Independent evolution of matrotrophy in the major classes of Bryozoa: transitions among reproductive patterns and their ecological background

Andrew N. Ostrovsky[1,4,*], Dennis P. Gordon[2], Scott Lidgard[3]

[1]Department of Invertebrate Zoology, Faculty of Biology & Soil Science, St. Petersburg State University, Universitetskaja nab. 7/9, 199034, St. Petersburg, Russia

[2]National Institute of Water & Atmospheric Research, Private Bag 14901, Kilbirnie, Wellington, New Zealand

[3]Department of Geology, Field Museum of Natural History, 1400 S. Lake Shore Dr., Chicago, Illinois 60605, USA

[4]*Present address:* Department of Palaeontology, Faculty of Earth Sciences, Geography and Astronomy, Geozentrum, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria

ABSTRACT: Bryozoa are unique among invertebrates in possessing placenta-like analogues and exhibiting extraembryonic nutrition in all high-level (class) taxa. Extant representatives of the classes Stenolaemata and Phylactolaemata are evidently all placental. Within the Gymnolaemata, placenta-like systems have been known since the 1910s in a few species, but are herein reported to be widespread within this class. Placental forms include both viviparous species, in which embryonic development occurs within the maternal body cavity, and brooding species, in which development proceeds outside the body cavity. We have also identified an unknown reproductive pattern involving macrolecithal oogenesis and placental nutrition from a new, taxonomically extensive anatomical study of 120 species in 92 genera and 48 families of the gymnolaemate order Cheilostomata. Results support the hypothesis of evolution of oogenesis and placentation among Cheilostomata from oligolecithal to macrolecithal oogenesis, followed by brooding, through incipient matrotrophy combining macrolecithal oogenesis and placentation, to oligolecithal oogenesis with subsequent placental brooding. The distribution of reproductive patterns within the phylum suggests that variations of placentation evolved in all 3 bryozoan classes, and possibly several times within both gymnolaemate orders. We infer that extraembryonic nutrition may be advantageous to species through enhanced developmental plasticity, and, in fast-growing ephemeral colonies, simultaneous volumetric growth and embryonic development may facilitate earlier larval release and occupation of vacant space.

KEY WORDS: Matrotrophy · Placenta · Reproductive patterns · Evolution · Bryozoa

INTRODUCTION

Matrotrophy, or extraembryonic nutrition (EEN), is considered the most complex nutritional relationship between a parent and an embryo, enhancing offspring fitness under certain circumstances (Wourms & Lombardi 1992, Mousseau & Fox 1998, Trexler & DeAngelis 2003, Marshall & Uller 2007). It occurs in both viviparous and some brooding animals by a variety of methods (oophagy, adelphophagy, histophagy, placental nutrition). The most complex variant is pla-

centation, involving intimate contact or even fusion of the fetal and parental tissues and 'nutrient transfer via cell secretions or blood constituents' to the embryo or its enclosing space (Crespi & Semeniuk 2004, p. 638). The distribution of matrotrophy in the Eumetazoa is strikingly scattered. Basically, a few species in some genera or families within a class or phylum exhibit matrotrophy, whereas the others lack it. For instance, nutrient transfer from the maternal organism to the embryo is known in 1 scyphozoan jellyfish, a few cestode flatworms, a polychaete, several species of gas-

tropods and of bivalve molluscs, 2 kamptozoans, and 3 echinoderms. Matrotrophy is more common within the Arthropoda, in which EEN is characteristic of 2 families of scorpions, several isopod crustaceans, some genera in a few orders of insects, and 2 genera of mites. It is also found in 2 families of Onychophora, 2 species of Ascidiacea, numerous families of elasmobranch and bony fishes, and in some amphibians and reptiles. Most species in these groups are either oviparous or viviparous, but not matrotrophic (Giese & Pearse 1974, 1975a,b, 1977, Giese et al. 1979, 1987, 1991, Wourms et al. 1988, Adiyodi & Adiyodi 1989, 1990, Blackburn 1992, Charmantier & Charmantier-Daures 1994, Schwartz & Dimock 2001, Crespi & Semeniuk 2004, Korneva 2005, von Rintelen & Glaubrecht 2005, Glaubrecht et al. 2006, Koya & Munoz 2007, Reznick et al. 2007). Exceptions to patchy distribution of EEN are the Pseudoscorpionida, Salpida (Tunicata), and placental mammals, in which it occurs in all species (Weygoldt 1969, Bone 1998, Lombardi 1998, Mess & Carter 2007).

The phylum Bryozoa, all species of which are colonial suspension feeders, is an exception too, as we report below. All extant species of the class Stenolaemata (order Cyclostomata) are viviparous, possessing specialized nutritive tissue and embryos that are incubated intracoelomically in characteristic brooding zooids (gonozooids) (Harmer 1893, 1896, 1898, Borg 1926). Insofar as these gonozooids are known in fossil cyclostomes (Taylor & Michalik 1991, Lidgard et al. 1993), matrotrophy is inferred to have existed in this order at least since the Late Triassic. Similarly, all species of the class Phylactolaemata studied so far have EEN by either spot- or ring-like placental analogues, developing inside a brooding sac the cavity of which is external relative to the maternal body cavity (Braem 1890, Brien 1953). In Gymnolaemata, the largest bryozoan class with >1000 genera, matrotrophy was, until recently, known only in relatively few taxa — in the viviparous family Epistomiidae (genera *Epistomia*, *Synnotum*) and in the families Bugulidae (*Bicellariella*, *Bugula*), Candidae (*Scrupocellaria*), and Hippothoidae (*Celleporella*). These taxa are among the majority of gymnolaemates that brood their embryos in extrazooidal incubation chambers (ovicells) (Marcus 1938, 1941, Woollacott & Zimmer 1972, 1975, Dyrynda 1981, Dyrynda & King 1982, 1983, Dyrynda & Ryland 1982, Hughes 1987, Santagata & Banta 1996, Ostrovsky 1998).

We report here the results of an extensive light-microscopic anatomical study, revealing that EEN is far more common in gymnolaemates than previously realized. The results point out seemingly independent appearances of matrotrophy. To the extent that broad similarities — and independent acquisition — evidenced in these cases hold true, they imply that transitions in reproductive patterns have occurred repeatedly among gymnolaemate lineages. We also offer some provisional ecological considerations based on our survey, increasing awareness of the importance of maternal provisioning among marine animals, and recent ecological studies of cheilostome bryozoans.

MATERIALS AND METHODS

Specimens were collected by various methods and fixed either in 2.5% glutaraldehyde (buffered in 0.1 M Na-cacodylate with 10.26% sucrose, pH 7.3) or Bouin's fluid without acetic acid. While still in fixative they were decalcified for 6 to 12 h using a few drops of a 2 N solution of hydrochloric acid; gradually dehydrated in an ethanol series (40–50–60–70–80–90–96%), embedded in plastic (epoxy resin type TAAB 812), sectioned (1.0 µm thick) with a glass knife, and stained with Richardson's stain (1% water solution of methylene blue, Na-tetraborate and azur II, mixed in proportions 1:1:2) using standard methods (Richardson et al. 1960). Sections were observed and digital images were made with Nikon 104 and Nikon 118 FXA dissecting light microscopes.

Altogether, sections of 120 species belonging to 92 genera and 48 families of the gymnolaemate order Cheilostomata were prepared and studied (Table 1). Our criteria for recognizing extraembryonic nutrition include comparing the size of the zygotes/early embryos and late embryos/larvae, and/or comparing the epithelial lining of empty and incubating brood chambers, since EEN is mediated via the hypertrophied epithelial cells (embryophore) that develop inside these chambers (Fig. 1). Simultaneously anatomical study of oogenesis was undertaken aiming to recognize the type and numbers of oocytes.

RESULTS

Anatomical data

In addition to the above-mentioned taxa, we found EEN in the families Flustridae (genera *Gregarinidra*, *Isosecuriflustra*, *Klugeflustra*), Beaniidae (*Beania*), Cellariidae (*Cellaria*), Microporidae (*Micropora*), Cribrilinidae (*Figularia*), Catenicellidae (*Costaticella*, *Cribricellina*, *Pterocella*), Watersiporidae (*Watersipora*), Lanceoporidae (*Calyptotheca*), Myriaporidae (*Myriapora*), and Urceoliporidae (*Reciprocus*, *Urceolipora*).

Placental analogues are represented structurally by hypertrophied epithelial cells (embryophore) of the maternal body wall transporting nutrients to the brooding cavity by exocytosis in Cheilostomata. In its
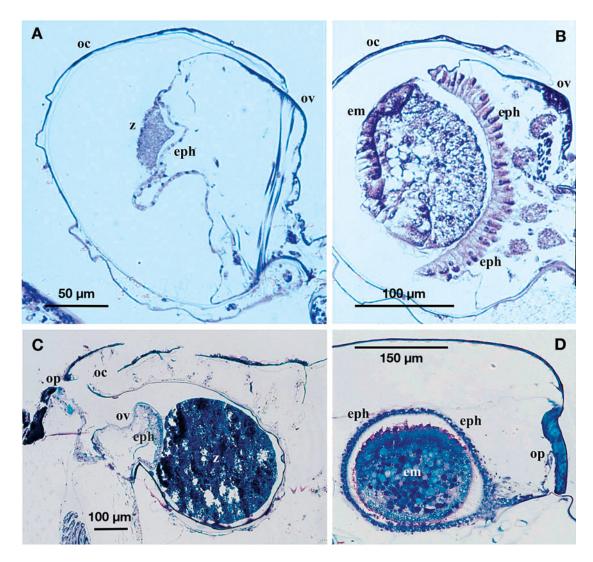
Fig. 1. Longitudinal sections through brood chambers with placental analogues in 3 cheilostome bryozoans (light microscopy). (A,B) *Bugula flabellata* (Bugulidae) (Pattern III): (A) ovicell with an oligolecithal zygote and non-developed embryophore and (B) partly grown embryo and fully developed embryophore. (C) Ovicell of *Myriapora truncata* (Myriozoidae) with an embryophore and macrolecithal zygote (Pattern IV). (D) Internal brood sac of *Reciprocus regalis* (Urceoliporidae) with partly grown embryo (Pattern III). em: embryo; eph: embryophore; oc: protective fold of the ovicell; op: zooidal operculum; ov: ooecial vesicle; z: zygote

turn, the embryo consumes them from a surrounding liquid by endocytosis (Woollacott & Zimmer 1975, Hughes 1987). The embryo is either freely suspended within a brooding cavity, or in contact with an embryophore. Normally (but not always), a zygote/young embryo is suspended and does not touch the wall of the brood chamber. During its growth it gradually occupies most or all of the brooding cavity and nestles close to the embryophore.

Placental analogues occur within both ovicells (Fig. 1A–C) and internal brooding sacs (Fig. 1D). Maximal recorded increase in embryo volume during development was 257.7-fold (*Reciprocus regalis*); minimal increases were 1.27- and 1.49-fold (*Isosecuriflustra*

angusta and *Figularia figularis*, respectively). Increases reported in the literature range from 2.1- (*Scrupocellaria ferox*) to 500-fold (*Bugula neritina*) and even 1000-fold (*Epistomia bursaria*) (Santagata & Banta 1996, Woollacott & Zimmer 1972, Dyrynda & King 1982).

Based on the type of oogenesis and presence or absence of extraembryonic nutrition, 4 reproductive patterns were recognized (Table 1). The least common is the oviparous pattern (Pattern I) accompanied by a production of many small oligolecithal oocytes (little or no yolk), whereas the most common pattern involves consecutive embryonic incubation of a few large macrolecithal oocytes (relatively large yolk) without

Table 1. Distribution of reproductive patterns (Patterns I to IV) among the cheilostome taxa studied. Pattern I: oligolecithal oogenesis, no brooding, planktotrophy; Pattern II: macrolecithal oogenesis, brooding, lecithotrophy; Pattern III: oligolecithal oogenesis, brooding, placentation, lecithotrophy; Pattern IV: macrolecithal oogenesis, brooding, placentation, lecithotrophy. Generic name of *Biflustra perfragilis* is preliminary

No.	Taxa	I	II	III	IV
	Electridae Stach, 1937				
1	*Electra pilosa* (Linnaeus, 1767)	+			
	Calloporidae Norman, 1903				
2	*Callopora lineata* (Linnaeus, 1767)		+		
3	*Callopora dumerilii* (Audouin, 1826)		+		
4	*Cauloramphus spiniferum* (Johnston, 1832)		+		
5	*Cauloramphus cryptoarmatus* Grischenko, Dick & Mawatari, 2007		+		
6	*Crassimarginatella* sp.		+		
7	*Tegella unicornis* (Fleming, 1828)		+		
8	*Tegella armifera* (Hincks, 1880)		+		
9	*Bryocalyx cinnameus* Cook & Bock, 2000		+		
10	*Gontarella* sp.		+		
	Hiantoporidae Gregory, 1893				
11	*Hiantopora ferox* (MacGillivray, 1869)		+		
	Farciminariidae Busk, 1852				
12	*Columnella magna* (Busk, 1884)		+		
	Cupuladriidae Lagaaij, 1952				
13	*Cupuladria exfragminis* Herrera-Cubilla, Dick, Sanner & Jackson, 2006			+	
14	*Discoporella cookae* Herrera-Cubilla, Dick, Sanner et Jackson, 2008				+
15	*Discoporella marcusorum* Herrera-Cubilla, Dick, Sanner et Jackson, 2008				+
	Flustridae Fleming, 1828				
16	*'Biflustra' perfragilis* MacGillivray, 1881		+		
17	*Gregarinidra inarmata* (Hincks, 1881)			+	
18	*Gregarinidra serrata* MacGillivray, 1869		+		
19	*Isosecuriflustra tenuis* (Kluge, 1914)		+		
20	*Isosecuriflustra angusta* (Kluge, 1914)		+		
21	*Klugeflustra antarctica* (Hastings, 1943)			+	
22	*Nematoflustra flagellata* (Waters, 1904)		+		
23	*Spiralaria florea* Busk, 1861		+		
	Bugulidae Gray, 1848				
24	*Bugula neritina* (Linnaeus, 1758)			+	
25	*Bugula flabellata* (Thompson *in* Gray, 1848)			+	
26	*Camptoplites retiformis* (Kluge, 1914)		+		
27	*Cornucopina pectogemma* (Goldstein, 1882)		+		
28	*Dimetopia cornuta* Busk, 1852		+		
29	*Nordgaardia cornucopioides* d'Hondt, 1983		+		
	Beaniidae Canu & Bassler, 1927				
30	*Beania bilaminata* (Hincks, 1881)			+	
	Candidae Busk, 1852				
31	*Amastigia* cf. *funiculata* (MacGillivray, 1886)		+		
32	*Bugulopsis monotrypa* (Busk, 1852)		+		
33	*Canda simplex* Busk, 1884		+		
34	*Menipea roborata* (Hincks, 1881)		+		
35	*Scrupocellaria scruposa* (Linnaeus, 1758)				+
	Microporidae Gray, 1848				
36	*Micropora notialis* Hayward et Ryland, 1993				+
37	*Mollia multijuncta* (Waters, 1879)		+		
	Steginoporellidae Hincks, 1884				
38	*Steginoporella* cf. *magnilabris* (Busk, 1854)		+		
39	*Steginoporella perplexa* Livingstone, 1929		+		
	Cellariidae Fleming, 1828				
40	*Cellaria tenuirostris* (Busk, 1852)		+		
41	*Cellaria fistulosa* (Linnaeus, 1758)			+	
42	*Steginocellaria magnimandibulata* (Gordon, 1986)				+
43	*Euginoma conica* Gordon, 1986		+		
	Cribrilinidae Hincks, 1879				
44	*Cribrilina punctata* (Hassal, 1841)		+		
45	*Cribrilina annulata* (Fabricius, 1780)		+		
46	*Corbulipora inopinata* Bock & Cook, 1998		+		
47	*Figularia figularis* (Johnston, 1847)				+
	Euthyroididae Levinsen, 1909				
48	*Euthyroides episcopalis* (Busk, 1852)		+		
	Bifaxariidae Busk, 1884				
49	*Diplonotos* sp.		+		
	Catenicellidae Busk, 1852				
50	*Cribricellina cribraria* (Busk, 1852)		+		
51	*Costaticella solida* (Levinsen, 1909)			+	
52	*Costaticella bicuspis* (Gray, 1843)			+	
53	*Pterocella scutella* (Hutton, 1891)			+	
	Eurystomellidae Levinsen, 1909				
54	*Eurystomella foraminigera* (Hincks, 1883)		+		
55	*Selenariopsis gabrieli* Maplestone, 1913		+		
	Hippothoidae Busk, 1859				
56	*Antarctothoa bougainvillei* (d'Orbigny, 1847)		+		
57	*Antarctothoa* sp.		+		
58	*Celleporella hyalina* (Linnaeus, 1767)				+
	Arachnopusiidae Jullien, 1888				
59	*Arachnopusia unicornis* (Hutton, 1873)		+		
	Lepraliellidae Vigneaux, 1949				
60	*Lepraliella contigua* (Smitt, 1868)		+		
61	*Sinuporaria* sp.		+		
	Bryocryptellidae Vigneaux, 1949				
62	*Porella minuta* Norman, 1869		+		
63	*Porella smitti* Kluge, 1907		+		

Table 1 (continued)

No.	Taxa	I	II	III	IV
64	Rhamphostomella ovata (Smitt, 1868)		+		
65	Rhamphostomella radiatula (Hincks, 1877)		+		
66	Rhamphostomella bilaminata (Hincks, 1877)		+		
67	Rhamphostomella costata Lorenz, 1886		+		
	Romancheinidae Jullien, 1888				
68	Arctonula arctica (M. Sars, 1851)		+		
69	Escharella immersa (Fleming, 1828)		+		
70	Lageneschara lyrulata (Calvet, 1909)		+		
	Umbonulidae Canu, 1904				
71	Desmacystis sandalia (Robertson, 1900)		+		
	Sclerodomidae Levinsen, 1909				
72	Cellarinella sp.		+		
	Smittinidae Levinsen, 1909				
73	Smittina majuscula (Smitt, 1868)		+		
74	Smittina concinna (Busk, 1854)		+		
75	Smittina antarctica (Waters, 1904)		+		
76	Smittoidea reticulata (J. MacGillivray, 1842)		+		
77	Parasmittina crosslandi (Hastings, 1930)		+		
78	Bostrychopora dentata (Waters, 1904)		+		
	Bitectiporidae MacGillivray, 1895				
79	Schizomavella lineata (Nordgaard, 1896)		+		
80	Schizomavella cuspidata (Hincks, 1880)		+		
81	Schizomavella mamillata (Hincks, 1880)		+		
82	Hippoporina reticulatopunctata (Hincks, 1877)		+		
83	Hippoporina ussowi (Kluge, 1908)		+		
84	Hippoporina propinqua (Smitt, 1868)		+		
	Watersiporidae Vigneaux, 1949				
85	Watersipora subtorquata (d'Orbigny, 1852)				+
	Schizoporellidae Jullien, 1883				
86	Schizoporella unicornis (Johnston, 1847)		+		
87	Schizoporella sp.		+		
	Phorioppniidae Gordon & d'Hondt, 1997				
88	Quadriscutella papillata Bock & Cook, 1993		+		
	Margarettidae Harmer, 1957				
89	Margaretta barbata (Lamarck, 1816)		+		
	Myriaporidae Gray, 1841				
90	Myriapora truncata (Pallas, 1766)				+
	Pacificincolidae Liu & Liu, 1999				
91	Pacificincola insculpta (Hincks, 1882)		+		
	Gigantoporidae Bassler, 1935				
92	Cylindroporella tubulosa (Norman, 1868)		+		
	Lanceoporidae Harmer, 1957				
93	Calyptotheca variolosa (MacGillivray, 1869)				+

No.	Taxa	I	II	III	IV
94	Emballotheca quadrata (MacGillivray, 1869)	+			
95	Parmularia smeatoni (MacGillivray, 1890)	+			
	Cryptosulidae Vigneaux, 1949				
96	Cryptosula pallasiana (Moll, 1803)	+			
	Microporellidae Hincks, 1879				
97	Microporella ciliata (Pallas, 1766)	+			
98	Fenestrulina sp.	+			
	Calwelliidae MacGillivray, 1887				
99	Calwellia bicornis Wyville Thomson, 1858	+			
100	Calwellia gracilis Maplestone, 1882	+			
	Petraliidae Levinsen, 1909				
101	Petralia undata (MacGillivray, 1869)	+			
	Petraliellidae Harmer, 1957				
102	Mucropetraliella ellerii (MacGillivray, 1869)	+			
	Buffonellodidae Gordon & d'Hondt, 1997				
103	Kymella polaris (Waters, 1904)	+			
	Eminooeciidae Hayward & Thorpe, 1988				
104	Eminooecia carsonae (Rogick, 1957)	+			
105	Isoschizoporella tricuspis (Calvet, 1909)	+			
106	Isoschizoporella secunda Hayward & Taylor, 1984	+			
	Urceoliporidae Bassler, 1936				
107	Urceolipora nana MacGillivray, 1881			+	
108	Reciprocus regalis Gordon, 1988			+	
	Mamilloporidae Canu & Bassler, 1927				
109	Mamillopora sp.	+			
	Crepidacanthidae Levinsen, 1909				
110	Crepidacantha kirkpatricki Brown, 1954	+			
	Cleidochasmatidae Cheetham & Sandberg, 1964				
111	Characodoma porcellanum (Busk, 1860)	+			
	Celleporidae Johnston, 1838				
112	Galeopsis porcellanicus (Hutton, 1873)	+			
113	Turbicellepora crenulata Hayward, 1978	+			
114	Turbicellepora avicularis (Hincks, 1860)	+			
115	Celleporina caminata (Waters, 1879)	+			
116	Celleporina sp.	+			
	Hippoporidridae Vigneaux, 1949				
117	Hippoporella hippopus (Smitt, 1867)	+			
118	Trematooecia aviculifera (Canu & Bassler, 1923)	+			
	Phidoloporidae Gabb & Horn, 1862				
119	Reteporella sp.	+			
	Lekythoporidae Levinsen, 1909				
120	Poecilopora anomala MacGillivray, 1886	+			

EEN in the brood chamber (Pattern II). Two other reproductive patterns involve both brooding and matrotrophy, with production of either a few small oligolecithal (Pattern III) or a few large macrolecithal oocytes (Pattern IV). Patterns I to III have previously been described (and enumerated) in the literature (Harmer 1926, Woollacott & Zimmer 1975, Reed 1991), whereas Pattern IV is recorded here for the first time.

Different patterns involving brooding and EEN were sometimes met within one and the same family and even the same genus. Patterns II and IV occur in *Isosecuriflustra*, *Celleporella* Candidae, Microporidae, Cribrilinidae, and Hippothoidae; Patterns II and III in *Gregarinidra* and Bugulidae; Patterns III and IV in *Cellaria* and Catenicellidae (also, possibly, Pattern II in the latter family, see Marcus 1938); and Patterns II, III, and IV in Flustridae and Cellariidae.

Data from the literature

Reanalysis of bryozoan taxonomic literature also shows that matrotrophy has been described several times in cheilostomes by earlier scholars, but these findings were either not understood or were overlooked. Based on published descriptions and illustrations, EEN also exists in *Retiflustra* (Flustridae), *Poricellaria* (Poricellariidae), *Catenicella* (Catenicellidae), *Adeona* and *Adeonellopsis* (Adeonidae), *Adeonella, Laminopora* (Adeonellidae), and *Hippopodina* (Hippopodinidae) (Harmer 1902, 1926, Waters 1912, 1913, Marcus 1938; summarized in Ostrovsky 2008, Ostrovsky et al. 2008). Thus, 18 families and 29 cheilostome genera are now known to exhibit EEN. There is also evidence that it exists in *Crassimarginatella falcata* (Calloporidae) (Cook 1985). So far, all examined species of *Bugula*, *Cellaria*, Catenicellidae, Adeonidae, Adeonellidae, and Urceoliporidae have placental analogues.

A substantial increase in embryo size has been reported in 8 brooding species of the gymnolaemate order Ctenostomata — in the families Flustrellidridae (*Flustrellidra*), Sundanellidae (*Sundanella*), Nolellidae (*Nolella*), Walkeriidae (*Walkeria*), Mimosellidae (*Mimosella*), and Vesiculariidae (*Zoobotryon*) (Joliet 1877, Prouho 1892, Pace 1906, Waters 1914, Braem 1939, Silén 1942, 1944, Banta 1968). This suggests they possess EEN. The structure of the 'ectodermic cushion' described in the embryo sac of the 'protoctenostome' *Labiostomella gisleni* (see Silén 1944) also suggests that it could be a placental analogue. The above-mentioned family-level taxa (those examined in our and previous studies and those inferred from the literature) are representative of almost half of the gymnolaemate superfamilies with extant species. Such a wide distribution within the phylum thus makes Bryozoa unique among invertebrates. At our present state of understanding, matrotrophy in Bryozoa can be regarded as ubiquitous in 2 living classes (Stenolaemata and Phylactolaemata) and broadly distributed in the Gymnolaemata.

DISCUSSION

Origin of bryozoan placental analogues

The question arises as to the origin of bryozoan placental analogues. The phylum Bryozoa lacks a well-resolved, robust phylogenetic framework. Relationships among both traditional higher level taxa, and lower level instances of various reproductive patterns, are inevitably subject to validation as this framework is developed, which is beyond the scope of the present paper. Our discussion thus relies on: current understanding of inter-group relationships; concordance or discordance among higher taxonomic groups, many of which are putatively monophyletic; diverse skeletal morphological characters (many 'non-reproductive' in nature) that presently differentiate these groups; temporal sequences in the fossil record; and comparative patterns of sexual reproduction.

Bryozoans are simultaneous hermaphrodites with spermcast mating (Bishop & Pemberton 2006). Aquatic spermatozoa are released and subsequently captured to inseminate retained eggs within or near an ovary. In oviparous species, many small oligolecithal oocytes are produced simultaneously and spawned freely into the seawater, each developing into a long-lived planktotrophic larva (cyphonautes). This oviparous pattern of reproduction (Pattern I) is restricted to relatively few gymnolaemates, both ctenostomes and cheilostomes. A second pattern (II) is the most common, in which a few large macrolecithal oocytes are produced sequentially and develop within the vestibulum or lophophoral tentacle sheath or in specialized brood chambers. Most gymnolaemates appear to follow this pattern. In the third pattern (III), a few small oligolecithal oocytes are produced sequentially and receive extraembryonic nutrition during embryogenesis in specialized brood chambers. This pattern is characteristic of some gymnolaemates (Fig. 1A,B,D). Patterns II and III both result in short-lived lecithotrophic (coronate) larvae. Cheilostomata exhibit all 3 patterns (Harmer 1926, Woollacott & Zimmer 1975, Reed 1991), facilitating comparisons that can inform us about the relative likelihoods of different evolutionary scenarios.

Oviparity, characteristic of the earliest and less-derived malacostegan cheilostomes, is conventionally considered to be the ancestral pattern (e.g. Todd 2000). Basic differences between this and Pattern II are the types of oogenesis and broadcasting versus brooding.

The origin of Pattern II is obviously based on a shift in oogenesis towards the production of a few large macrolecithal oocytes instead of many small oligolecithal ones. This shift would eventually result in the evolution of the non-feeding coronate larva that is characteristic of most cheilostomes, considered to be a trigger for cheilostome diversification (Taylor 1988). Also, this development is inferred to have been correlated with the origin of extrazooidal incubation of embryos in brood chambers, since all known bryozoan species with non-feeding larvae are brooders. We suggest that the evolution of extrazooidal brooding may be correlated with greater embryonic survival, offsetting a decrease in fecundity following the described shift in oogenesis (cf. Strathmann 1985, 2007).

Although cheilostome bryozoans with reproductive Patterns I and III share a common character — oligolecithal oocytes — it is unlikely that the third pattern would originate from the first. All cheilostome families and genera with extant representatives having placental analogues are well-nested within higher level groups whose other constituent taxa have reproductive Pattern II, which is the most common. Families and genera with living placental species also appear later in the fossil record than their non-placental brooding relatives. The earliest ovicell-like brood chambers in the cheilostome fossil record evolved from external spines, and are thought to have given rise to other lineages with more complete ovicell morphotypes, yet the earliest forms lack any overt indication of placental nutrition (Ostrovsky & Taylor 2005). Thus, we hypothesize that reproductive Pattern III appeared last in cheilostome evolution; the placenta evolved first, followed by a shift in oogenesis from macrolecithal to oligolecithal. In testing this hypothesis through our survey, we expected to find a pattern combining the characteristics of Patterns II and III, i.e. species with a few macrolecithal oocytes consecutively developing in the ovary and later receiving EEN at the brooding site via a placental analogue during embryogenesis.

Detailed anatomical study of oogenesis supports our hypothesis. We found a new pattern (Pattern IV) in 11 genera of 10 cheilostome families, combining macrolecithal oogenesis and placentation, which can be considered incipient matrotrophy (Fig. 1C, Table 1). In general, species having Pattern IV have a less-developed embryophore and an embryonic increase in volume smaller than in species with Pattern III, which are mainly dependent on EEN. We can thus infer that, whereas brooders ancestrally had large yolky oocytes, no placenta and EEN (Pattern II), they later acquired a placenta and EEN without any change in the type of female gametic production (Pattern IV). The next step was likely a precocious oviposition of submature oocytes, because part of the nutrients can be moved to it via the placental analogue (embryophore) in a brooding site. Progressively earlier oviposition required more placental activity, and finally embryophores began to play a major role in providing nutrition to the progeny. Placental cells became larger and more active, whereas the female gonad gradually changed to production of smaller oocytes (Pattern III). Altogether, these events resulted in a shift in oogenesis, since the ovary restricted its activity to the early stages of oocytic growth. We infer that nutrient distribution to the oocytes in the ovary became supplemented by, or dominated by, distribution to the embryos in the brood chamber. A similar shift from large to small (but macrolecithal) oocytes during a transition to the intraovarian incubation accompanied by cannibalism, has been hypothesized for some viviparous sea stars (Byrne 1991, 1996, Byrne & Cerra 1996). In this case, such a shift might be connected with a transition to the early onset of cleavage occurring within a gonad.

The occurrence of matrotrophy cannot be established definitively from cheilostome fossils, but what is presently known of cheilostome phylogeny (Gordon 2000) supports the above hypothesis. Also, the existence of different reproductive patterns, which are 'adjacent' to one another in a hypothetical series, within the same families and sometimes the same genera underlies the sequence of evolutionary transitions that we have suggested above, exemplified by *Isosecuriflustra*, *Celleporella*, Candidae, Microporidae, Cribrilinidae, and Hippothoidae (Patterns II and IV), *Cellaria* and Catenicellidae (Patterns III and IV), and Flustridae and Cellariidae (Patterns II, III, and IV). This taxonomic distribution strongly supports the idea that such transitions were not intractable evolutionarily and that EEN and placental analogues evolved multiple times within the Cheilostomata.

Viviparity in cheilostomes, known in the family Epistomiidae, could be considered as an additional, fifth reproductive pattern that evolved from Pattern II or III when embryos began to develop directly in the ovary and received EEN. External brood chambers likely disappeared in this lineage. An analogous pattern occurs in the Cyclostomata, although it almost certainly evolved independently (see below).

The taxonomic pattern of the distribution of matrotrophy within the phylum strongly supports the idea of its independent evolution in all 3 bryozoan classes and possibly several times within both gymnolaemate orders, reminiscent of the situation within vertebrates, in which EEN evolved independently numerous times in different lineages of fishes, amphibians, and reptiles (Blackburn 1992, Wourms & Lombardi 1992, Lombardi 1998, Trexler & DeAngelis 2003, Crespi & Semeniuk 2004).

Suggesting independent origins of placentation within the major bryozoan classes and orders of the

phylum, we specifically considered conventional views of major group relationships, distribution of the reproductive patterns (planktotrophy versus lecithotrophy), and differences in the origin of brood chambers. Considering the Ctenostomata (Gymnolaemata) to be a paraphyletic stem group for the Stenolaemata and Cheilostomata (Gymnolaemata) (Todd 2000), and recognizing planktotrophy in at least 3 ctenostome superfamilies, we suggest that the first cheilostomes also possessed a planktotrophic larva. Further, brooding and lecithotrophy evolved in cheilostomes, and the presence of 2 and sometimes 3 reproductive patterns (1 or 2 of which are placental) within the same families and even genera supports the idea that placentation evolved numerous times within this order. Increase in embryo size during brooding has been recorded in 4 ctenostome superfamilies. In 2 of them, planktotrophy also has been recorded. Thus, a conservative inference is that ctenostomes acquired placentation at least twice.

Cyclostomata (Stenolaemata) are viviparous. There are no viviparous ctenostomes known as yet. Placental ctenostomes brood their embryos outside the body cavity, either within brooding sacs (body wall invaginations) or within the introvert. Their placental organs are derivatives of the zooidal body wall. In contrast, placental organs in cyclostomes are derivatives of the ovary and coelothelium. Even if the ctenostome ancestor of Cyclostomata was a brooder, placentation in the ovary should evolve anew in this order.

The most problematic case is presented by the Phylactolaemata, whose precise relationships with the rest of the Bryozoa remain very obscure. Stark differences in morphology suggest their very early origin, probably from a ctenostome ancestor. Phylactolaemata are all placental, brooding their embryos inside brood sacs (body wall invaginations) similar to some placental ctenostomes from the superfamily Victorelloidea and in *Labiostomella* ('Protoctenostomata') (Ström 1977, Silén 1944, Todd 2000). Victorelloidea are thought to be among the youngest ctenostome superfamilies, not closely allied with *Labiostomella*. Overall sexual reproductive patterns of *Labiostomella* and Phylactolaemata are similar, but Phylactolaemata possess a ring- or spot-like placental structure, quite unlike the hypertrophied epithelial lining that exists in the placental victorelloids and 'ectodermic cushion' recorded in *Labiostomella*. Modes of oviposition are also different in the phylactolaemates and ctenostomes.

Ecological and evolutionary considerations of matrotrophy in cheilostome Bryozoa

Matrotrophy can be considered a maternal or parental effect, a form of phenotypic plasticity that spans gener-

ations (Uller 2008). Effects such as matrotrophy (and the plasticity they express) may carry proximate selective advantages in generational or ecological time, under certain circumstances. These circumstances could include: temporal or spatial fluctuations in the environment; conditions for offspring that are predictable from the parental conditions; low costs of interaction and transmission for both parents and offspring; and low levels of parent–offspring conflict, such that different optimal plasticity levels for parents and offspring do not reduce the fitness in either. Yet parental effects are not uniformly adaptive. They involve trade-offs (Trexler & DeAngelis 2003), and the costs and benefits are mediated by the respective strengths of selection on parents versus offspring, depending upon ecological contexts (Marshall & Uller 2007, Marshall et al. 2008a, Uller 2008).

In evolutionary time, differential allocation patterns to oocytes and to embryos are explicit among the reproductive patterns recognized in bryozoans, and both proximate and ultimate factors are in play (Wourms & Lombardi 1992, Uller 2008). Even *within* certain of these reproductive patterns, flexibility in parental investment in offspring (Marshall & Keough 2008a,b, Marshall et al. 2008b) is likely greater than in others. In particular, the degree of matrotrophy can be quite variable. Parent–offspring conflict influencing these transitions is also likely: How are parent and offspring fitness conditions that have been established under one reproductive pattern influenced in such a way as to make possible novel evolution of another pattern? We may conjecture, on the basis of multiple putative transitions in the direction of matrotrophy in bryozoans, that both natural selection and 'developmental bias' (Arthur 2004) may have played roles in (possibly convergent) acquisition and retention of novel reproductive patterns. Accepting that the implications of transitions in reproductive patterns and of parental investment are not yet clear (Reznick et al. 2007, Uller 2008), we offer some preliminary considerations about their existence in cheilostome bryozoans.

Bryozoan matrotrophy, variable maternal provisioning, and offspring size are all probably related interactively to areal and temporal environmental variation at several scales (Marshall & Keough 2008a,b, Marshall et al. 2008a,b). In the simplest form, an increase in the maternal provisioning to gamete or embryo may lead to larger, fitter offspring, but potentially at the cost of lowered fecundity because of the higher energy and space investment per offspring. Pattern I species with oligolecithal oogenesis and no brooding produce planktotrophic larvae, the reproductive strategy with the least developmental plasticity and the least maternal investment. To the extent that they persist in the plankton much longer than nonfeeding larvae, they

are more likely to encounter habitats different from and less predictable than that of the parents. However, this persistence may also enable them to maintain selectivity among habitats for longer periods of time (Elkin & Marshall 2007). Provisioning of lecithotrophic larvae, by contrast, provides a greater scope of size variation and often a means of buffering the next generation against stresses in the environment, increasing offspring fitness. For example, Marshall & Keough (2003) showed that in the cheilostome genera *Bugula* and *Watersipora*, both with variable sizes of lecithotrophic larvae, larger larvae could delay metamorphosis in the absence of settlement cues. Larger larvae of *B. neritina* also grow more quickly, survive better, reproduce sooner and more abundantly, and produce colonies in the next generation with larger larvae than do smaller initial larvae (Marshall et al. 2003). Similar size effects were found by Marshall & Keough (2004) for *W. subtorquata*. However, the size effects are not uniform, as subsequent experiments with *B. neritina* showed that larval duration interacts with size to produce complex effects after metamorphosis (Marshall & Keough 2006). Different intensities of post-metamorphic competition in *B. neritina*, conditioned according to the density of colonies, were used by Allen et al. (2008) to show that large offspring size is not always optimal; mothers produced smaller larvae at low colony densities. Producing larvae too large for a given time and habitat presumably has a cost in lost fecundity. This suggests that within-species plasticity in maternal provisioning can act to maximize both maternal and offspring fitness. Plasticity in bryozoan maternal provisioning and offspring size may also be adaptive at inter-population scales and with changing seasonal conditions (Marshall & Keough 2008b, Marshall et al. 2008a). Interestingly, both *B. neritina* and *W. subtorquata* are placental species, with reproductive Patterns III and IV, respectively (Table 1).

Matrotrophy may be favored where offspring conditions are predictable from parental conditions, or where environmental fluctuations occur. Lecithotrophic bryozoan larvae have limited dispersal, and some are philopatric or settle gregariously near conspecifics (Jackson 1986), ensuring predictable environments across generations. In fluctuating or unpredictable environments, flexibility in matrotrophy may facilitate 'bet-hedging' strategies, enabling mothers to produce a range of offspring sizes, potentially maximizing reproductive success across narrow, changing fitness optima; this strategy appears to hold for *Bugula neritina* and may be common (Marshall et al. 2008b). Sperm storage may be widespread in lecithotrophic gymnolaemates (Bishop & Pemberton 2006), and may increase developmental plasticity in concert with matrotrophy, possibly in response to varying environmen-

tal conditions. *Celleporella hyalina* with reproductive Pattern IV can adjust matrotrophic allocations based on receipt of sperm (Bishop et al. 2000, Hughes et al. 2002). Together with sperm storage, this would possibly give greater flexibility in response to adverse or fluctuating environmental conditions. Egg–sperm fusion occurs at or near the time of ovulation in oviparous gymnolaemates, whereas it is very early (precocious) and intraovarian in all brooding cheilostomes studied, including placental ones. Insemination by stored sperm can trigger normal oogenesis, which results in oviposition and the beginning of EEN in placental species. If mothers have some control over the induction of vitellogenesis and over allocation and larval provisioning in response to environmental cues, developmental plasticity is increased with regards to any of these processes acting alone.

The transition from lecithotrophic brooding without matrotrophy to matrotrophy via a placental analogue is a dramatic shift in the timing of resource allocation: from a major investment in offspring yolk resource before a fusion of male and female pronuclei in an inseminated oocyte to an investment after such fusion and through gestation (irrespective of prior yolk development in the oocyte in the second case). With this shift, parent–offspring interaction is accentuated, as these individuals are different genotypes. Selection on the parent can sometimes favour parental effects that are detrimental to offspring fitness, while selection on offspring is sometimes oblivious to parent fitness (Marshall & Uller 2007, Uller 2008 and references therein). Crespi & Semeniuk (2004), in considering vertebrates, argued that parent–offspring conflict over the degree of maternal investment was one of the main selective factors in evolutionary transitions among reproductive modes, independent of environmental and ecological factors.

Many of their supporting arguments might also be made for bryozoans, but as yet we have only scant data to evaluate this hypothesis. Multiple male sperm donors and the likelihood of sperm storage could represent a source of genotypic diversity, possibly advantageous in patchy or temporally variable environments (Bernasconi et al. 2004). Mothers may engage in cryptic selection through differential allocation of both resources and male genotypes, increasing their own lifetime fitness, possibly by contributing more to EEN when times are good and favoring flexibility or reduction in matrotrophic allocation in certain unfavorable times (Hunter & Hughes 1995). Offspring, in their own 'self-interest' could be selected for deriving maximum nourishment from their mothers, consistent with evolutionary transitions toward greater EEN. Marshall (2008) demonstrated that in *Bugula neritina*: 'when offspring cannot exercise any control over parental investment, parents might be able to impose their own

optimal allocation to offspring within and between broods, despite negative effects on offspring' (Uller 2008, p. 433; see also Marshall & Uller 2007, Allen et al. 2008). When *B. neritina* colonies experience tissue loss owing to predation, larvae produced immediately after the event are smaller and less fit (Marshall & Keough 2004). These examples reflect flexibility in resource allocation, where variable larval size can maximize both current and future reproductive returns. It has also been argued that (at least in mammals), once placentation is initially established, parent–offspring conflict will fuel further evolution and diverse morphological expression (Haig 1993). This appears to hold for bryozoans. Thus, we expect that the evolutionary transitions we infer would lead to enhanced fitness of *both* parents and offspring in order to be sustained under natural selection.

Our survey also revealed an unsuspected pattern among fast-growing ephemeral species with reproductive Pattern III, whereby placentation may confer an advantage in the time devoted to embryonic development. All examined cheilostome species with this ecological mode are relatively lightly calcified (suggesting fast growth), forming erect, flexible colonies that are often jointed. Insofar as incubation involves EEN, embryonic development and volumetric growth occur simultaneously. When starting reproduction, Pattern III species form the first small oocyte relatively quickly, transferring it to the brood chamber for further nutrition and development. Altogether these events can take less time than in species with Patterns II and IV, which require a longer time to form the first large (macrolecithal) oocyte. Also, the period of brooding in the latter 2 cases is of the same duration as oogenesis. Thus, the first larva, produced from a small egg with the help of the 'placenta', should be released earlier — speeding initial recruitment onto vacant substratum space. For instance, it takes 6 wk to develop a larva from the early oocyte in the perennial cheilostome *Chartella papyracea* (Pattern II), and just 3 wk in the ephemeral cheilostome *Bugula flabellata* (Pattern III) (Dyrynda & Ryland 1982). Pattern V (Epistomiidae) demonstrates the ultimate step in this evolutionary sequence, theoretically allowing fastest larval production (Dyrynda 1981, Dyrynda & King 1982). Although EEN is often accompanied by prolonged embryonic development in other groups of animals, it is, in contrast, faster in at least some placental bryozoans. This difference may be maximized at times or places where food resources are abundant, according to predictions of Trexler & DeAngelis (2003).

We reiterate our caution that these considerations are subject to validation by future phylogenetic analyses and ecological studies, but also borrow from Reznick et al. (2007, p. 2581) a thought about the value of our results. They are raw materials for the study of matrotrophy and evolution of complexity. Throughout their history, bryozoans have been an important component of benthic ecosystems. Tracing back to the early Ordovician, they survived all mass extinctions, becoming one of the dominant epibenthic groups in modern seas. Among the factors that have been linked to their episodes of radiation are growth plasticity, highly developed zooidal polymorphism, the evolution of complex body walls, and the existence of different larval types (Taylor 1988, McKinney & Jackson 1989, Jablonski et al. 1997). We suggest that evolution of a variety of reproductive patterns and lability during development contribute to that success by offering a range of mechanisms for resource allocation (allowing different permutations and combinations of oogenesis and brooding), playing a significant role in their diversification.

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