Calcite/aragonite ratio fluctuations in Aptian rudist bivalves: Correlation with changing temperatures

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Calcite/aragonite ratio fluctuations in Aptian rudist bivalves: Correlation with changing temperatures

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ABSTRACT

Understanding how bivalves responded to past temperature fluctuations may help us to predict specific responses of complex calcifiers to future climate change. During the late-Early Aptian, aragonite-rich rudist bivalves decreased in abundance in northern Tethyan carbonate platforms, while rudists with a thickened calcitic outer shell layer came to dominate those of Iberia. Seawater cooling and variations in calcium carbonate saturation states may have controlled this faunal turnover. However, our understanding of how rudist lineages responded to changing environmental conditions is constrained by a lack of quantitative data on the evolution of thickness, size, and mineralogy of the shell. This study is based on volumetric measurements of the shell and shows the transition in lineages of the family Polyconitidae from aragonite-rich mineralogy in the earliest Aptian, to low-Mg calcite-dominated mineralogy in the middle Aptian, returning to aragonite-dominated composition in the latest Aptian. The platform biocalcification crisis that occurred at the Early-Late Aptian boundary in the Tethys was marked by a relative increase of calcite and a decrease in skeletal thickness and commissural diameters. The highest calcite/aragonite (Cc/A) ratios in polyconitid rudists accompanied the late Aptian cold episode, and the lowest values were reached during the warmer intervals of the earliest and latest Aptian. These results imply a correlation between Cc/A ratio values and temperature and suggest that some bivalves adapted to less favorable calcification conditions by changing calcite and aragonite proportions of their bimineralic shells and decreasing skeletal thickness, thereby reducing the metabolic cost of shell growth.

INTRODUCTION

The effects of the present variations in calcium carbonate saturation states and seawater temperature on benthic marine calcifiers, especially on bivalves, are still poorly understood, making it difficult to predict the responses of modern carbonate-producing biota to climate change. Previous studies have shown that bivalves exposed to their thermal tolerance limits reduce metabolic activity (Pörtner, 2008). Decrease in calcium carbonate saturation is known to have detrimental effects on marine calcifying organisms; consequences in bivalves include depressed rates of calcification and growth (Beniash et al., 2010). Evolutionary responses to thermal extremes and reduced conditions for calcification have not yet been detected in the field or laboratory due to temporal constraints on observation (e.g., Ries et al., 2009). Alternatively, the question of evolutionary adaptation to biocalcification crises can be addressed by studying the geologic past. Most time intervals of the Phanerozoic had higher atmospheric CO_2 concentrations than today, exceeding those predicted for upcoming centuries. For example, high atmospheric CO_2 levels during the Aptian (125–112 Ma) arose from the emplacement of large igneous provinces and led to major oscillations of temperature (Steuber et al., 2005; McAnena et al., 2013), and hypothetically of oceanic pH and carbonate ion concentrations in seawater (Weissert and Erba, 2004). In addition, Aptian seas were characterized by low Mg/Ca ratios (Steuber and Rauch, 2005). The interaction of these environmental constraints has been identified as the prime cause of postulated Aptian calcification crises among calcareous plankton (Erba et al., 2010) and benthic calcifiers (Masse, 1989) in the mid-Early Aptian and mid-Aptian, respectively. Rudist bivalves (Order Hippuritida) possessed large shells consisting of an outer calcitic and an inner aragonitic layer (see Fig. DR1 in the GSA Data Repository[1]); they underwent extinctions and radiations closely associated with changes in their mode of life and composition of the shell (Skelton, 2003).

Changes through time of shell size, mineralogy, and thickness were investigated in *Polyconites* and *Horiopleura*, two lineages of polyconitid rudists, in order to determine evolutionary responses of these bivalves to calcification crises, and long-term changing temperatures. Quantitative trends in calcite/aragonite (Cc/A) and shell/cavities (Sh/Cav) ratios were measured and plotted against a summarized paleotemperature curve for the Aptian, within a well-constrained chronostratigraphic framework based on biostratigraphy and Sr isotope dating.

GEOLOGICAL SETTING OF THE STUDIED SPECIMENS

Specimens of the rudist genera *Polyconites* and *Horiopleura* analyzed here were sampled from Aptian platform carbonates across Iberia (Fig. 1), from the Cresmina section (Fig. DR2A) in the Lusitanian Basin in Portugal (Burla et al., 2008), Barranco de la Hoz (Fig. DR2B) and Pico Rope (Fig. DR2B) sections in the South Iberian Basin in Spain (Mas, 1981), and Las Mingachas (Fig. DR2C), Barranco de las Corralizas (Fig. DR2D), Barranco de la Serna (Fig. DR2E), and Las Cubetas sections in the Maestrat

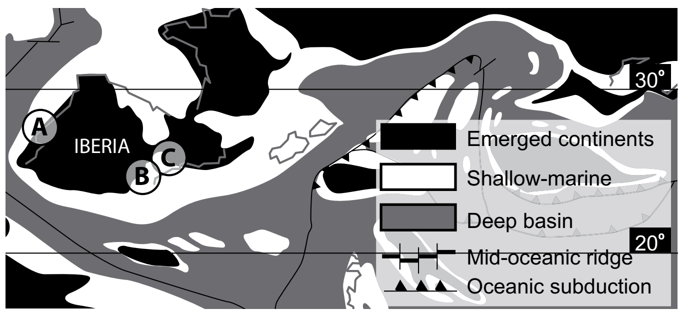

Figure 1. Paleogeography of the Aptian showing the localities of collected specimens (modified from Skelton and Gili, 2012; map based on Masse et al., 2000). A—Lusitanian Basin; B—South Iberian Basin; C—Maestrat Basin.

†Deceased

[1]GSA Data Repository item 2016035, digitalized tomograms, stratigraphic position of studied specimens, ontogenetic Cc/A ratio value variations, all Cc/A ratios by tomogram throughout time, size changes in *Polyconites*, Sr isotopes, summary table with Cc/A and Sh/Cav ratios, and Cc/A ratio statistics, is available online at www.geosociety.org/pubs/ft2016.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

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Basin in Spain (Bover-Arnal et al., 2010). These sedimentary successions were calibrated by Sr isotopic age estimates (Fig. DR2; Table DR1). The Sr isotope data were complemented by rudist and benthic foraminiferal and ammonite biostratigraphy (Mas, 1981; Masse et al., 1998; Masse, 2003; Burla et al., 2008; Moreno-Bedmar et al., 2010; Skelton et al., 2010).

METHODS

Cc/A and Sh/Cav ratios were measured on 16 specimens of polyconitids (Tables DR2 and DR3). The specimens were serially ground and scanned by a flatbed scanner (see details in Pascual-Cebrian et al., 2013). The state of preservation of the shells was evaluated optically. Shells with major breakage and dissolution were rejected. Calcitic shell layers preserve the original fibrous-prismatic microstructures while originally aragonitic shell layers are replaced by blocky calcite cements. The areas corresponding to internal cavities and to outer calcitic and inner aragonitic shell layers of 1064 tomograms were digitized (Figs. DR3 and DR4). Pixels matching the internal cavities and the calcitic and aragonitic shell layers were counted separately (Figs. DR1 and DR3), and used to calculate the Cc/A and Sh/Cav ratios (Figs. 2A and 3). To estimate specimen size variations in the successive chronospecies of the *Polyconites* lineage (*P. hadriani* and *P. verneuili*), the average values between the dorso-ventral and antero-posterior commissural diameters of 214 specimens were calculated for each sample (Fig. DR5).

RESULTS

Cc/A ratios range between 0.24 and 0.65 for *Horiopleura* and between 0.66 and 2.37 for *Polyconites* (Fig. 2A; Table DR2). The lowest values were identified for *Horiopleura* during the earliest and latest Aptian (Cc/A = 0.27, 0.24), whereas the highest values were shown by the genus *Polyconites* during the early-Late Aptian (Cc/A = 2.37). On average, there was an 83.6% positive shift in the Cc/A ratio in *Polyconites* between 122.3 Ma and 120.9–118.5 Ma, followed by a 52.8% decrease at 114.1 Ma. The *P. hadriani* shells analyzed from the late-Early Aptian are significantly more calcitic (Cc/A ratio mean = 1.11; n = 6) than shells of *H. dumortieri*, for which the measured mean Cc/A ratio is 0.46 (n = 2). The Sh/Cav ratio values in *Polyconites* vary between 0.46 and 2.27, and in *Horiopleura* vary between 0.86 and 1.85 (Table DR2; Fig. 3). Average ratio values were

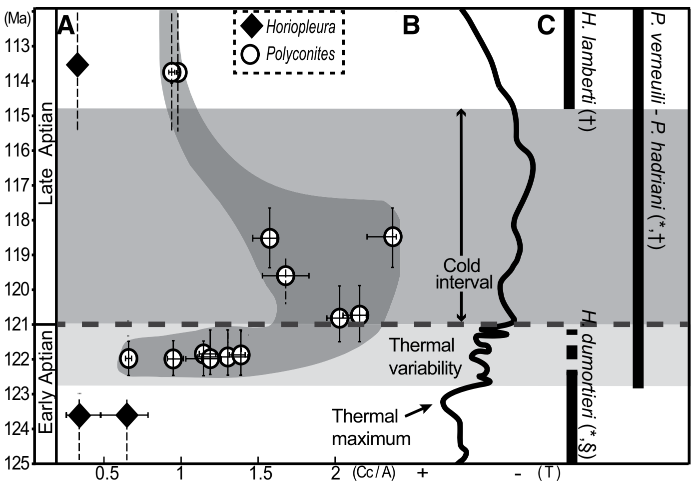

Figure 2. A—Calcite/aragonite (Cc/A) fluctuations in polyconitids. B—Generalized paleotemperature trends modified from Skelton and Gili (2012) and incorporating the late Aptian cold episode from Bottini et al. (2015). *T*—temperature. C—Stratigraphic ranges: (*) Skelton et al. (2010); (†) Masse et al. (1998), and including Paquier (1905), who described *Horiopleura almerae* Paquier in Castellví de la Marca; (§) Masse (1996). P.—*Polyconites*; H.—*Horiopleura*. Dashed line—mid-Aptian biocalcification crisis.

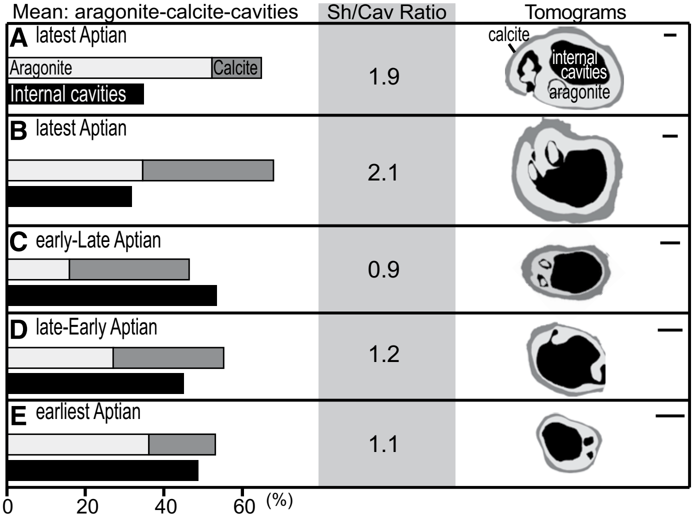

Figure 3. Correlation summary of mean values of shell mineralogy (calcite and aragonite) and internal cavities expressed in relative percentages; shell/cavities ratios (Sh/Cav R.); representative tomograms (scale 10 mm). A: *Horiopleura lamberti*: RP01. B: *Polyconites verneuili*: CH01 and CH02. C: *P. hadriani*: CH10, CH15, AZ08, BC01, and BC02. D: *P. hadriani,* LSM01, LSM02, LSC01, LM01, LM02 and LM03. E: *H. dumortieri*: Dm01 and Dm02.

constant in *Horiopleura* and *Polyconites* between the earliest Aptian and the early-Late Aptian (Sh/Cav ~ 1; Figs. 3C–3E), but values increased to >1.9 during the latest Aptian, which corresponds to the time interval with highest values observed for both genera (Figs. 3A and 3B).

During the Aptian, commissural diameters of *Polyconites* ranged between 20 and 77 mm (Fig. DR5). The smallest commissural diameters were identified during the first appearance of the taxon during the middle-Early Aptian, and were followed by an increase of 42 mm during the latest Early Aptian. From the latest Early Aptian to the earliest Late Aptian, the commissural size decreased to mean and maximum values of 25 mm and 36 mm, respectively. Subsequently, they showed a progressive increase until the latest Aptian; mean and maximum values of 72 and 77 mm, respectively, were measured.

DISCUSSION

During the earliest Aptian, rising relative sea level, climatic warmth, and low-latitude aridity permitted a phase of widespread carbonate platform growth that extended northward around the Atlantic and northern Tethyan margins (Burla et al., 2008; Skelton and Gili, 2012; Masse and Fenerci-Masse, 2013). While platform-top environments hosted abundant requieniid rudists of clinger morphotype, in which thickening of the outer (calcitic) shell layer was most likely adaptive for broad shell attachment, the platform margins were dominated by large, free-lying recumbent or shallowly implanted caprinids, with a thinned outer shell layer and therefore with low Cc/A ratios (Masse, 2003; Skelton and Gili, 2012).

The environmental changes leading to oceanic anoxic event 1a (OAE1a) were associated with a reduction of calcium carbonate saturation states (Weissert and Erba, 2004), followed by an increased rate of burial of organic carbon (Fig. 2B; late OAE1a) and associated drawdown of atmospheric CO_2 that may have caused colder conditions (Kuhnt et al., 2011; Mutterlose et al., 2014). The late-Early Aptian increase in Cc/A ratios observed in Iberia can directly be associated with changing temperatures, as in lower paleolatitudes with warmer seawater (e.g., Arabia), platform-margin rudist communities were still dominated by caprinids (e.g., Hughes, 2000), and thus remained aragonite-dominated (Skelton and Gili, 2012). In Iberia, however, a progressive decline in the relative abundance of caprinids on the platform margins was associated with cooling (Bover-Arnal et al., 2015). Polyconitids, by contrast, thrived in the late-Early Aptian seas with the appearance of a new genus, *Polyconites*, derived from the previously somewhat sparsely represented *Horiopleura* (Skelton et al., 2010). *Polyconites hadriani* increased the proportion of calcite in the shell (average Cc/A ratio = 1.5) with respect to its ancestor. This new calcite-dominated mineralogy could explain its successful adaptation to the new environmental conditions, as indicated by its abundance on the carbonate platforms of Iberia. Moreover, a rapid phyletic size increase is observed in the *Polyconites* lineage, from its first appearance to the latest Aptian (Fig. DR5).

The late Aptian was likely a period with intensified cooling (Kuhnt et al., 2011; Bottini et al., 2015; Fig. 2B). This change in climatic conditions was accompanied by a biocalcification crisis around the boundary between the Early and Late Aptian (Masse, 1989). Across this boundary, rudist biodiversity decreased (Steuber, 2002), and aragonite-rich rudist bivalves largely disappeared from the Tethyan record until the latest Aptian (Masse, 1989; Skelton and Gili, 2012). In Iberia, *Polyconites* maintained its abundance, although individual shell size decreased (Fig. DR5), and Cc/A ratio values increased from <1.39 to >1.58 (Fig. 2A). Colder seawater, possibly accompanied by a biocalcification crisis, likely favored calcite-rich families, while low Mg/Ca ratio values of the seawater may have contributed to this mineralogical turnover (Steuber, 2002).

An increase in temperature during the latest Aptian (Steuber et al., 2005; Bottini et al., 2015; Fig. 2B) was accompanied by an increase in rudist diversity in Iberia (Masse et al., 1998), favoring aragonite-rich taxa such as the genus *Horiopleura* that reappeared in the record (Fig. 2C) after ~6–8 m.y. of absence. Ameliorating conditions for biocalcification are inferred from the highest Sh/Cav ratio values, recorded in both *Horiopleura* and *Polyconites* (Figs. 3A and 3B), and the increase of the proportion of aragonite in the shell of *Polyconites* (average Cc/A ~ 0.95). Temperature curves for the Aptian correlate to the measured Cc/A ratio values (Figs. 2A and 2B). High Cc/A ratio values were detected for the colder conditions of the middle Aptian, and low Cc/A ratios were identified for the earliest and latest Aptian warmer periods.

The relative increase, during colder periods, in the Cc/A ratio is consistent with the thermal potentiation hypothesis of Carter et al. (1998), who suggested that cold waters kinetically favor the precipitation of calcite, a polymorph that may subsequently be promoted due to its mechanical advantages. However, this hypothesis alone cannot explain the mineralogical changes, as bivalves have a strong biological control on mineralization. A direct correlation between cooling and calcite-dominated shells is not necessarily given in the geological record (Hautmann, 2006), and additional factors such as seawater chemistry, ecological factors, specific demands of a mode of life, and metabolic costs of biomineralization must be considered. The mineralogical changes observed here support a relative increase of calcite during a cold episode, without shedding enough light on the possible promotion of calcite due to mechanical advantages. Skelton et al. (2010) proposed that the expansion of the calcitic outer shell layer of *Polyconites* with respect to *Horiopleura*, along with other morphological changes, allowed for a wider growth extension of the ventral valve margin and hence closer packing of clustered individuals. Nevertheless, this possible ecological advantage would not explain mineralogical fluctuations documented here for the *Polyconites* lineage.

Thickening of the outer calcitic shell layer could also confer a selective advantage against dissolution, by virtue of the greater resistance of calcite to dissolution in aragonite-undersaturated seawater (Taylor and Reid, 1990). If so, a thickened outer calcitic shell layer, as seen in *Polyconites* with respect to its ancestor, could have favored this genus in the theorized scenario of latitudinal cooling owing to CO_2 drawdown, in the context of still relatively high atmospheric CO_2 levels and therefore lowered aragonite saturation. The latter hypothesis remains to be tested, but recent studies indicate high atmospheric CO_2 levels during the Aptian, 4–6× pre-industrial levels, with peaks during the earliest and latest Aptian (Li et al., 2014). Shell microstructures and periostracum may also play an important role in controlling shell dissolution, rather than the polymorph type alone (Harper, 2000).

The geological record suggests that rudist bivalves had narrow thermal tolerance windows, and thus were sensitive to thermal shifts. For example, cooling episodes during the Hauterivian and Barremian restricted some families to low latitudes (Masse and Fenerci-Masse, 2008). Physiologically, bivalves exposed to their thermal tolerance limits respond by changing their geographical distribution or by reducing their metabolic activity (Pörtner, 2008). This may explain why aragonite-rich bivalves, mostly the caprinoid clade of rudists (Skelton, 2013), spread around the Atlantic-Tethyan-Pacific platforms during relatively warm periods (Skelton et al., 2013), whereas colder temperatures led to a contraction of their geographical range to the central and southern Tethyan margins (Skelton and Gili, 2012). The Aptian cold episode (Fig. 2B) may thus have metabolically stressed the precipitation and maintenance of thick aragonite-rich shells, especially on the northern margin of the Tethys, and favored calcite-rich shells that offered the advantage of lowering metabolic costs of shell secretion (Hautmann, 2006). The progressive increase in Cc/A ratio values observed in *Polyconites* may therefore explain the successful adaptation of this lineage to the Aptian cold interval. Phyletic size decrease (Fig. DR5) may also reflect the necessity of balancing metabolic costs. Consequently, the change from aragonite-dominated to calcite-dominated shells would mainly represent an evolutionary adaptation to adverse thermal regimes. This hypothesis is also reinforced by the coeval proliferation of the Radiolitidae, with a thickened calcitic outer layer as well as an innovative mesostructure of hollow cells, interpreted as an adaptive strategy to minimize the metabolic cost of shell secretion (Fenerci-Masse et al., 2006).

The reappearance in Iberia of the genus *Horiopleura*, postdating the late Aptian cold episode (Fig. 2C), and the contemporaneous decrease in Cc/A ratios and shell thickening observed in *Polyconites* (Figs. 2A and 3) suggest that with the return of favorable conditions, aragonite-rich shells were preferred, because they offered better properties for their mode of life.

CONCLUSIONS

Our results indicate that an inverse correlation existed between Cc/A ratios in polyconitid rudists and paleotemperatures. A progressive increase in Cc/A ratios is observed during the mid-Aptian cold episode, while lower Cc/A ratios and shell thickening are correlated to warmer periods. Temperature variability is considered a major environmental stress factor in an Aptian world characterized by low and stable Mg/Ca ratios and high but variable pCO_2 concentrations. This is especially the case for hypercalcifying bivalves with thick aragonite-rich shells and narrow thermal tolerance windows that responded to adverse temperatures by changing geographical ranges or reducing costs for shell growth.

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Calcite/aragonite ratio fluctuations in Aptian rudist bivalves: Correlation with changing temperatures

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