

Nutrient Forcing on the Late Middle Eocene to Early Oligocene (~40-31 Ma) Evolution of the Coccolithophore *Reticulofenestra* (Order Isochrysidales)

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The first size reduction (FSR) of coccolithophores of the Order Isochrysidales, which occurred in early Oligocene (~32 Ma), is of great significance for understanding the lilliput effect that has affected all coccolithophores from late Eocene to this day and generally interpreted as reflecting a global $p\text{CO}_2$ decline. Here we offer a complementary mechanism based on the results of a comprehensive morphometric analysis on the coccoliths of *Reticulofenestra* species that lived during late middle Eocene to early Oligocene (~40-31 Ma), using marine sediments from the South Atlantic Ocean. The results show increased size and decreased abundance of the large group during the late Eocene and early Oligocene, leading to the disappearance of the large *Reticulofenestra* at the FSR and a concurrent decrease in the size variability of the small-medium coccoliths whose diameter of the central opening had become very reduced. We interpret these results in the light of an ecological model designed to link coccolith morphology and trophic strategy: in sunlit oceanic waters the small- to medium-sized, r-selected coccolithophores with smaller coccolith central opening live in deeper, nutrient-rich waters where they rely little on mixotrophy; larger, K-selected species with larger coccolith central opening live in the oligotrophic surface waters where they strongly rely on mixotrophy. On this basis, we propose that the FSR is the mid-term result of the environmental destabilization that occurred at ~35.5 Ma caused by the expansion of eutrophic environments following the establishment of overturning circulation in the Atlantic Ocean.