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CALCAREOUS MICROBIALITES AND ASSOCIATED BIOTA IN THE MEDITERRANEAN COASTAL LAGOONS AND PONDS OF SOUTHERN FRANCE: A KEY FOR ANCIENT BIOCONSTRUCTIONS?

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Abstract. Microbialites were found in various lagoons of the Mediterranean coast of southern France. They preferentially develop on pebbles on the edge of semi-enclosed water bodies, which can be temporarily dewatered and desiccated. The microbialitic building is achieved episodically with variations in the characteristics of the different layers. Its cerebroid and pustular appearance is the most remarkable macroscopic feature. Occasionally, other organisms may be involved in the construction, such as bryozoans and serpulid worms that form also in other places small unconsolidated bioconstructions. The analogy of these phenomena with bryozoans-serpulid-microbialite reefs occurring during Miocene in Paratethys, like those noticed in Romania, proposed by some authors, is considered unlikely, despite some common features.

Key words: mediterranean, coastal lagoons, microbial mats, biomineralization, serpulids, bryozoans, Miocene.

1. INTRODUCTION

The Mediterranean coast of Languedoc and Roussillon comprises numerous coastal lagoons that differ very much in size (Fig. 1). Many studies looked into the environmental aspect, the biodiversity, fisheries and shellfish farming, subject to the conditions of an unstable complex system, especially, regarding the fluctuating salinity. Nevertheless, some works based on observations made in the French Mediterranean coastal lagoons proved that salinity is not the only factor of life distribution and led to the biological concept of confinement (Guélorget et al., 1983) and a better understanding of the paralic realm. The confinement corresponds to the water renewal time and/or intake of marine-origin elements at a given point. Thus, the settlements of lagoons are organized from the sea to continental borders of lagoons according to confinement gradient. The confinement at a given point is characterised, in fact, by the lack of an element (or more) of marine origin at this point. Bioconstructions considered

as reefs (Lepareur *et al.*, 2013) were reported in such paralic settings, including worms, bryozoans and more or less associated barnacles.

Following the discovery of well developed microbialites in coastal ponds in Sardinia (Saint Martin and Saint Martin, 2015), it was interesting to know whether this phenomenon is common to other coastal areas of the Mediterranean. The Mediterranean coast of Languedoc and Roussillon may, thus, have similar physical-geographic conditions, with confined and/or isolated environments and temporary communications with the sea. A verification of this assertion, therefore, needed to be performed. So, using satellite images, we focused our investigation in similar sites with the potential to support microbialite development. Bibliographic resource about this topic is very scarce, with only a unique short communication without any image support of Boekschoten (1995), during the 2nd European Regional Meeting of ISRS (International Socie-



Fig. 1. A. Location of the studied area in France; B. Map of the Languedoc-Roussillon coast with the numerous coastal lagoons.

ty for Reef Studies). This author reported the presence of small mineralized bioconstructions, with presumption of microbial intervention in a brackish pond, named by him "Lac d'Evêque" (SE of Gruissan), but, formally unknown under this name in the local toponymy. He evokes stromatolite limestone crusts developed underneath algal mats on pebbles and small bioherms made of serpulids and the bryozoan *Electra* and compares these structures to Miocene buildups of Paratethys.

The first objective of this study was to investigate the whole region housing potentially microbialites sites, including the one mentioned by Boekschoten (1995), in order to assess their extensive distribution, to observe *in situ* the possible bioconstructions and to take samples for further studies. Consecutively, our explorations finally led to the discovery of microbialites in various lagoons that are distributed from south to north: la Palme Lagoon, Ayrolle Lagoon, and Portiragne Lagoon, near Agde (Figs. 1,2).

The second objective is to compare the expected observations about current lagoonal mineralized bioconstructions with the data acquired during our work on Sarmatian (Middle Miocene) microbial buildups in Romania (Saint Martin and Pestrea, 1999; Saint Martin *et al.*, 2013) in order to determine if they are, according Boekschoten (1995), really identical phenomena.

2. REGIONAL SETTING

The part of the studied Mediterranean coast extends from Leucate, south, to Agde, north (Figs. 1, 2). Most lagoons in this area are in communication with the sea by passages called "graus" and supplied with fresh water by a set of versants. The "graus" of studied lagoons have not been artificially modified and they are the last to operate naturally on the French Mediterranean coast. The lagoons are characterised by the presence of large seagrass areas and salinity gradients corresponding to diverse environments: reeds, rushes, sansouires, salt steppes... The lagoons are of recent formation: the coastal plain was flooded in Flandrian and gradually filled by Quaternary fluvial inputs. They are bordered by massive limestone reliefs with karstic networks that play an important role in fresh or brackish water supply. The lagoons are located in the northern zone of

Mediterranean climate, with mild winters and hot summers, relatively low annual rainfall and intense summer drought. Significant seasonal salinity variations occur, up from 10 g/l of salt in the winter, after heavy rainfall, to more than 40 g/l in summer, due to the phenomenon of evaporation. The instability of the environment is also reflected by changes in the trophic quality with risk of eutrophication related to excess nutrient inputs, causing blooms of algae macrophytes and, probably, cyanobacterial mat development. The average water depth is between 0.5 and 1 m, but the fluctuations in water level can be significant (\pm 0.5 m), depending on the speed and wind direction. In general, the edges of the lagoons were not very urbanized. Agricultural activity is occasionally operating, with, mostly, vine crops causing potential supplementary pressure on water quality of the nearby lagoons.

3. MATERIAL AND METHODS

Microbialites covering pebbles were sampled in the different sites. Petrographic thin sections of standard thickness of 30 microns, with a cover-slip, were prepared in order to perform observations under, both optical, and confocal microscopy.



Fig. 2. Coastal lagoons in the studied area at the La Palme (1), southwest of Gruissan (2) and Portiragnes coast (3), Google Earth source.

For optical microscopy, the thin sections were studied under a microscope Zeiss Axioscope 40 at x2,5, x10, x40, x63 and x100 (oil immersion Zeiss) magnifications.

Confocal Laser Scanning Microscopy (CLSM) observations (see Saint Martin and Saint Martin, 2015) were performed on a Leica TCS SP5 microscope, at the University Pierre et Marie Curie at x20, x40 and x 60 magnifications.

Examinations and EDS microanalysis in Scanning Electron Microscope (SEM) were performed using a Hitachi SU 3500 hosted in the Muséum National d'Histoire Naturelle de Paris.

4. RESULTS

4.1. DESCRIPTION OF SITES BEARING MICROBIALITES

4.1.1. La Palme lagoon

The La Palme Lagoon (600 ha) communicates with the sea by the natural grau of Franqui (Fig. 2) whose outlines and openings vary over time (Larue *et al.*, 2009). A general synthesis of hydrobiological functioning and eutrophication state (Wilke and Boutière, 1999, 2000; Souchu *et al.*, 2001; Ifremer, 2002-2012) shows that the watershed con-

sists, mainly, of limestone, partially, occupied by vineyards. The freshwater inflows are, mainly, provided by constant flow resurgences located in the northern part. From the west, mainly temporal streams very dependent on rainfall can partially supply the lagoon with fresh water. The monitoring studies found a good general state of the lagoon which shows no signs of eutrophication (Ifremer, 2002-2012).

Two locations have led to the discovery of microbialites (Fig. 2), one, to the south edge of pond and grassy areas, and, the other, northwest, near the La Palme town. At the south, several sub-lagoon expanses are lined by dense pebbles accumulations (Fig. 3A). The pebbles are easily distinguishable by their black surface color. They also have a brain appearance with small meandering ridges and pustules (Fig. 3B-C). These characteristics correspond to more or less developed and thick microbialitic crusts. Some pebbles are largely covered by the encrusting organisms, such as serpulids, bryozoans and balanids (Fig. 3D).

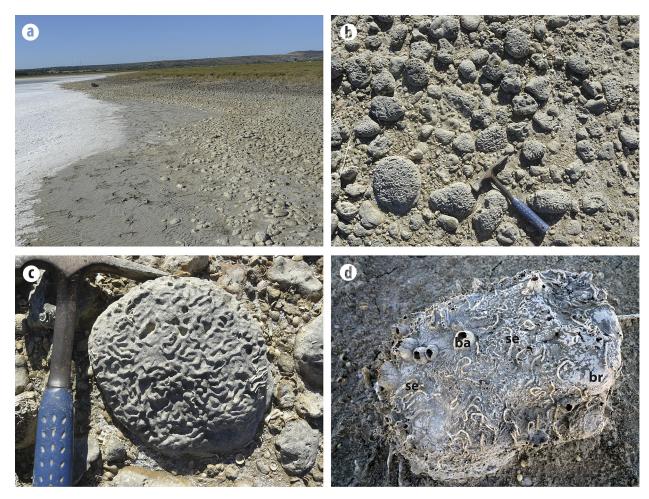


Fig. 3. Site of La Palme. **A.** View of the lagoon edge with accumulation of pebbles; **B.** Pebbles with the microbialitic crust; **C.** Detail of pebble showing the characteristic cerebroid aspect of the crust surface; **D.** Pebble covered by the serpulid (se)-bryozoan (br)-balanid (ba) consortium.

4.1.2. Ayrolle lagoon

The Ayrolle lagoon covers a vast area (1400 ha), south of the calcareous Clape mountain between Sigean lagoon and the sea, in direct communication with the sea in its southern part by a natural grau (Fig. 2). Freshwater inputs and freshening are, mostly, associated with contributions from the Campignol lagoon located northwest that serves as a buffer zone in case of flooding in the Aude low plain and small resurgences (Souchu et al., 2001). Its perimeter being barely urbanized, this ecosystem is not receiving effluents; when it does, it is on a small part. South of Gruissan, there is Saint-Martin Island, mainly made of Mesozoic carbonates. South of the island, near the Evêque site, occur small ponds, often partially dried, separated from the main Ayrolle lagoon by a cordon of 100-200 m width and surrounded by cultivated fields of vineyards and Mesozoic limestone (Fig. 4A). These small ponds include the one called Gassot occupying the central part, where there were observed, in fact, the bioconstructions cited by Boekshoten (1995) and studied in detail in this work. On the shore, pebble concentric accumulations crop out (Fig. 4B). The pebbles are characterised by a black cerebroid-pustular aspect, corresponding to the microbialitic coating (Figs. 4C-E). Some pebbles are colonized by various encrusting organisms, such as serpulids, bryozoans and balanids (Fig. 4F). During the dry season, the pebble accumulations are covered by bleached cyanobacterial filaments (Fig. 4F). The pond bottom is full of monospecific shell accumulation of the cardiid bivalve Cerastoderma glaucum (Bruguière, 1789) (Fig. 4G).

4.1.3. Lagoon and channels near Portiragnes

South of the Portiragnes town, a water body forms a small lagoon (Fig. 5A), but with varying dimensions, depending on season, and leading on the beach Portiragnes-Plage. This is, actually, the spreading area of the Ancien Grau du Libron, itself formerly involved in the natural outlet of the Libron coastal river. The entire outlet of Libron went, recently, through development management in the region, especially, for the prevention of floods, mitigating the natural settings. So, there remains a grau currently not directly related to the Libron flow

In the lagoon, only scattered pebbles (Fig. 5B) occur and the samples were collected during a dry period. These rare pebbles, mainly made of volcanic rocks, probably, resulting from the erosion of nearby outcrops of Pliocene volcanoes, are covered by thin microbialitic crust with pustular surface (Fig. 5C). Behind the pond, several channels connected to the Ancien Grau du Libron are noteworthy for the presence of bioconstructions dominated by worm tubes and bryozoans, also observed and sampled (Fig. 5D-E).

4.2. MICROBIALITE FEATURES

Macroscopically, the microbialite crusts are characterised by their black surface and their arrangement on pebbles or rocky substrate, according to a meandering ridges and pustules pattern. The combination of different observation techniques used in this work allow complementary information and a good understanding of the microbialitic phenomenon in the studied sites (Figs. 6-8). The principal feature is that pustules and ridges are formed by the successive episodes of development of erected filamentous cyanobacteria and laminated or wavy layers accompanied by Mg calcite micritic mineralization. The erected filaments correspond to *Scytonema*-like cyanobacteria exhibiting a thick lamellar sheath and false branching.

Pustules match digitations not exceeding the length of a few centimeters. Depending on the site, the age of the microbialite and the density of the mineralization, carpet filamentous cyanobacteria appear clearly, sometimes, revealing the preserved remains of sheaths (Fig. 6A-B, 7A-D,). Several stages in the mineralization process are distinguished from poorly cemented layers where micrite is relatively sparse (Fig. 8A-C) to dense micrite layers corresponding to a very consistent and solid crust (Fig. 8E-F). When the mineralization is more consistent, the location of cyanobacterial filaments is marked by elongate voids (Figs. 6C-D, 8E-F). Both ways can follow one another in the thickness of the microbialite (Figs. 6A-D, 7A-C, 7E, 8E). In some cases, we clearly noticed that the poorly cemented external part consists of cynaobacterial filaments gathered in tufts explaining, probably, the pustular appearance (Figs. 6E, 7E, 8D). Such a feature is known from Scytonema mats (Dupraz et al., 2006; Dupraz et al., 2013). The direct encrustation of pebble substrates may occur through erected filamentous carpets (Fig. 7D), or dense micritic crusts (Figs. 6E, 7E).

Other encrusting organisms providing some cohesion to mineralized microbial mats are present, either on the surface "sealing" the construction, in the case of bryozoans (Fig. 6A-B), or incorporated in the microbialite, as noticed in Portiragnes, in the case of serpulids (Figs. 6F, 7C).

These microscopical observations allow to highlight the sequence of events involving settlement phenomena on substrates, development of microbial mats and mineralization. These various events are marked by lines of growth stops, a more or less density of produced micrite and variations in color.

4.3. ASSOCIATED BIOTA

4.3.1. Invertebrates

Three main types of invertebrates with mineralized parts (skeleton or protecting tube) are involved in the constitution of bioconstructions, in various crusts on the pebbles and rocky substrates, or in the formation of microbialite: serpulids, bryozoans and barnacles.

The main contributor to bioconstructions found in the studied coastal area is the polychaete serpulid *Ficopomatus enigmaticus* Fauvel, 1923 (Figs. 3, 4). This invasive species is considered a, reef-builder in estuaries or brackish temperate environments and colonizes many areas in the world in

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Fig. 4. Site of Gassot ponds, southwest of Gruissan. A. General view showing the examined ponds situated between the main lagoon and the land characterised by cultivated fields of vineyards and Mesozoic limestone outcrops; B. View of the pond river with pebble accumulations; C-D. Pebbles with microbialitic coating exhibiting the characteristic cerebroid aspect; E. Detail of pustular cerebroid surface of microbialitic crust; F. Pebble colonized by the serpulid (se) - bryozoan (br) - balanid (ba) consortium and covered by cyanobacterial filaments; G. Monospecific shell accumulation on the pond bottom of the cardiid bivalve Cerastoderma glaucum.



Fig. 5. Site of Portiragnes. A. General view of the pond with few scattered pebbles (arrow); B. Pebble covered by thin microbialitic crust;
C. Detail of the pustular crust surface (arrow); D. Internal channels invaded by constructions with serpulid worms and bryozoans; E. Individual construction with serpulid worms (se) and bryozoans (br).

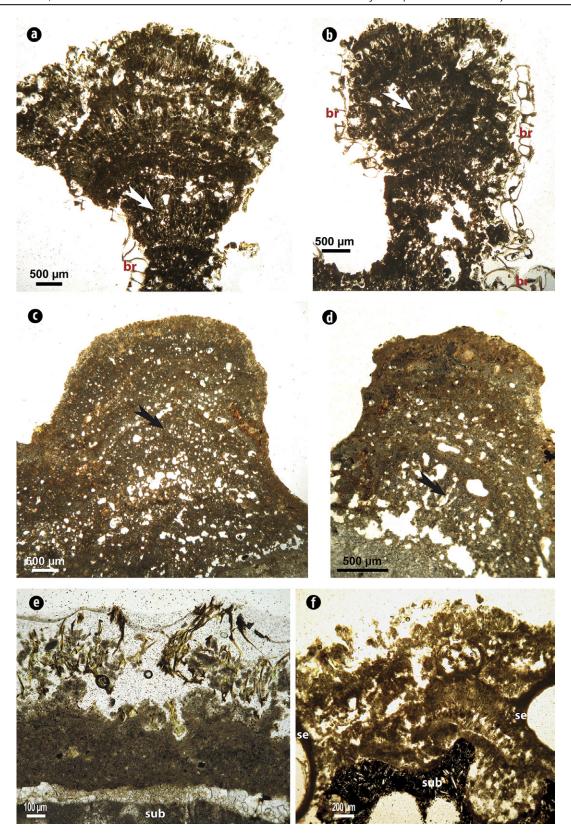


Fig. 6. Microbialite petrographic thin sections. **A-B.** Microbialitic digitations of successive filamentous poorly mineralized layers and covered by bryozoans colonies (br), Evêque; **C-D.** Microbialite pustules on pebble substrate made of alternation of filamentous layers (arrows) and micritic layers, La Palme; **E.** Crust on pebble substrate (sub) exhibiting a dense wavy micritic layer (m) at the base, followed by a poorly cemented layer of cyanobacterial filaments forming terminal tufts, La Palme. **F.** Filamentous crust on pebble substrate (sub) encompassing serpulid tubes (se), Portiragnes.

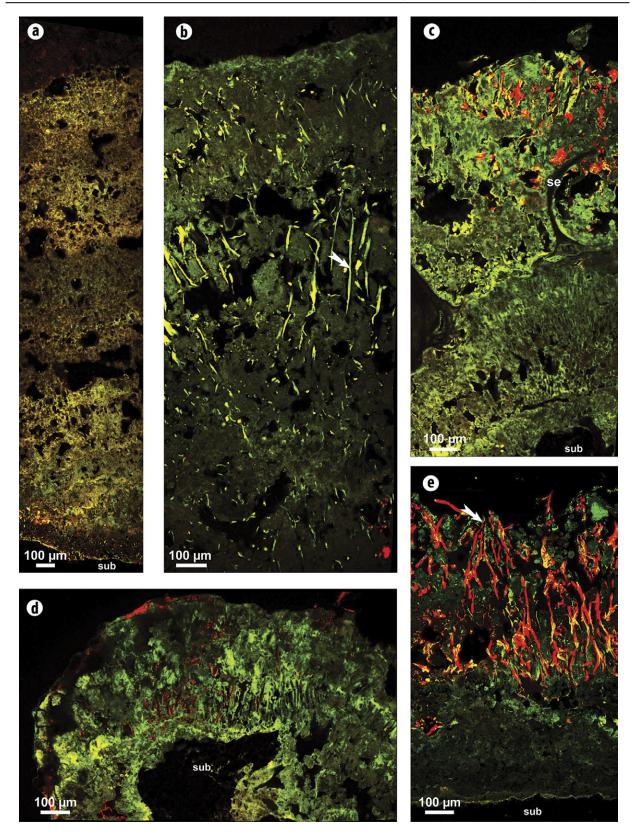


Fig. 7. Petrographic thin sections studied under CLSM (Confocal Laser Scanning Microscopy) technique restituting the autofluorescence signal inside the microbialite. A. Transect along a digitation exhibiting the alternation of finely laminated, wavy and filamentous mineralized layers, (sub: rocky substrate), La Palme; B. Transect along a digitation with partially preserved cyanobacterial sheath (arrow), Evêque; C. Microbialite with successive filamentous crusts encompassing serpulid tubes (se), (sub: rocky substrate), La Palme; D. Thin filamentous crust on rocky substrate (sub), La Palme; E. Filamentous crust ending by tufts (arrow) of cyanobacterial filaments, (sub: rocky substrate), Pradel.

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comparable environments with the Mediterranean coastal lagoons (Schwindt et al., 2001; Luppi and Bas, 2002; Schwindt et al., 2004; Nonnis Marzano et al., 2007; Dittmann et al., 2009; Bazterrica et al., 2012). The main constructions of Ficopomatus, known here under the local name of "cascails", are especially identified in the channels, but also within the lagoons. The abundant development of the serpulids trigger the repeated destroying of the reefs that threatened to obstruct or fill passage ways or water bodies making difficult the navigation and the hydraulic circulation (Lepareur et al., 2013). However, these reefs, even though they are reinforced by the presence of bryozoan colonies, are not cemented and not directly associated with the microbialite formation. The Ficopomatus tubes can only form limited encrustations on the microbialite surface and, more rarely, may be incorporated into the microbialite development (Figs. 6F, 7C).

The role of the serpulid *Serpula vermicularis* Linnaeus, 1767 is reduced to a few encrusting tubes on the pebbles or microbialite surface.

Bryozoans are represented by the species *Conopeum seurati* (Canu, 1928) (determination by P. Moissette, personal communication). The identification as *Electra* species proposed by Boekschoten (1995) needs, thus, to be rejected. Lightly calcified colonies of *Conopeum seurati* are ubiquitous in recoveries on microbialites (Fig. 6A-B) and pebbles, and in the "worm reefs", but never seen inside the microbial crusts. On even substrata, colonies form regular lacy sheets, while on uneven surfaces colonies become irregular, and the zooid size and shape can vary substantially (O'Dea and Okamura, 1999). *Conopeum seurati* is one of the few euryhaline bryozoan species that live, mostly, in desalinated water (estuaries, lagoons, etc), especially found in the Mediterranean coastal lagoons (Maluquer and Barangé, 1987).

Barnacles play an insignificant role in crusts on pebbles and microbialite (Figs. 3, 4). We identified (determination by R.P. Carriol, personal communication) *Amphibalanus amphitrite amphitrite* (Darwin, 1854). It is a cosmopolitan euryhaline species of tropical to warm temperate waters that tolerates brackish water (Kerckhof, 2002), but does not survive for a very long time in desalinated water (Newman and Abbott 1980). Species usually inhabit the intertidal zone, often, in brackish water on rocks, shells, in the mangroves, and, also, on vessels (Henry and McLaughlin, 1975). This species is also very common in polluted areas (Kerckhof and Cattrijsse, 2001).

4.3.2. Diatoms

The importance of diatoms associated with microbial mats and microbialite is now well proven and supported by numerous recent works (for more details, see Saint Martin and Saint Martin, 2015). Because of the fragility of their frustules, conservation is often poor and determination can be difficult. Moreover, diatoms are partly represented by spe-

cies of very small size, also, making them difficult to specific determination

The examination under optical microscopy allowed the observation of diatom frustules that are uniformly distributed on the microbialite surface. There is a monospecific population of *Rhopalodia gibberula* var. *musculus* (Kützing) Cleve-Euler 1952. Some frustules seem to be attached to the "substrate" (Fig. 9A). Indeed *Rhopalodia* is known as epilithic or epiphytic genus (Round, 1984).

Inside the microbialite, the dense material hides information concerning the presumed presence of diatoms. So, in order to access these data, microbialite broken samples were investigated under SEM. Effectively, this inside observation revealed numerous diatom frustules belonging to genera Diploneis, Navicula and Nitzschia, the latest being the most frequent (Figs. 9B-F). Attentive examination depicts the relation between diatoms and cyanobacteria. Very minute frustules (5 µm) of Nitzschia cf. frustulum (Kützing) Grunow in Cleve & Grunow 1880 and of Navicula cf. cryptocephala var. veneta (Kützing) Rebenhorst 1864 seem to be attached to the intertwined cyanobacteria filaments (Fig. 9B). The frustules of Diploneis cf. bombus (Ehr.) Ehrenberg 1853 and Nitzschia sp. are progressively coated by EPS (Extra Polymeric Substances) cyanobacterial biofilm (Fig. 9B, E) going up to the complete embedding. The electron micrographs document the epiphytic and interstitial lifestyle of the entrapped diatoms into the microbialite and provide, also, information on different stages of diatom preservation. Some frustules are still well to moderate preserved, such as Diploneis cf. bombus (Fig. 9B) and Nitzschia cf. frustulum (Fig. 9D), respectively. Other frustules, like Diploneis sp., appear to be corroded (Fig. 9C). We also observed imprints of frustules preserved in a more calcified material; morphological details are inscribed with more or less fidelity (Fig. 9F).

The recorded diatom community is typical for the microphytobenthos in shallow coastal waters that may be subject to salinity variations (Witkowski, 1990, 1991; Sundbäck and Snoeijs, 1991; Vilbaste *et al.*, 2000).

5. DISCUSSION

5.1. MICROBIALITE FORMATION AND ENVIRONMENTAL VARIATIONS

The microbialites covering the pebbles or the rare *in situ* bedrock in the studied area show an aspect and formation processes exactly like those highlighted in Sardinia by Saint Martin and Saint Martin (2015). However, the microbialites described in the present paper are less developed and remain limited to a few centimeter thick, at most. So, according to Saint Martin and Saint Martin (2015), the observed lamination more or less clearly expressed in the French microbialite reflects the irregular temporal sequence of environmental changes, such as impoundment or, at the contrary aerial exposure, the season succession (water temperature, wetting and drying), the nutrient supplies, the salinity fluctuations,

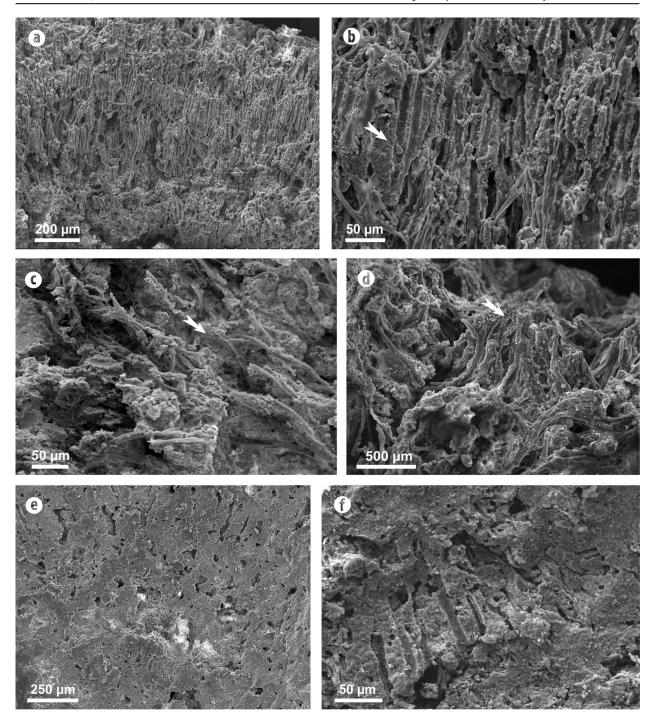


Fig. 8. SEM views of the microbialite. A. General view of relatively poorly mineralized microbialite constituted by dense erected filaments, Portiragnes; B. Detail of filamentous microbialite with micrite cement (arrow) between the filaments, Portiragnes; C. Detail of filamentous microbialite with micrite cement (arrow) between the filaments, Evêque; D. Cyanobacterial erected filaments forming tufts at the crust surface, La Palme;

E-F. Filamentous crust with elongate voids indicating the original presence of cyanobacterial filaments, La Palme.

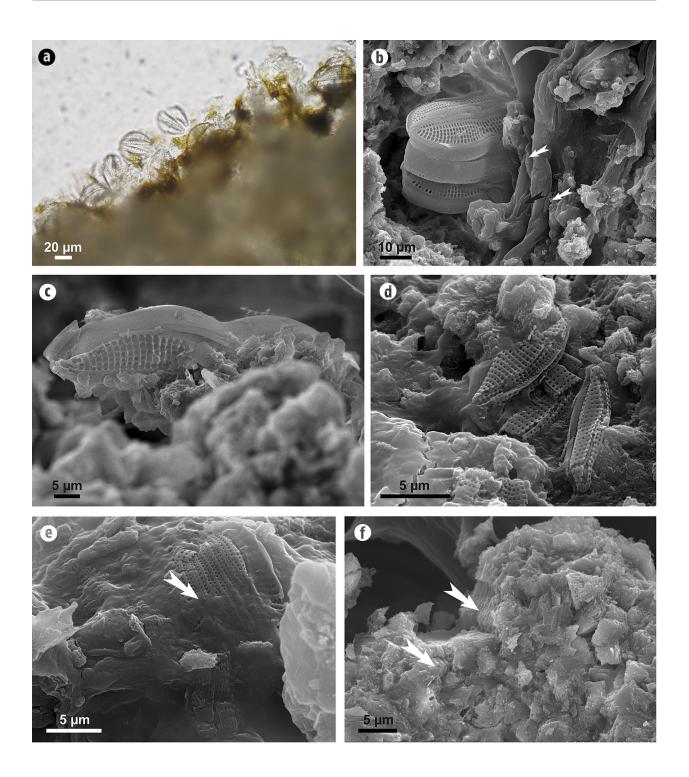


Fig. 9. Diatoms associated with the microbialite. A. Thin section showing frustules of the diatom *Rhopalodia gibberula* var. *musculus* (Kützing) Cleve-Euler 1952 colonizing the surface of microbial mat (arrows); B. Frustules of *Diploneis* cf. *bombus* (Ehr.) Ehrenberg 1853 between intertwined cyanobacterial filaments and minute frustules of *Nitzschia* cf. *frustulum* Kützing) Grunow in Cleve & Grunow 1880 (white arrows) and *Navicula cryptocephala* var. *veneta* (Kützing) Rebenhorst 1864 (black arrow); C. Corroded frustule of *Diploneis* sp.; D. Frustules of *Nitzschia* cf. *frustulum*; E. Partially dissolved frustules of *Nitzschia* sp. entrapped in degraded Extra Polymer Substances (EPS); F. Casts of diatom frustules (arrows) in micrite.

favoring the development of successive specific microbial mat layers and, then, their mineralization. The thinness of the French microbialites shows that it is a limited phenomenon in time, in this region. This led to question about the mineralization processes in action (Saint Martin and Saint Martin, 2015) and, also, their initiation. We can remark that there are no microbialites in the nearly coastal open marine conditions or in the lagoons center. Monitoring studies are needed to determine the exact time of microbialite formation regarding the lagoon water level, the rainfalls impact and the influence of marine inputs through the passage ways ("graus"). But, unfortunately, we cannot exclude that the relevant phenomena are very discontinuous in time and, therefore, difficult to define precisely. Other parameters are also considered by Boekschoten (1995), such as the very low relief of the French coastal region and the faint ecological gradient keeping the potential reef-builders spatially isolated. Under these conditions, he suggested that the stromatolite/serpulid/bryozoan "reefs" would develop along Mediterranean coasts as soon as favourable conditions (varied lagoon bottom topography, rise of brackish water level, and decrease of clastic influx) arise. However, our field investigations show that the stromatolite/serpulid/bryozoan "reefs" do not really exist, but, on the one hand, the microbialitic crust with some limited serpulids/ bryozoans/barnacles encrusting setup and, on the other hand, the serpulids/bryozoan "reefs" without microbialites!

An additional question could be related to the location of microbialites relative to confinement. We can observe that the Gassot site, but, also, to a lesser extent, that of La Palme correspond to a shift away from direct exchange areas with the marine environment. Given an identical situation in Sardinia, where direct interactions with the marine environment are only temporary or occasional (Saint Martin and Saint Martin, 2015), we can ask whether the concept of confinement in paralic realm may be applied, not only to common biota (invertebrates, fishes...), but also to the consortium of microbial organisms needed for the microbialite formation.

5.2. A MODERN ANALOGUE TO ANCIENT BIOCONSTRUCTIONS?

According to Boekschoten (1995) the stromatolite-serpulids-bryozoans consortium, like those observed in the Gruissan area, have built reefs from the Carboniferous times, always in marginally marine environments under shallow hypo- or hypersaline water, particularly with the massive bioherms along the Miocene coast of the Paratethys in Poland and Russia. Similarly, Bijma and Boekschoten (1985) consider that the bryozoan reefs and stromatolite observed on the Dutch coast in an artificial men-made environment have fossil counterparts with the Miocene bryozoan/stromatolite reefs in the Paratethys. These reefs were specifically established during the Sarmatian (Middle Miocene), throughout the whole Paratethys. They are well represented in Romania, where we could perform observations useful for comparisons (Saint Martin and Pestrea, 1999; Saint Martin *et al.*, 2013).

Indeed, in the present lagoons and in the Miocene bioconstructions, we generally found partly similar components, especially with brackish affinities, but this direct comparison requires a closer examination of the specific characteristics of each situation. In addition, the Sarmatian is, in fact, characterised by two successive periods, each with specific types of constructions and contents. In the lower part of the Sarmatian, during Volhynian, thick buildings containing interlinked serpulid colonies and abundant micrite are mostly developed. Later, during Bessarabian, there are less voluminous bioconstructions consisting of small reefs made by dominant bryozoans associated with foraminifers (nubecularids) and calcareous algae, the microbialite intervention being restricted. Table 1 summarizes the key features and shows disparities that need to be discussed.

The first observation concerns the microbialite size. Thus, macro-oncoids observed in Sardinia and the microbial crusts from the lagoons of France remain quite small, compared to the, sometimes, very important, Sarmatian reefs (Fig. 10A). This is due, of course, primarily to the fact that current microbialite develop over a short period of time in a very shallow environment (few centimeters to decimeters deep). The distribution of current microbialite is very punctual and their extension is limited. Yet, all ponds laced in identical conditions do not necessarily host microbialite formations. Sarmatian reefs show, on the contrary, a much more significant scope and a very broad distribution (Bucur et al., 1992; Pisera, 1996; Jasionowski, 1996; Jasionowski et al., 2002; Jasionowski et al., 2003; Jasionowski, 2006), sometimes almost continuous in the case of the Moldavian platform (Saint Martin and Pestrea, 1999; Saulea, 1995). Another notable difference is the absence in the current constructions of calcareous algae and encrusting foraminifera as nubecularids, the microbialitic features and the associated biota (Tabl. 1). Finally, the microbialitic fabric of Sarmatian reefs is significantly different exhibiting mainly clotted and/or peloidal micrite (Fig. 10B, C) and, also, fibrous calcite rims around the serpulid tubes (Bucur et al., 1992; Saint Martin and Pestrea, 1999) (Fig. 10D).

In summary, despite some similarities, it is difficult to establish strict analogies between biosedimentological events, separated in time and space, as suggested by Bijma and Boekschoten (1985) and Boekschoten (1995). Time, space and bio-physico-chemical features have to be considered. The current microbial structures were developed in limited time and particularly changing environmental conditions, in small water bodies with enormously variable hydrology, determined, primarily, by floods, caused by sea storms and/ or heavy rains and subsequent summer desiccation. On the other side, the Miocene reef structures are part of a longer biological and paleogeographic history marked by specific physico-chemical conditions, including alkalinity which seems to have played a significant role, ruling in a sea of great extension (Harzhauser and Piller, 2004; Piller and Harzhauser, 2005; Jasionowski, 2006; Harzhauser and Piller, 2007; Piller et al., 2007).

Table 1. Summary table of the main features of current microbialites from Sardinia (Saint Martin and Saint Martin, 2015) and France (this work) and Early and Middle Sarmatian (Miocene) reefs of the Paratethys realm.

	CURRENT MI	IT MICROBIALITES	MIOCENE (SARMATIAN) MICI	MIOCENE (SARMATIAN) MICROBIALITES FROM ROMANIA
MAIN FEATURES	Sardinia	French coast	Volhynian buildups	Bessarabian buildups
Thickness	Up to ten centimeters	Few centimeters	Several tens of meters	Decimeters to meters
Repartition	Scaterred	Scaterred	Whole Paratethysian area	Whole Paratethysian area
Geographic/ paleogeo- graphic context	Ponds, often, temporarily isolated from the open sea	 Lagoons communicating with the sea by narrow passageways semi-enclosed ponds 	Within a vast intern sea inherited of ancient Tethys	Within a vast intem sea inherited of ancient Tethys
Main distinguishable microbial composition	 Filamentous (Scytonema) and coccoid cyanobacteria Diatoms 	 Filamentous (Scytonema) and coccoid cyanobacteria Diatoms 	No clearly identifiable microbial remains	No clearly identifiable microbial remains
Macroscopic features	 Oncolite or crusts around pebbles Digitations Laminations Surface with a pustular cerebroid aspect 	 Oncolite or crusts around pebbles Digitations Laminations Surface with a pustular cerebroid aspect 	Masses forming variously sized reliefs (from limited patches to bioherms)	Generally, small hemispheric reefs
Associated biota		 Serpulids and bryozoans only as encrusters Few serpulid tubes incorporated in the microbialite 	 Serpulids and bryozoans incorporated in the buildup sparse nubecularids and calcareous algae 	Consortium of bryozoans, foraminifers (nubecularids), serpulids and calcareous algae
Otherfeatures		Presence of small reefs with serpulids and bryozoans without microbialite in confined lagoons and channels	Oolitic deposits	Abundant oolitic deposits
Main surrounding biota		Bivalves (cardiids)barnaclescrabs	 Bivalves (cardiids, mytilids) Gastropods (rissoids, potamids) 	 Diversified bivalve fauna Diversified gastropod fauna
Biosedimentology	Dense micritic product organized in fine laminations or wavy layers	Dense micritic product organized in fine laminations or wavy layers	 Clotted, peloidal micrite. Few small and isolated stromatolites 	 laminated microbial mats composite crusts

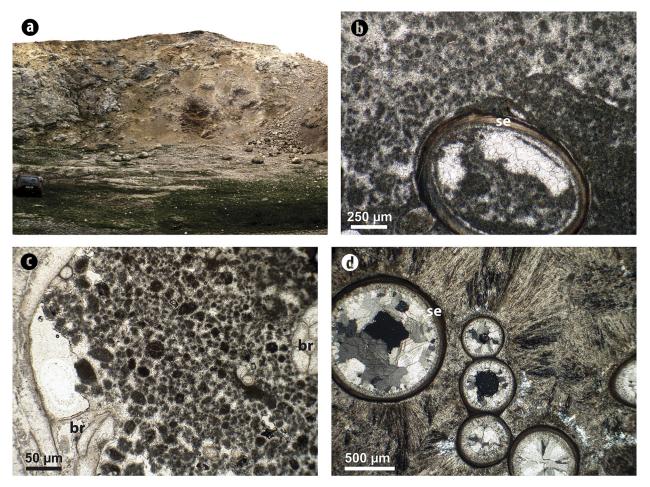


Fig. 10. Sarmatian reef features (Northeastern Romania); **A.** General view of a massive reef (scale: the car at the bottom left of the picture); **B.** Clotted to peloidal micritic layers embedding serpulid tubes (se); **C.** Peloidal micrite embedding bryozoan colonies (br); **D.** Fibrous calcite rims around serpulid tubes (se).

6. CONCLUSION

We have shown that the phenomenon of microbialite formation in the context of lagoons or smaller ponds was quite widespread in the Mediterranean, at least, in the state of current knowledge in Sardinia and France. It is likely that many other lagoons show similar features that can, therefore, be regarded as specific in their composition and their appearance. Systematic research must, now, be undertaken in all Mediterranean areas susceptible to host this type of microbialite.

Contrary to common ideas, current microbialites constructions associated or not with different metazoans cannot always be simply transposed to explain microbialitic old buildups, even for fairly similar time as the Miocene. It is absolutely necessary to take into account, not only the components of these microbialites, but all the parameters that govern aquatic environments and, also, the environments characterised by major rapid fluctuating conditions.

ACKNOWLEDGEMENTS

We thank Lilian Cazes and Severin Morel (Muséum National d'Histoire Naturelle) for their remarkable lab work. We thank Catherine Rausch, Cyril Willig and Caroline Dalle (PTME, Muséum National d'Histoire Naturelle, Paris) for their assistance with scanning electron microscopy. This work was partly supported by the ATM «Interactions Minéral-Vivant» of the MNHN (Muséum National d'Histoire Naturelle de Paris). Confocal work was carried out at the Institute of Biology Paris-Seine Imaging Facility that is strongly supported by the "Conseil Regional Ile-de France", the French National Research Council (CNRS) and Sorbonne University, UPMC Univ. Paris 06. Useful information was nicely provided by Pierre Moissette for bryozoans and René Pierre Carriol for barnacles. The authors are grateful to Iulia Lazăr and Ioan Bucur for their helpful comments on the manuscript.

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REFERENCES

- BAZTERRICA, M.C., BOTTO, F., IRIBARNE O., 2012. Effects of an invasive reef-building polychaete on the biomass and composition of estuarine macroalgal assemblages, *Biological Invasions* 14, 765-777.
- BOEKSCHOTEN, G.J., 1995. Incipient stromatolite/bryozoan/serpulite reefs in a Mediterranean lagoon near Narbonne (France), *Publ. Serv. Géol. Lux.* 29, 105.
- BIJMA J., BOEKSCHOTEN G. J., 1985. Recent Bryozoan Reefs and Stromatolite Development in Brackish Inland Lakes, SW Netherlands, Senckenbergiana maritima 17 (1-3), 163-185.
- Bucur, I.I., Nicorici, E., Huică, I., Ionesi, B., 1992. Calcareus microfacies in the Sarmatian deposits from Romania. *Studia Universitatea Babeş-Bolyai*, Geologia 2 (XXXVII), 9-16.
- DITTMANN, S., ROLSTON, A., BENGER, S.N., KUPRIYANOVA, E.K., 2009. Habitat requirements, distribution and colonisation of the tubeworm *Fico-pomatus enigmaticus* in the Lower Lakes and Coorong, *Report for the South Australian Murray-Darling Basin Natural Resources Management Board*, Adelaide, 99p.
- Dupraz, C., Fowler, A., Tobias, C., Visscher, P.T., 2013. Stromatolitic knobs in Storr's Lake (San Salvador, Bahamas): a model system for formation and alteration of laminae, *Geobiology* 11, 527-548.
- Dupraz, C., Patissina, A.R., Verrecchia, E.P., 2006. Simulation of stromatolite morphospace using 'DLA-CA' growth model': translation of energy in morphology, *Sedimentary Geology* 185, 185-203.
- Guélorget, O., Frisoni, G. F., Perthuisot, J. P., 1983. La zonation biologique des milieux lagunaires: définition d'une 'échelle de confinement dans le domaine paralique méditerranéen, *Journal de Recherche Océanographique* 8, 15-36.
- Harzhauser, M., Piller, W.E., 2004. Integrated stratigraphy of the Sarmatian (Upper Middle Miocene) in the western Central Paratethys, *Stratigraphy* 1 (1), 65-86.
- Harzhauser, M., Piller, W.E., 2007. Benchmark data of a changing sea-Palaeogeography, Palaeobiogeography and events in the Central Paratethys during the Miocene, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 253, 8–31.
- Henry, DP, McLaughlin, PA., 1975. The barnacles of the *Balanus amphitrite* complex (Cirripedia, Thoracica), *Zool. Verh.* 141, 1-254.
- IFREMER. 2002-2012. Réseau de Suivi Lagunaire du Languedoc-Roussillon: Bilan des résultats. Rapports RSL/02-RSL/11.
- Jasionowski, M., 1996. Budowle serpulowo-mikrobialitowe sarmatu na Roztoczu: niezwyk³e joint-venture, *Prz. Geologiczny* 44, 1044-1048.
- Jasionowski M., 2006. Facje i geochemia dolnosarmackich raf z północnych obrzeży Paratetydy na Roztoczu (Polska) i Miodoborach (Ukraina): implikacje paleośrodowiskowe, *Prz. Geologiczny* 54, 445-455.
- Jasionowski M., Studencka B., Hara U., Peryt D., Poberezhskyy, A., 2003. Early Sarmatian serpulid-microbialite buildups of the Carpathian Foredeep (Central Paratethys) in Poland and Ukraine, *Acta Mineralogica-Petrographica*, Abstract Series **4**: 19.

- Jasionowski, M., Studencka, B., Poberezhskyy, A., 2002. Early Sarmatian serpulid-microbialite carbonate buildups of the Miodobory region (western Ukraine), *Geologica Carpathica* 53 special issue, 3 p.
- Kerckhof, F., 2002. Barnacles (Cirripedia, Balanomorpha) in Belgian waters, an overview of the species and recent evolutions, with emphasis on exotic species, *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, Biologie 72-Suppl., 93-104.
- Kerckhof, F., Cattrusse, A., 2001. Exotic Cirripedia (Balanomorpha) from buoys off the Belgian coast, *Senckenbergiana Maritima* 31 (2), 245-254.
- LARUE, J.P., BOUABDALLAH, M., ÉTIENNE, R., 2009. Un littoral sableux en progradation: le lido entre Leucate et Port-la-Nouvelle (Aude, Golfe du Lion, France), *Physio-Géo* 3, 151-173.
- LEPAREUR, F., BERTRAND, S., PAPUGA, G., RICHEUX, M., 2013. État de conservation de l'habitat 1150 « Lagunes côtières », Méthode d'évaluation à l'échelle du site, Guide d'application. Rapport SPN 2013-14, Muséum National d'Histoire Naturelle/Service du Patrimoine naturel, Pôle-relais lagunes méditerranéennes/CEN-LR, 107 pages.
- Luppi, T.A., Bas, C.C., 2002. Rol de los arrecifes del poliqueto invasor *Ficopomatus enigmaticus* Fauvel 1923 (Polychaeta: Serpulidae) en el reclutamiento de *Cyrtograpsus angulatus* Dana 1851 (Brachyura: Grapsidae), en la laguna costera Mar Chiquita, Argentina, *Ciencias Marinas* 28, 319–330.
- Maluquer, P., Barangé, M. 1987. Briozoos de una laguna costera de la Isla de Mallorca, *Boll. Soco Hist. Nat. Balears* 31, 115-122.
- Newman, WA, Abbott, D.P., 1980. Cirripedia: the barnacles. *In*: Morris R.J., Abbott D.P., Haderlie, E.C., editors. Intertidal invertebrates of California. Stanford (CA): Stanford University Press, 504-535.
- Nonnis Marzano, C., Baldacconi, R., Fianchini, A., Gravina, F., Corriero, G., 2007. Settlement seasonality and temporal changes in hard substrate macrozoobenthic communities of Lesina Lagoon (Apulia, Southern Adriatic Sea), *Chemistry and Ecology* 23 (6), 479-491.
- O'Dea, A., Okamura, B., 1999. Influence of seasonal variation in temperature, salinity and food availability on module size and colony growth of the estuarine bryozoan *Conopeum seurati, Marine Biology* 135, 581-588.
- PILLER, W.E., HARZHAUSER, M., 2005. The myth of the brackish Sarmatian Sea, *Terra Nova* 17, 450-455.
- PILLER, W.E., HARZHAUSER, M., MANDIC, O., 2007, Miocene Central Paratethys stratigraphy-current status and future directions, *Stratigraphy* 4 (2/3), 151-168.
- PISERA, A., 1996, Miocene reefs of the Paratethys: a review, SEPM Concepts in Sedimentology and Paleontology 5, 97-104.
- ROUND, F.E., 1984. The ecology of algae, Cambridge University Press, 664 p.
- SAINT MARTIN, J.P., PESTREA, S., 1999. Les constructions à serpules et microbialites du Sarmatien de Moldavie, Acta Palaeontologica Romaniae 2, 493-469.
- SAINT MARTIN, J.P., LETENNEUR, C., BUCUR, I.I., SAINT MARTIN, S., ANDRÉ, J.P., MOIS-SETTE P., 2013. La mer du Sarmatien en Dobrogea du sud : para-

- mètres d'une reconstitution. *In J.P. Saint Martin (éd.) Recherches croisées en Dobrogea, Editura Amanda Edit, Bucarest, 49-60.*
- SAINT MARTIN J.P., SAINT MARTIN, S., 2015. Discovery of calcareous microbialites in coastal ponds of western Sardinia (Italy), *Geo-Eco-Marina* 21, 35-54.
- SAULEA, E., 1995. Récifs et faciès détritiques du Sarmatien moyen de la partie centrale de la Bessarabie, *Mémoires de l'Institut Géologique de Roumanie* 35, 98 p.
- Schwindt, E., Bortolus, A., Iribarne, O.O., 2001. Invasion of a reef-builder polychaete: direct and indirect impacts on the native benthic community structure, *Biological Invasions* 3, 137-149.
- Schwindt, E., De Francesco, C.G., Iribarne, O.O., 2004. Individual and reef growth of the invasive reef-building polychaete *Ficopomatus enigmaticus* in a south-western Atlantic coastal lagoon, *J. Mar. Biol. Ass. U.K.* 84: 987-993.
- Souchu, P., Laugier, T., Dusserre, K., Marobin, D., 2001. Suivi des paramètres trophiques dans l'eau des étangs de la Narbonnaise, *Rapport Ifremer DEL/ST*, 41 p.

- Sundbäck, K., Snoeijs, P., 1991. Effects of nutrient enrichment on microalgal community composition in a coastal shallow-water sediment system: an experimental study, *Botanica Marina* 34, 341-358.
- VILBASTE, S., SUNDBÄCK, K., NILSSON, C., TRUU, J., 2000. Distribution of benthic diatoms in the littoral zone of the Gulf of Riga, the Baltic Sea, *European Journal of Phycology* 35, 373-385.
- WILKE, M., BOUTIÈRE, H., 1999. Synthèse générale du fonctionnement hydrobiologique de l'étang de La Palme, *Rapport CEH*, *Perpignan*, 173 p. + annexes.
- Wilke, M., Bouthère, H., 2000. Hydrobiological, physical and chemical characteristics and spatio-temporal dynamics of an oligotrophic mediterranean lagoon: the Etang de La Palme (France), *Vie et Milieu* 50, 101-115.
- Witkowski, A., 1990. Fossilization processes of the microbial mat developing in clastic sediments of the Puck Bay (Southern Baltic Sea, Poland), *Acta Geologica Polonica* 40, 1-27.
- Witkowski, A., 1991. Diatoms of the Puck Bay coastal shallows (Poland, Southern Baltic), *Nordic Journal of Botany* 11, 689-701.