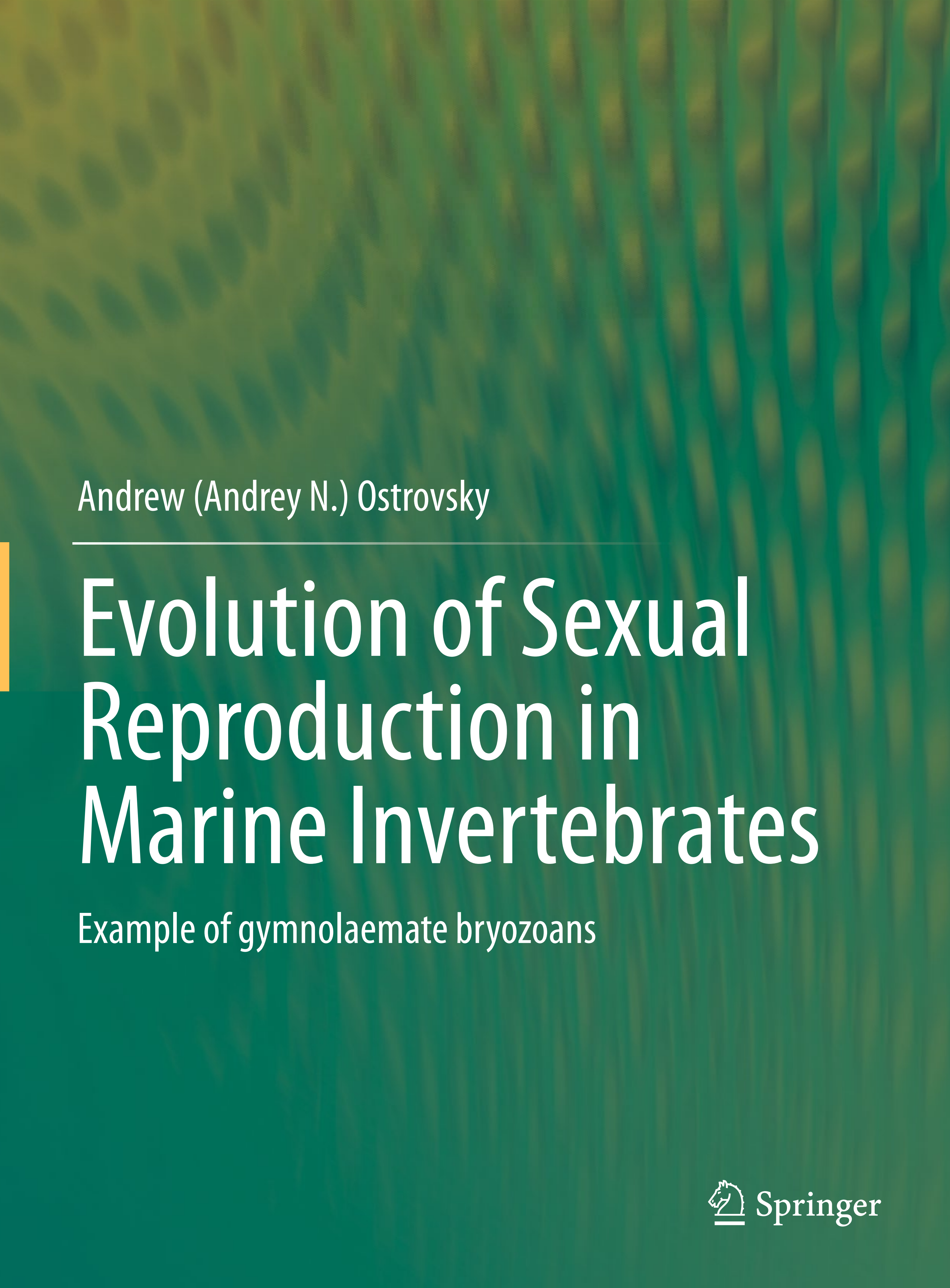

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Example of gymnolaemate bryozoans

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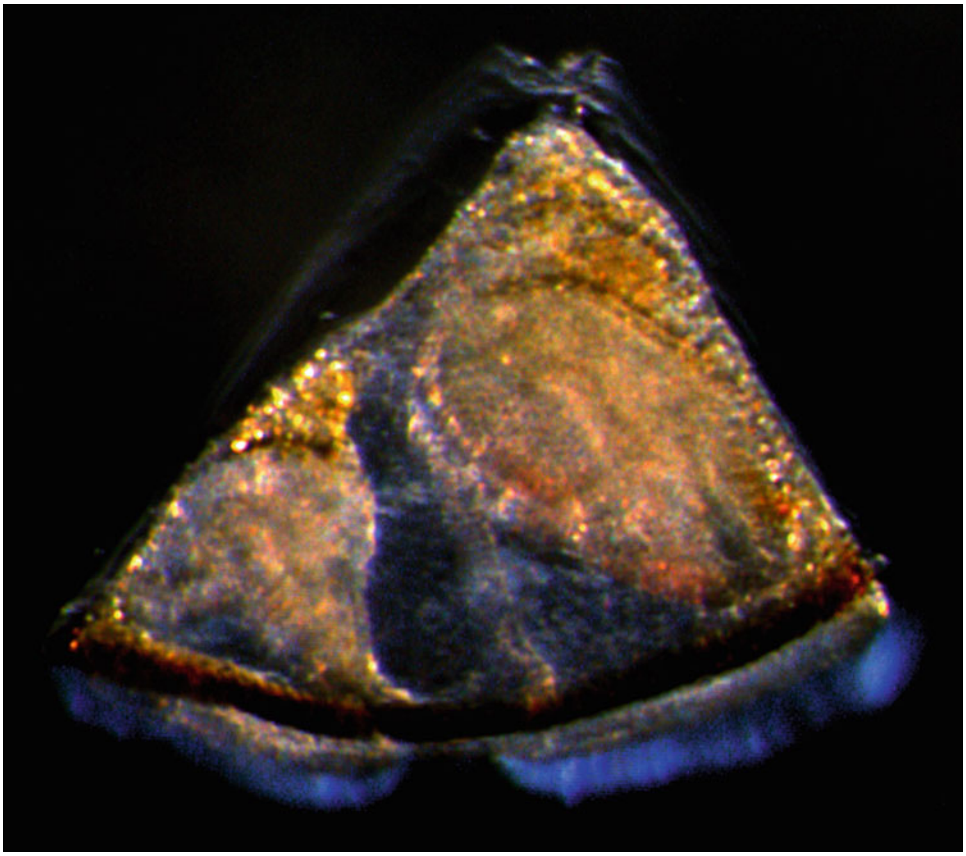

Planktotrophic cyphonautes larva of cheilostome bryozoan *Membranipora membranacea* (Photo by Olga Kotenko)

Andrew (Andrey N.) Ostrovsky

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Example of gymnolaemate bryozoans

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In memory of Christopher G. Reed and Frank K. McKinney
—whose examples I try to follow

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Contents

Introduction

Sex was a key novelty in the evolutionary history of the Eukaryota, and for most Metazoa a combination of sex and replication is the only way of reproducing (Barnes et al. 2001; Cavalier-Smith 2002). Sexual reproduction typically involves gonadogenesis, gametogenesis, fertilization, embryogenesis (often accompanied by incubation of the embryos) and, in species with a larval stage, larval ontogenesis and metamorphosis. These reproductive stages are implemented by means of various provisional and permanent structures, such as gonads, gonoducts and associated glands, organs responsible for gamete release into the environment, their transfer to the partner and for their storage, incubation chambers and various larval organs. Although having a general similarity in different metazoan groups, the reproductive stages vary greatly in their phenomenology as do the organs in their structure. This diversity is expressed in: (1) gender (unisexuality or gonochorism vs. different variants of hermaphroditism), (2) the structure of gonads as well as the sources, ways, timing and sites of their origin and final location, and their maturation time and duration of functioning, (3) gametic structure and development, (4) place, time and methods of insemination and fertilization and the structures ensuring these processes, (5) incubation modes and structures, (6) modes of embryogenesis, (7) larval types, and (8) modes of metamorphosis (reviewed in Franzén 1956; Raven 1961; Adiyodi and Adiyodi 1983, 1989, 1990; Wourms 1987; Giese et al. 1987; Eckelbarger 1994; McEdward 1995; Ivanova-Kazas 1995; Drozdov and Ivankov 2000; Schmidt-Rhaesa 2007; etc.). This broad range of diversity indicates that sexual reproduction has been evolving in concert with the organisms themselves. Being stable in the essentials, sexual reproduction has been constantly changing in its details.

Various combinations of the reproductive characters listed above can be taken as representing particular reproductive patterns – specific variants or stable complexes of the sexual traits characteristic of a species or a group of living organisms. Note, however, that in biological literature the term "reproductive pattern" is often not quite correctly understood as a synonym of "reproductive strategy." In general, a reproductive strategy is a method of energy input into the offspring defined by the amount of resources allocated for the production and parental care of a single offspring (Vance 1973). These methods may be quite different, representing the so-called r–K continuum (MacArthur and Wilson 1967; Pianka 1999). Besides, each strategy is characterized by a specific set of features ensuring reproduction, that is, by the reproductive pattern, and similar strategies may have different patterns. For instance, during lecithotrophic and placentotrophic development, the offspring obtains the necessary resources in different ways and at different stages. The result, however, is very much the same. To sum up, the term "reproductive strategy" describes the general character of resource allocation (for which data on seasonal dynamics of reproduction are usually necessary; see, for instance, Dyrynda and Ryland 1982), whereas the term "reproductive pattern" refers to a specific complex of reproductive traits, including the mode of oogenesis, method of gamete manipulation (spawning, copulation), time and site of syngamy, incubation mode, larval type, etc. It should be noted that marine invertebrates are sometimes said to possess larval (planktotrophic and lecithotrophic) and embryonic (lecithotrophic and placentotrophic) reproductive strategies (Thorson 1950; Mileikovsky 1971; Kasyanov 1989; Levin and Bridges 1995). This classification is based on the *ways* in which the embryos and larvae obtain resources during different phases of their development.

Also Chia (1974) classified "developmental patterns", combining larval types (feeding vs. non-feeding) and their "habitat" during development (pelagic, benthic, brooded, viviparous).

What are the prerequisites, causes and consequences of the emergence of different reproductive strategies and patterns? And what are the trends in the evolution of their key components: gametogenesis, fertilization and parental care? Finally, can we use data on sexual reproduction for reconstructing stages in the evolutionary history of life, for instance, in specifying phylogenies and constructing evolutionary scenarios?

Since the main objective of zoology is the study of diversity, evolution and phylogenetic relations among different animal groups, evolutionary studies of sexual reproduction would appear to have a very important role. Traditionally, such information is widely applied when reconstructing the historical past of organisms, since it concerns two key aspects of their existence: their structure and its replication. Changes in sexual reproduction are directly reflected in the evolutionary trajectories of the various groups. For instance, the transition from a long-lived feeding larva to a short-lived non-feeding one, associated with changes in the mode of oogenesis, should result in the isolation of distant populations, thus accelerating speciation rates (Jablonski 1986, 2005; Jablonski and Lutz 1983). The origin of parental care certainly resulted in better survival of progeny, and thus might have influenced the evolutionary success of the animal group (Clutton-Brock 1991).

Investigations conducted within the framework of traditional morphological methodology are usually confined to the comparative anatomy of reproductive systems, the results of this kind of analysis being then applied to evolutionary and phylogenetic constructions. Numerous studies also deal with the comparative morphology of gametes, the features of gametogenesis, fertilization, and incubation and the structures responsible for them. However, the multi-sided approach, integrating data from the various aspects of reproduction, is rare and the reviews on reproduction in most invertebrate groups are often incomplete and fragmentary as well as lacking recent data. Besides, for obvious reasons, the evolution of sexual reproduction in most groups is reconstructed mainly on the basis of information about living organisms.

The state of knowledge about sexual reproduction in marine invertebrates can be exemplified by bryozoans (phylum Bryozoa Ehrenberg, 1831). An analysis of the literature shows that over 230 articles and monographs published since the pioneering works of Ellis (1753, 1755) and Pallas (1766) contain data on various aspects of sexual reproduction in more than 350 species of marine gymnolaemates (class Gymnolaemata Allmann, 1856). Notwithstanding, information adequate enough to allow a comprehensive picture of reproductive cycles can be found in fewer than two dozen publications covering about 30 species (see Appendix I for the species list and history of studies). As for the most abundant bryozoan order, Cheilostomata Busk, 1852, comprising more than 1,060 genera and 150 families (Gordon 2012), reproduction has been studied in some detail in just 10 species representing 10 families. This is the factual basis for the best review on sexual reproduction in the Bryozoa (published by Reed 1991). Can we extrapolate these data to present an adequate picture for the whole phylum? Obviously we cannot. As a result, the evolution of sexual reproduction in bryozoans is hardly ever discussed in the literature, even oogenetic changes appear to have played a crucial role in the emergence of the lecithotrophic larva and possibly the consequent radiations of bryozoan clades (Taylor 1988; Ostrovsky 2009).

At present, researchers working with marine invertebrates tend to pay much more attention to the study of larval types. Several explanations for this tendency may be proposed (discussed in Strathmann 1978, 1986). Firstly, many structural features of planktotrophic larvae, being highly conservative, have played a traditionally important role in evolutionary morphological and phylogenetic reconstructions (e.g. Schneider 1869; Hatschek 1877, 1878, 1888–91; Ostroumoff 1886a, b, c; Garstang 1951; Nielsen 1971, 1977, 1995, 1998, 2001, 2008, 2013; Jägersten 1972; Zimmer 1973; Farmer 1977; Ivanova-Kazas 1986, 1995; Wray 1995a; Hall and Wake 1999; Hickman 1999; Rouse 1999; Williamson 2001; Malakhov 2004).

Secondly, major differences in the dispersal of planktotrophic and lecithotrophic larvae have formed the basis of zoogeographical studies as well as studies of genetic exchange between populations (e.g. Thorson 1950; Mileikovsky 1971; Sheltema 1971; Jablonski 1986; Strathmann 1986; Kasyanov 1989; Poulin and Féral 1994, 1996; McEdward 1995; Levin 2006).

Thirdly, the transition from planktotrophy to lecithotrophy, which occurred repeatedly in the history of different groups of marine invertebrates, has enabled studies of the evolutionary ecology of larval types and reconstructions of the evolution of life cycles (e.g. Vance 1973; Smith and Fretwell 1974; Strathmann 1977, 1985, 1993, 2007; Christiansen and Fenchel 1979; Kasyanov 1989; Havenhand 1995; Nielsen 1998; Hall and Wake 1999; Pechenik 1999; Hickman 1999; Peterson 2005).

Fourthly, the presence of different larval types within the same taxon affords an opportunity to study the molecular basis of the emergence and further evolution of the new larval types as well as developmental changes accompanying this process (Strathmann 1978; Sinervo and McEdward 1988; Byrne and Barker 1991; Wray and Raff 1991; Wray 1995b; Byrne 1995; Byrne and Cerra 1996; Raff 1996).

On the whole, most researchers have focused their attention not on the causes but on the consequences of the transition to a new larval type or else on the adaptive costs and benefits of the retention of larval types under changed environmental conditions (see McEdward 1995). The fact that the emergence of new larval types is caused by changes in reproductive processes in the maternal organism, which is also subject to external influences, is generally left without comment.

In my opinion, the situation calls for a synoptic approach, with all the important components of sexual reproduction such as gametogenesis, fertilization, incubation of embryos and development of larvae being studied together in a holistic evolutionary dynamic. Especially promising in this regard are clades including both living taxa with different reproductive patterns and fossil taxa with identifiable reproductive characters. Comparison of reproductive strategies and the corresponding patterns, the analysis of their distribution within clades and information about the time of their origin allow us to formulate ideas about the directions and stages of the evolution of sexual reproduction. This information may then be used for reconstruction of the evolutionary history and phylogenetic relationships of these groups.

This approach seems to hold much promise. For instance, successful attempts have recently been made to use data on the distribution of planktotrophy, lecithotrophy and parental care for reconstructions of the evolution and phylogeny of echinoderms, in particular, sea stars and sea urchins (e.g. Wray 1996; Smith 1997; Jeffery 1997; Byrne 2006). Owing to the extensive fossil record of Echinoidea, this kind of analysis was able to embrace both Recent and fossil species and turned out to be very fruitful, confirming previous phylogenetic relationships constructed on the basis of morphological (skeletal) characters.

Bryozoa are another promising model for such research. With their high diversity of reproductive patterns and larval types, as well as their extensive fossil record, they are in fact ideally suited for the application of the synoptic approach mentioned above.

Phylogenetic Relationships of the Phylum Bryozoa

Bryozoans (=Ectoprocta Nitsche, 1869) had been traditionally assigned, together with phoronids and brachiopods, to the group Tentaculata (Hatschek 1888–91; Marcus 1958; Ivanova-Kazas 1977; Hadorn and Wehner 1978; Westheide and Rieger 2007). Later, this name was superseded by its synonym Lophophorata (Hyman 1959; Emig 1982, 1984; Willmer 1990; Brusca and Brusca 2003; Malakhov 2004). The validity of Lophophorata as a monophyletic group and its position amongst the Metazoa remains ambiguous (Willmer 1990; Nielsen 2001, 2002a; Dewel et al. 2002; Ruppert et al. 2004; Valentine 2004). On the basis of comparative embryological and morphological data, most zoologists considered lophophorates as protostomes (Marcus 1958; Hyman 1959; Beklemishev 1969; Hadorn and Wehner 1978; Remane et al. 1989; Malakhov 2004; Nielsen 2012), whereas some assigned them, either altogether or in part, to Deuterostomia (Zimmer 1973; Meglitsch and Schram 1991; Eernisse et al. 1992;

Ruppert and Barnes 1994; Nielsen 2001) or placed them together within Lophodeuterostomia (Ruppert et al. 2004) or Radialia (Westheide and Rieger 2007). Many zoologists pointed to the fact that the lophophorates combined the characters of protostomes and deuterostomes (e.g. Zimmer 1973; Ivanov 1976; Willmer 1990; Ruppert and Barnes 1994; d'Hondt 1997). As a result, Lophophorata (or members thereof) have often been placed at the base of the evolutionary bifurcation between Protostomia and Deuterostomia, being put closer either with the former or with the latter or being treated as a "transitory", stem or sister group of Deuterostomia (Marcus 1958; Hyman 1959; Hennig 1979; Dogiel 1981; Salvini-Plawen 1982; Willmer 1990; Schram 1991; Ax 1995; Lüter and Bartolomaeus 1997; Sørensen et al. 2000; Brusca and Brusca 2003; Westheide and Rieger 2007; see also discussions in Zrzavy et al. 1998; Passamaneck and Halanych 2004; Helmkampf et al. 2008a, b; Gruhl 2008). For instance, Anderson (2001) interpreted lophophorates to be protostomatous in origin, having acquired morphological and embryological characters of deuterostomes as a result of convergent evolution.

Molecular data are not supportive of Lophophorata as a monophyletic group. At present, Bryozoa, Phoronida and Brachiopoda are included in the Lophotrochozoa or Spiralia within Protostomia (Halanych et al. 1995; Halanych 1996, 2004; Mackey et al. 1996; Cohen and Gawthrop 1996; Erber et al. 1998; Abouheif et al. 1998; Peterson and Eernisse 2001; Waeschenbach et al. 2006; Baguña et al. 2008; Helmkampf et al. 2008a; Bourlat et al. 2008; Dunn et al. 2008; Giribet et al. 2009; Jang and Hwang 2009; Hejnol et al. 2009; Sun et al. 2009, 2011; Mallatt et al. 2010, 2012; Edgecombe et al. 2011; Nesnidal et al. 2011; Shen et al. 2012, see also Giribet 2002, 2008; Passamaneck and Halanych 2004). However, their exact positions within the Lophotrochozoa are still not resolved.

Zoologists have traditionally affiliated bryozoans with phoronids, treating them as sister groups originating from pro(to)lophophorates or protophoronids or deriving Bryozoa from Phoronida (i.e. considering early Phoronida as the stem group for Bryozoa) (Caldwell 1882; Korschelt and Heider 1893; Borg 1926; Cori 1941; Marcus 1958; Hyman 1959; Brien 1960; Farmer et al. 1973; Jebram 1973, 1986; Farmer 1977; Emig 1984; Malakhov 1995; Gorjunova 1996; Ruppert et al. 2004). Silén (1944, p. 100) wrote that phoronids are not "true ancestors of the Bryozoa", but there is "perhaps … a parallelism as to certain features of the two groups". Emig (1982, p. 79) considered brachiopods and bryozoans to be "blind branches" of a trunk whose evolution resulted in the emergence of the phoronids, in his opinion the most advanced lophophorates. In contrast, Beklemishev (1969) and d'Hondt (1986) viewed brachiopods as a group separate from bryozoans and phoronids. Resurrecting the old view (see Van Beneden 1845; Leidy 1851; Allman 1856; Hatschek 1877), Nielsen (1971, 1995, 2000, 2001, 2002a, b) united Bryozoa and Kamptozoa (Entoprocta) into a superphylum Bryozoa (see also Cuffey 1973) within the protostomes and considered Phoronida and Brachiopoda as related basal deuterostomes. Recently, however, this author included Brachiozoa (Brachiopoda + Phoronida) in the Spiralia (Nielsen 2012; see also below).

Molecular studies and a combined "morphomolecular" analysis usually also place Bryozoa apart from Phoronida and Brachiopoda (whether uniting phoronids and brachiopods or setting them apart) (Halanych et al. 1995; Halanych 1996; Cohen and Gawthrop 1996; Mackey et al. 1996; Littlewood et al. 1998; Zrzavý et al. 1998; Abouheif et al. 1998; Cohen et al. 1998; Winnepenninckx et al. 1998; Cohen 2000; Peterson and Eernisse 2001; Waeschenbach et al. 2006; Baguña et al. 2008; Dunn et al. 2008; Bleidorn et al. 2009; Hejnol et al. 2009; Hausdorf et al. 2010; Mallatt et al. 2012; Edgecombe et al. 2011; Nesnidal et al. 2011; see also discussion in Gruhl 2008; Giribet et al. 2009). Also, different authors refute (Mallatt et al. 2010, 2012) or, on the contrary, support (Hausdorf et al. 2007, 2010; Helmkampf et al. 2008a; Hejnol et al. 2009; Bleidorn et al. 2009; Witek et al. 2009; Philippe et al. 2011; Edgecombe et al. 2011) a close relationships between bryozoans and entoprocts (see also Abouheif et al. 1998; Baguñá et al. 2008; Giribet et al. 2009; Nesnidal et al. 2011; Fuchs 2011). Recently Bryozoa, Entoprocta and Cycliophora have been united under the name Polyzoa (Cavalier-Smith 1998; Hejnol et al. 2009; summarized in Hejnol 2010; Nielsen 2012).

Moreover, some molecular data (Halanych et al. 1995; Halanych 1996; Mackey et al. 1996; Winnepenninckx et al. 1998; Giribet et al. 2009; Peterson and Eernisse 2001; Helmkampf et al. 2008a; Mallatt et al. 2010, 2012) indicate bryozoans as basal to the Phoronida–Brachiopoda "group", which, though hypothetically possible, does not correspond to paleontological data (Conway Morris et al. 1996; see also Cohen and Gawthrop 1996; Zrzavý et al. 1998; Halanych 2004). In contrast, Dewel et al. (2002) united phoronids and brachiopods, placing them in a position basal to Bryozoa, while in the analysis by Hejnol et al. (2009) these three spiralian groups are distant to each other, with Phoronida being the basal-most. In the multigene analysis of Helmkampf et al. (2008b), bryozoans and phoronids (to the inclusion of annelids) form a monophyletic group, while brachiopods were considered basal to them; although nodal support was low for these inferences. On the other hand, Bourlat et al. (2008) united bryozoans and brachiopods without making any connection to the phoronids. Analysis of complete mitochondrial genomes made by Jang and Hwang (2009) showed bryozoans forming a monophyletic clade with brachiopods, while the sister group to the phoronids was unresolved. Conversely, analyses of the mitochondrial protein-coding genes at the amino acid level by Sun et al. (2009, 2011), Shen et al. (2012) and Waeschenbach et al. (2006) resolved chaetognaths to be the sister group to Bryozoa, a finding which is likely to be the result of long-branch attraction. Nesnidal et al. (2011, p. 1) demonstrated that "the relationships of the lophophorate lineages within Lophotrochozoa differ strongly depending on the data set and the used method". Earlier Jenner and Littlewood (2008, p. 1508) wrote in this context: "Taxa such as … Ectoprocta behave like phylogenetic renegades, residing in as many different clades as there are studies", whereas Hejnol (2010) pointed to the problem of the phylogenetic placement of the Polyzoa (Ectoprocta + [Entoprocta + Cycliophora]) within Spiralia (see also Nielsen 2012). Thus, at the moment we can only state that lophotrochozoan affinities are well supported for these three groups, but much more research is needed to reveal their exact position.

The evolution of views on the origination sequence of different bryozoan groups and their phylogenetic relations can be summarized as follows. Phylum Bryozoa comprises three classes: Stenolaemata (exclusively marine bryozoans), Gymnolaemata (mostly marine, rarely brackish-water and freshwater bryozoans) and Phylactolaemata (exclusively freshwater bryozoans). According to early hypotheses, Phylactolaemata, which shares greatest morphological similarity with the phoronids, is the most ancient bryozoan group (Caldwell 1882; Korschelt and Heider 1893, see also Hyman 1959 for discussion), Gymnolaemata is derived from the Phylactolaemata (Gerwerzhagen 1913) (i.e. phylactolaemates are paraphyletic, and the ancient phylactolaemates are the stem group for gymnolaemates), and gymnolaemates and stenolaemates share a common ancestor ("ancestral Gymnolaemata") that originated from the ancient phylactolaemates (Jebram 1973, 1986). Although not mentioning a common ancestor, Silén (1944) speculated that phylactolaemates and stenolaemates originated from an ancestral form with a primitive colonial structure and that gymnolaemates ("Cheilo-Ctenostomata") could have evolved from ancient Phylactolaemata. A diametrically opposed viewpoint is that Phylactolaemata is the most derived group, originating from the more primitive marine gymnolaemate (ctenostome) bryozoans (Schneider 1869; Kraepelin 1887; Marcus 1924; Bassler 1953). Borg (1926) suggested that all three bryozoan classes were independent lineages that evolved from the common ancestral group "Pro-bryozoa", with phylactolaemates and stenolaemates being somewhat more closely related to each other than to gymnolaemates (see also Silén 1942, 1944; Hyman 1959). Lemche (1963) derived marine bryozoans from early phoronids, and, curiously, freshwater bryozoans from the "Prae-Rhizostomeae" (rhizostome medusae). Yet another hypothesis allows the possibility that marine and freshwater bryozoans evolved independently from different phoronid-like ancestors, while stenolaemates evolved from Gymnolaemata (Mundy et al. 1981) (for additional discussion see also Larwood and Taylor 1979; McKinney and Jackson 1989; Todd 2000; Taylor and Ernst 2004; Wood and Lore 2005; Ernst and Schäfer 2006; Hausdorf et al. 2010). It should be noted that some molecular studies question the monophyly of bryozoans (Cohen and Gawthrop 1996; Helmkampf et al.

2008b). For instance, the data of Helmkampf et al. (2008b) suggest that phylactolaemate bryozoans are more closely related to phoronids than to gymnolaemate bryozoans.

Yet other molecular studies show the Phylactolaemata as the sister group to the clade uniting sister groups Stenolaemata and Gymnolaemata (Fuchs et al. 2009; Hausdorf et al. 2010; Waeschenbach et al. 2012; Mallatt et al. 2012; see also the cladogram in Todd 2000). Another combined analysis unites Phylactolaemata and Stenolaemata as sister taxa, making this clade a sister group to Gymnolaemata (Fuchs et al. 2009). Anstey (1990) found Phylactolaemata to form a monophyletic group with Stenolaemata, suggesting a sister relationship of this group with the gymnolaemate order Cheilostomata, however. The third variant of interactions between the classes was presented by Cuffey (1973), who united phylactolaemates with gymnolaemates, considering this clade as a sister to stenolaemates (see also Cuffey and Blake 1991). At present, bryozoan researchers tend to support the first hypothesis (discussed also in Gruhl 2008).

Brief Overview of Bryozoa

Bryozoa, predominantly marine epibionts, are active suspension-feeders consuming phytoplankton, bacteria and dead organic matter in diverse habitats from the intertidal zone to hadal depths exceeding 8,000 m (Ryland 1967, 1970, 1976, 1982, 2005; Kluge 1975; Boardman et al. 1983; McKinney and Jackson 1989; Taylor 1999; Gordon 2003; Gordon et al. 2009). All bryozoans are colonial organisms consisting of modules, so-called zooids, which are usually less than a millimetre long. The pelago-benthic life cycle of Bryozoa includes the formation of gametes in a hermaphrodite colony, sperm release followed by internal fertilization and development of an exotrophic (planktotrophic) or incubated endotrophic (lecithotrophic or matrotrophic) free-swimming larva, which, when competent, finds a place for settlement, attaches to the substratum and undergoes catastrophic (phylactolaemates excepted) metamorphosis. The result is the formation of a founder zooid (ancestrula) or group of zooids (ancestrular complex) that begins to bud the daughter generations of zooids. On attaining maturity, the colony starts gametogenesis (reviewed in Reed 1991). Budding is traditionally considered as asexual reproduction though in case of colonial organisms it would be more correct to call it colonial growth, since in these organisms budding is never complete, the colony members remaining physically interconnected and physiologically dependent throughout their life time. Besides, the zooids are genetic copies while the colony is a modular organism forming genetically ‘identical’ gametes.

According to the latest estimation, about 6,000 species of extant marine bryozoans and over 15,000 species of extinct bryozoans (Gordon et al. 2009) have been described. These figures, however, are likely to represent as little as one third of the actual diversity of this group (Taylor, personal communication, 2007).

Traces of boring non-skeletal ctenostome bryozoans (class Gymnolaemata) and fossilized skeletons of stenolaemate bryozoans are known from marine sediments beginning with the Early Ordovician (Taylor and Curry 1985; Hu and Spjeldnaes 1991; Todd 2000; Xia et al. 2007; Zhang et al. 2009). Thus, both classes of marine Bryozoa and, according to Todd (2000), all superfamilies of the order Ctenostomata already existed at that time. A recent report on the finding of Cambrian stenolaemate bryozoans (Landing et al. 2010) is highly dubious. However, on the basis of the basal position of bryozoans in gene trees relative to brachiopods and molluscs, whose fossilized remains are known from Early Cambrian sediments, Passamaneck and Halanych (2006) suggested that the origin of Bryozoa dates back at least to the Early Cambrian. In turn, Buge (1952), Brien (1960) and Emig (1984) argued that bryozoans originated as early as the Precambrian (see also Hyman 1959). Fossil statoblasts (resting buds) of Phylactolaemata are known from Middle–Late Triassic deposits (Kohring and Pint 2005; Schcerbakov 2008).

Ctenostomata is one of the oldest surviving groups of bryozoans lacking a mineralized skeleton, traditionally considered as ancestral to all other groups of marine bryozoans (Banta

1975; Larwood and Taylor 1979; Cheetham and Cook 1983; Taylor and Larwood 1988, 1990; Todd 2000). Stenolaemata, with their calcified zooids, probably evolved from a ctenostome ancestor in the Late Cambrian; molecular analysis showed sister relationships between Stenolaemata and Gymnolaemata (see above). The explosive evolution of Stenolaemata resulted in five orders – Cyclostomata, Trepostomata, Cystoporata, Cryptostomata and Fenestrata – which achieved a high taxonomic diversity and played an important role in the benthic communities of Paleozoic seas (Taylor and Larwood 1990; Anstey and Pachut 1995; Taylor and Ernst 2004). One of the contributing factors in the evolutionary success of Stenolaemata might have been the origin of parental care. The existence of embryonic incubation was suggested by Dunaeva (1968) and Astrova (1978) for Trepostomata and by Buttler (1991) for Cystoporata. Putative embryo incubation chambers are an important character in the systematics of the order Fenestrata (Tavener-Smith 1966; Stratton 1975, 1981; Southwood 1985; Bancroft 1986, 1988; Morozova 2001; see also Ernst and Schäfer 2006).

Orders Cyclostomata, Trepostomata and, possibly, Cystoporata survived, though with losses, the global Permian-Triassic extinction event, but, with the exception of Cyclostomata, became extinct in the Triassic (Cryptostomata and Fenestrata disappeared in the Permian) (Taylor and Larwood 1988; Taylor and Ernst 2008). In contrast, the diversity of cyclostome bryozoans, previously far outshone by their more successful relatives, began to increase. The cyclostome heyday was the second half of the Mesozoic (Taylor and Larwood 1990; Lidgard et al. 1993; McKinney et al. 2001; McKinney and Taylor 2001).

There are several sound arguments in favour of the hypothesis that the Paleozoic cyclostomes became extinct without leaving any descendants, and a very similar group appeared in the Triassic that survives to this day (Ernst and Schäfer 2006; Taylor and Ernst 2008). Whatever the case, during the Late Cretaceous extinction, the Cyclostomata again sustained heavy losses (Taylor and Larwood 1988, 1990; Boardman et al. 1983; McKinney et al. 2001). Nevertheless, bryozoans from this order are rather common in present-day bottom communities. Again, as with Paleozoic stenolaemates, embryonic incubation is considered a key factor in the progress of the Mesozoic cyclostomes, whose incubation chambers (gonozooids) are known from the Late Triassic onward (Taylor and Michalik 1991; Lidgard et al. 1993). Details of gonozooid structure are important in the systematics of fossil and living cyclostomes (Borg 1926; Brood 1972; McKinney 1987; Schäfer 1991; Viskova 1992; Ostrovsky 1991, 1995, 1998a, b; Ostrovsky and Taylor 1996).

In the Late Jurassic, the Ctenostomata gave rise to a new gymnolaemate order, the Cheilostomata (Pohowsky 1973; Banta 1975; Taylor 1981, 1986a, 1988, 1990, 1994; Taylor and Ernst 2008). In the Late Cretaceous, after 60 Ma of low diversity, cheilostomes went through a phase of explosive radiation, quickly becoming the dominant bryozoan group and retaining this position until the present day (Cheetham and Cook 1983; McKinney and Jackson 1989; Taylor 2000). Jebram (1992) considered cheilostomes to be polyphyletic, a possibility discussed by some other authors (Taylor 1988; Todd 2000).

Cheilostomes are one of the most diverse and numerous groups of marine colonial epibionts. Represented by 150 families and more than 1,060 genera, they make up about 95% of the diversity of Recent Bryozoa (Gordon 2012). Moreover, cheilostomes are among the most abundant marine foulers: for instance, in the Antarctic they may cover up to 90% of all rocky surfaces, achieving densities in 1,000s colonies per square meter and being inferior in biomass only to sponges, annelids and ascidians (Ryland 1967, 1982; Hayward 1995; Barnes and Brockington 2003). Able to colonize all possible substrata – hard and soft, moving and immobile – cheilostome bryozoans are a key component of biocenoses, providing ample shelter as well as settlement and feeding substrata for other organisms (Ryland 1970, 1976; McKinney and Jackson 1989; Hayward and Ryland 1998, 1999; Ryland 2005).

The evolutionary success of the Cheilostomata can be explained by high integration of modules within the colony and the extreme morphological and physiological plasticity underlying the most diverse forms of colonial growth coupled with the emergence of an astonishing morphological and functional diversity of zooids (polymorphism) (Hyman 1959;

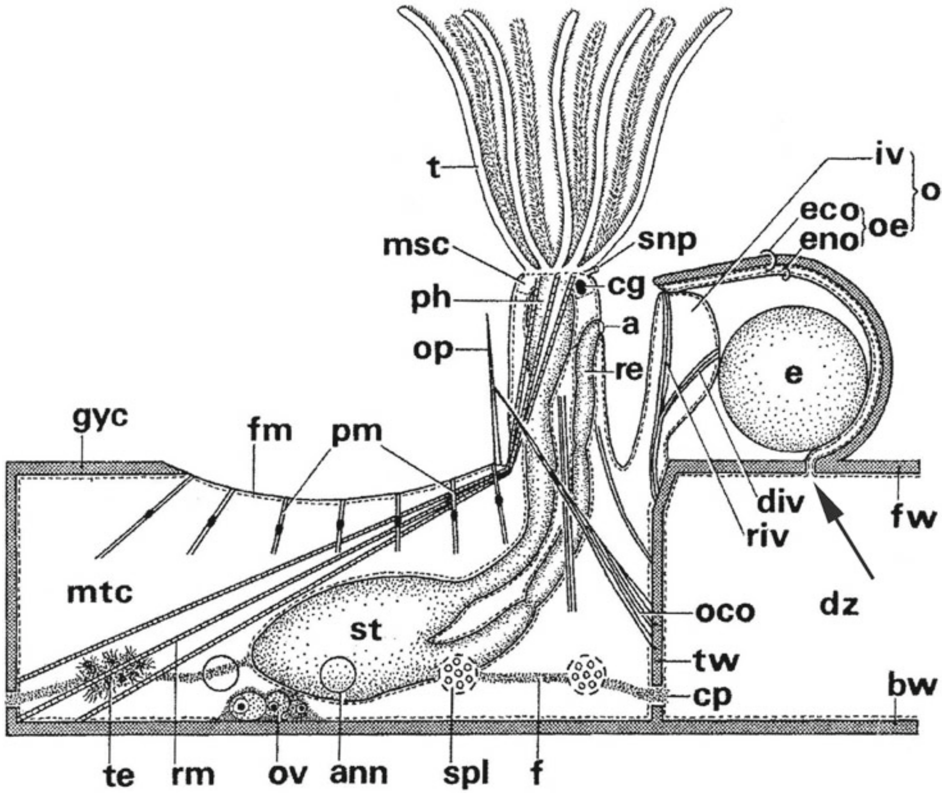

Fig. 1 Generalized scheme of zooid structure in Cheilostomata (e.g. superfamily Calloporoidea). The ooecial communication pore is *arrowed*. Abbreviations: *a* anus, *ann* annulus of mural pore chamber, *bw* basal wall, *cg* cerebral ganglion, *cp* communication pore, *div* depressor muscle of inner (ooecial) vesicle, *dz* distal zooid, *e* embryo, *eco* ectooecium, *eno* entooecium, *f* funiculus, *fm* frontal membranous wall, *fw* frontal wall, *gyc* gymnocyst, *iv* inner vesicle, *msc* mesocoel (ring coelom), *mtc* metacoel (visceral coelom), *oc* ovicell, *oco* opercular muscle, *oe*, ooecium, *op* operculum, *ov* ovary, *ph* pharynx, *pm* parietal muscles, *re* rectum, *riv* retractor muscle of inner (ooecial) vesicle, *rm* retractor muscle of polypide, *snp* supraneural pore, *spl* pore plate (septulum) in lateral wall, *st* stomach, *t* tentacle, *te* testis, *tw* transverse wall (From Ryland 1970, with modifications, courtesy of John Wiley & Sons)

Beklemishev 1969; Cook 1979; Ryland 1979; Cheetham and Cook 1983; McKinney and Jackson 1989; Reed 1991; Viskova 1992; Taylor 1999; Lidgard et al. 2012).

Like many other kinds of colonial epibionts, bryozoans can regenerate very well (Levinsen 1907; Winston 1983; Ostrovsky 1997; O'Dea 2006; O'Dea et al. 2008), reproducing not only sexually but also asexually. In some cases, asexual reproduction by fragmentation dominates over sexual reproduction. This often depends on the growth form of the colony: for example, half or even most of the increase in the abundance of populations of some bryozoans with tree-like colonies is due to fragmentation (Winston 1983; Thomsen and Håkansson 1995; Cheetham et al. 2001). Among free-living species (with non-attached colonies) there are those reproducing mostly by fragmentation and those relying mostly on sexual reproduction (O'Dea et al. 2004, 2008; O'Dea 2006). There are also species actively using both these means (O'Dea et al. 2010). Some encrusting forms are known to "switch" from sexual reproduction to asexual in response to changes in environmental conditions. It has been shown that in populations reproducing mostly asexually, the number of fertile zooids (those forming ovaries) in the colonies is much lower than in populations where sexual reproduction dominates (Thomsen and Håkansson 1995). In any case, sexual reproduction is an obligatory component of the bryozoan life cycle and for many the only possible way to reproduce.

The feeding zooid (autozooid) in Cheilostomata (Fig. 1) is an organic module consisting of the cystid (receptacle of the polypide) and the polypide (retractable tentacular crown with a centrally positioned mouth, loop-shaped intestine and associated muscles) (Ryland 1970; Boardman et al. 1983; Mukai et al. 1997). The cystid is sac-like or box-like, its wall consisting of an external cuticle and a calcified layer underlain (and formed) by a thin epithelium and loose peritoneum. In some cheilostomes the frontal wall is not calcified and, as parietal muscles contract, it flexes inwards, thus applying pressure to the coelomic fluid and resulting in the protrusion of the tentacular crown. In many cases, however, there is a frontal skeletal wall and the parietal muscles are attached to the floor of a special compensatory sac (ascus) serving as the hydrostatic apparatus. The polypide is retracted with the help of two retractor muscles and the zooidal orifice is closed by a chitinized fold (operculum). The only ganglion is located near the pharynx. The coelomic cavity is represented by two communicating parts: the main visceral coelom and the lophophoral coelom (circular peripharyngeal canal with radiating tentacular coeloms). The peritoneum of the body wall is connected with the peritoneal lining of the intestine by funicular strands, considered as homologues of blood vessels by Carle and Ruppert (1983). The cavities of neighbouring zooids communicate by means of pores closed by the specialized pore-cell complexes associated with funicular strands. Polypides are renewed in the course of degeneration and regeneration cycles, and their remnants are either removed or kept inside zooids as so-called brown bodies. There are no specialized excretory organs.

Bryozoan colonies are hermaphroditic, consisting of sterile and gonochoric and/or hermaphroditic zooids (Reed 1991; Ostrovsky 2009). The gonads are located either on the internal surface of the cystid walls or on the gut. In both cases they are associated with funicular strands or occur on the strands themselves. Fertilization is internal. Sperms are released into the environment via pores in the tentacle tips, and enter the maternal coelom via the intertentacular organ or the supraneural coelomopore. In non-brooding species, planktotrophic larvae with a cuticularized bivalve shell, known as cyphonautes larvae, are formed from the spawned eggs. In brooding species, embryos develop to become endotrophic coronate larvae. It is worth noting that the non-feeding larvae of some gymnolaemate species have retained some features characteristic of cyphonautes such as the shell and/or a rudimentary intestine. Cleavage is complete, biradial, equal at early stages and unequal at later stages, asynchronous and non-determined. Gastrulation is by invagination or by immersion of four cells of the presumptive mesentoderm into the blastocoel (Zimmer and Woollacott 1977; Reed 1991; Temkin 1994, 1996; Mukai et al. 1997; Gruhl 2008, 2010). Depending on the species, larval production either peaks in a certain season or is more or less even throughout the year (reviewed in Ryland 1967; Reed 1991; Seed and Hughes 1992).

Order Cheilostomata is subdivided into four suborders (Gordon 2012). The paraphyletic suborder Malacostegina exhibits primitive zooidal morphology, planktotrophic larvae and no parental care. Suborder Flustrina (=Neocheilostomina), considered to be monophyletic, comprises the overwhelming majority of brooding cheilostomes, except those in the suborders Inovicellina and Scrupariina. A characteristic feature of all brooding bryozoans is endotrophic larvae that develop in incubatory chambers. Malacostegina is considered as ancestral to brooding cheilostomes, but whether or not the other suborders are monophyletic remains an open question (Taylor 1988).

The first findings of fossil cheilostomes are from the Late Jurassic (Taylor 1981, 1986a, 1994). During the Early Cretaceous this group had low taxonomic diversity, being represented only by two families of Malacostegina, Electridae and Wawaliidae (summarized in Taylor 1986b; Ostrovsky et al. 2008). However, starting from the Middle Cretaceous, the Cheilostomata entered a phase of rapid diversification (Taylor 1988), which, alternating with periods of extinction and gradual decline, continued for about 90 Ma (Voigt 1985; Taylor and Larwood 1988; Lidgard et al. 1993; Macleod et al. 1997; McKinney et al. 1998; Sepkoski et al. 2000; Taylor 2000).

The first evidence of parental care in the Cheilostomata, namely the presence of brood chambers, is from the Late Albian (Cheetham 1954, 1975; Cheetham et al. 2006). This means that the emergence of larval brooding shortly preceded the onset of the above-mentioned diversification phase. Based on this evidence, Taylor (1988) suggested that the presence of brood chambers in cheilostomes meant that their larvae had become non-feeding (lecithotrophic). According to this idea, lecithotrophy would have enhanced speciation, triggering the subsequent dramatic radiation within the order. The transition to lecithotrophy must have greatly reduced the duration of the dispersal phase, which in planktotrophic cyphonautes larvae may last 1–2 months, resulting in the isolation of distant populations. It is the disruption of genetic exchange between populations that is considered as a direct cause of speciation (allopatric and parapatric models) (Jablonski and Lutz 1983; Jablonski 1986; Poulin and Féral 1994; discussed in Havenhand 1995). Modern data support this scenario: bryozoan species with endotrophic larvae are much more genetically heterogeneous than those with planktotrophic larvae that also have wider geographical range (Goldson et al. 2001; Porter et al. 2002; Watts and Thorpe 2006).

However, as emphasized above, the emergence of a non-feeding larva is the result of dramatic changes in the maternal organism, namely, a shift in oogenesis. Transition from an exotrophic larva to an endotrophic one is based on an increase in the amount of energy input into a single offspring with an accompanying decrease in the number of descendants, and this means a change in reproductive strategy. Besides, *all* incubating Bryozoa, marine as well as freshwater, have an endotrophic larva. Does this mean that the transition to a new larval type in bryozoans was in some way associated with the origin of parental care?

So far the only well-substantiated and non-contradictory explanation of the Late Cretaceous radiation of Cheilostomata appears to be the hypothesis suggested by Taylor (1988). While agreeing with it in general, Gordon and Voigt (1996) nevertheless asked: could lecithotrophy, once acquired, have sustained high speciation rates for so long? The above authors put forward their own hypothesis, according to which the progressive evolution of cheilostome bryozoans was based on the emergence of new types of protective skeletal structures, the frontal shields. The evolution of non-feeding larvae and brooding is seen as a trigger of radiation, later sustained by the evolution of skeletal structures. Jablonski et al. (1997) posited that Taylor's hypothesis is contradicted by the fact that in cyclostome bryozoans (which usually coexist with cheilostomes), the acquisition of gonozooids (and, possibly, of an endotrophic larva) in the Late Triassic (Taylor and Michalik 1991) resulted only in moderate diversification (see also Taylor and Larwood 1990; Lidgard et al. 1993). At the same time, these authors stressed that the available data were insufficient for any final judgement. However, the fact that endotrophic larvae and incubation are widespread in bryozoans indicates that these novelties might have played a very important role in their evolution.

Parental care is a common phenomenon. In particular, invertebrates are known to have different variants of brooding (Porifera, Cnidaria, Annelida, Mollusca, Arthropoda, Kamptozoa, Echinodermata, Brachiopoda, Phoronida, Pterobranchia), viviparity and matrotrophy (found in representatives of more than twenty of the 34 known phyla) (Giese and Pierse 1974, 1975a, b, 1977; Giese et al. 1979, 1987, 1991; Adiyodi and Adiyodi 1989, 1990; Levin and Bridges 1995; Batygina et al. 2006). Bryozoans are no exception: parental care is characteristic of most representatives of the phylum. All cyclostomes (and, presumably, some others of the Paleozoic stenolaemates) as well as the cheilostome family Epistomiidae are viviparous. All phylactolaemates and most gymnolaemates brood their offspring in specialized brood chambers. The question is, how and under what circumstances did different modes of parental care evolve? What were the evolutionary consequences of these innovations? Why and in what directions was sexual reproduction within the order Cheilostomata and other bryozoan groups evolving, and how did this influence the evolutionary fate of these epibiotic organisms?

About This Book

This monograph is the result of a long period of comparative-anatomical study of oogenesis, fertilization, brooding and associated organs and structures in cheilostome bryozoans. Altogether, 258 recent and fossil species from 148 genera and 66 families have been studied using light and scanning electron microscopy (see Appendix II: Materials and Methods and List of Taxa Studied). Comparative analysis of the data obtained made it possible to reconstruct the main stages and to reveal the major trends in the evolution of sexual reproduction in the Cheilostomata during their history. The results of this study indicate that the evolutionary success of Cheilostomata may have been based on changes in sexual reproduction, namely, the evolution of new reproductive strategies and patterns involving the origin of parental care. Importantly, the complex approach applied during this study was instrumental in revealing numerous examples of parallelisms and convergent evolution. The large suite of new data on bryozoan reproduction was also useful for understanding trends in the evolution of sexual reproduction in marine invertebrates in general.

The monograph consists of three chapters. The first chapter is devoted to comparative analysis of reproductive patterns in Bryozoa: first of all, oogenesis, fertilization and brooding in the Cheilostomata. Detailed consideration is given to the position of gonads, the sexual structure of the colonies, sexual polymorphism and oviposition. The second chapter deals with the structural diversity, independent origin and evolution of brood chambers in different cheilostome groups. These two chapters are mostly based on the results of original research, which is compared with information in the literature. The third chapter contains an analysis of the main directions in the evolution of sexual reproduction in bryozoans and a reconstruction of the stages: changes in modes of oogenesis and fertilization and their consequences, the transition to the non-feeding larva, the origin of embryonic incubation, and repeated evolution of matrotrophy and placental analogues. The trends that emerge from this analysis are compared with analogues in the evolution of the bryozoan order Ctenostomata as well as other marine invertebrate groups (predominantly, echinoderms, molluscs and annelids). The conditions under which the cheilostomes radiated in the Late Cretaceous are considered in detail, and the consequences of the transitions to new reproductive patterns are analyzed. Finally, the stages in the evolution of sexual reproduction in other bryozoan groups (classes Phylactolaemata and Stenolaemata) are reconstructed. The monograph contains 12 tables, including those with data on the sexual structure of colonies, the position of gonads in zooids and the size and number of the oocytes at various stages of development, embryonic increase during incubation, etc., as well as a review of the history of study of sexual reproduction in the Gymnolaemata with a list of the species studied. This review also references the major publications on bryozoan life cycles, which are not analyzed in the main body of the text.

The first version of this monograph was published by the Publishing House of Saint Petersburg State University (Unipress) in 2009 under the title "Evolution of sexual reproduction in the bryozoan order Cheilostomata (Gymnolaemata)" (Ostrovsky 2009). Since that time, new data emerged that led to a critical reassessment of some parts of the book. As a result the text of the present English edition has been considerably rewritten and supplemented. In particular, bryozoan reproduction is compared throughout the monograph with that in other aquatic invertebrates. These changes called for a change in the title of the book.

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