

Diversity dynamics and evolutionary patterns of Devonian Bryozoa

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Received: 18 January 2012 / Revised: 22 March 2012 / Accepted: 16 April 2012 / Published online: 24 May 2012
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Abstract Bryozoan diversity during the Devonian period displays a persistent rise from the Pragian to the early Givetian, significantly dropping in the late Givetian in the wake of the Taghanic Event. In contrast, two other important events during the Devonian, the Frasnian/Famennian Event and the Hangenberg Event at the Devonian/Carboniferous boundary, were less significant and resulted mainly in shifts in faunal composition. Diversity dynamics of Devonian Bryozoa was apparently controlled by extrinsic and intrinsic factors. Global palaeogeographic settings influenced faunal provincialism to which bryozoans seem to be sensitive. Sea-level fluctuations and subsequent changes in suitability of habitats influenced biodiversification processes in bryozoans. Intrinsically, bryozoans show some patterns consistent with diffuse co-evolution with potential predators and, possibly, prey. Observed trends in the morphological evolution of Devonian bryozoans include some obvious anti-predator adaptations (protective structures, strengthened skeletal walls). Moreover, Devonian bryozoans often developed various internal modifications, which apparently influenced the activity of polypides. This pattern is regarded here as apparent improvement of feeding, possibly as a response to diminishing food in the course of the mid-Palaeozoic Phytoplankton Blackout.

Keywords Bryozoans · Morphology · Adaptation · Coevolution · Ecology

Introduction

Palaeozoic bryozoans belong mainly to the Class Stenolaemata and are often diverse and abundant in different marine sediments from Ordovician to Permian times (Taylor and Allison 1998). Due to their stable calcitic skeletons, bryozoans usually show better preservation than many other animals, making them an important fossil group. As sessile animals, bryozoans show manifold interactions with their environment. This makes them valuable for investigation of different aspects of evolution, ecology and biogeography. Their morphological complexity, often well represented in the skeleton, is an excellent field for evolutionary studies.

Bryozoan diversity through the Phanerozoic shows similar patterns to those of marine invertebrates in general, as reflected by the similarity between the bryozoan family diversity curve (e.g. Taylor and Larwood 1990) and the Sepkoski marine invertebrate family curve (e.g. Sepkoski 1981). The bryozoan family diversity experienced the rapid climb during the Ordovician to a level that is maintained as a plateau through most of the Palaeozoic, followed by a dramatic decline at the end of this era and renewed diversification in the post-Palaeozoic.

Bryozoans are abundant and diverse in the Devonian worldwide (Cuffey and McKinney 1979). This period was a time of important changes in the structure and global composition of bryozoan faunas (Bigey 1988a). Devonian bryozoan faunas represent a transition between trepostome cystoporate-dominated communities of the Early Palaeozoic and fenestrate cryptostome communities of the Carboniferous and Permian.

The Devonian period, particularly the Mid-Late Devonian (Givetian-Frasnian), is characterised by the global expansion of reefs (Copper 1989, 2002), correlating with “greenhouse” conditions and high sea level. Late Silurian orogenesis resulted in

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the formation of the Old Red Continent in the northern hemisphere (e.g. Scotese and McKerrow 1990). A series of variously scaled extinction events (Walliser 1996) characterises the Devonian.

This paper aims to analyse bryozoan diversity dynamics during the Devonian and to investigate their evolutionary patterns. A dataset on bryozoan diversity and distribution has been compiled from the literature and my own unpublished research records to document genus-level patterns of bryozoan diversity through the stages of the Devonian. The recorded variations in diversity patterns are used to interpret extrinsic and intrinsic forcing factors. Observed patterns of morphological development of bryozoans during the Devonian are analysed in order to reveal their adaptive importance.

Material illustrated in this paper is housed at the Senckenberg Museum, Frankfurt am Main, Germany (SMF), Nationaal Natuurhistorisch Museum (Naturalis) in Leiden, Netherlands (RGM), and the Geological Centrum Göttingen, Germany (GZG).

Diversity dynamics of Devonian Bryozoa

Data set and time slices

For the purposes of this study, information on 209 bryozoan genera (Stenolaemata and Ctenostomata) occurring in the Devonian worldwide was compiled. The compilation was based primarily on species databases; the sources were literature from former studies and results of my own investigations on Devonian Bryozoa (Ernst 2008a, b, c, 2009, 2010, 2011; Ernst and Bohatý 2009; Ernst and Buttler 2012; Ernst and Herbig 2010; Ernst and Königshof 2010; Ernst and May 2009, 2012; Ernst and Mohammadi 2009; Ernst and Schröder 2007; Ernst et al. 2009, 2011a, b; Ernst et al. 2012a, b, c, d, e; Tolokonnikova and Ernst 2010; Tolokonnikova et al. 2011). Besides an extensive revision of the previously known bryozoan species and genera, 65 new species and 11 new genera were established during database compilation. In addition to the data on the entire group, diversity dynamics for three major orders of Devonian Bryozoa (Trepotomata, Fenestrata, and Cystoporata) were quantified. The diversity charts were calculated for genera, because the available taxonomic and stratigraphic data on species are not adequate in comparison with the generic dataset.

The Paleobiology Database (PBDB, podb.org) has been consulted during the compilation. However, my personal database was preferred in order to avoid some problems. Firstly, more than half of the bryozoan genera involved were described or re-evaluated in the course of my investigation. In this way, a bias produced by a monographic inhomogeneity has been reduced. In contrast, the PBDB contains data from different sources, and its reliability depends on

their authors (Crampton et al. 2003; Harnik 2009). Furthermore, my own database was adapted for the present investigation to contain information on morphology, which is absent in PBDB.

The Devonian Period is divided into 7 stages with durations from 4.2 to 15 My (million years) (Ogg et al. 2008). Information on bryozoan distribution often suffers from imprecise dating. However, the dataset compiled in Tolokonnikova and Ernst (2010) for palaeobiogeographical overview allowed splitting of the longest stage Famennian (15.3 My) into three sub-stages. In this way, the occurrence of bryozoan genera has been compiled according to 9 time slices, with a range of 3.5 to 10.8 My and an average stage duration of 6.3 My.

Counting the diversity

Raw data on diversity have some weaknesses, such as geographical variations in sampling intensity (for example, European and North American localities are better studied than those in Africa or Mongolia), sample and locality sizes, stratigraphic bias, incompleteness of the fossil record and the effects of preservation, monographic effort, rock volume and sea-level bias, etc. (e.g. Alroy 2010; Butler et al. 2011; Crampton et al. 2003; Peters 2005; Peters and Foote 2001; Sepkoski 1975; Smith and McGowan 2007, 2011). Various methods have been suggested to reduce the influence of these effects. While application of bias-correcting methods would undoubtedly bring some improvement, this is beyond the scope of the present publication. Some of these biases (e.g. monographic or sampling effect) are reduced due to the use of a personal database while others are relatively low for bryozoans, for example, high preservation potential of their skeletons (McKinney and Jackson 1989). Therefore, a few simple methods are used for evaluating bryozoan diversity in the present study.

There are different ways to estimate the diversity. The most straightforward method is to count the number of taxa recorded within a time unit. However, this method will overestimate true ranges because few species ranges will completely span the zones in which they first appear or last appear or to which they are confined. To compensate for this, Sepkoski (1975) devised a diversity measure referred to here as the normalized diversity measure (Fig. 1). This is the sum of species that range from the interval below to the interval above, plus half the number of species that range beyond the time interval but originate or become extinct within it, plus half those that are confined to the time interval itself. This metric also normalizes for variability in time interval duration to the extent that the longer a time interval is, the more species will begin or end within it or are confined to it (Copper 2002; Foote 2000b; Sepkoski 1975).

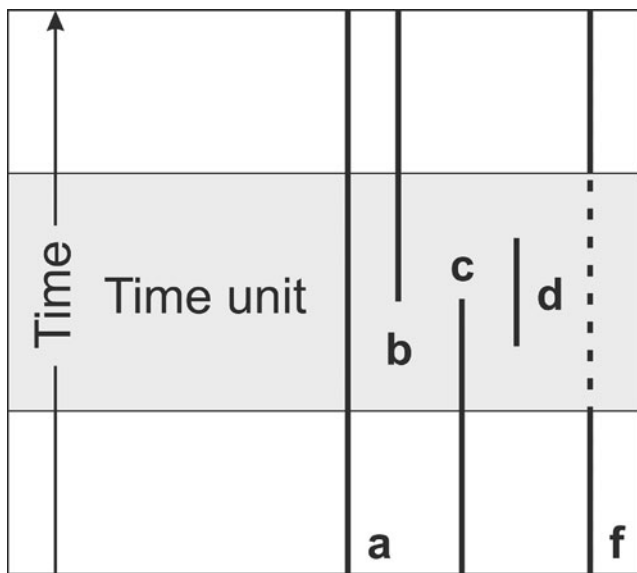


Fig. 1 Different types of taxa occurrences in respect to the time slice: **a** range through; **b** originate within the interval and range beyond it; **c** range into the interval and terminate within it; **d** confined to the time interval, **f** Lazarus species (modified from Copper 2002)

Another metric to estimate diversity is the number of taxa per 1 My. This reduces the influence of different durations of time intervals (Copper 2002; Sepkoski and Koch 1996).

Diversity is actually a function of originations and extinctions (Bambach et al. 2004; Copper 2002). If originations exceed extinctions, then diversity increases, and, conversely, if extinctions exceed originations, then diversity decreases (Taylor 2004). Data on evolutionary changes (turnover rates) are very important in order to reveal patterns of diversification, mass extinction or recovery of the group after a crisis.

At this point, it is important to mention so-called singleton taxa. These are taxa which are constrained within the same time interval (case d, Fig. 1). Some authors suggest that singleton taxa must be removed from the diversity analyses because they might result from preservational biases rather than evolutionary processes (e.g. Sepkoski 1996; Foote 2000a, b; Lu et al. 2006). Sepkoski (1996) defined that singleton taxa result mainly from taxonomic (synonymy, monographic effect) and preservational biases (Lagerstätten), whereas Foote (2000a, b) argued that various duration of time intervals make singleton taxa to an additional noise in the analysis. In contrast, other authors suggest that singleton taxa can be useful and should be included in the analysis (e.g. Fitzgerald and Carlson 2006; Uhen and Pyenson 2007). Fitzgerald and Carlson (2006) show using an example of Palaeozoic terebratulide brachiopods that many biases are low because of stable skeleton material (low magnesium calcite) and wide distribution of brachiopods in various biotopes. Moreover, the use of my own database reduces

the monographic bias. The same argument is followed here (high preservation of bryozoan skeletons, own practical experience with extensive collections) in order to retain the singleton genera in the analysis.

Partial compensation for the incompleteness of the fossil record can be achieved by consideration of Lazarus taxa. The Lazarus effect is an interruption in the range of taxa because of incompleteness of the fossil record, the taxa being missing from the studied unit but present in units before and after the unit (Fara 2001; Jablonski 1986; Wignall and Benton 1999).

The following methods were used to estimate the generic diversity dynamics of Devonian Bryozoa: total and normalized diversity, genera per 1 My, generic turnovers (Fig. 2a–c), as well as normalized diversity and evolutionary changes in three major groups (Figs. 2d and 3a–b).

Ctenostomes and cyclostome stenolaemates are negligible elements of the Devonian bryozoan faunas, while cryptostomes (rhabdomesines and ptilodictyines) are diverse and abundant in many Devonian communities. However, three groups—Trepotomata, Cystoporata, and Fenestrata—appear to be the most important not only in the Devonian but also throughout the Palaeozoic. Therefore, this paper describes the diversity dynamics of these three groups in detail, considering normalized diversity (plus Lazarus) curves and generic turnovers for the three groups during the Devonian (Figs. 2d and 3a–b).

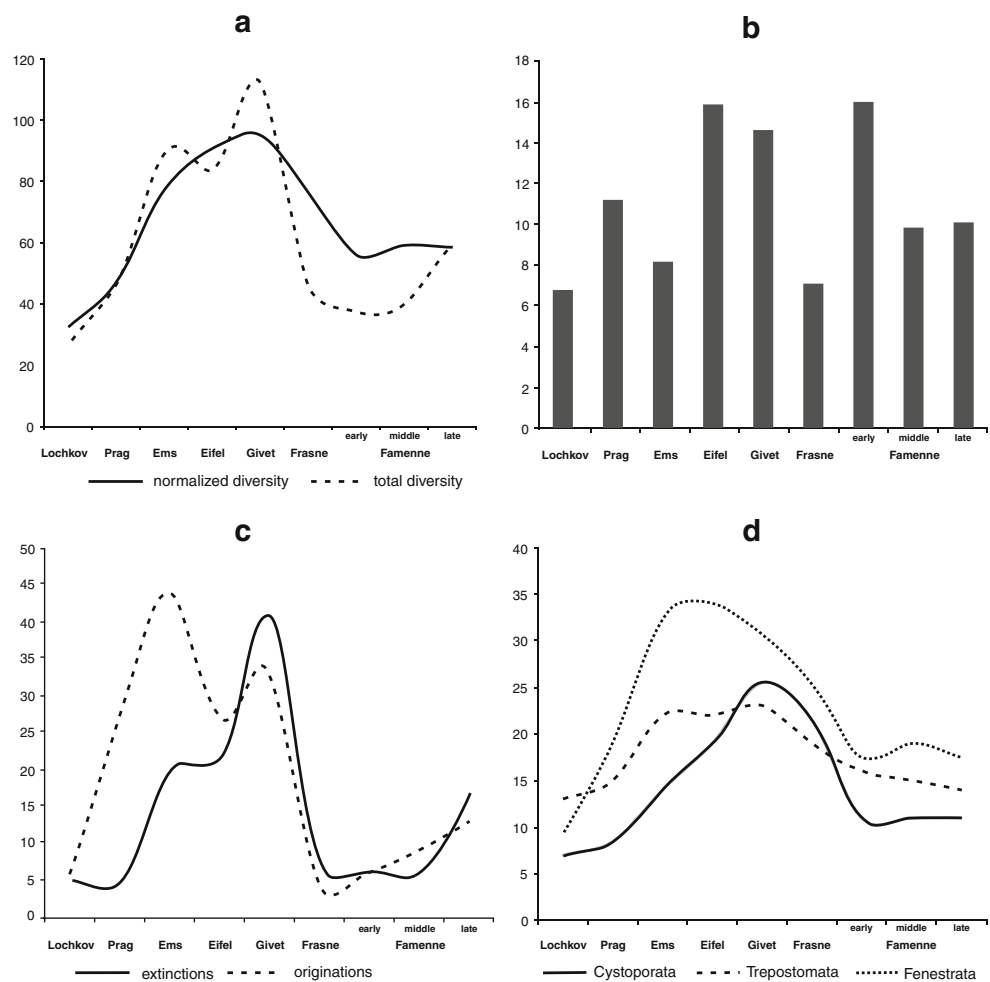
Morphological evolution and evolutionary trends in Devonian Bryozoa

Stenolaemate Bryozoa were a successful animal group in Palaeozoic seas, exhibiting various adaptive morphologies. In the course of the extensive taxonomic study and compilation of the available literature, three main trends in the morphological development of Devonian Bryozoa were recognised: (1) development of structures in fenestrate bryozoans assumed to have defensive functions; (2) modifications in trepostomes and cryptostomes of the exozonal wall microstructure and development of rod-like structures which apparently reinforced these skeletal walls; and (3) internal (zooecial) structures in all groups in the form of lateral projections of autozooecial walls.

Protective strategies in fenestrates

Fenestrate bryozoans developed characteristic erect colonies attached in different ways to a hard or firm substrate. The budding of autozooecia produced unilaminar arborescent colonies in which the autozooecial apertures open only on one side of the branch (Morozova 1987; McKinney and Jackson 1989). The Devonian genus *Schischcatella* represents

Fig. 2 Diversity dynamics of Devonian Bryozoa. **a** Total and normalized generic diversity (including Lazarus genera). **b** Genera per My. **c** Generic turnovers. **d** Generic diversity for three major bryozoan groups (normalized and including Lazarus genera)



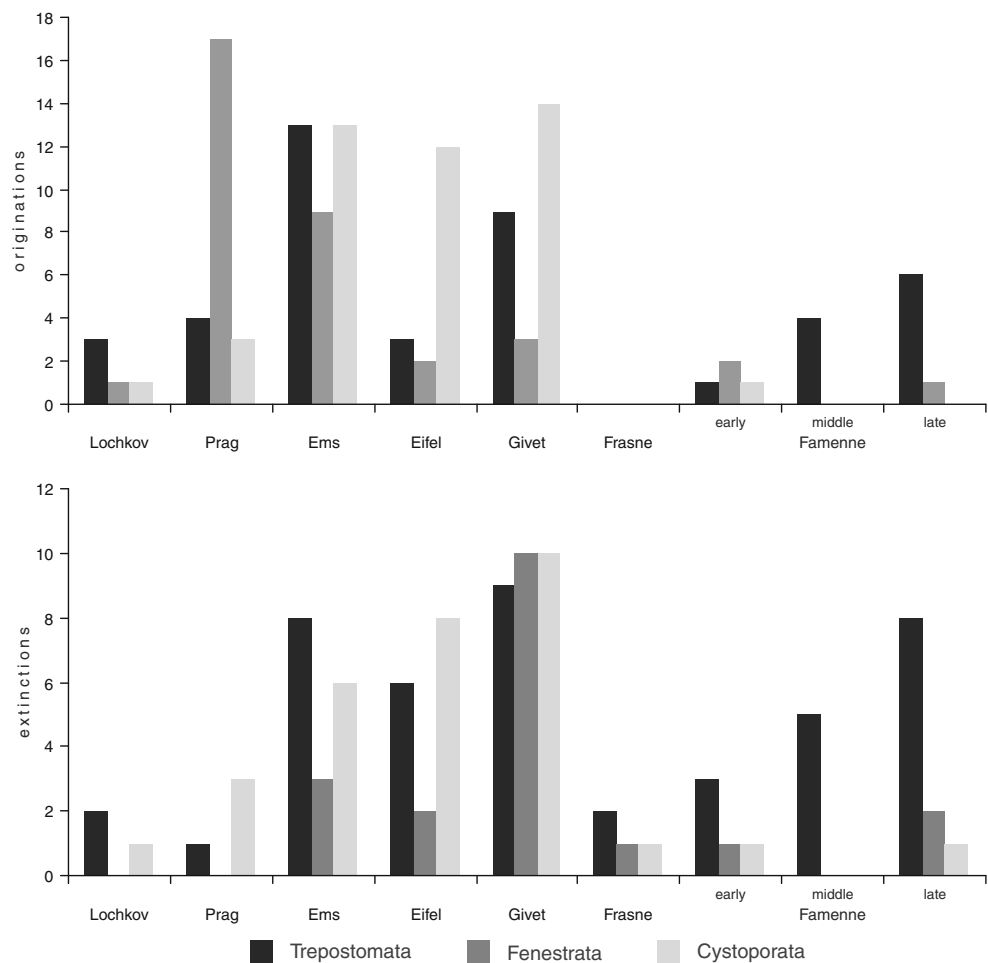
the only known exception in being encrusting, producing erect bifoliate fronds (Ernst and Bohatý 2009; Morozova 2001; Waschurova 1964).

The majority of fenestrates possessed reticulate colonies produced by connecting branches by sterile dissepiments or simple branch fusion. In such colonies water currents flowed towards the obverse surface and out through the open spaces (fenestrules) between branches to the reverse side (McKinney 1977; McKinney and Jackson 1989). The obverse surface contained autozoecial apertures and is potentially vulnerable to predators. Fenestrates developed different strategies thought to provide protection against predators. These can be classified into three groups: protective superstructures, apertural spines and polymorphic zooids (aviculomorphs, parazoecia).

Some fenestrates are able to produce skeletal structures on the frontal side of branches which are called superstructures (McKinney 1987). These range from simple high and broadened keels forming apical laths (Figs. 4c, d and 5), to nets produced by fusion of nodes on keels (Fig. 4a, b). Their importance is assumed to be in protection (Cumings 1904; Tavener-Smith 1975; Bancroft 1986; McKinney 1987) or strengthening of the colony (Cumings 1904). Sixteen

fenestrate genera are known to produce superstructures (Morozova 2001): *Hinganotrypa*, *Pseudounitrypa*, *Hemitrypa*, *Ignotrypa*, *Eosemicoscium*, *Pseudoisotrypa*, *Semicoscium*, *Quadrisemicoscium*, *Fenestrapora*, *Loculipora*, *Unitrypa*, *Wjatkella*, *Bigeyina*, *Mirifenestella*, *Ikelarchimedes* and *Tectulipora* (Table 1).

Among these, *Pseudounitrypa* occurred from the Early Carboniferous to the Early Permian, and *Hinganotrypa* and *Wjatkella* in the Permian. *Loculipora* and *Unitrypa* appeared in the Silurian and became extinct during the Middle Devonian. *Hemitrypa* ranges from Silurian to Early Carboniferous. The genus *Quadrisemicoscium* ranges from Early Devonian to Early Carboniferous. Of the 16 genera with obvious superstructures, 12 occurred during the Devonian. Moreover, 7 armored fenestrate genera are restricted to the Devonian: *Pseudoisotrypa*, *Semicoscium*, *Fenestrapora*, *Bigeyina*, *Mirifenestella*, *Ikelarchimedes*, and *Tectulipora*. Among the Devonian and pre-Devonian armored taxa, 5 genera (*Hemitrypa*, *Semicoscium*, *Eosemicoscium*, *Quadrisemicoscium* and *Tectulipora*) survived into the Late Devonian, with only *Hemitrypa* and *Quadrisemicoscium* persisting until the Early Carboniferous.

Fig. 3 Generic turnovers in three major bryozoan groups

During the Devonian, the ratio of armored fenestrates was high until the end of the Middle Devonian (Fig. 6). The highest ratio is observable in the Lochkovian.

The majority of armored genera became extinct by the end of the Middle Devonian.

Many fenestrates developed long spines surrounding autozoocelial apertures (Fig. 4g, h). In modern cheilostomes, similar spines can serve as protection against grazing by nudibranchs (Dyrynda 1986; Harvell 1984a). Taylor and Lewis (2003) described a cyclostome bryozoan with eight apertural spines supposed to have a similar protective function. However, these spines are produced by a frontal wall which is absent in double-walled Palaeozoic stenolaemates. Remarkably, those Devonian genera possessing protective superstructures usually lack apertural spines.

Two Devonian fenestrates, *Fenestrapora* and *Mirifenestella*, developed apparent polymorphic zooids which resemble the avicularia of cheilostome bryozoans and the eleozoids of cyclostomes. These structures were named "aviculomorphs" (McKinney 1998; Fig. 4e, f). Morozova (1974) described similar structures which she called "parazoecia". They occur in pairs on the reverse side in the genus *Mirifenestella*. The function of such structures is

supposed to be cleaning or defensive (McKinney 1998; McKinney et al. 2003; Morozova 1974, 2001).

Wall structure

Stenolaemate bryozoans secrete basically laminated calcitic walls (e.g. Armstrong 1970; Blake 1973a, b; Boardman 1971; Hickey 1987; Tavener-Smith 1969a, b; Tavener-Smith and Williams 1972). A number of genera developed various inhomogeneities in their skeletons, such as tubules and spherules, as well as rod-like structures which are largely or completely embedded in the exozonal skeleton: paurostyles, aktinostyles, mural spines, microstyles, cryptostyles etc. Many Devonian bryozoans contained such morphological modifications in their exozonal walls.

Spherules and tubules are deflections in the wall laminations, associated with some trepostomes and cryptostome (ptilodictyine and rhabdomesine) bryozoans (Fig. 7e–h). Mural spines or microstyles are rod-like structures completely embedded or slightly protruding on the colony surface and into the autozoocelial chambers (Fig. 7a–d). In contrast to spherules and tubules, microstyles have hyaline cores.

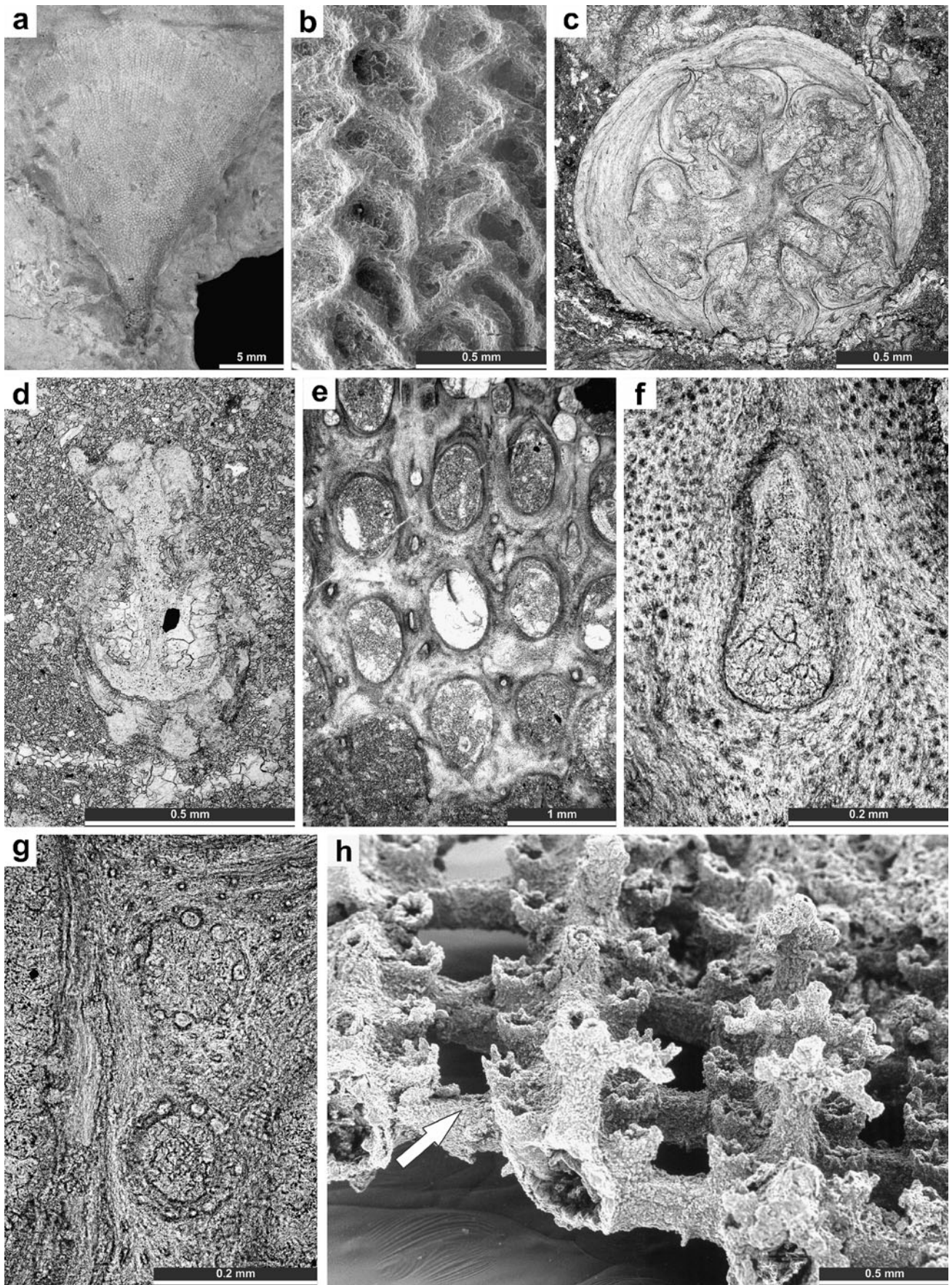


Fig. 4 Protecting morphologies in fenestrate bryozoans. **a** *Hemitrypa* sp. SMF 21.685, Middle Devonian (lower Givetian), Rhenish Massif, Germany. External view of the colony. **b** *Hemitrypa* sp. SMF 21.686, Middle Devonian (lower Givetian), Rhenish Massif, Germany. Close view of protecting structure represented by diverging and fused nodes on the median keel (voids are filled with sediment). **c, d** *Tectulipora tuberculata* Ernst et al., 2012b. Lower Devonian (Pragian), Cantabrian Mountains, NW Spain. **c** SMF 21.369, transverse section of conical colony at its base showing branches and superstructure. **d** SMF 21.380, branch transverse section showing massive nodes on the reverse side and superstructure formed by high roofed keel. **e, f** *Fenestrapora transcaucasica* Morozova and Lavrentjeva, 1998. Middle Devonian (Eifelian), Rhenish Massif, Germany. **e** Reverse side of the colony with aviculamorphs and massive nodes. **f** Aviculamorph. **g** *Rectifenestella exiliformis* Ernst et al., 2012b. SMF 21.326, tangential section showing autozooeical apertures with nodes. Lower Devonian (Pragian), Cantabrian Mountains, NW Spain. **h** *Cervella* sp. RGM 211 520c, Pennsylvanian, Cantabrian Mountains, NW Spain. Protecting superstructure in form of branched nodes on keels and apertural spines (arrow)

The Suborder Timanodictyina of the Order Cryptostomata is characterised by skeletal walls containing abundant microstyles (Gorjunova 1994, 1996; Morozova 1970). The origin of this group (which may be polyphyletic) is not clear. The earliest timanodictyines are known from the Early Devonian, and the peak of their diversity was in Permian (Gorjunova 1994).

Other structures include generally larger rod-like constructions such as acanthostyles, paurostyles, aktinostyles etc. (Armstrong 1970; Blake 1973a, b; Blake 1983; Tavener-Smith 1969a). Only acanthostyles protrude significantly on the colony surface, having probably at least in part a defensive function (Figs. 8a, i, k). Other style types do not protrude or form low nodes on the colony surface. Cryptostyles are massive embedded styles described in the Middle Devonian cryptostome (ptilodictyine) genus *Cryptostylocia* Ernst et al. 2009 (Figs. 7i–k).

Aktinostyles (called also "stellatopores" by some Russian scientists) occur in cryptostomes and trepostomes. These are rods with lateral projections (Figs. 7l, m and 8a, b). Long protruding and massive imbedded styles are known in Devonian cryptostomes (Fig. 8i, k). Embedded styles in

Vidronovella Gorjunova, 2006 produce conical elevations between the autozooeical apertures (Fig. 8g–j) and have been called "fastigia" (Gorjunova 2006).

Figure 6 shows changes in the ratio of trepostome genera having walls with potentially reinforcing structures; data on cryptostomes are omitted here. The number of genera with such modified walls rose during the Early to Middle Devonian, reaching a peak in the Givetian (Fig. 6).

In the Carboniferous, only a few trepostomes as well as cryptostomes are known to possess any kind of wall-strengthening structures. Curiously, some Permian trepostomes and cryptostomes subsequently redeveloped walls with skeletal inhomogeneities (e.g. *Ulrichotrypella*, *Hinganella*, *Neoeridotrypella*), correlating with Permian fenestrates having protective superstructures (*Wjatkella*, *Hinganotrypa*; see Table 1).

Internal morphology

Stenolaemate bryozoans are characterised by tubular zooecia in the most basic case (Borg 1926; Boardman 1971). As only a few Recent cyclostome bryozoans have structures within the autozooeical chambers, and their function is scarcely discussed in the literature (Boardman 1983). Three cyclostome species *Harmelinopora indistincta* (Canu and Bassler 1929), *Tubulipora hemiphragmata* Harmelin 1976 and *T. zigzag* Harmelin 1976 from the Mediterranean Sea were reported to have shelf-like lateral projections (hemisepta in *Harmelinopora indistincta* and hemiphragms in *Tubulipora hemiphragmata* and *T. zigzag*). It was shown that these structures play an important role for attachment of retractor muscles and therefore for polypide retraction and protrusion (Schäfer 1985; Boardman 1998). In *Harmelinopora indistincta*, the polypide retracts behind a pair of skeletal hemisepta to the bottom of the living chamber, and polypides in *Tubulipora hemiphragmata* and *T. zigzag* can actively bend around hemiphragms during their movement (Boardman 1983).

Fig. 5 Protective superstructure of *Fenestrapora* sp. Middle Devonian (Eifelian), Rhenish Massif, Germany. **a** SMF 21.688, colony external view. **b** SMF 21.689, SEM image of colony fragment with the superstructure in form of widened keel (right). On the left side, the superstructure is eroded

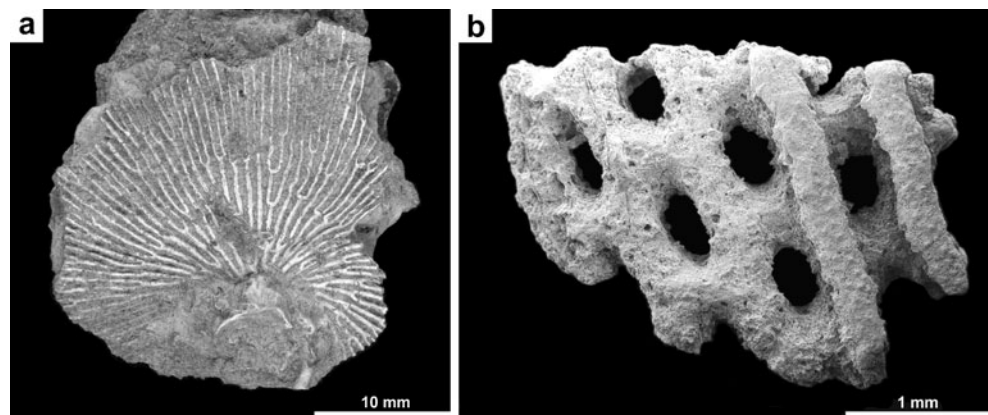


Table 1 Distribution of armoured fenestrates in the Palaeozoic

Species	Period									
	S ₁	S ₂	D ₁	D ₂	D ₃	C ₁	C ₂	P ₁	P ₂	
<i>Bigeyina</i>			X	X						
<i>Fenestrapora</i>			X	X						
<i>Eosemicoscium</i>	X	X	X	X	X					
<i>Hemitrypa</i>	X	X	X	X	X	X				
<i>Hinganoitrypa</i>										X
<i>Ignotrypa</i>			X							
<i>Ikelarchimedes</i>				X						
<i>Mirifenestella</i>			X	X						
<i>Loculipora</i>		X	X	X						
<i>Pseudisotrypa</i>			X							
<i>Pseudounitrypa</i>						X	X	X		
<i>Quadriseemicoscium</i>			X	X	X	X				
<i>Semicoscium</i>			X	X	X					
<i>Tectulipora</i>			X	X	X					
<i>Unitrypa</i>	X	X	X	X						
<i>Wjatkella</i>								X	X	

S Silurian, D Devonian, C Carboniferous, P Permian

In contrast, the Palaeozoic Stenolaemata possess numerous internal structures. Besides hemisepta and hemiphragms, previously mentioned, cystiphragms, ring septa and heterophragms are known in Palaeozoic bryozoans. They seem to have a direct relationship with polypide morphology and certainly have high taxonomic significance (Boardman 1971, 1983, 1998, 1999, 2001; Schäfer 1985).

Taxonomic study of Devonian bryozoan faunas and analysis of the available literature reveals an exceptional richness and abundance of internal structures among different bryozoan taxa. Lateral projections of different types are known in all four large groups of stenolaemate bryozoans (Cryptostomata, Trepostomata, Fenestrata, and Cryptostomata). The most sophisticated structures are found in rhabdomesine cryptostomes. Usually, these are juxtaposed inferior and superior hemisepta, both curved proximally and situated near the transition between endozone and exozone (Fig. 8g, h). However, a great variety of arrangements can occur in cryptostomes: only superior or inferior hemisepta can be present, and these can be simple, complex or multiple (Figs. 7n and 8j). Fenestrates are known to develop either inferior and superior hemisepta, or only superior hemisepta (Morozova 2001).

Cystoporate and trepostome bryozoans can possess hemiphragms, cystiphragms, ring septa and heterophragms (Boardman 1999, 2001; Boardman and McKinney 1976; Duncan 1939; Ernst and Voigt 2002). Moreover, some trepostomes, notably the Devonian genus *Leptotrypella*, occasionally possess inwardly curved mural spines (Boardman 1960; Ernst 2010). Such structures are also known in Recent cyclostomes, and are assumed to be attachment sites for

retractor muscles (Boardman 1983; Farmer 1979; Taylor 1999). Hemiphragms and heterophragms are usually situated alternating and juxtaposed (Fig. 8l), but they can be also arranged on one side (usually proximal regarding to growth direction) of the autozoecial chamber (Fig. 8c, d, m). Several Devonian trepostomes develop complex internal structures like corrugated heterophragms (Fig. 8f), or even a combination of cystiphragms and hemiphragms (Fig. 8c, d). Cystoporate bryozoans rarely contain any internal structures, but some Devonian genera have hemiphragms, either juxtaposed and alternating, or arranged on one side of the autozoecial chamber (Fig. 8l, m).

Discussion

Overview of the diversity graphs

The graphs presented here reveal various patterns in the diversity dynamics of Devonian Bryozoa. The total diversity curve (raw data) shows stronger fluctuation than the normalized diversity curve with Lazarus taxa (Fig. 2a). The reason is apparently an artefact caused by incomplete fossil record (Lazarus effect) and overestimation of diversity. The normalized diversity curve shows a steady increase in generic diversity from the Early Devonian to the late Middle Devonian (Givetian).

The normalized diversity (plus Lazarus taxa) per 1 My (Fig. 2b) shows a somewhat different pattern with stronger fluctuations. Remarkably, diversity is low in the Emsian and Frasnian, and the highest diversity is in the Eifelian and early Famennian.

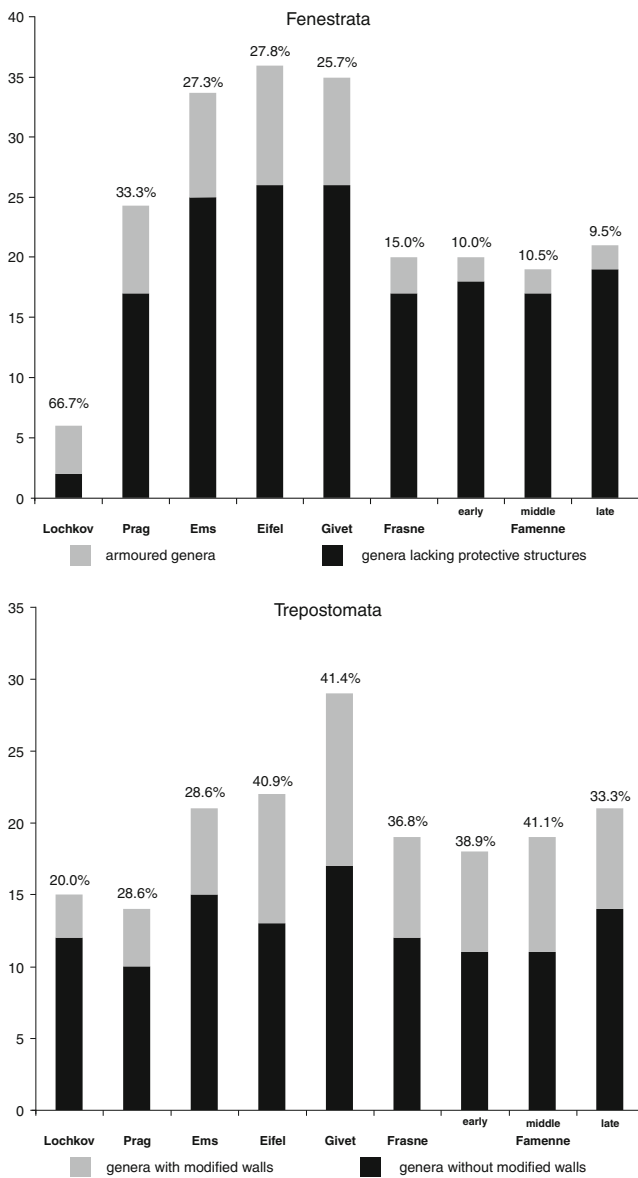


Fig. 6 Morphological patterns in fenestrates (ratio of genera with protecting superstructures), and in trepostomata (ratio of genera with modified walls)

Generic turnover (Fig. 2c) shows a steady increase in originations from the Lochkovian to the Eifelian. The number of extinctions is low in the Early Devonian, increasing towards the Givetian. In the Givetian extinctions exceed originations, whereas in Frasnian both parameters are equally low. For the early to middle Famennian, extinctions drop whereas originations increase. Towards the end of Devonian, extinctions rise again, while originations continue to increase. A similar pattern is visible at the beginning of the Devonian (Pragian-Emsian).

The normalized diversity curve shows that the three main groups (Trepostomata, Cystoporata, and Fenestrata) had different diversity dynamics during the Devonian (Fig. 2d). Fenestrates had their diversity peak in the Eifelian, whereas

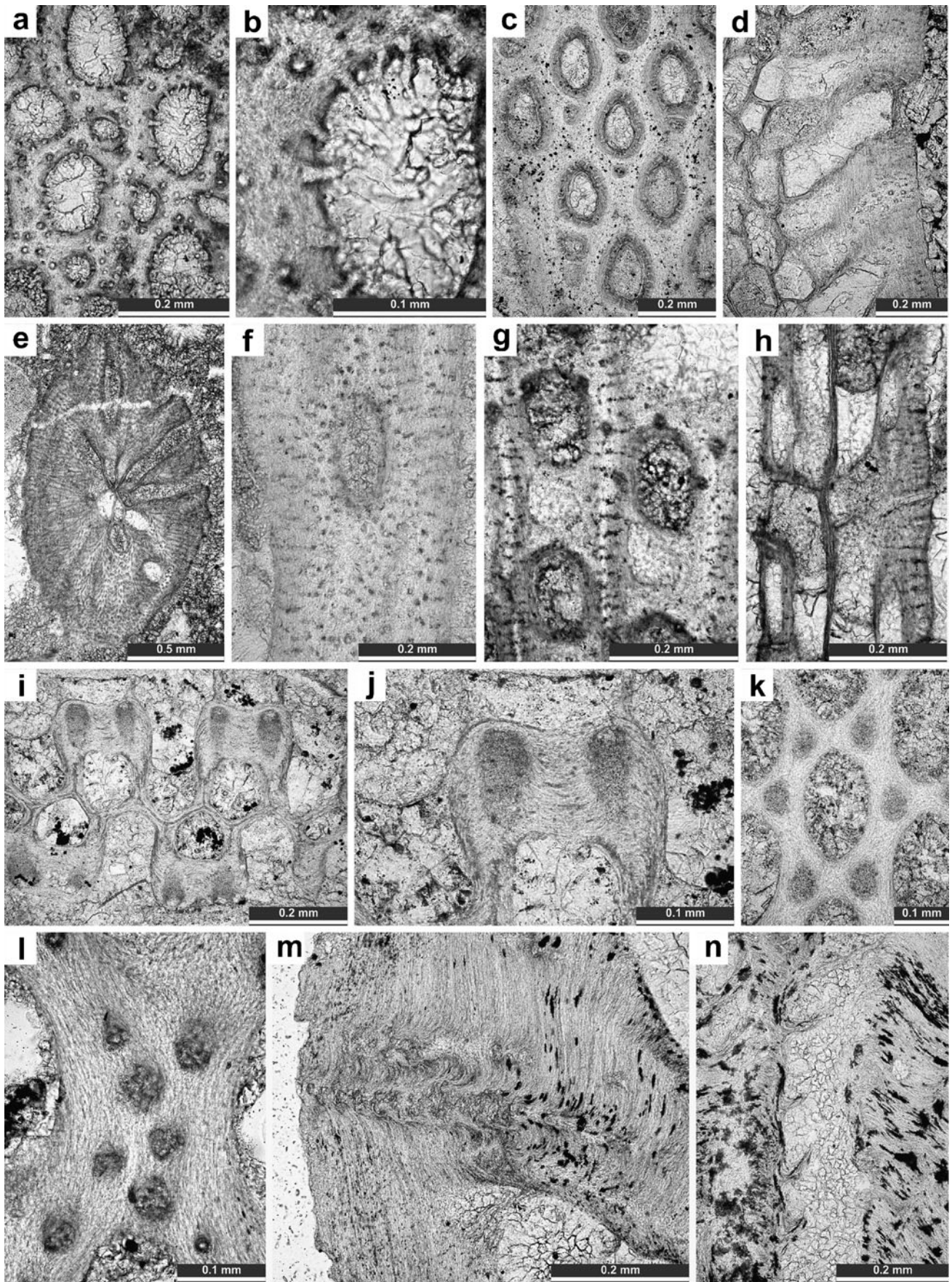
trepostomes achieved their highest diversity in the Givetian. Cystoporates were diverse from the Emsian to the Givetian. Whereas fenestrates and trepostomes experienced a similar drop and subsequent recovery during the Famennian, cystoporates show a gradual decline towards the end of the Devonian. The generic turnover data show that fenestrates had the fastest diversification during the Pragian, with very high origination values and no extinctions. In the Emsian, cystoporates and trepostomes had equally high origination rates, but trepostomes suffered more extinctions than cystoporates. In the Eifelian, cystoporates had high origination rates accompanied by relatively high extinction rates. Extinction rates were high for all three groups during the Givetian, whereas fenestrates produced fewer new genera during this stage. Extinction rates were low for all three groups during the Frasnian, but much more remarkable is the absence of origination. In the Famennian, a slight recovery for fenestrates can be detected and gradual increase in extinctions of trepostomes is evident.

Predation on bryozoans

Predation is an important agent of natural selection and a major determinant of ecological structure (Anderson and Underwood 1997; Bambach 1999; Huntley and Kowalewski 2007; Vermeij 1977, 1987, 1993). Bryozoans are eaten by various animals (see comprehensive overviews in McKinney et al. 2003 and Lidgard 2008), including fishes (Choat 1982; Osburn 1921), nudibranchs and other gastropods (e.g. Barnes and Bullough 1996; Chadwick and Thorpe 1981; Harvell 1984b; Nybakken and McDonald 1981; Todd and Havenhand 1989), arthropods (e.g. Buss and Iverson 1981; Fry 1965), and echinoderms (Day and Osman 1981). The most common types of predators are single zooid predators (some nudibranchs and pycnogonids), or grazers, which attack whole colonies or their parts (urchins, nudibranchs, fish) (Nybakken and McDonald 1981; Ryland 1976; Seed 1976; Todd 1981; Yoshioka 1982). The freshwater Phylactolaemata lacking calcitic skeletons are also known to be heavily preyed upon by gastropods (Wood et al. 2006).

There is also some evidence from the fossil record that bryozoans were actively preyed upon in the past. Remains of fenestrate bryozoans have been reported from coprolites of the Permian fish *Janassa* (Malzahn 1972; Schaumberg 1979).

However, many predators do not leave visible damage in the bryozoan skeleton (Berning 2008; McKinney et al. 2003). Indirect evidence of predation can be obtained from adaptations which seemingly serve a protective function. Bryozoans react to predation in different ways (McKinney et al. 2003). Morphological defences often involve various protective structures such as spines, armour or heterozooids (Harvell



◀ **Fig. 7** Wall microstructure, styles and internal morphology in trepostome (a, b) and cryptostome (c–n) bryozoans. a, b *Microcampylus regularis* Ernst, 2008a. SMF 20.112, Middle Devonian (Eifelian), Rhenish Massif, Germany. Tangential section showing mural spines in autozoecial walls. c, d *Acanthoclema distilum* Bigey, 1988b. Middle Devonian (Eifelian), Rhenish Massif, Germany. Tangential (c), SMF 21.656, and longitudinal (d), SMF 21.643, sections showing mural spines in autozoecial walls. e, f *Lenapora pulchra* Ernst and Königshof, 2010. Middle Devonian (Eifelian), Rhenish Massif, Germany. Branch oblique (e), SMF 20.151, and tangential (f), SMF 20.152, sections showing autozoecial walls with abundant tubules. g, h *Euspilopora spinigera* Ernst and Königshof, 2010. Middle Devonian (Late Givetian), Sabkhat Lafayrina reef complex, Tindouf Basin, Western Sahara. Tangential (g), SMF 20.499, and longitudinal (h), SMF 20.508, sections showing tubules in autozoecial walls, acanthostyles and vesicles. i–k *Cryptostyloecia hexapuncta* Ernst et al., 2009. Middle Devonian (Late Givetian), Sabkhat Lafayrina reef complex, Tindouf Basin, Western Sahara. Branch transverse (i, j), SMF-HF-18, SMF-HF-7, and tangential (k), SMF-HF-16, sections showing cryptostyles in autozoecial walls. l–n *Lunostoma pulchra* Ernst et al., 2012a. Middle Devonian (lower Givetian), Rhenish Massif, Germany. Tangential (l), SMF 20.925, and longitudinal (m), SMF 20.917, sections showing aktinostyles. n SMF 20.924, longitudinal section showing multiple hemisepa

1984a, 1986, 1992; Taylor and Lewis 2003; Yoshioka 1982). Especially fenestrates among fossil bryozoans are known to produce morphologies presumed to have a protective role (Bancroft 1986; Cumings 1904; McKinney 1987; Tavener-Smith 1975). The high ratio of fenestrates with superstructures and trepostomes with modified walls in the Devonian gives a clue that there may have been an increasing predator pressure during this time (Table 1; Fig. 6).

Similar tendencies were observed in Devonian brachiopods, which developed spines, extensive ornamentation of shells, and pseudopunctate shells (e.g. Leighton 1999, 2001, 2002, 2003). Pseudopunctate brachiopod shells penetrated by calcite rods (taleolae) are assumed to be an adaptation against predation (e.g. Alexander 1986, 2001; Brett and Walker 2002). There is evidence that, at the beginning of the Middle Devonian, and continuing into the Carboniferous, the number of genera of durophagous predators markedly increased (Bambach 1999; Sallan et al. 2011; Signor and Brett 1984).

Among specialised partial predators, nudibranch gastropods apparently represent the most active and diverse group feeding on modern shallow-water bryozoans (Lidgard 2008). Their attacks on bryozoans can occur by boring through the skeleton with their radula (e.g. Taylor 1982), or by placing their buccal mass on the orifice and sucking out the polypide, leaving no visible damage in the skeleton (McKinney et al. 2003). However, it is uncertain whether nudibranchs were present in the Devonian to prey on bryozoans. Nudibranchs belong to Opisthobranchia (Göbbeler and Klussmann-Kolb 2011; Grande et al. 2002), and the earliest shelled opisthobranch gastropods are known from the Early Carboniferous (Gosliner 1981). Molecular studies

also show that nudibranchs possibly did not appear before the Carboniferous or Permian (Jörger et al. 2010). However, non-nudibranch gastropods are also known to prey on bryozoans, and they were a significant predatory group in the Devonian and Carboniferous (Smith et al. 1985; Brett and Walker 2002). Arthropods could also be possible partial predators on bryozoans in the Devonian (Brett and Walker 2002; Moy-Thomas and Miles 1971), as early taxa of pycnogonids are reported from the Early Devonian Hunsrück Shale in Germany (Bergström et al. 1980; Dunlop and Arango 2005). Pycnogonids usually gain access to the polypide by inserting their proboscis into the zooidal chamber through the orifice.

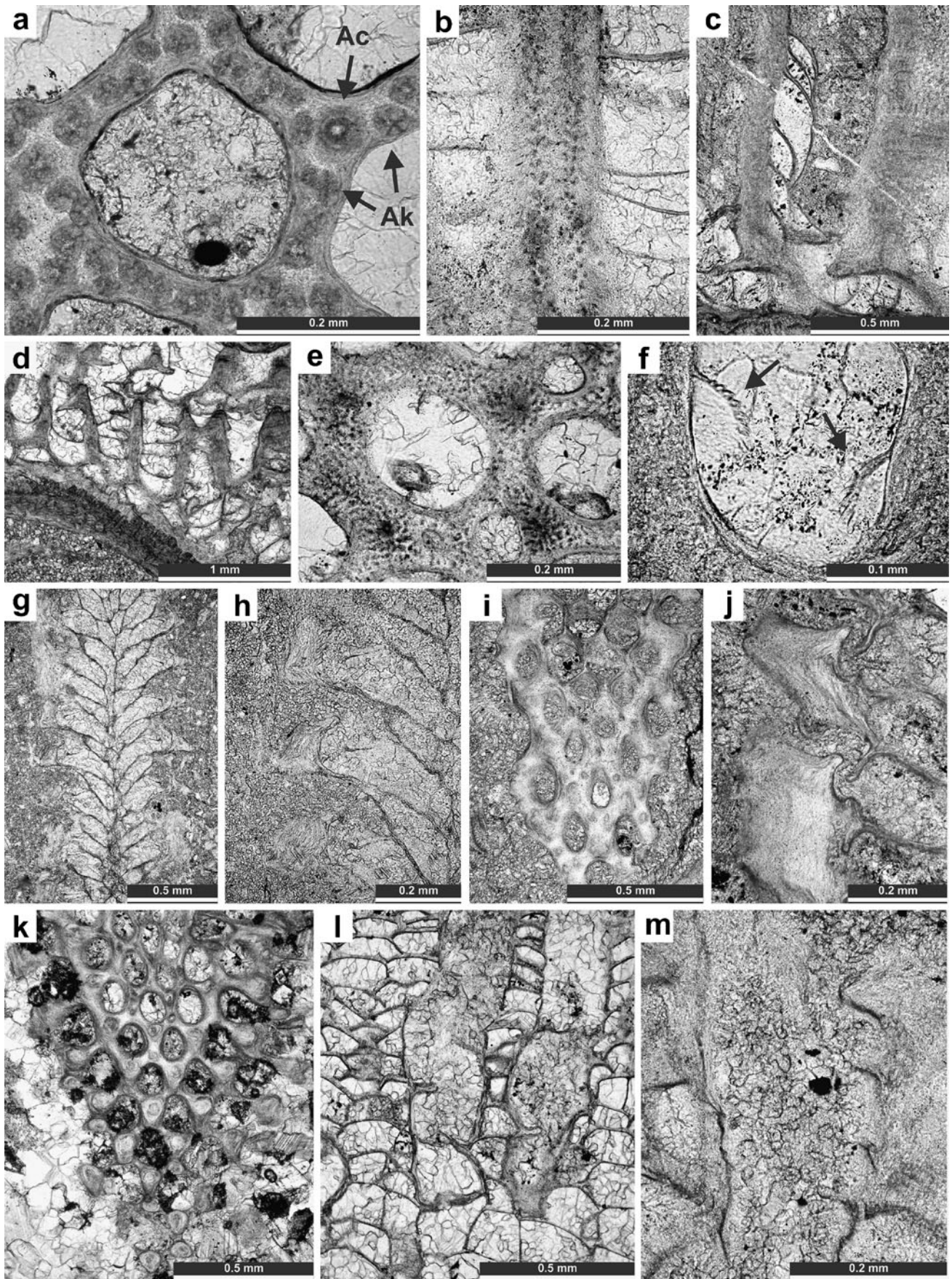
Whatever the predator, protection from partial predation will be achieved by prohibiting the predator from accessing the polypide by (1) increasing the thickness and/or strength of the exterior skeleton in order to impede boring or rupturing by predators aiming at the frontal wall; and/or (2) formation of structures around the orifice to impede mouthparts of predators. Both types of structural features have increasingly evolved in bryozoans from the Early Devonian onwards.

Anstey (1991) supposed that an increase of zoecial depth was a distinct trend in Palaeozoic stenolaemates. Using the example of trepostome bryozoans, he showed that the Lower Palaeozoic genera had generally shallow autozoecia, whereas the genera with intermediate and deep autozoecia dominated from the Late Silurian to the Late Permian (Anstey 1991, p. 244). He explained this trend as response to increasing predation. In the Devonian bryozoans, the deeper autozooids are often combined with internal structures like hemiphragms.

Thus, the observed coincidence between the rise of diversity (Fig. 2) and increasing predator stress (Fig. 6) can be inferred to represent a diffuse coevolutionary response of the bryozoans to their predators. The peak of this process occurred near the transition between the Early and Middle Devonian. Bryozoans responded to predation with various strategies such as development of protecting superstructures, increasing spinosity and strengthening/thickening of skeletal walls. The production of such defensive structures is associated with high costs for bryozoans. This implies that heavily armoured taxa need more food and are potentially disadvantaged compared with unarmoured taxa in situations when no predator stress occurs. It may also explain why many of these taxa became extinct at the end of the Devonian when food became scarce.

Bryozoan feeding

An increase in the complexity of internal structures of Devonian bryozoans can have several explanations. Internal



◀ **Fig. 8** Wall microstructure, styles and internal morphology in trepostome (a–f), cryptostome (g–k) and cystoporate (l, m) bryozoans. **a, b** *Eostenopora clivosa* (Schlüter, 1889). Middle Devonian (Eifelian), Rhenish Massif, Germany. Tangential (a), SMF 20.097, and longitudinal (b), SMF 20.096, sections showing acanthostyle (Ac) and aktinostyles (Ak). **c–e** *Diphragmoides paradoxus* Ernst, 2008a, **b, c**. Middle Devonian (Eifelian), Rhenish Massif, Germany. **c, d** GZG.IN.0.010.540e, longitudinal section showing tubules in autozooeal walls, basal diaphragms, hemiphragms and cystiphragms in autozoecia. **e** SMF 20.115, tangential section showing tubules in the autozooeal wall. **f** *Trachytoechus globosus* Ernst et al., 2011b. SMF 21.511, Middle Devonian (Eifelian), Rhenish Massif, Germany. Oblique section showing heterophragms (arrows). **g, h** *Vidronovella elegantula* Ernst et al., 2012b. SMF 21.296, Lower Devonian (Pragian), Cantabrian Mountains, NW Spain. Longitudinal section showing hemisepta. **i, j** *Vidronovella intricata* Ernst 2011. Lower Devonian (Emsian), Cantabrian Mountains, NW Spain. **i** RGM 211 542-3-5, tangential section showing imbedded styles (fastigia sensu Gorjunova 2006) and paurostyles. **j** RGM 211 542-3-6, longitudinal section showing complex hemisepta. **k** *Klaucena (Spira) devonica* Ernst, 2011. RGM 211 542-3-5, Lower Devonian (Emsian), Cantabrian Mountains, NW Spain. Tangential section showing massive acanthostyles. **l** *Fistuliphragma eifelensis* sp. SMF 2729, Middle Devonian (Eifelian), Rhenish Massif, Germany. Longitudinal section showing hemiphragms. **m** *Cliotrypa cystota* sp. SMF 2751, Middle Devonian (Eifelian), Rhenish Massif, Germany. Longitudinal section showing hemiphragms

skeletal structures have a relationship with polypide morphology and can influence the feeding activities of bryozoans (Schäfer 1985; Boardman 1998). Early and primitive forms of Stenolaemata lack any internal structures (Larwood and Taylor 1979; Taylor and Larwood 1990; Taylor and Rozhnov 1996) and there can have been various reasons for their development: (1) increasing demand of food (e.g. due to energetic expenses for protection against predators), or (2) reduction of food supply. The first situation appears reasonable, especially because a combination of protecting and internal morphologies often occurs. The second is difficult to prove. Bryozoans are active suspension feeders, they generally feed on phytoplankton including green algae, diatoms, cyanobacteria, but also microscopic crustaceans (Winston 1977). Possible links can be made to the development of phytoplankton during the Palaeozoic. The Devonian period is regarded as the destabilisation phase before the so-called mid-Palaeozoic Phytoplankton Blackout (Riegel 2008; Strother 2008). The relation between phytoplankton productivity and its consumers is evident (Tappan 1970). The increasing complexity of bryozoan internal morphology could be a reaction to diminishing food in order to optimize feeding capacity.

Bryozoans and Devonian bioevents

Geological history has witnessed several global events which crucially changed the biosphere of the Earth (e.g. Benton 1995; Jablonski 2004; Hallam and Wignall 1999;

House 2002; Racki and Wrzolek 2001). During the evolutionary history of Bryozoa from Ordovician to Recent, the severest crisis occurred at the P/T transition, with mass extinction of the majority of bryozoan taxa that impacted most orders (Bambach et al. 2004; Gorjunova et al. 2004; Morozova and Viskova 1977; Raup and Sepkoski 1982).

During the Devonian, several bioevents of smaller scale occurred (Walliser 1986, 1996). Bryozoans show a slightly different sensitivity to these events than other fossil groups (Bigey 1988a; Morozova et al. 2002). The Choteč Event at the Emsian–Eifelian boundary strongly affected brachiopods and trilobites, whereas corals and bryozoans did not show any noticeable changes in their diversity (Chlupáč and Kukal 1986, 1988; Ernst et al. 2012c). The compiled graphs of bryozoan generic diversity dynamics (Figs. 2 and 3) do not identify any significant reduction in diversity. This event is recognisable on the total diversity chart but is not evident in the normalized diversity curve with Lazarus taxa (Fig. 2a). The number of genera per 1 My (Fig. 2b) is even higher in the Eifelian than in the Emsian. However, generic turnovers display a weak signal expressed in decreasing origination and increasing extinction rates during the Eifelian (Figs. 2c and 3).

The highest bryozoan diversity is recorded for the Givetian. Unfortunately, the compiled graphs do not use time slices sufficiently fine to show diversity dynamics within the stages. At least for the Givetian in Europe, the peak in the diversity coincides with the early Givetian (Ernst 2008c). Late Givetian bryozoan faunas, such as those in northern Africa, are rare (Ernst and Königshof 2008, 2010). Generic turnover data shows the onset of origination decrease and rapid increase in extinction rates, so that extinctions exceed originations (Figs. 2c and 3). During the Givetian 40 bryozoan genera became extinct (Table 2), which means 36.3 % diversity loss. During the Givetian, 33 new genera appeared, but this does not significantly balance the diversity loss (Fig. 2a). In the subsequent Frasnian stage, the drop in bryozoan diversity is dramatic. Generic turnover is equally low for the Frasnian. For the three major groups (Trepostomata, Fenestrata, Cystoporata), no originations were recorded during the Frasnian (Fig. 3). The compiled bryozoan diversity charts document a significant drop in diversity, which implies a strong extinction event in the time between the Givetian and Frasnian. Horowitz et al. (1996) previously suggested a major change in bryozoan diversity between the Givetian and Frasnian stages (see also Taylor and Larwood 1988).

The Givetian/Frasnian bryozoan extinction most probably corresponds to the late Givetian Taghanic bioevent (Boucot 1990; House 1985; May 1996). This crisis represents a series of faunal changes (Baird and Brett 2008), with the impact on different groups shifted in time (Ebert 1993).

Table 2 Bryozoan generic loss during the Taghanic and Hangenberg events

Taghanic event (late Givetian)	Hangenberg event (late Famennian)
<i>Abakana</i>	<i>Anastomopora</i>
<i>Acanthostictoporella</i>	<i>Boardmanella</i>
<i>Acrogenia</i>	<i>Coelocaulis</i>
<i>Ascodiction</i>	<i>Cyphotrypa</i>
<i>Bactropora</i>	<i>Eodyscritella</i>
<i>Bigeyina</i>	<i>Eridotrypella</i>
<i>Botryllopora</i>	<i>Fitzroyopora</i>
<i>Canutrypa</i>	<i>Geranopora</i>
<i>Ceramella</i>	<i>Mysticella</i>
<i>Chondraulus</i>	<i>Neotrematopora</i>
<i>Clonopora</i>	<i>Percyopora</i>
<i>Coscinella</i>	<i>Pseudoascopepora</i>
<i>Diphragmoides</i>	<i>Reteporina</i>
<i>Dissotrypa</i>	<i>Schulgina</i>
<i>Dyoidophragma</i>	<i>Tamaroclema</i>
<i>Eifelipora</i>	<i>Vidronovella</i>
<i>Eliasopora</i>	
<i>Euspilopora</i>	
<i>Fenestrapora</i>	
<i>Fistuliporella</i>	
<i>Fistuliporidra</i>	
<i>Kysylschinipora</i>	
<i>Lenapora</i>	
<i>Loculipora</i>	
<i>Loxophragma</i>	
<i>Monotrypa</i>	
<i>Phractopora</i>	
<i>Pileptrypella</i>	
<i>Pinacotrypa</i>	
<i>Polycylindricus</i>	
<i>Prolixicella</i>	
<i>Ptilocella</i>	
<i>Ptiloporina</i>	
<i>Scalaripora</i>	
<i>Schischcatella</i>	
<i>Semiopora</i>	
<i>Stictocella</i>	
<i>Trachytoechus</i>	
<i>Trematella</i>	
<i>Viscovia</i>	

This bioevent coincided with the final disappearance of the Eastern Americas Realm and its remaining endemic taxa, as well as the disappearance of a few final Malvinokaffric Realm stragglers (Boucot 1988, 1990). The Taghanic event was considerable for such groups as ammonoids (House 1996), trilobites (Chlupáč 1994; Feist 1991) and corals

(Oliver and Pedder 1994). It was apparently caused by transgression and marked the end of faunal provincialism, which had persisted since Early Devonian times (Johnson 1970). This may also explain its heavy impact on bryozoans because they seem to be sensitive to changes in provincialism, as shown for the Ordovician (Taylor and Ernst 2002; Tuckey 1990). Increase of cosmopolitanism and reduction of available habitats as a result of the Taghanic transgression (with subsequent deepening of carbonate platforms) seem to bias bryozoan generic diversity.

In contrast to the Taghanic event, the Frasnian/Famennian bioevent did not greatly affect bryozoans (Bigey 1988a; Morozova et al. 2002). Indeed, there are even signs of a slight recovery of bryozoan faunas during the early Famennian (Figs. 2 and 3). During the late Famennian, 16 genera became extinct (Table 2), which means 28.0 % diversity loss. Different causes for the Frasnian/Famennian bioevent (the so-called Kellwasser event) have been discussed, ranging from the worldwide anoxia (McGhee et al. 1986; McGhee 1996; McLaren 1970; Schindler 1990; Walliser 1984, 1986, 1996) to an asteroid shower (Sandberg et al. 2002).

The Hangenberg bioevent at the Devonian/Carboniferous boundary was apparently caused by a strong drop in sea level due to glaciation (Caplan and Bustin 1999; Kaiser 2007; Kaiser et al. 2006, 2008; Paproth and Streeb 1984). Sallan et al. (2011) suggested that during the Hangenberg event a significant restructuring of vertebrate predator faunas occurred. They stated possible links between changes in the composition of the predator faunas (durofagous fishes) and diversity of crinoids. The decrease in crinoid diversity during the Hangenberg event was interpreted as a result of higher predator pressure. In contrast, the following crinoid diversification is regarded as a release of predation because of reduction in diversity of predators.

The consequence of the Hangenberg event was a significant shift in the composition of many animal groups including bryozoans (Gutak et al. 2008; Horowitz and Pachut 1993; Simakov 1993; Tolokonnikova and Ernst 2010). Whereas generic turnovers for the Famennian (Fig. 2c) show a typical recovery pattern with an initial drop in extinction rates and increase in originations in the early to middle Famennian, near the Devonian/Carboniferous boundary extinction rates are almost as high as origination rates. Among the three major groups, generic turnover changes significantly in trepostomes.

An important factor affecting the bryozoan diversity in the Late Devonian was strong endemism of some faunas (Tolokonnikova and Ernst 2010). Especially faunas from Northern China, Iran, Afghanistan and Australia display high endemism, and those genera became extinct during the late Famennian.

Conclusions

The diversity of Devonian Bryozoa displays a persistent rise from the Pragian to the early Givetian, before dropping significantly in the late Givetian corresponding to the Taghanic Event. Bryozoans experienced a slight decline during the F/F Event, beginning their recovery during the middle Famennian. The Hangenberg bioevent at the Devonian/Carboniferous boundary resulted mainly in shifts of faunal composition.

These dynamics can be explained by abiotic and biotic changes. Abiotic causes included changes in global palaeogeography which controlled faunal provincialism. Increased provincialism had a positive influence on bryozoan diversity, whereas an increase in cosmopolitanism during the late Givetian resulted in a significant drop in bryozoan diversity.

Biotic causes for bryozoan diversity changes include diffuse coevolution between bryozoans and their predators and, possibly, their prey. Observed trends in the morphological evolution of Devonian bryozoans include development of protective structures (in fenestrates) and strengthening of zooecial walls (in other bryozoans with calcareous skeletons). These morphologies can be interpreted as responses to increasing predator pressure.

Another trend concerned the feeding of bryozoans, including development of various internal modifications, which apparently influenced the activity of polypides in order to improve feeding capacity, possibly in response to diminishing food supply during mid-Palaeozoic Phytoplankton Blackout.

Acknowledgments Björn Berning, Linz, Paul Taylor, London, and Timothy Wood, Dayton, are thanked for valuable comments and language correction of the manuscript. Robert Anstey, East Lansing, and Hans Arne Nakrem, Oslo, are thanked for their helpful and constructive reviews. The present study is part of the project ER 278/4-1 and 2 supported by the Deutsche Forschungsgemeinschaft (DFG). It is also a contribution to the IGCP 596 “Mid-Paleozoic climate and biodiversity”.

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