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The Early Evolution of Eukaryotic Heterotrophy

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Primary production is the basis for all life on Earth, but the secondary utilization of that resource, including the recycling of nutrients, is no less essential for sustaining the biosphere. Most heterotrophic activity on Earth has always been carried out by prokaryotes; however, it is the diverse habits of heterotrophic eukaryotes that have driven, and account for, most organismal diversity.

Biomarker analyses suggest that eukaryotes were ecologically minor constituents of marine ecosystems through the Late Archean and much of the Proterozoic. Body fossils of convincing eukaryotes are first encountered at ca. 1850 Ma, but until the Late Mesoproterozoic (1200-1000 Ma) are limited to simple spheroidal acritarchs and undifferentiated filaments. Morphologically complex eukaryotes make their first appearance in the Late Mesoproterozoic in the form of large ornamented acritarchs and complex multicellular algae. Along with various "problematica", these groups undergo a conspicuous diversification through the Neoproterozoic.

A number of (pre-Vendian) Neoproterozoic fossils might be interpreted as early eukaryotic heterotrophs, but the only convincing case is for certain "vase shaped microfossils" which compare with modern testate amoebae. Preservational biases will inevitably under-represent heterotrophs in the fossil record and a more accurate estimate of heterotrophic activity can be inferred from co-evolved adaptations in plant protists and problematica. Morphological elaboration is both energetically and evolutionarily costly; thus, the marked Meso-Neoproterozoic diversification of ornamentation and large size provides clear evidence of increasingly complex ecological interactions, including eukaryotic heterotrophy. This may have been limited to a single-celled grade of organisation, but there is no reason to rule out multicellular heterotrophs at this time. The first unambiguous record of metazoans appears in the terminal Proterozoic in the form of trace fossils and Ediacaran-type body fossils.

Mophological elaboration during the Meso-Neoproterozoic was limited largely to shallow-water benthos (perhaps accounting for the limited contribution of eukaryotes to the biomarker record). The onset of the Phanerozoic, however, witnessed a major radiation of ornamented phytoplankton, implying an evolutionary migration of grazing metazoans into the water column. Such an interpretation is supported by the Early Cambrian occurrence of arthropodan zooplankton and acritarch-laden faecal strings, as well as the marked perturbations in contemporaneous biogeochemistry.

The "Cambrian explosion" of ca. 540Ma can be considered a massive diversification of the heterotrophic habit, linking multicellular, often motile, food-gathering devices to sophisticated chemical processing plants. The fossil record documents the rapid appearance of diverse trophic strategies, including primary, secondary and tertiary carnivores. Despite their superficially modern aspect, however, these early metazoan ecosystems appear to have lacked the web-like interconnectedness of more recent trophic structures. Such simple structures are singularly susceptible to perturbation (as in modern trophic cascades) and may account for both the rapid evolutionary turnover and accompanying geochemical fluctuations of the Early Cambrian.