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Earth-Science Reviews 78 (2006) 287–306
EARTH-SCIENCE REVIEWS
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Skeletal mineralogy of bryozoans: Taxonomic and temporal patterns

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Received 28 July 2005; accepted 1 June 2006
Available online 22 August 2006

Abstract

Skeletal carbonate mineralogy of 1183 specimens of marine bryozoans from the literature was examined for phylogenetic patterns in order to elucidate the effects of bryozoan mineralogy on geochemical and paleoenvironmental analysis. Colonies are composed of calcite (66% of specimens), aragonite (17% of specimens) or various mixtures of the two (17% specimens) (phylum mean = 72.9 wt.% calcite, $n = 1051$). When calcite is present, it ranges from 0.0 to 13.7 wt.% $MgCO_3$ (mean = 5.0 wt.% $MgCO_3$, $n = 873$). Most (61%) calcitic specimens are formed of intermediate-Mg calcite (4 to 8 wt.% $MgCO_3$), others (28%) of low-Mg calcite (0 to 4 wt.% $MgCO_3$), and few of high-Mg calcite (>8 wt.% $MgCO_3$). The phylum occupies at least 63% of the theoretical mineralogical "space" available to biomineralisation. Most of this variation occurs in the class Gymnolaemata, order Cheilostomata, suborder Neocheilostomata. Fossil and Recent stenolaemate taxa are generally low- to intermediate-Mg calcite (mean = 99.7 wt.% calcite, 2.6 wt.% $MgCO_3$, 17% of available biomineral space). Variability among families is related in a general way to first appearance datum: families younger than 100 Ma display greater mineralogical complexity than older ones. The cheilostome infraorder Flustrina includes unusual free-living aragonitic families, dual-calcite skeletons (mainly low-Mg calcite, but with secondary high-Mg calcite), and some genera with considerable mineralogical variability. Families (e.g., Membraniporidae and Phidoloporidae) and species (e.g., *Schizoporella unicornis*) with the highest degree of variability have potential for environmental correlations with mineralogy, paleoenvironmental interpretation, and possibly molecular investigation for potential cryptic species. Stenolaemate families, genera and species with low variability, on the other hand, are well-suited for geochemical work such as stable isotope analysis. Variability in the skeletal mineralogy of bryozoans suggests that they may be useful in geochemical, phylogenetic, and paleoenvironmental studies, with careful choice of study material.

Keywords: bryozoans; carbonate mineralogy; biomineralization; calcite; aragonite

1. Introduction

Marine bryozoans have precipitated calcium carbonate skeletons since at least the Lower Ordovician (Taylor and Ernst, 2004); over the last 500 Ma they have evolved through both icehouse periods when aragonite was more likely to be precipitated in the sea, and greenhouse periods when calcite was the favored polymorph (e.g., Sandberg, 1983a; Hardie, 1996). It has been suggested that bryozoan evolution, at least in the post-Cretaceous order Cheilostomata, has been driven in part by secular changes in sea-water chemistry over that time (Stanley and Hardie, 1998, p. 15). Shifts in the Mg:Ca ratio in sea-water, it is argued, have affected skeletal mineralogy of evolving families, providing selective pressure resulting

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doi:10.1016/j.earscirev.2006.06.001

in a wide range of carbonate skeletal mineralogy seen in bryozoans today.

Marine bryozoans from the classes Gymnolaemata and Stenolaemata do show a wide range of mineralogies in their skeletal carbonate (Smith et al., 1998). Early studies (particularly Schopf and Manheim, 1967; Schopf and Allan, 1969; Rucker and Carver, 1969; Poluzzi and Sartori, 1973, 1974; Hickey, 1987) revealed a complex mineralogical suite of mixtures in the phylum. Later workers tried to summarize bryozoan mineralogy, noting the dominance of calcite (e.g., Lowenstam and Weiner, 1989, p. 211), the addition of aragonite in secondary calcification (Sandberg, 1983b, p. 269), the presence of entirely aragonitic bryozoans (Sandberg, 1983b, p. 267), and the presence of bimineralic forms, some with highly organized biominerals and others with fairly amorphous mixtures (Bone and James, 1993, p. 253). More recently the presence of two distinct calcites (dominant low-Mg calcite and subdominant high-Mg calcite) has been documented in a few anascan cheilostomes (Smith et al., 1998).

While mineralogy in bryozoans has generally increased in complexity over time, it appears likely that the development of calcareous skeletons evolved separately in the two major clades which have been studied. Cyclostome bryozoans (along with other stenolaemates) developed their low-Mg calcite skeletons in the Ordovician (Taylor and Ernst, 2004), whereas Cheilostome bryozoans evolved their skeletons independently in the Jurassic.

Bryozoans, as temperate colonial carbonate-producers with a long fossil record, are well-suited for investigation into some of the larger questions about the effects of global sea-level and secular sea-water chemistry on invertebrate evolution and development over the Phanerozoic. Environmental and temporal variations, however, cannot be interpreted without a clear understanding of the mineralogical variability present within the phylum, and how that variability is related to phylogenetic clades. Variation within individuals, among individuals, and within species has been considered elsewhere (see Poluzzi and Sartori, 1974; Smith et al., 1998). Here we collate mineralogical information from the literature and examine it at a range of taxonomic levels in order to understand the phylogenetic patterns of carbonate skeletal mineralogy in bryozoans.

2. Methods

An extensive literature search resulted in a list of 46 papers from 1885 to 2005 in which carbonate mineralogy was reported for identified bryozoan species (Walther, 1885; Nichols, 1906; Clarke and Wheeler, 1917, 1922; Chave, 1954; Lowenstam, 1954, 1964a, b; Schopf and Manheim, 1967; Cheetham et al., 1969; Greeley, 1969; Rucker and Carver, 1969; Schopf and Allan, 1970; Smith, 1970; Sandberg, 1971, 1973, 1975, 1977, 1983a, b; Siesser, 1972; Tavener-Smith and Williams, 1972; Poluzzi and Sartori, 1973, 1974; Jørgensen, 1975; Ristedt, 1977; Healey and Utgaard, 1979; Masuda and Sakagami, 1982; Keane, 1986; Boardman and Cheetham, 1987; Pätzold et al., 1987; Agegian and Mackenzie, 1989; Bone and Wass, 1990; Williams, 1990a,b; Borisenko and Gontar, 1991; Bone and James, 1993, 1997; Smith and Nelson, 1993; Rahimpour-Bonab et al., 1997; Taylor and Monks, 1997; Smith et al., 1998; Taylor and Wilson, 1999; Crowley and Taylor, 2000; Grischenko et al., 2002; Machiyama et al., 2003; Taylor and Schindler, 2004; Steger and Smith, 2005). The lack of replication in most of these studies is notable. Only 12 of the 45 papers examined more than one specimen within a species, only two papers measured mineralogy of more than 10 replicates within species (Machiyama et al., 2003; Steger and Smith, 2005).

Studies which refer only to “bryozoans” were not included. Reported mineralogy was recorded in a database, along with details of location, morphology and age, if given. For each of the 1183 measurements recorded, taxonomic position of the species was determined. We recorded the species names given by the original authors, then noted any subsequent revisions. We have classified cheilostome bryozoans using the Interim Classification of Gordon (2005). For stenolaemate bryozoans, we have relied on the Treatise of Invertebrate Paleontology (Bassler, 1953; Boardman et al., 1983) as well as the more recent work by Taylor (1993). These references also provided First Appearance Data for higher taxa (with ages chosen conservatively from the top of the stage after Palmer and Geissman, 1999). The collated database is available in its entirety as a Microsoft Excel X file of 464 kb from website in Appendix A.

The usefulness of the data varies greatly depending on source. Early studies used chemical titration and staining methods (e.g. Clarke and Wheeler, 1917; 1922) and reported elemental concentration, of which Mg content is the most relevant to carbonate mineralogy. Rucker (1968) and Rucker and Carver (1969) did some of the earliest X-ray diffraction (XRD) work on bryozoans (following the pioneering work by Lowenstam, 1954), but they did not report on sample locations. They appear to have had some reservations about the precision of the wt.% $MgCO_3$ determination by peak shift (Chave, 1954), because they reported Mg content in a series of ranges (0–4, 4–8, 8–12, >12 wt.% $MgCO_3$). Schopf and Manheim (1967) and Schopf and Allan (1969) reported Mg content to one decimal place, and subsequent authors have retained this practice. As XRD trace interpretation has moved from manual measurements to computerized peak identification, more decimal places have become available. The precision of this technique, however, is still probably no better than 0.1 wt.% $MgCO_3$.

Sometimes XRD traces show ragged or flat-topped peaks at the calcite position. Bone and James (1993) reported that such peaks result from interference between closely spaced low-Mg and high-Mg calcite peaks. Both Bone and James (1993) and Smith et al. (1998) described several anascan bryozoan species which appear (at least sometimes) to precipitate discrete minerals of low-Mg and high-Mg calcite. We have no way of knowing if previous workers disregarded "ragged" peaks or if they never happened to encounter dual-calcitic species.

3. Skeletal carbonate mineralogy

Carbonate mineralogy is ordinarily expressed as a combination of two variables (calcite:aragonite ratio and Mg content), each with a limited continuum. The proportion of the two major $CaCO_3$ polymorphs is often expressed as a ratio of calcite:aragonite or as percent calcite (with percent aragonite assumed to equal 100 minus percent calcite). Either way, this variable can only vary from 0 to 1 or 0% to 100%. The degree of substitution by $MgCO_3$ in calcite (expressed in mol% $MgCO_3$, wt.% MgO, wt.% Mg and other units, but here recalculated to wt.% $MgCO_3$) varies in biological calcite from 0 to 22 wt.% $MgCO_3$ (Lowenstam and Weiner, 1989). There is no measurable Mg substitution in aragonite (though there may be trace amounts, see Chave, 1954).

For convenience, the degree of Mg substitution has been divided into low-Mg calcite (LMC) and high-Mg calcite (HMC) with the boundary about 4 wt.% $MgCO_3$ (e.g., Tucker and Wright, 1990). More recently, intermediate-Mg calcite (IMC) has been added to the classification, with variously defined boundaries. Here we adopt the classification boundaries of Rucker and Carver (1969), with LMC from 0 to 4 wt.% $MgCO_3$, IMC ranging from 4 to 8 wt.% $MgCO_3$, and HMC greater than 8 wt.% $MgCO_3$. The main reason for choosing these rather arbitrary boundaries is that species with some mineralogical consistency appear to stay within these bounds. The data themselves offer little assistance; there is no obvious modality in the distribution of $MgCO_3$ in bryozoan calcite (Smith et al., 1998).

Carbonate mineralogy of a group of specimens may be outlined by an area described by the ranges of these two variables (wt.% calcite and wt.% $MgCO_3$ in calcite). Other statistical measurements of variability (which could usefully reduce the influence of outliers), such as 95% confidence limits or standard error, are not properly used with data, such as these, with defined boundaries. Consequently we calculate and present only the ranges for sets of mineralogical data.

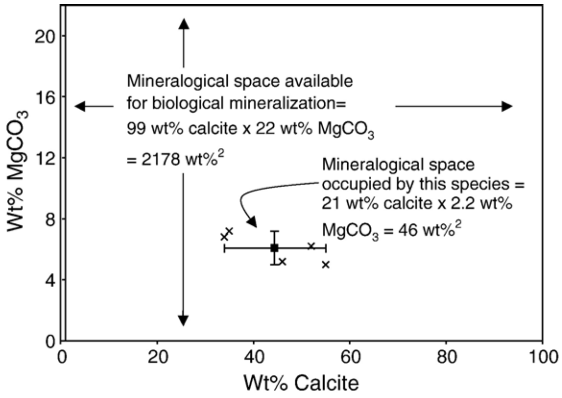

Fig. 1. Model of "mineralogical space" available for biomineralization, showing calculation of percentage occupation by a group of four theoretical specimens.

In order to describe mineralogical variability within the limits of the data, we have considered the space available for biological calcification (0 to 100 wt.% calcite, 0 to 22 wt.% $MgCO_3$, with the exception of a small area where wt.% calcite is less than 1, any Mg content thus being undetectable; see Fig. 1). Mineralogical "area" available to biological precipitation of calcium carbonate is thus 2178 wt.%^{2} (that is, 99 wt.% calcite times 22 wt.% $MgCO_3$). The mineralogical space occupied by a group of data (for example, within a family) is given by the product of the ranges (Fig. 1). When this area is divided by the total biomineralogical space available, it gives the dimensionless "percent coverage" of the group — or an indication of how widely the group varies over the possible mineralogies available.

For each measurement given in the database, then, we report wt.% calcite and wt.% $MgCO_3$ in calcite, and for each taxon investigated we also give biomineralogical percentage of the total possible (abbreviated "minspace"). 132 specimens had a qualitative reports of mineralogy which were not amenable to numerical rendering.

4. Results

4.1. Phylum bryozoa

Of the 1183 specimens in the database, 1051 specimens had wt.% calcite reported, ranging from 0 to 100%, with a mean of 72.9 wt.% calcite. By far the most common mineralogy was 100% calcite: 694 specimens (66%) were

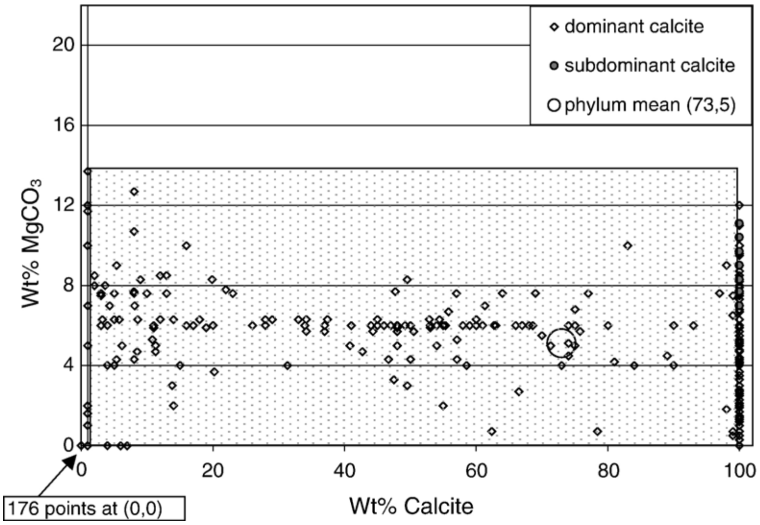

Fig. 2. Skeletal carbonate mineralogy of 1051 specimens of marine bryozoans (both fossil and extant). Shaded box indicates maximum mineralogical "space" occupied by the phylum (63% of total available biomineralogical space).

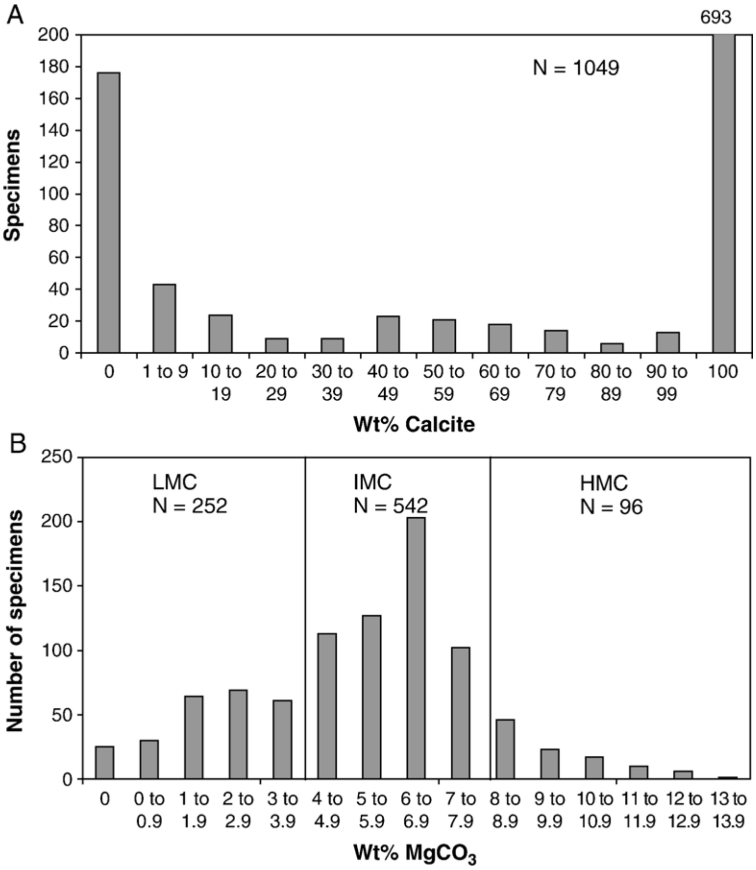

Fig. 3. Frequency distributions for A) calcite content and B) Mg content in 1051 bryozoan specimens. LMC — low-Mg calcite; IMC — intermediate-Mg calcite; HMC — high-Mg calcite.

entirely formed of calcite. Aragonitic specimens (0% calcite) were the second most common type (177 specimens, or 17% of those tested). Mixtures of the two polymorphs were found in another 17% of specimens (180 in total) spread fairly evenly across the range from 1 to 99% calcite (Fig. 2).

Only 873 specimens had wt.% $MgCO_3$ in calcite reported, ranging from 0.0 to 13.7, with a mean of 5.0. The majority (61%) of specimens with some calcite fell into the intermediate class (4–8 wt.% $MgCO_3$), with another 28% forming low-Mg calcite. Far fewer (11%) were composed of high-Mg calcite. In 24 of low-Mg calcite specimens, a second subdominant high-Mg calcite was found, ranging from 7.0 to 11.0 wt.% $MgCO_3$, with a mean of 9 wt.% $MgCO_3$ (Fig. 3).

The mineralogical "space" occupied by the phylum is 1400 wt.%^{2}, 63% of the possible area available for biomineralization (Fig. 2).

4.2. Class stenolaemata

"All stenolaemates have calcareous skeletons. All skeletons are calcitic except for one reportedly aragonitic species from the Triassic." (Boardman and Cheetham, 1987, p. 511). In general we find this sweeping statement to be mostly true (Table 1). Of 212 specimens from the class Stenolaemata covering all five orders (comprising 20 fossil specimens from the four extinct orders and 192 fossil and Recent specimens from the extant order Cyclostomata), only 7 specimens show any aragonite, and five of them are less than 2% aragonite. The argonitic stenolaemates reported from the Triassic are probably sponges or corals rather than bryozoans (Engeser and Taylor, 1989; Schäfer and Grant-Mackie, 1998.) Mean wt.% calcite for the class is thus 99.7, even though the measured range is 62.4 to 100 wt.% calcite (Table 1).

There are 174 published Mg contents for stenolaemates (all in the order Cyclostomata), ranging from 0 to 9.6 wt.% $MgCO_3$. The mean of 2.6, however, reflects the overall dominance of low-Mg calcite: 72% of specimens ($n=126$) have less than 4.0 wt.% $MgCO_3$. Another 27% ($n=47$) fall into the intermediate Mg calcite category, leaving only 1 specimen with wt.% $MgCO_3$ greater than 8.0 (Table 1).

Stenolaemata take up only 17% of available biomineralogical space, which is less than a third of the space the phylum Bryozoa occupies. The majority of the variability

Table 1
Skeletal carbonate mineralogy of higher taxa in the phylum Bryozoa

Higher taxonomy of bryozoan mineralogy								Mean mineralogy		Biomineral space (% possible)
Phylum	Classes	Orders	Suborders	Families	Genera	Species	Specimens*	Wt.% calcite	Wt.% $MgCO_3$**	
Bryozoa	2	6	15	101	206	389	1176	72.9	5.0	63
	Stenolaemata	5	12	36	54	73	235	99.7	2.6	17
		Cyclostomata	7	17	33	53	215	99.6	2.6	17
			Articulata	1	3	7	8	100.0	3.0	0
			Tubuliporina	9	19	27	127	99.5	2.5	17
			Cancellata	1	2	6	51	100.0	1.8	0
			Cerioporina	3	5	7	14	99.8	2.7	1
			Rectangulata	1	2	4	12	99.9	4.9	0
			Paleotubuliporina	2	2	2	2	100.0		
		Cryptostomata	2	3	3	3	3	100.0		
			Ptilodictyina	2	2	2	2	100.0		
			Rhabdomesina	1	1	1	1	100.0		
		Cystoporata	2	5	5	5	5	100.0		
			Ceramoporina	1	1	1	1	100.0		
			Fistuliporina	4	4	4	4	100.0		
		Fenestrata	1	3	3	3	3	100.0		
			Fenestelloidea	3	3	3	3	100.0		
		Trepostomata	n/a	7	9	9	9	100.0		
	Gymnolaemata	1	3	65	152	315	941	67.1	5.6	63
		Cheilostomata	3	65	152	315	941	67.1	5.6	63
			Scrupariina	1	1	1	3	100.0	4.7	0
			Malacostega	2	5	14	27	95.2	7.6	1
			Neocheilostomina	62	146	300	911	65.8	5.7	63

*The database also includes 7 specimens with no taxonomic identification which do not appear in this table.
**Excluding secondary calcite which occurs in 24 specimens (all Neocheilostomina) and has a mean of 9 wt.% $MgCO_3$ (range 7 to 11).
Taxa without data are omitted.

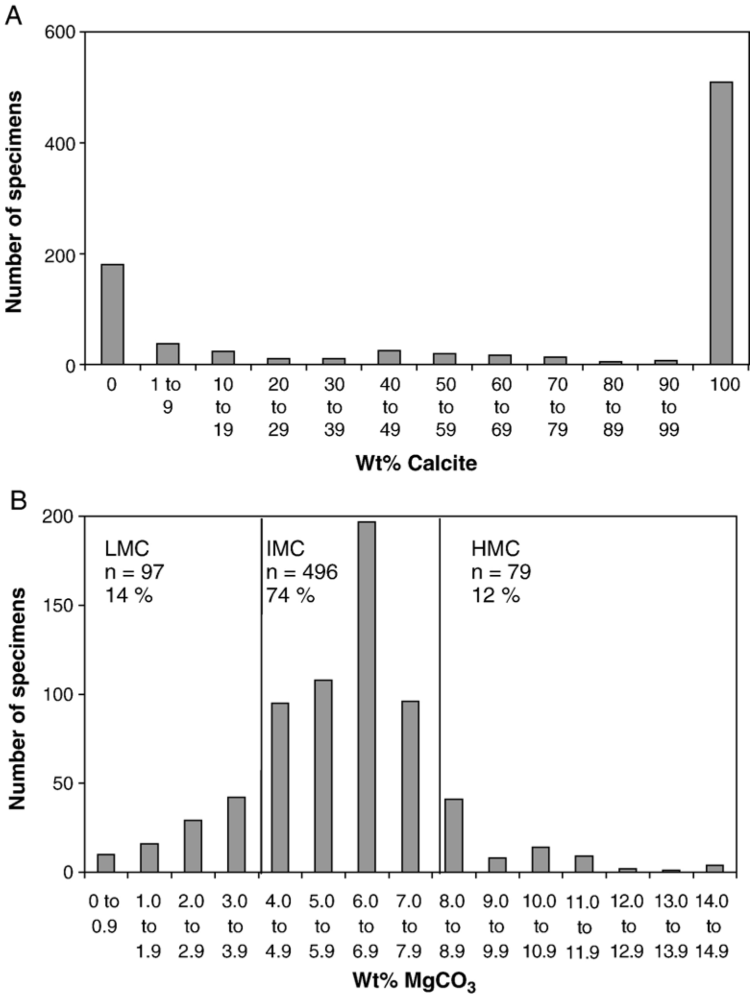

Fig. 4. Frequency distributions of A) calcite content and B) Mg content in the bryozoan class Gymnolaemata, order Cheilostomata.

is provided by the extant order Cyclostomata. Seven cyclostomate suborders including 18 families are in the database (specimens = 215). Extant suborders Cancellata, Cerioporina, and Articulata and fossil suborder Paleotubuliporina all precipitate low-Mg calcite (means of 2–3 wt.% $MgCO_3$). The suborder Rectangulata, in contrast, is the only group of stenolaemates consistently to produce intermediate-Mg calcite. The mean wt.% $MgCO_3$ of the suborder Rectangulata (mean = 4.8, $n = 10$) is significantly more than the mean wt.% $MgCO_3$ of the extant suborders Articulata, Cancellata, Cerioporina, and Tubuliporina combined (mean = 2.3, $n = 185$)(Mann–Whitney U-Test, $P < 0.0005$). The vast majority of cyclostomate specimens are in the suborder Tubuliporina ($n = 127$), which, perhaps not coincidentally, also shows the most variability and covers the widest mineralogical area. Eight fossil cyclostomate specimens, ranging from the Ordovician to the Cretaceous, are all low-Mg calcite (Table 1).

The Paleozoic order Cystoporata contains two suborders; both are represented here. A single specimen from the sole family of the suborder Ceramoporina is composed of low-Mg calcite. In the other cystoporate suborder, the Fistuliporina, four of 11 families are represented. Two specimens are identified as being made of high-Mg calcite, the other two of low-Mg calcite (but with no numerical data given). All cystoporate specimens measured occur in the Ordovician or the Mississippian. Similarly, the order Cryptostomata is also represented in the database by 3 specimens from the Ordovician and the Mississipian. Two of eight families in the cryptostome suborder Ptilodictyina and one of six families in the suborder Rhabdomesina all show calcitic skeletal mineralogy. In the order Trepostomata, seven of 23 families are represented, all calcitic with two specimens showing high-Mg calcite. All three representatives of the order Fenestrata show calcitic mineralogy (Table 1).

4.3. Class gymnolaemata

Mineralogical complexity in the class Gymnolaemata is well documented. This class has assumed dominance over the last 100 Ma, rapidly evolving since the Cretaceous into an abundant and diverse clade (Boardman and Cheetham, 1987) typical of temperate waters. Of the 941 specimens in the class Gymnolaemata, order Cheilostomata, 59% are entirely calcite and 21% are entirely aragonite, with 20% with some degree of bimineralic mixing (Fig. 4). The mean Mg content of the group is 5.6 wt.% $MgCO_3$ and 74% of specimens contain intermediate-Mg calcite. Nevertheless, Mg content ranges from 0 to 14.0, with 14% of specimens low-Mg calcite, and 12% high-Mg calcite (Fig. 4).

The mineralogical space occupied by class Gymnolaemata is 63% of the total available biomineralogical space (see Fig. 2) and accounts for all the variability seen in the phylum as a whole.

Suborder Malacostega, the oldest cheilostomate suborder here (Late Jurassic to Recent), is represented in the database by two of its four families; 27 specimens cover 5 genera and 14 species. All specimens except two are composed of calcite, varying from low to high-Mg calcite (2–14 wt.% $MgCO_3$). The two specimens which contain aragonite are from the common species *Membranipora membranacea*. Mean Mg content in this suborder is 7.4 wt.% $MgCO_3$ (Table 1). Suborder Scrupariina (Upper Cretaceous to Recent) is represented by only one of its three families. All three specimens are composed of intermediate-Mg calcite (mean = 6.0 wt.% $MgCO_3$).

By far the most mineralogically variable suborder in the Bryozoa is the Neocheilostomata, (arising in the mid-Cretaceous, the suborder includes the infraorders Flustrina and Ascophora). Mineralogy varies from entirely aragonite to entirely calcite with a wide range of mixtures, mean 65.9 wt.% calcite. Mg content varies from 0 to 13.7, with a mean of 5.7 wt.% $MgCO_3$. This wide range of mineralogies

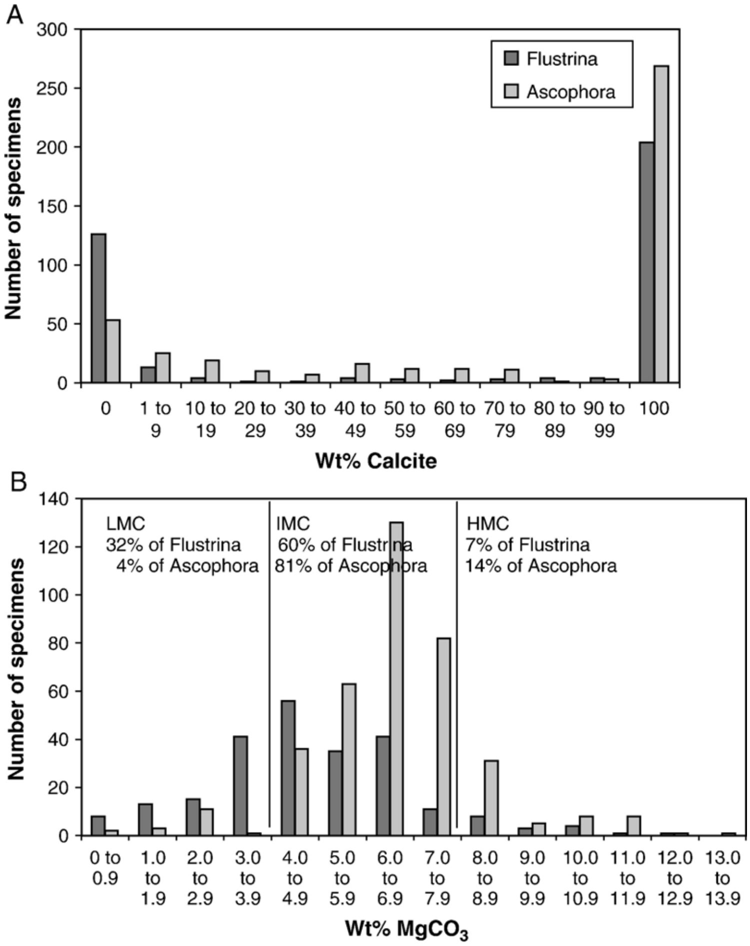

Fig. 5. Frequency distributions of A) calcite content and B) Mg content in the neocheilostomate infraorders Flustrina and Ascophora.

covers 63% of available biomineralogical space, comprising the entire range of mineralogical space occupied by the phylum as a whole.

The infraorder Flustrina (which contains the group formerly known as anascans) is represented in the database by 385 specimens in 108 species, 50 genera, and 22 families. Calcite content varies from 0 to 100, with a mean of 59.6 wt.% calcite (Fig. 5A). It is the aragonitic free-living families (Cupuladriidae, Lunulitidae, Otionellidae) which bring the mean down. Most of the Flustrina are either calcite (55%) or aragonite (34%), but admixtures are rare (only 11% of specimens). Mg content ranges from 0 to 12.7 wt.% $MgCO_3$, with a mean of 4.6 wt.% $MgCO_3$ (Fig. 5B). All cases of dual calcite (dominant low-Mg calcite with subdominant high-Mg calcite) are found in this infraorder (3 species, 2 genera, 2 families). Mineralogical space occupied by the Flustrina is 58% of biomineralogically available space (Fig. 5).

Infraorder Ascophora is represented by 494 specimens in 186 species, 92 genera and 41 families. Calcite content is higher than in the Flustrina (mean = 70.7) but the range is just as great. While calcite specimens are the majority in this group (61%), specimens with mixed mineralogy (26%) outnumber entirely aragonitic ones (12%) (Fig. 5A). Mg content ranges from 0 to 13.7 wt.% $MgCO_3$, with a mean of 6.3 wt.% $MgCO_3$ (Fig. 5B). The biomineralogical space occupied by this group is the same as that occupied by the phylum, 63%.

Mineralogical variation in the higher bryozoan taxa can be low (as in most fossil taxa) or very high (particularly in the relatively young suborder Neocheilostomina). Younger taxa appear to contain the greatest variability, particularly in calcite:aragonite ratio (Fig. 6). Variation in wt.% calcite does not necessarily co-vary with variation in Mg content (Fig. 2). The suborder Malacostega, for example, has the highest range of wt.% $MgCO_3$ among suborders, but a very low variability in % calcite. With a wide degree of variation in the higher taxa, and a great deal of variability in its extent, the degree of consistency within lower taxa becomes relevant.

4.4. Families

In all we have collated data for 101 families within the phylum Bryozoa (Table 2). Many of the families are represented by only one or two species, though some include as many as 23 species. While some families comprise only a single specimen, and are thus of limited use, the mean number of specimens per family is 11, and the maximum is 120, allowing some generalizations to be made. Coverage of known genera within families ranges from 3% to 100% (Table 2).

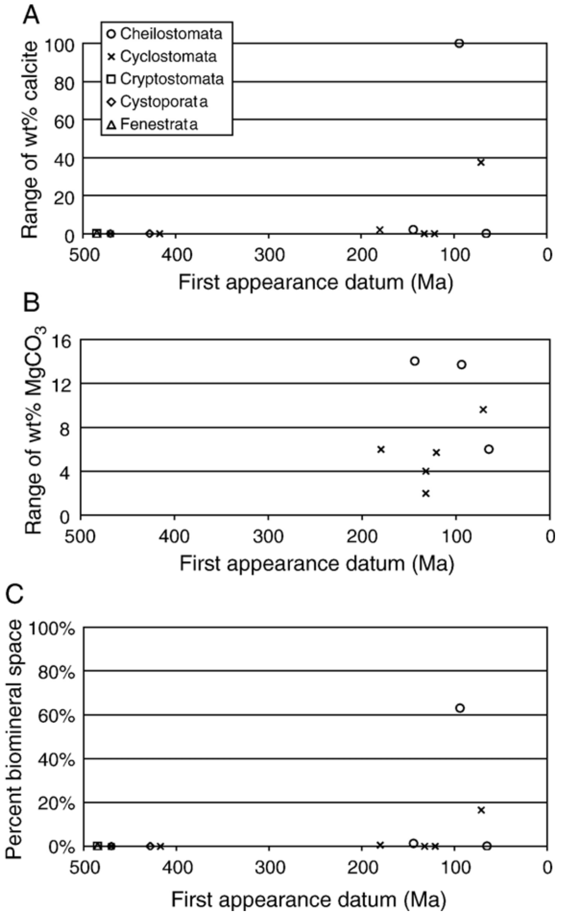

Fig. 6. Degree of mineralogical variation in suborders of the Bryozoa related to time of first appearance. Suborders without numerical mineralogical data are omitted. In range of A) calcite content, B) range of Mg content, and C) percent of available biomineralogical space, variation is greater in younger taxa.

Bryozoan families fall into three rather amorphous overlapping groups (Fig. 7). A few families (5%) are mostly aragonite, with Mg contents ranging from 2 to 6 wt.% $MgCO_3$. More families (20%) are of variable mixed mineralogy, with wt.% calcite ranging from 20% to just under 100%, and mostly intermediate Mg content. Most families (75%) are low- to intermediate-Mg calcite-dominated, with a few as high as 10 wt.% $MgCO_3$ in calcite.

Some families are consistent in their mineralogy, with little or no variation. Among them are the low-Mg calcite families Crisiidae (*n* = 8), Mecynoeciidae (*n* = 5), and Theonidae (*n* = 27). Intermediate-Mg calcite is precipitated by bryozoans in the families Beaniidae (*n* = 4), Diastoporidae (*n* = 5), Electridae (*n* = 5), Porinidae (*n* = 7), and Umbonulidae (*n* = 5). The Catenicellidae (*n* = 4) and Myrioporidae (*n* = 5) precipitate high-Mg calcite.

Table 2
Mineralogical characteristics of 101 bryozoan families

Family	Genera	Species	Specimens	Overall mineralogy	Mean wt.% calcite	Mean wt.% MgCO3	Range wt.% Calcite	Range wt.% MgCO$_3$	Biomin space %	FAD stage	Age at top (Ma)	Total genera	Coverage of genera
Adeonellidae	1	2	3	Calc dom mix	98.0	6.3				Priabonian	33.7	2	50
Adeonidae*	3	8	46	Arag dom mix	6.8	2.8	59.0	8.0	22	Ypresian	49.0	14	21
Anolotichiidae**	1	1	1	Calcite	100.0					Arenigian	470.0	7	
Antroporidae	1	1	1	Calcite	100.0	10.0				Maastrichtian	65.0		
Arachnopusiidae*	2	5	15	IMC, some A	86.0	5.3	63.0	3.0	9	Santonian	83.5	9	22
Beaniidae	1	3	4	IMC	100.0	5.5	0.0	2.3	0	Bartonian	37.0	2	50
Biporidae	2	3	4	Calc dom mix	83.0	4.2	50.0	0.3	1	Ypresian	49.0	8	25
Bitectiporidae*	6	12	35	Calc arag mix	59.3	7.2	100.0	6.8	31	Ypresian	49.0	13	46
Bryocryptellidae	3	6	8	HMC	100.0	6.2	0.0	4.0	0	Ypresian	49.0	13	23
Bugulidae	4	12	15	Calcite	100.0	6.0	0.0	8.0	0	Recent	0.0	29	14
Calescharidae	3	3	11	C or A or mix	51.6	4.5	100.0	7.6	35	Burdigalian	16.4	3	100
Calloporidae	6	9	34	Calc Arag mix	61.1	6.5	96.0	8.3	37	Albian	99.0	76	8
Calwelliidae	1	1	1	Calcite	100.0	7.0				Recent	0.0	7	14
Candidae	5	16	22	Calcite	99.1	4.9	20.0	3.3	3	Maastrichtian	65.0	26	19
Catenicellidae	3	3	4	Calcite	100.0	7.6	0.0	4.0	0	Maastrichtian	65.0	28	11
Cellariidae*	2	10	49	Calcite (often dual)	100.0	3.2	0.0	11.4***	0	Santonian	83.5	25	8
Celleporidae	8	17	92	Calcite	97.8	6.4	87.0	4.2	17	Priabonian	33.7	20	40
Ceramoporidae**	1	1	1	Calcite	100.0					Llandeilian	458.0	10	10
Cerioporidae*	2	2	2	Calcite	100.0					Toarcian	180.0		
Chaperiidae	2	3	9	Calc-dom mix	73.6	5.0	89.2	3.0	12	Maastrichtian	65.0	13	15
Chorizoporidae	1	1	1	Calcite	100.0	5.9				Serravallian	11.2	1	100
Cinctiporidae	1	1	32	Calcite, some A	98.2	0.7	37.6	3.7	6	Maastrichtian	65.0		
Constellariidae**	1	1	1	Calcite	100.0					Llandeilian	458.0	2	
Corynotrypidae**	1	1	1	Calcite	100.0					Arenigian	470.0		
Cribrilinidae	4	5	7	Calcite	100.0	6.9	0.0	4.5	0	Cenomanian	93.5	108	4
Crisiidae	4	7	8	Calcite	100.0	3.0	0.0	2.2	0	Maastrichtian	65.0	8	
Cryptosulidae	1	2	15	Calcite, some A	93.7	5.3	50.0	2.2	5	Tortonian	7.1	2	50
Cupuladriidae*	2	4	9	Arag, some C	2.0	2.0	11.0	4.0	2	Thanetian	54.8	5	40
Cystodictyonidae**	1	1	1	Calcite	100.0					Givetian	370.0	11	
Densiporidae	1	1	1	Calcite, some A	98.0	6.5				Bajocian	169.0		
Dianulitidae**	1	1	1	Calcite	100.0					Arenigian	470.0		
Diaperoeciidae*	5	10	35	Calcite	100.0	2.8	0.0	9.6	0	Hauterivian	127.0	9	
Diastoporidae	3	3	5	Calcite	100.0	5.7	0.0	1.3	0	Pliensbachian	190.0	29	
Electridae*	2	5	5	Calcite	100.0	5.7	0.0	1.7	0	Oxfordian	155.0	22	9
Escharoporidae**	1	1	1	Calcite	100.0					Llandeilian	458.0	6	
Eucrateidae	1	2	3	Calcite	100.0	4.5	0.0	4.0	0	Recent	0.0	1	100
Euthyroididae	1	2	2	Calc dom mix	74.8	8.2	50.5	0.3	1	Recent	0.0	1	100
Exechonellidae	1	1	1	Calc dom mix						Lutetian	41.0	5	20
Fenestellidae**	1	1	1	Calcite	100.0					Caradocian	449.0	30	3

(continued on next page)

Table 2 (*continued*)

Family	Genera	Species	Specimens	Overall mineralogy	Mean wt.% calcite	Mean wt.% MgCO3	Range wt.% Calcite	Range wt.% $MgCO_3$	Biomin space %	FAD stage	Age at top (Ma)	Total genera	Coverage of genera
Fistuliporidae**	1	1	1	Calcite	100.0					Ashgillian	443.0	29	
Flustridae	7	10	15	Calcite	100.0	5.2	0.0	6.0	0	Recent	0.0	14	50
Frondiporidae	2	2	4	Calcite	100.0	3.8	0.0	5.8	0	Bathonian	164.0	7	29
Gigantoporidae	1	4	6	Arag-dom mix	28.6	4.2	86.2	5.0	20	Priabonian	33.7	7	14
Halloporidae**	1	1	1	Calcite	100.0					Arenigian	470.0	5	20
Heliodomidae	1	2	3	Calcite	66.7	6.3	100.0	0.0	0	Danian	61.0	2	50
Heteroporidae*	2	4	11	Calcite, some A	99.6	2.5	1.0	3.5	0	Toarcian	180.0	23	9
Heterotrypidae**	1	1	1	Calcite	100.0					Llanvirnian	464.0	11	9
Hippopodinidae	1	2	2	Calcite	100.0	6.0	0.0	4.0	0	Priabonian	33.7	4	25
Hippoporidridae*	3	4	5	Arag dom mix	45.6	7.7	100.0	2.0	9%	Priabonian	33.7	4	75
Hippothoidae	2	2	6	Calcite	100.0	3.0	100.0	7.0	32	Coniacian	85.8	9	22
Horneridae	2	6	51	Calcite	100.0	1.8	0.0	5.7	0	Barremian	121.0	2	100
Lacernidae	1	1	2	Calcite	100.0	6.3	0.0	0.0	0	Priabonian	33.7	10	10
Lanceoporidae	1	1	4	Aragonite	0.0		0.0		0	Priabonian	33.7	3	
Leioclemidae**	1	1	1	Calcite	100.0								
Lekythoporidae	1	1	1	Calcite	100.0	6.3				Chattian	23.8	8	13
Lepraliellidae*	1	9	19	Calc dom mix	65.4	5.7	100.0	5.0	23	Santonian	83.5	18	6
Lichenoporidae	2	4	12	Calcite	100.0	4.6	0.0	4.7	0	Cenomanian	93.5	13	
Lunulariidae	1	1	1	Calcite, some A	60.0	6.0				Burdigalian	16.4	1	
Lunulitidae*	3	8	10	Arag dom mix	50.0	6.0	5.0	4.0	1%	Santonian	83.5	6	17
Macroporidae	1	1	1	Calcite (often dual)	100.0	2.3				Thanetian	54.8	3	33
Mamilloporidae*	1	1	3	Aragonite	0.0		0.0			Ypresian	49.0	2	50
Margarettidae	1	2	8	Calc dom mix	68.3	8.0	88.0	1.5	6	Ypresian	49.0	1	100
Mecynoeciidae	1	2	5	Calcite	100.0	3.0	0.0	1.5	0%	Aalenian	176.0		
Membraniporidae	3	8	19	Calcite, some A	94.4	7.8	100.0	12.0	55	Priabonian	33.7	3	100
Mesotrypidae**	1	1	1	Calcite	100.0					Llanvirnian	464.0		
Metrarabdotosidae	1	3	16	Calc dom mix	79.5	5.6	52.0	4.0	10	Priabonian	33.7	6	17
Microporellidae	3	7	8	Calcite, some A	90.6	5.2	47.0	5.2	11	Aquitanian	20.5	9	33
Microporidae*	5	5	17	Calc dom mix	86.2	6.2	96.0	5.0	22	Cenomanian	93.5	29	17
Monticuliporidae**	1	1	1	Calcite	100.0					Llanvirnian	464.0	13	8
Myriaporidae	1	3	5	Calcite, some A	100.0	6.7	0.0	3.5	0	Priabonian	33.7	4	25
Onychocellidae	1	1	4	Calcite	100.0	8.5	0.0	0.0	0	Cenomanian	93.5	24	4

Otionellidae	1	5	120	Arag, some C	1.4	1.6	100.0	8.3	38	Rupelian	28.5	5	20
Pasytheidae	2	3	3	Mixed	40.0	6.5	100.0	3.0	14	Ypresian	49.0	6	33
Petraliellidae*	2	5	6	Calcite, some A	95.0	6.0	10.0	4.0	2	Ypresian	49.0	9	22
Petraliidae	1	2	3	Calcite	92.2	7.4				Recent	0.0	1	100
Phidoloporidae*	10	25	63	Calcite, some A	92.2	7.7	100.0	12.7	58	Danian	61.0	24	42
Phylloporinidae**	1	1	1	Calcite	100.0					Llandeilian	458.0	11	9
Plagioeciidae	1	1	1	Calcite	100.0					Pliensbachian	190.0	12	8
Polyporidae**	1	1	1	Calcite	100.0								
Porinidae	2	2	7	Calcite, some A	99.9	6.6	0.0	1.6	0	Ypresian	49.0	7	29
Quadricellariidae	1	1	1	Calcite	100.0	10.0				Cenomanian	93.5	6	17
Rhinidictyidae**	1	1	1	Calcite	100.0					Llanvirnian	464.0	11	9
Rhomboporidae**	1	1	1	Calcite	100.0					Eifelian	380.0	6	
Romancheinidae	3	8	10	Calc dom mix	61.3	7.5	52.0	7.0	17	Campanian	71.3	32	9
Sagenellidae**	1	1	1	Calcite	100.0					Caradocian	449.0		
Schizoporellidae*	3	9	54	Calc Arag mix	54.1	5.7	100.0	7.0	32	Ypresian	49.0	6	50
Sclerodomidae	1	1	1	Calcite	100.0	5.0				Piacenzian	1.8	4	25
Selenariidae	1	1	2	Aragonite	0.0		0.0		0	Burdigalian	16.4	1	100
Setosellidae	1	1	1	Aragonite	0.0					Thanetian	54.8	1	100
Smittinidae*	4	8	11	Arag, some C	5.4	6.0	26.0	4.0	5	Ypresian	49.0	25	16
Steginoporellidae	2	7	77	Calcite, some A	95.6	4.0	100.0	5.0	23	Lutetian	41.3	5	40
Terviidae	1	1	1	Calcite	100.0	1.7				Ypresian	49.0	4	25
Tessaradomidae	1	2	2	Calcite	100.0	5.9				Danian	61.0	1	100
Thalamoporellidae	1	4	5	Calcite, some A	98.6	5.0	7.0	4.0	1	Lutetian	41.3	6	17
Theonoidae	1	2	27	Calcite	100.0	2.8	0.0	2.6	0	Toarcian	180.0	10	10
Trematoporidae**	2	2	2	Calcite	100.0	0.0				Arenician	470.0	14	14
Trypostegidae	1	1	2	Calcite	100.0	8.5	0.0			Santonian	83.5	13	8
Tubuliporidae*	3	11	16	Calcite	100.0	3.9	0.0	4.2	0	Campanian	71.3	25	12
Umbonulidae	4	5	5	Calcite	100.0	6.5	0.0	1.9	0	Lutetian	41.3	6	67
Watersiporidae	2	2	3	Calcite	100.0	2.0				Messinian	5.3	4	50
Minimum	1	1	1		0.0	0.7	0.0	0.0	0		0.0	1	3
Mean	2	4	12		84.4	5.4	36.2	4.3	7		134.5	12	35
Maximum	10	25	120		100.0	10.0	100.0	12.7	58		470.0	108	100

*One or more specimens in the family is fossil.

**Family is extinct.

***Secondary calcite included in calculation.

NOTE: 23 Incertae sedis not included

Range and % minspace not calculated if only one data point.

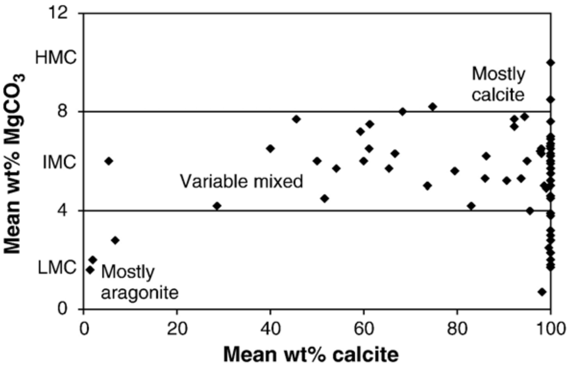

Fig. 7. Mean skeletal carbonate mineralogy of 101 bryozoan families.

Another group of families are particularly consistent in their calcite:aragonite ratio even though Mg content is quite variable. The 51 specimens from the Horneridae, for example, are all calcitic, though they range from low to intermediate Mg calcite (0 to 5.7 wt.% $MgCO_3$). Similarly, the Cellariidae specimens range from 0 to 11.4 wt.% $MgCO_3$, but are always calcitic (in some species consisting of a mixture of dominant low-Mg calcite and subdominant high-Mg calcite). In contrast, there are a few families where Mg content varies very little but calcite:aragonite ratio is highly variable, such as the Conescharellinidae ($n=4$), Heliodomidae ($n=3$), Hippoporidridae ($n=5$), and Margarettidae ($n=8$).

In particular, families that are aragonite-dominated appear to show little mineralogical variability. The Cupuladriidae ($n=9$), Mamilloporidae ($n=3$), Otionellidae ($n=119$ if we disregard one very anomalous measurement of *O. squamosa*), Selenariidae ($n=2$), and Setosellidae ($n=1$) are 95 to 100% aragonite. Interestingly, all these families are flustrinid cheilostomes. Two ascophoran cheilostome families, Lanceoporidae and Cleidochasmatidae, appear to have a similar aragonitic mineralogy, but in each case only one species has been studied.

The most variable family studied here is the Phidoloporidae (58% of biomineral space, $n=63$), closely followed by the Membraniporidae (55% minspace, $n=22$). Both families arose during the post-Cretaceous radiation of cheilostomes; the Philoporidae first appeared in the Danian (61 Ma), whereas the Membraniporidae appeared in the Priabonian (33.7 Ma). In fact, all bryozoan families that demonstrate some mineralogical variability arose after about 100 Ma (Fig. 8), though some variation in Mg content predates that time.

4.5. Genera and species

Carbonate mineralogy recorded for 203 genera (including two genera for which family is uncertain) shows that 64% of genera are all calcite, 5% are all aragonite, and 31% are mixed to some degree. As with families, many genera have a great deal of internal consistency, but some are extremely variable. For example, *Margaretta barbata* ($n=5$) is all intermediate-Mg calcite; *Margaretta cereoides* ($n=3$) is mostly aragonite, including on average 15% high-Mg calcite. In cases like this, the mean for the genus is neither accurate nor useful. The species, a more consistent measure and also one with biological significance, is a more useful unit for analysis.

Carbonate mineralogy data for 383 bryozoan species are given in the database (see Appendix A). Mineralogical space was calculated only for those with more than 2 specimens, a total of 87 species (Table 3). Among these are species such as *Adeonellopsis* sp. ($n=31$, percent of available biomineral space$=3\%$), which has highly variable Mg content but consistently low calcite content (Fig. 9). Some other aragonitic species are almost always aragonite, with only a few specimens showing a little calcite (such as *Otionellina proberti* $n=37$, minspace$=3\%$). *M. cereoides* is rare in being mainly but never entirely aragonitic, and having consistently high-Mg content ($n=3$, minspace$=0.3\%$). Some all-calcite species, such as *Galeopsis polyporus* ($n=14$, minspace$=0\%$), are not very variable, whereas others such as *Celleporina costazii* ($n=20$, minspace$=6\%$) have a much wider range of Mg content. Species with mixed mineralogy can be widely variable, such as *Schizoporella unicornis* ($n=28$, minspace$=17\%$).

Most species have a range of Mg contents less than 4, such that they are always or nearly always within a single Mg category. *Hornera robusta*, for example, is almost always low-Mg calcite (Fig. 9). Only 14 species have a range of Mg contents greater than 4, the greatest being *Bugula neritina* (range of 6.0 wt.% $MgCO_3$) and *S. unicornis* (range of 7.0 wt.% $MgCO_3$, though the range without an outlier would be 3.6 wt.% $MgCO_3$).

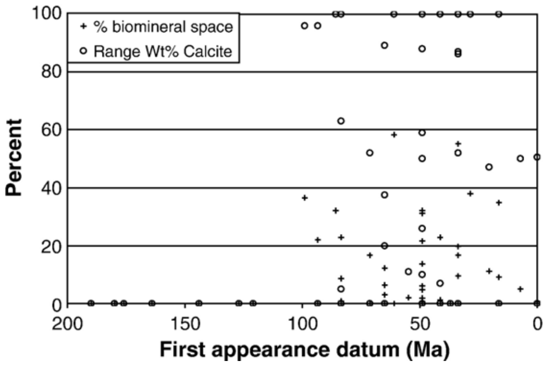

Fig. 8. Skeletal carbonate mineralogy in 101 bryozoan families related to their time of first appearance.

Table 3
Variability in skeletal carbonate mineralogy of 88 bryozoan species with more than 2 specimens studied

				Wt.% Calcite				Wt.% $MgCO_3$				Mineralogical	
Genus	Species	N	Mineralogy*	Mean	Min	Max	Range	Mean	Min	Max	Range	Area	% total
Adeona	grisea	3	A	0.0	0.0	0.0	0.0						
Adeonellopsis	sp.	31	A/A(IMC)/A(HMC)	3.1	0.0	11.3	11.3	6.0	4.0	9.0	5.0	56.5	3
Adeonellopsis	sulcata	4	A/A(tr LMC)	0.0	0.0	1.0	1.0	1.0					
Arachnopusia	unicornis	11	IMC/IMC(A)/A (IMC)	90.1	37.0	100.0		5.3	4.0	7.0	3.0	0.0	0
Biflustra	savartii	4	IMC	100.0				6.0	4.0	8.0	4.0	0.0	0
Bugula	neritina	3	IMC	100.0	100.0	100.0	0.0	7.3	5.0	11.0	6.0	0.0	0
Caleschara	denticulata	5	A/LMC	40.0	0.0	100.0	100.0	0.0	0.0	4.0	4.0	400.0	18
Calpensia	nobilis	7	IMC(A)	81.1	73.0	90.0	17.0	4.3	4.0	5.1	1.1	18.7	1
Cellaria	immersa	25	LMC(HMC)/LMC	100.0	100.0	100.0	0.0	2.1	0.3	4.3	4.0	0.0	0
Cellaria	tenuirostris	5	LMC (HMC)/LMC/ IMC	100.0	100.0	100.0	0.0	2.5	0.5	6.0	5.5	0.0	0
Cellaria	rigida	5	IMC/LMC	100.0	100.0	100.0	0.0	3.7	0.5	4.8	4.3	0.0	0
Cellaria	sp.	3	IMC	100.0				6.3					
Celleporaria	agglutinans	7	IMC	100.0				5.2	4.3	6.3	2.0	0.0	0
Celleporaria	vagans	4	A/A(IMC)/IMC(A)	44.8	0.0	100.0	100.0	6.0	4.0	8.0	4.0	400.0	18
Celleporina	grandis	10	IMC	100.0	100.0	100.0	0.0	5.0	4.0	5.3	1.3	0.0	0
Celleporina	costazii	20	IMC/HMC	98.8	75.8	100.0	24.2	5.9	4.3	10.0	5.7	137.9	6
Chaperia	granulosa	5	A(IMC)/A(LMC)/ IMC/LMC	52.5	10.8	100.0	89.2	4.1	3.7	5.3	1.6	142.7	7
Chaperiopsis	tintinnabula	3	IMC	100.0				6.0	5.7	6.7	1.0	0.0	0
Chiastosella	splendida	6	IMC	100.0	100.0	100.0	0.0	5.7	4.3	6.0	1.7	0.0	0
Cinctipora	elegans	32	LMC	98.2	62.4	100.0	37.6	0.7	0.0	3.7	3.7	139.1	6
Cribrilaria	radiata	3	IMC/HMC	100.0	100.0	100.0	0.0	8.5					
Cryptosula	pallasiana	14	IMC/LMC	93.1	50.0	100.0	50.0	5.3	2.0	6.0	4.0	200.0	9
Cupuladria	canariensis	3	A(tr IMC)	0.0	0.0	0.0	0.0						
Diaperoecia	cf *purpurascens*	21	LMC/IMC	100.0	100.0	100.0	0.0	1.7	0.0	5.0	5.0	0.0	0
Diaperoecia	sp.	5	LMC/IMC	100.0	100.0	100.0	0.0	3.7	2.7	5.7	3.0	0.0	0
Discoporella	umbellata	3	A/A(IMC)	2.3	0.0	4.0	4.0	6.0	4.0	8.0	4.0	16.0	1
Disporella	sp.	6	LMC/IMC	100.0	100.0	100.0	0.0	4.5	2.3	7.0	4.7	0.0	0
Escharina	waiparensis	3	IMC	100.0	100.0	100.0	0.0	6.2	5.7	6.5	0.8	0.0	0
Flustra	foliacea	5	IMC	100.0	100.0	100.0	0.0	4.3	1.2	6.0	4.8	0.0	0
Frondipora	verrucosa	3	IMC/LMC	100.0				3.4	0.2	6.0	5.8	0.0	0
Galeopsis	porcellanicus	28	IMC	100.0	100.0	100.0	0.0	6.4	4.7	8.3	3.6	0.0	0
Galeopsis	polyporus	14	IMC	100.0	100.0	100.0	0.0	7.1	5.3	7.7	2.4	0.0	0
Gigantopora	regularis	3	A(tr LMC)/A(tr IMC)	13.8				4.0	2.0	7.0	5.0	0.0	0
Heteropora	cf *neozelanica*	5	LMC/LMC(A)	100.0	50.0	100.0	50.0	1.0	0.5	1.7	1.2	60.0	3
Heteropora	pelliculata	4	IMC	100.0	100.0	100.0	0.0	3.9	3.5	4.0	0.5	0.0	
Hippellozoon	novaezelandiae	9	IMC	100.0	100.0	100.0	0.0	6.7	6.0	7.3	1.3	0.0	0
Hippomenella	vellicata	11	IMC/IMC(A)	94.5	68.6	100.0	31.4	5.1	4.1	6.0	1.9	59.7	3
Hippoporina	pertusa	3	IMC/A/IMC(A)	43.0	0.0	100.0	100.0	6.2	6.0	6.3	0.3	30.0	1
Hippothoa	hyalina	4	LMC	100.0				2.0	0.0	4.0	4.0	0.0	0
Hornera	robusta	32	LMC/IMC	100.0	100.0	100.0	0.0	1.5	0.0	4.3	4.3	0.0	0
Hornera	striata	6	LMC	100.0	100.0	100.0	0.0	2.3	1.0	4.2	3.2	0.0	0
Hornera	foliacea	3	LMC/IMC	100.0	100.0	100.0	0.0	2.7	1.0	5.7	4.7	0.0	0
Idmidronea	sp.	4	LMC, IMC	100.0	100.0	100.0	0.0	3.5	2.3	4.7	2.4	0.0	0
Idmidronea	atlantica	4	IMC	100.0	100.0	100.0	0.0	5.1	5.0	5.1	0.1	0.0	0
Iodictyum	yaldwyni	10	IMC	100.0	100.0	100.0	0.0	7.1	5.7	8.5	2.8	0.0	0
Jellyella	tuberculata	6	C	100.0	100.0	100.0	0.0	13.0	10.0	14.0	4.0	0.0	0
Lanceopora	reniformis	4	A	0.0	0.0	0.0	0.0						
Mamillopora	cupula	3	A	0.0	0.0	0.0	0.0						
Margaretta	barbata	5	IMC/HMC	100.0	100.0	100.0	0.0	7.8	7.0	8.2	1.2	0.0	0
Margaretta	cereoides	3	A(HMC)	15.3	12.0	22.0	10.0	8.3	7.8	8.5	0.7	7.0	0
Mecynoecia	proboscidea	3	LMC/IMC	100.0	100.0	100.0		3.0	2.5	4.0	1.5	0.0	0
Melicerita	chathamensis	3	HMC/IMC	100.0	100.0	100.0	0.0	7.7	6.7	8.3	1.6	0.0	0

(continued on next page)

Table 3 (*continued*)

				Wt.% Calcite				Wt.% $MgCO_3$				Mineralogical	
Genus	Species	N	Mineralogy*	Mean	Min	Max	Range	Mean	Min	Max	Range	Area	% total
Membranipora	membranacea	4	A, LMC	33.0	0.0	100.0	100.0	2.0					
Menipea	zelandica	3	IMC	100.0	100.0	100.0	0.0	4.7	4.3	5.7	1.4	0.0	0
Metrarabdotos	tenue	7	IMC	100.0	100.0	100.0	0.0	6.0	4.0	8.0	4.0	0.0	0
Metrarabdotos	unguiculatum	8	IMC(A)/A(IMC)	59.0	48.0	75.0	27.0	6.0	4.0	8.0	4.0	108.0	5
Metroperiella	mucronifera	11	IMC/HMC/A(IMC)	94.8	47.7	100.0	52.3	7.6	6.3	8.5	2.2	115.1	5
Microporina	articulata	4	HMC/IMC	100.0	100.0	100.0	0.0	8.0	5.0	9.0	4.0	0.0	0
Mollia	patellaria	3	IMC	100.0	100.0	100.0	0.0	7.2	6.3	7.6	1.3	0.0	0
Myriapora	truncata	3	HMC	100.0	100.0	100.0	0.0	8.5	8.5	8.5	0.0	0.0	0
Nevianipora	sp.	4	LMC	100.0	100.0	100.0	0.0	1.1	0.5	1.3	0.8	0.0	0
Odontionella	cyclops	23	IMC/A(IMC)/IMC (A)	63.3	34.2	100.0	65.8	6.0	4.3	7.5	3.2	210.6	10
Oligotresium	jacksonensis	3	A(IMC)	48.0	45.0	50.0	5.0	6.0	4.0	8.0	4.0	20.0	1
Onychocella	antiqua	4	HMC	100.0	100.0	100.0	0.0	8.5	8.5	8.5	0.0	0.0	0
Otionellina	proberti	37	A/A(IMC)	0.6	0.0	15.0	15.0	2.0	0.0	4.0	4.0	60.0	3
Otionellina	squamosa	20	A/A(IMC)/A(HMC)/ IMC	5.3	0.0	100.0	100.0	6.0	4.0	8.3	4.3	430.0	20
Otionellina	zelandica	35	A/A(LMC)	0.2	0.0	6.0	6.0	0.0					
Otionellina	symmetrica	26	A/A(LMC)	0.5	0.0	14.0	14.0	2.0					
Parasmittina	spathulata	3	A(IMC)/A	6.0	0.0	17.0	17.0	6.0	4.0	8.0	4.0	68.0	3
Patinella	radiata	4	IMC	100.0	100.0	100.0	0.0	5.9	5.9	5.9	0.0	0.0	0
Pentapora	foliacea	7	A(IMC)/C(A)	35.6	12.0	72.0	60.0	5.6	2.7	6.3	3.6	216.0	10
Plagioecia	patina	3	IMC	100.0	100.0	100.0	0.0	6.3	6.3	6.3	0.0	0.0	0
Porella	cervicornis	3	IMC	100.0	100.0	100.0	0.0	6.3	6.3	6.3	0.0	0.0	0
Porina	gracilis	6	IMC	100.0	100.0	100.0	0.0	6.4	6.0	7.9	1.9	0.0	0
Retehornera	foliacea	8	LMC	100.0	100.0	100.0	0.0	1.8	1.4	2.0	0.6	0.0	0
Reteporella	septentrionalis	3	IMC	100.0	100.0	100.0	0.0	6.5	6.3	7.0	0.7	0.0	0
Reteporella	bilaminata	4	HMC	100.0				10.8	10.0	11.0	1.0	0.0	0
Reteporella	lata	11	HMC/HMC(A)	99.8	98.0	100.0	2.0	10.0	8.0	11.0	3.0	6.0	0
Schizomavella	arrogata	4	A(HMC)	2.5	2.0	3.0	1.0	7.9	7.5	8.5	1.0	1.0	0
Schizomavella	auriculata	4	IMC(A)/A(IMC)	32.8	1.0	60.0	59.0	6.7	6.3	7.6	1.3	76.7	4
Schizoporella	unicornis	28	A(IMC)/IMC(A)	43.9	22.0	75.0	53.0	5.7	0.6	7.6	7.0	371.0	17
Steginoporella	perplexa	7	IMC/LMC/LMC(A)/ A(LMC)/A(IMC)	79.5	42.7	100.0	57.3	3.9	2.7	4.7	2.0	114.6	5
Steginoporella	magnifica	16	IMC/LMC/IMC(A)	97.4	58.5	100.0	41.5	4.4	2.3	5.7	3.4	141.1	6
Steginoporella	neozelanica	49	IMC/LMC/A(LMC)	99.0	49.5	100.0	50.5	3.8	2.3	5.3	3.0	151.5	7
Tegella	unicornis	3	IMC/LMC	100.0				4.0	2.0	6.0	4.0	0.0	0
Telopora	buski	26	LMC/IMC	100.0	100.0	100.0	0.0	2.8	0.7	4.3	3.6	0.0	0
Tretosina	flemingi	4	IMC/IMC(A)	89.3	57.1	100.0	42.9	4.9	4.3	6.0	1.7	72.9	3
Turbicellepora	coronopus	5	IMC	100.0	100.0	100.0	0.0	6.1	5.9	6.3	0.4	0.0	0

* A — aragonite, C — calcite, LMC — low-Mg calcite, IMC — intermediate Mg calcite, HMC — high-Mg calcite. Brackets enclose subdominant mineral.

Listed in order of frequency of occurrence in the database.

The greatest mineralogical variability is achieved by species which contain specimens which are entirely aragonitic and entirely calcitic. In the case of *Otionella squamosa* (minspace = 20%), 119 measurements show it to be aragonitic, and there is one all-calcite specimen. It might be reasonable to assume experimental error in this case. In the cases of *Caleschara denticulata* ($n = 5$, minspace = 18%) and *Celleporaria vagans* ($n = 4$, minspace = 18%), there are too few measurements to ascertain the degree of variation with confidence. On the other hand, *Pentapora foliacea* ($n = 7$, minspace = 10%), *Odontionella cyclops* ($n = 23$, minspace = 10%) and *S. unicornis* ($n = 28$, minspace = 17%) are genuinely variable and show great potential for further investigations of controls on mineralogy. No other species show more than 10% mineralogical variation.

5. Discussion

Bryozoans have no single characteristic mineralogy. Some invertebrate taxa do have quite predictable mineralogies: hydrozoan and scleractinian corals are usually

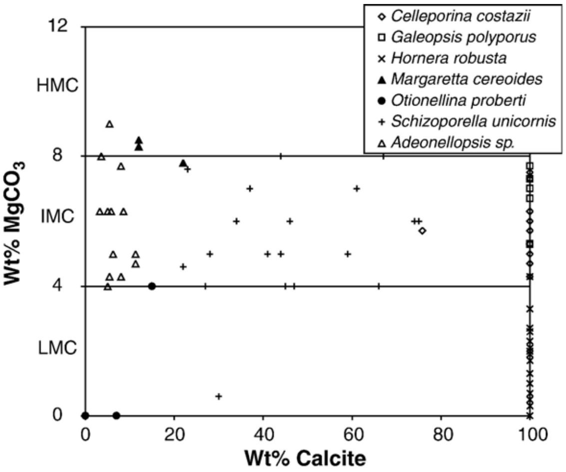

Fig. 9. Skeletal carbonate mineralogy of seven representative bryozoan species.

aragonite; octocorals are usually calcite (Milliman, 1974). Even some of the more phylogenetically advanced phyla, such as echinoderms (almost all high-Mg calcite) show a general consistency in skeletal mineralogy (Milliman, 1974). Groups with more complex mineralogies, such as molluscs or barnacles, have been described as 'active' mineralizers which exert physiological control over skeletal composition (Lowenstam and Weiner, 1989). One theory is that passive mineralizers produce calcium carbonate by nucleation on external templates, whereas active mineralizers calcify through their cellular tissues (Milliman, 1974). Given the complexity and wide range of variability in bryozoan skeletal carbonate, it appears likely that at least some bryozoans are active mineralizers. Typical short summaries of bryozoan mineralogy usually fail to take into account this degree of variation (e.g., Tucker and Wright, 1990).

We have described carbonate mineralogy of the phylum Bryozoa, but 1183 specimens of 383 species is a very small proportion of those available. There are probably some 6000 extant species, of the 20,000 species that once existed (Horowitz and Pachut, 1994). No more than 6% of extant bryozoan species, and 2% of all have been actually tested. The most we can claim is that bryozoans for which carbonate mineralogy has been examined fall in this range, and others may be found which may expand it further.

The influence of phylogenetic position on carbonate mineralogy of invertebrate skeletons is often assumed but not usually investigated. For example, the observation that bivalves are generally aragonite, except for oysters and scallops (Ostreidae and Pectenidae) is commonly made (Lowenstam and Weiner, 1989). This assumption that higher level taxa have consistent mineralogies is not always backed up by further investigation and certainly doesn't apply to all bryozoans (see especially Poluzzi and Sartori, 1973, 1974; Smith et al., 1998). Within a single genus (e.g. *Margaretta*), two species may have distinct mineralogies. In some cases it may even be impossible to cite a single carbonate mineralogy for a given species (see, e.g., *M. membranacea*).

On the other hand, some broad generalizations are possible. Most bryozoan species are either entirely calcitic (about 65%) or entirely aragonitic (about 15%). The remainder, those with mixed mineralogies, can lie anywhere between the two. Most bryozoans secrete intermediate-Mg calcite (mean = 5 wt.% $MgCO_3$), though the range lies between 0 and 14 wt.% $MgCO_3$.

Stenolaemata bryozoans are almost always calcitic, usually of low-Mg calcite. Within the Cyclostomata, only the Rectangulata (one of the younger suborders which arose in the Cretaceous) consistently produces intermediate-Mg calcite. The most variable stenolaemate taxon is also the most recently developed: the Triassic cyclostome suborder Tubuliporina. All the older stenolaemate orders and suborders (mostly arising in the Ordovician) are dominated by low-Mg calcite. Some fossil stenolaemates (e.g. *Nicholsonella*) may have been composed of aragonite (McKinney, 1971; Johnson and Walker, 1986) or high-Mg calcite (Sandberg, 1983a; Taylor and Weedon, 1999), an interpretation based on the diagenetic alteration of their skeletal ultrastructure. The ancestral mineralogy for bryozoans is, however, almost certainly low- to intermediate-Mg calcite with aragonite being more derived (Rucker, 1968; Poluzzi and Sartori, 1975; Boardman and Cheetham, 1987; Borisenko and Gontar, 1997; Taylor and Monks, 1997; Taylor and Schindler, 2004).

Since the Cretaceous, however, bryozoan mineralogy has been expanding its range. The adaptive radiation of gymnolaemate bryozoans through the Paleogene consists of groups which are much more variable, particularly in the Neocheilostomina (both malacostegans and scruparinids are dominated by intermediate-Mg calcite). The infraorder Flustrina contains a number of special mineralogies not found elsewhere: the free-living aragonitic families Otionellidae, Lunulitidae and Cupuladriidae, the genera *Cellaria* and *Macropora* which sometimes produce dual-calcite skeletons, and the unusual high-Mg low-calcite species *M. cereoides*. Species with the highest degree of variability (>10% minspace) are always found in the Neocheilostomina, about equally divided between Ascophora and Flustrina.

Free-living (or vagrant) aragonitic bryozoans are unusual in several ways. They are the only bryozoans that can be considered motile, living as they do on shifting sandy substrates (Greeley, 1969; Rosso, 1996). They form a group of families that are very similar in colonial growth form (shaped rather like a lentil), mineralogy (dominated by aragonite) and lifestyle (motile, shifting substrate). The Selenariidae, Otionellidae, Lunulariidae, Lunulitidae and Cupuladriidae, all part of the infraorder Flustrina, form this group. First appearance data suggest that this lifestyle arose during the late Cretaceous, when the Lunulitidae appeared (this family and its sister family the Lunulariidae have the highest calcite content). The other three families arose during the Palaeogene, with increasing amounts of aragonite the younger they are (Table 4) (see also Haakansson, 1986).

It is tempting to speculate that an abrasive lifestyle among the sand grains requires the use of stronger and denser (but energetically more costly) aragonite for these bryozoans. The trend of increasing aragonite over time may reflect the colonization of high-energy shifting substrates by benthic bryozoans. Alternatively, the development of aragonitic skeletons (probably not in response to sea-water chemistry, see Key et al., submitted for publication) could have allowed the new lifestyle to develop.

Dual-calcite mineralogy is unusual among bryozoans. It has only been found in the flustrinid genera *Cellaria* and *Macropora*. In both cases the dominant calcite is low in Mg content, but the subdominant secondary calcite is among the highest in Mg content within the phylum. Smith et al. (1998) found 21 of 25 specimens of *Cellaria immersa* had secondary calcite ranging from 7 to 11 wt.% $MgCO_3$. Primary calcite was much lower: 0.4 to 4.3 wt.% $MgCO_3$. While they found dual calcite mineralogy in two other species (*C. tenuirostris* and *Macropora grandis*) the sample numbers were very small. Why would a temperate bryozoan colony produce high-Mg calcite (which is more soluble and energetically demanding in cool water than low-Mg calcite)? In the case of *Cellaria*, at least, it is possible that the answer lies in the ontongeny of the flexible articulated colony. Perhaps more-soluble high-Mg calcite is produced at the points along the internodes where new joints will arise. The various calcium carbonate polymorphs are often considered to have little adaptive significance (e.g., Lowenstam and Weiner, 1989, but see Cairns and MacIntyre, 1992). Calcite is less dense, less hard, more stable and has more perfect cleavage than aragonite. Lower density and higher stability makes calcite more economical to produce and allows rapid calcification to occur (Carter, 1980). For colonial organisms that often reproduce asexually through fragmentation (McKinney, 1983), perfect cleavage may also be advantageous, concentrating fractures and allowing larger pieces to result from physical stress (Cairns and MacIntyre, 1992). Why then would a clade evolve to utilize aragonite? Perhaps the increased strength of aragonite is sufficient advantage, or perhaps the difference is insufficient to exert selective pressure and aragonite precipitation is a by-product of some other factor.

Mineralogical diversity within the cheilostomate Bryozoa has been increasing in complexity since at least the Early Cretaceous (see Fig. 8). Stanley and Hardie (1998) argued that a geochemical shift in sea-water chemistry, from a calcite sea to the modern aragonite sea, could have driven this adaptive radiation in cheilostomes: that as sea-water chemistry allowed aragonite precipitation to occur, cheilostomes evolved an increasingly complex mineralogy. Our data do not support this interpretation (see Key et al., submitted for publication). The transition from Calcite II to Aragonite III occurred, according to Stanley and Hardie (1998) about 39 Ma. Cheilostomate mineralogical complexity began to develop about 100 Ma. By the time sea-water had changed enough to have any effect, cheilostomes had been evolving more complex skeletal carbonate for some 60 Ma. A more likely scenario is that mineralogical complexity arose in cheilostomes in conjunction with post-Coniacian evolution of the ascophoran frontal shield, frontal budding, secondary calcification, and robust colony growth (McKinney and Jackson, 1989; Gordon and Voigt, 1996; Gordon, 2000). It is also possible that mineralogical diversification is simply only a by-product of the extensive radiation of this order.

The genus *Margaretta*, as noted before, includes both the high-Mg low-calcite species *M. cereoides* and the

Table 4
Correlation between first appearance datum (FAD) and percent calcite in free-living aragonitic families of the cheilostome infraorder Flustrina

Family	FAD (stage)	FAD (Ma)	Genera	Species	Specimens	Mean wt.% Calcite
Lunulariidae	Burdigalian	16.4	1	1	1	60.0
Selenariidae	Burdigalian	16.4	1	1	2	0.0
Otionellidae	Rupelian	28.5	1	5	119	0.5
Cupuladriidae	Thanetian	54.8	4	4	9	2.0
Lunulitidae	Santonian	83.5	3	8	10	47.0

consistently intermediate-Mg calcite species *M. barbata*. This inconsistency may be an example where mineralogy could provide some utility as a phylogenetic/taxonomic character. It could be advisable to re-consider the congeneric nature of these two species. Within the coral family Stylasteridae, a detailed carbonate mineralogical study showed that mineralogy and phylogeny were closely linked, and reconsideration of relationships based on mineralogy was fruitful (Cairns and MacIntyre, 1992).

Species with the highest degree of variability (>10% minspace) are found in the Neocheilostomina, about equally divided between infraorders Ascophora and Flustrina. The most variable mixed-mineralogy species in the database is *S. unicornis* ($n=28$, wt.% calcite is 22 to 75, wt.% $MgCO_3$ varies from 0.6 to 7.6, minspace = 17%). This degree of variability may be environmentally controlled. Lowenstam's (1954) choice of this species for his study of temperature and calcite:aragonite ratio in Bermuda was extremely felicitous. It is precisely this kind of plastic and variable species (most likely to be found in the Neocheilostomina) that has the greatest potential for environmental correlations with mineralogy, and possibly paleoenvironmental interpretation.

Alternatively, species with high mineralogical variability, such as *S. unicornis* and *B. neritina*, may be excellent candidates for detailed systematic work. Molecular studies of these species could reveal a suite of cryptic species, each with a characteristic mineralogy. Cryptic species have been found in other morphologically-similar bryozoan species such as *Celleporella hyalina* (e.g., Navarrete et al., 2004).

Families, genera and species with low variability, such as those in the Stenolaemata, are good candidates for geochemical work where consistent mineralogy is important, such as stable isotope analysis. The great variability in the phylum Bryozoa does not mean bryozoans have limited potential in geochemical, phylogenetic or environmental analysis of mineralogy. It does mean that with careful choice of study colonies, bryozoans may be ideally suited for all of them.

6. Summary and conclusions

Bryozoans cover a range of skeletal carbonate mineralogy, occupying 63% of the theoretical "space" available to biomineralizers. While only a small proportion of bryozoans living and fossil have been studied (1183 specimens of 387 species), they do allow some phylogenetic patterns to be elucidated. Some higher taxa have consistent mineralogies, particularly among the class Stenolaemata (17% of minspace). Others are extremely variable, particularly within the class Gymnolaemata (63% minspace). Most bryozoans are either entirely calcitic (about 65%) or entirely aragonitic (about 15%). The remainder, those with mixed mineralogies, can lie anywhere between the two. Most bryozoans secrete intermediate-Mg calcite (mean = 5 wt.% $MgCO_3$), though the range lies between 0 and 14 wt.% $MgCO_3$.

Stenolaemata bryozoans almost always precipitate low-Mg calcite. Within the Cyclostomata, only the Rectangulata produce intermediate-Mg calcite. The most variable stenolaemate taxon is the Triassic cyclostome suborder Tubuliporina. All the older stenolaemate orders and suborders (mostly arising in the Ordovician) are dominated by low-Mg calcite, probably the ancestral biomineral of the bryozoans.

In the gymnolaemate suborder Neocheilostomata, however, more variation occurs. The infraorder Flustrina contains a number of special mineralogies not found elsewhere: unusual free-living aragonitic families, dual-calcite skeletons (mainly low-Mg calcite, but with secondary high-Mg calcite), and within-genus mineralogical variability. Families (especially the Membraniporidae and Phidoloporidae) and species with the highest degree of variability (>10% minspace) are found in the Neocheilostomina, about equally divided between Ascophora and Flustrina. Increasing mineralogical complexity over the last 100 Ma appears to coincide with a period of increasing zooidal calcification, but begins 60 Ma earlier than increasing Mg/Ca ratios in seawater.

The most variable species in the database is *S. unicornis*, a plastic and variable species of the type which has potential for environmental correlations with mineralogy, paleoenvironmental interpretation, and possibly molecular investigation for potential cryptic species. Taxa with a high degree of mineralogical variability might well bear taxonomic reconsideration and/or molecular study.

Stenolaemate families, genera and species with low variability, on the other hand, are well-suited for geochemical work such as stable isotope analysis. Variability in the phylum Bryozoa means that they can be useful in geochemical, phylogenetic, and paleoenvironmental analysis of mineralogy, with careful choice of study material.

Acknowledgements

Dr. Paul D. Taylor of the Natural History Museum in London provided some useful first appearance data. Daryl Coup from the Department of Marine Science, University of Otago, assisted with design of the database. The

Department of Geology at Dickinson College graciously provided support and space to the senior author. Thanks to Anna Wood and two reviewers who commented on and improved the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.earscirev.2006.06.001.

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