***Carnets Geol.* 20 (20)**

E-ISSN 1634-0744
DOI 10.2110/carnets.2020.2020

The biosignature of sparite permits the distinction between gravitational cement and endostromatolites

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Abstract: Following a brief summary of some fundamentals in carbonate sedimentology (sedimentary petrography) that highlights the significance of organic matter, some examples of biocrystals in carbonate grains/particles, such as bioclasts or ooids, are provided as an introductory chapter to a discussion on gravitational cements versus endostromatolites. The gravitational cements, either marine (fibrous) or continental (dog-tooth), are made of hyaline (*i.e.*, translucent) sparitic crystals whereas endostromatolites are made of colored sparitic crystals and/or micrite. Gravitational cements forms in the vadose zone whereas endostromatolites grow in small rock cavities in the marine phreatic zone. As such the latter can grow centripetally in all directions (not only downward).

Key-words:

- asymmetrical cement;
- geopetal infills;
- endostromatolites;
- microbes;
- vadose zone;
- phreatic zone

Citation: GRANIER B.R.C. (2020).- The biosignature of sparite permits the distinction between gravitational cement and endostromatolites.- *Carnets Geol.*, Madrid, vol. 20, no. 20, p. 407-419.

Résumé : *La biosignature de la sparite permet de distinguer un ciment gravitationnel des endostromatolithes.-* Après à un bref rappel de quelques principes fondamentaux de la sédimentologie (pétrographie sédimentaire) des carbonates qui met en évidence l'importance de la matière organique, quelques exemples de biocristaux dans les grains calcaires, tels que les bioclastes ou les ooïdes, sont présentés dans un chapitre d'introduction à une discussion portant sur la distinction entre ciments gravitationnels et endostromatolithes. Les ciments gravitationnels, qu'ils soient marins (fibreux) ou continentaux (en "dents de chien"), sont constitués de cristaux sparitiques hyalins (c'est-à-dire translucides) tandis que les endostromatolithes sont constitués de cristaux sparitiques colorés et /ou de micrite. Les ciments gravitationnels se forment dans la zone vadose alors que les endostromatolithes poussent probablement dans de petites cavités de la roche dans la zone phréatique marine. En tant que tels, ces derniers peuvent pousser de manière centripète dans toutes les directions (et pas seulement vers le bas).

Mots-clefs :

- conservation exceptionnelle (silicification) ;
- bivalves rudistes ;
- *Laluzia* ;
- *Caribbea* ;
- *Parastroma* ;
- Hippuritidae ;
- Porto Rico ;
- Crétacé

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Published online in final form (pdf) on November 20, 2020
[Editor: Michel MOULLADE; language editor: Phil SALVADOR; technical editor: Bruno GRANIER]

1. Introduction

In his PhD thesis, the present author (Granier, 1987: p. 96-97, Pl. 14, fig. a; Pl. 15, fig. d; Pl. 16, figs. c-d; Pl. 17, figs. a-b; Pl. 51, figs. h-i) described from uppermost Jurassic strata in "Sierra Helada" (Serra Gelada, Alicante, Spain) "des ciments [*sic*] asymétriques" [asymetric cements] made of layers of radiating fibrous sparitic crystals with an amber yellow color and micritic laminae or bulges. Granier (1987) pointed out that these structures present in former rock cavities grew in various directions, *i.e.*, they were not necessarily formed under gravitational dynamics, and that, accordingly, they should not be called "microstalactites". He interpreted them to be of microbial origin and more specifically "endostromatolites" *sensu* Monty (1980, 1982) because these structures have grown up in cavities. It appears that, in the scientific literature, such features are commonly erroneously interpreted as pendant or microstalactitic cement (*e.g.*, "gravitational cement" in Flügel, 2004: Pl. 34, fig. 6), and even as microstalacmitic (!) features (*e.g.*, Arnaud-Vanneau, 1980; Arnaud, 1981: vol. 3, Figs. IV, VII, Pls. 33-34). Recent publications document limestones exhibiting similar features from Italy (Amadio *et al.*, 2018) with "dendritic shrub-like fabric" and Algeria (Belkhedim *et al.*, 2019) with "asymmetric fibrous cements (AFC)". In the present author's view, all these structures, being partly of a microbial nature, should not be considered as "cements" (*i.e.*, a word the use of which should be restricted to crystals resulting of the purely chemical precipitation from a brine in voids) but as microbial crusts growing in cavities, *i.e.*, "endostromatolites", as shown through the following simple and naturalistic approach.

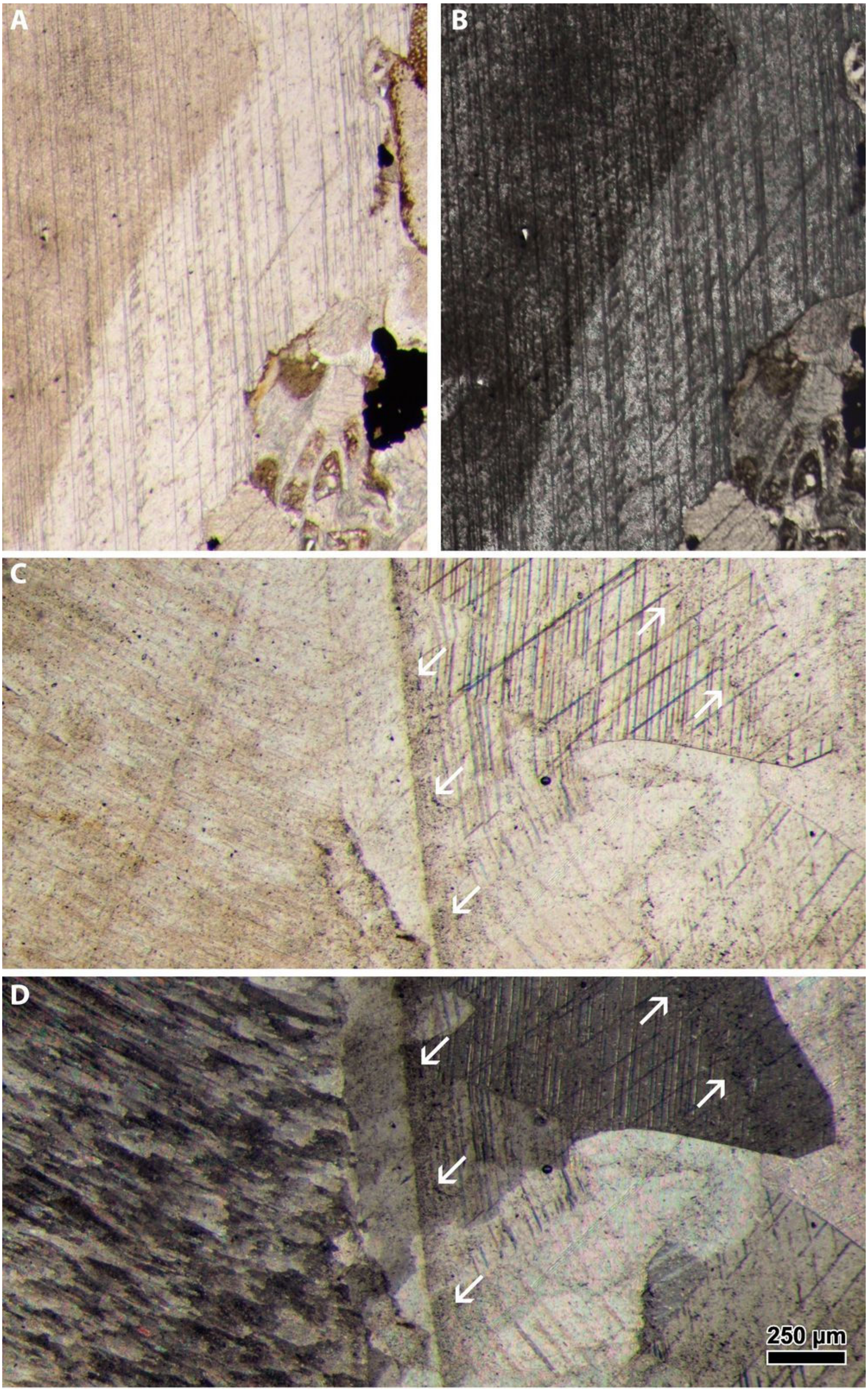
2. Material and method

The studied material is from the present author's collection (currently stored at University of Western Brittany in Brest). It comprises a set of thin sections from various origins (France, Iran, Spain, and Ukraine), which are used either as references (*e.g.*, bioclasts and ooids) for comparison or as case specimens illustrating either endostromatolites (Spain) or gravitational cements (France), or both of them (Ukraine).

The significance of organic matter in carbonate sedimentology is still noticeably undervalued, which brings us to summarize some essentials on carbonate petrography under a standard microscope with focus on biocrystals. Obviously, small amounts of iron oxides or hydroxides, for example, may contribute to coloring quartz or calcite crystals, but organic matter may contribute too, even more significantly, particularly in biocrystals. With the support of modern techniques (SEM, AFM, EDS-energy dispersive spectroscopy, NanoSIMS, TOF-SIMS, microXANES, fluorescence X, high resolution episcopic microscopy, synchrotron XR fluorescence), recent publications (*e.g.*, Dauphin, 2005, 2016; Stolarski & Mazur, 2005; Gorzelak *et al.*, 2012; Cuif *et al.*, 2018, and older references therein) document how organic matter is incorporated within biocrystals during biomineralization processes. Although none of these techniques are available to the present author, the presence of organic matter within biocrystals, *i.e.*, the biosignature of sparite, can be revealed by their natural colors with transmitted light or with reflected light using the "white card" technique (*e.g.*, Granier, 2017) on a standard microscope.

According to Dunham (1962), most limestones are basically either made of components bound together at deposition, *i.e.*, boundstones, or made of components not bound together at deposition and ranging from mudstone, wackestone, packstone, and grainstone with respect to the arrangement and amount of micrite (former calcareous mud), allochems (calcareous grains), cement and residual porosity. It is worth mentioning that this cardinal classification lumps together all "recrystallized" limestones (*e.g.*, dolomitized limestones) in the broad category of "crystalline limestones" (Dunham, 1962). Micrite refers to the microscopic appearance with transmitted light of crystals smaller than 10 µm in size, *i.e.*, less than one third or half the thickness of the ca. 25 µm thick rock slice affixed on the glass slide, the whole forming the petrographic thin section. Accordingly, micrite is dark, not translucent, in transmitted light. Allochems, as well as components bound together at deposition, can be partly or fully micritic but some also comprise yellowish sparite parts whereas others may comprise hyaline (*i.e.*, translucent) sparite parts. The yellowish sparite is either **1)** primary, *i.e.*, consisting of genuine biocrystals that constitute calcitic skeletons, tests or shells, or **2)** secondary, *i.e.*, resulting from the mosaic replacement of primary biocrystals of aragonite or high-Mg calcite. As summarized by Granier *et al.* (2016), "Replacement of aragonite by calcite (*i.e.*, calcitization) commonly results in a mosaic of crystals of a similar size, with a brownish pseudopleiochroism due to the preservation of the original organic matter of the bioclast". The color and the pseudopleiochroism are directly related to the organic matter

▶ **Figure 1: A-B)** Echinoderm (crinoid) remains --colored part on the left-hand side-- with its syntaxial overgrowth --translucent part on the right-hand side--. The whole feature is behaving like a single crystal. Thin section B.12566, exact location unknown, Brittany (France), Paleozoic. A) transmitted light; B) cross polars. **C-D)** Rudist shell with a coarsely fibrous primary calcitic part to the left and a secondary calcitic part to the right. The latter consists of a mosaic of calcite crystals that replaced the original aragonitic part. Ghosts of the primary structure are locally preserved, such as the vertical lining in the middle of both pictures (white arrowheads). Thin section HL 74 (B) 45x60, Serra Gelada, L'Alfàs del Pi, Alicante (Spain), "Calcaires à Rudistes et à Huîtres", lower Albian. C) transmitted light; D) cross polars. All photos same scale bar = 250 µm.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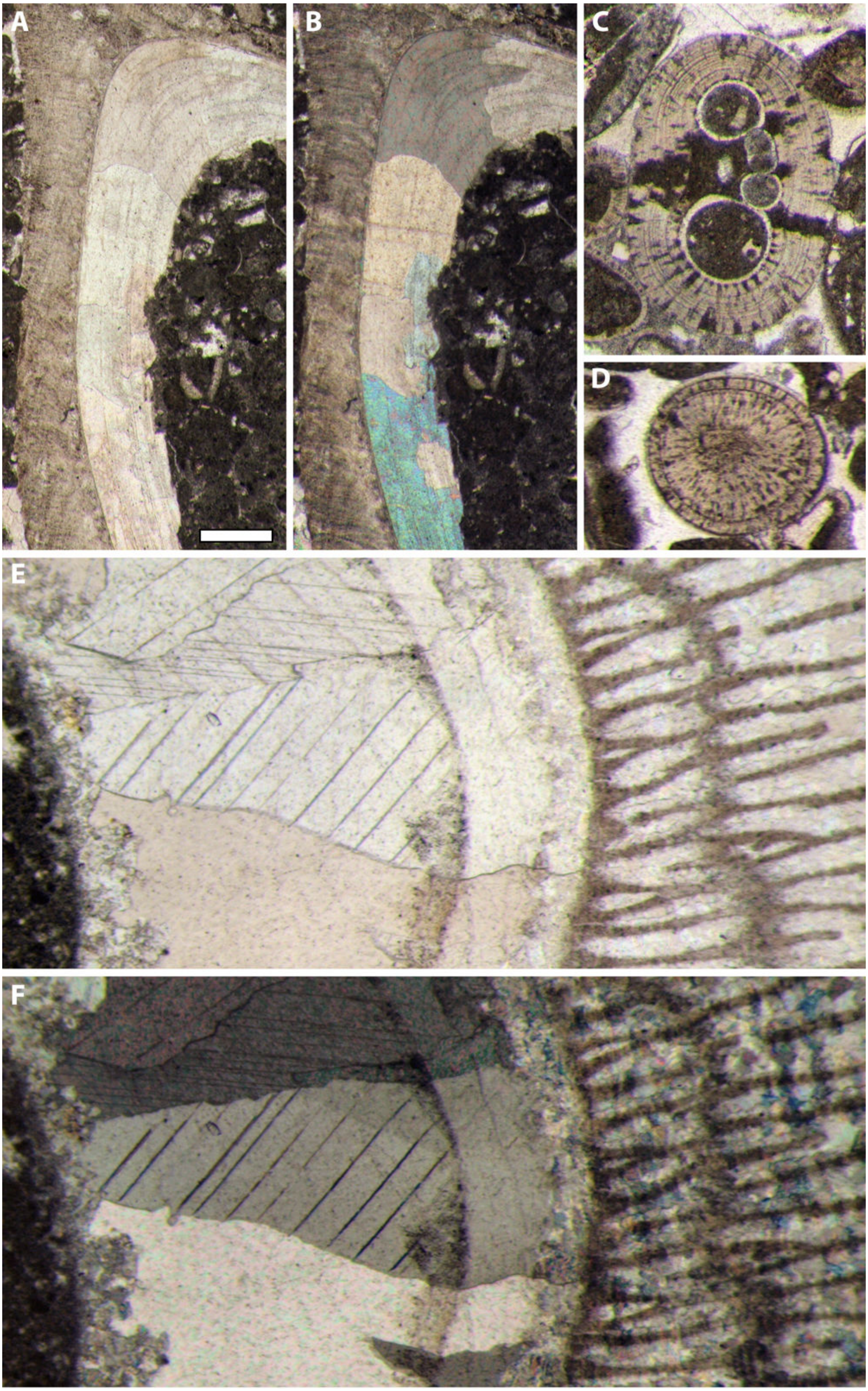
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◀ **Figure 2: A-B)** Rudist shell with a colored primary calcitic part to the left and a secondary calcitic part to the right. The latter consists of a mosaic of calcite crystals that replaced the original aragonitic part. Ghosts of the primary structure, *i.e.*, many linings, are locally preserved. Thin section HL 42 bis (A) 45x60, Serra Gelada, L'Alfàs del Pi, Alicante (Spain), "Calcaires à Rudistes et à Huîtres", lower Albian. A) transmitted light; B) cross polars. **C-D)** Radial fibrous sparitic marine ooids. Thin section BR 2530, Golian, Shirwan, North Khorasan (Iran), Tirgan Formation, upper Barremian. Transmitted light. **E-F)** Rudist shell (*Eoradiolites*) with a secondary calcitic part to the left and a primary calcitic cellular part to the right. The cellular part (right) consists of walls made of yellowish primary calcite and vugs cemented by a translucent drusy sparitic cement. The secondary calcitic part (left) consists of a mosaic of calcite crystals that replaced the original aragonitic part. Ghosts of the primary structure are locally preserved, such as the irregular curved lining in the middle of both pictures. Thin section HL 74 (A) 45x60, Serra Gelada, L'Alfàs del Pi, Alicante (Spain), "Calcaires à Rudistes et à Huîtres", lower Albian: E) transmitted light; F) cross polars. All photos same scale bar = 250 µm.

contents of these calcite crystals. In contrast, hyaline sparite is a translucent cement resulting from the direct precipitation of calcite from a brine in vugs to form palisadic or drusic cements, or it could be the mosaic replacement of a primary aragonite or high-Mg calcite cement. Consequently, most hyaline calcite crystals that result from chemical precipitation should be treated as cement *sensu stricto*, whereas most colored calcite crystals are either primary biocrystals or recrystallized biocrystals and accordingly they should NOT be treated as cement.

A short list of seminal books helping on identification of bioclasts in sedimentary petrography includes BØGGILD (1930), MIŠÍK (1966), MAJEWSKE (1969), HOROWITZ and POTTER (1971), SAMUEL *et al.* (1972), FLÜGEL (1982, 2004, 2010), or the more recent DIAS-BRITO *et al.* (2017), amongst many others. They provide illustrations of **1)** primarily calcitic bioclasts (*e.g.*, echinoids, Fig. 1.A-B herein), **2)** primarily aragonitic bioclasts (*e.g.*, gastropods), eventually secondarily replaced (*e.g.*, bivalves, Fig. 4.E herein) or dissolved and later secondarily cemented (*e.g.*, gastropods, Fig. 4.B herein), and **3)** dual calcitic-aragonitic bioclasts (*e.g.*, serpulids or rudists, Figs. 1.C-D, 2.A-B, .E-F herein). Primary biocrystals and replaced biocrystals are amber yellow colored or "cloudy" due to their residual organic matter content. A few examples are documented and illustrated herein.

3. Examples of primary biocrystals and replaced biocrystals

Radial ooids - samples BR2530 (Fig. 2.C-D): The material was originally collected at Golian, 10 km south of Shirwan, North Khorasan Province, Iran (GPS coordinates: 37°14'13.8"N 57°54'17.3"E). The microfacies of this rock sample from the lower part of the Tirgan Formation, upper Barremian, is typically a floatstone of *Balkhania balkhanica* MAMONTOVA and *Pseudoactinoporella iranica* BUCUR *et al.* with a bioclastic-oolitic grainstone matrix. Nobody ever questioned the role of organic matter in bioclasts whereas fierce debates have taken place regarding its role in ooids (*e.g.*, DANGEARD, 1936; O'REILLY *et al.*, 2017; DIAZ & EBERLI, 2019, and references therein) and in microbial crusts or stromatoids *sensu* KALKOWSKY (1908). Microbes and mucilage (*i.e.*, extracellular polymeric substances or EPS) were well documented in modern and fossil stromatolites and oncoids. On the opposite side until recently (*e.g.*, BREHM *et al.*, 2004; O'REILLY *et al.*, 2017; DIAZ & EBERLI, 2019, and references therein), their role in the ooid factory was still questioned. Iranian ooids are calcitic with a radial fibrous fabric suggesting they were originally formed as high-magnesium calcite. Their cortices are light brown, which implies that organic matter is embedded in their crystal framework.

Rudist shells - samples HL (Figs. 1.C-D, 2.A-B, .E-F): The material was originally collected at Morro de Sant Jordi, Parc Natural de la Serra Gelada, L'Alfàs del Pi, Province of Alicante, Spain (GPS coordinates: 38°34'03.0"N 0°03'21.8"W). Per definition rudist floatstones with wackestone to *bacinella* bindstone (GRANIER, 2012, and in prep.) matrices from the "Calcaires à Rudistes et à Huîtres" (GRANIER, 1987), lower Albian, yield numerous bivalve shells. In both samples (HL42bis: Requienidae, and HL74: Requienidae and *Eoradiolites* gr. *davidsoni* HILL), the originally aragonitic inner layer of the rudist shells is replaced by a mosaic of large calcite crystals that retain few organic ghosts of the primary structure (Figs. 1.C-D, 2.A-B, .E-F).

Bivalve shell - sample 65 (Fig. 4.E): The material was originally collected on the side of the parking area near the Fierney cable-car station of Crozet, Ain Department, France (GPS coordinates: 46°17'03.3"N 6°00'22.0"E). The bioclastic grainstone facies from the uppermost part of the Chambotte Formation (BÖKER, 1994; GRANIER, 2019a), lower Valanginian, yield numerous large benthic foraminifers, including *Pfenderina neocomiensis* (PFENDER) and *Pseudocyclammina lituus* (YOKOYAMA) (Fig. 4.F). Surprisingly all primary aragonitic bioclasts were not dissolved to form micritic envelopes (*e.g.*, Fig. 4.B); some were replaced by a mosaic of calcite crystals that retains some organic ghosts of the primary structure (Fig. 4.E). It is suggested here that the original amount of organic matter in the original biocrystals, as well as its later degree of oxidation and the mesh density of the original aragonite needles, could be clues to this structural difference.

4. Gravitational cement from the lowermost Cretaceous (lower Valanginian) of E France

Gravitational cement - sample 65 (Figs. 3.C, 4): Same as above for the "Bivalve shell - sample 65", the material was originally collected on the side of the parking area near the Fierney cable-car station of Crozet (GPS coordinates: 46°17' 03.3"N 6°00'22.0"E), from the lower Valanginian part of the Chambotte Formation.

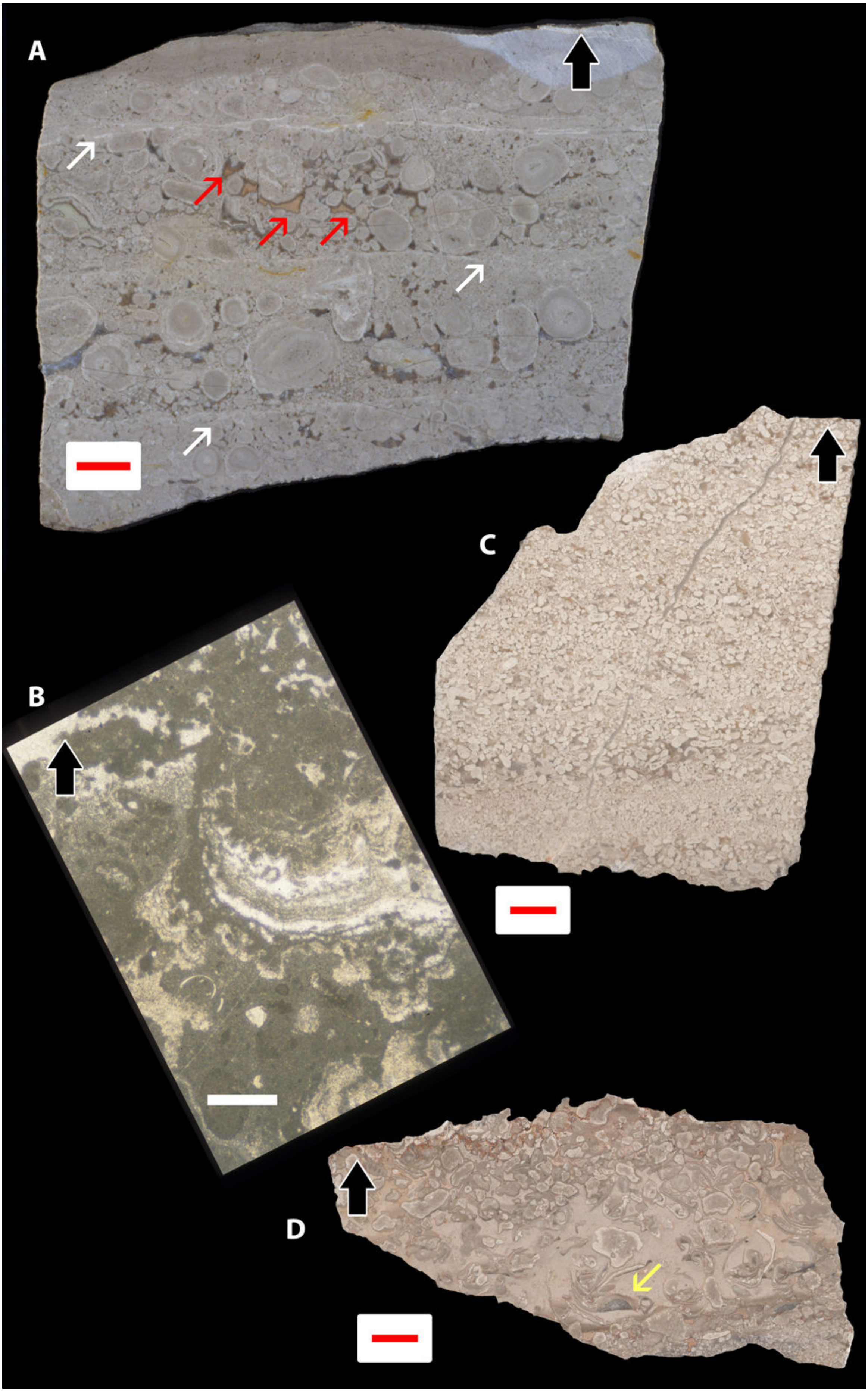
The fabric is dominantly grain-supported with well-sorted and commonly coarse grains (Fig. 3.C). It is a beach-rock facies as evidenced by the fibrous (hence marine) gravitational cement that developed in intergranular cavities below the largest grains (Fig. 4.B, blue arrowheads). This gravitational cement documents a marine vadose setting where beach-rocks form. Some micrite is also partly infilling cavities, including some micritic envelopes following the leaching of the primarily aragonitic bioclasts (Fig. 4.B). A thin isopachous palisadic cement is locally observed (Fig. 4.B), which predates the leaching of aragonite. It suggests an initial marine phreatic setting for diagenesis, hence the occurrence of a short episode of (subaqueous) hardground formation preceding emersion and (subaerial) beach-rock formation. Not all the aragonitic bioclasts were leached. As documented above, a few were replaced by calcite (Fig. 4.E). The micrite, which later percolated through the porous network (*i.e.*, intergranular, intragranular and moldic porosity), commonly displays a geopetal layout (Fig. 4.B, .E, .G-H, .J-L, orange arrowheads). It postdates the leaching that in turn postdates the gravitational cement. Finally, the remaining porosity was cemented by a meteoric phreatic cement and then a deep-burial drusy sparitic cement.

5. Endostromatolites from the uppermost Jurassic of SE Spain

Endostromatolites - samples SHJ (Figs. 3.A-B, 5): The material was originally collected at Morro de Sant Jordi, Parc Natural de la Serra Gelada, L'Alfàs del Pi, Province of Alicante, Spain (GPS coordinates: 38°33'07.3"N 0°03'32.0"W). The stratigraphic unit was improperly named "Mud mounds à Clypéines" (GRANIER, 1987), Tithonian-lower Berriasian. Although the fabrics are dominated by microbial macrostructures (oncoids, algal mats, stromatolites, ...) and comprise various microstructures (such as *Bacinella*, *Cayeuxia*, *Ortonella*, *Girvanella*, *Gakhumella huberi*, coccoids, ... and microbial crusts /stromatoids/ growing in cavities, hence endostromatolites), this unit should have been interpreted as biostromes (Fig. 3.A) rather than as bioherms. In addition, a correct labeling should have been "*Clypeina* Limestones" (GRANIER, 2019a) or better "*Aloisalthella* Limestones", based on the latest systematics of the algal epynom (GRANIER & LETHIERS, 2019).

The rock sample corresponds to a microbial boundstone (Fig. 3.A), probably formed in a very shallow-water setting. Some large cavities between grains were sites for endostromatolitic growth. These commonly zoned endostromatolites comprise yellowish fibrous sparitic crusts and micritic crusts and bulges. Although they commonly look like they were formed under some gravity control, there are places where that was obviously not the case (Fig. 5.C-D). As already documented by GRANIER (1987), the remainder of the cavities were then filled with **1)** dog-tooth like sparitic cements (Fig. 5.C, .E, white arrowheads), which are the mark of a continental phreatic setting, **2)** red-colored marine micrites that have percolated downward through the remaining porous network and a fracture network, and finally **3)** a drusy sparitic cement, which corresponds to the deep burial setting. At Serra Gelada, the Tithonian-lower Berriasian "*Aloisalthella* Limestones" are topped by an angular unconformity (GRANIER, 1987, Pl. 13, fig. d) in the form of a bored surface, a feature which suggests the occurrence of at least one episode of emersion and erosion preceding a flooding. The fracture network is post-early Valanginian in age (see GRANIER, 1987; GRANIER *et al.*, 1995). It was polyphasic, as documented by several episodes of fracturing, phreatic cementation and red-colored micrite infill (*e.g.*, GRANIER, 1987, Pl. 16, fig. a), which have occurred over part of the late Valanginian – earliest Aptian time interval.

▶ **Figure 3: A)** Polished slab of an oncoid floastone to bindstone facies from Serra Gelada, L'Alfàs del Pi, Province of Alicante (Spain), "*Aloisalthella* Limestones", Tithonian-lower Berriasian. White arrowheads point to stratiform binding micritic films, red arrowhead points to a patch of red-colored micrites corresponding to upper Valanginian – lower Aptian pelagic mud that has percolated downward into the porous network. Sample SH 19; **B)** Detail of a colored fibrous sparitic cauliflower-like structure growing in a cavity of the "*Aloisalthella* Limestones" (GRANIER, 1987, Pl. 15, fig. d). Thin section SHJ 1B, Serra Gelada, L'Alfàs del Pi, Province of Alicante (Spain); **C)** Polished slab of the beachrock facies from Crozet, Ain Department (France), Chambotte Formation, lower Valanginian. Sample 65; **D)** Polished slab of a coquina facies from Bukivna/Буківна, Ivano-Frankivsk Oblast (Ukraine), "Niźniower Kalkstein", Tithonian-lower Berriasian. The yellow arrowhead points to a former shelter cavity below a bivalve shell, now fully cemented. Sample F3. Thick black arrowheads are upward-oriented; scale bars: red = 1 cm, white = 500 µm.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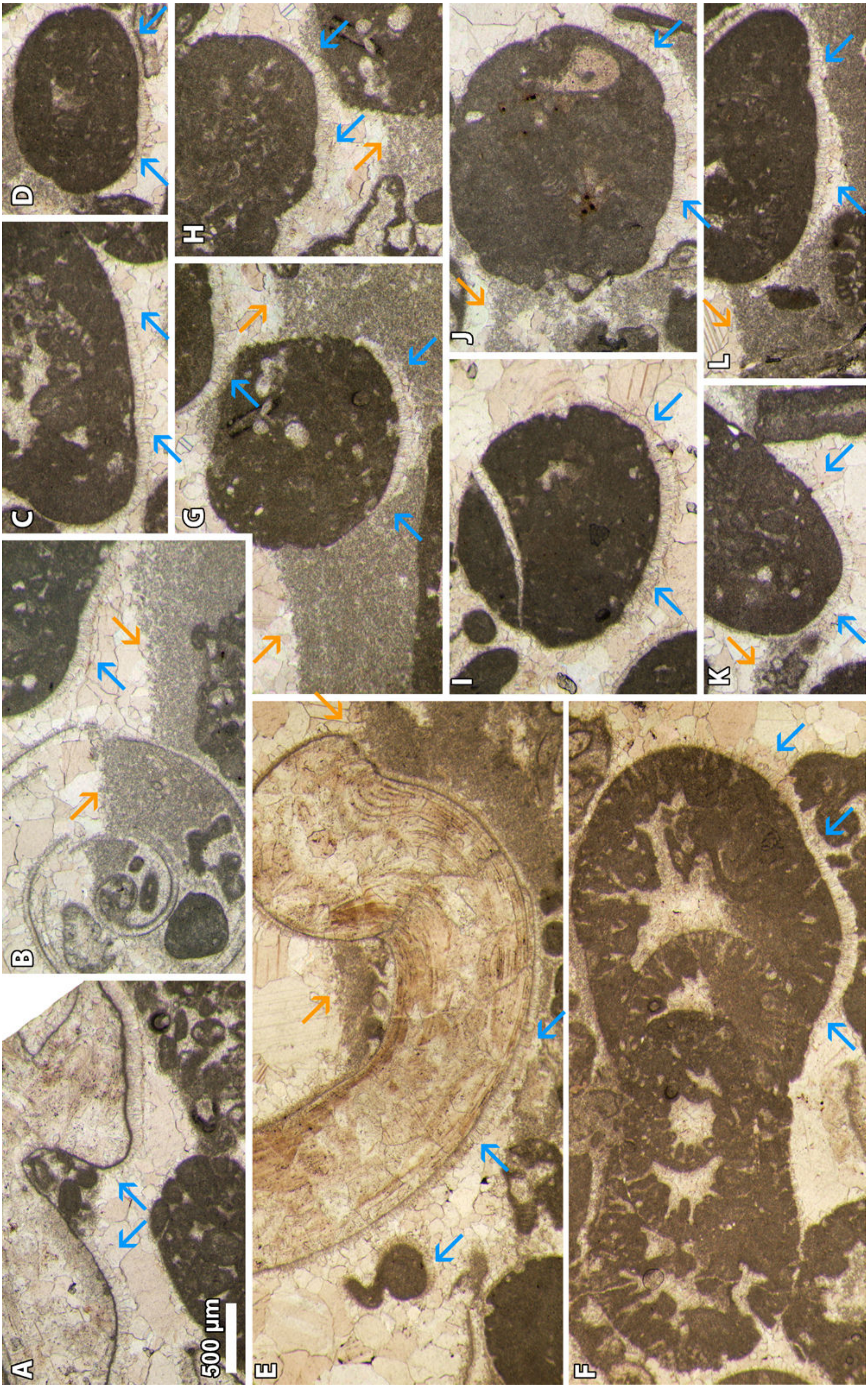
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◀ **Figure 4:** Early gravitational cement (blue arrowheads) and late geopetal micritic infills (orange arrowheads) from Crozet, Ain Department (France), Chambotte Formation, lower Valanginian. **A, D, I, L)** Thin section Bb1995/65c. **B-C, K)** Thin section BR 2594. **E-F)** Thin section BR 2595. **G-H, J)** Thin section Bb2003/65c'''. All photos same scale bar = 500 µm.

6. Endostromatolites and gravitational cement from the uppermost Jurassic of W Ukraine

Endostromatolites and gravitational cement – sample F3 (Figs. 3.D, 6): The material was originally collected near Bukivna/Буківна, Ivano-Frankivsk Oblast/Province, Ukraine (GPS coordinates: 48°59'04.5"N 24°58'07.4"E). The stratigraphic unit corresponds to the "Niźniower Kalkstein" (ALTH, 1882; GŁAŻEWSKI, 1937; GRANIER, 2019b, 2020), upper Tithonian-lower Berriasian, the stratum typicum of *Actinoporella podolica* (ALTH, 1878) (see GRANIER, 2019b), that of *Aloisalthella sulcata* (ALTH, 1882) (see GRANIER & LETHIERS, 2019), and also that of some agglutinated foraminifers described by CUSHMAN and GŁAŻEWSKI (1949).

The rock sample corresponds to a coquina (Fig. 3.D), probably in a supratidal wash-over setting. Its texture is that of floatstone to rudstone because the allochems are large, including numerous gastropods, some corals, sponges, *Arabicodium* sp. (*i.e.*, a large Bryopsidalean alga), and *Cayeuxia* microstructures. The related large cavities between grains or inside them were sites for endostromatolitic growth (Fig. 6). Although the yellowish fibrous sparitic layers commonly look like they were formed under gravity control, that is not obvious in some places. These endostromatolites, commonly zoned, also comprise micritic bulges, either embedded or developing on the side of the crust. The emersion that affected the "Niźniow" limestones led to the dissolution of most aragonitic shells, leaving behind micritic envelops, in a (?) continental vadose setting. The development of non-isopachous, hence partly gravitational, dog-tooth sparitic cement in all cavities, including in the micritic envelops, means that the rock remained in a dominantly continental vadose setting (with at least one episode in a phreatic setting). The micrite, which percolated later through the porous network in a marine phreatic setting and almost completely filled in the cavities, postdates the dog-tooth cementation and is probably the mark of the Late Cretaceous marine transgression in the area.

7. Conclusions

As documented above, sparite crystals forming gravitational cements, whether they are **1)** fibrous in shape and the signature of a vadose marine setting (*e.g.*, in the French sample, Figs. 3.C, 4) or **2)** dog-tooth shaped and the signature of a vadose continental setting (*e.g.*, in the Ukrainian sample, Figs. 3.D, 6), are hyaline/translucent. In contrast, sparitic biocrystals that form bioclasts are commonly colored by organic matter, which is also the case of sparitic crystals forming colored crusts in some rock cavities and that should be assigned a biogenic origin. Such individual colored crusts are here called endostromatoids whereas the assembly of colored sparitic and/or clotted micritic crusts in a similar setting is called endostromatolite, not cement. Besides being colored, contrary to the crystals forming gravitational cements that are always hyaline, endostromatolitic biocrystals are not necessarily growing gravitationally as documented herein (*e.g.*, Fig. 5). Because no specific laboratory investigation of the organic contents of such endostromatolites has hitherto been attempted, it is felt that the features given above should serve as a preliminary guide to distinguish between endostromatolites (*e.g.*, "gravitational cement" in FLÜGEL, 2004: Pl. 34, fig. 6) and genuine gravitational cement (*e.g.*, "pendant (or gravitational) cement" in FLÜGEL, 2004: Pl. 33, fig. 4).

Acknowledgments

The manuscript also benefited from the constructive reviews of Bogusław KOŁODZIEJ and George PLEȘ. The author would like to thank Phil SALVADOR for his appreciated help with the original (English) text and Robert W. SCOTT for the final touch. He would like to acknowledge the support of Alin OPRIȘA, Volodymyr KHOMYN, Lev MONCHAK, and Natalia SHKOLNA for fieldwork in Ukraine (2019), and that of Zinat HASANZADE, Javad PAKRAVAN, and Morteza TAHERPOUR KHALIL ABAD for fieldwork in Iran (2017).

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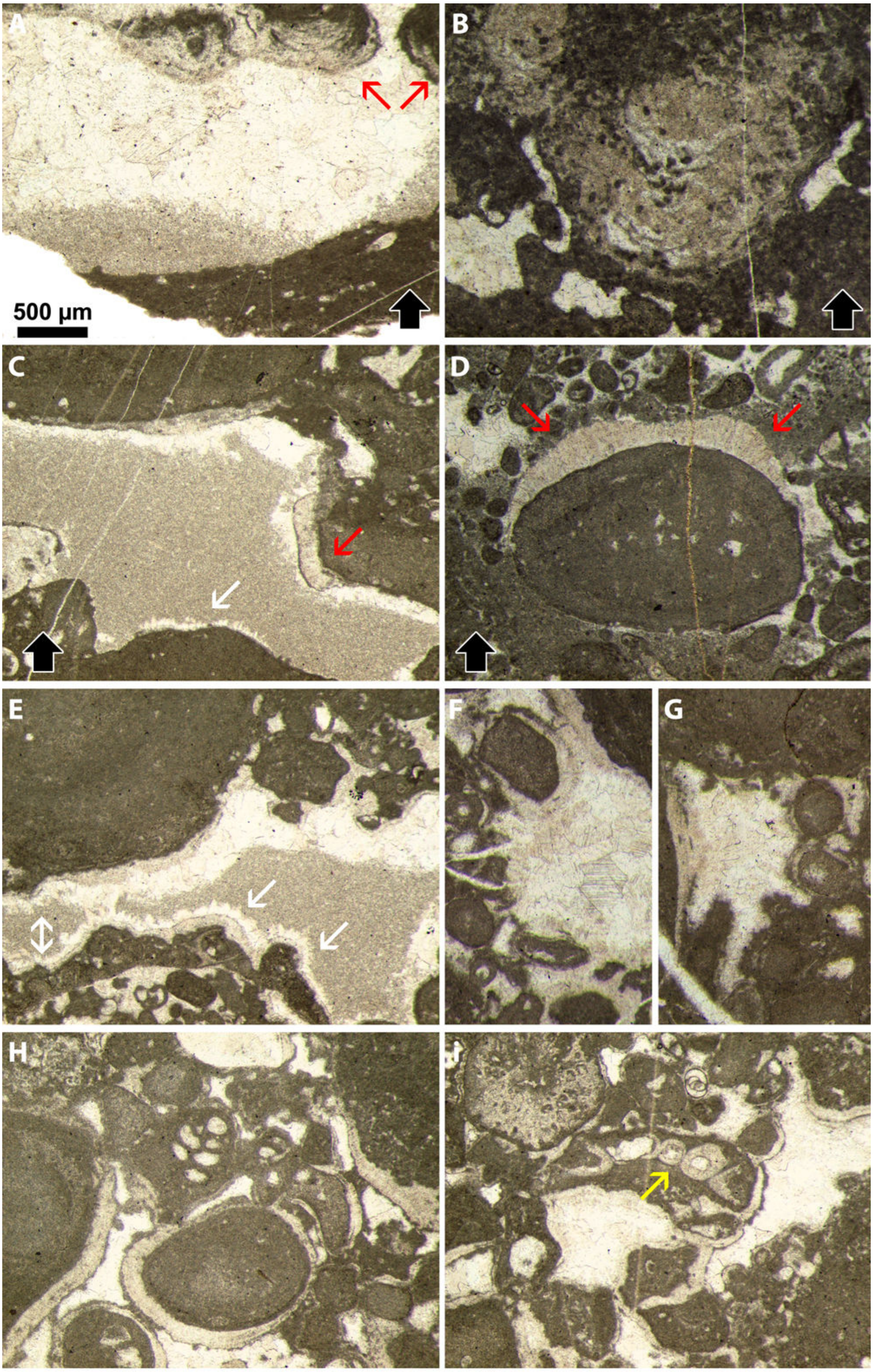
▶ **Figure 5:** Endostromatolites (red arrowheads) from Serra Gelada, L'Alfàs del Pi, Province of Alicante (Spain), "*Aloisalthella* Limestones", Tithonian-lower Berriasian. Thick black arrowheads in A-D are upward-oriented; E-I are oblique or horizontal sections (*i.e.*, oblique or parallel to stratification). **A)** infill, cf. GRANIER, 1987, Pl. 51, fig. h. The red arrowheads point to non-strictly gravitational crusts. Thin section SHJ 1B; **B)** Thin section SHJ1 b; **C)** The red arrowhead points to a non-gravitational crust whereas the white arrowhead points to a dog-tooth like sparitic cement. Thin section SHJ1B (uncovered); **D)** The red arrowheads point to a non-gravitational crust. Thin section SHJ 2 (A); **E)** The white arrowheads point to the dog-tooth like sparitic cement. Thin section SHJ 1B (?); **F)** Thin section SHJ1B (covered); **G)** Thin section SHJ1B (covered); **H)** Thin section SHJ 1B (?); **I)** The yellow arrowhead points to verticil of *Aloisalthella sulcata* (ALTH), the calcification of which is yellowish-colored as the endostromatolitic crusts. Thin section SHJ 1B (?). All photos same scale bar = 500 µm.


A
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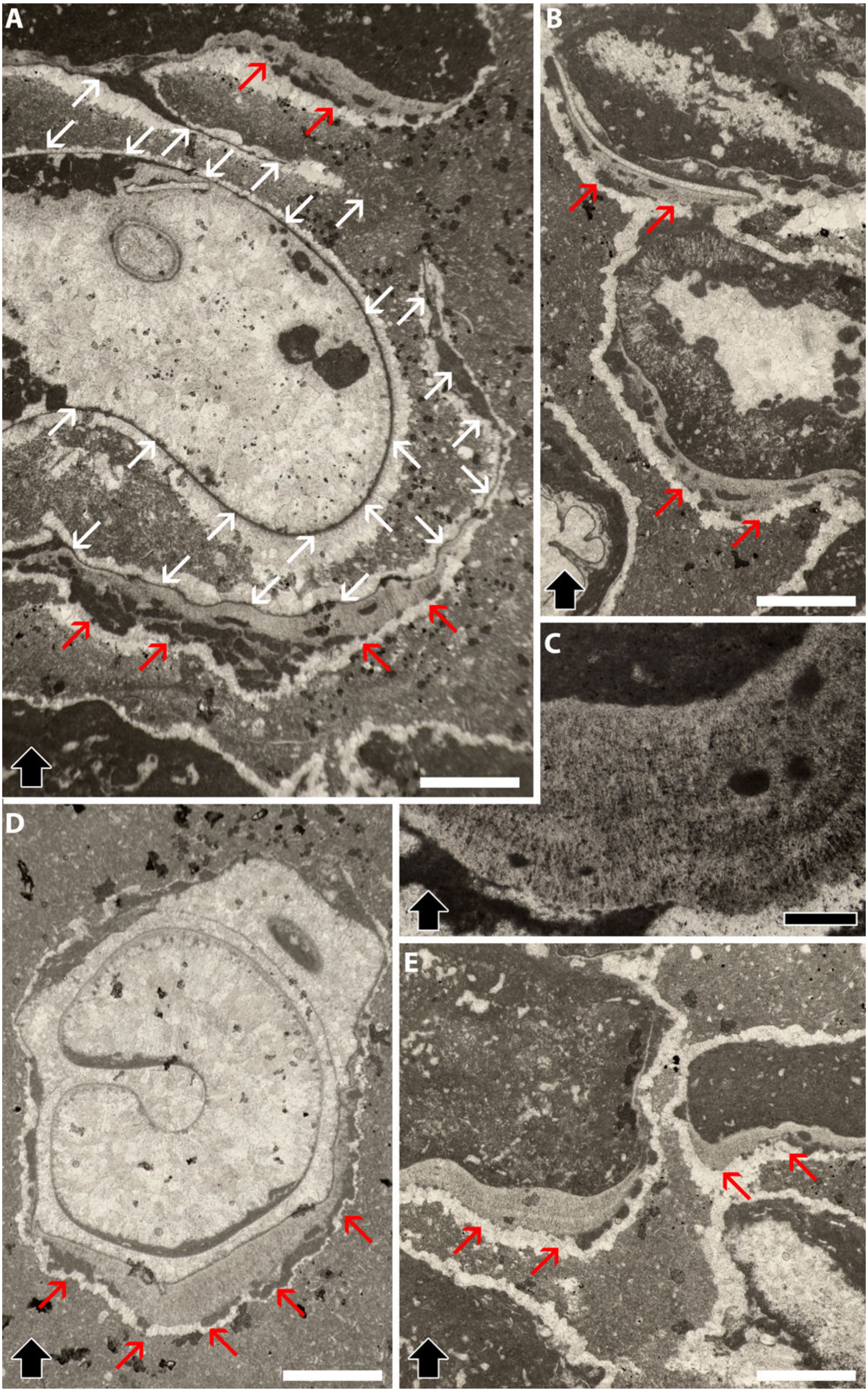
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◀ **Figure 6:** Endostromatolites (red arrowheads) from Bukivna/Буківна, Ivano-Frankivsk Oblast (Ukraine), "Niźniower Kalkstein", Tithonian-lower Berriasian. **A)** White arrowheads point to the micritic envelop of a former aragonitic gastropod shell. Thin section BR 3008. **B)** As in the previous picture, the micritic infill of the interparticular and moldic cavities postdates a phreatic cementation, that in turn postdates the dissolution of aragonitic shells. Thin section BR 3005. **C)** Detail of a colored fibrous sparitic crust growing in a cavity. Thin section BR 3008. **D)** Colored fibrous sparitic crusts in a cavity below a gastropod shell. Thin section BR 3010. **E)** Colored fibrous sparitic crusts growing in cavities. Thin section BR 3006. Red arrowheads point to endostromatolites (crusts); thick black arrowheads are upward-oriented; scale bars: white = 1 mm, black = 250 µm.

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