

Article

Latitudinal influences on bryozoan calcification through the Paleozoic

Catherine M. Reid* , Patrick N. Wyse Jackson, and Marcus M. Key Jr.

Abstract.—Bryozoans are active non-phototrophic biomineralizers that precipitate their calcareous skeletons in seawater. Carbonate saturation states varied temporally and spatially in Paleozoic oceans, and we used the Bryozoan Skeletal Index (BSI) to investigate whether bryozoan calcification was controlled by seawater chemistry in Paleozoic trepostome and cryptostome bryozoans. Our results show that cryptostome bryozoan genera were influenced by ocean chemistry throughout the Paleozoic and precipitated the most calcite at lower latitudes, where carbonate saturation states are generally higher, and less in mid-latitudes, where carbonate will be relatively undersaturated. Trepostome bryozoan genera show a similar but weaker trend for the Ordovician to Devonian, suggesting that, like the cryptostomes, they were unable to metabolically overcome falling saturation states and simply precipitated less robust skeletons at higher latitudes. Carboniferous to Triassic trepostomes differ, however, and show a trend toward increased calcification at higher latitudes, indicating an ability to overcome unfavorable carbonate saturation states. Analysis of Permian trepostomes at the species level indicates this is most pronounced in the Southern Hemisphere, where calcification is matched by increased feeding capacity. It is proposed that this increased feeding capacity allowed trepostomes to metabolically overcome unfavorable carbonate saturation states. The differing responses of trepostome and cryptostome bryozoans to carbonate saturation states suggest that bryozoans should not be considered as a single group in marine extinctions linked to ocean chemistry changes. Likewise, it would suggest that modern stenolaemate and gymnolaemate bryozoans should be treated separately when considering their response to modern ocean chemistry changes.

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Accepted: 1 August 2022

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Introduction

Marine bryozoans are calcified colonial suspension-feeding invertebrates and have an extensive fossil record through the Paleozoic in both warm and cold marine waters (Taylor and Allison 1998). The first records of non-calcified bryozoans are now known from the Cambrian (Zhang et al. 2021), and all Paleozoic stenolaemate orders (Cryptostomata, Cyclostomata, Cystoporata, Estonioporata, Fenestrata, and Trepostomata) were established by the Early Ordovician (Ma et al. 2014). Almost all Paleozoic stenolaemate bryozoans disappeared during the end-Paleozoic extinction, with the

trepostomes and cystoporates persisting until the Late Triassic (McKinney and Jackson 1991). The cyclostomes were relatively sparse in the Paleozoic but are the only Paleozoic stenolaemate order to survive to the Recent. The gymnolaemate Cheilostomata that dominate modern oceans only appeared in the Jurassic (Taylor 1994).

Bryozoans, like other marine invertebrates with calcareous hard parts, must precipitate their skeletons in seawater. Paleozoic stenolaemate bryozoans had calcitic skeletons (Taylor 2020) and are not known to have hosted photosymbionts (Key et al. 2005). Many

phylogenetically more primitive calcareous organisms, particularly phototrophic ones, are passive calcifiers, and they were influenced by changes in ocean chemistry through the Phanerozoic (Stanley and Hardie 1998, 1999), and bryozoans were initially proposed to be among this passive calcifying group. Paleozoic bryozoans are now known to be active biomineralizers (Taylor and Kuklinski 2011; Key et al. 2022) rather than passive calcifiers and show no response to secular changes in ocean calcite-aragonite chemistry. Bryozoans, however, must still accommodate biomineralization issues associated with $p\text{CO}_2$ fluctuations and temperature-controlled changes in marine carbonate saturation state and the availability of skeleton-building ions (James and Jones 2015). Modern bryozoan growth rates are usually higher during warmer months in areas with higher seasonal temperature variation (Lombardi et al. 2006), and some produce distinct growth checks in colder months (e.g., Patzgold et al. 1987; Barnes 1995; Key et al. 2018) linked to seasonal food availability (Brey et al. 1998; Smith 2007). Cenozoic gymnolaemate bryozoans may have calcite, aragonite or bimineralic skeletons, and the occurrence of aragonite and bimineralic forms increases markedly toward the tropics (Taylor et al. 2009). Additionally, in modern bimineralic bryozoans, the proportion of calcite to aragonite skeleton precipitated by the zooid varies seasonally (Lombardi et al. 2008), indicating bryozoans are responding to saturation states. Therefore, it might be expected that Paleozoic bryozoans should have larger or more robust skeletons in warmer lower-latitude waters and would be smaller or less robust in colder water at higher latitudes in response to the decreased saturation state with increasing latitude. Following on from Taylor and Kuklinski's (2011) and Key et al.'s (2022) finding that bryozoans are active and not passive biomineralizers, this paper investigates the influence of paleolatitude on the calcification of selected Paleozoic stenolaemates (Trepotomata and Cryptostomata) and the potential difficulty of calcium carbonate precipitation in these bryozoans driven by oceanographic variation in carbonate saturation state. As carbonate saturation state cannot be directly measured from the fossil record, we use paleolatitude as a proxy.

Materials and Methods

The Bryozoan Skeletal Index (BSI) of Wyse Jackson et al. (2020) was used as proxy for the degree of calcification in bryozoans. Skeletal parameters gathered for trepostome and cryptostome colonies were mean autozoecial aperture diameter (MZD; mean diameter for circular apertures, and mean of minimum and maximum dimensions for oval apertures), exozone width (EW), and zoecial wall thickness in exozone (ZWT). The width of the zoarium (or thickness) (ZOW) was also recorded where available. The BSI measures the relative proportion of skeletal carbonate to intra-zoarial void space in stenolaemate bryozoan colonies (Fig. 1) and is calculated using the following equation:

$$\text{BSI} = [(\text{EW} \times \text{ZWT})/\text{MZD}] \times 100 \quad (1)$$

The multiplication factor of $\times 100$ ensures that BSI is a whole number. Higher numbers represent higher levels of calcification.

Data were gathered from the literature for all genera globally of the stenolaemate bryozoan orders Trepotomata and Cryptostomata from the Lower Ordovician to the Upper Triassic. Data were primarily gathered from original type species descriptions; however, where original descriptions did not include all required parameters, additional data were gathered from published works on the same species in the same location, unit, or age. Where possible, skeletal data were gathered from published data tables, but where numeric values were not available, we measured directly from published photomicrographs. For all species for which data were collected, relative age of the collection horizon was recorded and a numerical age derived from the updated International Commission of Stratigraphy chronostratigraphic chart (Cohen et al. 2013). Data were gathered for all colony morphologies; however, the BSI calculation strongly favors massive and encrusting forms that may have multilayered sheets. As cryptostomes have primarily ramose forms, only ramose forms were analyzed when comparing Ordovician to Triassic trepostome and cryptostome genera.

An additional dataset was gathered for 119 Permian trepostome bryozoan species to

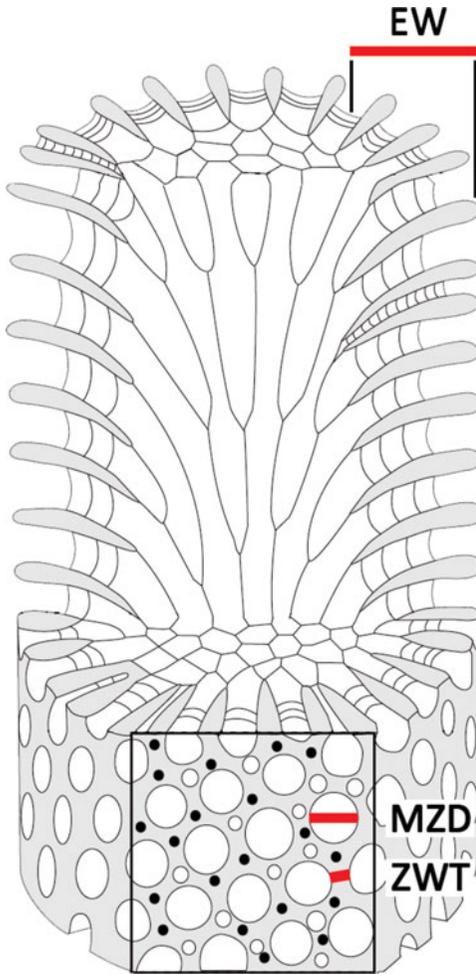


FIGURE 1. Morphological characters used to derive the Bryozoan Skeletal Index (BSI) on a ramose zoarium. From Wyse Jackson et al. (2020: fig. 2). Abbreviations: EW, exozone width; MZD, autozoecial aperture diameter; ZWT, zoecial wall thickness.

investigate the distribution of bryozoans from low to high paleolatitudes. Species recorded in more than one sedimentary basin were entered as data points for each basin where location-specific measurements were available. Where multiple colony morphologies were recorded, ramose colonies took precedence as the primary classification, followed in descending preference by encrusting, massive, and foliose colonies.

The same BSI parameters for all available trespustome bryozoan species were gathered from each depositional basin and were not restricted to type species occurrences. Permian Southern

Hemisphere basins and locations included eastern Australia (Tasmania, Sydney, and Bowen Basins) (Crockford 1941, 1943, 1945; Wass 1968; Reid 2001, 2003; Morozova 2004), Western Australia (Crockford 1957), Timor (Bassler 1929), and southern Thailand (Sakagami 1968, 1970, 1973, 1975, 1999). Permian Northern Hemisphere basins and locations included Novaya Zemlya and the Russian Arctic (Morozova and Krutchinina 1986), data in Morozova (1970), Spitsbergen and Arctic Canada (Nakrem 1994; Key et al. 2001; Ernst and Nakrem 2007; Nakrem et al. 2009), Primorsky Krai and Khabarovsk Krai (Romanchuk 1967; Romanchuk and Kiseleva 1968; Kiseleva 1982), and Nevada, U.S.A. (Gilmour 1962, 2014; Gilmour and Snyder 1986, 2000; Gilmour et al. 1997).

Paleolatitude for all species occurrence locations was determined to the nearest 5 Myr age interval. For stable craton locations, the online interactive tool of van Hindsbergen et al. (2015) was used. For early and mid-Paleozoic Iapetus and Rheic Ocean terranes and blocks, the paleogeographic maps of Scotese (2001), Golonka et al. (2003), and Golonka and Gawęda (2012) were assessed, and a latitude was determined from van Hindsbergen et al. (2015) for the nearest relevant stable craton. For exotic Tethyan and Panthalassa terranes of the late Paleozoic, paleolatitudes were estimated from Jadoul et al. (1990), Scotese (2001), Shi (2006), Adams et al. (2007), Brayard et al. (2009), and Metcalfe (2013).

Statistical Analyses.—Data were managed, BSI values calculated, graphs plotted, and summary statistics (mean, r^2) derived in Excel. Normal distribution tests (Anderson-Darling) and correlation coefficients were performed in PAST v. 4.03 (Hammer et al. 2001). A Pearson's correlation test was performed for data with a normal distribution; the nonparametric Spearman's r_s was applied for data with a nonnormal distribution.

Results

In total, BSI and paleolatitude data were gathered on type species of 184 genera of Trespustomata (125 exhibiting ramose colony form) and 63 genera of Cryptostomata (all ramose) from the Ordovician to Triassic

(Supplementary Table 1). Data for an additional 119 trepostome (all colony forms) species from the Permian were also gathered (Supplementary Table 2).

Trepostomata.—The BSI values for the 184 foliose, ramose, massive, and encrusting trepostome type species range from 3.0 to 210.7 over the Tremadocian (Lower Ordovician) to Norian (Upper Triassic). Paleolatitudes for trepostome type species range from 50°N to 74.5°S. When plotted against normalized paleolatitude, BSI values show no clear trend, either as a group or when considered by morphological form (Fig. 2A). The most common zoarial habit of the Trepostomata is ramose ($N=125$), and the BSI in this group also shows no statistically significant response to paleolatitude ($r_s = -0.104$, $p > 0.05$) (Fig. 2B).

For Ordovician to Devonian ramose taxa, there is a visible trend of highest BSI values at lower latitudes (Fig. 3A,C), however, this trend is not statistically significant, as low BSI

values also occur at all latitudes. When BSI values are compared for each geologic period (Fig. 4A), weak trends of larger BSI at lower latitudes are apparent for the Ordovician and Devonian, with a slightly stronger relationship ($r_s = -0.670$, $p < 0.05$) for the Silurian, although over fewer genera. In contrast, the BSI values for Carboniferous to Triassic taxa are highest at higher latitudes (Fig. 3A,C), but again this is not statistically significant, as low BSI values also occur at all latitudes. When each period is assessed separately (Fig. 4B), all show weak positive correlation for higher BSI values at higher latitudes, with Permian taxa showing the strongest correlation ($r_s = 0.200$) with marginal statistical significance ($p > 0.05$) (Fig. 4B). Permian trepostomes are considered in more detail in “Permian Trepostome BSI Parameters.”

Cryptostomata.—BSI values range from 0.5 to 179.4 for the 82 ramose cryptostome genera from the Sandbian (Upper Ordovician) to

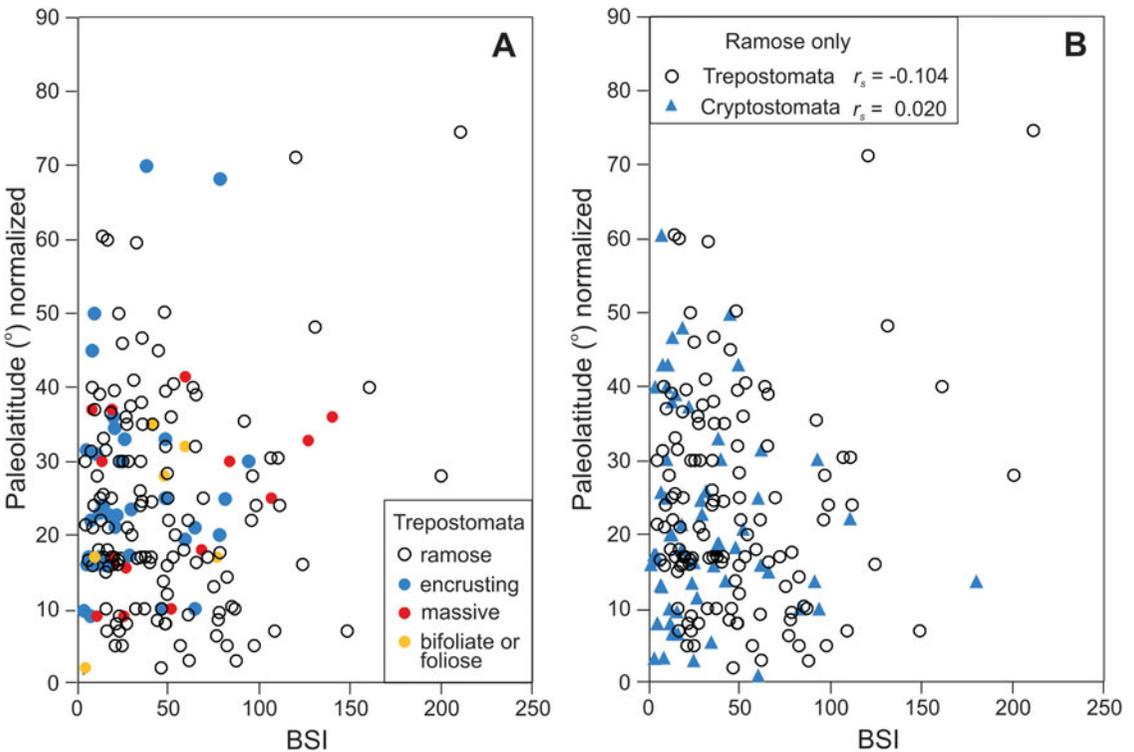


FIGURE 2. Bryozoan Skeletal Index (BSI) plotted against normalized paleolatitude. A, Trepostome genera (Ordovician to Triassic) differentiated by colony form. B, Ramose trepostome genera (Ordovician to Triassic) and cryptostome ramose genera (Ordovician to Permian).

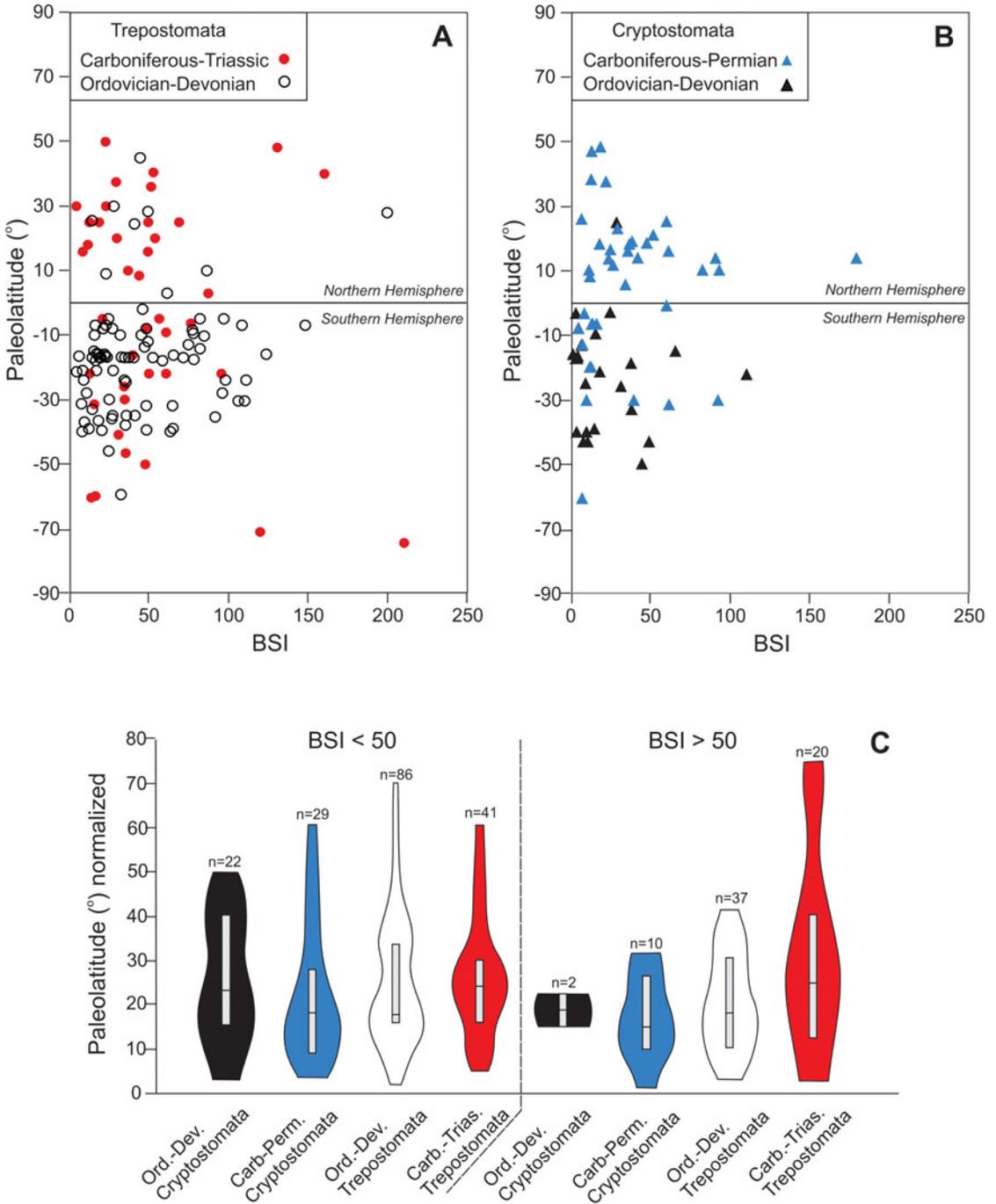


FIGURE 3. Bryozoan Skeletal Index (BSI) for trepostome and cryptostome genera plotted against true paleolatitude. A, Trepostome bryozoans differentiated into Ordovician to Devonian and Carboniferous to Triassic. B, Cryptostome bryozoans differentiated into Ordovician to Devonian and Carboniferous to Permian. C, Violin and box plots showing paleolatitude distribution of Ordovician to Devonian and Carboniferous to Triassic cryptostomes and trepostomes at lower (<50) and higher (>50) BSI values. See color keys in A and B. Boxes show 25th to 75th percentiles, and horizontal bar shows the median.

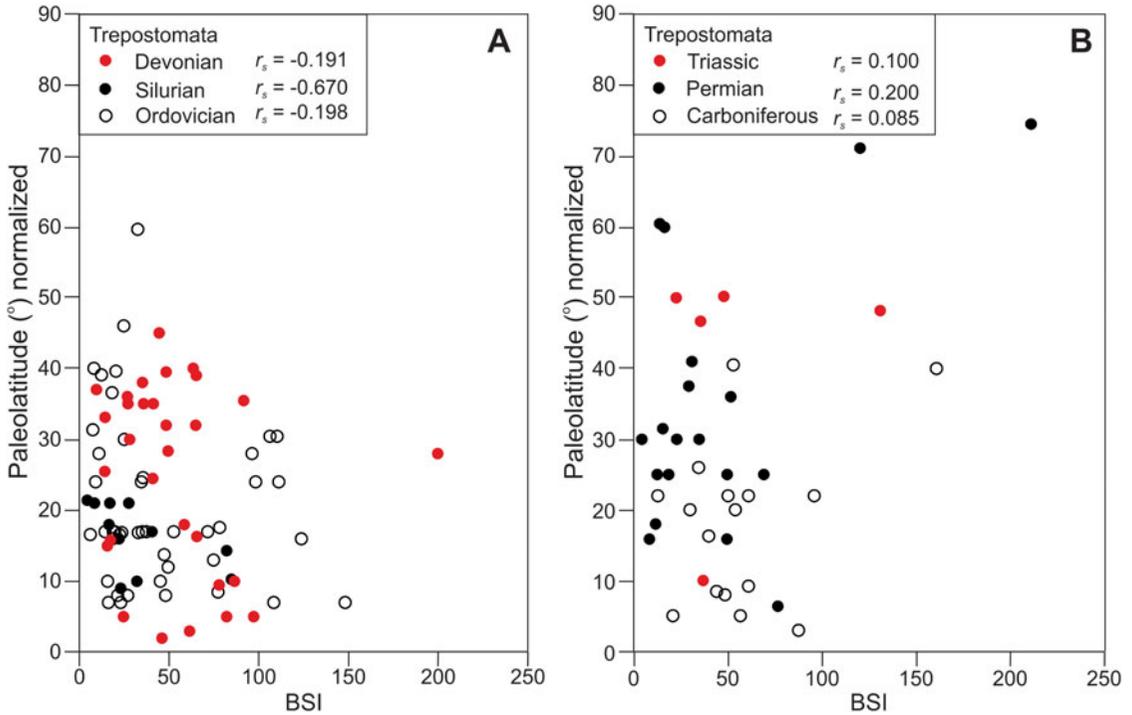


FIGURE 4. Trepostome genera Bryozoan Skeletal Index (BSI) vs. normalized paleolatitude. A, Ordovician to Devonian, differentiated by period. B, Carboniferous to Triassic, differentiated by period.

Wordian (Guadalupian, Permian). The paleolatitudes of type species in 64 locations range between 48°N and 60.5°S. When plotted against normalized paleolatitude, BSI values show a weak but insignificant positive correlation (Fig. 2B). When BSI values are plotted by hemisphere, a distinct peak of higher values at lower latitudes is apparent (Fig. 3B). This distribution is broadly similar in both the Ordovician to Devonian and Carboniferous to Permian, where BSI values <50 are found over a range of paleolatitudes and those >50 are restricted to lower latitudes (Fig. 3C).

Permian Trepostome Species BSI.—In total 98 ramose, 15 encrusting, 5 massive, and 1 foliose-only form were recorded. Plotted against normalized paleolatitude (Fig. 5A) massive forms show a clear positive correlation ($r_s = 0.872$) of increasing BSI at higher latitudes; however, there are few data in this group. The correlations for encrusting and ramose forms are weakly positive ($r_s = 0.231$ and 0.283 , respectively) and significant ($p < 0.001$ and < 0.05 , respectively). When BSI values are

considered by hemisphere (Fig. 5B), the highest values are found in higher southern latitudes (i.e., southern Gondwana), with BSI ranging up to 632 (*Stenopora rugosa* Crockford, 1945) (mean = 90.9, SD = 112.1, $n = 65$). Northern Hemisphere BSI values range up to 195 (*Tabulipora arcturusensis* Gilmour, 1962) (mean = 42.8, SD = 38.8, $n = 54$). A Spearman's correlation test for BSI in Southern Hemisphere shows a weak but significant correlation of increasing BSI with higher southern latitudes ($r_s = 0.313$, $p = 0.01$) (Fig. 5B). The same test for Northern Hemisphere samples shows no correlation ($p > 0.1$).

Permian Trepostome BSI Parameters.—To investigate these high-latitude high BSI values, we assessed which parameters (EW, ZWT, and MZD) used in the BSI equation had the greatest influence on results. For Permian trepostome species, only the BSI parameter ZWT shows a normal distribution (Anderson-Darling $p = > 0.1$), and Pearson's correlation can be applied. Parameters EW and MZD have a nonnormal distribution (Anderson-Darling $p = < 0.001$ for both), and the nonparametric Spearman's

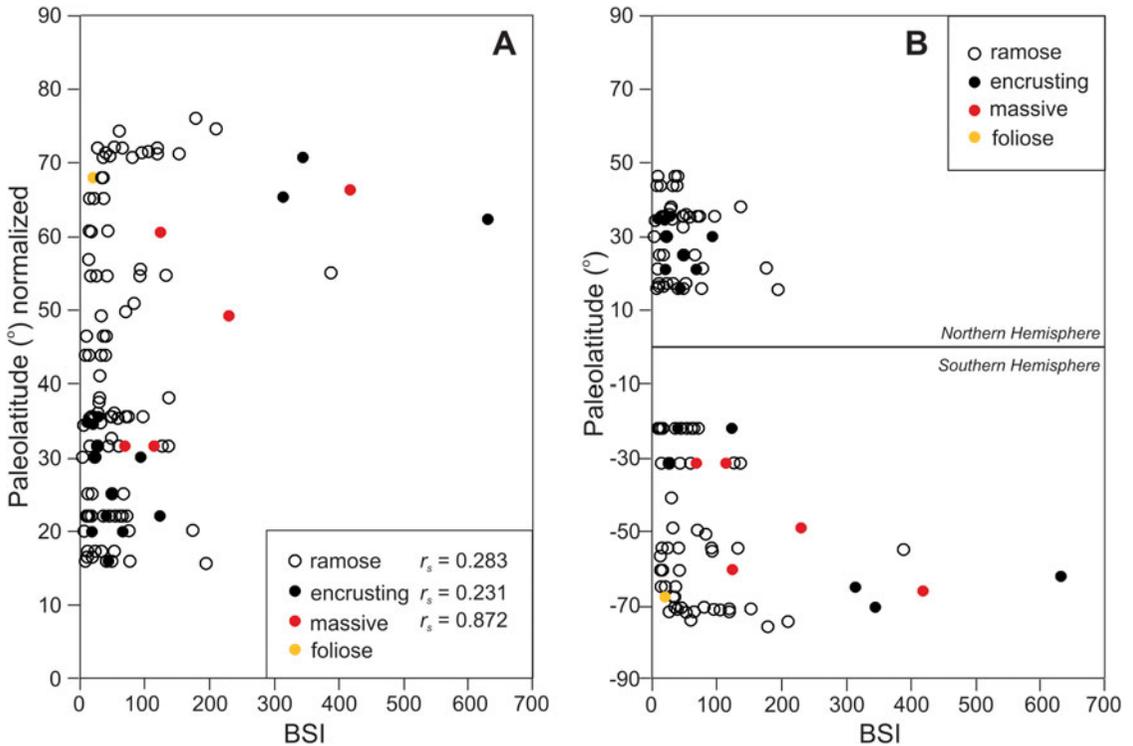


FIGURE 5. Bryozoan Skeletal Index (BSI) for Permian trepostome species. A, Normalized paleolatitude differentiated by colony form. B, Northern and Southern Hemisphere BSI distribution, differentiated by colony form.

correlation must be used. When the control these parameters have on BSI results is considered, exozone width has the strongest control ($r_s = 0.861$, $p < < 0.001$), with thicker exozones resulting in higher BSI values (Fig. 6A). This is also partly reflected by higher BSI values with greater colony thickness (endozone + exozone). Calcite contributed from zooecial walls (ZWT) does not correlate to higher BSI values ($R^2 = 0.011$; Fig. 6B). Autozooecial aperture diameter (MZD), which accounts for space in the BSI calculation, does show a weak positive correlation ($r_s = 0.291$, $p < 0.05$) whereby larger autozooecial apertures are linked to higher BSI values (Fig. 6C). Aperture diameter also increases with increasing southern paleolatitudes ($r_s = -0.472$), but there is no apparent correlation in the Northern Hemisphere ($r_s = 0.032$) (Fig. 6D).

Discussion

The BSI approximates the relative amount of calcium carbonate precipitated within bryozoan colonies. In stable alkaline conditions,

carbonate saturation in seawater and ease of precipitation of calcium carbonate decrease with temperature (and pressure) and thus are relatively lower at higher latitudes (Table 1). If carbonate saturation state influenced the amount of calcite precipitated per colony, it might be expected that there would be higher BSI values at lower paleolatitudes.

Paleozoic Trepostome and Cryptostome Genera.—Trepostome bryozoans when considered over the duration of the Ordovician to Triassic, show no apparent relationship between BSI and paleolatitude (Fig. 2). In other words, the BSI of trepostome taxa does not appear to be uniformly controlled by carbonate saturation state through the Paleozoic, just as trepostome taxa do not respond to calcite-aragonite sea transitions (Key et al. 2022). When examined in more detail, however, earlier Paleozoic forms of the Ordovician to Devonian show, like the cryptostomes, a weak trend of higher BSI at lower latitudes (Figs. 3A,C, 4A). From the Carboniferous to the Triassic there is a trend of higher BSI values or more calcite per

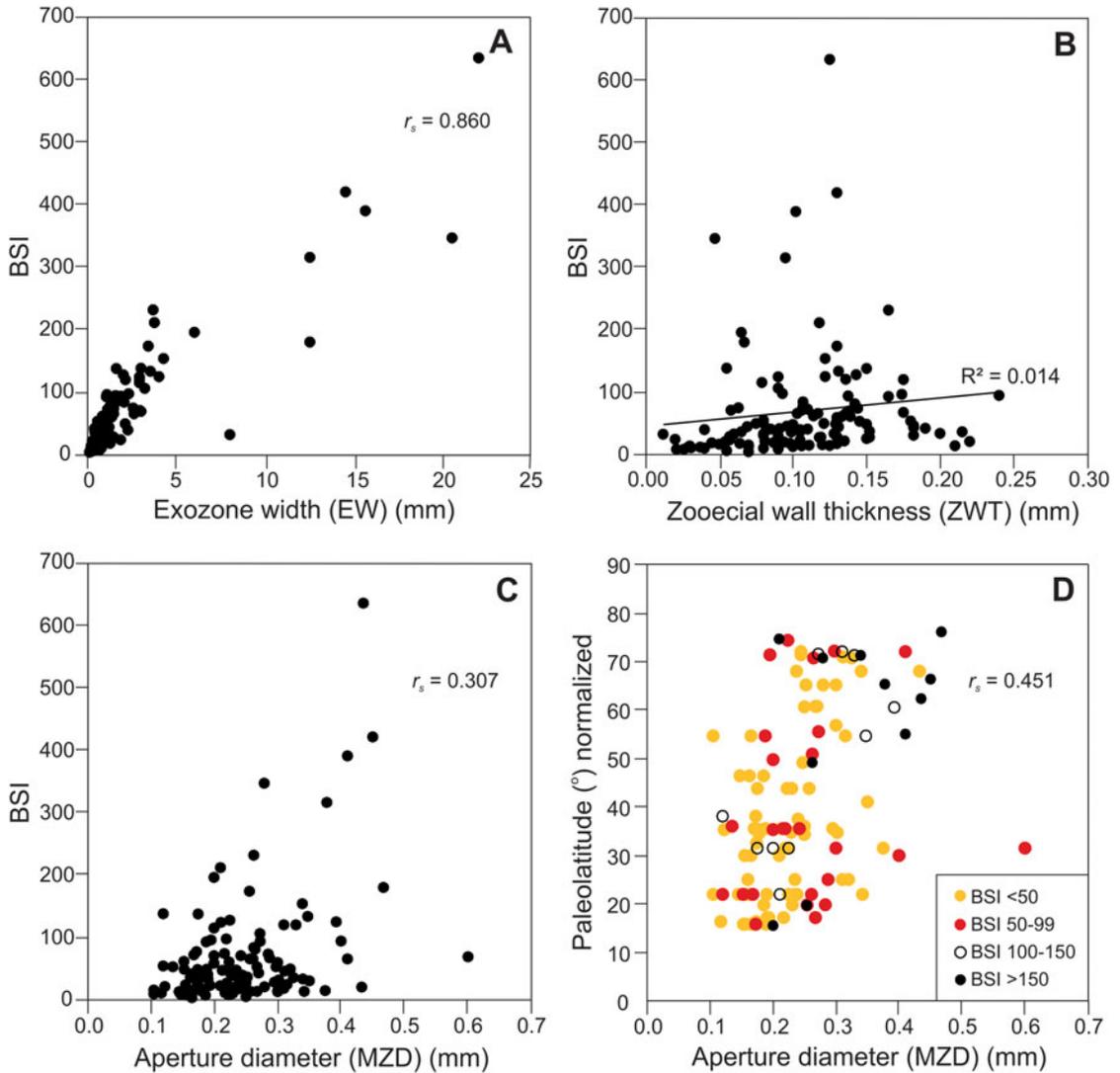


FIGURE 6. Comparison of Bryozoan Skeletal Index (BSI) values to skeletal characters for Permian trepostome species of all colony forms. A, Exozone width (EW) vs. BSI. B, Zooecial wall thickness (ZWT) vs. BSI. C, Mean apertural diameter (MZD) vs. BSI. D, Mean apertural diameter (MZD) vs. normalized paleolatitude, plotted by BSI.

zooid at higher latitudes (Fig. 3C). This trend is weak for the Carboniferous and Triassic, but more pronounced for the Permian (Fig. 4B). In contrast, for cryptostome bryozoans, there is a clear peak of higher BSI values at lower latitudes (Fig. 3B,C), with lower BSI values at mid- and high latitudes. This pattern exists for both earlier Paleozoic (Ordovician to Devonian) and later Paleozoic (Carboniferous to Permian) forms regardless of hemisphere. Based on this observation, cryptostomes appear to have been more responsive to carbonate

saturation state and to have precipitated more robustly calcified zoaria in warmer lower-latitude waters.

In the early Paleozoic, many continental blocks and their sedimentary basins were positioned equatorially (Scotese 2001). It is possible the trend of higher BSI values at lower latitudes may be an artifact of this paleogeography, with fossil records being concentrated equatorially. However, both cryptostome and trepostome taxa do range well into the midlatitudes (30°–60°) in the Ordovician and Devonian,

TABLE 1. Summary of anticipated response of bryozoans to carbonate saturation and observed response according to group and temporal range. BSI, Bryozoan Skeletal Index; Carb-Perm, Carboniferous to Permian; Carb-Trias, Carboniferous to Triassic; Ord-Dev, Ordovician to Devonian; Ord-Perm, Ordovician to Permian; Ord-Trias, Ordovician to Triassic.

Carbonate saturation state proxy	Relative carbonate saturation state	Anticipated response
Low-latitude (warm) bryozoans	High	Easier to precipitate carbonate = higher BSI
High-latitude (cool) bryozoans	Low	More difficult to precipitate carbonate = lower BSI
Observed response		
Dataset	Age range	BSI vs. latitude (carbonate saturation state)
Trepostome genera	Ord-Trias	No apparent relationship (Fig. 2)
Trepostome genera	Ord-Dev	Weak trend of higher BSI at low latitudes (Figs. 3A,C, 4A)
Trepostome genera	Carb-Trias	Weak trend of higher BSI values at higher latitudes (Fig. 3C)
Trepostome genera	Permian	Weak trend of higher BSI values at higher latitudes (Fig. 4B)
Cryptostome genera	Ord-Perm	Distinctly higher BSI values at lower latitudes, with lower BSI values at mid- and high latitudes (Fig. 3B,C)
Cryptostome genera	Ord-Dev	As for Ord-Perm (Fig. 3B,C)
Cryptostome genera	Carb-Perm	As for Ord-Perm (Fig. 3B,C)
Trepostome species	Permian	Clear trend of highest BSI values in southern high latitudes (Fig. 5A,B)

and BSI values are lower (Figs. 3A,B, 4A). With the final amalgamation of Pangea by the late Paleozoic and its north–south orientation, continents and associated sedimentary basins extend into higher latitudes (Scotese 2001). While growth depth is not known for the species used here, they are likely mostly from the upper few hundred meters of bathymetry, and the gradient with respect to carbonate saturation would be weak. Additionally, if depositional depth was the control on BSI, species distribution with respect to paleolatitude should be random.

In the late Paleozoic the trepostomes with higher BSIs, range into higher latitudes; however, cryptostomes do not, and instead maintain a trend of higher BSI at lower latitudes (Table 1). Thus, it would appear that paleolatitude per se is not controlling BSI in bryozoans, but that bryozoans of these two ordinal groups respond to latitudinally driven oceanographic change differently. The Permian has a range of species present across high and low latitudes, especially in Gondwana, and this period is examined in more detail.

Permian Trepostome Species.—Data on individual species were examined for the Permian, with the intention of sampling as wide a latitudinal range as possible. Trepostome species in the Permian Southern Hemisphere have distinctly higher BSI values at higher latitudes

(Fig. 4B, Table 1). Modeled $p\text{CO}_2$ and carbonate saturation state through the Phanerozoic reveal that, in this time interval, Permian carbonate saturation states were very similar to those of modern oceans (Riding and Liang 2005; Berner 2006; Mackenzie and Andersson 2013). At these Permian latitudes (50°S–74°S), carbonate would have been relatively undersaturated with respect to aragonite and calcite, and sedimentologically, these higher southern latitudes record cold-water carbonates (Rogala et al. 2007; James and Lukasik 2010). Therefore, it should be metabolically more challenging to precipitate calcite skeletons at higher latitudes, and it would be expected that Permian trepostomes would be more lightly calcified and thus have lower BSI values.

While there are limited data on carbonate production and direct response to saturation state for modern bryozoans, *Pentapora* colonies are shown produce more carbonate per year in Mediterranean waters (Cocito and Ferdeghini 2001) than in cooler Atlantic waters (Lombardi et al. 2008). Likewise, in the Southern Hemisphere, bryozoan colonies in cool temperate New Zealand waters (Smith et al. 2001) have been shown to produce more carbonate per year than Antarctic bryozoans (Smith 2007). Furthermore, in summer growth bands of *Pentapora*, the weight percent of aragonite was higher than in winter growth periods

(Lombardi et al. 2008), suggesting bryozoans are also responsive to seasonal variation in saturation state of carbonate mineral species. Therefore, the premise that Permian forms should show less skeletal calcite (or lower BSI) at high latitudes is not without basis. So why is BSI higher at high latitudes rather than higher at low latitudes as might be expected?

When investigating the drivers of BSI values in the Permian data, the thickness of the exozone is the strongest predictor of BSI values (Fig. 6A). This is hardly surprising, as the thicker the exozone, the more calcite will be present. Interestingly, although the thickness of the wall arithmetically contributes positively to BSI, there is no correlative relationship (Fig. 6B). Examination of autozoecial aperture diameter (MZD), the parameter that accounts for space in the skeleton, reveals a positive relationship to BSI (Fig. 6C). It might be expected that larger apertures, representing more space in the skeleton, would reduce BSI.

The size of the aperture in modern cheilostome and cyclostome bryozoans is known to be correlated to the size of the mouth and lophophore of the soft-bodied zooid (Winston 1977; Tamberg and Smith 2020; Reid and Tamberg 2021). In turn, the size of the mouth controls the size of food particles that can be ingested (Winston 1977; McKinney and Jackson 1991; Sanderson et al. 2000). Larger lophophores are linked to higher pumping rates (Riisgård and Manriquez 1997), which together would increase the food intake of larger-aperture bryozoans. We speculate that this increased feeding capacity is providing more caloric resources for precipitating more skeletal carbonate. While these polar Permian waters did not show evidence of seasonality in the skeletons (C.M.R. personal observation) common to modern temperate bryozoans, it cannot be discounted that the large aperture had an impact similar to what is reported in modern species, where aperture size increases with spring and autumn nutrient availability, driving zooid growth during these seasons (O'Dea 2005; Key et al. 2018).

As BSI increases with higher southern latitudes so does aperture size (Fig. 6D). This suggests that the correspondingly larger mouth and lophophore size and associated feeding

abilities supported these high-latitude bryozoans to metabolically overcome the challenges of living in seawater undersaturated with respect to calcite and not only continue to precipitate but precipitate skeletons with more calcite. The same trend is not seen in Northern Hemisphere taxa, for which there are only data into the midlatitudes and few taxa have BSI values over 100 (Fig. 5B).

Permian high southern latitude species diversity of bryozoan faunas decreases with increasing latitude, as cystoporates and cryptostomes largely disappear, and the faunas are overwhelmingly composed of trepostomes and fenestrates (Reid and James 2008). In comparison, low-latitude faunas include all orders, as do Northern Hemisphere low and midlatitude faunas of the Sverdrup and Arctic Basins (Reid and James 2010). Thus, the near absence of cystoporates and cryptostomes from southern high-latitude Permian faunas allowed the trepostomes to diversify into this ecospace and take advantage of food resources not previously available to them (Reid and Tamberg 2021). It appears that this access to additional resources and enhanced feeding rates in high latitudes also allowed trepostomes to metabolically mediate the additional challenges of reduced carbonate saturation at these latitudes. But to achieve this they must have been capable of biological mediation of skeletal precipitation in adverse saturation conditions. In modern bryozoans, feeding current speeds (Sanderson and Thorpe 1996) and clearance rates of particles (Menon 1974; Riisgård and Manriquez 1997) increase with temperature, and therefore the larger mouths (apertures) in Permian high-latitude forms may have been a function of the need to increase the range of ingestible food particles to overcome slower rates (cf. Reid and Tamberg 2021) and maintain stable caloric intake. There may be other causes for larger mouth size, such as overall larger polypide size or differing food resources, or the absence of competing cystoporates, as suggested by Reid and Tamberg (2021). It also needs to be asked what benefit trepostome bryozoans gained in precipitating more calcium carbonate given the lower calcite saturation states. Just because they may have had the caloric intake to do so, does not mean they did. It is worth noting

that these southern high latitudes are known for large bryozoan colonies alongside a diverse brachiopod and molluscan fauna (Reid and James 2008) and that the typical algal, sponge, and tabulate coral reef formers of the Permian (Kiesling 2002) are absent at these high latitudes. Unitary brachiopods and mollusks are unable to grow far above the substratum, and in the absence of phototrophic reef-formers, the bryozoans may have been filling this ecospace.

If trepostome bryozoans, as discussed earlier, are capable of biological mediation of calcite precipitation through increased feeding to overcome lowered saturation states, the converse may also be true for the cryptostomes. Perhaps cryptostomes were unable to metabolically mediate calcite precipitation to overcome lower saturation states and were only successful at lower latitudes. The skeletal structure of fenestrate bryozoans does not align well with the BSI calculation and thus cannot be assessed in this way. The vesicular structure of cystoporate bryozoans, which is not usually numerically accounted for in systematic descriptions, also makes them difficult candidates for accurate BSI analysis. However, based on distribution patterns in the Permian Southern Hemisphere, it could be implied that fenestrates, like trepostomes, were also able to biologically mediate calcite precipitation in lower saturation states and that the cystoporates, like the cryptostomes, could not. Whereas it is possible that the ability of trepostomes to biologically overcome lower saturation states at higher latitudes through the Permian contributed to their survival of the end-Permian extinction and associated very low calcite saturation states (Jurikova et al. 2020), this would need to be examined in more detail across all Paleozoic bryozoan groups.

Implications for Modern Bryozoans.—Paleozoic stenolaemate bryozoans appear to have had variable responses and capacity to respond to changing ocean chemistry. If the trepostome bryozoans respond differently than cryptostomes, we should not presume that modern stenolaemate (Cyclostomata) and gymnolaemate (Cheilostomata) behave in a uniform way with respect to ocean chemistry. In consideration of current ocean acidification concerns and the importance of bryozoans as habitat formers (Wood and Probert 2013), each group

needs to be investigated separately, and one should not expect all bryozoan groups to respond in the same way.

Conclusions

Paleozoic marine bryozoans had variable responses to paleolatitude and inferred carbonate saturation states. Cryptostome bryozoan genera precipitated the most calcite per colony at lower latitudes, where carbonate saturation states would be higher, and less in midlatitudes, where carbonate would be undersaturated. This implies they were unable to metabolically overcome the increased pressures of precipitating calcium carbonate at higher latitudes.

Trepostome bryozoan genera show a similar but weaker trend for the Ordovician to Devonian. However, in the Carboniferous to Triassic, they show a trend toward more calcium carbonate per colony at higher latitudes, indicating they were able to overcome unfavorable carbonate saturation states. Analysis of Permian trepostome species indicates this was most pronounced in the Southern Hemisphere, where they were able to metabolically overcome unfavorable carbonate saturation states at higher latitudes supported by increased feeding capacity.

The fact that trepostome and cryptostome bryozoans responded differently to carbonate saturation states shows that bryozoans cannot be treated as a single group in extinction events influenced by ocean chemistry and has important implications for modern bryozoans. Modern stenolaemate and gymnolaemate bryozoans need to be considered separately in studies of their response to ocean acidification.

Acknowledgments

We are grateful to C. Buttler, who provided access to the genus descriptions and plates for the forthcoming Trepostome volume of the *Treatise on Invertebrate Paleontology*. We thank S. Pruss and an anonymous reviewer for constructive feedback on the original article.

Data Availability Statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.1zcrjdfvm>.

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