

Chapter 7

Summarizing discussion

The studies in the preceding chapters have all focussed on morphological characters of the Bryozoa that are potentially of phylogenetic significance, but suffer from a lack of knowledge or ambiguous scoring. Both molecular analyses and morphology-based phylogenies have so far failed to provide a consistent hypothesis of the position of the Bryozoa in the phylogenetic system. Further questions that are controversially discussed include the internal relationships of Bryozoa and their monophyly. In the following section, I will review these problems and discuss in synopsis the impact of the present results on the different hypotheses.

Relationships within Bryozoa

The relationships between the recent bryozoan higher taxa are still relatively uncertain and so far only few phylogenetic accounts exist (Cuffey and Blake 1991, Todd 2000). Phylactolaemata and Cheilostomata are generally regarded as monophyletic (Mundy et al. 1981, Taylor 1990, Okuyama et al. 2006), whereas some evidence, mainly from palaeontology argues for paraphyly of ctenostomes (Taylor and Larwood 1990, Todd 2000). Stenolaemata are also suggested to be paraphyletic (Ernst and Schäfer 2006), but Cyclostomata, their only recent representatives are likely monophyletic (Borg 1927, Schäfer 1991, Taylor and Weedon 2000, but see Boardman 1998). Traditionally, Phylactolaemata are thought to be sister-group to the remaining Bryozoa (e.g., Silén 1942, Marcus 1958, Hyman 1959, Ax 2001). However, Cuffey and Blake (1991) regard Stenolaemata as sister to a taxon comprising Phylactolaemata and Gymnolaemata.

Considerable morphological differences have long been recognized between Phylactolaemata on the one side and Stenolaemata and Gymnolaemata on the other (Allman 1856, see Hyman 1959, Ryland 1970, Mukai et al. 1997 for review). Phylactolaemata possess soft-walled, often tubular cystides with ring musculature. The zooids are monomorphic, mostly widely connected by their body cavities. The lophophore is U-shaped and an epistome is present at the anal side of the mouth opening. All species exhibit a unique form of asexual propagation via encapsulated resting buds, so-called statoblasts. In contrast Gymnolaemata and Stenolaemata have circular lophophores lacking an epistome. The cystide of Cheilostomata and Stenolaemata are calcified. Zooids exhibit polymorphism and are usually connected via

communication pores. Budding occurs at oral surface of the zooids in phylactolaemates, but at the aboral surface in the remaining groups (Jebram 1973). Further differences concern the sexual reproduction. Larvae in phylactolaemates are hollow bilayered spheres that already have formed the first polypide buds. Thus they are often regarded as swimming juvenile colonies. Gymnolaemates exhibit planktotrophic cyphonautes larvae, as well as several types of lecithotrophic larvae (Zimmer and Woollacott 1977, Reed 1991). The latter are brooded outside the body cavity in various types of brooding structures, whereas in phylactolaemates, embryos develop in internal pouches in the coelom (Ström 1977).

Detailed statements on the ground-pattern of Bryozoa suffer from the unresolved internal relationships, especially the unclear position of the phylactolaemates. Many authors regard characters found in phylactolaemates as plesiomorphic, but these assumptions are mostly biased by the unproved affinity to phoronids and brachiopods, thus should be avoided. On the other hand, the relatively recent occurrence of phylactolaemates in the fossil record contrasts their assumed basal phylogenetic position, especially concerning the long record of for example Stenolaemata, which are known from the Ordovician. However, Kohring and Hörnig (1998) identified statoblasts already in Upper Triassic strata.

Monophyly of Bryozoa

A number of molecular studies were unable to support bryozoan monophyly (e.g., Mackey et al. 1996, Helmkampf et al. 2008, Passamanek and Halanych 2006). One reason for this might be insufficient taxon sampling, because often only one representative of each bryozoan higher group is used. A sister-group relationship of phylactolaemates to phoronids has been suggested only in one analysis of 18S rDNA data (Wood and Lore 2006) and one of protein-coding genes (Helmkampf et al. 2008), in both cases with weak support.

Based on morphology, bryozoans are mostly regarded as monophyletic. At least a common ancestry of Stenolaemata and Gymnolaemata has to my knowledge never been questioned. However, as already pointed out, phylactolaemate morphology clearly differs from that of gymnolaemates and stenolaemates. Some characters, like e.g., statoblasts, lack of calcification, or modifications in the larval form, can easily be explained as specific adaptations to the limnetic habitat, while others are more often interpreted as primitive. The latter include the U-shaped lophophore with an epistome, worm-like cystides with soft ectocysts, and ring musculature. These characters have been suggested to show similarities to phoronids, especially to *Phoronis ovalis*, the only modular phoronid species (Hyman 1959, Farmer et al. 1973, Farmer 1977, Mundy et al. 1981). Budding in *P. ovalis* takes place at the oral side (Marcus 1949), similar as in phylactolaemata (Jebram 1973). Hence, Mundy et al. (1981) suggested Phylactolaemata to share a common ancestor with Phoronida, rather than with

Gymnolaemata and Stenolaemata. Furthermore, Backus and Banta (2002) pointed to similarities of phoronid fat bodies to phylactolaemate statoblasts.

Despite the morphological differences, several synapomorphies of Phylactolaemata, Gymnolamata and Stenolaemata can be identified. However, due to the uncertain phylogenetic position of Bryozoa, only such character states that do not occur in any putative out-group can be taken into account: (1) adult feeding mechanism as upstream-collecting system with multiciliated lateral cells and stiff laterofrontal cilia (Riisgard and Manriquez 1997, Nielsen and Riisgard 1998, Riisgard et al. 2004). Phoronids and brachiopods have monociliated lateral cells, entoprocts and all other spiralian exhibit multiciliated cells, but downstream-collecting system. (2) Funiculus, a tissue-cord connecting the zooids of a colony. (Bobin 1977, Ryland 1979, Carle and Ruppert 1983) (3) Absence of nephridia (see Mukai et al. 1997 and discussion in chapter 3) (4) Formation of brown bodies (Gordon 1977) (5) Budding. Differences occur between subgroups, thus a reexamination is needed (see Nielsen 1971, Reed 1991 for review). (6) Retractable lophophore. In all bryozoans the lophophore can be retracted into the remaining body, although mechanisms of retraction and protusion differ (Taylor 1991).

The data from the present studies on phylactolaemate ultrastructure (chapters 2 and 3) do not provide any further support for a phoronid affinity of phylactolaemates. Though, as shown in chapter 2, the cerebral ganglion of phylactolaemates is distinct from that of gymnolaemates in its histological structure as a hollow, epithelial vesicle, its location beneath the pharyngeal epithelium corresponds to that in gymnolaemates (Gordon 1974, Lutaud 1973, Lutaud 1977, 1993). In contrast, the nervous center in phoronids is formed by a concentration of the basiepithelial plexus in the epidermis outside the ring of tentacles (Fernandez et al. 1996). The position of the ganglion might thus also be considered as potential bryozoan autapomorphy, but since the orientation of the body axes in adult bryozoans is uncertain, comparisons to other taxa remain difficult. The epistomes in phylactolaemates and phoronids are found at similar locations inside the lophophore and have traditionally been regarded as homologous (Remane 1950, Hyman 1959), especially in connection with the hypothesized trimeric coelomic organization. Furthermore, a close resemblance in the function of the epistome in the context of ciliary feeding has been suggested (Gilmour 1978). The results in chapter 3, however, show no resemblance in the body cavity composition of this organ between phylactolaemates and phoronids rendering a convergent origin of the epistome possible. Furthermore, neither this study, nor any preceding studies show coelomic trimery in phylactolaemates.

Thus, so far no convincing arguments from morphology exist that would support a closer relationship of Phylactolaemata to Phoronida or any bryozoan taxon to any non-bryozoan bilaterian group. The list of characters that support bryozoan monophyly is certainly not

overwhelming, but, as long as no contrary hypothesis can be put forward consistently, sufficient. However, the discussion about a remote position of Phylactolaemata emphasizes once more their importance for phylogenetic inference.

Position of Bryozoa in the Phylogenetic System

The classic dispute is whether Bryozoa are related to the Deuterostomia or to the Protostomia. The former hypothesis is advocated by most comparative morphological accounts and usually implicates a close affinity of Bryozoa to Brachiopoda and Phoronida in the either mono- or paraphyletic Lophophorata (Hyman 1959, Jefferies 1986, Ax 1989, Brusca and Brusca 2003). A placement within the protostomes is supported by nearly all modern molecular phylogenetic analyses, which consistently show evidence for a clade Lophotrochozoa uniting spiralian and the lophophorate taxa (e.g., Halanych 2004, Dunn et al. 2008). Morphology-based arguments for a protostome affinity have so far mainly been arguments for a close relationship to Kamptozoa (Nielsen 1971, 1977, 2001).

An affinity to Brachiopoda and Phoronida in the taxon Tentaculata (Hatschek 1891) or Lophophorata (Hyman 1959) is by far that theory which has persisted for the longest time, evidenced today by its presence in most current text-books. As indicated by the names given to this taxon, the lophophore was the crucial feature that led to erect it. This theory has been disputed on mainly two lines of argumentation. Firstly, under the rise of consequent phylogenetic methods, some authors argued that the lophophore in fact represents an ancient feature (Jefferies 1986, Ax 1989, 2001), as a resembling structure also exists in hemichordates (Dilly 1972, Halanych 1993). Thus it provides an argument for a common ancestry of tentaculates and deuterostomes, but not for the monophyly of the former. However, the three taxa were still placed closely to each other as a paraphyletic assemblage at the base of the deuterostome lineage. Secondly, homology of the lophophore itself was questioned, mainly because of differences in body cavity composition and ciliary band architecture between Bryozoa and the other two groups (Nielsen 1971, Nielsen and Riisgard 1998, 1977, 2001). As already pointed out in the first section, several similarities, between phoronids and phylactolaemate bryozoans like the epistome, U-shaped lophophore etc. have also been taken as arguments for a phoronid-bryozoan sister-group relationship (Farmer et al. 1973, Farmer 1977).

Many molecular as well as morphological data show good support for a close affinity of Phoronida and Brachiopoda, either as sister-taxa (e.g., Mackey et al. 1996, Lüter and Bartolomaeus 1997, Anderson et al. 2004, Peterson and Eernisse 2001, Glenner et al. 2004, Dunn et al. 2008) or with Phoronida as an ingroup of Brachiopoda (“Phoronozoa”) (Cohen 1998, 2000, Cohen and Weydmann 2005). However, Lophophorata are never supported

and only few analyses show some (weak) support for a close placement of Bryozoa and Brachiopoda (Waeschenbach et al. 2006) or Bryozoa and Phoronida (Helmkamp et al. 2008).

Taking a closer look at the arguments for a deuterostome affinity, it turns out that most of them do not directly apply for Bryozoa. This means, that some putative synapomorphies are found for Brachiopoda, Phoronida, and Deuterostomia, whereas Bryozoa are only enclosed because of a putative relationship to Brachiopoda and Phoronida.

Deuterostomy, the origin of the adult anus from the blastopore has sometimes been suggested for Brachiopoda and Phoronida, but is certainly absent, as shown by many recent embryological studies (e.g., Freeman 2000, 2003, Lüter 2000 for Brachiopoda, Freeman and Martindale 2002, Santagata 2004, Grobe 2008 for Phoronida). In Bryozoa, deuterostomy is mentioned in some older text-books; only Brusca and Brusca (2003) code this character state in their matrix. In most data matrices, blastopore closure, i.e. no connection between mouth/anus and blastopore is coded. This has actually been stated in older embryological descriptions (Prouho 1890, 1892), but the data from *Membranipora membranacea* presented in chapter 6 argue for persistence of the blastopore as mouth opening in the cyphonautes larva. However, the catastrophic metamorphosis obscures any connection between larval and adult intestinal tract in bryozoans.

The long-held view of a trimeric body and coelom organization is certainly overcome, since recent studies have denied this character for Brachiopoda and Phoronida (Bartolomaeus 2001, Lüter 1996, 1998, Gruhl et al. 2005). Also my data from Phylactolaemata (chapter 3) show, in accordance with many older descriptions (e.g., Braem 1890, 1892, Brien 1953), no trace of a tripartite coelom. However, a significance of mesoderm and coelom origin might still apply. Lüter (2000) has argued for an archenteric origin of coelomic mesoderm as synapomorphy of Deuterostomia and Brachiopoda. However, mesoderm origin might be not uniform in Brachiopoda (Nielsen 1991, Freeman 2003), and in Phoronida mesoderm formation takes place at the ectoderm/endoderm boundary (Freeman and Martindale 2002). In the present results on mesoderm formation in *M. membranacea* no material originating from endoderm or blastopore rim has been observed, but instead ingression from the ectoderm. This parallels in part the situation in spiralian where two sources of mesoderm, one ectodermal and one from the 4d-micromere exist (Boyer et al. 1996, Boyer and Henry 1998).

Concerning larval nervous system characters, Hay-Schmidt (2000) found resemblance in the distribution of serotonergic cells between phoronids, brachiopods and deuterostomes (see discussion in chapter 5). Bryozoan larvae, however, were found to exhibit similar patterns as spiralian. This was corroborated in the present study. Assumptions basing on the adult nervous system are difficult, because polarities of the adult body in bryozoans are unclear. Furthermore, basal deuterostomes, as well as phoronids and brachiopods exhibit only simple

central nervous systems, possibly due to their sedentary lifestyle (Holland 2003, Lowe et al. 2003).

Kamptozoa (Entoprocta) were for a long time included within the Bryozoa. Nitsche (1869) drew attention on differences in the position of the anus and the morphology of the tentacle crown, hence proposed Entoprocta as sistergroup to the Ectoprocta. During the rise of comparative developmental biology in the late 19th century, the recognition of more fundamental differences in cleavage pattern and body cavity composition led to the separation of both groups (e.g., Hatschek 1891). More recently this relationship has been revived by Nielsen (1971, 1977, 2001) mainly based on similarities of metamorphosis and larval morphology. However, since Kamptozoa are well-founded acoelomate spiralian, a sistergroup relationship to Bryozoa would require many unparsimonious assumptions like loss of spiral cleavage in Bryozoa, loss or independent evolution of coelom etc. Furthermore, this theory is in opposition to the morphology-based hypothesis of a molluscan affinity of kamptozoans (Bartolomaeus 1993, Ax 1999, Wanninger et al. 2007, Haszprunar and Wanninger 2008). Although most molecular studies (see above) provide evidence for a lophotrochozoan affinity of Bryozoa, the only support so far for an entoproct-ectoproct sister-group relationship is from a study of protein-coding genes (Hausdorf et al. 2007). That study, however, offers only limited insights, since representatives of several taxa, especially Phoronida and Brachiopoda were not included. The results from the present study do not support a bryozoan-kamptozoan clade. The neural architecture of gymnolaemate larvae, as analyzed in chapter 5, shows similarities to a generalized spiralian pattern, but no close connection to Kamptozoa is indicated. The analysis of early embryology in chapter 6 does not give evidence for a spiral cleavage, but mesoderm origin may offer a link to spiralian. However, embryological data from Kamptozoa which could serve for a direct comparison are still missing.

Conclusion and prospects

The data on mesoderm formation, body cavity composition as well as larval nervous systems, acquired in the present study mostly argue for a spiralian affinity of Bryozoa. This is in accordance with the majority of the molecular data. Thus, a serious conflict between molecular and morphological data does not exist to the extent as had been suggested earlier. Indeed many morphological data, that served as arguments for a the classic hypothesis of a deuterostome affinity have been identified as lesser well-founded than proposed earlier. The studies included in this thesis do not provide arguments for a closer relationship to one of the candidate sistergroups Entoprocta, Phoronida or Brachiopoda. However, it is shown that many morphological characters of Bryozoa that are utilized for phylogeny reconstruction deserve critical reexamination, as was already suggested for metazoan data matrices in a more general context (Jenner 2001, Jenner 2004). The most promising approach at the moment in will be to maintain discussion on the entries in these matrices and to reevaluate the given

states. This can be either be done by critically reviewing the literature on each character, or by reexamination of the characters. Especially the utilization of new microscopic techniques has the potential to deliver further phylogenetically significant data.

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