

Ovicell structure in *Callopora dumerilii* and *C. lineata* (Bryozoa: Cheilostomatida)

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Abstract

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Anatomical and SEM-studies of the brood-chambers (ovicells) in two bryozoans (*Callopora dumerilii* and *C. lineata*) were undertaken to resolve a long-term controversy existing in the literature about the origin of the ovicells. In contrast with the interpretation of Silén (1945), both species investigated possess hyperstomial ovicells with the oecium formed by the distal (daughter) zooid. The oecial coelomic cavity communicates with the zooidal coelom through a pore-like canal or canals remaining after the closure of an arch-shaped slit. The slit forms during ovicellogenesis. The communication canals are normally plugged by epithelial cells, however incompletely closed canals were also found in *Callopora lineata*. SEM-studies of noncleaned, air-dried specimens showed a relationship between membranous and calcified parts during early ovicellogenesis. It starts from a transverse wall as the calcification of the proximal part of the daughter zooid frontal wall, and has the shape of two flat rounded plates. There are no knobs or any other outgrowths. Conditions and phenomenology of hyperstomial ovicell formation are discussed.

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Introduction

Brooding is widespread among cheilostomate bryozoans, and most of them keep their young in special chambers called ovicells. There are several morphological types of ovicells (Levinsen 1909; Bassler 1953; Hayward and Ryland 1998). Most common are hyperstomial ones that often look like hemispherical bubbles or helmets on the colony surface. The hyperstomial ovicell usually consists of a two-walled fold (oecium) with a coelomic cavity inside and a basal wall situated at the proximal wall of the zooid distal to the maternal zooid (that produces the eggs), together surrounding the brooding cavity (Fig. 1). The outer oecial wall is called ectooecium, that surrounding the brooding cavity the entoecium (Levinsen 1902; Ryland 1968). The ovicell opening is closed either by the operculum of the maternal zooid or by an evagination of the maternal cystid wall called an oecial (inner) vesicle or oecial plug (see Ryland 1968; Woollacott and Zimmer 1972, and Hayward and Ryland 1998 for terminology and diagrams).

The origin of the oecial fold can be followed during its development and evidenced in the fully formed ovicells by a connection between the zooid and oecium. Direct observations of the oecial development from distal autozooid were made by Nielsen (1981, 1985; see also illustrations in Levinsen 1909 and Harmelin 1973a). A number of authors (for instance, Calvet 1900; Woollacott and Zimmer 1972; Santagata and Banta 1996) have found that the oecial coelom is confluent with the body cavity of the daughter zooid through a narrow pore which is either open or closed by nonspecialized epithelial cells. Woollacott and Zimmer (1972) interpreted the oecia with communication pores plugged by nonspecialized cells as kenozooids. In species where the pores are not plugged (see illustrations and descriptions in Cheetham and Cook 1983; Santagata and Banta 1996), the oecia should be interpreted as outgrowths of the zooid frontal wall. In species where a terminally budded daughter zooid is absent, the hyperstomial ovicell appears to be formed directly from the maternal zooid, but communication between the zooidal coelom

Fig. 1—Schema of the longitudinal section of decalcified specimen of *Callopora dumerilii* (the partly plugged communication canal between the oocelial coelom and the general body cavity is arrowed). Abbreviations: bc = brooding cavity, cec = calcified part of ectooecium, dz = coelomic cavity of daughter autozoid, en = entoecium, fs = funicular strands, fw = frontal wall of distal zooid, m = muscle bundles of oocelial vesicle, mec = membranous part of ectooecium, mz = coelomic cavity of maternal autozoid, oc = oocelial coelomic cavity, of = ocellular floor, op = operculum, ov = oocelial vesicle, s = sclerite, tw = transverse zooidal wall, v = vestibulum.

and the ovicellar coelom is usually through pores with special pore-cell complexes, and oocelia of this type must therefore be considered as true kenozooids (Ostrovsky 1998).

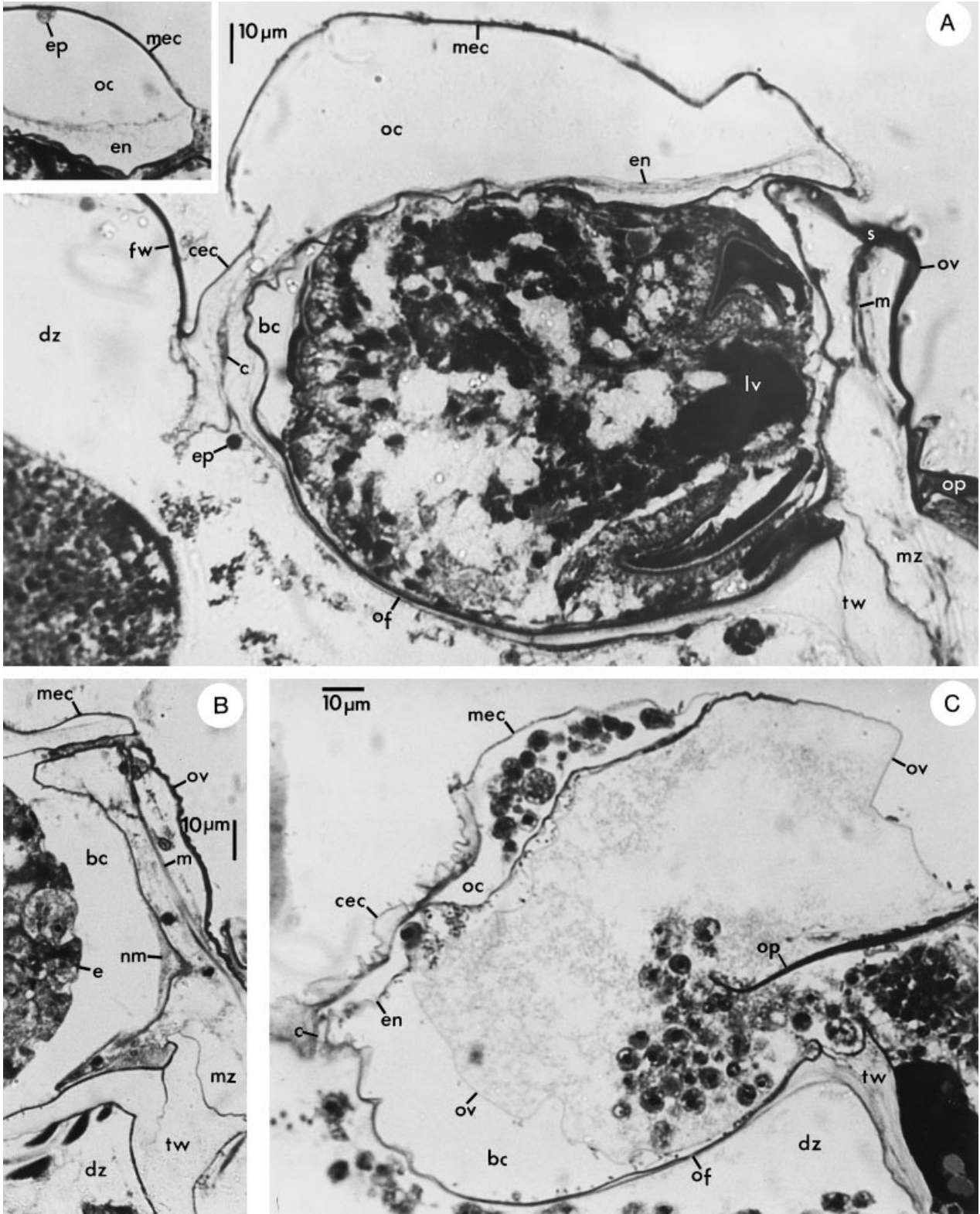
Silřn (1944, 1945) reported that ovicells situated on the frontal wall of the distal zooid in several species are formed as direct outgrowths from the maternal zooid, and he proposed that this is the general structure of hyperstomial ovicells. An uncertainty about this has therefore crept into the literature (see, for example, Ryland 1979; Reed 1991; Mukai et al 1997). It was therefore decided to reinvestigate *Callopora dumerilii* (Audouin, 1826) on which Silřn based much of his argumentation, and *C. lineata* (Linnaeus, 1767) (type species of the genus *Callopora* Gray 1848), in order to check the basis for his generalization. A detailed description of the history of investigation of ovicell formation and structure is given in Ostrovsky (in press).

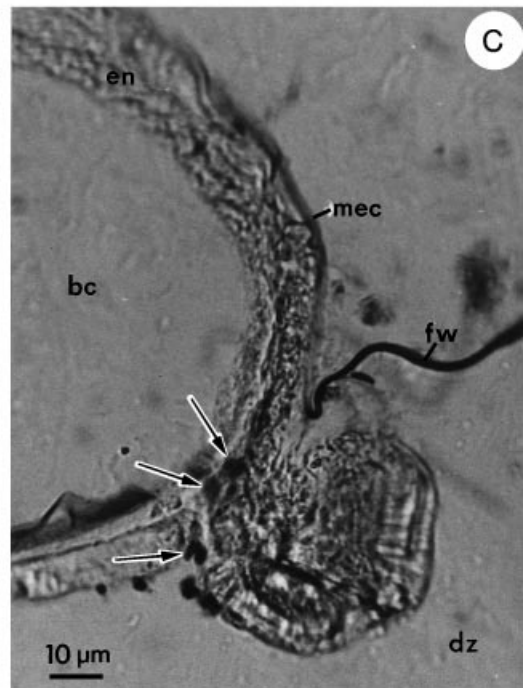
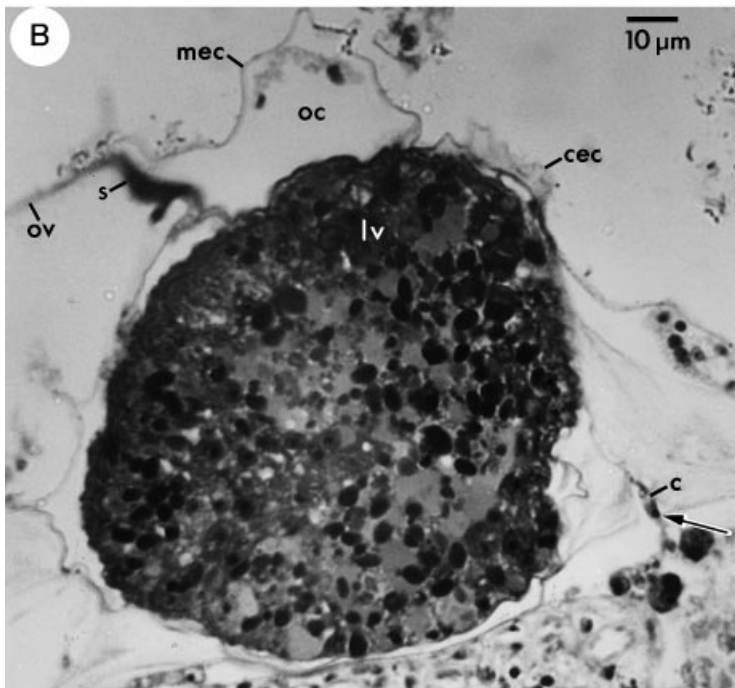
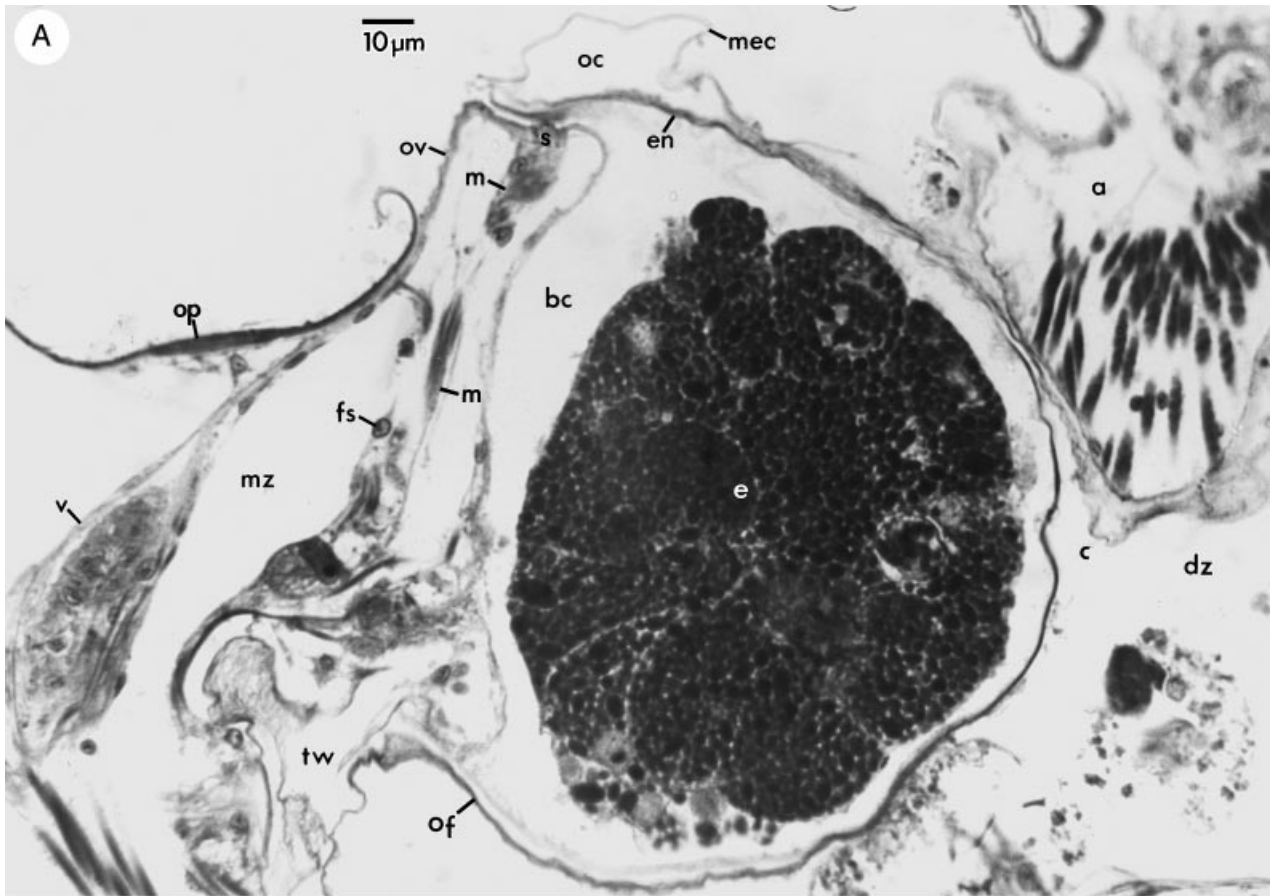
Materials and methods

Colonies of *Callopora dumerilii* were collected 05 August 1997 by trawling at 16–29 m depth on the stone reef Herthas Flak (North Kattegat, Baltic Sea), and 12 June 1997 by SCUBA from the 22 m depth near Riou Island (West Mediterranean). Colonies of *C. lineata* were collected 14 June 1995, 03 July 1995 and 17 August 1996 by dredging and SCUBA from 3 to 7 m depth near Sredniy and Matrenin Islands in the Chupa Inlet (Kandalaksha Bay, White Sea). Specimens were fixed in Bouin's fluid without acetic acid (sometimes with formalin neutralized by calcium carbonate) and 70% alcohol. For light microscopy, colonies decalcified in Bouin's fluid were embedded in plastic (epon), sectioned (1–2.5 µm thick) and stained with toluidine blue using standard methods. For SEM studies, colonies fixed in alcohol were cleaned in 7.5% solution of sodium hypochlorite,

Fig. 2—A, B. *Callopora dumerilii*; C. *lineata*—A. longitudinal section of ovicell with larva (communication canal is plugged by cells), insert † distal edge of the oocium—B. oocelial vesicle—C. tangential section of developing ovicell (communication canal is still open). Abbreviations: bc = brooding cavity, c = communication canal, cec = calcified part of ectooecium, dz = coelomic cavity of

daughter autozoid, e = embryo, en = entoecium, ep = nucleus of epithelial cell, fw = frontal wall of distal zooid, lv = larva, m = muscle bundle of oocelial vesicle, mec = membranous part of ectooecium, mz = coelomic cavity of maternal autozoid, oc = oocelial coelomic cavity, of = ocellular floor, op = operculum, ov = oocelial vesicle, s = sclerite, tw = transverse zooidal wall.





dehydrated in absolute alcohol, air-dried and coated with gold. Also some colonies fixed in 'neutral' Bouin's fluid were dehydrated and either air or critical-point dried for SEM study.

Results

Ovicell structure

Anatomical investigations showed that both *Callopora dumerilii* and *C. lineata* possess hyperstomial ovicells with oecia formed by the distal (daughter) zooid (Figs 1–5). In the complete ovicell the basis of the oecium is a continuation of the proximal gymnocyst of the daughter zooid. The majority of the ovicells was formed by autozooids, but one ovicell formed by a kenozooid was also found in *C. dumerilii* from the Mediterranean locality (Fig. 4B) (a similar case is shown in Zabala and Maluquer 1988; Pl. 3C). In this species the development of ovicell-bearing zooids was sometimes suppressed by the formation of an adjacent zooidal row (Fig. 4C). In one such case two fused ovicells with brooding cavities separated by a calcified wall were encountered (Fig. 4C,D).

Ovicells are helmet-shaped, and their chambers are slightly flattened dorsoventrally. The opening of the ovicell is not closed by an operculum (acleithral type) but is plugged by an oecial vesicle (Figs 1, 2A, 3A).

The oecial fold consists of two walls: outer (ectooecium) and inner (entooecium), with the coelomic lumen in between (Figs 1–3). In *C. dumerilii* the ectooecium is membranous except for the narrow basal part (Figs 2A, 4E, 4F). In *C. lineata* the calcified ectooecium is characterized by a big membranous window (lucida) near the oecial edge (Figs 3B, 5A) (see also Ryland and Hayward 1977 for comparison). The ectooecial cuticle is markedly thinner than the cuticle of the frontal zooidal wall (Fig. 2A).

The entooecium is always completely calcified and thickened along the oecial orifice (Figs 1, 2A and insert). In older zooids this thickening appears as a prominent lip. Its edge has a flattened area at the point of contact with the oecial vesicle. The surface of the entooecium facing the brooding cavity is smooth (Figs 4H, 5E), with concentric lines of growth and often nondistinct radial wrinkles. The coelomic surface of the entooecium is either more or less even (*C. lineata*) or granulated (*C. dumerilii*). Prenant and Bobin (1996) described and pictured a short medial suture in the entooecium of *C. lineata*, and a similar, small medial furrow was observed in one ovicell of this species in the material studied here.

The coelomic cavity of the oecium is lined by epidermal and peritoneal cells (Fig. 2A insert). Extensions of the latter sometimes cross the cavity. As calcification increases, the lumen becomes narrower, finally slit-like, but is never reduced completely. The oecial cavity communicates with a cavity of the daughter zooid through a flattened pore-like canal. The opening of the canal into the zooidal coelom is usually placed near the left or, sometimes, the right 'corner' of the oecial fold basis (Fig. 4G). In two cases, the canal was seen to communicate with the zooidal cavity by a couple of such openings in *C. dumerilii* (Fig. 4H). Each communication canal is a rudiment of an arch-shaped slit, formed during ovicellogenesis and connecting oecial and zooidal coeloms during that time. In younger zooids with complete ovicells this slit is already closed, but still clearly seen (Fig. 5F). In older zooids it is recognizable by an arch-shaped groove (Fig. 4G,H). As a rule, the canal is plugged by epithelial cells (not special pore-cell complexes) (Figs 2A, 3, 5F), so free circulation of the coelomic fluid is obviously absent. However, some completely formed ovicells of *C. lineata* had an open the communication canal, lined by epithelial cells, but not plugged (Fig. 3A). The oecial vesicle is a hollow evagination of the distal wall of the maternal autozooid that plugs the ovicell opening (Figs 1, 2A,B, 3A,B). In many cases observed, the vesicle was recumbent on the distal edge of the operculum. The cuticle of the vesicle wall that faces into the ovicell cavity is thinnest. The part of the vesicle in contact with the flattened area of the entooecium edge is characterized by a thickened cuticle forming a sclerite (see Santagata and Banta 1996). Its outer surface bears cuticular ribs, making the closure of the ovicell tighter (Fig. 1). The inner surface possesses a transverse (triangular in section) rib to which the upper bundle of the muscles is fixed (Figs 2A, 3A,B).

Paired sets of the bilateral muscles of the oecial vesicle originate laterally either at the basal wall of the maternal zooid (*C. dumerilii* from the Baltic locality) (Fig. 1) or at the transverse wall (*C. lineata*), near the corner between these walls. In *C. dumerilii* from the Mediterranean the muscles were found originating at the basal wall in some cases, and at the transverse wall in others; the transverse wall was more inclined, and more often the muscles were fixed at the basal wall. Sometimes the muscles originated exactly in the corner between the walls. The upper (larger) muscle set inserts on the sclerite rib (Figs 1, 2A,B, 3A). The middle set consists of four bundles which distally insert on the inner wall of the oecial vesicle in its middle part. Lower (smaller) set distally

Fig. 3—**A–B**, *Callopora lineata*, **C**, *C. dumerilii*—**A**. longitudinal section of ovicell with embryo (communication canal is open) —**B**, **C**. tangential section of ovicell (communication canal is plugged by cells, nuclei of epithelial cells arrowed). Abbreviations: a = avicularium, bc = brooding cavity, c = communication canal, cec = calcified part of ectooecium, dz = coelomic cavity of daughter autozooid, e = embryo, en = entooecium, ep = nucleus of

epithelial cell, fs = funicular strand, fw = frontal wall of distal zooid, lv = larva, m = muscle bundle of oecial vesicle, mec = membranous part of ectooecium, mz = coelomic cavity of maternal autozooid, nm = noncellular material within brooding cavity, oc = oecial coelomic cavity, of = ovicellar floor, op = operculum, ov = oecial vesicle, s = sclerite, tw = transverse zooidal wall, v = vestibulum.

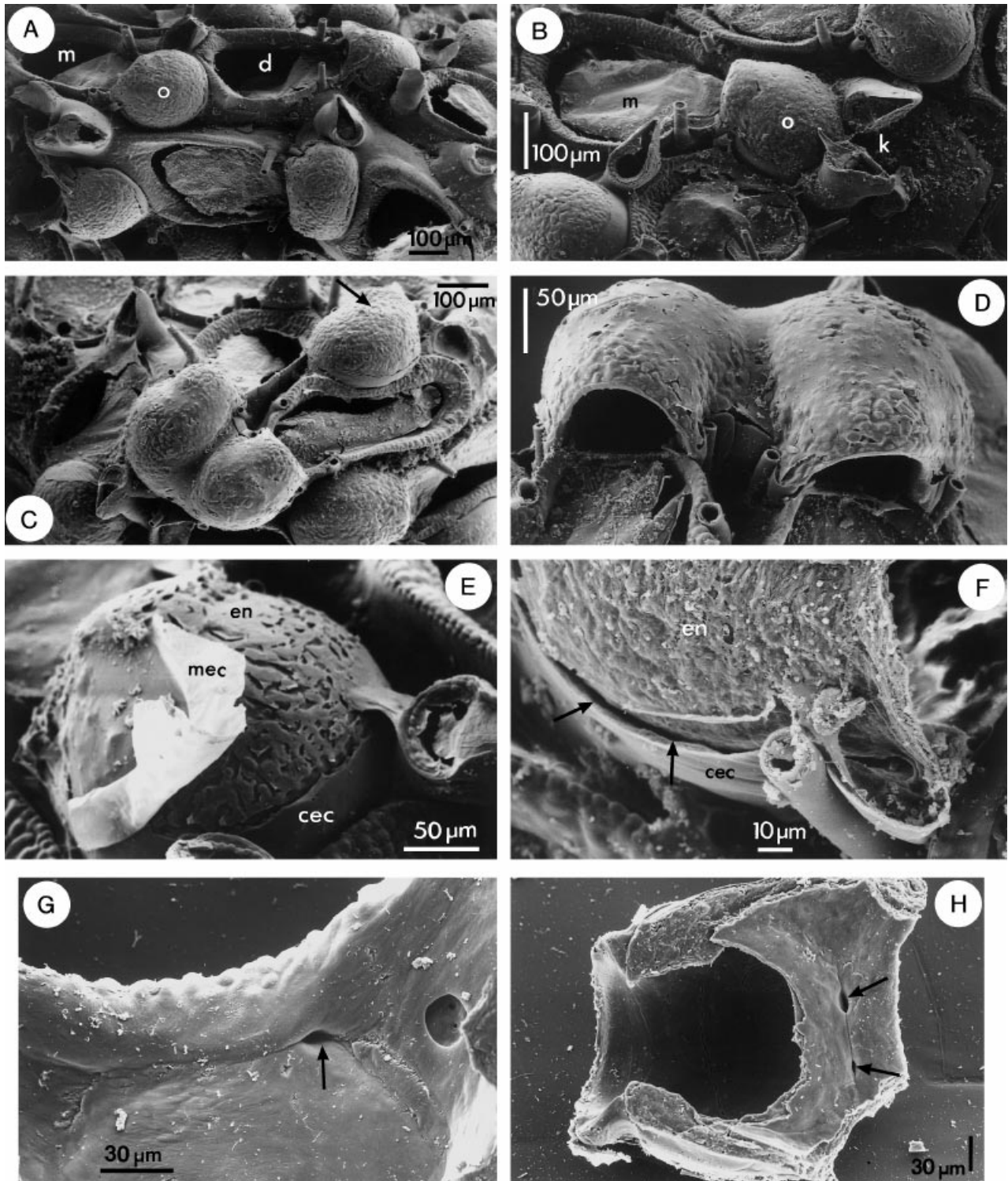


Fig. 4—*Callopora dumerilii*. —**A**. ovicells formed by distal autozooids —**B**. ovicell formed by distal kenozooid (ooecium bordered by two avicularia) —**C, D**. fused ovicells (**C**, ovicell of the zooid suppressed by the formation of an adjacent zooidal row arrowed) —**E**. ovicell distal view (membranous part of the ectooecium detached) —**F**. slit between endooecium and calcified

basal part of ectooecium (arrowed) —**G, H**. detached ooecia with one (**G**) and two (**H**) communication pores (arrowed) (trace of closed arc-shaped slit is clearly seen). Abbreviations: cec = calcified part of ectooecium, d = daughter autozooid, en = endooecium, k = distal kenozooid, m = maternal autozooid, mec = membranous part of ectooecium, o = ovicell.

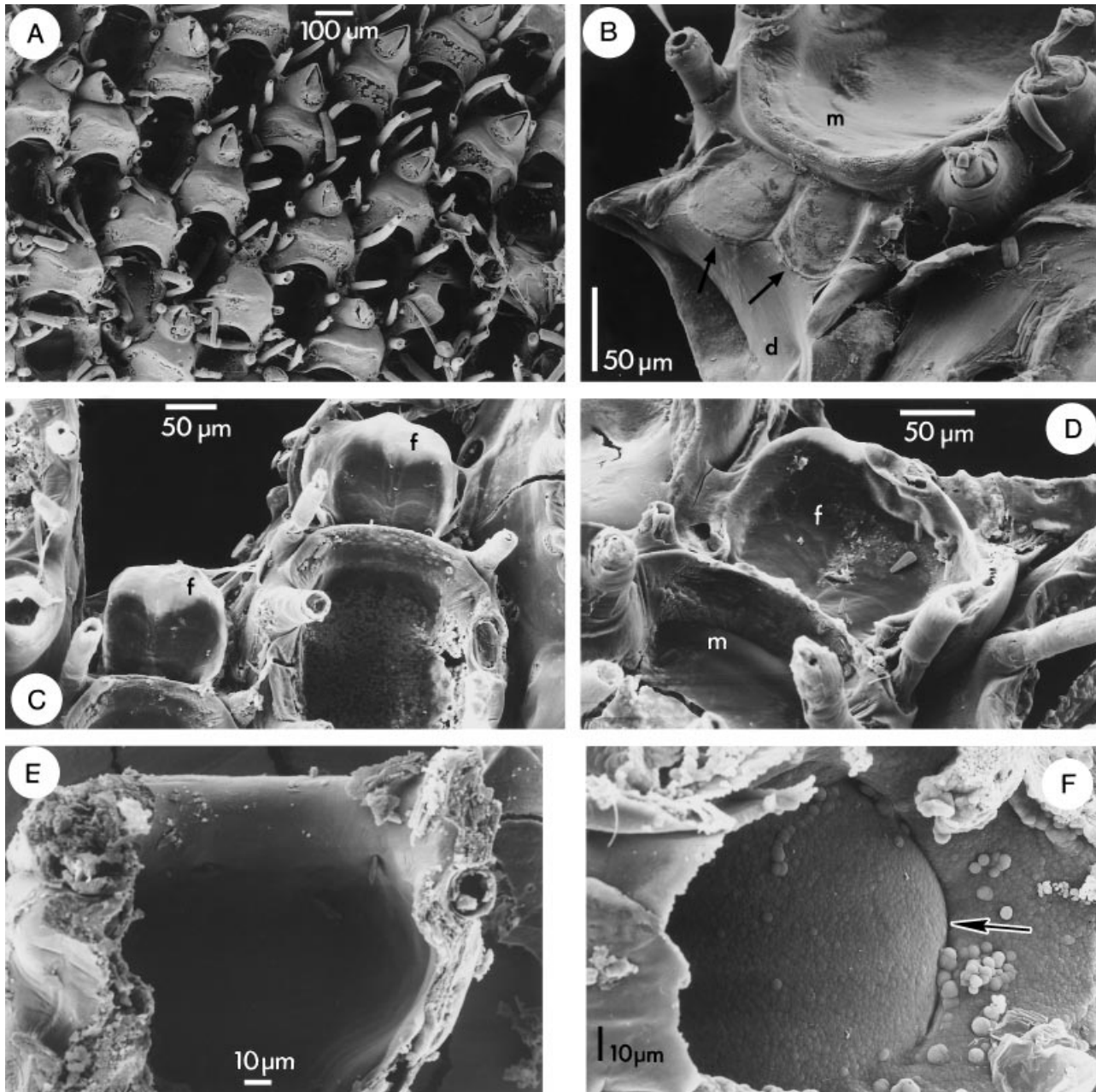


Fig. 5—*Callopora lineata* —**A.** part of colony with ovicells —**B–D.** early stages of oocial development: —**B.** distal zooidal bud with bilobate calcification (arrowed) —**C.** stage of bilobate plate with medial suture (two forming ovicell are seen) —**D.** stage of

semicircular fold —**E.** detached oocium (inner view) —**F.** arc-shaped communication slit (arrowed) with collapsed epithelial cells. Abbreviations: d = daughter autozooid, m = maternal autozooid, f = forming ovicell.

inserts on this wall in its lower part. The distance between these smaller sets (middle and lower) varies depending on the ovicell. In *C. dumerilii* they sometimes insert in upper and middle parts of the vesicle. Compared with the parietal muscle bands of the frontal zooidal wall, the muscles of the oocial vesicle are much wider, having longer zones of attachment to the body wall. Silén (1945) believed that there is a single muscle bundle.

The wall of the oocial vesicle is lined by flat epithelial and peritoneal cells, which are in contact with funicular strands that run into the zooidal coelom (Figs 1, 3A). No sign of cell hypertrophy was found in the oocial vesicles of the ovicells containing embryos or in the empty ones. There was also no special evagination on the inner wall of the vesicle as described by Silén (1945), and only late embryos sometimes deformed it. A thin layer of noncellular material was often

seen on the surface of the vesicle inner wall facing the brooding cavity (Fig. 2B). It was clearly seen in the wrinkles of the wall caused by muscle retraction.

Each embryo contained in the ovicell is surrounded by a very thin fertilization envelope. These were also found in empty ovicells, indicating that the brood chambers had been used at least once.

Early ovicellogenesis

The earliest stages of ovicell formation were investigated in *Callopora lineata*. The oocelial fold originates as a proximal outgrowth of the frontal wall of the daughter zooid bud. Before folding, an area of its membranous frontal wall begins to calcify. Calcification starts from the transverse zooidal wall and expands distally, having a shape of two rounded flat plates. The plates originate independently of one another and sometimes have different sizes (Fig. 5B). Finally, they fuse forming a bilobate plate with a medial suture (Fig. 5C). Calcification continues to expand centrifugally along the frontal wall of the zooidal bud, forming a shallow depression – the future floor (basal wall) of the ovicell. At this stage the calcified area loses its bilobate shape, but the medial suture is often still seen. It disappears at a later stage when the semicircular fold of the future ooeonium starts to grow (Fig. 5D). The oocelial coelomic cavity communicates with the zooidal perigastric coelom through the arch-shaped slit that gradually closes (Figs 2C and 5F).

Discussion

The ovicells of the two species of *Callopora* studied here definitely develop as special outgrowths from the frontal wall of the zooid distal to the maternal, not from the maternal zooid itself, as proposed by Silén (1945). An analysis of text-Fig. 18 in Silén (1944) (representing a longitudinal section of the ovicell in *Scrupocellaria scabra* (van Beneden, 1848)), and the accompanying description shows that Silén could not find a communication between an oocelial fold and a distal zooid because of the strong shrinkage of the specimen fixed in alcohol. Studying three other species, Silén (1945) did not make sections and referred to the wrongly interpreted structure of *Scrupocellaria*. On the basis of recent and previous findings (Levinsen 1909; Nielsen 1981; Lobastova and Ostrovsky 1994; see also Nielsen 1985 and Santagata and Banta 1996), Silén's (1944, 1945) conclusions concerning ovicell structure in *Scrupocellaria scabra*, *Callopora dumerilii*, *Fenestulina malusii* (Audouin, 1826) and *Escharella immersa* (Fleming, 1828) must be regarded as incorrect, and his generalization rejected.

The picture of brood chamber formation in cheilostomatids is not simple. Initially, Harmer (1902; p. 248) noted that the ooeonium can be part of 'the distal' zooid (type 1) or belong to the 'fertile (proximal)' zooid (type 2), and this has been confirmed (reviewed in Reed 1991; Ostrovsky 1998). In con-

trast with the opinion of Silén, type 1 is much more common than type 2. In the Cribrilinidae both types can sometimes be found within one and the same taxon and even in the same colony (see Ristedt 1985; Bishop and Househam 1987). Both types of ovicells are also known in Calloporidae, Romancheinidae and some other families (see illustrations in Levinsen 1909, 1916; Harmelin 1973b; Gordon 1984, 1986; Hayward 1995, etc.). Type 2 could have evolved from type 1 by a gradual reduction of the distal zooid (discussed in Bishop and Househam 1987; Ostrovsky 1998). Thus, the vast majority of the type 2 ovicells studied are found in species where a terminally budded daughter zooid is absent, and this was not the case in the species investigated by Silén. He believed that the development of an ovary triggers ovicell formation in the same zooid. Nielsen (1981) however, clearly showed that ovicellogenesis in distal zooids is induced by the proximal ones in fused colonies of *Fenestulina malusii*: fertile zooids from one colony had induced zooids from the other colony to form the ovicells (see also Nielsen 1990). Two fused ovicells on one zooid have been sometimes formed in such cases (one from maternal, the second from the 'neighbour'), but it is difficult to gauge the reason for the fusion of two ovicells in the colony of *C. dumerilii* studied (see above).

The first sign of the ovicellogenesis in *Callopora* is a calcification in the shape of two flat areas (rounded plates) extending from the proximal edge and along the frontal surface of the distal zooidal bud (see also Levinsen 1893, 1894, 1909; Harmelin 1973a for comparison). Silén (1945) described the first stage as a pair of knobs, but this was probably the result of observing only with a dissecting microscope (see also Ryland 1979). Believing that an ooeonium develops from the maternal zooid as paired knobs, Silén (1977) supported Harmer's (1902) hypothesis on the evolution of the ooeonium from the distal pair of oral spines (see Ryland 1979 and Ostrovsky 1998 for further discussion).

In cleaned specimens subsequent stages in calcification of the entoocium appear to develop from the transverse wall between zooids (see, for instance illustrations in Harmelin 1973a; Nielsen 1985, etc.). This probably explains the diversity of opinions concerning the mixed origin of the ooeonium. Since the paper of Levinsen (1902), it was suggested that the entoocium derives from the maternal zooid, and the entoocium from the daughter zooid (Harmelin 1973a; Soule 1973; Cook 1977, 1979, 1985; Ryland 1979; Morris 1980; Cook and Chimonides 1981; Wass and Banta 1981; Ristedt 1985). Calcification, however, is only a part, not the whole of ovicellogenesis, and it is incorrect, we believe, to consider the maternal zooid as a locus for entoocium only because the calcification of the latter starts from the transverse wall equally belonging to both maternal and daughter zooids. Nielsen (1981, Fig. 20) concluded that the entoocium is formed by the distal zooid (see also Ostrovsky 1998 and Ostrovsky (in press) for further discussion).

Further growth of the oocelial fold leads to the appearance of a helmet-shaped ooeonium, the lumen of which initially is

confluent with a cavity of the daughter zooid (Fig. 2C), thus, the oecium is simply an outgrowth of the zooid, although in most cases quite complicated. The communication slit is then subsequently getting narrowed by increasing calcification of the oecial walls. If the pore-like canal(s) remaining after the slit closure is free of cell obstruction (Fig. 3A), the oecium remains as an outgrowth of the zooidal wall as in *Figularia figularis* (Johnston, 1847), *Scrupocellaria ferox* (Busk, 1852), and some colonies of *Callopora lineata* (Cheetham and Cook 1983; Santagata and Banta 1996; our data). If the canal is plugged by the epithelial cells (Figs 2A, 3B,C), the oecium transforms to some kind of heterozooid (but not a true kenozooid) as in the cases of *Bugula neritina* (see Woollacott and Zimmer 1972) and two species of the genus *Callopora* studied. The epithelial lining of an oecium receives nutrients probably by intercellular transport. Finding closed and nonclosed communication canals in completely formed ovicells of *C. lineata* can reflect ontogenetical changes when older oecia finally should be ‘closed’ by cells, however, it is also still possible that some canals can stay open during the whole existence of particular ovicells. If so, there is only a formal reason to credit oecia as being a special heterozooid or ‘morph’ (Woollacott and Zimmer 1972; Ryland 1979; p. 214; see also Nielsen 1985 for discussion).

Oecia of type 2 start their development in the same manner as ordinary zooids (Ostrovsky 1998). They bud from the maternal zooids, becoming true kenozooids after the development of the transverse wall with pores closed by special pore-cell complexes.

In the calloporid *Amphiblestrum flemingii* (Busk, 1854) (as *Membranipora*), Calvet (1900, Fig. 45) pictured cells of the inner wall of the oecial vesicle as larger than all other epithelial cells. The same impression is gained from the schema of the *Securiflustra securifrons* (Pallas, 1766) (as *Flustra*) (Flustridae) (Calvet 1900, Fig. 44), however there is no sign of extra-embryonal feeding and subsequent hypertrophy of the epithelial cells in two species of the genus *Callopora* studied (Figs 2A,B, 3A). We suggest that Calvet, being impressed by his finding of an embryophore in the inner vesicle of *Bugula simplex*, incorrectly extrapolated these data to other species. At the moment, placental brooding is known in three bryozoan families: Bugulidae, Candidae, and Hippothoidae (Woollacott and Zimmer 1972; 1975; Dyrinda and King 1983; Hughes 1987; Santagata and Banta 1996; Ostrovsky 1998). In contrast, an egg receives all the nutrients while still in the ovary in Calloporidae. Silén (1945) noted that embryos died if they were removed from the brood chamber to the sea-water in *C. dumerilii*, but the processes involved are completely unknown.

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