

The rise of predators

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Despite their abundance, diversity, and importance today, organisms with mineralized skeletons are a relatively recent introduction. For the first three billion years of its history, life was soft-bodied, inducing mineralized structures passively, if at all. Beginning ca. 550 Ma, however, more than two dozen clades—primarily animal, but also protistan—independently evolved mineralized skeletons within a geologically short interval of time (Fig. 1; Bengtson, 1992). Now a new report by Cohen et al. (2011; p. 539 in this issue of *Geology*) describing beautifully intricate scale-like microfossils from the Fifteenmile Group, Yukon Territory, provides definitive evidence for mineralized skeletons some 150–250 m.y. earlier. These scale-like microfossils were first reported over two decades ago (Allison and Hilgert, 1986), but neither their age nor their mineralogy were well constrained. Work by Cohen and her colleagues has now shown that these scales (which perhaps enveloped a single-celled green alga) are between ca. 717 and ca. 812 Ma in age and composed of primary phosphate (Macdonald et al., 2010; Cohen et al., 2011). This adds to earlier suggestive evidence for mineralization at this time: the ca. 770–742 Ma vase-shaped microfossil (VSM) *Melicerion poikilon*, interpreted on the basis of taphonomic models to be a euglyphid amoeba whose organic-walled test was embedded with mineralized scales, possibly siliceous (Figs. 1B and 1C; Porter and Knoll, 2000; Porter et al., 2003); the mid-Neoproterozoic *Tenuocharta cloudii*, a multicellular, sheet-like fossil whose calcareous cell walls may reflect primary (Horodyski and Mankiewicz, 1990) or early diagenetic (Knoll, 2003) mineralization; and ca. 650 Ma millimeter- to centimeter-scale asymmetric bodies permeated with a network of canals and interpreted to be sponge-like organisms perhaps lightly mineralized with carbonate (Maloof et al., 2010b).

Numerous hypotheses have been posed to explain the sudden appearance of skeletons in the latest Ediacaran and early Cambrian (e.g., Wood, 2011), but the most widely favored is that they evolved for defense against macrophagous predators—animals capable of consuming large prey (e.g., Bengtson, 1994). Animals most likely weren't around in the mid-Neoproterozoic, but single-celled predators were (herein the term predator refers to eukaryotes that eat other living organisms, including algae). Given the strong selective influence protistan predators have on microbial communities today (e.g., Smetacek, 2001; Tillmann, 2004), and that the primary function of many protistan skeletons seems to be for defense (e.g., Hamm et al., 2003; Tillmann, 2004), it is reasonable to think that mineralized skeletons may have appeared ca. 750 Ma as a response to protistan predation. Single-celled predators obtain their food by engulfing or piercing their prey, and the (modest) diversity of skeletons in mid-Neoproterozoic rocks might reflect a comparable diversity of predation styles. Scale microfossils, in particular *Characodictyon*, with its central, pronged shaft (Fig. 1A), might have restricted the ability of single-celled predators to engulf the cell by effectively increasing its size, and VSM tests—both those with mineralized scales and those that are entirely organic-walled—might have deterred predators that used pseudopods to pierce their prey (e.g., Old, 1978). The earliest direct fossil evidence for protistan predators are the VSMs themselves (Porter et al., 2003), as well as biomarkers of the same age thought to be derived from ciliates (Summons et al., 1988). Fossils of eukaryotic algae as old as 1200 Ma (Butterfield, 2000) provide indirect evidence for the presence of protistan predators much earlier, however, as the origin of plastids (the sites of photosynthesis in eukaryotic

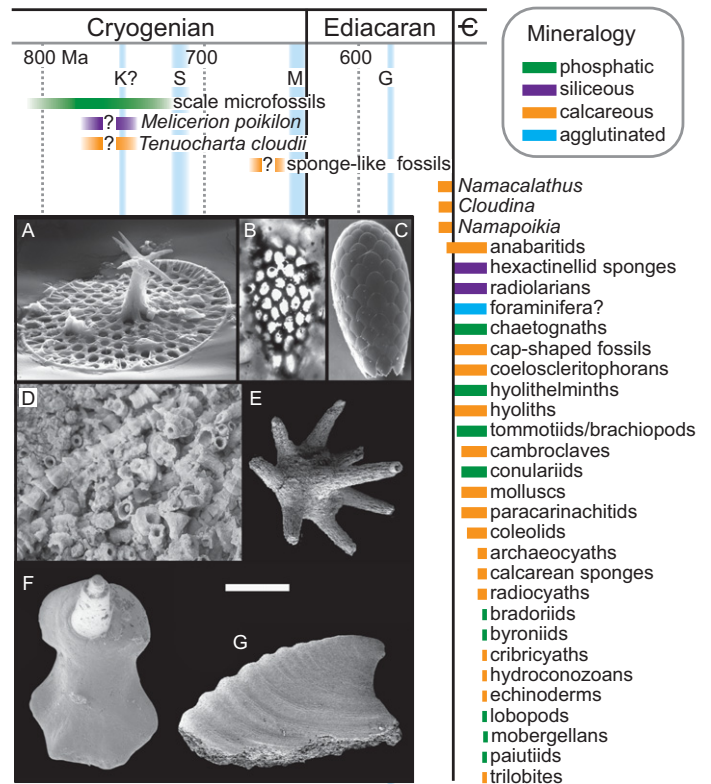


Figure 1. Independent origins of mineralized skeletons during the Cryogenian, Ediacaran, and early Cambrian (through the Atdabanian) and images of selected skeletons (A–G). Ediacaran and Cambrian occurrences from Bengtson (1992), Maloof et al. (2010a), and Porter (2010). See text for Cryogenian references. K?—possible Kaigas glaciation; S—Sturtian glaciation; M—Marinoan glaciation; G—Gaskiers glaciation. Age constraints on glaciations are from Macdonald et al. (2010, and references therein). A: The scale microfossil *Characodictyon*. B: The vase-shaped microfossil *Melicerion poikilon*, interpreted to be a euglyphid amoeba. C: Test of the modern euglyphid amoeba *Euglyphid tuberculata*. D: Silicified tubes of *Cloudina carinata*. E: Chancelloriid sclerite (Coeloscleritophora), one of many that covered the animal's body like the spines of a cactus. F: Sclerite of the cambroclavate *Cambroclavus fangxianensis*, part of an array of interlocking sclerites. G: Internal mold of the mollusc *Mellopegma georginense*. Image in A is courtesy of P. Cohen; images in B, C, and E are reprinted with permission from the *Journal of Paleontology*; image in D is courtesy of I. Cortijo; image in F is courtesy of J. Moore. Scale bar equals 5 μ m in A, 50 μ m in B, 35 μ m in C, 10 mm in D, 100 μ m in E, 150 μ m in F, and 500 μ m in G.

algae) involved the host cell engulfing another cell. The absence of protistan predators in older rocks probably reflects (at least in part) the limited preservation potential of many protozoan groups. However, it is also possible that the appearance of protistan skeletons in the mid-Neoproterozoic reflects a shift in the taxonomic contributors to primary productivity (Knoll, 2007). Both biomarker ratios and body fossils suggest increasing dominance of eukaryotic algae from the early Mesoproterozoic to the late

Neoproterozoic, perhaps caused by a change from euxinic, nitrogen-poor oceans to increasingly oxic oceans richer in nitrogen (Knoll, 2007). Protistan predators thus may have been common in Mesoproterozoic oceans, but primarily feeding on bacteria. As eukaryotic algae began to increase in abundance, however, more protistan predators would have become adapted to eating eukaryotes, and eukaryotic algae would have responded by evolving a variety of defenses, including skeletons. The ability to engulf large prey (eukaryotes tend to be much larger than bacteria) also meant that protistan predators would have had the capacity to consume other protistan predators, which in turn would have evolved defenses of their own (or stolen them from their prey: some modern testate amoebae incorporate into their own tests mineralized scales they acquired from the tests of their prey [e.g., Ogden, 1991]). Some protistan skeletons could also have evolved to function in predation; some radiolarians, for example, use their spiny skeletons both for protection and for mechanical support as they extend pseudopods to ensnare prey (Anderson, 1983). The convergent evolution of macroscopic size and multicellularity in numerous clades in the early Ediacaran (e.g., Yuan et al., 2011; Xiao and Laflamme, 2009) could also reflect increasing predation pressure by protists, as large size is one form of defense against becoming engulfed (Stanley, 1973; Boraas et al., 1998).

Future insights into late Proterozoic food webs depend on determining the taxonomic affinities of Precambrian fossils, most of which are obscure. Recent studies that use ultrastructural and microchemical characters as well as morphology have yielded promising results (e.g., Javaux and Marshal, 2006); these need to be paired with studies on modern protists that establish the distribution of those characters in the eukaryotic tree. In addition, taphonomic studies may yield information about the behavior of early predators. For example, numerous 2–3 μm circular perforations in the ca. 750 Ma microfossil *Cerebrosphaera buickii* (Butterfield et al., 1994) may have been produced by protistan predators that pierced the tough organic wall; ~20 μm semicircular holes in some VSM tests may have a similar origin (Porter et al., 2003).

One of the most striking discoveries that has come from studies of protistan biology is evidence for convergent evolution between protists and animals (Leander, 2008). Protists must contend with many of the same problems animals do, and, despite their unicellular organization, often have evolved similar solutions. The appearance of protistan skeletons in the mid-Neoproterozoic, and, 200 million years later, the appearance of skeletons in animals, may be another example of these two different groups converging on the same answer to a shared problem: the rise of predators.

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