The V/R model of heterococcoliths biomineralisation 30 years on: Unanswered questions and continuing relevance

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The V/R model of coccolith biomineralization was first published by Young et al. (1992), and so 30 years ago. Broadly this consisted of: (1) Observation that the biomineralization of heterococcolith-rims commonly commenced with nucleation of calcite microcrystals with alternately sub-vertical (V) and sub-radial (R) crystallographic c-axis orientations. (2) Observation that this pattern was conserved through the 230 Ma evolutionary history of heterococcoliths and so likely provided a key to studying homology between taxa. (3) An hypothesis that the nucleation might be controlled by a plicated macromolecular template located around the rim of the cellulosic baseplate.

The model has generally held up well, with support both from application across the biodiversity of extant and fossil heterococcoliths, and from detailed studies of biomineralization in particular species. Nonetheless numerous questions posed by the model remain unanswered and perhaps more surprisingly many taxonomists largely ignore it. This talk will discuss some of the unanswered questions related to the V/R model and why it continues to be a key tool to understand coccolith evolution and taxonomy. Unanswered questions include: Is there a precursor template for the nucleation template, and if not how does the biological system precisely control orientation and spacing of nuclei? Are the V/R orientations precisely 90° apart or does this vary? Nucleation spacing varies around the rim of coccoliths, is this geometrically determined or altered by design? Is variation in nucleation spacing and chirality phylogenetically significant? Nucleation in holococcoliths, in many heterococcolith central-areas and in many nannoliths does not show the V/R pattern, are these radically different biomineralisation modes or are they modifications of the typical V/R mode? Do Syracosphaeraceae really show a V/R/T pattern of nucleation?

The relevance of the V/R model, to practical taxonomy will be discussed with reference to Palaeogene placoliths, such as *Aliculosphaera, Centumgemina, Ericsonia, Hornibrookina*, and *Toweius*. More generally it will be argued that nannofossil taxonomy requires: (1) Tracing of the interconnections of elements to form crystal-units, (2) Determination of the c-axis orientation of crystal-units, and so, (3) Integrated use of electron microscopy and light microscopy (including use of accessory plates and phase contrast).