

Interactive comment on “Algal constraints on the Cenozoic history of atmospheric CO₂?” by J. Henderiks and R. E. M. Rickaby

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Authors' response to Reviewers - Introduction

Our manuscript on the potential use of modern coccolithophores for placing upper constraints on palaeo-pCO₂ over the Cenozoic has received constructive Interactive Comments by three anonymous Referees (on, respectively, 16/01, 22/01 and 28/02/07) and Ulf Riebesell (on 16/02/07). Herewith we would like to respond to the main points brought forward in these reviews. They can be summarised as follows:

1. Adaptation
2. Evolution - potential mechanisms for 'evolutionary memory'
3. What parameter(s) drive(s) calcification?
4. Coccolithophore cell size through time
5. Future Implications

6. Terminology

These specific topics will be consecutively addressed below. We would like to rectify the notion of Referee 2 that *'They do not bring new data or analyses to comfort their hypothesis'*. In fact, we present an extensive new data set in Fig. 1b on coccolith size variability of the *C. pelagicus* morphospecies, in 99 deep-sea sediment samples derived from combined high- and low latitude sites. These data are discussed in context of the grouping between the coccolithophore lineages under discussion (see below). We prefer to present further details of this dataset elsewhere, and focus the present manuscript on our hypothesis in light of current scientific knowledge. However, we will change the reference to this data set from 'Henderiks, unpublished data' to read 'this study', with further clarifications in footnote 1.

1. Adaptation

'The hypothesis presented by Henderiks and Rickaby basically challenges the suggestion that populations of planktonic micro-organisms can adapt very fast to their changing environment' (Ref2)

'Response of Calcidiscus leptoporus typically indicates evolutionary adaptation to present-day values of pCO₂, and cannot be used to reconstruct past pCO₂' (Refs1 and 2)

'broad tolerance in C. pelagicus rather than preference for high pCO₂, indicating that pCO₂ did depart from those limits since this species originated' (Ref3)

We agree with Referee 1 and 2 that the response of *Calcidiscus leptoporus* to variable pCO₂ in culture is consistent with evolutionary adaptation on glacial-interglacial time scales, and that this morphospecies/strain would be unsuitable to use as a palaeo-proxy for pCO₂. The broad, and apparent insensitive, response by *Coccolithus pelagicus* also suggests adaptation to present-day pCO₂ values, but with conservation of the ability to calcify normally under lower, as well as much higher CO₂ concentrations, and therefore potentially represents an 'evolutionary memory' of both the glacial low-pCO₂ and high-pCO₂ Palaeogene worlds.

Indeed, in the marine realm, it would be expected that populations of planktonic microorganisms could quickly adapt to a changing environment. We don't argue against adaptation - obviously, all extant coccolithophores appear to do physiologically well under present-day natural conditions - but we propose to explore whether the calcification mechanism of certain "ancient" coccolithophore morphospecies would still contain its adaptations to pCO₂ levels of the past. From long-term coccolith size evolution, in particular, it appears that the different morphospecies may fall into two groups: morphospecies which are highly adaptive to changing ocean chemistry in terms of their calcification and size, and morphospecies which are highly conservative. Both the evolutionary lineages of *C. leptoporus* and the reticulofenestrid ancestors of *G. oceanica* and *E. huxleyi* demonstrate size ranges which vary widely and probably in concert with the environment. In comparison, based on our morphometric data, *C. pelagicus* has experienced minor long-term change in size during the entire Cenozoic which points to its conservative nature, and its optimal candidacy for retaining an "evolutionary memory".

2. Evolution

'The statement that a complex, most probably multi-functional, physiological process such as calcification is 'frozen' within a given morphotype, is rather strong and needs to be balanced on several aspects' (Ref2)

'Do the authors imply that certain species will preserve a "physiological memory" while others won't? Please explain' (Ref2)

At this point, it is not possible to constrain the likely means by which "evolutionary memory" to calcify under "ancient" levels of pCO₂, may be preserved. Nonetheless, other evidence supports the phenotypic plasticity of biomineralisation. Intriguing evidence that this plasticity reflects past ocean chemistry conditions comes from the results of Maldonado et al. (1999). Relict modern populations of sublittoral silicious demosponges (genus *Crambe*), which have Jurassic ancestry, modulate the phenotypic expression of their spicules depending on the experimental concentrations of silicic

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acid. These organisms only produce lightly silicified spicules in their natural environment, which is likely silicon limited. Under “ancient” chemical conditions of elevated silica concentrations, *C. crambe* proves genetically capable of producing spicule types that are not normally found in natural populations, but have high resemblance to fossil morphotypes (Maldonado et al., 1999). An “ancient” and unexpressed mineralisation pathway becomes activated by changing ambient conditions to be reminiscent of the past. One further piece of anecdotal evidence points to the adaptation of birds and their ability to sustain the most aerobic exercise of flying at extreme high altitudes (Ward, 2006). It has been hypothesized that this physiological adaptation arises due to their shared ancestry with dinosaurs whom developed a unique form of breathing optimized for the low oxygen levels at the time of their origination.

The ability to calcify has most likely evolved only once in haptophytes, in the late Triassic. The presence of non-calcifying taxa within the typical ‘coccolithophore’ phylogenetic clades suggests that the biochemical pathways involved in coccolithogenesis have been shut down and possibly reactivated several times in the course of their evolution (deVargas and Probert, 2004). Still, a relatively simple phylogenetic pattern can be derived based on life-cycle observations and related modes of biomineralisation (Young and Bown, 1997). For example, *C. pelagicus* and *C. leptoporus* produce both heterococcoliths (in diploid phase) and holococcoliths (haploid phase), while *E. huxleyi* and *G. oceanica* appear to have lost the ability to produce holococcoliths (they only produce organic scales in haploid phase). The close phylogenetic affinity of *E. huxleyi* and *G. oceanica* to the non-calcifying haptophyte genus *IsochrYSIS* (Sáez et al., 2004) also suggests that the genetic encoding for calcification is subject to variable evolutionary selection within this organism group, and is susceptible to phenotypic plasticity.

2.1. Potential mechanisms for retaining “evolutionary memory”

Potential mechanisms for retaining an “evolutionary memory” lie in relict genes within the genetic codes of calcification whose expression is triggered by environmental conditions reminiscent of the past. The high proportion of duplicate genes within plant

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and algae genomes is indicative of a high rate of retention of duplicate genes (Lynch and Connery, 2000). Gene duplications contribute to the establishment of new gene functions, and may underlie the origin of evolutionary novelty. Duplicate genes can exist stably in a partially redundant state over a protracted evolutionary period (Moore and Purugganan, 2005). A half-life to silencing and loss of a plant gene duplicate is estimated at 23.4 million years such that remnant duplicate genes, which can be re-activated by environmental conditions to encode calcification within coccolithophores under “ancestral” conditions representative of 60 Ma, appears reasonable.

Additionally (or, alternatively), adaptation to a new ecological niche may result in a “cost” in terms of lost ancestral capabilities (e.g. Bell, 1997; Kassen, 2002) such that the modern *E. huxleyi* has lost the ability to succeed at high $p\text{CO}_2$. These capabilities may be lost either because they are no longer under selection (neutral) or because of a deleterious effect on fitness in a new niche. By contrast, the preservation of *C. pelagicus*’ calcification ability may be enhanced because this species prefers a high $p\text{CO}_2$ niche, which may have played a role in its progressive biogeographic restriction during the Neogene (e.g. Sato et al., 2004; Henderiks, unpublished data). Recent studies are beginning to suggest that adaptation to new ecological niches is associated with gene inactivation. Therefore, evolution of the lightly calcified *Gephyrocapsa* and *E. huxleyi* with fast growing, small cells provides the advantage of investing energy in cell growth, and an ability to outcompete more heavily calcified coccolithophores in a low $p\text{CO}_2$ world. These considerations of the ecological niche or adaptive behaviour do not undermine our hypothesis of proxy application from the environmental tolerance of extant species, but merely provide an alternative insight into how such characteristics of different species may develop, and be preserved.

2.2. Evolution of atmospheric $p\text{CO}_2$

Why would upper tolerance of $p\text{CO}_2$ correspond to time of origin, and not from another period of time later, when $p\text{CO}_2$ was particularly high? How could one, in this context, use the “physiological memory” as a proxy?’ (Ref2)

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Our hypothesis relies on the preservation of physiological plasticity of “ancient” coccolithophore taxa, being recalled by ocean chemistry reminiscent of the past. This would imply the preservation both of the maximum, and minimum values of parameters of influence on coccolithogenesis. We argue that this parameter could be past $p\text{CO}_2$. The proxy, therefore, would allow placement of an envelope of maximum, and minimum $p\text{CO}_2$ experienced by the ancestry of the given morphospecies, backtracking to the emergence of the morphospecies.

In the case of a gradual Cenozoic $p\text{CO}_2$ decline from the Palaeocene into Miocene - with maximum levels during the Palaeocene and lowest $p\text{CO}_2$ in the Miocene - the proposed proxy would indeed place an upper constraint on Palaeocene $p\text{CO}_2$. However, at this stage we cannot exclude that the maximum would reflect particularly high $p\text{CO}_2$ experienced later along the morphospecies' evolutionary lineage, for example, during the late Eocene. Still, we would argue that such a ‘direct’ palaeo-proxy would add great value to the verification of available ‘indirect’ palaeo- $p\text{CO}_2$ proxies.

3. What parameter(s) drive(s) calcification?

As mentioned in our manuscript, the carbonate saturation state and pH are inversely proportional to $p\text{CO}_2$ in the modern ocean as well as in culture experiments. On geological time scales, these parameters were likely decoupled. Tyrrell and Zeebe (2004) argue against large shifts in average surface ocean carbonate saturation state (defined as the product between carbonate ion and Ca^{2+} concentrations). However, their model suggests a secular increase in $[\text{CO}_3^{2-}]$ (from 50 to 200 $\mu\text{mol kg}^{-1}$) and pH (from 7.5 to 8.2) over the last 100 million years, consistent with Cenozoic decline in $p\text{CO}_2$.

For our proposed palaeo- $p\text{CO}_2$ approach to work, the photosynthetic or calcification potential of a (morpho)species must be optimised for an aspect of ocean carbonate chemistry directly related to $p\text{CO}_2$ at the time of origin and, become preserved within the genetic make-up since the ocean and atmosphere chemistry changed. In order for calcification to take place, the coccolithophores must expend energy pumping ions to create a supersaturation within an intracellular vesicle in terms of Ca^{2+} concentra-

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tion, carbonate ion and likely pH. Calcification, therefore, could depend on any carbonate system parameter and without further culture experiments of decoupled carbonate system parameters, such as saturation state, pH and $p\text{CO}_2$, it is impossible to resolve which aspect of ocean chemistry, and which physiological pathway is fundamental to coccolithogenesis.

Still, there exists an intrinsic coupling between photosynthesis and calcification, and between ocean pH and $p\text{CO}_2$. Therefore, we relate our discussion of whether all extant coccolithophore species possess an “evolutionary memory” and how such physiological pathways could be preserved, to $p\text{CO}_2$ as the variant parameter.

As Ulf Riebesell points out, the tight and compensatory coupling between calcification and photosynthesis is not supported by the CO_2 sensitivity of photosynthesis in *C. pelagicus* and *E. huxleyi*. Nonetheless, average PIC/POC ratios of the different species appear to indicate the priority of energy partitioning to photosynthesis and calcification. *E. huxleyi* and *G. oceanica* cells are produced with an average PIC/POC ratio of 0.6-0.8 compared to 1.6-1.8 for both *C. leptoporus* and *C. pelagicus* (Zondervan et al., 2001; 2002; Langer et al., 2006) which could imply a different partitioning priority for energy between photosynthetic carbon fixation and calcification as a result of the $p\text{CO}_2$ at their time of origin. This would imply that both *C. leptoporus* and *C. pelagicus* precipitate more CaCO_3 per mole of C fixed and are efficient calcifiers. By contrast *E. huxleyi* prioritises photosynthetic carbon fixation under low $p\text{CO}_2$ conditions and the cost of calcification to *E. huxleyi* and *G. oceanica* is proportionately larger and expendable as the ocean becomes more acidic.

3.1. The available palaeo- $p\text{CO}_2$ proxies

The authors claim: “At face value, the levels of $p\text{CO}_2$ tolerated in cultures of the different coccolithophorid morphospecies coincide with the levels of $p\text{CO}_2$ from proxy reconstructions at the time of their emergence”. This is not true, the maximum value of $p\text{CO}_2$ tested for pelagicus (915 ppmv) is much lower than available proxies’ estimation (>3000 ppmv) for its time of origination’ (Ref2)

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Currently there is no reliable constraint on palaeo- $p\text{CO}_2$ during the Cenozoic as both boron isotopes (for palaeo-pH) and the carbon isotopic composition in alkenones each suffer from major uncertainties, hence the need for a novel approach. For example, Tyrrell and Zeebe (2004) point out that the magnitude of the rise in pH in their reconstruction for the past 100 My is only half as great as that in Pearson and Palmer (2000). In their model, atmospheric $p\text{CO}_2$ estimates for the Palaeogene level off at 1000 μatm , much lower than the >3000 ppmv estimates of Pearson and Palmer (2000), who calculated atmospheric $p\text{CO}_2$ from past pH estimates based on boron isotopes in foraminiferal carbonate, combined with an assumption that $[\text{Ca}^{2+}]$ has remained proportional to alkalinity. Recently, the boron method has come under further scrutiny due to theoretical uncertainties, constraints on the budget of boron isotopes on long timescales (Pagani et al., 2005), and the importance of environmental factors in controlling the partitioning of isotopes into the carbonate (Wara et al., 2003). Consequently, boron-based high $p\text{CO}_2$ estimates are not highly reliable for the Palaeocene.

4. Coccolithophorid size through time

'The relation between size and CO_2 should either be stated clearly, or rejected' (Ref 3)
'Palaeocene small coccolithophores had to be adapted to high CO_2 values as well as the largest ones'(Ref 3) *'As far as I know, coccoliths were tiny during most of the Paleocene, when $p\text{CO}_2$ was the highest for the Cenozoic?'* (Ref 2)

In terms of our hypothesis, we primarily use the evolution of cell size as an indicator of the conservative nature of the *C. pelagicus* lineage and potentially adaptive behaviour of the reticulofenestrads.

Indeed, both very small and larger coccolithophores co-exist today, and this has been the case throughout the evolutionary history of calcareous nannofossils, since the Mesozoic. This implies that both large and small cells were adapted to the contemporaneous levels of $p\text{CO}_2$. Nevertheless, evidence for evolutionary selection against large coccoliths and heavily calcified nannoliths (e.g. discoasterids) over the Cenozoic supports the notion that larger haptophyte cells (and heavy calcifiers) would be

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more prone to extinction under decreasing $p\text{CO}_2$ and related environmental change (e.g. global cooling, variable nutrient availability, paleoceanography) than would be the smaller morphospecies. Evidently, small taxa also went extinct, contributing to the macroevolutionary trend of coccolithophorid diversity loss since the late Eocene (Bown, 2005). But the presence of small taxa during the Palaeocene does not contradict a potential link between palaeo- $p\text{CO}_2$ and macroevolutionary size patterns in coccolithophores.

5. Future Implications

'Unlikely that Coccolithus pelagicus, although unaffected by increased $p\text{CO}_2$, would expand its niche to become the main blooming coccolithophore' (Ref3)

We do not want to imply that larger, more heavily calcified coccolithophores will take over the cosmopolitan role of *E. huxleyi*. In terms of calcification, we would speculate (as future implications are, by definition, speculations) that the “ancient” *Coccolithus pelagicus* will likely remain unaffected by elevated $p\text{CO}_2$, whereas *E. huxleyi* may adapt to high levels of $p\text{CO}_2$, never before experienced during its Pleistocene evolution, by giving less priority to coccolithogenesis.

6. Terminology

The Referees asked for us to clarify some of the concise terms used in our manuscript. In the revised manuscript, we will remove opaque terms or define terms more precisely, particularly:

‘evolutionary degradation’: this term alluded to evolutionary changes (selection) in the coccolithophore genome, which would result in the loss of genes encoded for calcification under “ancient” sea water chemistry. This would result in reduction of the envelope of potential physiological plasticity. For our proxy to work, such alteration to the genome should not have occurred in *Coccolithus* - however, it appears that *E. huxleyi* has not inherited such physiological plasticity from its reticulofenestrated ancestors, which experienced high levels of $p\text{CO}_2$ (both large and small).

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'calcification tolerance': the tolerance to variable pCO₂ of coccolithophores with respect to calcify normally (with no malformation/incomplete coccolithogenesis).

'calcification ability': the ability to produce coccoliths with no, or only minor, decrease in PIC/POC ratio from those during optimum conditions.

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