

# Pattern of occurrence of supraneural coelomopores and intertentacular organs in Gymnolaemata (Bryozoa) and its evolutionary implications

Andrew N. Ostrovsky · Joanne S. Porter

Received: 17 October 2008/Revised: 26 January 2011/Accepted: 1 February 2011/Published online: 18 February 2011  
© Springer-Verlag 2011

**Abstract** The evolution of bryozoan female gonopores (the supraneural coelomopore (SNP) and the intertentacular organ (ITO)) is considered in the light of two alternative hypotheses. In the first hypothesis it is proposed that the ITO originated from the shortening and fusion of two tentacles possessing terminal pore(s), with further transformation into a simple pore. In the alternative hypothesis it is suggested that the ITO evolved from a coelomopore with a contribution from the basal parts of two disto-medial tentacles in an ancestor. Favouring the second hypothesis, in this paper we present a hypothetical scenario, according to which the earliest gymnolaemate bryozoans with uniserial growth and a broadcasting reproductive pattern possessed the supraneural coelomopore (SNP). This could serve both as a female gonopore and as a conduit for sperm entry. Evolution of large colonies of closely packed zooids led to development of the tube-like intertentacular organ (ITO) that is formed by epithelial proliferation of the basal parts of two dorso-medial tentacles. This prevented egg

swallowing in the situation when water exchange was hampered within the large colony. The ITO independently evolved in both ctenostome and cheilostome gymnolaemates when multiserial colonies appeared. Evolution of brooding in species with colonies of closely packed zooids led to reduction of the ITO, except for the cheilostomes *Tendra* and *Thalamoporella* that acquired brooding independently. A rudimentary ITO also “survived” in two ctenostomes with the “mixed” type of brooding. An alternative, analogous organ—the ovipositor—has evolved in the cheilostome taxon *Schizoporella*.

**Keywords** Gonopore · Fertilization · Spawning · Evolution · Bryozoa

## Introduction

Despite their importance in the final stage of reproduction, bryozoan gonopores and their evolution have rarely been discussed in the literature. The pattern of the occurrence of two different female gonopore types (supraneural coelomopore and intertentacular organ) throughout the taxon Gymnolaemata (Ctenostomata and Cheilostomata) shows interesting correlations with colony growth form and patterns of sexual reproduction. From these, it is feasible to explore possible trends in the evolutionary change of female gonopores. In this paper we propose a hypothesis connecting evolution of the female gonopore and the intertentacular organ with colony morphology and reproduction, and discuss the possible evolutionary transitions between these reproductive structures.

Traditionally Bryozoa are classified into the limnetic Phylactolaemata, the marine Stenolaemata (Cyclostomata) and the primarily marine Gymnolaemata consisting of

---

Communicated by T. Bartolomaeus.

A. N. Ostrovsky (✉)  
Department of Invertebrate Zoology,  
Faculty of Biology and Soil Science,  
St. Petersburg State University, Universitetskaja nab. 7/9,  
199034 St. Petersburg, Russia  
e-mail: oan\_univer@yahoo.com

A. N. Ostrovsky  
Department of Palaeontology, Faculty of Earth Sciences,  
Geography and Astronomy, Geozentrum, University of Vienna,  
Althanstrasse 14, 1090 Vienna, Austria

J. S. Porter  
School of Life Sciences, Centre for Marine Biodiversity  
and Biotechnology, Heriot-Watt University,  
John Muir Building, Gait 1, Edinburgh EH14 4AS, UK

Ctenostomata and Cheilostomata. Recent molecular studies (Fuchs et al. 2009; Tsyganov et al. 2009) confirm the monophyly of all three groups and support the traditional view of a monophyletic taxon Phylactolaemata, which is the sister group of the remaining Bryozoa, Stenolaemata and Gymnolaemata (Ax 2001: 79–81). In the analyses by Fuchs et al. (2009), sistergroup relationship of Phylactolaemata and Cyclostomata is equally well supported. Monophyly of both subgroups of the Gymnolaemata, Ctenostomata and Cheilostomata remains questionable due to classical and molecular studies, indicating that at least Ctenostomata are paraphyletic with respect to the Cheilostomata (Fuchs et al. 2009; Tsyganov et al. 2009).

All bryozoans are characterized by spermcast mating (Bishop and Pemberton 2006). The sperm is released via the terminal pores of all, or in some cases two disto-medial tentacles (Silén 1966, 1972; Bullivant 1967; Temkin 1994), although it has yet to be confirmed in phylactolaemates (see Lützen et al. 2009). Sperm enters the body cavity via intertentacular organ (ITO) or supraneural pore (SNP), both being also used for the egg release. Fertilization (syngamy) is universally internal, either intracoelomic or intraovarian. Fusion of the female and male pronuclei occurs after spawning or oviposition, whereas egg activation (except Cyclostomata and cheilostome Epistomiidae) is obviously triggered during a passage of the egg through the female gonopore (Temkin 1994, 1996; Ostrovsky 2008a, 2009).

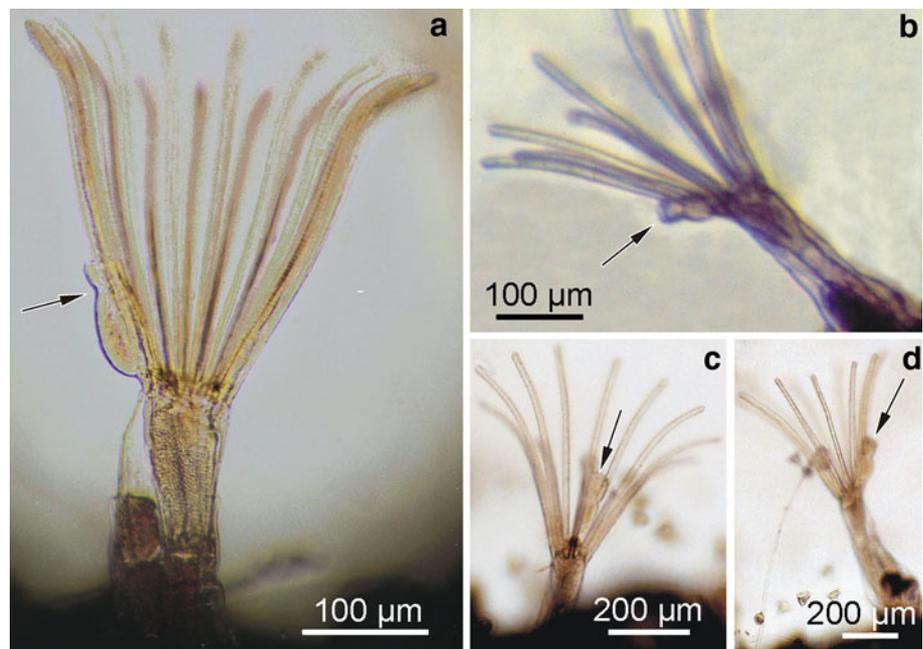
Thus, in Bryozoa the coelomic cavity communicates with the external medium via (1) terminal tentacular pores (male gonopores) and (2) the female gonopore, represented either by a supraneural coelomopore or by a terminal opening of the intertentacular organ (Calvet 1900; Hyman

1959; Silén 1966; Reed 1991; Temkin 1994; Mukai et al. 1997; Woollacott 1999). The coelomopore and the intertentacular organ occupy the same position at the base of the crown of ciliated tentacles, close to the ganglion and between the bases of the two dorso-medial tentacles (Figs. 1, 2, 3b, 4b). Silén (1945) considered the ITO and the SNP as homologous structures as they have the same position and function. Later, Reed (1991: 140) called the ITO an extension of the female gonopore.

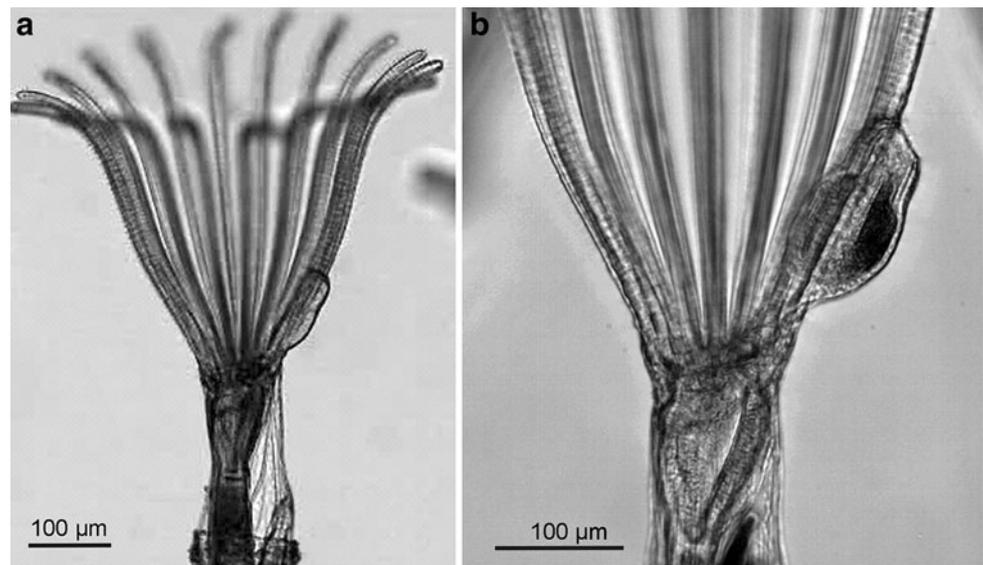
The ITO is known only in gymnolaemates. It is a two-chambered organ, ranging from about one-quarter to one-third of the tentacle length. The proximal chamber has a glandular structure (Temkin 1994). The distal pore is directed away from the funnel of the lophophore (Figs. 1, 2, 4b). The intertentacular organ is heavily ciliated internally (Fig. 3) and connected with an internal ciliated gutter in the broadcasting cheilostome *Membranipora serrilamella* Osburn 1950 (Hageman 1981; Reed 1991). Similar internal ciliated structures have been recorded in the brooding ctenostomes *Alcyonidium polyoum* (Hassal, 1841) and *Bowerbankia gracilis* Leidy, 1855 (Matricon 1963; Reed 1988). Both species have a SNP, which is associated with the internal ciliated funnel in *A. polyoum*, and with a pair of longitudinal ciliated ridges (also internal) in *B. gracilis*. Reed (1991) suggested that these structures (ciliated gutter, funnel and longitudinal ridges) are homologous.

In *M. serrilamella*, the ITO develops at the onset of oogenesis, and the whole process lasts about 2 days. The outer epithelium differentiates from rows of abfrontal and frontolateral cells of the two dorso-medial tentacles. The internal cells of the ITO differentiate from lateral cells of the tentacles which lose the cilia and later on develop a new ciliation

**Fig. 1** Expanded lophophore with the intertentacular organ (arrows). **a** Ctenostome *Alcyonidium mytili* Dalyell, 1848 (photograph by P. Cadman, courtesy J.S. Ryland); **b** Cheilostome *Conopeum tenuissimum* (Canu, 1928) (photograph courtesy J.E. Winston); **c, d** Cheilostome *Electra pilosa* (Linnaeus, 1767) (photograph courtesy A. Ernst)



**Fig. 2** Expanded lophophore with the intertentacular organ in cheilostome *Membranipora membranacea* before (a) and during (b) egg release (photographs courtesy M.H. Temkin)



(Hageman 1981). The differentiation of the ITO is not connected with polypide replacement (Cori 1941; Jebram 1975; Reed 1991; see also Cook 1962; Silén 1966; Jebram 1973a; Cadman and Ryland 1996). It is not yet known whether a supraneural pore is present before the formation of the ITO or whether it is found in non-fertile zooids.

The supraneural coelomopore (SNP) (the term introduced by Marcus 1926, 1938a) is so tiny that it was only encountered during the observation of egg spawning in the ctenostome *Farrella repens* (Farre, 1837) (as *Laguncula*) (van Beneden 1844, see also Marcus 1926; Ostrovsky et al. 2008; Ostrovsky 2008a, 2009). The ITO was initially discovered in the ctenostome *Alcyonidium duplex* Prouho, 1892 (as *Halodactylus diaphanus*, see Prouho 1892) by Farre (1837: 408) who asked “does it indicate a difference of sex?” Later the ITO was observed apparently releasing sperm in the cheilostome *Electra pilosa* (Linnaeus, 1767) (as *Membranipora*) by Hincks (1851) who introduced the term “intertentacular organ” (see also Hincks 1880). Ehlers (1876) observed the presence of an ITO in almost all the zooids of an unidentified cheilostome (as *Lepralia*). Although Ehlers referred to the results of the earlier work (Farre 1837; Hincks 1851), he suggested that the ITO was an attached parasitic infusorian. Later, Hincks (1880) and Harmer (1892) ascribed an excretory function to the ITO.

The ITO was later shown by several observers to be similar in function to the SNP, serving as a route for the release of eggs (Fig. 2B) in a variety of species (Prouho 1889, 1892; Schulz 1901; Silén 1966; Mawatari 1975; Jebram 1975; Temkin 1994; Ryland 2001; Temkin and Bortolami 2004). The ITO also serves as the entry point for sperm (Temkin 1994). This function has also been ascribed (but not documented) to the SNP. Hincks (1880) and Prouho (1892) interpreted from the observations of Hincks (1851)

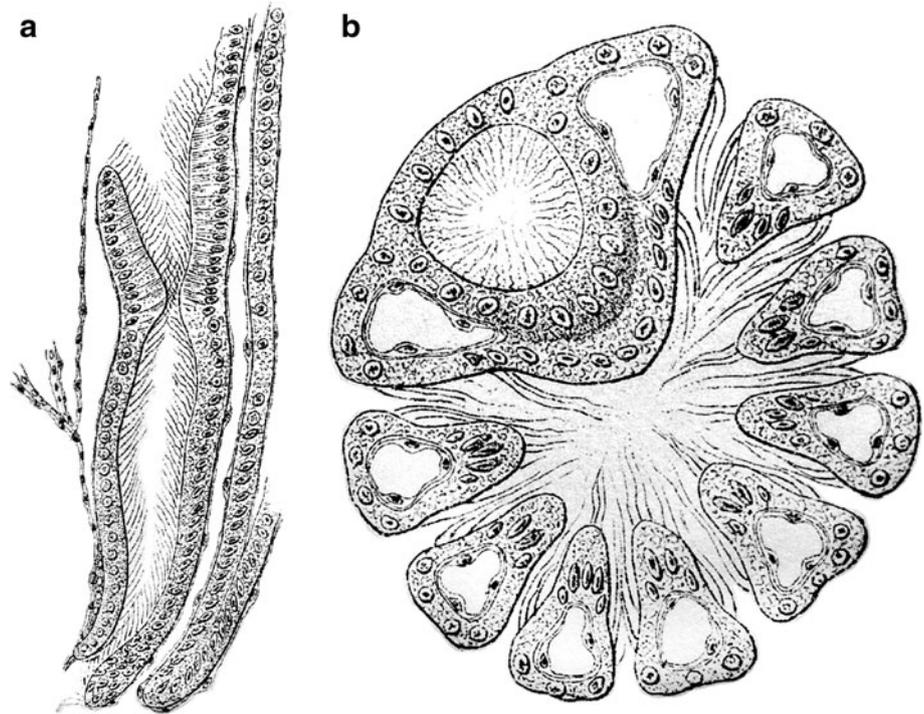
that there could be an additional function of sperm release by the ITO. They speculated that this could enable the expulsion of the remaining sperm at the end of the reproductive period. Later, Temkin (1994) suggested that the squeeze of the inseminated oocyte through the ITO may trigger activation of the egg by either i) physical stress or ii) chemical stimulation. It was also shown that both a passage of eggs and an entering of sperm via the ITO are regulated by a terminal sphincter muscle in *M. membranacea* (Temkin 1994).

The presence of an ITO is strongly correlated with a broadcasting reproductive pattern involving production of numerous small yolk-poor eggs that develop into long-lived planktotrophic larvae. This pattern of reproduction is considered to be an ancestral one by most scholars, and it is also rather rare (but probably underreported) among Bryozoa. Within the Gymnolaemata, it is typical of the earliest cheilostome group Malacostega, possessing primitive skeletal organization, and also broadcasting ctenostomes, and absent in the Stenolaemata and Phylactolaemata (Ryland 1970, 1976; Boardman et al. 1983; McKinney and Jackson 1989; Reed 1991). There are also a few gymnolaemate brooders possessing an ITO and a few broadcasters with a SNP, but these are exceptions.

### Competing hypotheses on the origin and the function of the intertentacular organ

Two hypotheses for the origin of the supraneural coelomopore and intertentacular organ are considered here. In the first, postulated by Silén (1945), the ITO and SNP evolved by transformation of two tentacles through their “shortening”: an intertentacular organ might have evolved at the expense of the tentacles with terminal (coelomo)pores, becoming

**Fig. 3** Longitudinal (a) and transverse (b) section of the ITO in *Electra pilosa* (from Calvet, 1900, Plate VI, Figs. 8, 10) (the relationships between the cell layers are obviously wrong)



reduced at a later stage to a simple pore. In this paper we propose an alternative hypothesis, where the ITO evolved from a female gonopore as an extension developing from the fusion of the basal parts of two dorso-medial tentacles. This is in accordance with the development of the ITO as described by Hageman (1981) and Reed (1991) who called the ITO an extension of the female gonopore.

Silén (1944) speculated that in Phylactolaemata and primitive brooding Gymnolaemata (such as *Labiostomella gisleni* Silén, 1944), the ovulated egg never leaves the zooidal cavity and enters an “embryonary” or “embryo sac” formed on the internal surface of the maternal zooid body wall. Upon maturation the larva is released from this brood chamber either by rupture of the body wall or through the zooidal orifice after polypide degeneration. In this scenario there was no requirement for a female ‘birth’ pore in the ancestral bryozoans, although there is a need for a pore serving for the entry of allosperm. The simultaneous presence of the supraneural coelomopore and “embryonary” in the ctenostome *Nolella* species led Silén (1945: 24) to develop the idea that the ITO and the SNP initially evolved not for the spawning of eggs, but for the entry of sperm, and secondarily acquired the spawning function in descendants. This idea was presumably caused by two different observations. (1) According to Cori (1941), the ITO is formed by the fusion of two neighbouring tentacles (see also Fig. 3b). This could lead Silén (1945: 25) to suggest that the ITO and the SNP were possibly homologous with tentacles, so that ITO pore and SNP pore were comparable to terminal

tentacular pores. (2) Cori (1941) recorded spermatozoids in the coelomic lumen of the tentacles in the ctenostome *Zoobotryon verticillatum* (Delle Chiaje, 1828) that might influence Silén to suggest a sperm entry via tentacle pores. It should be noted that, despite Silén’s assumption, there is no evidence to date that the terminal pores of tentacles were ever used by bryozoans as a conduit for the entry of sperm. In some phoronids the sperm lyses through the wall of the tentacles, however (Zimmer 1991). Twenty years later it was discovered by Silén himself that the terminal tentacular pores are the male gonoducts in Bryozoa (Silén 1966, 1972; see also Bullivant 1967; Temkin 1994).

The example of the *Nolella* species, however, cannot be used as a supportive argument in this case, since its eggs leave the maternal zooid via a supraneural coelomopore and are then immersed into the body wall from the outside, a mode also found in the ctenostomes *Victorella muelleri* (Kraepelin, 1877) and *Sundanella sibogae* (Harmer, 1915) (see Ström 1977 for details and discussion). Silén’s speculations concerning evolution of brooding, oviposition and larval types in Gymnolaemata, are highly disputable (criticized by Santagata and Banta 1996; Ostrovsky 2009).

According to the second hypothesis, the earliest Bryozoa had a female gonopore (supraneural coelomopore) that was originally used for both spawning and for the entry of alien sperm, whereas terminal (coelomo)pores of the tentacles served as male gonopores for sperm release. The inter-tentacular organ evolved later as an extension of the female gonopore retaining its functions.

The difference between the two hypotheses on the origin of the ITO is that in the first case, it supposedly evolved by fusion of two entire dorso-medial tentacles, accompanied by shortening and functional modification (as a conduit for egg release and entering sperm), while in the other, the ITO is formed by the fusion of the basal parts of two dorso-medial tentacles and did not change its function. In the first case the terminal pore of the ITO corresponds to the male gonopore, whereas in the second it is originated from the female one.

### Origin of the supraneural coelomopore

Broadcasting is generally considered as an ancestral reproductive pattern in marine invertebrates (Jägersten 1972; Levin and Bridges 1995; Havenhand 1995) including bryozoans (Zimmer and Woollacott 1977; Strathmann 1978; Taylor 1988). In agreement with this idea, Reed (1991) wrote that the presence of an ITO was a primitive condition.

We agree that the intertentacular organ evolved early in the Bryozoa in broadcasting ctenostomes and cheilostomes. Nonetheless, we suggest that the initial state of this character was a simple female gonopore that served for both sperm entry and spawning in the earliest bryozoans. In Phylactolaemata a coelomopore in a vestibular wall through which statoblasts, and, incidentally, sperm are released has been recorded by Marcus (1941, 1942) and Wiebach (1953). Position of this pore below the anus, at duplicature (i.e. at the cystid wall) and not at the lophophore base, questions its homologicity with the SNP in gymnolaemates (see also Marcus 1941). It may serve as a route for the alien sperm. In the same time, it is not known if it is used for oviposition. According to Brien (1953), the eggs move from the ovary to the embryo sac through its wall by diapedesis in this group, and larvae obviously escape through the body wall rupture. If so, the function of coelomopore has been changed from the egg to the statoblast release. Terminal tentacular pores are known in Phylactolaemata (Hyatt 1866-1868; Nitsche 1868; Braem 1890, Marcus 1934), although the sperm release via them has yet to be confirmed (see also Lützen et al. 2009).

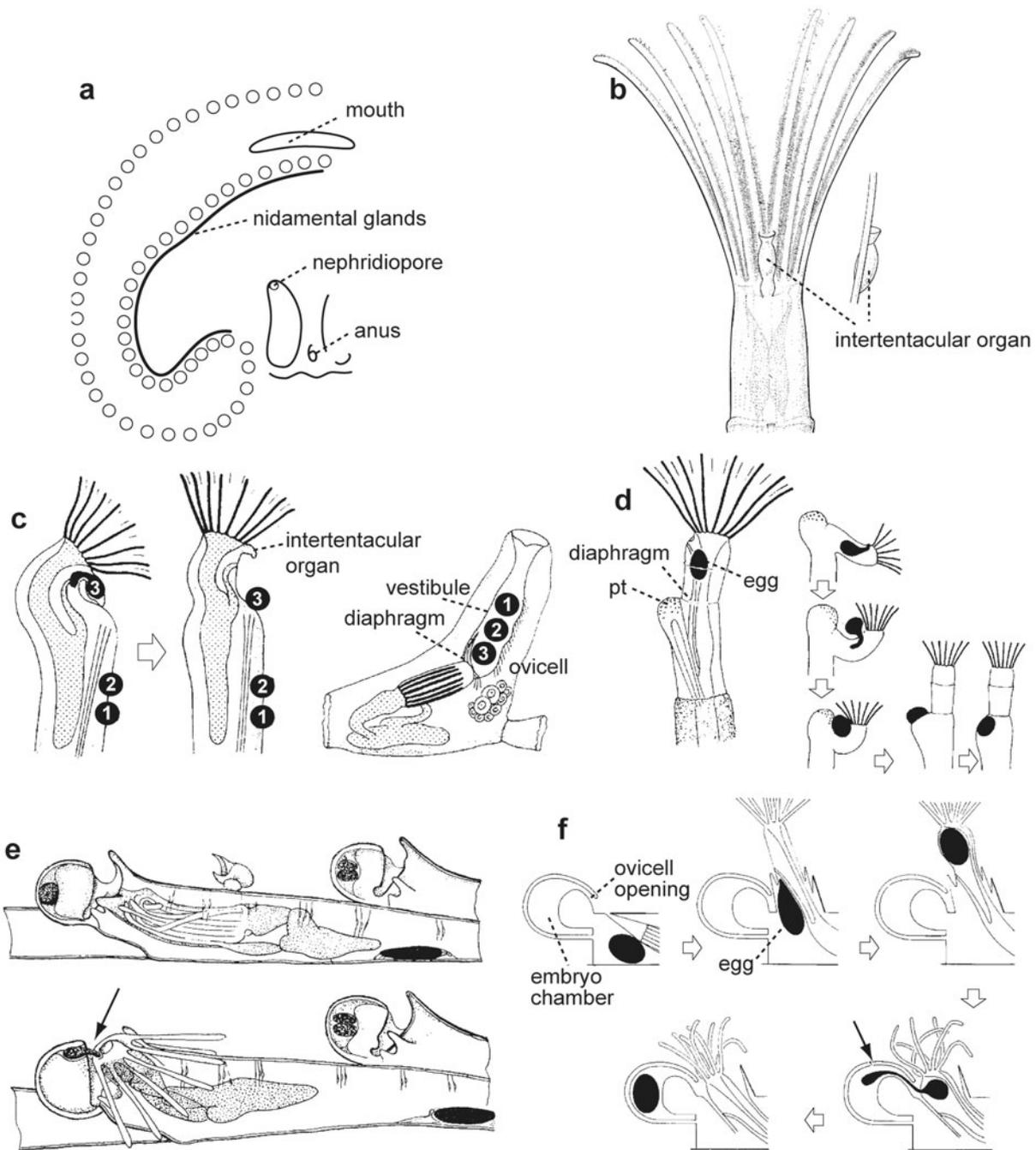
There are no data on the occurrence of the SNP in the Stenolaemata (Cyclostomata). Spawning is absent since their larvae develop intracoelomically, later escaping via the gonozooidal orifice. The route for the sperm is not known, but supposedly is via SNP. Since the tentacular pores are obviously not involved in its entry, other theoretical options are (1) penetration of the tentacle wall or even (2) ingestion.

We suggest that both Stenolaemata (Cyclostomata) and Phylactolaemata possess derived patterns of sexual

reproduction. Both these taxa have small oligolecithal or mesolecithal eggs (Reed 1991) that could have been spawned via the female gonopore in their ancestor(s). Later in evolution, a shift in the reproductive pattern involving viviparity (cyclostomes) and brooding (phylactolaemates) could have lead to the loss of the primary function (egg release) by the female gonopore. In both groups the egg does not leave the maternal coelom: in Cyclostomata an egg starts cleavage in the ovary, whereas in Phylactolaemata the egg moves to the brooding sac (i.e. outside the coelom) without being released (Brien 1953; Reed 1991). The female gonopore (SNP) is, however, supposedly used for the entry of sperm.

Theoretically, the existing SNP could have been either a female gonopore or nephridiopore in origin. In the Phoronida, which are traditionally (but not invariably) considered as a related or even ancestral group for bryozoans (Hyman 1959; Farmer et al. 1973; Farmer 1977; Ruppert et al. 2004; but see Emig 1982; Nielsen 2001), the sexual products are released via paired nephridiopores of metanephridia. Similar to the bryozoan supraneural coelomopore, these pores are positioned between the lophophore arms dorso-medially, near the anus (Emig 1982; Zimmer 1991; Mukai et al. 1997) (Fig. 4a). It should be noted that both the phoronid and the phylactolaemate pore(s) under discussion lead to the main coelom (metacoel), whereas in Gymnolaemata a female gonopore leads to the lophophoral coelom that, in turn, is connected to the main coelom (Hyman 1959; Mukai et al. 1997).

Considering the possible phylogenetic relationships of Phoronida and Bryozoa, we examined recent molecular papers. Some molecular data suggested that bryozoans and phoronids are not closely related (Passamanek and Halanynch 2006; Helmkamp et al. 2008a; Hausdorf et al. 2009). In contrast, Helmkamp et al. (2008b) used a multigene approach of seven housekeeping genes and concluded that Bryozoa, Brachiopoda and Phoronida are more closely related to molluscs and annelids than either deuterostomes or ecdysozoans, and phoronids share a common ancestor more recently with bryozoans than with brachiopods. Again, multigene analysis made by Dunn et al. (2008) did not support close relationships between Bryozoa and Phoronida. Despite this uncertainty, the similarity in position of pore(s) for gametic release is obvious in the two groups in question. We suggest it is possible that an ancestor of Bryozoa could have a pore(s) similar to that of phoronids through which female gametes were passed from the visceral coelom to the sea water, and which also served for the entry of allosperm. The ciliated internal structure associated with the pore, reminiscent of the phoronid metanephridia, would have been used to direct the sexual products. In extant species, it was found in both ctenostomes and cheilostomes in the form of a ciliated funnel,



**Fig. 4** **a** Left part of the lophophore in *Phoronis psammophila* Cori, 1889 (from above) (from Zimmer, 1991); **b** Expanded lophophore with the ITO in the ctenostome *Alcyonidium mytili* (dorso-medial and lateral views) (drawings by P. Cadman, courtesy J.S. Ryland); **c–f** Stages of oviposition in ctenostome (**c, d**) and cheilostome (**e, f**) Bryozoa; large arrows indicate successive stages. **c** *Bulbella abscondita* (modified from Braem 1951): Release of the zygote via an intertentacular organ (left). As soon as it free, it attaches to the introvert wall (middle) and stays there above the previously released and stuck zygotes. When polypide is withdrawn, the zygotes are inside the vestibulum—the distalmost part of the inverted introvert (right). **d** *Victorella muelleri* (modified from Braem 1951): The egg is near a supraneural coelomopore, ready for oviposition (left). Note the protuberance (pt)—a place in which a zygote will be immersed after release via a coelomopore.

Successive stages of this release are shown in the vertical column with 3 images. Once released the zygote attaches to the protuberance and immerses into it (right). **e** *Bugula avicularia* (Linnaeus, 1758) (modified from Gerwerzhagen 1913): Upper image Zooid with oviceil incubating a zygote (left) and zooid with oviceil containing two-cell stage (right). Lower image, left: polypide in a special ‘birth’ pose for squeezing a zygote through the supraneural coelomopore into the oviceil. **f** *Callopora dumerilii* (Audouin, 1826) (modified from Silén 1945): Upper left zygote in a coelom, empty oviceil, polypide withdrawn. Upper middle zygote uprises towards the coelomopore, polypide expanded. Upper right zygote is near the coelomopore, polypide expanded. Lower right polypide in a special ‘birth’ pose to squeeze zygote through the supraneural coelomopore into the oviceil. (c, d, f after Ström 1977; e after Prenant and Bobin 1966)

lateral ridges and ciliated gutter. A good argument for a former excretory function would be the occurrence of a SNP also in sterile zooids. On the other hand, these internal ciliated structures might have evolved anew. Both scenarios suggest that the earliest Bryozoa could inherit a pore leading from the coelom to the outside and used for evacuation of eggs (and sperm?). As mentioned previously, a coelomopore is placed near the tentacle base above the anus and leads to the lophophoral coelom in Gymnolaemata, whereas it is at the duplicature below the anus leading to the main coelom in phylactolaemates, but it is difficult to judge what this difference means. Were they evolved independently in these groups, and if not what state is derived then?

The female gonopore later evolved into an ITO. Formation of this organ involved a contribution from the basal parts of two disto-medial tentacles that are closest to the SNP (Fig. 3b). Such a process involves formation of two pairs of lateral epithelial proliferations in the lower part of the two tentacles, and their fusion allows a development of the new specialized tube organ.

It should also be noted that in contrast with the hypothesis of Silén (1945), our scenario requires fewer evolutionary steps and corresponds to accepted ideas on the evolution of bryozoan sexual reproduction (Boardman et al. 1983; Taylor 1988; Reed 1991; Ostrovsky and Taylor 2004, 2005; Ostrovsky et al. 2009; Ostrovsky 2009).

### Pattern of distribution of the ITO and SNP among gymnolaemate bryozoans

In the vast majority of cases the ITO has been recorded in the fertile (hermaphroditic and female) autozooids of broadcasting (non-brooding) ctenostome and cheilostome species (see Table 1). In contrast, brooding species have no ITO, except for the ctenostomes *Alcyonidium duplex* Prouho, 1892, and *Bulbella abscondita* Braem, 1951 (reduced ITO), and the cheilostomes *Tendra zostericola* Nordmann, 1839, and *Thalamoporella evelinae* Marcus, 1939 (Farre 1837; Prouho 1892; Braem 1951; Jebram and Everitt 1982; Paltschikowa-Ostroumowa 1926; Braiko 1967; Marcus 1941). Furthermore, two cheilostomes from the taxon *Schizoporella* possess a special ovipositor reminiscent of the ITO. In *S. cf. pungens* Canu et Bassler, 1828 and *S. cf. errata* (Waters, 1878), “a movable finger-like tube” with a tapered end is formed dorsally at the base of the lophophore of the fertile zooid, originating from the extended introvert just above the frontal surface of the colony (Maturio 1991: 572–573; R. Zimmer, pers. obs.). This tube is described as being “very flexible and contractile” and would enter the brood chamber (ovicell) within which it would move around fairly actively. The mature egg moves

into the extended tube, deforming like a “squirt of toothpaste” and is eventually deposited into the ovicell. Except six aforementioned species, in the vast majority of gymnolaemate brooders oviposition occurs through the supra-neural coelomopore (Fig. 4e, f).

On the other hand, there are two broadcasting ctenostome species—*Farrella repens* and *Hypophorella expansa* Ehlers, 1876—that release eggs via a coelomopore (Table 1). Thus, most brooders possess a SNP, and only a few species have an ITO or its analogue. Vice versa, majority of broadcasters have ITO, and only two—SNP.

It is interesting to note that all of those bryozoans that possess an ITO also have colony morphologies in the form of multiserial structures, taking the shape of large crusts, mats, anastomosing networks or dense turfs of closely packed zooids. The ctenostomes *Victorella pavida* Saville Kent, 1870, *Alcyonidium albidum* Alder, 1857 and *Arachnidium fibrosum* Hincks, 1880 all possess an ITO and form not only dense clumps (the first species), sheets (the second species) and dense patches of closely juxtaposed zooids (the third species), but also diffuse or uniserial chains (Prenant and Bobin 1956; Hayward 1985; De Blauwe 2009). Narrow encrusting lobes are also formed in the colonies of malacostegan cheilostomes from the genus *Electra*, also possessing an ITO (Hincks 1880: 137; Prenant and Bobin 1956: 201; Kluge 1975; Ryland and Hayward 1977). In contrast, there are no known species possessing an ITO that display strictly uniserial, runner-like growth of colonies with diffuse chains of zooids.

### Evolution of the ITO in relation to colony growth form

Reed (1991) suggested that the use of the terminal tentacular pores for sperm release in Bryozoa provided a mechanism by which the trapping of sperm by the parental and adjacent autozooids could be avoided. Could it be then that the terminal pores of the tentacles acquired the function of sperm release as a consequence of the evolution of colonies with dense positioning of zooids? Could it also follow then that the ITO evolved in a similar way? We suggest that elevating the gonopore to a higher position away from the base of the large colony of closely packed zooids would enhance the chances of both successful spawning of the eggs (as opposed to eggs being swallowed by the parental or neighbour lophophore) and spermcasting.

In large encrusting multiserial colonies, feeding polypides produce a broad ‘layer’ of descending water (Winston 1978, 1979; Lidgard 1981; Dick 1987; Shunatova and Ostrovsky 2002). In this situation the spawned oocytes in broadcasting species are forced into the zone of high water pressure that is created underneath the lophophores (Dick

**Table 1** Distribution of the intertentacular organ (ITO) and supraneural coelomopore (SNP) in broadcastling and brooding gymnoelaemate Bryozoa (based on the data from the literature and personal observations, SNP has been either detected during direct observations of oviposition/spawning or anatomical studies, or inferred from an absence of the ITO in reproducing zooids and the presence of brooding)

Intertentacular organ	Supraneural coelomopore
<b>Ctenostomata</b>	
<i>Alcyonidium albidum</i> Alder, 1857—broadcaster (Prouho 1889, 1892)	<i>Alcyonidium diaphanum</i> (Hudson, 1762)—brooder (Porter et al. 2001; Porter 2004)
<i>Alcyonidium mytili</i> Dalyell, 1848—broadcaster (Hincks 1880; Cadman and Ryland 1996; Ryland and Porter 2000, 2006)	<i>Alcyonidium</i> sp. (as <i>A. mamillatum</i> )—? (Marcus 1938a)
<i>Alcyonidium duplex</i> Prouho, 1892—“ <b>mixed</b> ” brooding (few embryos) (Farre 1837; Prouho 1892)	<i>Alcyonidium gelatinosum</i> (Linnaeus, 1761)—brooder (Ryland and Porter 2000, 2006)
<i>Alcyonidium antarcticum</i> Waters, 1904—broadcaster (Waters 1904)	<i>Alcyonidium disciforme</i> Smitt, 1872—brooder (Kuklinski and Porter 2004)
<i>Alcyonidium cellarioides</i> Calvet, 1900—broadcaster (Calvet 1900)	<i>Alcyonidium eightsi</i> Winston & Hayward, 1994—brooder (Porter and Hayward 2004)
<i>Alcyonidium flustroides</i> Busk, 1886—broadcaster? (Marcus 1922)	<i>Alcyonidium polyoum</i> (Hassall, 1841)—brooder (Matricon 1963; Ryland and Porter 2006)
<i>Alcyonidium</i> sp. (as <i>A. polyoum</i> )—broadcaster? (Marcus 1938b)	<i>Alcyonidium hirsutum</i> (Fleming, 1828)—brooder (Owrid and Ryland 1991, Ryland and Porter 2006)
<i>Alcyonidium polypylum</i> Marcus, 1941—broadcaster? (Marcus 1941)	<i>Alcyonidium parasiticum</i> (Fleming, 1828)—brooder (Porter, pers. obs.)
<i>Alcyonidium argyllaceum</i> Castric-Fey 1971—broadcaster? (Castric-Fey 1971)	
<i>Alcyonidium sanguineum</i> Cook, 1985—broadcaster? (Cook, 1985)	
<i>Alcyonidium nodosum</i> O'Donoghue & Wattleville, 1944—broadcaster (Ryland 2001)	
<i>Alcyonidium condylocinerum</i> Porter, 2004—broadcaster (Porter 2004; De Blauwe 2009)	
<i>Alcyonidium mamillatum</i> Alder, 1857—broadcaster (Porter, pers. obs.)	
<i>Alcyonidium hydrocoelatum</i> Porter, 2004—broadcaster (Porter 2004)	
<i>Alcyonidium australe</i> D'Hondt & Moyano, 1979—broadcaster? (ITO wanted) (Porter and Hayward 2004)	
<i>Alcyonidium flabelliforme</i> Kirkpatrick, 1902—broadcaster (ITO wanted) (Porter and Hayward 2004)	
<i>Alcyonidium epispiculum</i> Porter & Hayward, 2004—broadcaster (Porter and Hayward 2004)	
<i>Alcyonidium scolecoideum</i> Porter & Hayward, 2004—broadcaster? (ITO wanted) (Porter and Hayward 2004)	
<i>Alcyonidium simulatum</i> Porter & Hayward, 2004—broadcaster? (ITO wanted) (Porter and Hayward 2004)	
<i>Alcyonidium parasiticum</i> (Fleming, 1828)—broadcaster (De Blauwe 2009)	
<i>Victorella pavida</i> Saville Kent, 1870—broadcaster (Braem 1951, Carter, pers. obs.)	<i>Victorella muelleri</i> (Kraepelin, 1887) (as <i>Tanganella</i> )—brooder (Braem 1951)
<i>Victorella pseudoarachnidia</i> Jebram & Everitt, 1982—broadcaster (Jebram and Everitt 1982)	<i>Victorella appendiculata</i> (Jebram & Everitt, 1982)—brooder (Jebram and Everitt 1982)
<i>Bulbella abscondita</i> Braem, 1951—“ <b>mixed</b> ” brooding (few embryos) (ITO reduced) (Braem 1951; Jebram and Everitt 1982)	
<i>Cryptoarachnidium argilla</i> (Banta, 1967) (as <i>Victorella</i> )—broadcaster? (Banta 1967)	

**Table 1** continued

Intertentacular organ	Supraneural coelomopore
<i>Arachnidium fibrosum</i> Hincks 1880—broadcaster? (De Blauwe 2009)	<i>Triticella flava</i> Dalyell, 1848—external brooding (numerous eggs) (Ström 1969, 1977) <i>Panolicella nutans</i> Jebram, 1985—external brooding (few eggs) (Jebram 1985) <i>Potsiella erecta</i> (Potts, 1884)—external brooding (few eggs) (Smith et al. 2003) <i>Paludicella articulata</i> (Ehrenberg, 1831)—external brooding (few? eggs) (Braem 1896) <i>Notella stipata</i> Gosse, 1855—brooder (Marcus 1938a) <i>Bowerbankia gracilis</i> Leidy, 1855—brooder (Braem 1951; Reed 1988) <i>Farrella repens</i> (Farre, 1837)—broadcaster (van Beneden 1844; Marcus 1926) <i>Hypophorella expansa</i> Ehlers, 1876—broadcaster (Joyeux-Laffuie 1888; Prouho 1892) <i>Hislophia malayensis</i> Annandale, 1916—broadcaster (Wood, pers. obs.) The rest of brooding Ctenostomata
<b>Cheilostomata</b>	(?) <i>Membranipora commensale</i> (Kirkpatrick & Metzelaar, 1922) (as <i>Conopeum</i> )—broadcaster (Corrêa 1948)
<i>Membranipora membranacea</i> (Linnaeus, 1767)—broadcaster (Hincks 1880; Temkin 1994; Temkin and Bortolami 2004) <i>Membranipora serrilamella</i> Osburn, 1950—broadcaster (Mawatari 1975; Mawatari and Mawatari 1975; Hageman 1981) <i>Conopeum seurati</i> (Canu, 1928)—broadcaster (Cook 1960, 1962; Jebram 1973b, 1975) <i>Conopeum reticulatum</i> (Linnaeus, 1767)—broadcaster (Cook 1964) <i>Conopeum tenuissimum</i> (Canu, 1928)—broadcaster (Dudley 1973) <i>Electra pilosa</i> (Linnaeus, 1767)—broadcaster (Farre 1837; Hincks 1851, 1880; Smitt 1866; Prouho 1892; Calvet 1900; Marcus 1926; Borg 1926) <i>Electra repiachowi</i> (Ostroumoff, 1886)—broadcaster (Paltschikowa-Ostroumowa 1926) <i>Electra crustulenta</i> (Pallas, 1766)—broadcaster (Schulz 1901; Borg 1947; Cook 1960, 1962; Silén 1966) <i>Electra monostachys</i> (Busk, 1854)—broadcaster (Cook 1964) <i>Electra posidoniae</i> Gautier, 1854—broadcaster (Silén 1966) non-identified cheilostome (as <i>Lepralia</i> ) (Ehlers 1876) <i>Tendra zostericola</i> Nordmann, 1839— <b>brooder</b> (Paltschikowa-Ostroumowa 1926; Braiko 1967) <i>Thalamoporella evelinae</i> Marcus, 1939— <b>brooder</b> (Marcus 1941) <i>Schizoporella</i> cf. <i>pungens</i> Canu & Bassler, 1828— <b>brooder</b> (ovipositor) (Maturro 1991) <i>Schizoporella</i> cf. <i>errata</i> (Waters, 1878)— <b>brooder</b> (ovipositor) (Zimmer, pers. obs.)	
	<i>Thalamoporella prominens</i> (Levinsen, 1909)—brooder (Marcus 1938b) <i>Schizoporella floridana</i> Osburn, 1914—brooder (the coelomic pore between the two distal tentacles) (Cook 1985) The rest of brooding Cheilostomata

Brooders with an ITO and broadcasters with SNP are highlighted in bold. "Mixed" brooding is also highlighted in bold: this refers to the situation whereby when the polypide is retracted, the embryos are placed into the introvert and when the polypide is protruded, the embryos are attached onto the exposed outer surface of the introvert wall

1987; Grünbaum 1995). This zone, especially in large colonies, is characterized by a relatively low rate of water exchange. Additionally, a proportion of the exhalant water is refiltered (Lidgard 1981; Grünbaum 1995; Shunatova and Ostrovsky 2001, 2002; also discussed in Ryland 2001). As a consequence of these two processes, the oocytes are at risk of being swallowed. During observations of spawning in *Electra pilosa*, Borg (1926) recorded the sequential transfer of released eggs from lophophore to lophophore by tentacle ‘claps’ (see also Winston 1978; Shunatova and Ostrovsky 2001) towards the colony periphery. In contrast, swallowing of the oocytes by the maternal as well as neighbouring polypides has been repeatedly observed in some broadcasters (Marcus 1926; Cook 1962; Mawatari 1975; Mawatari and Mawatari 1975). Interestingly, Marcus (1926) and Mawatari (1975) wrote that swallowed eggs had not been digested and were subsequently released via the anus with faecal pellets in *E. pilosa* and *Membranipora serrilamella* without undergoing any external changes. We doubt, however, that normal embryogenesis would occur after an excursion through the digestive tract. A swallowed egg would undergo both physical and chemical influences that make its future development highly improbable.

During spawning the tentacles of the polypide sometimes take up a special position. Cook (1960: 261) described spawning through the ITO in *Electra crustulenta* (Pallas, 1766). According to her observations, the polypide was fully extended, but the tentacles were closely opposed and deflected to a position parallel to the frontal wall of the zooid. In such a position the intertentacular organ was thus protruded as far as possible above the surface of the colony. It should be noted that when adopting such a horizontal position, the tentacular ciliature creates an upstream (ascending) water current (see Shunatova and Ostrovsky 2001), thus allowing the movement of spawning eggs away from the colony surface.

In contrast, the problem of egg swallowing is absent in uniserial colonies due to their comparatively distant lophophores. We therefore suggest that the acquisition of the intertentacular organ might be connected with the evolution of large colonies with closely packed zooids in the Gymnolaemata. The terminal opening of the ITO is rather higher than its base (where the supraneural coelomopore is positioned) (Figs. 1, 2), so released eggs could be placed in a zone with a relatively higher level of water exchange. This mechanism could provide a more effective process for transport of the released eggs away from the parent colony. The fossil record suggests that both the earliest Ctenostomata and the Cheilostomata were uniserial (Banta, 1975; Pohowski 1978; Boardman et al. 1983; Taylor 1990, 1994; Todd 2000), and the multiserial colonies evolved in them independently (Silén 1944; Boardman et al. 1983; see also McKinney and Jackson 1989). It is possible therefore that

the ITO could also have evolved independently in both orders of Gymnolaemata.

The ctenostomes *Farrella repens* and *Hypophorella expansa* possibly show an ancestral situation. These broadcasters with their loose zooidal arrangement have a supraneural coelomopore rather than ITO. We suggest that the ITO might also be absent in primitive uniserial malacostegans, such as *Pyroporopsis* and *Pyripora* that possibly evolved from uniserial broadcasting ctenostomes with SNP (Banta 1975; Taylor 1994). The evolution of colonies of closely packed zooids (multiserial and others) could have been a trigger for the evolution of the ITO. From a different perspective, the broadcaster *Membranipora commensale* (Kirkpatrick et Metzelaar, 1922) forms multiserial colonies with polypides that Corrêa (1948) reported as possessing a coelomopore. This is the one of two exceptions known to date, and there is some doubt as to whether this is really the case as Corrêa did not mention whether she observed mature reproducing colonies of *M. commensale* (as *Conopeum*). Later work showed that the ITO developed at the onset of oogenesis, and thus only in mature colonies, thus it is possible that Corrêa observed non-fertile colonies. The broadcasting freshwater ctenostome *Hislopia malayensis* Annandale, 1916 with multiserial colonies is devoid of an ITO (T. Wood, pers. comm.), and this may be connected with the small number of zooids. Because of that there should be a high rate of water exchange in a colony quickly taking eggs outside and, thus, preventing them from becoming swallowed. We also speculate that some broadcasters that secondarily acquired the uniserial growth might inherit the ITO from their multiserial broadcasting ancestors.

### Secondary loss of the ITO

It is feasible that the ITO could be lost secondarily due to the (1) secondary acquisition of uniserial budding in broadcasters and/or (2) the evolution of brooding.

Secondary loss of the intertentacular organ (ITO) in multiserial brooders might occur because there was no longer the requirement for oocytes to be transported away from the parent colony. In gymnolaemates eggs are incubated either on the colony surface or inside of specialized brood chambers (Ostrovsky 2008b, c). Within Cheilostomata the ITO theoretically could have been present in early brooders (Calloporidae) with multiserial colonies and ovicells constructed of spines (Ostrovsky and Taylor 2004, 2005). With assistance from the ITO, it is possible that the mature eggs were passed directly to the brooding cavity. Such activity has been recorded in the cheilostome *Tendra zostericola*, where both the intertentacular organ and the

tentacle crown entered the cavity where embryonic incubation takes place during the process of oviposition (Paltschikowa-Ostroumowa 1926; Braiko 1967).

However, the enlargement of the oocytes during the transition to the lecithotrophic larva in brooders (see Taylor 1988; Ostrovsky et al. 2009) could make oviposition via the SNP more effective, and the ITO might be lost. On the other hand, the large oocyte size is obviously not an obstacle in some instances, since large oocytes are very elastic in gymnolaemate bryozoans. They squeeze not only through a tiny supraneural coelomopore (Gerwerzhagen 1913; Silén 1945) (Fig. 4e, f), but also through a tube-like ovipositor in *Schizoporella* (Maturó 1991; R. Zimmer, personal communication). Large oocytes and a large ITO are also described in the ovicellate brooder *Thalamoporella evelinae* (Marcus 1941). Additionally, it should be mentioned that the secondarily uniserial brooders could inherit the SNP from their multiseriate brooding ancestors.

Evidence from the literature shows that four brooding species possess the ITO either in its complete or reduced (*Bulbella abscondita*) form. Why should this be the case? In *B. abscondita*, the ITO has a role where it specifically manipulates the eggs, attaching them to the introvert (Fig. 4c) (Braem 1951). There is no specific activity of the ITO mentioned in the case of *Alcyonidium duplex* (Proucho 1892). In *Tendra zostericola*, the ITO enters large brood chamber during oviposition, and it is possible that similar activity occurs in *Thalamoporella evelinae*. It should be noted that several embryos are simultaneously incubated in the same brood chamber in these two species, which is rare among gymnolaemates (Ostrovsky et al. 2008).

Based on the above considerations and the pattern of distribution of the ITO throughout Gymnolaemata (Table 1), we suppose that the ITO has been lost independently in congeneric species of *Alcyonidium*, *Victorella*, *Thalamoporella*, and maybe *Membranipora* within both of the gymnolaemate taxa: all these genera include species both with and without the ITO (see also Reed 1991). The majority of species from the ctenostome genus *Alcyonidium* are broadcasters possessing the ITO. The rest are introvert brooders with a SNP, and only *A. duplex* has the ITO and mixed type of brooding possibly representing the transitional stage from broadcasting to internal brooding. All of them (except, to some extent, *A. albidum*) form multiseriate colonies.

It was suggested earlier that the brood chambers in *Tendra* and *Thalamoporella* evolved independently of conventional ovicells in the Cheilostomata (Harmer 1926; Ostrovsky and Taylor 2005). The presence of an ITO in *Tendra zostericola* and *Thalamoporella evelinae* supports this. We suppose that both tendrids and thalamoporellids could have inherited the ITO from their broadcasting malacostegan ancestors, but later it was lost in some

species (for instance, *Thalamoporella prominens* (Levinson, 1909), see Marcus 1938a). In contrast, in the cheilostome genus *Schizoporella*, the ovipositor could be a secondary novelty that evolved anew, since it is positioned some distance from the normal site of a supraneural pore (R. Zimmer, M. Temkin, personal communication). Information given by Reed (1991) about oviposition via the genital pore in the ooecial vesicle in a non-identified *Schizoporella* species actually describes the ovipositor (R. Zimmer, personal communication). Cook (1985: 49) recorded oviposition via the coelomic pore between the two distal tentacles in *S. floridana* Osburn, 1914, however. Thus, as with *Alcyonidium* and *Thalamoporella*, different structures for oviposition (SNP and ITO) can be present within the same genus.

On the other hand, some primitive cheilostome lineages probably never possessed an ITO. For instance, some uni-/biserial cheilostome erect brooders (Eurateidae, Leiosalpingidae, Scrupariidae, Alysidiidae) could have independently evolved from the uniserial malacostegans with a supraneural coelomopore, and Aeteidae from the uniserial ctenostome ancestor (Jebram 1992). The idea of the independent origin of these groups is also supported by the obviously independent evolution of brooding in these taxa (Osburn 1950; Taylor 1988; Ostrovsky and Taylor 2005), suggesting that ctenostomes are paraphyletic and cheilostomes are polyphyletic.

Similarly, ctenostome uniserial brooders (for example, *Paludicella*) could inherit a SNP from their uniserial broadcasting ancestor. Unfortunately, there are no data on both SNP and ITO in uniserial cheilostomes as yet.

In his 1944 and 1945 works Silén came to the conclusion that the broadcasting reproductive pattern, the intertentacular organ (ITO) and the supraneural coelomopore (SNP) have been secondarily derived in the Bryozoa. Palaeontological data and the pattern of distribution of reproductive patterns throughout Bryozoa contradict this. Broadcasting (malacostegan) cheilostomes appeared first in the palaeontological record (Pohowsky 1973; Taylor 1994). The primitive nature of the broadcasting pattern is also confirmed by the distribution of the larval planktotrophy among high-level ctenostome taxa (see Todd 2000): most of them include species with a planktotrophic larva. We agree that the ITO is a derived structure, but suggest that it has evolved as an extension of the previously existing SNP. According to our hypothetical scenario, in the Gymnolaemata the ITO might have evolved twice (in Ctenostomata and Cheilostomata) and was secondarily lost on several occasions (in all the taxa where both ITO and SNP are present). We suppose that the evolution of the ITO could be connected with the acquisition of close zooidal packing like multiseriate and dense anastomosing growth, and its loss with the adoption of a brooding reproductive

pattern in multiserial species or the return to uniserial growth in broadcasters.

### Critical assessment

This hypothesis could be disputed, however. There are both broadcasting species with the ITO and brooders with the SNP within the same ctenostome taxon *Victorella*. All of them primarily form diffuse uniserial chains of zooids. Thus, the suggestion about the loss of the ITO in a connection with evolution of brooding is supported. Interestingly, the brooding ctenostome *Victorella muelleri* with a supraneural coelomopore (SNP) shows similar behaviour to another brooding victorellid *B. abscondita* with the reduced ITO: its polypide bends ventrally when attaching the eggs to its introvert (Braem 1951) (Fig. 4d).

From the other hand, the example of victorellid ctenostomes does not support a suggestion that the origin of the ITO is a result of evolution of multiserial colonies. Also the two-chambered ciliated structure of the ITO, which is very similar in ctenostomes and cheilostomes, provides evidence for its singular origin. If this is true, the above ideas would need to be re-considered. In such a circumstance, multiserial broadcasters could have inherited the ITO from their uniserial broadcasting ancestors and then lost it in most cases when brooding evolved. We also note that the role of egg swallowing could be overestimated as most of the observations of egg spawning were not made under natural flow conditions. On the other hand, in cheilostomes the uniserial growth pattern could have evolved secondarily from the multiserial one numerous times. Thus, uniserial broadcasters with the ITO cannot be considered as an ultimate evidence against the hypothesis presented. The intertentacular organ could be inherited from their ancestors with multiserial colonies.

It is possible that evolution of the ITO could be connected with the prevention of intracoelomic embryonic development by delayed activation of the internally fertilized oocytes. Since the ITO proximal chamber has a glandular structure, and zygotes are typically retained within the ITO for variable although brief periods of time, chemical stimulation for egg activation has been suggested by Temkin (1994). If so, then brooders could secondarily lose this mechanism, substituting it for another. In theory, egg activation can be caused by a mechanical deformation of the zygote during its release or by its contact with sea water in different species (discussed also in Temkin 1996). In contrast, intracoelomic cleavage has been incidentally recorded in both broadcasting and brooding cheilostomes (Gerwerzhagen 1913; Lutaud 1961), and thus the egg activation could not be triggered neither by the external chemical nor by physical influence in these cases.

### Conclusion

Despite two and a half centuries of observations, our knowledge on the sexual reproduction of Bryozoa is still inadequate and incomplete. The evolution of new reproductive strategies involves gametogenesis, fertilization and brooding, where gamete manipulation (broadcast spawning, oviposition, and the release and uptake of sperm) is one of the most crucial aspects of the whole life cycle. Future studies in this area should focus on checking the hypothesis presented here. Specifically, it would be useful to get more data on both brooding and non-brooding gymnolaemates with uniserial colonies. Further observations on both the formation of the intertentacular organ and spawning in multiserial broadcasters, presence of the supraneural pore in non-ferile zooids, anatomical research on the differences in a structure of the ITO between Ctenostomata and Cheilostomata as well as presence of the SNP in Stenolaemata (Cyclostomata) would be of particular significance.

**Acknowledgments** Financial support for ANO was provided by the Lise Meitner Foundation, the FWF Grants P19337-B17 and P22696-B17 (Austria) and the RFBR Grants 07-04-00928a and 10-04-00085-a (Russia). Aberystwyth University provided financial support for JSP. Thanks to Dr Michael Winson (Heriot-Watt University), Professors John S. Ryland (Swansea University), Russel Zimmer (University of Southern California), Michael H. Temkin (St Lawrence University) and Dr Alexander Gruhl (Free University of Berlin) for constructive criticism on the early versions of the text and for illustrations. Dr Judith Winston (Virginia Museum of Natural History) and Dr Peter S. Cadman (Swansea University) provided some illustrations. Professor Timothy S. Wood (Wright State University) and Dr M. Carter (Heriot-Watt University) are acknowledged for unpublished data on *Hislopia malayensis* and *Victorella pavidia*. Hans De Blauwe (Belgium) provided information on the ITO in *Arachnidium fibrosum* and *Alcyonidium parasiticum*. We also thank Professor Thomas Bartolomaeus (University of Bonn) and anonymous reviewers whose suggestions substantially helped to improve the manuscript.

### References

- Ax P (2001) Multicellular animals. Order in nature—system made by man. Springer, Heidelberg, pp 1–317
- Banta WC (1967) A new species of *Victorella* from Southern California (Bryozoa, Ctenostomata). Proc US Nat Mus 122(3593):1–18
- Banta WC (1975) Origin and early evolution of cheilostome Bryozoa. In: Pouyet S (ed) Bryozoa 1974. Doc Lab Géol Fac Sci Lyon HS 3(2):565–582
- Bishop JDD, Pemberton AJ (2006) The third way: spermcast mating in sessile marine invertebrates. Int Comp Biol 46(4):398–406
- Boardman RS, Cheetham AH, Blake DB, Utgaard J, Karklins OL, Cook PL, Sandberg PA, Lutaud G, Wood TS (1983) Bryozoa (Part G, revised). In: Robinson RA (ed) Treatise on Invertebrate Paleontology. Geological Society of America, Boulder, Colorado; University of Kansas, Lawrence, 1:1–625
- Borg F (1926) Studies on recent cyclostomatous Bryozoa. Zool Bidr Uppsala 10:181–507

- Borg F (1947) Zur Kenntnis der Ökologie und des Lebenszyklus von *Electra crustulenta*. Zool Bidr Uppsala 25:344–377
- Braem F (1890) Untersuchungen über die Bryozoen des süßen Wassers. Biobl Zool Stuttg 6:1–134
- Braem F (1896) Die geschlechtliche Entwicklung von *Paludicella Ehrenbergii*. Zool Anz 19(493):54–57
- Braem F (1951) Über *Victorella* und einige ihrer nächsten Verwandten, sowie über die Bryozoenfauna des Ryck bei Greifswald. Zoologica 102(37):1–59
- Braiko VB (1967) Biology of reproduction of *Membranipora zostericola* Nordm. (Bryozoa). Zool Zhurn 46:1119–1121 (in Russian)
- Brien P (1953) Etude sur les Phylactolemates. Ann Soc R Zool Belgique 84:301–440
- Bullivant JS (1967) Release of sperm by Bryozoa. Ophelia 4:139–142
- 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 Ltd, Wellington, pp 237–242
- Calvet L (1900) Contribution a l'histoire naturelle des Bryozoaires Ectoproctes marins. Trav Inst Zool Un Montpellier, NS 8:1–488
- Castric-Fey A (1971) Sur quelques bryozoaires de l'archipel de Glénan (Sud-Finistère). Vie Millieu 22:69–86
- 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 (1964) The development of *Electra monostachys* (Busk) and *Conopeum reticulum* (Linnaeus), Polyzoa, Anasca. Cah Biol Mar 5:391–397
- Cook PL (1985) Bryozoa from Ghana. Zool Wetens Mus R Afr Centr Tervuren Belgique 238:1–315
- Cori CJ (1941) Bryozoa. Ordnung der Tentaculata. Handb Zool III 2(5):263–374, 375–502
- Corrêa DD (1948) A embriologia de *Bugula flabellata* (J. V. Thompson) Bryozoa Ectoprocta. Bol Fac Fil Ci Letr Univ S Paulo Zool 13:7–71
- De Blauwe H (2009) Mosdiertjes van de Zuidelijke Bocht van de Noordzee. Determinatiewerk voor België en Nederland, Uitgave Vlaams Instituut voor de Zee, Oostende
- Dick MH (1987) A proposed mechanism for chimney formation in encrusting bryozoan colonies. In: Ross JRP (ed) Bryozoa: present and past. Western Washington University, Bellingham, WA, pp 73–80
- Dudley JW (1973) Observations on the reproduction, early larval development, and colony astogeny of *Conopeum tenuissimum* (Canu). Chesapeake Sci 14(4):270–278
- Dunn CW, Hejnol A, Matus DQ, Pang K, Browne WE, Smith SA, Seaver E, Rouse GW, Obst M, Edgecombe GD, Sørensen MV, Haddock SHD, Schmidt-Rhaesa A, Okusu A, Kristensen RM, Wheeler WC, Martindale MQ, Giribet G (2008) Broad phylogenomic sampling improves resolution of the animal tree of life. Nature 452:745–749
- Ehlers E (1876) *Hypophorella expansa*. Ein Beitrag zur Kenntniss der minirenden Bryozoen. Abh Physik Class Königl Gesells Wiss Göttingen 21:3–157
- Emig CC (1982) Biology of Phoronida. In: Russell FS, Yonge CM (eds) Advances in marine biology. Academic Press, London 14:1–89
- Farmer JD (1977) An adaptive model for the evolution of the ectoproct life cycle. In: Woollacott RM, Zimmer RL (eds) Biology of bryozoans. Academic Press, New York, pp 487–517
- Farmer JD, Valentine JW, Cowen R (1973) Adaptive strategies leading to the ectoproct ground-plan. Syst Zool 22:233–239
- Farre MB (1837) Observations on the minute structure of some of the higher forms of polypi, with views of a more natural arrangement of the class. Phil Trans R Soc Lond 1:387–426
- Fuchs J, Obst M, Sundberg P (2009) The first comprehensive molecular phylogeny of Bryozoa (Ectoprocta) based on combined analyses of nuclear and mitochondrial genes. Mol Phyl Evol 52:225–233
- Gerwerzhagen A (1913) Untersuchungen an Bryozoen. Sitzungsber Heidelb Akad Wiss Math-nat Kl B 9:1–16
- Grünbaum D (1995) A model of feeding currents in encrusting bryozoans shows interference between zooids within a colony. J Theor Biol 174:409–425
- 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
- Harmer SF (1892) On the nature of the excretory processes in marine Polyzoa. Quart J Micr Sci 33:123–167
- Harmer SF (1926) The Polyzoa of the Siboga expedition. II. Cheilostomata Anasca. Rep Siboga Exp, EJ Brill. Leiden 28b:181–501
- Hausdorf B, Helmkamp M, Nesnidal MP, Bruchhaus I (2009) Phylogenetic relationships within the lophophorate lineages (Ectoprocta, Brachiopoda and Phoronida). Mol Phyl Evol 55:1121–1127
- Havenhand JN (1995) Evolutionary ecology of larval types. In: McEdwards L (ed) Ecology of marine invertebrate larvae. CRC Press, Boca Raton, pp 9–121
- Hayward PJ (1985) Ctenostome bryozoans. Syn Brit Fauna 33:1–169
- Helmkamp M, Bruchhaus I, Hausdorf B (2008a) Phylogenomic analyses of lophophorates (brachiopods, phoronids and bryozoans) confirm the Lophotrochozoa concept. Proc R Soc B 275:1927–1933
- Helmkamp M, Bruchhaus I, Hausdorf B (2008b) Multigene analysis of lophophorate and chaetognath phylogenetic relationships. Mol Phyl Evol 46:206–214
- 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 (1880) A history of the British marine Polyzoa. Van Voorst, London
- Hyatt A (1866–1868) Observations on Polyzoa. Suborder Phylactolaemata. Proc Essex Inst 4–5:1–103
- Hyman LH (1959) The invertebrates: smaller coelomate groups. McGraw-Hill Book Company, New York
- Jägersten G (1972) Evolution of the metazoan life cycle. Academic Press, New York
- Jebram D (1973a) 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 Press, London, pp 565–576
- Jebram D (1973b) Preliminary observations of the influences of food and other factors on the growth of Bryozoa with the description of a new apparatus for cultivation of sessile plankton feeders. Kiel Meeresf 29:50–57
- Jebram D (1975) Effects of different foods on *Conopeum seurati* (Canu) (Bryozoa Cheilostomata) and *Bowerbankia gracilis* Leidy (Bryozoa Ctenostomata). In: Pouyet S (ed) Bryozoa 1974. Doc Lab Géol Fac Sci Lyon HS 3(2):97–108
- Jebram D (1985) *Panolicella nutans*, gen. et sp. n., its description, development, and laboratory cultivation. Zool Scr 14:11–18
- Jebram D (1992) The polyphyletic origin of the Cheilostomata (Bryozoa). Z Zool Syst Evol 30:46–52
- Jebram D, Everitt B (1982) New victorellids (Bryozoa, Ctenostomata) from North America: the use of parallel cultures in bryozoan taxonomy. Biol Bull 163:172–187

- Joyeux-Laffuie J (1888) Description du *Delagia chaetopteri* (J. J.-L.), type d'un nouveau genre de Bryozoaires. Arch Zool Exp Gén 6:135–154
- Kluge GA (1975) Bryozoa of the northern seas of the USSR. Fauna USSR Publ Zool Inst Acad Sci USSR, Amerind Publishing Co, New Delhi 76:1–711
- Kuklinski P, Porter JS (2004) *Alcyonidium disciforme*: an exceptional Arctic bryozoan. J Mar Biol Assoc UK 84:267–275
- Levin LF, Bridges TS (1995) Pattern and diversity in reproduction and development. In: McEdwards L (ed) Ecology of marine invertebrate larvae. CRC Press, Boca Raton, pp 1–48
- Lidgard S (1981) Water flow, feeding and colony form in an encrusting cheilostome. In: Larwood GP, Nielsen C (eds) Recent and Fossil Bryozoa. Olsen and Olsen, Fredensborg, pp 175–182
- Lutaud G (1961) Contribution à l'étude de bourgeonnement et de la croissance des colonies chez *Membranipora membranacea* (L), Bryozoaire Chilostome. Ann Soc R Zool Belgique 91:157–300
- Lützen J, Jespersen Å, Nielsen C (2009) Ultrastructure of spermiogenesis in *Cristatella mucedo* Cuvier (Bryozoa: Phylactolaemata: Cristatellidae). Zoomorphology 128(4):275–283
- Marcus E (1922) Bryozoen von den Aru Inseln. Abh Senckenberg Natur Ges 35:421–446
- Marcus E (1926) Beobachtungen und Versuche an lebenden Meer-sbryozoen. Zool Jahrb Abt Syst Ökol Geogr Tier 52:1–102
- Marcus E (1934) Über *Lophopus crystallinus* (Pall.). Zool Jahr Abt Anat Ont Tier 58:501–606
- Marcus E (1938a) Bryozoaírios marinhos brasileiros, II. Bol Fac Philos Sci Letr Univ S Paulo IV Zool 2:1–196
- Marcus E (1938b) Bryozoen von St. Helena. Videns Med Dan Natur For København 101:183–252
- Marcus E (1941) Sobre Bryozoa do Brasil. Bol Fac Philos Sci Letr Univ S Paulo XXII Zool 5:3–208
- Marcus E (1942) Sobre Bryozoa do Brasil. II. Bol Fac Philos Sci Letr Univ S Paulo XXV Zool 6:57–106
- Matricon I (1963) Dégénérescence du polypide femelle et formation d'une poche incubatrice chez *Alcyonidium polyoum* (Hassall) (Bryozoaire Ctenostome). Arc Zool Exp Gén 102:79–93
- Maturo FJS (1991) A new bryozoan structure: an ovipositor. In: Bigey FP (ed) Bryozoaírios Actuels et Fossils: Bryozoa Living and Fossil. Bull Soc Sci Nat Oues France, Mém HS 1:572–573
- Mawatari SF (1975) The life history of *Membranipora serrilamella* Osburn (Bryozoa, Cheilostomata). Bull Libr Art Sci Cour 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 Géol Fac Sci Lyon HS 3(1):13–18
- McKinney FK, Jackson JDC (1989) Bryozoan evolution. Unwin Hyman, Boston
- Mukai H, Terakado K, Reed CG (1997) Bryozoa. In: Harrison FW (ed) Microscopic anatomy of invertebrates, 13. Wiley-Liss, New York, pp 45–206
- Nielsen C (2001) Animal evolution: interrelationships of the living phyla, 2nd edn. Oxford University Press, Oxford
- Nitsche H (1868) Beiträge zur Anatomie und Entwicklungsgeschichte der phylactolaemen Süßwasserbryozoen, insbesondere von *Alcyonella fungosa* Pall. Akadem.-Dissertation, Berlin, pp 1–57
- Osburn RC (1950) Bryozoa of the Pacific coast of America. Part 1, Cheilostomata-Anasca. Allan Hancock. Pacific Exp 14(1):1–269
- 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) Brood chambers in cheilostome Bryozoa: diversity and revised terminology. In: Hageman SJ, Key MM, Winston JE (eds) Bryozoan Studies 2007. Proceedings of the 14th international bryozoology association conference, Boone, North Carolina. Virg Mus Nat Hist Spec Publ, vol 15, pp 195–204
- Ostrovsky AN (2008c) 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 (2009) Evolution of the sexual reproduction in the bryozoan order Cheilostomata (Gymnolaemata). St Petersburg State University [in Russian with English Summary]
- Ostrovsky AN, Taylor PD (2004) Systematics of Upper Cretaceous calloporid bryozoans with primitive spinose ovicells. Palaeontology 47(3):775–793
- Ostrovsky AN, Taylor PD (2005) Brood chambers constructed from spines in fossil and Recent cheilostome bryozoans. Zool J Linn Soc 144:317–361
- 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 Progr Ser 378:113–124
- Owrid GMA, Ryland JS (1991) Sexual reproduction in *Alcyonidium hirsutum* (Bryozoa: Ctenostomata). In: Bigey FP (ed) Bryozoaírios Actuels et Fossils: Bryozoa Living and Fossil. Bull Soc Sci Nat Oues France, Mém HS, vol 1, pp 317–326
- Paltschikowa-Ostroumowa MW (1926) Kurze Bemerkung über den Ovidukt bei den Bryozoen. Zool Anz 65:100–102
- Passamanek Y, Halanych KM (2006) Lophotrochozoan phylogeny assessed with LSU and SSU data: evidence of lophophorate polyphyly. Mol Phyl Evol 40:20–28
- Pohowski RA (1978) The boring ctenostomate Bryozoa: taxonomy and paleobiology based on cavities in calcareous substrata. Bull Amer Paleont 73(301):1–192
- Pohowsky RA (1973) A Jurassic cheilostome from England. In: Larwood GP (ed) Living and fossil Bryozoa. Academic Press, London, pp 447–461
- 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
- Prenant M, Bobin G (1956) Bryozoaires. 1. Entoproctes, Phylactolèmes, Ctenostomes. Faune France 60:1–398
- Prenant M, Bobin G (1966) Bryozoaires. 2. Chilostomes Anasca. Faune France 68:1–647
- Prouho H (1889) Sur la reproduction de quelques Bryozoaires ctenostomes. Comp Rend Hebd Séan Acad Sci Paris 109:197–198
- Prouho H (1892) Contribution à l'histoire des Bryozoaires. Arch Zool Exp Gén 10:557–656
- 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, VI. Echinoderms and Lophophorates. Boxwood Press, Pacific Grove, pp 85–245
- Ruppert EE, Fox RS, Barnes RD (2004) Invertebrate zoology: a functional evolutionary approach, 7th edn. Thomson Brooks, Cole
- Ryland JS (1970) Bryozoans. Hutchinson University Library, London
- Ryland JS (1976) Physiology and ecology of marine bryozoans. In: Russell FS, Yonge CM (eds) Advances in marine biology, 14. Academic Press, London, pp 285–443
- 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, Hayward PJ (1977) British anascan bryozoans. *Syn Brit Fauna* 10:1–188
- 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
- Santagata S, Banta WC (1996) Origin of brooding and ovicells in cheilostome bryozoans: interpretive morphology of *Scrupocellaria ferox*. *Invert Biol* 115(2):170–180
- Schulz K (1901) Untersuchungen über den Bau der Bryozoen mit besonderer Berücksichtigung der Exkretionsorgane. *Arch Natur* 67(1):115–144
- Shunatova NN, Ostrovsky AN (2001) Individual autozooidal behaviour and feeding in marine bryozoans. *Sarsia* 86:113–142
- Shunatova NN, Ostrovsky AN (2002) Group behaviour and chimneys in marine bryozoans. *Mar Biol* 140(3):503–518
- Silén L (1944) The anatomy of *Labriostomella gisleni* Silén (Bryozoa Protocheilostomata). *Kungl Sven Vetenskap Handl, Ser 3(21)*:1–111
- Silén L (1945) The main features of the development of the ovum, embryo and oecium in the oociferous Bryozoa Gymnolaemata. *Ark Zool* 35A(17):1–34
- Silén L (1966) On the fertilization problem in the gymnolaematus Bryozoa. *Ophelia* 3:113–140
- Silén L (1972) Fertilization in the Bryozoa. *Ophelia* 10(1):27–34
- 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 (1866) Kritisk Förteskning öfver Scandinaviens Hafsbryozoernas. *Aft Öfvers Kongl Vetensk-Akad Förh* 23:395–533
- Strathmann RR (1978) The evolution and loss of feeding larval stages of marine invertebrates. *Evolution* 32(4):894–906
- Ström R (1969) Sexual reproduction in a stoloniferous bryozoan, *Triticella koreni* (G. O. Sars). *Zool Bidr Uppsala* 38:113–128
- 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 (1988) Major radiation of cheilostome bryozoans: triggered by the evolution of a new larval type. *Hist Biol* 1:45–64
- Taylor PD (1990) Bioimmured ctenostomes from the Jurassic and the origin of the cheilostome Bryozoa. *Palaeontology* 33:19–34
- Taylor PD (1994) An early cheilostome bryozoan from the Upper Jurassic of Yemen. *N Jb Geol Palaeont Abh* 191:331–344
- Temkin MH (1994) Gamete spawning and fertilization in the gymnolaemate bryozoan *Membranipora membranacea*. *Biol Bull* 187:143–155
- Temkin MH (1996) Comparative fertilization biology of gymnolaemate bryozoans. *Mar Biol* 127(2):329–339
- 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
- Todd JA (2000) The central role of ctenostomes in bryozoan phylogeny. In: Herrera Cubilla A, Jackson JBC (eds) Proceedings of the 11th international bryozoology association conference. Smithsonian Tropical Research Institute, Republic of Panama, pp 104–135
- Tsyganov A, Hayward PJ, Porter JS, Skibinski DOF (2009) Bayesian phylogenetics of bryozoa. *Mol Phyl Evol* 52:904–910
- van Beneden PJ (1844) Recherches sur l'organisation des *Laguncula* et l'histoire naturelle des différens polypes Bryozoaires qui habitent la côte d'Ostende. *Nouv Mém Acad Roy Bruxelles* 18:1–29
- Waters A (1904) Bryozoa. Résultats du Voyage du S.Y. "Belgica" en 1897–1898–1899. *Exp Antarct Belge Zool Anvers*, pp 1–114
- Wiebach F (1953) Über den Ausstoss von Flottoblasten bei Plumatellen. *Zool Anz* 151(9–10):266–272
- Winston JE (1978) Polypide morphology and feeding behaviour in marine ectoprocts. *Bull Mar Sci* 28(1):1–31
- Winston JE (1979) Current-related morphology and behaviour in some Pacific coast bryozoans. In: Larwood GP, Abbott MB (eds) Advances in bryozoology. Systematics association special vol 13. Academic Press, London, pp 247–268
- Woollacott RM (1999) Bryozoa (Ectoprocta). In: Knobil E, Neill JD (eds) Encyclopedia of reproduction, vol 1. Academic Press, London, pp 439–448
- Zimmer RL (1991) Phoronida. In: Giese AC, Pearse JS, Pearse VB (eds) Reproduction of marine invertebrates, VI. Echinoderms and Lophophorates. Boxwood Press, Pacific Grove, pp 85–245
- Zimmer RL, Woollacott RM (1977) Structure and classification of gymnolaemate larvae. In: Woollacott RM, Zimmer RL (eds) Biology of Bryozoans. Academic Press, New York, pp 57–89