

# Calcitic shells in the aragonite sea of the earliest Cambrian

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## ABSTRACT

The initial acquisition of calcium carbonate polymorphs (aragonite and calcite) at the onset of skeletal biomineralization by disparate metazoans across the Ediacaran-Cambrian transition is thought to be directly influenced by Earth's seawater chemistry. It has been presumed that animal clades that first acquired mineralized skeletons during the so-called “aragonite sea” of the latest Ediacaran and earliest Cambrian (Terreneuvian) possessed aragonite or high-Mg calcite skeletons, while clades that arose in the subsequent “calcite sea” of Cambrian Series 2 acquired low-Mg calcite skeletons. Here, contrary to previous expectations, we document shells of one of the earliest helcionelloid molluscs from the basal Cambrian of southwestern Mongolia that are composed entirely of low-Mg calcite and formed during the Terreneuvian aragonite sea. The extraordinarily well-preserved *Postacanthella* shells have a simple prismatic microstructure identical to that of their modern low-Mg calcite molluscan relatives. High-resolution scanning electron microscope observations show that calcitic crystallites were originally encased within an intra- and interprismatic organic matrix scaffold preserved by aggregates of apatite during early diagenesis. This indicates that not all molluscan taxa during the early Cambrian produced aragonitic shells, weakening the direct link between carbonate skeletal mineralogy and ambient seawater chemistry during the early evolution of the phylum. Rather, our study suggests that skeletal mineralogy in *Postacanthella* was biologically controlled, possibly exerted by the associated prismatic organic matrix. The presence of calcite or aragonite mineralogy in different early Cambrian molluscan taxa indicates that the construction of calcium carbonate polymorphs at the time when skeletons first emerged may have been species dependent.

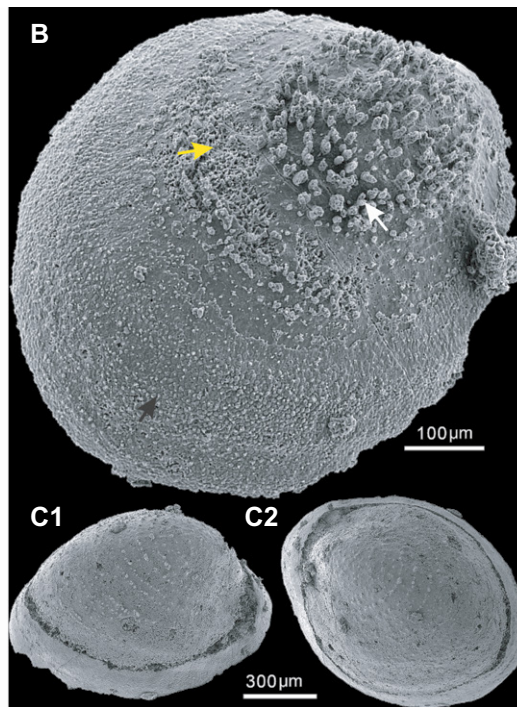
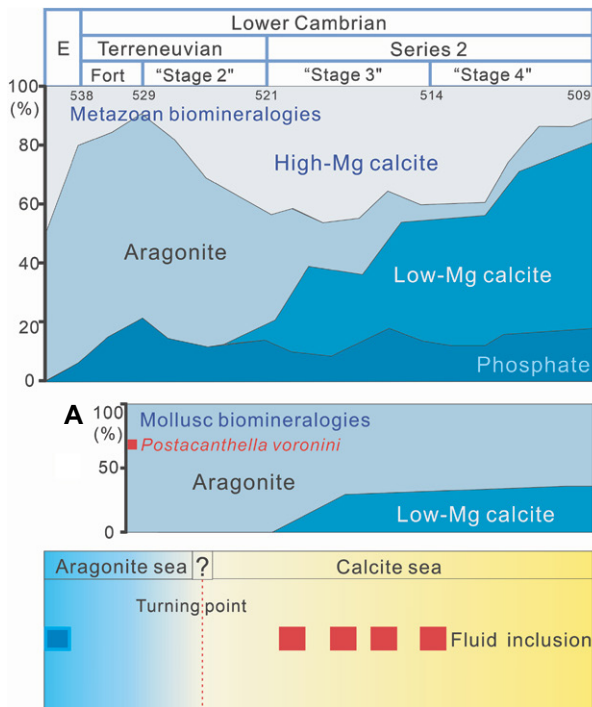
## INTRODUCTION

Changes in the CaCO<sub>3</sub> polymorphs (aragonite and high- and low-magnesium calcite) in abiotic marine cements, ooids, and hypercalcifying reef builders and sediment producers have been suggested to have vacillated throughout Earth's history with the secular variation of seawater ion compositions, particularly the magnesium/calcium molar ratio (*mMg:Ca*) (Stanley, 2006; Ries, 2010). However, the effect of oscil-

lating seawater chemistry on CaCO<sub>3</sub> polymorphs of metazoan skeletons formed by organically mediated biologically controlled mineralization (BCM) remains elusive. Porter (2007, 2010) proposed that the initial selection of aragonite and calcite polymorphism was directly influenced by the chemical condition of oceans at the time when skeletal animals first emerged in the Cambrian “explosion”. This hypothesis was supported by paleontological evidence, given

that the earliest carbonate small shelly fossils, which represent a wide range of Ediacaran and earliest Cambrian (Terreneuvian) animal phyla, are interpreted to have been originally composed exclusively of high-Mg calcite or aragonite, formed in a favorable aragonite sea (*mMg:Ca* > 2). Low-Mg calcitic skeletons are perceived to have appeared slightly later but rapidly rose to dominance in the subsequent calcite-sea environment (*mMg:Ca* < 2) (Zhuravlev and Wood, 2008; Maloof et al., 2010; Wood and Zhuravlev, 2012; Murdock, 2020). Quantitative observations of molluscan mineralogy in the early Cambrian show a similar trend (Vendrasco et al., 2016; Li et al., 2017). Geochemical evidence (e.g., fluid inclusions, calcium isotope [ $\delta^{44}\text{Ca}$ ] and strontium [Sr] content data) and statistical analyses of skeletal mineralogy suggests that the dramatic shift of seawater chemistry from the Terreneuvian aragonite sea to the subsequent calcite sea occurred around Cambrian Stages 3 and 4 (Brennan et al., 2004; Wei et al., 2022) (Fig. 1A).

However, contrary to previous studies that considered that all molluscan taxa produced an aragonitic shell in the earliest Cambrian, we confirm the existence of low-Mg calcitic mollusc shells at the time of the Terreneuvian aragonite sea. The extraordinarily well-preserved shell organic matrix (SOM) that regulated biomineralization is also discovered among Cambrian molluscs for the first time, which permits precise reconstruction of the shell microstructure and



**Figure 1. Changes in metazoan skeletal mineralogy in oscillating seawater conditions across the Ediacaran-Cambrian transition. (A) Animal skeletal mineralogy from Wood and Zhuravlev (2012) (top); mollusc data from Li et al. (2017) (middle); and constraints on seawater chemistry derived from Porter (2007) (bottom). Boxes denote fluid inclusions in marine evaporite deposits; dashed line denotes the possible turning point of seawater chemistry from the Terreneuvian aragonite sea to subsequent calcite sea. E—Ediacaran; Fort—Fortunian. (B) Specimen NRM Mo196849 showing preservation of phosphatic infillings (white arrow), prismatic organic matrix (yellow arrow), and delicate polygonal textures (black arrow) on the**

**face of the internal molds. (C) Specimen NRM Mo196850 showing overall morphology of *Postacanthella voronini*.**

recognition of its original calcitic constituents on different microscopic scales.

## MATERIALS

Hundreds of phosphatic internal mold specimens identified as the helcionelloid mollusc *Postacanthella voronini* Zhegallo by Esakova and Zhegallo (1996) (Figs. 1B and 1C) were recovered from the Cambrian Terreneuvian Bayangol Formation at Bayan Gol in the Zavkhan Basin, southwestern Mongolia (Topper et al., 2022). All specimens occur within the *Purella* shelly biozone of the measured BAY2 section (46°42'11.0"N, 96°18'44.5"E) in southwestern Mongolia, equivalent to the *Purella antiqua* assemblage biozone in Siberia, upper Fortunian, ca. 535 Ma, formed during an aragonite sea (Kouchinsky et al., 2017). Helcionelloids are widely considered as a stem group of shell-producing conchiferan molluscs (e.g., Thomas et al., 2020), and the simple cap-shaped shells of *Postacanthella* represent one of the earliest members of helcionelloids from the basal Cambrian (see the Supplemental Material<sup>1</sup> for geological settings and methods).

## RESULTS

Our scanning electron microscope (SEM) observations show that *Postacanthella* shells were composed entirely of a prismatic micro-

structure and associated SOM was exquisitely replicated by aggregates of apatite during early diagenesis. The three-dimensional inter- and intraprismatic organic framework of *Postacanthella* (Fig. 2D) is closely comparable to that of modern *Pinctada* shells in which encased calcitic polycrystallites have been partly dissolved during laboratory decalcification but acid-resistant SOM is preserved (Fig. 2B). The only minor difference is that the interprismatic organic envelope surrounding a mineral prism in *Postacanthella* is much smaller in size (ranging 1–10 μm in diameter) (Fig. 2C) relative to columnar prisms (megaprisms, >10 μm in diameter) of *Pinctada* (Fig. 2A).

The interprismatic organic membrane in *Postacanthella* is ~0.5 μm thick. On the membrane surface, organic growth increments (lines) are visible, and numerous longitudinal short, straight, and incomplete segments developed (Figs. 3A and 3D). Many small incipient prisms, ~1 μm in diameter, occur adjacent to the thick interprismatic organic membrane of large prisms. Small prisms tend to disappear toward the internal surface of the shell due to crystal growth competition with large prisms (Fig. 3M). Mineral prisms are more or less polygonal in cross section, vertical to highly reclined, parallel mutually, and tightly adjacent to each other (Fig. 3B). Each columnar prism consists internally of second-order structural subunits, originally encased within a relative thin layer of organic sheath and parallel to the long axis of the prism (Figs. 3E–3G and 3I–3L). Large mineral prisms are separated by sinu-

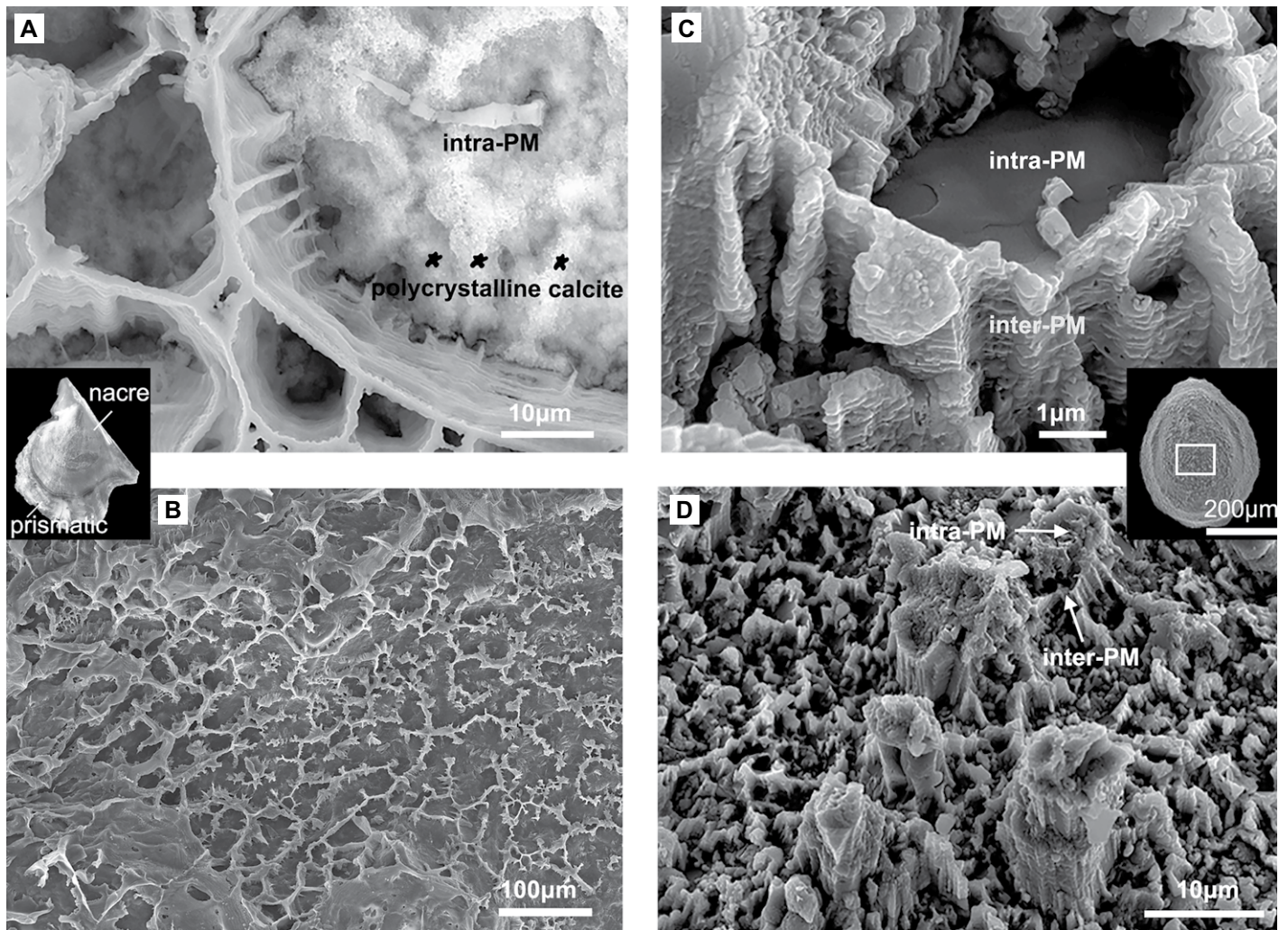
ous and tortuous intraprismatic organic membranes, reminiscent of the calcitic polycrystalline prisms seen in *Pinctada* (Figs. 3C and 3H). Furthermore, well-defined polygonal textures are very common on the surface of our specimens (Fig. 3P). The polygons, each ~10 μm in diameter and slightly convex and cell-like, commonly exhibit intricate interdigitating margins that correspond closely to the short and incomplete segments of thick interprismatic organic wall of SOM (Figs. 3N and 3O).

## DISCUSSION

### Microstructure, Mineralogy, and Organic Matrix

It has been extensively recognized that microstructural details of Cambrian mollusc shells can be preserved on the surface of phosphatic internal molds (Runnegar, 1985; Vendrasco et al., 2016; Li et al., 2017). Many microstructures, such as prismatic and crossed-lamellar fabrics that are commonly observed in modern representatives, have been documented from early Cambrian molluscan taxa (Vendrasco et al., 2010; Li et al., 2022). However, the self-assembled SOM, which directs crystal growth, polymorphism, crystallography, and orientation, has never been documented from the Cambrian, most likely because of diagenesis that obscures these intricate features. The SOM, incorporated within the mineral phase, generally accounts for <5% of shell weight and plays a key role in controlling the entire calcification process (Marin et al., 2012). But the labile proteinaceous SOM easily decomposes and generally disappears

<sup>1</sup>Supplemental Material. Geological settings and methods. Please visit <https://doi.org/10.1130/GEOL.S.21191092> to access the supplemental material, and contact [editing@geosociety.org](mailto:editing@geosociety.org) with any questions.



**Figure 2.** Prismatic organic matrix of Terreneuvian *Postacanthella* and modern *Pinctada* shells. (A,B) Digital and scanning electron microscope (SEM) observations of partly decalcified *Pinctada* prisms showing three-dimensional organic matrix framework (specimen NRM Mo196851). (C,D) SEM details of interprismatic and intraprismatic organic matrix of a Cambrian Terreneuvian *Postacanthella* shell (specimen NRM Mo196852). PM—prismatic organic membrane.

during complex diagenetic processes and thus is rarely fossilized. Laboratory experimental diagenesis has also showed that post-mortem diagenetic alterations start immediately after burial, with organic degradation within skeletons followed by a series of fluid-solid interactions through time (Pederson et al., 2019). Direct physical evidence of preserved SOM in fossil shells has so far been reported only from much younger Mesozoic and Cenozoic deposits (Clark, 1999; Myers et al., 2018).

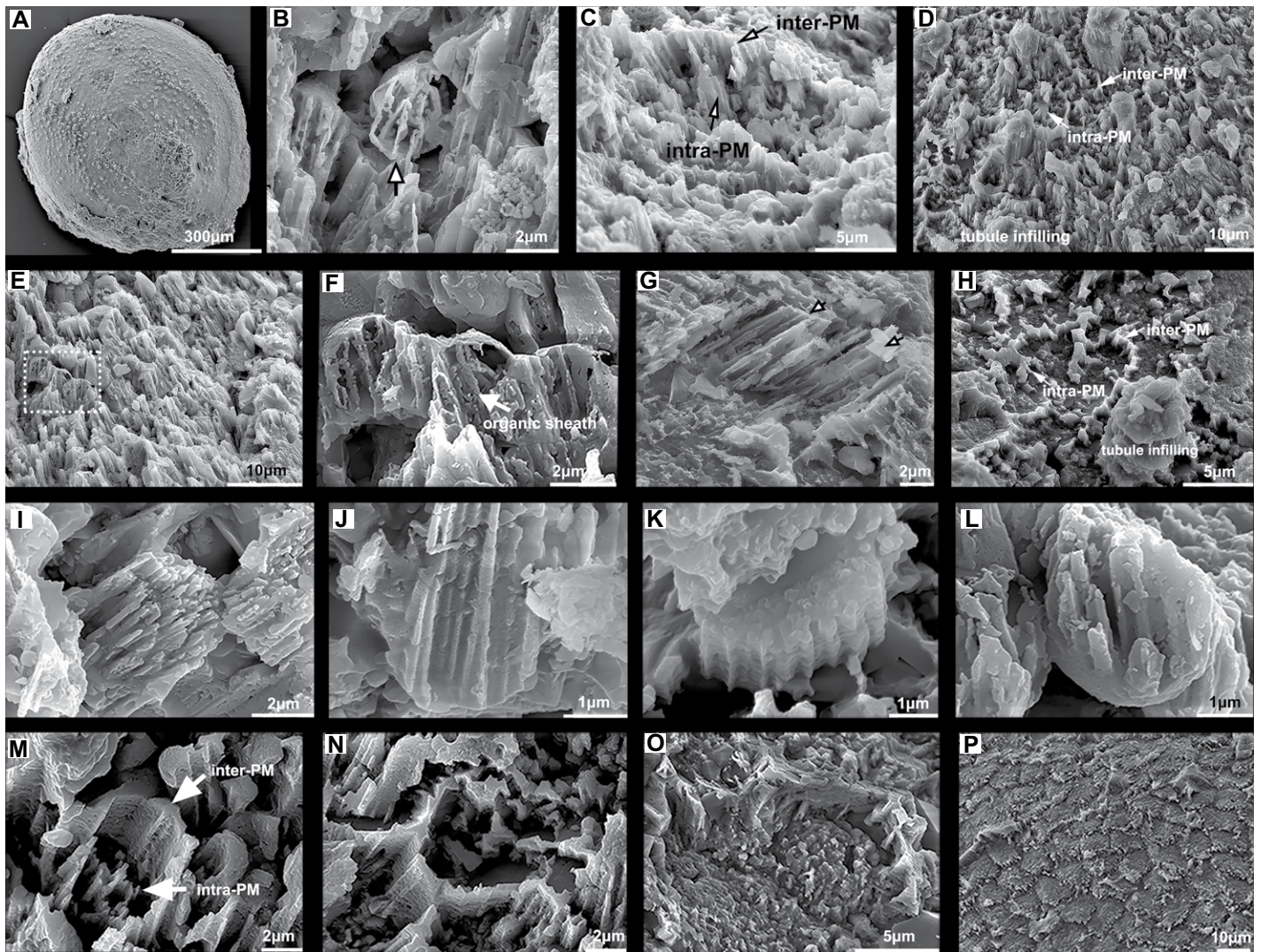
Specimens from southwestern Mongolia demonstrate, however, that it is possible for the SOM to be preserved in delicately phosphatized early Cambrian calcareous shells. Although pristine organic compounds, isotopic signature, and encased primary crystallites cannot survive after decay and diagenetic overprinting, their morphological features, e.g., shape, size, and arrangement, can be precisely replicated by phosphate and preserved (to microscopic levels) on the surface of phosphatic internal molds. The well-preserved SOM documented here indi-

cates that *Postacanthella* shells had a prismatic microstructure.

Prismatic microstructure commonly forms the external shell layer and muscle attachment layer (myostracum) in molluscs. Previous studies of Terreneuvian molluscs showed preservation of polygonal textures and fiber and/or lath-shaped substructural units on the surface of internal molds, which were considered to be formed by a spherulitic prismatic microstructure, made up of aragonite, from the external layer of associated shells (Runnegar, 1985; Ventrascio et al., 2010). Our study further demonstrates that these delicate polygons are produced by interprismatic organic envelopes of columnar prisms. But differently, in *Postacanthella*, second-order lath-like building blocks coated by organic sheaths tend to be parallel to the long axes of prisms rather than in a radiating or fan-like pattern of spherulitic prisms, thus indicating a typical simple prismatic microstructure.

In mollusc shells, simple prismatic microstructure may be composed of either aragonite

or calcite in monocrystalline or polycrystalline forms (Cuif et al., 2020). Of these, aragonitic prisms are commonly characterized by an initial central zone with divergent elongated crystallites at the periphery (Dauphin et al., 2020). These resemble spherulitic prisms but clearly differ from the mutually parallel building blocks of calcitic prisms and from the microstructure illustrated herein. In addition, in *Postacanthella*, small incipient prisms contain numerous parallel, lath-like crystals of equal size, suggesting a monocrystalline structure, while large adult prisms are internally separated by tortuous and irregular intraprismatic organic membranes, indicating a polycrystalline fabric. This likely occurred because of a gradual transition from mono- to polycrystalline calcitic constituents along the prisms, also seen in the calcitic prisms of living molluscs like *Pinctada* (Checa et al., 2016; Dauphin et al., 2019). Together, these observations strongly indicate a primary low-Mg calcitic composition of *Postacanthella* shells.



**Figure 3.** Calcitic simple prismatic microstructure of *Postacanthella*. (A) Scanning electron microscope (SEM) images of specimen NRM Mo196853 showing overall morphology of *Postacanthella voronini*. (B,E,F) Small prisms with parallel second-order crystal subunits. (C,H) Inter- and intrapismatic organic membranes of large mature prisms. (D) Prismatic organic matrix. (G) Two adjacent small prisms and mutually parallel second-order structural subunits. (I–L) Small individual prisms with numerous lath-like second-order subunits encased within organic sheaths. (M–P) Well-defined polygonal texture formed by interprismatic organic membranes. PM—prismatic organic membrane.

### Taxon-Specific Response to Ambient Seawater Chemistry

Several studies have highlighted the correlation between seawater chemistry and carbonate skeletal mineralogy at the time when mineralized skeletons were first acquired in particular clades (Zhuravlev and Wood, 2008; Porter, 2010). It is assumed that during the initial acquisition of a mineralized skeleton, seawater chemistry plays a defining role in which a calcium carbonate polymorph is produced by that particular lineage. After they initially acquire the ability to biomineralize, sophisticated BCM metazoans—in contrast to simple hypercalcifiers and inorganic carbonate deposits—rarely switch mineralogy regardless of seawater ion perturbations (Porter, 2010). These taxa are able to maintain production of particular carbonate polymorphs through time because mineralogies are strictly controlled by the SOM within

the skeletons, not ambient seawater chemistry, especially involving different expressions of particular SOM genes that underpin the ability to counteract changing seawater  $mMg:Ca$  (Janiszewska et al., 2017).

However, the direct correlation of seawater chemistry and carbonate skeletal mineralogy early in the history of a clade is not ubiquitous (Zhang and Shu, 2021). There is evidence that micrabaciids, a lineage of aragonitic scleractinian corals, first appeared during the Cretaceous calcite sea (Janiszewska et al., 2017). Additionally, laboratory experiments have shown that calcitic bivalves can produce aragonite in a simulated aragonite sea (Checa et al., 2007) and that serpulid polychaetes that inhabit environments below the carbonate compensation depth can continue to precipitate calcitic tissues in the modern aragonite sea (Kupriyanova et al., 2014). Moreover, temperature may also play a signifi-

cant role by influencing physiological activity of skeletogenesis, and aragonitic skeletons have formed in warm-water environments in calcite seas throughout the Phanerozoic (Morse et al., 1997; Balthasar and Cusack, 2015). These studies demonstrate that acquisition of biomineralization pathways is vastly more complex than the influence of seawater chemistry on aragonite and calcite polymorphism.

Molluscs are exceptional among biocalcifying organisms because of their ability to fabricate elaborate biomineralic microstructures and for the controls exerted by the SOM over the biocalcification processes (Checa, 2018). During the Terreneuvian aragonite sea, molluscs preferred to precipitate aragonite as aragonitic prismatic, foliated aragonite, and various regular-irregular fibrous microstructures (Runnegar, 1985; Vendrasco et al., 2016; Li et al., 2017). In contrast, calcitic shells, represented by foliated

calcite and calcitic semi-nacre microstructures, first emerged in the subsequent calcite sea of Cambrian Stage 3 (Vendrasco et al., 2010). But contrary to this general correlation between shell mineralogy and seawater chemistry in early Cambrian molluscs, our current work demonstrates the rare occurrence of molluscs capable of biomineralizing low-Mg calcitic shells in the Terreneuvian aragonite sea. The secretion of a prismatic microstructure made up of mono- and polycrystalline calcite in *Postacanthella* was strictly controlled and selected by the associated prismatic organic matrix rather than being triggered by the aragonitic chemistry of the surrounding seawater.

It is clear that the initial selection of CaCO<sub>3</sub> polymorphs at the onset of skeletal acquisition within a clade cannot be readily ascribed to the ambient seawater chemistry. The range of calcium carbonate polymorphs present in early Cambrian molluscs suggests that while the mineralogy of BCM skeletons was influenced by seawater chemical compositions, the effect may have been species dependent, and further attention is needed to study the influence of biological factors that influence the production of carbonate mineralogy.

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