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SIZE VARIABILITY IN
PLANKTIC FORAMINIFERS

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ABSTRACT

Planktic foraminifers are a major marine calcareous microfossil group. Their shells are abundant in most oceanic sediments. This unique pelagic sediment record of the deep sea was used to investigate macro-evolutionary changes in the test size of planktic foraminiferal assemblages, the impact of physical factors on morphological diversity and the biotic response to environmental perturbations. The pelagic sedimentary record is exceptionally complete, with global coverage available from well-dated deep-sea cores recovered by international drilling programs (DSDP, ODP).

Previous work has shown that test size of planktic foraminiferal species can be related to ecological factors such as temperature (Bé et al. 1973; Hecht 1976), upwelling intensity (Naidu and Malmgren 1995) and environmental variability (Bé and Duplessy, 1976; Naidu and Malmgren, 1995) (Chapter 1). In addition, it has been shown that test size changes during evolution (Malmgren et al., 1983; Corfield and Shackleton, 1988; Kucera and Malmgren, 1998). Most studies of evolutionary size changes in planktic foraminifers have focused on single species or lineages (e.g. Malmgren and Kennett, 1981; Arnold, 1983; Malmgren et al., 1983; Spencer-Cervato and Thierstein, 1997; Kucera and Malmgren, 1998; MacLeod et al., 2000).

This study rather focuses on changes in the entire planktic foraminiferal assemblages, which holds the potential of gaining insights into long-term macro- evolutionary processes. The maximum diameter of more than 1.6 million foraminifers was measured with an automated light microscope for three different data sets (Chapter 2). In each sample, the size spectrum of the entire assemblage was measured. Since size spectra are strongly skewed towards large size, the value separating the largest 5% from the smallest 95% of the assemblage was taken as an estimator for assemblage size changes and called assemblage size.

Ecological influences on size are identifiable in analyses of Holocene assemblages. The correlation between ecological changes and test size changes has been tested and confirmed in late Quaternary records. These new insights are used to interpret the Cenozoic planktic foraminiferal size record.

In the Holocene, geographical variations in the size distribution within the entire foraminiferal assemblage are related to environmental gradients, e.g. temperature and primary productivity, in the ocean (Chapter 3). Temperature-related effects, the main driving force behind assemblage size changes, results in an increase in size from polar to tropical biogeographic zones. However, this increase is not linear, and deviations are the result of secondary environmental factors such as primary productivity and the dynamics of frontal

systems. Upwelling areas and frontal systems are regions of high environmental variability associated with decreased sizes with respect to the temperature-size trend.

In the Quaternary, environmental control of size change in planktic foraminiferal species has been documented in the Pleistocene (Bé and Duplessy, 1976; Malmgren and Kennett, 1978; Naidu and Malmgren, 1995). The size response to temporal environmental changes during glacial-interglacial cycles mimics the spatial Holocene size variations. The same processes, which drive geographic assemblage size changes in the Holocene, are correlated with short term temporal size variations in the Quaternary. The amplitude of assemblage size variation is directly related to the amplitude of the Quaternary climatic fluctuations (Chapter 4). More stable environments display the least assemblage-size variation. Assemblage-size variation may either be the result of species replacement or intraspecific size variation, or both. The relative importance of these processes depends on the environmental setting. In the subtropics and tropics, small temperature variations cause strong changes in the composition of the largest species in the assemblage since the temperature optima of the species are very close to each other. In the subpolar environment, the temperature optima of individual species differ greatly and the species have a wider temperature tolerance. Therefore, intraspecific size changes without species replacement are more likely to happen in this environment. During the Quaternary, species distributions and sizes oscillated along a north-south gradient. This implies that species are adapted to certain environmental conditions and persist as long as a suitable habitat can be found and occupied.

On longer time scales, evolutionary size changes become important. Results from previous studies suggest that climatic change is the principal instigator of evolutionary change within planktonic foraminiferal faunas in the Cenozoic (e.g. Ciffeli, 1969; Lipps 1970), and more specifically, that there is a fundamental linkage between amplitude of changes and steepness of surface water gradients and periods of speciation or extinction.

The size record in the Cenozoic can be divided into three different intervals, a time of dwarfs from the K/T boundary up to the late Eocene, a transition period from the late Eocene to the Mid-Miocene and a time of giants from the Mid-Miocene to Recent (Chapter 5). The early Paleogene is characterised by an increase in size ranges after the K/T reduction and similar foraminiferal assemblage size is at all latitudes, indicating little provincialism. In the middle Eocene, high latitude and low latitude assemblage sizes became decoupled as a consequence of the steepening of the latitudinal temperature gradients caused by cooling in the high latitudes (Lear et al., 2000). In the early Miocene, subtropical and tropical assemblage size become differentiated. A

pronounced size increase in the Neogene is observable in all warm water sites studied, whereas high-latitude records display size stability during this period.

The large sizes of warm water late Neogene planktic foraminiferal assemblages are unprecedented in the geological record. This suggests that this increase in size is a reaction to niches partitioning as a consequence of the intensification of vertical and latitudinal temperature gradients. Size changes in the assemblage reflect a stronger stratification of the upper water column rather than temperature per se. Stratification results in an increase in the number of ecological niches, which allows for specific adaptations within the planktic foraminifers, including growth to large size. The similarity of size evolution of globorotaliid and globigerinid species (*G. menardii*, G. *sacculifer*, G. *ruber,* O. *universa*) argues against a lineage-specific explanation for large size.

At times of low species richness, such as the Paleocene and the Oligocene, the paleo-productivity of the surface oceans rather than the temperature structure seems more closely correlated to planktic foraminiferal size. This suggests a dependency of foraminifers on fertility and the importance of fertility after the breakdown in food chains following the K/T mass extinction (d'Hondt, 1998), and during the dominance of a "global upwelling" fauna proposed for the Oligocene (Hallock, 1987).