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A basin redox transect at the dawn of animal life

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ABSTRACT

Multiple eukaryotic clades make their first appearance in the fossil record between ~810 and 715 Ma. Molecular clock studies suggest that the origin of animal multicellularity may have been part of this broader eukaryotic radiation. Animals require oxygen to fuel their metabolism, and low oxygen levels have been hypothesized to account for the temporal lag between metazoan origins and the Cambrian radiation of large, ecologically diverse animals. Here, paleoredox conditions were investigated in the Fifteenmile Group, Ogilvie Mountains, Yukon, Canada, which hosts an 811 Ma ash horizon and spans the temporal window that captures the inferred origin and early evolution of animals. Iron-based redox proxies, redox-sensitive trace elements, organic carbon percentages and pyrite sulfur isotopes were analyzed in seven stratigraphic sections along two parallel basin transects. These data suggest that for this basin, oxygenated shelf waters overlay generally anoxic deeper waters. The anoxic water column was dominantly ferruginous, but brief periods of euxinia likely occurred. These oscillations coincide with changes in total organic carbon, suggesting euxinia was primarily driven by increased organic carbon loading. Overall, these data are consistent with proposed quantitative constraints on Proterozoic atmospheric oxygen being greater than 1% of modern levels, but less than present levels. Comparing these oxygen levels against the likely oxygen requirements of the earliest animals, both theoretical considerations and the ecology of modern oxygen-deficient settings suggest that the inferred oxygen levels in the mixed layer would not have been prohibitive to the presence of sponges, eumetazoans or bilaterians. Thus the evolution of the earliest animals was probably not limited by the low absolute oxygen levels that may have characterized Neoproterozoic oceans, although these inferred levels would constrain animals to very small sizes and low metabolic rates.

1. Introduction

A number of eukaryotic groups first appear in the fossil record between the Bitter Springs isotope excursion at ~810 Ma and the Sturtian glaciation at ~715 Ma (Macdonald et al., 2010). This apparent radiation includes the first unequivocal appearances of groups such as the vase-shaped microfossils, interpreted to be related to lobose, and perhaps filose, testate amoebae (Porter and Knoll, 2000; Porter et al., 2003), scale microfossils of uncertain phylogenetic affinity (Cohen et al., 2011; Cohen and Knoll, 2012), and simple multicellular and coenocytic green algae (Butterfield et al., 1994). Interestingly, molecular clock studies suggest that the origin of animal multicellularity may have been part of this broader radiation. Studies utilizing different taxa, genes, calibration points and clock models have converged on an estimated divergence of ~800 Ma for the last common ancestor of animals (Berney and Pawlowski, 2006; Lartillot et al., 2009; Sperling et al., 2010; Erwin et al., 2011; Parfrey et al., 2011). Similar results in these studies, despite broad methodological differences, suggest this divergence estimate is approximately correct. This age finds further support in the appearance of presumed demosponge-specific biomarkers beneath ca. 635 Ma Marinoan glacial deposits (Love et al., 2009; Kodner et al., 2008); as demosponges represent a derived lineage within animals, the origin of the animal crown group must be even deeper in time. If the molecular clock ages and biomarker data are accurate, the lack of metazoan body and trace fossils throughout the Cryogenian and early Ediacaran periods presents a conundrum (Erwin et al., 2011). It has been hypothesized that animal body size and diversity may have been limited by relatively low levels of oxygen in the Proterozoic atmosphere and oceans. In such oceans, it is posited that animals could have been restricted to small and thin body plans that did not fossilize well, with the explosion of larger and ecologically diverse organisms in the late Ediacaran and Cambrian related in part to increasing O_2 levels (Cloud, 1968; Rhoads and Morse, 1971; Runnegar, 1982a; Knoll and Carroll, 1999). Consistent with this hypothesis, different geochemical redox proxies support

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a directional change toward more oxygenated conditions in the latest Proterozoic (reviewed by Och and Shields-Zhou (2012) and Kah and Bartley (2011)).

What remains highly uncertain, however, are the atmospheric and oceanic oxygen concentrations prior to and during earliest animal evolution, specifically during the Cryogenian period (850–635 Ma). Oxygen levels are generally assumed to have been relatively low in Cryogenian oceans (e.g. Kump, 2008), but given the lack of widespread paleoenvironmental documentation, the extent to which early animals were limited by low oxygen levels remains unknown. Specifically, the physiological requirements of small animals with low-energy lifestyles that may have characterized the Cryogenian period were likely different from the larger, more active and muscular organisms preserved in Cambrian rocks. This difference needs to be considered when comparing physiological requirements against the constraints provided by geochemical proxies.

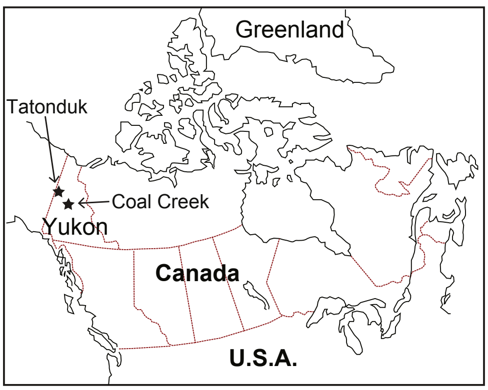

Fig. 1. Location map of the Coal Creek and Tatonduk inliers, Yukon Territory, Canada, with stars marking the location of the inliers.

Here, we investigate the environmental context of early animal evolution and compare inferred redox constraints with the likely physiological requirements associated with different grades of organization in early animal evolution. Previous iron speciation and sulfur isotope studies of the pre-Sturtian Chuar Group (Canfield et al., 2008; Nagy et al., 2009; Johnston et al., 2010) provide insight into Cryogenian environments, but are limited to a single section deposited between ca. 770 and 742 Ma (Karlstrom et al., 2000). Here we report geochemical redox proxies through seven sections along two parallel platform-to-basin transects in the early Cryogenian Fifteenmile Group in the Tatonduk and Coal Creek inliers, Ogilvie Mountains, Yukon, Canada (Figs. 1 and 2). The Fifteenmile Group was deposited in a basin that originated during an episode of continental extension (Macdonald et al., 2012) prior to 811.51 $\pm$ 0.25 Ma, the U–Pb zircon date on a tuff in the upper portion of the Reefal Assemblage (green line in Mt. Harper Section, Figs. 3 and 6; Macdonald et al., 2010). Thus the Fifteenmile Group spans a time period that significantly preceded the earliest macroscopic multicellular forms in the Ediacaran period (Narbonne, 2011) but overlaps with molecular-clock estimates for the divergence of crown-group animals (Erwin et al., 2011, and references above).

The paleoredox state of shale samples collected from measured stratigraphic sections was investigated using a multi-proxy approach. Specifically, iron speciation data are integrated with major-element and redox-sensitive trace element abundances, total organic carbon (TOC) percentages, and pyrite sulfur isotope values to obtain an estimate of overall water-column redox profiles. Together, the geochemical data from these stratigraphic sections provide the first early Neoproterozoic basin redox transect and give insight into paleoenvironmental conditions in this basin at the dawn of animal life. These

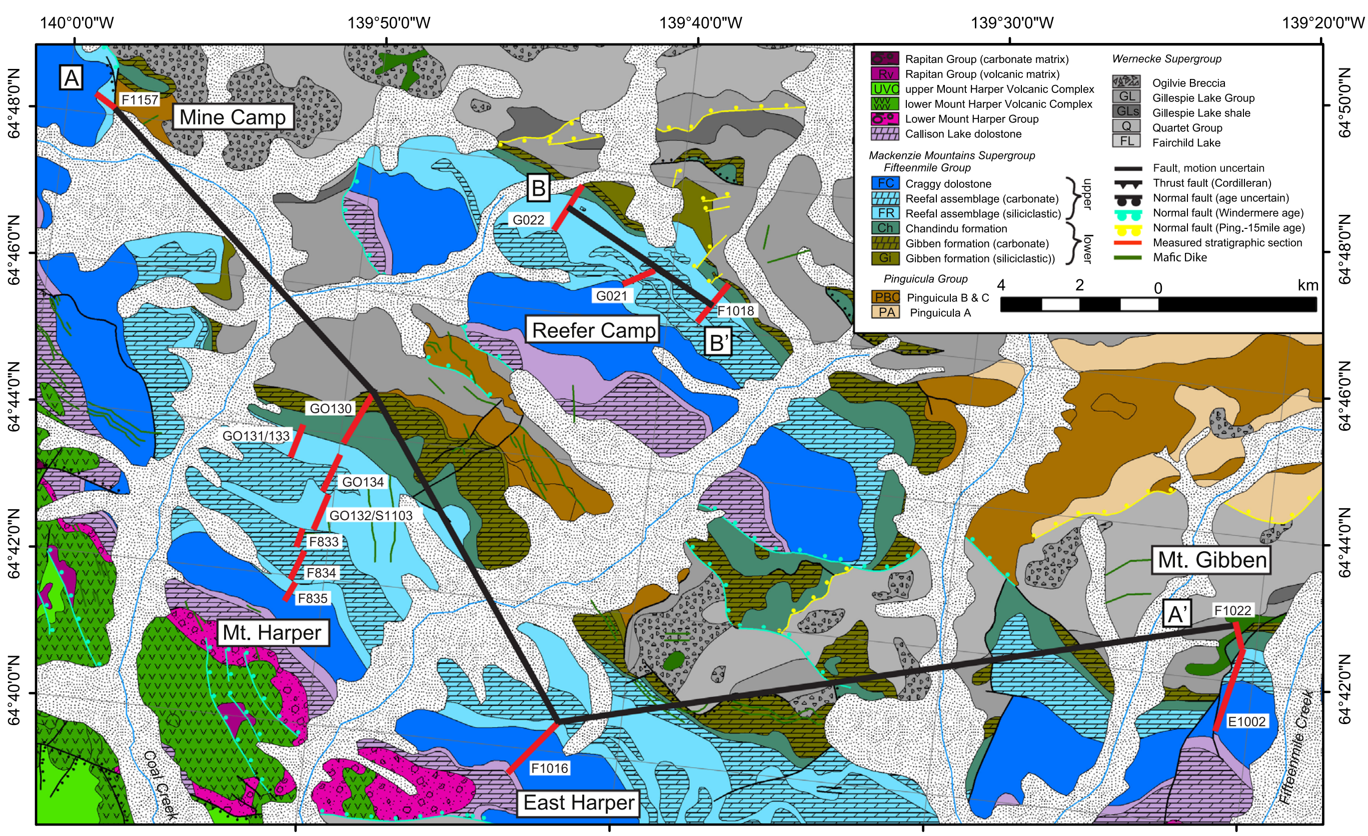

Fig. 2. Geological map of the Coal Creek inlier, Ogilvie Mountains, Yukon Territory, showing sections (in red) studied in this paper. The stratigraphic framework for basin transects A–A′ and B–B′ are found in Figs. 3 and 4. The units studied as part of this paper are the informal Gibben formation, Chandindu formation and Reefal Assemblage of the Fifteenmile Group. Geological mapping by Macdonald et al. (2012). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)