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Tempo and mode of planktonic foraminiferal evolution

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Planktonic foraminifera are among the most thoroughly studied fossil groups because of their more complete fossil record and more intensive investigation by a larger number of workers. A scrutiny of the tempo(s) and mode(s) of planktonic foraminiferal evolution will not only greatly enhance their biostratigraphic value but also significantly improve the theory of evolution. Since their initial appearance in the Jurassic, planktonic foraminifera have undergone four major episodes of evolutionary radiation and suffered three major extinctions. All major extinctions wiped out morphologically advanced and complex forms and left a few survivors with simple, generalized morphologies. Each radiation begins with ecological expansion and morphological diversification of survivors. Several morphological trends are iteratively shared by different radiations, such as the development of planispiral tests, clavate chambers, complex umbilical structures, supplementary apertures, increase in number of chambers, and enlargement in test size. These are modifications of the simple morphology of survivors, which are characterized in general by trochospiral tests, umbilical apertures, fewer chambers, smaller size, and globular chambers, and probably represent adaptation-related functional adjustment as a result of natural selection. Even more important is the addition of progressively new characters in later radiations, such as the first occurrence of peripheral keels in the Albian, double keels in the Cenomanian, multiserial tests in the Coniacian, spines in the Danian, spherical tests in the Ypresian, and corticated tests in the Serravallian. The evolution of some new characters is probably related to co-evolution. For example, the development of spines is very likely related to the evolution of floating algal symbionts in the early Danian. Rate of speciation varies significantly and it accelerates after major extinctions. In addition, opportunist species have lower background speciation rate but recover more rapidly following catastrophic extinction event. For example, during their entire >60 Ma range in the Cretaceous, only three species of *Guembelitria* have been recognized, and they are all morphologically similar and probably represent the same biological species. In contrast, only ~30 kyr after the K/T mass extinction, six new species with significantly distinct morphologies evolved from the single survivor species *Guembelitria cretacea*. In contrast, the normal perforate *Hedbergella* clade has moderate speciation rate during background evolution and the rate of speciation accelerated only slightly after the K/T event. Approximately 50k years into the Danian, only six new species have evolved from the rest two K/T survivors (*H. monmouthensis* and *H. holmdelensis*). All of these early Danian normal perforate species can be traced back to corresponding hedbergellid morphotypes in the Campanian and Maastrichtian. In addition, these two survivors had already undergone morphological variation in the Late Cretaceous. Apparently, although the rate of speciation accelerated after the K/T mass extinction, the pace of speciation of the Danian normal perforate planktonic foraminifera from the Late Cretaceous Hedbergellids clearly reflects phyletic gradualism. The quick rise and demise of the opportunists and rapid subsequent replacement by stable mainstream normal perforate planktonic foraminifera indicates that natural selection is operative. Allopatric speciation and stasis are the two key elements of punctuated equilibrium theory (sensu Eldredge & Gould, 1972). While cases of allopatric speciation exist, stasis is not apparent in planktonic foraminiferal evolution. The most important modes of planktonic foraminiferal speciation are cladogenesis, sympatric speciation, variable phyletic "gradualism", and probably phyletic transformation. This is more consistent with the speciation process presented by Charles Darwin, except that the rate of "gradual" change may accelerate more rapidly than the traditional gradualism allows.