



Evolutionary changes in coccolithophorid cell geometry: Implications for past pCO₂ reconstructions

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Reconstructions of atmospheric pCO₂, based on $\delta^{13}\text{C}$ values of diunsaturated alkenones and estimates of the total carbon isotopic fractionation during photosynthetic carbon fixation ($\varepsilon_{p37:2}$), show a distinct decline in pCO₂ during the Oligocene, as well as regionally confined, short-term fluctuations in $\varepsilon_{p37:2}$ during the Miocene. Additional to surface water [CO₂(aq)], $\varepsilon_{p37:2}$ values are controlled by algal growth rates and cell geometry; specifically the ratio of the cell volume to surface area of the cell. Here, we confirm for the first time that substantial evolutionary changes in coccolithophorid cell geometry, based on coccolith morphology, warrant a re-evaluation of pCO₂ reconstructions and interpretations of $\varepsilon_{p37:2}$ trends.

Only a few modern species of haptophyte algae are known to produce alkenones. Their Cenozoic ancestors are species belonging to the *Reticulofenestra* genus, which thus would have been the most probable alkenone producers during that time.

A portion of the $\varepsilon_{p37:2}$ signal during specific events in the Miocene can be strongly explained by changes in cell geometry, in part resolving apparent contradictions between $\varepsilon_{p37:2}$ values and independent nutrient-proxy data from the Miocene record.

Paleogene nannofossil biostratigraphy is marked by the extinction of one of the largest coccolithophorid species, *Reticulofenestra umbilica*, at ~ 31.7 Ma, which falls conspicuously close to a distinct decrease in the long term $\varepsilon_{p37:2}$ trend. Hence, the long term signal cannot be explained by the observed size variability, which in fact implies a steeper slope of change in $\varepsilon_{p37:2}$ during the Oligocene and possibly higher pCO₂ estimates during the late-middle Eocene.