The microscale exoskeletal reconstruction of the genus *Nannoconus* - taxonomic insights

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Among calcareous nannofossils, the genus *Nannoconus* was the major biocarbonate producer of Early Cretaceous seas (~152 to ~120 Ma). With its heavy calcitic exoskeleton (~200–1100 picograms), it produced massive carbonate accumulations for approximately 30 million years. However, its taxonomic position and biological affinity are not well known. A better understanding of the calcification process from the microstructural arrangement of the exoskeleton can help to close this gap. The *Nannoconus* skeleton is physically characterized by the interlocking arrangement of calcitic laminae (length ~0.5–1 µm, thickness ~100–500 nm) around a central canal. This arrangement results from sets of laminae with two different angles of inclination. Different morphogroups of *Nannoconus* have been classified based on the variability of these angles. A set of ptychography X-ray computed tomography (PXCT) and synchrotron radiation at SWING Beamline of SOLEIL (French synchrotron) was applied to several well-preserved *Nannoconus* skeletons in order to understand the microstructural arrangement at the nanometer level (finer than the thickness of an individual lamina).

The result of the experiment was a series of tomographic image slices (3D resolution ~30 nm) for the exoskeleton of each specimen. One lamina for each species of *Nannoconus* was virtually separated from the image slices using ORS-Dragonfly software. This lamina was used again to reconstruct virtually the entire exoskeleton of *Nannoconus* in the same software. Based on these results, we propose two different models of construction:

Model 1: Two separate layers of plates are formed. The laminae in each layer have a specific inclination. The entire exoskeleton is built by alternatively placing these two layers one above the other.

Model 2: One segment of laminae is created. Each segment is formed by alternately stacking laminae of two different inclinations. The exoskeleton is built by joining several such segments.

Both models show that the exoskeleton was formed by the arrangement of laminae, but each model has a unique growth pattern during calcification. However, model 2, in which segments constitute the building blocks of *Nannoconus*, agrees with scanning electron microscope (SEM) illustrations and descriptions of the structure of *Nannoconus*

and other homococcoliths in the Order Braarudosphaerales, which includes the genus *Braarudosphaera*. Calcification in the latter genus thus provides a good model for the calcification of *Nannoconus* on an external organic template. In the case of *Braarudosphaera*, the template for each segment has a pentagonal shape and the laminae form on vertical columnar stacks. In the case of *Nannoconus*, the template for each segment is of triangular shape and the segments slant in a sinistral direction.