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Sexual reproduction in gymnolaemate Bryozoa: history and perspectives of the research

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1. Introductory note
2. Brief characteristic of the sexual reproduction in Bryozoa
3. 18th and 19th centuries – primary accumulation of data and first reviews
4. First half of the 20th century – more results
5. Second half of 20th century – a period with large reviews and new discoveries
6. Recent works
7. General conclusions and future research
8. Acknowledgements
Appendix (Chronological list of papers and gymnolaemate species, in which different aspects of sexual reproduction have been either studied or observed)

1. Introductory note

The Bryozoa are a mainly marine phylum of oligomerous coelomate invertebrates with a long fossil history stretching back to the Lower Ordovician. They form colonies that are frequently a conspicuous part of the sessile epifauna in many marine habitats, from the intertidal to depths of 8000 m. Bryozoans are active suspension feeders, ingesting living and non-living particles from the surrounding medium. Many species are structurally significant in seafloor biotopes, forming bushy and coral-like growths that are ecologically important as habitats for a wide range of other organisms.[1-2]

Apart from the obscure phylogenetic affinities of Bryozoa that are a long-term source of scientific interest and speculation, there are a remarkable array of reproductive and

developmental patterns within the phylum, ranging from planktotrophy to lecithotrophy, and from viviparty to brooding, and extra-embryonic nutrition.[3] This diversity affords opportunities for comparative and experimental studies, and gives insight into the role of larval dispersal and hence gene flow in evolutionary diversification.[4] The variety of reproductive patterns and larval types offers a wide scope for speculation on the evolutionary trends of sexual reproduction of marine invertebrates in general. Owing to a rich fossil record, where bryozoans with different strategies can be recognized, we can explore the relationship of recent data to the past, and make comparisons of evolutionary fate with those of other similar marine organisms.

Research on the sexual reproduction of marine bryozoans has attracted zoologists since the beginning of the 19th century. Existing reviews on the topic[5-14] show that since this time considerable information has been accumulated. However, there is no single historical review that represents the key names and works published since the 19th century, and early 20th century knowledge has never really been evaluated properly. Many early scholars analyzed and reassessed existing data, but most of these works, especially short papers, have been often neglected if not forgotten. One can also find reviews in some old[15-19] and more recent monographs and textbooks,[20-24] but little attention has been paid to these as most of them were written in German or French. An attempt to review both old and recent literature concerning brooding structures and oviposition in Cheilostomata, and fertilization in Bryozoa has recently made by Ostrovsky (see this volume).[25-26] Similarly, in this review we aim to chronicle the main steps in the history of the research of sexual reproduction (origin of the germ cells, gonado- and gametogenesis, fertilization, oviposition and some aspects of brooding) in marine gymnolaemate bryozoans with particular emphasis placed on the observation and recording of different structures and development of the modern understanding of the specific processes involved. It should be stressed that, apart from many data and ideas that have been completely forgotten, later authors sometimes incorrectly interpreted the hypotheses or conclusions of the previous researchers. Sometimes, mistaken traditional opinions survived for many years despite the emergence of new facts and contradicting data as has happened, for instance, in the case of bryozoan fertilization.[27] We aim to highlight these contradictions where appropriate. In an effort towards making the review as comprehensive as possible, we have analyzed many obscure papers and listed small descriptive details in all species studied. This gave us the opportunity to resurrect many forgotten names and facts simultaneously, thus the review represents an integrated picture of the available literature on bryozoan sexual reproduction and associated taxonomic diversity. It should be noted however, that some difficulties were encountered in trying to trace a small number of short papers and some incidental reports on the reproductive organs in several works.

2. A brief outline of the characteristics of sexual reproduction in Bryozoa

The most recent and complete review on bryozoan reproduction was that published by Reed.[28] We have extracted (and modified where necessary) the main items from it in order

to introduce readers to this field of research.

There is wide variation in the manner of sexual reproduction in extant marine Bryozoa (Stenolaemata and Gymnolaemata). Their reproductive system consists simply of the gonads since gonoducts are missing, and gametes are released through the coelomopores. Separation of sexes among colonies has not been documented. All bryozoans are colonial hermaphrodites, with testes (spermatogenic tissue) and ovaries developing either within the same zooid (zooidal hermaphroditism) or in different zooids within the same colony (zooidal gonochorism). Thus, in the marine classes of bryozoans the autozooids in a colony may be sterile, male, female or hermaphroditic, and a colony can be considered as a dynamic system characterized by the different time of appearance, maturation and functioning of gonads in the different generations of zooids. The reproductive activity of zooids, including morphological specialization, is intimately connected with polypide recycling and seasonality that, in turn, are correlated with a length of a colony life and life history. In species with zooidal hermaphroditism, the autozooids may be protandrous, protogynous, or simultaneous hermaphrodites. In species with zooidal gonochorism, the colonies may be protandrous, protogynous, or simultaneous hermaphrodites, and the male and female zooids sometimes exhibit sexual dimorphism. Morphological distinctions between male and female zooids are correlated with spawning and brooding, and may involve the polypide (tentacle crown associated with a gut), the cystid (receptacle of the polypide, body wall), or both. In some species there are gonochoristic and hermaphroditic zooids within the same hermaphroditic colony.

In bryozoans, totipotential cells in the cystid of each zooid may either differentiate as somatic cells to generate a new zooid or to regenerate a polypide, or they may differentiate as germ cells to initiate the process of sexual reproduction. When colonies form there is an alternation of differentiation of totipotential cells into somatic tissue and apparent dedifferentiation of somatic cells into totipotential cells during the modular replication of the zooids. The spermatogonia typically develop within the cystid mesothelium that lines the main body cavity, and the oogonia usually appear between the epithelial and mesothelial layers of the polypide bud. Release of sperm is through the terminal tentacular pores. Fertilization occurs either inside the ovary or in the zooidal coelomic cavity just after ovulation has taken place. Despite the fact that most bryozoans are hermaphroditic, cross-fertilization does normally occur, but self-fertilization was also encountered in some experiments (see below). The release of eggs is via the intertentacular organ or supraneural pore, found in both brooding and non-brooding ctenostomes and cheilostomes (sometimes, within the same genus e.g. in the ctenostome *Alcyonidium*).

The organization of the ovary and the pattern of oogenesis varies throughout the phylum depending upon the particular pattern of sexual reproduction and its consequences for larval nutrition. Three basic patterns have been recognized among the Bryozoa. In the first, and least common pattern, many small oligolecithal eggs are produced simultaneously and spawned freely into the seawater, where each develops into a planktotrophic larva called a cyphonautes. This pattern of reproduction is restricted to relatively few gymnolaemates. Far more common is a second pattern of sexual reproduction, in which

a few large macrolecithal eggs are produced sequentially and develop within a tentacle sheath or in specialized brood chambers. The majority of gymnolaemates follow this pattern. In the third pattern, one or a few small oligolecithal eggs are produced sequentially and receive extra-embryonic nutrition during embryogenesis in specialized brood chambers or when still in the ovary. This pattern is characteristic of some gymnolaemates as well as stenolaemates (and Phylactolaemata, although their bryozoan affinities are currently under question). The second and third patterns both result in short-lived lecithotrophic larvae, and egg development is aided by the nurse-cell in cheilostomes here.

However, it is important to bear in mind that all the generalizations made above are based on the studies of just a handful of species, and that further extensive research is much needed in order to create a comprehensive view of sexual reproduction in marine bryozoans.

3. 18th and 19th centuries – primary accumulation of data and first reviews

During the period of the 18th to the beginning of the 19th century, understanding of bryozoan sexual reproduction was poor, and only represented by a few brief, and often unclear notes in the descriptive works of several early naturalists. Until the middle of the 19th century, as Huxley wrote, even 'the precise position of ... ovaria and testis has not been ... determined'.[29] Analysis of the literature shows that this was true not only for 'cheilostome Polyzoa', but for all Bryozoa. During those times fresh-water bryozoans were chosen for studies much more often than were marine bryozoans, due to their accessibility and also because of the transparency of their body walls. For instance, in the 'Polype à Panache' (first described phylactolaemate *Lophopus crystallinus* (Pallas, 1768)) Trembley[30] observed small spherical bodies moving by cavity fluid from one zooid to another, and suggested that they were eggs. Similar to Reaumur and Jussieu, Trembley also understood statoblasts to be the same as eggs, since these researchers observed the development of the first polyp from them.[31] Statoblasts were considered as eggs even a century later.[32-34]

As for marine bryozoans, Pallas expressed the point of view that 'bullas' (ovicells – chambers for embryonic incubation) were ovaria in encrusting cheilostomes. He speculated that both ovicells and avicularia (zooidal polymorphs) could serve for fertilization, and sometimes called them 'Nectariums'.[35] Ellis agreed with the opinion of Pallas, additionally suggesting that ovicells could detach from a branch, drop and fix to the substratum below, thereby giving rise to a new animal.[36]

The authority and reputation of these scientists was so high that their suggestions were not reconsidered for almost a century. Lamouroux,[37] Milne Edwards,[38] Lamarck,[39] Reid,[40] Johnston,[41] and Hincks[42-44] all thought that ovicells were ovaria.[45] Additionally, some researchers considered brown bodies to be a special kind of egg, finding them in zooids with degenerated polypides.[46-48] However, an accumulation of data on other bryozoan groups, whose representatives had no ovicells (ctenostomes as well as some non-

Figure 1. Robert Edmond Grant (photograph courtesy of Jack Ashby, © The Grant Museum of Zoology, University College London)

ovicellate cheilostomes), contradicted the traditional point of view. For instance, Thompson[49] observed 'an ovum or ovarium' on the body wall inside the autozooid of '*Vesicularia*', and Milne-Edwards[50] also mentioned it there in '*Cellariae*'.

It should be noted here, that until the last third of the 19th century, microanatomical sectioning techniques had not been used by scientists studying Bryozoa. Therefore, observations on the internal structure were restricted to species having a transparent body wall. Also, the strongest magnification available at that time could not be used with thick preparations, whether the tissues were living or fixed. On the other hand, such observations allowed the three-dimensional reconstruction of the animals studied and records were made from specimens that were often still alive.

One of the first detailed descriptions on sexual reproduction in marine bryozoans was made by Robert Edmond Grant (1793-1874) (Figure 1).[51] His paper was one of the most valuable sources of information on this topic for a long time. Studying the cheilostomes *Carbasea carbasea* (Ellis and Solander, 1786) (as *Flustra*) and *Flustra foliacea* (Linnaeus, 1758), he found eggs [oocytes] developing inside the zooids: in the distal part of the cystid beneath the polypide in the first species, and in the proximal part in the second, being unconnected with the polypide. Grant therefore suggested that the eggs were produced by the posterior [basal] zooidal wall. In *C. carbasea* egg formation is accompanied by polypide degeneration, and it was supposed that regeneration took place after egg release

[in fact, Grant may have confused some eggs with embryos, developing inside the internal brood sac in this species; polypide recycling occurs after oviposition]. The mature egg is always single, occupying one third of the cystid volume. Grant carefully described the pattern of the distribution of the egg-bearing zooids throughout the colony. He followed the embryonic growth, larval release, their swimming behaviour and settlement. He was also probably the first to describe larval metamorphosis in cheilostomes. In *F. foliacea* the polypide generally degenerates during the development of the first egg. The mature egg occupies the distal part of the cystid, later being placed further away and becoming surrounded by 'a distinct wide helmet-shaped capsule [ovicell]', that separates 'it from the cavity of the cell [zooid]'. Grant observed moving larvae inside the brood chamber, their release, settlement and metamorphosis, and noted that the polypide undergoes recycling during oogenesis and brooding. It regenerates when the 'egg has escaped from the cell'. Grant concluded that the same zooid repeatedly 'produce[s] the ova and polypi'.[52] Also, he possibly observed spermatozoids, describing them as 'numerous monads and other animalcules busily imployed in consuming the remains of the dead [degenerated] polypus'.[53]

Farre[54] discovered, illustrated and described in detail an intertentacular organ and the movements of its cilia in the ctenostome *Alcyonidium duplex* Prouho, 1892 (as *Halodactylus diaphanus*), and also recorded and depicted it in the cheilostome *Electra pilosa* (Linnaeus, 1767) (as *Membranipora*).[55] This author did not recognize its function, but asked the question 'does it indicate a difference of sex?'[56] He also observed moving spermatozoids inside the zooidal cavity in *A. duplex* and *Walkeria uva* (Linnaeus, 1758) (as *Valkeria cuscuta*), and even saw sperm release in the first species, but called the male cells 'parasites' and 'cercariae', not being able to ascertain the exact locus of their expulsion since the polypide was half-retracted. Farre wrote that they were 'issued from the centre of the tentacula'.[57] Based on this observation, he correctly supposed the existence of communication between the body cavity and the external medium. From four to six embryos ('ciliated gemmules') were found brooded internally in the 'transparent sac' of *A. duplex*. Additionally, 'ova' were recorded inside the zooidal cavity of *Bowerbankia imbricata* (Adams, 1798) (as *B. densa*), but Farre doubted their nature since there were two kinds of them – brown and 'milky-white', and brown 'eggs' were often found inside young zooids with a developing polypide bud.

Johnston[58] briefly discussed the known facts on bryozoan reproduction in the first edition of his famous monograph *A history of the British zoophytes*. Notably he stressed the existing contradiction in opinions on the position of the ovary.

Some observations of Farre were restated and explained by Thomas Hincks,[59] who described the structure of the ciliary intertentacular organ in the cheilostome *Electra pilosa* (as *Membranipora*) and recorded sperm release through it. This is in contradiction with the more recent observations of Silén,[60] who described sperm release through the pores on the tips of the tentacles in two other species of *Electra* (see below). However, the description of Hincks is so detailed and convincing that one can be in no doubt of whether the sperm expulsion may really sometimes possible through the intertentacular organ in

Figure 2. Henri Prouho (photograph courtesy of Jean-Loup d'Hondt)

Electra pilosa. In connection with this Henri Prouho (Figure 2)[61] suggested that this could happen if the rest of the sperm moved out at the end of the reproductive period. Hincks[62] suggested that the intertentacular organ could also be used for the release of eggs after their ovulation and fertilization in the body cavity, and this was later proved by Prouho,[63] who described egg liberation in the ctenostome *Alcyonidium albidum* Alder, 1857. Additionally, Hincks[64] observed sperm in *Bowerbankia* sp., and larval release in *A. hirsutum* (Fleming, 1828) (as *Cycloum papillosum* Hassall).

Kölliker[65] recorded a presence of eggs and sperm in *Alcyonidium* sp. (as *A. gelatinosum* Johnston), and pointed out that the 'cercariae' of Farre were spermatozoids, which he described, measured and precisely depicted. Kölliker believed that the gonads were contained not inside the zooids, but between them in the branches of the colony.

Hassall[66] observed developing embryos, that he called 'ciliated eggs', in groups of six-seven arranged in a circle in *Alcyonidium hirsutum* (as *Cycloum papillosum*). He mentioned that they were surrounded by a thin wall, which was obviously an incubatory chamber. In *Alcyonidium polyoum* (Hassall, 1841) (as *Sarcochitum polyoum*) this author observed larval release.

Van Beneden[67] described and illustrated ovaries containing up to seventeen oocytes, and testes inside the hermaphroditic zooids of ctenostome *Farella repens* (Farre, 1837) (as *Laguncula*). He found an ovary on the body wall, whereas the testis was observed on the funiculus, near its attachment to the stomach. Van Beneden also observed ovulated eggs as well as spermatozoids moving inside the visceral coelom. Additionally, he found a special opening [supraneural pore] near the base of the tentacles, and described the eggs' release. Van Beneden was sure about intrazooidal self-fertilization, and this is the first mentioning of this phenomenon in Bryozoa that we could find. In another paper[68] Van Beneden described and depicted sperm inside the body cavity of *Bowerbankia* cf.

imbricata (as *B. densa*), isolated young polypides of *Flustra foliacea* with an egg, and also eggs and moving embryo inside zooids in *Alcyonidium* sp. (as *Holodactyle diaphane*). In addition, the 'testicule' was recorded in *Flustra* and the sperm was separately illustrated for the two latter species. In *Alcyonidium* sp. Van Beneden recorded eggs, obviously still inside the ovary, in zooids that were generating a new polypide.

Reid[69] observed developing embryos inside the ovicells in cheilostomes *Scrupocellaria reptans* (Linnaeus, 1767), *S. scruposa* (Linnaeus, 1758) (as *Cellularia*), a non-identified cheilostome (as *Flustra avicularis*) and *Bugula flabellata* (as *C. avicularis*). In the latter species he recorded an increase in the thickness of the membranous wall [of the ooecial vesicle] that obviously, was the first observation of an embryophore in bryozoans (see below). Reid stated that ovicells ('ovary-capsules') contain the ovaries.

Johnston[70] expanded a review on bryozoan sexual reproduction in the second edition of his monograph. Based on the data of Grant, Reid and Van Beneden, he stated that bryozoans are hermaphrodites whose eggs are formed from the epithelium of the body wall, and after maturation move to the zooidal cavity. There they are prepared for fertilization, provided by the sperm that forms inside the same zooid too. Following general opinion (see above), Johnston noted that in many genera eggs are formed in the ovicells.

Dalyell[71] observed developing embryos, and swimming and settling larvae in a few cheilostomes, among which were *Carbasea carbasea* (as *Flustra*), *Flustra foliacea* and *Securiflustra securifrons* (Pallas, 1766) (as *Flustra truncata*). In *Bowerbankia imbricata* (as *B. densa*) he described and illustrated mature oocytes in the ovary and an embryo brooded in the tentacle sheath of a zooid without a polypide.

Hancock[72] observed an egg, surrounded by a 'delicate membranous sac' [ovarian wall], in the place of the funicular attachment to the cystid wall in the fresh-water ctenostome *Paludicella* (as *P. procumbens*) (obviously, *P. articulata* (Ehrenberg, 1831)). He also observed moving spermatozoids, an embryonic enlargement inside the 'eneveloping membrane' [introvert] and larval release in *Bowerbankia* sp.

Allman[73] carefully described the shape, position and content of male and female gonads in the phylactolaemate *Plumatella fungosa* (Pallas, 1768) (as *Alcyonella*) and fresh-water ctenostome *Paludicella articulata* (as *P. ehrenbergi* Van Beneden). In the gonads he found numerous eggs and sperm at various developmental stages, and stressed that they simultaneously developed inside the same zooids in these bryozoans, rejecting the opinion of Van Beneden[74] who first stated the gonochoristic nature of the zooids, and then thought that there are male, female and hermaphroditic zooids in one colony.[75] In contrast with *Farella*, the testis was reported on the body wall proximally, in the place of the funicular attachment in *Paludicella*. An ovary, containing numerous oocytes, was found on the body wall being associated with another funicular strand too, but this time in the distal part of the zooid. Allman also described the gametic structure, divisions of spermatogonia, movement of spermatozoids, their concentration in the body cavity and grouping around the ovary. Interestingly, since Allman believed that the polypide and cystid are distinct individuals (zooids), budding one from another, he suggested that ovarium and testis

could be simplified zooids too. Some scientists followed Allman, for instance, Salensky[76] (see also discussion in the papers of Nitsche[77-78] and Joliet[79]). Finally, Allman presented a brilliant review of the studies on fresh-water Bryozoa, pointing out many of the most intriguing discoveries made at this time (for the references of the early works on Phylactolaemata see works of Bronn,[80] Hyatt,[81] Hincks,[82] Vigelius,[83] and Cori[84]).

The true function of the ovicell as a 'marsupial pouch' was first recognized by Huxley,[85] although similar observations were published earlier by Grant.[86] Studying the cheilostome *Bugula avicularia* (Linnaeus, 1758) (as *B. avicularis*), Huxley also found a growing egg [ovary] being 'attached to the funiculus ... close to the stomach' (and described the changes in its coloration from pale to reddish), and the testis on the zooid basal wall at the place where the funiculus attaches to this wall. Huxley wrote that the form and structure of the testis are similar, and the position is the same in three more cheilostomes he dealt with. Nonetheless, he noted that the ovary, that normally contains one or two ova, is not directly connected with the funiculus, being placed in the middle of the basal wall in *B. flabellata* (Thompson in Gray, 1848), at the 'apex of the back' [obviously, in a corner between basal and distal transverse wall] in *B. plumosa* (Pallas, 1766), and in the distal part of the basal wall in *Scrupocellaria scruposa*. Huxley noted ova 'commonly possessing a double germinal spot' in *Bugula avicularia*, that could be the nucleoluses of the oocytic doublets not recognized by him. The final conclusion of Huxley was that after 'impregnation' [self-fertilization] 'the ovum passes ... into the ovicell'.

Redfern[87] observed 'ova or statoblasts', surrounded by 'clear and highly refractive nucleated cells' [obviously, follicle], and 'egg with cilia' [embryo], when studying *Flustrellidra hispida* (Fabricius, 1780) (as *Flustrella*). This author was one of the first who both described and illustrated in detail the postlarval development in marine bryozoans, but his paper has unfortunately been forgotten.

Bronn made a general review of the previous observations on bryozoan reproduction in his textbook,[88] in which he repeated common opinion at that time regarding bryozoan self-ferilization, based on the simultaneous presence of both sperm and eggs within a cavity of the same zooid.[89] One can also find a similar brief overview in the book by Busk.[90]

Smitt[91] described and beautifully illustrated some aspects of the gametic development and gonadal structure of four species of cheilostome and one cyclostome bryozoan. In three instances Smitt depicted the ovarian wall, partially consisting of cells. The majority of reseaches illustrated ovarian [follicle] wall as a simple line in those times, describing it as a membrane. Later Salensky[92] wrote that the ovary consists of two layers, one being internal and composed of roundish cells [oocytes] and the other being external and composed of flat and spindle-shaped cells [wall of the ovary]. Repiachoff[93] and Calvet[94] called the follicle wall 'cell membrane', meaning 'consisting of cells'. Smitt[95] also observed the stages of oocytic growth in ovaries of *Escharella immersa* (Fleming, 1828) (as *Lepralia peachii*) and *Scrupocellaria scruposa* (Linnaeus, 1758), showing the gonadal position in the corner between the basal and lateral walls in the middle or distal part of the zooid in the first species, and between the basal, lateral and distal transversal wall in the

second. *S. scruposa* was recognized as having both, ovary and spermatogenic tissue (in the proximal part of the cystid on its transverse, lateral and basal walls) simultaneously within the same zooid. One of Smitt's main findings (that he depicted, but did not understand himself) was an interesting oocytic development occurring in pairs (doublets). In the ovaries of *S. scruposa* he recorded up to four oocytic doublets (plus additional small cells that were possibly oogonia), clearly showing in drawings the differences between the leading and following doublets as well as between the oocyte and its nurse-cell in older doublets. The leading oocyte is larger than its sibling (nurse-cell) and has numerous yolk granules in the cytoplasm. In *Membranipora membranacea* (Linnaeus, 1767) (as *Flustra*) both ovary and testis were recorded in the same zooid too: the female gonad is found lying on the basal wall in the middle, and the male one is placed on the transverse, lateral and basal walls in the proximal part of the zooid. There are about 40 small oocytes of approximately the same size in the ovary and five ovulated oocytes in the distal part of the zooid. Smitt illustrated the difference between the mature oocytes, poor of yolk (oligolecithal) in *Membranipora* and rich in yolk (macrolecithal) in *Scrupocellaria*. In *Escharella immersa* he found eggs in the zooidal cavity and developing embryo in the ovicell. Later this fact was used by Claparède[96] as evidence in favour of Huxley's hypothesis on the exclusively brooding function of the ovicells (see above). Additionally, Smitt recorded an embryonal development inside autozooids in *Cryptosula pallasiana* (Moll, 1803) (as *Lepralia*). Since he did not find sperm in some species, Smitt suggested that, in contrast with normal eggs, fertilized in the zooidal cavity, some bryozoans possess a special kind of egg, which develops into embryos without fertilization. According to him, this could happen either inside the ovicell [gonozooid] in *Crisia* or inside the zooid in *C. pallasiana*. Remarkably, Smitt depicted embryos [probably, artificially released] surrounded by the fertilization envelope in this species. In a subsequent paper, he recorded an intertentacular organ in *Electra pilosa* (as *Membranipora*).[97]

The observations of Nitsche[98] were in accordance with the conclusions of Huxley.[99] Studying *Bugula flabellata*, *B. plumosa* (Pallas, 1766) and *Bicellariella ciliata* (Linnaeus, 1758) (as *Bicellaria*), Nitsche proved that ovicells are not ovaria, but rather the chambers for incubation. He also considered the data of Smitt[100] on *Scrupocellaria scruposa* as further evidence for it. In addition, Nitsche was the first to precisely describe ovicell development and structure in cheilostomes, taking *B. ciliata* as an example. In all the above species he described the development of spermatogenic tissue in the proximal part of zooids. Later, mature spermatozoids were seen in the rest of the perigastric cavity. Nitsche thought that there was no special ovary in *B. ciliata* (and also other bugulids studied), and that two-three oocytes (in all probability, there is an oocytic doublet pictured in his Tafel I, figure 15) were developed on the internal surface of the 'endocyst' [epithelial lining of the cystid wall], being surrounded by a thin membrane [squamose follicular cells]. In contrast, Joliet[101] mainly found ovary developing within a funiculus in this and some other species. He wrote that he was able to find female gonad on the cystid wall in a few instances only.

Nitsche[102] described oocytic growth, accumulation of yolk (granular structure of a

cytoplasm) and ovulation accompanied by the breakdown of the nucleus and subsequent disappearance of the 'membrane' [rupture of the follicular wall]. As with Huxley, he showed that all three species studied possessed simultaneously hermaphroditic zooids. Nitsche proposed that the possible method for oviposition was through the pore placed between the basal parts of the ooecium and the ooecial vesicle in the base of the ovicell, he briefly described and illustrated embryonic development and larval morphology, and mentioned firm external membrane ('feste aussere Membran'), surrounding an embryo in the ovicell [possibly, fertilization envelope].

Claparède's[103] findings in *Scrupocellaria scruposa* and *Bugula avicularia*, supported the data of Huxley and Smitt, and noted that the fertilized egg should be transferred to the ovicell. Describing oogenesis in the first species, he recorded the difference in the development of a pair of oocytes ('gepaarte Eizellen') usually found in the ovary laying on the basal wall in its distal part: one egg [the leading oocyte] rapidly increases in size, becomes brightly red and shows the granular cytoplasm, whereas another [nurse-cell] stays small and colourless. Further, the mature egg leaves the ovary, whereas the small one, as Claparède thought, is ready to divide. Actually, the nurse-cell either leaves an ovary together with its sibling or stays. In both cases it degenerates, whereas a new oocytic doublet is developed following the division of one of the primary oogonia. Claparède's[104] paper also depicted the ovarian wall consisting of squamous cells. Confirming the data of Huxley and Smitt, he found that in *S. scruposa* the ovary is positioned on the basal wall in the distal part of the cystid, whereas in *B. avicularia* the female gonad has been developing on the upper part of the funiculus, and the testis in its lower part. However, Claparède observed an incipient ovary inside young zooidal buds, when both the cystid and the polypide is not completely formed, and there is no trace of the funiculus at this stage. He also noted a change in the position of the early ovarium with respect to the developing polypide. Since ovaries were mainly (with few exceptions) found on the cystid wall, it was implied that the female gonad developed from 'endocyst' [epithelial lining of the cystid wall] at that time. Observations of Claparède showed that its development is connected with a polypide bud instead. Later Joliet[105] confirmed these data, describing development of the gonads on the funiculus – part of 'endosarc' – in several species. Hincks[106] discussed this controversy in detail.

Studies of Repiachoff[107] and Reinhard[108] on the reproduction of *Tendra zostericola* Nordmann, 1839, showed that simultaneously hermaphroditic zooids occurred in this species. This contradicted the first description of sexual dimorphism in Bryozoa – 'cellules males' and 'cellules femelles' – made by Nordmann,[109] who found developing embryos in the zooids with acanthostegous brood chambers of spines, and testes inside the zooids without them. Apart from the hermaphroditic, Repiachoff also mentioned male and female zooids in this species, but was in doubt whether there was true gonochorism or whether it was a result of the non-simultaneous development of the gonad in the same zooids. Repiachoff found ovaries in both, zooids with normal morphology as well as in those with brood chambers, and confirmed the data of Claparède on the early appearance of the ovary in the young zooids with developing polypides, mentioning that he met a

group of the cells indistinguishable from the incipient ovary close to very young polypide bud once. Up to ten oocytes were found in one ovary, with their colour varying from pale to brown and black during their development [vitellogenesis]. Ovulated oocytes (up to three) stayed in the perigastric coelom for some time until oviposition. Reinhard described a spermatogenic tissue being developed at both lateral walls of the cystid and in the proximal part, and an ovary lying on the basal wall either in the middle or in the proximal half of the fertile zooid.

Although not understanding the actual structure of the zooids with acanthostegous brood chambers Repiahoff suggested that they played a role similar to that of the ovicells. Following Repiahoff (and, obviously, Nordmann), Reinhard thought that embryos developed inside the body cavity of specialized zooids in this species. However, he believed that they could not be compared with ovicells since they possessed a polypide and an ovary. Reinhard criticized the statement of Nordmann, who thought that sperm could enter the female zooids through the opening in the [transverse] wall between subsequent zooids.[110] He also challenged the opinion of Salensky[111] on ovarian structure (see above), stating that there were not two layers in it, but a gradual change in shape and size from large and roundish cells in the middle to smaller elongated cells at the periphery. Reinhard[112] described and depicted some details of the egg and sperm formation not only in *Tendra*, but also in *Cryptosula pallasiana* (as *Lepralia*) and *Smittoidea reticulata* (J. Macgillivray, 1842) (as *Lepralia*).

Ostroumoff[113] was the first to recognize the actual position of the developing embryos in the space [epistege] between the frontal membrane and the overarching spines in *T. zostericola*. Later Paltschikowa-Ostroumowa[114] and Braiko[115] described oviposition with the help of the intertentacular organ, and the tentacle crown entering the epistege in this species. The intertentacular organ was discovered first by Paltschikowa-Ostroumowa in both *T. zostericola* and *Electra repiachowi* Ostroumoff, 1886 (as *Membranipora*), whose colonies were often considered as the same species by previous authors. Paltschikowa-Ostroumowa suggested that the formation of the acanthostegal brood-chamber by the distal zooid is influenced by hormones produced by the maternal zooid in the former species.

Further, Repiahoff,[116] working on *Cryptosula pallasiana* (as *Lepralia*), described more precisely the ovarian structure in cheilostomes. According to him, eggs are surrounded by (1) a thin cellular layer (that Repiachoff often calls 'cell membrane') [and that is a follicular epithelium], that is connected with a (2) group of the cells, forming the base of the ovary. Together, these two cell groups form the ovarian wall. In one of the schemes[117] a vitellogenic oocytic doublet is seen, consisting of a leading macrolecithal oocyte and a nurse-cell that is distinguished by its large nucleus, occupying a major part of the cell volume. There are cells obviously belonging to two-three oocytic doublets in each ovary figured. This author was possibly the first to describe clusters of spermatozoids – since he differentiated between thin and thick moving 'threads', and even suggested that the latter might consist of several of the former. It is not clear, however, if these clusters were spermatozeugmata, but not the quartets of spermatids around the cytophore. In the same

work Repiachoff briefly described and depicted oocytes in the ovary of *Electra repiachowi* Ostroumoff, 1886 (as *Tendra* species). It is particularly interesting to see that some of them are lobate.

Ehlers's study[118] of the ctenostomate bryozoan *Hypophorella expansa* Ehlers, 1876 showed that both male and female gonads occur on the internal surface of the body wall, and paired testes have an irregular shape. This scientist carefully described spermato- and oogenesis, being one of the first to make measurements of spermatozoids, ovaria and eggs, the latter at different stages of their development. Ehlers observed up to 30 growing oocytes in the ovary, suggesting that the new portion of them would develop after the ovulation of the older ones. Interestingly, he found that the ovulated eggs were different in size, and that they continued to increase in diameter in the perigastric coelom [possibly, absorbing a water]. He noted the strange folded shape of the eggs saying that it reminded him of developing embryos. He also once observed a structure that he thought was 'Ausführungsapparat' [intertacular organ] in the retracted polypide of *Hypophorella*, and stated that he saw it in almost all zooids in a non-identified cheilostome (as *Lepralia*). However, although knowing about similar findings of Farre[119] and Hincks,[120] Ehlers decided that it was a parasitic infusorian. Later Prouho[121] showed that there is a supraneural pore in *H. expansa*.

Joliet[122] observed gametogenesis in ten gymnolaemate bryozoans, cheilostome and ctenostome. This author stated that formation of the sexual cells is connected with a polypide,[123] showing that both testes and ovaria are formed at the expense of the funiculus. In hermaphroditic zooids the female gonad is placed in the upper part near the caecum, and the male one in the lower part. In gonochoristic zooids the gonad is in the place where the funiculus approaches the cystid wall, connecting with its funicular network. Thus, Joliet came to the conclusion that different gonads and, subsequently, gametes should have the same origin. Considering examples when the ovary was observed on the cystid wall, he showed that the female gonad could be moved from the funiculus to the body wall during its development in some species (for instance, in *Farella repens*) (as *Laguncula*),[124] and he described two different kinds of eggs, one developing on the funiculus and another ('parietal') on the body wall in other species (among those *Bicellariella ciliata*) (as *Bicellaria*).[125] However, Joliet supposed that the parietal eggs should originate in connection with the funicular strands passing through the mural pores. Since the work of Smitt[126] the funicular system was considered as 'colonial nervous system' by some authors. Joliet also used this term although thought that an origin of the germ cells in a funiculus was a strong argument against its 'nervous nature'. An ovary was recorded on the funiculus of the zooid with the incipient polypide in *Bugula avicularia*, and the early male germ cells near the young polypide bud in *F. repens*. In the ctenostome *Walkeria uva* (as *Valkeria cuscuta*) he also recorded formation of the spermatogenic tissue and ovary on the funiculus of the early polypide bud, and described spermatogenesis in detail. Joliet also described the release of sperm, but could not recognize a pore through which mature sperm leaves the zooidal cavity. In this species Joliet carefully investigated larval brooding in the tentacle sheath, stressing that the eggs do not degenerate in the ovarium

during the polypide recycling, but that one of them begins to grow faster instead. Much later Dyrynda and Ryland[127] found that vitellogenesis commences during polypide recycling in the cheilostome *Chartella papyracea* (see below). In Joliet's case a modified polypide without tentacles develops before oviposition in the fertile zooid. It can be seen in the illustrations[128] that the brooded embryo increases in size, and this is obviously evidence of extraembryonic feeding in the species. Joliet's description and pictures show that he often saw developing oocytic doublets in cheilostomes, where only one of the cells [leading oocyte] grows, whereas the second [nurse-cell] stays small. In agreement with Claparède,[129] Joliet believed that the second cell waits its turn to develop.[130] His description of oogenesis in *Lepralia martyi* (non-identified cheilostome) is rather curious: Joliet wrote that he observed a transparent cavity, developing in the ovary, in which two eggs originate. In this species he recorded up to six eggs formed during the life of the fertile zooid. Stating that the majority of the species studied possessed hermaphroditic autozooids, he showed the presence of gonochoristic zooids in *L. martyi*. In spite of the general opinion, Joliet remarked that cross-fertilization takes place in some species, ctenostomes as well as cheilostomes, where protandrous zooidal hermaphroditism or zooidal gonochorism occurs. Differences in the timing of gametic maturation, massive production of spermatozoids and their possibility to actively swim in the surrounding water led him to believe that cross-fertilization is the rule. He suggested that fertilization by the alien sperm, 'distinguished' by an absence of the nucleus in the egg, has a place in different species (1) inside the maternal zooid (within the tentacle sheath in the brooding ctenostomes studied or within the zooidal cavity), (2) during oviposition, or even (3) in the ovicell. Joliet wrote that he also observed embryonic development inside the introvert in *Bowerbankia imbricata* (Adams, 1898) and *Farella repens* (as *Laguncula*). The second case is wrong as Marcus[131] noted. Joliet thought that the sperm was released through the thin wall of the tentacle sheath during a sharp withdrawal of the polypide. Finally, he showed that each ovicell could be used repeatedly, and noted that a fertilization envelope was invariably present after the egg enters the brood chamber in the species studied.

An extensive review on bryozoan sexual reproduction was included in the monograph by Thomas Hincks,[132] who, apart from the analysis of the results of the previous authors, also mentioned his own observations.[133-134] Summarizing the data and opinions of the early scientists, he wrote that 'the testicle is all, but universally derived from the funiculus, invariably from some portion of the endosarc [mesenchymatous tissue] – that the ova in the considerable number of species also developed in the funiculus – that in one case at least they originate from the endosarc apart from this organ [funiculus], but in connection with a communication-plate – and that in several cases they are placed on the cell[zooid]-wall, but whether they are a product of the endocyst [epidermal epithelium] or endosarc is still undetermined'.[135] In the ctenostome *Alcyonidium mytili* Dalyell, 1848, he recognized female and male zooids, and mentioned the intertentacular organ (also in *Alcyonidium* sp. (as *A. gelatinosum*) and *Membranipora membranacea*). In another ctenostome *Vesicularia spinosa* (Linnaeus, 1767), Hincks described embryonic brooding accompanied by the embryo enlargement, the change of its coloration and the polypide degeneration. He

observed a 'delicate envelope' [introvert] surrounding the embryo, following the thinking that embryo develops inside the zooidal cavity, and this was subsequently extrapolated to all brooding Ctenostomata.[136] Later Calvet[137] showed that brooding has a place inside the introvert in this species. In *Nolella stipata* Gosse, 1855 (as *Cylindroecium giganteum*) Hincks found that three 'eggs' of different sizes were found near the top of the cystid, and he described them as 'previous to escape'.[138] Judging from their gradually increasing size, these were brooded embryos, incorporated into the cystid wall. This observation, again not understood, was later rediscovered by Prouho in *N. dilatata*.[139] Admitting the existence of cross-fertilization in some species, Hincks, however, believed that on the whole, self-fertilization prevailed in Bryozoa. Following Joliet,[140] he thought that two ovaries could be developed in succession within the same funiculus, confusing them with follicles developing one after another. Giving the general description of oogenesis, he mentioned that 'frequently two ova are produced [oocytic doublet], which are either matured in succession [successive growth of the oocytic doublets], or one of them perfects its development at the expense of the other, which is atrophied' [degeneration of the nurse-cell].[141] Remarkably, though he agreed with the opinion of Huxley, Nitsche and Joliet about the merely brooding function of the ovicell, Hincks continued to insist that it could also produce eggs in some cases.

The most complete and precise descriptions of cheilostome reproduction at this time were made by Vigelius,[142-144] who, in addition to observations of living colonies, studied serial anatomical sections. The majority of latter researchers employed this technique. Vigelius continued the discussion about the source of the ovarian origin: is it developed from the 'endocyst' or from the 'endosarc' (see above)? Studying *Terminoflustra membranaceotruncata* (Smitt, 1868) (as *Flustra membranaceo-truncata*), he found forming ovaries on the basal wall in distal parts of young zooids with developing polypide buds, and stated that they are formed 'on the internal surface of the endocyst' since gonads are clearly isolated from the polypide, and cell layers of the body wall and the ovary wall are continuous. According to his description, cells of the incipient ovary are formed from the cells of the parietal layer [epithelial lining of the body wall that was not differentiated into epidermis and peritoneum at that time], they further actively divide and move to the zooidal cavity to build an ovary that initially consists of the compact group of roundish cells of the same size. He stressed their similarity to the early cells of the male gonad and common origin from the parietal layer, calling them homologous. A similar suggestion about homology of the sex cells was made earlier by Joliet.[145] Apart from the ovicell structure and development, Vigelius gave exhaustive and beautifully illustrated descriptions of oogenesis and ovarian structure in his papers: differentiation of two-three early oocytes[146] being surrounded by smaller cells [ovarian wall] in the young ovary, growth of the leading oocyte [judging from his illustrations, macrolecithal], surrounded by the 'Dottermembran' [yolk membrane], and accompanied by the changes in its cytoplasm during vitellogenesis and, finally, degeneration of its nurse-cell [that Vigelius considered as a struggle for an existence between the cells]; the structure of the ovarium, forming the follicle (Vigelius was one of the first, who used the term 'follicle' describing bryozoan

oogenesis) and consisting of the intensively pigmented, pear-shaped and cylindrical cells on the side, adjoining the basal wall, and more light, flattened cells on its opposite side; differences in the ovarian shape and, sometimes, position. This researcher was sure that the cells of the ovarian wall never transformed into the germinal ones, but that their number increased by division as the follicle grew. He described ovulation, accompanied by a gradual flattening and, finally, resorption of the follicular cells, stages of the breakdown of the nucleus preceded by a shrinkage of the nuclear membrane, and removal of the mature egg, that occupies the large part of the cystid cavity, towards the distal transverse wall. He suggested that oviposition could be performed by the activity of the parietal muscles of the zooidal frontal wall, contraction of which increases the pressure of the perigastric fluid, and leads to the rupture of the ooecial vesicle wall. According to Vigelius the egg is moved to the ooecial vesicle first, later transferring through the hole to the incubation cavity of the ovicell. This idea was later adopted by Calvet,[147] but some authors, for instance, Korschelt and Heider[148] and Gerwerzhagen[149] ascribed the authorship to Calvet.

In *Terminoflustra* Vigelius found male, female (more numerous) and, occasionally, hermaphroditic zooids in the same colonies. Because of the simultaneous presence of the three variants of sexual zooids in the colony, Vigelius supposed that they could transform from female to hermaphroditic and back to female depending on the conditions. It was observed that the male gonads in the males appear later than ovaries in female zooids in the protogynous colony. However, the sperm mature at approximately the same time as the eggs. Separation of the sexes between zooids, simultaneous maturation of gametes in them, and, in contrast, different (as a rule) terms of the gamete maturation in hermaphroditic zooids [possibly, protogyny] led him to believe that cross-fertilization should characterize this and the majority of other species, although it seems he meant intracolonial self-fertilization [zooidal cross-fertilization within the same colony]. According to Vigelius's Figures 69 and 71 (Table V),[150] the mature oocyte is surrounded by the fertilization envelope when still in the ovary. The envelope wall is seen on the side of the partially ovulated oocyte that is exposed to the zooidal cavity. Challenging the statement of Joliet,[151] Vigelius found that the testes developed on the zooidal wall, but not within a funiculus. Similar to Ehlers,[152] he described the irregular shape, sometimes paired, and wide distribution of the spermatogenic tissue across the zooidal wall in the proximal part of the cystid and noted that the ovary does not degenerate after the first ovulation, but continues to produce new eggs. Vigelius thought that the new ovary originated from the remains of the previous one, or could be built up again from the parietal epithelium. Moreover, functioning ovaries were observed in zooids with a brown body and regenerating polypide, and these observations were used as evidence against Joliet's statements on the 'polypide' origin of the ovary. There is also a detailed description of spermatogenesis in his papers. Vigelius thought that the release of sperm was possible through the zooidal aperture only after polypide degeneration and destruction of the body wall. Fertilisation itself he supposed to occur externally, inside the ovicell.

In his later paper, Vigelius[153] studied sexual reproduction in *Bugula calathus* Norman,

1868, including the structure and development of its ovicells. Here the ovary is suggested to be a product of 'mesenchymatous parenchyma' (we also found a similar opinion in the paper of Ostroumoff[154]), developing on the basal wall of the cystid. Vigelius noted that some ovaries lost their contact with a basal wall during oogenesis, either lying free [suspended] in the body cavity [actually connected with several funicular strands] or connected with a basal wall by the single parenchimatous [funicular] strand. Comparing the ovarian structure in *B. calathus* and *Terminoflustra membranaceotruncata* Vigelius stressed the striking difference between these species: in contrast with the female gonad of *Terminoflustra*, with its basal part consisting of large, cylindrical, tightly packed cells, the ovary of *Bugula*, is represented by few small, flat cells with a loose arrangement. It is noteworthy, that in two instances this scientist depicted some tiny bodies inbetween the oocytes and the ovarian wall. It is now clear that he saw so-called 'basal ovarian cells' (the term, introduced by Hageman after his non-published TEM-studies of *Membranipora membranacea*, see reference in Reed 1991). Judging from his illustrations,[155] Vigelius often saw oocytic doublets, young as well as mature. In one of these illustrations, a small oocyte [actually, the nurse-cell] was depicted with a nucleus occupying the major part of the cell in a mature doublet. Vigelius also described a large transparent vacuole, seen in the nucleoluses of many oocytes, change (from the central to the excentric) of the nucleus position during the course of the egg's growth and vitellogenesis. Despite mentioning the brown granules of yolk, he called the eggs of *Bugula* alecithal [correctly, oligolecithal]. The simultaneous presence of male and female gametes in the same zooids forced him to admit intrazooidal self-fertilisation in this species. One of the most interesting findings of Vigelius was the discovery of cylindrical epithelium in the ooecial vesicle, and unusual 'bodies' with granulate cytoplasm, associated with its cells. It should be mentioned that this hypertrophied cell layer, now known as an embryophore[156-159] was probably found first by Reid in *B. flabellata*. Reid wrote 'this membranous partition [distal wall of the ooecial vesicle] was much thickened, … and contained a number of nucleated cells'.[160] 'Thickened … wall [of the ooecial vesicle], that shows very distinctly' was also mentioned by Hincks[161] in some *Bugula* and *Bicillariella*. An increase of incubated embryos in size (that, as known at the moment, is a consequence of the placental brooding) has been also either described or illustrated by several authors in bugulids.[162-167]

Kraepelin[168] described and depicted the position of gonads in the hermaphroditic zooids of two ctenostomes. In *Victorella pavida* Saville Kent, 1870 both gonads are placed on the cystid wall, an ovary in the distal part of the zooid, whereas testis occurs in the middle part. In *Paludicella articulata* (as *P. ehrenbergi*) spermatogenic tissue develops on the funiculus and, partially, cystid wall in the proximal part of the zooid, and ovary on the cystid wall in its middle part. Kraepelin also described the shape and movement of the sperm in the latter species. He believed that both types of sexual cells developed from the peritoneum.

In contrast with all previous observations published, Jullien[169] decribed and depicted single and paired 'testicule glandulaire' with deducing channels in *Figularia figularis* (Johnston, 1847) (as *Lepralia*), and depicted ovaria with one oocytic dublet in this species

and in *Beania* sp. (as *Diachoris costata*).[170] In all probability, this author confused opercular glands with testes. In *Celleporella hyalina* (Linnaeus, 1767) (as *Hippothoa*) Jullien distinguished ordinary, male and female zooids, and proposed that oviposition might occur with the help of the tentacle sheath, since he did not find a polypide in the females.

Pergens[171] briefly described oogenesis and ovulation in *Fenestrulina malusii* (Audouin, 1826) (as *Microporella*). He stated that ovary develops from the parietal layer of the zooidal wall in this species. Development of the ovary starts from a group of three-five small cells. Some of them are resorbed, but two are increased in size [oocytic doublet] and one is transformed to an egg. Other ovarial cells surround this pair, 'serving them for feeding'. The ovulated egg is surrounded by the 'Chorion' [fertilization envelope] that is distinguished just after ovulation. Pergens was the first to record oviposition in cheilostomes, noting that this is accompanied by a strong compression of the egg and occurs when the polypide degenerates. Until now, Gerwerzhagen[172] was considered to be the first scholar to describe this phenomenon. Nielsen[173] described oviposition in *Fenestrulina miramara* Soule, Soule and Chaney, 1995 (described as *F. malusii*), as being undertaken by an everted lophophore and almost without the egg deformation (see below). However, Pergen's description is very realistic, and one can suggest that he could observe different species. A further important observation was that the ovary continued with oogenesis during polypide recycling, this coincided with the observations of Van Beneden[174] and Vigelius.[175] Although finding only gonochoristic zooids, Pergens believed that the sex of the zooid could change since he recorded 'spermatosporen' in ovicellated zooids.

The classical works of Henri Prouho (Figure 2)[176-177] revealed different methods of brooding in several ctenostome bryozoans, as well as demonstrating the presence of both brooding and non-brooding species within the same ctenostome genus *Alcyonidium*. Among non-brooders is *A. albidum* Alder, 1857. It has simultaneous hermaphroditic zooids, with an ovary developing on the funiculus and the spermatogenic tissue – found on the cystid wall in the proximal region. The female gonad is depicted as a central mass of oocytes with a peripheral wall of flattened cells. Judging from the illustrations the ovary contains up to eighteen oocytes [obviously, oligolecithal] plus up to three ovulated eggs seen in the body cavity. Prouho described the 'transparent and … delicate shell' [fertilization envelope] surrounding the ovulated eggs and observed their release through the intertentacular organ, proving that it is an oviduct.[178] It is not clear from the Prouho's text how he connected formation of the 'shell' with the fertilization event. He only suggested that fertilization possibly occured before the 'shell's' appearance.

In addition Prouho investigated the structure of the intertentacular organ of *Electra pilosa* (as *Membranipora*) and *Alcyonidium duplex* in section. Egg release was observed through the 'genital pore' [supraneural pore] in the non-brooding ctenostome *Hypophorella expansa* thus showing that Ehlers[179] was mistaken when he wrote that he observed an intertentacular organ in the retracted polypide in this species. Brooding within the introvert was described in four species: *Pherusella tubulosa* (Ellis and Solander, 1786) (as *Pherusa*), *Flustrellidra hispida* (as *Flustrella*), *A. variegatum* Prouho, 1892 and *A.*

duplex. In three of them the polypide degenerates, and several embryos are brooded simultaneously: four-five in the first two species (there can be up to eight embryos in *F. hispida* according to Hayward),[180] and six to eight in the last one (it is not clear from the Prouho's description how many embryos are simultaneously brooded in *A. variegatum*). In *A. duplex* the male germ cells are developed on the funiculus of the first polypide, in the place of its attachment to the stomach. Further they migrate to the body wall, establishing the gonad. An ovary is formed in the place where the funiculus of the second polypide (whose bud co-exists for some time with the first one) attaches to the body wall. There are seven to nine (up to eleven) oocytes seen in the ovary in Prouho's illustrations. Similar to other species studied, the ovulated eggs are irregular in shape. In contrast with the first polypide, that finally degenerates, the polypide forming the ovary has an intertentacular organ. Released eggs stick to the polypide diaphragmal region [obviously, by their fertilization envelopes], being submerged to the vestibulum during the polypide retractions, and exposed when it expands. Later the third polypide forms new ovary, and has the same structure as the second one that degenerates. No new testis develops in the zooid. In addition, Prouho recorded two polar bodies in the perivitelline space of recently spawned zygotes surrounded by the fertilization envelope in *E. pilosa*, *A. albidum* and *H. expansa*. The elevation of the fertilization envelope is described during the passage of the eggs through the intertentacular organ in *E. pilosa* and *A. albidum*.

In *Nolella dilatata* (Hincks, 1860) (as *Cylindroecium dilatatum*) Prouho found, as he thought, internal brooding. According to his description and figure explanations,[181] two-three eggs are brooded, adhering to the internal surface of the zooidal wall. Larvae were supposed to leave the zooidal coelom through the rupture of this wall. Later Marcus[182] wrote that the eggs are surrounded by the sac, but it is not clear whether he meant an invaginated body wall in this case.[183] It is also documented that the embryos are enlarged during brooding, with the youngest (=smallest) being uppermost in the zooid, and this could be evidence for extraembryonic nutrition. Prouho was tending to believe that self-fertilisation was the rule among bryozoans, since in those species where he recorded the sexual products, they often matured simultaneously. He observed that spermatozoids were concentrated around the ovary in *Alcyonidium albidum*. However, this scientist admitted that the male and the female gonads began their formation non-simultaneously in some zooids in *A. duplex*, and that if cross-fertilisation existed it should happen during the egg's passage through the intertentacular organ. Finally, he rejected the idea that alien sperm could enter the zooidal cavity using the same organ, since the activity of its cilia was directed towards the outside.

Braem[184] confirmed the data of Allman[185] on gonadal position in the fresh-water ctenostome *Paludicella articulata* (as *P. ehrenbergi*). He specified that the male gonad was paired, described vitellogenesis and made egg measurements. He documented that released eggs were surrounded by the fertilization envelope and sometimes stuck to the maternal colony. In his later papers Braem[186-187] briefly described the structure and made measurements of spermatozoids in the ctenostomes *Paludicella* sp. [obviously, *P. articulata*] and *Triticella* sp.

Figure 3. Louis Calvet in 1901 (photograph courtesy of Jean-Loup d'Hondt)

Waters[188] discovered the external brooding sacs (that he called as 'ovicells') and an ovary in *Aetea sica* (Couch, 1844) (as *A. anguina* forma *recta*). Later this was confirmed by Robertson[189] and Mawatari.[190] The female gonad is positioned inside the adnate, horizontal part of the maternal zooid, and contained four young oocytes.

Delage and Hérouard[191] briefly overviewed bryozoan sexual reproduction in their handbook, but the number of original papers used was quite small.

The monograph of Louis Calvet (Figure 3)[192] became an important landmark in the development of our knowledge about bryozoan anatomy, including the reproductive system. Apart from the structure of brooding chambers in several cheilostome species, and finding the embryophore in cheilostomes *Bugula simplex* Hincks, 1886 (as *B. sabatieri* Calvet, 1900) and *Cellaria fistulosa* (Linnaeus, 1758),[193] he described brooding in the tentacle sheath in the ctenostomes *Bowerbankia pustulosa* (Ellis and Solander, 1786), *Amathia lendigera* (Linnaeus, 1761), *Amathia semiconvoluta* (Lamouroux, 1824) and *Vesicularia spinosa* (Linnaeus, 1767). The intertentacular organs of *Electra pilosa* (as *Membranipora* var. *dentata*) and *Alcyonidium cellarioides* Calvet, 1900 were studied in sections. This author recorded protandrous zooidal hermaphroditism in ten cheilostome species, and simultaneous zooidal hermaphroditism in six cheilostomes and two ctenostomes. He stressed that the early zooids did not reproduce sexually in the colony. It was mentioned that the position of the mature ovary is generally constant for the same species, but can be somewhat variable for the whole group as well as for the same species. In the majority of the species studied it is placed 'parietally' [on the zooidal wall, mainly,

basal], although it could be suspended on the funicular strands or attached to the polypide, and this explained the apparent controversies of Joliet[194] (see above). Male gonads were recorded on the lateral and basal walls in the proximal region of the cystid. Dividing bryozoans into oviparous and viviparous, Calvet showed the striking difference in egg number contained by the ovaries: there are many more oocytes in the former. In the latter [actually, brooders] the eggs are often pictured in pairs [oocytic doublets], some of them degenerating inside the ovary [mature nurse-cells]. It is also clearly seen from the illustrations that cheilostomes, except *Electra* species (as *Membranipora*), possess less eggs in the ovary than the ctenostomes studied. Calvet observed spermatogenesis in twenty-three species (nineteen cheilostomes, two ctenostomes and two cyclostomes), illustrating in detail the different stages of spermatozoid development in *Bugula simplex* and *Cryptosula pallasiana*, and stating that the initial 'cellule spermatoblastique' originated from the mesenchymatous tissue in young zooidal buds. This author also recorded clusters of spermatozoids (spermatozeugmata) in *Electra pilosa* and described their dissagregation.

Calvet carefully investigated the ovarian structure, oogenesis and spermatogenesis in simultaneous hermaphroditic zooids of *B. simplex*, resolving several important problems. According to his observations, the position of the ovary varies in this species. The female gonad is found, being either suspended to the funicular strands in the zooidal cavity, or attached to the peritoneal lining of the zooidal wall or stomach. Calvet mentions the rare occurence of two ovaries in some zooids. In one instance he depicted an ovary resting on the zooidal wall[195] and, additionally, 'cellules ovulaires' inside the funiculus, as if there were two locations for eggs in the same zooid. Wherever it was positioned, an important conclusion was that the ovary always 'belongs to the mesenchymatous tissue' and its cells 'come directly, and by simple differentiation, from' it.[196] This was in accordance with the statements of Vigelius for *Bugula calathus*.[197-198] However, in contrast with the data of the latter, Calvet found early ovaries located near the developing polypide in young zooidal buds. In zooids with the polypides at more advanced stage, young ovary was then either found within the polypide peritoneum or more often, within the peritoneum of the cystid wall, or being suspended to the funicular strands.[199] He stated that female gonads incidentally appeared in terminal zooids with developed polypides, specifically within the funicular tissue or peritoneal cover. Calvet described oocytic growth and accompanying changes in the egg structure as well as the transformation of the ovarian cells. Some of them are flattened, thus forming the follicle, whereas the rest kept their shape and formed either a narrow (pedunculate) or wide basal part of the ovary that was often connected with the cystid wall. It is clear from his illustrations that Calvet saw the basal cells in some ovaries too. According to his description, the early 'ovular cells' after their differentiation are further enveloped by the multiplying peritoneal cells in different species of *Bugula* and in the ctenostome *Bowerbankia pustulosa* (Ellis and Solander, 1786). In all, but one[200] of the other bryozoans studied, the process is said to be different. After being differentiated from the 'mesenchymatous elements', the female germ cells that differ from all others in having the bubble-like shape, more intense staining and larger diameter, divide once each. Judging from his figures, Calvet saw two-four oogonia in the incipient ovaries. Calvet

wrote that all of them had the same characteristics and were 'young ovules' at that stage.[201] In this cell cluster peripheral cells developed into the 'follicular membrane' [ovarian cells], whereas the central ones began to grow and accumulate yolk granules, resulting in mature eggs. However, only some of these cells develop, whereas others degenerate [supposedly, nurse-cells]. This researcher thought that growing eggs were fed at the expense of the degenerated ones. Actually, in the vast majority of brooding cheilostomes, including bugulids, only one vitellogenic oocyte (plus its nurse-cell) develops in the ovary in the same time. Since the eggs are oligolecithal in *Bugula*, Calvet probably counted all the oocytes (vitellogenic and previtellogenic), simultaneously presented in the ovary.

Calvet believed in the idea of intrazooidal self-fertilization, and stated that he observed it inside the zooidal cavity in *Bugula simplex*, being preceded by a formation of two polar bodies expelled from the mature, but non-fertilized egg that is surrounded by the thin vitelline membrane. It was suggested that each regenerating polypide produced new ovary and new testis in the hermaphroditic zooids, and the eggs that are formed were at the expense of the first polypide, and were fertilized by the sperm of the testis formed by the second polypide.

Thus, towards the end of the 19th century the following features or conditions were recognized:

-Except for sterile zooids, gymnolaemate colonies may consist of either hermaphroditic or gonochoristic autozooids with simultaneous or non-simultaneous maturation of gametes in both cases; those thought to be gonochoristic, may in fact be hermaphroditic depending on the time of appearance of the gonad.

-Germ cells originate at the expense of the mesenchyma [mesothelium], and formation of the early female cells is sometimes connected with early polypide buds.

-An ovary develops on the caecum, funicular strand (often on that connecting the caecum and the cystid wall) or on the body wall (being connected with a funicular system too), and its position is the subject of some variation.

-With one exception (*Farella repens*), testes (sometimes, paired) are formed in the proximal part of the zooid on the cystid wall, often in the place where the funiculus attaches to the wall.

-The main stages of both oogenesis and spermatogenesis have been described. There are clear differences in the amount of yolk deposited in the eggs of different species.

-There are oviparous and brooding species among Gymnolaemata. The former produce numerous eggs, releasing them through the intertentacular organ or genital pore. The number of eggs in the latter is much less, and they are brooded in a variety of types of incubation chambers.

-The polypide often degenerates and embryos are enlarged during brooding in Ctenostomata. Increase in embryo size also occurs in some brooding Cheilostomata.

-A thin membrane envelopes ovulated eggs and developing embryos, whether brooded or released.

4. First half of the 20th century – more results

Schulz[202] presented some data on the reproduction of *Electra crustulenta* (Pallas, 1766) (as *Membranipora membranacea*), briefly describing gametogenesis in this species. Both male and female gametes mature simultaneously, and the ovary develops at the expense of the funicular tissue, often close to the pylorus. Interestingly, Schulz wrote that several ovaries are often formed in one zooid. Spermatogenic tissue is formed partially on the funicular strands, partially on the cystid walls. Because of the simultaneous zooidal hermaphroditism, Schulz suggested that self-fertilization has a place in this species. He described an intertentacular organ, stressing that he could observe it in sexually reproducing colonies only. He rejected an idea about it having an excretory function[203] stating that it was used exclusively as an oviduct.

Harmer[204] was the first to write that the embryo 'receives its yolk while in the [brooding] sac' in *Retiflustra schoenaui* Levinsen, 1909 (as *Flustra cribriformis* Busk), and this was obviously influenced by the comparison made between the small oviposed egg and large embryo. Later Harmer described 'a secretory epithelium' of the brooding sac wall, saying that the embryo towards the end of its development 'occupies nearly two thirds' of the cavity of the fertile zooid in this species.[205] He stressed that 'while the eggs which develop into Cyphonautes are always small, with little or no yolk, and are produced in considerable numbers … the egg which develops in an ovicell is, with few exceptions, single and usually has from the first a considerable amount of yolk'. The exceptions noted are the species of *Bugula* 'where the ovum is small when it first passes into the brood-space. Its increase in size is presumably due to nutriment supplied through the membranous vesicle, which thus acts as a placenta'.[206] Thus, Harmer was actually the first person to recognize three major reproductive patterns in Bryozoa.

The papers of Waters are usually considered as being taxonomical, although they contain valuable information on bryozoan anatomy and reproduction. For instance, anatomical figures from Waters's works were widely used in the monographs of Canu and Bassler.[207-208] Waters applied sectioning, where he was trying to get some anatomical characters for the purposes of classification. In this way, he began to count the number of tentacles first, then describing muscles, glands and gonads. In some instances, this information can be found simply by examining his illustrations (for instance, there is an ovary with eight oocytes depicted inside the sectioned zooid of *Menipea roborata* (Hincks, 1881) (as *Flabellaris*);[209] also in *Cystisella saccata* (Busk, 1856) (as *Porella)* testes and ovary are figured in obviously gonochoristic zooids,[210] and a developing embryo in the tentacle sheath is pictured in the ctenostomes *Walkeria uva* (as *Valkeria*) and *Bowerbankia imbricata*[211]). In other papers there are brief remarks in the taxonomical descriptions.[212-215] For instance, he wrote: 'No doubt the nature, size, shape and position of the ovaria will have to be used in the classification of Alcyonidiidae'.[216] Additionally, an intertentacular organ was found in the simultaneously hermaphroditic zooids of *Alcyonidium antarcticum* Waters, 1904. Waters[217-218] was the first to find the external brooding sac and ovary in *Aetea sica* and *A. anguina* (Linnaeus, 1758). Waters's study of

the peristomial ovicells in *Margaretta chuakensis* Waters, 1907 (as *Tubucellaria ceroides* var. *chuakensis*) revealed that the ovary is normally below the dwarf polypide, although ovaries may occur on the lateral walls in different places, being frequently associated with a funicular strand near the point where it enters one of the distal mural rosette-plates.[219] Waters stated that the dwarf polypide is formed not by polypide recycling, but by a modification of the original polypide, and he was in doubt as to whether it could serve for larval release. At the same time Waters showed that the dwarf polypide has a cuticular terminal plug, closing the entrance to the ovicell in the maternal zooid. Thus, the polypide itself cannot release the larva, but by moving this plug it could open the entrance for the larva to escape. Waters's schemes show macrolecithal eggs, forming within the ovary of the cylindrical epithelial cells in this species. In the ovicells of *Thalamoporella rozieri* (Audouin, 1826) he found up to three embryos of different ages all surrounded by fertilization envelopes. He mentioned an unusual structure of the ovary where 'ovarian cells are partly surrounded by a coarse cellular network' in this species.[220]

Additionally to some observations on internal brooding, in a small number of cheilostomes from the genera *Adeona*, *Adeonella*, *Adeonellopsis*, *Laminopora, Beania* and *Watersipora* (as *Lepralia*),[221] there was the obvious discovery of extraembryonal nutrition in most of them.[222] Waters wrote that embryos occupied half or even the major part of the zooidal cavity in 'adeonid' genera, but that the eggs found were from small to moderate size. He also briefly described gonads in 'Adeonidae'. He further wrote that testes could be said to fill almost all of the zooidal cavity [obviously, in male zooids] in *Laminopora contorta* Michelin, 1842, and that ovary is positioned in the distal part of zooid, near the proximal part of the brooding sac. It contains two, occasionally, three small oocytes, of which only one reaches the moderate size in *Adeona foliifera fascialis* Kirchenpauer, 1880 (as *A. foliacea* var. *fascialis*). Waters proposed to divide all Bryozoa into two groups according to their ovarian structure, and discussed their 'classificatory assistance'. He defined (1) 'bicellular' ovaria 'with only two, or perhaps three, small ovarian cells [oocytes], neither of which grows to any large size, but passes into the ovicell quite small', and (2) 'multicellular ovaria with many ovarian cells, one or more of which often attain to a considerable size', noting that 'multicellular forms may pass through a stage somewhat like the bicellular'.[223] This author considered *Bugula* (and obviously the 'Adeonidae' described) as an example of the 'bicellular' variant, and *Scrupocellaria* as an example of the 'multicellular' one.

In a later paper Waters[224] described and depicted the hypertrophied epithelium of the brooding sac in *Adeonella platalea* (Busk, 1854). According to his description the small egg begins its growth in the small brooding sac, hanging below the zooidal operculum in *Poricellaria complicata* Reuss, 1869 (as *Diplodidymia*). Further they both enlarge to such an extent that they fill most of the zooidal cavity. In both these cases, Waters did not understand that he had discovered placental nutrition. However, he obviously realised this in the case of *Catenicella elegans* (Busk, 1852) (as *Vittaticella*). Waters wrote that there are 'several fleshy bands or tubes by which … material for growth is transferred to the ovicell', containing a large embryo in this species.[225] The position of the gonads and the

number of eggs in the ovary was recorded in sixteen cheilostome species. For three other species there are data about the positions of embryos in the brood-chambers: for instance, embryos surrounded by a membrane were suggested to be brooded in the 'internal ovicell'[226] in *Steginoporella magnilabris* (Busk, 1854) (as *Steganoporella*). A similar finding was made by Marcus[227] next, who recorded embryos enveloped by the membrane and the ovary in *Steginoporella haddoni* (Harmer, 1900) (as *Steganoporella*). Waters further considered that the size and position of the ovary and the size and the number of eggs formed might be used as a character of the generic status. He grouped together the genera *Canda*, *Caberea*, *Scrupocellaria*, *Bugulopsis* and *Menipea* as having a large, distal ovary with several eggs, one of which grew quite large before oviposition occurred. In contrast, *Bugula* and *Bicellariella* (as *Bicellaria*) possess a small, proximal ovary with only two (rarely three-four) small eggs one of which is transferred to the ovicell [being small]. For instance, Waters supported an idea to remove *Dendrobeania murrayana* (Bean in Johnson, 1847) from the genus *Bugula* on the basis of ovarian structure. Actually, this division reflected an existence of two different reproductive patterns, involving placental and non-placental brooding in Cheilostomata, but an appreciation of it came much later. It should be noted that Waters's idea was in accordance with the observations of Vigelius,[228] who noted the marked difference in the structure of the ovarian wall in *Bugula* and *Terminoflustra*.

The data on the presence and position of gonads are incidentally met in the taxonomic works of Harmer,[229-230] but, in contrast with Waters, Harmer rarely discussed his findings. In the ctenostome *Nolella papuensis* (Busk, 1886) Harmer[231] found embryos, both immersed into the zooidal cavity and attached to the zooidal wall (being surrounded by the thin envelope), and described them according to the point of view of Prouho[232] as if they were brooded internally further escaping through the 'hernia-like protrusion'. In the cheilostome genus *Steginoporella* (as *Steganoporella*) he found embryos in the ovisacs, ovaries on the lateral wall of A-zooids, and sperm in both A- and B-zooids. In this monograph Harmer also briefly discussed some points concerning the ovicell structure, oviposition, and oviparity and viviparity in Gymnolaemata.[233]

Pace[234] studied reproduction in the ctenostome *Flustrellidra hispida* (as *Flustrella*) in detail. He was one of the first to record gonadal activity throughout the different seasons, noting that the simultaneous presence of male and female gonads in the same zooid does not coincide with their simultaneous maturation. Both male and female germ cells are confirmed as originating from the mesenchyme with the testes positioned at the body wall, and the ovary on the funiculus. Incipient ovary is stated to originate from the 'protoplasmic mass' with nuclei,[235] but with no indication of the cell walls. Similarly Owrid and Ryland[236] wrote that the boundaries between young oocytes were occasionally indistinct in the developing ovary in *Alcyonidium hirsutum* (see below). These appear later, dividing the 'mass' into cells. Four to five of them differentiate into growing eggs, simultaneously developing in the ovary, whereas the rest develop into follicular cells. The number of follicular cells increases as egg maturation proceeds. Pace carefully described oocytic growth with the corresponding changes in their structure, including the fate of so-called

"yolk nucleus". Upon egg maturation, the polypide degenerates and up to five oocytes then move to the tentacle sheath for simultaneous brooding. Similar observations were also made by Prouho.[237] In one instance Pace found the fertilization envelope and two polar bodies appearing soon after oviposition, but he could not ascertain the exact moment of fertilization. During their development, the embryos increase in size, eventually filling the entire zooidal cavity providing what could be evidence for extraembryonic nutrition.

In contrast with previous authors, Silbermann[238] stated that the ovary originates from the ectoderm of the cystid wall in the ctenostome *Alcyonidium mytili*. Silbermann followed its development, formation of the follicle and oocytic growth. Similar to the development in *Flustrellidra hispida*, each large oocyte is enveloped by its own follicle. Testes are described as being paired, forming on zooidal wall in the proximal region of the cystid. Hermaphroditic zooids are rare, however. Moreover, since the author never saw mature eggs and ripe sperm together, he concluded that self-fertilisation is impossible in this case, that resembles protogyny. He described the intertentacular organ in this species, depicting it sectioned, but Marcus[239] stated that it was a mistake.

Retzius[240-244] investigated spermatogenesis and sperm structure in four gymnolaemate species, undertaking one of the most complete and detailed studies at that time. In the same period the prominent papers of Bonnevie[245-246] were published. Working on *Electra pilosa* (as *Membranipora*) and *Membranipora membranacea*, she revealed that their colonies consist of male, female and hermaphroditic zooids throughout the reproductive season. However, all of them are actually hermaphrodites possessing either (1) mature sperm and early ovary, or (2) mature eggs and degenerating sperm tissue, or (3) sperm and eggs [probably, ripe or maturing]. Judging from this, the protandry is manifested in a different degree, and there is also simultaneous gonadal maturation in some zooids. Bonnevie suggested that the sex changes follow from male to hermaphroditic, and then back to the female state in some zooids, but also that the appearance of the different gonads might repeatedly alternate during the life span of the zooid. Both gonads are said to develop from the cystid parietal wall. Spermatogenic tissue develops on the lateral walls. Studying spermatogenesis, Bonnevie recorded sperm clusters – spermatozeugmata (called 'spermosyzygien' or 'spermozeugmen') and described their structure and behaviour in both species. She noted that spermatozeugmata move independently, as if they were a single thing, and thought that this phenomenon is an adaptation for 'Polyspermie': fertilization by several spermatozoids that was suggested to happen just after ovulation. Using sections, Bonnevie described several male pronuclei inside the egg, at first being positioned close together, but then later distributed more widely throughout the cytoplasm and acquiring the spiral shape. She speculated that the clustering of spermatozoids could enhance their locomotory power, but admitted that this contradicts her own belief in either intrazooidal or intracolonial self-fertilization. Judging from her description, she considered polyspermy as a rule, ascribing it a special physiological function. Additionally, Bonnevie studied the ovarian structure and oogenesis of *E. pilosa*, describing zonality of the female gonad with young and mature oocytes having different shapes and being concentrated in different regions (peripheral and central, subsequently), and the intermediate stages

inbetween. This author paid great attention to the changes in the nuclear apparatus and cytoplasmic inclusions of the developing female cells. Based on nuclear structure, Bonnevie suggested that multiplication of the cells occurs in the zone with young oocytes. Further development of the oocyte is said to be accompanied by its fusion with a 'Nährzelle' 'nutritive/feeding cell', 'belonging to the ovarian wall'.[247] Fusion is described as a slow process, and the nucleus of the 'nutritive cell' is seen in the oocyte cytoplasm for a long time afterwards. This reminds the oocytic doublets in Neocheilostomata and needs checking. At the beginning of vitellogenesis, subsequent changes in the oocytic shape and germinal vesicle breakdown have been recorded. Bonnevie speculated that nucleoplasm ('cell juice') is moved from the nucleus outside the egg membrane, forming the special hyaline layer, and the nucleus itself then degrades. Meiosis begins (Bonnevie observed meiotic events and recorded a set of eleven chromosomes; later Temkin[248] recorded a set of twelve chromosomes in the primary oocytes of *Membranipora membranacea*) while the mature egg is still in the ovary, but does not continue after ovulation. Further ovulated eggs increase in size, acquiring variable shapes in *E. pilosa*. Supposedly, it is not growth, but rather an enlargement caused by water entering the cytoplasm.

Similar to Silbermann,[249] Römer[250] found that the early germ cell, which he called an egg, develops within the epidermal layer of the cystid wall, being not connected with a bud of regenerating polypide in *Alcyonidium* sp. (as *A. mytili*). He suggested that the main reason for the polypide degeneration is the development of the sexual cells and growth of the embryo that later fills the major part of the zooid.

Levinsen[251] discovered numerous modifications of the ovicells and their development in different cheilostome taxa, and introduced some basic terminology that is commonly used now. However, since he studied dried and cleaned material his results were actually never checked or used.[252] He proposed that oviposition might occur either underneath the zooidal operculum, or through the zooidal opening before entering the ovicell.

In their handbook Korschelt and Heider[253] briefly characterized ovicell structure, based on the works of Nitsche,[254] Vigelius,[255-256] Calvet[257] and Levinsen.[258] They pointed out the unsolved problem of oviposition, mentioning the hypotheses of Vigelius[259] and Levinsen. This question worried many researchers at that time, but the observation of Pergens[260] was overlooked. In addition to the hypotheses mentioned above and in agreement with the idea of Nitsche,[261] Prouho[262] supposed that there is a connection between the ovicell incubation cavity and the visceral coelom of the maternal zooid in Cheilostomata.

Three years after the publication of Korschelt and Heider's[263] textbook and twenty-four years after the paper of Pergens,[264] oviposition was observed and described by Gerwerzhagen[265] in *Bugula avicularia*. He found that ovulation is caused by the activity of the polypide that pushes and presses the ovary. Fertilization occurs just after ovulation, since numerous sperm are present in the zooidal cavity at that moment. Oviposition is accompanied by violent exertions of the polypide, thanks to which the ovulated egg moves into close proximity of the 'Geburtsöffnung' [birth opening or supraneural pore]. Gerwerzhagen observed this pore between the bases of two dorsal tentacles. Next the

everted polypide takes up a special postion close to the ovicell opening, lowers its tentacles, and pushes the egg to the brooding cavity. The contradiction between the relatively large size of the egg and small diameter of the pore is solved by the unusual plasticity of the egg that stretches out into a narrow cord. Gerwerzhagen supposed that this process could be facilitated by the sucking activity of the ovicell itself via the contraction of the muscles in the ooecial vesicle, but could not find any evidence in favour of the suggestion. Accomplishing the oviposition, the polypide retracts, rests for some time, and finally begins to feed again. If the polypide degenerates before the egg was oviposed, the process occurs after polypide regeneration. Gerwerzhagen noted that he once observed the two-cell stage of embryonal development inside the maternal zooid. In theory, it is possible that embryogenesis starts before oviposition when the polypide does not regenerate. In *Membranipora membranacea* developing embryos inside zooids were observed by Lutaud.[266]

Friedl[267] made one of the first seasonal observations on the reproductive ecology of marine Bryozoa, recording the presence of larvae in the colonies and 'cyphotauteses' in the plankton. Some data on the reproductive ecology of *Bugula flabellata* are documented by Grave.[268]

Marcus[269] investigated sexual reproduction in the ctenostome *Farella repens* and the cheilostome *Electra pilosa*, and his observations supported the data of Van Beneden[270] and Bonnevie.[271] In particular, the testis was found on the funiculus and the ovary on the cystid wall, and their development was both simultaneous and non-simultaneous in the hermaphroditic zooids in *Farella*. Observing the mature spermatozoids and eggs (up to ten in number) within the same zooids, Marcus tended to believe in self-fertilization. However, he recorded that the sperm stuck to the tentacle crown, suggesting that (1) this could be a result of accidental release simultaneously with liberation of the eggs, and (2) that the sperm should enter the zooidal cavity, again, through the coelomopore if cross-fertilization occured in this ctenostome. Trying to observe cross-fertilization in *Electra*, Marcus put ovulated eggs and sperm in water together, but the spermatozoids died. Ovary has been reported on the cystid [basal] wall, often in the proximal region of the zooid in this species. There were ten-twenty ovarian oocytes found in it after ovulation of the mature eggs. Up to seventeen ovulated oocytes of various shapes were recorded in the zooidal cavity. Spermatogenic tissue develops in separate locations on the zooidal [lateral and basal] walls too. Marcus recorded the simultaneous presence of male, female and hermaphroditic zooids in the same colonies, suggesting that all of them are hermaphroditic and were at different phases of their sexual cycle. He described egg liberation in detail, mentioning the strong deformation of the eggs during their passage through the intertentacular organ in *Electra*. He also recorded that some eggs were swallowed, and then defaecated without undergoing any external changes! The fertilization envelope became visible and the two (?) polar bodies were expelled soon after release. In *Farella* up to ten ovulated eggs were recorded, also passing through the coelomopore. Interestingly, Marcus thought that the eggs of non-brooding bryozoan species were richer in yolk than those of brooding forms.

Following Waters and Harmer, Hastings noted some reproductive structures in her taxonomic papers. In simultaneously hermaphroditic zooids of *Bugula uniserialis* Hincks, 1885 the ovary is said to be located in the funicular tissue just below the tip of the caecum, and the sperm fills the proximal region of the zooid. The female gonad contains either four small or one large egg in *Alderina irregularis* (Smitt, 1873), and sperm and eggs were also simultaneously found in the hermaphroditic zooids of *Discoporella umbelata* (Defrance, 1823). Hastings described heteromorphic female polypides in *Thalamoporella californica*. They are considerably smaller than that in other zooids, and Hastings suggested that their only function is that of oviposition. Up to four embryos are contained in the ovicells.[272] There is also some information on reproduction of *Stylopoma schizostoma* (MacGillivray, 1869) in her paper published two years later.[273] This author followed the successive stages of egg development, polypide cycling and ovicell formation in this species. Upon maturation of the large first egg, the first polypide degenerates and the ovicell starts to grow in this species. Egg enlargement continues during the polypide degeneration. Hastings criticized as non-substantiated the statement of Canu and Bassler,[274-275] who wrote that the female polypide constructed the ovicell in *S. spongites* (Pallas, 1766). In 1941 Hastings[276] recorded simultaneous brooding of up to seven embryos in the ovicells of *Scruparia chelata* (Linnaeus, 1758) (three embryos were recorded in this species by S. Mawatari in 1973[277]), comparing this phenomenon with the case of *Thalamoporella* and stressing the 'two-valved' apperance of their ovicells.

Faulkner[278] investigated the early germ cells in *Alcyonidium gelatinosum*, resulting in the formation of the ovary, and his data are largely in accordance with the descriptions of Calvet.[279] Sexual zooids are described as gonochoristic, simultaneously occurring in the colonies of this species. The prospective germ cells ('neoblasts') first appear in the zone of the actively dividing cells of the developing polypide bud. In this zone the epithelial layers of the zooidal wall and the polypide rudiment are confluent. 'Neoblasts' clearly differed from the other cells by the large size, nuclear characteristics, staining and position. They supposedly migrate between layers of the bilayered polypide bud, proliferate, and form a group ('neoblastic morula') between the epithelium of the developing caecum and mesothelial lining at the confluence of the funiculus. These cells stay undifferentiated, however. These totipotential cells may then either migrate through the basal membrane and take part in the development of the polypide gut (in the prospective sterile zooids) or form an ovary (in the case of the female zooids). Thus, 'neoblasts' should be considered as totipotential cells. Faulkner[280] noted that Silbermann[281] saw these cells, but did not recognize them.[282]

Zirpolo[283] confirmed the observations of Waters,[284] observing brooding in the tentacle sheath in *Zoobotryon verticillatum* (Delle Chiaje, 1828). In contrast, Braem[285] described embryos developing inside a special sac in the ctenostome *Sundanella sibogae* (Harmer, 1915) (as *Victorella*). Judging from his illustrations, this sac is an invagination of the zooidal body wall. The changes of structure in their walls during brooding together with the very large increase of embryonal size implies that he discovered a placenta in this bryozoan: the polypide degenerates and the mature embryo occupies most of the zooidal

cavity. Braem supposed that the embryo escaped through the 'neck' – a narrow distal part of the incubation sac with a narrow lumen inside. Silén[286-287] found similar sacs in the ctenostome *Nolella papuensis*, describing its wall as thick when containing the large embryo, and as thin when the embryo is small. It seems that placental brooding is represented in this species too. However, Silén's interpretation of the sac structure was that it is formed not by wall invagination, but by epidermal cell immigration (see below).

Stach[288] studied reproduction in the cheilostome *Carbasea indivisa* Busk, 1852; colonies consisted of sterile, male, female and occasionally, hermaphroditic zooids. Presence of both gonohoristic and hermaphroditic zooids might be evidence that all sexual zooids are actually hermaphroditic with strong protandry/protogyny in this species. The ovary contained four-seven oocytes, these being suspended on the funicular strands near the proximal transverse and lateral walls. The polypide usually undergoes recycling during oogenesis. Spermatogenic tissue develops on both lateral and transverse (distal and proximal) walls. It is reported that after fertilization ovulated oocytes increase in size, and have an irregular outline. Oviposition was not observed, but three-seven released eggs become attached to the lower surface of the zooidal operculum, being surrounded by the transparent 'brood-sac'. The brood-sacs are described as developing from the distal portion of the tentacle sheath [obviously, vestibulum] that forms the inner wall of the operculum. There are some differences in the timing of embryo development, apparently depending on differences in the timing of egg liberation. The second generation of oocytes often appears in zooids bearing the embryos. Larvae escape from the brood sac supposedly through the rupture of its wall. One can suggest that the 'brood-sacs' are fertilization envelopes sticking to the operculum.[289]

A brief review on sexual reproduction was published by Marcus in his book on Bryozoa.[290] The following papers by this author are an outstanding combination of data on taxonomy, morphology and reproductive biology.[291-293] Like many of the works of this prominent zoologist they were written in Portuguese (with an English summary). Marcus showed a sequence of the appearance of male and female zooids in colonies of the cheilostome *Celleporella hyalina* (as *Hippothoa*), calling them protandrous, and stressing that self-fertilisation is impossible when the male and female sexual cells mature at different times in gonochoristic zooids. He did not find the parietal muscles of the ascus in females and was sure that the rudimentary polypide could not protrude in this species (these muscles were later found by Ostrovsky[294]). In contrast, protrusions of the rudimentary male polypides of six tentacles [obviously, non-ciliated] were incidentally observed, and spermatozoids were discovered in the zooidal cavities of all three zooidal types. Based on this, Marcus suggested that sperm 'in search of the eggs'[295] could migrate through the pore-chambers, being accepted first by the expanded lophophores of autozooids, in which he found the coelomopore. He discovered spermatozeugmata in the cheilostome *Biflustra savartii* (Audouin, 1826) (as *Acanthodesia*), but showed that fertilization is monospermic. In this and sixteen more gymnolaemate species either the supraneural pore (Marcus's term) or intertentacular organ were found. Marcus gives a list of species and papers where similar observations were described.

Among the most interesting and important findings was a discovery of the precocious intraovarian fertilization [insemination] in a number of cheilostomes and two ctenostomes (*Alcyonidium mamillatum* Alder, 1857 and *Nolella stipata* Gosse, 1855 (as *N. gigantea*)). As mentioned above, previous authors believed that this event occurs after ovulation or later. Marcus believed that this finding connects the timing of gonadal maturation with fertilization. He wrote that fully grown ovary in zooids without testes may already contain the [alien] sperm suggesting cross-fertilization. However, distinct protandry [in hermaphroditic zooids] 'by no means indicates that there must be reciprocal fertilization'[296] since even early oocytes can be inseminated in the same zooid by its own sperm. From this finding it also follows that simultaneous maturation of the gametes in a zooid or colony cannot be evidence for self-fertilization if the fusion of the male and female cells is precocious (in other words, it occurred before own sperm maturation). Marcus noted that fusion of the male and female cells happens 'in the beginning of their [oocytes] second growing period'.[297] In fact, the diameter of inseminated oocytes found was about 20 μm in *Celleporina costazii* (Audouin, 1826) (as *Siniopelta*) and *Rhynchozoon phrynoglossum* Marcus, 1937, when vitellogenesis did not start yet. In the ctenostomes *A. mamillatum* and *N. stipata*, sperm was found in the oocytes 'which are still growing'.[298] Four of Marcus's figures[299] (Estampa III, figure 8B, Estampa XXI, figures 58-60) of cheilostome ovaria show previtellogenic or early vitellogenic oocytes or oocytic doublets with a male pronucleus inside. The ovary contains several inseminated oocytes, and the sperm heads were also found between the ovarian cells. Mature oocytes are decribed as being not completely covered with follicular cells, but partially exposed to the zooidal coelom. Confirming the data of Prouho,[300] Marcus found internally brooded embryos on the wall in the ctenostome *Nolella dilatata*, *N. stipata* and *N. alta* (Kirkpatrick, 1888), but wrote that they develop in sacs (without any comments about the sac structure). Eggs were desribed as differing in the amount of yolk – 'scarce in *Bugula*, considerable in *Hippopodina*' [oligo- and macrolecithal, correspondingly].[301] Maturation divisions started in the ovary or just after ovulation [Marcus obviously meant a breakdown of the germinal vesicle]. In contrast with all other oviparous species studied, *Electra bellula* (Hincks, 1882) shows only one egg, that is however larger than the eggs in the brooding species. It is not clear if *Electra bellula* actually belongs to malacostegans. We found no mention in Marcus's paper that he observed its egg or larval release, saying only that it 'shows only one mature ... egg'.[302] Thus, it could be an internal brooder.

Marcus clearly understood the role of the hypertrophied epithelium in the oocial vesicle in cheilostomes. He recognized the presence of extraembryonic feeding in *Bugula avicularia* and *Celleporella hyalina* (as *Hippothoa*), comparing them with non-placental cheilostome brooders and mentioning the similar finding of Waters[303] in the catenicellid cheilostome *Catenicella elegans* (as *Vittaticella*). He noted that the placenta develops after the beginning of cleavage and is reduced after larval release, he also mentioned that hypertrophied cells of the embryophore supply the embryo with an 'albuminous liquid' in *Bugula*. His data on size of the mature eggs and early and late embryos show the possibility of extraembryonal nutrition in *Hippopodina feegensis* (Busk, 1884) and

Catenicella elegans. However, Marcus stated that there is no such nutrition in *C. contei* (Audouin, 1826), again comparing size of the egg and the embryo. He suggested that synchronized growth of both the next egg in the ovary and the nourishing embryo in the ovicell is regulated hormonally. Studying the embryognesis of *Bugula* species, Marcus recorded the formation of two polar bodies that remain within the fertilization envelope.

In his 1941 paper,[304] the most valuable information was that regarding the reproductive biology of *Thalamoporella evelinae* Marcus, 1939. This species was described as having gonochoristic zooids. In contrast with male and sterile zooids, females are characterized by a smaller polypide with fewer tentacles, a very large intertentacular organ (later Maturo[305] described a tube-like 'ovipositor' – in cheilostome *Schizoporella* cf. *pungens*) and two operculae, separately closing the ovicell and the zooidal orifice. These were described first by Levinsen[306] (see also works of Harmer[307] and Hastings[308]). Spermatozoids united in pairs, supposedly leaving the male zooid via the coelomopore and entering the female coelom through the intertentacular organ. Insemination is intraovarian and monospermic. Ovary develops from the peritoneal cells of the basal cystid wall in the distal part of the female zooid. A thin and perhaps incomplete follicle envelops the growing oocyte, whereas the basal pedunculate part consists of somewhat elongated cells with pale cytoplasm surrounding the 'ovarian channel' [slit-like lumen between the cells in the lower part of the ovary]. Marcus discovered that oocytes develop in pairs (according to his illustrations, an ovary can contain up to five oocytic doublets), in which one of the cells plays the role of nurse. Actually, he saw and depicted this phenomenon in the previously discussed paper too,[309] but did not mention it. According to his description, the nurse cell fuses with another oocyte when both reach 20-30 µm in diameter (in all other neocheilostomes the oocytic doublets are the result of the arrested cytokinesis), and its cytoplasm is incorporated to that of the latter. Shortly after fusion the 'twin oocyte' is fused with a spermatozoid. The doublet grows, and when it reaches the final size, the nurse-cell nucleus migrates through the cytoplasm to the vegetal pole where it is expelled. Marcus also thought that the oocyte could be nourished on account of the 'yolk stored in the peritoneal cells', and by the special location of hypertrophied peritoneal cells adjoining the leading oocyte. Cells of the ovarian wall accumulate presumptive yolk granules, exocytosing them to the 'ovarian channel', from which location they could be accepted by the growing oocyte. Up to six embryos of different ages were recorded as being brooded in the ovicell. Marcus described an intertentacular organ in *Alcyonidium polypylum* Marcus, 1941. The ovary is placed in the proximal region, whereas spermatogenic tissue occurs in the proximal as well as distal regions of hermaphroditic zooids of this species.

In the same year Marcus[310] published a paper on the cheilostome *Synnotum* sp. (as *S. aegyptiacum*), in which he discovered intracoelomic brooding (viviparity). In this species different gonads appear simultaneously in paired gonochoristic zooids. Females are larger than males. The ovary in this case produces two-three oocytes, one of which develops into an embryo inside the maternal zooid whose polypide degenerates. Marcus 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'.[311] The late embryo is fifty to sixty times larger than the mature ovum before cleavage, this is good evidence for extraembryonic nutrition.

Cori[312] reviewed bryozoan sexual reproduction in his textbook. It mainly correctly characterizes this complex phenomenon, except that polyspermy and autogamy are considered to be common for all Bryozoa, and ooecium was said to develop as a part of the maternal autozooid. It should be noted, that studying *Zoobotryon verticillatum* (as *Z. pellucidum*), Cori found and depicted spermatozoids in the coelomic lumen of the tentacles. Later Brien[313] mentioned this, suggesting that sperm is released via the terminal tentacular pores. Cori presented one of the most complete lists of the literature on Bryozoa for this period.

Silén[314] investigated the ctenostome *Labiostomella gisleni* Silén, 1941 (as a cheilostome), recording more than one hundred oocytes simultaneously occurring in its very long ovary. However, he came to the conclusion that only one embryo is developed during the life span of each fertile zooid. Zooids are stated to be hermaphroditic and protogynous. Silén described the different stages of oocytic growth, measured them, discussed ovulation and fertilization, and noted accumulation of the ovulated oocytes in the distal part of the autozooid. He also noted the presence of male nuclei inside them. Since no ripe spermatozoids were found in testes, he suggested that the the sperm came from outside, fusing with eggs in the distal region of the zooid. One embryo per zooid developed inside an embryo sac [with the structure implying a presence of extraembryonic nutrition] within the coelom of the maternal zooid; this is accompanied by polypide degeneration. Silén admitted that the sac is an invagination of the body wall, but speculated that its formation is strongly modified, developing by migration of the ectodermal cells inside the zooidal cavity, these overgrowing and enveloping the fertilized egg. Comparing this embryo sac with that found in ctenostomes *Sundanella* and *Nolella*, he came to the conclusion that they are homologous, having the same type of development. It was suggested that larval release occurs through the rupture of the sac and the zooidal aperture. Based on these findings and the ovicell anatomy of cheilostome *Scrupocellaria scabra* Silén proposed a hypothesis suggesting that cheilostome ovicells originated from an embryo sac such as that of *Labiostomella*. He also considered the brooding structures throughout the phylum to be homologous, originating from the modified polypide. The cyphonautes is stated to be a derived larval type.

Several years later Braem,[315] investigating the ctenostomes *Bulbella abscondita* Braem, 1951 and *Victorella muelleri* (Kraepelin, 1877) (as *Tanganella*) showed that oviposed zigotas stick either to the vestibulum or to the external zooidal wall. In *Bulbella*, the ovary is positioned on the cystid wall in the middle region of the zooid. Between four and six eggs are released through the reduced intertentacular organ, being further brooded in the cavity of the vestibulum when the polypide is retracted and exposed outside when it is extended. If eggs became separated from the maternal zooid they did not develop successfully. In *Victorella* both ovary and spermatogenic tissue are on the cystid wall in the distal part of the hermaphroditic zooid. Eggs are numerous, but, similar to *Bulbella*, they mature in succession, being released through the supraneural pore, and sinking into

the special protuberance of the body wall that forms the invagination or brooding sac. When the polypide is retracted, embryos (normally three) are placed in the vestibulum. Thus, Silén's suggestion about the structure of embryo sacs in ctenostomes was not supported.[316] Braem[317] also recorded brooding in the vestibulum of *Bowerbankia gracilis* Leidy, 1855 (as *B. caudata*) after polypide degeneration. The ovary is in the middle part of the hermaphroditic zooid, being positioned on the cystid wall in the place of the funiculus attachment. Spermatogenic tissue was found on the cystid wall too, but more proximally. The mature egg is pushed through the pore in the rudiment of the tentacle sheath of the replacement polypide and into the vestibulum. These findings were in accordance with the observations of Joliet, who found the same phenomenon in *Walkeria uva* (as *Valkeria cuscuta*). Additionally, both ovary and spermatogenic tissue were found on the cystid wall in the distal part of the hermaphroditic zooids in the non-brooding ctenostome *Victorella pavida*. In contrast with all species mentioned above, its oocytes are small, and mature and ovulate in cohorts. After ovulation they possess an irregular shape. In addition an intertentacular organ was found and studied in histological sections. We should note that much confusion exists with this species that has been considered as a brooder in the monographs of Hyman[318] and Hayward.[319] This contradiction is discussed and explained by Jebram and Everitt.[320]

Despite the fact that many researchers kept bryozoans alive for a long time, there are very few records concerning observations on the reproductive activities of living animals in the literature. In his next paper Silén[321] documented the results of some summer observations on the reproductive biology of several gymnolaemate species under experimental conditions, comparing brooding and non-brooding species. Simultaneous hermaphroditic zooids were recorded in *Membranipora membranacea*. In *Callopora dumerilii* (Audouin, 1826) (as *C. dumerili*) (also referring to *Escharella immersa* and *Fenestrulina malusii* (as *F. malusi*)) he observed, carefully described and measured the duration of the oocytic growth, ovulation, post-ovulatory period (following Gerwerzhagen,[322] Silén stated that the destruction of the follicular wall is triggered by the moving caecum of the polypide that further carries the ovulated egg to the distal part of the maternal zooid), oviposition and synchronized development of the embryo and the following oocyte, repeating the idea of Marcus[323] about hormonal regulation of this synchrony. Development of the ooecium is said to be triggered by the beginning of the ovarian activity through hormonal regulation. In *Callopora dumerilii* at least three to four eggs are successively developed in the female gonad during the reproductive season in experiments, and it takes approximately two weeks for each egg to mature. Embryonic development takes the same time in the ovicell, and these events are correlated in time. Thus, the repeated use of the ovicell was proven.[324] It was also suggested that the limited space of the incubation cavity restricted the number of oocytes produced in the ovary. The '*Membrana vitellina*' [fertilization envelope] surrounding the embryo was found to appear in the ovicell. Since embryos could not develop outside the ovicell, it was concluded that the chemical composition of fluid inside the incubation cavity differs from the sea-water, and the ooecial vesicle is responsible for that. The intertentacular organ and coelomopore were

considered as homologous and secondarily evolved structures, used not only for oviposition, but also, possibly, for the acceptance of alien sperm. Thus, Silén tended to favour the concept of cross-fertilization. Larval release through the 'embryonary' is suggested as a primitive condition. Such 'embryonary' [actually, invagination of the cystid wall] seems to have been found in the ctenostome *Nolella,* but that species also has a supraneural pore (recorded by Marcus[325]) that Silén thought initially evolved in connection with some other function.

Crucially, it was realized that further progress in research on bryozoan reproduction would be impossible without seasonal observations and studies of life history. Borg[326] undertook an investigation of the life cycle of cheilostome *Electra crustulenta* (Pallas, 1766), using material collected throughout the year. Judging from his description, zooids are simultaneously hermaphroditic in this species. Borg correctly noted that the term 'testis' could hardly be applied to the diffuse male elements that started their development from the mesodermal lining of the cystid wall as well as on the funicular strands, further moving to the visceral coelom. He described ovaries as being one or several, developing in a connection with the caecum. Borg often referred to the paper of Schulz[327] (see above), who also mentioned the plural nature of the ovarium in this species. The maximal number of eggs in one ovary was up to sixteen. Borg recorded the presence of gonads and the state of the polypide throughout the seasons, suggesting a correlation between polypide cycling and sexual reproduction. Moreover, he stated that the main function of the cycling is not excretion, and that 'the de- and regeneration of the polypides must have begun in connection with sexual reproduction in order to empty the genital cells and supply food for the growing brood'.[328] Another of his conclusions was that the formation of an intertentacular organ is indispensably combined with polypide replacement. Later Silén,[329] studying living material, challenged this statement because he observed that this organ forms in the existing polypide upon the maturation of eggs, this was further supported by Jebram,[330] Hageman[331] and by Cadman and Ryland.[332]

Studying reproduction of the cheilostome *Bugula flabellata*, Corrêa[333] described colonial zonality, based on the polypide and sexual cycling of a Brazilian population. She observed spermato- and oogenesis, developing ovicells, the oviposition of the mature egg into the ovicell, and development and regression of the hypertrophied epithelium of the ooecial vesicle on the onset and the completion of brooding. She also found the sperm head in early intraovarian oocytes in accordance with the findings of Marcus,[334-335] calling the eggs as oligolecithal-homolecithal and stating that (self-)fertilization is monospermic in this species. Interestingly, in a British population of this species, protogyny was recorded,[336] whereas Corrêa noted slight zooidal protandry. Three polar bodies have been recorded being surrounded by the fertilization envelope together with a zigota. Remarkably, Corrêa recorded two embryos in the same ovicell, being in the same stage of cleavage, and suggested that they were oviposited by the polypides of two neighbouring zooids. Additionally, she found a supraneural pore in *Membranipora commensale* (Kirkpatrick and Metzelaar, 1922) (as *Conopeum*).

Silén[337-338] discovered specialized brooding zooids ('gonozooids') with external incubation sacs in three burrowing ctenostomes from the genus *Penetrantia*. According to the original description, the wall of the brooding sac is made of cuticle, but the method of its formation and the exact structure are not clear. Silén called it a 'pouch of the exterior wall',[339] suggesting that the 'gonozooid was composed of two zooids, an older, dead one and a younger, living one developed inside the former'.[340] Thus, the brooding cavity is explained as a space between two cuticular walls – external (wall of the first zooid in which epithelial cells vanished) and internal (belonging to the new zooid). However, Ström[341] speculated that the brooding sac might be a thickened fertilization envelope. Additionally, Silén described an ovary in *P. densa* Silén, 1946, stating that the embryo starts its development inside the zooidal cavity, later being transferred to the incubation pouch. He suggested three possible variations for oviposition, but further research is necessary to figure out the brooding phenomenon in this group. Silén also found an embryo brooded within the tentacle sheath in *Immergentia californica* Silén, 1946.

5. Second half of the 20th century – a period with large reviews and new discoveries

Soule and Soule largely confirmed the findings of Silén. A number of burrowing ctenostome brooders with both types of brooding mentioned were described in a series of their papers.[342-346] In particular, focus was placed on the genera *Penetrantia* (brooding in 'gonozoid') and *Spathipora*, *Immergentia* and *Terebripora* (brooding in introvert). Bobin and Prenant[347] confirmed the data of Soule, describing brooding in the introvert in *T. comma* Soule, 1950 (for the records on reproduction and brooding in Ctenostomata see works of Prenant and Bobin,[348] d'Hondt,[349] and Hayward[350]).

In 1951 S. Mawatari published a paper,[351] dealing with the cheilostome *Tricellaria occidentalis* (Trask, 1857), and there is some information on its reproduction. Zooids are said to be non-simultaneously hermaphroditic in this species. Also Mawatari briefly described oogenesis, and it is clear from his text and illustrations that the oocytes developed in pairs.

In the next year the same author[352] published the results of his detailed study on *Watersipora subtorquata* (d'Orbigny, 1842) (as *W. cucullata* Busk). According to his description zooids are simultaneously hermaphroditic, that is why self-fertilization is considered usual for this species. Spermatogenic tissue develops in different sites on the surface of the lateral and proximal transverse cystid walls and compensation sac. The ovary is positioned on the lateral or transverse walls in the distal part of the maternal zooid, and four to five oocytes are said to develop within it. It is clear from the illustrations that they are arranged in doublets. One or more sperm heads were detected in the growing oocyte, but fertilization is stated as being monospermic. The large leading oocyte ovulates, 'moves ... under the vestibule, and is enveloped within the embryo sac'.[353] Mawatari's figures 20-38 and 44 show the embryo sac as an evagination of the vestibulum, but the author did not go into detail regarding its structure. The polypide degenerates at

the onset of brooding, during which time an embryo occupies the distal part of the zooidal cavity. A new oocyte begins its growth in the ovary after larval release and polypide cycling. Unfortunately, it is impossible to state whether there is or is not extraembryonal nutrition during brooding in this species, since the size of the eggs and embryos has been not mentioned, and scale bars and magnifications are absent in the paper. However, there is some indirect evidence, such as the appearance of the embryonal sac wall during brooding, and the relative size of the early and late embryos. Also Zimmer[354] recorded that the embryo grows during embryogenesis in *W. arcuata* Banta, 1969.

The splendid text-book of Hyman[355] ranked among the main sources consulted by two generations of zoologists. Apart from the extensive review on bryozoans (including their sexual reproduction), Hyman made a very complete list of references. Concerning reproduction, quite a number of data included were, unfortunately, not precise (or just wrong) or wrongly interpreted, and this part of the monograph represents mainly historical interest at the moment. The same can be said of the text-books authored by Brien[356] and Kaestner.[357] Interestingly, in discussing possible methods by which mature spem might leave the zooidal cavity, Brien notes liberation through the 'pore génital', the terminal pores of the tentacles (mentioning the finding of the sperm inside the tentacle cavity made by Cori[358]) and during the polypide recycling. In the latter case, it is said that sperm could be released by the regenerating polypide, being incorporated in the brown body first. We suppose that this idea is based on the suggestions of Borg,[359] who thought that the polypide cycling is mainly 'to empty the genital cells'. Following previous authors, Brien discussed both (auto- and cross-) opportunities for fertilization in Bryozoa.

A series of papers on ctenostome reproductive biology were published during the 1950s and 1960s. It started with the classical work of Braem,[360] who described several different variations of brooding (see above), and who critically suggested an evolutionary trend towards better protection of the embryos. Chrétien[361] studied development of the ovary in *Alcyonidium diaphanum* (Hudson, 1762) (as *A. gelatinosum*). She recognized 'cellules initiales femelles' [oogonia] by the presence of enlarged nuclei, lying between epithelium and mesothelium at the proximal end of the polypide bud, at a stage when the latter comprises the hollow vesicle – future gut and rudiment of the lophophore. Oogonia are said to be of 'mesenchymatic origin', and the statements of Faulkner[362] about their origin from the region of the polypide bud proliferation was rejected. Following mitotic divisions [and differentiation], a group of six to ten small 'young oocytes' is formed in which cell membranes appear a little later. A similar picture was painted by Pace[363] in *Flustrellidra hispida*, and it is not clear if the cell membranes are absent or were not distinguished. Chrétien identified a series of stages showing related events in the development of the ovary and polypide cycle, following these events through the autumn in the aquarium. 'Cytoplasmatic growth' of the oocytes begins before the complete differentiation of the polypide, and nutrition is supposedly provided by the specialized caecal cells: in the place where the ovary is in the contact with a gut, the special cells with tongue-like parts and papillae were protruded into the caecal lumen. Peritoneal cells multiply, spreading over the oocytes to form a follicle. Commencement of the vitellogenesis

is accompanied by further multiplication of the follicle cells, forming a double layer. Later such a double-layered follicle was recorded in *Alcyonidium hirsutum* by Owrid and Ryland.[364] Polypide degeneration begins before vitellogenesis starts, and, judging from the description, fertilization occurs only after complete regression of the polypide, intraovarialy. Four to five oocytes reach maturity, whereas the rest are aborted. Mature oocytes occupy most of the zooidal cavity, and their follicles are flattened at this stage. Chrétien carefully described vitellogenesis, starting from the successive formation of several ribosomal aggregations ('caps') by the nucleolus. Yolk granules are accumulated at the periphery first, and then throughout the ooplasm. Additionally, in vitellogenic oocytes she demonstrated the presence of large amounts of protein and polysaccharides as well as numerous lipid droplets that appear at the later stages, using histochemistry.

Bobin and Prenant[365] showed that polypide degeneration is connected with the maturation of the ovary in *A. gelatinosum*. Grellet[366] investigated the structure of the testis and spermatogenesis in *A. diaphanum* (as *A. gelatinosum*), mentioning that spermatogenic tissue is associated with a funiculus that possibly supplies it with nutrients, being independent from the polypide. He also noted the male germ cells in the cystid peritoneum. Ranzoli[367] studied cytological characters of the oocytes in *Zoobotryon verticillatum*. Matricon[368] found that ovary develops in a connection with the polypide, and brooding of four to six embryos takes place inside the incubation pouch, developing after polypide degeneration between the vestibule and degenerated tentacle sheath in *Alcyonidium polyoum*. Matricon suggested that eggs enter the brooding pouch through the newly developed ciliary funnel leading to supraneural pore. In another paper Matricon[369] recorded testes developing on the lateral and basal cystid walls in this species. Banta[370] described larval brooding in the tentacle sheath in *Mimosella cookae* Banta, 1968. Since the volume of the embryo strongly increases during its development, one can suppose that extraembryonic nutrition occurs in this species. Similar enlargement was depicted by Joliet[371] in *Walkeria uva* (as *Valkeria cuscuta*). Ström[372] discovered external brooding in the ctenostome *Triticella flava* Dalyell, 1848 (as *T. koreni*) that is strongly reminiscent of the case of *Paludicella articulata*[373] (later a similar type of brooding was also described[374] in *Panolicella nutans* Jebram, 1985). However, in contrast with *P. articulata*, there are up to twenty embryos in the sticky fertilization envelopes that attach to the maternal zooid in *Triticella* (see also Eggleston[375]). Only early development takes place in such a position (discussed in Ström[376]). Ström found the spermatozoids attached to the tentacles of the expanded lophophores in this species, and showed that two polar bodies remain within the fertilization envelope. Castric-Fey[377] recorded the presence of an intertentacular organ in *Alcyonidium argyllaceum* Castric-Fey, 1971.

Cook published a series of papers dealing with the early larval development of several malacostegan cheilostomes. In *Electra crustulenta* and *Conopeum seurati* (Canu, 1928) (as *Membranipora*) she observed development of the intertentacular organ and deflecting behaviour of the tentacles during extrusion of the eggs (after which some of them were incidentally swallowed by the neighbour lophophores). The intertentacular organ was thus protruded as far as possible above the surface of the colony.[378-379] Egg liberation

through the intertentacular organ was recorded in *Electra monostachys* (Busk, 1854) and *Conopeum reticulum* (Linnaeus, 1767).[380] The number of eggs per zooid, their average size and duration of the egg extrusion were measured. Studying the cheilostome *Steginoporella buskii* (Harmer, 1900) (as *Steganoporella*), Cook[381-382] recorded the internal brooding in this species, and noted that the polypide degenerates and the cryptocyst is strongly reduced as the embryo grows. She found that there is a direct correlation between the size of the embryo and reduction of the zooidal cryptocyst.

In 1966 Silén published his famous paper[383] in which he described the liberation of sperm via the terminal pores of the two distomedial tentacles in three species of *Electra* and *Membranipora membranacea*. The long-term enigma of bryozoan cross-fertilization was solved, although many questions remained. All the main events of gonado- and gametogenesis and their duration as well as the later destiny of the sexual cells was followed by observing living colonies of *Electra posidoniae* Gautier, 1961 and *E. crustulenta*. Here colonies consist of hermaphroditic zooids that are either protandrous or, occasionally, simultaneous in the former species, and simultaneous in the latter. There are also males developing towards the end of reproduction in *E. posidoniae*. Spermatogenic tissue develops laterally beneath the frontal and, obviously, basal cystid walls except the distal region of the zooid. The ovary is placed proximally on the funiculus, and usually eight to nine (up to twenty) eggs are developed in *E. posidoniae* while six are depicted in Figure 5 for *E. crustulenta*. An intertentacular organ develops only in the existing polypide of the hermaphroditic zooids when they reach maturity. Evacuation of both eggs and sperm may be synchronized in the large parts of the colony (also observed in *Membranipora membranacea* by Zimmer[384]) and often involves several neighbouring colonies. However, the sperm and the eggs are released non-simultaneously in the same colony. The lophophores, liberating sperm, do not retract sometimes for several hours. Spermatozoids from the body cavity travel along the lumens of two dorsomedial tentacles, escape from them via the terminal pores, and then drift away with the seawater. Being captured by the feeding current of a nearby lophophore, they actively stick to the non-ciliated abfrontal surface of the tentacles, then move towards the intertentacular organ when the eggs enter it in *E. posidoniae*. In *E. crustulenta* sperm was observed inside the intertentacular organ. Silén ascribed an important role to chemotaxis, during the process where the spermatozoids are searching for the egg. The fertilization envelope appears approximately one hour after the egg is released. Based on this, Silén suggested that fertilization takes place externally in the first species and inside the intertentacular organ in the second. A similar suggestion was made by Prouho[385] (see above). Nevertheless, Silén admitted that theoretically sperm could enter the zooidal cavity through the intertentacular organ or supraneural pore too, and cross-fertilization could occur in the body cavity. Returning to the earlier idea of Joliet,[386] Silén speculated that fertilization in larviparous forms could be achieved during oviposition. Strangely, the data of Marcus[387] who discovered precocious intraovarian fertilization in brooding Gymnolaemata are overlooked or ignored, despite his paper being cited. Also Silén's[388] own finding of the male nuclei inside the ovulated oocytes in *Labiostomella gisleni* was not mentioned or discussed.

Bullivant[389] confirmed the data of Silén,[390] recording sperm release through the terminal pores of all the tentacles in the ctenostome *Zoobotryon verticillatum* and cheilostome *Schizoporella unicornis* (Johnston in Wood, 1844). Except for 'passive' evacuation, numerous spermatozoids were released on retraction of the lophophore. In his second paper on the 'fertilization problem' Silén[391] added eight cheilostome and two cyclostome species to this list. It should be noted that only malacostegan cheilostomes released their sperm via two distomedial tentacles.

At approximately the same time, male heteromorphic polypides were recorded in several Cheilostomata. Earlier the first observations of the protruded male polypides were made by Marcus[392] in *Celleporella hyalina* in which he counted six tentacles (see above). Four tentacles were found in males of *Celleporella tongima* Ryland and Gordon, 1977 (as *Hippothoa*).[393] In *Odontoporella adpressa* (Busk, 1854) (as *Hippopodinella*) Gordon[394] described them as having a few (later Cook[395] recorded eight - four short and four elongated) long, unciliated tentacles, which are not expanded in the usual bell-shape and possessing distinct behaviour. Skeletally these zooids do not differ from others, possibly developing normal feeding polypides after degeneration of the male ones. Similarly, Carter and Gordon[396] described male polypides with eight tentacles and a vestigial gut in *O. bishopi* Carter and Gordon, 2007. Cook[397] recorded heteromorphic lophophores in larger zooids, possessing six non-ciliated tentacles of the different length, and described their behaviour in *Hippoporidra senegambiensis* (Carter, 1882). Male polypides demonstrated rapid sweeps in one plane, but in different directions, being protruded for five to ten minutes. Identical behaviour of the polypides of four tentacles was recorded in *H. littoralis* Cook, 1964.[398] Groups of male zooids with lophophores of two long tentacles without cilia were also recorded in *Hippoporidra* sp. Concerning sperm dispersal, Cook[399-400] suggested that these groups may also act as passive excurrent outlets. Chimonides and Cook[401] observed a special behaviour of the elongated lophophores of paired, unciliated tentacles in *Selenaria maculata* Busk, 1852. These male zooids develop on the periphery of the colony, and their lophophores often protrude simultaneously in small groups. Sections confirmed the presence of the sperm inside their zooidal cavity. Also sperm was found in several large ovarian oocytes, developing in the subperipheral female zooids. Zonal position of the zooids of the different sexes corresponds with the direction of the colonial water currents – the sperm should be moved from the colony without being caught by the female zooids in such forms. Detailed reviews on the sexual zooidal polymorphism in Bryozoa have been published by Silén,[402] who proposed a modified terminology, and by Cook.[403]

Franzén[404-412] published a series of papers and reviews on bryozoan sperm morphology, development and fertilization biology, analysing both his own results and those of others. In addition, oocytic structure and oogenesis were briefly described in his review on bryozoan spermatogenesis published in 1977. Special attention was paid to the comparison of spermatozoid ultrastructure within the three main bryozoan groups – Phylactolaemata, Stenolaemata and Gymnolaemata. Eventually, the sperm structure supported a hypothesis that two latter classes are more closely related with each other than either of them is with

the Phylactolaemata. Franzén concluded that the sperm of bryozoans appears to be highly modified from the morphology that she considered representative of the primitive condition, and characteristic of external fertilization. According to his hypothesis, the morphology of bryozoan sperm is indicative of internal fertilization. Franzén[413-414] confirmed the data of Bonnevie[415] on the presence of spermatozeugmata in *Membranipora membranacea* and *Electra pilosa*. Some aspects of the sperm ultrastructure in *Bugula* sp. and *Membranipora* sp. were studied by Reger[416] and Zimmer and Woollacott[417] correspondingly, and it was shown that spermatozeugmata consist of thirty two or sixty four spermatozoids in *Membranipora*.

Woollacott and Zimmer[418] redescribed the placenta and confirmed the data of previous authors on the ooecial development from the distal zooid in *Bugula neritina*.[419] In their two following papers they presented the results of a TEM-investigation of the placental system in this species. The embryophore was reported to consist of two main elements – hypertrophied epidermis of the ooecial vesicle and associated funicular strands, presumably transporting nutrients for embryonal development. Adjacent to the embryophore part of the embryo, the epithelium is differentiated for the uptake of nutrients. At the onset of brooding, the embryophore undergoes a dramatic transformation in size, cell structure and morphology, and the funicular plexus enlarges to cover a large surface area over the basal ends of the hypertrophied cells, these show obvious signs of synthetic and transport activities. Apical parts of the epidermal cells of both the ooecial vesicle and the embryo are folded, developing microvilli (in embryophore) and infoldings (in embryo), and performing exo- and pinocytosis correspondingly. Woollacott and Zimmer suggested that this transport might be bi-directional, and that the embryophore could also accept waste from the embryo. It is particularly interesting that the transfer of matter should occur through the cuticle of the ooecial vesicle inferring an osmotic gradient mechanism. The fertilization envelope, surrounding the early embryo, was not evident at the advanced stage. It was recorded that the embryo increases by about 500 times in volume during brooding. Additionally, these authors stated the presence of three reproductive patterns, based on the types of oogenesis and brooding in Bryozoa.[420-421]

In the late-1960s and 1970s research on bryozoan reproductive anatomy and behaviour was extended by the addition of ecological studies.[422-427] Among others[428-429] are the papers of Gordon[430] and Eggleston,[431-432] who undertook investigations on bryozoan reproductive ecology, studying their breeding seasons in particular and life-cycles in general. Among twenty-three species of the New Zealand Bryozoa studied, Gordon, recognized three 'breeding patterns' depending on the season and duration of the reproductive activities. He also made an attempt to classify their 'brooding habits'. Interstingly, in making sections of *Macropora levinseni* Brown, 1952 (as *Macropora grandis* (Hutton) var. *levinseni* Brown), Gordon found two to four simultaneously brooded embryos in the ovicells. It was the third cheilostome genus (except *Scruparia* and *Thalamoporella*), which broods several embryos in these incubation chambers. Eggleston studied the term and duration of both reproductive season and colony longevity, recording gonadal acivity, brooding, spawning and larval settlement with pictures and descriptions in more than fifty

bryozoan species from the Isle of Man. He divided all the species studied into four groups (those living less than a year, annuals, biennials and perennials), depending on the longevity of life of their colonies and the number of breeding/non-breeding generations presented through the seasons. It was shown that the number of embryo-bearing zooids in the colony and the embryo size and speed of embryonal development are related to the longevity of the colony of the species. In general, lesser longevity means that a higher percentage of zooids brood, their larvae are smaller and their development is faster. The size at which the colony begins to reproduce is related to the length of the breeding season and the longevity of the colony. Most shore species have a short breeding period that is probably connected with instability of the environment on the shore. Eggleston also suggested that internally brooded embryos are better protected against environmental variations, so internal brooders frequently occur in the upper littoral, where they are often exposed to drying. In *Bicellariella ciliata* Eggleston described sexual colonial zonality (sometimes repeated), and discovered external brooding in the 'membrane sacs' in *Eucratea loricata* (Linnaeus, 1758) along with internal brooding of several embryos simultaneously in *Oshurkovia littoralis* Hasting, 1944 (as *Umbonula*). Internal brooding in this species was recorded first by Hastings.[433] Later she mentioned an 'internal ovisac' in it.[434]

Dudley[435] observed reproduction in the cheilostome *Conopeum tenuissimum* (Canu, 1928), recording the timing of the appearance of the gonadal and the subsequent release of the gametes. Zooids in this case are protandrous hermaphrodites, with the intertentacular organ developing after the first polypide cycle in this species. Mawatari[436] and Mawatari and Mawatari[437] studied the similar life cycle of *Membranipora serrilamella* Osburn, 1950. Zooids are protandrous hermaphrodites. Testes develop just beneath the lateral and proximal region of the frontal membrane, whereas ovary develops in the distal half of the zooid [the wall is not specified]. These authors recorded more than forty ovulated eggs per zooid in this species. Two or more eggs are usually found in the intertentacular organ during their release. The eggs that were incidentally swallowed are defaecated soon afterwards. A fertilization envelope is formed after the liberation of the zygote that transforms from a flattened circular disk to a sphere with a diameter about half the size. Interestingly, despite the numerous observations made by these authors they failed to observe polar bodies, suggesting that these break away and degrade at an early stage in this species.

Ryland reviewed sexual reproduction in Bryozoa in his books.[438-439] Both reviews are rather short, but they include all the main discoveries made from the time of the monograph of Hyman,[440] pointing out the most important unsolved problems. In his 1976 review Ryland characterized in detail three bryozoan reproductive patterns defined by Harmer[441] and Woollacott and Zimmer,[442] and suggested that by-products from the degenerated polypide could be used for extraembryonal nutrition. Among the most interesting of Ryland's[443] conclusions based on the data of Marcus[444] is that there are different methods of brooding, either involving the placental feeding or not, among related groups and, sometimes, within the same genus. Ryland also usefully summarised the

available data on the increase in larval volume during placental brooding. Describing, after Silén,[445] the pattern of oogenesis of *Callopora dumerilii*, he wrote that the oocyte enlarges in the ovary, reaching a size of 120 mm, then ovulates into the coelom where it continues to expand until it reaches 200 mm. Enlargement of the ovulated eggs in the visceral coelom was recorded by Ehlers[446] in the ctenostomate *Hypophorella expansa* (see above). Silén[447] did not describe the increase in *Callopora*, although this could be inferred from his text. Theoretically, such an increase might be possible through the absorption of water, and this is possibly the case for broadcasting species. However, there is no evidence in the literature that this is also true for the brooders.

A very complete review on brooding in the Gymnolaemata was published by Ström.[448] Until now this is one of the most valuable sources of the heterogenous information concerning parental care in Bryozoa. There is also a short review on brooding in Gymnolaemata in the 1983 volume of the *Treatise on Invertebrate Palaeontology* written by Cheetham and Cook.[449]

Several important papers on bryozoan reproduction were published in the 1980s. Nielsen[450] undertook a complex study, working on *Pacificincola insculpta* (Hincks, 1882) (as '*Hippodiplosia*') and *Fenestrulina miramara* (as *F. malusii*). He recorded the duration of synchronized events, including oocyte growth, oviposition and embryonal development in their repeated successions. In the first species with gonochoristic zooids, maturation of the first oocyte terminates with degeneration of the polypide, substituted by a new dwarf, non-feeding one. Oviposition is beneath the closed zooidal operculum, so the pore was not observed. The egg is just slightly deformed during the passage to the ovicell, becoming about two to three times longer than its diameter. In the second species oviposition is provided by the normal polypide and, in general, similar to the process described by Gerwerzhagen[451] and Silén.[452] However, the transfer itself is much faster than in other forms, when 'the egg is suddenly squeezed through the pore into the ovicell almost without becoming deformed'.[453] Additionally, this author found distal zooids with two ovicells (whose formation was induced by two different maternal zooids) in both species, and, thus the suggestion of Silén that the fertile zooid triggers ovicell formation by the distal zooid was confirmed.

Jebram and Everitt[454] corroborated the data of Braem[455] on reproduction of the ctenostomes *Bulbella abscondita*, *Victorella* and *Tanganella*. Similar to *V. pavida*, an intertentacular organ was recorded in the non-brooding *V. pseudoarachnidia* Jebram and Everitt, 1982. Also, a genital pore and the brooding of up to six embryos in the pockets of the body wall were described in *T. appendiculata* Jebram and Everitt, 1982, this is similar to *Victorella muelleri*.

Dyrynda with co-authors succesfully united anatomical and ecological research, studying bryozoan sexual reproduction. Following Marcus,[456] intracoelomic brooding was discovered in the cheilostome *Epistomia bursaria* (Linnaeus, 1758).[457-458] In this species colonies are hermaphroditic with gonochoristic zooids, where females are larger and more rare. There is only one generation of the polypide in each zooid, and the polypide develops in the autozooid as it forms. Male polypides persist until the zooid is between

five and ten zooid pairs from the growing tip of the colony, whereas the female polypide degenerates at a distance of only two to four zooid pairs. Each female produces only one larva. A TEM-study was undertaken to investigate both spermato- and oogenesis. Testis develops proximally on the axial funicular cord, and all the nutrients for spermatogenesis are probably developed intrazooidally, since it ceases when the polypide degenerates. The ovary is accosiated with the funicular cord too, but, in contrast with the testis, it becomes established in the disto-medial corner and its nutrient supply is intrazooidal during oogenesis and mainly extrazooidal during embryogenesis, although the polypide recycling by-products might be used. A single small alecithal oocyte was completed by the time of onset of polypide degeneration. It is surrounded by the 'follicle' or 'nurse' cells that are presumably of germ origin. Authors explain this speculation by the existence of cytoplasmic bridges between the single oocyte and 'follicle' cells. Out of the suggested initial syncytial cluster of germ cells, the central one may differentiate into the oocyte, whereas the rest may become the 'follicle' that was also called 'nurse' cells in the Plate II caption. Fertilization is intraovarian, since the embryonic cleavage starts inside the 'follicle'. Extraembryonic feeding is obvious: the embryo increases about 1000 fold in volume, and the axial funicular cord hypertrophies during this time. Additionally, if the polypides of the neighouring zooids degenerate, the embryo fails to develop. Colonial self-fertilisation is described: colonies produced embryos growing in isolation. 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 polypide cycling and extracoelomic brooding may have evolved.

In his 1981 paper Dyrynda[459] also gave a brief description of the reproductive cycle of *Chartella papyracea* (Ellis and Solander, 1786), noting a formation of the 'oocyte nurse cell syncytial duplet' in this species. Soon Dyrynda and Ryland[460] published an excellent paper, comparing the reproductive strategies and life histories of the non-placental (*C. papyracea*) and the placental (*Bugula flabellata*) cheilostome brooders in detail. Colonial and zooidal sexual changes were described in relation to seasonality and polypide cycling, and they explained that the interrelationship between polypide and sexual cycling controls nutrient budgeting for sexual and other processes within zooids and colony. In *C. papyracea* sexes are separated, and male zooids appear first in the colony. The fronds, however, are hermaphroditic since females develop at the end of the first reproductive season. The switch from the male to female zooid production coincides with a summer peak of water temperature. Nutrient intensive stages of gametogenesis (late spermatogenesis and late vitellogenesis) only take place in the presence of a feeding polypide, except in the first polypide generation that never produces gonads. Male germ cells are formed on the proximal transverse wall, and the testis develops with spermatogenesis progressing on the proximal and lateral walls during the lives of the next two polypides. As soon as the second [actually, the third] polypide degenerates, the testis regresses, but the male cycle recommences as the next polypide nears completion, and it is repeated for each polypide generation (it is not known, is the new testis established or the old one renovated). A cluster of the female germ cells is said to develop 'in the coelom of the female zooid, opposite

the first polypide bud'[461] where it is suspended by funicular cords seen on Dyrynda's Figure 6A. Vigelius[462] stated that ovary develops on the zooidal wall in flustrid *Terminoflustra membranaceotruncata* (see above). In contrast, it seems that the female gonad develops being associated with a polypide bud in *Chartella* discussed. Then it migrates towards the middle of the lateral cystid wall to establish an ovary, and the ovicell is formed [by the distal zooid] at the same time. Oocytes develop in doublets that, in contrast with the description of Marcus, was stated as a result of arrested cytokinesis.[463] According to the description of Marcus,[464] the nurse cell fuses with another oocyte when both reach 20-30 mm in diameter in *Thalamoporella evelinae*. The polypide starts to feed at the moment of the appearance of the first doublet. Previtellogenic growth takes place through the rest of the polypide cycle. Vitellogenesis commences during polypide cycling, becoming rapid when the next polypide starts to feed. This polypide transfers the ovulated egg to the ovicell in a way similar to that described by Gerwerzhagen[465] and Silén.[466] After oviposition, the polypide degenerates, and the ovarian cycle is repeated for each subsequent polypide cycle. If the oocyte is not ovulated before the polypide degenerates, it will be transferred by the next polypide. In contrast, larval release may occur without a polypide since the ooecial vesicle musculature and innervation are part of the cystid. Ovaries regress in winter when the polypides fail to regenerate in the female zooids, and the reversal of sex takes place next spring – in many of them testes develop. The authors suggested that in normal female zooids, the ovary produces a factor, suppressing the male cells, showing therefore that female autozooids may not in fact be gonochoristic after all. In *Bugula flabellata* mature sperm and an egg, which develops into a larva, are produced for each polypide generation including the first in hermaphroditic autozooids. There is protogyny: the egg matures at approximately the halfway point of the polypide life, whereas the sperm mature just before the polypide degenerates. Ovary is placed on the basal wall in the proximal part of the zooid, spermatogenic tissue – on the lateral and proximal transverse walls. Oocytes grow in pairs [oocytic doublets]. The ovicell completes its formation as the first egg ovulates, both events occurring halfway through the life of the first polypide. After oviposition, the egg receives extraembryonic nutrition via a placenta, thereafter increasing about 6.5 times in volume, much less than in *B. neritina* described by Woollacott and Zimmer.[467] Embryogenesis continues through the rest of the first polypide cycle and into the second with larval release taking place when the new polypide starts to feed. The authors suggested that polypide degeneration may be utilised for the onset of gametogenesis, and that evolution of the placental brooding provides uninterrupted embryonal feeding through the polypide cycling by 'spreading the nutrient demands' over two polypide generations.[468] This corresponds with the need to maximise larval productivity in those species with ephemeral colonies.

    The above research was aided by the light and TEM-microscopical study of the spermato- and oogenesis conducted by Dyrynda and King.[469] In *Chartella papyracea* the initial cluster of the female germ cells is established in the maternal coelom on the funicular cords, later migrating on to the lateral wall. Partially dividing enlarged oogonium forms an oocyte-nurse cell doublet, in which cells are identical in their structure

and connected via an intercellular bridge. Each doublet is enclosed by follicular cells, that have no peritoneal covering. Dyrynda and King described oogenesis in detail and made measurements, showing a 175 fold enlargement of the oocyte during vitellogenesis. During early and mid- vitellogenesis yolk platelets (autosynthesized yolk) appear throughout the oocyte cytoplasm, the oolemma forms numerous microvilli with pinocytosis (heterosynthesized yolk) occuring between their bases, and the vitelline envelope begins to form. Pinocytosis ceases during the middle vitellogenic stage, microvilli are withdrawn, and the fertilisation envelope differentiates into two layers prior to maturation. The nurse-cell also performs pinocytosis between its microvilli and has a fertilisation envelope. It produces ribosomes, transporting them to the sibling via the cytoplasmic bridge. Additionally it forms protein platelets, but there is no evidence of their transport. The follicular epithelium is decribed as differentiating into two layers of squamous (inner) and columnar (outer) cells, the latter performing the synthetic activity and possibly transporting the yolk to the oocyte. Sperm heads were recorded in both pre- and vitellogenic oocytes. Cytokinesis occurs during ovulation, after which the nurse-cell and follicular cells degrade. The mature telolecithal oocyte contains numerous protein platelets and lipid inclusions, and is oviposited being surrounded by a fertilization envelope. Prior the transfer to the ovicell it envelops the terminal parts of the gut, and constricted to a diameter of approximatelly 10 mm (from 140 mm) during its passage through the supraneural pore. Brooding is non-placental, so the embryo size is the same like the size of the mature oocyte. In *Bugula flabellata* the ovarian cycle is similar, and oocytes develop in doublets, again connected by the cytoplasmic bridge and a series of plate desmosomes. Both cells in a pair are surrounded by a fertilization envelope, form microvilli and perform pinocytosis. Also the nurse-cell produces few protein platelets and numerous ribonucleoproteins, being characterized by a large convoluted nucleus (similar to that described for *Chartella*). The number of ovarian cells is much less in *Bugula*. At the onset of vitellogenesis follicle cells differentiate into a continuous layer of squamous and few columnar cells. Striking difference between flustrid *Terminoflustra membranaceotruncata* and bugulid *Bugula calathus* in the number of the ovarian cells was first recorded by Vigelius[470] (see above). Both auto- and heterosynthesized sources of yolk are suggested. The egg volume is increased by approximately 29 times during vitellogenesis, and the embryo volume enlarges by about seven times during placental brooding. Nutrient storage cells were discovered, being associated with periotoneal lining, funicular cords and gonads. It should be noted that the mature egg is described as being telolecithal in *B. flabellata*, and it is also shown at the figures. Instead Reed[471] called eggs 'small mesolecithal' in this species. According to Woollacott and Zimmer,[472] Ryland[473] and Reed[474] there are three basic patterns of sexual reproduction in Bryozoa (see above). Combination of the telolecithal, i.e. macrolecithal egg, further brooded with placenta, should be considered either as a fourth pattern.

Additionally, Dyrynda and King checked twenty-eight cheilostome species, finding the placenta in bugulids only (genera *Bugula* and *Bicellariella*). In contrast with *Bugula neritina*, in which the embryo grows about 500 times larger,[475] the increase factor varied

between 7.1 and and 32.7 times in them: in general the larger an egg, the lesser the nutrient input during the embryonic stage.

In 1983 a review on bryozoan oogenesis was published by Hayward.[476] Despite the rather few studies consulted, he correctly pointed out the existing imbalance in the research of bryozoan reproduction. Furthermore, whereas spermatogenesis, embryology and larval morphology have attracted great attention, the processes of oogenesis and fertilization are still relatively understudied. The great variety of reproductive patterns and associated morphologies recorded in the relatively restricted number of species studied makes the current picture very confused, showing that further research is urgently needed to verify many of the data and conclusions made by earlier authors. Hayward stressed the most important problems and questions in this field of study. Among others there are variations in the site of ovarian origin and final position, the temporary relationship between the appearance and development of the polypide bud and early ovary, source of the ovarian cells, and almost unknown cytology of the ovary. Additionally, Hayward presented sections of the female gonad of *Alcyonidium hirsutum* for comparative purposes.

Jebram[477] described the ctenostome *Panolicella nutans* Jebram, 1985[478] as being a protandrous hermaphrodite. Spermatogenic tissue developed on the basal wall in the proximal part of the zooid, ovary – at the funiculus at the end of the caecum. Ovary contains several oocytes, but only one becomes ripe at a time. After ovulation it is released through the supraneural pore. The maternal zooid simultaneously broods four to five embryos that are externally attached to the maternal cystid wall obviously by the sticky fertilization envelope. Embryos of different ages are sometimes positioned chaotically, but often form a line in which the oldest embryo is the lowest. This is probably because the cystid continues its growth. The most distal egg can be withdrawn and sheltered inside the vestibulum during polypide retractions. Judging by the time of appearance of the perivitellar membrane [fertilization envelope], Jebram suggested that fertilization takes place during egg release.

D. Hughes[479] investigated the reproductive biology and anatomy of *Celleporella hyalina*. He carefully described formation of both male and female autozooidal polymorphs, and presented the results of the light and ultrastructural studies of their gonads. The coelomic cavity of males is largely filled with spermatogenic tissue. The ovary is positioned on the basal wall of the female, while the distal part of the zooid contains the cells providing the placental nutrition. Oocytes develop in doublets, being surrounded by the squamous follicle cells at least at an early vitellogenetic stage. The source of nutrients for the early stages of vitellogenesis is unclear (and may be connected with the activity of the nurse-cell), since there is no pinocytosis until the enlarged leading oocyte breaks through the thin follicular layer and its surface is partially exposed to the maternal coelom. The oolemma in the exposed region becomes microvillous, possibly allowing nutrient uptake directly from the coelomic fluid. The source of nutrients could be some peritoneal cells with numerous yolk-like inclusions that supposedly represent nutrient storage cells. It is possible that these cells actually belong to the funicular tissue forming part of the

placenta. Sperm heads were found between the ovarian cells, and insemination is suggested to occur during the pre- or vitellogenetic phase of the development. However, the route of the sperm to the ovary was not explained, since Hughes thought that the rudimentary female polypide is not able to protrude. The mature oocyte is said to fill most of the coelom, accumulating many large yolk inclusions. This is also seen in Hughes' Plate Vb. Thus, the egg is probably macrolecithal, and this example should be considered as a separate reproductive pattern, combining the yolk-rich oocytes and placental nutrition (see above). The embryo is increased by 15.6 times in volume receiving extraembryonal nutrition in the ovicell. Initially it is not in contact with the distal wall of the maternal zooid, which consists of hypertrophying epithelium covered with a two-layered cuticle. Despite this barrier, the soluble metabolites are obviously released to the fluid in the brooding space, where they are taken up by the embryo. There is no evidence of the pinocytosis in the early embryo, surrounded by the fertilization envelope, but its uptake is shown clearly in the mature one, where the cell surface becomes highly microvillous between the ciliary bases. Cilia fill the space between the placental epithelium and the late embryo in which fertilization envelope is not seen anymore. Finally, Hughes suggested that the ovicells evolved as merely protective structures, later transforming into a site for accessory nutrition in some forms.

Additionally, a number of papers on cheilostome bryozoan life cycles and reproductive ecology were also published in the 1980s and 1990s. Among those works were Winston,[480-482] Jackson and Wertheimer,[483] D. Hughes,[484] d'Hondt,[485] R. Hughes with co-authors,[486-489] and Cancino with co-authors,[490-493] who mainly work on the cheilostome *Celleporella hyalina*. Experimental studies of isolated colonies showed that self-fertilisation was either not possible (oogenesis failed to complete in *Membranipora isabelleana* (d'Orbigny, 1847) or never started in *C. hyalina*),[494] or leads to frequent embryonal abortion and reduced fittnes of the offspring.[495] Inbreeding capability resulting in normal progeny was recorded in one population of *C. hyalina* only.[496-497] Finally, it was concluded that outbreeding is a rule in this species, and occasional selfing might be connected with a reduced opportunity for outbreeding in some instances. Sperm liberation (often, synchronous[498] at stagnant or low-flow conditions) from the central, longest tentacle of male zooids has been observed, when their lophophores were bending to release the sperm to the exhalant currents of adjacent feeding lophophores, and evidence was obtained that *C. hyalina* might store the alien sperm.[499–501] Moreover, the mechanisms of allosperm storage and translocation are already present at the three-zooid stage of astogeny: colonies consisting merely of the ancestrula and two autozooids obtained and stored alien sperm, further using it to fertilize eggs for a maximum period of four to six weeks.[502] Returning to the old idea of Marcus,[503] it was suggested that the sperm can travel through the colony from autozooids to females via communication pores, using the funicular system.[504] Further research revealed that egg growth is absent in reproductively isolated colonies, and allosperm is a trigger of vitellogenesis.[505] Additionally, it was shown that some of the basal and frontal autozooids become male after polypide cycling in *Celleporella hyalina*.[506] Similar changes, presumably connected with polypide recycling were described by

Rogick[507] and Powell[508] in *Celleporella bougainvillei* (d'Orbigny, 1847) (as *Hippothoa*). Also sex reversal sometimes happens in this species: some female zooids change to males. In both cases, these events involve obvious skeletal changes.

Among more recent publications there are a comparative study by Wood and Seed[509] on the reproduction of the ctenostomes *Alcyonidium hirsutum* and *Flustrellidra hispida* growing together on algal fronds, and a study by Barnes and Clarke[510] on seasonality of polypide cycling and sexual reproduction in three Antarctic cheilostomes. A review on reproductive strategies of epialgal bryozoans was published by Seed and Hughes.[511]

Reed[512] investigated reproduction of the ctenostomes *Bowerbankia gracilis* and *B. gracilis* var. *aggregata* O'Donoghue and O'Donoghue, 1926 in detail, and this work greatly aided the original observations of Braem.[513] Both spermatogenesis and oogenesis were described. Autozooids are protandrously hermaphroditic, developing their gonads asynchronously. So, there may be functional male and female zooids within the colony in the same time. Spermatogenic tissue developed on the proximo-lateral cystid wall in connection with a funicular strand. However, it sometimes covers the caecum and gizzard of the polypide. Formation of the ovary occcurs during polypide degeneration, and is accompanied by the appearance of a ciliated gutter that will be involved in the ovulation and oviposition. Ovary development on the lateral cystid wall is supplied by a funicular strand, and is not directly associated with degenerating polypide. However, it is suggested that the nutrients can be transferred from the polypide to the ovary via funicular tissue. Mature female gonad is said to contain one to two vitellogenic [macrolecithal] and several previtellogenic oocytes that develop in succession. The ovary wall consists of the squamous (enveloping previtellogenetic oocytes) and cuboidal (eneveloping vitellogenetic ones) follicular epithelium. Using TEM, Reed described the ultrastructure and the changes occuring in the oocytes and follicular cells during oogenesis. It was shown that during the vitellogenetic phase follicular cells are enlarged and transform from squamous to cuboidal, actively producing and secreting proteinase product into the narrow space around the vitellogenic oocyte, which consume it by endocytosis. Reed notes that follicular epithelium may synthesize yolk precursors or modify these, which are transported to the ovary by the funicular system. The oocyte is obviously able to synthesize yolk too. Ovulation is accompanied by the activity of the ciliary gutter that further transfers the egg to the tentacle sheath, presumably via the coelomopore. Similar organs were described by Matricon[514] in the ctenostome *Alcyonidium polyoum* and Hageman[515] in the cheilostome *Membranipora serrilamella*. The tentacle sheath then everts, exposing the egg to the ambient water, as Reed thought, for fertilisation. Being retracted afterwards, the egg is surrounded by the fertilization envelope. Similar behaviour was described by Joliet[516] in *Walkeria uva* and *Bowerbankia imbricata*. However, later Temkin[517] showed intracoelomic fertilisation in *B. gracilis* (see below).

In a similar study by Owrid and Ryland[518] the main features of the gonado- and gametogenesis in the ctenostome *Alcyonidium hirsutum* were revealed. It was shown that this species is hermaphroditic, with distinct protandry at both colonial and zooidal levels. Spermatogenic tissue differentiates before the development (in the new zooid) or

regeneration (in the existed zooid) of the polypide from the peritoneum of the proximal part of the cystid wall. Primary oogonia originate in the rudiment of newly developing polypide [obviously from its peritoneum], and from the gut peritoneum in the replacement polypide. Thus, gonads develop each time before or during the formation of the new functioning polypide. Peritoneal cells proliferate to form the follicular cover, surrounding the young oocytes. In the place where the ovary is in the contact with a gut, the special cells with tongue-like parts protruding into the caecal lumen were found. These cells were recorded first by Chrétien[519] who studied *Alcyonidium diaphanum* (see above). Authors suggested that they could play a nutritive role. Finally, each of several growing oocytes is enveloped by its own follicle, which becomes two-layered, and the ovary appears to be no longer in contact with the caecum [possibly, suspended on the funicular strands]. Increase in the size of the ovary during vitellogenesis is accompanied by degeneration of the polypide that disappears when the ovary attains its full size. At the end of vitellogenesis the follicular layer becomes very thin, and the new small polypide without tentacles is developed. A similar process was described by Joliet[520] in *Walkeria uva* (see above). Mature eggs ovulate and are transferred to the polypide sac [modified tentacle sheath] via the coelomopore. The authors believed that they are fertilized prior or just after oviposition. From four to eleven larvae were recorded being simultaneously brooded. Cadman and Ryland[521] studied reproduction in *Alcyonidium mytili*. They showed that the ovary develops on the funicular strand, and confirmed the presence of an intertentacular organ that formed within the existing lophophore in this species.

Four reviews on bryozoan sexual reproduction appeared during the 1990s. In 1990 Nielsen published a short chapter, in which he stressed that in addition to the three basic reproductive patterns known in Bryozoa, there are 'a large number of intermediate types'.[522]

The ultimate review by Reed,[523] despite the inevitable inaccuracies connected with the large gaps in our knowledge, is the most complete compilation of the discussed topic at present. Six years later a short chapter on bryozoan sexual reproduction was included in the monograph of Mukai, Terakado and Reed,[524] in which some of the gaps in knowledge were addressed. In addition to the descriptions and examples, Reed widely discusses and interprets the data on bryozoans, comparing them with other invertebrate groups. In particular, he arranged scanty data on the origin of the germ cells in Bryozoa in a logical system of facts and suggestions, creating the modern view of this topic. It should be noted that Reed often included non-published results of observations and studies made by other authors. For instance, he mentioned the finding of the genital pore in the ooecial vesicle in a non-specified cheilostome *Schizoporella* made by Zimmer. Of special interest are the data from the Ph.D. dissertation of Hageman[525] who, except for one short note,[526] never published the results of his studies on the cheilostome *Membranipora serrilamella*. However, these results are of great value. In this malacostegan species spermatogenic tissue develops as diffuse clusters of spermatogonia from the coelomic peritoneum on the lateral and basal walls in protandrously hermaphroditic zooids. Earlier Mawatari and Mawatari[527] reported that the spermatogonia develop beneath the frontal membrane in this

species. Unlike the majority of gymnolaemates in which female gonad differentiates from mesothelium of the first polypide bud (see above), the ovary differentiates in the somatic peritoneum of one of the lateral walls in the proximal region of the zooid, at the confluence of several funicular cords. The ovarian wall consists of follicular cells of the peritoneal origin, enveloping the oogonia and oocytes, and there is so-called 'subovarian space' between the ovary and cystid epidermis. This is confluent with the lumina of the funicular cords, and is lined by special 'basal cells' [of the peritoneal origin too]. In the ovarian peripheral germinal zone follicular cells completely surround the oogonia and early previtellogenic oocytes, which remain connected by cytoplasmic bridges. Hageman suggested that the follicle cells may regulate vitellogenesis by compartmentalizing the ovary, synchronize the oocyte differentiation and transport low molecular weight precursors or metabolites. Interestingly, it was also shown that the follicle cells phagocytosed degenerating oocytes. In the central growing zone follicular epithelium is not complete basally, and the oocytes in various stages of vitellogenesis are in contact with the subovarian space. Additionally, the early vitellogenic oocytes share gap junctions with the overlying follicular cells. 'Basal cells' secret yolk precursors that are endocytosed by the oocytes from the 'subovarian space' (heterosynthetic source of yolk), and incorporated into yolk granules (autosynthetic source) in the oocytes. Later the vitelline envelope forms at the oolemma. Further, oocytes move into the centro-apical ovulatory zone where they are partially exposed to the zooidal cavity. The late oocytes form microvilli on the surface exposed to the coelom. A similar situation described by D. Hughes[528] in *Celleporella hyalina* (see above). Upon germinal vesicle breakdown, the mature oocytes ovulate, and up to twenty-five of them are accumulated in the zooidal cavity. The ovulated eggs and spermatozeugmata are transported to the base of the lophophore by the ciliated pharyngeal gutter that differentiates at the onset of spermatogenesis. During the male phase of reproduction, sperm are transported to the lumina of the dorsomedial tentacles by the ciliary tracts lateral to the gutter. During the female phase, the eggs are transported along the ciliated gutter's floor into the base of the two-chambered intertentacular organ. It forms at the onset of oogenesis from the epithelium of two dorsomedial tentacles, is completed in approximately two days, and this process does not involve polypide replacement.

A very detailed review on bryozoan fertilization has been published by Ryland and Bishop,[529] who, among others, mentioned some of the results of Temkin.[530] In contrast with the data of Cancino with co-authors,[531] in whose experiments *Membranipora isabelleana*[532] failed to complete oogenesis being in isolation, the reproduction was successful in isolated colonies of *Membranipora* sp. This was in accordance with the results of Maturo,[533] in whose experiments five gymnolaemate species produced larvae, when grown from single ancestrulae in isolation. In spite of this, it was concluded that cross-fertilisation is usually a rule among Bryozoa, and selfing, if really exists, might be used in an 'emergency' situation. Precocious insemination and the ability to store sperm make it important to carefully isolate colonies grown from ancestrulae at an early stage of their development in future experiments.

The excellent experimental works on bryozoan fertilization conducted by Temkin[534-535] resulted in a reconsideration of some generally accepted opinions. It was shown that fertilization is internal in gymnolaemate bryozoans: either intracoelomic or intraovarian. In *Membranipora membranacea*, spermatozeugmata are pushed through the tentacle lumen by an undulating movement of the midpiece region and spawned via the terminal pores of the two distomedial tentacles – tail ends first – into the exhalant current created by the colony. Temkin suggested that this should increase the chances for the sperm to be removed from the colony (and, thus, prevent intracolonial self-fertilization), for which purpose the tips of the distomedial tentacles bend towards the exhalent current. This contradicts the opinion of Silén,[536] who thought that releasing sperm through the tentacle tips would position it outside of the feeding currents of the parental zooid. Being entrapped by the feeding currents of another lophophore, sperm attaches to the tentacles and performs undulating movements (although is sometimes eaten, rejected with the food particles or ensnared in the tentacles). Those spermatozeugmata that have been attached nearby the distal opening of the intertentacular organ, using a 'random search process',[537] enter it head end first. The intertentacular organ actively regulates the passage of the spermatozeugmata to the zooidal coelom, closing its opening. However, it does not discriminate between the alien and its own sperm, produced by the same colony. Spermatozoids have been found on the ovarian surface, and egg-sperm fusion is said to happen during or shortly after ovulation. Judging from the description, nuclear breakdown happens at approximately the same time. A polyspermic oocyte containing at least fourteen sperm nuclei was observed on one occasion.[538] Temkin described egg release, its maturation, activation and syngamy in detail. Activation is delayed and this is considered as a possible adaptation for liberation/oviposition of the egg through the small opening of the supraneural pore.

In his following paper[539] Temkin studied fertilization in two ctenostome and seven cheilostome species. For all nine species intraovarian monospermic sperm-egg fusion was found. In both egg broadcasters studied – *Alcyonidium* sp. and *Electra pilosa* – sperm fuses with late stage ovarian oocytes after the germinal vesicle breakdown at or near ovulation. In the ctenostome brooder *Bowerbankia gracilis* sperm were only found inside the late stage ovarian oocytes before the germinal vesicle breakdown,[540] and sperm fuses with early ovarian oocytes in all the cheilostome brooders studied. In the latter Temkin described the oocytic doublets and illustrated the cytoplasmic bridges between nurse-cells and their siblings in some species. Only one cell of each oocytic doublet is inseminated, and this cell will become an egg. Sperm tails and midpieces were found resorbing either in the oocyte cytoplasm (*Watersipora arcuata*) or outside the oocyte (*Dendrobeania lichenoides* (Robertson, 1900)). There is only one vitellogenic doublet in each ovary, but other previtellogeneic doublets, are all possessing sperm too. Ovaria are said to consist of squamous, cuboidal or columnar cells. Spermatozoids are suggested to enter the maternal coelom through the intertentacular organ or supraneural pore, accumulate on the ovarian surface, and later move between ovarian cells. All these findings show that internal fertilization is a rule among Gymnolaemata, providing high levels of fertilization success

in this group. Additionally, Temkin counted the number of the oocytes/oocytic doublets in the ovaria and measured them. Recently, this author published the results of his experimental study on the movements of the spermatozeugmata in *Membranipora membranacea*.[541-542]

The same species was an object of experiments conducted by Harvell and Helling.[543] They demonstrated large and localized shifts (acceleration) in the timing and pattern of reproduction in response to simulated damage by predators (trimming the colony periphery) and by overgrowing of conspecific neighbour colonies.

Santagata and Banta[544] investigated brooding in the cheilostome *Scrupocellaria ferox* Busk, 1852. They discovered the embryophore, consisting of the hypertrophied eputhelium and funicular system, and showed that the embryos more than double in volume while in the ovicell. The ovary is found in association with a funicular cord in the basal perigastric coelom. Additionally, these authors investigated ovicell anatomy in this species and proposed a hypothesis whereby vestibular brooding preceeded brooding in ovicells.

Ostrovsky[545] studied ovicell anatomy and reproductive patterns in *Cribrilina annulata* (Fabricius, 1780) and *Celleporella hyalina*. Both species are protandrous colonial hermaphrodites with male and hermaphroditic autozooids in the first case, and male and female dwarf autozooidal polymorphs in the second. It was revealed that dwarf zoids are hermaphroditic autozooids, not females in *C. annulata*, and their 'dwarfism' is not connected with sexuality as Powell thought.[546] Presumptive ovary contains a couple of large female cells, that might be either two oogonia or the first oocytic doublet, surrounded by the peritoneal cover, and is associated with the proximal part of a differentiating polypide bud. Further ovary is either located on the basal cystid wall or suspended on the funicular strands. In *C. annulata* complete female gonad contains up to six oocytic doublets (one being vitellogenetic), and mature oocyte is macrolecithal-telolecithal. Ovarian wall consists of columnar cells in its lower and squamous cells in its upper part. Columnar epithelium surrounds a central area of the polygonal [basal] cells with numerous intercellular spaces. Similar ovarian structure was described in *Thalamoporella evelinae* by Marcus.[547] Ovary is said to consist of polygonal cells in *C. hyalina*. It contains up to three doublets, and the mature oocyte is said to be microlecithal-homolecithal. This contradicts the illustrations and description of Hughes,[548] who found the eggs full of yolk in this species (see above). Additional research showed that the eggs are macrolecithal in the population from the White Sea (Ostrovsky, unpublished). Sperm are frequently found between ovarian cells. Insemination is precocious: spermatozoids penetrate the early previtellogenetic oocytes. Syngamy and egg activation are delayed: the sperm heads were found in late oocytes as well. Musculature of the compensation sac has been discovered in female polymorphs of *C. hyalina*, and this fact was used to propose a possible mechanism of oviposition through the genital pore. Among unusual findings are three large sterile colonies of *C. annulata*, and sperm-like bodies inside the ooecial coelomic cavity in *C. hyalina*. The latter fact further supports the idea that sperm can travel through the colony. Additionally, an unknown intracellular parasite was encountered in the oocytes of *C. annulata*.

6. Recent works

Apart from the above-mentioned works of R. Hughes with co-authors, among the recent publications there are several works of Porter and Ryland with co-authors[549-555] on the ctenostome genus *Alcyonidium*. Authors distinguished the type of reproductive pattern by the presence of intertentacular organs, lipid granules or brooded embryos in thirteen species of *Alcyonidium*, revealing some unusual aspects of their reproductive biology. For instance, in several species numerous small eggs were recorded in absence of an intertentacular organ. Either intertentacular organ was not found, or it is completely absent in these specis, and eggs are spawned through the supraneural pore. However, oviparous species with the supraneural pore, although they exist among Ctenostomata, are not known within *Alcyonidium*. In *Alcyonidium disciforme* Smitt, 1871 only one embryo per time is brooded in the tentacle sheath, although several embryos are a rule for that genus.

In 2003 Smith, Werle and Klekowski[556] investigated reproduction of the ctenostome *Pottsiella erecta* (Potts, 1884). An ovary develops on the cystid wall, and spermatogenic tissue – on the funicular strands, are both present in the middle region of zooids that are simultaneous hermaphrodites. Since both gonads develop in close proximity, it was suggested that self-fertilization has a place in this species. This is obviously wrong (see above), but requires checking. The most intriguing finding is that the egg (occasionally two eggs) is brooded externally in a sticky coat connected with a maternal zooid by a flexible, elastic strand. Authors consider the coat as being a fertilization envelope, and the strand is thought mucoid. The embryo remains outside the parent whether the polypide is extended or withdrawn, and the strand possibly lengthens with time.

7. General conclusions and future research

At the moment there are data about sexual reproduction for sixty ctenostome and more than one hundred and sixty cheilostome species in the literature. They belong to twenty-six genera and nineteen families, and ninety-two genera and fifty-two families respectively (see Appendix). These numbers are not complete in extent, since we were not able to collect all of the existing sources. However, we are sure that we analyzed more than 95% of works published since the times of Trembley and Ellis in this review.

It is important to state here, that despite the apparently large numbers mentioned in this review, reproduction was properly studied in just a few gymnolaemates (actually, in about ten species). Among ctenostomes these are a few species of *Alcyonidium* and *Bowerbankia gracilis*, among the cheilostomes – *Celleporella hyalina*, a few species of *Bugula*, *Chartella papyracea*, *Epistomia bursaria*, *Cribrilina annulata*, *Membranipora serrilamella* and *Terminoflustra membranaceotruncata*. It should be emphasized that there are many gaps in the current knowledge even for these species. All, but one, of these forms are anascans, but the vast majority of cheilostomes are ascophorans. Actually, for many of the gymnolaemates some details of their reproduction were described in passing as part of

systematical works.

Another problem is that the most of the data accumulated at the moment were obtained by early scholars, and many of them need checking. Thus, our knowledge is still very fragmented and generalities given in textbooks and reviews are based on rather rare and heterogenous information.

In addition to the general need of new data and the extension of the research to as many taxa as possible, several important problems still await attention.

7.1 Early gonado- and gametogenesis

Despite several authors describing early female cells in Gymnolaemata, identification of the oogonia is a very obscure business. Most descriptions are superficial and do not specify the oogonial stage, others are confusing. Theoretically, after differentiation from the mesothelial cell of the first polypide bud the primary oogonium should divide, giving two primary oogonia that further should create an oogonial pull in the ovary, and divide forming primary oocytes.[557] It is possible that namely such division was mentioned by Calvet[558] and Chrétien.[559] However, we have no idea about this process, similarly we do not know about the numbers of the early female cells and their destiny (degeneration, growth and divisions). It is obvious that the appearance (size, shape and coloration) of the primary oogonia does not differ strongly (at least, at the light microscopical level) from early primary oocytes. Also the result of the primary oogonium division can be easily confused with the early oocytic doublet. Can new oogonia form during the life span of the ovary or there is an initial pull inherited from the first polypide? TEM-studies of the early polypide buds at the different stages of their development should be helpful in answering these questions.

7.2 Site of gonadal origin and final location

According to the accounts of different authors, the source of the germ cells is the local proliferation of peritoneal cells. The site of origin and final position of the male gonads does not differ strongly, and the main difference is that mature spermatogenic tissue occupies a much larger area than does the immature testi(e)s on the zooidal wall or funicular cords.

In contrast, the sites of the female germ cells origin and the position of the complete ovary may not coincide. The early female cells can be moved from the site of their origin in the polypide bud towards the final position of the ovary, and this could be facilitated by the growing funicular network. The site of origin is mainly connected with the developing polypide bud, although it is also reported on the cystid wall. The latter was suggested by Vigelius[560] and Pergens.[561] However, their data need checking since they did not make sections of the polypide buds. Also Hageman[562] found that ovary differentiates in the somatic peritoneum of one of the lateral walls in the proximal region of the zooid,

at the confluence of several funicular cords. The final position of the female gonad is on the polypide gut (within the peritoneal lining of the caecum or nearby), in the funicular cord or within the peritoneal cover of the cystid wall (always with association with a funicular strand). Additionally, the final position of the ovary within the zooid varies both between and within species. Although the peritoneal origin of the ovary makes a good explanation for such variation, the rather restricted number of species studied (mainly, by the early authors) means that further investigation is required in order to check the existing data and to be able to recognize the patterns of the ovarian origin/position within the group. The time of appearance of the female germ cells seems to be different in relation to the stage of polypide bud formation, but the data are so scarce that it also requires additional study. Also divisions, differentiation, (possible) degeneration and cytomorphological characteristics of oogonia have not been studied. We also do not know how new oogonia appear in the mature ovary.

7.3 Ovarian structure and functioning

Structure of the ovary is poorly known in both Ctenostomata and Cheilostomata until now. In cheilostomes there are actually two cell groups (except oogonia and oocytes) constituting the female gonad – peripheral (follicular) and subovarian (basal) – that strongly differ in morphology and presumably, function. These groups are easily recognizable, however, the majority of researchers, although depicting basal cells, mention the follicular ones only. Moreover, there is a subovarian lumen that has been recorded in two cheilostomes. Ovarian ultrastructure is described in a few species only, and most of these descriptions are rather superficial. Function of the ovarian cells is poorly understood. Some evidence exists regarding either synthetic or transport activities, or both. However, the number of species studied is so small that we only have general ideas about the functioning of ovarian cells. This is also true of the processes of oogenesis and vitellogenesis.

7.4 Origin of the ovarian cells

Cells forming the ovary wall are described as originating either from the peritoneal cells (majority of the cases described) or from the cluster of germ cells. In the latter case, the central cells of the cluster differentiate into oocytes whereas the peripheral ones form the follicle (stated for *Bugula simplex* by Calvet[563] and suggested for *Epystomia bursaria* by Dyrynda and King[564]). In the third case (in *Nolella dilatata*), there are no ovarian cells at all (see Calvet[565]). Two last variants are reported only once and should be restudied. Differentiation of the basal cells is also obscure.

7.5 Time of the sperm-egg fusion in brooding Ctenostomata

This event has been recorded in four species. In brooding *Bowerbankia gracilis*

insemination occurs before germinal vesicle breakdown. Only one late stage ovarian oocyte per gonad contains a sperm nucleus, and it was suggested that the rupture of the follicle cell layer might expose the oocyte to sperm.[566] In *Alcyonidium mamillatum* (broadcaster) and *Nolella stipata* (brooder), the sperm penetrates the oocytes while they are still growing,[567] but it is not clear from the description when. Also, we do not know if Marcus really worked with *Alcyonidium mamillatum*, since the intertentacular organ and oviparity has been recently recorded in this species.[568] Additionally, it was shown that sperm fuse with late growth stage ovarian oocytes after collapse of the nuclear membrane at or near ovulation in broadcasting *Alcyonidium* sp.[569] This variation needs further research. Additional questions are connected to the fact that the polypide degenerates during vitellogenesis in some ctenostomes, not permitting fertilization during polypide cycling.

7.6 Placental brooding

Reed[570] suggested that extra-embryonic nutrition has arisen independently numerous times within Bryozoa. Among Ctenostomata there are several reports on the increase in size of embryos whilst in the brood-chamber (in *Walkeria uva*,[571] *Nolella stipata*,[572] *Nolella dilatata*,[573] *Flustrellidra hispida*[574] and *Mimosella cookae*[575]), sometimes accompanied by the changes in the structure of the wall surrounding the embryo (in *Zoobotryon verticillatum*,[576] *Sundanella sibogae*[577] and *Nolella papuensis*[578]). A transfer of nutrients from the maternal zooid must clearly take place, but the mechanism and placental structure have not been studied.

Similarly, extraembryonal nutrition have been described in a few cheilostome species only (in *Retiflustra schoenaui*, *Catenicella elegans*, seven species of *Bugula*, *Bicellariella ciliata*, *Synnotum* sp., *Epystomia bursaria*, *Celeporella hyalina* and *Scrupocellaria ferox*, see above), although placental brooding is apparently much more common than was originally thought.[579]

7.7 Brooding structures

Sites of embryonal incubation are highly variable in structure, showing that brooding evolved independently several times within Cheilostomata. Reed[580] suggested that the ooecium is not a homologous structure throughout this order, and ovicell evolved numerous times. Further, brooding chambers are often strongly modified in the forms of apparently a monophyletic origin.[581-585] The simultaneous presence of planktotrophic larvae and brooding within some families as well as different types of brooding show that the same is true for Ctenostomata as well.[586] However, much more should be done to describe and estimate the variety mentioned, and understand the role that brooding played in the evolution of Gymnolaemata.

7.8 Dynamics of the colonial and zooidal sexual structure and life cycles

The vast majority of data on the sexual structure of bryozoan colonies reflects the colony state at the moment of the collection. However, this structure is the subject of change on both the short- as well as long-term time scale, being intimately connected with polypide recycling and colony longevity. More comprehensive studies are needed to determine sexual dynamics based on seasonal observations.

8. Acknowledgements

APPENDIX

Chronological list of papers and gymnolaemate species, in which different aspects of sexual reproduction have been either studied or observed:[587]

Grant (1827)
   Carbasea carbasea (Ellis and Solander, 1786) (as *Flustra*) (Flustridae)
   Flustra foliacea (Linnaeus, 1758) (Flustridae)
Thompson (1830)
   '*Vesicularia*' (Ctenostomata)
Milne-Edwards (1836)
   '*Cellariae*' (Cheilostomata)
Farre (1837)
   Alcyonidium duplex Prouho, 1892 (as *Halodactylus diaphanus*) (Alcyonidiidae)
   Walkeria uva (Linnaeus, 1758) (as *Valkeria cuscuta*) (Walkeriidae)
   Bowerbankia imbricata (Adams, 1798) (as *B. densa*) (Vesiculariidae)

Electra pilosa (Linnaeus, 1767) (as *Membranipora*) (Electridae)

Nordmann (1839)

Tendra zostericola Nordmann, 1839 (Tendridae)

Kölliker (1841)

Alcyonidium sp. (as *A. gelatinosum* Johnston) (Alcyonidiidae)

Hassall (1841)

Alcyonidium hirsutum (Fleming, 1828) (as *Cycloum papillosum*) (Alcyonidiidae)

Alcyonidium polyoum (Hassall, 1841) (as *Sarcochitum polyoum*) (Alcyonidiidae)

Van Beneden (1844a)

Farella repens (Farre, 1837) (as *Laguncula*) (Triticellidae)

Van Beneden (1844b)

Bowerbankia cf. *imbricata* (as *B. densa*) (Vesiculariidae)

Flustra foliacea (Linnaeus, 1758) (Flustridae)

Alcyonidium sp. (as *Holodactyle diaphane*) (Alcyonidiidae)

Reid (1845)

Scrupocellaria reptans (Linnaeus, 1767) (as *Cellularia*) (Candidae)

Scrupocellaria scruposa (Linnaeus, 1758) (as *Cellularia*) (Candidae)

Bugula flabellata (Thompson in Gray, 1848) (as *Cellularia avicularis*) (Bugulidae)

non-identified cheilostome (as *Flustra avicularis*)

Dalyell (1847-1848)

Carbasea carbasea (Ellis and Solander, 1786) (as *Flustra*) (Flustridae)

Flustra foliacea (Linnaeus, 1758) (Flustridae)

Securiflustra securifrons (Pallas, 1766) (as *Flustra truncata*) (Flustridae)

Bowerbankia imbricata (Adams, 1798) (as *B. densa*) (Vesiculariidae)

Hancock (1850)

Paludicella sp. (as *P. procumbens*) (obviously, *P. articulata* (Ehrenberg, 1831) (Paludicellidae))

Bowerbankia sp. (Vesiculariidae)

Hincks (1851)

Bowerbankia sp. (Vesiculariidae)

Alcyonidium hirsutum (Fleming, 1828) (as *Cycloum papillosum* Hassal) (Alcyonidiidae)

Electra pilosa (Linnaeus, 1767) (as *Membranipora*) (Electridae)

Allman (1856)

Paludicella articulata (Ehrenberg, 1831) (as *P. ehrenbergi* van Beneden) (Paludicellidae)

Huxley (1856)

Bugula avicularia (Linnaeus, 1758) (as *B. avicularis*) (Bugulidae)

Bugula flabellata (Thompson in Gray, 1848) (Bugulidae)

Bugula plumosa (Pallas, 1766) (Bugulidae)

Scrupocellaria scruposa (Linnaeus, 1758) (Candidae)

Redfern (1858)

Flustrellidra hispida (Fabricius, 1780) (as *Flustrella*) (Flustrellidae)

Hincks (1861)

Bugula flabellata (Thompson in Gray, 1848) (Bugulidae)

Bugula turbinata Alder, 1857 (Bugulidae)

Bicellariella ciliata (Linnaeus, 1758) (as *Bicellaria*) (Bugulidae)

Smitt (1865)

Membranipora membranacea (Linnaeus, 1767) (as *Flustra*) (Membraniporidae)

Scrupocellaria scruposa (Linnaeus, 1758) (Candidae)
Escharella immersa (Fleming, 1828) (as *Lepralia peachii*) (Romancheinidae)
Cryptosula pallasiana (Moll, 1803) (as *Lepralia*) (Cryptosulidae)

Smitt (1866)
Electra pilosa (Linnaeus, 1767) (as *Membranipora*) (Electridae)

Nitschce (1869)
Bicellariella ciliata (Linnaeus, 1758) (as *Bicellaria*) (Bugulidae)
Bugula flabellata (Thompson in Gray, 1848) (Bugulidae)
Bugula plumosa (Pallas, 1766) (Bugulidae)

Claparède (1871)
Bugula avicularia (Linnaeus, 1758) (Bugulidae)
Scrupocellaria scruposa (Linnaeus, 1758) (Candidae)

Hincks (1873)
Vesicularia spinosa (Linnaeus, 1767) (Vesiculariidae)
Bugula purpurotincta (Norman, 1868) (as *Bugula fascigiata*) (Bugulidae)
Bicellariella ciliata (Linnaeus, 1758) (as *Bicellaria*) (Bugulidae)

Salensky (1874)
Bugula plumosa (Pallas, 1766) (Bugulidae)

Repiachoff (1875)
Tendra zostericola Nordmann, 1839 (Tendridae)

Reingard (1875)
Tendra zostericola Nordmann, 1839 (Tendridae)
Cryptosula pallasiana (Moll, 1803) (as *Lepralia*) (Cryptosulidae)
Smittoidea reticulata (J. Macgillivray, 1842) (as *Lepralia*) (Smittinidae)

Repiachoff (1876)
Cryptosula pallasiana (Moll, 1803) (as *Lepralia*) (Cryptosulidae)
Electra repiachowi Ostroumoff, 1886 (as *Tendra*) (Electridae)

Ehlers (1876)
Hypophorella expansa Ehlers, 1876 (Hypophorellidae)
non-identified cheilostome (as *Lepralia*)

Joliet (1877)
Bowerbankia imbricata (Adams, 1898) (Vesiculariidae)
Walkeria uva (Linnaeus, 1758) (as *Valkeria cuscuta*) (Walkeriidae)
Farella repens (Farre, 1837) (as *Laguncula*) (Triticellidae)
non-identified ctenostome (as *Lagenella nutans*)
Membranipora membranacea (Linnaeus, 1767) (Membraniporidae)
Bugula avicularia (Linnaeus, 1758) (Bugulidae)
Bugula flabellata (Thompson in Gray, 1848) (Bugulidae)
Bicellariella ciliata (Linnaeus, 1758) (as *Bicellaria*) (Bugulidae)
Scrupocellaria scruposa (Linnaeus, 1758) (Candidae)
non-identified cheilostome (as *Lepralia martyi*)

Hincks (1880)
Alcyonidium mytili Dalyell, 1848 (Alcyonidiidae)
Alcyonidium sp. (as *A. gelatinosum*) (Alcyonidiidae)
Vesicularia spinosa (Linnaeus, 1767) (Vesiculariidae)
Nolella stipata Gosse, 1855 (as *Cylindroecium giganteum*) (Nolellidae)

Membranipora membranacea (Linnaeus, 1767) (Membraniporidae)
Vigelius (1882, 1884a, 1884b)
Terminoflustra membranaceotruncata (Smitt, 1868) (as *Flustra membranaceo-truncata*) (Flustridae)
Vigelius (1886)
Bugula calathus Norman, 1868 (Bugulidae)
Ostroumoff (1886)
Tendra zostericola Nordmann, 1839 (Tendridae)
Electra repiachowi Ostroumoff, 1886 (as *Membranipora*) (Electridae)
Kraepelin (1887)
Victorella pavida Saville Kent, 1870 (Victorellidae)
Paludicella articulata (Ehrenberg, 1831) (as *P. ehrenbergi*) (Paludicellidae)
Jullien (1888a)
Figularia figularis (Johnston, 1847) (as *Lepralia*) (Cribrilinidae)
Jullien (1888b)
Beania sp. (as *Diachoris costata*) (Beaniidae)
Pergens (1889)
Fenestrulina malusii (Audouin, 1826) (as *Microporella*) (Microporellidae)
non-identified cheilostome (as *Amphiblestrum patellarium* Moll)
Bugula simplex Hincks, 1886 (Bugulidae)
Bugula turbinata Alder, 1857 (Bugulidae)
Prouho (1889)
Alcyonidium albidum Alder, 1857 (Alcyonidiidae)
 Alcyonidium duplex Prouho, 1892 (Alcyonidiidae)
Prouho (1892)
Alcyonidium albidum Alder, 1857 (Alcyonidiidae)
Alcyonidium variegatum Prouho, 1892 (Alcyonidiidae)
Alcyonidium duplex Prouho, 1892 (Alcyonidiidae)
Hypophorella expansa Ehlers, 1876 (Hypophorellidae)
Pherusella tubulosa (Ellis and Solander, 1786) (as *Pherusa*) (Pherusellidae)
Flustrellidra hispida (Fabricius, 1780) (as *Flustrella*) (Flustrellidae)
Nolella dilatata (Hincks, 1860) (as *Cylindroecium dilatatum*) (Nolellidae)
Electra pilosa (Linnaeus, 1767) (as *Membranipora*) (Electridae)
Braem (1896)
Paludicella articulata (Ehrenberg, 1831) (as *P. ehrenbergi*) (Paludicellidae)
Waters 1896(1898)a
Menipea roborata (Hincks, 1881) (as *Flabellaris*) (Candidae)
Waters 1896(1898)b
Aetea sica (Couch, 1844) (as *A. anguina* forma *recta* Hincks) (Aetiidae)
Beania magellanica (Busk, 1852) (Beaniidae)
Waters (1900)
Cystisella saccata (Busk, 1856) (as *Porella)* (Bryocriptellidae?)
Calvet (1900)
Alcyonidium cellarioides Calvet, 1900 (Alcyonidiidae)
Bowerbankia pustulosa (Ellis and Solander, 1786) (Vesiculariidae)
Amathia lendigera (Linnaeus, 1761) (Vesiculariidae)

Amathia semiconvoluta (Lamouroux, 1824) (Vesiculariidae)
Vesicularia spinosa (Linnaeus, 1767) (Vesiculariidae)
Nolella dilatata (Hincks, 1860) (as *Cylindroecium dilatatum*)
Aetea anguina (Linnaeus, 1758) (Aetiidae)
Electra pilosa (Linnaeus, 1767) (as *Membranipora* and *M. pilosa* var. *dentata*) (Electridae)
Membranipora tenuis (Desor, 1848) (as *M. pilosa* var. *tenuis*) (Membraniporidae)
Amphiblestrum flemingi (Busk, 1854) (as *Membranipora*) (Calloporidae)
Securiflustra securifrons (Pallas, 1766) (as *Flustra*) (Flustridae)
Bugula simplex Hincks, 1886 (as *B. sabatieri* Calvet, 1900) (Bugulidae)
Bugula avicularia (Linnaeus, 1758) (Bugulidae)
Bugula turbinata Alder, 1857 (Bugulidae)
Bugula calathus Norman, 1868 (Bugulidae)
Bugula neritina (Linnaeus, 1758) (Bugulidae)
Cellaria fistulosa (Linnaeus, 1758) (Cellariidae)
Cellaria salicornoides Lamouroux, 1816 (Cellariidae)
Umbonula ovicellata Hastings, 1944 (as *U. verrucosa*) (Umbonulidae)
Schozomavella auriculata (Hassall, 1842) (Bitectiporidae)
Cryptosula pallasiana (Moll, 1803) (as *Lepralia*) (Cryptosulidae)
Fenestrulina malusii (Audouin, 1826) (as *Microporella*) (Microporellidae)
Microporella ciliata (Pallas, 1766) (Microporellidae)
Savygniella lafontii (as *Eucratea*) (Savygniellidae)
Schizoporella unicornis (Johnston in Wood, 1844) (Schizoporellidae)
Schizobrachiella sanguinea (Norman, 1868) (as *Schizoporella*) (Schizoporellidae)
Cellepora pumicosa (Pallas, 1766) (Celleporidae)
Turbicellepora avicularis (Hincks, 1860) (as *Cellepora avicularia*) (Celleporidae)
non-identified cheilostome (as *Retepora cellulosa*)

Schulz (1901)
Electra crustulenta (Pallas, 1766) (as *Membranipora membranacea*) (Electridae)
Harmer (1902)
Cheiloporina haddoni (Harmer, 1902) (as *Lepralia*) (Cheiloporinidae)
Retiflustra schoenaui Levinsen, 1909 (as *Flustra cribriformis* Busk) (Flustridae)
Waters (1904a)
Systenopora contracta Waters, 1904 (Sclerodomidae)
Spigaleos horneroides (Waters, 1904) (as *Cellepora*) (Celleporidae)
Osthimosia clavata Waters, 1904 (Celleporidae)
Turritigera stellata Busk, 1884 (Lekythoporidae)
Orthoporidra compacta (Waters, 1904) (as *Orthopora*) (Lekythoporidae)
Alcyonidium antarcticum Waters, 1904 (Alcyonidiidae)
Waters (1904b)
Alcyonidium gelatinosum (Linnaeus, 1761) (Alcyonidiidae)
Alcyonidium sp. (Alcyonidiidae)
Retzius (1904)
Alcyonidium gelatinosum (Linnaeus, 1761) (Alcyonidiidae)
Robertson (1905)
Aetea anguina (Linnaeus, 1758) (Aetiidae)

Retzius (1905)
  Flustra foliacea (Linnaeus, 1758) (Flustridae)
Retzius (1906)
  Triticella flava Dalyell, 1848 (as *T. korenii*) (Triticellidae)
Römer (1906)
  Alcyonidium sp. (as *A. mytili* Dalyell, 1848) (Alcyonidiidae)
Waters (1906)
  non-identified cheilostome as *Lepralia clivosa* n. sp.
  non-identified cheilostome as *Smittina praestans* (Hincks, 1882)
Pace (1906)
  Flustrellidra hispida (Fabricius, 1780) (Flustrellidridae)
Silbermann (1906)
  Alcyonidium mytili Dalyell, 1848 (Alcyonidiidae)
Bonnevie (1907)
  Electra pilosa (Linnaeus, 1767) (as *Membranipora*) (Electridae)
  Membranipora membranacea (Linnaeus, 1767) (Membraniporidae)
Waters (1907)
  Margaretta chuakensis Waters, 1907 (as *Tubucellaria ceroides* var. *chuakensis*) (Margarettidae)
Braem (1908a, b)
  Paludicella sp. (obviously, *P. atriculata* (Ehrenberg, 1831)) (Paludicellidae)
  Triticella sp. (Triticellidae)
Retzius (1909)
  Triticella flava Dalyell, 1848 (as *T. korenii*) (Triticellidae)
  Scrupocellaria reptans (Linnaeus, 1767) (Candidae)
Waters (1909)
  Thalamoporella rozieri (Audouin, 1826) (Thalamoporellidae)
  Watersipora cucullata (Busk, 1854) (as ?*Lepralia*) (Watersiporidae)
Waters (1910)
  Bowerbankia imbricata (Adams, 1898) (Vesiculariidae)
  Walkeria uva (Linnaeus, 1758) (as *Valkeria*) (Walkeriidae)
Retzius (1910)
  Alcyonidium gelatinosum (Linnaeus, 1761) (Alcyonidiidae)
Waters (1912)
  Adeona foliifera fascialis Kirchenpauer, 1880 (as *A. foliacea* var. *fascialis*) (Adeonidae)
  Adeonellopsis distoma (Busk, 1858) (Adeonidae)
  Adeonellopsis sp. (Adeonidae)
  Adeonella platalea (Busk, 1852) (Adeonellidae)
  Adeonella polymorpha Busk, 1884 (as *A. polymorpha* and *Adeonella lichenoides* (Lamarck,
  1816)) (Adeonellidae)
  Adeonella polystomella (Reuss, 1847) (Adeonellidae)
  Laminopora contorta Michelin, 1842 (as *Adeonella*) (Adeonellidae)
  Beania magellanica (Busk, 1852) (Beaniidae)
  Watersipora cucullata (Busk, 1854) (as *Lepralia*) (Watersiporidae)
Waters (1913)
  Aetea anguina (Linnaeus, 1758) (Aetiidae)
  Caulibugula zanzibariensis (Waters, 1913) (as *Stirparia*) (Bugulidae)

Caulibugula dendrograpta (Waters, 1913) (as *Stirparia*) (Bugulidae)
Menipea roborata (Hincks, 1881) (as *Flabellaris*) (Candidae)
Scrupocellaria wasinensis Waters, 1913 (Candidae)
Halysisis diaphanus (Busk, 1860) (as *Catenaria diaphana*) (Savygniellidae)
Catenicella elegans (Busk, 1852) (as *Vittaticella*) (Catenicellidae)
Adenifera armata (Hasswell, 1880) (Calloporidae)
Nellia tenella (Lamarck, 1816) (as *Farcimia oculata* Busk) (Quadricellariidae)
Poricellaria complicata Reuss, 1869 (as *Diplodidymia*) (Poricellariidae)
Chlidonia pyriformis (Bertolini, 1810) (as *Chlidonia cordieri* Audouin) (Chlidoniidae)
? *Cellaria wasinensis* Waters, 1913 (Cellariidae)
Steginoporella magnilabris (Busk, 1854) (as *Steganoporella*) (Steginoporellidae)
Calyptotheca wasinensis (Waters, 1913) (as *Schizoporella nivea* Busk) (Lanceoporidae)
Trypostega venusta (Norman, 1864) (Trypostegidae)
Hippopodina feegensis (Busk, 1994) (as *Lepralia*) (Hippopodinidae)
Serripetraliella chuakensis (Waters, 1913) (as *Petralia*) (Petraliellidae)
Celleporaria columnaris (Busk, 1881) (as *Holoporella*) (Lepraliellidae)
Adeonella platalea (Busk, 1854) (Adeonellidae)
Adeonellopsis crosslandi Waters, 1913 (Adeonidae)

Gerwerzhagen (1913)
Bugula avicularia (Linnaeus, 1758) (Bugulidae)

Waters (1914)
Zoobotryon verticillatum (Delle Chiaje, 1828) (as *Z. pellucidum* Ehrenberg) (Vesiculariidae)

Harmer (1915)
Nolella papuensis (Busk, 1886) (Nolellidae)

Waters (1921)
Cupuladria canariensis (Busk, 1859) (as *Cupularia*) (Cupuladriidae)

Marcus (1922)
Steginoporella haddoni (Harmer, 1900) (as *Steganoporella*) (Steginoporellidae)

Marcus (1926)
Farella repens (Farre, 1837) (Triticellidae)
Electra pilosa (Linnaeus, 1767) (Electridae)

Harmer (1926)
Retiflustra schoenaui Levinsen, 1909 (Flustridae)
Himantozoum taurinum Harmer, 1926 (Bugulidae)
Calyptozoum operculatum Harmer, 1926 (Bugulidae)
Bugula longicauda Harmer, 1926 (Bugulidae)
Bugula johnstonae (Gray, 1843) (Bugulidae)
Euoplozoum cirratum (Busk, 1884) (Euoplozoidae)
Steginoporella magnilabris (Busk, 1854) (as *Steganoporella*) (Steginoporellidae)
Steginoporella dilatata (Harmer, 1926) (as *Steganoporella*) (Steginoporellidae)
Steginoporella lateralis (MacGillivray, 1895) (as *Steganoporella*) (Steginoporellidae)

Paltschikowa-Ostroumowa (1926)
Tendra zostericola Nordmann, 1839 (as *Membranipora*) (Tendridae)
Electra repiachowi Ostroumoff, 1886 (as *Membranipora*) (Electridae)
Conopeum reticulum (Linnaeus, 1767) (as *Membranipora*) (Membraniporidae)

Hastings (1930)
  Bugula uniserialis Hincks, 1885 (Bugulidae)
  Alderina irregularis (Smitt, 1873) (Calloporidae)
  Antropora tincta (Hastings, 1930) (as *Crassimarginatella*) (Antroporidae)
  Floridina antiqua (Smitt, 1873) (Onychocellidae)
  Discoporella umbelata (Defrance, 1823) (Cupuladriidae)
  Thalamoporella californica (Levinsen, 1909) (Thalamoporellidae)
Hastings (1932)
  Stylopoma schizostoma (MacGillivray, 1869) (Schizoporellidae)
  Stylopoma spongites (Pallas, 1766) (Schizoporellidae)
  Sinupetraliella litoralis (Livingstone, 1932) (as *Petralia*) (Petraliellidae)
Faulkner (1933)
  Alcyonidium gelatinosum (Linnaeus, 1761) (Alcyonidiidae)
Zirpolo (1933)
  Zoobotryon verticillatum (Delle Chiaje, 1828) (Vesiculariidae)
Stach (1938)
  Carbasea indivisa Busk, 1852 (Flustridae?)
Marcus (1938a)
  Alcyonidium mamillatum Alder, 1857 (Alcyonidiidae)
  Nolella dilatata (Hincks, 1860) (Nolellidae)
  Nolella stipata Gosse, 1855 (as *N. gigantea* Busk) (Nolellidae)
  Nolella alta (Kirckpatrick, 1888) (Nolellidae)
  Electra (?) *bellula* (Hincks, 1882) (Electridae)
  Chartella tenella (Hincks, 1880) (as *Electra*) (Flustridae)
  Biflustra savartii (Audouin, 1826) (as *Acanthodesia*) (Membraniporidae)
  Biflustra tenuis (Desor, 1848) (as *Acanthodesia*) (Membraniporidae)
  Securiflustra securifrons (Pallas, 1766) (as *Flustra*) (Flustridae)
  Antropora leucocypha (as *Crassimarginatella*) (Marcus, 1937) (Antroporidae)
  Bugula avicularia (Linnaeus, 1758) (Bugulidae)
  Kinetoskias smittii Daniellsen, 1868 (Bugulidae)
  Steginoporella buskii (Harmer, 1900) (as *Steganoporella*) (Steginoporellidae)
  Thalamoporella prominens (Levinsen, 1909) (as *T. gothica* var. *prominens*) (Thalamoporellidae)
  Beania hirtissima (Heller, 1867) (Beaniidae)
  Membraniporella aragoi (Audouin, 1826) (Cribrilinidae)
  Catenicella elegans (Busk, 1852) (as *Vittaticella*) (Catenicellidae)
  Vittaticella contei (Audouin, 1826) (as *Catenicella*) (Catenicellidae)
  Celleporella hyalina (Linnaeus, 1767) (as *Hippothoa*) (Hippothoidae)
  Hippoporina americana (as *Hippodiplosia*) (Bitectiporidae)
  Schizoporella unicornis (Johnston in Wood, 1844) (Schizoporellidae)
  Celleporaria carvalhoi (Marcus, 1939) (as *Schizoporella*) (Lepraliellidae)
  Celleporaria mordax (Marcus, 1937) (as *Holoporella*) (Lepraliellidae)
  Microporella ciliata (Pallas, 1766) (Microporellidae)
  Hippopodina feegensis (Busk, 1994) (Hippopodinidae)
  Watersipora cucullata (Busk, 1854) (Watersiporidae)
  Hippoporella gorgonensis Hastings, 1930 (Hippoporidridae)
  Celleporina costazii (Audouin, 1826) (as *Siniopelta*) (Celleporidae)

Rhynchozoon phrynoglossum Marcus, 1937 (Phidoloporidae)
Marcus (1938b)
Alcyonidium sp. (as *A. polyoum* (Hassal, 1841)) (Alcyonidiidae)
Braem (1940)
Sundanella sibogae (Harmer, 1915) (as *Victorella*) (Victorellidae)
Cori (1941)
Zoobotryon verticillatum (Delle Chiaje, 1828) (as *Z. pellucidum*) (Vesiculariidae)
Hastings (1941)
Scruparia chelata (Linnaeus, 1758) (Scrupariidae)
Silén (1942)
Nolella papuensis (Busk, 1886) (Nolellidae)
Marcus (1941a)
Alcyonidium gelatinosum (Linnaeus, 1761) (Alcyonidiidae)
Alcyonidium polypylum Marcus, 1941 (Alcyonidiidae)
Thalamoporella evelinae Marcus, 1939 (Thalamoporellidae)
Marcus (1941b)
Synnotum sp. (as *S. aegyptiacum*) (Epistomiidae)
Hastings (1944)
Oshurkovia littoralis (Hasting, 1944) (as *Umbonula*) (Umbonulidae)
Silén (1944)
Labiostomella gisleni Silén, 1941 (Labiostomellidae)
Nolella papuensis (Busk, 1886) (Nolellidae)
Scrupocellaria scabra (van Beneden, 1848) (Candidae)
Silén (1945)
Alcyonidium gelatinosum (Linnaeus, 1761) (Alcyonidiidae)
Alcyonidium polyoum (Hassal, 1841) (Alcyonidiidae)
Membranipora membranacea (Linnaeus, 1767) (Membraniporidae)
Electra pilosa (Linnaeus, 1767) (Electridae)
Callopora dumerilii (Audouin, 1826) (as *C. dumerili*) (Calloporidae)
Escharella immersa (Fleming, 1828) (Romancheinidae)
Fenestrulina malusii (Audouin, 1826) (as *F. malusi*) (Microporellidae)
Securiflustra securifrons (Pallas, 1766) (Flustridae)
Silén (1946, 1947)
Penetrantia densa Silén, 1946 (Penetrantiidae)
Penetrantia brevis Silén, 1946 (Penetrantiidae)
Penetrantia concharum Silén, 1946 (Penetrantiidae)
Immergentia californica Silén, 1946 (Immergentiidae)
Borg (1947)
Electra crustulenta (Pallas, 1766) (Electridae)
Corrêa (1948)
Membranipora commensale (Kirkpatrick and Metzelaar, 1922) (as *Conopeum*)
(Membraniporidae)
Bugula flabellata (Thompson in Gray, 1848) (Bugulidae)
Soule (1950a)
Penetrantia sileni Soule, 1950 (Penetrantiidae)

Soule (1950b)
   Terebripora comma Soule, 1950 (Terebriporidae)
Braem (1951)
   Victorella pavida Saville Kent, 1870 (Victorellidae)
   Bulbella abscondita Braem, 1951 (Victorellidae)
   Victorella muelleri (Kraepelin, 1877) (as *Tanganella*) (Victorellidae)
   Bowerbankia gracilis Leidy, 1855 (as *B. caudata*) (Vesiculariidae)
Mawatari (1952)
   Tricellaria occidentalis (Trask, 1857) (Candidae)
Mawatari (1952)
   Watersipora subtorquata (d'Orbigny, 1842) (as *W. cucullata* Busk) (Watersiporidae)
Bobin and Prenant (1954)
   Terebripora comma Soule, 1950 (Terebriporidae)
Chrétien (1957)
   Alcyonidium diaphanum (Hudson, 1762) (as *A. gelatinosum*) (Alcyonidiidae)
Bobin and Prenant (1957)
   Alcyonidium gelatinosum (Linnaeus, 1761) (Alcyonidiidae)
Grellet (1958)
   Alcyonidium diaphanum (Hudson, 1762) (as *A. gelatinosum*) (Alcyonidiidae)
Matricon (1960)
   Alcyonidium polyoum (Hassal, 1841) (Alcyonidiidae)
Lutaud (1961)
   Membranipora membranacea (Linnaeus, 1767) (Membraniporidae)
Cook (1961)
   Electra crustulenta (Pallas, 1766) (Electridae)
Cook (1962)
   Conopeum seurati (Canu, 1928) (as *Membranipora*) (Membraniporidae)
   Electra crustulenta (Pallas, 1766) (Electridae)
Ranzoli (1962)
   Zoobotryon verticillatum (Delle Chiaje, 1828) (Vesiculariidae)
Matricon (1963)
   Alcyonidium polyoum (Hassal, 1841) (Alcyonidiidae)
Cook (1962)
   Conopeum reticulum (Linnaeus, 1767) (Membraniporidae)
   Electra monostachys (Busk, 1854) (Electridae)
Cook (1964)
   Steginoporella buskii (Harmer, 1900) (as *Steganoporella*) (Steginoporellidae)
Silén (1966)
   Electra posidoniae Gautier, 1961 (Electridae)
   Electra crustulenta (Pallas, 1766) (Electridae)
   Electra pilosa (Linnaeus, 1767) (Electridae)
   Membranipora membranacea (Linnaeus, 1767) (Membraniporidae)
Bullivant (1967)
   Zoobotryon verticillatum (Delle Chiaje, 1828) (Vesiculariidae)
   Schizoporella unicornis (Johnston in Wood, 1844) (Schizoporellidae)

Braiko (1967)
Tendra zostericola Nordmann, 1839 (Tendridae)
Banta (1968)
Mimosella cookae Banta, 1968 (Mimosellidae)
Gordon (1968)
Odontoporella adpressa (Busk, 1854) (as *Hippopodinella*) (Hippoporidridae)
Cook (1968)
Steginoporella buskii Harmer, 1900 (as *Steganoporella*) (Steginoporellidae)
Smittipora levinseni (Canu and Bassler, 1917) (Onychocellidae)
Onychocella allula Hastings, 1930 (Onychocellidae)
Hippoporidra senegambiensis (Carter, 1882) (Hippoporidridae)
Ström (1969)
Triticella flava Dalyell, 1848 (as *T. koreni* G.O. Sars) (Triticellidae)
Eggleston (1971)
Triticella flava Dalyell, 1848 (as *T. koreni*) (Triticellidae)
Reger (1971)
Bugula sp. (Bugulidae)
Castric-Fey (1971)
Alcyonidium argyllaceum Castric-Fey, 1971 (Alcyonidiidae)
Silén (1972)
Cellaria fistulosa (Linnaeus, 1758) (as *Cellaria salicornia* Pallas) (Cellariidae)
Bugula flabellata (Thompson in Gray, 1848) (Bugulidae)
Chorizopora brongniartii (Audouin, 1826) (as *C. brongniarti*) (Chorizoporidae)
Schizoporella unicornis (Johnston in Wood, 1844) (Schizoporellidae)
Reteporella septentrionalis (Harmer, 1933) (as *Sertella*) (Phidoloporidae)
Celleporina caminata (Waters, 1879) (Celleporidae)
Turbicellepora avicularis (as '*Schismopora*') (Hincks, 1860) (Celleporidae)
Myriapora truncata (Pallas, 1766) (Myriaporidae)
Woollacott and Zimmer (1972a, 1972b)
Bugula neritina (Linnaeus, 1758) (Bugulidae)
Jebram (1973)
Conopeum seurati (Canu, 1928) (Membraniporidae)
Dudley (1973)
Conopeum tenuissimum (Canu, 1928) (Membraniporidae)
Mawatari (1973a)
Aetea anguina (Linnaeus, 1758) (Aetiidae)
Aetea truncata (Landsborough, 1852) (Aetiidae)
Mawatari (1973b)
Scruparia chelata (Linnaeus, 1758) (Scrupariidae)
Zimmer and Woollacott (1974)
Membranipora sp. (Membraniporidae)
Woollacott and Zimmer (1975)
Bugula neritina (Linnaeus, 1758) (Bugulidae)
Mawatari (1975)
Membranipora serrilamella Osburn, 1950 (Membraniporidae)

Mawatari and Mawatari (1975)
  Membranipora serrilamella Osburn, 1950 (Membraniporidae)
Soule and Soule (1975)
  Spathipora sp. (Spathiporidae)
  Terebripora sp. (Terebriporidae)
  Penetrantia sp. (Penetrantiidae)
  Immergentia sp. (Immergentiidae)
Soule and Soule (1976)
  Spathipora mazatlanica Soule and Soule, 1976 (Spathiporidae)
Franzén (1976)
  Triticella flava Dalyell, 1848 (as *T. korenii* G.O. Sars) (Triticellidae)
  Flustra foliacea (Linnaeus, 1758) (Flustridae)
Cook (1977)
  Hippoporidra sp. (Hippoporidridae)
Ryland and Gordon (1977)
  Celleporella tongima Ryland and Gordon, 1977 (as *Hippothoa*) (Hippothoidae)
Nielsen (1981)
  Pacificincola insculpta (Hincks, 1882) (as '*Hippodiplosia*') (Pacificincolidae)
  Fenestrulina miramara Soule, Soule and Chaney, 1995 (as *F. malusii*) (Microporellidae)
Dyrynda (1981)
  Epistomia bursaria (Linnaeus, 1758) (Epistomiidae)
  Chartella papyracea (Ellis and Solander, 1786) (Flustridae)
Chimonides and Cook (1981)
  Selenaria maculata Busk, 1852 (Selenariidae)
Hageman (1981, 1983)
  Membranipora serrilamella Osburn, 1950 (Membraniporidae)
Jebram and Everitt (1982)
  Bulbella abscondita Braem, 1951 (Victorellidae)
  Victorella pseudoarachnidia Jebram and Everitt, 1982 (Victorellidae)
  Tanganella appendiculata Jebram and Everitt, 1982 (Victorellidae)
Dyrynda and King (1982)
  Epistomia bursaria (Linnaeus, 1758) (Epistomiidae)
Dyrynda and Ryland (1982)
  Chartella papyracea (Ellis and Solander, 1786) (Flustridae)
  Bugula flabellata (Thompson in Gray, 1848) (Bugulidae)
Dyrynda and King (1983)
  Chartella papyracea (Ellis and Solander, 1786) (Flustridae)
  Bugula flabellata (Thompson in Gray, 1848) (Bugulidae)
  Bugula turbinata Alder, 1857 (Bugulidae)
  Bugula calathus Norman, 1868 (Bugulidae)
  Bugula neritina (Linnaeus, 1758) (Bugulidae)
  Bugula plumosa (Pallas, 1766) (Bugulidae)
  Bugula fulva Ryland, 1960 (Bugulidae)
  Bugula stolonifera Ryland, 1960 (Bugulidae)
  Bicellariella ciliata (Linnaeus, 1758) (Bugulidae)

Hayward (1983)
   Alcyonidium hirsutum (Fleming, 1828) (Alcyonidiidae)
Kayser (1984)
   Panolicella nutans Jebram, 1985 (as *Nolella pusilla*) (Panolicellidae)
Cook (1985)
   Odontoporella adpressa (Busk, 1854) (as *Hippopodinella*) (Hippoporidridae)
   Hippoporidra senegambiensis (Carter, 1882) (Hippoporidridae)
   Hippoporidra littoralis Cook, 1964 (Hippoporidridae)
Jebram (1985)
   Panolicella nutans Jebram, 1985 (Panolicellidae)
Hughes (1987)
   Celleporella hyalina (Linnaeus, 1767) (Hippothoidae)
Reed (1988)
   Bowerbankia gracilis Leidy, 1855 (Vesiculariidae)
   Bowerbankia gracilis var. *aggregata* O'Donoghue and O'Donoghue, 1926 (Vesiculariidae)
Owrid and Ryland (1991)
   Alcyonidium hirsutum (Fleming, 1828) (Alcyonidiidae)
Cancino, Castañeda and Orellana (1991)
   Membranipora isabelleana (d'Orbigny, 1847) (Membraniporidae)
   Celleporella hyalina (Linnaeus, 1767) (Hippothoidae)
Zimmer (in Reed 1991)
   Membranipora membranacea (Linnaeus, 1767) (Membraniporidae)
   non-specified *Schizoporella* (Schizoporellidae)
   Watersipora arcuata Banta, 1969 (Watersiporidae)
Maturo (1991a)
   Schizoporella cf. *pungens* Canu and Bassler, 1928 (Schizoporellidae)
Maturo (1991b)
   Bowerbankia gracilis Leidy, 1855 (Vesiculariidae)
   Buskia sp. (Buskiidae)
   Bugula neritina (Linnaeus, 1758) (Bugulidae)
   Antropora leucocypha (Marcus, 1937) (Antroporidae)
   Hippoporina verrilli Maturo and Schopf, 1968 (Bitectiporidae)
   Schizoporella cf. *pungens* Canu and Bassler, 1928 (Schizoporellidae)
Wood and Seed (1992)
   Alcyonidium hirsutum (Fleming, 1828) (Alcyonidiidae)
   Flustrellidra hispida (Fabricius, 1780) (Flustrellidridae)
Harvell and Helling (1993)
   Membranipora membranacea (Linnaeus, 1767) (Membraniporidae)
Temkin (1994)
   Membranipora membranacea (Linnaeus, 1767) (Membraniporidae)
Temkin (1996)
   Alcyonidium sp. (Alcyonidiidae)
   Bowerbankia gracilis Leidy, 1855 (Vesiculariidae)
   Electra pilosa (Linnaeus, 1767) (Electridae)
   Dendrobeania lichenoides (Robertson, 1900) (Bugulidae)
   Tricellaria gracilis (Smitt, 1867) (Candidae)

Cribrilina corbicula (O'Donoghue, 1923) (Cribrilinidae)
Schizoporella serialis (Heller, 1867) (Schizoporellidae)
Watersipora arcuata Banta, 1969 (Watersiporidae)
Pacificincola insculpta (Hincks, 1882) (as *Hippodiplosia*) (Pacificincolidae)

Santagata and Banta (1996)
Scrupocellaria ferox Busk, 1852 (Candidae)

Cadman and Ryland (1996)
Alcyonidium mytili Dalyell, 1848 (Alcyonidiidae)

Franzén (1998)
Electra pilosa (Linnaeus, 1767) (Electridae)

Ostrovsky (1998)
Cribrilina annulata (Fabricius, 1780) (Cribrilinidae)
Celleporella hyalina (Linnaeus, 1767) (Hippothoidae)

Ryland and Porter (2000)
Alcyonidium reticulum Ryland and Porter, 2000 (Alcyonidiidae)
Alcyonidium gelatinosum (Linnaeus, 1761) (Alcyonidiidae)
Alcyonidium mytili Dalyell, 1848 (Alcyonidiidae)

Ryland (2001)
Alcyonidium nodosum O'Donoghue and de Watteville, 1944 (Alcyonidiidae)
Hippoporidra dictyota Ryland, 2001 (Hippoporidridae)

Porter, Hayward and Spencer Jones (2001)
Alcyonidium diaphanum (Hudson, 1778) (Alcyonidiidae)

Temkin (2002)
Membranipora membranacea (Linnaeus, 1767) (Membraniporidae)

Smith, Werle and Klekowski (2003)
Pottsiella erecta (Potts, 1884) (Pottsiellidae)

Temkin and Bortolami (2004)
Membranipora membranacea (Linnaeus, 1767) (Membraniporidae)

Porter (2004)
Alcyonidium condylocinereum Porter, 2004 (Alcyonidiidae)
Alcyonidium diaphanum (Hudson, 1778) (Alcyonidiidae)
Alcyonidium hydrocoalitum Porter, 2004 (Alcyonidiidae)

Porter and Hayward (2004)
Alcyonidium australe d'Hondt and Moyano, 1979 (Alcyonidiidae)
Alcyonidium eightsi Winston and Hayward, 1986 (Alcyonidiidae)
Alcyonidium epispicule Porter and Hayward, 2004 (Alcyonidiidae)
Alcyonidium flabelliforme Kirckpatrick, 1902 (Alcyonidiidae)
Alcyonidium scolicoideum Porter and Hayward, 2004 (Alcyonidiidae)
Alcyonidium simulatum Porter and Hayward, 2004 (Alcyonidiidae)

Kuklinski and Porter (2004)
Alcyonidium disciforme Smitt, 1871 (Alcyonidiidae)

Ryland and Porter (2006)
Alcyonidium diaphanum (Hudson, 1778) (Alcyonidiidae)
Alcyonidium gelatinosum (Linnaeus, 1761) (Alcyonidiidae)
Alcyonidium hirsutum (Fleming, 1828) (Alcyonidiidae)
Alcyonidium mytili Dalyell, 1848 (Alcyonidiidae)

Alcyonidium polyoum (Hassal, 1841) (Alcyonidiidae)
Carter and Gordon (2007)
   Odontoporella bishopi (Carter and Gordon, 2007) (Hippoporidridae)

Notes

1   R.S. Boardman, A.H. Cheetham, D.B. Blake, J. Utgaard, O.L. Karklins, P.L. Cook, P.A. Sandberg, G. Lutaud and T.S. Wood, '*Bryozoa (Part G, revised)*', *Treatise on Invertebrate Paleontology,* edited by R.A. Robinson, vol. 1, (Geological Society of America, Boulder, Colorado, and University of Kansas, Lawrence, 1983), 1-625.

2   F.K. McKinney and J.D.C. Jackson, *Bryozoan evolution*, (Unwin Hyman, Boston, 1989), xiii, 238.

3   C.G. Reed, 'Bryozoa', in *Reproduction of Marine Invertebrates*, edited by A.C. Giese, J.S. Pearse and V.B. Pearse, vol. VI. Echinoderms and Lophophorates, (Boxwood Press, Pacific Grove, 1991), 85-245.

4   P.D. Taylor, 'Major radiation of cheilostome bryozoans: triggered by the evolution of a new larval type', *Historical Biology,* 1 (1988), 45-64.

5   Å. Franzén, 'On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates', *Zoologiska Bidrag från Uppsala*, 31 (1956), 355-481.

6   Å. Franzén, 'Gametogenesis of bryozoans', in *Biology of Bryozoans,* edited by R.M. Woollacott and R.L. Zimmer (Academic Press, New York, 1977), 1-22.

7   Å. Franzén, 'Comparative ultrastructural studies of spermatids and spermatozoa in Bryozoa and Entoprocta', in *Recent and Fossil Bryozoans,* edited by G.P. Larwood and C. Nielsen (Olsen and Olsen, Fredensborg, 1981), 83-92.

8   Å. Franzén, 'Bryozoa Ectoprocta. Vol. II, Spermatogenesis and sperm function', in *Reproductive Biology of Inveretebrates*, edited by K.G. Adiyodi and R.G. Adiyodi, Vol. IV, Part B (John Wiley and Sons, Chichester, 1983), 491-504.

9   L.H. Hyman, '*The Invertebrates: smaller coelomate groups*', vol. 5: VIII, (McGraw-Hill, New York, 1959), 1-783.

10 R. Ström, 'Brooding patterns of bryozoans', in *Biology of Bryozoans,* edited by R.M. Woollacott and R.L. Zimmer, (Academic Press, New York, 1977), 23-56.

11 P.J. Hayward, 'Bryozoa Ectoprocta', in *Reproductive Biology of Invertebrates,* edited by K.G. Adiyodi and R.G. Adiyodi, vol. I: Oogenesis, oviposition and oosorption, (John Wiley and Sons, Ltd., 1983), 543-560.

12 C. Nielsen, 'Bryozoa Ectoprocta', in *Reproductive Biology of Inveretebrates*, edited by K.G. Adiyodi and R.G. Adiyodi, Vol. IV, Part B: Fertilization, development and parental care (Oxford and IBH Publishing Co. Pvt. Ltd, New Delhi, Bombay, Calcutta, 1990), 185-200.

13 Reed, note 3.

14 H. Mukai, K. Terakado and C.G. Reed, 'Bryozoa', in *Microscopic Anatomy of Invertebrates*, edited by F.W. Harrison, vol. 13, (Wiley-Liss, New York, 1997), 45-206.

15 H.G. Bronn, 'Moostierchen: Bryozoa Ehrb. (Bryacephala)', in *Die Klassen und Ordnungen des Their-Reichs*, *wissenschaftlich dargestellt in Wort und Bild,* (C.F. Winter'sche Verlagshandlung, Leipzig, Heidelberg, 1862-1866), Band III, Malacozoa, I Abtheilung (1862), 19-102, II Abtheilung (1862-1866), Pls I-VIII.

16 T. Hincks, *A history of the British marine Polyzoa*, 2 vols (Van Voorst, London, 1880), 601.

17 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.

18 Y. Delage, E. Hérouard, 'Bryozoaires. – Bryozoaria', in *Traité de Zoologie Concrète, Les Vermidiens – Vermidea*, 5, edited by S. Frères, (Librairie C. Reinwald, Paris, 1897), 47-155.

19 E. Korschelt and K. Heider, 'Bryozoen', *Lehrbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Thiere*, 4 (2) (1910), 632-694, 892-894.

20 E. Marcus, 'Beobachtungen und Versuche an lebeden Meeresbryozoen', *Zoologische Jahrbücher Abteilung für Systematik, Ökologie und Geographie der Tiere*, 52 (1926), 1-102.

21 E. Marcus, 'Mosdyr (Bryozóa eller Polyzóa) ', *Danmarks Fauna*, 46 (1940), 1-401.

22 C.J. Cori, 'Bryozoa. Ordnung der Tentaculata', *Handbuch der Zoologie* III, 2 (5) (1941), 263-374, 375-502.

23 P. Brien, 'Classe des Bryozoaires', in *Traité de Zoologie*, edited by P.-P. Grassé, (Masson, Paris, 1960), 1053-1379.

24 A. Kaestner, 'Klasse Bryozoa Moostiere'. in *Lehrbuch der speciellen Zoologie. Teil I*: *Wirbellose*, (Veb Gustav Fisher Verlag, Jena, 1963), 1068-1100.

25 A. Ostrovsky, 'The history of study on the parental care in cheilostome bryozoans', this volume.

26 A. Ostrovsky, '*External* versus *Internal* and *Self-* versus *Cross-*. Fertilization in Bryozoa: transformation of the view and evolutionary considerations', this volume.

27 Ostrovsky, note 26.

28 Reed, note 3.

29 T.H. Huxley, 'Note on the reproductive organs of the cheilostome Polyzoa', *Quarterly Journal of Microscopical Science*, 4 (1856), 191-192 (191).

30 A. Trembley, *Memoires pour servir a l'histoire d'un genre de polypes d'eau douce, a bras en forme de cornes*, 2 vols (Jean and Herman Verbeek, Paris, 1744), xvi, 324. For an account of some of Trembley's work see also paper by G.C. Cadée, 'Early bryozoan studies in the Netherlands', in *Annals of Bryozoology,* edited by P.N. Wyse Jackson and M.E. Spencer Jones, (International Bryozoology Association, Dublin, 2002), 31-43.

31 Mentioned in G. Allman, *A monograph of the fresh-water Polyzoa, including all the known species, both British and foreign* (Ray Society, London, 1856), 120.

32 F.V. Raspail, 'Histoire naturelle de l'*Alcyonella fluviatile* (*A. stagnorum,* Lamk.) et de tous les genres voisins, consideres, soit sous le rapport de leur organisation et de leur identite specifique, sout sous le rapport physiologique de leurs tentacules avec les branchies des mollusques et des animalcules ou infusoires ou sermatiques', *Memoires de la Societe d'Histoire Naturelle de Paris*, 4 (1828), 75-165, 246.

33 M.P. Gervais, 'Recherches sur les Polypes d'eau douce des genres *Plumatella*, *Cristatella* et *Paludicella*', *Annales des Sciences Naturelles,* 2 Serie, 7 (Masson, Paris, 1837), 74-93

34 G. Allman, 'On the larva state in *Plumatella*', *Proceedings of the Royal Irish Academy*, 3 (1847), 218-219, 220-222. For further references see Allman, note 31.

35 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).

36 J. Ellis and D. Solander, *The natural history of many curious and uncommom Zoophytes, collected from 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.

37 J.V.F. Lamouroux, *Histoire des Polypiers Coralligènes flexibles, vulgairement nommés Zoophytes* (Poisson, Caen, 1816), 559.

38 H. Milne Edwards, 'Recherches anatomiques, physiologiques et zoologiques sur les Eschares',

Annales des Sciences Naturelles, Zoologie 2, VI (1836), 5-53.

39 J.B.P.A.M. de Lamarck, *Histoire naturelle des animaux sans vertèbres*, 2 èdition, Vol. II, (J.B. Baillière, Paris, 1836), 683.

40 J. Reid, 'Anatomical and physiological observations on some Zoophytes', *The Annals and Magazine of Natural History*, 16 (1845), 385-400.

41 G. Johnston, *A history of British Zoophytes*, Vol. 1, (Van Voorst, London, 1847), 488.

42 T. Hincks, 'Note on the ovicells of the cheilostomatous Polyzoa', *Quarterly Journal of Microscopical Science*, *New Series*, 1 (1861), 278-281.

43 T. Hincks, 'Contributions to history of Polyzoa', *Quarterly Journal of Microscopical Science*, (N.S.) 13 (1873), 17-37.

44 Hincks, note 16.

45 See Ostrovsky, note 25.

46 Hincks, note 42, page 280.

47 Later reviewed in Hincks, note 43.

48 Bronn, note 15.

49 J.V. Thompson, 'On Polyzoa, a new animal discovered as an inhabitant of some zoophytes with a description of the newly instituted genera of *Pedicellaria* and *Vesicularia* and their species', *Zoological researches and illustrations*, 4 (5) (1830), 89-102 (96).

50 Milne-Edwards, note 38.

51 R.E. Grant, 'Observations on the structure and nature of Flustrae', *Edinburgh New Phylosophical Journal*, 3 (1827), 107-118, 337-342. For information on Grant see S.E. Parker, *Robert Edmond Grant (1793-1874) and his Museum of Zoology and Comparative Anatomy* (London, Grant Museum of Zoology, University College London, 2006).

52 Grant, note 51, pages 341-342.

53 Grant, note 51, page 117.

54 A.B. Farre, 'Observations on the minute structure of some of the higher forms of polypi, with views of a more natural arrangement of the class', *Philosophical Transactions of the Royal Society of London*, 1 (1837), 387-426.

55 Later Calvet (note 17) studied it in sections in this species.

56 Farre, note 54, page 408.

57 Farre, note 54, page 409.

58 G. Johnston, '*A history of the British zoophytes*', (Edinburgh, London, Dublin, 1838), 341.

59 T. Hincks, 'Notes on British Zoophytes, with descriptions of some new species', *The Annals and Magazine of Natural History*, *2nd Series*, 8 (47) (1851), 353-362.

60 L. Silén, 'On the fertilization problem in gymnolaematous Bryozoa', *Ophelia*, 3 (1966), 113-140.

61 H. Prouho, 'Contribution a l´histoire des bryozoaires', *Archives de Zoologie expérimentale et générale*, 10 (1892), 557-656.

62 Hincks, note 59.

63 H. Prouho, 'Sur la reproduction de quelques Bryozoaires cténostomes', *Comptes Rendus Hebdomadaires des Séances de l'Ácadémie des Sciences, Paris*, 109 (1889), 197-198.

64 Hincks, note 59.

65 A. Kölliker, *Beiträge zur Kenntniss der Geschlechtsverhältnisse und der Samenflüssigkeit wirbelloser Thiere, nebst einem Versuch über das Wesen und die Bedeutung der sogenanten Samenthiere* (Berlin, 1841), 88.

66 A.H. Hassall, 'Description of two new genera of Irish Zoophytes', *The Annals and Magazine*

of Natural History, 7 (46) (1841), 483-486.

67 P.J. Van Beneden, 'Recherches sur l'organisation des *Laguncula* et l'histoire naturelle des différents polypes Bryozoaires qui habitent la côte d'Ostende', *Nouveaux Mémoires de l'Academie Royale de Bruxelles*, 18 (1844), 1-29.

68 P.J. Van Beneden, 'Recherches sur l'anatomie, la physiologie et l'embryologie des Bryozoaires qui habitent la cote d'Ostende', *Mémoires de l'Academie Royale de Belgique*, 18 (1844), 1-44.

69 Reid, note 40.

70 Johnston, note 41.

71 J.G. Dalyell, *Rare and remarkable animals of Scotland, represented from living subjects: with practical observations on their nature,* 2 vols (Van Voorst, London, 1847-1848), vol 1, xii, 268, vol 2, iv, 322.

72 A. Hancock, 'On the anatomy of the freshwater Bryozoa with description of three new species', *The Annals and Magazine of Natural History*, 2nd Series, 5 (27) (1850), 173-204.

73 Allman, note 31.

74 P.J. Van Beneden, 'Quelques observations sur les Polypes d'eau douce', *Bulletin de l'Academie Royale des Sciences et Belles-Lettres de Bruxelles*, 6 (1839), 276-279.

75 B.C. Dumortier and P.J. Van Beneden, 'Histoire naturelle des Polypes d'eau douce', *Mémoires de l'Academie Royale des Sciences et Belles-Lettres de Bruxelles*, 16 (complement) (1850), 1-96.

76 W. Salensky, 'Untersuchungen an Seebryozoen', *Zeitschrift für wissenschaftliche Zoologie,* 24 (1874), 343-348.

77 H. Nitsche, 'Beiträge zur Kenntniss der Bryozoen. IV. Über die Morphologie der Bryozoen', *Zeitschrift für wissenschaftliche Zoologie*, 21 (1871), 471-498.

78 H. Nitsche, 'On some interesting points concerning the mode of reproduction of the Bryozoa', *Quarterly Journal of Microscopical Science*, 11 (1871), 155-162.

79 L. Joliet, 'Contributions à l'histoire naturelle des Bryozoaires des côtes de France', *Archives de Zoologie expérimentale et générale*, 6 (1877), 193-304.

80 Bronn, note 15.

81 A. Hyatt, 'Observations on Polyzoa. Suborder Phylactolaemata', *Proceedings of the Essex Institute*, vols 4 and 5, (Salem, 1866-1868), iv, 103 (9).

82 Hincks, note 16.

83 W.J. Vigelius, 'Die Bryozoen, gesammelt während der dritten und vierten Polarfahrt des "Willem Barents" in den Jahren 1880 und 1881', *Bijdragen tot de Dierkunde*, 11 (1884), 1-104.

84 Cori, note 22.

85 Huxley, note 29, pages 191-192.

86 Grant, note 51.

87 P. Redfern, '*Flustrella hispida* and its development', *Quarternaly Journal of Microscopical Science*, 6 (1858), 96-102.

88 Bronn, note 15.

89 Noteworthy, this opinion survived for more than one and half centuries. See: Ostrovsky, this volume, note 26.

90 G. Busk, *A monograph of the fossil Polyzoa of the Crag* (Palaeontological Society, London, 1859), 136.

91 F.A. Smitt, 'Om Hafs-Bryozoernas utveckling och fettkroppar', *Aftrych ur Öfversigt af Kongliga Vetenskaps-Akademiens förhandlingar*, 1 (1865), 5-50.

92 Salensky, note 76.

93 W. Repiachoff, 'Zur Naturgeschichte der chilostomen Bryozoen', *Zeitschrift für wissenschaftliche Zoologie,* 26 (1876), 139-160 (140).

94 Calvet, note 17, page 293.

95 Smitt, note 91.

96 E. Claparède, 'Beiträge zur Anatomie und Entwicklungsgeschichte der Seebryozoen', *Zeitschrift für Wissenschaftliche Zoologie*, 21 (1871), 138-174.

97 F.A. Smitt, 'Kritisk Förteskning öfver Scandinaviens Hafs-Bryozoernas', *Aftrych ur Öfversigt af Kongliga Vetenskaps-Akademiens förhandlingar*, 23 (1866), 395-533.

98 H. Nitsche, 'Beobachtungen über die Entwicklungsgeschichte einiger chilostomen Bryozoen', *Zeitschrift für wissenschaftliche Zoologie*, 20 (1) (1869), 1-13.

99 Huxley, note 29.

100 Smitt, note 91.

101 L. Joliet, 'Contributions à l'histoire naturelle des Bryozoaires des côtes de France', *Archives de Zoologie expérimentale et générale*, 6 (1877), 193-304.

102 Nitsche, note 98.

103 Claparède, note 96.

104 Claparède, note 96.

105 Joliet, note 79.

106 Hincks, note 16.

107 W. Repiachoff, 'Zur Entwicklungsgeschichte der *Tendra zostericola*', *Zeitschrift für wissenschaftliche Zoologie*, 25 (1875), 129-142.

108 W.W. Reinhard, 'Neskolko soobschceniy iz istorii razvitija mschanok', *Trudy Obschcestva Ispytateley Prirody pri Imperatorskom Kharkovskom universitete*, 9 (1875), 1-39.

109 M.A. Nordmann, 'Recherches microscopiques sur l´anatomie et le développement du *Tendra zostericola*, espèce de polype de la section des Bryozoaires', *Annales des Sciences Naturelles*, Paris: Masson, Serie 2, 11 (1839), 185-191.

110 Similar to Nordmann, Braiko (note 115) thought that the transverse wall between these zooids degenerates.

111 Salensky, note 76.

112 Reinhard, note 108.

113 A. Ostroumoff, 'Die Bryozoen der Bucht von Sebastopol. Vollständigere Ausgabe mit einem ganz neuen Theile über die Morphologie der Bryozoen', *Trudy Obschcestva Ispytateley Prirody pri Imperatorskom Kharkovskom universitete*, 16 (2) (1886), 1-124.

114 M.W. Paltschikowa-Ostroumowa, 'Kurze Bemerkung über den Ovidukt bei den Bryozoen', *Zoologischer Anzeiger,* 65 (1926), 100-102.

115 V.B. Braiko, 'Biologija razmnozhenija *Membranipora zostericola* Nordm. (Bryozoa)', *Zoologicheskiy Zhurnal,* 46 (1967), 1119-1121.

116 Repiachoff, note 93.

117 Repiachoff, note 93, Plate 6, figure 1.

118 E. Ehlers, '*Hypophorella expansa*. Ein beitrag zur Kenntniss der minirenden Bryozoen', *Abhandlungen der physikalischen Classe der königlichen Gesellschaft der Wissenschaften zu Göttingen*, 21 (1876), 3-157.

119 Farre, note 54.

120 Hincks, note 59.

121 Prouho, note 61.

122 Joliet, note 101.

123 Both Nitsche and Joliet considered the cystid and polypide as distinct individuals of the 'compound animal' (Nitsche, note 78, page 161), although Nitsche thought that sexual reproduction was one of the functions of the cystid, but Joliet – of the polypide (see also above).

124 Joliet's observation, although criticized by Hincks (note 16), is actually correct: in many instances an ovary is removed from the developing polypide bud (where it originates) to the basal cystid wall.

125 In contrast with Nitsche (note 98) (see reference above), Joliet found ovaries on both funiculus and cystid wall in *Bicellariella ciliata*. Interestingly, he stated that he never saw the ovicells, formed by the fertile zooid in the second case. Was it the egg?

126 Smitt, note 91.

127 P.E.J. Dyrynda and J.S. Ryland, 'Reproductive strategies and life histories in the cheilostome marine bryozoans *Chartella papyracea* and *Bugula flabellata*', *Marine Biology*, 71 (1982), 241-256.

128 Joliet, note 101, Plate XIII, figures 5-9.

129 Claparède, note 96.

130 It could be correct if Joliet and Claparède also saw previtellogenetic doublets.

131 Marcus, note 20.

132 Hincks, note 16.

133 Hincks, note 42.

134 Hincks, note 43.

135 Hincks, note 16, pages xlix-l.

136 Hincks, note 43.

137 Calvet, note 17.

138 Hincks, note 16, see legend for figure 4 (Plate 77).

139 Prouho, note 61, Plate XXIV.

140 Joliet, note 101.

141 Hincks, note 16, page xci.

142 W.J. Vigelius, 'Zur Enstehung und Entwicklung der Geschlechtsprodukte bei chilostomen Bryozoen', *Biologisches Zentralblatt*, 2 (1882), 435-442 (436).

143 W.J. Vigelius, 'Morphologische Untersuchungen über *Flustra membranaceo-truncata* Smith', *Biologisches Zentralblatt*, 3 (23) (1884), 705-721.

144 Vigelius, note 83.

145 Joliet, note 101.

146 Actually, there are either 1-2 oocytic doublets or one doublet and one mature primary oogonium. However, Vigelius often mentioned that eggs develop in pairs.

147 Calvet, note 17.

148 Korschelt and Heider, note 253.

149 Gerwerzhagen, note 172.

150 Vigelius, note 83.

151 Joliet, note 79.

152 Ehlers, note 118.

153 W.J. Vigelius, 'Zur Ontogenie der marinen Bryozoen', *Mittheilungen aus der zoologischen Station zu Neapel zugleich ein Repertorium für Mittelmeerkunde*, 6 (1886), 499-541 (509).

154 Ostroumoff, note 113.

155 Vigelius, note 153, Tafel 26, figures 3-4, 40.

156 See also: Calvet, note 17.

157 E. Marcus, 'Bryozoarios marinhos brasileiros, II', *Boletins da Faculdade de Philosophia, Sciências e Letras. Universidade de São Paulo IV,* Zoologia, 2 (1938), 1-196.

158 R.M. Woollacott and R.L. Zimmer, 'Origin and structure of the brood chamber in *Bugula neritina* (Bryozoa)', *Marine Biology*, 16 (1972), 165-170.

159 R.M. Woollacott and R.L. Zimmer, 'A simplified placenta-like system for the transport of extraembryonic nutrients during embryogenesis of *Bugula neritina* (Bryozoa)', *Journal of Morphology*, 147 (1975), 355-378.

160 Reid, note 40, page 398.

161 Hincks, note 42, page 280.

162 Reid, note 40.

163 Hincks, note 42.

164 Nitsche, note 98.

165 Hincks, note 43.

166 Vigelius, note 153.

167 Calvet, note 17.

168 K. Kraepelin, 'Die Deutschen Süsswasser-Bryozoen. Anatomish-systematischer Teil', *Abhandlungen aus dem Gebiete der Naturwissenschaft herausgeben von dem Naturwissenschaftlicher Verein in Hamburg,* 10 (1887), 1-168.

169 J. Jullien, 'Du testicule chez la *Lepralia figularis* Johnston, 1847, et des variétés de cet organe chez les bryozoaires en général', *Mémoires de la Société Zoologique de France*, 1 (1888), 270-273.

170 J. Jullien, 'Bryozoaires', *Mission scientifique du Cap Horn, 1882-83,* 6 (Zoologie Part 3) (1888): 1-92.

171 E. Pergens, 'Untersuchungen an Seebryozoen', *Zoologischer Anzeiger*, 12 (317, 318) (1889), 504-510 (510), 526-533.

172 A. Gerwerzhagen, 'Untersuchungen an Bryozoen', *Sitzungsberichte der Heidelberger Akademie der Wissenschaften, Mathematische-naturwissenschaftliche Klasse B*, 9 (1913), 1-16.

173 C. Nielsen, 'On morphology and reproduction of *'Hippodiplosia' insculpta* and *Fenestrulina malusii* (Bryozoa, Cheilostomata)', *Ophelia*, 20 (1981), 91-125.

174 Van Beneden, note 68.

175 Vigelius, note 83.

176 Prouho, note 63.

177 Prouho, note 61.

178 Prouho, note 63, page 197.

179 Ehlers, note 118.

180 P.J. Hayward, 'Ctenostome bryozoans', *Synopses of the British Fauna*, 33 (1985), 1-169.

181 Prouho, note 61, Plate XXIV, figures 14-17.

182 Marcus, note 157.

183 See also: Ström, note 10.

184 F. Braem, 'Die geschlechtliche Entwicklung von *Paludicella Ehrenbergii*', *Zoologischer Anzeiger*, 19 (493) (1896), 54-57.

185 Allman, note 31.

186 F. Braem, 'Die Spermatozoon der Süsswasser-Bryozoen', *Zoologischer Anzeiger*, 32 (1908), 671-673.

187 F. Braem, 'Die Spermatozoen von *Paludicella* and *Triticella*', *Zoologischer Anzeiger*, 33 (11) (1908), 380-381.

188 A. Waters, 'Notes on Bryozoa from Rapallo and other Mediterranean localities. – Chiefly Cellulariidae', *Journal of the Linnean Society, London, Zoology*, 26 (166) (1896(1898)), 1-21.

189 A. Robertson, 'Non-encrusting chilostomatous Bryozoa of the West coast of North America', *Publications of the University of California, Zoology*, 2 (5) (1905), 235-322.

190 S. Mawatari, 'Studies on Japanese Anascan Bryozoa. 1. Inovicellata', *Bulletin of the National Science Museum, Tokyo*, 16 (3) (1973), 409-428.

191 Delage and Hérouard, note 18.

192 Calvet, note 17.

193 Both these findings were not understood by the author, although he noted that the size of the cells of the brooding sac wall correlated with the developmental stage of the embryo in *Cellaria*: the more advanced the embryo is, the larger the cells are.

194 Joliet, note 79.

195 Calvet, note 17, Planche III, figure 14.

196 Calvet, note 17, pages 75, 295.

197 Vigelius, note 153.

198 Calvet criticized the opinion of the early authors, for instance, Nitsche (note 98), about the ovarian origin from the 'endocyst'. Actually, Nitsche, who did not used sections for his work, could not see perithoneal epithelium of the cystid wall.

199 See also Joliet, note 101.

200 Unusual ovary, developing on the caecum and, partially, funiculus, was described in the ctenostome *Nolella dilatata* (as *Cylindroecium dilatatum*). Except numerous eggs Calvet could not distinguish any accessory cells in it.

201 Calvet, note 17, page 296.

202 K. Schulz, 'Untersuchungen über den Bau der Bryozoen mit besonderer Berücksichtigung der Exkretionsorgane', *Archiv für Naturgeschichte*, 67 (1) (1901), 115-144.

203 For details see the paper of S.F. Harmer, 'On the nature of the excretory processes in marine Polyzoa', *Quarterly Journal of Microscopical Science*, 33 (1892), 123-167.

204 S.F. Harmer, 'On the morphology of the Cheilostomata', *Quarterly Journal of Microscopical Science*, 46 (182) (1902), 263-350 (301).

205 S.F. Harmer, 'The Polyzoa of the Siboga Expedition. II. Cheilostomata Anasca', *Reports of the Siboga Expedition*, 28b (E. J. Brill, Leiden, 1926), 181-501 (253).

206 Harmer, note 205, page 203.

207 F. Canu and R.S. Bassler, 'North American Early Tertiary Bryozoa', *Bulletin of the United States National Museum*, 106 (1920), I-XX, 1-879.

208 F. Canu and R.S. Bassler, 'Bryozoa of the Philippine region', *Bulletin of the United States National Museum*, 100 (9) (1929), I-XI, 1-685.

209 A. Waters, 'Observations on Membraniporidae', *Journal of the Linnean Society, London, Zoology*, 26 (172) (1896(1898)), 126-133.

210 A. Waters, 'Bryozoa from Franz-Josef Land, collected by the Jackson-Harmsworth expedition, 1896-1897', *Journal of the Linnean Society, London, Zoology*, 28 (179) (1900), 126-133.

211 A. Waters, 'Reports on marine biology of the Sudanese Red Sea, from collections made by Cyril Crossland, M.A., B.Sc., F.Z.S.; together with collections made in the Red Sea by Dr. R. Hartmeyer. – XV. The Bryozoa. Part II. – Cyclostomata, Ctenostomata and Endoprocta',

Journal of the Linnean Society, London, Zoology, 31 (1910), 231-256.

212   A. Waters 'Bryozoa from Franz-Josef Land, collected by the Jackson-Harmsworth expedition, 1896-1897. – Part II. Cyclostomata, Ctenostomata and Endoprocta', *Journal of the Linnean Society, London, Zoology*, 29 (190) (1904), 161-184.

213   A. Waters, 'Bryozoa from Chatham Island and d'Urville Island, New Zealand, collected by Professor H. Schauinsland', *Annals and Magazine of Natural History*, Serie 7, 17 (97) (1906), 12-23.

214   Brooding in the introvert was described in *Zoobotryon verticillatum* (as *Z. pellucidum*) in A. Waters, 'The marine fauna of British East Africa and Zanzibar, from collections made by Cyril Crossland, M.A., B.Sc., F.Z.S., in the years 1901-1902. Bryozoa-Cyclostomata, Ctenostomata and Endoprocta', *Proceedings of the Zoological Society of London*, Parts 3-4 (1914), 831-858.

215   A. Waters, 'Observations upon the relationships of the (Bryozoa) Selenariidae, Conescharellinidae, etc., Fossil and Recent', *Journal of the Linnean Society, London, Zoology*, 34 (1919(1921)), 399-427.

216   A. Waters, *Bryozoa. Résultats du Voyage du S. Y. "Belgica" en 1897-1898-1899, Expèdition Antarctique Belge, Zoologie* (Anvers, 1904), 114 (86).

217   Waters, note 188.

218   A. Waters, 'The marine fauna of British East Africa and Zanzibar, from collections made by Cyril Crossland, M.A., B.Sc., F.Z.S., in the years 1901-1902. Bryozoa-Cheilostomata', *Proceedings of the Zoological Society of London*, 32 (1913), 458-537.

219   A. Waters, '*Tubucellaria*: its species and ovicells', *Journal of the Linnean Society, London, Zoology*, 30 (1907), 126-133.

220   A. Waters, 'Reports on marine biology of the Sudanese Red Sea, from collections made by Cyril Crossland, M.A., B.Sc., F.Z.S.; together with collections made in the Red Sea by Dr. R. Hartmeyer. – XII. The Bryozoa. Part I. – Cheilostomata', *Journal of the Linnean Society, London, Zoology*, 31 (1909), 123-181 (141).

221   The case of *Watersipora* is dicussed below. See also: Ostrovsky, note 25.

222   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.

223   Waters, note 222, pages 496-497.

224   Waters, note 218.

225   Waters, note 218, page 485.

226   Waters, note 218, page 500.

227   E. Marcus, 'Bryozoen von den Aru Inseln', *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 35 (1922), 421-446.

228   Vigelius, note 153.

229   Harmer, note 204.

230   Harmer, note 205.

231   S.F. Harmer, 'The Polyzoa of the Siboga Expedition. I. Entoprocta, Ctenostomata and Cyclostomata', *Reports of the Siboga Expedition*, 28a (E.J. Brill, Leiden, 1915), 1-180 (56).

232   Prouho, note 61.

233   Harmer, note 205.

234   R.M. Pace, 'On the early stages in the development of *Flustrella hispida* (Fabricius), and on the existence of a "yolk nucleus" in the egg of this form', *Quarterly Journal of Microscopical*

Science, 50 (1906), 435-478.

235 Pace, note 234, page 441.

236 G.M.A. Owrid and J.S. Ryland, 'Sexual reproduction in *Alcyonidium hirsutum* (Bryozoa: Ctenostomata)', in *Bryozoaires Actuels et Fossiels*: *Bryozoa Living and Fossil*, edited by F.P. Bigey, *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France, Mémoire Hors Série*, 1 (1991), 317-326.

237 H. Prouho, 'Recherches sur la larve de *Flustrella hispida*: structure et métamorphose', *Archives de Zoologie expérimentale et générale*, 8 (2) (1890), 409-459.

238 S. Silbermann, 'Untersuchungen über den feineren Bau von *Alcyonidium mytili*', *Archiv für Naturgeschichte*, 72 (1906), 265-308.

239 Marcus, note 20.

240 G. Retzius, 'Zur Kenntnis der Spermien der Evertebtraten', *Biologische Untersuchungen*, *N.S.*, 11 (1) (1904), 1-32.

241 G. Retzius, 'Zur Kenntnis der Spermien der Evertebtraten. II. Die Spermien der Leptocardier, Teleostier und Ganoider', *Biologische Untersuchungen*, *N.S.*, 12 (9-10) (1905), 79-115.

242 G. Retzius, 'Die Spermien der Enteropneusten and der Nemertinen. Die Spermien der Turbellarien. Die Spermien der Bryozoen', *Biologische Untersuchungen*, *N.S.*, 13 (2-4) (1906), 37-48.

243 G. Retzius, 'Spermien der Insecten, *Aurelia aurita* (L.) Nereiden, Cestoden, Trematoden, Chaetognaten, Bryozoen und *Nassa reticulata* (L.)', *Biologische Untersuchungen*, *N.S.*, 14 (2-8) (1909), 54-78.

244 G. Retzius, 'Zur Kenntnis der Spermien der Echinodermen. Weitere Beiträge zur Kenntnis der Spermien mit besonderer Berücksichtigung der Kernsubstanz', *Biologische Untersuchungen*, *N.S.*, 15 (2-3) (1910), 54-82.

245 K. Bonnevie, 'Physiologische Polyspermie', *Archiv for Matematik og Naturvidenskab*, (1906), 27 (13), 275-289.

246 K. Bonnevie, 'Untersuchungen über Keimzellen. II. Physiologische Polyspermie bei Bryozoen', *Jenaische Zeitschrift für Naturwissenschaft*, 42, N.F. 35 (1907), 567-598.

247 Bonnevie, note 246, page 585.

248 M.H. Temkin, 'Gamete spawning and fertilization in the gymnolaemate bryozoan *Membranipora membranacea*', *Biological Bulletin*, 187 (2) (1994), 143-155.

249 Silbermann, note 238.

250 O. Römer, 'Untersuchungen über die Knospung, Degeneration und Regeneration von einigen marinen ectoprocten Bryozoen', *Zeitschrift für wissenschaftliche Zoologie*, 84 (3) (1906), 446-478.

251 G.M.R. Levinsen, *Morphological and systematic studies on the Cheilostomatous Bryozoa*, (F. Bagge, Copenhagen, 1909), 431.

252 Ostrovsky, note 25, this volume.

253 Korschelt, Heider, note 19.

254 Nitsche, note 98.

255 Vigelius, note 143.

256 Vigelius, 153.

257 Calvet, note 17.

258 Levinsen, note 251.

259 Actually, Korschelt and Heider thought that the suggestion about the rupture of the ooecial vesicle was made by Calvet first (see above).

260 Pergens, note 171.

261 Nitsche, note 98.

262 Prouho, note 61.

263 Korschelt and Heider, note 19.

264 Pergens, note 171.

265 Gerwerzhagen, note 172.

266 G. Lutaud, 'Contribution à l'étude de bourgeonnement et de la croissance des colonies chez *Membranipora membranacea* (L), Bryozoaire Chilostome', *Annales de la Société Royal Zoologique de Belgique*, 91 (1961), 157-300.

267 H. Friedl, 'Kolonienbildung. Besiedelung und Wachstum bei marinen Bryozoen', *Arbeiten aus dem Zoologische Institut der Universität Innsbruck*, 2 (3) (1925), 139-168.

268 B.H. Grave, The natural history of *Bugula flabellata* at Woods Hole, Massachusets, including the behaviour and attachment of the larva', *Journal of Morphology*, 49 (1930), 355-379.

269 Marcus, note 20.

270 Van Beneden, note 67.

271 Bonnevie, note 246.

272 A.B. Hastings, 'Cheilostomatous Polyzoa from the vicinity of the Panama Canal collected by Dr. C. Crossland on the cruise of the S.Y. 'St. George'', *Proceedings of the Zoological Society of London*, 4 (47) (1930), 697-740.

273 A.B. Hastings, 'The Polyzoa with a note on an associated hydroid', *Scientific Reports of the Great Barrier Reef Expedition 1928-29*, 4 (12) (1932), 399-458.

274 F. Canu and R.S. Bassler, 'North American Later Tertiary Bryozoa', *Bulletin of the United States National Museum*, 125 (1923), I-VII, 1-244.

275 F. Canu and R.S. Bassler, 'Fossil and recent Bryozoa of the Gulf of Mexico region', *Proceedings of the United States National Museum*, 72 (2710) (1928), 1-165.

276 A.B. Hastings, 'The British species of *Scruparia* (Polyzoa)', *The Annals and Magazine of Natural History, 11 Series,* 7 (41) (1941), 465-472.

277 S. Mawatari, 'Studies on Japanese Anascan Bryozoa. 2. Division Scrupariina', *Bulletin of the National Science Museum, Tokyo*, 16 (4) (1973), 605-624.

278 G.H. Faulkner, 'The relation between somatic and germ cells in the asexually produced polyps of the polyzoon *Alcyonidium gelatinosum*', *The Annals and Magazine of Natural History,* 10 Series, 11 (63) (1933), 255-269.

279 Calvet, note 17.

280 Faulkner, note 278.

281 Silbermann, note 238.

282 For further discussion see Reed, note 3.

283 G. Zirpolo, '*Zoobotryon verticillatum* (Delle Chiaje)', *Memorie dell'Academia Pontifica dei Nuovi Lincei*, 2, 17 (1933), 109-442.

284 Waters, note 214.

285 F. Braem, '*Victorella sibogae* Harmer', *Zeitschrift für Morphologie und Ökologie der Tiere*, 36 (1940), 267-278.

286 L. Silén, 'Carnosa and Stolonifera (Bryozoa) collected by Prof. Dr. Sixten Bock's expedition to Japan and the Bonin Islands 1914', *Arkiv för Zoologi*, 34A (8) (1942), 1-33.

287 L. Silén, 'The anatomy of *Labiostomella gisleni* Silén (Bryozoa Protocheilostomata)', *Kungliga Svenska Vetenskapsakademiens Handlingar, Serie 3*, 21 (1944), 1-111.

288 L.W. Stach, 'Observation on *Carbasea indivisa* Busk (Bryozoa)', *Proceedings of the*

Zoological Society of London, *Series B*, 108 (3) (1938), 389-399.

289 Ström, note 10.

290 Marcus, note 21.

291 E. Marcus, 'Bryozoen von St. Helena', *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København*, 101 (1938), 183-252.

292 Marcus, note 157.

293 E. Marcus, 'Sobre Bryozoa do Brasil', *Boletins da Faculdade de Filosofia, Ciências e Letras. Universidade de São Paulo XXII,* Zoologia 5 (1941), 3-208.

294 A.N. Ostrovsky, 'Comparative studies of ovicell anatomy and reproductive patterns in *Cribrilina annulata* and *Celleporella hyalina* (Bryozoa: Cheilostomatida)', *Acta Zoologica*, 79 (4) (1998), 287-318.

295 Marcus, note 157, page 119.

296 Marcus, note 157, page 120.

297 Marcus, note 157, page 119.

298 Marcus, note 157, page 81.

299 Marcus, note 157, Estampa III, figure 8B, Estampa XXI, figures 58-60.

300 Prouho, note 61.

301 Marcus, note 157, page 121.

302 Marcus, note 157, pages 88-89, 120.

303 Waters, note 218.

304 Marcus, note 293.

305 F.J.S. Maturo, 'A new bryozoan structure: an ovipositor', in *Bryozoaires Actuels et Fossiels*: *Bryozoa Living and Fossil*', edited by F.P. Bigey, *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France, Mémoire Hors Série*, 1 (1991), 572.

306 Levinsen, note 251.

307 Harmer, note 205.

308 Hastings, note 272.

309 Marcus, note 157, Estampa XXI, figures 58-60.

310 E. Marcus, 'Sobre o desenvolvimento do bryozoario *Synnotum aegyptiacum*', *Arquivos de Cirurgia Clínica e Experimental*, 5 (1941), 227-234.

311 Marcus, note 310, page 232.

312 Cori, note 22.

313 Brien, note 23.

314 Silén, note 287.

315 F. Braem, 'Über *Victorella* und einige ihrer nächsten Vermandten, sowie über die Bryozoenfauna des Rysk bei Greifswald', *Zoologica*, 102 (37) (1951), 1-59.

316 Discussed in: Ström, note 10.

317 Braem, note 315.

318 Hyman, note 9.

319 Hayward, note 180.

320 D. Jebram and B. Everitt, 'New victorellids (Bryozoa, Cenostomata) from North America: the use of parallel cultures in bryozoan taxonomy', *Biological Bulletin*, 163 (1982), 172-187.

321 L. Silén, 'The main features of the development of the ovum, embryo and ooecium in the ooecioferous Bryozoa Gymnolaemata', *Arkiv för Zoologi*, 35A (17) (1945), 1-34.

322 Gerwerzhagen, note 172.

323 Marcus, note 157.

324   Joliet, note 101.

325   Marcus, note 157.

326   F. Borg, 'Zur Kenntnis der Ökologie und des Lebenszyklus von *Electra crustulenta*', *Zoologiska Bidrag från Uppsala*, 25 (1947), 344-377.

327   Schulz, note 202.

328   Borg, note 326, page 375.

329   Silén, note 60.

330   D. Jebram, 'The importance of different growth directions in the Phylactolaemata and Gymnolaemata for reconstructing the phylogeny of the Bryozoa' in *Living and Fossil Bryozoa*, edited by G.P. Larwood, (Academic Press, London, 1973), 565-576.

331   G.S. Hageman, 'Accessory reproductive structures in *Membranipora serrilamella*: a fine structural study', in *Recent and Fossil Bryozoa*, edited by G.P. Larwood and C. Nielsen, (Olsen and Olsen, Fredensborg. 1981), 311.

332   P.S. Cadman and J.S. Ryland, 'The characters, reproduction, and growth of *Alcyonidium mytili* Dalyell, 1848 (Ctenostomatida)', in *Bryozoans in Space and Time,* edited by D.P. Gordon, A.M. Smith and J.A. Grant-Mackie, (National Institute of Water and Athmospheric Resarch Ltd, Wellington, 1996), 237-242.

333   D.D. Corrêa, 'A embriologia de *Bugula flabellata* (J. V. Thompson) Bryozoa Ectoprocta', *Boletim da Faculdade de Filosofia, Ciências e Letras. Universidade de São Paulo,* Zoologia, 13 (1948), 7-71.

334   Marcus, note 157.

335   Marcus, note 293.

336   Dyrynda, Ryland, note 127.

337   L. Silén, 'On two new groups of Bryozoa living in shells of molluscs', *Arkiv för Zoologi*, 38B (1) (1946), 1-7.

338   L. Silén, 'On the anatomy and biology of Penetrantiidae and Immergentiidae (Bryozoa)', *Arkiv för Zoologi*, 40A (4) (1947), 1-48.

339   Silén, note 338, page 20.

340   Silén, note 338, page 34.

341   Ström, note 10.

342   J.D. Soule, 'Penetrantiidae and Immergentiidae from the Pacific (Bryozoa: Ctenostomata)', *Transactions of the American Microscopical Society*, 69 (4) (1950), 359-367.

343   J.D. Soule, 'A new species of *Terebripora* from the Pacific (Bryozoa Ctenostomata)', *Journal of the Washington Academy of Sciences*, 40 (11) (1950), 378-381.

344   J.D. Soule and D.F. Soule, 'Systematics and biogeography of burrowing bryozoans', *American Zoologist*, 9 (1969), 791-802.

345   J.D. Soule and D.F. Soule, '*Spathipora*, its anatomy and phylogenetic affinities', in *Bryozoa 1974*, edited by S. Pouyet, *Documents du Laboratoire de Géologie de la Faculté des Sciences de Lyon, Hors Série*, 3 (1) (1975), 247-253.

346   J.D. Soule and D.F. Soule, '*Spathipora mazatlanica*, a new species of burrowing Bryozoa (Ctenostomata) from Mazatlan, Sinaloa, Mexico', *Bulletin of the Southern California Academy of Sciences*, 75 (1) (1976), 38-42.

347   G. Bobin and M. Prenant, 'Sur un Bryozoaire perforant, *Terebripora comma* (Soule), trouvé en Mediterranée', *Archives de Zoologie expérimentale et générale*, 91 (1954), 130-144.

348   M. Prenant and G. Bobin, 'Bryozoaires. 1. Entoproctes, Phylactolèmes, Cténostomes', *Faune de France*, 60 (1956), 1-398.

349 J.-L. d'Hondt, 'Tubular keys for identification of Recent Ctenostomatous Bryozoa', *Mémoires de l'Institut océanographique*, *Monaco*, 14 (1983), 1-134.

350 Hayward, note 180.

351 S. Mawatari, 'On *Tricellaria occidentalis* (Trask), one of the fouling bryozoans in Japan. Studies on fouling Bryozoa in Japan No 7', *Contributions from the Research Institute for Natural Resources*, No 501, 8 (22) (1951), 9-16.

352 S. Mawatari, 'On *Watersipora cucullata* (Busk) II', *Miscellaneous Reports of the Research Institute for Natural Resources*, 28 (1952), 17-27.

353 Mawatari, note 352, page 20.

354 Personal communication in: Reed, note 3.

355 Hyman, note 9.

356 Brien, note 23.

357 Kaestner, note 24.

358 Cori, note 22.

359 Borg, note 326, page 375.

360 Braem, note 315.

361 M. Chrétien, 'Histologie et dévelopment de l´ovaire chez *Alcyonidium gelatinosum* (L.) (Bryozoaire cténostome)', *Bulletin de la Laboratoire Maritime de Dinard*, 43 (1957), 25-51.

362 Faulkner, note 278.

363 Pace, note 234.

364 Owrid and Ryland, note 236.

365 G. Bobin and M. Prenant, 'Les cellules cystidiennes et les phénomènes d'histolyse et de phagocytose chez *Alcyonidium gelatinosum* (L.) (Bryozoaire Cténostome)', *Bulletin biologique de la France et de la Belgique*, 49 (1957), 205-224.

366 P. Grellet, 'Histologie du testicule et spermatogénèse chez *Alcyonidium gelatinosum* (L.) (Bryozoaire cténostome)', *Bulletin de la Laboratoire Maritime de Dinard*, 43 (1958), 1-24.

367 F. Ranzoli, 'Ovogenesi e strutture Feulgen-positive in *Zoobothryon verticillatum* (Delle Chiaje)', *Atti della Accademia delle Scienze dell´Instituto di Bologna*, 9 (1962), 139-143.

368 I. Matricon, 'Dégénérescence du polypide femelle et formation d'une poche incubatrice chez *Alcyonidium polyoum* (Hassal) (Bryozoaire Cténostome)', *Archives de Zoologie expérimentale et générale*, 102 (1963), 79-93.

369 I. Matricon, 'Etude histologique d´*Alcyonidium polyoum* (Hassall), caractères structuraux spécifiques d´*Alcyonidium mytili* Dalyell', *Cahiers de Biologie Marine*, 1 (1960), 359-395.

370 W.C. Banta, '*Mimosella cookae*, new species (Bryozoa, Ctenostomata) with a review of the family Mimosellidae', *Bulletin of the Southern California Academy of Sciences*, 67 (1968), 245-254.

371 Joliet, note 101.

372 R. Ström, 'Sexual reproduction in a stoloniferous bryozoan, *Triticella koreni* (G. O. Sars)', *Zoologiska Bidrag från Uppsala*, 38 (1969), 113-127.

373 Braem, note 184.

374 D. Jebram, '*Panolicella nutans*, gen. et sp. n., its description, development, and laboratory cultivation', *Zoologica Scripta*, 14 (1985), 11-18.

375 D. Eggleston, 'Synchronization between moulting in *Calocaris macandreae* (Decapoda) and reproduction in its epibiont *Triticella koreni* (Polyzoa Ectoprocta)', *Journal of the Marine Biological Association of the United Kingdom*, 51 (1971), 404-410.

376 Ström, note 10.

377 A. Castric-Fey, 'Sur quelques bryozoaires de l'archipel de Glenan (Sud-Finistère)', *Vie Millieu*, 22 (1971), 69-86.

378 P.L. Cook, 'The development of *Electra crustulenta* (Pallas) (Polyzoa, Ectoprocta)', *Essex Naturalist*, 30 (4) (1961), 258-266.

379 P.L. Cook, 'The early larval development of *Membranipora seurati* (Canu) and *Electra crustulenta* (Pallas), Polyzoa', *Cahiers de Biologie Marine*, 3 (1) (1962), 57-60.

380 P.L. Cook, 'The deveopment of *Electra monostachys* (Busk) and *Conopeum reticulum* (Linnaeus), Polyzoa, Anasca', *Cahiers de Biologie Marine*, 5 (1964), 391-397.

381 P.L. Cook, 'Polyzoa from west Africa. I. Notes on Steganoporellidae, Thalamoporellidae and Onychocellidae (Anasca, Coilostega) ', *Annales de l'Institut Oceanographique*, (Calypso IV), 41 (1964), 43-78.

382 P.L. Cook, 'Observations on living Bryozoa', *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 108 (1968), 155-160.

383 Silén, note 60.

384 Zimmer, personal communication in Reed, note 3.

385 Prouho, note 61.

386 Joliet, note 101.

387 Marcus, note 157.

388 Silén, note 287.

389 J.S. Bullivant, 'Release of sperm by Bryozoa', *Ophelia*, 4 (1967), 139-142.

390 Silén, note 60.

391 L. Silén, 'Fertilization in the Bryozoa', *Ophelia*, 10 (1) (1972), 27-34.

392 Marcus, note 157.

393 J.S. Ryland and D.P. Gordon, 'Some New Zealand and British species of *Hippothoa* (Bryozoa: Cheilostomata)', *Journal of the Royal Society of New Zealand*, 7 (1) (1977), 17-49.

394 D.P. Gordon, 'Zooidal dimorphism in the polyzoan *Hippopodinella adpressa* (Busk)', *Nature*, 219 (1968), 633-634.

395 P.L. Cook, 'Bryozoa from Ghana', *Zoologische Wetenschappen Musee Royal l'Afrique centrale Tervuren, Belgique*, 238 (1985), 1-315.

396 M.C. Carter and D.P. Gordon, 'Substratum and morphometric relationships in the bryozoan genus *Odontoporella*, with a description of a new paguridean-symbiont species from New Zealand', *Zoological Science*, 24 (2007), 47-56.

397 Cook, note 382.

398 Cook, note 395.

399 P.L. Cook, 'Colony-wide water currents in living Bryozoa', *Cahiers de Biologie Marine*, 18 (1977), 31-47.

400 P.L. Cook, 'Some problems in interpretation of heteromorphy and colony integration in Bryozoa', in *Biology and Systematics of Colonial Organisms*, edited by G.P. Larwood and B.R. Rosen, Systematics Association Special vol. 11, (Academic Press, London, New York, 1979), 193-210.

401 P.J. Chimonides and P.L. Cook, 'Observations on living colonies of *Selenaria* (Bryozoa, Cheilostomata). II', *Cahiers de Biologie Marine*, 22 (2) (1981), 207-219.

402 L. Silén, 'Polymorphism', in *Biology of Bryozoans,* edited by R.M. Woollacott and R.L. Zimmer, (Academic Press, New York, 1977), 184-232.

403 Cook, note 400.

404 Franzén, note 5.

405 Å. Franzén, 'Phylogenetic aspects of the morphology of spermatozoa and spermiogenesis', In: *Comparative spermatology*, edited by B. Baccetti, (Academic Press, New York, 1970), 29-46.

406 Å. Franzén, 'On the ultrastructure of spermiogenesis of *Flustra foliacea* (L.) and *Triticella korenii* G.O. Sars (Bryozoa)', *Zoon* (*Stockholm*) 4 (1976), 19-29.

407 Franzén, note 6.

408 Franzén, note 7.

409 Franzén, note 8.

410 Å. Franzén, 'Sperm ultrastructure in the Bryozoa', in *Bryozoa: Present and Past*, edited by J.R.P. Ross (Western Washington University, Billingham, 1987), 89-96.

411 Å. Franzén, 'Spermatogenesis', in *Reproduction of Marine Invertebrates*, edited by A.C. Giese, J.S. Pearse and V.B. Pearse, Vol. IX. General aspects: seeking unity in diversity, (Boxwood Press, Pacific Grove, 1987), 1-47.

412 Å. Franzén, 'Spermatogenesis, sperm structure and spermatozeugmata in the gymnolaematous bryozoan *Electra pilosa* (Bryozoa, Gymnolaemata)', *Invertebrate Reproduction and Development*, 34 (1) (1998), 55-63.

413 Franzén, note 5.

414 Franzén, note 412.

415 Bonnevie, notes 245-246.

416 J.F. Reger, 'A fine structure study on spermiogenesis in the entoproct, *Bugula* sp.', *Journal of submicroscopical Cytology*, 3 (1971), 193-200.

417 R.L. Zimmer and R.M. Woollacott, 'Morphological and biochemical modifications of the spermatozoan mitochondria of *Membranipora* sp.', *Journal of Cell Biology*, 63 (1974), 385a.

418 Woollacott and Zimmer, note 158.

419 For futher discussion see: Ostrovsky, note 25, this volume.

420 R.M. Woollacott and R.L. Zimmer, 'A simplified placenta-like brooding system in *Bugula neritina* (Bryozoa)', in *30th Annual Proceedings of the Electron Microscope Society of America*, edited by C.J. Arceneaux, (Claitor's Publishing Division, Baton Rouge, 1972), 30-31.

421 Woollacott and Zimmer, note 159.

422 T. Kawahara, 'Analysis of ecological phenomena in the community of the sessile organisms. (2). Growth, maturation and propagation in *Bugula neritina* Linné', *Reports of the Faculty of Fisheries of the Prefecture University of Mie*, 3 (1960), 573-581.

423 Y.V. Gautier, 'Recherches écologiques sur les Bryozoaires chilostomes en Méditerranèe Occidentale', *Recueil de Travaux de la Station Marine d'Endoume*, 39 (1962), 1-434.

424 J.S. Ryland, 'Systematic and biological studies on Polyzoa (Bryozoa) from western Norway', *Sarsia*, 14 (1963), 1-59.

425 M.B. Abbott, 'Seasonal diversity and density in bryozoan populations of Block Island Sound (New York, U.S.A.)', in *Living and Fossil Bryozoa*, edited by G.P. Larwood, (Academic Press, London, 1973), 593-599.

426 M.B. Abbott, 'Relationship of temperature to patterns of sexual reproduction in some Recent encrusting Cheilostomata', in *Bryozoa 1974*, edited by S. Pouyet, *Documents du Laboratoire de Géologie de la Faculté des Sciences de Lyon, Hors Série*, 3 (1) (1975), 37-50.

427 P.J. Hayward and J.S. Ryland, 'Growth, reproduction and larval dispersal in *Alcyonidium hirsutum* (Fleming) and some other Bryozoa', *Pubblicazioni Stazioni Zoologica Napoli*, 39 (supplement) (1975), 226-241.

428 For review and references see: J.S. Ryland, 'Polyzoa', *Annual Review in Oceanography and Marine Biology*, 5 (1967), 343-369.

429 J.S. Ryland, 'Physiology and ecology of marine bryozoans', in *Advances in Marine Biology*, vol. 14, edited by. F.S. Russell and C.M. Yonge, (Academic Press, London, 1976), 285-443.

430 D.P. Gordon, 'Reproductive ecology of some northern New Zealand Bryozoa', *Cahiers de Biologie Marine*, 11 (1970), 307-323.

431 D. Eggleston, 'Marine fauna of the Isle of Man. Supplement 1. Entoprocta and Ectoprocta', *Reports of the Marine Biological Station at Port Erin*, 81 (1969), 57-80.

432 D. Eggleston, 'Patterns of reproduction in the marine Ectoprocta of the Isle of Man', *Journal of Natural History*, 6 (1972), 31-38.

433 A.B. Hastings, 'Notes on Polyzoa (Bryozoa).-I. *Umbonula verrucosa* auctt.: *U. ovicellata*, sp. n. and *U. littoralis*, sp. n.', *The Annals and Magazine of Natural History, 11 Series,* 11 (77) (1944), 273-284.

434 A.B. Hastings, 'The cheilostomatous Polyzoa *Neoeuthyris woosteri* (MacGillivray) and *Reginella doliaris* (Maplestone)', *Bulletin of the British Museum (Natural History)*, Zoology, 11 (3) (1964), 243-262.

435 J.E. Dudley, 'Observations on the reproduction, early larval development, and colony astogeny of *Conopeum tenuissimum* (Canu)', *Chesapeake Science* 14 (4) (1973), 270-278.

436 S.F. Mawatari, 'The life history of *Membranipora serrilamella* Osburn (Bryozoa, Cheilostomata)', *Bulletin of the Library of Arts and Science Course, School of Medicine, Nihon University*, 3 (1975), 19-57.

437 S. Mawatari and S.F. Mawatari, 'Development and metamorphosis of the cyphonautes of *Membranipora serrilamella* Osburn", in *Bryozoa 1974*, edited by S. Pouyet, *Documents du Laboratoire de Géologie de la Faculté des Sciences de Lyon, Hors Série*, 3 (1) (1975), 13-18.

438 J.S. Ryland, *Bryozoans* (Hutchinson University Library, London, 1970), 175.

439 Ryland, note 429.

440 Hyman, note 9.

441 Harmer, note 205.

442 Woollacott and Zimmer, note 158.

443 Ryland, note 429.

444 Marcus, note 157.

445 Silén, note 321.

446 Ehlers, note 118.

447 Silén, note 321.

448 Ström, note 10.

449 A. Cheetham and P.L. Cook, 'General features of the class Gymnolaemata', in *Bryozoa (Part G, revised). Treatise on Invertebrate Paleontology,* edited by R.A. Robinson, vol. 1, (Geological Society of America (Boulder, Colorado) and University of Kansas (Lawrence), 1983), 138-207.

450 Nielsen, note 173.

451 Gerwerzhagen, note 172.

452 Silén, note 321.

453 Nielsen, note 173, page 114.

454 Jebram, Everitt, note 320.

455 Braem, note 315.

456 Marcus, note 310.

457 P.E.J. Dyrynda, 'A preliminary study of patterns of polypide generation-degeneration in marine cheilostome Bryozoa', in *Recent and Fossil Bryozoa*, edited by G.P. Larwood and C. Nielsen, (Olsen and Olsen, Fredensborg, 1981), 73-81.

458 P.E.J. Dyrynda and P.E. King, 'Sexual reproduction in *Epistomia bursaria* (Bryozoa: Cheilostomata), an endozooidal brooder without polypide recycling', *Journal of Zoology, London*, 198 (1982), 337-352.

459 Dyrynda, note 457.

460 Dyrynda and Ryland, note 127.

461 Dyrynda and Ryland, note 127, page 248.

462 Vigelius, notes 83 and 143.

463 Marcus, note 293.

464 See also: P.E.J. Dyrynda and P.E. King, 'Gametogenesis in placental and non-placental ovicellate cheilostome Bryozoa', *Journal of Zoology, London*, 200 (1983), 471-492.

465 Gerwerzhagen, note 172.

466 Silén, note 321.

467 Woollacott and Zimmer, note 159.

468 Dyrynda and Ryland, note 127, page 255.

469 Dyrynda and King, note 464.

470 Vigelius, note 153.

471 Reed, note 3.

472 Woollacott and Zimmer, notes 159 and 420.

473 Ryland, note 429.

474 Reed, note 3.

475 Woollacott and Zimmer, note 159.

476 Hayward, note 11.

477 Jebram, note 374.

478 Actually, this bryozoan was discovered earlier by Kayser (H. Kayser, '*Nolella pusilla* (Bryozoa, Ctenostomata): cultivation, biology and first record from the German Bight', *Helgoländer Meeresuntersuchungen*, 38 (1984), 35-36), and there is some information on its reproduction in his paper.

479 D.J. Hughes, 'Gametogenesis and embryonic brooding in the cheilostome bryozoan *Celleporella hyalina*', *Journal of Zoology, London*, 212 (1987), 691-711.

480 J.E. Winston, 'Marine bryozoans (Ectoprocta) of the Indian river area (Florida)', *Bulletin of the American Museum of Natural History*, 173 (1982), 99-176.

481 J.E. Winston, 'Patterns of growth, reproduction and mortality in bryozoans from the Ross Sea, Antarctica', *Bulletin of Marine Science*, 33 (3) (1983), 688-702.

482 J.E. Winston, 'Life history studies of *Disporella* and *Drepanophora* in Jamaica', in *Bryozoa: Ordovician to Recent*, edited by C. Nielsen and G.P. Larwood, (Olsen and Olsen, Fredensborg, 1985), 350.

483 J.B.C. Jackson and S.P. Wertheimer, 'Patterns of reproduction in five common species of Jamaican reef-associated bryozoans', in *Bryozoa: Ordovician to Recent*, edited by C. Nielsen and G.P. Larwood, (Olsen and Olsen, Fredensborg, 1985), 161-168.

484 D.J. Hughes, 'Variation in reproductive strategy among clones of the bryozoan *Celleporella hyalina*', *Ecological Monographs*, 59 (4) (1989), 387-403.

485 J.-L. d'Hondt, 'Etat des connaissances sur les cycles de developpement chez les Bryozoaires', *Bulletin de la Société zoologique de France*, 119 (3) (1994), 275-283.

486 D.J. Hughes and R.N. Hughes, 'Life history variation in *Celleporella hyalina* (Bryozoa)', *Proceedings of the Royal Society of London*, B 228 (1251) (1987), 109-224.

487 E. Hunter and R.N. Hughes, 'Self-fertilization in *Celleporella hyalina*', *Marine Biology*, 115 (1993), 495-500.

488 E. Hunter, R.N. Hughes and A. Goldson, 'Environmental and genetic control of somatic and sexual performance in *Celleporella hyalina* (L.)', in *Bryozoans in Space and Time*, edited by D.P. Gordon, A.M. Smith and J.A. Grant-Mackie, (National Institute of Water and Atmospheric Research Ltd., Wellington, 1996), 149-156.

489 P.J. Wright and R.N. Hughes, 'A comparison of the early astogeny and life history of *Celleporella carolinensis* and *Celleporella hyalina*', in *Bryozoan Studies 2001*, edited by P.N. Wyse Jackson, C.J. Buttler and M.E. Spencer Jones, (A.A. Balkema Publishers, Lisse, 2002), 353-357.

490 J.M. Cancino, 'Marine macroalgae as a substratum for sessile invertebrates: a study of *Celleporella hyalina* (Bryozoa) on fronds of *Laminaria saccharina* (Phaeophyta)', *Monografias Biológicas*, 4 (1986), 279-308.

491 J.M. Cancino and R.N. Hughes, 'The effect of water flow on growth and reproduction of *Celleporella hyalina* (L.) (Bryozoa: Cheilostomata)', *Journal of Experimental Marine Biology and Ecology*, 112 (1987), 109-131.

492 J.M. Cancino and R.N. Hughes, 'The zooidal polymorphism and astogeny of *Celleporella hyalina* (Bryozoa: Cheilostomata)', *Journal of Zoology, London*, 215 (1988), 167-181.

493 J.M. Cancino, B. Castañeda and C. Orellana, 'Reproductive strategies in bryozoans: experimental test of the effects of conspecific neighbours', in *Bryozoaires Actuels et Fossiles*: *Bryozoa Living and Fossil*', edited by F.P. Bigey, *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France, Mémoire Hors Série*, 1 (1991), 81-88.

494 Cancino, Castañeda and Orellana, note 493.

495 Hunter and Hughes, note 487.

496 P.O. Yund and M.A. McCartney, 'Male reproductive success in sessile invertebrates: competition for fertilization', *Ecology*, 75 (1994), 2151-2167.

497 R.N. Hughes, P. Wright, P.H. Manríques and J.D.D. Bishop, 'Predominance of obligate outbreeding in the simultaneous hermaphrodite *Celeporella hyalina* sensu lato', in *Bryozoan Studies 2001*, edited by P.N. Wyse Jackson, C.J. Buttler and M.E. Spencer Jones, (A.A. Balkema Publishers, Lisse, 2002), 159-162.

498 Zimmer observed synchronous spawning among male zooids in non-specified *Schizoporella* (personal communication in: Reed, note 3).

499 K. Hoare, R.N. Hughes and A.J. Goldson, 'Molecular genetic evidence for the prevalence of outcrossing in the hermaphroditic brooding bryozoan *Celleporella hyalina*', *Marine Ecology Progress Series*, 188 (1999), 73-79.

500 E. Hunter and R.N. Hughes, 'Environmental and genetic components of variation in sexual allocation by an epialgal bryozoan', *Marine Ecology Progress Series*, 120 (1995), 193-201.

501 P.H. Manríques, R.N. Hughes and J.D.D. Bishop, 'Age-dependent loss of fertility in water-borne sperm of the bryozoan *Celleporella hyalina*', *Marine Ecology Progress Series*, 224 (2001), 87-92.

502 P.H. Manríques, R.N. Hughes and J.D.D. Bishop, 'Female investment is retarded pending reception of allosperm in a hermaphroditic colonial invertebrate', *Proceedings of the National Academy of Sciences of the United States of America*, 99 (23) (2002), 14884-14886.

503 Marcus, note 157.

504 Manríques, Hughes and Bishop, note 502.

505 J.D.D. Bishop, P.H. Manríquez and R.N. Hughes, 'Water-borne sperm trigger vitellogenic egg growth in two sessile marine invertebrates', *Proceedings of the Royal Society, London,* B 267 (2000), 1165-1169.

506 Cancino and Hughes, note 492.

507 M.D. Rogick, 'Studies on marine Bryozoa. VII. *Hippothoa*', *The Ohio Journal of Science*, 56 (3) (1956), 183-191.

508 N.A. Powell, 'Polyzoa (Bryozoa) - Ascophora - from north New Zealand', *Discovery Reports*, 34 (1967), 199-394.

509 V. Wood and R. Seed, 'Reproduction and growth of *Alcyonidium hirsutum* (Fleming) and *Flustrellidra hispida* (Fabricius) (Bryozoa: Ctenostomata) within a *Fucus serratus* community. *Cahiers de Biologie Marine*, 33 (1992), 347-363.

510 D.K.A. Barnes and A. Clarke, 'Seasonality of polypide recycling and sexual reproduction in some erect Antarctic bryozoans', *Marine Biology*, 131 (1998), 647-658.

511 R. Seed and R.N. Hughes, 'Reproductive strategies of epialgal bryozoans', *Invertebrate Reproduction and Development*, 22 (1-3) (1992), 291-300.

512 C.G. Reed, 'The reproductive biology of the gymnolaemate bryozoan *Bowerbankia gracilis* (Ctenostomata: Vesiculariida)', *Ophelia*, 29 (1) (1988), 1-23.

513 Braem, note 315.

514 Matricon, note 368.

515 Hageman, see note 331.

516 Joliet, note 101.

517 M.H. Temkin, 'Comparative fertilization biology of gymnolaemate bryozoans', *Marine Biology*, 127 (2) (1996), 329-339.

518 Owrid and Ryland, note 236

519 Chrétien, note 361.

520 Joliet, note 101.

521 Cadman and Ryland, note 332.

522 Nielsen, note 12, page 185.

523 Reed, note 3.

524 Mukai, Terakado and Reed, note 14.

525 G.S. Hageman, 'A fine structural analysis of ovarian morphology, oogenesis, and ovulation in marine bryozoan *Membranipora serrilamella* (Cheilostomata, Anasca)', Ph.D. dissertation, (University of Southern California, Los Angeles, 1983), 488.

526 Hageman, note 331.

527 Mawatari and Mawatari, note 437.

528 Hughes, note 479.

529 J.S. Ryland and J.D.D. Bishop, 'Internal fertilization in hermaphroditic colonial invertebrates', *Oceanography and Marine Biology Annual Review*, 31 (1993), 445-477.

530 M.H. Temkin, 'Fertilization in the gymnolaemate Bryozoa', Unpublished Ph.D. Thesis, University of Southern California (1991), 139, (cited from Ryland and Bishop 1993).

531 Cancino, Castañeda and Orellana, note 493.

532 According to Cancino with co-authors (note 493) sexual zooids are markedly protandrodrous in this species: sperm and mature oocytes were never observed to occur simultaneously on the coelom. However, zooids with either sperm or oocytes co-occurred in the same colonies.

533 F.J.S. Maturo, 'Self-fertilisation in gymnolaemate Bryozoa', in *Bryozoaires Actuels et*

Fossiels: *Bryozoa Living and Fossil*', edited by F.P. Bigey, *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France, Mémoire Hors Série*, 1 (1991), 572.

534 Temkin, note 248.

535 Temkin, note 517

536 Silén, note 60.

537 Temkin, note 248, page 151.

538 See discussion of the Bonnevie's paper, note 246.

539 Temkin, note 517.

540 Temkin suggested that the rupture of the follicle cell layer may expose the oocyte to sperm, and this may explain why only late stage ovarian oocytes contain a sperm nucleus in this species. However, Marcus (note 157, page 81) wrote that in ctenostomes *Alcyonidium mamillatum* and *Nolella stipata* (as *N. gigantea*)), 'we have verified the presence of spermatozoids in ovocytes which are still growing'.

541 M.H. Temkin, 'The effects of increased external Ca++ and K+ concentrations on the waveform dynamics of bryozoan spermatozeugmata', in *Bryozoan Studies 2001*, edited by P.N. Wyse Jackson, C.J. Buttler and M.E. Spencer Jones, (A.A. Balkema Publishers, Lisse, 2002), 315-320.

542 M.H. Temkin and S.B. Bortolami, 'Waveform dynamics of spermatozeugmata during the transfer from paternal to maternal individuals of *Membranipora membranacea*', *Biological Bulletin*, 206 (1) (2004), 35-45.

543 C.D. Harvell and R. Helling, 'Experimental induction of localized reproduction in a marine bryozoan', *Biological Bulletin*, 184 (3) (1993), 286-295.

544 S. Santagata and W.C. Banta, 'Origin of brooding and ovicells in cheilostome bryozoans: interpretive morphology of *Scrupocellaria ferox*', *Invertebrate Biology*, 115 (1996), 170-180.

545 Ostrovsky, note 294.

546 N.A. Powell, 'Sexual dwarfism in *Cribrilina annulata* (Cribrilinidae-Bryozoa)', *Journal of the Fisheries Research Board of Canada*, 24 (9) (1967), 1905-1910.

547 Marcus, note 293.

548 Hughes, note 479.

549 J.S. Ryland and J.S. Porter, '*Alcyonidium reticulum* sp. nov., a common intertidal bryozoan from south-west Britain', *Journal of the Marine Biology Association of the United Kingdom*, 80 (2000), 563-564.

550 J.S. Ryland, 'Convergent colonial organization and reproductive function in two bryozoan species epizoic on gastropod shells', *Journal of Natural History* 35 (2001), 1085-1101.

551 J.S. Porter, P.J. Hayward and M.E. Spencer Jones, 'The identity of *Alcyonidium diaphanum* (Bryozoa: Ctenostomatida)', *Journal of the Marine Biology Association of the United Kingdom*, 81 (2001), 1001-1008.

552 J.S. Porter, 'Morphological and genetic characteristics of erect subtidal species of *Alcyonidium* (Ctenostomata: Bryozoa)', *Journal of the Marine Biology Association of the United Kingdom*, 84 (2004), 243-252.

553 J.S. Porter and P.J. Hayward, 'Species of *Alcyonidium* (Bryozoa: Ctenostomata) from Antarctica and Magellan Strait, defined by morphological, reproductive and molecular characters', *Journal of the Marine Biology Association of the United Kingdom*, 84 (2004), 253-265.

554 P. Kuklinski and J.S. Porter, '*Alcyonidium disciforme*: an exceptional Arctic bryozoan',

Journal of the Marine Biology Association of the United Kingdom, 84 (2004), 267-275.

555 J.S. Ryland and J.S. Porter, 'The identification, distribution and biology of encrusting species of *Alcyonidium* (Bryozoa: Ctenostomatida) around the coasts of Ireland', *Proceedings of the Royal Irish Academy* 106B (2006), 19-33.

556 D.G. Smith, S.F. Werle and E.J. Klekowski, 'The anatomy and brooding biology of *Pottsiella erecta* (Potts, 1884) (Ectoprocta: Gymnolaemata: Ctenostomata) with an expanded diagnosis of the Pottsiellidae, *Hydrobiologia*, 490 (2003), 135-145.

557 J.P. Wourms, 'Oogenesis', in *Reproduction of Marine Invertebrates*, *vol. IX. General aspects: seeking unity in diversity,* edited by A.C. Giese, J.S. Pearse and V.B. Pearse, (Boxwood Press, Pacific Grove, 1987), 49-178.

558 Calvet, note 17.

559 Chrétien, note 361.

560 Vigelius, note 83.

561 Pergens, note 171.

562 Hageman, note 525.

563 Calvet, note 17.

564 Dyrynda and King, note 458.

565 Calvet, note 17.

566 Temkin, note 517.

567 Marcus, note 157.

568 J.S. Porter, personal observation.

569 Temkin, note 517.

570 Reed, note 3.

571 Joliet, note 101.

572 Hincks, note 16.

573 Prouho, note 61.

574 Pace, note 234.

575 Banta, note 370.

576 Waters, note 214.

577 Braem, note 285.

578 Silén, notes 286-287.

579 Ostrovsky, unpublished data.

580 Reed, note 3.

581 A.N. Ostrovsky, 'Brood chambers in cribrimorphs evolved by fusion of costae: further arguments', in *Bryozoan Studies 2001*, edited by P.N. Wyse Jackson, C.J. Buttler and M.E. Spencer Jones, (A.A. Balkema Publishers, Lisse, 2002), 247-255.

582 A.N. Ostrovsky and P. Schäfer, 'Ovicell structure in *Callopora dumerili* and *C. lineata* (Bryozoa, Cheilostomatida)', *Acta Zoologica,* 84 (1) (2003), 15-24.

583 A.N. Ostrovsky, P. Schäfer and D.P. Gordon, 'Ultrastructure and development of the ooecial walls in some calloporid bryozoans', *Zoologischer Anzeiger*, 242 (3) (2003), 223-240.

584 A.N. Ostrovsky and P.D. Taylor, 'Brood chambers constructed from spines in fossil and Recent cheilostome bryozoans', *Zoological Journal of the Linnean Society*, 144 (2005), 317-361.

585 A.N. Ostrovsky, A.V. Grischenko, P.D. Taylor, P. Bock and S.F. Mawatari, 'Comparative anatomical study of internal brooding in three anascan bryozoans (Cheilostomata) and its taxonomical and evolutionary implications', *Journal of Morphology*, 267 (6) (2006): 739-

        749.
586 J.A. Todd, 'The central role of ctenostomes in bryozoan phylogeny', in *Proceedings of the 11th International Bryozoology Association Conference*, edited by A. Herrera Cubilla and J.B.C. Jackson, (Smithsonian Tropical Research Institute, Republic of Panama, 2000), 104-135.
587 Works where the data on the reproductive ecology and the ovicell structure are merely presented are not included in this list.