

Evolution of skeletal mineralogy in cheilostome bryozoans from calcite to aragonite seas

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ABSTRACT

Under the calcite-aragonite seas hypothesis, the evolutionary history of calcifying marine organisms reflects changes in global seawater chemistry, alternately favoring precipitation of skeletons made of calcite or aragonite. Most calcifying groups including corals, coccolithophores, and stromatoporoids do not switch mineralogies in response to these changes; instead, they expand and dwindle as their favored seawater conditions come and go. Cheilostome bryozoans have been suggested as an exception to this rule, apparently transitioning between aragonite and calcite many times. These changes have never been surveyed in detail, but have important consequences for material properties, fossil preservation, and the capacity of marine organisms to adapt to environmental change. We used new large-scale phylogenetic, paleontological, and mineralogical data sets to analyze the evolution of skeletal mineralogy in cheilostomes as they diversified across the early Cenozoic calcite-aragonite seas transition. Ancestral state reconstructions and stochastic character maps indicate at least 50 independent acquisitions of partly or fully aragonitic skeletons from calcitic ancestors, with many more transitions toward the aragonitic state than away from it. Fossil faunas are dominated almost entirely by calcitic species in the Cretaceous, but bimineralic species become common by the Oligocene, and aragonitic species by the Pliocene–Pleistocene. Phylogenetic and fossil analyses reveal a coherent timeline consistent with the shift to aragonite seas. Cheilostome skeletal development may be predisposed to mineralogical flexibility, with adaptive consequences for colony construction and modularity.

INTRODUCTION

The calcite-aragonite seas hypothesis holds that changes in oceanic chemistry over the Phanerozoic led to changes in the favored calcium carbonate polymorph in abiotic precipitates and in the skeletons of calcifying marine organisms (Stanley and Hardie, 1998). When marine molar Mg/Ca ratios were <2 during intervals of sea-floor spreading in the middle Paleozoic and Cretaceous, carbonates were predominantly low-Mg calcite; during intervals of continental coalescence in the late Paleozoic to Jurassic and early Cenozoic to Recent, Mg/Ca rose to >2 and high-Mg calcite and aragonite were

favored (Stanley and Hardie, 1998). The mineralogy of major groups of calcifying organisms appears to generally track these changes (Stanley, 2006). Curiously, calcifiers appear to be mostly “locked in” to the skeletal mineralogy they originate with (Murdoch, 2020), dwindling or going extinct rather than switching to calcite or aragonite when their favored ocean chemistry changes (Porter, 2010). For example, the mostly aragonitic scleractinian corals ceased to be major carbonate producers during the Cretaceous “calcite seas” interval, only rebounding in the mid-Cenozoic aragonite seas (Ries et al., 2006; Stolarski et al., 2007); the calcitic, chalk-forming coccolithophores show the opposite trajectory (Stanley et al., 2005).

In contrast with the tendency of most calcifiers to use only calcite or aragonite, cheilostome

bryozoans are suggested to have undergone multiple evolutionary transitions in skeletal mineralogy (Stanley, 2006). This widespread group of colonial marine invertebrates are the most successful bryozoans today, comprising ~5500 of the ~6500 (85%) described species (WoRMS, 2024). While all other bryozoan orders are either calcitic or non-mineralizing, cheilostome skeletons can be aragonitic, calcitic, or both, with aragonitic and bimineralic forms concentrated at low latitudes where aragonite precipitates more readily (Piwoni-Piórewicz et al., 2024). Cheilostomes are thought to be ancestrally calcitic (Taylor et al., 2009), but it is not known how many times they transitioned toward aragonitic skeletons, or whether these transitions happened concurrently with the early Cenozoic shift to aragonite seas (Smith et al., 2006; Taylor et al., 2014). Trends in skeletal mineralogy are important to understand from an evolutionary and ecological perspective because they constitute changes in the mechanical properties and preservation potential (Foote et al., 2015) of important habitat constructors. Such trends may also shed light on how marine organisms differ in their adaptations to environmental change. We used new mineralogical, phylogenetic, and fossil occurrence data sets to conduct the most comprehensive analysis of the evolution of skeletal mineralogy in cheilostome bryozoans.

METHODS

BryoMinBase (Piwoni-Piórewicz et al., 2024) compiles new and literature-sourced measurements of skeletal mineralogy in 981 extant cheilostome species, in the form of percent weight (wt%) aragonite content estimated with X-ray diffraction (XRD). To analyze this data set in a phylogenetic context, we timescaled

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a large (720 tips) molecular phylogeny from Orr et al. (2022) with penalized likelihood using the software treePL (Smith and O'Meara, 2012), including a constraint that crown cheilostomes be no older than the earliest fossil cheilostome (see Section 1 in the Supplemental Material¹). The resulting timetree shared 250 species with BryoMinBase (see Section 2 in the Supplemental Material). Each tip in the phylogeny was assigned as “calcitic,” “aragonitic,” or “bimineralic” when the median wt% aragonite was 0 (calcitic), 100 (aragonitic), or in between (bimineralic).

We inferred the evolutionary history of mineralogy using ancestral state reconstructions and stochastic character mapping, implemented in the R package *phytools* (Revell, 2012). Because our mineralogy trait is discretized from a continuous feature (wt%), we modeled its evolution using an ordered Mk model (Lewis, 2001) in which transitions between aragonitic and calcitic states must pass through a bimineralic state (see Section 3 in the Supplemental Material). We fit rates for our character evolution model and used the model for marginal ancestral state reconstructions. To further explore the evolutionary trends implied by this model, we used it to generate 100 stochastic character maps of mineralogy on the phylogeny and summarized the results with lineage-through-time plots and by counting transitions for each mapping.

We sought to complement this extant-only phylogenetic view with data on mineralogy in fossil communities, because such data provide more direct evidence for the timing of change and because the calcite-aragonite seas hypothesis makes predictions not just about lineages but especially about the ecological prevalence of different mineralogies (Stanley and Hardie, 1998). Directly and reliably measuring mineralogy across an entire fossil bryozoan fauna is challenging (Taylor et al., 2014; Di Martino et al., 2018) and outside the scope of the present study. However, indirect information on the ecological prevalence of different mineralogies is available by using taxonomy as a proxy for mineralogy.

We estimated the proportions of different mineralogies in fossil cheilostome communities using taxonomy by combining a compilation of cheilostome-bearing fossil localities by Lidgard et al. (2021) with BryoMinBase. We also supplemented BryoMinBase with a new compilation of 172 XRD measurements of skeletal mineralogy in fossil cheilostomes across 70 genera from four previous studies (Smith et al., 2006; Taylor et al., 2009, 2014; Di Mar-

tino et al., 2018). To estimate mineralogy for fossil species, we first assigned each genus in BryoMinBase a mineralogical category based on median wt% aragonite within that genus. Fossil species were then assigned the mineralogy of their genus, if available: 57% of fossil occurrences could be assigned to genera with mineralogical information, and the rest were excluded (see the Section 4 in the Supplemental Material). We visualized trends in the proportion of each mineralogy across localities through time and analyzed these using correlation tests and LOESS curves. For comparison, we plotted results alongside Eocene–Oligocene faunas studied with XRD by Taylor et al. (2014). Because skeletal mineralogy has a strong latitudinal signal (Reid et al., 2023; Piwoni-Piórewicz et al., 2024), we determined paleo-latitudes and longitudes for all fossil localities using the R package *chronosphere* (Kocsis and Raja, 2019) and analyzed trends by latitude. Multiple tests failed to detect any aragonite bias in our data set (see Section 5 in the Supplemental Material). We validated our approach to estimating mineralogy by comparing estimates made with BryoMinBase to those made using the fossil XRD compilation for 31 genera present in both data sets. Our method may overestimate the proportion of bimineralic species due to estimating mineralogy at the genus, rather than the species, level but appears otherwise unbiased (see Section 5 and Fig. S4 in the Supplemental Material).

RESULTS

Phylogeny

Although calcite is the most common crystal form in cheilostomes, bimineralic skeletons are phylogenetically widespread, as are the rarer aragonitic lineages (Fig. 1). Marginal ancestral state reconstruction recovers early cheilostomes as almost entirely calcitic, consistent with previous inferences (Taylor et al., 2009): calcite skeletons are inferred at all nodes before the Late Cretaceous and at all Late Cretaceous nodes outside the Schizoporellidae and Adeonidae. Most major clades arising in the Cenozoic are ancestrally calcitic, but transitions toward aragonite occur throughout the tree during this time.

Stochastic character maps indicate that cheilostomes acquired partly aragonitic skeletons ~57 times, with ~21 further transitions from the bimineralic to the aragonitic state (Fig. 2). Given that the phylogeny includes only 250 species, the true number of transitions could be much higher. There are over three times as many transitions away from the calcitic state ($N = 78$) as toward it ($N = 22$). Lineage-through-time plots (Fig. 2) show bimineralic species diversity is close to zero before the Late Cretaceous, as is aragonitic diversity before the Cenozoic. The diversity of cheilostomes with at least some aragonite has increased by a factor of 3.7 since

the start of the Cenozoic, while that of calcitic species has increased by a factor of 1.7.

Fossil Faunas

Inferring mineralogy from taxonomy indicates that the proportion of aragonitic and bimineralic species in fossil faunas has increased since the Cretaceous (Fig. 3). Before the Cenozoic, bimineralic species are rare and aragonitic species virtually absent. As in the phylogenetic results, the rise of non-calcitic forms is gradual. The proportion of bimineralic forms reaches modern levels by the Eocene, but aragonitic forms are rare until the Neogene, and especially the Pliocene–Pleistocene. Localities at high absolute paleolatitude ($>40^\circ$) have more calcitic and fewer aragonitic species (Fig. S3). Non-calcitic forms increase through time in both high- and low-latitude subsets of the data (Fig. S1), with similar trends in both north and south hemispheres (Fig. S2). Correlations between age and mineralogy (Fig. S2) are stronger at low latitudes. Six Eocene–Oligocene localities (Taylor et al., 2014) are consistent with our estimates of the proportion of aragonitic and calcitic species, although the proportion of bimineralic forms is overestimated relative to Taylor et al. (2014) (Fig. 3).

DISCUSSION

We recovered a coherent, global signal from independent phylogenetic and paleontological data sets of an evolutionary trend toward bimineralic and, later, aragonitic skeletons in cheilostome bryozoans. This trend is gradual and began in the Late Cretaceous among bimineralic forms and by the Paleocene among aragonitic forms. This aligns with observations that the representation of aragonitic forms does not jump abruptly across the Eocene–Oligocene boundary (Taylor et al., 2014) and confirms a previous inference from first appearances of cheilostome families of an origin of aragonite skeletons at ca. 100 Ma (Smith et al., 2006). If the transition from calcite to aragonite seas was a globally synchronous event near the Eocene–Oligocene boundary, as is sometimes implied (Smith et al., 2006; Taylor et al., 2014), then that transition is too young to have caused the evolutionary changes we document in cheilostomes. Some Mg/Ca proxies and models agree with this young age (Stanley and Hardie, 1998), but others put it as old as >100 Ma (Wilkinson and Algeo, 1989), with broad consensus only on a transition sometime between the Cretaceous–Paleogene and Eocene–Oligocene boundaries (Horita et al., 2002). Furthermore, aragonite precipitation depends on temperature in addition to Mg/Ca, so warm areas could have been favorable to aragonite by the start of the Late Cretaceous (Balthasar and Cusack, 2015). Because models agree that Mg/Ca has been rising for at least the past 100 m.y., those parts of the ocean suitable for the precipitation

¹Supplemental Material. Code and data files necessary to replicate all analyses. Please visit <https://doi.org/10.1130/GEOLOGY.S.29873825> to access the supplemental material; contact editing@geosociety.org with any questions.

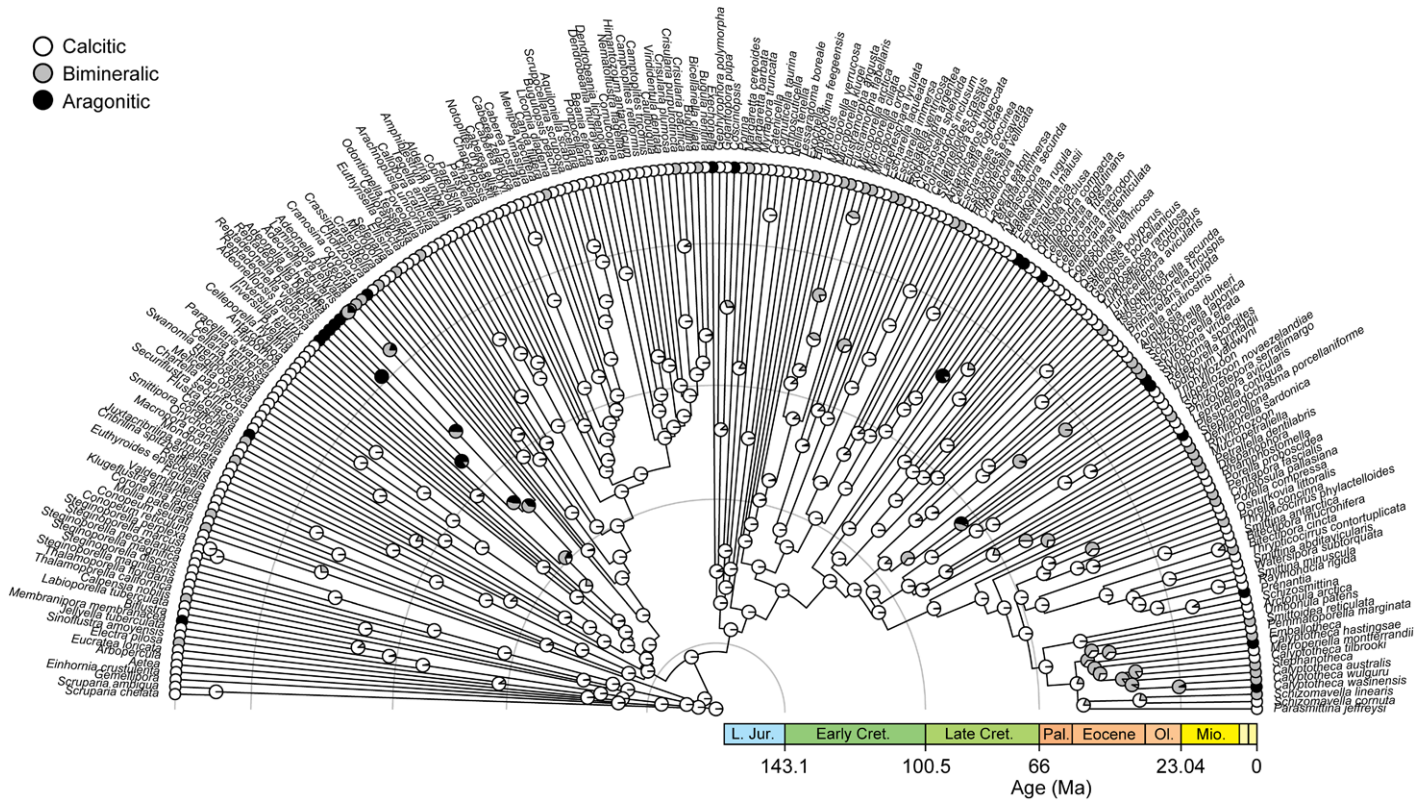


Figure 1. Phylogeny of cheilostome bryozoans with ancestral state reconstructions of mineralogy. Species names are omitted where mineralogical and phylogenetic data match only at the genus level. Jur.—Jurassic; Cret.—Cretaceous; Pal.—Paleocene; Ol.—Oligocene; Mio.—Miocene; L.—Late.

of aragonite were likely expanding during the entire interval studied (Balthasar and Cusack, 2015). Thus, our findings are consistent with the hypothesis that cheilostome mineralogy evolved in response to the shift from calcite to aragonite seas, though future developments in geochemistry could overturn this. An alternative is that cheilostome mineralogical evolution is neutral with respect to calcite-aragonite seas, but this is hard to reconcile with experimental evidence for the effect of Mg/Ca ratio on the fitness of calcifiers (Stanley et al., 2005; Ries et al., 2006; Cole et al., 2023).

Perhaps most surprisingly, we recovered at least 50 independent acquisitions of aragonite skeletons in cheilostomes—likely an underestimate due to our incomplete phylogenetic sampling. Environmental plasticity in skeletal mineralogy could lead us to overestimate the amount of evolutionary change in this group, but cheilostomes with contrasting mineralogies frequently co-occur, indicating that much of their mineralogical diversity results from genetic change. Scleractinians apparently maintain aragonitic skeletons under calcite sea-type conditions through regulating production of proteins

involved in skeletal organic matrix and calcium ion transport (Conci et al., 2024); similar mechanisms may explain both how cheilostomes stabilize skeletal mineralogy across variable environments and how heritable differences in mineralogy arise between lineages. Given that many major groups, including coccolithophores, echinoderms, octocorals (Quattrini et al., 2020), most foraminiferan orders (de Nooijer et al., 2023), and stenolaemate bryozoans never transition out of the calcitic state (Taylor et al., 2009; Key et al., 2022), what makes cheilostomes so evolvable in this respect? Cheilostomes evolved

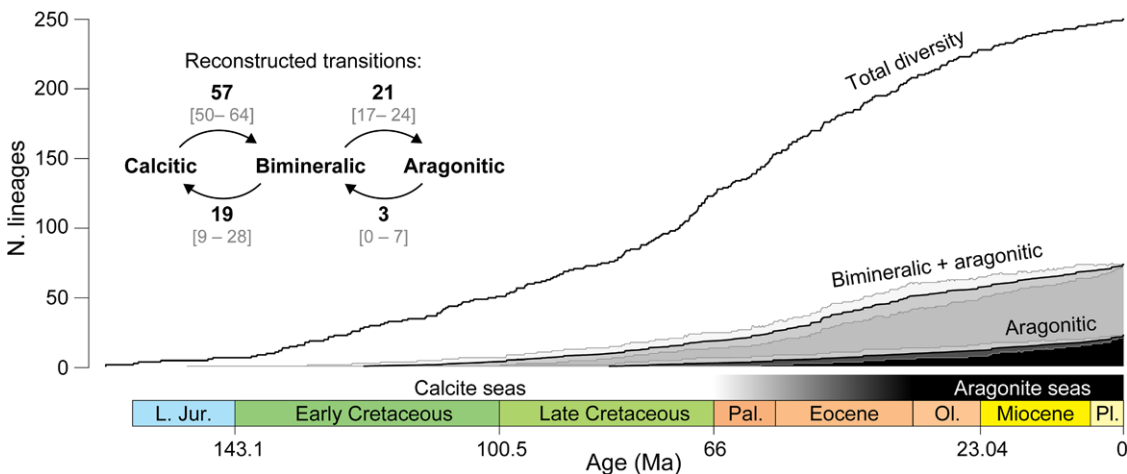


Figure 2. Lineage-through-time plot summarizing 100 stochastic character maps of cheilostomes. Average number (N.) of lineages in each state is shown by the bold black line, with 5th and 95th percentiles shown by gray lines. Inset shows median numbers of transitions between states, with 2.5th to 97.5th percentile range in gray. Jur.—Jurassic; Pal.—Paleocene; Ol.—Oligocene; Mio.—Miocene; Pl.—Pliocene; L.—Late.

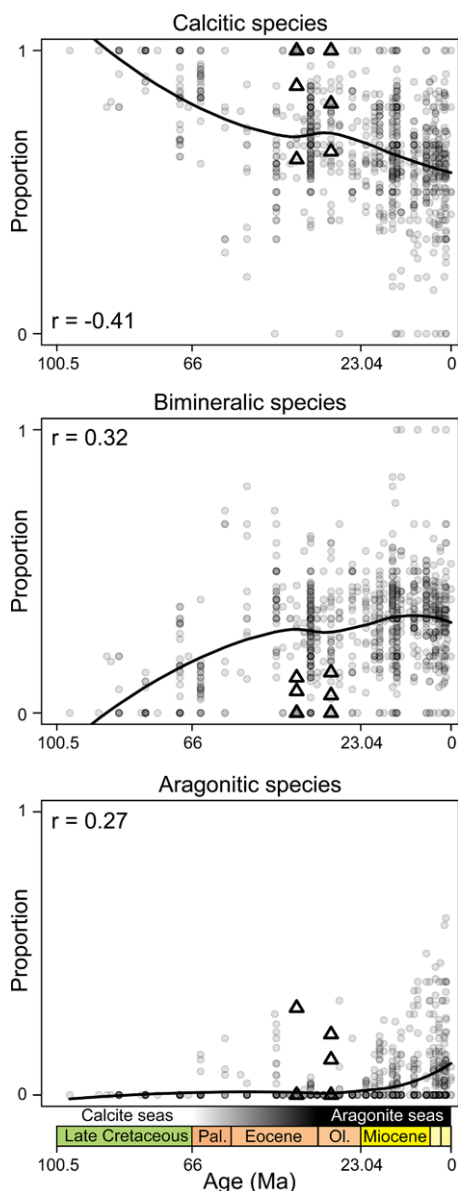


Figure 3. Proportion of cheilostome species in each mineralogical state (calcitic, bimineralic, aragonitic) through time across 911 localities. Circles show proportions inferred from taxonomy, along with the LOESS regression curve. Triangles show proportions from six faunas in Taylor et al. (2014) analyzed with X-ray diffraction. Pearson correlation between mineralogy and time is also shown. Pal.—Paleocene; Ol.—Oligocene.

from a non-mineralized ctenostome-like ancestor, representing the second instance of bryozoans evolving skeletons (Taylor et al., 2009). Relative to other bryozoans, cheilostomes build their skeletons from a uniquely diverse range of ultrastructural fabrics, or patterns of crystal growth (Taylor et al., 2015). Some of these are associated with aragonitic mineralogy, including the wall-perpendicular (prismatic) fabrics unique to cheilostomes (Taylor et al., 2015). Thus, cheilostomes may have arisen with ultrastructural fabrics that are predisposed to ara-

gonitic composition. These features could be associated with dramatic chromosomal rearrangements at the base of Bryozoa and on the branch leading to cheilostomes, which have been suggested to play a role in biomineralization (Lewin et al., 2025).

Does skeletal mineralogy have adaptive consequences for cheilostomes? An aragonite skeleton is almost certainly maladaptive in a calcite sea, as demonstrated in corals (Ries et al., 2006); the shift to aragonite seas must therefore have had a profound effect on the adaptive landscape in cheilostomes, opening up a range of new viable phenotypes incorporating aragonite. In modern aragonite seas, aragonitic skeletons are probably not always fitter than high-Mg calcite, but the combination of permissive ocean chemistry and evolvable skeletonization in cheilostomes probably enables adaptive scenarios that would otherwise not be realizable. For example, bimineralic cheilostomes are known to deploy aragonite as a superficial “frosting” over a colony with a calcitic core (Benedix et al., 2014), paralleling the arrangement in a bimineralic coral (Stolarski et al., 2021). Aragonite is slightly denser and energetically more expensive than calcite, so building a thin, external aragonite layer may lead to a robust, but inexpensive, colony structure. Likewise, in bimineralic bryozoans, specialized modules are sometimes associated with particular mineralogies. Mineralogical evolvability may therefore be related to the exceptional diversity of modules in cheilostomes (Schack et al., 2019). Modularity promotes evolvability by allowing beneficial changes within modules while minimizing deleterious correlated changes across the organism (Hansen, 2003); thus, a novel mineralogy arising in a single module might be more likely to persist than one affecting the entire colony.

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