GEOCHEMICAL MODEL FOR PROTEROZOIC STROMATOLITE DECLINE

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ABSTRACT. There are three principal periods of decline of stromatolites in the stratigraphic record: the first occurred sometime after about 1000 Ma, followed by further decline at the base of the Cambrian, and a final decline after the early Ordovician. In the first case, the decline in Proterozoic stromatolites is commonly thought to result from the advent of grazing and burrowing metazoan organisms (Walter and Heys, 1985). It is shown here that the temporal gap between the decline of stromatolites and the first occurrence of preserved metazoans is much greater than previously assumed, perhaps on the order of 400 my. This brings into question the validity of the foregoing model.

An alternative explanation for the decline of stromatolites is based on the evidence for a decrease in the carbonate saturation of seawater through the Proterozoic. Since the essential stromatolite-forming processes of precipitation and/or trapping and binding both ultimately depend on the rate of supply of carbonate sediment, any decrease in the saturation of seawater will eventually result in decreased carbonate sediment production and subsequent delivery. Stromatolite diversity and abundance, both taxonomic measures, decline at some point between about 1000 and 575 Ma. Stromatolite density, a measure of the abundance of individual stromatolites regardless of taxonomic designation, also is thought to decrease during this time.

Stromatolite density is thought to be high in the early Proterozoic, whereas taxonomic diversity and abundance are low. The fastest sedimentation rates of the early Proterozoic would have impeded stromatolite microstructure diversification by overwhelming biologic or environmental effects through sediment inundation during prolific whitings or direct precipitation of laminae. Whereas individual stromatolites would have been very abundant, the number of taxa would have been low due to the homogenizing effect of high sedimentation rates.

INTRODUCTION

Extensive work on Proterozoic stromatolites over the past two decades has demonstrated a decline in the diversity and abundance of stromatolite taxa\(^1\) near the end of Proterozoic time (Awramik, 1971:

\(^1\) Use of the Linnean system for the classification of stromatolites has been popular since the work of James Hall and Charles Walcott near the turn of the century. However, it should be acknowledged that stromatolites are not individual organisms but rather a record of the possible activity of benthic microbial mats. These mats probably consisted of a consortium of distinct microbial communities. Therefore, stromatolites cannot be strictly treated, in an evolutionary sense, as individual organisms have been. Biologic interpretations of the taxonomic diversity of stromatolites must infer the overriding effect

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Walter and Heys, 1985). This decline precedes two subsequent additional declines of stromatolites at the base of the Cambrian and after Early Ordovician time (Fischer, 1965: Pratt, 1982). In both cases, a variety of hypotheses had been offered to account for these events, including competitive exclusion by higher algae and metazoans (Fischer, 1965: Monty, 1973; Pratt, 1982), non-competitive ecologic restriction by grazing and burrowing/boring metazoans (Garrett, 1970: Awramik, 1971; Stanley, 1973; Walter and Heys, 1985), and changes in seawater chemistry (Fischer, 1965: Monty, 1973).

The first hypothesis was developed primarily to account for the post-Lower Ordovician decline of stromatolites (Fischer, 1965: Monty, 1973: Pratt, 1982) but may also be applicable to the decline of Proterozoic stromatolites where evidence for late Proterozoic higher algae are being documented in increasing amounts (Hofmann, 1985; Butterfield, Knoll, and Swett, 1988; Knoll and Swett, this volume). The potential importance of this mechanism should be recognized in addition to the geochemical arguments developed here. The second hypothesis has found especially strong support in view of the distribution of modern stromatolites which are restricted to environments where hypersalinity, high temperature, desiccation, and high current velocities tend to exclude grazing and burrowing organisms (Garrett, 1970), as well as potential competitors. For the Proterozoic decline, arguments have been developed that link the apparent coincidence of late Proterozoic stromatolite decline with the advent of grazing/burrowing metazoans (Awramik, 1971; Walter and Heys, 1985).

The hypothesis for changes in seawater chemistry (Fischer, 1965: Monty, 1973) has never been accepted owing to a lack of sufficient evidence. Disfavor of this model is best expressed by Walter and Heys (1985), who note that "While they may well have been perturbations to the chemical composition of seawater during the later Proterozoic and early Paleozoic, as there were during later geological history, there is no evidence for a unidirectional change in carbonate chemistry such as would be required to explain the stromatolite record." However, new evidence for unidirectional changes in the carbonate chemistry of seawater has recently been summarized by Grotzinger (1989).

The purpose of this paper is to present the evidence for and develop a geochemical model that can help explain the Proterozoic decline in stromatolites. The model satisfactorily explains the published evidence for the timing of stromatolite decline as well as some heretofore unappreciated events in stromatolite evolution. Furthermore, it eliminates the uncomfortable problem of the temporal gap between the actual decline of most Proterozoic stromatolites and the first evidence for metazoans, previously accounted for by invoking a cryptic metazoan "prehistory."

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of biotic control on stromatolite microstructure and/or morphology. However, because stromatolites are not fossil organisms, the diversity of stromatolite "taxa" may be otherwise interpreted.
It is acknowledged that the geochemical mechanism outlined here most likely worked in combination with other potentially important factors such as competitive exclusion by higher algae.

PREVIOUS WORK

The decline of Proterozoic and lower Paleozoic stromatolites was first noted by Fischer (1965), who invoked competitive exclusion by higher algae or chemical changes in seawater. The former idea was elaborated on by Monty (1973) and Pratt (1982). Pratt additionally suggested that the decline was possibly apparent due to the smothering effect of increased carbonate sediment production by more efficient post-Lower Ordovician calcified algae and metazoans. Pratt considered that Proterozoic sediment production rates were lower when, in fact, the opposite may be true (Grotzinger, 1989).

The hypothesis of changes in seawater chemistry was expanded by Monty (1973) who noted that production of calcified algal structures is enhanced by increased concentrations of dissolved CO₂. Monty suggested that Proterozoic seawater may have been enriched in CO₂ due to increased volcanism in the middle and late Proterozoic. Stromatolite decline was attributed to demise of these conditions with time.

Garrett (1970) observed that modern stromatolites are restricted to environments where hypersalinity, high temperature, desiccation, and high current velocities tend to exclude grazing and burrowing organisms. The effects of grazing and burrowing on algal mat preservation were measured and considered to be inimical to the widespread development of stromatolite meadows in open marine conditions. Garrett concluded that the decline of Phanerozoic stromatolites was due to the evolution and diversification of grazing metazoans which feed on algal mats and burrowing metazoans which destroy sedimentary laminae.

Awramik (1971) compiled Proterozoic stromatolite diversity data and demonstrated a decline of columnar forms during late Proterozoic time. He attributed this decline to the advent of Ediacaran soft-bodied metazoans which may have been capable of similar grazing/burrowing activities observed by Garrett (1970) for worms and shelly invertebrates. Awramik’s model generally has been accepted (Stanley, 1973; Walter and Heys, 1985), with some exceptions (Monty, 1973; Pratt, 1982).

Walter and Heys (1985) added substantially to the database supporting the interpretation of a decline in the diversity and abundance of stromatolite taxa during the Late Proterozoic. Their study considered and corrected for the number of basins preserved, the number of authors reporting stromatolites from each time interval (but not the number of publications), the long duration of individual taxa, and time intervals of unequal duration. Diversity was defined and computed as the number of taxa per interval of time (fig. 1A). Abundance, a biogeographic metric, estimates how widespread the taxa are per interval of time. It represents the number of taxa in each basin, summed for all basins in each time interval (fig. 1A). Because of this, abundance is
**Fig. 1(A)**  Method for computation of diversity and abundance of stromatolite taxa as executed by Walter and Heys (1985). Diversity is the number of taxa per interval of time. Abundance represents the number of taxa in each basin, summed for all basins in each time interval. (B) Diversity of stromatolite taxa for the (early) early Proterozoic (2.5-2.2 Ga), (late) early Proterozoic (2.2-1.65 Ga), early Riphean (1.65-1.35 Ga), middle Riphean (1.55-1.05 Ga), late Riphean (1.05-675 Ga), Vendian (0.675-0.570 Ga), and Cambrian (0.570-0.500 Ga) time. (C) Abundance of stromatolite taxa for the same time intervals as in (B). The final abundances are normalized for the deviation in the number of basins between time intervals. Data for (B) and (C) from Walter and Heys (1985).
strongly dependent on the diversity. Differences between abundance and diversity reflect true environmental distributions and/or variations in the number of basins. Therefore, the final estimate is normalized for the deviation in the number of basins between time intervals.

Walter and Heys (1985) suggested that the diversity of stromatolites reached a maximum in the middle Riphean, remained constant through the later Riphean, and declined during the Vendian (fig. 1B). Stromatolite taxa were most “abundant” during the late Riphean and declined thereafter (fig. 1C). It is important to note that Walter and Heys did not develop any method of gauging the density (number of stromatolites per unit of rock) of individual stromatolites (as opposed to abundance of taxa) in carbonate platforms over time. This is potentially a very useful parameter that, although difficult to quantify, would constitute an additional proxy of microbial evolution. The implications of saturation by numbers, as opposed to taxa, are discussed further below.

It is possible that Ediacaran metazoan fossils are younger than 600 Ma (Jenkins, 1984) based on a number of U-Pb zircon ages on volcanic rocks within or bracketing fossiliferous sections (Jenkins, 1984; Benus, 1988). This may not be so surprising given that the base of the Cambrian is also now thought to be younger than previously assumed (as young as 530 Ma; Conway Morris, 1988). On the other hand, the decline of stromatolites could have started as early as 1000 Ma (see below). This 400 my gap is inextricable if stromatolite decline is related to the advent of metazoan organisms that graze and burrow. Walter and Heys (1985) recognized this temporal misfit, although they considered it to be much shorter than what the data allow (see below). They attributed it to an early metazoan “prehistory,” unrecorded by fossils, but invoked by the need to explain the advanced state and diversity of the Ediacaran fauna (Glaessner, 1983; Cloud, 1986). It should be recognized that even if unpreserved metazoans (for example, some form of meiofauna as suggested by Walter and Heys) were present, their effect on mat disruption may have been negligible as argued by Farmer (1989) who has studied modern mat-meiofauna relations.

Knoll (in press) cautions that the data of Walter and Heys (1985) should properly be plotted as a histogram. The data is replotted in figure 2 for comparison. Knoll emphasizes that the data can only be interpreted as representing a significant decline somewhere between the Late Riphean and the Vendian—not over the interval beginning 700 to 800 Ma as Walter and Heys contend. Additional time points and subdivisions are required in order to achieve this level of resolution. The implications of this misinterpreted data set are significant and suggest that the timing of the actual decline could have been earlier in the Late Riphean than has been previously argued. In any event, the correlation in time between the origin of grazing/burrowing metazoans and the decline of stromatolites is weak.

Finally, following a synthesis of the facies, stratigraphic relationships, and evolution of several Archean through late Proterozoic carbon-
ate platforms, Grotzinger (1989) suggested that several secular changes in platform facies probably relate to long-term, unidirectional changes in the carbonate chemistry of seawater. For lack of evidence, Walter and Heys (1985) had previously dismissed changes in seawater as a cause of stromatolite decline. However, this evidence is now available and summarized below as it specifically pertains to the interpretation of Proterozoic stromatolite decline.

PROTEROZOIC CARBONATE PLATFORMS AND SEAWATER CHEMISTRY

Carbonate platforms with most of the essential features of Phanerozoic platforms (fig. 3) were well developed by 2.6 to 2.3 Ga (Grotzinger, 1989). Proterozoic carbonate platforms include ramps and rimmed shelves. These generally show strong paleogeographic zonation as reflected by the distribution of stromatolitic buildups, including reefs, relative to other deeper and shallower water facies (fig. 4). Ramps may be homoclinal (fig. 4B) or distally steepened and have fringing reefs, barrier reefs, or isolated buildups. Examples include the early Proterozoic Monteville Formation, middle Proterozoic Dismal Lakes Group,
Fig. 3. Stratigraphic cross section of the Campbellrand Subgroup. Note prominence of various stromatolitic facies in overall construction of platform. After Beukes (1987).
Fig. 4. General distribution of specific stromatolite types across Proterozoic carbonate platforms. (A) Rimmed shelf as high-energy (windward) margin characterized by barrier reef complex of strongly elongate stromatolite mounds and columns. Conical stromatolites may form below wave-base as foreslope deposits; domal stromatolites of the inner-shelf lagoon are weakly- to non-elongate as a result of their restricted, low-energy setting; tufas (including microdigitate stromatolites) form by precipitation on tidal flats. (B) Ramp as moderate-energy platform. Elongation of stromatolite mounds and columns is dependent on relative amount of wave surge and/or tidal strength; for low-energy settings elongation will be minimal. Note decrease of stromatolite mound size toward both deeper and shallower settings; elongation may show a similar relationship. After Grotzinger (1989).
and late Proterozoic Little Dal. Rimmed shelves are developed as both accretionary and bypass margins and may include intrashelf basins. Examples include the early Proterozoic Rocknest Formation and Reivilo Formation and late Proterozoic carbonates of the Gourma basin.

The evolution of many Proterozoic carbonate platforms is strikingly similar to that of younger counterparts and indicates that the critical stages of development, including growth, diversification, and expansion, were not dependent on the presence of carbonate-secreting metazoans or higher algae. This relationship demonstrates that zones of Proterozoic carbonate production and accumulation must have been nearly identical to Phanerozoic counterparts.

Composition of Proterozoic seawater.—Changes in the composition of Precambrian seawater, particularly factors influencing carbonate equilibria, have been discussed by Ronov (1968), Holland (1972, 1984), Walker (1983), Kempe and Degens (1985), and Kasting (1987). In general, it is thought that no great changes have occurred to alter significantly the precipitation of chemical sediments relative to Phanerozoic and modern analogues. However, Grotzinger (1989) proposed that abundance and possibly the sequence of minerals precipitated may have changed. While not a major modification of previous models, it may have significantly affected the chemical basis of stromatolite-forming processes. Kempe and Degens (1985) propose a more severe deviation from standard models of seawater composition.

Faith in the apparent similarity between Precambrian and Phanerozoic seawater is strongly dependent on the acceptance that Precambrian evaporative sequences bear evidence for precipitation of carbonate, followed by gypsum and then halite (Holland, 1972). This relationship is partially supported by the Precambrian rock record, which contains preserved mineral assemblages or pseudomorphs of “vanished” assemblages (Holland, 1972: Walker and others, 1983). However, these relationships have not been firmly established, particularly for the Archean and early Proterozoic record. Reports of “evaporite” pseudomorphs, most notably gypsum, are often unsubstantiated by reliable criteria. Furthermore, the context in which documented pseudomorphs occur is seldom discussed in terms of paleoenvironments, and also to what extent the mineralogy may have been influenced by influx of non-marine waters (sensu Hardie, 1984).

In the rare instance where it has been possible to document convincingly the former presence of primary, probably evaporative gypsum (now preserved as barite; Buick and Dunlop, 1987), it is not clear whether or not this occurrence was marine or lacustrine. Furthermore, if the occurrence was marine, it is likely that there was a considerable influence on the local composition of seawater through influx of “continental”-derived calcium-rich waters from erosion of highly basaltic surrounding source areas. As pointed out by Hardie (1984), even if a marine depositional setting is established independently, say on sedimentologic evidence from enclosing deposits, the hydrologic restriction
required to precipitate salts º... cannot fail to put a strong non-marine stamp on both the geochemistry and the sedimentology of the deposit” (Hardie, 1984). Consequently, evaporite deposits interlayed with marine sediments may not necessarily yield the correct sequence of evaporite minerals predicted by precipitation from normal seawater.

For the Archean, large calcite fans, previously interpreted as calcite-replaced gypsum (Walter, 1983; Hofmann, 1971; Wilks, 1986; Martin, Nisbet and Bickle, 1981), alternatively may be calcite pseudomorphs after giant aragonite fans. This interpretation has been historically disfavored, with one exception (Martin, Nisbet, and Bickle, 1981), and is considered by Grotzinger (1989) as the better option. These fans, which have radii up to 1 m (Hofmann and others, 1985) appear to be characteristic of many late Archean sequences but are rare in younger sequences. If the fans were originally aragonite, then they may constitute evidence for the relative ease of precipitation of abiotic calcium carbonate, perhaps under highly supersaturated conditions. Specific possible occurrences of former Archean aragonite are evaluated in Grotzinger (1989).

The interpretation of calcitized Archean gypsum has strongly influenced models for the composition of Precambrian seawater. Past recognition of these assumed “gypsum” pseudomorphs in part forms the basis for justification of a uniformitarian model for seawater composition in which precipitation of calcium carbonate is sequentially followed by calcium sulfate and halite (Walker, 1983). However, if the aragonite interpretation for the fibrous fans is correct, true gypsum precipitation may have been rarer than previously thought and perhaps did not follow as the “normal” precipitate after calcium carbonate (Grotzinger, 1989).

The precipitation of carbonate was a common phenomenon in Proterozoic marine settings (Grotzinger, 1989). It occurred in normal marine environments where there is no evidence or need to invoke evaporation to concentrate dissolved components. Precipitation occurred in all environments represented by the Phanerozoic carbonate record, including the pelagic realm in certain cases (for example, Pethei Platform: Hoffman, 1974). Supersaturation with respect to calcite and aragonite is documented by the widespread occurrence of marine cements in shallow as well as deep marine environments.

Supersaturation of Proterozoic seawater with respect to calcite and aragonite is further supported by the presence of abundant tidal-flat tufas (microdigitate stromatolites; Hoffman, 1975; Grotzinger and Read, 1983; Grotzinger, 1986b) in many early Proterozoic carbonate platforms. The significance of these tufas was not previously recognized, and it was suggested (Grotzinger, 1989) that these facies represent the precipitation of mesoscopically crystalline calcium carbonate (probably aragonite: Grotzinger and Read, 1983; Hofmann and Jackson, 1988) on tidal flats under normal to mildly evaporative conditions. The apparent restriction of this facies after about 1.7 Ga may suggest that early Proterozoic seawater had a higher degree of saturation than in younger times when carbonate precipitation may have been less abundant (Grotz-
Grotzinger (1989) proposed that Archean, early Proterozoic, and to a lesser extent, middle to late Proterozoic seawater favored surplus "abiotic" carbonate precipitation as aragonite and (hi-Mg?) calcite, in comparison to younger times. "Normal" seawater possibly was highly oversaturated, and any perturbation such as microbially-induced uptake of CO$_2$ might have caused immediate and prolific precipitation of calcium carbonate. The ratio of [HCO$_3^-$] to [Ca$^{2+}$] may also have been increased relative to Phanerozoic seawater, so that 2[HCO$_3^-$] was close to or even greater than [Ca$^{2+}$]. Seawater might have precipitated abundant carbonate in excess quantities and induced the "carbonate factory" to exploit new realms such as tidal flats where tufas might form. In the process, most or all available calcium would be extracted simply by precipitation of carbonate and, during an evaporative situation, little or no calcium sulfate could have precipitated except near sites of continental runoff (for example, deltas) where influx of additional calcium might be expected.

This model is compatible with theoretical studies that suggest that atmospheric CO$_2$ was greatly increased in the Precambrian (Walker, 1983; Kasting, 1987). By implication, the concentration of total dissolved inorganic carbon in the oceans would have also been increased. Precipitation of carbonate would have been favored provided that the excess negative charge represented by increased bicarbonate was balanced by an increase in the concentration of major cations.

The model is also supported by geologic data. Bedded or massive gypsum formed in primary evaporative environments is absent in the Archean and early Proterozoic record. These sediments first appear in the middle Proterozoic (about 1.7–1.5 Ga) MacArthur Basin (Jackson, Muir, and Plumb, 1987), with others in the about 1.2 Ga Borden Basin (G. Jackson and Ianelli, 1981) and about 0.8 Ga Amundsen Basin (Victoria Island, Canada; Young, 1981). Furthermore, the best documented early Proterozoic gypsum casts are not associated with the major evaporitic carbonate platforms such as the Rocknest or Campbellrand platforms. Rather, they are often developed in sequences that may have formed adjacent to deltaic regimes where locally high concentrations of calcium might occur. For example, the widely cited gypsum casts of the Great Slave Supergroup (Badham and Stanworth, 1977) occur almost exclusively in siliciclastic facies, some of which are deltaic (Hoffman, 1969). None are present in the regionally extensive Pethei carbonate platform (Great Slave Supergroup), and it should be noted that halite casts (and not gypsum) are present in the transitional "evaporite" facies between deep basinal carbonate precipitates and an overlying evaporite solution-collapse breccia (Stark Formation: Hoffman, 1969). These relationships further underscore the possibility that calcium sulfate was not a common phase in early Proterozoic evaporative sequences.
Significantly, the demise of the early Proterozoic tidal-flat tufas (microdigitate stromatolites) approximately coincides with the first appearance of middle Proterozoic bedded sulfate deposits. This relationship suggests that as total calcium carbonate saturation and the [HCO₃⁻]/[Ca²⁺] ratio decreased with time toward average Phanerozoic values, less precipitation of carbonate occurred leaving more calcium available to form sulfates during development of evaporative sediments.

**Stromatolites and Proterozoic carbonate production.**—Stromatolites, constructed by sediment accreted through the trapping-and-binding and/or precipitation-inducing activities of microbial communities, or as a result of entirely abiotic processes, occupied every major ecological niche known to be important in the construction of Phanerozoic platforms by more complex and environmentally sensitive organisms (Grotzinger, 1989). Therefore, it is reasonable to suspect that stromatolites, in part, may be the result of prolific in situ carbonate production in the form of major buildups and reefs, some of which are comparable in scale to the largest of Phanerozoic barrier and pinnacle reefs. In addition, stromatolites often formed veneers over the interiors of carbonate platforms and thus contributed significantly to the growth and aggradation of the overall platform.

Traditionally, stromatolites have been viewed as carbonate depo- sitories, rather than factories, forming principally through the trapping-and-binding of carbonate sediments derived externally to the stromato- lite lithotope (Black, 1933; Logan, Rezak, and Ginsburg, 1964). However, the large volume of stromatolitic sediment in most Proterozoic (particularly early Proterozoic) platforms requires that stromatolitic facies tracts be regarded not only as carbonate deposits but also as actual carbonate factories on the basis of mass balance arguments (Grotzinger, 1986a, 1989). This is important since the substantial volume of stromatolitic sediment in many Proterozoic carbonate platforms generally has not been previously appreciated (compare, Pratt, 1982).

In addition to mass balance arguments, there is also growing direct evidence for the role of in situ precipitation in the development of at least some stromatolites. Locally abundant marine cementation has been documented in the vicinity of stromatolites as cements between component particles of stromatolites and as actual stromatolitic laminae (Kerans, 1982; Grotzinger and Read, 1983; Grotzinger, 1986a,b; Hofmann and Jackson, 1988; Kerans and Donaldson, 1989). The presence of substrate-parallel layers of neomorphic fibrous or blocky cement that coat and form adjacent to stromatolites are evidence for in situ precipita- tion of accretionary layers. Similarly, the preservation of radial fibrous fabrics in neomorphic carbonates that constitute “microdigitate” stromatolites (tufas) of early Proterozoic tidal flat facies is also evidence for volumetrically important in situ sediment accumulation by precipitation (Grotzinger, 1989). Other arguments also apply with a correspondingly lower degree of confidence. For example, the minimal incorporation of quartz sand grains into stromatolitic laminae where stromatolites are
strongly admixed with siliciclastic sediments is a common field observation (Donaldson, 1963; Serebryakov and Semikhatov, 1974). In addition the fine lamination of Proterozoic stromatolites has been cited as evidence of possible precipitation, in contrast to Phanerozoic “trapping-and-binding” stromatolites which often show less well developed lamination (Cloud and Semikhatov, 1969; Walter, 1972).

It is likely that the literature of stromatolitic microfabrics potentially misrepresents the importance of precipitation in the formation of stromatolites. In some cases, recrystallized cements in Proterozoic stromatolitic laminae may have either not been recognized or been misidentified as recrystallized clastic carbonate (micrites, et cetera). Studies of recrystallization of Phanerozoic marine cements, ooids, and skeletal grains have only recently provided reliable criteria for the recognition of former aragonite versus calcite cements and how they can be distinguished from recrystallized micrites (compare Sandberg, 1985). Future investigations of Proterozoic stromatolites will have to consider the wide variety of possible fabrics, and their origins, that are associated with neomorphically recrystallized marine sediments and cements.

The role of in situ precipitation in the development of stromatolitic lamination is interpreted here to be a time dependent process. It is suggested that it was most important in the early Proterozoic and possibly negligible in the late Proterozoic, a relationship supported by Knoll and Swett (this volume). The transition through time is ultimately interpreted to be partially responsible for the decline of Proterozoic stromatolites as a result of their reduced capacity to accrete sediment.

Growth mechanisms of stromatolites.—There are four possible mechanisms involved in the formation of calcareous microbialites including trapping and binding of sediment, inorganic calcification, biologically influenced calcification, and skeletal calcification (Burne and Moore, 1987). They suggest that only trapping and binding and inorganic calcification are important in the formation of stromatolites. Skeletal calcification (or silification) is a “process in which metabolism produces an organized mineralized structure with a predetermined form.” This would include organisms such as diatoms and red algae, which are generally not important in the formation of benthic microbial mats, nor which are believed to have been important in the Proterozoic.

Biologically influenced calcification as defined by Burne and Moore (1987) essentially involves calcification of cyanobacterial or eucaryotic algal sheaths. It can result from a variety of biological processes including photosynthesis or degradation of organic matter. In the case of photosynthesis carbonate precipitation is induced when \( \text{CO}_2 \) is extracted from seawater, and \( \text{pH} \) is lowered within and adjacent to sheaths. Burne and Moore suggest that eucaryotes are better equipped to promote calcification and that cyanobacteria are not as effective, if at all. Calcification of sheaths has not been an important factor in the growth of most Proterozoic stromatolites, in contrast to Phanerozoic stromatolites and thrombolites (Kennard and James, 1986). However, it should be noted
that there are a few reported occurrences of possible late Proterozoic calcified sheaths (Swett and Knoll, 1985; Horodyski and Mankiewicz, this volume).

The third mechanism is inorganic calcification where microbes are only incidentally associated with the precipitated carbonate (Burne and Moore, 1987). Precipitation occurs exclusively in response to physicochemical changes in seawater. However, it seems likely that in a situation where precipitation does not take place in or on sheaths, a microbial community may still be capable of influencing seawater chemistry through extraction of CO₂ during photosynthesis. This is a potentially very important process where a carbonate platform is covered with stromatolite-forming cyanobacteria that do not precipitate carbonate on or in sheaths. Such a process could result in direct precipitation of cement crusts as stromatolitic laminae (fig. 5A) or as micritic whittings that would settle to form laminae (fig 5B); the stromatolites formed would be nearly impossible to distinguish from what Burne and Moore (1987) consider to be true inorganic calcification. The early Proterozoic tidal flat tufas of Grotzinger (1986b) are thought to have been produced by microbially-influenced inorganic calcification (although it is equally possible that they are entirely abiotic in origin). In the past these have been classified as microdigitate stromatolites (Donaldson, 1963), asperiform stromatolites (Grey and Thorne, 1985), and ministromatolites (Hofmann and Jackson, 1988). Although they are indeed stromatolites, they are considered to have a precipitated origin and therefore may be classified as microbial tufas in the scheme of Burne and Moore (1987).

The fourth mechanism involves trapping and binding clastic carbonate by filamentous and/or gelatinous benthic microbial communities (Burne and Moore, 1987). The sediment of most Proterozoic stromatolitic laminae appears to have been generally micritic, excepting those instances where cement crusts (tufas) may have been important (Grotzinger, 1989; Knoll and Swett, this volume). Awramik and Riding (1988) suggest that this results from the dominance of mat communities by

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**Fig. 5.** Mechanisms for growth of Proterozoic stromatolites. (A) Direct precipitation of inorganic or biologically-influenced cement crusts as laminae. (B) Inorganic or biologically influenced precipitation of micrite as whittings; sediment is subsequently trapped and bound. (C) Import of clastic carbonate sediment from laterally adjacent source area: sediment is subsequently trapped and bound.
cyanobacteria which are incapable of sequestering coarser-grained material. They argue that coarse-grained stromatolites are a Phanerozoic phenomenon resulting from prolific coarse-grained skeletal sediment production initiated at the base of the Paleozoic and continuing on to the Recent. Algal eucaryotes, in contrast to more primitive cyanobacterial microbes, would have been capable of binding these coarse skeletal sediments.

However, it is not clear why algal eucaryotes, which evolved during the middle Proterozoic, should not have been able to trap and bind the locally copious coarse sediments that do occur in the middle and late Proterozoic as coarse to very coarse oolitic and intraclastic grainstones and packstones (Knoll and Swett, this volume; Grotzinger, 1989). In such settings, stromatolites are still dominantly micritic. This apparent contradiction of the Awramik and Riding hypothesis can be resolved if relative volumes of sediment production are considered. If coarse-grained sediments are the only sediments available, then it follows that eualgal stromatolites would be coarse grained. However, if fine-grained as well as coarse-grained sediments are both available, then it becomes a trade off between which sediment type might dominate. Many authors (most recently Grotzinger, 1989; Knoll and Swett, this volume) have suggested that carbonate sediment production in the form of micritic “whitings” may have been higher in the late Proterozoic relative to the Phanerozoic. In this case, despite the presence of coarser-grained sediment (transported as bed load), the micritic sediment (transported as suspended load) would dominate the total sediment contribution to stromatolitic lamination. Furthermore, it is suggested that even under conditions of a 1:1 micritic to coarse sediment ratio, the micritic fraction would tend to be incorporated selectively. This would result from the tendency of coarse sediment to be transported as bed load and micrite as suspended load. As the synoptic relief of any given stromatolite increased, the supply of coarse sediment would be proportionately decreased due to the mechanical difficulties of transporting bed load sediment over obstacles such as protruding domes, or, worse yet, columns. Consequently, the dominance of late Proterozoic micritic stromatolites that could have been colonized by both cyanobacterial and eucaryotic mats is interpreted to reflect a high rate of micrite production. Therefore, the rise of coarse-grained columnar stromatolites at the base of the Phanerozoic would not only result from a dramatic increase in the volume of coarse-grained sediment (Awramik and Riding, 1988) but also to a decrease in the available micritic sediment. These observations and interpretations are consistent with the overall model for increased Proterozoic carbonate production discussed below.

The trapping and binding model for stromatolite growth can be advanced further by distinguishing between stromatolites that form by the accretion of micrite precipitated directly from the surrounding water column versus sediment imported from laterally adjacent non-stromatolitic environments (compare fig. 5B and C). In the former case,
the benthic microbial communities may play an indirect role by changing local water chemistry and inducing carbonate precipitation as whittings and also an active role by subsequently trapping-and-binding the sediment that is precipitated. In the latter case, the benthic microbes only serve actively to fix sediment produced outside the stromatolitic area. The latter mechanism has been invoked to account for most stromatolites of both Proterozoic and Phanerozoic age.

It is extremely important to recognize that in any of these models the rate and efficiency of stromatolite growth is ultimately entirely dependent on the rate of supply of carbonate sediment. In the model involving precipitation of cements to form laminae, the rate of growth is determined by the rate of precipitation. This is clearly the most efficient mechanism, because each unit of sediment precipitated is translated into one unit of equivalent lamination. In the second model, precipitation of micrite from the surrounding water column is less efficient because volume may be lost by transport of suspended sediments away from the stromatolites by various currents. Furthermore, "trapping-and-binding" is not as efficient in accreting sediment as direct in situ precipitation: once deposited, currents may erode sediments unless they are immediately cemented. Finally, in the third model, incorporation of sediment produced externally to the zone of stromatolites is the least efficient mechanism. Because sediment must be produced at an external site, the growth of stromatolites is dependent on favorable currents to import suspended and/or traction loads. This process is likely to be highly variable, dependent on platform morphology, tidal regime, wave regime, and the influences of storms and oceanic currents. In the most favorable circumstances this model might be as efficient as the precipitated micrite model: in general, it is probably very inefficient.

These arguments all emphasize that the optimal growth rate of stromatolites is directly related to the rate of sediment production and the efficiency of the mechanism by which sediment is accreted as laminae. Accordingly, whatever factors are important in controlling sediment production and sediment accretion will ultimately determine the growth potential of stromatolites. Sediment accretion occurs by precipitation and/or trapping and binding. As discussed above, precipitation is more efficient than trapping and binding, and early cementation of trapped and bound sediment will prevent subsequent erosion by currents (or burrowing by metazoans in younger stromatolites). Therefore, the efficiency of laminae accretion is interpreted to be directly proportional to the saturation state of seawater with respect to calcium carbonate. As saturation is increased, marine cementation would start sooner, and ultimately cements would be precipitated directly on the sediment surface as laminae.

Similarly, the integrated total sediment production of a Proterozoic carbonate platform also is related directly to the saturation state of seawater with respect to calcium carbonate. Higher levels of saturation would promote excessive carbonate precipitation and therefore rapid
growth of stromatolites. It is likely that microbes might have further enhanced carbonate precipitation by extracting dissolved CO₂ from surrounding seawater during photosynthesis. However, at lower levels of saturation the microbial influence over precipitation would be correspondingly reduced and stromatolite growth would be diminished.

THE RISE AND FALL OF PROTEROZOIC STROMATOLITES

The best developed Proterozoic carbonate platforms are primarily of early Proterozoic age (Grotzinger, 1989). Most early Proterozoic platforms are constructed principally of stromatolites which constitute, by volume, the most important facies. Furthermore, early Proterozoic stromatolites show abundant evidence for direct precipitation of laminae (Grotzinger, 1989), although trapping-and-binding of precipitated micrite probably also was common. Therefore, it becomes meaningful to evaluate the decline of stromatolites in terms of an additional parameter, designated here as stromatolite density, and defined as the average volume of stromatolitic sediment per unit of carbonate platform.² Independent of taxonomic classification, stromatolites saturated nearly every available environment on early Proterozoic platforms, and their density was high (fig 6) Although it is hard to constrain quantitatively, it seems that the stromatolite density decreased in the middle Proterozoic. For the late Proterozoic, it appears that stromatolitic facies were also less important in the construction of carbonate platforms (Eby, 1977; Knoll and Swett, this volume).

As summarized above, Grotzinger (1989) provided evidence for increased carbonate saturation of Proterozoic seawater relative to the Phanerozoic. Saturation is proposed to have been highest in the early Proterozoic decreasing through the middle and late Proterozoic. Late Proterozoic levels are interpreted to be somewhat higher than Phanerozoic levels, consistent with data and interpretations of Knoll (in press) and Knoll and Swett (this volume). An obvious implication of this model is that the decline of Proterozoic stromatolites could, in part, be related to a global reduction in carbonate saturation through time.³ The growth of any stromatolite formed of carbonate sediment would be subject to changes in this condition as discussed above. As saturation decreased, direct precipitation of laminae would have stopped, and eventually

² At this time, it is not possible to assign specific values of density to the various periods of time. Accordingly, the "curve" of figure 6 is an interpretation based principally on field work in several Proterozoic platforms, the middle to late Proterozoic Belt basin, and the late Proterozoic Pahrump Group, and extensive review of the literature (Grotzinger, 1989). The present significance of this parameter is to emphasize the increased importance of stromatolites in the construction of early Proterozoic carbonate platforms compared to their younger Proterozoic counterparts. Such a role is greatly underestimated by the extremely low values for early Proterozoic diversity and abundance presented by Walter and Heys (1985).

³ It must be acknowledged, however, that the increased density of early Proterozoic stromatolites may also have been promoted by the potential lack of competition imposed by higher algae believed to have been present in the late Proterozoic (Butterfield, Knoll, and Swett, 1988).
whittings would have become more restricted in frequency as well as area. In this manner, the amount of sediment available to become incorporated in stromatolites was decreased, thereby restricting the distribution of stromatolites themselves.

It is revealing that the microdigitate stromatolites (tuftas) decline at the end of the early Proterozoic (Grey and Thorne, 1985; Grotzinger, 1989), followed by the coniform stromatolites that decline at the end of the middle Proterozoic, prior to the decline of most other stromatolite taxa (Walter and Heys, 1985). Of all the stromatolite groups, the mechanisms for growth of these two can be most obviously related to direct precipitation (Grotzinger, 1989). Whereas the microdigitate stromatolites formed on tidal flats, the coniform stromatolites are of subtidal origin. As carbonate saturation of seawater decreased through the Proterozoic, it can be expected that subtidal environments would have remained more productive, where a constant supply of calcium and bicarbonate was available.

The model developed here can also explain the increase in stromatolite diversity and abundance in the early Proterozoic, assuming that the data are reliable. A comparison of figures 1 and 6 shows that stromatolite diversity, abundance, and density all decreased through the late Proterozoic. However, for the early Proterozoic, stromatolite density is inferred to be high, while diversity and abundance are low. This aspect of Proterozoic stromatolite diversity has not been directly addressed in previous studies (Awramik, 1971; Walter and Heys, 1985).

As discussed above, the high density of stromatolites is interpreted to have resulted partially from the increased saturation of seawater with respect to calcium carbonate during that time (the other likely effect being a lack of competition by higher algae of the late Proterozoic; Knoll
and Swett, this volume). However, it should be noted that the terms "diversity" and "abundance" refer to stromatolite taxa rather than actual numbers ("density"). Therefore, it is worth reviewing the basis for taxonomic classification of stromatolites.

Initially, stromatolites were classified according to morphological characteristics, particularly styles of branching (Raaben, 1969). However, for the past decade, stromatolites have been classified principally according to their microstructure, with lesser emphasis on morphology (Semikhatov and others, 1979) owing to the realization that various forms may have greater temporal ranges than previously thought (Donaldson, 1976: Hofmann, 1977). It is thought that microstructure principally reflects the assemblage of microorganisms originally present in the mat covering the stromatolite surface. Therefore, evolutionary changes in the history of microbes will be recorded in the succession of microfabrics exhibited by stromatolites.

It is possible that the range of individual stromatolite taxa do record the evolution of microorganisms, as has been generally suggested (Walter, 1972). However, it seems likely that the proposed Proterozoic decrease in carbonate saturation of seawater must have had some effect on the diversification of stromatolites in the first half of the Proterozoic. Almost paradoxically, the increase in diversity, just as the decline, is attributed here to the same long-term decrease in carbonate saturation of seawater. According to the model presented so far, one may have predicted that if a decrease in carbonate saturation results in a decrease in stromatolite diversity, then high saturation might have resulted in high diversity. In fact, the opposite is true: an attempt to resolve this seeming paradox is presented below.

The microstructure of stromatolites reflects a number of features including: grain-to-grain and crystal-to-crystal relationships, the thickness of lamination, the relief, along individual laminae, and the distribution of organic matter and of elements associated with organic matter (Semikhatov and others, 1979). Since the microstructure of stromatolites is dependent on the interplay of these factors—then the more these factors vary the greater the range of potential microstructural relationships. The biological imprint on microstructure is created through the orientation of filaments and unicells, the motility of major filamentous forms, and the adhesiveness and abundance of the microbial sheath material (Semikhatov and others, 1979). Non-biologic influences on microstructure include: rate of sedimentation of elasic carbonate, rate of accretion of precipitated carbonate, rate of lithification, and subsequent degradation of fabrics during diagenesis (Semikhatov and others, 1979). It is suggested that under conditions of greater carbonate saturation a lower range of fabrics would be achieved for stromatolites due to the homogenizing effect of rapid rates of sedimentation associated with regimes of high precipitation. In the form of in situ accretion of cement layers, this process would dominate the fabric due to high growth rates. Similarly high rates of growth would occur during "fall-out of micrite
during possibly prolific whittings. Consequently, there would be little diversity in microstructure owing to little deviation in the processes of formation (or subsequent modification).

Three possible explanations can account for the increase in diversity of stromatolites (microstructures) through the first half of the Proterozoic. First, the diversity of microbes was already high in the early Proterozoic, but the high rates of sediment production overwhelmed the potentially variable influences of different microbial assemblages on development of unique microstructures. Extremely rapid early lithification would have helped to prevent subsequent modification of fabrics. In the second scenario, microbial diversification in the middle Proterozoic was real and occurs simultaneously with a decrease in carbonate saturation. Perhaps diversification results from pressure to respond to a waning source of “easy” sediment supply as growth by precipitation becomes less viable. In the third model, the diversification records primarily changes in external conditions over time (that is, microbial evolution has little to do with microstructure development). In this case, low diversity caused by the homogenizing effect of rapid precipitation (as laminae or whiting-derived micrite) in the early Proterozoic is replaced by conditions where sedimentation rates are somewhat lower and early cementation is less rapid in the middle Proterozoic. As a result, other variables such as currents and climate begin to influence the overall system as well as specific environments such that stromatolites become more sensitive to these variables. Eventually, the myriad external factors that control sediment distribution become progressively more important as precipitation and sediment supply become progressively less important. The stromatolitic microstructures reach a maximum. The subsequent decline is then attributed to further degradation of the carbonate producing system so that the previously influential external factors become detrimental to the robust growth of stromatolites.

CONCLUSIONS

1. Proterozoic seawater may have been highly oversaturated with respect to calcium carbonate; the ratio of \([\text{HCO}_3^-]\) to \([\text{Ca}^{2+}]\) may also have been increased relative to Phanerozoic seawater. The middle and late Proterozoic possibly saw a decrease in both of these variables. However, late Proterozoic seawater is still thought to have had a higher carbonate saturation than Phanerozoic seawater.

2. The decline of stromatolites, in part, may be directly related to the proposed decrease in carbonate saturation of seawater. Precipitation, sediment production, and stromatolite growth rates would have been highest in the early Proterozoic, decreasing progressively through time. This is reflected in the decrease in stromatolite diversity, abundance, and density during the second half of the Proterozoic.

3. The increase in stromatolite diversity in the first half of the Proterozoic may also be related to a decrease in sediment production
rates. The fastest sedimentation rates of the early Proterozoic would have impeded stromatolite microstructure diversification by overwhelming biologic and/or environmental effects through direct precipitation of laminae or sediment inundation during prolific whittings. Accordingly, the middle Proterozoic is interpreted to represent a time interval when sediment production rates were just right for the maximum diversification of stromatolite microstructure—enough to insure adequate growth, but not so high as to suppress other influences.

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CARBONATE DEPOSITION DURING THE LATE PROTEROZOIC ERA: AN EXAMPLE FROM SPITSBERGEN

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ABSTRACT. Carbonate sediments reflect the physico-chemical and biological circumstances of their formation; thus, features of limestones and dolomites may provide insights into both environmental and evolutionary change through geological time. The Upper Proterozoic (approx 800–700 Ma) Akademikerbreen Group, Spitsbergen, comprises 2000 m of carbonates, with only minor intercalations of quartz arenite and shale. Although Proterozoic carbonates are often seen as predominantly dolomitic, the Akademikerbreen Group is about 45 percent limestone. Stromatolites are conspicuous in outcrop but constitute only 25 percent of the total section. Micrites and coarser intraclastic carbonates derived mainly from micritic precursors comprise 60 percent of the group, while oolites make up the remaining 15 percent. Distinctive sedimentary features of the group include giant (up to 16 mm) ooids, very early diagenetic calcite nodules and cements, micrites containing subaqueous shrinkage cracks filled with equant microspar cement, and strong 13C enrichment in both carbonates and co-occurring organic matter. The principal features of Akademikerbreen carbonates are widely distributed in coeval successions. However, these rocks appear to differ from older limestones and dolomites in their relative abundance of grainstones and, perhaps, micrites, as well as their paucity of tufa-like laminates and columnar or coniform stromatolites that preserve petrographic evidence of in situ precipitation as a dominant means of carbonate accretion. Upper Proterozoic carbonates also differ from Paleozoic accumulations, but the transition is not abrupt. Most changes accompanying the Proterozoic/Phanerozoic transition can be interpreted in terms of the consequences rather than the causes of metazoan and metaphyte evolution, including the evolution of biomineralization. Carbonate sedimentology reinforces data from other sources which indicate the last 200 to 300 Ma of the Proterozoic Eon was a distinctive interval of Earth history.

INTRODUCTION

In the present day oceans, CaCO₃ precipitation is predominantly a biological process mediated by skeleton-forming invertebrates, algae, and protozoa (Bathurst, 1975). Although the earliest known skeletonized organisms appeared near the end of the Proterozoic Eon, approx 600 Ma ago (Germs, 1972; Grant, 1990; Grant, Knoll, and Germs, in press), thick and laterally extensive carbonates are characteristic components of earlier Proterozoic sedimentary successions. How do these Proterozoic carbonates compare or contrast with the predominantly biogenic limestones and dolomites of the Phanerozoic Eon?

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