Reports

Phanerozoic Stromatolites: Noncompetitive Ecologic Restriction by Grazing and Burrowing Animals

Abstract. *The abundance of stromatolites (algal laminated sedimentary structures) in the Precambrian followed by a decline in the Phanerozoic is explained by the evolution and diversification during the Phanerozoic of grazing animals which feed on surface algal mats and of burrowing animals which destroy sedimentary laminations.*

Stromatolites are laminated sedimentary structures built by dense mats primarily of blue-green algae, which selectively trap and bind sediment particles among their mucilaginous filaments (*1*). Stromatolites range in age from the early Precambrian (*2*) to the Recent, although, unlike most other fossil groups, they reached their acme in the Precambrian, and declined markedly from the middle Ordovician onward to become scarce in the Cenozoic (*3*). The unusual geologic history requires an explanation.

Fischer (*3*) speculated that although stromatolites probably grew subtidally in the Precambrian, their Phanerozoic range has been limited to the intertidal zone either because of competition with other plants, or because they became less mineralized and were therefore less readily preserved. To properly understand the factors limiting stromatolites, however, it is necessary to study these factors in Recent stromatolite localities.

Such localities exist on the west coast of Andros Island, Bahamas, where carbonate sediments are being deposited today in shallow water and littoral environments in an area approximately 150 miles long by 50 miles wide. The littoral environments where most of my observations were made form part of a tidal flat complex with beach ridges, tidal channels, levees, and ponds (*4*). Elevation, which is the chief factor controlling the distribution of organisms on the tidal flats, ranges from subtidal and intertidal in the channels and ponds, to supratidal on the beach ridges and levees.

Filamentous blue-green algae occur abundantly in almost all surface sediments of the tidal flat and shallow marine environments of the Bahama Banks. Strongly cohesive algal mats (*5*), however, are only developed in supratidal zones, and beneath them mostly planar stromatolites are developed. In intertidal zones the algae are usually present only as a clotted scum on the sediment surface, and in subtidal zones mats are usually only weakly developed.

Grazing and burrowing animals (Table 1) are common on and in the tidal flat and shallow marine sediments and to varying degrees are important in the biogenic reworking of the sediments. Grazers are animals that feed on the sediment surface. On the Andros tidal flats they include two small cerithid gastropods, *Cerithidea costata* and *Batillaria minima*, which appear to prevent the intertidal formation of algal mats. Several lines of evidence point to this conclusion. First, the distribution of the mats and the gastropods is mutually exclusive, the gastropods living in the intertidal zone, the mats being developed in the supratidal and subtidal zones.

Table 1. Common grazing and burrowing animals from the west coast of Andros Island, Bahamas. +, Deposit-feeders; –, deposit-movers; * grazers.

Supratidal

+ oligochaete worm
– ants
– insect larvae
– *Cardisoma guanhumi* (crab)
– *Sesarma curacaoense*

Intertidal

* *Cerithidea costata* (gastropod)
* *Batillaria minima* (gastropod)
+ *Marphysa sanguinea* (polychaete)
+ *Perinereis* cf. *anderssoni* (polychaete)
+ ? *Ceratonereis tridentata* (polychaete)
+ *Dasybranchus lumbricoides* ? (polychaete)
+ nematode worms
– *Apseudes* sp. (shrimp)
– *Alpheus heterochaelis* (shrimp)

Subtidal

* *Elops saurus* (the bonefish)
* *Mugil* sp. (the mullet)
* ostracods
+ *Myriochele* sp. (polychaete)
+ *Armandia maculata* (polychaete)
+ nematode worms
– *Callianassa* sp. (shrimp)
– *Callinectes sapidus* (crab)

Secondly, two critical field experiments demonstrated the potential of the gastropods for preventing mat formation. In the first, several gastropods were placed on a piece of wet supratidal mat. They crawled slowly over the mat, feeding on the surface layers and leaving behind a trail of rod-shaped fecal pellets. By using the size of these pellets (0.026 mm^3), their rate of excretion (about 100 per hour), the number of gastropods (average concentration in intertidal, 500 to 1500/m^2), and the time they spend feeding (average: 12 hr/day, while the tide is in), I calculated that they would devour the topmost millimeter of sediment in 1 month. That this is sufficient to prevent the formation of a cohesive algal mat was shown by the second experiment. In this, 0.25 m^2 was enclosed in the intertidal zone to prevent the gastropods from feeding. In 2 months the surface of this area had developed a cohesive mat, although it was as yet thin and rather easily broken.

Final proof of the relationship between mats and gastropods came from an unusual area of the tidal flats—a sort of mud beach lying seaward of the beach ridge. There, a cohesive algal mat is developed intertidally because the gastropods are periodically washed away by storm waves. Where the gastropods do occur, they live together in small "herds," grazing on fresh mats and leaving behind a trail of pellets on a mat-free surface (Fig. 1A).

Subtidal mats are generally less cohesive than those in the supratidal zone, and laminations are not preserved beneath them because of the activities of tiny syllid polychaetes, ostracods, and cumaceans which feed on the algal coatings that bind the grains of sediment together, and otherwise disorganize the grains while moving through

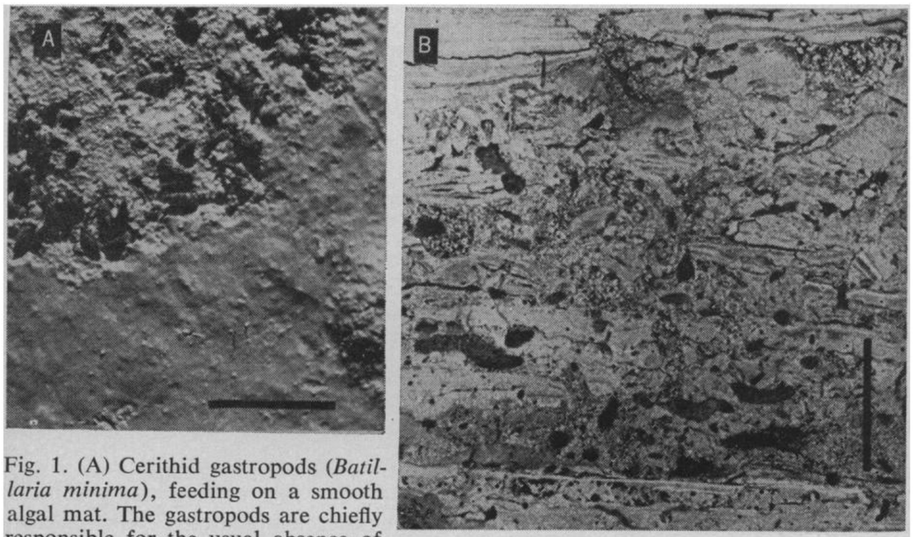

Fig. 1. (A) Cerithid gastropods (*Batillaria minima*), feeding on a smooth algal mat. The gastropods are chiefly responsible for the usual absence of intertidal algal mats on the tidal flats on the northwest coast of Andros Island, Bahamas. Scale, 5 cm. (B) Slabbed and polished core of supratidal levee sediments, showing burrows and patches of pelleted sediment cutting the stromatolitic laminations and laminated intraclasts. Both the burrows and the pellets are made by worms, ants and insect larvae, whose activities destroy the original laminated structure. Scale, 1 cm.

the mats (*6*). In addition, several fish such as the bonefish and mullet ingest mouthfuls of surface sediment and can be considered as partially responsible for the poor development of subtidal mats.

Algal laminations, once formed, may later be destroyed by burrowing animals which homogenize sediments beneath the surface by moving sedimentary particles around. Among these burrowers, deposit-feeders such as errant polychaetes and nematodes move through the sediment, ingesting it and excreting it as pellets behind them.

Deposit-movers do not ingest sediment, but instead burrow into it for temporary or permanent shelter. They include such groups as filter feeders, detritus feeders, scavengers, and predators. Most deposit-movers construct their burrows by picking at the sediment and removing material to the surface—some of them construct elaborate subsurface tunnels and galleries (*7*).

Some burrowers destroy supratidal laminations (Fig. 1B). Because there are fewer burrowers in supratidal zones, and because those that are present are not particularly active in moving large quantities of sediment, the laminations formed in the supratidal zone of the Bahamas are never completely destroyed.

To summarize, the grazers eat the mats or surface sediments, thus preventing laminations from forming, and the burrowers churn the sediment so that any laminations that may be present are progressively destroyed. This has the effect of limiting algal laminated deposits on Andros to supratidal zones, where grazing animals are absent and burrowing animals few. A similar distribution has been described from Florida Bay (*8*), where laminated stromatolitic sediment is restricted to the upper intertidal because of the abundance of burrowing and surface-grazing polychaetes in the lower intertidal.

Small head-shaped stromatolites and algal laminated balls (oncolites) have been reported from subtidal zones in Bermuda and the Bahamas (*9*). That such structures can exist in normal marine situations is no doubt due to their location in environments such as tidal channels, where the occurrence of invertebrate grazers and the settling of burrowing larvae is limited by strong currents and high sediment movement.

The most prolific growth of stromatolites known anywhere in the Recent occurs in Hamelin Pool, Western Australia (*10*). This is a hypersaline lagoon, where there are no grazers or burrowers to limit stromatolite growth and preservation.

There are many stromatolitic sequences in the Phanerozoic fossil record that can be interpreted as having been deposited in littoral environments (*11*). Among these it is notable that the stromatolitic (laminated) beds are not usually fossiliferous, even though fossiliferous (usually bioclastic or burrowed) beds occur within the same sequences. This suggests a spatial separation of environments, (i) with algal mats but without animals, and (ii) without preserved algal mats but with animals, as in the Bahamas today.

Puzzling exceptions to the usual restriction to littoral environments, are the well-developed stromatolites reported from among reef assemblages of Silurian through Lower Cretaceous age (*12*). These present a special problem, since stromatolites have not been reported from modern reefs. Several factors may account for this anomaly. First, invertebrate grazers are typically motile epifaunal animals that are easily detached from their substrate, and are therefore uncommon on modern and ancient reefs. Second, the chief grazers of modern reefs are teleost fishes such as the parrotfish and surgeon fish (*13*) —none of these had evolved before the Tertiary (*14*). Third, reef stromatolites may have become cemented penecontemporaneously like some modern reef sediments (*15*)—they would then have been less susceptible to destruction by burrowers. In any case, we know, at least for Permian reefs, that "there is no evidence that the mollusks, echinoids, and larger worms played an important role [as reef-rock borers], as they do today" (*16*).

According to Fischer (*3*), "stromatolites were dominant up to middle Ordovician times, and then declined through the Paleozoic to play a very minor role in Mesozoic marine limestones and to virtually disappear in the Cenozoic." This gradual decline of stromatolites can probably be correlated with the evolution of new grazing and burrowing animals, their radiation into new habitats and environments, and finally their toleration of such extreme conditions as are typical of tidal flats and reefs. The greater abundance of Cambrian and Lower Ordovician stromatolites may correlate with the low diversity of animal life before the Ordovician expansion (*17*).

In Precambrian rocks there is little sign of metazoan life (*18*), so it is hardly surprising that we find the greatest stromatolite development here. That stromatolites did in fact reach their acme in the Precambrian is illustrated by the extent to which they have been used by Russian workers (*19*) as stratigraphic guide fossils. In North America, a great variety of stromatolites has been described from the Belt Series

(*20*) and the Pethei Formation (*21*)—the 2-billion-year-old Pethei stromatolites are of particular interest, because Hoffman (*21*) believes that the different forms grew in a great variety of environments extending from the shore to shelf-edge reefs. To consider a modern equivalent we would have to imagine the entire Bahama Banks covered with stromatolites.

Blue-green algae today inhabit an enormous range of environments (*22*). It is their remarkable ecologic tolerance that has enabled stromatolites to persist to the present time. The compelling evidence for restriction of stromatolites by animals is especially important in that few, if any, similar relationships have been well documented in the fossil record. In contrast to the many well-known examples of ecologic displacement of groups by better-adapted competitors, the stromatolite example is one of suppression of a group by interacting but noncompetitive organisms, so that the fossil record of that group is limited ecologically and areally to the narrow extremes of its broad adaptive range.

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Deformation Twins in Hornblende

Abstract. *Hornblende deformation twins with twin planes parallel to ($\bar{1}01$) are produced experimentally in single crystals by compression parallel to the* c *axis. Twinning occurs at confining pressures from 5 to 15 kilobars and temperatures from 400° to 600°C (strain rate, 10^{-5} per second).*

Lamellar features approximately parallel to (100) and ($\bar{1}01$) are commonly reported for clinoamphiboles. Recently, numerous amphibole minerals containing lamellae were examined by x-ray single crystal, optical, and microprobe techniques (*1, 2*). These studies clarify the relations between the optical direc-

Table 1. Pressure-temperature conditions for twinning in hornblende. Test conducted at a strain rate of 10^{-5} per second.

Test	Confining pressure (kb)	Temperature (°C)	Longitudinal strain (%)	Twins (No.)	Development*
A1-63	5	400	9.5	25	2
A1-72	5	600	10.0	10	3
A1-54	10	400	10.5	18	2
A1-55	10	600	13.0	10	3
A1-58	15	400	12.2	100	1
A1-59	15	600	10.0	100	1
A1-78	20	400	10.9	15	2
A1-61	20	400	11.3	12	2
A1-73	20	600	9.0	14	3

* 1, excellent; 2, fair; 3, poor.

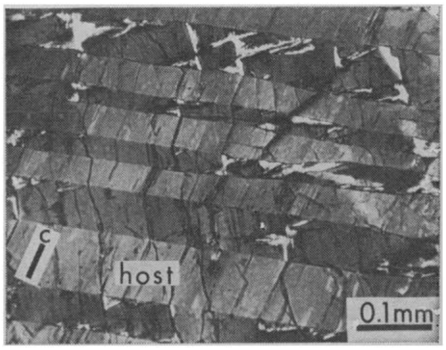

Fig. 1 (left). The ($\bar{1}01$) twin lamellae developed in deformed cylinder of hornblende (Al-58T). Crystallographic *c* axis approximately parallel to length of cylinder, which is also direction of maximum compression. Diagonal, light-colored area is ductile zone. Note pronounced parting along ($\bar{1}01$) planes. Confining pressure, 15 kb; temperature, 400°C. Length of cylinder is 7 mm. Fig. 2 (right). Magnified view of ($\bar{1}01$) twin lamellae in Fig. 1. The NE-SW (100) cleavages are deflected at twin boundaries by the twinning shear. White areas within ($\bar{1}01$) twin lamellae are (100) twins.