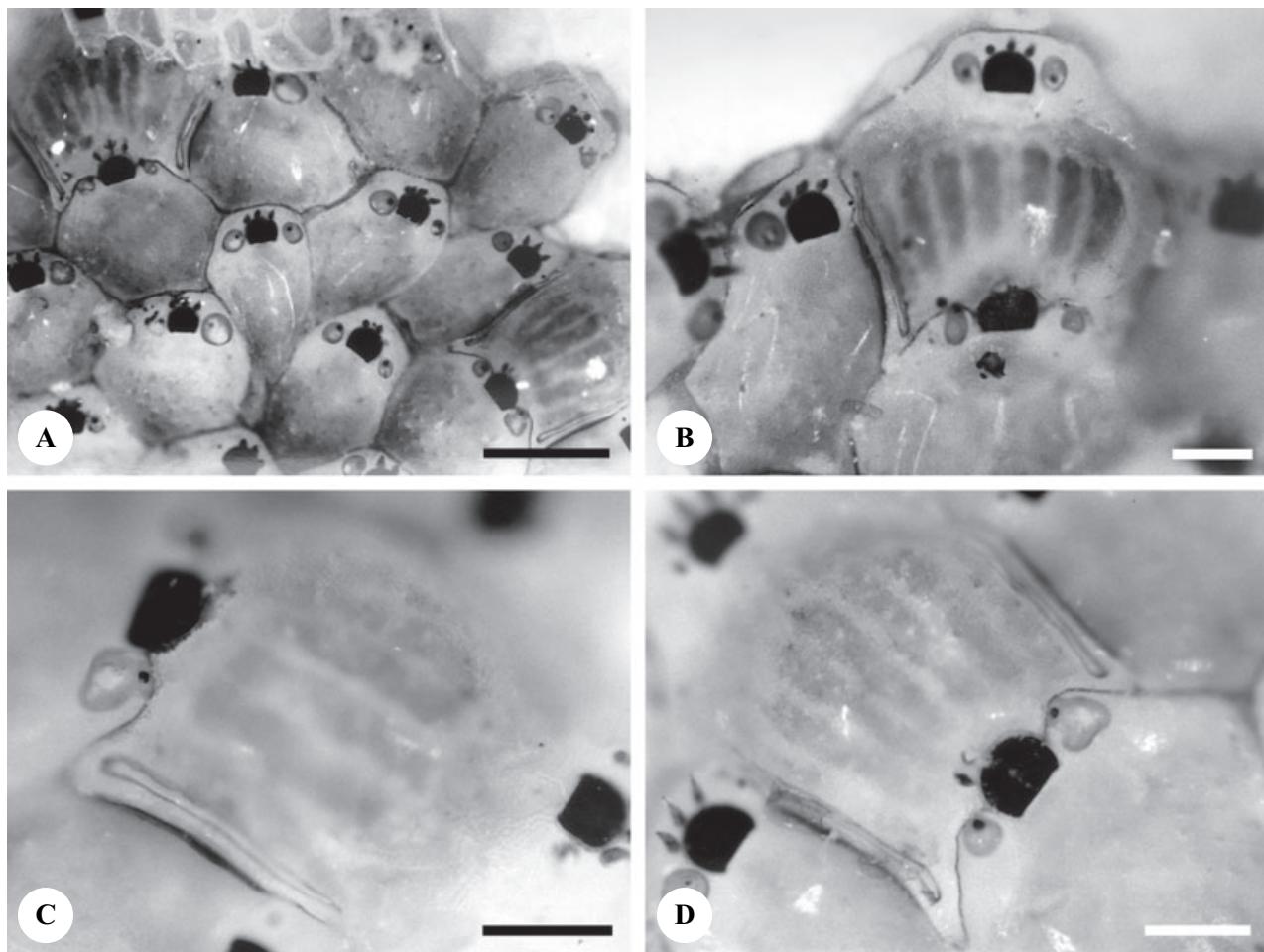


Figure 12. *Monoporella nodulifera* (Hincks), photographed wet; Recent, Australia. A, autozooids and two ovicells (top left and bottom right). B, ovicell showing costal banding. C, slightly oblique view of ovicell (orientated top left to bottom right), showing lateral foramen (black slit) parallel to the lateral ovicell groove. D, another ovicell (orientated bottom right to top left), with costal coelomic lumens visible as pale bands in the ovicell roof. Scale bars: A = 500 µm, B–D = 200 µm.

ovicell lead to an anastomosing system of coelomic lacunae that pierce the calcified cryptocystal layer and open as chains of pores on the cryptocystal insertions between the costae on the underside of the ooecium (Fig. 11D–F). Thus, the upper and lower parts of the ovicell hypostegal coelom are connected not only at the ooecial edge but also via these pores. Connections are also provided by fissures between the costal bases. In contrast, the coeloms of individual costae, visible as 6–7 longitudinal dark stripes in wet specimens (Fig. 12), are confluent with the perigastric cavity of the brooding zooid.

The ovicell floor is distinctly concave, trapezoidal in shape and gymnocystal. However, cryptocystal overgrowths may occur between the costal bases in developing ovicells (Fig. 13C). Lateral foramina are present, located above cryptocystal facets in the frontal shields of the two zooids laterally adjacent to the

ovicell (Figs 12B–D, 13B, D, 23D). Ovicells therefore possess three openings: the main proximal opening plus the two lateral foramina.

Remarks: Unbleached ovicells were first figured in this species by Harmer (1926: pl. 20, fig. 21) who described a wet specimen (p. 311) with ‘four deep longitudinal grooves . . . on the distal half of the entooecium’ (cf. Fig. 12 herein). Canu & Bassler (1929: pl. 17, fig. 10) published a photograph of a bleached colony fragment with an ovicell having four fissures (as *M. fimbriata carinifera* Canu & Bassler, 1929). The most detailed description of the ovicell was given by Hayward (1974; see also references therein for synonymy and localities), who stressed that the number of fissures (slits) varies from four to at least nine. He also noted that the slits could be eventually closed by progressive calcification.

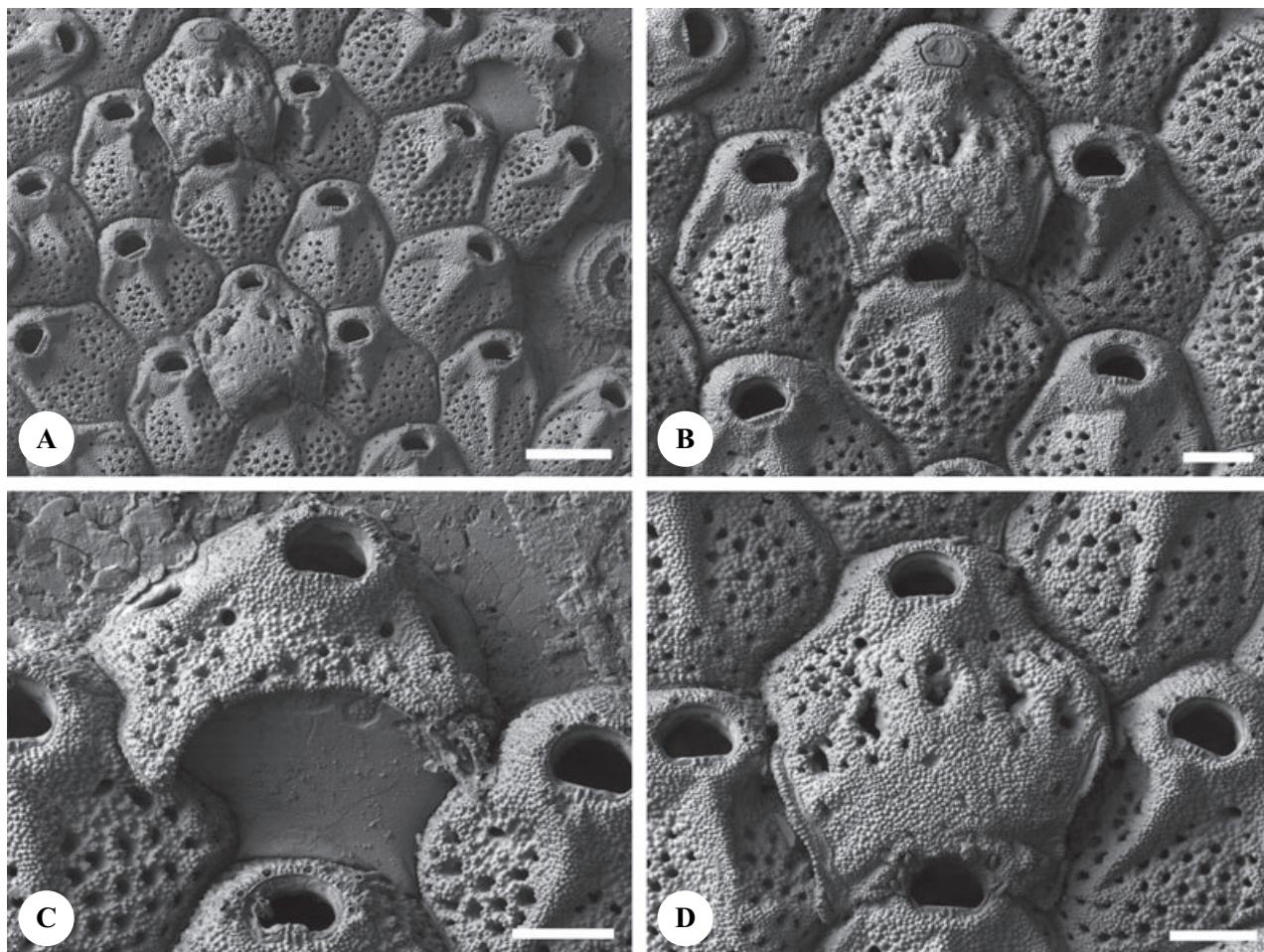


Figure 13. *Monoporella nodulifera* (Hincks) *sensu lato*, Recent, Chios, Mediterranean, NHM 1975.1.12.405pt. A, group of zooids with two complete and one incomplete ovicell. B, ovicell showing maternal zooid, distal zooid with orifice plugged by operculum, and lateral foramina. C, incomplete ovicell with cryptocystal overgrowths on the gymnocystal ovicell floor. D, complete ovicell. Scale bars: A = 500 µm; B–D = 200 µm.

The structure of the ovicell in thin section was illustrated by Cheetham & Cook (1983: fig. 72). Their photographs show that the roof of the ovicell consists of an external membrane and a calcified wall, with a hypostegal coelom between (their fig. 72.1). The calcified wall comprises a thin lower layer and a thick upper layer, described by them (p. 166) as the ‘initial layer’ and ‘superficial layer’, respectively. As is evident in their figure 72.1, the boundary between these layers can be a very narrow slit, possibly representing the coelomic cavities of the costae. The lower layer is a direct continuation of the gymnocystal ovicell floor, whereas the upper layer seems to be continuous with the cryptocyst of the brooding zooid. However, the boundary between costae and overgrowing cryptocyst is also seen as a weak line in figure 72.1 of Cheetham & Cook (1983). The main ovicell opening is closed by the zooidal operculum, whereas the lateral foramina

are closed by frontal membranes of the laterally neighbouring zooids (their fig. 72.2) (see also Figs 22B, C, 23A, C, D).

An SEM image of an Australian specimen of this species can be found on P. E. Bock’s web page (<http://www.civgeo.rmit.edu.au/bryozoa/cheiostomata/monoporellidae/mononod.html>) where it is noted that Mediterranean material putatively belonging to this species is not conspecific.

Additional data from the literature: The comb-like ovicells of *Monoporella prisca* Favorskaya, 1987 (Cretaceous, Upper Maastrichtian, Scheikhardy range, eastern Turkmenistan) are characterized by having a very conspicuous ‘spinose’ appearance. The ovicell roof is constructed of 8–9 juxtaposed spines whose bases are arranged in a wide, slightly distally convex arch (Fig. 24J). Taylor & McKinney (2002)

noted the similarity between the ovicell of *M. prisca* and those of *Stichomicropora*.

Ovicells in *Monoporella exsculpta* (Marsson, 1887) from the Lower Maastrichtian (Basbeck, near Hemmoor, Germany) and Upper Maastrichtian (St. Pietersberg, near Maastricht, The Netherlands) were briefly described and illustrated by Voigt (1989: 45–46, pl. 19, figs 1–3) (see also Fig. 24J). Their structure is very similar to *M. nodulifera* but only three fissures are visible in the ovicell roof (pl. 19, fig. 1). The broken base of an ovicell shows an oval slit (pl. 19, fig. 3) that may be the coelomic cavity of a costa overgrown by the cryptocyst. Contrary to Taylor & McKinney (2002), ovicells in this species are not bilobate.

The Recent species *M. fimbriata* Canu & Bassler, 1929 from the Philippines possesses ovicells with bases perforated by short parallel fissures, reminiscent of the patterns seen in *M. nodulifera* and *M. exsculpta*, but with more numerous fissures.

FAMILY MACROPORIDAE UTTLEY, 1949
GENUS *MACROPORA* MACGILLIVRAY, 1895
MACROPORA CRIBRILIFERA MAPLESTONE, 1901
(FIGS 14A–C, 23B, 24R)

Material: NMV P311815. Lower Miocene, Mount Gambier Limestone, limestone quarry about 1 km west of Mount Shanck (37°57'S, 140°43.2'E), South Australia, collected by P. E. Bock.

Description: The hyperstomial ovicells are normally constructed by distal autozooids but one observed example was formed by a distal kenozooid. Ovicells are large, occupying the entire zooidal frontal surface except for the orifice/opesia, and consist of 16 spine-like ribs (costae) arranged in a radial pattern and separated by distinct slits (Figs 14A–C, 23B, 24R). The two most proximal ribs are wider than the others (Fig. 14A, C), and the shortest ribs are sometimes found in the distal part of the ovicell (Fig. 14B). The costae are flattened, with the lumen confluent with the chamber of the distal brooding zooid. Their ends are fused along the midline of the ovicell to form a median ridge. Laterally, the costae are also fused periodically with neighbouring costae. Intercostal slits have the appearance of rows of elongated pores (Fig. 14A–C). Usually there are one or two pores on each side of the costal bases, with additional pores occasionally developed further along the costae (Fig. 14A–C). Judging from the presence of pores and the granular external texture, each costa was enveloped (at least externally) by cryptocyst, and the ovicell roof in this fossil species was probably originally covered by an outer membrane with a hypostegal coelom beneath. This coelom would have been confluent both with the hypostegal coelom of the distal brooding zooid

as well as the visceral coelom of the maternal zooid through the pores in the costal bases (Fig. 23B). Since the majority of the frontal surface of the distal, brooding zooid is occupied by the ovicell, parietal muscles deforming the frontal membrane during tentacle crown protrusion presumably passed through the pores in the costal bases. The slightly concave ovicell floor is mainly gymnocystal, as are the undersides of the costae facing into the brooding cavity. The arch-like opening of the ovicell is placed just above the maternal zooid orifice, probably being closed by the zooidal operculum (cleithral type).

Remarks: Maplestone (1901) described and illustrated *Macropora cribrilifera* from the Miocene of Australia (Mitchell River, near Bairnsdale, Victoria) (see also Canu & Bassler, 1929). SEM images of this species can be found on the website of P. E. Bock: (<http://www.civgeo.rmit.edu.au/bryozoa/cheilostomata/macroporidae/macrcrcri.html>). Superior preservation of the ovicells depicted here shows that each costa (except the most proximal pair) has a medial longitudinal keel. It is possible that this keel is a very narrow longitudinal strip of gymnocyst. The surfaces of both the median ridge of the ovicell as well as the perimeter around the opening of the ovicell are smooth, possibly also representing gymnocyst.

MACROPORA WAIMATUKUENSIS (UTTLEY, 1949)
(FIGS 14D–F, 24R)

Material: CM zb51, holotype, ?Miocene, right bank of Waimatuku River, Southland, New Zealand. NIWA, Eocene, Runangan (Priabonian), Alma, Oamaru, North Otago, New Zealand. NHM BZ5201, Eocene, Runangan (Priabonian), Fortification Road cutting, Oamaru, North Otago, New Zealand, P. D. Taylor & M. J. Weedon Collection.

Description: The hyperstomial ovicell occupies the entire frontal surface of the distal brooding autozooid, apart from the orifice, and is constructed of 16 costae/ribs arranged radially with slits between (Figs 14D–F, 24R). The costae are hollow with their lumens fused distally. Surface texture is granular, and there is an oval pore at the base of some of the costae. Thus, the costal surface is cryptocystal and would have been enveloped by hypostegal coelom with an outer membranous wall during life. Possible exceptions are the central area of the ovicell roof (medial ridge) where the costae are fused (Fig. 14D, F), and the narrow stripes along the midline of some (all?) costae that are possibly gymnocystal. The arch-like opening of the ovicell is formed by the widest proximal costae. It is placed just above the maternal zooid orifice, and would have been closed by the zooidal operculum (cleithral type).

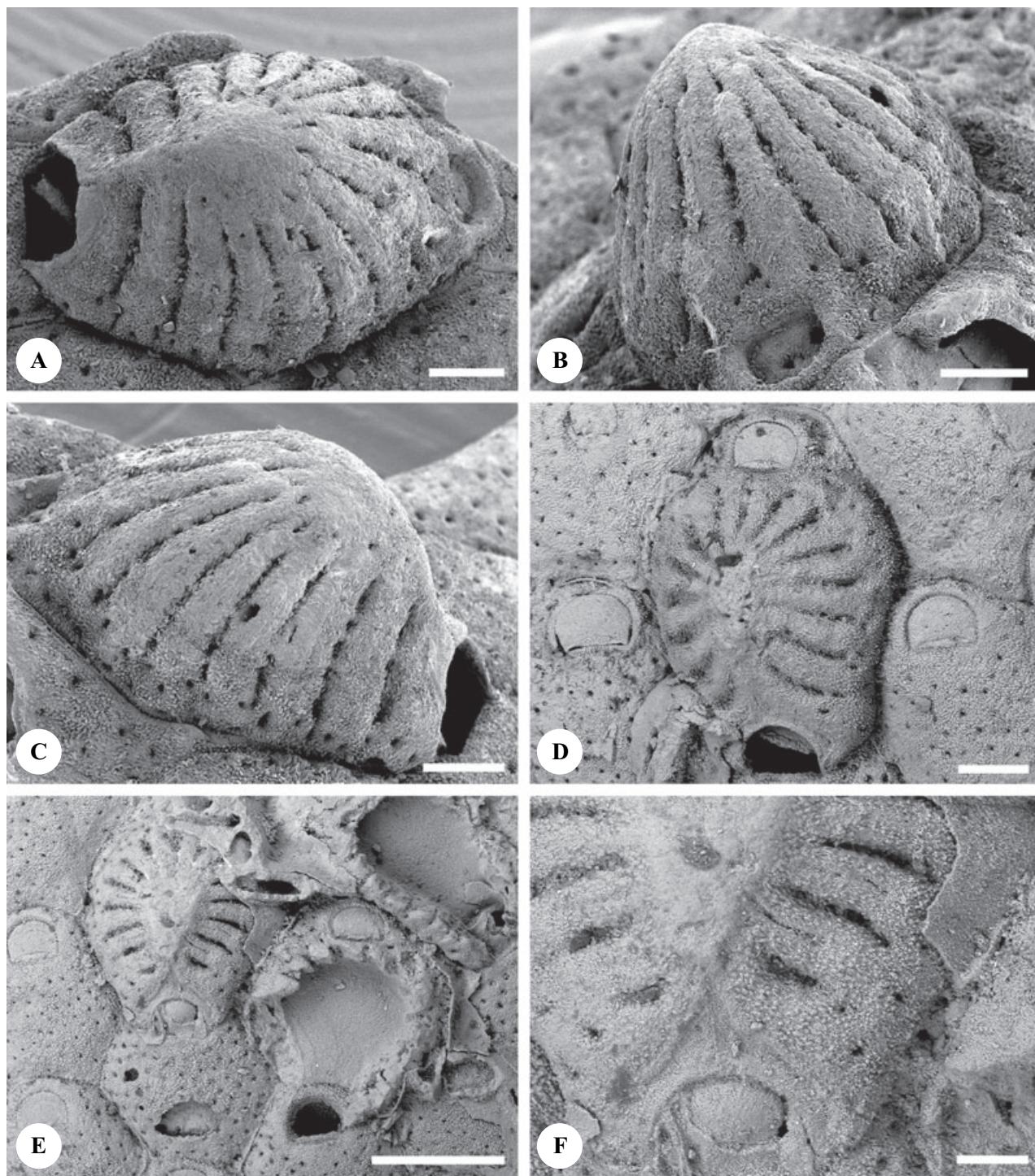


Figure 14. A–C, *Macropora cibrilifera* Maplestone, Lower Miocene, South Australia, NMV P311815. A, ovicell in oblique frontal view. B, ovicell viewed from the distal side (orifice of distal zooid bottom centre). C, lateral view of ovicell, showing intercostal slits and pores. D–F, *Macropora waimatkuensis* (Uttley). CM zb51, ?Miocene, Southland, New Zealand. D, complete ovicell; note calcified opercula in distal and two lateral zooids. E, complete and broken ovicells. F, proximal part of ovicell showing cryptocystal costal fabric. Scale bars: A–D = 200 µm; E = 500 µm; F = 100 µm.

Remarks: Uttley (1949: 180) described and illustrated ovicells consisting of 16–18 ‘rounded costules’ in this species (as *Macroporella*) from the Lower Oligocene (Whaingaroan) of Kakanui, North Otago, and the Lower Miocene of Waimatuku River, Southland, New Zealand. Additionally, he mentioned ‘costulate’ ovicells in *M. waimatukuensis* var. *trisinuata* Uttley, 1949 from the Upper Oligocene of North Otago and Middle Miocene (Waiauan) of North Canterbury.

MACROPORA SP. 1
(FIGS 15A, B, 23B, 24R)

Material: NHM BZ5202–3, Miocene, Otaian (Burdigalian), Waitemata Group, Parnell Grits, Faulkner Bay–Waikowhai section, Manukau Harbour, Auckland, New Zealand, P. D. Taylor Collection.

Description: The hyperstomial ovicell is very large, occupying the entire nonorificial frontal surface of the distal autozooid except for the orifice, and consists of 14–15 costae arranged in a radial pattern with broad intercostal slits (Figs 15A, 23B, 24R). The two most proximal costae are wider than the others. A median ridge or boss is formed by the fusion of the distal ends of the flattened costae. The surface texture of the costae is granular, resembling the cryptocystal frontal shield. Therefore, it can be inferred that the costae were covered by a hypostegal coelom beneath a membranous external wall in the living bryozoan (Fig. 23B). Worn ovicells expose the flat floor and show the presence of pores between the costal bases (Fig. 15B). The arch-like opening of the ovicell is placed just above the maternal zooid orifice, and was probably closed by the zooidal operculum (cleithral type). Distal (brooding) autozooids have noticeably smaller orifices than nonbrooding autozooids.

MACROPORA SP. 2
(FIGS 15C, 24R)

Material: NIWA, Recent, NIWA Stations Kah 0204/22 (34°4.68'S, 174°4.72'E, depth 610 m) and Kah 0204/27 (34°7.21'S, 174°5.64'E, depth 554 m), Cavalli Seamounts, New Zealand, collected 16 April 2002.

Description: Zooids possess 4–6 small, articulated oral spines. Brooding (distal) autozooids have large, hemispherical hyperstomial ovicells that occupy all of the zooid frontal surface except for the orifice. Maternal autozooids are shorter and wider than sterile autozooids. The opening of the ovicell is placed just above the orifice of the maternal zooid and is closed by the operculum (cleithral type). Externally, the calcified ovicell roof has a cryptocystal texture with pits, 12 short radial fissures and a medial furrow. The outer body wall above the ovicell calcified wall was evidently membranous, enclosing a hypostegal coelom confluent

with that of the brooding zooid. Broken ovicells reveal that the internal structure of the roof comprises flattened, hollow costae, proximally with slits flanked by cryptocystal calcification (Fig. 15C) but distally (at the summit of the roof) comprising fused, entirely gymnocystal costae. Costal lumens are confluent through slit-like openings with the perigastric cavity of the distal zooid but not with one another. The ovicell floor is gymnocystal.

MACROPORA UTTLEYI LÓPEZ DE LA CUADRA &
GARCÍA GÓMEZ, 1997
(FIGS 15D–F, 24R)

Material: NIWA, Recent, NIWA Stations Kah 0204/22 (34°4.68'S, 174°4.72'E, depth 610 m) and Kah 0204/27 (34°7.21'S, 174°5.64'E, depth 554 m), Cavalli Seamounts, New Zealand, collected 16 April 2002.

Description: Large hyperstomial ovicells are produced by a flat distal kenozoid that forms the base of the brood chamber. Maternal autozooids are smaller than the other autozooids (Fig. 15D–F). The arch-like opening of the ovicell is placed just above the orifice of the maternal zooid, apparently being closed by the zooidal operculum (cleithral type). Externally, the calcified ovicell roof has a granular cryptocystal fabric with pits and pores arranged in an ill-defined radial pattern. It was evidently covered by an external membranous wall enclosing a hypostegal coelom. Broken ovicells show that the roof actually consists of about a dozen fused and flattened costae (Figs 15E, F, 24R). The surfaces of costae facing into the brooding cavity are gymnocystal, separated from one another by porous bands of cryptocyst. The pores connect the external ooecial hypostegal coelom with longitudinal hypostegal cavities between the costae on the ooecial internal surface. Coeloms within the lumens of the costae (Fig. 15F) are apparently confluent with the perigastric cavity of the brooding zooid but not with each other. The ovicell floor is gymnocystal, its calcification smoothly continuous with that of the costae.

Remarks: López de la Cuadra & García-Gómez (1997) described and illustrated the radially arranged pores in the ovicells of this species from off Three Kings Island, New Zealand.

MACROPORA LEVINSENI BROWN, 1952
(FIGS 16A–C, 17A, B, 23E, 24R)

Material: NIWA, Recent, NIWA Station U1012, depth 35 m, east of New Zealand (39°56.35'S, 174°25.55'E).

Description: The large hyperstomial cleithral ovicell is produced by the distal kenozoid (Figs 16A, C, 23E)

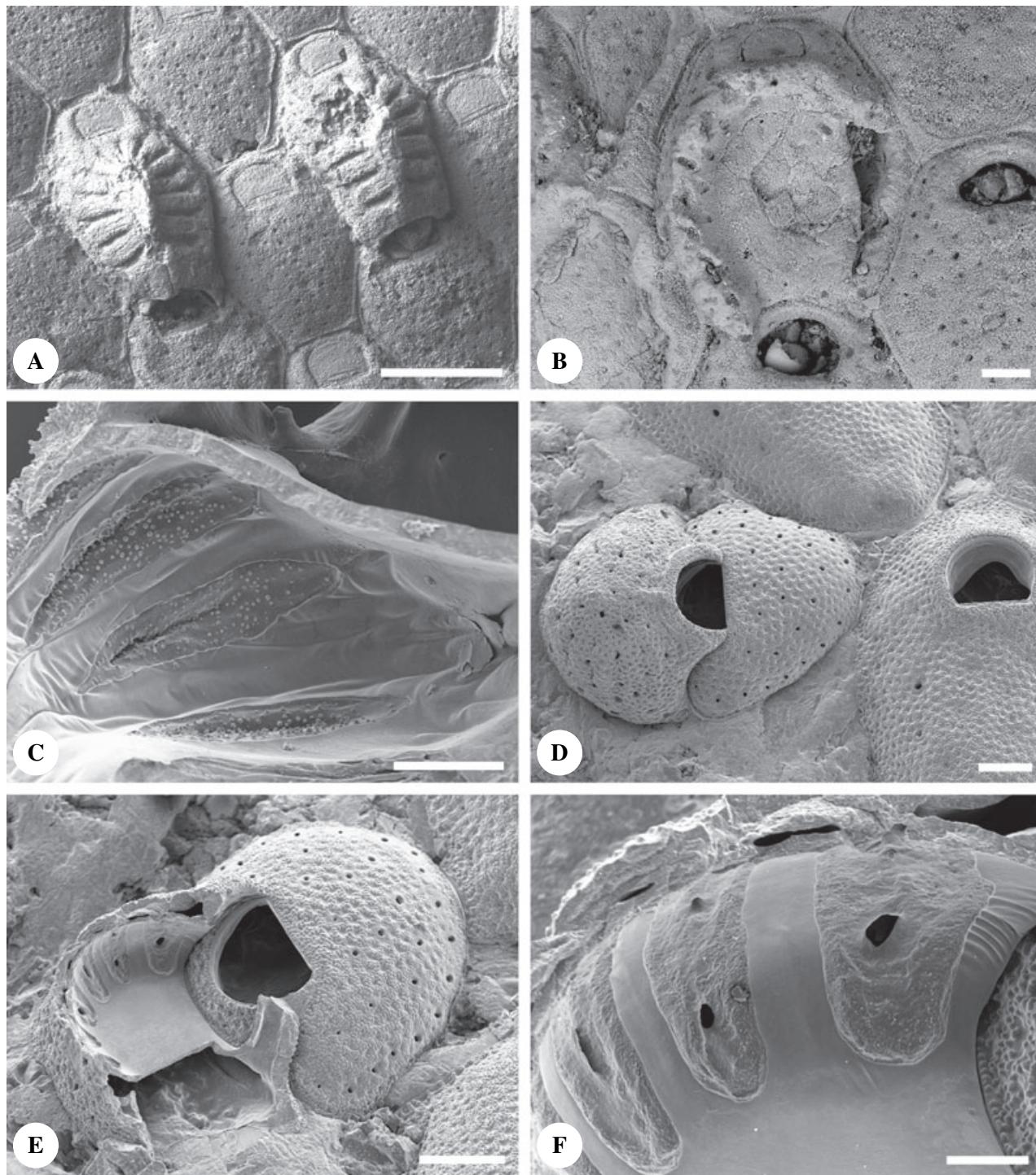


Figure 15. A, B, *Macropora* sp. 1., Lower Miocene, Auckland, New Zealand. A, colony with one complete and one damaged ovicell; NHM BZ5202. B, broken ovicell; NHM BZ5203. C, *Macropora* sp. 2, Recent, Cavalli Seamounts, New Zealand, NIWA. Ovicell from the inside, showing gymnocystal costal surfaces and intercostal spaces with cryptocystal fabric and fissures between them. D–F, *Macropora uttleyi* López de la Cuadra & García Gómez, Recent, Cavalli Seamounts, Pacific Ocean, NIWA. D, ovicellate zooid. E, broken ovicell, showing gymnocystal floor and inner costal surfaces. F, detail of ovicell interior, showing flat-surfaced costae and intercostal spaces with pores and cryptocystal fabric. Scale bars: A = 500 µm; B, C = 100 µm; D, E = 200 µm; F = 50 µm.

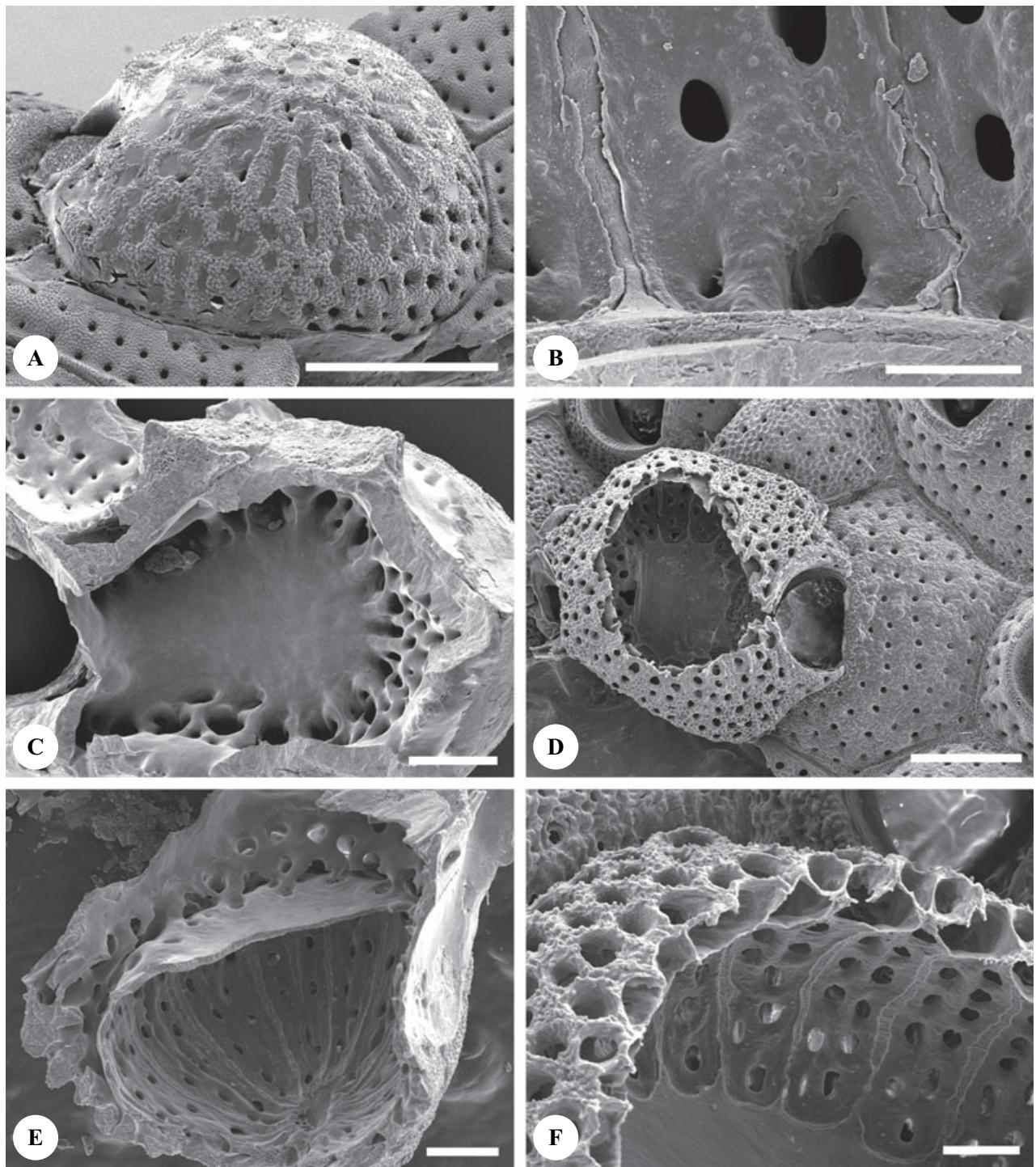


Figure 16. A–C, *Macropora levinsoni* Brown, Recent, New Zealand, NIWA. A, partly bleached ovicell, viewed laterally. B, interior of brooding cavity, showing bases of ooecial costae overgrown by cryptocysts; gymnocystal ovicell floor is below. C, ovicell upside down, showing the pores in its floor. D–F, *Macropora polymorpha* (Philips), Recent, New Zealand, NIWA. D, developing ovicell, showing gymnocystal floor and intercostal spaces with cryptocystal fabric. E, upside-down ovicell, showing the kenozooidal supporting zooid (top) and peripheral pores in the ovicell floor. F, part of the developing ovicell, showing costal coelomic lumina connected with lacunae in the cryptocystal matrix. Scale bars: A, D = 500 µm; B, F = 100 µm; C, E = 200 µm.

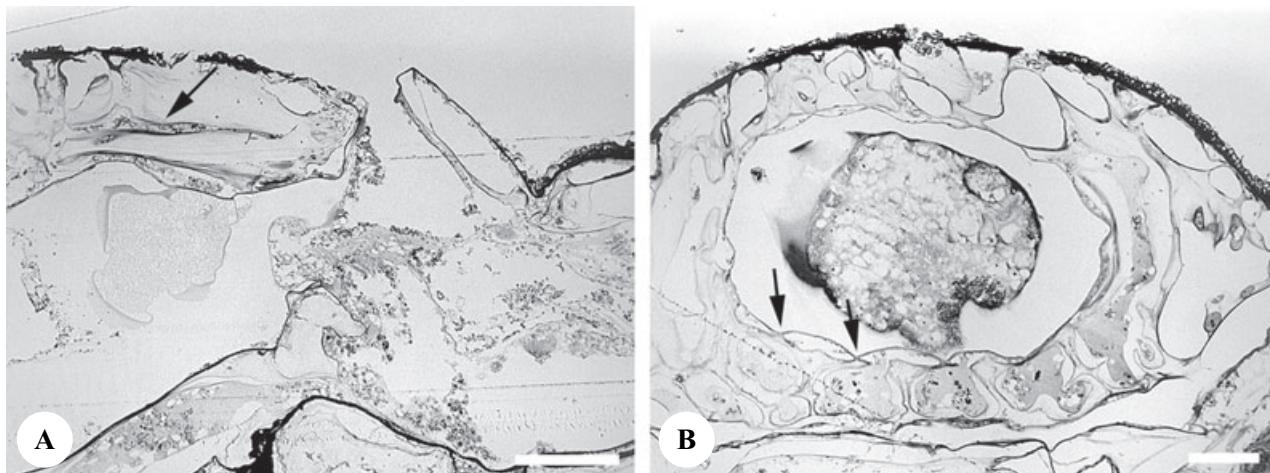


Figure 17. *Macropora levinseni* Brown, Recent, New Zealand. A, longitudinal section of an ovicell, showing costal lumen (arrowed) and zooidal operculum (right of arrow). B, saggital section of ovicell with embryo, showing attachments (arrowed) of the internal membranous ooecial wall to the calcified part of the ooecium; note thick external membranous ooecial wall. Scale bars = 100 µm.

which has pore chambers in contact with neighbouring autozooids. Compared with other autozooids, maternal autozooids are shorter whereas ovicells are longer. The calcified part of the ooecium consists of about 10–12 hollow costae embedded in a perforated cryptocystal matrix (Figs 16B, 17A, 23E, 24R). This complex wall is enveloped, both externally and internally (Figs 16A, 17A, B, 23E), by the membranous outer body wall with its underlying hypostegal coelom. The external (upper) membranous ovicell wall is thicker than the internal (lower) one. Basal parts of the costae facing into the brooding cavity are gymnocystal (Fig. 16B), not covered by the membranous wall and associated hypostegal coelom. In cleaned specimens longitudinal grooves visible on the internal ovicell surface correspond with costae.

From the outside the skeletal ooecial wall is a latticework of radial ribs, with granular surface texture, and subcircular and elliptical pores (Fig. 16A). However, only some of these ribs correspond to the costae visible internally; others are exclusively cryptocystal. The subcircular pores are mainly concentrated around the ovicell base, and the elliptical pores on the ovicell roof. Pores lead to the anastomosing lacunar system piercing the cryptocystal matrix and connecting the upper and the lower hypostegal coeloms (Figs 17B, 23E). Costae, except for their basal parts facing into the brooding cavity, are covered with cryptocyst and their narrow coelomic cavities open into its lacunar system. In sections of decalcified specimens the costal skeleton stains differently from the surrounding cryptocyst. The arch-like opening of the ovicell is placed

just above the orifice of the maternal zooid and is closed by the zooidal operculum (cleithral).

Most of the ovicell floor is gymnocystal except for the periphery where the costal bases and intervening cryptocystal overgrowths are covered by a membranous wall continuous with the internal membranous wall. Viewed from underneath, the peripheral area of the ovicell floor is also perforated by large and small pores (Figs 16C, 23E). Some of the large pores lead to the costal cavities, thereby connecting the costal coeloms with the kenozooidal coelom. Others are either fused with the former or pierce the floor linking the kenozooidal coelom with the hypostegal coelom above the ovicell floor.

Remarks: This extant species was first described as *Macropora grandis* (Hutton) var. *levinseni* by Brown (1952) based on material from Wanganui, New Zealand. There is at least one additional species, *Macropora grandis* (Hutton, 1873), recorded from the Lower Miocene-Recent of Australia and New Zealand, with a similar or identical ovicell structure (for synonymy and localities, see Brown, 1952; Gordon, 1984; López de la Cuadra & García-Gómez, 1997).

Gordon (1984: 57) noted that the ovicell can be 'resting on a distal [auto]zooid' as well as on a distal kenozooid in *Macropora grandis*. Following Brown (1952), he also commented that there was no distal kenozooid in some instances, and 'the ovicell apparently rests directly on the substratum'. Judging from the ovicell structure in *M. levinseni*, this statement is almost certainly incorrect and is based on the existence of

ovicells formed by very low and flat kenozooids that are difficult to observe.

MACROPORA POLYMORPHA (PHILIPPS, 1899)
(FIGS 16D–F, 24R)

Material: NIWA, Recent, NIWA Station Z9695, depth 89 m, Tom Bowling Bay, northern North Island, New Zealand (22°00'S, 173°00.01'W), collected 27 January 1999.

Description: Zooids possess 3–4 small, articulated oral spines. The large hyperstomial ovicell is produced by a kenozooid (Fig. 16D, E) distal of the maternal zooid which has pore chambers in contact with neighbouring autozooids. Compared to other zooids, the maternal autozooid is shorter whereas the ovicell is about the same size. Externally, the ooecial wall has a granular surface with oval or subcircular pores in radial rows (Fig. 16D, F) and is clearly cryptocystal. The calcified part of the ooecium consists of more than a dozen hollow costae, embedded in a perforated cryptocystal matrix (Figs 16E, F, 24R). This wall is apparently covered by a membranous wall, with underlying hypostegal coelom, on both the external and internal sides. The underside of the ooecial roof facing into the brooding cavity has narrow, raised strips of smooth, nonporous skeleton separated by broader regions of porous obviously cryptocystal skeleton (Fig. 1E, F). Each strip corresponds to a costa, having a short gymnocystal base. However, it is uncertain whether the narrow strips are gymnocystal; similar regions in *M. levinseni* are cryptocystal. Pores in the walls of the ooecium lead to the wide costal coelomic cavities and anastomosing lacunar system connecting the inferred upper and lower hypostegal coeloms (Fig. 16F). The arch-like opening of the ovicell is placed just above the maternal zooid orifice, being closed by the zooidal operculum (cleithral).

Most of the ovicell floor is gymnocystal (Fig. 16D). However, the peripheral region is cryptocystal and perforated by pores (Fig. 16D, F). Some of the larger pores lead into the costal cavities whereas others possibly pierce the floor of the ovicell, thereby connecting the kenozoidal coelom with the hypostegal coelom above the ovicell floor.

Remarks: López de la Cuadra & García-Gómez (1997) described and illustrated ovicells with radially arranged pores in furrows in material of this species from the Loyalty Islands (Pacific Ocean).

Additional data from the literature: Uttley (1949: 178) described and illustrated ‘strongly costulate’ ovicells consisting of 18–28 ‘ribs’ in *M. retusa* (Uttley, 1949) (as *Macroporina*) from the Whaingaroan (Lower Oligocene) of Kakanui, North Otago, New Zealand.

Scanning electron microscopy of Uttley’s material shows that the ovicell is formed by a distal kenozooid and constructed of 19 costae whose tips are fused along the median suture. Costal fusion leaves two groups of large oval slits, an upper group between the costal tips and a lower group between the costal bases. Each costa has a longitudinal furrow, possibly gymnocystal, whereas the rest of the surface has a cryptocystal relief. The base of the ooecium is encircled by round pores.

Radially striated ovicells with large marginal pores were described and figured by López de la Cuadra & García-Gómez (1997) in *M. georgiensis* López de la Cuadra & García Gómez, 1997. In this species from the Recent of South Georgia (Atlantic Ocean) they illustrated developing ovicells, showing the gymnocystal ovicell floor, bases of the costae and intervening cryptocystal overgrowths with pores similar to those seen in *M. levinseni*, *M. polymorpha* (see above) and also in *M. centralis* MacGillivray, 1895 (Miocene, Muddy Creek, south-eastern Australia). The latter species has been depicted on the web-site of P. E. Bock: (<http://www.civgeo.rmit.edu.au/bryozoa/cheilostomata/macroporidae/maercri.html>). Ovicells with radial striations and marginal slits also occur in *M. africana* Hayward & Cook, 1983 (Recent, eastern South African coast), and in *M. operculata* (Canu, 1908) (as *Hippoporella*) (Miocene, Chubut, Patagonia, Argentina). These strongly suggest a similar or identical ovicell structure to the species described above, with costae overgrown by cryptocyst.

FAMILY CRIBRILINIDAE HINCKS, 1879

GENUS LEPTOCHEILOPORA LANG, 1916

LEPTOCHEILOPORA TENUILABROSA LANG, 1916
(FIGS 18A–C, 22D, 24O)

Material: NHM D28892, Cretaceous, Santonian, *Marsupites* Zone, Upper Chalk, Brighton, Sussex, England. NHM D21210, Cretaceous, Santonian, *Marsupites* Zone, Upper Chalk, Roke Farm, south-east of Odham, Hampshire, England. NHM D29901, Cretaceous, Santonian *coranguinum* Zone, Upper Chalk, Houndsdown Bottom, west of Lewes, Sussex, England.

Description: Non-maternal zooids possess 2–4 small oral spines (four according to Lang, 1921 and Larwood, 1962). Occasionally two oral spines can be found in maternal autozooids. The frontal shield consists of 14–23 costae (14–15 according to Lang, 1921 and 17–22 according to Larwood, 1962) (Fig. 18A) with brooding zooids having fewer costae than nonbrooding zooids. There is no evidence for the existence of the ‘intercostal spaces’ described by Larwood (1962: 107–108).

The hyperstomial ovicells are formed on the proximal gymnocyst of the distal (brooding) autozooid. Their

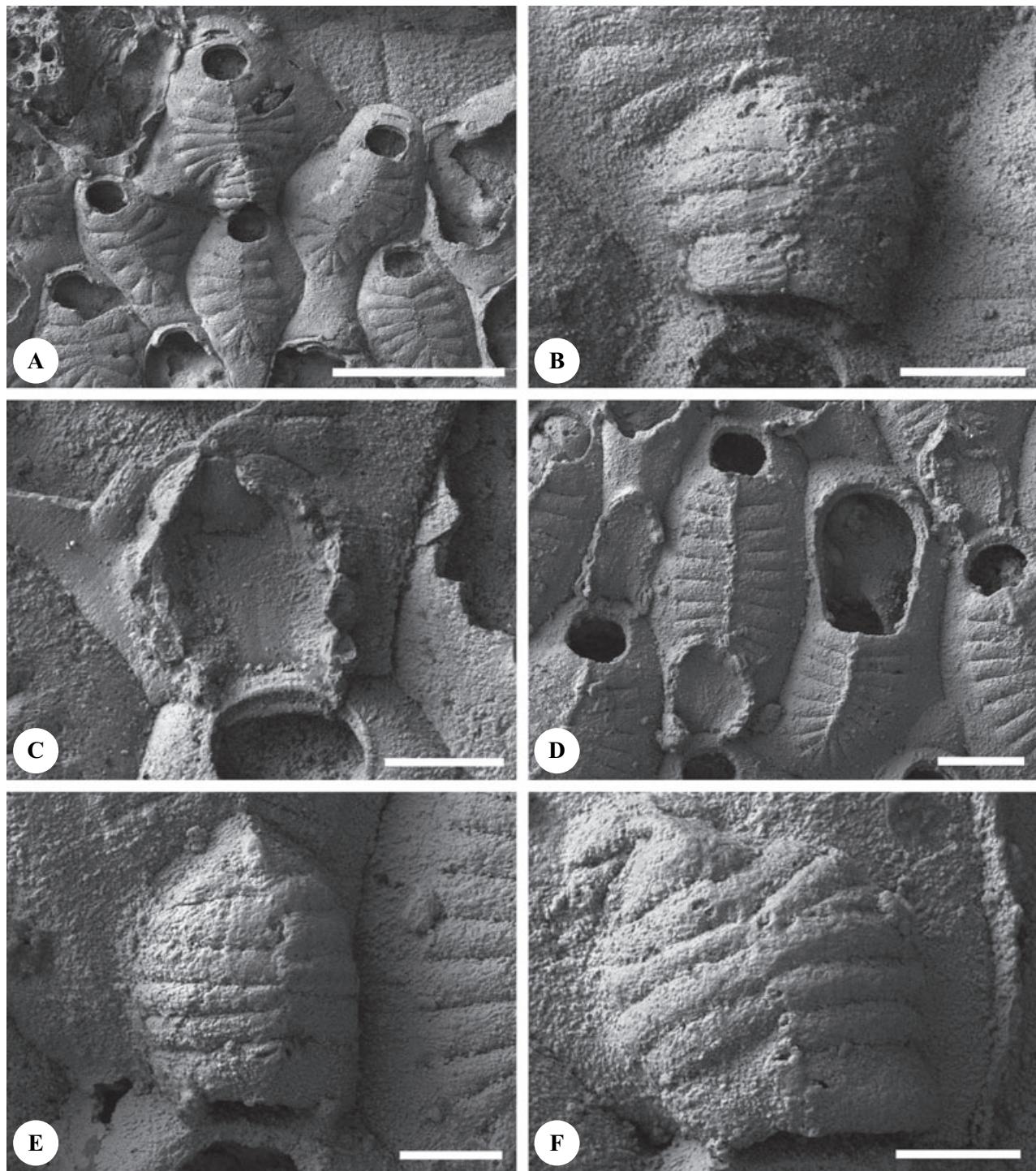


Figure 18. A–C, *Leptocheilopora tenuilabrosa* Lang. A, group of zooids and an ovicell (centre); Santonian, Hampshire, England, NHM D21210. B, complete ovicell, showing costae; Santonian, Sussex, England, NHM D28892. C, broken ovicell; Santonian, Hampshire, England, NHM D21210. D–F, *Leptocheilopora* sp. 1, Campanian, Norfolk, England, NHM D55505. D, three broken ovicells and a heterozooid with an enlarged orifice (right centre). E, complete ovicell. F, another complete ovicell. Scale bars: A = 500 µm; B, C, E, F = 100 µm; D = 200 µm.

external surface is distinctly costate, and they have a longitudinal medial suture that is aligned with the medial suture of the frontal shield of the distal zooid. Each ovicell roof consists of 11–14 tightly juxtaposed, centripetally orientated costae (Figs 18A, B, 23D). The bases of the costae are arranged in a semicircular (horseshoe) pattern (Figs 18C, 24O). Their distal tips meet and sometimes overlap on the midline of the ovicell roof. Ovicell costae have the same width as frontal shield costae, within the normal limits of variation. Distalmost ovicell costae are the shortest, often having a subtriangular shape, and are juxtaposed with the proximal (and shortest) frontal shield costae of the distal zooid. The two most proximal ovicell costae are located close to the distal boundary wall of the maternal zooid. The ovicell floor, surrounded by the costal bases, is slightly depressed. Larwood (1962: 109) described ‘occasional minute pores along . . . mid-lines’ of the ovicell costae but these have not been confirmed.

Costae of the only undamaged ovicell seen in specimen NHM D21210 expand and contract in width at intervals along their lengths in concert with neighbouring costae. The resultant wave-like form of the edges of the costae gives the impression that the costae fuse at intervals (Fig. 18A; see also text-fig. 1B of Ostrovsky & Taylor, 2004).

Remarks: The first illustrated description of costate hyperstomial ovicells in any cheilostome was made for this species by Lang (1921). The same author had earlier (1916: 396) diagnosed *L. tenuilabrosa* in a species key as having ‘Ovicells formed like the intraterminal front wall’, indicating that he had already recognized their costal structure. When describing ovicells in his new species *Cribrilina tumuliformis*, which was subsequently placed by Lang (1921) in synonymy with *L. tenuilabrosa*, Brydone (1917: 51) remarked that ‘in a favourable light it can be discerned that these ooecia are ribbed like the zooecia.’ Larwood (1962) described and illustrated ovicells in *L. tenuilabrosa*, writing that ‘costae . . . cover the ovicell’. He was uncertain if ‘the costae may form an ectooecium’ (p. 109). Ryland (1979: 214) followed Larwood in suggesting that ‘the ooecium was either formed by or covered with a series of spines’, whereas Ostrovsky (2002) showed the ooecial wall to be formed entirely of costae.

LEPTOCHEILOPORA SP. 1 (FIGS 18D–F, 22D, 24O)

Material: NHM D55505, Cretaceous, Campanian, *mucronata* Zone, low in the Weybourne Chalk, Keswick Chalk Pit, near Norwich, Norfolk, England, P. Whittlesea Collection.

Description: All autozooids possess two small oral spines. In nonbrooding autozooids, the frontal shield

comprises 21–22 costae whereas in brooding autozooids there are 15–19 costae, closely juxtaposed and without intervening slits (Fig. 18D).

The hyperstomial ovicells are formed on the proximal gymnocyst of the distal brooding autozooid. Their roof is composed of 12–13 hollow juxtaposed costae, whose distal tips meet to form a low median keel which is aligned with the medial keel of the frontal shield (Figs 18E, F, 22D). Ovicell costal bases are arranged in a semicircular (horseshoe) pattern (Figs 18D–F, 24O). The two most proximal ovicell costae are located close to the distal boundary wall of the maternal zooid. The gymnocystal ovicell floor is almost flat or slightly concave (Figs 18D, 22D). Judging from the positions of occasional closure plates, which tend to be secreted immediately underneath the operculum in cheilostomes, the ovicell opening may not have been closed by the operculum during life (acleithral). Ovicell costae have approximately the same width as the frontal shelf costae. The two most proximal ovicell costae are the widest, whereas the most distal ovicell costae are the shortest. The latter juxtapose the proximalmost (also the shortest) costae of the frontal shield of the distal zooid. In one instance an ovicell is separated from the costate frontal shield of the brooding zooid by a substantial expanse of proximal gymnocyst (Fig. 18D).

LEPTOCHEILOPORA SP. 2 (FIGS 19A–D, 22D, 24O)

Material: NHM BZ5204–6, Cretaceous, Lower Maastrichtian, *Porosphaera* Beds, Sidestrand, Norfolk, England, P. Whittlesea Collection.

Description: There are no oral spines. Non-brooding zooids possess 21–29 costae and brooding zooids 15–19. The costae are tightly juxtaposed with their neighbours and have one or two small lumen pores (pelmatidia) near their distal ends (Fig. 19A, B).

The hyperstomial ovicells are constructed of 14–15 juxtaposed costae on the proximal gymnocyst of the distal brooding zooid (Figs 19A–D, 22D, 24O). One example has been found of an ovicell formed by an intramural reparative autozooid (Fig. 19B). Distal ends of the overarching costae meet to form a median keel or sometimes a suture (Fig. 19A, C). These structures are in alignment with the median keel of the frontal shield. Costal bases of the ovicells are arranged in a semicircular (horseshoe) pattern. The ovicell floor is slightly concave and is longitudinally elongated or equidimensional (Fig. 19B). The two most proximal ovicell costae are positioned close to the distal boundary wall of the maternal zooid and are wider than the other costae. The distalmost ovicell costae are the shortest, often having a subtriangular shape. They are juxtaposed with the short, proximal costae of the

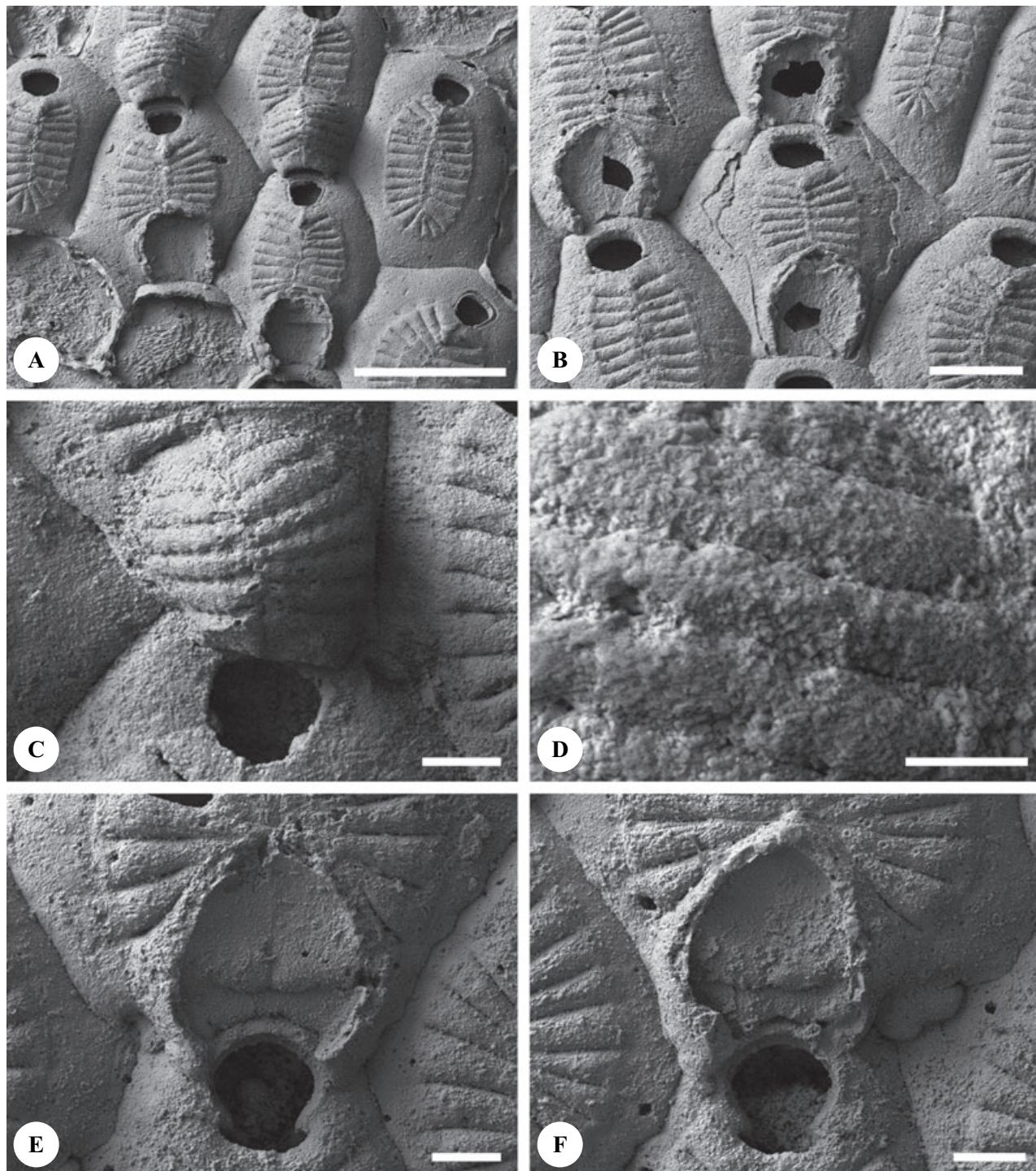


Figure 19. A–D, *Leptocheilopora* sp. 2. Lower Maastrichtian, Norfolk, England. A, group of zooids with complete and broken ovicells; NHM BZ5206. B, broken ovicells, that in the centre associated with an intramurally budded reparative zooid; NHM BZ5205. C, complete ovicell; NHM BZ5204. D, the same ovicell at higher magnification, showing apparent lateral fusions between costae. E, F, *Leptocheilopora magna* Lang, Campanian, Norfolk, England, NHM BZ5207. E, broken ovicell, showing horizontal slit. F, another broken ovicell. Scale bars: A = 500 µm; B = 200 µm; C, E, F = 100 µm; D = 50 µm.

frontal shield of the distal zooid. Ovicell costae are of roughly the same width as frontal shield costae.

As in the specimen (NHM D21210) of *Leptocheilopora tenuilabrosa* described above, junctions between ovicell costae have a wavy appearance, with intercostal sutures alternating with small pits (Fig. 19C, D). This gives the appearance of lateral costal fusions, although there is a clear demarcation line (suture) between the seemingly fused parts of the costae.

Remarks: Larwood (1962) suggested that *Leptocheilopora magna* Lang, 1916, with which this species can be compared, possessed costate ovicells. Unfortunately, there were no intact ovicells of *L. magna* at our disposal, although examination of broken ovicells in NHM BZ5207 suggests that Larwood's opinion may be correct. The base of broken ovicells shows oval flattened elements, possibly broken costal bases, with an inverted T-shaped arrangement of closed slits (Fig. 19E, F). This resembles the bilaterally symmetrical fold on the ovicell floor described in some Recent species of the cribrimorph *Puellina* (Ostrovsky, 2002).

Lang (1921) and Larwood (1962) recorded costate ovicells in the Cretaceous cribrimorphs *Andriopora homunculus* Lang, 1916, *Pliophloea striata* Lang, 1916, *Aeolopora distincta* Lang, 1916 and *Castanopora dibleyi* (Brydone, 1906). We have reinvestigated the specimens described by these two authors using SEM and have been unable to find any trace of costae in the ovicells of any of these species.

Additional data from the literature: Voigt (1994) described and illustrated a new cribrimorph, *Craticulacella schneemilchae* Voigt, 1994, from the Lower Campanian of Lägerdorf, near Hamburg, Germany. A broken costate ovicell is seen in Voigt's plate 5, figure 1. It is represented by an estimated 8–10 costal bases arranged in a semicircular (horseshoe) pattern on the proximal gymnocyst of the distal zooid. The two most proximal ovicell costae are positioned close to the two oral spines, which are of similar size, and to the distal boundary wall of the maternal zooid. In contrast with species of *Leptocheilopora*, ovicell costal bases are spatially separated. Coupled with the fact that the costae forming the frontal shield have open slits between them, this feature suggests that intact ovicells probably had intercostal gaps, at least around the edges of the ovicell.

A similar ovicell structure is found in the undescribed cribrimorph *?Thoracopora* sp. (Lower Cenomanian, Mülheim, Germany), illustrated by Ostrovsky & Taylor (2004: text-fig. 1C). A half-broken ovicell has seven flat costae borne on the proximal gymnocyst of the distal zooid. Preserved parts of the costae are juxtaposed, but there are distinct sutures between

them that may possibly be very narrow slits. An interesting point is that there are no distal (medial) spine bases in the two other, almost completely broken ovicells in this specimen. Thus, the ovicells of *?Thoracopora* sp. were probably formed by two lateral rows of costal bases. This may also be true for *Craticulacella schneemilchae* (Fig. 24N).

Judging from the illustrations, costate ovicells may also occur in the cribrimorph *Lekythoglena ampullacea* Marsson, 1887 (pl. 9, fig. 7) but this needs to be confirmed using SEM.

GENUS *BELLULOPORA* LAGAAIJ, 1963
BELLULOPORA BELLULA (OSBURN, 1950)
 (FIGS 20A–F, 22E)

Material: NHM 1986.8.14.20, Recent, Florida, Atlantic Ocean, Station GOS 736, depth 60–90 m.

Description: Non-ovicellate autozooids have only one or two small articulated oral spines (Fig. 20A) (Osburn, 1950 recorded 2–4 oral spines), except for the ancestrula which is tatiform and has numerous spines encircling the opesia. The ovicell is produced by a flat distal kenozoid (Figs 20A–F, 22E). The roof of the ovicell is constructed of 6–7 radial ribs which meet at the summit of the ovicell (Fig. 20A–F). Ribs are joined to their neighbours via short lateral fusions, leaving rows of bean-shaped lacunae between fusions (Figs 20D, E, 22E). Sea water can apparently gain entry into the brooding cavity through these lacunae in living colonies. The two proximalmost ribs are significantly wider than the others and form a transverse bar that overlies the distal part of the maternal zooid (Figs 20A, B, 22E). The medial part of each rib is concave and possesses a surface fabric typical of cryptocysts, although without granulation. Therefore, a longitudinal strip of hypostegal coelom can be inferred to be present. The concave medial strips belonging to the most proximal pair of ribs are always joined, indicating continuity of the hypostegal coelom across the top of the ovicell. Similar strips in the more distal ribs may also reach the summit of the ovicell and join the strips of other ribs (Fig. 20A, B). However, in other instances cryptocystal strips terminate before contacting those of neighbouring ribs, indicating that the hypostegal coeloms would not have linked with those of the other ribs.

Externally, each costa has a basal pore leading to a short canal through which the costal hypostegal coelom apparently communicates with the main visceral coelom of the kenozoid that forms the oocium (Figs 20D, 22E). The entrance to this canal from the inside is identical in appearance to the pores leading to the pore-chambers (Fig. 20E). Pores opening into costae and pore chambers alternate around the internal perimeter of the ovicell (Fig. 20D). Unusually for

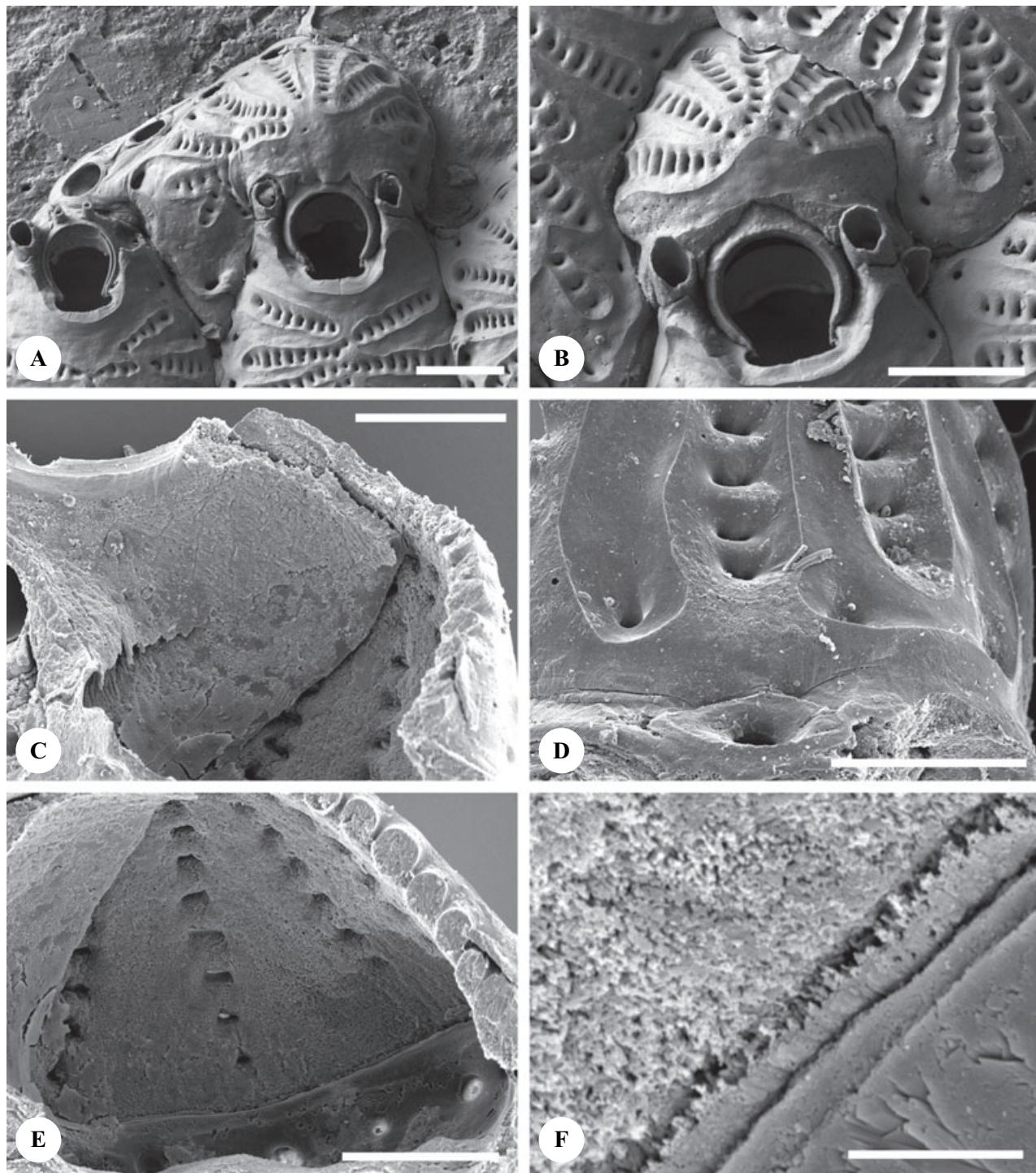


Figure 20. *Bellulopora bellula* (Osburn), Recent, Florida, Atlantic Ocean, NHM 1986.8.14.20. A, ovicell at colony growing edge. B, complete ovicell. C, interior of the ovicell, showing part of the peristome underlying the ovicell opening. D, basal pore chamber (centre bottom), two costal pores and intercostal fusions. E, interior of the ovicell; lower part is the cavity of a kenozooid (floor partly visible) that communicates with its pore chambers through the pores; upper part is the brooding cavity. F, higher magnification of the boundary between the wall of the cavity of the kenozooid (lower right) and the internal wall of an ovicell rib (upper left). Scale bars: A, B = 100 µm; C–E = 50 µm; F = 5 µm.

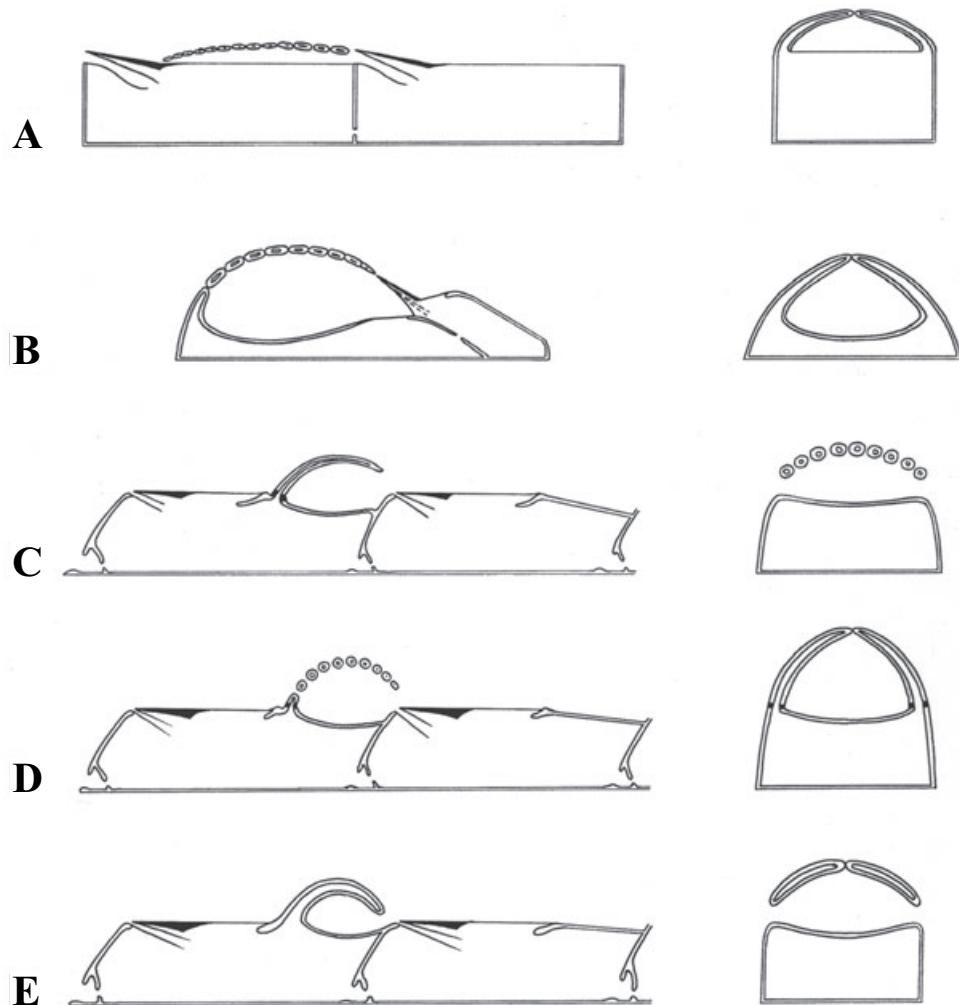


Figure 21. Schematic diagrams of brood chambers in Tendridae (A, B) and Calloporidae (C–E) in longitudinal and transverse section, showing maternal and distal zooids (fossil spinose ovicells reconstructed). A, *Tendra zostericola*. B, *Heterocodium* sp. C, *Distelopora bipilata* and *D. langi*. D, *Distelopora spinifera*, *Unidistelopora krauseae*. E, *Gilbertopora larwoodi*.

ovicells, the frontal wall of the brooding kenozooid that forms the floor of the ovicell is membranous rather than being a calcified gymnocystal layer. The boundary between the main kenozooidal coelomic cavity and the brooding cavity of the ovicell is clearly seen as a demarcation line separating areas of different skeletal ultrastructure (Fig. 20E, F). Ovicells are presumed to be cleithral.

Remark: Osburn (1950) was the first to describe *Bellulopora bellula* (as *Colletosia*) from the Recent of the Gulf of California and the Pleistocene of southern California. He noted ‘the primary ovicell [possibly, kenozooid]’ that ‘is small . . . , smooth, hemispherical’, and ‘soon becomes covered by an ectooecium which is composed of 3 or 4 pairs of radiating costules’ (pp. 188–189). Larwood (1962: 111) repeated Osburn’s descrip-

tion. However, Moyano (1984), when describing *B. bellula* from central Chile, came very close to understanding the unusual and enigmatic structure of its ovicell. He correctly recognized the kenozooidal nature of the ovicell in this species, and stated that ‘the ovicell external wall (= ectooecium) has the same structure as the frontal shield’ (p. 62). However, he thought that the hypostegal coelom of each costa connected with ‘a dietella [basal pore chamber] lying at the base of the lateral walls’ (p. 59; see also Moyano, 1991). He also found the ‘horizontal membrane that seems to be homologous to the frontal zooidal membrane’ (p. 62), but, unfortunately, did not appreciate that it represented the floor of the ovicell. Moyano described ‘a calcified globular structure (= the entooecium) positioned ‘inside [?] the ectooecium’. This is actually part of the peristome of the maternal zooid

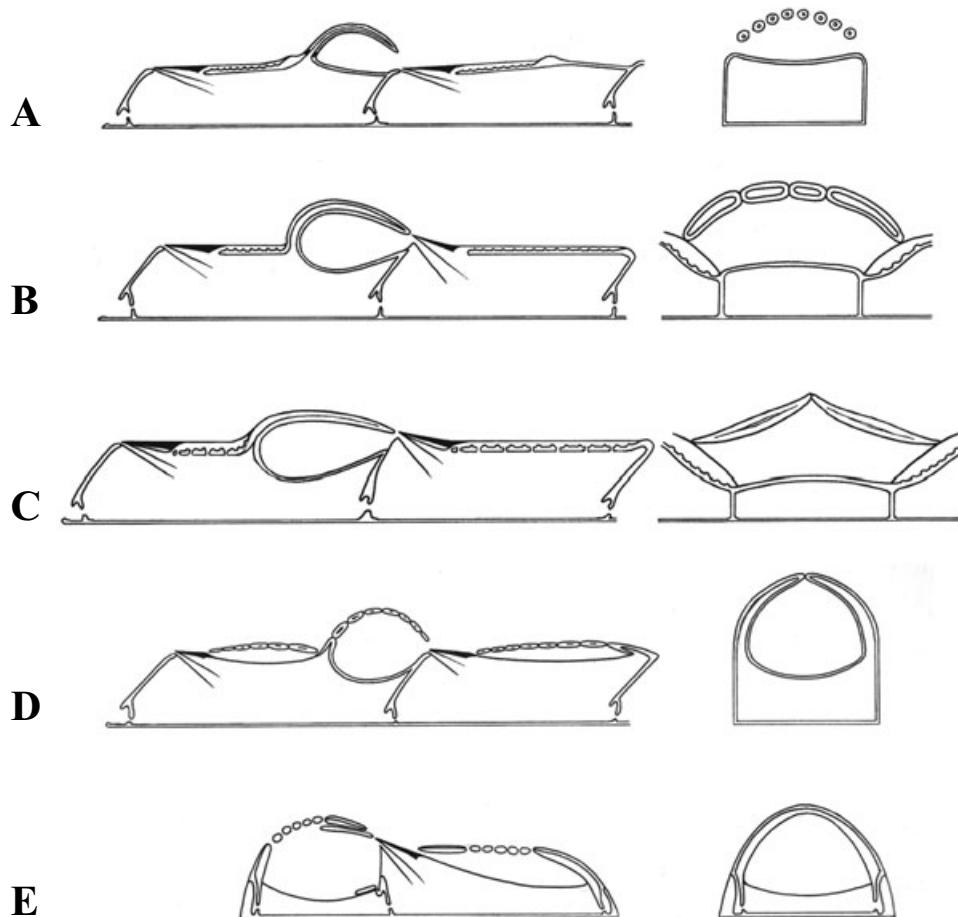


Figure 22. Schematic diagrams of brood chambers in Monoporellidae (A–C), Cribritlinidae (D, E) in longitudinal and transverse section, showing maternal and distal zooids (fossil spinose ovicells reconstructed). A, *Stichomicropora* spp. with articulated ovicell spine bases; B, *Stichomicropora baccata*. C, *Monoporella multilamellosa*. D, *Leptocheilopora* spp. E, *Bellulopora bellula*.

underlying the ovicell opening (Figs 20C, 22E) (for further discussion, see Gordon, 2000; Ostrovsky, 2002).

Brief descriptions of this species were also given by Lagaaij (1963) and Moyano & Melgarejo (1977), based on material, respectively, from the Gulf of Mexico and central Chile.

Additional data from the literature: There are several Recent cribritimorphs described in the literature whose ovicells resemble costate frontal shields and apparently have the same structure. Among these are *Figularia clithridiata* (Waters, 1887), *F. tahitiensis* Waters, 1929, *F. pulcherrima* Tilbrook *et al.*, 2001, *Puellina modica* Bishop & Househam, 1987 (see Ostrovsky, 2002).

DISCUSSION

The data presented above show that brood chambers constructed of spines, including costae, are not uncom-

mon among cheiostomes. They are widely distributed in the Upper Cretaceous, especially in Europe, with at least 28 species having spinose ovicells. An additional 19 species with spinose ovicells are known from the post-Cretaceous, including 11 Recent species. Taxonomically, spinose brood chambers are distributed among the following families: Calloporidae (five species in the genera *Distelopora*, *Unidistelopora* and *Gilbertopora*), Monoporellidae (23 species in *Stichomicropora* and *Monoporella*), Macroporidae (ten species in *Macropora*), Cribritlinidae (six species in *Leptocheilopora*, *Craticulacella*, *?Thoracopora* and *Bellulopora*), and Tendridae (three species in *Tendra* and *Heteroecium*). These numbers do not include *Macropora grandis*, *M. georgiensis*, *M. operculata* and *M. africana* and some Recent cribritlinids, all of which have yet to be adequately studied. In terms of geological distribution, spinose ovicells occur in Lower Cenomanian–Lower Campanian calloporids, Lower

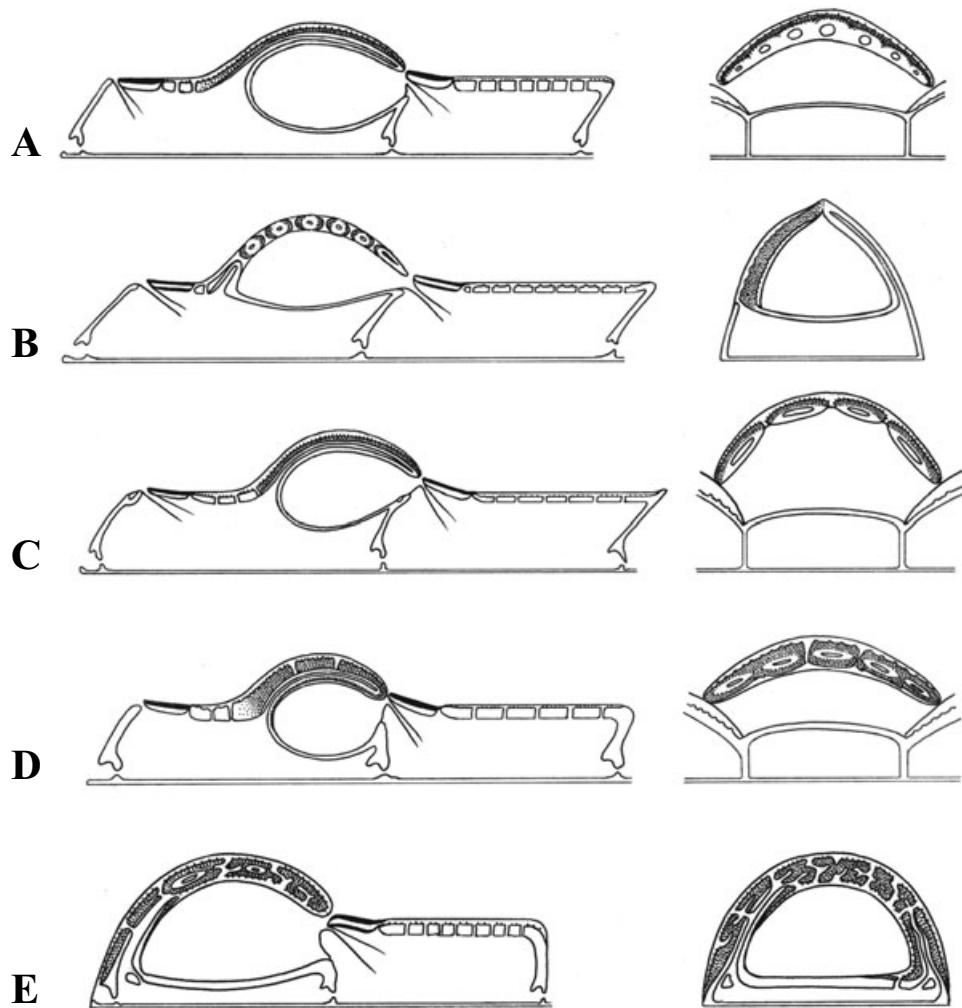


Figure 23. Schematic diagrams of brood chambers in Monoporellidae (A, C, D) and Macroporidae (B, E) in longitudinal and transverse section, showing maternal and distal zooids; cryptocystal ooecial matrix is shadowed. A, *Monoporella* sp. 1. B, *Macropora* sp. 1 and *M. cibrilifera* (transverse section made through cryptocystal (left) and gymnocystal (right) components of the ribs). C, *Monoporella* sp. 2. D, *Monoporella nodulifera*. E, *Macropora levinseni*.

Cenomanian–Recent monoporellids, Upper Eocene–Recent macroporids, and Lower Cenomanian–Recent cribrilinids. The acanthostegal brood chambers of the Tendridae are known only from the Recent.

The earliest geological records of ovicells are in the Upper Albian calloporid genera *Wilbertopora* and *Marginaria* (Cheetham, 1954, 1975; Taylor, 1988). These species have nonspinose ovicells that slightly antedate the oldest spinose ovicells. However, arguments based on morphology (see below) suggest that spinose ovicells represent the more primitive condition, implying the existence of still earlier species with spinose ovicells not yet recorded as fossils. All three of the oldest neocheilostome superfamilies (Calloporoidea, Microporoidea and Cribrimorpha) include Cenomanian species with primitive spinose ovicells.

It must be emphasized at the outset that the following discussions of ovicell origins and early morphological evolution are preliminary, pending a proper cladistic analysis of cheilostome phylogeny incorporating data on nonnovicellular characters which is beyond the scope of the current study.

A viable model for ovicell origin entails modification of mural spines previously used to protect the vulnerable frontal membrane. Precursors of the first brooding cheilostomes are probably to be found among early Cretaceous taxa assigned to *Spinicharixa* Taylor, 1986. This genus lacks ovicells but preserves the bases of articulated mural spines that encircle the opesia where the vulnerable frontal membrane was located during life. By analogy with Recent malacostegans such as *Villicharixa strigosa* (Uttley, 1951) and

V. pilosissima (Moyano, 1982) (see Gordon, 1989), a palisade of long articulated spines would have shielded this frontal membrane. It is easy to envisage some of these spines being co-opted for the additional function of protecting eggs (probably surrounded by a sticky fertilization envelope) laid onto the proximal gymnacyst of the distal zooid by the polypide of the maternal zooid. Curvature or re-orientation of the proximal mural spines away from the frontal membrane of the distal zooid and towards the proximal, maternal zooid can be hypothesized as the first step towards the acquisition of a specialized brood chamber for the developing larvae.

Morphologically, the most basic spinose ovicells are found in species of the calloporids *Distelopora* and *Unidistelopora*, and some species of the monoporellid *Stichomicropora*. These ovicells are represented by a row of articulated spines differing in location minimally from the mural spines found in many anascans (Fig. 24A, B). Often the medial ovicell spine bases are situated on or very close to the mural rim of the distal zooid. In *Distelopora* and *Unidistelopora* the mural spine bases and distalmost (medial) ovicell spine bases may form a continuous line (Fig. 24P), with the distalmost ovicell spines in the same position as the most proximal mural spines in nonbrooding zooids.

The exact arrangement of ovicell spine bases varies among Cretaceous cheilostomes and it is possible to propose a morphoseries leading from the primitive condition described above to more derived arrangements in which the configuration of the spines was probably more suitable for the protection of the brooded embryo. A distally concave arrangement of articulated ovicell spine bases can be interpreted as the least modified because it more closely resembles the arrangement of spine bases around the mural rim of the distal zooid. This arrangement is often seen in *Stichomicropora* sp. 1 and *S. oceanii* (excepting the two lateral spine bases). Seemingly more advanced is a state in which the majority of ovicell spine bases are arranged transversely in a straight line, as in some or all ovicells of *Stichomicropora* sp. 1, *S. oceanii*, *Stichomicropora* sp. 3, *Stichomicropora* sp. 5, *S. sicksi* and *S. sulcata*. Further modification to give a distally convex arch may be found in *Stichomicropora* sp. 1, *Stichomicropora* sp. 2, *Stichomicropora* sp. 3, *Stichomicropora* sp. 4, *S. sicksi*, *S. sulcata*, *S. erecta*, *S. biconstricta*, *S. cf. clathrata*, *S. punctilla*, *Distelopora bipilata* and *D. langi*. Note that all three of these basic arrangements can occur in a single species (*Stichomicropora* sp. 1) (Fig. 24A, D, G). Finally, a horseshoe-shaped pattern is known in *Distelopora bipilata* (occasionally), *D. spinifera* and *Unidistelopora krauseae* (Fig. 24).

Ovicells with gently arched and straight-line patterns of spine bases can be reconstructed as having a

canopy of proximally bent spines, leaving the ovicell open laterally. In contrast, horseshoe-shaped patterns probably resulted in a cage-like structure that provided protection from all sides (see also text-fig. 2 of Ostrovsky & Taylor, 2004). Thus, changes in spine base patterning can be linked with the transition from a primary function of protection for the frontal membrane of the distal zooid, towards progressively better protection of the developing embryos. The isolation of two lateral spine bases, as seen in some *Stichomicropora* ovicells, may represent an early stage in the change from a distally concave arch or straight line configuration to a distally convex arch (Fig. 24B, E, H). This change in spine base arrangement requires that some spines begin to develop on the gymnacyst away from the mural rim, a feature seen also in the Recent malacostegan *Villicharixa strigosa*. Ovicells may eventually lose contact with the mural rim; in some ovicells of *Distelopora bipilata* and *D. spinifera* even the median ovicell spine bases, which are normally close to the mural rim, are placed some distance from it and conventional spines may develop on the mural rim.

Similar variations in configuration are also seen among cheilostomes with nonarticulated, basally fused ovicell spines. Spine bases in distally concave and distally convex arches as well as straight lines have been observed in *Stichomicropora* sp. 6 (Fig. 24C, F, J), whereas straight line and distally convex arches occur in *S. baccata*, and distally convex arches in *Stichomicropora* sp. 7, *S. subquadrata*, *Monoporella nodulifera*, *M. exsculpta*, *M. prisca*, *Monoporella* sp. 1 and *Monoporella* sp. 2 (Fig. 24F, J). Although consisting of only two flattened spines, ovicell spine bases are arranged in a straight line in *M. multilamellosa*, and in a distally convex arch in *Gilbertopora larwoodi* (Fig. 24K, M). A third species, *Monoporella*(?) *vincenztownensis*, appears to exhibit both variations judging from published figures. The costae forming the ovicells of species of *Macropora* and *Leptochelopora* have a semicircular or horseshoe-shaped basal pattern. A similar pattern, but with the apparent absence of medial spines, occurs in *?Thoracopora* sp. and *Craticulacella schneemilchae* (Fig. 24N).

The presence of arch-like, distally convex patterns of ovicell spine arrangement in both calloporids and monoporellids is strong evidence for the monophyletic origin of the ovicell in these two groups. In addition, semicircular patterns of spine base arrangement provide a possible phylogenetic linkage between calloporids and cribrimorphs (see Ostrovsky & Taylor, 2004). Further evolution of the ovicells in cribrimorphs involved strong modification of the spines, with loss of basal articulations and flattening, transforming them into costae. Ovicells are noncostate in most Cribrilinidae, fossil as well as Recent, but often have a

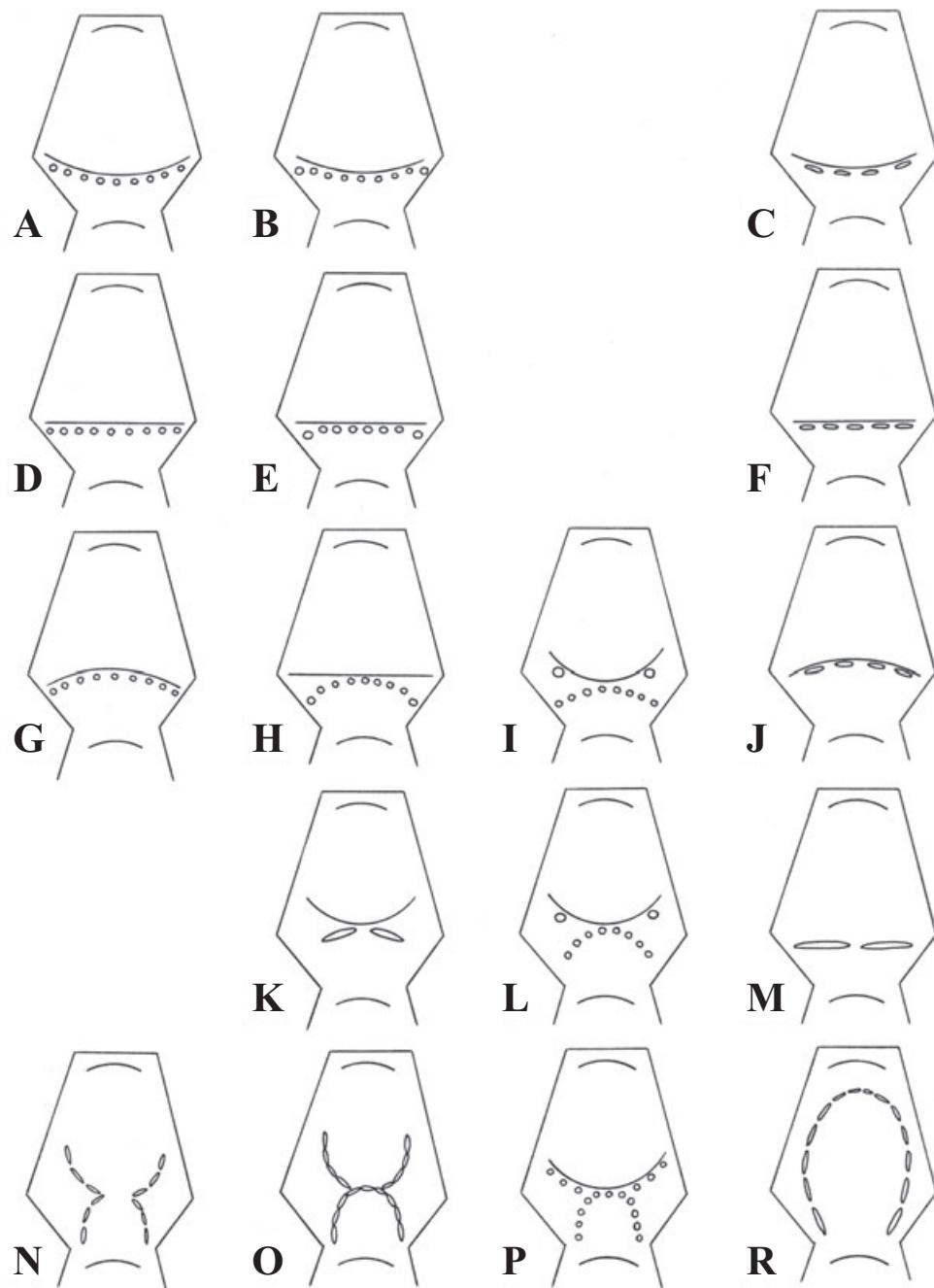


Figure 24. Schematic diagrams showing the shape of the mural rim and positioning of ovicell spine bases in frontal aspect; number of spines in *Stichomicropora* is approximate. Note that variable species may appear more than once. A, *Stichomicropora* sp. 1. B, *S. oceanii*. C, *Stichomicropora* sp. 6. D, *Stichomicropora* sp. 1, *S. sicksi* and *S. sulcata*. E, *S. oceanii*, *Stichomicropora* sp. 3, and *Stichomicropora* sp. 5. F, *Stichomicropora* sp. 6 and *S. baccata*. G, *Stichomicropora* spp. 1, 2 and 4, *S. sicksi*, *S. sulcata*, *S. erecta*, *S. biconstricta*, *S. cf. clathrata* and *S. punctilla*. H, *S. marginula*, *Stichomicropora* sp. 3; I, *Distelopora bipilata* and *D. langi*. J, *Stichomicropora* spp. 6 and 7, *S. baccata*, *S. subquadrata*, *Monoporella* spp. 1 and 2, *M. prisca*, *M. nodulifera*, and *M. exculpta*. K, *Gilbertopora larwoodi* or *Wilbertopora mutabilis*. L, *Distelopora bipilata*. M, *Monoporella multilamellosa* and *M.?* *vincentownensis*. N, ?*Thoracopora* sp. and *Craticulacella schneemilchae*. O, *Lepotocheilopora tenuilabrosa*, *Leptocheilopora* sp. 1, and *Leptocheilopora* sp. 2. P, *Distelopora spinifera* and *Unidistelopora krauseae*. R, *Macropora* spp.

bilobate appearance because of the presence of a medial keel or suture. Each lobe of the ovicell communicates with the distal zooidal chamber via a long lateral slit (Ostrovsky, 2002). Judging from the external ovicell morphology of *Leptocheilopora* sp. 2 and the Hampshire specimen of *L. tenuilabrosa*, it can be suggested that bilobate ovicells in cribrimorphs may have originated through costal fusion, similar to the fusion of costae seen in cribrimorph frontal shields. The seeming absence of medial costae in the ovicells of ?*Thoracopora* sp. and *Craticulacella schneemilchae* may also point to loss of costae during the evolution of cribrimorph ovicells. The resulting large distal gap could be closed by progressive flattening and enlargement of the two bordering costae, leaving just horizontal slits similar to those present in Recent *Puellina* (Ostrovsky, 2002) and Cretaceous *Leptocheilopora magna* (see above).

Loss of basal articulation, together with flattening and fusion of the spines, also characterized ovicell evolution in monoporellids. The costate ovicells seen in *Stichomicropora baccata* bear a marked resemblance to the costate frontal shields of cribrimorphs. A further step in monoporellid ovicell evolution saw the gradual spreading of hypostegal coelom over the ovicell spines, allowing secretion of cryptocyst. Ovicell spine bases with a cryptocystal surface fabric have been found in the Eocene species *Monoporella multilamellosa*. Two Recent species (*Monoporella* spp. 1 and 2) have a membranous wall covering the external surface of the ovicell that is continuous with the frontal membrane, while in *M. nodulifera* this membrane envelops the ovicell both externally and internally. The calcified part of the oocium is represented by costae partially or completely immersed in cryptocyst. Levinson (1902: 14–15) referred to such ovicells as ‘hyperstomial oocia with a cryptocyst’, noting that its ‘calcareous layer . . . is really formed by the fusion of two layers’. In *M. prisca* ovicells are very similar to those found in most species of *Stichomicropora*, having a gently curved, distally convex pattern, and spines juxtaposed with each other as in *S. baccata*. Unfortunately, it is impossible to tell from Favorskaya’s (1987) description and small illustration whether the spine surface has a cryptocystal or gymnocystal fabric.

Better protection of the brooded embryos apparently could be achieved by plugging the ovicell openings. Early spinose ovicells were probably aleithral, with the main, proximal entrance to the ovicell open. Later in evolution this opening was closed by the operculum of the maternal zooid. A transverse section of the ovicell in *M. nodulifera* (Cheetham & Cook, 1983: fig. 72.2) illustrates how the lateral ovicell openings (foramina) are plugged by the frontal membranes of the two neighbouring zooids. The maternal, distal and

two lateral zooids represent a ‘cluster of polymorphic autozooids forming [the] brooding structure’ (Cheetham & Cook, 1983: 166). The brooding cavity is isolated from the external medium (text-fig. 1k, see also G, H, J, K) by the lateral zooids. This could explain why a semicircular pattern of spine bases did not evolve in monoporellid ovicells – there was no need to protect the brooding cavity laterally since the lateral ovicell openings were closed by the frontal walls of the lateral zooids.

Species of *Macropora*, another coilostegan, differ in having a semicircular or horseshoe-shaped pattern of ovicell costae (Fig. 24R), without the lateral foramina seen in costate ovicells of *Monoporella* and *Stichomicropora*. Cryptocrystal overgrowth of the ovicell costae, either externally or all over, is another feature of *Macropora* that is shared with *Monoporella*. In *Macropora* sp. 2 and *M. uttleyi* the ooecial wall facing into the brooding cavity is mainly gymnocystal, whereas in *M. levinseni* and *M. polymorpha* it is mainly cryptocystal. Lateral fusion of the costae can be demonstrated by comparing ovicells in *M. waimatukuensis*, *M. cibrilifera*, *Macropora* sp. 1 and *Macropora* sp. 2 with those of *M. retusa* and *M. uttleyi*, the former group having slits and the latter radiating pores. External longitudinal strips of apparent gymnocyst were developed in the ovicells of some fossil species (*Macropora retusa*, *M. cibrilifera* and possibly *M. waimatukuensis*) but are unknown in Recent species. Fused, contiguous costal coelomic cavities characterize the ovicells of *M. waimatukuensis*, contrasting with the majority of *Macropora* species where only the costal wall itself is apparently fused.

Ovicells in the calloporid *Gilbertopora larwoodi* and the monoporellids *Monoporella multilamellosa* and *M. (?) vincentownensis* show marked similarities. They are bipartite, consisting of two modified spines that are flattened and nonarticulated, and have four openings. Ostrovsky & Taylor (2004) suggested that the ovicell structure of *G. larwoodi* could result from a reduction in the number of ovicell spines to two, accompanied by flattening and enlargement of these two spines. The same may be possible for the monoporellids. However, in contrast with the likely condition in the calloporid *Gilbertopora*, lateral foramina in monoporellids were probably closed by the frontal membrane of the neighbouring lateral zooids (see above), and the distal opening possibly by the frontal membrane of the distal zooid.

Another feature that can be inferred to have evolved independently among the three superfamilies in question is the gradual immersion of the ovicell floor. This would give more space for the developing embryo and/or provide better protection. Until the Maastrichtian when such species as *Stichomicropora baccata*, *Monoporella subquadrata* and *M. prisca* appeared, the

ovicell floor was flat or only slightly depressed. In contrast all Tertiary and Recent species possess a distinctly concave ovicell floor.

The earliest hyperstomial ovicells are known in calloporids from the Upper Albian and are nonspinose. Unless there is a long but undiscovered earlier history of ovicellate cheilostomes, it seems likely that the inferred evolution of nonspinose from spinose oovicells occurred very rapidly. Nevertheless, spinose oovicells have survived in some clades to the present day. In addition, many calloporids and cribrimorphs possess oovicells with a bipartite appearance (Ostrovsky, 2002). Radial striations present in some Recent cheilostomes could be a remnant of their spinose origin, although such an appearance may also be a fabric resulting from the centripetal calcification of the oocium.

As already noted, oovicell evolution cannot be properly understood without a phylogeny, which is currently not available. However, the most parsimonious interpretation is that oovicells evolved only once in the Cheilostomata and were initially spinose. Such features as reduction in spine number, distally convex curvature of the row of spine bases, spine flattening, loss of basal articulations, closure of gaps between spines and sinking of the gymnacyst forming the oovicell floor, all appear to have evolved to varying degrees in parallel in calloporids, microporoideans (monoporellids and macroporellids) and cribrilinids.

In the great majority of cheilostomes each oovicell broods only one embryo at a time. However, simultaneous brooding of several embryos within a single oovicell can occur in species having costate oovicells. In the costate oovicells of *Macropora levinsoni* Brown, 1952 (as *M. grandis* (Hutton) var. *levinsoni*), Gordon (1970) noted the presence of 2–4 embryos. Similarly, a costate oovicell of *Monoporella nodulifera* studied by us contained three embryos of similar size. While it is impossible to know how many larvae were simultaneously brooded in the spinose oovicells of primitive fossil neocheilostomes, their close relationship with malacostegans, which produce a large number of small embryos, together with the occurrence of more than one embryo per oovicell in *Macropora levinsoni* and *Monoporella nodulifera*, suggests that simultaneous brooding of multiple embryos may have occurred.

Brood chambers in the Tendridae probably evolved in a similar way to calloporid oovicells from a malacostegan ancestor through modification of mural spines. However, whereas calloporid oovicells originated by the bending towards the maternal zooid of a small cluster of proximally situated mural spines belonging to the distal zooid, in tendrids all of the mural spines surrounding the opesia of the distal zooid contributed to brood-chamber formation. These mural spines became bent towards the midline of the brooding zooid, resulting in formation of the calcified

frontal shield of spines that constitute the characteristic acanthostegal brood chamber. The brood-chamber floor in tendrids is formed by the frontal membrane of the distal zooid and is uncalcified, in contrast to that of neocheilostome oovicells, which is derived from the proximal gymnacyst of the distal zooid and is calcified.

Describing *Heteroecium amplexens*, Hincks (1892: 333) perceptively remarked that this special chamber for the reception of the embryo ‘... bears a close resemblance in structure of the front wall of the *Cribripline* zooecium, and like it has originated in a modification and adaptation of the marginal spines’. As in the Cribrilinidae, tendrids possess both articulated (oral) and nonarticulated ('brooding') spines (costae). It is quite possible that acanthostegous brood chambers constructed of articulated spines were precursors of the costate brood chambers seen in modern tendrids. However, this would be difficult to recognize in fossil tendrids where articulated spines are routinely lost.

The structure of the brooding complex in *Heteroecium*, consisting of the maternal zooid plus a kenozooid forming the brood chamber, resembles the condition known in some ovicellate neocheilostomes belonging to the Calloporidae, Cribrilinidae, Catenicellidae and Hippothoidae. The Tendridae also show a trend towards reduction of the distal brooding zooid like that described by Bishop & Househam (1987) in the Cribrilinidae (for further details and discussion, see Ostrovsky, 1998), and also evident in *Macropora*, where the brooding zooid can be an autozooid or, in apparently more advanced species, a kenozooid.

The seemingly unique oovicell structure of *Bellulopora* deserves comment. As with the acanthostegous brood chamber of *Tendra*, the brood-chamber floor is membranous and water can apparently enter into the brooding cavity. The membranous floor of the oovicell in *Bellulopora* could have originated through the secondary loss of a calcified, gymnacystal floor. Alternatively, the *Bellulopora* oovicell may be nonhomologous with those of other cribrimorphs, with the floor originating from the frontal membrane of the brooding zooid in the same manner as the acanthostegous brood chamber of *Tendra*.

Despite commonalities in brood-chamber construction among cheilostomes – embryos are always brooded in a space between a frontal wall and a roof made of or derived from modified spines – it seems likely that spinose brood chambers evolved at least twice in the Cheilostomata, once in the neocheilostomes and a second time in the tendrids. It is also possible that *Scruparia*, *Alysidium* and *Thalamoporella*, with their characteristic bivalved oovicells originating from the maternal zooid, represent an additional instance/s of independent evolution of brooding (see Ostrovsky & Taylor, 2004). However, further anatomi-

cal, morphological and phylogenetic studies will be necessary before such ideas can be properly evaluated.

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