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Evolution and environmental significance of digitate planktonic foraminifera

H. Coxall (1), P. Wilson (2), P. Pearson (1), P. Sexton (1,2)

1. School of Earth, Ocean and Planetary Sciences, Cardiff University, UK, (2) School of Ocean and Earth Science, National Oceanography Centre, Southampton, UK

Planktonic foraminifera with digitate shell morphologies have evolved repeatedly during the Cretaceous and Cenozoic and three species exist today. Digitate species have never been common in typical open-ocean assemblages but at several times in the Cretaceous and Eocene, and in some modern ocean regions of semi-permanent upwelling, they are or have been a more conspicuous component, leading to the suggestion that the morphology represents an environmental specialization. Here we explore the environmental significance of digitate foraminifera by investigating the palaeoecology and distribution of fossil and living species. δ^{13}C and δ^{18}O values of six extinct and two modern digitate species, from six time slices (Cenomanian, Turonian, Eocene, Miocene, Pleistocene and Holocene) show similar isotopic depth ecologies, consistently registering the most negative δ^{13}C and usually the most positive δ^{18}O compared to other coexisting species. These results indicate a similar deep-water ($>$150 m) habitat for all the digitates, probably within or below the thermocline, characterized by lower temperatures and enrichment of dissolved inorganic carbon (DIC). This is consistent with modern water-column plankton studies that provide insight into the depth preferences of modern digitate species; out of 32 observations all occurred below 35 m and 25 were found in nets towed at depths of 150 m or greater. The correlation between digitate species and a deep dwelling habitat across multiple epochs suggests that elongated chambers evolved as an adaptation to a deep mesopelagic environment, possibly within or close to an expanded OMZ, where light is absent and food is scarce. We suggest that the function of digitate chambers was as a feeding specialization that increased the effective size of the foraminifera, and therefore the volume of water that could be searched for food, at minimum metabolic cost. Our results provide evidence of convergent evolution by adaptation to a deep pelagic habitat and highlight the potential of digitate species to act as indicators of palaeo-upwelling, including expansion of the OMZ, across geological epochs.