

## Ultrastructure in the Order Braarudosphaerales

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The Order Braarudosphaerales is a group of coccolithophorids with coccoliths that share a structure of circular to polygonal discs made up of a number of radially-arranged, thin polygonal calcite plates that abut or partially overlap each other. In each individual coccolith, multiple discs are vertically stacked upon each other. The number of discs in each coccolith varies greatly between species, resulting in a great range in coccolith height. A central pore in each disc may be present, resulting in a central canal along the long axis of the coccolith. In each disc, the calcite *c*-axis of each of the calcite plates making up the disc is always tangential relative to the centre of the disc.

From genetic studies, it has been shown that the modern species *Braarudosphaera bigelowii* is a coccolithophorid, even though it does not form either hetero- or holococcoliths. The coccoliths of *B. bigelowii* are formed extracellularly, and constitute a third major type of coccolith in the coccolithophorids. It is assumed here that all members of the Order Braarudosphaerales (based on their clearly-shared ultrastructure) are coccolithophorids that form coccospheres of externally-calcified coccoliths.

The Braarudosphaerales originated in the Early Tithonian, with the appearance of *Nannoconus beckmannii* from an unknown ancestor. *Nannoconus beckmannii* is the first member of the Family Nannoconaceae, and possesses coccoliths that are low in height, with 6–10 elements in each disc, with some overlap between adjacent elements. Nannoconid coccolith height and complexity rapidly increased through a long-ranging lineage that went extinct in the Campanian. The number of discs in each coccolith varies greatly between species, from very low (giving an overall form of a thin, flat disc) in *N. magnadiscus*, to very high (giving the form of a tall tapering cylinder) in *N. steinmannii*.

The Family Braarudosphaeraceae originated from *N. beckmannii* with the evolution of *Polycostella senaria* in the mid-Tithonian. Species in the Braarudosphaeraceae have a fixed number of elements in the discs of each coccolith and have no overlap between adjacent elements in each disc, unlike in the Nannoconaceae. With a reduction in the number of elements in each disc from six to five, *Polycostella* gave rise to *Micrantholithus* in the earliest Berriasian, and hence to the long-ranging lineage of pentoliths that continue to the present day. Five elements per disc allow a dodecahedral coccosphere, which further allows the coccosphere to completely enclose the living cell. Completely enclosing the cell isolates it from its environment, which seems to be key for surviving the highly variable chemical and physical conditions in the coastal environments favoured by modern *B. bigelowii*.