

Ultrastructure and taxonomy of the Order Arkhangelskiales

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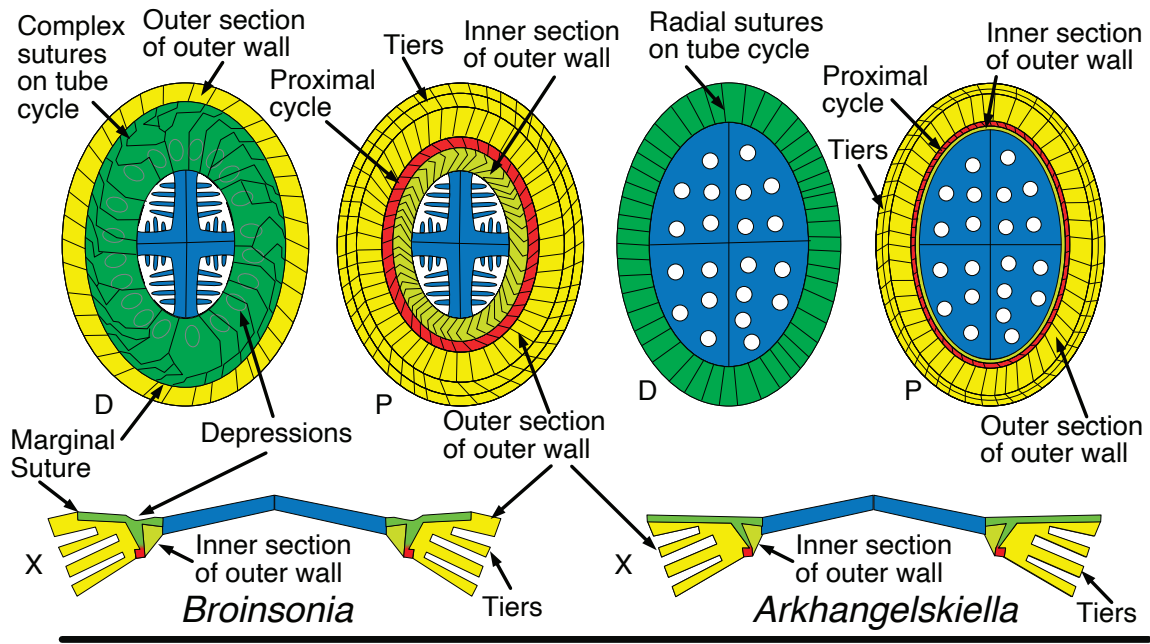
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The Order Arkhangelskiales is a group of Cretaceous heterococcoliths that are united by a common ultrastructure. They are muraliths with a thin and narrow R-unit proximal cycle, a tall and wide V-unit outer wall, an R-unit tube cycle, and a central-area structure (Figure 1). The key innovation that separates the Arkhangelskiales from other Cretaceous muraliths is that the outer wall is wide and grows inward of the tube cycle so that the tube-cycle elements grow upwards through the outer wall, which is not seen in any other group. This divides the outer wall into inner and outer sections, and results in a superficially complex ultrastructure. Another key feature of taxa in the order is the presence of lateral ridges that extend outward from the outer wall, resulting in a tiered appearance in lateral view that superficially resembles placolith morphology. It is unclear whether all taxa within this order have tiers, although most do. In most species, the inner and outer sections of the outer wall meet distally at a marginal suture. A central-area structure is present inside the inner section of the outer wall, usually with a perforate plate or axial cross, and it sometimes has accessory bars.

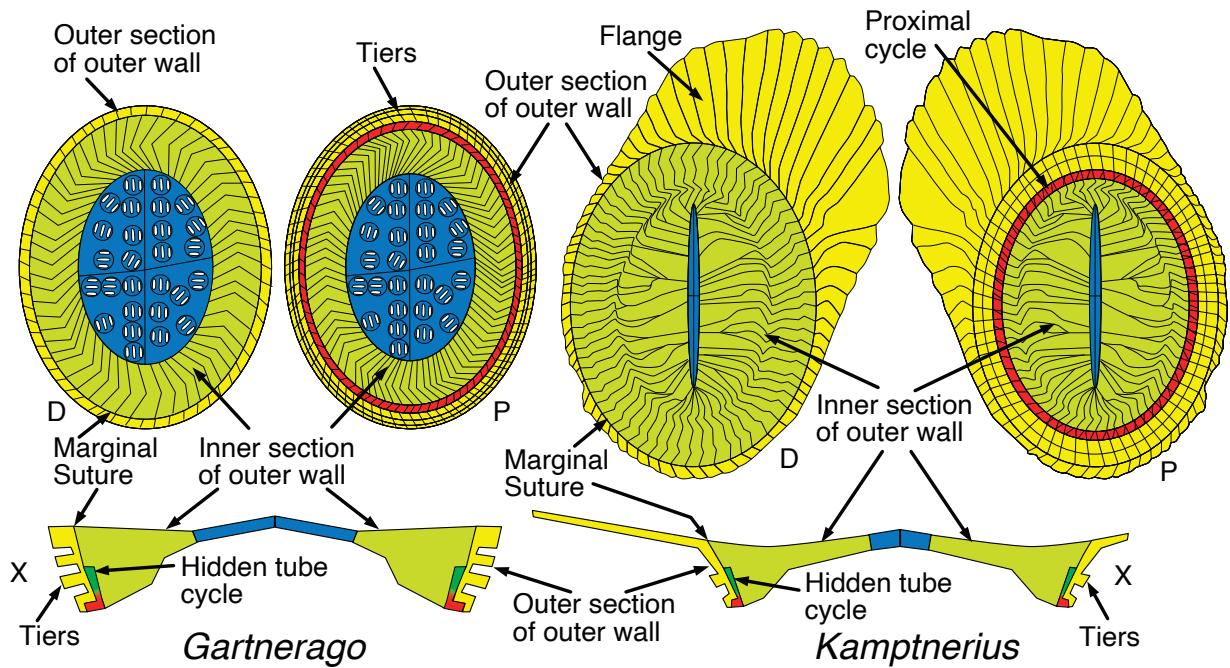
There are two families within the order, the Arkhangelskiellaceae and Kamptneriaceae. These two families have superficially different ultrastructures but clearly have a common origin because they share the key characteristics of the outer wall growing inward of the tube cycle and tiers being present on the outer wall. The evolutionary origin of the order is unclear. The first unambiguous member of the order is *Broinsonia* in the Arkhangelskiellaceae, which appeared in the early Albian. In *Broinsonia* and the closely related *Aspidolithus*, the tube cycle grows up through the outer wall and grows laterally on top of the distal surface of the outer wall where it shows a complex suture pattern between adjacent elements. Outside of the marginal suture, a narrow outer section of the outer wall is present on the distal surface. A single cycle of subcircular depressions is present on the distal surface of the tube cycle in many species of *Broinsonia* and *Aspidolithus*. *Arkhangelskiella* evolved from *Aspidolithus* in the Santonian–Campanian with the tube cycle growing laterally on the distal surface to cover the outer wall mostly or completely, and the complex tube-cycle sutures of *Aspidolithus* became simple radial sutures in *Arkhangelskiella*.

In the Albian–Cenomanian, the Kamptneriaceae evolved from *Broinsonia* through loss of the distal portion of the tube cycle, leaving the distal surface of the inner section of the outer wall exposed. The tube cycle in *Gartnerago* is much narrower than in *Broinsonia*, and on the distal surface it is completely covered by the outer wall, making it visible in the light microscope but not in the electron microscope. The marginal suture marks, where the inner and outer sections of the outer wall meet on the distal surface, completely cover the tube cycle. In *Kamptnerius*, the distal part of the outer section of the outer wall extends laterally to form an asymmetrical flange. The inner section of the outer wall is much wider than in *Gartnerago*, and the central plate is correspondingly reduced in width. The inner section of the outer wall may be perforate.

Correctly characterizing species in the Arkhangelskiales requires careful observation of the tube cycle, both the inner and outer sections of the outer wall, the position of the marginal suture, and the nature of the central-area structure.



ARKHANGELSKIACEAE



KAMPTNERIACEAE

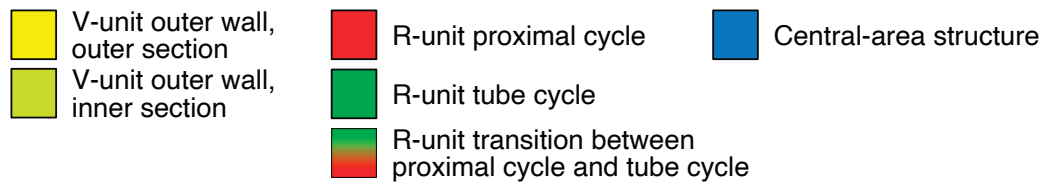


Figure 1. Schematic ultrastructure of the Order Arkhangelskiales. D = distal side, P = proximal side, X = cross section.