SYSTEMATICS OF UPPER CRETACEOUS CALLOPORID BRYOZOANS WITH PRIMITIVE SPINOSE OVICELLS

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ABSTRACT. The majority of fossil and Recent cheilostome bryozoans brood their larvae in ovicells. These double-walled, hood-like skeletal structures are thought to have arisen through modification of spines belonging to the zooid distal of the maternal zooid. Support for this hypothesis comes from the existence of ovicells constructed of multiple spines in a few Upper Cretaceous species belonging to two groups, microporids and cribrimorphs. Here we report the discovery of similar multispinose ovicells in a third group, calloporids, which are closely related to primitive cheilostomes that do not brood their larvae. The genus *Distelopora* Lang, 1915 from the Cenomanian ('Chalk Marl') of Cambridge is taken out of synonymy and shown to comprise the type species (*D. bipilata*) and two new species (*D. langi* and *D. spinifera*) of multiserial calloporids. Between 5 and 15 spine bases are arranged in a crescent on the gymnocyst of the zooid distal of each maternal (egg-producing) zooid in *Distelopora*. This indicates the presence of an ovicell formed by a cage of basally articulated spines. Similar ovicells represented by 18–19 spine bases occur in a uniserial calloporid from the German Campanian *Allantopora krauseae* Voigt and Schneemilch, 1986, which is made the type species of the new genus *Unidistelopora*. Another calloporid from the Cambridge Cenomanian has ovicells constructed by two claw-like, flattened, non-articulated and laterally juxtaposed spines. Described as *Gilbertopora larwoodi* gen. et sp. nov., this multiserial species provides a link between *Distelopora* and more typical cheilostome ovicells. The spines forming primitive ovicells provide a good example of exaptations, co-opted from their original function protecting the polypide of the distal zooid.

KEY WORDS: Bryozoa, Cheilostomata, Cretaceous, Europe, systematics, evolution.

CHEILOSTOMES have been the dominant order of marine bryozoans since the Late Cretaceous. All pre-Albian cheilostomes belong to the paraphyletic malacostegans whose extant representatives release planktotrophic larvae directly into the sea (Ström 1977). Larval brooding can be interpreted as a key evolutionary innovation in cheilostomes because it correlated with the onset of an explosive increase in diversity (Taylor 1988a). As with other benthic invertebrate groups, an evolutionary switch from planktotrophic, non-brooded to lecithotrophic, brooded larvae would have had profound ecological and macroevolutionary consequences. Brooded larvae spend a significantly shorter time in the plankton, are less vulnerable to plankton-eating predators and vagaries in phytoplanktonic food sources, and have a restricted dispersal capability, resulting in a more heterogeneous population genetic structure. The restricted gene flow within and between populations would have favoured allopatric speciation (including parapatric speciation) and may have had an important role in triggering evolutionary radiation.

The great majority of brooding cheilostomes (neocheilostomes) use ovicells for larval brooding. Although a variety of brooding structures is known in living cheilostomes, the scattered taxonomic distribution of these other modes suggests that ovicellular brooding was the primitive form of brooding from which other modes evolved. Because ovicells are calcified structures they are commonly well preserved in fossils and can be recognised with relative ease as small, hood-like chambers located just distally of the orifice of fertile feeding zooids. Accordingly, the fossil record can contribute to our understanding of the evolution of ovicells in cheilostomes. The oldest ovicells occur in two Upper Albian genera of calloporid cheilostomes, *Wilbertopora* and *Marginaria* (Cheetham 1954, 1975; Taylor 1988a).

Our purpose in this paper is to describe a previously overlooked and some undescribed Cenomanian and Campanian calloporid cheilostomes which provide important evidence bearing on the origin and early

evolution of ovicells. These taxa have multispinous ovicells which lend strong support to the hypothesis that ovicells originated as modified spines formed by the zooid distal of the maternal zooid. From such multispinose ovicells evolved more conventional non-spinous ovicells through reduction in spine number, loss of basal articulation, spine flattening and complete fusion to form a single rigid structure affording better protection to the embryo within.

Repository details. NHM, The Natural History Museum, London; SM, Sedgwick Museum, Cambridge; VC, Voigt Collection, currently in Hamburg but destined for the Senckenberg Museum, Frankfurt.

SYSTEMATIC PALAEONTOLOGY

Order CHEILOSTOMATA Busk, 1852
Suborder FLUSTRINA Smitt, 1868
Family CALLOPORIDAE Norman, 1903

Genus DISTELOPORA Lang, 1915

Type species. *Distelopora bipilata* Lang, 1915, Lower Cenomanian, 'Chalk Marl' (=Lower Chalk, Porcellaneous Beds), Cambridge, England.

Other species. *Distelopora langi* sp. nov. and *D. spinifera* sp. nov., Lower Cenomanian, 'Chalk Marl' (=Lower Chalk, Porcellaneous Beds), Cambridge.

Revised diagnosis. Calloporidae with encrusting, multiserial colonies often forming small lobate expansions. Autozooidal apertures and opesiae pear-shaped, oval or egg-shaped; gymnocyst well developed proximally; cryptocyst wide and shelf-like to narrow and inwardly sloping; mural spines numbering 6–21, sometimes paired, distributed around most of circumference of aperture, often indenting the mural rim. Ovicell represented by a crescent of 5–15 spine bases on gymnocyst of distal zooid, floor very slightly concave. Avicularia absent or present and vicarious, spatulate and about same size as an autozooid. Closure plates and intramural buds unknown. Pore chambers present, the large distal pore chamber with a transverse window opening frontally. Ancestrula budding either one distal zooid, or one distal plus two distolateral zooids.

Remarks. *Distelopora* was erected by Lang (1915, p. 502) as a monospecific genus with *D. bipilata* Lang, 1915 as the type species. Except for Voigt (1930) who described a new species as *Distelopora sparsa*, the genus has been neglected by later bryozoologists. This may be because Bassler (1935), repeated in the Treatise (Bassler 1953), placed *Distelopora* in synonymy with the malacostegan genus *Pyripora* d'Orbigny, 1849, with which it bears no close relationship. Lang (1915) somewhat misleadingly described the genus in a paper entitled 'New uniserial Cretaceous cheilostome Bryozoa' even though *Distelopora* is not strictly uniserial. The only post-Treatise mention that we could find is in a paper by Thomas and Larwood (1960) who compared the zooidal morphology of *Distelopora* with that of the malacostegan *Rhammatopora* Lang. The latter, however, has strongly caudate zooids, quite unlike those of *Distelopora*, and a runner-like colony-form.

The most striking feature of *Distelopora* is the multiplicity of spine bases representing the ovicell. Although this feature was not described by Lang in his paper of 1915, it is apparent from a pencil drawing on the reverse of a cavity slide containing a specimen (NHM D21876) of *Distelopora* that he had observed these spine bases. There is no indication that he understood their identity as ovicells. Fully intact ovicells have not been observed in *Distelopora* but, by analogy with similar spine bases found in modern calloporids, though not associated with ovicells, it can be inferred that a narrow, hollow spine was borne on each spine base, articulating by an uncalcified cuticular ring. A double ring structure seen in some of the spine bases is similar to that observed in articulated spines of modern bryozoans, further supporting the inference that the ovicell spines of *Distelopora* were basally articulated.

In overall zooidal morphology and distribution of mural spines, *Distelopora* is reminiscent of the

Cenomanian calloporid *Ornatella ornata* (d'Orbigny, 1853), the type species of *Ornatella* Canu, 1900, and also *Flustrellaria fragilis* d'Orbigny, 1853, the type species of *Flustrellaria* d'Orbigny, 1853. Other multiserial calloporid species, often referred incorrectly to '*Membranipora*' or '*Allantopora*' (e.g. Brydone 1929; Voigt 1930; Canu and Bassler 1933, 1935), can also resemble *Distelopora* but none that we know of has multispinose ovicells. In the absence of ovicells, the assignment of *Distelopora sparsa* Voigt, 1930 to this genus cannot at present be upheld; it is much more likely to belong to one of the commoner calloporid genera such as *Flustrellaria*.

Three species of *Distelopora* are recognised here, all from the Lower Cenomanian Chalk Marl of Cambridge. They differ from one another in the number of mural spines, number and arrangement of ovicell spines, and development of the cryptocyst.

Distelopora bipilata Lang, 1915

Plate 1, figures 1–6

1915   *Distelopora bipilata* Lang, p. 503, pl. 17, figs 8–9.

Holotype. NHM D23019, incomplete colony, consisting of nine autozooids, all without ovicells, with a proximal uniserial part, encrusting bivalve shell fragment; figured by Lang (1915, pl. 17, figs 8–9); Chalk Marl (Lower Cenomanian), 10 ft (3·05 m) from the base, Cambridge, F. Möckler Colln.

Other material. NHM D21876, D21879–21883, Chalk Marl (Lower Cenomanian), Cambridge, F. Möckler Collection; Lang labelled these specimens as paratypes on the cavity slides containing them but they are not mentioned as paratypes in his paper (Lang 1915). NHM BZ4958, encrusting an inoceramid shell fragment, Lower Cenomanian (?*carcitanense* Subzone), Porcellaneous Beds (= Chalk Marl), Barrington Chalk Pit, Cambridgeshire, collected by A. N. Ostrovsky and P. D. Taylor, October 2002.

Revised diagnosis. *Distelopora* with rhombic ovoidal autozooids, with a pear-shaped aperture and oval or pear-shaped opesia. Mural rim raised, indented by 6–8 mural spine bases, including a typically large distal pair and two small pairs of distal (oral) spine bases. Gymnocyst well developed; cryptocyst pustulose, wide, normally forming a proximal shelf tapering distally. Avicularia not observed. Hyperstomial ovicells comprising 5–10 spine bases arranged in a curved arc on gymnocyst of distal zooid.

Description. Colonies are encrusting, multiserial, often uniserial in early astogeny (Pl. 1, fig. 1), before becoming lobate (Pl. 1, fig. 2). Pore chambers are evident distally, distolaterally and proximolaterally, the large distal pore chamber having a transverse, slit-like window opening frontodistally (Pl. 1, fig. 3). All ancestrulae are worn, the best example (Pl. 1, fig. 3) measuring 267 µm long by 248 µm wide, and budding a distal and two distolateral daughter zooids. The presence of spines in the ancestrula cannot be ascertained.

Autozooids are rhombic ovoidal in shape (Pl. 1, fig. 4), non-caudate, usually widest mid-length or just proximal of mid-length, 195–404 µm long by 192–280 µm wide. The aperture occupies approximately two-thirds of the frontal surface and is usually pear-shaped, more rarely oval, widest in the proximal half and constricted in the distal third, 128–216 µm long by 99–160 µm wide. The opesia is oval, sometimes slightly wider proximally, 118–176 µm long by 68–101 µm wide. A prominent mural rim is formed by the raised outer edge of the cryptocyst, and is indented by 6–8 mural spine bases. These are usually paired on either side of the zooid, encircling the entire mural rim except for the most proximal part which is free of spines. The most proximal pair of spine bases usually have the greatest diameter, are sometimes considerably larger (Pl. 1, fig. 4) and indent the mural rim more than the others, whereas the most distal of the two pairs of oral spine bases is the smallest. The proximal pair of oral spine bases coincides with an apertural constriction. The gymnocyst is well developed especially proximally and proximolaterally. The cryptocyst is pustulose, moderate to wide, often forming a proximal shelf (Pl. 1, fig. 5), tapering and disappearing distally.

Ovicells are represented by a gently curved row of spine bases on the proximal gymnocyst of the distal autozooid (Pl. 1, figs 5–6). Usually numbering six or seven but with a total range of 5–10, ovicell spine bases are approximately the same diameter as the distalmost oral spines. The median ovicell spines are usually positioned adjacent to the proximal edge of the mural rim of the distal zooid but are sometimes separated from it by a very narrow strip of gymnocyst. The outermost spine bases are often well separated from the distal edge of the maternal zooid. In one example ovicell spine bases are arranged in a semicircle. The distance between adjacent ovicell spine bases is equal to

or greater than their diameter. Formed by the proximal gymnocyst of the distal zooid, the floor of the ovicell is slightly concave. Ovicells measure 67–110 μm in length and are 142–207 μm wide. Zooids bearing ovicells have 6–7, usually six, mural spines.

   Avicularia, closure plates and intramural buds are all unknown.

Remarks. This species can be distinguished by its small number of mural spines, bilateral pairing of these spines, with the most proximal pair of spine bases being the largest, and the development in many zooids of a broad, shelf-like proximal cryptocyst. However, these last three characters may vary: some colonies have unpaired proximal spines, not appreciably larger than the other spine bases; and the cryptocyst is not always shelf-like. In his original diagnosis Lang (1915, p. 502) noted the '. . . termen [mural rim] with eight spines of which the proximal pair are widely separated from the distal three pairs and much larger than them'. A wide separation does often occur between the most proximal mural spines and the others but this is not always true.

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Disteloporalangi sp. nov.

Plate 2, figures 1–6

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Derivation of name. Named to honour William Dickson Lang, former Keeper of Geology at the British Museum (Natural History) and author of the genus *Distelopora*.

Holotype. NHM D23059, incomplete colony consisting of 16 autozooids and one broken ovicell, encrusting inoceramid shell fragment; Chalk Marl (Lower Cenomanian), 10 ft (3·05 m) from the base, Cambridge, F. Möckler Colln.

Paratypes. NHM D21873–21875, D21878, D23111, BZ 4961, BZ 4962, seven small colonies and colony fragments encrusting bivalve shells, and, in one instance, overgrowing a cyclostome colony; occurrence details as for holotype.

Diagnosis. *Distelopora* with rhombic ovoidal autozooids, aperture either oval or, more rarely, pear-shaped, and opesia widest proximally. Mural rim raised, surrounded by 9–16 indenting spine bases, proximal spines normally larger than distal; 4–6 pairs of oral spines. Gymnocyst well developed; cryptocyst rather narrow, sloping inwardly, pustulose. Avicularia not observed. Hyperstomial ovicells comprising 7–8 spines arranged in a gently curved arc usually reaching mural rim of distal zooid.

Description. Colonies are encrusting, multiserial, lobate (Pl. 2, figs 3, 6). Pore chambers are present, the distal pore chamber having a transversely oval window facing distofrontally (Pl. 2, fig. 5). A probable ancestrula (Pl. 2, fig. 1) is poorly preserved, about 305 μm long by 220 μm wide, and buds a distal and one distolateral daughter zooid. Another apparent ancestrula measures 282 μm long by 236 μm wide and buds one distal and two distolateral daughter zooids (Pl. 2, fig. 3).

   Autozooids are rhombic ovoidal, non-caudate, widest just proximal of mid-length, 232–423 μm long by 181–345 μm wide. The aperture is oval or pear-shaped, widest proximal of mid-length, 188–243 μm long by 116–160 μm wide. The opesia is oval or pear-shaped, widest proximal of mid-length, and measures 172–219 μm long

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EXPLANATION OF PLATE 1

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Figs 1–6. *Distelopora bipilata* Lang, 1915 from the Cenomanian Chalk Marl of Cambridge, England. Back-scattered scanning electron micrographs of uncoated specimens. 1, NHM D23019, holotype, a small colony with the oldest zooids arranged uniserially, commencing from what is probably a periancestrular zooid (lower left); ×46. 2–3, NHM BZ4958, Barrington Chalk Pit. 2, showing typically lobate colony-form; ×18. 3, early zooids including the worn ancestrula (lower centre); ×54. 4, NHM D21880, three zooids with enlarged proximolateral spine bases and one ovicell (just right of centre); ×77. 5–6, NHM D21883. 5, zooid with shelf-like proximal cryptocyst and gymnocyst bearing a cresent of spine bases which forms the ovicell for the proximal, maternal zooid; ×128. 6, detail of an ovicell comprising nine spine bases; ×230.
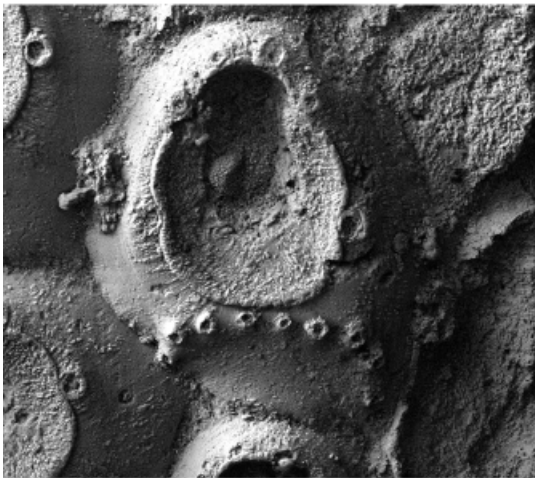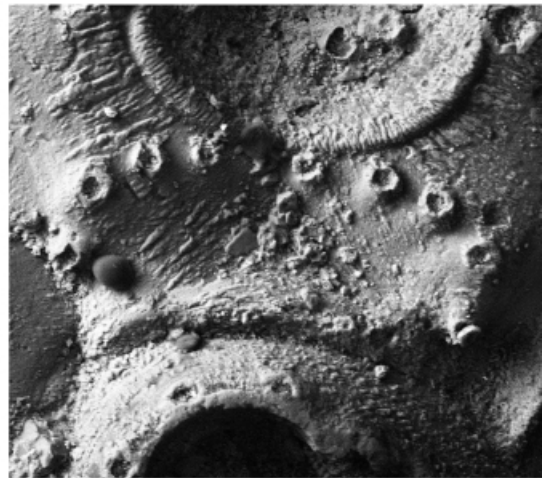
PLATE 1

OSTROVSKY and TAYLOR, *Distelopora*
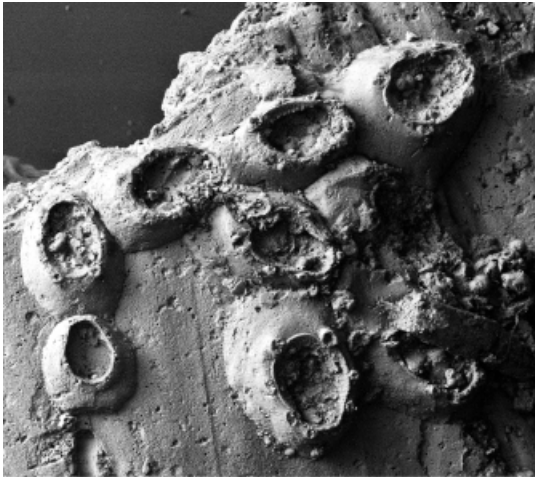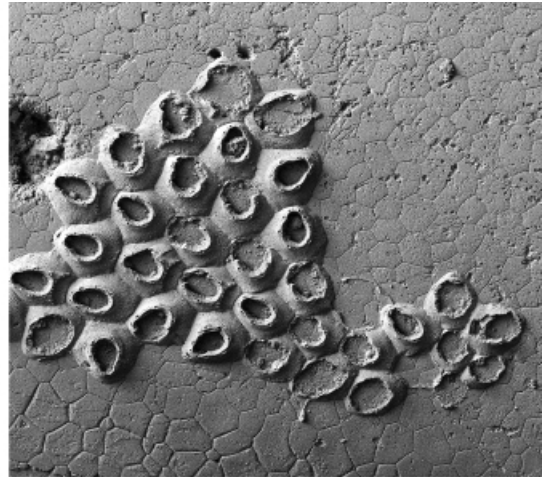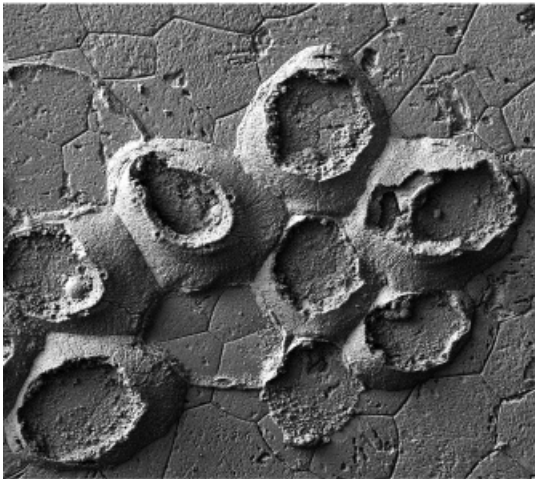
by 94–117 μm wide. A prominent mural rim, formed by the outer edge of the raised cryptocyst, is indented by usually 9–11 but up to 16 mural spine bases. There are typically four oral mural spine bases although as many as six can be present. Proximal spine bases are often slightly larger than distal spine bases. However, this feature is variable and the largest spine bases can be in any position except the most distal. The gymnocyst is well developed, especially proximally and proximolaterally (Pl. 2, fig. 5). The sloping cryptocyst is pustulose, narrow to moderately wide, never forming a proximal shelf, and tapers and disappears distally.

Ovicells are represented by 7–8 spine bases on the proximal frontal wall of the distal zooid, which is slightly concave (Pl. 2, fig. 4). These are approximately the same diameter as distal oral spines but can be somewhat smaller or larger. They are arranged in a gently curved arch, with the median spines typically aligned along the proximal edge of the mural rim of the distal zooid. The distance between ovicell spine bases is equal to or smaller than spine diameter. Ovicells measure 69–103 μm long by 155–200 μm wide.

Avicularia, closure plates and intramural buds have not been observed. Two small elongate structures in the holotype may be kenozooids (Pl. 2, fig. 2).

Remarks. Superficially *Distelopora langi* is strongly reminiscent of *D. bipilata*; the shapes of the autozooids and of their apertures are very similar, as is the patterning of spine bases forming the ovicells. However, there are some important differences between the two species. Autozooids in the zone of astogenetic repetition are larger in *D. langi* and have a narrower, more sloping cryptocyst never prolonged into a proximal shelf. A larger number of mural spines are present in *D. langi* and they are distributed evenly around the aperture. The distal pore window is more circular than in *D. bipilata*.

Distelopora spinifera sp. nov.

Plate 3, figures 1–7

Derivation of name. In reference to the large number of mural and ovicell spines.

Holotype. NHM D21651, two fragments of one colony, consisting of more than 30 zooids with seven ovicells and two avicularia, encrusting a bivalve shell fragment; Chalk Marl (Lower Cenomanian), Cambridge, F. Möckler Colln.
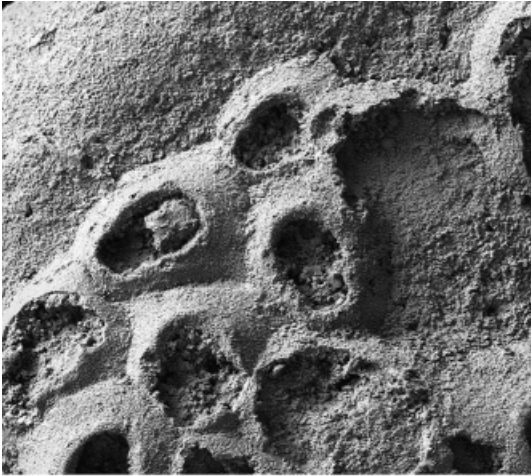
Paratypes. NHM D21652–21653, D21667, D21894, D21897–21899, D21901, D23308, nine small colonies and colony fragments, encrusting bivalve shell fragments; occurrence details as for holotype.

Diagnosis. *Distelopora* with rhombic ovoidal autozooids, an extensive, egg-shaped or, more rarely, oval aperture and opesia. Mural rim double in appearance comprising the raised outer edge of the cryptocyst plus a chain of elongated mural spine bases numbering 14–24, typically 18–21. Gymnocyst well developed; cryptocyst very narrow, crenulated. Vicarious avicularia with rounded rostra and spine bases around mural rim. Hyperstomial ovicells represented by 11–15 closely-spaced spine bases located on a low, semicircular ridge.

Description. Colonies are encrusting, multiserial, possibly with a uniserial initial part. Pore chambers are present, the window of the distal pore chamber being transversely elliptical (Pl. 3, fig. 6). The ancestrula and early budding pattern are unknown.
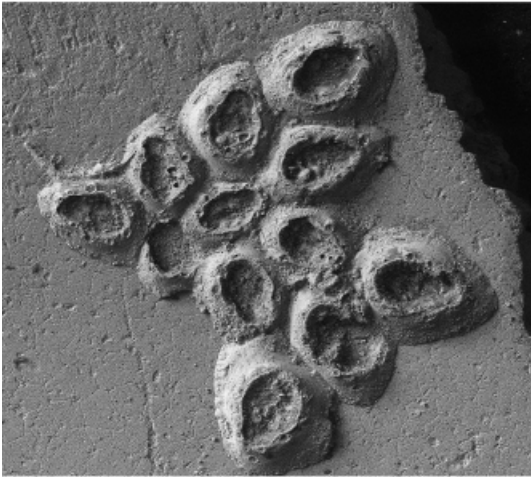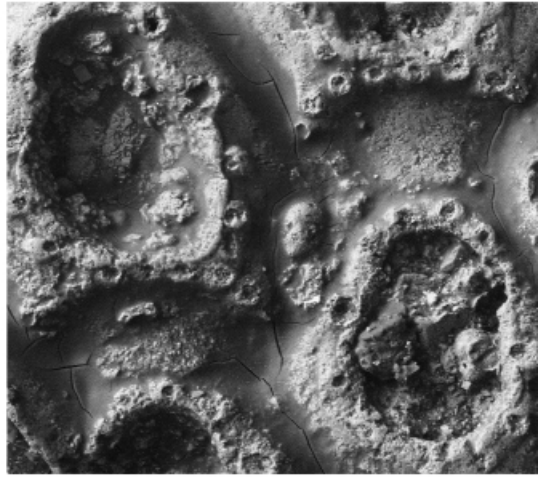

PLATE 2

OSTROVSKY and TAYLOR, *Distelopora*
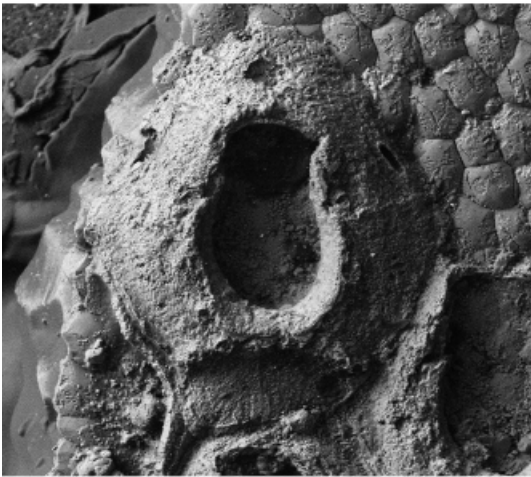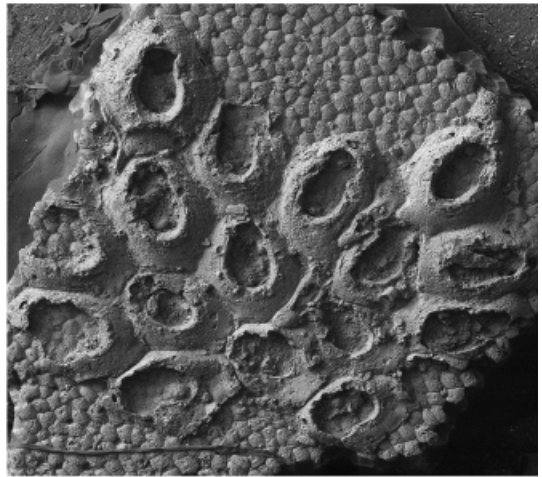
Autozooids are non-caudate, rhombic ovoidal (Pl. 3, fig. 1), longer than wide, usually attaining maximum width proximally of mid-length, 363–602 µm long by 331–518 µm wide. The aperture is extensive, usually egg-shaped, more rarely oval, widest proximally of mid-length, 320–425 µm long by 212–273 µm wide. The opesia is either egg-shaped or oval, 288–372 µm long by 168–238 µm wide. A double appearance of the mural rim (Pl. 3, fig. 7) is due to the combination of the raised outer edge of the cryptocyst enclosed by a chain of mural spine bases of subequal diameter that indent the cryptocyst. Mural spine bases are distributed all around the aperture (Pl. 3, figs 1, 4) and range in number from 14–24 but are usually 18–21 with smaller zooids tending to have fewer spines. There are four larger oral spines: two distal and two disto-lateral. Gymnocyst is well developed, surrounds the aperture on all sides, and is widest proximally and proximolaterally. The cryptocyst is very narrow, inwardly sloping, crenulated, and absent altogether in the distal part of the zooid.

Ovicells are represented by 11–15, often 14, spine bases on the slightly concave proximal gymnocyst of the distal autozooid (Pl. 3, fig. 2). Ovicell spine bases are markedly smaller in diameter than the nearby distal oral spines, and are arranged in a semicircular pattern, usually extending very close to the mural rim of the distal zooid but sometimes with an intervening area of gymnocyst. Spine bases are closely spaced and located on a slight ridge. The two most proximal ovicell spines are located close to the distal wall of the maternal zooid. Spacing between the ovicell spine bases is approximately equal to their diameter, although a greater separation is often found in the distal part of the ovicell. Ovicells measure 83–96 µm long by 80–107 µm wide.

Vicarious avicularia are sporadically present (Pl. 3, figs 3, 5). They are larger than the autozooids, measuring 692–745 µm long by 470–586 µm wide, and have broader gymnocysts distolaterally. The rostrum is rounded and slightly spatulate. Spine bases are closely spaced and number about 14 in the proximal part of the opesia but are distantly spaced and about four in number on the rostrum. Avicularian apertures are 439–541 µm long by 286–302 µm wide. Neither condyles nor a pivot bar are evident. Reparative intramural budding may occur (Pl. 3, fig. 3) but closure plates have not been observed.

Remarks. This species is readily distinguished from the two other species of *Distelopora* by its larger zooids, the greater number of mural and ovicell spine bases, the semicircular arrangement of the ovicell spine bases (Pl. 3, fig. 2), and the presence of vicarious avicularia. Further differences are evident in the shape of the aperture and the double structure of the mural rim.

On the reverse side of all three wooden cavity slides containing specimens of *Distelopora spinifera*, Lang made pencil sketches showing egg-shaped apertures, the 'double' mural rim and the large number of mural spines. Thus, it is clear that he recognized the difference between this and the other species.

Genus UNIDISTELOPORA gen. nov.

*Derivation of name*. A *Distelopora*-like calloporid having uniserial colony-form.

Type species. *Allantopora krauseae* Voigt and Schneemilch, 1986, Lower Campanian, Germany.

Diagnosis. Calloporid with encrusting, runner-like uniserial colonies ramifying by the formation of distolateral buds. Autozooids ovoidal, with oval or elliptical aperture and opesia, surrounded by 20–25 mural spine bases. Mural rim indistinct. Gymnocyst moderately wide, forming a short to moderate cauda; cryptocyst very narrow, pustulose. Pore chambers present, pore windows transversely elliptical.


EXPLANATION OF PLATE 3

Figs 1–7. *Distelopora spinifera* sp. nov. from the Cenomanian Chalk Marl of Cambridge, England. Back-scattered scanning electron micrographs of uncoated specimens. 1–2, 5–7, NHM D21651, holotype. 1, group of autozooids showing multiple mural spine bases and three ovicells; ×43. 2, remains of ovicell comprising a semicircle of about 14 spine bases which are noticeably smaller than the two visible oral mural spine bases of the maternal zooid (bottom); ×312. 5, vicarious avicularium; ×72. 6, marginal zooid with large distal pore chamber window; ×77. 7, double appearance of the mural rim; ×300. 3, NHM D21894, paratype, group of zooids including a vicarious avicularium (right) and a regenerative bud (centre); ×58. 4, NHM D21667, paratype, two autozooids with small ovicells and numerous mural spine bases; ×61.
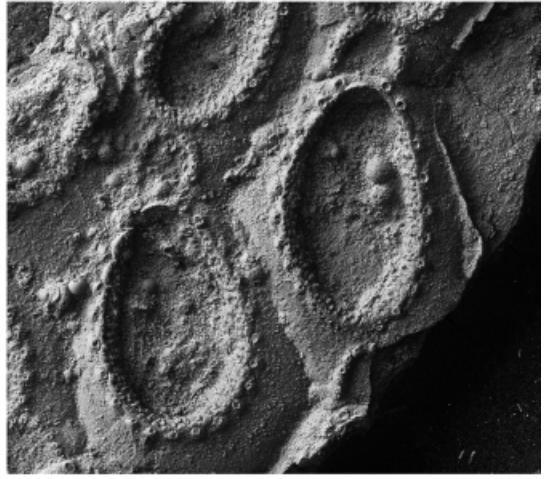
PLATE 3

OSTROVSKY and TAYLOR, *Distelopora*
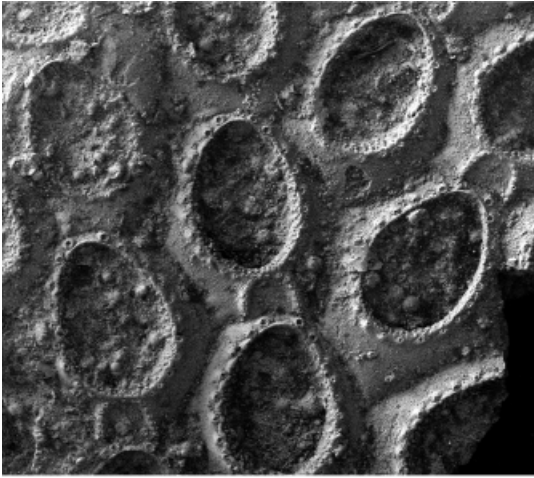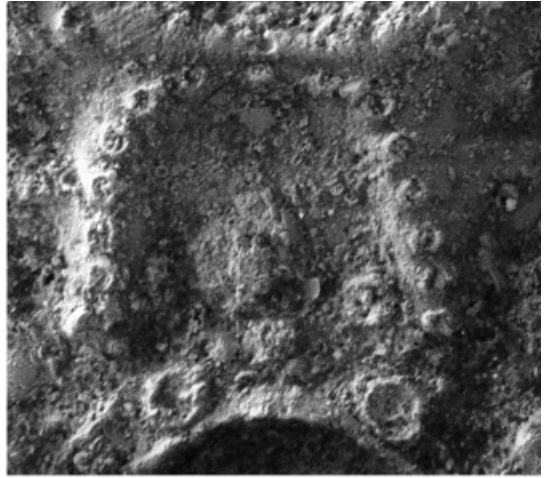
Avicularia unknown. Hyperstomial ovicells represented by a semicircle of 18–19 spine bases on a slight ridge.

Remarks. The distinctive uniserial colony-form of this new monospecific genus immediately distinguishes it from *Distelopora*. No other uniserial calloporids are known to have multispinose ovicells (see Rosso and Taylor 2002 for a review of uniserial calloporid genera). This includes *Allantopora* Lang to which the type species of *Unidistelopora* was originally referred. The morphology of the spine bases in *Unidistelopora* is identical to that seen in *Distelopora* and there is little doubt that the spines were also basally articulated in this genus.

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Unidistelopora krauseae (Voigt and Schneemilch, 1986)

Plate 4, figures 1–6

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1986   *Allantopora krauseae* Voigt and Schneemilch, p. 114, pl. 1, figs 1–7.

Holotype. VC 11025, Lower Campanian, Grube Allemania, Höver, near Hannover; colony encrusting a piece of octocoral (not studied).

Other material. VC T10580, Lower Campanian, Grube Alsen, Lägerdorf, near Hamburg, Germany; colony encrusting a fragment of echinoid test. VC T10581, Lower Campanian, Grube Breitenburg, Germany; colony encrusting a piece of echinoid test.

*Revised diagnosis*. See generic diagnosis.

Description. Colonies are encrusting, runner-like (Pl. 4, fig. 1), comprising long branched chains of uniserial zooids with occasional small patches of biserial growth. Branches ramify through the production of one or two distolateral buds in addition to a distal bud (Pl. 4, figs 2, 4). Very occasionally two distolateral buds are formed by a parental zooid without a distal bud. The ancestrula and early astogeny are unknown. Pore chambers are present distally, distolaterally and proximolaterally, all having transversely elliptical pore windows (Pl. 4, fig. 3) which are largest for the distal pore chambers.

   Autozooids are elongate ovoidal, attaining maximum width at or just proximal of mid-length, 529–728 μm long by 378–520 μm wide. The aperture is large, usually oval or elliptical, more rarely egg-shaped, 347–462 μm by 242–301 μm wide. The opesia is either egg-shaped or oval, 288–372 μm long by 168–238 μm wide. Mural spine bases surround the aperture and number 20–21 in ovicellate zooids, 24–25 in non-ovicellate zooids. Distal spine bases tend to be slightly larger, particularly the four 'oral' spine bases (Pl. 4, fig. 3). The gymnocyst is moderately wide, surrounding the aperture on all sides but better developed proximally where it forms a short to moderate, broad cauda. The cryptocyst is very narrow, inwardly sloping, pustulose, and tapers to nothing in the distal part of the zooid. Closely adjacent zooids from different branches may have irregular prolongations apparently growing towards proximolateral pore chambers (Pl. 4, fig. 5).

<div align="center">

EXPLANATION OF PLATE 4

</div>

Figs 1–6. *Unidistelopora krauseae* (Voigt and Schneemilch, 1986) from the Lower Campanian of northern Germany. Back-scattered scanning electron micrographs of uncoated specimens. 1, 3–4, VC T10580, Grube Alsen. 1, runner-like uniserial colony; ×8·5. 3, ovicell remains consisting of 18 spine bases significantly smaller than the oral mural spine bases of the maternal zooid; ×178. 4, distal and two distolateral daughter zooids budded by a zooid hosting an intramural reparative bud; the oval window of the distal pore chamber is visible in the left distolateral zooid; ×38. 2, 5–6, VC T10581, Grube Breitenburg. 2, three zooids, the most proximal being ovicellate and containing an intramural bud whereas its distal daughter zooid hosts two generations of intramural buds; ×46. 5, converging branches with the zooid furthest left having a prolongation from a sibling zooid extending towards the position of its proximolateral pore chamber window; ×32. 6, three subparallel branches of which one contains a bipolar pair of zooids (lower centre) formed by regenerative growth from the fractured proximal end of a severed branch; two intramural kenozooids are visible in the upper right; ×23.

PLATE 4
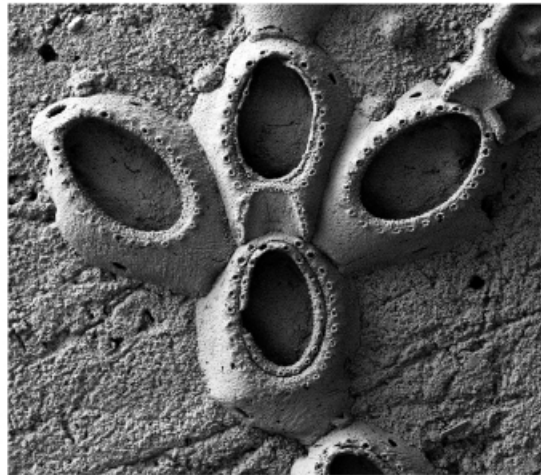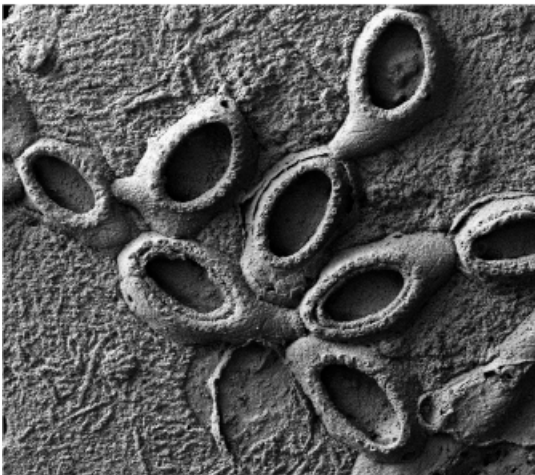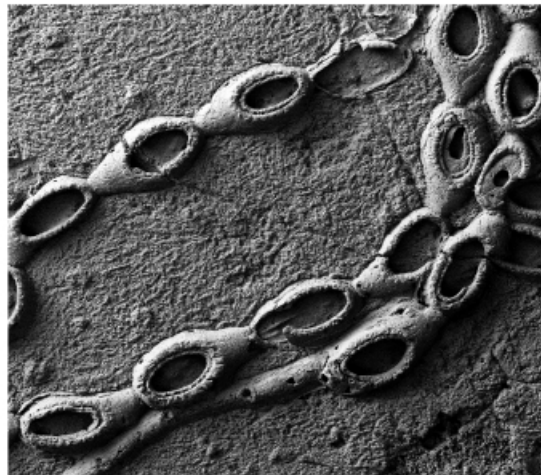

OSTROVSKY and TAYLOR, *Unidistelopora*
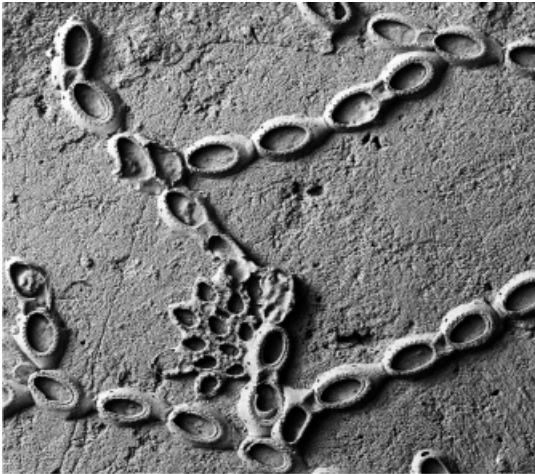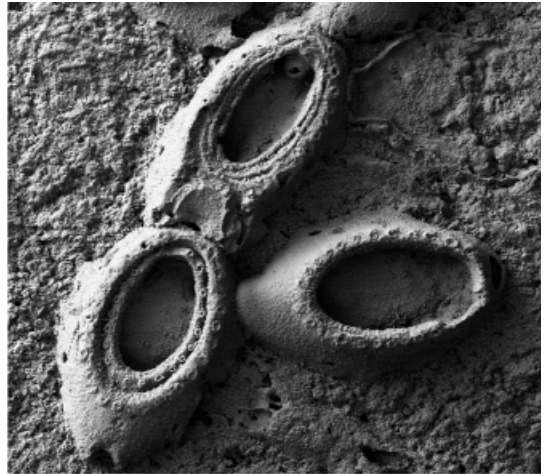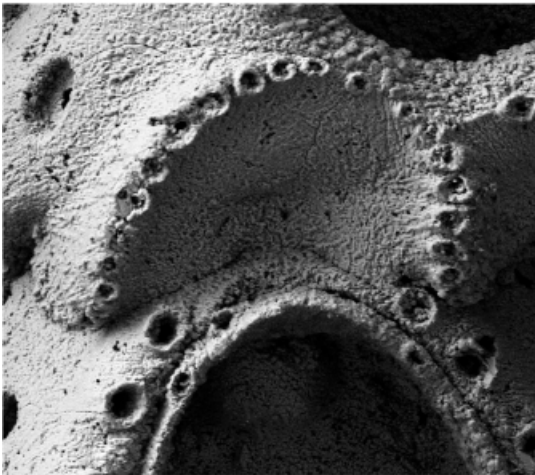
Ovicells are represented by 18–19 spine bases arranged on a semicircular ridge elevated significantly above the ovicell floor, which is formed by the concave proximal gymnocyst of the distal zooid (Pl. 4, fig. 3). The diameter of ovicell spine bases is markedly smaller than that of mural spines, notably the nearby oral spine bases of the maternal zooid. Distal, median ovicell spine bases are located on the mural rim of the distal zooid. The two most proximal spine bases are positioned very close to the distal wall 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. Ovicells measure 104–111 μm long by 170–191 μm wide.

Avicularia are unknown. Kenozooids (Pl. 4, fig. 6) sometimes occur as intramural reparative buds (*sensu* Taylor 1988*b*) within host autozooids but most reparative buds comprise autozooids within autozooids (Pl. 4, figs 2, 4). Some autozooids contain two intramural buds one inside the other. Mural spine bases are smaller and fewer in number in intramurally budded autozooids than in the host autozooid. Extramural reparative budding can also occur if the proximal part of the zooid was damaged, resulting in a new branch of opposite polarity (Pl. 4, fig. 6). Closure plates are unknown.

Remarks. Although having a very different colony-form, this species resembles *Distelopora spinifera* in aspects of its zooidal morphology, notably in having a large number of mural as well as ovicell spines, and in the semicircular arrangement of the ovicell spines. In general, the description made by Voigt and Schneemilch (1986) is accurate even though these authors failed to notice the multispinose ovicells. This may be because they had only one damaged ovicell in their material; abrasion of the ovicells beneath the level of the spine bases obliterates their multispinose condition.

Genus GILBERTOPORA gen. nov.

Type species. *Gilbertopora larwoodi* sp. nov., Lower Cenomanian, 'Chalk Marl' (= Lower Chalk, Porcellaneous Beds), Cambridge, England.

Derivation of name. The genus and type species are named in honour of the late palaeobryozoologist Gilbert Larwood, with allusion of the genus to the related Cretaceous calloporid *Wilbertopora*.

Diagnosis. Calloporidae with multiserial encrusting colonies. Pore chambers present. Autozooids rhombic ovoidal with elliptical or oval aperture and opesia; mural rim narrow; gymnocyst moderately well developed, cryptocyst narrow; spines restricted to two short, knob-like oral spines with closed ends present in some non-ovicellate zooids. Hyperstomial ovicells small, bispinose with two claw-like flattened spines, a wide and shallow aperture, plus one distal and two lateral openings.

Remarks. This genus differs from all known calloporids (and other cheilostomes) in its unique bispinose ovicells with four openings.

*Gilbertopora larwoodi* sp. nov.

Plate 5, figures 1–6

Holotype. NHM D23297, fragmentary colony preserving ten autozooids with three complete and three damaged ovicells, encrusting a piece of bivalve shell; Chalk Marl (Lower Cenomanian), 10 ft (3·05 m) from the base, Cambridge, F. Möckler Colln.

Figs 1–6. *Gilbertopora larwoodi* sp. nov. from the Cenomanian Chalk Marl of Cambridge, England. Back-scattered scanning electron micrographs of uncoated specimens. 1, 5, NHM D28297, holotype. 1, broken colony, encrusting a fragment of bivalve shell, with small ovicells present in all of the visible zooids; ×33. 5, bases of the two spines of a broken ovicell; ×230. 2–4, NHM D28298, paratype. 2, frontal view of an ovicell showing the median suture between the two spines; ×224. 3, oblique lateral view of an ovicell illustrating the lateral foramen; ×345. 3, opening formed between the bases of the two spines of an ovicell viewed from the distal side (mural rim of the distal zooid visible in the lower right); ×320. 6, NHM BZ 4955, paratype, fragment of colony with non-ovicellate zooids having small oral spines (best seen in the zooid on the right); ×60.
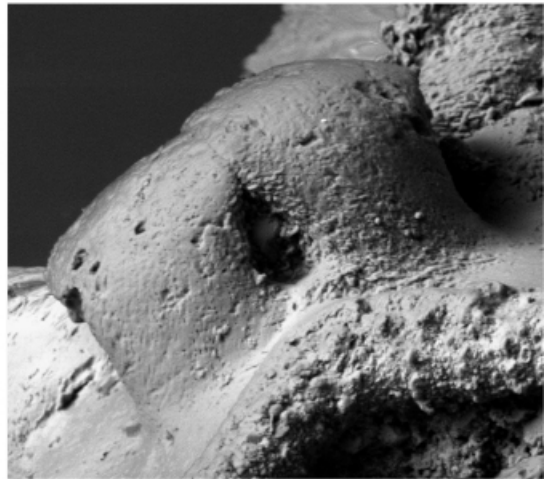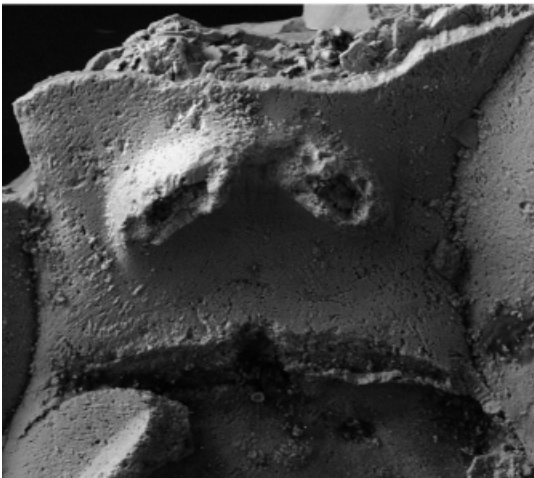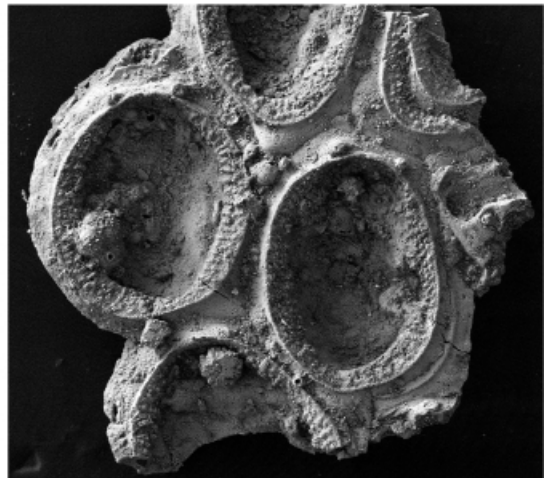
PLATE 5
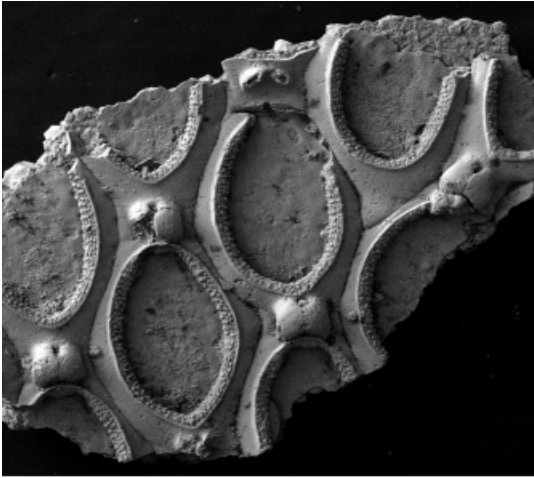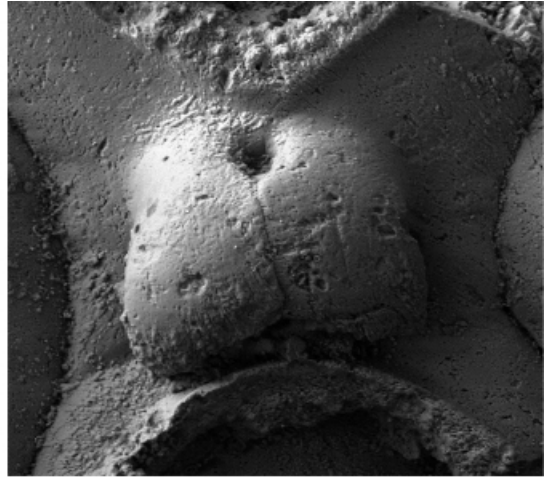
Paratypes. NHM D23298, small fragment with two complete and one broken ovicell; details as for holotype. NHM BZ 4954–4957, details as for holotype but 20 ft (6·1 m) from base of Chalk Marl.

Diagnosis. As for genus.

Description. Colonies are encrusting, multiserial (Pl. 5, fig. 1). The ancestrula and early astogeny are unknown. Pore chambers have been observed distolaterally and may be present elsewhere.

Autozooids are non-caudate, rhombic ovoidal (Pl. 5, figs 1, 6), longer than wide, attaining maximum width about mid-length, and measure 618–635 μm long by 451–483 μm wide. The large aperture is usually elliptical or egg-shaped, 498–510 μm long by 342–367 μm wide. The opesia has same the shape as the aperture but is 434–453 μm long by 259–272 μm wide. Gymnocyst is moderately well developed and surrounds the aperture on all sides. The cryptocyst is pustulose, inwardly-sloping, not shelf-like, of moderate width, broadest proximally and laterally, tapering to nothing in the most distal part of the zooid. Two small knob-like oral spines with closed ends and probably not basally articulated occur in some of the non-ovicellate zooids (Pl. 5, fig. 6).

Ovicells are hyperstomial, small, 96–107 μm long by 132–143 μm wide. They are bispinose, constructed of two claw-like, arched, flattened spines (Pl. 5, fig. 2), and originate on the proximal gymnocyst of the distal zooid which forms the concave floor of the ovicell. Basally the hollow spines are narrow and separate (Pl. 5, fig. 5), but they broaden during proximofrontal growth to become juxtaposed along the median line of the zooid where a suture is developed (Pl. 5, fig. 2). A medially fractured ovicell shows that the internal cavities of the spines are not confluent. The brood chamber has four openings to the exterior. A teardrop-shaped distal opening is present between the bases of the two spines (Pl. 5, fig. 4). An elliptical lateral opening (foramen) occurs on each side of the ovicell between the arched spines and the floor of the ovicell (Pl. 5, fig. 3). The proximal aperture of the ovicell opening towards the maternal zooid is a wide, very low arch.

Avicularia or other polymorphs and closure plates have not been observed. Intramural buds may occur.

Remarks. All our material of this species comprises small fragments of delicate colonies often encrusting thin shells of inoceramid bivalves. Unfortunately, early astogenetic stages are not preserved and the limited material means that features which are often of sporadic occurrence, such as avicularia, may be present but have not been sampled. Nonetheless, the structure of the ovicells is highly distinctive and has considerable relevance to an understanding of early ovicell evolution, as discussed below.

DISCUSSION

Harmer (1902) first proposed that ovicells in cheilostome bryozoans evolved from spines. His hypothesis was further developed and modified by several subsequent authors (Lang 1921; Larwood 1962; Braiko 1967; Silén 1977; Santagata and Banta 1996); for recent reviews, see Ostrovsky (1998, 2002) and Taylor and McKinney (2002). Harmer's original idea was that two distal oral spines of the maternal zooid were the evolutionary precursors of ovicells. Although this may be true for a few cheilostomes (e.g. *Scruparia* and *Thalamoporella*), it is now believed that ovicells in the vast majority of cheilostomes originated by modification of mural spines on the proximal part of the next distal zooid in series. According to this idea, two separate zooids are involved in larval brooding: the proximal maternal zooid produces the eggs, while the distal zooid constructs the brood chamber (ovicell) where the fertilised eggs develop into larvae. The discovery in four calloporid species described here of ovicells comprising multiple spines borne on the gymnocyst of the distal zooid strongly corroborates the hypothesis that ovicells are derived from spines of the distal zooid. These multispinose ovicells comprise a row of spines showing a clear resemblance to the spines arranged around the mural rim in some non-ovicellate cheilostomes such as the Aptian–Albian genus *Spinicharixa* Taylor, 1986, the Cretaceous–Recent genus *Villicharixa* Gordon, 1989, and some extant species of *Electra* Lamouroux, 1816 (e.g. Winston 1982, fig. 32).

Mural spines probably evolved to protect the vulnerable frontal membrane and underlying polypide from physical and biological damage, including predation. Their subsequent role in constructing the larval brooding chamber of the proximal zooid provides an example of exaptation. Not only has the functional role of the spines changed through time, but the focus of their functionality has also shifted from the distal to the maternal zooid.

Prior to the current paper, confirmable multispinose (or multicostate) ovicells had been noted only in
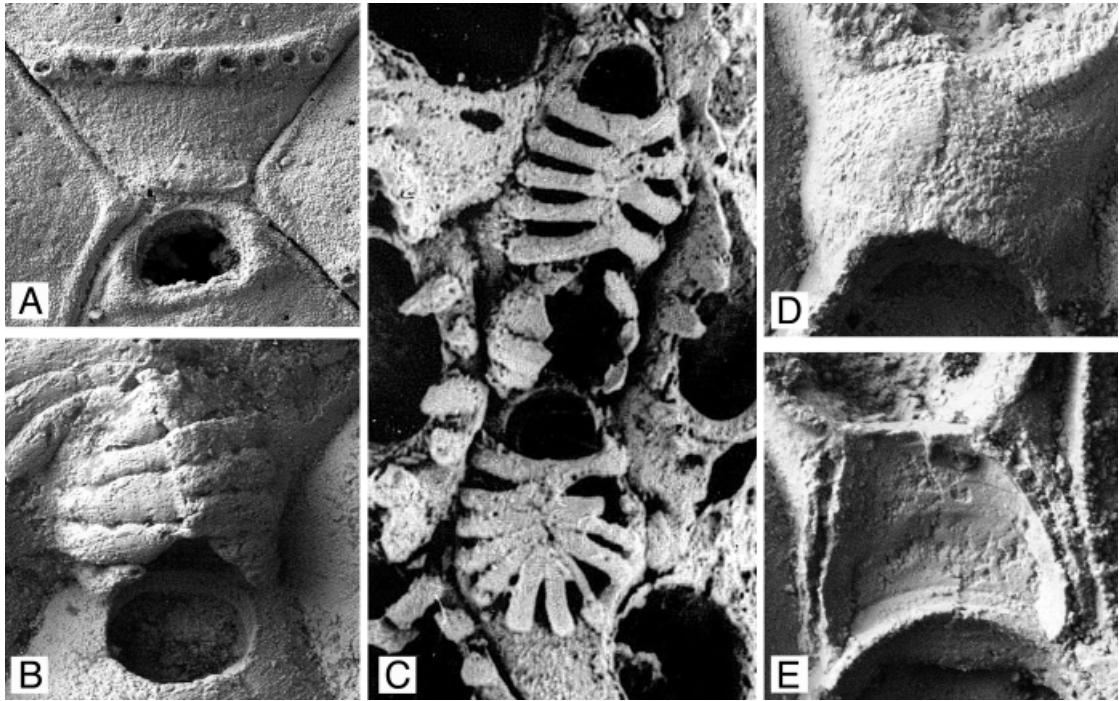
TEXT-FIG. 1. Spinose and other primitive ovicells in some Cretaceous cheilostomes. A, *Stichomicropora* sp., multispinose ovicell represented by a curved row of spine bases on the zooid distal of the maternal zooid whose semicircular orifice is at the bottom of the picture; NHM D42263, Campanian, *mucronata* Zone, Earlham Lime Works, Norwich, England; ×75. B, *Leptocheilopora tenuilabrosa* Lang, ovicell formed by overarched costae abutting along the median line; NHM D21210, Santonian, *Marsupites* Zone, Odiham, Hampshire, England; ×143. C, ?*Thoracopora* sp., part of a colony showing maternal and distal zooids and a broken ovicell evidently constructed of spines similar to those forming the frontal shields of the zooids (micrograph courtesy of Professor E. Voigt); Lower Cenomanian, Mülheim, Westfalia, Germany, VC 11330; ×125. D–E, bilobate ovicell of the oldest known brooding cheilostome, *Wilbertopora* from the mid-Cretaceous. D, intact ovicell of *W. mutabilis* Cheetham with median ridge; NMH D47068, Albian, Fort Worth Limestone, Kaum, Denton County, Texas, USA; ×190. E, damaged ovicell of *Wilbertopora* sp. showing the two double-walled lobes forming the roof of the ovicell; NHM D57378, Cenomanian, Grayson Formation, Lake Waco Dam, Denton County, Texas, USA; ×172.

two Cretaceous genera: the coilostegan *Stichomicropora* Voigt, 1949 (Text-fig. 1A) and the cribrimorph *Leptocheilopora* Lang, 1916 (Text-fig. 1B) (Lang 1921; Voigt 1949, 1967, 1989; Larwood 1961; Favorskaya 1987; Ostrovsky 2002; Taylor and McKinney 2002). Another undescribed cribrimorph, ?*Thoracopora* sp. (Text-fig. 1C) from the German Cenomanian, also has multispinose ovicells but exhibits a loosely costate frontal shield morphology quite different from the closely-spaced costae seen in *Leptocheilopora*. Taylor and McKinney (2002) interpreted multispinose ovicells as primitive for neocheilostomes in general. This hypothesis is strengthened by the discovery of multispinose ovicells in the calloporids *Distelopora* and *Unidistelopora* because the simple skeletal morphology of calloporids suggests that they occupy a basal position within the neocheilostomes. Indeed, some calloporids are almost indistinguishable in skeletal morphology from non-brooding malacostegans, save for the presence of the defining ovicells.

The oldest known calloporid, *Wilbertopora mutabilis* Cheetham from the Upper Albian of Texas, has bilobate ovicells with a median suture or carina (Cheetham 1954, 1975) (Text-fig. 1D–E). The two lobes of the ovicell have been interpreted as flattened spines fusing along the mid-line of the zooid. Taylor and
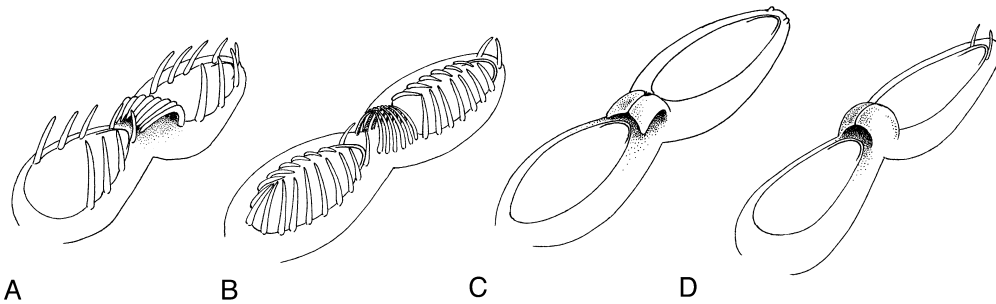
TEXT-FIG. 2. Simplified reconstructions of some primitive cheilostome ovicells seen in oblique views of the maternal and distal zooids. A, multispinose ovicell of the type found in *Distelopora bipilata* and *D. langi* in which the ovicell spine bases are arranged in a gently bowed row. B, multispinose ovicell of the type developed in *Distelopora spinifera* and *Unidistelopora krauseae* with ovicell spine bases arranged in a semicircle. C, bispinose ovicell of *Gilbertopora larwoodi*. D, more conventional, bilobate ovicell of *Wilbertopora mutabilis*.

McKinney (2002) regarded the bilobate ovicells of *Wilbertopora* as homologous with the multispinose ovicells in *Stichomicropora*, while Ostrovsky (2002) was impressed by the strong similarities shown between ovicells in *Leptocheilopora* and other cribrimorphs and those in calloporids, including *Wilbertopora*. It now seems reasonable to infer that *Stichomicropora*, *Leptocheilopora* and ?*Thoracopora* sp. (Text-fig. 1c) all inherited their multispinose ovicells from a *Distelopora*-like calloporid ancestor.

Ovicell spine bases in *Distelopora bipilata* and *D. langi* are arranged in a gently curved arc, resembling the pattern seen in species of *Stichomicropora* (Taylor and McKinney 2002). In contrast, these spine bases in *D. spinifera* (and *Unidistelopora krauseae*) form a semicircle, an arrangement similar to that seen in the cribrimorphs *Leptocheilopora tenuilabrosa* Lang and ?*Thoracopora* sp. This may point to phylogenetic links between the *D. pilata/D. langi* and coilostegans on the one hand, and between *D. spinifera* and cribrimorphs on the other. However, a full phylogenetic analysis incorporating all skeletal characters, which is beyond the scope of the current paper, is needed to test this suggestion.

It is possible to propose a model for the evolution of multispinose ovicells from the proximal mural spines of the distal zooid. In the first stage, these spines are bent backwards to form a protective roof with two large lateral gaps (Text-fig. 2A). Such gaps are likely to have existed in the complete ovicells of *Distelopora bipilata* and *D. langi*. Subsequently, a semicircular pattern of ovicell spine bases evolved, as in *D. spinifera*, making a more complete cage that provided greater protection for the developing embryo (Text-fig. 2B). Later stages involved the loss of basal articulation of the ovicell spines and their close lateral and terminal juxtaposition. This transition from a multispinose to a multicostate ovicell would give a more rigid structure like that seen in *Leptocheilopora* and in some later species of *Stichomicropora* such as *S. baccata* (Canu and Bassler) (see Taylor and McKinney 2002).

Bilobate ovicells constructed by the distal zooid (Text-fig. 2D), as seen in the Albian–Cenomanian species *Wilbertopora mutabilis* (see Cheetham 1954, 1975), can be viewed as morphological intermediates between multicostate ovicells and the single-valved hemispherical ovicells that characterise the majority of fossil and living neocheilostomes. Two alternative scenarios for the transition from multicostate to bilobate ovicells can be envisaged: (1) spine fusion resulting in an ovicell made from two composite spines, or (2) reduction in spine number, with the retention and enlargement of only the two most distal spines. The unusual bispinose ovicells of *Gilbertopora* (Text-fig. 2C) support the second suggestion, at least for calloporids. In both *Gilbertopora* and *Wilbertopora* communication between the ovicell lumen (i.e. the coelomic cavity between entooecium and ectooecium) and the distal zooid is through two short slits (Pl. 5, fig. 5). If spine fusion had occurred a longer arch-like slit would be expected, perhaps expanding in width at intervals corresponding with the positions of the original multiple spine bases. The bilobate ovicells of *Wilbertopora* can be derived from the bispinose ovicells of *Gilbertopora* by the further enlargement and lateral fusion of the two spines. Complete fusion would result in a single-valved hemispherical ovicell of modern type.

The ovicells of *Gilbertopora* are notable for having four openings to the exterior: a proximal opening, adjacent to the orifice of the maternal zooid; a distal opening between the two overarching claw-like spines of the ovicell; and two lateral openings at the sides of the spines. Whereas the proximal opening is common to ovicells in all cheilostomes, the other three openings are not ubiquitous. Lateral openings are inferred for the two *Distelopora* species which have multispinose ovicells and spine bases arranged in a gently-curved arc. They also occur in the coilostegan genus *Stichomicropora* where they have been described as lateral foramina (Taylor and McKinney 2002). In all multispinose ovicells, additional gaps would almost certainly have existed between the adjacent spines. The presence of appreciable gaps to the exterior in the ovicells of all the species described here implies that the developing embryos in these bryozoans were bathed in sea water. Ovicells of modern type completely isolate the embryo from the sea water because the only opening, the aperture, is sealed by the ooecial vesicle and/or the zooidal operculum during the time that the embryo undergoes development. Silén (1945) noted that embryos of *Callopora dumerilii* (Audouin) died when removed from ovicells and placed in sea water. Evolution towards ovicells of modern type may have been accompanied by loss of ability of immature embryos to survive outside the brood chamber. Further experimental research on modern cheilostomes, including the coilostegan *Monoporella* which has ovicells with lateral foramina, will be necessary to confirm this suggestion. However, it does suggest important physiological differences in larval brooding between the primitive ovicells described here in some Cretaceous taxa and ovicells of modern type.

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