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Algal constraints on the Cenozoic history of atmospheric CO$_2$?

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Abstract

An urgent question for future climate, in light of increased burning of fossil fuels, is the temperature sensitivity of the climate system to atmospheric carbon dioxide (pCO$_2$). To date, no direct proxy for past levels of pCO$_2$ exists beyond the reach of the polar ice core records. We propose a new methodology for placing an upper constraint on pCO$_2$ over the Cenozoic based on the living geological record. Specifically, our premise is that the contrasting calcification tolerance of various extant species of coccolithophore to raised pCO$_2$ reflects an "evolutionary memory" of past atmospheric composition. The different times of first emergence of each morphospecies allows an upper constraint of past pCO$_2$ to be placed on Cenozoic timeslices. Further, our hypothesis has implications for the response of marine calcifiers to ocean acidification. Geologically "ancient" species, which have survived large changes in ocean chemistry, are likely more resilient to predicted acidification.

1 Introduction

Anthropogenic pCO$_2$ is absorbed largely by the oceans, causing acidification of the biologically productive surface waters (The Royal Society, 2005; Kleypas et al., 2006). Corals, foraminifera and pteropods decrease their calcification in response to increased acidification (Gattuso et al., 1999; Kleypas et al., 1999; Bijma et al., 1999; Orr et al., 2005). Despite the intracellular nature of coccolithophore calcification, culture experiments confirm that *Emiliania huxleyi* and its close relative *Gephyrocapsa oceanica* also decrease calcification as pCO$_2$ increases (Riebesell et al., 2000; Zondervan et al., 2001). Decreased calcification is a negative feedback to acidification on the short term (Zondervan et al., 2001) but poses a serious threat to the sensitive ecologic balance. Ultimately, the rate at which populations acclimatise or adapt to changing ocean chemistry will determine the operation of feedback mechanisms on future climate.

Long-term patterns in coccolithophorid evolution and success seem, however, coun-

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terintuitive to this paradigm of low calcification under high pCO$_2$. Coccolithophore diversity and abundance peaked during the greenhouse Cretaceous world and have since declined (Bown, 2005). In addition, and by contrast to the tests on *E. huxleyi* and *G. oceanica* (Riebesell et al., 2000; Zondervan et al., 2001), recent acidification exper-

5 iments testing the environmental tolerance of different extant coccolithophore species reveal that the calcification response is species-specific (Langer et al., 2006). Calcification ability in the species *Coccolithus pelagicus* is unaffected by values of pCO$_2$ up to at least 920 ppmV, and even though calcification ability declines, coccoliths are still produced up to much higher levels (S. Krug, personal communication). *Calcidiscus lep-*

10 *toporus* shows an "optimum" calcification ability close to modern day pCO$_2$ (Langer et al., 2006). Species-specific effects must be considered when evaluating whole ecosystem response to elevated pCO$_2$. Although representative of few algal strains, these culture results raise a major question: why do different species respond differently to pCO$_2$?

15 **2 Methodology and Hypothesis**

With a geological perspective, the ability of different coccolithophore species to calcify in culture under a range of ocean acidity correlates with likely levels of atmospheric pCO$_2$ since the emergence of their corresponding morphospecies during the Cenozoic (Fig. 1a). Modern *E. huxleyi* and *G. oceanica* are distinct genetic outliers to most other

20 extant coccolithophore (Fujiwara et al., 1994; Sáez et al., 2003), and group together with other alkenone-producing haptophytes such as the non-coccolith bearing species *Isochrysis galbana*. The morphospecies *E. huxleyi* had a first occurrence ~291-268 ka and has risen to global dominance since 85 ka, while *G. oceanica* evolved at 1.7 Ma (Thierstein et al., 1977; Raffi et al., 2007). In contrast, the morphospecies *Calcidiscus*

25 *leptoporus* originated at 23 Ma (Knappertsbusch, 2000) and *Coccolithus pelagicus* in the Palaeocene, ~63 Ma (Haq and Lohmann, 1976). At face value, the levels of pCO$_2$ tolerated in cultures of the different coccolithophorid morphospecies coincide with the

levels of pCO_2 from proxy reconstructions at the time of their emergence (Pagani et al., 2005; Pearson and Palmer, 2000). This evolutionary view of the culture results places an upper constraint on pCO_2 of at most 920 ppmV (and likely higher) since 63 Ma, and 360 ppmV since 23 Ma. Our novel proxy validates the accuracy of the indi-
5 rect alkenone proxy for pCO_2 (Pagani et al., 2005), and concurs with an emerging view of different climate sensitivities before and after the marked draw-down of pCO_2 at the early Oligocene (Lowenstein and Demicco, 2006). We predict, with further experiments to push the calcification tolerance of *C. pelagicus* and additional modern representa- tives of ancient morphospecies, a tight bracketing of palaeo-pCO_2 estimates for the
10 Palaeogene, especially in combination with a fixed minimum early Eocene pCO_2 of 1125 ppmV, as reconstructed by stability fields of sodium carbonates (Fig. 1a; Lowen- stein and Demicco, 2006).

3   Discussion

Our statement that genetically "older" extant species are able to calcify at higher pCO_2
15 in these culture experiments, and that this envelope of ability may constrain past pCO_2 estimates, requires detailed consideration.

Which of the carbonate system parameters dictates the calcification ability of different coccolithophore species? To date, this remains unclear. Calcification and photosyn- thesis are intricately coupled due to the energy requirement for the transport of Ca^{2+}
20 and CO_3^{2-} into the coccolithophore cells, and control of intracellular pH. In the culture experiments, as in the modern ocean, the carbonate saturation state and pH are in- versely proportional to pCO_2, with coherence between lower energetic requirement for calcification at high saturation and pH, and lower photosynthetic energy available from low pCO_2. Rather than a calcification dependency on saturation state, pH or $[CO_3^{2-}]$
25 alone, the critical factor determining the calcification tolerance of different species may be the photosynthetic capacity to harvest energy from CO_2. In the geological past, carbonate saturation state and pCO_2 were likely decoupled (Tyrrell and Zeebe, 2004).

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But in culture, *C. pelagicus* tolerates conditions (Krug pers. comm.) beyond the limit of modern surface waters (Orr et al., 2005) and indicative of a different past carbonate system or pH.

Is evolutionary capability preserved without degradation? The modern species *Cruciplacolithus neohelis* produces coccoliths that are highly similar to its Palaeogene counterpart, and persistently secretes low Mg-calcite in the high Mg/Ca modern ocean and in culture manipulations (Stanley et al., 2005). This evidence implies that calcification ability can be determined, in an "ancient" species, by the chemical composition of seawater at the time of origin and conserved for many millions of years. The preservation of calcification tolerance may occur through genetic redundancy (Wagner, 1999), variance in genetic expression or ecological generalism versus specialism (Richmond et al., 2005). Our proposed evolutionary perspective requires that the coupled photosynthetic and calcification potential of the various taxa is optimised for ocean carbonate chemistry at their time of origin and has been locked into genetic make-up since pCO_2 declined. Currently, little is known about genetic controls on calcification (e.g. Marsh, 2003; Nguyen et al., 2005), or the detailed photosynthetic mechanism of coccolithophores. Cells optimise their photosynthesis by increasing surface area to volume, maximizing light acquisition, increasing Rubisco specificity (Tortell, 2000), and carbon concentrating mechanisms (Giordano et al., 2005). Coupling of calcification with species-specific Rubisco specificity provides a tangible means to preserve the CO_2/O_2 composition at the time of origin of photosynthetic phyla (Giordano et al., 2005; Tcherkez et al., 2006).

Using cell size as an indicator of photosynthetic capacity, today, *E. huxleyi* stands out as one of the smallest coccolithophores alive, and is best adapted to low pCO_2 values, whereas *C. pelagicus* represents one of the largest. Further, the morphological template and the mean coccolith size, linearly related to cell size, have remained largely constant for *Coccolithus* during the Cenozoic decline of pCO_2 (Fig. 1b; Henderiks, unpublished data[1]). In contrast, the Cenozoic ancestors of *Gephyrocapsa* and *Emiliania*,

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[1]Coccolith morphometric data on 99 deep-sea sediment samples, ranging in age 2.2 ka–

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within the *Reticulofenestra* genus, have greatly varied in coccolith size, with largest morphospecies (14–20 μm) occurring during the late Eocene (Backman and Hermelin, 1986). The presence of large, heavily calcified *C. pelagicus* since the Palaeogene, and recent origination of small, lightly calcified *E. huxleyi* corroborates our hypothesis that the photosynthetic potential or calcification ability is set by the conditions at the time of emergence and can be preserved over millions of years despite large changes in pCO_2. Indeed the preservation of *C. pelagicus*' calcification ability may be enhanced because this species prefers a high pCO_2 niche. *C. pelagicus* prevailed in Palaeocene equatorial regions (Haq and Lohmann, 1977), and was only restricted to high pCO_2 subpolar and upwelling niches since the late Pliocene (Sato et al., 2004).

4 Concluding remarks

A direction for future research is to diversify, with more ancient species, investigation into calcification and photosynthesis under a range of ocean carbonate conditions, nutrient levels and temperatures. Nonetheless, our ideas have implications for the future ocean. With fossil fuel burning and a predicted decrease in pH of ∼0.3 over the next 100 years (The Royal Society, 2005), the larger species will likely have an advantage over the now prosperous *E. huxleyi*, as the carbonate system of the ocean reverses towards the acidity of the past. *C. pelagicus* has weathered large and abrupt changes in conditions in the geological past, e.g. the Palaeocene-Eocene thermal maximum (Gibbs et al., 2006), with no apparent impact on physiology, but the adaptive speed of newcomer *E. huxleyi* may not suffice. If anything, large coccolithophores will be more successful calcifiers, and could act to release CO_2 to the atmosphere with positive feedback on global warming.

57.3 Ma. Mean coccolith size was determined from 100-200 individual coccolith measurements per sample using 4 replicate sprayed slides under polarised light microscopy (Henderiks and Törner, 2006)

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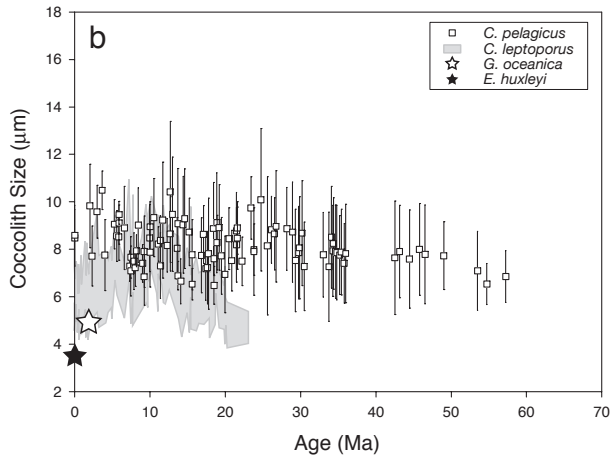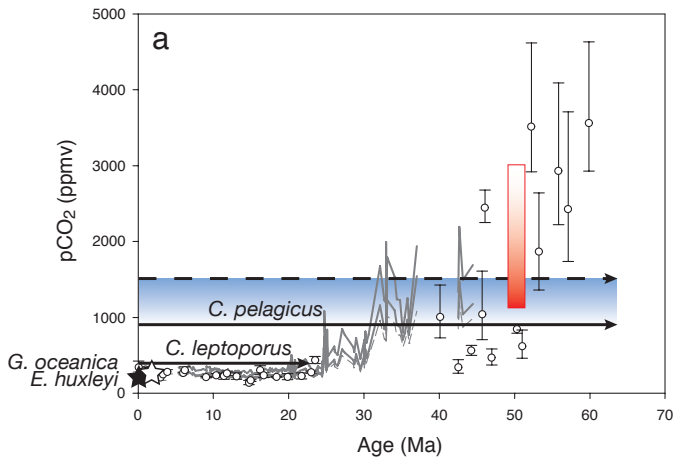Full Screen / Esc

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Fig. 1.

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Fig. 1. **(a)** At face value, the levels of pCO$_2$ tolerated by different coccolithophore species for calcification in culture experiments (Riebesell et al., 2000; Langer et al., 2006) coincide with levels of pCO$_2$ from marine proxy reconstructions, based on alkenones (solid and dashed lines; Pagani et al., 2005) and boron isotopes in planktic foraminifera (open circles; Pearson and Palmer, 2000), at the time of emergence of each respective morphospecies; marked by a star for *E. huxleyi* (291–268 ka; closed star) and *G. oceanica* (1.7 Ma; open star), and solid arrows for *C. leptoporus* (23 Ma) and *C. pelagicus* (∼63 Ma). The upper pCO$_2$ tolerance range for *C. pelagicus* is indicated by the blue box with a solid arrow at the maximum pCO$_2$ at which its calcification remains unaffected (Langer et al., 2006), and dashed arrow showing the potential for this species to determine the Palaeogene maximum pCO$_2$. The red box depicts the pCO$_2$ range in which the sodium carbonate nahcolite precipitates (Lowenstein and Demicco, 2006), fixing minimum early Eocene pCO$_2$ at 1125 ppmV.
(b) Mean coccolith size, a proxy for coccolithophore cell size, has remained largely constant for *Coccolithus* during the Cenozoic decline of pCO$_2$ (open squares ±1 stdev; Henderiks, unpubl. data), and for *Calcidiscus* (grey envelope ±1 stdev; Knappertsbusch, 2000) since the Miocene. Both genera are significantly larger than *E. huxleyi* (closed star), which stands out as one of the smallest, but most prolific calcifying coccolithophore alive today and represents the youngest evolutionary addition (291–268 ka) to the fossil record of calcifying haptophytes.