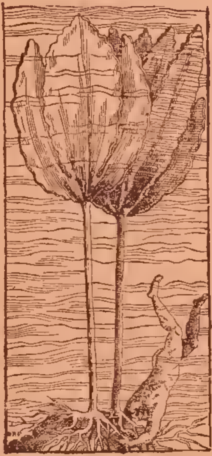
Nouvelle Série, Tome XIV, Fasc. 3 1979

ISSN 0035-0702

REVUE ALGOLOGIQUE



LABORATOIRE DE CRYPTOGAMIE
MUSÉUM NATIONAL D'HISTOIRE NATURELLE
12, RUE DE BUFFON - 75005 PARIS

Publication Trimestrielle *Sorti des presses le 31 octobre 1979*

OUVRAGE PUBLIÉ AVEC LE CONCOURS DU CENTRE NATIONAL DE LA RECHERCHE SCIENTIFIQUE

Éditeur : A. D. A. C.

Nouvelle Série, Tome XIV, Fasc. 3 1979

REVUE ALGOLOGIQUE

Fondée en 1922 par P. ALLORGE et G. HAMEL

Directeurs : P. BOURRELLY et R. LAMI

Secrétariat de Rédaction : M. RICARD

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LES DIATOMEES LACUSTRES PLIO-PLEISTOCENES DU GADEB (ETHIOPIE) SYSTEMATIQUE, PALEOECOLOGIE, BIOSTRATIGRAPHIE

par Françoise GASSE
(Ecole Normale Supérieure, 92260, Fontenay aux Roses, France)

210 pages, 62 planches, 150 références, broché.
Prix de souscription : 260 FF, parution : déc. 1979.

L'auteur étudie dans cet ouvrage les diatomées d'une séquence continentale, lacustre puis fluvio-lacustre, de 45 m d'épaisseur, d'âge plio-pléistocène (2.7-0.7 millions d'années), récoltées sur les hauts plateaux volcaniques d'Ethiopie (2300 m d'altitude).

La première partie est consacrée à la description de la flore : 392 taxons appartenant à 31 genres ont été inventoriés. Cette étude taxinomique contient la description de nombreux taxons nouveaux ou intéressants et s'appuie sur 62 planches photographiques réalisées en microscopie photonique et électronique à balayage : près de 900 clichés représentant 265 taxons et leurs variations spécifiques.

Dans la deuxième partie, les associations successives des diatomées de la phase franchement lacustre (2.71-2.35 millions d'années) sont définies et interprétées. Ces associations sont très diversifiées et leur composition floristique s'explique par l'évolution écologique du milieu et l'âge ancien des dépôts. Des fluctuations climatiques globales paraissent, en partie, responsables des changements écologiques enregistrés par les diatomées. L'ancienneté de la flore se manifeste principalement dans le groupe des centriques (*Melosira, Cyclotella, Stephanodiscus*) et se traduit par l'abondance d'espèces éteintes ou d'aire biogéographique actuellement restreinte. Leur valeur biostratigraphique est soulignée par l'analyse de leur paléogéographie et paléostratigraphie mondiale. Certaines espèces vivant encore actuellement présentent des caractères archaïques et l'existence de nombreuses formes intermédiaires reflète une période d'intense évolution spécifique.

L'analyse des diatomées lacustres plio-pléistocènes du Gadeb est la première étude d'une séquence épaisse, continue et très bien située dans le temps par de nombreuses datations radiométriques. Seul, ce type d'étude permet des corrélations interrégionales et intercontinentales pouvant apporter des conclusions générales sur l'évolution des milieux continentaux, la paléobiogéographie et la phylogénie des diatomées. De plus, la richesse et la qualité de l'illustration en font un important document sur la systématique et la biogéographie des diatomées lacustres plio-pléistocènes.

LES DIATOMEES LACUSTRES PLIO-PLEISTOCENES DU GADEB (ETHIOPIE)
SYSTEMATIQUE, PALEOECOLOGIE, BIOSTRATIGRAPHIE
par Françoise GASSE

BON DE RESERVATION

Ce bon de réservation est destiné à préciser le nombre de personnes intéressées par l'achat de cet ouvrage. En juillet 1979, les personnes ayant renvoyé ce bon recevront un bon de commande leur permettant d'acquérir ce livre au prix de souscription.

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PLIO-PLEISTOCENE LACUSTRINE DIATOMS FROM THE GADEB (ETHIOPIA) SYSTEMATIC, PALEOECOLOGY, BIOSTRATIGRAPHY

by Françoise GASSE
(Ecole Normale Supérieure, 92260 Fontenay aux Roses, France)

210 pages, 62 plates, 150 references, bound.
Subscription price : 260 FF, issue on Dec. 1979.

In this paper, the author presents the diatom study of a continental (lacustrine and fluvio-lacustrine) sequence of 45 m thick and dated from 2.7 to 0.7 million years. The geographical and geological setting of the sediments, taken from the volcanic uplands (2300-2350 m in elevation) of Ethiopia, is briefly described in the introduction.

The first part is relative to the systematical study of the rich diatom flora : 392 taxa belonging to 31 genera. This taxonomical chapter is based on 62 photographic plates in photonic (28 plates) and scanning microscopy (34 plates). 265 of the taxa are represented, taking into account their specific variations.

In the second part, the successive diatom assemblages of the entire typical lacustrine phase (2.71-2.35 million years) are defined and interpreted. Their floristic composition depends on the ecological evolution of the biotope and on the Plio-Pleistocene age of the deposits. Ecological changes deduced from the diatom flora seem to be partly due to global climatic fluctuations. The age of the flora appears clearly through the Centric diatoms (*Melosira, Cyclotella, Stephanodiscus*). It is registered by the abundance of species now extinct or with today restricted biogeographical area. The study of their paleogeographical distribution and their stratigraphical range throughout the world indicates they are excellent biostratigraphical markers. Many species present transitional forms indicating that the Plio-Pleistocene was a period of intensive specific evolution.

The analysis of the plio-pleistocene lacustrine diatoms of the Gadeb represents the first diatom study on a thick and continuous continental sequence set within a radiometrically dated time scale. Only this type of study allows interregional and intercontinental correlations and will lead to general conclusions concerning the ecological evolution of the continents, the paleobiogeography and the phylogeny of the diatoms. The numerous illustrations make this an important work for the systematic and the biostratigraphy of the plio-pleistocene lacustrine diatoms.

PLIO-PLEISTOCENE LACUSTRINE DIATOMS FROM THE GADEB (ETHIOPIA) SYSTEMATIC, PALEOECOLOGY, BIOSTRATIGRAPHY

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MICROSTRUCTURES IN METEORITES

or Fossilized Ideas About Ideal Fossils

George Claus*

RÉSUMÉ. – Les termes «éléments organisés» furent introduits en 1961 pour désigner des microstructures, découvertes dans des météorites carbonées du Type I, et censées représenter des restes de microfossiles. Bien que ces structures aient été facilement découvertes dans les laboratoires où de telles météorites étaient examinées, différents chercheurs fournirent des explications variées concernant leur nature et leur origine. Dans cet article sont présentés les résultats des examens microscopiques électroniques à transmission et à balayage de fragments intacts de microstructures provenant de la météorite d'Orgueil. Ces observations décrivent des éléments organisés intimement enrobés dans une matrice constituée de roches, ce qui exclut totalement l'hypothèse d'une contamination pour expliquer la présence de ces éléments. Ces éléments ont été analysés par diffraction aux rayons X et les résultats obtenus indiquent que certains de ces corps contiennent du carbone ainsi que des éléments minéraux. La discussion finale fait ressortir la difficulté de préciser l'origine des fossiles précambriens et des microstructures météoritiques.

ABSTRACT. – In 1961 the term «organized elements» was introduced to designate indigenous microstructures discovered in Type I carbonaceous meteorites, which were believed to represent remains of microfossilia. Although these structures were easily found in laboratories where such meteorites were investigated, different researchers offered varied alternative explanations as to their nature and origin. They were identified as mineral grains, terrestrial contaminants, prebiological organic structures, or any combination of these. Later extensive work has demonstrated that the question of terrestrial contamination had been greatly overemphasized, and the claim that the majority of the organized elements are mineral grains is no longer asserted. The currently favored idea is that they are organic, indigenous forms, but are the result of abiogenesis. Results of transmission and scanning electron microscopic investigations on intact fragments of the Orgueil meteorite are presented, depicting organized elements intimately embedded in the matrices of the stone, thus excluding the possibility that these objects are contaminants. The elemental composition of individual microstructures is defined with energy dispersive X-ray analysis, and it is shown that some of the bodies, even after HF treatment, contain carbon as well as minerals, the latter having elemental abundances comparable to those of the stone, attesting both their organic and indigenous nature. Fine morphological characteristics of different types

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Rev. Algol., N. S., 1979, XIV, 3: 197-233.

of structures are illustrated and described, and the question of their biogenic nature is raised. After discussing the various proposals for establishing the biogenecity of many early Precambrian microfossils, it is concluded that unless new criteria are devised, it is equally impossible to prove the vital origin of simple Precambrian fossils as that of the organic meteoritic microstructures.

This paper has a threefold purpose: to recount the furor which erupted after the suggestion was made that the organized elements in carbonaceous chondrites are indigenous microfossils; to present results of ultrastructural investigations which are not incompatible with the correctness of this interpretation; and to examine whether, within the framework of prevailing scientific dogmata, proof for this contention could be arrived at by any means.

INTRODUCTION

About 17 years ago to date, together with a colleague of mine, I published a paper in the *British scientific weekly Nature* in which - having conducted some investigations on two Type I carbonaceous chondrites, the Orgueil and Ivuna meteorites - I had the temerity to propose that these bodies carry remains of autochthonous microfossils of extraterrestrial origin (1). This statement initiated an explosive controversy which has not yet been settled, at least not to the satisfaction of all parties concerned. The ensuing debate was often acrimonious, and by the late 1960s it appeared advisable to let matters stand where they were, and to temporarily withdraw from the battle.

In 1961, the idea of finding extinct life forms in certain meteorites did not seem particularly strange to me; in fact, for a time I could hardly comprehend the viciousness of many of the subsequent attacks, which I thought quite unwarranted by the nature of our results. After all, it had been known for close to 100 years that the Orgueil meteorite contains considerable quantities of organic carbon compounds (about 5% by weight), and these had been identified by CLOEZ as similar to terrestrial humates a few weeks after the stone fell, in France, in 1864 (2, 3). The studies of BOATO (4) demonstrated that this meteorite (and three others, known together as WIIK's Type I carbonaceous chondrites (5, 6)) contains as much as 20% water, in the main of extraterrestrial origin; and as it was accepted at that time, on the basis of the mineral suite present in the stone, that the parent body had had a low temperature, aqueous environment (7, 8), there seemed to be but little difficulty in the interpretation offered for the results of our microscopic studies. What I was not yet aware of at that time was the fundamentally conservative nature of the scientific endeavor itself - a factor frequently alluded to in historical or philosophical analyses on the process of discovery (9, 11) - but which, as a practicing member of the scientific community and also a curious member of the human race, I could not accept. It happened, however, that the publication of our simple observational results had implications far beyond the assertion that microfossils had been found in two meteorites: a number of cherished and well-established hypotheses regarding the origin of life, of meteorites, and even of the solar system would have had to be modified had these findings been accepted.

In retrospect, it seems evident that one major obstacles to acceptance was the purported history of the meteorites' parent body. Since it is not the subject of this paper to review the divergent concepts about the parent body, it should only be mentioned that meteorites are thought to originate in the belt between Mars and Jupiter as a result of collisions among asteroids, the latter representing the condensation products of primordial gases of the solar nebula which never formed a planet. Carbonaceous chondrites are taken to be the most primitive matter in the solar system, as they have supposedly undergone the least amount of chemical fractionation since the time of their accretion, shown by their elemental distributions, which are closest to those of the sun. The fact that no single hypothesis about the origin of meteorites can satisfactorily explain the peculiarities of the carbonaceous chondrites - especially the petrology of the Type I stones - is known (12), but not much discussed. As asteroid-sized bodies could not hold an atmosphere and liquid water for any appreciable time, the argument goes, and since they are so far from the sun that their free energy is slight, conditions which would have permitted the development of life on asteroids were well-nigh impossible. Of course, the synthesis of the improbably high quantities of organic matter in carbonaceous meteorites is also unlikely under the presumed conditions. As SAGAN has written: «About $10^{-2}\%$ of all meteoritic material which has fallen on the Earth is organic matter. For comparison, the mass of the Earth is 6×10^{27} gm; the mass of the biosphere - all the living and non-living organic matter on Earth - is a few times 10^{17} gm. Thus, the Earth is composed of something like $10^{-8}\%$ organic matter, and most of this is of biological origin. Why is there a million times more organic matter in the asteroid belt than on the Earth?» (13, p. 335).

An alternative concept - frequently debated and equally frequently rejected - is the hypothesis that the asteroids are the remaining debris of a once-existing planet which exploded as the result of some unknown cause. The first serious consideration of this problem in recent years is represented by the work of OVENDEN (14), who has shown that discrepancies between the orbital eccentricities of the planets in our system and the masses of the presumed perturbing bodies could best be resolved by assuming the prior existence of a massive planet between Mars and Jupiter. The means by which such a large body could be disrupted are unknown. OVENDEN wrote: «Two major problems remain. First, what physical process caused the sudden dissipation of A (the huge mass which should be in the present asteroidal belt)? From the point of view of the dynamical arguments presented here, it is porbably true that A was always in the form of a ring. But while it may be difficult to «explode» a planet, it would seem even more difficult to dissipate a ring suddenly after it has been quiescent for 4.5×10^{9} yr. Second, only ~ 0.1 $M_{\oplus}$/Earth mass/ seems now to reside in the asteroid belt. What has happened to the other 89.9 $M_{\oplus}$?» (14).

A confirmation of this work was supplied in 1976 by Van FLANDERN, who showed that backwards integration of the previous perihelion passages of 60 well-observed comets of long period demonstrates that most of these intersect at nearly the same point. He concluded: «Taken in conjunction with the already-existing evidence, these new results leave little room to doubt that a Saturn-sized planet did exist between Mars and Jupiter 16 million years ago, and then violently exploded». (15).

It is, of course, beyond my competence to judge the correctness of these findings. It may be remarked, however, that were it true that a planet of 90 times Earth mass existed in the present asteroidal belt 16 million years ago, then life could indeed have developed at such a distance from the sun, and it would be feasible that its remains should reach the Earth embedded in the carbonaceous meteorites. *En passant*, it was recently emphasized that carbonaceous chondrites have approximate cosmic exposure ages of 15 million years (16).

The identity of the organized elements

In our original report, we gave the name «organized elements» to the microstructures observed in the investigated meteorites, and for the sake of simplicity and purposes of identification, we described five types, or broad morphological categories. As alternatives to our interpretations, others offered variations or combinations of four explanations relating to the nature and origin of the organized elements.

1) In the initial stages of the debate, the main argument of the critics was that the organized elements were terrestrial contaminants - at least all but the smallest and simplest, relatively featureless spheroids, which were said to be mineral grains (17-19). The most frequently voiced view was that those organized elements which exhibited complex morphologies were spores or pollen grains originating either in the laboratory, or having entered the stones at the place of fall or during museum storage.

2) A second interpretation - especially favored later in the debate - was that practically all of the organized elements were actually mineral grains, which we had simply mistaken for fossils on account of their «biological appearance». Among the analytical techniques applied to individual organized elements, or such which were embedded in the minerals of the stones, was an electron microprobe study undertaken by myself and colleagues (20). The results unquestionably demonstrated that the forms in question had mineral compositions which corresponded to those of the meteorite, and that they were indigenous to the stones. After publication, these findings were interpreted as admissions on our part that the organized elements are simple mineral grains (19, 21). Furthermore, those objects which has been demineralized in order to demonstrate their organic matrix were claimed to represent the unorganized organic matter of the meteorite (22). Thus, either mineral grains became endowed with complex morphologies (23), or objects clearly containing organic

matter, which had had sufficiently complex morphologies to be earlier seen as probable terrestrial contaminants (19, 21), suddenly became featureless. This chemical probe of selected, individual organized elements showed that they were indeed mineralized (in our view, fossilized) objects. The result was that their indigenous nature was then acknowledged, but their biogenicity denied. Such reinterpretation seems to rest on circuitous logic and to ignore completely the fact that three-dimensionally preserved fossilia (as distinct from imprints) are, in most cases, permineralized.

It is also of a certain historical interest that a single object, the «type 5 organized element,» was definitely identified by different critics as an indigenous mineral grain (a rare pseudomorph of troilite) by MUELLER (23) and as an altered terrestrial contaminant (a ragweed pollen grain) by FITCH and ANDERS (24). This disagreement among our opponents was authoritatively settled in 1966 by BOSTROEM and FREDRIKSSON (25) in favor of Mueller's view. These authors rejected Fitch and Anders' pollen grain identification, since it had been based «entirely on morphological argument». That Mueller's claim about the disputed form being a troilite particle had also been based exclusively on morphological interpretation was not mentioned by the later authors.

3) Still other critics recognized that some of the organized elements might indeed be indigenous, and might consist at least partially of organic matter. MORRISON, for instance, who was impressed by the varied crystalline growth patterns of ice snowflakes, hypothesized that the meteoritic organic matter may similarly show elaborate structures, without being biogenic (26). In a series of papers from the Soviet (22, 27-29), organic matter in the stones was described to be present in three forms: a) dispersed, oily bituminous matter; b) small conglomerations around minute mineral condensation nuclei; and c) coatings around larger mineral grains. All of these inclusions were obviously abiogenic.

4) It was perhaps only to be expected that investigators involved in experimental synthesis of prebiotic organic forms thought that the organized elements were, in effect, indigenous masses of organized but non-biogenic objects, resembling their own laboratory products. Thus FOX proposed that at least the simpler forms were similar to his proteinoids (30, 31), and PERTI (32) suggested that the *Jeevanu* or «particles of life» synthesized by BAHADUR, PERTI and others of their group (33, 34) had remarkable resemblances with the organized elements found in meteorites.

5) At a rather late stage in the debate, two papers appeared by ORCEL and ALPERN (35, 36), which actually denied the very existence of structured aggregates of indigenous organic matter in the stones. In their first publication, the authors dismissed our findings as obvious contaminants and proceeded to show in thin section and ultrathin section studies that the inclusion bodies they saw were all minerals. Their second paper was a microprobe analysis of the distribution of organic carbon in the Orgueil and the Cold Bokkeveld stones. They found «... une dispersion assez régulière du carbone dans le ciment

silicate. . .» (36). However, they admitted that, because of the limitations of their technique, they could not state that this dispersion is absolutely homogenous, i. e., that, there is only amorphous carbon present.

One interesting example of how these various reinterpretations were combined - sometimes on the basis of distortious of our own findings - is represented in a 1964 publication of VDOVYKIN (22). Following his own description of certain mineral phases in the Orgueil meteorite, which he in part identified with the organized elements, he wrote, in connection with our 1963 microprobe study, «. . . there appeared a paper by NAGY et al. . . . which fully confirms the conclusions presented above. The authors show by means of local X-ray analysis that the globular microstructures in the Orgueil and Ivuna chondrites, morphologically identical with the organized elements, contain up to 40% Fe, 6% Mg, 10% Si, 20% Ca, 2% Ni, up to 10% S and 3% Cl, are essentially hydrous ferromagnesian silicates (chlorite - serpentine). Some of the particles contain no elements with $Z > 11$; these are inclusions of carbonaceous matter.» (22). It is remarkable that the Russian author could so blatantly misread figures presented in a table, where the elemental composition with Z number above 11 of 21 isolated, untreated organized elements was presented, plus that of three untreated objects in thin sections, three demineralized pellicles, and a mineral control. No object studied contained more than four of the above-named elements, the majority only two: iron and chlorine, or iron and nickel. One object out of the 28 analyzed showed calcium and sulphur, and it was pointed out that this was probably a gypsum-containing particle. The high magnesium and silicon values mentioned were taken by Vdovykin from the chlorite mineral which had been used as a *control*. Vdovykin's «inclusions of carbonàceous matter» were, of course, those isolated objects which had been demineralized by HCl treatment. As though all of this were not enough, it may be noted that the author had earlier dismissed the organized elements as terrestrial contaminants through an equally blatant misrepresentation of two of our earlier publications (1, 37), as well as those of STAPLIN (38) and of PALIK (39). It goes without saying that in all of these works, controls were run for laboratory contaminants and for contaminants present in the stones. In this connection, VDOVYKIN wrote: «. . . the carbonaceous chondrite contains. . . a certain amount of biogenic contaminations which cannot be completely removed because of the porous character of carbonaceous chondrites. These impurities may be spores, pollen grains, and even paper fibers described as «organized elements». . .» (22). *None* of the papers cited ever identified these items as organized elements: the authors had simply pointed out that a few spores, pollen grains and cellulose fibers were occasionnally observed in preparations as obvious terrestrial contaminations.

This particular paper was probably unique in combining three explanations of our findings - i. e., that everything which we had considered as an organized element was a mineral, a terrestrial contaminant, or an aggregation of featureless organic matter - and in simultaneously misrepresenting our work by incorrectly inferring that we ourselves had proven these points in our own studies. But while this publication represents an extreme case, it was not entirely atypical for the period.

By the 1970s, the situation respecting organic inclusion bodies in carbonaceous chondrites had changed considerably. The assertion that the stones had undergone large-scale contamination by terrestrial organisms during their post-fall histories was no longer a primary claim, since in the intervening years the results of extensive studies had shown that the number and weight of contaminating structures and/or microorganisms were unexpectedly low (40-43). Furthermore, the idea that our simpler forms (organized elements of types 1 and 2, which constituted the bulk of the numerical counts) were obvious mineral grains, was thrown into doubt by two studies (44, 45) appearing in 1973 and 1971, respectively. The first of these was a fluorescence investigation of embedded fragments of the Orgueil meteorite, in which the authors demonstrated that organic aggregates of $< 2\mu m$ size are present in massive numbers in the amorphous matrix of the stone. The researchers also published transmission electron micrographs of submicronsize particles which they took to correspond to the fluorescing material. In the second paper (45), a palynological study of the Orgueil stone, the presence of large numbers of indigenous, organised, organic particles in the 2 to $50\mu m$ range, with a majority about $9\mu m$ in size, was demonstrated. This latter paper will be treated in some detail later.

In the context of these renewed assertions that indigenous, organized, organic particles are indeed present in Type I carbonaceous chondrites, the results of transmission and scanning electron microscopic investigations of the Orgueil meteorite are presented below.

MATERIALS AND METHODS

The Orgueil meteorite sample originated from the collection of the Montauban Museum in France, and was obtained through the courtesy of Dr. A. Cavaillé. It represented originally a complete stone with fused crust weighing ~ 80g, from which a 49.27 g piece was brocken off. This rock has been kept since 1962, wrapped in aluminium foil in a hermetically-sealed glass jar. Several prior experiments have been conducted on specimens from this stone (20, 41, 45,46, 47). Fragments were separated from the breakage surface with sterile instruments, and a selected piece was placed between aluminium foils and pressured by the thumb. Particles from the fragment thus crushed, in the size range of 1 or 2 mm or smaller, were picked out with a sterile forceps for the investigations.

For the transmission electron microscopic (TEM) studies, the meteorite grains were impregnate with and embedded into Spurr low-viscosity medium (Polysciences, Inc., Warrington, Pennsylvania), using the standard formulation (48). Infiltration was carried out for 24 hr under continuous agitation on a rotary shaker, while oven-dry gelatin capsules served as casts for embedding. Curing took place at 70°C for 24 hr. No dehydration or staining of the specimen was undertaken. Silver sections were cut on a Porter-Blum MT 2 ultramicrotome using a 3 mm edge Dupont diamond knife. The ribbons were mounted on 300 mesh Formvar coated grids, and were viewed in a Phillips 200 electron microscope at 60 KV. Pictures were printed on Kodak polycontrast paper.

Two types of preparations were made for the scanning electron microscopic (SEM) investigations: intact meteorite grains were mounted on the usual aluminium discs, gold coated to $\sim$ 300 Å thickness, and viewed in a Cambridge «Stereoscan» microscope, at 20 KV, equipped with an energy dispersive X-ray analyzer (EDAX International) operated from 9 to 50 KeV, with a resolving power of 800 Å ^{2} and elemental detection capability of 10^{-18} g above $Z > 5$; all elements present appearing in a simultaneous display. This instrument has a built-in computer which automatically strips the display from noise, high background levels, and overlapping secondary peaks, and determines peak heights in relation to an internal standard (49). Elemental analyses were performed on each selected object and on its surroundong area.

In the second type of preparation, the sample holder disc was covered with a sterile polyethylene sheath, upon which were placed the meteorite fragments. The preparation was then etched with 48% HF. After drying under cover (about 24 hr), the samples were gold coated and investigated as described above. This treatment permitted the *in situ* visualization of HF resistant organic remains. No washing of these preparations was attempted; nor was the HF treatment followed up with HCl extraction to remove the rest of the inorganic material.

A piece of the Gunflint chert served as a positive control in these experiments. It was obtained with the cooperation of Dr. A. A. Ekdale, and came from the collection of the Department of Geological and Geophysical Sciences, University of Utah, Salt Lake City. It originated from the Biwabik Banded Iron (Minnesota) portion of this formation, showing the typical stromatolitic structure. This particular shale has been dated at 1.8 eons. Petrographic thin sections, kindly prepared by Prof. Dr. A. Papp, Micropaleontological Institute, University of Vienna, Austria, exhibited the typical Gunflint flora of filaments and unicells (50, 51). The chert was treated identically to the meteorite samples, with the exception that no TEM studies have been performed on it.

During all sample preparations, extreme measures at cleanliness, as usual with meteoritic studies, were adhered to, the details of which have been reported several times elsewhere (2, 37, 46, 47).

RESULTS

Transmission electron microscopic studies

The results of the transmission electron microscopic studies were in agreement with earlier findings. The minerals within the matrix (by which is meant the inorganic or organic amorphous or slightly crystalline matter) exhibited a great variety of forms. Lathe-like filaments, as described earlier on the EM level (12, 52-54), embedded in the common non-crystalline matrix (see at A), are illustrated in fig. 1. Flaky, layer-lattice silicates have been found, a specimen of which is shown in fig. 2. It is similar to those depicted by previous workers (53-56). On fig. 3, a portion of the meteorite matrix with fewer crystalline structures can be seen, although the curved edges of the typical silicate minerals are plainly visible in the lower middle portion of the picture (area C). Rhomboidal crystals occur on both sides (underneath A), while clearly amorphous material is present in the lower left corner (B). What might be magnetite globules (highly electron-dense, more or less spherical structures exhibiting some hexagonal faceting) occupy the upper right corner (D). In the center of the figure is a microstructure with an electron-transparent interior, delimited from the surrounding material with what seems to be a double wall, at least on its right side. It has the following dimensions: length, 0.51μm; width, 0.36μm.

The pseudohexagonal shape of this form should not be confused with those structures first described from the light microscope and named by STAPLIN as *Caelestites sexangularis* (38), and in subsequent studies designated as «box-like objects» (57-59). (Findings relating to such objects will be discussed in another publication). The present form and most of those on the next plate seem to be similar to the organized organic matter found in ultrathin sections of unextracted meteorite stones by Van LANDINGHAM et al. (60), and later by ALPERN and BENKHEIRI (44). The majority of these objects have apparently one or two less electron-dense areas in their centers. It should be pointed out that such transparent areas could hardly represent a mineral grain, around which the organic matter would have condensed (as presumed by the French authors (44)), since such a crystal would have shown up in the thin sections. No materials which could have served as condensation nuclei are evident in the published micrographs.

At low magnification, all the individual bodies on Plate 2 with the exception of fig. 13 could be identified with one or another of the forms in the published micrographs of these two teams of authors. At higher magnifications, however, details emerge which have not been described by the previous investigators. In fig. 4, 6, 7, 8, and 9, structures of the same object are presented at three magnifications. The body might have had either a spherical or an elliptical form, cut somewhat tangentially, with a long axis of 0.56μm and a short axis of 0.46μm. Fig. 4 shows that the structure is completely embedded in the undisturbed mineral matrix, which exhibits relatively poor crystallinity at this place. Comparing the pores in the matrix with the size of the object, it is obvious from this and other micrographs that the pore size of the Orgueil meteorite is typically much below the 1μm diameter; thus it is impossible that even these relatively small structures should have become lodged in the stone as a result of contamination.

In fig. 6, the object is shown at higher magnification, permitting the observation of the spines on the external surface of its wall (left side); the layered wall, best visible on its right; the attachment of the stalk; and the peculiar, centrally-located vesicular system. The average height of the spines is 30nm, and some show either a canal with an internal diameter of 3 nm, or at least a pore in their tips (see arrows in fig. 7). Apparently the spines cover the whole surface, with the exception of the area where the stalk is attached. The wall is double layered (fig. 8), with great similarities to the structure of gram negative microorganisms, especially that of *Cyanophyta*; therefore, the designations of YOST (61) will be used. L4 + L3 (Pl) = 11 nm; L2 + L1 = 4 nm; Cm = 3 nm. Thus, the total wall thickness is 18 nm, approximately one-half that of a typical blue-green algal cell wall (62). One has to point out, however, that no terrestrial bacterium or blue-green alga is known which would have such a spinous cell envelope.

The attachment of the stalk to the object is shown enlarged in fig. 7. It is evident that the stalk is a cylindrical structure, with a broadening collar at the place of attachment to the body. The diameter of the stalk itself is 140 nm; while at the top of the neck it is 180 nm wide. It penetrates through the wall of the body to a depth of 35 nm. Its total length cannot be established, but its visible length is 0.56 μm.

In the center of the body a peculiar structure, composed of at least six vesicles, is visible (fig. 9). The largest measurement of the total complex is 0.2μm, and the length of the elliptical upper vesicle, which is the best preserved, is 80 nm. At least three of the vesicles have spots of electron-dense material within their centers, and they also possess their own limiting membrane, measuring, where visible, 3nm. Microtubule-like branching canals seem to pass from the vesicles to the surroundings (fig. 9, arrows).

Fig. 5 is taken with the same magnification as fig. 4, but from a different preparation. It represents basically the same kind of object, except that it is apparently a mirror image, with the remnants of the stalk (at arrow) attached on the lower right corner. The diameter of the body is 0.5μm; the height of the well-visible spine in the upper left corner is 48nm. Where the wall can be seen, its structure and dimensions are the same as those of the previous object. The visible portion of the stalk has a diameter of 74 nm, with a width at the collar of 102 nm, and a length of 48 nm.

Fig. 10 represents an object resembling a terrestrial yeast undergoing budging. Its total length is 0.46μm, that of the main body 0.3μm, and of the bud 0.16μm. The width of the main body is 0.18μm, and of the bud 0.14μm. The wall is similar in structure to those of the previously-described objects, but it is clearly visible only on the lower side of the main body; at other places it is partially or completely covered with some extraneous material. Within the main body there are two, more electron-dense profiles, one circular (above and to the right of A) and the other elliptical (above and to the right of B): The circular feature has a diameter of 42nm. The elliptical structure, at high magnification, is seen to be composed of two vesicles, each with an internal electron-dense spot. They closely resemble those of the object in fig. 9. The length of the better preserved one is 74 nm.

A fine, reticular, fibrillar network is discernible in the central portion of what appears to be the bud, mimicking DNA strands. The width of these fibrils, which are of two types, is 1.5 and 2 nm, respectively (about the same as blue-green algal DNA (63)).

The object in fig. 12 is, in general, similar to those in fig. 5 and 11, except that it has several small protrusions on its surface. Fig. 13 shows what is most probably an euhedral magnetite crystal. It is the same approximate size range as the two bodies in fig. 11 and 12, having a diameter of 0.23μm. The electron-opaque nature of this mineral clearly distinguishes it from the organic material.

Fig. 14 to 16 depict the cross section of an object with an exceedingly thick internal wall layer. The external layer (L4 + L3), best seen at arrow, has approximately the same thickness as in the form in fig. 4, i. e., 11 nm. However, L2 + L1 varies from 54 to 88 nm with an average of 66 nm. Cm = 6 nm; the average total wall thickness is ~ 80 nm. (It should be noted that the thin electron-light layer surrounding the whole object is not part of the wall, a fact which can be ascertained from its continuation around the sickle-shaped white area above the body). The length of the object is 0.66μm; its width, 0.54μm. On its lower left side, the body shows a neck with a base of 240 nm and a height of 88 nm, resulting in a total wall thickness of 168 nm in this area. A feature within the wall is suggestive of the presence of at least one canal traversing it, connecting the inside of the body with the exterior. This is manifested within the neck on the lower left side (above A), where the electron lucidity of the area, compared with the rest of the wall, is indicative of the presence of a channel just below the plane of sectioning. The interior of the entire form is filled with unidentifiable debris. The structure of the left of the neck (between arrows) does not belong to the body, but is part of the surrounding matrix.

Fig. 15 is an over-illumined view of the body and its surrounding at the place of junction between the external object and the neck (arrows). It is clear from this picture that the object is merely appressed to the body.

The light, sickle-shaped area above the form was apparently an empty space prior to impregnation with the resin. However, the slight opacities in it indicate that it was penetrated by the embedding medium. Thus, the body was not torn from its matrix during sectioning, but was moved from its original position before processing. Fig. 16 shows that the object indeed fits the space from which it was displaced, proving that originally it was intimately embedded in the matrix, but was turned by approximately 180° (note location of neck canal at A). During displacement, an electron-dense granule apparently became pressed into the wall (see at B).

As a whole, this object is closely reminiscent of a terminal heterocyst of a Nostocacean Cyanophyte, such as a member of the *Rivulariaceae*. However, it also resembles a cross section of the abundant marine fossil of unknown affinities, *Tasmanites sommeri* Winslow.

Scanning electron microscopy

Some of the findings of the SEM investigations are illustrated in Plates 4, 5, and 6. Plate 4 depicts objects which are, for the most part, familiar from the literature. Fig. 17 and 18 compare two spherical bodies of approximately equal diameter (6.8 and 6.2μm, respectively), one (fig. 17) after HF treatment, the other from native preparation. The irregularities on the surface of the first body seem to be the result of deposition of materials after the evaporation of the acid, and should not be mistaken for layering. Some surface layering can, however, be discerned in the structure shown in fig. 18 - a feature found also in the SEM picture of one of the acid-treated «hollow spheres» from the Orgueil meteorite of ROSSIGNOL-STRICK and BARGHOORN (45) (Plate 3, fig. 2). The indigenous, organic nature of objects of this type has been established by these investigators, and is now confirmed: they contain carbon, in addition to iron, but hardly any silicon. Whether they are prebiological or biogenic is still an open question.

In fig. 19, a discoidal body with notable surface structure is shown. Its diameter is 5.6μm; height, 2.6μm. Several similar structures have been illustrated by JEDWAB, both from petrographic thin sections (64) and from density-gradient separated material viewed by means of SEM (65). This author interpreted such forms as one of several extraterrestrial types of magnetite. In fig. 20 the EDAX spectrum of this object is presented, taken at 10 KeV. The body unquestionably contains considerable quantities of iron, but the relative amounts of aluminium, silver, potassium and sulphur make it an interesting species of magnetite from the point of view of composition as well as that of morphology.

The well-delineated objects in fig. 21 (measuring approximately 4μm in length) are basically composed of iron, with some traces of copper. (These were the only structures found in the whole investigation which showed the presence of copper). Since oxygen could not be determined, it is impossible to decide whether these particles represent magnetite or limonite. However, the peculiar feature of radiating spokes (underneath A) in the object at the left of the figure is quite reminiscent of similar details described several times from petrographic sections in the light microscope and held to be characteristic for meteoric magnetite (12, 25, 35, 64, 65).

Another supposed extraterrestrial form of magnetite, as described by JEDWAB (65, 67), is shown in fig. 22. Here are seen submicron-size particles, identical to each other in dimensions, forming an aggregate of irregular shape. According to JEDWAB, such «magnetite aggregates» usually develop in cavities where they cover the concave walls. The picture shows that these particles occupy a highly convex surface, and they continue on the right side, below the area visible in this micrograph. The individual particles have diameters of 0.1μm, are connected with each other by some kind of fibrillar material, usually have a prominent spot on their surface, and sometimes are enveloped jointly in a more or less transparent mass (see under A), which is much more easily recognized at lower magnification. Some apparent faceting is observable, interpreted in similar aggregates by KERRIDGE (66) and by NAGY (12) as representing possible crystal faces of magnetite. On account of their small size, KERRIDGE could not define the elemental composition of the individual grains by microprobe; but since he observed occasional concavities in their surfaces, he pointed out that such structures occur in terrestrial spinels. It should be noted, on the other hand, that the faceting on the surface of these particles is not necessarily indicative of crystalline nature, since it could equally well be the result of compression.

According to our studies, these objects are definitely not magnetite, as we were able to take elemental spectra from individual granules. The composition of these forms (averaged from five determinations), expressed relative to Fe as unity, is as follows: $Fe_{1.00}Si_{0.74}Al_{0.24}Mg_{0.22}Ca_{0.22}Ag_{0.11}Mn_{0.08}Ni_{0.07}Cl_{0.08}C_{0.26}S_{trace}$. The composition of the particles would seem also to rule out a number of other possible mineral identities.

In fig. 23, on the other hand, may be seen individual granules of similar size (from 0.2 to 1.2μm), scattered in the matrix among other mineral grains, which seem from their elemental composition to be indeed magnetite particles.

Fig. 24 and 25 on Plate 5 depict some highly siliceous objects embedded in silica matrices - the first from an untreated Orgueil meteorite specimen; the second from an untreated fragment of the Gunflint chert. The texture and cleavage patterns of the matrices are remarkably similar, as are also their elemental compositions. This type of almost pure silicate matrix, which does occur in Orgueil and is suggestive of the chalcedony of the chert, contrasts sharply with the apparently layer-lattice silicate matrices shown in fig. 18 and 23.

A third and again fundamentally different type of matrix in Orgueil may be discerned in fig. 26 and 27. In the former, a spinous object is also visible, apparently torn out from its matrix, as evidenced by the hole beneath it, in which are retained some of the spines (at B). This spheroid has a diameter of 2.4μm, and the length of the spines varies from 0.3 to 0.6μm, with an average diameter of 0.1μm (68). Its immediate surrounding does not show much surface structure, but lower magnification (fig. 27) reveals that the body is lying on top of a meteorite fragment. The darkness of this figure is the result of the deep location of the entire structure, which is well below the uppermost surface of the fragment, the latter being indicated by the ridge (at A) in fig. 27. B designates the area in the hole from which the EDAX readings were taken, and C the region of the matrix which was probed. The results obtained for the elemental compositions of the spinous body, the area of the hole, and that of the matrix are given in Table I. It is noteworthy that the material making up the side of the hole is intermediary in composition between that of the body and the pure matrix. This might result from the inclusion of retained spines in the analysis of the hole. The presence of silver in this matrix is also interesting, since it has not been observed in other matrices investigated, but rather appeared only in discreet particles. Here also, both the matrix and the object are carbonaceous.

Fig. 28 shows what appears to be a partially collapsed, fossilized spore from the Gunflint chert after HF etching. Its diameter is 11μm, and its height

Table I. — Relative Elemental Composition of Complex in fig. 27.

	Matrix	«Hole»	Object
C	0.11	0.12	0.17
Mg	0.02	trace	—
Al	0.08	0.06	0.07
Si	0.18	0.21	0.18
Cl	0.03	0.03	0.02
Ca	0.07	0.08	—
Ti	—	0.09	0.09
Cr	0.13	0.12	—
Mn	—	0.18	0.20
Fe	1.00	1.00	1.00
Ni	0.13	0.12	0.11
Ag	0.22	0.16	0.13
W	0.13	0.15	0.09

— : not found.

9.6μm. In a series of articles, BOUREAU (69, 70) demonstrated that most of the spheroidal structures found in Precambrian materials are stages in the agglomeration of bacteria, which eventually become surrounded with solidified mucilagineous matter to form distinct colonies. However, the structure depicted in this figure could not represent one of these forms, because even with very high magnification under the scanning electron microscope (50,000 x) no surface details other than the fact that the wall is porate and covered with small spines, about 0.1μm in height, can be visualized. The body has one visible dimple on its lower left side, 1μm wide and 0.8μm deep, and a protuberance on the right side of approximately the same dimensions. The general structure is very similar to the oospheres occuring in the *Vaucheriaceae*; although the fossil is only about one-sixth the size of that typical for extant members of the genus *Vaucheria*. It might, however, also represent a single, extinct tetraspore.

In fig. 29, one can see a dichotomously dividing portion of a filament from an HF-etched Gunflint fragment. In the foreground there are two parallel main branches, each measuring 35μm in width. Before bifurcation (at A), the filament is 60μm wide. Two side branches are present, one in the front (B) and the other coming from underneath the main filament (C), the first having a width of 10μm, the second of 20μm. The second side branch also bifurcates (at U), giving rise to two 10μm-wide filaments. Since there is no sign of cross walls, the entire habit of this structure is reminiscent of the syphonaceous organization of members of the Xanthophycean *Vaucheriaceae* family, or that of the green alga *Protosyphon*. However, the marked diversity in width exhibited among the main filament and the primary and secondary branches is a characteristic not found in any of the modern yellow-green or green algae. On the other hand, this habit is quite characteristic for certain *Florideaceae*, such as some *Ceramium* or, especially, *Bostrychium* spp. The extant representatives of these forms, however, are always multicellular.

Such highly developed plant remains as those depicted in fig. 28 and 29 have not yet been reported from the Gunflint formation. As mentioned above, the affinities of the filament are uncertain; however, its complex structure and large dimensions seem to attest its possible eukariotic nature (71, 72).

Although these samples were etched with HF, their EDAX spectra indicate that considerable amounts of minerals are still present. In addition to iron and other cations, quantities of silicon remain in these microfossils. Their excellent state of preservation is undoubtedly due to their thorough permineralization. The results of the elemental analyses are given in Table 2, together with those for the filament complex of fig. 34, Plate 6.

Table 2. — Relative Elemental Composition of Objects Depicted in fig. 28, 29, 34 and 35.

	28	29	35 Crystal	34 Main Filament	34 Matrix	34 Narrow Filament
C	0.17	0.19	—	0.21	—	0.35
N	trace	0.02	—	0.03	—	trace
Mg	0.02	0.04	—	—	—	—
Al	0.04	0.08	0.14*	0.12*	0.30*	0.17*
Si	0.25	0.16	0.30	0.20	0.16	0.12
S	0.06	—	0.22	—	0.14	—
Cl	0.02	0.06	—	—	—	0.11
Ca	0.03	0.09	0.16	0.06	0.12	0.07
Ti	—	0.11	—	0.12	—	0.09
Cr	0.06	0.11	—	—	—	—
Mn	0.04	—	—	0.19	—	—
Fe	1.00	1.00	1.00	1.00	1.00	1.00
Ni	—	0.05	1.16	0.18	0.07	0.14
W	0.06	0.08	—	—	—	—

— : not found; *: The high values may result in part from the fact that during storage the stone was wrapped in aluminium foil.

On Plate 6 are depicted only filamentous structures, some clearly minerals, others of debatable nature and origin.

The hollow filament shown in fig. 30 is from an HF-treated sample of the Orgueil stone. Its width is 1.2 μm, with a total wall thickness of 40 nm (68). Note that the double lines visible on the sides of the filament do not represent double layering, but are rather an optical phenomenon, resulting from the translucency of the object. The EDAX spectrum of this structure, when expressed in terms of Fe as unity, is as follows: $C_{1.2}N_{0.13}Fe_{1.0}Si_{1.0}Al_{1.0}Mg_{0.4}$.

The proportional expression of elements is somewhat misleading here, since the major elements (iron, silicon, aluminium) all gave very low absolute readings. Such was also the case with several other objects (to be illustrated elsewhere) which were apparently quite thoroughly demineralized by HF etching. The fact, however, that the major elements were found, together with carbon, in about equal proportions, indicates that this structure is indigenous to the meteorite.

The next figure (31) shows a filamentous form with a diameter of only 0.6 μm from an untreated Orgueil fragment. It is so intimately embedded in its surrounding matrix that it serves as a bridge across a fissure. This form is reminiscent of that shown by KERRIDGE (52, 53) and tentatively designated as sepiolite, an identification questioned by NAGY (12, 55). From the EDAX analysis of the object, it would seem to be mineralized organic matter, and in any case, is certainly not sepiolite, having the composition : $C_{0.2}S_{0.09}Fe_{1.0}Si_{0.09}Al_{0.22}Ni_{0.04}$.

Fig. 32 and 33 each depict rounded (A) and prismatic (B) filaments (C indicates location of matrix analyses), those of fig. 32 from an untreated Orgueil sample, and those of fig. 33 from untreated chert. The rounded forms have diameters of 0.8 μm. All five objects contain various proportions of iron and silicon (with the latter in dominance) and the matrices are almost completely silicaceous. None of these filaments contains any carbon, and they show only trace amounts of magnesium; thus, they do not appear to be sepiolite either.

In fig. 34, a group of two types of filaments can be seen. There are clearly septated, larger filaments, more visible towards the upper right side of the picture, on top of which a bundle of narrower filaments is lying. The whole assemblage is partially covered by finely crystalline matter, which is evidently the result of the recrystallization of the meteorite's matrix after HF treatment. The large filaments are 18 to 20 μm wide, with a narrow sheath on the one to the left, enclosing a trichome of 16 μm width, constricted at the cross walls; the cells are barrel-shaped, shorter than wide, 5 to 10 μm long, with end cells pointed. The exact shape of the end cells is not discernible because of overlaying material, but from the portions which are not covered, a pointed conical form can be deduced (see at A). The total length of the assemblage, which presumably corresponds to the length of the large filaments, is approximately 550 μm. With the exception of one or possibly two filaments (to the right of B), the other large filaments are collapsed. Whereas the left one is simply collapsed to a form a U-shape or a longitudinal burrow, the one on the right (to the left of C) is completely compressed, its end representing the probable remnants of a cross wall,, the presence of which is signified by the line of submicroscopic pores (visible only at high magnification, but here indicated by arrow) at the place of their junction. The sheath of the filament to the left is frayed at its end, and throughout its length shows a flaky, fragile structure. The filaments to the right apparently have no sheaths. The whole structure seems to have been heavily mineralized, as several breakage marks are present (for instance, to the left of D), suggestive of rigidity.

Two structures not belonging to the filaments have to be mentioned: at E is seen a bipyramidal prism in the lumen of a large filament (shown also in fig. 35 at higher magnification), predominantly made up of nearly equal amounts of iron and nickel (cf., Table 2). At F a pseudohexagonal object is visible, which is identical to *Caelestites sexangulatus* Staplin (38), or the «box-like» bodies of other investigators - forms very commonly found in Type I carbonaceous chondrites. As mentioned earlier, the description of these bodies from both TEM and SEM findings will be the basis of another paper.

The bundle of small filaments is composed of basically 1.5μm wide individual trichomes without regularly visible septae, the presence of which, however, is occasionally indicated (see to the left of G). The length of these filaments is up to 200μm; their ends are obtusely conic.

If terrestrial, both the larger and the smaller filaments would belong to the *Oscillatoriaceae* family, the broader ones representing the genus *Lyngbya* and the small ones *Microcoleus*. The unsheathed nature of the filaments to the right (at B) might suggest a primary state, and in that case one would be dealing with an *Oscillatoria*; on the other hand, if these represent only hormogonia, then they may, indeed, be *Lyngbyae*.

The facts that the top surface of the meteoritic matrix is visible around the bottom portion of the picture (H), on which the filaments are apparently lying, further that they are all covered with recrystallized minerals, are associated with a body known from this type of meteorite (*Caelestites*) and with an iron-nickel mineral (E), would all support the view that these structures are not terrestrial contaminants, but are indigenous to the stone. Their fragility and their individual EDAX spectra (Table 2) confirm that they are mineralized with elements present in the meteorite. The differences in elemental abundances among the matrix, the large filaments and the small filaments argue against the possibility that they became imbibed with these elements as a result of the HF treatment.

Forms corresponding to the major filaments were identified and described at the light microscopic level by PALIK (39, 43) and Van LANDINGHAM (42), from the Orgueil meteorite. The small filament was first recognized by PALIK (39) and photographed and shown by NAGY et al. (20), also from Orgueil.

DISCUSSION

The fine morphology of meteoritic structures

In the whole of the literature, there is only one work which is devoted specifically to the ultrastructural analysis of organic matter in intact carbonaceous chondrites with transmission electron microscopy on direct thin sections (60). There is a second paper containing several TEM micrographs (44), and four other publications showing at least one picture from untreated meteoritic sections.

The first micrograph seems to have been published by MANTEN in 1966 (71), the specimen having been prepared by the LKB laboratories of Stockholm. MANTEN does not give a description of the object, which is a small (0.3μm diameter) spheroid with an electron-translucent, homogenous internal area, showing an electron-light center. It is partially delimited from its surrounding by what might be called a wall. It is torn from its matrix, and the wall is missing on the detached side. This picture was republished by NAGY in 1974 (12). Also shown in NAGY's book are four micrographs prepared by ALGY PERSSON in 1963, depicting peculiar configurations in the matrix suggestive of preferred orientation. In 1966, NAGY published a paper (72) in which the micrograph of a tripartite object composed of three spheres was incorporated. An external layer, which might have been considered to be a wall, was present. The general structure of this form is highly reminiscent of some inclusions found in high temperature minerals and identified as such by NAGY himself, on the light microscopic level, from Precambrian basalts (73). It is probably for this reason that the early picture of the object no longer appears in the 1974 treatise (12).

Also in 1966, two electron micrographs appeared in the mineralogical study of ORCEL and ALPERN (35). One of them clearly represents small magnetite grains, whereas the authors could only speculate about the identity of the object on the second, which was too small to microprobe (0.3μm). In the text, they state that the body looks like a microorganism with an internal structure; however, they presume that it must be an olivine microchondrule, and the micrograph is already so captioned.

In 1973, ALPERN, together with BENKHEIRI (44), decided to publish several additional pictures obtained in 1966, but not included in his work with ORCEL of that date. In these micrographs, which contain electron-translucent particles assumed to be identical with the investigators' fluorescing particulate organic matter, it is interesting to note the presence of developed, double-layered walls, especially well preserved in the objects of their fig. 8 and 9. These are not, however, mentioned in the text. Measuring from the printed photographs, the walls have a thickness of $\sim$ 14 nm. A wealth of other details are also visible in the several forms of their EM figures; it is not, however, our task to discuss them here, since they were not described by the authors.

The difficulties of preparing ultrathin sections of intact meteorites have led to several alternate methods of TEM studies, such as investigation of powdered samples, acid treated residues without sectioning, sectioned organic residues, and replicas. Since these are not of direct concern in this paper, only TAN and Van LANDINGHAM's work on exhaustively extracted organic residues from the Orgueil meteorite will be mentioned (74). Direct investigations on a Formvar grid of these air-dried materials revealed a number of objects, mostly in the $< 1\mu$m size range, which resembled the acid-resistant walls of bacteria-like or other filamentous microstructures. The majority of the longer filamentous forms showed small electron-dense globules, regularly placed in their interiors. The wall thickness of the objects was estimated as less than 25 nm.

In the ultrathin section investigation by Van LANDINGHAM et al. (60), ten organic structures are depicted on six electron micrographs. Because of the low magnification, it is somewhat difficult to evaluate these pictures. However, the presence of a well-developed limiting wall around most of the objects is easily discernible. The walls are described as measuring approximately 20 nm. There are other visible features as well. The wall of the object in fig. 2 can be resolved to be composed of layers, whereas that of fig. 3 shows a number of protuberances, in addition to layering. An internal electron-light area is well visible in the structures of fig. 3, one of which is essentially identical to the objects of fig. 7 and 8 in (44), or to those of fig. 4, 5, 11, and 12 of this study.

The sizes of the microstructures depicted from TEM works are admittedly very small: in their majority less than one micron. This is also true for the present study. Nevertheless, these objects are not likely to have become lodged in the stone after its entrance into the terrestrial atmosphere, since they are found thouroughly embedded in matrices where the pore sizes are well under 0.1 μm. We had already in 1964 pointed out (75) that our petrographic studies indicated a general pore size of less than one micron for the Orgueil meteorite, and the present investigations seemed to confirm this statement. The finding reported above of essentially identical structures in two different specimens of the meteorite (fig. 4 and 5) further substantiates the claim that the objects described on the TEM level are autochthonous.

It is pertinent to note that there are known terrestrial microorganisms which fall in the size range of the meteorite organic forms described from the TEM studies. These were first found in argillaceous speleo-sediments (76) and later in soils (77, 78). The recent discovery of this «dwarf flora» of soils, the individuals of which are barely visible in the light microscope, seems to be of considerable significance; and recognition of their existence was strictly dependent on investigations utilizing the electron microscope. (The fact that microorganisms of comparable size range to the objects described from the meteorite occur in soil should not, on the other hand, be taken as an indication that the meteoritic microstructures might result from contamination by these forms, since the morphologies of the latter are decidedly different on the ultrastructural level. Further, as just pointed out, the pore size of the stone is even smaller than the measurements of these organisms).

Respecting the use of TEM technique on ultrathin sections of intact meteorites, NAGY has written that such a project is «difficult and time consuming», and that the «. . . results of these examinations do not lead to much more definite conclusions regarding the origin of the organized elements than the examination in the light microscope» (12, p. 627-628). I can agree that such studies are time consuming, for it takes approximately eight solid hours of microscope time just to find one appropriately sectioned object. Thus it is not too surprising that KERRIDGE, for instance, failed to see any of the «notorious microfossils» in his EM investigations (53), particularly as he is a mineralogist who was looking for minerals. He might, however, have spared the pejorative adjective. As BACON wrote: «They are ill discoverers that think there is no land, when they can see nothing but sea».

I would question, on the other hand, whether such investigations are no more conclusive than light microscopic studies. It is possible to demonstrate with the aid of TEM studies that indigenous, highly structured organic bodies are present in the Orgueil meteorite, well embedded in the matrix. In view of the complexity of their fine morphologies, not much room is left for argument about their biological or abiogenic origin.

Bodies in the size range reported above were also encountered in the SEM investigations, and their partially organic nature was ascertained through the demonstration of their carbon contents by EDAX. They are not depicted in the present study, however, because the simplicity of their surface morphology relative to the other objects scanned did not seem to warrant their inclusion.

Surface morphology of meteoritic inclusions.

As is the case with TEM investigations, studies of Type I carbonaceous chondrites involving SEM techniques are very few in number. Nine publications were found in which SEM pictures of meteoritic components appear, but in most of these the micrographs serve mainly an illustrative, ancillary role, rather than representing results from which conclusions are drawn.

In three consecutive publications, NAGY (79, 80, 12) has provided SEM images of four objects (alternately, ovoids and one spherical form, only ovoids, etc.), photographed by DREW in 1968 from the «freshly broken surfaces of the Orgueil meteorite, «implying that no treatment was employed before the fragments were scanned. (These would then be the only pictures of «native» organized elements prior to those presented in this paper, since in other investigations dealing with presumed organic objects, the residue from acid-treated samples was photographed). The bodies were described as possibly hollow, with a relatively thin, elastic, organic wall showing beaded surface sculpturing. NAGY speculated that they might have been produced from collapsed membranes under the vacuum of the gold coating process. The objects were relatively large: the ovoids having lengths of $\sim 30\mu$m and widths of $\sim 28\mu$m, while the sphere was 28μm in diameter. These forms have not been found again since 1968.

BROOKS and MUIR (59) attempted to compare the structured organic matter of the Orgueil and Murray meteorites with that of the lower Onverwacht strata (Lower Precambrian). Whereas they discovered spheroids in the Precambrian material, which they likened to SCHOPF's SEM pictures of some forms described from the Bitter Springs Formation (Upper Precambrian) (81), they found only the «hexagonal box-shaped bodies» in the meteorites. This is surprising in view of the fact that organized elements are quite abundant in at least the Type I stones, even after acid treatment, as has been shown earlier (37) and recently confirmed by ROSSIGNOL-STRICK and BARGHOORN (45). The precambrian forms of the English authors exhibit, in effect, a striking similarity to structures found in this study both before and after acid treatment (cf. fig. 17 and 18).

ROSSIGNOL-STRICK and BARGHOORN (45) show SEM images of three isolated organic objects (one fragmented), recovered after acid treatment. The authors interpreted the remarkable surface layering of one of their forms as the result of debris deposition from the organic matrix on the wall. Fig. 18, which is substantially identical with their Plate 3, fig. 3, but is from an untreated sample, exhibits the same surface layering, indicating that it is apparently a characteristic of the body in question rather than a preparatory artifact. If this is accepted, then the authors' statement about the absence of any surface morphology in such structures is thrown into question.

Papers devoted to the mineralogical study of carbonaceous chondrites also carry occasional SEM pictures. Thus ORCEL et al. (56) depict a gypsum particle and a flaky layer-lattice mineral (rather similar to the TEM object in fig. 2 of this study); and KERRIDGE and MACDOUGALL (82) illustrate two isolated olivine crystals. The most extensive mineralogical studies, however, are undoubtedly those of JEDWAB (65), who utilized SEM for a detailed investigation of a great number of microstructures separated through a density gradient technique from Type I carbonaceous chondrites. The author identified all of the depicted objects as representing different types of magnetite. As far as one can ascertain from the methodology employed, the whole identification proceedure was based solely on the facts that these forms were not soluble in CCl_4 and had a density greater than 3.3 (X-ray diffraction measurements and identifications were carried out on only a few objects in petrographic thin sections). The variety of shapes found by this investigator is remarkable; he even created a special systematic order to accomodate them, since most are completely unlike terrestrial magnetite in their form. Among the more notable are disc-like and spiral stacks of platelets, framboidal structures, individual plates with supposed corrosion features showing diverse morphologies, aggregates of small spherules, spherical clusters, etc. Pictures of the «perfect» framboidal structure and one of the longest spirals yet to be found were produced by LEWIN as decorative illustrations for a recent popular paper on carbonaceous chondrites (83).

It has already been noted that many of Jedwab's magnetite specimens, in both petrographic thin sections (64) and SEM (65) preparations, show remarkable resemblances to biological forms (12). One cannot but agree with this observation; and many similarities could be brought to attention. Thus: JEDWAB (64) fig. 10 with SCHOPF (84) fig. 56a; JEDWAB (64) fig. 11 with BOURRELLY (85) Plate 24, fig. 2; JEDWAB (64) fig. 12 with STAPLIN (38) fig. 6 or with Van LANDINGHAM (42) fig. 7; JEDWAB (64) fig. 24 with OBERLIES and PRASHNOVSKI (86) fig. 5; JEDWAB (65) fig. 1 with FISHER et al. (87) fig. 1a; JEDWAB (65) fig. 18 with VOZZHENNIKOVA (88) Plate 1, fig. 1 or with VENKATACHALA and SHARMA (89) Plate 1, fig. 21; JEDWAB (65) fig. 31 with BROOKS and SHAW (90) fig. 11, 14b; JEDWAB (65) fig. 43 with LOPUCHIN (91) fig. 3d; JEDWAB (65) fig. 45 with BROOKS and MUIR (59) fig. 1 or with KERRIDGE and MACDOUGALL (82) fig. 2; JEDWAB (65) fig. 48 with ENGEL et al. (73) fig. 2b; JEDWAB (65) fig. 51 with BOURRELLY (92) Plate 8, fig. 11a; JEDWAB (65) fig. 52 with NAGY (79) fig. 2b or with ROSSIGNOL-STRICK and BARGHOORN (45) Plate 3, fig. 1 or with

SCHOPF (81) Plate 1, fig. 4 or with BROOKS et al. (93) fig. 1a; JEDWAB (65) fig. 58 with BOURRELLY (85) Plate 40, fig. 9 - an assemblage which consists of minerals other than magnetite; biological forms both recent and extinct, some from marine ooze; possibly mineralized, prebiotic organic matter resembling some terrestrial Precambrian microfossils; skeletons of marine microorganisms; and forms occuring in air pollution samples, with particles of terrestrial origin.

Of course, it would be patently unscientific on my part to claim that these resemblances constitute identifications. Nevertheless, one would like to know how it is possible that JEDWAB's complex array of non-terrestrial forms, described strictly on morphological grounds, can be accepted without opposition as being magnetite, when no positive identification has been supplied for the pictured structures?

From the above it would follow that the usefulness of the scanning electron microscope in investigations of meteoritic microstructures is rather restricted, where unknown entities are in question, since only surface morphology is obtained. If the identity of a structure has been more or less established with the aid of other techniques and only some additional information about surface structure is required, then the use of SEM is obviously valuable. The combination of SEM pictures with another analytical tool, such as the simultaneous determination of the elemental composition of the particle in question, can also yield more discriminating data than microscopic images alone. For instance, such a gross error as identifying as magnetite the small particles depicted in fig. 22 was easily avoided. Even such combined systems are not adequate, however, to provide proof of the biogenicity of an object showing simple morphology. The considerable amount of carbon occuring in the two spheroids of fig. 17 and 18 seems to indicate that they have a carbonaceous matrix. Their biogenicity now rests on their morphology, which is arguable. Such clearly biologically appearing objects, on the other hand, as the filaments in fig. 34 could be claimed to represent recent terrestrial contaminants, had their spectra not shown that they were thoroughly mineralized. Furthermore, the fact that the elemental composition of the narrow filaments is different from that of the underlying large ones makes it highly improbable that the elemental enrichment found in these forms resulted from the HF treatment.

The issue of biogenicity.

The 1971 paper of ROSSIGNOL-STRICK and BARGHOORN (45) has already been mentioned, in which was reported the successful isolation in relatively large numbers, from the Orgueil meteorite, of what the investigators called «hollow spheres». They applied rigorous palynological techniques to separate the organic material from the mineral fraction, the former including the amorphous organic residue and organized organic structures. Although they described several morphological types from the light microscope, their investigations were concentrated on hollow, spherical bodies only (94). Through electron-probe microanalysis they showed that these spheres were composed mainly of carbon, with equivocal quantities of nitrogen, phosphorus and potassium. In 1963, when we performed our microprobe study of organized elements (20), instrumental limitations of the time precluded direct analysis for carbon; therefore, these authors are the first to have demonstrated the organic nature of the acid-resistant pellicles by such technique. The arguments put forth against the possibility that the forms might be contaminants are probably acceptable even to skeptics (at least in so far as the references is to purported abiogenic structures), although they are almost the same as those which were advanced already in the early 1960s. Thus, these workers have provided irrefutable evidence for the presence of indigenous, organized, organic microstructures in the Orgueil meteorite.

Having shown that the objects in question were neither minerals nor contaminants, there remained only one interpretive problem respecting the origin of the forms: are they extraterrestrial microfossils or prebiological organic structures? To deal with this «crucial question of biogenicity», the authors postulated two types of criteria: intrinsic and extrinsic. The intrinsic criteria are familiar, being essentially the same as those offered for many years by paleontologists working with relatively simple fossil forms from various strata of the Precambrian (see, for instance, in (95)): a) degree and constancy of organization; b) chemical composition showing the presence of organics; c) abondance; and d) narrow size distribution for objects of the same type. The meteoritic «hollow spheres» satisfy these requirements as well as many forms described from such Precambrian strata as the South African Fig Tree Series (3.2 x 10^9 yr old); thus, the intrinsic criteria for biogenicity are said to be met.

By extrinsic criteria, the authors refer to the environment from which the forms in question originate. They discuss only one such criterion in this connection : the necessity for a sedimentary structure. They write : «On Earth, fossils are found only in sedimentary layers. . .» and «. . . there is no sedimentary structure in the Orgueil meteorite. . .» Of the three references cited in support of this last statement (96,35, 97), the one paper authored by scientists with specific expertise in petrography (35) contains no such generalization. Further, ROSSIGNOL-STRICK and BARGHOORN recognized that a long-term aqueous environment on the parent body has been admitted (98, 54), but they qualify: «. . . considered at best as an interstitial filling of the accreted matrix, depositing magnesium sulfate in the veins, too scarce to postulate an aqueous sedimentary environment». One must ask : so considered by whom? Certainly neither of the two references offered contains any such qualification. The authors grant that a parallel to such «aberrant» sediments as pyroclastic tuffs settling in water was described for the meteorite by UREY (97) but do not deal with the implications of this description. In addition, they fail to quote the one detailed study on the petrography of the Orgueil stone (55). Following a series of references treating the possible presence of olivine in the meteorite, which supposedly argues against any aqueous stage, they conclude, in what seems to be an almost complete non-sequitur: «Therefore, the meteoritic texture does not conform satisfactorily with the usual sedimentary requirement associated with true fossils». All of these points proving the failure of the meteorite to provide the proper environment for fossils are dealt with in 17 condensed lines, and, on this basis, the authors reached the decision that the organic microstructures they studied must be abiotic (99).

In connection with the above, three points should be brought out :

1) The authors have reached a decision with respect to one much debated and very important interpretive problem about the meteorite (the issue of the biogenicity of the microstructures) by erroneously implying that two other areas of dispute (the complex petrology of the stone versus its supposed primitive nature and the question of whether or not the parent body ever contained a hydrosphere) have been settled. In order to achieve this implication, they had to rely on selective and improper use of citations. What they did, in essence, was to resolve two unknowns by fiat (there is no sedimentary structure in the meteorite and there was no true aqueous phase), and from this concluded that the third unknown was solved : the «hollow spheres» are not biogenic.

2) Had the investigators made the intrinsic criteria more stringent, much of the work of the second author on Precambrian fossils would have been thrown into doubt as to biogenicity. Thus, they needed a double standard, since they were apparently unwilling even to leave open the possibility that the Orgueil forms might be biogenic.

3) Even if one accepts their very restricted idea of the «usual sediments» which are possible environments for «true fossils,» the researchers unintentionally confirmed that the forms found in the Lower Onverwacht Series ($\sim 3.3 \times 10^9$ yr old) - the biogenicity of which has been questioned by some (102) and asserted by others (91, 92) - are true fossils, for these meet both the intrinsic (103) and extrinsic criteria postulated.

In the event, once having «established» an abiogenic origin for the meteoritic microstructures, the authors apparently felt it necessary to explain how these forms might have arisen. It is not worthwhile to discuss their hypothesis in detail, since it is rather convoluted and highly inclusive - i. e., at least fourteen different and often mutually contradictory models of events in early solar system history leading to the formation of carbonaceous chondrites are invoked, without comparison of their merits. Four solid pages of text are devoted to these theoretical considerations and to a final explanation of how the extraterrestrial organic spheres could have had an abiogenic genesis.

In 1971, it was not yet known that forms approximating the «hollow spheres» found in the meteorite could be produced in the laboratory through prebiotic synthesis (the work of the Indian authors mentioned earlier (32, 34) having apparently been forgotten). Only four years after the publication of ROSSIGNOL-STRICK and BORGHOORN's paper, however, dramatic findings were reported by FOLSOME et al. (104) and FRAZER and FOLSOME (105). Utilizing a Miller-Urey type procedure, the investigators produced «massive yields of discrete groups of highly structured morphological entities» in less than a day (104). Among these - depicted through the use of various microscopic methods - were bacteria-like forms, larger, more complex membrane-bound systems, and «hollow tubes», some of which even showed suggestions of septation. The FOLSOME group felt that their laboratory products could explain virtually all of the early findings about organic structures in carbonaceous chondrites, and that the error had been only in mistaking prebiotic forms for biogenic fossils.

FOLSOME and his coworkers do not recognize double standards for early terrestrial «fossils» and for those described from meteorites, and since (at least according to their first publication) their structures meet all the criteria of biogenicity accepted by most specialists working on the Precambrian, it is only natural that they question the validity of many early fossils. Their claim that their laboratory-produced forms show more spectacular morphologies than do many presently accepted terrestrial fossils would seem, from visual evidence alone, to have some merit (106). Among findings from ancient terrestrial strata, they accept as unquestionably biogenic only the Transvaal Sequence of South Africa (2.2 x 10^9 yr old), in which has been discovered *Petraphera vivescenticula* (107, 108), the earliest known fossil evidencing cellular diversification. The implication, of course, is that the validity of all work on the Fig Tree Group (100, 101, 109-111), the Soudan Iron Formation (95, 112), etc., is thrown into doubt, not to mention fossil discoveries in still older strata.

It would seem that ROSSIGNOL-STRICK and BARGHOORN would have two logical choices for reinterpretation of their findings in the face of this new abiogenic synthesis work. 1) If they want to retain the original set of criteria, they would have to admit that the extrinsic criterion has been met for the meteorite, since the kind of Miller-Urey synthesis employed by the FOLSOME group requires the presence of liquid water. If, however, an aqueous environment must be admitted even for abiogenesis, then the necessary condition for the deposition and preservation of true fossils would have been present on the parent body; there would have been no necessity to invoke abiogenic processes; and the organic spheres could be interpreted as biogenic. 2) If they still wished to maintain that the meteoritic forms are abiogenic, they would have to grant the inadequacy of their intrinsic criteria and accept the conclusion of the FOLSOME group that the biogenicity of terrestrial microfossils which areolder than 2.2 x 10^9 yr is not demonstrable.

To be fair to FOLSOME et al. (104), it should be mentioned that - being aware that there must have been some truly living terrestrial forms which preceded the advent of cellular diversification - they review non morphological criteria for hiogenicity which have been proposed (carbon isotope ratios; the presence of porphyrins, even numbered fatty acids, odd numbered aliphatic hydrocarbons, or isoprenoids; evidence of enzymatic activity; finding of optically active amino acids; etc.) and conclude that all are unreliable for one or another reason. We are thus left with the ultimate agnostic implication that **there is no way to prove that any simple unicellular form or filament composed of the same type of cells found in an isolated assemblage - even if younger than 2.2 x 10^9 yr - was once living.**

If the face of such a drastic situation, one might be tempted to propose yet other approaches to the proof of the biogenicity of simple fossil forms, but that is beyond the scope and intent of this paper.

Concluding remarks

The results of the investigations presented above can be interpreted from several different standpoints. The assumption that the described forms are representatives of advanced prebiotic chemical synthesis would seem to be a desirable choice, especially in view of the remarkable advances made by PERTI (32) and BAHADUR (33, 34) in this area of endeavor. Fig. 54 of PERTI (32), for instance, is strikingly similar to my micrograph in fig. 26, although the chemical composition and measurements of the bodies differ. The more recent achievements in this field, such as the objects presented in the papers of FOLSOME and his coworkers (104, 105), do not even come close in variety of forms and beauty of structure to those produced with the aid of a little sunshine by the Indian authors. However, notwithstanding some minor but bothersome values in the publications of the FOLSOME group - such as light microscopic pictures with asserted resolution of 0.028μm (104, fig. 1f), an interference contrast image taken at 3200 x (105, fig. 1), and so on - it may be that these new abiotic creations mimicking biological forms have already solved the nagging problem of the presence in carbonaceous chondrites of indigenous, organic microstructures.

The fact that, according to the results of the EDAX analyses, the organized elements described from the SEM investigations all contain minerals, naturally would substantiate the view that they represent inorganic concretions. Their strikingly biological appearance is actually not unfamiliar to some students of minerals, and under no conditions would it be acceptable as attesting their biogenic origin. In effect, the remarkable array of magnetite forms described from Type I carbonaceous chondrites - never found before on Earth but established basically on morphological grounds - could lend further credence to the hypothesis that all structures discussed above are simple mineral grains or growths. (Elongated, dendritic types of magnetite have recently been added to the shapes of this versatile mineral (12), completing the series needed to identify any and every organized element as a magnetite pseudomorph, if necessary).

Also, one can argue that the unquestionable biological «looks» of at least the large filamentous structures make it hard to believe that they are either minerals or the result of prebiotic chemical synthesis. They are therefore biotic forms, and, as such, must represent terrestrial contaminants. The finding that the elemental composition of the larger and smaller filaments are somewhat different from each other but, to a certain degree similar to that of the matrix, can best be explained by applying differential diffusion rates to them during the period of HF etching, which process solubilized the meteorite minerals and deposited them in the filaments. (The same process does not necessarily hold true for the controls. On the contrary, such discrepancies in elemental composition between them, after treatment, might be used to prove the indigenous nature of the microfossils).

As can be seen, each one of the enumerated hypotheses, or any preferered combination thereof, can serve as a «scientific explanation» for the presence of highly organized microstructures in the meteorite without the necessity of recourse to the irksome notion that they are remains of extraterrestrial life.

«But O how dull hath Occam's razor grown!».

I am greatly indebted to Drs. E. DEBERNARDO and K. BOLANDER, without whose valuable help this paper could not have been written. Thanks are also due to Dr. S. KUNEN and Mr. C. WAKE.

(manuscrit accepté le 10 avril 1979)

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96. For the most part, the actual results seem clear and straightforward, but there are two points to which attention should be brought. First, it seems puzzling that in a palynological study of what were apparently gram quantities of this meteorite, no truly filamentous forms, none of the «box-like» structures, no other entities with complex morphology were found, since the presence of such has been repeatedly described and confirmed from Type I carbonaceous chondrites (38, 42, 43, 57-59). Secondly, the authors flatly state that their organic spheres could not be stained with safranin.

This is used, on the one hand, as a demonstration that the objects are not recent terrestrial contaminants, and on the other hand, as an indication that they are not biogenic. Although STAPLIN (38) and one of our papers (46) are quoted - in which publications it is clearly stated that the described objects stain with safranin - these references are not mentioned in connection with their own negative results. Furthermore, staining with safranin is not a criterion of either biogenicity or abiogenesis. Safranin is a simple adsorptive stain, and as such it will indiscriminately dye the most varied substrates. One wonders why the authors' materials have failed to take the stain. Staining experiments on organized elements with safranin and an additional 19 biological stains have been described at some length in (46), where the non-specificity of this color has been discussed in particular.

97. CLOUD, P.E., Jr., LICARI, G.R., 1968 – *Proc. Natl. Acad. Sci. U.S.A.* 61: 779.

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101. It should be pointed out that the implicit reasoning behind the authors' conclusion that the meteorite could not have a proper environment for the deposition of fossils is actually the denial of a period when the parent body would have a hydrosphere, rather than the claim that the (undefined) sedimentary requirement is not met. Space does not permit the detailed textual analysis which would be necessary to prove this contention; however, another paper now in preparation will include a thorough examination of this passage and other questionable generalizations in this publication.

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107. FRAZER, C.L., FOLSOME, C.E., 1975 – *Origin Life* 6: 429.

108. By comparing photographic evidence of prebiotic forms with materials on Precambrian structures, one has to admit that fig. 3, 21, 37, 39, 41, and 50 of PERTI (32) more convincingly depict nuclei-like profiles than exhibited by the fossils in the micrographs in fig. 50 and 51 of SCHOPF (86), or those of CLOUD and his coworkers (fig. 39 and 40) as quoted by SCHOPF in (86). Also, one can see more details in the prebiotic filament exhibiting incipient septation of FOLSOME et al. (106) (fig. 1c) than in the microfossils shown by CLOUD and LICARI (97) (fig. 3, 5, and 6). On the other hand, in fig. 1a of FOLSOME et al. (106) where the materials are supposed to be contamination free, a nice *Gloeocapsa* (Cyanophyta) can be seen; while fig. 45 of PERTI (32) could easily be identified as a *Cosmarium* species (Chlorophyta).

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FIGURE LEGENDS

Plate 1

1: Lathe-like minerals in matrix. 2: A layer-lattice silicate flake. 3: Mineral matrix with organic structure in center. Lines represent 0.1 µm.

Plate 2

4: Stalked object embedded in matrix. 5: Similar object found in another preparation. 6: Object of fig. 4 at higher magnification. Note the spinous wall, the stalk, and the central vesicular profile. 7: Area of stalk; arrows point to canals or pores in wall. 8: Layering of wall. 9: Details of vesicular structure. Microtubule-like formations at arrows. 10: Object resembling budding yeast. Circular inclusion to the right of A, vesicles at B. 11 and 12: Two additional organic structures. 13: Magnetite grain. Lines represent 0.1 µm.

Plate 3

14: Object with massive wall. External layer of wall at black arrow. Appressed foreign particle between white arrows. Neck canal above A. Allochtonous foreign body in wall below B. 15: Over-exposed portion of wall to show demarkation between neck and external object. 16: Body cut from its matrix and rotated 180° to demonstrate that originally it was positioned in the sickle-shaped electron-luscent area in fig. 14. Lines represent 0.1 µm.

Plate 4

17: Spheroid after HF treatment of meteorite . 18: Same as above in native stone. 19: Particle in native meteorite. 20: EDAX of above particle. 21: Possible magnetite grains. Note radiating spokes under A. 22: Microspheres which are definitely not magnetite. 23: Scattered magnetite microspheres. Lines represent 2 µm.

Plate 5

24: Siliceous object and matrix from untreated Orgueil Specimen. 25: Similar complex from the untreated chert. 26: Spinous object, torn from its matrix, untreated Orgueil. Some spines retained in hole, at B. 27: Same as above, with lower magnification to show configuration of matrix and object. A is ridge at uppermost surface of fragment; B and C, areas where EDAX readings were taken. 28: Collapsed possible oosphere from treated chert. 29: Dichotomously branching filament from chert. A, main filament before branching; B, front branch; C, hind branch; U, secondary branches. All lines represent 2 µm, except that of fig. 29, which equals 20 µm.

Plate 6

30: Filament fragment from HF treated Orgueil. 31: Similar filament to the above, without treatment, bridging a fissure. 32: Pencil-shaped and lathe-like filaments in untreated Orgueil. A, B, and C: areas where EDAX analyses were carried out. 33: Same types of objects as in fig. 32, but from untreated chert. A, B, and C: areas where EDAX analyses were carried out. 34: Filamentous complex from Orgueil with bundles of broad and narrow filaments, partially covered by recrystallized minerals of the matrix after HF treatment. See text for meaning of labeling. 35: Detail from above complex at higher magnification, showing the frayed sheath, a bipyramidal crystal (E) in the lumen, and the site of two cross walls. All lines equal 2 µm, except that of fig. 34, which represents 20 µm.

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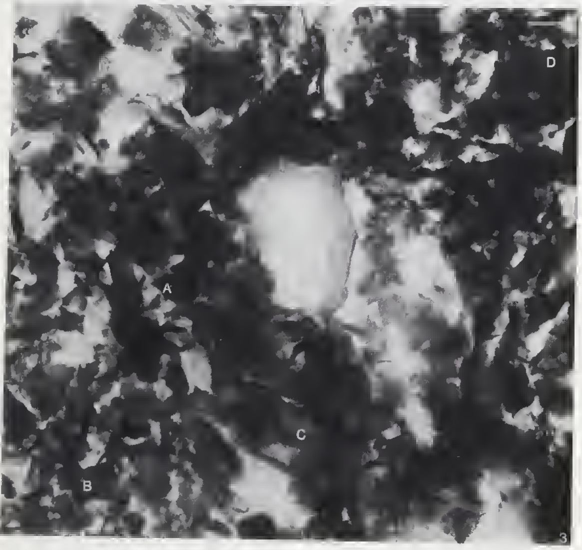

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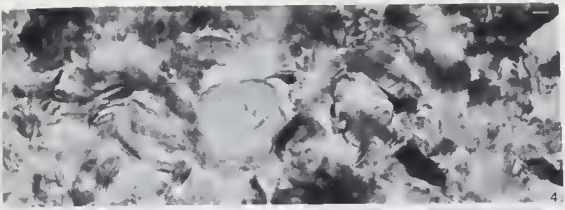
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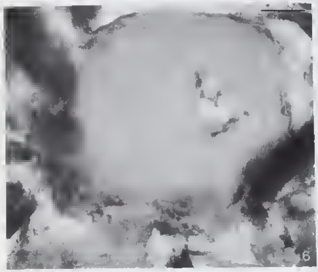
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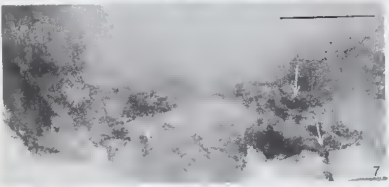
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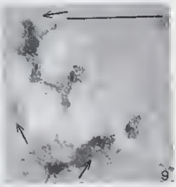
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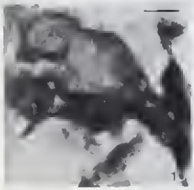
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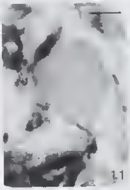
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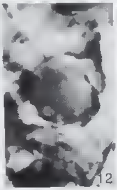
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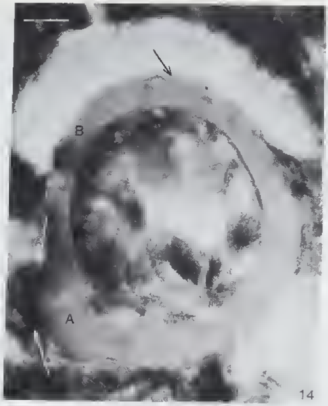
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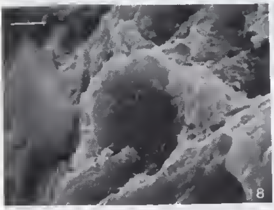
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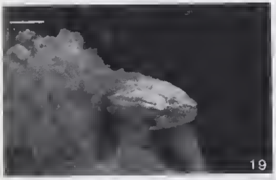
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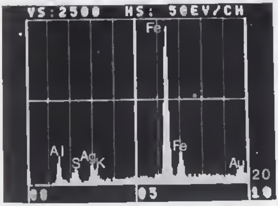
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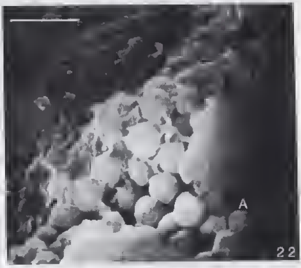
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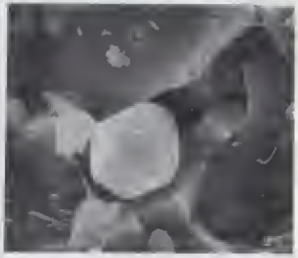


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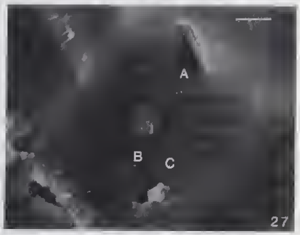
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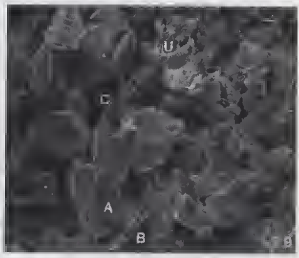
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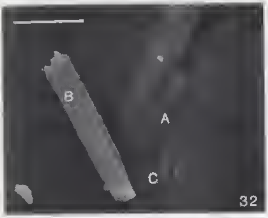
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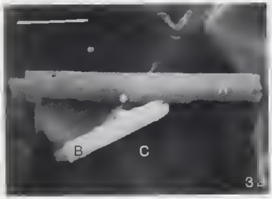
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PORES IN THE APICAL CELL OF *OSCILLATORIA LIMOSA* AG.

Carlo ANDREIS *

ABSTRACT. – This paper deals with occurence and function of pores in the cell wall of Cyanophyceae. The distribution model and the size of the pores could be a systematic character.

RÉSUMÉ. – Cet article traite de la présence et de la fonction des pores dans la paroi cellulaire des Cyanophyceae. La distribution et la taille de ces pores peut être dans certains cas, un caractère systématique utile pour l'identification des Cyanophyceae.

Occurence and function of pores in the cell wall of Cyanophyceae is a problem not yet completely solved.

Plasmodesma-like structures, having about 17 nm in diameter, have been observed in the cross wall of *Symploca muscorum* (PANKRATZ et BOWEN, 1963). Also in cross-wall of *Oscillatoria princeps* plasmodesma-like structures, termed junctional pores, have been observed (HALFEN et CASTENHOLZ, 1971).

Pores of similar diameter have been described in the external cell wall of *Oscillatoria sancta, O. tenuis, O. chalibea, O. okeni* and *O. borneti*, and also in *Microcoleus vaginatus*, *Porphyrosiphon notarisii* and *Symploca muscorum* (DRAWERT et METZNER, 1958; FRANK et al., 1962; METZNER, 1956; RIS et SING, 1961; SCHULZ, 1955).

LAMONT observed that the pores reach the L_3 layer of the cell wall (LAMONT, 1969). On the contrary HALFEN and CASTENHOLZ observed that they reach only the L_2 layer (HALFEN et CASTENHOLZ, 1971).

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Rev. Algol., N.S., 1979, XIV, 3: 235-238.

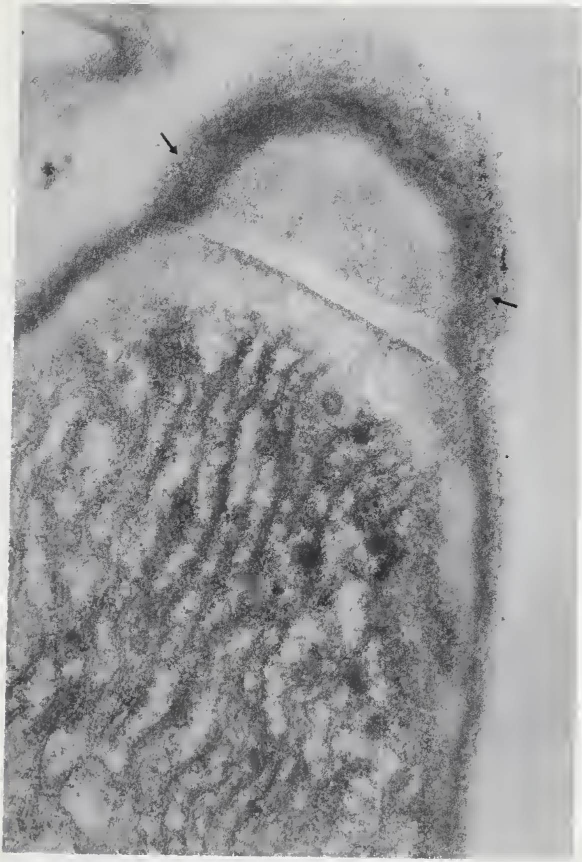

Fig. 1. — Apical and subapical cell of *Oscillatoria limosa* Ag. (x 50,000).

Pores about 60 nm in diameter much bigger than the ones described before, have been observed in the external cell wall of *Oscillatoria princeps* (RIS et SING, 1961).

We do not know exactly how to interprete these pores, that up to now have been observed only in the Hormogonales. They have been correlated with mucilage secretion (PANKRATZ et BOWEN, 1963; WALSBY, 1968) which, according to SCHULZ, could help these filamentous algae in the movement (SCHULZ, 1955). However, according to WALSBY, SCHULZ's interpretation is not based on experimental evidence (WALSBY, 1968). Also HALFEN and CASTENHOLZ object this interpretation : really they proposed that the gliding motility in the Hormogonales is caused by fibrils arranged on the surface of L_2 layer (HALFEN et CASTENHOLZ, 1971).

Studying the ultrastructure of *Oscillatoria limosa* Ag. we have observed the presence of pores in the external cell wall near the transversal wall, delimiting the apical cell from the subapical one. They are about 5 nm in diameter and arranged in parallel lines about 30 nm apart. The single pores are 40 nm apart and the lines are 40/2 nm shifted (fig. 1). This arrangement is similar to the one described by PANKRATZ and BOWEN (1963) but it differs in size and distribution of the pores. However the alternate disposition of pores in neighbouring lines completely differs from the one reported by previous Authors. In the external part of the cell wall we can see pores placed in the mucilagenous layer.

Therefore we can find regarding the arrangement and the size of pores. The distribution model and the size of the pores could be a systematic character. According to FJERDINGSTAD the ultrastructural features are sometimes diagnostic characters useful in uncertain cases for the classification of the Cyanophyceae (FJERDINGSTAD et FJERDINGSTAD, 1976).

(manuscrit accepté le 27 mars 1979)

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STUDIES ON SOUTH INDIAN SOIL ALGAE : *GLOEOCYSTIS GIGAS* COLLINS (TETRASPORALES)*

V.S. SUNDARALINGA, A.K.S.K. PRASAD and S. SUBBALAKSHMI**

RÉSUMÉ. — *Gloeocystis gigas* Collins, ordre des tétrasporales, a été observé et isolé à partir de substrats sableux de Mahabalipuram, dans le sud de l'Inde. Les présentes observations réalisées sur des cultures montrent que *Gloeocystis gigas* est une algue palmelloïde qui se reproduit par zoospores.

ABSTRACT. — *Gloeocystis gigas* Collins a member of tetrasporales has been recorded and isolated from sandy soils of Mahabalipuram, South India. The present observations on culture show that the alga *Gloeocystis gigas* Collins is a palmelloid one and reproduces by zoospores.

INTRODUCTION

Masses of green algae growing as palmelloid colonies exhibiting spherical to ellipsoidal cells embedded in concentric mucilaginous sheaths, are classified since NÄGELI's basic work (1848) on one celled algae, as belonging to the genus *Gloeocystis* Nageli. NÄGELI laid emphasis on the lack of motile reproductive cells. However, the diagnosis of the genus reproduced in the classic Süsswasser flora of Pascher made one change that the species reproduce occasionally by zoospores. Since then the genus has been conceived by later authors differently (WEST and G.S. WEST, 1902; LEMMERMANN, 1915; FOTT and NOWAKOVA, 1971; IYENGAR, 1971; FOTT, 1972 and HINDAK, 1978). Thus, as HINDAK (1978) has pointed out, the genus *Gloeocystis* has become an example of misinterpretation.

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* Memoir N° 292 from Centre for Advanced Study in Botany.

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Rev. Algol., N.S., 1979, XIV, 3: 239-245.

Gloeocystis is one of the several algae isolated during a study on soil algae of South India. Earlier, IYENGAR (1971) reported *Gl. ampla* and *Gl. planctonica* from South India and described a new species *Gl. banneergattensis*. The present paper deals with the report of a fourth species of the genus occuring in South India.

MATERIAL AND METHODS

Approximately 10.0 g of soil samples from Mahabalipuram were inoculated into 250 ml. Erlenmeyer flask containing 100ml of sterile liquid modified Bristol medium (NICHOLAS and BOLD, 1965). The flasks were then incubated under standard conditions.

When sufficient growth was observed (after 2-3 weeks) a portion of the material was removed with a sterile pipette and was then centrifuged for about 5 minutes at 5000 r.p.m. to give a uniform suspension of algal cells. The suspension was then aspirated on to a plate of BBM agar. Upon illumination algal colonies appeared from which unialgal cultures were isolated.

Colonies of different organisms, as differentiated by their colony morphology observable with a dissecting microscope were removed from the Petri plates and inoculated into tubes of liquid BBM. The observations of fresh mounts were often supplemented by using stain-crystal violet to determine the presence or absence of gelatinous matrices. A dilute I_2KI solution was used to test the presence or absence of starch and also to study flagellation.

Zoospores were induced when the alga was shifted from agar to liquid medium. Swarmer production was indicated by a green scum near the surface of the water.

OBSERVATIONS

The following description is based on the study of the alga in culture (fig. 1-16).

The alga has gelatinous colonies which are bright green, hemispherical to flat, soft, measured about 0.01 mm to 0.2 mm in diameter. The other colonies are up to 0.25 mm. The cells are mostly spherical (rarely oblong) which are often united and embedded in the mucilage. Cells are frequently arranged in groups of four, each group being enclosed by a separate gelatinous and even the individual cell envelopes are lamellated. The stratification is either concentric or eccentric. (This is clearly observed in crystalviolet-stained material).

The cells show a thin cell wall and measure 8.3µm-(9.13)-11.6µm in diameter. Young cells contain a single massive cup shaped chloroplast, with a single pyrenoid. Contracted vacuoles are not observed. Older cells measure up to 13µm in diameter with slightly thickened walls (akinetes?) and have a diffuse chloroplast completely filling the cell and contain numerous starch granules. (At this stage pyrenoid is not distinguishable). Multiplication or vegetative reproduction is by means of formation of 2-4 daughter cells, which secrete individual envelopes later.

Asexual reproduction is by the production of biflagellated zoospores which are of *Chlamydomonas* type. Zoospores are mostly spherical, rarely oblong, measuring $5\mu m$-$8.3\mu m$ (6.3) in diameter. Flagella are equal, the length of the flagellum is twice as long as the body of zoospore. Zoospores possess a cup-shaped chloroplast with a single pyrenoid and a distinct eye spot is also observed. Papilla is not observed.

Sexual reproduction has not been observed.

DISCUSSION

The present alga resembles tetrasporalean genera *Gloeocystis* Nag., *Sphaerellocystis* Ettl. and *Chlamydocapsa* Fott. Tetrasporalean algae differ from the coccoid ones in the presence of contractile vacuoles. *Sphaerellocystis* (ETTL, 1960) and *Chlamydocapsa* Fott (FOTT, 1972) possess contractile vacuoles. It is not clearly known whether the type species of *Gloeocystis* and the other species have them. However, IYENGAR (1971) observed 1 or 2 contractile vacuoles in *Gl. ampla*. NOVAKOVA (1964) transfers this species to *Sphaerellocystis* as *S. ampla* since the structure of the cell is tetrasporine. *Gloeocystis* Nag. includes species lacking contractile vacuoles. The present alga resembles more closely these species in having the cells grouped in colonies-exhibiting a palmelloid habit, a stratified gelatinous envelope , a cup shaped chloroplast with a pyrenoid and in the absence of contractile vacuoles. It differs from *Sphaerellocystis* in having a palmelloid condition and in the absence of contractile vacuoles and from *Chlamydocapsa* mainly in the absence of contractile vacuoles. The present alga resembles otherwise to one species of *Sphaerellocystis (S. globosa)* which does possess a mucilaginous covering. Naturally one could expect this species to form palmelloid colonies under certain conditions. Thus the present alga is assigned to the genus *Gloeocystis*.

It is quite probable that many species presently included in this genus are merely palmelloid stages of other motile algae. IYENGAR (1971) retained the genus in the Tetrasporales, rightly pointed out that some species of *Chlamydomonas* are known to get into a palmelloid condition or «*Gloeocystis* condition» and unless one investigates the organism fully, it is difficult to decide whether it is a *Gloeocystis* or a *Chlamydomonas* in a «*Gloeocystis* stage». It is rather difficult to draw the line of demarcation between a *Chlamydomonas* in *Gloeocystis* stage and a *Gloeocystis*. One does not know whether it is proper to reduce all species of *Gloeocystis* to species of *Chlamydomonas* which spend most of their time in palmelloid condition to either *Gloeocystis* or *Palmella* species (IYENGAR, 1971). It may be worth mentioning that young colonies of *Hormotila* have much the same appearance as *Gloeocystis* and each of the spherical cells is enclosed in a thick layered gelatinous envelope. Observations for a series of years of *Gl. vesiculosa* and *Gl. rupestris* have shown great uniformity (COLLINS, 1909). The present observations in culture showed that the present alga is a palmelloid one.

LEMMERMAN (1915) conceived this genus in a broad sense and referred six species to it. They are *Gl. planctonica* (W. et G.S. West) Lemmermann, *Gl. vesiculosa* Näg., *Gl. botryoides* Näg., *Gl. rupestris* (Lyngb.) Rabenh., *Gl. ampla* Kütz. and *Gl. major* Gerneck. *Gl. vesiculosa* Näg. is the type. COLLINS (1909), besides the type and *Gl. rupestris*, recognized five species. They are *Gl. gigas, Gl. fenestralis, Gl. parotiniana, Gl. zostericola* and *Gl. scopularum*. The latter two species are marine. HEYING (1962) described a species, *Gl. hercynica*. MAINX (1928) described a species *Gl. maxima* which is a latter homonym of *Gl. maxima* Gutwins. Therefore, DESIKACHARY (in IYENGAR, 1971) renamed it as *Gl. mainxii*. IYENGAR (1971) while reporting the indian records for *Gl. ampla* and *Gl. planctonica*, described a new species *Gl. banneergattensis*. HINDAK (1978) besides the type species *Gl. vesiculosa* Näg., included one more species *Gl. polydermatica* (Kütz.) Hindak. The distinction among the species of *Gloeocystis* is based on the shape of the cells and cell dimensions.

The present alga comes very close to *Gl. gigas* Collins and therefore it is placed under this species. The alga also resembles *Gl. vesiculosa* but differs slightly in having generally larger cells 8-11.6 μm in diameter. LEMMERMANN (1915) indicated reproduction by zoospores in three species, *Gl. vesiculosa, Gl. ampla* and *Gl. major*. The present observations show that *Gl. gigas* also reproduces by zoospores.

ACKNOWLEDGEMENTS

The authors are thankful to Prof. T.V. Desikachary for his comments and for critically going through the manuscript and to Prof. M.S. Balakrishnan for his suggestions. The financial assistance from the University Grants Commission of India for one of the authors (A.K.S.K.P.) is gratefully acknowledged.

(manuscrit accepté le 8 septembre 1979)

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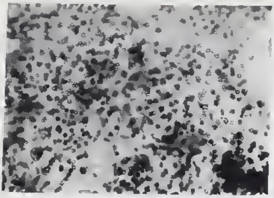
Plate I: fig. 1-10

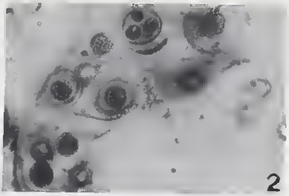
Gloeocystis gigas Collins. — 1: Thallus organization at low magnification (crystal violet stained) ca. x 140. 2 & 3: Vegetative cells in colonies (note the individual envelope and the common envelopes) (crystal violet stained) ca. x 550. 4: Cells showing concentric lamellations of the mucilage envelope (crystal violet stained) ca. x 770. 5: Biflagellated zoospores (Iodine stained) ca. x 1000. 6: A zoospore at higher magnification (note the eyespot) ca. x 1600. 7: Vegetative cells stained with Iodine, ca. x 780. 8: Old cells showing numerous starch granules (Iodine stained) ca. x 780. 9: A mature diad (Iodine stained) ca. x 1200. 10: Stratified envelopes without the cell (crystal violet stained) ca. x 1200.

Plate 2 : fig. 11-16

Gloeocystis gigas Collins. — 11: A portion of the thallus at low magnification. 12: An enlarged portion of the vegetative cells in colonies (note the individual and the common envelopes). 13: Colony of 4 cells (note the individual and the common envelopes). 14: Cells embedded in lamellated sheaths. 16: Biflagellated zoospores.

Fig. 11: scale = 50μm; fig. 12-16: scale = 10μm.





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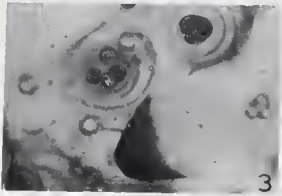

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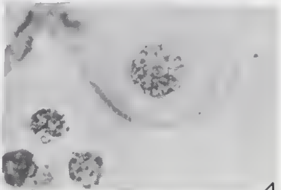

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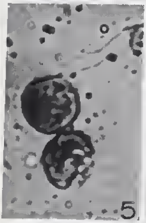

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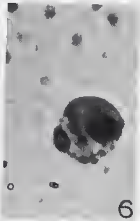

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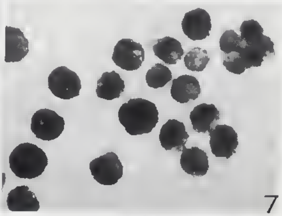

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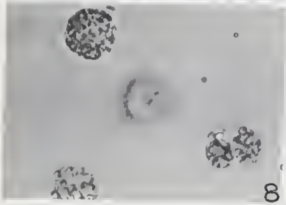

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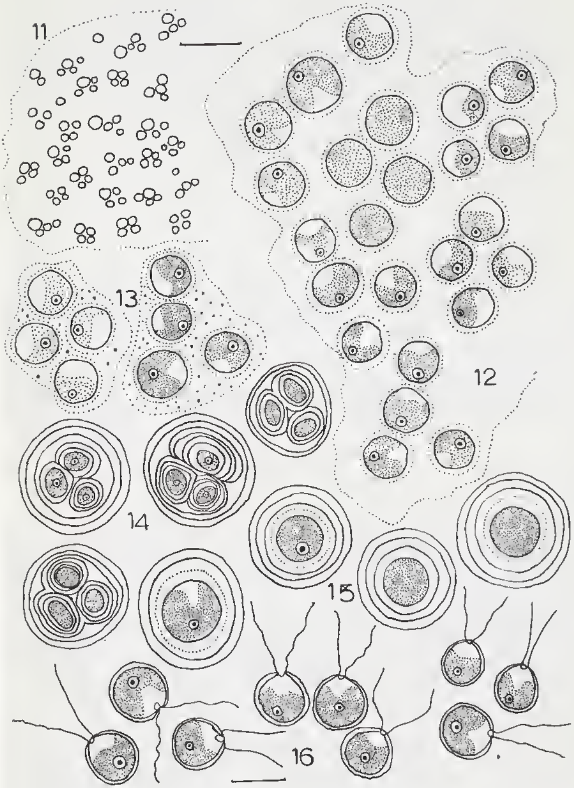
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PARADOXIA PELLETIERI, NOV. SP.
NOUVELLE ESPECE DE CHLOROCOCCALES DE FRANCE (CHLOROPHYCEAE)

J.C. DRUART et O. REYMOND**

RÉSUMÉ. — Les auteurs décrivent une nouvelle espèce de Chlorophycée du genre *Paradoxia* récoltée au lac du Bourget (Savoie, France). Cette algue est toujours unicellulaire. Son pôle antérieur est effilé et porte une ancre peu visible. Le pôle postérieur est arrondi. La cellule porte des soies, principalement sur la partie postérieure.

SUMMARY. — The authors describe a new species of Chlorophyceae of the genus *Paradoxia* found in the lac du Bourget (Savoie, France). This alga is always single-celled; its anterior pole is sharp and surmounted with a hardly visible anchor. Some setae surround the cell, particularly at the posterior end.

Au cours de prélèvements faits sur le lac du Bourget (Savoie), l'observation du matériel planctonique recueilli de juillet à septembre 1978 nous a fait découvrir un organisme non encore décrit, et que nous proposons de nommer *Paradoxia pelletieri* (fig. 1).

Cet organisme est toujours unicellulaire. Les cellules sont fusiformes et hétéropolaires. Le pôle antérieur (voir la terminologie employée pour *Ankyra* par SWALE et BELCHER, 1971) est effilé, et son extrémité est bien visible au contraste de phase. Cette extrémité porte une ornementation très faiblement

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Rev. Algol., N. S., 1979, XIV, 3: 247-252.

Fig. 1

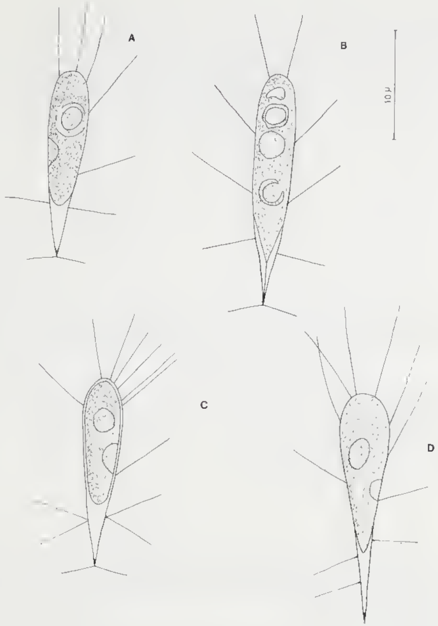

Fig. 1. — *Paradoxia pelletieri* nov. sp. Quatre cellules A, B, C, D.

contrastée qui, en coupe optique, a la forme d'une ancre souvent à peine visible (fig. 1, D).

Cette ancre pourrait être identique à celle observée par KISSELEV (1955) chez *Ankyra calcarifera* (Kisselev) Fott (1957) (fig. 2), ou décrite et dessinée par SMITH (1916), FOTT (1974) et REYMOND (1979) chez *Ankyra judayi* (Smith) Fott (1957) (fig. 3, 4 et 7).

Il faut noter que les organismes des genres *Paradoxia* Swirenko (1928) et

Fig. 2

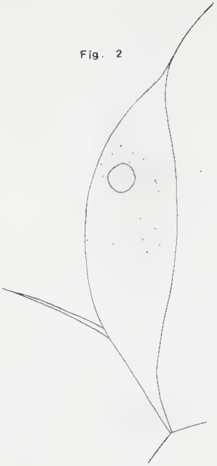

Fig. 3

Fig. 4

Fig. 2. — *Ankyra calcarifera* (Kisselev) Fott (dessin d'après Kisselev, 1955). Fig. 3. — *Ankyra judayi* (Smith) Fott. Smith (1916) décrit le pied comme un disque, et non des appendices en forme d'ancre (voir fig. 7) (dessin d'après Smith, 1916). Fig. 4. — *Ankyra judayi* (Smith) Fott. Cellule de culture. Le pied, bien que représenté par des appendices en forme d'ancre, est en réalité un disque plus ou moins aplati (voir fig. 7) (dessin d'après Fott, 1974).

Ankyra Fott (1957) sont généralement surmontés d'une ancre. Cette dernière peut être de deux types. Elle est formée soit par deux appendices foliacés (fig. 5 et 6), possédant une ultrastructure en lame très particulière (SWALE et BELCHER, 1971; REYMOND, 1979), soit par un disque fait de fibrilles rayonnant à 360° (fig. 7) et ne s'aggrégeant pas en un tissu comme dans le cas précédent (les fibrilles formant ce disque s'agglomèrent quelquefois entre elles et forment un appendice, dit en queue de cheval, REYMOND, 1979).

Le pôle postérieur est arrondi, comme chez *Paradoxia multiseta* Swirenko (1928) (fig. 6). Une dizaine de soies environ recouvrent le corps cellulaire. Elles sont plus contrastées et plus serrées que sur le pôle postérieur de la cellule. Vers l'extrémité antérieure de l'algue, les soies sont perpendiculaires à l'axe cellulaire, et sont parfois doubles (fig. 1 C). Le contraste de phase est indispensable pour leur examen.

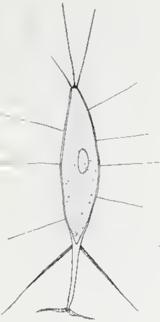

Fig. 5

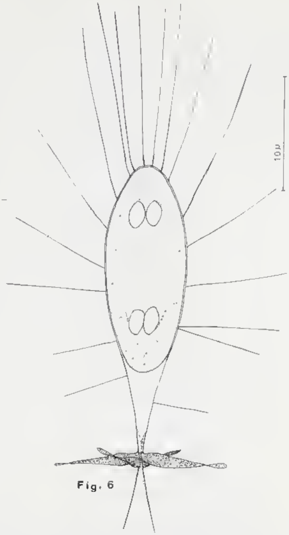

Fig. 6

Fig. 7

Fig. 5. — *Ankyra paradoxioides* Cirik. On remarque la présence de soies sur toute la cellule. Les deux appendices antérieurs sont foliacés et bien distincts (matériel fourni par Mme Cirik). Fig. 6. — *Paradoxia multiseta* Swirenko. Une seule cellule est représentée en entier. Les appendices foliacés de chacune des cellules se croisent avec un angle de 90°. Les cellules ne sont accrochées entre elles que par leur apex (résultats optiques et électroniques) (matériel provenant du lac de Bret près de Lausanne, Suisse, et récolté en septembre 1976). Fig. 7. — Représentation schématique faite à partir d'observations en microscopie optique et électronique d'apex de *Ankyra judayi.* On ne trouve plus une organisation foliacée (fig. 5 et 6) mais des fibrilles peu organisées, formant un cône plus ou moins aplati (REYMOND, 1979). L'appendice antérieur de *Paradoxia pelletieri* a probablement une structure identique.

Le corps cellulaire mesure de 18 à 22µm de long, et de 3 à 4µm de large (sans soies, ni ancre). Les soies atteignent 15µm de longueur. La largeur de l'ancre est de 7µm.

Les cellules possèdent un plaste important, avec un pyrénoïde (rarement deux). Le noyau est généralement placé en position légèrement antérieure et latérale.

A la suite de recherches faites au microscope électronique par SWALE et BELCHER (1971) sur *Ankyra*, et par REYMOND (1979) sur *Paradoxia* et *Ankyra*, il s'est révélé que la frontière entre les deux genres était très ténue. C'est pourquoi par la présence de soies, d'un pôle arrondi et malgré l'absence de cénobes, l'organisme que nous décrivons se rapproche plus de *Paradoxia* Swirenko (1928) que de *Ankyra* Fott (1957).

Paradoxia multiseta Swirenko (1928) (fig. 6), *Ankyra calcarifera* Kisselev (1955) (fig. 2), et *Ankyra paradoxioides* Cirik (1978) (fig. 5) sont proches de notre nouveau taxon, mais s'en différencient par la présence d'appendices antérieurs foliacés et nettement visibles (fig. 5 et 6), de cénobes (fig. 6), de parties cellulaires postérieures plus ou moins effilées (fig. 2 à 5), d'épines antérolatérales épaisses non perpendiculaires à l'axe de l'algue (fig. 2 et 5), et d'axes cellulaires légèrement recourbés (fig. 2).

Paradoxia pelletieri a été recueillie au moyen d'un appareil permettant un prélèvement intégré (brevet INRA, 1978) dans la couche d'eau allant de la surface à 10 m de profondeur. Elle coexistait avec les Chlorophycées suivantes : *Ankyra judayi* (Smith) Fott, *Ankyra spatulifera* (Korschikov) Fott, *Scenedesmus ecornis* Chodat, *Oocystis solitaria* Wittrock. Cet organisme a été trouvé dans le plancton pélagique, mais il n'est pas impossible qu'il soit également benthique, son appendice antérieur servant alors d'organe de fixation. L'abondance de cette nouvelle espèce est restée très faible durant la période citée, environ une cellule par millilitre.

Les plages de variations des principaux paramètres physico-chimiques de l'eau, de juillet à septembre 1978, période de développement de cette algue, sont récapitulées dans le tableau suivant :

	Temp. °C	pH	Ca mg/l	Mg mg/l	TAC mé/l	SO_4 mg/l	NO_3 mg P/l	PO_4 mg P/l	P. total mg P/l
minimum	16°3	8,2	33,6	3,8	1,90	15,3	0	0,009	0,039
maximum	22°8	8,2	50,2	5,8	2,74	17,9	0,26	0,018	0,059

Le cycle de reproduction de *Paradoxia pelletieri* n'est pas encore connu.

Diagnose latine :

Cellula fusiformis, solitaris, libera, heteropolaris (L = 18-22µm, l = 3-4µm). Unus polus ornatus processus insignificanti in coni forma qui anchora similis est. Apex poli qui hanc appendicum fert dilucidissimus est. Alter polus rotundus est. Cellula tenuissimis radiantibus setis ornata, maxime in posteriori polo. Chromatophorus unum centralem pyrenoidum fert. Iconotypus: fig. 1 (A, B, C, D). Locus classicus: lacu burgetense (Gallia).

Nous remercions le professeur BOURRELLY qui nous a fait bénéficier de son expérience et nous a encouragé à publier cet article.

(manuscrit accepté le 22 février 1979)

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L'ÉVOLUTION DE LA STRUCTURE CLADOMIENNE chez les CHARALES et les CÉRAMIALES

Étude comparative

Marius CHADEFAUD*

RÉSUMÉ. — Le thalle des *Chara* est formé de cladomes à phyllidies, non à pleuridies, cela au terme d'une évolution qui a conduit de cladomes à pleuridies (*Draparnaldiopsis*) à des cladomes à phyllidies de type simple *(Nitella)*, puis à des cladomes à phyllidies de type complexe (*Chara*). Une évolution analogue mais toutefois non identique, se retrouve chez les Céramiales.

SUMMARY. — The thallus of the *Chara* is composed of cladoms with phyllidia, not with pleuridia. This is the result of an evolution which led from cladoms with pleuridia (*Draparnaldiopsis*) to cladoms with phyllidia of a simple type (*Nitella*), then to cladoms with phyllidia of a complex type (*Chara*). An analogous evolution, but not identical, is to be found in the Ceramiales.

Parmi les Algues vertes, les Charales sont particulièrement intéressantes, parce que ce sont les plus évoluées des «Chorophycées à phragmoplastes», lesquelles sont, selon PICKETT-HEAPS et MARCHANT (1972) les plus proches des plantes supérieures (cf. CHADEFAUD, 1976 et 1977).

Elles ont fait l'objet de nombreux travaux, dont les plus récents et les plus précis sont ceux de SUNDARALINGAM (1954, 1960 : étude morphologique) et de DUCREUX (1974: morphogenèse, étude expérimentale). En 1960, nous leur avions attribué une structure cladomienne, en supposant leur thalle formé de cladomes uniaxiaux, garnis de verticilles de pleuridies. Aujourd'hui, nos idées sur les cladomes ayant évolué, notamment grâce aux travaux de Mmes L'HARDY-HALOS (1966 à 1975) et ARDRÉ (1967a, 1967b; GINSBURG-ARDRÉ, 1964, 1966), nous avons modifié cette interprétation, en constatant

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Rev. Algol., N. S., 1979, XIV, 3: 253-273.

que les verticilles des *Chara* et *Nitella* sont constitués de phyllidies, et non de pleuridies.

Rappelons ici que, d'une façon générale, les cladomes uni-axiaux sont formés d'un filament axial (α) garni sur ses flancs, soit de pleuridies (π), composées de filaments pleuridiens, soit de phyllidies (φ), composées de filaments phyllidiens (v. CHADEFAUD, 1960). Le filament axial a une croissance indéfinie, assurée par une cellule initiale apicale. Les filaments phyllidiens (β 1, porteurs des β 2, porteurs à leur tour des β 3) et les filaments pleuridiens n'ont au contraire qu'une croissance définie, parce que leur initiale cesse vite de fonctionner. Mais les filaments phyllidiens, contrairement aux pleuridiens, constituent des «brachyblastes» c'est à dire des systèmes de petits cladomes, ou «brachycladomes» réduits chacun à son axe, et nés les uns des autres. Autrement dit, dans une phyllidie, les filaments β sont en réalité les filaments axiaux (à croissance limitée) de brachy-cladomes, formant un brachyblaste de formule : un β 1 + des β 2 + des β 3, etc.

Ces données étant rappelées, nous allons montrer comment elles s'appliquent aux Charales, et ensuite comparativement aux Céramiales, de l'étude desquelles d'ailleurs elles proviennent (CHADEFAUD, 1954). Nous observerons ainsi, dans ces deux groupes pourtant non apparentés, une évolution de la structure cladomienne, rattachable à un même modèle fondamental.

A. — CHARALES

Nous prendrons comme point de départ, pour suivre l'évolution de leur structure cladomienne, le *Draparnaldiopsis indica* Bharad., qu'on ne range pas parmi les Charales, mais qui nous paraît être une «Proto-Charale», encore planogame et digénétique, tandis que les Charales sont oogames et monogénétiques. Cela dit :

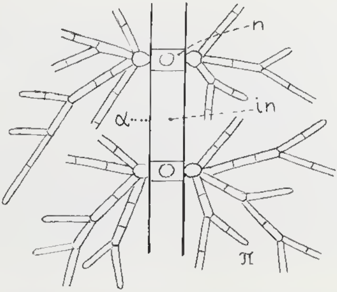

Fig. 1. — *Draparnaldiopsis indica*. — Cladome à pleuridies. Axe cladomien((α), avec sous-segments nodaux (n) et internodaux (in); sur les nodaux, cycles de quatre pleuridies (π).

a) Le *Draparnaldiopsis* (fig. 1) est formé de **cladomes à pleuridies**, comprenant chacun : 1. un filament axial (α), dont chaque segment est subdivisé en un sous-segment nodal (distal et court) et un sous-segment internodal (proximal et long), qui ne se cloisonnent ni l'un ni l'autre; 2. des pleuridies (π), insérées sur les sous-segments nodaux, en un verticille de quatre sur chaque sous-segment.

b) Les *Nitella* (fig. 2), Charales qu'on considère comme peu évoluées, sont au contraire formés de **cladomes à phyllidies**. Chez eux, il n'y a plus de pleuridies : n'existent que des filaments axiaux constitués, comme ceux du *Draparnaldiopsis*, de segments subdivisés chacun en deux sous-segments, l'un nodal, l'autre internodal. De plus, une **hiérarchisation** fait que certains de ces filaments axiaux sont des filaments **caulidiens** (= simulant des tiges) à allongement indéfini, et les autres des filaments **phyllidiens**, moins gros que les caulidien, et à croissance limitée. Dans le filament caulidiens (α) les sous-segments nodaux, au lieu de rester indivis, se subdivisent en cellules centrales entourées de péricentrales (fig. 2 B), et sur chacune de celles-ci se développe un filament phyllidien primaire (β 1); de même, sur les nodaux de ce phyllidien primaire naissent les phyllidiens secondaires (β 2), etc. Les β 1, β 2, etc., sont des axes de brachycladomes, et l'ensemble de chaque β 1, avec ses β 2, β 3, etc..., forme une **phyllidie** (φ) (fig. 2 A).

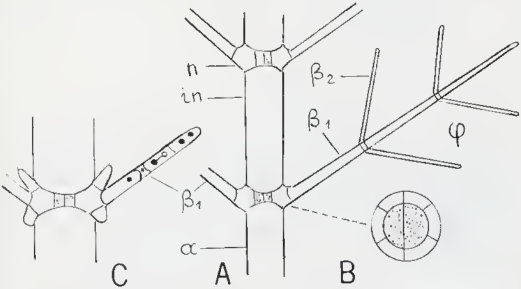

Fig. 2. — *Nitella* : Cladome à phyllidies (schéma). — A: Axe caulidien (α), avec sous-segments nodaux (n) et internodaux (in); sur chaque nodal, verticille de phyllidies (φ) formées d'un axe phyllidien (β 1) porteur d'axes phyllidiens (β 2); B: Coupe transversale schématique d'un sous-segment nodal formé de cellules centrales (encore non redivisées) et de cellules péricentrales; C: Développement d'un axe β 1 à partir d'une des péricentrales de α.

Ainsi, du type *Draparnaldiopsis* au type *Nitella*, l'évolution a comporté, corrélativement : 1. la suppression des pleuridies; 2. la hiérarchisation des filaments axiaux, devenant les uns caulidiens (α), les autres phyllidiens (β 1, β 2...);

3. La disposition coordonnée des phyllidiens pour former les phyllidies (φ).

D'après cela, du moins chez les Charales, **les phyllidies ne sont pas des pleuridies évoluées** : phyllidies et pleuridies sont des formations différentes, et **la formation des phyllidies est en corrélation avec la suppression des pleuridies.**

c) Les *Chara* (fig. 3 à 6), plus évolués que les *Nitella*, ont une organisation analogue, mais plus complexe et plus sophistiquée. On retrouve chez eux des axes cladomiens, à segments subdivisés en sous-segments internodaux et nodaux, ceux-ci cloisonnés en centrales et péricentrales (fig. 3, 4 et 5), mais il y a (fig. 3 et 4) :

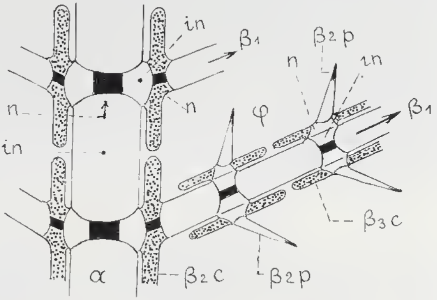

Fig. 3. — *Chara* : cladome à phyllidies (schéma). — Axe caulidien (α) avec sous-segments internodaux (in) et nodaux (n), ceux-ci subdivisés en cellules centrales (en noir) et péricentrales. — Axes phyllidiens (β 1): un verticille sur chaque sous-segment nodal de α; segment coxal dérivé d'une péricentrale de α, et subdivisé en un sous-segment internodal (in) et un sous-segment nodal (n); autres segments constitués comme ceux de α (cellules centrales en noir). — Axes phyllidiens β 2 corticants (β 2 C): nés des péricentrales du sous-segment nodal des segments coxaux de β 1, ils sont les uns ascendants, les autres descendants, et cortiquent α. Axes phyllidiens β 2 réduits à une penne (β 2 p), nés des péricentrales des sous-segments nodaux des autres segments de β 1 (un verticille sur chacun de ces sous-segments) segment coxal dérivé d'une de ces péricentrales, et subdivisé en un sous-segment internodal (in) et un sous-segment nodal (n); le reste réduit à une penne. — Axes phyllidiens β 3 corticants (β 3 C), nés des sous-segments nodaux des segments coxaux des β 2 p, ils sont les uns ascendants, les autres descendants, et cortiquent les β 1. Phyllidie $\varphi = \beta 1 +$ les $\beta 2 +$ les β 3.

- des α caulidiens; ils sont «orthotropes» (DUCREUX, 1974);
- sur chaque nodale de ceux-ci, un verticille de β 1; ils sont «plagiotropes», et terminés par des segments «imparfaits», ce qui est en rapport avec leur allongement défini (v. plus loin);
- sur le segment coxal des β 1, deux β 2 corticants (β 2 C), l'un ascendant, l'autre descendant, appliqués sur le α;

- sur les autres sous-segments nodaux des β 1, un verticille de β 2 réduits à des «pennes» (β 2 p);

- sur le segment coxal de chacune de ces pennes, deux β 3 corticants (β 3 C), l'un ascendant, l'autre descendant, appliqués sur le β 1;

- sur les sous-segments coxaux des β corticants, deux β corticants secondaires (β C'), qui ont valeur de β 3 sur les corticants β 2, et de β 4 sur les corticants β 3 (fig. 5, C_1 et C_2).

De plus, les sous-segments coxaux des β 2 portent deux «stipulodes» (fig. 5A) et les sous-segments nodaux des β corticants deux «acicules» (fig. 5 C). Celles-ci sont peut-être les stipulodes de β abortifs, qui auraient valeur de β 3 sur les β 2 corticants, de β 4 sur les corticants β 3.

On notera en outre :

1. Que sur le filament caulidien α, le mode de cloisonnement des sous-segments nodaux, donnant les péricentrales, indique une **bilatéralité** du segment, marquée dès le début par la position de la première cloison, **a - b** (la disposition des cloisons suivantes rappelle celle des cloisons séparant les péricentrales des *Polysiphonia*) (fig. 5 B);

2. Que d'après l'orientation de la cloison **a - b** sur les sous-segments nodaux successifs, l'axe cladomien α possède une **infra-structure hélicoïdale** (on peut la rapprocher de celle qu'indique la disposition hélicoïdale des phyllidies des *Polysiphonia*) (fig. 10 B);

3. Que sur les filaments axiaux caulidiens (α) les péricentrales deviennent les segments coxaux des β 1; de même sur ceux-ci les péricentrales deviennent les segments coxaux des β 2, etc... Ces segments coxaux, comme les autres, se subdivisent en un sous-segment internodal et un sous-segment nodal, celui-ci à son tour cloisonné en centrales et péricentrales (fig. 3 et 4);

4. Qu'à partir du zygote générateur, le premier cladome, qualifié (à tort) de «protonémien», a une organisation plus simple que les suivants. Chez le *Chara vulgaris*, il est formé de deux segments non cortiqués, encore subdivisés en un demi-segment internodal et un nodal, puis d'une série de segments imparfaits, non subdivisés, à l'extrémité de laquelle la cellule initiale, cessant de fonctionner, devient elle-même un tel segment. Sur le noeud du premier segment naissent des rhizoïdes, sur celui du second, un cycle de β 1, sans pennes ni cortex (fig. 6 A).

5. Enfin, que les β 1 normaux se terminent comme le filament α «protonémien», par des segments imparfaits (fig. 4)*, que le segment coxal des β corticants se cloisonne autrement que les autres, pour former un petit massif parenchymateux (**k**), d'où partent des rhizoïdes (lesquels sont peut-être des β très simplifiés) (fig. 5 A 2).

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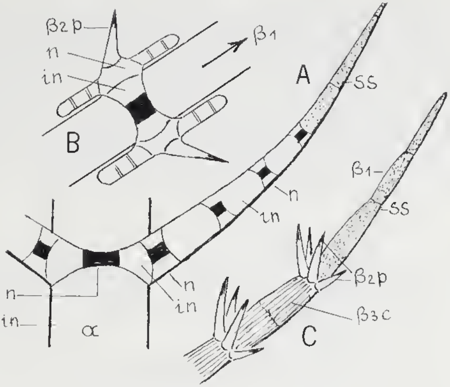
* Cela montre que les β sont bien de même nature que les α, malgré leur allongement défini.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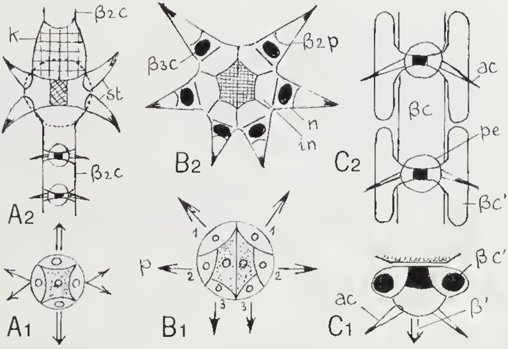
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Fig. 4 – *Chara* : phyllidie. – A - Sur un axe caulidien (α) développement des axes phyllidiens (β 1): sous-segments internodaux (in) et nodaux (n) de l'axe α, puis du segment coxal de β 1, puis des autres segments de β 1; segment coxal de β 1, dérivé d'une péricentrale de α; dans les sous-segments nodaux, centrales en noir; ss, segments imparfaits constituant la partie distale de β 1. – B - Sous-segment nodal de β 1, avec cellules centrales (en noir) et péricentrales, celles-ci devenues les segments coxaux des β p (pennes), subdivisés en un sous-segment internodal (in) et un sous-segment nodal (n); sur ce dernier, axes phyllidiens corticants (β 3 C). – C - Phyllidie adulte, avec segments de β 1 parfaits, revêtus d'axes corticants (β 3 C) et garnis de verticilles de pennes (β 2 p), et segments imparfaits (ss).

Fig. 5. – *Chara* : sous-segments nodaux des axes phyllidiens (schéma). – A1 - Axe β 1, sous-segment nodal coxal: centrale et péricentrales; axes corticants β 2 C et stipulodes st. – A2 - id.: sous-segment nodal coxal en pointillé; st, stipulodes; β 2 C, axes corticants, l'un descendant, l'autre ascendant. De celui-ci, le premier segment (k) est parenchymateux. – B1 - Axe β 1, sous-segment nodal normal: centrales et péricentrales; ordre des cloisonnements séparant les péricentrales; axes β 2 p indiqués par des flèches. – B2 - id.; axes β 2 p réduits à des pennes, avec segment coxal dérivé d'une péricentrale de β 1, et subdivisé en un sous-segment internodal (in) et un sous-segment nodal (n); sur celui-ci (en noir), départ d'axes corticants β 3 C. – C1 - Axe corticant (β C) : centrale (en noir); péricentrales latérales portant des axes corticants supplémentaires (β C', insertions en noir); péricentrale externe portant deux acicules (ac); elle devrait aussi porter un axe β', mais il ne se développe pas. – C2 - Idem - pe, péricentrale externe;ac, acicule;βC', axe corticant supplémentaire.

Quant à la formation de **cladomes axillaires**, dans l'aisselle des phyllidies du cladome principal, ils sont engendrés par une péricentrale de celui-ci, de laquelle dérivent, d'abord le filament β 1 de la phyllidie, ensuite le filament axial α' du cladome axillaire (fig. 6B). Celui-ci demeure d'ailleurs généralement à l'état de bourgeon, du fait d'une action inhibitrice émanant de l'apex du cladome principal (DUCREUX, 1974), et il est flanqué de deux bourgeons axillaires accessoires.

Pour la situation des organes reproducteurs, v. la fig. 6, C et D : les organes mâles terminent des β 2, et les organes femelles des β 3, ceux-ci homologues à des β 3 corticants.,

Ainsi, les *Chara* montrent que les cladomes à phyllidies, dépourvues de pleuridies et entièrement formés de filaments cladomiens axiaux (α, puis β 1, β 2...), homologues à ceux du *Draparnaldiopsis*, peuvent évoluer vers un type complexe, comportant des différenciations importantes. Comme ces algues sont des Chlorophycées «à phragmoplastes», et que celles-ci semblent apparentées aux plantes supérieures ou Cormophytes, on peut se demander si ce n'est pas une évolution analogue, mais toutefois différente (et «plus poussée») qui a conduit au «cormus» des plus primitives de celles-ci.

En résumé, du *Draparnaldiopsis* aux *Chara*, s'observe une évolution du type cladomien conduisant des cladomes à **pleuridies** aux cladomes **à phyllidies**, puis **à un type évolué de ceux-ci**. Et cette évolution montre que les phyllidies

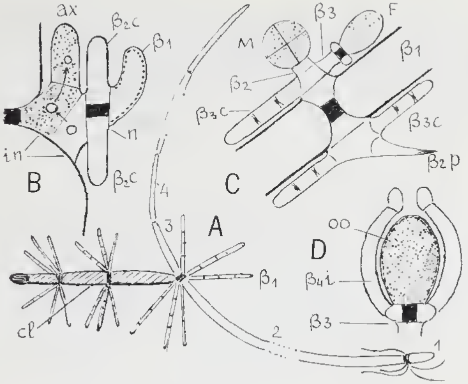

Fig. 6. — *Chara* (fin). — A - Cladome primaire du thalle, prétendu protonémien. Segment 1 très court, avec rhizoïdes sur le sous-segment nodal. Segment 2 très long, également avec verticille de β 1, sur le sous-segment nodal. Segments suivants (3-4...) imparfaits. (cf. A et C, fig. 4). Pas d'axes recouvrants. Premier cladome normal (cl) dans l'aisselle d'un des β 1. — B - Segment coxal d'un axe phyllidien β 1 donnant naissance à l'axe caulidien α x d'un cladome-fils axillaire. Dans le sous-segment internodal (in) de ce segment des cloisons ont délimité le segment coxal de α x. Du segment nodal (n) sont nés des axes corticants β 2 C (schéma). — C - Disposition des organes reproducteurs (schéma) : organe mâle (M) au sommet d'un axe β 2 (homologue aux β 2 p) ; organe femelle (F) au sommet d'un axe β 3 (homologue aux β 3 C). — D - Organe femelle (schéma). Sur le sous-segment nodal de son segment coxal (avec centrale en noir), verticille de cinq axes involucraux (β 4 i) enveloppant l'oocyste (o o), autour duquel ils sont en réalité torsadés.

ne sont pas des pleuridies évoluées, et qu'elles ne sont pas forcément portées par des axes à structure sympodiale. Elles peuvent toutefois remplacer les pleuridies des cladomes primitifs.

B. — CÉRAMIALES

Ce que nous apprennent ainsi les Charales peut être mis en parallèle avec ce que montrent les Céramiales (cependant sans parenté avec les Charales), parmi lesquelles on trouve :

a) Des espèces formées de cladomes à pleuridies. Ex.:

- le *Halurus equisetifolius* (dont les cladomes rappellent ceux des *Batrachosper-*

mum et des *Dudresnaya*);

- le *Crouania attenuata,* avec sur chaque segment un verticille de quatre pleuridies;
- le *Wrangelia penicillata*, dont les verticilles de pleuridies comportent: une pleuridie primaire, indiquant une bilatéralité (cf. *Nitella* et *Chara*) et dont les segments se séparent de l'initiale apicale par un cloisonnement oblique (cf. Rhodomélacées; v. plus loin). De cette obliquité dépend la position de la pleuridie primaire; de plus, elle varie de chaque segment au suivant selon un mode scorpioïde (= en zig-zag) de sorte que la disposition des pleuridies primaires est elle aussi scorpioïde (fig. 7).

Cette espèce montre ainsi que les cladomes à pleuridies peuvent subir une importante évolution progressive, sans pour autant devenir des cladomes à phyllidies.

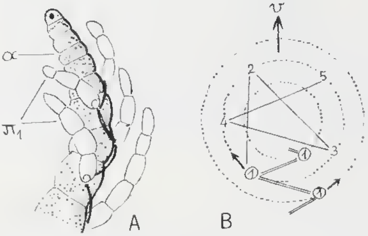

Fig. 7. — *Wrangelia penicillata* : ordre «phyllotaxique» des pleuridies. — A - Très jeune cladome: disposition «scorpioïde» (en zig-zag) des pleuridies I (α, axe cladomien; noter sa dorsiventralité; π 1, pleuridies I, insérées sur le dos de l'axe, alternativement à droite et à gauche de sa ligne médiane; autres pleuridies encore non développées). — B - Diagramme de trois verticilles pleuridiens successifs. Dans chaque verticille, cinq pleuridies (1.2.3.4.5.) en ordre approximativement quinconcial (div. 2/5). Dans les verticilles successifs, disposition scorpioïde de la pleuridie I (cf. A), et ordre quinconcial, alternativement dextre et sénestre (v, côté ventral).

b) Des espèces au contraire formées de **cladomes à phyllidies.** Exemples :

- l'*Antithamnion cruciatum* (fig. 8, A), avec: segments de l'axe caulidien (α) non subdivisés en deux sous-segments; sur chacun d'eux, près de son sommet, un cycle de quatre phyllidies (φ), dont deux majeures, en croix avec deux mineures (qui peuvent manquer); des phyllidies formées d'axes β 1 porteurs de β 2; à la base de chaque phyllidie, un segment coxal (cf. *Chara*); les organes reproducteurs sont sur les β 1, sur lesquels les tétrasporocystes remplacent chacun un β 2 (cf. *Chara*, dont les organes mâles terminent des β 2, et les organes femelles des β 3).

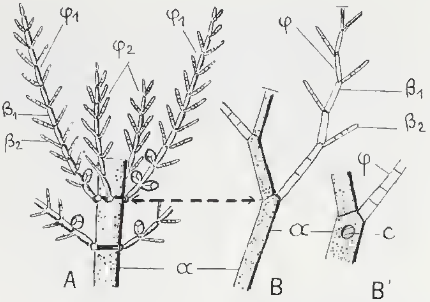

Fig. 8. — Céramiales: cladomes à phyllidies. — A - *Antithamnion cruciatum*. En principe quatre phyllidies φ par segment de l'axe caulidien α: deux majeures (φ 1) et deux mineures (φ 2), qui peuvent manquer. β 1 et β 2, axes phyllidiens. — B - *Callithamnion dudresnayi* (= *purpurascens* Harvey): une seule phyllidie (φ = la première des φ 1) par segment de α. — B' - Idem: segment fertile d'un axe α d'un thalle femelle: en plus de la phyllidie φ, deux coxales (c) de phyllidies mineures (?) ou de pleuridies (?). On sait que l'une d'elles porte un filament carpogonial et que toutes deux se divisent pour donner une cellule auxiliaire.

Une telle structure est tout à fait comparable à celle des cladomes à phyllidies des Charales, sauf toutefois que les segments caulidiens ne se subdivisent pas en deux sous-segments. Comme dans le cas des Charales, elle doit résulter de l'évolution d'un type à pleuridies, comportant la disparition de celles-ci. On doit en effet remarquer que, d'une façon générale, sur les cladomes à pleuridies de certaines espèces, les cladomes-fils remplacent chacun une pleuridie. Dans les cladomes à phyllidies de l'*A. cruciatum*, toutes les pleuridies seraient ainsi remplacées par des cladomes-fils, mais ceux-ci réduits à des phyllidies (= brachyblastes), formées de brachy-cladomes β. On retrouve ainsi l'idée selon laquelle (cf. Charales) les phyllidies ne sont, ni des pleuridies évoluées, ni forcément subordonnées à un axe α sympodial.

- les *Callithamnion*, tels que le *C. dudresnayi* Crouan (= *purpurascens* Harvey) (fig. 8, B). Ils ne diffèrent de l'*A. cruciatum* que parce que chaque segment caulidien ne porte plus qu'une seule phyllidie : la majeure I.

Toutefois, sur les segments fertiles femelles il y a encore deux coxales qui, étant placées plus bas que la phyllidie, ne sont peut-être pas les coxales de phyllidies mineures, homologues à celles de l'*Antithamnion*; elles peuvent être les coxales de deux pleuridies (non développées), non remplacées par des phyllidies, donc être pleuridiennes, non phyllidiennes (?) (V. plus loin: Rhodomélacées, fig. 10 et 11).

La réduction du nombre des phyllidies à un seul par segment caulidien est le résultat d'une bilatéralité analogue à celle des segments du *Wrangelia*, mais plus accusée. D'autre part, l'ordre «phyllotaxique» est hélicoïdal distique et non scorpioïde.

c) Des espèces **également à phyllidies, mais évoluées,** à la façon des *Chara*, bien que ce soit autrement, et d'ailleurs diversement. Exemples :

- L'*Antithamnion plumula* (fig. 9 A), dont l'évolution s'est manifestée par une **tagmatisation des cladomes à phyllidies** (cf. CHADEFAUD, 1954).

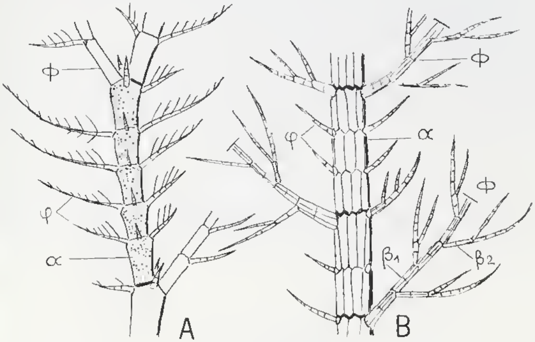

Fig. 9. — Céramiales à cladomes tagmatisés. — A - *Antithamnion plumula*. Tagme de 5 segments portant chacun 4 phyllidies φ (deux majeures, en croix avec 2 mineures; cf. *A. cruciatum*, mais mineures beaucoup plus réduites); sur le dernier segment, l'une des φ est développée en une Φ; bilatéralité: grandes φ majeures toutes à gauche; d'un tagme au suivant, inversion de la bipolarité: par suite, Φ alternativement à droite et à gauche. Cette inversion traduit un ordre hélicoïdal distique des tagmes. — B - *Heterosiphonia plumosa*. Deux tagmes, l'un de 2, l'autre de 3 segments. Même disposition que chez l'*A. plumula*, mais axe caulidien, axes phyllidiens β 1 et partie inférieure de certains des β 2 revêtus de péricentrales (cf. fig. 10 A).

Comme chez l'*A. cruciatum*, chaque segment caulidien porte quatre phyllidies, dont deux majeures, I et II, et deux mineures rudimentaires en croix avec les précédentes; chaque phyllidie majeure = 1 β_1 + des β_2 et des β_3. Mais l'axe caulidien est formé de **tagmes** successifs, comportant tous le même nombre de segments. Ces tagmes ont une bilatéralité telle que, sur chacun d'eux, les phyllidies majeures I sont toutes du même côté. Cette bilatéralité s'inverse, de chaque tagme au suivant, selon un ordre hélicoïdal distique (cf. *Callithamnion*).

Les tagmes successifs sont séparés par des cloisons obliques (cf. *Wrangelia* et, plus loin, Rhodomélacées). Au sommet de chaque tagme, la dernière phyllidie majeure I, ou phyllidie Φ se développe en un cladome-fils: cela illustre que les phyllidies sont des brachyblastes, et non des pleuridies évoluées.

Cette structure traduit un **rythme** dans le développement de l'axe caulidien (α), donc dans le fonctionnement de sa cellule initiale apicale. Selon un rythme défini, celle-ci se cloisonne d'abord plusieurs fois transversalement, pour donner les segments normaux de cet axe, puis obliquement, pour donner son dernier segment, celui qui porte la phyllidie Φ. On remarquera que sans les cloisons transversales on retrouverait le cas des *Callithamnion*, chez lesquels un tel rythme n'existe pas (à moins qu'il ait été supprimé?).

- Les Rhodomélacées, parmi lesquelles nous examinerons seulement les *Polysiphonia*, les *Heterosiphonia* et les *Pterosiphonia*.

On retrouve chez ces Algues une tagmatisation analogue à celle de l'*Antithamnion plumula*, mais avec **des axes caulidiens (α) et parfois aussi les axes phyllidiens (β), formés de cellules dites «centrales», entourées de cellules «péricentrales»**, qui sont les coxales de pleuridies. Quand celles-ci sont développées, ce qui n'est pas toujours le cas, leur ensemble forme un **cortex pleuridien**. En ce qui concerne les segments caulidiens, cela donne ce qu'on observe notamment chez les *Polysiphonia*, chez lesquels chacun des segments de l'axe α porte latéralement, près de son sommet, une phyllidie Φ, (réduite à un trichoblaste incolore et caduc), et plus bas un cycle de coxales pleuridiennes ou péricentrales, qu'entoure un cortex pleuridien chez certaines des espèces, mais non chez toutes (fig. 10 A).

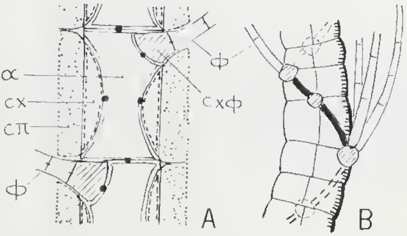

Fig. 10. — *G. Polysiphonia* : structure et disposition des segments de l'axe caulidien des cladomes. — A - Un segment: cellule axiale α (= centrale); tout autour, verticille de pleuridies, avec coxales cx (= péricentrales) et cortex pleuridien cπ; près du sommet, coxale cx Φ d'une phyllidie Φ (= réduite à un trichoblaste). Pour une interprétation possible de cette coxale, v. fig. 12. — B - Disposition hélicoïdale des segments successifs, indiquée par celle des Φ. Péricentrales seules figurées; espèces à 4 péricentrales par segment caulidien; par suite, entre les Φ successives, div. = 1/4.

Cette structure, qu'on doit qualifier de «rhodoméloïde», peut être interprétée, quant à son origine phylogénétique, en prenant comme point de départ: 1. le *Wrangelia penicillata* (fig. 7) dont chaque segment caulidien porte, près de son sommet, un verticille de pleuridies disposées (approximativement) en ordre quinconcial, et dont la première seule peut porter, sur sa base, un cladome-fils; 2. les *Callithamnion* (fig. 8 B), dont chaque segment caulidien porte, près de son sommet, une phyllidie unique (qui peut se développer en un cladome-fils) et plus bas une paire de coxales, peut-être pleuridiennes (présentes seulement sur les segments fertiles des thalles femelles).

On se trouve là en présence de deux variantes de la structure fondamentale représentée par le diagramme A de la fig. 11, comportant une pleuridie dorsale a, une pleuridie ventrale b, et des pleuridies latérales en ordre scorpioïde (en zig-zag). Chez le *Wrangelia*, du fait d'une dorsiventralité accusée et de la bilatéralité des axes caulidiens, les pleuridies a et b ont été déplacées, alternativement vers la gauche ou vers la droite, l'une des pleuridies latérales proches de b a été

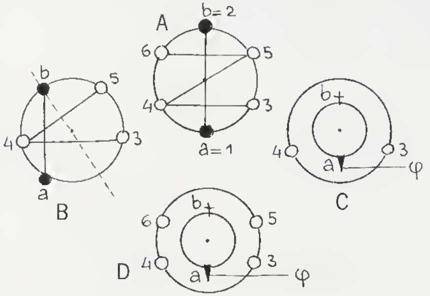

Fig. 11 — G. *Polysiphonia* : origine possible de l'organisation des segments caulidiens (diagrammes schématiques). — A - Segment caulidien primitif (théorique): seulement un verticille de pleuridies, mais bilatéralité nette. Pleuridies a (= 1), dorsale, et b (= 2), ventrale, dans le plan de symétrie; pleuridies suivantes (3,4,5,6) en ordre scorpioïde (en zig-zag). — B - *Wrangelia penicillata* (cf. fig. 7) : a et b déportées vers l'un des côtés (ici, côté gauche); pleuridie 6 supprimée; en conséquence, pleuridies en ordre quinconcial et plan de symétrie oblique. — C - *Callithamnion* (cf. fig. 8) : verticille dédoublé; verticille supérieur portant seulement la pleuridie a (remplacée par la phyllidie φ; b supprimé (+); verticille inférieur avec seulement les pleuridies 3 et 4, présentes seulement sur les segments femelles fertiles, et réduites à leurs coxales. — D - *Polysiphonia* : espèce à quatre péricentrales par segment (cf. fig. 10): verticille également dédoublé; verticille supérieur ne portant également que a (= phyllidie φ); mais verticille inférieur portant encore les pleuridies 3,4,5 et 6 du *Wrangelia*, en ordre scorpioïde. Chez d'autres espèces, ces pleuridies sont plus nombreuses; il y a alors un nombre plus élevé de péricentrales par segment.

supprimée, et il en est résulté une disposition quinconciale, avec axe géométrique oblique (diagr. B) (1). Chez les *Callithamnion* n'ont été conservés que la pleuridie dorsale a, remplacée, par une phyllidie, et (sur les segments femelles fertiles) l'un des couples des pleuridies latérales (réduites à leur coxale). De la sorte, le verticille pleuridien de A a été dédoublé en un verticille phyllidien et un verticille demeuré pleuridien, celui-ci situé plus bas sur les flancs de la cellule axiale (diagr. C). En combinant ces deux évolutions, on arrive au diagr. D, comportant un verticille de deux phyllidies, dont la ventrale peut manquer, et plus bas un verticille de pleuridies latérales, dont le nombre peut d'ailleurs être supérieur à quatre : c'est là précisément le diagramme des segments caulidiens «rhodoméloïdes» : tels que ceux des *Polysiphonia* (fig. 10 A).

Le dédoublement du verticille pleuridien du diagramme A en un verticille phyllidien superposé à un verticille demeuré pleuridien n'est pas sans rappeler la subdivision des segments des Charales en un sous-segment nodal porteur de phyllidies, et un sous-segment internodal. Mais celui-ci ne porte pas de pleuridies, et d'autre part il n'y a pas, chez les Rhodomélacées, de cloison transversale entre les deux verticilles, à moins toutefois qu'on admette que, dans la cellule axiale des *Polysiphonia*, la petite cellule portant la phyllidie est l'équivalent très réduit, du sous-segment nodal des Charales (fig. 12) (?).

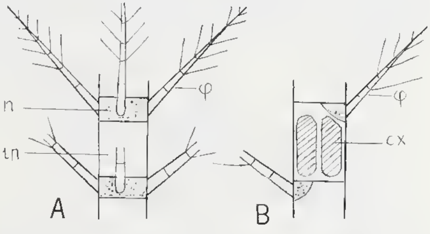

Fig. 12 — *Polysiphonia* : comparaison possible avec les Charales. — A - Schéma d'un segment caulidien de Charale, avec sous-segments internodal in et nodal n, celui-ci porteur d'un verticille de phyllidie φ. Pas de pleuridies. — B - Schéma d'un -id- de *Polysiphonia* : sous-segment nodal réduit à la coxale d'une phyllidie unique φ (= trichoblaste); sous-segment internodal entouré de coxales pleuridiennes cx (= péricentrales).

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(1) Cette transformation d'un diagramme hexagonal, de 2 + 4 pièces, en un diagramme pentagonal quinconcial est exactement celle qui a donné le calice pentamère quinconcial de la plupart des Dicotylédones. Il y a là un remarquable exemple de parallélisme entre des groupes extrêmement éloignés et, si l'on veut, un argument en faveur des théories structuralistes (cf. CHADEFAUD, *C. R. Ac. Sc.*, Paris 1955, 240: 1129-1131.

Cela dit, la tagmatisation des axes caulidiens ou phyllidiens des Rhodomélacées est indiquée par la présence sur le segment terminal de chaque tagme, d'une phyllidie Φ, parfois deux, distincte des autres parce qu'elle peut porter un cladome-fils, ou être remplacée par un tel cladome. De la sorte :

1. L'*Heterosiphonia plumosa* (fig. 9, B) est directement comparable à l'*A. plumula* (fig. 9, A), avec tagmes caulidiens porteurs de deux rangées de phyllidies, rectilignes et opposées, et sur leur dernier segment une phyllidie Φ, dont la position indique que de chaque tagme au suivant il y a inversion de la bilatéralité, donc que les tagmes successifs sont en ordre hélicoïdal distique. Mais ces tagmes ne sont que de deux ou trois segments, et ceux-ci sont revêtus de péricentrales (= coxales pleuridiennes). Dans les phyllidies Φ l'axe β 1 est formé de tagmes à deux segments, également revêtus de péricentrales; les axes β 2 débutent par un tagme à deux segments, parfois pareillement revêtus; le reste n'est pas tagmatisé; les β 3 ne le sont pas non plus.

2. Une organisation semblable se retrouve chez les *Pterosiphonia*, par ex. le *P. parasitica* (fig. 13, A), sauf qu'ils n'ont pas de phyllidies φ, et que leurs phyllidies Φ sont entièrement revêtues de péricentrales. Les tagmes caulidiens sont de deux segments; les β 1 sont formés d'un tagme plurisegmenté, suivi de tagmes à deux segments; les β 2 ne sont pas tagmatisés. Chez le *P. complanata* les β 2 portent des β 3. Chez le *P. pennata*, au contraire, il n'y a pas de β 2. Dans tous les cas, les axes β sont disposés en séries rectilignes opposées, comme chez l'*A. plumula* et l'*H. plumosa*, et les tagmes successifs sont en ordre distique.

On peut penser que par rapport à l'*Antithamnion*, les *Pterosiphonia* sont plus évolués, leur évolution s'étant traduite par la suppression des phyllidies φ et par la formation d'un revêtement complet de péricentrales sur les β. Cela est d'ailleurs justifié par la comparaison avec les *Brongniartella* et *Boergeseniella*, car :

- Chez le *Brongniartella byssoides* (fig. 13, B) les φ n'ont pas encore disparu, mais dans les Φ (= brachyblastes) on observe un revêtement de péricentrales sur l'axe β 1 et sur la partie basale de certains des β 2. Le sommet de ceux-ci, et les autres β 2, au contraire encore dépourvus de péricentrales, sont des trichoblastes (pigmentés et non caducs);
- chez le *Boergeseniella fruticulosa* (fig. 13, C), dont la tagmatisation est très régulière, l'organisation est presque celle des *Pterosiphonia*, sauf qu'existent encore des phyllidies φ (= trichoblastes), et que leur Φ et φ sont en ordre hélicoïdal non distique.

3. Les *Polysiphonia* (fig. 10, 13 B, 14 et 15) diffèrent au contraire davantage de l'*H. plumosa*, et leurs caractères semblent indiquer une évolution différente: leurs phyllidies Φ et φ sont en effet disposées, non pas en ordre distique, mais en ordre hélicoïdal polystique, avec divergence variable selon les espèces. De plus, on trouve, chez certains d'entre eux une disposition aberrante des phyllidies Φ, et chez toutes les espèces les φ sont réduites à des trichoblastes, incolores et caducs.

La tagmatisation indiquée par les Φ est plus ou moins irrégulière, le nombre des segments variant d'un tagme à l'autre. Ainsi, le long de l'axe caulidien,

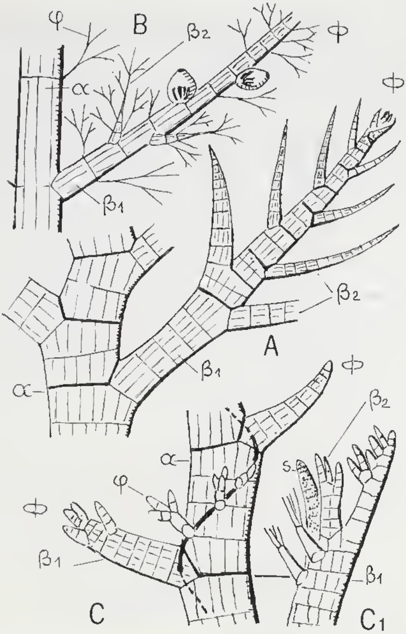


Fig. 13. — *Pterosiphonia* : Phyllidie Φ (= brachyblaste) du *P. parasitica*, comparée à celles du *Brongniartella byssoïdes* et du *Boergenseniella fruticulosa* (v. le texte). — A - *Pterosiphonia* : axe caulidien α et axes phyllidiens β 1 et β 2 entièrement revêtus de péricentrales; tagmatisation régulière de α, avec tagmes de 2 segments; premier tagme de β 1 à 5 segments, les suivants à deux; β 2 non tagmatisés (ou peut-être réduits à leur premier tagme plurisegmenté); pas de trichoblastes. — B - *Brongniartella* : axes α et β 1 également revêtus de péricentrales, mais ne l'est que seulement la base de certains des β 2; tagmatisation moins régulière, les tagmes étant de un ou deux segments; encore des phyllidies φ, et des trichoblastes, formés par ces φ, et par le sommet ou la totalité des β 2. — C - *Boergeseniella* : axes α et β 1 des phyllidies entièrement revêtus de péricentrales, ainsi que certains des β 2 phyllidiens, mais encore des trichoblastes sur α (= des φ) et sur les β des Φ; tagmatisation très régulière (tagmes caulidiens à 2 segments): ordre hélicoïdal régulier des φ et Φ sur les axes caulidiens. En C1, β 1 (avec sommet S), β 2 normaux et β 2 réduits à des trichoblastes d'une phyllidie Φ.

il varie de 3 à 13 chez le *P. furcellata* (fig. 14, A) et de 5 à 7 chez le *P. urceolata*. Mais chez le *P. nigrescens*, il est constamment de 2 ou 3 (et de 2 chez le *Borgeseniella fruticulosa* : fig. 13, C).

Sur chaque tagme, les phyllidies sont disposées sur une hélice dextre, et l'hélice de chaque tagme continue celle du précédent. D'un tagme à l'autre on ne retrouve donc pas l'inversion observée chez l'*A. plumula*, l'*Heterosiphonia* et les *Pterosiphonia*. La phyllidie du dernier segment est une phyllidie Φ, portant sur sa cellule coxale, et à sa gauche, un cladome-fils. Peut-être faudra-t-il plutôt penser qu'elle est représentée par ce cladome-fils, avec une phyllidie Φ (= trichoblaste) sur sa cellule coxale, et à sa droite. Chez certaines espèces, une partie des segments sont dépourvus de phyllidies φ : ainsi il n'y en a pas du tout chez le *P. lanosa (= fastigiata)*, ce qui peut être le résultat d'une évolution régressive.

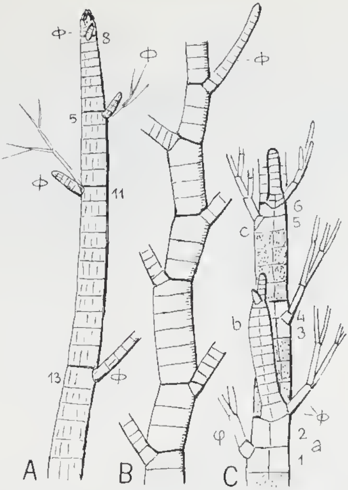
Entre les phyllidies des segments successifs, la divergence varie selon les espèces. Elle dépend du nombre de péricentrales par segment. Quand ce nombre est 4, la div. = 1/4 (fig. 10, B).

Chez certaines espèces, cette organisation est perturbée par l'intercalation entre les tagmes successifs, d'**inter-tagmes non hélicoïdaux**. Nous l'avons déjà signalé autrefois (CHADEFAUD, 1967). En fait, chaque inter-tagme constitue la base du tagme suivant et de la sorte chaque axe caulidien a pour base un inter-tagme plus ou moins long, dépourvu de phyllidies. Ont des axes caulidiens à inter-tagmes, par ex. :

- Le *Polysiphonia sertularioïdes*. Sur l'axe représenté par la fig. 14, C, les tagmes hélicoïdaux sont de deux segments portant, le premier une phyllidie φ (= trichoblaste), le second une phyllidie Φ (= trichoblaste + cladome-fils). L'hélice de chaque tagme continue celle du précédent. Les inter-tagmes sont de trois ou quatre segments. Mais on observe aussi des axes à structure différente.

- Le *P. tenerrina*. Ses tagmes hélicoïdaux ont un nombre variable de segments, et là encore il y a continuité de leurs hélices. Ils ne portent généralement que des phyllidies φ. Entre eux, les inter-tagmes ont de un à trois segments, dont l'un porte généralement une phyllidie Φ, représentée par un cladome-fils. D'après les dispositions de cette phyllidie et des phyllidies φ, on peut penser que fondamentalement les inter-tagmes étaient de trois segments, à disposition orthomère, avec deux rangées rectilignes et opposées de phyllidies, donc avec une organisation semblable à celle des tagmes de l'*A. plumula* (cf. fig. 9, A). Mais une seule des phyllidies se développe (une Φ), qui peut même manquer; les autres demeurent virtuelles. Les fig. 15, B, C, D, montrent certains des cas réellement observés: inter-tagmes réduits à deux segments, puis à un seul; disposition variable de l'unique phyllidie Φ, et absence des autres phyllidies.

Si le schéma A est valable, il peut indiquer qu'ancestralement les *Polysiphonia* ont eu l'organisation et la tagmatisation de l'*A. plumula*, de l'*Heterosiphonia plumosa*, par rapport auxquels ils seraient d'un type plus évolué, leur évolution ayant réduit un sur deux des tagmes orthomères à des inter-tagmes, qui ensuite ont généralement disparu, tandis que les autres devenaient hélicomères.


Φ
8
Φ
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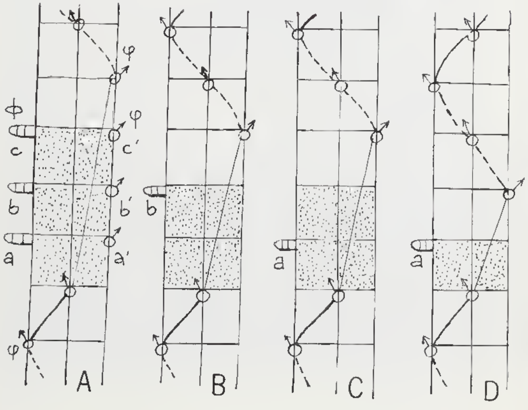
φ
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Fig. 14. — *Polysiphonia* : cladomes; tagmatisation indiquée par les Φ ou par les cladomes-fils. — A - *P. furcellata* : tagmatisation très irrégulière; tagmes de 13, 11, 5 et 8 segments. Mais cette irrégularité tient peut-être à la présence d'intertagmes (?), cf. C. — B - *P. thuyoïdes* : tagmatisation presque régulière; tagmes de 2 ou 4 segments (rarement davantage). — C - *P. sertularioïdes (= macrocarpa* Harvey) : alternance de tagmes (en blanc) et d'intertagmes (pointillés). Tagmes a, b, c de deux segments portant le premier une φ (= trichoblastes), le second une Φ (= trichoblaste + ébauche de cladome-fils; pour b, celui-ci n'est pas visible); φ et Φ en ordre hélicoïdal, avec divergence = 1/4. Segments des tagmes numérotés de 1 à 6.

Fig. 15. — *Polysiphonia tenerrima* : intertagmes. — A - Structure fondamentale probable (?) des intertagmes: 3 segments en ordre rectiligne (orthomérie), avec deux rangs opposés, l'un de phyllidies Φ(a, b, c), l'autre de phyllidies φ (a', b', c',). Sur les tagmes, seulement des φ, en ordre hélicoïdal, avec div.: 1/4. La présence des intertagmes n'altère pas cet ordre et cette divergence. De tels intertagmes ont été réellement observés, mais sans Φ ni φ. — B à D - Intertagmes observés, portant seulement l'une des Φ (a ou b), et réduits à 2 segments ou un seul. Dans quelques cas, les deux rangées de phyllidies des intertagmes réelles ou virtuelles) étaient en quadrature, et non opposées.

C. — CONCLUSION

En définitive, il résulte de l'étude comparative des Charales et des Céramiales que, malgré des différences qu'on ne saurait négliger, on retrouve dans ces deux groupes une structure cladomienne évoluant selon le même schéma, de sorte qu'on y trouve, d'abord des cladomes à pleuridies, ensuite des cladomes à phyllidies d'un type encore simple, enfin des cladomes à phyllidies d'un type évolué, plus ou moins complexe et sophistiqué.

Charales et Céramiales n'étant nullement apparentées, cela signifie que le type cladomien et son évolution ont pu apparaître, d'une manière polyphylétique, indépendamment dans les divers phylums d'Algues, et que par conséquent ils résultent d'une tendance évolutive commune à la plupart d'entre eux, sinon à tous. Dès leur origine, cette tendance devait être inscrite dans leur génome, comme si elle avait, dans le super-embranchement des Algues, un caractère fondamental. Mais ensuite elle ne s'est manifestée qu'à partir d'un certain niveau de l'évolution, qui n'a été atteint qu'en fonction d'autres tendances génotypiques, et sans doute aussi contrôlé par l'action du milieu.

Toutefois, on doit remarquer que la structure cladomienne n'a pas été également réalisée dans tous les groupes d'Algues : elle l'a été très bien chez les Floridées et diverses Phéophycées, mais beaucoup moins chez les Chlorophycées, ou seules les Charales (et à un moindre degré les *Draparnaldia*) sont franchement cladomiennes; dans les autres groupes il n'y a presque pas d'espèces cladomiennes; encore ne le sont-elles pas parfaitement, ou même il n'y en a pas du tout (1).

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(1) Pourtant, il y en a déjà chez les Cyanophycées: cladomes (à la vérité imparfaits) du *Stigonema mamillosum*, par ex.

On remarquera ici que les groupes dans lesquels la tendance cladomienne ne s'est que rarement manifestée, ou fait défaut, sont par contre ceux dans lesquels abondent les espèces monadoïdes : Volvocales, Euglénomonadines, Cryptomonadines, Chrysomonadines, etc., tandis qu'au contraire il n'y a chez les Floridées et les Phéophycées, si souvent cladomiennes, aucune espèce flagellée nageuse. Ainsi, Floridées et Phéophycées ont manifesté des tendances essentiellement «végétales», tandis que dans les autres groupes on observe une tendance «animale» accusée. Autrement dit, de par leur génome initial, certains phylums sont purement végétaux, tandis que les autres conduisent au Règne animal.

A propos des Charales, on a vu que la rareté, chez les Chlorophycées, des formes cladomiennes, peut tenir en partie à une autre cause : chez celles qui ont atteint le stade cladomien, celui-ci a pu être dépassé, de sorte qu'au lieu d'un thalle cladomien elles ont un **cormus**, en principe feuillé. Selon PICKETT-HEAPS et MARCHANT (1972), puis CHADEFAUD (1977), cela concerne les Chlorophycées «à phragmoplastes», dont les plus évoluées sont les Charales, et dont les formes surévoluées à cormus, seraient les Cormophytes (= Archégoniates).

Enfin, la notion de surévolution des cladomes, ainsi envisagée, conduit à remarquer que, sans quitter les Algues, on trouve aussi des espèces **métacladomiennes**, dont le thalle est formé de **cladomes surévolués**, sans pour autant être devenu un cormus. La surévolution en jeu peut se concevoir par comparaison avec ce que montrent les *Gracilaria* (selon BODARD et KLING, 1978) : le sommet de leurs cladomes est typiquement cladomien, avec filament axial hélicomère et cortex pleuridien, mais dans leur partie plus âgée la structure cladomienne s'efface, du fait que les cellules axiales et celles de la partie interne du cortex pleuridien forment un pseudo-parenchyme médullaire. Cette partie du thalle devient ainsi méta-cladomienne, et il est possible que ce soit aussi le cas des autres Floridées à rameaux composés d'une moelle et d'un cortex. Mais d'autres Algues n'ont pas une structure cladomienne reconnaissable sans doute pour une autre raison : elles auraient évolué sans passer par un stade cladomien typique, et seraient donc **para-cladomiennes**. Tels sont peut-être les Fucales, les Dictyotales, les Laminariales (?).

(manuscrit accepté le 15 mai 1979)

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P. BOURRELLY, M. RICARD

BERTHOLD, W.H., 1978 – **Ultrastrukturanalyse der endoplasmatischen Algen von *Amphistegina lessonii* d'Orbigny, Foraminifera (Protozoa) und ihre systematische Stellung.** *Arch. Protistenk.*, 120: 16-62.

L'auteur observe des algues unicellulaires dans le cytoplasme d'un foraminifère des îles Hawaï.

L'étude en microscopie électronique permet, d'après le mode de division nucléaire, de penser qu'il s'agit de diatomées. Ces diatomées conservent leurs caractères cytologiques mais la carapace siliceuse est fragmentée et très réduite. Les symbiotes connus chez les foraminifères sont le plus souvent des Dinophycées, plus rarement des Chlorophycées et des Cryptophycées. Jusqu'au mémoire de BERTHOLD, un seul cas de symbiose de foraminifère et diatomées avait été observé par DIEZ-ELBRÄCHTER (1971).

Le travail de BERTHOLD est étayé par une illustration très démonstrative de 45 photographies d'ultrastructure en microscopie électronique.

FINDLAY, D.L. and KLING, H.J., 1978 – **A species list and pictorial reference to the phytoplankton of central and northern Canada.** *Fisheries and Marine Service, Manuscript Rep.* 1503, part I: 619p.; part II: 619 p.

Ces deux ouvrages constituent un ouvrage pratique destiné à aider les chercheurs appelés à travailler sur les lacs du centre et du nord canadien dans des domaines touchant à l'algologie.

615 taxons sont regroupés, appartenant aux Cyanophycées, Euglénophycées, Chlorophycées, Chrysophycées, Diatomophycées et Dinophycées. Chaque espèce fait l'objet d'une fiche indiquant sa taille, les lieux et périodes de récolte et une figure reprise sur des ouvrages d'auteurs spécialisés: HUBER-PESTALOZZI, SKUJA, SMITH, UHERKOVICH, HUSTEDT, etc. En dehors de quelques Desmidiées au dessin trop sommaire, les illustrations sont, dans l'ensemble, bien choisies, suffisamment claires et détaillées. Le nom de l'auteur des figures, souvent différent de celui de l'éditeur qui a effectué la révision globale d'un groupe, n'est pas mentionné.

Une mise à jour, à l'aide des travaux d'algologie récents, serait utile pour supprimer quelques lacunes ou inexactitudes: certains noms d'espèces sont encore orthographiés avec une majuscule; *Marssoniella elegans* est signalé parmi les Cyanophycées alors que les observations de KOMAREK & VAVRA (1967) ont démontré qu'il s'agit d'un groupement de spores d'une microsporidie parasite des ovocytes de *Cyclops*; quelques Xanthophycées sont signalées parmi les Chrysophycées et une bactérie est répertoriée dans les Pyrrophytes; la classification des Desmidiées serait à revoir. Enfin, il n'est pas fait état du troisième tome de l'ouvrage de base de P. BOURRELLY (1970) sur les Algues d'eau douce.

L'index complet placé à la fin de chacun des deux volumes facilite l'emploi de cette liste illustrée, indispensable à tous ceux qui s'intéressent au phytoplancton lacustre de ces régions du Canada.

GRANHALL, U., ed., 1978 — **Environmental role of Nitrogen fixing Blue-green Algae and asymbiotic Bacteria.** *Ecological Bulletins*, N.F.R. Stockholm, 26: 1-391, 100 Sw. Cr., broché.

Ce volume est le compte-rendu d'un symposium tenu à Uppsala en 1976. Les algologues seront intéressés par les deux premiers chapitres se rapportant au rôle des Cyanophycées aquatiques et subaériennes. Il s'agit de communications originales. Citons simplement G.E. FOGG : Nitrogen fixation in the Ocean; R.H. BURRIS & R.B. PETERSON: Nitrogen-fixing blue-green algae, their H_2 metabolism and their activity in freshwater lakes; J.R. GALLON : Calcium and nitrogen fixation by *Gloeocapsa*; P.A. REYNAUD & P.A. ROGER: N_2 fixing algal biomass in Senegal rice fields; J.K. JONES & R.E. WILSON: the fate of nitrogen fixed by a free-living blue-green alga; J. SKUJINS & B. KLUBEK: Nitrogen fixation and cycling by blue-green algae- lichen- crusts in arid rangeland soils.

Le troisième chapitre est consacré à la fixation d'azote par les Cyanophycées symbiotiques des lichens, des *Azolla* et des *Anthoceros*. Remarquons spécialement les communications de W.D.P. STEWART & G.A. RODGERS : Studies on the symbiotic blue-green algae of *Anthoceros, Blasia* and *Peltigera* et de J.H. BECKING: Ecological and physiological adaptations of *Anabaena* in the *Azolla-Anabaena azollae* symbiosis.

Le quatrième chapitre est réservé aux bactéries fixatrices d'azote.

La simple énumération de ces communications montrera, nous l'espérons, tout l'intérêt que présente cet ouvrage, aussi bien pour les algologues que pour les physiologistes.

Rappelons la réimpression, dans la même série, d'un intéressant ouvrage consacré aux cycles de l'azote, du phosphore et du soufre : Nitrogen, Phosphorus and Sulphur - Global cycles. *Ecological Bulletins*, n° 22, NFR Stockholm, SVENSSON B.H. and SODERLUND R. ed.: 192 p., 1976, 2nd reprinted ed. 1979, 40 Sw. Cr., broché.

KUROKAWA, S., 1979 — **Studies on Cryptogams of Papua New Guinea.** *Academia Scientific Book Inc.*, Tokyo: 150 p.

Ce volume présenté par KUROKAWA groupe une série d'études faites sur le matériel récolté en 1975, lors de l'expédition botanique japonaise en Nouvelle Guinée. En algologie nous trouvons quatre articles :

1. – Les algues d'eau douce: algues filamenteuses vertes par T. YAMAGISHI et M. WATANABE avec 44 taxons dont *Cloniophora plumosa* et *Cylindrocapsopsis indica*.

2. – Desmidiées de Woitape par M. WATANABE, G.W. PRESCOTT et Y. YAMAGISHI. Les auteurs signalent 45 taxons avec des nouveautés pour les genres : *Cylindrocystis, Closterium, Spinoclosterium, Euastrum, Cosmarium* et *Staurastrum*.

3. – Les Cyanophycées d'eau douce par M.M. WATANABE, M. WATANABE et T. YAMAGISHI avec 49 taxons dont *Rivularia vieillardii*.

4. – Le dernier article de S. WATANABE est consacré aux algues du sol. L'auteur obtient 13 taxons en culture dont une nov. sp. de *Chlorella (Palmellococcus)* et une de *Cloeocystis (Palmogloea)*.

Cet ensemble, fort intéressant pour une région encore très mal connue, est soigneusement illustré, mais il est dommage que la répartition géographique des algues identifiées ne soit pas indiquée.

MATVIENKO, O.M. et DOGADINA, T.V., 1977 – **Visnatchik prisnovodnich vodorostej Ukrainskoj, R.S.R. - III, 2 - Pyrrophyta**. Kiev, 1 vol. rel.: 386 p.

Dans ce volume, les auteurs décrivent et figurent les espèces de Pyrrophytes connus d'Ukraine. C'est en quelque sorte une «Süsswasserflora» régionale. Ce volume est consacré aux Chloromonadines, Cryptophycées, et Dinophycées. L'embranchement *Pyrrophyta* est divisé en 3 sous-embranchements *Chloromonadophytina, Cryptophytina* et *Dinophytina*.

Les *Cryptophytina* groupent deux classes: *Cryptomonadophyceae* et *Cryptococcophyceae* et les Dinophytina cinq classes : *Dinorhizophyceae, Dinomonadophyceae, Dinocapsophyceae, Dinococcophyceae* et *Dinotrichophyceae*. Cette hiérarchisation ne nous satisfait guère, car il s'agit, à notre avis, d'ordres qui sont élevés au rang de classes.

De plus les *Chloromonadines* très proches des *Xanthophyceae* n'ont pas leur place dans les *Pyrrophytes*.

Le livre, bien illustré, mais avec très peu de dessins originaux rendra des services aux algologues pouvant lire et comprendre l'ukrainien.

MATVIENKO, O.M. et DOGADINA, T.V., 1978 – **X - Xanthophyta**. Kiev, 1 vol. rel.: 511 p.

Comme dans le volume précédent, les auteurs relèvent d'un cran la hiérarchie: les Xanthophycées forment un embranchement des Xanthophyta avec 6 classes: *Xanthorhizophyceae, Xanthomonadophyceae, Xanthocapsophyceae, Xanthococcophyceae, Xanthotrichophyceae*, et *Xanthosiphonophyceae*. Pour nous, ces classes sont des ordres.

Signalons que les auteurs rangent dans les Xanthophycées les *Microthamnion* (d'après SKUJA, 1956, qui ne justifie pas cette place) et *Actidesmium* : ces algues à zoospores à deux flagelles égaux et à réserve d'amidon sont des Chlorophycées.

Malgré cela, ce volume nous renseigne de façon très précise sur la flore ukrainienne et son illustration sera précieuse pour les espèces endémiques de cette région.

MONTGOMERY, R.T., 1978 – **Environmental and ecological studies of the benthic diatoms communities associated with the coral reefs of the Florida Keys.** *Ph. D. Thesis, Florida State Univ. Coll. Arts Sci.*, vol. I: 320 p., man.

MONTGOMERY, R.T. and MILLER III, W.I. – *Ibid.*, **A Taxonomic study of Florida Keys benthic diatoms based on scanning electron microscopy.** *Ibid.*, vol. II: 204 pl., man.

La première partie de ce travail est consacrée à l'étude de l'environnement et de l'écologie des communautés de diatomées benthiques associées aux récifs coralliens de la côte de Floride. L'auteur analyse la composition spécifique et la structure des communautés des populations de diatomées de divers habitats des Florida Keys. Ces habitats sont riches en diatomées mais chacun est caractérisé par une flore propre comme en témoignent les indices d'affinité. Sur les substrats coralliens proprement dits, les densités de diatomées sont plus importantes sur les parties mortes que sur les parties vivantes ce qui laisserait supposer que, continuellement, le corail vivant se débarasse des diatomées épibiontes.

Les études de peuplement de 5 types de substrat, placés dans des habitats colonisés par des *Thalassia* et par des madrépores, montrent qu'il existe une relation positive entre la diversité spécifique et la complexité de l'habitat : celui-ci semble être le facteur réglant la composition et la structure des communautés benthiques. Les modalités de peuplement des substrats coralliens, nettoyés de toute matière organique puis replacés dans le milieu, indiquent que la composition spécifique, plutôt que la densité, est le facteur dominant dans la détermination du degré de compétition au cours de la colonisation d'un substrat. Sur des supports en plexiglas, à la différence des études antérieures, le nombre d'espèces n'augmente pas proportionnellement à la surface de peuplement; néanmoins, cet accroissement de la surface influe sur la composition spécifique et sur la structure des communautés de diatomées.

La deuxième partie, réalisée en collaboration avec W.I. MILLER, se présente comme un album photographique des divers taxons de diatomées benthiques récoltées dans les Florida Keys. Ces nombreuses microphotographies, il y en a plus de 1600, ont toutes été réalisées en microscopie électronique à balayage et sont d'une qualité remarquable. Les auteurs présentent ainsi un nombre considérable de taxons dont l'identification est soit complète soit incomplète et ouverte. Sous cette forme il s'agit là d'un remarquable outil de travail dont l'utilisation se trouve facilitée par la présence d'un répertoire alphabétique des divers genres et espèces.

En conclusion le travail de MONTGOMERY, auquel a collaboré en partie MILLER, est remarquable par la quantité d'informations tant écologiques qu'iconographiques qu'il livre à tous les diatomistes, et en particulier à ceux travaillant sur les écosystèmes récifaux. Malheureusement, et nous souhaitons que ce ne soit que temporaire, cet ouvrage volumineux ne figure qu'à l'état de manuscrit tiré à un nombre réduit d'exemplaires. Ces deux volumes doivent être suivis d'un troisième consacré aux descriptions taxinomiques, nous l'attendons avec impatience.

PARA, O.O. et GONZALEZ, M., 1977 – **Desmidiacéas de Chile III. Desmidiacéas de la Isla de Chiloé.** *Gayana, Bot.*, 34: 103 p.

Dans cette île chilienne, les auteurs reconnaissent 150 taxons, dont 47 sont nouveaux pour le Chili.

Les *Closterium* avec 32 taxons, sont les plus nombreux, suivis par les *Staurastrum*,29 et les *Cosmarium*, 28.

Une illustration abondante de 235 figures, suivie d'un index, terminent cet inventaire descriptif.

SIMONSEN, R., Ed., 1979 – ***BACILLARIA*. International Journal for diatom Research.** J. Cramer print., vol. 2: 214 p., 10 fig., 38 pl., relié, 60 DM.

Après *BACILLARIA 1* paru en 1978, voici le deuxième volume de cette revue destinée aux seuls diatomistes. Le sommaire comporte 7 articles dont le plus volumineux est celui de SIMONSEN: The diatom system: Ideas on Phylogeny. L'auteur expose ici ses conceptions sur la phylogénie des diverses familles de diatomées, conceptions qui se sont développées et précisées au cours des dernières années comme en témoignent ses exposés au cours des deux derniers Symposiums sur les diatomées d'Oslo et d'Anvers. SIMONSEN conserve la division classique en deux ordres, les Centrales et les Pennales, eux-mêmes divisés en cinq sous-ordres et 21 familles. Cet intéressant article est complété par deux appendices: une clef d'identification conduisant aux familles et une classification des diatomées. Cette classification n'est pas sans intérêt mais ne sera pas adoptée par tous les diatomistes, en particulier en ce qui concerne la division des Pennales qui, de quatre sous-ordres, est ramenée à deux sous-ordres seulement: les Araphidineae et les Raphidineae. La raison de cette modification est l'importance injustifiée accordée, par les précédentes classifications, aux Raphidoidineae et aux Monoraphidineae. Si l'on suit le raisonnement de l'auteur l'on ne comprend pas, alors, la fragmentation de certains genres peu représentés comme le genre *Attheya*, 3 espèces seulement, scindé en deux sans que cela apparaisse vraiment nécessaire.

Parmi les autres articles de *BACILLARIA 2* citons plus particulièrement ceux de G.R. HASLE: *Thalassiosira decipiens* (Grun.) Jörgensen; R.A. GIBSON: *Protoraphis atlantica* sp. nov., a new marine epizoic diatom; W.H. HOLMES et A.L. BRIGGER: The marine fossil diatom genus *Entogonia* Greville. L'article de H. LANGE BERTALOT, *Simonsenia* : a new genus with morphology intermediate between *Nitzschia* and *Surirella*, présente également un grand intérêt car la création de ce nouveau genre, intermédiaire entre les *Nitzschia* et les *Surirella*, ne manquera pas de soulever à nouveau les nombreux problèmes taxinomiques posés par de nombreuses *Nitzschia* à l'exemple de *N. delognei* : citons par exemple le cas de *N. apiculata*.

Ce deuxième volume de *BACILLARIA* tient les promesses du premier, grâce aux efforts de son éditeur, et sera du plus grand intérêt pour ses lecteurs.

WATANABE, Masayuki, 1978 – **A taxonomic study of the *Closterium calosporum* Complex** *(1)-2. Bull. Nat. Sc. Mus. Tokyo*, Sér. B (Bot.), 4 (4): 133-154 et 1979: id. 5 (1): 1-23.

L'auteur étudie, dans la nature et en culture, 35 clones de *Closterium* du groupe *calosporum*. Grâce à ces cultures il peut évaluer, statistiquement, les variations des cellules végétatives et des zygotes en fonction des milieux nutritifs et de la température.

Il peut ainsi reconnaître, et décrire avec précision dans ce complexe à côté de *C. calosporum* Wittr. var. *calosporum*, 2 variétés dont l'une nouvelle, ainsi que 3 variétés nouvelles de *C. spinosporum* Hodgetts. Il décrit de plus une nouvelle espèce.

L'excellente illustration en 11 planches, et les diagnoses très précises des divers taxons étudiés permettent de mettre de l'ordre dans ce groupe difficile.

Commission paritaire N° 28588 - Dépôt légal : n° 659 - Octobre 1979 - Imp. Vial, 91410 Dourdan

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DOCUMENTATION GRATUITE SUR SIMPLE DEMANDE

Editions du CNRS
15 quai Anatole France. 75700 Paris