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Phylogeny and the evolutionary history of planktonic foraminiferal test size

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Body size is interesting to (paleo)biologists owing to its association with a large number of ecological, developmental, and functional constraints. Investigations of size-related phenomena are arguably of more importance to micropaleontologists because of the wide range of sizes characteristic of microscopic organisms and our lack of experience-based intuition regarding how small organisms are constrained by many environmental variables. Until recently, the analysis of body size changes—along with changes in other metric variables—was undertaken with scant attention paid to the phylogenetic context within which such variations occurred. This approach assumes all taxa included in the study have equal phylogenetic relations to one another; obviously an incorrect assumption. Such an approach also leads to confusion of distinct concepts (e.g., describing decreases in the mean size of a multi-taxon assemblages as examples of 'dwarfing', which is a lineage-specific phenomenon) with consequent confusion over the correct interpretation of hypothesis tests. A recent study of planktonic foraminifera test size variation (Schmidt *et al.*, 2004. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 212:159–180) recognized three time-ordered patterns of change that appeared to correlate with temperature and productivity fluctuations in the world ocean. However this study ignored the phylogenetic component of relations among species. The conclusions of this study may be valid in their own context, but they may also not fully express lineage specific trends. Certainly they cannot be used to test macroevolutionary hypotheses. A clade-specific, comparative investigation based on 17 different planktonic foraminifer lineages has identified five distinct modes of evolutionary test-size variation and allowed the relative frequency of these modes to be estimated. Results of this phylogeny-based analysis using the maximum parsimony analysis reveals important patterns undocumented by the Schmidt et al. study. Planktonic foraminifera are characterized by high lineage-specific phylogenetic test size differentials (= net increase-decrease in test size relative to ancestral conditions) during the Lower Cretaceous, but these rates fall off markedly throughout the Upper Cretaceous. Upper Cretaceous planktonic are large, but only because they evolved from large ancestors. Trans-K-T lineages are characterized by modest levels phyletic size decrease at the intra-specific level, a result consistent with many morphometric studies, but not recovered by Schmidt *et al.*. After the K-T turnover phylogenetic test size differentials increased progressively to an early Paleocene maxima after which it fell to zero in the early Eocene, picked up again in the middle Eocene, and soared to a pronounced peak in the late Eocene. Neogene phylogenetic test size differentials also exhibit a phased character with maxima in the early Miocene and a sustained plateau of dramatically elevated phylogenetic test size differentials for the late Miocene-Recent. Overall, this pattern differs strongly from that proposed by Schmidt *et al.* (2004), especially through the Cretaceous and Palaeogene. Much more work needs to be done in documenting global patters of planktonic foraminiferal test size variation. However, the results obtained by this investigation illustrate the importance of adopting an explicitly phylogenetic approach if the richness of planktonic foraminiferal evolutionary dynamics is to be revealed.