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Microtaphonomy of bioclasts and paleoecology of microencrusters from Upper Jurassic spongiolithic limestones (External Prebetic, Southern Spain)

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Abstract Microencrusters and microtaphonomic features of the Oxfordian spongiolithic limestones of the External Prebetic were studied using thin-section analysis. The spongiolithic limestone is a bioclastic-rich packstone with common echinoderm, mollusc and brachiopod remains. The bioclasts show a high fragmentation index and frequent microborings. The encrustation index (E_i) is higher for fragments of serpulids, ammonoids and bivalves, and increases with the initial grain-size of bioclasts. The main microencrusters consist of benthic microbial communities (BMC) and nubeculariids, as well as subordinate calcareous and siliceous agglutinated foraminifera, serpulids and bryozoans. BMC are usually the first colonizers, and encrusting foraminifera mainly appear on bioclasts larger than 2 mm. BMC dominate in well-developed encrustations on upward facing surfaces of larger bioclasts that are also colonized by foraminifera (nubeculariids and *Subdelloidina*). *Bullopora*, serpulids and bryozoans are more common on lower surfaces. The fact that the values of encrustation index, encrustation thickness and diversity of the microencrusters increase with the size of bioclasts is related to a higher stability and exposure time of the available bioclastic substrate. The microencruster distribution on upper and lower surfaces of large bioclasts may be related to photic control, space competition and/or predation avoidance.

Keywords Microencrusters · Paleoecology · Taphonomy · Upper Jurassic · Southern Iberia

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Introduction

Microbialites and other microencrusters have been amply analysed in reefal habitats through much of the Phanerozoic, where they play an important role by frame-building and sediment-trapping (Fagerstrom 1987; Webb 1996; Riding 2002). We thus already know a considerable amount about the Upper Jurassic microencrusters from carbonate build-ups (Gaillard 1983; Leinfelder et al. 1993a, b, 1994; Nose 1995; Dupraz and Strasser 1999; Ourribane et al. 2000; Olivier et al. 2003, 2004; Shiraisi and Kano 2004). These works have provided valuable paleoecological information concerning microencrusters and microbialites. However, studies of these organisms from Jurassic non-built facies are less common (Rat 1966; Nose 1995; Schmid 1996; Mišik and Sucha 1997; Gradzinski et al. 2004; Reolid et al. 2005).

In the Upper Jurassic of the Prebetic Zone (Betic Cordillera, southern Spain), Reolid et al. (2005) show the importance of the microbialites for palaeoenvironmental interpretations and the participation of encrusting foraminifera, annelids and bryozoans in the microbial fabrics. A taphonomic study recently carried out in the so-called Upper Jurassic lumpy facies from the Prebetic by Olóriz et al. (2004) focused on microborings, but included an analysis of the microencrustations. Nevertheless, a detailed study of the microencrusters is still lacking. The present microtaphonomic study of Upper Jurassic microencrusters places special emphasis on the preferences of microencrusters regarding bioclastic substrate (type and size), and the relationships among microencrusters.

Location and geological setting

The studied samples originate from the Prebetic Zone, which is the outermost sector of the Betic Cordillera (Fig. 1). The External Prebetic corresponded to a mid-shelf environment during the Late Jurassic. The spongiolithic limestones of the External Prebetic show the colonization

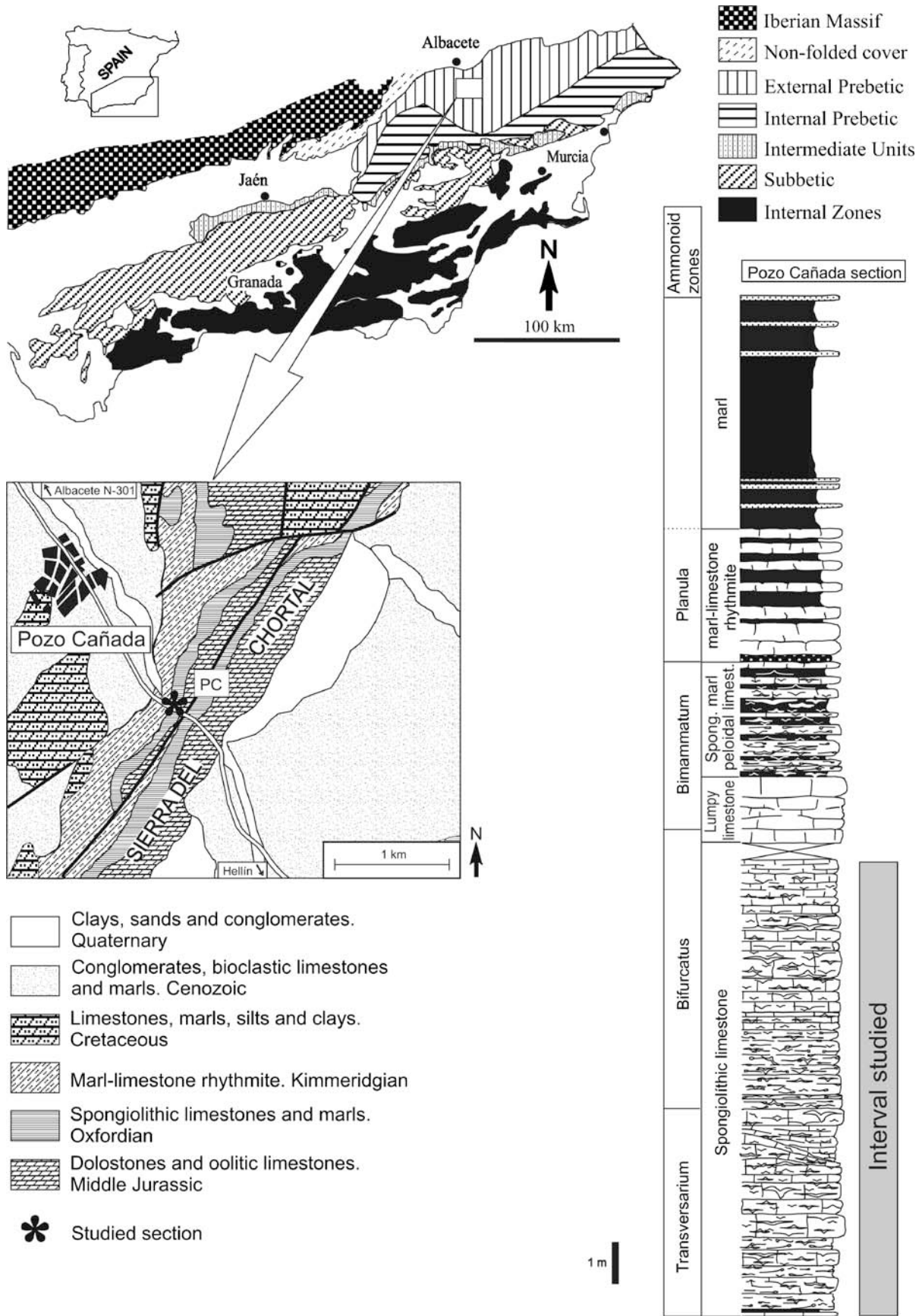


Fig. 1 Geological setting and Pozo Cañada section (PC)

of the mid shelf sea-bottom by siliceous sponges, forming a sponge meadow in a mixed siliciclastic-carbonate ramp. The studied section is located in the eastern sector of the External Prebetic. Oxfordian sponge facies of the southern Iberian margin have a long history of study, including Behmel (1970), Geyer and Pelleduhn (1979), Deusch et al. (1990, 1991), Pisera (1991), Krautter (1995, 1998), Nose (1995) and Olóriz et al. (2003).

The studied outcrop is located on a small gully to the SE of the village of Pozo Cañada (province of Albacete). The section extends along the whole northern slope of the Sierra del Chortal (Fig. 1). The Middle Oxfordian-Lowermost Kimmeridgian deposits (26 m thick, Fig. 1) are made up of spongiolithic limestones (Transversarium and Bifurcatus Zones), spongiolithic marl-peloidal limestones (Bimammatum Zone), marl-limestones and marls (Planula Zone) (Reolid 2005). The microtaphonomic analysis of bioclasts and their microencrusters was carried out on samples from the spongiolithic limestones.

Materials and methods

In order to obtain a detailed analysis of microencrusters and microtaphonomic traits, we studied 5,640 bioclasts in 42 thin-sections from 20 samples taken bed-by-bed at the Pozo Cañada section (Transversarium to Bimammatum Zones, Oxfordian). For each sampling level, over 250 bioclasts were analysed, taking into account the type of bioclast and the taphonomic characteristics as put forth by Olóriz et al. (2004): size, fragmentation (fragmentation index, F_i), microboring (microboring index, MB_i) and, in particular, microencrustations (encrustation index, E_i).

The technique used for grain-size analysis was area counting. Yet the grain sizes derived from thin sections are apparent, not true grain sizes; and we therefore refer to maximum size observable (Carozzi 1988). The mean value of the maximum apparent grain size (apparent diameter s , Carozzi 1988) is an approximation of the real size and it proves very useful for comparing sets of data involving different types of bioclasts and beds, for example. In the encrustation study, particular attention is paid to two aspects: the degree and the index of encrustation (E_i). For the former, three levels were established (Olóriz et al. 2004): high, medium and low, depending on the intensity of encrustation (occupied periphery of the bioclast and thickness of the encrustation). The degree of encrustation was defined as high (HED) when the proportion of encrusted periphery exceeded 60%; less than 10% was considered to be a low encrustation degree (LED), while 10–60% was considered a medium degree of encrustation (MED). Several bioclasts showed no signs of encrustation. The E_i refers to the degree of encrustation among a set of specimens, and it was calculated as the mean value obtained by summing the product of the number of samples (n) showing different degrees of microencrusting $\times 100$ (HED), $\times 50$ (MEB), $\times 1$ (LED), then dividing the resulting value by the total

number of samples considered (N), including those without evidence of microencrusting:

$$E_i = \frac{[(n\text{HED} \times 100) + (n\text{MED} \times 50) + (n\text{LED} \times 1)]}{N}$$

The F_i , MB_i and E_i are weighted averages. They varied between 0 and 100 and can be expressed as a percentage (Olóriz et al. 2004). We analysed microencrustation according to mean apparent size of bioclasts, and according to five selected size intervals; fine ($< 250 \mu\text{m}$), medium (250–500 μm), coarse (0.5–1 mm), very coarse (1–2 mm), and even coarser grains ($> 2 \text{ mm}$). Bioclasts less than 150 μm were not been studied and the foraminifera were not analysed because they are generally not encrusted.

In each encrusted bioclast, the microencrusters are identified. To identify the role of the substrate in the control of colonization by microencrusters, our analysis of each microencruster took into close account the type of bioclastic substrate and the location of the encrustation. The relative abundance of the different organisms and the sequence of colonization were noted. Microencruster relationships were studied both in lithoclasts and bioclasts using the overgrowth ability index of Taylor (1979). This index was calculated for each microencruster using Taylor's formula:

$$\begin{aligned} &\text{Overgrowth ability index} \\ &= \frac{(\text{Frequency as an overgrower}) \times 100}{(\text{Frequency as an overgrower} + \text{frequency overgrown})} \end{aligned}$$

This simple index expresses the number of successful overgrowths as a percentage of the total number of overgrowth interactions. Lateral and frontal overgrowths among microencrusters are not differentiated, being impossible in several cases with observations only in thin-sections. Overgrowth ability index is treated in this paper as an approximation to the true relationships among microencrusters, since overlapping is a complex three-dimensional phenomenon.

Facies studied

Sponge facies of the Prebetic and Celtiberic domains occur in the Transversarium Zone (Middle Oxfordian) to the Planula Zone (lowermost Kimmeridgian). They show their widest geographic range in the Bifurcatus Zone (Upper Oxfordian, Krautter 1998). Although most of the Oxfordian lithofacies of the Prebetic Zone contain sponge remains, sponges are particularly characteristic in the spongiolithic limestone lithofacies. Spongiolithic limestones from the Pozo Cañada section are well bedded (12 to 50 cm thick) and contain abundant remains of siliceous sponges (Olóriz et al. 2002, 2003), which constitute a fundamental component of the rock (> 40 –50%). Ammonoids, brachiopods, bivalves, crinoids, irregular and regular echinoids, annelids and gastropods are also very common.

The fabric is grain- to matrix-supported, and microbial laminated fabrics occur locally on the sponges (Olóriz

Table 1 Abundance of the different skeletal types for each size interval

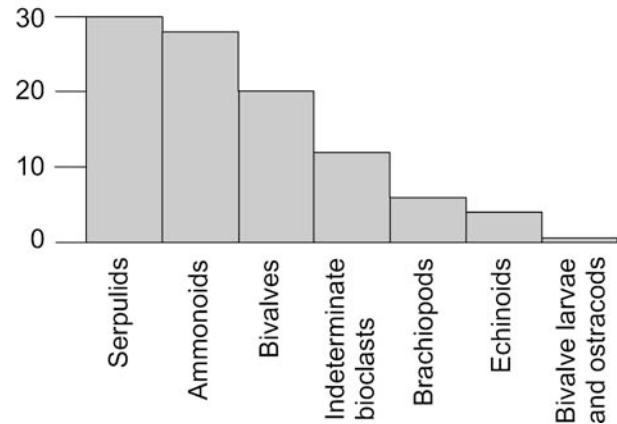
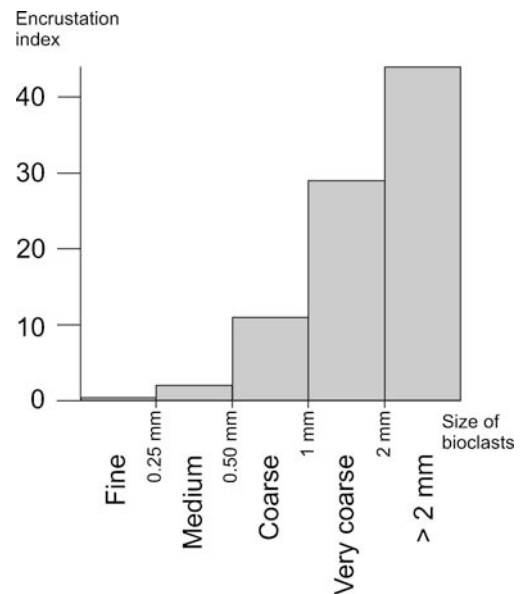
Type of bioclasts (%)	Size intervals				
	Fine fraction	Medium fraction	Coarse fraction	Very coarse fraction	>2mm
Ahermatypic corals				<1	1
Ammonoids	<1	<1	1	4	9
Belemnoids		<1	<1	<1	<1
Bioclasts	10	22	30	33	31
Bivalve larval shells	23	13			
Bivalves	<1	<1	7	9	16
Brachiopods	<1	2	6	9	17
Bryozoans			<1	<1	1
Echinoids	62	58	51	38	20
Gastropods		<1	<1	<1	<1
Ostracods	4	1	<1		
Serpulids	<1	1	4	4	3
<i>Terebella</i>			<1		
Plant remains				<1	

et al. 2003; Reolid et al. 2005). The microfacies, which is characterized by packstone (locally wackestone), is dominated by lumps (24%), bioclasts (24%), peloids (18%), tuberoids (11%), oncoids (10%) with subordinate ooids, aggregate grains and quartz grains (Olóriz et al. 2003). We use the term lump to denote subspherical lime-mud intraclasts ranging between 0.4 and 1 cm. The term tuberoid (Fritz 1958; Flügel 1982; Gaillard 1983) is used to describe darkish, subrounded grains derived from sponges, ranging between 0.2 and 2 mm, and showing variable microstructures. The most abundant bioclasts are echinoderm remains (55%), indeterminate mollusc bioclasts (21%) and bivalves (15%, which possibly are 68% larval shells); and secondarily, brachiopod, ammonoid and gastropod fragments, serpulids, and ostracods. The abundance of the different skeletal types, expressed as a percentage, is summarized in Table 1 for the five size intervals. Foraminifera, radiolaria, sponge spicules and bioclasts < 150 μm size were not included.

Bioclast composition and preservation

The bioclasts studied consist mainly of sand-size remains. The size distribution of the bioclasts is: 32% fine, 38% medium, 20% coarse, 7% very coarse and 3% > 2mm. The bioclast fragmentation is high ($F_i = 55\%$), though it varies depending on the type of bioclasts. Higher values of F_i correspond to remains of brachiopods (87%), ammonoids (84%), and indeterminate mollusc bioclasts (79%), whereas lower values of F_i are seen with bivalve larval shells (3%) and ostracods (2%). The frequency of microborings likewise varies, being greatest on ammonoid remains ($MB_i = 43\%$), and indeterminate mollusc bioclasts (34%). Lower values correspond to ostracods and bivalve larval shells. The MB_i values increase along with bioclast size, from 2% for fine grains, to 48% for grains larger than 2 mm.

Encrustation index

**Fig. 2** Encrustation index values according to bioclast type**Fig. 3** Encrustation index values according to bioclast size intervals

Microencrusted bioclasts usually correspond to macroinvertebrate fragments (Fig. 2), while microencrusters are scarce or absent in small complete shells. E_i is higher in serpulids and ammonoids, followed by bivalves (20%, excluding larval shells). Lower E_i is shown by echinoderms, bivalve larval shells and ostracods. E_i and MB_i increase with the size of the bioclasts (Fig. 3), showing a similar trend (Table 2). A comparison of fragmentation and E_i points to the independence between these microtaphonomic features.

Microencrusters

Microbes and encrusting foraminifera (mainly nubeculariids) are the main encrusters. Nubeculariids are comparatively more abundant on the largest bioclasts; yet benthic microbial communities (BMC) may constitute thick coats. Less common are calcareous foraminifera (*Tubiphytes* and

Table 2 Relation between the encrustation degrees and fragmentation (F_i) and microboring (MB_i) index

Encrustation		Fragmentation index (F_i)	Microboring index (MB_i)
Absent		55	6
Low	LED	59	27
Medium	MED	59	45
High	HED	57	66

LED lower encrustation degree; MED medium encrustation degree; HED high encrustation degree

Bullopورا), siliceous agglutinated foraminifera (*Tolypammina*, *Thurammina* and *Subdelloïdina*), serpulids and bryozoans (Figs. 4, 5).

The BMC formed microbialites through the trapping and/or binding of fine detritic sediment or carbonate precipitation (e.g., Burne and Moore 1987; Leinfelder et al. 1993a). We use the term agglutination as proposed by Riding (2002) for trapping and binding processes, though a possible biologically forced calcification of minipeloids can not be dismissed (Reitner and Schumann-Kindel 1997; Schumann-Kindel et al. 1997). Encrustations by microbes frequently appear as a locally dark micrite or thin dark coat around bioclusters. These films are composed of dense, homogeneous, cryptocrystalline micrite, which is characterized by its dark colour as compared to the surrounding micrite. When the microbialite is well developed, it may present the minipeloidal laminated fabrics described by Reolid et al. (2005), with concentric (microbial oncoids) and planar structures (microbial laminated fabrics).

Encrusting porcelaneous nubeculariids are commonly associated with microbialites (Gaillard 1983; Reolid et al. 2005). They are mainly represented by *Vinelloidea* [usually termed *Nubeculinella* but see Voigt (1973) and Loeblich and Tappan (1988)] without excluding the possible presence of *Nubecularia*. Sections sometimes allowed for the identification of the proloculus and an initial coiled stage, while a later uniserial stage is easily recognizable. The section of chambers is generally ovate. *Tubiphytes* shows an inner porcelaneous wall and a micritic coat. It is a controversial organism, interpreted as a foraminifera-microbe consortium (Flügel 1981; Bernier 1984; Leinfelder et al. 1993a; Nose 1995; Schmid 1995, 1996; Dupraz and Strasser 1999). We assume here that *Tubiphytes* could correspond to the symbiotic coexistence of a sessile porcelaneous foraminifer (*Nodophthalmidium* or *Nubeculinella* s. Leinfelder et al. 1993a; Nose 1995) and a microbial crust. It is observed encrusting along the substrate and above its surface. *T. morronensis* is a typical microencruster from the mid-outer shelf (Leinfelder et al. 1993; Schmid 1996; Dupraz and Strasser 1999) and is usually associated with siliceous sponges.

Bullopورا (Polymorphinidae) has a calcareous test consisting of a series of hemispherical to elongated chambers of circular to ovate outline, variable in size and linked by stolon-like necks. They correspond mainly to *B. tubercu-*

lata, characterized by spines irregularly distributed in the test. It is common to but not exclusive of cryptic microhabitats (Olivier 2004).

Subdelloïdina (Lituolidae) has a siliceous coarse agglutinated test, featuring a proloculus followed by irregularly arranged or rectilinear chambers that increase in size as they are added. It participates in the microbial fabrics together with nubeculariids (Gaillard 1983; Olóriz et al. 2004).

Ammodiscidae with a siliceous finely agglutinated test characterized by a proloculus followed by an elongated tubular chamber showing an irregular morphology, according to the substrate were assigned to *Tolypammina*. It is very common in sheltered parts of bioclusters or inside microborings, *Bullopورا* and *Thurammina* chambers (Fig. 5J) and spicule meshes of hexactinellid sponges (Kazmierczak 1973; Gaillard 1983; Olóriz et al. 2004; Guibault et al. 2006).

Thurammina (Saccaminidae) has a test made up of agglutination of small quartz grains (Fig. 5H, I). It shows an irregular to subglobular morphology with many short conical protuberances. It is frequent within siliceous sponge structures (Kazmierczak 1973; Gaillard 1983; Reolid 2005; Guibault et al. 2006). The studied specimens possibly correspond to *T. hausleri*.

Only *Plagioecia* (Bryozoa, order Cyclostomata) was recognised from the observation in thin-section. Cyclostome bryozoans in thin section are difficult to differentiate, and here they collectively called the “*Berenicea* group” (Leinfelder et al. 1993a; Schmid 1996). Bryozoans occur in diversified and thick encrustations, being locally associated with serpulids.

Serpulids are typical epibionts of sponges. Morphologies can be attributed to *Cycloserpula*, *Dorsoserpula* and, locally, to *Tetraserpula* and *Pentaserpula*. In hand samples some serpulid species (*Glomerula gordialis* and *Neovermilia limata*) and an agglutinated annelid (*Terebella lapilloides*) were identified.

Microencrusters and grain size

An analysis of the relationships between the type of microencrusting organism and the selected grain sizes was carried out to explore the role of bioclast size in colonization (Fig. 6, Table 3). An increase of encrustation with increasing grain size is observed from 2% in the fine fraction to 86% in bioclusters > 2 mm. The BMC and nubeculariids are dominant (Table 3), with decreasing proportions of BMC encrustation compensated by increasing percentages of nubeculariids. Assemblages are more diversified in the very coarse and > 2 mm fractions, where siliceous foraminifera, serpulids and bryozoans have their highest values. The encrustations in bioclusters from coarser fractions are sometimes thicker and contain more microencrusters. The nubeculariids participate in a higher percentage of encrustations than BMC in the > 2 mm size fraction. In this fraction, when nubeculariids and BMC appear jointly, the nubeculariids usually precede BMC in the sequence of substrate colonization.

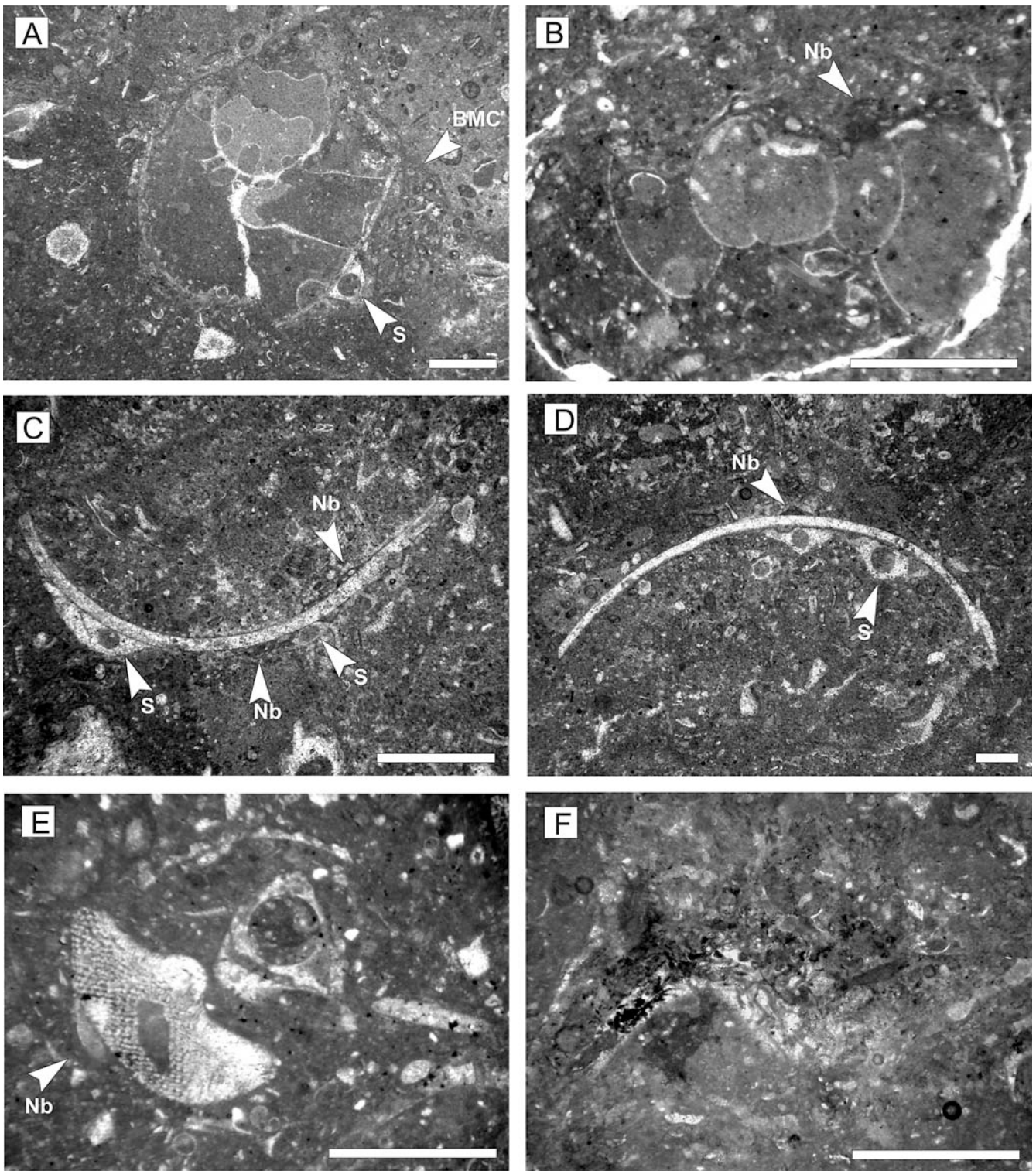


Fig. 4 Microtaphonomic features of bioclasts from spongiolithic lithofacies. **A** Ammonoid fragment showing encrustations by BMC, nubeculariids and serpulid. **B** Mould of ammonoid encrusted by nubeculariids on upper flank. **C** Fragment of bivalve encrusted by serpulids and nubeculariids on lower surface and nubeculariids on upper surface. **D** Fragment of bivalve with serpulids on lower surface

and local encrustation by nubeculariids on upper surface. **E** Bioclasts showing microboring and microencrustation. **F** Indeterminate mollusc bioclast showing high density of microborings and microencrustations. *Scale bar* 1 mm. *BMC* benthic microbial communities; *Nb* nubeculariids; *S* serpulids

Microencrusters and bioclast types

BMC are the dominant microencrusters whatever the type of bioclastic substrate, except for brachiopod remains. In the fine and medium fractions, BMC are practically the only microencrusters, as well as the first ones to colonize the substrate. Serpulids show the highest proportions of encrustations by BMC in medium and coarse-grained sediments. Nubeculariids are the second most important microencrusters on the main types of bioclasts (Fig. 7), being the most common on serpulid remains (in medium and coarse-grained sediments). On larger bioclasts, nubeculariids are more common on bivalves, echinoderms and ammonoids. The greater the bioclast size, the greater the relative proportion of nubeculariids with respect to BMC, although BMC are normally dominant in thickness. Nubeculariids are preferentially located on the upper side of the substrates. This distribution agrees with observations by Palmer and Fürsich (1974), Gaillard (1983), Leinfelder et al. (1993a), Gradzinski et al. (2004) and Reolid et al. (2005).

As for secondary encrusters, *Bullopore* occurs on all type of bioclasts, yet mainly on bivalves and serpulids. *Tolypammina* is most common on indeterminate mollusc bioclasts, ammonoids and bivalves (Fig. 7). It was not observed on brachiopods. It is more frequent in the sheltered part of the bioclasts, inside microborings and the spicule meshes of siliceous sponges. A similar habitat was described for *T. gregaria* by Benjamini (1984) from the Anisian of Israel. *Thurammina* shows preference for larger ammonoid fragments (> 2 mm), and spicule framework of siliceous sponges. *Subdelloidina* is commonly associated with serpulid aggregates (substrates > 2 mm). It is more frequent inside well-developed microbial laminated fabrics occurring on the upper surfaces of plate-shaped sponges, than directly on bioclasts. Encrustations of bioclasts by *Tubiphytes* are very infrequent. *Tubiphytes* appears mainly on brachiopod fragments, but very commonly encrusts lithoclasts as lumps and tuberosities (Olóriz et al. 2003; Reolid et al. 2005). It prefers interval sizes where other sessile foraminifera are absent. Serpulids are especially abundant encrusting other serpulids and bivalve remains. They are very rare in bioclasts < 2 mm (Fig. 7), except for encrustations over other serpulids forming aggregates. There is no record of serpulids encrusting brachiopods. Meanwhile, bryozoans are scarce and mainly encrust bivalves.

As opposed to nubeculariids, BMC can encrust smaller bioclasts. Both participate in oncolid formation (Fig. 8) around bioclasts and lithoclasts (Reolid et al. 2005). The first coating around the small grains (< 500 µm) corresponds to BMC, while the nubeculariids appear when oncolid development reaches approximately 750 µm in size. The proportion of crusts with nubeculariids increases sharply on the coarse fraction: they are the most numerous microencrusters on bioclasts > 2 mm. All encrusting foraminifera are typical of bioclasts > 2 mm, and are found very rarely on bioclasts < 1 mm. Siliceous agglutinated foraminifera do not encrust lithoclasts and only occur

either directly on bioclasts or on previous BMC encrustations, nubeculariids and serpulids. The largest bioclasts show distinctive orientations of the microencrusters. BMC and nubeculariids are more abundant on the upper surfaces of bioclasts (Figs. 4C–E and 5E–F), whereas serpulids and bryozoans usually occupy the sheltered and shadowed parts, which normally represent the lower surfaces of clasts.

Microencruster relationships

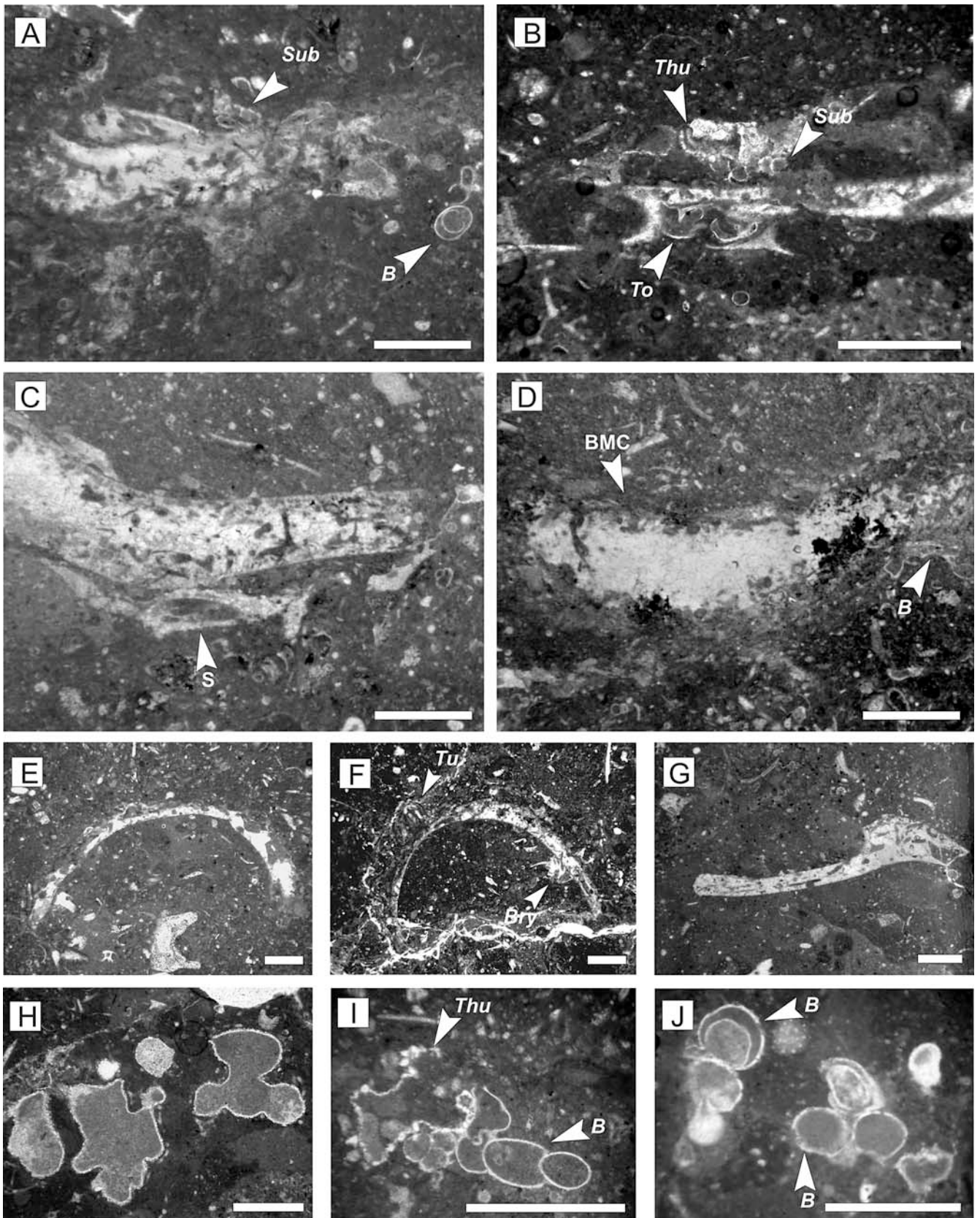
Distribution and overgrowth interactions among the different microencrusters have been analysed both for bioclasts and lithoclasts. BMC are mainly encrusted by nubeculariids (51%) and *Subdelloidina* (21%), and secondarily by serpulids and *Bullopore* (Fig. 9). The main microencrusters on nubeculariids are BMC (39%), *Subdelloidina* (24%) and serpulids (13%). The determination of colonization on upper or lower surfaces in sand-size bioclasts is more difficult because these grains possibly moved before, during and after encrustation. Comparison with well-known examples from larger macroinvertebrate remains is very illustrative in this sense (Gaillard 1983; Lescinsky 1993; Nebelsick et al. 1997; Olóriz et al. 2002). In well-developed encrustations of upper surfaces of plate-shaped sponges and larger bioclasts, BMC dominate, forming laminated fabrics colonized by nubeculariids and *Subdelloidina*, and occasionally serpulids, *Bullopore* and bryozoans. Since *Tolypammina* and *Thurammina* are restricted almost exclusively to sheltered lower surfaces and encrust directly over bioclasts, their interaction with other microencrusters is scarce. We do not differentiate between encrustations of the same types of microencruster, because it is often impossible to differentiate individuals in thin sections.

The analysis of the overgrowth ability index (Taylor 1979) shows higher values for sessile foraminifera and bryozoans (> 60%, except *Tolypammina*) and lower ones in serpulids (40%) and BMC (21%) (Table 4). If the microbial encrustations are excluded from analysis, the overgrowth ability index decreases for most microencrusters.

Discussion: paleoecology of microencrusters

Relationships of microencrusters with the bioclastic substrate

The data obtained allow us to confirm an increase in the encrustation index (E_i) and the proportion of encrusted bioclasts with greater grain size. This association, seen both in the thickness and in the diversity of microencrusters, is probably related to the higher stability and longer time of exposure of the available bioclastic substrate. Colonization and exposure time are also influenced by the durability of the host bioclasts (Rodland et al. 2006). Low sedimentation rates mean longer exposure, thereby favouring the colonization of bioclasts by microencrusters. It is widely



known that the development of microencrusts, microbialites and complex biologic crusts calls for a low rate of sedimentation, in view of the slow growth rate of encrusters (Schneider 1970; Gaillard 1983; Leinfelder et al. 1993a, 1993b, 1994; Brunton and Dixon 1994; Dromart et al. 1994; Martín-Algarra and Vera 1994; Schmid 1996; Martín-Algarra and Sánchez-Navas 2000; among others). Microencrusts are also very sensitive to any influx of fine, clay-rich sediments (Leinfelder et al. 1994; Reolid et al. 2005). Low sedimentation rates and low terrigenous input would be well indicated by the thicker encrustations developed over larger bioclasts. In other ways, these large bioclasts offer better possibilities for larval fixation and growth. Thus, fragments of ammonoids, serpulids, bivalves and indeterminate mollusc bioclasts display higher E_i . Contrariwise, smaller bioclasts such as ostracods, bivalve larval shells and very small echinoderm fragments are rarely encrusted, because they provide a reduced surface and are easily reworked and buried. The presence of microborings shows this same pattern. Reolid et al. (2005) emphasized the importance of substrate size and stability as a major factor controlling the presence and morphology of encrustations.

Phases of colonization

All the evidence described here points to the colonization of skeletal parts mostly after the death of organisms. Only some *Tolypammina* and *Thurammina* observed inside sponges (Gaillard 1983; Olóriz et al. 2003) could be interpreted as the colonization of living specimens. According to Kazmierczak (1973), the *Tolypammina*-sponge association could be a commensal relationship, where foraminifera found shelter in sponge canals and also profited from water currents that brought them food. In the studied bioclasts, however, these foraminifera were found encrusting shell fragments, their occurrence clearly corresponding to a biotratinomic process. Notwithstanding, some encrustation of exhumed and reworked remains may be possible.

Microboring and microencrusting are the two main taphonomic processes derived from the relationships between bioclasts and microorganisms, commonly observed

◀ **Fig. 5** Microborings and microencrustations. **A** Microbored bioclast encrusted by BMC, nubeculariids and *Subdelloidina*. **B** Densely microbored bioclast colonized by agglutinated sessile foraminifera (*Thurammina*, *Subdelloidina* and *Tolypammina*). **C** Microbored bioclast encrusted by nubeculariids and a serpulid. **D** Microbored bioclast with encrustation by BMC, nubeculariids and *Bullopore*. **E** Fragment of bivalve microbored and encrusted by BMC and nubeculariids (upper surface). **F** Fragment of bivalve showing microboring and encrustation mainly formed by BMC and nubeculariids. **G** Indeterminate mollusc bioclast with microborings. **H** *Thurammina* inside a lithistid sponge structure. **I** Association of *Thurammina* and *Bullopore*. Note the quartz-agglutinated test of *Thurammina*. **J** *Tolypammina* located inside *Bullopore tuberculata* chambers. Scale bar 1 mm. B, *Bullopore*; BMC, benthic microbial communities; Bry bryozoans; Nb nubeculariids; S serpulids; Tu *Thurammina*; To *Tolypammina*; Tu *Tubiphytes*; Sub *Subdelloidina*

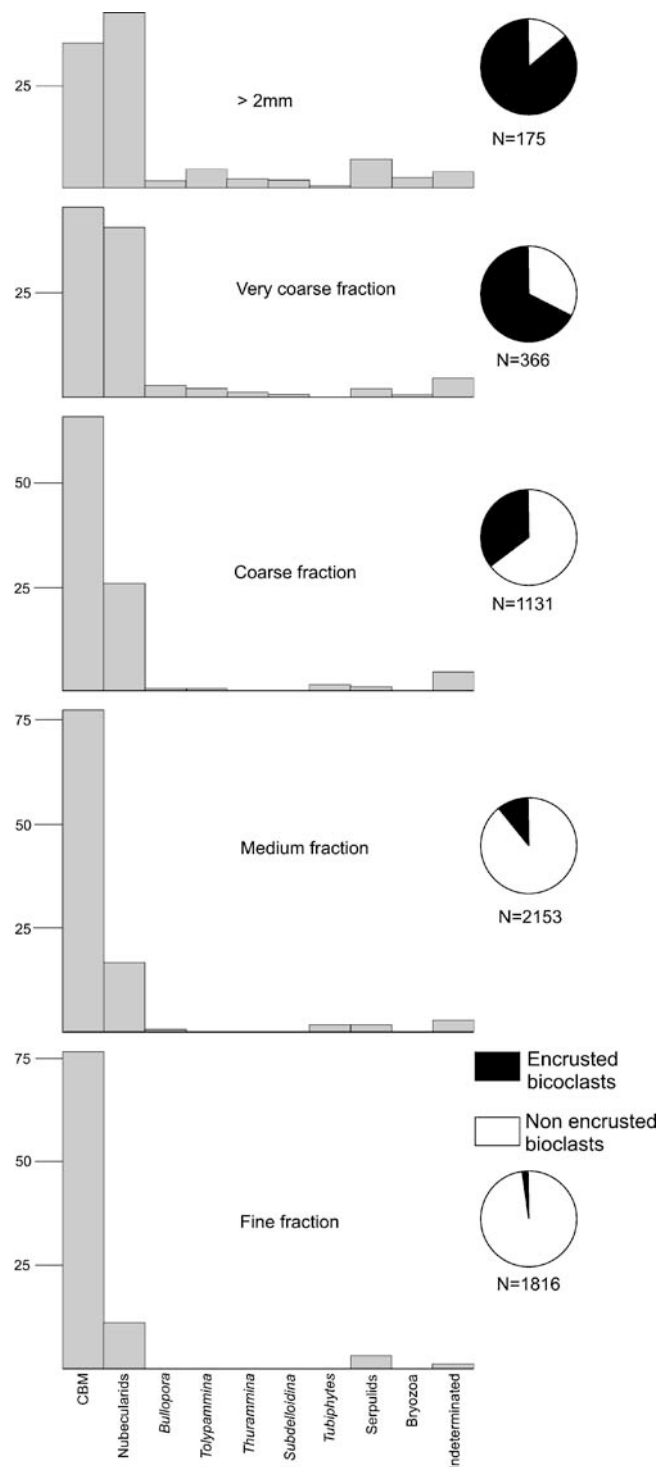


Fig. 6 Relative proportions of microencrusters registered in each bioclast size interval (bar diagrams) and proportion of encrusted bioclasts (pie diagrams)

in the spongiolithic limestones. Several encrusted bioclasts were colonized by microborers previous to encrustation; and normally encrustations occur on fragments of macroinvertebrates, sometimes forming a coat around the bioclast (oncoids), thus evidencing encrustation post-mortem. Rapid rates of microbial activity have also been measured

Table 3 Proportions of microencrusters according to bioclast size intervals

Microencrusters (%)	Size of the bioclasts				
	Fine fraction	Medium fraction	Coarse fraction	Very coarse fraction	>2mm
BMC	78	78	66	47	35
Nubeculariids	11	17	26	41	42
<i>Tubiphytes</i>		1	1		<1
<i>Bullopora</i>		<1	<1	3	1
<i>Tolypammina</i>			<1	2	4
<i>Thurammina</i>			<1	<1	2
<i>Subdelloidina</i>				<1	2
Serpulids	3	1	1	2	7
Bryozoans			<1	<1	2
Indeterminates	8	2	5	4	4

from experiments in carbonate substrates in shallow areas, with initial phases of microendolithic organism infestation occurring during the first week, and intense colonization occurring after a few months (Perkins and Tsentas 1976; Kobluk and Risk 1977; Bromley et al. 1990; Chazottes et al. 1995). As for encrustation, MB_i is related to a low sedimentation rate allowing the colonization of bioclasts by microborers.

Microboring and microencrusting are two opposite taphonomic features, the first being an early destructive process and the second a later process of conservation. Microborings, through their penetrative action, weaken carbonate skeletal substrates and make them more susceptible to physical destruction (Young and Nelson 1988; Olóriz et al. 2004); they also increase the porosity and surface area of the substrate, making it more prone to dissolution, maceration and microbial invasion of organic laminae. Destruction of the protective organic matrix coating the carbonate crystals within a shell facilitates its disintegration (Kennedy and Hall 1967; Lewy 1981; Nelson et al. 1988; Young and Nelson 1988; Zuschin et al. 2003). In contrast, encrustation may enhance shell preservation, protecting damaged surfaces of bioclasts. Cases of encrustation in previously microbored surfaces are common, but encrustation showing microboring was not observed (except on encrustation by serpulids). Thus, an initial phase of microboring activity could be halted by later colonization by encrusting organisms. Olóriz et al. (2004) interpret the absence of microbored encrustation as related to BMC composition and the abundance of porcelaneous shells of nubeculariids.

According to these interpretations, the time for settlement was higher for encrusters than for microborers, yet under favourable environmental conditions, encruster growth could be very rapid. For example, the growth of recent serpulids in similar marine environments is very rapid (up to 75 mm 1 year after settlement, Simon-Papyn 1965). Shroba (1993) observed that within 3 days the test of dead foraminifera was coated in algal scum and diatoms. Shroba (1993) speculated that this coating may inhibit or prevent impact and abrasion of the test. Both rates of microencrustation and of microboring are related to planktonic productivity and burial (Walker et al. 1998; Lescinsky et al.

2002). In encrustations with various microencrusters, BMC are usually the first colonizers; the nubeculariids appear to be the pioneer microencrusters only in grains > 2 mm. The relation between the thickness of encrustations and diversity of microencruster assemblages can be explained by the improved substrate conditions for colonizers resulting from an increased thickness of microbial encrustations (that is, a greater surface, though possible changes in ecological and chemical properties of the microhabitat can not be disregarded).

Spatial and paleoecological relationships among microencrusters

Competition for substrate

The interpretation of spatial relationships is complicated by the possibility that interacting organisms did not live contemporaneously (Palmer and Palmer 1977; Taylor 1979). However, the small grain size allows us to infer a brief exposure time of the grains, and therefore a higher probability of a contemporaneous interaction between microencrusters. The microencruster relationships suggest that active competition for substrate space did indeed occur. In general, it is assumed that competitively superior microencrusters overgrew the skeletons of less adept competitors, although in some cases, fossilised overgrowths may result from encrustation over an already dead organism (Lescinsky 1997). The lower values of the overgrowth ability index of the microbial encrustations (21%) can be the result of:

- A lesser ability of BMC than sessile foraminifera, serpulids and bryozoans to compete for the available substrate. BMC would be opportunistic, pioneer organisms colonizing the substrate. Then, more specialized microencrusters would appear when the grains reached a more favourable size. This illustrates an ecological succession and explains the higher diversity of microencrusters in the largest encrustations analysed. In this sense, Olivier et al. (2004) propose a first layer of microbialite (millimetric crust of dense micrite). Examples from build-ups of the Prebetic (Olóriz et al. 2003; Reolid et al. 2005), however, show very thick microbial encrustations (up to 7 cm) without a clear ecological succession in microencruster assemblages consisting almost exclusively of BMC and nubeculariids.
- The colonization of BMC by other organisms occurs when the BMC are dead. Some thicker encrustations are laminated, showing rhythmic growth of BMC, as Olóriz et al. (2003) and Reolid et al. (2005) proposed for microbial laminated fabrics from Oxfordian sediments of the Prebetic. For these authors, growth breaks would be favourable for nubeculariid settlement. Leinfelder et al. (1993a) interpret the frequency of sparitic peloidal crust fabrics, even within a general micritic setting, as an indicator of the early hardening of encrusting structures resulting from encrustation episodes. If this

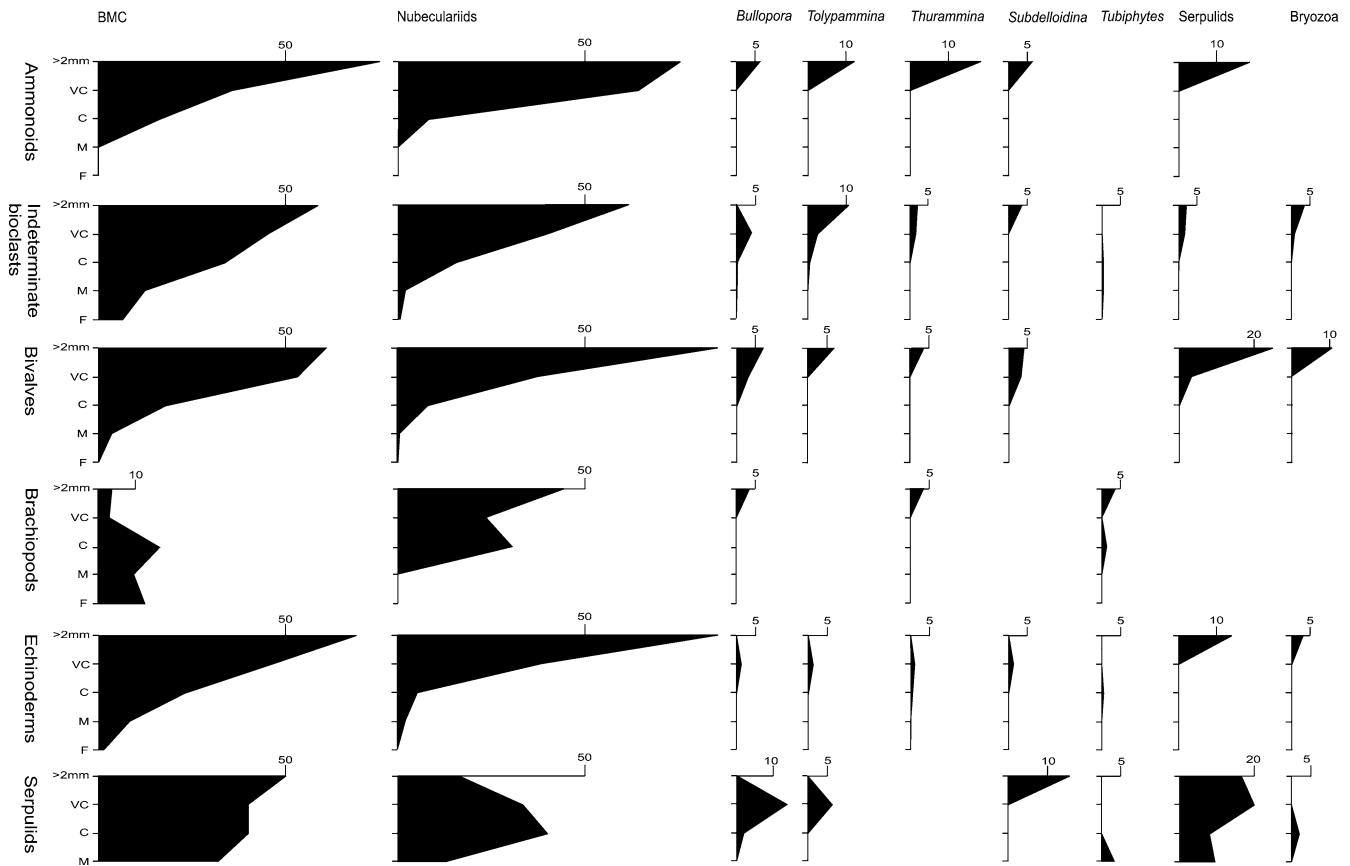


Fig. 7 Importance of different microencrusters (BMC, nubeculariids, *Bullopora*, *Tolypammina*, *Thurammina*, *Subdelloidina*, *Tubiphytes*, serpulids and bryozoans) in relation to nature (ammonoids,

indeterminate mollusc bioclasts, bivalves, brachiopods, echinoderms and serpulids) and size of bioclasts. *F* fine, *M* medium, *C* coarse; *VC* very coarse

possibility is correct, we must consider the overgrowth ability index of BMC as invalid, because the encrustation over BMC was not produced during the life of the microbes. This possibility is incompatible with a commensal relationship between microbes and nubeculariids as proposed by Gradzinski et al. (2004). However, laminated encrustations of BMC are not very frequent in the microfacies studied, and they appear mainly on larger siliceous sponges (Olóriz et al. 2003).

- (c) BMC might present a rhythmic growth with faster and slower growth stages. The encrustation on BMC by other organisms would occur during slower growth phases. But this possibility would only be applicable to thicker, laminated encrustations developed over larger macroinvertebrate remains (sponges and ammonoids) as described by Olóriz et al. (2002, 2003, 2004) and Reolid et al. (2005). In those examples, nubeculariids are located mainly—but not exclusively—inside the microbialite.

We cannot reject a combination of these three possibilities. Reolid et al. (2005) consider an aggressive growth of the BMC, with other microencrusters only growing during slower growth phases or after the BMC died (except for nubeculariids and *Subdelloidina*, which may have co-existed with the microbes). The problem in interpreting microencruster fossil assemblage successions lies in deter-

mining interactions among contemporaneously living organisms.

Possible trophic relationships

Until now, we have considered the foraminifera-BMC record as a competition for space, but it is also possible to consider it as a close interspecific interaction (mutualism and commensalism). The co-occurrence of sessile foraminifera and BMC is not fortuitous according to Peryt and Peryt (1975), who consider this to be a life association, and possibly symbiotic (*Tolypammina*?-cyanophytic algae). The relation between the thickness of microbial encrustations and the diversity of microencruster assemblages has been linked with possible changes in ecological and chemical properties of the microhabitat. In this sense, foraminifera were probably very dependent on nutrient availability, using microbes as a stable food source, like certain present-day foraminifera (Bernhard and Bowser 1992). The abundance of microbial encrustations with nubeculariids could be interpreted as a close interspecific interaction of microbes and foraminifers well adapted to oligotrophic conditions, according to Gradzinski et al. (2004). For these authors, sessile foraminifera (nubeculariids and *Tolypammina*) and microbes (possibly

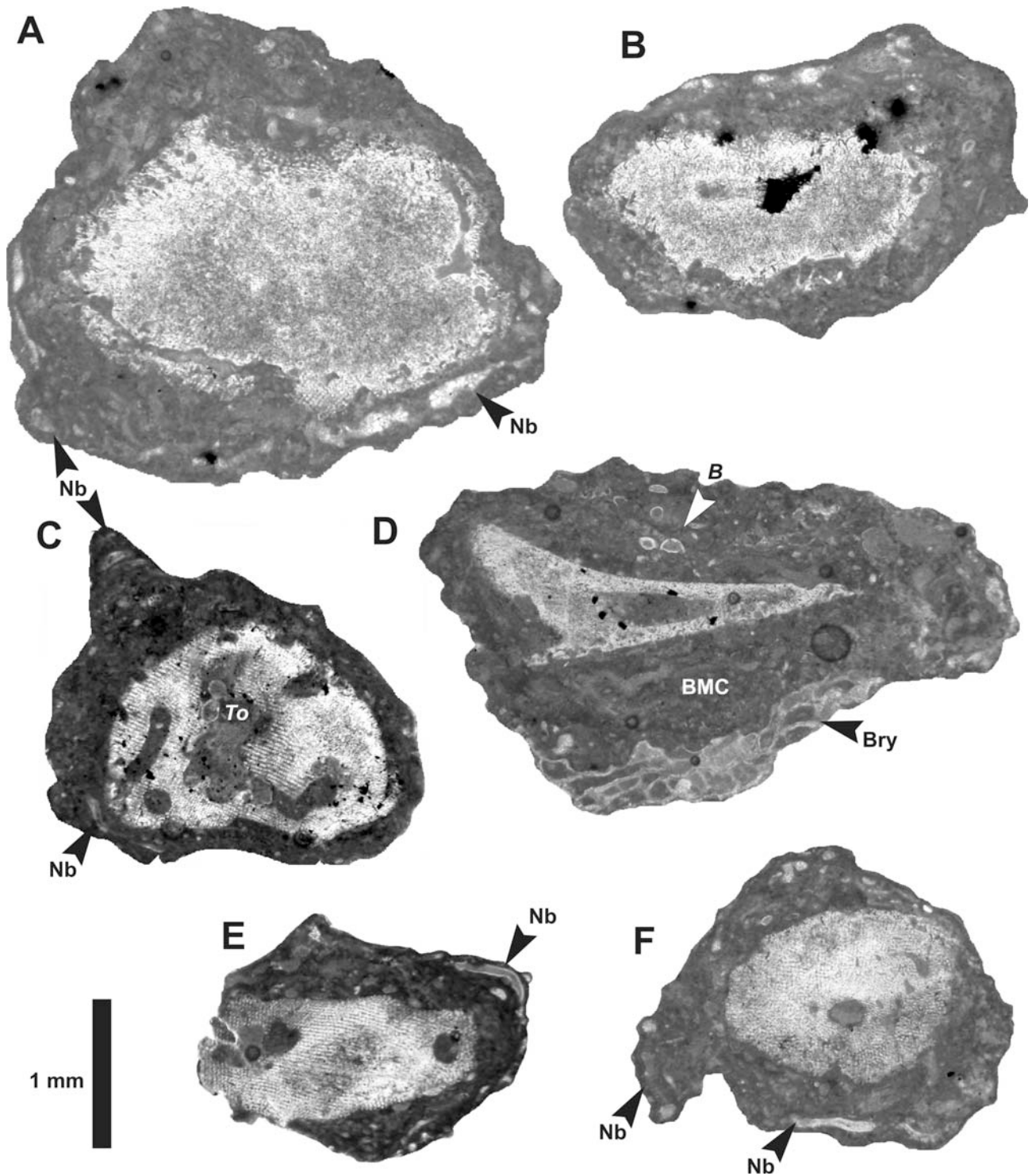


Fig. 8 Microencrustations on fragments of echinoderms forming oncoïds. **A** Oncoïd showing a nucleus with long superficial microborings and a thick coat composed of BMC and nubeculariids. **B** Typical oncoïd where the nucleus is a microbored fragment of echinoderm coated by BMC and nubeculariids. **C** Idem. The nucleus is densely microbored and shows some *Tolypammina* inside a microboring. **D**

Idem. The coat is very thick and locally includes bryozoans and *Bulloporea*. **E–F** Idem. The coat shows several superimposed generations of nubeculariids forming an irregular lamination. *Scale bar* 1 mm. *B* *Bulloporea*; *BMC* benthic microbial communities; *Bry* bryozoans; *Nb* nubeculariids; *To* *Tolypammina*

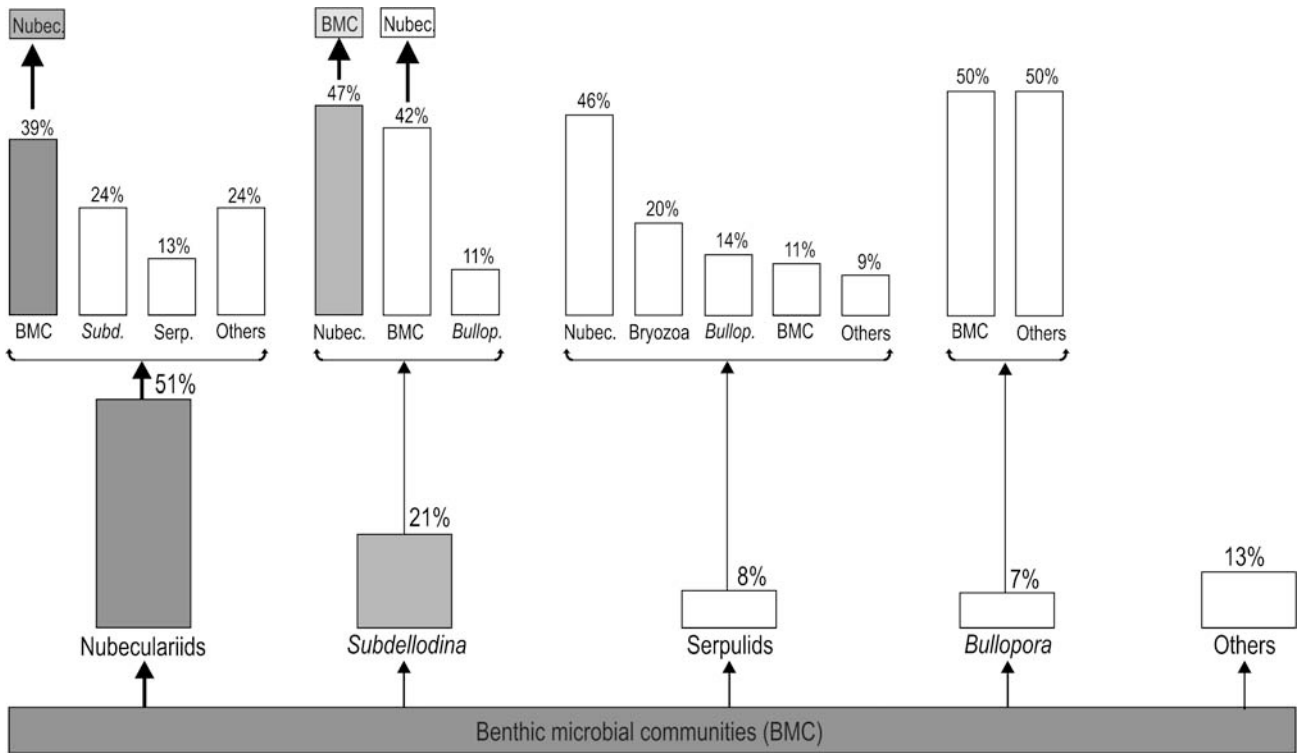


Fig. 9 Inferred interactions among microencrusters, illustrated by the different observed encrustation sequences. The most probable sequence is shown in a darker colour

cyanobacteria) were closely related through commensal relationships, where microbes and biofilms served as a food source for encrusting foraminifers. Moreover, the possibility that BMC took advantage of nutrient-rich foraminiferal excretions can not be rejected. Peryt and Peryt (1975) indicate that the sessile foraminifera-cyanophytic algae association was probably symbiotic. Competition and commensal relationships are equally difficult to demonstrate from fossil assemblages. Nonetheless, *Tubiphytes* is widely interpreted as representing a symbiotic coexistence between a nubeculariid foraminifera and microbial crust (s. Leinfelder et al. 1993a; Nose 1995; among others).

Preferential colonization

The differential colonization of siliceous sponges by microencrusters is well known in Jurassic microbialitic deposits (Palmer and Fürsich 1974; Gaillard 1983; Leinfelder et al. 1993a; Olóriz et al. 2003; Olivier 2004). Interestingly, this phenomenon has also been observed here, with very

small substrates. The largest bioclusters studied exhibit microencrusters that are significantly different on their upper and lower surfaces. This is clearly related to the stability of the substrate and also evidences a fundamentally low-energy environment (Reolid et al. 2005). The development of coated grains, meanwhile, indicates a free movement of grains on the seafloor during colonisation by encrusting organisms; yet it does not imply high water energy, given the high porosity and low density of oncoids (Verrecchia et al. 1997). BMC, nubeculariids and *Subdellodina* preferentially occur on upper surfaces while serpulids and *Bullopora* display a preference for lower surfaces. *Thurammina*, *Tolypammina* and bryozoans are found almost exclusively in lower surfaces, occupying protected, less illuminated parts of bioclusters, and thus showing cryptobiontic behaviour (Kobluk 1988). This microencruster distribution might be attributed to three phenomena that are not mutually exclusive:

- (a) Possible photic control. BMC are probably cyanobacteria which need light for photosynthesis, whereas some

Table 4 Overgrowth ability index (Taylor 1979) of the microencruster, including BMC (upper row) and excluding BMC (lower row)

Microencrusters	BMC	Nubec.	Bullop.	Tolyp.	Thuram.	Subde.	Serpulids	Bryozoa	Tubiphy.
Overgrowth ability index	21	69	82	54	61	77	40	74	69
		49	83	58	25	62	22	73	75

microencrusters, such as bryozoans or serpulids, are sciaphilous (Gaillard 1983; Fernández-López 1987).

- (b) The possibility of avoiding space competition with BMC, which thrives on upper surfaces. Sessile animals are concentrated on lower surfaces of available substrates, which are easier to colonize (Palmer and Fürsich 1974; Gaillard 1983). In the case of bryozoans, they are interpreted as poor space competitors (McKinney and Jackson 1989; Nebelsick 1992).
- (c) The possibility of avoiding predation, with a preferential location of small sessile animals on undersurfaces of available substrates, where microencrusters are less visible and situated in a better protected habitat.

Conclusions

In this paper, we analysed the microtaphonomic traits of the Upper Jurassic spongiolithic limestones from Pozo Cañada section with special attention given to microencruster assemblages. The bioclasts studied are the remains of echinoderms, molluscs, brachiopods, serpulids and ostracods, mainly of the sand size interval and the minority coarser fraction. The main conclusions of this study are:

- (1) The bioclasts show high fragmentation and frequent microborings, the latter increasing according to bioclast size. Microencrustation is higher in serpulids and mollusc (ammonoids and bivalves) bioclasts and lower in bivalve larval shells and ostracods.
- (2) The main components of microencrustations are BMC and nubeculariids. Secondary components are calcareous foraminifera (*Bullopore*, *Tubiphytes*), siliceous agglutinated foraminifera (*Tolypammina*, *Thurammina*, *Subdelloidina*), serpulids and bryozoans.
- (3) Encrustation increases along with the size of bioclasts, both in thickness and in microencruster diversity. This is probably related to a higher stability and time exposition of the available bioclastic substrate.
- (4) Colonization of skeletal parts was mainly after the death of organisms, first by microendolithic organisms and later by microencrusters.
- (5) BMC were usually the first microencrusters, located principally on the upper surface of bioclasts. Nubeculariids are more frequent in the coarse (up to > 2 mm) size interval. Other foraminifera encrust almost exclusively on bioclasts > 2 mm.
- (6) Microencruster relationships can be interpreted as active competition for substrate space, but the possibility of a foraminifera-BMC consortium is considered as an alternative. Both competition and commensal relationships are difficult to demonstrate from fossil assemblages.
- (7) The largest bioclasts studied exhibit a differential distribution of microencrusters in their upper and lower surfaces. BMC, nubeculariids and *Subdelloidina* preferentially occur on upper surfaces, while serpulids and *Bullopore* show a preference for lower surfaces.

Thurammina, *Tolypammina* and bryozoans encrust almost exclusively lower surfaces, occupying protected, less illuminated parts of bioclasts. Such a pattern of microencruster distribution could be related to photic control, space competition with BMC, and/or predation avoidance.

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