

Carbon isotopic evidence for photosynthesis in Early Cambrian oceans

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ABSTRACT

Were the first metazoan reefs ecologically similar to modern tropical reefs, enabling them to persist under oligotrophic conditions? We tested the hypothesis of ecological similarity by employing a geochemical approach. Petrography, cathodoluminescence, trace elements, and stable isotope analyses of primary precipitates of the Lower Cambrian Ajax Limestone, South Australia, indicate preservation of original C isotopic composition. All primary carbonate components exhibit C isotopic values similar to the composition of inorganically precipitated fibrous marine cements, suggesting that archaeocyaths and the calcimicrobe *Epiphyton* precipitated skeletal carbonate in equilibrium with ambient seawater in the absence of vital effects. Such data do not support the contention that archaeocyaths possessed photosymbionts. However, a +0.5‰ shift in $\delta^{13}\text{C}$ occurs in reefs developed under shallower-water conditions relative to deeper reefs. This shift suggests the stratification of primary production in Early Cambrian oceans. The pattern is similar to that seen in the modern ocean, whereby significant photosynthesis modulates the C isotopic composition of the photic zone.

INTRODUCTION

Lower Cambrian limestones record the origins of metazoan reef communities. Much of our understanding about this important period in the history of life has been gathered through the carbonate petrology of the rocks and interpretation of fossils. Although these approaches provide valuable information about the paleobiology of the animals and the environmental conditions surrounding them, other paleoecological and paleoceanographic characteristics can best be determined through geochemical investigation, provided the original chemical composition of the rocks and fossils are preserved. Were Early Cambrian reefs ecologically similar to modern tropical reefs (James and Debrenne, 1980; Debrenne et al., 1981; Rowland, 1984; Rowland and Gangloff, 1988) in that photosymbiosis allowed their radiation into oligotrophic environments? Our study is confined to upper Atdabanian and lower Botomian (Gravestock, 1984) bioherms and biostromes of the Ajax Limestone in the Flinders Ranges, South Australia. We examined C and O isotopic compositions of carbonate components to determine whether (1) original isotopic compositions are preserved, (2) $\delta^{13}\text{C}$ values of shallow-water carbonates are more positive than $\delta^{13}\text{C}$ values of deeper-water carbonates due to surface productivity,

(3) archaeocyaths contained photosymbionts, and (4) *Epiphyton* was a photosynthesizing organism.

Biological and chemical processes, which lead to the precipitation of skeletal and inorganic carbonate, are commonly recorded in the isotopic variations preserved in ancient limestones. For example, processes that are dominated by photosynthetic fixation of ^{12}C result in enrichment of ambient waters in ^{13}C and are reflected by positive $\delta^{13}\text{C}$ values in phases precipitated in isotopic equilibrium with seawater (Swart, 1983). Such records include inorganic marine cements and skeletal carbonate that is passively precipitated. In contrast, many organisms control the isotopic composition of body fluids from which carbonate is secreted, such that the isotopic composition of this reservoir varies according to the relative contributions of C derived from metabolic processes (respiration and photosynthesis) and from exchange with ambient waters. Other workers have documented such disequilibrium precipitation in numerous photosymbiont-bearing organisms (e.g., corals—Swart, 1983; McConnaughey, 1989; Wefer and Berger, 1991; foraminifera—Erez, 1978; D'Hondt et al., 1994; bivalves—Romanek et al., 1987; see, however, Romanek and Grossman, 1989). Thus, in the fossil record, assuming diagenesis under relatively closed conditions (see Given and Lohmann, 1985), an enrichment or depletion of ^{13}C in skeletal carbonate relative to the composition of phases precipitated in equilibrium with seawater implies photosymbiosis (e.g., Stanley and Swart, 1995) or some other vital effect. In this study, we compare the $\delta^{13}\text{C}$ values of archaeocyathan skeletons and

coeval marine cements within and across photic and subphotic environments to test for the presence of photosymbiosis. To imply photosymbiosis, both of the following conditions must be met: (1) among samples from shallow, photic settings, archaeocyath $\delta^{13}\text{C}$ differs from $\delta^{13}\text{C}$ of coeval marine cements; and (2) among samples from deeper, subphotic settings, archaeocyath $\delta^{13}\text{C}$ is similar to $\delta^{13}\text{C}$ of coeval marine cement. If the $\delta^{13}\text{C}$ of archaeocyath and inorganically precipitated carbonate are the same for both environments, this finding would argue against the presence of photosymbionts and metabolic vital effects during precipitation of skeletal carbonate. If archaeocyaths differ in their composition relative to marine cements from shallow, photic and deeper, subphotic settings, the existence of a vital effect is supported. However, in this case, the process causing the isotopic offset cannot be determined. Comparing the isotopic composition of organically and inorganically precipitated phases within and across environments allows us to discriminate disequilibrium effects related to photosymbiosis from other disequilibrium vital effects.

Converse to those disequilibrium effects induced through photosynthesis, degradation of organic matter (OM) can also modulate the isotopic composition of carbonate precipitated from seawater. Aerobic decay of OM liberates isotopically light CO_2 , enriching the local C pool in ^{12}C (Kroopnick, 1985). Thus, the $\delta^{13}\text{C}$ of carbonates precipitating in equilibrium with seawater should be lower in deeper, subphotic environments relative to shallow, photic environments. Differences

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in $\delta^{13}\text{C}$ of unaltered primary carbonates from shallow and deeper environments can, therefore, reflect depth effects induced by photosynthesis and aerobic decay of OM.

METHODS

Samples were collected from eight horizons from a section of the Ajax Limestone (Fig. 1). Trace element variations were determined via cathodoluminescence (CL) and inductively coupled plasma (ICP) analyses.¹ We analyzed 27 samples under CL and mapped areas of bright, dull, and nonluminescence to identify appropriate sites for isotopic and trace element analyses.

We analyzed isotopically 200 powdered microsamples (20–50 μg). Billets microdrilled for isotopic analyses were examined under CL before and after drilling to ensure microsamples did not cross luminescent boundaries. Precision of the instrument is $>0.1\%$ for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values. We used standard techniques in all geochemical analyses (e.g., Dettman and Lohmann 1995).

RESULTS AND DISCUSSION

Lower Cambrian carbonate buildups from the Ajax Limestone occur in high-energy, shallow, photic and low-energy, deeper, subphotic environments (James and Gravestock, 1990; Savarese, 1995; Surge and Savarese, 1995a, 1995b). High-energy, shallow-water reefs contain a diverse assemblage dominated by archaeocyaths and calcimicrobes (predominantly *Epiphyton*; Fig. 1). Phosphatic small shelly fossils, gastropods, and monoplacophorans make up part of the fauna associated with the shallow-water bioherms. Archaeocyathan, spicule-rich buildups, devoid of calcimicrobes, characterize deeper, low-energy environments (Fig. 1). A diverse microfauna of calcareous (nonphosphatic) small shelly fossils occurs in the deeper water buildups. Archaeocyaths from both environments and *Epiphyton* exhibit dull luminescence. Early diagenetic features in both environments include dull to nonluminescent, Fe- and Mn-poor, fibrous marine cements and scalenohedral sparry cements forming at the time of deposition. The remaining porosity was occluded by brightly luminescent, Fe- and Mn-rich, late-stage blocky spar.

Trace chemistry, CL and isotopic analyses suggest that the ^{13}C contents of primary precipitates in these samples have been minimally altered by diagenesis. Late-stage blocky spars are depleted in ^{18}O and form a population that is distinct from early marine cements (Fig. 2). Fibrous marine cements and skeletal material from deeper environments have lower $\delta^{13}\text{C}$ values than those in more shallow environments (Fig. 3). These populations are statistically distinct ($p < 0.001$; t-test and Scheffé F-test) and exhibit the predicted pattern of

¹GSA Data Repository item 9728, ICP data, is available on request from Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301. E-mail: editing@geosociety.org.

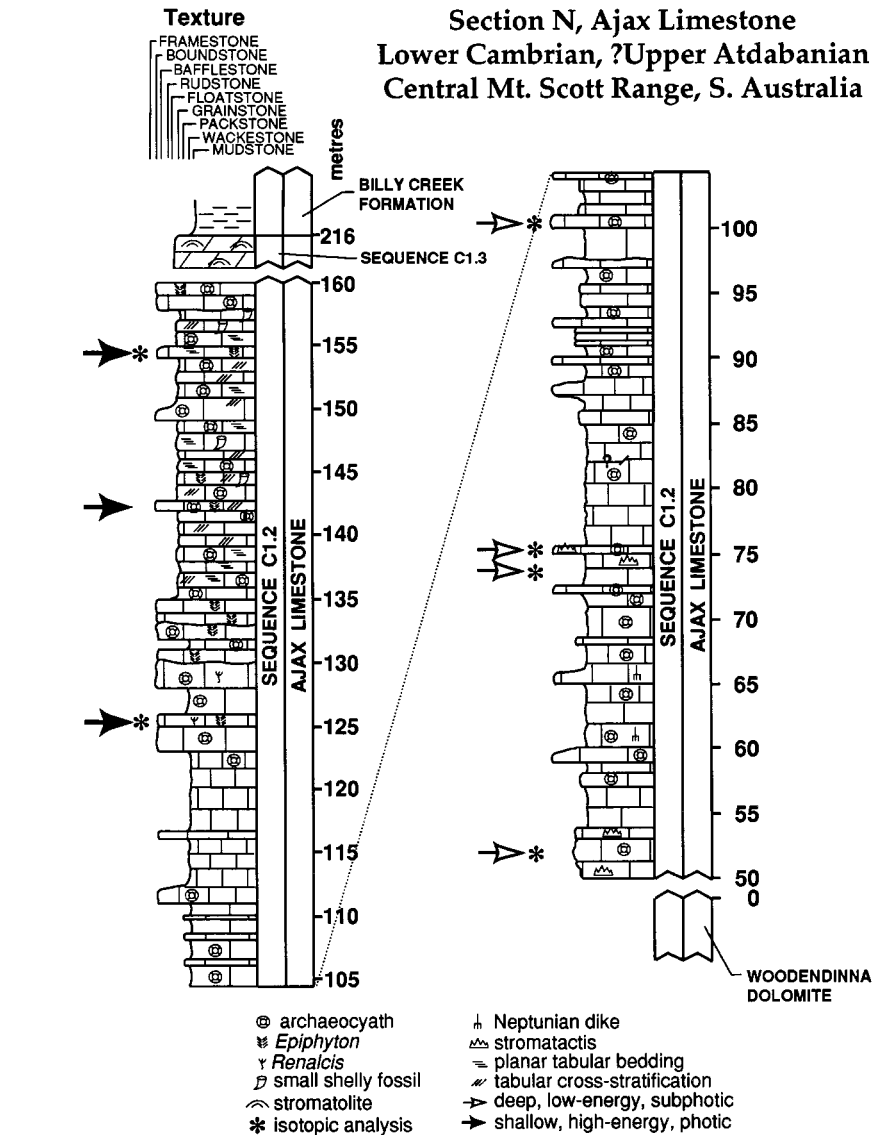


Figure 1. Stratigraphic column of the Ajax Limestone, Section N (see James and Gravestock, 1990, for locality), illustrating lithological textures (J. Mount, personal commun.) and horizons sampled. Open arrows = deep, low-energy, subphotic environments. Filled arrows = shallow, high-energy, photic environments. Horizons marked by an asterisk were sampled for isotopic analysis. Total stratigraphic distance between basal and uppermost sampled horizons is 100 m. Stratigraphic distance between environmental end members is ~25 m; stratigraphic intervals of environmental end members are ~50 m (deeper, subphotic) and ~30 m (shallow, photic). Sequence designations from Gravestock and Hibbert (1991).

^{13}C enrichment in photic settings and depletion in subphotic settings, indicating that the C isotopic compositions are original. Moreover, values of $\delta^{13}\text{C}$ do not covary with $\delta^{18}\text{O}$, suggesting that C isotopic compositions are independent of $\delta^{18}\text{O}$ and that original C isotopic composition is preserved (see Lohmann, 1982, 1988; Meyers and Lohmann, 1985). In addition, the data do not converge to a mean C isotopic composition with increasingly negative $\delta^{18}\text{O}$ (Fig. 2), as expected if diagenesis changed the original C isotopic composition. Such convergence would suggest progressive alteration of $\delta^{13}\text{C}$ from the original values. These results differ from those reported by Whittaker et al. (1994); however, their study focused on lime-

stones of the Wilkawillina Formation in a different tectonic regime and geographic region of the Flinders Ranges. The isotopic composition of O is more variable than that of C, resulting from differential alteration.

The difference in $\delta^{13}\text{C}$ between environments is best explained by changes in productivity at shallow and deep sites. Differences between shallow and deeper samples suggest that primary productivity and oxidation of OM resulted in an isotopic stratification of Early Cambrian oceans similar to that observed in modern oceans. Kroopnick (1985) demonstrated by sampling through the water column that surface-water values of $\delta^{13}\text{C}$ are as much as 3‰ more positive than $\delta^{13}\text{C}$

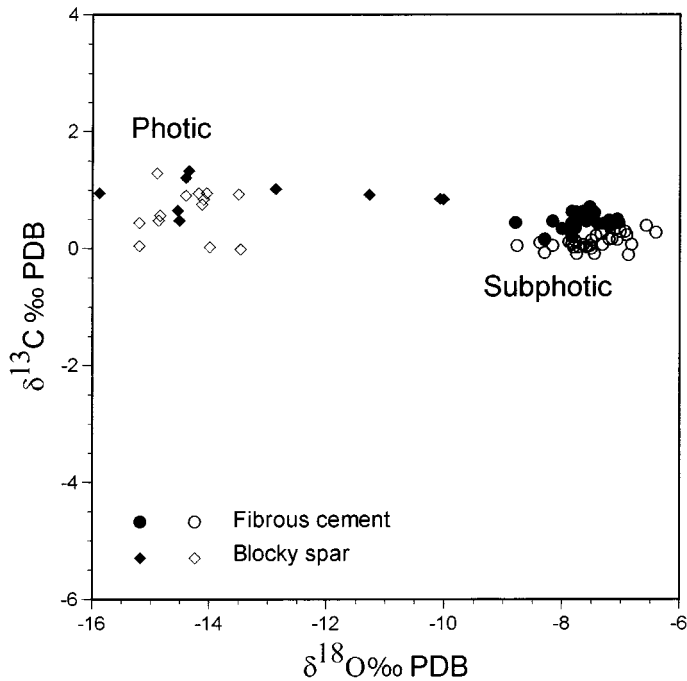


Figure 2. Isotopic cross-plot of early marine cements (circles) and late-stage blocky spars (diamonds) from deeper (open symbols) and shallow (filled symbols) environments. Isotopic compositions are reported in per mil units relative to PDB (Peedee belemnite).

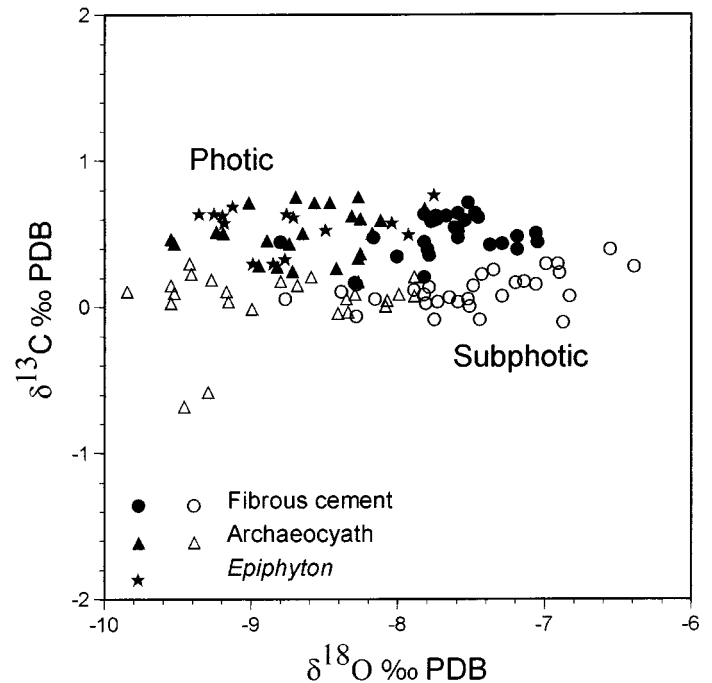


Figure 3. Isotopic cross-plot of early marine cements (circles), archaeocyaths (triangles), and *Epiphyton* (diamonds) from deeper (open symbols) and shallow (filled symbols) environments.

values at several hundred metres depth. The reported variation of $\delta^{13}\text{C}$ in the Ajax is consistent (in direction if not in magnitude) with these observations. In addition, the presence of phosphatic microfossils in the shallow, photic settings suggests an abundance of phosphorus (P) (an essential nutrient for plants) in the environment and argues against oligotrophic conditions wherein biolimiting nutrients are scarce. Although phosphatic microfossils in themselves are not evidence for the presence of photoautotrophs, they do imply that ecological conditions were favorable for a photoautotrophic community. Brasier (1991) and Brasier et al. (1994) have reached similar conclusions about abundant biolimiting nutrients in Cambrian oceans.

Although previous workers have reported secular excursions in global $\delta^{13}\text{C}$ of Early Cambrian seawater (e.g., Tucker, 1989; Magaritz, 1991; Brasier et al., 1994), the lack of stratigraphic discontinuities within the section, the expected positive shift in $\delta^{13}\text{C}$ from subphotic to photic environments, and the consistent $\delta^{13}\text{C}$ values reported among bioherms within the same environment (deep vs. shallow) imply that the $\sim 0.5\%$ difference in $\delta^{13}\text{C}$ between samples from deep-water vs. shallow-water settings seen through the study interval probably is not due to secular variation. Although the deeper and shallow environments under investigation are separated stratigraphically (Fig. 1), no obvious disconformity occurs between deep and shallow reefs. The isotopic shift occurs in the predicted negative to positive direction through

the stratigraphic interval where environments change from deep to shallow water. Moreover, consistent values of $\delta^{13}\text{C}$ come from samples within a single environment that encompass a stratigraphic interval greater than the stratigraphic separation between environments (Fig. 1). Six pairwise comparisons of $\delta^{13}\text{C}$ values between these shallow and deep horizons do not support secular variation by Scheffé-F test at $p = 0.05$ (two horizons from the deeper environment had too few samples to compare). If secular variation of $\delta^{13}\text{C}$ produced the $\sim 0.5\%$ positive shift from deeper- to shallow-water settings, it would have coincidentally occurred at the point of environmental change. Therefore, we conclude that secular variation is an unlikely explanation for the positive trend in $\delta^{13}\text{C}$.

Carbon isotopic compositions of archaeocyaths and marine cements occurring within a single environment have low variability and are statistically indistinguishable (shallow: $p = 0.84$; deep: $p = 0.57$; t test; Fig. 3). These results suggest that C isotopic compositions of archaeocyaths and cements were in equilibrium with seawater. Brasier et al. (1994) also concluded equilibrium precipitation of archaeocyathan skeletons on the basis of data from shallow-water carbonates in Siberia. Thus, the archaeocyaths probably lacked photosymbionts. Although photosymbiosis cannot be conclusively disproven (i.e., archaeocyaths might have possessed symbionts, but they produced no C isotopic effect), the data are consistent with an asymbiotic relationship. Kinetic fractionation

among modern reef zooxanthellate corals is highly variable for corals growing in different parts of the reef (Haggerty et al., 1980), resulting in highly variable C isotopic compositions. This effect occurs because of the inherent biochemical complexities induced by algal symbionts. Therefore, the low variability in C isotopic compositions of archaeocyathan skeletons also implies equilibrium precipitation and, hence, a lack of photosymbiotic activity. *Epiphyton*, thought by some workers to be photosynthetic (Riding, 1991), also has $\delta^{13}\text{C}$ values that are statistically indistinguishable from marine cements ($p = 0.23$; t-test; Fig. 3), suggesting that these calcimicrobes did not photosynthesize. Some workers have reported that *Epiphyton* can grow cryptically under minimal light conditions and that growth may have been achieved through chemosynthesis rather than photosynthesis (Rowland and Gangloff, 1988). Although cements and archaeocyaths can be microsampled confidently, the small size and intricate geometry of *Epiphyton* increases the likelihood of sample contamination from surrounding matrix. Alternatively, if sample contamination was inconsequential and $\delta^{13}\text{C}$ values of *Epiphyton* are representative of skeletal $^{13}\text{C}/^{12}\text{C}$ ratios, this calcimicrobe may have precipitated its skeleton passively, thereby imposing no vital effects. Consequently, we view the test for photosynthesis in *Epiphyton* as equivocal. Perhaps a comparison of stable isotopes of *Epiphyton* from photic and cryptic environments would help determine if *Epiphyton* was photosynthetic.

If archaeocyaths, the primary frame builders,

lacked photosymbionts. Early Cambrian reefs were fundamentally different from modern reefs. Significant surface productivity and the probable absence of photosymbiosis suggest that these Early Cambrian reefs persisted under conditions in which biolimiting nutrients were relatively abundant, unlike oligotrophic conditions surrounding modern reefs. Hallock (1981) demonstrated that photosymbiosis is ecologically favored when dissolved inorganic nutrients (DIN) are less abundant than particulate organic matter (POM). She also demonstrated that when DIN are more abundant than POM, heterotrophs and free-living photoautotrophs out compete photosymbiont-bearing animals. According to Hallock's (1981) model, asymbiotic, suspension-feeding archaeocyaths and free-living autotrophs would suggest the latter condition. Moreover, the abundance of phosphatic microfossils associated with shallow-water bioherms implies a P-rich environment, supporting our interpretation of available nutrients. Brasier (1995) discussed the utility of fossil indicators to evaluate past nutrient levels. Other workers have reached similar conclusions about nutrients (Brasier, 1991) and photosymbiosis (Wood, 1993) in the Early Cambrian based on other lines of evidence.

Our results cast doubt on the dependence of reef development upon oligotrophic conditions and algal symbiosis. Although younger reef ecosystems throughout the Phanerozoic, like modern reefs, may have required algal symbiosis to overcome a paucity of DIN, perhaps not all reefs in history developed under such nutrient-limiting conditions. Consequently, this uniformitarian assumption (Hallock, 1981; Cowen, 1988) may not be universally applicable. The Early Cambrian archaeocyathan reefs are the most ancient example of metazoan reef development, but how soon after archaeocyath extinction did the evolution of photosymbiosis occur? Perhaps a disruption of biolimiting nutrient levels in tropical waters contributed to their extinction and caused the hiatus in metazoan reef building between the Lower Cambrian and Ordovician. Previous workers proposed that archaeocyaths and Cambrian reefs became extinct because of excess nutrients (Brasier, 1991; Debrenne, 1991). Our results suggest that these ancient communities may have become extinct because of a lack of nutrients.

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