Evolutionary change in crystallographic orientation and morphology of Cenozoic coccoliths: Insights from *Toweius*, *Reticulofenestra*, and *Umbilicosphaera*

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The interlocking crystal units that form heterococcoliths have two different crystal orientations: near-vertical c-axis (V-unit) and near-horizontal c-axis (R-unit) (Young et al., 1992). The taxonomy of coccolithophores and V/R composition is consistent, suggesting that the crystallographic orientation in coccoliths has a common phylogenetic origin. Comparison of crystallographic orientation among closely related species and between families and genera should show how crystallography contributed to differences in morphology during the evolutionary process. We measured crystallographic orientations of the genera *Umbilicosphaera* (Miocene–Pleistocene), *Reticulofenestra* (Miocene), and *Toweius* (Eocene). The top of the coccolith surface was analyzed using scanning electron microscopy (SEM) and electron back-scattered diffraction (EBSD). If the shield surface was too steep for the electron beam to hit it, as was the case for *Toweius* spp., a cross section of the coccolith was prepared with focused ion beam (FIB) sectioning and analyzed using transmission electron microscopy (TEM). The crystallographic orientation of the distal shield of *Reticulofenestra* was not found to be significantly different from that of the closely related extant genera *Emiliania* and *Gephyrocapsa*, with the c-axis inclined 20˚–30˚ toward the central opening. *Toweius* has two distinct crystal units showing different c-axis directions. The crystallographic orientation of the elements forming the proximal shield and inner cycle of the distal shield was closer to the R-units of *Reticulofenestra*, whereas the c-axis of the outer cycle element of the distal shield seems to be the V-unit. This suggests that evolution from *Toweius* to *Reticulofenestra* was accompanied by loss or miniaturization of the V-unit. The *Umbilicosphaera* lineage shows species-specific differences (e.g., element morphology, presence of bridge, etc.) due to subtle changes in crystallographic orientation and element growth direction (~10˚ in c-axis) (Utsunomiya & Kogure, 2024), but crystallographic orientations of their V- and R-units are clearly different from those of *Toweius* and *Reticulofenestra*. Therefore, crystallographic orientation is considered to have changed with the evolution of the coccolithophores.

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