geologicaacta

Jurassic Fe-Mn macro-oncoids from pelagic swells of the External Subbetic (Spain): evidences of microbial origin

MATIAS REOLID [*] and LUIS MIGUEL NIETO

Departamento de Geología, Universidad de Jaén
Campus Las Lagunillas, 23071 Jaén, Spain

* Corresponding autor. E-mail: mreolid@ujaen.es

⊣ **A B S T R A C T** ⊢

Ferromanganesiferous macro-oncoids are distinctive from the External Subbetic Zone (Betic Cordillera, SE Spain) in relation to a major heterochronic unconformity, with a Middle Bathonian-Lower Oxfordian minimum hiatus and a Lowest Bathonian-Lowest Kimmeridgian maximum hiatus. The Fe-Mn macro-oncoids (43 mm mean-size) consist of microbial laminae with planar and arborescent to dendrolitic morphologies. Under petrographic microscopy, the planar morphologies are made up by condensed fibrillar meshworks whereas the dendrolitic ones are similar to *Frutexites*. Alternation between these two types of laminae reveals a rhythmic growth in the Fe-Mn macro-oncoids. Bacterial and fungal filaments are observed in SEM analyses as microbial mats constituted by a disperse web of filaments exhibiting a branching tube-like morphology with diameters ranging between 2 and 10 μm. Aggregates of coccoid-shaped forms are also registered by SEM analyses. Taxonomical approximation of the microbiota is complex, though in the thin section the condensed fibrillar meshworks look like cyanobacteria, and in SEM images the morphology of the filaments resembles fungal hyphae and green algae, whereas coccoids are assigned to cyanobacteria. The precipitation of Fe-Mn is related to the chemoorganotrophic behaviour of the benthic microbial communities, probably corresponding to the fungal mats and other chemosynthetic microbes. Inorganic precipitation mechanisms are regarded as insufficient for the accumulation of a significant amount of MnO. An efficient precipitation of Mn from natural water largely depended on the presence of Mn-oxidizing microorganisms. Sediment-starved zones of pelagic swells of the External Subbetic, located in the deep euphotic zone, were the best places for microbially mediated authigenesis.

KEYWORDS | Macro-oncoids. Biogeochemical origin. Hardground. Jurassic. External Subbetic.

INTRODUCTION

The stratigraphic record from the Bathonian to Oxfordian is characterized by common events of different origins: eustatic changes (e.g. Vail et al., 1987; Hardenbol et al., 1998), and tectonic processes on local and regional scales (Wilson et al., 1989; Leinfelder, 1993; Vera, 2001; Azeredo et al., 2002) related to changes in the position of the mid-

oceanic ridge of the North Atlantic (Wilson et al., 1989), or to rifting processes involving both the North Atlantic and the western Tethys (Leinfelder, 1993). Alternatively, Dromart et al. (2003a, b) propose global climatic changes that produced important fluctuations in the extent of the carbonate platforms. These events have been recorded as stratigraphic unconformities, represented by hardgrounds, neptunian dykes, condensed levels, and Fe-Mn and/or phosphatic banded crusts and macro-oncoids.

The texture and geochemistry of the Fe-Mn crusts and macro-oncoids have been studied in different alpine domains (e.g. Wendt, 1969, 1970; Jenkyns, 1970a, b; Drittenbas 1979; Bourbon, 1980; Krajewski, 1984; Gygi, 1992; Pomoni-Papaioannou, 1994; Burkhalter, 1995). The study of this type of deposits is a common subject in recent marine environments (Usui, 1994; Usui and Mita, 1994; Bu et al., 2003; Han et al., 2003; Buatier et al., 2004; Glasby et al., 2006; González et al., 2007; Usui et al., 2007). In some such recent crusts and nodules, the proposed origin for the precipitation of Fe-Mn oxyhydroxides is biochemical, with the mediation of bacteria and fungi in highly oxydizing hydrothermal environments.

These macro-oncoids and planar laminated crusts have been described as pelagic stromatolites (Krajewski et al., 2000; Martín-Algarra and Sánchez-Navas, 2000; Chacón and Martín-Chivelet, 2008). Studies regarding Fe-Mn and phosphatic macro-oncoids in the Betic External Zones (Southeastern Spain) are abundant (Martín-Algarra and Vera, 1994; Vera and Martín-Algarra, 1994; Martín-Algarra and Sánchez-Navas, 1995, 2000; Jiménez-Espinosa et al., 1997; Nieto, 1997; Jiménez-Millán and Nieto, 2008). Most papers characterize the stratigraphical and sedimentological meaning of these deposits, while others describe the mineralogical and geochemical composition. However, a detailed study of the microbial assemblages has not been put forth to date.

The objective of the present paper is to characterize the components of the benthic microbial communities (BMC) from thin section and electron microscopy analyses. The paleoecological study of the microbial assemblage composition allows us to interpret the light availability and the paleobathymetry in which the Fe-Mn microbialite developed. In fact, the most important aim of this research is to interpret the role of the activity of these microorganisms in the authigenic precipitation of Fe-Mn oxyhydroxides and the growth of the macro-oncoids.

GEOLOGICAL SETTING

The studied outcrops are located in the External Subbetic Zone (Southeastern Spain, Fig. 1), in turn be-

longing to the Betic External Zones. At the Middle-Late Jurassic boundary, the Subbetic was the pelagic domain of the Southern Iberian Continental Palaeomargin (Vera, 2001). This domain comprised two strings of pelagic swells with low subsidence (External and Internal Subbetic, respectively), located to the North and South of a more subsident central trough named the Median Subbetic.

In the External Subbetic (northern pelagic swells), the most characteristic facies of the Middle-Upper Jurassic are the *ammonitico rosso* (Upper Ammonitico Rosso Formation; ARS Fm in Fig. 1D). Complex intra-Bathonian-Oxfordian events, such as changes in relative sea-level, tectonic events, erosional processes and sedimentary reworking (Molina, 1987; Rey, 1993; Nieto, 1997; Vera, 2001; e.g.) are recorded in this formation. The associated first order unconformities involve a stratigraphic hiatus ranging between Upper Bathonian (minimum) and Middle Bathonian-Lower Kimmeridgian (maximum) (Ruiz-Ortiz pers. comm., 1997). Erosive surfaces, neptunian dykes, hardgrounds, Fe-Mn crusts and condensed levels are recognized in these materials.

The rocks studied in this research belong to the Lúgar-Corque and Reclot Tectonic Units (Figs. 1 and 2), pertaining to the External Subbetic of the Murcia and Alicante provinces (Nieto, 1997). The simplified stratigraphic sections of these tectonic units are shown in Figure 1D. The Upper Ammonitico Rosso Fm. in both tectonic units exhibits an average thickness of 60 m. Lower and upper members can be distinguished in this formation (ARS Fm in Fig. 1D).

The lower member of the Upper Ammonitico Rosso Fm. is made up of well compacted red nodular limestones. The microfacies of these rocks are wackestone to packstone of "filaments" attributed to *Bositra buchi*; other allochems are peloids, sponge spicules, crinoids, radiolaria, foraminifera (*Protopeneroplis striata*, *Globuligerina* sp.) and unclassified bioclasts. An incipient hardground appears at the top of this member, where some trace fossils, attributed to *Thalassinoides*, are observed (Fig. 2).

Over previous incipient hardground, there lies a very compacted level of up to 70 cm thickness that laterally disappears (Fig. 2). It is a calcarenite with a packstone of "filaments" (*Bositra buchi*) featuring peloids, crinoids, *Globuligerina* and unclassified bioclasts (see Lugar section 62-1 in Fig. 2). Subspherical Fe-Mn macro-oncoids are embedded in the calcarenite level. Another hardground is developed at top of the calcarenite. The two hardgrounds overlap each other when the calcarenite level is not present, in which case a Fe-Mn oxide crust, 2-3 cm thick, is observed (Fig. 2). Large ammonite moulds (*Procerites* and *Wagericeras*) and some trace fossils (*Thalassinoides*) are seen in this hardground.
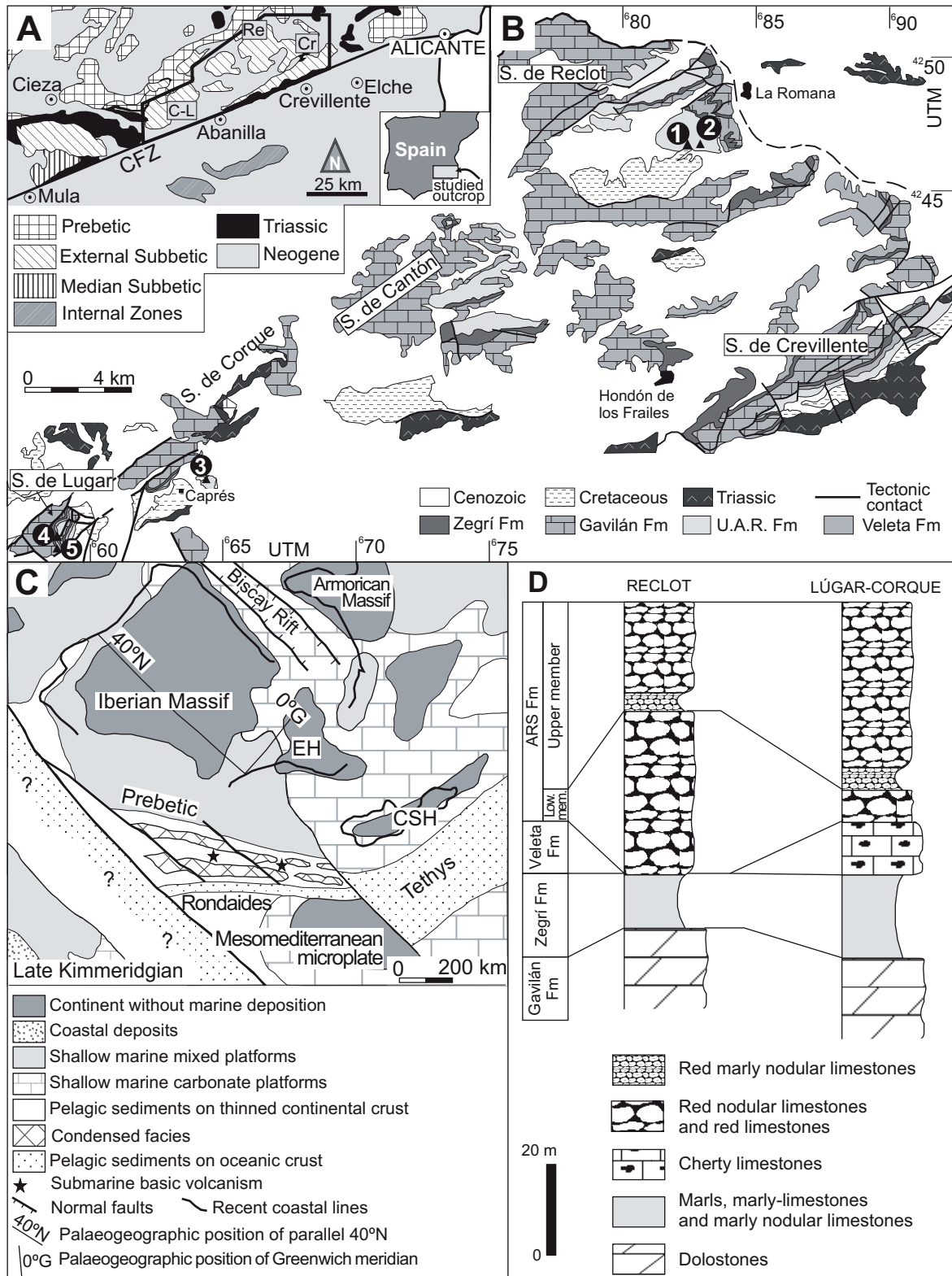
FIGURE 1 | **A) Geographical and geological location of the studied area. CFZ: Crevillente Fault Zone; Re: Sierra de Reclot; Cr: Sierra de Crevillente; C-L: Sierras de Corque y Lúgar. B) Geological map of the studied area with position of the stratigraphic sections of figure 2. 1: Rambla Honda-1; 2: Rambla Honda-2; 3: Caprés; 4: Section 62-1; 5: Section 62-2. C) Palaeogeographic reconstruction of the Southern Iberian Continental Paleomargin for the Late Kimmeridgian after Vera (2001). D) Synthetic Jurassic stratigraphic sections for the Reclot and Corque-Lúgar Tectono-stratigraphic Units.**
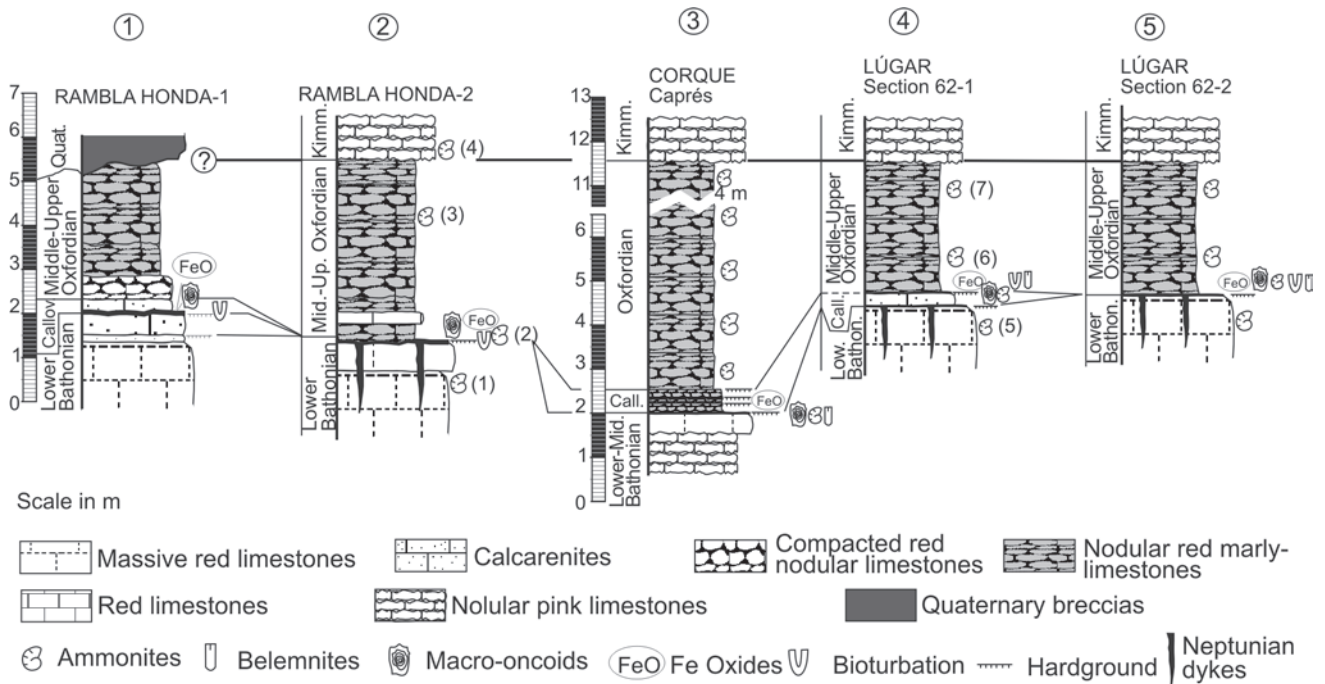
FIGURE 2 | **Detailed stratigraphic sections for the intra-Bathonian-Oxfordian materials (See geologic and geographic position in the map of figure 1B). Specifications of the number of the ammonoids: 1.** *Nannolytoceras tripartitum*; **2.** *Holcophylloceras* sp., *Dichotomoceras bifurcatus*, *Dichotomosphinctes* sp.; **3.** *Epipeltoceras* sp., *Sowerbyceras tortisulcatum*; **4.** *Mesosimoceras* sp.; **5.** *Morphoceras patescens*; **6.** *Dichotomosphinctes* sp., *Orthosphinctes* sp., *Discosphinctes* sp. *Epipeltoceras* sp.; **7.** *Orthosphinctes* sp.

The upper member of the Upper Ammonitico Rosso Fm. is made up of marly nodular red limestones and red nodular limestones with *Globuligerina* and *Saccoccoma* mudstone - wackestone microfacies, respectively.

Nieto (1997) studied the stratigraphy of this formation in the Lúgar-Corque and Reclot tectonic units, and showed the base heterochrony (Fig. 3): while in the Lúgar-Corque Unit this surface was dated as Late Bajocian (*Strenoceras niortense* biozone), in the Reclot Unit it was dated as Early Bajocian (*Hyperlioceras discites* biozone). The top of the lower member is also heterochronic (Fig. 3), being Early Bathonian (*Zigzagiceras zigzag* biozone) in age in the Reclot, and Early-Middle Bathonian in the Lúgar-Corque Unit. The base of the upper member has a Middle Oxfordian age (*Dichotomoceras bifurcatus* biozone) in the Reclot Unit while in the Lúgar-Corque Unit this surface has an age comprised between Early Oxfordian and Early Kimmeridgian. The top of the Upper Ammonitico Rosso Fm. has been dated as Early Berriasian (*Berriasella jacobi* biozone) in the Reclot Unit and Late Tithonian-earliest Berriasian in the Lúgar-Corque Unit.

The hiatus between the two members of this formation (Fig. 3) has a minimum time span from the *Cadomites bremeri* biozone to the *Quenstedtoceras*

lamberti biozone, both included; according to the chronostratigraphy indicated in Figure 3 (after Ogg, 2004), this time interval is equivalent to 4.8 Ma. The maximum time included in this hiatus is from the *Procerites aurigerus* biozone to *Crussoliceras divisum* biozone that is equivalent to 14.2 Ma.

MATERIALS AND METHODS

Five outcrops, evidencing the Bathonian-Oxfordian unconformity and showing Fe-Mn crusts and macro-oncoids, were selected from three localities (Figs. 1 and 2): Rambla-Honda (Reclot Unit), Corque and Lúgar (Lúgar-Corque Unit). Petrographic microscopy was used to determine the textures of the rock and the Fe-Mn macro-oncoids and crusts from 40 thin sections. Analysis of the Fe-Mn macro-oncoids (characterization of the cortical structure, total diameter, nucleus size, and coat thickness) was obtained from 90 Fe-Mn macro-oncoids from the hardgrounds of Rambla-Honda sections and 65 Fe-Mn macro-oncoids from the outcropping hardgrounds of the Lúgar sections (Fig. 2).

The mineral composition of the Fe-Mn crusts and the Fe-Mn coated grains was determined by X-ray diffractometry
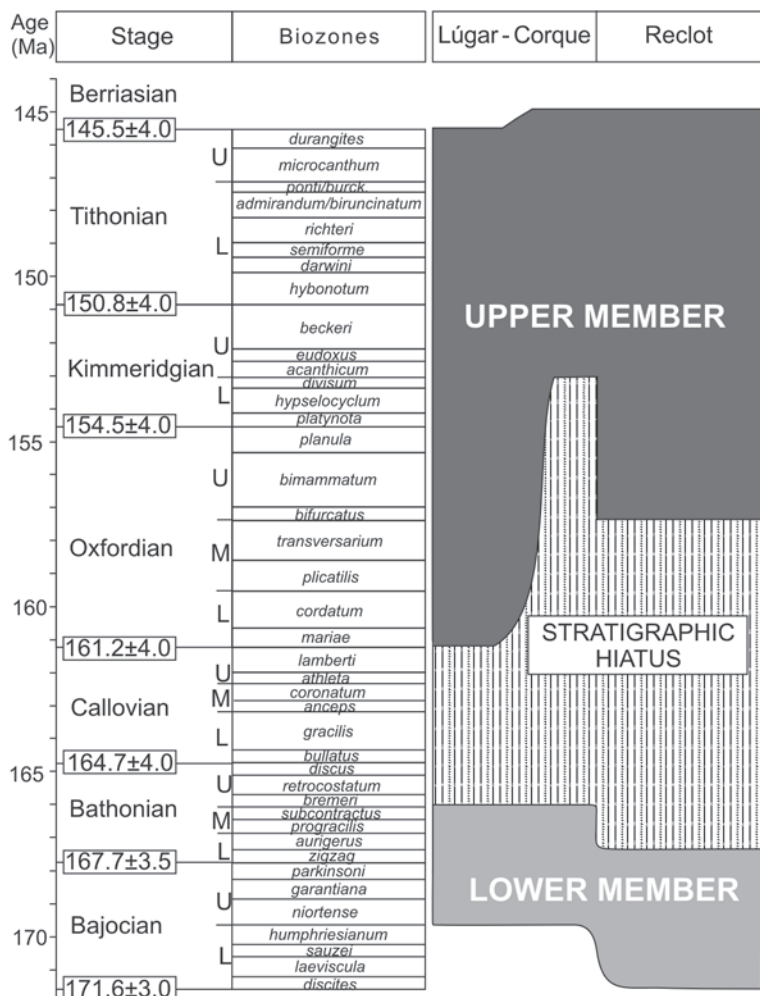
FIGURE 3 | **Chronostratigraphic diagram of the Upper Ammonitico Rosso Formation. The chronometry is according to Ogg (2004).**

(XRD), scanning electron microscopy (SEM), using back-scattered electron (BSE) imaging and energy-dispersive X-ray (EDX) analysis (see Jiménez-Millán and Nieto, 2008 for a detailed description of these methods).

In addition, Fe-Mn coated grains were split and the broken pieces from the innesr laminae of the coating were mounted, coated with carbon and gold, and examined directly under the SEM using secondary electrons to study their internal ultrastructure and crystal morphology using a Zeiss DSM 950 SEM at the University of Granada's Scientific Instruments Centre (CIC) and a SCI Quanta 400 at the Centro Andaluz de Medio Ambiente (CEAMA), as well as a Jeol 5800 electron microscope at the Research Technical Services (STI) of the Universidad de Jaén (Spain).

Thin sections were also stained using the nuclear counterstains DAPI (4',6-diamidino-2-phenylindole) and PI (Propidium Iodide), which are fluorescent stains that bind strongly to DNA. This allowed us to rule out recent microbes. Analysis of the staining techniques was carried out with a Nikon E-800 fluorescence microscope and a Hamamatsu CCD camera at the Department of Experimental Biology (Universidad de Jaén). A Nikon DAPI-FITC filter set was designed for optimal detection of DAPI and the AnalySIS 2.11.005 program was used to process the images.

MORPHOLOGY AND STRUCTURE OF THE Fe-Mn CRUSTS AND MACRO-ONCOIDS

The Fe-Mn crusts and macro-oncoids extend over the hardground surface. In general, they are characterized by brown and reddish colours. The Fe-Mn crusts are 4-5 mm mean thickness and develop directly over the hardground. The Fe-Mn macro-oncoids are macroscopic components of calcarenitic levels overlying the hardground and crust. A Fe-Mn oxyhydroxide coating envelops the nucleus (Figs. 4 and 5). These coated grains range from 10 to 108 mm in diameter, and they are 43 mm mean-size. The coat is usually less than 30 mm thick. However, in some macro-

oncoids this coating is much thicker (see Figs. 4B and 5A). The outer shape is irregular in outline, and subrounded, spheroidal to elongated (Figs 4A, B). The type of nucleus has a strong influence on the outer shape of these macro-oncoids. The nucleus is made up of pebbles (Fig. 4C) or bioclasts (Fig. 4D); ammonoid shells and moulds are typical cores of the macro-oncoids studied.

The crusts have a poorly developed laminated structure, while the macro-oncoids have a very well developed laminated structure. In the macro-oncoids from the Reclot section, two different types of laminated bands may be differentiated on the basis of colour of the coating: the first inner band is pale brown, and the second outer band is reddish brown in colour (Fig. 4B). The bands are almost concentric and symmetrically related to the nucleus.

The bands consist of partially overlapping laminae, usually alternating between light and dark laminae (Figs. 5A, B). The banded coatings consist of laminae with planar (Fig. 5B) and arborescent or club-shaped morphologies (Figs. 5C-E). Arborescent morphologies develop from an initial planar lamination; among them, some small spokes are filled by pelagic sediment, mainly valves of filaments (possibly *Bositra buchi*, Figs. 5D, E). The surface of the macro-oncoids is frequently mammillated, expressing the internal texture with arborescent morphologies (Fig. 5F). Some arborescent morphologies evolve to dendrolitic ones (Figs. 5D, E) with a dominant growth axis normal to the lamination (finger-like columns).

In general, the laminae range from 20 to 140 μm thick. Petrographic microscopy shows laminae pairs to consist of a thicker clear lamina (130 μm mean thickness) and a thinner dark lamina (30 μm mean thickness). These laminae pairs are grouped in alternating thicker clear intervals (0.7 mm) and thinner dark intervals (0.25 mm). These groups of laminae constitute a rhythmic pattern in the Fe-Mn macro-oncoids and crusts. Moreover, scarce carbonate laminae with pelagic sediment are intercalated
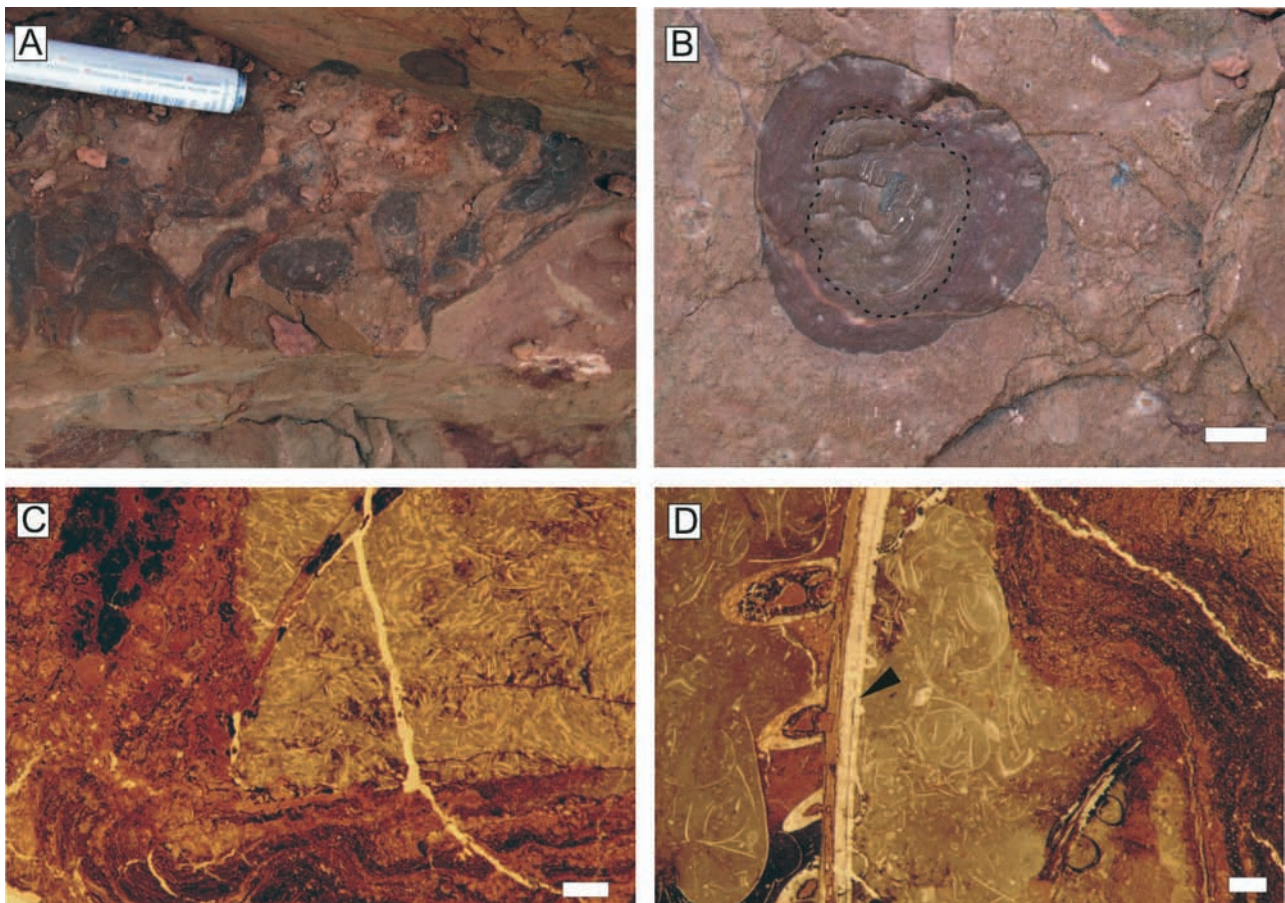

FIGURE 4 | **A) Hardground surface with Fe-Mn banded crusts and macro-oncoids (Rambla Honda-1 section). B) Detail of a Fe-Mn macro-oncoid with two phases of development (Rambla Honda-2 section, scale bar 1 cm). C) Core of Fe-Mn macro-oncoid composed by a pebble constituted by a wackestone-packstone of filaments, scale-bar 1 mm (Lúgar section 62-1, scale bar 1 mm). D) Core of Fe-Mn macro-oncoids constituted by a mould of ammonoid with wackestone of filaments (Rambla Honda-1 section, scale bar 1 mm). Note that inner walls of the ammonoid shell are preserved (arrow).**

within laminae dominated by Fe-Mn oxyhydroxides (Fig. 5B). The different scales of the superimposed rhythms in the growth of the macro-oncoids clearly show a well-developed hierarchy.

According to the morphology of the laminae, the rhythms can be classified as planar lamina-bearing rhythms and as arborescent lamina-bearing rhythms. The planar lamina-bearing rhythms feature a dominant thick and clear laminated interval and a reduced reddish brown laminated interval. The planar lamina-bearing rhythms are 920 μm mean-thick and comprise minor cycles 350 μm thick. The arborescent lamina-bearing rhythms are constituted by a thick clear phase with small finger-like columns made up
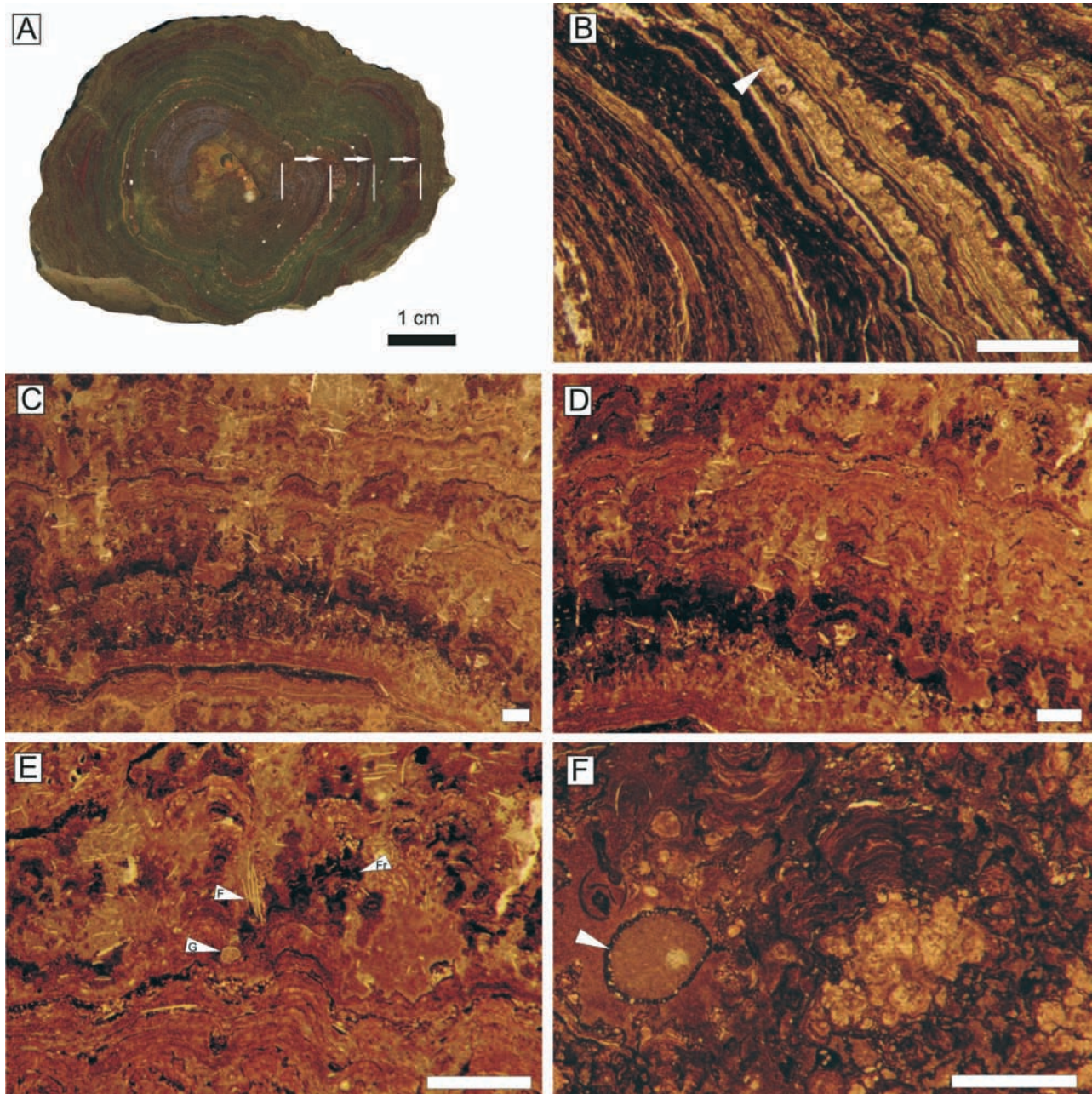

FIGURE 5 | **A) Polished section of a macro-oncoid from Lúgar section 62-1 showing a clear rhythmic growth. B) Detail of lamina pairs grouped in alternating thicker clear intervals and thinner dark intervals, with calcitic laminae intercalations (arrow). C and D) Laminated textures with alternation between planar and arborescent morphologies revealing rhythmic growth. E) Pockets of sediment between the finger-like columns with G: *Globuligerina* and F: bivalve filaments. Dendrolitic microstructures are assigned to Fr: *Frutexites*. F) Club-shaped lamination and *Thurammina* (arrow). Scale bar 1 mm.**

of convex laminae, which coalesce at the top in a thinner and darker interval with planar to wavy lamination that smoothes out underlying irregularities. The dendrolitic structures are dark and can be found included among the pelagic sediment (Fig. 5E). The bands with arborescent lamina-bearing rhythms are limited by bands with planar lamination. The thickness of the arborescent lamina-bearing rhythms is 2.43 mm, greater than that of planar lamina-bearing rhythms (0.92 mm).

Similarities have been found between these rhythms and those described by Han et al. (2003) in Pacific ferromanganese nodules, and by Martín-Algarra and Vera (1994) in phosphate stromatolites from the Penibetic (Betic Cordillera, Spain).

CHEMICAL AND MINERALOGICAL COMPOSITION

The mineral assemblage of these crusts and oncoids comprises goethite, calcite, lithiophorite and cryptomelane. In general, the Fe_2O_3 proportion in crust and macro-oncoids (mean value = 34.5%) is between 3 and 9 times the European Shale Composite (ESC) content. However, the Mn content is always <20% (mean value = 9.6%). The Fe/Mn ratios are usually <30%. A strong enrichment in Co, Ni, As and Sb is observed. The content in REE shows values similar to those of recent Fe-Mn crusts formed by hydrogeneous processes (Fleet, 1983; Fromm et al., 2005; Jiménez-Millán and Nieto, 2008). Noteworthy is the important positive anomaly in Ce. The Ce/Ce* ratio (after Baar et al., 1988) is almost 3 (see discontinuity D3 in Jiménez-Millán and Nieto, 2008). More extended information about the mineralogical and chemical composition of these Fe-Mn macro-oncoids and crusts, as well as the analytical method used to obtain the several results, was previously published by Jiménez-Millán and Nieto (2008).

MICROBIOTA

Benthic microbial communities (BMC)

Below, we describe some microstructures with potentially microbial origin, and propose what kind of potential microorganism they may represent.

Under petrographic microscopy, the lamination can be attributed to the activity of BMC. Planar and arborescent laminated textures have been traditionally interpreted as microbialites, mainly in the case of carbonates (Burne and Moore, 1987; Dromart et al., 1994; Reolid et al., 2005; Nose et al., 2006; Perri and Tucker, 2007; among others). Detailed analysis of the planar laminae reveals frequent microspheres with spherical to ovoid shapes and an average diameter of 40 μm. They probably correspond to microbes. Filamentous microstructures parallel to lamination are observed in relation to these microspheres, with an average width of 8 μm (Fig. 6A). In some cases the filamentous microstructures, which constitute fibrillar meshworks, contain small spheres forming a trichomal arrangement (Fig. 6B). Taxonomical assessment of the microbiota forming microspheres and filamentous microstructures is difficult, though the morphology resembles filamentous cyanobacterium *Microcoleus* (see Figure 6 in Gerdes et al., 2000). The cyanobacteria are identified in some of the planar rhythms, forming condensed fibrillar meshworks.

The arborescent to dendrolitic microstructures are assigned to *Frutexites* shrubs (Fig. 5E). This structure has been typically described in relation to crusts of Fe-Mn oxyhydroxides (Wallace et al., 1991; Böhm and Brachert, 1993; Nicoll and Playford, 1993; Mamet and Préat, 2006; Cavalazzi et al., 2007). However, it is not clear what type of microbe is involved in *Frutexites*. It has frequently been assigned a cyanobacterial origin (Walter and Awramik, 1979; Riding, 1991; Nicoll and Playford, 1993) and attributed to chemosynthetic bacteria (Cavalazzi et al., 2007).

Filamentous cyanobacteria and *Frutexites* could not be identified under SEM analyses, most likely hidden by the diagenesis. Differences between observations with thin section and with SEM may be related to the intense iron mineralization of the microbial structures. Dahanayake and Krumbein (1986) indicate that the filaments can become undetectable due to iron encrustation.

The negative results of the thin sections stained with DNA stains (DAPI and PI) allow us to rule out the presence of recent microbes from the laminated inner bands of the Fe-Mn crusts and macro-oncoids. Some broken pieces from the inner laminae of these Fe-Mn macro-oncoids were analysed by SEM.

The SEM analyses of the Fe-Mn macro-oncoid laminae allow us to characterize three types of microbial structures made up by calcite with Fe-Mn oxyhydroxide coatings or exclusively of Fe-Mn oxyhydroxides (Figs. 7 and 8):

a) The most abundant microbial structure appears as straight to slightly curved cylindrical filaments ranging from 2-3.5 μm in diameter and more than 0.7 mm in length (Fig. 7). Occasionally these filaments are seen to branch without an apparent pattern. These filaments may be assigned to multicellular hyphae forming a fungal mycelium preserved by Fe-Mn oxyhydroxides.

b) Other less common components are aggregates of coccoid-shaped forms with a maximum size of
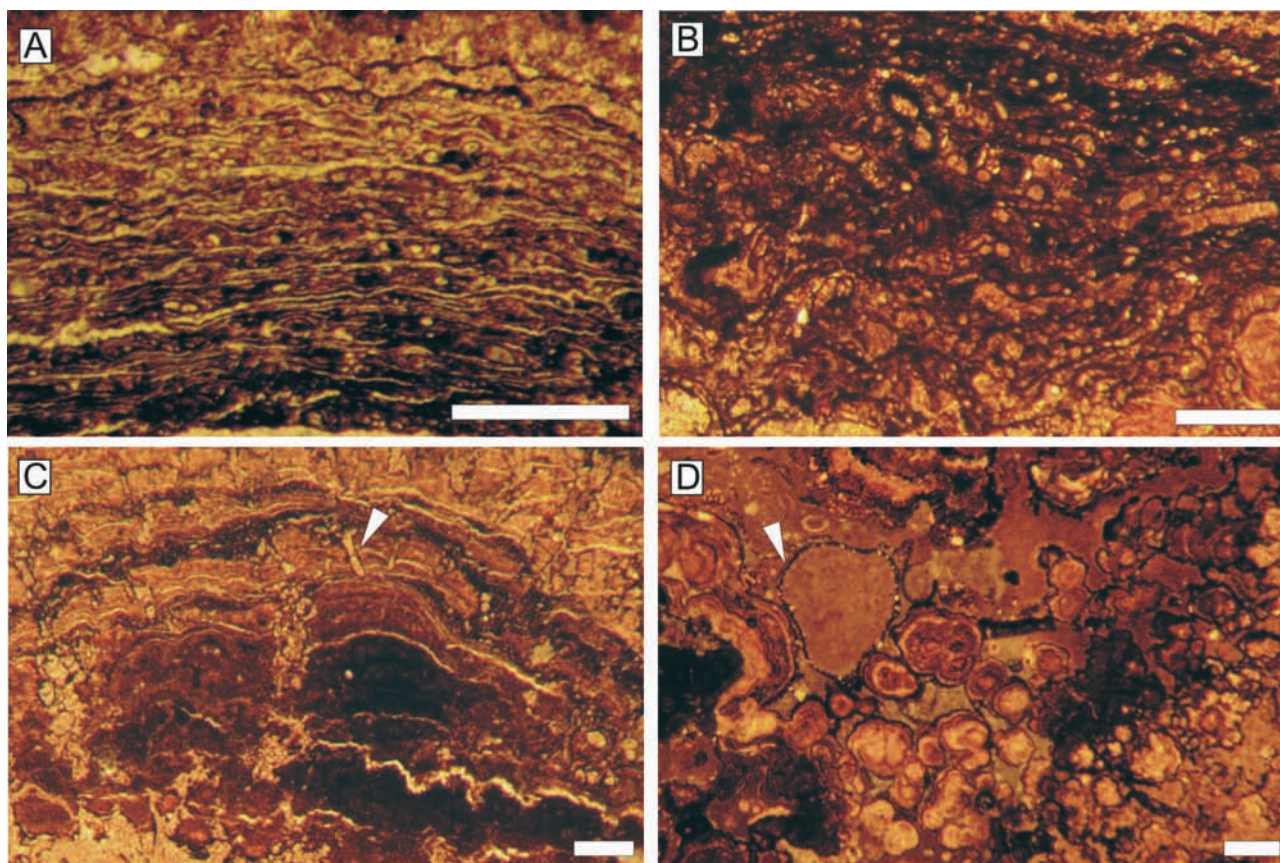
FIGURE 6 | **A) Detail of the planar laminated texture with fibrillar meshwork resembling to a possible *Microcoleus* mat, arranged with their long axes parallel to the surface of the core of the macro-oncoid. B) Filamentous microstructures constituted by microspheres forming trichomal arrangements. C) Arborescent laminae with microboring (arrow) in Fe-Mn macro-oncoids, which is evidence of synsedimentary consolidation of the microbialite. D) Shell of *Thurammina* (arrow) adapted to spaces allowed by the club-shaped morphologies. Scale bar 0.5 mm.**

~2 µm (Fig. 8A, B). These forms are very probably related to cyanobacteria, yet other possible types of eubacteria related to Fe and Mn oxidation cannot be ruled out.

c) The least frequent microbial structure is a dense network consisting of thin, straight main filaments close to the substrate surface with frequent dichotomous branching, and slightly thinner filaments that exhibit antler-like terminal swellings (Fig. 8C). The cylindrical to flattened filaments are between 5-10 µm in diameter. Second order filaments emerge mostly at right angles and bifurcate dichotomously (5-6.5 µm in diameter). The reticulate network resembles that of some green algae (chlorophycea). Thus, tube enlargements are interpreted to be sporangia. Very similar morphologies were described by Glaub (1994) in the analysis of casts of the ichnotaxon *Reticulina elegans*, whose recent equivalents are produced by the green alga *Ostreobium quekettii* (Budd and Perkins, 1980; Vogel et al., 1995; Glaub and Bundschuh, 1997). However, a fungal origin is not ruled out as a possibility.

Foraminifera

Some agglutinated foraminifera are registered in the Fe-Mn crusts and macro-oncoids, including *Thurammina*, *Placopsilina* and *Tolypammina*. They are formed by quartz grains of silt size, bound by calcareous cement (Figs. 5F and 6D). The plano-convex irregular shell of these foraminifera is generally attributed to a sessile epifaunal mode of life and passive herbivore or suspension-feeder strategy (Reolid et al., 2008). These forms cannot graze, and so must feed on organisms they harvest with their pseudopodia near the attachment site (Jones and Charnock, 1985). According to Gooday and Haynes (1983) and Lipps (1983) these passive herbivores presumably feed on bacteria. In Oxfordian deposits of the neighbouring Prebetic (Betic Cordillera), *Placopsilina* and *Tolypammina* are typical encrusting taxa occurring in association with microbial fabrics and encrustations (Reolid et al., 2005; Reolid and Gaillard, 2007). With respect to other organisms, in some cases the surface of the laminae present microborings and marks of grazers (Figs. 6C and 9). Other organisms are recorded within the macro-oncoids, such as filaments and planktic foraminifera.

DISCUSSION

Origin of Fe-Mn macro-oncoids

Previous work concerning the origin of these Fe-Mn macro-oncoids and associated crust may be considered under two main interpretations: a) organic origin, and b) diagenetic precipitation. Martín-Algarra and Sánchez-Navas (2000) interpret that the Fe-Mn and phosphatic macro-oncoids and crusts associated to the stratigraphic discontinuity surfaces as synsedimentary microbial accretions. Other authors (Sandoval and Checa, 2002; among others) point to a diagenetic origin. The latter interpretation implies that the macro-oncoids most likely formed within the shallow sediment due to concentration and diffusion of Fe-Mn mineral-containing fluids through dissolution surfaces during early diagenetic stages. However, the features described in the present research suggest that the Fe-Mn macro-oncoids were an accretionary synsedimentary deposit and not a diagenetic precipitate.

The following features point to synsedimentary origin:

a) the finely laminated structure;

b) the intercalation of non-ferruginized carbonate grains included in the Fe-Mn oxyhydroxide laminae;

c) the existence of discrete sediment laminae between Fe-Mn oxyhydroxide laminae and occurrence of pelagic sediment between the columns in the arborescent rhythms;

d) the existence of encrusting foraminifera inside Fe-Mn macro-oncoids;

e) an abundance of filamentous microbes seen through petrographic microscopy and SEM analyses.

We interpret the precipitation of Fe-Mn with regard to the chemoorganotrophic behaviour of the BMC, since iron oxides can form as a result of the direct metabolic activity of microbes or as a result of passive sorption and nucleation reactions (Fortin and Langley, 2005). According to Dahanayake and Krumbein (1986), iron-
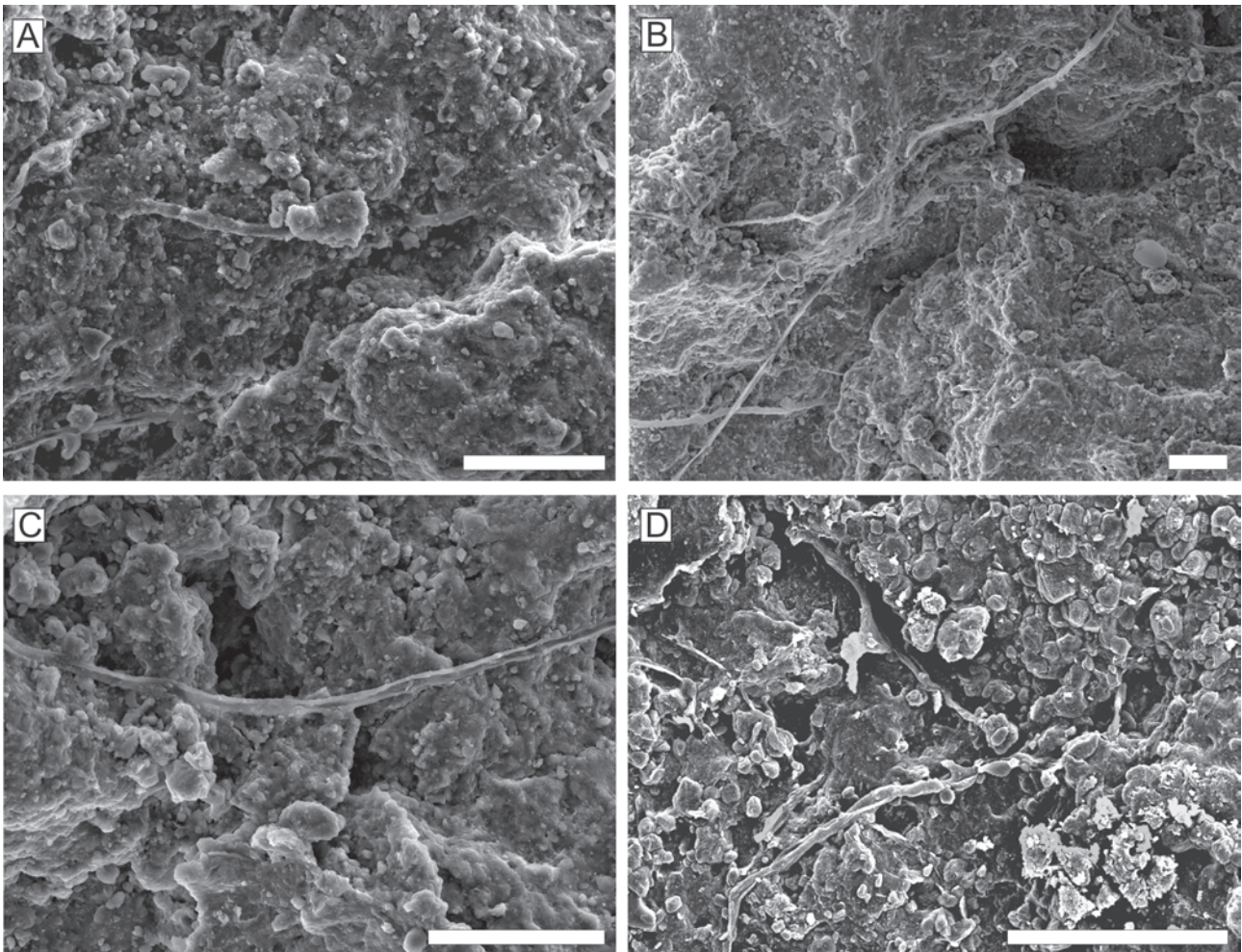

FIGURE 7 | **SEM images of microbial structures recorded within Fe-Mn macro-oncoids. Straight to slightly curved cylindrical filaments seen to branch without an apparent pattern, probably corresponding to multicellular hyphae of a fungal mat. Scale bar 10 μm., hyphae of a fungal mat. Scale bar 50 μm.**

secreting microbial mats are predominantly fungal in origin. However, many authors have interpreted different types of eubacteria inducing Fe and Mn mineralizations (see Frankel and Bazylinski, 2003). Fe- and Mn-oxidizing bacteria, both mesophilic autotrophic (such as

Acidithiobacillus ferrooxidans and *Leptospirillum* sp.) and chemoheterotrophic bacteria (such as *Sphaerotilus*, *Leptothrix* and *Siderocapsa*) are known to induce the precipitation of Fe-Mn oxyhydroxides under acidic and neutral conditions where Fe^{3+} and Mn^{4+} are soluble (Southam, 2000; Frankel and Bazylinski, 2003; Hanert, 2006). The presence of *Frutexites* is commonly associated to Fe-Mn crusts and they are interpreted as chemosynthetic and cryptobiontic microorganisms (Böhm and Brachert, 1993; Chafetz et al., 1998; Cavalazzi et al., 2007).

Interesting enough is the interpretation of the Mn content of the macro-oncoids. The origin of Mn-oxides may be related to inorganic and organic processes. However, inorganic precipitation mechanisms are considered to be insufficient for accretion of significant amounts of MnO in natural environments (Ostwald, 1990). It is well recognized that, in recent environments, efficient precipitation of Mn from natural water depends basically on the presence of Mn-oxidizing microbes (Nealson and Stahl, 1997; Francis and Tebo, 2002; Frankel and Bazylinski, 2003). Some types of eubacteria can induce the precipitation of Mn-oxides 4 to 5 orders of magnitude more readily than by abiotic precipitation (Hasting and Emerson, 1986; Francis and Tebo, 2002). Monty (1973), Greenslate (1974), Ehrlich (1975) and Krumbein (1983) have suggested the influence of microbes in the reactions of Mn in deep-sea manganese nodules, whereas Schaefer et al. (2001) propose Mn precipitation that is biogenically controlled in shallow water oncoids.

Specific Fe and Mn enrichment by microbes highlights the importance of microbial biocoenoses as a catalyzer, also serving as a specific trap of these elements (Krumbein and Jens, 1981; Nealson, 1983; Dahanayake and Krumbein, 1986; Frankel and Bazylinski, 2003). Iron and manganese are concentrated by extracellular traps in the microbial wall. In the studied macro-oncoids, the former existence of mucilaginous substances around the microbes and their role as an iron chelating compound (siderophore) secreted by microorganisms in the precipitation of authigenic minerals can be reasonably inferred by the presence of branching filamentous microstructures that evoke hyphae. According to Lewin (1984), siderophores produced by microbes could trap and transfer Fe^{3+} into the cell interior. Authigenesis occurred by means of the Fe and Mn previously enriched by the siderophores as amorphous precursor phases that can later be precipitated as Fe-Mn oxyhydroxides. Préat et al. (2000) propose very low oxygen concentrations for similar microstromatolithic crusts of the Bajocian from Normandy (France), with conditions of greater Fe^{2+} stability. Iron could thus serve as an electron donor in the metabolism of iron-oxidizing microbes. Alternative chemical processes have been expounded by other authors (for more information see Frankel and Bazylinski, 2003; Fortin and Langley,
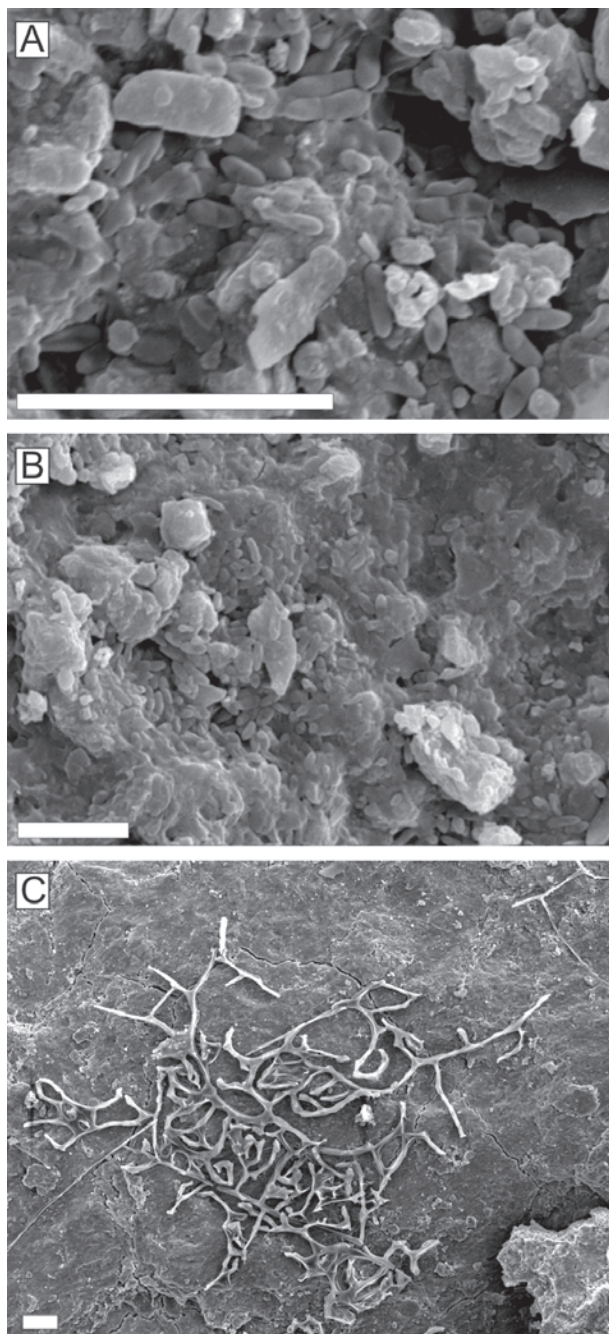

FIGURE 8 | **SEM images of microbial structures recorded inside Fe-Mn macro-oncoids. A-B) Aggregates of coccoid-shaped microbes from Fe-Mn macro-oncoids. C) Dense network composed by straight flattened filaments with many dichotomous branching filaments potentially interpreted as chlorophycea but fungal origin is not ruled out. Scale bar 10 µm.**
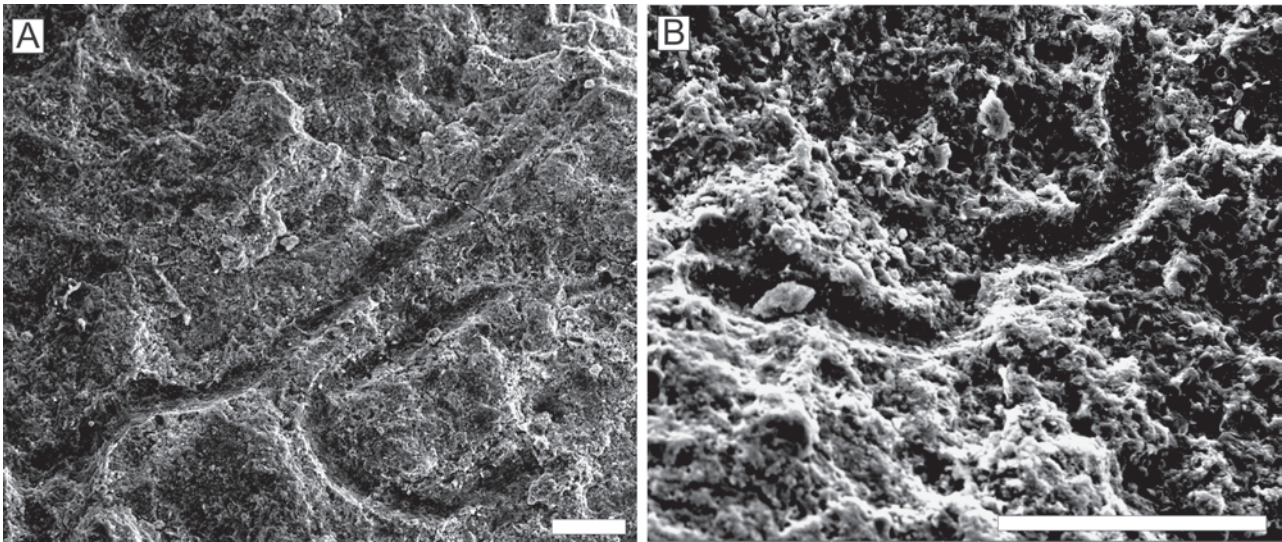
FIGURE 9 | **SEM images of the surface of planar lamina with marks of grazer organisms recorded inside Fe-Mn macro-oncoids, scale bar 100 μm.**

2005); yet in our opinion, any interpretation is merely an approach to the mechanisms of Fe-Mn deposition in the absence of a detailed taxonomic classification of the microbes. At any rate, the common presence of microbes in Fe-Mn crusts in the geological record must be taken into account when explaining their genesis (Dahanayake and Krumbein, 1986; Martín-Algarra and Sánchez-Navas, 2000; Préat et al., 2000; Schaefer et al., 2001; Mamet and Préat, 2003; Schelble et al., 2004; Cavalazzi et al., 2007; among others).

The Ce enrichment, in turn, could be adequately explained by oxidative scavenging of Ce^{4+} from normal seawater by Fe-Mn oxyhydroxides formed in close genesis to microbes (Martín-Algarra and Sánchez-Navas, 1995). The pelagic swells of the External Subbetic were favourable places for microbially mediated authigenesis due to: a) the sediment-starved conditions, and b) the injection in seawater of Fe, Mn, trace elements and REE related to the contemporary volcanic processes recorded in the Median Subbetic (Puga et al., 1989; Vera et al., 1997).

Not all the microbes identified in the Fe-Mn macro-oncoids would be related with the precipitation of Fe-Mn oxyhydroxides (chemosynthetic organisms), because some laminae have substantial $CaCO_3$ contents. The record of cyanobacteria and potentially chlorophycea confirm the presence of photosynthetic organisms. Furthermore, we must take into account the possibility of Fe oxyhydroxide formation by Fe^{2+} oxidizing photosynthetic bacteria (Kappler and Newman, 2004; Fortin and Langley, 2005).

The existence of other organisms in the Fe-Mn crusts and macro-oncoids, such as encrusting foraminifera,

has palaeoecological implications. The association of encrusting foraminifera with microbial films of cyanobacteria and fungi closely resembles commensalism, where the biofilms served as a food source for the encrusting foraminifera, while the cyanobacteria and fungi took advantage of the nutrient-rich foraminiferal excretions. Gradzinski et al. (2004) suggested this kind of relationship for the occurrence of nubeculariids and *Tolypammina* in microbial-foraminiferal oncoids in the Toarcian of the Tatra Mountains (Poland). Veillette et al. (2007) studied the sessile foraminifera from modern manganese nodules and surmised that food particles could be obtained either from suspension or from microbial films present on the nodule surface.

Rhythms and sedimentation rate

The laminated crusts and oncoids are constituted by microbial laminae with planar and arborescent morphologies. In this way, the macro-oncoids may be considered microbialites sensu Burne and Moore (1987). In general, the development of microbialites calls for a low rate of sedimentation because their growth is very slow (e.g. Leinfelder et al., 1993; Dromart et al., 1994; Martín-Algarra and Vera, 1994; Reolid et al., 2005). They are also very sensitive to any unfavourable influx of fine, clay-rich sediment. Thus, microbialites are good indicators of the rate of siliciclastic influx (Leinfelder et al., 1994). Other studies in Fe-Mn crusts support low sedimentation rates both in ancient (0.5-1 mm Myr^{-1} according to Martín-Algarra and Sánchez-Navas, 2000) and modern examples (7-18 mm Myr^{-1} reported by Allouc et al., 1999; 4.2-4.8 mm Myr^{-1} by Han et al., 2003). However, fast growth in Fe-Mn nodules has

been also described in modern examples (Hlawatsch et al., 2002; González et al., 2007).

Alternation between laminae with planar and arborescent morphologies may respond to minor changes in sedimentation rate. In the case of calcareous microbialites, the columnar morphologies in the microbial encrustations reflect slight increases in the sedimentation rate (cf. Dromart et al., 1994). That means relatively higher values of sedimentation rate in arborescent rhythms than in planar rhythms. Another possibility to be taken into account when interpreting the rhythmic growth is the type of microbes forming the planar laminae (cyanobacteria) and dendrolitic structures (*Frutexites*), which may reflect changes in environmental features (sedimentation rate or oxygenation degree). However, such observations pertain only to thin section analysis as these microstructures are not identifiable under SEM analyses.

Interruptions in the oncoid growth and early lithification are evidenced through colonization by encrusting foraminifera and unidentified microborers (Fig. 6C).

Palaeobathymetry

Rey (1993) and Nieto (1997) suggested a maximum of 200 m depth for the genesis of crusts and oncoids, according to the record of hummocky cross stratification

in some levels of the lower member of the Upper Ammonitico Rosso Fm. Préat et al. (2000) studied the Oolithe Ferrugineuse de Bayeux Fm (Bajocian of Normandy, France) and showed that the sedimentation of these rocks took place below the photic zone and below or near the storm wave base, at a depth of around 100 m. Meanwhile, Martín-Algarra and Sánchez-Navas (2000) propose an origin in the aphotic zone for these macro-oncoids based on the similarities in morphology and type of encrusting foraminifera between these structures and the recent deep sea nodules, as well as the presence of endostromatolites (s. Burkhalter, 1995). Having studied the microbial assemblages from the ammonitico rosso lithofacies from the Verona area (north Italy), Mamet and Préat (2003) propose a relatively deep environment below the normal wave base level, entailing dysaerobic conditions with weak oxygen gradients that trigger the growth of ferrobacteria and fungi. In the particular case of *Frutexites*, a preference for oxygen deficient environments is described by Böhm and Brachert (1993).

The environment where Fe-Mn crusts and macro-oncoids developed must have been an epioceanic swell (sensu Olóriz, 2000), in view of the pelagic nature of the trapped sediment. Interpretation of palaeobathymetry is complicated because chemosynthetic (fungi) and photosynthetic (cyanobacteria) microbes coexist. Possibly high luminosity was not necessary for the microbial
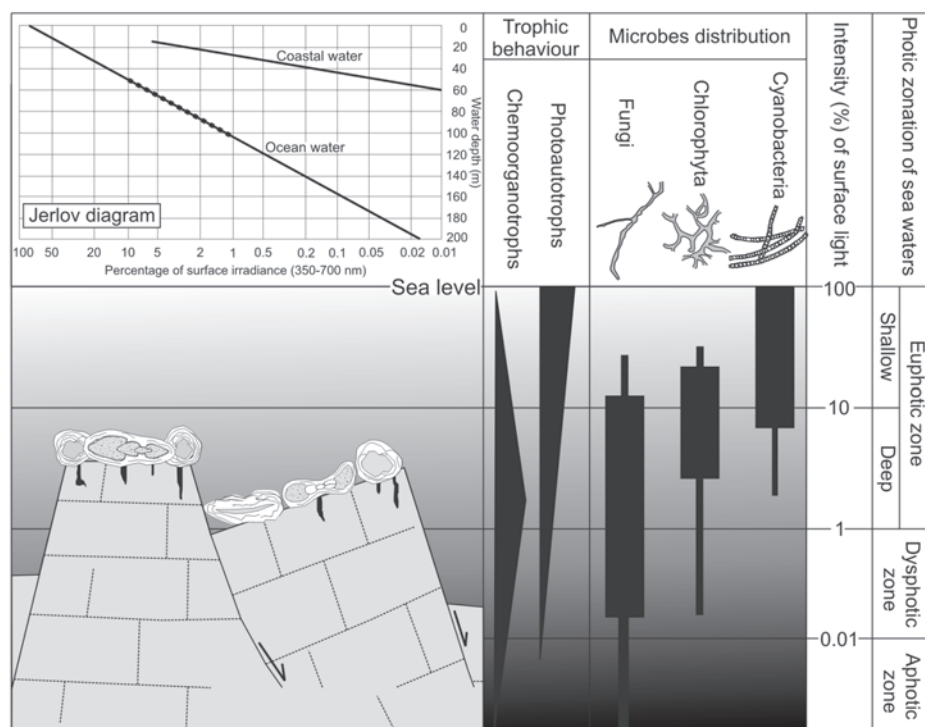

FIGURE 10 | **Relative distribution of the main benthic microbes in Jurassic sea water environment compared with the photic zones proposed by Vogel et al. (1995, 2000) and location of the Fe-Mn macro-oncoids of the External Subbetic. The Jerlov diagram indicates the intensity of surface light related to water depth in recent tropical ocean and coastal waters (modified after Jerlov, 1976).**

community, consisting of abundant fungal mats. The record of *Frutexites* is congruent with scarce light availability. Böhm and Brachert (1993) related the record of *Frutexites* with aphotic stromatolites and evoked a non-phototrophic behaviour in Jurassic examples from Germany. Contrariwise Kazmierczak and Kempe (2006) registered Fe-Mn dendrolitic mineralizations (*Frutexites*-like) in modern shallow stromatolites. A cryptobiontic life style of the organisms originating *Frutexites* has been interpreted by Myrow and Coniglio (1991), Böhm and Brachert (1993) and Cavalazzi et al. (2007).

Thus, we assume deep euphotic zone conditions (sensu Vogel et al., 1995), where scarce light availability favoured the predominance of eucaryotes (fungi and chlorophyta); and cyanobacteria are secondary (Budd and Perkins, 1980; Vogel et al., 1995, 2000; among others) (Fig. 10). According to Vogel et al. (1995, 1999) the deep euphotic zone is correlated to a less illuminated portion of the subtidal zone and extends to a depth where light intensity decreases to approximately 1% of the surface light.

Development in the deep euphotic zone is compatible with a dominating chemosynthetic behaviour of the microbes, which in turn favoured the precipitation of authigenic minerals. If the sea bottom were in the shallow euphotic zone (s. Vogel et al., 1999), autotrophic photosynthetic cyanobacteria would be dominant and authigenic minerals would be absent. The deep euphotic zone in ocean waters would be located between 50 and 100 m in depth (Glaub, 1994; Vogel et al., 1999), depending on the optical water conditions (see Jerlov, 1970).

The record of bacterial and fungal communities related to Fe-Mn crusts in modern examples from submarine caves in the northwestern Mediterranean confirms the growth of such Fe-Mn coatings in reduced light conditions (Allouc and Harmelin, 2001). These crusts are thicker and have a higher Mn/Fe ratio when the confinement of the submarine cave is greater.

Depth determination is a tentative approach since interpretation is based only on fossil microstructures; and while other non-fossilized microbes may be involved in the bioconstruction of the Fe-Mn macro-oncoids, they cannot be specified at present.

CONCLUSIONS

Detailed analysis of the Fe-Mn macro-oncoids and crusts related to the major unconformity of the Middle Bathonian-Middle Oxfordian hiatus in the External Subbetic has improved the knowledge of the microbial assemblages as well as the environmental conditions in

which the authigenic precipitation of Fe-Mn oxyhydroxides occurred. The main conclusions of the present research study can be summarized as follows.

Under petrographic microscopy, two main laminae morphologies are observed: 1) planar and 2) arborescent, vertically evolving to finger-like columns. The laminae are grouped in pairs representing a rhythmic growth in the Fe-Mn macro-oncoids.

Two types of filamentous microstructures are recorded in the Fe-Mn macro-oncoids from thin section analyses: 1) fibrillar meshworks with microspheres (~ 8 µm in diameter) interpreted as cyanobacteria and 2) dendrolitic microstructures assigned to *Frutexites* shrubs (cyanobacteria or chemosynthetic microbes).

Three types of organic components are recorded within Fe-Mn macro-oncoids from SEM images: 1) cylindrical filaments (2-3.5 µm in diameter) with irregular branching interpreted as a fungal mat comprising a disperse web of thread-like filaments (hyphae) that form a mycelium; 2) coccoid-shaped forms (~2 µm) assigned to cyanobacteria; and 3) a dense network containing straight flattened filaments (5-10 µm in diameter) with many dichotomous branching filaments potentially interpreted as chlorophycea.

The palaeobiocoenoses observed in the Fe-Mn macro-oncoids are made up of benthic microbial communities corresponding to dominant fungi and cyanobacteria, and scarce chlorophycea. Secondarily, agglutinated foraminifera (*Thurammina*, *Placopsilina* and *Tolypammina*) were recorded.

The Fe-Mn macro-oncoids and crusts are accretionary synsedimentary microbialites generated in pelagic swells, where sediment-starved conditions were present. The precipitation of Fe-Mn oxyhydroxides is related to the chemoorganotrophic behaviour of the benthic microbial communities. Inorganic precipitation mechanisms are regarded as insufficient for the accumulation of a significant amount of MnO; an efficient precipitation of Fe-Mn oxyhydroxides from natural water depends largely on the microbial catalyzation. The genesis of these macro-oncoids occurred in environments whose palaeobathymetry is near 50 to 100 m in depth, that is, in the deep euphotic zone, where the coexistence of chemosynthetic fungi and photosynthetic cyanobacteria is possible.

REFERENCES

Allouc, J., Harmelin, J.G., 2001. Les dépôts d'enduits manganoferrifères en environnement marin littoral. L'exemple de grottes sous-marines en Méditerrée nord-occidentale. Bulletin de la Société Géologique France, 172, 765-778.

Allouc, J., Hilly, J., Ghanbaja, J., Villemin, G., 1999. Phénomènes biosédimentaires et genèse des croûtes et enduits polymétalliques. L'exemple des dépôts hydrogénétiques de la marge ouest africaine et de la Mediterranée. Geobios, 32, 769-790.

Azeredo, A.C., Wright, V.P., Ramalho, M.M., 2002. The Middle-Late Jurassic forced regression and disconformity in central Portugal: eustatic, tectonic and climatic effects on a carbonate ramp system. Sedimentology, 49, 1339-1370.

Baar, H.J.W., German, C.R., Eldelrfield, H., van Gaans, P., 1988. Rare earth element distribution in anoxic waters of the cariaco trench. Geochimica et Cosmochimica Acta, 52, 1023-1219.

Böhm, F., Brachert, T.C., 1993. Deep-water stromatolites and *Frutexites* Maslov from the Early and Middle Jurassic of S-Germany and Austria. Facies, 28, 145-168.

Bourbon, M., 1980. Évolution d'un secteur de la marge nord-Tethysienne en milieu pélagique: La Zone Briançonnaise près de Briançon entre le début du Malm et l'Éocene inférieur. Doctoral Thesis. Strasbourg (Cedex), Université Louis Pasteur Strasbourg, 580 pp.

Bu, W.R., Shi, X.F., Peng, J.T., Qi, L., 2003. Geochemical characteristics of seamount ferromanganese nodules from mid-Pacific ocean. Chinese Sciences Bulletin, 48, 98-105.

Buatier, M.D., Guillaume, D., Wheat, C.G., Hervé, L., Adatte, T., 2004. Mineralogical characterization and genesis of hydrothermal Mn oxides from the flank of the Juan de Fuca Ridge. American Mineralogists, 89, 1807-1815.

Budd, D.A., Perkins, R.D., 1980. Bathymetric zonation and paleoecological significance of microborings in Puerto Rican shelf and slope sediments. Journal of Sedimentary Petrology, 50, 881-904.

Burkhalter, R.M., 1995. Ooidal ironstones and ferruginous microbialites: Origin and relation to sequence stratigraphy (Aalenian and Bajocian, Swiss Jura mountains). Sedimentology, 42, 57-74.

Burne, R.V., Moore, L.S., 1987. Microbialites: Organosedimentary deposits of benthic microbial communities. Palaios, 2, 241-254.

Cavalazzi, B., Barbieri, R., Ori, G.G., 2007. Chemosynthetic microbialites in the Devonian carbonate mounds of Hamar Laghdad (Anti-Atlas, Morocco). Sedimentary Geology, 200, 73-88.

Chacón, B., Martín-Chivelet, J., 2008. Stratigraphy of Paleocene phosphatic pelagic stromatolites (Prebetic Zone, SE Spain). Facies, 54, 361-376.

Chafetz, H.S., Akdim, B., Julia, R., Reid, A., 1998. Mn- and Fe-rich black travertine shrubs: bacterially (and nanobacterially) induced precipitates. Journal of Sedimentary Research, 68, 404-413.

Dahanayake, K., Krumbein, W.E., 1986. Microbial structures in oolitic iron formations. Mineralium Deposita, 21, 85-94.

Drittenbas, W., 1979. Sedimentologie und Geochemie von Eisen-Mangan führenden Knollen und Krusten im Jura der Trento-Zone (östliche Südalpen, Norditalien). Eclogae Geologicae Helvetiae, 72, 313-345.

Dromart, G., Gaillard, C., Jansa, L.F., 1994. Deep-marine microbial structures in the Upper Jurassic of western Tethys. In: Bertrand-Sarfati, J., Monty, C. (eds.). Phanerozoic Stromatolites II. Dordrecht, Kluwer Academic Publishers, 295-318.

Dromart, G., Garcia, J.-P., Gaumet, F., Picard, S., Rousseau, M., Atrops, F. Lécuyer, C., Shepard, S.M.F., 2003a. Perturbation of the carbon cycle at the Middle/Late Jurassic transition: geological and geochemical evidence. American Journal of Science, 303, 667-707.

Dromart, G., Garcia, J.-P., Picard, S., Atrops, F. Lécuyer, C., Shepard, S.M.F., 2003b. Ice age at the Middle - Late Jurassic transition? Earth and Planetary Science Letters, 213, 205-220.

Ehrlich, H.L., 1975. The formation of ores in the sedimentary environment of the deep sea with microbial participation: The case for ferromanganese concretions. Soil Science, 119, 36-41.

Fleet, A.J., 1983. Hydrotermal and hydrogenous ferromanganese deposits: do they from a continuum? The rare evidence. In: Rona, P.A., Boström, K., Laubier, L., Smith, Jr.,K.L. (eds.). Hydrothernal Processes at Seafloor Spreading Centers. New York, Plenum Press, 535-555.

Fortin, D., Langley, S., 2005. Formation and occurrence of biogenic iron-rich minerals. Earth-Science Reviews, 72, 1-19.

Francis, C.A., Tebo, B.M., 2002. Enzymatic manganese (II) oxidation by metabolically dormant spores of diverse *Bacillus* species. Applied and Environmental Microbiology, 68, 874-880.

Frankel, R.B., Bazylinski, D.A., 2003. Biologically induced mineralization by bacteria. Reviews in Mineralogy and Geochemistry, 54, 95-114.

Fromm, R., Hachicha, T., Smykatz-Kloss, W., 2005. Aridic crusts and vein mineralization in the playa Areg el Makrezene, South Tunisia. Chemie der Erde Geochemistry, 65, 357-373.

Gerdes, G., Klenke, T., Nofke, N., 2000. Microbial signatures in peritidal siliciclastic sediments: a catalogue. Sedimentology, 47, 279-308.

Glasby, G.P., Cherkashov, G.A., Gavrilenko, G.M., Rashidov, V.A., Slovtsov, I.B., 2006. Submarine hydrothermal activity and mineralization on the Kurile and western Aleutian island arcs, NW Pacific. Marine Geology, 231, 163-180.

Glaub, I., 1994. Mikrobohrspuren in augewählten Ablagerungsräumen des europäischen Jura und der Unterkreide (Klassifikation und Palökologie). Courier Forschungsinstitut Senckenberg, 174, 1-319.

Glaub, I., Bundschuh, M., 1997. Comparative study on Silurian and Jurassic/Lower Cretaceous microborings. Courier Forschungsinstitut Senckenberg, 201, 123-135.

González, F.J., Somoza, L., Lunar, R., Martínez-Frías, J., Martín-Rubí, J.A., Torres, T., Ortiz, J.E., Díaz-del-Río, V., 2007. Fe-Mn nodules associated with hydrocarbon seeps: A new discovery in the Gulf of Cádiz (eastern central Atlantic). Episodes, 30, 187-196.

Gooday, A.J., Haynes, J.R., 1983. Abyssal foraminifers, including two new genera, encrusting the interior of *Bathysiphon rusticus* tubes. Deep-sea Research, 30, 591-614.

Gradzinski, M., Tyszka, J., Uchman, A., Jach, R., 2004. Large microbial-foraminiferal oncoids from condensed Lower-Middle Jurassic deposits a case study from the Tatra Mountains, Poland. Palaeogeography Palaeoclimatology Palaeoecology, 213, 133-151.

Greenslate, J., 1974. Microorganisms participate in the construction of manganese nodules. Nature, 249, 181-183.

Gygi, R.A., 1992. Structure, pattern of distribution and paleobathymetry of Late Jurassic microbialites (stromatolites and oncoids) in northern Switzerland. Eclogae Geologicae Helvetiae, 85, 799-824.

Han, X., Jin, X., Yang, S., Fietzke, J., Eisenhauer, A., 2003. Rhythmic growth of Pacific ferromanganese nodules and their Milankovitch climatic origin. Earth and Planetary Science Letters, 211, 143-157.

Hanert, H.H., 2006. The genus *Siderocapsa* (and other iron- and manganese-oxidizing eubacteria). Prokaryotes, 7, 1005-1015.

Hardenbol, J., Thierry, J., Farley, M.B., Jacquin, T., De Graciansky, P.C., Vail, P.R., 1998. Jurassic Sequence Chronostratigraphy. In: De Graciansky, P.C., Hardenbol, J., Jacquin, T., Vail, P.R. (eds.). Mesozoic and Cenozoic Sequence Stratigraphy of European Basins. Tulsa, Society for Sedimentary Geology (SEPM), 60(Special Publication), charts 1 and 6, 3-13.

Hasting, D., Emerson, S., 1986. Oxidation of manganese by spores of a marine bacillus: kinetic and thermodynamic considerations. Geochimica and Cosmochimica Acta, 50, 1819-1824.

Hlawatsch, S., Neumann, T., van den Berg, C.M.G., Kersten, M., Harff, J., Suess, E., 2002. Fast-growing, shallow-water ferro-manganese nodules from the western Baltic Sea: origin and modes of trace elements incorporation. Marine Geology, 182, 373-387.

Jenkyns, H.C., 1970a. Fossil manganese nodules from the West Sicilian Jurassic. Eclogae Geologicae Helvetiae, 63, 741-774.

Jenkyns, H.C., 1970b. The genesis of condensed sequences in the Tethyan Jurassic. Lethaia, 4, 327-352.

Jerlov, N.G., 1970. Light. General introduction. In: Kinne, O. (ed.). Marine Ecology 1, Environmental factors. London, Wiley Interscience, 195-102.

Jerlov, N.G., 1976. Marine optics. Amsterdam, Elsevier, 231pp.

Jiménez-Espinosa, R., Jiménez-Millán, J., Nieto, L.M., 1997. Factors controlling the genesis of Fe-Mn crusts in stratigraphic breaks of the eastern Betic Cordillera (SE Spain) deduced from numerical analysis of geological data. Sedimentary Geology, 114, 97-107.

Jiménez-Millán, J., Nieto, L.M., 2008. Geochemical and mineralogical evidence of tectonic and sedimentary factors controlling the origin of ferromanganese crusts associates to stratigraphic discontinuities (Betic Cordilleras, SE of Spain). Chemie der Erde, 68, 323-336.

Jones, R.W., Charnock, M.A., 1985. "Morphogroups" of agglutinating foraminifera. Their life position and feeding habits and potential applicability in (paleo)ecological studies. Revue de Paléobiologie, 4, 311-320.

Kappler, A., Newman, D.K., 2004. Formation of Fe(III) minerals by Fe(II)-oxidizing photoautotrophic bacteria. Geochimica et Cosmochimica Acta, 68, 1217-1226.

Kazmierczak, J., Kempe, S., 2006. Genuine modern analogues of Precambrian stromatolites from caldera lakes of Niuafo'ou Island, Tonga. Naturwissenschaften, 93, 119-126.

Krajewski, K.P., 1984. Early diagenetic phosphate cements in the Albian condensed glauconitic limestones of the Tatra Mountains, Western Carpathians. Sedimentology, 31, 443-470.

Krajewski, K.P., Lesniak, P.M., Lacka, B., Zawidzki, P., 2000. Origin of phosphatic stromatolites in the Upper Cretaceous condensed sequence of the Polish Jura Chain. Sedimentary Geology, 136, 89-112.

Krumbein, W.E., 1983. Microbial geochemistry. London, Blackwell Scientific Publisher, 330pp.

Krumbein, W.E., Jens, K., 1981. Biogenic rock varnishes of the Negev Desert (Israel), an ecological study of iron and manganese transformation by cyanobacteria and fungi. Oecologia, 50, 25-38.

Leinfelder, R.R., 1993. A sequence stratigraphic approach to the Upper Jurassic mixed carbonate - siliciclastic succession of the central Lusitanian Basin, Portugal. Profil, 5, 119-140.

Leinfelder, R.R., Nose, M., Schmid, D.U., Werner, W., 1993. Microbial crust of the Late Jurassic: composition, palaeoecological significance and importance in reef constructions. Facies, 29, 195-230.

Leinfelder, R.R., Krautter, M., Laternser, R., Nose, M., Schmid, D.U., Schweigert, G., Werner, W., Keupp, H., Brugger, H., Herrmann, R., Rehfeld-Kiefer, U., Koch, R., Zeiss, A., Schweizer, V., Christmann, H., Menges, G., Luterbacher, H., 1994. The origin of the Jurassic reefs: current research developments and results. Facies, 31, 1-56.

Lewin, R., 1984. How microorganisms transport iron. Science, 225, 401-402.

Lipps, J.H., 1983. Biotic interactions in benthic foraminifera. In: Tevesz, M.J.S., McCall, P.L. (eds.). Biotic interaction in

modern and fossil benthic communities. New York, Plenum Press, 331-376.

Mamet, B., Préat, A., 2003. Sur l'origine bactérienne et fongique de la pigmentation de l'Ammonitico Rosso (Jurassique, région de Vérone, Italie du nord). Revue de Micropaléontologie, 46, 35-46.

Mamet, B., Préat, A., 2006. Jurassic microfacies, Rosso Ammonitico limestone, Subbetic Cordillera, Spain. Revista Española de Micropaleontología, 38, 219-228.

Martín-Algarra, A., Sánchez-Navas, A., 1995. Phosphate stromatolites from condensed cephalopod limestones, Upper Jurassic, Southern Spain. Sedimentology, 42, 893-919.

Martín-Algarra, A., Sánchez-Navas, A., 2000. Bacterially mediated authigenesis in Mesozoic stromatolites from condensed pelagic sediments (Betic Cordillera, Southern Spain). In: Marine Authigenesis: From Global to Microbial. Tulsa, Society for Sedimentary Geology (SEPM), 66(Special Publication), 499-525.

Martín-Algarra, A., Vera, J.A., 1994. Mesozoic pelagic phosphate stromatolites from the Penibetic (Betic Cordillera Southern Spain). In: Bertrand-Sarfati, J., Monty, C. (eds.). Phanerozoic Stromatolites II. Dordrecht, Kluwer Academic Publishers, 345-391.

Molina, J.M., 1987. Análisis de facies del Mesozoico en el Subbético Externo (Provincia de Córdoba y Sur de Jaén). Doctoral Thesis. Granada, Universidad de Granada, 518pp.

Monty, C.L.V., 1973. Les nodules de manganese sont des stromatolites océaniques. Comptes Rendus de l'Academie des Sciences Paris D, 276, 3285-3288.

Myrow, P.M., Coniglio, M., 1991. Origin and diagenesis of cryptobiontic *Frutexites* in the Chapel Island Formation (Vendian to Early Cambrian) of southeast Newfoundland, Canada. Palaios, 6, 572-585.

Nealson, K.H., 1983. The microbial iron cycle. In: Krumbein, W.E. (ed.). Microbial geochemistry. Oxford, Blackwell Scientific Publications, 159-190.

Nealson, K.H., Stahl, D.A., 1997. Microorganisms and biochemical cycles: What can we learn from layered microbial communities? Reviews in Mineralogy, 35, 5-34.

Nicoll, R.S., Playford, P.E., 1993. Upper Devonian iridium anomalies, conodont zonation and the Frasnian-Fammenian boundary in the Canning Basin, Western Australia. Palaeogeography, Palaeoclimatology, Palaeoecology, 104, 105-113.

Nieto, L.M., 1997. La cuenca subbética mesozoica en el sector oriental de las Cordilleras Béticas. Doctoral Thesis. Granada, Universidad de Granada, 562pp.

Nose, M., Schmid, D.U., Leinfelder, R.R., 2006. Significance of microbialites, calcimicrobes, and calcareous algae in reefal framework formation from the Silurian of Gotland, Sweden. Sedimentary Geology, 192, 243-265.

Ogg, J.G., 2004. The Jurassic Period. In: Gradstein, F.M., Ogg, J.G., Smith, A.G. (eds.). A Geologic Time Scale 2004. Cambridge, Cambridge University Press, 307-343.

Olóriz, F., 2000. Time-averaging and long-term palaeoecology in macroinvertebrate fossil assemblages with ammonites (Upper Jurassic). Revue de Paléobiologie, 8, 123-140.

Ostwald, J., 1990. The biochemical origin of the Groote Eylandts manganese oxide pisoliths and ooliths, Northern Australia. Ore Geology Reviews, 5, 469-490.

Perri, E., Tucker, M., 2007. Bacterial fossils and microbial dolomite in Triassic stromatolites. Geology, 35, 207-210.

Pomoni-Papaioannou, F., 1994. Palaeoenvironmental reconstruction of a condensed hardground-type depositional sequence at the Cretaceous-Tertiary contact in the Parnassus-Ghiona zone, central Greece. Sedimentary Geology, 93, 7-24.

Préat, A., Mamet, B., De Ridder, C., Boulvain, F., Gillan, D., 2000. Iron bacterial and fungal mats, Bajocian stratotype (Mid-Jurassic, northern Normandy, France). Sedimentary Geology, 137, 107-126.

Puga, E., Portugal, M., Díaz de Federico, A., Bargossi, G.M., Morten, L., 1989. The evolution of the magmatism in the external zones of the Betic Cordilleras during the Mesozoic. Geodinamica Acta, 3, 253-266.

Reolid, M., Gaillard, C., 2007. Microtaphonomy of bioclasts and paleoecology of microencrusters from Upper Jurassic spongiolithic limestones (External Prebetic, Southern Spain). Facies, 53, 97-112.

Reolid, M., Gaillard, C., Olóriz, F., Rodríguez-Tovar, F.J., 2005. Microbial encrustation from the Middle Oxfordian-earliest Kimmeridgian lithofacies in the Prebetic Zone (Betic Cordillera, southern Spain): characterization, distribution and controlling factors. Facies, 50, 529-543.

Reolid, M., Rodríguez-Tovar, F.J., Nagy, J., Olóriz, F., 2008. Benthic foraminiferal morphogroups of mid to outer shelf environments of the Late Jurassic (Prebetic Zone, Southern Spain): Characterization of biofacies and environmental significance. Palaeogeography, Palaeoclimatology, Palaeoecology, 261, 280-299.

Rey, J., 1993. Análisis de la Cuenca Subbética durante el Jurásico y el Cretácico en la transversal Caravaca - Vélez Rubio. Doctoral Thesis. Granada, Universidad de Granada, 460pp.

Riding, R., 1991. Calcified Cyanobacteria. In: Riding, R. (ed.). Calcareous algae and stromatolites. Berlin, Springer, 21-51.

Sandoval, J., Checa, A., 2002. Taphonomy of cephalopod concentrations in the Jurassic of the Subbetic (Southern Spain). In: De Renzi, M., Pardo-Alonso, M.V., Belinchón, M., Peñalver, E., Montoya, P., Márquez-Aliaga, A. (eds.). Current Topics on Taphonomy and Fossilization. Valencia, Ajuntament de Valencia, 223-230.

Schaefer, M.O., Gutzmer, J., Beukes, N.J., 2001. Late Paleoproterozoic Mn-rich oncoids: Earliest evidence for microbially mediated Mn precipitation. Geology, 29, 835-838.

Schelble, R.T., Westall, F., Allen, C.C., 2004. ~ 1.8 Ga iron-mineralized microbiota from the Gunflint Iron Formation, Ontario, Canada: implications for Mars. Advances in Space Research, 33, 1268-1273.

Southam, G., 2000. Bacterial surface-mediated mineral formation. In: Lovley, D.R. (ed.). Environmental microbe-mineral interactions. Washington, American Society for Microbiology Press (ASM), 257-276.

Usui, A., 1994. Manganese nodule facies in the Western Part of the Penrhyn Basin, South Pacific (GH83-3 Area). Geological Survey of Japan Cruise Report, 23, 87-163.

Usui, A., Mita N., 1994. Mineralogy, geochemistry and internal growth structure of manganese nodules in the western part of the Penrhyn Basin, South Pacific (GH83-3 Area). Geological Survey of Japan Cruise Report, 23, 165-185.

Usui, A., Graham, I.J., Ditchburn, R.G., Zondervan, A., Shibasaki, H., Hishida, H., 2007. Growth history and formation environments of ferromanganese deposits on the Philippine Sea Plate, northwest Pacific Ocean. Island Arc, 16, 420-430.

Vail, P.R., Colin, J.P., Chene, J., Kuchly, J., Mediavilla, F., Trifilief, F., 1987. La stratigraphie séquentielle et son application aux correlations chronostratigraphiques dans le Jurassique du basin de Paris. Bulletin de la Société Géologique France, 7, 301-321.

Veillette, J., Juniper, S.K., Gooday, A.J., Sarrazin, J., 2007. Influence of surface texture and microhabitat heterogeneity in structuring nodule faunal communities. Deep-Sea Research I, 54, 1936-1943.

Vera, J.A., 2001. Evolution of the Iberian Continental Margin. Mémoires du Muséum National d'Histoire Naturel de Paris, 186, 109-143.

Vera, J.A., Martín-Algarra, A., 1994. Mesozoic stratigraphic breaks and pelagic stromatolites in the Betic Cordillera (Southern Spain). In: Bertrand-Sarfati, J., Monty, C. (eds.). Phanerozoic Stromatolites II. Dordrecht, Kluwer Academic Publishers, 319-344.

Vera, J.A., Molina, J.M., Montero, P., Bea, F., 1997. Jurassic guyots in the Southern Iberian Continental Margin: a model of isolated carbonate platforms on volcanic submarine edifices. Terra Nova, 9, 163-166.

Vogel, K., Balog, S.J., Bundschuh, M., Gektidis, M., Glaub, I., Krutschinna, J., Radtke, G., 1999. Bathymetrical studies in fossil reefs, with Microendoliths as paleoecological indicators. Profil, 16, 181-191.

Vogel, K., Bundschuh, M., Glaub, I., Hofmann, K., Radtke, G., Schmidt, H., 1995. Hard substrate ichnocoenoses and their relations to light intensity and marine bathymetry. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 195, 49-61.

Vogel, K., Gektidis, M., Golubic, S., Kiene, W.E., Radtke, G., 2000. Experimental studies on microbial bioerosion at Lee Stocking Island, Bahamas and One Tree Island, Great Barrier Reef, Australia: implications for paleoecological reconstructions. Lethaia, 33, 190-204.

Wallace, M.W., Keays, R.R., Gostin, V.A., 1991. Stromatolitic iron oxides: evidence that sea-level changes can cause sedimentary iridium anomalies. Geology, 19, 551-554.

Walter, M.R., Awramik, S.M., 1979. *Frutexites* from stromatolites of the Gunflint Iron Formation of Canada, and its biological affinities. Precambrian Research, 9, 23-33.

Wendt, J., 1969. Stratigraphie und Paläogeographie des Roten Jurakalks im Sonnwendgebirge (Tirol, Österreich). Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 132, 219- 238.

Wendt, J., 1970. Stratigraphische Kondensation in triadischen und jurassischen Cephalopodenkalken der Tethys. Neues Jahrbuch für Geologie und Paläontologie Monatshefte, 1970, 433-449.

Wilson, R.C.L., Hiscott, R.N., Willis, M.G., Gradstein, F.M., 1989. The Lusitanian Basin of West - Central Portugal. Mesozoic and Tertiary tectonic, stratigraphy and subsidence history. American Association of Petroleum Geologists (AAPG) Memoir, 46, 341-362.