Annales de la Société Géologique de Belgique, T. 96, 1973, pp. 585-624 1974

PRECAMBRIAN BACKGROUND AND PHANEROZOIC HISTORY OF STROMATOLITIC COMMUNITIES, AN OVERVIEW (*)

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ABSTRACT

The environmental situation and the ecological circumstances of precambrian stromatolites are first considered. Four main problems are discussed : (1) the morphological evolution of stromatolitic structures (2) the gigantism of precambrian stromatolites (3) the ecological restrictions imposed upon the development of these communities and (4) the Vendian decline of precambrian stromatolites and the rise of invertebrates.

During the Phanerozoic, stromatolites underwent a continuous and steady decline the most significant phases of which occurred after mid-Ordovician times and after the radiation of Rhodophytes early in the Cenozoic. This decline is correlated with at least four main factors : (1) the Early Paleozoic transformation of marine ecosystems, with a net increase in niche diversity and a resulting decrease of optimal modal niche sizes, resulting in severe problems for stromatolites; (2) the development of animal communities adapted to use the abundant food provided by Blue-green algae; (3) the development of better-adapted, encrusting and reef building animal communities which greatly restricted marine reefoid stromatolitic algae; and (4) the rise of better-adapted red and green algal communities, which partially replaced calcareous blue-greens in the shallow marine settings and contributed to confining the proeminence of stromatolites, as rock builders, to very marginal settings and to fresh water settings.

RÉSUMÉ

La situation des stromatolithes au Précambrien et leurs relations avec le milieu général sont considérées dans une première section. Quatre problèmes principaux y sont discutés : (1) l'évolution morphologique des structures stromatolithiques, (2) le gigantisme des stromatolithes précambriens, (3) les restrictions écologiques qui ont freiné le développement de ces communautés et (4) le déclin, d'âge Vendien, des stromatolithes précambriens et l'apparition des invertébrés.

Le déclin des stromatolithes enregistré au cours du Phanérozoïque est mis en relation avec quatre faits majeurs : (1) La profonde transformation qui affecta les écosystèmes marins au début du Paléozoïque; l'accroissement considérable de diversité des niches et la diminution conséquente de leurs dimensions optimales causa de sérieux problèmes aux communautés à stromatolithes; (2) le développement des communautés animales adaptées à utiliser la nourriture riche et abondante constituée par le matériel cyanophytique; (3) la différenciation de communautés animales encroûtantes et récifales, caractérisées par des niches plus restreintes et de meilleures adaptations aux nouvelles conditions du milieu, limita considérablement l'omnipotence des stromatolithes marins; (4) le développement progressif de communautés algaires à base de rhodophycées et de chlorophycées, beaucoup plus perfectionnées sous l'angle biologique, les amenèrent peu à peu à remplacer les algues bleues calcaires dans les milieux marins peu profonds et à contribuer à limiter la puissance constructrice des stromatolithes aux domaines marginaux, puis aux eaux douces.

(*) Communication présentée le 9 mars 1971, manuscrit déposé le 11 juillet 1973.

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WORKING METHODS AND METHODOLOGICAL BASIS

The present paper is the first attempt to reconstruct and interpret the history of stromatolitic communities from Precambrian times onward. This long meandering and difficult history is rooted and has known its most fascinating episodes in the wide mysterious Proterozoic, almost in another world. The conceptual and factual problems cannot be solved by one man at one time; as such, the present overview is far from being complete. It only proposes a general scheme, a methodology and lines of reasonning which will hopefully lay out basis for constructive discussion; by the same token, it attempts to propose embryonic solutions to obvious but yet unexplained situations on the sole assumptions drawn from the observation of natural systems.

This study is based first on *stratal evidence,* which give us, at any period of time, a wealth of objective informations about the past situation of stromatolites. It is a most reliable approach to stick to stratal evidence, to let it speak and to avoid biasing its informations by unrefrained, untested transposition of the Present. The Present is *but* a resultant of past situations before being a key to them.

Accordingly, the first step is to follow as objectively as possible the paleontological record from Precambrian times to the Recent and to collect a sound learning all the way. This historical wandering leads to the understanding of the present-day real status of Cyanophyta and algal mats, a status rooted in geohistory. Once we know what this Present means with respect to the Past, we know how to handle it, what to take of it in order to understand the past, what to sift from it in order not to misunderstand the past.

The study is based secondly on a critical knowledge of the general ecology and habits of present-day Cyanophyta and algal mats, of the various single environmental situations in which they are found, and of their reactions with respect to each particular situation.

Once we know the intrinsic mechanisms of the dynamic of blue-green algal coenoses in the various Recent settings, once we know moreover what their present-day occurences represent with respect to the past, we can organize the second step of the approach, i.e. the regressive analysis from the present to the past. Furthermore, with the help of theoretical basic principles and the understanding of historical situations, we can guess *what* part of the present can give us clues to *what* part of the past, and *how* to make the transposition.

Accordingly, the elaboration of this paper was based on a threefold analysis : (1) following onward the objective stratal evidence up to the Present to recognize all the evolutionary meanders as well as the historical and intrinsic significance of the Present; (2) then a pause in the journey to decipher the rules of the game in the Present; (3) then going backward by regressive analysis to interpret the past situations after having isolated in the right Present the right keys applicable to the right analogous or homologous past situations. Of course, this paper does not follow this scheme but is a synthesis of the reported methodology and results from it.

INTRODUCTION

1. *General*

Precambrian strata record the progressive development of procaryotic coenoses, from the ancestral « Eobacterium » to the important blue-green algal reef building coenoses of the Middle and Late Proterozoic (Cloud, 1968; Schopf, 1970).

Ecological pressures favored those forms which, among other things, had evolved highly efficient photosynthetic systems (Olson, 1970); their rise had a most fundamental influence on the physico-chemical conditions at both atmospheric and biospheric levels (Fischer, 1965, 1972; Cloud, 1968).

The acme of benthonic calcareous blue-green algae occurred in the Younger Precambrian seas — from about 1.65 to 0.65 eons (Cloud, and Semikhatov, 1969) — and widespread significant stromatolitic deposits can be traced through the Precambrian record until mid-Ordovician times (Fischer, 1965). This progressive rise resulted in the colonization of all suitable habitats (1) from (deep) subtidal to interdital zones (Mohan, 1968; Krüger, 1969; Donaldson, 1963; Awramik, 1971; Bertrand-Sarfati, 1972; Walter, 1972).

From Latest Proterozoic and undoubtedly mid-Ordovician times onward however, stromatolites suffered a progressive decline. The acceleration of this decline coincides roughly with the Cambro-Ordovician burst of animal and eukariotic communities; this observation suggests that stromatolites suffered the impact of an apparently major biological event which inaugurated the Phanerozoic eon (see for instance Fischer, 1965; Garrett, 1970; Awramik, 1971).

The purpose of this paper is an attempt to place the history of stromatolitic communities — considered as *encrusting calcareous structures* — into a broad evolutionary framework and to focus upon the history of the niche.

2. *Applicable niche concepts*

The niche concept may be important in understanding the history of stromatolites. The niche (Elton, 1927) represents the *functional* properties of a species, or the functional aspect of a population; it summarizes its environmental requirements, tolerances and potentials (Valentine, 1969). Each population has a place — or a niche — « in the economy of its surroundings, as it consumes resources or is itself resource for its predators and interferes or aids, other populations » (Valentine, 1968, p. 225). The niche of a species or any population may be conceptually visualized in its prospective and realized aspects.

The *prospective niche* is « the collection of all the points representing the range of conditions under which a species may possibly exist » (Valentine, 1969, p. 905). The size of the prospective niche depends on the range and variety of potential environmental interactions with which species are basically provided by their genetic pool at any time given. Among other things the size of the prospective niche is related to this multidimensional region which is the environment.

Thus there is a second basic concept, the concept of hyperspace, which was developed by Hutchinson (1957, 1967; see also Simpson, 1953). If one visualizes each single parameter of the environment as a geometric dimension, the « total environment » may be represented by a multidimensional space or hyperspace. The *prospective environmental hyperspace* is defined by the maximum « geometric » dimension of all possible environmental parameters.

These notions of prospective niche and prospective hyperspace can be best visualized by the paleontologist who deals with coenoses spanning 3 billion years of earth history, surviving the most drastic environmental changes.

At any time and place, however, only a small fraction of the total range of the prospective environmental parameters is materialized; this local instantaneous set of parameters defines the *realized environmental hyperspace*. Similarly, only a part of the prospective niche of a population (or species) is fulfilled at a given time because it happens to overlap with the then realized hyperspace : this part of the prospective niche is called the *realized niche*. The sizes of the realized niches are more severely controlled than the sizes of the prospective niche as « they are controlled partly by the range of environmental conditions, physical and biological, that happen to be

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(1) With the exception of acidic water bodies, as blue-green algae apparently cannot thrive in pH's lower than 5 (Brock, 1973).

realized in the living region of the species, and they fluctuate as environment fluctuates » (Valentine, 1969, p. 907).

ACKNOWLEDGEMENTS

This study was supported by a grant of the « Fonds National de la Recherche Scientifique » to which I am very grateful. I am also endebted to D. R. Lawrence, University of South Carolina, who revised the second part of the manuscript and improved the text.

THE PRECAMBRIAN BACKGROUND

1. *Some significant facts*

Precambrian stromatolitic assemblages reveal a series of particular trends, two of which appear rather unique in the history of the group : (1) the rather common realization of big individual or biohermal structures (Cloud, 1968; Donaldson 1969, etc...) the size of which will never be *significantly* (1) reached again after the dawn of the Phanerozoic.

(2) The worldwide distribution of well defined growth forms and microstructures, many of which do not cross, as such, the Precambrian-Cambrian boundary; the most conspicuous among them include *Conophyton* and a variety of very particular columnar forms (Cloud and Semikhatov, 1969; Valdiya 1969; Awramik, 1971; Bertrand-Sarfati, 1972; Walter 1972, etc...).

Furthermore, there has « apparently been a time related change in the morphology of Proterozoic stromatolites and... the changes involved appear to be roughly contemporaneous in widely separated parts of the world » (Cloud and Semikhatov, 1969, p. 1022). These changes affected the microstructure of individual stromatolites (Glaessner, 1971; Bertrand-Sarfati, 1972; Walter, 1972), the characteristic features of the individual colonies (the stromatoid of Kalkowsky, 1908) and the overall pattern of the resulting « reefs », in such a way that a biostratigraphical scheme has been set up and is being checked all over the world (Keller et al. 1960; Semikhatov, 1962; Krylov, 1963, 1967; Koma et al., 1964; Komar et al 1965; Raaben, 1964, 1969; Nuzhnov, 1967; Cloud and Semikhatov, 1969; Valdiya 1969; Glaessner, Preiss and Walter, 1969; Bertrand-Sarfati and Raaben, 1970; Glaessner, 1971; Walter 1972).

Finally, as shown by Awramik (1971) and Bertrand-Sarfati (1972), the generalized increase in the diversity of columnar stromatolites, which is commonly recorded from pre-Riphean to Middle-Late Riphean times is followed by a rather marked decreased in diversity from Late Riphean to Early Vendian-Cambrian times.

This apparent evolution led to a *first crisis* which started about 800 m.y. ago (Awramik 1971, fig. 1; Bertrand-Sarfati, 1972) and which is marked, from Latest Precambrian to Early Cambrian times by — (1) the progressive extinction of many stromatolitic groups, hence a loss in organic diversity;

— (2) a loss in the morphological and microstructural definition of growth

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(1) I say significantly, because scattered occurences are known in younger strata such as the Early to Middle Cambrian of Siberia (Nechaeva, 1945) or the Devonian of the Canning Basin, N.W. Australia (Playford, personnal communication).

forms, or the appearance of new types of microstructures (Glaessner 1971, p. 1331; Walter 1972, pp. 85-87);

— (3) a rather brutal decrease in the sizes of the construction, generally speaking (Glaessner, id.; Walter, id.).

This will not prevent stromatolitic communities from being still very abundant until mid-Ordovician times, but with lesser sizes and greater confusion in the (micro)-structures.

2. *General comments on the recorded evolution of Precambrian stromatolites*

If laterally, within a given basin, stromatolitic units may be time-transgressive — as is the case for so many lithological units —, it is however clear that on a broader scale, we are confronted with a unique succession of stromatolitic types; most authors agree with the fact that the recorded changes appear to be time-controlled and cannot be paralleled with lithological changes, nor accounted for by the geological evolution of sedimentary basins (Valdiya, 1969; Keller et al. 1960; Edgell 1964; Cloud and Semikhatov 1969; Glaessner 1971,...). Also, the recorded appearance of new microstructural types of stromatolites cannot be explained in terms of particular diagenesis or different preservation (Walter, 1972, p. 86). There is little doubt left then that the reported observations record true evolutionnary trends. The problems arise as to which natural factors are we going to relate these trends in stromatolites history, remembering that we are not dealing with the evolution of one organism but of complex communities?

Confronted with the reported evolutionnary facts, Glaessner (1971, p. 1331) focusses on the *morphological* evolution of the participating algae as the prime factor leading to the observed changes in the form of stromatolites as well as in their microstructure (« Es ist sehr warscheinlich, dass die beobachteten Formänderungen der Stromatolithen mit evolutionären Formwandlung der sie erzeugenden Algen in Verbindung stehen »... « in anderen (Formen) beginnt eine Veränderung der Feinstruktur der sie aufbauenden Lagen, die gewiss mit evolutionären Veränderung der Algen in Zusammenhang steht »). Stated in such a simple way, this healthy, biological approach could be ruined by the evidence that the evolution of Blue-green algae has been rather slow through the Precambrian, and that, moreover, many of them show striking morphological similarities with Recent ones (Schopf 1968, 1969, 1970). In fact, in view of the morphological conservatism of individual blue-green algae through time (Cloud and Semikhatov 1969, p. 1022; Schopf, 1970, p. 337, 345; 1972, p. 76, etc...) as revealed by the numerous studies carried on material preserved in cherts *below* (see review in Schopf 1970) and *above* (Starmach, 1963; Adamczak, 1963...) the Precambrian/Cambrian boundary, the marked differences recorded in the overall characters of stromatolites (size, diversity,...) cannot apparently be closely related to important and determinant morphological evolution of the algae themselves, at least not as such.

We must accordingly frame the discussion in a wider scope and consider the problem in terms of algal evolution, of coenose evolution and of environmental evolution.

Algal evolution itself is not so much important in terms of the progressive changes affecting the morphology of the filaments or of the cells — morphology which is rather conservative as seen above — but in terms of extinction, emergence and radiation of individual algal taxa. Such changes imply replacement of the « personnalities » which have led the building up of the recorded stromatolites.

With this in mind, it seems evident that there has been significant changes in Precambrian cyanophytic communities : comparisons made by Schopf (1968) of the Gunflint microflora (ca. 1800 m.y.) with that of the Belt (1200 m.y.) and that of the Bitter Spring (800-900 m.y.) have revealed the succession of very different assemblages having few or no taxa in common. I completely agree with Schopf (1968) and Walter (1972) that these differences are time related rather than due to different facies relationships. Algal analysis of Recent stromatolites coming from very different environments and localities (freshwaters, normal marine waters, hypersaline waters, from the Bahamas, from Florida, Australia, etc.) show that whereas the dominant algae may be different, they are always accompanied by about the same ubiquitous forms whatever may be the conditions. Accordingly, if the differences recorded in the coenotic composition of Precambrian stromatolites were due to local ecological factors only, the recorded taxonomical differences would never be as drastic as reported, and a collection of identical ubiquitous species would probably have been found.

We arrive then to the conclusion that, whereas blue-green algae are a rather conservative group showing limited *morphological* evolution during Precambrian times, the processes of speciation and extinction may have been quite effective in the modification of stromatolites properties. The extinction of given species, or the arrival in a given mat community of a new taxon with its particular behavior and abilities, will undoubtedly originate greater or lesser changes in the mat organization and structure, depending on the rôle played by that particular taxon in the stromatolite. (Monty, 1967, 1972; Walter 1972, p. 87).

When considering this factor of « algal evolution » during Precambrian times, we must also consider the impact of the rise of new algal groups like the greens and the reds (somewhere in the Riphean, see Schopf, 1968). Some filamentous or coccoid representatives of these groups happen to belong nowadays to the stromatolitic community or even build laminated calcareous crusts of their own (see review in Monty 1965). Accordingly, beside the fact that the time related arrival of these new participants may originate progressive changes in the stromatolites configuration, we are allowed to consider, as concluded by Walter (1972), that « the evolution of new algal phyla may be the cause of at least some of the stromatolites now known ».

Accordingly, more than the evolution of algal morphology, the evolution of Pre-cambrian *algal assemblages* is a most important factor to consider when dealing with stromatolites evolution. The influence of the algal coenose, of the ecological, ethological and physiological properties of the leading algae on the growth form and on the microstructure of the colony has been stressed by the author in the Recent, and the problem has been brillantly reviewed by Walter (1972) in the case of Precambrian stromatolites.

Let us come now to a second point. « If there must be a connection between algal and stromatolite evolution, this does not exclude the possibility that sequential environmental changes were a factor in stromatolite changes » (Walter 1972, p. 88). It is the author's conviction that both the recorded morphological (and microstructural) evolution of Precambrian stromatolites and the first crisis that they suffered around Vendian times « might involve some deeper connection with the evolving ecology of stromatolites supporting environments or even broader features of the developping primitive atmosphere and hydrosphere » as is, among other reasons, suggested by Cloud and Semikhatov (1962, p. 1022).

Undoubtedly, the fundamental and *unidirectionnal* atmospheric and hydrologic changes that characterized these times strongly shifted the physico-chemical hyperspacial parameters and were likely to constantly and progressively modify the *bulk composition* and the potentialities of the successive algal coenoses, hence of the resulting stromatolites. The geospheric evolution was a powerful drain acting upon the evolving algal assemblages and strengthening the pressure of evolution. As the overall conditions changed, new dominant species or ecophenes with proper biological characteristics would rise, lead the algal coenose and impose particular types of mats. The basic properties of the resultant mat communities together with the possible range of the environmental parameters (turbulence, depth, alkalinity...) would yield a limited number of *possible* stromatolitic morphologies and microstructures. Considering then the continuous atmospheric, hydrologic... changes during the Precambrian, one can visualize a worldwide succession of some basic stromatolitic types that we can order in an evolutionnary sequence (together with some non typical, non stratigraphical ones, resulting from relict or eurybiontic less sensitive communities).

3. *The Problem of gigantism*

Precambrian stromatolites are well known for their unusual large sizes and this problem also merits some discussion; it has received various accounts some of which will be reviewed briefly.

Tides. Relying on Shark Bay occurences described by Logan (1961), Cloud (1968) relates the unusual size of Precambrian stromatolitic structures to high tidal amplitudes resulting from the greater proximity of the moon to the earth. However, as Walter (1970) notes it, this conclusion is unwarranted, the more that most Precambrian stromatolites were surely not intertidal but subtidal (Fischer, 1965; Walter, 1970; Bertrand-Sarfati, 1972, etc.). Even if tides were much higher in Proterzoic times they would not have been a determinant factor of gigantism as will be shown in later sections.

Rates of subsidence and environmental stability. Other arguments could be found in eventual appropriate rates of subsidence keeping pace with algal growth so that the resulting bioherms could reach important sizes whereas the growing portions would always remain in hospitable fitting environments.

One may also think of greater environmental stabilities so that growth can proceed for considerable time without being interrupted, and the colonies destroyed, by seasonnal climatic fluctuations or constant microenvironmental changes.

Undoubtedly, these factors may be significant in that they delineate environments where rock builders — whatever they are — can *potentially* grow impressive colonies. But the « subsidence vs. growth » argument is neither unequivocal nor historical; it should furthermore evaluate the mutual relationships between the rate of subsidence itself, the rate of algal growth (these two occurring at a very different order of magnitude), the eurybionticity of the growing community or population, the sites and depths of water where growth proceeds, etc... Furthermore, ideal balances must yet have been realized after the Precambrian, but stromatolitic gigantism did not occur anymore significantly. Similarly, proper environmental stabilities have undoubtedly been realized in Phanerozoic times, although marine stromatolites kept on and on reducing their size (1), whereas other successive groups

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(1) Walter (1972, p. 85) for instance notes that typical post-Ordovician columnar stromatolites built columns less than 15 cm. high and often much less.

(Stromatoporoids, Tabulates and rugose corals, Hexacorals, etc...), replaced them and were able to build impressive colonies or reefs.

Fitting temperatures. Blue-green algae are well known to favor warm temperatures and to grow profusely in the tropics (Fritsch 1907) whereas in temperate climates most of them bloom but during the warmest months of the year. According to Fogg (1956) 35° C. appears to be the optimum temperature for their development from the point of view of the number of species. No doubt that proper temperatures would have favored optimal metabolism and, if stable, a continuous « enhanced » growth.

But what might have been these fitting temperatures in Precambrian times? No one knows. Studying hot spring algae, Marrè (1962, p. 548) concludes that « the fact that the thermophilic species, able to withstand extremely high temperatures, are found almost exclusively among so-called primitive organisms, the Cyanophyta and the bacteria, suggests that these species are survivors from a period when the common environment was characterized by high temperature and high CO2 pressures and that the thermophily may be a primitive rather than an adaptive character ». This statement would give us an other range for optimal temperature conditions during Precambrian times, somewhere between, say, 40 and 70° C. However, most of these hot spring Cyanophyta not only have a rather *slow growth* (Marrè, id., p. 545) — a most probable consequence of the lowered solubilities of CO2 and oxygen — but Marrè's conclusions are most unwarranted; one argument against his conclusions lies in the fact that *all* blue-green algae have a very stable protoplasm (Fogg, 1956, Marrè et al., 1958) and that this particular property may well be utilized nowadays by *some* of them to escape competition (Fogg, 1956, Marrè, 1962) and live in environments characterized by abnormally high temperatures. In that case, thermophilic algae would exploit some sort of « pre-adaptations » resulting from particular proteidic linkage, and their present situation would not be characteristic of precambrian temperature conditions. Vouk (1923, 1948, 1950) reached similar conclusions from a different approach, as he thinks that thermophilic life results from high metabolical specialization.

Whatever may be the right interpretation of thermophilic algae, their prolific growth depends on well defined relations between temperature, light intensity and availability of CO2 (Bünning and Herdle, 1946), relations that we cannot evaluate for precambrian times. Even if that fraction of the realized hyperspace could be defined, we would not know *how* to use it for our purpose; indeed, « much is known of the effects and conditions such as light intensities, temperature, hydrogen ion concentration on the rates of individual metabolic processes and on their final expression in terms of growth in cell numbers, yet we are largely ignorant of the differential effects that these conditions may have on different processes » (Fogg, 1964).

Another problem arises when attempting to appreciate the actual influence of « fitting temperatures ». Blue-green algae have indeed developped many *cold water* species; some of them do bloom in winter or even in the ice (Skulberg, 1964); more interesting for us is the case of the blue greens which build various calcified crusts in cold water alpine lakes (see review in Monty 1965) or various creeks such as the Hoyoux river (Belgium, Symoens 1950; Symoens et al., 1961; personnal observations) which is invaded by various algal incrustations and dams actively built by species of *Lyngbya* and *Schizothrix* although the water temperature averages 11° C.

It is clear from what preceeds that it would be difficult to account for the gigantic precambrian stromatolites but by an eventual range of favorable temperatures;

blue green algae *are so constituted* that they can bloom and/or be efficient rock-building participants in a very wide range of temperatures. Accordingly, the latter factor is not the intrinsic unequivocal one we are looking for, the more that « proper temperatures » whatever they may be, have had many chances to be realized during the Phanerozoic without originating recurring giant stromatolites.

4. *Proposed approach to gigantism*

The gigantism of precambrian stromatolites probably results from a combination of algal intrinsic factors with several historical factors that all worked together in the same direction.

The algal aspect. Among the most important intrinsic factor, is the fantastic exponential growth rate of Blue-Green algae. Nowadays, the signifiance of this exponential growth rate can be visualized in planktonic and benthonic blooms (see detailled review in Monty 1965). Phytoplanktonic blooms are well known in lacustrine environments where sizeable lakes become covered, in less than a few days, with a thick algal scum which completely chokes the water body; similarly in marine settings, the formation of red tides, many of which are due to the exponential development of populations of the Blue-green *Trichodesmium erythreum*, are quite impressive. Blooms of benthonic species are as much significant and may cover lake floors with loose organic deposits originating organo-laminated sediments (Ljungvist, 1914; Nauman, 1925a, 1925b); describing the bloom of a unicellular species on a swedish lake floor, Nauman (1925a, p. 26) concludes : « Das Massenauftreten dieser Art in Sabysjön ist ein Schauspiel von grosster Produktionbiologischer und geologischer Bedeutung gewesen ».

Water blooms appear and evolve very rapidly; they are the expression of the explosive development of a rather restricted community as, most of the time, they are characterized by one dominant species, or a small number of dominant species, which are replaced by another population through the season or the year.

Fogg (1965) gave interesting figures with respect to the rate of exponential growth of the algae : he showed that the doubling time for *Anabaena cylindrica* was about 10.6 hours at 25° C and for *Anacyctis nidulans*, 2 hours at 41° C. Considering an exponential increase, and supposing that no daughter cell is lost ,one can easily calculate that the volume of the generated cells would equal the volume of the earth within a few months. Furthermore, many blue greens can, at a given time, split their filaments into a number of motile hormogones which, at once, grow as many daughter filaments (Desikashary, 1959; Monty 1971, fig. 1).

Accordingly, as blue green algae may be nearly considered as «perfect» organisms obtaining nitrogen and CO2 from the atmosphere and requiring little else than water (Tappand and Loeblich 1970, p. 281) — elements which were readily available during precambrian times — one can visualize from its present-day behavior, the fantastic *potential* possibilities of the group.

The environmental and historical aspect. To account ecologically for gigantism, we have to check whether these blue-green algae could reach their maximum growth rate, i.e. realize their « biotic potential » (Odum, 1959, p. 178) in the prevailing precambrian environmental conditions. They will approach their biotic potential if the environmental resistance is low or nil (Odum, id.). We shall discuss this problem in terms of energetic sources (light), nutrients and competition. As the literature on Proterozoic realized hyperspaces is most controversial, which is quite normal with such conjectural problems, I shall limit the discussion to some lines of thoughts.

Energetic sources. Historically, the utilization of light in the synthesis reactions was not an early process. The geological record seems to indicate that Blue-green algae originated in atmospheric reducing conditions and undoubtedly their original metabolism was anoxygenic. Some of the oldest floras recovered from cherts contained — beside chemosynthetic bacteria — an important proportion of Blue-green algae belonging to the Oscillatoriacaea (and to the Nostocacaea); nowadays, these groups contain many obligate or temporary heterotrophic species able to produce important benthonic blooms on oxygen-depleted lake floors (Monty, 1965) (1).

The acquisition of photosynthesis and the subsequent onset of oxydant conditions at the surface of the earth was a most important step, although a very slow one. In the beginnings, photosynthetic and hydrocatalytic Blue-green algae still lived in a reducing hyperspace : the oxygen released by the breakdown of water was partly immediatly recycled, partly trapped as bubbles in the mucilaginous material and used up by bacterial activities; that tiny fraction of oxygen that might eventually escape the algal site was at once utilized in geological reactions (2).

For a while, some given basins kept remaining extremely poor in oxygen or even anoxygenic (due to the physiography of the water body, or various types of impossibility to build up a positive budget between the O_2 produced and the O_2 consummed); these would be colonized by sorts of « relict » or eurybiontic communities able to thrive and build stromatolites as they did at previous epochs; other regions of the earth, in equilibrium with the progressing atmospheric parameters were colonized by new metabolically more modern communities. So that stromatolitic construction kept going on all over the earth.

If blue-green algae were to photosynthesize and eventually produce oxygen, they needed suitable light. What were the light conditions in the span of the Proterozoic, and were Blue-green algae able to utilize it conveniently? As was long ago suggested by Tilden (1933), the pigmentation of Blue-green algae may well result from an early adaptation to the color and intensity of the light available at the surface of the primitive earth. Whatever may have been the light properties and the way these changed during the Precambrian, Blue-green algae were most probably equipped to use it conveniently as the combination of their three pigments (Chlorophyll *a*, Phycoerythrin, Phycocyanin) covers the greater part of the visible spectrum (Monty, 1971). Beside the fact that phycoerytrin and phycocyanin are effective pigments, as the energy they absorb is tranferred to the chlorophyll and utilized in the synthesis, they also act at low light intensities where their production is enhanced provided there is a supply of nitrogen.

So, we have good reasons to think that Blue-green algae were able to use efficiently the Precambrian light conditions. Furthermore, as pointed in Monty (1971) the structure of their protoplasm and their genetic organization rendered them rather resistant to eventual noxious radiations.

Nutrients. From thermophilic to cold water crust-building cyanophyta, an

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(1) The revovery of algal filaments, morphologically similar to extant ones as in the Gunflint or the Bitter Springs (Schopf, 1968, 1972) does not automatically and unequivocally point to a photosynthetic metabolism as generally considered. There is no gross fossilizable difference, in Recent Cyanophyta, between the photosynthetic, hydrocatalytic ones, and those that temporarily or usually have other types of metabolism.

(2) This means that the recovery of supposed photosynthetic derivatives in the sediments does not necessarily imply the presence of free oxygen in the atmosphere.

enhanced growth and the building up of calcified structures (¹) is closely dependant on the abundance of CO_2, we could even say, in many cases, of abnormally high concentrations in CO_2. This point has been lengthily emphasized by Pia (1926), Ruttner (1961, namely p. 244-45), Honsell (1879), Bauman (1911) etc... For instance in a careful analysis of the blue-green calcareous deposits from the Lake of Constance (Switzerland), Bauman (1911, p. 27) notes that « Diese Algen bedürfen zu ihrer Existenz beständiger Erneuerung von Kohlensäurehaltigen Wasser und finden sich nur, wo dieses eine Geschwindigkeit hat... » Although studying rather different settings, Prescott (1951) also concludes that « cyanophycean lakes », i.e. lakes most favorable to blue-green algal growth, are characterized by an abundance in free or half-bound CO_2, richness in nitrogen and alkaline pH's ranging from 7.2 to 9.5 (²).

An abundance of free or half-bound CO_2 is most likely to enhance photosynthesis and hence, in calcium rich waters, precipitation of calcium carbonate around the algal coenoses (³). Both unrestricted availability of H_2O, CO_2 and of nitrogen should permit and stimulate algal growth and division as well as the production of carbohydrates on the one hand, and that of proteins on the other. The synthesis of the proteins itself is most important for the elaboration of the blue and red pigments of Cyanophyta (Heocha, 1962) and contributes much to their protoplasmic substances which are conspisuously rich in nitrogen (Prescott, 1948, 1959).

These conditions were realized in Middle to Early Late Proterozoic times. The CO_2 was probably more abundant than to-day and its accumulation may have been enhanced by the « great episodes of volcanism that characterize that part of the geological column » (Cloud, 1966a, p. 16). At first sight, we might expect these higher CO_2 pressures to have lowered the oceanic pH's down to levels perhaps unfavorable to Blue-green algae (cfr. above and to the precipitation of carbonates. The geological record shows that this was not the case as limestones become more and more conspicuous; how come?

First of all, the intense development of blue-green algae may have built up a biochemical screen between the atmosphere and the sea; continuous enhanced algal metabolism would fix important quantities of atmospheric CO_2 into carbohydrates, preventing its accumulation in the ocean and hence the atmosphere-ocean equilibration.

Secondly, the abundance of carbonates precipitated at that time supposes that the alkaline reserves of the ocean were high; such high alkaline reserves, while originating environmental conditions very favorable for Cyanophyta, would have allowed an abundance of carbonate ions and rather high pH's in the sea in spite of high CO_2 atmospheric pressures, the equilibration being constantly delayed.

Finally, the clay mineral buffer, in front of higher atmospheric pCO_2, would also tend to keep the oceanic pH's to normal values (Holland, 1965; MacIntyre, 1970); MacIntyre (Id. p. 112) has indeed shown that even if the CO_2 present atmospheric

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(¹) By calcification, I do not mean simple *inorganic cementation* as occurs in some crusts or heads of hypersaline settings.

(²) pH's measurements made by the author in the Hoyoux creek (Belgium), the lake of Constance (Switzerland) and Bahamian fresh water lakes, where Blue-green algal growth were most prolific, ranged between 7.2 and 8.5.

(³) Experiments conducted by the author in aquarium show that as soon as one reduces the availability of CO^2, precipitation by Blue-green algae suddenly drops and then disappears (as opposed to what occurs with aragonitic green algae and magneso-calcitic red algae, which metabolize their skeleton).

content would doubble, the effect on oceanic pH's would be really negligeable because of the equilibration with marine sediment, what he calls the pH-stat.

Accordingly, the combination of the previous factors — the enhanced growth due to the abundance of atmospheric CO_2, the maintenance of alkaline pH's in the sea, and the great availability of non-demanded carbonate ions in the absence of skeletal organisms — could but favor a rapid building up of calcareous stromatolitic structures. This is only true, however if there were no limitations in the key nutrients, i.e. nitrates and phosphates, that we shall consider now.

Nowadays, many blue-green algae can fix elementary nitrogen that they convert into nitrogenous compounds, and the group as a whole is one of the most effective agents of nitrification of the oceans (Allen, 1963; Goering et al., 1966; Carpenter, 1972). Being given their normally high protoplasmic demands for nitrogenous compounds, nitrogen fixation was probably an early adaptation and was an effective process in precambrian times before the inorganic nitrates (formed by electrical discharges in the atmosphere) began to accumulate (1). Now, beside the stromatolitic cyanophyta we know of by the structures they left, the oceans were probably crowded at many levels with non calcareous benthonic and planktonic Blue-green algae (2); these ones were also fixing nitrogen, and yield nitrates upon dying. These organic nitrates were mostly reclycled to blue-green algae and to bacteria, i.e. to the stromatolitic and other blue-green algal communities, in the absence of zooplanktonic and metazoarian animals.

Accordingly, we can deduce from the blue-green algal nitrogen fixation, the rapid recycling of nitrate and the absence of competitors, that nitrates were no limitating nutrients.

The phosphorus — supplied by weathering in amounts which do not seem to have changed much (Fischer, 1972, p. 161) — is also a key element of productivity in the ecological requirements of Blue-green algae (Prescott, 1951; Shapiro, 1973). Once more, in precambrian times the only important biological demand for phosphorus came from Blue-green algae alone.

From what preceeds, we can conclude that most of the precambrian Blue-green algae lived under *very low environmental resistance, that is in a somewhat infinite environment* that they could exploit thanks to their physiological and metabolical characteristics. These factors made it possible for these exponentially growing organisms to reach effectively their biotic potential and build, during that period of time, the largest and most widespread stromatolitic deposits ever found in the earth history.

Competition. Now other historical factors enhanced this situation and were also favorable to the building up of huge algal deposits; we shall only retain two of them in this discussion.

The first originates in the absence (or at least in the rarity) of organisms feeding on stromatolitic blue-green algal cells. Accordingly, all the cells generated by division were used in the thourough building up of mats.

A second very important factor is the absence of other competitive encrusting,

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(1) As shown by Holland (*in* Fischer, 1972, p. 161), « the amount of inorganic nitrate is directly related to the oxygen content of the atmosphere », and oxygen was just slowly accumulating at these times.

(2) Nowadays, planktonic blue-green algae have been recorded to depths of 1000 m. at least (Drouet, 1963; Bernard, 1963).

or hard substrate dwelling, organisms that could disorganize the stromatolitic growth, overwhelm it or more simply displace it (as will occur in Phanerozoic times). In Precambrian times, a stromatolitic Blue-green algal community could be invaded but by another Blue-green algal community whenever possible (¹).

A clear example would be provided by the *Jacutophyton* type of stromatolites that may cap the upper parts of *Conophyton* and grow an overall branched structure as described and illustrated by Bertrand-Sarfati (1972, figs. 35, e, f). The same author extends these observations to many other instances : « *Baicalia mauritanica, B. anastomosa, Jacutophyton, Tilemsina digitata,* se développent sur des troncs de *Conophyton* sans interruption notable de la construction » (id. p. 168) (²). This process, as opposed to the action of competitive communities in Phanerozoic times (encrusting stromatoporoid, tabulates, bryozoans, foraminifera, etc...) could but increase the overall dimensions of the stromatolitic body.

Conclusions. This historical background, the various environmental pathways that stromatolitic communities had to follow between 3 b.y. and 0.8 b.y. are responsible for the wide prospective niche they still have to-day and for the fact that the most important in their Precambrian evolution was physiological rather than morphological. That cyanophyta were able to cope with this changing earth is shown by direct stratal evidence, i.e. the importance of the deposits they originated in the successively realized hyperspaces (for instance that of Bulawayan times, of Gunflint times and of Bitter Spring times to take three major steps). This implies that the overall conditions prevailing at the surface of the earth, as hard as they may appear to us, fell well within the range of inherited tolerance of Blue-green algae.

Accordingly, the extension and gigantism of precambrian stromatolites are a direct response of exponentially growing procaryotes to optimal realized hyperspaces which, generalized at this time, will be met again but very sporadically and locally afterwards (see Phanerozoic section). Among the most important parameters of this success stand the possibility of optimal use of energetic sources, the unrestricted availability of nutrients, and the absence of encrusting competitive groups.

However when trying to solve this problem of the success of precambrian stromatolites, we find ourselves facing another one, at least as much important: which might well have been the environmental factors that lowered or limited the catastrophic exponential growth of Blue-green algae? What prevented them from overcrowding the infinite environment they lived on?

5. *Ecological restrictions of precambrian Blue-green algal communities*

Factors that might have restricted blue-green algal growth during precambrian times have been briefly discussed by Tappan & Loeblich (1970, p. 282) and Awramik (1971) but they do not appear to be fully convincing. Indeed, the effect of *ultraviolet radiation* is uneasy to appreciate, as Cyanophyta can not only withstand noxious wavelengths (Monty 1971), but furthermore can shield their cells with protective mucilages and carbonate grains (Fischer, 1967; Monty, 1971), can

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(¹) Even in Latest Precambrian times, competition by encrusting Red or Green algal communities does not seem very probable according to the record.

(²) an interesting discussion on « variants » which sort of overgrow previous stromatolites without leaving any structural discontinuity will be found in Walter (1972, pp. 25-26). Such overgrowths record the progressive alteration of the initial coenose and its replacement by an other one more adapted to the marginal ecological conditions reached by the growing stromatolite.

glide and move toward shelters during insolation (deeper zones of the mat, in the sediment, etc...) or yet colonize rather deep waters free from dangerous radiations (Monty, 1971). Finally the evaluation of the real effect of U.V. radiations relies on the determination of the amount of free oxygen and subsequent ozone, a problem wich is rather disputed (see Fischer, 1972).

Temperature limitations is another factor difficult to evaluate in view of what has been said before.

Rates of sedimentation that would have exceeded the growth of microorganisms (Awramik, 1971) would have constituted but a local factor, and cannot account for significant limitation at the scale of the ecosystem (the more that much of the carbonate composing many precambrian stromatolites appears to have been precipitated in the mat and not entrapped, Bertrand-Sarfati, 1972). Furthermore, Blue-green algae are well known for their ability to cope with important sedimentation. Experiments carried with Recent filamentous forms and observation under sea (Monty, 1965, 1967; Ginsburg et al. 1654) revealed that they could rapidly permeate detrital layers and establish a new mat on top of them; this is achieved either by gliding upward in between the grains, or by sending motile reproductive cells, or hormogones, that will multiply rapidly if surface life-conditions are proper. Finally, many Blue-green algae, when provided with abundant basic nutrients, can show impressive growth rates that will cope with environmental sedimentation; as has been discussed before, precambrian Blue-green algae were most probably endowed with abnormal growth rate potentials, so that restrictions by high sedimentation rates were undoubtedly very local factors.

It is still difficult to find equilibrating factors in *extreme tidal actions* (Tappan & Loeblich, 1970), or the development of *rigorous environments* due to the presence of *strong currents* and *wave action* (Awramik, 1971). High tides due to the formation and the capture of the moon are rather hypothetical in the presently known historical context, but nevertheless, Logan (1961) has shown that algal mats and stromatolites could grow on exposed headlands; if Logan's theory were directly applicable to the Precambrian, high tides would have originated belts of giant stromatolites rather than preventing them from growing. Finally, the development of blue-green algal tufa and dams in fast flowing portions of streams (connexion between the Bodensee and the Rhine River, Hoyoux creek,...) demonstrate their remarquable resistance to turbulence, a turbulence that they accentuate as they build up their calcareous masses. Anyhow, even if effective, the presence of strong currents delineating rigorous environments could have determined but *local* ecological restrictions too.

Availability of suitable space (Tappan & Loeblich, 1970) as such could have restricted the eventual catastrophic development of Cyanophyta; however, (1) as the sea floor was apparently bare of encrusting or reef-building communities other than Blue-greens and (2) as these algae can range from shallow to rather deep waters (Monty, 1971), they had at hand a very wide range of uncompeted habitats.

Proposed approach. The only way to understand *worldwide* factors that regulated Blue-Green algal growth during precambrian times is to turn one more time to some basic ecological facts and observations on Recent algal growth.

The type of calculation presented p. 594, based on measured doubling time of blue green algae and its consequence on the crowding of the earth surface, merits some basic corrections. Natural laws are such that any catastrophic population increase is always, sooner or later, limited by some homeostatic regulating factors (see below). Furthermore, algal population growth is very seldomly continuous but presents a cyclic pattern in temperate as well as in tropical regions; this cyclicity breaks down the figures which might be expected from simple exponential growth calculations. Let us take some examples; the algal film is the lowest structural unit of a stromatolite and its growth pattern is relevant to our discussion. I have described elsewhere (Monty 1965, 1967, 1972) the growth pattern of *Schizothrix* films : the filaments constituting the film start dividing at sunrise, then pass by a phase of exponential growth which rapidly thickens the concerned lamina during the day; this multiplication brutally stops at sunset and a relaxation phase follows. Such a pattern of population increase illustrate the J-shaped growth form of Odum (1959, p. 182). Accordingly, at the lowest fundamental scale of the algal film the exponential growth is limited by a resistant environmental parameter : light.

Now, considering the whole stromatolite, we can go a step further. I have shown elsewhere (Monty 1965, 1967) that in the Andros lagoon the frequency of the *Schizothrix* domes presented a cyclic seasonnal pattern : the dome population is small and scattered from January to May; then, it increases in density during the Summer months when the domes become conspicuous all over the place; the domes washed away by the tides, because of their too large size which offers too much resistance to currents, are constantly replaced by younger fully growing ones, so that an equilibrium status is reached and maintained. Then in Fall, growth recesses and the dome population becomes more and more scattered while showing smaller and smaller structures.

Although it is difficult to pinpoint the external factors ruling seasonnally this rythmic development, one may think that water temperatures, turbulence as well as light intensity and composition may play a significant rôle.

Other interesting types of limitations can be understood by analysing the situation in lakes and ponds where benthonic and planktonic Blue-green algae do seasonnally bloom. The seasonnal bloom relies on the availability of nutrients accumulated during the Winter and starts when fitting Spring temperatures are reached. Algal exponential growth leads rapidly to the formation of conspicuous scums choking the lake, or thick mats spreading over the bottom. Exponential algal growth itself leads automatically to a « crowding effect » which slows down and then stops any further population increase; this phenomenon results from several processes : (1) the rapid depletion in nutrients (phosphates, nitrates...); (2) the isolation of subpopulations from the surface or from the overlying normal water body (case of benthonic species) by an impervious mass of cells and mucilages; the isolated subpopulations start to rot and are invaded by Bacteria; (3) this phenomenon joined to the overconsumption of oxygen leads the lake to anoxygenic conditions, or at least to drastic impoverishments; (4) the accumulation of metabolites, excreted by the algae, and of decay products, resulting from rotting processes, originates an autointoxication which inhibits any further growth.

Finally, competition between Blue-green algae themselves is another very effective growth-limiting factor. When competition arises in a given water body, some Blue-green algae release an abundance of growth-inhibiting substances as well as various toxins which prevent and block the development of other cyanophyta (Prescott, 1960, Fogg, 1956, 1962, Lefèvre 1952, 1964). The « winner » then blooms freely for a while at a tremendous rate; sooner or later, however, the toxin producer will be dangerously affected by the accumulation of its own toxins and will die out.

These comments show that the notion of exponential growth must be handled with care when applied to natural systems where homeostatic feedbacks always control its course. The rôle of environmental resistances (physical, chemical, biological...) which progressively build up as a response to algal growth is fundamental in shaping population growth form. Furthermore the rythmicity in the value and the quality of the various environmental parameters (light, temperature, nutrients...) restricts the exponential growth to some limited period of the year.

Accordingly, simple ecological concepts and observations give us clues as to the type of universal processes that might have limited an eventual catastrophic proliferation of Blue-green algae during precambrian times. Of course, very locally, these processes inherent to population growth may have been helped by punctual factor such as excess of sedimentation, scouring by currents, etc... but the latter are not the basic agents we were looking for.

Now, if we consider the overall development of stromatolitic communities during precambrian times (number of occurences vs. time) we find it to follow a sigmoïdal curve with a phase of initiation (Bulawayam times), then a phase of acceleration, then during Early to Middle Late Precambrian the curves flattens asymptotically. The *environmental carrying capacity* (Odum, 1958, p. 183) is approached; all the suitable habitats are colonized, growth and stromatolitic spreading becomes density-controlled. The carrying capacity of precambrian seas for stromatotes was of course much higher than that of later seas as no other community would compete for space, nutrients, etc...; but nevertheless this carrying capacity fixes an upper limit, a stage of equilibrium between abundance of stromatolites and environmental availabilities beyond which no further population enlargment can take place. This was the ultimate factor which limited stromatolitic development in the originally unlimited precambrian environment. I say « originally unlimited » because the overcrowding by stromatolites themselves built up limitations in the ecosystem potentialities.

6. *Late Precambrian decline of Stromatolites vs. rise of Metazoans.*

Current hypothesis. As mentionned earlier in this paper, the stromatolites underwent a first and marked decline in Late precambrian (Vendian) times. The present-day interpretation of this and later (Ordovician) declines postulates that stromatolites were eliminated by the rising metazoans which burrowed them and fed upon them (Garrett, 1970; Awramik, 1971). Although there may be *some* truth in this statement, it does not seem to me to rely on stratal nor on ecological evidences.

(i) *stratal evidence :* we have absolutly no evidence indicating that Riphean and Vendian stromatolites became more and more infested with burrowing organisms. The enormous amount of detailled microstructural studies on Late Precambrian stromatolites failed to record any increase, upsequence, of burrowing activity, if any at all. In all reported cases, the stromatolitic laminations are biologically undisturbed, and we never find in precambrian algal reefs or mats anything comparable or even reminiscent of what can be seen in modern reef rocks be they corallian or red algal in origin. So the stratal evidence is definitly negative.

(ii) *ecological evidence :* in terms of evolution, it seems logical to postulate that the first metazoans were « generalized » organisms with little or no specialization. If they fed on Blue-green algae, they probably did so on the « easiest » preys, i.e. the phytoplankton on the one hand, the loose algal mats and blankets that most probably covered precambrian sea floors, as occurs today, on the other. Indeed, feeding on variously mineralized and/or cemented stromatolites (such as the Shark Bay ones) requires special physiological and anatomical well delineated adaptations. Such adaptations are not likely to exist in archetypic metazoans (Valentine, 1960). For instance, the paleontological record shows that the teleost fishes acquired the faculty of chopping pieces of corals but early in the Tertiary (Romer, 1969) whereas the radiation of the boring bivalves was delayed until the appearance of an adaptative innovation, the development of a siphon, that is in Mesozoic times (Raup and Stanley, 1971). Finally, being given the toxicity of many Blue-green algae and of their by-products (see below), further physiological adaptations would have been required for the metazoan to assimilate them safely; that is why Odum (1971, p. 306) points out that « many species of Blue-green algae are resistant to grazing ».

Accordingly, if early metazoans fed on algae they probably did so on the phytoplankton and the loose algal masses not on the stromatolitic structures.

We may however push the discussion one step further and see what might well have happened, if by some process of fast adaptative evolution some bottom feeders would have acquired the faculty of boring and grazing the stromatolitic masses.

It is the author's experience that, once feeding or habitat relationships get established between two or several populations of a community, an equilibrium is to be maintained if the community has to survive. An example will first be taken in the reef building communities that later replaced Blue-green algae, i.e. the Tertiary to Recent coralgal community. This community shelters innumerable borers, such as clams, sponges, worms, algae, mycetes, etc..., and grazers such as these fishes which directly eat the polyps or chew the reef rock. The actual prolific growth of coral colonies and algal nodules or crusts appears to cope quite perfectly with the boring and grazing activities of these reef dwellers. The latter have a proper niche, the realization of which is bound to the preservation and the perpetuation of the host in function of which they developped special adaptations. Nothing is more infested than a coralgal reef rock, but this situation *never* brought about the extinction of hexacorals nor of red algae.

Similarly, gastropods would never completely clean up the algal mats on which they feed and to the assimilation of which they became adapted, or so they would readily starve. The well known association of calcareous Blue-green algae and gastropods that lives in hard fresh waters (see Baumann, 1911, for instance) is another example of positive equilibrium : the gastropods feed on the algae but do not prevent them from building oncolites (quite often around dead gastropods shells), sizeable crusts or dams.

So, even if boring and grazing activity were recorded or simply postulated in precambrian stromatolites, the argumentation drawn from the later paleontological record and from the Recent would by no means allow us to say that this activity was *the* cause of the recorded stromatolite decline. All we could do would be to note the establishment of a new and more complex stromatolitic reef community.

Accordingly, stratal and ecological evidences do not support the idea that the first (and later) decline of stromatolites is directly bound to the evolution of bottom deposit feeders and burrowing metazoans that would have eaten them up or disorganized their rock-building activity. Furthermore, as noted earlier, this decline is bound to worldwide ans significant reduction in stromatolites *diversity* (Awramik, 1972) and to changes in the overall caracteristics of algal structures (morphology, microstructures...); this seems to indicate that broader ecological and evolutionnary factors were acting.

The decline of Blue-green algae permitted the rise of invertebrates. Before going any further, it might be interesting to investigate a provocative question : was the decline of precambrian stromatolites due to the rise of soft bodied metazoans, or were the latter allowed to emerge because the historical decline of Blue-green algae originated more suitable biochemical environments? To make an interesting comparison, we still do not know for sure the reasons why Dinosaurs dissappeared in mesozoic times, but what we know is that this is the historical situation which was the key factor permitting the rise and radiation of land mammals.

It is a well known fact that the colonization of water bodies by Blue-green algae is most of the time a dangerous nuisance. To understand what the situation might well have been in Precambrian times, and look for a valid recent analog, we have to turn to water bodies where blue-green algae are nowadays dominant, i.e. the fresh waters, and where the oxygen content is normally *low*, i.e. the standing bodies.

The intense development of Blue-green algae in to-day's fresh water settings, can disturb the aquatic environment by two main types of effet : the depletion in oxygen and the liberation of toxic substances.

The first objectionable effet — the depletion of oxygen — results in the killing of animal by suffocation. The abundant development of filamentous algae results in the formation of dense floating mats stabilizing the waters and screening the sunlight (1). Under optimal conditions, this mat becomes thick and a decaying layer appears at its lower surface; this layer is at once crowded with oxygen-consuming bacteria which still lower the oxygen content of the surrounding waters; if this content is already low, as observed in shallow waters during hot still nights, the tremendous decomposition activity of bacteria may depleat the oxygen below 3 ppm., i.e. below the point which would support most fish life (Prescott, 1948).

The second origin of suffocation results from the fact that during the night, when respiration alone goes on, the algal metabolism must rely on the oxygen dissolved in the water; if the original level of dissolved oxygen is low (4-5 ppm.) the algal nightly demand for O_2 may lead to a dangerous impoverishment and the dissolved oxygen drops to zero as observed by Prescott (1951); the immediate result reported by this author is that within a few hours not a single living animal could be found in the surveyed lake; even bottom organisms adapted to low oxygen supply were killed.

This means that even if today, with high atmospheric and hydrologic oxygen level, extreme critical situations can developpe in lakes as a result of blue-green algal exponential growth, the more reasons have we to think that extreme situations could be rather frequent in Precambrian basins where oxygen levels were low; this would somewhat limit Fischer's hypothesis (1965) according to which algal mats or algal domains would have been oases for the first metazoans to develop. In fact these sites would have been oases but for Bacteria.

The second objectionable effect of intense Blue-green algal development is poisonning. Poisonning by Blue-green algae and before all by cyanophytic blooms are virtually worldwide in occurence (Gorham, 1964). Many striking occurences are

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(1) Such mats can be scums of plantonic species or yet benthonic formations floated to the surface by the accumulation of photosynthetic gases as described and illustrated by Monty (1972).

known at every level. There is evidence of their toxicity to *zooplankton* (Hardy, 1936; Braginskii, 1955; Dillenberg and Dehnef, 1960, etc...); we know also that they can poison other *algae* (Lefèvre 1964; Lefèvre et al., 1952). Saunders (1957) has shown that the toxins of some Blue-green algae « may accumulate to lethal levels in *grazing* and *filter feeding animals* during the periodic bloom ». Finally, Steyn (1945) reported an almost legendary case where thousands of *cattle*, sheeps and other animals were killed in Transvaal after having drunk the waters of a reservoir poisoned by a bloom of *Microcystis*.

Without accounting in detail for all the sources of poisoning by Blue-green algae, we can focuss here on two types of processes :

(1) The decay of important masses of Cyanophyta, rich in proteins and nitrogen-bearing substances (Prescott, 1948) releases noxious substances among which methane, H2S and a poisonous protein, the hydroxilamine.

(2) the action of these decaying substances must be separated from that of the toxins secreted or released by living Blue-green algae; these toxins appear nowadays as a powerful death factor able to kill a full grown cow in half an hour or less (Gorham, 1964). Moreover, these toxins are specific in that a given toxin may be lethal but to one type or species of organism (Gorham, id.).

A geological insight on the lethal activity of Blue-green algae on animal communities can be obtained from those varved lacustrine sediments where periodic blooms of Cyanophyta are associated with periodic catastrophic death of fishes, arthropods, etc... (see discussion in Monty, 1965, pp. 73-77 as well as the case of the Green River Formation, Bradley 1931, 1929a, 1929b, 1963).

What were the overall condition in precambrian times is difficult to guess, but the overdominance of Blue-green algae as can be guessed from the tiny record left (stromatolites, carbonaceous cherts, etc...) and the consequence of inter-algal competition (see above) presuppose that the environment was not as good for invertebrates as generally supposed in the geological literature.

Considering all the objectionable effects of Blue-green algal growth, their omnipotence in precambrian times, the normally very low levels of dissolved oxygen, *it might well be that the Reign of benthonic and planktonic Cyanophyta (and of Bacteria) hindered for a long time the radiation of invertebrates which slowly kept on evolving in some « unpolluted » place.* In this hypothesis, the decline of Blue-green algae in Late Precambrian times, like later the decline of dinosaurs, change some key biosperic conditions to the point that the metazoan could now spread and radiate in less hostile biochemical environments. This was the « big explosion » after the so-called « Lipalian interval ».

7. *About the first decline of Late Precambrian (Vendian) stromatolites*

This first crisis of stromatolitic communities is an historical fact reported by Awramik (1971), Bertrand-Sarfati (1972) Walter (1972) etc... It follows the zenith in evolutionnary diversification and ecologic importance that Blue-green algae reached some 900 m.y. ago (Schopf, 1972; Awramik, 1971, fig. 1). I have tried, in the previous section, to show that this crisis could not be bound to the only rise of bottom feeding invertebrates, as claimed by Awramik (1971) but, on the contrary, had favored their emergence leading to important ecological shifts as will be shown in the Phanerozoic section.

As is the case for all of the periods of paleontological crisis, no satisfactory account has yet been provided, for we cannot grasp the nature of the complex factors which originated these crisis; most of these factors are « unfossilizable » and have not been recorded in the geological column. The problem is still more complex with the Late Precambrian decline of stromatolites as we are dealing with a highly conjectural period, the ecospacial coordinates of which are very poorly known.

Undoubtedly, this first crisis reflects a decreased efficiency of the rock-building potentials of precambrian Blue-green algae. The decrease in the phenotypic diversity of columnar stromatolites (Awramik, 1971; Bertrand-Sarfati, 1972) and in the diversity of microstructures reflects a coenotic evolution that has been discussed earlier in this paper and that has been paralleled with overall hydro-atmospheric modifications. We have good reasons to believe (1) that the bulk of *active* blue-green algal coenoses diminished, whereas (2) the constructionnal activity of the remaining ones was somewhat hindered. All this reflects generalized modifications in the hyperspacial parameters that had permitted the former climax of Blue-green algae, modifications that mark the beginning of the alternation of the former marine ecosystem as a whole.

In view of what has been said before, the overall decrease in the CO_2 content of the atmosphere (Cloud, 1968a, 1968b; Fairbridge 1967, fig. 13, p. 418, p. 419) may have been one prominent factor, among others, that first limited the rock-building potentials of Cyanophyta; such a decrease would have affected the rates of photosynthesis as well as the abilities of Blue-green algae to precipitate carbonate (phenomenon which is closely dependant on CO_2 pressures as said before).

The continuous building-up of oxygen progressively diminished the nuisances of planktonic and benthonic blue-green algal blooms (mainly the depletion of basins in oxygen and the pouring of toxins due to bacterial decomposition); this in turn favored the rise of eukariotic organisms which introduced important shifts in the general nutrient budget. Furthermore, the arrival of Green and Red algae in Late Proterozoic times, that is of better organized plants, definitly marks a period of incipient severe inter-algal competition that will go on increasing during Phanerozoic times.

This first crisis that stromatolites underwent in Vendian times does not appear very important with respect to the one they will suffer after mid-Ordovician times. It is however a significant scar in their period of acmé and in the evolution of their communities. It underlines the first step of the drastic modifications that the whole biosphere is ready to face.

8. *Remarks*

In the previous pages, stromatolites have only been discussed in terms of Blue-green algal coenoses. We have indeed good reasons to believe that the bulk of fossil stromatolites was due to the activity of Blue-green algae, and magnificent floras have been recovered from many cherty horizons. However, the concept of stromatolites has been recently enlarged and applied to the monerans as a whole, i.e. the Cyanophyta and the Bacteria (Walter, 1972a; Monty, 1973a, 1973b). This new approach has two major incidences; the first one brings further limitations to the correlation generally made between stromatolitic development and evolution of oxygen. As noted by Walter (1972a), if some Precambrian stromatolites were bacterial in origin, the reported correlation would not be valid since bacteria do not evolve oxygen; the fact is, however, that the correlation between stromatolites and evolution of oxygen is *always* unsafe; indeed, even if we were certain that the Bulawayan and subsequent stromatolites were Blue-green algal in origin, we could *by no mean* postulate any significant evolution of oxygen as has been irreverantly done up to now. We first of all know that many Blue-green algae may have an obligatory or facultative anaerobic metabolism and we do not know at all the metabolism of their Precambrian representatives. Secondly, morphological gross analogies between Precambrian filaments released from cherts and Recent Blue-green algal ones *do not imply* as such that the former had acquired the oxygen-releasing photosystem II. We have no direct paleontological evidence which would indicate *when* Precambrian algae adjoined on the original photosystem I the more modern Photosystem II (see Olson, 1970). It is finally clear from the discussions reported before that proliferation of Blue-green algae did not mean pouring of oxygen in the surrounding waters nor in the atmosphere.

Accordingly the notion of eventual bacterial Precambrian stromatolites does nothing but to drive us to a greater carefulness when drawing oxygen models for that period of time.

We must however be aware that some reported Precambrian stromatolites may well have been either bacterial in origin (see the hot spring siliceous deposits of Walter, 1972a, b), or even inorganic (the geyserites of Walter, 1972b). It is a fact that there is, in the Recent, many structures in marine settings which appear to be classic stromatolites but which are either non biogenic (i.e. the calcareous pseudostromatolites of Purser, 1973) or bacterial (i.e. the oceanic manganese nodules, Monty, 1973a, 1973b). Some of the latter should be easily recognized in the geological record by their particular microstructure. There remains however a possibility that Precambrian stromatolitic communities were enriched in bacteria with respect to the present-day algal mats consortia. Bacterial degradation of Blue-green algal mucilage, if on a large scale, would have tremendeously enhanced the carbonate precipitation in the mats (Monty, 1965, 1967).

As for the geyserites or the pseudostromatolites of Purser (id.) they do not appear to have originated an important fraction of the bulk of Precambrian stromatolites. The reverse would have yielded a uniform succession of undifferenciated and monotonous stromatolites; we would have never noted the worldwide and contemporaneous evolution of overall morphologies and microstructures reported at the beginning of this paper. In my opinion and in that of many authors, this evolution does but reflect the progressive ecological and morphological modification of algal coenoses playing a most fundamental role in the shaping and building up of stromatolitic structures.

Furthermore, the fact that most Precambrian stromatolites offer many interesting analogies with Recent Blue-green algal mats and crusts (be the latter marine or non-marine), that, not unfrequently, preserved calcareous filaments, molds of filaments or residual streaks can be observed in some stromatolites whereas others have yielded significant cynaophytic floras, lead me to believe that considerng most Precambrian calcareous stromatolites as Blue-green algal in origin, is a most reasonable assumption; finally, whatever may be the restrictions I have made to rapid and unjustified correlations between stromatolites and oxygen, we have *in fine* to account for the progressive building up of an oxydant atmosphere; and here the paleontological record indicates but one evidence : Blue-green algae.

We must however always keep in mind that, in some particular occurences, stromatolitic structures may be bacterial or non biogenic in origin as is still the case to-day; this means that we must refine our methods of investigation and stick to more critical conclusions.

THE PHANEROZOIC HISTORY

Introduction

Stromatolites have a very broad prospective niche. Besides the fact that most stromatolites result from a close association of different algae, which enlarges the adaptative range of the resultant consortium (as discussed in Monty, 1967), the very broad size of the prospective niche of Blue-green algae can be accounted for by several historical factors.

First of all, during Precambrian times they evolved in an uncrowded biosphere and did not have to develop elaborate specializations (factors which reduce the modal niche) in order to successfully compete; accordingly their average niche size may be expected to be broad.

Secondly, they successively spanned very different realized hyperspaces in the evolving Precambrian biosphere. Doubtless the environmental uncertainty which resulted from temporal variability — though on a broad scale here — originated the selective pressures towards a broad niche (see R. Levins, 1968).

In addition to possible and important atmospheric changes, the dawn of the Phanerozoic Eon is marked by two important events which thoroughly modified the ecological structure of the biosphere; they include (1) the (apparently) sudden and well known development of invertebrates and (2) the progressive rise of other algal groups (Red and Green ones) including calcified forms (Johnson, 1965, 1966; Maslov, 1956, Wray, 1971).

The resulting enrichment of the ecosystems originated pressures that worked towards a reduction of the realizable niche size of the cyanophytes and hence towards *niche partitioning*. Indeed, as a result of the action of these newcomers and of the interactions between them and Blue-green algae, the enrichment of ecosystems :

(1) modified the habitat, the realized hyperspace controlling the niche of Blue-green algae;

(2) originated an overall increase in niche density; and

(3) modified the balance of the so-called « consumable ecological factors » (i.e. the factors altered in quality or in quantity by organisms).

1. PALEOZOIC STROMATOLITES

Effects of the rise of invertebrates. The rise of the invertebrates had both positive and negative effects upon the Blue-green algae. The hard parts of the invertebrates, including individual skeletons as well as the stony communities represented by the successive types of reefs, constituted new and everchanging substrates for Blue-green and other algae. Biological adaptations originated new niches for the species utilizing these newly realized hyperspaces.

For example, the appearance of the first animal reefs, built by archaeocyathids, brought about the intense development of the epibiontic algae *Epiphyton*; the very narrow prospective niche of this alga, closely adapted to the new substrate and to the new, elusive biological association, is reflected in the very short geological existence (essentially Lower and Middle Cambrian, Johnson, 1966, p. 16). Other new niches are illustrated by boring Blue-green algae which, as soon as Ordovician times, infested trilobite carapaces, crinoid ossicles, etc... (Toomey, 1970, fig. 11).

The rise of invertebrates was somewhat inimical to the further dominance of Blue-green algae for at least two main reasons : predation and competition.

Doubtless, benthonic and planktonic cyanophytes played a fundamental rôle in the newly developing trophic pyramids. Given their rapid growth rate and their generally high protein content, Blue-green algae were most probably an important source of food for the successive animal communities *which had realized the required physiological adaptations* (toxins immunity).

Direct competition by the invertebrates included competition for the available space on the sea floor, the available nutrients and the required chemicals (phosphates, nitrates, calcium, carbon dioxide, oxygen, etc.). I shall restrict further discussion to the competitive influence of reef or mound-building and encrusting organisms.

Before Cambrian times, Blue-green algae were more or less the only reef or mound-builder and lime-depositing organisms in the sea; from the Cambrian onward, important portions of the sea floor became covered with calcareous communities and deposits built by archaeocythids and various sponges, bryozoans, echinoderms, stromatoporoids and corals. The resulting space competition is reflected in the various reciprocal overgrowths of algae, tabulate corals, stromatoporoids, bryozoans, etc. found in many Paleozoic reefs where one can see that Blue-green algae were no longer pre-eminent (Dangeard, 1948; Manten, 1971; Murray, 1966; Tsien, 1971; Bain, 1967, Toomey, 1970, etc.).

The rising eukariotic organisms, provided with a truly biogenic skeletons, differenciated and produced a great number of species with narrow niches. The eukariotes were most probably severe competitors with Blue-green algae and overwhelmed the « reef-building » potentials of the latter.

The basic encrusting niche was probably dominated in mid-Paleozoic marine settings by the stromatoporoids and to a lesser extent by encrusting tabulates and bryozoans. Like the previously dominant Blue-green algae, stromatoporoids occured in a range of settings; they could build encrusting sheets, round colonies or various biohermal accumulations (Manten, 1971, fig. 226). They could differenciate these growth forms in response to changing environments (Lecompte, 1956, 1960; Manten, 1971). In addition, the compact and solid skeleton of stromatoporoids offered a far better protection against predation and scraping than did the calcareous encrustations of stromatolitic algae.

Faced by the colonization of the sea floor by such efficient and more advanced competitors, the activity of Blue-green algae was generally limited to a secondary rôle : that of accompanying organisms, building oncolites and various overgrowths or occuring as bundles or scattered masses of *Girvanella* (Manten, 1971; Hadding, 1933, 1941; Dangeard, 1948; Brown, 1963). However, when *local* conditions were such that Blue-green algae became temporarily advantaged, they « bloomed » and originated reefoid stromatolites (see below) or almost pure oncolitic beds, very reminiscent of the deposits built nowadays by red algae on continental shelves or by blue-greens in fresh water lakes.

Effects of the development of green and red algae. Green siphonous algae developed suddenly in Early Silurian times and became important constituents of some calcareous beds, such as the ones built by *Anthracoporella* in Kazakhstan (Maslov, 1956). They spread into lagoonal waters and extended towards reef environments where stromatolites were still locally important rock builders (as in the Swedish Leptaena Limestone, Haddings, 1941).

Red algae were still poorly diversified (the acme of the phylum being reached in Cretaceous times) but *Solenopora* and *Parachaetetes* underwent an important phase of development in Silurian seas. Altough these rhodophytes had not yet fully realized their present-day fundamental niche in reef building, they were already conspicuous components of some Siluro-Devonian calcareous beds or reefs (Manten, 1971, p. 73; Brown, 1963, p. 178, 180; Wray, 1971).

The ecological pressures, stemming from the rise of more advanced calcareous algae (rhodo- and chlorophytes) became the strongest in the shallow warm carbonated seas where the greatest organic diversity flourished. Competition related to this taxonomic development brought about an ever increasing biotic specialization which progressively altered the niche size and frequency patterns. Eventually, the optimal niche size in these growing communities became smaller than the wide niche size of many stromatolitic Blue-green algae. Other plant groups, more able to specialize, thus may have developed species with relatively small and adequate niches, species which rose in diversity and finally produced an environment inimical to the successful colonization of the sea floors by Blue-green algae. A broad niche indeed — such as that of stromatolitic Blue-greens — is often related to a weakened fitness, and a negative relation has been suggested between the rate of increase in the best environment and the breadth of the niche (Levins, 1968, p. 338) : « This would be manifested in the frequent occurence, among groups of similar species, of a dominant species which outcompetes the others in the best environments but cannot invade the marginal situation where these others, with broader niches, survive ». Some aspects of limnic ecology may help to visualize what might have happened during Early Paleozoic times. It is well known that while limnic *planktonic* Blue-green algal communities are successful competitors with other algal groups which they can eliminate or inhibit temporarily, the *benthonic* Blue-green algae (including the stromatolite builders) are much less aggressive; they are quite often expelled from favorable lake floors by other algal groups (such as the green Cladophorales, as well as some red or brown algae) and relegated to grow with little competition on inhospitable shores subjected to periodic drought during low water levels (cfr. review in Monty, 1965; Monty, 1972).

The broad niche of cyanophytes enabled them to flourish undisturbed in such marginal situations, and the increasing ecological pressures during Paleozoic times most probably resulted in the *concentration* (*not* the limitation, though) of blue-green algal activity on tidal or supratidal flats where they most frequently occur. (See also Fischer, 1965).

The biotic pressures of other algae, resulting in habitat splitting, may have also tended to concentrate some Blue-green algae towards the other extreme of the marginal niche situation, i.e. the deep waters. As developed elsewhere (Monty, 1971), Blue-green algae, as opposed to chlorophytes, are well suited for thriving successfuly in deep waters; we have such geological examples (Playford & Cockbain, 1969) and they are by no means a « special problem » as Garrett (1970) postulates. This other end of the marginal niche situation was however less successful than the tidal flats, for Blue-green algae were first overwhelmed by many « deep water » encrusting invertebrates (such as some stromatoporoids and other sponges, bryozoans, hydrozoans, etc.) and later by red algae which also have special pigments accomodating deep water light conditions (Biebl, 1962).

Other effects. The ecological pressures building up in the sea, the resulting habitat and niche splitting, originating the concentration of cyanophytes around the shorelines, may have had another important consequence : while life was crowding the seas, a realm remained free — the continents, now certainly exposed to a near present-day oxygenic atmosphere and to much less lethal radiations than during Precambrian times. If we consider present-day Blue-green algae, we find them to be the first organisms to invade and colonize any new available land such as volcanic islands. « A dramatic example of such colonization is provided by the island of Krakatoa... which was denuded of all visible plant life by its cataclysmic volcanic explosion of 1883. Filamentous Blue-green algae were the first plants to appear on the pumice and volcanic ash; within a few years they had formed a dark green gelatinous growth. The layer of Blue-green algae formed in such circumstances eventuelly becomes thick enough to provide a soil rich in organic matter for the growth of higher plants » (Echlin, 1966, p. 80). In such cases the action of blue-greens is at least twofold : (1) they desintegrate the surficial rock and enhance the formation of soil; (2) they enrich the surficial materials in nitrates and other organic substances thus opening the way for further colonization. It might well be that a similar process occured during very early Paleozoic times; it led the way to the establishment of land vegetation by originating proper and fitting soils on the one hand, and by enriching marshes and ponds in organic and easily assimilable mineral matter on the other hand, at a time when the O_2 level was no longer a barrier. In the early days, this initial colonization of the bare lands was greatly facilitated by the motility of Blue-green algae, able to move down in the soils in order to escape the eventual noxious radiations, as well as by their mucilaginous and mineral cover which shielded them also.

The ecological pressures, as well as the required optimal niche size, may have finally forced some Blue-green species to become symbiotic with other plants or animals.

Summary — Importance of niche alteration. That the decline of marine stromatolitic constructions from Ordovician times onward is not due to waning growth potentials, as has been sometimes postulated, but is related to the process of niche alteration resulting from the evolution of the biotic world, is shown by the local development of significant stromatolitic reef or calcareous banks throughout the Paleozoic : Devonian of the Canning Basin, Australia (Playford & Cockbain, 1969), Carboniferous of England (Wolfenden, 1958), Permian of England (Smith, 1958) and of New Mexico (Newell et al., 1953). This is no puzzling problem for, at *these times and places,* the niche of reefoid Blue-green algae may have been narrower than that of comtemporaneous competiting algae and invertebrates; also, some given link in the complex biotic feed back may have been such that Blue-green algae were momentarily advantaged (see also Valentine, 1969, p. 914).

The net result of all the reported interactions stemming from the transformation of Early Paleozoic ecosystems is that, as far as we can judge, much of the Paleozoic stromatolites appear to be inter- to supratidal whereas growths in subtidal settings became generally less impressive in size and diversity. Furthermore, growth in the inter-and supratidal settings could not yield impressive bioherms or reefs as was the case for many subtidal precambrian stromatolites, because of the restrictions imposed by the water table and the periodic inhibitions due to climatic factors. This is reflected in the growing abundance of *algal mat limestones* from Mid-Ordovician on (Fischer, 1965).

Although preservational bias make it difficult to ascertain when stromatolites first spread toward continental settings, we know that by Late Carboniferous times at least, they were already active in various brackish, fresh water and hypersaline *continental* settings (Bertrand-Sarfati and Fabre, 1972a).

2. MESOZOIC STROMATOLITES

Mesozoic stromatolites have been relatively poorly studied; this may appear paradoxical for the term « stromatolithi » was first applied to Mesozoic structures (Kalkowsky, 1908). Although they are still found in various marine and perimarine habitats, their decline seems to go on; the realized niche of marine stromatolites appears to be more and more confined to the margins of their prospective niche. Furthermore, competition by other algal groups became stronger in Mesozoic times than during the Paleozoic.

The *Dasycladaceans*, crowding the shallow water favorable environments, reached their zenith during the Late Triassic and the Jurassic; this was the time when they developed the largest number of genera and species, and evolved the most complex structures (Johnson, 1964); moreover, many of these genera had a very short geological range. All these facts point towards a high specialization and a strong tendancy to reduce the modal niche size considerably. By the same token, these forms must have been very active competitors in the environments and microhabitats that they invaded. A clear example of mutual ecological exclusion between dasyclads and stromatolites, confined to littoral environments, has been illustrated by d'Argenio (1966).

Among *Red algae*, two important facts should be mentioned : the Solenoporaceae reached their acme during the Jurassic (Johnson, 1969), whereas the Corallinaceae, the most powerful competitive group that crowded the seas from the end of the Mesozoic on, began to appear with such forms as *Archaeolithothamnium*, *Lithothamnium*, *Lithophyllum* and the coralline *Archamphiroa* (Johnson, 1969; Wray, 1971). This started the zenith of red algae. After a slow evolution in the Paleozoic, the group evolved continuous specializations in the organization of their tissues, a modernization of their sexual organs, and showed a progressive diversification of their mode of growth. These facts lead to the same conclusions as the ones drawn from the evolution of dasyclads, i.e. they became active competitors which moreover appropriated the basic encrusting niche.

All these events resulted in an inhibition of the growth and constructional abilities of Blue-green algae in the sea, and accounted for the subsequent explosion of fresh water stromatolites later during Cenozoic times.

Mesozoic stromatolites are most abundantly reported from inter- to supratidal settings (for example, Fischer, 1964; D'Argenio, 1966; Szulcewski, 1963) where they withstood severe conditions : in the Dachstein of the Northern Calcareous Alps, they constitute a unique facies of cyclothemic formations, capping a deeply weathered and prism-cracked limestone member. The Dachstein occurences overlie a sedimentation discontinuity and record the return of a transgressive sea (Fischer, 1964).

Many Mesozoic subtidal stromatolites record similar conditions; first of all they seem to have developed in most extreme shallow water positions, as notes Szulcewski (1968, p. 89) with respect to Polish Jurassic stromatolites; secondly, stromatolitic thin beds frequently occur at the base of a transgressive sequence where they overgrow a basal conglomerate or blocks from the substrate (Bajocian, Rioult, 1962; Bathonian, Szulcewski, 1963, 1967; Albian, Niegodzisz, 1965).

Finally, and more generally, they accompany stratigraphical gaps or condensed sections (Szulcewski, 1968; Arkell, 1956; Radwanski & Szulcewski, 1966; Jenkyns, 1971...). In the latter case, they are often associated with a rich fauna as opposed to most stromatolitic beds; the associated fossils (ammonites, belemnites guards, brachiopods, etc.) are obviously reworked, corroded and/or bored by polychaetes or lithophagous lamellibranchs. These stromatolites, which may intergrow with serpulids or bryozoans, developed during periods of very low sedimentation and of unstable ecological conditions accompanying environmental changes; they seem to preceed a new, well adapted and strongly competitive biocenose or new sedimentary environments which will prohibit their growth (see for instance Royant et al. 1970).

Finally, as in Paleozoic times, stony stromatolite encrustations were still found on reefs, in deep water, although the occurences reported up to now are still unfrequent. An intersting example is found in the intergrowth of Blue-green algae and stromatoporoid in the deepest phase of a Cretaceous reef described by Achauer and Johnson (1969); Jenkyns (1971) has also interpreted Jurassic stromatolites associated with manganese nodules and crusts, and lying in condensed sequences, as capping deep water seamount terraces. Observations of Jurassic calcareous stromatolites from the Holy Cross Mountains (Poland) by Bernoulli has revealed an abundance of coccoliths in the stromatolites as well as in the surrounding limestone, which would point to their formation in plain oceanic conditions (Bernoulli, personnal communication).

All these occurences reflect once more the marginal ecologic situation to which the *bulk* of Blue-green algae were now confined. This does not mean, however, that stromatolite communities were no longer active in « normal » marine conditions for, at times, and for some particular unknown ecological conditions, they could still play a significant rôle even though they were diluted in a diverse biotic community. For instance, Kutek and Radwanski (1965) described poorly layered oolitic and organodetrital limestones crowded with oncolites which locally may concentrate (lag deposit ?) to form true oncolitic limestones; in the present case stromatolites were found to be associated with a rich benthonic community including solenoporoids, corals, brachiopods, gastropods, pelecypods, etc. (see also Radwanski, 1968).

Unlike Recent algal biscuits, the Jurassic oncolites were still hard lithified objects (Kutek and Radwanski, 1965) : they show nicely preserved borings by pelecypods (*Lithophaga*), polychaetes (*Potalimma*) as well as encrustation by bryozoans, serpulids, pelecypods (*Exogyra*), red algae, etc. These organic interrelations give an idea of the ecological pressures with which the Blue-green algae had to cope.

In conclusion, although Mesozoic stromatolites were still found in a wide range of environments, from the supratidal flats down to deep waters, they no longer built impressive deposits in the sea where their individual size remains quite smal (1); the most remarquable stromatolitic limestones were of supratidal origin. In the sea, they generally grew during very brief preiods and in unstable ecological conditions accompanying environmental changes, as reflected by their frequent occurence at the base of transgressive sequences or around stratigraphical gaps or condensations. Locally, the oncolitic mode of growth contributed significant materials to calcareous deposits for red algae had not yet filled that particular niche.

3. CENOZOIC AND RECENT STROMATOLITES

As far as can be appreciated from the geological record of stromatolites, their realized niche changed drastically from the beginning of the Cenozoic onward; fossilizable stromatolites are indeed very rare in Cenozoic marine sediments but extremely abundant in lacustrine deposits from all over the world. It is interesting

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(1) As observed in the Paleozoic section, exceptions to this generality can yet occur in priviliged sites : in the Roumanian Jurassic, for instance, the author has seen giant stromatolites underlying and later associated with reef building hexacorals (unpublished material by A. DRAGANESCU).

to note that most of these lacustrine stromatolitic deposits — either bedded, reefoid, or oncolitic — show a variety of growth forms that evokes — at a smaller scale though — many pre-Cenozoic subtidal stromatolites (see for instance Bradley, 1929; Johnson, 1937).

In my opinion, two main factors must be considered if we wish to account for the present-day paucity of stromatolites in marine sediments : (1) the climax recently reached by red algae (2) the process of mineralization and the general lack of lithification in Recent marine Blue-green algal colonies.

Consequences of the acme of rhodophytes. Crustose rhodophytes, wich progressively differenciated during the Mesozoic, and the coralline rhodophytes which appeared sometimes in the Cretaceous, invaded the sea floor from the beginning of the Cenozoic onward. Provided the environment be of « normal » salinity and frequently replinished in marine waters, Recent red algae colonize many hard (and even soft) substrates from the intertidal zone down to depths of 100 to 200 meters, and from the tropics to the high latitude cold waters (Lemoine, 1940). Thus they occur in many habitats where stromatolites could potentially flourish. Considering now the geological and present-day record, it appears that, from Late Cretaceous time on, red algae have almost totally outcompeted lime depositing cyanophytes in the sea. They have outcompeted calcareous Blue-green algae in shallow lagoonal waters where the reds build small knobby and dendritic calcified structures or encrust any available debris, sometimes in competition with foraminifera, bryozoans, serpulids, etc. This situation is quite reminiscent of many Paleozoic and Mesozoic intergrowths of Blue-green algae with encrusting invertebrates. Also, they have overwhelmed calcareous Blue-green algae in reefs where the reds range from the intertidal reef-flat to the slope (they may even be at times the most prominent reef builder). In addition, they have nearly excluded calcareous Blue-green algae from the soft or hard bottoms of continental shelves or internal seas where the reds now develop important algal beds variously known as « maerl » off N.W. France, « wild coral » in Ireland, « secca di chiaja » in the Gulf of Naples, or various boulder beds like the « Challenger Bank » 9 miles south of Bermuda where red algae build nodules up to 30 cm in diameter and form extensive deposits at depths ranging from 54 to 90 meters (Lemoine, 1940).

Many of these Recent formations are represented in Cenozoic sediments by algal limestones in which colonies of red algae *have replaced* the Blue-green algal oncolites of pre-Cenozoic times.

The present-day pre-eminence of rhodophytes, which have invaded many classical habitats of fossil stromatolites, reflects their better co-adaptation in equilibrium with a more advanced stage of the algal world and of the biosphere in general. Both reds and blue-greens have a similar pigment assortment (chlorophyll and phycobillins). Thus the reds can compete with cyanophytes even in the deepest or light impoverished habitats (which is not the case for chlorophytes). In addition, red algae have several advantages over blue-greens. First of all, red algae are eukariotic, generally stenohaline organisms which have developed many specialized free or encrusting forms (Lemoine, 1940); the latter overlap an important portion of the adaptative zone of Blue-green algae and can outcompete them because of the reds narrower niche.

Secondly, the intraorganic mode of calcification of red algae (where the microcrystals orient themselves on the cellulosic framework of the cell walls, Walter Levy & Strauss, 1961) is far more efficient than the external mineralization of blue-green algal filaments or colonies (Fritsch, 1945); the latter process is indeed more dependant on the environmental physico-chemical conditions than in the red algae where internal metabolical processes are the dominant factor; these processes can precipitate a skeleton independantly of (and in chemical desiquilibrium with) the external environmental conditions. Moreover, the tough and solid crusts built by rhodophytes are generally more resistant to predation than the concretions built by Recent Blue-green algae in fresh waters.

The spread of these highly competitive red algae, plus the ecological pressures that we have traced from the Paleozoic onward and that kept driving Blue-green algae towards the margin of their prospective niche, account for the present-day situation, i.e. the poor representation of Cyanophyta in marine environments. The following figures, drawn from Humm and Hildebrand (1962) clearly illustrate the way in which Cyanophyta are overwhelmed in the ocean by other algal groups and above all by Red algae :

	TEXAS & MEXICO		FLORIDA
	Number of species	*Percent*	*Percent*
Rhodophyta	92	48	52
Chlorophyta	46	24	25
Phaeophyta	31	16	13
Cyanophyta	24	12	10

This trend was confirmed by Echlin (1966) who stated that as far as organic diversity is concerned, only one fifth of all (Recent) Blue-green algae live in saline environments.

Effects of the lack of lithification in Recent marine stromatolites. The other point to be considered, when accounting for the paucity of marine stromatolites from the Early Cenozoic onward, is the general lack of calcification in Recent marine Blue-green algal colonies. The paleontological record may indeed have been biased by the non preservation of colonies similar to the Recent gelatinous algal biscuits, whereas the apparent loss of lithification may have seriously lessened their resistance to algae feeders. Personnal observations carried along Eastern Andros Island (Bahamas) revealed that when laminated blue-green algal consortia are traced from fresh waters toward marine lagoonal waters, there is a rapid decrease in the precipitated fine grained carbonate around algal filaments, wheras the entrapment of ready-made detrital calcareous grains becomes dominant (cfr. Monty, 1967, 1972). *Schizothrix calcicola* illustrates the case quite well : this Blue-green alga is responsible for heavy encrustations and deposition of calcium carbonate in many fresh water settings (Monty, 1965); it also grows actively in the sea where it forms the biscuits described by Monty (1965, 1967) and Gebelein (1969). These biscuits show no trace of precipitation (except for very local bacterial deposition); the mineral matter found in their regular calcareous layers originates in the daily entrapment and binding of various skeletal grains.

Similarly, *Lyngbya* and *Oscillatoria* are responsible for active lime deposition and crust building in many alkaline lakes and rivers. In the sea, however, they simply, form organic mats, stabilizing sedimentary particles (Monty, 1965, 1967; Bathurst, 1967; Scoffin, 1970; Neuman et al., 1970). It seems that, nowadays, precipitation and lithification are somehow inhibited in marine subtidal blue-green algal mats; all the latter can do is entrap and bind ready-made particles. Only one case of impressive but *inorganic cementation* has been reported to date from the inter- and subtidal zones (Logan, 1961; Playford, personnal communication). This is not much with respect to the abundance of *soft subtidal* structures on the one hand and the universal occurence of blue-green algal stony structures underwater or around the shores of most carbonate rich lakes and creeks, on the other hand. Such a unique occurence (Shark Bay), contrasting with the general situation in the sea, may somehow be correlated with the *local* occurences of deep water reefoid stromatolites in Paleozoic times (see previous section). Both instances reflect the development of a unique set of environmental parameters defining a hyperspace in which stromatolitic construction is momentarily enhanced whereas eventual competitors are tempo-ratily eliminated.

The general lack of lithification in Recent subtidal shallow water stromatolites may be interpreted along two lines of reasonning.

First of all, progressive changes in the chemical composition of sea water due to biological factors as well as to climatic ones may have somehow broken a link in the ecological requirements of stromatolitic Blue-green algae and deprived them of faculty of building significant lithified structures in marine shallow water settings. The cyanophyceans lakes, where Blue-green algae contribute important calcareous deposits and lithified structures, are characterized by a relatively high content in nitrates and phosphates as well as by an abundance of free and half bound CO2 (Prescott, 1951). In such settings, as well as in many cold and hardwater streams, the abundance of free CO_2 enhances blue-green algal photosynthesis and greatly facilitates the deposition of calcium carbonate while the competition for calcium and CO_2 is much less dramatic than in present-day lagoonal and impoverished back-reef waters. In the latter settings, organisms with an internally controlled mineralisation are greatly advantaged; that is for instance the case for rhodophytes, dasyclads and most skeletonized invertebrates that crowd these waters.

Secondly, the Recent soft, non-preservable biscuits and mats, trapping detrital grains, *may represent an obligatory variety* of shallow marine stromatoliti cconstructions, a particular adaptation habit, the preponderance of which was favored by the actual physicochemical parameters of seawater on the one hand, and by the ecological pressures enforced by red algae on the other hand. By trapping ready-made particles and erecting gelatinous but otherwise coherent structures, Recent subtidal stromatolites survive and cope with the present chemical situation of marine environments. By the same token, they focuss their activities toward a niche which is very different from that of rhodophytes; accordingly they do not meet the latter's competition. In this sense, this particular growth habit represents yet another case of niche partitioning which was necessary for some species, or consortia of species, to survive in the sea in the face of competitive opponents.

A most important consequence of this lack of calcification in Recent subtidal stromatolitic domes and biscuits associated with lagoonal and reef organisms, is that they cannot accumulate to constitute an important fraction of calcareous deposits; furthermore, they can no more significantly alter or influence the marine environment by building reefoid structures, oncolitic beds, solid calcareous heads, in short by forming new and constantly renewed hard substrates. *This niche nowadays overwhelmingly belongs to the rhodophytes in the sea,* wheras Blue-green algae have transposed the occupation of this niche to fresh water settings and very marginal marine settings (tidal flats), where they escape their competitors and are the leading encrusting and lime depositing algae.

4. CONCLUSIONS AND FINAL COMMENTS

The decline of Phanerozoic stromatolites is the story of eurybiontic encrusting communities which have been continuously displaced by more specialized, better adapted, competitive organisms provided with narrower niches.

Marine stromatolitic communities probably spread very early toward the shores, the intertidal zone, and from there, later, toward the bare land; this movement was however dependant on a decrease in the noxious radiations that hit the earth, though the mineralization of stromatolites could somewhat shade the cells (Fischer, 1965). Originally, this spread was probably dictated by the acme that marine stromatolites reached in Late-Precambrian-Earliest Paleozoic times, an acme which allowed them to colonize all suitable substrates. From Cambro-Ordovician times onward, animal and plant *competition for niche*, *substrate* and *nutrients* originated a drastic *habitat and niche splitting* in stromatolitic communities, the results of which appears to-day as a net displacement of the latter towards very marginal marine (and later non marine) settings; under these pressures, the intertidal habitat s.l. was then found most satisfactory, in view of the various competitive communities rising in the sea.

The rise of eukariotic algae originated a progressive drop in the organic diversity of the bulk of marine benthonic cyanophytes which eventually resulted in the present-day situation, i.e. their very poor representation in the photic zone when compared with other algae. Furthermore, the *calcareous* blue-green algal species, in the shallow seas, were progressively dispossessed of their niche, i.e. of their function as rock-building encrusting communities, by a series of strongly competitive organisms from stromatoporoids to red algae. These organisms diversified and produced a great number of species endowed with basic biological advantages, provided with narrow niches, and able to build stony calcareous skeletons independantly of the local and instantenous physicochemical conditions of the sea. Very soon then stromatolites were concentrated around the harsh inter- supratidal habitats, where Blue-green algae could live uncompeted on grounds which did not fit the requirements of their highly specialized competitors in the sea.

Another habitat existed where Blue-green algae could escape the high organic diversity of the shallow seas and the green algae competition, this habitat was the deep waters where blue-green algae could grow successfully. However, several animal communities invaded parts of these settings where rhodophytes furthermore extended later. Accordingly, stromatolites as a rule did not concentrate in the deep waters, although from time to time, they found adequate realized hyperspaces there.

In between these two extremes, the tidal flats and the deep waters, stromatolites became less and less conspicuous, during the Mesozoic, in the shallow seas where they occasionally spread, during periods of generally unfavorable conditions for their competitors; their constructions remained however small as a whole.

Nowadays, soft, non competitive blue-green algal colonies subsist in shallow waters (various subtidal biscuits, mats and films); the bulk of marine stromatolitic deposits is found along calcareous shores or flats, where they can grow with little competition to form leathery mats and earthy deposits.

Finally, that part of the former marine niche, represented by the building of lithified calcareous crusts, heads, oncolites and « reefs » was transposed to alkaline non marine environments as is illustrated by the paleontological record from Cenozoic times onward.

All the developped considerations show that the present day status of stromatolites does not result from « non competitive ecologic restriction by grazing and burrowing animals » as Garrett (1970) proposed. Indeed, as said in the Precambrian section, successful freshwater stromatolites can cope with grazing by gastropods as well as burrowing or various bioturbations introduced by worms and arthropods. The arguments presented by Garrett (id.) to show that browsers and borers would have restricted stromatolites to the supratidal flats would also imply the decline of subtidal red algae due to the rise of various boring invertebrates and grazing fishes (Fritsch, 1959, p. 511). Furthermore, in view of Garrett's arguments, it seems somewhat paradoxical that the non lithified blue-green algal structures (biscuits, mats, films), i.e. the *most easily accessible to browsers and grazers, have not* been eliminated from the sea, whereas blue-green algal solid crusts, heads and the like, i.e. the more resistant to predation, would have been confined and restricted to non marine environments. (see also discussion p. 602).

The present overall temperature at the surface of the biosphere, apparently lower than that of some of the previous geological epochs, may be thought of as an explanation for the eventual diminution of the growth potential of Blue-green algae as well as for a shortened growth period per year. This would lead to the formation of smaller structures exposed to die and disappear during poor growing seasons, prohibiting in that way the building up of important structures. There may be some truth in this argument for Blue-green algae as a whole are warm water forms. As Fritsch (1907) tentatively stated, this affinity for warm temperatures may be a relict and inherited ecological factor : « in view of the exceeding abundance of this group of algae in the tropics, one can scarcely resist the assumption that their habitats in these regions are more in accord with their former condition of existence than the habitats of temperate regions. A considerable number of Cyanophytes have indeed become acclimatized to the changed conditions in these latter parts of the world but the group is prevalently tropical ». However, two points suggest that this argument is not fundamental to the history of stromatolites.

First of all, the decline of stromatolites has progressed since mid-Ordovician times and there is no apparent correlation between any proposed scheme of past temperature fluctuations and the greater or lesser abundance of stromatolites.

Secondly, as said earlier in this paper, Recent Blue-green algae have developed many cold water stenotherms which are very active as rock builders in streams and lakes where they replicate many stromatolitic structures of the past. There is no reason to think that such cold stenotherms did not exist from Precambrian times onward and perhaps even became prominent during glaciations or cool periods. Therefore, we should not *ipso facto* interpret stromatolitic biostromes as typical of shallow warm waters.

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