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EARLY DIAGENESIS OF SKELETAL REMAINS IN MARINE SEDIMENTS : A 10 YEARS STUDY

by

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Mots-clés : *diagenèse précoce, biodégradation, biosédimentologie, formations squelettiques.*

SUMMARY. A 10 years long experimental approach of weathering processes affecting "fresh" organoclastic material at various depths (0 - 4800 meters) in different regions of the world allowed us to characterize, from an ecological point of view, the endolithic populations and associated microorganisms and to evaluate their role in the maturation of organoclastic sediments. We defined the rules governing the settling, growth and succession patterns of the microborers communities. The diagenetic phenomenons related to the microborers populations depend on environmental conditions (depth, t°, pO_2,...) in a way that will enable future modelisation work.

From a general point of view, the prime alteration affecting skeletal remains is of biological origin. It is due to microorganisms growing onto and inside the skeletons, at the precise level of the organic matrices, that weather the organic compounds of these matrices by discharging specific hydrolases at their contact. A fast step of extraction of the most labile compounds (high speed constant) precedes a much slower biodegradation step of refractory compounds.

Anaerobic biodegradation takes place after aerobic biodegradation. Other kinds of microorganisms appear implicated but anaerobic biodegradation processes do not intrinsically differ and do not develop slowlier. Its apparent slowness mainly proceeds from the fact that only refractory compounds of the skeletal matrices usually reach the anoxic layers of the sediments. Anaerobic microbiocenoses associated with skeletal carbonates appear adapted to the biodegradation of such less labile compounds of the organic matrices.

Early biological diagenesis events have important repercussions on other diagenetic, physical as well as chemical processes. From a mechanical standpoint, the biological extraction of the organic "cement" between skeletal crystallites fasten abrasion processes by reducing the general cohesion of the skeleton. Moreover, grazing and browsing organisms seeking for endolithic microflora contribute to such abrasion and disruption phenomenons. This leads to an appreciable increase of the $CaCO_3$ *content of the fine grain size fraction of sediments. From a chemical point of view, the disparition of the organic sheaths protecting* $CaCO_3$ *joined to crushing and abrasion effects greatly increase the carbonate dissolution phenomenons and, paradoxally, even in thermodynamically supersaturated media like shallow tropical environment. From that point of view, the importance of high magnesian calcites, their microstructures and organic content, have to be stressed in connection with the control of the buffering capacity of marine waters.*

FOREWORD

This paper is a compilation of results that were first exposed in several other publications where they are discussed and illustrated with more details. We do not expose here new data. All the papers published about this subject are listed as references.

INTRODUCTION

The prime question in all biogeochemical studies concerns the stability of the organic remnants in a diagenetic environment. The bulk of the original biogenic polymers (proteins, chitin, cellulose,...) is eliminated during the early stages of diagenesis. Although microbes undoubtly control to a large extent the fate of organic compounds, it is surprising how little is known concerning their occurence, type of populations, distribution and biochemical activities in various sedimentological materials. While most geochemical papers are devoted to the modelisation of settling and decomposition of particulate organic matter, very little is known about the kinetics of early diagenesis of the organic compounds screened within mineralized skeletons.

As a contribution to the fullfilling of this gap, an experimental analysis of weathering processes affecting detritic skeletal material sampled in shallow and deep sea sediments in different regions of the world was conducted to characterize, from an ecological point of view, the endolithic microbiocenoses present and to evaluate the role of microborers in the alteration of shallow and deep sea carbonates.

MATERIAL AND METHODS

This study is based primarily on direct examination of skeletal substrates (shells, cuticles,...) that were laid down at and below sediment-water interface in different settings and recovered periodically by diving. Moreover samples were collected from a wide variety of sites in order to clarify the weathering patterns of organoclastic remains in different environmental conditions in comparison with experimental material.

RESULTS AND DISCUSSION

AEROBIC BIODEGRADATION

Growth characteristics of the microborers populations in mollusk shells

The colonization and attack by boring microorganisms proceed very rapidly. Even after only 4 days some boreholes were already detectable on some substrates, and marked penetration after only 15 days. Within a few hours after immersion of a new substrate, its surface begin to be covered by epilithic microflora (diatoms, bacteria, yeasts,...) and after one week the surface is completely covered by a slimy coating of algae, bacteria, diatoms,... of which a few percent are true endoliths but much more will later behave as chasmoliths. There is few variation between the different experimental sites [Calvi (Mediterranean Sea), Roscoff (Channel) and Virgin Islands]. Early colonization stages are the most unstable as frequent removal of microorganisms repeatedly exposes new settling areas.

The further steps of the growth of endolithic populations (all "species" confused) lead to the classical sigmoid growth curve of a mixed population colonizing a new substrate. In shallow water (fig. 1), the number of borings approximately increases during the first 15 to 18 months of experiment, regardless of the origin of the sample. Of these borings, only 5 to 15% are effectively occupied by a living microorganism (Fig. 1, black dots). The steady state is maintained (after the exponential growing phase) at about 400.000 borings cm^{-2}, of which approximately 20.000 to 50.000 are "alive". Most of the live filaments are

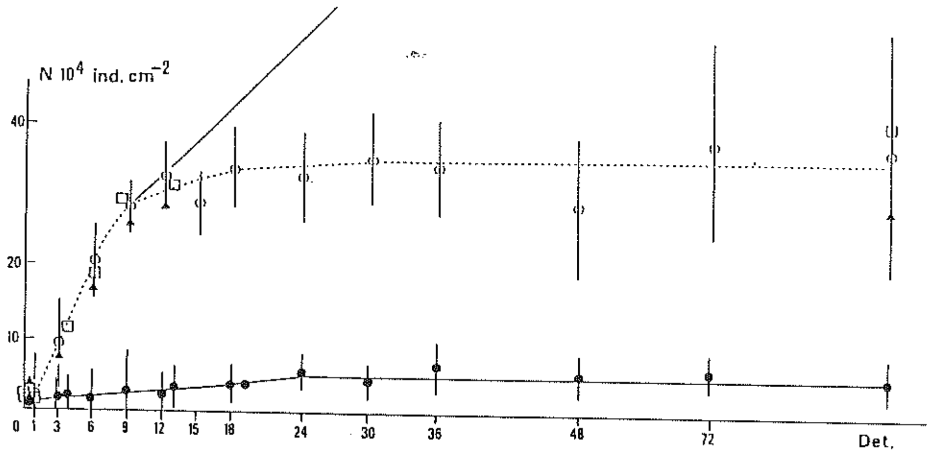

Fig. 1 : Growth curve of the populations of microborers in mollusk shells in shallow water conditions.

○: number of microborings cm^{-2} in Calvi experimental site;
▲: number of microborings cm^{-2} in Roscoff experimental site;
□: number of microborings cm^{-2} in Virgin Islands experimental site;
●: number of live filaments cm^{-2} in Calvi experimental site;
straight line : estimation of erosion rate and browsing effects;
Time is expressed in months. Det. : detritic shells in surrounding sediment, each value is a mean of 75 counts +/- S.D.

to be found in the deepest bored layers in the substrate.

In abyssal conditions (- 4.200 meters depth), indirect estimations (based on statistical estimations of population structure) yield similar results : a sigmoidal growth curve culminating at about 300.000 borings cm^{-2} of which 5.000 to 20.000 are effectively occupied.

After thoroughful penetration in a calcified substrate, the further course of boring activity will be determined by gradients in some critical ecological factors within the shell environment. Population density and penetration depth by photosynthetic algae are restricted to the "photic zone" (which seems to be a thin cortical layer of 100 to 1.000 µm, depending on the microstructure of the shell considered, the amount of incident light and the species of algae considered) : close to the "light compensation depth" within the substrate, algal penetration slows down and the living biomass stabilizes. Other critical factors (for fungi) include O_2 permeation and nutrient supply.

Carbonate substrates once weakened by microborers are rasped away by grazing mollusks (limpets, chitons,...) in shallow and deep-water. The removal of the altered cortical layers of the shells results in a modification of the substrate (accessibility of light and of O_2, exposure of organically less impoverished regions,...) so that algal and fungal penetration can go on. This appears thus as a homeostatically regulated system where substrate weathering will result of mutually adjusted rates of microorganisms growth and penetration within the substrate on one hand, and grazing or erosion of the cortical layers on the other hand (fig. 1).

Microborers successional patterns and interactions

Boring by microorganisms mostly includes blue-green algae, microscopic eucaryotic algae and fungi that actively penetrate hard substrates and produce boreholes conforming to the shapes of their thalli. A detailed survey of succession patterns in endolithic communities of mollusk shells was undertaken in the Calvi area (- 37 m depth) over a six year period (fig. 2).

At each moment, the microborers community is composed of a different set of forms, more and more diversified with time. The bulk of endolith biomass is composed of fungi and blue-green algae. During the first year of experiment, cyanophyta dominate the other components of the microbiocenosis, reaching a dominance of 75 to 95 % of the whole community. After a remarkable spreading during the first months of experiment, the dominance of blue-green algae diminishes for the next two years, to keep an almost constant level, representing approximately 15 to 25 % of the effective borers during the following four years. simultaneously to blue-green algae decrease, fungi progressively increase their biomass during the first three years of experiment, reaching a constant dominance of about 50 %, and keeping it almost unchanged for the next three years (fig. 2).

The other microorganisms encountered are much less abundant in the conditions of the experiment. Filamentous green algae regularly increase their population to reach about 10 % of the number of living filaments after about two years of experiment. Yeasts and filamentous bacteria populations remain almost unchanged during the whole experiment : they represent 2 to 5 % of the microorganisms present at each moment. The other organisms (red algae, sponges, nematods, gastrotrichs,...) are even less abundant, around 1 to 2 % of the population.

Except in the case of fungi and blue green-algae, the variability of the counts is very high reflecting the extent of heterogeneity in microborers community structures. We did not detect any significant difference in the colonization pattern of various microstructures, including mother-of-pearl and crossed-lamellar structures (fig. 2).

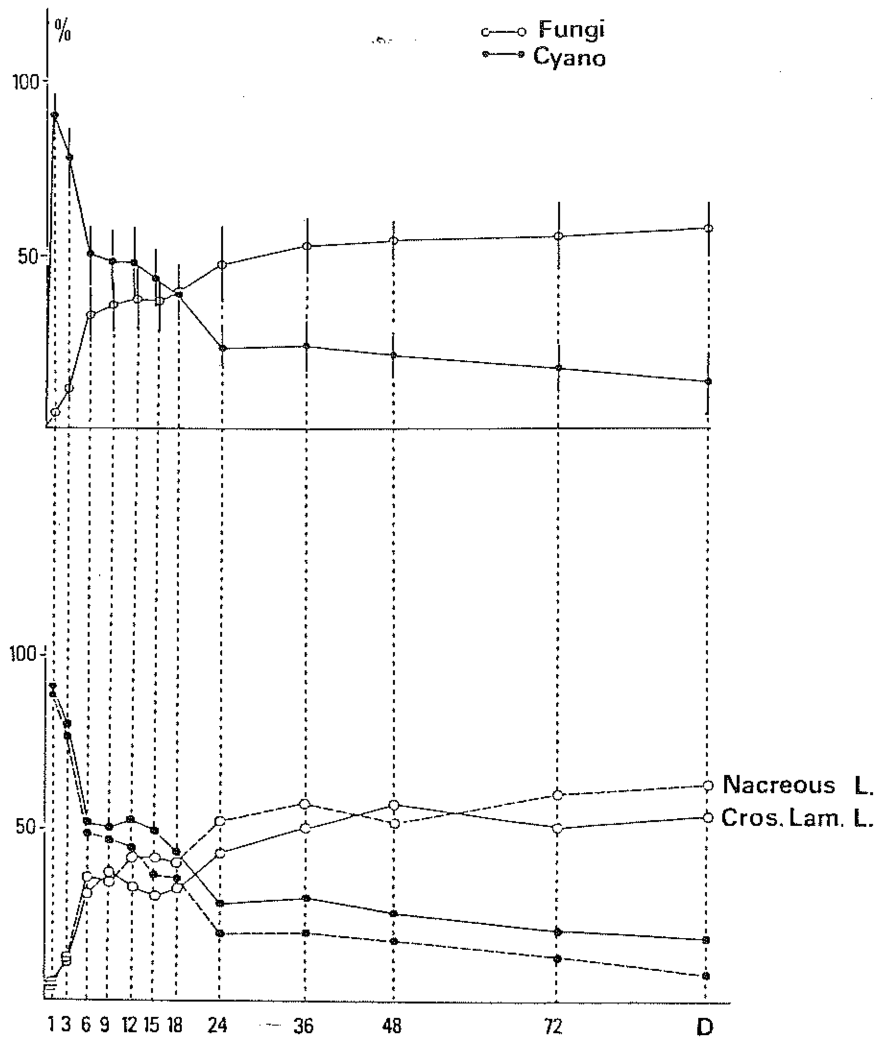

Fig. 2 : Dominance pattern of fungi and blue-green algae during colonization of mollusk shells at experimental site Calvi (-37 m depth). Above, all microstructures confused (crossed lamellar, foliated, prismatic nacrous and homogenous). Bottom, variations in the colonization of two different microstructures, crossed lamellar versus mother of pearl.

The comparison of the three experimental sites shows that there is much geographical differences in the colonization pattern of a same substrate but immersed in different areas. Even if the majority of algal borers genera are distributed worldwide, the associations and dominances appear to vary in different parts of the world. The qualitative composition of the microorganisms populations boring into shell substrates will have much importance on the kinetics and ways of shell matrix consumption through their different properties concerning secretion of hydrolytic enzymes.

In abyssal sediments, a succession pattern is also obvious, even if the endolithic community superficially looks more uniform and less diversified : sporangia-bearing fungi (oomycetes), together with filamentous bacteria occur almost alone during the first half of the population exponential growing phase. Then tubular fungi of different kinds and yeasts invade the shells, sharing dominance with sporangia-bearing fungi. They are soon followed by ascomycetes and sponges. When the microborers population density reaches its highest level, some filamentous "agressive" mycetes settle in the weathered shells, seeming to feed upon other microborers (ascomycetes, sponges, tubular forms,...).

In a general way, some interactions apparently occur between different microborers species. Some filamentous bacterial clumps (streptomycetes) always appear surrounded by a clear growth inhibitory zone that most other microorganisms manage to avoid. A subsequent growth of the bacteria appear to kill the other too close endoliths, just as if an antibiotic-like or mycostatic substance diffused from the colony. This kind of relationship is found at any depth but is much more frequent in deep-waters.

Repeated observations suggest that some endolithic fungi seek out other forms (fungi or sponges in deep water biocenoses, several kinds of algae in shallow water), presumably as a nutrient source. This occurs mainly in very biodegraded shells. It is difficult to determine in each case whether this represents parasitic, saprophytic or symbiotic relationships. In deep waters, some particularly well preserved samples make obvious the existence of predator-prey like relationships between different kinds of fungi, or between fungi and sponges.

<u>Aerobic biodegradation of the organic matrices of skeletal substrates</u>

There is a general consensus that microborers and associated microorganisms in shells and other skeletal substrates use the organic matrix of the skeletons as source of nutrients and energy. From a more quantitative point of view, when plotting the organic matter content of detritic mollusk shells sampled in different kinds of sediments (temperate shallow water sediments and abyssal sediments) as a function of the number of microborers, we observed a progressive decrease in organic matter content with increasing density of microborers (fig. 3).

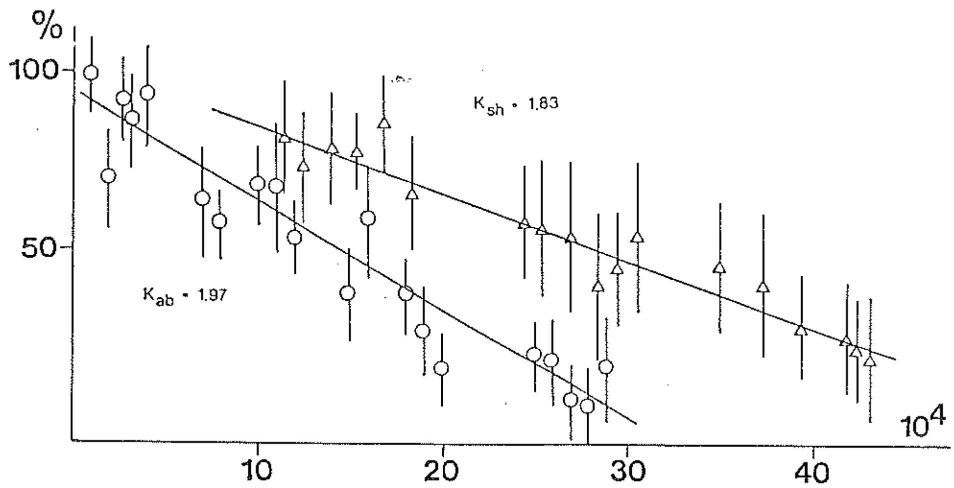

Fig. 3 : Relations between the density of microborers (N cm^{-2}) and the organic content of mollusk shells (expressed as % of the initial content) in shallow sediments (40 to 120 meters depth, Δ) and in abyssal sediments (2800 to 4800 meters depth, O). Each value mean of 10 samples.

From a statistical approach, it appears that there is a direct (linear) relation between the number of endoliths (all forms confused) and the amount of organic matter extracted (correlation coefficient and values highly significant). The angular coefficient of regression lines is slightly higher in the case of abyssal samples (K_{ab} = 1.97) than in the case of shallow-water samples (K_{sh} = 1.83). This means that the abyssal endolithic microflora is more efficient in extracting the organic matrix (even with lower density) than shallow water communities. This can be attributed to a different composition of the endolithic communities of microorganisms. Generally, the microorganisms living within more or less altered skeletons are found in close contact with the organic matrices wrapping the calcified crystallites. They are thus able to use the polymers constituting these matrices as substrates and source of nutrient and energy thanks to the secretion of hydrolytic enzymes. We verified by different approaches that some microorganisms encountered within our experimental material were able to secrete the hydrolases required to weather the macromolecular assemblages of polysaccharides, proteins and lipids constituting the organic sheaths wrapping the mineral units constituting the skeletons (table I).

The histoenzymological approach performed on isolated colonies of microorganisms indeed shows that most of them have wide hydrolytic equipment (table II). The photosynthetic blue-green and green algae are an exception.

TABLE I : Hydrolytic activities in experimental and detritic skeletal material (Calvi experimental site, 37 meters depth). All activities expressed as nM hydrolysed substrate per hour per gram wet weight.

ENZYMES		Nacrous layer 12 months imm.	Nacrous layer 72 months imm.	Nacrous layer detritic (1)	Nacrous layer detritic (2)	Crossed-lamell. detritic (3)	Crustacean cuticle detritic	Echinod. test detritic
PHOSPHATASIC ACTIVITY	(4)	97.2	206.5	147.3	233.8	192.3	511.5	400.7
LIPOLYTIC ACTIVITY	(5)	197.4	186.4	111.3	148.3	116.3	445.7	200.3
PROTEOLYTIC ACTIVITY	(6)	126.0	44.7	30.2	49.3	133.6	115.1	150.0
GLYCOLYTIC ACTIVITY	(7)	98.4	66.1	48.8	75.1	119.5	233.9	18.8

(1) 120 000 borings cm^{-2}
(2) 300 000 borings cm^{-2}
(3) 150 000 borings cm^{-2}
(4) Acid-, alkaline phosphatases plus phosphoamidasic activity
(5) C_4, C_8, and C_{14} esterasic and lipolytic activities
(6) Trypsin, α-chymotrypsin, Val-, Cys- and Leu-arylaminidasic activities
(7) α- and β-glucosidasic and galactosidasic activities, β-glucuronidase, N-acetylglucosaminidase, fucosidase and mannosidase activities.

These last two groups of microorganisms are of course restricted to shallower sediments (above light compensation depth), and, when present, spread relatively cortically in the shells. Fungi (Asco-, and Oomycetes) and bacteria (bacilli and cocci), that are generally found in close contact with the organic matrices inside the skeletons, are able to weather the chitinoproteic or collagenic compounds of the matrices. In the case of chitinolytic activity, the enzymes are effectively secreted within the shells or in the cuticles. That activity is actually located in the areas with high microborers biomass : the thoroughly bored cortical layers, the organic matter of which has been extracted show a very low (not significant) activity, just as the deepest layers of the shells not yet reached by microborers. In contrast, the subcortical layers, sustaining the highest microorganisms biomass, exhibit the maximal activity.

We tried to assess more quantitatively the phenomenons of organic matrix weathering by microorganisms, taking into account the differences in initial organic composition and mineralogies of the skeletal remnants.

In order to define a kinetic model of the degradation of the compounds tested, all data were expressed at each moment of the experiments as percent of the initial weight of the studied compound. This results in a model we called "multi-first order weathering kinetic model", in which all phenomenons can be characterized by a set of three first order speed constants : K_1, K_2 and K_3. K_1 is characteristic of the initial phase of biodegradation, when the microorganisms population constitutes itself and is not yet well defined (low diversity and fluctuating biomass). This phase is the most variable and will not be discussed here. K_2 is characteristic of the most active weathering phase : high speed of biodegradation due to high hydrolytic enzyme secretion by stable populations of microorganisms (high and stable diversity and biomass). K_3 is characteristic of the last weathering phase, when nearly all the organic compounds are exhausted and only more refractory compounds remain in the experimental material.

Mollusk shells are aragonitic (crossed-lamellar and helicoidal layers, mother-of-pearl) or calcitic (prismatic layer) with a chitinoproteic matrix. Actually all K_2 values are of the same order of magnitude (2.7 to 20.3 for whole organic matrix, 4.6 to 30.5 for proteins and 7.7 to 26.2 for chitin). Except in crossed-lamellar layer (where its amount is very low, around 0.01 %), chitin is extracted at a greater rate than proteins, leading to complete disruption of the organic framework (structured on chitinous fibril architecture). There is no fundamental differences between calcitic and aragonitic layers. The K_2 constants in tropical condition are generally higher than in temperate environments (11.6 to 20.3 versus 2.7 to 12.0), reflecting a higher metabolism and thus an increased biodegradation speed.

TABLE II : Histoenzymological demonstration of proteolytic, chitinolytic, amylolytic and laminarinolytic activities of microorganisms isolated from experimentally weathered shells (mother-of-pearl, Calvi experimental site, 37 meters depth, 18 months immersion).

ORGANISMS	CHITINASE	PROTEASE	AMYLASE	LAMINARINASE
BLUE-GREEN ALGAE				
Hyella sp.	0	+	0	0
Mastigocoleus testarum	0	+	+?	0
FUNGI				
Oomycete Strain 1	++	++	+	+
Oomycete Strain 2	+++	++	++	0
Ascomycete unident.	+	++	++	+
BACTERIA				
Bacilli Strain 1	+	++	++	+
Bacilli Strain 2	+	++	+++	0
Bacilli Strain 3	+	++	+++	++
Cocci Strain 4	+++	+	++	++
Cocci Strain 5	++	+++	+++	++
CHLOROPHYTA				
Oestrobium sp.(queckettii?)	0	0?	+	+

0 : no detectable activity

+, ++, +++ : increasing levels of hydrolytic activity.

Crustacean cuticles and echinoderm skeletons share the same mineralogy, high magnesian calcite, but with different organic content although (high chitino-proteic content in crustacean skeletons, low amounts of proteins without chitin in echinoid stereom). The K_2 constants of whole matrix and protein biodegradation kinetics are very close (64.97 to 67.58), and close to the K_2 degradation constant of chitin in crustacean skeletons (78.96). This constant is much higher than the K_2 constant of mollusk shells in the same environment (2.7 to 12.0). Taking into account the differences between cuticles and echinoid skeletons (structure, composition and abundance of organic matter), this observation has to be correlated with mineralogical data. The relative instability of high magnesian calcites in marine environment leads to a quick dissolution of such skeletal pieces in thermodynamically undersaturated solutions. This dissolution occuring preferentially at organic-mineral interface leads to some king of "freeing" of the organic matrix screened within such skeletons, and thus to increase its accessibility to microorganisms : in *Carcinus* cuticles, more than 60 % of the organic matrix and more than 75 % of the chitin content disappear in more or less two weeks whereas 80 to 90 % of the organic compounds of echinoid tests disappears within the same time. The same result is only attained after 6 to 12 months in immerged mollusk shells, either aragonitic or calcitic ones.

The K_3 constant, characteristic of the last phase of early biodegradation is very homogenous (0.29 to 2.50) whatever the structure, mineralogy and organic content of the skeletons. The observations that there is a pool of organic matter very hard to extract from the skeletons and of which biodegradation kinetics is very slow lead to the idea that refractory organic matter can be formed very soon during biodegradation events.

Anaerobic biodegradation

Anoxic conditions occur to a rather limited extent in the ocean. But although they cover only 10 % of the sea-floor anoxic superficial sediments underlie most of the shallow highly productive areas of the world ocean. These sediments accumulate more than 90 % of the total organic matter buried in sediments annually, so processes of anaerobic decomposition are of utmost importance to determine to what extent the organic compounds supply "survives" the surface biotic layers of rapid mineralization and is buried long term.

An important difference between aerobic and anaerobic decomposers is that most aerobic microorganisms can oxidise a wide range of substrates to CO_2, while individual anaerobic microorganisms metabolize a rather restricted range of molecules, often incompletely. However, anaerobic communities can be very efficient in decomposing relatively refractory molecules. Most organic polymers (proteins, cellulose, chitin and other polysaccharides,...) can be decomposed by

TABLE III : Hydrolytic activities estimated in experimental skeletal material weathered under aerobic and anaerobic conditions (Calvi experimental site, -37 meters). All activities are calculated after a 3 months summer immersion as nM hydrolysed substrate per hour incubation, per gram wet weight.

MATERIAL		AEROBIC CONDITIONS N = 5	ANAEROBIC CONDITIONS N = 3
Mother of pearl			
Phosphatasic activity	(4)	1311.3 - 2379.7	1867.2 - 3550.9
Lipolytic activity	(5)	1165.6 - 2088.3	1120.3 - 2663.2
Proteolytic activity	(6)	777.1 - 2719.7	466.8 - 3373.3
Glycolytic activity	(7)	1019.9 - 3933.8	653.5 - 6214.7
Sum of activities		3982.4 - 10393.1	4107.8 - 9801.5
Echinoid test			
Phosphatasic activity	(4)	339.8 - 777.0	359.9 - 365.2
Lipolytic activity	(5)	291.4 - 1238.5	359.9 - 469.5
Proteolytic activity	(6)	341.4 - 631.3	102.8 - 130.4
Glycolytic activity	(7)	146.7 - 1019.9	0 - 104.3
Sum of activities		1117.0 - 2428.3	822.7 - 1199.8

(4), (5), (6), (7) : see Table I , same significations.

aquatic anaerobic communities.

As in the case of aerobic biodegradation processes, the hydrolytic activities related to the presence of microorganisms inside the skeletons in anoxic experimental conditions can be detected using the APIZYM test.

The results exposed in Table III show that there is no significant differences between the hydrolytic activities associated with mollusk shells in aerobic compared to anaerobic conditions. All classes of enzymes are present with a similar activity. The variability of results in anaerobic conditions is greater than that in aerobic conditions but this is probably connected to confinement of the samples in closed jars, reflecting and multiplicating the local variability of aerobic sediments.

Trying to assess quantitatively the phenomenons of organic matrix weathering by anaerobic microorganisms, we used the same formalism as in aerobic conditions.

The kinetic constants for anaerobic weathering of the organic matrix of mollusk shells are very close to that observed under aerobic conditions (2.7 to 12.0), reflecting the same kind of enzymatic activities observed inside the skeletons even if the microorganisms concerned are quite different. As in aerobic media, the crossed lamellar layer is weathered more quickly than the other microstructural layers (K = 13.56 versus 6.29 - 8.50), probably due to the low organic content of this microstructure.

High magnesian calcite skeletons, either crustacean cuticles or echinoid stereom, have characteristic K_2 values greater than that of aragonitic or calcitic mollusk shells, but much lower than that of same skeletons in aerobic conditions (K_2 = 67.58). The intensity of weathering activities is probably linked, as in aerobic conditions, to (Ca-Mg) CO_3 dissolution phenomenons, occuring in somewhat acidifying interstitial medium. This trend may be restricted by confinement in the experimental containers.

The K_3 kinetic constant values are low, of the same magnitude than the same constants in aerobic conditions. In anoxic media, there is thus also some kind of refractory organic matter. But the composition of these refractory compounds may be somewhat different in the two experimental conditions as is shown by the results of transfer experiments (fig. 4).

After a quick decrease of the organic content during the six first months 70% biodegradation), the extraction of the organic compounds slows down, as classical in the refractory phase (K_{AE} = 0.91). But the material then transferred to anaerobic conditions is weathered three times faster than if remaining in aerobic conditions (K_{ANA} = 3.00). This can be interpreted as some kind of adaptation of the anaerobic microbiocenoses to biodegradation of less labile compounds remaining after aerobic degradation activity.

The cumulative effect of both processes (aerobic and anaerobic weathering) results in optimisation of the recycling of the organic matter of skeletal substrates. Through this kind of adaptation of microorganisms living in anoxic environments, most carbon and nitrogen containing molecules of the organic matrices of animal skeletons are quickly recycled, even the most refractory ones, and the energy produced by these metabolic pathways can be further reinjected in biogeochemical cycles and trophic webs.

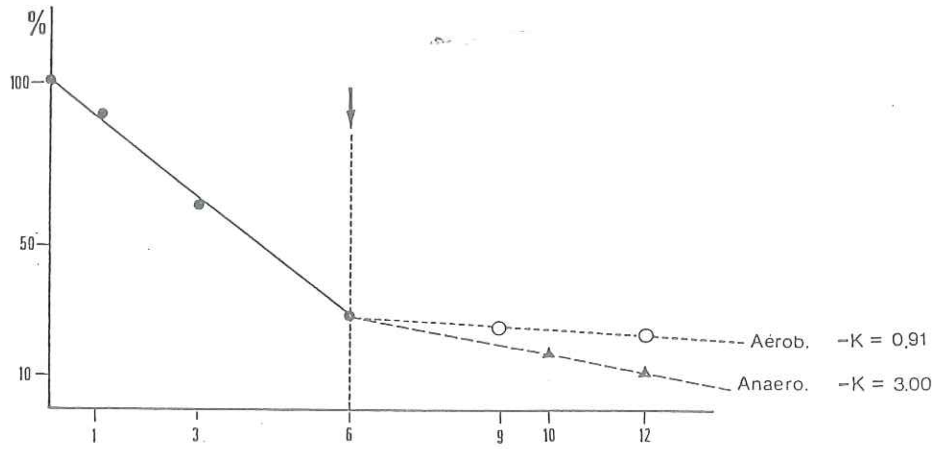

Fig. 4 : Kinetic of organic matrix biodegradation in nacreous layer of mollusk shells. 6 first months of experiment under aerobic conditions (black dots), then transfer (arrow) of part of the material under anaerobic conditions (Anaero), when the other part remains in aerobic conditions (Aerob.).

SUMMARY AND CONCLUSIONS

In this paper, we tried to clear up some biological phenomenons occuring during early diagenesis of skeletal remains in marine sediments and to stress the importance of these phenomenons in a sedimentological and oceanographical perspective.

In most circumstances, the prime alteration affecting skeletal remains is of biological origin. It is due to microorganisms growing onto and inside the skeletons, and to microborers that settle at the precise level of the organic matrices and weather the organic compounds of these matrices by discharging specific hydrolases at their contact. A fast step of extraction of the most labile components precedes a much slower biodegradation step of refractory compounds.

Anaerobic biodegradation takes place after aerobic biodegradation. Other kinds of microorganisms appear implicated but anaerobic biodegradation processes do not intrinsically differ and do not develop slowlier. Its apparent slowness mainly proceeds from the fact that only refractory compounds of the skeletal matrices reach anoxic layers of the sediments. Anaerobic microbiocenoses associated with skeletal carbonates appear adapted to the biodegradation of the less labile compounds of the organic matrices.

Early biological diagenesis events have important repercussions on other diagenetic, physical (mechanical) as well as chemical processes. From a mechanical standpoint, the biological extraction of the organic "cement" between skeletal crystallites fastens abrasion processes by reducing the general cohesion of the skeleton. Moreover, grazing and browsing organisms seeking for endolithic microflora contribute to such abrasion and disruption phenomenons. These phenomenons lead to an appreciable increase of the $CaCO_3$ content of the fine grain size fraction of sediments. From a chemical point of view, the disparition of the organic sheaths "protecting" $CaCO_3$ joined to crushing and abrasion effects greatly increases the $CaCO_3$ dissolution phenomenons and, paradoxally, even in thermodynamically supersaturated media like shallow tropical environment. From that point of view, the importance of high magnesian calcites, their microstructures and organic content have to be stressed in connection with the control of the buffering capacity of marine waters.

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DISCUSSION

L. HOFFMANN : *Comment distinguez-vous si un organisme est vivant ou mort dans une perforation ?*

R : *Il faut différencier deux approches : au SEM, après infiltration par une résine, on reconnaît seulement la présence et l'organistion tridimensionnelle des GALERIES, occupées ou non par le microorganisme qui l'a creusée ou par un chasmolithe. En microscopie photonique et au TEM, la présence de cellules intactes au sein des galeries nous fait considérer le microorganisme comme vivant.*

L. HOFFMANN : *Est-ce qu'il y a une variabilité dans la colonisation avec la profondeur ?*

R : *Oui. Les communautés endolithes peuvent être utilisées, dans une certaine mesure, comme indicateurs bathymétriques. On distingue les communautés intertidales des communautés infralittorales, circa-littorales et, a fortiori, bathyales et abyssales. Mais des travaux plus précis, au niveau taxonomique notamment, sont nécessaires pour affiner cet aspect de nos connaissances.*

L. HOFFMANN : *Est-ce que ce sont les algues bleues qui sont responsables de la perforation, ou est-ce que ce sont les bactéries associées aux algues bleues ?*

R : *C'est assez difficile à dire. Les cyanophycées endolithes sont presque toujours accompagnées de bactéries dans leurs gaines notamment (symbiontes, parasites, saprophytes... ?) et on ne peut faire clairement la part des deux microorganismes dans l'activité de pénétration des substrats calcifiés. On peut toutefois souligner que certaines espèces de cyanophycées en culture axénique sont à même de pénétrer des rhomboèdres de calcite (travaux de LeCampion).*