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Origin of planktonic foraminifera as a result of biotic recovery from the Permian-Triassic boundary crisis

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Planktonic foraminifera are important marine pelagic calcifiers. Steady rain of their calcite shells has contributed to thick deposits of biogenic carbonates on the sea floor that regulate ocean chemistry and carbon cycle and serve as a unique archive of past climate change. Despite the importance of the group to marine biogeochemistry and paleobiology, its origin, and therefore also the origin of the climatic regulation that their biomineralisation affords, remain shrouded in mystery. Despite the Precambrian origin of Foraminifera and Devonian origin of biomineralisation in the group, the oldest planktonic foraminifera have been identified in Jurassic deposits. The relationship of these early forms to the present-day representatives of the group and the reason for the delayed timing of the transition of foraminifera into the plankton remain unclear. Using the tychopelagic (living both in plankton and benthos) Bolivina as a model, earlier research has shown that the ecological transition into the plankton likely proceeded by making use of pre-adaptations to pelagic life that evolved independently, multiple times, for other reasons, and did not immediately lead to a transition into the plankton. Here we take this research further by analyzing the identity of foraminifera sequences found in the recently available global metabarcoding datasets from the plankton. These sequences represent genuinely planktonic species and a small contribution from specimens of primarily benthic species that have in some way detached from the substrate and are found, presumably alive, in the surface layer of the ocean. Through recent advances in barcoding of the genuinely planktonic foraminifera, we are now in the unique position to filter out the planktonic signal and analyse these rare escapees from the benthos. As expected, we found that the escapee signal has a bias towards the coast, confirming that the plankton is not the primary habitat of these taxa but at most a temporary home after their detachment from the substrate. Do these specimen represent a passive entrainment of individuals mobilized during storms? Remarkably, the analysis of the composition of the encountered sequences shows that this is not the case. The escapee metabarcode is almost exclusively comprised of rotaliids. The same genetic methods have consistently showed that benthic foraminifera metabarcode composition is dominated by monothalamids and the virtual absence of miliolids in the escapee sequences is at odds with the shallow-water affinity of the group making them potential “passive entrainers”. We interpret the rotaliid dominance as evidence of the presence of an ancient common adaptation in the clade to survive in the plankton at least for some time and speculate that such adaptation could initially facilitate dispersal. This observation opens up the possibility that the origin of planktonic lifestyle in foraminifera is linked to the evolution of this particular adaptation and that planktonic foraminifera therefore could first originate after the evolution of the rotaliids, in the aftermath of the biotic recovery from the Permian/Triassic crisis.