Cheilostome Brood Chambers: Structure, Formation, Evolution

2

Abstract

This chapter focuses on brood-chamber structure and evolution in different cheilostome lineages. Following a review of the history of studies on brooding in the order Cheilostomata, different variants of brood-chamber structure and development are described, most for the first time. Their classification is developed and the terminology involved has been clarified. The data obtained show that cheilostome brooding evolved independently several times from modified mural spines, kenozooids, outgrowths of the zooid wall and fertilization envelopes. Accordingly, suborder Flustrina as currently conceived is considered polyphyletic. Major trends in the evolution of skeletal brood chambers (ovicells) are reconstructed using living and fossil taxa. The early evolution of conventional ovicells included curvature of the most proximal mural spines, their flattening, and reduction in number as well as loss of joints and fusion. Further changes were intimately connected with the evolution of complex frontal zooidal shields.

Keywords

Brood chambers • Diversity • Frontal shields • Independent evolution • Kenozooids • Ovicells • Spines

2.1 History of Studies of Cheilostome Brood Chambers

Cheilostome bryozoans possess a broad range of methods for embryonic incubation. Embryos are brooded in the external membranous sacs, skeletal (calcified) chambers and internal brood sacs formed by non-calcified zooidal walls, or develop intracoelomically in viviparous species. In some instances extraembryonic nutrition (EEN) has evolved.

Most cheilostomes temporarily house their offspring in skeletal chambers called ovicells. The presence or absence of ovicells, and their morphology, are important characters in cheilostome taxonomy. There are several morphological types, the commonest being hyperstomial ovicells that often look like prominent hemispherical bubbles or helmets on the colony surface. Basically, the hyperstomial ovicell consists of (1) a double-walled, calcified protective fold (ooecium) with a coelomic cavity between the two walls, (2) a non-calcified part of the distal wall of the egg-producing maternal autozooid, and (3) the brood cavity between these two components (see Fig. 1 in Introduction, Figs. 2.1, 2.3, and 2.5).

Ovicells were first described by Ellis (1753, 1755) who suggested that they were snail-like "neritae," formed from the "polypes," able to detach from a branch (to drop, fix to the substratum, and give rise to a new animal) or to lay eggs (see also Ellis and Solander 1786) (Fig. 2.2). Following Linnaeus (1758), Pallas (1766, p. 36) opined that these "bulla[e], galeae" [helmet-like bubbles, i.e. ovicells] might be ovaria. He speculated that both ovicells and avicularia might serve for fertilization and sometimes called them "Nectariums" (see also Ostrovsky 2008a, and Appendix I for details and discussion).

Later authors followed Linnaeus and Pallas, calling ovicells "corps vesiculaires", "corps globuleux" (Lamouroux 1816), "vesicules gemmifères", "capsules gemmifères" (Milne Edwards 1836), "vesiculae gemmifèrae" (de Lamarck 1836), "ovary-capsules" (Reid 1845), "calcareous capsules" (Johnston 1847), "ovarian capsules" (Landsborough 1852), and considering them as ovaries. This concept came to be

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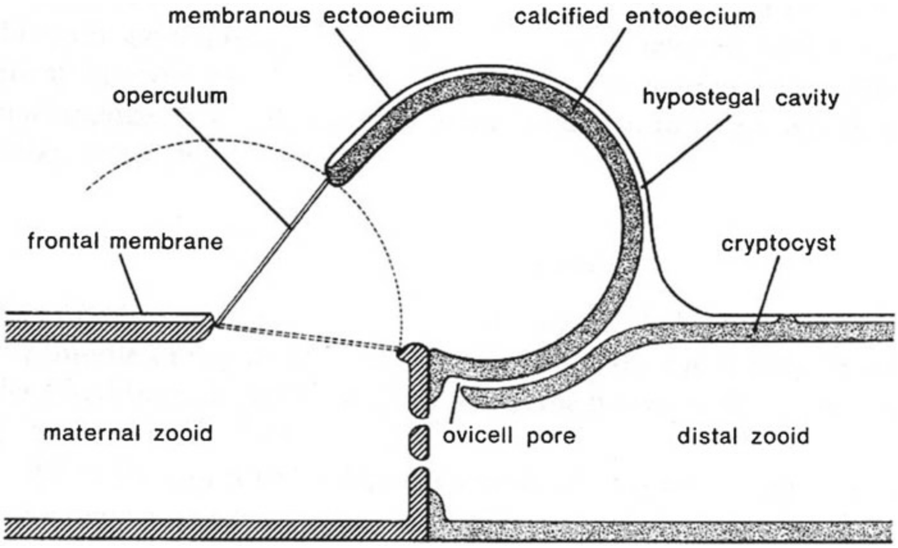

Fig. 2.1 Schematic depiction of ovicell structure in *Fenestrulina miramara* (From Nielsen 1981, courtesy of Taylor & Francis Ltd., http://www.tandfonline.com/doi/abs/10.1080/00785236.1981.10426564)

reflected in the term "ovicell," introduced by Busk (1852), augmenting it with such descriptive terms as "subglobose and terminal", "galeriform" (for *Scrupocellaria*), "globose, subpedunculate" (*Bicellariella*, as *Bicellaria*), "arcuate" (*Caberea*), "conical" (*Beania*, as *Diachoris*) and "subglobular" (*Cellepora*).

One of the first observers to contradict this view was Grant (1827, p. 341). Studying *Flustra foliacea*, he recorded an egg growing inside the zooid, whereas, when mature, it was seen to be surrounded by a helmet-shaped capsule [ooecium] that separates the egg "from the cavity of the cell [zooid]". Grant did not discuss this difference in relation to the accepted terminology, however.

The older view that ovicells are capsules containing ovaries was first disputed by Huxley (1856, p. 192). In *Bugula avicularia* (as *B. avicularis*) he observed eggs inside an autozooid with an empty ovicell that was later seen to contain an egg. Accordingly, he interpreted the ovicell as a "marsupial pouch" [brood chamber].

Hincks (1861), who investigated *Bugula flabellata*, *B. turbinata* and *Bicellariella ciliata* (as *Bicellaria*), challenged this opinion, but was later forced to admit the correctness of Huxley's observations (Hincks 1873, 1880). However, Hincks also stressed that he had "grounds for believing that in some cases, and under conditions which [he could not] explain, ova are also produced within [ovicells]" (1880, p. xciii). He further speculated that there are two kinds of eggs formed in marine Bryozoa; some are produced in ovicells, others in autozooids, being "the equivalent of the statoblast[s] of the Phylactolaemata" (Hincks 1861, 1873, p. 19). Smitt (1865) held a similar view concerning the existence of two types of eggs that develop with or without fertilization (see Appendix I for historical review). As evidence, Hincks (1861) adduced Smitt's (1863, 1865) findings. Smitt had first recorded embryo development inside the gonozooid (at that time also called an ovicell) of the cyclostome *Crisia eburnea* and inside the autozooid (in fact, in an internal brood sac that he referred to as a "membrane") of the cheilostome *Cryptosula pallasiana* (as *Lepralia*).

In his monograph, Hincks (1880, p. xcii) also expressed the opinion that the ovicell "interior is in direct communication with the perigastric cavity" of the maternal autozooid but he was unsure of the method of oviposition. In *Chartella papyracea* (as *Flustra*) he described an egg "jerking itself spasmodically" and wrote further that "it might pass by means of the contraction and extension of its substance from the cell [cystid] to the ovicell" (Hincks 1880, p. xciv). Earlier, he had observed how the ovulated egg in *Bugula* was moved within the zooid, being affected by excursions of the polypide, and suggested that "the action of the polypide might be mainly instrumental in effecting the transference to the marsupium" [ovicell] (Hincks 1873, p. 31). In the same paper Hincks (1873) introduced the term "ooecium" (by analogy with "zooecium") which he used synonymously with the "ovicell" of Busk (1852), and later indicated that "ooecia" can be "prominent", "subimmersed" or "immersed", depending on the extent to which they protrude at the surface of the colony (Hincks 1880). Busk (1884) accepted the term ooecium, describing the variety of shapes as "cucullate", "mitriform", "acuminate" and "subcarinate", and introduced the terms "erect" and "recumbent".

The first investigation of the structure and development of so-called hyperstomial ovicells was made by Nitsche (1869) on *Bicellariella ciliata* (as *Bicellaria*), and one of his figures was schematically redrawn by a later colleague as a non-numbered text-figure (Vigelius 1884a, p. 50). Nitsche found

Fig. 2.2 Colony of *Bugula neritina* with ovicells and supposed spirorbid tubes. (**A, a**), General view of the colony; (**B**), fragment of the branch showing its basal side; (**C**), lateral view of the branch (From Ellis 1755)

that each ovicell was formed as two outgrowths – “helmförmige Blase” [ooecium] and “rundliche Blase” or “Deckelblase” [ooecial vesicle] with two groups of muscles – on the distal margin of the maternal zooid in this species. The external wall of the ooecium was described as calcified, and its ‘internal’ wall [entooecium] as membranous, similar to the ooecial vesicle. The ooecial vesicle that plugs the opening of the brood chamber, and its rhythmical contractions, were first described by Reid (1845) in *Bugula flabellata* (as *Flustra avicularis*) (see also Hincks 1873, 1880). In accord with the opinion of Huxley (1856), Nitsche (1869) came to the conclusion that ovicells were merely brood chambers and that “the ovicells or ooecia in the Chilostomata” were modified individuals (Nitsche 1871a, b, p. 162). Following Allman (1856), Nitsche believed that bryozoan colonies were “composed of two different classes of zoïds, the ‘cystoid zoöids’ [cystid] and the ‘polypoid zoöids’ [polypide]”, with the latter being produced by budding inside the former. Accordingly, he considered ovicells to be a variety of “cystoid zoöid” (Nitsche 1871b, p. 162). It is noteworthy that Busk (1852, p. 5) believed that ovicells “are clearly transformed cells [zooids]” (see also Calvet 1900). Nitsche (1869) also proposed a possible mechanism for oviposition via a hypothesized pore between the basal parts of the ooecium and the ooecial vesicle. Communication between the incubation cavity and the visceral coelom of the maternal zooid was also suggested by Prouho (1892).

Claparède (1871) and Joliet (1877) made observations on ovicells in several cheilostomes but, in contrast to Nitsche (1869, 1871a, b), provided no new information about ooecial structure. In *Scrupocellaria scruposa*, Claparède noted that ovicell development began when the first mature egg and sperm were seen in the maternal zooid. This statement was criticized by Vigelius (1882) who observed the earliest stages of ovicellogenesis in zooids with incipient ovaries and stated that the growth of the first egg was accompanied by the formation of the brood chamber in *Chartella membranaceotruncata* (as *Flustra membranaceo-truncata*). Vigelius (1886) noted that the ovicell appeared slightly later than the ovary in *Bugula calathus*. Interestingly, Claparède (1871) and Nitsche (1869) used Smitt’s (1865) findings to argue against the hypothesis that the egg originates inside ovicells, since they were certain that it would have to be transferred to the brood chamber for further development.

Vigelius (1884a, b, 1886) was the first to section bryozoans. He described the structure and development of the so-called endozooidal ovicells of *Chartella membranaceotruncata* and clearly showed that two successive zooids contribute to the formation of the brood chamber in this species – the “Helm” (ooecium) originates from the daughter zooid whereas the “Deckel” (ooecial vesicle) originates from the maternal zooid (1884a, b). At the same time he accepted the opinion of Nitsche (1869) that the distal zooid is not involved in the formation of the brood chamber and the ovicell is merely an evagination of the maternal zooid in *Bicellariella ciliata*. Vigelius believed that, despite the different positions of “external” (hyperstomial) and “internal” (endozooidal) brood chambers in *B. ciliata* and *C. membranaceotruncata*, respectively, their structure showed obvious similarities. He opined that the simpler ovicell of *Chartella* is more likely to be a specialised organ, not a “Cystidindividuen” as Nitsche (1871a, b) stated. He also suggested a possible mechanism for oviposition through the rupture hole in the ooecial vesicle, which was accepted by Delage and Hérouard (1897) and by Calvet (1900). A similar idea was subsequently suggested by Waters (1913).

In his later paper, Vigelius (1886, p. 512) described ovicell structure in *Bugula calathus*, briefly outlining its formation. He interpreted the brood chamber as developing “from the free distal wall of the sexually mature animal” [maternal zooid]. He also found “Cylinderzellenschicht” (cylindrical epithelium) on the inner surface of the distal wall of the ooecial vesicle, giving a detailed description of its musculature, which consisted of two perpendicular groups of bands. He thought that one of the muscle groups was responsible for the rupture of the wall of the ooecial vesicle during oviposition.

Jullien (1888, p. 1.56) used the terms "coïtis" (Greek, "cradle") for the thick external ovicellar wall [ectooecium] and "sparganile" (Greek, "swaddling-cloth") [entooecium] for the thin internal wall in his description of the cheilostome *Exochella longirostris* (see also Jullien and Calvet 1903). In classifying cheilostomes, he introduced the new "tribes" Inovicellata, Subovicellata and Superovicellata based on the presence/absence of the ovicells and position of the ovicell opening in relation to the orifice of the maternal autozooid, and was the first to propose new terms for the different types of ovicell closure, dividing cheilostomes into "aneucleithrien(s)" (with ovicells not closed by the zooidal operculum) and "cleithrien(s)" (with ovicells closed by it) (see also Canu and Bassler 1920). These terms were subsequently modified to "acleithral" and "cleithral" by Ryland (1968).

Delage and Hérouard (1897) cited both Nitsche's (1869) opinion that brood chambers were formed by the maternal zooid and Vigelius's (1884a) view that maternal and daughter zooids might both be involved in ovicell formation, favouring the former. Harmer (1902, p. 284) was the first to consider three possibilities concerning ovicell [meaning its protective capsule, ooecium] development: the "ovicell" can (1) belong to the "fertile (proximal)" zooid, (2) belong to the "distal" zooid, or (3) be "a modified individual, as believed by Nitsche and others". In describing the ooecium in *Euthyroides episcopalis*, Harmer suggested (but did not prove) that "the ovicell is formed by the fusion of a pair of greatly expanded oral spines, the bases of which should communicate with the fertile zooecium on each side of the operculum" of the maternal zooid (1902, p. 283). He also stressed that "it is impossible not to be struck by the resemblance between the development of the ovicell and that of the frontal bars" [zooidal costae] in this species.

Waters (1889, 1904, 1907, 1909, 1912, 1913) made sections of ovicells in a number of cheilostome species. While his descriptions and figures showed that there are two ways of forming ooecia, either from the maternal or the daughter zooid, he did not discuss this distinction. In his study of tube-like brood chambers ("peristomial ooecia" in the terminology of Levinsen 1902) in *Margaretta chuakensis* (as *Tubucellaria ceroides* var. *chuakensis*), Waters (1907) found a peculiar modified polypide with a special terminal plug closing the entrance to the ovicell. In his paper briefly describing and illustrating ovicell formation in *Bugula neritina* (Waters 1909), he also mentioned that "the ovum passes for development into a sac at the distal end by the basal wall" in *Watersipora cucullata* (as *Lepralia*). He called this internal brood sac "a concealed ovicell" (p. 151). Waters (1913) depicted the ovicell of *Halysisis diaphanus* (as *Catenaria diaphana*) as consisting of a small kenozooidal ooecium (budded from the fertile zooid) and brood sac. In this paper he also applied the characters of ovicell shape and position to the classification of Catenicellidae and described the developmental stages of the ovicell in *Triphyllozoon* (as *Retepora monilifera* var. *umbonata*). The latter data were further supported and verified by Okada (1920), Buchner (1924) and Harmer (1934), who described ovicellogenesis in several confamilial species of Phidoloporidae.

Calvet (1900) carefully investigated the anatomy of brood chambers in a number of marine bryozoans, including cheilostomes, making sections of decalcified specimens. He noted that, compared to the majority of cheilostomes and ctenostomes that incubate their offspring, there are some that do not. In *Bugula simplex* (as *B. sabatieri*) he described early ovicellogenesis as the formation of two hollow vesicles, one of which, formed from a maternal zooid, was a rudiment of the ooecial vesicle ("vésicule ovicellienne inférieure"), whereas the second, originating from a daughter zooid, was a rudiment of the ooecium ("vésicule ovicellienne supérieure") (Calvet 1900, p. 132; p. 57, fig. 10; pl. 2, fig. 14; pl. 3, figs. 5–6). Calvet suggested that this ovicell type, in which two parts of the ovicell (ooecium and inner vesicle) belong to different subsequent zooids, is the commonest among cheilostomes. He thought that *Bicellariella ciliata*, the ovicells of which were studied by Nitsche (1869), should not be an exception to this rule. A recent study has confirmed the correctness of Calvet's suggestion (Moosburgger et al. 2012).

One of Calvet's most important findings was a communication pore in the septum between ooecial and daughter-zooid coeloms (Calvet 1900, p. 58, fig. 10) (Fig. 2.3). Unfortunately, this communication, which was conclusive evidence of ooecial formation from the distal zooid, was overlooked or ignored by most subsequent authors. In the ooecial vesicle of *B. simplex* Calvet found a sclerite (a thickening of the cuticle corresponding to the zone of contact between the ooecium and ooecial vesicle), a plexus of mesenchymatous cells (funicular strands), and, similar to Vigelius (1886), musculature and embryophore. He described and illustrated the structure of the endozooidal ovicell in *Securiflustra securifrons* (as *Flustra*), depicting longitudinal sections of the hyperstomial ovicells of *Amphiblestrum flemingi* (as *Membranipora*) and *Fenestrulina malusii* (as *Microporella*).

Until now, Calvet (1900) remains the only researcher to have studied the anatomy of endotoichal ovicells in the genus *Cellaria* (in *Cellaria fistulosa* and *C. salicornioides*). One of the most interesting characters found in these peculiar internal brood chambers was an additional operculum (actually, part of the modified ooecial vesicle), closing the ovicell opening. Calvet wrote that the brood cavity [as he called the space around the brood sac] is connected with

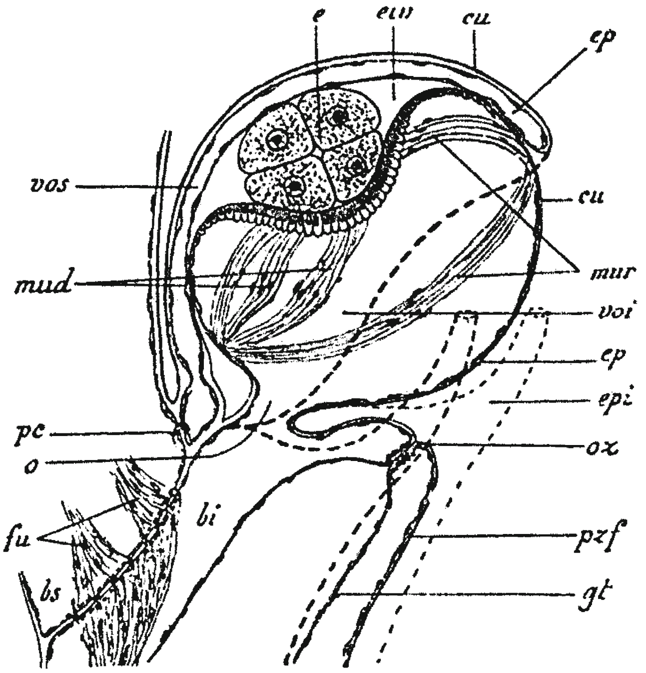

Fig. 2.3 Calvet's (1900) depiction of ovicell structure in *Bugula simplex*. Abbreviations: *bi* coelom of maternal autozooid, *bs* coelom of daughter autozooid, *cu* cuticle, *e* embryo, *eiv* brood cavity, *ep* epidermis, *epi* oral spine, *fu* funicular strands, *gt* wall of tentacular sheath, *mud* muscles-depressors of brooding cavity, *mur* muscles-retractors of ooecial vesicle, *o* communication between the cavity of ooecial vesicle and the cavity of maternal zooid, *oz* zooidal orifice, *pc* communication pore between the coelomic cavity of ooecium and the visceral coelom of the distal zooid, *pzf* frontal wall of maternal autozooid, *voi* ooecial vesicle cavity, *vos* ooecial coelomic cavity

the coelomic cavity of the maternal zooid and considered it part of the latter.

The comprehensive studies of Levinsen (1893, 1894, 1902, 1909, 1916, 1925) (who intentionally did not use the term "ovicell," possibly because it reflected the erroneous idea that eggs can be formed in them), revealed "numerous modifications" of "hyperstomial ooecia" and showed a basic similarity in their structure, where "the two layers [walls] of the actual ooecium are formed by the frontal membrane [wall] of the distal zooecium [daughter zooid]" (Levinsen 1909, p. 60). He also described and depicted some species with ooecia formed either by distal kenozooids or avicularia, but stated that the above-mentioned "type of the ooecium … appears in the majority of the Cheilostomata". Likewise, in considering endozooidal ovicells, he categorized them into "ooecia which are enclosed in autozooecia" and "ooecia which are surrounded by kenozooecia" (Levinsen 1909, pp. 56, 59). He did not mention the communication between ooecial and distal zooidal coeloms discovered by Calvet (1900) in *Bugula*, or depict a communication pore in his schema of the ovicell of *Bugula* (Levinsen 1909, pl. 24, fig. 13). However, he carefully illustrated it in many other cases (Levinsen, 1893, 1894, 1909). One explanation may be that Levinsen mainly dealt with cleaned (but often sectioned) skeletons in which communication pores are not always clearly visible.

In total, Levinsen described ovicell structure and development in more than 80 cheilostome species, but, except for his terminology, his data were practically never used (see Ostrovsky 2008a, b). He classified cheilostome brood chambers according to their structure, the position of the ooecium relative to the zooidal orifice, and degree of ovicell immersion, introducing the terms "endozooecial", "hyperstomial", "peristomial", "endotoichal", "double-valved" and "acanthostegous," most of which are currently in use (Levinsen 1902, 1909). He also categorized hyperstomial ovicells as (1) "ooecia without a cryptocyst" and "ooecia with a cryptocyst" (Levinsen 1902), and (2) "dependent" and "independent" according to the number of ooecial walls and the size of the contact between the ooecial base and the distal zooid wall (Levinsen 1909). He often used the terms "ooecial fold" for the entire ooecium, "ooecial operculum" for the ooecial vesicle, and "ectoOoecium" and "endoOoecium" for the external and 'internal' [surrounding a brood cavity] ooecial walls (Levinsen 1902, p. 13, 1909, p. 60). He also described the earliest stages of ovicellogenesis (in dried specimens) which, according to him, start from the development of either "two small distal calcareous plates" or "a continuous plate" (depending on the taxon), arising "from the frontal edge of the distal [zooidal] wall" (Levinsen 1909, pp. 60–61; see also Ostrovsky and Taylor 2005a). In the same monograph he suggested that the egg should leave the maternal zooid before entering the ovicell, aided by the tentacle sheath as suggested by Jullien (1888) in *Celleporella hyalina* (as *Hippothoa*) or "by an independent movement of the egg" (p. 67).

Subsequent authors either accepted without discussion, or supported, or just ignored the findings of previous workers on ooecial structure. Korschelt and Heider (1910) briefly described ovicell structure in *Bugula* subsequent to Calvet and copied the schema of the ovicell in sagittal section from his monograph (Calvet 1900, fig. 10) without comment. Canu and Bassler (1920), although criticizing Levinsen (1902, 1909), gave very similar schemata of different ovicellar types (see also Bassler 1922, 1953). These authors sectioned a number of species with ovicells and introduced the term "subcleithriens" for cheilostomes with ovicells closed by the partly elevated operculum. Canu and Bassler (1920) substituted Levinsen's term "independent ooecia" for "recumbent" [Ryland (1968) criticized this move] and reproduced Calvet's schema for the *Bugula* ovicell (see Canu and Bassler 1929). These authors also applied the characters of ovicell structure (immersion and closure) to the classification of "Membraniporae" (Canu and Bassler 1923).

Harmer (1926, 1934, 1957) considered ovicell structure in all three cheilostome volumes of his famous monograph "The Polyzoa of the Siboga Expedition". In the 1926 volume he used slightly modified schematics of endozooidal and hyperstomial ovicells (fig. 1A–C) published by Calvet (1900). Harmer also modified Levinsen's (1902, 1909) spelling of "ectoooecium" and "endoooecium" to "ectooecium" and "entooecium", and used "entozooecial ovicells" instead of "endozooecial". In the final "Siboga" volume Harmer, following Levinsen (1909), depicted three schemes of ovicell structure, with ooecia consisting of two external non-calcified walls (ecto- and entooecium) and a double inner wall (cryptocyst) between (Harmer 1957, fig. 15B–D). In all cases, ooecial walls were depicted as a continuation of the daughter-zooid frontal wall.

Interestingly, when using Calvet's (1900, fig. 10) schema for *Bugula*, Harmer (1926, fig. 1C) for some reason did not mention or illustrate the communication pore of the ooecium (the same omission was made by Levinsen in his 1909 monograph, see above). It is all the more strange since he discussed Calvet's finding in an earlier work (Harmer 1902, p. 284) and stressed that "the vestigial … ovicell is … definitely shown to be a derivative of the distal zooecium" in *B. longicauda* (Harmer 1926, p. 451). Marcus (1926, fig. 19, 1940, fig. 54), on the other hand, depicted this pore, using the modified schema of *B. avicularia* from the work of Gerwerzhagen (1913, textfig. 1).

Contrary to all previous authors, Cori (1941, fig. 343) modified the scheme of Calvet (1900, fig. 10) and pictured communication between ooecial and maternal-zooid coeloms instead. The reason for this is unclear, since Cori did not himself make sections of ovicells. It is quite possible that he was influenced by the opinions of earlier authors such as Nitsche (1869), Vigelius (1884a, 1886), and Delage and Hérouard (1897).

Cori's figure was approved by Silén (1944, 1945), however. It should be noted that Silén was probably the first to realize the importance of the communication between coelomic cavities (instead of a continuity of zooidal walls) in regard to ooecial origins. Based on histological sections, Silén (1944, figs. 18–19) reconstructed ovicell anatomy in *Scrupocellaria scabra* (Fig. 2.4), and described the ooecial coelom as confluent with that of the maternal autozooid.

Silén (1945) then published his very influential paper, "The main features of the development of the ovum, embryo and ooecium in the ooeciferous Bryozoa Gymnolaemata." This prominent study dealt with many aspects of bryozoan structure and reproductive biology, including the development and structure of the ooecia of three cheilostomes: *Callopora dumerilii*, *Escharella immersa* and *Fenestrulina malusii*. In this paper Silén refuted the view of earlier researchers concerning the existence of a connection between the ooecial coelom and the perigastric cavity of the distal zooid. Based on sections of *Scrupocellaria scabra* (see Silén 1944) he stated that in all three species studied an ooecial fold originates from the maternal zooid, the cavity of which communicates with that of the fold. He showed that the ooecium starts to develop when the first oocyte begins to grow in the ovary, and this was suggested as being regulated by hormones. Silén apparently implied that if ovicellogenesis was triggered by the maternal zooid (its ovary), the ooecium was formed at its expense as well. He obviously overlooked Calvet's (1900) finding of the communication pore in *Bugula simplex*, unjustly and rather aggressively criticizing him for not "understanding of the nature of the" ooecium, and considering his anatomical schemes of the ovicells of *Amphiblestrum flemingi* and *Securiflustra securifrons* as "misapprehended" or "entirely wrong" (Silén 1945, pp. 12–13, see also Ryland 1976 for discussion). Admitting the correctness of the Levinsen's data on ooecial development, Silén criticized his view on the connection between the ooecium and ooecium-producing zooid. The illustrations of Levinsen clearly showing the origin of the ooecium from the daughter zooid were considered wrong or were ignored (for instance, for *S. scabra*, see 1893, tab. 1, fig. 8, 1894, tab. 1, fig. 22; for *E. immersa*, see 1909, pl. 17, fig. 3a; for *C. aurita*, see 1909, pl. 24, fig. 16; for *Tegella unicornis* (as *Membranipora*), see 1893, tab. 2, fig. 24; 1894, tab. 4, fig. 19). The earliest stage of ovicellogenesis was described as "a flat and narrow prominence from the frontal part of distal wall [of the mother zooid] … composed of two separate knobs" (Silén 1945, p. 9; see also Ryland 1979). In accord with Nitsche (1869), the external wall of the ooecial fold was said to be calcified whereas the inner one was membranous. Finally, Silén extrapolated these statements to all bryozoans with hyperstomial and endozooidal ovicells (for review and discussion see also Woollacott and Zimmer 1972a). It is noteworthy that in his previous paper Silén (1944, captions for text-figs. 20–24) wrote that the ooecium is formed by the distal zooid in endozooidal ovicells.

Silén's view that the ooecium originates from the maternal zooid was influenced by Harmer (1902), who suggested that the ooecium originated from the two oral spines in the cribrimorph *Euthyroides episcopalis* (discussed in Ostrovsky 1998, see also above). Based on this, and his own inferences concerning the evolution of spines in Gymnolaemata, Silén (1942, 1945, p. 17) speculated that the ooecium "is possibly a structure composed of transformed zoid-buds".

Silén's (1945) study was so comprehensive, and his arguments so convincing, that they have been accepted or mentioned by the authors of most large reviews and handbooks on Bryozoa up to the present time (Brown 1952; Hyman 1959; Brien 1960; Larwood 1962; Prenant and Bobin 1966; Powell 1967; Ryland 1970, 1976, 1979; Kluge 1975; Ryland and Hayward 1977; Ström 1977; Hayward and Ryland 1979, 1998, 1999; Reed 1991; Viskova 1992;

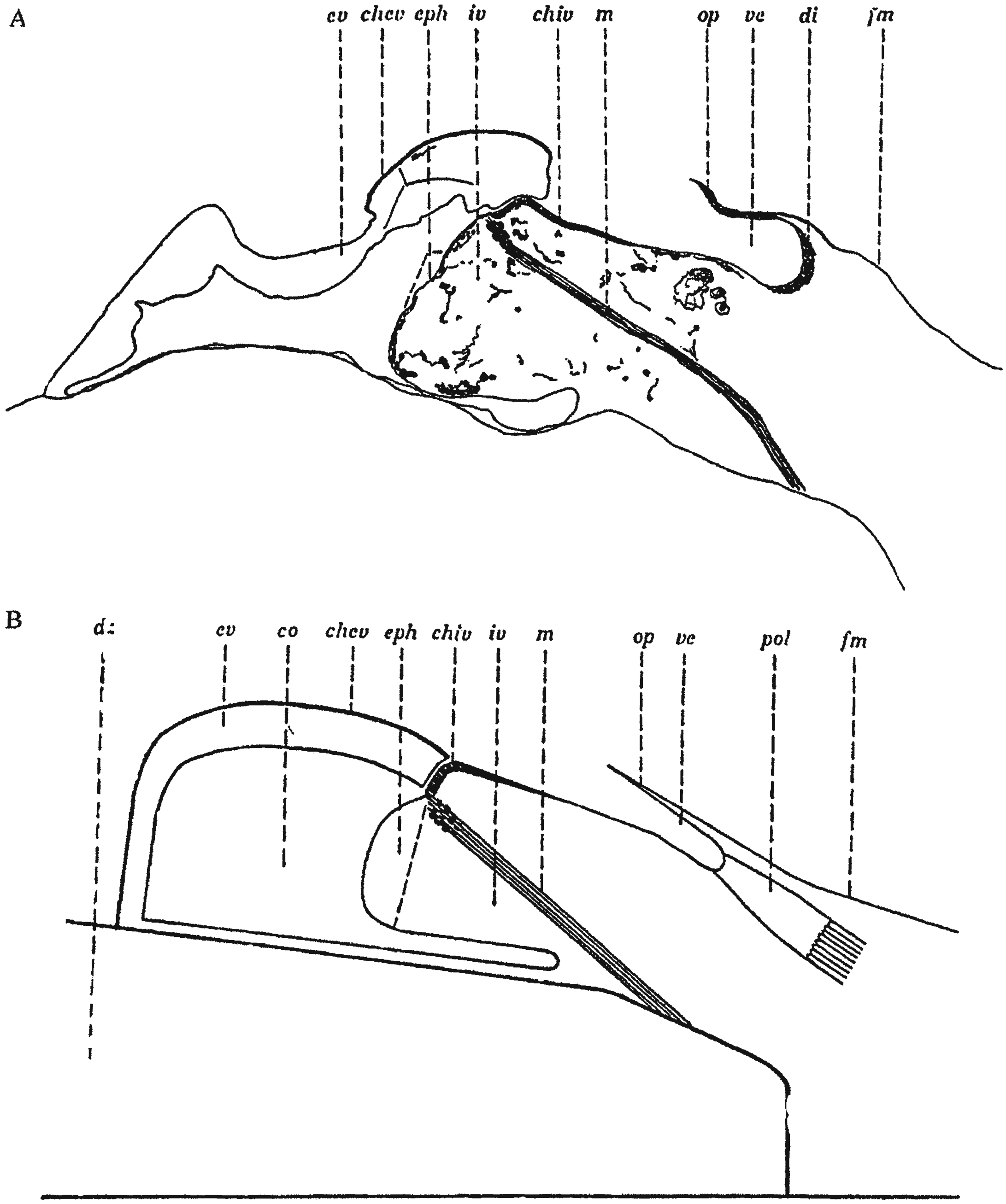

Fig. 2.4 Silén's (1944) schematics of ovicell structure in *Scrupocellaria scabra*: (**A**) longitudinal section of an ovicell in a decalcified specimen. (**B**) Diagrammatic reconstruction of the section. Abbreviations: *chev* ectooecium, *chiv* sclerite of ooecial vesicle, *co* brood cavity, *cv* ooecial coelomic cavity, *di* diaphragm, *dz* daughter (distal) zooid, *eph* distal part of ooecial vesicle, *fm* frontal membrane of daughter zooid, *iv* inner (ooecial) vesicle, *m* muscles of ooecial vesicle, *op* operculum, *pol* distal end of tentacle sheath, *ve* vestibulum

Mukai et al. 1997). Some (Powell 1967; Viskova 1992) also accepted the changes in terminology made by Silén, who used the term "ectooecium" for the entire ooecial fold and "entooecium" for the ooecial vesicle (criticized by Ryland 1968). Notably, Calvet had called the ooecial vesicle a "vésicule ovicellienne inférieure", Levinsen (1909) an "ooecial operculum", Harmer (1926) a "membranous vesicle", Cori (1941) "Untere Blasé des Ooeciums", Silén (1944) "interior vesicle", and Ryland (1970) an "inner vesicle". The common term "ooecial vesicle" was introduced by Woollacott and Zimmer (1972a), and later Banta (1977) and Santagata and Banta (1996) used "median vesicle" and "ovicell plug" for this structure correspondingly.

Interestingly, figures 1–8a from Silén's (1945) paper, often reproduced, have never been modified, whereas the communication pore to the ooecium in figure 10 of Calvet

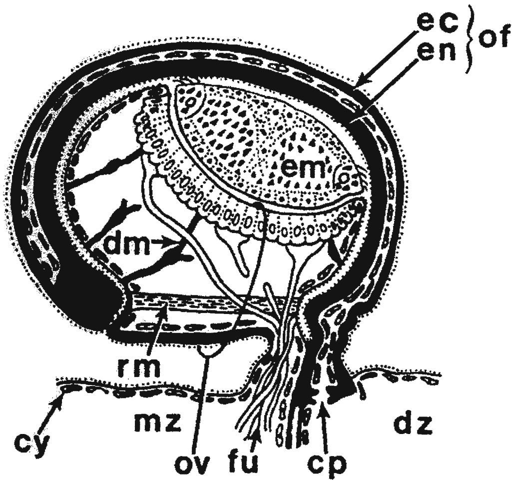

Fig. 2.5 Ovicell structure in *Bugula neritina.* Abbreviations: *cp* communication pore, *cy* cystid wall of maternal zooid, *dm* depressor muscle of inner (ooecial) vesicle, *dz* distal zooid, *em* embryo, *ec* ectooecium, *en* entooecium, *fu* funicular cords, *mz* maternal zooid, *of* ooecial fold (ooecium), *ov* ooecial vesicle, *rm* retractor muscle (from Woollacott and Zimmer 1972a, courtesy of Springer Verlag, http://link.springer.com/article/10.1007/BF00347954)

(1900) has often been omitted without comment (Hyman 1959; Brien 1960; Prenant and Bobin 1966). This may have happened because Calvet stressed that he did not find this pore in any of the species with hyperstomial ovicells other than *Bugula simplex*, even though the connection between ooecial and visceral coeloms was described and depicted by him in the endozooidal ovicell of *Securiflustra securifrons* (see Calvet 1900, fig. 44).

Other than Hass (1948, fig. 32), who correctly depicted the lumen of the ooecial fold connected with the visceral coelom of the distal zooid via "Oözialporus" in a phidoloporid cheilostome (as *Sertella*), no-one challenged Silén's generally accepted opinion during the next three decades. Ryland (1962, 1965, 1968) and Moyano (1968) depicted ooecia either resting on the frontal wall of the distal zooid or immersed in it, but gave no details of their communication with the visceral coelom. In the latter work, Ryland (1968) discussed terminological problems subsequent to the works of Jullien (1888), Levinsen (1902, 1909), Canu and Bassler (1920), and Silén (1944, 1945) and selected the most appropriate terms that are currently in use (see also Ryland 1976, 1982; reviewed in Ostrovsky 2008a).

Woollacott and Zimmer (1972a) investigated ovicell structure in *Bugula neritina* (Fig. 2.5), validating Calvet's (1900) findings. They also studied a placental analogue in this species (Woollacott and Zimmer 1972b, 1975). Silén (1977) was then moved to admit that Calvet had been right in regard to the species mentioned (see also Ryland 1979) but stressed that the ooecium ought always to be formed by the maternal zooid in species where the distal zooid is absent from a longitudinal zooidal row (series). Finally, Silén repeated the idea of Harmer (1902) that the ooecium is formed in different ways in different taxa.

A number of studies have since presented further evidence in favour of ooecium formation from the daughter zooid in the cheilostome families Calloporidae, Phidoloporidae, Bitectiporidae, Candidae, Bugulidae, Microporellidae, Cribrilinidae and Petraliellidae (see Cheetham 1975; Banta 1977; Sandberg 1977; Carson 1978; Nielsen 1981, 1985; Cheetham and Cook 1983; Lobastova and Ostrovsky 1994; Santagata and Banta 1996). For instance, Sandberg (1977, p. 176) wrote that the ooecium is a flattened, expanded spine or spines, whose lumen "connects with the distal individual, not the fertile zooid." Importantly, the same genera or species as Silén studied have been investigated by subsequent workers, allowing direct comparisons. Nielsen (1981, 1985) studied, inter alia, *Scrupocellaria varians*, *Bugula pacifica* and *Fenestrulina miramara* (as *F. malusii*) (Fig. 2.1) (see also Nielsen 1990). Following Levinsen (1909), he showed that the initial stage of ovicell formation could be either bilobate or single in different taxa. Lobastova and Ostrovsky (1994) and Santagata and Banta (1996) studied sections of *S. scabra*, *Callopora aurita* and *S. ferox*. They all confirmed that ooecia are formed by the daughter zooid (already regarded as basic by Nielsen 1985), and ooecial and visceral coeloms are interconnected via a communication pore(s) or slit. As a consequence of these findings, the previously dominant view in the literature shifted to reflect both those of Silén and Levinsen-Calvet (Ryland 1979; Reed 1991; Mukai et al. 1997).

Terminology has also varied. Following Levinsen (1902, 1909), Woollacott and Zimmer (1972a) used "ooecium" as a synonym of "ovicell", comprising the ooecial fold and ooecial vesicle. Ryland (1976), however, distinguished the two terms, stressing that "ooecial fold" could not be used for taxonomy. Thus, he referred to the entire structure as an ovicell, comprising the ooecium (the protective skeletal walls), the ooecial vesicle and the incubation space between them (see also Ryland 1979). Actually, a division into three parts – "the ectooecium, the entooecium, and the embryo chamber" – was first proposed by Silén (1945, p. 32). I consider the definition of Ryland the most acceptable and precise for descriptive-anatomical and taxonomic purposes (Ostrovsky 2008b).

Following Calvet (1900), Levinsen (1909) and Woollacott and Zimmer (1972a), Ryland and Hayward (1977) published schematic drawings of hyperstomial and endozooidal ovicells in their bryozoan "Synopses of the British Fauna" (see also Hayward and Ryland 1979, 1998, 1999). These two schemata are correct, but three others show communication of the ooecial coelom with the maternal zooid, apparently influenced by the above-mentioned paper of Silén (1945) (see also similar schemata in Lutaud 1976; Occhipinti Ambrogi 1981).

Since calcification of the incipient entooecium starts from the upper margin of the transverse wall between the maternal (proximal) zooid and the distal bud (or zooid), such that the wall and entooecium are continuous, a further idea for ooecial formation was suggested – that the entooecium is derived from the maternal zooid and the ectooecium is derived from the daughter zooid. This idea was first mentioned by Levinsen (1902, p. 13), who wrote that "it is obvious that the inner layer (the endoooecium) can be regarded as a continuation of the distal [transverse] wall while the outer layer (the ectoooecium) is formed from the front wall of the distal zooecium". Following the papers of Soule (1973) and Harmelin (1973a), this point of view reappeared in the literature as a compromise between the two earlier conflicting opinions (cf. Cook 1977a, 1979, 1985; Ryland 1979, 1982; Humphries 1979; Morris 1980; Cook and Chimonides 1981a; Wass and Banta 1981; Ristedt 1985). For instance, Harmelin (1973a) interpreted ovicell formation in the calloporid *Corbulella maderensis* (as *Crassimarginatella*) and Cook (1979) in *Doryporella alcicornis* and *Scrupocellaria* (Candidae) in this way. However, their morphological data clearly show that all these authors described ooecia formed by the daughter zooid and that the ooecial fold should be considered in its entirety (Ostrovsky 1998; see also Nielsen 1981).

Cook (1979) and Cook and Hayward (1983) outlined different variants of brood-chamber formation in Cheilostomata, including that in several Lekythoporidae, in which zooids have a distinctive orientation. Judging from their generalized schematic for the family, they depicted the ooecium as formed by the maternal autozooid, although polypide orientation shows that the ooecium obviously originated at the expense of the distal zooid in an ancestral form.

An important landmark was the paper of Bishop and Househam (1987), who described three categories of ovicells [ooecia] "based on the timing of production of the ovicell in relation to the budding of the maternal autozooid and of the zooid distal to it" in the genus *Puellina* (Cribrilinidae). The ovicell "is a proximal component of the distal zooid" in category A, and "of the kenozooid … distal to the maternal autozooid" in category B. "The ovicell appears to be a distal component of the maternal zooid" in category C (Bishop and Househam 1987, p. 4). Two years previously, Ristedt (1985) illustrated the same three ovicell categories in *Puellina harmeri* (as *Cribrilaria*). Ostrovsky (1998) discussed these findings in the context of ooecium formation from the maternal zooid in confamilial *Cribrilina annulata*. Further analysis of the literature and my own data led me to recognize two main ovicell types in Cheilostomata, assigning ooecia in categories A and B of Bishop and Househam (1987) to one type and category C to a second (Ostrovsky 1998; see also below).

However, since *Callopora dumerilii* has not been restudied, Silén's (1944, 1945) statements that ooecia are formed by the maternal autozooid in it, *Scrupocellaria scabra* and other cheilostomes, could be neither refuted nor ignored. I therefore investigated ovicell structure (anatomy and external morphology) and development in *C. dumerilii* and *C. lineata* (type species of *Callopora*), with the aim of resolving this long-standing controversy (Ostrovsky and Schäfer 2003; Ostrovsky et al. 2003). It was confirmed that ooecia were formed by daughter zooids in both species. Early stages of ovicellogenesis in *C. lineata* were studied, and no knobs or any other outgrowths were found. An analysis of text-figure 18 in Silén (1944) (representing a longitudinal section of the ovicell in *Scrupocellaria scabra*) (Fig. 2.4) and the accompanying description showed that he could not have discovered any communication between the ooecial fold and the distal zooid because of strong shrinkage in alcohol-fixed specimens. Studying three other species, Silén (1945) did not make sections and referred to the misinterpreted structure of *Scrupocellaria.* Interestingly, Silén himself explained the difference between his and Calvet's results for the same reason – he suggested that the latter author worked with shrunken material. On the basis of these and previous findings, Silén's (1944, 1945) conclusions concerning ovicell structure were taken to be incorrect, and his generalization was rejected. Since it has often been stressed that both ooecial types exist among cheilostomes (Harmer 1902; Silén 1977; Ostrovsky 1998, 2008b; see also Ostrovsky et al. 2009a), sometimes in the same taxon, further research was deemed necessary to verify what types are characteristic of different taxa (Ostrovsky and Schäfer 2003).

A commonly expressed viewpoint in bryozoological literature is that the ooecium is a heterozooid (Ström 1977; Silén 1977; Ryland 1976, 1979, 1982; Cook 1979; Reed 1991) and that brood-chamber formation is thus an expression of the zooidal polymorphism that reflects the high level of colonial integration in bryozoans (Viskova 1992). Woollacott and Zimmer (1972a) found a calcified septum with a pore and a cell plug separating ooecial and visceral coeloms in *Bugula neritina* (see also Calvet 1900), thereby suggested that the ooecium might be a heterozooid (kenozooid). Ooecial lobes indeed appear to be kenozooids in Scrupariidae and Alysidiidae (see below). In other cheilostomes, ooecia are kenozooids only if they bud from the maternal autozooid (type II, see below) and there are specialized pore-cell complexes that plug communication pores. As for cheilostomes with ooecia formed by the distal zooid (type I), subsequent research has shown that they are not kenozooids. Santagata and Banta (1996) described in detail ovicell anatomy in *Scrupocellaria ferox* and showed that the wide communication slit connecting the coeloms of the distal zooid and the ooecium have no traces of a septum or cell plug. Open communication pores have been found in *Callopora lineata* (see Ostrovsky and Schäfer 2003). Even when communication pores are completely plugged by cells (in strongly calcified old ooecia), the absence of specialized pore-cell complexes does not allow one to consider such ooecia as polymorphs (Ostrovsky and Schäfer 2003; Ostrovsky et al. 2009a). To sum up, in the majority of cheilostomes, ooecia are body-wall outgrowths, not heterozooids (an alternative viewpoint is endorsed by Viskova 1992). At the same time, ooecia evolved from spines (except in *Scruparia*, *Alysidium* and *Catenicula*; see Ostrovsky and Taylor 2004, 2005a), which are obviously modified modular polymorphs (Silén 1942; see also Lidgard et al. 2012).

Ultrastructure and development of ovicells have been studied in additional calloporids (*Callopora*, *Tegella*, *Corbulella*) (Ostrovsky et al. 2003). Taylor and MacKinney (2002) and Ostrovsky (2002) described the structure of so-called "costate" ovicells in some fossil and Recent Microporidae and Cribrilinidae, correspondingly, and discussed the origin of ovicells in cheilostomes. Ostrovsky and Taylor (2004) described four calloporid species in which the brood chambers were formed by spines of the daughter zooid in Middle Cretaceous material from England and Germany. Such primitive ovicells looked like a cage, on the one hand supporting Harmer's hypothesis (1902) that the ovicell originated from mural spines, and on the other hand according with Nielsen's view (1985) that category A ovicells (ooecium formed by the distal autozooid) are basic in ovicell evolution. A detailed survey of the fossil and Recent cheilostomes whose brood chambers consist of spines or costae has been published by Ostrovsky and Taylor (2005a).

The development of the ooecium has additionally been investigated in the earliest cheilostome brooders, belonging to the genus *Wilbertopora*. Interestingly, it is different from ovicellogenesis in Recent calloporids, being more reminiscent of that in Recent cribrimorphs such as *Puellina* (discussed in Ostrovsky and Taylor 2005b).

More recently, research has been presented on the anatomy of ovicells and internal brood sacs in a number of anascan cheilostomes (Ostrovsky et al. 2006, 2007, 2009a, b) as well as two large reviews on brooding structures and the history of research on cheilostome parental care (Ostrovsky 2008a, b).

In the sections that follow, the main types of cheilostome brood chambers (both development and structure) are described using correlated light-microscopic and SEM techniques. An emended classification and terminology are proposed. Hypotheses on the origin of chambers for embryo incubation are discussed together with the main trends in their evolution.

2.2 Classification and Terminology

Chambers for embryo incubation are among the most important characters in the systematics of Bryozoa, particularly in the Cheilostomata (Viskova 1992; Ostrovsky 2004, 2008b). However, a review of the literature shows that many authors used the terms introduced by the early scholars (Hincks 1880; Jullien 1888; Levinsen 1902, 1909; Canu and Bassler 1920) rather arbitrarily, and there is much inconsistency in older taxonomic descriptions. Many taxonomists still rely on the terminology and schematic illustrations of Bassler (1953), who applied the terms of Levinsen (1902, 1909) to the schematics of Canu and Bassler (1920) (see above). Ryland (1968, 1970, 1976, 1979) and Ryland and Hayward (1977) simplified and improved the terminology, stressing the main principles upon which such terminology should be based (see Ostrovsky 2008b). However, cheilostome brood chambers are very diverse, and in the absence of a clear understanding of their internal structure, the situation has been far from satisfactory. The terminology of the earlier authors that later became standard has carried with it the baggage of over-simplified, even erroneous, ideas about brood-chamber structure (discussed in Ostrovsky 2008b). As a result, taxonomists have continued to use the terms that they prefer, which are often in contradiction with the actual structure of the brood chamber.

An extensive review of cheilostome brooding structures was recently published, aiming to correct this situation (Ostrovsky 2008b). It featured descriptions of the range of different morphologies and a revision of terminology commonly used in taxonomic descriptions. The traditional morpho-functional terminological approach has been supplemented by a developmental approach. In the following section, a revised and expanded version of this review is presented.

Four main groups of embryo-incubation chambers are known in Cheilostomata: (1) external membranous sacs (*Aetea*, *Eucratea loricata*, "*Carbasea*" *indivisa*, *Leiosalpinx australis*); (2) skeletal (calcified) chambers, including all ovicells and brood chambers formed by spines (most cheilostomes); (3) internal brood sacs formed by non-calcified zooidal walls (in at least 22 families); and (4) female zooids for intracoelomic incubation (Epistomiidae). This division is based on wall composition and positioning of the brood chamber (Ostrovsky 2008a, b).

We still do not know how the chamber wall is formed in the first group and of what it consists (Fig. 2.52). Various authors have suggested it to be an outgrowth of the introvert wall, a cuticular chamber produced by the external cystid wall or a sticky fertilization envelope (Stach 1938; Cook 1977b; Ström 1977). In any case, the term "external membranous brood sac" should be applied to them all. Notably, all cheilostomes possessing these sacs have simple skeletal morphology and are considered to be less derived.

The second group covers the majority of incubation chambers known in Cheilostomata. Apart from the acanthostegal brood chambers of Tendridae ("acanthostegous ooecia" of Levinsen 1902, 1909), which are represented by adjoining zooidal mural spines, the frontal wall (including frontal membrane), and the epistegal space between them (see Ostrovsky and Taylor 2005a) (Figs. 2.50, 2.51, and 2.59A, B), all of these chambers are known as "ovicells" (Figs. 1.17, 1.18A, B, 1.19B–D, 1.20D–E, 1.25A, 1.27D, 1.28C–D, 1.29B, 1.30A, B, 1.32A, B, 1.36, 2.1, 2.3, 2.4, 2.5, 2.6a, b(A–D, F), 2.7a, b(A, B, F), 2.8, 2.9, 2.10, 2.11, 2.12, 2.13, 2.14, 2.15, 2.16, 2.17, 2.18, 2.19, 2.20, 2.21, 2.22, 2.23, 2.24, 2.25A, 2.26, 2.27, 2.28, 2.29, 2.30, 2.31, 2.32, 2.33, 2.34, 2.35, 2.36, 2.37, 2.38, 2.39, 2.40, 2.41, 2.42, 2.43, 2.44, 2.45, 2.48, 2.49, 2.54, 2.55, 2.56, 2.57, 2.58, 2.59C–E, 2.60, 2.61, 2.62, 2.63, 2.64, and 2.65).

In general, each ovicell consists of a two-walled, completely or partially calcified protective ooecial fold (ooecium) with an enclosed coelomic lumen, a non-calcified part of the distal wall of the maternal (egg-producing) autozooid that plugs the ovicell opening, and the topologically exterior brood cavity between them (see Fig. 1 in Introduction, Figs. 2.6, 2.7 and 2.8) (Ryland 1976; Ostrovsky 2008a, b). Among cheilostomes, ooecium size and shape vary from prominent and hemispherical to vestigial and cap-like. The outer ooecial wall is ectooecium; that surrounding the brood cavity, entooecium. The lower concave part of the entooecium, proximally continuous with the transverse wall of the zooid, is the ovicell floor. The upper part of the ovicell capsule (ooecium) is sometimes called a roof, whereas the sides are vertical walls. Both include parts of the ento- and ectooecium. The ovicell opening is closed either by the operculum of the zooidal aperture, or by a non-calcified part of the distal wall of the maternal cystid, or both. Often this wall forms an evagination called an ooecial (inner) vesicle. This vesicle can be contracted by special muscle bands, thereby opening the ovicell entrance. In some species, ovicells are permanently open (see below), and the maternal zooid does not contribute to ovicell closure. Depending on the type of formation, the ooecial coelomic cavity communicates either with the coelom of the daughter or maternal zooid through communication pore(s). If the ooecium is formed by the daughter zooid, these pores are often (but not always) plugged by non-specialized epithelial cells, so that the coeloms are not confluent. If the ooecium is budded from the maternal zooid, the communication pore(s) is plugged by the pore-cell complex that is normally found in a septular pore. In both cases, an ovicell is a complex structure (colonial organ), involving at least two zooids in its formation (for original terms and additional schemes see Levinsen 1909; Harmer 1926, 1957; Woollacott and Zimmer 1972a; Ryland 1968, 1976; Ryland and Hayward 1977; Santagata and Banta 1996; Hayward and Ryland 1979, 1998, 1999; Ostrovsky 1998, 2008a, b; Ostrovsky and Schäfer 2003; Ostrovsky et al. 2003, 2009a).

In many taxa, however, ooecial structure is more complex than this. Levinsen (1902, p. 14, 1909) was the first to separate "ooecia with a cryptocyst" from those without it (see also Harmer 1957; Woollacott and Zimmer 1972a, for discussion). A complex ovicell roof with a "cryptocystal matrix" was recently discovered in some *Macropora* and *Monoporella* species (Ostrovsky and Taylor 2005a).

The terms "ovicell" and "ooecium" (reflecting an early supposition that the chamber contains an ovary) were introduced by Busk (1852) and Hincks (1873), and have been effectively regarded as synonymous. However, as soon as anatomical descriptions appeared (Vigelius 1884a, b, 1886; Calvet 1900) it became clear that such synonymy is misleading. One problem is that the terms "ovicell" and "ooecium" are generally applied to both the externally visible part of the brood chamber and the entire structure. The most obvious example is the often-used phrase "vestigial ovicell," which is terminologically nonsensical, since "vestigial" can apply only to the protective fold (ooecium), whereas the actual brood cavity is always capacious. An ovicell cannot be vestigial. In another example, an immersed ovicell is typified by a brood cavity that is situated below the colony surface, whereas its ooecium is an external structure and cannot be immersed. The same is true of endozooidal ovicells possessing an internal cavity for embryo incubation and externally projecting ooecia. Interestingly, Busk (1884), who introduced the term "ovicell", in his famous description of the collection of the "Challenger" expedition, used Hincks's term "ooecium".

The terminological changes made by Ryland (1976) and Reed (1991) reflect the need to distinguish the entire brood chamber from its parts, namely the protective hood (ooecium or ooecial outfold), brood cavity, and closing device (either a non-calcified part of the distal wall of the maternal cystid or the ooecial vesicle) (see also Silén 1945; Ryland and Hayward 1977; Ryland 1979; Hayward and Ryland 1979). This need reflects the fact that the brood-chamber complex in Cheilostomata is "usually produced by a collaboration between the maternal zooid and the next distal [daughter] zooid" (Reed 1991, p. 149).

2.2.1 Ooecium Formation

This aspect of ovicell structure is particularly complex and cannot be elucidated without recourse to anatomical study or at least examining fractured or sectioned skeletons. Analysis of the literature and my own anatomical studies show that all ovicells can be classified according to the ooecium-producing zooid and the nature of the ooecium itself. Two types of ooecium formation can be formally defined (1st and 2nd types in Ostrovsky 1998). In "type 1" the ooecium is formed either by the distal autozooid ("category A" of Bishop and Househam 1987), or by an avicularium or kenozooid ("category B") with or without a distally

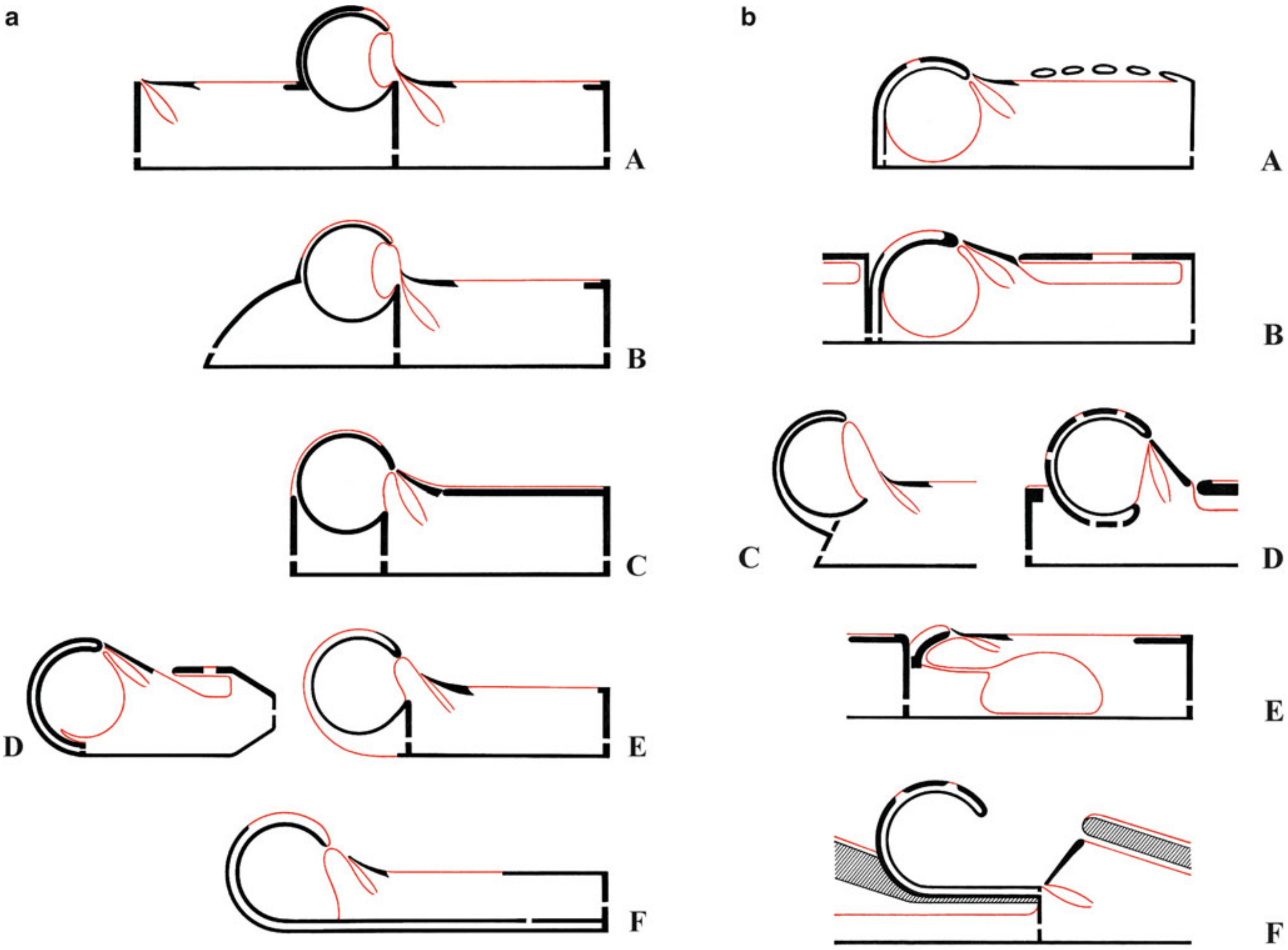

Fig. 2.6 (**a**) Schematic diagrams of various types of ooecium formation. **A**–**C**, **E**, **F**, type 1: ooecial outfold and ovicell floor are formed by the distal (auto/keno)zooid (**A**, *Callopora lineata*, *Tegella armifera*; **B**, *Callopora dumerilii*; **C**, *Micropora notialis*; **E**, *Bryocalyx cinnameus*), or basal kenozooid (**F**, *Cornucopina pectogemma*). **D**, intermediate type: kenozooidal ooecium budded from the maternal autozooid, the distal part of the ovicell floor is formed by the ooecium and the proximal part formed by the distal wall of the maternal autozooid (*Costaticella solida*). In **A**–**C**, **E** and **F** the ooecial coelom communicates with the ooecium-producing distal (basal in **F**) zooid via a communication slit or pore(s), often plugged by non-specialized epithelial cells (not shown), whereas ooecium-producing zooids themselves communicate with the maternal zooid via a septular communication pore(s) plugged by a pore-cell complex (not shown). In **D**, the coelom of the kenozooidal ooecium communicates with the maternal zooid via septular communication pores plugged by a pore-cell complex (not shown). In **A**, **B** and **E** ovicells are acleithral, in **C** and **D** cleithral, and in *F* semicleithral. Diagrams **C**–**F** represent terminal ovicells. Calcified walls and zooidal opercula are shown in *black*, membranous walls in *red*. (**b**) Schematic diagrams of various types of ooecium formation. **A**, **B**, **E**, type 2: kenozooidal ooecium budded from the maternal autozooid, the floor of the brood chamber is formed entirely by the distal wall of the maternal autozooid (**A**, *Cribrilina annulata*; **B**, *Eurystomella foraminigera*; **E**, *Cauloramphus spinifer*). **C**, intermediate type: kenozooidal ooecium budded from the maternal autozooid, the distal part of the ovicell floor is formed by the ooecium, the proximal part formed by the distal wall of the maternal autozooid (*Chaperiopsis cervicornis*). **D**, **F**, type 1: ooecial outfold and ovicell floor formed by the distal kenozooid (**D**, *Omanipora pilleri*; **F**, *Turbicellepora crenulata*). In **A**–**C** and **E** the coelom of the kenozooidal ooecium communicates with the maternal zooid via septular communication pores plugged by a pore-cell complex (not shown). In **D** and **F** the ooecial coelom communicates with the ooecium-producing distal kenozooid via a communication slit, whereas ooecium-producing zooids themselves communicate with the maternal zooid via a septular communication pore(s) plugged by a pore-cell complex (not shown). In **F** the basal part of the ooecial fold and the distal (ooecium-producing) kenozooid lie on the proximal part of the daughter autozooid. In **A**, **B** and **D** ovicells are cleithral, in **C** acleithral, and in **F** non-cleithral. Diagrams **A** and **C** represent terminal ovicells (in fact, in **B** and **F** they are terminal too). Calcified walls and zooidal opercula are shown in *black* and by hatching, membranous walls (including pseudopores) in *red*

distinct frontal part (see also Ristedt 1985; Harmelin and Arístegui 1988). The ooecium itself is the frontal or distal outgrowth (outfold) of this distal (daughter) zooid – autozooid, avicularium or kenozooid (Figs. 1.36, 2.1, 2.3, 2.5, 2.6a (A–C, E), b (D, F), 2.7a (A–I), b (A, B), 2.8, 2.13, 2.14, 2.15A, B, 2.16, 2.17, 2.22, 2.23, 2.24, 2.25A, 2.26, 2.27, 2.28, 2.30, 2.31, 2.32, 2.33, 2.34, 2.35, 2.36, 2.40, 2.41, 2.42, 2.43, 2.44, 2.45, 2.55, 2.56, 2.57, 2.58, 2.59C-E, 2.60, 2.61, 2.63, 2.64, and 2.65). The ooecium-producing kenozooid can also have a basal position (Fig. 2.6a(F)). In all these cases the floor of the brood cavity is entirely or mainly formed by the distal (ooecium-producing) zooid, which is sometimes strongly flattened (Figs. 1.36B, C, 2.6a(F), b(D, F), and 2.42). The basal part of the ooecial fold can be positioned near the transverse wall between the maternal and distal zooids or at a distance from it (compare Fig. 1 in Introduction and Figs. 2.3, 2.6a(A), and 2.7a(A)). Distal budding in ooecium-producing zooid is, as a rule, retained.

If the distal kenozooid has no distally distinct frontal part, the entire structure (ooecial fold plus distal kenozooid) may be considered as a kenozooid that is formed by the maternal autozooid, exemplifying so-called "terminal" ovicells (Figs. 1.27D, 1.30B, 1.36, 2.6a(C, E, F), 2.23A, 2.33D, and 2.42B) (Ostrovsky 1998). In fact, in this case, the maternal autozooid first forms the distal bud (kenozooid), which in turn forms the ooecial outfold (vertical walls and roof of the ooecium) (Figs. 1.36B, C, 2.6a(C, E), 2.17A, B, 2.23A, and 2.42B). Thus, the upper wall of the distal kenozooid serves as the floor of the brood cavity and the ooecium itself is an outgrowth of this basally placed "ooecial kenozooid" (Ostrovsky 2008b, see also illustrations in Levinsen 1909). In other words, the entire skeletal structure consists of two well-defined elements, only one of which is a kenozooid.

The "type 2" ooecium is itself a kenozooid, budded from the maternal autozooid, and ovicells with such ooecia can be also called terminal in some species (Figs. 1.25A, 1.28C, D, 2.6a(D), b(A–C), and 2.29). The base (basal part adjacent to maternal zooid) of such a "kenozooidal ooecium" is homologous with the strongly reduced distal kenozooid in ovicells with "type 1" ooecia, whereas the rest of the ooecium is an outfold. In contrast to "type 1", the floor of the brood cavity in ovicells with "type 2" ooecia is formed entirely or partially by the distal wall of the maternal zooid. Kenozooidal ooecia show various degrees of reduction (Figs. 1.25A, 1.28C, D, 1.32A, B, 2.6a(D), b(A–C, E), 2.7b(C), 2.25B, and 2.29), with the two types representing a clear evolutionary trend towards reduction of the distal, ooecium-producing zooid (Ostrovsky 1998, 2008b, 2009; Ostrovsky et al. 2009a, see also illustrations in Levinsen 1909). Two examples with intermediate morphology have been found (Figs. 1.25A, 2.6a(D), and b(C)) that may be referred to as an "intermediate type". Here, a kenozooidal ooecium is budded from the maternal autozooid. The distal part of the ovicell floor is formed by the ooecium, whereas the proximal part is formed by the distal wall of the maternal autozooid (see also pl. 12, fig. 1h in Levinsen 1909).

It should be noted that the above categorization is a little different from that introduced earlier (Ostrovsky 1998), in which ooecia of all terminal ovicells (i.e. ovicells without a distally distinct distal zooid) were considered to be formed from the maternal zooid (discussed also in Ostrovsky 2008b). For instance, according to Bishop and Househam (1987), all ooecia formed by the ooecium-producing distal kenozooid with no distinct frontal part [not visible in frontal view] (Figs. 2.6a(C, E), b(F), 2.23A, and 2.42) should be considered as maternally derived and placed in "category C" (see also Ostrovsky 1998). Instead, I propose that the term "category C" should be used only for kenozooidal ooecia (Figs. 1.25A, 1.28C, D, 1.32A, B, 2.6a(D), b(A–C), and 2.29). Recently, Berning and Ostrovsky (2011) described ooecia that are budded from the distofrontal wall of the maternal autozooid in *Omanipora pilleri*, stating that similar "kenozooidal ooecia" (i.e. category C) are formed in the genera *Celleporina*, *Galeopsis* and *Turbicellepora* s. str. (Fig. 2.42). However, I have reconsidered this interpretation; the basal part of the brood chamber corresponds to a strongly reduced distal ooecial kenozooid (Fig. 2.6b(D)) that forms both the ovicell floor and the ooecial outfold in these cheilostomes. Thus, these ooecia should belong to category B.

Recognizing the locus of ooecium formation and interpreting its structure can be difficult without making sections (compare, for instance, Fig. 2.6a(A) with Fig. 2.6b(B, F)): compact zooidal budding, very narrow communications between ooecial and zooidal coeloms, and structural variability often hamper this work. To avoid confusion, it is better not to describe the type of ooecium formation if it is uncertain. In the case of ovicells in which the underlying distal zooid is not visible in frontal view (regardless of which type of ooecium formation) (Figs. 1.25A, 1.27D, 1.28C, D, 1.30B, 1.32A, B, 1.36, 2.6a(C–F), b(A–C), 2.17A, B, 2.23A, 2.29, 2.33D, 2.42B, 2.60E, and 2.61E), the descriptor "terminal" is proposed instead (see above), which may serve as a compromise until their proper structure is determined. Terminal ovicells are commonly (but not invariably) present at the colony periphery, and are afterwards distinctly separated from the zooids distal to them by a suture/slit between the skeletal walls (Harmelin and Arístegui 1988) (Figs. 1.28D and 2.6b(B)).

2.2.2 Immersion of Brood Cavity

Another character used in ovicell classification is the degree to which the brood cavity is immersed in relation to the colony surface.

The commonest type of ovicell in this regard is "hyperstomial", i.e. positioned above the cavity of the underlying (distal) zooid ("seated over the zooecia" in Levinsen 1902, p. 13, and "situated outside the cavity of the zooecium" in Levinsen 1909, p. 60), although the word itself reflects more the position of the brood chamber relative to the opening of the maternal zooid. Earlier, Busk (1884) had used "erect" for such ooecia, and Jullien (1888) described variants of this position as "superovicellate" and "subovicellate" (discussed in Ryland 1968). However, most researchers have used and

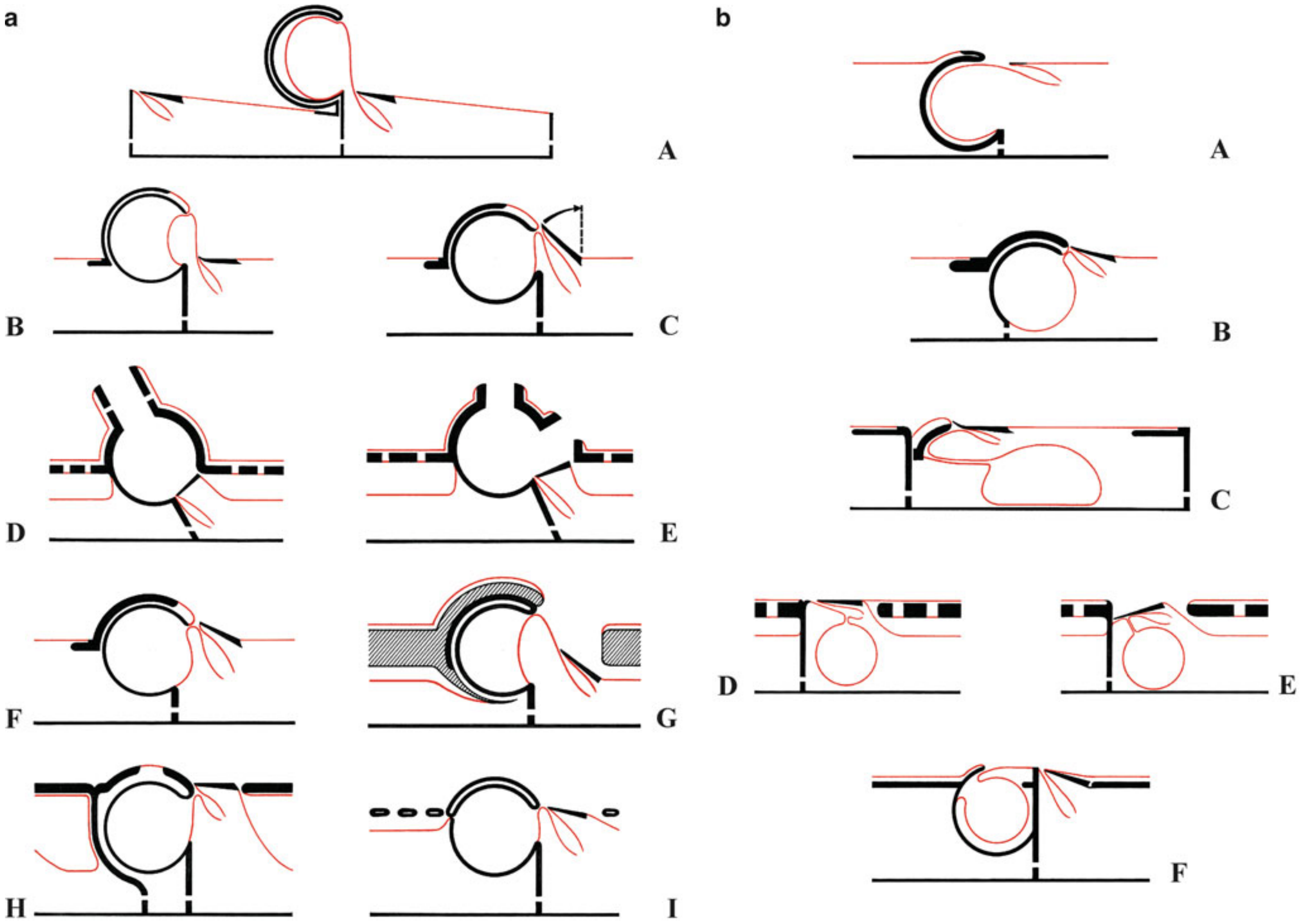

Fig. 2.7 (**a**) Schematic diagrams of the position of the brood cavity relative to the colony surface. **A**–**C**, hyperstomial (prominent) ovicells (**A**, *Bugula neritina*; **B**, *Notoplites tenuis*, *Tricellaria gracilis*; **C**, *Corbulella maderensis*). **D**, **E**, peristomial ovicells (**D**, *Margaretta barbata*; **E**, *Cylindroporella tubulosa*). **F**, **G**, **I**, subimmersed ovicells (**F**, *Valdemunitella lata* – each lobe of bilobate ooecium communicates with visceral coelom via separate pore; **G**, *Porella smitti* – ectoooecium covered with secondary calcification; **I**, *Puellina radiata* – each lobe of bilobate ooecium communicates with visceral coelom via separate slit or pore). **H**, endozooidal ovicell (*Selenariopsis gabrieli*). In **A**–**C** and **F**–**I** the ooecial coelom communicates with the ooecium-producing distal zooid via a communication slit or pore(s), often plugged by non-specialized epithelial cells (not shown). In **D** and **E** the ooecial coelom is confluent with the hypostegal coelom of the ooecium-producing distal zooid. In **A**, **B** and **G** ovicells are acleithral, in **C**, **F** and **H** cleithral, and in **I** semicleithral. Calcified walls and zooidal opercula are shown in black and by hatching, membranous walls (including pseudopores) in *red*. (**b**) Schematic diagrams of the position of the brood cavity relative to the colony surface. **A**, endozooidal ovicell (*Chartella membranaceotruncata*). **B**, immersed ovicell (*Crassimarginatella* sp.). **C**, internal brood sac with rudimentary ooecium (*Cauloramphus spinifer*). **D**, **E**, internal brood sacs (**D**, *Cryptosula pallasiana*; **E**, *Watersipora subtorquata*). **F**, endotoichal ovicell (*Cellaria tenuirostris*). In **A** and **B** the ooecial coelom communicates with the ooecium-producing distal zooid via a communication slit or pore(s), sometimes plugged by non-specialized epithelial cells (not shown). In **C** the coelom of the kenozooidal ooecium communicates with the maternal zooid via a septular communication pore(s) plugged by a pore-cell complex (not shown). In **D** the internal brood sac communicates with the vestibulum of the fertile zooid. In **E** the internal brood sac opens to the environment independently of the vestibulum. In **A** ovicell is acleithral, in **B** cleithral. Calcified walls and zooidal opercula are shown in *black*, membranous walls (including pseudopores) in *red*

continue to use "hyperstomial" or "prominent" (introduced by Hincks 1880) to define any ovicell whose roof is well above the colony surface (see Fig. 1 in Introduction, Figs. 2.1, 2.3, 2.5, 2.6a(A–C), b(C, D, F), 2.7a(A–C), and 2.8A–E). The limits of the ovicell opening (mostly between the upper edge of the calcified transverse wall of the zooid and the lower edge of the ovicell roof) relative to the zooidal orifice (not always reflected in the skeleton) are often difficult to recognize without studying internal structure. In this regard, the terminology of Jullien (1888) is of dubious value. This also concerns the term "hypostomial," provisionally introduced by Ryland (1968).

The terms "erect" and "recumbent" (Busk 1884), and "dependent" and "independent" (Levinsen 1909), should be mentioned in this context. The first pair was obviously introduced to reflect the position of the ooecium relative to the frontal plane of the colony, whereas the second pair reflects the relation between the basal part of the ooecium and the proximal part of the frontal wall of the distal (ooecium-producing) zooid, i.e. the extent of the "common wall" between them (see also Canu and Bassler 1920). Ryland (1968) was critical of "recumbent" as a term, but it still appears in taxonomic descriptions. "Dependent" (the ovicell floor is broad-based on the distal zooid, constituting a considerable part of its frontal wall; see, for instance, see Fig. 1 in Introduction, 2.6a(A) and 2.22) and "independent" (ooecia have a narrow base, with the ovicell floor either situated above or constituting a small part of the frontal wall of the distal zooid; see Figs. 2.3, 2.5, 2.7a(A), and 2.41) have not been adopted, partly because the basal part of the ooecium is often obscured by neighboring zooids, "secondary calcification" or both. It would be logical therefore to retain the well-known term "hyperstomial" or its synonym "prominent (raised)" for ovicells with ooecia of both types (1 and 2), in which half or more of the spherical brood cavity appears above the colony surface (Figs. 1.18A, B, 1.20E, 2.11A, 2.12D, E, 2.13, 2.14A, C–F, 2.15B, 2.16, 2.17C, D, 2.19, 2.22, 2.23, 2.26A, B, 2.27A, 2.33A–D, F, 2.34, 2.35A, B, D, 2.36, 2.40A, B, 2.41, 2.42, 2.43, 2.44, 2.45, 2.48, 2.49, 2.63, and 2.65).

When well-exposed terminal ovicells are positioned at the edge of the colony, they could also be termed prominent or hyperstomial despite the fact that more than half or even the entire brood cavity may be situated below the colony surface, corresponding to "subimmersed" and "immersed" ovicell types (Figs. 1.25A, 1.27D, 1.28C, 1.30B, 1.32A, B, 1.36, 2.6a(D–F), b(A), 2.17B, 2.29, 2.33D, and 2.60E) (see also illustrations in Levinsen 1909; Wass and Banta 1981). Most of the "spinose" and "costate" ovicells recently described in some fossil and Recent cheilostomes (Ostrovsky and Taylor 2004, 2005a, Gordon and Taylor 2008) belong to the hyperstomial/prominent type (Figs. 2.10C–F, 2.54A–C, 2.57C, D, 2.58A–E, 2.59C–E, 2.60A, B, D, and 2.61), although in some species they show some degree of immersion (see for instance Figs. 2.56, 2.57A, B, and 2.60C).

If less than half the brood cavity is above the colony surface, then the ovicell can be termed "subimmersed" (Figs. 2.7a(F, G, I), 2.8F, 2.15A, 2.24, 2.56, 2.57A, B, and 2.60C) (Hincks 1880; Ryland 1968). As is often the case with transitional morphologies, this definition is not very precise since, again, it is difficult to estimate the size of the immersed part without sectioning. The term "subimmersed" could be applied to all ovicells that are less prominent than hyperstomial but more raised than immersed and endozooidal (that are "seated internally between two contiguous zooecia but as a rule chiefly project[ing] into the bottom" of the distal zooid (Levinsen 1902, p. 11), and "enclosed in autozooecia" (Levinsen 1909, p. 56)). In the latter two instances, the entire or near-entire brood cavity is below the colony surface (Figs. 2.6b(B), 2.7a(H), and 2.7b(A, B)), whereas in subimmersed types about one-third of the brood cavity is above the colony surface (Figs. 2.7a(F, G, I) and 2.15A). Such ovicells are widespread among the Cheilostomata, characterizing an evolutionary trend towards immersion of the incubation chamber (Ostrovsky and Taylor 2004; Ostrovsky et al. 2009a). For instance, some calloporids and cribrilinids possess both prominent (Figs. 2.13A, 2.19A, C, and 2.27A) and subimmersed (Figs. 2.7a(I) and 2.15A) ovicells, sometimes found in the same species (*Callopora lineata*, *Puellina radiata*).

The terms "immersed" (Hincks 1880) and "endozooidal" ["endozooecial" of Levinsen (1902, 1909), "entozooecial" of Harmer (1926) and "entozooidal" of Ryland (1970); modified by Silén (1945) and Ryland (1968)], are often considered synonymous. However, it would be preferable, following tradition, to reserve "endozooidal" for ovicells whose brood cavity is in the proximal part of the distal zooid, as in many flustrids (Figs. 1.17, 2.7b(A), 2.31, and 2.32), some cribrilinids (Figs. 2.27B, C, E, G and 2.28) and eurystomellids (Fig. 2.7a(H)), and some catenicellids (Fig. 1.24A) and candids (Fig. 2.30A), and "immersed" for those with the brood cavity in the distal part of the maternal zooid as occurs in some microporids (Fig. 1.28C, D), cribrilinids (Figs. 2.6b(A) and 2.29), eurystomelids (Fig. 2.6b(B)), calloporids (Figs. 2.7b(B) and 2.25A) and candids (Fig. 2.30B) (see also Hastings 1945 for discussion). In both cases, the ooecium is level with the colony surface or only very slightly above it. Species of the cribrimorph genus *Puellina* possess prominent (Fig. 2.27A), subimmersed (Fig. 2.7a(I)) and endozooidal ovicells (Figs. 2.27B, C, E, G and 2.28), sometimes in the same species (Figs. 2.7a(I), 2.27A, and 2.28A).

It should be stressed that, when viewed using SEM, ooecia often appear more prominent in cleaned (i.e. bleached to show the skeleton only) than non-cleaned colonies, which retain their cuticularized surfaces (compare Fig. 2.14B, C). In addition, in many ascophorans the ovicell is transformed in ontogeny from hyperstomial/prominent to subimmersed depending of the degree of subsequent secondary calcification ("ooecial" or "ovicellar cover", or "secondary calcareous layer" in Levinsen 1909, Ryland 1968, Ryland and Hayward 1977; Banta 1977; discussed in Zágoršek et al. 2011) (Figs. 2.7a(G), 2.8E, F, 2.40A, B, and 2.41A). Thus, varying degrees of ovicell immersion may be found in the same colony. In extreme cases when the ovicell completely "sinks" into a matrix of secondary calcification, the term "endozooidal" can be provisionally used, even though the ooecium is immersed into the frontal shield of the distal zooid, not its cavity (see Levinsen 1909, pl. 24, fig. 18; Moyano 1968, figs. 1.20, 1.23, 1.25; Carson 1978, pl. 3, figs. 12, 14; Sandberg 1977, pl. 6. fig. 3).

"Peristomial" ovicells (Levinsen 1902, 1909), in which the ooecial capsule is incorporated into the zooidal peristome, comprise subimmersed or sometimes endozooidal types (Figs. 2.7a(D, E) and 2.37).

Further immersion of the brood cavity in the maternal zooid, concurrent with reduction of the ooecial fold, eventually results in "internal sacs," "internal embryo sacs," or "membranous diverticula" (Waters 1912; Ström 1977; Cook 1979), in which the cavity can be connected with that of the introvert or open independently of it to the outside (Figs. 1.22, 2.7b(D, E), 2.46, and 2.47) (summarized in Ostrovsky et al. 2006, 2009b; Ostrovsky 2008a, b). Brood sacs belong to the third group of brood chambers as defined above. *Beania bilaminata* (Fig. 1.22) and species of *Cauloramphus* are intermediate with respect to ovicells and internal brood sacs (Figs. 2.6b(E), 2.7b(C), and 2.25B) (Ostrovsky et al. 2007, 2009a). All three elements of the ovicell are present – kenozooidal ooecium (reduced, cap-like), incubation cavity and ooecial vesicle – and their brooding apparatus is fairly similar to the immersed ovicells of the calloporid *Crassimarginatella* sp. (cf. Figs. 2.7b(B, C) and 2.25A, B). It should be emphasized once again that the much-used phrase "vestigial/reduced ovicell" (see, for instance, Harmer 1926; Hastings 1945) is inaccurate, since the brood cavity, as part of the ovicell, is always well developed. The term "vestigial" [small or rudimentary] can be true only of the ooecium. The brood chambers of *Cauloramphus* and *Beania bilaminata*, although evolved from ovicells, are internal brood sacs that have retained vestigial ooecia (see also Ostrovsky et al. 2007).

In some taxa (e.g. Adeonidae) internal brooding is combined with changes in cystid shape and size, being an example of sexual zooidal dimorphism. For such zooids (often enlarged) it would be correct to use the term "autozooidal polymorph with an internal brood sac" (see Sect. 2.3.3).

"Endotoichal" ovicells (Levinsen 1902, 1909), known only in the family Cellariidae, are a special case (see Sect. 2.3.2). Their anatomy was first described by Calvet (1900) and recently restudied (Ostrovsky 2009). The skeletal walls of the brood chamber belong to 1–3 distal zooids, whereas the embryo is enveloped by the modified ooecial vesicle formed by the maternal zooid (Figs. 1.19B–D, 1.20A, B, D, 2.7b(F), 2.38, and 2.39). Basically, the endotoichal ovicell is a highly modified endozooidal ovicell.

2.2.3 Ovicell Closure

Yet another approach to ovicell classification is based on their closure method. Ovicells that are closed only by the ooecial vesicle are called "acleithral" (see Fig. 1 in Introduction, Figs. 1.17, 1.18A, 2.4, 2.6a(A, B, E, F), b(C), 2.7a(A, B, G), b(A), 2.8A, F, 2.14B, 2.15A, B, 2.16, 2.22A, 2.23, 2.30A, 2.31B, 2.32, 2.36, 2.44A, and 2.63B, C), whereas those closed by the zooidal operculum (plus the underlying ooecial vesicle or non-calcified distal wall of the maternal zooid) are called "cleithral" (Figs. 1.24A, 1.25, 1.27D, 1.28A, B, 1.30, 1.32A, B, 1.36, 2.6a(C, D), b(A, B, D), 2.7a(C, F, H), b(B), 2.8B, D, 2.22B, 2.24, 2.25A, 2.29, 2.30B, 2.33A, F, 2.34, 2.41, 2.44B, 2.45, 2.49B, 2.57C, 2.60B, C, E, 2.61, and 2.63A, D). An intermediate position pertains to "semicleithral" ovicells (Figs. 1.28C, D, 2.7a (I), 2.8C, and 2.28), in which the zooidal operculum closes the ovicell opening incompletely (Ostrovsky 2008b). Isolation of the brood cavity from the external medium is here provided by the ooecial vesicle since the distal edge of the operculum does not reach the margin of the ovicell opening. I have encountered a number of examples of such closure in fixed material, and both cleithral and semicleithral ovicells were sometimes found in the same species. Thus, one should be alert to the possibility of confusion caused by shrinkage of the frontal membrane or ascus wall during fixation or drying, because the operculum is connected to this membrane/wall (also discussed in Cook 1977a). It should be stressed that the more the brood cavity is immersed, the greater is the probability of it being semicleithral or cleithral.

In contrast to species with cleithral ovicells that raise their opercula during larval extrusion (Figs. 2.7a(C) and 2.8B) (e.g. *Smittipora levinseni*, see Cook 1985), in *Pacificincola insculpta* (as '*Hippodiplosia*') and *Fenestrulina miramara* (as *F. malusii*) the operculum is lowered during larval release (see Nielsen 1981) (Figs. 2.8D and 2.45). This variant of the cleithral type can be termed "subcleithral," as modified by Ryland (1968, p. 233) [who described this type as having two "closed positions, the upper sealing off the ovicell, the lower sealing the [zooidal] orifice only"] and based on the term "subcleithrian(s)" of Canu and Bassler (1920). Ryland (1968) stated that this type exists in *Pentapora* (see also Carson 1978). Observations on living material are necessary to distinguish this type of ovicell closure.

The term "pseudocleithral", proposed by Ryland (1968), describes a situation in which the operculum closes the ovicell opening for a brief moment during polypide protrusion or retraction. While the tentacle crown is everted, the operculum maintains a vertical position. When the tentacle crown is retracted, the operculum closes the zooidal orifice and the ovicell opening is plugged by the ooecial vesicle (Fig. 2.8F). Judging from the length and position of the operculum, this variant of the acleithral type possibly exists in *Schizomavella cuspidata*. In two other species of this genus (*S. lineata, S. mamillata*) I found acleithral ovicells which, judging from the position of the operculum, cannot be closed by it during excursions of the polypide.

Levinsen (1909) was the first to note that, in some ovicells, the opening is not closed at all, since the zooidal operculum is distant and an ooecial plug is absent (Figs. 2.6b(F), 2.8E, and 2.42)

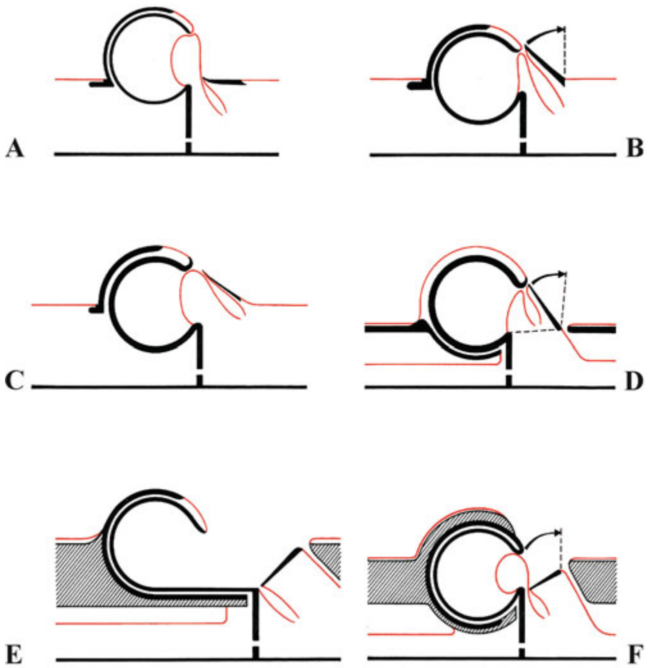

Fig. 2.8 Schematic diagrams of ovicell closure (**A**) acleithral (*Notoplites tenuis*). (**B**) Cleithral (*Corbulella maderensis*). (**C**) Semicleithral (*Scrupocellaria elongata*). (**D**) Cleithral (subcleithral) (*Fenestrulina* sp.). (**E**) Non-cleithral (*Reteporella* sp.). (**F**) Acleithral (pseudocleithral) (*Schizomavella cuspidata*). In (**B**) vertical position of the operculum during larval release and polypide feeding shown by *dotted line*. In (**D**) *dotted lines* show positions of the operculum during polypide feeding (*vertical*) and larval release (*horizontal*). In (**F**) vertical position of the operculum during polypide feeding shown by *dotted line*. In (**E**) the basal part of the ooecial fold lies on the proximal part of the daughter autozooid. The ooecial coelom communicates with the ooecium-producing distal zooid via a communication slit or pore(s), usually plugged by non-specialized epithelial cells (not shown). In (**A–D**) ovicells are hyperstomial (prominent), in (**E**) and (**F**) subimmersed. Calcified walls and zooidal opercula are shown in *black* and by hatching, membranous walls in *red*

(see also Harmer 1957; Banta 1977). The term "non-cleithral" is proposed for this variant (Ostrovsky 2008b).

2.3 Structure and Development of Brood Chambers in Cheilostomata

Classification of brooding structures in Cheilostomata is hampered by the profusion of structural variants. Although essentially similar, they vary as to the degree of immersion of the brood cavity, manner of closure, position and structure of communication slits or pores, degree of calcification of ooecial walls, details of ovicellogenesis, degree of reduction of the distal zooid and the ooecium itself and so on. Moreover, different combinations of these variable characters are often found in the same supraspecific taxon. To gain a better understanding of the structure, development and evolution of brood chambers in different groups of cheilostomes it is convenient to start with the Calloporidae.

2.3.1 Brood Chambers of Calloporidae: Basic Type and Structural Diversity

Calloporids possess a broad range of brooding structures. This is unsurprising, given that it is the oldest-known cheilostome family with brood chambers and the second-largest family by number of genera (currently 77) after Cribrilinidae (118) (Gordon 2012). Most calloporids possess hyperstomial ovicells, but subimmersed and immersed ovicells and internal brood sacs are also found (Ostrovsky et al. 2006, 2007, 2009a). In addition, in some fossil calloporids ooecia were constructed from spines (Ostrovsky and Taylor 2004, 2005a).

2.3.1.1 Spinose Hyperstomial Ovicells

Several fossil calloporids with ooecia constructed from spines are known. Three species of *Distelopora* (Figs. 2.9 and 2.59C, D) and one of *Gilbertopora* (Figs. 2.10C–F and 2.59E) occur in the Lower Cenomanian (Cretaceous) of England; a single species of *Unidistelopora* occurs in the Lower Campanian (Cretaceous) of Germany (Fig. 2.10A, B). In most cases, the ooecia themselves are not preserved and we can deduce their form only from the bases of the spines of which they were constructed. More information can be deduced from ovicell structure in some other fossil and Recent bryozoans with similar incubation chambers (see below).

The ooecium in *Distelopora* and *Unidistelopora* consisted of several jointed spines. The preserved basal parts are arranged in a gently curving distal arch or, more rarely, a semicircle (*D. bipilata*, *D. langi*) or elongated semicircle (horseshoe) (*D. spinifera*, *U. krauseae*) on the proximal gymnocyst of the distal zooid (Figs. 2.9, 2.10A, B, and 2.62 I, L, P). In the former case, the ooecium must have looked like a comb and in the latter, like a cage (Fig. 2.54A, B and 2.59C, D). The ovicell floor, formed by the proximal gymnocyst of the distal zooid, was flat or slightly concave.

In *Gilbertopora larwoodi*, the ooecium (roof and walls of the ovicell) consisted of two costae, that is, flattened, convex, hollow modified inarticulate spines (Figs. 2.10C–F, 2.54C, 2.59E, and 2.62K). They also formed on the proximal gymnocyst of the distal autozooid, covering the slightly concave ovicell floor. The rather narrow bases of the costae are somewhat apart from each other. In the middle and distal parts of the ooecium they become broader, adjoining each other along the midline, thus forming a medial ooecial suture. The cavities of the costae do not merge and neither do their walls. The ooecium bears four openings; the distal foramen is situated between the bases of flattened spines and has a drop-like, oval or rounded shape (Fig. 2.10C, F); elliptic foramina are located on the sides of the brood chamber between the lower surface of the costae and the ovicell floor (Fig. 2.10D); the main proximal opening of the ovicell is a low, broad arch (Fig. 2.10E). The gaps/slits and openings between the ooecium-forming spines and costae in these species suggest that water was able to enter the brood cavity (Ostrovsky and Taylor 2004, 2005a).

Significantly, spinose and costate ooecia are characteristic of some other fossil and Recent cheilostomes too. In the cribrimorph genus *Leptocheilopora* (Upper Cretaceous), hyperstomial ovicells consist of costae homologous to those of the frontal shield (Lang 1921; Larwood 1962; Ostrovsky and Taylor 2005a). Edges of ooecial costae are closely adjoined and their bases are arranged in an elongated semicircle (horseshoe) (Figs. 2.26A, B, D, 2.60D, and 2.62O) similar to the calloporids *Distelopora spinifera* and *Unidistelopora krauseae* (Fig. 2.62P). In one specimen, the costal edges were all gently sinuous and tightly apressed (Fig. 2.26D).

Costae are also used for construction of ooecia in *Bellulopora bellula*, but it is doubtful that they are homologous to cribrilinid costae. They are more likely to be kenozooids, judging from the fact that their cavities communicate with that of the distal kenozooid (forming the non-calcified ovicell floor) through pores with a cuticular annulus identical to conventional interzooidal communication pores of Cheilostomata (Fig. 2.60E) (Ostrovsky and Taylor 2005a). Thus, the example of Belluloporidae indicates that cheilostome spines may originally have been zooid polymorphs as was suggested by Silén (1942, 1977).

Ooecia constructed from spines and costae are also characteristic of fossil and Recent representatives of the families Monoporellidae (*Stichomicropora*, *Monoporella*) and Macroporidae (*Macropora*) (Figs. 2.55, 2.56, 2.57, 2.58, 2.60A–C, and 2.61). In species of the extinct genus *Stichomicropora*, ooecial spine bases are arranged in a straight line or gently curving (concave or convex) arch (Fig. 2.62A–H, J) as the in calloporids *Distelopora bipilata* and *D. langi* (Fig. 2.62I, L). In *Monoporella*, the ooecium is constructed from several costae or just two broad costae (Figs. 2.57, 2.60C, 2.61A, C, D, and 2.62J, M). If several costae, their bases are arranged in a gently curving arch as in the *Distelopora* species mentioned above; if two broad costae, ooecial structure is similar to that in the calloporid *Gilbertopora* (Fig. 2.62K). In *Macropora* (Figs. 2.58, 2.61B, E, and 2.62Q), spine bases are arranged in an elongated semicircle (horseshoe), as in the calloporids *Distelopora spinifera* and *U. krauseae* (Fig. 2.62P) and cribrilinids of the genus *Leptocheilopora* (Fig. 2.62O) (Ostrovsky and Taylor 2005a; Gordon and Taylor 2008). Similarities in ooecia are important for reconstructing evolutionary transformation of brooding structures within related bryozoan groups (see Sects. 2.4.3, 2.4.4, and 2.4.5).

2.3.1.2 Structure and Development of Hyperstomial Ovicells in *Wilbertopora*

Distelopora and *Gilbertopora*, with spinose ooecia, are stratigraphically somewhat younger than confamilial *Wilbertopora* with a hood-like ooecium (Upper Albian–Lower Cenomanian) (Cheetham 1954, 1975; Cheetham et al. 2006) – the earliest cheilostome genus known to possess ovicells.

The hyperstomial ooecia of *Wilbertopora* (Figs. 2.11A and 2.12D–F) are formed by the distal zooid, whether an autozooid, kenozooid or avicularium. In some species, primitive avicularia may also initiate the formation of ooecia by the distal zooid, whether an autozooid or avicularium (Fig. 2.12E). The ooecial roof consists of two lobes adjoining each other along the midline, similar to the arrangement in *Gilbertopora* and often forming a low longitudinal crest (Fig. 2.12D). The coelomic cavities of the lobes and their adjoining walls apparently do not merge, as indicated by ooecia fractured along the medial suture (Fig. 2.12F). The bases of the lobes are rather narrow (Figs. 2.12A and 2.62K). The floor of the brood chamber is rather deeply depressed in the proximal area of the gymnocyst of the daughter zooid (Ostrovsky and Taylor 2005b).

As in Recent calloporids, ovicells are formed at the periphery of the colony, close to its growing edge (Fig. 2.11A). Brood chambers are always arranged in groups, with the youngest ovicells positioned distally. Ovicellogenesis starts in the developing autozooid long before its cystid is completed. The first indication of ooecium formation is calcification of the proximal part of the frontal wall of the distal autozooid. Calcification starts from the transverse wall between maternal and distal zooids, spreads distally and forms, contrary to Recent calloporids, a simple narrow plate with a rounded edge (Fig. 2.11B–D). The shape of the plate indicates that it could have been surrounded by the arched ooecial fold of the frontal wall. This membranous outgrowth is not preserved in fossils, but has been described in living calloporids (Ostrovsky and Schäfer 2003; Ostrovsky et al. 2003). Nevertheless, it is also possible that instead of an ooecial fold, two soft outgrowths, predecessors of ooecial lobes, were formed (see below). Calcification continues to expand centrifugally, bordered by two lateral slits (Fig. 2.11E) (see also Cheetham 1975, p. 553). The resulting gymnocystal ovicell floor is concave (Fig. 2.11E–H). In zooids without brood chambers, the proximal gymnocyst is flat or only slightly concave (Ostrovsky and Taylor 2005b).

As calcification continues, the lateral slits gradually decrease in length and become separated from one another (Fig. 2.11F), as a consequence of which the common ooecial fold (if it existed at all) would have been transformed into two hollow symmetrical outgrowths, the future ooecial lobes. As noted above, they could also form somewhat earlier. Each lobe communicates with the proximal part of the distal zooid through a large oval opening (the former lateral slit) (Fig. 2.12B, C). The lobes start growing to form the vertical walls of the ooecium (Fig. 2.12A). Each lobe overgrows the gymnocyst in a proximal direction towards the opening of the maternal zooid (Fig. 2.11F–G). For this reason, the communication opening is always much smaller than the total length of the basal part of the lobe. Thus, each lobe has a relatively narrow base and a broad body. The frontal edges of the lobes grow upwards and fuse along the midline of the zooid to form a hemispherical hood-like ooecial roof, retaining the medial suture (Figs. 2.11H and 2.12D) (Ostrovsky and Taylor 2005b).

2.3.1.3 Hyperstomial Ovicells in Recent Calloporids

In Recent calloporids, ooecia are usually formed by the distal autozooid (type 1, category A) (Figs. 2.6a(A), 2.13, 2.14, 2.15, and 2.16), but in *Callopora dumerilii* and *Corbulella maderensis*, the ooecium is also formed by the distal kenozooid (type 1, category B) (Figs. 2.6a(B) and 2.17C, D) [similar cases are illustrated by Zabala and Maluquer (1988, pl. 3C) and Gordon (1984), pl. 1D]. Colonies of *C. craticula* in which ooecia are formed by the distal autozooid were also found to contain ovicells with ooecia formed by peripheral “interzooidal” avicularia (type 1, category B) (Fig. 2.17A) as well as two instances of terminal ovicells with ooecia formed by distal kenozooids lacking a prominent frontal part (type 1, category B) (Fig. 2.17B). In *Concertina cultrata* and *Bryocalyx cinnameus*, hyperstomial ovicells are formed at the periphery of the colony, in which growth ceases soon after. The ooecium is formed by the distal kenozooid (type 1, category B), which in *C. cultrata* can bud one more distal autozooid (Figs. 2.6a(E) and 2.23) (Ostrovsky and Schäfer 2003; Ostrovsky et al. 2003, 2009a).

In most studied calloporids ovicells are acleithral, with the opening closed by the ooecial vesicle (Figs. 2.6a(A, B, E), 2.7a(A, B), 2.14B, 2.15A, B, 2.16, 2.22A, and 2.23). The ooecial fold consists of inner (entooecial) and outer (ectooecial) walls with a narrow coelomic lumen between them. The upper parts of ecto- and entooecium make up the ooecial roof, merging at the edge of the ooecial fold surrounding the ovicell opening. The ectooecium is more or less heavily calcified in most species. Sometimes the only non-calcified area is an elongated arched or triangular membranous (cuticular) window at the outer edge of the ectoooecium (Figs. 2.6a(A), 2.7a(C), 2.8B, 2.13A, B, 2.14A–C, E–F, 2.15A, B, 2.16, 2.17B, C, 2.19A, B, and 2.22). In *C. craticula* and *Tegella unicornis* this window often has a prominent calcified “collar” (Figs. 2.14C and 2.17B). In contrast, in *C. dumerilii* the ectooecium is non-calcified except for a narrow basal part (Figs. 2.6a(B), 2.13C, 2.14D, and 2.17D). Another exception is *Bryocalyx cinnameus*, in which most of the ectooecial wall is also non-calcified (Figs. 2.6a(E) and 2.23A).

Entooecium is entirely calcified. Its lower, moderately concave part (ovicell floor) proximally joins the upper part of the transverse wall between maternal and distal zooids and the wall of the ooecial vesicle. The entooecial surface facing the brood cavity is smooth, with concentric growth lines and indistinct radial folds reflecting its formation. The entooecial surface facing the coelomic cavity of the ooecial fold is more or less smooth (Figs. 2.13B and 2.14F) or pustulose, its relief resembling that of the zooidal cryptocyst (Figs. 2.13C and 2.14D). In a single instance in both *C. lineata* and *T. unicornis* there was a medial groove at the edge of the ooecium similar to that found in *C. lineata* by Prenant and Bobin (1966). Also, a short medial keel with a suture was found on the inner ooecial surface in *Corbulella maderensis*. The keel is on the inner (facing the brood cavity) side of the entooecium, disappearing more or less opposite the place where there is a small outgrowth of ectooecium externally (Fig. 2.22B). In *Concertina cultrata* a medial suture runs along the midline of the elongated ooecium with its pointed apex (Ostrovsky et al. 2009a).

The bilobate ooecium of *Bryocalyx cinnameus* also has a longitudinal median suture and corresponding septum, symmetrically dividing the ooecial roof into two parts. The septum results from merging of the ooecial lobes. The entooecium is entirely calcified, whereas most of the ectooecium is membranous except for the narrow calcified edges of the ovicell opening and medial suture, and two flat diagonal ribs coming from these edges. (Fig. 2.23A) (see also Cook and Bock 2000). All of these calcified elements form a rigid framework of ectooecium. Two large oral spines surround the ovicell opening from above. The bases of the ooecial lobes fuse into a common unpaired base, while the coeloms of the lobes communicate directly with the cavity of the distal kenozooid. The latter in turn communicates with the visceral coelom of the maternal autozooid via a few groups of pores in the intervening transverse wall (Fig. 2.23A), plugged by pore-cell complexes typical of cheilostomes (Fig. 2.15C) (Ostrovsky et al. 2009a).

The ooecial coelom is lined with flat epidermal and peritoneal cells (with projections that sometimes stretch across the lumen) and communicates with the cavity of the distal zooid via its communication pore (Figs. 2.15A, B, 2.16, 2.21, and 2.22A) in the left or, more rarely, the right “corner” of the ooecial base. There are sometimes 2–3 such pores (Fig. 2.21D), representing the remnants of the arched communication slit (Fig. 2.20) that forms when the ooecium is formed. In young zooids this slit, though closed, remains plainly visible as an arched suture (Fig. 2.21A); in older zooids a shallow groove is retained (Fig. 2.21B, C) (Ostrovsky and Schäfer 2003).

Thickening of ooecial walls, characteristic of most calloporids, results in progressive narrowing of the ooecial coelom. In developing and young fully formed ovicells it looks like a narrow slit-like lumen (Figs. 2.15A, B, 2.16, 2.20, and 2.22A). Further calcification results in partial merging of the ento- and ectooecium (Fig. 2.20). The ooecial coelom transforms into a network of flat anastomosing lacunae connecting the coelom of the ooecial roof with the visceral coelom of the distal zooid, sometimes disappearing completely as in *Corbulella maderensis* (Fig. 2.22B). Similarly, the arched communication slit formed early in the course of ovicellogenesis is gradually reduced to become small communication pores (Figs. 2.20 and 2.21), usually plugged by non-specialized epithelial cells. In the deep-water taxa *Bryocalyx* and *Concertina*, calcification is very weak, and the structure of the ooecium does not appear to change with age (Ostrovsky and Schäfer 2003; Ostrovsky et al. 2009a).

As a rule, the communication pore(s) is plugged with non-specialized epithelial cells (Figs. 2.15B, 2.16, and 2.22A), and it appears that coelomic fluid is unable to circulate freely between the ooecium and distal zooid. Nevertheless, the groups of epithelial cells that have been seen at the base of the ooecial fold in sections of the developing ooecium do not plug the entire slit-like entrance to its cavity. Moreover, in *C. lineata*, two complete ovicells with embryos were found whose communication pores were also free of cells (at least partially) (Fig. 2.15A). Thus, in both cases, coelomic fluid should freely circulate between the cavity of the ooecium and that of the parent zooid. The discovery of ooecial folds with open communication and a lack of specialized pore-cell complexes in the plugged communication pores together indicate that such ooecia are not kenozooids (see discussion in Sect. 2.1). As for ovicells with communication pores plugged by epithelial cells, ongoing calcification of ooecial walls indicates that necessary substances are transported to their lining across epithelial cells and intercellular spaces (Ostrovsky and Schäfer 2003).

The inner vesicle is a hollow non-calcified evagination of the distal wall of the maternal autozooid that closes the ovicell opening (Figs. 2.14B, 2.15A, B, 2.16, 2.22, and 2.23). The cuticle of the vesicle wall facing the brood cavity is very thin whereas that of the wall adjoining the flattened area of entooecium (ooecial edge surrounding the ovicell opening) in *Callopora* and *Tegella* is thickened to form a “sclerite” (sic, Santagata and Banta 1996). The outer sclerite surface forms numerous tiny parallel “ribs,” presumably tightening the contact between the vesicle and the ooecial edge; such ribs are sometimes also found at the surface of the vesicle proximal wall. The sclerite bears a transverse crest (triangular in section) serving for attachment of the largest muscular bundle of the ooecial vesicle (Figs. 2.15A, B, 2.16, and 2.22A) (Ostrovsky and Schäfer 2003; Ostrovsky et al. 2009a).

The proximal (lower) ends of the muscle bundles that effect contraction of the ooecial vesicle during larval release are attached to the basal wall of the maternal autozooid (near its intersection with the distal transverse wall) or to the lower part of the transverse wall (Fig. 2.22A). In *C. dumerilii*, attachment may occur at both locations or even at the intersection itself. The distal end of the largest (upper) muscle bundle (presumably consisting of two broad muscle bands) is attached to the sclerite (Figs. 2.15A, B and 2.16). The second group of muscles consists of several fine bundles attached to the inner middle surface of the ooecial vesicle wall (Figs. 2.15B and 2.22A). The lower group of very thin muscle strands is attached to the inner lower part of the vesicle wall (Figs. 2.16A and 2.22A). These data are preliminary and require checking with confocal laser microscopy. The distance between the attachment sites of the middle and the lower groups of muscles varies depending on the ovicell. In *C. dumerilii* these two groups of muscles are sometimes attached to the wall surface in the upper half of the vesicle. Compared to the parietal muscles of the frontal wall of the zooid, the muscle bundles of the ooecial vesicle are much broader and have larger attachment zones. Whereas Silén (1945) thought that the ooecial vesicle of *C. dumerilii* contains only one muscle bundle, Calvet’s (1900, fig. 45) findings in confamilial *Amphiblestrum flemingi* (as *Membranipora*) more or less accord with my own results (Ostrovsky and Schäfer 2003; Ostrovsky et al. 2009a).

The cuticle of the ooecial vesicle is lined with flat epidermal and peritoneal cells (Figs. 2.15A, B and 2.16). The latter are connected by their projections to the cells of the funicular cords that cross the vesicle cavity (Fig. 2.15A). There is no indication that these cells enlarge during incubation. A fine layer of non-cellular substance was often present at the surface of the vesicle wall facing the brood cavity, especially in the folds of the wall (Ostrovsky and Schäfer 2003).

The ooecial vesicle retains its shape by means of coelomic pressure. Its elastic wall collapses readily during contraction of its internal musculature. Larvae may exit the ovicell whether or not the maternal zooid contains a functional polypide. The musculature of the ooecial vesicle, being part of the parietal muscular system, does not degenerate during polypide recycling, a feature noted by Dyrynda and Ryland (1982) in *Chartella papyracea* that presumably also occurs in other cheilostomes (Ostrovsky 1998). The mature larva with its actively beating cilia rotates in the brood cavity, leading to contraction of the muscles of the ooecial vesicle and opening of the ovicell entrance (Silén 1945). Once the larva leaves the brood chamber (Fig. 1.20D, E), the vesicle recovers and the ovicell entrance is closed. It may be conjectured that contraction of the muscle bundles of the ooecial vesicle during larval release and their subsequent relaxation are followed by contraction of the cystid parietal muscles, resulting in redistribution of coelomic fluid and recovery of the vesicle. Muscular contractions of the ooecial vesicle possibly also occur during oviposition.

The ovicell of *Corbulella maderensis* is cleithral, its opening closed by the zooidal operculum and the underlying ooecial vesicle – a small outgrowth of the upper part of the distal wall of the maternal autozooid (Figs. 2.7a(C), 2.8B, and 2.22B). The lower part of the vesicle may protrude slightly into the brood cavity. It lacks a sclerite and is filled with numerous funicular cells that give it a parenchymatose appearance in some sections. Two thin muscle bundles attach to the distal wall in upper and middle parts of the vesicle (Ostrovsky et al. 2009a).

2.3.1.4 Development of Hyperstomial Ovicells in Recent Calloporids

The fertile maternal autozooid initially forms a distal bud, which later results in the distal zooid with the ooecium (Fig. 2.18A–D, F). Sometimes an ovicell is developed and even starts brooding long before the formation of the daughter zooid is completed.

In general, the ooecium originates as a vertical outgrowth of the membranous frontal wall in the proximal part of the developing distal zooid (type 1). The ooecial fold is produced by intussusception in the same manner as an autozooid (reviewed in Ryland 1976), recognizable as an expansion of cuticle by a group or zone of dividing epithelial cells. The first indication of ovicellogenesis is a localized calcification of the frontal wall of the distal zooid. Starting from the upper edge of the transverse wall dividing maternal and distal zooids, it spreads centrifugally, giving the impression, in the early stages, of two rounded plates (often referred to as the "ooecial rudiment") (Figs. 2.13B and 2.18A). The plates originate independently and may differ in size. Eventually they merge to form a bilobate plate often with a weakly expressed medial suture or low keel. This calcified zone enlarges further to form a concave area, the ovicell floor (Fig. 2.18B–D), i.e. the proximal part of the entooecium. At this stage the bilobate shape of calcification is normally lost, although the trace left by the two merged plates often can be seen (Ostrovsky and Schäfer 2003; Ostrovsky et al. 2003, 2009a).

Contemporaneous with formation of the frontally visible proximal part of entooecial calcification is an additional calcified layer underlying it, with a different crystalline structure (Fig. 2.20A–C). This layer starts from the transverse and lateral walls of the distal zooid bud and, together, the two layers form the more-or-less flat-shelved ovicell floor (Fig. 2.18B). This underlying layer was first described by Nielsen (1985) in *Tegella aquilirostris*, *Scrupocellaria varians* and *Tricellaria occidentalis* and referred to as a cryptocyst because of its shape and position. This layer spreads downwards to cover the vertical walls of the zooid, and its external borders are usually clearly discernible (Fig. 2.20) (Ostrovsky et al. 2003).

The fully formed concave ovicell floor thus consists of a very thin cuticle and two calcified layers, its frontally expressed exterior surface nominally a gymnocyst. At its periphery the ovicell floor is bordered by a protruding membranous fold of future ooecium (Figs. 2.18D–F and 2.20A–C), the coelomic lumen of which communicates with the visceral coelom of the distal zooid via an arched communication slit that later closes (Fig. 2.21). The ooecial fold grows upwards, its calcification being slightly retarded (Figs. 2.18D–F, 2.19A, B, and 2.20A–C). Calcification of the ectooecium starts from the lateral walls of the distal zooid that are continuous with the base of the ooecial fold. As the ooecium grows, calcification of the vertical ectooecial wall (also of two calcified layers) takes the form of two symmetrical elongated lateral lobes that merge to form a distal hood over the developing entooecium. A thin coelomic lumen is retained between the entooecium and the ectooecium (Fig. 2.20C, F) (Ostrovsky et al. 2003).

In the process of forming the ovicell roof, the upper part of the ooecial fold generally develops evenly, with centripetal calcification (Figs. 2.13B and 2.19A). There can be exceptions, encountered, for example, in *Callopora lineata* and *Tegella armifera* in which the ooecial roof was formed by fusion of two flat lateral lobes emerging late in development (Fig. 2.19B–D). Normally these lobes, initially non-calcified, grow towards each other and fuse leaving no trace of a median suture (Ostrovsky et al. 2003). It is possible that the above-mentioned medial groove found on the inner entooecial surface of a specimen of *C. lineata* formed in this way.

Calcification of ooecial walls proceeds in tandem with development of the fold with only a slight delay, following its growth except for non-calcified areas of the ectooecium (Fig. 2.19). In most of the species of *Callopora* and *Tegella* examined in the course of this study, as well as in *Amphiblestrum inermis*, the ooecium is associated with an adventitious avicularian chamber (Figs. 2.13A, 2.14A, C, F, 2.15A, 2.16, 2.19, and 2.22A). In these cases, its interior wall (cryptocyst) forms the vertical ectooecial wall, separating the coeloms of the ooecium and the avicularium (Fig. 2.20D–F) (Nielsen 1985; Ostrovsky et al. 2003, 2009a).

The ooecial vesicle is formed at the same time as the ooecial fold, as an outgrowth of the upper part of the distal wall of the maternal autozooid (Fig. 2.20C, F) (Silén 1945; Ostrovsky and Schäfer 2003).

2.3.1.5 Subimmersed Ovicells

Formed at the expense of the distal autozooid (type 1, category A), ovicells of *Valdemunitella lata* are traditionally described as prominent and bilobate (cf. Gordon 1986). Since more than half the volume of the brood cavity is below the colony surface

(Figs. 2.7a(F) and 2.24), however, they should be classified as subimmersed. The ovicells are cleithral, i.e. the brood cavity is closed by the ooecial vesicle, which is overlapped proximally from above by the zooidal operculum. [Note that these ovicells are erroneously referred to as semicleithral in Ostrovsky (2008b); but see Ostrovsky et al. (2009a).] As in *Wilbertopora*, *Bryocalyx* and possibly *Concertina*, the ooecium consists of two symmetric halves (lobes) separated by a transverse medial suture easily seen in the interior and generally also the exterior of the ooecium (see also Gordon (1986, pl. 6A), showing the developing ooecium). Its proximal edge is flanked by a narrow non-calcified area.

On the inner surface of the ooecium, the medial suture ends as a closed horizontal slit, more or less as in the cribrilinids *Puellina*, *Figularia* and *Corbulipora* (see Sect. 2.3.2) though somewhat different in shape. The adjoining lateral surfaces of the ooecial lobes merge to form a two-layered longitudinal septum corresponding to the outer and inner medial suture. As in *Figularia*, the ooecial coelomic cavity is represented by the lumen of each lobe communicating with each other underneath the membranous wall of the non-calcified area on the proximal edge of the ooecium. The paired lumina of the ooecium also communicate with the visceral coelom of the parent zooid via two symmetric communication pores situated directly below the ooecial lobes (Fig. 2.24). In younger zooids they appear as non-parallel slits but later transform into oval pores. Judging from the volume of the ooecial coeloms and the size of the pores, the latter were open in life, potentially allowing circulation of coelomic fluid. It is possible, however, that these pores later become plugged by non-specialized epithelial cells (Ostrovsky et al. 2009a).

The bases of the ooecial halves are rather narrow (in this regard resembling the ovicells of extinct *Wilbertopora*, see above). As the bases are formed, the lobes become broader. Their lower edge grows proximally, first adjoining the proximal gymnocyst of the distal zooid and then overgrowing the lateral wall of the maternal zooid (see also Gordon (1986, pl. 6A)). As in *Wilbertopora*, a suture remains between the lower surface of the ooecial lobes and the zooidal surface.

Only about half the ovicell floor is represented by the calcified wall. The remaining half is formed by the thin non-calcified distal wall of the maternal autozooid (Figs. 2.7a(F) and 2.24). Its upper part forms the ooecial vesicle, the wall of which has a thickened, sclerite-like, zone of cuticle. The internal muscle bundles of the vesicle, inserting on its middle and lower wall, effect opening of the ovicell by contracting the vesicle. At their opposite ends, these bundles attach compactly to the basal wall of the maternal autozooid (Ostrovsky et al. 2009a).

2.3.1.6 Immersed Ovicells

Compared to *Valdemunitella lata*, the incubation chamber of the immersed ovicell in *Crassimarginatella* sp. lies completely in the distal part of the maternal autozooid (Figs. 2.7b(B) and 2.25A). The vestigial ooecium, slightly protruding above the colony surface, is formed by the distal autozooid (type 1, category A). It is represented by two thick walls, the outer ectooecium and inner entooecium, which fuse because of strong calcification. Initially, the coelom of the ooecium is a slit-like lumen lined with epithelial cells and communicating with the parent coelom via an arched slit. Later, because of increased calcification, the ooecial coelom is reduced to a crescentic pit at the proximal edge of the ooecium and the narrow canal that connects the pit with the visceral coelom. The arched communication slit becomes a closed groove with several pores or a single pore at the bottom. In some old ooecia the communication canal is completely closed and the pores at both ends are also not retained.

The brood sac is a deep invagination of the distal wall of the maternal autozooid (Figs. 2.7b(B) and 2.25A). Distally, the wall of the brood sac is attached to the transverse wall at the base of the ooecium, whereas proximally it forms a kind of ooecial vesicle overlapping the embryo from above. It was not found to contain either a sclerite or specialized musculature, and yet it closes the entrance to the brood cavity in the same manner as an actual ooecial vesicle. Several muscle bundles are attached to the sac wall in its proximal part, their opposite ends being attached to the basal wall of the maternal autozooid. They appear to extend the brood chamber during oviposition and larval release. Immersed ovicells are also characteristic of the calloporid genera *Aplousina* and *Cranosina* and the related family Antroporidae (Ostrovsky et al. 2009a).

2.3.1.7 Internal Brood Sac with Vestigial Ooecium in *Cauloramphus*

In the genus *Cauloramphus*, all components of the brood chamber are formed solely at the expense of the maternal autozooid (type 2) (Ostrovsky 2008b; Ostrovsky et al. 2007, 2009a). The vestigial kenozooidal ooecium is budded at the distal rim of the maternal autozooid, while its base merges with the upper part of the distal wall of this zooid (Figs. 2.6b(E), 2.7b(C), and 2.25B). The ooecial cavity communicates with the visceral coelom via 1–3 communication pores with pore-cell complexes (Fig. 2.25B). The outer wall of the ooecium (ectooecium) is uncalcified except for its base as a consequence of which, in cleaned specimens, it is mostly entooecium that is visible, appearing as a prominent cap in some species, while in *Cauloramphus spinifer* it appears as a small plate with an arched outline. The ooecial cavity is a deep groove. In older zooids, its lower part is partly reduced by wall calcification. This results in the formation of 1–3 coelomic canals, each leading to a communication pore. These canals are connected with each other only in the upper part of the ooecium, under the membranous area of the ectooecium. The lumina of these canals are partly filled with loose epithelial and peritoneal cells. The position of the ooecium does not prevent distal budding of the maternal autozooid.

The brood cavity is immersed in the distal part of the maternal autozooid and looks like a spacious sac with thin non-calcified walls. It consists of a main chamber and a flat neck leading to the exterior. The entrance to the brood cavity is tightly closed by a specialized part of the distal wall of the maternal autozooid functioning as an ooecial vesicle. When it is displaced, the brood cavity communicates directly with the outside world and not with the vestibulum. At the site where the ooecial vesicle tightly adjoins the entooecial surface, its wall has a cuticular thickening that appears to be a homologue of the sclerite in other calloporids (Fig. 2.25B). A group of muscles (possibly paired) that ensure displacement of the fold and opening of the brood chamber during oviposition and larval release is attached to the wall of the fold above and below the sclerite. At their opposite ends, these muscles are presumably attached to the lateral walls of the cystid. Groups of muscles are also attached to the neck and main chamber of the brood sac (Ostrovsky et al. 2007, 2009a).

A vestigial kenozooidal ooecium is formed in *Cymulopora uniserialis* (see Winston and Håkansson 1986), but the structure of the brood chamber in this species remains unknown.

Thus, the family Calloporidae (sensu lato) has a diverse range of brood chambers, indicating the existence of several trends in the evolution of this earliest group of brooding cheilostomes. These trends include reduction of the distal ooecium-bearing zooid, immersion of the brood cavity accompanied by its proximal displacement and reduction in ooecium size, as well as closure of the ovicell opening by the zooidal operculum (transition from acleithral to cleithral type). Recently, it has been suggested that *Gontarella*, with internal brooding and lacking an ooecium, belongs to the Calloporidae (see Ostrovsky et al. 2009b), in which case calloporids span the entire morphological series from external ovicells to internal incubation.

2.3.2 Structure and Development of Ovicells in Other Cheilostome Families

Apart from ovicells with ooecia constructed from spines and costae (see Sects. 2.3.1, 2.4.3, 2.4.4, 2.4.5, and 2.4.6), there are at least five other variants of ooecium structure in cheilostome brooders, all of them modifications of the basic calloporid plan known since the Cenomanian. The main criteria used for delimiting these variants are (1) the mode of ooecial-wall calcification, (2) degree and mode of contact of ooecial walls with the skeletal elements of the frontal wall/shield of the distal zooid, (3) mode of communication between the ooecial coelom and the zooidal (visceral or hypostegal) coelom, and (4) details of ovicellogenesis. All of these characters are subject to variation within the 'frame' of the particular variant, whereas in some species ovicell structure combines characters of different variants. Moreover, variability characterizes the early stages of ooecial-fold formation, methods of ovicell closure, degree of immersion of the brood cavity, structure of the ooecial vesicle including shape and size, degree of sclerite development, number of muscular bundles and the loci of their attachment as well as some other characters. In fact, structural variability is so great that one can present only a brief comparative analysis of ovicell diversity across the major cheilostome clades. In order to do this, it is convenient to refer to the major variants as "calloporiform," "escharelliform," "lepralielliform" and "microporelliform" in the account that follows.

2.3.2.1 The Calloporiform Ooecium

Despite the vast structural diversity, ooecial morphology in most studied cheilostomes conforms to the calloporiform type (see Fig. 1 in Introduction, Figs. 2.15A, B, 2.16, and 2.22). This type of ooecium is a double-walled hemispheric outgrowth with a completely calcified entooecium, a completely or partly calcified ectooecium and a slit-like coelomic cavity between them. The ooecial coelom communicates with the zooidal coelomic cavity via an arched slit or pores derived from it, which may be open or plugged by non-specialized epithelial cells, or via communication pore(s) with a pore-cell complex. Apart from calloporids (Figs. 2.6a(A, B, E), 2.7a(C, F), b(B), 2.8B, 2.11A, 2.12D, E, 2.13, 2.14, 2.15, 2.16, 2.17, 2.18, 2.19, 2.20, 2.21, 2.22, 2.23, 2.24, and 2.25A), such an ooecium – whether well-developed or vestigial, complete or bilobate (with lobes fused to varying degrees), an outgrowth of the distal zooid or a kenozooid budded from the maternal autozooid – is characteristic of (1) the anascan flustrine superfamilies Calloporoidea (e.g. families Chaperiidae, Hiantoporidae, Farciminariidae) (Fig. 2.6b(C)), Flustroidea (Flustridae, except for species with internal brood sacs lacking an ooecium) (Figs. 1.17, 2.7b(A), 2.31, and 2.32), Buguloidea (Candidae, some Bugulidae) (Figs. 2.6a(F), 2.7a(B), 2.8A, C, and 2.30), and Microporoidea (some Microporidae) (Figs. 2.33F and 2.63A–C); (2) the acanthostegan families Cribrilinidae, Euthyroididae, Bifaxariidae, Catenicellidae, and Eurystomellidae (Figs. 1.24A, 1.25A, 1.32A, B, 2.6a(D), b(A, B), 2.7a(H, I), 2.27, 2.28, and 2.29); (3) the gymnocystal-shielded ascophoran family Hippothoidae (Figs. 1.27D, 1.30B, and 1.36); (4) some members the umbonuloid-shielded family Arachnopusiidae; and (5) some members of the "lepraliomorph" family Smittinidae (at least two species) (Vigelius 1884a, b; Calvet 1900; Levinsen 1909; Woollacott and Zimmer 1972a; Wass and Banta 1981; Nielsen 1985; Lobastova and Ostrovsky 1994; Santagata and Banta 1996; Ostrovsky 1998, 2002; Ostrovsky and Schäfer 2003; Ostrovsky et al. 2003, 2009a, unpublished data). The base of the ooecial fold is in all the cases a continuation of the gymnocystal wall of the ooecium-producing zooid.

The vast majority of ooecia are complete. On the other hand, in some calloporids (*Wilbertopora*, *Valdemunitella*, *Bryocalyx*, *Concertina*, see above) and in many Cribrilinidae ooecia have a median suture (Ostrovsky 1998, 2002, 2009) and may be called bilobate. Species of the cribrilinid genera *Figularia*, *Corbulipora*, *Euthyroides* and *Puellina* have a horizontal slit running perpendicular to the median suture on the inner surface of the ooecium (Figs. 2.7a(I), 2.27C–E, G, and 2.28; note that similar slit exists in a costate ooecium of the fossil *Leptocheilopora magna*, see Fig. 2.26C). The coeloms of the ooecial lobes communicate with the visceral coelom of the distal zooid via two lateral communication slits (Fig. 2.27G, H). The same ooecial structure occurs in the Bifaxariidae (*Diplonotos*), which is related to Cribrilinidae. Communication slits later become communication pores, which sometimes close because of ooecial-wall calcification. The median suture and independent lateral communication slits indicates that the left and right halves of the ooecium initially form independently, as two outgrowths. Later they merge to form the hemispherical brood chamber typical of fossil and Recent calloporids like *Wilbertopora* and *Valdemunitella* (see above). The early stages of ovicell-floor calcification in calloporids and cribrilinids with bilobate ooecia, are represented by a non-paired plate (discussed in Ostrovsky and Taylor 2005b).

Cribrilina macropunctata, *C. punctata* and *C. cryptooecium*, on the other hand, have complete ooecia, lacking a longitudinal suture. In these species the ooecial coelom communicates with the zooidal coelom via a narrow arched slit, retained from ovicellogenesis, just as in Recent calloporids. Likewise, early stages of ovicell-floor calcification in Recent cribrilinids and calloporids with complete ooecia are represented by a paired plate (Levinsen 1909, pl. 9, figs. 11a–c; Bishop 1994, fig. 17; Ostrovsky and Schäfer 2003; Ostrovsky et al. 2003, 2009a, unpublished data).

Cribrilina annulata has a kenozooidal ooecium. It appears as a terminal cap on the distal wall of the maternal autozooid. The space between the inner calcified ooecial wall (entooecium) and non-calcified distal wall of the maternal autozooid is the brood chamber of the ovicell (Figs. 2.6b(A) and 2.29). In this species, the ooecial coelom communicates with that of the maternal autozooid via communication pores plugged by specialized pore-cell complexes (Ostrovsky 1998). Ovicells with an ‘intercalary’ kenozooidal ooecium in *Eurystomella* (Eurystomellidae) have a similar structure (Fig. 2.6b(B)) (see also Levinsen 1909, pl. 18, fig. 14c).

Calloporiform ooecia form at the colony periphery (Figs. 2.13B and 2.18). As noted above, the initial stage of ovicell-floor calcification may be a paired or a non-paired plate (Figs. 2.11C, D, 2.13B, and 2.18A). Paired plates occur in the calloporid genera *Callopora*, *Tegella*, *Crassimarginatella*, *Amphiblestrum* and *Parellisina* (inter alia), the candid genera *Menipea*, *Scrupocellaria* and *Tricellaria*, cribrilinid genera *Collarina* and *Cribrilina* and the arachnopusiid genus *Arachnopusia*, while non-paired plates occur in the calloporid genera *Wilbertopora* and *Valdemunitella*, cribrilinid genera *Corbulipora* and *Puellina*, Euthyroididae and Hippothoidae.

Most of the bryozoans listed above have hyperstomial, prominent ovicells, while subimmersed, endozooidal or immersed ones are less common, with different ovicell types often found within one and the same family (for instance, in Calloporidae), sometimes in the same genus (*Puellina*) or even species (*Callopora lineata*, *Puellena radiata*) (compare Figs. 2.13A and 2.15A).

Endozooidal ovicells occur in species of Candidae (*Caberea*) (Fig. 2.30A), Cribrilinidae (*Puellina*, *Figularia*) (Figs. 2.27B, C, E and 2.28), Eurystomellidae (*Selenariopsis*) (Fig. 2.7a(H)) and Catenicellidae (*Catenicella*, *Pterocella*) (Fig. 1.24A). However, they are especially characteristic of Flustridae (Figs. 1.17, 2.7b(A), 2.31, and 2.32). Most or all of the brood cavity is immersed/enclosed in the distal zooid; only in *Flustra foliacea* does the brood chamber of the ovicell go deeply into the cavity of the maternal autozooid (see also Levinsen 1909, pl. 24, figs. 6–8). The vestigial ooecium is cap- or knob-shaped, with its base merging with the frontal wall of the distal zooid. The ooecial coelom in this instance communicates with the visceral coelom of the distal autozooid via a broad arched slit. The brood cavity and entooecium appear to be formed as a result of invagination of the non-calcified proximal part of the distal zooid. The entooecium presumably increases in size by intercalary growth, while the ectooecium grows little, if at all (Fig. 2.31D–H) (see Sect. 2.4.8). In empty ovicells of some species the ooecial vesicle occupies nearly all or most of the brood cavity (Figs. 1.17A, 2.7b(A), and 2.32A), but it may also be only weakly or moderately developed (Fig. 2.32B).

Immersed ovicells are found in Antroporidae (Ostrovsky et al. 2009a, b) and *Bugulopsis monotrypa* (Candidae) (Fig. 2.30B). Some calloporids (Figs. 2.6b(E), 2.7b(C), and 2.46C), some flustrids (Fig. 2.46A, B) and Beaniidae (Fig. 1.22) have internal brood sacs with or without a vestigial ooecium.

Two types of ovicell structure are found in the Microporidae, indicating an evolutionary connection between them – the calloporiform type in *Opaeophora* and *Micropora* and the escharelliform type (see below).

2.3.2.2 The Escharelliform Ooecium

This ooecial variant seems to have evolved independently from the calloporiform type in the anascan families Microporidae and Onychocellidae (Figs. 2.33A–C and 2.34), the umbonulomorph families Romancheinidae, Lepraliellidae, Sclerodomidae, and Metrarabdotosidae (Figs. 2.35A–D and 2.36) and lepraliomorph families Phorioppniidae, Margarettidae (Fig. 2.37), Gigantoporidae, Cheiloporinidae, Cyclicoporidae and Urceoliporidae (Fig. 1.23B). Thus, this ooecium seems to appear once a hypostegal coelom and complex frontal wall have evolved.

The escharelliform ooecium is characterized by complete or partial reduction of ectooecial calcification and by fusion of the entooecium with the cryptocyst or calcified wall of the frontal shield of the distal zooid. Uncalcified ectooecium continues to the membranous frontal wall of this zooid, while the coelom of the ooecial fold is represented by a narrow cavity communicating directly with the hypostegal coelom of the distal zooid (Figs. 2.34, 2.36, and 2.37). A number of species (for instance, *Escharella immersa*) retain communication pores or a closed arched slit (Figs. 2.35C, H and 2.36A), highlighting ooecial communication with the visceral coelom during the early stages of ooecial-fold formation (and evolution). Ooecia form at the colony periphery (Fig. 2.35E–H). The early stage of calcification of the provisional ovicell floor appears as a non-paired plate (Fig. 2.35E, G) (see also Levinsen 1909, pl. 17, fig. 3a). As it forms, the ovicell floor fuses with the simultaneously forming cryptocyst or the calcified wall of the frontal shield of the distal zooid (Fig. 2.35F, H).

If the distal autozooid is reduced, the ooecial coelom communicates with that of the ooecium-producing distal kenozooid (via one or more pore that remain after closure of the communication slit, presumably plugged by non-specialized cells (in some species of *Micropora*; see Figs. 2.6a(C) and 2.33D)) or the maternal autozooid (via one or more pores with a pore-cell complex (*Mollia multijuncta*) (Fig. 1.28C, D)). In these two cases, ooecial structure fully corresponds to the calloporiform type.

Crepis longipes (recently moved from the Chlidoniidae to the Calloporidae) has partially calcified ooecia formed by the distal autozooid or distal kenozooid (see Harmelin and d'Hondt 1992; Reverter-Gil et al. 2011). In the former case the ooecial coelomic cavity communicates directly with the hypostegal coelom of the distal zooid – a situation unknown in calloporids. In the latter, the ooecial coelom communicates with that of the ooecium-producing distal kenozooid. Both variants are known among Microporidae.

In *Margaretta barbata*, the maternal autozooid and the ovicell open into the lumen of the elongated, distally bent tube of the peristome (Figs. 2.7a(D) and 2.37). Such ovicells are referred to as peristomial. The walls of the entooecium and the peristome are continuous, being represented by a thick calcified layer perforated by pseudopores and covered from the outside by the hypostegal coelom and membranous frontal wall.

Immersed escharelliform ovicells, correspond in all their main features (except for the non-calcified ectooecium and ooecial communication with the hypostegal coelom) to the above-described ovicells of *Crassimarginatella* sp. (Calloporidae), are found in *Onychocella* (Onychocellidae) and *Cheiloporina* (Cheiloporinidae). Endozooidal ovicells are found in *Cellarinella* (Sclerodomidae) and *Polirhabdotos* (Metrarabdotosidae) (see Levinsen 1909, pl. 24, fig. 10; Harmer 1957, fig. 94).

The endotoichal ovicells of cellariids, which resemble endozooidal ovicells because of complete immersion of the brood cavity, should be attributed to the same group since their ooecia are represented by external membranous and internal calcified walls and the ooecial coelom communicates with the hypostegal coelom(s) of the ooecium-producing autozooid(s). Although the ovicell opens into the distal part of the frontal surface of the maternal autozooid (Fig. 2.38D, F–H), the brood chamber is immersed in the proximal part of the distal zooid and, often, the neighbouring distolateral zooids, and its walls, except for the proximal (transverse) wall, comprise the skeletal walls of these zooids (Figs. 1.19B–D, 1.20D, 2.7b(F), and 2.39) (see also Calvet 1900, pl. 6, fig. 11). The brood cavity is limited from above by the proximal and lateral areas of the frontal wall of the distal zooid and/or two distolateral zooids (Fig. 1.20D) as well as by the upper horizontal part of the transverse zooid wall (proximal part of the ooecial roof). The entrance to the brood chamber is closed by a modified ooecial vesicle, which plays the role of ovicell operculum and brood sac at the same time (Figs. 1.19B–D, 2.7b(F), and 2.39). Its coelomic cavity communicates with the hypostegal coelom of the maternal autozooid laterally from the zooidal opening. The distal area of the maternal zooid's frontal membrane continues into the wall of the ooecial vesicle. The cuticle of the vesicle wall just below the distal edge of the ovicell opening thickens to form a sclerite (Figs. 1.19B, D and 2.39). It is approached by a group of thick muscle bundles, the proximal ends of which are attached to the transverse wall between the brood chamber and the cavity of the maternal zooid. Inside the brood cavity the thin wall of the ooecial vesicle serves as a sheath surrounding the embryo in the ovicell (Figs. 1.19B–D, 1.20A, B, 1.29B, and 2.39). The distal part of the ooecial vesicle is attached to the calcified floor or roof of the ovicell (Figs. 2.7b(F) and 2.39).

2.3.2.3 The Lepralielliform Ooecium

As with the escharelliform type, the general form of construction of the lepralielliform variant corresponds to the calloporid ooecium. The main differences from the escharelliform are (1) partly or completely calcified ectooecium, (2) communication of the ooecial coelom with that of the distal zooid via a central communication pore (in most cases), (3) secondary calcification overgrowing the ooecium (several exceptions), and (4) reduced ooecial base and early calcification of the ooecial fold as a "double disc" (some exceptions). The lepralielliform ooecium occurs in some hiantoporid and bugulid anascans (*Bugula*, *Bicellariella*) (Figs. 1.18A, B, 2.3, 2.5, and 2.7a(A)) and a number of ascophorans, e.g. some species in the umbonulomorph families Arachnopusiidae and Lepraliellidae and presumably in all Bryocryptellidae and Umbonulidae (Figs. 2.7a(G), 2.40, and 2.41) and in the lepraliomorph families Smittinidae, Bitectiporidae, Stomachetosellidae, Lanceoporidae, Cleidochasmatidae, Phidoloporidae, Hippoporidridae, Celleporidae, Lekythoporidae, Petraliidae, and Petraliellidae (Figs. 2.8E, F, 2.40, 2.41, and 2.65A).

In *Bugula* and *Bicellariella*, the ooecium develops as a small terminal evagination of the distal zooid bud, having a narrow base (Nielsen 1985; Moosburgger et al. 2012). As the initially funnel-shaped evagination enlarges, it broadens distally. Calcification lags slightly behind ooecium formation. Ooecial coelomic cavity communicates with the visceral coelom of the distal zooid via a communication pore that is partly or completely plugged by non-specialized epithelial cells (Woollacott and Zimmer 1972a; Moosburgger et al. 2012). As in the ascophorans described below, the following stage of ooecial formation in bugulids is a slightly concave "double disc".

In most ascophorans with a lepralielliform ooecium, the ectooecium is calcified with small to medium-sized pseudopores, oval, rounded or irregular and evenly or unevenly scattered on the surface. In some species the ectooecium has membranous windows; in rare cases only the ectooecium base is calcified. In many species, as the colony ages, ooecia are immersed completely or almost completely in secondary calcification (Figs. 2.7a(G), 2.8F, 2.40B, and 2.41A) of the frontal shield of the distal zooid and often 2–5 distolateral autozooids. The boundaries of calcification formed by the adjacent zooids appear as sutures or crests (see Levinsen 1909, pl. 18, fig. 13a, pl. 24, fig. 5a). The presence of such sutures led some researchers to interpret the ooecia of such ovicells as cormidial, i.e. formed by several zooids. In other species secondary calcification is weakly developed (Fig. 2.41B, C). The ooecium may also become immersed in the colony by frontal budding of hypostegal coeloms, forming additional zooid layers.

The ooecial cavity communicates with the visceral coelom of the distal autozooid via a narrow communication canal with a central pore (Figs. 2.7a(G), 2.8E, F, 2.40E, 2.41, and 2.65A). The pore is located close to the transverse wall between maternal and distal zooids or at some distance from it. The lumen of the communication canal is plugged by non-specialized epithelial cells (Fig. 2.41). If the distal autozooid is reduced, the ooecial coelom communicates via a narrow slit with the coelom of the flattened, ooecium-producing distal kenozooid that in turn is connected with a maternal autozooid via a communication pore(s) plugged by a pore-cell complex (Figs. 2.6b(D, F) and 2.42). In this case, ooecial structure can be described as calloporiform, whereas early stages of ovicellogenesis correspond to the lepralielliform "double disc".

Ooecia originate at the colony periphery (Fig. 2.40A, C). In general, ovicellogenesis starts with the formation of a flat hollow outgrowth (ooecial fold), which has the shape of a semicircle with a narrow base surrounding the communication pore (Fig. 2.40C, E, F) (Banta 1977). Early stages of ooecial floor calcification are represented by a paired (*Porella smitti*, *Smittina mucronata*) (Fig. 2.40C, E) or non-paired (most species studied) plate. This plate represents the initial calcification of the ooecial fold, which begins development at the proximal part of the frontal shield of the distal zooid before its calcification is completed (Fig. 2.40C–E). The lower lateral areas of ooecial-fold calcification grow toward each other together with the lateroproximal parts of the developing frontal shield (Fig. 2.40D). The fusion of these areas and the formation of the calcified base of the ectooecium result in separation of the coelomic cavity of the growing ooecial fold from the hypostegal coelom of the distal zooid and formation of the central communication pore (Fig. 2.40E). Continued growth of the ooecial fold occurs at its uncalcified edge (Fig. 2.40 inset) (see also Levinsen 1909, pl. 19, fig. 4a).

The lower wall of the ooecial fold (provisional ectooecium) overgrows the proximal part of the distal autozooid, tightly adjoining its outer (frontal) non-calcified wall (Fig. 2.40F), as a consequence of which both elements (autozooidal frontal membrane and ectooecial cuticle) become immured between the subsequent ectooecial calcification and that of the frontal wall (i.e. frontal shield). The hypostegal coelom in the zone of overgrowth is compressed and obliterated (Fig. 2.41A, C) (Banta 1977). At this stage the ooecial fold becomes a double disc consisting of the upper non-paired plate (provisional entooecium, ovicell floor) and the lower plate (ectooecium) (Fig. 2.40F). After the horizontal part of the ooecium has been formed, its vertical growth starts, accompanied by a more-or-less synchronous overgrowing of the ooecium by a matrix of secondary calcification at the expense of the thickening frontal shield of the distal zooid. When forming the roof, the edges of the ooecium grow from the periphery to the centre.

A careful description and schematic of ovicellogenesis in *Reteporellina evelinae* were published by Banta (1977) (for illustrations of ovicellogenesis see also Hass (1948), Soule (1973), Cook (1977a), Cook and Hayward (1983) and Gordon and Grischenko (1994)). Cook (1977a) and Cook and Chimonides (1981a) carefully described and illustrated ooecium formation in a number of species of Arachnopusiidae and Petraliellidae. However, since they did not make sections, both cuticular and calcified walls (some excessive) in their SEM-based descriptions and schemata are shown in a confusing manner.

In *Rhamphostomella ovata*, *Palmiskenea* sp. and some other species, development of the ooecial fold differs from that described above – formation of the double disk stage is postponed. Instead, there is an arched groove containing a slit-like communication pore in the proximal part of the incompletely formed frontal shield of a developing ooecium-producing autozooid at the colony periphery. The groove is covered by a cuticular wall, and its coelomic cavity is isolated from the hypostegal coelom of the distal zooid by a narrow arch of calcification (the base of the provisional ectooecium); the communication pore leads to the visceral coelom of the distal bud. The entire structure (groove and pore) comprises the base of the developmentally retarded provisional ooecial fold. Thus, whereas base of the ooecium originates at the colony periphery, the actual ooecial fold can be formed later when the ooecium-producing zooid is no longer at the periphery.

2.3.2.4 The Microporelliform Ooecium

This variant is found only in lepraliomorph ascophorans (e.g. families Microporellidae, Pacificincolidae, Schizoporellidae, Myriaporidae, Porinidae) (Figs. 2.43A–D, 2.44, and 2.65C; see also fig. 17 showing a schematic of ovicell anatomy. *Pacificincola insculpta* (as '*Hippodiplosia*') in Nielsen 1981).

The ooecium is again an outgrowth of the proximal part of the frontal shield of the distal autozooid and consists of two walls with a coelomic cavity between them (Figs. 2.43C, D, 2.44, and 2.65C). The outer wall (ectooecium) is non-calcified, being a continuation of the frontal wall of the distal autozooid (as in the escharelliform ooecium). The calcified inner wall (entooecium) is connected with the proximal part of the frontal shield of the distal zooid. The ovicell floor is represented by a horizontal area of entooecium that is fused with the calcified proximal part of the distal frontal shield by several crossbar-like ridges. A narrow coelomic space is retained between the entooecium and the proximal part of the frontal shield, communicating (as does the rest of the ooecial coelom), with the hypostegal coelom of the distal autozooid (Figs. 2.43C and 2.44). There are no pores, hence no communication, between ooecial and visceral coeloms.

Ovicellogenesis proceeds at a considerable distance from the colony periphery. It involves the formation of an arched ooecial fold, accompanied by gradual calcification of the proximal part of the frontal shield of the distal zooid. The provisional ovicell floor initially appears as an unpaired semicircular plate extending from the transverse wall (see also illustrations in Nielsen 1981; Mawatari et al. 1991; Suwa and Mawatari 1998; Mawatari and Suwa 1998; Suwa et al. 1998). Its calcification overgrows the proximal hypostegal coelom and frontal shield of the underlying distal zooid, fusing with its calcified wall by means of protuberances or crests of the wall (sometimes present only at the edge of the ovicell floor) transforming to skeletal crossbars. The fully developed flat ovicell floor is skirted by a low ooecial fold of the non-calcified frontal wall of the distal zooid. This fold grows vertically and then centripetally, accompanied by progressive thickening of the calcified entooecium.

2.3.2.5 The Case of *Fenestrulina*

In species of *Fenestrulina* (Microporellidae), the floor of the brood cavity comprises entooecium fused with the proximal area of the frontal shield of the distal autozooid by means of several (16–18) radial crossbars; spaces between them describe an arch of pores around the entooecial base (Figs. 2.1, 2.8D, 2.43E, F, 2.45, and 2.65B). Between the ovicell floor and the proximal part of the frontal shield, a narrow coelomic space is retained that communicates with the ooecial coelom via the pores between the crossbars. The entooecium is surrounded by a raised lip, with a narrow rim of gymnocyst (Fig. 2.43E–F), that represents the calcified base of the ectooecium and the site where its non-calcified part is attached to the frontal shield. Because of this lip, the ooecial coelom is isolated from the hypostegal coelom of the distal zooid. The narrow ooecial cavity communicates with the visceral coelom of the distal autozooid via a central slit-like pore; it is arched and located near the transverse wall between the maternal and distal zooids (Figs. 2.1, 2.8D, 2.45, and 2.65B; see also Nielsen 1981, fig. 18B).

The ooecium is formed as an arched fold in the proximal part of peripheral zooid buds in which formation of the frontal shield is underway (Nielsen 1981, figs. 17–19). The earliest stage of calcification of the provisional ovicell floor is an unpaired tongue-like plate initiated from the transverse zooidal wall. Further growth of the ooecial fold resembles that in the lepralielliform variant although a double disc is not formed (see Fig. 2.40 and description above).

The lower lateral areas of calcification of the ooecial fold grow towards each other, together with the proximal areas of the developing frontal shield. Fusion of these areas beneath the provisional ovicell floor (horizontal part of the entooecium) and formation of the calcified base of ectooecium result in separation of the coelomic cavity of the growing ooecial fold from the hypostegal coelom of the distal zooid and in the formation of the proximal part of its frontal shield with central communication in the form of a slit-like pore (Figs. 2.1, 2.8D, and 2.45; see also Nielsen 1981, Figs. 1.17B, 1.18). Further, the frontal shield fuses with the ovicell floor by means of radial crossbars.

Fusion of the horizontal area of the entooecium with the frontal shield and the lack of a double disc are microporelliform, whereas isolation of the ooecial and hypostegal coeloms, the presence of the communication pore and early ovicellogenesis are lepralielliform. It should also be noted that, judging from the description of Nielsen (1981), *F. miramara* (as *F. malusii*) has cleithral ovicells. In contrast, Calvet (1900, fig. 21) depicted an acleithral ovicell in *F. malusii* (as *Microporella*).

Table 2.1 Occurrence of internal brooding and prominent ovicells in cheilostomes

Taxon	Internal brood sacs, immersed ovicells and endozooidal ovicells	Prominent ovicells	References
Flustrina			
Calloporidae	IBS, IMO, IBS/VO	+	
Cranosina	IBS	–	Harmer (1926)
Gontarella	IBS	–	Ostrovsky et al. (2006)
Cauloramphus	IBS/VO	–	Ostrovsky et al. (2007, 2009a)
Crassimarginatella	IMO	+	Cook (1968a, 1985), Ostrovsky et al. (2009a)
Aplousina	IMO	+	Cook (1968a)
Cymulopora	IMO	–	Winston and Håkansson (1986)
Septentriopora	*	+	Kuklinski and Taylor (2006a)
Vibracellina	IMO	–	Winston and Håkansson (1986)
Antroporidae	IMO, EZO	–	Hastings (1930), Cook (1968a), Gordon (1986), Tilbrook (1998), Tilbrook and Grischenko (2004)
Chaperiidae	IBS	+	
Chaperia	IBS	–	Gordon (1970, 1982, 1984), Gordon and Mawatari (1992)
Quadricellariidae	*	+	
Quadricellaria	*	–	Harmer (1926), Mawatari (1974), Gordon (1984)
Bryopastoridae	*	–	
Bryopastor	*	–	Gordon (1986)
Pseudothyracella	*	–	d'Hondt and Gordon (1999)
Farciminariidae	IBS	+	
Farciminellum	IBS	–	Harmer (1926)
Heliodomidae	*	+	
Setosellina	*	+	Harmer (1926), d'Hondt and Schopf (1984), Lagaaij (1963)
Cupuladriidae	IBS	–	
Cupuladria	IBS	–	Waters (1919 [1921]), Cook (1965, 1985), Ostrovsky et al. (2009b)
Discoporella	IBS	–	Winston and Håkansson (1986), Ostrovsky et al. (2009b)
Reussirella	IBS	–	Waters (1919 [1921]), Winston and Håkansson (1986), Winston (1988)
Flustridae	IBS, EZO	+	
majority of genera	EZO	+	Vigelius (1884a, b), Calvet (1900), Levinsen (1909), Hayward (1995)
Carbasea	IBS	–	Grant (1827), Hayward (1995)
Nematoflustra	IBS	–	Ostrovsky et al. (2006)
"*Biflustra*" *perfragilis*	IBS	–	Ostrovsky et al. (2006)
Bugulidae	IBS, IMO	+	
Bugula	IMO	+	Ryland (1962), Hastings (1943), Prenant and Bobin (1966)
Caulibugula	*	+	Harmer (1926), Liu (1985)
Himantozoum	IBS, IMO	–	Harmer (1926), Hastings (1943), Hayward (1995)
Cornucopina	IMO	+	Hayward (1995)
Camptoplites	IMO	+	Kluge (1914), Hastings (1943), Hayward (1995)
Beaniidae	IBS, IBS/VO, IMO(?)	+	
Beania	IBS, IBS/VO, IMO(?)	+	Jullien (1888), Waters (1912, 1913), Harmer (1926), Hastings (1943), Marcus (1955), Gautier (1962), Prenant and Bobin (1966), Gordon (1970), Ryland and Hayward (1977), Cook (1968b, 1985)
Candidae	IBS, IMO, EZO	+	
Menipea	IBS, IMO, EZO	+	Hastings (1943), Gordon (1986), Hayward (1995)
Bugulopsis	IMO	–	Hastings (1943)
Caberea	EZO	+	Hastings (1943), Gordon (1984, 1986)
Microporidae	*	+	
Calpensia	*	–	Hayward and Ryland (1998)
Microporina	*	–	Canu and Bassler (1929), Kluge (1975)
Ogivalia	*	–	Hayward (1995)

(continued)

Table 2.1 (continued)

Taxon	Internal brood sacs, immersed ovicells and endozooidal ovicells	Prominent ovicells	References
Lunulitidae	IMO, EZO	–	
Lunulites	IMO	–	Håkansson (1975), Håkansson and Voigt (1996)
Pavolunulites	IMO, EZO		Håkansson and Voigt (1996)
Lunulariidae	IBS, IMO	–	
Lunularia	IBS, IMO	–	Cook and Chimonides (1986)
Otionellidae	IBS	–	
Otionella	*	–	Cook and Chimonides (1985), Bock and Cook (1998)
Otionellina	IBS	–	Cook and Chimonides (1985), Bock and Cook (1998)
Petatosella	IBS	–	Bock and Cook (1998)
Helixotionella	*	–	Cook and Chimonides (1984)
Kausiaria	*	–	Bock and Cook (1998)
Selenariidae	EZO, IMO	–	
Selenaria	EZO, IMO	–	Chimonides and Cook (1981), Bock and Cook (1999)
Onychocellidae	IMO, EZO	+	
Aechmella	EZO	–	Taylor and McKinney (2006)
Onychocella	IMO	–	Cook (1985)
Smittipora	IMO	–	Cook (1968c, 1973, 1985)
Floridina	IMO	–	Hastings (1930)
Steginoporellidae	IBS	–	
Steginoporella	IBS	–	Waters (1913), Marcus (1922), Harmer (1926), Cook (1964, 1968c, 1985), Winston (1984)
Labioporella	IBS	–	Cook (1985)
Chlidoniidae	IBS	–	
Chlidonia	IBS	–	Waters (1913), Harmer (1926)
Crepis	*	–	Harmer (1926)
Poricellariidae	IBS/VO	–	
Poricellaria	IBS/VO	–	Waters (1913)
Ascophora			
Cribrilinidae	IMO, EZO	+	
Jullienula	*	–	Osburn (1950), Hayami (1975)
Anaskopora	*	–	Arnold and Cook (1997), Bock and Cook (2001a)
Cribrilina	IMO, EZO	+	Hayward and Ryland (1998), Ostrovsky (1998)
Puelleina	EZO	+	Hayward and Ryland (1998), Ostrovsky (2002)
Eurystomellidae	IMO, EZO	–	
Eurystomella	IMO	–	Gordon et al. (2002)
Integripelta	IMO	–	Gordon et al. (2002)
Zygoplane	IMO	–	Gordon et al. (2002)
Selenariopsis	EZO	–	Bock and Cook (1996)
Pasytheidae	*	–	
Pasythea	*	–	Cook (1985)
Gemellipora	*	–	Cook (1985)
Exechonellidae	IBS	–	
Exechonella	*	–	Gordon (1984), Cook (1985)
Triporula	IBS	–	Cook (1985)
Anexechona	*	–	Osburn (1950)
Adeonidae	IBS	–	
Adeona	IBS	–	Waters (1912)
Adeonellopsis	IBS	–	Waters (1913)
Reptadeonella	IBS	–	Winston (1984)
Adeonella	IBS	–	Waters (1912, 1913)
Laminopora	IBS	–	Waters (1912)

(continued)

Table 2.1 (continued)

Taxon	Internal brood sacs, immersed ovicells and endozooidal ovicells	Prominent ovicells	References
Inversiulidae	*	–	
Inversiula	*	–	Harmer (1926), Powell (1967), Gordon (1984), Hayward (1995)
Romancheinidae	IBS	+	
Arctonula	IBS	–	Gordon and Grischenko (1994)
Umbonulidae	IBS, IMO	+	
Oshurkovia	IBS	–	Hastings (1944, 1964), Eggleston (1972)
Desmacystis	IMO	–	Gordon and Grischenko (1994)
Sclerodomidae	EZO	+	
Cellarinella	EZO	–	Hayward (1995)
Cellarinelloides	EZO	–	Hayward (1995)
Watersiporidae	IBS	–	
Watersipora	IBS	–	Waters (1909, 1913), Mawatari (1952), Cook (1985), Zimmer (personal communication in Reed 1991)
Uscia	*	–	Banta (1969)
Veleroa	*	–	Osburn (1952)
Stomachetosellidae	*	+	
Fatkullina	*	–	Grischenko et al. (1998)
Tetraplariidae	*	+	
Tetraplaria	*	+	Harmer (1957)
Porinidae	EZO	+	
Porina	EZO	–	Ostrovsky, unpublished data
Myriaporidae	EZO	–	
Myriapora	EZO	–	Ostrovsky, unpublished data
Cheiloporinidae	IMO	+	
Cheiloporina	IMO	–	Ostrovsky, unpublished data
Cryptosulidae	IBS	–	
Cryptosula	IBS	–	Smitt (1863), Calvet (1900), Gordon (1977), Zimmer (personal communication in Reed 1991), Gordon and Mawatari (1992)
Harmeria	IBS	–	Kuklinski and Taylor (2006b)
Urceoliporidae	IBS/VO	+	
Reciprocus	IBS/VO	–	Ostrovsky, unpublished data
Euthyrisellidae	IBS	–	
Euthyrisella	IBS	–	Cook and Chimonides (1981b)
Pleurotoichus	IBS	–	Cook (1979)
Tropidozoum	IBS	–	Cook and Chimonides (1981b)
Siphonicytaridae	*	–	
Siphonicytara	*	–	Bock and Cook (2001b)
Hippoporidridae	IBS	+	
Odontoporella	IBS	–	Gordon (1970, 1989a), Carter and Gordon (2007)

This table is based on personal observations and data from the literature. The type of brooding was either recorded anatomically or inferred from the presence of embryos in reproducing colonies. Bryozoans with immersed (IMO) and endozooidal (EZO) ovicells are classified as internal brooders because their embryos are incubated inside an internal brood cavity below the colony surface. *Cauloramphus*, *Poricellaria*, *Reciprocus* and some species of *Beania* represent a special case as they have both an internal brood sac (IBS) and a vestigial kenozooidal ooecium (VO)
Asterisks indicate cases in which brooding in the internal sac is suggested by the absence of ooecia or the presence of polymorphic zooids. The families Epistomiidae and Cellariidae were not included in the list because the former is viviparous and the latter has endotoichal ovicells. Note that the genera *Gontarella* and *Vibracellina* are provisionally placed in the family Calloporidae

2.3.3 Internal Brood Sacs

Brooding of the embryo in internal sacs is widespread among Cheilostomata (summarized in Table 2.1; see also Ostrovsky et al. 2009b). This phenomenon was first discovered by Grant (1827) in *Carbasea carbasea*. He observed eggs, developing embryos and larval release, but did not recognize the brood sac, which had not been studied. Similarly, intrazooidal development of the embryo was recorded by Smitt (1863, 1865) in *Cryptosula pallasiana* (as *Lepralia*) and developing larvae were observed by Jullien (1888) inside zooids of *Beania costata* (as *Diachoris*). Later Calvet (1900) described the internal brood chamber (pouch or diverticulum of the vestibulum) in *C. pallasiana*, noting the muscles attached to its walls and the "membrane vitelline" [fertilization envelope] surrounding the early embryo. A similar "ovisac" "with delicate walls" and "inserted muscle-fibres" was recorded "at the distal end of the zooecium" in *Cheiloporina haddoni* (as *Lepralia*) by Harmer (1902, p. 300).

Waters (1909, 1912, 1913) recorded internal brooding in *Watersipora* (as *Lepralia*), *Adeona*, *Adeonella*, *Adeonellopsis*, *Laminopora*, *Beania*, *Poricellaria* and *Catenicella* (as *Vittaticella*) and discussed the possible value of brood chambers for bryozoan classification. Embryos were said to be brooded inside an internal "sac near the distal end of the zooecium" – a specialized enlarged "gonoecium" in Adeonidae. Incubation sacs were also found in *Beania* (see Waters 1912, pp. 492–493). This author termed the internal brood sac of *Watersipora cucullata* (as *Lepralia*) "a concealed ovicell" (Waters 1909, p. 151)

Waters (1913, p. 500) found membrane-bounded embryos in *Steginoporella magnilabris* (as *Steganoporella*), referring to them as "internal ovicells". He also found an internally brooded embryo in *Chlidonia pyriformis* (as *C. cordieri*) in sections, but gave no details about structure. Marcus (1922) made a similar finding while studying *Steginoporella haddoni* (as *Steganoporella*). Harmer (1926, p. 271) described internal brooding in "a spacious, thin-walled ovisac" in *S. magnilabris* (as *Steganoporella*) that extended almost to the zooidal basal wall, attaching "to the lateral walls … by a number of muscle-fibres", but was unable to determine if it was connected with the vestibulum. Studying the same species, Cook (1964, pp. 52–53) stated "when the egg [i.e. embryo] has reached the largest size observed it can be seen beneath the operculum within the ovisac which is attached to the lateral walls of the zooecium."

Hastings (1944, pp. 273–274) recorded "zooecia … [with] embryos in the body-cavity, although they had no ovicells and showed no external difference from the non-fertile zooecia" in *Oshurkovia littoralis* (as *Umbonula*). Hastings (1964, p. 251) subsequently referred to "internal ovisacs" in this species, confirmed by Eggleston (1972) who noted simultaneous internal brooding of several embryos. The structure of the brooding apparatus is unknown, however.

Mawatari (1952, p. 20) studied aspects of sexual reproduction in *Watersipora subtorquata* (as *W. cucullata*). He mentioned "the embryo sac" enveloping the developing embryo; his figures 34–35 and 44 show it to be an evagination of the vestibulum, confirmed by Zimmer (personal communication in Reed 1991) for *W. arcuata*. Similarly, Cook (1979, p. 200) mentioned "membranous diverticula housed within zooid body wall" as a brood chamber in dimorphic female zooids of *Tropidozoum cellariiforme*. According to Gordon and Mawatari (1992), internal brooding is characteristic of *Chaperia granulosa* (Chaperiidae) (reviewed in Ostrovsky 2008b).

My data have contributed to further understanding of the anatomy of cheilostome internal brooding. In addition to the calloporid genus *Cauloramphus* (see Sect. 2.3.1), a number of species with internal incubation sacs were studied from the families Calloporidae, Cupuladriidae, Flustridae, Beaniidae, Steginoporellidae, Chlidoniidae, Romancheinidae, Watersiporidae, Cryptosulidae, Euthyrisellidae and Urceoliporidae (Ostrovsky 2009; Ostrovsky et al. 2006, 2007, 2009a, b and unpublished data).

In *Nematoflustra flagellata* (Flustridae), the brooding zooid differs in external appearance from non-brooding ones. The frontally visible inner vesicle (a presumed homologue of the ooecial vesicle in an ovicell-bearing ancestor) is a hollow fold of the distal wall of the maternal autozooid that adjoins the arched proximal wall of the distal autozooid (Fig. 2.46A). The entrance to the brood sac is closed by this vesicle, which, displaced, allows the brood cavity to communicate directly with the environment rather than the vestibulum. The vesicle bears a large sclerite, attached to which is a group of muscles that open the entrance to the brood sac during oviposition and larval release. These muscles are anchored to the cystid basal wall behind the proximal end of the brood sac. This sac is a voluminous oval invagination of the non-calcified distal wall of the maternal autozooid and consists of a capacious chamber and a neck that tapers towards the opening. The sac wall is thin and easily deformed, being composed of a cuticular layer and underlying flat epithelial cells. The muscle bundles that change the shape of the sac during oviposition and larval release are attached to its wall proximally and distally. The lower ends of the muscle bundles are attached to the basal and transverse walls of the cystid (Fig. 2.46A).

In "*Biflustra*" *perfragilis* (family incertae sedis) and *Gontarella* sp. (?Calloporidae) (Fig. 2.46B, C), brooding zooids cannot be externally distinguished from non-brooding ones. The opening of the incubation sac is closed by the upper part of the distal wall of the maternal autozooid playing the role of the inner vesicle. Wall cuticle is thicker in this area but there is no sclerite. As in *Nematoflustra*, the brood cavity communicates with the environment independently of the vestibulum and is not closed by the zooidal operculum. The neck of the brood sac is very short in "*B.*" *perfragilis* and long in *Gontarella* sp.

The brood-sac neck is also long in *Beania bilaminata* (Beaniidae) (Fig. 1.22). A brood chamber containing a late embryo occupies most of the coelom of the maternal autozooid. The chamber opening communicates with the environment independently of the vestibulum and is normally closed by an ooecial vesicle with a sclerite and stout muscle bundles. Strikingly, the ooecium in *Beania* is developed to varying degrees in different species studied. In *Beania* sp. it is formed at the expense of an underlying basal kenozooid that is budded from the maternal autozooid; in *B. bilaminata* a vestigial kenozooidal ooecium is retained as a small, somewhat bent, calcified hollow visor-like outgrowth at the distal edge of the maternal autozooid (Fig. 1.22). Overall, the structure of the brood chamber in this species is as in the calloporid genus *Cauloramphus* (Figs. 2.6b(E), 2.7b(C), and 2.25B) (Ostrovsky et al. 2007, 2009a).

A long neck also characterizes the brood sac of *Arctonula arctica* (Romancheinidae), which may contain two embryos at a time. In this instance, the chamber of the sac occupies most of the coelom of the maternal autozooid. The brood-chamber opening communicates with the environmental independently of the vestibulum, beneath the zooidal operculum.

Internal brood sacs develop in all Cupuladriidae. Sexual zooidal polymorphism is lacking and the neck of the brood sac communicates with the vestibulum. The distal wall of the vestibulum bears a cuticular thickening (flap) above the place where the neck opens into the vestibular cavity. This flap may act like a cover, plugging the brood chamber and providing additional isolation from the vestibulum (Ostrovsky et al. 2009b). In *Steginoporella perplexa* (Steginoporellidae), the brood sac is situated under the zooidal operculum as a large outpocket of the vestibulum. In *Watersipora subtorquata* (Watersiporidae) (Figs. 2.7b(E) and 2.47B), the neck of the brood sac and the vestibulum open to the exterior very near but independently of each other, contradicting the photos of Mawatari (1952) in which they fuse. This discrepancy could indicate that different species were studied. My data on *Cryptosula pallasiana* (Cryptosulidae) confirm Calvet's (1900) findings that the internal brood sac communicates with the vestibulum (Figs. 2.7b(D) and 2.47A).

In all the above species, there is no sexual zooidal polymorphism. In contrast, in *Chlidonia pyriformis* (Chlidoniidae), *Adeonella calveti* (Adeonidae) and *Reciprocus regalis* (Urceoliporidae), embryos develop in large female polymorphs. In the former species the brood sac and vestibulum fuse immediately beneath the zooidal operculum. In the latter two species the brood sac and vestibulum open independently and the inner vesicle plugging the entrance to the brood cavity has a sclerite. A similar cuticular thickening was found in *Pleurotoichus clathratus* (Euthyrisellidae), the fertile zooids of which are characterized by an unusually broad operculum base; its brood sac does not communicate with the vestibulum.

Thus, although probably evolving independently in different cheilostome families (Ostrovsky et al. 2009b; see also Sect. 2.4.8), internal brood sacs have obvious morphological similarities, differing mainly in mode of communication, presence/absence of the inner vesicle and its sclerite, and accompanying musculature.

2.3.4 Bivalved Ovicells

"Bivalved" brood chambers are characteristic of *Scruparia* and *Brettiopsis* (Scrupariidae), *Alysidium* (Alysidiidae), and *Thalamoporella* (Thalamoporellidae), which is why Hyman (1959) united them in a "two-valved" ovicell grouping. Earlier, Harmer (1926) had compared thalamoporellid ovicells with those of alysidiids, and Hastings (1941) noted simultaneous brooding of several embryos in "two-valved ovicells" in *Scruparia* and *Thalamoporella*.

Busk (1852) first reported the brood chambers of *Alysidium parasiticum* that were later studied in detail by Levinsen (1902, 1909). Each consists of two semispherical hollow plates or "valves", forming a protective chamber in the distal part (top) of the maternal zooid. Each valve is attached to the maternal zooid by a cuticular base that permits them to bend outwards. Levinsen (1902, p. 16) called these brood chambers "bivalvular" or "double-valved ooecia", interpreting their valves as equivalent to oral spines in non-fertile zooids. He subsequently showed that the ooecial valves are true kenozooids whose cavity is separated from the visceral coelom of the maternal zooid by a pore plate (Levinsen 1909, p. 66).

An unusually complex brood chamber (termed a synecium) of six flat plates (presumable kenozooids) was discovered by O'Donoghue (1924, p. 28) in the confamilial genus *Catenicula* (see also O'Donoghue and Watteville 1944, p. 423). The plates "all curve over the opesium" [sic] of the fertile zooid, forming "a globular basket-like arrangement in which the early development of the young animal takes place." Each plate is attached to the maternal zooid or an adjacent plate by an elastic cuticular joint. Hyman (1959, p. 337) considered this arrangement to be "related to the two-valved type". Cook (1979, p. 202) has used the modified term "synoecium".

In *Scruparia* (Scrupariidae), embryos are brooded in large terminal ovicells (Fig. 2.48). For instance, *Scruparia ambigua* has a high, galeate, terminally pointed ooecium (Fig. 2.48B, D) made of two halves. It has a medial longitudinal septum with a corresponding suture visible externally and internally, ending on the outer basal surface as an arched horizontal slit (Fig. 2.48C). The septum results from the medial fusion of two symmetrical, hollow, elongated lobes, the coeloms of which are completely separated from each other. They presumably communicate with the visceral coelom of the maternal autozooid via communication pores with pore-cell complexes in the distal wall of the latter, but, in the absence of fixed material, this could not be confirmed anatomically. If so, each ooecial lobe is a kenozooid budded from the maternal autozooid. The ectooecium is mostly membranous (except for the edges of each lobe), whereas the entooecium is completely calcified. Ovicells are semicleithral or acleithral (see Mawatari 1973a) – the ovicell opening is closed by the distal wall of the maternal autozooid with the operculum above it. The distal margin of the operculum is situated close to the proximal border of the ovicell but does not adjoin it.

The ovicells of *Thalamoporella* are distinctive. Levinsen (1902, p. 15) referred to them as "epistomial" but later considered them to be hyperstomial (Levinsen 1909). Harmer (1926, p. 291) suggested that they are non-homologous to hyperstomial ovicells in other Cheilostomata, proposing that they evolved from the "adoral tubercles" of the maternal zooid. Marcus (1941a, pl. 4, fig. 11) presented the stages of ovicellogenesis and a schematic of a longitudinal section of the ovicelled autozooid of *T. evelinae*. It gives the impression that the ooecium consists of three walls in this species. Marcus did not show any communication organs between ooecial and zooidal coeloms.

My study of *Thalamoporella* sp. showed that the ooecium of the cleithral ovicell is formed from the maternal autozooid, which has a larger orifice than non-ovicelled zooids (Fig. 2.49A, D). This is a special type of bivalved ovicell, formed at the frontal surface of the maternal autozooid around its orifice (see also Levinsen 1902; Harmer 1926). The intermediate stage of ovicellogenesis superficially resembles ooecial-fold development in calloporids (Fig. 2.49D). The calcified ooecium results from the fusion of two symmetrical, hollow hemispherical lobes along the midline of the ooecium, leaving a medial suture visible externally and internally (Fig. 2.49B, C, E, F, see also pl. 4, fig. 7 in Marcus 1941a). In contrast with the calloporid *Bryocalyx cinnameus*, in which the ooecial lobes are separated by a double longitudinal septum in the distal part of the ooecium, the lobes in *Thalamoporella* are separated by a septum only at the ooecial base (Fig. 2.49E); in the upper part there is no septum and the ooecial roof is thus complete even though the medial suture is retained (Fig. 2.49F). Waters (1909, p. 142) termed the ovicells of *Thalamoporella* "bilobate," but also stated that "there is no complete divisional wall in" them. The nature of the internal "wall" in the ooecium seen in the above-mentioned illustration of Marcus is puzzling since it was not shown in another of Marcus's figures (1941a, pl. 5, fig. 12a).

The ooecial coelom communicates directly with the visceral coelom of the maternal autozooid via two large, symmetrical arched openings at the sides of its aperture (Fig. 2.49C). Thus, in this case, although the ooecium is formed at the expense of the maternal autozooid, it is not a kenozooid but a paired outgrowth of the frontal zooidal wall.

2.3.5 Acanthostegal Brood Chambers

These structures, made of flattened mural spines, are known only in three living species of Tendridae (Cheilostomata) (Hincks 1892; Levinsen 1909; Ostrovsky and Taylor 2005a). Repiachoff (1875), Reinhard (1875) and Ostroumoff (1886a, b, c) studied them in *Tendra zostericola*. Although mistaken in their understanding of the construction of these brood chambers, and believing that embryos were developed inside the body cavity of specialized zooids, Repiahoff (1875) nevertheless suggested that they play the role of ovicells, and Reinhard (1875, p. 25) stated that "*Tendra* will represent a transition between bryozoans without ovicells to those that possess them". Ostroumoff (1886a) was the first to understand that the embryos are brooded in the space [epistege] between the frontal membrane and the over-arching spines in this species (see also Appendix I for historical review).

In *Tendra zostericola*, the brooding zooid produces a pair of articulated oral spines and, at the mural edge, two (sometimes one) lateral rows of horizontally inclined inarticulate spines that are flattened at the base. These long, pointed spines closely adjoin each other and the spines of the opposite row, forming the acanthostegal (literally "spine-roofed") brood chamber; the space between it and the underlying frontal membrane is the brood cavity (Figs. 2.50 and 2.59A). Each lateral row typically consists of 10–15 spines (up to 17 (Repiachoff 1875; Levinsen 1909), 13–18 (Occipinti Ambrogi 1981; Occhipinti Ambrogi and d'Hondt 1981)). The proximal edge is free of spines, providing an opening for oviposition and larval release (Fig. 2.50B). It may remain open but is usually closed by the operculum of the proximal (maternal) autozooid, as in the case of the cleithral ovicells of other cheilostomes.

The so-called brooding "zooids" of *Heteroecium amplectens* are a complex of two zooids – the proximal (maternal) autozooid (apparently an autozooidal polymorph) and a distal kenozooid (Figs. 2.51A, B and 2.59B). At the mural edge of the latter, up to 15–17 flattened inarticulate spines form the roof of the brood chamber, similar to the situation in *Tendra*. They closely adjoin each other, leaving no spaces between, their ends fusing along the midline of the kenozooid to form a low longitudinal keel. The brood chamber has the shape of an elongated hemisphere with a single proximal opening closed by the operculum of the maternal zooid, similar to cleithral closure in other cheilostomes. The brood-cavity floor is calcified, except for a proximal membranous area where there are two lateral outgrowths (Fig. 2.51C, D and 2.59B) facing the kenozooidal coelomic cavity. It may be conjectured that this area of kenozooidal frontal wall is a rudiment of the frontal membrane of the autozooid, with parietal musculature. The lateral outgrowths would then serve for attachment of these muscles (Ostrovsky and Taylor 2005a).

In conclusion, despite two and a half centuries of investigation, the general picture of cheilostome brood-chamber structure and development remains incomplete. The largest single published source of information is Levinsen's (1909).

This prominent researcher studied whole, sectioned and developing ovicells in more than 80 cheilostome species in 62 genera, but, since he mostly worked with cleaned bryozoan skeletons, his conclusions can be misleading (discussed in Silén 1945; Woollacott and Zimmer 1972a; Ostrovsky 2009). As a result, Levinsen's results have been rarely used, and careful restudy of these species is necessary. Ovicell anatomy should also be reinvestigated in some recently studied species. For instance, Nielsen's (1981) schematic of *Fenestrulina miramara* (as *F. malusii*), based only on the skeleton, differs from that presented Calvet (1900, fig. 21) in *Fenestrulina malusii* (as *Microporella*) based on decalcified sections. My data on *Fenestrulina* (see above) do not contradict these papers, but better, fixed material is required to draw definitive conclusions.

2.4 Evolution of Brood Chambers in Cheilostomata

The vast structural diversity of incubational chambers in cheilostome bryozoans led researchers to believe that these structures are not homologous in different cheilostome groups and that their similarities could be explained by convergence (Harmer 1926; Osburn 1950; Ryland 1974; Cook 1979; Cook and Hayward 1983; Reed 1991; Santagata and Banta 1996; see also Taylor 1988). If so, the questions to be answered are: How many times, when and in which lineages did embryo incubation evolve? How did different brood-chamber types evolve in cheilostomes and what were the main trends during their further transformation?

2.4.1 External Membranous Brood Sacs

The simplest brood chambers are external membranous sacs, although the questions surrounding their origin and wall composition are still open. Waters (1896 [1898], p. 4, pl. 1, figs. 1–3, 1913, pl. 64, fig. 1) discovered them (calling "ovicells") in *Aetea sica* (as *A. anguina* forma *recta*) and *A. anguina*, depicting them on top of the dorsal side of the erect portion in autozooids. In contrast, Robertson (1905, p. 246) recorded a "membranous bag", situated "on the ventral side" of the zooid "below the operculum but exterior to the aperture" in *A. anguina*. She suggested that the curvature of the tubular part of the zooid "afford[s]… protection to the delicate ooecium and its contents". In considering the "great transparency" and position of this brooding structure, Levinsen (1909, p. 93), concluded that "the supposed ovicellular wall [is] only … a shell membrane surrounding the egg," a view accepted by Ström (1977). Waters (1913) challenged it, saying that the position of all the brood sacs he saw was consistent. He referred to Osburn (1912), who also depicted the brood sacs at the top of the autozooid, distal to the operculum in *A. anguina*. Waters (1913, p. 464) additionally wrote: "One section shows the zooecial wall bulging out and the ovum partly in this portion, which is the commencement of the ovicell." Although membranous brood sacs have nothing to do with true ovicells, this observation is in accord with the later suggestion of Cheetham (personal communication in Cook 1977b) that this sac might be an outgrowth of the cystid wall with a coelomic space inside.

Further researchers have supported both opinions on the position of these "ooecia" or "ovisacs". It has been described as attached to the frontal membrane proximal to the operculum (Marcus 1937; Hastings 1943, pp. 471–472; Gautier 1962, p. 27; Mawatari 1973b, p. 413) and to the dorsal side (Marcus 1940, pp. 103–105; Cook 1968b, p. 137, 1977b, 1985) (reviewed in Prenant and Bobin 1966 and Cook 1968b). Problematically, all of the above authors have described the "ovisac" as either proximal or distal in the same species, *Aetea anguina* (see also Ryland and Hayward 1977; Cook 1985). Cook (1968b, p. 137) stressed that "the occurrence of ovisacs either in the dorsal or ventral position is remarkably consistent in the populations where they are abundant," suggesting also that different authors may in fact have been dealing with different species. For instance, among more than 100 membranous sacs studied by Cook (1968b, fig. 2D), all were dorsal, though asymmetrical (dorsal or dorsolateral). Occhipinti Ambrogi (1981) described these sacs as situated either proximal or distal to the operculum in *A. anguina* (also cited in Hayward and Ryland 1998). Both positions are also reported in *A. sica* (summarized in Ryland and Hayward 1977; Hayward and Ryland 1998; see also Prenant and Bobin 1966).

Hastings (1943) noted that sacs containing an early embryo were closely applied to the zooidal frontal membrane, whereas those with an advanced embryo were attached to the membrane by a narrow distal zone that is also evident in empty sacs (1943, fig. 57). Similarly, a narrow basal part of "the membranous ovicelligeous sac" was described and depicted by Mawatari (1973b, p. 414, fig. 1E, F). Also Hayward and Ryland (1998, p. 100) wrote that those "ovisacs" that were situated proximal to the autozooidal orifice were at first appressed to the frontal membrane, but later became free except for an attachment site proximal to the operculum. According to Cook (1977b, p. 59), the sac is "closely apposed to the dorsal part of the zooid body wall but attached only in its distal end."

Interestingly, Mawatari (1973b, p. 414) misinterpreted Busk (1849, but mistakenly referenced as 1884) as having observed a "membranous ovicelligeous sac" in *Aetea*, comparing it with "the bag of the pelicans beak". Busk's (1849, p. 125) text in fact speaks of the membranous frontal wall in this way, not the brood sac.

After studying anatomical sections of brooding *A. anguina* Cook (1977b, p. 59) stated that the "brood chamber is covered by a cuticular layer", and that there was no opening in sacs containing a developing embryo. In one population of this species, she also described and illustrated a slight proximal and ventral calcification of the sac wall on the side apposed to the zooidal wall, although it is not obvious if it is actual calcification in the only illustration published (Fig. 2.52, bottom). She suggested that the ovisac is a product of the exterior zooidal wall, not an external diverticulum of the tentacle sheath, since there is no tissue passing from the zooidal opening to the sac. Finally, she noted that, in a significant number of zooids, two embryos were simultaneously contained within and released from the same brood sac.

A similar type of brooding in "transparent membranous … ooecia … placed singly at the distal edge of the operculum" was recorded in *Eucratea loricata* (Eucrateidae) by Eggleston (1963, p. 29). This author also noted that "ooecia … appear to extend into the zooidal cavity", but his meaning is unclear. In his following paper Eggleston (1972, pp. 34–35) added, "the embryos are brooded singly in membraneous sacs above the orifice (as in *Aetea* spp.)" (see also Ryland and Hayward 1977; Hayward and Ryland 1998). Stach (1938, p. 397) discovered a similar type of external "brood-sac" in malacostegan-like "*Carbasea*" *indivisa* (family incertae sedis); each brooding zooid possesses 3–7 such sacs, "developed from the distal portion of the tentacle-sheath forming the inner wall of the operculum". Larvae presumably escape from the sacs through a rupture of the wall. Additionally, Gordon (1986, p. 45) recorded "1–2 membrane-bounded embryos" attached to the frontal membrane adjacent to the zooidal opening in *Leiosalpinx australis* (Leiosalpingidae).

The lack of constancy in the position of the external membranous sacs in *Aetea* (see above), the fact that they are present during the reproductive period only (Winston 1982) as external flexible transparent sacs without a cellular lining, and the apparent lack of an opening appear to support the suggestion of Levinsen (1909) and Ström (1977) that they are a fertilization envelope. Formation of sticky fertilization envelopes is known in a number of ctenostome brooders with external embryonic incubation (see Sect. 3.4.4). Against this idea is the partial calcification of the sac wall reported by Cook (1977b) (Fig. 2.52, bottom). Further study is necessary to check both hypotheses, but if Levinsen and Ström are correct, this is the most primitive variant of external brooding in cheilostomes, similar to that in some ctenostome bryozoans (discussed in Chap. 3).

External membranous brood sacs thus occur in different families and even suborders: *Aetea* (Aeteidae, suborder Inovicellina), *Eucratea* and *Leiosalpinx* (Eucrateidae and Leiosalpingidae, suborder Scrupariina), and "*Carbasea*" *indivisa* (family and suborder incertae sedis). All the species in these taxa have a simple anascan morphology, consistent with the idea that their incubation chamber is actually a fertilization envelope. Such a simple brooding mode might be the most primitive form of parental care that, as in ctenostomes, could have evolved in primitive anascans de novo or have been inherited from one or more ctenostome ancestors. For example, in a paper proposing polyphyly in Cheilostomata, Jebram (1992) conjectured that *Aetea* may be related to *Pottsiella*-like ctenostomes, which also brood embryos in external membranous sacs (Smith et al. 2003). Another primitive trait in *Aetea* is a small setigerous collar in the vestibulum, which, with few exceptions, is a ctenostome character (reviewed in Prenant and Bobin 1966; Banta et al. 1995; McKinney and Dewel 2002). A recent molecular analysis nested *Aetea* with primitive non-brooding (malacostegan) cheilostomes (Waeschenbach et al. 2012).

Despite their identical mode of brooding, the families Aeteidae (Inovicellata), Eucrateidae and Leiosalpingidae (Scrupariina) differ so much in zooidal morphology and the time of their inferred stratigraphic origination, that it would seem they acquired parental care independently. Further, in addition to species with membranous sacs, suborder Scrupariina currently includes genera with bilobate ovicells (*Scruparia* and *Brettiopsis*) (Scrupariidae). The question arises if this clade is natural then (see also Eggleston 1972). Molecular analysis should answer this question, but if yes, then ovicells, as more complex and advanced brood chambers, must have replaced membranous sacs in the evolution of parental care in this clade. It would also mean that very different brood chambers evolved twice in Scrupariina.

2.4.2 Origin of Brooding in Cheilostomata: Overview of the Major Hypotheses

According to Silén (1944, p. 21), the earliest brood chamber was an "embryo sack" or "embryonary" – an invagination of the body wall of the egg-producing zooid formed by "extensive inward migration of ectodermic cells". He considered this invagination as "homologous to the polypide bud" (p. 46). Later in evolution, the "embryo sack" moved towards the zooidal opening, while two oral spines of the maternal autozooid transformed to become an ooecium (Silén 1944, 1977; see also Ström 1977). This hypothesis was based on the finding of a brood sac on the body wall of the ctenostome *Labiostomella gisleni*, considered by Silén as a "protocheilostome" with many primitive characters (see also Silén 1942). Santagata and Banta (1996) justly criticized Silén's hypothesis as purely speculative in the absence of fossil evidence and data on oviposition. We may note that Silén (1944) considered all bryozoan brood chambers as homologous, and thus very ancient structures, interpreting the lack of brooding in some Recent cheilostomes (Malacostega) as secondary.

Santagata and Banta (1996, p. 178) proposed an alternative hypothesis, according to which "vestibular brooding preceded evolution of ovicells among cheilostomes." They suggested that, as in some ctenostomes, released zygotes stuck to the everted vestibulum of the polypide in the hypothetical "membraniporoid ancestor", being withdrawn into its cavity during polypide retraction. Embryo enlargement (as a result of placental nutrition via the vestibular wall) finally led to the removal of the embryo from the vestibulum. The latter was still partially connected with the embryo and transformed to the ooecial vesicle, phyletically accompanied by the origin of a skeletal incubation chamber (ooecium). These authors argued that the ooecium could have originated through "excavation or evagination" of the "proximal end of the next distal zooid" or/and modification of its proximal spine(s) to form the protective capsule (Santagata and Banta 1996, p. 177). It was also suggested that internal incubation [in internal brood sacs] evolved from vestibular incubation.

My own data and an analysis of the literature show that the ideas of Santagata and Banta (1996) concerning the vestibulum as the original receptacle for embryon incubation are based on a misinterpretation (Ostrovsky 2002; Taylor and McKinney 2002; Ostrovsky et al. 2006); vestibular or introvert brooding is unknown in cheilostomes as is external brooding accompanied by an everted vestibulum.

Dyrynda and King (1982, p. 337), who worked with *Epistomia bursaria* (Epistomiidae), suggested that the combination of intracoelomic incubation, "larval viviparity" and a single polypide generation is primitive. In their opinion, the subsequent origin of external brooding enabled polypide recycling, thereby increasing fecundity. This idea is not supported by paleontological data, however. Moreover, if the embryo is already protected by the zooid, the benefits of a shift to external brooding are dubious. It is much more likely that this mode of embryo incubation evolved secondarily (see also Sect. 2.4.8).

A fourth hypothesis was suggested by Hughes (1987), who thought that brood chambers were originally protective structures that later assumed the function of extraembryonic nutrition in some species. Hughes did not specify which brood chambers, but, since he was studying ovicells, he probably had them in mind. The variety of brood chambers, their distribution among cheilostomes and fossil evidence are supportive of this hypothesis. If true, the question arises, how did the ooecium evolve?

Harmer (1902) suggested that it originated from two oral spines of the maternal autozooid. Using Levinsen's unpublished data on the structure of the bivalved ooecium in *Alysidium parasiticum*, he speculated that ovicells were formed from two expanded oral spines whose bases communicate with the maternal zooid. Levinsen (1902) himself first supported then later criticized this view, leaning towards the idea that ovicells in *Alysidium* originate from two daughter autozooids (Levinsen 1909). Supporting Harmer's idea, Silén (1944, 1945, 1977) offered in support the paired initial calcification of the ovicell floor (interpreted to be a rudiment of allegedly lost spines) and the absence, in some species, of the two disto-medial oral spines in maternal autozooids initiating ooecium formation (see Harmelin 1973a). It should be noted that the latter argument is contradicted by the fact that some smittinid and microporellid species retain the distalmost oral spines until the end of ooecium formation, after which they break off or are resorbed (Soule 1973; Nielsen 1981) (see also Fig. 2.43D, F).

My data fully support the idea that the ooecium originated from modified spines. Harmer (1902), who was the first to suggest it, emphasized the striking similarity between the development of the ooecium and the frontal costae (modified spines) in *Euthyroides episcopalis* (discussed in Ostrovsky 1998, 2002). Spines as the basis of ooecium formation have been mentioned in several studies (Lang 1921; Larwood 1962; Ryland 1979, 1982; Santagata and Banta 1996; discussed in Ostrovsky 1998). The critical factor, however, is the zooid to which the ooecial spines belong. In the absence of paleontological and new anatomical data, compromise solutions were proposed. For instance, Ryland (1982, p. 463) wrote that the paired ooecial rudiment is formed at the expense of the maternal zooid and the unpaired at the expense of the distal zooid. In his opinion, this was associated with the possible origin of the ooecium from paired maternal oral spines in some species and from a "proximally situated spinelike zooid" on the distal zooid in others.

The above data and paleontological evidence do not support the idea that the ooecium originated from two oral spines. Instead, as Nielsen (1985) demonstrated, ooecium formation from the distal zooid is fundamental in cheilostomes. Thus, ooecia are derivatives of spines developing on the proximal wall of the distal zooid. Kenozooidal ooecia are budded directly from the maternal autozooid when the distal zooid is vestigialized (often accompanied by reduction of the ooecial fold itself) (see Sect. 2.2).

Lang (1921, p. xxxv) was the first to state explicitly that ooecia originate from modified periopesial spines (i.e. of the distal zooid): the "ovicell origin [in some cribrimorphs] from costae is evident." Larwood (1962) agreed. Santagata and Banta (1996) suggested that in *Bugula* and *Scrupocellaria* the ooecium may originate from one or a pair of proximal spines [of the distal zooid]. Braiko (1967) and Santagata and Banta (1996) also suggested that the acanthostegal brood chambers of *Tendra* may represent a primitive stage in the evolution of cribrimorph ovicells such as are found in *Figularia* (a similar opinion was earlier expressed by Reinhard 1875; see Sect. 2.1). Ostrovsky (2002) also considered this idea plausible, offering a detailed hypothetical explanation of how the space between the spinocyst and the frontal membrane of the distal zooid could be divided into a brooding and epistegal cavity in a *Tendra*-like ancestor. Subsequent new data on ovicell structure in fossil calloporids, cribrimorphs and monoporellids have refuted this hypothesis. Now we may be fairly sure that ooecia of the vast majority of cheilostomes originated from the mural spines of the proximal part of the distal autozooid in a calloporid ancestor (see Sects. 2.3.1.1 and 2.4.3), whereas tendrid brood chambers evolved independently (Ostrovsky and Taylor 2005a; see also Silén 1944).

Spines (articulated or non-articulated) are common in both fossil and Recent cheilostomes. Presumably they originated as protective structures (Larwood and Taylor 1981; Taylor 1999). A protective function is evidenced not only by their shape and position; it was experimentally shown that the formation, increase in number and size of spines (or spinules) may be induced by nudibranch predators, strong water turbulence or abrasion resulting from frequent contact between a colony and neighbouring algal thalli (Yoshioka 1982; Harvell 1984, 1986, 1992; Whitehead et al. 1996; Bayer et al. 1997; reviewed in McKinney et al. 2003).

Gymnolaemate spines are very varied, ranging from stout hollow structures interpreted to be modified zooids (kenozooids or spinozooids) to simple cuticular outgrowths of the membranous body wall (Smitt 1868, 1872; Nitsche 1871a, b; Calvet 1900; Levinsen 1909; Borg 1931; Cori 1941; Silén 1942, 1944, 1947, 1977; Ryland 1979, 1982; Harvell 1984, 1986). Whatever their origin, the spines/costae of all, but one Recent cheilostomes that have been studied are outgrowths of the zooidal body wall; there are no pore plates with specialized pore-cell complexes between hollow spines and the visceral coelom (Silén 1947; Bobin 1968; Ostrovsky 1998). In contrast, costae of *Bellulopora bellula* are supposedly true kenozooids. They have a long strip of hypostegal coelom confluent with visceral coelom of autozooid via a communication pore with a cuticular annulus identical to communication pores of Cheilostomata.

2.4.3 Early Stages in Ovicell Evolution

The fact that mural spines are situated around the frontal membrane indicates that their origin may have been associated with the protection of this most vulnerable part of the zooidal surface. Later, the spines on the proximal gymnocyst became specialized for the protection of the embryo.

Spinose and costate brood chambers are not uncommon among Cheilostomata. They were widespread in the Late Cretaceous (28 species). In the Cenozoic 19 other species are known, 11 of them Recent. Spinose and costate brood chambers are found in the families Calloporidae (*Distelopora*, *Unidistelopora*, *Gilbertopora*; see Sect. 2.3.1), Monoporellidae (*Stichomicropora*, *Monoporella*), Macroporidae (*Macropora*), Cribrilinidae (*Leptocheilopora*, *Craticulacella*, (?)*Thoracopora*), Tendridae (*Tendra*, *Heteroecium*) and in the genus *Bellulopora* (summarized in Ostrovsky and Taylor 2005a). As for their geochronological distribution, the timelines are as follows: Calloporidae – Early Cenomanian to Early Campanian; Monoporellidae – Early Cenomanian to Recent; Macroporidae – Late Eocene to Recent; Cribrilinidae – Early Cenomanian to Early Campanian; *Bellulopora* – Pleistocene to Recent. Acanthostegal brood chambers are known only in living bryozoans of the family Tendridae. Importantly, the three oldest superfamilies of brooding cheilostomes (Calloporoidea, Microporoidea and Cribrilinoidea) include Cenomanian species with primitive spinose or costate ovicells. Microporids and cribrimorphs are generally considered as calloporid descendants (Gordon 2000).

The earliest ovicells are recorded in the calloporids *Wilbertopora* and *Marginaria* from the Late Albian (Cheetham 1954, 1975; Taylor 1988; Cheetham et al. 2006). Strikingly, species belonging to these genera have complete ooecia (except for a medial suture in *Wilbertopora*) and appeared somewhat earlier in the geochronological record than known calloporids with spinose ooecia. Nevertheless, spinose ooecia are more primitive structurally, which indicates that they must have occurred in calloporids preceding those with complete ooecia. Such forerunners need not have occurred much earlier in time – it appears likely that the transition from spinose and costate ovicells to complete ooecia was relatively fast in geological terms, corresponding to the time gap between *Wilbertopora* (the earliest known cheilostome with ooecia) and *Distelopora* (the earliest cheilostome with spinose ooecia) (see Ostrovsky and Taylor 2004), i.e. about 10 million years.

As indicated, the main event in ovicell evolution was the modification of mural spines initially protecting the vulnerable membranous frontal wall of autozooids. A search for the ancestors of the first brooding cheilostomes leads us to Early Cretaceous bryozoans similar to *Spinicharixa* (see Taylor 1986). In this malacostegan genus ovicells are absent, but the opesia is surrounded by the bases of articulated spines. So, as in Recent malacostegans like *Villicharixa strigosa* (see Gordon 1989b) (Fig. 2.53), the frontal membrane in *Spinicharixa* and in the first cheilostome brooders was protected by a palisade of long spines. These spines also presumably protected eggs laid on the frontal surface of the distal zooid by the polypide of the maternal one. If the eggs were surrounded by sticky fertilization envelopes (see Sect. 3.4.3), this could additionally prevent their removal from the colony.

The first step towards a specialized brood chamber was bending or growth re-orientation of proximal spines towards the opening of the maternal zooid (Fig. 2.54A) (Ostrovsky and Taylor 2004, 2005a). Spinose ovicells with the simplest morphology are found in the Late Cretaceous genera *Distelopora* and *Unidistelopora* (Calloporidae) as well as in several *Stichomicropora* species (Monoporellidae). Their ooecia were represented by a straight or bent row of articulated spines on the gymnocyst of the distal zooid (Figs. 2.9, 2.10A, B, 2.54A, B, 2.55, 2.59C, D, 2.60A, and 2.62A, B, D, E, G, H, I, L, P). The bases of the medial spines of the ooecium are often situated close to or on the mural (opesial) rim of the distal zooid. Because of this, in *Distelopora* (as a rule) and in *Unidistelopora* (always) the bases of the mural spines of the distal zooid and those of the medial spines of the ooecium together form an uninterrupted row (Figs. 2.9B, D, 2.10A, B, and 2.62P), with the latter occupying the position of proximal mural spines. This circumstance is direct evidence for the origin of ooecial spines – they clearly evolved from mural spines.

Variations in the morphology and arrangement of ooecial spines throughout the Late Cretaceous demonstrate how transitions from simple to advanced character states may have occurred. A distally concave arch formed by the bases of the ooecial spines represents a less-derived character state, in essence corresponding to the arrangement of the usual mural spines in the proximal part of the opesia of the distal zooid (*Stichomicropora*; Figs. 2.55A–D and 2.62A, B). A more-derived character state is when most of the ooecial-spine bases are arranged transversely in a more or less straight line (*Stichomicropora*; Figs. 2.55A, C, D, and 2.62D, E). The next step, a distally convex arch of spine bases, characterizes species of *Stichomicropora* (Monoporellidae) (Figs. 2.55D–F and 2.62G, H) and *Distelopora* (Calloporidae) (Figs. 2.9A–E, 2.54A, and 2.62I, L). It should be stressed that all three basic stages can be found in a single species – Campanian *Stichomicropora* sp. 1, which had articulated spines similarly to calloporids (Figs. 2.55C, D and 2.62A, D, G) (Ostrovsky and Taylor 2005a, see also Taylor and McKinney 2002). Finally, a horseshoe arrangement of ooecial-spine bases is found in the calloporids *Distelopora spinifera* (Figs. 2.9F–H and 2.54B), *Unidistelopora krauseae* (Figs. 2.10A, B and 2.62P) and, sometimes *D. bipilata* (Fig. 2.9B). The monoporellid genus *Stichomicropora* is, in fact, younger than most of these calloporids, from which we may infer that the Calloporidae in the Late Cretaceous would have included species with ooecia having distally concave and transverse spine arrangements.

This morphoseries agrees well with the idea that the protective function of the ooecium was enhanced in the course of evolution. Proximally inclined ooecial spines, their bases arranged as a gently curving arch or a straight line, formed the roof of the ooecium, the brood cavity of which opened to the environment on three sides (Fig. 2.54A). In contrast, the horseshoe arrangement resulted in the formation of a cage-like ooecium opening on one side only (Fig. 2.54B) (see Ostrovsky and Taylor 2004, 2005a). Thus, a shift in ooecial-spine arrangement may have been associated with a change in function, that is, from protection of the membranous frontal wall of the distal zooid to more effective protection of developing embryos. This change required some of the spines to develop directly on the proximal gymnocyst of the distal zooid, beyond the edge of the opesia. This developmental variant is found, for instance, in the living malacostegan *Villicharixa strigosa* (Fig. 2.53B). Finally, ooecia could completely lose contact with the opesial rim; in some ovicells of *Distelopora bipilata* and *D. spinifera*, even the medial ooecial spines, usually located near the rim, may be positioned at some distance from it (Fig. 2.9H). In this instance substitute spines occupy the position on the opesial rim.

Further evolution of ovicells in calloporids was probably associated with a reduction in the number of ooecial spines to two, accompanied by their flattening and enlargement as well as the loss of articulation. Ooecia of *Gilbertopora larwoodi* consist of two costa-like lobes. Apart from the main ovicell opening, the brood cavity communicates with the external environment via two lateral foramina and a distal opening between the basal parts of the lobes (Figs. 2.10C–F, 2.54C, and 2.59E). The next stage is represented by complete ooecia with a medial suture, as seen in *Wilbertopora* (Figs. 2.11A, 2.12D–F, and 2.54D).

In addition to the species of *Stichomicropora* with articulated spines, similar variants of the position of ooecial spine bases also occurred in *S. ostrovskyi* and in the genus *Monoporella* with non-articulated ooecial spines being arranged in distally concave row. (Fig. 2.62C), across the daughter zooid (Figs. 2.56C and 2.62F) or in a distally convex arch (Figs. 2.57C, D and 2.62J). A reduction in spine number to two, accompanied by flattening, also occurred in both these genera (Figs. 2.57A, B, 2.60C, and 2.62M) (Ostrovsky and Taylor 2005a; Taylor and McKinney 2006).

Ooecium-forming costae in *Macropora* (Macroporidae) and *Leptocheilopora* (Cribrilinidae) are arranged in a semicircular or horseshoe pattern (Figs. 2.26, 2.28, 2.60D, and 2.62N–O, R) (Ostrovsky and Taylor 2004, 2005a).

2.4.4 Evolution of Ovicells in the Family Cribrilinidae

The existence of ovicells constructed of spines in calloporids and monoporellids is supportive of a monophyletic origin of these two groups, with Calloporidae basal. As was mentioned above, the Calloporidae in the Late Cretaceous would have included species with ooecia having a distally concave spine arrangement that was supposedly inherited by their monoporellid descendants. The further evolution of ooecia – involving a transition to the distally convex spine arrangement, loss of spine articulation, spine flattening and reduction in number – in both clades was probably independent (see above).

The semicircular arrangement of spines may also indicate a relationship between Calloporidae and Cribrilinidae (see Ostrovsky and Taylor 2004, 2005a). In the course of the further evolution of ovicells, the structure of spines in cribrilinids changed considerably – they lost their basal joints and became flattened. Thus, mural and ooecial spines transformed into costae. The scutum protecting the frontal wall in many species of Candidae is a good example of how spines can flatten to become a kind of shield (Silén 1977).

Theoretically, cribrilinids could have inherited ovicells from their ancestors according to two possible scenarios: (1) ovicells of early cribrimorphs could have been inherited from one or more calloporids that had ooecia with a horseshoe arrangement of spines (as in *Distelopora spinifera*); (2) in *Tricephalopora saltdeanensis* (Cribrilinidae) the ooecial surface appears to be implicitly costate (Lang 1922, pl. 1, fig. 7), appearing to retain traces of fused costae. These are not arranged in a horseshoe pattern (as in *Leptocheilopora*) but “linearly” (as in some *Stichomicropora*). If these traces are indeed left by fused costae, then cribrilinids, having inherited the linear/arched arrangement of ooecial spines from calloporids, evolved the horseshoe arrangement independently (as did calloporids and monoporellids).

In some species of the latter two families, the number of spines was reduced to two and the remaining spines became flattened and enlarged. In this way cribrilinids also independently underwent reduction in spine number to a single pair. On the one hand, not only fossil but also some Recent cribrilinids (genera *Figularia* and *Puellina*) possess costate ooecia, indicative of their origin (reviewed in Ostrovsky 2002). On the other hand, ovicells with bilobate ooecia (in cribrimorph genera *Puellina*, *Figularia*, *Filaguria*, *Corbulipora* and *Euthyroides*) are structurally more or less identical to those of the calloporids *Wilbertopora* and *Valdemunitella*. Moreover, the development of the ooecium from two originally independent ooecial halves/folds (demonstrated in *Corbulipora* and *E. episcopalis* and suspected in *Puellina* and *Figularia*) closely resembles ovicellogenesis in *Wilbertopora* and *Valdemunitella* (Gordon 1986; Ostrovsky and Taylor 2005b; Ostrovsky, unpublished data).

The presence of both costate and bivalved ooecia within the same genus (as in *Figularia* and *Puellina*) is especially remarkable. In this context, the transformation from spinose to bilobate ooecia in cribrilinids could be imagined to result from: (1) reducing the number of spines to two, their flattening and enlargement (as probably occurred in calloporids), or (2) fusion of spines and formation of the left and right ooecial halves. Judging from the external appearance of the ooecium in the Cretaceous cribrilinid *Leptocheilopora* sp. 2 (Fig. 2.26B, D), the two-lobed ovicells of cribrimorphs may have evolved by fusion of spines, as happened in spinocysts of more-advanced cribrilinids such as *Cribrilina* (see Ostrovsky and Taylor 2005a). Fusion of buds of forming zooids is well-known in Gymnolaemata (Jebram 1978); as long as they are not calcified, cystid walls can merge cuticular and cellular layers. Finally, both above variants could be realized in different cribrimorph groups (Ostrovsky et al. 2009a).

To summarize, the two-lobed ooecium seems to have originated independently in Calloporidae, Monoporellidae and Cribrimorpha. However, the evidence that this structure resulted from spine fusion is present only in cribrilinids (Ostrovsky and Taylor 2005a), and it is not known if this variant is basic. In the course of subsequent evolution (and in parallel with calloporids), both sides of the two-lobed ooecium in some cribrilinids fused to form a unitary ooecium with a common communication slit (*Cribrilina macropunctata*, *C. punctata*, *C. cryptooecium*, Ostrovsky, unpublished data). As in calloporids, the non-paired rudiment of the ovicell floor was retained in species with a bilobate ooecium, whereas the paired rudiment was probably independently evolved by cribrilinids together with the unitary ooecium (Ostrovsky and Taylor 2005b).

2.4.5 Evolution of Ovicells in the Genera *Monoporella* and *Macropora*

The loss of articulation, the flattening and fusion of ooecial spines and shift in their arrangement from distally concave to convex, were also characteristic of ovicell evolution in *Monoporella* (Monoporellidae) (Figs. 2.57, 2.60C, 2.61A, C, and 2.62J, M, see also above). In this genus, ooecial spines are also overgrown by a cryptocystal matrix (Figs. 2.57D–F and 2.61A, C, D) (Ostrovsky and Taylor 2005a). Secondary calcification similarly covers the ooecium in many ascophorans (see Sect. 2.3.2), producing more-robust brood chambers.

Better protection of embryos may be also achieved by closure of the brood-chamber opening. Early spinose ovicells appear to have been non-cleithral (non-closed), later transforming into acleithral (closed by the ooecial vesicle) then cleithral, with the ovicell opening closed by the operculum of the maternal autozooid. Lateral foramina in the ovicells of some species also became closed, as can be seen in transverse sections of *Monoporella* ovicells (Fig. 2.61A, C, D); the foramina are plugged by the membranous frontal wall of each laterally adjacent zooid so that the brood cavity is isolated from the environment (see also Cheetham and Cook 1983, fig. 72.2). It seems that lateral foramina were similarly plugged in ovicells of some species of *Stichomicropora*, whereas they remained open in others with a more-developed proximal gymnocyst (compare Fig. 2.55A, E, and C, D). This fact may explain why semicircular or horseshoe arrangements of ooecial spines did not evolve in monoporellids (Figs. 2.62A–H, J, M) – in contrast to calloporids and cribrilinids, the lateral openings became closed by the frontal membranes of the lateral zooids. Similarly, such openings (two lateral and one distal) were probably closed in the monoporellid *Monoporella multilamellosa* (Fig. 2.57A, B), which had an ooecium of two flattened, non-articulated spines (Figs. 2.60C and 2.62M). Lateral foramina were probably likewise closed by adjacent frontal membranes while the distal foramen was closed by that of the distal zooid. In contrast, lateral and distal ooecial openings in the calloporid *Gilbertopora larwoodi* with a similar ooecial structure most probably remained open (Figs. 2.10C–F, 2.54C, and 2.59E), with water able to enter the brood cavity.

In contrast, in *Macropora* (Macroporidae) the bases of ooecial spines are arranged in a horseshoe, while the ooecium has no lateral foramina (Figs. 2.58, 2.61B, E, and 2.62Q). At the same time, as in some monoporellids, the ooecial costae of macroporids are overgrown, exteriorly and completely, by a cryptocystal matrix, i.e. secondary calcification.

Zooidal morphology and especially the well-developed cryptocyst indicate that a species of *Stichomicropora* (with spinose ooecia) could have been ancestral to *Micropora* (Microporidae) (with complete ooecia) [both of these genera evolved in the Cenomanian] or these two genera could have shared a common ancestor. However, if this were the case, there should have been species of *Micropora* with spinose ooecia, demonstrating a transitional stage to a unitary ooecium as seen in Calloporidae, Monoporellidae and Cribrilinidae. So far, no such microporids are known and it is almost certain that the ancestral microporid inherited a complete ooecium from a calloporid precursor. To note, a medial suture has been found on the internal surface of the ooecium in *Micropora notialis* (Fig. 2.33E). I therefore formally propose a superfamily Monoporelloidea for the Monoporellidae (see Appendix II for diagnosis). The idea that *Macropora* could have evolved from *Micropora* (Banta et al. 1997) is not supported by any evidence, since the former has fundamentally costate ovicells and the latter has not; *Macropora* is also a considerably younger genus. *Macropora* could have evolved from *Monoporella* but the genera are separated by a time interval of 15–17 million years. At the same time, no *Macropora* species has the arched arrangement of ooecial spines and foramina characteristic of *Monoporella*. Nevertheless, the two genera have much in common and Macroporidae may provisionally be included in the Monoporelloidea.

2.4.6 Acanthostegal Brood Chambers of Tendridae and Ovicells of *Bellulopora*

The acanthostegal brood chambers of Tendridae appear to have evolved, as did the calloporid ovicell, by the modification of periopesial spines in a malacostegan ancestor. However, whereas the calloporid ovicell originated by differentially inclining of a small group of proximal opesial spines of the distal zooid towards the maternal autozooid, the tendrid brood chamber involved all of the periopesial spines of the distal autozooid. These mural spines are inclined towards the midline of the zooid to form a frontal shield (Figs. 2.50 and 2.59A). The uncalcified floor of the acanthostegal chamber in *Tendra* comprises the membranous frontal wall of the brooding (distal) zooid, in complete contradistinction to the calcified floor (proximal gymnocyst of the distal zooid) of calloporid ovicells (Ostrovsky and Taylor 2005a).

When describing *Heteroecium amplectens*, Hincks (1892, p. 333) quite correctly remarked that its “ribbed roofing … bears a close resemblance in structure of the front wall of the *Cribriline* zooecium, and like it has originated in a modification and adaptation of the marginal spines”. Tendrids, like cribrilinids, have both articulated oral spines and non-articulated costal spines that form the brood chamber. It is possible that acanthostegal brood chambers formed from costae were preceded by similar chambers formed from articulated mural spines.

The brood-chamber complex of *Heteroecium* (Figs. 2.51 and 2.59B), consisting of the maternal zooid and the distal kenozooid, structurally resembles ooecia formed by the distal kenozooid in Calloporidae, Cribrilinidae, Catenicellidae, Hippothoidae (e.g. Fig. 1.36B, C) and some other families. This means that the trend towards reduction of the distal zooid, characteristic of these cheilostome groups, is observed in tendrids as well (see Sect. 2.4.8). This trend is also found in *Macropora*, in which the ooecium may be formed by the distal autozooid or the kenozooid (Fig. 2.61B, E).

Bellulopora ovicells are unique. Their costae are kenozooids (see Sect. 2.3.1); the brood-cavity floor is uncalcified (Fig. 2.60E) and water enters the cavity freely as in fossil species with primitive ovicells and in *Tendra*. The ovicell floor may have lost calcification secondarily or is a rudiment of the membranous frontal wall of the distal zooid. If the latter is true, then the *Bellulopora* brood chamber evolved independently of ovicelled cribrimorphs in a manner reminiscent of Tendridae (from the distal zooid). It is not inconceivable that *Bellulopora* and *Tendra* are related (Ostrovsky and Taylor 2005a). It should be noted that the calcification of the brood-cavity floor (homologous to the frontal wall of the autozooid) appears to be secondary in *Heteroecium*. It has, however, retained a small membranous area (Fig. 2.51C, D), of uncertain function.

2.4.7 Evolution of the Unitary Ooecium and Frontal Shield

As discussed above, spinose brood chambers could have evolved three times in Cheilostomata (in Tendridae, Calloporidae and *Bellulopora*). Also, structural and developmental differences indicate that ooecia (and ovicells in general) could have evolved at least five times: in Scrupariidae (from a pair of distal kenozooids), Thalamoporellidae (from a pair of frontal outgrowths of the fertile autozooid), Alysidiidae (from two to several distal kenozooids), *Bellulopora* (from kenozooidal costae) and Calloporidae (from articulated mural spines). Ooecia constructed of spines (the latter variant) were obviously inherited by monoporellids and cribrimorphs. Reductions in the number and flattening of spines, the acquisition of the distally convex arrangement of spine bases, loss of articulation, fusion of costae and immersion of the ovicell floor apparently occurred independently within Calloporoidea, Monoporelloidea (Monoporellidae and Macroporidae) and Cribrilinoidea, all of these trends being expressed in them to varied degrees (Ostrovsky and Taylor 2005a).

Given that spinose and costate ooecia are the ancestral structural variant, further evolution resulted in first, bilobate and then unitary (complete) calloporiform ooecia (see Sect. 2.3.2). An example of such a transition to unitary ooecia is provided by fossil and Recent calloporids. *Wilbertopora* (Albian–Cenomanian) and *Gilbertopora* (Cenomanian) are characterized by bilobate ooecia and a pair of communication openings, while *Callopora*, which evolved in the Cenomanian and survived until the present, has a complete ooecium and a common communication slit (later reduced to a pore). In Recent calloporid genera such as *Alderina*, *Callopora*, *Concertina*, *Crassimarginatella*, *Corbulella*, *Copidozoum*, *Retevirgula*, *Leptinatella* and *Bryocalyx* (see Canu and Bassler 1933; Prenant and Bobin 1966; Harmelin 1973a; Gordon 1986; Tilbrook 1998; Cook and Bock 2000), ovicells have a medial suture or a keel, demonstrating different degrees of fusion of ooecial lobes (summarized in Ostrovsky 2002). For instance, the ooecial base is complete (with no traces of the paired origin) in *Concertina* and *Bryocalyx*, whereas the proximal edge is bilobate. In *Corbulella maderensis* a short medial keel is retained on the inner ooecial surface. In *Callopora lineata* and *Tegella unicornis* there is instead a medial groove in the proximal ooecial rim. In Recent *Valdemunitella* ooecia are bilobate, with narrow bases and a pair of communication slits as in confamilial *Wilbertopora* from the Middle Cretaceous. The ooecial rudiment (initial calcification of the ovicell floor) is single in species with bilobate ooecia and paired in those with complete ooecia (see Sect. 2.3.2).

A similar transition from bilobate to complete ooecia presumably occurred among cribrimorph cheilostomes. Species of *Figularia*, *Euthyroides* and *Corbulipora* have bilobate ooecia with lateral communication slits and a single ooecial rudiment, which is very similar to that in the calloporid *Wilbertopora* (Ostrovsky and Taylor 2005b). Ovicells in most Recent cribrimorphs (e.g. *Membraniporella*, *Cribrilina*, *Puellina*, *Collarina*, *Reginella*) and some early fossil cribrimorphs (e.g. *Pliophloea*, *Anaptopora*, *Monoceratopora*, *Lagynopora*, *Castanopora*) have a more or less expressed medial suture and/or keel, indicative of fusion of ooecial halves (summarized in Ostrovsky 2002). Sometimes the medial suture is mostly visible at the inner ooecial surface (*Cribrilina annulata*) (Ostrovsky 1998). Thus, traces of paired ooecial structure have been retained throughout bryozoan evolutionary history. At the same time, some cribrilinids have a complete ooecium, a common communication slit and a paired rudiment of the ovicell floor (*Cribrilina cryptoecium*, *C. punctata*) (see also Sect. 2.4.4).

Thus, the most advanced ooecial morphology (unitary) appears to have been acquired independently in Calloporidae and Cribrilinidae. As the latter family is considered ancestral to the former (Silén 1942; Gordon 2000), this trend may be regarded as exemplifying parallelism.

The calloporiform ooecium co-occurs with all known types of frontal wall – simple anascan (malacostegan), cryptocystal (coilostegan), spinocystal (cribrimorph), gymnocystal ascophoran (hippothoomorph), and umbonuloid and lepralioid ascophoran – in which a relatively wide area of proximal gymnocyst does not prevent the formation of an arch-like ooecial outfold. A narrow ooecial base of lepralielliform ooecia forming on a “wide” proximal gymnocyst is known only in bugulids and the causes of this modification are uncertain. It is clear only that these ooecia evolved in Bugulidae independently from advanced ascophorans with a similar narrow ooecial base.

The transition from a calloporiform to an escharelliform ooecium may have first occurred in a coilostegan. Taxonomically, its lineage would presumably have been within the calloporidae (see, for instance, Voigt 1991), in which there was a gradual expansion of the cryptocyst beneath the membranous frontal wall (reviewed by Silén 1942). In contrast, the calcification of the ectooecium shows varying degrees of reduction. The evolution of the escharelliform ooecium in microporids was accompanied by fusion of the entooecium with the cryptocyst and the establishment of direct communication of ooecial and hypostegal coeloms. The loss of ectooecial calcification and fusion of the ooecial floor with the zooidal cryptocyst (Fig. 2.63B, C) resulted in closure of the ooecial communication slit once the ooecial fold was formed (Fig. 2.63D). In this situation, ooecial epithelia could remain viable only if ooecial and hypostegal coeloms were united. All stages of the calloporiform–escharelliform transition are found in the Microporidae (Fig. 2.63A, D; see also Figs. 2.33 and 2.34), with the less-derived calloporiform condition occurring in *Micropora*. For instance, the ectooecium in the majority of species in the ancient families Microporidae and Onychocellidae (Microporoidea) is mostly uncalcified (as a rule, only the proximal rim is calcified) (Figs. 2.33, 2.34, and 2.63). In many species ooecia also have direct communication with the hypostegal coelom of the distal zooid, and the ovicell floor is fused with its cryptocyst (Figs. 2.34 and 2.63D). Genera such as *Onychocella* and

Aechmella (Onychocellidae) had this type of ooecium as early as in the Cenomanian (Voigt 1989). The genus *Micropora* evolved at the same time, but there is currently no information about the ooecium in any Cenomanian species. Presumably it was calloporiform, with a calcified ecto- and entooecium and the ooecial coelom connected with the visceral cavity of the distal zooid (as in Recent *Micropora gracilis*) (Fig. 2.63A).

There is no obvious reason why the ectooecium would have trended towards reduced calcification (see Sect. 2.4.8). There may have been a shift in the locus of the calcium carbonate deposition consequent upon evolution of the coilostegan cryptocyst – the more $CaCO_3$ is deposited into an enlarging cryptocyst, the less it is deposited into the ectooecium, which would make sense energetically.

The endotoichal ovicells of Cellarioidea are structurally similar to the ooecia of Microporidae and Onychocellidae. Common features include a lack of ectooecial calcification, communication of ooecial and hypostegal coeloms and fusion of the entooecium with the cryptocyst of the distal zooid(s) (compare Figs. 2.34 and 2.39). Endotoichal ovicells were probably formed by immersion of the ovicellar brood cavity in the colony (see Sect. 2.3.2), which is one of the major trends in the evolution of brooding structures in Cheilostomata. Another important aspect of endotoichal ovicell evolution was the development of the ooecial vesicle, which formed a sac inside the brood cavity. That this sac is a modified ooecial vesicle is evidenced by the presence of the sclerite and numerous muscle bundles within it. These considerations are supportive of the origin of the endotoichal ovicell within Microporoidea, including the evolution of Cellarioidea (known since the Santonian) from an ancestor within Microporidae (known since the Cenomanian). The specific hypothesis that *Cellaria* evolved from *Micropora* (Banta et al. 1997) is supported by a comparison of ooecial structure.

The primitive calloporiform ooecium is found in umbonulomorph and lepraliomorph ascophorans. It is the basic ooecial type from which escharelliform and lepralielliform variants evolved in ascophorans. As mentioned earlier in this chapter, the latter two variants are also both found in umbonulomorphs (including the family Lepraliellidae) and lepraliomorphs.

According to the least-contradictory and best-supported hypothesis, the lepralioid frontal shield repeatedly evolved from umbonuloid precursors. The umbonuloid shield itself apparently originated when frontal (adventitious) kenozooids overgrew the zooidal spinocyst of cribrimorphs (Fig. 2.64A1). Kenozooids like these have been found in cribrimorphs from the Cretaceous (including the Santonian) to the Holocene and the present day (Gordon and Voigt 1996; Gordon 2000). Thus, in accord with this hypothesis, umbonulomorph ancestors would have been cribrilinoidean taxa with a calloporiform ooecium (Figs. 2.64A2, C) inherited by the early umbonulomorphs. For instance, the combination of a calloporiform ooecium and umbonulomorph frontal shield exists in some Recent Arachnopusiidae.

It is likely that the early progressive development of frontal kenozooids and the formation of hypostegal coelom (derived from the laterally expanded kenozooidal coelom) of the frontal shield influenced the formation of the ooecial fold, thus reducing the size of the ooecial base. In the calloporiform ooecium the ooecial fold starts its formation around the simple gymnocystal floor of the future brood chamber, whereas in the lepralielliform variant formation of the fold begins much earlier, with the ovicell floor placed (partially or completely) above the horizontal part of the ectooecium and the frontal shield (compare Figs. 2.22 and 2.41). The "double disc" developmental stage characteristic of the latter variant is in fact a somewhat more compact version of the ooecial fold of calloporids and cribrimorphs (compare Figs. 2.18 and 2.40). Reduction of the ooecial base influenced the shape and size of the communication pores – a central pore was formed instead of an arched slit. Expansion of the frontal kenozooids accompanied by the diminution of the ooecial base resulted in coordinated development of the umbonulomorph frontal shield and the lepralielliform ooecium (Fig. 2.64B), characteristic of some Recent species from the families Arachnopusiidae, Lepraliellidae, Bryocryptellidae and Umbonulidae. In the latter family, species of *Rhamphostomella* exhibit this reduction to varying degrees (Fig. 2.41). It may be additionally supposed that the kenozooids that formed the umbonuloid shield overgrew not only the cribrimorph spinocyst but also the ooecial base and the ooecium itself, giving rise to secondary calcification.

Paralleling the transformation in the anascan family Microporidae, the escharelliform variant in umbonulomorphs presumably evolved from a calloporiform ooecium (Fig. 2.64C). This would have involved a reduction of ectooecial calcification and fusion of the basal part of the entooecium (ovicell floor) with the proximal part of the calcified wall of the frontal shield. The combined umbonulomorph frontal shield and escharelliform ooecium thus emerged (Fig. 2.64D). The ooecial coelom began to communicate with the hypostegal coelom of the distal zooid, and the communication canal between the ooecium and the visceral coelom was closed (with few exceptions, see Sect. 2.3.2). Among others, this type of ooecium characterizes modern species of Lepraliellidae and Romancheinidae (Figs. 2.35 and 2.36).

According to Gordon and Voigt (1996) and Gordon (2000), the lepraliomorph frontal shield (whether pseudoporous or centrally imperforate) originated by progressive reduction of the umbonuloid component by the distal expansion of the proximal part of the frontal shield (gymnocyst concealed by transformed frontal kenozooids) and ascus formation. Some lepraliomorph cheilostomes (few smittinids, see below) have calloporiform ooecia (Fig. 2.64E), perhaps inherited from umbonulomorph ancestors (Fig. 2.64A2). As described above in umbonulomorphs, the early establishment of the frontal shield and hypostegal coelom may have resulted in reduction of the basal part of the ooecium, origination of the "double disc" stage and corresponding changes in communication structures. This trend is easily traceable in *Smittina* – ooecial and visceral coeloms communicate via an arched slit in *S. antarctica* with a calloporiform ooecium, while all other studied species of the genus have a central pore in combination with either a calloporiform or lepralielliform ooecium; correspondingly, the simple gymnocystal part of the ovicell floor is developed to a different degree in *Smittina*, as in umbonulomorph *Rhamphostomella* (Ostrovsky, unpublished data). The combined lepralioid frontal shield and lepralielliform ooecium, found in Smittinidae and Bitectiporidae inter alia, may have evolved in this way (Fig. 2.64F).

Another combination is that of the lepralioid frontal shield and the escharelliform ooecium (Fig. 2.64G), found in some cheilostome families (see Sect. 2.3.2). If we accept that the lepralioid frontal shield evolved from an umbonuloid precursor and the escharelliform ooecium evolved from a calloporiform precursor, then we may suggest that the lepralioid/escharelliform combination could have evolved from (1) early lepraliomorphs with a calloporiform ooecium (Fig. 2.64E) or (2) umbonulomorphs with an escharelliform ooecium (Fig. 2.64D).

The above hypothetical scenarios of ooecium evolution in lepraliomorphs do not contradict Gordon and Voigt's (1996) and Gordon's (2000) ideas about the polyphyletic origin of this morphological grade. Moreover, the fact that there are different variants of ooecial structure among lepraliomorphs may indicate that lepralielliform and/or escharelliform ooecia could have been inherited from different umbonuloid ancestors that also possessed them.

The microporelliform ooecium and the variant described in *Fenestrulina* are found only in the Schizoporelloidea (e.g. Microporellidae, Pacificincolidae, Schizoporellidae, Myriaporidae, Porinidae). These variants may demonstrate stages in the transformation of the lepralielliform ooecium. Ooecial structure in *Fenestrulina* may be interpreted as transitional between lepralielliform and microporelliform (Fig. 2.65) (*Fenestrulina* and "microporelliform" taxa have a single initial calcification of the ovicell floor). *Fenestrulina* and *Microporella*, exhibiting two variants of ooecial structure, belong to the same family Microporellidae.

As with the escharelliform ooecium (Fig. 2.64C, D and above), the presumed transition from calloporiform to microporelliform may have occurred through reduction of ectooecial calcification, fusion of entooecium with the frontal shield, and consequent loss of communication between ooecial and visceral coeloms but establishment of communication between ooecial and hypostegal coeloms (Fig. 2.65). In *Fenestrulina*, with its intermediate structure of ooecium, the latter coeloms are separated, as indicated by an ooecial communication pore and calcareous ectooecial thickening around the base of the vertical part of the entooecium (Figs. 2.1, 2.45, and 2.65B; see also Nielsen 1981). Later in evolution, the entooecium fuses with the calcified wall of the lepralioid frontal shield of the distal zooid via several calcified bars (Figs. 2.43E, F and 2.65B). Further modification towards the microporelliform ooecium may have led to the establishment of the connection between ooecial and hypostegal coeloms and loss of the communication pore. The calcified wall of the frontal shield partly fuses with the ovicell floor via knob-like outgrowths, while the entooecium thickens as a consequence of overgrowth by the calcareous matrix of the frontal shield (Fig. 2.65C).

As in the vast majority of cheilostomes with calloporiform and lepralielliform ooecia, those of *Fenestrulina* are formed at the periphery of the colony, possibly indicating a connection between these structural variants. As the microporelliform ooecium evolved, calcification of the entooecium began to proceed independently of that of the distal frontal shield. Thus, in some families (Microporellidae, Schizoporellidae) ooecia are formed several zooid rows distant from the colony periphery. In contrast, ooecia begin their formation on peripheral zooids in the Pacificincolidae and Porinidae (which have the same ooecial structure) in association with the proximal part of the developing frontal shield.

2.4.8 Major Trends in the Evolution of Cheilostome Ovicells

The origination of new ooecial variants and new patterns of ovicellogenesis were accompanied by a number of additional changes characteristic of the evolution of brooding structures. These changes occurred independently in different cheilostome families, though in some cases they may be indicative of relatedness among distant groups.

2.4.8.1 Integration of Ovicell-Forming Zooids

A major trend in the evolution of brooding in Cheilostomata was the integration of maternal (egg-producing) and distal (ooecium-producing) zooids (sometimes reduced to kenozooidal ooecia) as or within a special morphofunctional module – a "colonial organ" of reproduction or cormidium in the terminology of Beklemishev (1969). A close connection between these two zooids is ensured not only morphologically but also hormonally, resulting in a high degree of synchronization of their development and functioning (oogenesis, oviposition, brooding). In such a cormidium the ooecium (formed by the daughter zooid) plays the role of the protective capsule and the ooecial vesicle (formed by the maternal zooid) isolates the brood cavity from the external medium and, in the case of matrotrophic species, also ensures extraembryonic nutrition.

In most ovicellate cheilostomes, this complex is formed by two successively budding zooids. At the same time, in Monoporellidae, the non-calcified frontal walls of the two distolateral zooids that close the lateral foramina play an important role in the isolation of the brood cavity from the environment. In this way, the maternal, distal and neighbouring zooids are combined into a "cluster of polymorphic autozooids forming [the] brooding structure" (Cheetham and Cook 1983, p. 166, fig. 72.2; Ostrovsky and Taylor 2005a; see also Sect. 2.4.5). In Cellariidae the brood cavity is limited by the walls of 2–3 distal and/or distolateral zooids, and so the entire complex consists of 3–4 zooids. Similar cormidia independently evolved in *Heterooecium* (Tendridae). Its acanthostegal brood chambers comprise an egg-producing autozooidal polymorph and a distal kenozooid that forms a costate brood chamber.

Interestingly, the highest level of integration associated with the formation of brooding structures can be found in some rectangulate Cyclostomata, in which large, colonial brood chambers occur (Borg 1926; Beklemishev 1969; Schäfer 1991; Reed 1991).

2.4.8.2 Reduction of Ectooecial Calcification

Levinsen (1909) was the first to pay attention to differences in ooecial-wall calcification in cheilostomes. For instance, in *Callopora* there are species with a completely calcified ectooecium (*C. minuta*, see Harmelin 1973b) and species in which it is mostly membranous with only the base calcified (*C. dumerilii*; see Levinsen 1909; Prenant and Bobin 1966; Zabala and Maluquer 1988; Ostrovsky and Schäfer 2003; Ostrovsky et al. 2003, 2009a). While the early calloporids *Wilbertopora* and *Gilbertopora* have a completely calcified ooecium, most Recent calloporids have cuticular windows of different sizes and shapes in their ooecia. Analysis of the literature and my own data show that most cheilostome families are characterized by some degree of reduction of ooecial calcification. This reduction is expressed as membranous windows or pseudopores or as a complete loss of calcification of the ectooecium, which then often becomes a direct continuation of the non-calcified frontal membrane of the distal zooid (in escharelliform and microporelliform ooecia). All these facts indicate the presence of an evolutionary trend towards gradual reduction of ectooecial calcification, expressed within the order Cheilostomata independently in several distant lineages.

Such an evolutionary trend begs the question of the biological expedience of lessening of the mechanical strength of a protective structure. Calcification has an energetic cost and reducing it can be an advantageous trade-off in favour of some other benefit. Inter alia, the formation of ovicells increases overall colony volume and existing non-calcified surfaces may become insufficient for normal gas exchange. Cuticular windows in ooecia might mitigate this negative aspect, an idea indirectly supported by the fact that secondary calcification, characteristic of many cheilostomes, does not typically overgrow non-calcified ooecial areas such as pseudopores and membranous windows; for example, in Smittinidae, Umbonulidae (Fig. 2.41A) and Bitectiporidae secondary calcification does not close the ovicell roof where pseudopores are located. Significantly, Navarrete et al. (2005) noted a latitudinal trend in the number of pseudopores in the ovicells of *Celleporella* species along the Chilean coast, suggesting that the north–south decline was modulated in relation to temperature and dissolved oxygen.

Levinsen (1909) noted that the calcified entooecium is usually thicker in species with a membranous ectooecium and my data would seem to confirm this. In such cases, ooecial structure is like that of a frontal zooidal shield with a hypostegal coelom (Sandberg 1977). Such shields are developed in a majority of cheilostome species, even though the outer (frontal) wall is non-calcified, and it is apparent that such an arrangement must be advantageous. [Inter alia, it allows for the possibility of frontal budding and colony strengthening (Gordon and Voigt 1996).] Since the gap between the outer membraneous wall and the underlying skeletal wall is very small, the whole construction has a high assurance factor. The pressure exercised upon the surface of such a frontal complex would be instantly transmitted to the calcified wall. At the same time, gas exchange is not hindered in any way. The situation in ovicells may be analogous (Figs. 2.34, 2.36, 2.44, and 2.45) (Ostrovsky et al. 2009a).

2.4.8.3 Reduction of the Distal Ooecium-Producing Zooid

This trend in brood-chamber evolution culminated in terminal ovicells and kenozooidal ooecia; (1) In the former case the ooecium is formed by the distal kenozooid, which constitutes the base of the brood chamber. The distally protruding part of the kenozooid is absent (Figs. 1.30B, 1.36, 2.6a(C, E), b(D, F), 2.23, and 2.42). (2) In the latter case the only part of the distal kenozooid remaining in kenozooidal ooecia is a small area (the originating "chamber") at the site of contact with the maternal autozooid (Figs. 1.22, 1.25A, 2.6a(D), b(A–C, E), 2.7b(C), 2.25B, and 2.29).

In many cheilostome genera and families, terminal ovicells co-occur with ooecia formed by distal autozooids, kenozooids (with the distal part protruding) and avicularia. Moreover, ovicells of two different categories may be found within a single species or colony (in *Cribrilina punctata*, *Puellina harmeri*, *Callopora craticula*) (see Levinsen 1909; Ristedt 1985; Harmelin and Arístegui 1988; Bishop 1994; Ostrovsky et al. 2009a). In some other taxa the ooecia are always formed by the distal kenozooid

(*Euginoma*, *Didymozoum*, *Anoteropora*, hippothoomorphs, Celleporidae, etc.) or only the kenozooidal ooecium is present (*Cauloramphus*) (Ostrovsky et al. 2007).

Notwithstanding, why is the distal (auto)zooid reduced and terminal ovicells formed? According to Bishop and Househam (1987), the transformation of one type of ooecium into another is not an overly complex evolutionary step. Judging from the fact that two categories of ooecia may be present in one and the same colony, this supposition is likely to be true. Nevertheless, the reasons for the reduction of the distal zooid remain obscure.

The developing ooecium-producing distal zooid bud is structurally identical to a kenozooid with an ooecium (compare Figs. 2.6a(B) and 2.18F). The origin of this type of ooecium (type 1, category B) may be associated with the cessation of distal autozooidal development after ooecium formation. Why development ceases is, however, unclear. Harmelin and Arístegui (1988) suggested that the formation of terminal ovicells of category C (sensu Bishop and Househam 1987) may be indicative of an r-strategy. Conversely, ovicells that are a product of two autozooids (category A) indicate a K-strategy. In other words, they concluded that, whereas terminal ovicells (first variant) ensure rapid formation of ooecia (and early brooding), normal ovicells (second variant) are formed less quickly but provide better protection for the embryo.

In many instances ooecia formed by the distal kenozooid develop only at the colony periphery (in some Calloporidae and Cribrilinidae) or on terminal areas of branches (in some Calloporidae, Flustridae and Catenicellidae). For example, terminal kenozooid-produced ovicells can be found at the colony periphery in *Callopora* while autozooid-produced ovicells occur at some distance from the periphery. It appears that further budding of distal autozooids at the colony periphery is suppressed at the end of the growth period of the whole colony, and because of that ooecia are formed by the distal kenozooids there. This means that, at least in some cases, terminal ovicells may result from age-related and/or astogenetic changes. On the other hand, in hippothoomorphs, Celleporidae and Crepidacanthidae, the formation of terminal ovicells does not depend on cessation of colony growth, since these are the only kind of ovicells in the colony (Ostrovsky et al. 2009a). Corresponding examples among cribrilinids are *Cribrilina annulata* and *C. watersi* and, among chaperiids, *Chaperiopsis cervicornis*.

Insofar as all hippothoomorphs and the families Celleporidae and Crepidacanthidae have terminal ovicells, they probably inherited this character from their ancestors. If so, the taxa of special interest would be those in which this trend is best represented. Unsurprisingly, these are the most ancient lineages of brooding cheilostomes – Calloporidae, Microporidae and cribrimorphs. Three categories of ooecia are found among them as well as in the stratigraphically younger Bugulidae and Catenicellidae. This is unambiguous evidence that terminal ovicells evolved independently in different cheilostome clades by reduction of the ooecium-producing zooid.

To return to the earlier question concerning the reason for reduction of the distal zooid in cases when growth processes are not an explanation – it may be conjectured that the evolution of terminal ovicells, which culminated in kenozooidal ooecia (as in *Cribrilina annulata* and *Cauloramphus*), was associated with immersion of the brood cavity into the colony (between zooids), which afforded better protection. Comparative morphology shows that the brood cavity of terminal ovicells is situated further below the colony surface than that of hyperstomial ovicells formed by the distal autozooid (compare Figs. 2.6a(A, B, D, E) and b(A, B). Thus, reduction of the distal zooid resulted in both immersion of the brood cavity and in a transition from prominent to terminal ovicells (corresponding to endozooidal and immersed ovicells as regards the position of the brood cavity).

In the earliest stage of this transition, the distal autozooid was substituted by the distal kenozooid. Its degree of reduction in different species varies, and terminal ovicells are not always formed. Further reduction of the distal zooid resulted in kenozooidal ooecia in some taxa, with the brood cavity situated inside the maternal zooid (Figs. 2.6b(A, B) and 2.29). In some cases the ooecium was reduced to a vestigial kenozooidal ooecium, as in *Cauloramphus* (Figs. 2.6b(E) and 2.25B; see also Ostrovsky et al. 2007) and some Beaniidae (Fig. 1.22). In some species the kenozooidal ooecium may still bud distal zooids (Fig. 2.6b(B); see also Ostrovsky 1998), while in others distal budding proceeds from the basal pore chambers of the maternal zooid (Fig. 2.6b(C, E)).

The proportion of umbonulomorph and lepraliomorph families and genera among bryozoans with terminal ovicells is on the whole strikingly low. One family that does not conform to this rule is Celleporidae; all studied species have ooecia formed by the distal kenozooid without distally distinct frontal part (Figs. 2.6b(F) and 2.42).

2.4.8.4 Immersion of the Brood Cavity and Reduction of the Ooecium

As noted above, many brooding cheilostomes are characterized by immersion of the incubation cavity in the maternal or distal zooid or in the colony (between zooids). This immersion, presumably ensuring better protection of the developing embryo, may be implemented in several ways. Apart from terminal ovicells, it may be achieved by the formation of a more concave ovicell floor, formed by the distal zooid, representing the gradual transition from hyperstomial to subimmersed to endozooidal (see Viskova 1992) or endotoichal ovicells. A third possibility involves invagination of the distal wall of the maternal zooid, accompanied by reduction of the calcified brood-cavity floor and thus the transition to immersed ovicells. Later, endozooidal and immersed ovicells could serve as the basis for the evolution of internal brood sacs. A fourth way is associated with overgrowth of the ooecium by secondary calcification. The effect is similar – the brood cavity becomes immersed, in this case into the frontal shield of the distal zooid.

Analysis of the literature and my own data indicate a trend towards immersion of the brood cavity, accompanied by reduction and, in some cases, the complete disappearance of the ooecium. These changes occurred repeatedly within the Cheilostomata (Ostrovsky and Taylor 2004). Levinsen (1909, p. 72) and Harmer (1926, p. 405) were the first to note that related, sometimes congeneric, species may exhibit both well-developed ooecia and reduced ooecia or none at all. Hastings (1964, p. 250) also discussed the simultaneous presence of hyperstomial and the "reduced and vestigial ovicells" within the same cheilostome genera (see also Cook 1968a). It is important to note that, while Harmer (1926, p. 202) wrote concerning "the entozooecial ovicell … to have preceded the hyperstomial ovicell in evolution, and to have given rise to it", on page 405 he described "forms with well developed ovicells, which are in a course of reduction in this genus, as has probably occurred in other lineages of cheilostome evolution".

Among the bryozoan groups that I have studied, this trend is most prominent in the Calloporidae, in which hyperstomial (*Wilbertopora*, *Gilbertopora*, *Callopora*, *Tegella*, *Corbulella*, *Concertina*, *Bryocalyx*, *Amphiblestrum*) and subimmersed (*Valdemunitella*) ovicells with well-developed ooecia are found alongside immersed ovicells with vestigial ooecia (*Crassimarginatella*) and internal brood sacs with vestigial kenozooidal ooecia (*Cauloramphus*) (Ostrovsky et al. 2007, 2009a). *Gontarella*, characterized by internal brood sacs and no ooecium, may also belong to this family (Ostrovsky et al. 2006). It should be noted that the more the brood cavity is immersed and the ooecium reduced in Calloporidae, the smaller is the gymnocyst of the ovicell floor.

Endozooidal ovicells in Flustridae appear to have resulted from a change in the growth processes at the edge of the developing ooecial fold. Two descriptions of ovicellogenesis in flustrids are those of Vigelius (1884a, p. 50, non-numbered text-fig.) and Levinsen (1909, pp. 57–58, pl. 19, fig. 8b-n). According to the former author the formation of the ovicell floor and brood cavity is because of the invagination of the proximal part of the frontal wall of the distal zooid. According to Levinsen (1909) it is the distal wall of the maternal zooid that invaginates. In both descriptions, however, formation of the ovicell is accompanied by the growth and curvature of the transverse wall between the maternal and daughter zooids. One may suggest that such ovicellogenesis might involve activity of the intercalary growth zone formed on the margin of the ooecial fold. If so, the newly formed parts of the originally non-calcified entooecium should become immersed and not raised as in hyperstomial ovicells. Additional studies of ovicellogenesis in flustrids are necessary to determine the details of this process.

Different expressions of ooecium reduction and the corresponding immersion of the brood cavity are found in many cheilostome families. Both hyperstomial and immersed ovicells may be present within the same genus (*Bugula*, *Camptoplites*) (Robertson 1905; Harmer 1926; Osburn 1950; Bobin and Prenant 1963; Prenant and Bobin 1966; Ryland and Hayward 1977, 1992; Gordon 1986; Hayward 1995; Soule et al. 1995), and the same genus may contain some species with immersed ovicells and others with internal brood sacs (*Himantozoum*, *Caulibugula*) (Harmer 1926; Hastings 1943, 1945, 1964; Gordon 1986; Hayward 1995). The same trend is found in *Farciminellum* (Farciminariidae), *Menipea* (Candidae) and *Beania* (Beaniidae), which include some species with well-developed ooecia, others with vestigial oecia, and some with none at all (i.e. with internal brood sacs) (Harmer 1926; Hastings 1943; Osburn 1950; Gordon 1984, 1986; Zabala and Maluquer 1988; Hayward 1995; Ostrovsky, unpublished data).

The trend towards immersion of the brood cavity and reduction of the ooecium is also observed in Recent species of *Cellaria* (Cellariidae) (see illustrations in Hayward 1995; Ostrovsky, unpublished data). Judging from illustrations published by Cook and Chimonides (1985, 1986, 1987), Cadée et al. (1989), Parker and Cook (1994), Håkansson and Voigt (1996), and Bock and Cook (1999), species of *Lunularia* (Lunulariidae), *Pseudolunularia* and *Selenaria* (Selenariidae), and *Lunulites* and *Pavolunulites* (Lunulitidae) have ovicells with a vestigial ooecium and brood sac immersed into the cavity of the maternal autozooid. The vestigial ooecium may be developed to varying degrees – it is sometimes quite distinct but more often barely discernible. In *Setosellina* (Heliodomidae), ooecia may be present or absent (Harmer 1926; Harmelin 1977).

A similar trend is found at family level (Ostrovsky et al. 2006, 2009a; see also Table 2.1). Most genera in the following families have ovicells, exceptions being *Oshurkovia* (Umbonulidae) (Hastings 1944, 1964; Eggleston 1972; Grischenko and Mawatari 2005), *Arctonula* (Romancheinidae) (Kluge 1975; Gordon and Grischenko 1994; Hayward and Ryland 1999), *Fatkullina* (Stomachetosellidae) (Grischenko et al. 1998) and *Odontoporella* (Hippoporidridae) (Canu and Bassler 1929; Osburn 1950; Prenant and Bobin 1966; Ryland and Hayward 1977; Gordon 1989a; Hayward 1995), with internal brooding. Actual brood sacs have been demonstrated by thin section in *Arctonula arctica* (Ostrovsky, unpublished data) but the remainder of these genera have not been studied anatomically.

The Microporidae contains genera with well-developed ooecia (*Micropora*, *Mollia*, *Apiophragma*), vestigial ooecia (*Rosseliana*) and no ooecia (*Calpensia*, *Ogivalia*, *Microporina*) (Prenant and Bobin 1966; Hayward and Ryland 1998). The same is true of the Umbonulidae; most genera have hyperstomial or prominent ovicells, *Desmacystis* has immersed ovicells with vestigial ooecia and *Oshurkovia* has no ovicells at all (Hastings 1944, 1964; Eggleston 1972; Gordon and Grischenko 1994; Grischenko and Mawatari 2005). Recent Onychocellidae have vestigial ooecia. For instance, Cook (1973) reported brooding in internal brood sacs of *Smittipora levinseni*, in which a small ooecium is present (see Levinsen 1909, pl. 24, fig. 10). At the same time, some onychocellids from the Cretaceous have well-developed ooecia (Voigt 1989; Ostrovsky, unpublished data).

Varying degrees of reduction of the ooecium and immersion of the brood cavity can be found in the Urceoliporidae. Endozooidal and immersed ovicells are also present in species of Cheiloporinidae, Sclerodomidae, Metrarabdotosidae, Myriaporidae and Porinidae. Remarkably, the cheiloporinid *Cheiloporina haddoni* is strikingly similar to the calloporid *Crassimarginatella* sp. in the mutual arrangement of the brood-chamber components, whereas the brooding structures of *Reciprocus regalis* (Urceoliporidae) are very similar to those in *Beania bilaminata* (Beaniidae) (Ostrovsky, unpublished data). Thus, phylogenetically distant species have convergently evolved extremely similar structures for embryo incubation.

Within the family Cribrilinidae, fossil *Leptocheilopora* (Fig. 2.26) and Recent *Corbulipora*, *Euthyroides* and some *Puellina* (Fig. 2.27A) have hyperstomial ovicells, whereas subimmersed and endozooidal ovicells are also found in *Puellina* (Figs. 2.7a(I), 2.27B–E, and 2.28), and endozooidal in *Figularia* and *Cribrilina* (Ostrovsky, unpublished data). The conclusion that a trend towards immersion of the brood cavity is widespread in this group also emerges from an analysis of descriptions of various fossil cribrimorphs (see Lang 1916, 1921, 1922; Larwood 1962). Cribrimorph bryozoans with subimmersed and endozooidal ovicells were common as early as the Cretaceous. As in other groups, this trend was accompanied by reduction of the ooecium. In Recent *Cribralaria austrinsulensis* (Gordon 1989a), *Cribrilina dispersa* and *C. simplex* (see Florence et al. 2007), ooecia seem to be completely lacking. Ovicells are also unknown in *Jullienula*. Accordingly, cribrimorphs also possesses the whole range of brood structures from hyperstomial ovicells to internal brood sacs. Lang (1921) cited cribrimorphs from the Upper Cretaceous with endozooidal ovicells, the first of them appearing as early as the Cenomanian (*Calpidopora*). The transitional series from hyperstomial to endozooidal ovicells in Late Cretaceous Onychocellidae was described by Voigt (1991). Thus, this trend in brood-chamber evolution was expressed in the earliest cribrimorphs and onychocellids, which are among most ancient clades of brooding cheilostomes.

The same situation obtains in the Chaperiidae, showing the range from hyperstomial and prominent (*Chaperiopsis*, *Notocoryne*, *Larnacicus*, *Icelozoon*, *Exallozoon*, *Pyrichaperia*, *Exostesia*) to subimmersed (*Clipeochaperia*) to endozooidal (*Patsyella*) (Gordon 1982, 1992). Species *Chaperia* have no ovicells and brood embryos internally, as was recorded in *C. granulosa* (Gordon and Mawatari 1992).

Levinsen (1909) remarked quite correctly that endozooidal ovicells are found in different families. On the basis of this observation, however, he suggested that this type of brood chamber structure was "old" (primitive) and "common" and subject to later substitution by other types. A similar opinion was expressed by Harmer (1926) (see above). My data indicate the contrary. Though the trend towards immersion of the brood cavity manifested itself early in the evolutionary history of flustrines, their first ovicells were hyperstomial.

Thus, immersion of the brood cavity and reduction of the ooecium are interrelated trends in the evolution of cheilostome brooding structures. The deeper the brood cavity lies in the zooid, the less it protrudes and the smaller the ooecium. If ovicell immersion is achieved by overgrowth of a layer of secondary calcification, reduction of the ooecium does not occur.

It should be noted that protection of the brood chamber may be achieved not only by ovicell immersion. Additional protective structures may also evolve. For instance, in *Isoschizoporella tricuspis* and *Petralia undata*, ovicells are formed in groups associated with spinose avicularia taller than the ovicells (Ostrovsky, unpublished data).

2.4.8.5 Evolution of Internal Brood Sacs

The above examples show that the evolutionary trend expressed in the immersion of the brood cavity into the colony is manifested in many taxa. This phenomenon has been noted in at least 41 families (Ostrovsky et al. 2009b; see also Table 2.1). Thus, a quarter of the known cheilostome families, belonging to several superfamilies, include species with different expressions of this trend. Half of these families have species with internal brood sacs and no ooecia, and in most such families species with ovicells also occur. These facts give evidence that the transition from ovicells to internal brood sacs occurred repeatedly in cheilostomes (Ostrovsky et al. 2006, 2007, 2009b).

Internal brood sacs are the only incubational structures in the Cupuladriidae (Ostrovsky et al. 2009b), Chlidoniidae (Waters 1913; Harmer 1926; Ostrovsky, unpublished data), Steginoporellidae (Waters 1913; Marcus 1922; Harmer 1926; Osburn 1950), Pasytheidae (Gordon 1984), Adeonidae (Waters 1912, 1913), Exechonellidae (Fransen 1986), Watersiporidae (Waters 1912; Mawatari 1952), Cryptosulidae (Calvet 1900) and Inversiulidae (Gordon 1984; Hayward 1995). In most of these taxa the presence of brood sacs was registered in studies made on live or fixed (wet) colonies with embryos or else in studies involving anatomical sections (Fig. 2.47). For the others, the existence of brood sacs is only inferred. For instance, all species and genera of Bryopastoridae, Euthyrisellidae and Didymosellidae are thought to have internal brooding in "ovisacs" of zooidal polymorphs (Cook 1979; Cook and Chimonides 1981b; Gordon 1986; Zabala and Maluquer 1988). There are no data on the brooding structures in a number of genera (see above) including *Carbasea carbasea* (Flustridae), the first cheilostome reported to have internal brooding (Grant 1827; Zabala and Maluquer 1988; Ostrovsky et al. 2006, 2008).

Internal brood sacs could have evolved as modifications of ovicells, endozooidal as well as immersed. This possibility is supported by the fact that, in species with brood sacs (e.g. *Cauloramphus*, *Beania bilaminata*, *Nematoflustra flagellata* and *Reciprocus regalis*), the ooecial vesicle is retained, together with its sclerite and musculature. Whatever the ovicell type was, the origin of internal brood sacs should have been accompanied by reduction of the calcified floor of the brood cavity, invagination of the distal wall of the maternal zooid and disappearance of the ooecium. A strongly reduced ooecium is retained in species with immersed ovicells (*Crassimarginatella* sp., *Bugulopsis monotrypa* and some others) and with brood sacs (*Cauloramphus*, *Beania*). In most flustrids, the brood cavity of endozooidal ovicells lies in the proximal part of the distal autozooid. In contrast, the internal brood sacs of *Nematoflustra flagellata* and "*Biflustra*" *perfragilis* lie in the distal half of the maternal zooid (Fig. 2.46A, B). Thus, immersion of the brood cavity in flustrids should have been accompanied by its proximal displacement and a change in the position of its opening.

The structure of the internal brood sac in the presumed calloporid *Gontarella* sp. is almost identical to that in the calloporid *Cauloramphus* (compare Figs. 2.25B and 2.46C). This variant could be the result of complete reduction of the ooecium. On the other hand, modification of immersed ovicells, as in *Crassimarginatella* sp., could have brought about the same result. Thus, even within the Calloporidae, the transition to internal brooding may have been achieved in different ways (Ostrovsky et al. 2006, 2009a).

It seems evident that immersion of the incubation chamber is associated with better protection of the developing embryo – immersed and endozooidal ovicells are less exposed than other ovicells and thus less likely to be damaged. On the other hand, the reduction and even complete disappearance of the calcified ooecial roof may be thought to decrease protection of the embryo. In an attempt to explain this phenomenon, Hastings (1964) looked for correlations between the presence or absence of ovicells within the same genus and for differences in vertical, geographical and climatic distribution of species, but failed to find any. Eggleston (1972) noted that internal brooding is characteristic of intertidal species and suggested the embryos of such species might be better protected against exposure to air than in species with ovicells.

Having studied internal brooding anatomically, I have suggested several other alternative or complementary scenarios (Ostrovsky et al. 2006, 2009b):

1. Since ovicell formation requires considerable amounts of materials and energy, reduction of the ooecium and associated structures could release some resources for somatic growth. The result could be a higher growth rate or enlargement of the colony.
2. The zooid cavity is more capacious than the ovicell, and a large zooid has enough room for a large larva, which is likely to be more competitive after settlement. Therefore, a transition to internal brooding might be associated with the acquisition of a larger larva. In the Adeonidae, the transition to internal brooding appears to have caused the origin of female zooidal polymorphs.
3. Internal brooding may have been an evolutionary response to predators feeding on embryos contained in ovicells (such as acleithral). Small species of nudibranchs and pycnogonids have been shown to feed on individual zooids (McBeth 1968; Wyer and King 1973; Lidgard 2008a, b; reviewed in McKinney et al. 2003).

Santagata and Banta (1996) suggested that the internal brood sac is a modification of the expanded vestibulum, and internal brooding was the initial mode of incubation in the Cheilostomata (see Sect. 2.4.2). Ryland (1970, p. 95) also proposed that "incubation in an embryo sac suspended in the coelom might have been the primitive arrangement". The geological record does not support these hypotheses; species with internal brooding mostly emerged in the Middle Eocene and later. For instance, *Watersipora* and *Cryptosula* appeared in the Late Miocene. A much more ancient brooding type was incubation in a cage-like hyperstomial ovicell made of spines formed by the distal autozooid (Taylor and McKinney 2002; Ostrovsky and Taylor 2004, 2005a). It is much easier to interpret internal brooding as the final stage of the transition from hyperstomial to endozooidal and immersed ovicells, which occurred independently in several cheilostome clades (Ostrovsky et al. 2006).

Interestingly, some families with internal brooding, e.g., Cryptosulidae, contain both species with sexual zooidal dimorphism (*Harmeria*) and without it (*Cryptosula*). This may also be true of Watersiporidae; *Uscia mexicana* colonies form heteromorphic zooids but it is not known if they are sexual (female) or defensive (avicularian). At the same time, there are no polymorphs in *Watersipora*.

The origin of intracoelomic embryo incubation in the Epistomiidae remains an open question (Marcus 1941b; Dyrynda 1981; Dyrynda and King 1982). This variant may have evolved through the loss of brooding in ovicells or internal sacs and a transition to viviparity when cleavage starts in the ovary. This shift might have somewhat accelerated reproduction, which is important for ephemeral species such as epistomiids (see Chap. 3).

2.4.8.6 Change in the Method of Ovicell Closure

Analysis of the literature supports my own data on the existence of different modes of ovicell closure in the same family or genus. For instance, acleithral and cleithral ovicells are known in the Calloporidae, Flustridae, Bugulidae, Romancheinidae and Smittinidae. These facts point to another evolutionary trend frequently manifested within the Cheilostomata – a change in the ovicell closure mechanism.

One can suggest that the non-cleithral character state (if not secondary, see below) is plesiomorphic and that cleithral is apomorphic, whereas all the other states represent intermediate stages (and their variants) in the evolution of ovicell closure for better protection of the embryo. The calcified unitary ooecium certainly protects the embryo better than spinose, and the most vulnerable aspect is the brood-chamber opening. The first step towards an acleithral ovicell (Fig. 2.8A) was probably the plugging of this opening. The ooecial vesicle as a protective structure could have evolved as an outgrowth of the non-calcified wall of the maternal zooid distal to the operculum. Its musculature should then be homologous with the distalmost parietal muscles of the zooidal frontal wall.

Acleithral ovicells appear to have evolved early. Judging from the arrangement of skeletal elements, the ooecial vesicle may have been already present in *Wilbertopora* and in several Late Cretaceous cribrimorphs (*Leptocheilopora*, *Pancheilopora*, *Eucheilopora*, *Aeolopora*) (see illustrations in Lang 1921).

The next step could be the origin of a cleithral ovicell – instead of an elastic membrane, the brood-chamber opening was closed by the operculum of the maternal zooid (Fig. 2.8B). This transformation involved the displacement of the zooidal operculum relative to the ooecium. In the light of this, it is logical to conclude that semicleithral ovicells (Figs. 2.7a(I), 2.8C, and 2.28B) illustrate an intermediate stage between acleithral and cleithral. Ryland (1968) had also considered cleithral ovicell as advanced. Subcleithral ovicells, in which the operculum lowers to open the entrance of the ovicell, may be regarded as a cleithral variant (Fig. 2.8D). The pseudocleithral ovicell, which Ryland (1968) considered to be primitive, is a variant of the acleithral type (Fig. 2.8F).

It is likely that the ooecial vesicle became less important once the cleithral ovicell appeared. It is the transition from acleithral to cleithral that may explain a certain diminution of the ooecial vesicle in *Corbulella maderensis* compared to *Callopora* and *Tegella*; the ooecial vesicle has a contributory role in ovicell closure in the former, but closure is most effectively performed by a strongly cuticularized operculum (Ostrovsky et al. 2009a) (see also Fig. 2.22). The ooecial vesicle merely isolates the ovicell cavity from the environment during feeding excursions of the polypide. In some species with cleithral and subcleithral ovicells the ooecial vesicle is mostly or completely reduced.

That the loss of the ooecial vesicle might have been secondary was first mentioned by Santagata and Banta (1996). In non-cleithral ovicells the opening should be closed by the protruding introvert during polypide feeding and open at all other times. Sections of species with such brood chambers show that the operculum of the maternal zooid is located much more proximally than the ovicell opening and cannot close it (Figs. 2.6b(F), 2.8E, and 2.42) (Banta 1977). The reason why some ascophorans abandoned ovicell closure remains unclear. In some groups this might have been associated with modification of the ovicell opening, such as flattening (some Phidoloporidae and Celleporidae) or incorporation into a peristome. In both cases the potential predator is much less likely to be able to thrust its mouth parts into the brood cavity. This cannot be said, however, of *Lepraliella contigua* and *Sinuporaria* sp. (Lepraliellidae) – their large brooded embryos partly protrude from the opening of non-cleithral ovicells. Note, however, that in species with such brood chambers the embryos are as a rule surrounded by an especially thick fertilization envelope. Whatever the case, further evidence supporting the idea that the transition to non-cleithral ovicells was secondary is the age of the families in which these ovicells occur. The earliest, Lepraliellidae, evolved in the Santonian, while the next such family, Phidoloporidae, appeared in the Danian.

The broad occurrence of the ooecial vesicle, its musculature and sclerite in cheilostomes indicates that these three characters may be synapomorphies of Flustrina. An early origin of these structures is also indicated by the fact that they are rather common in calloporids, the most ancient family of brooding cheilostomes. The lack of the ooecial vesicle, sclerite and/or musculature in some cheilostomes would seem to be secondary. As noted above, the disappearance of the ooecial vesicle may have been associated with the transition to cleithral ovicells.

The loss of the sclerite (substituted in some species by a thickened cuticle) in many bryozoans was not associated with loss of the musculature. Flustrids with a weakly developed ooecial vesicle have no sclerite (*Isosecuriflustra angusta*, *Klugeflustra antarctica*). Apparently, the effort necessary for vesicle retraction is not great and thus there is no need for a thickened structure for muscle attachment. Species with and without the sclerite occur in most families, which may indicate yet another evolutionary trend. However, the information presently available is insufficient for any far-reaching conclusions.

2.4.8.7 Evolution of Peristomial Ovicells

Peristomial ovicells are known in the Margarettidae (*Margaretta*), Lacernidae (*Cylindroporella*), Lekythoporidae (*Poecilopora*) and Cribrilinidae (*Haplocephalopora*, *Pachydera*) (Lang 1916; Voigt 1993; Ostrovsky, unpublished data) (Figs. 2.7a(D, E) and 2.37). The patchy distribution of these taxa in the phylogenetic tree indicates that the transition from hyperstomial to peristomial ovicells is a distinct evolutionary trend originating independently in at least four distant families. Evolution of the peristomial ovicell was associated with the fusion of the ooecium and the peristome (the collar- or tube-like calcified wall around the orifice of the maternal zooid). Peristomes evolved as modifications of the zooidal orifice and/or frontal shield, and were probably protective structures preventing predation through forcing of the operculum.

Since the ooecium is situated near the zooidal orifice, it is naturally incorporated into the peristome wall, and the brood chamber cannot open directly to the environment but into the peristome cavity. It may be noted that formation of peristomial ovicells may be accompanied by immersion of the brood cavity into the colony (*Margaretta*, *Poecilopora*).

2.4.8.8 Proximal Displacement and Reduction of the Ooecial Base

Levinsen (1909, pp. 62–63) was the first to note the difference in the size of the "common wall for zooecium [zooid] and ooecium", i.e. the size of the ooecial base in different, sometimes congeneric, cheilostomes. He observed that the "common wall" is large in some species whereas in others the ooecium has a "narrow … pedunculate basal part," terming the former ooecia "dependent" and the latter "independent" (see Sect. 2.2).

Since the ooecia of the most ancient cheilostome brooders (including Calloporidae) are developed as an arch-like fold on the frontal gymnocyst of the distal zooid, their base is represented by the ovicell floor surrounded by the basal part of the ooecial vertical walls. Thus, the ovicell floor (horizontal part of the entooecium) constitutes a considerable part of the frontal wall of the ooecium-producing zooid. In many species, however, this "common wall" is much smaller or absent and the ooecium and the frontal wall of the distal zooid are connected via a narrow (and often very short) "stalk" with calcified walls surrounding a communication pore. The pattern of distribution of these two structural variants across Cheilostomata points to a trend, in some cases presumably associated with the evolution of new types of frontal shield and the reduction of the proximal area involved in the formation of the ooecium (see Sect. 2.4.7). In the course of this transformation, the broad ooecial base, shaped as an arched fold (Fig. 2.18D–F) became a "double disc" (a fold with a narrow base) (Fig. 2.40C–F).

This trend, evident within superfamilies, families and genera, appears repeatedly within the Cheilostomata. For instance, the proximal position of the narrow ooecial base is characteristic of the Hiantoporidae and some Bugulidae among anascans and of a number of umbonulomorph (Fig. 2.41) and lepraliomorph ascophorans with lepralielliform ooecia (see Sects. 2.3.2 and 2.4.7). In all of them the developing ooecium has the shape of a "double disc" – the displacement of the ooecial base towards the transverse wall between maternal and distal zooids precludes the development of a "broad" ooecial fold such as is observed in *Callopora*, for example. Further, ovicell floor formation starts with single (unpaired) rudiment of calcification, and the general reduction of the ooecial base may have been also a reason for the secondary acquisition of the shape of the initial calcification.

Together with the reduction of the ooecial base a communication slit transforms to a central pore. Whereas most Bugulidae have such a pore, *Nordgaardia cornucopioides* has a communication slit and a broader base, indicating the plesiomorphic state of this character. Similarly, both the communication slit and pore occur in different species of *Smittina* (see Sect. 2.4.7).

Reduction of the ooecial base and the transformation of a slit to a pore in ascophorans with lepralielliform ooecia was also accompanied by a proximal displacement of the ooecial communication pore, enlargement of the horizontal ectooecial part (and thus its contact area with the frontal shield of the distal zooid) (Fig. 2.41) and, in some cases, the character of ovicellogenesis. Such correlations among these three characters exist in the Bryocryptellidae, Smittinidae and Bitectiporidae. It is only in rare cases (e.g. in *Hippoporina* *propinqua*, *Characodoma porcellanum* and some others) that the proximal position of the pore is combined with the distal position of the ectooecium base, which appears to be associated with the way in which the ovicell floor fuses with the proximal area of the calcified wall of the frontal shield. At the same time, different combinations of proximal and distal positions of the pore and ectooecial base can be found in the same genus (*Porella*, *Rhamphostomella*) or family (Bryocryptellidae, Smittinidae).

As for ovicellogenesis, in most species with the ectooecial base in a "distal" position (the plesiomorphic condition), the ooecial fold begins to form at the colony periphery long before the frontal shield of the distal zooid is completed. In contrast, in species with the ooecial base proximal, the "double-disc" stage often develops from the edge of the narrow membranous window (in fact, a membrane-covered groove with a communication pore at the bottom; see Sect. 2.3.2) after the distal zooid has been completed. In this case, formation of the lepralielliform ooecium is not connected with the formation of new zooids at the colony periphery, and can be postponed. A similar correlation exists in ascophorans with microporelliform ooecia (see Sect. 2.3.2).

2.4.9 Brood Chambers in the Scrupariidae, Thalamoporellidae and Alysidiidae

In ovicells with "bivalved" or "bilobate" ("bivalvular," "double-valved," "two-valved," see Levinsen 1902, 1909; Waters 1909; Hyman 1959) ooecia, the protective capsule is constructed of two symmetrical halves. Such ovicells are patchily distributed among the Cheilostomata, some of which are closely related and some phylogenetically distant (Calloporidae, Cribrilinidae, Euthyroididae, Scrupariidae, Thalamoporellidae, Alysidiidae) (see also Sects. 2.3.1, 2.3.2, and 2.3.4).

In *Scruparia*, *Brettiopsis*, *Alysidium* and *Catenicula*, each valve/plate is obviously kenozooidal (although anatomical study is needed in all these cases), budded either from the maternal zooid or from each other, whereas in *Thalamoporella* they are fused hollow outgrowths of the frontal surface around the orifice of the maternal autozooid, a unique instance among cheilostomes. In contrast, in *Wilbertopora*, *Gilbertopora*, *Bryocalyx*, *Valdemunitella*, *Euthyroides*, *Corbulipora*, *Puellina*, *Figularia*, and *Filaguria* the ooecial halves are outgrowths of the distal zooid – either an autozooid, an avicularium or a kenozooid. A special type of brood chamber (synoecium) is found in *Catenicula* that consists of eight flattened elements (presumed kenozooids) (O'Donoghue 1924; O'Donoghue and Watteville 1944). I additionally propose to designate the synoecium a "multivalved brood chamber".

Thus, bilobate ovicells are not homologous throughout the Cheilostomata, supporting the hypothesis of independent evolution of brooding (Taylor 1988; Ostrovsky and Taylor 2005a; see also discussion in Santagata and Banta 1996). Many other cheilostomes have a median suture in their ovicells (Ostrovsky 2002; Ostrovsky et al. 2009a), but the use of the term "bivalved" for them is less appropriate, since the suture is normally short and often restricted to a part of the ovicell roof (see Ostrovsky 1998).

Scruparia and *Brettiopsis* (Scrupariidae) have bivalved terminal ovicells consisting of a pair of lobes, presumably kenozooids. Appearing in the Maastrichtian, scrupariids have traditionally been separated from the rest of the brooding cheilostomes owing to a set of morphological and anatomical differences. That embryo incubation in scrupariids evolved independently of other cheilostomes was first suggested by Osburn (1950; see also Ryland 1974). Waeschenbach et al. (2012) molecular analysis supports this idea, with *Scruparia* nested among malacostegans in their phylogeny (see also Sect. 3.4.1). In addition, species of *Scruparia* have a setigerous collar (Prenant and Bobin 1966; Banta et al. 1995) and brood several embryos simultaneously. Both of these characters, considered to be primitive, are known in ctenostomes. Finally, the larva of *Scruparia*, illustrated by Barrois (1877), strongly resembles the larva of the ctenostome *Flustrellidra hispida* (see Zimmer and Woollacott 1977).

Alysidium has bivalved brood chambers with a similar structure but the valves are connected to the maternal zooid by a cuticular base that permits them to bend outwards. This difference and zooid structure mediate against a relationship with *Scruparia*. The Alysidiidae also includes *Catenicula* but it is unclear if its multivalved brood chamber is homologous to that of *Alysidium*. Levinsen (1909) interpreted the ooecial valves of *Alysidium* to be modified autozooids. The coelomic cavity of the valve (kenozooid) is separated from the visceral coelom by a pore plate. In other words, alysidiid ovicells also appear to have evolved independently of other cheilostomes. Unfortunately, this conclusion sheds little light upon the phylogenetic connections of this family, which may well turn out to be unrelated to the other Flustrina.

The origin of brooding in the Thalamoporellidae is a complicated and essentially unresolved question. This is partly because of a lack of information about the structure of the brood chamber as well as the uncertain position of the family in cheilostome classification. Harmer (1926, pp. 291, 293–294) regarded the bilobate ovicells of *Thalamoporella* as non-homologous to the ovicells of other cheilostomes (see also Ryland 1974), being "modifications of the adoral tubercles … borne by the ordinary zooecia". Specifically, the ooecial lobes are not kenozooids, as in *Scruparia* and

Alysidium. In fact, *Thalamoporella* ovicells are unlike those of any other cheilostome, raising the question (similar to Alysidiidae) of the taxonomic relatedness of the family to the rest of the Flustrina. An independent origin of Thalamoporellidae is also supported by the fact that *Thalamoporella* ovicells contain several embryos at a time. Also in *T. evelinae*, zygotes are transferred to the brood chamber with the help of an intertentacular organ, which is predominantly characteristic of gymnolaemate broadcasters. These plesiomorphic characters indicate that thalamoporellids evolved directly from malacostegans (see also Ostrovsky and Porter 2011).

The presumed relatedness of Thalamoporellidae and Steginoporellidae (Harmer 1926; Gordon 2000) further complicates the situation. Both families appeared in the Middle Eocene and have a well-developed cryptocyst, but steginoporellids brood embryos in internal brood sacs. As shown above, this incubation type in cheilostomes is secondary, its origin having been accompanied by the loss of ovicells. Can it be, then, that Thalamoporellidae is ancestral to Steginoporellidae?

Harmer (1926) compared the bivalved ovicells of *Thalamoporella* with the brood chambers of *Alysidium*, based on their external appearance. Hastings (1941), having found as many as seven embryos in the ovicell of *Scruparia chelata*, compared its multiple incubation and "bivalved" ovicells with these features in *Thalamoporella*. A third argument in favour of the relatedness of *Thalamoporella* and *Scruparia* is the external appearance of their larvae (Marcus 1939; discussed in Zimmer and Woollacott 1977). Nevertheless, zooidal and ooecial structure in *Scruparia* and *Thalamoporella* are very different; inter alia, the lobes of the bipartite ooecium, have a different structure and origin in these two taxa.

Finally, Hyman (1959) suggested that the bivalved ovicells of *Scruparia*, *Thalamoporella*, *Alysidium* and *Catenicula* were modified spines and considered them as kenozooids. Mawatari (1973a) held the same view concerning *Scruparia*. The ooecial valves in *Scruparia*, *Alysidium* and, possibly, *Catenicula* are indeed kenozooids budded from the maternal zooid, whereas in *Thalamoporella* they are outgrowths of the frontal wall of the maternal zooid.

The structure and development of the brood chambers discussed in this section indicate that they evolved independently and that their resemblance to the bipartite ooecia of some calloporids and cribrimophs is a result of convergent evolution. Accordingly, the Thalamoporellidae (plus *Bellulopora* and Tendridae) are removed from the suborder Flustrina and separate suborders designated for them (see Appendix II for diagnoses). An additional study is required to confirm if the Alysidiidae deserve a similar status, which is highly likely. Note too, that further evidence of the independent origin of brooding in *Tendra* and *Thalamoporella* may be the intertentacular organ, presumably inherited from their non-brooding ancestors (Ostrovsky and Porter 2011) (see also Sect. 1.3.9).

2.5 Conclusions

The various types of brood chambers found in living and fossil Cheilostomata vividly exemplify the evolution of these structures in this order. The differences in their morphology and the pattern of their distribution in the Cheilostomata show that chambers for incubation of the embryo evolved in this group at least seven times – in Aeteidae, "*Carbasea*" *indivisa*, Scrupariidae, Thalamoporellidae, Calloporidae, Tendridae, *Bellulopora* and possibly Alysidiidae. The inevitable conclusion is that the Flustrina (=Neocheilostomina), as currently conceived, is polyphyletic. Some of these brooding structures underwent considerable modification in the course of further evolution, probably associated with enhancement of their protective function. All of this, as well as the broad distribution of brood chambers within the order, points to the paramount role of parental care in the evolutionary success of Cheilostomata. Taylor (1988), who in general tended to think that brooding cheilostomes were monophyletic, nevertheless noted that *Aetea*, *Scruparia* and *Eucratea* could have evolved brooding independently of other "neocheilostomes". This suggestion was supported by Ostrovsky and Taylor (2005a). I agree with my respected colleague that bryozoans that evolved brooding independently play a relatively unimportant role in the overall taxonomic diversity of Cheilostomata. Nevertheless, the early idea that "other types of larval brooding … are likely to be secondarily derived from the ovicellar brooding" (Taylor and Larwood, 1990, p. 224) cannot be correct.

In conclusion, it should be noted that an important feature of brood-chamber evolution is the abundance of parallelisms and convergence, which hampers the search for phylogenetic connections between the taxa within this order. As for the phylum Bryozoa as a whole, my data convincingly show that the brooding structures of cheilostomes evolved independently from those in other bryozoan orders and classes. Therefore, the hypothesis that incubation chambers in the various orders of Bryozoa are homologous (Silén 1944) is erroneous (see Sect. 2.4.2). On the other hand, the presence of external membranous brood sacs in some primitive cheilostomes (e.g. *Aetea*) may indicate either their relatedness to some brooding ctenostomes (Jebram 1992).

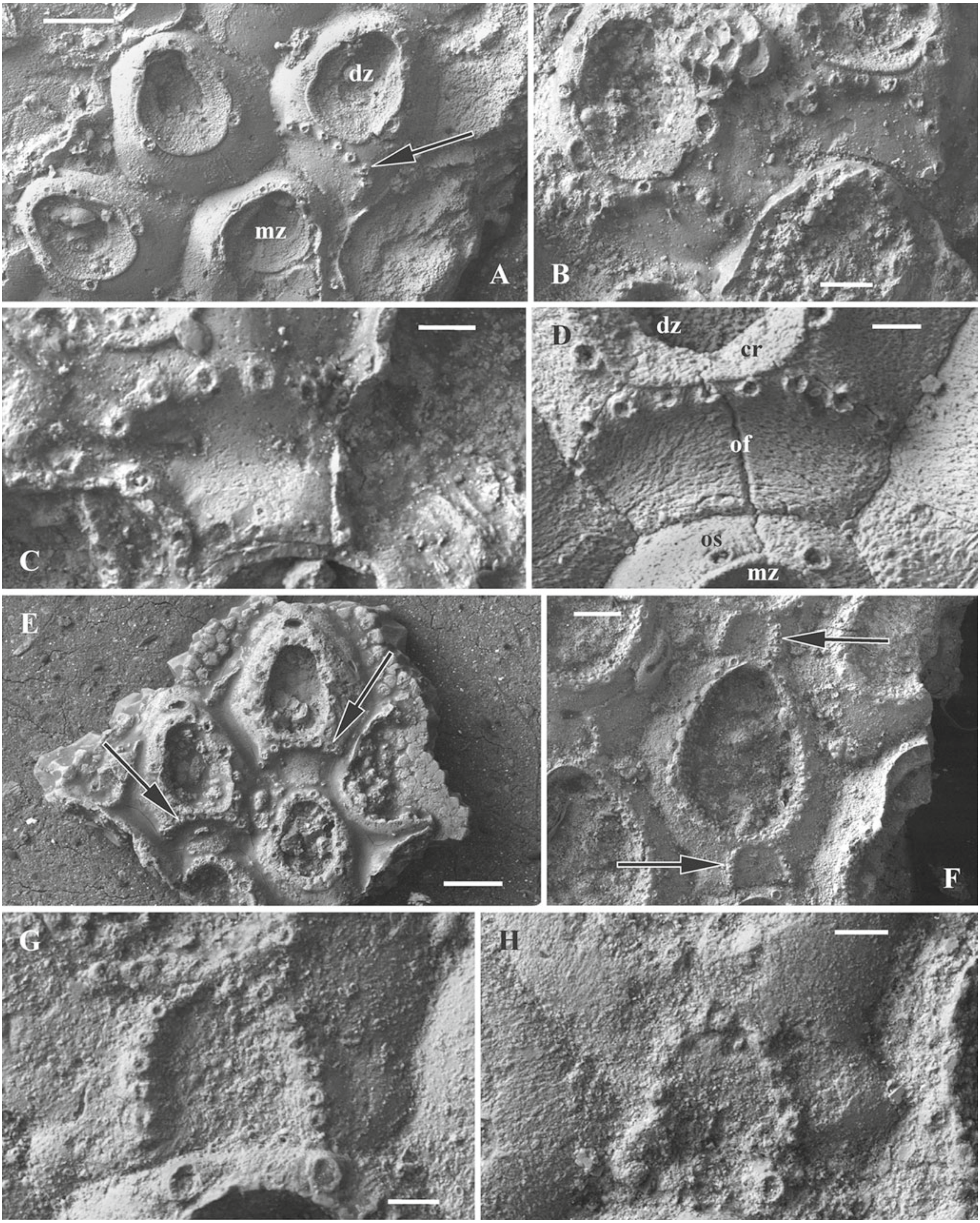

Fig. 2.9 Position of spine bases in spinose ooecia. (**A**–**D**) *Distelopora bipilata*; (**E**) *Distelopora langi*; (**F**–**H**) *Distelopora spinifera*. (**A**) Part of colony with non-brooding autozooids and a damaged ovicell (arrowed); (**B**) ooecial spine bases arranged in a regular semicircle; (**C**) ooecial spine bases located at some distance from the mural rim of the distal autozooid; (**D**) ooecial spine bases arranged in a gently curved arc (medial spines adjacent to mural rim). (**E**) Part of colony with non-brooding autozooids and two damaged ovicells (ooecial spine bases form gently curving arcs (*arrowed*); medial spines adjacent to mural rim). (**F**–**H**) Ooecial spine bases arranged as a horseshoe (*arrowed* in (**F**); in (**H**) ovicell spine bases are located at some distance from the mural rim of distal autozooid) (From Ostrovsky and Taylor 2005a, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.2005.00179.x/abstract). Abbreviations: *cr* cryptocyst, *dz* distal autozooid, *mz* maternal autozooid, *of* ovicell floor, *os* oral spine. Scale bars: **A**, 127 µm; **B**, 58.8 µm; **C**, 37 µm; **D**, 29.4 µm; **E**, 125 µm; **F**, 100 µm; **G**, 28.6 µm; **H**, 40 µm

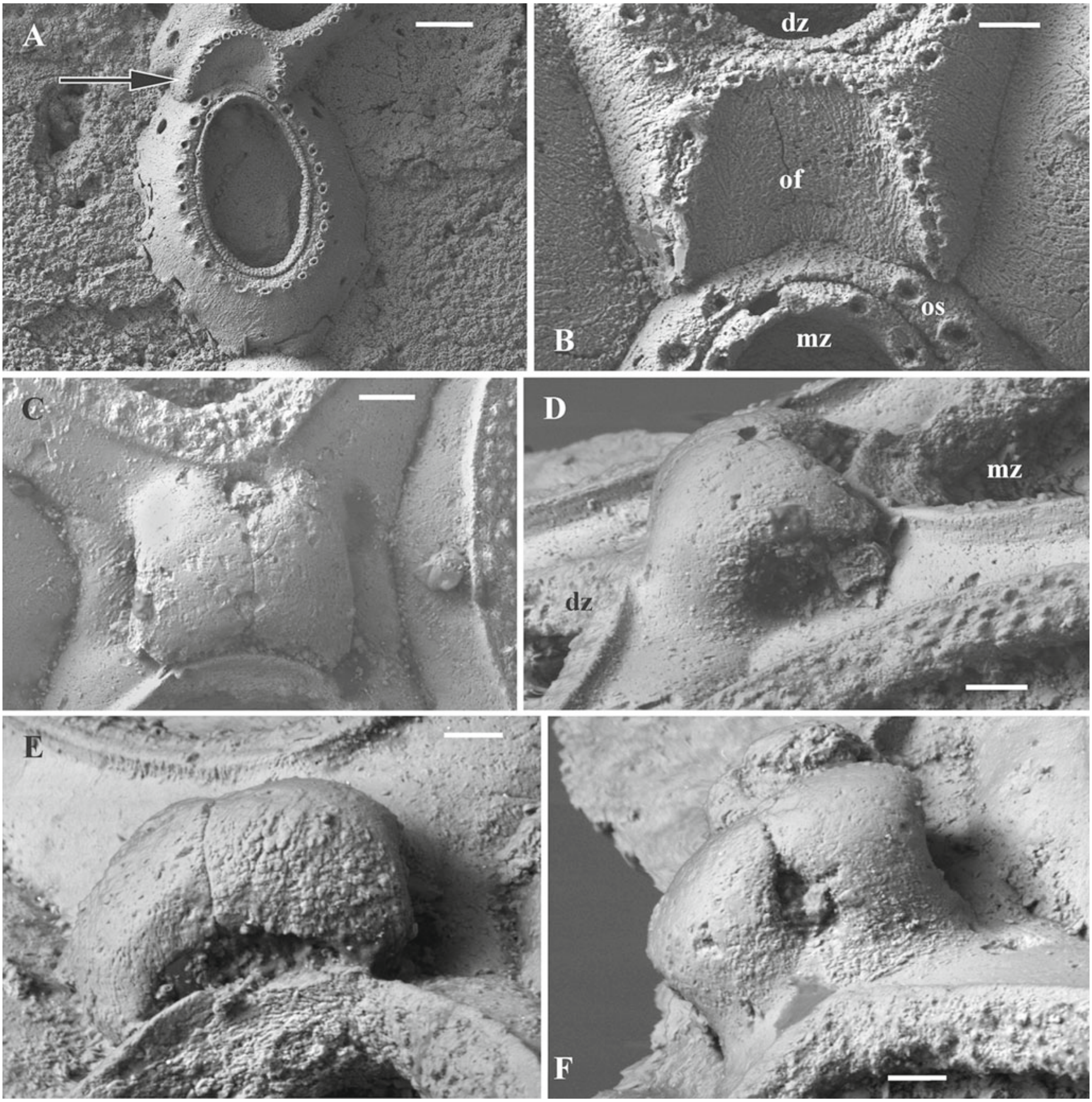

Fig. 2.10 Damaged spinose ooecium in *Unidistelopora krauseae* (**A**, **B**) and complete bilobate ooecium in *Gilbertopora larwoodi* (**C**–**F**). (**A**), Maternal autozooid with a damaged ovicell (*arrowed*) and an intramural bud; (**B**), ooecial spine bases arranged in a horseshoe pattern (medial spines adjacent to the mural rim). (**C**), Complete ooecium of two large flattened spines viewed from above; (**D**), the same ooecium viewed from the side, showing a lateral foramen; (**E**), the same ooecium in proximal view showing the main opening of the ovicell; (**F**), the same ooecium showing a distal opening (distal view) (from Ostrovsky and Taylor 2005a, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.2005.00179.x/abstract). Abbreviations: *dz* distal autozooid, *mz* maternal autozooid, *of* ovicell floor, *os* oral spine. Scale bars: **A**, 130 µm; **B**, 43.5 µm; **C**, 34.5 µm; **D**, 31.3 µm; **E**, 23.3 µm; **F**, 26.3 µm

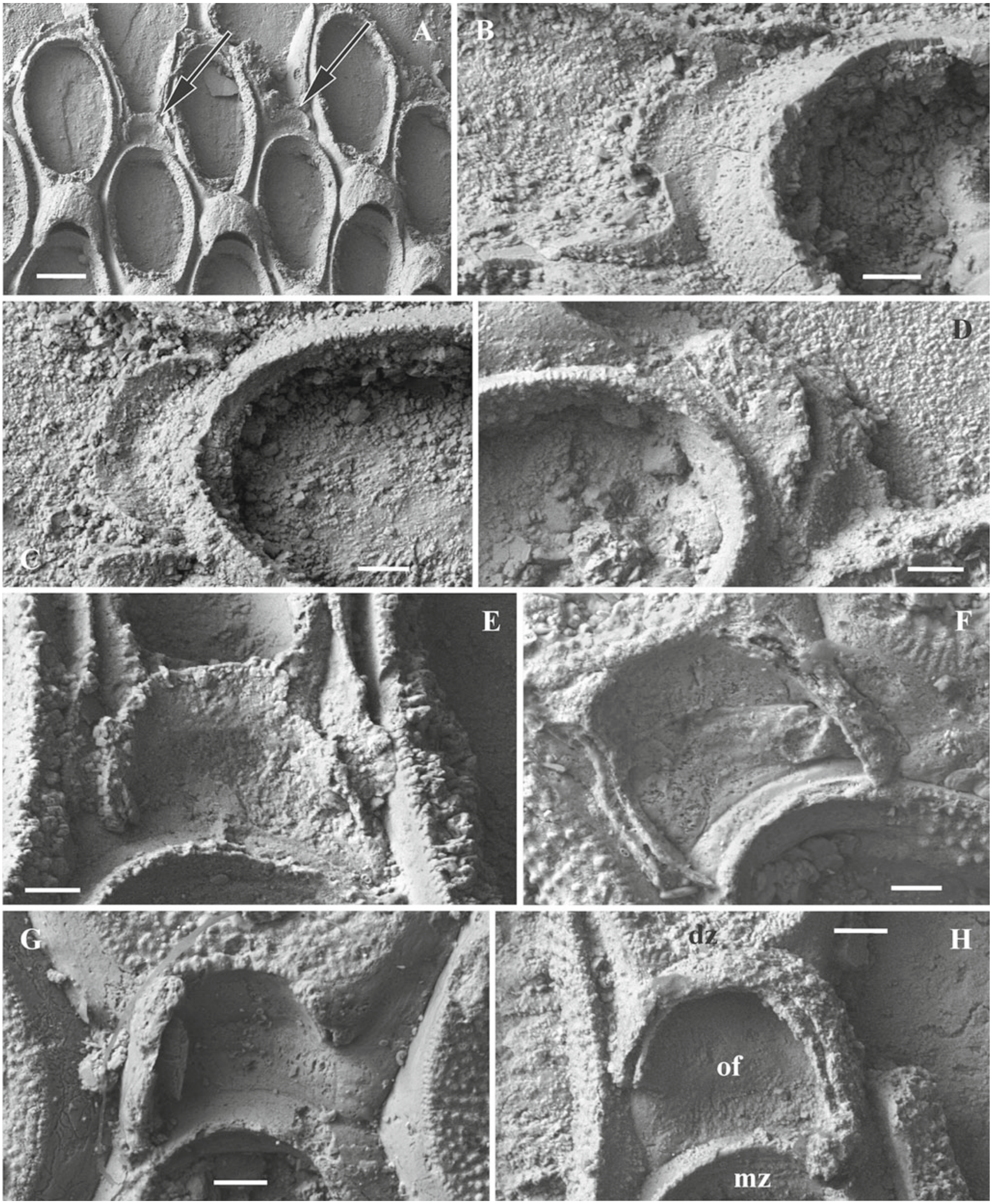

Fig. 2.11 Early stages of ooecium formation in: (**A**–**E**, **H**) *Wilbertopora listokinae*; (**F**, **G**), *Wilbertopora tappanae*. (**A**) Peripheral part of colony with complete and developing ovicells (*arrowed*); (**B**–**H**) successive stages of ovicellogenesis: (**B**–**D**) single ooecial rudiment of initial calcification of ovicell floor; (**E**) formation of concave ovicell floor, showing skeletal layer underlying both the lateral zooidal walls and the ovicell floor. (**F**, **G**) Broken ooecia with their lateral lobes partially destroyed (their communication openings seen in Fig. 2.12C); (**G**) developing ooecium with its right lateral lobe mostly detached (short base of this lobe can be seen), and the lower edge of the left lobe overgrowing the proximal gymnocyst; (**H**) intermediate stage of ooecial development showing a hemispherical fold formed from fused lateral lobes and a broken left lateral lobe ((**B**–**H**) – From Ostrovsky and Taylor 2005b, courtesy of Taylor and Francis Ltd.). Abbreviations: *dz* distal autozooid, *mz* maternal autozooid, *of* ovicell floor. Scale bars: **A**, 125 μm; **B**, 27 μm; **C**, **D**, 30.3 μm; **E**, 24.4 μm; **F**, 20.8 μm; **G**, 29.4 μm; **H**, 35.7 μm

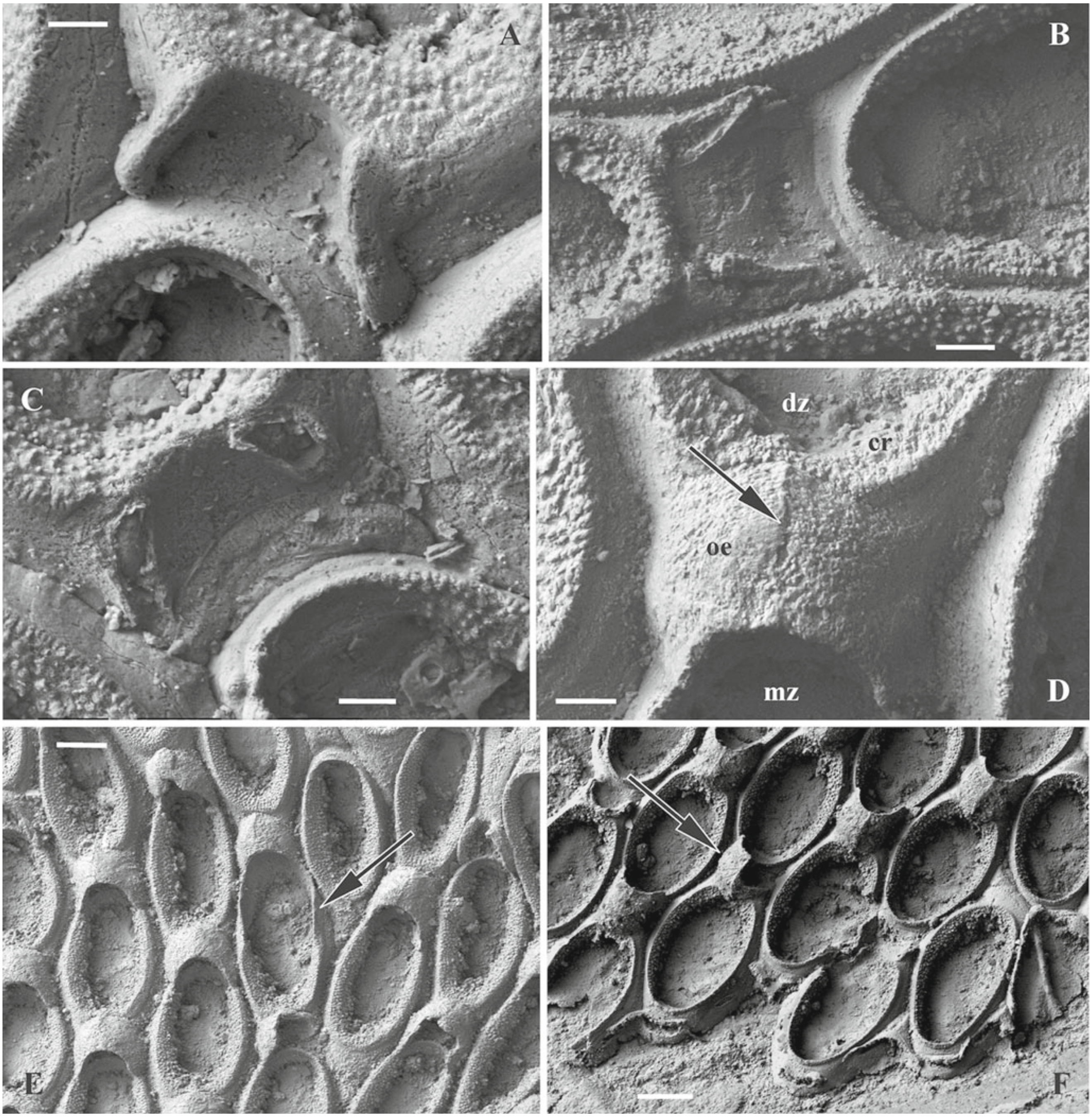

Fig. 2.12 Ovicell structure in: (**A**, **B**, **E**, **F**) *Wilbertopora listokinae*; (**C**, **D**) *Wilbertopora tappanae*. (**A**–**C**) Developing (**A**) and damaged (**B**, **C**) lateral lobes of an ooecium (in **C**, communication openings can be seen connecting cavities of the lobes with the visceral coelom of the distal autozooid). (**D**) Frontal view of complete ooecium (medial suture arrowed). (**E**) Part of colony with ovicells (*arrow* points to the cryptic avicularium that initiated the formation of the ooecium by the distal autozooid). (**F**) Oblique view of growing edge with three ovicells whose ooecia fractured (*arrow*) along the median suture ((**A**–**C** and **F**) – From Ostrovsky and Taylor 2005b, courtesy of Taylor and Francis Ltd.). Abbreviations: *dz* distal autozooid, *cr* cryptocyst, *mz* maternal autozooid, *oe* ooecium. Scale bars: **A**, 27.8 μm; **B**, 40 μm; **C**, 25.6 μm; **D**, 34.5 μm; **E**, 152 μm; **F**, 156 μm

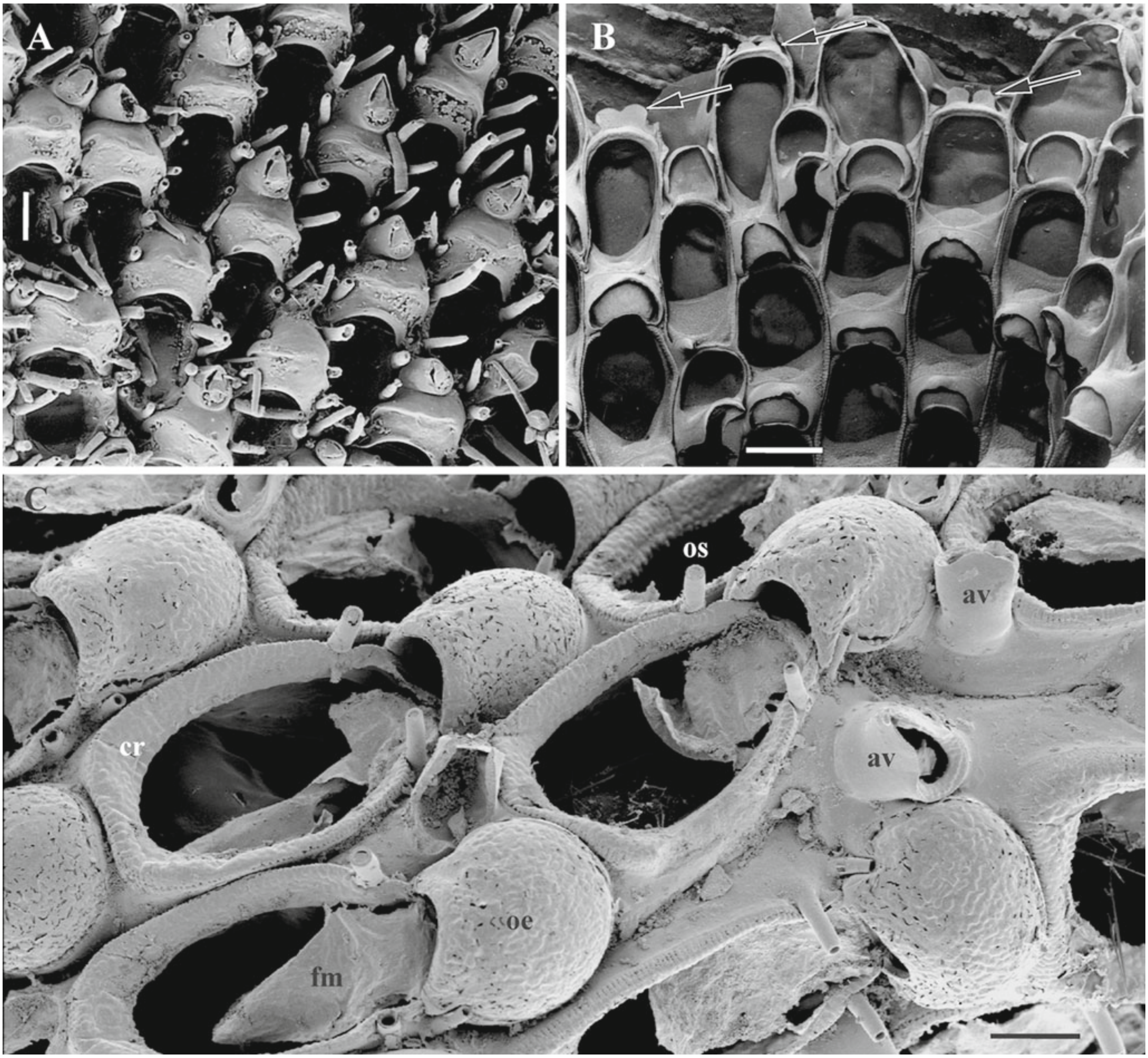

Fig. 2.13 General view of colonies with hyperstomial ovicells. (**A**) *Callopora lineata* (non-cleaned colony). (**B**) *Parellisina* sp. (peripheral part of cleaned colony with ovicells at different stages of formation, with bipartite rudiments of calcification of ovicell floor *arrowed* (photo courtesy of P. Bock). (**C**) *Callopora dumerilii* (non-cleaned colony) ((**A**) – From Ostrovsky and Schäfer 2003, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1046/j.1463-6395.2003.00121.x/abstract). Abbreviations: *av* avicularium, *cr* cryptocyst, *fm* frontal membrane, *oe* ooecium, *os* oral spine. Scale bars: **A**–**C**, 100 μm

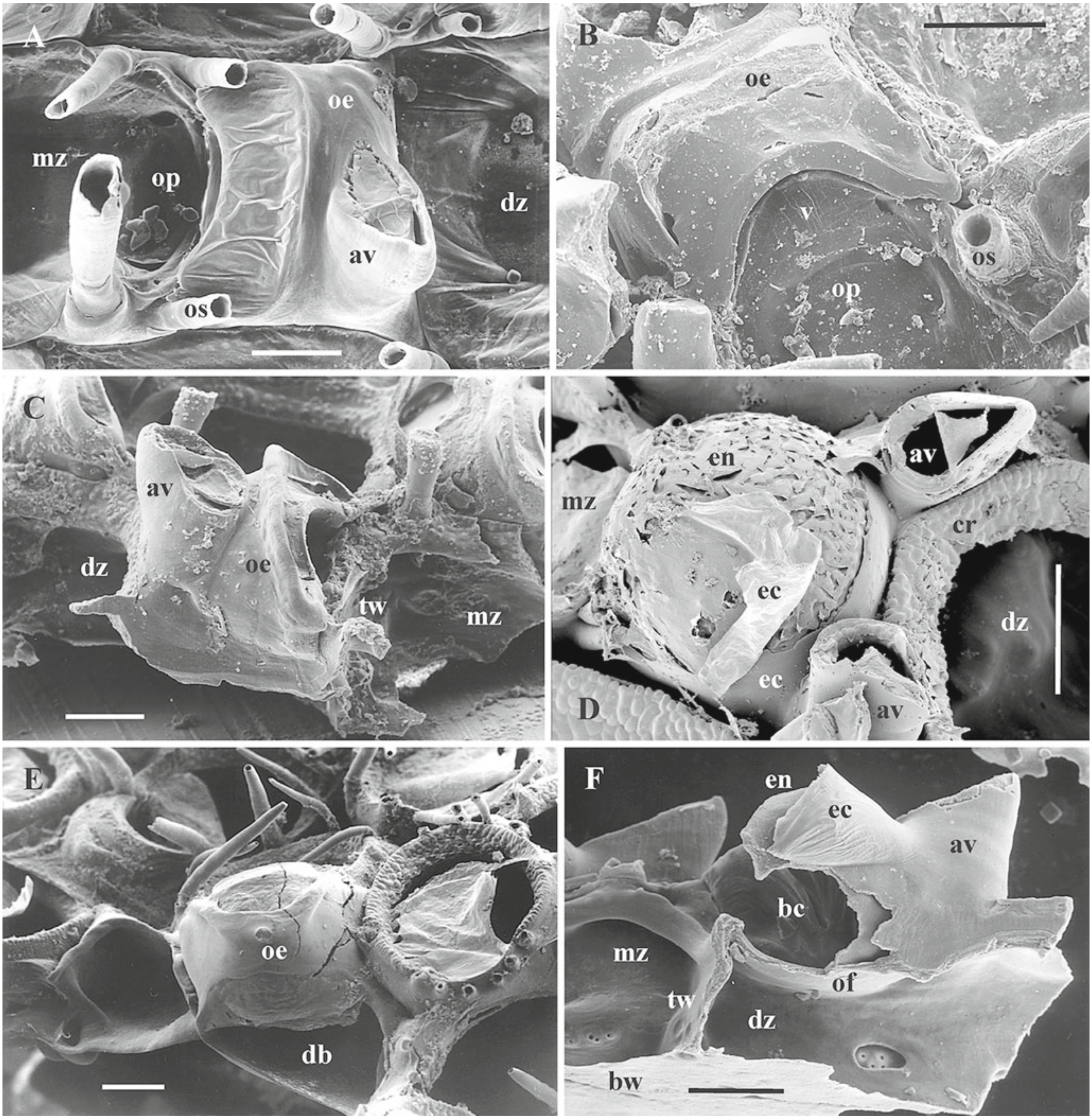

Fig. 2.14 Morphology of hyperstomial ovicells and ooecial structure in: (**A**, **F**) *Tegella armifera*; (**B**, **C**) *Tegella unicornis*; (**D**) *Callopora dumerilii*; (**E**) *Corbulella maderensis*. (**A**) Non-cleaned air-dried ovicell (frontal view). (**B**) Non-cleaned critical-point-dried young ovicell with opening closed by ooecial vesicle (frontal view). (**C**) Non-cleaned mature ovicell with a prominent "collar" around the membranous window (lateral view). (**D**) Non-cleaned ovicell with partially detached membranous part of ectooecium (laterofrontal view). (**E**) Ooecium formed by bud of distal zooid (distal view). (**F**) Cleaned fractured ooecium showing the main elements of the brooding capsule (lateral view) (From Ostrovsky et al. 2009a, courtesy of Springer Verlag, http://link.springer.com/article/10.1007/s00435-008-0070-8). Abbreviations: *av* avicularium, *bc* brood cavity, *bw* basal wall, *cr* cryptocyst, *db* bud of distal zooid, *dz* distal autozooid, *ec* ectooecium, *en* entooecium, *mz* maternal autozooid, *oe* ooecium, *of* ovicell floor, *op* operculum, *os* oral spine, *tw* transverse wall, *v* ooecial vesicle. Scale bars: **A**–**F**, 100 μm

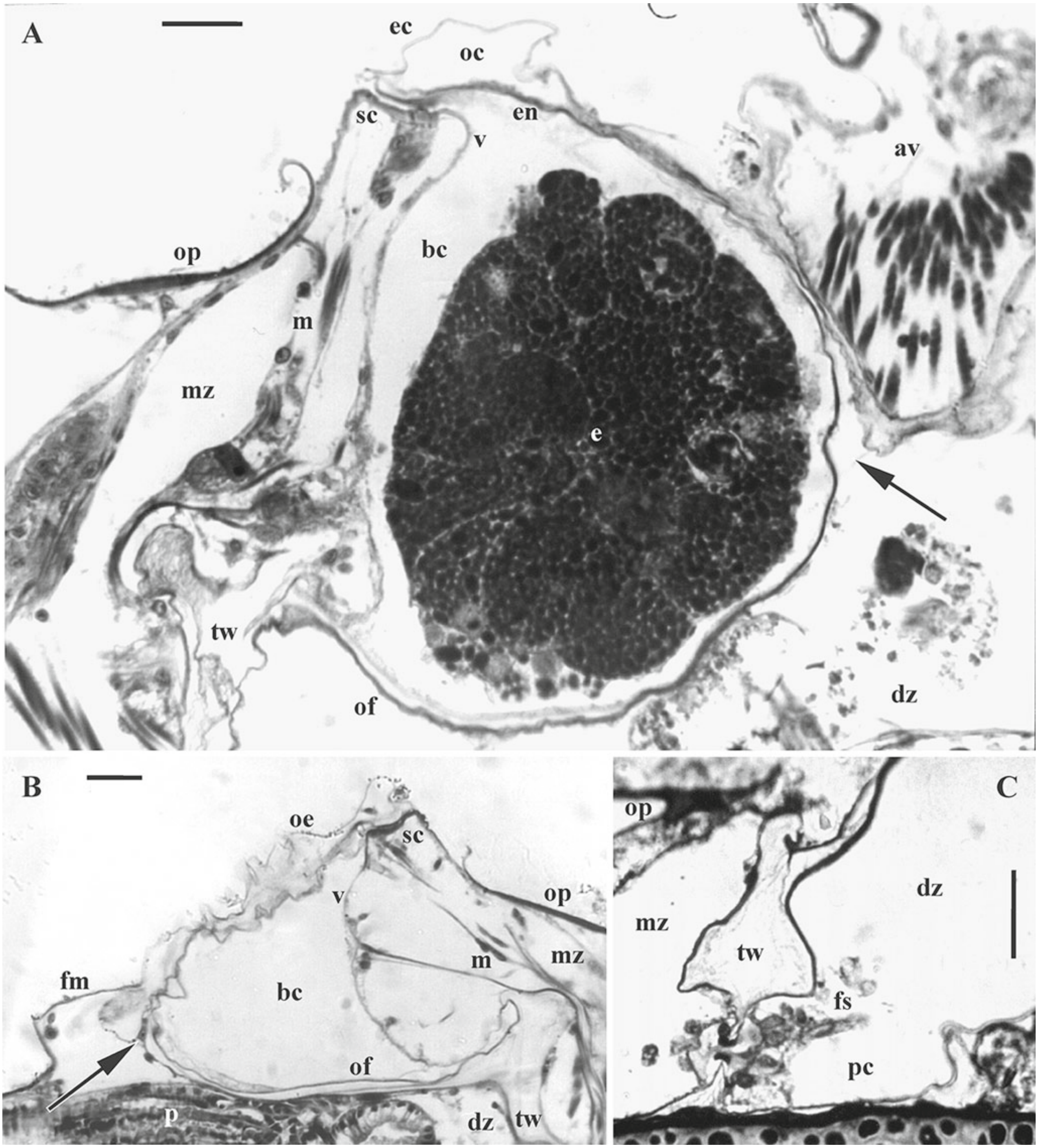

Fig. 2.15 Ovicell anatomy in: (**A**) *Callopora lineata*; (**B**) *Callopora craticula*. Basal pore chamber in (**C**) *Callopora dumerilii* (decalcified specimens). (**A**) Longitudinal section of subimmersed acleithral ovicell with early embryo (open communication pore of ooecium *arrowed*). (**B**) Longitudinal section of empty hyperstomial ovicell (*arrow* indicates communication pore plugged by non-specialized epithelial cells). (**C**) Longitudinal section through the basal pore chamber (the pore-cell complex formed by "special" dumbbell-shaped cells and limiting cells is clearly seen) ((**A**) – From Ostrovsky and Schäfer 2003, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1046/j.1463-6395.2003.00121.x/abstract). Abbreviations: *av* avicularium, *bc* brood cavity, *dz* distal zooid, *e* embryo, *ec* ectooecium, *en* entooecium, *fm* frontal wall, *fs* funicular strand, *m* muscle strands of ooecial vesicle, *mz* maternal zooid, *oc* ooecial coelom, *oe* ooecium, *of* ovicell floor, *op* operculum, *pc* basal pore chamber, *sc* sclerite of ooecial vesicle, *tw* transverse wall, *v* ooecial vesicle. Scale bars: **A**, **B**, 20 µm; **C**, 10 µm

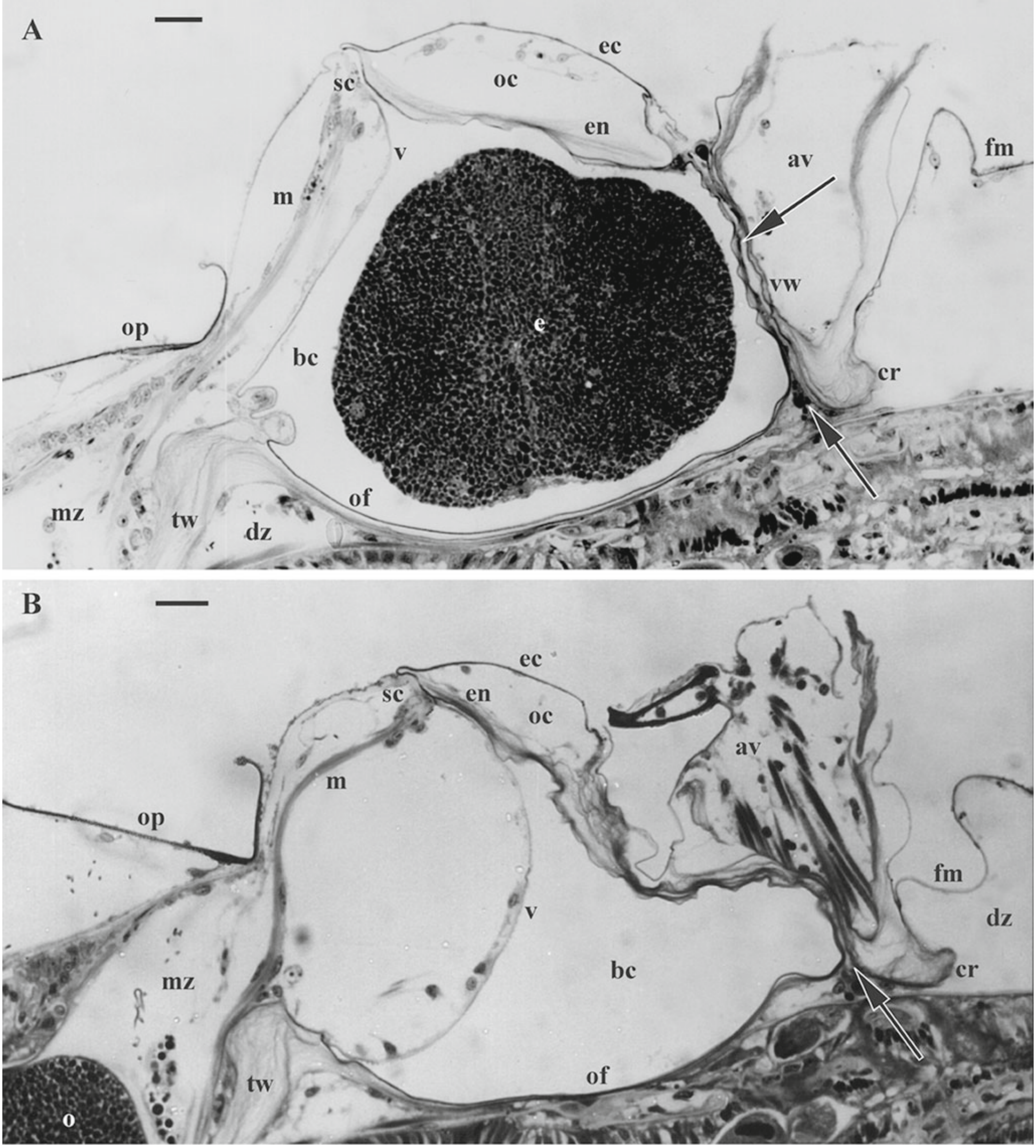

Fig. 2.16 Ovicell anatomy in *Tegella unicornis* (decalcified specimens). Longitudinal section of hyperstomial acleithral ovicell with early embryo (**A**), and ovicell without an embryo, the ooecium slightly folded (**B**). *Arrows* indicate ooecial communication pore plugged by non-specialized epithelial cells (**A**, **B**) and coelomic cavity of ooecium (**A**) (From Ostrovsky et al. 2009a, courtesy of Springer Verlag, http://link.springer.com/article/10.1007/s00435-008-0070-8). Abbreviations: *av* avicularium, *bc* brood cavity, *cr* cryptocyst, *dz* distal zooid, *e* embryo, *ec* ectooecium, *en* entooecium, *fm* frontal membranous wall, *m* muscle strands of ooecial vesicle, *mz* maternal zooid, *oc* ooecial coelom, *of* ovicell floor, *op* operculum, *sc* sclerite of ooecial vesicle, *tw* transverse wall, *v* ooecial vesicle, *vw* vertical wall between coelomic cavities of ooecium and avicularium. Scale bars: **A**, **B**, 20 μm

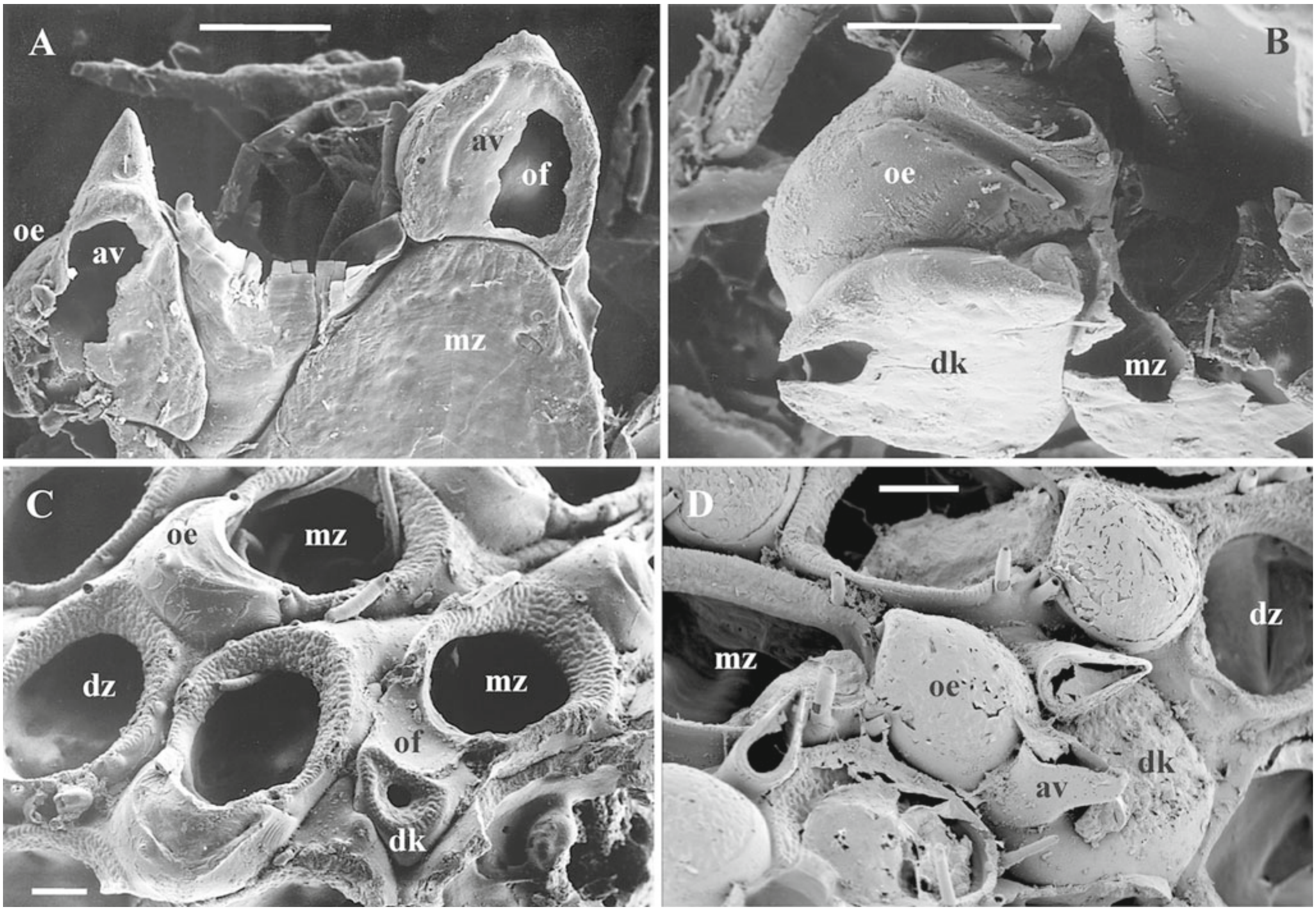

Fig. 2.17 Types of ooecium formation in: (**A**, **B**) *Callopora craticula*; (**C**) *Corbulella maderensis*; (**D**) *Callopora dumerilii*. (**A**) Ooecia formed by 'interzooidal' avicularia at the periphery of the colony (basal view). (**B**) Ooecium formed by distal kenozooid (basolateral view). (**C**) Fractured ooecium (at *right*) with roof missing, formed by a distal kenozooid with prominent frontal part. (**D**) Ooecium and two adventitious avicularia formed by a distal kenozooid (adjacent ooecium formed by a distal autozooid can be seen above it in same photo) ((**A–C**) – From Ostrovsky et al. 2009a, courtesy of Springer Verlag, http://link.springer.com/article/10.1007/s00435-008-0070-8; (**D**) – From Ostrovsky and Schäfer 2003, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1046/j.1463-6395.2003.00121.x/abstract). Abbreviations: *av* avicularium, *dk* distal kenozooid, *dz* distal zooid, *mz* maternal zooid, *oe* ooecium, *of* ovicell floor. Scale bars: **A–D**, 100 μm

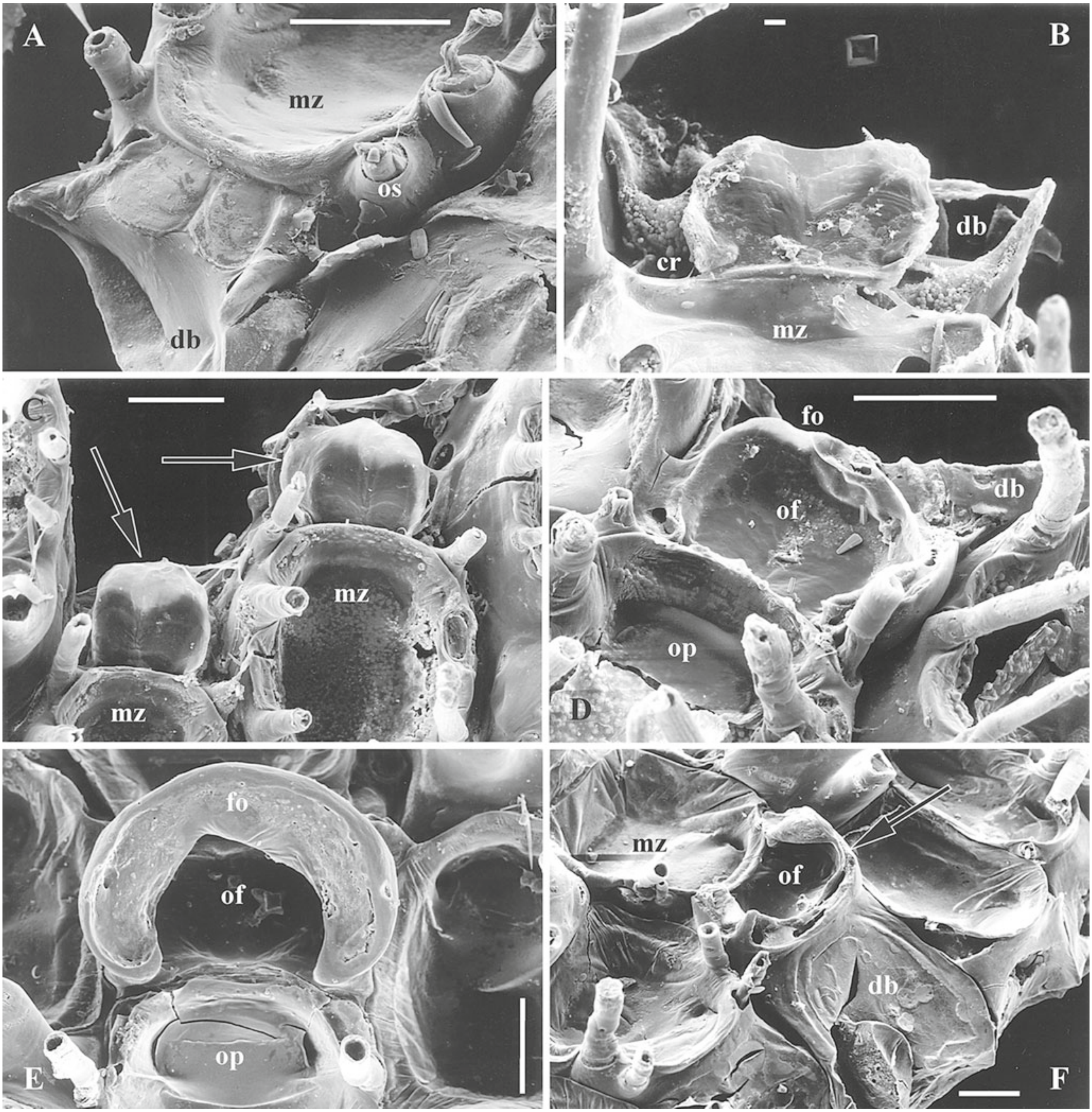

Fig. 2.18 Early ovicellogenesis in: (**A**–**D**) *Callopora lineata*. (**E**, **F**) *Tegella armifera* (critical-point-dried non-cleaned specimens). (**A**, **B**) Earliest stage of ovicell-floor calcification in the form of a bilobate plate (a small area of cryptocyst can be seen to the *left* of the ooecial primordium in **B**). (**C**) Calcification of ovicell floor (initial part of entooecium *arrowed*). (**D**–**F**) Formation of ooecial fold (*arrowed* in **F**) ((**A**, **C**, **D**) – From Ostrovsky and Schäfer 2003, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1046/j.1463-6395.2003.00121.x/abstract; (**B**, **E**) – From Ostrovsky et al. 2003, courtesy of Elsevier, http://www.sciencedirect.com/science/article/pii/S0044523104701047). Abbreviations: *cr* cryptocyst, *db* bud of distal zooid, *fo* ooecial fold, *mz* maternal zooid; *of* ovicell floor, *op* operculum, *os* oral spine. Scale bars: **A**–**F**, 100 μm

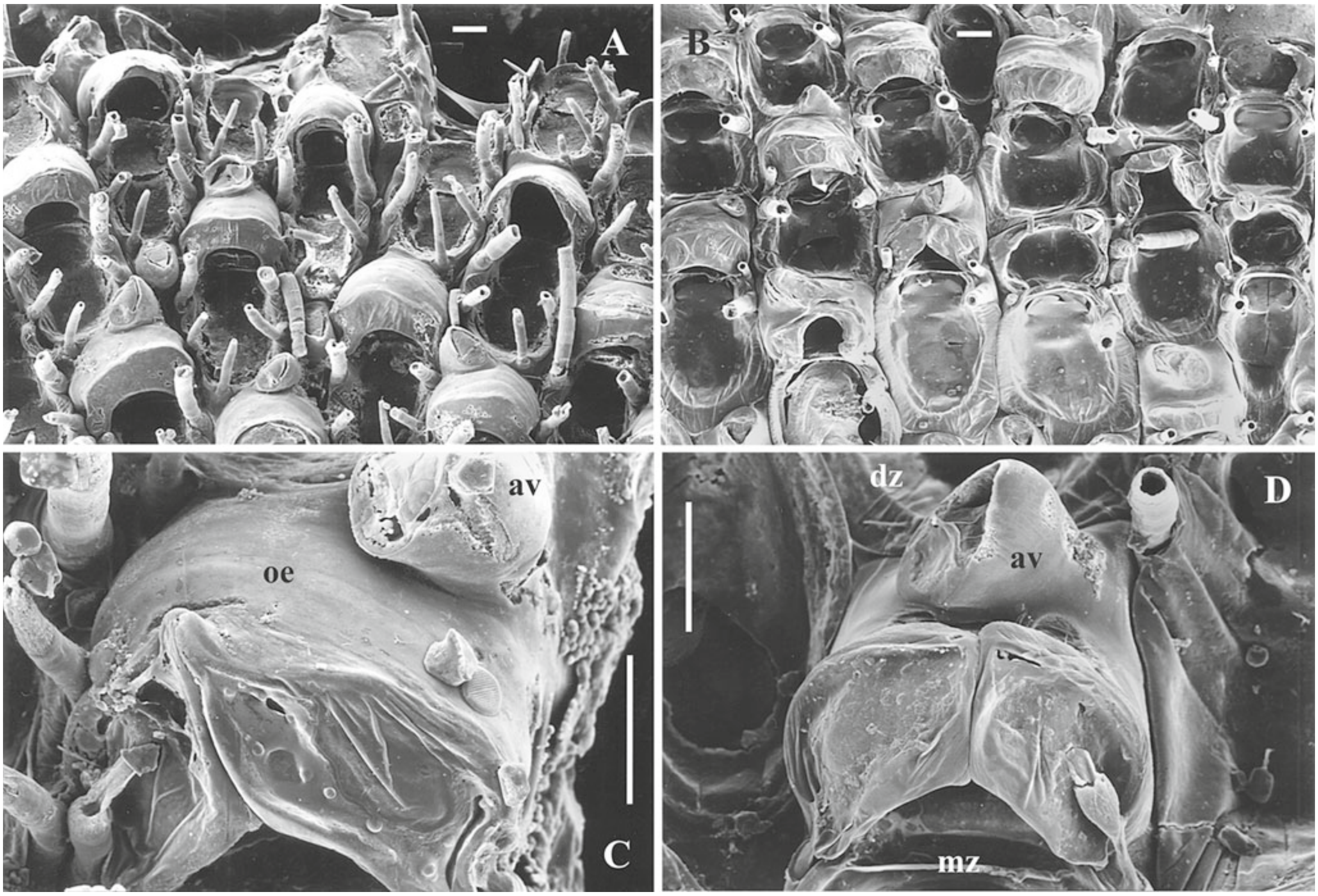

Fig. 2.19 Final stages of ovicell-roof formation in: (**A**, **C**) *Callopora lineata*; (**B**, **D**) *Tegella armifera* (air-dried non-cleaned colonies). (**A**) Peripheral part of colony with centripetally growing ooecial edge. (**B**) Centripetal and bilobate variants of ooecial-roof growth. (**C**, **D**) ooecial-roof growth by fusion of two lateral lobes (From Ostrovsky et al. 2003, courtesy of Elsevier, http://www.sciencedirect.com/science/article/pii/S0044523104701047). Abbreviations: *av* avicularium, *dz* distal zooid, *mz* maternal zooid, *oe* ooecium. Scale bars: **A**–**D**, 100 µm

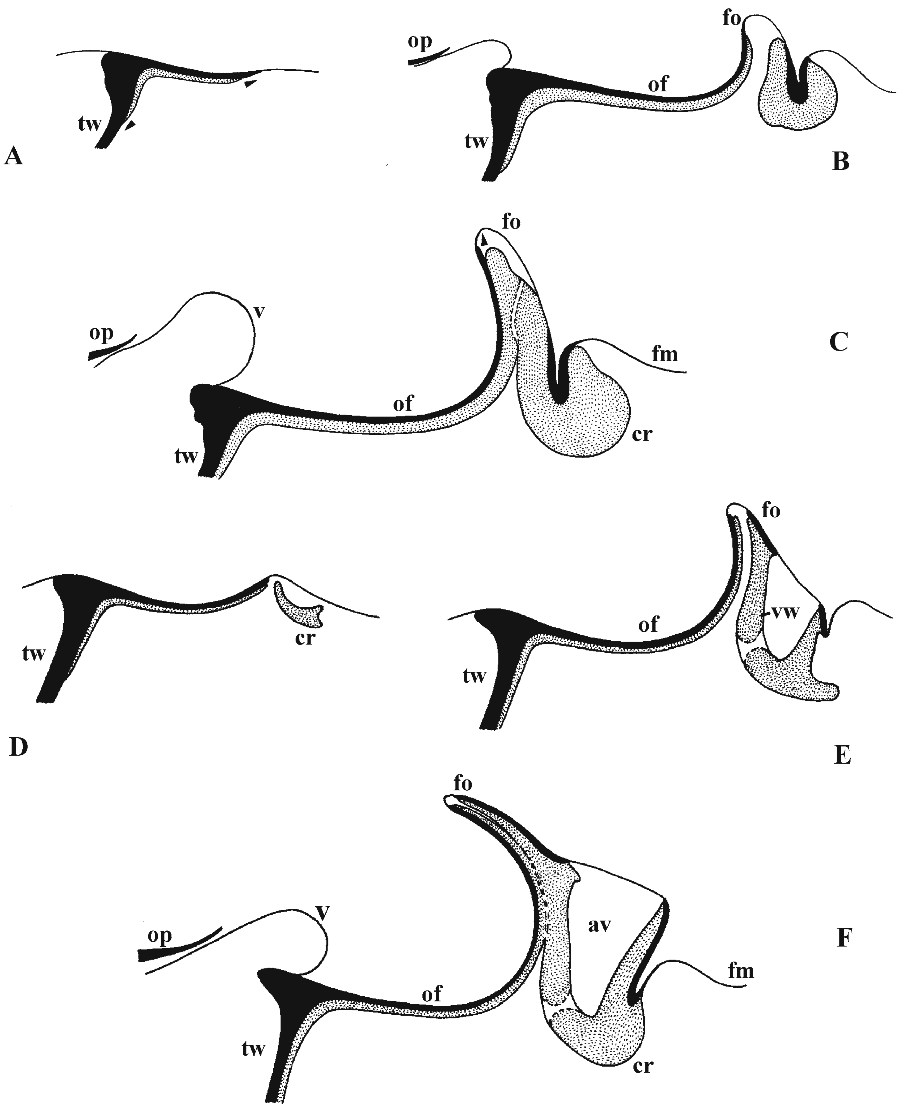

Fig. 2.20 Reconstruction of early ovicellogenesis in calloporids in the absence (**A**–**C**) and presence (**D**–**F**) of an adventitious avicularium (outer calcification *black*, underlying calcification *dotted*, *arrowheads* showing growth directions, ooecial communication canal and pores shown by *dotted lines*) (From Ostrovsky et al. 2003, courtesy of Elsevier, http://www.sciencedirect.com/science/article/pii/S0044523104701047). Abbreviations: *av* avicularium, *cr* cryptocyst, *fm* frontal membranous wall, *fo* ooecial fold, *of* ovicell floor, *op* operculum, *tw* transverse wall, *v* ooecial vesicle, *vw* vertical wall between coelomic cavities of ooecium and avicularium

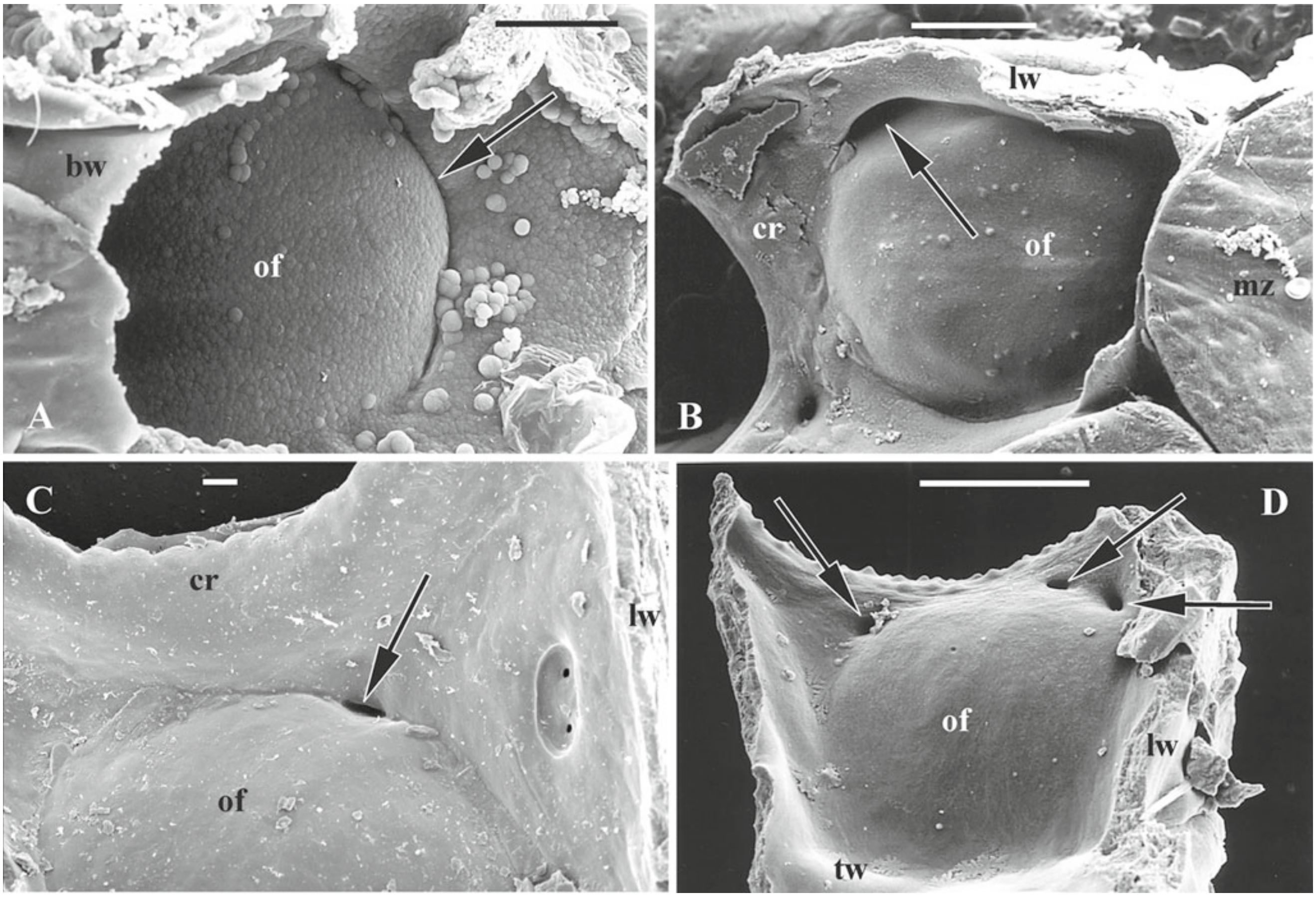

Fig. 2.21 Age-related gradual sealing of the communication slit, with formation of communication pores, in calloporid ooecia: (**A**) *Callopora lineata*; (**B**) *Callopora craticula*; (**C**) *Callopora dumerilii*; (**D**) *Tegella unicornis*. (**A**) Arc-like communication slit (*arrowed*) in young ovicell. (**B**) Partly closed communication slit (*arrowed*). (**C**, **D**) One (**C**) and three (**D**) communication pores (*arrowed*) remaining after the closure of the communication slit ((**A**) – From Ostrovsky and Schäfer 2003, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1046/j.1463-6395.2003.00121.x/abstract; (**B**) – From Ostrovsky et al. 2009a, courtesy of Springer Verlag, http://link.springer.com/article/10.1007/s00435-008-0070-8; (**D**) – From Ostrovsky et al. 2003, courtesy of Elsevier, http://www.sciencedirect.com/science/article/pii/S0044523104701047). Abbreviations: *bw* basal wall, *cr* cryptocyst, *lw* lateral wall, *mz* maternal zooid, *of* ovicell floor, *tw* transverse wall. Scale bars: **A**, **B**, 30 µm; **C**, 10 µm; **D**, 100 µm

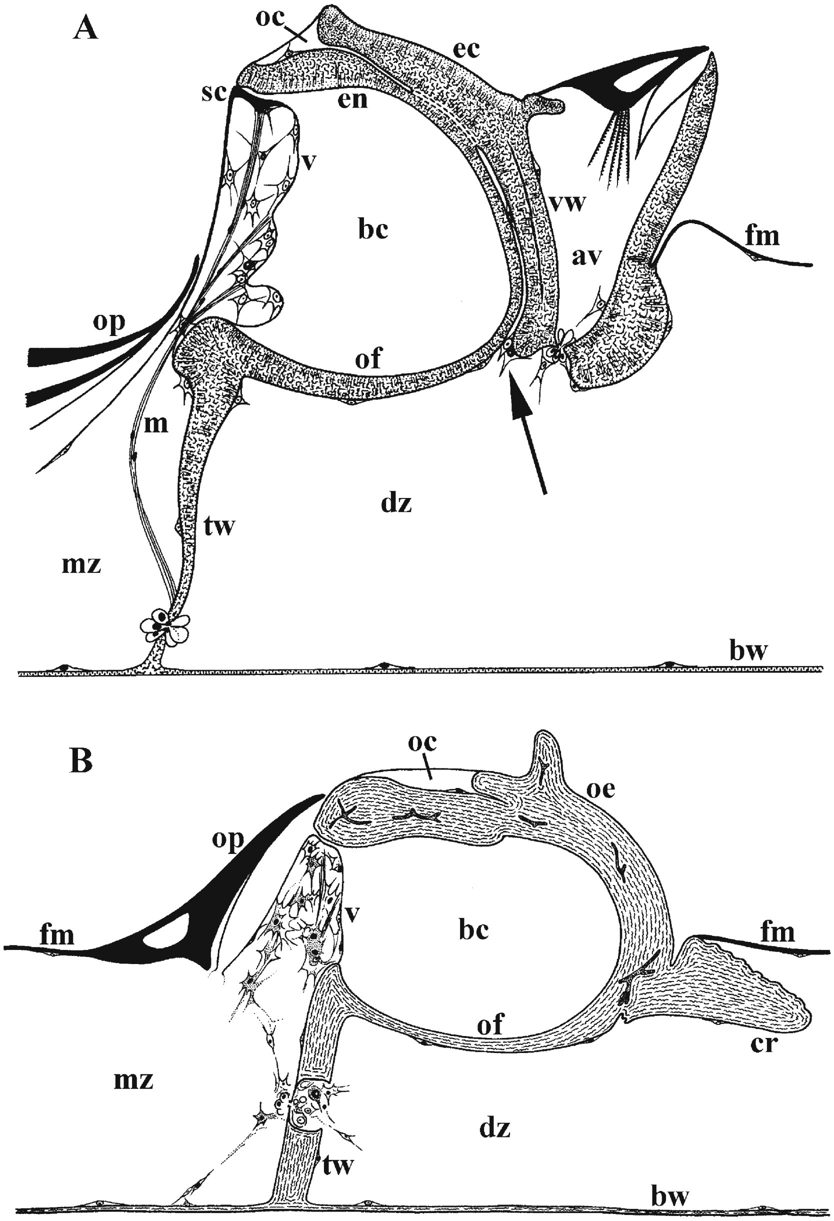

Fig. 2.22 Schematic longitudinal sections of hyperstomial ovicells in: (**A**) *Tegella armifera* (ovicell acleithral; *arrow* indicates ooecial communication pore plugged by non-specialized epithelial cells); (**B**) *Corbulella maderensis* (ovicell cleithral; ooecial walls fused to form a solid common wall, which is perforated by fungal hyphae) (From Ostrovsky et al. 2009a, courtesy of Springer Verlag, http://link.springer.com/article/10.1007/s00435-008-0070-8). Abbreviations: *av* avicularium, *bc* brood cavity, *bw* basal wall, *cr* cryptocyst, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *fm* membranous frontal wall, *m* muscle strands of ooecial vesicle, *mz* maternal zooid, *oc* ooecial coelom, *oe* ooecium, *of* ovicell floor, *op* operculum, *sc* sclerite of ooecial vesicle, *tw* transverse wall, *v* ooecial vesicle, *vw* vertical wall between coelomic cavities of ooecium and avicularium

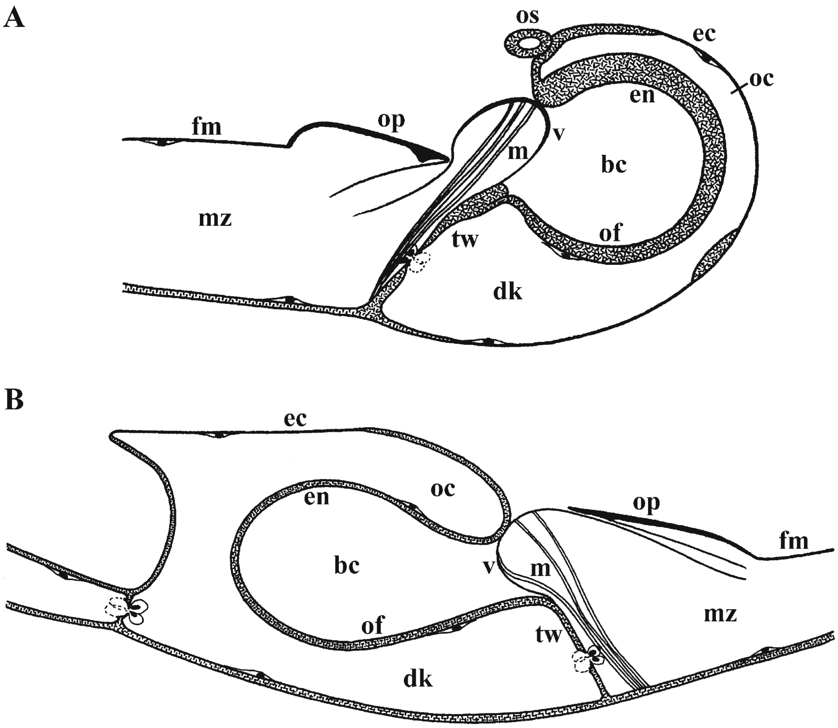

Fig. 2.23 Schematic longitudinal sections of hyperstomial acleithral ovicells in: (**A**) *Bryocalyx cinnameus* (terminal ovicell); (**B**) *Concertina cultrata* (From Ostrovsky et al. 2009a, courtesy of Springer Verlag, http://link.springer.com/article/10.1007/s00435-008-0070-8). Abbreviations: *bc* brood cavity, *dk* distal kenozooid, *ec* ectooecium, *en* entooecium, *fm* membranous frontal wall, *m* muscle strands of ooecial vesicle, *mz* maternal zooid, *oc* ooecial coelom, *of* ovicell floor, *op* operculum, *os* oral spine, *tw* transverse wall, *v* ooecial vesicle

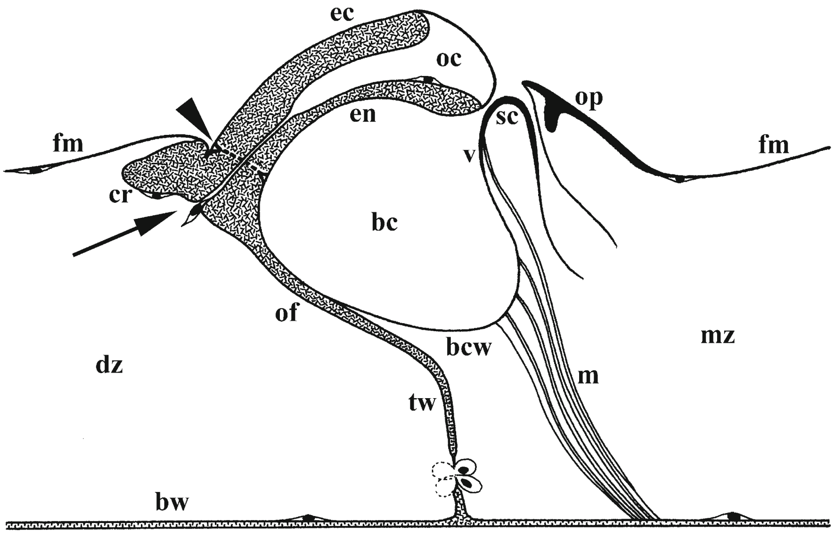

Fig. 2.24 Schematic longitudinal section of subimmersed cleithral ovicell in *Valdemunitella lata* (*arrowhead* indicates horizontal slit of ooecium, *arrow* indicates communication pore of an ooecial lobe plugged by non-specialized epithelial cells) (From Ostrovsky et al. 2009a, courtesy of Springer Verlag, http://link.springer.com/article/10.1007/s00435-008-0070-8). Abbreviations: *bc* brood cavity, *bcw* brood-cavity wall, *bw* basal wall, *cr* cryptocyst, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *fm* frontal membranous wall, *m* muscle strands of ooecial vesicle, *mz* maternal zooid, *oc* ooecial coelom, *of* ovicell floor, *op* operculum, *sc* sclerite of ooecial vesicle, *tw* transverse wall, *v* ooecial vesicle

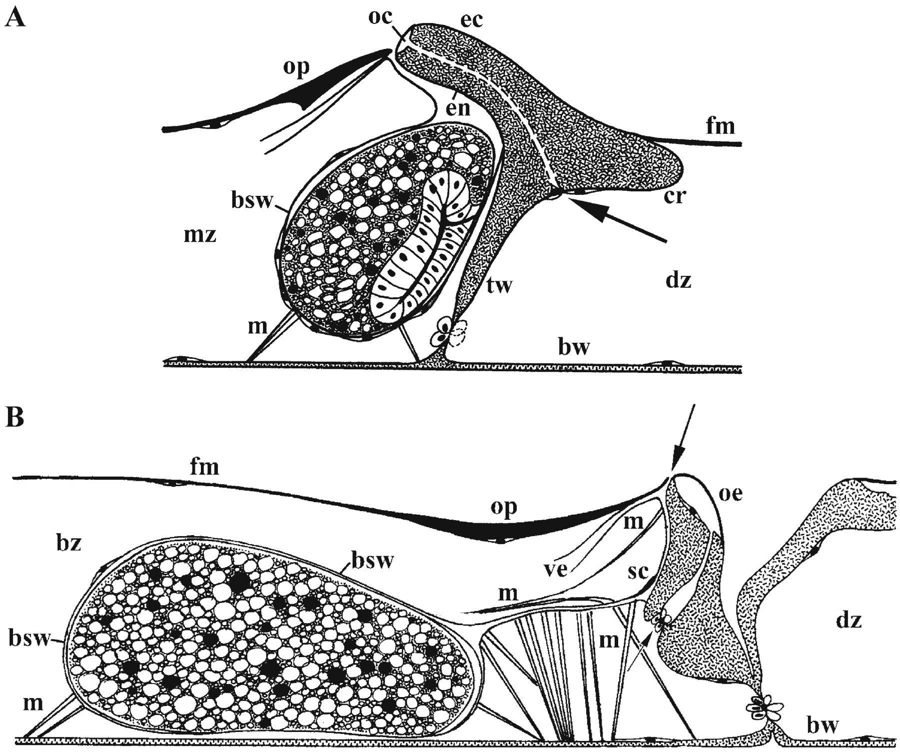

Fig. 2.25 Schematic longitudinal sections of: (**A**) immersed cleithral ovicell in *Crassimarginatella* sp. (*arrow* indicates communication pore plugged by non-specialized epithelial cells); (**B**) internal brood sac with vestigial ooecium in *Cauloramphus spinifer* (*larger arrow* indicates a common opening leading to vestibulum and entrance to brood sac; *smaller arrow* indicates ooecial communication pore plugged by a pore-cell complex) ((**A**) – From Ostrovsky et al. 2009a, courtesy of Springer Verlag, http://link.springer.com/article/10.1007/s00435-008-0070-8; (**B**) – From Ostrovsky et al. 2007, courtesy of Zoological Society of Japan, http://www.bioone.org/doi/abs/10.2108/zsj.24.1187?journalCode=jzoo). Abbreviations: *bsw* brood-sac wall, *bw* basal wall, *cr* cryptocyst, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *fm* membranous frontal wall, *m* muscle strands of ooecial vesicle and brood sac, *mz* maternal zooid, *oc* ooecial coelom, *oe* kenozooidal ooecium, *of* ovicell floor, *op* operculum, *sc* sclerite of ooecial vesicle, *tw* transverse wall

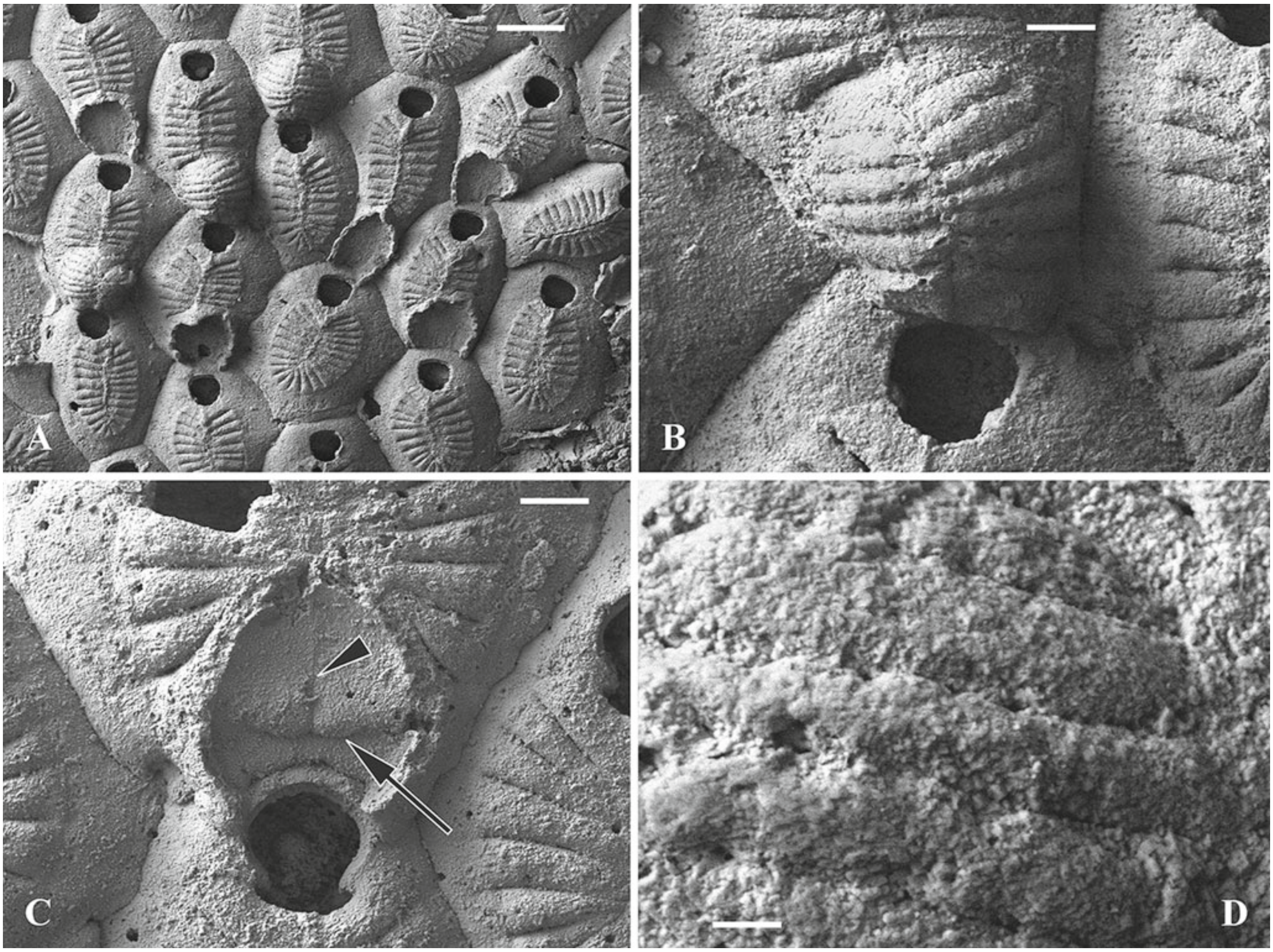

Fig. 2.26 Structure of costate ooecia in: (**A**, **B**, **D**) *Leptocheilopora* sp. 2; (**C**) *Leptocheilopora magna*. (**A**) Part of colony with whole and fractured ovicells. (**B**) General view of ooecium. (**C**) Fractured ooecium (closed horizontal slit and medial suture of ooecium *arrowed*). (**D**) Part of ooecial surface showing close lateral appression of costae, possibly even incipient costal fusion) ((**B**–**D**) – From Ostrovsky and Taylor 2005a, b, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.2005.00179.x/abstract). Scale bars: **A**, 286 µm; **B**, 71.4 µm; **C**, 83.3 µm; **D**, 19.6 µm

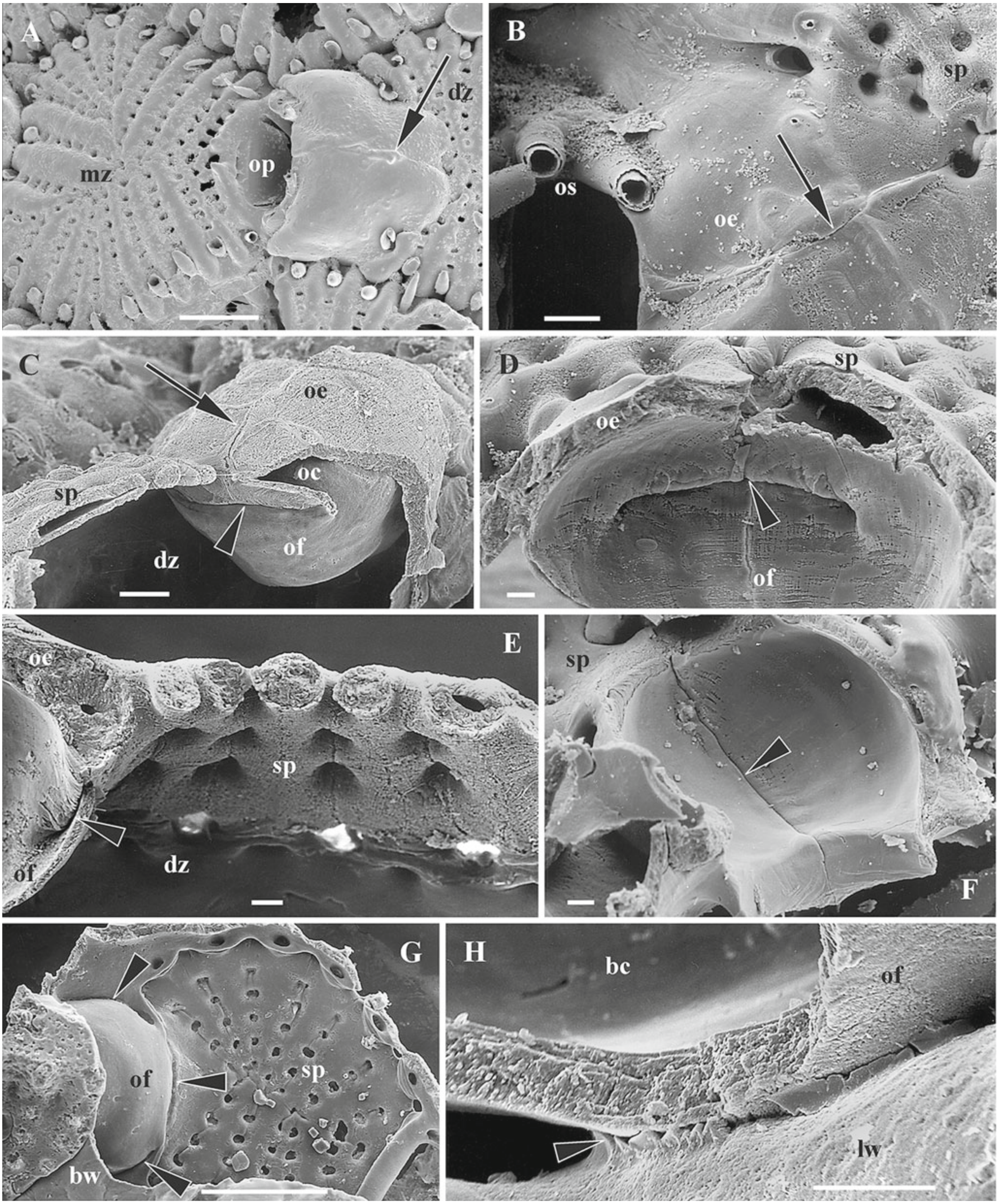

Fig. 2.27 Ovicell structure in: (**A**) *Puellina radiata* (prominent ovicell); (**B**–**E**) *Puellina hincksi* (endozooidal); (**F**–**H**) *Puellina denticulata* (endozooidal). (**A**) Maternal zooid with ooecium formed by distal autozooid (non-cleaned specimen; medial ooecial suture *arrowed*). (**B**) Ooecium and frontal shield of distal zooid (a tiny pelmatidium can be seen in the ooecium and a costa above, *arrow* indicates the medial suture). (**C**) Structure of distal part of ooecium (spinocyst of distal zooid and part of ectooecium are removed; *arrow* indicates medial suture, *arrowhead* indicates closed horizontal slit of ooecium). (**D**) Inner surface of ooecium (*arrowhead* indicates closed horizontal slit). (**E**) Longitudinal fracture through ooecium and spinocyst of distal zooid (*arrowhead* indicates closed horizontal slit). (**F**) Inner surface of ooecium (*arrowhead* indicates medial suture). (**G**) Basal view of ovicell floor (at *left*) and spinocyst of distal zooid (*arrowheads* indicate closed horizontal slit and lateral communication slits). (**H**) Area of lateral communication slit partly closed by calcification (*arrowhead*) of lateral zooidal wall ((**E**, **G**) – From Ostrovsky 2002, courtesy of Taylor and Francis Ltd.). Abbreviations: *bc* brood cavity, *bw* basal wall, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *lw* lateral wall, *mz* maternal zooid, *oc* ooecial coelom, *oe* ooecium, *of* ovicell floor, *op* operculum, *os* oral spine, *sp* spinocyst. Scale bars: **A**, **G**, 100 µm; **B**, 20 µm; **c**, 30 µm; **D**–**F**, **H**, 10 µm

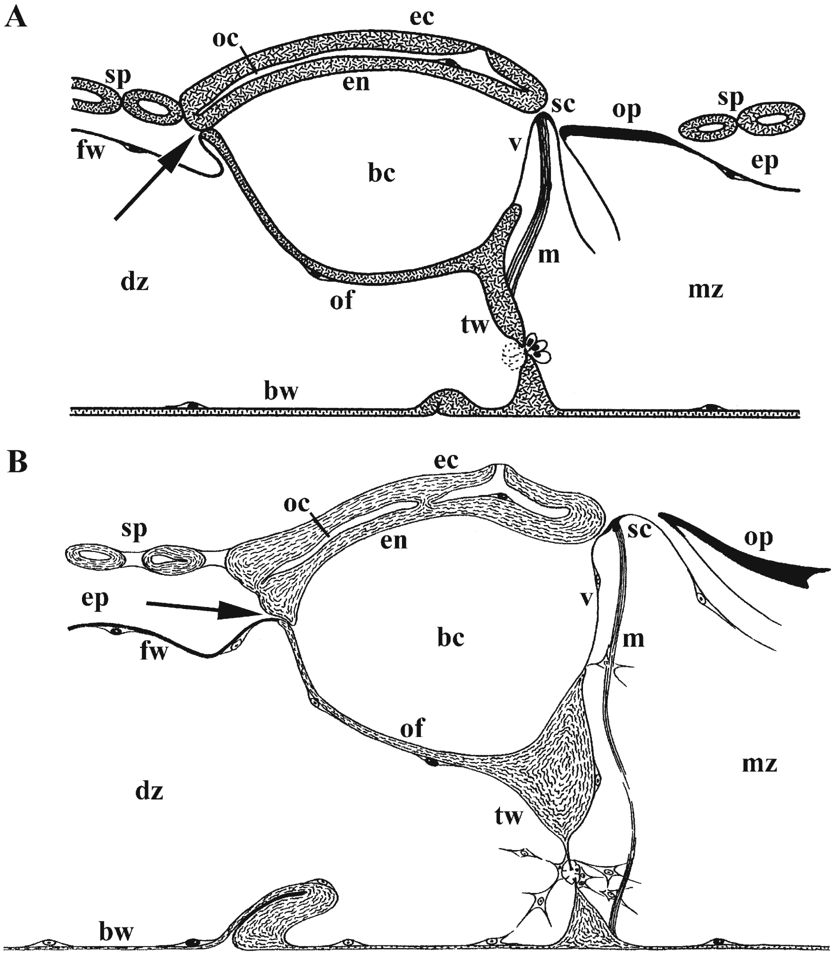

Fig. 2.28 Schematic longitudinal sections of endozooidal semicleithral ovicells in: (**A**) *Puellina radiata*; (**B**) *Puellina hincksi* (each ooecium shows a pelmatidium; closed horizontal slit of ooecium *arrowed*) ((**B**) – From Ostrovsky 2002, with modifications, courtesy of Taylor and Francis Ltd.). Abbreviations: *bc* brood cavity, *bw* basal wall, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *ep* epistege, *fw* membranous frontal wall, *m* muscle strands of ooecial vesicle, *mz* maternal zooid, *oc* ooecial coelom, *of* ovicell floor, *op* operculum, *sc* sclerite of ooecial vesicle, *sp* spinocyst, *tw* transverse wall, *v* ooecial vesicle

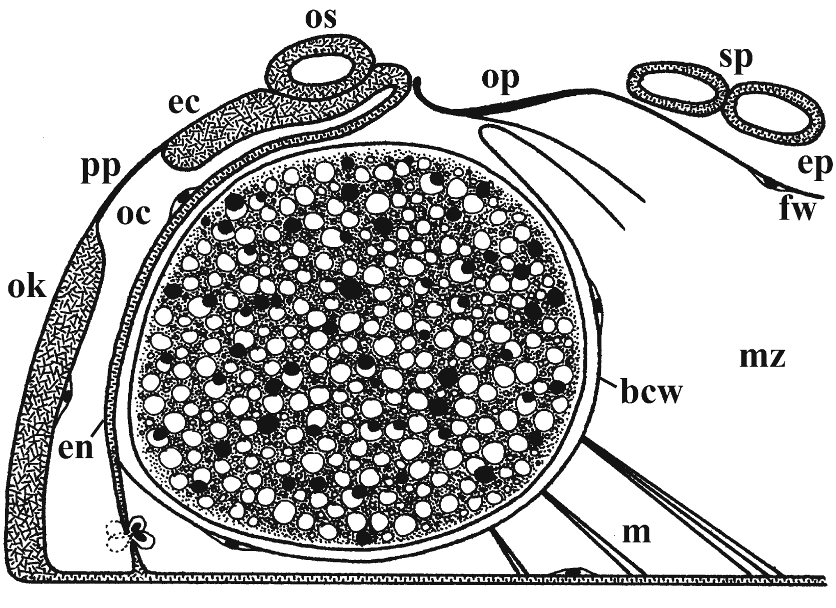

Fig. 2.29 Schematic longitudinal section of terminal cleithral ovicell in *Cribrilina annulata*. Abbreviations: *bc* brood cavity, *bcw* brood-cavity wall, *ec* ectooecium, *en* entooecium, *ep* epistege, *fw* frontal membranous wall, *m* muscular bundles of brood-cavity wall, *mz* maternal zooid, *oc* ooecial coelom, *ok* kenozooidal ooecium, *op* operculum, *os* oral spine, *pp* pseudopore, *sp* spinocyst

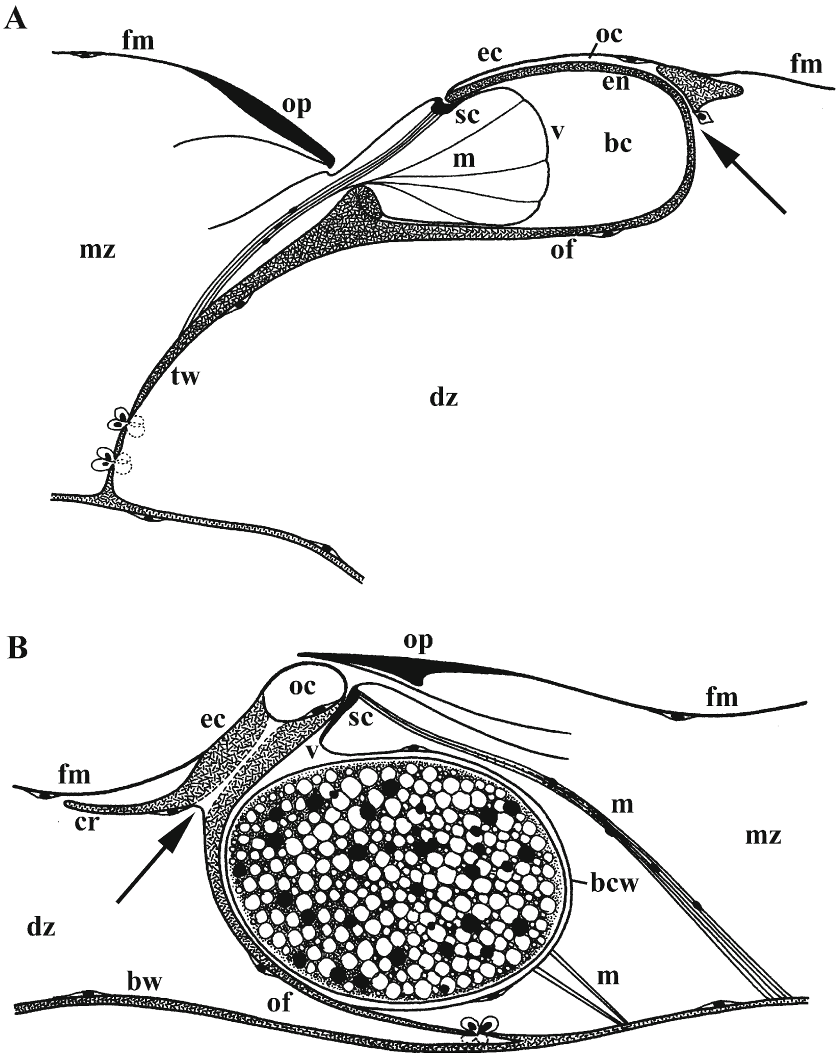

Fig. 2.30 Schematic longitudinal sections of ovicells in: (**A**) *Caberea solida* (endozooidal acleithral ovicell); (**B**) *Bugulopsis monotrypa* (immersed cleithral ovicell) (communication pores of ooecia *arrowed*). Abbreviations: *bc* brood cavity, *bcw* brood-cavity wall, *bw* basal wall, *cr* cryptocyst, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *fm* membranous frontal wall, *m* muscle strands of ooecial vesicle, *mz* maternal zooid, *oc* ooecial coelom, *of* ovicell floor, *op* operculum, *sc* sclerite of ooecial vesicle, *tw* transverse wall, *v* ooecial vesicle

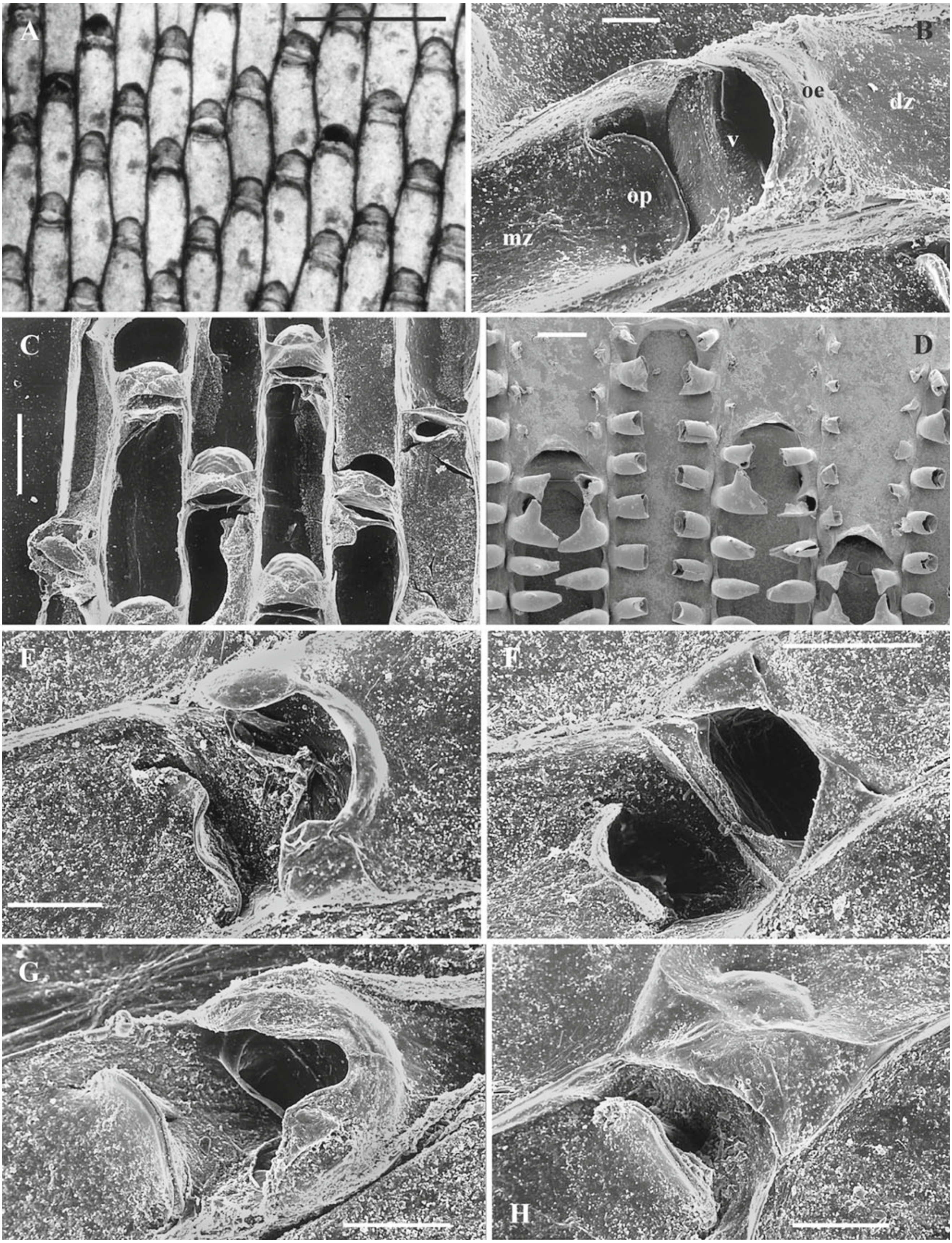

Fig. 2.31 Structure and development of endozooidal ovicells in: (**A**–**C**, **E**–**H**) *Chartella membranaceotruncata*; (**D**) *Gregarinidra serrata*. (**A**, **C**) Areas of non-cleaned colonies with ovicells (**A** wet specimen, **C** air-dried specimen). (**B**) Mature non-cleaned ovicell, showing the operculum of the maternal zooid and a collapsed ooecial vesicle. (**D**) Early stages of ovicellogenesis. (**E**–**H**) Stages of ovicell formation. Abbreviations: *dz* distal zooid, *mz* maternal zooid, *oe* ooecium, *op* operculum, *v* ooecial vesicle. Scale bars: **A**, 1 mm; **B**, **D**–**H**, 100 μm; **c**, 300 μm

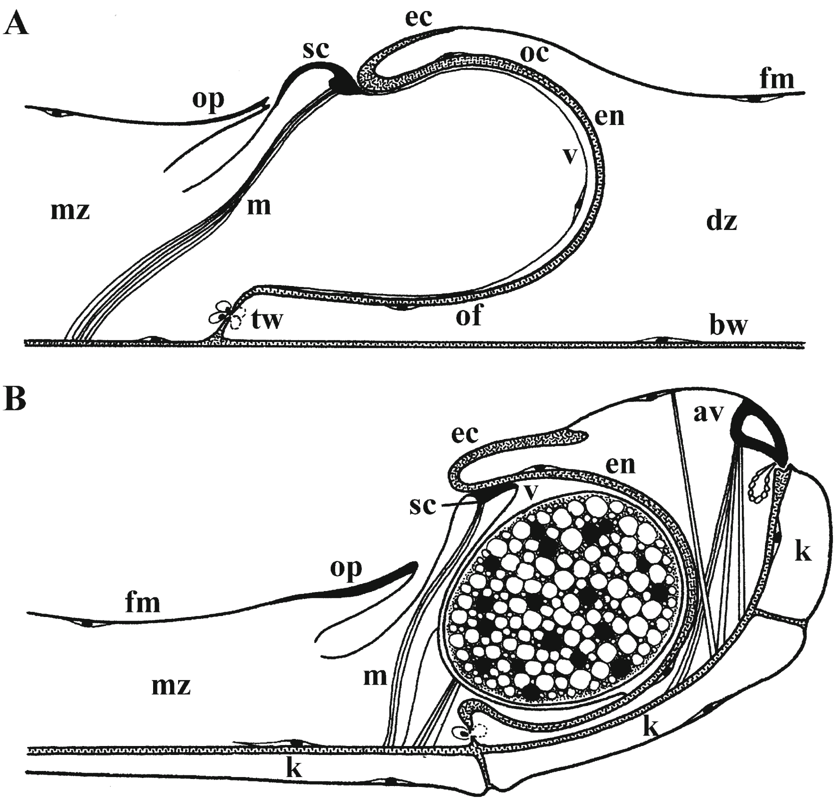

Fig. 2.32 Schematic longitudinal sections of endozooidal acleithral ovicells in: (**A**) *Securiflustra securifrons*; (**B**) *Spiralaria florea*. Abbreviations: *av* avicularium, *bw* basal wall, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *fm* membranous frontal wall, *k* kenozooid, *m* muscle strands of ooecial vesicle, *mz* maternal zooid, *oc* ooecial coelom, *of* ovicell floor, *op* operculum, *sc* sclerite of ooecial vesicle, *tw* transverse wall, *v* ooecial vesicle

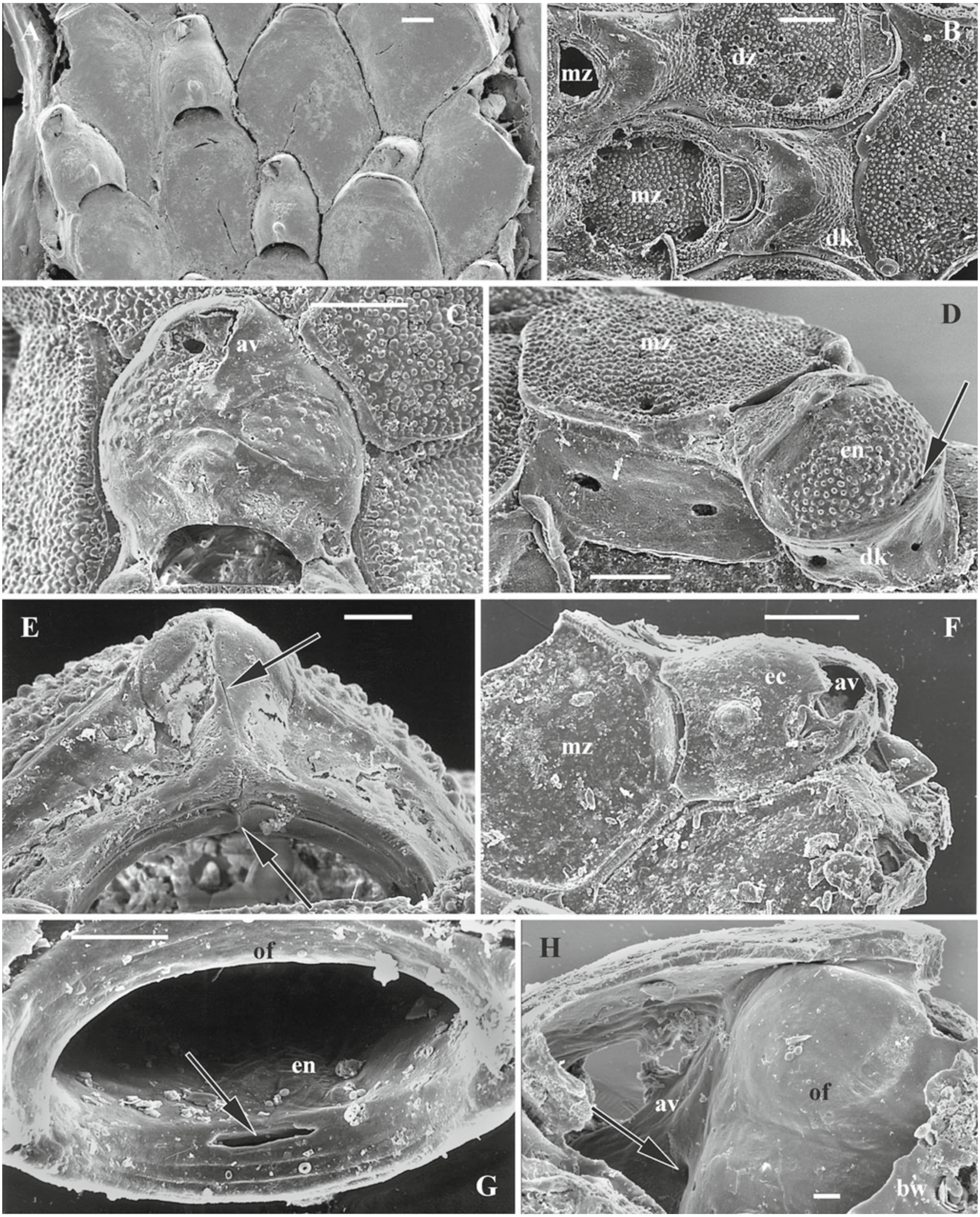

Fig. 2.33 Structure of hyperstomial cleithral ovicells in: (**A**) *Micropora brevissima*; (**B**) *Micropora variperforata*; (**C**–**E**) *Micropora notialis*; (**F**–**H**) *Micropora gracilis*. (**A**) Part of non-cleaned colony with ooecia formed by interzooidal avicularia. (**B**) Part of cleaned colony with ooecia formed by distal autozooid (*top left*) and distal kenozooid. (**C**, **D**) Cleaned specimens with ooecia formed by interzooidal avicularium (**C**) and distal kenozooid (**D**) (*arrow* indicates communication pore of ooecium). (**E**) Proximal edge of cleaned ooecium (*arrows* indicate medial sutures of ectooecium and entooecium). (**F**) Non-cleaned specimen with ovicell, the ooecium of which is formed by an interzooidal avicularium. (**G**) Non-calcified window (*arrowed*) on internal surface of entooecium. (**H**) Cavity of interzooidal avicularium and ovicell floor (*arrow* indicates communication pore of ooecium). Abbreviations: *av* avicularium, *cr* cryptocyst, *dk* distal kenozooid, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *mz* maternal zooid, *of* ovicell floor. Scale bars: **A**–**D**, **F**, 100 µm; **E**, **G**, 30 µm; **H**, 10 µm

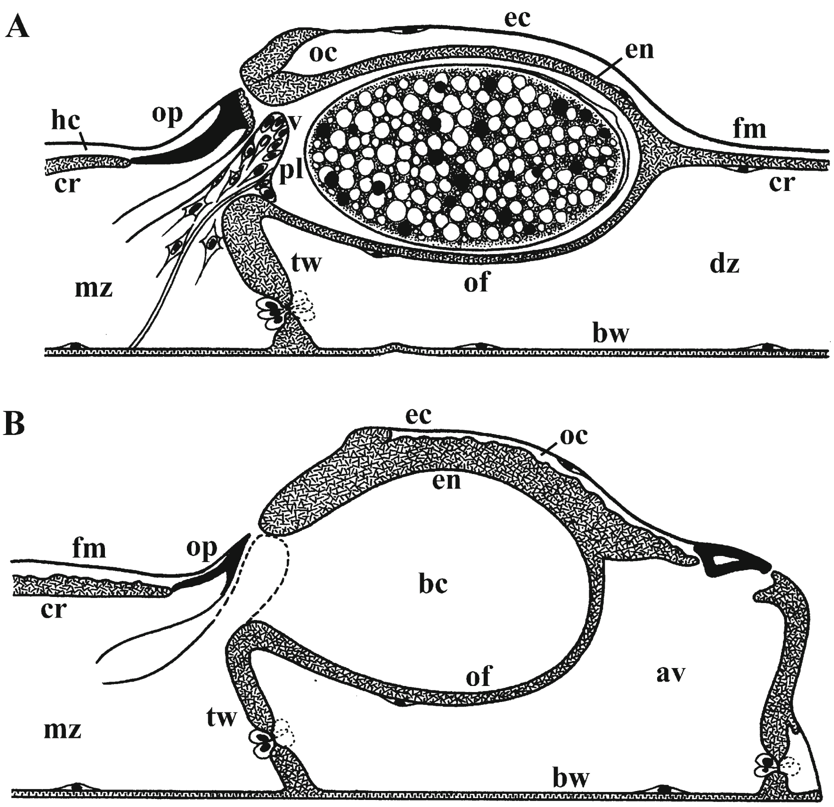

Fig. 2.34 Schematic longitudinal sections of hyperstomial cleithral ovicells in: (**A**) *Micropora notialis* (ooecium formed by distal autozooid); (**B**) *Micropora brevissima* (ooecium is formed by an interzooidal avicularium). Abbreviations: *av* avicularium, *bc* brood cavity, *bw* basal wall, *cr* cryptocyst, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *fm* membranous frontal wall, *hc* hypostegal coelom, *m* muscle strands of ooecial vesicle, *mz* maternal zooid, *oc* ooecial coelom, *of* ovicell floor, *op* operculum, *pl* placental analogue, *tw* transverse wall, *v* ooecial vesicle

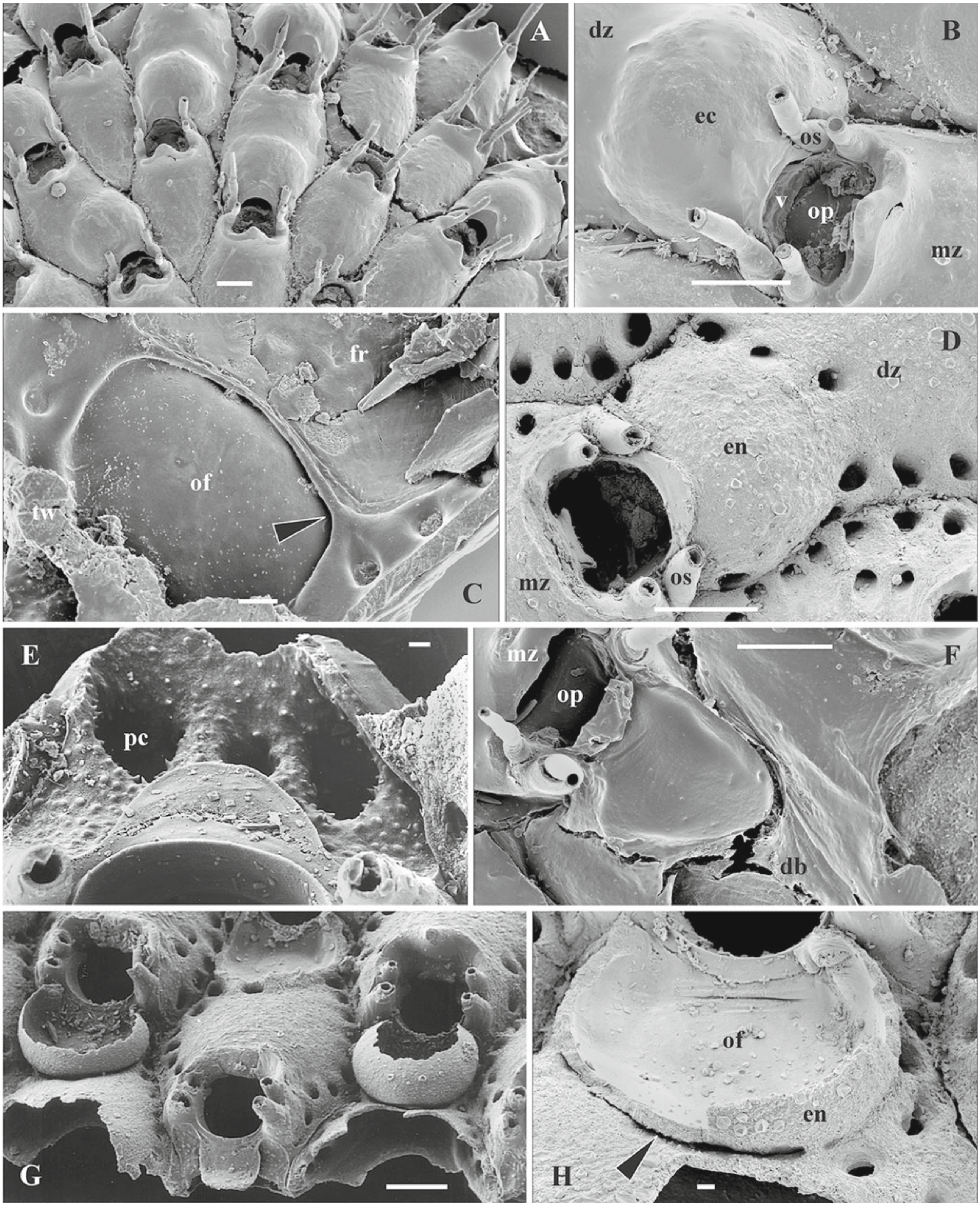

Fig. 2.35 Structure and development of hyperstomial acleithral ovicells in *Escharella immersa*. (**A**) Part of non-cleaned colony with ooecia formed by distal autozooids. (**B**, **D**) General view of ovicell (**B**, non-cleaned specimen with ooecial vesicle and operculum visible). (**C**) Basal view of ovicell floor and part of frontal shield (arc-like communication slit *arrowed*). (**E**–**H**) Early and intermediate stages of ovicellogenesis (**F**, non-cleaned preparation; in **H** *arrowhead* points to yet-unsealed communication slit). Abbreviations: *db* bud of distal zooid, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *fr* frontal shield, *mz* maternal zooid, *of* ovicell floor, *op* operculum, *os* oral spine, *pc* basal pore chamber, *tw* transverse wall, *v* ooecial vesicle. Scale bars: **A**, **B**, **D**, **F**, **G**, 100 μm; **C**, 20 μm; **E**, **H**, 10 μm

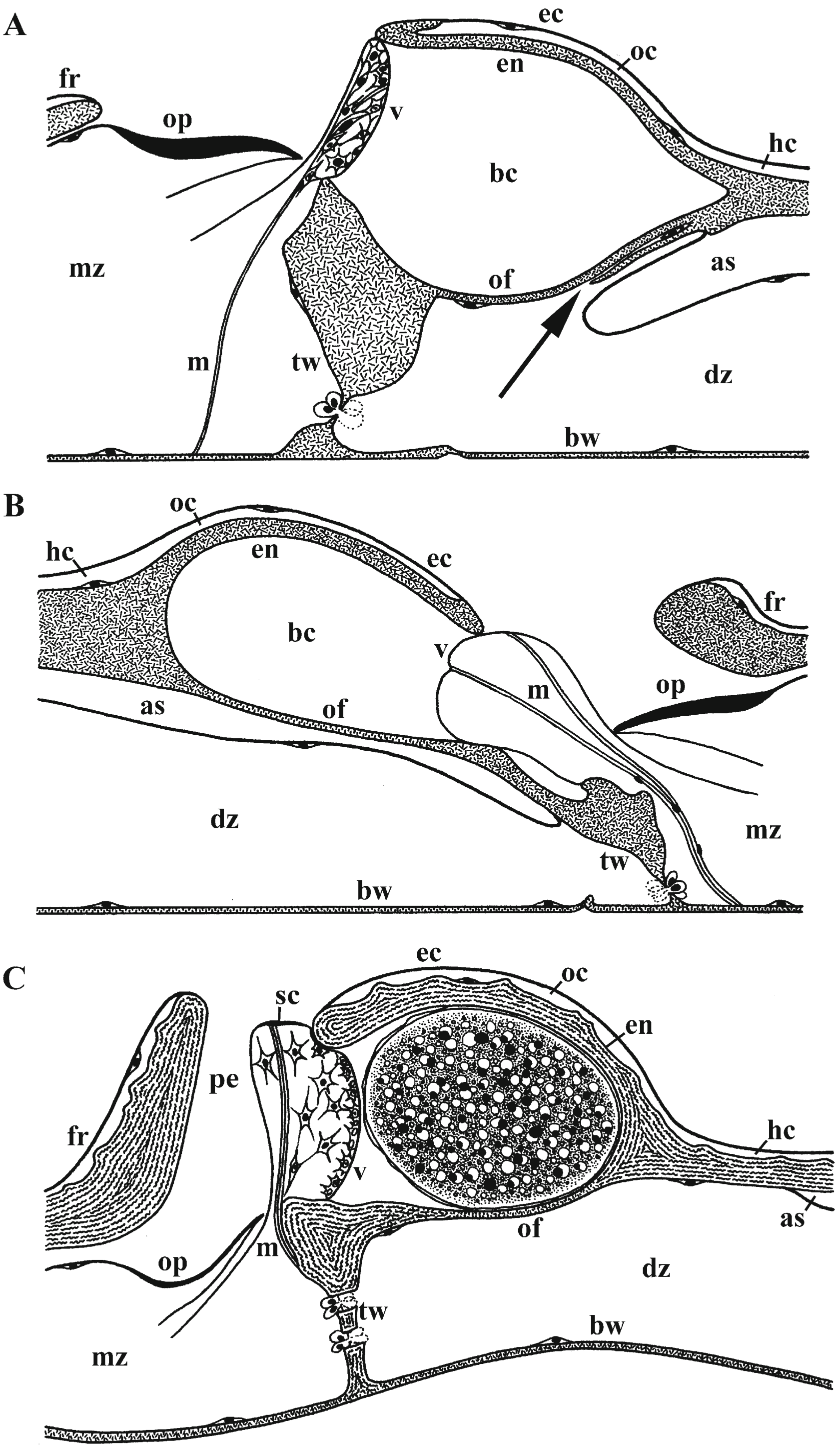

Fig. 2.36 Schematic longitudinal sections of hyperstomial acleithral ovicells in: (**A**) *Escharella immersa* (communication slit of ooecium *arrowed*); (**B**) *Exochella* sp.; (**C**) *Lageneschara lyrulata*. Abbreviations: *as* ascus, *bc* brood cavity, *bw* basal wall, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *fr* frontal shield, *hc* hypostegal coelom, *m* muscle strands of ooecial vesicle, *mz* maternal zooid, *oc* ooecial coelom, *of* ovicell floor, *op* operculum, *pe* lumen of peristome, *sc* sclerite of ooecial vesicle, *tw* transverse wall, *v* ooecial vesicle

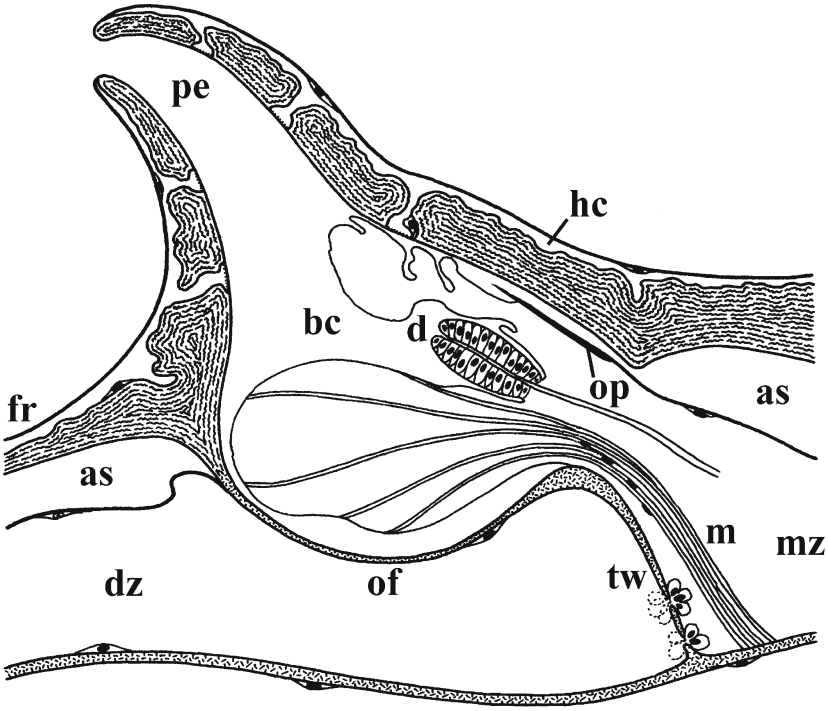

Fig. 2.37 Schematic longitudinal section of peristomial ovicell in *Margaretta barbata*. Abbreviations: *as* ascus, *bc* brood cavity, *d* diaphragm, *dz* distal zooid, *fr* frontal shield, *hc* hypostegal coelom, *m* muscle strands of ooecial vesicle, *mz* maternal zooid, *of* ovicell floor, *op* operculum, *pe* lumen of peristome, *tw* transverse wall

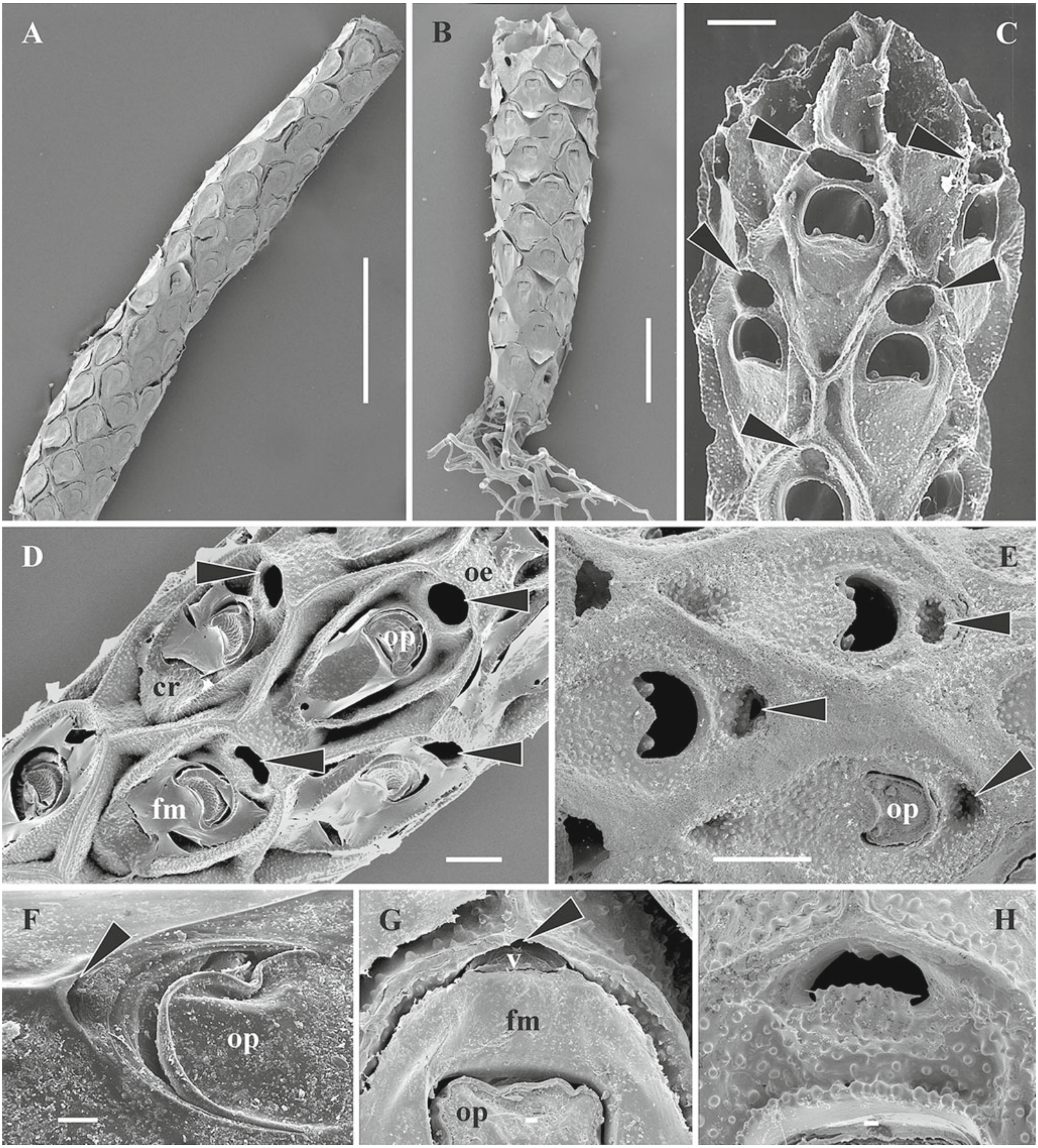

Fig. 2.38 Morphology and development of endotoichal ovicells in: (**A**, **E**) *Cellaria tenuirostris*; (**B**, **G**, **H**) *Cellaria aurorae*; (**C**, **D**) *Cellaria fistulosa*; (**F**) *Cellaria diversa*. (**A**, **B**) General view of non-cleaned colonies (in **A** ovicell-bearing parts of colony are inflated). (**C**) Terminal (growing) part of cleaned colony with ovicells (*arrowed*) at different stages of development. (**D**) Partly cleaned colony fragment showing changes in the shape of ovicell openings (*arrowed*) in the course of calcification of zooid walls. (**E**) Progressive closure of ovicell openings (*arrowed*) in old part of colony by calcification of skeletal walls. (**F**–**H**) Openings of fully formed ovicells (**F**, **G**) Non-cleaned air-dried specimens; openings *arrowed*). Abbreviations: *cr* cryptocyst, *fm* membranous frontal wall, *oe* ooecium, *op* operculum, *v* ooecial vesicle. Scale bars: **A**, **B**, 1 mm; **C**–**E**, 100 μm; **F**, 30 μm; **G**, **H**, 10 μm

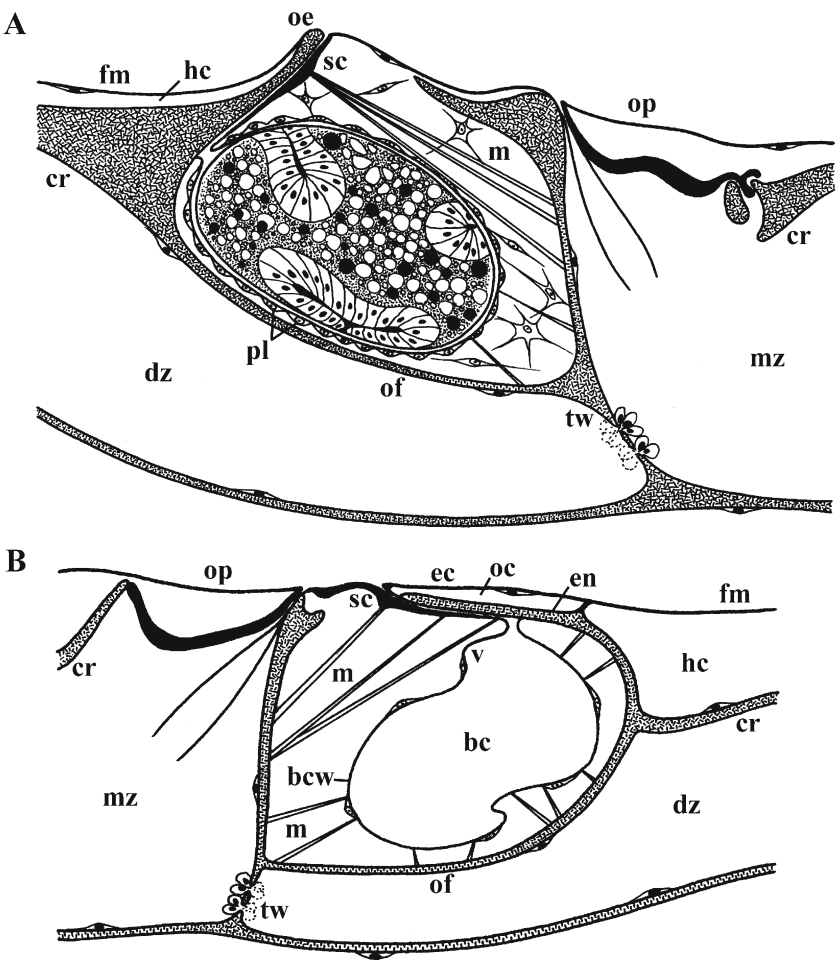

Fig. 2.39 Schematic longitudinal sections of endotoichal ovicells in: (**A**) *Cellaria tenuirostris*; (**B**) *Cellaria diversa*. Abbreviations: *bc* brood cavity, *bcw* brood-cavity wall, *cr* cryptocyst, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *fm* membranous frontal wall, *hc* hypostegal coelom, *m* muscle strands of ooecial vesicle, *mz* maternal zooid, *oc* ooecial coelom, *oe* ooecium, *of* ovicell floor, *op* operculum, *pl* placental analogue (embryophore), *sc* sclerite of ooecial vesicle, *tw* transverse wall, *v* ooecial vesicle

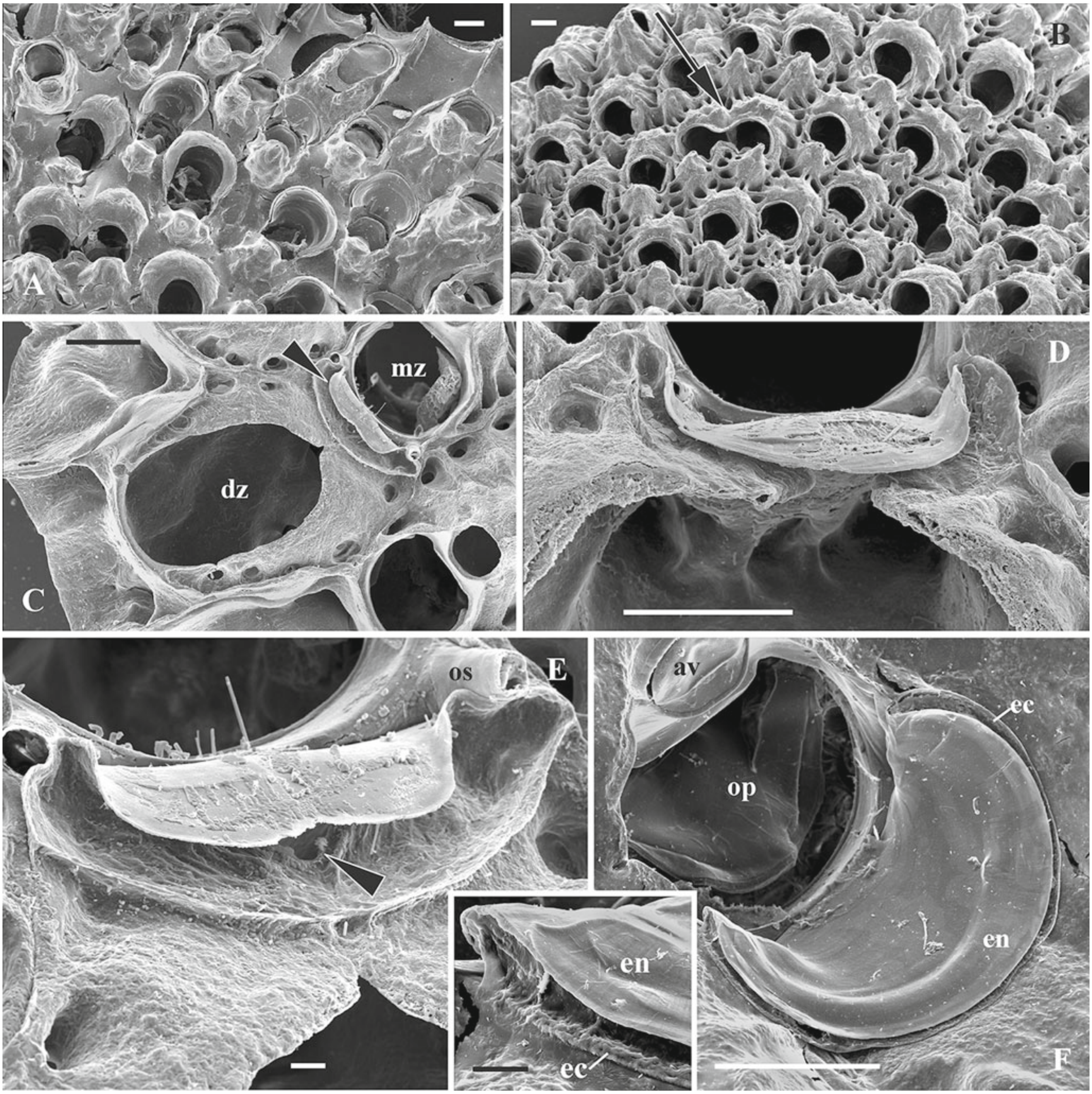

Fig. 2.40 Ovicell formation in *Porella smitti*. (**A**) Peripheral part of non-cleaned air-dried colony with developing ovicells. (**B**) Part of cleaned colony with fully formed ooecia (*arrow* indicates fused ooecia). (**C**, **E**) Peripheral zooids with developing frontal shield and ooecium (early stage of ovicell-floor calcification in the form of a bilobate plate; *arrow* indicates developing communication pore of ooecium). (**D**) Earliest stage of ooecial-fold formation (lobes of developing frontal shield grow towards each other beneath the ovicell floor). (**F**) Double-disk stage (non-cleaned specimen); *inset*, edge of non-cleaned ooecial fold starting to overgrow frontal surface of distal zooid. Abbreviations: *av* suboral avicularium, *cr* cryptocyst, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *mz* maternal zooid, *op* operculum, *os* oral spine. Scale bars: **A**–**D**, **F**, 100 µm; **E**, *inset*, 10 µm

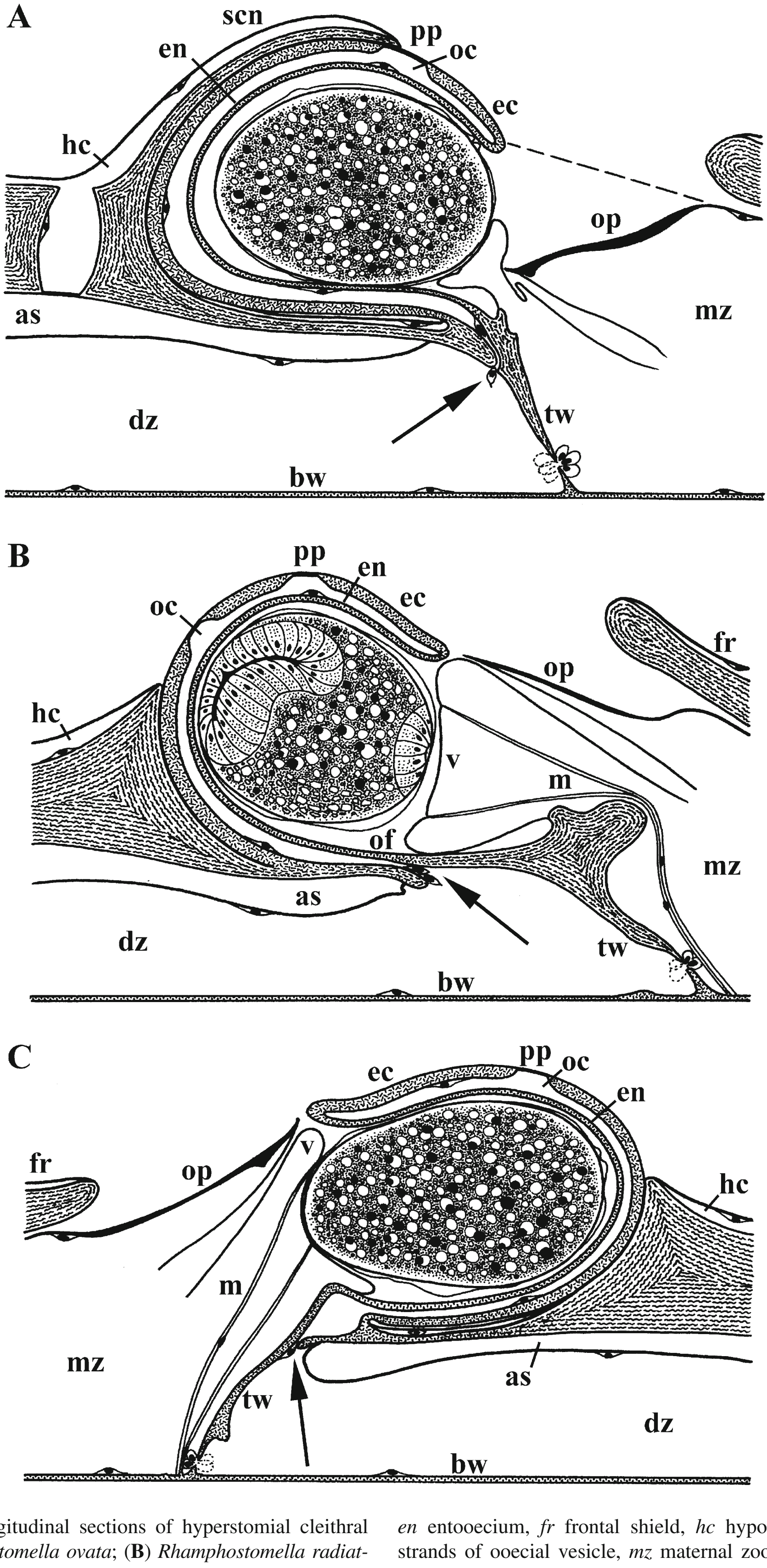

Fig. 2.41 Schematic longitudinal sections of hyperstomial cleithral ovicells in: (**A**) *Rhamphostomella ovata*; (**B**) *Rhamphostomella radiatula*; (**C**) *Rhamphostomella costata* (*arrows* indicate ooecial communication pores; in **A** normal position of operculum shown by *dotted line*). Abbreviations: *as* ascus, *bw* basal wall, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *fr* frontal shield, *hc* hypostegal coelom, *m* muscle strands of ooecial vesicle, *mz* maternal zooid, *oc* ooecial coelom, *of* ovicell floor, *op* operculum, *pp* pseudopore, *scn* secondary calcification, *tw* transverse wall, *v* ooecial vesicle

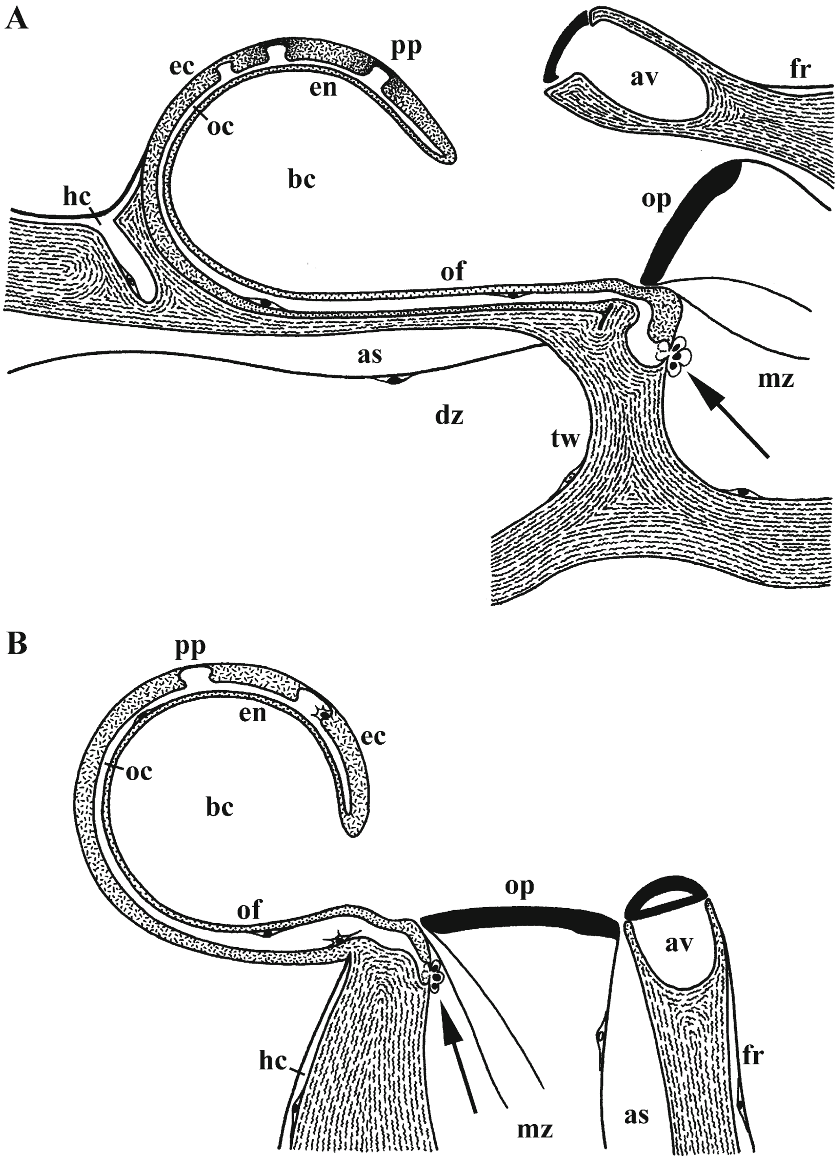

Fig. 2.42 Schematic longitudinal sections of hyperstomial noncleithral ovicells in: (**A**) *Turbicellepora crenulata*; (**B**) *Turbicellepora avicularis* (*arrows* indicate communication pores connecting distal kenozooidal and maternal autozooidal coeloms). Abbreviations: *as* ascus, *av* avicularium, *bc* brood cavity, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *fr* frontal shield, *hc* hypostegal coelom, *mz* maternal zooid, *oc* ooecial coelom, *of* ovicell floor, *op* operculum, *pp* pseudopore, *tw* transverse wall

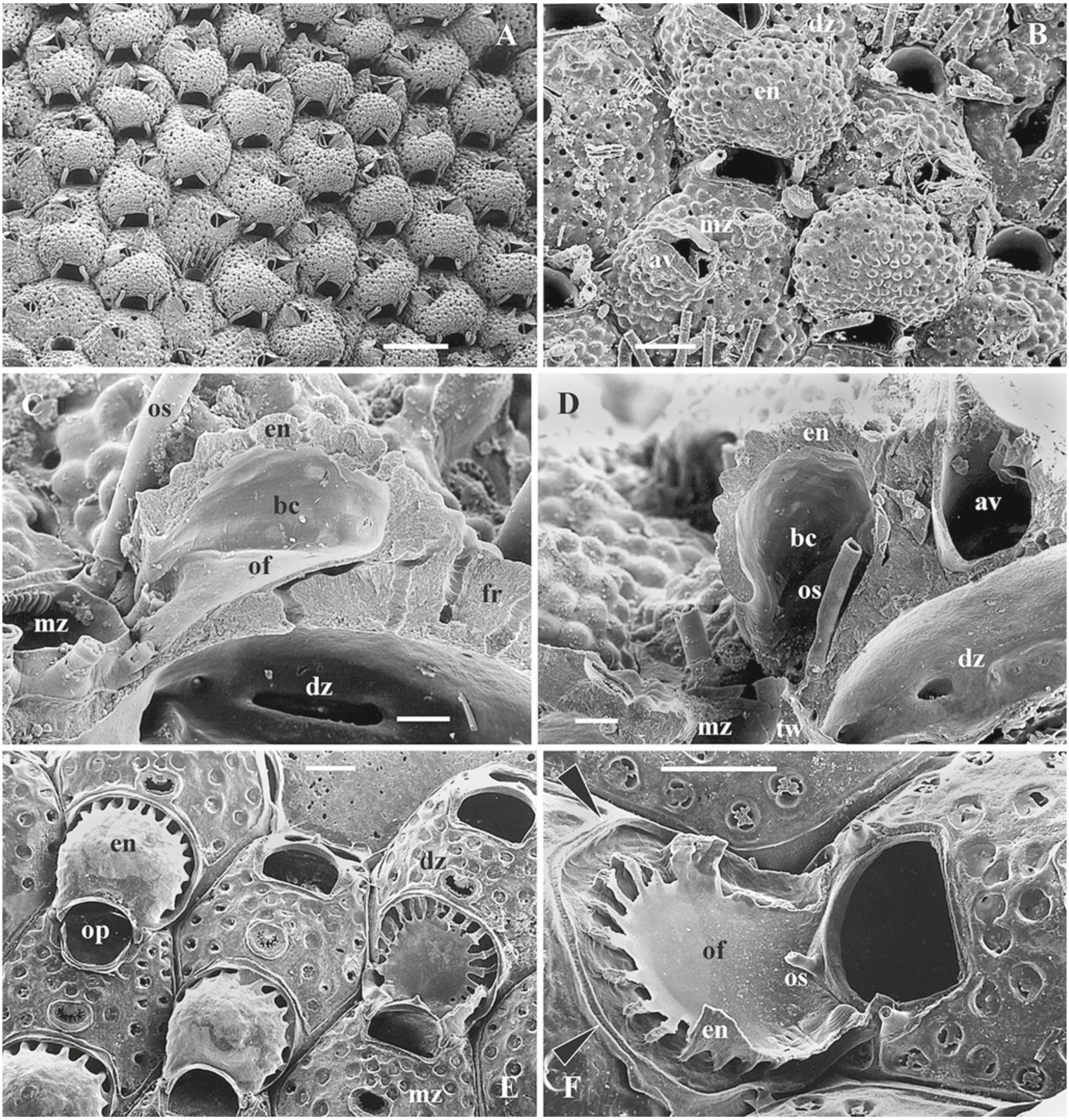

Fig. 2.43 Structure of ooecia of hyperstomial ovicells in: (**A**–**D**) *Microporella ciliata*; (**E**, **F**) *Fenestrulina malusii*. (**A**, **B**, **E**) Parts of cleaned colonies with fully formed ooecia. (**C**, **D**) Longitudinal fractures of ooecia (oral spine can be seen in brood cavity in (**D**)). (**F**) Lateral view of fractured ooecium (*arrowheads* indicate peripheral elevation surrounding entooecial base). In (**E**) ovicell (at *left*) closed by zooidal operculum. Abbreviations: *av* avicularium, *bc* brood cavity, *dz* distal zooid, *en* entooecium, *fr* frontal shield, *mz* maternal zooid, *of* ovicell floor, *op* operculum, *os* oral spine, *tw* transverse wall. Scale bars: **A**, 300 μm; **B**, **E**, **F**, 100 μm; **C**, **D**, 30 μm

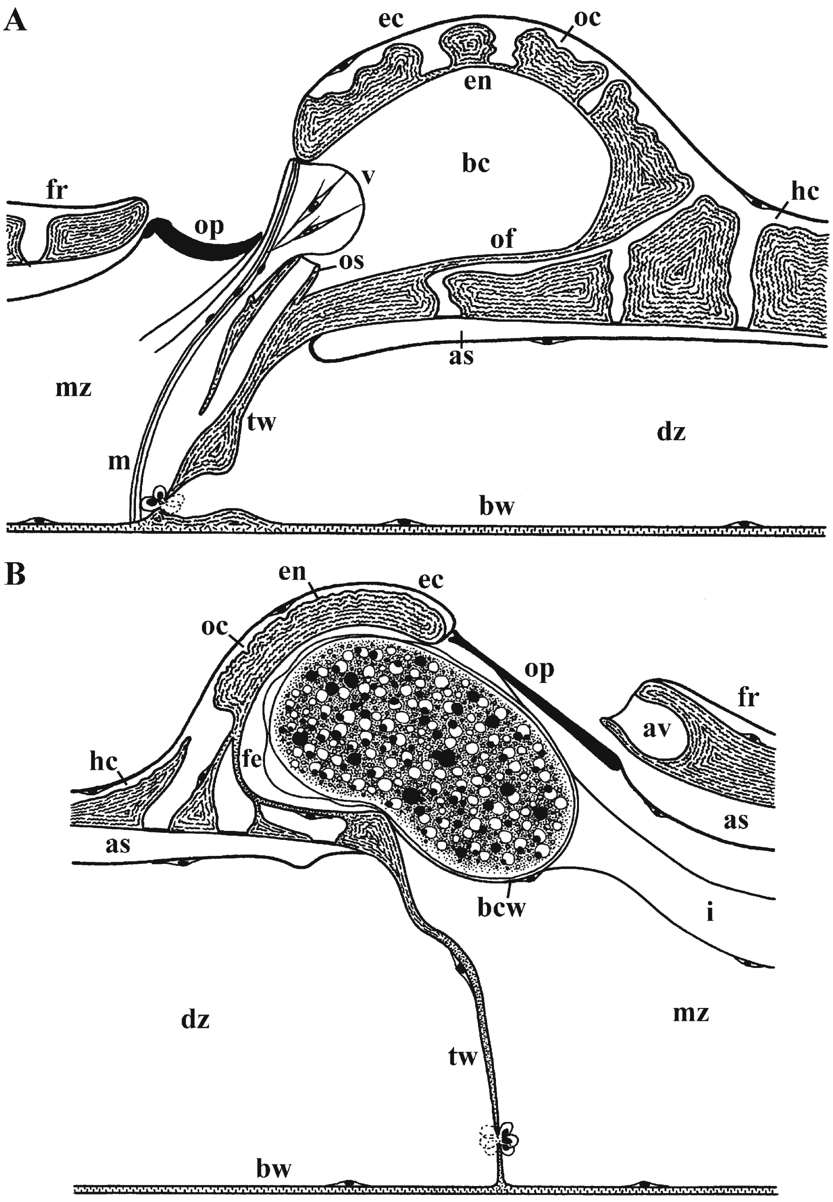

Fig. 2.44 Schematic longitudinal sections of hyperstomial ovicells in: (**A**) *Microporella ciliata* (ovicell acleithral); (**B**) *Pacificincola insculpta* (ovicell subcleithral). Abbreviations: *as* ascus, *av* avicularium, *bc* brood cavity, *bcw* brood-cavity wall, *bw* basal wall, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *fe* fertilization envelope, *fr* frontal shield, *hc* hypostegal coelom, *i* introvert, *m* muscle strands of ooecial vesicle, *mz* maternal zooid, *oc* ooecial coelom, *of* ovicell floor, *op* operculum, *os* oral spine, *tw* transverse wall, *v* ooecial vesicle

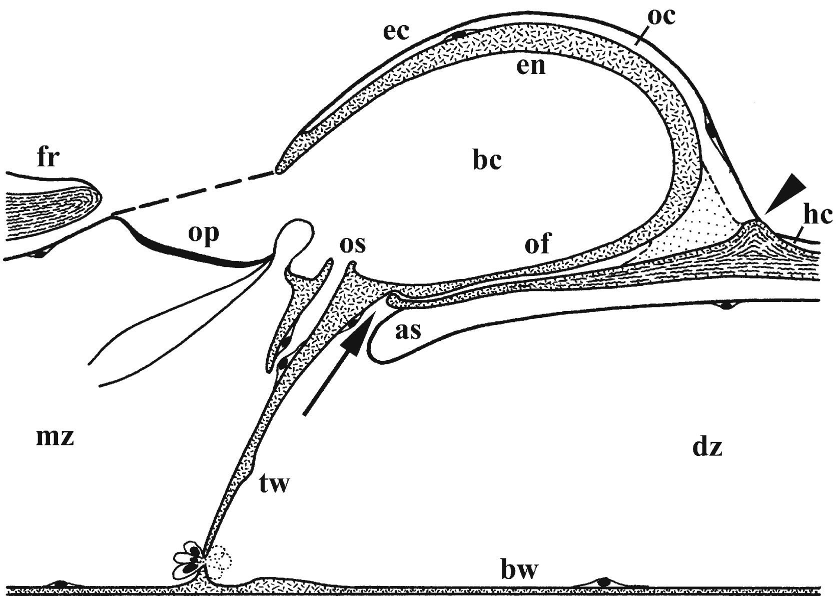

Fig. 2.45 Schematic longitudinal section of hyperstomial subcleithral ovicell in *Fenestrulina malusii* (*arrow* indicates ooecial communication pore; *arrowhead* indicates calcified elevation surrounding entooecium base; position of operculum during embryonic incubation shown by *dotted line*). Abbreviations: *as* ascus, *bc* brood cavity, *bw* basal wall, *dz* distal zooid, *ec* ectooecium, *en* entooecium, *fr* frontal shield, *hc* hypostegal coelom, *mz* maternal zooid, *oc* ooecial coelom, *of* ovicell floor, *op* operculum, *os* oral spine, *tw* transverse wall

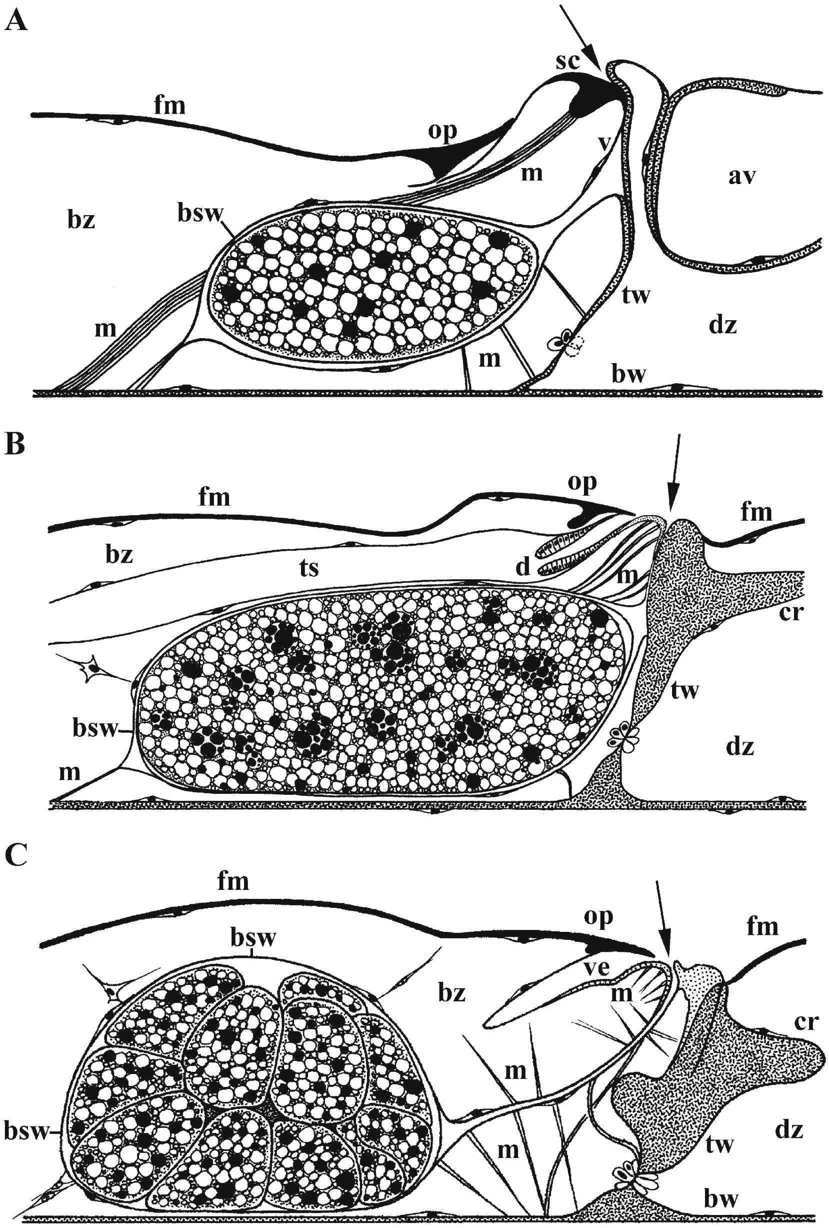

Fig. 2.46 Schematic longitudinal sections of brooding zooids with internal brood sacs in: (**A**) *Nematoflustra flagellata*; (**B**) "*Biflustra*" *perfragilis*; (**C**) *Gontarella* sp. (*arrows* indicate communication between the brood-sac cavity and the environment) (From Ostrovsky et al. 2006, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1002/jmor.10438/abstract). Abbreviations: *av* vibraculum (setiform avicularium), *bsw* brood-sac wall, *bz* brooding zooid, *bw* basal wall, *cr* cryptocyst, *d* diaphragm, *dz* distal zooid, *fm* membranous frontal wall, *m* muscle strands of ooecial vesicle and brood sac, *op* operculum, *sc* sclerite of ooecial vesicle, *ts* tentacle sheath, *tw* transverse wall, *v* ooecial vesicle, *ve* vestibulum

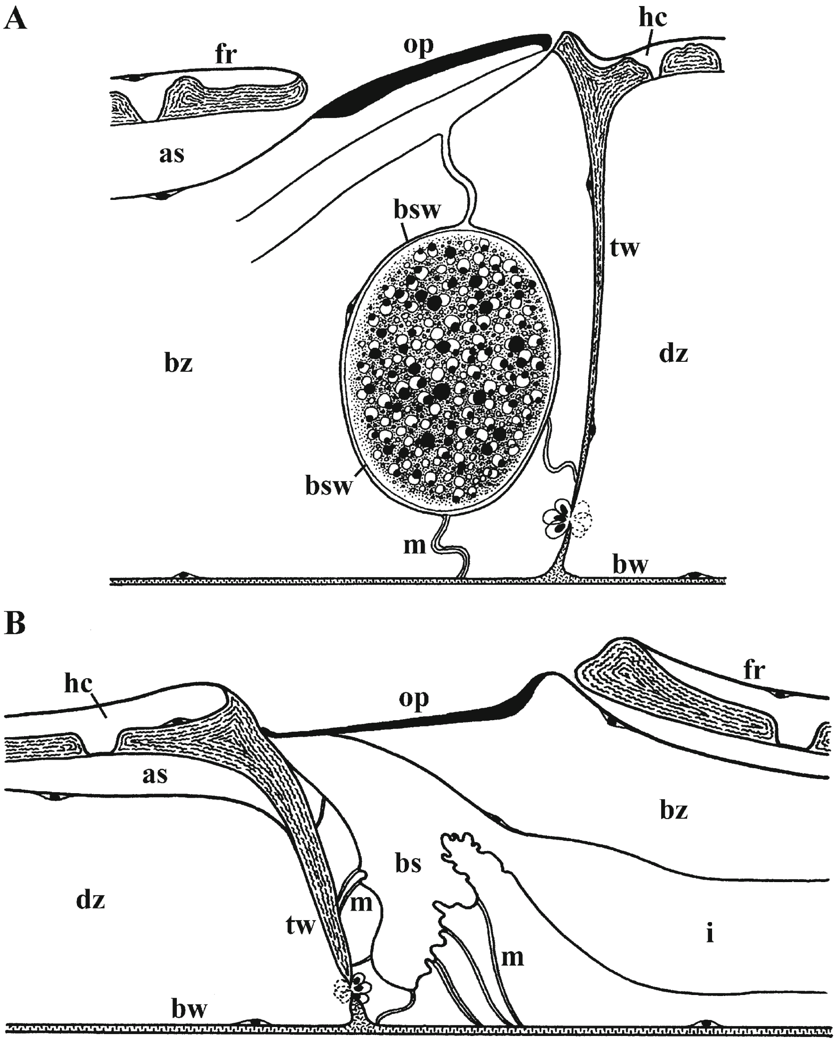

Fig. 2.47 Schematic longitudinal sections of brooding zooids with internal brood sacs in: (**A**) *Cryptosula pallasiana*; (**B**) *Watersipora subtorquata*. Abbreviations: *as* ascus, *bs* brood sac, *bsw* brood-sac wall, *bw* basal wall, *bz* brooding zooid, *dz* distal zooid, *fr* frontal shield, *hc* hypostegal coelom, *i* introvert, *m* muscle strands of brood sac, *op* operculum, *tw* transverse wall

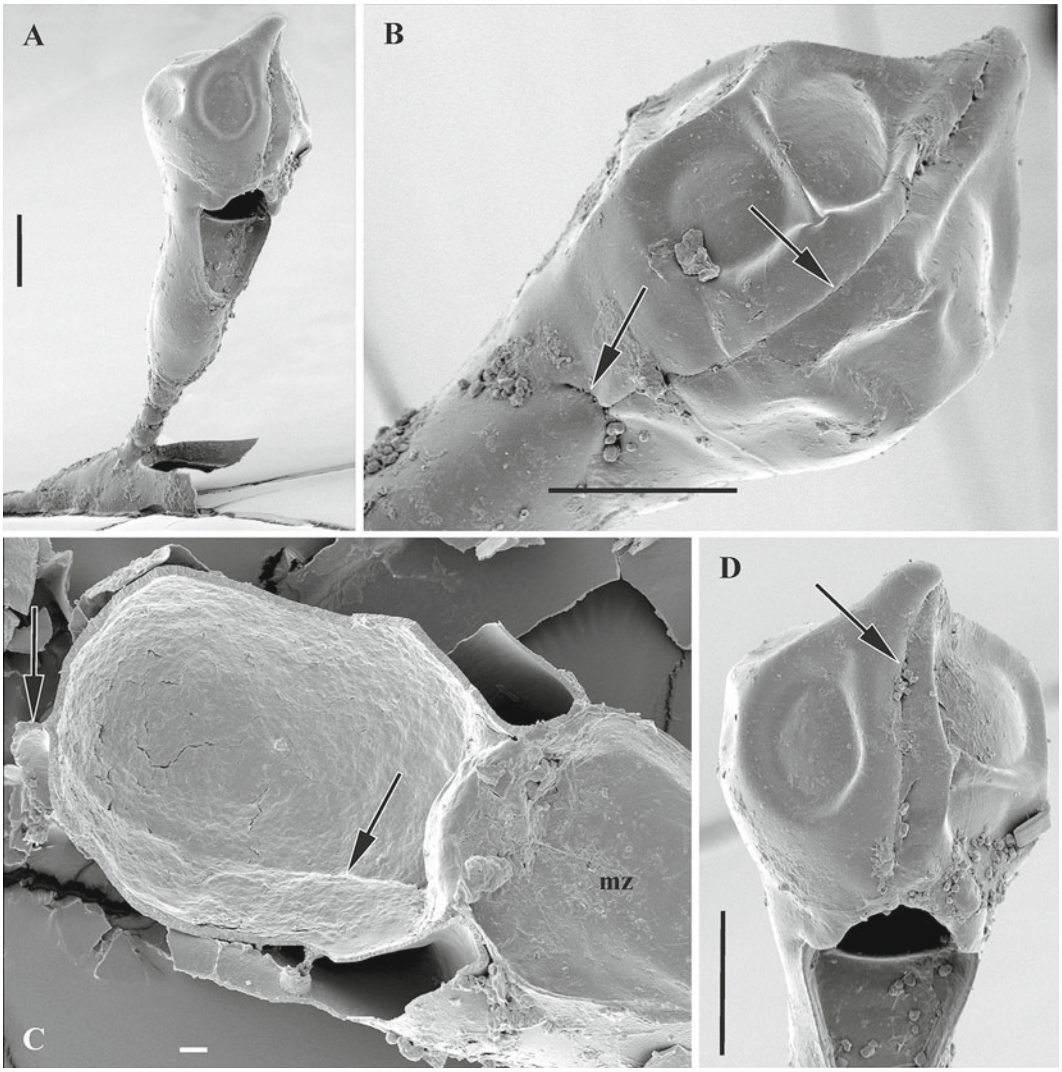

Fig. 2.48 Structure of bilobate ovicell in *Scruparia ambigua*. (**A**) General view of fertile zooid with ovicell. (**B**) Basal view of ooecium (medial suture and horizontal slit *arrowed*). (**C**) Fractured ooecium (cavities of ooecial lobes can be seen; *arrows* indicate medial suture and septum). (**D**) Frontal view of ooecium (medial suture *arrowed*). Abbreviations: *mz* maternal zooid. Scale bars: **A**, **B**, **D**, 100 μm; **C**, 10 μm

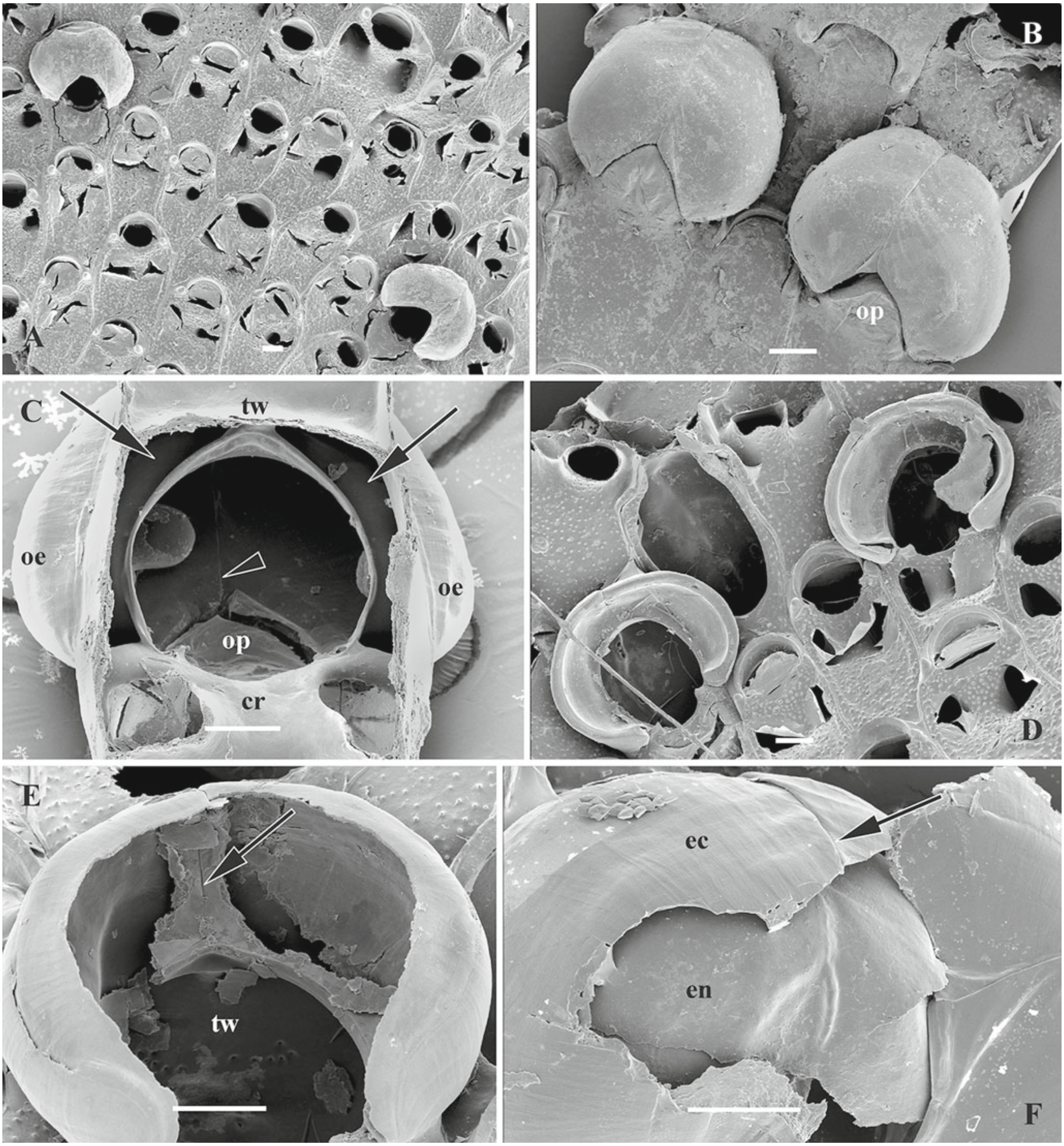

Fig. 2.49 Structure and development of bilobate cleithral ovicell in *Thalamoporella* sp. (**A**) Part of non-cleaned colony. (**B**) General view of two ovicells. (**C**) Basal view of zooidal orifice and paired communication openings (shown by *arrows*) of ooecium (*arrowhead* indicates medial suture). (**D**) Developing ooecia at colony periphery. (**E**) Fractured ooecium (*arrow* indicates medial suture corresponding to longitudinal septum between bases of ooecial lobes). (**F**) Ooecium with fractured ectooecium showing entooecium (longitudinal septum absent, medial suture of ectooecium *arrowed*). Abbreviations: *cr* cryptocyst, *ec* ectooecium, *en* entooecium, *oe* ooecium, *op* operculum, *tw* transverse wall. Scale bars: **A**–**F**, 100 µm

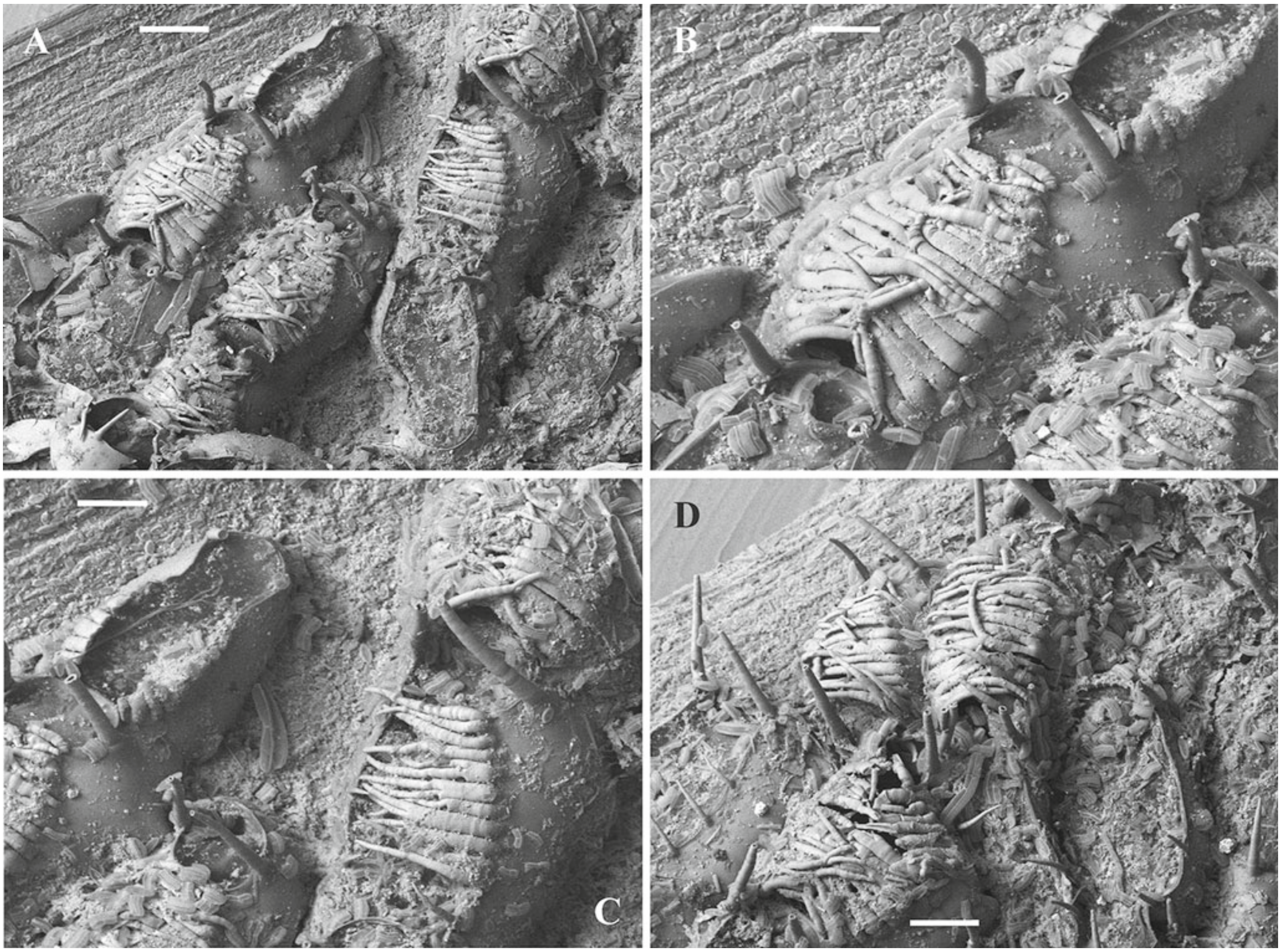

Fig. 2.50 Acanthostegal brood chambers of *Tendra zostericola*. (**A**) Part of non-cleaned colony with brooding and non-brooding autozooids. (**B**) General view of acanthostegal brood chamber (spines overlapping). (**C**) Part of non-cleaned colony with developing brood chamber (at *left*) and brood chamber represented only by spines from right half of zooid (at *right*). (**D**) Part of non-cleaned colony with three brooding zooids showing variations in spine arrangement (non-brooding zooids at right with several short mural spines) (From Ostrovsky and Taylor 2005a, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.2005.00179.x/abstract). Scale bars: **A**, 250 µm; **B**, 111.1 µm; **C**, 125 µm; **D**, 166.7 µm

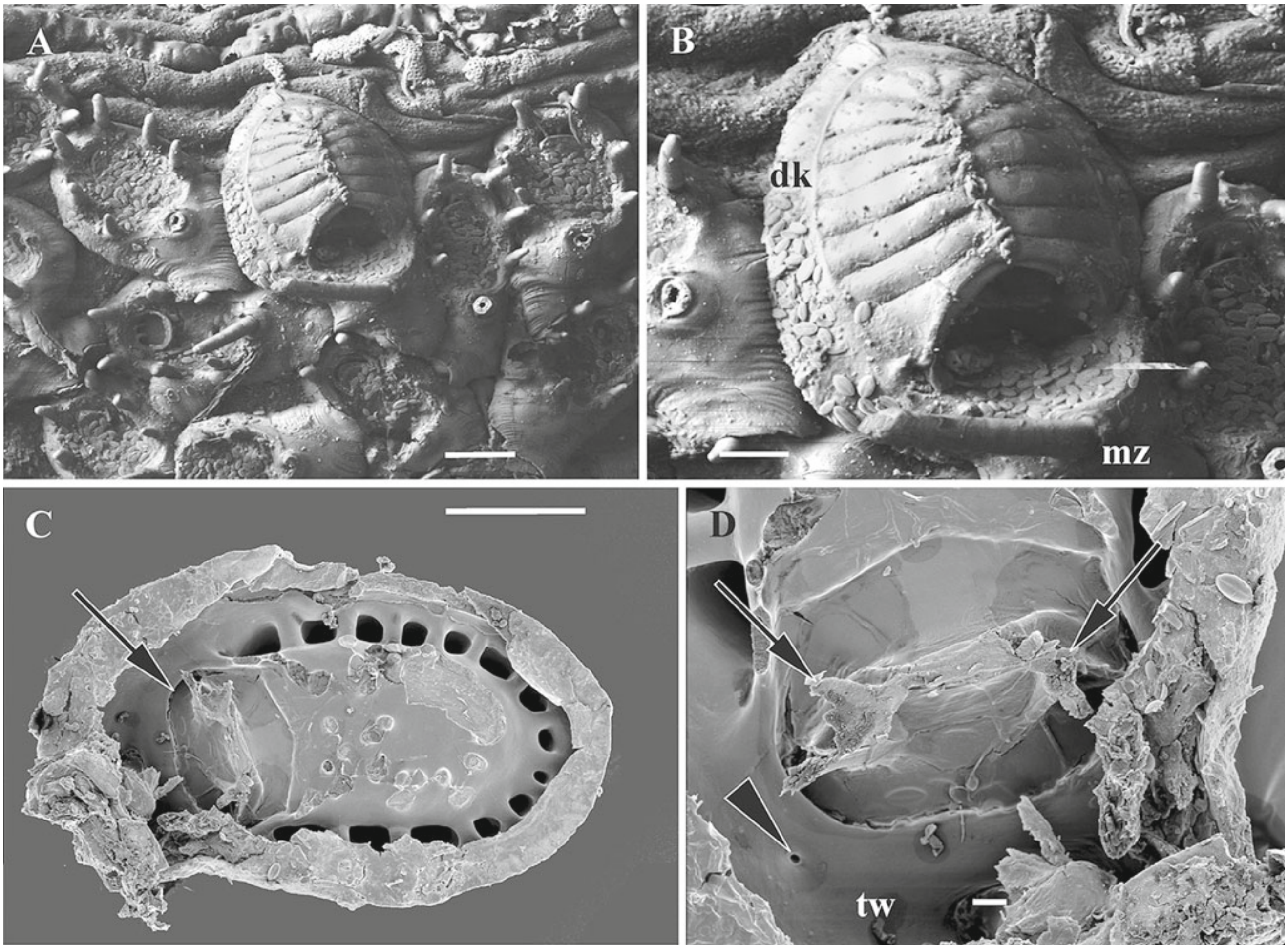

Fig. 2.51 Acanthostegal brood chambers of *Heteroecium amplectens*. (**A**) Part of non-cleaned colony with brooding complex and non-brooding autozooids. (**B**) General view of brooding complex. (**C**) Basal view of brooding complex (*arrow* indicates membranous area of brood-chamber floor). (**D**) Membranous area of brood-chamber floor (*arrows* indicate outgrowths of membranous area; *arrowhead* indicates communication pore between maternal zooid and distal kenozooid). Abbreviations: *dk* distal kenozooid, *mz* maternal zooid, *tw* transverse wall (From Ostrovsky and Taylor 2005a, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.2005.00179.x/abstract). Scale bars: **A**, 100 µm; **B**, 47.6 µm; **C**, 100 µm; **D**, 10 µm

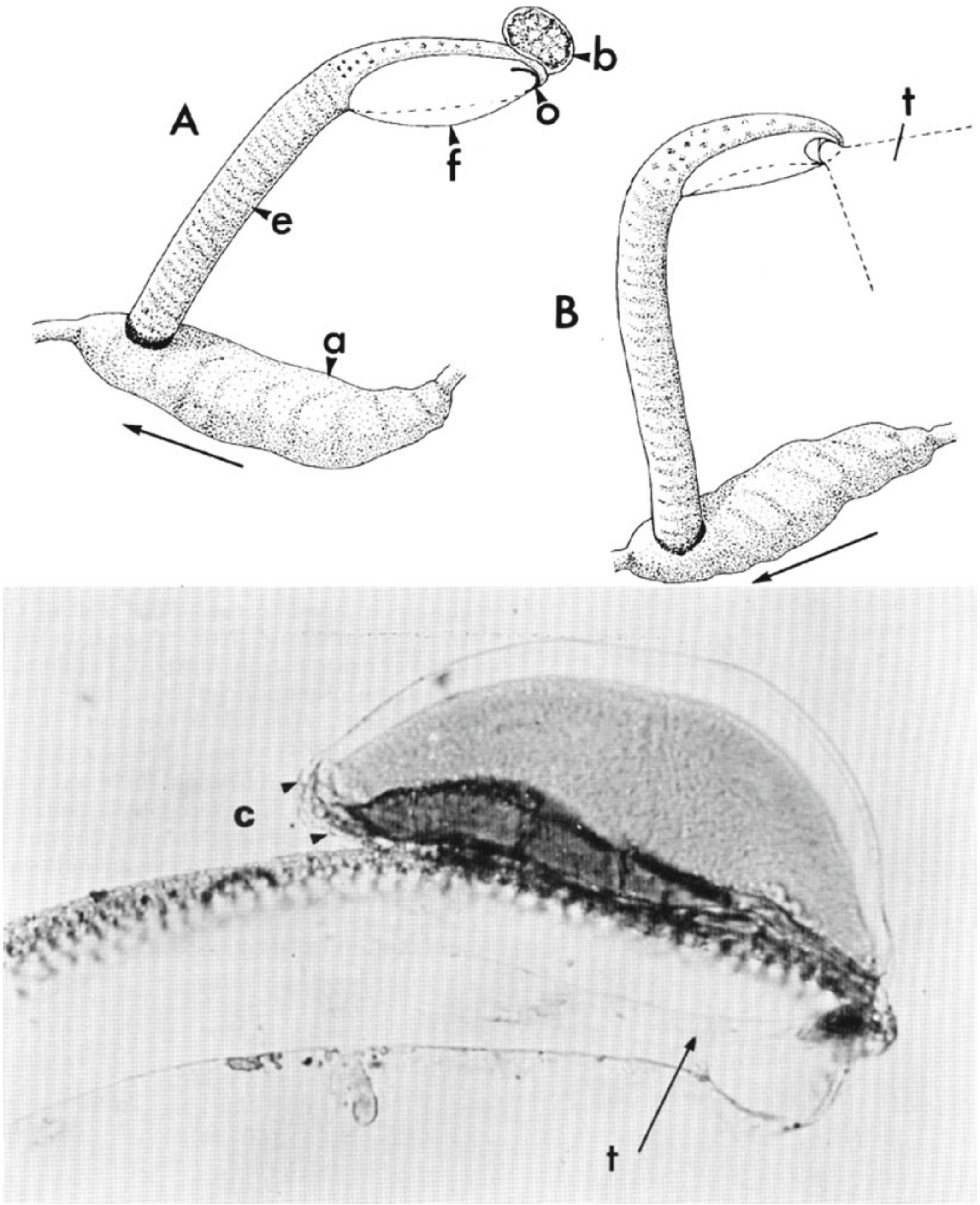

Fig. 2.52 External membranous brood sac of *Aetea anguina*. (**A**) Autozooid with retracted tentacles and brood sac. (**B**) Autozooid with extended tentacle crown (shown by *dotted lines*). *Bottom*: longitudinal section of terminal area of autozooid and membranous brood sac (From Cook 1977b, courtesy of Oxford University Press, http://icb.oxfordjournals.org/content/17/1/55.short). Abbreviations: *a* attached proximal part of autozooid, *b* brood sac, *c* calcified part of brood sac, *e* erect distal part of autozooid, *f* frontal membranous wall, *o* operculum, *t* tentacles

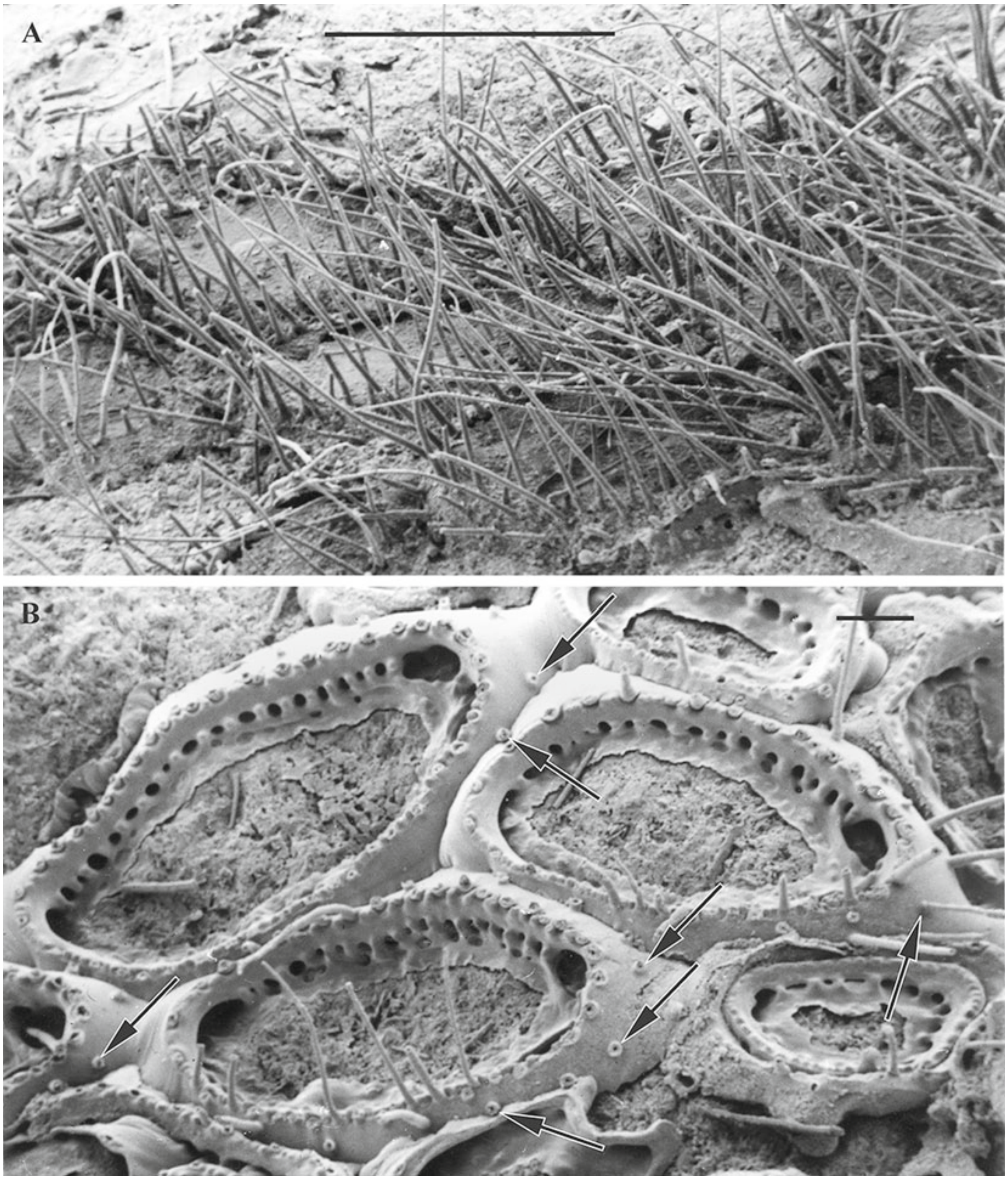

Fig. 2.53 General view of the colonies of *Villicharixa strigosa* (Photo courtesy of D.P. Gordon). (**A**) Part of non-cleaned colony. (**B**) Part of cleaned colony (*arrows* indicate bases of spines developing on the gymnocyst outside the mural rim). Scale bars: **A**, 500 µm; **B**, 100 µm

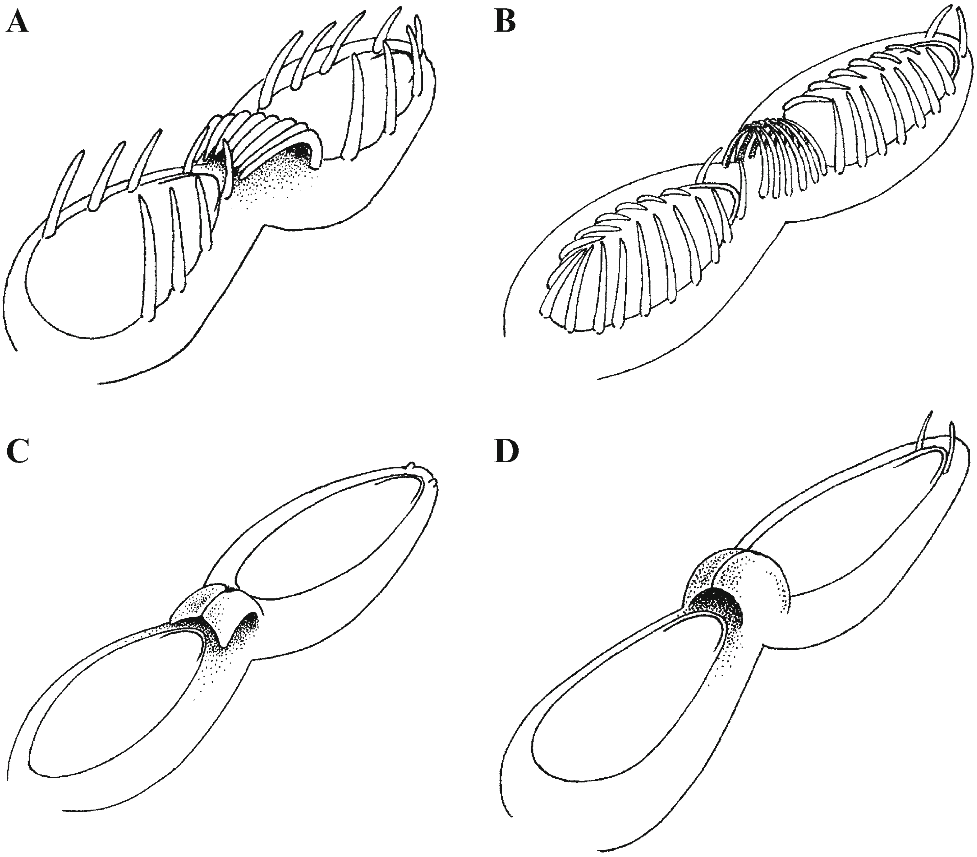

Fig. 2.54 Diagrammatic reconstructions of primitive ovicell types, reflecting successive stages in the early evolution of brood chambers in Neocheilostomina. (**A**) *Distelopora bipilata*; *Distelopora langi*; (**B**) *Distelopora spinifera*, *Unidistelopora krauseae*; (**C**) *Gilbertopora larwoodi*; (**D**) *Wilbertopora mutabilis* (From Ostrovsky and Taylor 2004, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1111/j.0031-0239.2004.00379.x/full)

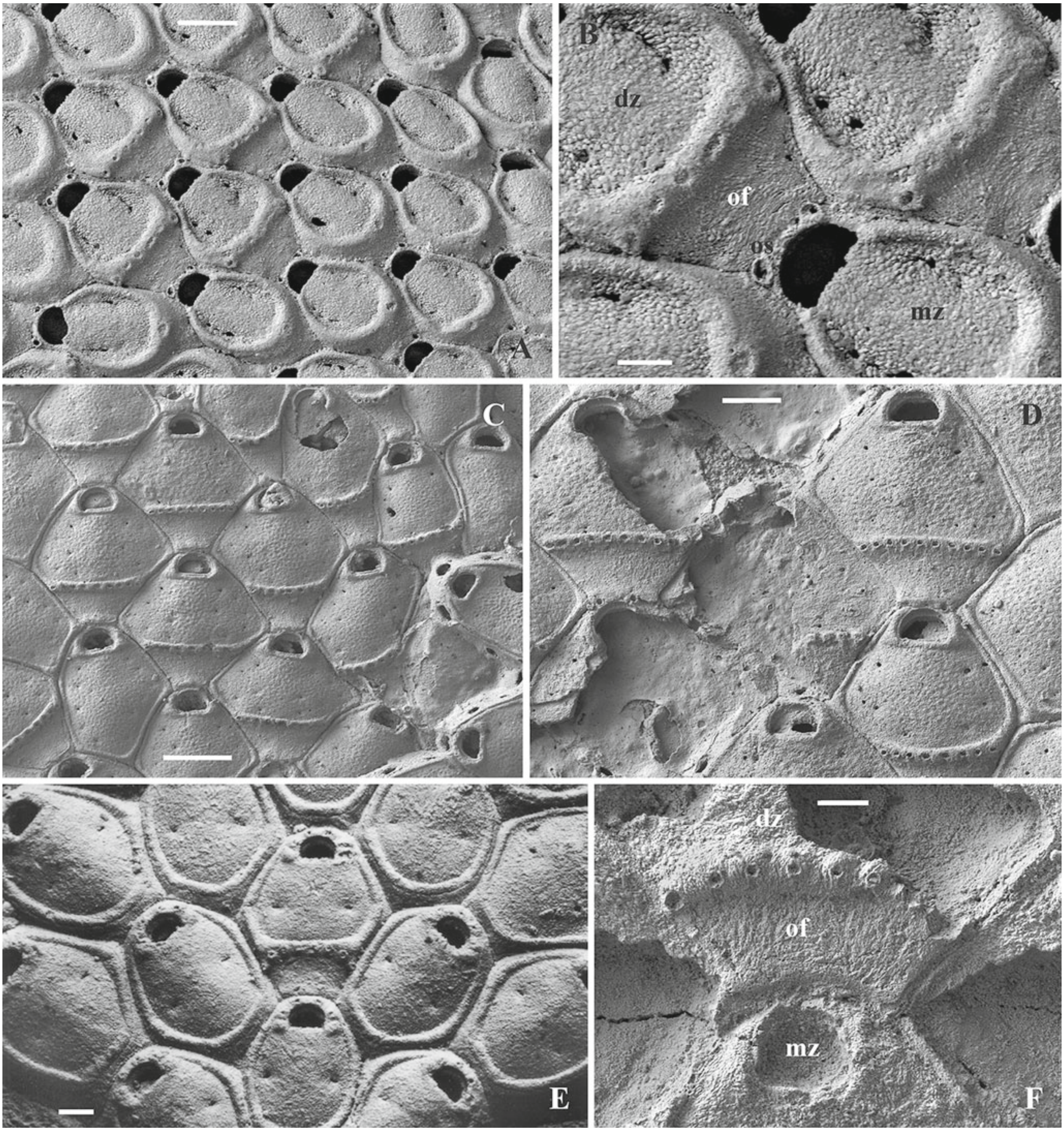

Fig. 2.55 Different arrangements of ovicell spine bases in: (**A**, **B**) *Stichomicropora oceani*; (**C**, **D**) *Stichomicropora* sp. 1; (**E**) *Stichomicropora marginula*; (**F**) *Stichomicropora* sp. 2. (**A**, **B**) Horizontal (straight), or very gently curving, proximally concave arc; outer spines situated at some distance from mural rim of distal zooid. (**C**, **D**) Horizontal and gently curving, proximally concave or distally convex arc. (**E**, **F**) Distally convex arc; (From Ostrovsky and Taylor 2005a, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.2005.00179.x/abstract). Abbreviations: *dz* distal autozooid, *mz* maternal zooid, *of* ovicell floor. Scale bars: **A**, 142.9 μm; **B**, 47.6 μm; **C**, 333 μm; **D**, 169 μm; **E**, 100 μm; **F**, 62.5 μm

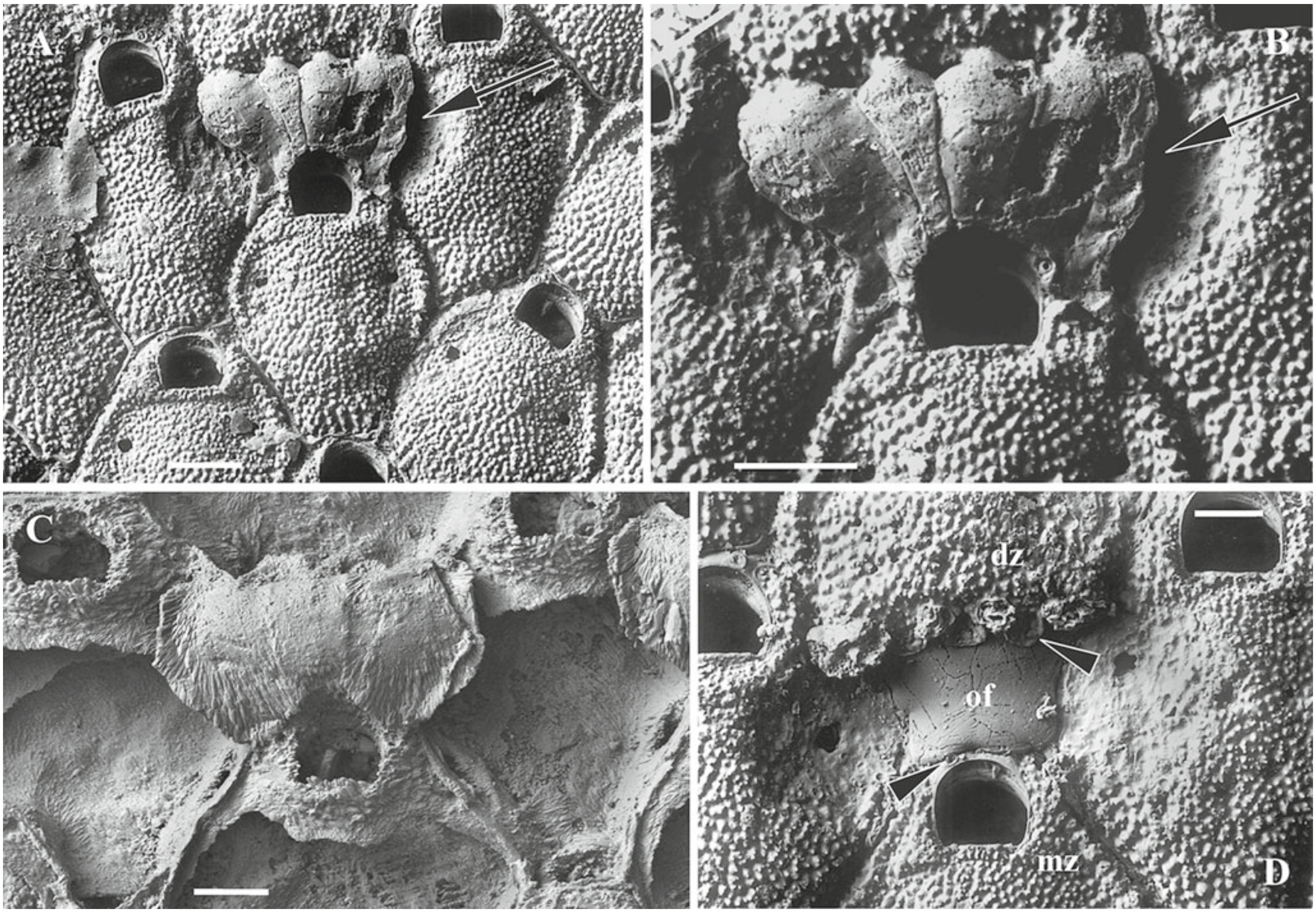

Fig. 2.56 Ooecial structure in: (**A**, **B**, **D**) *Stichomicropora baccata*; (**C**) *Stichomicropora ostrovskyi*. (**A–C**) General view of costate ooecium (lateral foramina *arrowed*). (**D**) Fractured ooecium showing a row of spine bases and ovicell floor (*arrowheads* indicate cryptocystal matrix encroaching on the ovicell spine bases and the base of a tiny oral spine) (From Ostrovsky and Taylor 2005a, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.2005.00179.x/abstract). Abbreviations: *dz* distal autozooid, *mz* maternal zooid, *of* ovicell floor. Scale bars: **A**, **B**, 100 µm; **C**, 76.9 µm; **D**, 66.7 µm

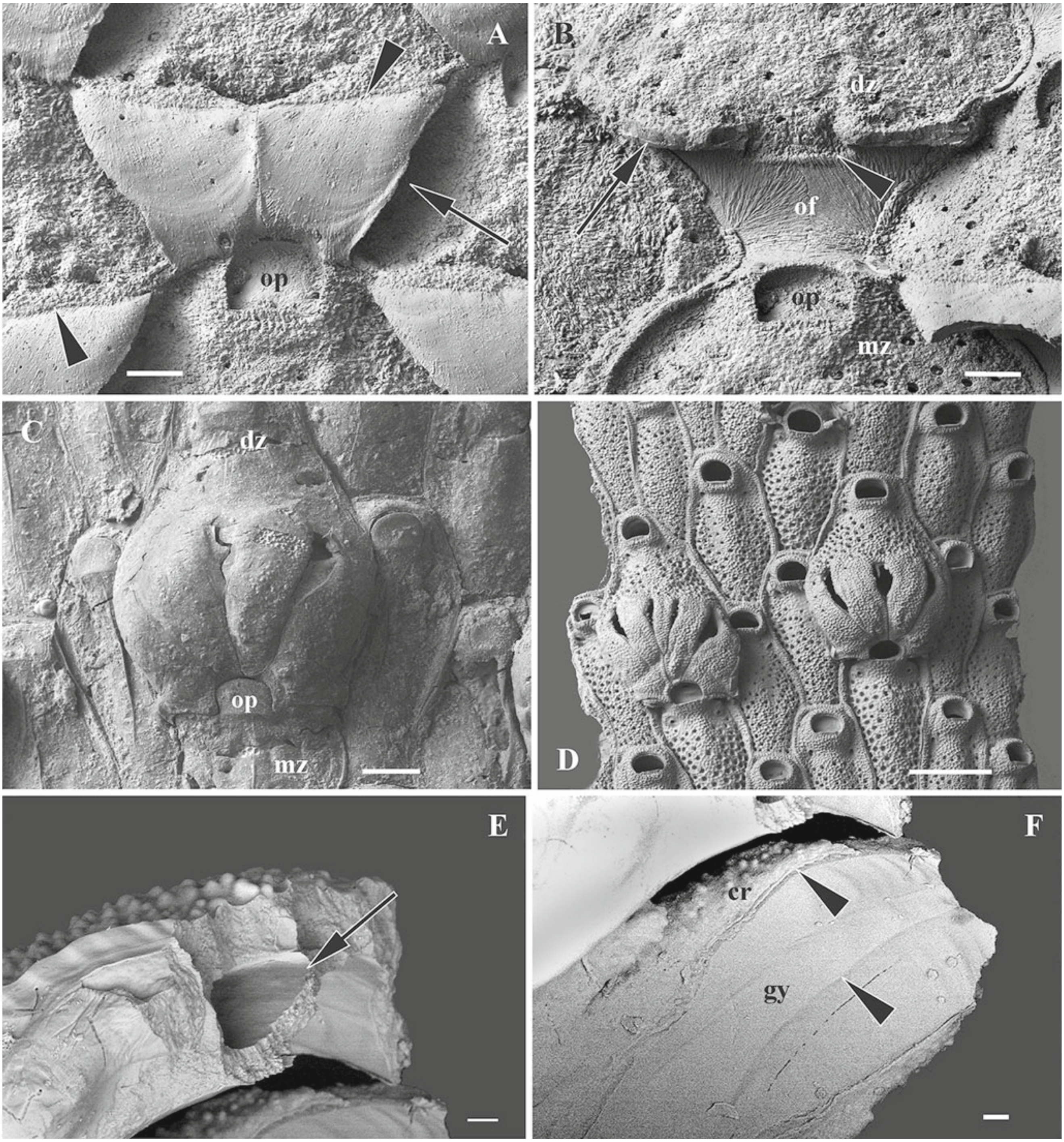

Fig. 2.57 Ovicell structure in: (**A**, **B**) *Monoporella multilamellosa*; (**C**–**F**) *Monoporella* sp. 2. (**A**) General view of ooecium (*arrow* indicates the lateral foramen; *arrowheads* indicate the edges of the cryptocystal matrix encroaching on the spine bases). (**B**) Fractured ooecium (*arrow* indicates boundary between upper and lower walls of an ooecial spine; *arrowhead* indicates cryptocystal border of distal autozooid). (**C**) General view of non-cleaned cleithral ovicell. (**D**) Part of cleaned colony showing two ooecia. (**E**) Damaged spine (costa) of ooecium (its coelomic cavity arrowed). (**F**) Internal ooecial surface (*arrowheads* indicate edge of cryptocystal 'matrix' and longitudinal grooves between two ooecial spines) (From Ostrovsky and Taylor 2005a, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.2005.00179.x/abstract). Abbreviations: *cr* cryptocyst, *dz* distal autozooid, *gy* gymnocyst, *mz* maternal zooid, *of* ovicell floor, *op* operculum. Scale bars: **A**, **B**, 83.3 µm; **C**, 238 µm; **D**, 769 µm; **E**, **F**, 20 µm

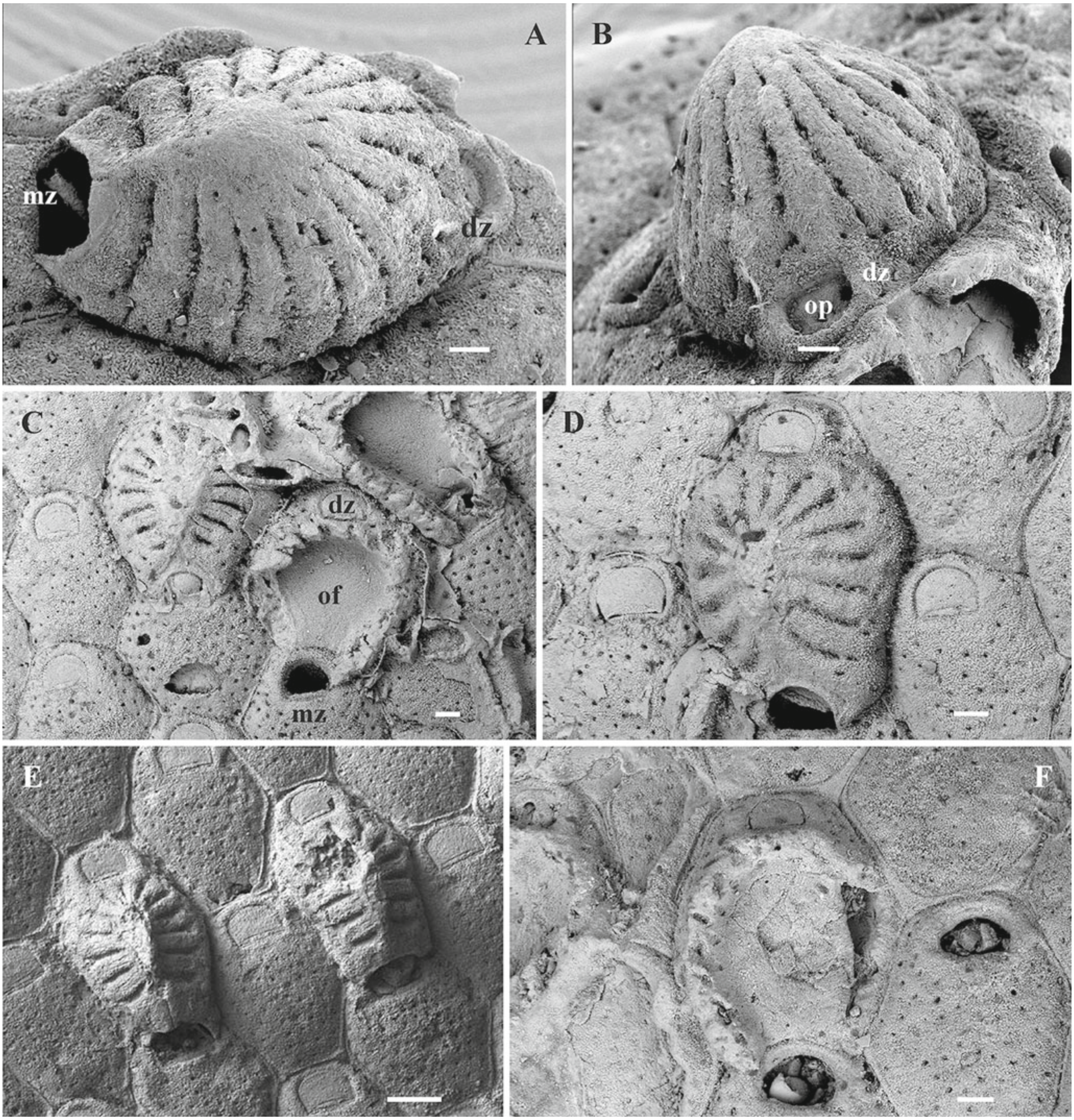

Fig. 2.58 Ooecial structure in: (**A**, **B**) *Macropora cribrilifera*; (**C**, **D**) *M*. *waimatakuensis*; (**E**, **F**) *Macropora* sp. 1. (**A**, **B**, **D**, **E**) General view of ooecia. (**C**, **F**) Whole and fractured ooecia (From Ostrovsky and Taylor 2005a, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.2005.00179.x/abstract). Abbreviations: *dz* distal autozooid, *mz* maternal zooid, *of* ovicell floor, *op* operculum. Scale bars: **A**–**D**, **F**, 100 μm; **E**, 238 μm

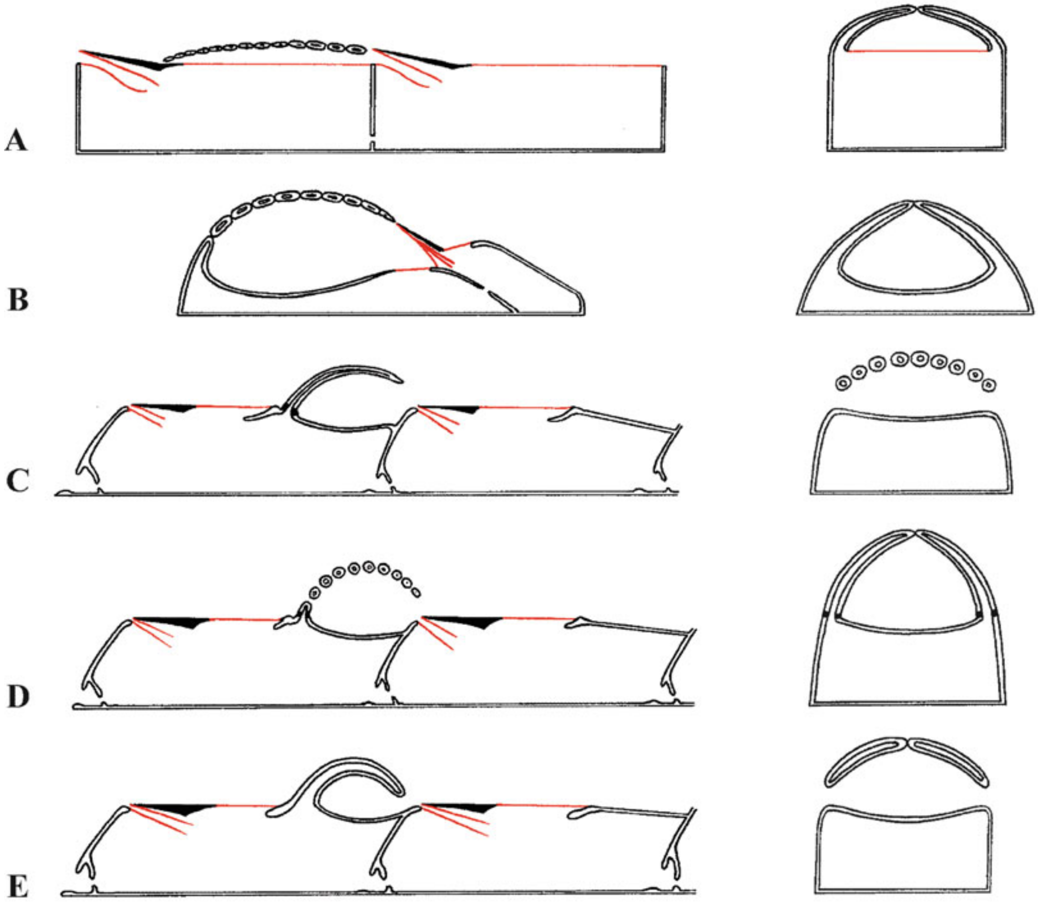

Fig. 2.59 Schematics of brood-chamber structure in Tendridae (**A**, **B**) and Calloporidae (**C**–**E**), presented as longitudinal and transverse sections of the maternal and distal zooids. (**A**) *Tendra zostericola*. (**B**) *Heteroecium* sp. (**C**) *Distelopora bipilata* and *Distelopora langi*. (**D**) *Distelopora spinifera* and *Unidistelopora krauseae*. (**E**) *Gilbertopora larwoodi* (From Ostrovsky and Taylor 2005a, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.2005.00179.x/abstract). Membranous walls shown in *red* (reconstructed for fossil species)

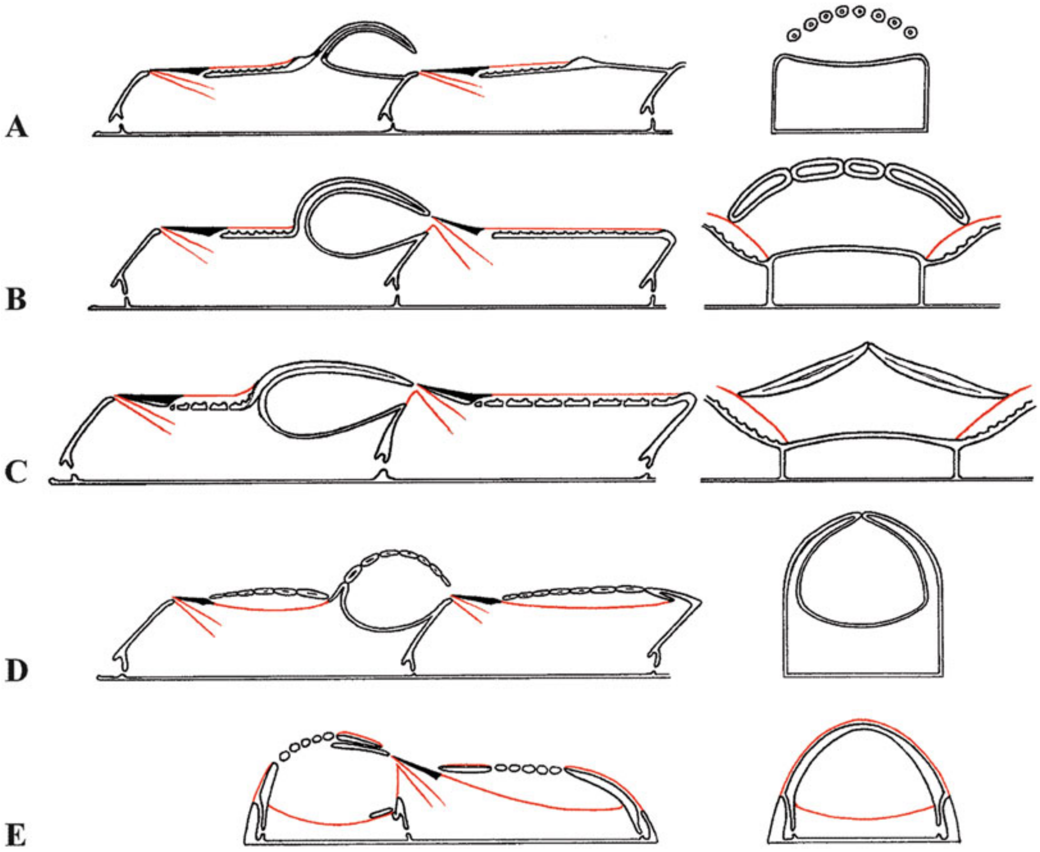

Fig. 2.60 Schematics of brood-chamber structure in Monoporellidae (**A**–**C**), Cribrilinidae (**D**) and Belluloporidae (**E**), presented as longitudinal and transverse sections of the maternal and the distal zooids. (**A**) *Stichomicropora* spp. with articulated ovicellar spine bases. (**B**) *Stichomicropora baccata*. (**C**) *Monoporella multilamellosa*. (**D**) *Leptocheilopora* spp. (**E**) *Bellulopora bellula* (From Ostrovsky and Taylor 2005a, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.2005.00179.x/abstract). Membranous walls shown in *red* (reconstructed for fossil species)

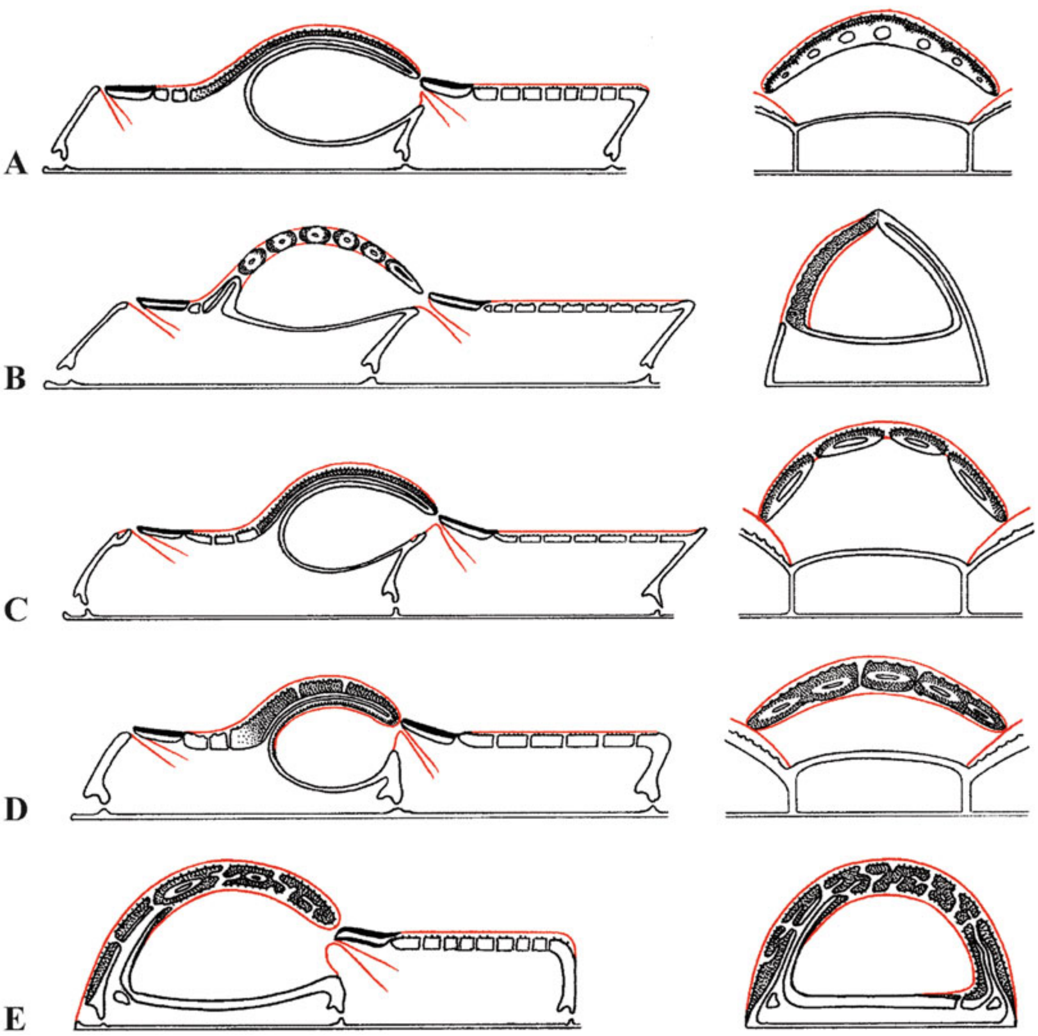

Fig. 2.61 Schematics of brood-chamber structure in Monoporellidae (**A**, **C**, **D**), and Macroporidae (**B**, **E**), presented as longitudinal and transverse sections of the maternal and distal zooids. (**A**) *Monoporella* sp.. (**B**) *Macropora* sp. 1 and *M*. *cribrilifera* (right-hand transverse section shows costal cryptocyst at *left* and costal gymnocyst at *right*). (**C**) *Monoporella elongata*. (**D**) *Monoporella nodulifera*. (**E**) *Macropora levinseni* (From Ostrovsky and Taylor 2005a), courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.2005.00179.x/abstract). Membranous walls in *red* (reconstructed for fossil species), cryptocystal 'matrix' shaded

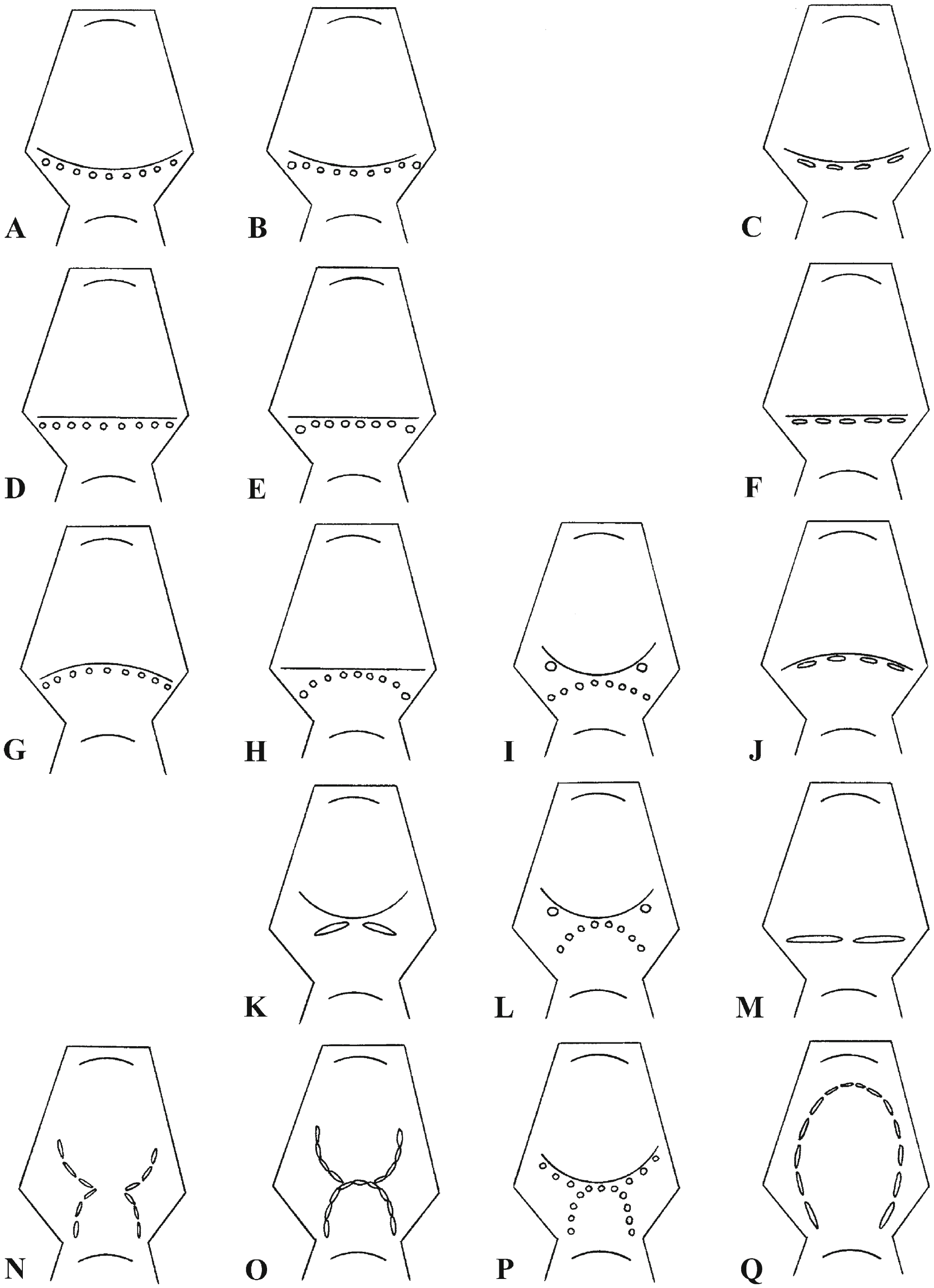

Fig. 2.62 Diagrams showing the shape of the mural rim and the arrangement of ovicell spine bases (in frontal view). Some species demonstrate variations in spine arrangement; the number of spines shown in the picture is approximate. (**A**) *Stichomicropora* sp. 1. (**B**) *Stichomicropora oceani*. (**C**) *Stichomicropora ostrovskyi*. (**D**) *Stichomicropora* sp. 1, *Stichomicropora sicksi* and *Stichomicropora sulcata*. (**E**) *Stichomicropora oceani*, *Stichomicropora* sp. 3 and *Stichomicropora* sp. 5. (**F**) *Stichomicropora ostrovskyi* and *Stichomicropora baccata*. (**G**) *Stichomicropora* sp. 1, *Stichomicropora* sp. 2, *Stichomicropora* sp. 4, *Stichomicropora sicksi*, *Stichomicropora sulcata*, *Stichomicropora erecta*, *Stichomicropora biconstricta*, *Stichomicropora* cf. *clathrata* and *Stichomicropora punctilla*. (**H**) *Stichomicropora marginula* and *Stichomicropora* sp. 3. (**I**) *Distelopora bipilata* and *Distelopora langi*. (**J**) *Stichomicropora ostrovskyi*, *Stichomicropora senaria*, *Stichomicropora baccata*, *Stichomicropora subquadrata*, *Monoporella* sp., *Monoporella elongata*, *Monoporella prisca*, *Monoporella nodulifera* and *Monoporella exculpta*. (**K**) *Gilbertopora larwoodi* and *Wilbertopora mutabilis*. (**L**) *Distelopora bipilata*. (**M**) *Monoporella multilamellosa* and *Monoporella? vincentownensis*. (**N**) ?*Thoracopora* sp. and *Craticulacella schneemilchae*. (**O**) *Leptocheilopora tenuilabrosa*, *Leptocheilopora* sp. 1 and *Leptocheilopora* sp. 2. (**P**) *Distelopora spinifera* and *Unidistelopora krauseae*. (**Q**) *Macropora* spp. (From Ostrovsky and Taylor 2005a, courtesy of John Wiley and Sons, http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.2005.00179.x/abstract)

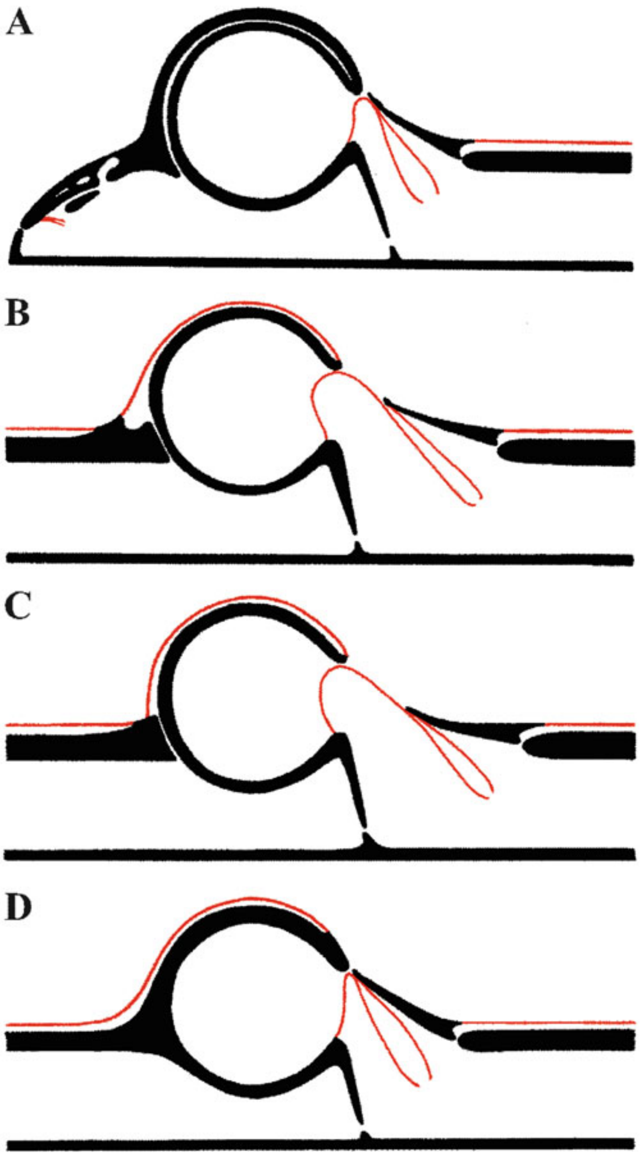

Fig. 2.63 Schematic hypothetical sequence of ooecium evolution in Microporidae illustrated by Recent species (from *top* to *bottom*): (**A**) *Micropora gracilis*; (**B**) *Opaeophora lepida*; (**C**) *Opaeophora monopia*; (**D**) *Micropora notialis*. Calcified walls and zooidal opercula shown *black*, membranous walls *red*

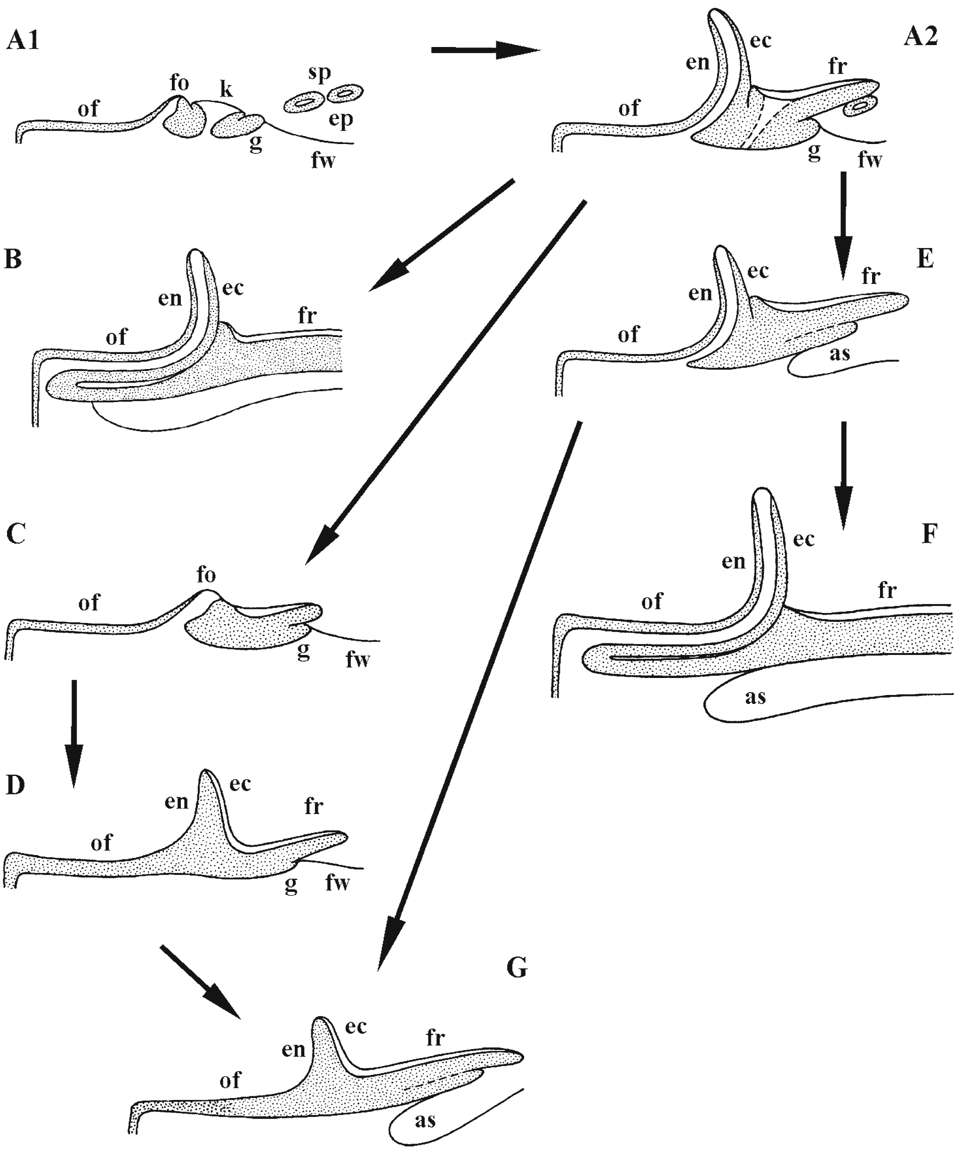

Fig. 2.64 Schematic hypothetical sequence of integrated frontal-shield and ooecial evolution (developing or fully formed calcified parts stippled): (**A1**) cribrimorph with frontal kenozooids and developing fold of calloporiform ooecium. (**A2**) Spinocystal umbonulomorph ancestor with frontal kenozooidal overgrowth and calloporiform ooecium. (**B**) Umbonulomorph with lepralielliform ooecium. (**C**) Umbonulomorph with developing fold of calloporiform ooecium. (**D**) Umbonulomorph with escharelliform ooecium. (**E**) Lepraliomorph with calloporiform ooecium. (**F**) Lepraliomorph with lepralielliform ooecium. (**G**) Lepraliomorph with escharelliform ooecium. Abbreviations: *as* ascus, *ec* ectooecium, *en* entooecium, *ep* epistege, *fo* ooecial fold, *fr* frontal shield, *fw* non-calcified frontal wall, *g* gymnocyst, *k* frontal kenozooid, *of* ovicell floor

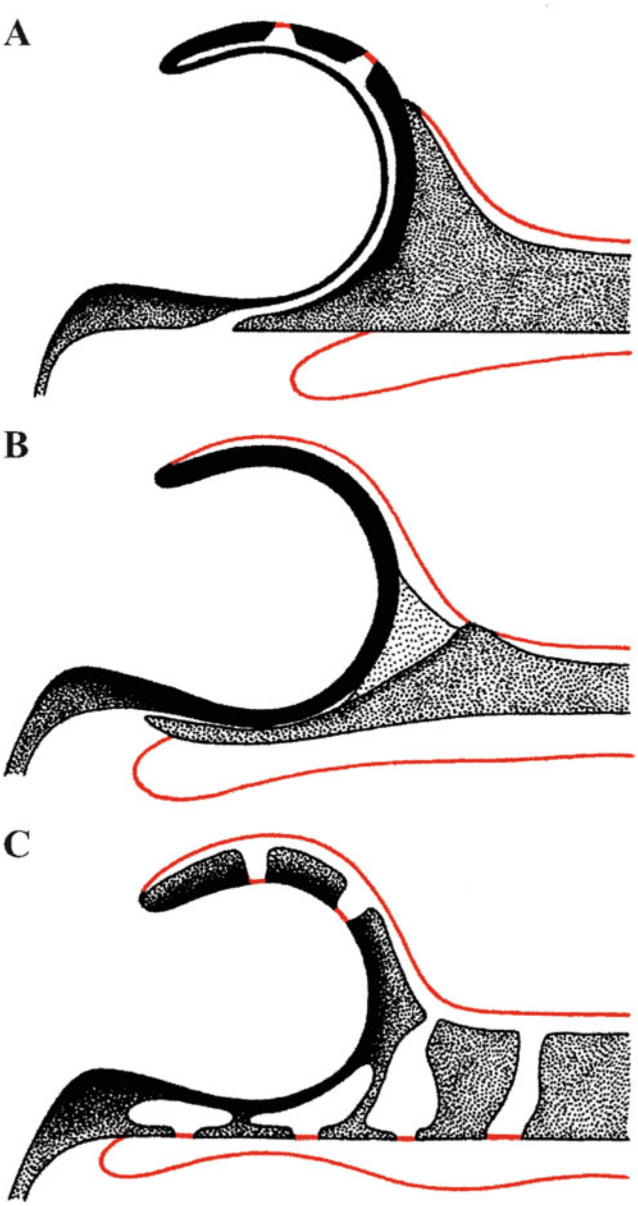

Fig. 2.65 Schematic hypothetical sequence of ooecial evolution in "lepraliomorphs", illustrated by Recent genera (from *top* to *bottom*): (**A**) *Smittina* (calloporiform ooecium). (**B**) *Fenestrulina*. (**C**) *Schizoporella* and *Microporella* (microporelliform ooecium). Calcified walls are shown in *black* and by hatching, membranous walls (including pseudopores) in *red*

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