Paper in:

The parental care in cheilostome bryozoans: a historical review

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

Most cheilostomes keep their young in the skeletal chambers called oovicells. Presence or absence of the oovicells as well as their morphology is considered to be important characters in the taxonomy of Cheilostomata. There are several morphological types of oovicells, and most common are hyperstomial ones that often look like hemispherical bubbles or helmets on the colony surface. Basically, the hyperstomial oovicell consists of a two-walled calcified fold (ooecium) with a coelomic cavity inside, a non-calcified distal wall of the maternal autozooid (that produces eggs), and the brooding cavity between them (Figure 1). The outer ooeial wall is called ectooecium; that surrounding the brooding cavity, entooecium. The oovicell opening is closed either by the operculum of the zooidal aperture, or by an evagination of the maternal cystid wall called an ooeial (inner) vesicle or ooeial plug. The ooeial vesicle can contract by the special muscle bands, opening the oovicell entrance. Depending on the type of formation, the ooeial coelom cavity communicates either with the coelom of the daughter or maternal zooid through communication pore(s). If the ooecium originates from the daughter zooid, the pore is normally plugged by non-specialized epithelial cells, and direct communication between the coelomic cavities mentioned becomes impossible. For this reason the ooeial fold is
conventionally considered to be a special polymorph, a kenozooid, and the ovicells evolution is thought to be a manifestation of the most interesting and important colonial phenomenon, that of zooidal polymorphism.7-10

1. Ovicells, oviposition and placental brooding

The first author who described ovicells in cheilostomes was John Ellis.11-12 In his famous book Essay towards a natural history of the corallines... he noted and figured ovicells in several species of the genera Bugula, Bicellariella and, probably, Flustra, and called them ‘Balls’, ‘testaceous Spherules’, or ‘testaceous Figures’.13 Describing ovicells in one of the ‘Corallines Celluleuses’ (Bugula neritina (Linnaeus, 1758) according to Levinsen14), Ellis suggested that they could be ‘Niduses or Matrices of certain testaceous Animals, like small snails or Neritae’,15 from the eggs of which the colony originates. This remarkable opinion was further expressed in the drawing of B. neritina, where the ovicells were pictured as spirorbid polychaetes, forameniferans and gastropods with a spiral shell (Figure 2).16 It could be that Ellis possibly saw in some cases actual spirorbids and foraminiferans attached to the bryozoan colonies, and confused them with brood chambers. Furthermore, he suggested that the similar relationship existed between some bryozoans and bivalves.17
Peter Simon Pallas expressed the view that ‘bullas’ (ovicells) are ovaria in encrusting bryozoans, and this opinion was retained for a century. Concerning ovicells in erect Bugula neritina and B. avicularia (Linnaeus, 1758) (both identified therein as Cellularia), this author suggested that they and avicularia are organs of similar nature, and could be somehow related with ovicells in encrusting ‘Eschara’. Pallas speculated that both ovicells and avicularia could serve for fertilization, and sometimes called them ‘Nectariums’.

In his later work, Ellis agreed with the opinion of Pallas, and admitted that the ‘pearl-like studs (bullulae supra cellulas)’ in Flustra and ‘little hemispherical covers’ in Bugula (as Cellularia) ‘appear rather to be what we have called Ovaries’. Ellis mentioned that Pallas called ovicells and avicularia ‘Nectariums’ comparing them with ‘the flowers of some plants’. At the same time, he suggested that ovicells could be the shell-bearing larvae in ‘Cellaria’, that detach from the branch, ‘drops and adheres to a proper substance as a base, beginning to form a Coralline like the parent animal’.

One of the first observations that contradicted this view was made by Robert Grant. Studing *Carbasea carbasea* (Ellis and Solander, 1786) (as *Flustra*) and *Flustra foliacea* (Linnaeus, 1758), he recorded the growing egg inside the zooid, whereas, when mature, it is surrounded by a helmet-shaped capsule [ovicell], that separates the egg “from the cavity of the cell [zooid]” in *Flustra*.

George Busk introduced the term ‘ovicells’, augmenting for them such descriptive terms as ‘subglobose and terminal’, ‘galeriform’ [*Scrupocellaria*], ‘globose, subpedunculate’ [*Bicellaria*], ‘arcuate’ [*Caberea*], ‘conical’ [*Diachoris*], and ‘subglobular’ [*Cellepora*].

However, the older view that ovicells are capsules, containing the ovaries, was first altered by Thomas Huxley (Figure 3). Huxley, who observed eggs inside autozooids and with empty ovicells that were seen to contain the egg later on in *Bugula avicularia* (as *B. avicularis*), proposed that an ovicell should be the ‘marsupial pouch’ [brood chamber]. Thomas Hincks, who investigated *Bugula flabellata* (Thompson in Gray, 1848), *B. turbinata* Alder, 1857 and *Bicellariella ciliata* (Linnaeus, 1758) (as *Bicellaria*), challenged Huxley’s opinion, but was forced to admit the truth of Huxley’s observations afterwards. However, Hincks stressed that he had ‘grounds for believing that in some cases, and under conditions which [he could not] explain, ova are also produced within [ovicells]’. Hincks suggested that there are two kinds of eggs formed in gymnolaemates: some eggs are produced in the ovicells, whereas others in the autozooids, being ‘the equivalent of the statoblast[s] of the Phylactolaemata’. For evidence he used Fredrik Smitt’s data, who...
first recorded embryonal development inside the gonozooid (at that time also called ovicells) in the cyclostome, *Crisia eburnea* (Linnaeus, 1758), and inside the autozooid in the cheilostome, *Cryptosula pallasiiana* (Moll, 1803) (as *Lepralia*). In the same 1880 monograph Hincks expressed the opinion that ‘its [ovicell] interior is in direct communication with the perigastric cavity’ of the maternal autozooid, but was in doubt concerning the method of the oviposition. He observed the very beginning of this process in *Bugula*, when ‘it seemed as if a vigorous movement [of the polypide] might at any moment discharge it [an egg] into the ovicell, and in *Chartella papyracea* (Ellis and Solander, 1786) (as *Flustra*). Hincks introduced the term ‘ooecium’ that he used as synonymous with ‘ovicell’, and indicated that the ovicells can be ‘prominent’, ‘subimmerged’ or ‘immersed’, depending how they protrude on the surface of the colony.

The first investigation of the structure and development of hyperstomial oovicells was made by Hinrich Nitsche on *Bicellariella ciliata* (as *Bicellaria*), and one of his figures was schematically redrawn by Vigelius. Nitsche found that each oovicell formed as two outgrowths - ‘helmförmige Blase’ (ooecium) and ‘rundliche Blase’ or ‘Deckelblase’ (ooecial vesicle) on the distal margin of the maternal zooid in this species. The inner vesicle serves as an operculum for the helmet-shaped part, and can be contracted by the work of special muscles during larval release (rhythmical contractions of the ooecial vesicle was described first by John Reid in *Bugula flabellata* (as *Flustra avicularis*)). Similar to the opinion of Huxley, Nitsche independently came to the conclusion that oovicells are merely brood chambers, and ‘the oovicells or ooecia in the Chilostomata’ were suggested to be modified individuals, but in a special sense. Following Allman, Nitsche believed that bryozoan colonies were ‘composed of two different classes of zooïds, the “cystoid zooïds” [cystide] and the “polypoid zooïds” [polypide], and the latter were produced by budding inside the former. Accordingly, he considered oovicells as a variety of “cystoid zooïd”. Busk believed that oovicells ‘are clearly transformed cells [zooids]’. Nitsche proposed a possible mechanism for oviposition through the hypothetical pore, placed between the basal parts of the ooecium and the ooecial vesicle.

Édouard Claparède and Lucien Jolivet made some observations on oovicells in several cheilostomes, but comparing with Nitsche, they provided no new information about ooecial structure in their publications. In *Scrupocellaria scruposa* Claparède noted that the development of the oovicell began when the first mature egg and sperm were seen in the maternal zooid. This statement was later criticised by Vigelius, who observed the earliest stages of the oovicellogenesis in the zooids with the incipient ovary and stated that the growth of the first egg was accompanied by the formation of the brood chamber in *Terminoflustramembranaceaotruncata* (Smitt, 1868) (as *Flustra membranaceao-truncata*). Interestingly, Claparède and Nitsche also used the data of Smitt, but to argue against the hypothesis of Hincks (see above), since they were sure that egg had to be moved to the oovicell for further development.

Willem Johann Vigelius described the structure and the development of the ‘endooecial’ (according to Levinsen) oovicells in *Terminoflustramembranaceaotruncata* in sections, and clearly showed that two successive zooïds contribute to the formation of
the brood chamber: ‘Helm’ (ooecium) originates from the daughter zooid whereas ‘Deckel’ (ooecial vesicle) from the maternal zooid.73 Vigelius believed that, despite the different origin of ‘external’ (in *Bicellariella ciliata*) and the ‘internal’ (in *Terminoflustra membranaceotruncata*) brood chambers,74 the ovicell structure shows obvious similarities in these species. He held the opinion that, an ovicell with its simple structure is more likely a specialised organ in *Terminoflustra*, not a ‘Cystidindividuen’ like Nitsche stated for *Bicellariella*. He also suggested a possible mechanism for oviposition through the rupture hole in the inner vesicle, and this idea was accepted by Delage and Hérouard75 and by Calvet.76 Later a similar idea was also suggested by Arthur Waters (Figure 4).77 In his later paper, Vigelius described the ovicell structure and briefly outlined its formation in *Bugula calathus* Norman, 1868, where he thought that the brood chamber developed ‘from the free distal wall of the sexually mature animal’ [maternal zooid].78 Vigelius also found ‘Cylinderzellenschicht’ (cylindrical epithelium) on the inner surface of the distal wall of the ooecial vesicle, and described precisely the musculature of the ooecial plug, which consisted of two groups of bands perpendicular to each other. He thought that one of the muscle groups was responsible for the rupture of the ooecial vesicle wall during oviposition. Interestingly, the hyperthrophied cell layer (mentioned above) that serves as an embryophore79-82 was probably discovered first by Reid, who wrote that the ‘membranous partition [ooecial vesicle] was much thickened, especially at the central part ..., and contained a number of nucleated cells’ in *B. flabellata*.83-84

Jules Jullien85 used the terms ‘coïtis’ (Greek, ‘cradle’) for the thick external ovicellar wall, and ‘sparganile’ (Greek, ‘swaddling-cloth’) for the thin internal one in the description of cheilostome *Exochella longirostris* Jullien, 1888.86 Classifying cheilostomes, he introduced the new ‘tribes’ Inovicellata, Subovicellata and Superovicellata based on the
presence and position of the ovicell opening in relation to the orifice of the maternal autozooid, and proposed the terms ‘aneucleithral’ and ‘cleithral’ for different types of the closure of the ovicell opening by the zooidal operculum. Jullien also illustrated larvae, developing inside zooids in *Beania* sp. (as *Diachoris costata*), and suggested that oviposition might occur with the help of the tentacle sheath in *Celleporella hyalina* (as *Hippothoa*).

Eduard Pergens was the first to record oviposition in cheilostomes, but his paper was overlooked and forgotten by later authors. Studying *Fenestrulina malusii* (Audouin, 1826) (described as *Microporella*), he noted that this was accompanied by a strong compression of the egg and occurred when the polypide degenerated.

Ives Delage and Edgar Hérouard in their book mentioned both opinions concerning the origin of the ovicells (Nitsche’s, that these brood chambers were formed by the maternal zooid, and Vigelius’s, that they originated from both the maternal zooid and the daughter zooid), but favoured Nitsche’s point of view. Sidney Harmer first noted that the ooecium can also be either a part of the ‘fertile (proximal)’ zooid or belong ‘to the distal’ zooid. As a third possibility he mentioned ‘that it is a modified individual, as believed by Nitsche and others’. He suggested that the ooecium as seen in in *Euthyroides episcopalis* (Busk, 1852), should communicate with a maternal zooid, although he could not prove this. Harmer’s idea was that ‘the ovicell is formed by the fusion a pair of greatly expanded oral spines, the bases of which should communicate with the fertile zooecium on each side of the operculum’. On the other hand, he wrote that ‘it is impossible not to be struck by the resemblance between the development of the ovicell and that of the frontal bars’ in this species. This contradiction and Harmer’s doubts overshadowed the true nature of these structures for a long time.

Harmer was the first to describe extraembryonic nutrition in cheilostomes when he stated that the embryo “receives …yolk while in the [brooding] sac” in *Retiflustra schoenaui* Levinsen, 1909 (described as *Flustra cribriformis* Busk).

Waters made sections of the ovicells in a number of cheilostome species. His descriptions and figures show that there are two ways of the ooecial formation, and the ooecium can be formed either by the maternal, or by the daughter zooid in the different taxa. One of the most informative papers was published in 1913. In this work, Waters depicted the ovicell consisting of the small kenozooidal ooecium (budded from the fertile zooid) and brooding sac in *Halysisis diaphanus* (Busk, 1860) (as *Catenaria diaphana*). Here he also applied the ovicell shape and position for classification of Catenicellidae, and described the developmental stages of the ovicell in *Retepora umbonata* MacGillivray, 1885. These data were later supported and verified by Yaichiro Okada, Paul Buchner and Sidney Harmer who described ovicellogenesis in several phidoloporids.

Louis Calvet carefully investigated anatomy of brooding chambers in several species, including cheilostomes, making sections of decalcified specimens. He noted that there are marine bryozoans (cheilostomes as well as ctenostomes) that do not brood their youth, whereas the majority of them are brooders. In *Bugula simplex* Hincks, 1886 (as *B.
sabatieri Calvet, 1900) he described early oovicellogenesis as the formation of two hollow vesicles, one of which, being formed from a maternal zooid, was a rudiment of the ooecial vesicle (‘vésicule oovicellienne inférieure’), whereas the second, originating from a daughter zooid, was a rudiment of the ooecium (‘vésicule oovicellienne supérieure’). Calvet suggested that this oivicell type in which its two parts (ooecium and inner vesicle) belong to the different subsequent zooids, is most common among cheilostomes. However, he thought that Bicellariella ciliata, in which oivicells were studied by Nitsche, should not be an exception from this rule, (despite an absence of the terminally budded distal zooid in this species), and this was later recognized by Harmer. One of Calvet’s most important findings was a communication pore in the septum between ooecial and daughter zooid coeloms (Figure 5). In the ooecial vesicle of the oivicells of B. simplex he found a sclerite - circular thickening of its cuticle corresponding to the place of contact between ooecium and ooecial vesicle, plexus of the mesenchymatous cells (obviously, funicular strands), and following Vigelius, complex musculature and embryophore. Calvet described growth of the embryo accompanied by the enlargement of the cells in the ooecial vesicle. It is also well seen in his illustrations: for instance, in the oivicell containing the zigote, the epithelium of the ooecial vesicle is not hypertrophied, whereas its cells have a cylindrical shape when there is the large embryo in the brood chamber. However, Calvet did not explain this. He described and illustrated the structure of the endozooidal oivicell in Securiflustra securifrons (Pallas, 1766) (as Flustra), also depicting the longitudinal sections of the hyperstomial oivicells in Amphiblestrum flemingi (Busk, 1854) (as Membranipora) and Fenestrulina malusii (Audouin, 1826) (as Microporella). Untill now Calvet is the only researcher who has studied the anatomy of endotoichal oivicells in the genus Cellaria (in Cellaria fistulosa (Linnaeus, 1758) and C. salicornioides Lamouroux, 1816). One of the most interesting characters found in these peculiar internal brood

chambers was a hypertrophied epithelium of the brooding sac and an additional operculum, closing the ovicell opening. Calvet wrote that the brooding cavity [as he called the space around the brooding sac] is connected with a cavity of the maternal zooid, and considered it as a part of the latter. He recorded the enlargement of the embryophore cells accompanying the growth of the embryo, but, again, failed to recognize its true function.

Waters\(^\text{115}\) studied tube-like brood chambers (‘peristomial ooecia’ according to Levinsen\(^\text{116}\)) in *Margaretta chuakensis* Waters, 1907 (as *Tubucellaria ceroides* var. *chuakensis*), and found a peculiar modified polypide with a special terminal plug, closing the entrance to the oovicell in the maternal zooid.

Harmer\(^\text{117}\) described ‘somewhat hood-like external ovicells’ and an ‘ovisac’ with associated muscles in ‘fertile zooecia’ of *Cheiloporina haddoni* (Harmer, 1902) (as *Lepralia*), but was not able to ascertain if the sac was a diverticulum of the vestibulum.

The comprehensive studies of Georg Levinsen (Figure 6),\(^\text{118-123}\) who intentionally did not use the term ‘ovicell’,\(^\text{124}\) revealed ‘numerous modifications’ of ‘hyperstomial ooecia’ and showed a basic similarity in their structure, where ‘the two layers [walls] of the actual ooecium are formed by the frontal membrane [wall] of the distal zooecium [daughter zooid]’.\(^\text{125}\) Levinsen also described and depicted some bryozoans with the ooecia formed either by the distal kenozooids or avicularia, but stated that the above mentioned ‘type of the ooecium ... appears in the majority of the Cheilostomata’.\(^\text{126}\) Similarly, considering endozooidal oovicells, he divided them on the “ooecia which are enclosed in autozoecia”, and “ooecia which are surrounded by kenozoecia”.\(^\text{127}\) In contrast with Calvet,\(^\text{128}\) Levinsen did not mention the communication between the ooecial and distal zooidal coeloms. He

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*Figure 6. Georg Levinsen (photograph courtesy of the Library of the Zoological Museum, University of Copenhagen).*
Levinsen described the oovicell structure and development in more than 80 cheilostome species, but, except for his terminology, his data were almost never used and were not revised.

Levinsen classified cheilostome brood chambers according to their structure and a position of the oovicell relative to the distal zooid (ovicell immersion), introducing the terms ‘endozooecial’, ‘hyperstomial’, ‘peristomial’, ‘endotoichal’, ‘double-valved’ and ‘acanthostegous’ that are currently in use. He also divided hyperstomial oovicells into (1) ‘ooecia without a cryptocyst’ and ‘ooecia with a cryptocyst’, and (2) ‘dependent’ and ‘independent’ according to the size of the wall contact between the ooeccial base and the distal zooid. For the entire ooeccium he often used the term ‘ooecial fold’, for the ooeccial vesicle - ‘ooecial operculum’, and for the external and internal ooeccial walls ‘ectoOoecium’ and ‘endoOoecium’ (‘coïtis’ and ‘sparganile’ of Jullien). He also described the earliest stages of oovicellogenesis (in dried specimens) which, according to him, in different taxa starts from the development of either ‘two small distal calcareous plates’ or ‘a continuous plate’, arising ‘from the frontal edge of the distal [zooidal] wall’. Levinsen suggested that the egg should leave the maternal zooid before entering the oovicell, however, oviposition has a place under the closed zooidal operculum in some species.

Subsequent authors either accepted without discussion, or supported or just ignored the data of the previous workers on the ooeccial structure. Eugen Korschelt and Karl Heider briefly described the oovicell structure in *Bugula* after Calvet and copied the scheme of the oovicell sagittal section from his monograph with no comments. Ferdinand Canu and Ray Bassler, although criticizing Levinsen, gave very similar schemes of the different oovicellar types. They sectioned a number of species with oovicells, and proposed modified terms ‘aneucleithrian’ (for the hyperstomial oovicells not closed by a zooidal operculum), ‘cleithrian’ (closed by the operculum), and introduced ‘subcleithrian’ (the oovicells is closed with the operculum rised). These authors substituted Levinsen’s term ‘independent ooecia’ for the ‘recumbent’ ones (criticized by Ryland), and they also copied Calvet’s scheme of the *Bugula* oovicell.

Harmer considered the oovicell structure in all three cheilostome volumes of his famous monograph *The Polyzoa of the Siboga Expedition*. Following Levinsen, he depicted several schemes of the oovicell structure with the ooeccia consisting of two external non-calcified walls (ecto- and entooecium), and the ooeccia with a double inner wall (cryptocyst) inbetween. In both cases the ooeccium is a continuation of the daughter zooid frontal wall. Copying Calvet’s scheme for *Bugula*, Harmer did not mention or illustrate the communication pore of the ooeccium for some reason. It is even more strange, since he discussed Calvet’s findings in his previous work, and stressed that “the vestigial ... oovicell is ... definitely shown to be a derivative of the distal zooeccium” in *B. longicauda* Harmer, 1926. In contrast, Ernst Marcus figured this pore, using the modified scheme of *B. avicularia* from the work of Adolf Gerwerzhagen. After Pergens, Gerwerzhagen was the first to observe the oviposition in cheilostomes, and this...
question was finally answered. Later the oviposition was also observed by several researchers.161-168

Marcus169 depicted the stages of oovicellogenesis and presented the scheme of the longitudinal section of oovicellated autozooid of *Thalamoporella evelinae* Marcus, 1941. Looking at this scheme, one has an impression that the ooecium consists of three walls in this species. However, the epithelial lining shows that there are actually two walls. Marcus did not illustrate any communication organs between ooecial and zooidal coeloms.170

Contrary to all previous authors, Carl Cori171 modified the scheme of Calvet172 and pictured the communication between ooecial and maternal zooid coeloms instead. The reason for this is unclear, since Cori did not make the sections of the oicells by himself. However, Cori’s figure was approved by Lars Silén (Figure 7).173-174 It should be noted that the last researcher was, probably, the first who realized the importance of communication between coelomic cavities (instead of a continuity of zooidal walls) to reveal the source of ooecial origin. After making sections, Silén reconstructed the oivicell anatomy of *Scrupocellaria scabra* (van Beneden, 1848).175 According to him, the ooecial coelom is confluent with the coelom of the maternal autozooid.

In 1945 Silén published his famous paper ‘The main features of the development of the ovum, embryo and ooecium in the ooeiferous Bryozoa Gymnolaemata’.176 This prominent study investigated many aspects of bryozoan structure and reproductive biology, including the development and structure of the ooecia of three cheilostome species: *Callopora dumerilii* (Audouin, 1826), *Escharella immersa* (Fleming, 1828) and *Fenestrulina malusii*. As a result of his work, Silén refuted the point of view of earlier scientists about
Figure 8. 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 ooecial vesicle, co – brooding cavity, cv – ooecial coelomic cavity, di – diaphragm, dz – daughter (distal) autozooid, eph – embryophore, fm – frontal wall of the daughter autozooid, iv – ooecial (inner) vesicle, m – muscles of the ooecial vesicle, op – operculum, pol – polypide, ve – vestibulum (from Silén, 1944, figures 18-19).
the existence of a connection between the ooeical coelom and the perigastric cavity of the
dughter zooid. Referring to his sections of *Scrupocellaria scabra* (Figure 8),\textsuperscript{177} he stated
that in all three species studied an ooeial fold originates from the maternal zooid, and its
cavity communicates with that of the latter. It was shown that the ooeium starts its
development when the first oocyte begins to grow in the ovary, and this was suggested as
being regulated by hormones. Silén obviously implied that if the ovicellogenesis is
triggered by the maternal zooid (its ovary), the ooeium is formed at the expense of it too.

Calvet\textsuperscript{178} finding of the communication pore in *Bugula simplex* as well as Levinsen’s
illustrations of the ooeell structure and development in *S. scabra*,\textsuperscript{179-181} *E. immersa*,\textsuperscript{182} and
calloporids *Callopora dumerilii*,\textsuperscript{183} *C. aurita* (Hincks, 1877),\textsuperscript{184} *Tegella unicornis*
(Fleming, 1828) (as *Membranipora*),\textsuperscript{185-187} and *T. arctica* (d’Orbigny, 1853) (as *T. sophiae*
(Busk, 1855)),\textsuperscript{188} where an ooeial origin from the daughter zooid is clearly seen, were
either criticized or ignored. The earliest stage of ovicellogenesis was described as ‘a flat
and narrow prominence from the frontal part of distal wall [of the mother zooid] ... composed of two separate knobs’, and the inner wall of the ooeial fold was said to be
membranous.\textsuperscript{189-190} Finally, Silén extrapolated these statements to all bryozoans with
hyperstomial and endozooidal ooeicles.\textsuperscript{191} It is noteworthy, that in his previous paper Silén
wrote that the ooeium is formed by the distal zooid in endozooidal ooeicles.\textsuperscript{192}

It should be mentioned here that the statement on the ooeial origin from the maternal
zooid was influenced by the early idea of Harmer,\textsuperscript{193} who suggested that the ooeium
originates from the two oral spines in the cribrimorph *Euthyroides episcopalis* (see
above). Based on this and his own inferences concerning evolution of the spines in
Gymnolaemata,\textsuperscript{194} Silén speculated that the ooeium ‘is possibly a structure composed of
transformed zoid-buds’.\textsuperscript{195} Later this author\textsuperscript{196} advocated these opinions in one of his
following papers.\textsuperscript{197}

Silén’s study was so comprehensive, and his arguments were so convincing, that they
have been accepted or mentioned by the authors of most large reviews and handbooks on
Bryozoa up to the present time (Brown,\textsuperscript{198} Hyman,\textsuperscript{199} Brien,\textsuperscript{200} Larwood,\textsuperscript{201} Kluge,\textsuperscript{202-203}
Prenant and Bobin,\textsuperscript{204} Powell,\textsuperscript{205} Ryland,\textsuperscript{206-209} Ryland & Hayward,\textsuperscript{210} Ström,\textsuperscript{211} Hayward
& Ryland,\textsuperscript{212-213} Reed,\textsuperscript{214} Viskova,\textsuperscript{215} Mukai et al.\textsuperscript{216}). Some authors\textsuperscript{217-218} also accepted the
changes in terminology made by Silén, who used the term ‘ectooecium’ for the entire
ooeical fold and ‘entooecium’ for the inner vesicle.\textsuperscript{219-220} Interestingly, figures 1-8a from
Silén’s paper,\textsuperscript{221} that have often been reproduced elsewhere, have never been subsequently
modified, whereas a communication pore of the ooeill in the text-figure 10 by Calvet\textsuperscript{222}
has been often omitted without comment.\textsuperscript{223-225} It could possibly have happened because
Calvet stressed that he did not find this pore in any of the species with hyperstomial
ooeicles other than in *Bugula simplex* (in the endozooidal ooeill of the *Securiflustra
securifrons* the connection between the ooeial and visceral coeloms was described and
depicted).\textsuperscript{226}

Nobody challenged Silén’s generally accepted opinion during next three decades,\textsuperscript{227-228}
except Hans Hass\textsuperscript{229} who provided very diagrammatical shemes of the ‘reteporid’
ooecia, formed by the daughter zooid.
Anna Hastings discussed interesting points concerning the simultaneous presence of the hyperstomial and the ‘reduced and vestigial ovicells’ within the same cheilostome genera. Hugo Moyano presented the diagrammatical schemes of the oovicells from four ascophoran genera, but gave not much detail on their structure. John Ryland discussed terminological problems accumulated since the works of Jullien, Levinsen, Canu and Bassler and Silén, and selected the most appropriate terms that are currently in use. Robert Woollacott and Russel Zimmer investigated ovicell structure in Bugula neritina (Figure 9) and completely verified the data of Calvet. They also studied a placental analogue. After this, Silén was forced to admit the correctness of Calvet in respect of the species mentioned. However, he stressed that the ooecium inevitably should be formed by the maternal zooid in forms where the daughter zooid is absent in a longitudinal zooidal row (series). Silén suggested that the ooecium is formed in different ways in different taxa. Subsequently, Alan Cheetham, William Banta, Philip Sandberg, Renate Carson, Claus Nielsen, Patricia Cook and Jim Chimonides, Alan Cheetham and Patricia Cook, Ekaterina Lobastova and Andrew Ostrovsky and Scott Santagata and William Banta presented further evidence in favour of ooecium formation from the daughter zooid in several cheilostome families (Calloporidae, Phidoloporidae, Bitectiporidae, Candidae, Bugulidae, Microporellidae, Cribrilinidae, Petraliellidae). Among others, the representatives of the same genera and, sometimes, the same species, which have been studied by Silén, were investigated. Nielsen studied, amongst others, Scrupocellaria varians Hincks, 1882, Bugula pacifica Robertson, 1905 and Fenestrulina miramara Soule, Soule & Chaney, 1995 (described as F. malusii) (Figure 10). Following Levinsen, he showed that the initial stage of ovicell formation can be either bilobate or single in different taxa. Lobastova and Ostrovsky and Santagata and Banta studied sections of S. scabra, Callopora aurita and S. ferox Busk, 1852 correspondingly. In all these cases the ooecia formed by the daughter zooid were found.
Parental care in cheilostome bryozoans: historical review.

Because calcification of the incipient entoecium starts from the transversal wall between the maternal (proximal) zooid and the distal bud (or zooid), and thus, the wall and the entoecium are continuous, one more explanation of the ooecial formation has been raised. It was suggested that the entoecium derives from the maternal zooid, and the ectoecium from the daughter zooid. The first mention of this, one can find in the paper of Levinsen, who wrote that ‘it is obvious that the inner layer (the endo-ooecium) can be regarded as a continuation of the distal [transversal] wall while the outer layer (the ecto-ooecium) is formed from the front wall of the distal zooecium’. Since the papers of Dorothy Soule and Jean-Georges Harmelin, this point of view has reappeared in the literature as a compromise between the two earlier conflicting opinions. For instance, Harmelin suggested this in the calloporid, Corbulella maderensis (Waters, 1898) (as Crassimarginatella), and Cook did the same for Doryporella alcicornis (O’Donoghue and O’Donoghue, 1923) and Scrupocellaria (Candidae). Nonetheless, Ostrovsky came to the conclusion that although the entoecium and transverse wall are continuous, one should consider the ooecial fold as a whole structure, and all the authors mentioned have dealt with ooecia formed by the daughter zooid.

Patricia Cook and Peter Hayward outlined different variants of the brood chamber formation within Cheilostomata, describing and illustrating the ovecells in some Lekythoporidae with unusual zooidal orientation. Judging from their figure, the ooecium is formed by the maternal autozooid in this case, although the polypide orientation shows that the ooecium obviously originated at the expense of the distal zooid in the ancestral forms.

As important landmark the paper of John Bishop and Bridgette Househam should be considered. In the genus Puellina they found the ovecells of three categories ‘based on the timing of production of the ovecell in relation to the budding of the maternal autozooid and of the zooid distal to it’. The ovecell ‘is a proximal component of the distal zooid’ in category A, and ‘of the kenozooid ... distal to the maternal autozooid’ in category B. ‘The ovecell appears to be a distal component of the maternal zooid’ in category C.
Ostrovsky investigated the structure and development of the ovicells in *Cribrilina annulata* (Fabricius, 1780) and *Celleporella hyalina* (Linnaeus, 1767), and analysed the current state of the ovicell research in detail. He recognized two main types of ovicells among the Cheilostomata, assigning ovicells of categories A and B to the 1st type, and of category C to the 2nd type.

However, since *Callopora dumerilii* has not been restudied, it was impossible to deny or ignore the statements of Silén, who sectioned *Scrupocellaria scabra* and reported on the ooecia formed by the maternal autozooid in this and other cheilostomes. Andrew Ostrovsky and Priska Schäfer investigated ovicell structure (anatomy and external morphology) in two calloporid bryozoans, *C. dumerilii* and *C. lineata* (Linnaeus, 1767) (the type species of the genus *Callopora* Gray, 1848), with the aim to finally resolve the long-term controversy described. It was confirmed that ovicells are formed by the daughter zooids in both these species. The early stages of ovicellogenesis in *C. lineata* were studied, and there were no knobs or any other outgrowths found. An analysis of text-figure 18 of Silén (representing a longitudinal section of the ovicell in *Scrupocellaria scabra*), and the accompanying description, showed that Silén could not find communication between an ooecial fold and a distal zooid because of the strong shrinkage of the specimen fixed in alcohol. Studing three other species, Silén did not make sections and referred to the wrongly interpreted structure of *Scrupocellaria*. Interestingly, Silén himself explained the difference between his and Calvet’s results using the same reason: he suggested that the latter author worked with shrinked material. On the basis of these and previous findings (see above) Silén’s conclusions concerning the ovicell structure were regarded as incorrect, and his generalization was rejected. It was stressed that both ovicell types exist among Cheilostomata, and sometimes within one and the same taxa, and further research is necessary to verify which types are characteristic for different taxa. Ostrovsky and Schäfer came to the conclusion that since there are no special pore-cell complexes associated with the ooecial communication pore(s), there is only a formal reason to credit ooecium as being a heterozooid. It is not a true kenozooid.

It should be mentioned here, that there is no clear distinction between the ooecia formed by the distal kenozooid and by the maternal zooid in many instances, since the kenozooid can be flat, non-prominent distally and not seen from the above. In such cases, the maternal zooid forms the flat, distal kenozooidal bud that, in its turn, forms the ooecium. Thus, the kenozooidal frontal wall serves as a floor of the brooding cavity, and the ooecium itself is an outgrowth of this basal kenozooid. The majority of so-called ‘terminal’ ovicells have such structure, but they are traditionally considered as being formed by the maternal autozooid. However, it would be better to reserve this definition for ooecia, where the distal kenozooid is strongly reduced (like in *Cribrilina annulata* and *Cauloramphus spinifer*).

Ultrastructure and development of the ovicells in a few more calloporids (*Callopora*, *Tegella*, *Corbulella*) have been further studied by Ostrovsky, Schäfer and Gordon. Paul Taylor and Ken MacKinney, and Ostrovsky investigated the structure of so-called ‘costate’ ovicells in some fossil and Recent Microporoidae and Cribrilinidae.
correspondingly, and discussed the origin of ovicells in cheilostomes. Ostrovsky and Taylor\textsuperscript{302} described four calloporid species with brood chambers formed by spines of the daughter zooid in the Mid-Cretaceous deposits of England and Germany. Such primitive ovicells looked like a cage, on one hand, supporting Harmer’s hypothesis on the ovicell originated from mural spines,\textsuperscript{303} and, on the other, mirrored Nielsen’s view\textsuperscript{304} about ovicells of the category A (ooecium is formed by the distal autozooid) as a basic form in ovicell evolution. Further more these authors published a detailed survey on all fossil and Recent forms known, whose brood chambers consists of spines or costae.\textsuperscript{305} Evolutionary scenarios on the ooecial transformations in Calloporoidae, Monoporellidae, Macroporidae and Cribrilinidae were proposed. The acanthostegal brood chambers of \textit{Tendra} were stated to be an example of independent evolution of brooding in the Cheilostomata.\textsuperscript{306}

The development of the ooecium has additionally been investigated in the earliest cheilostome brooders belonging to the genus \textit{Wilbertopora}. Interestingly, it is different from ovicellogenesis in the Recent calloporids, more reminicent of ooecial formation in some Recent cribrimorphs, for example, \textit{Puellina}.\textsuperscript{307}

2. Other types of external brood chambers with calcified walls

Wassiliy Repiahoff\textsuperscript{308}, Vladimir Reingard\textsuperscript{309} and Alexandr Ostroumoff\textsuperscript{310} investigated unusual brood-chambers from flattened mural spines (‘acanthostegous ooecia’ according to Levinsen\textsuperscript{311}) in \textit{Tendra zostericola} Nordmann, 1839, that were described first by M. Alexander Nordmann in 1839.\textsuperscript{312-314} Although being mistaken in the understanding of the construction of these brood-chambers and believing that embryos were developed inside the body cavity of specialized zooids, Repiahoff suggested that they play the role of ovicells, and Reingard was the first who stated that ‘…\textit{Tendra} will represent a transition between bryozoans without ovicells to those, that possess them…’.\textsuperscript{315} Ostroumoff\textsuperscript{316} first understood that embryos are brooded in the space \textit{[epistege]} between the frontal membrane and the over-arching spines in \textit{T. zostericola}.

Busk\textsuperscript{317} recorded brood chambers in \textit{Alysidium parasiticum} Busk, 1852, that were later studied by Levinsen\textsuperscript{318-319} in detail. Such an ‘ovicell’ consists of two semispherical hollow plates or ‘valves’, forming a protecting chamber in the distal part of the maternal zooid. Each ‘valve’ is connected with the maternal zooid by the cuticular base that permits them to bend outwards. Levinsen called these brood chambers ‘bivalvular’ or ‘double-valved ooecia’, suggesting first that they correspond to two \textit{[oral]} spines in non-fertile zooids.\textsuperscript{320} However, in his next paper he showed that ooecial ‘valves’ are true kenozooids whose cavity is separated from the visceral coelom of the maternal zooid by the pore-plate.\textsuperscript{321}

The ‘bivalve’ appearance of the brood-chambers is also characteristic of the genera \textit{Scruparia}, \textit{Alysidium} and \textit{Thalamoporella}, and that is why Libbie Hyman\textsuperscript{322} united them in the group of ‘two-valved’ ovicells.\textsuperscript{323-324} She also believed that the ‘synecium’ — an unusually complexed brood chamber of eight hollow flat plates discovered by O’Donoghue in \textit{Catenicula}\textsuperscript{325-326} was ‘related to the two-valved type’.\textsuperscript{327} Later Cook\textsuperscript{328} modified the term to ‘synoecium’.
Levinsen first called the ovicells of *Thalamoporella* ‘epistomial’, but later considered them as being hyperstomial. In his turn, Harmer suggested that ovicells in *Thalamoporella* are non-homologous to hyperstomial ovicells in other Cheilostomata, proposing that they evolved from the ‘adoral tubercles’ of the maternal zooid. Waters called ovicells ‘bilobate’ in this genus, but stated that ‘there is no complete divisional wall in’ them.

3. Internal brood chambers and intracoelomic brooding

The first observations of internal brooding in Cheilostomata were made by Grant in *Carbasea carbasea*. Grant saw eggs, developing embryos and larval release, but did not recognize the brooding sac, which has not been studied yet. Similarly intrazooidal development of the embryo was recorded by Smitt in *Cryptosula pallasiana* (as *Lepralia*). Later Louis Calvet described the internal brood chamber (pouch or diverticulum of the vestibulum), recording the muscles attached to its walls and the fertilisation envelope surrounding the early embryo in this species. It was stated that the envelope disappears later in development.

Waters recorded the internal brooding in several species from the genera *Watersipora* (as *Lepralia*), *Adeona*, *Adeonella*, *Adeonellopsis*, *Laminopora* and *Beania*, and discussed the possible value of such brood chambers for bryozoan classification. Embryos were said to be brooded inside the internal sac, placed in the distal part of the zooid (a specialized, and often enlarged ‘gonoecium’ in Adeonidae and Adeonellidae). In contrast with *Watersipora*, in which embryos were described and depicted being enveloped by the ‘thin-walled [brooding] sac’, all other cheilostomes mentioned have been characterized by the ‘thick-walled sac’. Judging from Waters data (that embryos occupied half or even most part of the zooidal cavity in four ‘adeonid’ genera, but the eggs found were from small to moderate size), there should be extraembryonic nutrition in them. In the following paper Waters described and depicted hypertrophied epithelium of the brooding sac in *Adeonella platalea* (Busk, 1854). In *Poricellaria ratoniensis* (Waters, 1887) (as *Diplodidymia complicata*) the small egg begins growth within the small brooding sac, hanging below the zooidal operculum. Further more they both enlarge to such an extent that they fill most of the zooidal cavity, but Waters did not understand that he had discovered an extraembryonic nutrition in both these species. However, he obviously realised this in the case of *Catenicella elegans* (Busk, 1852) (as *Vitaticella*), since he wrote that there are ‘several fleshy bands or tubes by which … material for growth is transferred to the ovicell’, containing large embryo in this species.

Additionally, Waters found embryos surrounded by a membrane inside some zooids of *Steginoporella magnilabris* (Busk, 1854) (as *Steganoporella*), calling such brooding structures ‘internal ovicells’. He also found an embryo brooded internally in *Chlidonia pyriformis* (Bertolini, 1810) (as *C. cordieri*) in sections, but did not mentioned the brooding organs in his paper. Marcus made a similar finding while studying *Steginoporella haddoni* (Harmer, 1900) (as *Steganoporella*). Later, Harmer described internal
brooding in ‘a spacious, thin-walled ovisac’ in *S. magnilabris*. He mentioned that it extends nearly to the zooidal basal wall, attaching ‘to the lateral walls … by a number of muscle-fibres’, but was not able to recognize whether it was connected with a vestibulum. Studing *S. buskii* (Harmer, 1900) (as *Steganoporella*), Cook345 recorded the internal brooding and noted that the cryptocyst is strongly reduced as the embryo grows which could be evidence of extraembryonic nutrition.

Marcus346 discovered viviparity (intracoelomic embryonic development) in *Synnotum* sp. (as *S. aegyptiacum*). He stated that the embryo ‘is nourished by the follicle cells which receive alimentary material from other parts of the colony and the maternal brown body, transported by the mesenchymatous tissue-cords’.347 The late embryo is 50-60 times larger than the mature ovum before cleavage, that is evidence of extraembryonic nutrition.

Hastings recorded ‘the zooecia …[with] embryos in the body-cavity, although they had no ovicells and showed no external difference from the non-fertile zooecia’ in *Oshurkovia littoralis* Hasting, 1944 (as *Umbonula verrucosa*).348 Later she mentioned ‘internal ovisacs’ in this species.349 The data were confirmed by David Eggleston350 who noted the internal brooding of several embryos simultaneously in *O. littoralis* (as *Umbonula*). The structure of the brooding organ is unknown, however.

Mawatari351 studied some aspects of the sexual reproduction in *Watersipora subtorquata* (d’Orbigny, 1842) (as *W. cucullata* (Busk)). He mentioned ‘the embryo sac’, which envelops the developing embryo, and his figures 20-38 and 44 show that it is evagination of the vestibulum.352 Similarly, Cook353 mentioned ‘membranous diverticula housed within zoooid body wall’ as a brood chamber in dimorphic female zooids of *Tropidozoum cellariiforme* Harmer, 1957.

Dyrynda discovered the intracoelomic brooding in *Epistomia bursaria* (Linnaeus, 1758).354-355 The embryonic cleavage starts inside the ‘follicle’ and the embryo increases about 1000 fold in volume, which is evidence of extraembryonic feeding. Finally it was suggested that the combination of endocoelomic brooding, larval viviparity and one polypide generation per zooid may be a primitive feature from which recycling and extracoelomic brooding may have evolved.

Recently, the anatomical structure of internal sacs for embryonic incubation has been studied in three cheilostome bryozoans, *Nematoflustra flagellata*, *Gontarella* sp. and ‘*Biflustra*’ *perfragilis* by Ostrovsky et al.356 In the evolution of brood chambers in the Cheilostomata, such internal sacs for embryonic incubation have been considered as a final step, being the result of immersion of the brooding cavity into the maternal zooid and reduction of the protective fold (ooecium). Possible stages and reasons for this transformation have been discussed, and the hypothesis of Santagata and Banta357 that internal brooding evolved prior to incubation in ovicells has been rejected.

4. External brooding sacs

Waters358 discovered the external brooding sacs (that he called ‘ovicells’) in *Aetea sica* (Couch, 1844) (as *A. anguina* forma recta) and *Aetea anguina* (Linnaeus, 1758).359 He
figured them on the top of the dorsal side of the erect portion in the maternal zooids. Alice Robertson recorded this ‘membranous bag’, being situated on the frontal side of the zooid below the operculum in the same species. She suggested that the curvature of the tubular part of the zooid ‘afford[s]... protection to the delicate ooecium and its contents’. Levinsen, considering the unusual appearance and position of this structure, concluded that ‘the supposed ovicellular wall [is] only ... a shell membrane surrounding the egg’.

Waters challenged Levinsen’s opinion, in saying that the position of all the brood chambers he saw, is very consistent. He referred to the paper of Raymond Osburn, who also found the brooding sacs at the top of the zooids, distally from the operculum. Further researchers supported both opinions: in *Aetea anguina* the brooding sac (ovisac) has been described on the frontal membrane, proximally to the operculum by Hastings, and distally to the operculum by Marcus. Hastings noted that embryo sacs with the early embryo are closely applied to the zooidal frontal membrane, whereas those with an advanced embryo are free from the membrane except to the distal narrow attachment. She also depicted this narrowest part in the ovisac with an embryo and in an empty one. Similar ‘commencement of the ovicell’ has been mentioned by Waters, and depicted by Shizuo Mawatari, who described ‘the membranous ovicelligeous sac at the distal extremity on one side of the frontal membrane just proximal to the opercular valve’. Patricia Cook, who observed the brood chambers on the zooidal dorsal side only, stated that they were covered by a cuticular layer. Additionally, in one population of *A. anguina* she also found the slight proximal and ventral calcification of its wall on the side apposed to the zooidal wall in sections. She suggested that the ovisac is a product of the exterior zooidal wall, and not of the external diverticulum from the tentacle sheath. Cook also noted that in a significant number of zooids two embryos were contained and released simultaneously from the same brooding sac. The inconsistency in positioning of the embryo sacs, its presence during reproductive periods only and an absence of the opening could be considered in favour of Levinsen’s hypothesis. In contrast, partial calcification of the ovisac wall and embryonal pairs met may be evidence against this hypothesis. Information concerning the ovisacs found in other species of the genus *Aetea*, is in the books of Prenant and Bobin, and Ryland and Hayward.

A similar type of brooding in the ‘membrane sac above the orifice’ was recorded by Eggleston in *Eucratea loricata* (Linnaeus, 1758). Leo Stach discovered external ‘brood-sac’[s] in *Carbasea indivusa* Busk, 1852. Each brooding zooid possesses three to seven such sacs. The author stated that they ‘are developed from the distal portion of the tentacle-sheath forming the inner wall of the operculum.’ Larvae escape from the sacs supposedly through the rupture of its wall. ‘1-2 membrane-bounded embryos’ attached to the frontal membrane adjacent to the zooidal opening were recorded by Dennis Gordon in *Leiosalpinx australis* (Busk, 1884).

In conclusion, it should be admitted that in spite of two and half centuries of investigations, the general picture of cheilostome brood chamber structure and development is still very incomplete. The largest existing source of data on that topic is Levinsen’s
illustrations and, in a lesser extent, his descriptions. As mentioned above, this prominent researcher studied the complete, sectioned and developing ovicells in more than 80 cheilostome species belonging to 62 genera, but since he worked with cleaned bryozoan skeletons only, it is often very difficult to estimate the correctness of the conclusions he made. As a result, Levinsen’s data were never used, and careful restudy is necessary in this case. Ovicell anatomy should also be reinvestigated in some recently studied species as well. For instance, Calvet’s schematical drawing of the ovicell in Fenestrulina malusii (as Microporella) made from the section of decalcified animal, differs from the diagram of the species Fenestrulina miramara (described as F. malusii) presented by Nielsen who only used the skeletal parts. It is clear now that a combined approach is the only adequate method for this kind of research. Further accumulation of data on brooding structures is necessary to make progress in our understanding of bryozoan phylogeny and evolution of their reproductive patterns.

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Notes


2 J.S. Ryland, ‘Physiology and ecology of marine bryozoans’, in Advances in Marine Biology,
7 Woollacott and Zimmer, note 3.
13 Ellis, note 11, pages 33-39.
15 Ellis, note 11, page 35.
16 Ellis, note 11, Plate XIX, A.
17 Ellis, note 11, Plate XV.
18 P.S. Pallas, Elenhus Zoophytorum sistens generum adumbrationes generaliores et specierum cognitarum succinctas descriptiones cum selectis auctorum synonymus (P. van Gleef, La Hagae, 1766), xvi, 451 (36).
19 Pallas, note 18, page 36.
20 J. Ellis and D. Solander, The natural history of many curious and uncommom Zoophytes, collected in various parts of the globe by the late John Ellis, systematically arranged and described by Daniel Solander, Vol. B, (White and Son, London, 1786), xii, 208 (11).
21 Ellis and Solander, note 20, pages 19-20.
22 Ellis and Solander, note 20, page 29.
23 Pallas, note 18.
24 J.V.F. Lamouroux, Histoire des Polypiers Coralligènes flexibles, vulgairement nommés Zoophytes (Poisson, Caen, 1816), 559.
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Annales des Sciences Naturelles, Zoologie 2, VI (1836), 5-53.
27 J. Reid, ‘Anatomical and hysiological observations on some Zoophytes’, The Annals and Magazine of Natural History, 16 (1845), 385-400.
33 Huxley, note 32, page 192.
37 Hincks, note 36, page XCIII.
38 Hincks, note 35.
39 Hincks, note 36, page 20. In this paper Hincks also admitted that he mistook the ‘germ-capsules’ [brown bodies] for ‘a sort of winter egg[s]’.
42 Internal embryonic development, accompanied by degeneration of the polypide, was also known among Ctenostomata, which possess no ovicells (see, for instance, papers of Claparède, note 63, and Hincks, note 35).
43 Hincks, note 36, page XCII.
45 Hincks, note 36.
46 Hincks, note 35.
47 Hincks, note 36.
50 W.J. Vigelius, ‘Morphologische Untersuchungen über Flustra membranaceo-truncata Smith’, Biologisches Centralblatt, 3 (23) (1884), 705-21 (page 50, non-numbered text-figure).
52 Reid, note 27.
53 See also: Hincks, note 35.
54 Huxley, note 32.
55 Nitsche, note 48.
56 See also: L. Joliet, ‘Contributions à l’histoire naturelle des Bryozoaires des côtes de France’, *Archives de Zoologie expérimentale et générale*, 6 (1877), 193-304.
59 G. Allman, *A monograph of the fresh-water Polyzoa, including all the known species, both British and foreign* (Ray Society, London, 1856), 120.
60 Busk, note 30, page 5.
61 See also: L. Calvet, ‘Contribution à l’histoire naturelle des Bryozoaires Ectoproctes marins’, *Travaux de l’Institut de zoologie de l’Université de Montpellier, Nouvelle Série*, 8 (1900), 1-488.
62 Communication between the incubation cavity and visceral coelom of the maternal zooid was later suggested by H. Prouho, ‘Contribution à l’histoire des bryozoaires’, *Archives de Zoologie expérimentale et générale*, 10 (1892), 557-656.
64 Joliet, note 56.
65 Nitsche, note 48.
66 In *Tendra zostericola* Repiachoff recorded the very beginning of the acanthostegal brood chamber formation in the zooidal buds that were preceded by the young zooids with ovarium. See W. Repiachoff, ‘Zur Entwicklungsgeschichte der *Tendra zostericola*’, *Zeitschrift für wissenschaftliche Zoologie*, 25 (1875), 129-142.
68 Vigelius wrote that the ovicell appears slightly later than an ovary in *Bugula calathus* (see note 78).
69 In *Escharella immersa* (Fleming, 1828) (referred as *Lepralia peachii*) and *Scrupocellaria scruposa*, Smitt (note 41) found eggs inside the zooids, and a developing embryo in the ovicell of *E. immersa*.
70 Vigelius, note 50.
73 See also page 50, non-numbered text-figure, and Plate III, figures 42-45 in Vigelius, note 50.
74 Vigelius (note 71) mentioned that in *Bicellariella ciliata*, unlike in *Terminoflustra membranaceotruncata*, the neighbouring zooids do not take part in the formation of the ovicell.
76 Calvet, note 61.
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79 See also: Calvet, note 61.
81 Woollacott and Zimmer, note 3.
83 Reid, note 27, page 398.
84 ‘Thickened ... wall [of the ooecial vesicle], that shows very distinctly’ also mentioned in Hincks (note 34, page 280).
86 See also: J. Jullien and L. Calvet, ‘Bryozoaires provenant des campagnes de l’Hirondelle (1886-1888)’, *Résultats des campagnes scientifiques accomplies sur son yacht par Albert Ier Prince Souverain de Monaco*, 23 (1903), 1-188.
87 Jullien, note 85.
89 Delage and Hérouard, note 75.
90 Nitsche, note 48.
91 Vigelius, note 71.
93 Harmer, note 92, page 283.
94 For details see Ostrovsky, note 6.
95 Harmer, note 92, page 301.
96 A. Waters, ‘Supplementary report on the Polyzoa collected by H.M.S. Challenger during the years 1873-1876’, *Report on the Scientific Results of the voyage of H.M.S. Challenger during the years 1873-1876*, Zoology, 31 (1889), 1-41.
100 Waters, note 77.
101 Waters, note 77.
102 Y. Okada, ‘Notes on some species of *Retepora* and *Adeonella* occuring in Japan, with description of one new variety and five new species’, *Annotationes Zoologicae Japonenses* 9 (V) (1920), 613-634.


Calvet, note 61.

Calvet, note 61, page 132, Plate II, figure 14, Plate III, figure 5.

Nitsche, note 48.

See: Prenant and Bobin, note 51.


Calvet, note 61, page 58, text-fig. 10.

Calvet (note 61) called those muscles that opened the ovicell opening - ‘retractors’, and those that expanded the brooding cavity – ‘dilatators’. He also wrote that the number of muscle bundles increased during embryonal development. It is possible that he confused some of them with funicular strands.

In the calloporid *Amphiblestrum flemingii* Calvet (note 61, Fig. 45) illustrated cells of the inner wall of the ooecial vesicle as larger than all other epithelial cells. The same impression is gained from his scheme of the flustrid *Securiflustra securifrons* (fig. 44), however, this requires checking.

Waters, note 98.

Levinsen, note 72.

Harmer, note 92, page 300.


Levinsen, note 72.

Levinsen, note 14.


The word ‘ovicell’ could imply a zooid [cell], producing an egg [ovum].

Levinsen, note 14, page 60.

Levinsen, note 14, page 60.

Levinsen, note 14, pages 56, 59.

Calvet, note 61.

Levinsen, note 14, Plate XXIV, figure 13.

Levinsen, note 118.

Levinsen, note 119.

Levinsen, note 14.
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133 Levinsen, note 72.
134 Levinsen, note 14.
135 Levinsen, note 72.
137 Levinsen, note 14.
138 Jullien, note 85.
139 Levinsen, note 14, pages 60-61, see also below.
140 Levinsen, note 14.
142 Calvet, note 61, text-figure 10.
144 See also: R.S. Bassler, ‘The Bryozoa, or moss animals’, Reports of the Smithsonian Institute, 2633 (1922), 339-80.
146 Canu and Bassler, note 143.
148 Canu and Bassler, note 143.
149 Canu and Bassler, note 143.
150 Ryland, note 1.
152 Levinsen, note 14.
153 Harmer, note 111.
155 Calvet, note 61, text-figure 10.
156 Harmer, note 111, figure 1C.
157 Harmer, note 92.
158 E. Marcus, ‘Mosdyr (Bryozoa eller Polyzóa)’, Danmarks Fauna, 46 (1940), 1-401 (figure 54).
159 A. Gerwerzhagen, ‘Untersuchungen an Bryozoen’, Sitzungsberichte der Heidelberger Akademie der Wissenschaften, Mathematische-naturwissenschaftliche Klasse B, 9 (1913), 1-16 (text-figure 1).
160 Pergens, note 88.
164 P.E.J. Dyrynda and J.S. Ryland, ‘Reproductive strategies and life histories in the cheilostome


167 R. Zimmer (pers. comm. in Reed, note 213).


170 Marcus, note 169, Plate 4, figure 11.


172 Calvet, note 61.


174 Silén, note 161.

175 Silén, note 173, figures 18-19.

176 Silén, note 161.

177 In the 1945 paper, it is mentioned as *Scrupocellaria scruposa* (Linnaeus, 1758), probably by mistake.

178 Calvet, note 61.

179 Levinsen, note 118, Plate I, figures 8-9.

180 Levinsen, note 119, Plate I, figures 21-22.

181 Levinsen, note 14, Plate II, figures 5a-f.

182 Levinsen, note 14, Plate XVII, figure 3a.

183 Levinsen, note 14, Plate IX, figure 3a.

184 Levinsen, note 14, Plate XXIV, figure 16.

185 Levinsen, note 118, Plate II, figure 24.

186 Levinsen, note 119, Plate IV, figure 19.

187 Levinsen, note 14, Plate IX, figures 5a-h.

188 Levinsen, note 14, Plate IX, figures 6a-c.


190 See also: Ryland, note 9.

191 For review and discussion see also: Woollacott and Zimmer, note 3.

192 See captions for Text-fig. 20-24 in Silén, note 173.

193 Harmer, note 92.


195 Silén, note 161, page 17.

196 Silén, note 8.

197 For further discussion see Ostrovsky, note 6.


Prenant and Bobin, note 51.


Ryland and Hayward, note 5.


Powell, note 205.

Criticised by Ryland, note 1.

Harmer (note 111) called the ooecial vesicle ‘membranous vesicle’, and Cori (note 171) termed it ‘Untere Blase des Ooeciums’.

Silen, note 161.

Calvet, note 61.

Hyman, note 199.

Brien, note 200.

Prenant and Bobin, note 51.

Calvet, note 61, figure 44.

228 J.S. Ryland, ‘Polyzoa’, *Catalogue of main marine fouling organisms (found on ships coming into European waters)*, 2 (1965), 1-83 (figure 1).


232 Ryland, note 1.
233 Jullien, note 85.
234 Levinsen, note 72.
236 Canu and Bassler, note 143.
237 Silén, note 173.
238 Silén, note 161.
239 See also: Ryland, note 2.
240 Woollacott and Zimmer, note 3.
241 Calvet, note 61.
243 Silén, note 8.
248 Nielsen, note 163.
Society of America (Boulder, Colorado) and University of Kansas (Lawrence), 1983), 138-207.


253 Santagata and Banta, note 4.

254 Nielsen, note 163.

255 Nielsen, note 249.


257 Levinsen, note 14.

258 Lobastova and Ostrovsky, note 252.

259 Santagata and Banta, note 4.

260 Nielsen, note 249.

261 See, for instance: Ryland, note 9.

262 Reed, note 214.

263 Mukai, Terakado and Reed, note 216.

264 Levinsen, note 72.


268 Cook, note 10.

269 Cook, note 166.

270 Ryland, note 9.


273 Cook and Chimonides, note 250.


277 Harmelin, note 266.

278 Cook, note 10.
Ostrovsky, note 6.

For further discussion see also: Nielsen, note 163.


Cook, note 10.

P.L. Cook, P.J. Hayward, ‘Notes on the family Lekythoporidae (Bryozoa, Cheilostomata)’, *Bulletin of the British Museum (Natural History), Zoology*, 45 (2) (1983), 55-76 (55, 57, Fig. 1).


Bishop and Househam, note 284, page 4.

Bishop and Househam, note 284, page 4.

Bishop and Househam, note 284.

Bishop and Househam, note 284.

Silén, note 173.

Silén, note 161.

Ostrovsky and Schäfer, note 281.

Silén, note 173.

Silén, note 161.

Silén, note 173.

Silén, note 161.

Also suggested by Harmer (note 92) and Silén in his later work (note 8).

See similar opinion in Ryland, note 276.

Ostrovsky, note 6.


Harmer, note 92.

Nielsen, note 249.


See also section “Other types of external brood chambers with calcified walls”.

Ostrovsky and Taylor, note 105.


311 Levinsen, note 72.


313 For further details see: M.W. Paltschikowa-Ostroumowa, ‘Kurze Bemerkung über den Ovidukt bei den Bryozoen’, *Zoolologischer Anzeiger*, 65 (1926), 100-102.


315 Reingard, note 309, page 25.

316 Ostroumoff, note 310.

317 Busk, note 30.

318 Levinsen, note 72.

319 Levinsen, note 14.

320 Levinsen, note 72.


322 Hyman, note 199.

323 Earlier Harmer (note 111) compared ovicells in *Thalamoporellidae* with those in *Alysidiidae*.


327 Hyman, note 199, page 337.

328 Cook, note 10, page 200.

329 Levinsen, note 72.


331 Harmer, note 111.

332 Waters, note 99, page 142.

333 Immersed and endozooidal ovicells are considered in the section “Ovicells, oviposition and placental brooding”.

334 Grant, note 29, page 342.

335 Smitt, note 40.

336 Calvet, note 61.

337 Waters, note 99.

338 A. Waters, ‘A structure in *Adeonella (Laminopora) contorta* (Michelin) and some other Bryozoa, together with remarks on the Adeonidae’, *The Annals and Magazine of Natural History*, 8 Series, 9 (53) (1912), 489-500.

339 Waters, note 99, Plate XV, figure 4.

340 Waters, note 77.
341 Waters, note 77, page 485.
342 Waters, note 77, page 500.
344 Harmer, note 111, page 271.
347 Marcus, note 346, page 232.
349 Hastings, note 230.
351 S. Mawatari, ‘On Watersipora cucullata (Busk) II’, Miscellaneous Reports of the Research Institute for Natural Resources, 28 (1952), 17-27.
352 This was also confirmed by Zimmer (in Reed, note 213), who additionally noted the embryonal enlargement during brooding in Watersipora arcuata Banta, 1969.
353 Cook, note 10, page 200.
357 Santagata and Banta, note 4.
359 Waters, note 77.
361 She believed that the difference in the ‘ooecium’ position is evidence for true distinction between Aetea anguina and A. anguina forma recta.
362 Levinsen, note 14, page 93.
363 Later this opinion was supported by Ström, note 211.
364 Waters, note 77.
366 A.B. Hastings, ‘Polyzoa (Bryozoa). I. Scrupocellariidae, Epistomiidae, Farciminariidae,
Bicellariellidae, Aetidae, Scrupariidae', *Discovery Reports*, 22 (1943), 301-510.


370 Marcus, note 158.

371 Personal communication in Ryland and Hayward, note 110.


374 Waters, note 77, page 464.

375 Interestingly, Mawatari (note 368) cited the monograph of G. Busk, ‘Report on the Polyzoa collected by H.M.S. Challenger during the years 1873-1876’, *Report on the Scientific Results of the voyage of H.M.S. Challenger during the years 1873-1876, Zoology*, 10 (30) (1884), 1-126, as if Busk often observed embryonal sacs in *Aetea*, comparing them with ‘the bag of the pelicans beak’. Unfortunately, Mawatari gave no page number from where he cited this phrase, and I was not able to find it in the Busk’s book. Otherwise, Busk should be credited as the first who recorded these structures in *Aetea*.

376 Mawatari, note 351, page 414.

377 Cook, note 373.


379 Prenant and Bobin, note 51.

380 Ryland and Hayward, note 110.

381 Eggleston, note 350.


383 Stach, note 382, page 397.

384 In the absence of sections, this strongly suggests that the ‘brood-sacs’ are fertilization envelopes sticking to the operculum. Their stalk-like proximal part reminiscent of that in similar sacs in *Aetea*.


386 Levinsen, note 14.

387 Discussed in Silén, note 161.

388 Woollacott and Zimmer, note 3.

389 Calvet, note 61, text-fig. 21.

390 Nielsen, note 249, figure 20.