

Biom mineralization and global change: A new perspective for understanding the end-Permian extinction

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ABSTRACT

We investigated the kill mechanisms of the end-Permian mass extinction by analyzing patterns in biomineralization of marine invertebrates. The microstructures of Upper Permian brachiopod organocarbonate shells show the demise of the production of fabrics with a columnar layer—which has less organic matrix—in favor of more organic-rich shells at the end of Permian. Also, in the 100–120 k.y. interval prior to the Permian-Triassic boundary (PTB), the Rhynchonellata had small calcite structural units (fibers) and thus a higher shell organic content, whereas the Strophomenata were not able to produce smaller units. This suggests that the two classes had a different capacity to cope with environmental change, with the Rhynchonellata being more able to buffer against pH changes and surviving the PTB, whereas the Strophomenata became extinct. The observed trends in biomineralization are similar to the patterns in extant marine invertebrates exposed to increasing $p\text{CO}_2$ and decreasing pH, indicating that ocean acidification could have been one of the kill mechanisms of the mass extinction at the PTB.

INTRODUCTION

The Late Permian was the time of the most dramatic biotic change in Earth's history: the end-Permian mass extinction (e.g., Erwin, 2006). The event approximately coincided with one of the largest known continental eruptions, the Siberian flood basalts (Burgess and Bowring, 2015), which, by the metamorphism of organic-rich shale, coal, and salts, could have generated more than 100,000 Gt of CO_2 , as well as CH_4 (e.g., Svensen et al., 2009; Polozov et al., 2016), and injected into the atmosphere ~6300–7800 Gt of sulfur (Black et al., 2014). This large amount of gas caused global warming (Brand et al., 2012; Joachimski et al., 2012) and acidification of both terrestrial and marine ecosystems, as shown by geochemical proxies (Hinojosa et al., 2012; Sephton et al., 2015). Acidification has been referred to as a kill mechanism (Clarkson et al., 2015), and recently it has been shown that the end-Permian atmosphere-ocean composition was compatible with low pH values (Brand et al., 2016). Heavily calcified organisms were less likely to survive (e.g., Clapham and Payne, 2011), but up to now, there has been no attempt to investigate the biominerals in order to understand these events. Since the best archive of biocalcification is the hierarchical microstructure of fossil shells, here we use a new approach to study end-Permian extinction with the aim of relating the microscale pattern of brachiopod biomineralization to the macroscale changes caused by the Siberian continental eruptions.

We focus on Rhynchonelliformea brachiopod shells because they are low-buffered organisms (Knoll et al., 2007), with an organocarbonate multilayered shell that is vulnerable to changes in the $p\text{CO}_2$ and CaCO_3 saturation state of seawater (Clapham and Payne, 2011). Also, they dominated Paleozoic benthic communities and showed a remarkable morphological and chemical-structural diversity (Williams and Cusack, 2007; Garbelli et al., 2014a), which make them valuable tools with which to trace end-Permian environmental and climate disruption and the consequent biotic crisis.

METHODS

We investigated the microstructure of Rhynchonelliformean organocarbonate shells, focusing on the classes Strophomenata and Rhynchonellata. Their shells are composed of two to three low-Mg calcite layers, which are made distinctive by the fabric of the secondary layer: laminar in the Strophomenata and fibrous in the Rhynchonellata (Williams and Cusack, 2007). The primary layer is rarely preserved, whereas the columnar tertiary layer, when present, is analogous in the two classes (Garbelli et al., 2014a). We used scanning electron microscopy (SEM) to investigate the fabrics (sensu Hobbs et al., 1976) of 443 brachiopod fossil shells belonging to 39 genera collected through several Upper Permian stratigraphic sections of Tethys Ocean sedimentary rocks deposited in different environments. The shells were classified into

two different types, based on the fabric of the multilayered shell (i.e., fibrous/laminar secondary layer and columnar tertiary layer; Fig. 1). A logistic regression on the probability of finding one of the two fabric types was applied to evaluate the effect of environmental parameters such as hydrodynamic energy (settings above vs. below the fair wave base), sedimentation (carbonate versus mixed siliciclastic-carbonate), paleolatitude (middle versus paleoequatorial latitudes), and stratigraphic position (Wuchiapingian, Changhsingian, extinction interval). We measured the size of the structural units of the secondary layer of pristine shells of selected taxa. In particular, we measured the thickness of the laminae for the Strophomenata ($N_{\text{specimens}} = 67$) and the width of the fibers, in cross section, for the Rhynchonellata ($N_{\text{specimens}} = 37$). Since the structural unit size in brachiopods is taxon diagnostic, it varies among taxa (i.e., McKinnon, 1974), and, as shown in recent calcifying organisms, its thickness or width can vary in response to environmental parameters (Olson et al., 2012). We measured the size variation across specimens of the same taxon to verify how it evolved in time (see the GSA Data Repository¹).

RESULTS

Based on the presence or absence of the columnar tertiary layer, we classified the shells into two main types. The shells of type 1 are composed of three layers: primary (not always preserved), secondary (laminar in the Strophomenata and fibrous in the Rhynchonellata), and tertiary (Figs. 1A and 1B). Type 2 shells include those only made of the fibrous or laminar secondary layer below the primary layer, when preserved (Figs. 1C and 1D). The two types of shells occur in both the Strophomenata and Rhynchonellata. In our database, the probability of finding a type 2 versus a type 1 fabric

¹GSA Data Repository item 2017005, information about provenance and stratigraphic position of the studied brachiopods, a complete list of the specimens investigated with SEM, and details of methods applied and relative results, is available online at www.geosociety.org/pubs/ft2016.htm, or on request from editing@geosociety.org.

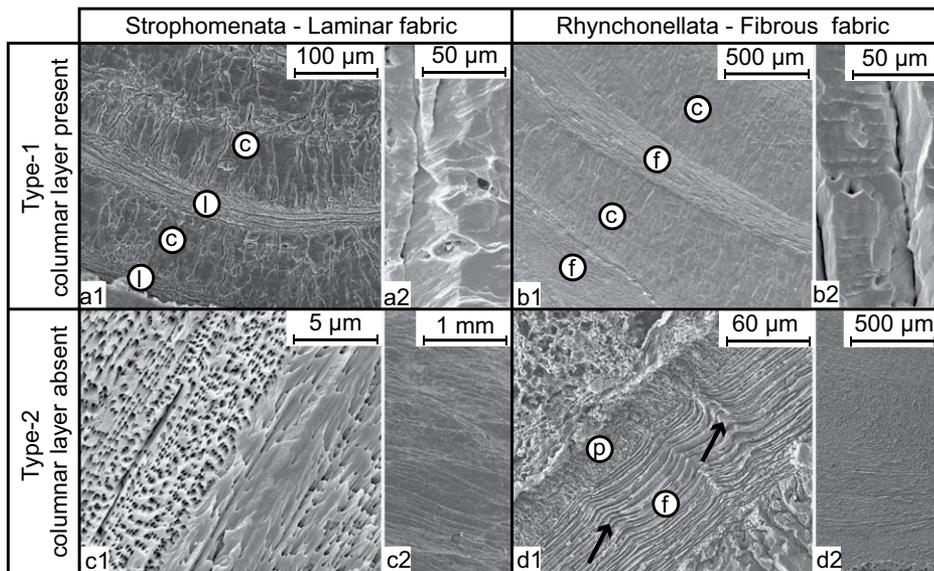


Figure 1. Types of brachiopod shell microstructures. a1 and b1: Type 1 shells of Strophomenata (*Spinomarginifera helica*) and Rhynchonellata (*Permophricodothyris iranica*), respectively. a2 and b2: Tertiary columnar layer of a Strophomenata and a Rhynchonellata specimen, respectively. c1 and d1: Type 2 shells of Strophomenata (*Haydenella* sp.) and Rhynchonellata (*Hustedia* sp.), respectively. c2 and d2: Type 2 shells of large Strophomenata (*Costiferina* sp.) and Rhynchonellata (*Peltichia* sp.), respectively. l—structural units of laminar secondary layer, c—tertiary columnar layer, f—structural units of fibrous secondary layer, arrows—endopunctae, p—primary layer.

is more controlled by the stratigraphic position than by environmental parameters such as hydrodynamic energy, substrate, or paleolatitude (Fig. 2). Fabrics of type 1 have a higher probability of occurring in the Wuchiapingian and are replaced by type 2 shells in the Changhsingian. Type 2 became the dominant fabric type in the extinction interval (Fig. 2). The size of the structural units of the secondary layer shows a significant trend of variation in the Late Permian. The fibrous fabric of the investigated Rhynchonellata shows a decrease of the average width of the fibers in the stratigraphic interval corresponding to 100–120 k.y before the Permian-Triassic boundary (PTB), both in South China and in Tibet (Fig. 3; Shen et al., 2011; Garbelli et al., 2016). This trend is not correlated with variations in shell thickness (e.g., *Paracrurithyris*). Instead, the laminar fabric of the studied Strophomenata shows a weak increase of the thickness of the laminae throughout the Late Permian (Fig. 3; see the Data Repository).

DISCUSSION

Based on our data, shells with type 2 fabric become dominant during the extinction interval (Fig. 2). Since type of substrate or environmental energy is not statistically significant, this change seems not to be related to any parameters that affect the mechanical properties (i.e., hardness) of brachiopod shells (Goetz et al., 2009). The absence of a massive columnar layer, which has less organic matrix (Goetz et al., 2009), indicates that type 2 shells have a total organic/inorganic content higher than those with

type 1 fabric. A higher ratio of organic/inorganic content could be an adaptation to low CaCO_3 saturation caused by increased $p\text{CO}_2$ and low pH of seawater, as shown by modern organisms through latitudinal gradients (see Watson et al., 2012, their figure 2). This is in agreement with the occurrence of small brachiopods in the latest Changhsingian (Zhang et al., 2015; Shi et al., 2016), which could be the result of adaptation to acidified seawater (Garilli et al., 2015), rather than adaptation to low-oxygen or low-nutrient conditions (He et al., 2016). In fact, it is difficult to explain the Late Permian decrease in size as the result of low-oxygen or low-nutrients conditions, because there are clear records of the occurrence of small shells—with type 2 fabric—in oxic and normal nutrient conditions during the latest Changhsingian in South China (Xiang et al., 2016) and north Iran (Garbelli et al., 2014b). Schobben et al. (2015) excluded the possibility of a productivity collapse at the end of the Permian.

It is noteworthy that medium to large shells are also present in several sections close to the boundary (e.g., species of *Peltichia* at Shangsi, or *Costiferina* at Gyanyima; see Shen and He, 1991; Shen et al., 2010). These have a type 2 fabric, which indicates a higher ratio of organic/inorganic content than species disappearing earlier, such as *Permophricodothyris* or *Tyloplecta*, which were equipped with a thick tertiary columnar layer.

Hence, toward the PTB, one of the strategies adopted by both Strophomenata and Rhynchonellata was to produce a more organic-rich

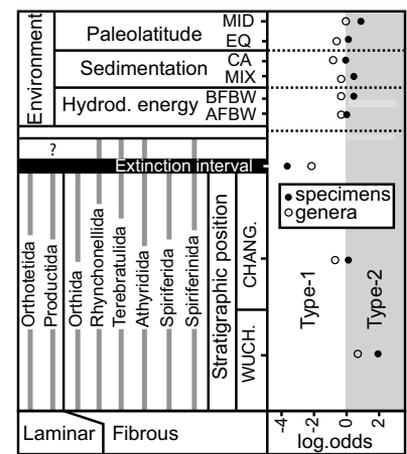


Figure 2. Log odds of fabric type for different stratigraphic positions and environmental parameters considered. On the left, stratigraphic ranges of the two main classes of brachiopod Rhynchonelliformea are plotted; a few species with laminar fabric are obviously reported after extinction interval; only taxa with fibrous fabric survived extinction and still occur today (Curry and Brunton, 2007). MID—middle (~35–45°) latitudes; EQ—equatorial latitudes; CA—carbonate; MIX—mixed siliciclastic-carbonate; AFBW and BFBW—above/below fair wave base, respectively; WUCH.—Wuchiapingian; CHANG.—Changhsingian.

fabric, eventually coupled with a small shell. The distribution of fabric types through the Late Permian has a potential parallel in extant brachiopods. For example, *Liothyrella uva*, an Antarctic species, has a shell with type 2 fabric (Peck et al., 1997) and lives at sites with a lower seawater CaCO_3 saturation state and pH (Watson et al., 2012) than the congeneric *L. neozelanica*, a temperate species with a type 1 shell (Williams et al., 1997). These extant brachiopods do not show variation in shell thickness (Watson et al., 2012), but they do have different shell microstructures.

This parallel with extant species suggests that the observed end-Permian pattern may have been driven by a decrease in pH. This scenario is consistent with our finding of a decrease of the size of the fibers in Rhynchonellata genera (Fig. 3), which implies an increase of the overall surface area of the organic component sheathing the structural units and thus a higher organic content of the shell. It has been proven that the metabolic cost of deposition of CaCO_3 is ~5% of that required for the proteinaceous organic fraction (per unit of shell; Palmer, 1992). The loss of the columnar tertiary layer and the reduction of fiber size suggest that, paradoxically, it was more difficult to induce and control carbonate deposition than secrete a more expensive organic fraction during end-Permian events, which is consistent with acidification.

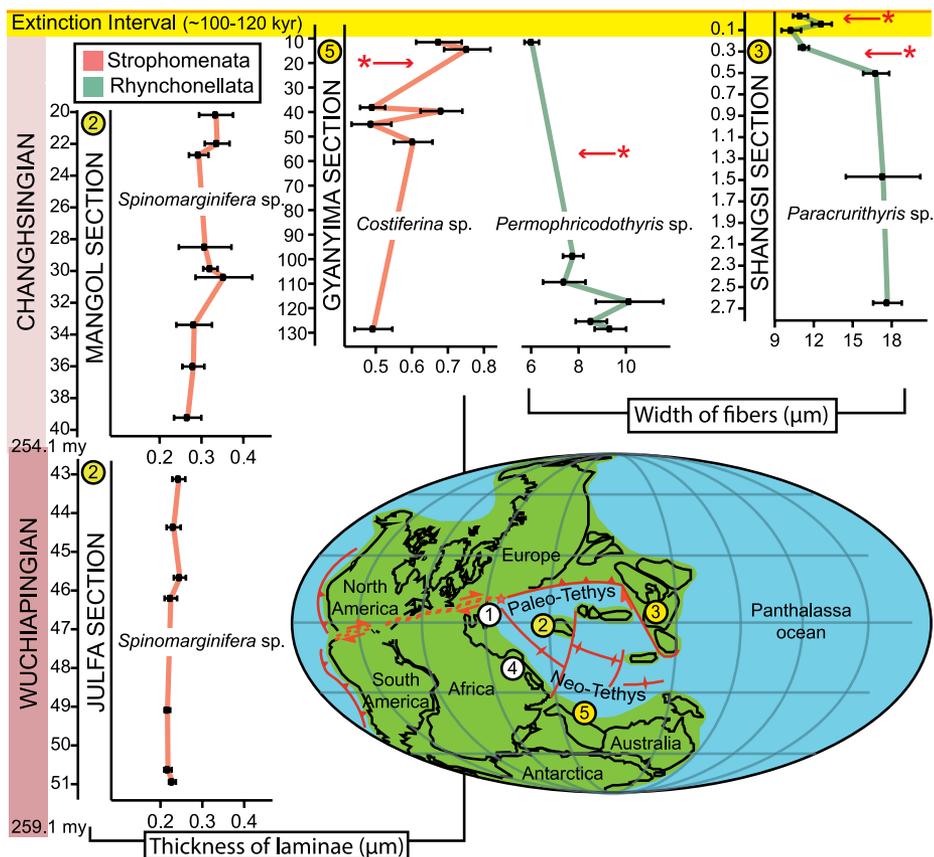


Figure 3. Mean and 95% confidence interval of measures of thickness of laminae (red) and width of the fibers (green) in different localities of the Tethyan Ocean; 1—Dolomites, 2—Iran, 3—South China, 4—Turkey, 5—Tibet. Red asterisks indicate where value is significantly different for two contiguous intervals following Welch *t*-test; red arrow indicates direction of change. Stratigraphic logs are in meters.

The pattern observed in type 2 shells of *Strophomenata* taxa before the PTB is less clear (Fig. 3). They have a weak tendency to increase the thickness of their laminae, suggesting a poor capacity to produce smaller structural units. The *Strophomenata*, besides having a different lifestyle and physiology (Pérez-Huerta and Sheldon, 2006), also had different secretion mechanisms to *Rhynchonellata*, as their calcitic units seem to have been secreted on impersistent protein strands exuded by collective cell surfaces (Williams and Cusack, 2007). This suggests that the two classes had a different capacity to cope with acidification. The *Rhynchonellata* were able to maintain calcification at low pH and to partially repair shell dissolution at sustainable metabolic costs, a trait that seems to be retained by some modern representatives of the group (Cross et al., 2015); however, the *Strophomenata* remained in an evolutionary dead end, since, after the loss of their type 1 fabric, they could not further reduce their calcite structural units. They became extinct at the end-Permian or in the earliest Triassic (Fig. 2; Curry and Brunton, 2007).

During acidification, end-Permian high seawater temperature (Brand et al., 2012) could have played a role in shell fabric modifications, enhancing metabolic rate for the organisms

(Gillooly et al., 2001). Oxygen depletion has been excluded because it is a local phenomenon, not associated with most of the sections investigated here. A primary production collapse would have favored the *Strophomenata*, which are better adapted to low nutrient supply (Pérez-Huerta and Sheldon, 2006), which is not consistent with the observed pattern.

CONCLUSIONS

Our new approach has led to the following conclusions:

(1) There was a change in the type of shell fabric in both *Strophomenata* and *Rhynchonellata* throughout the Late Permian. Just before and during the extinction, brachiopods preferentially produced shells composed only of secondary fabric and thus were more organic rich. The brachiopod taxa that adopted this strategy were initially able to cope with end-Permian environmental change.

(2) Modern fibrous *Rhynchonellata* continue shell production and repair under acidified conditions. It is clear that, also in the past, this group had a strong control over calcification; thus, they were able to reduce their calcification rates during the end-Permian, whereas the *Strophomenata*, after the loss of the tertiary layer, were

probably not able to further reduce the amount of carbonate in their shells.

(3) The study of brachiopod shell biomineralization suggests that the observed trend of shell size reduction is not unequivocally related to oxygen depletion or primary production collapse, but it could be related to the increased metabolic cost of precipitating a large carbonate shell as pH decreases.

(4) Because the observed changes are consistent with variations in seawater carbonate saturation state during the latest Permian (Brand et al., 2016), the rising of ocean acidification could have been one important kill mechanism of the mass extinction.

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