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Convergent evolutionary patterns of shell ornamentation in Cretaceous planktonic foraminifera: Was there method to the madness?

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Depth ecology models for Cretaceous planktonic foraminifera have suggested a positive correlation between the size, thickness and ornamentation complexity of foraminiferal shells relative to the depth at which the adult chambers grew. Small sized, thin-walled and weakly ornamented “primitive” species were thought to have had short life spans within the ocean mixed layer whereas larger, thicker walled “complex” species were thought to have had longer life cycles, reaching adult sizes at or near the thermocline. Stable isotope studies of well preserved planktonic assemblages ranging from the late Aptian through late Maastrichtian have suggested that there are a number of exceptions to this depth ecology model, with some “complex” species yielding $\delta^{18}O$ and $\delta^{13}C$ values indicative of growth at relatively shallow depths in the mixed layer and “primitive” species with values that indicate growth at or below the thermocline. However, interpretations of stable isotope cross-plots, from which the depth ecology inferences are based, are not unequivocal, as inter-species differences in stable isotopic signatures could also reflect offsets in the timing of population abundance peaks, with different species reaching abundance maxima during the cooler versus warmer seasons.

Studies of modern planktonic foraminifera have shown that the role of calcite mass in determining shell sinking rates may be significantly counterbalanced by the manufacture of low-density lipids or gases and a high surface area-to-volume ratio of the foraminiferal shell and protoplasm. Growth of thin, elongate spines provides one way for larger sized planktonic foraminifera to increase fluid drag and reduce their settling speed. While the option to grow elongate spines did not exist for Cretaceous planktonic foraminifera, since spinose shells did not evolve until the early Danian, we have to assume that Cretaceous planktonic foraminifera may have had the ability to manufacture lipids and/or gases, and thus could have offset some of the negative buoyancy effects of calcite addition to the shell.

Clues to whether shell morphology and ornamentation had functional significance in Cretaceous planktonic foraminifera may be revealed by interspecies comparison of stable isotopic signatures and biofacies distributions for shell features that have evolved repeatedly among independent lineages. Evidence for convergent evolution is based on iterative occurrences of the following shell ornamentation features:

1) pore mounds, which evolved independently at least four times in the Aptian, late Albian, Turonian, and late Campanian;
2) single peripheral keels, which evolved independently at least sixteen times during the late Albian, early Cenomanian, late Cenomanian, middle Turonian, late Santonian, late Campanian, early Maastrichtian and late Maastrichtian;
3) meridional costellae, which evolved independently three times during the late Albian, early Santonian, and middle Campanian; and
4) double peripheral keels, which evolved independently at least five times during the late Cenomanian, middle Turonian, late Turonian, early Maastrichtian, and late Maastrichtian.

It is noteworthy that the latter two ornamentation features never recur during the Cenozoic. In spite of the prediction that such a high recurrence of these shell features is an indication that they must have imparted adaptive advantages to the living organism, results from this investigation do not provide any new insight as to what those advantages might have been.