

Structural developments within the Family Ceratolithaceae

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The horseshoe-shaped nannoliths, which are commonly known as ceratoliths, have unique calcite crystals that may or may not show birefringence, depending on how they settle into a stable position during smear slide preparation. Raffi et al. (1998) pointed out that the horseshoe structure evolved three different times from *Orthorhabdus rugosus*, which usually does not show any birefringence because in its most stable position it has a middle blade oriented straight up. The c-axis is perpendicular to the length of the nannolith and parallel to this median blade, and at both sides there are two blades in about the same plane (Lancis et al., 2022). This rod-shaped and bladed nannolith has two pointed ends. With the sharper end pointing away from the observer and the median blade face up, the blade to the right is the dextral blade and the one to the left the sinistral blade.

The first two horseshoe developments do not show any birefringence because in their most stable layouts the c-axis points upward and basically coincides with the median blade. Both ceratolith horseshoe structures were produced by the sinistral blade becoming the sinistral arm and the median and dextral blade becoming the dextral arm. The *Amaurolithus branch* started with *A. primus*, which then evolved into *A. delicatus*. *Amaurolithus primus* became extinct in the late Messinian, whereas *A. delicatus* continued into the Pliocene. The second branch consists of only one species, the short lived *Nicklithus amplifiscus*.

From the end of the Messinian to the early Pliocene, a new genus, *Ceratolithus*, evolved from *O. rugosus*. The *Ceratolithus* horseshoe structure is formed by the *O. rugosus* sinistral blade producing the sinistral arm, the dextral arm is formed from the median blade, and the dextral blade becomes reduced to a keel. The genus *Ceratolithus* shows birefringence because the median blade of *O. rugosus* rotated to the right during the evolution of *C. finifer* to be parallel to the most stable layout, thus showing birefringence when observed with cross-polarized light (Lancis et al., 2024). Older specimens of *C. finifer* commonly have low birefringence, whereas younger specimens have high birefringence. The more recent *C. finifer* form evolved into three branches: (1) *C. acutus*, *C. armatus*, *C. cristatus*, and *C. larrymayeri*, (2) *C. atlanticus*, and (3) *C.? tricorniculatus*.

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