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The 'sediment dilemma' in fossil microbialites: a review of the factors controlling the 'trapping and binding' process

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KEYWORDS

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ABSTRACT

Trapping and binding of allochtonous grains by benthic microbial communities has been considered a fundamental process of microbialite accretion since its discovery in popular shallow-marine modern examples (Bahamas and Shark Bay). However, agglutinated textures are rare in fossil microbialites and, thus, the role of trapping and binding has been debated in the last four decades. Recently, renewed attention on this subject has produced new findings of fossil agglutinated microbialites (mainly formed by 'trapping and binding' and analogous to modern examples), but they are still few and geologically recent (post-Paleozoic) when compared to the 3.5 Ga long record of microbialites. This discrepancy in the presence of trapped grains between modern and fossil microbialites is known as the 'sediment dilemma'. Here, an extensive literature review is provided to create the first thorough database of modern and ancient agglutinated microbialites, which shows that all of them are formed in shallow-marine environments and most under tidal influence. In addition, a Lower Cretaceous case example is described, including very diverse microbialites, each of them formed in a particular paleoenvironment. Some of those microbialites developed in grainy settings, but only those formed in marginal-marine tide-influenced environments accreted mainly by trapping and binding the surrounding grains, being analogous of modern agglutinated microbialites, and matching the environmental pattern observed in the literature database. The combination of the literature review with the case study presented here allows to discuss the factors that control and enhance 'trapping and binding': a) occurrence of grains in the microbialite environment; b) frequent currents that mobilize the grains and supply them onto the microbialite surface; c) high concentration and diversity of electrolytes in water to increase the adhesiveness of the extracellular polymeric substances (EPS) of the microbialite surface; and d) $CaCO_3$ saturation state not so high as to promote early and strong carbonate precipitation within EPS, which would eventually decrease its availability to adhere grains. Therefore, this review shows that the keys to solve the 'sediment dilemma' may be environmental, because the conjuction of those hydrodynamic and hydrochemical parameters is preferentially achieved in shallow-marine

settings and especially in those influenced by tides, at least since Mesozoic times. This explains the limited environmental and stratigraphic distribution of microbialites mainly formed by 'trapping and binding', and opens new ways to look, geologically and microbiologically, at this process, so often cited and yet so rare.

1. INTRODUCTION

Microbialites are organosedimentary deposits formed or influenced by benthic microbial communities since ~3500 Ma (Burne & Moore, 1987; Riding, 1991a; 2011a; Dupraz et al., 2009; 2011). Many different biotic and abiotic processes are involved in the development of these deposits (e.g. Monty, 1976; Riding, 2000; 2011a; Arp et al., 2001a; 2012; Dupraz et al., 2009; 2011; Bosak et al., 2013), but the original definition of 'microbialites' highlighted two specific roles of the microbial communities (e.g. microbial mats, biofilms) in their origin: "trapping and binding detrital sediment and/or forming the locus of mineral precipitation" (Burne & Moore, 1987). Mineral precipitation within microbial communities is currently considered the main driving mechanism of microbialite formation (e.g. Dupraz et al., 2009; Bosak, 2011; Reitner, 2011; Riding, 2011a), but the process of 'trapping and binding' of allochtonous particles by microbialites has received historically much attention because it is the dominant accretion process in the well-studied modern specimens of Bahamas (e.g. Black, 1933; Dill et al., 1986; Reid et al., 2000) and Shark Bay, Australia (e.g. Logan, 1961; Reid et al., 2003; Jahnert & Collins, 2012). Despite the importance of 'trapping and binding' in these modern microbialites, fossil analogues mostly formed by this process (i.e. agglutinated microbialites) are scarce and, thus, the significance of this process in the long geological record of microbialites has been debated for more than four decades (e.g. Monty, 1972; Serebryakov & Semikhatov, 1974), with the consequent accumulation of different views and hypotheses and confusing terminologies.

The concept of 'sediment dilemma' was coined by Browne (2011) precisely to address the discrepancy between the popular modern agglutinated microbialites and the scarceness of

fossil analogues. “In comparing modern stromatolites with ancient examples, what do we do with the coarse sediment [*that modern examples agglutinate*]?” (Browne, 2011; p. 307). In fact, the literature review analyzed here shows that the processes behind grain agglutination by microbialites are not well understood yet: how, where and when do agglutinated microbialites exactly form?; which factors control them?; are those factors intrinsic (biotic) or extrinsic (environmental)? To answer these questions, Browne (2011) suggested that it may be necessary to look not only at marine examples, but to combine them with examples from other settings (e.g. alkaline and/or hypersaline; p. 308). Following that suggestion, this article presents a dual approach aiming to provide new keys for this long-standing dilemma, through the combination of a thorough literature review (covering modern and fossil microbialites formed in different settings) with a fossil case study. The case study is especially relevant because it presents Lower Cretaceous coastal deposits that show an unusual diversity of microbialites (not only stromatolites, Fig. 1), some formed by trapping and binding of grains and some others not, but with the peculiarity that each of them is associated with a different paleoenvironment, ranging from freshwater to hypersaline and including shallow marine examples, which allows to link each microbialite type to the specific factors that influenced their accretion processes. The combination of the results of this case study with the literature review shows that a complex interplay of factors is necessary for a microbialite to develop mainly through ‘trapping and binding’ (i.e. agglutinated microbialite), and it also shows that this process seems to have a strong environmental control, being highly influenced by the hydrodynamic and hydrochemical conditions where the microbialite develops. Furthermore, the exhaustive literature review of agglutinated microbialites (conducted here for the first time) suggests that those environmental conditions suitable for grain agglutination are most easily achieved in specific environments, mainly shallow marine, and especially those with tidal influence. Therefore, this study presents an in-depth approach to the four-decade long debate of agglutinated microbialites, not only pinpointing the factors that control the often-cited process of ‘trapping and binding’, but also opening new ways to discuss and to clarify the dilemma of its scarceness and its temporal and spatial distribution through the geological record.

2. TERMINOLOGY

The study field of microbialite research has now more than a century of history (Riding, 2011b) and during that time the discipline has accumulated a significant amount of terminology, which is continuously being discussed, revised and updated (e.g. Hofman, 1969; Walter, 1972; 1976; Krumbein, 1983; Grey, 1984; Riding, 1999; 2011a; Dupraz et al., 2011; Myshrall et al., 2012; Harwood Theisen & Sumner, 2016). Therefore, it is always advisable to clarify the meaning of the terms and methods used. In this article, the characterization of microbialites will follow the traditional multiscale approach (e.g. Preiss, 1976; Grey, 1984; Shapiro, 2000; Vennin et al., 2015), separately describing the macroscopic (i.e. outcrop), mesoscopic (i.e. hand specimen) and microscopic (i.e. thin section) features. The general classification of microbialites (e.g. stromatolite, thrombolite...) will be based, as commonly done, on their internal structure at mesoscale (presence/absence of lamination, etc.; e.g. Kennard & James, 1986; Braga et al., 1995; Dupraz et al., 2011). More specific classifications within the general categories (e.g. micritic stromatolite, agglutinated thrombolite, etc) are normally carried out according to microscopic features of microbialites (e.g. Riding, 1991; 2000; 2011a; Schmid, 1996; Dupraz et al., 2011). Here, the term 'microfabric' will be used to referer to the microscopic features of a particular area of a microbialite (a lamina, a clot…), since it is a term traditionally used in carbonate petrology (e.g. Bathurst, 1993; and references therein) that encompasses both textural and structural aspects (Flügel, 2010, p. 177). Thus, the description of the different microfabrics analyzed in this article will emphasize the relationships between the different components observed under the microscope (e.g. grains, matrix, cements…; cf. Rezak & Lavoie, 1990; Vennin et al., 2015; Harwood Theisen & Sumner, 2016). A microfabric of particular interest to this study is the 'agglutinated microfabric', and the microbialites dominated by this microfabric will be thus classified as 'agglutinated microbialites'. The term 'agglutinated' was first applied to microbialtes by Riding (1991a, p. 30) to refer to "stromatolites produced by trapping of particulate sediment" (Riding, 1999, p. 325, changed

'particulate sediment' for "allochtonous particles" in the definition), and it is preferred here to the term 'coarse-grained' (*sensu* Awramik & Riding, 1988, and often used as somehow synonymous, cf. Suarez-Gonzalez et al., 2014; Frantz et al., 2015), in order to avoid confusions with the Udden-Wentworth grain-size scale (cf. Folk, 1954). Thus, 'agglutinated' is applied here to microfabrics that are dominated by allochtonous, generally sand-sized particles, which can be confidently interpreted as trapped and bound by the original microbial community that formed the microbialite (see criteria in Frantz et al., 2015), as it is observed in popular modern agglutinated microbialites (e.g. Bahamas and Shark Bay). The scarcity of fossil analogues of these modern examples is the basis of the 'sediment dilemma' investigated here, and therefore it is fundamental for this study that the fossil agglutinated microfabrics are clearly comparable with the modern ones (i.e. rich in allochtonous, carbonate, sand-sized material). For this reason, 'fine-grained agglutinated' microbialites (*sensu* Riding, 1991a), those dominated by micritic microfabrics without sand-sized grains, but interpreted as formed by trapping and binding of the micrite, are not considered here, since they are very rarely described, their interpretation is challenging (Riding, 2000; Tosti & Riding, 2017), and they are not analogues of the aforementioned modern marine agglutinated examples.

3. MATERIAL AND METHODS

The literature review presented here has covered an extensive database, compiled by the authors, of research studies about microbialites of all ages and environmental settings. From this database, all the microbialite examples showing clear evidence of the accretion process of 'trapping and binding' were selected. Tables 1 and 2 show a compilation of all the examples found of modern and fossil agglutinated microbialites (i.e. those mainly formed by 'trapping and binding' of particles and which are analogous of the modern examples of Bahamas and Shark Bay where that process was first described). Examples of microbialites only partially

including agglutinated microfabrics are not listed in the tables, but are included and discussed in the text.

In addition to the literature review, this work includes a Lower Cretaceous case study that provides crucial insights into the addressed issues. The results presented from the case study are based on detailed geological works (see Suarez-Gonzalez, 2015), including geological mapping of the whole outcrop area of the unit (approximately 500 km^2, Fig. 2) and logging of 12 complete stratigraphic sections (Fig. 4), measured with a dm-resolution and logged at 1:100 scale (or larger where details made it necessary, especially in microbialite-bearing deposits). Throughout these sections and in additional relevant outcrops, more than 800 samples (~200 of them from microbialites) were collected and at least one thin section (of 46x25 mm and/or 80x50 mm size) was prepared for each of them.

4. A BRIEF HISTORY OF 'TRAPPING AND BINDING': AN OLD DILEMMA STILL UNCLEAR

The concept of microbialite accretion due to 'trapping and binding' of clastic sediment is rooted on the earliest works about modern marine microbialites, and it can be traced back to Black (1933), who studied coastal microbial structures in Andros Island (Bahamas). He described the development of some of the structures as "the colonization of newly deposited sediment by filamentous algae" (i.e. cyanobacteria), which "bind together the sediment" because they are "enclosed in a mucilaginous sheath, to which mineral particles very readily adhere", and therefore "sediment brought into the region is at once trapped amongst the filaments" (p. 168). Ginsburg et al. (1954) later found microbial structures in south Florida that also accreted by 'trapping and binding', and they were the first to suggest an extrapolation of this process to the fossil record, proposing two main criteria for the recognition of ancient stromatolites: "detrital texture" of the laminae and "structures indicative of sediment binding" (pp. 30-31). Logan (1961) recognized columnar shallow marine stromatolites in Shark Bay

(Australia) formed by "binding of mechanically deposited sediment" (p. 517), and using those examples as referents, Logan et al. (1964) proposed a general definition of stromatolites as "laminated organosedimentary structures composed of particulate sand, silt, and clay-size sediment, which have been formed by the trapping and binding of detrital sediment particles" (pp. 69, 81). Further studies of these modern examples, and the recognition of similar agglutinated microbialites in other modern shallow-marine settings, such as Bermuda (Gebelein, 1969; 1976a), led to what Monty (1977) called the "trapping and binding dogma" (p. 22): the assumption that most fossil examples would also have mainly formed by trapping and binding of particles. Quite early in the evolution of that idea, some researchers were already opposing it (see Monty, 1972; 1977; Serebryakov & Semikhatov, 1974; and references in them), noting that agglutinated textures were very rare in fossil microbialites, a claim that kept being supported later (see Awramik & Riding, 1988; Ginsburg, 1991). In fact, it was not until the 90's (Riding et al., 1991a) that a clear fossil agglutinated microbialite, analogous to modern specimens, was described.

In the last decades, the knowledge about modern agglutinated microbialites has increased significantly (e.g. Dravis, 1983; Dill et al., 1986; Riding et al., 1991b; Reid et al., 1995; 2000; 2003; Macintyre et al., 1996; 2000; Feldmann & McKenzie, 1998; Sprachta et al., 2001; Planavsky & Ginsburg, 2009; Jahnert & Collins, 2012; 2013; Suosaari et al., 2016a; see Table 1), but fossil counterparts are still rarely described (Table 2). Despite this scarcity, and although nowadays it is widely recognized that the main process of microbialite development is *in situ* mineral precipitation within microbial communities (e.g. Dupraz et al., 2009; Bosak, 2011; Reitner, 2011; Riding, 2011a), the 'trapping and binding dogma' seems to be still permeated in the general geological knowledge, as it can be seen in popular science books (e.g. Zalasiewicz, 2008, p. 97), many textbooks (e.g. Chernicoff et al., 1997, p. 934; Lunine, 1999, p. 134; Marshak, 2009, p. 301; Stanley, 2009, p. 119; Grotzinger & Jordan, 2014, p. 295; Tarbuck & Lutgens, 2014, p. 760), and even in more specialized sedimentological works (e.g. Collinson et al., 2006, p. 174). Maybe because of this persistence of the 'dogma', the 'sediment dilemma'

has recently gained new attention (Browne, 2011; Suarez-Gonzalez et al., 2014; Frantz et al., 2015), trying to shed light on this peculiar organo-sedimentary process, ubiquitous in scientific literature but elusive through geologic time.

5. AGGLUTINATING PRESENT AND PAST

The concept of 'trapping and binding' as an accretion process of microbialites was originally developed in modern examples, and then theoretically extrapolated to the fossil record (see previous sections), proposing that it may have been a fundamental and widespread accretion process of microbialites during their long geological history. Here, the published examples of modern and ancient agglutinated microbialites (summarized in Table 1 and 2), and even of those only partially including grains in some of their microfabrics, are compiled, compared and discussed.

5.1 Modern examples of agglutinated microbialites

The fact that sedimentary particles adhere very easily to the sticky surface of benthic microbial communities has long been realized (e.g. Carey & Oliver, 1918). Nevertheless, the discovery of agglutinated microbialites (accretionary organosedimentary structures with positive relief that build up mainly by binding successive layers of adjacent particles) is due to Black (1933), who described small domes in the coast of Andros Island (Bahamas), which were internally formed by grain-rich laminae (Table 1). And so was born the concept of microbialite accretion by 'trapping and binding', but it did not attain its later repercussion until Ginsburg et al. (1954) and Logan (1961) described similar structures in coastal settings of Florida (USA) and Shark Bay (Australia), respectively, proposing them as analogues for the whole geological record of microbialites. Since then, the specimens of Bahamas (e.g. Monty, 1965; 1967; Dravis, 1983; Dill et al., 1986; Reid & Browne, 1991; Riding et al., 1991b; Feldmann, 1995; 1997; Feldmann & McKenzie, 1998; Reid et al., 1995; 2000; Macintyre et al., 2000; Visscher et al., 2000; Andres & Reid, 2006; Planavsky et al., 2009; Planavski & Ginsburg, 2009; Bowlin et al.,

2012), Shark Bay (e.g. Logan et al., 1964; 1974; Playford & Cockbain, 1976; Hoffman, 1976; Playford, 1979; Golubic, 1985; Awramik & Riding, 1988; Reid et al., 2003; Jahnert & Collins, 2011; 2012; 2013; Burne & Johnson, 2012; Playford et al., 2013; Hagan, 2015; Suosaari et al., 2016a; 2016b) and Florida (Ginsburg, 1960; Gebelein, 1977) have been intensively studied (Table 1), but very few further examples have been found so far: Bermuda Islands (Gebelein, 1969; 1976a), French Polynesia (Sprachta et al., 2001) and Cuba (Bouton et al., 2016a). These examples are all agglutinated stromatolites or thrombolites, but also agglutinated oncoids have locally been described in the coasts of Florida (Ginsburg, 1960), Bahamas (Gebelein, 1976a) and Cayman Islands (Jones & Goodbody, 1985).

The environments where all modern agglutinated microbialites have been observed are consistently coastal and very shallow marine (normally <10 m deep, but on average <2 m, Table 1), with brackish, normal-marine or hypersaline salinities, and generally with tidal influence or within restricted lagoons (Table 1). This limited environmental distribution contrasts with the wide range of settings in which modern microbialites occur outside of the marine realm (e.g. Golubic, 1991; Dupraz et al., 2011; Della Porta, 2015; Chagas et al., 2016). In all those varied settings, 'trapping and binding' of grains is very seldom cited as a relevant accretion process in modern microbialites, which do not show clear well-developed agglutinated microfabrics, since grains are in general only locally or sporadically included within them (e.g. Jones, 1991; Winsborough et al., 1994; Castro-Contreras et al., 2014; Della Porta, 2015; Brasier et al., 2018). In fact, since the very first description of agglutinated microbialites, Black (1933) noted this interesting contrast in the distribution of 'trapping and binding', describing not only the marginal marine agglutinated specimens (see previous section 4), but also other structures developing in neighboring freshwater settings, which consisted of "radiating filaments, without much interstitial sediment" (p. 170). Therefore, the present-day microbialite record suggests an environmental distribution of the accretion process of 'trapping and binding' and of agglutinated microbialites, limited to coastal and shallow-marine settings, commonly with tidal influence.

5.2 Fossil analogues of agglutinated microbialites

Despite the popularity of the 'trapping and binding' process in the microbialite literature since the 60's, it was not until the 90's that actual fossil agglutinated microbialites, clearly analogous to modern counterparts, were described, and their geological record is still relatively poor (Table 2). Riding et al. (1991a) showed that 'trapping and binding' was the main accretion process of large Messininan (Miocene) microbialites in Almería, SE Spain. These specimens became very popular and have been further studied (Braga et al., 1995; Bourillot 2009; Bourillot et al., 2010a, b; Goldstein et al., 2013), being interpreted as formed in shallow-marine high-energy environments, in which the relative influence of waves, storms and tides is debated (Table 2). Similar Miocene agglutinated microbialites have been described in Mallorca (E Spain) by Arenas & Pomar (2010), being also interpreted as formed in shallow-marine environments with alternating calm and agitated periods. Other Miocene microbialites that may not be classified as agglutinated, but which also include some allochtonous grains in their microfabrics are described by Irtem (1987) from tidal flat paleoenvironments of E Saudi Arabia. In addition to all these Miocene examples, Pliocene shallow-marine oncoids from an uplifted atoll in New Caledonia display micritic microfabrics with abundant trapped grains (Pederson et al., 2015).

Older than the Miocene, agglutinated microbialites are very scarce. Suarez-Gonzalez et al. (2014; 2016a) described Lower Cretaceous agglutinated stromatolites from La Rioja (Spain), deposited in the distal tide-influenced areas of coastal wetlands. Some Upper Jurassic agglutinated microbialites have been cited by Matyszkiewicz et al. (2006; 2012) in shallow high-energy marine paleoenvironments from Poland, and three Triassic examples of agglutinated microbialites have been described (Woods, 2013, Nevada, USA; Vennin et al., 2015, Utah, USA; Mercedes Martín, 2013; Mercedes-Martín et al., 2013a, b, 2014, NE Spain), all of them formed in environments interpreted to be shallow-marine and commonly with tidal influence. Throughout the Mesozoic, there are other examples of microbialites that include trapped grains only in some of their microfabrics (Achauer & Johnson, 1969; Leinfelder et al.,

1994; Herrmann, 1996; Immenhauser et al., 2005; Rodríguez-Martínez et al., 2012; Quijada et al., 2015; 2016), but which are not considered agglutinated microbialites as a whole. All of these partly-agglutinated Mesozoic examples are also interpreted to be deposited in shallow-marine peritidal settings, with the exception of those described by Acosta et al. (1988) and Massari & Westphal (2011) in Jurassic deep marine *Ammonitico Rosso* facies, which also show trapped and bound grains in some of their microfabrics.

In Paleozoic rocks there is, to our knowledge, only one example of microbialites almost exclusively formed by trapping and binding of grains, those described by Chow & George (2004) from the Late Devonian of W Australia, interpreted as deposited in high-energy shallow-subtidal settings. Beside this case, other Paleozoic microbialites, formed in shallow marine peritidal settings (Słowakiewicz et al., 2013, Upper Permian; Wright & Wright, 1985, Lower Carboniferous; Warusavitharana & Parcell, 2013, Lower Ordovician; Harwood Theisen & Sumner, 2016, Cambrian) have been described to include allochtonous particles only in some of their microfabrics, and therefore are not analogues of modern agglutinated examples.

Also not clearly analogous to modern agglutinated examples (which trap mainly carbonate particles), are some rare cases of microbialites that include abundant siliciclastic sediment. These 'sandstone' (*sensu* Davis, 1968), 'sandy' (*sensu* Schwarz et al., 1975) or 'siliciclastic' (*sensu* Martín et al., 1993) microbialites have been described in the Miocene (Martín et al., 1993; Braga & Martín, 2000) and the Cretaceous (Marcinowski & Szulczewski, 1972) but mainly, although sporadically, through the Paleozoic: in the Cambrian (Soudry & Weissbrod, 1995), Ordovician (Davis, 1968), Devonian (Draganits & Noffke, 2005), Carboniferous (Bertrand-Sarfati, 1994), and Permian (Harwood, 1990). All these examples were formed in environments interpreted to be shallow marine or coastal, and most of them with tidal influence.

The aforementioned examples show that purely agglutinated microbialites are quite rare during the Phanerozoic (Table 2), but their scarcity is much more remarkable throughout their 3000 Ma-long Precambrian history. Throughout this long period, trapping and binding was an

infrequent accretion process (Awramik & Riding, 1988; Sami & James, 1996; Knoll & Semikhatov, 1998; Altermann, 2008; Planavsky & Grey, 2008; Bosak et al., 2013), with few mentions of microbialites that only partially or locally include grains within their microfabrics (Walter, 1972; Horodyski, 1976; Fairchild, 1991; Allwood et al., 2009; Martindale et al., 2015; Fedorchuk et al., 2016; Siahi et al., 2016), thus being not clear analogues of the modern marine examples.

In summary, the literature review presented here shows that fossil agglutinated microbialites have been continuously rare through Earth history, in comparison with the abundant and diverse spectrum of fossil microbialites. The few described agglutinated examples seem to be consistently formed in shallow- and marginal-marine settings under agitated conditions, commonly with tidal influence (Table 2). Moreover, the non-agglutinated microbialites that include trapped grains in some of their microfabrics are also mostly found in shallow-marine facies, with those of the Jurassic *Ammonitico Rosso* being the exception to this pattern. In fact, the literature also shows that in non-marine paleoenvironments allochtonous grains are rarely a significant component of microbialite microfabrics (Frantz et al., 2014; Bunevich et al., 2017; Vennin et al., 2018). When grains are observed, it is commonly not in accretionary laminae but filling primary cavities within the microbialite structure (e.g. Freytet & Plet, 1996; Freytet, 2000; Suarez-Gonzalez et al., 2016a) or in cases where marine influence has been suggested and should not be ruled out (Arp et al., 2005). Therefore, both the modern and ancient record of agglutinated microbialites suggest a link between the accretionary process of trapping and binding and shallow-marine environments often agitated and commonly by tidal currents, which deserves to be investigated in further detail.

6. A CRETACEOUS MICROBIAL PARADISE TO CLEAR UP THE DILEMMA

The Lower Cretaceous Leza Fm (La Rioja, N Spain) includes one of the few fossil examples of agglutinated stromatolites (Table 2), with some of its microfabrics being

remarkably similar to those of modern agglutinated counterparts, and also formed in marginal-marine settings (Suarez-Gonzalez et al., 2014). But besides the agglutinated specimens, this unit includes many other microbialites (Fig. 1; Table 3), some with and some without agglutinated microfabrics, and each of them formed in different paleoenvironments, ranging from alluvial to shallow-marine (Suarez-Gonzalez et al., 2015). Thus, this unit not only is an interesting case study to explore the environmental parameters that may influence microbialite development, but it is also an optimal example to scrutinize the environmental constraint of the trapping and binding accretion process (shown by the literature review presented here), and to shed light into the dilemma of why trapped and bound grains are so rare in the geological record of microbialites (Browne, 2011).

The Leza Fm belongs to the Cameros Basin (Fig. 2), which developed during the Late Jurassic (Tithonian)-Early Cretaceous (Early Albian) extensional phases of the Iberian Plate, over a pre-extensional Jurassic substrate, dominated by carbonates (Figs. 2C, 3A; Mas et al., 1993; Benito et al., 2001; Salas et al., 2001; Benito & Mas, 2002; 2006; Mas et al., 2002; 2011; Suarez-Gonzalez et al., 2013; 2016b; Omodeo Salè et al., 2014; Sacristán-Horcajada et al., 2015). Throughout its evolution, this basin recorded up to 6500m of siliciclastic, carbonate and minor evaporite sediments deposited in continental, coastal and shallow-marine environments (Mas et al. 2011; Quijada et al., 2013a; 2013b; 2016; Suarez-Gonzalez et al., 2013; 2016a; Omodeo Salè et al., 2014; Mas et al., 2018). During the late Barremian-early Aptian extensional phase, the Leza Fm was deposited at the distal northernmost margin of the basin (Fig. 2), in a series of small tectonic depressions formed by faulting of the Jurassic substrate of the basin (Fig. 3A; Suarez-Gonzalez et al., 2013). Erosion of the faulted substrate led to deposition of alluvial fans in the margins of the depressions, which changed laterally to carbonate coastal wetlands (Figs. 2D, 3A) formed by a complex mosaic of diverse environments with influence of both freshwater and marine water (Suarez-Gonzalez et al., 2015). Being a tectonically-controlled system, this unit shows significant variations in thickness and in facies distribution (Figs. 3, 4). Two main paleogeographic sectors are distinguished, western and eastern, with

relevant sedimentological differences between them (Figs. 2D, 4): input of clastic deposits was stronger in the western sector, whereas marine influence wass stronger and more direct in the eastern sector (Suarez-Gonzalez et al., 2015). However, a general trend of upwards increase in marine influence is observed in both sectors (Fig. 4; Suarez-Gonzalez et al., 2013). Given this general setting, the Leza Fm includes a wide variety of interrelated facies, grouped in five facies associations, all of them including microbialites, and each of them corresponding to a different paleoenvironmental setting (Figs. 2D, 4, 5), as described and interpreted in detail by Suarez-Gonzalez et al. (2015). Here, only the key features of each paleoenvironment are summarized, focusing later on the microbialites and the facies in which they occur.

6.1 General paleoenvironmental settings of the microbialites

The *alluvial fan paleoenvironments* were characterized by conglomerates and sandstones with very abundant lithoclasts from the Jurassic substrate of the Cameros Basin, being interpreted as systems that transported material eroded from the basin substrate (Figs. 2D, 3A, 5A). Alluvial fan facies are often interbedded with limestones that commonly include the same lithoclasts (Figs. 4, 5; and see below), suggesting that part of the material transported by the alluvial fans was deposited within the shallow water bodies that formed the carbonate coastal-wetlands of the Leza Fm (Suarez-Gonzalez et al., 2015). These paleoenvironments included locally oncoids, and paleosols were often developed over alluvial fan deposits. The *freshwater to marine-influenced wetland paleoenvironments* were characterized by black, fetid and locally bituminous limestones, and less common marls, which are the most widespread deposits of the unit (Figs. 2D, 4), being generally arranged in thickening upwards sequences up to 4 m thick, with abundant desiccation and edaphic features at their top (Figs. 5B-D). Thus, these deposits are interpreted as formed in wide wetland areas with abundant shallow water-bodies with continuous periods of desiccation and inundation, surrounded by vegetated areas. Lithoclasts of Jurassic rocks occur, indicating lateral association with the alluvial fan paleoenvironments and suggesting that the source of freshwater to the water bodies was related to the erosion and dissolution of the carbonate-dominated Jurassic substrate of the basin

(Suarez-Gonzalez et al., 2013; 2015). These wetland paleoenvironments had a rich biota, including ostracods, charophytes, dasycladales, gastropods and vertebrate remains, as well as abundant microbialites (oncoids, skeletal stromatolites and thrombolites). Oncoids are especially abundant, commonly forming sandy cross-bedded sequences interpreted as small oncoid-rich creeks associtated with the water bodies (Fig. 5D). Despite the presence of freshwater (e.g. charophytes) and marine (dasycladales) fossils, these do not typically occur together within the same sequence (Figs. 5B-C), pointing at different degrees of marine influence within these paleoenvironments, producing water bodies with diverse salinities, from fresh to near-marine (Suarez-Gonzalez et al., 2015). The *peritidal wetland paleoenvironments* were only distributed in the western sector of the studied area (Figs. 2D, 4) and are characterized by thinly-bedded gray limestone deposits, interpreted as formed in very shallow and often desiccated coastal water bodies with a marine signature stronger than the previous paleoenvironments (Suarez-Gonzalez et al., 2015), due to a different biotic composition, dominated by ostracods, miliolid foraminifers and gastropods, as well as fenestral laminites (Fig. 5E), which are widely interpreted as record of periodic accretion and desiccation of microbial mats in very shallow peritidal settings (e.g. Logan, 1974; Hardie & Ginsburg, 1977; Shinn, 1983; Mazzullo & Birdwell, 1989; Demicco & Hardie, 1994). Peloids, intraclasts and silt-sized quartz grains are also common in these facies, together with desiccation and edaphic features, which indicate alternating episodes of inundation and desiccation. The *tide-influenced oolitic paleoenvironments* were only recorded in the eastern sector (Figs. 2D, 4) and they were characterized by oolitic deposits with sedimentary structures that indicate influence of tidal currents (Suarez-Gonzalez et al., 2015; 2016a), laterally and vertically associated with agglutinated stromatolites, flat-pebble breccias and desiccation features (Fig. 5F). Locally pseudomorphs after evaporites occur within stromatolite laminae. Besides the stromatolites, the biotic community of these paleoenvironments included ostracods, and miliolid foraminifers. Therefore, these depostis are interpreted as formed in shallow tide-influenced areas of the distal part of the coastal wetland system, closer to the marine realm. These areas were commonly subaerially exposed and they were dominated by seawater, although salinity may have been

very variable due to influence of freshwater from proximal areas of the system and/or to desiccation (Suarez-Gonzalez et al., 2014; 2015). The *evaporitic paleoenvironments* were only distributed in the eastern sector and they were laterally associated with the tide-influenced oolitic paleoenvironments (Figs. 2D, 4). They were characterized by laminated dolomitic deposits with abundant pseudomorphs after gypsum and anhydrite and locally including micritic-evaporitic stromatolites (Fig. 5G). The biotic community of these paleoenvironments was very poor (only rare ostracods and miliolid foraminifers) and desiccation episodes were very common. Thus, these paleoenvironments were very shallow and relatively restricted marine-influenced areas, which commonly reached high salinity through evaporation (Suarez-Gonzalez et al., 2015).

6.2 Linking microbialite accretion processes and their paleoenvironments

The case study presented here includes a remarkable diversity of microbialites, comprising most of the wide array of macro-, meso- and micro-structures that characterize these organosedimentary deposits (Fig. 1; Table 3; cf. Kennard & James, 1986; Riding, 1991a; 2011a; Dupraz et al., 2011). Interestingly, each microbialite variety occurs within a particular facies and in a particular paleogeographic sector (Figs. 2D, 4, 5), suggesting an important environmental control in the development of microbial structures. Here the different microbialites will be described, highlighting their relationship with the surrounding sediment, in order to interpret their accretion processes and the environmental factors that may have controlled them.

6.2.1 Oncoids: Oncoids are the most abundant microbialites, occurring in the freshwater to marine-influenced wetland facies and in the alluvial fan facies, and in both eastern and western sectors (Figs. 2D, 4, 5B-D). They are most common in limestones rich in charophytes (which form often the nuclei of oncoids) and in clastic-rich limestone beds with cross-bedding and irregular bases (Figs. 5B, D, 6A-B). Therefore, oncoids developed in shallow water-bodies dominated by freshwater and in small channels or creeks associated with them and

linked to alluvial fans that delivered lithoclastic material eroded from the substrate of the basin (Figs. 2D, 5A-D). Most oncoids are <4cm in diameter, but specimens up to 15 cm have been observed and they range from ellipsoidal to subspherical (Fig. 6). Internally, oncoid cortices are very well laminated (Fig. 6C), with laminae (50 μm to 2 mm thick) that either surround completely the oncoid (i.e. "plenicinct", *sensu* Hofmann, 1969, or "concentric", *sensu* Freytet & Plaziat, 1972) or cover only a portion of it (i.e. "penecinct", *sensu* Hofmann, 1969, or "polarized", *sensu* Freytet & Plaziat, 1972). Erosive surfaces are also observed truncating previous laminae (Fig. 6C). Various microfabrics are observed in the oncoid laminae, including micritic and clotted-peloidal, but filamentous microfabrics are conspicuously predominant, characterized by well-preserved calcified filaments (<1 mm long with 5-15 μm lumina surrounded by thinner micritic walls), showing an erect orientation perpendicular to the laminae (Figs. 6C- F). Filaments are arranged either as closely-packed palisades or as tufts radiating from a single point (Figs. 6C, E). In spite of occurring in bioclastic and clastic-rich facies, oncoids do not commonly include allochtonous material in their microfabrics, with only local and minor silt-sized quartz grains being observed within micritic laminae. Some oncolitic levels show a laminated (i.e. stromatolitic) or dendritic overgrowth that covers various oncoids (Figs. 6B, E, F). Stromatolitic overgrowths have filamentous microfabrics markedly different than those of the oncoid cortices, with much thicker laminae (up to 7 mm thick) formed by fan-like structures of longer and thicker (13-30 μm lumina) filaments (Fig. 6F), which are similar to those of skeletal stromatolites (see section 6.2.3, below). Dendritic overgrowths are composed of millimetric shrub-like structures with common branching, formed by thin filaments similar to those observed within the oncoid laminae.

Accretion processes and paleoenvironment: Oncoid filaments have sizes and shapes consistent with those traditionally considered as the calcified sheath of fossil filamentous cyanobacteria (e.g. Pollock, 1918; Pia, 1927; Black, 1933; Johnson, 1961; Golubic, 1973; Pentecost, 1978; Merz, 1992), being almost identical to the filaments of many cyanobaterial-dominated modern freshwater and fluvial microbialites (e.g. Irion & Müller, 1968; Ordóñez et

al., 1986; Freytet & Plet, 1996; Freytet & Verrecchia, 1998; Arp et al., 2001b; Shiraishi et al., 2008; Arenas et al., 2014;2015; Auqué et al., 2014), and even to those formed in the freshwater-influenced areas of coastal systems (e.g. Bahamas, cf. Black, 1933; Monty, 1967; 1972; 1973). In fact, similar fossil filaments have been taxonomically classified as different cyanobacteria genera: *Scytonema*, *Phormidium*, *Calothrix* and/or *Dichothrix* (Monty, 1976; Schäfer & Stapf, 1978; Anadón y Zamarreño, 1981; Monty & Mas, 1981; Nickel, 1983; Leinfelder, 1985; Arenas et al., 2000; Hägele et al., 2006). The filaments that dominate the stromatolitic overgrowths of oncoids are clearly different and more similar to those of the cyanobacteria genus *Rivularia* (e.g. Schäfer & Stapf, 1978; Nickel, 1983; Leinfelder, 1985; Dragastan, 1985; Kuss, 1990). Thus, these oncoids could be classed within the 'cyanoid' variety (*sensu* Riding, 1983) and it is interpreted that the main process that formed them was the recurrent accretion and early mineralization of cyanobacteria-dominated biofilms that surrounded a clastic nucleus. The freshwater and fluvial paleoenvironments of these oncoids, linked to alluvial discharges of clastic material eroded from the carbonate-dominated substrate of the basin, suggest that they developed in aquatic environments rich in dissolved carbonate, which matches the environmental setting of modern oncoids rich in calcified filaments (e.g. Roddy, 1915; Jones & Wilkinson, 1978; Schäfer & Stapf, 1978; Rott, 1991; Freytet & Plet, 1996; Hägele et al, 2006). In these settings, the combination of carbonate supersaturation with the metabolic activity of cyanobacteria led to carbonate precipitation within their sheaths (e.g. Kempe & Kazmierczak, 1990; Merz-Preiß, 2000; Arp et al., 2001a). The grainy facies where the oncoid often occur, together with the presence of plenicinct laminae and truncations in the oncoid cortices, suggests that they accreted in agitated environments, but the presence of penecinct laminae indicates that there were also periods of quietness or periods when the hydrodynamic energy was not enough to continuously overturn the oncoids (cf. Dahanayake, 1977; Lanés & Palma, 1998; Campos-Soto et al., 2016). Nevertheless, despite the agitation of the environment and the abundance of particles, these were very rarely incorporated within the oncoid cortices, unlike in some modern (Ginsburg, 1960; Gebelein, 1976a; Jones & Goodbody, 1985) and fossil (Pederson et al., 2015) shallow-marine agglutinated oncoids. When the environment changed towards longer periods of

quietness and/or the oncoids were too large for common overturning, oncoid accumulations were covered by stromatolitic or dendritic overgrowths, probably formed by different microbial communities, as shown by their different microfabrics.

6.2.2 Thrombolites: Thrombolites also occurred in the freshwater to marine-influenced wetland paleoenvironments, but they have only been observed in one locality of the western sector (Leza River section, Fig. 4), and they occur in limestones rich in dasycladales (Fig. 5C). Thrombolites form either laterally continuous beds (biostromes), up to 30 cm thick (Fig. 7A), or irregular masses (bioherms), up to 50 cm tall and 1m wide, within thicker beds (Figs. 7B-D). Macro- and mesoscopically, these microbialites are not laminated and have irregular shapes with patchy or clotted fabrics, formed by interconnected mesoclots (*sensu* Shapiro, 2000) with a vague upwards-elongated distribution that suggests vertical growth (Figs. 7C-D) and, thus, they can be classified as thrombolites (cf. Aitken, 1967; Kennard & James, 1986; Shapiro, 2000; Riding, 2011a). The internal framework of mesoclots is very open, leaving many interstitial spaces (cf. fenestrae) that are currently filled by micrite and/or cement, commonly forming geopetal structures (Figs. 7E-H). Using the classes differentiated by Harwood Theisen & Sumner (2016), these examples would be either 'bushy', 'mottled' or 'amoeboid' thrombolites. In hand specimen, mesoclots are irregular, 0.1-1 cm wide masses (Fig. 7E), and under the microscope, their internal microfabric is typically poorly preserved and dominated by microsparitic textures with relicts of clotted-peloidal micrite (Figs. 7F-H). Locally, poorly preserved filamentous structures are observed (Fig. 7G). The interstitial space between mesoclots often includes dasycladales (Figs. 7H-I), and in the specimens richest in dasycladales, these are also included within the mesoclots (Fig. 7H).

Accretion processes and paleoenvironment: Thrombolites formed locally in areas of the coastal-wetland system with significant seawater influence (Fig. 2D), which allowed the development of abundant dasycladales (Suarez-Gonzalez et al., 2015). The clotted-peloidal microfabric of the thrombolite mesoclots is widely regarded as the product of carbonate precipitation within microbial mats (e.g. Monty, 1976; Kennard & James, 1986; Thompson et

al., 1990; Chafetz & Buczynski, 1992; Reitner, 1993; Arp et al., 1998; Dupraz et al., 2004; Riding & Tomás, 2006; Spadafora et al., 2010). Thus, it is interpreted that the thrombolites represent microbial communities that accreted developing buildups or laterally continuous beds, and which were relatively early lithified, in order to preserve their original framework. The highly porous and seemingly delicate appearance of this framework suggests a quiet environment, and the general absence of clastic particles in the thrombolites and in their adjacent sediment further support an overall quiet setting, also excluding trapping and binding as a significant process. Nevertheless, the local presence of dasycladales within the mesoclots indicates that these bioclasts could be transported by episodic currents from adjacent algal meadows, being eventually bound within the microbial communities. However, the fact that thrombolites developed mostly without incorporating dasycladales proves that trapping and binding was not relevant to their accretion. In any case, the close interrelation between dasycladales and microbialites is extremely rare (Martin & Delgado, 1980) and deserves further work to be fully understood.

6.2.3 Skeletal stromatolites: Stromatolites also occurred in the freshwater to marine-influenced wetland paleoenvironments, but only in the western sector (Figs. 2D, 4). They occur within sandy limestone and sandstone levels, up to 50 cm thick, which are composed of poorly-sorted quartz grains, ooids, Jurassic lithoclasts, bioclasts (ostracods, charophytes and gastropods) and intraclasts (Fig. 5B), interpreted as marginal areas of shallow fresh-water bodies with common input of clastic material, probably delivered by the alluvial fans of the system (Fig. 2D), which transported lithoclastic material eroded from the substrate of the Cameros Basin (Suarez-Gonzalez et al., 2015). Stromatolites typically show a morphology of laterally linked domes up to 30 cm high (Figs. 8A-B), and less commonly stratiform or columnar morphology, with columns up to 10 cm high and 5 cm thick (Fig. 8D). Mesoscopically, stromatolites are very well laminated with a clear alternation of darker and lighter laminae up to 8 mm thick (Figs. 8B-D). Laminae are wavy with very common 'cauliflower-like' or botryoidal micro-domes (up to 1 cm tall), and show moderate to very poor

inheritance (Figs. 8C-E). They are dominated by filamentous microfabrics (Figs. 8E-G) and, for this reason, they could be classified as biophoric stromatolites (*sensu* Hofmann, 1973), skeletal stromatolites (*sensu* Riding, 1977), porostromate stromatolites (*sensu* Monty, 1981) or filamentous-calcimicrobial stromatolites (*sensu* Turner et al., 2000). Although the term 'skeletal stromatolite' has been debated (Golubic & Campbell, 1981; Monty, 1981; Burne & Moore, 1987), it is preferred here due to its more widespread and recent use (e.g. Rasmussen et al., 1993; Arp, 1995; Arp et al., 2005; MacNeil & Jones, 2006; Sarg et al., 2013). Laminae of the skeletal stromatolites show different microfabrics (Suarez-Gonzalez et al., 2016a), but are dominated by the *filament fans microfabric*, formed by long erect filaments (<2 mm long with lumina 9-38 μm thick surrounded by a <10 μm thick micritic wall), which radiate from a single point, creating fan-like structures (Figs. 8C, E-F). Despite being laterally associated with grainy facies, particles of these facies are not constituents of the skeletal stromatolite microfabrics, although grain accumulations are observed in the space between stromatolite columns (Fig. 8D), in small depressions between filament fans (Figs. 8E, 9) or filling concave irregularities between successive stromatolite laminae in domal forms (Figs. 8B-C, E).

Accretion processes and paleoenvironment: The filaments that dominate the skeletal stromatolites correspond to those traditionally considered fossil filamentous cyanobacteria (e.g. Pollock, 1918; Pia, 1927; Black, 1933; Johnson, 1961; Golubic, 1973; Pentecost, 1978; Merz, 1992), and the size and shape of their abundant filament fans are equivalent to those interpreted as formed by cyanobacteria of the extant genus *Rivularia* (e.g. Schäfer & Stapf, 1978; Nickel, 1983; Leinfelder, 1985; Dragastan, 1985; Kuss, 1990; MacNeil & Jones, 2006), similar to the filaments observed in the overgrowths of oncoids (see section 6.2.1, above; compare Figs. 8E-G with Fig. 6F). The extraordinary preservation of the filament microstructure suggests a very early precipitation of carbonate in the mucilaginous sheath of cyanobacteria, which is favored by their photosynthesis, but it is a process strongly controlled by environmental factors, mainly carbonate saturation state (e.g. Kempe & Kazmierczak, 1990; Merz, 1992; Arp et al., 2001; 2012; Riding & Liang, 2005; Aloisi, 2008). The paleoenvironment of these skeletal stromatolites had probably a high carbonate supersaturation, given that it was

linked to alluvial discharges of clastic material eroded from the carbonate-dominated substrate of the basin (Figs. 2D, 3A, 5B). Clastic discharges were probably episodic, as shown by the thin grainy intercalations between stromatolite laminae or between filament fans (Figs. 8-9). However, within the stromatolites, the grains are only filling cavities or surface depressions, indicating that trapping and binding did not play a significant role in the development of these stromatolites, which mainly accreted through the early calcification of cyanobacteria-dominated microbial mats (Fig. 9). Similar modern stromatolites, dominated by well-preserved filamentous microfabrics, also occur in carbonate-rich freshwater settings (e.g. Caudwell, 1983; Pentecost, 1987; Obenlüneschloss, 1991) or within the freshwater-influenced areas of coastal systems (Portman et al., 2005; Smith et al., 2005; Gischler et al., 2008; 2011; Cooper et al., 2013; Castro-Contreras et al., 2014; Saint Martin & Saint Martin, 2015; Edwards et al., 2017), such as that of the studied skeletal stromatolites.

6.2.4 Agglutinated stromatolites: The tide-influenced oolitic paleoenvironments only occurred in the eastern sector (Figs. 2D, 4), and are characterized by lateral and vertical interrelation of oolitic deposits and stromatolites, which range from stratiform to domal, with domes up to 70 cm across and 40 cm tall (Figs. 5F, 10A-C). At mesoscale, they show a clear lamination formed by alternating darker and lighter laminae up to 4 mm thick (Figs. 10B-C; Suarez-Gonzalez et al., 2014). Under the microscope, these laminae show two end-member compositions: grainy and micritic microfabrics (Figs. 10D-E). The grains observed within the stromatolites are the same as those of the surrounding oolitic deposits (ooids, peloids, micritic intraclasts, ostracods and miliolid foraminifers), but generally finer-grained, and they occur throughout the stromatolite domes, including the steeply dipping flanks (Fig. 10D). Micritic laminae typically show clotted or clotted-peloidal microfabrics (Figs. 10D, 11D-E). Laminae of intermediate composition, including both micrite and grains, are also very common (Figs. 10D, 11, 12). In fact, lateral and vertical variations in the relative abundance of both components are often observed through the same lamina (Fig. 12). In addition, thin micritic crusts are also observed topping many stromatolite laminae, they have dense micritic or clotted textures and

show sharp upper surfaces commonly associated with micritized and truncated grains (Figs. 9, 10E, 11, 12; Suarez-Gonzalez et al., 2014). Filaments are not abundant but are observed within some laminae, typically preserved as vertically elongated clusters of clotted-peloidal micrite, which locally display fan-like arrangement (Fig. 11). Locally, rare pseudomorphs after sulfates (gypsum and anhydrite) have been observed in some samples, displacing and replacing stromatolite laminae (Suarez-Gonzalez et al., 2014).

Accretion processes and paleoenvironment: The most distinctive feature of these stromatolites is the abundance of grains in their laminae. The facts that grains are the same as in the adjacent deposits, but finer, and that they occur both in flat and dipping stromatolite laminae, prove that those grains were not deposited merely by gravity, but rather suggests that they were often mobilized by currents (tides, waves and storms, Suarez-Gonzalez et al., 2015; 2016a; Fig. 9) and eventually stuck to the mucilaginous surface of the microbial mats that formed the stromatolites (cf. the criteria used to interpret trapping and binding in modern agglutinated examples: e.g. Gebelein, 1969; Riding et al. 1991; Reid & Browne, 1991; Frantz et al., 2015). Therefore, trapping and binding can be considered a significant accretion process in them, and for this reason, they are classified as "agglutinated stromatolites" (*sensu* Riding, 1991a). Nevertheless, the presence of micritic laminae without trapped grains indicates that these stromatolites accreted not only when grains were supplied to the microbial mats, but also during periods of sediment stasis and no grain supply (Fig. 12; Suarez-Gonzalez et al., 2014), a fact that has only recently been suggested for the classical examples of modern agglutinated microbialites in Shark Bay (Hagan, 2015; Suosaari et al., 2016a). The presence of calcified filaments, which probably represent remains of filamentous cyanobacteria (cf. Monty, 1976; Reid et al., 1995; Planavsky et al., 2009), further indicates that the original microbial mats could accrete without grain supply. The fact that these filaments are scarce and poorly preserved (Fig. 11; unlike other microbialites of the same unit, i.e. oncoids and skeletal stromatolites, Figs. 6, 8) suggests that they did not undergo very early calcification, and that micrite of the agglutinated stromatolites precipitated during subsequent microbial degradation of the organic matter of the mat (Figs. 9, 12; cf. Chafetz & Buczynski, 1992; Reitner, 1993; Arp et al., 1998; Dupraz et al., 2004; Riding

& Tomás, 2006; Planavsky et al., 2009). In addition, laminae of mixed grainy-micritic composition record variations in grain supply and mat accretion even at the relatively short time-scale represented by a single stromatolite lamina (Fig. 12). Thin micritic crusts, common at the top of laminae, are strikingly similar to those thoroughly studied in modern marine agglutinated examples (e.g. Monty, 1976; Reid et al., 1995; 2000; 2003; Macintyre et al., 1996; Feldmann & McKenzie, 1998; Visscher et al., 2000) and, thus, they are similarly interpreted as the product of microbially induced alteration and precipitation at the top of microbial mats during hiatuses in stromatolite accretion (Figs. 9, 12; Suarez-Gonzalez et al., 2014).

6.2.5 *Micritic-evaporitic stromatolites*: Another type of stromatolite occurred locally in the evaporitic paleoenvironments, which were only developed in the eastern sector (Figs. 2D, 4). Stromatolites show domal morphologies with small laterally-linked domes up to 10 cm tall (Figs. 13A, C). They are very well laminated, and laminae are micritic with dense, clotted or clotted-peloidal microfabrics, which are often diagenetically altered (Figs. 13B, D). No filaments have been observed and grains occur very scarcely in rare laminae. Pseudomorphs after sulfates, from μm- to mm-scale, are very common within the stromatolites (Fig. 13D). The pseudomorphs displace and replace the surrounding micrite and they commonly disrupt lamination (Fig. 13D). Pseudomorphs also occur grouped in cm-scale macroscopic nodules (Fig. 13C).

Accretion processes and paleoenvironment: The restricted and evaporative marine-influenced areas, locally developed benthic microbial communities that accreted producing stromatolites. The absence of clear microbial filaments suggests that those microbial communities were not very early lithified and that micrite precipitation probably took place subsequently, induced during degradation of the organic matter of the mat (cf. Chafetz & Buczynski, 1992; Reitner, 1993; Arp et al., 1998; Dupraz et al., 2004; Riding & Tomás, 2006). The scarcity of grains in their paleoenvironment may explain that they are only rarely observed within the stromatolite laminae. Important evaporation produced significant supersaturation in

the interstitial waters within the stromatolites, allowing the precipitation of intrasedimentary evaporitic sulfates (cf. Schreiber and El Tabakh 2000; Warren 2006; Ortí 2010).

6.2.6 Fenestral laminites: The peritidal wetland paleoenvironments, only developed in the western sector (Figs. 2D, 4), included very abundant fenestral laminites (Fig. 5E). They are thinly-bedded and display flat irregular wrinkly lamination, formed by mm-scale alternations of micritic laminae and laminae of horizontally-elongated fenestrae (Figs. 14A-B). Fenestrae typically show irregular shapes (Figs. 14C-F) and locally have stromatactis-like structures with flat bases and irregular tops (Figs. 14D, F). Fenestral porosity is currently filled by geopetal sediment and cement (Figs. 14D-F), which locally shows gravitational or pendant growth texture. Micritic laminae have dense-micritic, clotted or clotted-peloidal microfabrics (Figs. 14D-F) with only local and poorly-preserved relicts of calcified filaments. Micritic laminae commonly include grains (Figs. 14D-E): peloids, carbonate intraclasts, quartz grains and bioclasts (ostracods and less common foraminifers). Some micritic laminae display vertical, often v-shaped, fractures filled by cement, which may represent mud-cracks (Fig. 14E).

Accretion processes and paleoenvironment: Fenestral laminites are widespread carbonate facies commonly found in peritidal carbonate settings from the Archean to the present (e.g. Logan, 1974; Hardie & Ginsburg, 1977; Pratt et al., 1992; Sumner & Grotzinger, 2004; Riding, 2008; Duda et al., 2016), being even considered "unequivocal intertidal deposits" (Tucker & Wright, 1990, p. 151). They are widely interpreted as being formed by the successive accretion, lithification and desiccation of microbial mats (e.g. Ham, 1954; Tebbutt et al., 1965; Shinn, 1983; Mazzullo & Birdwell, 1989; Demicco & Hardie, 1994). However, fenestral laminites are not commonly included in microbialite classifications, but they could be considered a type of stromatolite under most definitions of this term (see Riding, 1999). The clotted and clotted-peloidal micritic microfabrics observed in the studied examples confirm their microbial origin, as well as the rare relicts of calcified filaments. The fact that filaments are so rare and poorly-preserved, compared to other microbialites of the unit (i.e. oncoids and skeletal stromatolites), suggests that fenestral laminites did not undergo very early cyanobacterial

calcification, and that micrite precipitated during subsequent microbial degradation of the organic matter of the mat (cf. Chafetz & Buczynski, 1992; Reitner, 1993; Arp et al., 1998; Dupraz et al., 2004; Riding & Tomás, 2006). The grains observed within the micritic layers are the same as those observed in laterally associated facies (see section 6.1, above) and, thus, they were most likely mobilized from adjacent areas by waves or storms. In summary, fenestral laminites studied here were deposited in very shallow and commonly desiccated near-marine areas of a coastal-wetland system, which were often colonized by thin and flat microbial communities that evolved through successive episodes of accretion and desiccation, and which underwent input of grains that were trapped and bound within some of their laminae.

7. DISCUSSION

7.1 Can microbialite accretion processes be environmentally controlled?

Microbialites are extremely diverse organosedimentary structures and their diversity can be explained by the biotic complexity and variability of the microbial communities that formed them, as well as by the many different environments in which they develop (e.g. Dupraz et al., 2011; Riding, 2011a). This is especially appreciated in modern and ancient systems in which different microbialites occur in different settings (e.g. Black, 1933; Braga et al., 1995; Bourillot, 2009; Jahnert & Collins, 2013; Vennin et al., 2015). In this regard, the case study presented here shows an unusual abundance and diversity of microbial deposits, with six types of contrasting microbialites that occurred in different paleoenvironments (Figs. 1, 2D, 5, Table 3), ranging from alluvial-influenced freshwater to tide-influenced marginal marine. For this reason, this Lower Cretaceous example is a perfect field laboratory for analyzing the still open question of how biotic and abiotic factors interact for the development of microfabrics of fossil microbialites. Shedding light on that question is first necessary to later understand more concrete issues, such as the ‘sediment dilemma’, i.e. why are agglutinated microbialites so

scarce in the geological record and which factors control the 'trapping and binding' process that forms them.

7.1.1 Environmental controls on macroscopic aspects: Explaining the abundance and diversity of microbialites in the field laboratory presented here provides stimulating clues to unravel the development and distribution of fossil microbialites in general. The paleoenvironmental setting of this unit as a coastal wetland system was prone to a wide development of microbial deposits, because it was an extremely variable system, with many contrasting but adjacent subenvironments, which constantly underwent changes in salinity and/or inundation (Suarez-Gonzalez et al., 2015). This situation is common to many coastal systems (Frey & Basan, 1978; Baldwin et al., 2009; Wolanski et al., 2009; Davidson-Arnott 2010) and it is stressful for most metazoans (e.g. Brenchley & Harper, 1998) but typically favorable for the development of microbial communities (e.g. Telesh et al., 2013). This explains the relatively poor diversity of metazoan associations in the case study (Suarez-Gonzalez et al., 2015) and the strong productivity and preservation of organic matter (i.e. abundance of bituminous black limestones) and microbialites. In fact, modern coastal wetlands are considered one of the environments with highest productivity and preservation of organic matter, mainly microbial in origin (e.g. Amanieu et al., 1980; Guerloget & Perthuisot, 1992; Reed, 2005). But even more striking than the abundance of microbialites in the case study, is their diversity (Figs. 1, 2D). All the main macroscopic categories of microbialites (*sensu* Kennard & James, 1986; Riding, 1991; 2000; 2011; Schmid, 1996; Dupraz et al., 2011) are recorded: oncoids, stromatolites, thrombolites and fenestral laminites (Fig. 1). Each of these microbialite types occurred in a different paleoenvironment (Fig. 2D, Table 3), highlighting the traditional interpretation that environmental factors are the main controls of macrostructure and external morphology of microbialites (e.g. Logan et al., 1964; Hoffman, 1976; Semikhatov et al., 1979; Trompette, 1982; Ginsburg, 1991; Andres & Reid, 2006). However, this case study also shows that microscopic aspects of microbialites can be strongly dependent on external environmental parameters.

7.1.2 Environmental controls on microscopic aspects: Despite the remarkable macroscopic variety of microbialites in the case study, the highest diversity concerns their microstructures (Fig. 1, Table 3), because externally similar microbialites (e.g. domal and well-laminated stromatolites) may show different microfabrics (1 – skeletal; 2 – agglutinated; and 3 – micritic-evaporitic) when occurring in different paleoenvironments (1 – freshwater bodies with alluvial input; 2 – tide-influenced oolitic areas; and 3 – restricted evaporative areas), indicating that in each paleoenvironment a contrasting process dominated their accretion (1 – early filament calcification; 2 – 'trapping and binding' of grains; and 3 – pervasive micrite precipitation; Table 3, Figs. 1, 2D, 9). Development of microbialite microfabrics has been shown to be highly controlled by the intrinsic biotic composition and processes of the microbial communities that form them (e.g. Semikhatov et al., 1979; Trompette, 1982; Andres & Reid, 2006), but the fossil examples studied here, as well as some modern cases (Bowlin et al., 2012; Jahnert & Collins, 2013), show that the influence of extrinsic environmental factors in the variability of microbial communities (and, thus, on the diversity of microfabrics they produce) should not be underrated.

Another concrete example of environmental control on microstructures is provided by the fact that filamentous microbialites of the case study (oncoids and skeletal stromatolites, Figs. 6, 8) only occurred in freshwater-dominated paleoenvironments (Figs. 2D, 5), whereas the rest of microbialites (without abundant well-preserved filaments, Figs. 7, 10-14) occurred in paleoenvironments with various degrees of marine influence (Figs. 2D, 5). The most important factor controlling strong and early calcification of filamentous microbes (mainly cyanobacteria) is supersaturation in $CaCO_3$ of their ambient waters (e.g. Riding, 1982; Kempe & Kazmierczak, 1990; Merz, 1992; Arp et al., 2001; 2012; Riding & Liang, 2005; Aloisi, 2008), and therefore that is a crucial environmental requirement for the development of microbialites with filamentous microfabrics. In fact, it has long been noted that filamentous microbialites are extremely rare in marine environments since the Cretaceous until now, being practically restricted to freshwater settings (Monty, 1973; Gebelein, 1976b), a trend that has been explained

as due to the strong and continuous decline in $CaCO_3$ saturation state of surface sea-water at least since the Early Cretaceous (Arp et al., 2001; Ridgwell, 2005; Ridgwell & Zeebe, 2005; Riding & Liang, 2005; Planavsky et al., 2009; Aloisi, 2018). Therefore, the development of Cretaceous, Cenozoic and modern calcified filamentous microfabrics has been environmentally constrained to continental and coastal settings where freshwater could reach a strong $CaCO_3$ supersaturation, such as in the case study presented here (see sections 6.2.1 and 6.2.3, above).

The final link between microstructure and paleoenvironment provided by the studied unit concerns agglutinated microbialites. Both the case study and the literature review presented here, show that microbialites dominated by agglutinated microfabrics occur, throughout geological history, mainly in marginal marine environments, being especially abundant in those with evidence of tidal influence (see section 5 above and Tables 1-3). This pattern has not been studied in detail before, and it may be crucial for the resolution of the 'sediment dilemma' posed by Browne (2011), since it will provide clues to understand which biotic and environmental conditions favor 'trapping and binding' and which hinder it.

7.2 To trap or not to trap: factors controlling grain agglutination

Two main requirements have been traditionally referred to as essential for a microbialite to trap and bind the sedimentary grains of its surrounding (Burne & Moore, 1987; Riding, 2011a): a) most obviously, the presence of grains in the environment, together with the conditions necessary (i.e. sufficient water agitation) for the supply of those grains onto the microbialite surface; and b) a sufficient 'stickiness' of its surface.

7.2.1 Supplying grains: Microbialites are very often observed in grainy environments, particularly in those rich in carbonate particles (peloids, ooids, bioclasts…). The association of microbialites with grainy settings goes back to the Archean (e.g. Buck, 1980) and the Proterozoic (e.g. Horodyski, 1976; Grotzinger, 1989; Planavsky & Grey, 2008), and it is also common today (e.g. Bowlin et al., 2012; Jahnert & Collins, 2012; Bouton et al., 2016b). In the case study, various microbialite paleoenvironments were rich in grains that could potentially

be trapped within the microbialites (Fig. 15). Oncoids (Figs. 5A-D, 6), skeletal stromatolites (Figs. 5B, 8-9), fenestral laminites (Figs. 5E, 14), and agglutinated stromatolites (Figs. 5F, 9, 10-12), all occurred in grain-rich environments, but only those formed in marine-influenced settings (fenestral laminates and agglutinated stromatolites) trapped and bound those grains, especially the agglutinated stromatolites, formed in tide-influenced settings. In the freshwater examples (oncoids and skeletal stromatolites), grains are not significant components of their microstructures, dominated by filamentous textures (Figs. 6, 8-9). One possible explanation for this pattern could be that in the freshwater examples there was little and sporadic grain supply, or that the input of grains occurred after microbialite development. It is true that in the agglutinated stromatolites, the shallow marine tidal setting would provide continuous and cyclic currents (tides, waves and storms), facilitating a constant supply of grains onto the stromatolite surface. Nevertheless, many of the oncoids occur embedded in sandy matrix, and thus it is very likely that their freshwater environment was also continuously agitated (e.g. small channels or creeks; Suarez-Gonzalez et al., 2015), transporting the oncoids together with other smaller particles that, however, were not commonly incorporated into their laminae (Fig. 6). In the case of skeletal stromatolites, the grainy intercalations between stromatolite laminae or between filament fans (Figs. 8-9) show that grain input, although sporadic, was simultaneous with the stromatolite accretion. Similarly, many other fossil and modern examples of microbialites that developed in grainy and commonly agitated environments do not show significant grains trapped within their microfabrics (e.g. Kalkowsky, 1908; Cole & Picard, 1978; Neuhauser, 1987; Camoin et al., 1997; Paul & Peryt, 2000; Seard et al., 2013; Chidsey et al., 2015; Bouton et al., 2016b). In fact, only a few examples associated with shallow marine settings, and especially with tidal influence, do (Tables 1, 2). Therefore, other factors, in addition to the grain availability and the hydrodynamic agitation, are necessary to explain the environmental pattern observed in the distribution of agglutinated microbialites.

7.2.2 Sticking grains: Even if a microbialite accretes in a grainy environment, and if the grains are regularly and abundantly supplied onto it, those grains still have to be stuck

to its surface and bound by the microbial communities that form it, in order to achieve an agglutinated microfabric (Burne & Moore, 1987; Riding, 2011a; Frantz et al., 2015). The 'sticky' quality of these microbial communities is provided by their extracellular polymeric substances (EPS), which are responsible (among many other functions) for the cohesion of microbes with each other and for their adhesion to substrates (e.g. Sutherland, 1982; Characklis & Wilderer, 1989; Wingender et al., 1999). The mechanisms that provide this adhesive capacity to EPS are not fully understood yet (Gerbersdorf & Wieprecht, 2015), but many studies of microbial attachment to surfaces and of sediment biostabilization by microbial communities (e.g. Sutherland, 1982; Fletcher, 1988; Dade et al., 1990; Decho, 1990; Mayer et al., 1999; Staats et al., 1999; de Brouwer et al., 2005; Flemming et al., 2007; Spears et al., 2008; Gerbersdorf & Wieprecht, 2015; and references within them) have shown that one of its most relevant controls is the presence of abundant cations in the environment, facilitating electrostatic bridging between the anionic groups of polymers and the charged surfaces of substrates or sediment grains. Therefore, since EPS are secreted by the own microbes, the adhesiveness of a microbialite surface could be viewed as an intrinsic factor controlled by biotic features; however, given the influence of electrolyte concentration, extrinsic hydrochemical conditions of the environment could play a significant role. In this regard, some studies have described a pattern that relates the adhesive property of EPS with salinity: microbial communities of coastal and marine settings seem to stabilize sediment more effectively than those of freshwater settings, even though the latter may show higher abundance of EPS (Spears et al., 2007; 2008; Gerbersdorf & Wieprecht, 2015). Nevertheless, biostabilization of sediment by microbial EPS does also occur in freshwater environments (e.g. Droppo et al., 2007; Hagadorn & McDowell, 2012; Gerbersdorf & Wieprecht, 2015; Schmidt et al., 2015; Thom et al., 2015), but the higher abundance and diversity of dissolved ions in brackish and marine environments may enhance the ability of EPS to adhere to sediment grains (Spears et al., 2008). This present-day pattern is consistent with that shown by the literature review and the case study presented here, because modern and fossil agglutinated microbialites occur only in shallow marine environments, contrasting with the many non-marine microbialites that do not accrete mainly by 'trapping and

binding', despite occurring in grainy settings (e.g. Kalkowsky, 1908; Cole & Picard, 1978; Neuhauser, 1987; Camoin et al., 1997; Paul & Peryt, 2000; Seard et al., 2013; Chidsey et al., 2015; Bouton et al., 2016b; Suarez-Gonzalez et al., 2016; Table 3).

Furthermore, microbialite EPS form not only the sticky surface to which grains adhere, but they are also, and mainly, the locus of mineral precipitation (Burne & Moore, 1987; Dupraz et al., 2009; Riding, 2011a). Therefore, early mineral precipitation within the surface layer of microbialites should also be taken into account as another factor involved in the 'sediment dilemma'. In fact, studies approaching the 'trapping and binding' issue experimentally (using modern stromatolitic microbial communities), have considered the importance of this factor, pointing as a limitation of their tests the fact that they "did not evaluate the impact of mat calcification and stromatolite lithification" (Frantz et al., 2015; p. 417). The Cretaceous case study presented here may help to overcome that limitation through the analysis of its microbialites dominated by filamentous microfabrics (oncoids and skeletal stromatolites, Figs. 6, 8-9). As discussed above (sections 6.2.1, 6.2.3), those microbialites developed in freshwater environments where filamentous microbial communities (most likely cyanobacteria) were heavily calcified very early in their development, maybe even during their metabolic processes, as photosynthesis is known to promote the early precipitation of carbonate within filamentous cyanobacterial communities (e.g. Merz, 1992; Merz-Preiß, 2000; Arp et al., 2001). Since calcification takes place within and/or upon the EPS sheath of filamentous microbes (e.g. Golubic, 1973; Pentecost, 1978; Pentecost & Riding, 1986; Merz, 1992), the strong and early calcification would imply a significant reduction in the 'sticky' EPS available in the microbialite surface. Thus, very early and pervasive mineral precipitation could further decrease the ability of a microbial community to trap and bind sediment grains. This would explain the fact that the studied oncoids and skeletal stromatolites did not include abundant grains in their microfabrics (Fig. 15), despite being formed in grainy and agitated environments (Fig. 9). Conversely, microbes of the marine-influenced microbialites of the same sedimentary system (Table 3) were not as early, rapidly or pervasively calcified as in the freshwater examples

(probably due to a lower $CaCO_3$ saturation state, see section 7.1.2 above), allowing uncalcified 'sticky' EPS to be available for a longer time at the microbialite surface (Figs. 9, 12). Therefore, the ability of the surface EPS of a microbialite to adhere and include grains seems to be at least partially controlled by the hydrochemistry of its environment. In this regard, continental saline lakes are interesting environments to consider, because their hydrochemistry could provide abundant and diverse electrolytes to enhance EPS 'stickiness' (which could explain the local presence of trapped grains in sporadic examples, e.g. Brasier et al., 2018; Vennin et al., 2018), but at the same time saline lakes often have high alkalinity and reach high $CaCO_3$ saturation state (e.g. Arp et al., 1998; Dupraz et al., 2004; 2013; Brasier et al., 2018), which may trigger early precipitation within EPS and, thus, hinder the 'trapping and binding' process. Moreover, although continental saline lakes may have significant currents, these are less likely to be as common as in shallow-marine settings, continuously washed by waves, tides and storms. Thus, these hydrodynamic and hydrochemical features may explain the fact that agglutinated microfabrics are not widespread in modern or fossil microbialites formed in continental saline lakes; see section 5 above.

In summary, the previous discussion suggests that trapping and binding of grains by microbialites may be a process largely controlled by the following environmental factors (Fig. 15): a) the presence of grains in the environment, together with b) sufficient and continuous water agitation; and c) significant concentration and diversity of electrolytes, to increase the EPS 'stickiness', but d) with a $CaCO_3$ saturation state not so high as to promote early and strong carbonate precipitation in the EPS. Of course, intrinsic biotic factors also influence trapping and binding, as taxonomic differences between microbial communities entail differences in EPS production (e.g. Hu et al., 2003; Underwood & Paterson, 2003; Bahulikar & Kroth, 2008) or mineral precipitation (e.g. Obenlüneschloss & Schneider, 1991; Gautret et al., 2004). For example, some studies have shown that microbial communities with abundant eukaryotes (e.g. diatoms) are more effective in trapping and binding grains than purely bacterial communities (Awramik & Riding, 1988; Frantz, 2013; Frantz et al., 2015). but some of those works also

highlighted the role of extrinsic conditions (such as water flow) in the agglutination process (Frantz, 2013; Frantz et al., 2015), and thus, the environmental (sedimentological, hydrodynamic and hydrochemical) controls seem to be overall very strong (cf. Monty, 1972; Golubic, 1973; Gautret et al., 2006; Vennin et al., 2015).

7.3 Clearing up the 'sediment dilemma'

Ever since Black (1933) first described modern agglutinated microbialites in Bahamas and Logan (1961) in Shark Bay, the process of 'trapping and binding' was essential in microbialite research. But as much as it was essential, it was also misleading, because fossil agglutinated counterparts showing clear evidence of that process were extremely scarce (see section 4, above). This problem has been long debated (Monty, 1972; 1977; Serebryakov & Semikhatov, 1974; Awramik & Riding, 1988; Ginsburg, 1991) and is still unclear, leading Browne (2011) to pose the 'sediment dilemma', i.e. the question of why sediment particles are so rarely observed as main components of fossil microbialites, when they are so profusely trapped and bound within microbialites of Bahamas and Shark Bay. Interestingly, even the preponderance of the 'trapping and binding' process in those classical modern examples is also starting to be questioned (Suosaari et al., 2016a).

The present study pinpoints a series of environmental factors that seem to enable a microbialite to accrete mainly by trapping and binding allochtonous grains (see previous section 7.2). Both the literature review and the case study presented here show that only microbialites formed in environments that fully reach all the conditions show significant development of agglutinated microfabrics, and the best conjunction of conditions typically occurs in shallow-marine tide-influenced environments (Fig. 15, Tables 1-3). In fact, going back to the origin of the dilemma, Black's (1933) description of microbialites in the Bahamian coastal system, it is noteworthy that he already described that microbialites in freshwater-dominated areas of the system show early-calcified filamentous textures and lack trapped grains, whereas microbialites in adjacent shallow-marine areas (which can be even formed by the same microbes as the

freshwater speciments) lack significant early filament calcification and mainly accrete by trapping and binding, generating agglutinated microfabrics (Black, 1933; Monty, 1967; 1972; 1973). Moreover, microbialites of hypersaline areas of the Bahamian coastal systems typically develop micritic microfabrics, devoid of grains and of calcified filaments (Dupraz et al., 2004, 2013; Dupraz & Visscher, 2005), as it is also observed in the Cretaceous case study (Fig. 13, Table 3).

Furthermore, the geological record of agglutinated microbialites (reviewed here for the first time; Table 2), supports a strong environmental control on the process of trapping and binding, indicating that this process has been most easily achieved in shallow marine environments, especially those with tidal influence. According to the factors proposed here (Fig. 15), tides do not seem to be strictly necessary for 'trapping and binding'. In fact, other mechanisms such as waves or storms have also been proposed as relevant for the delivery of grains onto modern agglutinated microbialites (Dravis, 1983; Riding et al., 1991a; Feldmann & McKenzie, 1998; Sprachta et al., 2001). Actually, any grain-rich environment that would provide common agitation by any type of current, plus high electrolyte concentration to enhance EPS adhesiveness, and a carbonate supersaturation not too high as to promote strong early calcification of EPS, should be suitable for the development of agglutinated microbialites. Therefore, the answer to the 'sediment dilemma' may reside in the difficulty of reaching the "favorable conspiracy" (Bosak et al., 2013) of all those factors together and continuously, in order to promote 'trapping and binding' long enough to produce a whole agglutinated microbialite. That difficulty could explain why agglutinated microbialites have remained more an exception than a rule throughout their long geological history. For example, the scarcity of clearly agglutinated microfabrics in Precambrian microbialites might be linked to the commonly agreed interpretation that Precambrian oceans had a carbonate saturation state much higher than modern oceans (e.g. Grotzinger & Kasting, 1993; Grotzinger & Knoll, 1999; Bosak & Newman, 2003; Ridgwell & Zeebe, 2005; Aloisi, 2008). In the metazoan-dominated Phanerozoic world, microbialites in general were much less abundant than before (e.g. Riding, 1997; 2006;

Grotzinger & Knoll, 1999), but the decrease in seawater carbonate saturation allowed some agglutinated microbialites to develop, only sporadically and in local refuges: coastal or shallow-marine, often with tidal influence, where the rest of the factors controlling 'trapping and binding' were also achieved (Table 2). Furthermore, the rarity of agglutinated microfabrics outside marine or coastal settings, can be due to a combination of factors: a) that strong and continuously agitated conditions are more easily achieved in wave-, tide- and storm-swiped shallow-marine areas; b) that water in non-marine settings commonly includes lower electrolyte abundance and diversity than seawater (except in saline lakes, see section 7.2 above), probably decreasing EPS adhesiveness; and c) that microbialite-bearing environments in these settings (especially in saline lakes) are often supersaturated in $CaCO_3$, facilitating early mineral precipitation within EPS. Nevertheless, those factors are not necessarily unfeasible in continental settings, and the fact that some continental microbialites include sporadic grains within their microfabrics (e.g. Frantz et al., 2014; Della Porta, 2015; Bunevich et al., 2017; Brasier et al., 2018; Vennin et al., 2018), suggest that those conditions are at least locally and temporarily achieved.

Despite more than 50 years discussing about the 'trapping and binding' process in microbialites, it has continuously remained unclear, mainly due to the lack of a systematic and exhaustive review on that process and on the agglutinated microbialites that it produces. The last decade has seen great advancements on this issue, with the descriptions of the majority of fossil agglutinated examples (Table 2). The combination of a thourough literature review with an exceptional case study finally clears up the 'sediment dilemma', showing that agglutinated microbialites are rare throughout the geological record because the 'trapping and binding' process that forms them relies on a delicate combination of different factors, which seem to be most easily achieved only in some environments (shallow-marine, especially with tidal influence) and during some geological periods (mainly post-Paleozoic). The recent developments on this subject allow to foresee that future research will further enlighten the 'sediment dilemma', by finding new constraints on the 'trapping and binding' process in

microbialites, especially if new examples of agglutinated microbialites are described in pre-Mesozoic rocks or in non-marine settings.

8. CONCLUSIONS

This study provides the first exhaustive database of agglutinated microbialites (those mainly formed by 'trapping and binding' allochtonous particles) in modern and ancient settings. The database shows that agglutination of grains by microbialites, despite being an often-cited process, is relatively rare (a fact that has been noted before in the last four decades, but not comprehensively studied yet). Modern agglutinated microbialites have been found only in seven localities worldwide, all of them in shallow-marine environments, and most under tidal influence. Fossil agglutinated microbialites, analogous to modern examples, have been described only in nine localities worldwide, three Cenozoic in age, five Mesozoic and only one Paleozoic. All of them were formed in shallow-marine paleoenvironments and most are interpreted to have tidal influence. Therefore, the literature review shows that microbialites mainly formed by 'trapping and binding' are scarce throughout the long geological history of microbialites, and that they seem to be environmentally restricted to shallow-marine settings, and especially those influenced by tides.

A Lower Cretaceous case study is also presented here, which includes a wide diversity of microbialites (six different types) formed in a coastal wetland system, with paleoenvironments ranging from freshwater to shallow-marine and hypersaline. Four microbialite types occurred in grainy paleoenvironments, but those formed under freshwater conditions do not significantly include grains in their microfabrics, whereas those formed in marginal marine settings do, especially the agglutinated stromatolites, which developed in tide-influenced paleoenvironments. Thus, the case study supports the environmental pattern observed in the database of modern and fossil agglutinated microbialites.

The combination of literature review and case study prompts discussion about the parameters that control microbialite accretion processes and the microfabrics they produce, and it shows that environmental factors may have a stronger influence on microfabric development than previously thought. In particular, microbialite accretion through agglutination of allochtonous grains is mainly controlled by two extrinsic factors (occurrence of grains and continuous water agitation) and one intrinsic factor (presence of abundant 'sticky' EPS on the microbialite surface). However, literature suggests that the latter biotic factor may be largely influenced by two environmental parameters: high concentration and diversity of electrolytes in water, which increase EPS adhesiveness; and a $CaCO_3$ saturation state not so high as to promote early and strong carbonate precipitation within EPS, which would eventually decrease its availability to adhere grains. The combination of these hydrodynamic and hydrochemical parameters is not easily achieved, at least prolonged enough in time to produce a whole agglutinated microbialite. This is exemplified by the case study presented here and by the distribution of modern agglutinated microbilates, and it would explain the scareceness of agglutinated microbialites in the geological record. In addition, those parameters may also explain the environmental and stratigraphic distribution of agglutinated microbialites, because they are more prone to be attained in commonly agitated shallow-marine settings (especially those daily washed by tides), at least in post-Paleozoic times. Therefore, this review provides answers to the long-standing dilemma of the rarity of agglutinated microbialites and it also provides a starting point for future research on the widely cited but still intriguing process of 'trapping and binding' that forms them.

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FIGURE CAPTIONS

Table 1: Compilation of the examples of modern agglutinated microbialites found in the literature, including the information provided by the authors about their environment and their macro-, meso- and microstructures.

Table 2: Compilation of the examples of fossil agglutinated microbialites, clear analogues of the modern examples, found in the literature, including the information provided by the authors about their paleoenvironments and their macro-, meso- and microstructures.

Table 3: Summary of the main features of the Leza Fm microbialites, the Lower Cretaceous case study presented here, including information about their paleoenvironments and their macro-, meso- and microstructures.

Figure 1: Table illustrating the diversity of macro-, meso- and microstructures of the microbialites observed in the Lower Cretaceous case study (Leza Fm) used here to discuss the 'sediment dilemma'. Colors used in the microbialite names (left column) refer to the paleoenvironments of the microbialites, using the same color-code as in Figs. 2, 4, 5 and 15.

Figure 2: Geological setting of the case study presented in this work. **A:** Simplified geological map of the Iberian Peninsula, highlighting the location of the Cameros Basin within the Mesozoic Iberian Extensional System (MIES). **B:** Geological map of the Cameros Basin (modified after Mas et al., 2011) highlighting in green the outcrops of the Leza Fm, at the northern margin of the basin. Red square marks the location of the map included in D and in Fig. 4. **C:** Lithochronostratigraphic chart of the eastern area of the Cameros Basin, modified after Mas et al. (2011). **D:** Schematic paleogeographic reconstruction of the different paleoenvironments of the Leza Fm coastal wetland system, the case study presented here. Modified after Suarez-Gonzalez et al. (2015). Microbialite types are represented with the same symbol used in Fig. 5, and the color-code is equivalent to that used in Figs. 1, 4, 5 and 15. Note that some paleoenvironments and some microbialites have a widespread distribution throughout the unit, whereas others only occurred in particular geographical sectors (cf. Fig. 4). Location of

the map is shown in B, and letters refer to the main towns of the area (also shown in B and in Fig. 4): S=Soto en Cameros, SR=San Román de Cameros, A=Arnedillo, E=Enciso.

Figure 3: **A:** Reconstruction of the stratigraphic and paleogeographic relationships of the case study presented here (Leza Fm) with its adjacent units (see Figs. 2C-D), showing that the Jubera and Leza Fms are associated with the faulting and erosion of the Jurassic substrate of the basin. Modified after Suarez-Gonzalez et al. (2013). **B:** Panoramic field image showing the lateral facies change (yellow line) between the Jubera and the Leza Fms. See Suarez-Gonzalez et al. (2013) for further details.

Figure 4: Stratigraphic sections logged in the Leza Fm with their geographical location shown in the map at the right side (same map as Fig. 2D, see location in Fig. 2B). Modified after Suarez-Gonzalez et al. (2015). Colors in the sections (equivalent to the color-code of Figs. 1, 2D, 4, 5 and 15) are related to the different paleoenvironments interpreted for the unit, as described in the text. Colored arrows mark the stratigraphic location of the studied microbialites. Note that some paleoenvironments and some microbialites have a widespread distribution throughout the unit, whereas others only occurred in particular geographical sectors (cf. Fig. 2D).

Figure 5: Schematic logs of the different facies associations of the Leza Fm, with the interpretation of their general paleoenvironments. Modified after Suarez-Gonzalez et al. (2015). The color-code is equivalent to that of Figs. 1, 2D, 4, 5 and 15. **A:** Facies deposited in alluvial fan paleoenvironments, where oncoids occur. **B-D:** Facies deposited in freshwater to marine-influenced wetland paleoenvironments. **B:** Example of a charophyte-rich (i.e. freshwater-dominated) sequence where oncoids and skeletal stromatolites occur. **C:** Example of a dasyclad-rich (i.e. marine-influenced) sequence where thrombolites occur. **D:** Oncoid-rich facies deposited in freshwater-dominated creeks. **E:** Facies deposited in the peritidal wetland paleoenvironments, where fenestral laminites occur. **F:** Facies deposited in the tide-influenced oolitic paleoenvironments, where agglutinated stromatolites occur. **G:** Facies deposited in the evaporitic paleoenvironments, where micritic-evaporitic stromatolites occur.

Figure 6: Oncoids of the Leza Fm. **A:** Field image of the cross-bedded, clastic and oncoid-rich facies deposited in freshwater-dominated creeks (Figs. 2D, 5D). **B:** Field image of charophyte- and oncoid-rich facies deposited in freshwater bodies (Figs. 2D, 5B). Red arrows point to the stromatolitic overgrowth developing on the oncoid level. Yellow rectangle shows the location of E. **C:** Photomicrograph of one of the oncoids shown in A. Note abundant grains in the matrix surrounding the oncoid. Porous microfabrics are formed by filament tufts, whereas darker and denser microfabrics are formed by filament palisades. Yellow arrows point to truncation surfaces observed within the oncoid cortex. Green rectangle marks the location of D. **D:** Detail of the filaments, main components of the oncoid microfabrics. Note how they grow forming branching tufts. **E:** Detail of B, showing the stromatolitic overgrowth developing on the oncoid level. **F:** Photomicrograph of a stromatolitic overgrowth developing on two oncoids (darker, in the lower part). Note that the overgrowth microfabrics differ from those of the oncoids in that they include larger filament tufts and fans.

Figure 7: Thrombolites of the Leza Fm. **A:** Field image of a thrombolite occurring as a laterally-continuous bed (biostrome). Green arrow marks bed thickness. **B:** Field image of thrombolites (green arrows point to their margins) occurring as irregular masses (bioherms) within thicker beds (Fig. 5C). White rectangle marks the location of C. **C:** Field image of the macroscopic features of thrombolites, showing the characteristic mesoclots (dark color) and large irregular fenestrae (light color). **D:** Field image of the macroscopic features of thrombolites. Note the upwards-elongated distribution of mesoclots suggesting vertical growth. **E:** Polished hand specimen showing the mesostructure of thrombolites and the characteristic irregular interconnected mesoclots (black) and the surrounding sediment (brown) filling fenestrae between the mesoclots. **F:** Photomicrograph showing a detail of the thrombolite mesostructure with irregular mesoclots (light brown) and fenestrae filled with sediment (dark brown) and/or cement (white). Note many fenestrae with geopetal fillings. Yellow arrow points to a dasyclad. **G:** Detail photomicrograph of a mesoclot, showing clotted-peloidal microfabric with poorly-preserved filamentous structures. Note geopetal cavities to the left. **H:**

Photomicrograph of a thrombolite sample very rich in dasyclads, both in the sediment-filled fenestrae (dark colors, dasyclads pointed by yellow arrows) and within the mesoclots (light colors, dasyclads pointed by red arrows). **I:** Detail photomicrograph of the dasyclads.

Figure 8: Skeletal stromatolites of the Leza Fm. A green S marks each sandy intercalation between stromatolite levels, domes, columns or laminae. **A:** Field image of the stromatolite-bearing facies deposited in freshwater bodies with alluvial influence (Figs. 2D, 5B). White rectangles mark the location of B and C. **B:** Detail of A showing domal stromatolites adjacent to sandy levels (S) and including thin sandy intervals between some of their laminae (black arrows). **C:** Field detail of the stromatolite lamination. Red ovals mark fan-like filamentous colonies easily visible (the black square shows a close-up of one of the colonies). Note that sandy intercalations (S) occur infilling cavities and irregularities within or over the stromatolite laminae (see E). **D:** Detailed field image of skeletal stromatolites with columnar macrostructure. Note how sandy material (S) fills the space between columns. **E:** Photomicrograph of the skeletal stromatolites showing the predominant microfabric formed by filamentous fans. Note that sandy intercalations (S) are filling the irregularities over one of the stromatolite laminae. **F:** Detail of one of the filamentous fan-like colonies that form the skeletal stromatolites. **G:** Photomicrograph of a thin section cut parallel to stromatolite lamination, showing a transverse section of the filaments.

Figure 9: Contrasting accretion processes that generate skeletal and agglutinated stromatolites. Skeletal stromatolites accrete through the growth of colonies of filamentous microbes (probably cyanobacteria) and the early and pervasive precipitation of carbonate in the EPS sheath of their filaments. Thus, filaments are well-preserved, whereas grains supplied on the stromatolite surface are not trapped and bound in the microbial EPS, but only deposited between the filament fans (yellow arrows in photomicrograph). In the Cretaceous case study and in many other post-Cretaceous literature examples, skeletal stromatolites formed in $CaCO_3$-rich freshwater settings. Agglutinated stromatolites accrete through the development of thin biofilms simultaneous with abundant and cyclic grain supply. Filamentous microbes are not early

calcified (and thus only locally and poorly preserved, yellow areas in photomicrograph, see Fig. 11), whereas grains are profusely trapped and bound in the uncalcified EPS. Lithification of the biofilms may occur subsequently, through precipitation of clotted-peloidal micrite probably influenced by the degradation of EPS by heterotrophic microbes. Thin micritic crusts separating successive laminae (see Figs. 10E, 11) form during interruptions in accretion and in grain supply. In the majority of modern and fossil literature examples, agglutinated stromatolites formed in shallow-marine tide-influenced areas. See text and Tables 1-3 for further details and references.

Figure 10: Agglutinated stromatolites of the Leza Fm. See further images in Suarez-Gonzalez et al. (2014). **A:** Field view of a stromatolite level (green arrows) with a large dome (right), onlapped by thinly bedded oolitic deposits (yellow arrows). **B:** Close-up of a stromatolite bed showing stratiform to domal structures and clear thin bedding. **C:** Domal stromatolite level developed over oolitic deposits and showing clear lamination formed by alternating dark and light laminae. Note large intraclasts included within the stromatolite (yellow arrows). **D:** Photomicrograph of the side of a stromatolite dome, showing very abundant grains included within the stromatolite laminae, even at steep angles. Laminae dominated by micrite are marked with a yellow M. Note that most laminae have an intermediate composition with both grains and micrite. **E:** Photomicrograph showing grainy stromatolite laminae separated by thin micritic crusts (green arrows). Note that the crusts are associated to micritization of the grains of the underlying laminae.

Figure 11: **A-E** Photomicrographs of the rare filament remains observed in the agglutinated stromatolites of the Leza Fm. Note that filament remains (yellow arrows and ellipses) are poorly preserved, mostly as individual elongated clusters of clotted-peloidal micrite, being only locally associated in tufts (ellipses of C and E). Green arrows point to thin micritic crusts between successive laminae.

Figure 12: The detailed analysis of stromatolite laminae reveals, even at the small temporal and spatial scale of a single lamina, the complex interplay between microbial accretion and

sediment supply that produces the microfabrics of the Leza Fm agglutinated stromatolites. **A:** During some periods, a benthic microbial community could accrete on the stromatolite surface even with relatively low sediment supply. If early calcification occurred locally, some filament remains would eventually be preserved. **B:** During periods of low microbial accretion relative to the sediment supply, thin levels especially rich in grains developed. **C:** When the rates of microbial accretion and grain supply were balanced, grainy levels were recorded. Meanwhile, precipitation of clotted-peloidal micrite could start in underlying parts of the microbial community, probably induced by the degradation of EPS by heterotrophic microbes. **D:** Interruption periods of both microbial accretion and grain supply are recorded by thin micritic crusts caused by intense microbial activity at the top of the microbial community, which induced micritization and truncation of underlying grains and micrite precipitation. **E:** Photomicrograph of the final result in the fossil record.

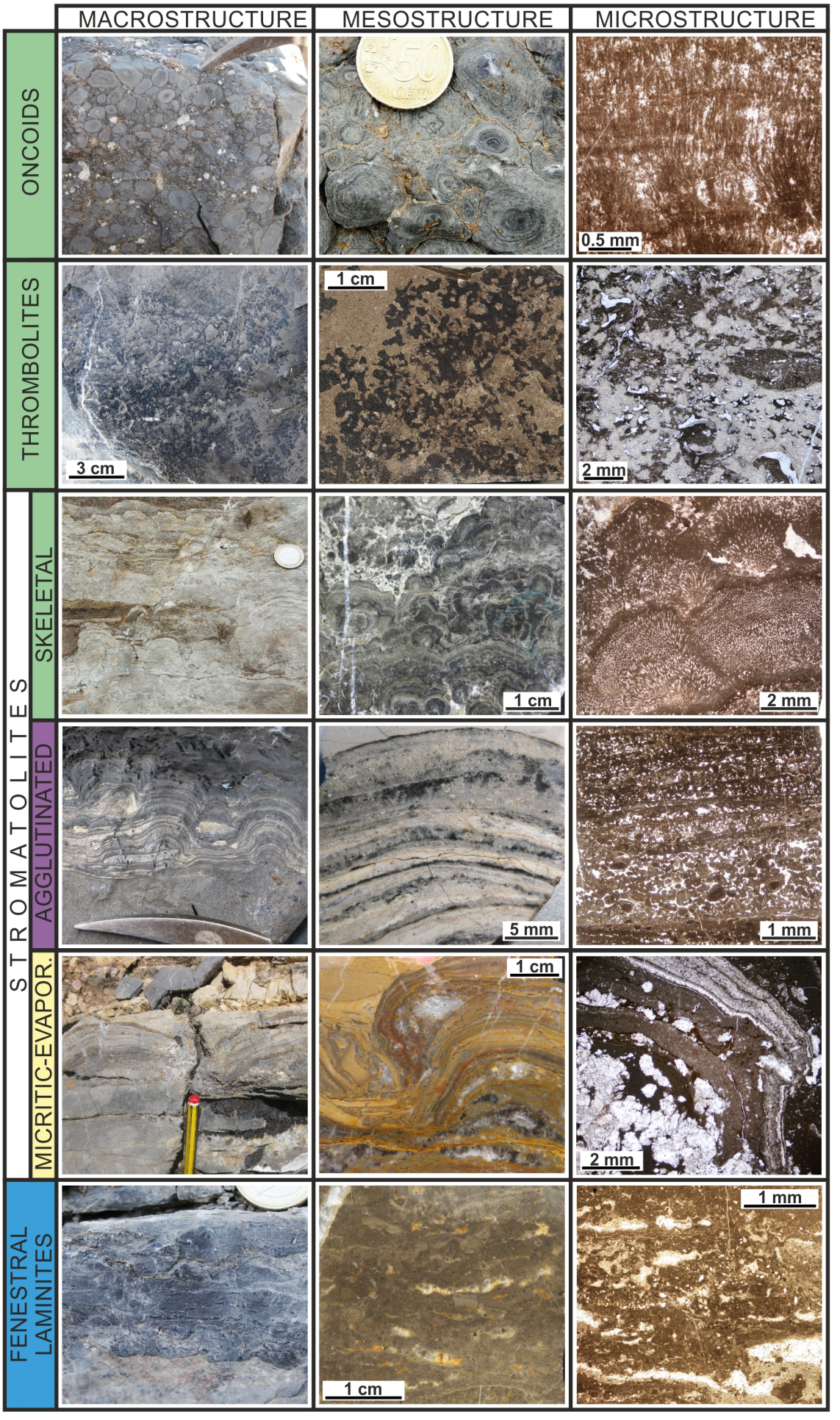
Figure 13: Micritic-evaporitic stromatolites of the Leza Fm. **A, C:** Polished hand specimens. **B, D:** Photomicrographs of the same specimens. Note abundant pseudomorphs after evaporites disrupting lamination both at meso- and micro-scale in C (crystalline white and gray areas) and D (yellow arrows), respectively.

Figure 14: Fenestral laminites of the Leza Fm. **A:** Field view of a thin level of fenestral laminites. **B:** Close-up view of fenestral lamintes, showing the thin lamination formed by horizontally elongated fenestrae (darker colors). **C:** Polished slab of fenestral laminites showing the irregular, horizontal, cement-filled fenestrae (white, gray and yellow colors). **D:** Photomicrograph showing fenestrae (light colors, some of them with darker geopetal fillings) and the micritic texture of the laminae, some of them including grains (mainly quartz). **E:** Photomicrograph of grain-rich microfabrics of the fenestral laminites. Green arrows point to subvertical cracks (some of them V-shaped) in many laminae. **F:** Photomicrograph showing stromatactis-like fenestrae, some of them with geopetal fillings.

Figure 15: Table summarizing the environmental factors (discussed in the text) that may control the accretion process of trapping and binding of allochtonous grains by microbialites.

The influence of these processes is exemplified by the diverse microbialites of the case study presented here. Color-code of the microbialite paleoenvironments is equivalent to that of Figs. 1, 2D, 4, 5. For each microbialite type, environmental factors that favor ‘trapping and binding’ are highlighted in red. Note that only the case in which all the favorable factors concur (agglutinated stromatolites) has ‘trapping and binding’ as its main accretion process. Microbialites occurring in environments where all favorable factors occur but some of them only locally or sporadically, develop some agglutinated microfabrics (i.e. fenestral laminintes), but they are not predominant.

Figure 1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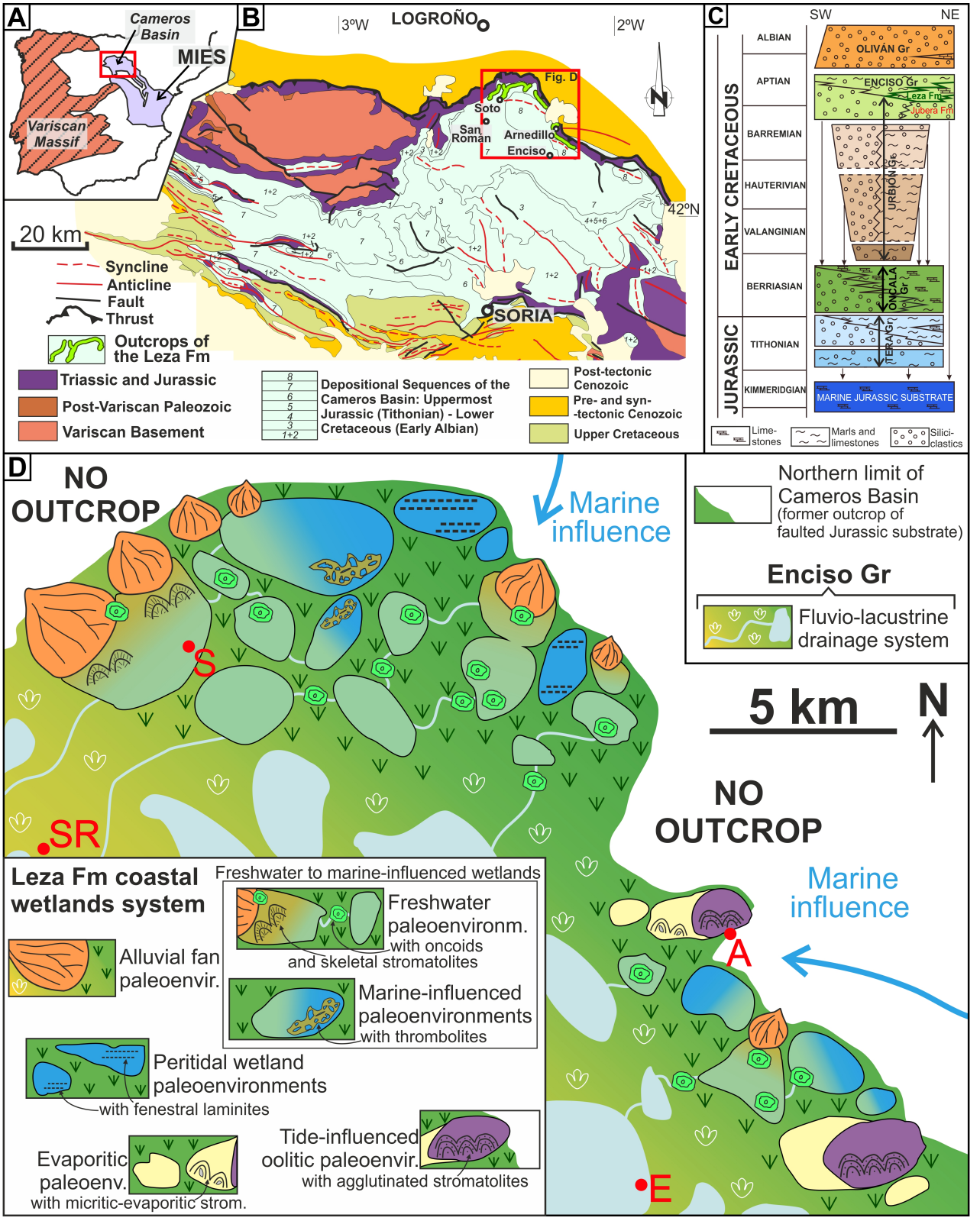
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Enciso
42ºN
20 km
Syncline
Anticline
Fault
Thrust
Outcrops of the Leza Fm
Triassic and Jurassic
Post-Variscan Paleozoic
Variscan Basement
Depositional Sequences of the Cameros Basin: Uppermost Jurassic (Tithonian) - Lower Cretaceous (Early Albian)
SORIA
Post-tectonic Cenozoic
Pre- and syn--tectonic Cenozoic
Upper Cretaceous
C
SW
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APTIAN
BARREMIAN
HAUTERIVIAN
VALANGINIAN
BERRIASIAN
TITHONIAN
KIMMERIDGIAN
OLIVÁN Gr
ENCISO Gr
Leza Fm
Lubera Fm
URBIÓN Gr
ONCALA Gr
TERAZO Gr
MARINE JURASSIC SUBSTRATE
Lime-stones
Marls and limestones
Silici-clastics
D
NO OUTCROP
Marine influence
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Northern limit of Cameros Basin (former outcrop of faulted Jurassic substrate)
Enciso Gr
Fluvio-lacustrine drainage system
5 km
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NO OUTCROP
Marine influence
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E
Leza Fm coastal wetlands system
Freshwater to marine-influenced wetlands
Alluvial fan paleoenvir.
Freshwater paleoenvironm. with oncoids and skeletal stromatolites
Marine-influenced paleoenvironments with thrombolites
Peritidal wetland paleoenvironments with fenestral laminites
Evaporitic paleoenv. with micritic-evaporitic strom.
Tide-influenced oolitic paleoenvir. with agglutinated stromatolites

Figure 2

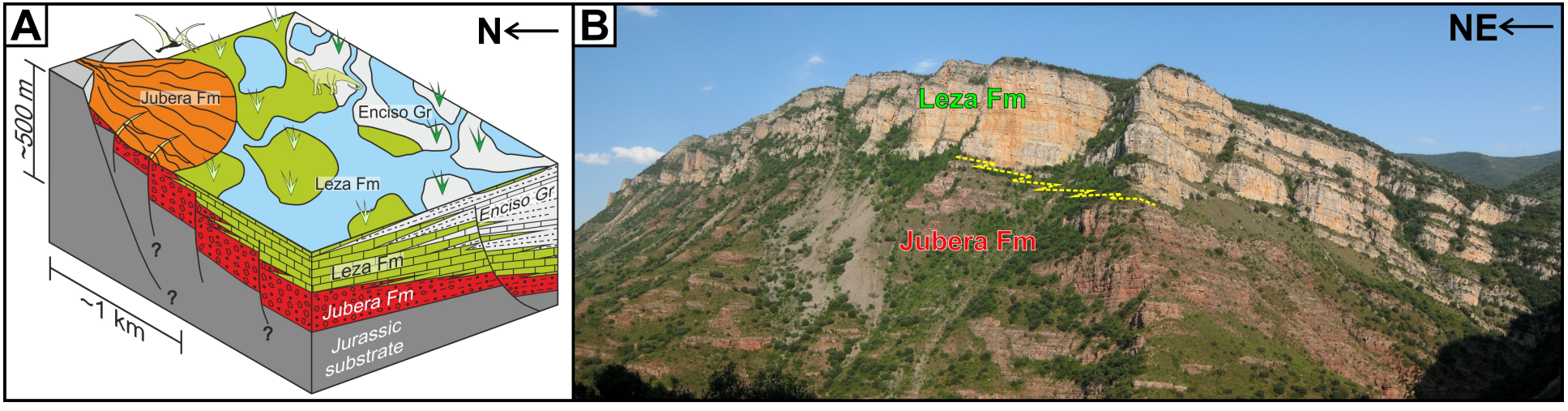
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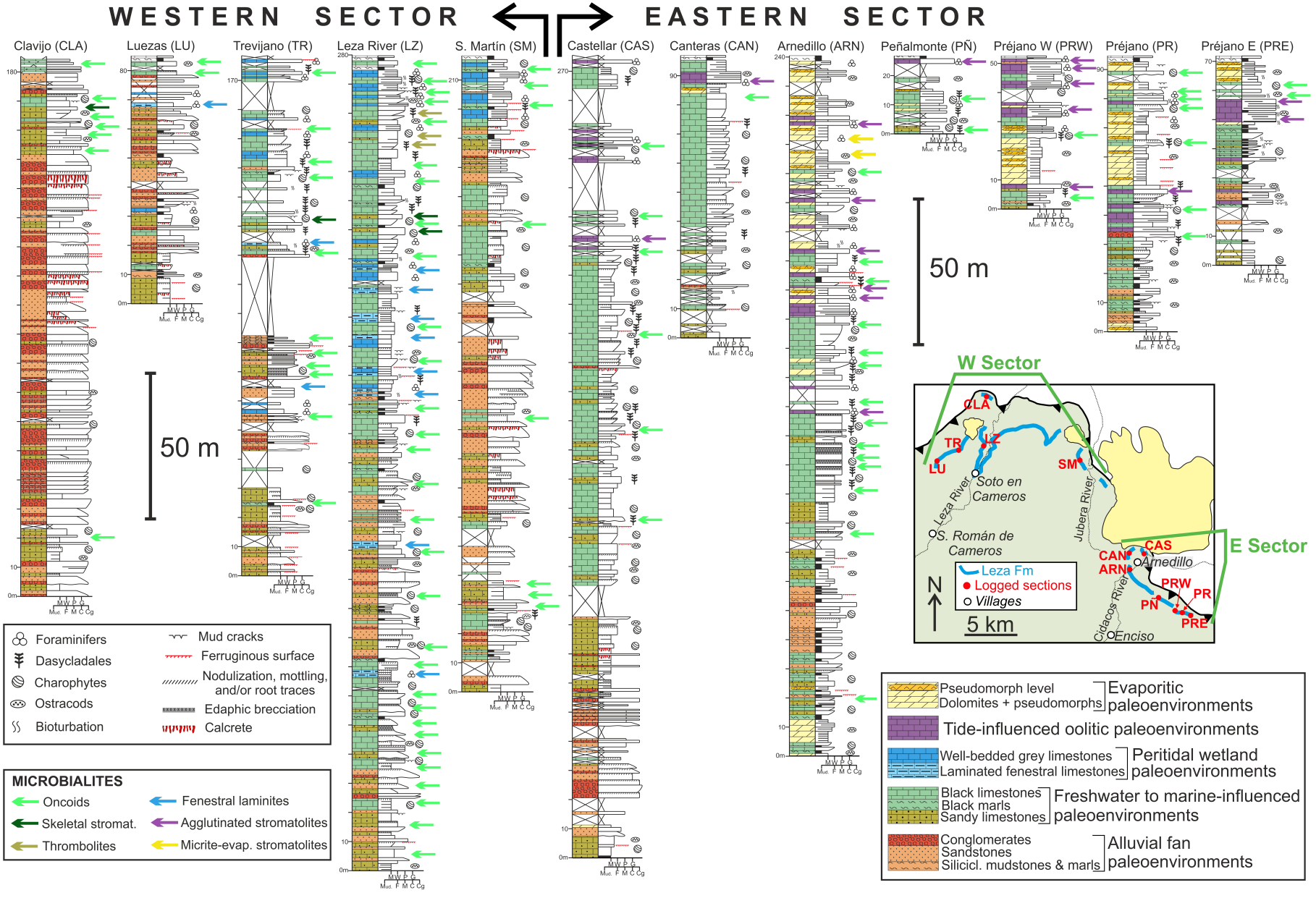
Figure 3

Figure 4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Castellar (CAS)
Canteras (CAN)
Arnedillo (ARN)
Peñalmonte (PÑ)
Préjano W (PRW)
Préjano (PR)
Préjano E (PRE)
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Dasycladales
Charophytes
Ostracods
Bioturbation
Mud cracks
Ferruginous surface
Nodulization, mottling, and/or root traces
Edaphic brecciation
Calcrete
MICROBIALITES
Oncoids
Skeletal stromat.
Thrombolites
Fenestral laminites
Agglutinated stromatolites
Micrite-evap. stromatolites
W Sector
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CLA
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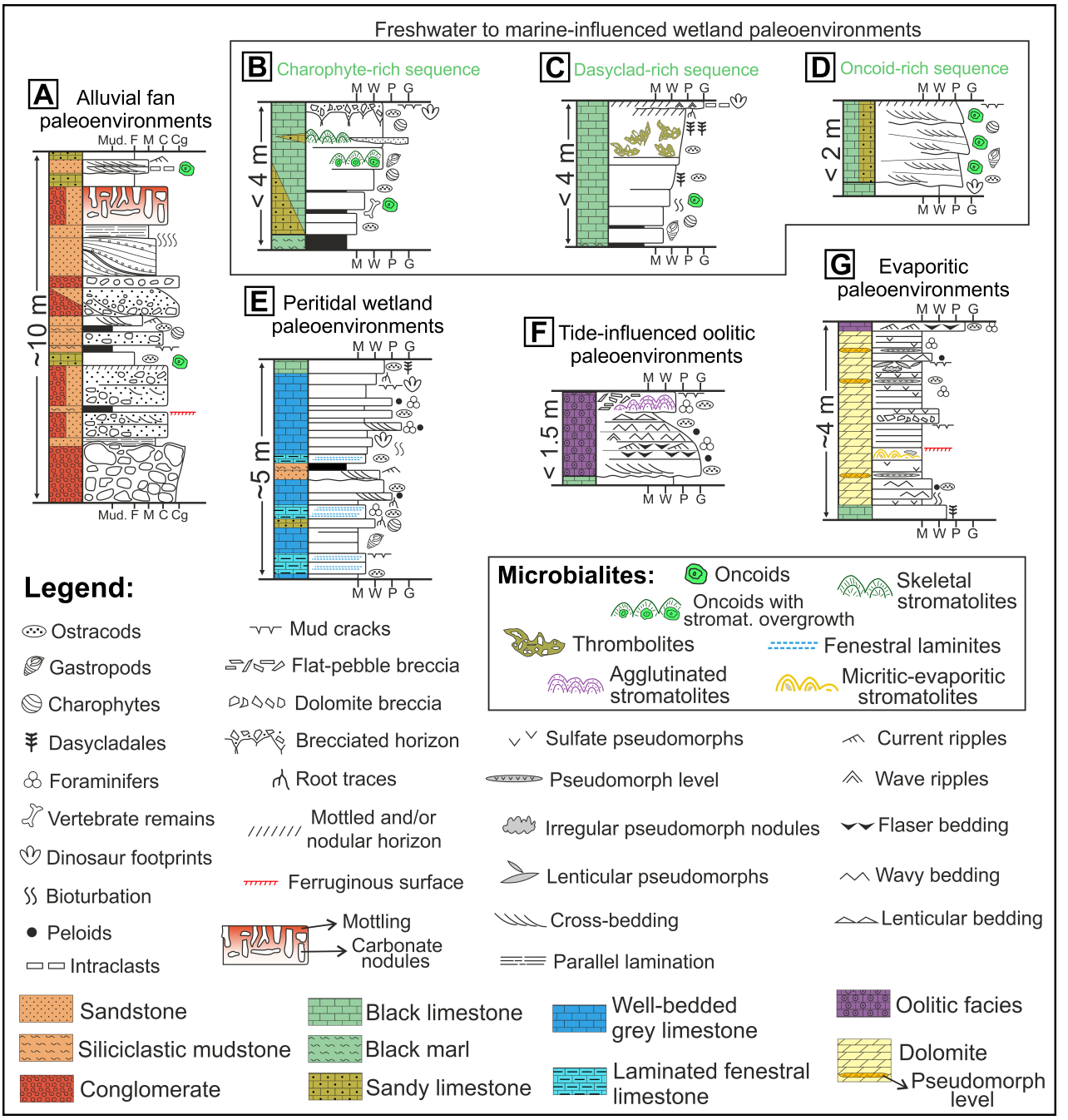
Soto en Cameros
S. Román de Cameros
Leza River
Jubera River
Cidacos River
Arnedillo
Enciso
Leza Fm
Logged sections
Villages
N
5 km
Pseudomorph level
Dolomites + pseudomorphs
Evaporitic paleoenvironments
Tide-influenced oolitic paleoenvironments
Well-bedded grey limestones
Laminated fenestral limestones
Peritidal wetland paleoenvironments
Black limestones
Black marls
Sandy limestones
Freshwater to marine-influenced paleoenvironments
Conglomerates
Sandstones
Siliciclastic mudstones & marls
Alluvial fan paleoenvironments


Freshwater to marine-influenced wetland paleoenvironments
A Alluvial fan paleoenvironments
Mud. F M C Cg
~10 m
B Charophyte-rich sequence
< 4 m
C Dasyclad-rich sequence
< 4 m
D Oncoid-rich sequence
< 2 m
M W P G
E Peritidal wetland paleoenvironments
~5 m
F Tide-influenced oolitic paleoenvironments
< 1.5 m
G Evaporitic paleoenvironments
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Legend:
Ostracods
Gastropods
Charophytes
Dasycladales
Foraminifers
Vertebrate remains
Dinosaur footprints
Bioturbation
Peloids
Intraclasts
Mud cracks
Flat-pebble breccia
Dolomite breccia
Brecciated horizon
Root traces
Mottled and/or nodular horizon
Ferruginous surface
Mottling
Carbonate nodules
Microbialites:
Oncoids
Oncoids with stromat. overgrowth
Thrombolites
Agglutinated stromatolites
Skeletal stromatolites
Fenestral laminites
Micritic-evaporitic stromatolites
Sulfate pseudomorphs
Pseudomorph level
Irregular pseudomorph nodules
Lenticular pseudomorphs
Cross-bedding
Parallel lamination
Current ripples
Wave ripples
Flaser bedding
Wavy bedding
Lenticular bedding
Sandstone
Siliciclastic mudstone
Conglomerate
Black limestone
Black marl
Sandy limestone
Well-bedded grey limestone
Laminated fenestral limestone
Oolitic facies
Dolomite
Pseudomorph level

Figure 5

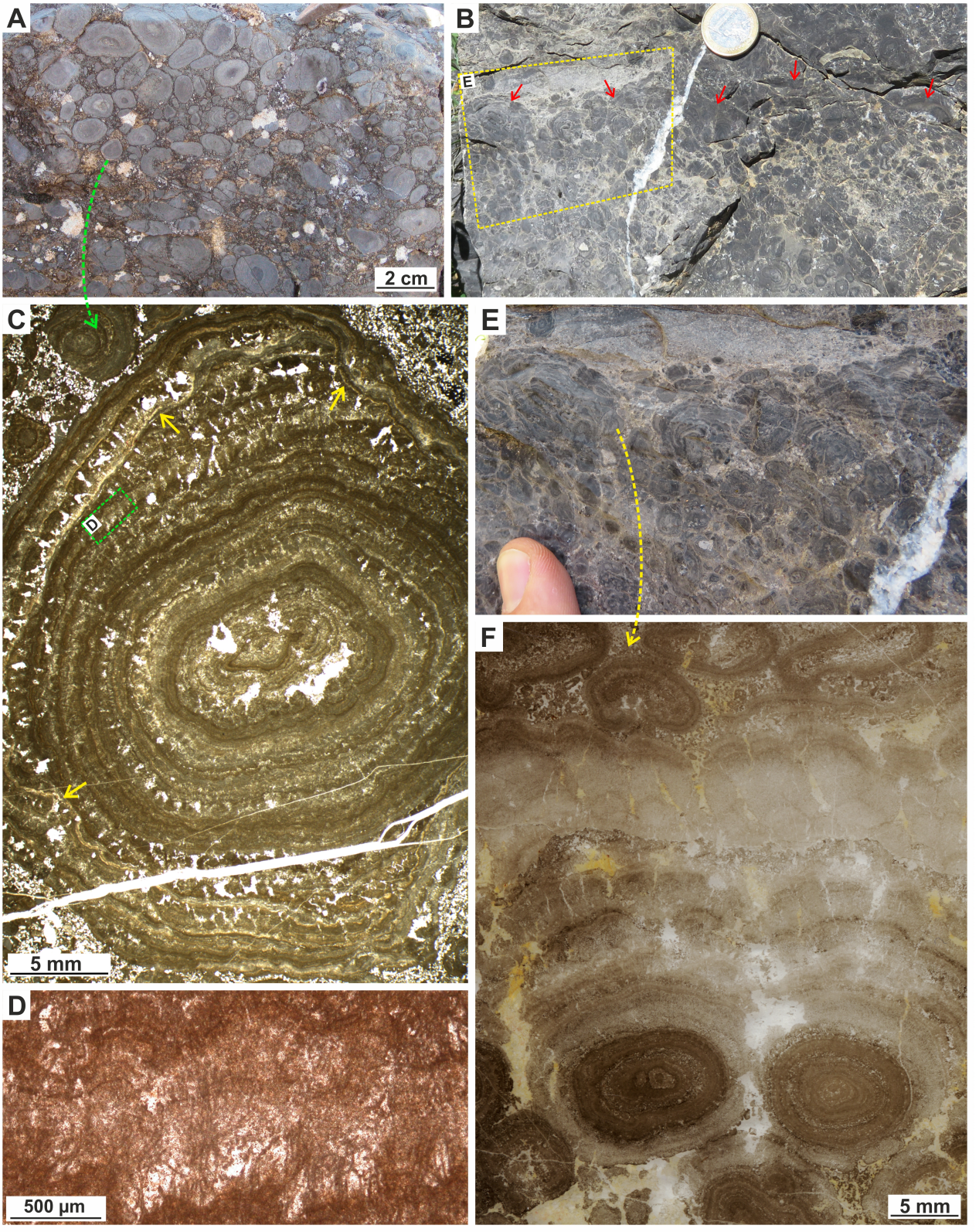

Figure 6

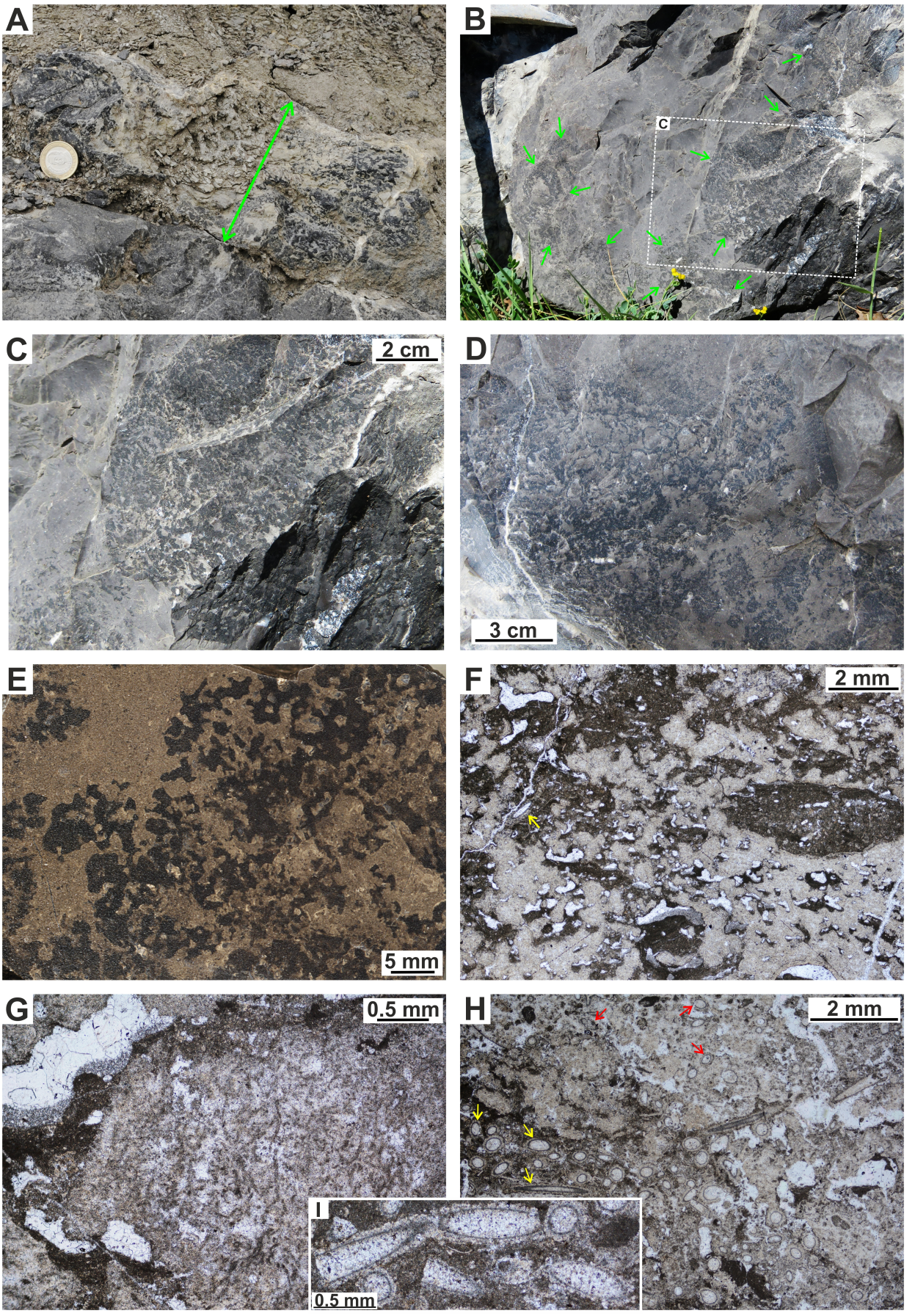

Figure 7

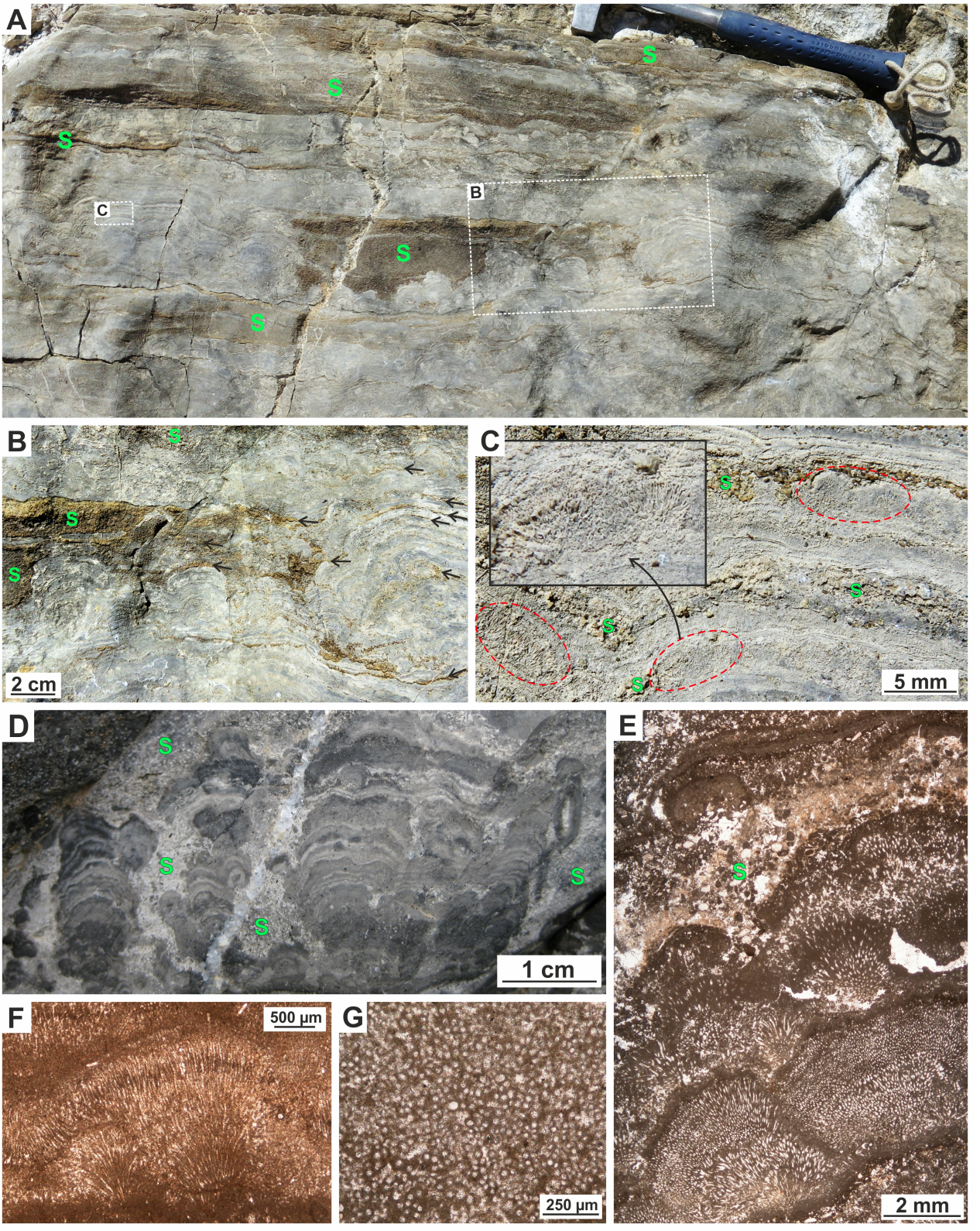

Figure 8

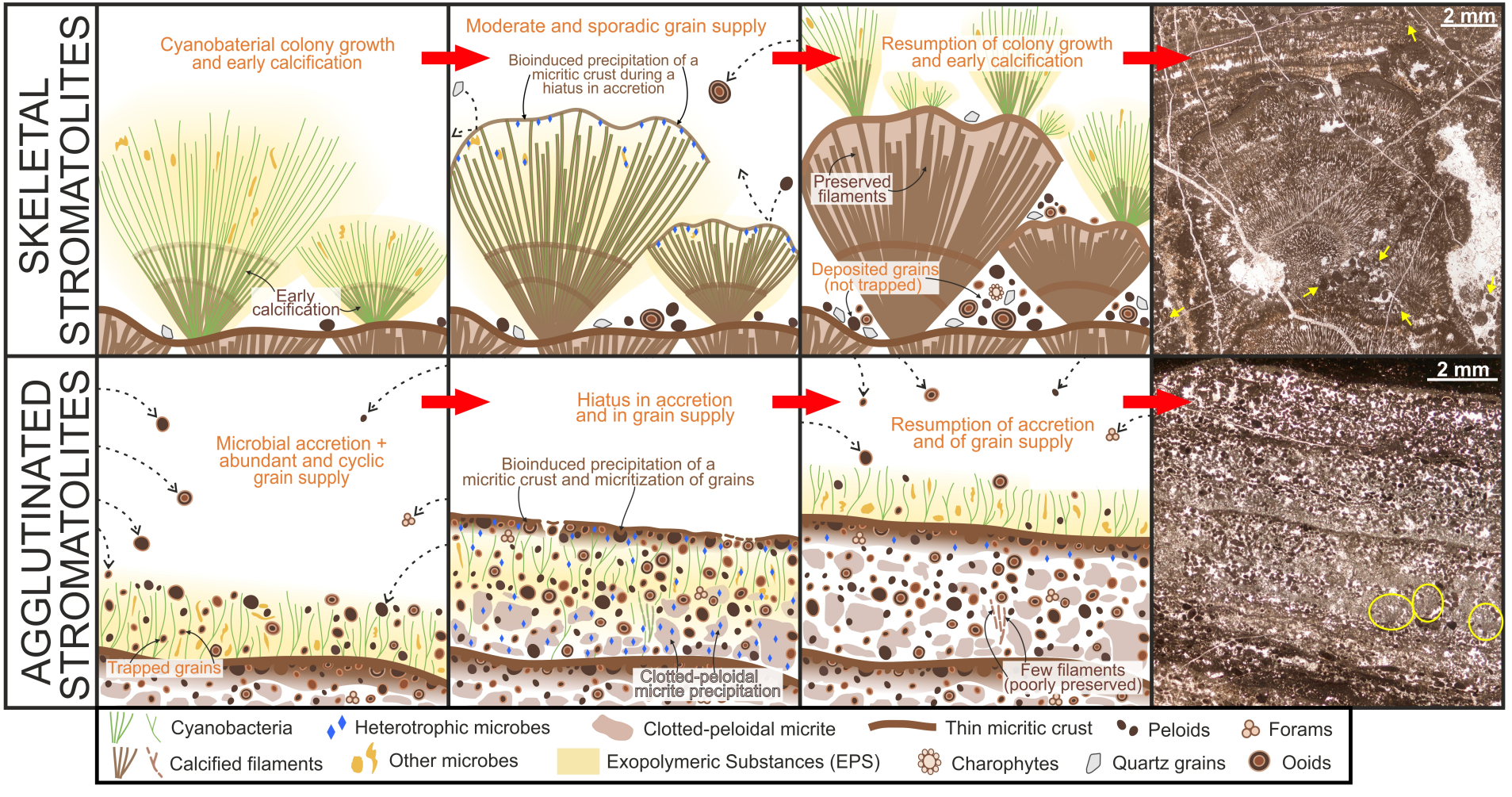
SKELETAL STROMATOLITES
Cyanobaterial colony growth and early calcification
Early calcification
Moderate and sporadic grain supply
Bioinduced precipitation of a micritic crust during a hiatus in accretion
Resumption of colony growth and early calcification
Preserved filaments
Deposited grains (not trapped)
2 mm
AGGLUTINATED STROMATOLITES
Microbial accretion + abundant and cyclic grain supply
Trapped grains
Hiatus in accretion and in grain supply
Bioinduced precipitation of a micritic crust and micritization of grains
Clotted-peloidal micrite precipitation
Resumption of accretion and of grain supply
Few filaments (poorly preserved)
2 mm
Cyanobacteria
Heterotrophic microbes
Clotted-peloidal micrite
Thin micritic crust
Peloids
Forams
Calcified filaments
Other microbes
Exopolymeric Substances (EPS)
Charophytes
Quartz grains
Ooids

Figure 9

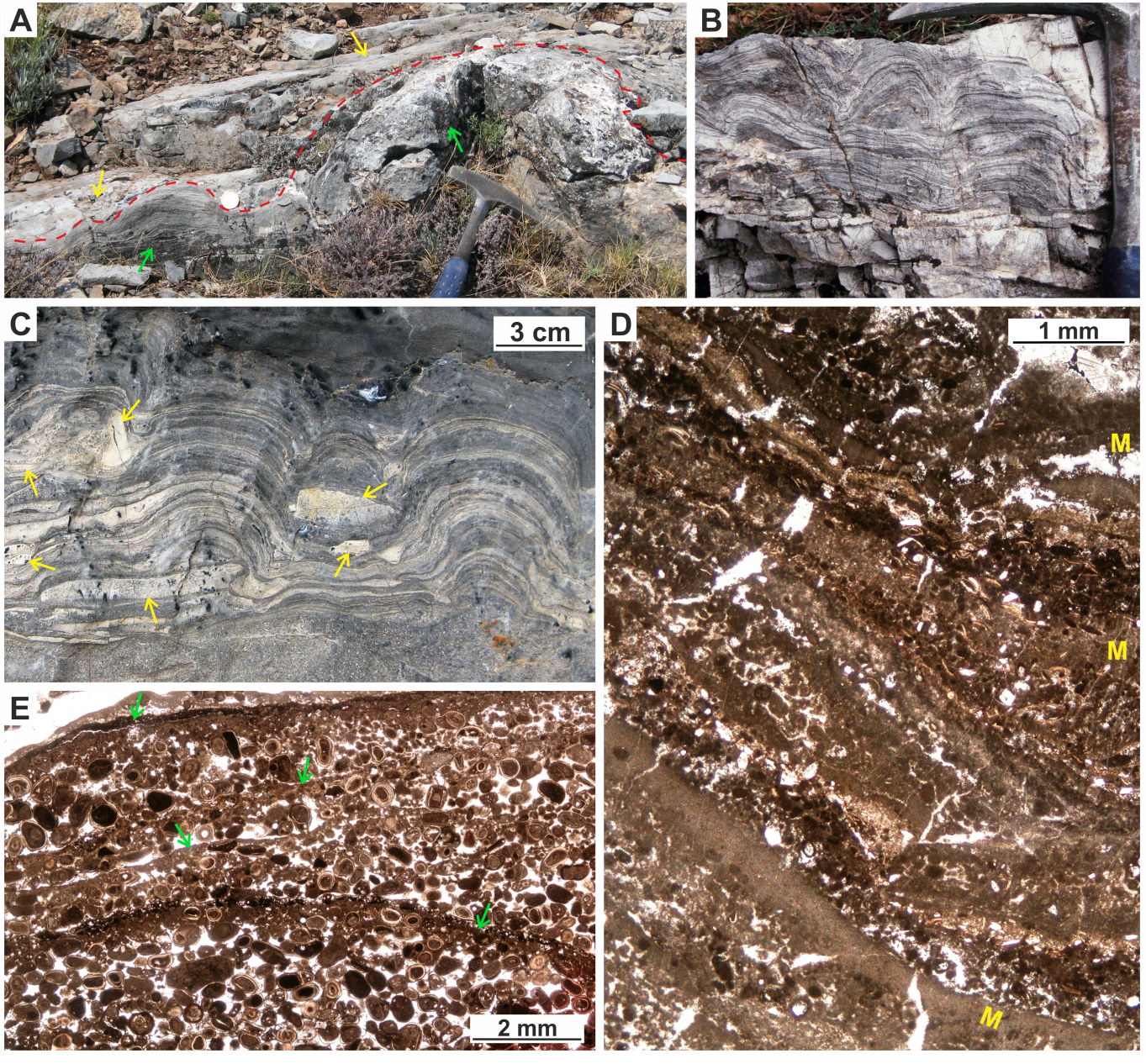

Figure 10

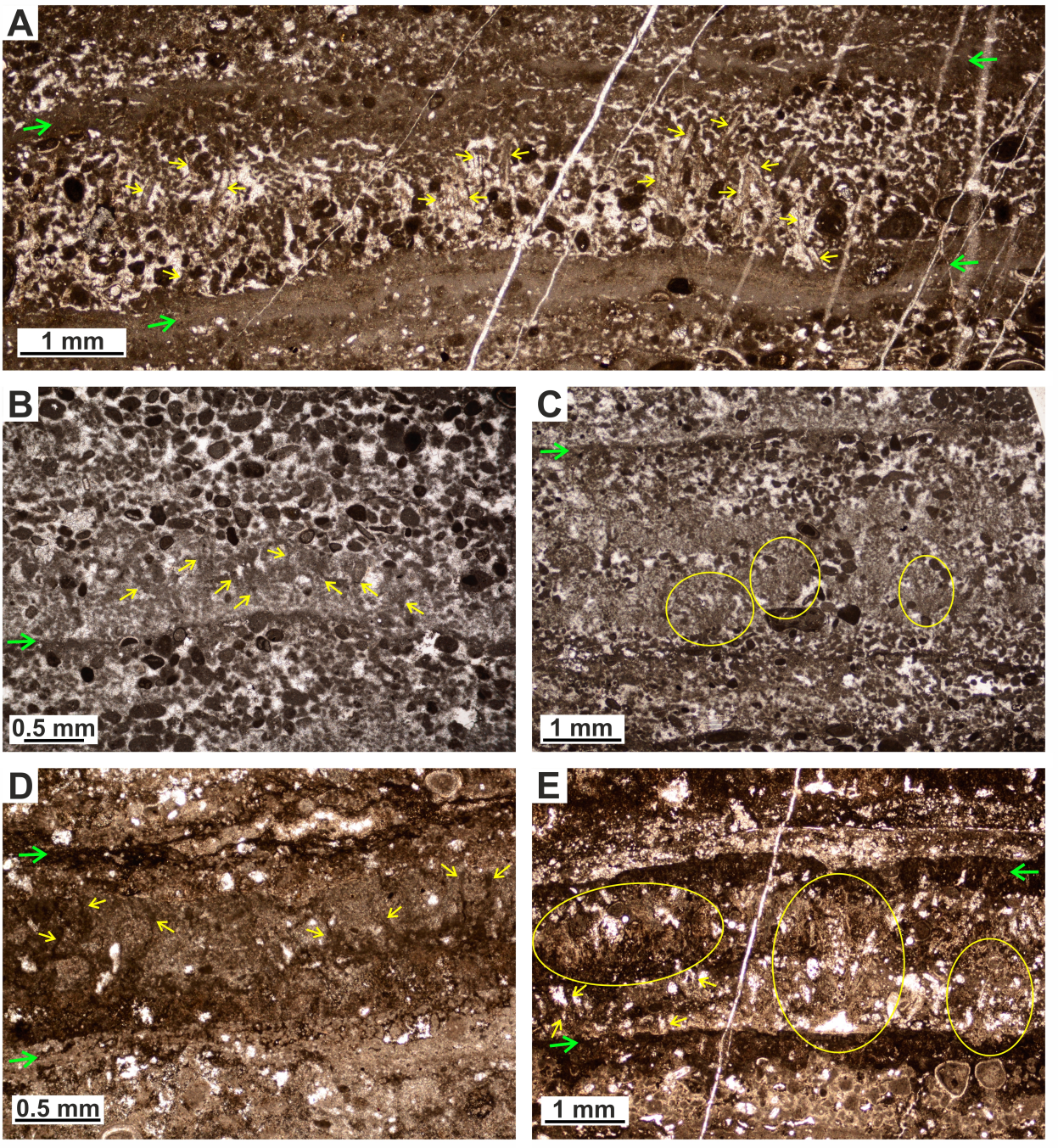

Figure 11

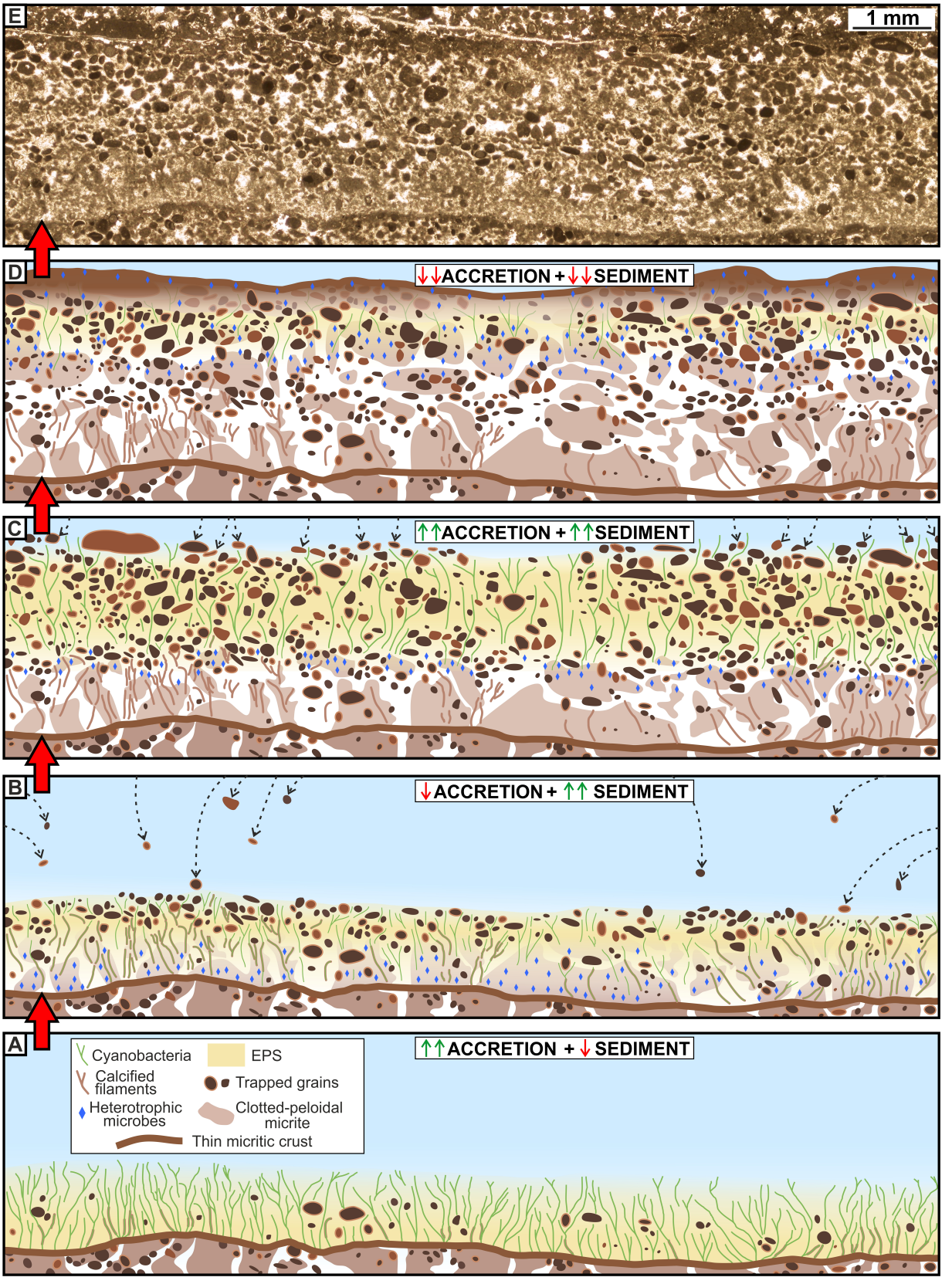
E
1 mm
D
↓↓ACCRETION + ↓↓SEDIMENT
C
↑↑ACCRETION + ↑↑SEDIMENT
B
↓ACCRETION + ↑↑ SEDIMENT
A
↑↑ACCRETION + ↓ SEDIMENT
Cyanobacteria
EPS
Calcified filaments
Trapped grains
Heterotrophic microbes
Clotted-peloidal micrite
Thin micritic crust

Figure 12

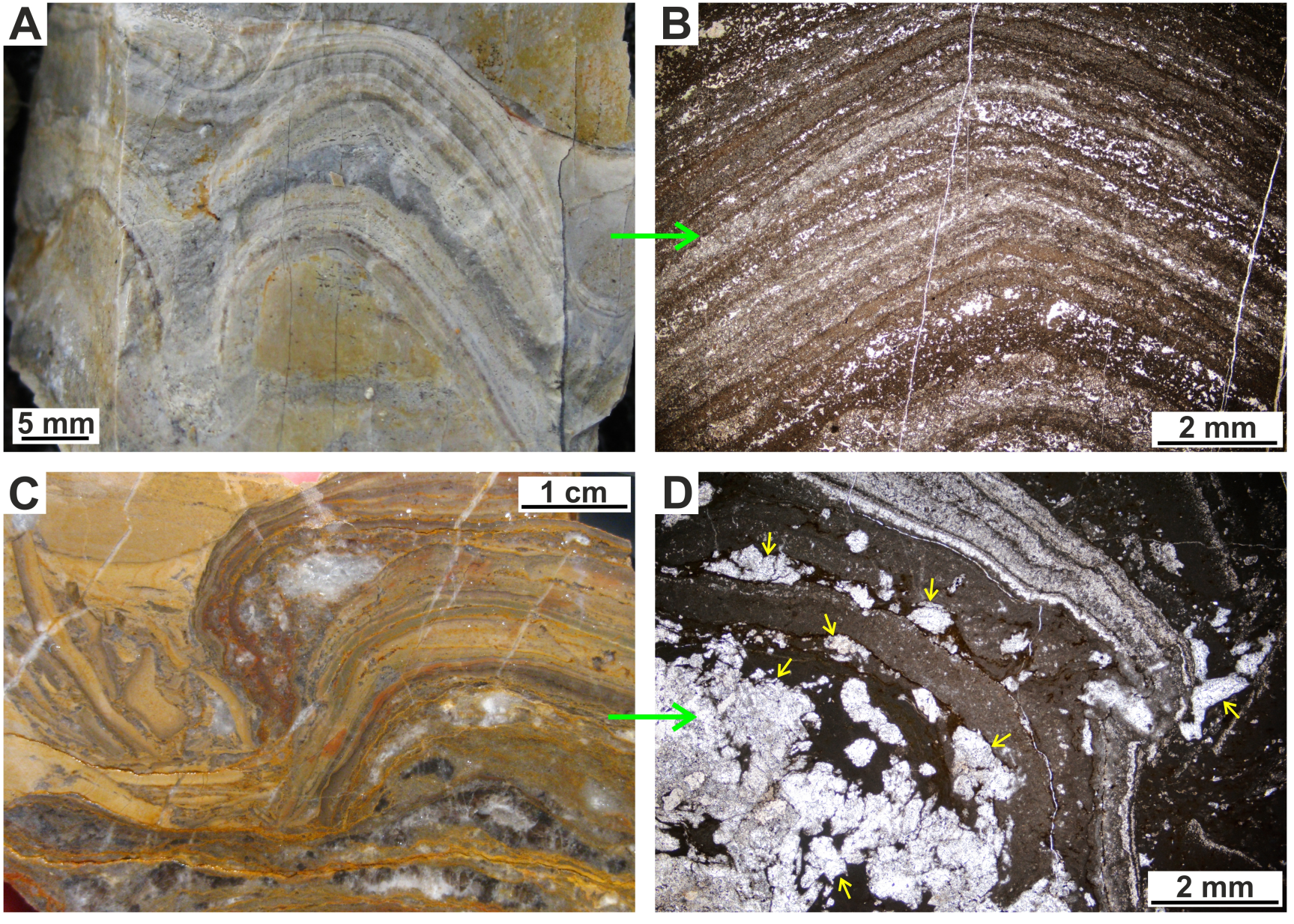

Figure 13

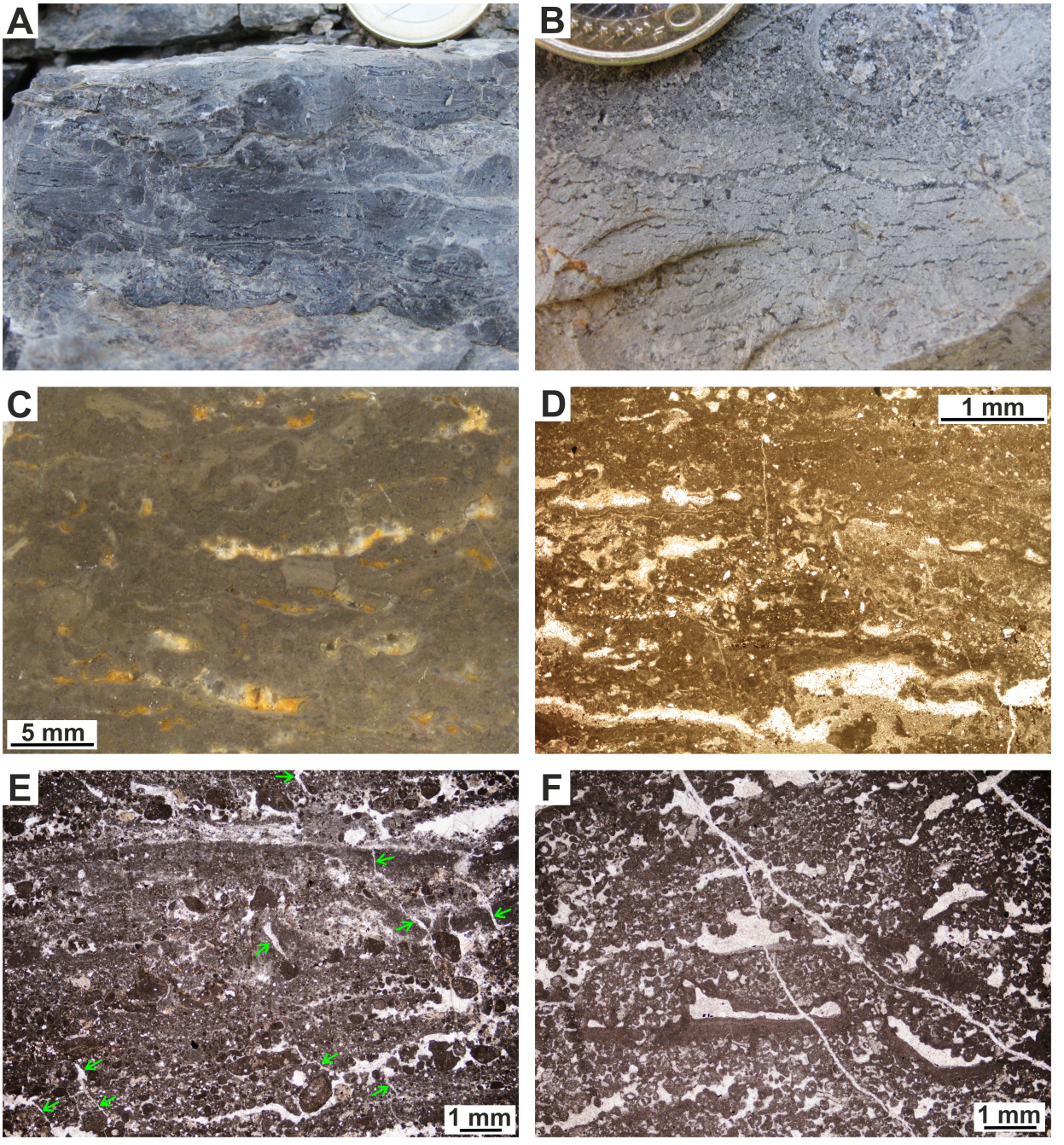

Figure 14

Figure 15

		ENVIRONMENTAL CONTROLS ON TRAPPING AND BINDING				
	Paleo-environment	Availability of **grains**	Common agitation by **currents**	**Electrolytes** to enhance EPS adhesiveness	**$CaCO_3$ supersaturation**	**Trapping and binding**
Oncoids	Small clastic-rich channels or creeks and shallow freshwater bodies	**Yes**	**Probably constant water flow within the channels**	Relatively low abundance and diversity in freshwater	Very high, due to hardwater sources, promoting early and strong precipitation	Not significant
Thrombolites	Shallow water bodies with marine influence and dasyclad meadows	No	Not significant	**Hig abundance and diversity due to marine influence**	**Relatively low in sea-water, hindering early and strong precipitation**	Not significant
Skeletal stromatolites	Shallow freshwater bodies with common clastic input from alluvial fans	**Yes**	Only sporadic, associated with discharges from fans	Relatively low abundance and diversity in freshwater	Very high, due to hardwater sources, promoting early and strong precipitation	Not significant
Agglutinated stromatolites	Marginal-marine tide-influenced water bodies	**Yes**	**Continuous and cyclic tidal currents in addition to waves and storms**	**High abundance and diversity due to marine influence**	**Relatively low in sea-water, hindering early and strong precipitation**	**Major accretion process**
Micritic-evap. stromatolites	Very shallow and restricted marginal-marine areas with sulfate precipitation	No	Not significant	**High abundance and diversity due to marine influence**	**Relatively low in sea-water, hindering early and strong precipitation**	Not significant
Fenestral laminites	Very shallow marine-influenced water bodies rich in ostracods and forams	Only locally	Probably waves and storms	**High abundance and diversity due to marine influence**	**Relatively low in sea-water, hindering early and strong precipitation**	Only partially in some specimens

Table 1 - Modern agglutinated microbialites

Publications	Locality		Environment	Modern agglutinated microbialites: main features		
				Macroscale	Mesoscale	Microscale
Black (1933)	BAHAMAS	Northern Andros Island, Bahamas	Supratidal-intertidal zones of tidal flats. Brackish-normal marine salinity	Low, rounded domes, 2.5-5 cm high and 10-13 cm in diameter	Parallel or concentric dark-light lamination	Thicker light laminae (0.5-1.75 mm), composed of soft and uncemented grains (0.1-1 mm grain-size), separated by thinner (~0.1 mm), dark, green-brown, organic-rich laminae
Monty (1965; 1967)		Eastern Andros Island, Bahamas	Intertidal-subtidal zones of back-reef lagoon. Brackish-normal marine salinity	Flat mats, mamillated structures, domes, and knobby or subspherical bodies. Up to 10 cm in diameter and 5 cm thick	Non-laminated and laminated	Non-laminated: well-sorted grains bound by filaments and eventually capped by 0.1 mm thick biofilm. Laminated: alternating grainy laminae and 0.2-0.9 mm filamentous laminae
Gebelein (1976a)		Joulters Cay, Bahamas	Subtidal (<1m) shoal areas and tidal channels	Oncoids (1 mm – 10 cm)	Laminated	Thicker laminae with vertical filaments and abundant trapped grains and thinner laminae with horizontal filaments and less grains
Dravis (1983)		Eleuthera Bank, Bahamas	1-5 m deep, high-energy, subtidal, oolitic bars. Normal marine salinity	0.1-1 m high hemispheroidal columns and elongated ridges	Crudely laminated with coarse fenestrae and borings	Trapped and bound, highly micritized, oolitic sediment and calcified filaments
Dill et al. (1986)		Channel between Normans Pond Cay and Lee Stocking Island, Bahamas	7-8 m deep, high energy subtidal field of giant oolitic megaripples. Normal marine salinity	>2 m high columns, individual or coalesced in fence-like rows	Convex-upward large-scale lamination and smaller-scale 1-4 cm-wide columns. Numerous voids and borings	Organically-bound and later cemented ooid and pelletal sand. Lamination caused by variations in grain size, cementation and alignment of pores
Riding et al. (1991b)		Mail Boat Channel and Iguana Cay Cut, Bahamas	6-8 m deep inter-island channels with subtidal ooid sand dunes. Normal marine salinity	<2.5 m high columns and domes	Conspicuous but crude and discontinuous lamination (mm-scale) with borings	Oolitic and peloidal fine-medium-grained sand, baffled, trapped and bound by microbial mat
Reid & Browne (1991)		Eastern Stocking Island, Bahamas	Lower intertidal zone landwards of a fringing-reef complex. Normal marine salinity	<0.5 m high, tabular forms and domes (0.5-1 m in diameter)	Discontinuous, wavy and often bored mm-scale lamination	Laminae are 1-3 mm thick, composed of carbonate sand (0.08-0.2 mm): peloids and skeletal fragments. Lamination is defined by differential lithification
Feldmann (1995; 1997), Feldmann & McKenzie (1998)		Lee Stocking Island and its NW channel, Bahamas	Subtidal (3-8 m deep) channel with ooid-sand dune fields and intertidal sandy embayment	Subtidal: up to 2 m high columns. Intertidal: few cm high columns	Laminated (stromatolitic) and non-laminated (thrombolitic) fabrics, even within the same specimen	Stromatolites: Clastic laminae (ooids, peloids, bioclasts, 0.1-0.2 mm grain-size) >1 mm thick, and micritic laminae <250 µm thick. Calcified filaments. Thrombolites: Micritic mesoclots few mm across with calcified filaments and grains in pockets between mesoclots
Reid et al. (1995), Macintyre et al. (2000)		Exuma Cays, Bahamas	Intertidal back-reefs, reef-flats and beaches, and subtidal (up to 10 m deep) sandy-embayments and passes with ooid shoals	Columnar, molar, linear, tabular and ridge-conforming shapes, up to 2.5 m high	Lamination (mm-scale) with knobby and digitate structures. Non-laminated thrombolites	Agglutinated carbonate fine sand (0.1-0.25 mm). Unlithified mm-scale laminae separated by lithified laminae, composed of thin (20-40 µm) micritic crusts overlying 0.2-1 mm of micritized grains. Some calcified filaments

Reid et al. (2000), Visscher et al. (2000), Andres & Reid (2006), Planavsky et al. (2009), Bowlin et al. (2012)		Highborne Cay, Bahamas	Back-reef zone (<1 m deep) of fringing-reef complex. Normal marine salinity	Ridges and columnar heads up to 0.5 m high	Lamination (mm-scale) formed by differences in lithification	Unlithified 1-5 mm thick laminae of trapped carbonate sand grains and lithified laminae, composed of thin (10-60 µm) micritic crusts overlying 1-2 mm of fused, microbored and micritized grains. Poorly preserved calcified filaments
Planavsky & Ginsburg (2009)		Adderley Channel, Bahamas	Subtidal (5-10 m deep) oolitic sand bar	Up to 2.5 m tall isolated columns and bioherms made up of coalesced columns	Stromatolites: poorly defined lamination. Thrombolites: patchy laminations, clotted appearance and vugs with or without sediment-filling	Stromatolites: laminae of uncemented fine-grained ooids and peloids, and laminae of cemented and micritized grains. Thrombolites: clots formed by dense clusters of sand grains and cements (micritic and fibrous aragonitic)
Ginsburg et al. (1954)	Florida, USA	Florida Keys and Florida Bay	Open intertidal rocky platforms (normal marine salinity) and island mud flats (brackish to hypersaline)	Flat mats and domes	Alternating dark organic-rich laminae and light sediment-rich laminae, with bubbles, undulations and unconformities	Laminae are 0.3-16 mm thick, and composed of detrital sediment (10-700 µm) and microbial organic matter as interstitial matter. No carbonate precipitation
Ginsburg (1960)		Florida Bay, Rodriguez Bank, Sandy Cay and Rickenbacker Causeway	Subtidal bay and sand bars (0.5-2.5 m deep), and intertidal flats and shoals	Stromatolitic domes and algal biscuits (oncoids)	Concentric, domal or crenulated lamination with boring/burrowing cavities	Sediment-rich laminae (lime clay, silt and fine-sand) up to 1 mm thick and organic-rich laminae up to 0.6 mm
Gebelein (1977)		Cape Sable, Florida	High intertidal zone of open mud flats	Flat-topped heads and hemispherical domes up to 6 cm high	Convex upward light-dark lamination that thins and pinches out along the sides. Abundant burrows	Thicker (200-500 µm) light laminae of peloidal bioclastic sediment (~50 µm grain size) and thinner (50-100 µm) dark laminae rich in microbial organic matter
Gebelein (1969; 1976a)	Castle Roads, Bermuda Islands		Subtidal (1-8m deep) channels between islands covered by rippled sand. Normal marine salinity	Head-shaped biscuits (<6 cm high) and ellipsoidal domes (<30 cm high)	Biscuits: convex upward smooth lamination of alternating grain-rich and organic-rich laminae. Domes: crude lamination	Laminae rich in trapped and bound sediment particles are 0.8-3 mm thick, organic-rich laminae with less grains are 75-200 µm thick. No carbonate precipitation
Jones & Goodbody (1985)	Pease Bay, Grand Cayman Island, Cayman Islands		Sides of seagrass banks, up to 1.5 m deep, facing strong currents	Elongate domal oncoids, up to 42 mm long, with a flattened base	Very vague lamination	Bioclastic, medium-sized (0.2-0.5 mm) sand (often micritized), trapped and bound by mucilaginous organic matter
Logan (1961), Logan et al. (1964), Logan et al. (1974)	SHARK BAY	Hamelin Pool, Shark Bay, Australia	Intertidal and supratidal zones of a large, enclosed, hypersaline, marine embayment. Only locally in some shallow subtidal (<2 m deep)	Flat-lying sheets, and relief structures (up to ~2 m tall) with various shapes: ridge and rill, ellipsoidal, club-shaped, calyx and columns	Crude convex-up lamination with porous, semi-indurated to indurated structure	Silt to very-fine grained detrital debris bound into the laminated structure by microbial mats and cemented by aragonite
Playford & Cockbain (1976), Playford (1979), Playford et al. (2013)		Flagpole Landing, Carbla Point and Booldah Well in Hamelin Pool, Shark Bay, Australia	Subtidal (up to ~4 m deep) and intertidal zones of a barred marine embayment, especially in the more saline areas	Flat algal mats and club-shaped, conical and cylindrical columns (<0.75 m tall), often elongate forming ridges	Unlaminated (thrombolites) and laminated (stromatolites), but most show only crude lamination	Trapped and bound sedimentary material, typically with fenestral fabrics. Lithification increases downwards due to aragonite cementation
Hoffman (1976)		Hamelin Pool, Shark Bay, Australia	Shallow subtidal (up to 2 m deep), intertidal and lower supratidal zones of a	Stratiform sheets, ovoid patches, circular and elongate columns (up to	Unlaminated, laminated, and digitate columnar internal structures	Trapped and/or bound sand, with irregular fenestrate fabrics, and simple-, scallop-,

	SHARK BAY		hypersaline marine embayment	1 m relief), and ridge-and-rill structures		ribbon- or multiconvex-lamination. Intergranular aragonite precipitation
Golubic (1985)		Hamelin Pool, Shark Bay, Australia	Subtidal and intertidal zones of a hypersaline marine embayment	Often elongated, headlike and domal (up to 1m high) stratiform structures and flat cushions	Laminated, perforated and fenestrated	Entrapped sediment (mostly carbonate skeletal fragments) and carbonate precipitation, which occurs either as crusts in distinct horizons, or as isolated concretions that later spread
Awramik & Riding (1988)		Hamelin Pool, Shark Bay, Australia	Subtidal and intertidal zones of a hypersaline marine embayment	Subtidal: cylindrical, domal and club-shaped columns, occasionally branching. Intertidal: Club-shaped columns.	Subtidal: poorly laminated with coarse laminoid fenestrae. Intertidal: finely laminated or unlaminated with irregular fenestrae	Subtidal: coarse- to very coarse-grained (0.5-2 mm) bioclastic-ooidal sand. Intertidal: fine-grained (125-250 µm) peloidal-ooidal sand lithified by aragonite cements
Reid et al. (2003)		Flagpole Landing and Carbla Point, Hamelin Pool, Shark Bay, Australia	Subtidal (up to 3-4 m deep) and intertidal zones of a shallow, broad, hypersaline marine embayment	Columns and mounds up to 1 m tall	Subtidal: lamination, although early obliterated. Lower intertidal: couplets of cemented and uncemented laminae. Mid-upper intertidal: patchy, non-laminated.	Subtidal: clotted micrite microfabrics with fenestrae. Lower intertidal: uncemented sandy laminae and thinner (20-500 µm thick) cemented and micritized laminae. Mid-upper intertidal: patches of grains with micritic matrix and fenestrae
Jahnert & Collins (2011; 2012; 2013)		Hamelin Pool, Shark Bay, Australia	Subtidal (up to 2.5 m deep) and intertidal zones of a hypersaline restricted embayment	Mats, ridges, subspherical heads, domes and columns with prismatic, ellipsoidal, calyx or club-shaped morphologies (up to 1.5 m high)	From well- or coarse-laminated stromatolitic fabrics to irregularly clotted thrombolitic and non-laminated cryptomicrobial fabrics	Laminated: grainy ooid-peloid-bioclastic laminae (2-10 mm thick) alternate with thin lithified micritic laminae (with micritized and fused grains). Non-laminated: subspherical patches of micrite, grainy clusters and abundant boring. Aragonite cement fills porosity
Burne & Johnson (2012)		Hamelin Pool, Shark Bay, Australia	Subtidal (up to ~3 m deep) and intertidal zones of a shallow, hypersaline, isolated, marine basin	Subtidal: isolated club-shaped forms and complex mounds (<1.5 m high). Intertidal: head-like and domical forms often elongated	Subtidal: coarsely laminated (stromatolites). Intertidal: laminated (stromatolites) and unlaminated (thrombolites)	Not studied
Hagan (2015), Suosaari et al. (2016a; b)		Hamelin Pool, Shark Bay, Australia	Subtidal (up to ~4m deep), intertidal and supratidal zones of a shallow, hypersaline, restricted, marine embayment	Extensive stratiform stromatolite sheets, and columnar stromatolites (individual or merged in tabular or elongate microbial buildups)	Poorly lithified (stratiform sheets) and lithified (columnar forms). Both can be laminated, moderately laminated or unlaminated	Different proportions of grains (peloids, ooids, bioclasts and quartz), red/brown micrite with dark inclusions and gray clotted micrite. Micritic crusts with micritized and fused grains. Locally micritic filaments.
Sprachta et al. (2001)	Tikehau Atoll, French Polynesia		Flanks of reef-pinnacles and small islets within an atoll lagoon, up to 26 m in depth. Normal marine salinity	Hemispherical and biscuit-shaped domes (up to 10 cm high)	Uneven layered fabrics with discontinuities. Locally, regular lamination	Fine-grained (up to 150 µm) detrital bioclastic particles trapped and bound within the organic network, and micropeloids and micritic patches of carbonate precipitates
Bouton et al. (2016)	Cayo Coco Island, Cuba		Shallow pond (<75 cm deep) of a hypersaline lagoonal network	Flat mats and hemispheroid, cerebroid or terrace structures (up to 20 cm relief)	Laminated	Alternating laminae rich in bioclastic-peloidal sand and laminae rich in microbially induced carbonate precipitation

Table 2 - Fossil agglutinated microbialites

Publications	Age and locality		Environment	Fossil agglutinated microbialites: main features		
				Macroscale	Mesoscale	Microscale
Pederson et al. (2015)	Late Pliocene. Maré Island, New Caledonia		Low-energy but periodically agitated, back-reef environment	Rounded to subrounded oncoids, 0.5-6.5 mm in diameter	Crudely-laminated or massive micritic cortex (up to 3 mm thick) around lithoclastic or bioclastic nucleus	Cortices are mainly composed of dense micrite with an irregular and crude lamination, and abundant trapped and bound sediment and skeletal fragments
Riding et al. (1991a)	Messinian, Almería (Spain)	Late Messinian (Miocene). El Joyazo, Almería, Spain	Shallow, wave-swept oolitic shoals on a platform. Probably normal marine salinity	Smooth inflated hemispherical domes up to 1.5 m high and 4 m wide.	Well-laminated fabrics (stromatolites) and irregular, blotchy and porous fabrics (thrombolites). They pass vertically into each other with sharp contacts	Fine-medium-grained peloids and ooids (packstone-grainstone fabrics). Stromatolites: small fenestrae and locally encrustring forams. Thrombolites: large fenestrae and locally bushy micrite patches
Braga et al. (1995)		Late Messinian (Miocene). Gochar and Cariatiz, Almería, Spain	Shallow wave-swept shelf and deeper storm-swept slope with oolitic shoals and siliciclastic fan-deltas. High-energy environment with normal marine salinity	Hemispherical and steep-sided domes up to 3 m high and 11 m across	Laminated fabrics (stromatolites), clotted fabrics (thrombolites) and structureless (leiolites)	Different mixtures of: a) fine-grained to pebble-size (commonly medium-coarse-grained) siliciclastic grains and ooids; b) dense, bushy or clotted micrite; c) fenestrae
Bourillot (2009), Bourillot et al. (2010a; b)		Late Messinian (Miocene). Sorbas, Cariatiz and Las Negras, Almería, Spain	High energy, tide-dominated oolitic shoals in the shoreface-foreshore, and moderate energy, shallow subtidal-intertidal lagoon/mud-flat. Salinity ranging from normal marine to fluctuating and slightly hypersaline	Crusts, stacked hemispheroids and columns (up to 4 m high and 3.5 m wide)	Laminated fabrics (stromatolites) and unlaminated/clotted fabrics (thrombolites). Both may occur within the same microbialite. *Lithophaga* perforations	Trapped and bound silt-sand-sized ooids, peloids, bioclasts and siliciclastic grains. Micrite precipitation, either laminated or clotted
Goldstein et al. (2013)		Late Messinian (Miocene). La Molata and Rellana-Ricardillo, Almería, Spain	High-energy, near-shore environment with normal marine salinity, and low-high energy near-shore, probably restricted, environment	Thrombolites up to 5 m thick and stromatolites up to 70 cm thick	Dark clotted texture: thrombolites. Fine planar lamination (stromatolites), locally with digitate structure	Thrombolites: peloids, ooids and bioclasts. Stromatolites: alternating coarser/finer laminae with ooids, peloids, micrite and volcaniclastic grains
Arenas & Pomar (2010)	Late Tortonian-Early Messinian (Miocene). Punta des Bous, Mirador des Pontàs and S'Estret des Temps, SE Mallorca, Spain		Shallow-water subtidal back-reef with alternating calm and agitated periods (wavy and flaser bedding). Normal marine salinity	Undulate oolitic microbial laminites (8 cm to 1 m thick) and irregular domes (up to 5 m thick), which widen from base to top (1-2.5 m wide)	Laminites: undulated and flat laminations. Domes: massive (thrombolitic) structure with crudely-laminated convex-up bands	Laminites: thick (<2 cm) grainstone laminae (medium-grained ooids and peloids) and thin (30-60 µm) dark, massive or clotted micritic laminae. Thrombolites: grainy (ooids, peloids and bioclasts) and micritic clots with large pores and micro-cavities
Suarez-Gonzalez et al. (2014; 2016a), this article	Late Barremian-Early Aptian (Early Cretaceous). Arnedillo-Préjano area, La Rioja, Spain		Distal, shallow and tide-influenced areas of coastal wetlands. Predominance of seawater but probable changes in salinity due to freshwater input and/or evaporation	Stratiform and laterally-linked domes up to 0.4 m high and 0.7 m across	Clear lamination (stromatolites) formed by alternating dark and light laminae (0.5-4 mm thick)	Thick (<4 mm) laminae composed by different proportions of grains (ooids, peloids, bioclasts, intraclasts and rare quartz grains), clotted-peloidal micrite, and poorly-preserved calcified filaments; and thinner (25-500 µm, average 140 µm) micritic crusts. Rare pseudomorphs after sulfates (gypsum/anhydrite)

Matyszkiewicz et al. (2006; 2012)	Oxfordian (Late Jurassic), Smoleń (Zegarowe Rocks), Czajowice, and Zabierzów, Poland	Microbial-sponge carbonate buildups on tectonic intraplatform highs. Shallow, normal marine, euphotic and high-energy environment, evolving into a more restricted periodically emerging intertidal flat	Thrombolitic buildups and agglutinated stromatolites, ca. 10 cm thick with vast lateral extent	Thrombolites: massive structure with stromatactis-like cavities. Agglutinated stromatolites: horizontal and variably dipping laminae 1-3 mm thick, with few fenestrae and local bioturbation.	Microbially-stabilized grains: ooids, peloids, micro-oncoids, bioclasts and coprolites (0.2-1 mm diameter). The top of agglutinated laminae shows thin micritized laminae or crusts of dense micropeloidal micrite
Mercedes Martín (2013), Mercedes-Martín et al. (2013a; b; 2014)	Ladinian (Middle Triassic), Catalan Coastal Ranges, Spain	Internal fore-shoals in the inner ramp: shallow marine environment (intertidal to subtidal) with alternation of high-energy and stasis conditions (herringbone and wavy lamination)	Low-relief hemielliptical buildups, stratiform stromatolites and microbial laminites (up to 3 m thick)	Vertically stacked, planar parallel and domal lamination (flat and undulate), mm to cm thick, with birdseye and fenestral fabrics and borings	Alternating grainy laminae (ooids, peloids, intraclasts, quartz grains), up to dm-thick, and dark massive or clotted micritic laminae, up to 2 cm thick
Woods (2013)	Spathian (late Olenekian, Early Triassic). Horse Spring Valley, Nevada, USA	Intertidal and shallow subtidal areas of a carbonate ramp	Tabular beds	Weak lamination at 2-3 mm scale, with an open fenestral fabric	Amalgamation of allochems: peloids, oncoids, ooids, intraclasts and rare skeletal grains
Vennin et al. (2015)	Smithian (early Olenekian, Early Triassic). Mineral Mountains, Utah, USA	Intertidal-subtidal high energy shoal and tide-dominated platform	Planar to wavy contorted crusts up to 50 cm thick	Vertically-stacked irregularly undulated planar, wavy to bulbous lamination with stromatactoid and sheet-like cavities	Grain-rich (ooids, oncoids and bioclasts) mm-thick laminae and thinner micritic or peloidal laminae. Small to large fenestrae
Chow & George (2004)	Famennian (Late Devonian). Chedda Cliffs, Canning Basin, W Australia	High-energy shallow-subtidal back-reef to reef-flat environment of a carbonate platform.	Nearly symmetrical (tepee-shaped) mounds, 0.3-1.3 m high and <2 m wide, with flat bases and chevron-shaped crest	Fenestral clotted fabric (thrombolitic) and wavy laminated (laminae <5 mm thick) fabric (stromatolitic), both within the same mound	Trapped and bound silt- to pebble-sized allochems (peloids, ooids, pisoids, oncoids, intraclasts and calcispheres). Thrombolite fabrics show clotted-micrite matrix between grains. Stromatolite fabrics show thin laminae of micrite or clotted micrite at the top of grainy laminae

Table 3 - Microbialites of the Leza Fm

Microbialite type	General paleoenvironmental setting and distribution	Facies (and detailed paleoenvironments)	Main microbialites features		
			Macroscale	Mesoscale	Microscale
Oncoids	Alluvial fan and freshwater wetland paleoenvironments developed throughout the studied area	Clastic-rich limestone beds with cross-bedding and irregular bases (creeks linked to alluvial fans). Charophyte-rich black limestones (shallow freshwater bodies)	Up to 15 cm in diameter, ellipsoidal to subspherical oncoids. External surface smooth or with small protrusions	Very well-laminated cortices with plenicinct and penecinct laminae (up to 2 mm thick). Truncation surfaces locally observed within cortices	Laminae have mainly filamentous microfabrics, with short and thin filaments in palisade or tuft arrangement. Micritic and clotted-peloidal microfabrics are also observed
Thrombolites	Marine-influenced wetland paleoenvironments developed in the western sector of the studied area	Black micritic limestones rich in dasycladales (quiet shallow water bodies with significant marine influence)	Laterally-continuous biostromes (up to 30 cm thick). Irregular bioherms (up to 0.5x1 m) within thicker beds	Non-laminated with patchy or clotted fabrics formed by interconnected mesoclots that create an open internal framework with a vague upwards-elongated distribution	Typically poorly preserved microfabrics dominated by microsparitic textures with relicts of clotted-peloidal micrite and locally of filaments
Skeletal stromatolites	Freshwater wetland paleoenvironments developed in the western sector of the studied area	Sandy black limestone and sandstone levels with quartz grains, ooids, Jurassic lithoclasts, bioclasts and intraclasts (marginal areas of shallow freshwater bodies with input of clastic material from alluvial fans)	Laterally-linked domes up to 30 cm high. Less commonly stratiform and columnar morphologies	Very well laminated, with laminae up to 8 mm thick, commonly botryoidal-shaped and with moderate to very poor inheritance	Filamentous microfabrics, commonly with long and thick filaments arranged in fan-like structures. Grain accumulations between columns and fans or filling irregularities between successive laminae
Agglutinated stromatolites	Tide-influenced oolitic paleoenvironments developed in the eastern sector of the studied area	Oolitic grainstones and grey mudstones with flaser, wavy and lenticular bedding and foraminifers (shallow tide-influenced areas in the distal parts of a coastal-wetland system)	Stratiform to domal morphologies, up to 40 cm thick	Very well laminated, with alternating dark and lighter laminae up to 4 mm thick	Grainy microfabrics, micritic (clotted, clotted-peloidal) microfabrics, and microfabrics of mixed grainy-micritic composition. Thin (~140 μm) micritic crusts at the top of many laminae, associated with micritized and truncated grains. Rare filament relicts
Micritic-evaporitic stromatolites	Evaporitic paleoenvironments developed in the eastern sector of the studied area	Thinly-bedded to laminated gray dolomites with pseudomorphs after sulfates, foraminifers and common desiccation features (very shallow and restricted marine-influenced areas often hypersaline)	Laterally-linked domes up to 10 cm tall	Very well laminated	Dense, clotted and clotted-peloidal micritic microfabrics. Pseudomorphs after sulfates commonly displace and replace the micrite.
Fenestral laminites	Peritidal wetland paleoenvironments developed in the western sector of the studied area	Gray limestone beds with foraminifers and common desiccation and edaphic features (wide, shallow and commonly desiccated near-marine water bodies)	Thin (<20 cm) laterally continuous beds	Irregular/wrinkly fenestral lamination: mm-scale alternation of micritic laminae and horizontally elongated fenestrae	Micritic laminae have dense, clotted or clotted peloidal microfabrics, which commonly include grains. Rare filament relicts. Fenestrae have locally stromatactis-like structure