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**INVERTEBRATE  
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## **Brood Chambers (Ovicells) of Cheilostome Bryozoans (Bryozoa: Gymnolaemata): Structure, Research History, and Modern Problematics**

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**Abstract**—The basic stages characterizing research of brood chambers (ovicells) in cheilostome bryozoans are reviewed, from their first description by J. Ellis in 1755 up to the present. The problems concerning contradictory views of researchers on the structure, formation, and function of ovicells are considered in detail. Special attention was paid to the development of modern terminology. Based on recent data, including paleontological data, the prospects are displayed of studying brood structures in Cheilostomata in order to better understand the phylogeny and evolution of their reproductive strategies.

**Key words:** brooding, ovicells, anatomy, Bryozoa, Cheilostomata, evolution.

Bryozoa is a widespread group of fouling suspension feeders, mostly marine, with a long geological history stretching back to the Early Ordovician [10]. Their colonies form a significant part of the fouling in many marine biotopes, from upper sublittoral horizons to depths exceeding 6000 m. Many bryozoans are extremely important components of such biotopes; they form shelter and are food for a broad spectrum of organisms inhabiting the sea floor.

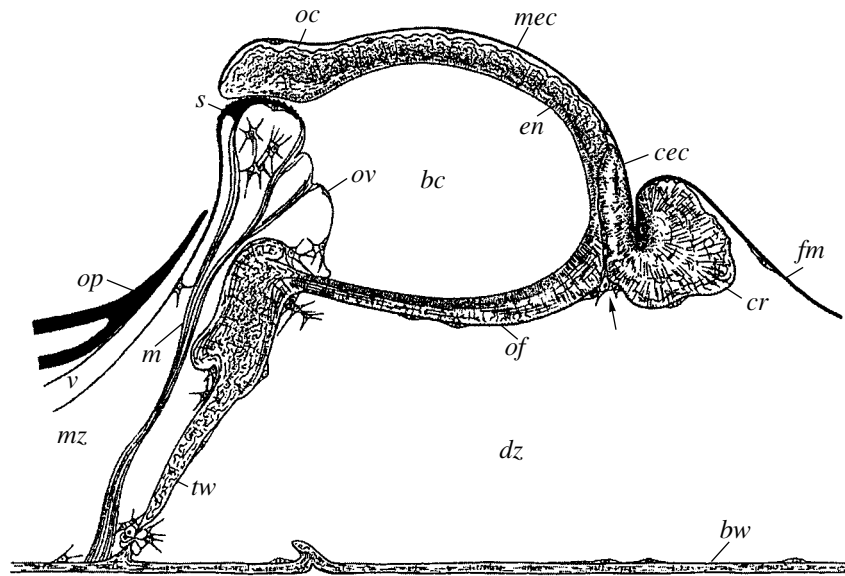
Over 6000 species of modern bryozoans, belonging to more than 1100 genera and 160 families, have been presently described [34]. Eighty percent of this diversity belongs to Cheilostomata (Bryozoa: Gymnolaemata).

The first fossils of Cheilostomata were dated from the Late Jurassic [88, 113]. During the rest of the Jurassic and the first half of the Cretaceous, that group was represented by only one family. However, after the Middle Cretaceous the Cheilostomata underwent a phase of rapid diversification, which lasted about 65 million years, until the Late Eocene.

It is noteworthy that at the end of the Early Cretaceous (Late Albian), Cheilostomata developed calcareous brood chambers—ovicells, the presence of which characterizes the type of development with endotrophic larva in modern forms. Based on that, well known English bryozoologist Taylor [112] suggested that the origin of short-lived larva and the evolution of brooding could interrupt genetic exchange between remote populations and trigger the mentioned radiation of cheilostomes. Related research on brooding structures in Cheilostomata becomes significant for understanding the evolution of the entire group, in general, as well as

its reproductive strategies, in particular. Moreover, as the vast majority of cheilostome bryozoans brood their larvae in special brood chambers called ovicells, the presence of ovicells and their morphology are considered relevant taxonomic characters in bryozoology.

Several morphological types of brood chambers have been distinguished, but the most widespread are ovicells that superficially resemble opaque or translucent bubbles protruding from the surface of the colony. Each hyperstomial ovicell consists of a hemispherical fold (oecium) with the coelomic cavity inside, and the distal wall of the maternal autozoid (forming eggs) and brooding cavity between them (Fig. 1). The outer wall of the oecium was named the ectoecium, and the wall that envelopes brooding cavity was called the endoecium. The ovicell opening is closed either by the wall protrusion of the maternal zoid, called the oecial (inner) vesicle or oecial plug, or by the operculum of the maternal autozoid. The oecial vesicle can be deformed due to contraction of special muscle bundles that open an entrance into the ovicell. Depending on the place of oecium formation, the oecial coelom is connected with the cavity of the daughter (distal) or maternal (proximal) zoid through communication pore(s) (see: [43, 73, 82, 83, 91, 97, 99, 104, 111, 124]). If the oecium is formed by the daughter zoid, these pores are often closed by epithelial cells, and direct contact between the coelomic cavities mentioned becomes impossible. For that reason, the oecial fold is considered a specific zooidal modification, kenozooid, and the development of ovicells is considered a manifestation of zooidal polymorphism, one of the most interesting



**Fig. 1.** The ovicell structure of *Callopora dumerili* (a longitudinal section of calcified specimen). Abbreviations: *bc*—brooding cavity, *bw*—basal wall, *cec*—calcareous part of ectoecium, *cr*—cryptocyst, *dz*—daughter (distal) autozooid, *en*—endoecium, *fm*—membranous frontal wall of daughter zooid, *m*—muscles of ooecial vesicle, *mec*—membranous part of ectoecium, *mz*—maternal (proximal) autozooid, *oc*—coelomic cavity of ooeonium *of*—ovicell floor, *op*—operculum, *ov*—ooecial vesicle, *s*—sclerit (a place of attachment of ooecial vesicle muscles), *tw*—transverse wall, *v*—vestibulum. The arrow points to communication pore.

phenomena specific to the colonial organisms [23, 100, 107, 124].

The first researcher who described ovicells in cheilostomes was Englishman J. Ellis, a rich London merchant and a brilliant naturalist. In his famous “An Essay Towards a Natural History of Corallines,” he mentioned and depicted the ovicells of several species of the genera *Bugula*, *Bicellariella*, and apparently *Flustra*, naming them “Balls,” “testaceous Spherules,” or “testaceous Figures” ([30], pp. 33–39). Describing ovicells of one of “Corallines Celluleuses” [in the opinion of Levisen [63], *Bugula neritina* (Linnaeus, 1758)], J. Ellis has assumed that they could be “Niduses or Matrices of certain testaceous Animals, like small snails or Neritae” from the eggs of which originated the colony (p. 35). This remarkable point of view was further expressed in drawings of *B. neritina*, where ovicells presented by the author were similar to the small shells of spirorbids, foraminiferas and small gastropods with helical shells (Fig. 2). It is quite possible that the researcher sometimes spotted the mentioned epibionts on colonies of bryozoans, but did not distinguished them from ovicells. It is also curious that J. Ellis considered the possibility that a relationship exists between bryozoans and bivalves.

One of the founders of natural science in France, the famous P.S. Pallas, assumed that the ovicells of some encrusting bryozoans were ovaries [86], and that opinion stood for the whole century. Concerning ovicells in erect colonies of *Bugula neritina* (Linnaeus, 1758) and *B. avicularia* (Linnaeus, 1758) (both species were attributed by P.S. Pallas to *Cellularia* genus), the

researcher put forth the opinion that they and avicularia (protective zooids) were organs of a similar nature, being somehow related to the ovicells in incrusting bryozoan *Eschara*. P.S. Pallas believed that ovicells and avicularia of “Cellularia” might serve for fertilization, and sometimes called them “Nectariums” ([86], p. 36).

In his next book, Ellis [31] agreed with P.S. Pallas and recognized that “pearl-like studs” in *Flustra* (p. 11) and “small hemispherical covers” in *Bugula* (as *Cellaria*) (pp. 19–20) “appear rather to be what we have called Ovaries.” J. Ellis mentioned that P.S. Pallas named ovicells and avicularia as “Nectariums,” comparing them with “the flowers of some plants.” At the same time, he had assumed that some *Cellaria* ovicells might be shell-bearing larvae, which detach from the branch, “it drops and adheres to a proper substance as a base, beginning to form a Coralline-like parent animal” ([31], p. 29).

Later researchers, following P.S. Pallas, named ovicells as “corps vésiculaires,” “corps globuleux” [57], “vésicules gemmifères,” “capsules gemmifères” [70], “vésiculæ gemmiferae” [56], and “ovary-capsules” [92] and considered them ovaries (see also: [50]). In the middle of the 19th century, the well-known English bryozoologist Busk introduced the term “ovicells” [14]. Approximately at the same time, the settled opinion that ovicells were capsules containing female gonads was challenged by his compatriot Huxley [48]. T. Huxley, observing *B. avicularia* (*B. avicularis*), noted that when the eggs were inside of autozooids, ovicells were empty. Later, eggs become visible in the

ovicells. Based on that, he suggested that the ovicell is merely a “marsupial pouch” ([48], p. 192).

Englishman Hincks [44], studying representatives of two genera from the family Bugulidae, *Bugula flabellata* (Thompson in Gray, 1848) and *B. turbinata* Alder, 1857, concurrently with *Bicellariella ciliata* (Linnaeus, 1758) (as *Bicellaria*), challenged that opinion (later, however, he had to recognize that it was correct [45, 46]). Nevertheless, T. Hincks emphasized that he had “grounds to believe that in some instances and under certain conditions, which I was unable to explain, eggs were formed in ovicells as well” ([46], p. XCIII). In his paper published in 1861, he assumed the presence of two types of eggs in Gymnolaemata: some eggs are produced in the ovicells, whereas the others are formed in autozooids, being an equivalent of statoblasts (wintering buds) of Phylactolaemata (fresh-water bryozoans). It is now clear that in the second instance T. Hincks took so-called brown bodies, regenerating polypids of autozooids, for eggs. It is interesting that this opinion was supported and developed by Swedish bryozoologist Smitt [108, 109], who was the first to record embryo development in the gonozooid (also named ovicell that time) of cyclostome bryozoan *Crisia eburnea* (Linnaeus, 1758) (Crisiidae) and in the autozooid of cheilostome bryozoan *Cryptosula pallasiana* (Moll, 1803) (Cryptosulidae). In F. Smitt’s opinion, finding the developing larvae inside a zooid confirmed the assumption of T. Hincks. In his two-volume monograph, T. Hincks asserted that “its [ovicell] interior is in direct communication with the perigastric cavity” of the maternal zooid, but was in doubt concerning the method of oviposition (transition of the egg into the brood chamber) ([46], Vol. I, p. XCII). He observed just the beginning of that process in *Bugula*, when “it seemed, as if a vigorous movement [of the polypid] at any moment can discharge it [an egg] into the ovicell” ([45], p. 31), and in *Chartella papyracea* (Ellis and Solander, 1786) (Flustridae) (as *Flustra*) (see: [46]). Hincks [45] introduced the term “oecium,” which he used as a synonym of the term “ovicell,” and he noted that, depending on the degree of protrusion of brood chambers above the colony surface, they may be “prominent,” “immersed” and “subimmersed” [46].

German naturalist Nordmann [80] described, for the first time, unusual brood chambers formed by flattened spines in *Tendra zostericola* Nordmann, 1839 (ELECTRIDAE), which were later named “acanthostegous oecia” by Levinsen [62]. Later, acanthostegous brood chambers were studied by several Russian zoologists: Repiachoff [93], Reingard [5], Ostroumov [4], Paltschikowa-Ostroumowa [87] and Braiko [1]. It is necessary to note that V. Reingard [5] was mistaken concerning the structure of brood formations, when he wrote: “*Tendra* is a transition from bryozoans without ovicells to those that possess them” (p. 25).

The first detailed description of the structure and development of hyperstomial ovicell was made by Ger-

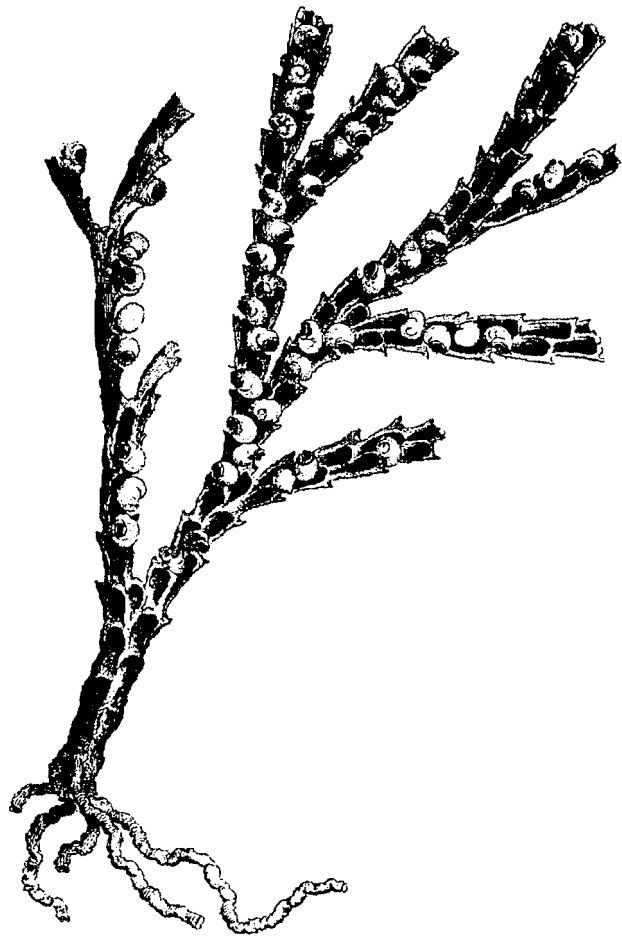
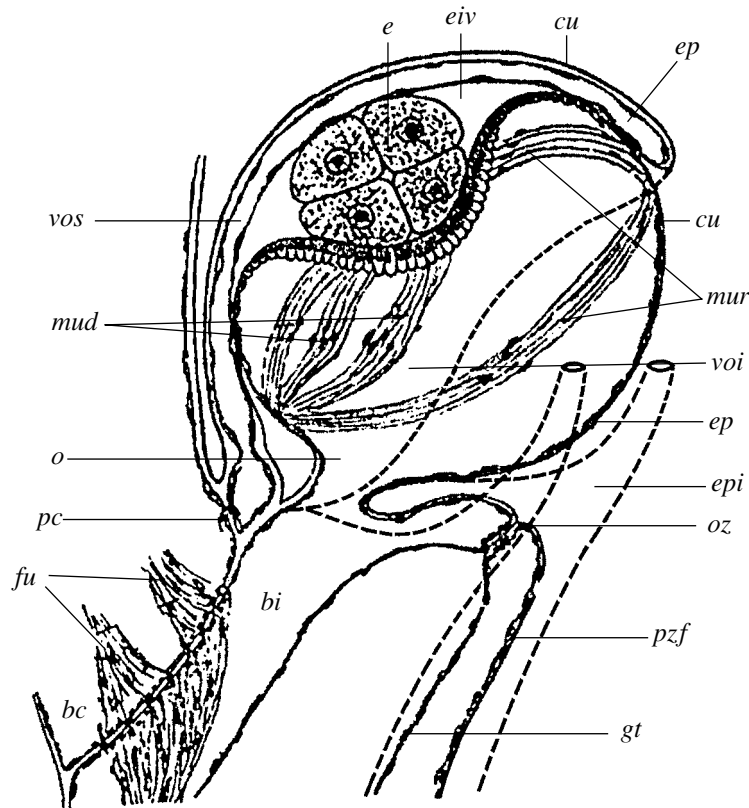


Fig. 2. Drawing of *Bugula neritina* with ovicells and adhered shells of polychaetes-spirorbids (from: [30], Tab. XIX, Fig. A).

man zoologist Nitsche [77], who studied *Bicellariella ciliata* (*Bicellaria*). One of his diagrams ([77], Figs. 10–13) was later used by Dutchman Vigelius ([115], p. 50, non-numbered figure in the text) for comparative purposes. G. Nitsche found that each ovicell in this species was formed by two protrusions, “helmförmige Blase” (German—“helmlike bubble”), i.e., oecium and “rundliche Blase” or “Deckelblase” (German—“rounded bubble,” “bubble lid,” i.e., by oecial, or the internal vesicle, according to modern terminology), formed at the distal edge of the maternal autozooid (see: [90]). The oecial vesicle functions as a lid (operculum), closing the entrance into the cavity of the helmet-shaped brood chamber. The vesicle can be contracted by special muscles during larva release. It is noteworthy that rhythmic contractions of the oecial vesicle were first described by English zoologist Reid [92] in *Bugula flabellata* (as *Flustra avicularis*) and also were observed by Hincks [45]. Not aware of the work of Huxley [48], G. Nitsche came to the conclusion that ovicells were exclusively brood structures (see also: [51]). Moreover, he suggested that “ovicells or oecia in



**Fig. 3.** Ovicell structure in *Bugula simplex*. Abbreviations: *bi*—visceral coelom of the maternal zooid, *bs*—visceral coelom of the daughter autozooid, *cu*—cuticle, *e*—embryo, *eiv*—brooding cavity, *ep*—epidermis, *epi*—oral spine, *fu*—funicular strands, *gt*—wall of the tentacle sheath, *mud*—muscles-depressors, *mur*—muscles of the oocel vesicle, *o*—communication between the oocel vesicle and the maternal autozooid, *oz*—zooidal orifice, *pc*—communication pore, *pzf*—frontal wall of the maternal autozooid, *voi*—oocel vesicle cavity, *vos*—oocel coelomic cavity (from: [15], Fig. 10).

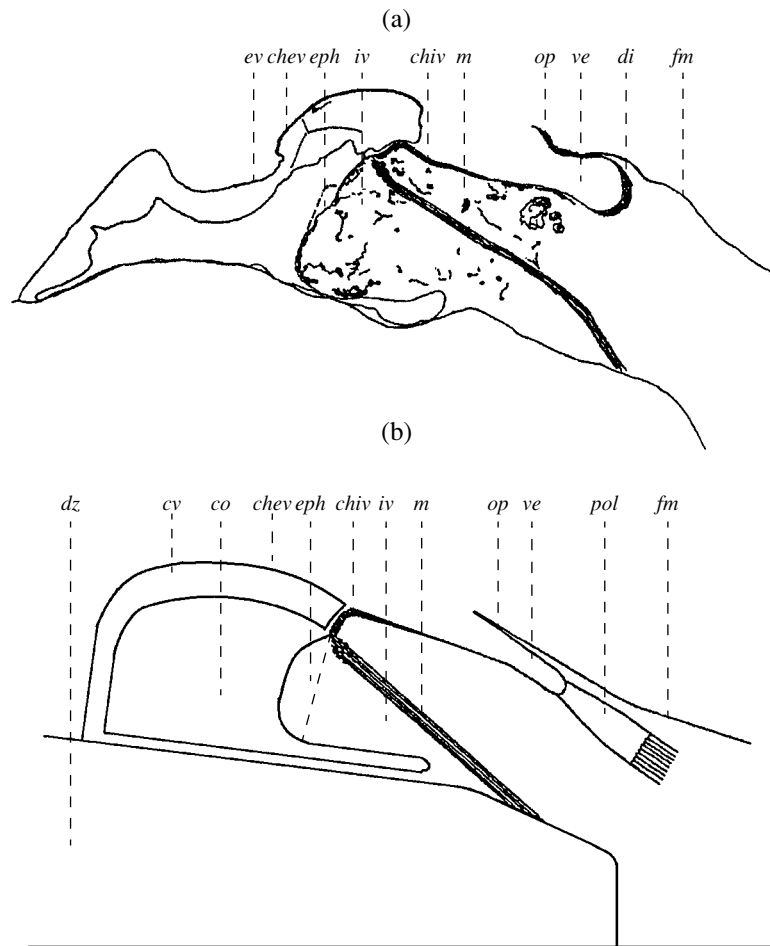
Chilostomata are modified individuals” ([78, 79], p. 161). It is necessary to emphasize that a similar conclusion was earlier drawn by J. Busk, who wrote that “ovicells are clearly transformed cells [zooids]” ([14], p. 5).

Some data on ovicell structure were published by French scientists Claparede [21] and Joliet [51], however, on the background of the Nitsche works [77–79] they did not obtain any new information.

Dutch researcher Vigelius was the first to apply anatomical sections to study the structure and development of brood chambers in bryozoans [115, 116]. Using that method he described immersed ovicells—“endozoocel oecia,” according to Levinsen’s terminology [62], in *Terminoflustra membranaceotruncata* (Smitt, 1868) (Flustridae) (as *Flustra*). W. Vigelius clearly showed that two successive zooids contribute to the formation of the brood chamber. The “Helm” (Ger.—“helmet,” i.e., oocelium) is formed by the daughter (distal) zooid, whereas the “Deckel” (Ger.—“lid,” i.e. oocel vesicle) is formed by the maternal (proximal) zooid. He also assumed that the egg entered the brooding cavity of the ovicell through a rupture in the wall of the oocel vesicle, an idea later supported by French zoologists Delage, Herouard [28] and Calvet [15]. In his next

paper, Vigelius [117] described the structure of ovicells in *Bugula calathus* Norman, 1868, having revealed cylindrical epithelium (Cylinderzellenschicht) on the inner surface of the oocel vesicle. It is necessary to add that this hypertrophied epithelium, directly adjoining the brooding cavity and taking the role of embryo-phore in brooding (see also: [15, 67, 124, 125]), was apparently already discovered by Reid [92], who wrote that the “membranous partition [oocel vesicle] was much thickened, especially in its central part, and contained a number of nucleated cells in *B. flabellata*” (p. 398).

French zoologist Jullien [52] used the terms “coïtis” (Greek—“cradle”) for the thick external oocel wall and “sparganile” (Greek—“swaddling cloth”) for the thin internal wall (p. I.56) describing the structure of ovicells in *Exochella longirostris* Jullien, 1888 (Romancheinidae). Suggesting a new macrosystem of cheilostome bryozoans, J. Jullien had distinguished “tribes”: Inovicellata, Subovicellata and Superovicellata, based on the presence or absence of an ovicell in those or other bryozoans, and on the position of the ovicell opening relative to that of the maternal autozooid.

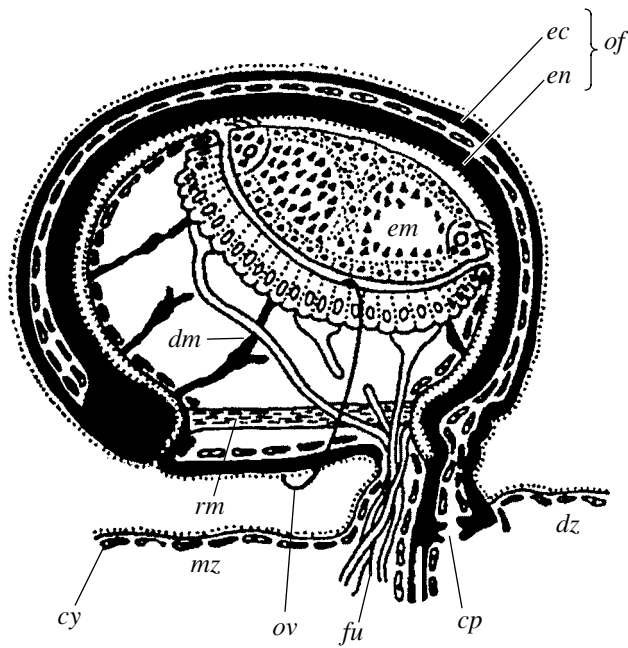


**Fig. 4.** *Scrupocellaria scabra*. (a) Drawing of the decalcified specimen, longitudinal section. (b) Reconstructed ovicell structure based on the above drawing. Abbreviations: *chev*—ectooecium, *chiv*—sclerit of the ooeical vesicle, *co*—brooding cavity, *cv*—ooeical coelomic cavity, *di*—diaphragm, *dz*—daughter (distal) autozoid, *eph*—embryophore, *fm*—frontal wall of the daughter autozoid, *iv*—ooeical (inner) vesicle, *m*—muscles of the ooeical vesicle, *op*—operculum, *pol*—polypide, *ve*—vestibulum (from: [105], Fig. 18–19).

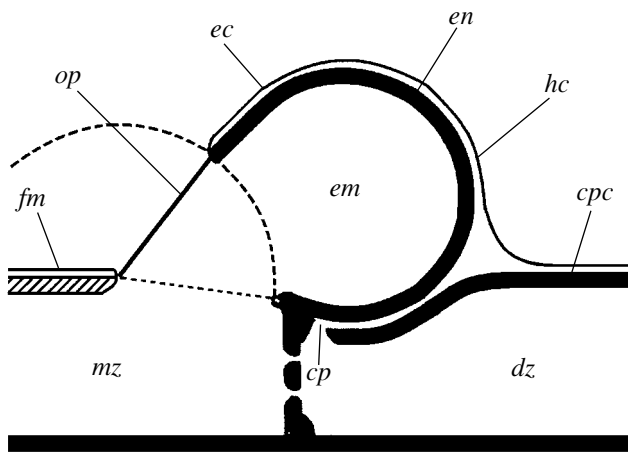
The previous year, Delage and Hérouard [28] had published their famous “Traité de zoologie concrète,” which mentioned both points of view on ovicell formation: Nitsche’s [77] opinion, that ovicells are formed by the maternal autozoid, and data of Vigelius [115, 116], who displayed by histological sections that both the maternal and the daughter autozooids took part in formation of those brood chambers. Nevertheless, the “Traité” authors preferred G. Nitsche’s point of view. This contradiction was resolved by one of the greatest English bryozoologists Harmer [36], who assumed that the ooeicum might be either a part of the “fertile (proximal) zoid,” or belong to the distal zoid” (p. 284). He assumed, for example, that in *Euthyroides episcopalis* (Busk, 1852) (Euthyroididae) the coelomic cavity should be connected with the maternal zoid. The validity of S. Harmer’s idea was confirmed by research of his compatriot Waters [119–123], who prepared and described anatomical sections of several cheilostomes. A. Waters showed the existence of both ways of ovicell

formation, though he did not discuss these findings. His illustrations showed that the ooeicum can be formed either by the maternal, or by the daughter zoid in different taxa. Waters [123] also described the developmental stages of ovicells in *Retepora umbonata* MacGillivray, 1885, and his data were later supported and verified by Japanese zoologist Okada [81], German researcher Buhner [13], and the previously mentioned Harmer (Harmer, 1934), who later described ovicellogenesis in several Reteporidae.

Basic studies of the Danish bryozoologist Levinsen [60–65], who intentionally did not use the term “ovicell,” revealed “numerous modifications of hyperstomial ooeicia” which manifested their basic similarity in the structure, where “two layers [walls] of the actual ooeicum are formed by the frontal membrane [wall] of the distal zoecium [daughter zoid]” ([63], p. 60). According to the classification subsequently proposed by Ostrovsky [82], this pattern of ovicell structure was



**Fig. 5.** Ovicell structure in *Bugula neritina*. Abbreviations: *cp*—communication pore, *cy*—cystid wall, *dm*—depressor muscles of the oocelial vesicle, *dz*—daughter (distal) autozoid, *em*—embryo, *ec*—ectooecium, *en*—entooecium, *fu*—funicular strands, *mz*—maternal zoid, *of*—oocium, *ov*—oocelial vesicle, *rm*—retractor muscle of the oocelial vesicle (from: [124], Fig. 2).



**Fig. 6.** Ovicell structure in *Fenestulina malusii*. Abbreviations: *cp*—communication pore, *cpc*—cryptocyst, *dz*—daughter (distal) autozoid, *ec*—non-calcified ectooecium, *em*—brooding cavity, *en*—calcified entooecium, *fm*—frontal membrane, *hc*—hypostegal coelom, *mz*—maternal (proximal) autozoid, *op*—operculum (from: [74], Fig. 20).

attributed to the first type. G. Levinsen also depicted several cheilostomes with ovicells generated by the maternal zoid (2nd type), however, he asserted that the

first “type of oocium appears in the majority of Cheilostomata” ([63], p. 60).

French zoologist Calvet [15] studied brooding structures in more than twenty species of marine bryozoans, preparing anatomic sections of decalcified specimens. In *Bugula simplex* (as *B. sabatieri* Calvet, 1900) Hincks had described and depicted the early stages of ovicellogenesis as the formation of two hollow vesicles, one of which was formed by the maternal zoid and a rudiment of the oocelial vesicle (vesicule oicellienne inferieure), whereas the second originated from the daughter zoid and was a rudiment of the oocium (vesicule oicellienne superieure) ([15], p. 132, Tab. II, Fig. 14, Tab. III, Fig. 5). L. Calvet assumed that this type of ovicells, where the two parts (oocium and internal vesicle) belong to different subsequent zooids, is the most common among cheilostomes. He considered that *Bicellariella ciliata*, the ovicells of which were studied by Nitsche [77], should not be an exception of this rule. This assumption is strange, since the distal zoid, by which the oocium could be formed, is absent in that species (see: [90, 102]). In completely formed ovicells of *Bugula simplex*, L. Calvet revealed a communication pore that connected coeloms of the oocium and the daughter zoid ([15], p. 58, Fig. 10) (see Fig. 3). On the contrary, G. Levinsen did not mention such communication anywhere. He did not picture it in the ovicell diagram of *Bugula* ([63], Tab. XXIV, Fig. 13), though he had carefully depicted it (without designation) in many other cases [60, 61, 63]. Furthermore, working with dried specimens Levinsen studied the early stages of ovicellogenesis, which, according to his descriptions, started their development in various taxa either from “two small distal calcareous plates” or from “a continuous plate,” arising “from the frontal edge of the distal [zooidal] wall” in various taxa ([63], pp. 60–61). This researcher classified brood chambers of cheilostomes according to their structure and the position of the ovicell relative to the distal zoid (immersion of ovicell into distal zoid), and introduced presently widely known terms. G. Levinsen distinguished “hyperstomial,” “peristomial,” “endotoichal,” “double-valved,” “acanthostegous” and “endozoocial” (now changed to “endozooidal”) ovicells ([62, 63]). Hyperstomial ovicells were subdivided by him into 1) “ooecia without cryptocyst” and “ooecia with cryptocyst” [62] and to 2) “dependent” and “independent,” according to the size of the wall contact between the base of the oocium and the distal zoid [63]. Levinsen [62] used the terms “ectooecium” and “entooecium” respectively for external and internal oocelial walls, thus replacing Julien’s “coitis” and “sparganile” [52] (see above). In contrast to Vigelius [115, 116], Levinsen [63] suggested that the egg leaves the autozoid cavity before entering the ovicell in some bryozoans, whereas this transition is carried out under a closed zooidal operculum in others. Subsequent researchers either accepted without discussion, confirmed, or simply ignored the aforementioned points of view on ovicell structure.

Thus, Korschelt and Heider [55] copied the ovicell diagram of *Bugula* from Calvet's monograph ([15], p. 58, Fig. 10) for their manual on zoology without any comment. Canu and Bassler [16] criticized G. Levinsen, but nevertheless presented very similar diagrams in their monograph (see also: [7, 8]). Furthermore, having studied sections of several species with ovicells, F. Canu and R. Bassler introduced the terms "aneucleithrian" (for hyperstomial ovicells, where the aperture is not closed by the zooidal operculum), "cleithrian" (for hyperstomial ovicells, where the aperture is closed by the zooidal operculum) and "subcleithrian" (the aperture of the ovicell is closed with the operculum raised) [16, 17]. These researchers also substituted the term "independent oecium," suggested by G. Levinsen (see above), for "recumbent," and were subsequently criticized for that by the known English bryozoologist J. Ryland [97].

Harmer [37] had also copied Calvet's diagram [15], but for some unknown reason he did not depict the oecial communication pore and did not mention it in the text. Even stranger, taking into account the fact that he discussed this finding of L. Calvet in his previous work [36]. However, that pore was drawn by E. Marcus ([68], Fig. 54), using a modified diagram of *B. avicularia* from the paper of his compatriot, German researcher Gerwerzhagen ([32], Fig. 1 in the text). A. Gerwerzhagen was the first to observe and describe oviposition—movement of eggs by a polypid from the cavity of the maternal autozooid into the ovicell through the so-called supraneural pore. The old problem on the location of egg formation and the actual functions of brood chambers (see above) was solved at last. It is remarkable that after A. Gerwerzhagen, oviposition has been observed only by five researchers [27, 29, 74, 106].

In the following work, Marcus [69] presented a longitudinal section with the ovicell of bryozoan *Thalamoporella evelinae* Marcus, 1941 (Thalamoporellidae), and showed that the oecium of that species consisted of three walls—"hyperstomial oecium with cryptocyst" according to the terminology of Levinsen [62, 63]. No communication between the oecial and zooidal coeloms was depicted in the diagram (see: [69], Tab. 4, Fig. 11).

As opposed to all the authors mentioned above, the German zoologist C. Cori modified Calvet's pattern ([15], p. 58, Fig. 10), presenting a communication pore between the coelomic cavity of the oecial fold and the perigastral coelom of the maternal autozooid ([26], Fig. 343). The reason for such an interpretation of Calvet's data remains unclear, as C. Cori himself did not make sections and did not study them. Probably, the work of Nitsche [77] and the opinion of Delage and Herouard [28] decisively influenced formation of his views on that problem.

Some time later, the point of view of C. Cori got support from the well-known Swedish bryozoologist Silen [105, 106]. It is necessary to note that this

researcher was, apparently, the first to realize the importance of a connection between coelomic cavities (instead of continuity of skeletal walls) of oecial fold origin. Having prepared sections, L. Silen reconstructed the ovicell structure of bryozoan *Scrupocellaria scabra* (van Beneden, 1848) (Candidae), and came to the conclusion that the oecial coelom was connected with the coelom of the maternal autozooid ([105], Fig. 18–19).

Silen [106] published the paper "The main features of the development of the ovum, embryo and oecium in the oeciferous Bryozoa Gymnolaemata." That outstanding research encompassed many aspects of the biology and morphology of cheilostome bryozoans, including the development and structure of the oecium in three species: *Callopora dumerilii* (Audouin, 1826) (Calloporidae), *Escharella immersa* (Fleming, 1828) (Romancheinidae) and *Fenestulina malusii* (Audouin, 1826) (Microporellidae). L. Silen rejected the point of view of his predecessors on the existence of communication between the oecial coelom and the visceral coelom of the daughter zooid. Referring to his sections of *S. scabra* [in the 1945 paper this species was mentioned as *S. scruposa* (Linnaeus, 1758), apparently by mistake], L. Silen asserted that in all three species studied, the oecial fold originated as an outgrowth of the maternal zooid, and its cavity was connected with the cavity of the latter (Fig. 4). Calvet's data [15] on the ovicell structure in *B. simplex* and G. Levinsen's illustrations, in which all basic details of structure and stages of ovicell development in *S. scabra* (see: [60], Tab. I, Fig. 8–9; [61], Tab. I, Fig. 21–22; [63], Tab. II, Fig. 5 a–f), *E. immersa* (see: [63], Tab. XVII, Fig. 3 a) and in representatives of family Calloporidae, *Callopora dumerilii* (see: [63], Tab. IX, Fig. 3 a), *C. aurita* [(Hincks, 1877) (see: [63], Tab. XXIV, Fig. 16)], *Tegella unicornis* (Fleming, 1828)—as *Membranipora* (see: [60], Tab. II, Fig. 24; [61], Tab. IV, Fig. 19; [63], Tab. IX, Fig. 5 a–h) and *T. arctica* (d'Orbigny, 1853)—as *T. sophiae* (Busk, 1855) (see: [63], Tab. IX, Fig. 6 a–c) where origination of the oecium from the daughter zooid is clearly visible, for some reason were ignored by L. Silen. Early stages of ovicell development were described by him as "a flat, narrow prominence from the frontal part of the distal wall [of the mother zooid]...., composed of two separate knobs" ([106], p. 9; see also: [100]). Finally, Silen extrapolated those results to all cheilostome bryozoans with hyperstomial and endozooidal ovicells (for discussion, see also: [124]).

Silen's work was so bright, and his arguments were so convincing, that they have been accepted or mentioned by authors of most large reviews and monographs on bryozoans up to the present [2, 3, 11, 12, 42, 43, 49, 54, 59, 73, 89–91, 98–100, 102, 111]. Some bryozoologists [2, 89] accepted the terminology proposed by L. Silen, who called the entire oecial fold "ectooecium" and the oecial vesicle "entooecium." Subsequently, English bryozoologist Ryland [97] reasonably criticized these changes. It is worth noting, that other

authors often copied Figs. 1–8a from Silen's paper [106] without changes, whereas the communication pore present in Fig. 10 of the Calvet monograph [15] was often omitted without any comment when copied in reviews (see, e.g.: [11, 49, 90]). The reason was probably due to L. Calvet's statement that he had not found that pore in any species studied, except for *B. simplex*. It is not absolutely true, as the communication between the oocial and visceral coeloms was shown in his scheme of the endozooidal ovicell of *Securiflustra securifrons* (Pallas, 1766) (Flustridae) (as *Flustra*) (see: [15], Fig. 44).

Except for Hass [40] and Harmer [39], who both gave very diagrammatical schemes of the oocia formed by the daughter zooid in their monographs (see also: [95], Fig. 3; [96], Fig. 1), nobody challenged the data and point of view of L. Silen for the next thirty years. It is interesting that S. Harmer, who briefly analyzed ovicell structure in all three volumes of his fundamental work "The Polyzoa of the Siboga Expedition," devoted to Cheilostomata [37, 38, 39], did not even mention L. Silen's work. Following Levinsen [63], he presented three schemes of ovicell structure ([39], Fig. 51B–D) in which the oocia consisted of two external uncalcified walls (ectoocium and endoecium), and a double inner wall of calcified cryptocyst that continued the skeletal walls of the daughter zooid.

Known English researcher A. Hastings analyzed the phenomenon of the simultaneous presence of hyperstomial and "reduced and vestigial" ovicells within some genera of Cheilostomata ([41], p. 250). Chilean bryozoologist Moyano [72] presented schematic figures of longitudinal sections of ovicells of four cheilostome genera in one of his first papers, but unfortunately they were uninformative. Ryland (Ryland, 1968) had discussed the terminological problems which have accumulated since the times of Jullien [52, 53], Levinsen [62, 63], Canu and Bassler [16], and also Silen [105, 106]. The terms chosen by him are currently used by bryozoologists (see also: [99]).

American zoologists Woollacott and Zimmer, [124] published results of anatomical research of the ovicells in *Bugula neritina* in 1972. They completely supported Calvet's data [15] (see Fig. 5). Silen was forced to admit the correctness of his descriptions concerning *Bugula* (see: [107]). Nevertheless, he stated that in species where the daughter zooid was absent in the longitudinal row, the oocium should be formed only by the maternal zooid. In conclusion, L. Silen assumed that the oocium was formed in different ways in different species.

Later, a number of researchers presented additional evidence in favor of oocium formation by the daughter zooid in several families of Cheilostomata: Calloporidae, Phidoloporidae, Bitectiporidae, Candidae, Bugulidae, Microporellidae, Cribrilinidae (see: [6, 18, 19, 20, 66, 74, 75, 103, 104]). Among others, representatives were studied of the same genera, and in some

instances, of the same species, as that studied by L. Silen. For example, known Danish zoologist Nielsen [74, 75] studied ovicell structure and development in several Cheilostomata, including *Bugula pacifica* Robertson, 1905, *Scrupocellaria varians* Hincks, 1882 and *Fenestulina malusii* (Fig. 6) (see also: [76].) It should be reiterated that L. Silen worked on *S. scabra*, *F. malusii* and *C. dumerilii* [105, 106]. Confirming Levinsen's data [63], C. Nilsen has shown that in different taxa, the initial stage of ovicell calcification can look like either a bilobate, or a single plate. Russian zoologists Lobastova and Ostrovsky [66] and American researchers Santagata and Banta [104] studied sections of *Callopora aurita*, *S. scabra* and *S. ferox* Busk, 1852 respectively. In all of them, the ovicells were formed by the distal zooid, and their coelomic cavity was connected with visceral coelom by the communication pore. Nielsen [75] presented the assumption, that this type of brood chamber was basic, from which other ovicell types could evolve. Owing to these finds, the prevalence of L. Silen's viewpoint was replaced by the coexistence of two opinions, that of L. Silen and that of G. Levinsen–L. Calvet (see: [73, 91, 100]).

In the beginning of the 1970s, another hypothesis appeared in the bryozoological literature. Based of the fact that calcification of endoecium starts from the transverse wall between the maternal (proximal) and the daughter (distal) zooids, and consequently, the oocium is an immediate continuation of this transverse wall, the assumption was made that it is formed by the maternal zooid, whereas the ectoecium is formed by the daughter zooid. The origin of this point of view is revealed in one of the early works of G. Levinsen, who wrote that "it is obvious, that the inner layer (the endoecium) can be regarded as a continuation of the distal [transversal] wall, while the outer layer (the ectoecium) is formed from the front wall of the distal zoocium" (Levinsen, 1902, p. 13). Since the publication of papers by the American researcher Soule [110] and the French bryozoologist Harmelin [35], this opinion has again appeared in the literature as a certain compromise between two conflicting hypotheses (see: [22, 23, 24, 25, 71, 94, 100, 101, 118]). For example, Harmelin [35] assumed that the ovicells were formed exactly that way in *Crassimarginatella maderensis* (Waters, 1898) (Calloporidae), and Australian researcher Cook [23] agreed, in *Doryporella alcicornis* (O'Donoghue, O'Donoghue, 1923) (Calloporidae) and *Scrupocellaria* (Candidae). Nevertheless, Ostrovsky [82] came to the conclusion that all the mentioned authors had dealt with ovicells formed by daughter zooids (see also: [74, 84]).

The paper of English scientists Bishop and Househam [9] was a major milestone in Cheilostomatida brood chamber research. Within the genus *Puellina* (Cribrilinidae) these authors have described three categories of ovicells "based on the timing of production of the ovicell in relation to budding of the maternal autozooid and the zooid distal to it" ([9], p. 4). According to the data of J. Bishop and B. Househam, the ovicell "is



a proximal component of the distal [auto]zooid" (category A), "of the kenozooid: distal to the maternal autozooid" in category B. "The ovicell appears to be a distal component of the maternal [auto]zooid" in category C ([9], p. 4). Thus, revealing different types of ovicell within the same cheilostome genus finally resolved the existing contradiction regarding their formation. Moreover, all three categories of ovicell were depicted (but not discussed) in *Puellina harmeri* (Ristedt, 1985) in the paper by German bryozoologist Ristedt [94]. It means that within the same species, ovicells can be generated by both maternal and daughter zooids (see also: [82]).

The author of the present paper has studied the structure and development of ovicells in *Cribrilina annulata* (Fabricius, 1780) (Cribrilinidae) and *Celleporella hyalina* (Linnaeus, 1767) (Hippothoidae) and has analyzed in detail the problems complicating work in this area of research [82]. As a result, the data of English scientist Hughes [47] who had described ovicells formed by the maternal zooid *C. hyalina* (see also: [20]) were confirmed. The same structural pattern was also found in *C. annulata*. Based on personal and literature data, A. Ostrovskii distinguished two main patterns of ovicell formation in Cheilostomata, attributing ovicells of categories A and B formed by the daughter zooid (see: [9]), to the first type, and ovicells of category C, formed by the maternal zooid, to the second [82].

Data that were accumulated in bryozoological literature by the end of the last century, contradicted the results and extrapolations of Silen [105, 106] and provided evidence for the existence of different patterns of structure and formation of brood chambers within Cheilostomata. However, as far as the species *Callopora dumerilii* was not reevaluated, L. Silen's statements continued to be valid, at least concerning that bryozoan. Aiming to verify the structure of calloporid ovicells, A. Ostrovskii and German researcher P. Schafer undertook a comparative anatomic-morphological research of the species *C. dumerilii* and *C. lineata* (Linnaeus, 1767) (the type species of the genus *Callopora* Gray, 1848). In their recently published paper it was shown that ovicells were formed from the daughter zooid in both species [84]. Study of the early stages of ovicellogenesis in *C. lineata* has confirmed the fact that calcification of the endooecium starts as a formation of two independent plates, corresponding to the data of Levinsen [63], instead of tubercles as Silen asserted [106]. Analysis of the depiction of an anatomical section of *S. scabra* ovicell made by L. Silen ([105], Fig. 18–19) showed that this researcher did not find a communication between the eoecial cavity and the visceral coelom due to shrinkage of the specimen fixed in alcohol (Fig. 4A). On the basis of these facts, the conclusions and generalizations of L. Silen were recognized incorrect. A. Ostrovskii and P. Schafer have emphasized that the two types of ovicells should be distinguished by their formation patterns in Cheilostomata (see also: [101]), which can exist within the same taxon

(species, genus, family), and sometimes within same colony. The necessity of further research is necessary, which would make it possible to distinguish the types of brood chambers that characterize different groups of Cheilostomata. The lack of specialized cell complexes in communication pores between the eoecial fold and the visceral coelom has led authors to the conclusion that use of the term "kenozooid" for the eoecium is inadequate.

Recently, English and American bryozoologists Taylor and MacKinney [114], and also Ostrovskii [83], have presented new data on ovicell structure of several fossil and modern representatives of families Microporidae and Cribrilinidae, and have considered various hypotheses concerning the early stages of evolution of brood chambers within these groups of bryozoans. Harmer was the first who assumed that ovicells of Cheilostomata could arise by spine modification [36], and later his idea was developed and modified by several authors [1, 58, 59, 104, 107]. Harmer's hypothesis was that the ovicell predecessors were two distal oral spines of the maternal autozooid. This assumption is probably valid for representatives of some groups with bivalved ovicells formed by the maternal autozooid (for example, within the *Scruparia* and *Thalamoporella* genera). At the same time, the majority of cheilostomes possess ovicells formed by the daughter zooid (see above). Therefore, it is relevant to mention the find of fossil cribrimorph bryozoan *Leptocheilopora tenuilabrosa* Lang, 1916, described by English bryozoologist Lang [58], who supposed that ovicells in that species were formed by several flattened spines (costa) in the proximal part of the distal autozooid.

In the upper Cretaceous deposits of England and Germany, Ostrovskii and Taylor (Ostrovskii, Taylor, in press) found four fossil species of Calloporidae (the earliest cheilostome with ovicells) with brood chambers formed by non-modified spines in the proximal part of the daughter zooid. Such primitive ovicells are reminiscent of a cage and confirm, on the one hand, Harmer's hypothesis [36] that brooding structures originated from spines in cheilostomes, and also Nielsen's assumption [75] that ovicells formed by the daughter zooid are a basic type.

Thus, despite the two and half centuries that have passed since naturalists began to pay attention to brood chambers in bryozoans, the general pattern of structure and development of ovicells remains fragmentary. However, data on brooding structures are extremely important for understanding cheilostome phylogeny and the evolution of their reproductive strategies. It is not in question that different patterns of brooding within the considered group of invertebrates originated repeatedly and independently. At the same time, ovicells, except for, apparently, bivalved and acanthostegous brood chambers, are synapomorphous in most Cheilostomata (for discussion see: [82, 83], Ostrovskii, Taylor, in press). Known New Zealand bryozoologist D. Gor-

don [33], based on a study of frontal shields, has come to a conclusion about the para- and polyphyletic nature of the formerly considered monophyletic taxa of the four largest infraorders of Cheilostomata, forming the suborder Ascophora. All those bryozoans possess ovicells that originated prior to the complex front shields, therefore, study of structure of the considered brood chambers is also extremely relevant for phylogeny. Research of various brooding patterns and structures associated with them is extremely important for analysis of the evolution of reproductive strategies of Cheilostomata, characterized by three different patterns of sexual reproduction. In two of them ovicells are involved, some of which are provided with an embryophore (see above), enabling extraembryonal feeding.

Proceeding from that stated above makes it obvious that further accumulation of data on the brood structures of cheilostomes is an imperative need. The most voluminous and still little used source of information is illustrations and, to a lesser degree, descriptions by Levinsen [63]. That remarkable zoologist investigated the structure and development of ovicells in 80 (!) species of Cheilostomata belonging to 62 genera. However, to assess the correctness of his diagrams is often rather problematic, as he worked only with cleared tissues and cuticle skeletal walls. For that reason, the results of the research by Levinsen were seldom discussed and even less often used by other zoologists. The solution to this situation is a thorough examination of Levinsen's data.

Data obtained by some modern zoologists also demand verification. For example, the ovicell diagram of *Fenestulina malusii* (as *Microporella*), obtained from longitudinal sections of a decalcified specimen by Calvet (see: [15], Fig. 21), greatly differs from the ovicell diagram of the same species quoted in Nielsen's paper ([74], Fig. 20), who exclusively studied skeletal structures. It is clear that the only adequate method for such research is the combined use of light and scanning microscopy, making it possible to obtain an integrated notion of such complex structures as ovicells.

Recent research has made it possible to ascertain and to bring incomplete and inconsistent data on the structure of hyperstomial ovicells of cheilostomes to a uniform system. These basic data are considered a necessary prerequisite to further progress in this area of research and will open prospects for study of the evolution of various brooding structures in bryozoans.

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