

Supplementary Results and Discussion

The Record of Precambrian Steroidal Hydrocarbons

The record of sterane and triterpane hydrocarbon biomarkers in Archean and Proterozoic sedimentary rocks has come under extremely thorough scrutiny in recent times. Concerns about contamination, and doubts about reports of steroidal hydrocarbons in the 2.7 billion year-old Fortescue Group sediments of the Pilbara Craton (Brocks et al., 1999), were initially raised in 2003 (Brocks et al., 2003). These potential problems became increasingly difficult to dismiss when new and improved types of geochemical analyses were devised and applied. For example, Brocks and colleagues showed that a selection of rock and sediment samples from a range of localities were ubiquitously contaminated with petroleum- and plastic-derived organic compounds (Brocks et al., 2008). Analyses of thin slices of sediment core showed that spatial distributions of hydrocarbons could be used to distinguish indigenous hydrocarbons from surface contaminants in Archean shales (Brocks, 2011). In another example, the carbon isotopic data values of *in situ* and insoluble kerogen and pyrobitumen in rock formations that had previously yielded biomarkers were discrepant from those of the extractable hydrocarbons, meaning that the latter could not be indigenous (Rasmussen et al., 2008). Experiments with passive sampling of laboratory aerosols provided further evidence of the pervasiveness of airborne petroleum-derived hydrocarbons in the environment (Illing et al., 2014). Irrespective of the geologic ages of samples being analyzed for biomarkers, these studies demonstrate that rocks that are lean in organic matter, or those which have seen elevated thermal histories, are particularly prone to contamination from anthropogenic pollutants (Gold et al., 2016b). Accordingly, we should be skeptical of all reports of biomarkers in pre-Cambrian rock sequences where the thermal history is high, where plasticizers or other demonstrable contaminants are detectable, or where the presence of incongruous combinations of extractable components casts reasonable doubt on the syngeneity of entrained hydrocarbons (Brocks et al., 2008).

The debate concerning the reliability, or not, of reports of freely extractable Archean biomarkers was ultimately settled through the collaborative Agouon Institute Drilling Project (AIDP). This was a program that combined rigorously clean drilling, collection, archival and analysis of the samples (French et al., 2015). Two sedimentary sequences that had previously yielded putative Archean biomarkers in samples obtained from early mineral exploration drill cores (Brocks et al., 1999; Eigenbrode et al., 2008) were re-drilled along with a third core through sequence of highly metamorphosed shales that served as a control. The results were unambiguous. No sterane or triterpane biomarkers were detected in any of the samples from the new ores and, instead, the extractable hydrocarbons were dominated by parent polyaromatic hydrocarbons and diamondoid hydrocarbons, the distributions of which were consistent with having come from rocks with thermal histories well beyond the 'oil window' and into the range where aliphatic hydrocarbons are being cracked to gas (Peters et al., 2005). Hydropyrolysis

experiments on kerogens from the same rocks afforded similar conclusions in that no steranes or triterpanes could be detected in the pyrolysates (French et al., 2015).

Given the absence of credible evidence for biomarkers being freely extractable from Archean sediments, it seems timely to also re-examine technologies for their recovery from alternative archives. For example, biomarkers including steranes, have been reported trapped in fluid inclusions in rocks of Archean and Paleoproterozoic ages (Dutkiewicz et al., 2007; Dutkiewicz et al., 1998; Dutkiewicz et al., 2006; George et al., 2008). Identification of the source rock for the migrating hydrocarbons and dating the emplacement of the fluid inclusions are factors to establish with confidence. Moreover, the enclosing minerals still need to be protected from the destructive effects of thermal metamorphism (Price, 1993) and ionizing radiation (Dahl et al., 1988; Landais, 1993; Lewan and Buchardt, 1989; Rasmussen et al., 1993). For example, in the case of the inclusions reported from the 2.45 Ga metaconglomerate of the Matinenda Formation, the authors state that these hydrocarbons were “exposed to upper prehnite–pumpellyite facies metamorphism (280–350 °C) either during migration or after entrapment” (George et al., 2008). Subsequent work by (French et al., 2015) shows that no hydrocarbons survived a milder thermal history of the Fortescue Group in the Pilbara. It follows, therefore, that the reports of biomarkers in hydrocarbon-bearing fluid inclusions should be re-appraised as exactly as those in extractable bitumens.

Brocks et al. (2011) and French et al. (2015) reported particular sampling, curation and analytical protocols that, if followed, reduce errors on the analysis of pre-Cambrian biomarkers. In doing so, they also identified criteria by which earlier reports of steranes, in particular, could be evaluated. Multiple studies of the 1.64 Ga Barney Creek Formation, which has been penetrated by wells drilled into terrains that are at or below the maturity threshold for oil generation (Crick et al., 1988) reveal the presence of a wide range of biomarker hydrocarbons including acyclic isoprenoids, tricyclic terpanes, pentacyclic hopanoid and gammacerane triterpanes, and C₄₀ carotenoid-derived saturated and aromatic hydrocarbons (Brocks et al., 2005; Brocks and Schaeffer, 2008; Summons et al., 1988). A rigorous examination of the steranes in Barney Creek Formation sediments shows their presence but with a unique distribution dominated by 4-methyl and desmethyl triaromatic steroids at levels of 60–130 p.p.m. but lacking in the side-chain methylation that is characteristic of the steroids produced by typical eukaryotes. Saturated sterane biomarkers typical of those found in Phanerozoic rocks were close to, or below, the methodological detection limits of ~1 p.p.m. Other biomarker studies of Archean, Paleoproterozoic and Mesoproterozoic sedimentary rocks, conducted in the era of heightened contamination awareness, reveal a similar picture of non-detection of eukaryote-specific 24-alkylated steranes (Blumenberg et al., 2012; Flannery and George, 2014; Hoshino et al., 2015) or their detection at levels than cannot be reliably distinguished from contamination (Luo et al., 2015; Zhang et al., 2016). Finally, new methodologies for evaluating the thermal regime experienced by sedimentary organic matter (Ferralis et al., 2016), the cleaning of contaminated rock samples prior to analysis (Jarrett et al., 2013) and a focus on directed identification and sampling of pockets of well-preserved Proterozoic and Archean sediments (Bruisten et al., 2013) suggest that the pre-Cambrian biomarker record can be elaborated and imbued with greater confidence.

Genetic Evidence for Early Sterol Biosynthesis, and the Reconciliation of Molecular and Geologic Data

While our analysis focused on the first two genes in the sterol biosynthesis pathway, it is worth reiterating that the last common ancestor of crown-group eukaryotes (LECA) most likely had the complete suite of genes necessary to produce complex sterols. This is based on several comparative genomic studies, which have concluded that the sterol biosynthesis pathway is present in the major eukaryotic clades, and that there is no compelling evidence for early horizontal gene transfer events between Eukaryotes (Desmond and Gribaldo, 2009; Gold et al., 2016a). This suite of genes includes *sterol 24-C-methyltransferase (SMT)*, which allows for the methylation of sterol side chains and the biosynthesis of canonical C₂₆-C₃₀ eukaryotic sterols. Our analysis dates the origin of LECA between ~1.30-2.17 Gyr ago, while multi-gene molecular clocks have estimated LECA between 0.95 and 1.87 Gyr ago (Berney and Pawlowski, 2006; Douzery et al., 2004; Parfrey et al., 2011). Subsequently, there is broad consensus that LECA evolved prior to the Neoproterozoic, and that it was capable of producing 24-methyl steroids.

Molecular clock studies strongly support the idea that both protosterol biosynthesis genes (this report) and crown-group eukaryotes significantly predate their biomarker record; this begs for a taphonomic or ecological explanation. There appears to be no significant taphonomic bias affecting the preservation of sterol versus bacteriohopanepolyol lipids. The derived steroidal and hopanoid hydrocarbons have similar thermodynamic stabilities and their concentrations in sedimentary rocks and petroleum decrease similarly as thermal maturity increases (Farrimond et al., 1998; Peters et al., 2005; van Graas, 1990). Yet the majority of Paleoproterozoic and Mesoproterozoic sedimentary rocks described that are known to preserve biomarkers appear to be devoid of eukaryotic steranes, but do contain C₂₇-C₃₅ hopane hydrocarbons of bacterial origin (Blumenberg et al., 2012; Brocks et al., 2005; Flannery and George, 2014; Luo et al., 2015). From a micro- and microfossil perspective, ample evidence exists for the presence of unambiguously eukaryotic fossil assemblages in the Mesoproterozoic (Butterfield, 2000; Javaux et al., 2001; Javaux et al., 2004; Knoll et al., 2006; Zhu et al., 2016). Accordingly, the failure to detect a concomitant record of eukaryotic steranes suggests that their membrane lipids contained limited amounts of steroids. However, it is possible that the majority of these organisms—with the exception of *Bangiomorpha pubescens* (Butterfield, 2000)—represent stem-group eukaryotes that had yet to evolve a complete sterol biosynthesis pathway.

An alternative explanation for the lack of Mesoproterozoic steranes is that crown-group eukaryotic biomass did not contribute significantly to organic matter that was ultimately preserved in the rock record or that eukaryote-derived organic matter was spatially restricted. Redox-sensitive bio-essential trace element abundances, iron and molybdenum in particular, have been invoked as factors constraining the marine nitrogen cycle and limiting nitrate availability for eukaryotes (Anbar and Knoll, 2002; Reinhard et al., 2013). In support of this hypothesis, recent work on bulk nitrogen isotopes suggests that severe offshore nitrate limitation was present in the Mesoproterozoic, which could have ecologically restricted many eukaryotes to near-shore environments until the

Neoproterozoic (Koehler et al., 2017; Stüeken et al., 2016). If this is correct, then low maturity, shallow water (carbonate) depositional environments might prove a more likely setting to find the missing evidence for pre-1.6Ga eukaryotic fossils and eukaryotic steroids.

The limited chemical fossil evidence that we have for the Barney Creek Formation indicates that protosterol biosynthesis was extant at least 1.64 billion years ago and is entirely consistent with the molecular clock analyses reported here. In addition, the abundance and diversity of fossil 24-alkylated steranes that is found in Cryogenian and Ediacaran rocks (Briggs and Summons, 2014; Brocks et al., 2016; Grosjean et al., 2009; Kelly et al., 2011; Pawlowska et al., 2013) matches what is known from the record of preserved physical fossils (Cohen et al., 2015; Knoll et al., 2006). Consistent with fossil evidence for an increasing presence and diversification of protists in the mid-Neoproterozoic (Butterfield, 2015; Cohen and Macdonald, 2015; Knoll, 2014), a recent study of well-preserved sediments from c. 800-750 Ma indicates steranes can be abundant in rocks of this age but that cholestane is dominant and its 24-alkylated counterparts are undetectable, a phenomenon that is not known at any other time in Earth's history (Brocks et al., 2016).

Improved biomarker and fossil records require targeted search and drilling programs to obtain additional samples of well-preserved, organic-rich Proterozoic and Archean sediments, as opposed to past approaches based on sampling of available drill cores. Efforts to reconstruct environmental pO_2 through this interval (Cole et al., 2016; Lyons et al., 2014) will provide further sampling guidelines. The results of these endeavors will ultimately determine how well the fossil, geochemical, and molecular records for the rise of complex life might be reconciled with those for environmental oxygenation.

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