

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

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16 **ABSTRACT**

17 Understanding how bivalves responded to past temperature fluctuations may help
18 us to predict specific responses of complex calcifiers to future climate change. During the
19 late-early Aptian, aragonite-rich rudist bivalves decreased in abundance in northern
20 Tethyan carbonate platforms, while rudists with a thickened calcitic outer shell layer
21 came to dominate those of Iberia. Seawater cooling and variations in calcium carbonate
22 saturation states may have controlled this faunal turnover. However, our understanding of

23 how rudist lineages responded to changing environmental conditions is constrained by a
24 lack of quantitative data on the evolution of thickness, size, and mineralogy of the shell.
25 This study is based on volumetric measurements of the shell and shows the transition in
26 lineages of the family Polyconitidae from aragonite-rich mineralogy in the earliest
27 Aptian, to low-Mg calcite-dominated mineralogy in the middle Aptian, returning to
28 aragonite-dominated composition in the latest Aptian. The platform biocalcification crisis
29 that occurred at the early-late Aptian boundary in the Tethys was marked by a relative
30 increase of calcite and a decrease in skeletal thickness and commissural diameters. The
31 highest calcite/aragonite (Cc/A) ratios in polyconitid rudists accompanied the late Aptian
32 cold episode, **[[SU: no quotes marks needed]]** and the lowest values were reached
33 during the warmer intervals of the earliest and latest Aptian. These results imply a
34 correlation between Cc/A ratio values and temperature and suggest that some bivalves
35 adapted to less favorable calcification conditions by changing calcite and aragonite
36 proportions of their bimineralic shells and decreasing skeletal thickness, thereby reducing
37 the metabolic cost of shell growth.

38 INTRODUCTION

39 The effects of the present variations in calcium carbonate saturation states and
40 seawater temperature on benthic marine calcifiers, especially on bivalves, are still poorly
41 understood, making it difficult to predict the responses of modern carbonate-producing
42 biota to climate change. Previous studies have shown that bivalves exposed to their
43 thermal tolerance limits reduce metabolic activity (Pörtner, 2008). Decrease in calcium
44 carbonate saturation is known to have detrimental effects on marine calcifying
45 organisms; consequences in bivalves include depressed rates of calcification and growth

46 (Beniash et al., 2010). Evolutionary responses to thermal extremes and reduced
47 conditions for calcification have not yet been detected in the field or laboratory due to
48 temporal constraints on observation (e.g., Ries et al., 2009). Alternatively, the question of
49 evolutionary adaptation to biocalcification crises can be addressed by studying the
50 geologic past. Most time intervals of the Phanerozoic had higher atmospheric CO₂
51 concentrations than today, exceeding those predicted for upcoming centuries. For
52 example, high atmospheric CO₂ levels during the Aptian (125–112 Ma) arose from the
53 emplacement of large igneous provinces and led to major oscillations of temperature
54 (Steuber et al., 2005; McAnena et al., 2013), and hypothetically of oceanic pH and
55 carbonate ion concentrations in seawater (Weissert and Erba, 2004). In addition, Aptian
56 seas were characterized by low Mg/Ca ratios (Steuber and Rauch, 2005). The interaction
57 of these environmental constraints has been identified as the prime cause of postulated
58 Aptian calcification crises among calcareous plankton (Erba et al., 2010) and benthic
59 calcifiers (Masse, 1989) in the mid-early Aptian and mid-Aptian, respectively. Rudist
60 bivalves (Order Hippuritida) possessed large shells consisting of an outer calcitic and an
61 inner aragonitic layer (see Fig. DR1 in the GSA Data Repository¹); they underwent
62 extinctions and radiations closely associated with changes in their mode of life and
63 composition of the shell (Skelton, 2003).

64 Changes through time of shell size, mineralogy, and thickness were investigated
65 in *Polyconites* and *Horiopleura*, two lineages of polyconitid rudists, in order to determine
66 evolutionary responses of these bivalves to calcification crises, and long-term changing
67 temperatures. Quantitative trends in calcite/aragonite (Cc/A) and shell/cavities (Sh/Cav)
68 ratios were measured and plotted against a summarized paleotemperature curve for the

69 Aptian, within a well-constrained chronostratigraphic framework based on
70 biostratigraphy and Sr isotope dating.

71 **GEOLOGICAL SETTING OF THE STUDIED SPECIMENS**

72 Specimens of the rudist genera *Polyconites* and *Horiopleura* analyzed here were
73 sampled from Aptian platform carbonates across Iberia (Fig. 1), from the Cresmina
74 section (Fig. DR2A) in the Lusitanian Basin in Portugal (Burla et al., 2008), the Barranco
75 de la Hoz (Fig. DR2B) and Pico Rope (Fig. DR2B) sections in the South Iberian Basin in
76 Spain (Mas, 1981), and the Las Mingachas (Fig. DR2C), Barranco de las Corralizas (Fig.
77 DR2D), Barranco de la Serna (Fig. DR2E), and Las Cubetas sections in the Maestrat
78 Basin in Spain (Bover-Arnal et al., 2010). These sedimentary successions were calibrated
79 by Sr isotopic age estimates (Fig. DR2; Table DR1). The Sr isotope data were
80 complemented by rudist and benthic foraminiferal and ammonite biostratigraphy (Mas,
81 1981; Masse et al., 1998; Masse, 2003; Burla et al., 2008; Moreno-Bedmar et al., 2010;
82 Skelton et al., 2010).

83 **METHODS**

84 Cc/A and Sh/Cav ratios were measured on 16 specimens of polyconitids (Tables
85 DR2 and DR3). The specimens were serially ground and scanned by a flatbed scanner
86 (see details in Pascual-Cebrian et al., 2013). The state of preservation of the shells was
87 evaluated optically. Shells with major breakage and dissolution were rejected. Calcitic
88 shell layers preserve the original fibrous-prismatic microstructures while originally
89 aragonitic shell layers are replaced by blocky calcite cements. The areas corresponding to
90 internal cavities and to outer calcitic and inner aragonitic shell layers of 1064 tomograms
91 were digitized (Figs. DR3 and DR4). Pixels matching the internal cavities and the calcitic

92 and aragonitic shell layers were counted separately (Figs. DR1 and DR3), and used to
93 calculate the Cc/A and Sh/Cav ratios (Figs. 2A and 3). To estimate specimen size
94 variations in the successive chronospecies of the *Polyconites* lineage (*P. hadriani* and *P.*
95 *verneuili*), the average values between the dorso-ventral and antero-posterior
96 commissural diameters of 214 specimens were calculated for each sample (Fig. DR5).

97 RESULTS

98 Cc/A ratios range between 0.24 and 0.65 for *Horiopleura* and between 0.66 and
99 2.37 for *Polyconites* (Fig. 2A; Table DR2). The lowest values were identified for
100 *Horiopleura* during the earliest and latest Aptian (Cc/A = 0.27, 0.24), whereas the highest
101 values were shown by the genus *Polyconites* during the early-late Aptian (Cc/A = 2.37).
102 On average, there was an 83.6% positive shift in the Cc/A ratio in *Polyconites* between
103 122.3 Ma and 120.9–118.5 Ma, followed by a 52.8% decrease at 114.1 Ma. The *P.*
104 *hadriani* shells analyzed from the late-early Aptian are significantly more calcitic (Cc/A
105 ratio mean = 1.11; n = 6) than shells of *H. dumortieri*, for which the measured mean
106 Cc/A ratio is 0.46 (n = 2). The Sh/Cav ratio values in *Polyconites* vary between 0.46 and
107 2.27, and in *Horiopleura* vary between 0.86 and 1.85 (Table DR2; Fig. 3). Average ratio
108 values were constant in *Horiopleura* and *Polyconites* between the earliest Aptian and the
109 early-late Aptian (Sh/Cav ~ 1; Figs. 3C–3E), but values increased to >1.9 during the
110 latest Aptian, which corresponds to the time interval with highest values observed for
111 both genera (Figs. 3A and 3B).

112 During the Aptian, commissural diameters of *Polyconites* ranged between 20 and
113 77 mm (Fig. DR5). The smallest commissural diameters were identified during the first
114 appearance of the taxon during the middle-early Aptian, and were followed by an

115 increase of 42 mm during the latest **early** Aptian. From the latest **early** Aptian to the
116 earliest **late** Aptian, the commissural size decreased to mean and maximum values of 25
117 mm and 36 mm, respectively. Subsequently, they showed a progressive increase until the
118 latest Aptian; mean and maximum values of 72 and 77 mm, respectively, were measured.

119 **DISCUSSION**

120 During the earliest Aptian, rising relative sea level, climatic warmth, and low-
121 latitude aridity permitted a phase of widespread carbonate platform growth that extended
122 northward around the Atlantic and northern Tethyan margins (Burla et al., 2008; Skelton
123 and Gili, 2012; Masse and Fenerci-Masse, 2013). While platform-top environments
124 hosted abundant requieniid rudists of **clinger** **[[SU: no quote marks]]** morphotype, in
125 which thickening of the outer (calcitic) shell layer was most likely adaptive for broad
126 shell attachment, the platform margins were dominated by large, free-lying recumbent or
127 shallowly implanted caprinids, with a thinned outer shell layer **and therefore** with low
128 Cc/A ratios (Masse, 2003; Skelton and Gili, 2012).

129 The environmental changes leading to oceanic anoxic event 1a (OAE1a) were
130 associated with a reduction of calcium carbonate saturation states (Weissert and Erba,
131 2004), followed by an increased rate of burial of organic carbon (Fig. 2B; late OAE1a)
132 and associated drawdown of atmospheric CO₂ that may have caused colder conditions
133 (Kuhnt et al., 2011; Mutterlose et al., 2014). The **late-early** Aptian increase in Cc/A ratios
134 observed in Iberia can directly be associated with changing temperatures; as in lower
135 paleolatitudes with warmer seawater (e.g., Arabia), platform-margin rudist communities
136 were still dominated by caprinids (e.g., Hughes, 2000), and thus remained **aragonite**
137 **dominated** (Skelton and Gili, 2012). In Iberia, **however**, a progressive decline in the

138 relative abundance of caprinids on the platform margins was associated with cooling
139 (Bover-Arnal et al., 2015). Polyconitids, by contrast, thrived in the late-early Aptian seas
140 with the appearance of a new genus, *Polyconites*, derived from the previously somewhat
141 sparsely represented *Horiopleura* (Skelton et al., 2010). *Polyconites hadriani* increased
142 the proportion of calcite in the shell (average Cc/A ratio = 1.5) with respect to its
143 ancestor. This new calcite-dominated mineralogy could explain its successful adaptation
144 to the new environmental conditions, as indicated by its abundance on the carbonate
145 platforms of Iberia. Moreover, a rapid phyletic size increase is observed in the
146 *Polyconites* lineage, from its first appearance to the latest Aptian (Fig. DR5).

147 The late Aptian was likely a period with intensified cooling (Kuhnt et al., 2011;
148 Bottini et al., 2015; Fig. 2B). This change in climatic conditions was accompanied by a
149 biocalcification crisis around the boundary between the early and late Aptian (Masse,
150 1989). Across this boundary, rudist biodiversity decreased (Steuber, 2002), and
151 aragonite-rich rudist bivalves largely disappeared from the Tethyan record until the latest
152 Aptian (Masse, 1989; Skelton and Gili, 2012). In Iberia, *Polyconites* maintained its
153 abundance, although individual shell size decreased (Fig. DR5), and Cc/A ratio values
154 increased from <1.39 to >1.58 (Fig. 2A). Colder seawater, possibly accompanied by a
155 biocalcification crisis, likely favored calcite-rich families, while low Mg/Ca ratio values
156 of the seawater may have contributed to this mineralogical turnover (Steuber, 2002).

157 An increase in temperature during the latest Aptian (Steuber et al., 2005; Bottini
158 et al., 2015; Fig. 2B) was accompanied by an increase in rudist diversity in Iberia (Masse
159 et al., 1998), favoring aragonite-rich taxa such as the genus *Horiopleura* that reappeared
160 in the record (Fig. 2C) after ~6–8 m.y. of absence. Ameliorating conditions for

161 biocalcification are inferred from the highest Sh/Cav ratio values, recorded in both
162 *Horiopleura* and *Polyconites* (Figs. 3A, 3B), and the increase of the proportion of
163 aragonite in the shell of *Polyconites* (average Cc/A ~ 0.95). Temperature curves for the
164 Aptian correlate to the measured Cc/A ratio values (Figs. 2A and 2B). High Cc/A ratio
165 values were detected for the colder conditions of the middle Aptian, and low Cc/A ratios
166 were detected for the earliest and latest Aptian warmer periods.

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

183 Thickening of the outer calcitic shell layer could also confer a selective advantage
184 against dissolution, by virtue of the greater resistance of calcite to dissolution in
185 aragonite-undersaturated seawater (Taylor and Reid, 1990). If so, a thickened outer
186 calcitic shell layer, as seen in *Polyconites* with respect to its ancestor, could have favored
187 this genus in the theorized scenario of latitudinal cooling owing to CO₂ drawdown, in the
188 context of still relatively high atmospheric CO₂ levels and therefore lowered aragonite
189 saturation. The latter hypothesis remains to be tested, but recent studies indicate high
190 atmospheric CO₂ levels during the Aptian, 4–6× pre-industrial levels, with peaks during
191 the earliest and latest Aptian (Li et al., 2014). Shell microstructures and periostracum
192 may also play an important role in controlling shell dissolution, rather than the
193 polymorph type alone (Harper, 2000).

194 The geological record suggests that rudist bivalves had narrow thermal tolerance
195 windows, and thus were sensitive to thermal shifts. For example, cooling episodes during
196 the Hauterivian and Barremian restricted some families to low latitudes (Masse and
197 Fenerci-Masse, 2008). Physiologically, bivalves exposed to their thermal tolerance limits
198 respond by changing their geographical distribution or by reducing their metabolic
199 activity (Pörtner, 2008). This may explain why aragonite-rich bivalves, mostly the
200 caprinoid clade of rudists (Skelton, 2013), spread around the Atlantic-Tethyan-Pacific
201 platforms during relatively warm periods (Skelton et al., 2013), whereas colder
202 temperatures led to a contraction of their geographical range to the central and southern
203 Tethyan margins (Skelton and Gili, 2012). The Aptian cold episode **[[SU: no quote**
204 marks]] (Fig. 2B) may thus have metabolically stressed the precipitation and
205 maintenance of thick aragonite-rich shells, especially on the northern margin of the

206 Tethys, and favored calcite-rich shells that offered the advantage of lowering metabolic
207 costs of shell secretion (Hautmann, 2006). The progressive increase in Cc/A ratio values
208 observed in *Polyconites* may therefore explain the successful adaptation of this lineage to
209 the Aptian cold interval. Phyletic size decrease (Fig. DR5) may also reflect the necessity
210 of balancing metabolic costs. Consequently, the change from aragonite-dominated to
211 calcite-dominated shells would mainly represent an evolutionary adaptation to adverse
212 thermal regimes. This hypothesis is also reinforced by the coeval proliferation of the
213 Radiolitidae, with a thickened calcitic outer layer as well as an innovative mesostructure
214 of hollow cells, interpreted as an adaptive strategy to minimize the metabolic cost of shell
215 secretion (Fenerci-Masse et al., 2006).

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

221 CONCLUSIONS

222 Our results indicate that an inverse correlation existed between Cc/A ratios in
223 polyconitid rudists and paleotemperatures. A progressive increase in Cc/A ratios is
224 observed during the mid-Aptian cold episode, while lower Cc/A ratios and shell
225 thickening are correlated to warmer periods. Temperature variability is considered a
226 major environmental stress factor in an Aptian world characterized by low and stable
227 Mg/Ca ratios and high but variable $p\text{CO}_2$ concentrations. This is especially the case for
228 hypercalcifying bivalves with thick aragonite-rich shells and narrow thermal tolerance

229 windows **that** responded to adverse temperatures by changing geographical ranges or
230 reducing costs for shell growth.

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370 **FIGURE CAPTIONS**

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

374

375 Figure 2. A—**Calcite/aragonite** (Cc/A) fluctuations in polyconitids. B—Generalized
376 paleotemperature trends modified from Skelton and Gili (2012) and incorporating the late
377 Aptian cold episode from Bottini et al. (2015). *T*—**temperature**. **[[SU: ok? italicize T in**
378 **figure]]** C—Stratigraphic ranges: (*) Skelton et al. (2010); (†) Masse et al. (1998), and
379 including Paquier (1905), who described *Horiopleura almerae* Paquier in Castellví de la
380 Marca; (§) Masse (1996). P.—*Polyconites*. Gray dashed line is mid-Aptian
381 biocalcification crisis.

382

383 Figure 3. Correlation summary of mean values of shell mineralogy (calcite and aragonite)
384 and internal cavities expressed in relative percentages; shell/cavities ratios (Sh/Ca R.);
385 representative tomograms (scale 10 mm). A: *Horiopleura lamberti*: RP01. B: *Polyconites*
386 *verneuili*: CH01 and CH02. C: *P. hadriani*: CH10, CH15, AZ08, BC01, and BC02. D: *P.*
387 *hadriani*, LSM01, LSM02, LSC01, LM01, LM02 and LM03. E: *H. dumortieri*: Dm01
388 and Dm02. **[[SU: in C, D, and E, should be lowercase Late and Early before Aptian,**
389 and should be hyphenated (e.g., “early-late Aptian”]]

390

391 ¹GSA Data Repository item 2016xxx, digitalized tomograms, stratigraphic position of
392 studied specimens, ontogenetic Cc/A ratio value variations, all Cc/A ratios by tomogram
393 throughout time, size changes in *Polyconites*, Sr isotopes, summary table with Cc/A and
394 Sh/Cav ratios, and Cc/A ratio statistics, is available online at
395 www.geosociety.org/pubs/ft2016.htm, or on request from editing@geosociety.org or
396 Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.