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Diversity of brood chambers in calloporid bryozoans (Gymnolaemata, Cheilostomata): comparative anatomy and evolutionary trends

Andrew N. Ostrovsky · Claus Nielsen · Norbert Vávra · Ekaterina B. Yagunova

Abstract Comparative anatomical studies of 12 species from 10 genera (*Callopora*, *Tegella*, *Amphiblestrum*, *Parellisina*, *Corbulella*, *Crassimarginatella*, *Valdemunitella*, *Bryocalyx*, *Concertina*, *Cauloramphus*) belonging to one of the largest and most diverse bryozoan taxa, the Calloporidae, and one species from the genus *Akatopora* belonging to the related taxon Antroporidae, were undertaken to elucidate the morphological diversity of brooding structures and to recognize main trends in their evolution. Most of the species studied possess ovicells (specialized brooding receptacles) formed by the distal and maternal (egg-producing) autozooids. The distal zooid can be an autozooid, a vicarious avicularium or a kenozooid. The calcified protective hood (ooecium) is an outgrowth from the distal zooid. Hyperstomial or prominent ovicells are most common. They were found in species of the genera *Callopora*, *Tegella*, *Amphiblestrum*, *Parellisina*, *Corbulella*, *Bryocalyx* and *Concertina*. Subimmersed ovicells were found in *Valdemunitella*, and immersed ovicells in *Crassimarginatella* and *Akatopora*. *Cauloramphus* has an internal brooding sac and a vestigial kenozooidal ooecium, budded by the maternal zooid. Based on the structure of the brooding organs, the following evolutionary trends can be recognized within the group: (1) reduction of the distal (ooecium-producing) zooid, (2) immersion of the brooding cavity correlated with a reduction of the ooecium and ooecial vesicle and with changes in the ovicell closure and the structure of the brood chamber floor, (3) reduction of the calcification of the ectooecium, and (4) transition from bilobate to entire ooecium. The trend towards immersion of the brooding cavity could have evolved repeatedly within the Calloporidae. Transition from bilobate to entire ooecium is characteristic of the related taxon Cribrilinidae, showing a good example of parallel evolution of the ooecium in two closely related clades. Possible causes for the transformations described are discussed.

Keywords Brooding · Ovicells · Internal sacs · Evolution · Cheilostomata

A. N. Ostrovsky · E. B. Yagunova
Department of Invertebrate Zoology, Faculty of Biology and Soil Science, St. Petersburg State University, Universitetskaja nab. 7/9, 199034 St. Petersburg, Russia

A. N. Ostrovsky (✉) · N. Vávra
Department of Palaeontology, Faculty of Earth Sciences, Geography and Astronomy, Geozentrum, Universität Wien, Althanstrasse 14, 1090 Wien, Austria
e-mail: oan_univer@yahoo.com

C. Nielsen
Zoological Museum, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen Ø, Denmark

Introduction

Parental care is generally interpreted as an evolutionary novelty improving offspring survival (see Adiyodi and Adiyodi 1989; Wray 1995 and references therein). The most common method is brooding, with strong variation in position and morphology of the brooding structures, often indicating different routes of evolution.

Except for a few broadcasting species, cheilostome bryozoans brood their embryos/larvae in special chambers. The variety of brooding methods and structures involved is high, including external membranous sacs, protective calcified chambers, epistegal space, and internal sacs (reviewed in Hyman 1959; Ström 1977; Nielsen 1990; Reed 1991; Mukai et al. 1997; Ostrovsky 2008a, b). Species of the taxon Epistomiidae are viviparous (Marcus 1941; Dyrynda 1981;

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Dyrynda and King 1982); this has somewhat confusingly been called intracoelomic brooding. The wide distribution and diversity of parental care clearly indicate that it has been of great importance for the evolutionary success of the clade. The diversity is obviously a result of independent evolution of brooding in several cheilostome lineages (Taylor 1988), but only one study has specifically aimed at proving this (Ostrovsky and Taylor 2005a).

The most common brooding organ is the ovicell, a complex protective structure consisting of (1) the calcified double-walled hood (ooecium) with an enclosed coelomic cavity, and formed either by the distal or the maternal zooid, (2) a space/cavity for embryonic incubation and, as a rule, (3) a closing structure (ooecial vesicle/plug or the non-calcified distal wall of the maternal zooid). Sometimes, it is also closed by the zooidal operculum. An ooecium produced by the distal zooid is an outgrowth of the zooidal wall, and its coelomic lumen communicates with a visceral coelom through a slit or pore(s), normally plugged by non-specialized epithelial cells. An ooecium produced by the maternal zooid is kenozooidal, with communication pores plugged by the special pore-cell complexes (Ryland and Hayward 1977; Nielsen 1981, 1985; Ostrovsky 1998, 2002; Ostrovsky and Schäfer 2003). The ooecial vesicle can be retracted by special muscle bundles, thus opening the entrance of the brooding cavity. Because the ovicell is formed by two zooids performing synchronized reproductive activities (oogenesis and embryonic incubation) it represents a colonial 'brooding organ' (see also Cheetham and Cook 1983).

The Calloporidae *sensu lato* includes 75 nominal genera (Gordon 2007). It is the second largest and the earliest taxon where ovicells evolved within the order Cheilostomata (Cheetham 1954, 1975; Cheetham et al. 2006), but the internal structure of their ovicells has been studied in detail in only few species of *Tegella* (Levinsen 1893, 1894), *Amphiblestrum* (Calvet 1900), and *Callopora* (Levinsen 1909; Ostrovsky and Schäfer 2003; Ostrovsky et al. 2003). Levinsen mainly studied cleaned skeletons, so the information about epithelia and tissues is often missing in his works. The anatomy of the internal brood chambers has been recently studied in eight species of the calloporid genus *Cauloramphus* (Ostrovsky et al. 2007).

Levinsen (1893, 1894, 1909) was the first author to publish illustrations of the developing ovicell, more specifically of its calcified parts, the ooecium, in four species of the genera *Tegella* and *Callopora*. Subsequently, ovicellogenesis has been studied in detail in representatives of the genera *Corbulella* and *Tegella* (Harmelin 1973a; Nielsen 1985). A brief description of the unusual ovicells of *Bryocalyx cinnameus* has been given by Cook and Bock (2000). Later, Ostrovsky et al. (2003) investigated the ultrastructure of the ovicells walls and the development of the ovicell in

six calloporids of the genera *Callopora*, *Tegella* and *Corbulella* (as *Crassimarginatella*). Recently, the development of the ovicell in the earliest known fossil calloporid *Wilbertopora*, has been described (Ostrovsky and Taylor 2005b).

Altogether, these studies seem to give a clear picture of ovicell anatomy and development in the Calloporidae. However, except *Cauloramphus*, only so-called hyperstomial or prominent ovicells have been studied, although the morphological diversity of the brood chambers is much higher within this group (see, for instance, Cook 1968; Gordon 1984, 1986; Soule et al. 1995; Tilbrook 2006). Apart of the diversity, the structure of Recent calloporid ovicells is of particular interest because they show both ancestral and derived characters (Ostrovsky and Schäfer 2003; Ostrovsky et al. 2003; Ostrovsky and Taylor 2004, 2005a, b).

Here we present a comparative study of the various types of brood chambers in 12 species of 10 genera from the cheilostome family Calloporidae. Additionally, we include data on ovicell structure of a species of *Akatopora* from the closely related group Antroporidae. The main aims of this paper are (1) to describe the morphological diversity of brooding structures in the Calloporidae, (2) to show the main trends in their evolution, and (3) to relate the new data to the evolution of brooding in the earliest cheilostome groups.

Materials and methods

Colonies of *Callopora craticula* (Alder, 1857) and *Tegella armifera* (Hincks, 1880) were collected on 17.08.1996 by dredge and SCUBA from 3 to 4 m depth near Bezymjanniy Island (66 18.23′N, 33 27.23′E), Chupa Inlet, Kandalarsha Bay, White Sea. *T. armifera* was collected by dredge on 03.09.1995, 04.08.1996, 19.08.1996, and 25.06.1998 from 3 to 10 m depth near Matrenin (66 18.36′N, 33 38.03′E) and Sredniy (66 17.12′N, 33 39.56′E) Islands, Chupa Inlet, Kandalarsha Bay, White Sea. *Cauloramphus spinifer* (Johnston, 1832) was collected by dredge on 13.06.1998 from 5 to 8 m depth near Sredniy Island (66 17.12′N, 33 39.56′E) Chupa Inlet, Kandalarsha Bay, White Sea (coll. Dr. N. N. Shunatova).

Colonies of *Tegella unicornis* (Fleming, 1828) were collected on 05.08.1997 by dredging from 16 to 29 m depth at the Herthas Flak-reef (57 27.50′N,10 35.21′E), North Kattegat, E of Skagen, Baltic Sea (coll. Dr A. N. Ostrovsky).

Colonies of *Callopora dumerilii* (Audouin, 1826) and *Corbulella maderensis* (Waters, 1898) were collected on 12.06.1997 by SCUBA from 22 m depth near Riou Island (43 10.36′N, 05 23.38′E), near Marseille, Mediterranean Sea (coll. Dr. J.-G. Harmelin).

Colonies of *Amphiblestrum inermis* (Kluge, 1914) and *Valdemunitella lata* (Kluge, 1914) were collected on

05.05.2000 by dredge from 99 m depth near King-George Island (62 17.40′S, 58 31.50′W), South Shetland Islands, Subantarctic (r/v "Polarstern", cruise ANTXVII/3, Station 190-1, coll. Drs. B. I. Sirenko and I. S. Smirnov).

A colony of *Parellisina* sp. was collected on 14.11.1981 from 56 m depth (40 43.9′S, 143 32.5′E) southern Australia (Bass Strait Survey, r/v "Tangaroa", cruise 81-T-1, Station 163). A colony of *Crassimarginatella* sp. was collected on 27.03.1981 by SCUBA from 25 m depth in Swashway Bay (39 27.7′S, 147 17.3′E), Erith Island, Bass Strait, southern Australia (coll. Dr. P. E. Bock).

Colonies of *Bryocalyx cinnameus* Bock et Cook, 2000 were collected on 06.10.1979 from 1,586 m depth near Bounty Trough (45 76′S, 174 51′E), New Zealand (NZOI/NIWA cruise, Station S151). A colony of *Concertina cultrata* Gordon, 1986 was collected on 03.10.1965 from 1,225 m depth near Bounty Trough (45 35′S, 171 95′E), New Zealand (NZOI/NIWA cruise, Station E416).

A colony of *Akatopora circumsaepta* (Uttley, 1951) was collected from 205 m depth near Stephens Hole (41 24.37′S, 174 25.46′E), Cook Strait, New Zealand (date and station unknown, NZOI/NIWA cruise).

Most specimens were fixed in Bouin's fluid without acetic acid or in 70% ethanol. For light microscopy, colonies were decalcified for 6–12 h using a few drops of a 2 N solution of hydrochloric acid, gradually dehydrated, embedded in plastic (epoxy resin type TAAB 812), sectioned (1–3 μm thick) with a glass knife, and stained with Richardson's stain (1% water solutions of methylene blue, Na-tetraborate and azur II mixed in proportions 1:1:2) using standard methods (Richardson et al. 1960). Sections were observed and digital images were made with Nikon 104 and Nikon 118 FXA dissecting light microscopes. In our preparations methylene blue non-selectively stained cells of all types in soft tissues, whereas azur II selectively stained decalcified skeletal tissue. We had only dry specimens of *Amphiblestrum inermis*, *Parellisina* sp. and *Akatopora circumsaepta* at our disposal. For SEM studies, colonies fixed in alcohol were cleaned in a 7.5% solution of sodium hypochlorite, rinsed, air-dried, and coated with gold. In addition, some colonies fixed in alcohol were dehydrated without cleaning, dried either under critical point or air-dried and coated with gold for SEM study. Specimens were observed with Jeol JSM-840, Jeol JSM-6400 and CAMSCAN-Serie-2-CS-44 scanning electron microscopes at 10 kV accelerating voltage.

Results

In describing the various ovicells, we classify them in three categories: **hyperstomial** or **prominent ovicells**, which have half or more of the brooding cavity protruding above the colony surface (Figs. 1, 2, 4, 5a, 8, 9, 12a, b); **subimmersed ovicells**, which have more than a half of the brooding cavity situated below the colony surface (Figs. 6a, b, 7a, 12d), and **immersed ovicells** in which the entire or almost entire brooding cavity is below the colony surface, situated in the distal part of the maternal autozooid (Figs. 7b, 11a, 12c). In contrast, *Cauloramphus* has an internal brooding sac with a vestigial kenozooidal ooecium (Figs. 10d–f, 11b, 12e, f).

Hyperstomial (prominent) ovicells with entire ooecia

The hyperstomial, prominent ovicells of the calloporids studied (species of the genera *Callopora*, *Tegella*, *Parellisina*, *Amphiblestrum* and *Corbulella*) are represented by a two-walled protective fold (ooecium) with enclosed coelom, and with an ooecial vesicle (or ooecial plug) closing the brooding cavity (Figs. 1, 2, 3b–d, 4, 5a). The outer ooecial wall (ectooecium) is partially calcified having a frontal membranous area of various shape and size (Figs. 1a–c, 2, 3c, d, 4, 5a), but it is mostly non-calcified in *Callopora dumerilii* (Fig. 1d). The internal ooecial wall (entooecium) that surrounds the brooding cavity is completely calcified (Figs. 1f, 4). The ooecium is formed by an outgrowth of the frontal wall of the autozooid distal to the maternal (egg-producing) autozooid. An ooecium formed by a distal kenozooid has been found in *Corbulella maderensis* (Fig. 3c), and several ooecia formed by a vicarious avicularium (Fig. 3a) or by the distal kenozooid (Fig. 3b) have been found on the colony periphery in *C. craticula*. The two latter variants were simultaneously present in the colonies where most of the ooecia were formed by the distal autozooid.

The ooecial coelomic cavity becomes very narrow because of the progressive calcification of the ooecial walls (Figs. 1f, 2, 4a). In older zooids it is reduced to slit-like lacunas. In *C. maderensis* it finally disappears except a small portion underneath the frontal membranous area (Fig. 4b). The ooecial coelom communicates with the coelomic cavity of the distal zooid via an arch-like slit that later becomes reduced to pore(s) (Figs. 3e–f, 5c–e). In completely formed ooecia these pores are plugged by non-specialized epithelial cells (Figs. 2, 4a), preventing free circulation of the coelomic fluid. Calcification of the ooecial walls also changes external morphology of the ooecium: in old parts of the colony ooecia acquire a prominent rim around the membranous area (compare Fig. 1b, c).

In *Tegella* and *Amphiblestrum* the ooecium is associated with an adventitious avicularium (Figs. 1a, c, f, 5a), with their coeloms separated by a vertical cryptocystal wall (Figs. 2, 4a, 5b).

With the exception of *Corbulella maderensis*, all species studied in this section have acleithral ovicells, with
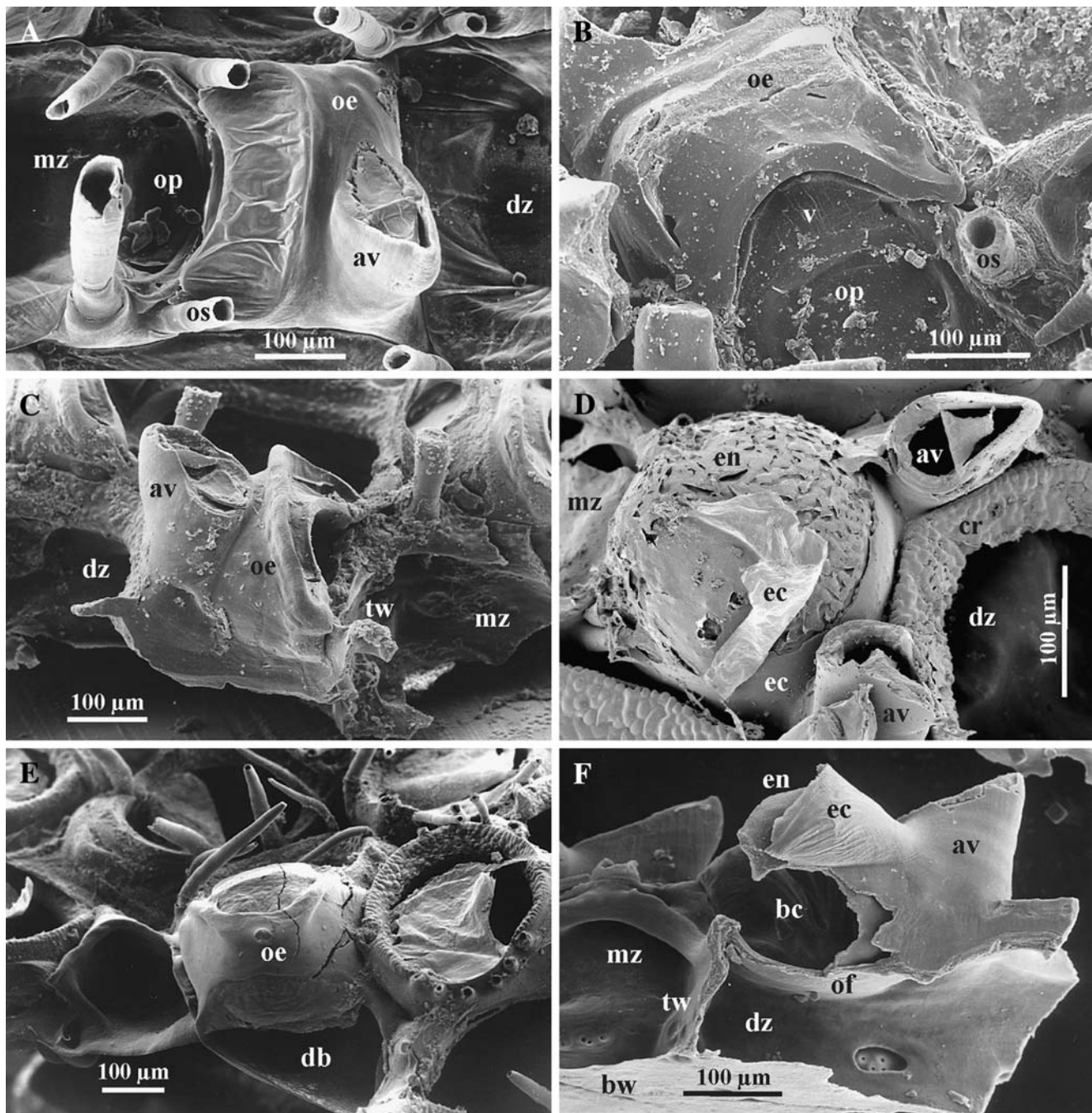
Fig. 1 Scanning electron microscopy. **a**, **f** *Tegella armifera*, **b–c** *T. unicornis*, **d** *Callopora dumerilii*, **e** *Corbulella maderensis*. **a** Non-cleaned air-dried young ovicell with large membranous area collapsed (seen from above), **b** non-cleaned critical-point dried young ovicell with the opening closed by the ooecial vesicle (*v*) (seen from above), **c** non-cleaned old ovicell with prominent rim around the membranous area of the ooecium (*oe*) (*lateral view*), **d** non-cleaned ovicell with partially detached membranous ectooecium (*ec*) (seen from above), **e** non-cleaned ovicell with the ooecium (*oe*) formed by the distal zooidal bud (*distal view*), **f** cleaned damaged ooecium (*oe*) (*lateral view*). Abbreviations: *av* adventitious avicularium, *bc* brooding cavity, *bw* basal wall, *cr* cryptocyst, *db* distal bud, *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

their opening being closed only by an ooecial vesicle (Figs. 1b, 2). Its wall facing the brooding cavity consists of a thin cuticle with epithelial layers. The distal edge of the vesicle has a thickened cuticle forming a prominent sclerite to which the largest (upper) paired bundles of muscles are attached (Figs. 2, 4a). There are smaller muscles attached to the middle and lower parts of the ooecial vesicle wall. These muscles originate on the
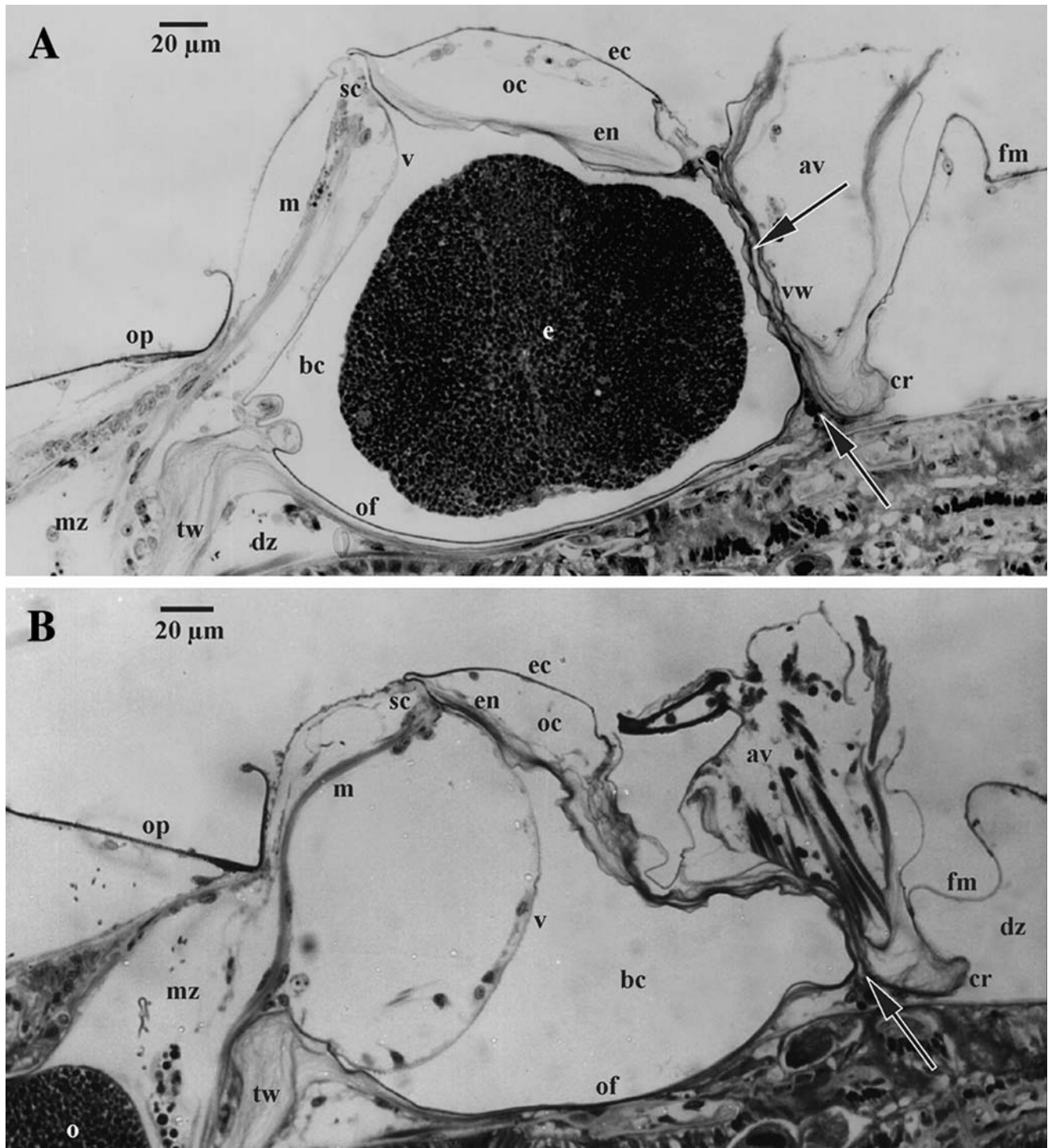
Fig. 2 Light microscopy. *Tegella unicornis*. Longitudinal section of the ovicell with an early embryo (*e*) **a**, and empty **b**. *Arrows* point at the narrow coelomic cavity (*oc*) of the ooecium (*oe*) and at the ooecial communication pore, plugged by non-specialized epithelial cells. Abbreviations: *av* adventitious avicularium, *bc* brooding cavity, *bw* basal wall, *cr* cryptocyst, *db* distal bud, *dz* distal autozooid, *e* embryo, *ec* ectooecium, *en* entooecium, *fm* frontal membrane, *m* muscle bundles of the ooecial vesicle, *mz* maternal autozooid, *oe* ooecium, *oc* ooecial coelom, *of* ovicell floor, *op* operculum, *sc* sclerite of the ooecial vesicle, *tw* transverse wall, *v* ooecial vesicle, *vw* vertical wall between coelomic cavities of the ooecium and avicularium

basal and/or lower part of transversal walls of the maternal cystid in the species of *Callopora* studied and on the lower part of the transversal wall in the species of *Tegella* (Fig. 4a, see also Ostrovsky and Schäfer 2003). When the ovicell is closed, the shape of the ooecial vesicle is maintained by the pressure of the coelomic
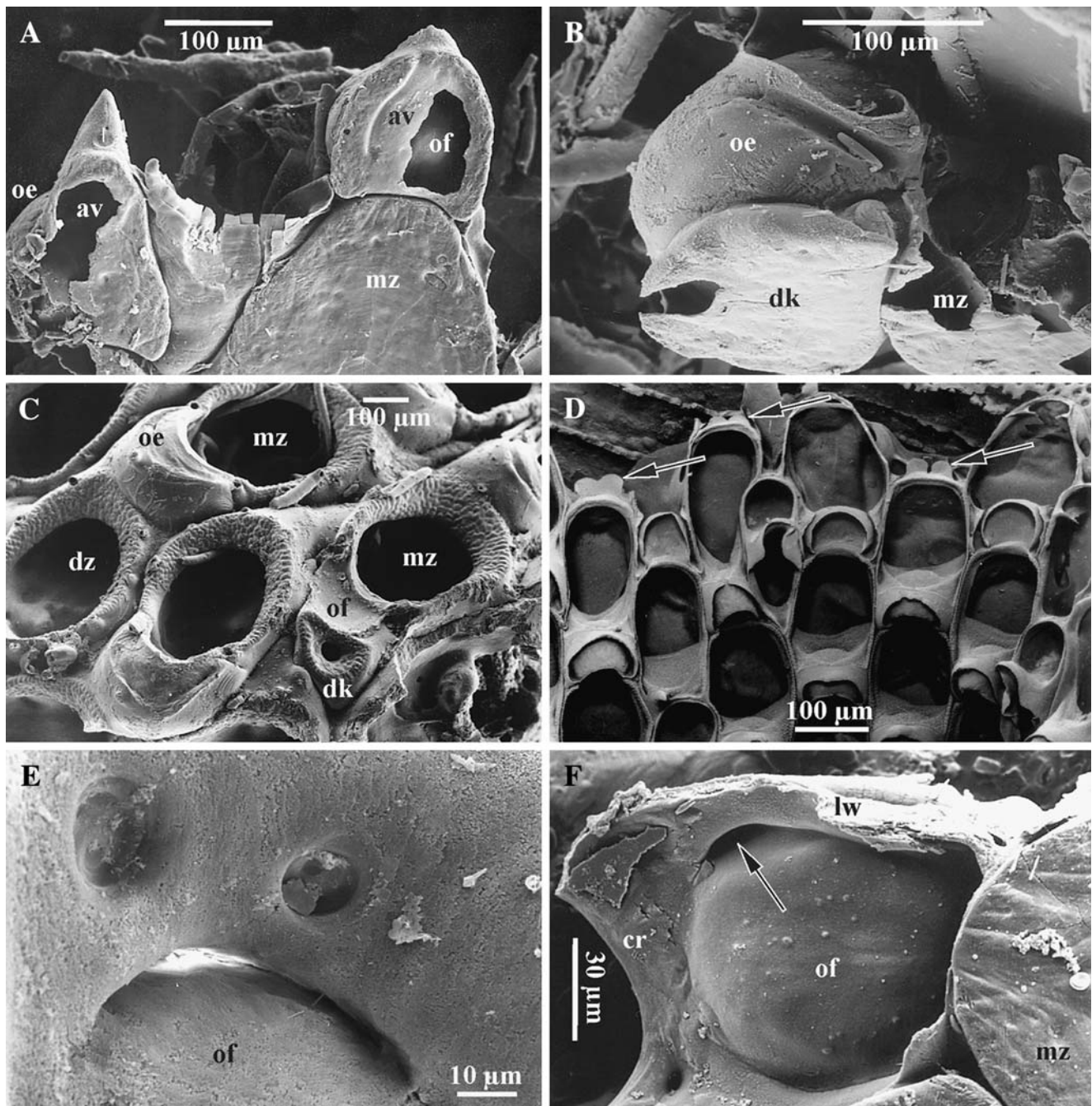
Fig. 3 Scanning electron microscopy (cleaned specimens). **a–b** *Callopora craticula*, **a** ooecia (*oe*) formed by the vicarious avicularia (*av*) on the colony periphery (seen from below), **b** ooecium (*oe*), formed by the distal kenozooid (*dk*) (*lateral view*), **c** *Corbulella maderensis*, two ooecia (*oe*) formed by the distal autozooids (*dz*) (*left*), and a damaged ooecium (*oe*) formed by the distal kenozooid (*dk*), **d** *Parellisina* sp., periphery of the colony with developing ooecia (*oe*) [*arrows* point at the paired rudiments of the calcifying ooecial floor (*of*)], **e** *Tegella armifera*, arch-like communication ooecial slit of the young ooecium (*oe*) (above are dietellae of two adventitious avicularia), **f** *Callopora craticula*, the remnant of the communication slit (*arrow*). Abbreviations: *av* vicarious avicularium, *cr* cryptocyst, *dk* distal kenozooid, *dz* distal autozooid, *lw* lateral wall, *mz* maternal autozooid, *oe* ooecium, *of* ovicell floor

fluid. During oviposition and larval release, the muscles contract to cause wrinkling of the vesicle that opens the entrance to the brooding cavity.

Ovicells are prominent and cleithral in *Corbulella maderensis* (Figs. 1e, 3c, 4b). The ovicell opening is closed by both the relatively small ooecial vesicle and the zooidal operculum. In contrast with other species, the ooecial plug is devoid of a sclerite and filled with funicular cells, giving it a 'parenchymatic' appearance in sections. Two thin muscle bundles are attached to the wall of the plug in its upper
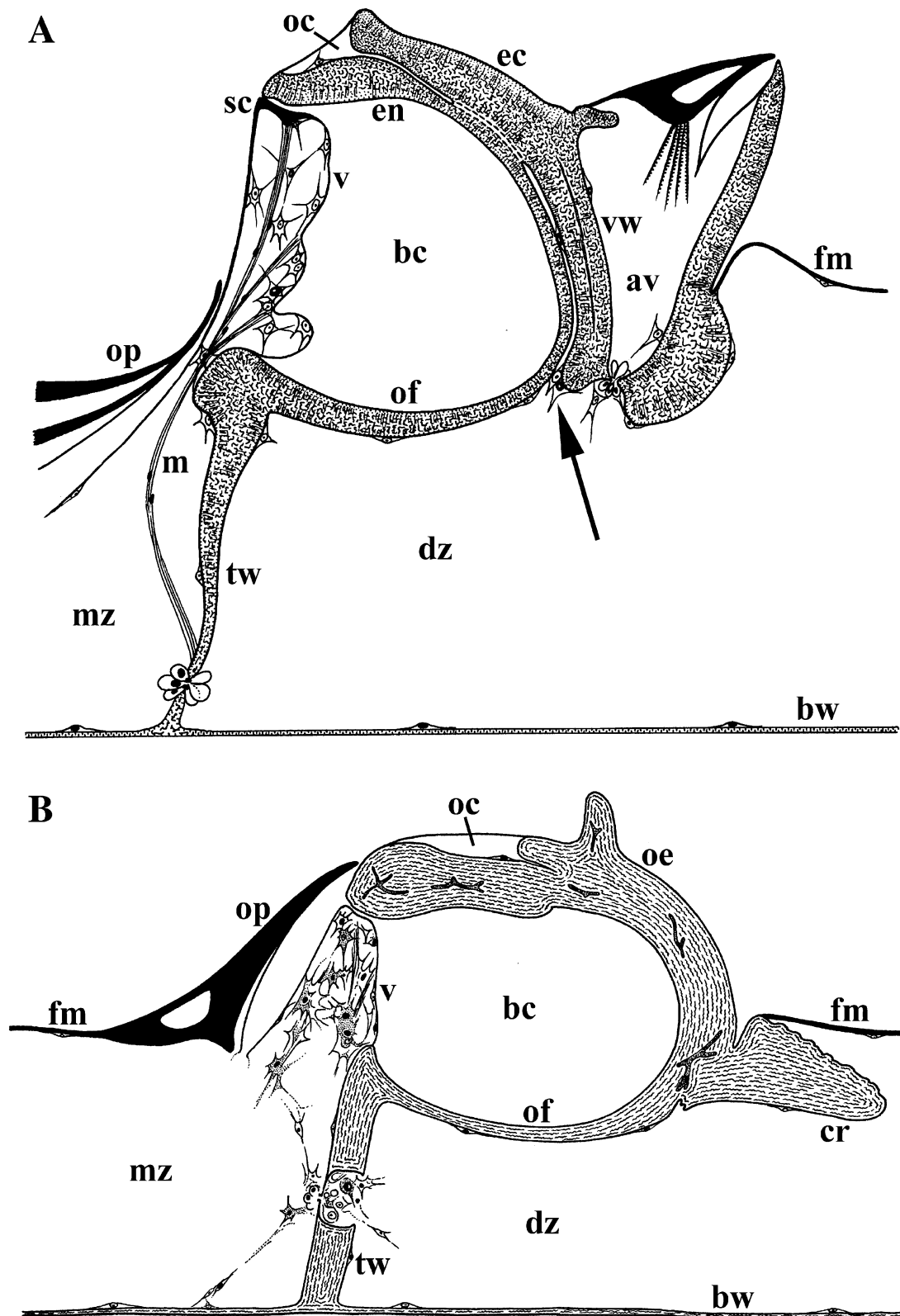
Fig. 4 Schematic longitudinal sections through ovicells. **a** acleithral, *Tegella armifera* (*arrow* points at the ooecial communication pore, plugged by non-specialized epithelial cells), **b** cleithral, *Corbulella maderensis* (ooecial walls fused together, fungal bore-holes are seen). Abbreviations: *av* adventitious avicularium, *bc* brooding cavity, *bw* basal wall, *cr* cryptocyst, *dz* distal autozooid, *ec* ectooecium, *en* entooecium, *fm* frontal membrane, *m* muscle bundles of the ooecial vesicle, *mz* maternal autozooid, *oc* ooecial coelom, *of* ovicell floor, *op* operculum, *sc* sclerite of the ooecial vesicle, *tw* transverse wall, *v* ooecial vesicle, *vw* vertical wall between coelomic cavities of the ooecium and avicularium
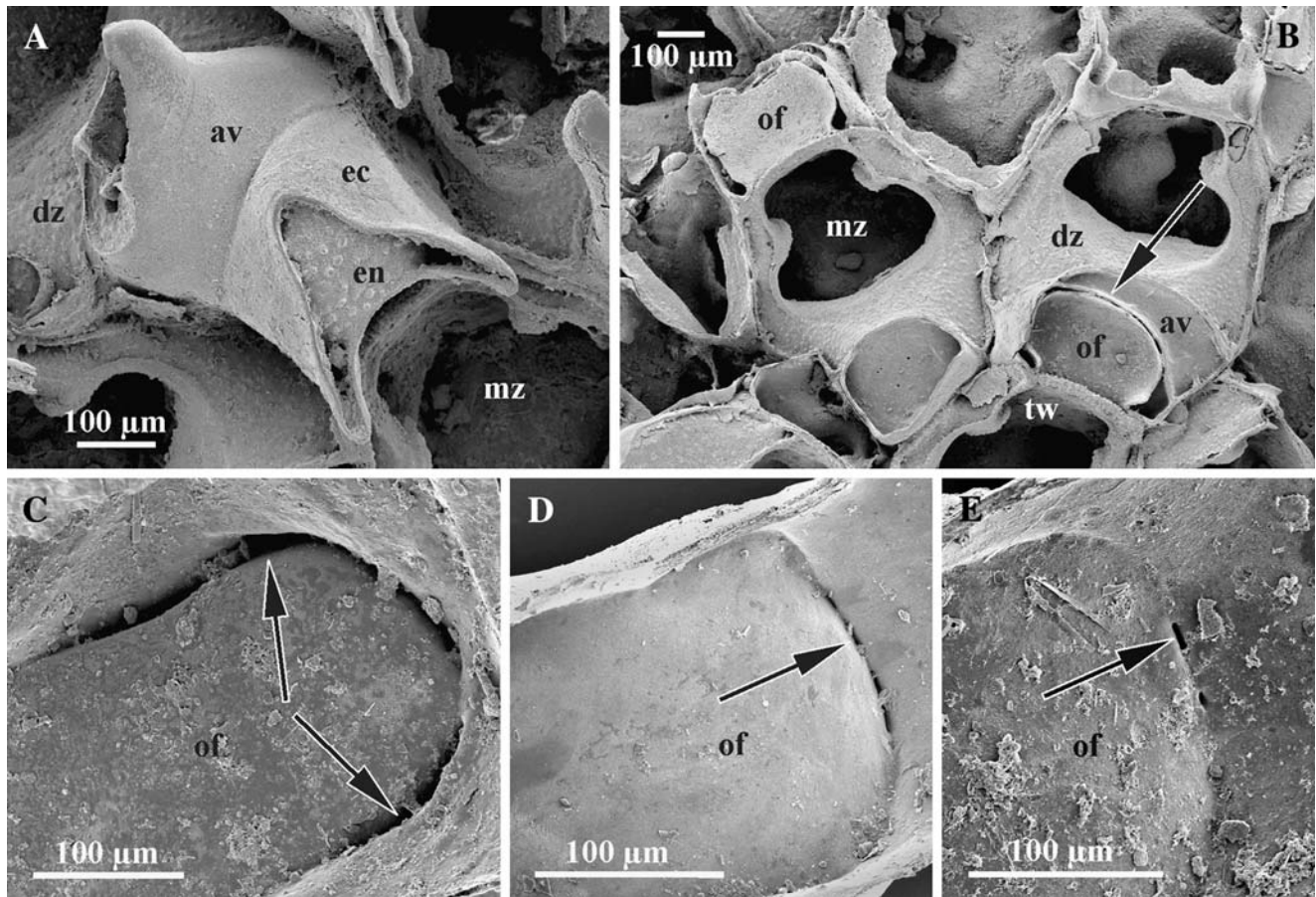
Fig. 5 Scanning electron microscopy (cleaned specimens). **a–e** *Amphiblestrum inermis*. **a** ooecium (*oe*) associated with adventitious avicularium (*av*), **b** forming ooecia (*oe*) [*arrow* points at the vertical wall between the coelomic cavities of the ooecium (*oe*) and avicularium (*av*)], **c–e** subsequent stages of the closure of the communication slit (the slit and residuary pores indicated by *arrows*). Abbreviations: *av* adventitious avicularium, *dz* distal autozooid, *ec* ectooecium, *en* entooecium, *mz* maternal autozooid, *of* ovicell floor, *tw* transverse wall

and middle parts. We were unable to find where their lower parts are fixed.

Development of the ooecium in all hyperstomial ovicells studied starts with a calcification of the provisory ovicell floor having a shape of two roundish plates (Fig. 3d). The ooecial walls grow as a semicircular fold (Fig. 5b) with subsequent calcification, forming the hemispherical protective hood.

Hyperstomial (prominent) and subimmersed ovicells with bilobate ooecia

Valdemunitella lata, *Concertina cultrata* and *Bryocalyx cinnameus* have ooecia of paired origin with a median suture (Figs. 6a, 8a, d).

In *Valdemunitella lata* this is best recognized in cleaned specimens. The ooecium consists of two lobes, fused along the median axis so that they form a double-walled longitudinal septum in the ooecium (Fig. 6b–c). The lower edges of each lobe are well-seen both internally and externally

(Fig. 6b). Each lobe possesses its own coelomic lumen that is connected with the visceral coelom of the distal autozooid via a separate slit (Fig. 6d) and later via an oval pore (Fig. 6f). Communication slits are open in young zooids, further closing by non-specialized epithelial cells in pores (Fig. 7a). The coeloms of the ooecial lobes are fused at the proximal edge of the ooecium, underneath the frontal membranous area where the medial suture on the longitudinal septum of the ooecium is not seen (Fig. 6b). However, the medial suture is seen on the cuticle of the membranous area in non-cleaned specimens, as if the coelomic cavities of two lobes were separated (Fig. 6a). The internal surface of the ooecium (facing the brooding cavity) bears the medial suture too, and it ends with a closed horizontal slit (Figs. 6c, 7a) that is also seen from the outside (Fig. 6a).

The ovicells are cleithral in *V. lata*, closed by both the zooidal operculum and the upper part of the maternal autozooid's distal wall (Figs. 7a, 12d). This wall might be considered as an ooecial plug, although it is not as well-developed as in hyperstomial ovicells. However, its upper
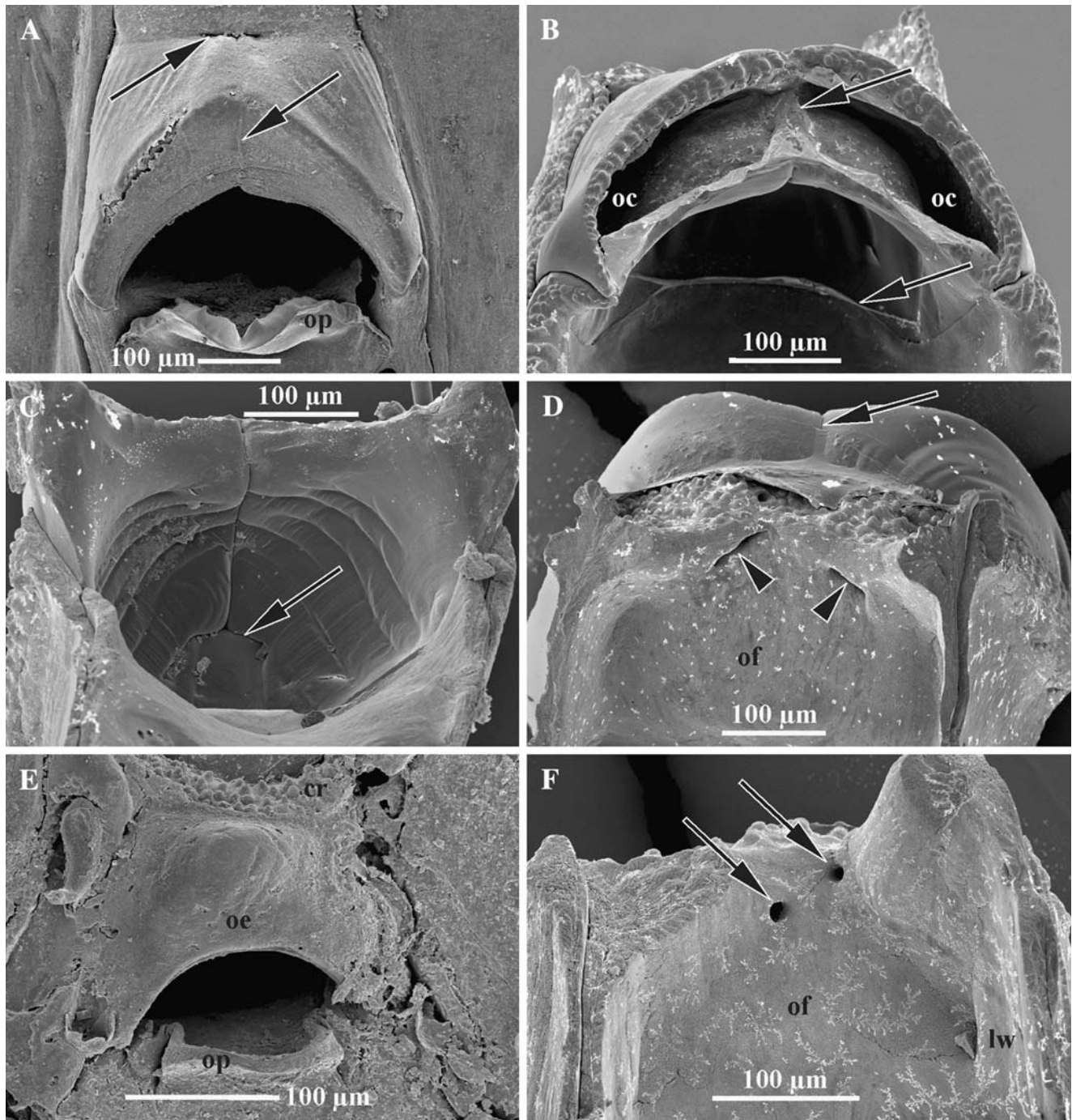
Fig. 6 Scanning electron microscopy. **a–d**, **f** *Valdemunitella lata*, **e** *Akatopora circumsaepta*. **a** non-cleaned air-dried ovicell (*arrows* point at the medial suture and the closed horizontal slit), **b** cleaned ovicell showing coeloms (*oc*) and basal parts of the ooecial lobes [*arrows* point at the longitudinal septum of the ooecium (*oe*), and at a zone of attachment of the distal wall of the maternal zooid], **c** internal surface of the brooding cavity (*arrow* points at closed horizontal slit), **d** floor (*of*) of young ovicell from the side of the distal zoid [*arrowheads* show the communication slits of the ooecial lobes, *arrow* points at the medial suture of the ooecium (*oe*)], **f** floor (*of*) of old ovicell from the side of the distal zoid (*arrow* points at the communication pores of the ooecial lobes), **e** non-cleaned air-dried ovicell. Abbreviations: *cr* cryptocyst, *lw* lateral wall, *oc* coelom of the ooecial lobe, *oe* ooecium, *of* ovicell floor, *op* operculum

part is provided with a thickened cuticle resembling a sclerite, and several thin muscle bundles are attached to its wall. The proximal parts of them are fixed on the basal wall of the maternal zooid (Fig. 7a).

The floor of the brooding cavity is mainly formed by the non-calcified distal wall of the maternal zooid, whereas the rest of it is a proximal gymnocyst of the distal autozooid, that continues with the upper part of the transverse wall.
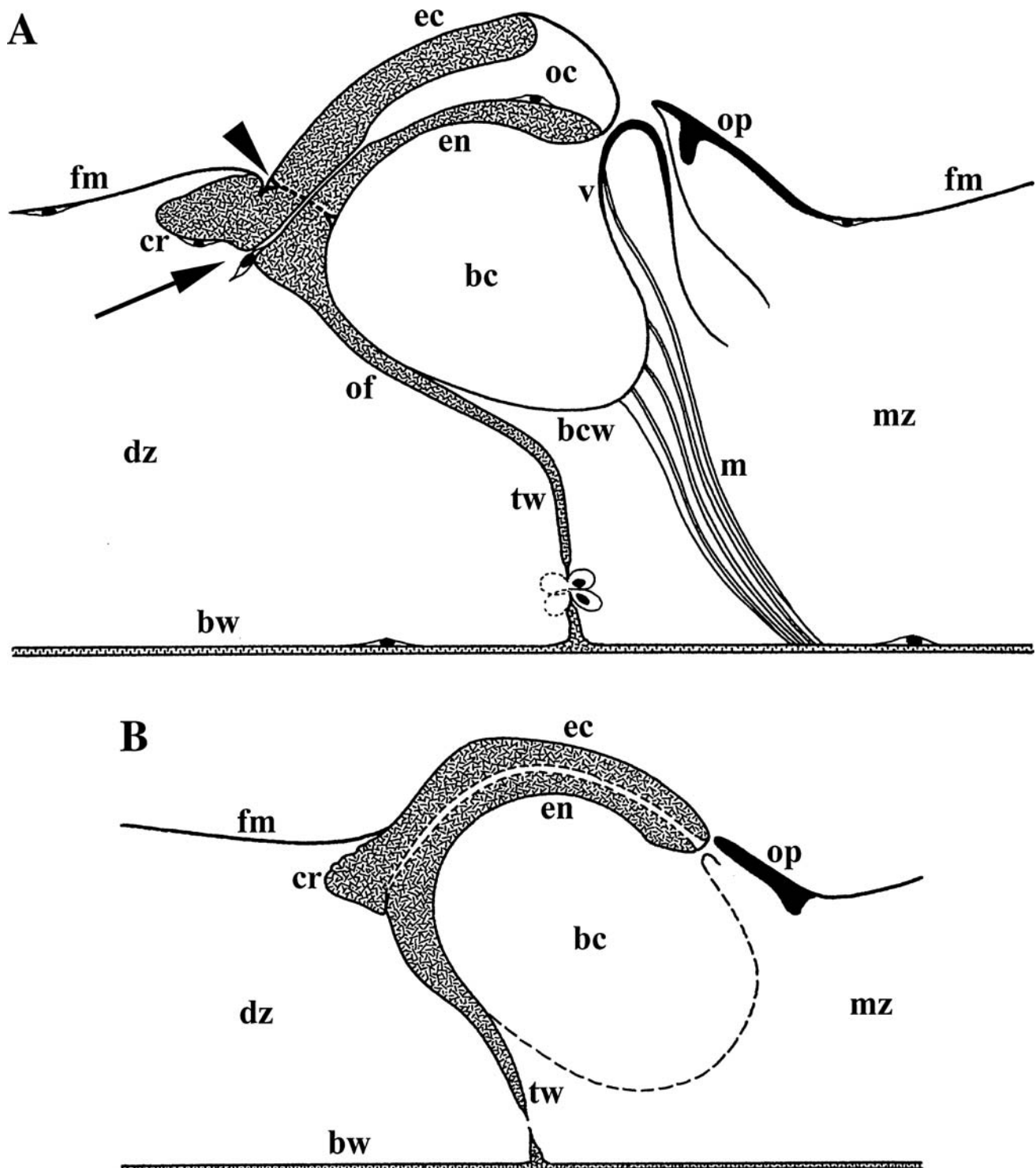
Fig. 7 Schematic longitudinal sections through cleithral ovicells. **a** *Valdemunitella lata* (*arrowhead* points at the position of closed horizontal slit given by *dotted line*, *arrow* points at the communication pore of one of the ooecial lobes), **b** *Akatopora circumsaepta* [suggested position of the distal wall of the maternal zooid (*mz*) forming part of the brooding cavity (*bc*) is given by *dotted line*]. Abbreviations: *bc* brooding cavity, *bcw* brooding cavity wall, *bw* basal wall, *cr* cryptocyst, *dz* distal autozooid, *ec* ectooecium, *en* entooecium, *fm* frontal membrane, *m* muscle bundles of the ooecial vesicle, *mz* maternal autozooid, *oc* ooecial coelom, *of* ovicell floor, *op* operculum, *tw* transverse wall, *v* ooecial vesicle

Since more than a half of the brooding cavity is below the colony surface in sections, we assign this ovicell to the subimmersed type (Figs. 7a, 12d).

In contrast, *Concertina cultrata* has prominent ovicells with half of the brooding cavity above the colony surface (Figs. 8d, 9b). The ooecium is formed by a distal kenozooid at the colony periphery (Figs. 9b, 12b). Gordon (1986) called this ovicell type vicarious. Sometimes, one more autozooid is budded from the kenozooid distally (Figs. 9b, 12b). The ooecium is elongate, with a medial suture along most of its roof (Fig. 8d). Scarcity of material prevented us from checking if the entooecium bears the medial suture as

well, and if the ooecial roof is divided in two lobes as in *Valdemunitella lata*. The basis of the ooecial fold is non-paired, with a wide arch-like communication slit leading from the distal kenozooid to the ooecial coelom (Figs. 9b, 12b), providing free circulation of the coelomic fluid. Calcification is very weak in both ecto- and entooecium. Moreover, in the central part of ectooecium it is so thin that it can hardly be detected in sections (Figs. 9b, 12b).

The ovicells are acleithral, with a medium sized ooecial vesicle. Several thin muscle bundles are attached to its upper and middle walls. Their proximal parts are fixed on the basal wall of the maternal zooid. There is no sclerite (Figs. 9b, 12b).
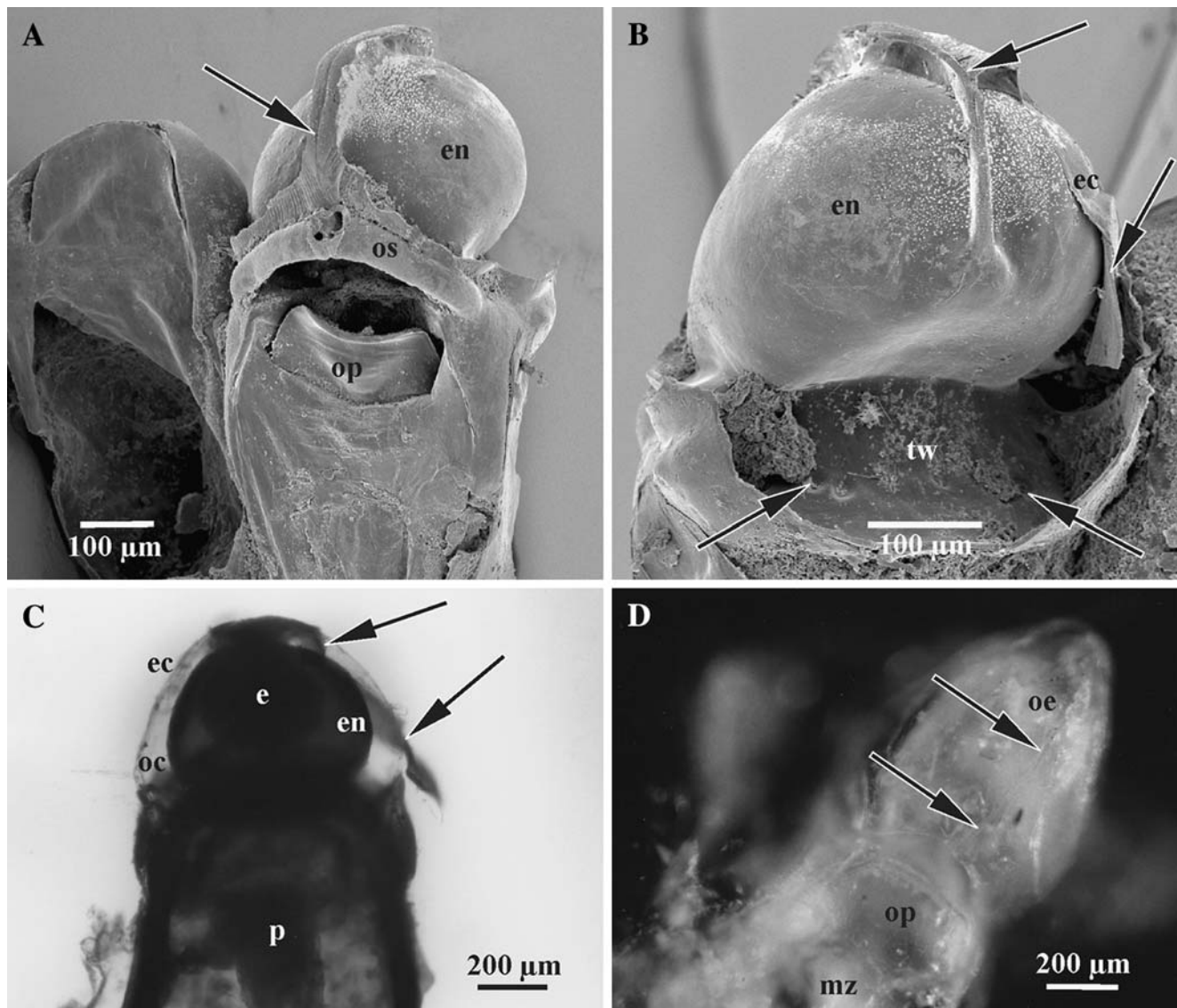
Fig. 8 Scanning electron and light microscopy. **a–c** *Bryocalyx cinnameus*, **d** *Concertina cultrata*. **a** air-dried ovicell with membranous parts of ectooecium (*ec*) removed (*arrow* points at the medial suture), **b** distal part of the ooecium (*oe*) and the cavity of the distal kenozooid [*arrows* point at the medial suture, at the calcified rib of ectooecium (*ec*), and at the communication pores of the distal kenozooid)], **c** wet specimen: maternal autozooid and terminal ovicell with the embryo (*e*) inside [*arrows* point at the calcified parts of the ectooecium (*ec*)], **d** wet specimen: maternal autozooid with terminal ovicell (*arrows* point at the medial suture). Abbreviations: *e* embryo, *ec* ectooecium, *en* entooecium, *mz* maternal autozooid, *oc* ooecial coelom, *op* operculum, *os* oral spine, *p* polypide, *tw* transverse wall
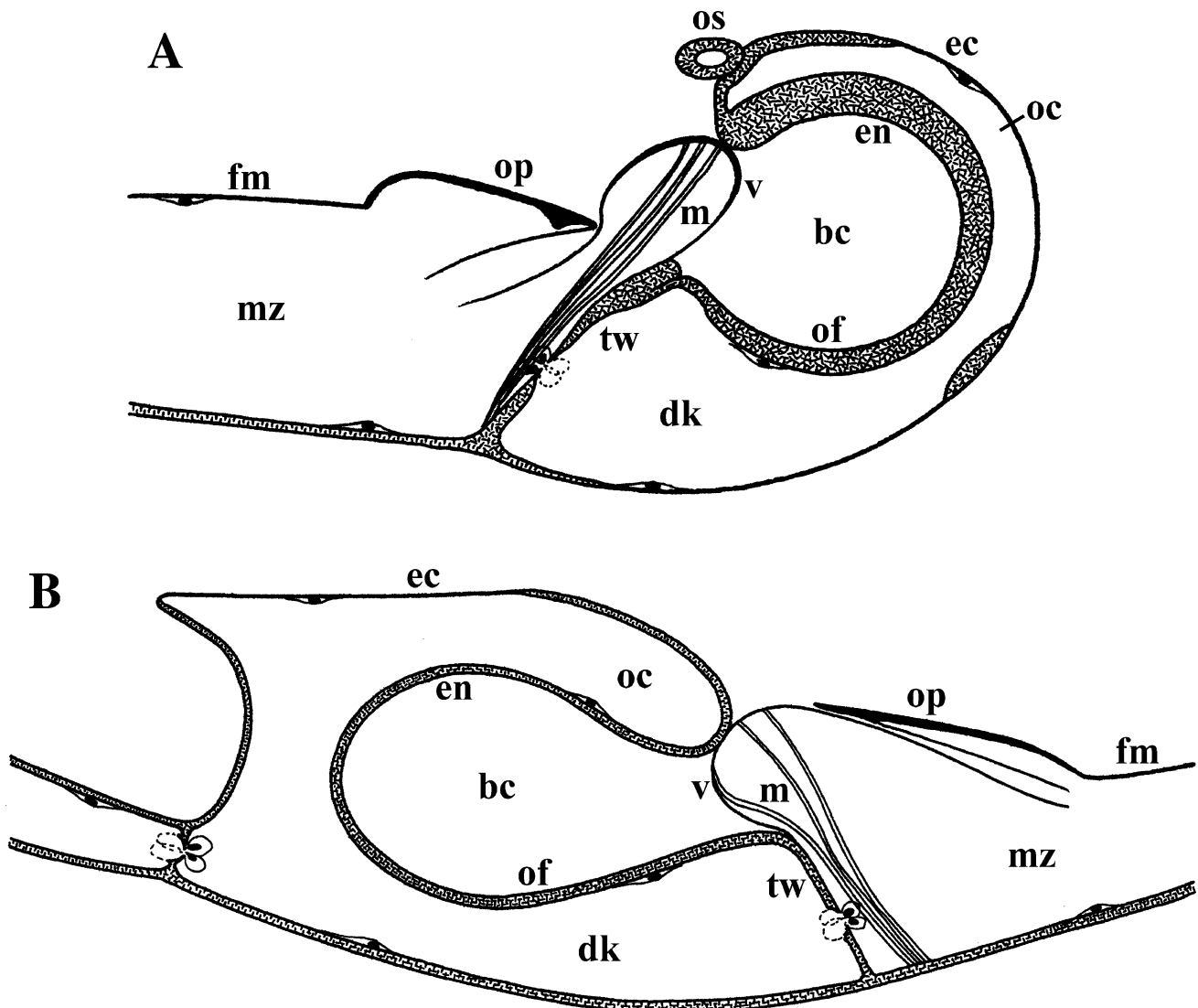
Fig. 9 Schematic longitudinal sections through cleithral ovicells. **a** *Bryocalyx cinnameus* (tangential section), **b** *Concertina cultrata*. Abbreviations: *bc* brooding cavity, *dk* distal kenozooid, *ec* ectooecium, *en* entooecium, *fm* frontal membrane, *m* muscle bundles of the ooecial vesicle, *mz* maternal autozooid, *oc* ooecial coelom, *of* ovicell floor, *op* operculum, *os* oral spine, *tw* transverse wall, *v* ooecial vesicle

Bryocalyx cinnameus has terminal hyperstomial ovicells. As in *C. cultrata*, the ooecium is formed by a distal kenozood, but it is more reduced in length (Figs. 9a, 12a). Most of the ooecium is bilobate. Lobes fuse with each other, forming a double longitudinal septum marked by a median suture like in *V. lata* (Figs. 8a, b, 12a). The coelom of each lobe opens into the coelomic cavity of the kenozooid via wide arch-like opening, permitting free circulation of the coelomic fluid (Figs. 9a, 12a). The ectooecial part of each lobe is membranous, except the narrow edges around the ovicell opening and along the medial suture, and two flat diagonal ribs coming from these edges (see also Cook and Bock 2000). All these calcified elements form a rigid frame of the ectooecium (Fig. 8a–c). Two large oral spines surround the ovicell opening from the above (Figs. 8a, 9a, 12a). The entooecium is completely calcified.

The ovicells are acleithral. The ooecial vesicle is well-developed, with thicker cuticle in its upper part where three muscle bundles are attached. Proximally they have an appearance of the single bundle being fixed on the basis of the transverse wall between the maternal autozooid and distal kenozooid (Figs. 9a, 12a).

Immersed ovicells

Akatopora circumsaepta and *Crassimarginatella* sp. possess immersed ovicells, with the embryos developing in an invagination of the uncalcified body wall of the maternal zooid, but still overarched by a small ooecium formed by the distal zooid.

Akatopora circumsaepta (Fig. 7b) has almost the entire brooding cavity below the colony surface, and the entire

brooding cavity of *Crassimarginatella* sp. (Figs. 11a, 12c) is completely below the surface. The brooding cavity is situated in the distal part of the maternal autozooid, as opposed to endozooidal ovicells where the brooding cavity is in the proximal part of the distal zooid (for instance, in Flustridae). In sections most part of the brooding cavity is surrounded by the non-calcified distal wall of the maternal zooid in *Crassimarginatella* sp. (Figs. 11a, 12c). Thus, this structure strongly resembles the internal brooding sac or might even be termed like this. Thin muscles are attached to its lower part, anchoring their proximal ends on the basal wall of the maternal zooid. We speculate that these muscles serve to expand the brood cavity during oviposition and larval release. Since only dry material was at our disposal, we were unable to study the brooding cavity in *A. circumsaepta*. We suggest that its structure might be similar to the brooding cavity of *Valdemunitella lata* (see Fig. 7a, b).

Ooecia in both species are vestigial, cap-like, with a small membranous area on the proximal side (*Crassimarginatella* sp.) (Figs. 10a–b, 11a) or on its edge (*A. circumsaepta*) (Figs. 6e, 7b). The same ooecial structure is known, for example, in *C. papulifera* (McGillivray, 1881) (see Gordon 1986; Tilbrook 1998). Initially the ooecial coelomic cavity is a slit-like space between the ecto- and entooecium, connected with a visceral coelom via arch-like slit (Figs. 7b, 10b, c, 11a). Later the ooecial coelom is reduced to a small furrow (underneath the membranous window) with a pore on its bottom (Fig. 10b) and a narrow communicative canal. The communication slit transforms to pores that often disappear. Thus, finally the ooecium is transformed to a thick, almost solid calcareous plate, similar to *Corbulella maderensis*.

These ovicells are cleithral. In *Crassimarginatella* sp. the upper part of the distal wall of the maternal zooid additionally plugs the opening of the brooding cavity in the shape of an ooecial vesicle (Figs. 11a, 12c). Sclerite and muscles were not seen. In *A. circumsaepta* zooidal opercula closing the ovicells are larger than normal opercula.

Internal brooding sac with vestigial kenozooidal ooecium

Cauloramphus spinifer possesses a special type of chamber for embryonic incubation showing the tendency towards further immersion of the brooding cavity. The maternal zooid buds a normal, distal zooid, and in addition a small, frontal kenozooid, which resembles the proximal part of the ooecium in a hyperstomial ovicell (Figs. 11b, 12e, f). This kenozooidal polymorph, located on the distal mural rim of the maternal autozooid being surrounded by oral spines, represents an ooecium. Its upper wall is a strongly reduced, non-calcified ectooecium, whereas the lower wall is a calcified entooecium (Figs. 11b, 12e, f). The border of the non-calcified ectooecium is obvious in cleaned specimens

(Fig. 10e). The basal part of the entooecium is fused with the distal wall of the maternal zooid.

In cleaned specimens the complete ooecium looks like a broad, rather deep cavity distal to a raised, crescentic lip (entooecium) (Fig. 10d, f). This cavity (ooecial coelom) consists of a larger upper part leading to a lower part comprising a narrow canal or canals (Figs. 10e, f, 11b, 12e, f). The lower part of the ooecial coelom (canal/s), which are often filled with non-specialized epithelial and mesenchymatous cells (Fig. 12e, f), connects to the visceral coelom of the maternal autozooid via 1–3 communication pore(s) plugged by a specialized pore-cell complexes (Figs. 10e, f, 11b, 12e, f).

The thin-walled brooding sac is an invagination of an uncalcified distal wall of the maternal zooid (Figs. 11b, 12e). There were no brooding sacs with embryos in the material studied, however we saw it functional in some other species (Ostrovsky et al. 2007). The brooding sac consists of a main chamber connecting with the exterior via a narrow neck. The opening of the sac is located near the vestibular opening beneath the distal edge of the closed zooidal operculum. It is independent of the vestibulum. The opening is closed by a distalmost part of the non-calcified frontal wall of the maternal zooid resembling the ooecial vesicle. A cuticular thickening of the wall is obviously a reduced sclerite (Figs. 11b, 12e, f).

One thin muscle bundle was detected, being attached to the basal wall of the neck of the brooding sac (Fig. 11b). Its proximal part might be anchored onto the transverse or basal wall. We were not able to find muscles inserting on the sclerite.

Discussion

Comparisons with previous observations

Our observations agree well with previous reports on hyperstomial ovicells in the Calloporidae. The first information about their structure was given by Levinsen (1893), (pl. 2, Figs. 20–25, 1894, pl. 4, Figs. 14, 19), who illustrated ovicells of *Tegella unicornis* (as *Membranipora*). The longitudinal sections correctly show the shape and relative position of the major elements including the continuity of the coelom of the ooecium and the visceral coelom of the distal autozooid (Levinsen 1893, pl. 2, Fig. 24, 1894, pl. 4, Fig. 19). As mentioned above, Levinsen mainly worked on cleaned specimens, so information on the soft parts is missing.

Soon after, Calvet (1900), (Fig. 45) published an anatomical scheme of a longitudinal section of the decalcified ovicell of *Amphiblestrum flemingi* (Busk 1854) (as *Membranipora*). It correctly reflects the main characters (including epithelia), but since the section was sagittal, Calvet did
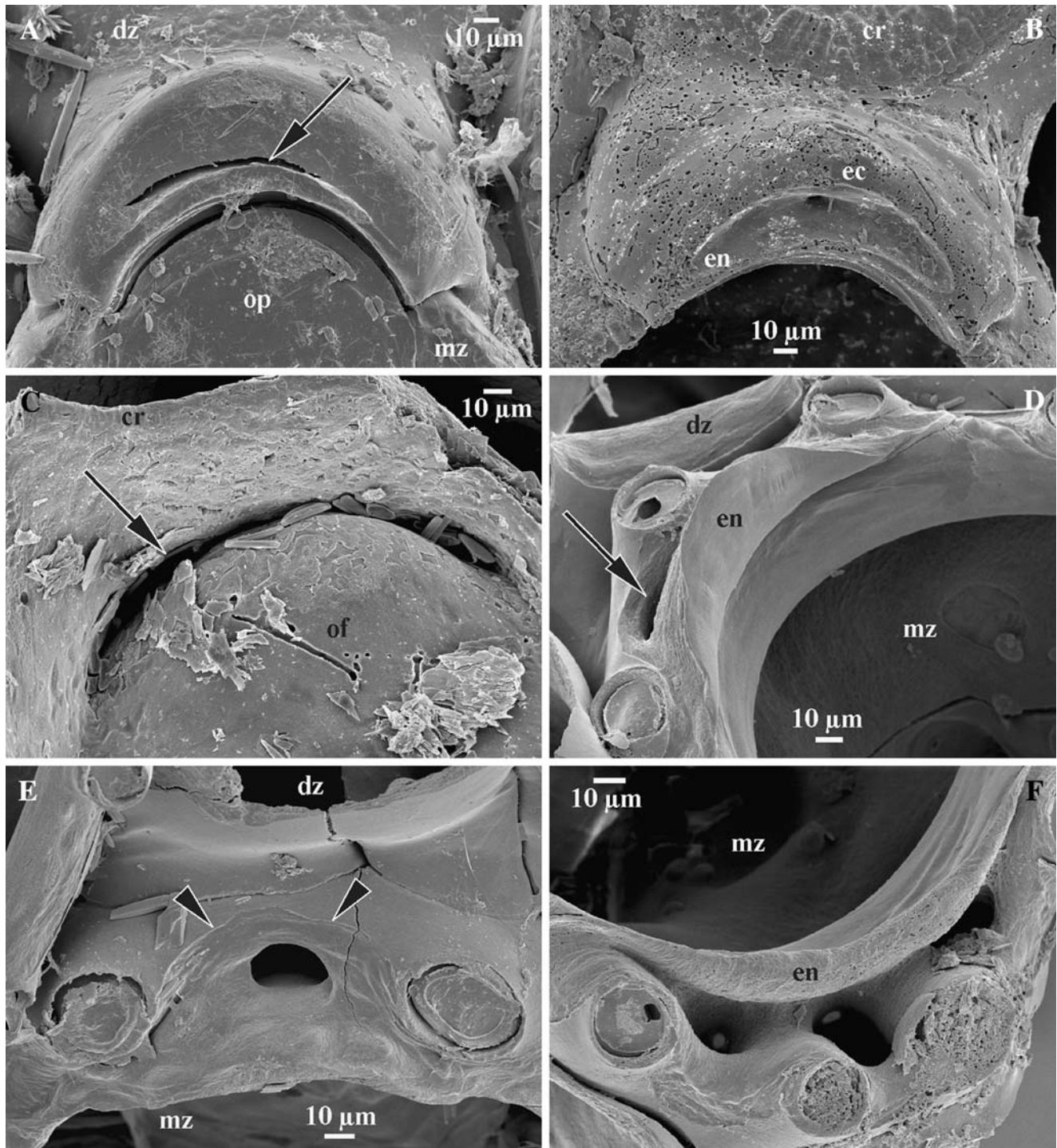
Fig. 10 Scanning electron microscopy. **a–c** *Crassimarginatella* sp., **d–f** *Cauloramphus spinifer*. **a** non-cleaned cleithral ovicell [*arrow* points at the crack in the membranous area of the ectooecium (*ec*)], **b** cleaned ooecium with part of its coelomic cavity and pore, located underneath of the membranous area, **c** arch-like communication slit (*arrow*) in the young ovicell [view from the side of the distal zooid (*dz*)], **d** distal part of the maternal autozooid (*mz*) with kenozooidal ooecium (*arrow* points at the ooecial coelom), **e–f** cleaned kenozooidal ooecia with one **e**, and three **f** communication pores [in **e** *arrowheads* show the limits of the removed membranous ectooecium (*ec*)]. Abbreviations: *cr* cryptocyst, *dz* distal autozooid, *ec* ectooecium, *en* entooecium, *mz* maternal autozooid, *of* ovicell floor, *op* operculum

not find the communication pore of the ooecium in this species. He pictured two muscle bundles attached to the wall of the upper and middle parts of the ooecial vesicle, with their proximal ends fixed on the transverse wall. A sclerite of the ooecial vesicle was not pictured, but since it was found in its closest relatives, in the species of the genera
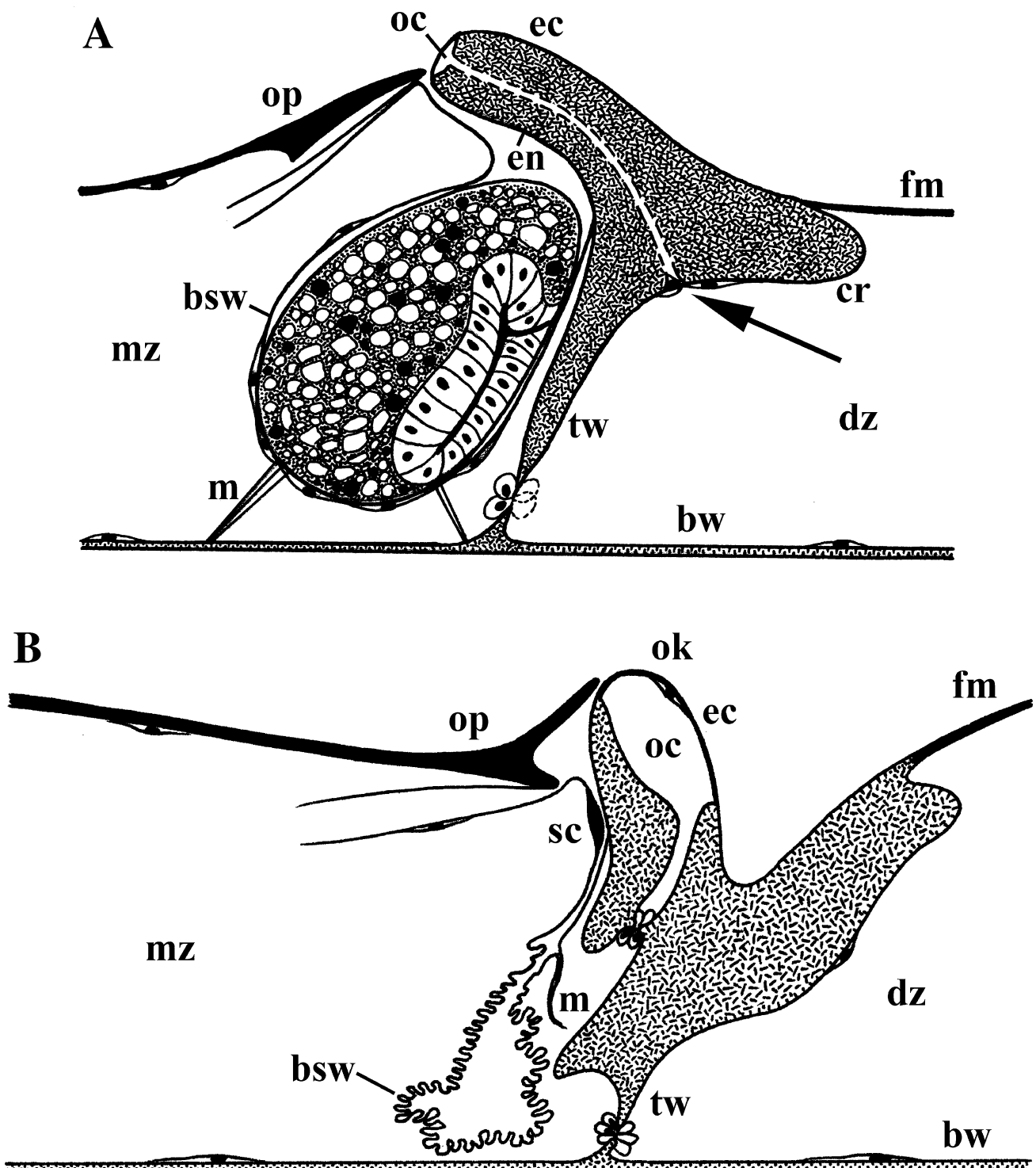
Fig. 11 Schematic longitudinal sections of brood chambers. **a** *Crassimarginatella* sp., immersed ovicell (*arrow* points at the communication pore, plugged by non-specialized epithelial cells), **b** *Cauloramphus spinifer*, internal brooding sac with vestigial kenozooidal ooecium (*ok*).

Abbreviations: *bsw* brooding sac wall, *bw* basal wall, *cr* cryptocyst, *dz* distal autozooid, *ec* ectooecium, *en* entooecium, *fm* frontal membrane, *m* muscle bundle, *mz* maternal autozooid, *oc* ooecial coelom, *ok* kenozooidal ooecium, *op* operculum, *sc* sclerite, *tw* transverse wall

Callopora and *Tegella*, we suspect that a sclerite is present also in *Amphiblestrum*.

A correct anatomical scheme of the hyperstomial ovicell of *Callopora aurita* (Hincks, 1877) with the ooecial com-munication pore, muscles of the ooecial vesicle and membranous area of the ectooecium was published by Levinsen (1909), (pl. 24, Fig. 16). There is only one muscle bundle of the ooecial vesicle in his scheme. Starting from the basal
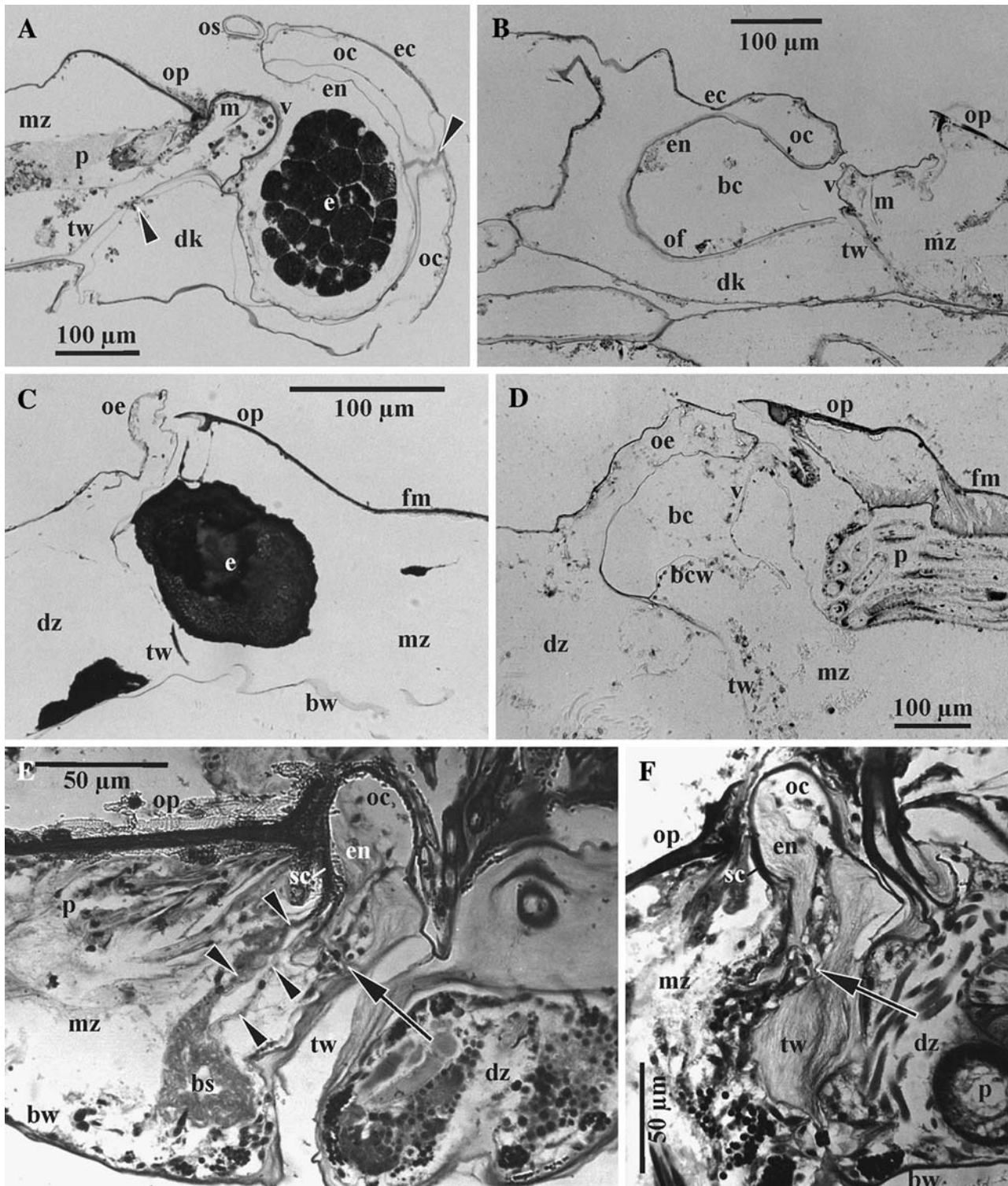
Fig. 12 Light microscopy. Longitudinal and oblique (*Bryocalyx cinnameus*) sections of brood chambers. **a** *Bryocalyx cinnameus*, terminal acleithral ovicell [*left arrowhead* points at communication pore, *right arrowhead* points at medial septum of the ooecium (*oe*)], **b** *Concertina cultrata*, prominent acleithral ovicell, **c** *Crassimarginatella* sp., immersed cleithral ovicell, **d** *Valdemunitella lata*, subimmersed cleithral ovicell, **e–f** *Cauloramphus spinifer*, internal brooding sac (*bs*) (folded in **e**) and vestigial kenozooidal ooecium (*arrows* point at the commu-nication pores of the kenozooidal ooecia plugged by special pore-cell complexes). Abbreviations: *bc* brooding cavity, *bcw* brooding cavity wall, *bs* brooding sac, *bw* basal wall, *dk* distal kenozooid, *dz* distal autozooid, *e* embryo, *ec* ectooecium, *en* entooecium, *fm* frontal membrane, *m* muscle bundles of the ooecial vesicle, *mz* maternal autozooi, *oc* ooecial coelom, *oe* ooecium, *of* ovicell floor, *op* operculum, *p* polypide, *sc* sclerite, *tw* transverse wall, *v* ooecial vesicle

wall of the maternal zooid, it attaches to the vesicle's wall in its upper part. A sclerite was not depicted.

A brief description and illustrations of the unusual ovicells in *Bryocalyx cinnameus* were given by Cook and Bock (2000). In general, these authors correctly reflected the relative position of calcified and non-calcified parts of the ooecium.

The anatomy of the hyperstomial ovicells of *Callopora lineata* (Linnaeus, 1767) and *C. dumerilii* was described in detail by Ostrovsky and Schäfer (2003) and Ostrovsky et al. (2003).

All the studies mentioned agree on that the ovicells in the Calloporidae are formed by the zooid distal to the maternal zooid, thus refuting Silén's (1944, 1945) idea of ovicells developing from the maternal zooid. *Cauloramphus* represents a special case (see below).

Antropora tincta (Hastings, 1930) (Antroporidae) broods in the immersed ovicells, which Hastings described as "endozooecial" (1930, p. 709, pl. 5, Fig. 17); in her scheme the embryo is seen through the operculum, located in the brooding sac situated beneath the vestibulum, proximal to the vestigial ooecium. Several muscle bundles are attached to the sac walls laterally on both sides. Thus, the ovicell structure in *A. tincta* is very similar or even identical to the immersed ovicell of *Crassimarginatella* sp. A similar position of embryo and vestigial ooecium was depicted by Cook (1968), (Text-Fig. 8) in the calloporid *Aplousina major* (Calvet, 1907).

The anatomical structure of the internal brood sacs has been recently studied in eight species of the genus *Cauloramphus* from the Pacific (Ostrovsky et al. 2007), including *C. spinifer*. In contrast, we investigated colonies of supposedly the same species from the White Sea, but found no difference in the internal structure of the brood sac. Kenozooidal ooecia, however, are less calcified in the specimens from the White Sea, and their coelomic cavity communicates with the maternal zooid via 1–3 communication pores.

Comparative anatomy and diversity of ovicells in Calloporidae

As concluded above, the structure of the hyperstomial ovicells in *Callopora*, *Tegella*, *Amphiblestrum*, *Parellisina* and *Corbulella* are of the same basic type, but there are several differences in the details: type of the distal (ooecium-producing) zooid, thickness of the ooecial walls, sites of the muscle bundles' attachment, shape and size of the membranous area of the ectooecium, method of the ovicell closure, shape of communication slits/pores, etc. *Callopora*, *Tegella*, *Amphiblestrum* (and, obviously) *Parellisina* have most similar anatomy. In these taxa all or most of the ovicell components are well-developed. In contrast, *Corbulella maderensis* has cleithral ovicells with reduced ooecial vesicle and its muscles and without a sclerite. It also possesses the heaviest calcification leading to almost complete reduction of the ooecial coelom.

In general, the anatomy of the ovicells with bilobate ooecia corresponds to those with conventional ovicells. They could be hyperstomial (*Bryocalyx*, *Concertina*), or subimmersed (*Valdemunitella*). The major difference is the bipartite structure of the ooecium and its coelom. In contrast to the rest of the calloporids studied, deep-water *Bryocalyx* and *Concertina* have weakly calcified skeletons, resulting in large communication slits and free circulation of the coelomic fluid between ooecium and the kenozooid which is rather large in *Concertina* and able to bud zooids distally. In contrast it is relatively small and never buds in *Bryocalyx*, forming a terminal ovicell. In both cases ovicells are acleithral, and possess no sclerite in their ooecial vesicle (except the thickened cuticle in *Bryocalyx*). Muscle bundles are relatively well-developed in both cases.

Bilobate ooecia with bipartite coelom are also characteristic of the subimmersed ovicells in *Valdemunitella lata*. In the antroporid *Akatopora circumsaepta* and the calloporid *Crassimarginatella* sp. the immersion of the brooding cavity is even stronger. In all three cases the size of the ooecium is distinctly less than in the hyperstomial ovicells. Calcification of the ooecial walls is strong, resulting in a gradual closure of the communication slit/pores and circulation of the coelomic fluid. Ovicells are cleithral with reduced ooecial vesicle. Muscle bundles and thickened cuticle are present in the vesicle of *Valdemunitella*, but there are no similar structures in *Crassimarginatella*. We suspect that *Antropora tincta* and *Aplousina major* possess ovicells of a similar structure.

In general, the anatomy of the brooding structure in *Cauloramphus spinifer* could be compared with the immersed ovicell of *Crassimarginatella* sp. However, in contrast to *Crassimarginatella* the ooecium is kenozooidal, i.e., not a zooidal wall outgrowth, and the deeply immersed brooding sac possesses a narrow passage (neck) to the exterior. Interestingly, the upper part of the maternal zooid's distal wall that works as an ooecial vesicle has retained a rudimentary sclerite in *Cauloramphus*. Thin muscle bundles attach to the non-calcified walls of the brood chamber in both cases.

Trends in ovicell evolution in Calloporidae

Reduction of the ooecium-producing zooid

The earliest cheilostome ovicells known (found in fossil calloporids of the Late Albian age of the Mid-Cretaceous) are hyperstomial (Cheetham 1954, 1975; Ostrovsky and Taylor 2004, 2005a, b; Cheetham et al. 2006), and several

evolutionary trends can be demonstrated in more modern cheilostomes. One trend is a reduction of the distal, ooecium-producing zooid, and judging from the literature this trend is seen in several groups of both anascans and cribrimorphs (Levinsen 1909; Ristedt 1985; Gordon 1984, 1986; Winston and Håkansson 1986; Bishop 1994; Ostrovsky 1998, etc.); however, its distribution should be studied more thoroughly and its adaptive importance is still unclear.

Most of the calloporid genera (including the earliest) possess ooecia formed by the autozooid distal to the maternal one, and this type is considered as a basic type within Cheilostomata (Nielsen 1985); this type was termed "category A" by Bishop and Househam (1987). The ooecial fold is sometimes formed by a distal zooidal polymorph—either a vicarious avicularium (in *Callopora* and *Wilbertopora*) or a kenozooid (in *Wilbertopora, Callopora*, *Corbulella*, *Concertina*, *Bryocalyx*) (see also Levinsen 1909; Zabala and Maluquer 1988; Ostrovsky and Schäfer 2003; Cheetham et al. 2006). The term "category B" of Bishop and Househam (1987) could be applied in these cases. In *C. craticula*, the ooecia in one colony may be of "category A" or formed by avicularia or kenozooids ("category B"). A similar variation has been reported in the Cribrilinidae (Ostrovsky 1998). The ooecial fold is produced by the distal zooid in both of these categories, and Ostrovsky (1998) classified them in the "1st type" (type 1). Noteworthy, both categories and all three variants of the ooecial formation have been recorded in the Upper Cretaceous (Lower Cenomanian) calloporid *Wilbertopora listokinae* (Cheetham et al. 2006).

The next stage in the trend in question is a formation of the kenozooidal ooecium. Till now it has been reported only in the cribrimorph *Cribrilina annulata* (Levinsen 1909; Ostrovsky 1998) and in *Cauloramphus* (Ostrovsky et al. 2007). In this type the ooecium is in itself a kenozooid, budded from the maternal autozooid. Only a small basal part of the ooecium is homologous to the distal kenozooid of the "category B". For ooecia of this type we apply here the terms "category C" and the "type 2" (Bishop and Househam 1987; Ostrovsky 1998). Initially these two terms included all terminal ovicells whose ooecia are formed either by the distal kenozooid without distally prominent frontal part (Bishop and Househam 1987; Harmelin and Aristegui 1988), or budded themselves from the maternal autozooid. However, the new interpretation is more accurate since it allows to separate terminal ovicells into two groups depending on their structure. In the terminal ovicells with the ooecium belonging to the type 1 (category B) the ooecium is an outfold of the distal kenozooid that forms the basal part of the entire structure and the floor of the brooding cavity. In the terminal ovicells with the ooecium belonging to the type 2 (category C), the ooecium

is a kenozooid itself, and the floor of the brooding cavity is formed by the expense of the maternal autozooid (compare Figs. 9a, 11b). *Cauloramphus* has an internal brooding sac and vestigial kenozooidal ooecium of the type 2 (category C).

It should be noted here that *Cribrilina annulata* and species of the genus *Cauloramphus* are only known exceptions that correspond to Silén's (1945) model of the ooecium formation from the maternal zooid. In other species studied the ooecium is formed by the distal zooid, however, and the above hypothetic scenario shows how such maternally derived ooecia could evolve without invoking Silén's idea on the ooecium origin from the oral spines of the maternal zooid.

In almost all cheilostomes studied the ooecium is an outgrowth of the zooidal wall, not a kenozooid. Since there is no specialized pore-cell complex(es) in the ooecial communication pore(s), the idea that such ooecia are heterozooids should be rejected (for discussion and details see Woollacott and Zimmer 1972; Ryland 1979; Nielsen 1981; Ostrovsky 1998; Ostrovsky and Schäfer 2003).

The presence of different ovicell categories within several cheilostome taxa and sometimes even within colonies (*Callopora*, *Puellina*) witnesses for an independent origin of this trend in a number of lineages. At the same time, all Hippothoomorpha including fossil species have only category B ovicells (Ostrovsky, unpublished data) that could be an ancestral state of the character in this clade.

Bishop and Househam (1987) thought that reduction of the distal zooid is not difficult evolutionary step. The presence of ovicells of categories A and B within the same genera, species and sometimes even colonies supports of this suggestion. But what is the reason for reduction of the distal autozooid? Another question, is whether the formation of the ooecia by the vicarious avicularia is an example of the zooidal reduction or modification?

Harmelin and Aristegui (1988) suggested that formation of the ovicell of category C (these authors meant all terminal ovicells) could be characteristic of r-strategists, whereas category A fits more to the K-strategy. According to their idea the ovicell is formed faster (and ready for brooding) if there is no need to produce a distal autozooid. However, we doubt if this suggestion is always correct, since the formation of the ovicell not always depends from the formation of the distal autozooid itself. For instance, in *Tegella armifera* ovicells could complete their formation and start to brood an embryo well in advance of the completion of the distal zooid formation.

In some instances terminal ovicells are formed on the colony periphery (*Callopora*) or on the terminal parts of the branches (*Bryocalyx*) only. In the *Callopora* species studied ovicells formed by the distal autozooids (category A) are found in the more central parts of the colony, whereas those

formed by the avicularia and kenozooids (category B) are always found at the very edge of the colony. Could it be that suppression of the distal autozooids is simply connected with a general cessation of the growth of the colony or its parts? If yes, formation of the terminal ovicells depends on age or astogenic changes at least in some instances. It is also possible that formation of the ovicells that requires a lot of energy, prevents the last generation of zooids from the completion of their growth in old/ageing colonies. On the other hand, only terminal ooecia are formed in Hippothoomorpha and some Cribrilinidae, and this clearly does not depend on the cessation of the colony growth in these cases (analysed in Ostrovsky 1998). The third suggestion is that the reduction of the distal zooid is a method to save energy that otherwise could be directed to reproduction or somatic growth. Different factors could cause the phenomenon in question in different taxa, acting separately or together, and more research is needed to estimate the distribution of the terminal ovicells within Cheilostomata first, and then to understand the circumstances in which they appear.

Immersion of the brooding cavity, reduction of the ooecium and changes in ovicell closure

Another evolutionary trend leads towards the immersion of the brooding cavity, also widespread within Cheilostomata. This could be connected to a better protection of the developing embryos, as well as with saving energy in building the ovicells, or acquirement of a larger space for incubation (see Ostrovsky et al. 2006 for detailed discussion). Sexual polymorphism found in *Akatopora circumsaepta* could be an argument in a favour of the latter suggestion: "internally" brooded embryos required a larger exit.

The earliest cheilostome ovicells known were hyperstomial (Cheetham 1954, 1975; Ostrovsky and Taylor 2004, 2005a, b; Cheetham et al. 2006). Progressive lowering of the ovicell floor culminates in the evolution of endozooidal ovicells with brooding cavity inside the proximal part of the distal autozooid in Flustridae and some Cribrilinidae, and immersed ovicells with brooding cavity in the distal part of the maternal autozooid in Calloporidae and Antroporidae. The species under our study represent the complete morphoseries demonstrating the subsequent immersion of the brooding cavity into the maternal zooid. Species of the genera *Callopora*, *Tegella*, *Amphiblestrum*, *Parellisina*, *Corbulella*, *Bryocalyx* and *Concertina* possess hyperstomial ovicells. Subimmersed ovicells were found in *Valdemunitella*, and immersed ovicells in *Crassimarginatella* and *Akatopora*. Further immersion is demonstrated by *Cauloramphus* having an internal brooding sac.

The immersion correlates with the size of the ooecium that is largest in the hyperstomial ovicells, and showing the different degrees of reduction in *Valdemunitella lata*, *Akatopora circumsaepta* and *Crassimarginatella* sp. (see also Ostrovsky et al. 2006). Again, it is smallest in *Cauloramphus*, although direct comparison is not correct because of the different type of the ooecial formation in these species. In our view, *Crassimarginatella* sp. and *Cauloramphus* represent two different calloporid lineages where the ooecium has been reduced together with and because of the immersion of the brooding cavity. In the second case the ooecium is reduced together with a distal ooecium-producing zooid, being transformed to a small kenozooidal polymorph. Its position does not prevent the distal budding, but the distal autozooid is not involved in the formation of the ooecia in its proximal part.

Immersion of the brooding cavity also correlates with the type of ovicell closure. All subimmersed and immersed ovicells studied are cleithral, and the only one example of cleithral prominent ovicell is that found in *Corbulella maderensis*. Changes in the ovicell closure are also connected with a reduction of the size of the ooecial vesicle and its components. We suggest that the reduction of practically all elements of the ooecial vesicle depends on the acquirement of the cleithral ovicells, providing better protection of the ovicell entrance by the zooidal operculum. However, the sclerite might be absent in some acleithral ovicells too, like in *Bryocalyx* and *Concertina* (see above). The thickened area in the upper wall of the ooecial vesicle that was found in some species might be a remnant of the reduced sclerite. Also there are changes in the structure of the brood chamber floor: the more the brooding cavity is immersed, the less the proximal gymnocyst of the distal zooid is involved, and the more the distal wall of the maternal zooid takes part in its formation (compare Figs. 7a, 11a).

Thus, the evolutionary trend under discussion includes correlated changes of several structures, representing the complex transformation of the entire brood chamber. This trend independently evolved in several cheilostome clades (discussed in Harmer 1926; Hastings 1964; Ostrovsky et al. 2006). Although the majority of calloporids have hyperstomial (prominent) ovicells, the taxa *Caulorhamphus* (Mawatari and Mawatari 1981; Dick and Ross 1988; Ostrovsky et al. 2007), *Cranosina* (Harmer 1926; Canu and Bassler 1929, 1933; Chimonides and Cook 1994) and *Cymulopora* (Winston and Håkansson 1986) consist exclusively of species with reduced ooecia and immersed brooding cavites. In *Cymulopora uniserialis* Winston et Håkansson, 1986, completely calcified vestigial ooecium is situated on the distal wall of the maternal autozooid. Such a position together with a fact that the distal zooid is not formed yet, shows that the ooecium is obviously kenozooid similar to those of *Caulorhamphus* (Winston and Håkansson 1986; Ostrovsky et al. 2007). Endozooidal ovicells or brooding zooids with a

slightly raised distal margin and larger opercula have been described in *Cranosina coronata* (Hincks, 1881), but its ooecia were never illustrated (Canu and Bassler 1929, 1933; Osburn 1950; Chimonides and Cook 1994; discussed in Hastings 1945). Harmer (1926), (p. 266) found "an embryo, lying in an ovisac", that is obviously an internal brooding sac in this species.

Small or vestigial ooecia are characterstic of the Recent species of the entire taxon Antroporidae (Hastings 1930; Osburn 1950; Cook 1968; Mawatari and Mawatari 1981; Winston and Håkansson 1986; Tilbrook 1998; Tilbrook et al. 2001; Tilbrook and Grischenko 2004). The embryo is incubated in the internal brooding sac situated beneath the vestibulum, proximal to the vestigial ooecium, in *Antropora tincta* (see above). Noteworthy, the Cretaceous (Maastrichtian) *Akatopora sulcata* (Canu et Bassler, 1926) possessed a well-developed ooecium in obviously subimmersed ovicells (Taylor and McKinney 2006). This could be considered as an argument towards independent evolution of the brooding cavity 'immersion' within this group.

Additionally, the genus *Crassimarginatella* includes both species with prominent (with well-developed ooecia) as well as immersed ovicells (with vestigial ooecia) (Gordon 1986; Tilbrook et al. 2001). Cook (1968), (pp. 141–142) described three types of ovicells in the calloporid genus *Aplousina*: (1) "endozooecial" acleithral with the brood cavity "protruding into the cavity of the next zooid", (2) probably, subimmersed cleithral, and (3) judging from the Text-Fig. 8, immersed ovicells with vestigial ooecia. In the two last cases the brooding cavity is placed in the distal part of the maternal zooid (see also above). Cook noted the existence of a transition from the second to the third type within the genus. Finally, Hastings (1964) and Cook (1968) described both well-developed and vestigial ooecia within the same colony fragments of *Crassimarginatella spatulifera* Harmer, 1926 and *Aplousina gigantea* Canu et Bassler, 1927. This shows that the degree of the ooecial development (and, thus, brooding cavity immersion) can vary within a family, a genus or even a colony.

Crassimarginatella sp. and species of the genus *Cauloramphus* have brood chambers reminding the brooding sacs of some internal brooders (see Ostrovsky et al. 2006). This, together with different type of the ooecium suggests a possibility for an independent evolution of the brooding sacs within Calloporidae. We speculate that the internal sacs for embryonic incubation known in *Gontarella* could evolve either by modification of the immersed ovicells like in *Crassimarginatella* sp., or from the brooding sacs with kenozooidal ooecium like in *Cauloramphus*. In both cases this involved the complete reduction of the ooecium (see also Ostrovsky et al. 2007). *Cranosina coronata* is obviously another example of such immersion and ooecial reduction (see above).

Reduction of the ectooecial calcification

Comparison of the ooecial morphology among calloporids shows the different degree of the ectooecial calcification, and this difference was noted already by Levinsen (1909). Within the taxon *Callopora* there are both species with completely calcified ectooecium (*C. minuta* Harmelin, 1973, *C. precocialis* Gordon, 1986, see Harmelin 1973b; Gordon 1986), and species in which only the basal part of the ectooecium is calcified (*C. dumerilii*, see Prenant and Bobin 1966; Zabala and Maluquer 1988; Hayward and McKinney 2002; our data). The oldest known ovicells in the calloporid taxon *Wilbertopora* possess ooecia that are completely calcified (Ostrovsky and Taylor 2005a, 2005b; Cheetham et al. 2006), whereas an analysis of the literature shows that the majority of the Recent species have ooecia bearing membranous areas of different shape and size. This could be a sign of the trend towards lesser calcification of the ooecial fold. However, more research is needed to support this suggestion.

But if this suggestion is correct, what adaptive value could a weakening of the protective structure have? Noncalcified areas, such as pseudopores, are generally considered as providing a gas exchange in Bryozoa (Ryland 1970). Formation of the ovicells leads to the increase of the colony volume, thus ectooecial membranous areas could enhance the rate of the gas exchange. In the same time, we agree with Levinsen (1909) who wrote that if the ectooecium is membranous, the calcified entooecium is, as a rule, thick. The structure of such ooecial fold is analogous to the structure of the frontal zooidal shield with a hypostegal coelom (see Sandberg 1977; Cheetham and Cook 1983). Such shields are characteristic of most cheilostomes despite their external wall being non-calcified. However, it is a good protection against mechanical damage since the hypostegal coelom is very narrow and the distance between the frontal membranous wall and calcified shield is very small. The strain applied to membranous wall will be immediately transferred to a calcified component of the shield. Thus, such structure should be equally effective as protective and gas-exchanging device. Similar suggestion could be correct for the ovicells too.

One more observation is that shallow or relatively shallow-water species (majority of calloporids studied) possess much thicker skeletons (including walls of the brood chambers) than fragile deep-water species (*Bryocalyx*, *Concertina*).

Origin and evolution of the ooecia

Among calloporids, bilobate ooecia is a generic character of *Valdemunitella*, *Bryocalyx* and *Gilbertopora*. Judging from the developmental stages and longitudinal suture it is

obviously bilobate in oldest calloporid *Wilbertopora* too (Ostrovsky and Taylor 2005b). Representatives of several calloporid genera, including *Concertina*, have ovicells with a medial suture (discussed in Ostrovsky 2002). In *Corbulella maderensis* short medial keel on the internal surface of the entooecium is seen in Fig. 6d in the paper of Ostrovsky et al. (2003). Thus, the paired nature (bilobate symmetry) of the ooecium is a common phenomenon in Calloporidae, as fossil as Recent, possibly showing the evolutionary stage towards the acquirement of most-common entire ooecia without any traces of partitioning.

The most primitive calloporid ooecia were constructed of several spines (Taylor and McKinney 2002; Ostrovsky and Taylor 2004, 2005a). Further evolution of the ooecium might be connected with a reduction of spines in number (up to two), their enlargement and subsequent fusion in this group. One of the transitional stages is represented by a peculiar bilobate ooecium of the Cenomanian (Upper Cretaceous) *Gilbertopora*. Additionally to the main opening, it had a distal opening between lobes and two lateral 'foraminae'. The ooecium of the Cretaceous *Wilbertopora* (Albian-Cenomanian) possesses the main opening only. The bilobate ooecium of the Recent *Valdemunitella* strongly resembles the ooecium of *Wilbertopora*, and all three genera in question possess paired communications (slits or pores) connecting the lobe's coelom with the visceral cavity of the distal autozooid. Moreover, the ovicellogenesis in *Valdemunitella* and *Wilbertopora* is very similar (compare Fig. 6d in Gordon 1986 and Figs. 1, 2 in Ostrovsky and Taylor 2005a, and descriptions therein). The only difference is a closed horizontal slit found in *Valdemunitella*. However, although the slit is unknown in *Wilbertopora* (since no internal surface of its brooding cavity has been studied in fossils), judging from the ooecial development we strongly suspect that it existed in *Wilbertopora* as well.

On the other hand, bilobate ooecia with horizontal slit and paired communications are also known in the genera *Puellina*, *Figularia*, *Euthyroides* and *Corbulipora* of the taxon Cribrilinidae (Ostrovsky 2002, and unpublished data), and ovicellogenesis in *Valdemunitella* and *Wilbertopora* is reminiscent the ooecial development in *Euthyroides* and *Corbulipora* (Harmer 1902, Ostrovsky, unpublished data). Also medial suture is present in many fossil and Recent cribrimorphs (discussed in Ostrovsky 2002).

If the generally accepted taxonomic position of the six last-mentioned genera is correct, we must conclude that bilobate ooecia were either inherited by cribrilinids from their calloporid ancestor or acquired independently. The last scenario is more probable since there are some fossil species of Cribrilinidae known with ooecia made of several costae. Such ooecia could transform to the bilobate ones either by fusion or reduction of the costae of the left and the right halves of the ooecium (Ostrovsky and Taylor 2005a).

Both cases would result in bilobate structures further transformed to the entire protective hood known in more recent cribrilinids. Thus, it could be an example of parallel evolution of the conventional ooecium in two closely related clades.

A presence of the plesiomorphic bilobate ooecia in both groups can also imply a possibility for repeated evolution of the entire ooecia within both Calloporidae and Cribrilinidae.

A comparison of the data on the early stages of ovicellogenesis from the literature shows its remarkable similarity throughout the calloporids with hyperstomial ovicells (see Levinsen 1893, 1894, 1909; Harmelin 1973a; Nielsen 1985; Ostrovsky and Schäfer 2003; Ostrovsky et al. 2003; our data—see Fig. 3d). However, the only cheilostome with bilobate ooecia in which the early stages of the ovicell formation has been studied is fossil *Wilbertopora*. In contrast to all other calloporids, it possesses not paired, but a single rudiment of the ooecial floor resembling the same stage in cribrimorphs (discussed in Ostrovsky and Taylor 2005b). These authors suggested that the acquirement of the double rudiment could be connected with a progressive 'shrinking' of the proximal gymnocyst of the distal zooid. The ovicell floor is then formed from the entooecium which has its origin from two flattened spines. Anyhow, the rudiment of the ooecial floor became paired, whereas the ooecium became entire in the majority of more recent calloporids.

Thus, the comparative analysis of the ooecial structure and development in cheilostomes with bilobate ooecia shows one more trend in the evolution of the parental care towards the entire (and, thus, more firm) protective hood without any traces of partitioning. In general, most of the trends recognized may be interpreted as evolution towards better protection of the embryos and/or economy of energy. There are also good arguments that these trends evolved numerous times not only within Calloporidae, but also in their close relatives.

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