tive correlation between incompatible element concentrations and MgO content.

The good correlation between Sr, Nd, and Pb concentrations and isotopic compositions at Pisgah and Amboy indicates that the basalts are mixtures of two magmas. The high-MgO, high-K_2O component has an isotopic composition similar to OIB and most likely represents a mantle-derived magma. The low-MgO component is tightly constrained by major and trace-element data to have $\sim 51\%$ by weight SiO_2, 4% MgO, 0.8% K_2O, an ε_{Nd} value of $\sim +1.5$, and a $^{87}Sr/^{86}Sr$ ratio of ~ 0.7055. Late Jurassic gabbros and Proterozoic diabases in the Mojave Desert have appropriate compositions and isotope ratios to be the source of the low-MgO mixing component (21). Large degrees ($\sim 50\%$) of partial melting of such mafic crustal rocks could produce the low-MgO basaltic magmas observed at Pisgah (9).

Recognition of subtle contamination of basalts may help to reconcile conflicting tectonic and isotopic views of the mantle in the southwestern United States. For example, basalts with low ε_{Nd} values and high $^{87}Sr/^{86}Sr$ ratios have been used as evidence that ancient lithospheric mantle underlies much of the area north and northeast of the Mojave Desert (1–3, 8, 14, 22). Tectonic studies, however, suggest that such mantle should have been stripped from beneath the Mojave Desert during shallow subduction in the late Mesozoic and early Cenozoic (17, 18). In the northern Mojave Desert and southern Sierra Nevada, where schists thought to be part of the subducted Farallon plate are found thrust directly beneath lower crustal rocks of the North American plate (18), there is thus little room for the preservation of thick, ancient, lithospheric mantle.

These observations can be reconciled in two ways. If the low ε_{Nd} values and high $^{87}Sr/^{86}Sr$ ratios of basalts north and northeast of the Mojave Desert originate from lithospheric mantle, then there must be a major boundary in the mantle near the Garlock fault that separates ancient mantle to the north from OIB-like mantle to the south. Alternatively, some of these anomalous isotopic ratios may result from cryptic contamination of OIB-like magmas. Delineation of the presence, location, and significance of a mantle boundary will require careful consideration of the effects of cryptic contamination.

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The Antiquity of Oxygenic Photosynthesis: Evidence from Stromatolites in Sulphate-Deficient Archaean Lakes

ROGER BUICK*

The Tumbiana Formation, about 2700 million years old, was largely deposited in ephemeral saline lakes, as judged by the unusual evaporite paragenesis of carbonate and halite with no sulfate. Stromatolites of diverse morphology occur in the lacustrine sediments, some with palimpsest fabrics after erect filaments. These stromatolites were probably accreted by phototropic microbes that, from their habitat in shallow isolated basins with negligible sulfate concentrations, almost certainly metabolized by oxygenic photosynthesis.

EARTH'S UNUSUALLY OXYGENATED atmosphere was not produced by abiogenic processes alone. Its redox state is clearly influenced by organisms metabolizing by oxygenic photosynthesis, that is, those that use water rather than exogenous reducing power as the electron donor for CO_2 reduction, liberating oxygen in the process. Just when organisms first evolved this ability to modify the atmosphere is unclear (1). Early Precambrian microfossils (2), stromatolite fabrics (3), and carbon isotope data (4) suggest, but do not prove, that aerobic photosynthesizers first appeared during the Archaean (1). Global mass balances of biogeochemically important elements (5) depend, for primeval times, upon poorly constrained quantities. Potentially, a more robust record of the early evolution of oxygenic photosynthesis is obtainable from microbial remains in environments isolated from external sources of reducing power. Here I report on a stromatolite assemblage from the late Archaean Fortescue Group of Western Australia, members of which were accreted by phototropic filamentous microorganisms in sulfate-deficient evaporative lakes. Their presence in such a setting indicates that by 2700 million years ago, complex microbial communities with a trophic hierarchy based on oxygenic photosynthesis were already extant.

The Fortescue Group unconformably overlies the early Archaean granitoid-supracrustal basement of the Pilbara Craton in northwestern Australia (Fig. 1). Northern exposures of Fortescue rocks are only slightly metamorphosed [sub-greenschist facies

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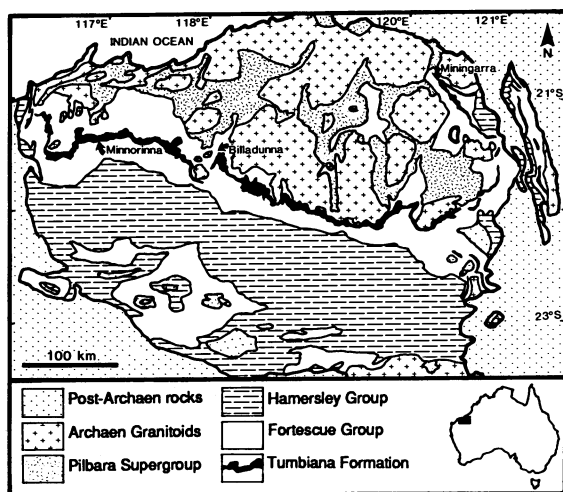
Fig. 1. Geological map of the Pilbara Craton.

Map legend:
- Post-Archaen rocks
- Archaen Granitoids
- Pilbara Supergroup
- Hamersley Group
- Fortescue Group
- Tumbiana Formation

(6)] and deformed [gentle folding (7)], with both increasing in intensity southwards. The group, at least 5000 m thick, has been divided into six formations (8), three of which are dominantly composed of tholeiitic flood basalts with subordinate felsic rocks (9). Intercalated with these are three largely sedimentary formations, the lower consisting mostly of terrigenous fluvial deposits and the upper of marine clastics and chert. The middle sedimentary horizon, called the Tumbiana Formation in northern areas [U-Pb zircon age of 2715 million ± 6 million years (10)], is rather different.

The Tumbiana Formation was examined at three localities: Minnorinna, Billadunna, and Miningarra (Fig. 1). The sections, all incomplete, ranged from 190 to 220 m thick (Fig.

Fig. 2. Schematic stratigraphy of the three Tumbiana localities.

Legend:
- Gabbro
- Terrigenous Arenite
- Kerogenous Lutite
- Carbonate
- Reworked Tuff
- Pyroclastic Tuff
- Basaltic Rudite
- Basalt

2); drilling indicates true stratigraphic thickness is up to 320 m. At all three sites, the Tumbiana Formation is underlain and overlain by massive or brecciated, coarsely amygdaloidal (1 to 10 mm, 1 to 40%) basalt with scoriaceous flow tops (similar rocks lie within the formation near Billadunna and Miningarra). The intervening sedimentary sequence can be divided into six facies associations, not all of which occur in all sections. Two are dominantly composed of terrigenous detritus. At Billadunna and Minnorinna, the basal rocks belong to the basaltic rudite association, very poorly sorted conglomerates that interfinger with trough cross-bedded tuffaceous arenites and wackes. The conglomerates are composed of angular to subrounded boulders and cobbles of scoriaceous basalt, identical to that immediately below, in a massive matrix of tuffaceous wacke. At the top of the Billadunna section and within the Minnorinna section lie rocks of the terrigenous arenite association, lenticular beds of trough cross-bedded (sets up to 0.5 m thick, 5 m broad) pebbly and gravelly sandstones overlying strongly scoured surfaces and grading up into rippled or plane-laminated siltstones. Quartz, microcline, and mica make up the bulk of the sediment along with lesser amounts of lithic detritus and volcanic ejecta, revealing that granitoids in the early Archaean basement were the main source.

The other four facies associations consist of volcanogenic or chemical sediment. The pyroclastic tuff association is composed of vitric wackes and arenites, generally very poorly sorted and massive to plane-laminated with partings of angular quartz sand. The kerogenous lutite association consists of massive organic-rich mudstones and rare rippled tuff-carbonate siltstones, both with abundant dewatering structures. The reworked tuff association contains shardy arenites and lutites with pervasive festoon cross-lamination. Straight to sinuous crested ripples, symmetri-

cal and commonly ladder-backed, are exposed on bedding surfaces, as are mud cracks and ripped-up intraclasts. Meter-thick interbeds of graded or cross-bedded accretionary lapilli rudite (grains up to 15 mm), often showing vigorous soft sediment deformation, may be present. The carbonate association (75% calcite and 25% dolomite) is composed of arenites, wackes, and lutites that are massive, rippled (symmetrical and occasionally ladder-backed), fenestral, or irregularly laminated. Mud cracks and teepees with associated breccias of imbricated tabular intraclasts are common. Calcarenites contain lutaceous peloids, coated intraclasts, cerebroid ooids (Fig. 3A) and tufa horizons that resemble microdigitate stromatolites (Fig. 3B). Pseudomorphs after hopper halite crystals occur in some calcilutite beds (Fig. 3C).

The Tumbiana Formation was evidently deposited on an emergent landmass (Fig. 4). The enclosing basalts were subaerially erupted, hence their massive structure, extreme vesicularity, and scoriaceous flow tops. The basaltic rudites resemble alluvial fan deposits in their sorting, rounding, and bed morphology; at Billadunna, they are adjacent to a regional growth fault that was active through much of Fortescue time (7, 9). The terrigenous arenites appear to be fluvial-deltaic deposits, the coarser sediments filling channels that gradually occluded. However, the four nondetrital associations were all deposited in standing water, judging from the ubiquity of symmetrical, and thus wave-generated, ripples. The pyroclastic tuffs and kerogenous lutites were probably laid down in deeper, stiller waters (indicated by poor sorting and scarcity of bedform structures), at times of high and low volcanogenic input, respectively. The reworked tuff and carbonate associations were deposited in more agitated, shallow to intermittently exposed settings (shown by the prevalence of mud cracks, teepees, intraclasts, fenestrae, and ooids), again under conditions of high and low volcanogenic influx respectively.

These standing water bodies were evidently lacustrine rather than marine (3). The interfingering relationships between the nondetrital sediments and terrestrial basalts and the alluvial fan and fluvial sediments suggest that marine transgressions did not interrupt nonmarine deposition. The prevalence of wave ripples and lack of unidirectional current structures indicate that tidal activity in the depository was negligible. The scarcity of dolomite in the carbonate sediments contrasts with the pervasive dolomitization of many similarly ancient marginal marine carbonates (11), suggesting that brines in the Tumbiana depository had lower Mg to Ca ratios than contemporary surficial seawater. Maybe most convincing, the curtailed evaporite paragene-
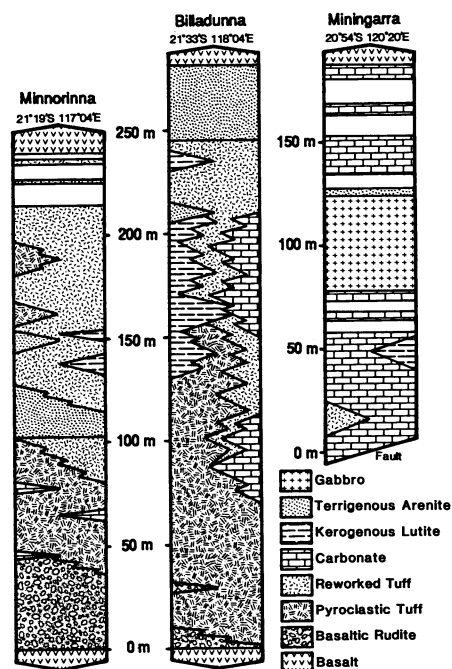
sis, from carbonate straight to halite without an intervening stage of sulfate precipitation (sulfates were clearly not removed by dissolution as collapse breccias are absent and sulfate pseudomorphs are nonexistent, although traces of even more soluble chlorides are abundant), is incompatible with a marine origin (12). As gypsum was both abundant and widespread in early Archaean marine evaporites (13), sulfate concentrations were appreciable in surficial oceanic water before the deposition of the Tumbiana sediments. So, to produce the Tumbiana paragenesis

from seawater, sulfate precipitation would have to be inhibited. This could be achieved by removing most sulfate before evaporite deposition, perhaps by microbial reduction to sulphide, or by consuming most calcium during carbonate precipitation, as might occur if increased atmospheric pCO_2 caused higher bicarbonate concentrations (14). However, the lack of significant sulfide mineralization in and around the evaporite beds indicates that the former did not occur. The calcic basalts of the hinterland would have supplied sufficient calcium to the evaporite

basins to overcome the effects of raised bicarbonate levels. It thus seems that the absence of sulfate minerals in the Tumbiana Formation results from an absence of sulfate ions in the basinal brines, testimony to a lacustrine environment.

All of the lacustrine sediment associations in the Tumbiana Formation contain stromatolites (3), with at least 12 distinct morphotypes developed. Three are restricted to the pyroclastic tuffs. These are nodular, complex bulbous (Fig. 3I), or ramifying columnar in macrostructure and are nucleated on coarse sandy partings, perhaps lag surfaces marking periods of volcanic quiescence. Their mesostructure of poorly inherited, moderately convex flexures is defined by scalloped microlaminae of chlorite, carbonate mud, and tuffaceous sand. The other morphotypes occur in the carbonate association and in carbonate-rich beds within kerogenous lutites and reworked tuffs. Some are interbedded with calcilutites containing halite pseudomorphs, others have mud-cracked upper surfaces that are overgrown by another generation of stromatolitic laminae. Their growth form is stratiform, nodular, pseudocolumnar, laterally linked, bulbous or columnar, with some of the latter branching (Fig. 3, F and G). In plan, they are round, ovate or markedly elongate. Most laminae have well-inherited, gently convex flexures, but some morphotypes have fenestral or cumulate mesostructures (Fig. 3H). On a microscopic scale, laminae are either continuous or crescentic and composed of fine carbonate mud or interlaminated carbonate mud, kerogenous lutite, and fine volcanic ash. Sandy ash laminae are often steeply inclined at angles near 90°. Tufted fabrics, of linked cuspate microflexures with curved axes and rare bifurcations (Fig. 3D), and palisade fabrics, of adjacent filamentary microstructures with sinuous traces and no bifurcations (Fig. 3E), are preserved in some fine-grained carbonate laminae.

The stromatolites are clearly biogenic. Their branching columns are more complex than those produced by inorganic processes alone (15). Their palisade and tufted fabrics closely resemble the palimpsests formed in younger microbialites after degradation of individual or clumped filamentous microorganisms of phototropic habit (3). Moreover, their sandy laminae inclined at angles far exceeding the normal maximum angle of repose indicate that accretion involved microbial binding. In diversity of morphotypes, the Tumbiana assemblage is comparable to those in many marine formations of Proterozoic age (16), though columnar forms are less significant. It is rather more varied than the most diverse younger assemblages of lacustrine origin (17), but not
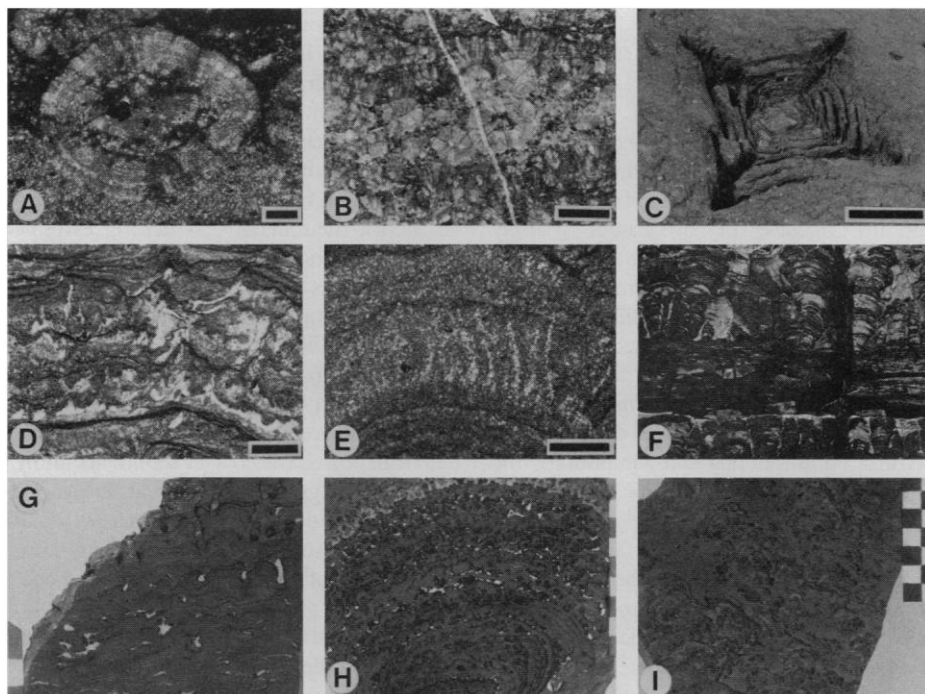

Fig. 3. Sediments and stromatolites from the carbonate association: (**A**) Cerebroid ooid with radial and concentric fabric (crossed polars); scale bar, 0.1 mm. (**B**) Microdigitate tufa with crystalline terminations (arrow) syntaxially overgrowing ooids; scale bar, 0.5 mm. (**C**) Mold of hopper halite crystal in tuffaceous calcilutite; scale bar, 10 mm. (**D**) Tufted fabric in bulbous stromatolite; scale bar, 1 mm. (**E**) Palisade fabric in bulbous stromatolite; scale bar, 0.5 mm. (**F**) Branching columnar stromatolites (hammer at left for scale). (**G**) Branching columnar stromatolite; scale bar, 1 cm. (**H**) Bulbous stromatolite with fenestral cumulate mesostructure; scale bar, 1 cm. (**I**) Complex bulbous stromatolite from pyroclastic tuff association; scale bar, 1 cm.
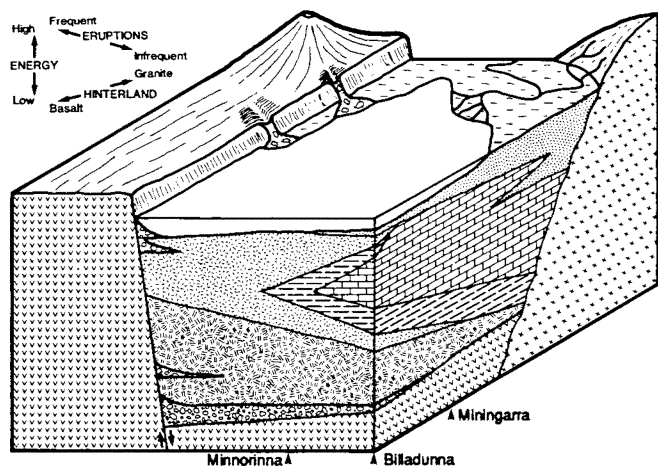

Fig. 4. Schematic reconstruction of the Tumbiana depositional environment (symbols as for Fig. 2).

markedly so. Thus, the Tumbiana stromatolite assemblage is noteworthy more for its age than for its aspect.

Most remarkable, however, is the fact that the metabolic capabilities of the constructing microorganisms can be determined. As the stromatolites accreted in evaporative lakes that occupied interior drainage basins on a basaltic plateau, essentially isolated ecosystems with negligible surficial inputs of energy and nutrients, heterotrophic metabolism of allochthonous organic nutrients cannot have been the basis of the local trophic hierarchy. The scarcity of sedimentary iron and sulfur mineralization indicates that volcanic and hydrothermal discharges into the Tumbiana lakes were minimal, so obligate consumers of juvenile hydrogen, hydrocarbons, or reduced sulfur must have been scarce. The sulfate deficit requires that anaerobic photosynthesis was insignificant. This leaves oxygenic photosynthesis as the only metabolic process capable of accounting for the abundance of biogenic material in the lakes. Given the equivocal nature of other data (1), the Tumbiana stromatolites thus constitute perhaps the firmest evidence of an Archaean trophic system based upon such metabolism.

Carbon isotope data (11, 18, 19) suggest both eubacteria and archaebacteria inhabited the Tumbiana lakes. Exceptionally light organic carbon (−40 to −50 per mil) associated with rather light carbonate carbon (0 to −4 per mil) implies that archaebacterial methanogens recycled carbon previously fixed by eubacterial photosynthesizers, the resulting methane being then consumed by methylotrophs (20). The isotopic differences between late Archaean lacustrine and marine kerogens (18) indicate that sulfate reducers had also evolved, largely excluding methanogens from oceanic environments by consuming most of the available organic substrate. Thus, the late Archaean biota had perhaps reached the maximum level of metabolic complexity and diversity possible in a suboxic world inhabited exclusively by prokaryotes. A period of evolutionary stasis apparently then ensued for about a billion years until the advent of eukaryosis (21) and a well-oxygenated atmosphere (22) in the latter part of the early Proterozoic.

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Interspecific Brood Parasitism in Blackbirds (Icterinae): A Phylogenetic Perspective

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An 852–base pair region of the cytochrome-b gene was sequenced for the brood parasitic cowbirds and 20 additional taxa of the New World blackbirds (Icterinae). The goal of the study was to determine (i) whether interspecific brood parasitism is multiply derived within the assemblage and (ii) the nature of the evolutionary transformation between various forms of interspecific brood parasitism. Cladistic analysis of the sequence data indicates that brood parasitism evolved a single time within the Icterinae. The primitive form of interspecific brood parasitism in this assemblage is host-specificity, with host-generality representing the derived condition.

AVIAN INTERSPECIFIC BROOD PARA-sitism (INTER), the laying of eggs by an individual of one species in nests of other species with subsequent care for the parasite young provided by the hosts, has been the subject of much interest over the past century (1–3). Most recently, avian brood parasitism has been proposed as an ideal system for the study of coevolution (3). However, studies of the evolution of this life history strategy have been hindered by the lack of explicit historical frameworks in the form of well-substantiated phylogenies for the taxa involved (4). Although a phylogeny does not necessarily fully resolve the sequence of events in the evolution of IN-TER, it does make possible the elimination of some alternative hypotheses (6).

Different species of avian brood parasites use from one to as many as 240 host species. Is this broad range of INTER connected by a simple evolutionary trajectory, and if so, does one extreme or the other represent the apomorphic condition? Theoretical investi-

gations of parasite-host coevolution (3, 7) suggest that as hosts develop defense mechanisms, brood-parasitic species may evolve in one of two ways: brood parasites may parasitize progressively fewer species over time as they develop responses to host defenses or, if naïve potential hosts are available, brood-parasitic species may alter their host selection. The former process could be characterized as an evolutionary transformation from host generalist to host specialist, whereas the latter could be characterized as maintenance of host number through time or perhaps a shift toward increasing generalization in host selection. A phylogeny for a group of birds that includes species that are specialized, intermediate, and generalized with respect to their selection of hosts provides a test of these predictions. If use of many host species is the initial stage in the evolution of INTER (5), then specialized species should form a monophyletic clade. Conversely, if use of one or a few host species is the primitive condition of INTER, then species parasitizing many host species should form a monophyletic clade. In either case, species parasitizing intermediate num-

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