

120 417

AN AUTOECOLOGICAL APPROACH OF INTERTIDAL AND DEEP WATER STROMATOLITES (*)

par C. L. V. MONTY (**)

(4 figures dans le texte)

ABSTRACT

The first section of this note lists some basic properties which enable blue green algae not only to survive but to grow successfully in the harsh inter- supratidal environments. Among other things, cytological, physiological and morphological features are briefly considered.

The second section tentatively accounts for deep water stromatolites; it is shown that the photosynthetic equipment of blue green algae joined to the eventual enhanced formation of red and blue pigments in deep waters enable blue green algae, and hence stromatolites, to grow successfully down to 150 meters or more provided the surrounding waters be rich in CO₂, nitrates and phosphates. It is suggested that Recent stromatolitic constructions should be searched for around these shelf edges submitted to significant upwelling.

RÉSUMÉ

Dans une première partie, l'auteur considère rapidement certaines propriétés fondamentales qui ont permis aux algues bleues non seulement de survivre mais aussi de prospérer dans les conditions rigoureuses rencontrées dans les zones intertidale et supratidale.

La seconde partie aborde le problème tant discuté des stromatolithes d'eau profonde; l'équipement photosynthétique des algues bleues, joint à leur faculté d'augmenter en eau profonde la production de pigments rouges et bleus photosynthétiquement actifs, permet aux cyanophycées de coloniser des fonds marins descendant jusqu'au moins 150 m, pour autant que les eaux environnantes soient riches en CO₂, en nitrates et en phosphates. Ces considérations permettent à l'auteur de suggérer la recherche de stromatolithes récents sur ces bordures continentales soumises à un upwelling significatif.

INTRODUCTION

The purpose of this note is to sort out some significant facts from neontological data in order to understand the accommodation of severely exposed environments (inter- to supratidal) by some stromatolitic communities, and of deep-water settings by some other ones.

A. WHAT PROPERTIES ENABLED BLUE-GREEN ALGAE TO ACCOMMODATE INTER- TO SUPRATIDAL SETTINGS?

Life in the intertidal and supratidal environments requires a series of particular physiological, cytological, morphological and behavioural adaptations as the orga-

(*) Communication présentée le 9 mai 1971. Manuscrit déposé le 20 août 1971.

(**) Laboratoire de Paléontologie animale de l'Université de Liège, 7, Place du XX Août, 4000 Liège.

nisms involved have to cope with extreme values of many leading ecological parameters. Four types of examples will briefly illustrate various steps of adaptation presented by blue green algae and accounting for the realization of this margin of their prospective niche.

1. Resistance to drought

Adaptation to the intertidal zone requires the possibility of surviving during the low tide exposures. Some chlorophytes like *Ulva* can lose important amounts of water without damage for their protoplasm; others, like the pheophyte *Fucus* are able to resist strong osmotic pressures and evaporation; they lose very little water which they can recuperate very quickly during the next high tide. In the intertidal zone however, we note that the highest algal belt is mostly composed of cyanophytes (such as *Entophysalis deusta*) withstanding conditions that no other algae can accommodate. Of course, the boring habit of some blue-green algae enables them to colonize microinterstices where sufficient amounts of humidity may remain trapped for a given period of time. However not all blue green algae have chosen this ecological adaptation for they have other ways of coping with life conditions on heavily exposed, often dried up shores or flats.

a) The most classical response to bad conditions is the production of resting spores or hormocysts, system which is not basically limited to blue green algae. *Hormocysts* (fig. 1) are non motile organs of perennation provided with a thick pigmented sheath surrounding enlarged cells full of food reserves; when germinating, these hormocysts grow into a new filament such as happens in the *Scytonemaceae* for

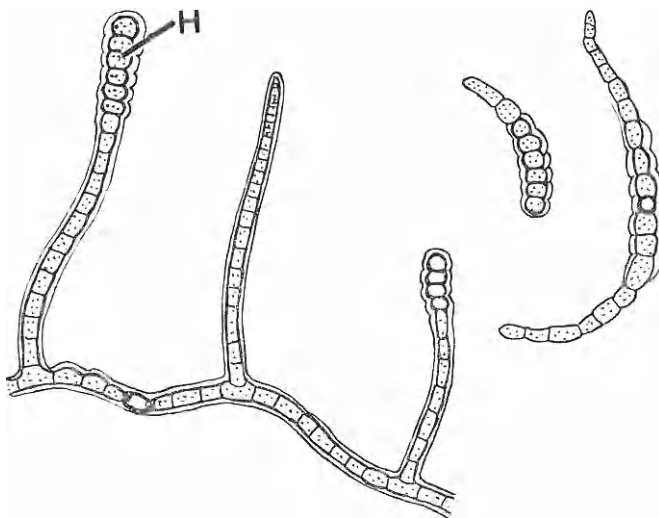


Fig. 1. — Formation and germination of hormocysts (H) in blue-green algal filaments : small parts of the trichome enclose themselves in a thick lamellated pigmented sheath protecting enlarged cells loaded with food reserves (left). These non motile hormocysts get then detached from the mother filament and on germinating (right) the two end grow a new plant. After Freyre in Desikashary 1959. Modified.

instance. In other algae (*Nostoc*, *Rivularia*, etc.) specialized cells of the trichomes inflate rapidly, are stuffed with granular food reserves and become completely isolated from the other cells whereas the walls thicken considerably and may develop coloration (fig. 2); such *resting spores* (or *akinetes*) constitute another way of securing perennation as they are very resistant to dessication and extreme exposure. Their content may germinate at once or after a resting period.

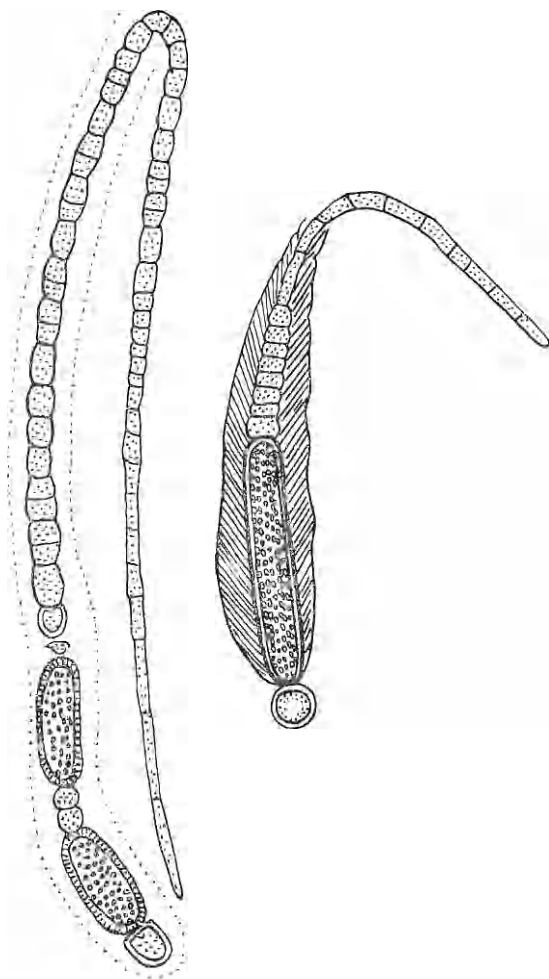


Fig. 2. — Individualization of resting spores or akinetes in blue-green algal filaments. These non motile perennating organs are loaded with food reserves and enclosed in a thick lamellated sheath. From Desikashary 1959, modified.

This enables algal mats to dry up for months upon tropical flats, where they may even turn to dust, and suddenly bloom again when the first rain comes.

b) The second mechanism does not rely anymore on concentration of the algal life potentials into specialized dormant cells, but on the development of a protective mucilaginous cover. This may be realized at three levels as Geitler (1930) points it out :

- Production of a thick mucilaginous mass which surrounds and limits the *whole* colony (such as in *Nostoc commune*). This jelly is very thick at the periphery of the colony where it is moreover surrounded by a strong cuticular membrane.
- Production of a thick and resistant sheath around the *individual* filaments (such as in *Scytonema myochrous*). Such sheaths are often deeply stained and protect the algal filament not only against dessication, but also against dangerous solar radiations (see below).
- Each cell assumes its own protection, such as occurs in some species of *Phormidium*.

c) Beside the production of resting spores or hormocysts, of thick coherent sheaths or watertight mucilaginous masses, there is a third way of coping with drought, i.e. the mode of growth. Two examples will be quoted after Fritsch (1907).

Fritsch noted the predominance, in the dry areas of Ceylan, of thin slippery films closely applied to the substratum. This « adhesive mode » of growth is mainly adapted to the preservation of the internal moisture; it is found in most unicellular gelatinous and encrusting forms (*Aphanocapsa*, *Aphanothece*, *Gloecoapsa*, etc...) as well as in some filamentous ones (*Nostoc*, etc...).

At the opposite is the « tufted mode » where algae such as *Tolypothrix*, *Scytonema*, etc. build up erected bundles of filaments. In this case, the filaments, encased in a protective sheath, project freely into their air. This mode, well adapted to the absorption of atmospheric humidity, will be favored in places where the atmospheric moisture is sufficient and the substrate somewhat dry, in such a way that the previous mode cannot grow successfully.

These two examples are by no means restrictive, nor are they diagnostic of a given environment : for instance, the adhesive mode which is presented here as an adaptation towards the retention of humidity, may in other settings, be a response to a different stimulus; this mode may for instance be prevalent in fast flowing streams because it offers the least resistance to the water flow.

2. Resistance to High temperature and protoplasmic stability

It is well known that blue green algae can withstand very high temperatures up to 60 to 70°C; ELENKIN (1914) even reports *Oscillatoria* and *Phormidium* accommodating temperatures of 85°C. Furthermore, INMAN (1940) found that thermophilic algae, living normally in hot springs around 60°C could be grown successfully at much lower temperatures (20°C); accordingly, in some cases at least, the adaptation to high temperature may be reversible. Finally, blue green algae can bloom in the ice or in the frigid lakes of the polar regions.

Such characteristics, reflect, among other things, a high stability of the blue green algal protoplasm. In fact, STANIER *et al* (1961) points out that one of the most striking feature of this protoplasm, is its immobility; FOGG (1956a) attributes this immobility to a high degree of viscosity, a rather rigid structure which does not permit streaming nor brownian movement; he explains the rigidity of the proteins of all blue green algae by their being cross-linked by primary bonds rather than solely by hydrogen bonds. Finally MARRÈ *et al* (1958) concluded that the protoplasmic thermo-resistance and non-coagulation as found in thermal algae appear as real properties of the protoplasm itself rather than as a result of the protective action of some biochemical agent.

Consequently, the stability of the blue green algal protoplasm, joined to the frequent development of protective films shading the underlying growth, makes it possible for these algae to withstand the very high temperatures that may be found on tropical flats.

3. *Resistance to lethal solar radiations*

Another important problem, that these inter- to supra-tidal algae have to cope with, originates in the lethal solar radiations.

As a rule, radiations of wave lengths shorter than 3000 Å are very noxious to plants, chiefly when in mixed light. Some blue green algae however can withstand radiations of the order of 2759 Å, radiations which are lethal for bacteria. Such a strong resistance is not yet well understood, but the following remarks have been put forward :

(i) The various pigments which occur in the peripheral region of the blue green algal protoplasm include carotenoids or CH groups and xanthophylls (their oxydated derivatives). Although the rôle played by the carotenoids in the photosynthetic reactions has not yet been completely elucidated (NAKAYAMA 1962), it has been proposed that the great number of double bonds in the carotenoidic structure might somewhat protect the protoplasm by absorbing at least part of the UV radiations. WITKIN (1966) and GIERE (1945) state that procaryotic cells (like that of blue green algae) are more resistant to UV radiation and resultant induced mutations than eucaryotic cells.

(ii) Furthermore, GODWARD (1962) points out that « Since cells of *Cyanophyta* have not been shown to possess nuclei or chromosomes like those of other plants, no radiation damage has been assessed cytologically.

(iii) The surficial layer of blue green algal mats is deeply stained by dark pigments which accumulate in the sheaths of the component filaments. This pigmented layer screens the noxious (*) light and protects the underlying algal cells or filaments which frequently contribute most of the thickening of the mat.

(iv) Two other points should also be considered : the frequent occurrence at the surface of mats or around filaments of detrital or precipitated calcareous grains which undoubtedly shade the cells. The mobility of the trichomes which eventually enables them to migrate deeper in the mat and escape momentarily the surficial layers hit by dangerous radiations.

4. *Nitrogen needs and fixation*

Most blue green algae appear to be very rich in proteins when compared to other algae (Table 1); this may account for their high demand for nitrogen (or nitrogen derivatives) and phosphates (PRESCOTT 1959). The case is illustrated by the prolific development of blue green algae in eutrophic lakes where the availability of phosphorus, and the abundance of nitrogen provide optimal life conditions for these algae; in such « Cyanophyceean lakes » they may thrive in enormous quantities reaching sometimes densities of several millions individuals/liter — situation that may have prevailed in primeaval seas. If nitrogen and phosphorus are readily available in normal seawater, and may reach optimal concentrations in particular lakes, the situation is quite different for the supratidal and terrestrial communities which spread their

(*) By its composition or and its intensity.

Organism	Nitrogen	Crude protein
<i>Cyanophyta</i>		
<i>Microcystis</i>	9,68	55,68
<i>Anabaena</i>	8,91	60,56
<i>Aphanizomenon</i>	10,05	62,83
<i>Lyngbya</i>	9,73	60,81
<i>Chlorophyta</i>		
<i>Spirogyra</i>	3,81	23,81
<i>Cladophora</i>	3,77	23,56

TABLE I.

Chemical analysis of various green and blue green algae stated in percentage of dry weight of the sample (Prescott 1948).

mats outside of the water and sometimes of freshly exposed bare rocks. We find here many species that have developed the ability to fix atmospheric nitrogen (*Nostoc*, *Anabaena*, *Calothrix*, ...); the process involved does not seem to be drastically different from the one encountered in *Azobacter* or *Rhizobium*, bacteria that crowd the tubercules of some leguminous phanerogames (FOGG 1956a).

The fixation of elementary nitrogen is also performed in the ocean by marine blue green algae, and this property has been apparently carefully preserved during the shift towards terrestrial environments (MONTY, in press.)

Accordingly, blue green algae are very well equipped cytologically (stability of the protoplasm, emission of resting spores...) physiologically (chemical absorption of UV radiation, fixation of atmospheric nitrogen...) morphologically (protective sheaths or colonial mucilages, mode of growth adapted to local conditions...) for surviving and even grow successfully in the harsh inter/supratidal environments.

B. DEEP WATER STROMATOLITES ARE NO SPECIAL PROBLEM

Not all of the fossil occurrences can be interpreted in terms of recent intertidal to supratidal algal mats. The paleontological record provides us with unequivocal examples of subtidal and even deep water stromatolites (PLAYFORD and COCKBAIN 1969; ACHAUER and JOHNSON 1969, etc.) although the possibility is often reluctantly accepted by geologists.

The question arises then : are such settings, characterized by impoverished light, compatible with the physiological and mainly with the photosynthetic requirements of blue green algae? Are the latter equipped for thriving in deep waters?

No doubt, the answer is yes : in fact, the maximum depth reached by blue green algae is actually unknown; *Oscillatoria profunda* has been found at — 70 m. in the Bodensee (GETTLER 1932) whereas *Schizothrix calcicola* — an important crust building alga — is reported at — 390 m. in the Dead Sea (DROUOT 1963) and *Nostoc* sp. is found in important quantities at — 1000 m. in the Indian Ocean. We shall not here discuss life in the bathyal zone but orient the argumentation towards the possibility for stromatolites to grow actively between 30 and 150 meters or so.

1. Photosynthetic pigments

The problem of photosynthesis and of the actual potentialities of the various pigments is far too complex and evolves too rapidly to be developed here. Moreover, the literature is flooded with detailed particular observations carried *in vitro* to the point that it is difficult to separate what is proper to the beaker from what is effective in nature. So, let us stick to some general comments.

The blue green algal chromoplasm contains the following pigments : *chlorophyll a* (green pigment with a strong absorption maximum in the red band), *phycocyanin* (blue pigment with an absorption maximum in the yellow-orange band), *Phycoerythrin* (red pigment with an absorption maximum in the green band) and the *carotenoids* i. e. carotene β and myxoxanthins (oxydated carotenoids) (fig. 3). The important thing for us is the presence of phycobillins (phycoc-erythrin, -cyanin) which are found in blue green and red algae, not in green nor in brown ones. As PÉRÈS (1961) points it out the combined action of the latter pigments and of the carotenoids together with the chlorophyll originates a high photosynthetic efficiency over most of the visible spectrum (fig. 3).

Let us now correlate the potentials of the pigments with the transparency of water for radiations of different wave lengths. Experimental work carried in lakes as well as in the ocean, shows that the water transparency decreases not only towards the longer wave lengths but also towards the shorter ones. Fig. 4 shows the intensity and spectral composition of light at various depths in an alpine lake (Lunzer Untersee). On fig. 3 the values of the coefficient of extinction K_0 for two types of marine waters have been superposed on the absorption peaks of the various blue green algal photosynthetic pigments. (data after STRICKLAND 1958 in PÉRÈS 1961). These figures show that the conditions of transmission are most favorable for the blue green and yellow radiations, whereas the red light is almost completely absorbed in the uppermost layers of the sea; this last phenomenon is an important limiting factor in the depth distribution of green algae since they mostly absorb in the red band. Red and blue green algae, on the contrary, are not dangerously affected by the differential pattern of light absorption by water; with increasing depth indeed, the remaining radiations shift toward the zone of absorption of their complementary pigments, i. e. the phycobillins (fig. 3).

This partly explains why red algae may abundantly colonize deep poorly illuminated bottoms : « they are suited to deeper water since the prevalent light consists essentially of the wavelengths most strongly absorbed by the algae themselves » (BIEBL, 1962); this has been confirmed by HAXO and BLINKS (1950) who showed that red algae exhibit their highest photosynthetic rates in the spectral regions absorbed by the phycobillins.

The situation is quite similar with blue green algae which, thanks to their phycoerythrin and phycocyanin can successfully utilize the blue-green-yellow radiations that most deeply penetrate sea-water; I say *successfully* because it has been proved that the energy drawn from these residual radiations can be transferred to the chlorophyll *a* which can therefore be an active photosynthetic pigment in waters where its proper radiation does not exist anymore.

Accordingly the photosynthetic equipment of blue green algae (and of red algae, their eventual competitors) enables them to colonize subtidal settings characterized by an impoverished spectrum, i. e. turbid or deep waters.

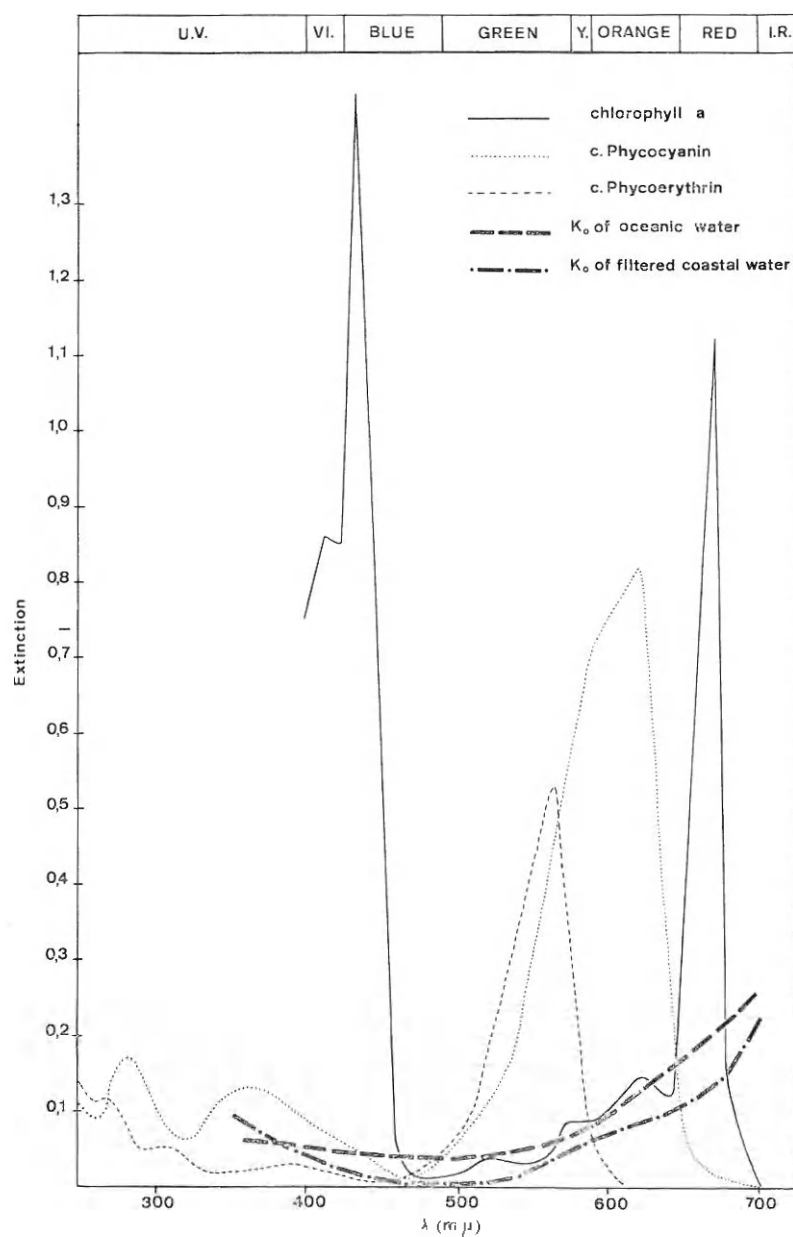


Fig. 3. — Pattern of the absorption spectrum of the leading photosynthetic pigments of cyanophyta (data obtained *in vitro*); the absorption spectrum of the carotenoids and xanthophylls, which has not been represented, range from about 420 $m\mu$ to 480 $m\mu$. The coefficients of extinction K_0 for the two types of marine waters have also been reported on the graph (data plotted are $10 \cdot K_0$, after Strickland 1958).

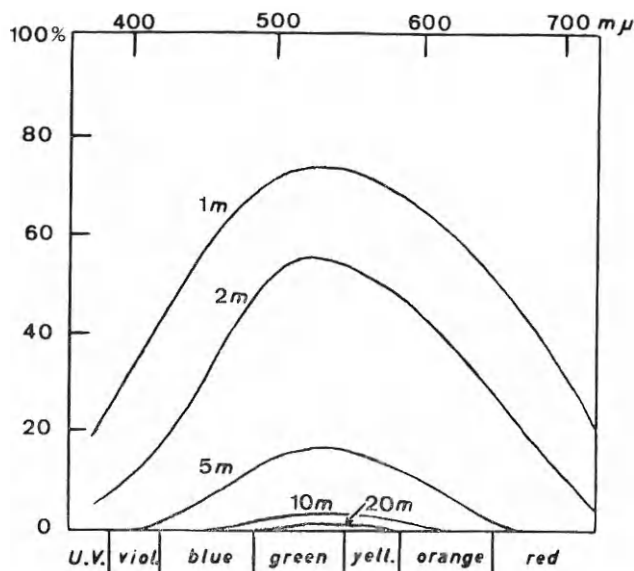


Fig. 4. — The intensity and spectral composition of light at various depths in Lunzer Untersee expressed as percentage of radiation reaching the surface (Summer averages at the mean elevation of the sun). From Ruttner 1964, fig. 5.

2. Chromatic adaptation

Blue green algae present a second fundamental property which is the enhanced formation of the pigment which most strongly absorbs the incident radiation; this so-called « complementary chromatic adaptation » appears to be only effective at low light intensity (BRODY & EMERSON 1959, HEOCHA 1962). This observation accounts for the fact that Cyanophyta collected in deep water (15-40 m) appear to be richer in red pigment than the surficial ones; this is for instance the case in alpine lakes where they are associated with red algae to form the so-called « deep red biocenose ». Accordingly, as FRITSCH (1959) states it « the capacity for adjustment to lights of different intensity and colour means that blue green algae are better adapted than other plants to utilize all the available light and this, combined with other characteristics, may account for their ubiquitous occurrence... ».

As phycoerythrin and phycocyanin are proteidic substances, their enhanced production requires the availability of nitrogenous compounds. However, blue green algae can fix elementary nitrogen in the sea, and vertical mixing or seasonal upwelling along continental shelves can bring up important amounts of available nitrogenous compounds.

The possession of efficient pigments devoted to the absorption of the deep penetrating radiations (blue green, yellow) as well as the possibility to enhance their formation in order to reach a better energetic efficiency, may not be fortuitous at all. It means that blue green algae are well equipped for thriving in rather deep water or in turbid environments (due to suspension of organic matter, for instance). Consequently if nowadays, algal mats and recent stromatolites have been reported but from supratidal to very shallow settings, the physiology of blue green algae is by no mean

prohibitive to the formation of deep water stromatolites such as seems to have occurred in the geological column. It also means that it might be most interesting to investigate these western shelf edges or even some reef fronts where upwelling of deep water brings up available free CO_2 , nitrates and phosphates which might originate a most satisfactory environments for modern deep water stromatolites.

3. Eventuality of very deep water stromatolites

We know that blue-green algae can live successfully in the dark on an appropriate substrate (FOGG, 1956); this has been observed *in vitro* but also *in vivo*; (1) MAGDEBOURG (1929) described laminated calcareous tufa built by an association blue-green algae/iron bacteria and growing in the complete darkness of caves. (2) BERNARD (1963) found abundant cyanophyta living at depths greater than 1000 m. in the Indian ocean. He furthermore states that nanoplanktonic cyanophyta would be more abundant in the aphotic than in the photic zone.

Such algae have undoubtedly acquired an heterotrophic metabolism and their growth relies on the presence of an appropriate organic substrate (*). Our knowledge of the concentration of nutrients in the aphotic zone of the oceans is still too scarce however to precise the processes involved, but some remarks may be interesting: MAGDEBOURG (*ibid.*) reports that in the caves, the required organic substrate would be provided by the associated chemosynthetic iron bacteria using the system $\text{Fe}^{++}/\text{Fe}^{+++}$ as a source of energy for their synthesis. Another interesting case is reported by NAUMAN (1924) from African lakes, where he found round colonies of *Nostoc* up to 2.5 cm in diameter, and showing periodic dark banding enriched in Fe^{+++} ; the iron is precipitated in the sheaths surrounding the filaments and the resulting dark laminae would correspond to yearly periods of growth. Finally many authors have reported yearly enrichment in iron and manganese in blue-green algal colonies or crusts (*cfr.* MONTY, 1965); the latter phenomenon being found sometimes in algae growing in the dark, sometimes in algae growing in daylight but in waters relatively rich in iron.

From what precedes (see also the important bibliography given by MAGDEBOURG 1929), it appears that blue-green algae can build laminated calcified structures, eventually enriched in iron and manganese, in the complete darkness. Up to now, we cannot say for sure whether some cyanophytes can, in given conditions, become autotrophic chemosynthetic organism using the Fe/Mn redox system as a source of energy, or whether they live as saprophytes feeding on the organic substrate provided by iron bacteria (one of the two processes has undoubtedly played during Meso-Proterozoic times); what we can say however is that there is no reason why blue-green algae could not build stromatolitic structures in the complete darkness of the aphotic zone down the 1000 m. or more. These structures, partly calcified or not, might show a lamination composed of alternating layers enriched in iron and manganese (corresponding to the full growth period) and eventual small layers of detrital material (as deep bayer cyanophytes do not seem to withstand strong influx of sediments, BERNARD 1963); the periodicity of the banding would be most probably related to the seasonal characteristics of the deep-water currents carrying the required nutrients. Such deep settings submitted to the influence of rather undepleted, nutrient-rich waters as well as to a very slow sedimentation could be found on oceanic seamounts, for instance.

(*) See bibliography in Fogg, 1956 and Magdebourg, 1929.

BIBLIOGRAPHY

- ACHAUER, C. W., and JOHNSON, J. H., 1969. — Algal stromatolites in the James Reef Complex (Lower Cretaceous) Fairway Field, Texas. *J. Sed. Petr.*, **39**, N° 4, 1466-1472.
- BERNARD, F., 1963. — Density of Flagellates and Myxophyceae in the heterotrophic layers related to environment. In « Symposium on marine microbiology », K. Oppenheimer Ed., C. Thomas publisher, Illinois pp. 215-228.
- BIEBL, R. 1962 : Seaweeds, in « Physiology and Biochemistry of Algae », R. A. Lewin Ed., Acad. Press., N. Y., pp. 799-815.
- BRODY, M., and EMERSON, R., 1959 : The effect of wavelength and intensity of light on the proportion of pigments in *Porphyridium cruentum*. *Am. Jour. Bot.* **26**, pp. 443-440.
- DESIKASHARY, T. V., 1959. — Cyanophyta. Indian Council of Agricultural research. New Delhi.
- DROUET, F., 1963 : Ecophenes of *Schizothrix calcicola*. *Proc. Acad. Nat. Sc. Philadelphia*, **115** n° 9, pp. 261-281.
- ELENKIN, A. A., 1914. — Ueber die thermophilen Algen-formationen. *Bull. Jardin Imp. Bot. Pierre le Grand*, **14**, pp. 62-110.
- FOGG, G. E., 1956a. — The comparative physiology and biochemistry of blue-green algae. *Bact. Rev.*, **20**, pp. 148-165.
- FOGG, G. E., 1956b. — Nitrogen fixation by photosynthetic organisms. *Ann. Rev. Physiol.* **7**, pp. 51-70.
- FOGG, G. E., 1956 : The comparative physiology and biochemistry of blue-green algae. *Bact. review*, vol. **20**, n° 3, p. 148-165.
- FRITSCH, F. E., 1907. — A general consideration of the subaerial and fresh water algal flora of Ceylon. — A contribution to the study of tropical algal ecology. Pt. I : Subaerial algae and algae of the inland fresh waters. *Proc. Roy. Soc. London*, se. B., **79**, pp. 197-254.
- FRITSCH, F. E. 1959. — The structure and reproduction of algae. Vol. II, Cambridge Univ. Press.
- GRÜTLER, L., 1930. — Cyanophyceae (Blaualgen) Deutschlands, Oesterreichs und der Schweiz mit Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete. *Rabenhorst's Kryptogamen Flora XIV Band*. Akad. Verlagsgesellschaft m. b. H. Leipzig.
- GIESE, A. G., 1945. — Ultraviolet radiations and life. *Physiol. zool.* **18**, n° 3. pp. 233-250.
- GODWARD, M. B., 1962. — Invisible radiations, in « Physiology and biochemistry of Algae » R. A. Lewin Ed., Acad. Press, N. Y., pp. 551-566.
- HAXO, F. T., and BLINKS, L. R., 1950. — Photosynthetic action spectra of marine algae. *J. Gen. Physiol.* **33**, pp. 389-442.
- HECHA, C. O., 1962. — Phycobilins, in Physiology and biochemistry of Algae. R. A. Lewin Ed., Acad. Press, N.Y., pp. 421-442.
- INMAN, O. L., 1940. — Studies on the Chlorophylls and photosynthesis of thermal algae from Yellowstone Park, California and Nevada. *J. Gen. Physiol.* **23**, pp. 661-666.
- MAGDEBOURG, P., 1929. — Organogene Kalkkonkretionen in Höhlen. *Naturfor. Gesellsch. Leipzig, Sitzungs-Berichte 1929-34*, pp. 14-36.
- MARRE, E., ALBERTARIO, M., and VACCARI, E., 1958 : Ricerche sull'adattamento proteico in organismi termoresistenti. III. Relativa insensibilità di enzimi di cianofite termali denaturanti che agiscono rompendo i ponti di idrogeno. *Atti. accad. nazl. Lincei Rend. Classe sci. fis. mat. e nat.*, **24**, pp. 349-353.
- MONTY, C. L. 1972. — The Phanerozoic history of stromatolite communities. *Lethaia*, in press.
- MONTY, C. L., 1965. — Geological and environmental significance of Cyanophyta, *Ph. D. Thesis*, 429 p., 89 Pls., 42 Figs., Princeton Univ., N. J., U.S.A., Microfilm N° 66-5003 Univ. Microf. Inc., Ann Arbor, Michigan.

- NAKAYANA, T. O., 1962. — Carotenoids, in « Physiology and Biochemistry of Algae », Lewin Ed., Acad. Press, N. Y., pp. 409-420.
- NAUMAN, E., 1924. — Notizen zur Systematik der Süßwasseralgen-X. *Arkiv för Botanik*, Band 19, N° 15, p. 1-7.
- PÉRÈS, J. M. 1961. — Océanographie biologique et biologie marine, tome 1 : La vie benthique. Presses Univ. France. 538 p.
- PLAYFORD, G., and COCKBAIN, A. E. 1969. — Algal stromatolites : deepwater forms in the Devonian of Western Australia. *Science*, **165**, n° 3897, pp. 1008-1010.
- PRESCOTT, G. W., 1948. — Objectionable algae with special reference to the killing of fish and other animals. *Hydrobiol.* **1**, pp. 1-13.
- PRESCOTT, G. W., 1959. — Fresh-water algal ecology with special reference to the Artic. *C. R. 9^e Congr. Int. Bot.*, **2**, Résumés, p. 309.
- RUTTNER, F., 1964. — Fundamentals of Limnology, 3rd Edition. Univ. Toronto Press.
- STANIER, R. Y., DOUDOROFF, M., ADELBERG, E. A., 1961 — The microbial world. Prentice Hall inc. Englewood Cliffs, N. J., USA.
- STRIKLAND, J. D. H., 1958. — The solar radiation penetrating the ocean. A review of requirements, data, and methods of measurement, with particular reference to photosynthetic productivity. *J. Fish Research Board Canada*, **15**, n° 3.
- WITKIN, E. M., 1966. — Radiation-induced mutations and their repair. *Science*, **152**, pp. 1345-1353.