Appendices

Appendix I: History of Research on Sexual Reproduction in Gymnolaemate Bryozoa

Introduction

Studies on sexual reproduction in marine bryozoans have attracted zoologists since the beginning of the nineteenth century. Many early naturalists analyzed and reassessed existing publications, but most of these works, especially short papers, have often been neglected if not forgotten. One can also find reviews on this topic in some old (Bronn 1862; Hincks 1880; Calvet 1900; Korschelt and Heider 1893, 1910; Delage and Hérouard 1897) and more recent monographs and textbooks (Marcus 1926a, b, 1938a, 1940; Cori 1941; Brien 1960; Kaestner 1963), but little attention has been paid to these, too, as most of them were written in German, French and Portuguese.

Reviews on bryozoan sexual reproduction published in English (Franzén 1956, 1977, 1981, 1983; Hyman 1959; Ryland 1974, 1976; Ström 1977; Hayward 1983; Nielsen 1990; Reed 1991; Woollacott 1999; Mukai et al. 1997) show that considerable information has been accumulated. However, they all aimed to characterize structures, patterns and processes rather than stages in the development of our understanding of this diversity, and many key names and works were not mentioned. Only Hageman (1983) undertook a review of this kind, but it was never published.

Three extensive reviews of both early and recent literature concerning the history of research on sexual reproduction in Bryozoa (predominantly Gymnolaemata) have recently been published (Ostrovsky 2008a, b; Ostrovsky et al. 2008), and this Section adds to them. I have chronicled the main steps in the history of research on the topic in question (dealing with the origin of the germ cells, gonado- and gametogenesis, fertilization, oviposition and embryo incubation) in marine gymnolaemate bryozoans, with particular emphasis on observation and recording of different structures and phenomena 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 happened, for instance, in the case of bryozoan fertilization (see Sect. 1.3.6 and Ostrovsky 2008a). I will highlight these contradictions where appropriate. In an effort towards making the review as comprehensive as possible, I have analyzed many obscure papers and listed small descriptive details in all species studied. This gave me the opportunity to resurrect many forgotten names and facts. Thus, this 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 of the reproductive organs in several works. Also, papers devoted exclusively to bryozoan embryogenesis and larval morphology are not discussed and referred to here.

Eighteenth Century: First Microscopic Observations and Suggestions

During the eighteenth and the beginning of the nineteenth century freshwater bryozoans were more popular objects for observations on their internal structure than were marine ones, mainly because of the transparency of their body walls (reviewed in Allman 1856).

As for marine Bryozoa, Ellis (1753, pp. 116–117) was the first to describe and illustrate ovicells ("spherical testaceous bodies") in the cheilostomes *Bugula plumosa* and *B. neritina* (as "upright feathered Coralline" and "snail bearing Coralline"). In observing brown bodies, Ellis supposed they were embryos that "swell … into spherical testaceous bodies…, burst through … [the frontal] membrane, and sit in the front of the cell [zooid] … till they come to maturity". His further suggestion was that these "rows of very small sea snails, or rather testaceous bodies, of the shape of the nautilus, [after maturation are] ready to drop off, and provide for themselves" (p. 116).

Later, in his famous "An essay towards a natural history of the corallines …" he modified this view. He realized that

"black Spots [brown bodies] are nothing, but the dead Polypes" (Ellis 1755, p. 34). Describing and depicting ovicells in several species of "Celliferous Corallines" and "Escharas" from the genera *Bugula*, *Scrupocellaria*, *Bicellariella*, *Flustra* and *Chartella*, Ellis called them "Balls", "testaceous Spherules", "testaceous Figures" or "shelly Figures … like small snails or Neritae" (pp. 34–37). In the case of *Bugula*, Ellis stated "that these little Snails are perfect Animals, no-body will doubt" (p. 35), supposing that "these little Shell-fish … in their mature state, may deposite on rocks, *Fucus*'s, and Shells, such curiously implicated Matrices or Ovaries, which, in time, may unfold and extend themselves into those many beautifil Tree-like Forms that we find them in" (p. xi).

He further wrote: "Let us suppose, that the testaceous Animal … lays its Eggs; these turn into vermicular-shaped Polypes, which, after they have fixed themselves to some marine Substance, rise up, and push forth in to branches of small Polypes [polypides] in their cells [zooids]. …From this state then of being small Polypes, we have observed that they changed into testaceous Animals [the small Polypes in the cells acquire a testaceous Covering, p. xi], connected to their cells [cystids] by the umbilical Ligament, till they are capable of providing for themselves". And else, "polypes turning into testaceous Bodies … grow large, and become capable of spawning the whole Coralline, in the same manner that the *Buccinum* … does its curious Matrices [egg batches]" (Ellis 1755, pp. 34–36).

This remarkable point of view (reminiscent of the metagenesis of salps and cnidarians that was discovered much later) was also reflected in illustrations (Ellis 1753, Tab. 5A; 1755, pl. XIX, fig. A), in which *Bugula neritina* ovicells were depicted as tubes of spirorbid polychaetes or spiral shells of small gastropods (see also Chap. 2, Fig. 2.38). Evidently, Ellis often met these epibionts on bryozoan colonies and could sometimes confuse them with ovicells (see also discussion in Levinsen 1909). Incidentally, the epithet "*neritina*" was attributed to this bryozoan species by Linnaeus (1758) because of the similarity to the-above mentioned "Neritae". In the same edition of "Systema Naturae…" (1758), the illustrious Swede used this name for a genus of gastropods. Interestingly, Ellis also considered the possibility of the similar connection between bryozoans and bivalves, writing that "there appears a great Probability of some of these being the Matrices or Ovaries of certain Species of Shell-fish, perhaps of the Bivalve Kind" (Ellis 1755, p. xv, discussed also in Levinsen 1909; Ostrovsky 2004, 2008b). In describing *Flustra foliacea* (as *Eschara*), he mentioned "at the Entrance of many of the Cells, a small testaceous Body, like a bivalve Shell" (p. 71). Thus, although in a confusing manner, Ellis clearly connected ovicells with the production of eggs, despite sometimes writing that colonies "may deposite … Ovaries" (Ellis 1755, p. xi).

Following the inclusion of Zoophyta in his "Systema Naturae …" in 1758, Linnaeus wrote of "capsulas seminiferas" (p. 643) in the "diagnosis" of this group in all the following editions (1760, 1767). He also divided Zoophyta-Sertularia into two sections, one with "Ovariis distinctis et exsertis instructae" (1758, p. 807), and the second with "Ovariis non distinctis, sed intra articulos latitantibus [hidden] (p. 814)." Since both cheilostome and cyclostome bryozoans with hyperstomial ovicells and gonozooids and hydroids with swollen gonothecae were included in Sertularia, it seems it was Linnaeus (possibly influenced by the works of Ellis with whom he was in correspondence) who formally termed all these structures as ovaries.

In his "Elenchus Zoophytorum …" Pallas (1766) expressed the view that "vesiculas" [gonozooids] known in crisiid cyclostomes (as Cellulariae) and "bulla[e], galeae" (helmet-shaped bubbles) [ovicells] in encrusting "*Escharas*" might be ovaria (1766, pp. 36, 60), and that "Galericulae" (small helmets) [ovicells] in erect *Bugula neritina* and *B. avicularia* (as *Cellularia*) could be somehow related ("subanalogae") to them. Comparing the latter two species, he also speculated that both ovicells ("bullulas inflatis") and avicularia ("galericula s. Nectarium inflato rostratum, aviculae caput referens") are organs of a similar nature, possibly destined for fertilization (pp. 60, 67, 69). In describing *B. plumosa*, Pallas objected to Ellis (1755), writing that the "corpuscula neritiformia" are not the progeny of "this small plant" (Pallas 1766, 1787), but organs, possibly ovaries, and may serve for "seminificationi" (p. 67) (see also Levinsen 1909 for discussion).

Ellis did not agree, however. On the one hand, he wrote in the diagnosis of "*Flustra* (The Sea Mat)" that "the ovaries appear to be the pearl-like studs (bullulae supra cellulas)", or "helmet-shaped bullae, that we find at the tops of the cell" (Ellis and Solander 1786, pp. 11, 16). Also, in the diagnosis of "*Cellaria* (Celleferous Coralline)" it is said that "the ovaries are uncertain, but most probably the little hemispherical covers, that appear over the cells, do that office" (p. 19).

Defending his initial idea, Ellis admitted that "the likeness to Nerits of its rows of little round adhering bodies, which are open on one side, together with their shell-like figure and pearly shining look, inclined me to believe at first that they were the young ones of such a small kind of shell-fish. But by comparing them with the figures of others of this genus, they appear rather to be what we have called Ovaries." But he continued "Or perhaps they are young of the animal defended by a testaceous covering like a little shell-fish, which at the time of its maturity separates from its umbilical cord … drops and soon adheres to a proper substance as a base, beginning to form a Coralline like the parental animal. This seems more probable, than to consider each of them as an ovary, which usually contains many eggs of the same animal" (Ellis and Solander 1786, p. 20). Describing *Bugula neritina* (as *Cellaria neritina* or Snail-bearing Coralline), Ellis writes that it has "a little egg [ovicell] on the outside of each" cell [zooid] "with an opening surrounded by a dark-colored margin"

(p. 22). Ellis also mentioned the suggestion of Pallas (1766) concerning ovicells ("pearl-like figures") and avicularia as "Nectariums, analogous to what is so called in the flowers of some plants" (p. 20).

Nineteenth Century: Primary Accumulation of Data and First Reviews

The suggestion that ovicells are ovaria was accepted and not reconsidered for almost a century (see Lamouroux 1816; Milne Edwards 1836; de Lamarck 1836; Reid 1845; Johnston 1847; Landsborough 1852; Hincks 1861, 1873, 1880). However, an accumulation of data on other bryozoan groups, whose representatives had no ovicells (ctenostomes as well as some non-ovicellate cheilostomes), contradicted the traditional point of view. For instance, Thompson (1830, p. 96) observed "an ovum or ovarium" on the body wall inside the autozooid of "*Vesicularia*", and Milne-Edwards (1836) also mentioned it on the zooidal wall in "*Cellariae*". Additionally, some researchers considered brown bodies to be a special kind of egg, finding them in zooids with degenerated polypides (Hincks 1861; Bronn 1862; reviewed in Hincks 1873).

It should be noted here that microanatomical sectioning techniques had not been used by researchers studying Bryozoa until the last third of the nineteenth century. Therefore, earlier observations on internal structure were restricted to species having a transparent body wall. Besides, 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 three-dimensional reconstructions of the animals studied and records were made from specimens that were often still alive.

One of the first detailed descriptions of sexual reproduction in marine bryozoans was made by Grant (1827, p. 116), who also discussed the data and statements of the previous authors (Basteri 1762; Pallas 1766; Lamouroux 1816; de Lamarck 1816). His paper was one of the most valuable and precise sources of information on this topic for a long time. Studying the cheilostomes *Carbasea carbasea* (as *Flustra*) and *Flustra foliacea*, he found a young "ovum … as a small yellow point" developing inside the zooid and being unconnected with the polypide. Grant wrote then that such eggs "appear to be produced by the posterior wall of the cell" [basal cystid wall] in the first species. He was not aware that *C. carbasea* is an internal brooder whose embryos develop in a brood sac. That is why he described oocyte growth (occurring in the perivisceral coelom "a little below the aperture of the cell, and behind the body of the polypus") and larval development as a single process of intrazooidal "ovum development", accompanied by polypide degeneration. It was supposed that regeneration took place after release of the ciliated "ovum" [larva] that occupied one third of the

cystid volume. Grant carefully described the pattern of distribution of egg-bearing zooids throughout the colony. He followed the release of larvae, their swimming behaviour and settlement. He was probably the first to describe larval metamorphosis and ancestrula formation in cheilostomes.

In *F. foliacea*, young "pale-red ova" are said to develop in the proximal part of zooids in which "the polypi … are generally removed [degenerated]" (Grant 1827, p. 341). The mature ovum [embryo] occupies the distal part of the cystid, becoming surrounded by "a distinct wide helmet-shaped capsule [ooecium of endozooidal ovicell]" that separates "it from the cavity of the cell [zooid]". Grant observed moving larvae inside the brood chamber, their release, settlement and metamorphosis. The polypide regenerates when the "ovum has escaped from the cell" and the same zooid repeatedly "produce[s] the ova and polypi" (1827, pp. 341–342). Grant may also have observed spermatozoids; he ambiguously wrote of "numerous monads and other animalcules busily employed in consuming the remains of the dead [degenerated] polypus" (p. 117).

Farre (1837) discovered, illustrated and described in detail an intertentacular organ and the movements of its cilia in the ctenostome *Alcyonidium duplex* (as *Halodactylus diaphanus*), and also recorded and depicted it in the cheilostome *Electra pilosa* (as *Membranipora*). This author did not recognize its function, but asked the question "does it indicate a difference of sex?" (p. 408). He was obviously the first to describe and depict spermatozoids moving inside the zooid cavity in *A. duplex* and *Walkeria uva* (as *Valkeria cuscuta*) and even saw sperm release in the first species. Farre called the male cells "parasites" and "cercariae", however, not being able to ascertain the exact locus of their expulsion since the polypide was half-retracted. In particular, it was written that they "issued from the centre of the tentacula" (p. 409). Based on this observation, Farre correctly supposed the existence of some form of communication between the body cavity and the external medium. Four to six embryos ("ciliated gemmules") were found brooded internally in the "transparent sac" of *A. duplex*. Additionally, two kinds of "rounded or oval bodies" – brown [obviously, brown bodies] and "milky-white", were recorded inside the zooid cavity of *Bowerbankia imbricata* (as *B. densa*). Farre tended to believe that both were connected "with the process of reproduction", but doubted if they were "ovaries or … immature ova" (pp. 400–401).

Based on the presence of sperm, eggs and embryos in zooids with acanthostegal (spinous) brood chambers, Nordmann (1839) described male zooids ("cellules males") and female zooids ("cellules femelles") in the cheilostome *Tendra zostericola*. He suggested that spermatozoids fertilize eggs intracolonially, entering female zooids via the "opening in the base of every cell" [zooid] (p. 191). This author also observed eggs (from four to seven per zooid), developing embryos and mature larvae rotating inside a

"chorion" [fertilization envelope] in the brood chamber. Nordmann also observed swimming larvae and mentioned their settlement, followed by development of the ancestrula.

Johnston (1838) briefly discussed the known facts on bryozoan reproduction in the first edition of his famous monograph "A history of the British zoophytes". He mainly followed and widely cited the paper of Grant (1827), writing that "the ova formed in the cells [zooids]" (p. 47).

Some observations of Farre (1837) were restated and explained by Hincks (1851), 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 (1966), who described sperm release through the pores in 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 left in no doubt whether sperm expulsion may really be sometimes possible through the intertentacular organ in *E. pilosa*. In connection with this, Prouho (1892) suggested that this could happen if the rest of the sperm [remaining after intrazooidal self-fertilization] exited at the end of the reproductive period. Hincks 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 proven by Prouho (1889), who described egg liberation in the ctenostome *Alcyonidium albidum*. Additionally, Hincks (1851) observed sperm in *Bowerbankia* sp. and larval release in *A. hirsutum* (as *Cycloum papillosum*).

Kölliker (1841) recorded the presence of eggs and sperm in *Alcyonidium* sp. (as *A. gelatinosum*) and pointed out that the "cercariae" of Farre were spermatozoids, which Kölliker described, measured and precisely depicted. He believed that the gonads were contained not inside the zooids, but between them in the branches of the colony.

Hassall (1841) observed developing embryos, which he called "ciliated eggs", in groups of six or 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 introvert. He also observed larval release in *Alcyonidium polyoum* (as *Sarcochitum polyoum*).

Van Beneden (1844a) described and illustrated testes, and ovaries containing up to eighteen oocytes, inside the hermaphrodite zooids of the ctenostome *Farrella repens* (as *Laguncula*). He found an ovary on the body wall, whereas the testis was observed on the funiculus, near its attachment to the stomach. Maturing eggs were said at the time of disappearance of the nuclear membrane to be surrounded by the "membrane externe vitelline ou le chorion" (p. 18). If this membrane was a fertilization envelope, recorded in the late ovarian oocytes of some Cheilostomata, then this should point to intraovarian fertilization in *Farrella*. Interestingly, Van Beneden, who believed that internal self-fertilization

occurred in Bryozoa, wondered if fertilization happened before the egg left the "ovisac" [follicle]. He 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 release of eggs. In another paper (1844b) Van Beneden described and depicted a testis and motile sperm inside the body cavity of *Bowerbankia* cf. *imbricata* (as *B. densa*), and sperm, eggs (both coelomic and isolated), an intrazooidal embryo and settling larvae in *Alcyonidium* cf. *hirsutum* (as *Halodactyle vélu*). In addition, sperm aggregation in *Flustra foliacea* and eggs (possibly still inside the ovary) in *A. parasiticum* (as *Halodactyle parasite*) were illustrated.

Reid (1845, p. 398) observed developing embryos inside the "ovary-capsules" [ovicells] of the cheilostomes *Scrupocellaria reptans*, *S. scruposa* (as *Cellularia*), *Bugula avicularia* (as *C. avicularis*) and *B. flabellata* (as *Flustra avicularis*), stating that ovicells were "filled with ovaries". In the latter species he described the ooecial vesicle and recorded an increase in the thickness of its "membranous lining [that] contained a number of nucleated cells". This increase was accompanied by "ovum" [embryo] enlargement and, obviously, was the first observation of an embryophore [placental analogue] in Bryozoa. Reid also observed larval release, swimming and settlement in *B. flabellata*. "Reddish brown nucleated cells inclosed in a membrane (ova)" were described in the broken zooids of *Alcyonidium* sp. (as *A. parasiticum*) (p. 394).

Johnston (1847, p. 262) expanded a review on bryozoan sexual reproduction in the second edition of his monograph. Based on the data of Grant (1827), Reid (1845) and Van Beneden (1844a), he stated that bryozoans are hermaphrodites whose eggs are formed "from the inner surface … of the skin or coat which lines the interior of the cell" [epithelium of the body wall]. Further "the ovum falls, when mature, into the space between it and the body of the polype; and in this cavity, which is always full of a fluid, probably seawater, it grows and appears to be rendered fruitful by admixture with the spermatozoa that are there prepared for this union.". At the same time, following general opinion (see above), Johnston noted that in many genera eggs are formed in the "calcareous capsules" [ovicells].

Dalyell (1848) observed developing embryos, and swimming and settling larvae in a few cheilostomes, among which were *Carbasea carbasea* (as *Flustra*), *Flustra foliacea* and *Securiflustra securifrons* (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 (1850, p. 193) observed an egg, surrounded by a "delicate membranous sac" [ovary wall], at the site of the funicular attachment to the cystid wall in the freshwater ctenostome *Paludicella* (as *P. procumbens*) (i.e. *P. articu-*

lata). He also observed motile intracoelomic spermatozoids and egg/embryo growth inside the "enveloping membrane" [introvert] accompanied by polypide degeneration, followed by larval release, in *Bowerbankia* sp.

Allman (1856) carefully described the shape, position and content of male and female gonads in *Paludicella articulata* (as *P. ehrenbergi*) with numerous eggs and sperm at various developmental stages. He stressed that they simultaneously developed inside the same zooids in this bryozoan. In contrast with *Farrella* studied by Van Beneden (1844a), the testis was reported proximally on the body wall, at the site of the funicular attachment in *Paludicella*. An ovary containing more than 40 oocytes was found on the body wall, also associated with another funicular strand, but this time in the distal part of the zooid. Allman also described 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 the ovary and testis could be simplified zooids too. Some scientists followed Allman, for instance, Salensky (1874) (for further discussion see Nitsche 1871a, b; Joliet 1877a). Finally, Allman presented a brilliant review of the studies on freshwater Bryozoa, pointing out many of the most intriguing discoveries made at this time [for references to the early work on Phylactolaemata see also Bronn (1862), Hyatt (1866–1868), Hincks (1880), Vigelius (1884b), Marcus (1934) and Cori (1941)].

The true function of the ovicell as a "marsupial pouch" was first recognized by Huxley (1856, pp. 191–192), although similar observations were published earlier by Grant (1827) (see above). In young zooids of *Bugula avicularia* (as *B. avicularis*), Huxley found a growing "ovum" "attached to the funiculus … close to the stomach" (and described the changes in its coloration from pale to reddish during its maturation), and the testis on the basal zooid wall at the site of attachment of the funiculus. Huxley wrote that the form and structure of the testis are similar and its location the same in three other cheilostomes he studied. Huxley stressed that an ovary with a ripening egg is situated at the top of the funiculus in *B. avicularia*. In contrast, he noted that the "ovarium", which "rarely presents more than one or two ova", is not directly connected with the funiculus, being placed in the middle of the basal wall in *B. flabellata*, at the "apex of the back" [i.e. in the corner between basal and distal transverse walls] in *B. plumosa*, and on the distal part of the basal wall in *Scrupocellaria scruposa*. Huxley noted ova "commonly possessing a double germinal spot" in *B. avicularia* – probably the nucleoli of the oocyte doublets unrecognized by him. Huxley's final conclusion was that, following "impregnation" [self-fertilization] "the ovum passes … into the ovicell".

Redfern (1858, p. 100) observed "ova or statoblasts" and "bodies [with] cilia", [presumably embryos], when studying *Flustrellidra hispida* (as *Flustrella*). This author was one of the first who both described and illustrated in detail postlarval development in marine bryozoans, but unfortunately his paper has been forgotten.

Bronn (1862) made a general review of previous observations on bryozoan reproduction in his textbook, in which he repeated the opinion, common at that time, regarding bryozoan self-fertilization, based on the simultaneous presence of both sperm and eggs in the same zooid. One can find a similar brief overview in the book by Busk (1859).

Smitt (1865, p. 34) described and beautifully illustrated aspects of gamete development and gonad structure in four species of cheilostome and one cyclostome. Notably, although describing the wall of the early "egg sac" [ovary] as a "common and clear membrane", in three instances Smitt depicted it as partially consisting of cells. In mature ovaries the ripening egg is described as being surrounded by an epithelium-like cellular cover. In contrast, the majority of researchers at that time illustrated it as a simple line, indicating a [non-cellular] membrane. Later Claparède (1871, p. 166), Repiachoff (1876, p. 140), Ostroumoff (1886a, p. 24, 1886b, p. 72) and Calvet (1900, p. 293) described the ovary wall as "zelligen Membran/Hülle [envelope]" or a "membrane cellulaire", consisting of cells. Salensky (1874) wrote that the ovary consists of two layers, one internal and composed of rounded cells [oocytes] and the other external and composed of flat and spindle-shaped cells [ovarian wall].

Smitt (1865) carefully described and measured the stages of oocyte growth in ovaries of *Escharella immersa* (as *Lepralia peachii*) and *S. scruposa*, showing the gonad positioned in the corner between basal and lateral walls in the middle or distal part of the zooid in the former species, and between basal, lateral and distal transverse walls in the latter. *Scrupocellaria 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 interesting findings (which he depicted but did not understand) was oocyte development occurring in pairs (doublets). In the ovaries of *S. scruposa* he depicted up to four oocyte doublets (plus additional small cells that were possibly oogonia), clearly showing in drawings the differences between the leading and succeeding doublets as well as between the oocyte and its nurse cell in older doublets. The leading oocyte has numerous yolk granules in the cytoplasm and eventually becomes blood-red in colour. Fertilization was said to be intrazooidal, with cleavage occurring in the ovicell.

In *Membranipora membranacea* (as *Flustra*) the ovary and testis were also both recorded in the same zooid: the ovary was found lying on the basal wall in the middle, and the testis on the transverse, lateral and basal walls in the proximal part of the zooid. There were about 40 small

oocytes of approximately the same size in the ovary and five ovulated oocytes in the distal part of the zooid. In *Escharella immersa* Smitt found eggs in the zooid cavity and a developing embryo in the ovicell. This finding was later used by Claparède (1871) as evidence supporting Huxley's hypothesis on the exclusively brooding function of the ovicells. Additionally, Smitt recorded oogenesis and embryo development in autozooids (in an internal brood sac that was described as a "membrane") in *Cryptosula pallasiana* (as *Lepralia*) and described and depicted its larvae, also mentioning their settlement and metamorphosis (see also Smitt 1863). Since he did not find sperm in some species, Smitt suggested that, in contrast with normal eggs, fertilized in the zooid cavity, some bryozoans possess a special kind of egg that develops into embryos without fertilization. According to him, this could happen either inside the ovicell [gonozooid] in *Crisia* or inside the autozooid in *C. pallasiana*. In a subsequent paper, Smitt (1866) recorded an intertentacular organ in *Electra pilosa* (as *Membranipora*).

Nitsche's (1869) observations were in accord with the conclusions of Huxley (1856). Studying *Bugula flabellata*, *B. plumosa* and *Bicellariella ciliata* (as *Bicellaria*), Nitsche proved that ovicells are not ovaries, but rather chambers for incubation. He also considered Smitt's (1865) data on *Scrupocellaria scruposa* as further evidence. In addition, Nitsche was the first to describe ovicell development and structure precisely in cheilostomes, taking *B. ciliata* as an example. Among other details he recorded an embryophore, describing it as an "epithelium of polygonal cells" (1869, p. 4). As with Huxley, he showed that all three species studied possessed simultaneously hermaphrodite zooids. In all of them spermatogenic tissue develops 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 or three oocytes (in all probability, there is an oocyte doublet pictured in his Tab. 1, fig. 15) were "budded" on the internal surface of the "Endocyste" [epithelial lining of the cystid wall]. Eggs are situated on the wall adjacent to the neighbouring zooid approximately in the middle part of the cystid, being surrounded by a thin membrane [ovary wall]. In contrast, Joliet (1877a) mainly found ovary development within a funiculus in this and some other species. He wrote that he was able to find the ovary on the cystid wall in a few instances only.

Nitsche (1869) described oocyte growth, accumulation of yolk [as the granular structure of the cytoplasm] and ovulation, accompanied by the breakdown of the nucleus and the subsequent disappearance of the "Membran" [rupture of the ovary wall] in *Bicellariella ciliata*. He proposed that the possible method for oviposition was through the pore situated between the basal part of the ooecium and the ooecial vesicle in the base of the ovicell. He also described and illustrated

larval morphology in all three species, and larval behaviour, settlement, metamorphosis and formation of the ancestrula in *B. flabellata*.

Based on his studies of *Scrupocellaria scruposa* and *Bugula avicularia*, Claparède (1871) supported the opinions of Huxley (1856) and Smitt (1865) 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") in the ovary lying on the basal wall in its distal part and surrounded by a common envelope [ovary wall] – one egg [the leading oocyte] rapidly increases in size, becomes bright red and shows granular cytoplasm, whereas another [the nurse cell] remains 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 the ovary together with its sibling or stays. In both cases it degenerates, whereas a new oocyte doublet is developed following division of the oogonium. Like Nitsche (1869), Claparède wrote that eggs develop via proliferation of the "Endocyste" in both species. By this term he presumably meant both the epithelium of the cystid wall and the polypide.

In contrast to *Scrupocellaria*, the ovary of *B. avicularia* is situated in the upper part of the funiculus and the later-developing testis in its lower part. Claparède was the first to observe and illustrate an incipient ovary, consisting of two small round cells at a time when both the cystid and the polypide are incompletely formed and there is no trace of the funiculus. Stressing the origin of the ovary from the "Endocyste", Claparède wrote that young doublet is adjacent to the pharynx of the polypide bud, being surrounded by the cell membrane [prospective ovary wall], the cells of which do not differ from the cells of the "Endocyste" [i.e. the peritoneal lining of the polypide]. As the polypide grows, the position of the ovary changes relative to it. Additionally, Claparède described and depicted larval settlement and metamorphosis and formation of ancestrula in *B. avicularia*.

Salensky (1874), reporting on ovary development in *Bugula plumosa*, stated that it corresponds to that of the polypide bud and is formed as a cell accumulation on the internal surface of the cystid, thus making these structures homologous.

Studies of Repiachoff (1875) and Reinhard (1875) on reproduction of *Tendra zostericola* showed that simultaneously hermaphrodite zooids occur in this species, contradicting Nordmann (1839), who described separate male and female zooids (see above). Apart from those zooids possessing both gonads simultaneously, Repiachoff did, however, also mention separate male and female zooids in colonies of this species, but was in doubt whether there was true gonochorism or non-simultaneous development of the gonad in

them. Ostroumoff (1886b, c, p. 561,) subsequently wrote that "sexes are usually separated" in zooids of *Tendra*. Repiachoff found ovaries on the basal wall in zooids with normal morphology as well as in those with brood chambers, and confirmed the data of Claparède (1871) on the early appearance of the ovary in young zooids with developing polypides; he described and depicted the incipient ovary adjacent to the polypide bud. The mature ovary contained up to ten oocytes, being surrounded by a membrane [ovarian wall]. Ovulated oocytes (up to three) remained in the perigastric coelom for some time until oviposition. Repiachoff also described and illustrated larval structure, metamorphosis and development of the ancestrula in detail (see also Repiachoff 1878).

Although not understanding the actual structure of zooids with acanthostegal brood chambers, Repiahoff (1875) suggested that they play a role similar to that of ovicells. Following him (and Nordmann 1839), Reinhard (1875) thought that embryos developed inside the body cavity of these 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 (1839), who thought that sperm could enter female zooids through opening in the [transverse] wall between subsequent zooids. He also challenged the opinion of Salensky (1874) on ovary structure (see above), stating that there were not two layers and that it exhibited a gradual change in shape and size from large and roundish cells in the middle to smaller elongated cells at the periphery. Reinhard recorded spermatogenic tissue developing on both lateral walls and proximally in the cystid, and an ovary lying on the basal wall either in the middle or in the proximal half of the fertile zooid. He was possibly the first to describe clusters of spermatozoids (spermatozeugmata), which, as he surmised, result from the grouping of originally single "seminal threads" with elongated heads. He further described and depicted aspects of egg and sperm formation not only in *Tendra*, but also in *Cryptosula pallasiana* and *Smittoidea reticulata* (both as *Lepralia*).

Ostroumoff (1886b, c) 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 brooding zooids of *T. zostericola*. Later Paltschikowa-Ostroumowa (1926) and Braiko (1967) described oviposition via 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* (as *Membranipora*), often considered to be 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.

Using *Cryptosula pallasiana* (as *Lepralia*), Repiachoff (1876) described the cheilostome ovary more precisely. He observed that the ovary is situated in the distal part of zooid on the basal wall, being in "genetic connection" with the "Endocyste". Eggs are surrounded by (1) a thin cellular layer (interpreted as a "cell membrane" [= ovary wall]) that is connected with (2) a group of cells forming the base of the ovary. Describing sperm, he differentiated between thin and thick moving "threads" [spermatozoids and spermatozeugmata], and even asked if the latter consist of several of the former. Cleavage, larval structure and development of the ancestrula were also studied in the same work.

Repiachoff (1876) also briefly described and depicted oocytes in the ovary of *Electra repiachowi* (as *Tendra*). It is particularly interesting that some of the oocytes were lobate. Sperm were also detected. Noteworthy, Ostroumoff (1886b, c) stressed that spermatozoids form bundles [spermatozeugmata?], reminiscent of tiny nematodes, in the latter species whereas they were single in *T. zostericola*. He further noted that the ovary is situated "near opercular surface [frontal wall]" in *Tendra* (1886b, p. 18), and "near basal surface [wall]" in *E. repiachowi* (p. 20). According to his description, zooids are hermaphrodite in the latter. Ostroumoff (1886b) also stated that the larva develops inside the tentacle sheath in *Cryptosula pallasiana*.

Ehlers's (1876) study of the ctenostome bryozoan *Hypophorella expansa* showed that both male and female gonads occur on the internal surface of the body wall of the same zooid. He described spermato- and oogenesis, being one of the first to make measurements of spermatozoids, ovaries and eggs, the latter at different stages of development. Ehlers observed up to 30 growing oocytes in the ovary, suggesting that the later-developed ones would develop after the ovulation of those developed earlier. He also noted a structure that he first thought was "Ausführungsapparat" [intertentacular 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 the similar findings of Farre (1837) and Hincks (1851), Ehlers decided that it was a parasitic infusorian. Later Prouho (1892) showed that there is a supraneural pore in *H. expansa*.

One of the most informative and influential (but almost forgotten) papers of that time was published by Joliet (1877a). This author observed gametogenesis in ten gymnolaemate bryozoans, both cheilostome and ctenostome. He stated that formation of the sex cells is connected with a polypide, showing that both testes and ovaries are formed at the expense of the funiculus. In hermaphrodite zooids the ovary is placed in the upper part [of the funiculus] near the caecum, and the testis in its lower part. In gonochoristic zooids the gonad is situated 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 gonad could be moved from the funiculus to the body wall in some species (for instance, in *Farrella repens*) (as *Laguncula*). This observation, although criticized by Hincks (1880), is actually correct; in several instances the ovary is removed from the developing polypide bud (where it originates) to the basal cystid wall obviously due to growth of funicular tissue (see Ostrovsky 1998; Moosbrugger et al. 2012).

Interestingly, Joliet (1877a) described two different kinds of eggs in different zooids of certain species, one developing on the funiculus and another ("parietal") on the body wall. For instance, in *Bicellariella ciliata* (as *Bicellaria*) he found ovaries on both the funiculus and the cystid wall [in different zooids], as recently observed by Moosbrugger et al. (2012). Puzzlingly, he stated that he never saw the ovicells, formed by the fertile zooid in the second case (was it an egg then?). Joliet supposed that the parietal eggs should originate in connection with funicular strands passing through the communication pores. Since the work of Müller (1860) the funicular system was considered as "colonial nervous system" by some authors (Smitt 1865; Claparéde 1871, discussed in Hincks 1878). Joliet also used this term although thought that the origin of germ cells in the funiculus was a strong argument against its "nervous nature". These doubts finally resulted in the introduction of the term "endosarc" for funicular tissue (see also Joliet 1877b). An ovary was recorded on the funiculus of a zooid with a developing polypide in *Bugula avicularia*, and early male germ cells near a young polypide bud in *F. repens*. In the ctenostome *Walkeria uva* (as *Valkeria cuscuta*) he also recorded formation of spermatogenic tissue and an ovary on the funiculus of the early polypide bud and described spermatogenesis in detail.

Joliet described the release of sperm in *W. uva*, but could not recognize the pore through which mature sperm leave the zooid cavity. In this species Joliet found that eggs do not degenerate in the ovary during polypide recycling, but that one of them begins to grow faster instead. Much later, Dyrynda and Ryland (1982) found that vitellogenesis commences during polypide recycling in the cheilostome *Chartella papyracea* (see below). In Joliet's case a modified polypide without tentacles develops prior to oviposition in the fertile zooid. It can be seen in his illustrations (1877a, pl. 13, figs 5–9) that the brooded embryo increases in size in the introvert, which is evidence of extraembryonic nutrition in that species. Joliet's description and illustrations show that he often saw developing oocyte doublets (in cheilostomes), of which one cell [the leading oocyte] grows and the other [nurse cell] remains small. In agreement with Claparède (1871), Joliet believed that the second cell waits its turn to develop or divide. Describing oogenesis in *Lepralia martyi* (a presently

unknown cheilostome taxon) Joliet wrote that he observed a cavity [intraovarian space?] developing in the ovary in which two eggs originate. He thought that upon ovulation, the new (second) ovary is established in place of the former one. In this species Joliet recorded up to six eggs formed during the lifetime of the fertile zooid. In stating that the majority of the species studied possessed hermaphrodite autozooids, he demonstrated the presence of gonochoristic zooids in *L. martyi*.

Going against general opinion, Joliet (1877a) remarked that cross-fertilization should occur in some species, ctenostomes as well as cheilostomes, in which protandrous zooidal hermaphroditism or zooidal gonochorism occurs. Differences in the timing of gamete maturation, massive production of spermatozoids and their possibility to swim actively in the surrounding water led him to believe that cross-fertilization is the rule. He suggested that fertilization by alien sperm, "distinguished" by the absence of the nucleus in the egg, occurs in different species (1) inside the maternal zooid (within the tentacle sheath in the brooding ctenostomes studied or within the zooid cavity), (2) during oviposition, or even (3) in the ovicell. Joliet wrote that he also observed embryo development inside the introvert in *Bowerbankia imbricata* and *Farrella repens* (as *Laguncula*). The second case is wrong, as Marcus (1926a) noted. Joliet thought that sperm was released through the thin wall of the tentacle sheath during a sharp withdrawal of the polypide. In cheilostomes he observed the egg positioned below the zooidal operculum prior to oviposition and suggested the presence of a "communication canal" for egg removal. Finally, from observations on colonies of *Bugula* spp., with serially positioned eggs and embryos in the ovicells along the branches, Joliet wrote that each ovicell could be used repeatedly.

There is some information on the structure and appearance of ripe oocytes in the embryological monograph of Barrois (1877).

An extensive review on bryozoan sexual reproduction was included in the monograph by Hincks (1880), who, apart from analyzing the results of previous authors, also mentioned his own observations (1861, 1873). Summarizing the earlier data and opinions, 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 connexion with a communication-plate – and that in several cases they are placed on the cell[zooid]-wall, but whether a product of the endocyst [epidermal layer of the cystid wall] or endosarc [associated funicular tissue] is still undetermined" (1880, pp. xlix–l). In the ctenostome *Alcyonidium mytili* 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*, Hincks (1873, 1880) described embryo brooding accompanied by a change of egg/embryo coloration and polypide degeneration. He observed a "delicate envelope" [introvert] surrounding the embryo, taking the view that the embryo develops inside the zooid cavity. Later Calvet (1900) showed that brooding takes place inside the introvert in this species. In *Nolella stipata* (as *Cylindroecium giganteum*), Hincks found three "ova" of different sizes near the apex of the cystid interior, describing their position as being "previous to escape" (see legend for pl. 77, fig. 4). Judging from their gradually increasing size, these were brooded embryos, incorporated into the cystid wall and nourished by it (indicative of matrotrophy). This observation, again not understood, was later made by Prouho (1892, pl. 24). While admitting the existence of cross-fertilization in some species, Hincks nevertheless believed that, on the whole, self-fertilization prevailed in Bryozoa. Following Joliet (1877a), he thought that two ovaries could be developed in succession within the same funiculus, confusing them with follicles of the same ovary developing sequentially. He gave a general description of oogenesis and mentioned that "frequently two ova [oocyte doublet] are produced, which are either matured in succession, or one of them [leading oocyte] perfects its development at the expense of the other, which is atrophied" [degeneration of the nurse cell] (1880, p. xci). Remarkably, although he agreed with the opinion of Huxley (1856), Nitsche (1869) and Joliet (1877a) 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 (1882, 1884a, b), who, in addition to observations of living colonies, studied serial anatomical sections. Most latter researchers employed this technique. Vigelius continued the discussion about the origin of the ovary – whether it is developed from the "endocyst" or from the "endosarc" (see above). In *Chartella membranaceotruncata* (as *Flustra membranaceo-truncata*), he found developing ovaries on the basal wall in distal parts of young zooids with late-developing polypide buds, and stated that they are formed "from the internal surface of the endocyst" (1882, p. 436), since gonads were clearly isolated from the polypide, and cell layers of the body wall and the ovary wall were continuous. According to his description, cells of the incipient ovary are formed from the cells of the parietal layer, "Parietalschicht" [epithelium of the body wall]. Furthermore, they actively divide to form an ovary that initially consists of a compact group of rounded cells of the same size. He stressed their similarity to the early cells of the male gonad and their common origin from the parietal layer, calling them homologous. A similar suggestion was made earlier by Joliet (1877a). It should be mentioned here that the data of Vigelius on the flustrid *Chartella* correspond to those of

Grant (1827), who observed the youngest eggs on the cystid wall without a connection with the polypide in two other flustrid species (see above).

Apart from the structure and development of the ovicell in *C. membranaceotruncata*, Vigelius (1882, 1884a, b) gave exhaustive and beautifully illustrated descriptions of oogenesis and ovarian structure, starting from differentiation of 2–3 early oocytes [in fact, oogonia] surrounded by smaller cells [ovary wall] in the young ovary. Like Joliet (1877a), Vigelius often mentioned that eggs develop in pairs, and described growth of the leading oocyte [judging from his illustrations, macrolecithal], surrounded by a "Dottermembran" [vitelline membrane] and accompanied by changes in its cytoplasm during vitellogenesis and, finally, degeneration of the nurse cell [which Vigelius considered as a struggle for existence between the cells]. The structure of the ovary with its follicle (Vigelius was one of the first to use this term in bryozoan oogenesis) was described as consisting of intensively pigmented, pear-shaped and cylindrical lateral cells, adjoining the zooid wall, and paler, flattened cells on its opposite side (1884b). Changes in ovary shape and sometimes position were also mentioned. Vigelius was sure that the cells of the ovary wall never transformed into germinal cells, but that their number increased by division as the follicle grew. He described ovulation, accompanied by a gradual flattening and eventual "resorption" of the follicle cells, stages in the breakdown of the nucleus preceded by shrinkage of the nuclear membrane, and removal of the mature egg that occupies the larger 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, leading to the rupture of the ooecial vesicle wall. The egg moved first to the ooecial vesicle, later transferring through the hole in its ruptured wall to the incubation cavity of the ovicell (Vigelius 1884a, b). This scenario was later adopted by Calvet (1900) and authors like Korschelt and Heider (1910) and Gerwerzhagen (1913) (based on Calvet).

In *Chartella* Vigelius found male, female (more numerous) and occasionally hermaphrodite zooids in the same colony. Because of the simultaneous presence of the three variants of sexual zooids in the same colony, Vigelius supposed that female zooids could transform to hermaphrodite and back to female depending on conditions. It was observed that the gonads in the males appear later than ovaries in female zooids in the colony. However, sperm mature at approximately the same time as the eggs. The separation of the sexes among zooids, the simultaneous maturation of their gametes, and, in contrast, the generally different timing of gamete maturation in hermaphrodite zooids [i.e. protogyny] led him to support the suggestion of Joliet (1877a) that cross-fertilization should characterize this and most other species, although it seems he meant intracolonial self-fertilization [zooidal cross-fertilization within the same colony]. The

mature oocyte was said to be surrounded by the "yolk membrane" [fertilization envelope] when still in the ovary (Vigelius 1884a, pl. V, figs 69, 71). The partially detached envelope wall is depicted on the side of the partially ovulated oocyte exposed to the zooid cavity. Challenging the statement of Joliet (1877a), Vigelius found that testes develop on the zooid wall but not within a funiculus. Like Ehlers (1876), he described the irregular shape, sometimes paired, and wide distribution of testes [spermatogenic tissue] across the zooid 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 (1877a) 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 achieved through the zooid 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 (1886) studied sexual reproduction in *Bugula calathus* including the structure and development of its ovicells. Here the ovary is suggested to be a product of "mesenchymatous parenchyma" (a similar opinion is also in the works of Ostroumoff (1886a, b), who wrote that both testes and ovary have a mesodermal origin), developing on the basal wall of the cystid. Vigelius noted that some ovaries lose their contact with the basal wall during oogenesis, either lying free [because of ovulation?] in the body cavity or connected to the basal wall by the single parenchymatous [funicular] strand. In comparing ovary structure in *B. calathus* and *Chartella membranaceotruncata*, Vigelius stressed the striking difference between these species; in contrast with the ovary of *Chartella*, with its basal part consisting of tightly packed large, cylindrical cells, the ovary of *Bugula* is represented by a few small, flat cells with a loose arrangement. It is noteworthy that in two instances Vigelius depicted some tiny bodies between the oocytes and the ovary wall (1884b, pl. 3, fig. 39, 1886, pl. 26, fig. 4) that might be so-called "basal ovarian cells", a term introduced by Hageman (1983) based on his ultrastructural studies. Judging from his illustrations (pl. 26, figs 3–4), Vigelius often saw oocyte doublets, young as well as mature, consisting of the oocyte and its nurse cell with a nucleus occupying the major part of the cell. Vigelius also described a large transparent vacuole, seen in the nucleoli of many oocytes, and a change in the position of the nucleus (from central to excentric) in the course of ovum growth and vitellogenesis. Though mentioning brown yolk granules, he termed the eggs of *Bugula* as alecithal. The simultaneous development of

male and female gametes in the same zooids persuaded him to accept intrazooidal self-fertilisation in this species. One of Vigelius's most interesting findings was the discovery of a cylindrical epithelium [embryophore] in the ooecial vesicle, and unusual "bodies" [possibly groups of the nutrient-storage cells] with granular cytoplasm, associated with its cells. This hypertrophied cell layer, now known as a placental analogue, was probably found first by Reid (1845) in *B. flabellata* (see above). Vigelius also depicted an increase in the size of incubated embryos (a consequence of placental brooding), but, like many of his contemporaries (Hincks 1861, 1873; Nitsche 1869; Joliet 1877a; Calvet 1900), did not recognized the importance of this finding.

Finally, Vigelius (1887a, b) published two papers in which he summarized the contemporary view on bryozoan anatomy, mentioning that sexual products are formed from "parenchymatous tissue". Judging from his description (1887a, p. 238) this "tissue" is of mesenchymatous origin and includes peritoneal and funicular cells.

Kraepelin (1887) described and depicted the position of gonads in the hermaphrodite zooids of two ctenostomes. In *Victorella pavida* both gonads are placed on the cystid wall – the ovary in the distal part of the zooid and the testis occurs in the middle part. In *Paludicella articulata* (as *P. ehrenbergi*), spermatogenic tissue develops on the funiculus and partly also on the cystid wall in the proximal part of the zooid, and the 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 "Peritonealepithel".

In contrast with all previous published observations, Jullien (1888a) described and depicted a "testicule glandulaire" with ducts in *Figularia figularis* (as *Lepralia*), and depicted ovaries with a single oocyte doublet in this species and in *Beania* sp. (as *Diachoris costata*) (Jullien 1888b). In all probability, he confused opercular glands with testes (which do not have ducts). In *Celleporella hyalina* (as *Hippothoa*) he 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 (Jullien 1888b).

Pergens (1889) briefly described oogenesis and ovulation in *Fenestrulina malusii* (as *Microporella*). He stated that the ovary develops from parietal tissue on the zooid wall in this species. Division of the cells of the parietal layer results in the development of the ovary in which a group of 3–5 larger cells becomes visible. Some of them are resorbed, but two [oocyte doublet] increase in size and one is transformed into an egg. Other ovary cells surround this pair, "serving them for feeding (p. 510)." The ovulated egg released from the follicle is surrounded by the "Chorion" [fertilization envelope] that is preserved until the end of larval development [in the ovicell]. Pergens was the first to record oviposition in cheilo-

stomes, noting that it is accompanied by strong compression of the egg and occurs when the polypide degenerates; up until now, Gerwerzhagen (1913) had been thought to be the first to describe this phenomenon. Nielsen (1981) has described oviposition in *Fenestrulina miramara* (described as *F. malusii*) as being undertaken by the everted lophophore and almost without the egg deformation (see also below); however, Pergen's (1889) description is very realistic, and it is unclear why oviposition is so different in congeneric species. A further important observation was that the ovary continued producing ova during polypide recycling, in accord with the observations of Van Beneden (1844b) and Vigelius (1884a). Although finding only gonochoristic zooids, Pergens believed that the sex of the zooid could change since he recorded "spermatosporen" in ovicelled zooids. He also observed a zygote and two polar bodies in the ovicell.

The classical works of Prouho (1889, 1892) 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*. Non-brooder *A. albidum* has simultaneously hermaphrodite zooids, with an ovary developing on the funiculus and spermatogenic tissue on the cystid wall in the proximal region. Judging from Prouho illustrations, the ovary contains up to 18 small oocytes and up to three ovulated eggs occur in the body cavity. Prouho (1889, p. 197) described the "transparent and … delicate shell" [vitelline membrane] surrounding the ovulated eggs and observed their release through the intertentacular organ, proving that it is an oviduct. He also suggested that fertilization possibly occurred prior to the appearance of the "shell."

Using anatomical sections, Prouho investigated the structure of the intertentacular organ in *Electra pilosa* (as *Membranipora*) and *Alcyonidium duplex*. He observed egg release through the "genital pore" [supraneural coelomopore] in the non-brooding ctenostome *Hypophorella expansa*, thus showing that Ehlers (1876) was mistaken when he wrote that he observed an intertentacular organ in the retracted polypides in this species. Brooding within the introvert was described in four species: *Pherusella tubulosa* (as *Pherusa*), *Flustrellidra hispida* (as *Flustrella*), *Alcyonidium variegatum* and *A. duplex*. In three of them the polypide degenerates, and several embryos are brooded simultaneously: 4–5 in the first two species [there can be up to eight embryos in *F. hispida* according to Hayward (1985)], and 6–8 in the third (it is not clear from Prouho's description how many embryos are simultaneously brooded in *A. variegatum*). According to his description, in *A. duplex* the male germ cells are developed on the funiculus of the first polypide, at the site of its attachment to the stomach; they then 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 7–9 (up to 11) oocytes seen in the ovary in Prouho's illustrations. The ovulated eggs are irregular in shape. In contrast with the first polypide, which finally degenerates, the polypide forming the ovary has an intertentacular organ. Released eggs stick to the polypide diaphragm region [presumably, by their fertilization envelopes], being withdrawn into the vestibulum during polypide retractions and exposed when it expands. Later the third polypide forms a new ovary and has the same structure as the second one that degenerates. No new testis develops in the zooid.

In three species with a cyphonautes larva (*Electra pilosa*, *A. albidum* and *H. expansa*) ovulated eggs are of irregular shape and are said to possess "slow ameboidal movements" in the zooid cavity (Prouho 1892, p. 608). They are surrounded by the "vitelline membrane" that was closely apposed to the oocyte, and the elevation of the fertilization envelope was described to occur after the passage of the eggs through the intertentacular organ or supraneural coelomopore. Prouho recorded the subsequent appearance of two polar bodies in the perivitelline space of recently spawned zygotes in these species.

In *Nolella dilatata* (as *Cylindroecium dilatatum*) Prouho found, as he thought, internal brooding. According to his description and figure explanations (1892, pl. 14, figs 14–17), 2–3 "eggs" are incubated, adhering to the internal surface of the zooid wall. Larvae were presumed to leave the zooid coelom through a rupture of this wall. It is also depicted that the embryos are enlarged during brooding, with the youngest (i.e. smallest) being uppermost in the zooid, and this could be evidence of extraembryonic nutrition. Prouho tended to believe that self-fertilisation was the rule among bryozoans, since in those species in which he recorded sexual products, they often matured simultaneously. He observed that spermatozoids were concentrated around the ovary in *Alcyonidium albidum*, but admitted that male and 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 zooid cavity using the same organ, since the activity of its cilia was directed towards the outside.

Braem (1896) confirmed Allman's (1856) findings on the position of the gonad in the freshwater 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 a fertilization envelope and sometimes stuck to the maternal colony. In his later papers Braem (1908a, b) briefly described the structure of spermatozoids and made measurements of them in the ctenostomes *Paludicella* sp. [*P. articulata*] and *Triticella* sp.

Waters (1896a [1898]) discovered the external membranous brooding sacs (which he termed ovicells) of

Aetea sica (as *A. anguina* forma *recta*) and an ovary. Later this mode of brooding was described by a number of authors (see Sect. 2.4.1 of Chap. 2). The ovary is positioned inside the adnate, horizontal part of the maternal zooid; Waters noted four young oocytes.

Delage and Hérouard (1897) briefly reviewed bryozoan sexual reproduction in their handbook, but the number of original papers upon which their account was based were relatively few.

The monograph of Calvet (1900) became an important landmark in the development of knowledge about bryozoan anatomy including the reproductive system. Apart from the structure of brood chambers in several cheilostome species, he described brooding in the tentacle sheath in the ctenostomes *Bowerbankia pustulosa*, *Amathia lendigera*, *A. semiconvoluta* and *Vesicularia spinosa*. Calvet discovered the embryophore in the cheilostomes *Bugula simplex* (as *B. sabatieri*) and *Cellaria fistulosa*, but did not understand its significance. He nevertheless noted that the size of the cells in the brood sac wall correlated with the developmental stage of the embryo in *Cellaria* – the more advanced the embryo, the larger the cells. The intertentacular organs of *Electra pilosa* (as *Membranipora* var. *dentata*) and *Alcyonidium cellarioides* were studied by anatomical section. Calvet recorded protandrous zooidal hermaphroditism in ten cheilostome species, and simultaneous zooidal hermaphroditism in six cheilostomes and two ctenostomes. He stressed that early zooids did not reproduce sexually. 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 in the same species. In the majority of the species studied the ovary is placed "parietally" [on the zooid wall, mainly basally], although it could be suspended on funicular strands or attached to the polypide, explaining existing controversies to some extent (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 types, Calvet showed the striking difference in egg number among ovaries – oviparous bryozoans have many more oocytes. In viviparous species the eggs are often pictured in pairs [oocyte doublets], some of them degenerating inside the ovary [mature nurse cells]. It is clearly seen from the illustrations that cheilostomes, except for *Electra* species (as *Membranipora*), possess fewer eggs in the ovary than the ctenostomes studied. Calvet observed spermatogenesis in 23 species (19 cheilostomes, two ctenostomes and two cyclostomes), illustrating in detail different stages of spermatozoid development in *Bugula simplex* and *Cryptosula pallasiana*, and stating that the initial "cellule spermatoblastique" originated from mesenchymatous tissue in young zooidal buds. This researcher also recorded clusters of

spermatozoids [spermatozeugmata] in *Electra pilosa* and described their disaggregation.

Calvet carefully investigated ovarian structure, oogenesis and spermatogenesis in simultaneously hermaphrodite zooids of *B. simplex*, resolving several important problems. According to his observations, the position of the ovary varies in this species. The fully formed ovary is either attached to the peritoneal lining of the zooid wall or stomach or suspended on funicular strands in the zooid cavity. He mentioned the rare occurrence of two ovaries in some zooids. In one instance he depicted an ovary resting on the zooid wall (pl. 3, fig. 14) and, additionally, "cellules ovulaires" inside the funiculus in the same zooid. An important conclusion was that, wherever it is positioned, the ovary is always "associated with the mesenchymatous tissue," and its cells "come directly, and by simple differentiation, from" it (pp. 75, 295), according with the statements of Ostroumoff (1886a, b) and Vigelius (1886). However, in contrast with the findings of the latter author, Calvet found early female cells "free" in the cavity of zooid buds containing a developing polypide. In zooids with polypides at a more advanced stage, these cells were then either found within the polypide peritoneum or the peritoneum of the cystid wall or suspended on funicular strands (see also Joliet 1877a). Calvet stated that female cells were also incidentally found in terminal zooids with developed polypides, specifically within the funicular tissue or peritoneal lining. He criticized the opinion of earlier authors, for instance Nitsche (1869), concerning the origination of the ovary from the "endocyst". Actually, Nitsche, who did not use thin sectioning, was unable to detect the peritoneum of the cystid wall.

According to Calvet's observations on oviparous species, ova within ovaries are surrounded by a few flattened cells whereas in viviparous species the ovary wall constitutes both flattened ("membrane folliculaire") and cylindrical cells forming either a narrow (pedunculate) or wide basal part that connects the ovary to the cystid wall. It is clear from his illustrations that Calvet saw basal cells in some ovaries too. A unusual type of ovary, developing on the caecum and partially the funiculus, was described in the ctenostome *Nolella dilatata* (as *Cylindroecium dilatatum*). Calvet could not distinguish any accessory cells in it, only numerous small eggs.

He described the development of the ovary and accompanying changes in female cell structure. According to his description, following their differentiation, the early "cellules ovulaires" are further enveloped by multiplying mesenchymatous cells in different species of *Bugula* and in the ctenostome *Bowerbankia pustulosa*. In all but one of the other bryozoans studied, the process is said to be different. Following differentiation from the "mesenchymatous elements", the female germ cells that differ from all others in having a bubble-like shape, more intense staining and a larger diameter, each divide once. Judging from his figures, Calvet may have seen 2–4 oogonia ("cellules ovariennes

initiales") in the incipient ovaries. He wrote that all of them had the same characteristics and were "young ovules" at that stage (p. 296). 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 [presumably nurse cells]. Calvet thought that growing eggs were nourished at the expense of those that degenerate.

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

Thus, towards the end of the nineteenth century the following features or conditions of gymnolaemate sexual reproduction were recognized:

- Except for sterile zooids, colonies may consist of either hermaphrodite and/or gonochoristic autozooids with simultaneous or non-simultaneous maturation of gametes in both cases; those thought to be gonochoristic may in fact be hermaphrodite depending on the time of appearance of the gonad.
- Germ cells originate at the expense of the mesenchyme [mesothelium], and the formation of early female cells is associated with either the zooid wall or the early polypide bud.
- An ovary is situated on the caecum, funicular strand(s) (often on that connecting the caecum and the cystid wall), or cystid wall (also connected to the funiculus), and its position is variable.
- With one exception (*Farrella repens*), testes (sometimes, paired) are formed in the proximal part of the zooid on the cystid wall, often at the site where the funiculus attaches to the wall.
- The main stages of oogenesis and spermatogenesis are known. There are clear differences in the amount of yolk deposited in the eggs of different species.
- There are oviparous and viviparous species among Gymnolaemata. The former produce numerous eggs, releasing them through the intertentacular organ or genital pore. The number of eggs in viviparous species is much smaller, and they are brooded in a variety of types of incubation chamber.
- Sexual reproduction is often accompanied by polypide degeneration.
- A thin membrane envelopes ovulated eggs and developing embryos, whether brooded or released.

First Half of the Twentieth Century – More Results

Schulz (1901) presented some findings on reproduction in *Einhornia crustulenta* (as *Membranipora membranacea*), briefly describing gametogenesis in this species. Both male and female gametes mature simultaneously, and the ovary that is covered by mesodermal epithelium [ovary wall] develops at the expense of funicular tissue, often close to the pylorus. Interestingly, Schulz wrote that several ovaries are often formed in one zooid, which is in accord with the data of Calvet (1900), who mentioned two ovaries in one zooid of *Bugula simplex* (see above). Spermatogenic tissue is formed partly on funicular strands, partly on cystid walls. Because of simultaneous zooidal hermaphroditism, Schulz suggested that self-fertilization took place in this species. He described an intertentacular organ, stressing that he could observe it in sexually reproducing colonies only. He rejected the idea that it has an excretory function (Harmer 1892), stating that it was used exclusively as an oviduct.

Data on the presence and position of gonads are incidentally contained in the works of Harmer (1902, 1915, 1926). Harmer (1902, p. 301) was the first to write that the embryo "receives its yolk while in the [brood] sac" in *Retiflustra schoenaui* (as *Flustra cribriformis*), and this was influenced by the comparison made between the small oviposited egg and the large embryo. Harmer (1926, p. 253) described "a secretory epithelium" in the brood-sac wall, stating that the embryo towards the end of its development "occupies nearly two thirds" of the cavity of the fertile zooid in this species. Comparing reproduction among cheilostomes, he stressed that "[1] while the eggs which develop into Cyphonautes are always small, with little or no yolk, and are produced in considerable numbers … [2] the egg which develops in an ovicell is, with few exceptions, single and usually has from the first a considerable amount of yolk". He noted as exceptions the species of *Bugula* "where [3] 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" (Harmer 1926, p. 203). Thus, Harmer was actually the first scholar to recognize extraembryonic nutrition and the three major reproductive patterns in Bryozoa.

In the ctenostome *Nolella papuensis*, Harmer (1915, p. 56) found embryos (surrounded by a thin envelope) immersed in the zooid cavity and also attached to the zooid wall, and described them from the viewpoint of Prouho (1892) as if they were brooded internally before escaping through a "hernia-like protrusion". In the cheilostome genus *Steginoporella* (as *Steganoporella*) Harmer described embryos in ovisacs, ovaries on the lateral wall of A-zooids and sperm in both A- and B-zooids (Harmer 1926).

Waters' papers give the appearance of being mainly taxonomic in character but in fact they frequently contain valuable information on bryozoan anatomy and reproduction. For instance, anatomical figures from his works were widely used in the monographs of Canu and Bassler (1920, 1929). Waters carried out thin-sectioning in order to use anatomical characters for the purposes of classification. Using sections, he counted tentacle numbers and described 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 a sectioned zooid of *Menipea roborata* (as *Flabellaris*) (Waters 1896b [1898]). In *Cystisella saccata* (as *Porella*), testes and an ovary are figured in obviously gonochoristic zooids (Waters 1900), and a developing embryo is pictured in the tentacle sheath of the ctenostomes *Walkeria uva* (as *Valkeria*) and *Bowerbankia imbricata* (Waters 1910). There are brief remarks on reproductive characters in taxonomic descriptions in other papers (Waters 1904a, 1906, 1914, 1919 [1921]). 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" (Waters 1904b, p. 86). Additionally, an intertentacular organ was found in the simultaneously hermaphrodite zooids of *Alcyonidium antarcticum*. Waters (1896a [1898], 1913) was the first to discover brooding in the external ovisacs of *Aetea* species (see above). His study of the peristomial ovicells of *Margaretta chuakensis* (as *Tubucellaria ceroides* var. *chuakensis*) revealed that a large ovary is normally situated below a dwarf polypide, although young ovaries may occur in different places, being frequently associated with a funicular strand near the point where it enters one of the lateral rosette-plates (Waters 1907). 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, he asked if the polypide could bring "spermatozoa … to the growing ova of the ovarium" (1907, p. 128). Waters' schemes show macrolecithal eggs forming within an ovary of cylindrical epithelial cells in this species. In the ovicells of *Thalamoporella rozieri*, he found up to three embryos of different ages all surrounded by fertilization envelopes. He mentioned the unusual structure of the ovary in this species, in which "ovarian cells are partly surrounded by a coarse cellular network" (Waters 1909, p. 141).

When studying internal brooding in a number of cheilostomes in the genera *Adeona*, *Adeonella*, *Adeonellopsis*, *Laminopora, Beania* and *Watersipora* (as *Lepralia*), Waters (1912) discovered (but again, did not understand) extraembryonic nutrition. He wrote that embryos were surrounded by a "thick-walled sac" [embryophore of the internal brood sac] and occupied half or even almost all zooid cavity in "adenoid" genera and *Beania*, but that the eggs found were

of small to moderate size. Briefly describing the female gonad in "adenoids", he wrote that the ovary is positioned in the distal part of the zooid, near the proximal part of the brood sac. It contains two, occasionally, three small oocytes, of which only one reaches a moderate size (in *Adeona foliifera fascialis* (as *A. foliacea* var. *fascialis*)). In this paper, Waters proposed to divide all Bryozoa into two groups according to ovarian structure, discussing the utility ("classificatory assistance") of this character. He defined (1) "bicellular" ovaries "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" (1912, pp. 496–497). He considered *Bugula* (and obviously the "adenoids") as an example of the "bicellular" variant, and *Scrupocellaria* as an example of the "multicellular" one, which corresponds with my data on oocyte number in matrotrophic and non-matrotrophic species (see Chap. 1). Testes were said to "nearly fill" the zooid cavity [obviously in male zooids] in *Laminopora contorta* (p. 498).

In a later paper Waters (1913) described and depicted the hypertrophied epithelium of the brood sac in *Adeonella platalea*. In *Poricellaria ratoniensis* (as *Diplodidymia complicata*) the small egg begins its growth in the small brood sac, hanging below the zooidal operculum. Both then enlarge to such an extent that they fill most of the zooid cavity. Once again, Waters did not understand that he had discovered placental nutrition in both these cases, but he did realize it in the case of *Catenicella elegans* (as *Vittaticella*), writing that there are "several fleshy bands or tubes [funicular strands] by which … material for growth is transferred to the ovicell", containing a large embryo in this species (1913, p. 485).

In this paper the position of the gonads and the number of eggs in the ovary were recorded in 16 cheilostome species. For three other species he gave data about the position of the embryo in the brood-chamber: for instance, embryos surrounded by a membrane were suggested to be brooded in the "internal ovicell" [brood sac] in *Steginoporella magnilabris* (as *Steganoporella*) (1913, p. 500). A similar finding was made by Marcus (1922), who recorded membrane-bounded embryos and ovary in *Steginoporella haddoni* (as *Steganoporella*). Waters (1913) further considered that the size and position of the ovary and the size and the number of eggs might be useful generic characters. 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*) had a small, proximal ovary with only two (rarely 3–5) small eggs, one of which is transferred to the ovicell. For this reason, Waters endorsed the segregation of

Dendrobeania murrayana (the type species of *Dendrobeania* Levinsen, 1909) from the genus *Bugula* on the basis of ovarian structure. In this regard, Waters was in accord with Vigelius (1886), who noted a marked difference in the structure of the ovary wall in *Bugula* and *Chartella*. Actually, this distinction reflected the existence of two different reproductive patterns, involving placental and non-placental brooding associated with micro- and macrolecithal oogenesis correspondingly, in Cheilostomata, the general appreciation of which came much later.

Pace (1906) studied reproduction in the ctenostome *Flustrellidra hispida* (as *Flustrella*) in detail. He was one of the first to record gonad activity throughout the different seasons, noting that the simultaneous presence of male and female gonads in the same zooid is not reflected in simultaneous maturation. Both male and female germ cells were reported as originating from the mesenchyme, with the testes positioned on the body wall and the ovary on the funiculus. The incipient ovary was stated to originate from a "protoplasmic mass," with nuclei but no indication of "cell-walls" (p. 441). Similarly, Owrid and Ryland (1991) 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 or five of them differentiate into growing eggs, simultaneously developing in the ovary, whereas the rest develop into follicle cells. The number of follicle cells increases as egg maturation proceeds in such a manner that each ripe "ovum is surrounded by a follicular membrane" (p. 442). Pace carefully described oocyte growth, with corresponding changes in its structure, including the fate of the 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 (1892). In one instance Pace found a "vitelline membrane" [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 increased in size, eventually filling the entire zooidal cavity providing what could be evidence for extra-embryonic nutrition.

In contrast with previous authors, Silbermann (1906) 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 oocyte growth. As with ovarian development in *Flustrellidra hispida*, each large oocyte is enveloped by its own follicle. Testes are described as being paired, forming on the zooid wall in the proximal region of the cystid. Hermaphrodite zooids are rare, however. Moreover, since the author never saw mature eggs and ripe sperm together [indicative of protogyny?], he concluded that self-fertilisation is impossible in this case. He described the intertentacular organ in this species, depicting it sectioned, but Marcus (1926a) stated that he was mistaken.

Retzius (1904, 1905, 1906, 1909, 1910) investigated spermatogenesis and sperm structure in four gymnolaemate species, undertaking one of the most complete and detailed studies of the time. During the same period the prominent papers of Bonnevie (1906, 1907) were published. Working on *Electra pilosa* (as *Membranipora*) and *Membranipora membranacea*, she revealed that their colonies consist of male, female and hermaphrodite zooids throughout the reproductive season. However, all of them are actually protandrous hermaphrodites, possessing either (1) mature sperm and an early ovary, (2) mature eggs and degenerating sperm tissue, or (3) sperm and eggs together [probably ripe or maturing]. Bonnevie suggested that changes in sex proceed from male to hermaphrodite, and then to the female state in some zooids, but also that the appearance of the different gonads may repeatedly alternate during the life span of the zooid. Both gonads are said to develop from the "parietal wall of coelom" (1907, p. 567). Spermatogenic tissue develops on the lateral walls. In her study of 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 a single unit, a possible adaptation for "Polyspermie" – fertilization by several spermatozoids, suggested to occur just after ovulation. Based on sections, Bonnevie described several male pronuclei inside the egg, at first positioned close together, but then later distributed more widely throughout the cytoplasm and with a spiral shape. She speculated that clustering of spermatozoids might enhance their locomotory power, but admitted that this would contradict her own belief in either intrazooidal or intracolonial self-fertilization. Judging from her description, she considered polyspermy to be the rule, ascribing to it a special physiological function.

Additionally, Bonnevie (1907) studied ovarian structure and oogenesis of *E. pilosa*, describing eventual internal zonation of the ovary with young and mature oocytes having different shapes and concentrated in different regions (peripheral and central), and the intermediate stages. She paid great attention to 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 was said to be accompanied by its fusion with a "Nährzelle" ("nourishing cell"), "belonging to the ovarian wall" (1907, p. 585). Fusion was described as a slow process, with the nucleus of the "nourishing cell" seen in the oocyte cytoplasm for a long time afterwards. Subsequent changes in oocyte shape and germinal-vesicle breakdown were recorded at the beginning of vitellogenesis. She speculated that nucleoplasm ("cell juice") is moved

from the nucleus outside the egg membrane, forming a special hyaline layer, the nucleus itself then degrading. Meiosis begins [Bonnevie observed meiotic events and recorded a set of 11 chromosomes in *Electra pilosa*; later Temkin (1994) recorded a set of 12 chromosomes in the primary oocytes of *Membranipora membranacea*] while the mature egg is still in the ovary, but does not continue in the zooid cavity after ovulation. Further ovulated eggs increase in size, acquiring variable shapes in *E. pilosa*. This increase is presumably not growth *per se*, but rather enlargement caused by water entering the cytoplasm.

Like Silbermann (1906), Römer (1906) interpreted the early germ cell, which he called an egg, as developing within the epidermal layer of the cystid wall, not being connected with the regenerating polypide bud in *Alcyonidium* sp. (as *A. mytili*). He suggested that the main reason for degeneration of the new polypide is the development of the sex cells and growth of the embryo that later fills the major part of the zooid.

Levinsen (1902, 1909) described numerous variants of ovicells and their development in different cheilostome taxa, and introduced some basic terminology that is in common use today. He stated that the egg should first leave the zooid via its opening before entering the brood chamber. Following Jullien (1888b), Levinsen (1909, p. 66) suggested that in some species, however, oviposition should occur underneath the operculum with the help of the tentacle sheath, since there is "an inner connection" between the maternal zooid and ovicell that "form a common cavity". The erroneous statement concerning a "common cavity" was a consequence of observations made on dried and cleaned material.

In their handbook, Korschelt and Heider (1910) briefly characterized ovicell structure based on the works of Nitsche (1869), Vigelius (1884a, b, 1886), Calvet (1900) and Levinsen (1909). They pointed out the unsolved problem of oviposition, mentioning the hypotheses of Vigelius (wrongly ascribed to Calvet) and Levinsen. This question puzzled many researchers at the time, but the observations of Pergens (1889) had been overlooked. In addition to the hypotheses mentioned above, and in agreement with the idea of Nitsche (1869), Prouho (1892) presumed that there is a connection between the ovicell incubatory chamber and the visceral coelom of the maternal zooid in Cheilostomata.

Three years after Korschelt and Heider's (1910) textbook and 24 years following Pergens' (1889) paper, oviposition was observed and described by Gerwerzhagen (1913) in *Bugula avicularia*. He found that ovulation is caused by the activity of the polypide, which presses upon and pushes the ovary. According to him, fertilization occurs just after ovulation, since numerous sperm are present in the zooid 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 coelomopore]. Gerwerzhagen observed this

pore between the bases of two [dorsomedial] tentacles. Next, the everted polypide takes up a special position close to the ovicell opening, lowers its tentacles, and pushes the egg toward the brood cavity. The contradiction between the relatively large size of the egg and the small diameter of the pore is solved by the unusual plasticity of the egg, which stretches out into a narrow cord. Gerwerzhagen supposed that this process could be facilitated by the sucking activity of the ovicell itself via contraction of the muscles of the ooecial vesicle, but he could not find supportive evidence. Having accomplishing oviposition, the polypide retracts, rests for some time, and finally begins to feed again. If the polypide degenerates before oviposition, the process takes place after polypide regeneration. Gerwerzhagen noted that he once observed the two-cell stage of embryo 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 were observed inside zooids by Lutaud (1961).

Friedl (1925) made one of the first seasonal observations on the reproductive ecology of marine bryozoans, recording the presence of yolky larvae within colonies of several species and cyphonautes larvae in the plankton. Some data on the reproductive ecology of *Bugula flabellata* were documented by Grave (1930).

Marcus (1926a) investigated sexual reproduction in the ctenostome *Farrella repens* and the cheilostome *Electra pilosa*, and his observations supported the data of Van Beneden (1844a) and Bonnevie (1907). In particular, the testis was found on the funiculus and the ovary on the cystid wall, and their development was both simultaneous and nonsimultaneous in the hermaphrodite zooids of *Farrella*. The co-occurrence of mature sperm and eggs (up to ten in number) within the same zooids, inclined Marcus to accept self-fertilization, but he also recorded sperm stuck to the tentacle crown, suggesting that (1) this could be the result of simultaneous accidental release with liberation of eggs and (2) that sperm should enter the zooidal cavity (again, through the coelomopore) if cross-fertilization did in fact occur. In an attempt to observe cross-fertilization in *Electra*, Marcus put ovulated eggs and sperm in water together, but the spermatozoids died.

The ovary has been reported on the basal cystid wall in this species, often in the proximal region of the zooid. Marcus noted 10–20 mature ovarian oocytes and up to 17 ovulated oocytes of various shapes in the zooid cavity. Spermatogenic tissue develops in separate locations on the lateral and basal walls also. Marcus more than once recorded the simultaneous presence of male, female and hermaphrodite zooids in the same colony, suggesting that all were hermaphrodite but 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 "Membrana vittelina" [fertilization envelope] became visible and one polar body was recorded soon after release. In *Farrella* up to ten ovulated eggs were recorded passing through the coelomopore. Interestingly, Marcus thought that the eggs of non-brooding bryozoan species were richer in yolk than those of brooding forms.

Like Waters and Harmer, Hastings (1930) remarked on reproductive structures in her taxonomic papers. For instance, in the simultaneously hermaphrodite zooids of *Bugula uniserialis* the ovary is said to be located in funicular tissue just below the tip of the caecum, and sperm filled the proximal region of the zooid. The ovary of *Alderina irregularis* was observed to contain either four small or one large egg, and sperm and eggs were also found together in the hermaphrodite zooids of *Discoporella umbellata*. She described heteromorphic female polypides in *Thalamoporella californica* that are considerably smaller than those of other zooids, and suggested that their only function is that of oviposition. Up to four embryos are contained in the ovicells. Hastings (1932) gave information on reproduction in *Stylopoma informata* and *S. schizostoma*. She followed successive stages of egg development, noting a change in structure of the ovary wall from "ordinary" to "columnar" [cells] (p. 423) and polypide degeneration and ovicell formation in the latter species. Upon maturation of the first large egg, the polypide degenerates and the ooecium starts to grow. Egg enlargement continues during polypide degeneration. Hastings rejected as unsubstantiated the statement of Canu and Bassler (1923, 1928), that the female polypide "constructed" the ovicell in *S. spongites*. Hastings (1941) recorded simultaneous brooding of up to seven embryos in ovicells of *Scruparia chelata* [three embryos were later recorded in this species by Mawatari (1973a)], comparing the species with *Thalamoporella* and stressing the "two-valved" appearance of their respective ovicells.

Faulkner (1933) investigated the early developmental stages of the polypide in *Alcyonidium gelatinosum*, accompanied by the formation of a so-called "neoblastic morula" [early stages of ovary formation]. Sexual zooids were described as gonochoristic, occurring simultaneously in the colonies of this species. Prospective germ cells ("neoblasts") first appear in the zone of actively dividing cells of the developing polypide bud attached to the cystid wall. In this zone the epithelial layers of the zooid wall and polypide rudiment are confluent. Here, one or two "neoblasts" [presumably primordial germ cells] appear, clearly distinguished from other cells by their large size, nuclear characteristics, staining and position. They further migrate distally between the layers of the bilayered polypide bud to its apex, proliferate, and form a "cell-colony" or "neoblastic morula" (pp. 257, 263) between the epithelium of the developing caecum and adjacent mesothelial lining [future ovary wall] at the confluence of the funiculus. According to Faulkner, these totipotential cells may then either migrate through the basal membrane and participate in the development of the polypide gut (in prospective sterile zooids) or form an ovary (in the case of female zooids). Faulkner noted that Silbermann (1906) saw "neoblasts" but did not recognize them (for further discussion see Reed 1991). A more-advanced stage of ovarian development is seen when its cells [oocytes] are aligned in a linear series. Further, each oocyte is surrounded by its own follicle.

Zirpolo (1933) confirmed observations of Waters (1914), observing brooding in the tentacle sheath of the ctenostome *Zoobotryon verticillatum*. In contrast, Braem (1940) described embryos developing inside a special sac in the ctenostome *Sundanella sibogae* (as *Victorella*). Judging from his illustrations, this sac is an invagination of the zooidal body wall. The structural changes in the sac walls during brooding, together with the very large increase in embryo size, implies that he discovered a placental analogue in this species, in which the polypide degenerates and the mature embryo occupies most of the zooid cavity. Braem supposed that the embryo escaped through the narrow distal "neck" of the incubation sac. Silén (1942, 1944) found similar sacs in the ctenostome *Nolella papuensis*, describing its wall as thick when containing the large embryo and thin when the embryo is small. It seems that placental brooding is present in this species also. It should be mentioned that extraembryonic nutrition has recently been confirmed at the ultrastructural level for *Zoobotryon verticillatum* (Ostrovsky and Schwaha 2011).

Stach (1938) studied reproduction in the cheilostome "*Carbasea*" *indivisa*. According to his description, colonies included both male and female zooids, although, occasionally, oocytes and sperm were seen in the same zooid. The presence of both gonochoristic and hermaphrodite zooids might be evidence that all sexual zooids are functionally hermaphrodite (see above). The ovary, with 4–7 oocytes, was found suspended on the funiculus 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. Stach reported that, following fertilization, ovulated oocytes increase in size and have an "irregular sinuate outline" (p. 395; see also pl. 1, fig. 2). The latter illustration also shows the angular shape of coelomic oocytes. Oviposition was not observed, but 3–7 released eggs become attached to the lower surface of the zooidal operculum, each egg being surrounded by a transparent, elongated "brood-sac". These chambers are described as developing from the distal portion of the tentacle sheath [i.e. vestibulum], which forms the inner wall of the operculum. As depicted in his illustrations, each sac has a thin stalk, situated close to those of neighbouring sacs. There are some differences in the timing of embryo development, apparently depending on differences in the

timing of egg liberation. A second generation of oocytes often appears in the zooids bearing embryos. Larvae escape from the brood sac presumably through the rupture of its wall. It is possible that these "brood-sacs" are fertilization envelopes that stick to the operculum (see Ström 1977).

Brief reviews of bryozoan sexual reproduction were published by Marcus (1926b, 1940). The following "Brazilian" papers of this author are an outstanding synthesis of data from the literature and his own results on taxonomy, morphology and reproductive biology, written in Portuguese with an English summary (Marcus 1937, 1938a, 1939, 1941a, b, 1942). Marcus described zooidal polymorphism and the sequential appearance of male and female zooids in two hippothoid cheilostomes (as *Hippothoa hyalina*), calling them protandrous, and stressing that self-fertilization is impossible when male and female sex cells mature at different times (1937, 1938a). He did not see any parietal muscles [eventually discovered by Ostrovsky (1998)] associated with the ascus in female zooids and was sure that the 2–3-tentaculate rudimentary polypide could not protrude in this species. On the other hand, he did witness protrusions of 6-tentaculate rudimentary male polypides, implicating them in sperm release. Spermatozoids were discovered in the coeloms of all three zooid types [sterile autozooids and sexual polymorphs], leading Marcus to suggest that sperm go "in search of the eggs" (1938a, pp. 77, 119), perhaps migrating within a colony via pore-chambers. It is logical to suggest that alien sperm are accepted first by the expanded lophophores of autozooids, in which Marcus reported the coelomopore, but this idea seems absent from his text. He discovered spermatozeugmata in the cheilostome *Biflustra savartii* (as *Acanthodesia*), but showed (from sections) that fertilization is monospermic. In this and 16 other gymnolaemate species, Marcus noted the presence of either the supraneural pore ("póro supraneural", p. 86) or intertentacular organ. He also gave a list of species and papers in which similar observations were described.

Among his most interesting and important discoveries was precocious intraovarian fertilization [syngamy] in two ctenostomes – *Alcyonidium* sp. (as A. *mamillatum*) and *Nolella stipata* (as *N. gigantea*) – and a number of cheilostomes. As mentioned above, previous authors believed that fertilization occurs after ovulation or later. Marcus (1938a) stated that this finding explains how the timing of gonadal maturation is connected with fertilization. He wrote that a fully grown ovary in zooids without testes may already contain [alien] sperm, suggesting cross-fertilization. However, distinct protandry [in hermaphrodite zooids] "by no means indicates that there must be reciprocal fertilization" since even early oocytes can be fertilized in the same zooid by its own sperm (p. 120). From this finding it also follows that simultaneous maturation of the gametes in a zooid or colony cannot be regarded as evidence for self-fertilization if the fusion of the male and female cells is precocious [i.e. occurs before sperm maturation]. Marcus noted that syngamy happens "in the beginning of their [oocytes] second growing period" (p. 119). In fact, the diameter of fertilized oocytes measured ca. 20.0 μm in *Celleporina costazii* (as *Siniopelta*) and *Rhynchozoon phrynoglossum*, prior to vitellogenesis. In the ctenostomes *Alcyonidium* sp. and *N. stipata*, sperm was found in oocytes "which are still growing" (p. 81). Four of Marcus's figures (1938a, pl. 3, fig. 8B, pl. 21, figs 58–60) of cheilostome ovaries show previtellogenic or early vitellogenic oocytes or oocyte doublets with a male pronucleus in the cytoplasm. Sperm heads were also found between ovarian cells. Mature oocytes were described as being not completely covered with follicular cells, but partially exposed to the zooidal coelom. Oocytes were described as differing in the amount of yolk, "scarce in *Bugula*, considerable in *Hippopodina*" [oligo- and macrolecithal, correspondingly] (p. 121). Maturation divisions [Marcus obviously meant the breakdown of the nuclear membrane] began in the ovary or immediately following ovulation. In contrast with all the other oviparous species studied, *Arbocuspis bellula* (as *Electra*) "shows only one mature … egg", which is, however, "bigger than in viviparous species" (pp. 88–89, 120). It is not clear if *A. bellula* actually belongs to malacostegans since it could be an internal brooder. Confirming the data of Prouho (1892), Marcus found internally brooded embryos on the zooid wall in the ctenostomes *Nolella dilatata* and *N. alta* (reviewed in Ström 1977).

Marcus clearly understood the role of the hypertrophied epithelium in the ooecial vesicle in cheilostomes. He recognized the presence of extraembryonic nutrition in *Bugula avicularia*, comparing this species with non-placental cheilostome brooders and noting a similar finding of Waters (1913) in the cheilostome *Catenicella elegans* (as *Vittaticella*). He noted that the placenta develops after the beginning of cleavage and is reduced after larval release, and that the hypertrophied cells of the embryophore supply the embryo with a presumed "albuminous liquid" (1938a, p. 120). Marcus also mentioned enlargement of embryophore cells, previously recorded by Vigelius (1886) and Calvet (1900). His data on the sizes of mature eggs, early embryos and incubated larvae showed the possibility of extraembryonic nutrition in *Celleporella* sp. (as *Hippothoa hyalina*), *Hippopodina feegensis* and *Catenicella elegans*. However, Marcus stated that there is no such nutrition in *Catenicella contei*, again comparing the size of the egg and the embryo (discussed also in Ryland 1976). He suggested that synchronized growth of both the next egg in the ovary and the nourished embryo in the ovicell is regulated hormonally. Studying embryogenesis of *Bugula* species, Marcus recorded the formation of two polar bodies that remain within the fertilization envelope.

Marcus (1941a) described the reproductive biology of *Thalamoporella evelinae*. 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 and two opercula, separately closing the ovicell and the zooidal orifice. These were described first by Levinsen (1909) (see also Harmer (1926) and Hastings (1930)). Spermatozoids united in pairs ("twin sperm", p. 142), presumably exiting the male zooid via the coelomopore and entering the female coelom through the intertentacular organ. Insemination is intraovarian and monospermic. The ovary develops from the peritoneal cells of the basal cystid wall in the distal part of the female zooid. A follicle from the squamose cells envelops the growing oocyte situated on top of the pedunculate part ("ovarian stalk"), the central area of which Marcus compared to a "nutritive channel" (p. 41). As seen from his Plate 6, fig. 16, the pedunculate part consists of a large subovarian space with young oocyte doublets on its periphery and containing alien sperm. Marcus was the first to note that oocytes develop in pairs (he depicts an ovary with up to four doublets), in which one of the cells plays the role of nurse. Actually, he saw and depicted this phenomenon in his 1938a paper also, but did not then describe it. According to his description, in *Thalamoporella evelinae* two young oocytes fuse when both reach 20–30 μm diameter (in all other known instances, cheilostome oocyte doublets are the result of arrested cytokinesis). Shortly after this fusion, syngamy takes place with one of the oocytes [that will become an egg], whereas the second cell becomes a nurse ("cellula auxiliar", p. 36). The doublet grows, and when it reaches its final size, the nucleus of the nurse cell migrates through the cytoplasm to the vegetal pole where it is expelled, with the nurse cell becoming incorporated into the oocyte. Marcus also wrote that the oocyte could be nourished on account of the "yolk stored in the peritoneal cells" of the lateral body wall (p. 142), and by the special area of "high [hypertrophied] peritoneal epithelium on the front wall", close to or adjoining the leading oocyte. Cells of the ovary (including follicle cells) accumulate yolk (provided by peritoneal storage cells), which is further transported to the oocyte "with the help of ovarian stroma". Up to six embryos of different ages were recorded as being brooded in the ovicell. Additionally, Marcus described an intertentacular organ in *Alcyonidium polypylum*; in this species the ovary is proximal, whereas spermatogenic tissue occurs proximally and distally in hermaphrodite zooids.

In the same year, Marcus (1941b) published a paper on the cheilostome *Synnotum* sp. (as *S. aegyptiacum*), in which he discovered intracoelomic embryonic incubation (viviparity). In this species, different gonads appear simultaneously in paired gonochoristic zooids. The ovary in this case produces 2–3 oocytes, one of which develops into an embryo inside the maternal zooid whose polypide degenerates. 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" (p. 232). The late embryo is 50–60 times larger than the mature ovum – good evidence of extraembryonic nutrition.

Cori (1941) reviewed bryozoan sexual reproduction in his textbook. In general, he characterized this complex phenomenon correctly, except that polyspermy and self-fertilization were considered to be common to all Bryozoa and the ooecium was said to develop as part of the maternal zooid. 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 (1960) mentioned this, suggesting that sperm is released via the terminal tentacular pores. Cori presented one of the most comprehensive lists of bryozoan literature for this period.

Silén (1944, p. 18) investigated the ctenostome *Labiostomella gisleni* (as a cheilostome), recording more than 100 oocytes simultaneously in its very long ovary surrounded by a "very thin … film [of] flattened cells" [ovary wall]. However, he came to the conclusion that only one embryo is developed during the "breeding season" of each fertile zooid. Zooids were stated to be hermaphrodite and protogynous. Silén described different stages of oocyte growth, measured them, discussed ovulation and fertilization, and noted that ovulated oocytes accumulate in the distal part of the autozooid. He also noted the presence of a male nucleus inside them. Since no ripe spermatozoids were found in testes, he suggested that the sperm came from outside, fusing with the eggs in the distal region of the zooid. One embryo per zooid developed inside an embryo sac [presumably possessing an embryophore, see Silén 1944, text-fig. 11], 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 inward migration of ectodermal cells that overgrow and envelop the fertilized egg. In comparing this embryo sac with that found in the ctenostomes *Sundanella* and *Nolella*, he concluded that they are homologous, having the same type of development. Larval release occurred through rupture of the internal wall of the sac and further via the zooid aperture. Based on these findings and ovicellar anatomy of the cheilostome *Scrupocellaria scabra*, Silén proposed a hypothesis suggesting that cheilostome ovicells originated from an embryo sac like that in *Labiostomella* (see also Ström 1977). He also considered brooding structures throughout the phylum to be homologous, originating from a modified polypide. The cyphonautes larva was stated to be a derived larval type (see Chap. 3 of the main text).

Several years later Braem (1951), investigating the ctenostomes *Bulbella abscondita* and *Victorella muelleri* (as *Tanganella*), showed that oviposited zygotes stick either to the everted vestibulum. In *Bulbella*, the ovary is positioned on the cystid wall in the middle region of the zooid.

Some 4–6 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. Eggs separated from the maternal zooid did not develop successfully. In *Victorella*, both ovarian and spermatogenic tissue are on the cystid wall in the distal part of the hermaphrodite zooid. Eggs are numerous, but, as in *Bulbella*, mature sequentially, exiting through the supraneural pore and sinking into the special protuberance of the body wall that forms the invagination or brood sac. When the polypide is retracted, embryos (normally three) are placed in the vestibulum. Thus, Silén's suggestion concerning the method of embryo-sac formation in ctenostomes was not supported (discussed in Ström 1977). Braem (1951) also recorded brooding in the vestibulum of *Bowerbankia gracilis* (as *B. caudata*) following polypide degeneration. The ovary is located in the middle part of the hermaphrodite zooid on the cystid wall at the site of attachment of the funiculus. Spermatogenic tissue was found on the cystid wall also, but more proximally. The mature egg moves via an intertentacular pore between the degenerating mouth and anus into the tentacle sheath. From there it is presumed to pass the diaphragm to be surrounded by the vestibular wall. These findings accorded with those of Joliet (1877a) on *Walkeria uva* (as *Valkeria cuscuta*). Additionally, both ovarian and spermatogenic tissue were found on the cystid wall in the distal part of the hermaphrodite zooids of the non-brooding ctenostome *Victorella pavida*. As in other broadcasters, its oocytes are small, maturing and ovulating in cohorts; after ovulation they are irregular in shape. In addition, an intertentacular organ was found and studied in histological sections. Much confusion surrounds this broadcasting species, which is considered to be a brooder in the monographs of Hyman (1959) and Hayward (1985). This contradiction is discussed and explained by Jebram and Everitt (1982).

Despite the fact that many researchers kept bryozoans alive for long periods, there are very few published observations on their reproductive activities. In his subsequent paper, Silén (1945) documented summer observations on the reproductive biology of several gymnolaemate species under experimental conditions, comparing brooding and non-brooding species. He noted simultaneously hermaphrodite zooids in *Membranipora membranacea*. In *Callopora dumerilii* (as *C. dumerili*) (and with reference to *Escharella immersa* and *Fenestrulina malusii* (as *F. malusi*)) he observed and carefully described ovicell development, oocyte growth, ovulation and a post-ovulatory period as well as larval behaviour. Silén stated that regression of the wall of the follicle containing a mature egg is triggered by movements of the polypide caecum (see also Gerwerzhagen 1913), which further result in shifting the ovulated egg to the distal part of the maternal zooid. He described oviposition and synchronized development of the embryo and the succeeding oocyte, repeat-

ing the idea of Marcus (1938a) about hormonal regulation of this synchrony. Development of the ooecium was said to be triggered by the onset of ovarian activity through hormonal regulation also. In aquaria, it took approximately two weeks for each egg to mature in the ovary of *C. dumerilii*. Development of the embryo in the ovicell has the same duration, and these events are correlated in time. Thus, the repeated use of the ovicell (at least three times) was proven (see Joliet 1877a). 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] was found to surround an embryo in the ovicell. Since embryos could not develop outside the ovicell when experimentally released through breakage, it was concluded that the chemical composition of the fluid inside the incubation cavity differs from that of sea-water, and the ooecial vesicle must be responsible for that. The intertentacular organ and coelomopore were considered homologous and secondarily evolved structures, used not only for egg release, but possibly also for the acceptance of alien sperm. Thus, Silén tended to favour the concept of cross-fertilization. Larval release through the body wall following development in an "embryonary" [brood sac] was suggested as the primitive condition. Such a condition seems to have been found in the ctenostome *Nolella,* but that taxon also has a supraneural pore (recorded by Marcus 1938a) that Silén thought initially evolved in connection with some other function, for instance sperm entry.

Crucially, it was realized that further progress in research on bryozoan reproduction would be impossible without seasonal observations and studies of life history. Kuznetzov (1941) was one of the first to make a comparative study of the life cycles about 60 bryozoan species, and proposed the first classification based on the number of generations, periods of their reproduction and duration of life span. Four patterns were identified based on the above combination of characters. Borg (1947) undertook an investigation of the life cycle of the cheilostome *Einhornia crustulenta* (as *Electra*), using material collected throughout the year. Judging from his description, zooids are simultaneously hermaphrodite in this species. He 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 funicular strands. He described ovaries as being one or several, developing in connection with the caecum, and often referred to the paper of Schulz (1901), who also mentioned the plural nature of the ovary in this species. The maximal number of eggs in one ovary was up to sixteen. Borg recorded the presence/absence of gonads and state of the polypide throughout the seasons, suggesting a correlation between polypide cycling and sexual reproduction. Moreover, he stated that the main function of 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" (p. 375). Another of his conclusions was that the formation of an intertentacular organ is indispensably combined with polypide replacement. Later Silén (1966), studying living material, challenged this statement because he observed that this organ forms in the existing polypide upon maturation of eggs and this was further supported by Jebram (1973), Hageman (1981) and Cadman and Ryland (1996).

Corrêa (1948) studied reproduction in the cheilostome *Bugula foliolata* (as *B. flabellata*), describing colonial zonality, based on the polypide and sexual cycling. 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 [embryophore] in relation to the onset and completion of brooding. The supraneural pore was stated to occur in both fertile and sterile zooids. She also found sperm heads in early intraovarian oocytes in accordance with the findings of Marcus (1938a, 1941a), terming the eggs oligolecithal-homolecithal and stating that early and monospermic fertilization "is almost certainly realized by sperms of the same zooid" in this species (Corrêa 1948, p. 46). Intracolonial self-fertilization was also suggested. Corrêa noted slight zooidal protandry in hermaphrodite zooids. It was mentioned that 2–3 "ovocytes" simultaneously growing in the ovary have different sizes. Egg maturation was said to occur in the zooid cavity. Judging from her description, Corrêa thought that the first polar body is formed inside the zooid before transfer to the ovicell together with the oocyte. Three polar bodies ("polocytes") are shown after oviposition surrounded by the fertilization envelope, together with a zygote, in her illustrations. Remarkably, Corrêa recorded two embryos in the same ovicell at 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 *Biflustra arborescens* (as *Conopeum commensale*).

Silén (1946, 1947) discovered specialized brooding zooids ("gonozooids") with external incubation sacs in three burrowing ctenostomes in the genus *Penetrantia*. According to the original description, the wall of the brood sac is made of cuticle, but its mode of formation and exact structure are unclear. Silén termed it a "pouch of the exterior wall" (1947, p. 20), suggesting that the "gonozooid was composed of two zooids, an older, dead one and a younger, living one developed inside the former" (p. 34). Thus, the brood cavity was explained as a space between two cuticular walls – external (pertaining to the first zooid in which epithelial cells had vanished) and internal (belonging to the new zooid). However, Ström (1977, p. 34) speculated that the "brood sac" may have been a "thickened embryonic membrane"

[fertilization envelope]. Additionally, Silén (1947) described an ovary in *P. densa*, stating that the embryo begins development inside the zooid cavity, later being transferred to the incubation pouch. He suggested three possible variations for oviposition, but further research is necessary to elucidate brooding in this group. Silén (1947) also found an embryo brooded within the tentacle sheath in *Immergentia californica*.

Second Half of the Twentieth Century: Extensive Reviews and New Discoveries

Soule and Soule largely confirmed the findings of Silén in regard to Ctenostomata. A number of burrowing ctenostome brooders with both types of brooding were described in a series of papers (Soule 1950a,b; Soule and Soule 1969a, b, 1975, 1976). They focused particularly on *Penetrantia* (brooding in a "gonozoid") and *Spathipora*, *Immergentia* and *Terebripora* (brooding in the introvert). Bobin and Prenant (1954) confirmed the data of Soule, describing brooding in the introvert in *T. comma* (for information on reproduction and brooding in ctenostomes, see also Prenant and Bobin (1956), d'Hondt (1983), and Hayward (1985)).

Mawatari (1951a, b) published two papers dealing with the cheilostomes *Bugula neritina* and *Tricellaria occidentalis* (currently generally called *T. inopinata* but it may be *T. catalinensis*) respectively. In *Bugula*, zooids were described as simultaneous hermaphrodites performing self-fertilization. Mawatari studied embryogenesis, larval structure, larval release and locomotion as well as larval attachment and metamorphosis. He also presented data on the *B. neritina* life cycle throughout the year, including peaks of reproduction and larval settlement and the rate of colony growth and maturation. In *Tricellaria*, zooids were said to be non-simultaneous hermaphrodites. Mawatari (1951b) briefly described oogenesis, and it is clear from his text and illustrations that oocytes develop in pairs in this species.

The following year, Mawatari (1952) made a detailed study of *Watersipora subtorquata* (as *W. cucullata*). According to his description, zooids are simultaneously hermaphrodite, which is why self-fertilization was considered usual for this species. Spermatogenic tissue develops at 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 4–5 oocytes were said to develop within it. It is clear from Mawatari's illustrations that they are arranged in doublets. One or more sperm heads were detected in the "developing egg", but fertilization was stated to be monospermic. The large leading oocyte ovulates, "moves … under the vestibule, and is enveloped within the embryo sac" (1952, p. 20). Mawatari's figures 20–38 and 44

show the embryo sac as an evagination of the vestibulum, which is confirmed by the following description of the "hatching" larva, which "moves at first out of the embryo sac into the vestibule … through the broadened passage of the sac" (p. 22). The polypide degenerates at the onset of brooding, during which time an embryo occupies most of the zooid cavity. A new oocyte begins its growth in the ovary after larval release and polypide regeneration. Unfortunately, it is impossible to state if there is extraembryonic nutrition during brooding in this species, since the size of the eggs and embryos was not given, and scale bars and magnifications are absent in the paper. However, there is some indirect evidence, such as the appearance of the brood-sac wall during brooding and the size of the mature oocyte and larva relative to the zooid size. Zimmer (personal communication in Reed 1991) recorded that the embryo grows during embryogenesis in congeneric *W. arcuata*.

The splendid textbook of Hyman (1959) ranked among the main sources consulted by two generations of zoologists. She gave an extensive review on bryozoans (including their sexual reproduction) and a very complete list of references. However, much of the information concerning reproduction was unfortunately imprecise, wrong or incorrectly interpreted, and this part of the monograph is now mainly of historical interest. The same can be said of the text-books by Brien (1960) and Kaestner (1963). Interestingly, in discussing possible situations in which mature sperm might leave the zooid cavity, Brien cited liberation through the "pore génital" [supraneural coelomopore], the terminal pores of the tentacles (mentioning Cori's 1941 finding of sperm inside the tentacle cavity) and during polypide recycling. In the latter case, it was said that sperm could be released by the regenerating polypide, being incorporated in the brown body first. This idea is similar to the suggestions of Borg (1947, p. 375) who thought that 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 (1951) (see above), who described several different variants of brooding, and who suggested an evolutionary trend towards better protection of the embryos (reviewed in Ström 1977). Chrétien (1958) studied development of the ovary and described oogenesis in detail in protandrous colonies (with gonochoristic zooids) of *Alcyonidium diaphanum* (as *A. gelatinosum*). She recognized "cellules femelles initiales" [oogonia] (p. 29) by the presence of enlarged nuclei, lying between the epithelium and mesothelium at the proximal end of the polypide bud, at a stage when the latter comprises a hollow vesicle – the future gut and rudiment of the lophophore. Early female cells were said to be of "mesenchymatic origin", and the statement of Faulkner (1933) about their origin from the

region of polypide-bud proliferation was rejected. Following mitotic divisions and differentiation, a group of 6–10 small "young oocytes" is formed in which cell membranes were deemed to appear a little later. A similar picture was recorded by Pace (1906) in *Flustrellidra hispida*, and it is not clear if the cell membranes were absent or simply not distinguishable by light microscopy. 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 began before complete differentiation of the polypide, and nutrition was presumed to be provided by specialized caecal cells – where the ovary contacts the gut, special cells with tongue-like and papillate extensions protrude into the caecal lumen. Peritoneal cells multiply, spreading over the oocytes to form a follicle. Commencement of vitellogenesis is accompanied by further multiplication of the follicle cells, forming a double layer. Such a double-layered follicle was later recorded in *Alcyonidium hirsutum* by Owrid and Ryland (1991). Judging from Chrétien's description, fertilization should occur within the ovary, at a late stage of oocyte development. On the other hand, polypide degeneration begins before vitellogenesis starts, i.e. alien sperm should be obtained by a zooid during much earlier stages of oocyte development. Some 4–5 oocytes reach maturity, whereas the rest are aborted. Mature oocytes occupy most of the zooidal cavity, and their follicles consist of flattened cells at this stage. Chrétien carefully described vitellogenesis, starting from the successive formation of several ribosomal aggregations ("caps") by the nucleolus. Yolk granules are accumulated first at the periphery, 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 are seen in later stages using histochemistry.

Bobin and Prenant (1957) showed that polypide degeneration is connected with the maturation of the ovary in *A. gelatinosum*. Grellet (1958) investigated testis structure and spermatogenesis in *A. diaphanum* (as *A. gelatinosum*), mentioning that spermatogenic tissue is associated with the funiculus, which possibly supplies it with nutrients independently of the polypide. He also noted male germ cells in the cystid peritoneum. Ranzoli (1962) studied the cytological characters of the oocytes in *Zoobotryon verticillatum*. Matricon (1963) found that the ovary develops in connection with the polypide and brooding of 4–6 embryos takes place inside the incubation pouch, developing, after polypide degeneration, between the vestibule and degenerated tentacle sheath in *Alcyonidium polyoum*. She suggested that eggs enter the brood pouch through the newly developed ciliary funnel leading to the supraneural pore. In another paper, Matricon (1960) recorded testes developing on the lateral and basal cystid walls in this species. Banta (1968) described larval brooding in the tentacle sheath in

Bantariella cookae (as *Mimosella*). Since the volume of the embryo increases markedly during development, one can assume that extraembryonic nutrition occurs in this species. Similar enlargement was depicted by Joliet (1877a) in *Walkeria uva* (as *Valkeria cuscuta*).

Ström (1969) discovered external brooding in the ctenostome *Triticella flava* (as *T. koreni*), strongly reminiscent of the situation in *Paludicella articulata* (see Braem 1896). Later a similar type of brooding was also described in *Panolicella nutans* by Jebram (1985). However, in contrast with *P. articulata*, there are up to 20 embryos in the sticky fertilization envelopes that attach to the maternal zooid in *Triticella* (see also Eggleston 1971). Only early development takes place in such a position (Ström 1977). Ström additionally found that both testis and ovary are situated on the dorsal cystid wall in the proximal half of the zooid (with the ovary more distal). Up to 60 ovulated eggs are accumulated in the coelom prior to spawning, which occurs [via the coelomopore] between the base of the dorsal tentacles. Since spermatozoids attached to the tentacles of the expanded lophophores were detected, Ström suggested that cross-fertilization occurs in this species. He also showed that two polar bodies are formed within the fertilization envelope after egg release (Ström 1969). He additionally described larval development and ancestrula formation. Castric-Fey (1971) recorded the presence of an intertentacular organ in *Alcyonidium argyllaceum*.

Cook published a series of papers dealing with early larval development in several malacostegan cheilostomes. In *Einhornia crustulenta* (as *Electra*) and *Conopeum seurati* (as *Membranipora*) she observed formation and functioning of the intertentacular organ. In the former species Cook described deflecting behaviour of the tentacles during egg extrusion (when tentacles were deflected to a position parallel to the frontal wall). The intertentacular organ was protruded as far as possible above the surface of the colony (Cook 1960, 1962). Egg liberation through the intertentacular organ was also recorded in *Electra monostachys* and *Conopeum reticulum* (Cook 1964a). The number of eggs per zooid, their average size and the duration of egg extrusion were all measured. Cook (1964b, 1968) recorded internal brooding in the cheilostome *Steginoporella buskii* (as *Steganoporella*), noting that the polypide degenerates and the cryptocyst is strongly reduced as the egg grows. She found that there is a direct correlation between the size of the egg [called an embryo in her 1968 paper] and reduction of the zooidal cryptocyst.

Silén (1966) published a landmark paper in which he described the liberation of sperm via the terminal pores of the two distomedial tentacles in the malacostegans *Electra posidoniae*, *E. pilosa*, *Einhornia crustulenta* (as *Electra*) and *Membranipora membranacea*. The long-standing enigma of bryozoan cross-fertilization was solved, although many questions remained. All of the main events of gonado-

and gametogenesis and their duration, as well as the later destiny of the sex cells, were followed by observing live colonies kept in aquaria. In *E. posidoniae* and *E. crustulenta* colonies consist of hermaphrodite zooids that are either protandrous or, occasionally, simultaneous. There are also males developing towards the end of reproduction in *E. posidoniae*. Colonies of *E. pilosa* and *M. membranacea* were described as protandrous [i.e. consistng of simultaneous hermaphrodite zooids]. In the two former species, spermatogenic tissue develops over lateral and proximal parts of the frontal wall and on the lateral cystid walls. The ovary is placed proximally on the funiculus, and usually 8–9 (up to 20) eggs are developed in *E. posidoniae*, while six are depicted in Silén's figure 5 of *E. crustulenta*. An intertentacular organ develops only in the existing polypide of hermaphrodite zooids when they reach maturity. Evacuation of both eggs and sperm may be synchronized over large parts of the colony (observed in *M. membranacea* by Zimmer who also saw synchronous spawning among male zooids in a species of *Schizoporella* (personal communication in Reed 1991)), often involving several neighbouring colonies. However, sperm and eggs are released non-simultaneously in the same colony. Lophophores liberating sperm may sometimes remain everted for several hours. Spermatozoids from the body cavity travel along the lumina of the two dorsomedial tentacles, escape from them via their 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 surface of the tentacles then move towards the intertentacular organ at about the same time that eggs enter it in *E. posidoniae*. In *E. crustulenta*, sperm were observed inside the intertentacular organ. Silén ascribed an important role to chemotaxis as spermatozoids "search for" the egg. A fertilization envelope appears approximately 1 h after egg release. Based on these observations, Silén suggested that fertilization takes place externally in the first species and inside the intertentacular organ in the second. Nevertheless, Silén admitted that, theoretically, sperm could also enter the zooid cavity through the intertentacular organ or supraneural pore and cross-fertilization could occur in the body cavity. Returning to the earlier idea of Joliet (1877a), Silén speculated that fertilization in larviparous forms could be achieved during oviposition. Strangely, the data of Marcus (1938a), who discovered precocious intraovarian fertilization in brooding Gymnolaemata, were overlooked or ignored, despite his paper being cited. Silén's (1944) own finding of male nuclei inside ovulated oocytes in *Labiostomella gisleni* was not mentioned or discussed either.

Bullivant (1967) confirmed the data of Silén, recording sperm release through the terminal pores of all the tentacles in the ctenostome *Zoobotryon verticillatum* and the cheilostome *Schizoporella unicornis*. Except for "passive" evacuation, numerous spermatozoids were released on retraction of

the lophophore. In his second paper on the "fertilization problem", Silén (1972) added eight cheilostome and two cyclostome species to the 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. The first observations on protruded male polypides were made by Marcus (1938a) in *Celleporella* sp., in which he counted six tentacles (see above). Four tentacles were found in males of *Celleporella tongima* (as *Hippothoa*) (see Ryland and Gordon 1977). In *Odontoporella bishopi* (as *Hippopodinella adpressa*), Gordon (1968) described male polypides with four long and four short unciliated tentacles, with the characteristic "rocking" behaviour and not expanding in the usual bell shape. Carter and Gordon (2007) also described the male polypide as having a vestigial gut. Skeletally, these zooids do not differ from others, possibly developing normal feeding polypides after degeneration of the male ones. Similarly, Cook (1968) recorded heteromorphic lophophores in larger zooids, possessing three pairs of non-ciliated tentacles of different length, describing their behaviour in *Hippoporidra senegambiensis* as rapid sweeps in one plane, but in different directions, while protruded for 5–10 min. Identical behaviour of four-tentacled male polypides was recorded in *H. littoralis* (see Cook 1985). Groups of male zooids with lophophores of two long non-ciliated tentacles were also recorded in *Hippoporidra* sp.

Concerning sperm dispersal, Cook (1977, 1979) suggested that the groups of male zooids may also act as passive excurrent outlets. Chimonides and Cook (1981) observed special behaviour of the elongated lophophores of paired, unciliated tentacles in *Selenaria maculata*. These male zooids develop on the periphery of the colony, and their lophophores often protrude simultaneously in small groups. Sections confirmed the presence of sperm inside their zooid cavity. Sperm were also found in several large ovarian oocytes in the subperipheral female zooids. The zonal positioning of the differently sexed zooids corresponds with the direction of the colonial water currents – sperm should be removed from the colony without being captured by the female zooids of the same colony. Detailed reviews on sexual zooidal polymorphism in Bryozoa have been published by Silén (1977), who proposed a modified terminology, and by Cook (1979).

Franzén (1956, 1970, 1976, 1977, 1981, 1983, 1987a, b, 1998) published a series of papers and reviews on bryozoan sperm morphology and development and fertilization biology, analysing both his own results and those of others. In passing, Franzén (1977) also briefly described oocyte structure and oogenesis. Special attention was paid to comparing sperm ultrastructure in the three main bryozoan groups, Phylactolaemata, Stenolaemata and Gymnolaemata, the results of which supported the hypothesis that latter two classes are more closely related to each other than either is to the Phylactolaemata. Franzén concluded that bryozoan sperm is departs considerably from the morphology that he considered representative of the primitive condition, which is characteristic of external fertilization. According to his hypothesis, bryozoan sperm morphology is indicative of internal fertilization. Franzén (1956, 1998) confirmed Bonnevie's (1906, 1907) findings on the presence of spermatozeugmata in *Membranipora membranacea* and *Electra pilosa*. Reger (1971) and Zimmer and Woollacott (1974) studied aspects of sperm ultrastructure in *Bugula* sp. and *Membranipora* sp., respectively, and it was shown that spermatozeugmata consist of 32 or 64 spermatozoids in *Membranipora*.

Woollacott and Zimmer (1972a) redescribed the placental analogue and confirmed the data of previous authors on ooecial development from the distal zooid in *Bugula neritina* (see discussion in Chap. 2). Woollacott and Zimmer (1972b, 1975) also 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 cells of the funicular strands, presumably transporting nutrients for embryo development. Cells of the embryo adjacent to the embryophore are said to differentiate for nutrient uptake. 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 of the basal ends of the hypertrophied cells, which 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 the embryophore) and infoldings (in the embryo) and performing exo- and pinocytosis, respectively. 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 occurs through the cuticle of the ooecial vesicle, inferring diffusion or an osmotic-gradient mechanism. The fertilization envelope surrounding the early embryo was not evident at an advanced stage. The embryo increases ca. 500-fold in volume during brooding. Woollacott and Zimmer (1975, p. 363) also identified three reproductive patterns "(planktonic, lecithotrophic and placenta-like)" in Bryozoa.

In the 1960s and 1970s, research on bryozoan reproductive anatomy and behaviour was extended by the addition of ecological studies (Kawahara 1960; Gautier 1962; Ryland 1963; Abbott 1973, 1975; Hayward and Ryland 1975 – reviewed in Ryland 1967, 1970, 1976, and Soule and Soule 1977). Among others are the papers of Gordon (1970) and Eggleston (1963, 1969, 1972), who undertook investigations on bryozoan reproductive ecology, studying their breeding

seasons in particular and life cycles in general. Gordon recognized three "breeding patterns" among 23 species of New Zealand intertidal bryozoans, depending on the season and duration of the reproductive activities. He also made an attempt to classify their "brooding habits". Interestingly, in dissected ovicells of *Macropora levinseni* (as *Macropora grandis*), Gordon found 2–4 simultaneously brooding embryos. Eggleston studied life cycles and reproductive patterns (terms and duration of reproductive season and colony longevity), recording gonadal activity, brooding, spawning and larval settlement in more than 50 species from the Isle of Man. He divided them into four groups (those living less than a year, annuals, biennials and perennials), depending on colony longevity and the number of breeding/non-breeding generations presented through the seasons. Interestingly, Gautier (1962), who studied Mediterranean bryozoans, found that seasonality is reflected in reproduction to depths of 20 m, whereas, at greater depths, the same species were breeding for the most of the year. Eggleston (1972) showed that the number of embryo-bearing zooids in the colony, the size at which the colony starts reproduction, embryo size and the rate of embryo development are related to the length of the breeding season and colony longevity. In general, shorter 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 length of the breeding season and the longevity of the colony. Most nearshore species have a short breeding period that is probably connected with the variability of the shore environment. Eggleston also suggested that internally brooded embryos are better protected against environmental variations, so internal brooders frequently occur in the upper intertidal, where they are often exposed to drying. In *Bicellariella ciliata*, Eggleston described sexual colony zonation (sometimes repeated), and discovered external brooding in the "membrane sacs" of *Eucratea loricata* along with internal brooding of several embryos simultaneously in *Oshurkovia littoralis* (as *Umbonula*). Internal brooding in this species was first recorded by Hastings (1944), subsequently using the term "internal ovisac" (Hastings 1964).

Dudley (1973) observed reproduction in the cheilostome *Conopeum tenuissimum*, recording the timing of gonad appearance and the subsequent gamete release. Zooids in this case are protandrous hermaphrodites, with the intertentacular organ developing after the first polypide cycle. Mawatari (1975) and Mawatari and Mawatari (1975) studied a similar life cycle in *Membranipora serrilamella*. Zooids are protandrous hermaphrodites. Testes develop just beneath the lateral and proximal region of the membranous frontal wall, whereas the ovary develops in the distal half of the zooid [the wall is not specified], and they recorded more than 40 ovulated eggs per zooid. Two or more eggs are usually found in the intertentacular organ during their release.

Accidentally swallowed eggs are defaecated soon afterwards. A fertilization envelope is formed after the liberation of the zygote, which transforms from a flattened circular disk to a sphere with a diameter about half the size of the disk. Interestingly, despite their numerous observations, they failed to observe polar bodies, suggesting that these break away and degrade at an early stage in this species.

Ryland (1970, 1974, 1976, 1982) reviewed sexual reproduction in Bryozoa, including all major discoveries made subsequent to Hyman (1959) and identifying the most important unsolved problems. Ryland (1976) characterized in detail three reproductive patterns outlined by Harmer (1926) and Woollacott and Zimmer (1975), and suggested that byproducts from the degenerated polypide could be used for extraembryonic nutrition. Among the most interesting of Ryland's conclusions based on Marcus's (1938a) findings is that there are different methods of brooding, with or without placental nutrition, among related groups, sometimes within the same genus. He also usefully summarised available data on the increase in larval volume during placental brooding. Describing the pattern of oogenesis of *Callopora dumerilii* based on Silén (1945), he wrote that the oocyte enlarges in the ovary, attaining a size of 120 μm, then ovulates into the coelom where it continues to expand until it reaches 200 μm Theoretically, such an increase might be achieved through absorption of water, which is possibly the case for broadcasting species but there is no evidence in the literature that this is also true for brooders.

One of the most valuable sources of the heterogenous information concerning parental care in Bryozoa was published by Ström (1977) in a comprehensive review of brooding in the Gymnolaemata. Cheetham and Cook (1983) gave a short review of brooding in Gymnolaemata in the *Treatise on Invertebrate Paleontology*.

Several important papers on bryozoan sexual reproduction were published in the 1980s. Nielsen (1981) undertook a complex study, working on *Pacificincola insculpta* (as 'Hippodiplosia') and *Fenestrulina miramara* (as *F. malusii*). He recorded the duration of synchronized events, including oocyte growth, oviposition and embryo development in repeated succession. In gonochoristic *P. insculpta*, maturation of the first oocyte ends with degeneration of the feeding polypide, which is replaced by a new dwarf, non-feeding one. Oviposition, which lasts less than a minute, occurs beneath the closed zooidal operculum, so the coelomopore was not observed. The egg is only slightly deformed during its passage to the ovicell, becoming about 2–3 times longer than its diameter. In *F. miramara*, oviposition is provided by the normal protruded polypide, generally as described by Gerwerzhagen (1913) and Silén (1945). However, the actual transfer takes place much faster than in other species, with the egg "suddenly squeezed through the pore into the ovicell almost without becoming deformed" (p. 114). In turn, this differs from

Pergens's (1889) observations on congeneric *F. malusii*, in which oviposition was described as being accompanied by strong compression of the egg, occurring when the polypide degenerates. Additionally, Nielsen found distal zooids with two ovicells (their formation being induced by maternal zooids from two different colonies), confirming the suggestion of Silén that the oncet of oogenesis triggers ovicell formation.

Jebram and Everitt (1982) corroborated Braem's (1951) results on reproduction in the ctenostomes *Bulbella abscondita* and *Victorella*. Like *V. pavida*, non-brooding *V. pseudoarachnidia* also has an intertentacular organ. A coelomopore and the brooding of up to six embryos in body-wall invaginations were also described in *Tanganella appendiculata*, similar to the situation in *Victorella muelleri*.

Dyrynda and coworkers successfully combined anatomical, ultrastructural and ecological research, studying bryozoan sexual reproduction. Following Marcus (1941b), intracoelomic brooding was discovered in the cheilostome *Epistomia bursaria* (Dyrynda 1981; Dyrynda and King 1982). Its colonies are hermaphrodite with gonochoristic zooids, the females being larger and rarer than males. There is only one polypide generation in each zooid, and the polypide in male zooids persists 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 2–4 zooid pairs. Each female produces only one larva. A TEM-study was undertaken to investigate both spermato- and oogenesis. The testis develops proximally on the axial funicular cord and all nutrients for spermatogenesis are probably developed intrazooidally, since it ceases when the polypide degenerates. The ovary is also associated with the funicular cord, but, in contrast with the testis, it becomes established in the distomedial corner and its nutrient supply is intrazooidal during oogenesis and mainly extrazooidal during embryogenesis, although the by-products of polypide cycling may perhaps be used. A single small alecithal oocyte matures by the onset of polypide degeneration. It is surrounded by "follicle" or "nurse" cells that are presumably of germ origin, suggested by the presence of cytoplasmic bridges between the oocyte and the "follicle" cells. In the inferred initial syncytial cluster of germ cells, the central one may differentiate into the oocyte, whereas the rest may become the "follicle" ("nurse" cells in their plate 2 caption). Fertilization is intra-ovarian, since cleavage of the embryo begins inside the "follicle". Extraembryonic nutrition is obvious – the embryo increases about 1,000-fold in volume and the axial funicular cord hypertrophies during this time. Additionally, if the polypides of the neighbouring zooids degenerate, the embryo fails to develop. Self-fertilization was assumed – isolated colonies are able to produce embryos. 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 (see Chap. 1 for the critical analysis of this hypothesis).

Dyrynda (1981) also gave a brief description of the reproductive cycle of *Chartella papyracea*, noting the formation of an "oocyte nurse cell syncytial duplet" (p. 78). Dyrynda and Ryland (1982) published an excellent paper comparing the contrasting reproductive strategies and life histories of brooding non-placental *C. papyracea* and placental *Bugula flabellata* in detail. Colonial and zooidal sexual changes were described in relation to seasonality and polypide cycling. It was suggested that the interrelationship between polypide and sexual cycling controls nutrient budgeting for sexual and other processes within zooids and the colony. Sexes are separate in *C. papyracea*, with male zooids appearing first. Fronds, however, are hermaphrodite since females develop at the end of the first reproductive season. The switch from the male to female zooid production coincides with the summer peak of water temperature. Nutrient-intensive stages of gametogenesis (late spermatogenesis and late vitellogenesis) take place only in the presence of a feeding polypide in a zooid, 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 life of the next polypide. As soon as the second 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 if the new testis is established or the old one is renovated. A cluster of female germ cells is said to develop "in the coelom [of the female zooid], opposite the first polypide bud" (p. 248) where it is suspended by funicular cords as seen in their figure 6A. It should be mentioned that Grant (1827) and Vigelius (1884a, b) wrote that the ovary develops on the zooid wall in species of Flustridae (see above). In contrast, it seems that the ovary of *C. papyracea* develops in association with the polypide bud, then migrates towards the middle of the lateral cystid wall to establish an ovary and the ovicell is formed at the same time. Oocytes develop in doublets, which, in contrast with the description of Marcus (1941a), was stated to be the consequence of arrested cytokinesis, not cell fusion (see also Dyrynda and King 1983). The polypide starts to feed when the first doublet appears. Previtellogenic growth takes place through the rest of the polypide cycle. Vitellogenesis commences during polypide cycling, speeding up when the next polypide starts to feed. This polypide transfers the ovulated egg to the ovicell as described by Gerwerzhagen (1913) and Silén (1945). Following oviposition, the polypide degenerates and the ovarian cycle is repeated with 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 musculature and innervation of the ooecial vesicle are part of the cystid. Ovaries regress in winter when polypides fail to regenerate in the female zooids, sex reversal taking place the following spring with spermatogenic tissue developing in many. The authors suggested that in normal female zooids the ovary produces a factor that suppresses male cells, thus female autozooids may not be gonochoristic after all.

In *Bugula flabellata* mature sperm and an egg that develops into a larva are produced by each polypide generation, including the first, in hermaphrodite autozooids. Protogyny prevails; the egg matures more or less half way through the life of the polypide, whereas sperm mature just before the polypide degenerates. The ovary is situated on the basal wall in the proximal part of the zooid, with spermatogenic tissue on the lateral and proximal transverse walls. Oocytes grow in pairs [oocyte doublets]. The ovicell completes its formation as the first egg ovulates, both events occurring halfway through the life of the first polypide. Following oviposition, the egg receives extraembryonic nutrition via a placenta, thereafter increasing about 6.5 times in volume, much less than in *B. neritina* as described by Woollacott and Zimmer (1975). 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 and prior to ovulation of the next egg. The authors suggested that the evolution of placental brooding provides uninterrupted extraembryonic nutrition throughout polypide cycling by "spreading the nutrient demands" over two polypide generations (Dyrynda and Ryland 1982, p. 255). Whilst there is no feeding polypide in the fertile zooid, extraembryonic nutrition can be provided from the degenerated-polypide resouces accumulated in "peritoneal nutrient storage cells". According to their suggestion, all this corresponds with the need to maximise larval productivity in species with ephemeral colonies.

The above research was aided by a light- and TEM-microscopic study of spermato- and oogenesis (Dyrynda and King 1983). In *Chartella papyracea* the initial cluster of female germ cells is established in the maternal coelom on funicular cords but later migrates to the lateral wall. The enlarged oogonium divides into an oocyte-nurse-cell doublet, the cells of which are identical in structure and connected by an intercellular bridge. Each doublet is enclosed by follicle 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 middle vitellogenesis, yolk platelets (described as autosynthesized yolk) appear throughout the oocyte cytoplasm, the oolemma forms numerous microvilli with pinocytotic vesicles (described as a source of heterosynthesized yolk) between their bases and the vitelline

envelope begins to form. Pinocytosis ceases during the middle vitellogenic stage, microvilli are withdrawn, and the "vitelline coat" differentiates into two layers prior to maturation. The nurse cell also performs pinocytosis between its microvilli and has a vitelline envelope. It produces ribosomes that are transported to the sibling via the cytoplasmic bridge. It additionally forms protein platelets but there is no evidence of their transport. The follicle epithelium is described as differentiating into two layers of squamous (inner) and columnar (outer) cells, the latter performing the synthetic activity. Sperm heads were recorded in both pre- and vitellogenic oocytes. Cytokinesis occurs during ovulation, after which the nurse cell and follicle cells degrade. The mature telolecithal oocyte contains numerous protein platelets and lipid inclusions. Prior to transfer to the ovicell, it envelops the terminal parts of the gut and is constricted to a diameter of approximately 10 μm (from 140 μm) during its passage through the supraneural pore. Brooding is non-placental, so the embryo is of the same size as the mature egg. The ovarian cycle is similar in *Bugula flabellata* and oocytes develop in doublets that are connected by the cytoplasmic bridge and a series of plate desmosomes. Both cells of a pair are surrounded by a vitelline envelope, form microvilli and perform pinocytosis. The nurse cell produces a 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*. Notably, there is also a striking difference between the flustrid *Chartella membranaceotruncata* and the bugulid *Bugula calathus* in the number of ovary cells, as first recorded by Vigelius (1886). Both auto- and heterosynthesized sources of yolk are suggested. Egg volume increases about 29-fold during vitellogenesis, and embryo volume enlarges by about seven times during placental brooding. Nutrient storage cells were discovered, being associated with the peritoneum, funicular cords and gonads. It should be noted that the mature egg is described as telolecithal in *B. flabellata*, as shown in the figures. Reed (1991) termed eggs of this species "small mesolecithal".

Additionally, Dyrynda and King checked 28 cheilostome species, recording embryo enlargement only in bugulids (*Bugula* and *Bicellariella*). In contrast with *Bugula neritina*, in which the embryo grows about 500 times larger (Woollacott and Zimmer 1975), the increase factor varied between 7.1 and 32.7 in other species; in general, the larger the egg the lesser the nutrient input during the embryonic stage.

In his unpublished Ph.D. dissertation, Hageman (1983) described the ultrastructure of the ovary and oogenesis in *Membranipora serrilamella*. In this malacostegan species spermatogenic tissue develops as diffuse clusters of spermatogonia from the coelomic peritoneum on the lateral and basal walls in protandrously hermaphrodite zooids. Earlier, Mawatari and Mawatari (1975) reported that the spermatogonia develop

beneath the frontal membrane in this species. 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 ovary wall consists of follicle cells of peritoneal origin, enveloping the oogonia and oocytes, and there is a 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 peritoneal origin also]. In the peripheral germinal zone, follicle cells completely surround the oogonia and early previtellogenic oocytes, which remain connected by cytoplasmic bridges after oogonial divisions. Hageman suggested that follicle cells may regulate vitellogenesis by compartmentalizing the ovary, synchronizing oocyte differentiation and transporting low-molecular-weight precursors or metabolites. Interestingly, it was also shown that follicle cells phagocytose degenerating oocytes. In the central growing zone, the follicle epithelium is not complete basally, and oocytes at various stages of vitellogenesis are in contact with the subovarian space. Additionally, early vitellogenic oocytes share gap junctions with the overlying follicle 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 apical zone, forming microvilli on that part of the surface exposed to the coelom. A similar situation was described by Hughes (1987) in *Celleporella hyalina* (see below). Upon breakdown of the germinal vesicle, the mature oocytes ovulate, with up to 25 accumulating in the zooid cavity. Ovulated eggs and spermatozeugmata are transported to the base of the lophophore by the ciliated pharyngeal gutter that forms 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 floor of the gutter into the base of the two-chambered intertentacular organ. It forms at the onset of oogenesis from the epithelium of the two dorsomedial tentacles and is completed in approximately 2 days. This process does not involve polypide replacement.

Hayward (1983) reviewed bryozoan oogenesis. Despite the relatively paucity of papers consulted, he correctly pointed out the existing imbalance in research on bryozoan reproduction. Whereas spermatogenesis, embryology and larval morphology had attracted considerable attention, the processes of oogenesis and fertilization were relatively understudied. Even today, 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, including variations in the site of origin and final position of ovaries, the temporary relationship between the appearance and development of the polypide bud and early ovary, the actual source of ovarian cells and the poorly known cytology of the ovary. He presented sections of the female gonad of *Alcyonidium hirsutum* for comparative purposes.

Jebram (1985) described the ctenostome *Panolicella nutans* as a protandrous hermaphrodite. [Actually, this bryozoan was described a little earlier by Kayser (1984), who gave some information on reproduction.] Spermatogenic tissue develops on the basal wall in the proximal part of the zooid and the ovary on the funiculus at the end of the caecum. The ovary contains several oocytes that mature sequentially and exit through the supraneural pore. The maternal zooid simultaneously broods 4–5 embryos that are externally attached to the maternal cystid wall 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. The distalmost egg can be withdrawn and sheltered inside the vestibulum during polypide retraction. Judging by the time of appearance of the "perivitellar membrane" [fertilization envelope], Jebram suggested that fertilization takes place during egg release.

Hughes (1987) 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-microscopic 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 cells providing placental nutrition [embryophore]. Oocytes develop in doublets, being surrounded by squamous follicle cells in at least the 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. Hughes suggested that the source of nutrients could be certain peritoneal cells with numerous yolk-like inclusions, presumably representing nutrient-storage cells. In fact, these cells belong to the funicular tissue forming part of the embryophore. Sperm heads were found among ovarian cells, and syngamy is suggested to occur during the previtellogenic or vitellogenetic phase of development. However, the route of the sperm to the ovary was not explained, since Hughes thought that the rudimentary female polypide could not protrude. The mature macrolecithal oocyte fills most of the coelom, accumulating many large yolk inclusions.

Following oviposition, the embryo increases in volume 15.6 times, receiving extraembryonic nutrition in the ovicell. Initially it is not in contact with the distal wall of the maternal zooid, which consists of hypertrophied embryophore epithelium covered with a two-layered cuticle. Despite this barrier, soluble nutrients are obviously released to the fluid in the brooding space, where they are taken up by the embryo. There is no evidence of pinocytosis in the early embryo surrounded by its fertilization envelope, but uptake is clearly evidenced in the mature embryo by the highly microvillous cell surface between the ciliary bases. Cilia fill the space between the embryophore and the late embryo in which the fertilization envelope is no longer seen. Finally, Hughes suggested that ovicells evolved as merely protective structures, later transforming into a site for accessory nutrition in some species.

A number of papers on cheilostome life cycles and reproductive ecology were also published in the 1980s and 1990s. Researchers included Winston (1982, 1983, 1985, 1988) Jackson and Wertheimer (1985), David Hughes (1989), d'Hondt (1994), Roger Hughes and coauthors (Hughes and Hughes 1987; Hunter and Hughes 1993; Hunter et al. 1996; Wright and Hughes 2002) and Cancino with coauthors (Cancino 1986; Cancino and Hughes 1987; Cancino et al. 1991), who mainly worked on *Celleporella hyalina*. Experimental studies by the latter authors on isolated colonies of two species showed that self-fertilisation was either impossible (oogenesis failed to complete in *Membranipora isabelleana* or never started in *C. hyalina*) (Cancino et al. 1991) or led to frequent embryo abortion and reduced offspring fitness (Hunter and Hughes 1993). Inbreeding capability resulting in normal progeny was recorded only within the *Celleporella angusta* clade (Hughes et al. 2002a; Hughes and Wright, in press). Finally, it was concluded that outbreeding is the rule in this species and occasional selfing might be connected with reduced opportunity for outbreeding in some instances. Sperm liberation (often synchronous in stagnant or low-flow conditions) from the central, longest tentacle of male zooids was observed, their lophophores bending to release sperm towards the exhalant currents of adjacent feeding lophophores. Evidence was obtained that *C. hyalina* might store alien sperm (Hoare et al. 1999; Hunter and Hughes 1995; Manríquez et al. 2001). Moreover, the mechanisms of allosperm storage and translocation were already present at the three-zooid stage of astogeny: colonies consisting merely of the ancestrula and two autozooids obtained and stored alien sperm, using it to fertilize eggs for a maximum period of 3–6 weeks (Hughes et al. 2002b). Returning to the earlier idea of Marcus (1938a), it was suggested that sperm can migrate through the colony from autozooids to females via communication pores, using the funicular system (Manríquez et al. 2002). Further research revealed that egg growth is absent in reproductively isolated colonies, and allosperm is a trigger of vitellogenesis (Bishop et al. 2000). Additionally, it was shown that some of the basal and frontal autozooids become male after polypide cycling in *Celleporella hyalina* (Cancino and Hughes 1988). Similar changes, presumably connected with polypide recycling, were described by Rogick (1956) and Powell (1967b) in *Antarctothoa bougainvillei* and *A. delta* (both as *Hippothoa*), respectively. Sex reversal also sometimes happens in *A. bougainvillei*: some female zooids change to males. In both cases, these events involve obvious skeletal changes.

More recent publications include those by Wood and Seed (1992) on reproduction in the ctenostomes *Alcyonidium hirsutum* and *Flustrellidra hispida* growing together on algal fronds and Barnes and Clarke (1998) on seasonality of polypide cycling and sexual reproduction in three Antarctic cheilostomes. A review on the reproductive strategies of epialgal bryozoans was published by Seed and Hughes (1992).

Reed (1988) investigated reproduction in the ctenostomes *Bowerbankia gracilis* and *B. aggregata* (as *gracilis* var. *aggregata*) in detail, greatly supplementing the original observations of Braem (1951). Both spermatogenesis and oogenesis were described. Autozooids are protandrous hermaphrodites, developing their gonads asynchronously. Thus, there may be functional male and female zooids within the colony at the same time. Spermatogenic tissue develops on the proximolateral cystid wall in connection with a funicular cord. However, it sometimes covers the caecum and gizzard of the polypide. Formation of the ovary occurs during polypide degeneration and is accompanied by the appearance of a ciliated gutter that will be involved in ovulation and oviposition. Ovary development on the lateral cystid wall is served by a funicular strand and is not directly associated with the degenerating polypide. However, it is suggested that nutrients can be transferred from the polypide to the ovary via the funiculus. The mature ovary is said to contain 1–2 vitellogenic [macrolecithal] and several previtellogenic oocytes that develop sequentially. The ovary wall consists of squamous (enveloping previtellogenetic oocytes) and cuboidal (enveloping vitellogenetic ones) follicle epithelium. Using TEM, Reed described the ultrastructure and the changes occurring in the oocytes and follicle cells during oogenesis. It was shown that, during the vitellogenetic phase, the follicle cells are enlarged and transform from squamous to cuboidal, actively producing and secreting proteinases into the narrow space around the vitellogenic oocyte, which is consumed by endocytosis. Reed (1991) noted that the follicle epithelium may synthesize yolk precursors or modify them. He suggested that the oocyte might also be able to synthesize yolk. Ovulation is accompanied by the activity of the ciliary gutter that further transfers the egg to the tentacle sheath, presumably via the supraneural coelomopore. Similar organs were described by Matricon (1963) in the ctenostome *Alcyonidium polyoum*

and Hageman (1981, 1983) 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 (1877a) in *Walkeria uva* (as *Valkeria cuscuta*) and *Bowerbankia imbricata*. However, Temkin (1996) showed intracoelomic fertilisation in *B. gracilis*.

In a similar study by Owrid and Ryland (1991), the main features of gonado- and gametogenesis in the ctenostome *Alcyonidium hirsutum* were revealed. This species is a protandrous hermaphrodite 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 bud of the newly developing polypide [presumably 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 follicle cover surrounding young oocytes. Where the ovary contacts the gut, special cells with tongue-like parts protruding into the caecal lumen were found. These cells were recorded first by Chrétien (1958) who studied *Alcyonidium diaphanum* (see above). Owrid and Ryland 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 funicular strands instead]. Increase in the size of the ovary during vitellogenesis is accompanied by degeneration of the polypide; it disappears when the ovary attains its full size. At the end of vitellogenesis the follicle layer becomes very thin and a new small polypide without tentacles is developed. A similar process was described by Joliet (1877a) in *Walkeria uva* (as *Valkeria cuscuta*) (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 to or just after oviposition. Some 4–11 larvae are brooded simultaneously. Cadman and Ryland (1996) studied reproduction in *Alcyonidium mytili*. They showed that the ovary develops on the funicular cord and confirmed the presence of an intertentacular organ that forms in the existing lophophore.

Four reviews on bryozoan sexual reproduction appeared during the 1990s. Nielsen (1990) 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" (p. 185).

Reed's (1991) review, despite the inevitable inaccuracies associated with large gaps in our knowledge, is the most complete compilation of this topic at present. In addition to the descriptions and examples presented, Reed widely discussed and interpreted the bryozoan data, comparing them with other invertebrate groups. In particular, he arranged the 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. Of special interest are the data from the Hageman's (1983) Ph.D. dissertation; except for one short note (Hageman 1981), he never published the results of his studies on the cheilostome *Membranipora serrilamella*. Brief account of bryozoan sexual reproduction was included in the book chapter of Mukai et al. (1997).

A detailed review of fertilization in hermaphrodite colonial invertebrates was published by Ryland and Bishop (1993). Inter alia, they mentioned some of the findings in the unpublished Ph.D. dissertation of Temkin (1991), who achieved bringing to reproduction isolated colonies of *Membranipora* sp. Cancino et al. (1991), on the other hand, did not achieve this in *Membranipora isabelleana*, which failed to complete oogenesis in isolation (sexual zooids are markedly protandrodrous in this species – sperm and mature oocytes were never observed to occur simultaneously in the coelom – however zooids with either sperm or oocytes co-occurred in the same colonies). Temkin's results accorded with those of Maturo (1991a). Six gymnolaemate species produced larvae in his experiments 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 at all existing, might be used in an "emergency" situation. Precocious insemination and the ability to store sperm (Hughes et al. 2002b) mean that it is important to carefully isolate colonies grown from ancestrulae early in their development in future experiments.

The excellent experimental work on bryozoan fertilization conducted by Temkin (1994, 1996) 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 tail-first via the terminal pores of the two distomedial tentacles into the exhalant current created by the colony. Temkin suggested that this should increase the chances for sperm to be removed from the colony (thus preventing intracolonial self-fertilization), for which purpose the tips of the distomedial tentacles bend towards the exhalant current. [Silén (1966) thought that releasing sperm through the tentacle tips would position them beyond the feeding currents of the parent zooid.] Being entrapped by the feeding currents of another lophophore, sperm attaches to the tentacles and performs undulating movements (although sperm are sometimes ingested, rejected with food particles or ensnared in the tentacles). Those spermatozeugmata that are attached near the

distal opening of the intertentacular organ enter it head-first using a "random search process" (Temkin 1994, p. 151). The intertentacular organ actively regulates the passage of the spermatozeugmata to the zooidal coelom, closing its opening. However, it does not discriminate between allosperm and its own sperm (produced by the same colony). Spermatozoids were been found on the ovary surface and egg-sperm fusion was said to happen during or shortly after ovulation. Nuclear-envelope breakdown appears to happen about the same time. A polyspermic oocyte containing at least 14 sperm nuclei was observed on one occasion (see discussion of Bonnevie's (1907) paper above). Temkin described egg release, activation, maturation and karyogamy in detail. Delayed activation was considered a possible adaptation for liberation/oviposition of the egg through the small supraneural pore.

Temkin (1996) studied fertilization in two ctenostome and seven cheilostome species. Intraovarian monospermic sperm-egg fusion was found in all nine species. In both egg-broadcasters studied, *Alcyonidium* sp. and *Electra pilosa*, sperm fuses with late-stage ovarian oocytes after germinal-vesicle breakdown at or near ovulation. In the ctenostome brooder *Bowerbankia gracilis*, sperm were found only inside late-stage ovarian oocytes before germinal-vesicle breakdown. Temkin suggested that the rupture of the follicle-cell layer may expose the oocyte to sperm, perhaps explaining why only late-stage ovarian oocytes contain a sperm nucleus in this species. However, Marcus (1938a, p. 81) wrote that in the ctenostomes *Alcyonidium* sp. (as *A. mamillatum*) and *Nolella stipata* (as *N. gigantea*), "we have verified the presence of spermatozoids in ovocytes which are still growing". Chrétien's (1958) results may indicate early intraovarian fertilization in *A. diaphanum* since polypide degeneration begins before the onset of vitellogenesis (see above).

Sperm fuses with early ovarian oocytes in all the cheilostome brooders studied by Temkin (1996). He described oocyte doublets and illustrated cytoplasmic bridges between nurse cells and their siblings in some species. Only one cell of each oocyte doublet is fertilized, and it will become an egg. Sperm tails and midpieces were found being resorbed in the oocyte cytoplasm (in *Watersipora arcuata*) or outside the oocyte (in *Dendrobeania lichenoides*). There is only one vitellogenic doublet in each ovary, but other previtellogeneic doublets may all possess sperm. Ovaries were described with squamose, cuboidal or columnar cells. Spermatozoids were suggested to enter the maternal coelom through the intertentacular organ or supraneural pore, accumulate on the ovary surface and later move among the cells of the ovary. All these findings show that internal fertilization is the rule in Gymnolaemata, providing high levels of fertilization success. Additionally, Temkin counted the number of the oocytes/oocyte doublets in ovaries and measured them. He later published the

results of his experimental study on the movements of the spermatozeugmata in *Membranipora membranacea* (Temkin 2002; Temkin and Bortolami 2004).

The same species was used in experiments conducted by Harvell and Helling (1993). They demonstrated large localized shifts (acceleration) in the timing and pattern of reproduction in response to simulated damage by predators (trimming the colony periphery) and overgrowth by conspecific neighbouring colonies.

Santagata and Banta (1996) investigated brooding in the cheilostome *Scrupocellaria ferox*. They discovered an embryophore, consisting of hypertrophied epithelium and funicular cells, 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. They also investigated ovicell anatomy in this species and proposed the hypothesis that vestibular brooding preceded ovicellar brooding (see Chap. 2 for critical analysis).

Ostrovsky (1998) studied ovicell anatomy and reproductive patterns in *Cribrilina annulata* and *Celleporella hyalina*. Both species are protandrous colonial hermaphrodites with sterile, male and hermaphrodite (dwarf and normal) autozooids in the first case, and sterile, male and female (both dwarf) autozooidal polymorphs in the second. It was discovered that dwarf zooids are hermaphrodite autozooids, not females in *C. annulata*, and their "dwarfism" is not connected with sexuality as Powell (1967a) thought. This species was stated to have reproductive pattern II. The presumptive ovary contains two large female cells that might be either oogonia or the first oocyte doublet, surrounded by peritoneum and associated with the proximal part of a differentiating polypide bud. The completely formed ovary is located on the basal cystid wall associated with the funicular cord. The complete female gonad contains up to six oocyte doublets (one being vitellogenetic) and the mature oocyte is macrolecithal-telolecithal. The ovary wall consists of columnar cells in its lower and squamous cells in its upper part. Columnar epithelium surrounds the central area [intraovarian space] of the polygonal [basal] cells, with numerous intercellular spaces. *Celleporina hyalina* was stated to have reproductive pattern III (but see Chap. 1 of the main text). A pair of oogonia develops in association with a polypide bud. The mature ovary consists of polygonal cells and is suspended on the funicular cords. It contains up to three oocyte doublets and the mature oocyte was described as microlecithal-homolecithal, contradicting the illustrations and description of Hughes (1987), who found macrolecithal eggs in this species. Subsequent research has confirmed the data of Hughes (see Chap. 1). Sperm are frequently found among ovarian cells in both species studied. Insemination is precocious, spermatozoids fusing with early previtellogenetic oocytes. Syngamy and egg activation are delayed, based on the finding of sperm heads in late oocyte. Muscles were

found associated with compensation sac in female polymorphs of *C. hyalina*, suggesting a possible mechanism for oviposition through the genital pore. Sperm-like bodies have been found inside the ooecial coelomic cavity in *C. hyalina*, supporting the idea that sperm can travel through the colony (discussed in Chap. 1). Additionally, an unknown intracellular parasite was encountered in oocytes of *C. annulata*.

Recent Works

Apart from the above-mentioned works of Hughes and coauthors, among recent publications there are several works by Ryland and Porter with coauthors (Ryland and Porter 2000, 2006; Ryland 2001; Porter et al. 2001; Porter 2004; Porter and Hayward 2004; Kuklinski and Porter 2004) on the ctenostome genus *Alcyonidium*. The authors distinguished the type of reproductive pattern by the presence of intertentacular organs, lipid globules in autozooids or brooded embryos in thirteen congeneric species, revealing some unusual aspects of their reproductive biology. For instance, in several species numerous small eggs were recorded in the absence of an intertentacular organ. Either the intertentacular organ was not found, or it is completely lacking in these species and eggs are spawned through the supraneural pore. However, although oviparous species with a supraneural pore are known among Ctenostomata, there are none in *Alcyonidium*. In *Alcyonidium disciforme*, only one embryo per time is brooded in the tentacle sheath, although several embryos are a rule for that genus.

Smith et al. (2003) investigated reproduction in the ctenostome *Pottsiella erecta*. An ovary develops on the cystid wall and spermatogenic tissue on the funiculus. Because both gonads appear in close proximity in the middle region of zooids that are simultaneous hermaphrodites, the authors erroneously inferred self-fertilization in this species, which is obviously not the case (see above). The most intriguing finding was that the egg (occasionally two) is brooded externally in a sticky coat connected with to the maternal zooid by a flexible, elastic strand. The authors considered the coat a fertilization envelope and the strand mucoid. The embryo remains outside the parent whether the polypide is extended or withdrawn, and the strand possibly lengthens with time.

A substantial body of experimental work on the reproductive biology of *Bugula neritina* and *Watersipora subtorquata* was undertaken by Marshall and coauthors (Marshall et al. 2003; Marshall and Keough 2003, 2004a, b, 2006, 2008a, 2009; Allen et al. 2008; Marshall 2008; Burgess et al. 2009; see also Marshall and Uller 2007, Elkin and Marshall 2007, Marshall and Keough 2008b, and Marshall et al. 2008 for general review and discussion). This wide research encompasses different aspects of larval, post-settlement and colonial performance and one of the most intriguing discoveries was the prolonged effect of larval size on colony life. Colonies that developed from larger larvae survived better, grew faster and reproduced sooner or formed more offspring than those from smaller larvae. This effect was observed over several consecutive generations.

Experiments of Johnson (2010) confirmed that self-fertilization is possible in isolated colonies of *Bugula stolonifera*. Such colonies produced viable larvae that successfully completed metamorphosis, but overall reproductive fitness was less than in control colonies and these larvae experienced reduced rates of initiation and completion of metamorphosis. Also the colonies that developed from such larvae in the field showed decreased survival and reproductive fitness.

Yagunova and Ostrovsky (2010) studied the fecundity of the cheilostome *Cribrilina annulata* living on stones and red algae, showing that it reproduces more actively (starts reproduction at a smaller size and forms more ovicells) on an algal substratum.

Five more papers recently published by the author of this monograph, with coauthors, were devoted to various aspects of the evolution of bryozoan gonopores (Ostrovsky and Porter 2011) and placental analogues (Ostrovsky et al. 2009; Ostrovsky and Schwaha 2011; Moosburger et al. 2012; Ostrovsky 2013). All are discussed in detail in Chaps. 1 and 3 of the main text.

Chronological list of papers and gymnolaemate species in which different aspects of sexual reproduction were studied or observed

(works merely presenting data on reproductive ecology and brood-chamber structure are not included in this list)

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)

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

Van Beneden (1844b)

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

Flustra foliacea (Linnaeus, 1758) (Flustridae)

Alcyonidium? *hirsutum* (as *Halodactyle vélu*) (Alcyonidiidae)

Alcyonidium parasiticum (as *Halodactyle parasite*) (Alcyonidiidae)

Reid (1845)

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

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

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

Bugula avicularia (Linnaeus, 1758) (as *Cellularia avicularis*) (Bugulidae)

Alcyonidium sp. (as *A. parasiticum*) (Alcyonidiidae)

Dalyell (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*) (= *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*) (Flustrellidridae)

Hincks (1861)

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

Bugula turbinata Alder, 1857 (Bugulidae)

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

Smitt (1863)

Escharella immersa (Fleming, 1828) (as *Lepralia peachii*) (Romancheinidae)

Cryptosula pallasiana (Moll, 1803) (as *Lepralia*) (Cryptosulidae)

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)

Nitsche (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)

Reinhard (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* species) (Electridae)

Ehlers (1876)

Hypophorella expansa Ehlers, 1876 (Hypophorellidae)

non-identified cheilostome (as *Lepralia*)

Joliet (1877a)

Bowerbankia imbricata (Adams, 1898) (Vesiculariidae)

Walkeria uva (Linnaeus, 1758) (as *Valkeria cuscuta*) (Walkeriidae)

Farrella 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, b)

Chartella membranaceotruncata (Smitt, 1868) (as *Flustra membranaceo-truncata*) (Flustridae)

Vigelius (1886)

Bugula calathus Norman, 1868 (Bugulidae)

Ostroumoff (1886b)

Tendra zostericola Nordmann, 1839 (as *Membranipora*) (Tendridae)

Electra repiachowi (Ostroumoff, 1886) (as *Membranipora*) (Electridae)

Conopeum sp. (as *Membranipora denticulata* Busk) (Membraniporidae)

Cryptosula pallasiana (Moll, 1803) (as *Lepralia*) (Cryptosulidae)

Braikovia turgenewi (Ostroumoff, 1886) (as *Discopora*) (Cribrilinidae)

Ostroumoff (1886c)

Tendra zostericola Nordmann, 1839 (as *Membranipora*) (Tendridae)

Electra repiachowi (Ostroumoff, 1886) (as *Membranipora*) (Electridae)

Braikovia turgenewi (Ostroumoff, 1886) (as *Discopora*) (Cribrilinidae)

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*) (Flustrellidridae)

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 (1896a [1898])

Aetea sica (Couch, 1844) (as *A. anguina* forma *recta* Hincks) (Aetiidae)

Beania magellanica (Busk, 1852) (Beaniidae)

Waters (1896b [1898])

Menipea roborata (Hincks, 1881) (as *Flabellaris*) (Candidae)

Waters (1900)

Cystisella saccata (Busk, 1856) (as *Porella*) (Bryocryptellidae?)

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)

Savignyella lafontii (as *Eucratea*) (Savignyellidae)

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)

Einhornia 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)

Hippadenella clivosa (Waters, 1906) (as *Lepralia clivosa*) (Buffonellodidae)

Escharoides angela (Hutton, 1873) (as *Smittina praestans* Hincks) (Romancheinidae)

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. (= *P. articulata* (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) (Adeonidae)

Adeonella polymorpha Busk, 1884 (as *A. polymorpha* and *Adeonella lichenoides* (Lamarck, 1816)) (Adeonidae)

Adeonella polystomella (Reuss, 1847) (Adeonidae)

Laminopora contorta Michelin, 1842 (as *Adeonella*) (Adeonidae)

Beania magellanica (Busk, 1852) (Beaniidae)

Watersipora cucullata (Busk, 1854) (as *Lepralia*) (Watersiporidae)

Waters (1913)

Aetea anguina (Linnaeus, 1758) (Aeteidae)

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 diaphana (Busk, 1860) (as *Catenaria diaphana*) (Savignyellidae)

Catenicella elegans (Busk, 1852) (as *Vittaticella*) (Catenicellidae)

Adenifera armata (Haswell, 1880) (Calloporidae)

Nellia tenella (Lamarck, 1816) (as *Farcimia oculata* Busk) (Quadricellariidae)

Poricellaria ratoniensis (Waters, 1887) (as *Diplodidymia complicata*)

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 feegeensis (Busk, 1994) (as *Lepralia*) (Hippopodinidae)

Petraliella dentilabris (Ortmann, 1892) (as *Petralia chuakensis* Waters) (Petraliellidae)

Celleporaria columnaris (Busk, 1881) (as *Holoporella*) (Lepraliellidae)

Adeonella platalea (Busk, 1854) (Adeonidae)

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 (1919 [1921])

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

Marcus (1922)

Alcyonidium flustroides Busk, 1886 (Alcyonidiidae)

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

Marcus (1926a)

Farrella repens (Farre, 1837) (Triticellidae)

Electra pilosa (Linnaeus, 1767) (Electridae)

Marcus (1926b)

Farrella repens (Farre, 1837) (Triticellidae)

Electra pilosa (Linnaeus, 1767) (as *Membranipora*) (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 umbellata (Defrance, 1823) (Cupuladriidae)

Thalamoporella californica (Levinsen, 1909) (Thalamoporellidae)

Hastings (1932)

Stylopoma schizostoma (MacGillivray, 1869) (Schizoporellidae)

Stylopoma spongites (Pallas, 1766) (Schizoporellidae)

Sinupetraliella litoralis (Hastings, 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 (incertae sedis)

Marcus (1938a)

Alcyonidium sp. (as *A. mamillatum*) (Alcyonidiidae)

Nolella dilatata (Hincks, 1860) (Nolellidae)

Nolella sp. (as *N. gigantea*) (Nolellidae)

Nolella alta (Kirkpatrick, 1888) (Nolellidae)

Arbocuspis bellula (Hincks, 1882) (as *Electra*) (Electridae)

Chartella tenella (Hincks, 1880) (as *Electra*) (Flustridae)

Biflustra sp. (as *Acanthodesia savartii*) (Membraniporidae)

Biflustra sp. (as *Acanthodesia tenuis*) (Membraniporidae)

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

Akatopora leucocypha (Marcus, 1937) (as *Crassimarginatella*) (Antroporidae)

Bugula avicularia (Linnaeus, 1758) (Bugulidae)

Kinetoskias smittii Daniellsen, 1868 (Bugulidae)

Steginoporella buskii (Harmer, 1900) (as *Steganoporella*) (Steginoporellidae)

Thalamoporella sp. (as *T. gothica* var. *prominens*) (Thalamoporellidae)

Beania americana Vieira, Migotto and Winston, 2010 (as B. *hirtissima* (Heller)) (Beaniidae)

Membraniporella sp. (as *Membraniporella aragoi*) (Cribrilinidae)

Catenicella sp. (as *Vittaticella elegans*) (Catenicellidae)

Catenicella sp. (as *Catenicella contei*) (Catenicellidae)

Celleporella sp. (as *Hippothoa hyalina*) (Hippothoidae)

Celleporella hyalina marcusi (Morris, 1980) (as *Hippothoa hyalina*) (Hippothoidae)

Pentapora americana (Verrill, 1875) (as *Hippodiplosia*) (Bitectiporidae)

Schizoporella sp. (as *Schizoporella unicornis*) (Schizoporellidae)

Pourtalesella carvalhoi (Marcus, 1939) (as *Schizoporella*) (Lepraliellidae)

Celleporaria mordax (Marcus, 1937) (as *Holoporella*) (Lepraliellidae)

Microporella sp. (as *Microporella ciliata*) (Microporellidae)

Hippopodina sp. (as *H. feegeensis* (Busk)) (Hippopodinidae)

Watersipora subtorquata (d'Orbigny, 1842) (as *W. cucullata* Busk) (Watersiporidae)

Hippoporella sp. (as *Hippoporella gorgonensis*) (Hippoporidridae)

Celleporina sp. (as *Siniopelta costazii*) (Celleporidae)

Rhynchozoon phrynoglossum Marcus, 1937 (Phidoloporidae)

Marcus (1938b)

Alcyonidium sp. (as *A. polyoum*) (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 sp. (as *Alcyonidium gelatinosum*) (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)

Einhornia crustulenta (Pallas, 1766) (as *Electra*) (Electridae)

Corrêa (1948)

Biflustra arborescens (Kirkpatrick and Metzelaar, 1922) (as *Conopeum commensale*) (Membraniporidae)

Bugula foliolata Vieira, Winston and Fehlauer-Ale 2012 (as B. *flabellata*) (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) (Victorellidae)

Bowerbankia gracilis Leidy, 1855 (as *B. caudata*) (Vesiculariidae)

Mawatari (1951a)

Bugula neritina (Linnaeus, 1758) (Bugulidae)

Mawatari (1951b)

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 (1958)

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 (1960)

Einhornia crustulenta (Pallas, 1766) (as *Electra*) (Electridae)

Cook (1962)

Conopeum seurati (Canu, 1928) (as *Membranipora*) (Membraniporidae)

Einhornia crustulenta (Pallas, 1766) (as *Electra*) (Electridae)

Ranzoil (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 (1964a)

Electra monostachys (Busk, 1854) (Electridae)

Conopeum reticulum (Linnaeus, 1767) (Membraniporidae)

Cook (1964b)

Steginoporella buskii (Harmer, 1900) (as *Steganoporella*) (Steginoporellidae)

Silén (1966)

Electra posidoniae Gautier, 1961 (Electridae)

Einhornia crustulenta (Pallas, 1766) (as *Electra*) (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)

Bantariella cookae (as *Mimosella*) Banta, 1968 (Mimosellidae)

Gordon (1968)

Odontoporella bishopi Carter and Gordon, 2007 (as *Hippopodinella adpressa*) (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

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)

Bugula neritina (Linnaeus, 1758) (Bugulidae)

Woollacott and Zimmer (1972b)

Bugula neritina (Linnaeus, 1758) (Bugulidae)

Jebram (1973)

Conopeum seurati (Canu, 1928) (Membraniporidae)

Dudley (1973)

Conopeum tenuissimum (Canu, 1928) (Membraniporidae)

Mawatari (1973a)

Scruparia chelata (Linnaeus, 1758) (Scrupariidae)

Mawatari (1973b)

Aetea anguina (Linnaeus, 1758) (Aetiidae)

Aetea truncata (Landsborough, 1852) (Aetiidae)

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 (L.) (Flustridae)

Cook (1977)

Hippoporidra sp. (Hippoporidridae)

Ryland and Gordon (1977)

Antarctothoa tongima (Ryland and Gordon 1977) (as *Hippothoa*) (Hippothoidae)

Ryland (1979)

Celleporella carolinensis Ryland, 1979 (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)

Alcyonidium sanguineum Cook, 1985 (Alcyonidiidae)

Crassimarginatella falcata Cook, 1968 (Calloporidae)

Odontoporella adpressa (Busk, 1854) (as *Hippopodinella*) (Hippoporidridae)

Hippoporidra senegambiensis (Carter, 1882) (Hippoporidridae)

Hippoporidra littoralis Cook, 1964 (Hippoporidridae)

Schizoporella floridana Osburn, 1914 (Schizoporellidae)

Jebram (1985)

Panolicella nutans Jebram, 1985 (Panolicellidae)

Hughes (1987)

Celleporella hyalina (Linnaeus, 1767) (Hippothoidae)

Reed (1988)

Bowerbankia gracilis Leidy, 1855 (Vesiculariidae)

Bowerbankia aggregata O'Donoghue and O'Donoghue, 1926 (as *gracilis* var. *aggregata*) (Vesiculariidae)

Owrid and Ryland (1991)

Alcyonidium hirsutum (Fleming, 1828) (Alcyonidiidae)

Cancino et al. (1991)

Membranipora isabelleana (d'Orbigny, 1847) (Membraniporidae)

Celleporella hyalina (Linnaeus, 1767) (Hippothoidae)

Zimmer (personal communications in Reed 1991)

Membranipora membranacea (Linnaeus, 1767) (Membraniporidae)

non-specified *Scizoporella* (Schizoporellidae)

Watersipora arcuata Banta, 1969 (Watersiporidae)

Maturo (1991a)

Bowerbankia gracilis Leidy, 1855 (Vesiculariidae)

Buskia sp. (Buskiidae)

Bugula neritina (Linnaeus, 1758) (Bugulidae)

Akatopora leucocypha (Marcus, 1937) (as *Antropora*) (Antroporidae)

Hippoporina verrilli Maturo and Schopf, 1968 (Bitectiporidae)

Schizoretepora cf. *pungens* (Canu and Bassler, 1925) (as *Schizoporella*) (Phidoloporidae)

Maturo (1991b)

Schizoretepora cf. *pungens* (Canu and Bassler, 1925) (as *Schizoporella*) (Phidoloporidae)

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 et al. (2001)

Alcyonidium diaphanum (Hudson, 1778) (Alcyonidiidae)

Temkin (2002)

Membranipora membranacea (Linnaeus, 1767) (Membraniporidae)

Smith et al. (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 Kirkpatrick, 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)

Ostrovsky and Schwaha (2011)

Zoobotryon verticillatum (Delle Chiaje, 1828) (Vesiculariidae)

Moosburgger et al. (2012)

Bicellariella ciliata (Linnaeus, 1758) (Bugulidae)

Ostrovsky (2013)

Bugula neritina (Linnaeus, 1758) (Bugulidae)

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

Beania bilaminata (Hincks, 1881) (Beaniidae)

Klugeflustra antarctica (Hastings, 1943) (Flustridae)

Isosecuriflustra angusta (Kluge, 1914) (Flustridae)

Gregarinidra serrata (MacGillivray, 1869) (Flustridae)

Micropora notialis Hayward and Ryland, 1993 (Microridae)

Cellaria fistulosa (Linnaeus, 1758) (Cellariidae)

Cellaria tenuirostris (Busk, 1852) (Cellariidae)

Mollia multijuncta (Waters, 1879) (Microporidae)

Figularia figularis (Johnston, 1847) (Cribrilinidae)

Cribricellina cribraria (Busk, 1852) (Catenicellidae)

Pterocella scutella (Hutton, 1891) (Catenicellidae)

Costaticella solida (Levinsen, 1909) (Catenicellidae)

Costaticella bicuspis (Gray, 1843) (Catenicellidae)

Celleporella hyalina (Linnaeus, 1767) (Hippothoidae)

Urceolipora nana MacGillivray, 1881 (Urceoliporidae)

Reciprocus regalis Gordon, 1988 (Urceoliporidae)

"Calyptotheca" variolosa (MacGillivray, 1869) (Lanceoporidae)

Watersipora subtorquata (d'Orbigny, 1852) (Watersiporidae)

Myriapora truncata (Pallas, 1766) (Myriaporidae)

Appendix II: Materials and Methods

Altogether, 258 species belonging to 148 genera and 66 cheilostome families have been studied. There were among them 35 fossil species belonging to 10 genera from five of the most ancient families. Thus, the collections included representatives of all but one (Inovicellina) of the known suborders of Cheilostomata, that is, Scrupariina, Malacostegina and Flustrina ("grades" Acanthostega, Hippothoomorpha, Umbonulomorpha, Lepraliomorpha). The type species of 65 genera were studied. The new suborders Tendrina, Thalamoporellina and Belluloporina, four new superfamilies, Tendroidea, Thalamoporelloidea, Monoporelloidea and Belluloporoidea, and the corresponding family Belluloporidae are established herein (see diagnoses at the end of the species list).

Living cheilostomes were sampled in the White, Barents, Baltic, Greenland, Mediterranean and Caribbean Seas as well as in the Pacific Ocean (Alaska, Japan, New Zealand), the Indian Ocean (Australia) and the Atlantic Ocean (Saint Helena, Canary Islands) and in the coastal waters of the Antarctic. Fossil material was collected in Australia, New Zealand, the USA and England. Sampling methods included trawling and dredging, manual collection in the intertidal zone, collection with the help of SCUBA and selection of fossils from sedimentary rocks. Some specimens were obtained from the Zoological Museum of Copenhagen, the Natural History Museum, London and Museum Victoria, Melbourne. The list of sampling sites with their detailed descriptions is available from the author on request.

Bryozoans were studied by light and scanning electron microscopy. To make histological sections, the collected specimens were fixed in 2.5% glutaraldehyde solution in 0.1 M sodium cacodylate buffer (pH 7.3), in Bouin's fluid (sometimes prepared without acetic acid or with chalk-neutralized formalin) or in 70% ethanol. Most of the specimens fixed in Bouin's fluid were additionally decalcified by adding a few drops of 2-normal hydrochloric acid to 70% ethanol during dehydration or 10% EDTA water solution for 6–24 h. Specimens fixed in glutaraldehyde were washed in a buffer with EDTA.

After removal of calcium carbonate and dehydration in an ascending alcohol series (40–50–60–70–80–90–96–100%), the specimens were embedded in resin (epoxy resin type TAAB 812) with the use of polypropylene according to the standard procedure. Semithin sections (1.0–3.0 µm) were made by ultramicrotomy and stained with toluidine blue or Richardson's stain (Richardson et al. 1960).

For studying oogenesis and brooding, the length and width (the longest and shortest diameters) of the oocytes, nurse cells and embryos were measured using the microscope eye-piece. Their average diameter and volume were then calculated to determine and compare their enlargement during the consecutive stages of oogenesis and incubation.

For scanning electron microscopy, specimens were cleaned in 7.5% sodium hypochlorite solution. Non-cleaned specimens were air- or critical-point-dried. Specimens were coated with gold or palladium and studied with the use of the following microscopes: Philips 003 M (Institute of Geology, Copenhagen), Jeol JSM-840 (Zoological Museum, University of Copenhagen), Jeol JSM-6400 (Geozentrum, University of Vienna), CAMSCAN-Serie-2-CS-44 (Institute for Earth Sciences, University of Kiel). Fossil specimens were examined without sputter-coating by environmental SEM (ISI ABT-55) (The Natural History Museum, London).

List of Taxa Studied

Phylum **Bryozoa** Ehrenberg, 1831
Class **Gymnolaemata** Allman, 1856
Order **Cheilostomata** Busk, 1852
Suborder **Scrupariina** Silén, 1941
  Superfamily **Scruparioidea** Gray, 1848
    Family **Scrupariidae** Busk, 1852
      Scruparia Oken, 1815
        Scruparia ambigua (d'Orbigny, 1841)
Suborder **Malacostegina** Levinsen, 1902
  Superfamily **Membraniporoidea** Busk, 1852
    Family **Electridae** d'Orbigny, 1851
      Electra Lamouroux, 1816
        Electra pilosa (Linnaeus, 1767) – type sp.
Suborder **Tendrina** subord. nov.
  Superfamily **Tendroidea** Vigneaux, 1949
    Family **Tendridae** Vigneaux, 1949
    Tendra Nordmann, 1839
      Tendra zostericola Nordmann, 1839 – type sp.
      Heteroecium Hincks, 1892
        Heteroecium amplectens (Hincks, 1881) – type sp.
Suborder **Thalamoporellina** subord. nov.
  Superfamily **Thalamoporelloidea** Levinsen, 1902
    Family **Thalamoporellidae** Levinsen, 1902
      Thalamoporella Hincks, 1887
        Thalamoporella sp.
    Family **Steginoporellidae** Hincks, 1884
      Steginoporella Smitt, 1873
        Steginoporella cf. magnilabris (Busk, 1854) – type sp.
        Steginoporella perplexa Livingstone, 1929
Suborder **Belluloporina** subord. nov.
  Superfamily **Belluloporoidea** suprafam. nov.
    Family **Belluloporidae** fam. nov.
      Bellulopora Lagaaij, 1963
        Bellulopora bellula (Osburn, 1950) – type sp.

Suborder **Flustrina** Smitt, 1868
  Superfamily **Calloporoidea** Norman, 1903
    Family **Calloporidae** Norman, 1903
      Wilbertopora Cheetham, 1954
        Wilbertopora mutabilis Cheetham, 1954 – type sp.
        Wilbertopora listokinae Cheetham, Sanner, Taylor and Ostrovsky, 2006
        Wilbertopora tappanae Cheetham, Sanner, Taylor and Ostrovsky, 2006
        Wilbertopora spatulifera Cheetham, Sanner, Taylor and Ostrovsky, 2006
        Wilbertopora attenuata Cheetham, Sanner, Taylor and Ostrovsky, 2006
        Wilbertopora improcera Cheetham, Sanner, Taylor and Ostrovsky, 2006
        Wilbertopora acuminata Cheetham, Sanner, Taylor and Ostrovsky, 2006
        Wilbertopora hoadleyae Cheetham, Sanner, Taylor and Ostrovsky, 2006
      Distelopora Lang, 1915
        Distelopora bipilata Lang, 1915 – type sp.
        Distelopora langi Ostrovsky and Taylor, 2004
        Distelopora spinifera Ostrovsky and Taylor, 2004
      Unidistelopora Ostrovsky and Taylor, 2004
        Unidistelopora krauseae (Voigt and Schneemilch, 1986) – type sp.
      Gilbertopora Ostrovsky and Taylor, 2004
        Gilbertopora larwoodi Ostrovsky and Taylor, 2004 – type sp.
      Callopora Gray, 1848
        Callopora lineata (Linnaeus, 1767) – type sp.
        Callopora craticula (Alder, 1856)
        Callopora aurita (Hincks, 1877)
        Callopora dumerilii (Audouin, 1826)
      Cauloramphus Norman, 1903
        Cauloramphus spinifer (Johnston, 1832) – type sp.
        Cauloramphus magnus Dick and Ross, 1988
        Cauloramphus cryptoarmatus Grischenko, Dick and Mawatari, 2007
        Cauloramphus niger Grischenko, Dick and Mawatari, 2007
        Cauloramphus multispinosus Grischenko, Dick and Mawatari, 2007
        Cauloramphus variegatus (Hincks, 1881)
        Cauloramphus multiavicularia Dick, Grischenko and Mawatari, 2005
        Cauloramphus tortilis Dick, Grischenko and Mawatari, 2005
      Crassimarginatella Canu, 1900
        Crassimarginatella sp.

      Corbulella Gordon, 1984
        Corbulella maderensis (Waters, 1898)
      Valdemunitella Canu, 1900
        Valdemunitella lata (Kluge, 1914)
      Tegella Levinsen, 1909
        Tegella unicornis (Fleming, 1828) – type sp.
        Tegella armifera (Hincks, 1880)
      Bryocalyx Cook and Bock, 2000
        Bryocalyx cinnameus Bock and Cook, 2000 – type sp.
      Concertina Gordon, 1986
        Concertina cultrata Gordon, 1986 – type sp.
      Amphiblestrum Gray, 1848
        Amphiblestrum inermis (Kluge, 1914)
      Gontarella Grischenko, Taylor and Mawatari, 2002
        Gontarella sp.
    Family **Akatoporidae** Vigneaux, 1949
      Akatopora Davis, 1934
        Akatopora circumsaepta (Uttley, 1951)
    Family **Chaperiidae** Jullien, 1888
      Chaperiopsis Uttley, 1949
        Chaperiopsis protecta (Waters, 1904)
        Chaperiopsis cervicornis (Busk, 1854)
      Chaperia Jullien, 1881
        Chaperia cf. acanthina (Lamoroux, 1825) – type sp.
    Family **Hiantoporidae** Gregory, 1893
      Hiantopora MacGillivray, 1887
        Hiantopora ferox (MacGillivray, 1869) – type sp.
        Hiantopora radicifera (Hincks, 1881)
        Hiantopora jucunda Gordon, 1984
    Family **Bryopastoridae** d'Hondt and Gordon, 1999
      Bryopastor Gordon, 1982
        Bryopastor pentagonus (Canu and Bassler, 1929) – type sp.
      Pseudothyracella Labracherie, 1975
        Pseudothyracella candelabra d'Hondt and Gordon, 1999
    Family **Farciminariidae** Busk, 1852
      Columnella Levinsen, 1914
        Columnella magna (Busk, 1884)
    Family **Cupuladriidae** Lagaaij, 1952
      Cupuladria Canu and Bassler, 1919
        Cupuladria exfragminis Herrera-Cubilla, Dick, Sanner and Jackson, 2006
      Discoporella d'Orbigny, 1852
        Discoporella cookae Herrera-Cubilla, Dick, Sanner and Jackson, 2006
        Discoporella marcusorum Herrera-Cubilla, Dick, Sanner and Jackson, 2006
        Discoporella sp.
  Superfamily **Flustroidea** Fleming, 1828

Family **Flustridae** Fleming, 1828
   Carbasea Gray, 1848
      Carbasea pisciformis Busk, 1852
   Flustra Linnaeus, 1761
      Flustra foliacea (Linnaeus, 1758) – type sp.
   Gregarinidra Barroso, 1948
      Gregarinidra inarmata (Hincks, 1881)
      Gregarinidra serrata (MacGillivray, 1869)
   Isosecuriflustra Liu and Hu, 1991
      Isosecuriflustra tenuis (Kluge, 1914) – type sp.
      Isosecuriflustra angusta (Kluge, 1914)
   Klugeflustra Moyano, 1972
      Klugeflustra antarctica (Hastings, 1943)
   Nematoflustra Moyano, 1972
      Nematoflustra flagellata (Waters, 1904) – type sp.
   Securiflustra Silen, 1941
      Securiflustra securifrons (Pallas, 1766) – type sp.
   Spiralaria Busk, 1861
      Spiralaria florea Busk, 1861– type sp.
   Chartella Gray, 1848
      Chartella membranaceotruncata (Smitt, 1868)
Incertae sedis
      "Biflustra" perfragilis MacGillivray, 1881
Superfamily **Buguloidea** Gray, 1848
  Family **Bugulidae** Gray, 1848
   Bugula Oken, 1815
      Bugula neritina (Linnaeus, 1758) – type sp.
      Bugula flabellata (Thompson in Gray, 1848)
      Bugula pacifica Robertson, 1905
   Bicellariella Levinsen, 1909
      Bicellariella ciliata (Linnaeus, 1758) – type sp.
   Camptoplites Harmer, 1923
      Camptoplites asymmetricus Hastings, 1943
      Camptoplites retiformis (Kluge, 1914)
      Camptoplites tricornis (Waters, 1904)
   Cornucopina Levinsen, 1909
      Cornucopina pectogemma (Goldstein, 1882)
      Cornucopina polymorpha (Kluge, 1914)
      Cornucopina sp.
   Dendrobeania Levinsen, 1909
      Dendrobeania murrayana (Johnston, 1837) – type sp.
      Dendrobeania fruticosa (Packard, 1863)
      Dendrobeania lichenoides (Robertson, 1900)
      Dendrobeania quadridentata (Loven, 1834)
   Dimetopia Busk, 1852
      Dimetopia cornuta Busk, 1852 – type sp.
   Nordgaardia Kluge, 1962
      Nordgaardia cornucopioides d'Hondt, 1983
  Family **Beaniidae** Canu and Bassler, 1927
   Beania Johnston, 1840

      Beania bilaminata (Hincks, 1881)
      Beania magellanica (Busk, 1852)
      Beania sp.
  Family **Candidae** Busk, 1852
   Amastigia Busk, 1852
      Amastigia cf. *funiculata* (MacGillivray, 1886)
   Bugulopsis Verrill, 1880
      Bugulopsis monotrypa (Busk, 1852)
   Caberea Lamouroux, 1816
      Caberea solida Gordon, 1986
   Canda Lamouroux, 1816
      Canda simplex Busk, 1884
   Menipea Lamouroux, 1812
      Menipea roborata (Hincks, 1881)
   Notoplites Harmer, 1923
      Notoplites tenuis (Kluge, 1914)
   Scrupocellaria van Beneden, 1845
      Scrupocellaria scruposa (Linnaeus, 1758) – type sp.
      Scrupocellaria elongata (Smitt, 1868)
      Scrupocellaria scabra (van Beneden, 1848)
   Tricellaria Fleming 1828
      Tricellaria gracilis (van Beneden, 1848)
      Tricellaria occidentalis (Trask, 1857)
Superfamily **Microporoidea** Gray, 1848
  Family **Microporidae** Gray, 1848
   Micropora Gray, 1848
      Micropora brevissima Waters, 1904
      Micropora notialis Hayward and Ryland, 1993
      Micropora variperforata Waters, 1887
      Micropora gracilis (Uttley, 1949)
   Mollia Lamouroux, 1816
      Mollia multijuncta (Waters, 1879)
   Opaeophora Brown, 1948
      Opaeophora monopia (Brown, 1952)
  Family **Onychocellidae** Jullien, 1882
   Onychocella Jullien, 1882
      Onychocella angulosa (Reuss, 1847)
      Onychocella sp. 1[1]
      Onychocella sp. 2
      Onychocella sp. 3
   Aechmella Canu and Bassler, 1917
      Aechmella sp.
  Family **Chlidoniidae** Busk, 1884
   Chlidonia Lamouroux, 1824
      Chlidonia pyriformis (Bertoloni, 1810) – type sp.
Superfamily **Cellarioidea** Fleming, 1828
  Family **Cellariidae** Fleming, 1828
   Cellaria Ellis and Solander, 1786
      Cellaria tenuirostris (Busk, 1852)

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[1]Species designated by numbers are still undescribed.

Cellaria fistulosa (Linnaeus, 1758)
Cellaria aurorae Livingstone, 1928
Cellaria diversa Livingstone, 1928
Steginocellaria David and Pouyet, 1986
    Steginocellaria magnimandibulata (Gordon, 1986)
Melicerita Milne Edwards, 1836
    Melicerita obliqua (Thornely, 1924)
Euginoma Jullien, 1883
    Euginoma conica Gordon, 1986
Superfamily **Monoporelloidea** Hincks, 1882
  Family **Monoporellidae** Hincks, 1882
    Stichomicropora Voigt, 1949
      Stichomicropora oceani (d'Orbigny, 1852)
      Stichomicropora marginula (Brydone, 1914)
      Stichomicropora baccata (Canu and Bassler, 1926)
      Stichomicropora ostrovskyi Taylor and McKinney, 2006
      Stichomicropora senaria Taylor and McKinney, 2006
      Stichomicropora sp. 1
      Stichomicropora sp. 2
      Stichomicropora sp. 3
      Stichomicropora sp. 4
      Stichomicropora sp. 5
    Monoporella Hincks, 1881
      Monoporella nodulifera (Hincks, 1881) – type sp.
      Monoporella multilamellosa (Canu and Bassler, 1920)
      Monoporella elongata Dick, 2008
      Monoporella sp.
  Family **Macroporidae** Uttley, 1949
    Macropora MacGillivray, 1895
      Macropora cribrilifera Maplestone, 1901
      Macropora waimatukuensis (Uttley, 1949)
      Macropora filifera Gordon and Taylor, 2008
      Macropora uttleyi López de la Cuadra and García Gómes, 1997
      Macropora levinseni Brown, 1952
      Macropora polymorpha (Philipps, 1899)
Superfamily Cribrilinoidea Hincks, 1879
  Family **Cribrilinidae** Hincks, 1879
    Leptocheilopora Lang, 1916
      Leptocheilopora tenuilabrosa Lang, 1916 – type sp.
      Leptocheilopora magna Lang, 1916
      Leptocheilopora sp. 1
      Leptocheilopora sp. 2
    Cribrilina Gray, 1848
      Cribrilina punctata (Hassal, 1841) – type sp.
      Cribrilina macropunctata Winston, Hayward and Craig, 2000

Cribrilina cryptooecium Norman, 1903
Cribrilina watersi Andersson, 1902
Cribrilina annulata (Fabricius, 1780)
Cribrilina spitzbergensis (Norman, 1903)
Collarina Jullien, 1886
    Collarina balzaci (Audouin, 1826) – type sp.
Puellina Jullien, 1886
    Puellina denticulata Harmelin and Aristegui, 1988
    Puellina hincksi (Friedl, 1917)
    Puellina radiata (Moll, 1803)
Corbulipora MacGillivray, 1895
    Corbulipora inopinata Bock and Cook, 1998
    Corbulipora tubulifera Hincks, 1881
Figularia Jullien, 1886
    Figularia figularis (Johnston, 1847) – type sp.
    Figularia carinata (Waters, 1887)
    Figularia mernae Uttley and Bullivant, 1972
    Figularia huttoni Brown, 1952
Family **Euthyroididae** Levinsen, 1909
  Euthyroides Harmer, 1902
    Euthyroides episcopalis (Busk, 1852) – type sp.
Family **Bifaxariidae** Busk, 1884
  Diplonotos Canu and Bassler, 1930
    Diplonotos sp.
Family **Catenicellidae** Busk, 1852
  Cribricellina Canu and Bassler, 1927
    Cribricellina cribraria (Busk, 1852) – type sp.
  Costaticella Maplestone, 1899
    Costaticella solida (Levinsen, 1909)
    Costaticella bicuspis (Gray, 1843)
  Pterocella Levinsen, 1900
    Pterocella scutella (Hutton, 1891)
Family **Eurystomellidae** Levinsen, 1909
  Eurystomella Levinsen, 1909
    Eurystomella foraminigera (Hincks, 1883) – type sp.
  Selenariopsis Maplestone, 1913
    Selenariopsis gabrieli Maplestone, 1913 – type sp.
Superfamily **Hippothooidea** Busk, 1859
  Family **Hippothoidae** Busk, 1859
    Hippothoa Lamouroux, 1821
      Hippothoa flagellum Manzoni, 1870
    Celleporella Gray, 1848
      Celleporella hyalina (Linnaeus, 1767) – type sp.
    Antarctothoa Moyano, 1986
      Antarctothoa bougainvillei (d'Orbigny, 1847) – type sp.
      Antarctothoa sp.
Superfamily **Arachnopusioidea** Jullien, 1888
  Family **Arachnopusiidae** Jullien, 1888
    Arachnopusia Jullien, 1886

Arachnopusia unicornis (Hutton, 1873)
Arachnopusia sp.
Superfamily **Adeonoidea** Busk, 1884
  Family **Adeonidae** Busk, 1884
    Adeonella Busk, 1884
    Adeonella calveti (Canu and Bassler, 1930)
Superfamily **Lepralielloidea** Vigneaux, 1949
  Family **Lepraliellidae** Vigneaux, 1949
    Lepraliella Levinsen, 1917
    Lepraliella contigua (Smitt, 1868) – type sp.
    Lepraliella sp. 1
    Lepraliella sp. 2
    Celleporaria Lamouroux, 1821
    Celleporaria sp.
    Sinuporaria Pouyet, 1973
    Sinuporaria sp.
  Family **Bryocryptellidae** Vigneaux, 1949
    Porella Gray, 1848
    Porella proboscidea Hincks, 1888
    Porella minuta Norman, 1869
    Porella smitti Kluge, 1907
    Porella fragilis Levinsen, 1914
    Palmiskenea Bishop and Hayward, 1989
    Palmiskenea sp.
  Family **Romancheinidae** Jullien, 1888
    Arctonula Gordon and Grischenko, 1994
    Arctonula arctica (M. Sars, 1851) – type sp.
    Escharella Gray, 1848
    Escharella immersa (Fleming, 1828)
    Exochella Jullien, 1888
    Exochella sp.
    Lageneschara Hayward and Thorpe, 1988
    Lageneschara lyrulata (Calvet, 1909)
    Antarcticaetos Hayward and Thorpe, 1988
    Antarcticaetos bubeccata (Rogick, 1955)
  Family **Umbonulidae** Canu, 1904
    Rhamphostomella von Lorenz, 1886
    Rhamphostomella ovata (Smitt, 1868)
    Rhamphostomella radiatula (Hincks, 1877)
    Rhamphostomella bilaminata (Hincks, 1877)
    Rhamphostomella costata Lorenz, 1886
  Family **Sclerodomidae** Levinsen, 1909
    Cellarinella Waters, 1904
    Cellarinella nutti Rogick, 1956
    Cellarinella sp.
  Family **Metrarabdotosidae** Vigneaux, 1949
    Polirhabdotos Hayward and Thorpe, 1987
    Polirhabdotos inclusum (Waters, 1904)
Superfamily **Smittinoidea** Levinsen, 1909
  Family **Smittinidae** Levinsen, 1909
    Smittina Norman, 1903
    Smittina obicullata Rogick, 1956
    Smittina majuscula (Smitt, 1868)

Smittina concinna (Busk, 1854)
Smittina antarctica (Waters, 1904)
Smittina mucronata (Smitt, 1868)
Smittina directa (Waters, 1904)
Smittoidea Osburn, 1952
Smittoidea reticulata (J. MacGillivray, 1842)
Parasmittina Osburn, 1952
Parasmittina crosslandi (Hastings, 1930)
Bostrychopora Hayward and Thorpe, 1988
Bostrychopora dentata (Waters, 1904) – type sp.
Pemmatoporella Hayward and Taylor, 1984
Pemmatoporella marginata (Calvet, 1909) – type sp.
Family **Bitectiporidae** MacGillivray, 1895
  Schizomavella Canu and Bassler, 1917
  Schizomavella lineata (Nordgaard, 1896)
  Schizomavella cuspidata (Hincks, 1880)
  Schizomavella mamillata (Hincks, 1880)
  Hippoporina Neviani, 1895
  Hippoporina reticulatopunctata (Hincks, 1877)
  Hippoporina ussowi (Kluge, 1908)
  Hippoporina propinqua (Smitt, 1868)
  Pentapora Fischer, 1807
  Pentapora foliacea (Ellis and Solander, 1786)
Incertae sedis
  Kymella Canu and Bassler, 1917
  Kymella polaris (Waters, 1904)
Family **Watersiporidae** Vigneaux, 1949
  Watersipora Neviani, 1896
  Watersipora subtorquata (d'Orbigny, 1852)
Family **Schizoporellidae** Jullien, 1883
  Schizoporella Hincks, 1877
  Schizoporella unicornis (Johnston, 1847) – type sp.
  Schizoporella sp.
  Stylopoma Levinsen, 1909
  Stylopoma informata (Lonsdale, 1845)
Family **Stomachetosellidae** Canu and Bassler, 1917
  Cigclisula Canu and Bassler, 1927
  Cigclisula sp.
Family **Phorioppniidae** Gordon and d'Hondt, 1997
  Quadriscutella Bock and Cook, 1993
  Quadriscutella papillata Bock and Cook, 1993 – type sp.
Family **Porinidae** d'Orbigny, 1852
  Porina d'Orbigny, 1852
  Porina gracilis (Lamarck, 1816) – type sp.
Family **Margarettidae** Harmer, 1957
  Margaretta Gray, 1843
  Margaretta barbata (Lamarck, 1816) – type sp.
Family **Myriaporidae** Gray, 1841
  Myriapora de Blainville, 1830
  Myriapora truncata (Pallas, 1766) – type sp.

Family **Pacificincolidae** Liu and Liu, 1999
   Pacificincola Liu and Liu, 1999
     Pacificincola insculpta (Hincks, 1882)
Family **Gigantoporidae** Bassler, 1935
   Cylindroporella Hincks, 1877
     Cylindroporella tubulosa (Norman, 1868) – type sp.
Family **Lacernidae Jullien**, 1888, 1957
   Calyptotheca Harmer, 1957
     Calyptotheca triangula (Hincks, 1881)
     "Calyptotheca" variolosa (MacGillivray, 1869)
   Emballotheca Levinsen, 1909
     Emballotheca quadrata (MacGillivray, 1869) – type sp.
   Parmularia MacGillivray, 1887
     Parmularia smeatoni (MacGillivray, 1890)
Family **Cheiloporinidae** Bassler, 1936
   Cheiloporina Canu and Bassler, 1923
     Cheiloporina haddoni (Harmer, 1902)
Family **Cryptosulidae** Vigneaux, 1949
   Cryptosula Canu and Bassler, 1925
     Cryptosula pallasiana (Moll, 1803) – type sp.
Family **Microporellidae** Hincks, 1879
   Microporella Hincks, 1877
     Microporella ciliata (Pallas, 1766) – type sp.
   Fenestrulina Jullien, 1888
     Fenestrulina malusii (Audouin, 1826) – type sp.
     Fenestrulina sp.
Family **Calwelliidae** MacGillivray, 1887
   Calwellia Wyville Thomson, 1858
     Calwellia bicornis Wyville Thomson, 1858 – type sp.
     Calwellia gracilis Maplestone, 1882
Family **Petraliidae** Levinsen, 1909
   Petralia MacGillivray, 1869
     Petralia undata (MacGillivray, 1869) – type sp.
Incertae sedis
   Isoschizoporella Rogick, 1960
     Isoschizoporella tricuspis (Calvet, 1909)
     Isoschizoporella secunda Hayward and Taylor, 1984
Family **Petraliellidae** Harmer, 1957
   Mucropetraliella Stach, 1936
     Mucropetraliella ellerii (MacGillivray, 1869) – type sp.
Family **Cyclicoporidae** Hincks, 1884
   Cyclicopora Hincks, 1884
     Cyclicopora longipora (MacGillivray, 1883) – type sp.
Family **Eminooeciidae** Vigneaux, 1949
   Eminooecia Hayward and Thorpe, 1988
     Eminooecia carsonae (Rogick, 1957) – type sp.
Superfamily **Urceoliporoidea** Bassler, 1936

Family **Urceoliporidae** Bassler, 1936
   Urceolipora MacGillivray, 1881
     Urceolipora nana MacGillivray, 1881 – type sp.
   Reciprocus Gordon, 1988
     Reciprocus regalis Gordon, 1988 – type sp.
Superfamily **Euthyriselloidea** Bassler, 1953
  Family **Euthyrisellidae** Bassler, 1953
   Pleurotoichus Levinsen, 1909
     Pleurotoichus clathratus (Harmer, 1902) – type sp.
  Incertae sedis
   Neoeuthyris Bretnall, 1921
     Neoeuthyris woosteri (MacGillivray, 1891) – type sp.
Superfamily **Mamilloporoidea** Canu and Bassler, 1927
  Family **Crepidacanthidae** Levinsen, 1909
   Crepidacantha Levinsen, 1909
     Crepidacantha kirkpatricki Brown, 1954
  Family **Cleidochasmatidae** Cheetham and Sandberg, 1964
   Characodoma Maplestone, 1900
     Characodoma porcellanum (Busk, 1860)
Superfamily **Celleporoidea** Johnston, 1838
  Family **Celleporidae** Johnston, 1838
   Galeopsis Jullien and Calvet, 1903
     Galeopsis porcellanicus (Hutton, 1873)
   Turbicellepora Ryland, 1963
     Turbicellepora crenulata Hayward, 1978
     Turbicellepora avicularis (Hincks, 1860)
   Celleporina Gray, 1848
     Celleporina caminata (Waters, 1879)
   Omalosecosa Canu and Bassler, 1925
     Omalosecosa ramulosa Busk, 1854 – type sp.
  Family **Hippoporidridae** Vigneaux, 1949
   Hippoporella Canu, 1917
     Hippoporella hippopus (Smitt, 1867) – type sp.
  Family **Colatooeciidae** Winston, 2005
   Trematooecia Osburn, 1940
     Trematooecia aviculifera (Canu and Bassler, 1923)
  Family **Phidoloporidae** Gabb and Horn, 1862
   Rhynchozoon Hincks, 1895
     Rhynchozoon solidum Osburn, 1914
     Rhynchozoon sp.
   Reteporella Busk, 1884
     Reteporella sp.
   Stephanollona Duvergier, 1920
     Stephanollona longispinata (Busk, 1884)
Superfamily **Conescharellinoidea** Levinsen, 1909
  Family **Lekythoporidae** Levinsen, 1909
   Poecilopora MacGillivray, 1886
     Poecilopora anomala MacGillivray, 1886 – type sp.

Diagnoses for the Newly Established Taxa

Suborder **Tendrina** subord. nov.

Diagnosis as in family.

Superfamily **Tendroidea** Vigneaux, 1949

Diagnosis as in family.

Family **Tendridae** Vigneaux, 1949

Diagnosis. Colony encrusting, uniserial to loosely pluri-serial and multiserial. Autozooids of malacostegan-grade structure, with well-developed smooth gymnocyst and large oval opesia. Mural spines normally present, articulated and non-articulated. No avicularia. Simultaneous incubation of several embryos of same age in acanthostegal brood chamber formed by mural spines of either autozooid (*Tendra*) or distal kenozooid (*Heteroecium*). In latter case it fuses with egg-producing autozooidal polymorph to form cormidial brood complex. Intertentacular organ may be present (recorded in *Tendra*). Lateral septula multiporous. Ancestrula autozooidal.

Time range: Recent.

Remarks. The structure of the acanthostegal brood chambers indicates that they (and the non-feeding larva) must have originated independently of the ovicells and larvae in Flustrina. The most recent ancestor of Tendridae was a mala-costegine cheilostome with an intertentacular organ and non-articulated mural spines. Multiplication and compaction of these spines was a necessary first step in the origin of the protective 'roof' of the brood chamber.

Suborder **Thalamoporellina** subord. nov.

Diagnosis as in superfamily.

Superfamily **Thalamoporelloidea** Levinsen, 1902

Diagnosis. Colony encrusting or erect. Zooids with depressed porous cryptocyst which generally reaches the opercular area; if so, one or a pair of large opesiules and a polypide tube are present, and there is a small opesia coinci-dent with the orifice. Internal free spicules usual. Avicularia, when present, vicarious or subvicarious/interzooidal. Embryos brooded in ovicells (Thalamoporellidae) or internal brood sacs (Steginoporellidae). Ovicells, when present, hyperstomial, cleithral, simultaneously incubating two to several embryos of different ages. Ooecium with median suture, formed from maternal autozooid. Large intertentacular organ may be present. Lateral septula multiporous or bipo-rous. Ancestrula autozooidal or kenozooidal.

Time range: Lutetian (Early-Middle Eocene) – Recent.

Remarks. Among both Thalamoporellidae and Steginoporellidae, *Thalamoporella* is exceptional in possess-ing ovicells whose structure, placement and inception indi-cate that they (and the non-feeding larva) must have originated independently of Flustrina. *Thalamoporella* and *Steginoporella*, both known from the Lutetian evidently had a malacostegine ancestor. *Thalamoporella* evolved by inde-pendently acquiring an extensive cryptocyst and bilobate ovicells formed by the extension and fusion of a pair of fron-tal tubercles. The evolution of brooding was accompanied by a shift from larval planktotrophy to lecithotrophy. Ovicells were substituted by internal brood sacs in steginoporellids and in other thalamoporellids. 'Marsupial' ovicell-like struc-tures situated proximal to the autozooidal orifice of the Recent *Marsupioporella*, and the reduction of the cryptocyst in *Hesychoxenia* were apparently later developments. Note that the Cretaceous genus *Dimorphomicropora* provisionally included by some in the Steginoporellidae, was probably an unrelated thalamoporelline homeomorph.

Suborder **Belluloporina** subord. nov.

Diagnosis as in family.

Superfamily **Belluloporoidea** superfam. nov.

Diagnosis as in family.

Family **Belluloporidae** fam. nov.

Diagnosis. Colony encrusting, multiserial. Autozooids of cribrimorph-grade organization, with very narrow smooth gymnocyst and frontal membranous wall overarched by cos-tae. Each costa a kenozooid with a long strip of hypostegal coelom confluent with visceral coelom of autozooid via a communication pore with a cuticular annulus. Costae joined to their neighbours via short lateral fusions, leaving rows of bean-shaped lacunae between fusions. Articulated oral spines present. Pedunculate adventitious avicularia on either side of zooidal aperture. Ovicell hyperstomial, cleithral, formed by fused costae of the distal kenozooid that has membranous frontal wall serving as ovicell floor. Basal pore chambers present. Ancestrula tatiform with mural spines sur-rounding frontal membrane.

Time range: Pleistocene – Recent.

Remarks. The kenozooidal nature of the ooecial costae indicates that these brood chambers must have originated independently of Flustrina. While the larva of *Bellulopora* has never been described, the suggestion that it is non-feeding is plausible. The putative ancestor of *Bellulopora* would have had a malacostegan-grade organization with numerous mural kenozooidal spines. Their fusion led to an independent origin of the spinocyst (and costate ooecia) in this genus. The exam-ple of Belluloporidae indicates that cheilostome spines may originally have been zooid polymorphs. It is rather probable that similar cheilostomes (both malacostegans and 'cribri-morphs') with kenozooidal spines should be more wide-spread, but their recognition in the fossil record is problematic since the organic annulus that is characteristic of conventional communication pores is not preserved.

Superfamily **Monoporelloidea** Hincks, 1882

Diagnosis. Colony encrusting (typically multiserial, sometimes uniserial or pluriserial) or erect (bilaminar-folded or dichotomously branching with flexible nodes). Zooids with opesiules and pores in an extensive cryptocyst, forming a small opesia coincident with the orifice. Gymnocystal rim

present or absent. Articulated oral spins typically present. Ovicells hyperstomial, cleithral, simultaneously incubating two to four embryos (*Monoporella, Macropora*). Ooecium constructed either from basally articulated spines (*Stichomicropora*) or costae (*Stichomicropora, Monoporella, Macropora*), formed from distal autozooid or kenozooid. In *Monoporella* and *Macropora* costae are partially or totally embedded into cryptocystal matrix covered by membranous wall with hypostegal coelom underneath. In *Stichomicropora* and *Monoporella* ovicell has two lateral foramina. Vicarious avicularia present in *Stichomicropora* and *Macropora*. Basal pore chambers present. Ancestrula autozooidal.

Time range: Cenomanian (Late Cretaceous) – Recent.

Remarks. The superfamily includes the families Monoporellidae (*Stichomicropora, Monoporella*) and Macroporidae (*Macropora*). *Stichomicropora* shares a primitive ooecium of articulated spines with calloporids of the same age (Cenomanian) that can be considered as an ancestral group. The earliest species of *Monoporella* is known from Maastrichtian when *Stichomicropora* became extinct. Both genera share a comb- or arch-like positioning of the ovicell spines/costae lateral ovicell foramina. *Macropora* evolved in the Thanetian (Late Paleocene), and, together with *Monoporella*, survived to the present day. In contrast with the latter genus, *Macropora* has a horse-shoe positioning of ovicell costae.

References

Abbott MB (1973) Seasonal diversity and density in bryozoan populations of Block Island Sound (New York, U.S.A.). In: Larwood GP (ed) Living and fossil Bryozoa: recent advances in research. Academic Press, London, pp 593–599

Abbott MB (1975) Relationship of temperature to patterns of sexual reproduction in some Recent encrusting Cheilostomata. In: Pouyet S (ed) Bryozoa 1974. Doc Lab Geol Fac Sci Lyon HS 3(1):37–50

Allen RM, Buckley YM, Marshall DJ (2008) Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. Am Nat 171(2):225–237

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

Banta WC (1968) *Mimosella cookae*, new species (Bryozoa, Ctenostomata) with a review of the family Mimosellidae. Bull So Calif Acad Sci 67:245–254

Banta WC (1969) *Uscia mexicana*, new genus, new species, a watersiporid bryozoan with dimorphic autozoids. Bull So Calif Acad Sci 68:30–35

Barnes DKA, Clarke A (1998) Seasonality of polypide recycling and sexual reproduction in some erect Antarctic bryozoans. Mar Biol 131:647–658

Barrois J (1877) Recherches sur l'embryologie des Bryozoaires. Trav St Zool Wimereux 1:1–305

Bassler RS (1953) Bryozoa. In: Moore RC (ed) Treatise on invertebrate paleontology. Part G. The University of Kansas Press for the Geological Society of America, Lawrence, pp 1–253

Basteri J (1762) Opuscula subseciva. J Bosch, Harlem

Bishop JDD, Manríquez PH, Hughes RN (2000) Water-borne sperm trigger vitellogenic egg growth in two sessile marine invertebrates. Proc R Soc B 267:1165–1169

Bobin G, Prenant M (1954) Sur un Bryozoaire perforant, *Terebripora comma* (Soule), trouvé en Mediterranée. Arch Zool Exp Gen 91:130–144

Bobin G, Prenant M (1957) Les cellules cystidiennes et les phénomènes d'histolyse et de phagocytose chez *Alcyonidium gelatinosum* (L.) (Bryozoaire Cténostome). Bull Biol France Belg 49:205–224

Bock PE, Cook PL (1998) Otionellidae, a new family including five genera of free-living lunulitiform Bryozoa (Cheilostomatida). Mem Sci Geol 50:195–211

Bonnevie K (1906) Physiologische Polyspermie. Arch Math Naturvid 27(13):275–289

Bonnevie K (1907) Untersuchungen über Keimzellen. II. Physiologische Polyspermie bei Bryozoen. Jen Z Naturwis 42, NF 35:567–598

Borg F (1947) Zur Kenntnis der Ökologie und des Lebenszyklus von *Electra crustulenta*. Zool Bid Uppsala 25:344–377

Braem F (1896) Die geschlechtliche Entwicklung von *Paludicella ehrenbergii*. Zool Anz 19(493):54–57

Braem F (1908a) Die Spermatozoen der Süßwasser-Bryozoen. Zool Anz 32:671–673

Braem F (1908b) Die Spermatozoen von *Paludicella* und *Triticella*. Zool Anz 33(11):380–381

Braem F (1940) *Victorella sibogae* Harmer. Z Morphol Okol Tiere 36:267–278

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

Braiko VB (1967) Biology of reproduction of *Membranipora zostericola* Nordm. (Bryozoa). Zool Zhurn 46:1119–1121 [in Russian]

Brien P (1960) Classe des Bryozoaires. In: Grassé P-P (ed) Traité de zoologie. Paris, Masson 5(2):1053–1379

Bronn HG (1862) Moostierchen: Bryozoa Ehrb. (Bryacephala). In: Die Klassen und Ordnungen der Weichthiere (Malacozoa), wissenschaftlich dargestellt in Wort und Bild. CF Winter'sche Verlagshandlung, Leipzig/Heidelberg

Brown DA (1952) The Tertiary cheilostomatous Polyzoa of New Zealand. Trustees of British Museum (Natural History), London

Bullivant JS (1967) Release of sperm by Bryozoa. Ophelia 4:139–142

Burgess SC, Hart SP, Marshall DJ (2009) Pre-settlement behavior in larval bryozoans: the role of larval age and size. Biol Bull 216:344–354

Busk G (1852) An account of the Polyzoa and sertularian zoophytes collected in the voyage of the Rattlesnake on the coasts of Australia and Louisiade Archipelago. In: MacGillivray J (ed) Narrative of the voyage H.M.S. Rattlesnake commanded by the late Captain Owen Stanley, during the years 1846–1850. T and W Boone, London, pp 343–402

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

Busk G (1884) Report on the Polyzoa collected by H. M. S. Challenger during the years 1873–1876. Rep Sci Res Voy HMS Challenger 1873–1876, Zool 10(30):1–216

Cadman PS, Ryland JS (1996) The characters, reproduction, and growth of *Alcyonidium mytili* Dalyell, 1848 (Ctenostomatida). In: Gordon DP, Smith AM, Grant-Mackie JA (eds) Bryozoans in space and time. National Institute of Water and Atmospheric Research, Wellington, pp 237–242

Calvet L (1900) Contribution à l'histoire naturelle des Bryozoaires Ectoproctes marins. Trav Inst Zool Univ Montp NS 8:1–488

Cancino JM (1986) Marine macroalgae as a substratum for sessile invertebrates: a study of *Celleporella hyalina* (Bryozoa) on fronds of *Laminaria saccharina* (Phaeophyta). Monogr Biol 4:279–308

Cancino JM, Hughes RN (1987) The effect of water flow on growth and reproduction of *Celleporella hyalina* (L.) (Bryozoa: Cheilostomata). J Exp Mar Biol Ecol 112:109–131

Cancino JM, Hughes RN (1988) The zooidal polymorphism and astogeny of *Celleporella hyalina* (Bryozoa: Cheilostomata). J Zool 215:167–181

Cancino JM, Castañeda B, Orellana C (1991) Reproductive strategies in bryozoans: experimental test of the effects of conspecific neighbours. In: Bigey FP (ed) Bryozoaires actuels et fossiels: Bryozoa living and fossil. Bull Soc Sci Nat Ouest France, Mem HS 1:81–88

Canu F, Bassler RS (1920) North American early Tertiary Bryozoa. Bull US Natl Mus 106:I–XX, 1–879

Canu F, Bassler RS (1923) North American later Tertiary Bryozoa. Bull US Natl Mus 125:I–VII, 1–244

Canu F, Bassler RS (1928) Fossil and recent Bryozoa of the Gulf of Mexico region. Proc US Natl Mus 72(2710):1–165

Canu F, Bassler RS (1929) Bryozoa of the Philippine region Bull US Natl Mus 100(9):I–I, 1–685

Carter MC, Gordon DP (2007) Substratum and morphometric relationships in the bryozoan genus *Odontoporella*, with a description of a new paguridean-symbiont species from New Zealand. Zool Sci 24:47–56

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

Cheetham AH (1954) A new early Cretaceous cheilostome bryozoan from Texas. J Paleontol 28(2):177–184

Cheetham AH, Cook PL (1983) General features of the class Gymnolaemata. In: Robinson RA (ed) Treatise on invertebrate paleontology, vol 1. Geological Society of America/University of Kansas, Lawrence/Boulder, pp 138–207

Chimonides PJ, Cook PL (1981) Observations on living colonies of *Selenaria* (Bryozoa, Cheilostomata). II. Cah Biol Mar 22(2):207–219

Chrétien M (1958) Histologie et dévelopment de l'ovaire chez *Alcyonidium gelatinosum* (L.) (Bryozoaire cténostome). Bull Lab Marit Dinard 43:25–51

Claparède E (1871) Beiträge zur Anatomie und Entwicklungsgeschichte der Seebryozoen. Z Wiss Zool 21:138–174

Cook PL (1960) The development of *Electra crustulenta* (Pallas) (Polyzoa, Ectoprocta). Essex Nat 30(4):258–266

Cook PL (1962) The early larval development of *Membranipora seurati* (Canu) and *Electra crustulenta* (Pallas), Polyzoa. Cah Biol Mar 3(1):57–60

Cook PL (1964a) The development of *Electra monostachys* (Busk) and *Conopeum reticulum* (Linnaeus), Polyzoa, Anasca. Cah Biol Mar 5:391–397

Cook PL (1964b) Polyzoa from west Africa. I. Notes on Steganoporellidae, Thalamoporellidae and Onychocellidae (Anasca, Coilostega). Ann Inst Oceanogr (Calypso IV) 41:43–78

Cook PL (1968) Observations on living Bryozoa. Att Soc Ital Sci Nat Mus Civ Stor Nat Milano 108:155–160

Cook PL (1977) Early colony development in *Aetea* (Bryozoa). Am Zool 17:55–61

Cook PL (1979) Some problems in interpretation of heteromorphy and colony integration in Bryozoa. In: Larwood GP, Rosen BR (eds) Biology and systematics of colonial organisms. Systematics Association special vol 11. Academic Press, London/New York, pp 193–210

Cook PL (1985) Bryozoa from Ghana. Zool Wet Mus Roy Afr Centr Tervuren Belgique 238:1–315

Cook PL, Bock PE (2000) Two new genera of Bryozoa (Calloporidae) from New Zealand. J Nat Hist 34:1125–1133

Cori CJ (1941) Bryozoa. Ordnung der Tentaculata. Handbuch der Zoologie III. 2 (5):263–374, 375–502

Corrêa DD (1948) A embryologia de *Bugula flabellata* (J. V. Thompson) Bryozoa Ectoprocta. Bol Fac Fil Ci Letr Univ S Paulo Zool 13:7–71

d'Hondt J-L (1983) Tubular keys for identification of recent Ctenostomatous Bryozoa. Mem Inst Oceanogr Monaco 14:1–134

d'Hondt J-L (1994) Etat des connaissances sur les cycles de developpement chez les Bryozoaires. Bull Soc Zool Fr 119(3):275–283

de Lamarck JBPAM (1816) Histoire naturelle des animaux sans vertèbres, vol 2. Verdière, Paris

de Lamarck JBPAM (1836) Histoire naturelle des animaux sans vertèbres, vol 2, 2nd edn. JB Baillière, Paris

Dalyell JG (1848) Rare and remarkable animals of Scotland, represented from living subjects: with practical observations on their nature. Vol 2. J Van Voorst, London

Delage Y, Hérouard E (1897) Bryozoaires. – Bryozoaria. In: Frères S (ed) Traité de zoologie concrète, Les Vermidiens – Vermidea, vol 5. Librairie C Reinwald, Paris, pp 47–155

Dudley JE (1973) Observations on the reproduction, early larval development, and colony astogeny of *Conopeum tenuissimum* (Canu). Chesapeake Sci 14(4):270–278

Dyrynda PEJ (1981) A preliminary study of patterns of polypide generation-degeneration in marine cheilostome Bryozoa. In: Larwood GP, Nielsen C (eds) Recent and fossil Bryozoa. Olsen and Olsen, Fredensborg, pp 73–81

Dyrynda PEJ, King PE (1982) Sexual reproduction in *Epistomia bursaria* (Bryozoa: Cheilostomata), an endozooidal brooder without polypide recycling. J Zool 198:337–352

Dyrynda PEJ, King PE (1983) Gametogenesis in placental and non-placental ovicellate cheilostome Bryozoa. J Zool 200:471–492

Dyrynda PEJ, Ryland JS (1982) Reproductive strategies and life histories in the cheilostome marine bryozoans *Chartella papyracea* and *Bugula flabellata*. Mar Biol 71:241–256

Eggleston D (1963) The marine Polyzoa of the Isle of Man. PhD dissertation, University of Liverpool

Eggleston D (1969) Marine fauna of the Isle of Man. Supplement 1. Entoprocta and Ectoprocts. Rep Mar Biol Stat Port Erin 81:57–80

Eggleston D (1971) Synchronization between moulting in *Calocaris macandreae* (Decapoda) and reproduction in its epibiont *Triticella koreni* (Polyzoa Ectoprocta). J Mar Biol Assoc UK 51:404–410

Eggleston D (1972) Patterns of reproduction in the marine Ectoprocta of the Isle of Man. J Nat Hist 6:31–38

Ehlers E (1876) *Hypophorella expansa*. Ein beitrag zur Kenntniss der minirenden Bryozoen. Abh Phys Clas Konig Ges Wiss Göttingen 21:3–157

Elkin C, Marshall DJ (2007) Desperate larvae: influence of deferred costs and habitat requirements on habitat selection. Mar Ecol Prog Ser 335:143–153

Ellis J (1753) Observations on a remarkable coralline, in a letter from Mr. John Ellis to the Rev. Thomas Birch, D. D. Secret. R. S. Philos Trans R Soc 48(pt 1):115–117

Ellis J (1755) An essay towards a natural history of the corallines, and other marine productions of the like kind, commonly found on the coasts of Great Britain and Ireland. A Millar, London

Ellis J, Solander D (1786) The natural history of many curious and uncommon Zoophytes, collected from various parts of the globe by the late John Ellis, Esq. F.R.S. Soc. Reg. Upsal. Soc. author of the natural history of English corallines and other works. Systematically arranged and described by the late Daniel Solander, M.D. F. R. S & c. Benjamin White and Sons, London

Farre AB (1837) Observations on the minute structure of some of the higher forms of polypi, with views of a more natural arrangement of the class. Philos Trans R Soc 1:387–426

Faulkner GH (1933) The relation between somatic and germ cells in the asexually produced polyps of the polyzoon *Alcyonidium gelatinosum*. Ann Mag Nat Hist, 10 Ser, 11(63):255–269

Franzén Å (1956) On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates. Zool Bidr Uppsala 31:355–481

Franzén Å (1970) Phylogenetic aspects of the morphology of spermatozoa and spermiogenesis. In: Baccetti B (ed) Comparative spermatology. Academic Press, New York, pp 29–46

Franzén Å (1976) On the ultrastructure of spermiogenesis of *Flustra foliacea* (L.) and *Triticella korenii* G.O. Sars (Bryozoa). Zoon 4:19–29

Franzén Å (1977) Gametogenesis of bryozoans. In: Woollacott RM, Zimmer RL (eds) Biology of bryozoans. Academic Press, New York/San Francisco/London, pp 1–22

Franzén Å (1981) Comparative ultrastructural studies of spermatids and spermatozoa in Bryozoa and Entoprocta. In: Larwood GP, Nielsen C (eds) Recent and fossil Bryozoa. Olsen and Olsen, Fredensborg, pp 82–92

Franzén Å (1983) Bryozoa Ectoprocta. In: Adiyodi KG, Adiyodi RG (eds) Reproductive biology of invertebrates, vol 2, Spermatogenesis and sperm function. John Wiley and Sons, Chichester, pp 491–504

Franzén Å (1987a) Sperm ultrastructure in the Bryozoa. In: Ross JRP (ed) Bryozoa: present and past. Western Washington University, Billingham, pp 89–96

Franzén Å (1987b) Spermatogenesis. In: Giese AC, Pearse JS, Pearse VB (eds) Reproduction of marine invertebrates, vol 9, General aspects: seeking unity in diversity. Boxwood Press, Pacific Grove, pp 1–47

Franzén Å (1998) Spermatogenesis, sperm structure and spermatozeugmata in the gymnolaematous bryozoan *Electra pilosa* (Bryozoa, Gymnolaemata). Invertebr Reprod Dev 34(1):55–63

Friedl H (1925) Kolonienbildung. Besiedelung und Wachstum bei marinen Bryozoen. Arb Zool Inst Univ Innsbruck 2(3):139–168

Gautier YV (1962) Recherches écologiques sur les Bryozoaires chilostomes en Méditerranèe Occidentale. Rec Trav Stat Mar Endoume 39:1–434

Gerwerzhagen A (1913) Untersuchungen an Bryozoen. Sitz Heidelb Akad Wiss Math Kl B 9:1–16

Gordon DP (1968) Zooidal dimorphism in the polyzoan *Hippopodinella adpressa* (Busk). Nature 219:633–634

Gordon DP (1970) Reproductive ecology of some northern New Zealand Bryozoa. Cah Biol Mar 11:307–323

Gordon DP (1982) The genera of the Chaperiidae (Bryozoa). NZ J Zool 9:1–24

Gordon DP (1984) The marine fauna of New Zealand: Bryozoa: Gymnolaemata from the Kermadec Ridge. NZ Oceanogr Inst Mem 91:1–198

Gordon DP (1986) The marine fauna of New Zealand: Bryozoa: Gymnolaemata (Ctenostomata and Cheilostomata Anasca) from the Western South Island continental shelf and slope. NZ Oceanogr Inst Mem 95:1–121

Gordon DP, Grischenko AV (1994) Bryozoan frontal shields: the type species of *Desmacystis*, *Rhamphostomella*, *Rhamphosmittina*, *Rhamphostomellina*, and new genus *Arctonula*. Zool Scr 23(1):61–72

Grant RE (1827) Observations on the structure and nature of Flustrae. Edinburgh New Phylos J 3:107–118, 337–342

Grave BH (1930) The natural history of *Bugula flabellata* at Woods Hole, Massachusetts, including the behaviour and attachment of the larva. J Morph 49:355–383

Grellet P (1958) Histologie du testicule et spermatogénèse chez *Alcyonidium gelatinosum* (L.) (Bryozoaire cténostome). Bull Lab Marit Dinard 43:1–24

Grischenko AV, Mawatari SF (2005) *Oshurkovia*: a new genus of Umbonulidae (Bryozoa: Cheilostomata) from the northwest Pacific. In: Moyano HIG, Cancino JM, Wyse Jackson PN (eds) Bryozoan studies 2004. AA Balkema Publishers, Lisse, pp 99–106

Hageman GS (1981) Accessory reproductive structures in *Membranipora serrilamella*: a fine structural study. In: Larwood GP, Nielsen C (eds) Recent and fossil Bryozoa. Olsen and Olsen, Fredensborg, p 311

Hageman GS (1983) A fine structural analysis of ovarian morphology, oogenesis, and ovulation in marine bryozoan *Membranipora serrilamella* (Cheilostomata, Anasca). PhD dissertation, University of Southern California

Hancock A (1850) On the anatomy of the freshwater Bryozoa, with descriptions of three new species. Ann Mag Nat Hist 5(27):173–204

Harmer SF (1892) On the nature of the excretory processes in marine Polyzoa. Q J Micr Sci 33:123–167

Harmer SF (1902) On the morphology of the Cheilostomata. Q J Micr Sci 46(182):263–350

Harmer SF (1915) The Polyzoa of the Siboga expedition. Part 1. Entoprocta, Ctenostomata and Cyclostomata. Rep Siboga Exp 28A:1–180, EJ Brill, Leiden

Harmer SF (1926) The Polyzoa of the Siboga expedition. II. Cheilostomata Anasca. Rep Siboga Exp 28b:181–501, EJ Brill, Leiden

Harmer SF (1957) The Polyzoa of the Siboga expedition. IV. Cheilostomata Ascophora. II. Rep Siboga Exp 28d:641–1147, EJ Brill, Leiden

Harvell CD, Helling R (1993) Experimental induction of localized reproduction in a marine bryozoan. Biol Bull 184(3):286–295

Hassall AH (1841) Description of two new genera of Irish Zoophytes. Ann Mag Nat Hist, 1 Ser 7(46):483–486

Hastings AB (1930) Cheilostomatous Polyzoa from the vicinity of the Panama Canal collected by Dr. C. Crossland on the cruise of the S.Y. "St. George". Proc Zool Soc Lond 4(47):697–740

Hastings AB (1932) The Polyzoa with a note on an associated hydroid. Sci Rep Great Barrier Reef Exp 1928–29 4(12):399–458

Hastings AB (1941) The British species of *Scruparia* (Polyzoa). Ann Mag Nat Hist, 11 Ser, 7,(41):465–472

Hastings AB (1943) Polyzoa (Bryozoa). I. Scrupocellariidae, Epistomiidae, Farciminariidae, Bicellariellidae, Aeteidae, Scrupariidae. Discov Rep 22:301–510

Hastings AB (1944) Notes on Polyzoa (Bryozoa).-I. *Umbonula verrucosa auctt.*: *U. ovicellata*, sp. n. and *U. littoralis*, sp. n. Ann Mag Nat Hist, 11 Ser, 11(77):273–284

Hastings AB (1964) The cheilostomatous Polyzoa *Neoeuthyris woosteri* (MacGillivray) and *Reginella doliaris* (Maplestone). Bull Br Mus (Nat Hist) 11(3):243–262

Hayward PJ (1983) Bryozoa Ectoprocta. In: Adiyodi KG, Adiyodi RG (eds) Reproductive biology of invertebrates, vol Oogenesis, oviposition and oosorption, 1. John Wiley and Sons, Chichester, pp 543–560

Hayward PJ (1985) Ctenostome bryozoans. Synopses Br Fauna 33:1–169

Hayward PJ, Ryland JS (1975) Growth, reproduction and larval dispersal in *Alcyonidium hirsutum* (Fleming) and some other Bryozoa. Pub Staz Zool Napoli 39(suppl):226–241

Hincks T (1851) Notes on British Zoophytes, with descriptions of some new species. Ann Mag Nat Hist, 2 Ser, 8(47):353–362

Hincks T (1861) Note on the ovicells of the cheilostomatous Polyzoa. Q J Micr Sci NS 1:278–281

Hincks T (1873) Contributions to history of Polyzoa. Q J Micr Sci NS 13:17–37

Hincks T (1878) Note of the movements of the vibracula in *Caberea Boryi*, and on the supposed common nervous system in the Polyzoa. Q J Micr Sci NS 18:7–9

Hincks T (1880) A history of the British marine Polyzoa. John Van Voorst, London

Hincks T (1892) Contributions towards a general history of the marine Polyzoa, 1880–91. – Appendix. Ann Mag Nat Hist, 6 Ser, 9(52):327–334

Hoare K, Hughes RN, Goldson AJ (1999) Molecular genetic evidence for the prevalence of outcrossing in the hermaphroditic brooding bryozoan *Celleporella hyalina*. Mar Ecol Prog Ser 188:73–79

Hughes DJ (1987) Gametogenesis and embryonic brooding in the cheilostome bryozoan *Celleporella hyalina*. J Zool 212:691–711

Hughes DJ (1989) Variation in reproductive strategy among clones of the bryozoan *Celleporella hyalina*. Ecol Monogr 59(4):387–403

Hughes DJ, Hughes RN (1987) Life history variation in *Celleporella hyalina* (Bryozoa). Proc R Soc B 228(1251):109–224

Hughes RN, Wright P, Manríquez PH, Bishop JDD (2002a) Predominance of obligate outbreeding in the simultaneous hermaphrodite *Celeporella hyalina* sensu lato. In: Wyse Jackson PN, Buttler CJ, Spencer Jones M (eds) Bryozoan studies 2001. AA Balkema Publishers, Lisse/Abingdon/Exton/Tokyo, pp 159–162

Hughes RN, Manríquez PH, Bishop JDD (2002b) Female investment is retarded pending reception of allosperm in a hermaphroditic colonial invertebrate. Proc Natl Acad Sci USA 99(23): 14884–14886

Hughes RN, Wright PJ (in press) Self-fertilisation in the *Celleporella angusta* clade and a description of *Celleporella osiani* sp. nov. In: Rosso A, Wyse Jackson PN, Porter J (eds) Bryozoan studies 2013. Proceedings of the 16th International Bryozoology Association conference, Catania. Stud Trent Sci Nat

Hunter E, Hughes RN (1993) Self-fertilization in *Celleporella hyalina*. Mar Biol 115:495–500

Hunter E, Hughes RN (1995) Environmental and genetic components of variation in sexual allocation by an epialgal bryozoan. Mar Ecol Prog Ser 120:193–201

Hunter E, Hughes RN, Goldson A (1996) Environmental and genetic control of somatic and sexual performance in *Celleporella hyalina* L. In: Gordon DP, Smith AM, Grant-Mackie JA (eds) Bryozoans in space and time. National Institute of Water and Atmospheric Research, Wellington, pp 149–156

Huxley TH (1856) Note on the reproductive organs of the cheilostome Polyzoa. Q J Microsc Sci 4:191–192

Hyatt A (1866–1868) Observations on polyzoa. Suborder Phylactolaemata. Proc Essex Inst 4–5:1–103

Hyman LH (1959) The invertebrates: smaller coelomate groups, vol 5: VIII. McGraw-Hill, New York

Jackson JBC, Wertheimer SP (1985) Patterns of reproduction in five common species of Jamaican reef-associated bryozoans. In: Nielsen C, Larwood GP (eds) Bryozoa: Ordovician to recent. Olsen and Olsen, Fredensborg, pp 161–168

Jebram D (1973) The importance of different growth directions in the Phylactolaemata and Gymnolaemata for reconstructing the phylogeny of the Bryozoa. In: Larwood GP (ed) Living and fossil Bryozoa: recent advances in research. Academic, London, pp 565–576

Jebram D (1985) *Panolicella nutans*, gen. et sp. n., its description, development, and laboratory cultivation. Zool Scr 14:11–18

Jebram D, Everitt B (1982) New victorellids (Bryozoa, Cenostomata) from North America: the use of parallel cultures in bryozoan taxonomy. Biol Bull 163:172–187

Johnson CH (2010) Effects of selfing on offspring survival and reproduction in a colonial simultaneous hermaphrodite (*Bugula stolonifera*, Bryozoa). Biol Bull 219:27–37

Johnston G (1838) A history of British Zoophytes. WH Lizars/S Highley/W Cuffy J, Edinburgh/London/Dublin

Johnston G (1847) A history of British Zoophytes. Van Voorst, London

Joliet L (1877a) Contributions à l'histoire naturelle des Bryozoaires des côtes de France. Arch Zool Exp Gen 6:193–304

Joliet L (1877b) Sur quelques points de l'organisation des Bryozoaires. Compt Rend Acad Sci Paris 85:406–408

Jullien J (1888a) Du testicule chez la *Lepralia figularis* Johnston, 1847, et des variétés de cet organe chez les bryozoaires en général. Mem Soc Zool France 1:270–273

Jullien J (1888b) Bryozoaires. Mission scientifique du Cap Horn, 1882–83, 6 (Zool Part 3):1–92

Jullien J, Calvet L (1903) Bryozoaires provenant des campagnes de l'Hirondelle (1886–1888). Res Camp Sci Monaco 23:1–188

Kaestner A (1963) Klasse Bryozoa Moostiere. Lehrbuch der speciellen Zoologie. Teil I: Wirbellose. Gustav Fisher Verlag, Jena, pp 1068–1100

Kawahara T (1960) Analysis of ecological phenomena in the community of the sessile organisms. (2). Growth, maturation and propagation in *Bugula neritina* Linné. Rep Fac Fish Univer Mie 3: 573–581

Kayser H (1984) *Nolella pusilla* (Bryozoa, Ctenostomata): cultivation, biology and first record from the German Bight. Helgol Meer 38:35–36

Kluge GA (1914) Die Bryozoan der Deutschen Südpolar-Expeditionen 1901–1903. 1. Die Familien Aetidae, Cellulariidae, Bicellaridae, Farciminaridae, Flustridae, Membraniporidae und Cribrilinidae. Deut Sudpol Exped 15, Zool 7:601–678

Kölliker A (1841) Beiträge zur kenntniss der geschlectsverhältnisse und der samen flüssigkeit wirbelloser thiere: nebst einem versuch über das wesen und die bedeutung der sogenannten samenthiere. W Logier, Berlin

Korschelt E, Heider K (1893) Lehrbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Thiere, vol 1. Gustav Fisher Verlag, Jena, pp 1–308

Korschelt E, Heider K (1910) Bryozoen. Lehrbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Thiere, 4(2):632–694, 892–894. Gustav Fisher Verlag, Jena

Kraepelin K (1887) Die Deutschen Süsswasser-Bryozoen. Anatomish-systematischer Teil. Abh Geb Nat Ver Hamburg 10:1–168

Kuklinski P, Porter JS (2004) *Alcyonidium disciforme*: an exceptional Arctic bryozoan. J Mar Biol Assoc UK 84:267–275

Kuznetzov VV (1941) Dynamics of the biocenosis of *Microporella ciliata* in the Barentz Sea. Proc Zool Inst Acad Sci USSR 7:114–139 [in Russian with French summary]

Lagaaij R (1963) New additions to the bryozoan fauna of the Gulf of Mexico. Publ Inst Mar Sci 9:181–236

Lamouroux JVF (1816) Histoire des Polypiers Coralligènes flexibles, vulgairement nommés Zoophytes. Poisson, Caen

Landsborough D (1852) Popular history of British zoophytes, or corallines. Reeve and Co, London

Lang WD (1916) A revision of the "Cribrimorph" Cretaceous Polyzoa. Ann Mag Nat Hist, 8 Ser, 18:81–112, 381–410

Levinsen GMR (1902) Studies on Bryozoa. Vid Med Dan Nat For København 54:1–31

Levinsen GMR (1909) Morphological and systematic studies on the Cheilostomatous Bryozoa. F Bagge, Copenhagen

Linnaeus C (1758) Systema naturae per regna tria naturae, 10th edn. Holmiae, Salvius, Stockholm

Linnaeus C (1760) Systema naturae per regna tria naturae, 11th edn. Curt, Halae Magdeburgicae

Linnaeus C (1767) Systema naturae per regna tria naturae, 12th edn. Holmiae, Salvius, Stockholm

Lutaud G (1961) Contribution à l'étude de bourgeonnement et de la croissance des colonies chez *Membranipora membranacea* (L), Bryozoaire Chilostome. Ann Soc Roy Zool Bel 91:157–300

Manríquez PH, Hughes RN, Bishop JDD (2001) Age-dependent loss of fertility in water-borne sperm of the bryozoan *Celleporella hyalina*. Mar Ecol Prog Ser 224:87–92

Manríquez PH, Hughes RN, Bishop JDD (2002) Female investment is retarded pending reception of allosperm in a hermaphroditic colonial invertebrate. Proc Natl Acad Sci USA 99(23):14884–14886

Marcus E (1922) Bryozoen von den Aru Inseln. Abh Senckenb Nat Ges 35:421–446

Marcus E (1926a) Beobachtungen und Versuche an lebeden Meeresbryozoen. Zool Jahrb Syst Oekol Geogr Tiere 52:1–102

Marcus E (1926b) Bryozoa. In: Grimpe G, Wagler E (eds) Die Tierwelt der Nord und Ostsee, Leipzig 4(7c): 1–100

Marcus E (1934) Über *Lophopus crystallinus* (Pall.). Zool Jahr Abt Anat Ont Tiere 58:501–606

Marcus E (1937) Bryozoarios marinhos brasileiros I. Bol Fac Phil Sci Letr Univ S Paulo I Zool 1:5–224

Marcus E (1938a) Bryozoarios marinhos brasileiros II. Bol Fac Phil Sci Letr Univ S Paulo IV, Zool 2:1–196

Marcus E (1938b) Bryozoen von St. Helena. Vid Med Dan Nat For København 101:183–252

Marcus E (1939) Bryozoarios marinhos brasileiros III. Bol Fac Fil Cie Letr Univ S Paulo XIII Zool 3:111–354

Marcus E (1940) Mosdyr (Bryozóa eller Polyzóa). Danmarks Fauna 46:1–401

Marcus E (1941a) Sobre Bryozoa do Brasil. Bol Fac Fil Cie Letr Univ S Paulo XXII Zool 5:3–208

Marcus E (1941b) Sobre o desenvolvimento do bryozoario *Synnotum aegyptiacum*. Arq Cirurg Clin Exp 5:227–234

Marcus E (1942) Sôbre Bryozoa do Brasil. II. Bol Fac Fil Cie Letr Univ S Paulo XXV Zool 6:57–106

Marshall DJ (2008) Transgenerational plasticity in the sea: context-dependent maternal effects across the life history. Ecology 89(2):418–427

Marshall DJ, Keough MJ (2003) Variation in the dispersal potential of non-feeding larvae: the desperate larva hypothesis and larval size. Mar Ecol Prog Ser 255:145–153

Marshall DJ, Keough MJ (2004a) Variable effects of larval size on post-metamorphic performance in the field. Mar Ecol Prog Ser 279:73–80

Marshall DJ, Keough MJ (2004b) When the going gets rough: effect of maternal size manipulation on larval quality. Mar Ecol Prog Ser 272:301–305

Marshall DJ, Keough MJ (2006) Complex life-cycles and offspring provisioning in marine invertebrates. Integr Comp Biol 46(5):643–651

Marshall DJ, Keough MJ (2008a) The relationship between offspring size and performance in the sea. Am Nat 171:214–224

Marshall DJ, Keough MJ (2008b) Offspring size plasticity in response to intraspecific competition: and adaptive maternal effect across life-history stages. Am Nat 171(2):225–237

Marshall DJ, Keough MJ (2009) Does interspecific competition affect offspring provisioning? Ecology 90(2):487–495

Marshall DJ, Uller T (2007) When is maternal effect adaptive? Oikos 116:1957–1963

Marshall DJ, Bolton TF, Keough MJ (2003) Offspring size affects the post-metamorphic performance of a colonial marine invertebrate. Ecology 84:3131–3137

Marshall DJ, Allen RM, Crean AJ (2008) The ecological and evolutionary importance of maternal effects in the sea. Oceanogr Mar Biol 46:203–250

Matricon I (1960) Dégénérescence du polypide femelle et formation d'une poche incubatrice chez *Alcyonidium polyoum* (Hassal) (Bryozoaire Cténostome). Arch Zool Exp Gen 102:79–93

Matricon I (1963) Etude histologique d'*Alcyonidium polyoum* (Hassall) caractères structuraux spécifiques d'*Alcyonidium mytili* Dalyell. Cah Biol Mar 1:359–395

Maturo FJS (1991a) Self-fertilisation in gymnolaemate Bryozoa. In: Bigey FP (ed) Bryozoaires actuels et fossiels: Bryozoa living and fossil. Bull Soc Sci Nat Ouest France, Mem HS 1:572

Maturo FJS (1991b) A new bryozoan structure: an ovipositor. In: Bigey FP (ed) Bryozoaires actuels et fossiels: Bryozoa living and fossil. Bull Soc Sci Nat Ouest France, Mem HS 1:572

Mawatari S (1951a) On the natural history of a common fouling bryozoan, *Bugula neritina* (Linnaeus). Misc Rep Res Inst Nat Res Tokyo 20:47–54

Mawatari S (1951b) On *Tricellaria occidentalis* (Trask), one of the fouling bryozoans in Japan. Studies on fouling Bryozoa in Japan № 7. Contr Res Inst Nat Res 501 8(22):9–16

Mawatari S (1952) On *Watersipora cucullata* (Busk) II. Misc Rep Res Inst Nat Res Tokyo 28:17–27

Mawatari S (1973a) Studies on Japanese anascan Bryozoa. 2. Division Scrupariina. Bull Nat Sci Mus Tokyo 16(4):605–624

Mawatari S (1973b) Studies on Japanese anascan Bryozoa. 1. Inovicellata. Bull Nat Sci Mus Tokyo 16(3):409–428

Mawatari SF (1975) The life history of *Membranipora serrilamella* Osburn (Bryozoa, Cheilostomata). Bull Libr Art Sci Sc Med Nihon Univ 3:19–57

Mawatari S, Mawatari SF (1975) Development and metamorphosis of the cyphonautes of *Membranipora serrilamella* Osburn. In: Pouyet S (ed) Bryozoa 1974. Doc Lab Geol Fac Sci Lyon, HS 3(1):13–18

Milne Edwards H (1836) Recherches anatomiques, physiologiques et zoologiques sur les Eschares. Ann Sci Nat Zool 2(6):5–53

Moosburgger M, Schwaha T, Walzl MG, Obst M, Ostrovsky AN (2012) The placental analogue and the pattern of sexual reproduction in the cheilostome bryozoan *Bicellariella ciliata* (Gymnolaemata). Front Zool 9:29

Morris PA (1980) The bryozoan family Hippothoidae (Cheilostomata-Ascophora), with emphasis on the genus *Hippothoa*. Allan Hancock Monogr Mar Biol 10:1–115

Mukai H, Terakado K, Reed CG (1997) Bryozoa. In: Harrison FW (ed) Microscopic anatomy of invertebrates, vol 13. Wiley-Liss, New York, pp 45–206

Müller F (1860) Das Kolonialnervensystem der Moosthiere, nachgewiesen an *Serialaria Continhii* n. sp. Arch Naturg 26(1):311–318

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

Nielsen C (1990) Bryozoa Ectoprocta. In: Adiyodi KG, Adiyodi RG (eds) Reproductive biology of invertebrates, vol 4, Part B: fertilization, development, and parental care. IBH Publishing Co Pvt Ltd, New Delhi/Bombay/Calcutta/Oxford, pp 185–200

Nitsche H (1869) Beobachtungen über die Entwicklungsgeschichte einiger chilostomen Bryozoen. Z Wiss Zool 20(1):1–13

Nitsche H (1871a) Beiträge zur Kenntnis der Bryozoen. III. Über die Anatomie und Entwickelungsgeschichte von *Flustra membranacea*. Z Wiss Zool 21(4):37–91

Nitsche H (1871b) On some interesting points concerning the mode of reproduction of the Bryozoa. Q J Microsc Sci 11:155–162

Nordmann MA (1839) Recherches microscopiques sur l'anatomie et le développement du *Tendra zostericola*, espèce de polype de la section des Bryozoaires. Ann Sci Nat, Ser 2, 11:185–191

O'Donoghue CH, de Watteville D (1944) Additional notes on Bryozoa from South Africa. Ann Natal Mus 10(3):407–432

Osburn RC (1950) Bryozoa of the Pacific coast of America. Part 1, Cheilostomata-Anasca. Allan Hancock Pacif Exp 14(1):1–269

Osburn RC (1952) Bryozoa of the Pacific coast of America, part 2: Cheilostomata-Ascophora. Allan Hancock Pacif Exp 14:271–611

Ostroumoff A (1886a) Contribution à l'étude zoologique et morphologique des Bryozoaires du Golfe de Sebastopol. Arch Slav Biol 2:8–25, 184–190, 329–355

Ostroumoff A (1886b) Research on bryozoans of the Sebastopol Bay in systematic and morphological respects. Works Soc Nat Imp Kazan Univ 16(2):1–124 [In Russian]

Ostroumoff A (1886c) Contribution à l'étude zoologique et morphologique des Bryozoaires du Golfe de Sebastopol. Arch Slav Biol 1:557–569

Ostrovsky AN (1998) Comparative studies of ovicell anatomy and reproductive patterns in *Cribrilina annulata* and *Celleporella hyalina* (Bryozoa: Cheilostomatida). Acta Zoologica 79(4):287–318

Ostrovsky (as Ostrovskii) AN (2004) Brood chambers (ovicells) of cheilostome bryozoans (Bryozoa: Gymnolaemata): structure, research history, and modern problematics. Russ J Mar Biol

30(3):169–182 [Russian version with English summary], 30(Suppl 1):S43–S55 [English version]

Ostrovsky AN (2008a) External versus internal and self- versus cross-fertilization in Bryozoa: transformation of the view and evolutionary considerations. In: Wyse Jackson PN, Spencer Jones ME (eds) Annals of bryozoology 2: aspects of the history of research on bryozoans. International Bryozoology Association, Dublin, pp 103–115

Ostrovsky AN (2008b) The parental care in cheilostome bryozoans: a historical review. In: Wyse Jackson PN, Spencer Jones ME (eds) Annals of bryozoology 2: aspects of the history of research on bryozoans. International Bryozoology Association, Dublin, pp 211–245

Ostrovsky AN (2013) From incipient to substantial: evolution of placentotrophy in a phylum of aquatic colonial invertebrates. Evolution 67(5):1368–1382

Ostrovsky AN, Taylor PD (2004) Systematics of Upper Cretaceous calloporid bryozoans with primitive spinose ovicells. Palaeontology 47(3):775–793

Ostrovsky AN, Vávra N, Porter JS (2008) Sexual reproduction in gymnolaemate Bryozoa: history and perspectives of the research. In: Wyse Jackson PN, Spencer Jones ME (eds) Annals of bryozoology 2: aspects of the history of research on bryozoans. International Bryozoology Association, Dublin, pp 117–210

Ostrovsky AN, Gordon D, Lidgard S (2009) Independent evolution of matrotrophy in the major classes of Bryozoa: transitions among reproductive patterns and their ecological background. Mar Ecol Prog Ser 378:113–124

Ostrovsky AN, Porter JS (2011) Pattern of occurrence of supraneural coelomopores and intertentacular organs in gymnolaematec bryozoans and its evolutionary implications. Zoomorphology 130:1–15

Ostrovsky AN, Schwaha T (2011) Ultrastructure of the placental analoge in ctenostome bryozoan *Zoobotryon verticillatum* (Delle Chiaje, 1828) (Gymnolaemata). In: Zaitseva OV, Petrov AA (eds) Modern problems of evolutionary morphology of animals. Proceedings of the 2nd all-Russian and international conference dedicated to the 105th anniversary of academician AV Ivanov. Zoological Institute of the Russian Academy of Sciences, St Petersburg, pp 254–256 [in Russian]

Owrid GMA, Ryland JS (1991) Sexual reproduction in *Alcyonidium hirsutum* (Bryozoa: Ctenostomata). In: Bigey FP (ed) Bryozoaires actuels et fossiels: Bryozoa living and fossil. Bull Soc Sci Nat Ouest France, Mem HS 1:317–326

Pace RM (1906) On the early stages in the development of *Flustrellidra hispida* (Fabricius), and on the existence of a "yolk nucleus" in the egg of this form. Q J Microsc Sci 50:435–478

Pallas PS (1766) Elenhus zoophytorum sistens generum adumbrationes generaliores et specierum cognitarum succinctas descriptiones cum selectis auctorum synonymus. P van Gleef, Hagae

Pallas PS (1787) Characteristic der Thierpflanzen, vol 1. Raspe, Nürnberg

Paltschikowa-Ostroumowa MW (1926) Kurze Bemerkung über den Ovidukt bei den Bryozoen. Zool Anz 65:100–102

Pergens E (1889) Untersuchungen an Seebryozoen. Zool Anz 12(317):504–510, (318):526–533

Porter JS (2004) Morphological and genetic characteristics of erect subtidal species of *Alcyonidium* (Ctenostomata: Bryozoa). J Mar Biol Assoc UK 84:243–252

Porter JS, Hayward PJ (2004) Species of *Alcyonidium* (Bryozoa: Ctenostomata) from Antarctica and Magellan Strait, defined by morphological, reproductive and molecular characters. J Mar Biol Assoc UK 84:253–265

Porter JS, Hayward PJ, Spencer Jones ME (2001) The identity of *Alcyonidium diaphanum* (Bryozoa: Ctenostomatida). J Mar Biol Assoc UK 81:1001–1008

Powell NA (1967a) Polyzoa (Bryozoa) – Ascophora – from north New Zealand. Discov Rep 34:199–394

Powell NA (1967b) Sexual dwarfism in *Cribrilina annulata* (Cribrilinidae-Bryozoa). J Fish Res Board Can 24(9):1905–1910

Prenant M, Bobin G (1956) Bryozoaires. 1. Entoproctes, Phylactolèmes, Cténostomes. Faune France 60:1–398

Prouho H (1889) Sur la reproduction de quelques Bryozoaires cténostomes. Compt Rend Hebd Sean Acad Sci Paris 109:197–198

Prouho H (1892) Contribution a l'histoire des bryozoaires. Arch Zool Exp Gen 10:557–656

Ranzoli F (1962) Ovogenesi e strutture Feulgen-positive in *Zoobothryon verticillatum* (Delle Chiaje). Atti Accad Sci Inst Bologna 9:139–143

Redfern P (1858) *Flustrella hispida* and its development. Q J Microsc Sci 6:96–102

Reed CG (1988) The reproductive biology of the gymnolaemate bryozoan *Bowerbankia gracilis* (Ctenostomata: Vesiculariida). Ophelia 29(1):1–23

Reed CG (1991) Bryozoa. In: Giese AC, Pearse JS, Pearse VB (eds) Reproduction of marine invertebrates, vol 6, Echinoderms and lophophorates. Boxwood Press, Pacific Grove, pp 85–245

Reger JF (1971) A fine structure study on spermiogenesis in the entoproct, *Bugula* sp. J Submicrosc Cytol 3:193–200

Reid J (1845) Anatomical and physiological observations on some Zoophytes. Ann Mag Nat Hist 16:385–400

Reinhard V (1875) Some communications on history of development of bryozoans. Works Soc Nat Imp Kharkov Univ 9:1–39 [in Russian]

Repiachoff W (1875) Zur Entwickelungsgeschichte der *Tendra zostericola*. Z Wiss Zool 25:129–142

Repiachoff W (1876) Zur Naturgeschichte der chilostomen Bryozoen. Z Wiss Zool 26:139–160

Repiachoff W (1878) Ueber die ersten embryonalen Entwicklungvorgänge bei *Tendra zostericola*. Z Wiss Zool 30(Suppl):411–423

Retzius G (1904) Zur Kenntnis der Spermien der Evertebtraten. Biol Untersuch NS 11(1):1–32

Retzius G (1905) Zur Kenntnis der Spermien der Evertebtraten. II. Die Spermien der Leptocardier, Teleostier und Ganoider. Biol Untersuch NS 12(9–10):79–115

Retzius G (1906) Die Spermien der Enteropneusten und der Nemertinen. Die Spermien der Turbellarien. Die Spermien der Bryozoen. Biol Untersuch NS 13(2–4):37–48

Retzius G (1909) Zur Kenntnis der Spermien der Insekten. Die Spermien von Aurelia aurita. Die Spermien der Nereiden. Die Spermien der Cestoden und der Trematoden. Die Spermien der Chaetognathen. Weiteres zur Kenntnis der Spermien der Bryozoen. Die Spermien von *Nassa reticulata*. Biol Untersuch NS 14(2–8):54–78

Retzius G (1910) Zur Kenntnis der Spermien der Echinodermen. Weitere Beiträge zur Kenntnis der Spermien mit besonderer Berücksichtigung der Kernsubstanz. Biol Untersuch NS 15(2–3):54–82

Richardson KC, Jarrett L, Finke EH (1960) Embedding in epoxy resins for ultrathin sectioning in electron microscopy. Stain Technol 35:313–323

Robertson A (1905) Non-encrusting chilostomatous Bryozoa of the West coast of North America. Publ Univ California Zool 2(5):235–322

Rogick MD (1956) Studies on marine Bryozoa. VII. *Hippothoa*. Ohio J Sci 56(3):183–191

Römer O (1906) Untersuchungen über die Knospung, Degeneration und Regeneration von einigen marinen ectoprocten Bryozoen. Z Wiss Zool 84(3):446–478

Ryland JS (1963) Systematic and biological studies on Polyzoa (Bryozoa) from western Norway. Sarsia 14:1–59

Ryland JS (1967) Polyzoa. Oceanogr Mar Biol 5:343–369

Ryland JS (1970) Bryozoans. Hutchinson University Library, London

Ryland JS (1974) Behaviour, settlement and metamorphosis of bryozoan larvae: a review. Thalassia Jugosl 10(1/2):239–262

Ryland JS (1976) Physiology and ecology of marine bryozoans. In: Russell FS, Yonge CM (eds) Advances in marine biology, vol 14. Academic Press, London/New York, pp 285–443

Ryland JS (1979) *Celleporella carolinensis* sp. nov. (Bryozoa Cheilostomata) from the Atlantic coast of America. In: Larwood GP, Abbott MB (eds) Advances in bryozoology. Systematics Association special vol 13. Academic Press, London/New York/San Francisco, pp 611–619

Ryland JS (1982) Bryozoa. In: Encyclopedia of science and technology, 5th edn. McGraw-Hill, New York, pp 458–466

Ryland JS (2001) Convergent colonial organization and reproductive function in two bryozoan species epizoic on gastropod shells. J Nat Hist 35:1085–1101

Ryland JS, Bishop JDD (1993) Internal fertilization in hermaphroditic colonial invertebrates. Oceanogr Mar Biol 31:445–477

Ryland JS, Gordon DP (1977) Some New Zealand and British species of *Hippothoa* (Bryozoa: Cheilostomata). J R Soc New Zeal 7(1):17–49

Ryland JS, Porter JS (2000) *Alcyonidium reticulum* sp. nov., a common intertidal bryozoan from south-west Britain. J Mar Biol Assoc UK 80:563–564

Ryland JS, Porter JS (2006) The identification, distribution and biology of encrusting species of *Alcyonidium* (Bryozoa: Ctenostomatida) around the coasts of Ireland. Proc R Irish Acad 106B(1):19–33

Salensky W (1874) Untersuchungen an Seebryozoen. Z Wiss Zool 24:343–348

Santagata S, Banta WC (1996) Origin of brooding and ovicells in cheilostome bryozoans: interpretive morphology of *Scrupocellaria ferox*. Invertebr Biol 115(2):170–180

Schulz K (1901) Untersuchungen über den Bau der Bryozoen mit besonderer Berücksichtigung der Exkretionsorgane. Arch Naturg 67(1):115–144

Seed R, Hughes RN (1992) Reproductive strategies of epialgal bryozoans. Invertebr Reprod Dev 22(1–3):291–300

Silbermann S (1906) Untersuchungen über den feineren Bau von *Alcyonidium mytili*. Arch Natur 72:265–308

Silén L (1942) Carnosa and Stolonifera (Bryozoa) collected by Prof. Dr. Sixten Bock's expedition to Japan and the Bonin Islands 1914. Ark Zool 34A(8):1–33

Silén L (1944) The anatomy of *Labiostomella gisleni* Silén (Bryozoa Protocheilostomata). Kongl Svenska Vetensk-Akad Handl Ser 3(21):1–111

Silén L (1945) The main features of the development of the ovum, embryo and ooecium in the ooecioferous Bryozoa Gymnolaemata. Ark Zool 35A(17):1–34

Silén L (1946) On two new groups of Bryozoa living in shells of molluscs. Ark Zool 38B(1):1–7

Silén L (1947) On the anatomy and biology of Penetrantiidae and Immergentiidae (Bryozoa). Ark Zool 40A(4):1–48

Silén L (1966) On the fertilization problem in gymnolaematous Bryozoa. Ophelia 3:113–140

Silén L (1972) Fertilization in the Bryozoa. Ophelia 10(1):27–34

Silén L (1977) Polymorphism. In: Woollacott RM, Zimmer RL (eds) Biology of bryozoans. Academic Press, New York, pp 184–232

Smith DG, Werle SF, Klekowski EJ (2003) The anatomy and brooding biology of *Pottsiella erecta* (Potts, 1884) (Ectoprocta: Gymnolaemata: Ctenostomata) with an expanded diagnosis of the Pottsiellidae. Hydrobiologia 490:135–145

Smitt FA (1863) Bidrag till Kännedomen om Hafs-Bryozoernas utveckling. Uppsala Univ Ars, Uppsala

Smitt FA (1865) Om Hafs-Bryozoernas utveckling och fettkroppar. Ofvers Kongl Vetensk-Akad Forh 1:5–50

Smitt FA (1866) Kritisk Förteskning öfver Scandinaviens Hafs-Bryozoernas. Ofvers Kongl Vetensk-Akad Forh 23:395–533

Soule JD (1950a) Penetrantiidae and Immergentiidae from the Pacific (Bryozoa: Ctenostomata). T Am Microsc Soc 69(4):359–367

Soule JD (1950b) A new species of *Terebripora* from the Pacific (Bryozoa Ctenostomata). J Wash Acad Sci 40(11):378–381

Soule JD, Soule DF (1969a) Systematics and biogeography of burrowing bryozoans. Am Zool 9(3):791–802

Soule JD, Soule DF (1969b) Three new species of burrowing bryozoans (Ectoprocta) from the Hawaiian Islands. Occ Pap Calif Acad Sci 78:1–9

Soule JD, Soule DF (1975) *Spathipora*, its anatomy and phylogenetic affinities. In: Pouyet S (ed) Bryozoa 1974. Doc Lab Geol Fac Sci Lyon HS 3(1):247–253

Soule JD, Soule DF (1976) *Spathipora mazatlanica*, a new species of burrowing Bryozoa (Ctenostomata) from Mazatlan, Sinaloa, Mexico. Bull So Calif Acad Sci 75(1):38–42

Soule JD, Soule DF (1977) Fouling and bioadhesion: life strategies of bryozoans. In: Woollacott RM, Zimmer RL (eds) Biology of bryozoans. Academic Press, New York, pp 437–457

Stach LW (1938) Observation on *Carbasea indivisa* Busk (Bryozoa). Proc Zool Soc Lond B 108(3):389–399

Ström R (1969) Sexual reproduction in a stoloniferous bryozoan, *Triticella koreni* (G.O. Sars). Zool Bidr Uppsala 38:113–127

Ström R (1977) Brooding patterns of bryozoans. In: Woollacott RM, Zimmer RL (eds) Biology of bryozoans. Academic Press, New York, pp 23–56

Taylor PD, McKinney FK (2006) Cretaceous Bryozoa from the Campanian and Maastrichtian of the Atlantic and Gulf Coastal Plains, United States. Scripta Geol 132:1–346

Temkin MH (1991) Fertilization in the gymnolaemate Bryozoa. PhD dissertation, University of Southern California

Temkin MH (1994) Gamete spawning and fertilization in the gymnolaemate bryozoan *Membranipora membranacea*. Biol Bull 187(2):143–155

Temkin MH (1996) Comparative fertilization biology of gymnolaemate bryozoans. Mar Biol 127(2):329–339

Temkin MH (2002) The effects of increased external Ca^{++} and K^+ concentrations on the waveform dynamics of bryozoan spermatozeugmata. In: Wyse Jackson PN, Buttler CJ, Spencer Jones M (eds) Bryozoan studies 2001. AA Balkema Publishers, Lisse/Abingdon/Exton/Tokyo, pp 315–320

Temkin MH, Bortolami SB (2004) Waveform dynamics of spermatozeugmata during the transfer from paternal to maternal individuals of *Membranipora membranacea*. Biol Bull 206:35–45

Thompson JV (1830) 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. Zool Res Ill 4(5):89–102

van Beneden PJ (1844a) Recherches sur l'organisation des *Laguncula* et l'histoire naturelle des différents polypes Bryozoaires qui habitent la côte d'Ostende. Nouv Mem Acad R Sci Belles-Lettr Bruxelles 18:1–29

van Beneden PJ (1844b) Recherches sur l'anatomie, la physiologie et le développement des bryozoaires qui habitent la cote d'Ostende. Mem Acad R Belg 18:1–44

Vigelius WJ (1882) Zur Enstehung und Entwicklung der Geschlechtsprodukte bei chilostomen Bryozoen. Biol Zbl 2:435–442

Vigelius WJ (1884a) Die Bryozoen, gesammelt während der dritten und vierten Polarfahrt des "Willem Barents" in den Jahren 1880 und 1881. Bijdr Dierkd 11:1–104

Vigelius WJ (1884b) Morphologische Untersuchungen über *Flustra membranaceo-truncata* Smitt. Biol Zbl 3(23):705–721

Vigelius WJ (1886) Zur Ontogenie der marinen Bryozoen. Mitt Zool Stat Neap 6:499–541

Vigelius WJ (1887a) Zur Morphologie der marinen Bryozoen. Zool Anz 10:237–240

Vigelius WJ (1887b) Contributions à la morphologie des bryozoaires ectoptoctes. Tijds Nederl Dierk Ver, 2 Ser, 1(3–4):77–92

Waters A (1896a [1898]) Notes on Bryozoa from Rapallo and other Mediterranean localities. – Chiefly Cellulariidae. J Linn Soc Zool 26(166):1–21

Waters A (1896b [1898]) Observations on Membraniporidae. J Linn Soc, Zool 26(172):126–133

Waters A (1900) Bryozoa from Franz-Josef Land, collected by the Jackson-Harmsworth expedition, 1896–1897. J Linn Soc Zool 28(179):126–133

Waters A (1904a) Bryozoa. Res Voy S.Y. Belgica 1897–1898–1899. Exp Ant Belge Zool 4:1–114

Waters A (1904b) Bryozoa from Franz-Josef Land, collected by the Jackson-Harmsworth expedition, 1896–1897. – Part II. Cyclostomata, Ctenostomata and Endoprocta. J Linn Soc Zool 29(190):161–184

Waters A (1906) Bryozoa from Chatham Island and d'Urville Island, New Zealand, collected by Professor H. Schauinsland. Ann Mag Nat Hist, Ser 7, 17(97):12–23

Waters A (1907) *Tubucellaria*: its species and ovicells. J Linn Soc, Zool 30:126–133

Waters A (1909) 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. J Linn Soc Zool 31:123–181

Waters A (1910) Reports on marine biology of the Sudanese Red Sea, from collections made by Cyril Crossland. Bryozoa. Part II. – Cyclostomata, Ctenostomata, and Endoprocta. J Linn Soc Zool 31:231–256

Waters A (1912) A structure in *Adeonella (Laminopora) contorta* (Michelin) and some other Bryozoa, together with remarks on the Adeonidae. Ann Mag Nat Hist, 8 Ser, 9(53):489–500

Waters A (1913) 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. Proc Zool Soc Lond, Parts 3–4, 32:458–537

Waters A (1914) 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. Proc Zool Soc Lond, Parts 3–4, 831–858

Waters A (1919 [1921]) Observations upon the relationships of the (Bryozoa) Selenariidae, Conescharellinidae, etc., fossil and Recent. J Linn Soc, Zool 34:399–427

Winston JE (1982) Marine bryozoans (Ectoprocta) of the Indian river area (Florida). Bull Am Mus Nat Hist 173:99–176

Winston JE (1983) Patterns of growth, reproduction and mortality in bryozoans from the Ross Sea, Antarctica. Bull Mar Sci 33(3):688–702

Winston JE (1985) Life history studies of *Disporella* and *Drepanophora* in Jamaica. In: Nielsen C, Larwood GP (eds) Bryozoa: Ordovician to recent. Olsen and Olsen, Fredensborg, p 350

Winston JE (1988) Life histories of free-living bryozoans. Nat Geogr Res 4:528–539

Wood V, Seed R (1992) Reproduction and growth of *Alcyonidium hirsutum* (Fleming) and *Flustrellidra hispida* (Fabricius) (Bryozoa: Ctenostomata) within a *Fucus serratus* community. Cah Biol Mar 33:347–363

Woollacott RM (1999) Bryozoa (Ectoprocta). In: Knobil E, Neill JD (eds) Encyclopedia of reproduction, vol 1. Academic Press, New York, pp 439–448

Woollacott RM, Zimmer RL (1972a) Origin and structure of the brood chamber in *Bugula neritina* (Bryozoa). Mar Biol 16:165–170

Woollacott RM, Zimmer RL (1972b) A simplified placenta-like brooding system in *Bugula neritina* (Bryozoa). In: Arceneaux CJ (ed) 30th annual proceedings of the Electron Microscope Society of America. Claitor's Publishing Division, Baton Rouge, pp 30–31

Woollacott RM, Zimmer RL (1975) A simplified placenta-like system for the transport of extraembryonic nutrients during embryogenesis of *Bugula neritina* (Bryozoa). J Morph 147:355–378

Wright PJ, Hughes RN (2002) A comparison of the early astogeny and life history of *Celleporella carolinensis* and *Celleporella hyalina*. In: Wyse Jackson PN, Buttler CJ, Spencer Jones M (eds) Bryozoan studies 2001. AA Balkema Publishers, Lisse/Abingdon/Exton/Tokyo, pp 353–357

Yagunova EB, Ostrovsky AN (2010) The influence of substrate type on sexual reproduction of the bryozoan *Cribrilina annulata* (Gymnolaemata, Cheilostomata). A case study from Arctic seas. Mar Biol Res 6(3):263–270

Zimmer RL, Woollacott RM (1974) Morphological and biochemical modifications of the spermatozoan mitochondria of *Membranipora* sp. J Cell Biol 63:385a

Zirpolo G (1933) *Zoobotryon verticillatum* (Delle Chiaje). Mem Acad Pont Nuov Lincei 2(17):109–442

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