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| Zitteliana | 20 | Hagn/Herm-Festschrift | 105-122 | München, 31. 12. 1993 | ISSN 0373-9627 |
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Systematic position and palaeoecology of the Upper Jurassic to Tertiary alga *Marinella lugeoni* PFENDER

By

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With 5 Text-figures, 1 Table and 3 Plates

ABSTRACT

The alga *Marinella lugeoni* PFENDER commonly occurs in Upper Jurassic and Lower Cretaceous sediments, and is known until the Oligocene. Originally described as a cyanophyte, most authors attributed the alga to the codiaceans whereas some reckoned a solenoporacean character. Features detected in the rich material from the Portuguese Upper Jurassic support a red algal character and reveal close relationships to the corallinaceans. Criteria for such interpretation are: (1) The microcrystalline character of tissue walls, (2) noticeable enrichment of Mg and lack of Sr indicating an originally Mg-calcite skeleton, (3) the small size of filaments which are subdivided by horizontal walls and occasionally bifurcate, (4) partial tissue differentiation, resulting in the development of an epithallial layer and probably of megacells, (5) auto-dissolution of skeletal material resulting in voids with pores which can be interpreted as reproductive organs, and (6) the frequent rhodolite growth form.

The simple structure of most of the thallial tissue and the radial arrangement of cell threads in *Marinella* are also features of solenoporacean red algae. Despite its similarities with both corallinaceans and solenoporaceans *Marinella* should not be taken as a 'missing link'. The longevity of the relative simple tissue features of *Marinella* indicates that corallinaceans did neither develop from solenoporaceans nor from *Marinella* but probably had a common, possibly uncalcified ancestor with *Marinella*.

Marinella occurs in a wide variety of marine shallow-water environments, but is most frequent in particle-rich, partly clayey limestones. It also occurs in settings of fluctuating salinities, where it indicates the more marine phases. Its success in highly abrasive settings such as unstabilized, quartz-rich ooid sands seems to be related to a high regeneration ability, a pathway which is followed by modern coralline algae.

1. INTRODUCTION

The alga *Marinella lugeoni* PFENDER is a common constituent of Upper Jurassic and Cretaceous shallow-water sediments of Europe (e. g. BERTHOU & POIGNANT 1969, BOUROULLEC & DELOFFRE 1968, BOLLIGER & BURRI 1970, LAUVERJAT & POIGNANT 1978, MISIK 1979, PEYBERNES 1979, RADOICIC 1970, RAMALHO 1971, 1981, REY 1972), the Middle and Far East (GOLLESTANEH 1979, IMAZUMI 1965), Africa (POIGNANT & LOBITZER 1962) as well as of North and Central America (BECKMANN & BECKMANN 1966, BENGTON & BERTHOU 1982, JOHNSON 1961, 1969, JOHNSON & KASKA 1965). BERTHOU & POIGNANT (1980) mention the alga also from Eocene sediments and, according to MOUSSAVIAN (1992: 132;

pers. commun. 1992), *Marinella lugeoni* still occurs in the Oligocene of the Alpine region. Attributions to this taxon recorded from rocks older than Upper Jurassic (PFENDER 1939: Bajocian - Bathonian of the Middle East; DIACONU & DRAGASTAN 1969: Upper Triassic of Romania) seem to be doubtful.

The holotype of *Marinella lugeoni* is derived from Spanish bedrocks of previously presumed Early Jurassic age (PFENDER 1939). However, according to FOURCADE (pers. commun., cited in RAMALHO 1971: 174; see also BARATTOLO & DEL RE 1985: 206) these rocks rather are to be attributed to the Late Jurassic.

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| | INCERTAE SEDIS | CYANOPHYTA/ CYANOBACTERIA | CHLOROPHYTA | RHODOPHYTA |
|--------------------------------------|----------------|---------------------------------|-----------------------|--|
| PFENDER 1939 | | ? Cyanophyceae | | |
| PIA, ANDRUSOV (fide PFENDER 1939) | | | | red alga |
| MASLOV 1961, 1964 | | | Codiaceae | |
| JOHNSON 1961 | | | ? Codiaceae | ? Corallinaceae |
| JOHNSON & KAFKA 1965 | | | Codiaceae | |
| IMAIZUMI 1965 | | | Codiaceae | |
| BECKMANN & BECKMANN 1966 | | | ? Codiaceae | |
| BOUROULLEC & DELOFFRE 1968 | | | Codiaceae | |
| JOHNSON 1969 | | | | red alga of uncertain affinity |
| RADOICIC 1970 | | | | Rhodophyta |
| BOLLIGER & BURRI 1970 | | | Codiaceae | |
| GOLONKA 1970 | | | | Rhodophyta, most probably corallinean family |
| MASSE & POIGNANT 1971 | | | Codiaceae | |
| RAMALHO 1971 | | | Codiaceae | |
| REY 1972 | | | Codiaceae | |
| SRIVASTAVA 1973 | | | | ? Rhodophyta |
| JAFFREZO 1974 | | | Codiaceae | |
| POIGNANT 1978 | incertae sedis | | | |
| LAUVERJAT & POIGNANT 1978 | incertae sedis | | | |
| CANEROT 1979 | incertae sedis | | | |
| FLÜGEL 1979 | | | | problematic red alga |
| GOLLESTANEH 1979 | | | presumed Codiaceae | |
| EMBERGER in MASSE 1979 | | Schizophytopides | | |
| TAPPAN 1980 | | | Udoteaceae | |
| CHERCHI, GUPTA & SCHROEDER 1984 | incertae sedis | | | |
| BARATTOLO & DEL RE 1985 | | | | Solenoporaceae resemblance to Melobesioidae |
| HOFLING 1985 | | (problematic) cyanobacterium | | |
| WERNER 1986 | | | | red alga |
| LEINFELDER 1986 | | | | Corallinaceae |
| REITNER 1987 | | | | problematic red alga |

Fig. 1: The different hypotheses about the systematic position of *Marinella lugeoni* since its first description by PFENDER 1939.

Despite the long stratigraphic range and the frequency in fossil shallow water environments the systematic position of *Marinella lugeoni* is matter of continuous discussion. To the present date, the alga is attributed to very different groups without any interpretation being generally accepted (Fig. 1). Most workers place the form to the chlorophyte group Codiaceae (e. g. JOHNSON 1961, 1964; BOUROULLEC & DELOFFRE 1968). PFENDER (1939), in her original description of *Marinella lugeoni*, places the alga to the Mixophyceae (i. e. Cyanophyta or Cyanobacteria), which is followed by MASSE (1979). PIA and ANDRUSOV (cited in PFENDER 1939) assume a solenoporacean or, in any case, red algal character.

PFENDER (1939) herself emphasized similarities with the alga „*Lithothamnion*“ *angolense* which was described from the Albion of Angola by ROMANES (1916). However, for *Marinella lugeoni*, PFENDER could not detect any conceptacle-like structures as they were mentioned by ROMANES for *L. angolense*. BECKMANN & BECKMANN (1966) consider both forms as possibly identic, whereas BOUROULLEC & DELOFFRE (1968) doubt any affinity of both taxa, because only the species *L. angolense* would exhibit individualized perithallial cells with well-marked transverse walls. Both ELLIOTT (1959) and BOUROULLEC & DELOFFRE (1968) refer to LEMOINE (1925) who is thought to have placed the species *angolense* to the genus *Lithophyllum*. However, such an attribution cannot be concluded from the works of LEMOINE (1925, 1939, 1978). On the contrary, the author rather pointed out the individuality of *Lithothamnion angolense*.

A possible red algal character of *Marinella* was subsequently assumed by several workers (JOHNSON 1969, RADOICIC 1970, SRIVASTAVA 1973, FLÜGEL 1979, DRAGASTAN 1982), without giving sufficient arguments for such interpretation. Consequently, CANEROT (1979) and POIGNANT & LOBITZER (1982) placed *Marinella lugeoni* to the algae incertae sedis. Only GOLONKA (1970), by interpreting sparitic fenestrae as possible conceptacles and mentioning vague horizontal walls, gave criteria for an assignment of the taxon as a corallinean red alga. BARATTOLO & DEL RE (1985), by investigating the species *Marinella yougoslavica*, doubted the existence of conceptacles. They interpreted the radial filament arrangement as diagnostic of a solenoporacean origin. A close relationship to the solenoporaceans is also assumed by REITNER (1987) and MOUSSAVIAN (1992: 130).

Based on rich Upper Jurassic material of Portugal the present authors independently reckoned a red algal, possibly corallinean character of *Marinella lugeoni* in 1986 (LEINFELDER 1986, WERNER 1986). Meanwhile additional material could be collected which allows us to shed more light on the systematic position and on the environmental demands of this frequent taxon.

Besides the type species a second species, *M. yougoslavica* MASLOV, 1962, was erected within this genus. According to MASLOV (1962) and, subsequently, BARATTOLO & DEL RE (1985), this species differs from *M. lugeoni* by its larger thallial sizes as well as by a higher rate and a less regular mode of ramification. The Portuguese material shows a high variation

of these parameters and of tissue characteristics (e. g. diameter of filaments). Therefore, in our opinion, a separation at the species level apparently is not justified.

The studied material was collected in the course of biofacies and microfacies analyses of Upper Jurassic, mainly Kimmeridgian to Tithonian shallow water successions of the Mesozoic Lusitanian Basin (west-central Portugal) and eastern Algarve Basin (southern Portugal) (e. g. LEINFELDER 1986, WERNER 1986, NOSE in prep.; see also for localities and stratigraphic

terms used in the present study). Sample types comprise calcareous hand specimens as well as isolated algal nodules from marls. The material was investigated by means of optic microscopy (polished slabs, thin sections, acetate peels), SEM and EDX analyses as well as wet chemical analyses. The reference material is deposited at the Bayerische Staatssammlung für Paläontologie und historische Geologie, München and the Institut für Geologie und Paläontologie, Universität of Stuttgart.

2. DESCRIPTION OF MATERIAL

2.1 GENERAL APPEARANCE

Marinella lugeoni forms thalli of variable shape. These can be subdivided into two basic types, i. e. encrusting thalli and the much more widespread erect, digitiform and branching thalli (pl. 1, figs. 9, 10). Encrusting forms overgrow skeletal hardparts (e. g. corals, mollusks, see pl. 1, fig. 3) or are incorporated within cyanobacterial oncoids, where *Marinella lugeoni* is often mutually overgrown by cyanobacterial crusts (pl. 1, figs. 4, 6). The encrusting *Marinella* thalli are hemispherical, dome- and kidney-shaped, or irregularly laminoid and attain sizes of 4 cm vs. 2 cm (length x height).

Besides the encrusting type, thalli can be attached to the substrate with a very narrow base only. They rapidly broaden during upwards growth and commonly form branches. Branches wax and wane. The narrow parts of the thalli are the sites where new branches originate. Individual digitiform branches may reach 0.9 cm in height. Their width varies largely between 0.18 and 0.5 mm.

Occasionally, *Marinella lugeoni* forms entire nodules up to 10 centimetres large. Sometimes, these are composed of slightly undulatory concentric layers forming fan-like hemispherical projections. More commonly, nodules consist of radially arranged, subparallel, dendroid digitiform branches. Also, both types may be realized within one nodule, with the subconcentric texture representing the inner, and the radial texture the outer part of the nodule (pl. 1, fig. 1, 6, 10). Particularly the radial texture leads to knobby, cauliflower-type nodules.

Upward branching forms are rarely preserved in growth position and entire *Marinella* nodules are rare. Most common is algal rubble of fragmented digitiform branches. It seems that the digitiform growth was the basic growth type of *Marinella lugeoni*, forming either small algal meadows, or more commonly, hemispherical to spherical structures. Due to the waxing and waning structure of the *Marinella* branches, the alga is mostly preserved as fragments. Commonly, these brittle fragments serve as nuclei for cyanobacterial oncol formation (pl. 1, fig. 7). Thallial fragments of *Marinella lugeoni* rarely exceed 5 mm in size.

2.2 TISSUE CHARACTERISTICS

In reflected light the *Marinella lugeoni* thalli mostly appear whitish-porcellaneous, whereas in thin-section their dense structure causes a dark grey coloration. Marginal parts are

often stained by brownish ironhydroxide. A tangential colour banding of lighter (thickness: 5 to 20 µm) and darker laminae (thickness: 15 to 40 µm) occurs in many specimens (pl. 1, fig. 8; pl. 2, fig. 5, 6).

The algal tissue is composed of radially oriented, densely packed, sometimes undulating fine filaments which sometimes branch dichotomously (pl. 2, figs. 3-5). Occasionally, very fine transverse walls occur (pl. 2, fig. 2, 4). They are either arranged in continuous tangential layers (pl. 2, fig. 3) or occur in irregular distribution. Bundles of filaments may show undulating deviations from the radial growth direction.

Both the side walls and the horizontal partitions of filaments are composed of very fine crystallites smaller than 2 µm (averaged size 0.5 to 1.5 µm). Filaments are filled by microspar (size of crystallites 1 to 4 µm). They exhibit a round to slightly polygonal cross-section (pl. 2, fig. 1). Filament diameter is very variable, ranging between 5 to 12 µm, and averages around 7 to 9 µm. Maximum and minimum value within one thallus can differ up to 5 µm. The thickness of the side walls is from 2 to 3 µm, horizontal partitions are even thinner. The spacing between horizontal partitions ranges around 8 to 15 µm. Wider spacing is apparently due to preservational loss of horizontal partitions.

In many specimens, isolated, small groups or short rows of intertwined, light coloured, rarely dichotomously branching filaments are arranged parallel to the normal filaments or even crosscut the tissue in an irregular radial direction (pl. 1, fig. 5; pl. 3, fig. 6). Their length is up to 150 µm with a diameter of 9 to 13 µm. Rarely, faint cross partitions can be observed (pl. 2, fig. 9). These conspicuous filaments are confined to small parts within the thallus.

Occasionally, an outer rim of coarse, spar-filled cells of 18-20 µm length and 8-10 µm width surrounds the algal thallus (pl. 3, figs. 4, 5, 7). These cells are placed at the ends of the tissue filaments and differ from the latter by an increase in diameter of the sparitic part and a partial decrease in thickness of the side walls. The cells often show a distinct inner and outer, very dark, dense wall which possibly contains an elevated amount of organic matter. In few cases the thin walls between these marginal cells are absent which probably is due to diagenetically alteration. This results in a continuous sparitic rim at the thallus margin. In very few cases, minute, dome-shaped voids measuring 30 to 90 µm are positioned directly beneath the outer wall (pl. 3, fig. 3).

Commonly, though not in all specimens, round to ovoid, spar-filled larger voids occur within the algal thallus (pl. 2, fig. 7-12). Their sizes mostly range between 20 to 40 μm , but rarely reach up to 110 μm in diameter. Some cavities exhibit a more ovate shape and sometimes wane which leads to sparitic, thread- to flagellum-like terminations ending in the filament tissue (pl. 2, fig. 11). The margins of the voids crosscut the filament tissue discordantly and in many cases are irregularly fringed whereby the end of tissue filaments project into the voids (e. g. pl. 2, fig. 8, 12). Some of these voids are situated close to the thallus margin. In a few cases, a small opening to the outer thallus surface could be detected (Pl. 2, fig. 7).

Occasionally, thalli show oval to elongated channel-like boreholes which reach 20 to 50 μm in diameter and are filled with sediment or microcrystalline sparite. In most cases these boreholes differ markedly from the above described voids by their general form, by their position more or less perpendicular to the thallial surface and by their type of filling.

In one case a tissue part situated at the extreme margin and slightly isolated from the main thallus exhibits a particular kind of differentiation. It consists of the typical *Marinella* filament tissue with proximal tissue folds and four distal pores (Pl. 3, fig. 1, 2). The diameter of pores is 7 μm .

Under SEM, in tangential section, the thalli show the typically dense, round to polygonal arrangement of filaments (pl. 3, fig. 9). Mostly, crystallites of the filament fillings are radially arranged. In radial section, these crystallites exhibit a growth direction more or less perpendicular to the filament wall or a slightly upwards directed growth (pl. 3, fig. 8). It is not clear whether this regular growth of crystallites after algal decay or during diagenesis is caused by the physico-chemical microenvironment within filaments of very small diameter or is induced by a possibly primary prismatic structure of the former filament wall as it is known from the secondary wall layer of corallinaceans (FLAJS 1977). It is noteworthy that

fillings of microboreholes in thalli of *Marinella* which have an only slightly greater diameter (15-25 μm) than the alga filaments (5-15 μm) consist of irregularly arranged blocky calcite.

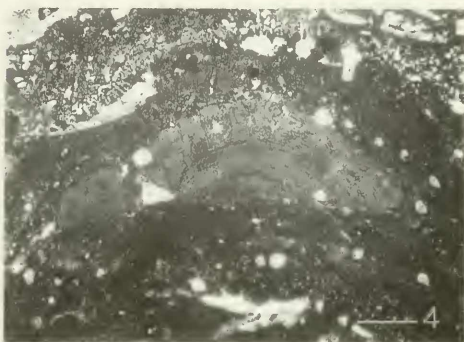
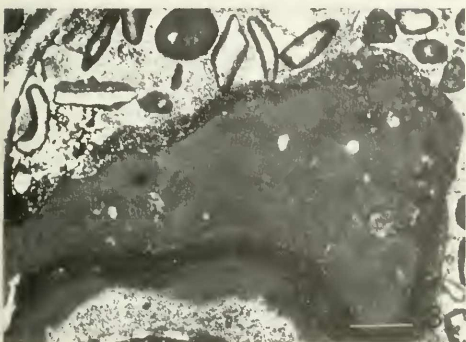
To evaluate the structural composition and mineralogy of the former algal skeleton qualitative and quantitative measurements of Mg and Sr were made with SEM, EDX and wet chemical analysis. Elevated Mg values would indicate an original high Mg-calcite skeleton which is typical of most extant corallinaceans (cf. MILLIMAN 1974, JOHANSEN 1981), whereas remarkable Sr values would point to a former aragonitic skeleton.

Most of the values of the EDX analyses are point measurements, some reflect the Mg and Sr contents of a small area. Due to the small dimensions of the filament wall and the filament fillings the data represent an averaged value of both structures. Therefore, originally elevated Mg values of the filament wall will be underrepresented in EDX data if the Mg content of the filament filling is lower. Analyzed *Marinella* specimens came from a fine conglomeratic rock in which *Marinella* is embedded as clasts together with rock fragments and other bioclasts, and from a bioclastic limestone with autochthonously embedded, large *Marinella* nodules.

The EDX analyses (tab. 1) revealed higher contents of Mg in *Marinella* (0,67-0,95 %, average: 0,8 %) than in rock particles and matrix (0,52-1,08 %; average: 0,53 %). In only one case, Mg values of rock pebble exceeded those of the alga. The wet chemical analysis of a specimen of the bioclastic limestone which was also measured by EDX revealed very low contents of Mg, whereby the slightly but not significantly higher Mg values in the alga correspond with the results of the EDX analysis. The only low differences in Mg content between algae and matrix may be due to the fact that small fragments of the alga contribute to the surrounding sediment and cannot be extracted for the chemical analysis. Qualitative microprobe

Plate 1

- Fig. 1 Large *Marinella lugeoni* thallus with dense subspherical basal growth, changing to branching digitiform growth. Lower Tithonian of S. Tiago dos Velhos; thin section SV26; length of bar 0,5 mm.
- Fig. 2 Spheroidal *Marinella* nodule with initial branching in the upper parts. Kimmeridgian of Consolação; C-3-36; length of bar 0,5 mm.
- Fig. 3 Asymmetrical crustose to subspheroidal growth of *Marinella lugeoni* on the cortex of a *Girvanella minuta* oncoid. The *Marinella* thallus is again covered by a thin layer of the cyanobacterium. Oncolithic rudstone, Lower Tithonian of S. Tiago dos Velhos; thin section SV31; length of bar 0,5 mm.
- Fig. 4 *Marinella* thallus with crustose growth. The alga forms part of the cortex of a *Girvanella minuta* oncoid. Kimmeridge of Patameira; thin section P37; length of bar 0,5 mm.
- Fig. 5 *Marinella* thallus with spherical basal part which is followed by the development of thick, closely arranged branches. Note the bundles of enlarged, light coloured, radial filaments in the branch tissue (middle and upper part of the figure). Kimmeridgian of Consolação; length of bar 0,2 mm.
- Fig. 6 *Girvanella minuta* oncoid with columnar-like overgrowth of a microbial crust sequence including a small *Marinella* thallus (arrow). Kimmeridgian of Consolação; length of bar 0,5 mm.
- Fig. 7 *Marinella* thallus forming the nucleus of a *Girvanella minuta* oncoid. Thin section SV26 (see Fig.1); length of bar 0,5 mm.
- Fig. 8 Thick branches of the marginal part of a *Marinella* thallus. Note the regular alternation of thick dark and narrow light coloured laminae. Lower Tithonian near Arruda dos Vinhos; length of bar 0,2 mm.
- Fig. 9 Extremely fine digitiform branching *Marinella lugeoni* thallus. Note the upward thickening of some branches. Kimmeridgian; Amaral Formation at Trancoso, near Arruda dos Vinhos; thin section 10F; length of bar 0,5 mm.
- Fig. 10 Digitiform branching *Marinella* thallus. The thallus exhibits numerous spar filled conceptacle-like voids and shows the alternation of light and dark coloured laminae ('banding'). Upper Kimmeridgian of Boieiro, near Arruda dos Vinhos; thin section BR V1; length of bar 0,5 mm.



| Marinella | A _{m1} | A _{m2} | A _{m3} | A _{m4} | B _{m1} | B _{m2} | \bar{x}_m |
|-----------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-------------|
| Mg | 0,95 | 0,72 | 0,97 | 0,77 | 0,67 | 0,72 | 0,8 % |
| Ca | 70,16 | 69,23 | 61,15 | 68,53 | 70,03 | 66,85 | 67,66 % |
| Sr | - | 1,14 | 1,62 | - | - | - | 0,46 % |
| Matrix | A _{s1} | A _{s2} | A _{s3} | | B _{s1} | | \bar{x}_s |
| Mg | 0,51 | 1,08 | - | - | 0,52 | - | 0,53 % |
| Ca | 64,73 | 65,27 | 67,52 | - | 55,98 | - | 63,38 % |
| Sr | 2,2 | 1,3 | 1,28 | - | 2,1 | - | 1,7 % |

Tab. 1: EDX-measurements of Mg, Sr and Ca content in specimens of *Marinella* (A_m; B_m) and the neighbouring matrix or bioclasts (A_s; B_s). A: specimens from the Kimmeridgian of Consolação; B: specimen from the Kimmeridgian near Arruda dos Vinhos.

measurements under SEM also revealed generally low but noticeable Mg values. However, differences between algal tissue and the surrounding matrix could not be registered by this method.

In contrast to the Mg values the EDX measurements for Sr clearly revealed considerably lower values for the algae (0-1,91 %, in four of the seven samples 0 %; average 0,70 %) and higher ones for the sediment matrix and rock fragments (1,51-2,6 %, average 2,04 %).

Often, the Mg and Sr contents in fossilized skeletal structures reflect the original mineralogical composition only to a minor degree due to various diagenetic alterations. This is particularly true for skeletons formerly rich in the instable high Mg-calcite which is dissolved or changed into Mg-poor calcite during early diagenesis (FUCHTBAUER 1988, MILLIMAN 1974). Additionally, extant calcifying red algae incorporate Mg in seasonally changing amounts (CHAVE & WHEELER 1965). Despite these limitations and although the present number of measurements on *Marinella* nodules is too small to allow statistically supported conclusions the comparison of the *Marinella* skeleton with the surrounding matrix and/or rock

particles shows a uniform trend and can be tentatively interpreted as relic features of the former mineralogy. The low to zero Sr content of the alga and a more remarkable content of this element in the matrix may reflect an original skeleton free of aragonite (cf. MILLIMAN 1974). Similarly, the higher Mg values of the algal tissue point to a former high Mg-Calcite skeleton which is a characteristic feature of most coralline red algae and cannot be observed in other algal groups.

2.3 SYSTEMATIC POSITION

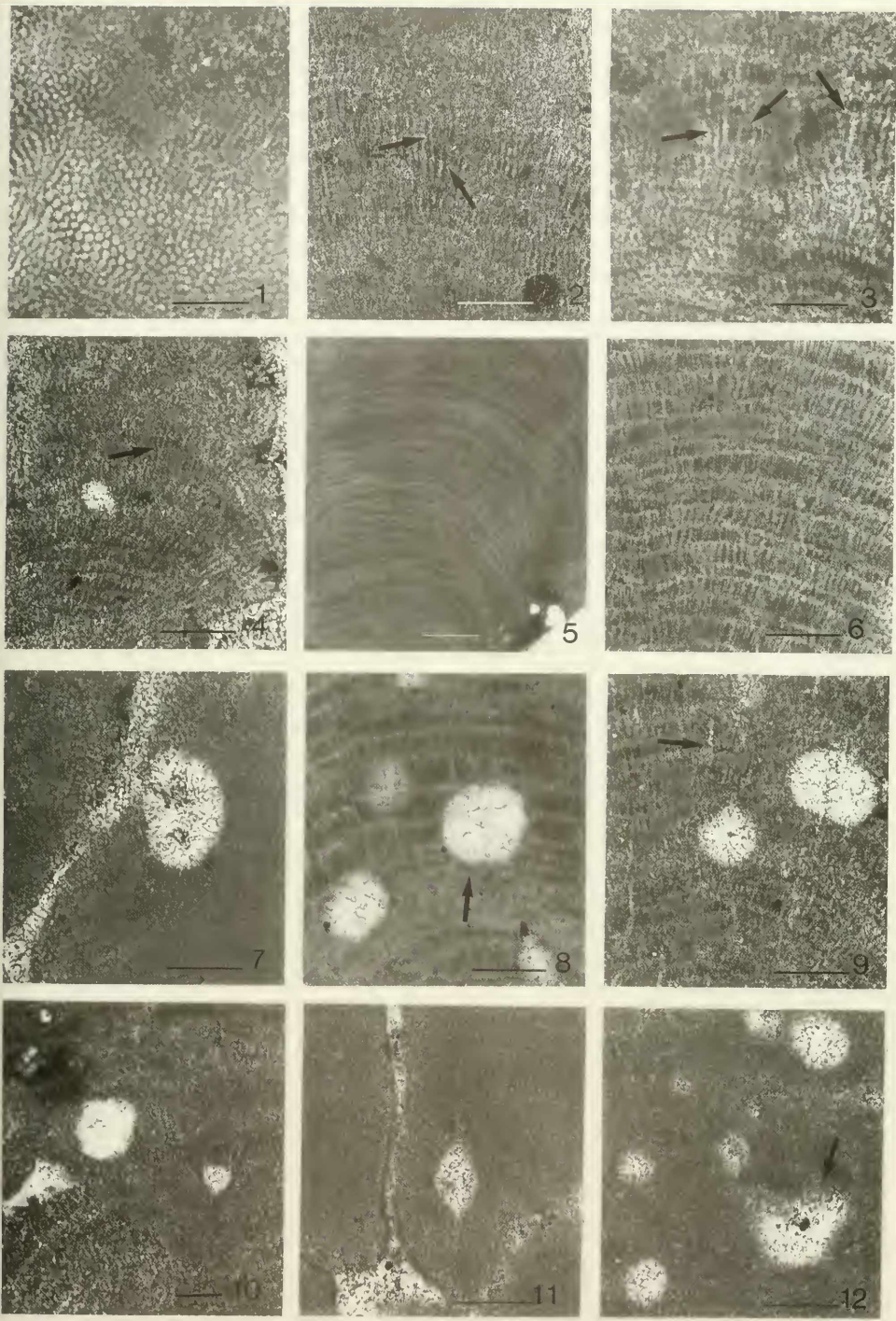
As outlined above, the systematic position of *Marinella lugeoni* is unclear ever since it was described first. As a matter of fact, the form shows affinities to the porostromate cyanobacteria, to the codiacean chlorophytes as well as to the red algae:

PFENDER (1939) and MASSE (1979) may have based their cyanophyte (i. e. cyanobacterial) interpretation on the somewhat irregular, undulating growth pattern of the minute radial filaments. The majority of authors dealing with *Marinella lugeoni* placed it in the codiacean chlorophytes. This seems to be a relic of the time, where all algae with a well defined thallus composed of radiating, often branching tubes like, e. g. the cayeuxiids, were attributed to the codiaceans (or Udoteaceae of the order Caulerpales). However, modern representatives as *Halimeda* exhibit a highly differentiated thallus composed of medullary and cortical filaments, which are arranged at a distinct angle to each other. This is why many of the classical bush-like fossil codiaceans as e. g. *Cayeuxia* and *Ortonella* are now grouped within the Cyanobacteria (rivulariaceans) (RIDING 1977, DRAGASTAN 1985, BARATTOLO 1991).

An attribution of *Marinella* to the rhodophyceans was mainly based on the interpretation of sparitic voids as conceptacles (GOLONKA 1970), the density of cell filaments and

Plate 2

- Fig. 1 Tangential section of *Marinella* tissue showing the dense arrangement and the round to polygonal outline of the filaments. Lower Tithonian; near Sapataria; thin section Si17; length of bar 0,1 mm.
- Fig. 2 Radial section of *Marinella* thallus. Note bifurcation of a filament (left arrow) and cross partitions (e. g. right arrow). Lower Tithonian of S. Tiago dos Velhos; thin section SV26a; length of bar 0,1 mm.
- Fig. 3 Radial section of *Marinella* thallus showing bifurcation (left arrow) and cross partitions (e. g. arrows at the right). In some parts of the section, cross partitions of neighbouring filaments form a continuous tangential layer (e. g. arrows at the right and lower part of the figure). Kimmeridgian of Consolação; thin section C-3-79/4; length of bar 0,1 mm.
- Fig. 4 Radial section showing bifurcation (arrow) and numerous cross partitions (e. g. lower part of the figure). Lower Tithonian of S. Tiago dos Velhos; thin section SV26; length of bar 0,1 mm.
- Fig. 5, 6 Radial section of a nodular *Marinella* thallus with alternation of dark and light coloured laminae ('banding'). The dark laminae are caused by diagenetic thickening of filament walls. Often, the filament walls of the light coloured laminae are poorly preserved and only blurred relics are visible. Kimmeridgian of Consolação; thin section C-3-79/4; 5: length of bar 0,2 mm; 6: 0,1 mm.
- Fig. 7-12 Conceptacle-like spar filled cavities within *Marinella* tissue. It is assumed that the alga itself produced the cavities by decalcification of thallus tissue. The margins of some voids exhibit a fringed outline with tissue filaments projecting into the cavities (e. g. arrows in Figs. 8, 12). This points to an incomplete dissolution of thallus tissue. Note also the thread- to flagellum-like terminations on both sides of some voids (Fig. 10: void at the right; Fig. 11).
- 7: Cavity with small opening to the interstitial space between two *Marinella* branches. 9: Note the enlarged radial filaments running parallel to or crossing the main tissue filaments; the enlarged filaments sometimes exhibit faint cross partitions (arrow at the upper left). 10: Spar-filled elongate, basally widened area to the left represents the interstitial space between two *Marinella* branches.
- In all figures, the growth direction is toward top of the figure. 7, 9, 11, 12: Lower Tithonian of S. Tiago dos Velhos; thin section SV26; 8: Upper Kimmeridgian of Boieiro near Arruda dos Vinhos; thin section BR VI; 10: Kimmeridgian of Bufarda; thin section B 17-20; length of bar of Figs. 7-12: 0,1 mm.



the shape of thallus and branches (BARATTOLO and DEL RE 1985). The good preservation of the Portuguese material allowed to detect additional criteria which support a rhodophyceean character for *Marinella lugeoni* and reveal a close affinity to the coralline algae. Such criteria are as follows:

- Well defined thallus composed of minute filaments with dense microcrystalline walls, giving the typical porcellaneous appearance
- Small size of the filaments which occasionally bifurcate and are divided by horizontal walls
- Differentiation in a ?perithallial tissue and an outer, epithallial-like cell layer, possibly exhibiting an over- and underlying cuticular sheet; possible existence of megacell layers
- Alternation of tangentially arranged darker and lighter laminae (banding) reflecting periodically changing variation in skeletal composition
- Development of voids by solution of skeletal material within the tissue which possibly may be used by the alga for reproduction
- The often rhodolite-like growth form
- An elevated content of Mg and the quasi absence of Sr

ad a): The density and systematic arrangement of the skeleton structure of *Marinella* thalli with regularly arranged filaments clearly reflect characteristics of an algal group with well organized structure. Actually, several extant freshwater to brackish cyanobacteria like *Phormidium* or *Scytonema* may exhibit comparable trichom diameters and an undulating growth habit. However, their calcification does not represent a true biologic skeleton but is only due to biologically controlled physico-chemical precipitation. Consequently, these forms are inhomogenously calcified and contain many irregular vugs, a pattern which is in contrast to the regular skeleton of *Marinella lugeoni*.

ad b): Bifurcation of filaments occurs in some cyanophytes (false branching) and is a common feature in filaments of the cortex of chlorophytes (e. g. WRAY 1977) but calcified horizontal walls dividing the filaments into cell-like segments have, to our knowledge, not yet been described. Moreover chlorophyceean, e. g. codiacean internal filaments are never as fine as the filaments of *Marinella lugeoni*.

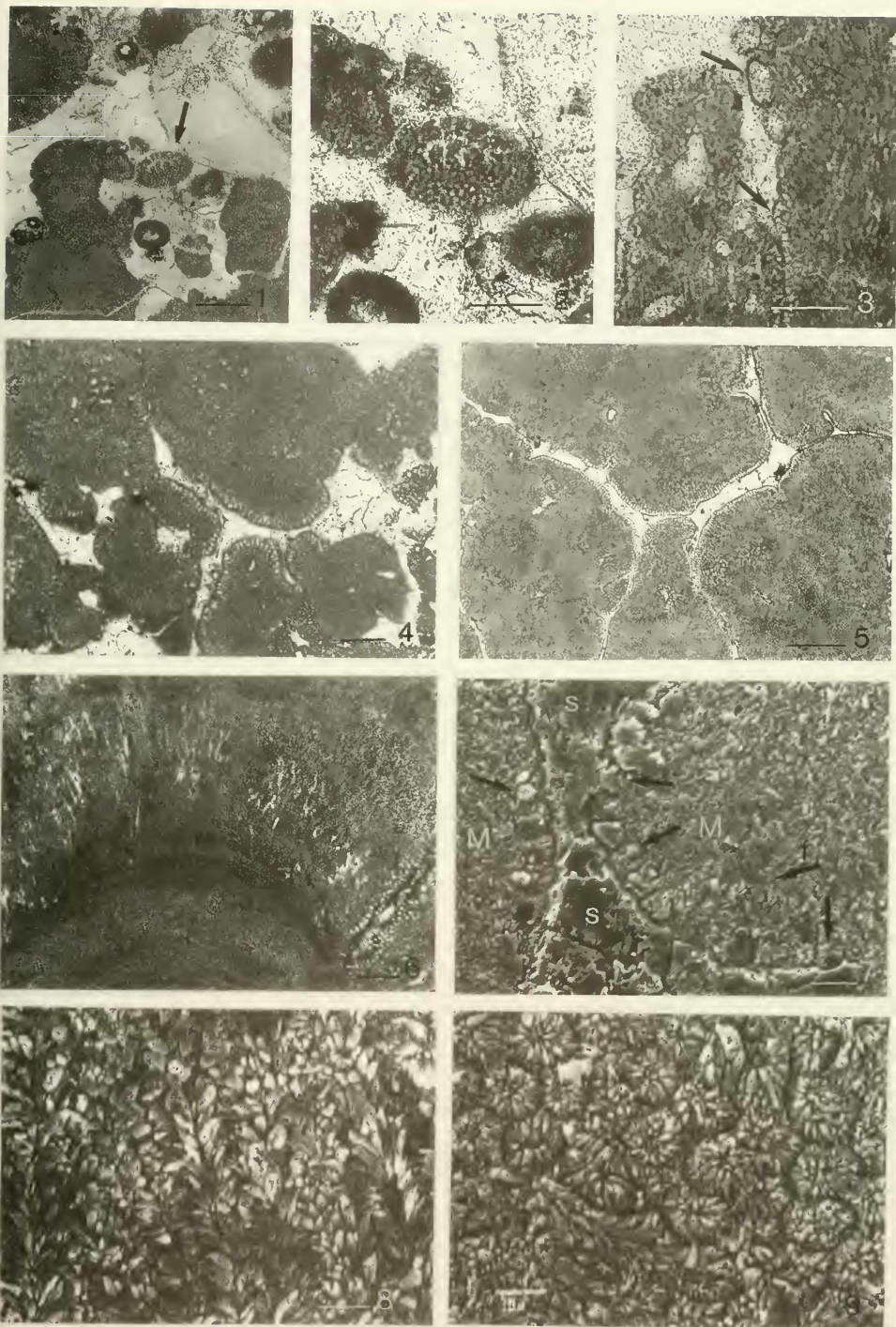
The fact that horizontal partitions have been recognized and described for *Marinella* in few cases only (e. g. IMAIZUMI 1965, BARATTOLO & DEL RE 1985), can be explained by the lesser chance of preservation of this skeletal element. In *Marinella lugeoni* the horizontal walls are mostly thinner than the radial filament walls and can be earlier destroyed during diagenesis than the latter. This is also true for the preservational loss of horizontal cross partitions in solenoporaceans which caused some confusions in taxonomy of this group (cf. MOUSSAVIAN 1989). Apart from the corallinaceans, thinner horizontal filament partitions are also mentioned in fossil squamariaceans (BUCHBINDER & HALLEY 1985) and seem to be a general feature of calcifying rhodophyceans.

ad c): Structural differentiation of the calcified thallus is an important feature to distinguish fossil algal groups. As already mentioned above, in modern codiaceans, the thallus is differentiated in medullary and cortical filaments. The inner, medullary part of fossil codiaceans may often be not or only poorly preserved (MU 1991: 151) and, therefore, the codiacean nature of fossil algae may not be visible. Even if taking this point into consideration, no affinities can be seen between the codiacean green algae and the dense, exclusively radial arrangement of filaments in *Marinella*.

Like the solenoporaceans (e. g. WRAY 1977, JOHANSEN 1981: 174, BOSENCE 1991, POIGNANT 1991) *Marinella* does not show a differentiation into hypothallus and perithallus. However, beside the main thallus filaments, some specimens of *Marinella* exhibit a layer of spar-filled cells forming an outer rim around the thallus. Since the lateral width of these cells corresponds to

Plate 3

- Fig. 1, 2 Partially collapsed *Marinella* thallus showing tissue differentiation around a marginal void with proximal folds and four distal pores (arrow in Fig. 1). Otherwise, the tissue exhibits the characteristics of the *Marinella* tissue. Lower Tithonian of Boieiro, near Arruda dos Vinhos; thin section Bo9; 1: length of bar 0,2 mm; 2: length of bar: 0,1.
- Fig. 3 Branch of a *Marinella* thallus covered with an outer epithallial-like layer of spar filled cells (arrow in lower part) and three voids (arrow at top). Note the wall structure of the lower void consisting of filamentous tissue similar to the algal tissue. Thin section as Fig. 1; length of bar 0,1 mm.
- Fig. 4, 5 *Marinella* thalli with development of a single outer layer of spar filled cells. These cells are interpreted as a separate tissue differentiation corresponding to the epithallial cells of extant corallinaceans. Note the dark overlying sheet which probably reflect a previous organic cover sheet. Kimmeridgian of Consolação; thin section C-3-79/1; 4: length of bar 0,1 mm; 5: length of bar 0,2 mm.
- Fig. 6 *Marinella* thallus showing rows of enlarged radial threads which rarely bifurcate (middle upper part of figure). They exhibit, in some aspects, similarities with megacells of some extant melobesoids. For some of the threads, an origin by boring activity of *Hyella*-like cyanobacterians cannot be ruled out. Note also the outer cell layer at the thallus margin (at the right, lower part). Detail from Pl. 1, Fig. 5; length of bar 0,1 mm.
- Fig. 7 SEM photograph of the ends of two neighbouring *Marinella* branches (M) which are separated by an interspace of blocky calcite (s). The margin of the thallus consists of the single ?epithallial layer of coarse sparitic cells (arrows). Arrow, 'f' within *Marinella* tissue indicates place of a filament wall (dark grooves). Kimmeridgian of Consolação; thin section C-3-79 St.14; length of bar 10 µm.
- Fig. 8 SEM photograph of the radial cross section of *Marinella* tissue. The crystallites of the filament filling are slightly but regularly inclined to the axe of the filament. Kimmeridgian of Consolação; thin section C-3-79 St.5; length of bar 10 µm.
- Fig. 9 SEM photograph of a tangential section of *Marinella* showing the characteristic round to polygonal outline of the filaments. Note the preferentially radial arrangement of the coarse extant crystallites (2-5 µm) of the filament filling. Due to the treatment of the specimen with acid and the dissolution of the fine crystallites of the filament walls (1-2 µm) the latter are visible as dark valleys. Kimmeridgian of Consolação; thin section C-3-79 St.7b; length of bar 10 µm.



the width of the subjacent filaments one could suppose that the outer cell layer would represent the young growth stage of filaments but with not yet calcified wall. If so, the base of the outer cells should correspond to the place of development of horizontal partitions. However, the length of the outer cells (18–20 μm) exceeds that of the distance between horizontal partitions within filaments where these are visible (8–15 μm). Therefore, the outer cells probably represent a different type of thallus tissue overlying the normal filamentous tissue. In location and function the cell layer may be compared with epithallial cells of extant corallineans. These were believed to remain uncalcified and thus to possess a very low preservational potential (WRAY 1977). However, as BOSENCE (1991) recently outlined, the epithallial cells can be well calcified and, therefore, such tissue may be preserved in fossil red algae. The outer rim cells of *Marinella* are preserved in some specimens only. Even in these cases, an epithallial layer mainly coats thallial branches of inner, more protected parts of the algal thallus. This fact and the dark rim of probable organic origin around the cells point to a predominantly organic and less calcified nature of the wall rather than a well calcified tissue.

The outer, well separated cell layer here described as possible epithallus analogon clearly stresses a rhodophycean character of *Marinella*. The calcification pattern of green algae with calcification outside of the filaments would cause a continuous precipitation of carbonate. As it is observed, an organic sheet separating the outer cell layer and the thallus filaments in *Marinella* cannot occur in such a calcification mode. Similarly, the precipitation in porostromate cyanobacteria does not show comparable differentiation, either.

With respect to the differentiation of the algal tissue *Marinella* exhibits close affinities to coralline algae rather than solenoporaceans. Despite the long stratigraphic range of the latter from the Palaeozoic through the Mesozoic no differentiation in tissue comparable to that of *Marinella* could be detected in solenoporaceans (cf. WRAY 1977, JOHANSEN 1981, MOUSSAVIAN 1989, BOSENCE 1991). Furtheron, *Marinella* differs from the solenoporaceans by its significantly smaller filament diameter.

ad d): Banding is a not uncommon feature in fossil rhodophytes such as solenoporaceans (HARLAND & TORRENS 1982, WRIGHT 1985). In comparison with modern analogues it is interpreted as a result of different diagenetic alteration of different skeletal structures which are probably due to seasonally controlled variable incorporation of magnesium and variable growth rates (WRIGHT 1985). Modern corallineans show seasonal differences in the magnesium content which may differ as much as 40 % between summer and winter growth (CHAVE & WHEELER 1965). Due to the instability of high-magnesium calcite, skeletal parts with high contents of magnesium undergo a stronger diagenetic alteration (cf. WRIGHT 1985). In *Solenopora jurassica* this led to a stronger recrystallisation of the skeletal structure and thinning of the wall, respectively. In *Marinella lugeoni* the dark coloured laminae are produced by a thickening of the microcrystalline filament wall and a corresponding reduction of the filament spacing. Occasionally the light coloured laminae exhibit only blurred relics of the filament walls. The regularity and the tangentially arranged occurrence of the laminae suggest that

differences in skeletal composition or calcification reflect periodical, primary changes.

Apart from rhodophyceans banding is reported from extant freshwater cyanobacteria such as *Rivularia haematites* (e. g. PENTECOST 1991). In this case the periodicity of growth pattern is caused by seasonal changes of growth and mode of calcification, with abiotic calcification during winter and a combination of abiotic and biotic (photosynthetic) growth during summer period. In contrast to this the regularity and continuous growth of *Marinella* filaments as well as their regular arrangement point to a biologically controlled calcification of a true algal taxon. Judging from the available literature, banding or a similar periodical growth pattern is not known from green algae.

ad e): Spar filled voids in *Marinella* have been mentioned in a few previous publications. BECKMANN & BECKMANN (1966) regarded this structures as secondary features and discussed an origin by dissolution, secondary resorption or parasitic infestation. IMAIZUMI (1965) interpreted the cavities as possible sporangia. In a further step GOLONKA (1970) concluded to 'Archaeolithothamnium- or *Solenopora*-like sporangia' and, consequently, he attributed *Marinella* to the rhodophytes. However, BARATTOLO & DEL RE (1985) could not see any connection with reproduction and believed that the cavities are caused by the activity of boring organisms rather than by the alga itself.

The Portuguese material includes specimens exhibiting cavities of round to elongate-ovate shape, with sediment or spar fillings. These voids are obviously caused by boring organisms. On the other hand, most of the spar-filled ovoid voids differ from these boreholes by the type of filling (no sediment), by the often not very sharp but rather fringed margin with ends of the filaments projecting into the voids, and by the sometimes flagellum-like terminations. This points to an origin not caused by borers attacking from the outside of the thallus. If these voids would represent boreholes, strongly elongated shapes and, at the surface of the thallus, openings of a similar diameter as the voids should be expected given the high number of studied thin sections. This is not the case. The cavities, particularly those with flagellum-like ends, rather can be explained by a dissolution of tissue produced by the alga itself. Dissolution processes are well known from modern corallineans where decalcification of cell walls is connected with the development of conceptacles and, in articulate corallineans, with the genicula development (CABIOCH 1971: 128, JOHANSEN 1981: 16, 70). Another possibility already discussed by BECKMANN & BECKMANN (1966), i. e. a parasitic infestation within thallus and a subsequent dissolution or mechanical destruction by the parasite, cannot be completely excluded but seems rather unlikely. In this case it would be difficult to explain how the parasite enters the dense thallus, as the filaments above and around the voids do not show any damage. Also, the search for food and oxygen requires a direct connection with the surface of the thallus.

If accepting that the voids are created by decalcification of the alga itself, the question remains which function the cavities of *Marinella* had and why they are found only in some specimens. As mentioned above, decalcification in extant coralline algae is a prerequisite for genicula and conceptacle

development. For genicula formation in articulate corallineans parts within the thallus branches decalcify. This process continues until the surface of the thallus is reached (JOHANSEN 1981: fig. 12, CABIOCH 1971). For *Marinella*, an interpretation of the voids as centres of decalcification for genicula formation is not convincing. Some of the fine, branching *Marinella* thalli with small branch bases exhibit, to a certain degree, similarities with modern articulate corallines, and voids in *Marinella* seem to be more frequent in branching thalli than in nodular specimens. However, sparitic voids in *Marinella* occur also in spheroidal nodules where a formation of genicular structures is not expected.

The *Marinella* voids show greater similarities with the sporangia and conceptacles of living and fossil corallineans. In these cases, decalcification takes place at the margin of thalli and, together with a differentiation of cuticular sheet and marginal cells, results in reproductive bodies which exhibit different shapes in different genera (see WRAY 1977, JOHANSEN 1981). With respect to the fossilizable structure three types can be distinguished: individual sporangia (e. g. *Archaeolithothamnium*) and single-pored (e. g. articulate corallines) or multi-pored conceptacles (WRAY 1977). In rare cases, marginally situated *Marinella* voids exhibit openings to the outside of the thallus which may be interpreted as pores (pl. 2, fig. 7). On the other hand, such pore-like structures are very rare in voids now preserved within the thallus. In the general shape and the scarcity of morphological features the *Marinella* voids show resemblance with some round simple sporangia of *Archaeolithothamnium*. GOLONKA (1970) therefore concluded an affinity with corallineans. However, in contrast to *Marinella* the reproductive cavities in *Archaeolithothamnium* are more or less systematically arranged. Additionally, no structures are preserved within the cavities which could be referred to reproduction. For this reason BARATTOLO & DEL RE (1985) doubt an interpretation of *Marinella* voids as sporangia or conceptacles. Although the detected features clearly indicate that the cavities were produced by the alga itself, the present study does not give more precise information about the function of these structures. However, the general shape and outline characteristics of the voids together with their often marginal position within the thalli suggests that a connection with reproductive processes is apparent.

In this context, the discovery of a *Marinella* specimen with particularly differentiated thallus tissue is interesting (pl. 3, fig. 1, 2). This specimen shows a marginal void which exhibits several proximal folds and four distal pores. This feature shows resemblance with multi-pored conceptacles of the Melobesioideae. However, only one example of such kind of tissue differentiation could be observed, a fact which does not support far-reaching conclusions.

A peculiar feature are the short, enlarged, irregular to subradial filaments with diameters of 7–9 µm crosscutting the algal tissue (e. g. pl. 3, fig. 5). They occur in bundles, short rows, or with irregular distribution within the thallus and exhibit, in some aspects, similarities with heterocysts/megacells of extant melobesoids (cf. WRAY 1977, JOHANSEN 1981: 33 f.). If so, a dissolution of cell and filament walls may have produced these structures in *Marinella*. However, in some morphological aspects (e. g. length of filaments, diameter), the enlarged

filaments can be compared with borings of the extant cyanobacterium *Hyella* and its fossil counterpart *Fasciculus* (cf. SCHMIDT 1992). Such boring organisms may also show bifurcation as observed in corresponding structures in *Marinella*. On the other hand, the frequent and repetitive occurrence of filaments obviously does not influence the mode of growth of *Marinella* tissue. Above the areas with such filaments an undisturbed, continuous development of algal tissue is observed and favours an interpretation of this structure as primary algal feature rather than the result of intermittent boring events. On the other hand, at the present state of knowledge, the latter cannot be ruled out completely.

ad f): Nodular growth form has often been mentioned from modern and fossil algal or 'algal'-like (e. g. cyanobacterial) organisms. This growth form occurs in both rhodophyceans and cyanobacteria. Nodules formed by red algae commonly are termed 'rhodolite' (BOSELLINI & GINSBURG 1971, see also for overview of algal nodules) whereas PERYT (1983) favours the term 'rhodoid'. They typically are composed of loosely to densely arranged, radially growing, arborescent, digitating branches growing on all sides which results in a flat to ovoid to subconcentric pustular nodule. Oncoids may be built by a variety of organisms, including heterotrophic forms (e. g. encrusting foraminifera), but are commonly dominated by cyanobacteria. They may be similar to dense rhodolites in outer morphology but differ in their inner structure which shows a predominantly tangentially arranged growth pattern and a nucleus. Based on this, rhodophyceans may both form rhodolites and red algal oncoids. The typical rhodolite nodules composed of radiating, long branches are mostly built by coralline algae whereas solenoporan nodules normally represent pustular to homogeneous rhodolites or laminated red algal oncoids.

According to literature calcareous green alga do not develop rhodolite-like or oncoidal growth form but prefer simple erect patterns (cf. MU 1991). 'Algal' nodules hitherto referred to green algae (e. g. JOHNSON 1964, BOSELLINI & GINSBURG 1971) have been built by taxa such as *Ortonella* and *Cayeuxia* which are now attributed to the cyanobacteria (see above; for discussion on the systematic position of filamentous nodular 'green' algae see MU 1991, 151 f., too).

If not preserved as fragments only, *Marinella* nodules are composed of densely packed radiating long branches very similar to typical modern rhodolites. This fact is another strong argument for the rhodophycan nature of the taxon. The functional advantages of the rhodolite growth form are not well known (BOSENCE 1983). Loosely packed branches in low energy regimes may prevent sinking into the substrate. Moreover, calcifying rhodophyceans seem to need more light than cyanobacteria so that in deeper setting the intranodular branching results in an enormous enlargement of outer, photoactive surfaces. In high-energy settings, abrasion will not affect the entire surface but only tangle the tips of branches, which can be easily repaired due to the high regeneration ability of coralline algae (cf. STENECK 1982, 1985). Due to the latter, partial fragmentation of branches can be tolerated and is even used for vegetative reproduction. Since *Marinella* occurs both in high-energy and shallow, low-energy settings (see below), parts of these strategies may have been realized already in the Upper Jurassic.

ad g): The data of the chemical analysis concerning Mg and Sr contents have to be interpreted with some reservations because of (1) possible periodically varying incorporation of these elements by the alga, (2) the not quantifiable diagenetic alterations and (3) some methodological uncertainties in measurement. On the other hand, the presented quantitative to semiquantitative analyses generally point to slightly raised Mg values and corresponding lower Sr values in the alga when compared with the surrounding sediment and other particles. This would confirm an original skeleton free of aragonite and enriched in magnesium calcite. If this is true, a close relationship to the corallineans is apparent. REITNER (1987: 210) also suggests a Mg-calcite, corallinean-like skeleton for *Marinella lugeoni*, without giving further information and submitting evidences for his opinion.

The majority of the modern members of the coralline algae are characterized by a high-magnesium calcite skeleton whereas other algae such as the green algae and even some corallineans use aragonite (MILLIMAN 1974, JOHANSEN 1981). For fossil red algae very scarce data about Mg and Sr measurements are available. WRIGHT (1985) detected low Sr values in *Solenopora jurassica* and stressed the affinity of the solenoporaceans to the calcitic corallineans.

In conclusion, the Portuguese material clearly stresses the rhodophycean character of *Marinella* and strongly supports an affinity with corallineans rather than solenoporaceans. Fig. 2 lists characteristics of the coralline algae, the solenoporaceans and *Marinella*. The previous opinion of a solenoporacean affinity was admitted because of an undifferentiated tissue, a generally similar growth habit, the growth direction of the filaments and the occurrence of cross partitions. However, the development of a marginal cell layer, the decalcification of algal tissue resulting in now sparitic voids, the very minute filament

diameter and, to some part, the typical rhodolite appearance of *Marinella* nodules are features pointing to a strong corallinean affinity. These features could not yet be detected in the long history of solenoporaceans.

2.4 PHYLOGENETIC ASPECTS

The phylogenetic interpretation of rhodophyte algae is troubled by differing and unsatisfactory systematic classifications. This is particularly caused by two opposing points of view as to the origin of rhodophytes. Some authors consider the rhodophytes as the most primitive group of floral eukaryotes (e. g. TAPPAN 1980: 138), whereas others assume that they stem from higher advanced ancestors but became secondarily simplified (LEE 1972 and McQUADE 1977, both in TAPPAN 1980: 137). We follow the more generally accepted conception that rhodophytes are a primitive group and that the corallineans are a mono- or oligophyletic homogenous natural family (POIGNANT 1979 a). However, phylogenetic relations between coralline algae depend on the features used for classification, i. e. tissue characteristics and reproductive bodies, and nature of secondary pit connections (e. g. WRAY 1977, POIGNANT 1979 b). Because the last feature is hardly ever recognizable in fossil specimens only few preservable skeletal features such as filament characteristics, cross partitions, sporangia and conceptacles remain for classification. Since their systematical value is evaluated for classification by different algal workers in a different way, several phylogenetic theories for the rhodophytes, particularly for the derivation of the Corallineaceae from the Solenoporaceae were established (cf. POIGNANT 1991). Additional confusion exists in taxonomy and nomenclature, particularly in solenoporaceans (cf. MOUSSAVIAN 1989). It was generally accepted that the modern corallineans derived from the solenoporaceans during Paleozoic or Mesozoic times (e. g. JOHNSON 1960, WRAY 1977; cf. POIGNANT 1991). However, according to MOUSSAVIAN (1989) who revised some genera of the Solenoporaceae, no connection can be seen between the modern corallineans and the solenoporaceans. As a consequence, he assumes that the Corallineaceae originated from ancestral corallines such as the Permian to Carboniferous taxon *Archaeolithophyllum* which is characterized by single-pored conceptacles. Due to their non-appearance during the lower Mesozoic an origin of the Corallineaceae from noncalcifying florideans may also be possible.

To evaluate the phylogenetic position of *Marinella* their morphological features and their affinities with the red algae families as well as the stratigraphical occurrence have to be considered. As mentioned above (see 2.3, Fig. 2) *Marinella* exhibits affinities with both solenoporaceans and corallineans. With the first group *Marinella* shares the lack of differentiation into hypothallus and perithallus, the dense radial arrangement of filaments and cells, and the horizontal walls dividing radial filaments into single cells. With the Corallineaceae, the alga has in common the minute filament diameter, the capability to a decalcification of skeletal tissue resulting in cell fusions and conceptacle-like cavities and the differentiation of an epithallial and, possibly, megacell tissue. Taking into account that the first appearance of *Marinella* is in the Late Jurassic and the first occurrence of corallineans is postulated

| | <i>Marinella</i> | Corallineans | Solenoporaceans |
|---|---|--|--|
| general outline | nodular rarely crustose | nodular (inarticulate C.) crustose | nodular crustose |
| growth form | spheroidal, digitiform, rarely cushion-like | spheroidal, digitiform, crusts | spheroidal, crusts, rarely digitiform |
| banding | + | + | + |
| diameter of cells | 5 - 15 μ m | 5 - 20 μ m | 20 - 100 μ m |
| differentiation of hypo- and perithallus | - | + | - |
| epithallus | outer rim of thin walled cells (? epithallus) | + | - |
| dominant direction of cell growth | radial filaments | tangential cell rows or radial filaments | tangential cell rows or radial filaments |
| dissolution of tissue resulting in cavities or enlarged cells | + | + | - |
| conceptacles/ sporangia | (+) | + | ? |
| megacells/ heterocysts | ? | + | - |

Fig. 2: Relationships in thallus characteristics between *Marinella*, corallineans and solenoporaceans.

for the Lower Cretaceous (MOUSSAVIAN 1989, 1991), one could attribute to *Marinella* the character of a 'missing link' between the solenoporaceans and the corallinaceans. However, as POIGNANT (1991) and, particularly, MOUSSAVIAN (1989) pointed out, the solenoporaceans seem to have had an own evolution since Paleozoic times. It is remarkable that no taxon of the solenoporaceans is known to have such a minute filament tissue as *Marinella*. With respect to the small filament diameter, only one example of solenoporaceans may be compared to some degree: CUIF (1969) described a certain tissue differentiation within Triassic solenoporaceans from Turkey and interpreted the corresponding structures as possible reproductive bodies. These have a significantly smaller filament size than normal tissue filaments. According to MOUSSAVIAN (1989), they are partly comparable with germs of Recent florideans rather than corallinaceans. Since these possible reproductive structures are very dissimilar to the *Marinella* features, no close systematic relation between both can be seen.

Marinella lugeoni is partly comparable with different taxa of extant species of coralline algae. The flabellate growth habit of cell threads closely resembles the articulate *Calliarthron* which, like *Marinella*, also exhibits a well developed layer of epithallial cells. If the enlargement of tangential cell rows discovered in *Marinella* represents heterocysts (or megacells), affinities to, for example, the non-articulated *Porolithon* or *Neogoniolithon* exist (cf. WRAY 1977). However, *Marinella* does not possess a

hypothallus and such highly differentiated sporangia and conceptacles as the corallinaceans. Nevertheless, *Marinella* possibly had simple mono-pored reproductive chambers (spare-filled cavities) and, possibly, multi-pored conceptacles (questionable tissue-differentiation, pl. 3, fig. 1, 2). In these features it clearly differs from the solenoporaceans.

Although the tissue characteristics of *Marinella* indicate very close relationships with the corallinaceans, the set of detected features cannot be correlated with a certain group or genus of the modern corallinaceans. This is partly caused by the uncertainty of the taxonomical significance of some of the skeletal features (cf. POIGNANT 1991). Therefore, at the present stage of research, a direct connection to one of the modern corallinacean taxa cannot be postulated. It is more likely that *Marinella* and the corallinaceans originated in the Jurassic from a common, possibly non-calcifying ancestor. The long persistence of the tissue parameters and in consequence this longevity of the species *Marinella lugeoni* from the Upper Jurassic up to the Oligocene also point to a separate evolutionary pathway of this taxon. If *Marinella* had been a direct ancestor of one of the modern corallinaceans it should have been most likely replaced by its evolutionary more successful descendants. For this reason, a derivation of the corallinaceans from the solenoporaceans with a relatively constant tissue pattern through time is unlikely as well.

3. PALAEOECOLOGY

3.1 MARINELLA HABITATS

Figs. 3 and 4 show that *Marinella* occurs in a wide variety of settings within the Kimmeridgian to Tithonian successions of both the Lusitanian and the Algarve Basin of Portugal. As a common factor these settings display shallow to very shallow water characteristics. Environments range from coral reef and reef debris settings to lagoonal and open platform/ramp systems to inner ramp and marginal marine settings. However, the alga had its largest success not in fully marine reef habitats with stable environmental conditions and firm substrate but rather occurred in unstable settings. These comprise unstabilized and highly abrasive high-energy environments often with a high influx of detrital quartz, muddy, commonly marly soft bottom habitats, or settings characterized by fluctuating, commonly hypohaline salinity conditions.

Marinella lugeoni typically occurs together with a set of characteristic microorganisms. Most common are lituolids (e. g. *Alveosepta jaccardi*, *Pseudocyclammia* spp., the euryhaline *Everticyclammia virguliana* and coarse agglutinating forms of the *Haplophragmium*-type). Other foraminifera, such as lenticulinids, *Glomospira* sp. and *Conicospirillina basiliensis* occur in some samples. In oncoid facies, and particularly in *Marinella*-rich floatstones, rudstones (e. g. pl. 1, figs. 1-3, 7) and coral reef facies other algae and algal-type microproblematica, such as *Permocalculus* sp., *Solenopora cayeuxiiformis*, *Lithocodium*, *Bacinella* and, 'cayeuxiid' algae sometimes occur as well (LEINFELDER 1986).

3.1.1 Oncoid facies with *Marinella*

Marinella lugeoni often occurs in high quantities in micritic oncoid rudstones which sometimes contain a moderate clay content. The oncoids are formed by the porostromate cyanobacterium *Girvanella minuta* and by spongiostromate forms, and typically exhibit fragments of *Marinella lugeoni* serving as oncoid nuclei. *Marinella* may also contribute to parts of the oncoid cortex, growing alternately with cyanobacteria. Often, such oncolitic beds are laterally extensive, and are intercalated in mixed salinity, marginal marine marl to siltstone successions or even in terrestrial facies (cf. LEINFELDER 1986, WERNER 1986).

Oncoid settings are characterized by a low sedimentation rate, resulting in the laterally extensive, but commonly short-term spreading of marly to calcareous oncolitic facies. Probably, the stop of sedimentation initially was accompanied by slightly elevated water energy and fairly normal salinity, giving rise to the establishment of attached *Marinella* meadows and small *Marinella* rhodolites. This was sometimes accompanied by the growth of small corals. Frequently, *Marinella*, was fragmented by the elevated water energy, possibly representing a strategy of reproduction. *Marinella* ceased growing when salinity went back to hyposaline, which possibly was accompanied by the onset of very low clay sedimentation. Consequently, *Marinella* and the few accompanying corals were encrusted by *Girvanella* and other cyanobacteria. Pure *Girvanella minuta* oncolites from the

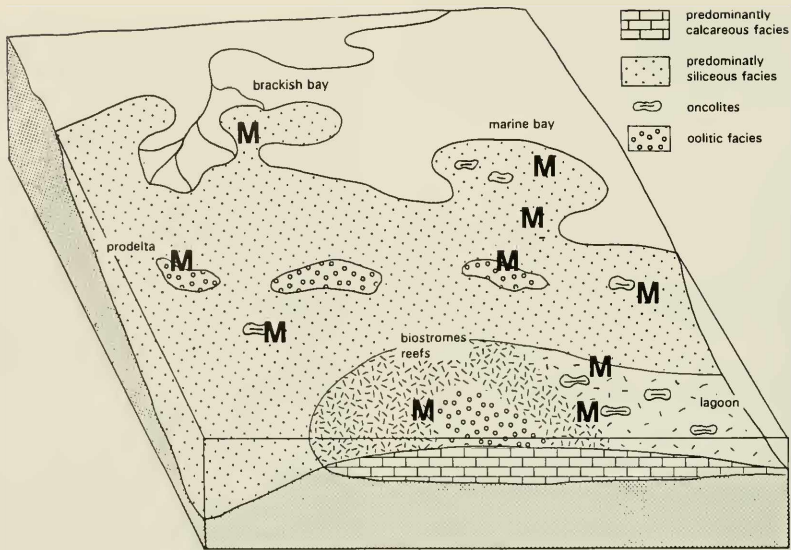


Fig. 3: Distribution of *Marinella lugeoni* (M) in Upper Jurassic settings of Portugal.

| | | REEFAL ENVIRONMENT | TRANSITION REEF/PLATFORM (bioclastic sands) | OPEN PLATFORM | INNER PLATFORM MARGINAL SETTINGS LAGOON |
|--------------------------|------------------|--------------------|---|---------------|---|
| Beckmann & Beckmann 1966 | Cret. - Eoc. | | | | |
| Höfling 1985 | U. Cret. | | | | |
| Reitner 1987 | L. - U. Cret. | | | | |
| Peybernés 1979 | L. Cret. | | | | |
| Rey 1972 | L. Cret. | | | | |
| Masse & Poignant 1971 | L. Cret. | | | | |
| Peybernés & Conrad 1979 | L. Cret. | | | | |
| Canerot 1979 | U. Jur./L. Cret. | | | | |
| Misik 1966 | U. Jur. | | | | |
| Flügel 1979 | U. Jur. | | | | |
| Persoz & Remane 1973 | U. Jur. | | | | |
| Golonka 1970 | U. Jur. | | | | |
| Bolliger & Burri 1970 | U. Jur. | | | | |
| present study | U. Jur. | | | | |

Fig. 4: Palaeoenvironmental distribution of *Marinella lugeoni* in Jurassic to Tertiary settings based on data from the literature and the present study of the Upper Jurassic of Portugal. (Dotted line: siliciclastics).

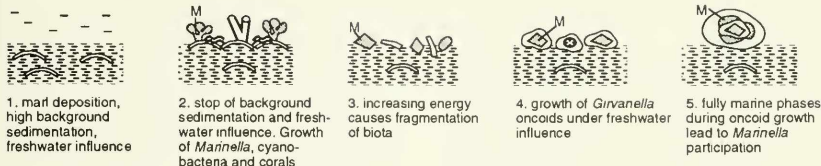
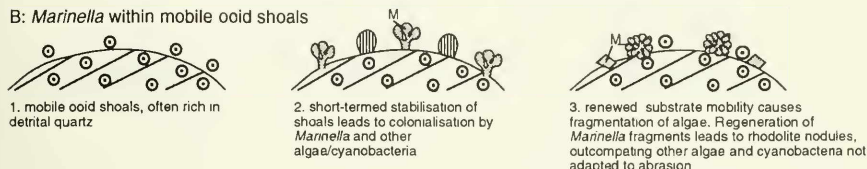
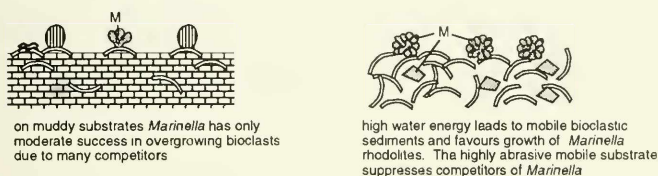
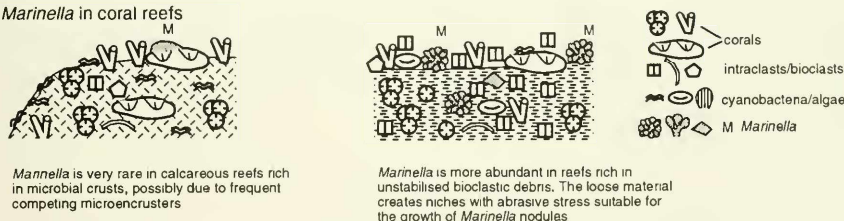
Upper Jurassic of Portugal are known to be adapted to slightly brackish environments (cf. LEINFELDER 1986, WERNER 1986, LEINFELDER et al. 1993). Episodic salinity improvement during the growth of oncoids is indicated in cases where *Marinella* occurs in distinct layers of the oncolitic cortex (Fig. 5a).

3.1.2 Oolites rich in *Marinella*

Marinella nodules with sizes of several decimetres, rarely with diameters up to 11 cm, occur in marly, oolitic packstone facies containing a low-diversity coral fauna (*Axosmilia* spp., *Ovalastrea* spp.). This type is intercalated in a thick series of oolitic grainstones and packstones which characteristically contain a high amount of lignite debris and detrital quartz, the latter of which commonly serves as ooid nuclei. In many ooid

grainstones, *Marinella* typically occurs as a common bioclastic constituent. Small fragments sometimes are encrusted by ooidal cortices.

Many of the ooid grainstones containing *Marinella* nodules and fragments are well sorted, cross-bedded, and do not contain autochthonous fauna. This indicates that they represent mobile, unstabilized ooid shoals which were difficult to colonize. Probably, *Marinella* was partly adapted to such a highly abrasive setting, as are many modern coralline algae both because of their repair capabilities and its ability to regenerate from broken fragments (cf. STENECK 1985). Repetitive short-term stabilization of ooid shoals and subsequent reworking suppressed other organisms and favoured the growth of *Marinella* (Fig. 5 b).

A: *Marinella* in marly oncoid faciesB: *Marinella* within mobile ooid shoalsC: *Marinella* in bioclastic limestonesD: *Marinella* in coral reefsFig. 5: Occurrence and palaeoenvironmental demands of *Marinella lugeoni* based on data from the Upper Jurassic of Portugal.3.1.3 Bioclastic wackestones, floatstones and rudstones with *Marinella*

Marinella is a subordinate, sometimes common constituent of bioclastic, partly nodular, wackestones and floatstones which contain fragments of corals, coralline sponges and echinoids. Often the alga appears in sediments rich in *Trichites* sp., a pinnacean fully marine bivalve which could possibly tolerate minor salinity fluctuations. More frequently, *Marinella* occurs in bioclastic rudstones. Occasionally, pure *Marinella* rudstones exist. In the rudstones, *Marinella* is mostly fragmented but sometimes forms large, centimetre-sized, rhodolite nodules.

The mud-supported facies represents low to medium energy, muddy substrates where *Marinella* had many competitors in colonizing the available bioclasts. This explains the moderate success of *Marinella* in such sediments. Generally increased water energy, or more likely, more frequent high-energy events gave rise to grain-supported, mobile substrates. This

hostile habitat suppressed other competitors for settling on bioclasts and favoured the growth of *Marinella* (Fig. 5 c).

Marinella also occurs in coral reef facies. It may be a common constituent in slightly marly reef limestones exhibiting a high amount of bioclastic debris, whereas it is very rare in purely calcareous reef rocks. In the well developed Kimmeridgian Ota Coral Reef of Portugal, for example, it only occurs as a very rare element in crust-rich boundstones, although the diversity of other algal-type taxa is very high (LEINFELDER 1992). Here, *Marinella* exhibits an encrusting growth habit and did not develop radially arborescent branches.

In purely calcareous reef settings *Marinella* obviously had little success. Possibly, the growth rate of *Marinella* was slower than for most of the other encrusting algal, algal-type and microbial forms (e.g. microbial crusts, *Bacinella*, *Lithocodium*, see LEINFELDER et al. 1993). Interestingly, in slightly marly reef settings, *Marinella* is much more frequent. It seems that

cyanobacterial crusts were more vulnerable to occasional clay sedimentation than *Marinella*. Additionally, many of these marly reefs contain more unstabilized debris than the calcareous reefs, where bioclasts are mostly cemented by microbial crusts. The unstabilized debris resulted in abrasive microenvironments within the reefs, which were the sites for *Marinella* settlement (Fig. 5 d).

3.2 DEMANDS AND ADAPTATIONAL STRATEGIES OF *MARINELLA*

The environmental demands for growth of *Marinella* differ significantly from other algal or microbial organisms of the Upper Jurassic. Although there is a wide overlap in distribution with other alga and cyanobacteria, *Marinella* is commonly outcompeted by others in classical environments for benthic algae such as reefs and lagoons. This might be particularly due to a very slow growth rate and a high demand of light for *Marinella*. The alga had a certain tolerance towards fluctuating salinities and had its maximum distribution in mixed salinity settings. Despite being a slightly euryhaline form, the occurrence of the alga pinpoints the maximum improvement of salinity in otherwise hypohaline or

hyperhaline settings as is indicated by the partial co-occurrence of small corals. Another ecological advantage was even more crucial. As many modern coralline meliobesoid algae, *Marinella* could thrive in highly abrasive settings. Some modern meliobesoids conquered the highest energy settings such as the reef rim, where water loaded with sediment particles is strongly abrasive. Encrusting corallines in tranquil settings are dependant on bioabrasion caused by grazing organism such as gastropods (STENECK 1982). Such abrasion is necessary to prevent settlement of other algae and microbes on the corallines. A certain damage of the skeletal tissue is tolerated since corallines have high regeneration abilities. The dominant occurrence and the partially large size of *Marinella* in abrasive settings such as cross-bedded ooid grainstones or sandy oolites clearly suggests that *Marinella* already had similar abilities. Probably, even fragmentation was tolerated since it helped the rapid distribution of branch fragments from which new thalli could develop. *Marinella* was a eurytopic form but had its maximum distribution in an ecological niche which previously was not occupied. This niche was characterized by mostly unstable substrates, abrasive events, input of terrigenous material and salinity excursions. Such adaption led to the more than 100 million year lasting success of *Marinella*.

ACKNOWLEDGEMENTS

We thank E. MOUSSAVIAN, Munich, for stimulating discussion on the phylogeny of red algae. M. NOSE and D. SCHMID, Stuttgart, provided additional material. R. LIEBREICH and M. WERNER, Munich, and A. FELS, Stuttgart, is thanked for SEM and EDX assistance. F. HOCK, Munich, performed most of the fotografic work.

Some of the field work was financially supported by the DEUTSCHE FORSCHUNGSGEMEINSCHAFT (DFG-projects SCHM-452/1,5 and LE 580/1).

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Jahr/Year: 1993

Band/Volume: [20](#)

Autor(en)/Author(s): Leinfelder Reinhold R.

Artikel/Article: [Systematic position and palaeoecology of the Upper Jurassic to Tertiary alga *Marinella lugeoni* Pfender 105-122](#)