# Functional Interpretation of the Evolution of Coccolith Morphology in Deep Time: Peering into the Biology of Coccolithophores

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## Abstract

Despite much field and laboratory research, the origin of calcification in coccolithophores remains indeterminate. While most experiments on living species are not applicable to extinct taxa, long-term morphologic changes in lineages under well constrained oceanographic conditions may help elucidate the primary forcing on coccolithophore evolution if examined in the context of fundamental requirements (e.g., nutrient availability) of the living cell. The Order Discoasterales (66–1.92 Ma) was among the most prolific (>600 species, 16 genera) with greatest abundance and diversity in warm oligotrophic waters. Their coccoliths tell a story of morphologic changes that affected also their constituent elements resulting in lightweight constructions that became increasingly cavernous as oligotrophy increased in the Paleocene ocean, leading to increase in surface/volume ratio in keeping with increase in cell size. This likely constitutes direct evidence that coccoliths were involved in regulating cell physiology, both by maintaining a sufficient surface for nutrient absorption when cell volume increases or when nutrient content in seawater decreases, and by determining sinking rates. The cavernous nature of coccoliths further suggest mixotrophic physiology. Calcification may thus have been the innovation permitting the migration of the ancestral coccolithophore from nutrient-rich coastal waters to the blue ocean.

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## INTRODUCTION

Anticipation of the effect(s) of global warming on coccolithophores (Haptophyta) requires identification of the **role of their coccoliths and coccospheres**. Ecologic experiments suggest a multitude of possibilities, among which enhancement of photosynthesis, photodamage protection and armor protection, in particular from grazing (1).

Long-term diversification of coccolithophores may help elucidate the **adaptive role of coccoliths** and bring a complementary perspective on the ecological significance of these abundantly secreted skeletal pieces which accumulate to form deep sea oozes and chalk.

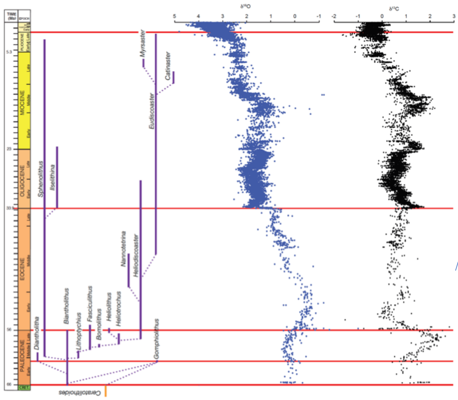

**Fig. 1a: Lineages of the Order Discoasterales and comparison with the Cenozoic history of temperature ($\delta^{18}O$) and nutrients ($\delta^{13}C$) (2, 3)**

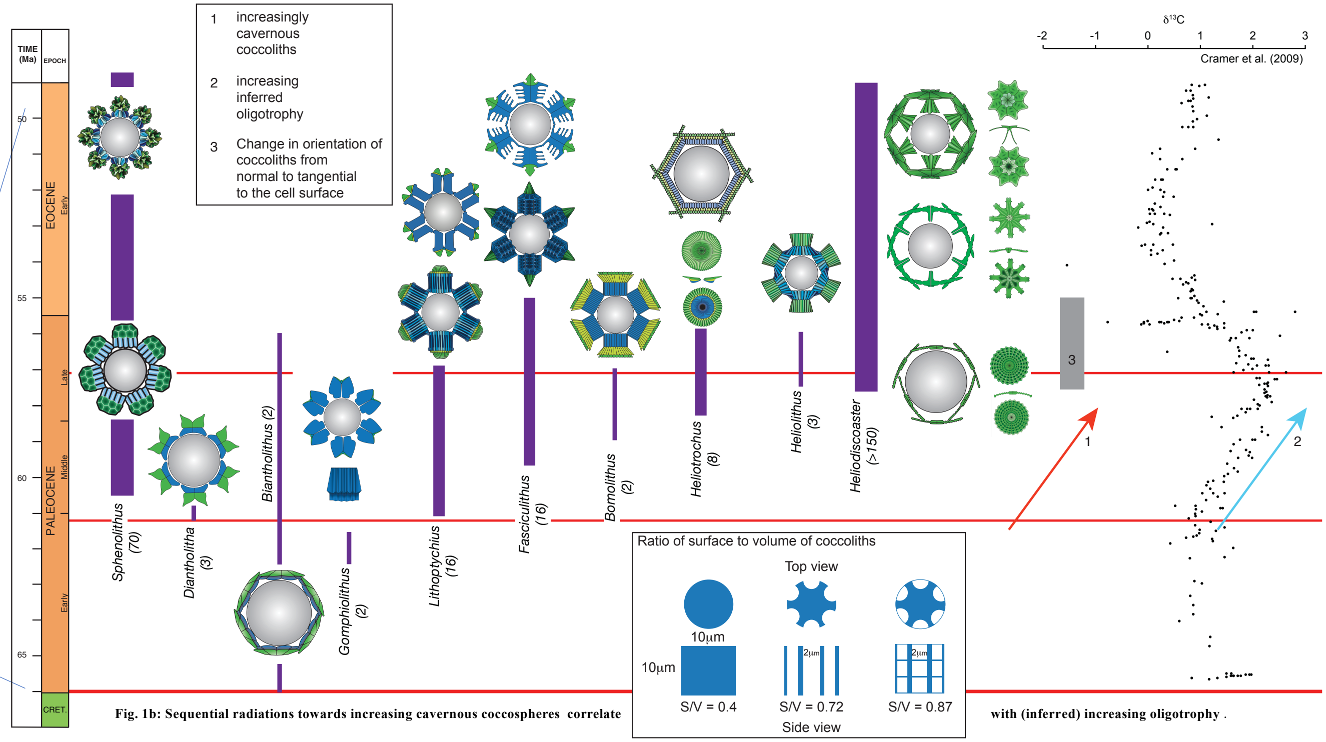


**Fig. 1b: Sequential radiations towards increasing cavernous coccospheres correlate with (inferred) increasing oligotrophy**.

## DISCUSSION

**Coevolution** of Discoasterales and the $\delta^{13}C$ of the ocean from a Middle to Late Paleocene (**4, 5**) evidenced by

a- Coccoliths increasingly more voluminous but also more cavernous through the Paleocene.

b- Evolution of morphology resulted in increase of Surface/Volume (S/V) ratio (**6**) suggesting:

c- Forcing of intensifying Late Paleocene oligotrophy on morphologic diversification

d- Cavernous coccospheres as support for mixotrophic and/or symbiotic activity

**Note: Discoasterales coccoliths and coccospheres were delicate, stiff, light structures— NOT robust and heavily calcified as generally thought.**

## METHODOLOGY

Cenozoic coccoliths of Order Discoasterales (66 Ma–1.92 Ma) are arguably the most diverse in the Cenozoic, representing 7 families, 16 genera and >600 (paleontologic) species (**7**)

This study is based on:

a) Characterization of **coccolith shape**
b) Analysis of **morphostructure** (# + position of cycles and shape + optical orientation + imbrication of elements)
c) Description of **texture** of elements
d) Reconstructions of **coccospheres**

## RESULTS

2 main superposed MSUs with wedge-shaped elements (Figs. 2, 3). Coccospheres modeled from *B. sparsus* (figs. 4, 5).

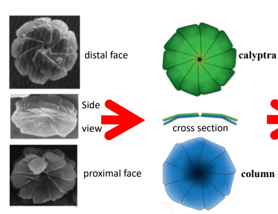


**Fig. 2: Fossil coccolith of ancestral taxon (*Biantholithus sparsus*) and interpretation of MSUs**

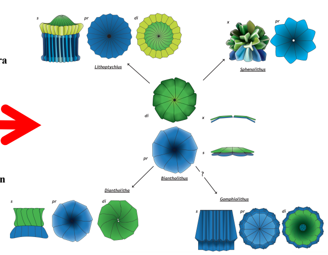

**Fig. 3: Modification of MSUs along selected lineages**

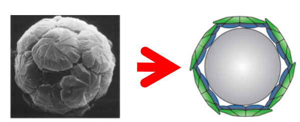

**Fig. 4: Fossil coccosphere of *Biantholithus* and graphic representation.**

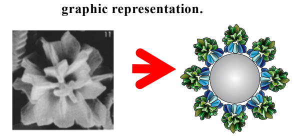

**Fig. 5: Fossil coccolith and graphic representation of corresponding coccosphere.**

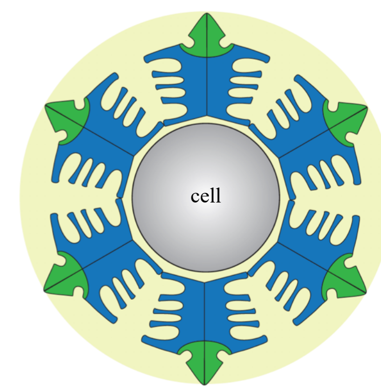


**Fig. 6: Interpretation of the living cell of a Fasciculithus species (Late Paleocene).**

Honeycombed coccoliths and underlying periplastic scales may have formed a structural ***feutrage*** that retained sea-water loaded with nutrients and metabolic products from the cell, offering spaces for **symbiotic and/or mixotrophic activity** (Fig. 6).

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