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The Environmental Context of the Cryogenian-Ediacaran Diversification of Metazoa

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Molecular clock estimates date the origin of animals to about 780 million years ago (Ma), with the diversification of most of the major clades occurring through the Cryogenian and early Ediacaran. Despite many attempts to constrain the origins of sponges, cnidarians, placozoans and even of Bilateria, the lack of sufficient Neoproterozoic calibration dates have made molecular clock estimates for these ancient metazoan divergences unreliable. Consequently it has been difficult to ascertain the relationship between the origins of major metazoan clades and extreme environmental perturbations, particularly the Sturtian (717-659 Ma) and Marinoan (>640-635 Ma) glaciations (possible Snowball Earths) and putative increases in oxygen levels in shallow marine settings. Comparative developmental biology has produced extensive information on the developmental capacity of the last common ancestors at various nodes on the metazoan tree, but these capacities have yet to be considered in light of environmental conditions. There has been extensive recent discussion over whether oxygen levels were sufficient for the origin of metazoan clades during the late Neoproterozoic, and when oxygen levels became sufficient for macroscopic metazoans. Here we discuss three alternative scenarios: an early-divergence model with sponges, cnidarians, placozoans and possibly other clades originating before the Sturtian; a Snowball model with divergences occurring during the glaciations, possibly with a burst of evolution during the interregnum between the Sturtian and Marinoan; and a late-divergence model in which most metazoan clades originated after the end of the Marinoan glaciation at 635 Ma. We present molecular and comparative developmental evidence relevant for each scenario, and discuss the implications of environmental evidence for each diversification pattern. Although none of these scenarios is likely to be entirely correct, this framework focuses attention on the distinctive challenges for early metazoans of the pre-Sturtian Cryogenian, the glacial interval and accompanying deglaciation phases, and the increasing oxygen of the Ediacaran.

