The contribution of calcareous green algae to the production of limestones: a review

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ABSTRACT

Calcareous green algae (CGA) are an artificially united but highly heterogeneous group of large unicellular benthic algae with one character in common: all have the capability of secreting a calcareous coating on the outer side of the cytoplasmic envelope. Today, they are a major contributor to carbonate sedimentation at all scales from clay-sized particles (aragonitic needles) to coarser grains (sand and gravel) and even to plurimetric sedimentary structures. There are fossil analogues to the features listed above. Phycologists know best *Halimeda*, *Penicillus*, *Acetabularia* and *Cymopolia*; micropaleontologists and carbonate sedimentologists are most knowledgeable about *Acicularia*, *Clypeina*, *Neoteutloporella*, *Salpingoporella*, *Anthracoporella*, *Boueina*, and *Eugonophyllum*. The CaCO$_3$ precipitated to form the coating is generally aragonite (the orthorhombic form) but there are short periods in the geologic record during which its calcite variant (the rhombohedric form) existed contemporaneously in discrete species. Recent studies on *Halimeda* have shown that some of the Bryopsidales have the capability to calcify strongly in the lower portion of the euphotic zone (where respiration becomes more important than photosynthesis in the process of mineralization) and to produce positive sedimentary reliefs (bioherms) *in situ* below the fair-weather wave base. Previous models of paleoenvironments considered the presence of Dasycladales or Bryopsidales to indicate shallow-water, that is the upper euphotic zone (from the sea surface down to –25 m), and predominantly low-energy, protected, lagoonal environments. When the algal remains were found in grain-supported facies, they were taken to have been subjected to dynamic transport and therefore indicative of high-energy environments of deposition. The new deeper-water finds have changed interpretations of the environments ascribed fossil algae. A current conception is that ancestral inarticulated Bryopsidales could have grown at depths as great as –120 m (near the base of the lower euphotic zone). This preliminary review concludes with suggestions about fields for continuing investigations.

KEY WORDS
Dasycladales,
Bryopsidales,
Halimeda,
bioherm,
euphotic zone,
phylloid,
aragonite,
calcite,
porosity,
epigenesis,
cementation.

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RÉSUMÉ

Contribution des algues vertes calcifiées à la production des calcaires : une ré-évaluation.
Les algues vertes calcaires (CGA) résultent du regroupement artificiel de grandes
algues unicellulaires benthiques qui ont pour caractère commun de présenter un
manchon calcifié développé sur la face externe de leur enveloppe cytoplasmique.
Aujourd'hui cet ensemble très hétérogène représente l'une des principales sources
de la sédimentation carbonatée et ce, à plusieurs échelles, depuis la fraction des
argiles (aiguilles aragonitiques) jusqu'aux granulométries plus grossières (fractions
des sables et des graviers) et même à l'échelle plurimétrique de structures sédimen-
taires. Il existe des analogues fossiles aux éléments mentionnés précédemment.
Si les phycologues connaissent bien *Halimeda*, *Penicillus*, *Acetabularia* ou *Cymo-
polia*, les micropaléontologues et les sédimentologues des carbonates sont, quant
à eux, plus familiers avec *Acicularia*, *Clypeina*, *Neoteutloporella*, *Salpingoporella*,
Anthracoporella, *Boueina* ou *Eugonophyllum*. Le CaCO$_3$ précipité à l'extérieur de
la cellule pour former le manchon est le plus souvent de l'aragonite (sa variété
orthorhombique) mais, au cours de certains intervalles stratigraphiques, il est
arrivé que de la calcite (sa variété rhomboédrique) existe concurremment dans
des espèces distinctes. Des études récentes sur *Halimeda* ont montré que quelques
Bryopsidales pouvaient être fortement calcifiées dans la tranche inférieure de la
zone euphotique (là où la respiration prend le pas sur la photosynthèse dans les
processus de minéralisation) et même qu'elles étaient capables de construire des
structures sédimentaires en relief (biohermes) *in situ* sous la limite inférieure d'action
des vagues. Les modèles paléoenvironnementaux précédents considéraient que la
présence de Dasycladales ou de Bryopsidales caractérisait les environnements d'eaux
peu profondes, c'est-à-dire la tranche supérieure de la zone euphotique (de 0 à
−25 m), et essentiellement protégés (lagon), à hydrodynamisme peu élevé ; lorsque
ces débris algaires sont rencontrés dans des faciès granulaires caractéristiques d'un
hydrodynamisme fort, ils sont alors considérés comme les indices d'un transport
sédimentaire significatif. Leur découverte en « eaux profondes » ouvre une brèche
dans les modèles pré-existants ; ainsi, par exemple, on peut désormais envisager
que les ancêtres inarticulés des Bryopsidales ont également pu se développer dans
la tranche inférieure de la zone euphotique (sous −25 m, voire jusqu'à −120 m).
Quelques clefs pour des recherches nouvelles sont proposées en conclusion de
cette courte revue préliminaire.

MOTS CLÉS
Dasycladales,
Bryopsidales,
Halimeda,
bioherme,
zone euphotique,
phylloïde,
aragonite,
calcite,
porosité,
épigenèse,
cimentation.

INTRODUCTION

Some large benthic chlorophyta may have a mineralized
"skeleton" and therefore are commonly pigeon-holed
as "calcareous green algae" (CGA). This grouping has
no meaning in Systematics for biologically it is highly
heterogeneous: on one branch are some of the Bryop-
sidales (e.g., *Halimeda*, *Penicillus*, *Rhipocephalus* and
Udotea) and on the other some of the Dasycladales
(e.g., *Acetabularia*, *Cymopolia* and *Neomeris*); both
orders are unicellular algae but Bryopsidales' filaments
are multinucleate cells without cross walls (coenocytic
organisms) whereas individual Dasycladales' thalli are
uninucleate cells during their vegetative stage. Apart
from the biological side this artificial grouping also
lacks consistency, for most genera or even species of the
same genus have discrete features or unique behaviors
which result in widely diverse contributions to CaCO$_3$
production in terms of volume, grain morphology
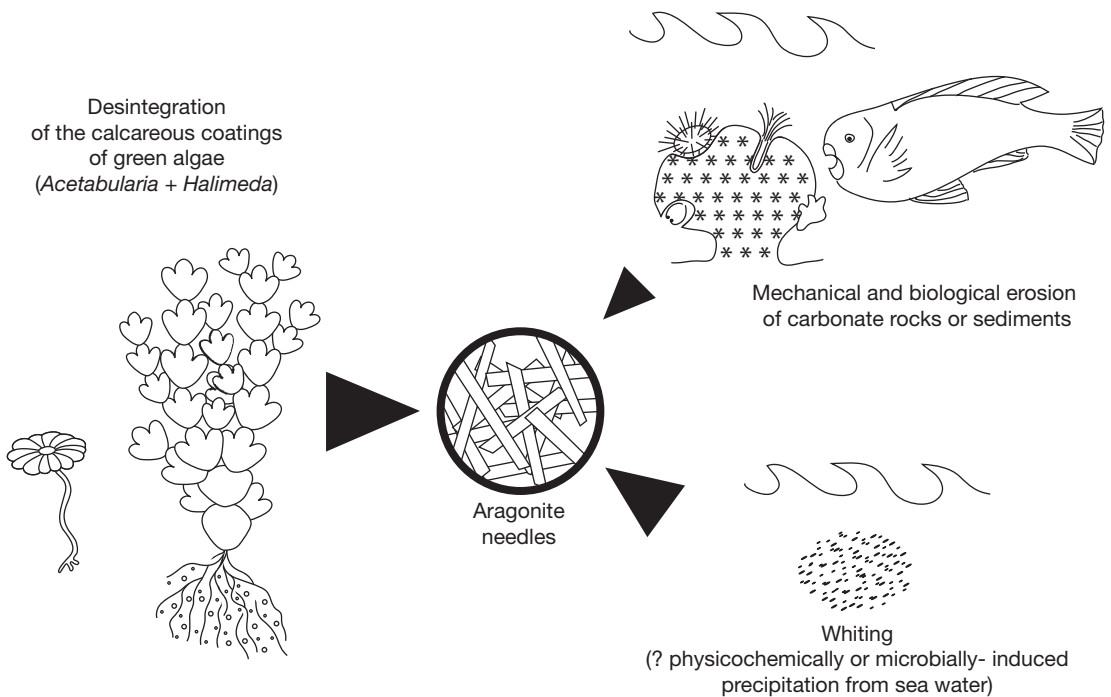and size. However sedimentologists commonly deal

Desintegration
of the calcareous coatings
of green algae
(*Acetabularia* + *Halimeda*)

Mechanical and biological erosion
of carbonate rocks or sediments

Aragonite
needles

Whiting
(? physicochemically or microbially- induced
precipitation from sea water)

Fɪɢ. 1. — "Carbonate factory": origin of calcareous muds.

with these CGA as a single major producer of the "carbonate factory" in the modern ocean, more specifically in the warm shallow-waters of the tropical and subtropical areas, for they contribute not just to the finest part of the sediment, i.e. the lime mud (Fig. 1), but also to the formation of calcareous sands and gravels, and even to the build up of relatively large biosedimentary structures. The aim of this paper is to review the available information on modern CGA, to draw conclusions therefrom, to discuss the extent to which its findings can be extrapolated to ancient representatives of these orders, and finally to suggest routes for future research.

A SHORT LIST OF LIVING CALCAREOUS GREEN ALGAE

Among the agencies most strongly promoting prolific occurrences of marine photosynthetic benthic algae are the intensity of light (it is inversely propor-

tional to bathymetric depth; Fig. 2)*,* nutrients and water temperature. These green algae are therefore abundant in warm shallow-waters that are usually supersaturated with calcium carbonate in tropical and subtropical realms. However few living Bryopsidales and Dasycladales have a calcareous "skeleton".

As CGA exhibit a great variety of thallus morphologies and sizes, this section illustrates their diversity through a summary presentation of some key genera.

Oʀᴅᴇʀ Bʀʏᴏᴘsɪᴅᴀʟᴇs
Five living genera calcify (Hillis 1991):
Genus Halimeda
One species is known as the "cactus alga" owing to its morphological similarities to the "paddle cactus" Opuntia. Its bushy thallus commonly attains a height of a half metre. Its articulated branches consist of highly mineralized segments up to 45 mm wide connected by flexible nodes. During the vegetative stage, segments may be detached through accident and give rise to new individuals: This form
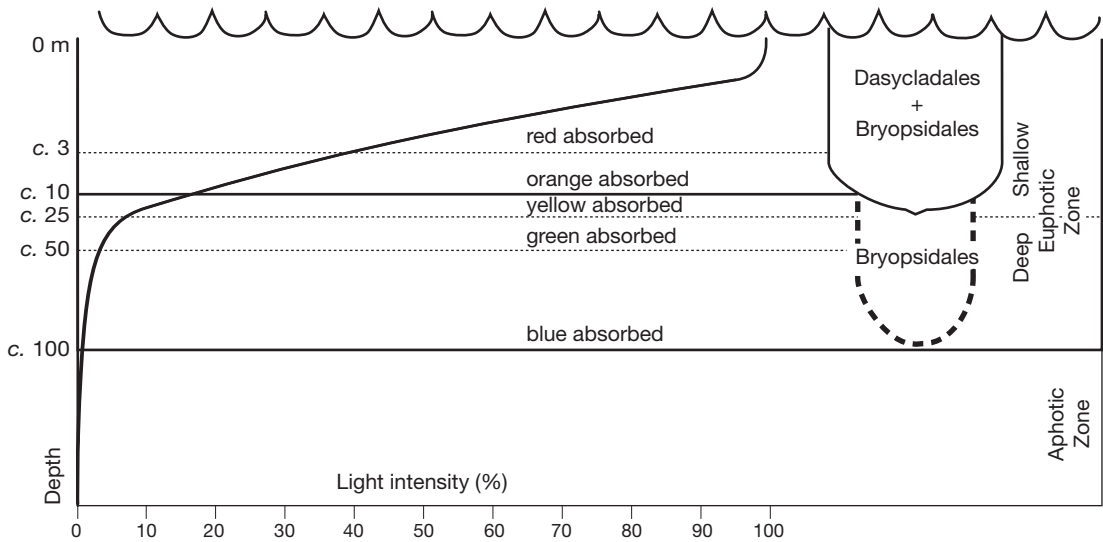
FIG. 2. — Photosynthesis (the curve) decreases exponentially with depth for it is a function of the intensity of light. But calcification is not necessarily a correlate of this process for under the same environmental conditions calcified and non-calcified representatives of the same genus live side-by-side. In this schematic sketch 60% of the sunlight is absorbed in the first 3 metres, 80% at about 10 metres and 99% at about 100 metres. This depth at which most of the cyan/blue rays have been absorbed is the lower limit of the euphotic zone. Obviously the depths in this model are estimates for the degree of transparency of water causes them to vary significantly. For instance, the base of the euphotic zone may be deeper: Roberts *et al.* (1988) report living *Halimeda* to about –120 m and Hillis-Colinvaux (1986) to about –140 m. In the upper euphotic zone (in our model to –25 m), calcification is mainly driven by photosynthesis in both Dasycladales and Bryopsidales. But in the lower euphotic zone respiration takes the lead: a few Bryopsidales, mostly *Halimeda* representatives, live and contribute to calcium carbonate production there.

of asexual reproduction ("bouturage") contributes significantly to the propagation of the species. Sexual reproduction involves emptying the cytoplasm from the alga (holocarpy) leaving behind many empty loose segments of calcium carbonate.

Genus Penicillus
The thallus, up to 0.2 m in height, consists of a holdfast bearing a tuft composed of thin articulated branches from 0.1 to 1.0 mm in diameter which give rise to its nickname, the "shaving-brush alga". Calcification of the segments is moderate for mineralization is only superficial.

Genera Udotea *(the "mermaid's fan alga")*
and Rhipocephalus *(the "pinecone alga")*
The height of the *Udotea* blade ranges up to 0.2 m and the *Rhipocephalus* stalk which has multiple blades is up to 0.1 m tall. The blades of both genera may be covered superficially by a thin and fragile crust of aragonite.

Genus Tydemania
The "Pom Pom alga". The thallus is up to 0.1 m in heigh; the main axis bears verticillated laterals that divide dichotomously several times and form successive spheres up to 10 mm in diameter.

ORDER DASYCLADALES
With the exception of *Batophora* and *Chlorocladus*, many representatives of the 9 remaining Recent genera calcify (Berger & Kaever 1992; Berger 2006). The three main morphologies of the thallus (umbelliform, necklace- or club-shaped) can be illustrated by:

Genus Acetabularia
The "mermaid's wine-glass alga", and related genera (Polyphysaceae, former Acetabulariaceae). The fertile thallus is umbelliform, with a tubular stalk up to 0.2 m long capped with a row up to 20 mm in diameter of elongated pluricystic ampullae (Fig. 3).
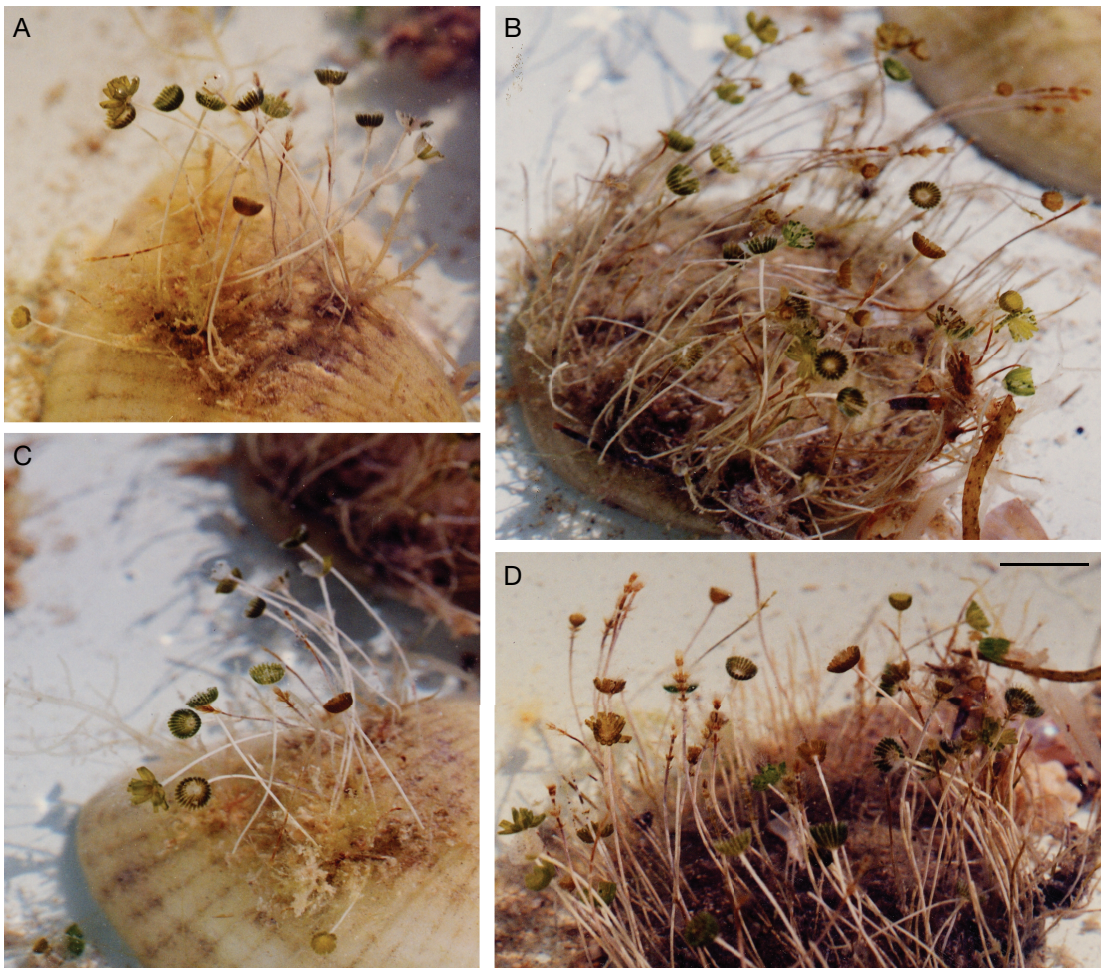
Fig. 3. — *Acetabularia caliculus* Lamouroux *in* Quoy & Gaimard, young specimens with whorls of sterile laterals and cap rays of mature specimens, attached to large shells (**A**, **C**) or lithoclasts (**B**, **D**). Sir Bani Yas Island, Abu Dhabi, United Arab Emirates.

Genus Cymopolia *(Dasycladaceae)*

The thallus is bushy, up to 0.2 m tall, with articulated branches up 5 mm in diameter consisting of mineralized ovoid (cylindrical, spherical…) segments up to 10 mm long connected through flexible nodes.

Genus Neomeris *(Dasycladaceae)*

Its thallus, cylindrical or club-shaped, is the smallest of all of them as it rarely exceeds 50 mm in height.

It is noteworthy that the way in which $CaCO_3$ is deposited and the amount of mineralization may vary considerably in the several species of the same genus.

BASIC INFORMATION
ON THE CALCIFICATION
OF MODERN GREEN ALGAE

The most heavily calcified Bryopsidales are found in representatives of the genus *Halimeda*. At least 200 g/m² of $CaCO_3$ are produced per year in the Great Barrier Reef (Drew 1983; Drew & Abel 1988a) and 800 in the Bahamas with estimates ranging up to 2400 (Freile *et al.* 1995). In any case, although they are commonly associated with the relatively weakly calcified *Penicillus*, *Rhipocephalus* and *Udotea*, the

vast majority of papers dealing with algal mineralization concerns *Halimeda* (Segonzac 1986). Among the Dasycladales, Marszalek (1975) estimates that crops of *Acetabularia* may produce up to 700 g/m² per year (this is the rate produced by the reproductive organs, stems are not included).

In all CGA most of the calcium carbonate precipitated is aragonite, the orthorhombic variety of $CaCO_3$. It has been documented by X-Ray diffraction in "*Acetabularia mediterranea*" (= *Acetabularia acetabulum*) (Walter Lévy & Strauss 1961), in *Halimeda tuna* (Walter Lévy *et al.* 1958; Walter Lévy & Strauss 1961), in several species of *Halimeda* (McConnel & Hillis Colinvaux 1967; Wilbur *et al.* 1969) and of *Penicillus* (Friedmann *et al.* 1972). But a little low-Mg calcite, the rhombohedric crystallographic variety of $CaCO_3$, may be present too. Its occurrence has been documented by X-Ray and chemical (arc spectrography and quantitative analysis of MgO) analyses in *Halimeda tuna*. Walter Lévy *et al.* (1958) reported the unique case of a specimen of "*Dasycladus clavaeformis*" (= *Dasycladus vermicularis*) from Ibiza (Balearic Islands) which consists predominantly of calcite with traces of aragonite: this specimen probably suffered strong diagenetic alteration. From a collection of *Tydemania expeditionis* preserved in formalin, McConnel & Hillis Colinvaux (1967) reported a very small quantity of calcite from 6 specimens but they found it might have been "recrystallization that take place while the samples were stored" and they concluded "the presence of calcite in the quantities observed does not indicate this species precipitates both forms of calcium carbonate". Milliman (1977) reminds us that "*Halimeda* fragments are susceptible to diagenetic alteration" and he also reports that "often this can happen within individual plates within a living plant", a statement that was supported by Macintyre & Reid (1995) through scanning electron microscope (SEM) observations on living specimens of *Halimeda*. Recently, experiments using artificial seawater found that depending on Mg/Ca ratios representatives of the genera *Halimeda* (Stanley *et al.* 2010), *Penicillus* (Ries 2005) and *Udotea* (Ries 2006) could produce a substantial proportion of skeletal low-Mg calcite: lowering the molar Mg/Ca ratio (from the *c.* 5.2 in modern "aragonite seawater") decreases total min-

eralization but produces increasing percentages of low-Mg calcite. As a conclusion, we can assume that in modern seas all CGA precipitate aragonite and the occurrence of calcite is related either to *in situ* alteration and conversion, to solution-deposition or to cementation in empty organic cavities. In addition to aragonite and low-Mg calcite there are a few records of minor (less than 2%) associated mineral components: $SrCO_3$ in *Halimeda* (Emery *et al.* 1954: table 11) and CaC_2O_4 in *Bornetella* (Berger & Kaever 1992), *Penicillus* (Friedmann *et al.* 1972; Ries 2005), *Rhipocephalus* and *Udotea* (Friedmann *et al.* 1972).

ULTRASTRUCTURE

Calcification is largely extracellular *sensu lato*: it occurs outside the cell wall in the gelatinous mucilage between the networks of adjacent filaments or laterals (i.e. extracellular but intercellular) or on the main axis and some laterals (i.e. extracellular *sensu stricto*). In the Bryopsidales reproductive organs are never calcified; in some Dasycladales calcification affects the cysts that are either discrete (they form "calcispheres") or aggregate into clusters ("spicules" or "buttons"). Lucas & Pobeguin (1954) were the first to investigate the ultrastructure of a Dasycladale, unfortunately they did not have a SEM. Wilbur *et al.* (1969) were the first to describe in *Halimeda* a three-fold sequence of calcification. In this sequence, later formally defined as the CGA calcification model by Flajs (1977a, b), calcification involves the development of:
– small crystal granules adjacent to the cell wall;
– needles (a typical crystal shape for aragonite) more or less perpendicular to the cell wall;
– needles without apparent orientation, commonly occupying the remainder of the intercellular space.

He also stated that the typical complete development occurs most of the time (Flajs 1977b: 83: "In den weitaus meisten Fällen ist jedoch die typische Abfolge ausgebilder") and that this applies to most modern Chlorophyta (*Cymopolia*, *Neomeris*, *Halimeda*, *Udotea*… see Figure 4A, B), although he admits that there are records of cases in which one or two of the three stages might be missing. This model was subsequently adopted by most authors (Bignot 1977; Bassoullet *et al.* 1979; Berger & Kaever 1992). While studying fossil *Neomeris* and *Zitellina*, Génot (1985,

2009) found mainly unoriented lathlike or prismatic needles demonstrating that here exception is the rule. In addition, Flajs himself (1977a, b) had already stated this model is not applicable in some algae (*Acetabularia*, *Penicillus* and related genera) or to parts of their thalli for example *Acetabularia* stalks (see Bassoullet *et al.* 1979: pl. I, figs 6-8; Loreau 1982: pl. 3, figs A-C; Berger & Kaever 1992: figs 2.14 & 2.15; Granier 1994: pl. 4, figs 5-9). In such cases calcification (Fig. 5) is extracellular *sensu stricto*, that is, it is not "extracellular but intercellular" as in the previous examples. Instead the intercellular space (ICS) is filled with mucilage which forms a true transitional zone between seawater and the cell itself (Borowitzka & Larkum 1977). It retains both CO_2 and Ca^{2+}, it has a discrete pH, and facilitates the precipitation of $CaCO_3$ as subhedral and euhedral crystals (needles). Extracellular calcification *sensu stricto* produces mostly anhedral and subhedral crystals (granules, never needles).

I now provide background information on photosynthesis and calcification, and on respiration and calcification.

CARBONATE CHEMISTRY

The reaction for the production of $CaCO_3$ by an organism (biocalcification) is:

$$Ca^{2+} + 2HCO_3 \Longleftrightarrow CaCO_3 \downarrow + H_2O + CO_2 \uparrow \; (1)$$

Before Goreau (1962), it was assumed that the calcification of CGA was an accompaniment of the extraction of CO_2 from seawater during the synthesis of their organic matter. A simplified form of the reaction to summarize the photosynthetic CO_2 uptake can be expressed as:

$$H_2O + CO_2 \rightarrow CH_2O + O_2 \uparrow \; (2)$$
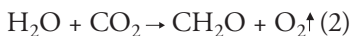
The CO_2 used in photosynthesis is derived from HCO_3 which is abundant in seawater. Accordingly the above reactions (1) and (2) can be combined to form the following:

$$Ca^{2+} + 2HCO_3 \rightarrow CaCO_3 \downarrow + CH_2O + O_2 \uparrow \; (3)$$

But Goreau (1962) reported that: "The Halimedas are exceptional among the calcareous Chlorophyta in that they tend to be more heavily calcified in deep than in shallow-water." It was found that *Halimeda* precipitates $CaCO_3$ during the day in connection with photosynthesis, a phenomenon reported as "light calcification", and also during the night, a phenomenon described as "dark calcification", that accompanies the alga's respiration.

A simplified form of the reaction to express the production of CO_2 during respiration is:

$$CH_2O + O_2 \rightarrow H_2O + CO_2 \uparrow \; (4)$$
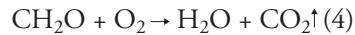
Accordingly the above reactions (1) and (4) can be combined to form the following:

$$Ca^{2+} + 2HCO_3 + CH_2O + O_2 \rightarrow CaCO_3 \downarrow + 2H_2O + 2CO_2 \uparrow * \; (5)$$
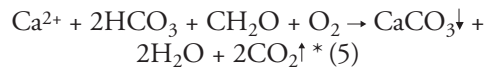
* This CO_2 stored at night in intercellular space will favour daytime photosynthesis.

In two species of *Halimeda* (*H. incrassata* and *H. opuntia*), Goreau (1962) found that dark calcification represents nearly 60% of the total.

Goreau's finding about dark calcification along with the identification of an extracellular but intercellular locus for calcification (Borowitzka & Larkum 1977; Böhm *et al.* 1978; Borowitzka 1986), the discovery of "deep-water" *Halimeda* bioherms in the Great Barrier Reef of northeastern Australia (at about –50 m; Davies & Marshall 1985) and in the eastern Java Sea (at about –120 m; Roberts *et al.* 1988), as well as the find of "deep-water" (at about –140 m) "vigorous and healthy" *Halimeda* in the Marshall Islands (Hillis-Colinvaux 1986; Blair & Norris 1988) led to the revival of scientific investigations on the CGA.

EXAMPLES OF MODERN CARBONATE PRODUCTION

PRODUCTION OF LIME MUDS (< 62 μm)
FROM FRAGILE GREEN ALGAE

Aragonite needles are common in the mud fraction of the shallow-water calcareous sediments of tropical and subtropical areas. According to Cloud (1962) "more than 95 percent" of the mud fraction of the recent sediments deposited West of Andros Island,

the Bahamas, consists of aragonite needles while "only 6 to 12 percent of the total sediment is calcite". In Florida Bay, another classical area for carbonate studies, aragonite needles are less abundant, ranging from 20 to 40% of the sediment.

Data from both areas, supplemented by other information from Bermuda and Jamaica, gave Lowenstam (1955) the initial evidence for an algal origin of aragonite needles. In his report he listed occurrences of representatives of *Acetabularia*, *Cymopolia*, *Neomeris*, *Halimeda*, *Penicillus*, *Rhipocephalus*, and *Udotea*. He stated that: "The calcareous hard parts of many of these algae […] consist wholly or partially of aragonite needles. These algally secreted needles are similar in habit and dimensions to sedimentary aragonite needles." So, contrary to the general consensus since the early 1900s that the origin of aragonitic muds involved mostly physicochemical processes, Lowenstam (1955) concluded that "this infers a largely algal origin for the sedimentary needles" (Fig. 1).

In most living representatives of the CGA the first layer coating the cell walls is composed of minute (less than 1 µm) granular crystals of aragonite. The remaining mucilage-filled space is more or less filled with 10 µm-long aragonitic needles. These needles were considered an important source of lagoonal muds by Neuman & Land (1975) but early on they may be altered to crystals of aragonite (later high-Mg calcite) that are less than 1 µm in size: this process was described as "early micritization" by Macintyre & Reid (1995). They found that, in consequence, less than 20% of the total carbonate in a *Halimeda* thallus retains the original acicular fabric (Macintyre & Reid 1995). So it is difficult to estimate the contribution of these modern algae to lime muds. In another approach to calculation of the quantity of $CaCO_3$ produced by algae, samples of plants are collected in natural environments. They are dried and segregated into organic and mineral components which are weighed: Marszalek (1975) calculated that *Acetabularia antillana* could produce up to 720 g/m^2 per annum of calcium carbonate while Drew (1983) found that *Halimeda* could produce 2234 g/m^2 per annum.

Lowenstam's (1955) views on the algal origin of the mud were considered "provocative" (Robertson

et al. in Cloud 1962) and he soon found other supporters: Lowenstam & Epstein (1957) on the basis of oxygen isotope ratios (but Shinn *et al.* 1989 use similar data to demonstrate the contrary), Mathews (1966) on the basis of strontium contents, Stockman *et al.* (1967) and Neuman & Land (1975) who compared rates of algal production of aragonite with rates of deposition of lime muds. Most of Lowenstam's detractors (Loreau 1982; Shinn *et al.* 1989; Macintyre & Reid 1992; Milliman *et al.* 1993) preferred the alternative hypothesis, that of whitings, so advocated chemical precipitation of aragonite to explain these phenomena. They pointed that the algal aragonite hypothesis raised a number of issues:

– Milliman *et al.* (1993) state that "because codiacean algae do not grow in the Persian Gulf, inorganic precipitation seems the only possible source of this fine-grained aragonite". But they neglected the fact that the Dasycladalean alga *Acetabularia* is particularly abundant in the area (Figs 3, 5; Loreau 1982: pl. 3, figs A-C);

– CGA do not produce only needles, but also a certain volume of granules, i.e. "nannograins" (Loreau 1982);

– cross-plots of the isotopic composition ($\delta^{18}O$‰ and $\delta^{13}C$‰) of carbonate sediment suspended in whitings and of that deposited on the sea floor produced two narrow clusters that overlap. But the algal aragonite cluster is wider and encloses the other two (Shinn *et al.* 1989);

– Sr concentrations are lower in algal aragonite than in those of non-skeletal grains and mud (Loreau 1982; Milliman *et al.* 1993);

– "SEM observations show that the characteristic shapes of algal differ from those of crystals commonly found in needle muds" (Macintyre & Reid 1992; Milliman *et al.* 1993). Needles of algal origin are larger than others and are commonly euhedral while the others have smooth rounded surfaces and terminations.

However none of these investigators recognized that algal material differs from mud and non-skeletal grains (ooids and peloids) in that the aragonitic algal coatings are almost pristine whereas the lime matrix and the allochems are older and may have been slightly altered diagenetically (Kobluk & Risk 1977; Chafetz 1986).
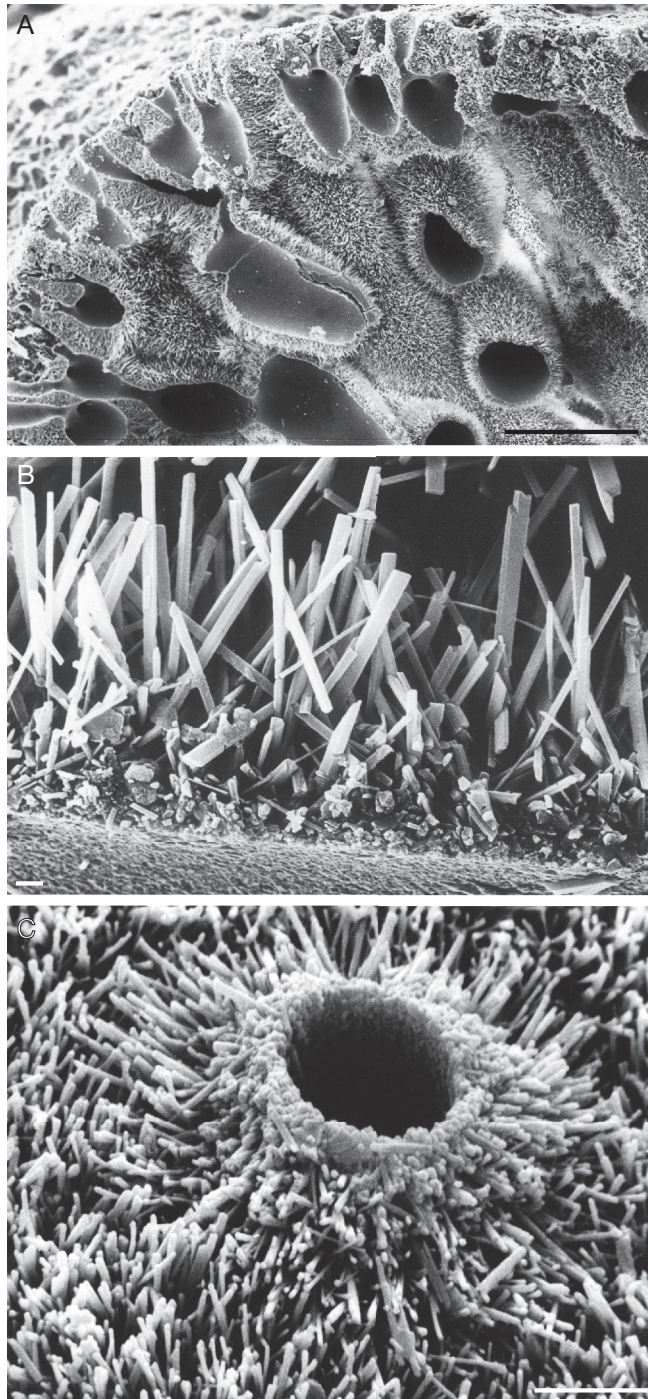
FIG. 4. — **A**, **B**, calcification in *Halimeda praeopuntia* L. & J. Morellet; Rupelian ("Stampian"); Gaas, Landes, France; Génot collection; **C**, aragonitic needles on the peduncle of a gametophore (= fertile ampulla) of *Neomeris arenularia* Munier-Chalmas *ex* L. & J. Morellet; Bartonian; Montagny, Oise, France; Génot collection. Scale bars: A, 100 µm; B, 1 µm; C, 10 µm.

I share Wilson's (1975) conclusions: "Data indicate that whatever its origin, much, if not most or all, fine lime sediment is organically derived."

LIME SANDS FROM GREEN ALGAE

Halimeda and *Cymopolia* are "important contributors to the sand fraction" (Stockman *et al.* 1967). Remains of these photosynthetic algae are the skeletal component that characterizes either the chloralgal facies or, when associated with hermatypic corals (the tissues of which host zooxanthellae, another type of photosynthetic algae), the chlorozoan facies. Both assemblages are markedly different from the temperate water assemblage known as the foramol facies (Lees & Buller 1972). However in quiet environments an algal origin (Dasycladales or Bryopsidales) cannot commonly be assumed for more than 20% of the coarse grains owing to micritization and degree of mineralization (Macintyre & Reid 1995).

For instance, fertile ampullae of *Acetabularia* are commonly found as nuclei of coated grains in the ooid shoals off Abu Dhabi, United Arab Emirates. But the presence of *Acetabularia* stems had not been recorded until Granier (*in* Kenig 1991) found a huge number of broken stems (Fig. 5) in a Holocene washover fan. These algal remains comprised more than 15% of the allochems in this grainy facies but were erroneously called "worm tubes/serpulids" by Strohmenger *et al.* (2010: fig. 17f, i [red arrows]; fig. 17h pars). They are preserved owing to their rapid burial that prevented an early diagenetic alteration.

Today the alga *Halimeda* grows in high-energy reefal environments as well as in lower-energy protected back-reef (lagoonal) settings. *Halimeda* flourishes in these lagoonal environments where it forms wide meadows and colonizes sandy substrates (Multer 1988). For the most part it reproduces vegetatively ("bouturage") but in sexual reproduction the thallus dies after having released the whole of its cytoplasm contents as gametes (holocarpy) and it disintegrates into individual segments (Drew & Abel 1988b). Locally these *Halimeda* segments are accumulated in the form of "corn flake" gravels (see Emery *et al.* 1954: pl. 25, figs 3, 4; pls 26, 27, fig. 1; pl. 29, figs 1-3; Cloud 1962: pl. 6, figs 1, 2): the texture is commonly grain-supported but these gravels are also found floating in finer-grained matrices. On the western margin of the Great Bahamas Bank the 15 m thick Holocene sequence consists predominantly of an *Halimeda*-generated sediment: Freile *et al.* (1995) assume that a significant volume went past the shelf break. In the southern Florida Keys, sand- and gravel-sized deposits consisting of more than 50% of broken *Halimeda* segments cover several tens of square kilometres in which their morphological expression is a field of sand waves with heights of as much as 5 m and an average crest-to-crest length of 200 m (Shinn *et al.* 1990).

PRODUCTION OF BIOLITHITES

Because *Acetabularia* has a short anchoring organ (Fig. 5; Granier 1994: pl. 4, figs 5-9), it has no capacity to bind and for fixation it prefers hard substrates (seagrasses: *Posidonia*, *Syringodium* and *Thalassia*, *Avicennia* roots, large shells, rocky bottoms…) On the contrary *Halimeda* anchors itself in the sediment with rhizoids and it has a binding capacity. When growing in a moderate-energy lagoonal environment the articulated thallus of modern *Halimeda* may act as a baffle to impede or restrain the flow of particles. This combination of binding and baffling tends to form small mounds on the sea floor. *Halimeda* mounds were first found in back-reef settings on the Great Barrier Reef of Australia (Davies & Marshall 1985; Davies *et al.* 1986; Marshall & Davies 1988; Orme & Salama 1988) and in the nearshore off northeastern Nicaragua-Honduras (Hine *et al.* 1988). These initial finds in "shallow-water" meadows were supplemented by reports from southeastern Borneo, Indonesia, of the presence of mounds in "deep-water" settings, still in the euphotic zone but below the fair-weather wave-base (swell). The first locality is an isolated platform, the Kalukalukuang Bank, in the eastern Java Sea (Roberts *et al.* 1987a, b, 1988; Phipps & Roberts 1988), and the second is at the shelf edge of the Makassar Strait seaward of the Mahakam delta (Fig. 6A; Granier *et al.* 1993, 1997; Roberts & Sydow 1996; Crumeyrolle *et al.* 2007).

These mounds can be mapped for they are identifiable using side-scan sonar and in traverses made with an echo sounder, a boomer or on shallow seismic
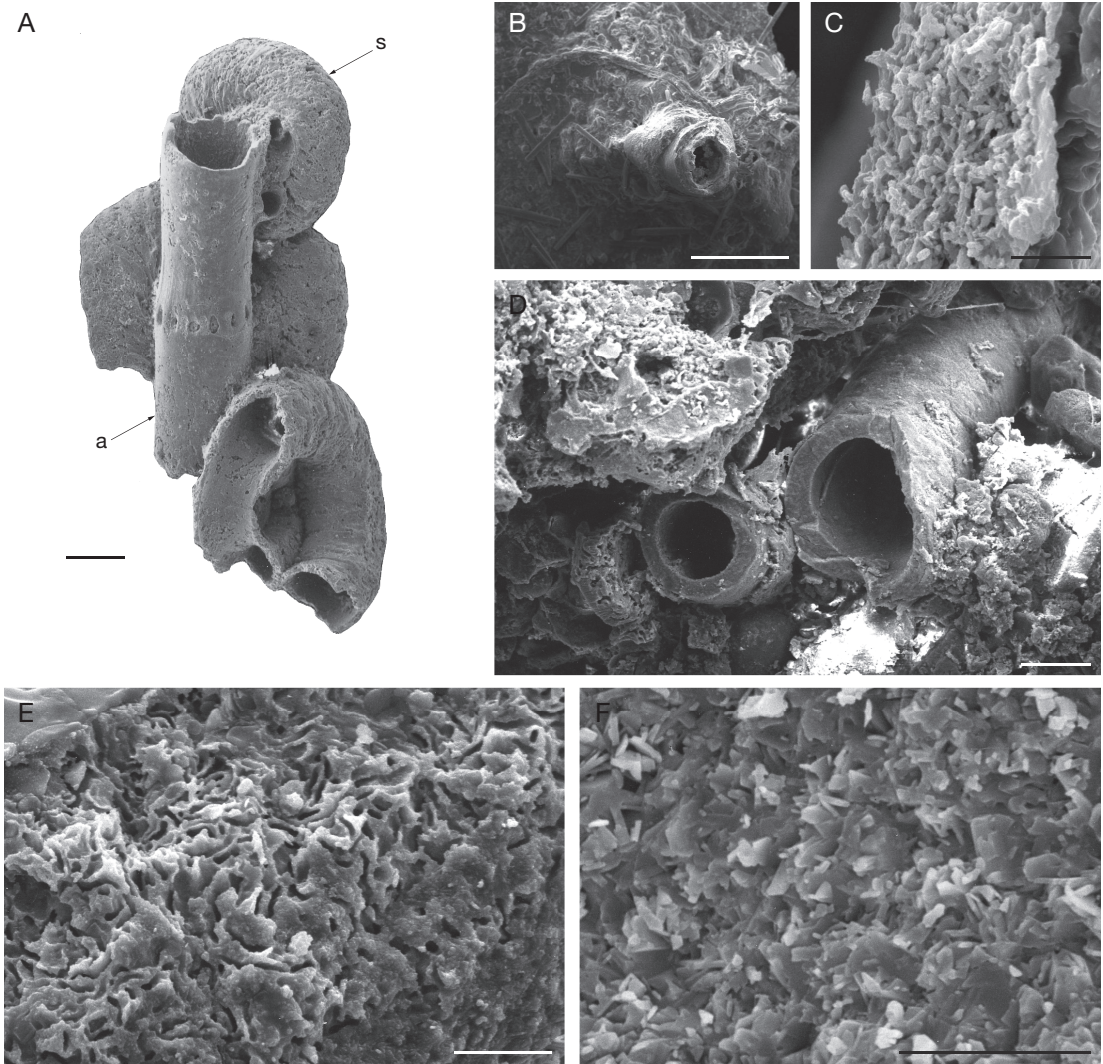
FIG. 5. — Remains of *Acetabularia caliculus* Lamouroux *in* Quoy & Gaimard: **A**, The annelid *Spirorbis* (**s**) encrusting a short portion of a stem (**a**) broken at the level of sterile whorls (scars of a median whorl are visible); **B**, calcified anchoring organ on a large shell; **C**, detail of its calcification; **D**, two broken stems; **E**, **F**, details of the stem wall, microborings on the outer surface (**E**) and calcification (**F**); Holocene; Mussafah, Abu Dhabi, United Arab Emirates. Scale bars: A, D, 100 µm; B, 500 µm; C, 5 µm; E, F, 10 µm.

records, but they have been cored only rarely and so are poorly documented at a macroscopic scale. Therefore we lack crucial ecological, micropaleontological, petrographical, sedimentological and taphonomical information about them.

In Indonesia below the modern *Halimeda* mounds seismic profiles reveal Holocene (Fig. 6A; Granier *et al.* 1993, 1997; Crumeyrolle *et al.* 2007) and even Pleistocene (Roberts & Sydow 1996) features of the same type. *Halimeda* mounds are also reported from strata dated as far back as the Miocene (Mankiewicz 1988; Braga *et al.* 1996; Martín *et al.* 1997). The oldest *Halimeda* mounds were found in the Upper Miocene succession of southern Spain (Braga *et al.*
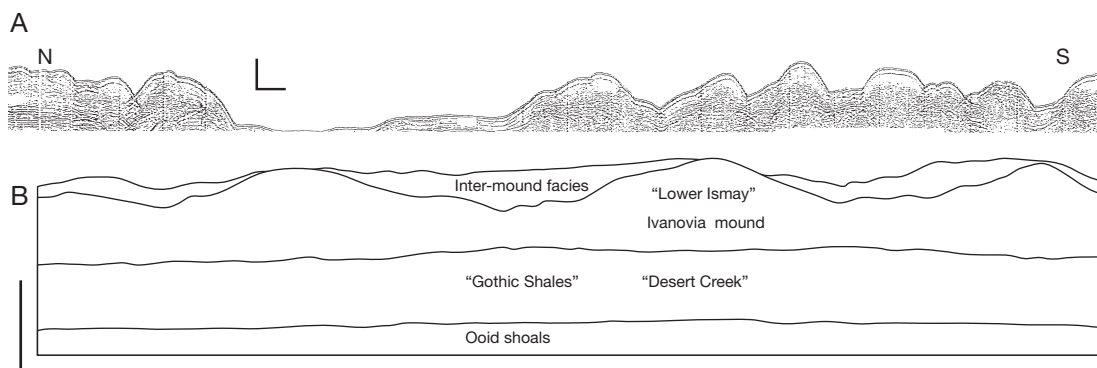
FIG. 6. — Comparison of: **A**, modern deep-water *Halimeda* bioherms; Kalimantan, Makassar Strait, Indonesia (modified after Granier *et al.* 1993, 1997); and **B**, moscovian "phylloid" algal mounds; Utah, USA (modified after Grammer *et al.* 2000). Scale bars: *c.* 10 m.

1996; Martín *et al.* 1997; remark: *Halimeda* beds described by Mankiewicz [1988] from a nearby area are ascribed to gravitational deposition on the basin slope). In those strata free empty segments of *Halimeda* thalli formed piles of gravel, the debris of their emptying during sexual reproduction. The intergranular space and part of the organic porosity of these segments are incompletely filled post-depositionally by percolated geotropic finer-grained sediment (commonly a micrite), and by thick botryoidal cement and clotted micrite (often considered microbial cement). The texture of the rock thus formed can be denominated as rudstone according to Embry and Klovan's classification (Fig. 10); it is not boundstone as none of the thalli are in the position of growth.

EXAMPLES OF ANCIENT CARBONATE PRODUCTION

PRODUCTION OF LIME MUDS

In fossil specimens the degree of calcification that has been used as a taxonomic criterion at the specific level may range widely within a single species depending on its stage of growth (age) and on environmental parameters. In addition, the calcareous coating breaks up into large or small bioclasts depending on whether or not the living specimen was weakly (loose needles) or strongly (dense acicular network) calcified. If indeed some of the largest fragments retain features allowing their ascription to the category of phycological

allochems, most of them have been micritized and consequently their origin is untraceable. Similarly the smaller remains are integrated into the muddy matrix so their origin is indeterminate too.

Owing to diagenesis, particularly as regards the conversion of micrometric needles of aragonite to microcrystalline calcite (micrite), it is not possible to answer Friedman's (1994) question "which processes formed the bulk of the micrites in the rock record".

PRODUCTION OF LIME SANDS
FROM SEGMENTED OR NOT GREEN ALGAE

In the fossil record bioclasts of CGA are usually pulverized and scattered. They commonly represent less than 10% of the components of most of the carbonate microfacies characteristic of shallow-water environments. However there are a few facies in which CGA are well preserved and may be the main component of the rock (more than 25%).

Dascladales

There are many examples of low-energy mud-dominated fabrics characteristic of chlorophytic meadows: e.g., the Tithonian *Clypeina sulcata* (Fig. 7D) and the Paleocene Dasyclad (Fig. 8A, C) wackestones. But we also see high-energy grain-dominated fabrics characteristic of submarine dune field, storm and beach deposits in which algal remains are preserved owing to their rapid burial: e.g., the Liassic *Tersella genotii* rudstones from Morocco (Fig. 7A; Barattolo *et al.* 2008).
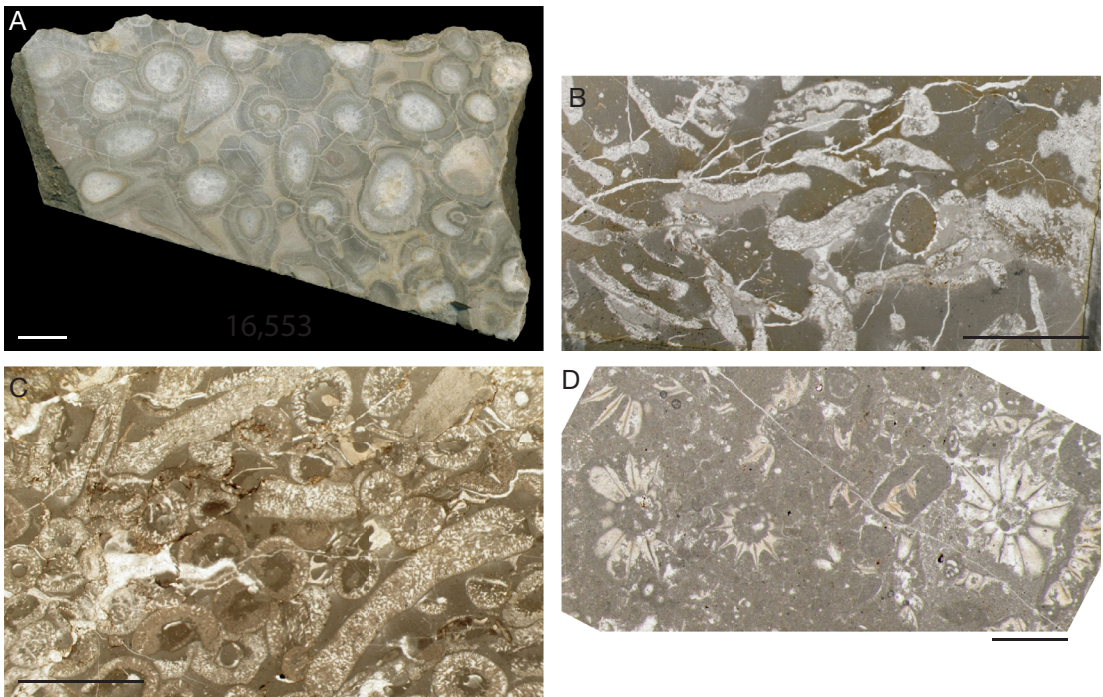
Fɪɢ. 7. — **A**, rudstone made up of various sections of *Tersella genotii* Barattolo & Bigozzi; Sinemurian; Ribat Al Khaïr, Morocco; Deloffre collection; **B**, floatstone with various sections of *Halimeda opuntia* (Linnaeus) Lamouroux; Calcare di Rosignano, Pliocene; Livorno, Italy; Deloffre collection, nr. Liv. 15; **C**, floatstone with various sections of *Boueina hochstetteri* Toula; Deloffre Collection, nr. o18940; **D**, bioclastic wackestone with oblique and transverse sections of *Clypeina sulcata* (Alth *ex* Pia) Granier & Deloffre; Kimmeridgian-Tithonian; Spain; Deloffre Collection, nr. Pe 1, c. 2, 519 m. Scale bars: A, 1 cm; B, C, 5 mm; D, 1 mm.

Mineralization in modern CGA is aragonite, the metastable polymorph of $CaCO_3$. But in fossils it may be calcite, as in some species of Dasycladales (Bassoullet *et al.* 1979): *Bucurella espichelensis* (Granier 2010), *Clypeina sulcata*, *Falsolikanella campanensis*, *Hamulusella durandelgai*, *Heteroporella lepina*, *Megaporella boulangeri*, *Pseudoclypeina distomensis*, *Salpingoporella* (*Hensonella*) *dinarica*, *S. urladanasi*, *Zergabriella embergeri*, etc. (Fig. 9). A plot of the distribution of these occurrences on a curve of the molar Mg/Ca ratio of seawater during the Phanerozoic shows no obvious relationship between the two forms of $CaCO_3$ that alternated in being predominate in seawater: calcite and aragonite, and the crystal form (orthorhombic or rhombohedral) of calcium carbonate comprising the tests of algae. The first occurrence of a calcitic alga (*Koninckopora* sp.) was in Visean times coincident with the end of the Paleozoic calcite sea; the second occurrence was restricted to the prelude and the closure of the Cretaceous-Paleogene calcite sea. The last occurrences, that of *Clypeina* ? *teakolarae* (Radoičić *et al.* 2011) and that of *C. helvetica* (Schlagintweit *et al.* 2011), are even more striking for they are isolated respectively in Early and Late Eocene times. In addition during these shorts intervals of geologic time calcitic and aragonitic species occurred together. So the problem of this co-occurrence is still to be solved.

Bryopsidales

Fossil *Halimeda* were not known before the work of the brothers L. & J. Morellet (1923) and their find of Eocene specimens (Fig. 7B). References to previous discoveries reported by these authors (see Unger 1847, 1850 and Fuchs 1894 *in* Morel-

let & Morellet 1923), are actually foraminifers of the genus *Arthrodendron* (Kaminsky *et al.* 2008).

As they share characters with modern *Halimeda* (articulation, patterns of the filaments) many fossil species ascribed to the genus have rounded rather than flattened segments (Bassoullet *et al.* 1983) and are therefore closer to the genus *Boueina*. Steinmann (1901) gives the following description of this genus: "Die einfachen, ungegliederten und unverzweigten, mehr oder weniger walzenförmigen Kalkkörper werden von einem System verzweigter Kanäle durchzogen, die alle unter einander ohne irgend welche sichtbare Trennung zusammenhängen." (Translation: "The simple more or less cylindrical calcareous thallus, inarticulated, unsegmented but branched, is furrowed by a system of irregularly branching channels that have no visible interruptions in their connectivity.") Remains of its representatives are commonly found in Cretaceous strata as bioclastic floatstones with muddy matrices (Fig. 7C). But so far there is no report of mound-like structure.

Another Late Cretaceous taxon, *Gosavisiphon paucimedullaris*, was formerly ascribed to the genus *Halimeda* for broken pieces of its thallus are flat and therefore very similar to *Halimeda* segments. While revising this material Schlagintweit (2010) demonstrated that its thallus is unsegmented and its flat elements are attached at angles to each other. Though it has a potentiality as a baffle for sediment, no phenomena of that kind have been reported to date.

Finally another genus, *Permocalculus*, and related forms, the thalli of which may display enigmatic ovoid structures, commonly interpreted as traces of reproductive organs, are attributed to the fossil family Gymnocodiaceae. Thought the termination "-codiaceae" suggests an attachment to the Chlorophytes, these problematic forms have been compared to the modern genus *Galaxaura* Lamouroux, a Rhodophyte (see Elliott 1965). No current data exist that would definitely validate or invalidate this attribution.

PRODUCTION OF ALGAL BIOLITHITES
In addition to *Halimeda* (for they may stabilize the sediment with their rhizoids), a number of fossil CGA produced biolithites:
– one is *Neoteutloporella socialis*, a member of the Order Dasycladales;

– a second is *Anthracoporella spectabilis*, originally described as a member of the Order Dasycladales, now treated as a member of the Order Bryopsidales;
– the Carboniferous-Permian ancestral Bryopsidales.

The Tithonian Neoteutloporella
Bodeur (1980, 1995) reports that in southern France Dasycladalean algae form "biolitites", a unique feature that comprises framestones made up of the Tithonian *Neoteutloporella socialis* (Fig. 8D). These small build-ups consist of discrete hemispherical colonies ranging from 0.1 to 0.5 m in diameter or of stacked colonies that may reach 2 m in width and up to 0.6 m in thickness. There are very few records of this species (see De Castro 1993 for review). Dragastan *et al.* (1987) also found small build-ups (up to 0.17 m in diameter) in Romania.

The Carboniferous Anthracoporella spectabilis
The Carboniferous-Permian alga *Anthracoporella spectabilis* (Fig. 8F) was long thought to be a Dasycladalean, it is now assumed to be a non-articulated Bryopsidalean (Granier & Hofmann 2003; Mu *et al.* 2003). *Anthracoporella* mounds have been described, most of them in the Carnic Alps (Krainer 1995; Samankassou 1997, 1998, 1999; Krainer *et al.* 2003). These algal thalli are rigid, commonly unbroken, and densely packed in an upright position, so the texture of the rock is that of a bafflestone or even that of a framestone in the Embry and Klovan classification.

The Carboniferous-Permian ancestral Bryopsidales
The word "phylloid" was introduced by Pray & Wray (1963) for those Carboniferous to Triassic algae of dubious systematic affinities but that share leaf-like shapes and sizes: "Phylloid: meaning, literally, leaf-like or resembling a leaf. This is the dominant character of the algal fragments so prevalent in shallow-water carbonate rocks of Pennsylvanian and Early Permian age. The algal genera, *Anchicodium*, *Archaeolithophyllum*, *Eugonophyllum*, *Ivanovia*, and possibly others are included. The term applies only to the shape of the algal remains as we now observe them. It can be applied without regard to biological classification and can be applied to forms of different growth habits. Thus, the term "phylloid" has no implication as to whether these
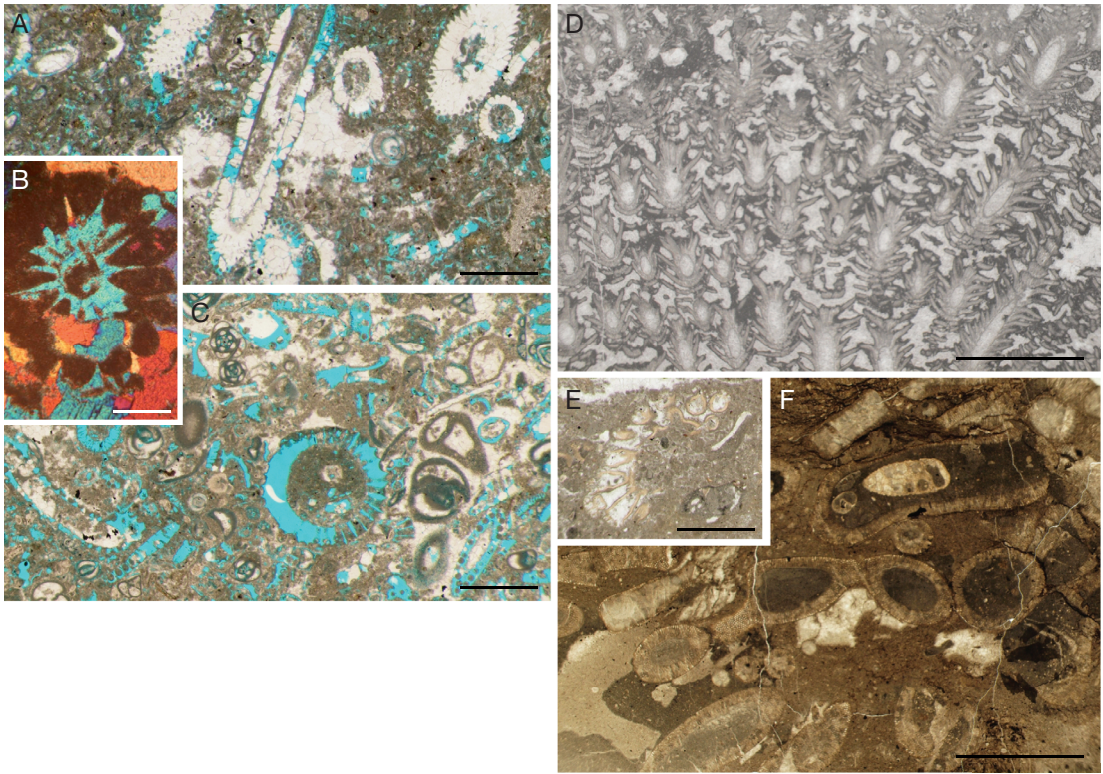
FIG. 8. — **A, C**, bioclastic wackestone with various sections of Dasycladales: *Acicularia*, *Neomeris*, etc; porosity is mainly moldic (**C**), residual moldic after partial drusic cementation (**A**); Paleocene; Sirte Bassin, Libya; **B**, oblique section of *Otternstella lemmensis*; the mold is filled by anhydrite (cross-polarized light); nr. 127/11711; Bu Haseer Formation, Tithonian-Berriasian transition; offshore Abu Dhabi, United Arab Emirates; **D**, subaxial sections of *Neoteutloporella socialis* (Praturlon) Bassoullet *et al*.; the texture is that of a framestone; Bodeur collection; **E**, oblique section of *Deloffrella quercifoliipora* Granier & Michaud; this specimen has retained its original aragonitic form; Tithonian-Berriasian; Bosnia-Herzegovina; J.-P. Masse collection; **F**, various sections of *Anthracoporella spectabilis* Pia; the texture is that of a bafflestone; Pia collection, nr. LXXII.5. Scale bars: A, C, E, 1 mm; B, 250 μm; D, F, 5 mm.

algae existed as encrusting 'mats' or upright 'leaves'. Such terms as 'blady', 'leafy', 'platy', and others have been previously applied to these algae. Certain of these terms have specific connotations which make them undesirable for general usage. None seems to characterize adequately the overall shape aspect of these algae, irrespective of their taxonomic identity or growth habit, and hence the term phylloid is here introduced to meet this need." But revision of some material suggests that the term should be abandoned. For instance although most of these algae have structural features that relate them to the Bryopsidales ("utricular molds" *sensu* Torres & Baars 1992a), *Archaeolithophyllum* (Johnson 1956) is an encrusting form with affinities to the Rhodophyceae (Wray 1964): the "Squamariaceae" (Vachard *et al.* 1989), i.e. the Peyssonneliaceae (James *et al.* 1988). In addition, remains of *Anchicodium* (Johnson 1946) that can be "several centimeters" long are not blade-shaped, for the thallus is "cylindrical and branched, much like modern *Codium*" (Baars & Torres 1991; Torres & Baars 1992b). Blades of the monospecific *Kansaphyllum* (Baars 1992) are "several centimeters long" and display utricular molds only on one side interpreted as their upper (photic) side, the lower side lay on the sea floor. The thalli of *Calcifolium* and *Falsofalcifolium* (Vachard & Cózar 2005), respectively with asymmetric and random pore settings, are constructed as a combination of variously arranged cones. They were long ascribed to the "Codiaceae"
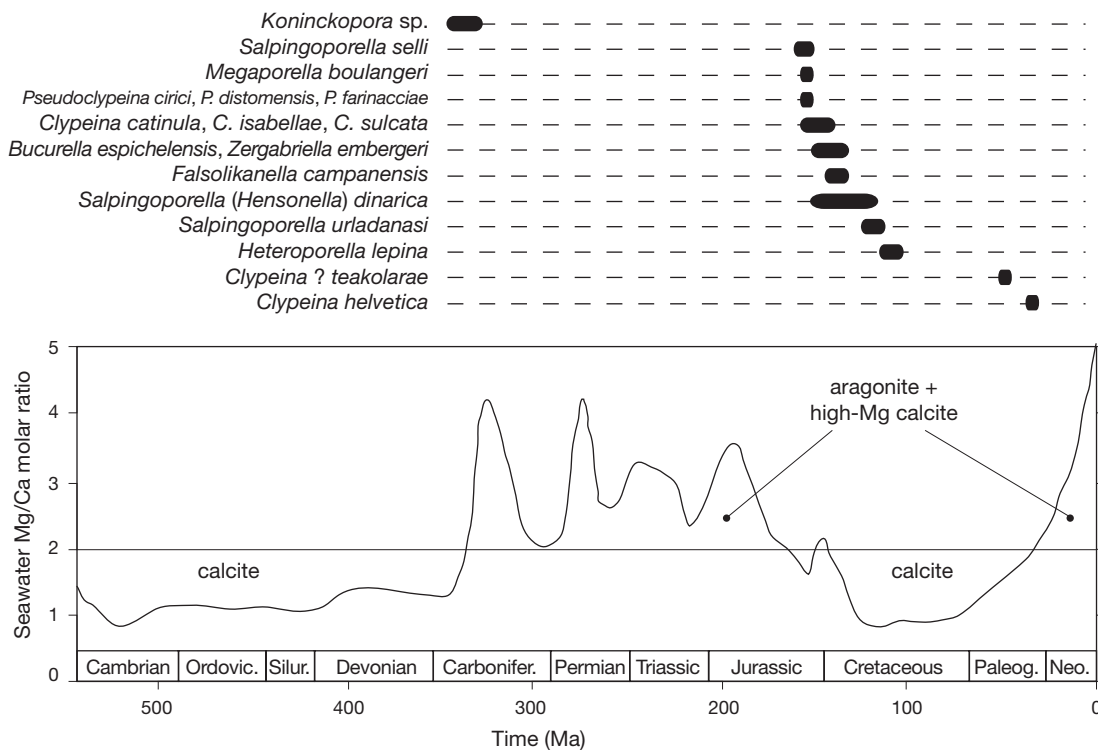
Fɪɢ. 9. — Stratigraphic distribution of the supposedly calcitic Dasycladales (*Koninckopora* sp. and *Salpingoporella selli* (Crescenti) Bassoullet *et al.*) and of the originally calcitic Dasycladales plotted against the molar Mg/Ca ratio of seawater during the Phanerozoic (after Ries 2006, modified from Lowenstein's publications).

(Skompski 1981) but are now ranged into a group of *incertae sedis* algae, the Calcifoliaceae (Vachard & Cózar 2005). Finally, whether or not fragments of phylloid algae "resemble leaves", the morphology of some species remains unknown:
– the monospecific *Calcipatera cottonwoodensis* (Torres *et al.* 1992) has a wide cup-shaped (cyathiform) membranous thallus: a single specimen is up to 180 mm wide and more than 40 mm high (Savin & West 2005). In axial section an obtuse angle near its proximal part characterizes it;
– thalli of *Ivanovia tebagaensis* and *I. triassica* are also cup-shaped, but are narrower and smaller (Torres 1995, 2003) for they attain scarcely 40 mm in both width and height;
– leaf-like remains of some *Eugonophyllum* are "several centimeters in length and width" but their small thalli (less than 20 mm wide) have been described as

having a folded-blade morphology (Cross & Klosterman 1981; Kirkland *et al.* 1993), or a wine-glass (Torres 1997) and a cup shape (Forsythe *et al.* 2002).

To summarize the use of the term phylloid that has confused Systematics should be abandoned. It has also hindered the sedimentological interpretations discussed below.

Harbaugh (1960) states that: "The modern alga *Halimeda* may provide a rough analogue to the leaf-like algal crusts of the Lansing limestones." He was the first to propose a relationship between the two. Konishi & Wray (1961) interpret certain algal bioherms or banks in the Upper Pennsylvanian-Lower Permian of New Mexico as having been built up through the influence of a sediment-trapping baffle mechanism of leaf-like algal fronds of the calcareous algae *Anchicodium*, *Eugonophyllum* (Fig. 6B) and *Ivanovia*. Cross & Klosterman (1981) state
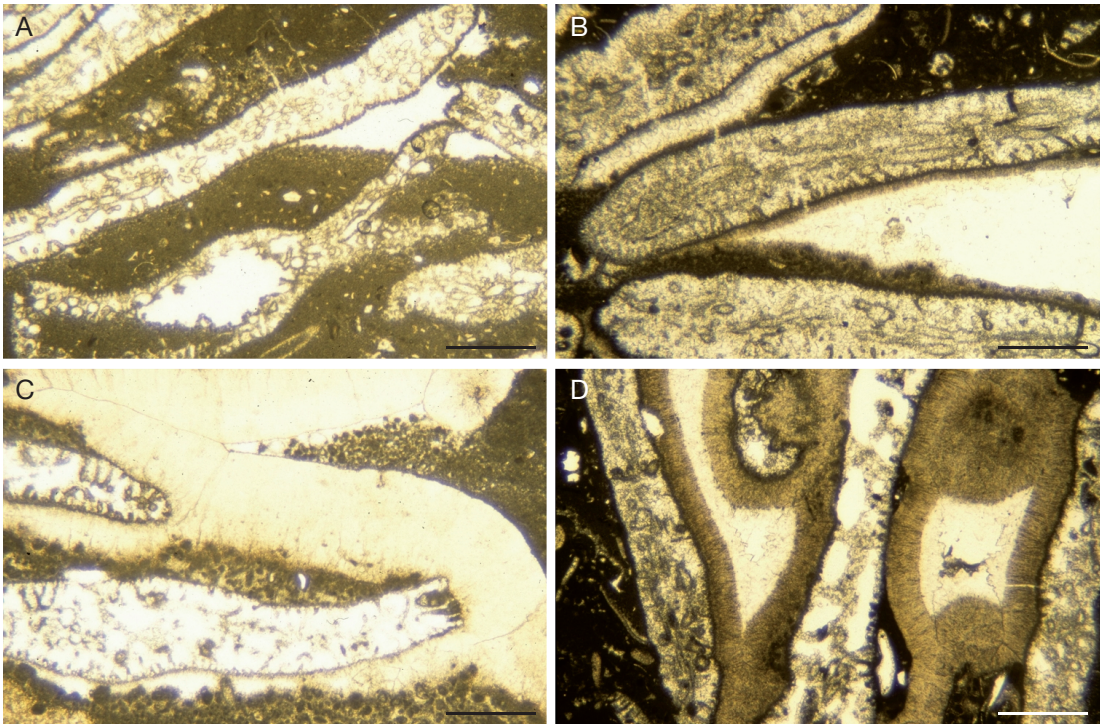
Fig. 10. — Miocene *Halimeda* facies, mostly *Halimeda* rudstones: **A**, micritic to clotted mud fills most of the intergranular space and the organic porosity; it is post-depositional for it took place by percolation; **B**, a fibrous calcitic fringe borders the shelter cavities beneath segments of *Halimeda*; **C**, a rather thick stage of botryoidal cementation is sandwished between two successive stages of post-depositional and geopetal clotted micrite; **D**, a yellowish fibrous-botryoidal cement borders the intergranular space and the rest of it is filled by a translucent drusy calcitic cement; Messinian; Sorbas, Spain. J. C. Braga Collection. Scale bars: 1 mm.

that: "In most reported occurrences, phylloid algal banks and mounds are parautochthonous detrital accumulations of phylloid algal debris in which the algal plates generally are fragmented, oriented subparallel to bedding, and are in either grain or matrix support."

Few *Halimeda* mounds are the *in situ* accumulation of disarticulated algal segments that are fossilized as grain-supported fabrics: rudstones. Most accumulations were transported by currents before final deposition to produce matrix-supported fabrics: floatstones. Most phylloid mounds consist of broken pieces of fragile inarticulated algae and were also dynamically-driven accumulations. There are very few reports of ancestral Bryopsidales found in growth position (Cross & Klosterman 1981; Torres *et al.* 1992; Kirkland *et al.* 1993; Torres 1995, res *et al.* 1992; Kirkland *et al.* 1993; Torres 1995,

1997, 2003; Savin & West 2005). In a 2-metre section measured by Savin & West (2005: fig. 2) the interval with *in situ Calcipatera* represents only ¼ of the total: a thick basal interval and the thin uppermost interval are "packstones" (actually floatstones) of fragmented specimens.

Konishi & Wray (1961) considered that: "*Eugonophyllum* inhabited sublittoral environment at a depth below normal wave agitation and possibly extended to depths of 100 feet [30 m] but occurred most abundantly in the shallow portion of its depth range." The paleodepth interpretation of Grammer *et al.* (2000) for their "phylloid" algal facies is based on this outdated view and does not discuss the alternative, that is a deep-water accumulation. Microbial inscrustations like those seen in the Miocene *Halimeda* mounds of southern Spain are described in *Eugonophyllum*

TABLE 1. — Key measurements of algal biosedimentary structures through time (data derived from a bibliographic compilation). Abbreviations: **Fm**, formation; **Lmst.**, limestone; **L**, length; **W**, width.

Algae	References	Total height	Relief	Height in living habit	W	L	Spacing/ wave lenght	Stratigraphy	Locality
Ivanovia	Pray & Wray 1963; Choquette 1983	> 3 m	2 m					Ismay Fm, Moscovian	Utah, USA
"phylloid" algae	Grammer *et al*. 2000	8-14 m	> 3 m				33-58 m		
?*Eugono- phyllum*	Samankassou & West 2002	1.4 m		0.3 m	4.2 m			Wyandotte Lmst. Fm, Kasimovian	Kansas, USA
"phylloid" algae	Doherty *et al*. 2002	< 30 m						Gzhelian	New Mexico, USA
Anthra- coporella	Samankassou 1997, 1998, 1999	12 m, up to 22 m		up to 12 m		60 m		Corona Fm and Lower Pseudos- chwagerina Lmst. Fm, Gzhelian	Tyrol, Italy; Austria
Anthra- coporella	Krainer *et al*. 2003	5.5-6 m		11- 12 m				Lower Pseudos- chwagerina Lmst. Fm, Gzhelian	Tyrol, Austria
Calcipa- tera	Savin & West 2005	5 m		0.5 m				Beattie Lmst. Fm, Permian	Kansas, USA
Eugono- phyllum	Cross & Kloster- man 1981	2.5 m, up to 10 m						Laborcita Fm, Lower Permian	New Mexico, USA
Halimeda	Davies *et al*. 1988	up to 25 m	10- 20 m		100 m	150 m		Holocene	Great Barrier Reef, Aus- tralia
	Roberts *et al*. 1988	20- 52 m	10- 20 m		10- 30 m	100- 450 m		Holocene	Kalukalu- kuang Bank, Indonesia

and ?*Ivanovia* bioherms (Cross & Klosterman 1981; Grammer *et al.* 2000: fig. 10d; Forsythe *et al.* 2002). Table 1 summarizes the diversity of sedimentary structures associated to successive taxa from the Late Carboniferous to date.

BY-PRODUCTS: ARAGONITE REPLACEMENT, POROSITY AND CEMENTS

Many papers state that "aragonite recrystallizes into calcite" although "recrystallization into calcite" (mosaic calcite with ghost structures) or "preservation as aragonite" are phenomena that are rarely the final state of preservation of fossil algae. For instance, the type-material of *Anthracoporella spectabilis* (Fig. 8F) is recrystallized: the large poikilitic honey-colored crystals show a pseudo-pleochroism owing to inclusions of organic matter. The oldest algae preserved as aragonite were found in Tithonian-Berriasian strata from Bosnia-Herzegovina: *Actinoporella podolica* (Granier 1994: pl. 3, figs 5-8) and *Deloffrella quercifoliipora* (Fig. 8E). In outcrop, i.e. in the vadose zone, geologists commonly collect molds filled with drusy calcite cement; in the phreatic zone, subsurface geologists find a huge number of empty molds. Dissolution of the aragonite leads to the formation of moldic vugs followed by the deposition of calcitic cements. Consider the following numbers:

Aragonite
mol. wt = 100
density = 2.93
vol = 100/2.93 = 34.1

Calcite
mol. wt = 100
density = 2.71
vol = 100/2.71 = 36.8

In a closed system, the complete dissolution of an aragonite filling creates an equivalent volume of porosity but asubsequent precipitation of calcite lessens the ultimate porosity with respect to the original porosity because of the larger volume occupied by calcite (the volume of solid mineral is increased by approximately 8%).

In subsurface rocks fossil CGA, along with other aragonitic bioclasts, are great contributors to the development of secondary porosity and to subsequent cementation by calcite (or less commonly by accessory minerals, such as anhydrite: Fig. 8B). Ancestral Bryopsidales have already a wide reputation for their accumulations formed historical oil reservoirs in the USA (Pray & Wray 1963; Wilson 1975; Choquette 1983; Doherty *et al.* 2002). The role of the Dasycladales is not neglictable in most carbonate reservoirs of the Middle East (Granier 2002, 2003), but most people dealing with these series are not able to identify their remains, mostly empty molds and micritic envelops.

CONCLUSIONS

While gathering information about the latest data on carbonate production by green algae in modern and ancient environments, the author found that few original works had been published: only a few short syntheses dealing only with *Halimeda* or on the contrary involving all sorts of "calcareous" algae (red algae, charophytes, cyanobacteria, coccolithophorids…) have been published, commonly as chapters in books with more eclectic ends. This preliminary review demonstrates that CGA have a broader diversity and therefore a greater impact on paleoenvironments than had been assumed to date, but does not answer all questions regarding algal contributions to accumulations of lime carbonates, for their importance in this area remains difficult to estimate. It concludes with six important points:
– though CGA contribute significantly to the clay-sized particles of modern lime mud, the origin of

aragonitic needles is still under discussion for many of them could be induced or controlled biologically, triggered by planktonic "algal" blooms, and the rest precipitated physicochemically directly from seawater (Fig. 1). It is even more difficult to get a rough idea of these ratios in ancient limestones for most needles and granules to lose their original texture due to diagenesis, i.e. their conversion to calcitic micrites;
– coarser (sand- and gravel-sized) algal-derived particles commonly suffer mechanical erosion (crushing and abrasion) as well as biologically-enhanced alteration, i.e. micritization. In addition the amount of calcification ranges widely in a single specimen or in its several parts. Furthermore, weakly calcified parts of a skeleton are rarely preserved;
– locally large algal remains are accumulated. If lithified in the position of growth, the rock is called a boundstone: it is either a bafflestone or a framestone. If these bioclasts have been subsequently more or less reworked discrete behaviours ensue, depending on whether the alga was articulated (e.g., *Halimeda*) or not (e.g., *Eugonophyllum*). Broken pieces of inarticulated Bryopsidales (e.g., *Eugonophyllum*) are commonly found imbricated in floatstone or rudstone textures suggesting they were transported by currents before final deposition. Most deposits made up of disarticulated segments of *Halimeda* are floatstones too, but in a few cases it can be proven that the accumulation was *in situ*: the "ecological reef" of living algae is replaced by a "geological reef" (bioherm), a cemented rudstone of *Halimeda* segments (not a boundstone); microbial communities are commonly envolved in these cementation processes;
– the use of the term phylloid that has confused Systematics should be abandoned;
– most of the CGA calcify as aragonite, but there are short intervals in the fossil record during which calcitic Dasyclad species lived in association with aragonitic species (Fig. 9);
– classically, CGA were considered as markers of shallow-water environments. However, although some taxa are restricted to the upper portion of the photic zone, others can grow and calcify in its lower portion at depths as great as −120 m (Fig. 2).

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APPENDIX

APPENDIX 1. — List of the taxa cited in this publication.

Acetabularia Lamouroux;
Acetabularia acetabulum (Linnaeus) Silva;
Acetabularia antillana (Solms-Laubach) Egerod;
Acetabularia caliculus Lamouroux *in* Quoy & Gaimard;
Acetabularia mediterranea Lamouroux;
Acetabulariaceae Nägeli;
Acicularia d'Archiac;
Actinoporella (Gümbel *in* Alth) Granier;
Actinoporella podolica (Alth) Conrad *et al.*;
Anchicodium Johnson;
Anthracoporella Pia;
Anthracoporella spectabilis Pia;
Archaeolithophyllum Johnson;
Arthrodendron Ulrich;
Avicennia Linnaeus;
Batophora J. Agardh;
Bornetella Munier-Chalmas;
Boueina Toula;
Boueina hochstetteri Toula;
Bryopsidales Schaffner;
Bucurella espichelensis (Deloffre & Ramalho) Granier;
Bucurella Granier;
Calcifoliaceae (G. Termier *et al.*) Vachard & Cózar;
Calcifolium Schvetzov & Birina;
Calcipatera Torres *et al.*;
Calcipatera cottonwoodensis Torres *et al.*;
Campbelliella Radoičić;
Chlorocladus Sonder;
Chlorophyta (Reichenbach) Pascher;
Clypeina (Michelin) Bassoullet *et al.*;
Clypeina catinula Carozzi;
Clypeina helvetica L. & J. Morellet;
Clypeina isabellae J.-P. Masse *et al.*;
Clypeina sulcata (Alth *ex* Pia) Granier & Deloffre;
Clypeina ? *teakolarae* Radoičić *et al.;*
Codiaceae Kützing;
Codium Stackhouse;
Cymopolia Lamouroux;
Dactylopora Lamarck;
Dasycladaceae Kützing;
Dasycladales Pascher;
Dasycladus clavaeformis (Roth) Agardh;

Dasycladus vermicularis (Scopoli) Krasser;
Deloffrella quercifoliipora Granier & Michaud;
Eugonophyllum Konishi & Wray;
Falsofalcifolium Vachard & Cózar;
Falsolikanella campanensis Azéma & Jaffrezo *ex* Granier;
Galaxaura Lamouroux;
Gosavisiphon (Schlagintweit & Ebli) Schlagintweit;
Gosavisiphon paucimedullaris (Schlagintweit & Ebli) Schlagintweit;
Gymnocodiaceae Elliott;
Halimeda Lamouroux;
Halimeda incrassata (Ellis) Lamouroux;
Halimeda monile (Ellis & Solander) Lamouroux;
Halimeda opuntia (Linnaeus) Lamouroux;
Halimeda paucimedullaris Schlagintweit & Ebli;
Halimeda praeopuntia L. & J. Morellet;
Halimeda tuna (Ellis & Solander) Lamouroux;
Halimedaceae Link;
Hamulusella durandelgai (Jaffrezo & Fourcade *ex* Jaffrezo *in* Bassoullet *et al.*) Barattolo;
Heteroporella lepina (Praturlon) Granier *et al.*;
Ivanovia Khvorova;
Ivanovia tebagaensis Vachard *et al.*;
Ivanovia triassica Torres;
Kansaphyllum Baars;
Koninckopora (Lee) Wood;
Megaporella boulangeri Deloffre & Beun;
Neomeris arenularia Munier-Chalmas *ex* L. & J. Morellet;
Neomeris Lamouroux;
Neoteutloporella Bassoullet *et al.*;
Neoteutloporella socialis (Praturlon) Bassoullet *et al.*;
Opuntia Miller;
Otternstella lemmensis (Bernier) Granier *et al.*;
Penicillus Lamarck;
Penicillus capitatus Lamarck;
Permocalculus Elliott;
Petrascula iberica (Dragastan & Trappe) Granier *et al.*;
Peyssonneliaceae Denizot;
Polyphysaceae Kützing;
Posidonia Koenig;
Pseudoclypeina cirici Radoičić*;*

Pseudoclypeina distomensis Barattolo & Carras*;*
Pseudoclypeina farinacciae Radoičić*;*
Pseudoschwagerina Dunbar & Skinner;
Rhipocephalus Kützing;
Salpingoporella (*Hensonella*) *dinarica* Radoičić;
Salpingoporella (Pia *in* Trauth) Conrad *et al.*;
Salpingoporella selli (Crescenti) Bassoullet *et al.*;
Salpingoporella urladanasi Conrad *et al.*;
Spirorbis Daudin, 1800 (annelid);
Squamariaceae Kylin;

Syringodium Kützing;
Tersella genotii Barattolo & Bigozzi;
Thalassia Banks & Solander *ex* Koenig;
Tydemania expeditionis Weber-van Bosse;
Tydemania Weber-van Bosse;
Udotea Lamouroux;
Udoteaceae Endlicher;
Zergabriella embergeri (Bouroullec & Deloffre), Granier;
Zitellina (L. & J. Morellet) Barattolo.