Origin and role of non-skeletal carbonate in coralligenous build-ups: new geobiological perspectives in the biomineralization processes

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Abstract. The coralligenous build-ups located in Mediterranean shelf in front of Marzamemi (SE - Sicily, Italy) represent useful natural examples to study the relationship between skeletal organisms and non-skeletal components in marine bioconstructions. Coralligenous build-ups are formed in open marine systems and their comparison with coeval bioconstructions (biostalactites) of confined environments, like submarine caves, allows depicting the complex interactions between metazoans and microbial communities in the formations of recent bioconstructions in different Mediterranean settings. In this study, two coralligenous build-ups were characterized in terms of organisms and sediments involved in their formation. The framework mainly consists of coralline algae and subordinate bryozoans and serpulids. Sponges affect the general morphology of the bioconstructions both interacting with skeletonised organisms and through bioerosion activity. The micrite or microcrystalline calcite is present in minor amount than other components that form the build-ups and consists of two types: autochthonous (*in situ*) and allochthonous (detrital). Fine autochthonous micrite mineralized directly inside the framework cavities and shows aphanitic or peloidal fabric, produced by organomineralization processes of soft sponge tissues and microbial metabolic activity, respectively. The detrital micrite occurring inside cavities derives from external sources or erosion processes of the bioconstructions themselves. This component has been classified as organic or inorganic based on the organic matter contents deduced by UV-Epifluorescence. A great amount of sponges lives in cavities of the coralligenous build-ups and compete with carbonatogenic bacteria for the same cryptic spaces limiting the production of microbialites. The sharing of a similar relationship between sponges and microbial communities by coralligenous concretion and biotic crusts of particular submarine caves suggests that this competition is not habitat specific. On the contrary, it may develop in a range of environmental settings, from open to cryptic systems, and could be used to clarify the role of metazoans *vs* microbialites in palaeoecological reconstructions.

Keywords: Coralligenous reefs; Sponges; Micrites; Geobiology; Mediterranean.

1. Introduction

Bioconstructions consisting of in-place reef-building organisms in temperate waters of the Mediterranean Sea shelf are known as Coralligenous (Pérès and Picard, 1964). The term Coralligenous (Coralligéne) is derived from the French literature (Marion, 1883; Pérès and Picard, 1964), and generally indicates mesophotic bioconstructions of the Mediterranean Sea, primarily built by crustose coralline algae. However, in recent years, the definition of Coralligenous is under review, also due to the exploration efforts in the deepest part of the shelf (Cerrano et al., 2019).

These structures are primarily made-up of calcareous red algae, which are able to develop algal-dominated frameworks characteristic for this basin (*e.g.*, Ballesteros, 2006). Pérès and Picard (1964) consider the Coralligenous a climax biocoenosis of the circalittoral zone, in which crustose coralline algae (CCA) and mineralized Peyssonneliales develop on primary or secondary hard bottoms, in dim-light conditions. The crustose coralline algae have an excellent fossil record from the Early Cretaceous onwards (Aguirre et al., 2010) but the fossil record of build-ups similar to Coralligenous dates back only to the Quaternary (Sartoretto et al., 1996; Bertolino et al., 2017a, 2017b; Basso et al., 2022).

Due to its importance as hot spot of biodiversity, the European Community considers the Coralligenous among the most important habitats to be monitored and protected (see: Ballesteros, 2006; Gennaro et al., 2020), considering also its low accretion rate of 0.06÷0.27 mm per year (Sartoretto et al., 1996; Di Geronimo et al., 2001; Bertolino et al., 2019; Basso et al. 2022). Coralligenous is usually considered to be an association of several communities (Ballesteros, 2006; La Rivière et al., 2021). Indeed, the external surface and the cavities of the build-ups host a rich association of calcareous red algae, sponges, bryozoans, serpulids, molluscs, and corals (Pérès, 1982; Bellan-Santini et al., 1994; Di Geronimo et al., 2002; Ballesteros, 2006; Rosso and Sanfilippo, 2009; Bertolino et al., 2017, 2019; Costa et al., 2019; Basso et al., 2022; Bracchi et al., 2022; Cipriani et al., 2023). Coralligenous build-ups: (i) modify the seafloor and the seascape (Laborel, 1961; Basso et al., 2007; Bracchi et al., 2015, 2017), (ii) promote the production of carbonate (Marchese et al., 2020), and (iii) may be recognized in the sedimentary succession (Bosence and Pedley 1982; Carannante and Simone 1996; Basso et al., 2007, 2009; Titschack et al., 2008; Bracchi et al., 2014, 2016, 2019). The presence of the coralligenous 3D structure and the related high biodiversity and biomass also determine the increase of available resources. These attract microorganisms such as ostracods and foraminifera which, while not contributing directly to the bioconstruction, raise its biodiversity (e.g., Hong, 1982; Ballesteros, 2006; Sciuto et al., 2023).

Unlike other aspects, geobiological features of the Coralligenous and the role of skeletonised and non-skeletonised (*e.g.,* bacteria) communities in forming these build-ups have so far not been explored in detail. The lack of this information produces a gap between the knowledge of the build-ups developed in the open settings of the Mediterranean Sea and those forming in confined environments, like the "biostalactites" of submarine caves. Actually, "biostalactites" from Apulia, Adriatic Sea (Onorato et al., 2003; Belmonte et al., 2009; Rosso et al., 2020; Guido et al., 2022), Sicily (Guido et al., 2012, 2017a; Sanfilippo et al., 2015), Lesvos Island, Aegean Sea (Sanfilippo et al., 2017; Guido et al., 2019a, 2019b); and Cyprus, Levantine Sea (Guido et al., 2017b; Jimenez et al., 2019) have been studied in detail and the biotic and abiotic processes involved in their formation have been clarified. These studies showed the fundamental role of bacteria in strengthening the bioconstructions, through the biomineralization processes of autochthonous micrite (Guido et al., 2013, Gischler et al., 2017a). Like these systems, it is conceivable that also the high porous framework of the Coralligenous could promote the development of non-skeletal biomineralization processes.

Biomineralization indicates a relationship between biotic activity or products and mineralization. Several biomineralization processes have been extensively investigated mainly in carbonate rocks (Riding, 2000, 2011; Van Driessche et al., 2019). Trichet and Défarge (1995) introduced the term organomineralization for mineral precipitation mediated by non-living microbial organic substrates *via* acidic macromolecules of extracellular polymeric substances

(EPS). These macromolecules provide a template for biofilm organomineralization. Dupraz et al. (2009) later utilized the term "organomineralization *sensu lato*" for not genetically controlled processes that mediate mineral precipitation on an organic matrix, including in the definition both the active (biologically induced, mediated by living organic substrates) and passive (biologically influenced, mediated by non-living organic substrates) processes. Summarizing, crystal nucleation in biomineralization processes can be: (i) controlled directly by the organisms (Blakemore, 1975; Mann, 1983; Mann, 2001; Weiner and Dove, 2003; Bazylinski and Frankel, 2004; Komeili, 2007; Altermann et al., 2009; Riding and Virgone, 2020); (ii) induced by microbial communities (Lowenstam and Weiner, 1989; Perry et al., 2007; Altermann et al., 2009; Dupraz et al., 2009; Borch et al., 2010; Phillips et al., 2013; Anbu et al., 2016; Riding and Virgone, 2020); or (iii) influenced by the presence of cell surface organic matter (Trichet and Défarge, 1995; Perry et al., 2007; Altermann et al., 2009; Dupraz et al., 2009). In all these cases, the formation of biominerals also depends on the chemical-physical conditions of the environment (Riding and Liang, 2005; Riding, 2011). Here the autochthonous micrite ("automicrites" *sensu* Wolf, 1965) was considered a product of induced or influenced biomineralization. To date no research has been addressed to this topic and, in the frame of the project "CRESCIBLUREEF", we aim to improve knowledge on the Coralligenous: (1) describing the origin of the sediments filling the cavities of the skeletal framework; (2) investigating the relationships between sponges and microbial processes through biomineralization-mediated processes; and (3) comparing the Coralligenous, formed in open marine systems, with the bioconstructions of submarine caves developed in confined marine settings.

2. Materials and methods

In the studied area, coralligenous bioconstructions, mostly columnar-shaped and distributed in more or less dense clusters, extend widely in a belt between ca 36 and 100 m depth. The image analysis and computed axial tomography reveals that the bioconstruction's framework is mainly formed of coralline algae and in minor amount of invertebrates (mostly serpulids and bryozoans) and cavities filled with sediment (Bracchi et al., 2022; Varzi et al., 2023). The surfaces of the studied build-ups were covered with a dense, up to 8–10 cm thick, canopy of fleshy algae and locally, also by subordinate erect bryozoan colonies (Bracchi et al., 2022; Donato et al., 2022; Rosso et al., 2022, 2023; Sciuto et al., 2023). The most abundant components are CCA and mineralized Peyssonneliales with a cover of up to about 61%. Fleshy algae are also abundant, up to about 32%. The faunal groups have negligible covers, except for bryozoans reaching about 12% (Bracchi et al., 2022).

Two build-ups called CBR2_3_7c and CBR2_4_21c from this coralligenous field located in the Ionian Sea were collected (Fig. 1). The build-up CBR2_3_7c (36° 43.394′ N; 15°09.469′ E) was sampled at 36,2 m depth in a zone covered by coralligenous hybrid banks (Bracchi et al., 2017), made of distinct, though sometimes coalescent, coralligenous columnar build-ups (Fig. 1b and d). The build-up CBR2_4_21c (36°43.454′ N; 15°09.657′ E) was collected at 36,7 m depth in an area characterized by sparse and distinct build-ups growing on biogenic gravel and sand substrate (Fig. 1c and e).
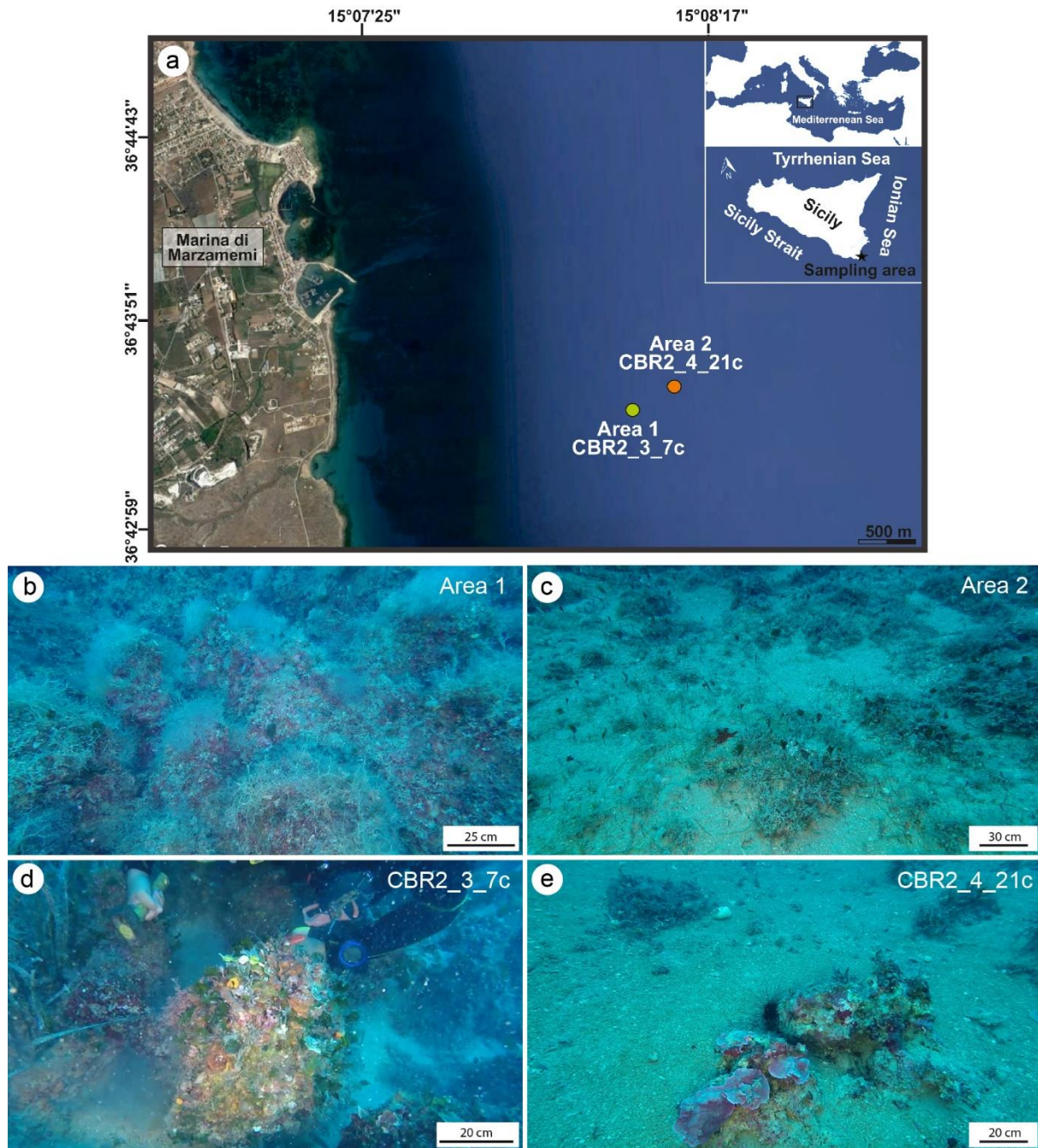
Figure 1 (**a**) Location of the study areas off the coast of Marzamemi village in the Ionian Sea. (**b-c**) Underwater photos of the sampling sites. (**d**) Area 1, characterized by high coralligenous cover, from where the CBR2_3_7c build-up was collected at 37 m. (**e**) Area 2, showing sparse and isolated coralligenous columnar bioconstructions, from where CBR2_4_21c build-up was sampled at 36 m.

After drying, the build-ups were cut with a diamond saw following the putative grow direction of the structures (Fig. 2a, b, d and e). The cutting planes showed that the coralline algae framework forms a highly porous structure with cavities filled with sediments (Fig. 2c and h). Photos at macroscale were acquired at the University of Milano-Bicocca with a Nikon D3500 camera. Photos at mesoscale were acquired at the University of Catania through a stereomicroscope Zeiss Discovery V8A stocked with an Axiocam MRC and a system for automatic acquisition of the images (Axiovision). To investigate the role of sediment in the growth and stabilization of the skeletal components (at micro and nano-scale) small fragments (Fig. 2g and h) and thin sections (Fig. 3) were analysed at the Laboratory of Geobiology of the Department of Biology, Ecology and Earth Science, University of Calabria.

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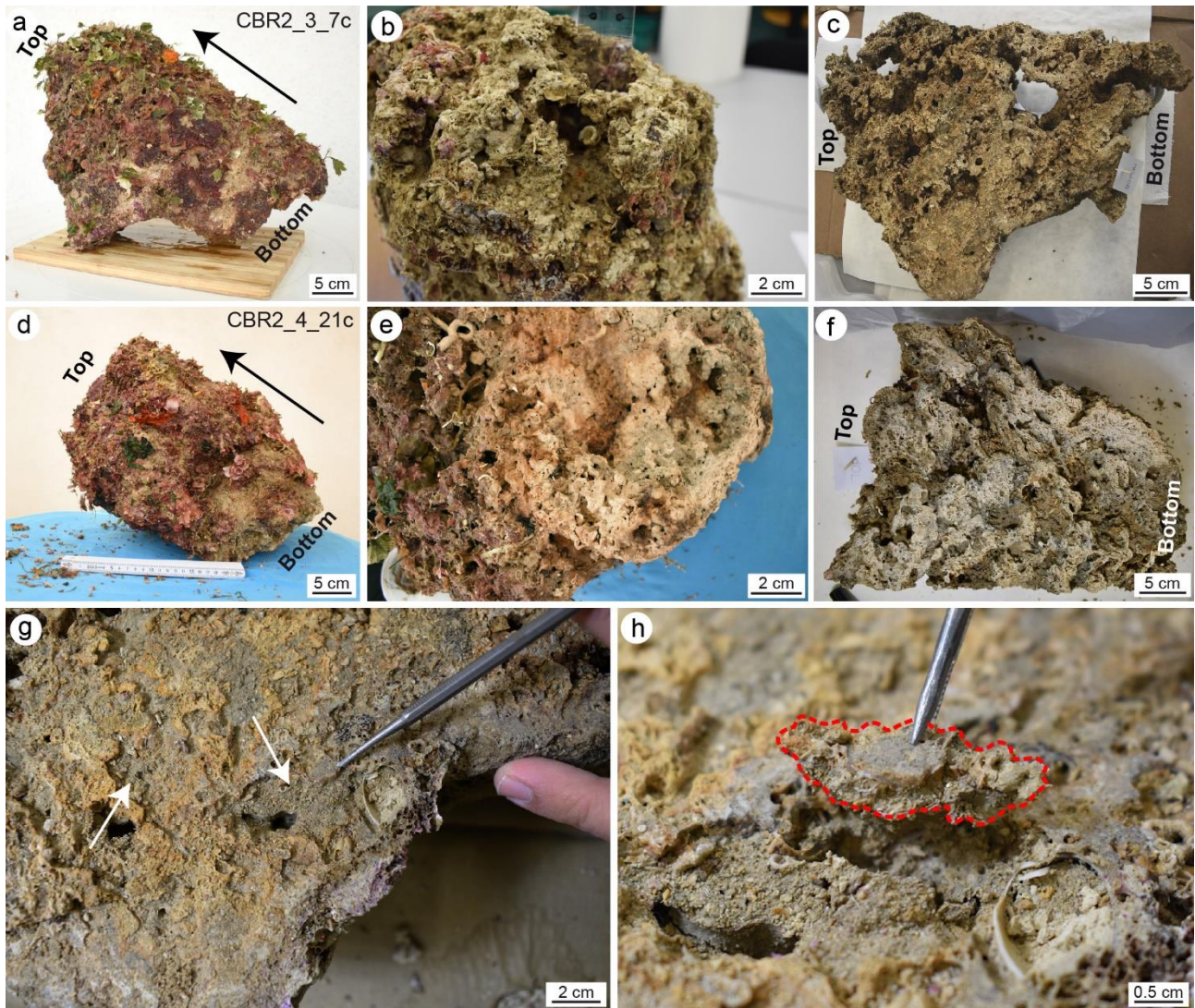


Figure 2 (**a** and **d**) Sampled coralligenous build-ups; note the high biogenic cover (largely consisting of soft-bodied organisms) on the external surfaces. Black arrows indicate the main growth direction. (**b** and **e**) Surfaces of detachment from the sea-bottom. (**c** and **f**) plane slab after the longitudinal cut of the build-ups showing the internal structure; note the high porous skeletal framework with cavities partly filled with sediment. (**g** and **h**) Selection and sampling of small micritic fragments from the cutting surfaces. (**g**) The white arrows point to cavities partly filled with sediment on a cutting plane of the CBR2_3_7c build-up; (**h**) detail of a fragment (red dotted line) sampled for the analyses. Bottom indicates the portion of build-ups detached from the substrate. **a**, **c**, and **h** adapted from Cipriani et al.,2023.

A total of twenty-nine small blocks, selected following a grid with sides of 5x3 cm on the cutting plane, have been utilized for thin sections preparation (Fig. 3). The blocks have been chosen based on the mesoscopic aspect and relative amount of skeletal components and micrite sediments. The fragments and thin sections have been investigated using an optical microscope (Zeiss Axioplan Imaging II) at different magnifications (2.5 x, 5 x, 10 x, 20 x, and 40 x). Thin sections were used for point counting analyses of the main components (skeletons, micrite and cavities). A total of 300 points per thin section were counted. Fluorescence intensity has been evaluated in incident light utilizing a Hg high-pressure vapour bulb and high-performance wide bandpass filters (band-pass filter 436/10 nm/long-pass filter 470 nm, no 488006, for the green light; and band-pass filter 450–490 nm/long-pass filter 515 nm, no. 488009, for the yellow light). UV-epifluorescence was used to discriminate the presence and distribution of organic compounds and to recognize, together with microfacies textures, biotic and abiotic components, especially in those cases showing a similar general aspect under reflected light (Neuweiler et al., 2000, 2003, 2023).

146 Selected fragments, used for Scanning Electron Microscopy (SEM) observations and Energy Dispersive X-ray

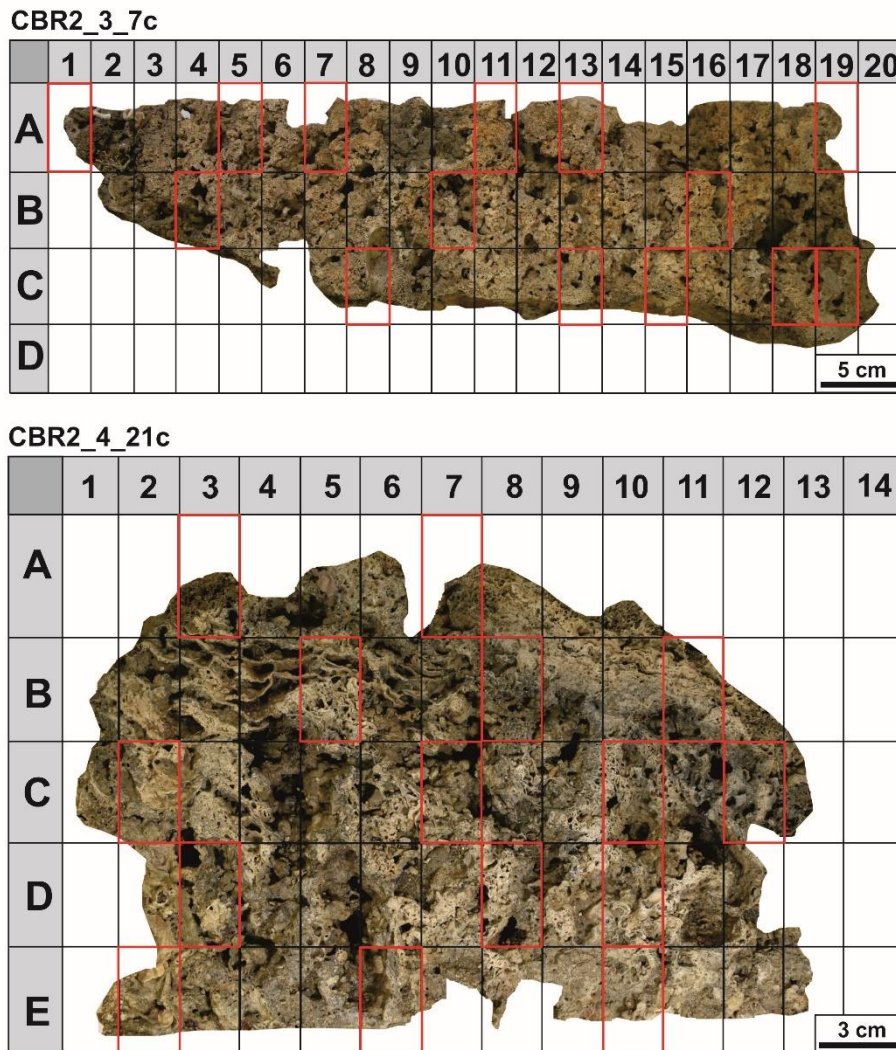
147 Spectroscopy (EDS) microanalysis, were carbon coated. The SEM apparatus was used is Ultra High Resolution (UHR-

148 SEM) – ZEISS CrossBeam 350. The working condition were: resolution 123 eV, high voltage 10 keV, probe current 100

149 pA and working distance 11 mm. Mineralogical and chemical compositions were investigated with an EDAX OCTANE

150 Elite Plus - Silicon drift type - Si3N4 Window apparatus under high voltage 15 keV, probe current 60 mm, working

151 distance 12 mm, take-off angle 40°, and live time 30 sec. The standardless quantitative analysis were checked on SPI

152 #02757-AB serial 4AK standard and were collected through the software AMETEK Apex Suite V2.

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154 **Figure 3** Cutting plane of the coralligenous build-ups with the superimposed grids of 5x3 cm sized rectangles. Cells
155 selected for thin sections are rimmed in red.

156 **3. Results**

157 **3.1 Morphology and framework at mesoscale observation**

158 The CBR2_3_7c build-up is 56 cm high, with circumferences of 59 cm at the base, 78 cm at the top and a maximum of

159 116 cm in between (Fig. 2a). The CBR2_4_21c build-up is 38 cm high, with circumferences of 71 cm at the base, 52.5

160 cm at the top and a maximum of 112 cm in between (Fig. 2d). Both build-ups show a prevalent upward growth and a

161 rough surface.

The surfaces of detachment (Fig. 2b and e, for CBR2_3_7c and CBR2_4_21c, respectively) and selected longitudinal plane slabs (Fig. 2c and f, for CBR2_3_7c and CBR2_4_21c, respectively) highlight the internal framework of the two build-ups, characterized by a primary skeletal framework forming a high porous structure, with cavities ranging from few millimeters to ten centimeters. Sometime, the cavities surfaces are encrusted by skeletonized organisms, mainly serpulids and bryozoans. In general, cavities show cylindrical-barrel shapes (like those produced by boring bivalves) or irregular shapes and may be empty or (partially or totally) filled with sediment. This appears either brownish-greyish or greenish. brown to grey/dark grey in colour. Brownish-greyish sediment is muddy, usually located in larger cavities, and includes a bioclastic component (planktonic and benthic foraminifer shells, small fragments of coralline algae, serpulids, bryozoans, ostracods, molluscs) and appears loose. Greenish coloured sediment is subordinate and distributed in smaller (millimetre- to centimetre- sized) cavities; it seems cemented and consists of mud lacking skeletal fragments, at mesoscale observation (Fig. 2g). This component mainly occurs along the borders of partly filled cavities possibly originally occupied by sponges, as testified by remains of their soft tissue connected with spicules (Fig. 4a and b). The two types of sediment (loose and cemented) seem distributed according to the size of the cavities but they do not show a preferential distribution, from the bottom to the top of the structures, inside the build-up frameworks.
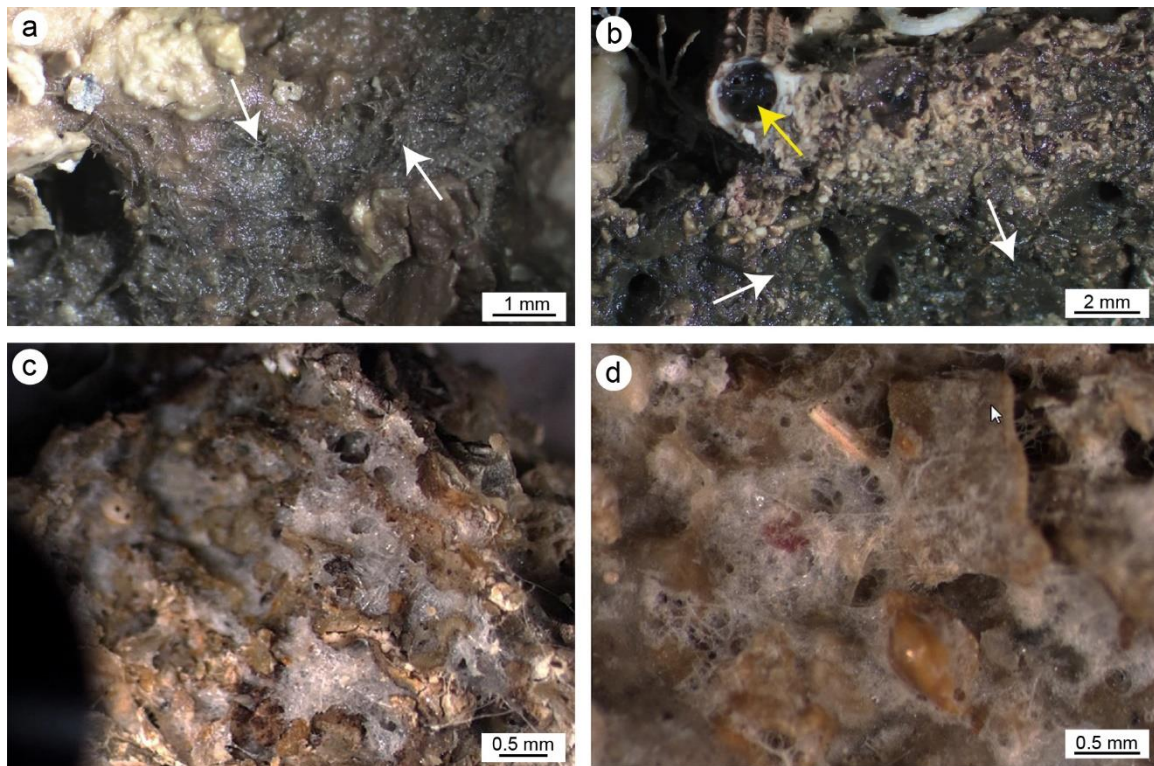
Figure 4 (**a**-**b**) Fine micritic sediment associated with remain of sponge tissue (white arrows) in internal cavities of the framework; the yellow arrow points to a sponge colonizing the internal cavity of a serpulid tube. (**c** and **d**) Pervasive colonization of sponges in internal cavities and the external surface, respectively.

3.2 Analyses of the fragments

The observation of the build-up fragments at the microscale (Fig. 2h and Fig. 5) highlight the superimposition of successive generations of different taxa producing the crusts. The skeletal framework is mainly composed of CCA (Fig. 5a-c). Serpulids (Fig. 5a, d and e) and bryozoans (Fig. 5a, f and g) participate subordinately to the formation of the structure. Sponges seem to concur to the general morphologies, regulating the direction of growth of the encrusting organisms, and altering the internal body of the build-ups through bio-erosive processes. The activity of sponges is evident both on the external surface and internal microcavities of the fragments testifying the pervasive colonization of these

organisms at different scales (Fig. 4). Spicules are sometimes associated with fine carbonate mud (Fig. 4a and b). In other cases, their original presence in empty cavities is testified by organic remains with spicules (Fig. 4c and d) and specific micro-morphologies of the cavity boundaries which testify the boring activity of these organisms. Molluscs and other skeletonized invertebrates make a negligible contribution to the build-up growth. Rare solitary corals are also present.
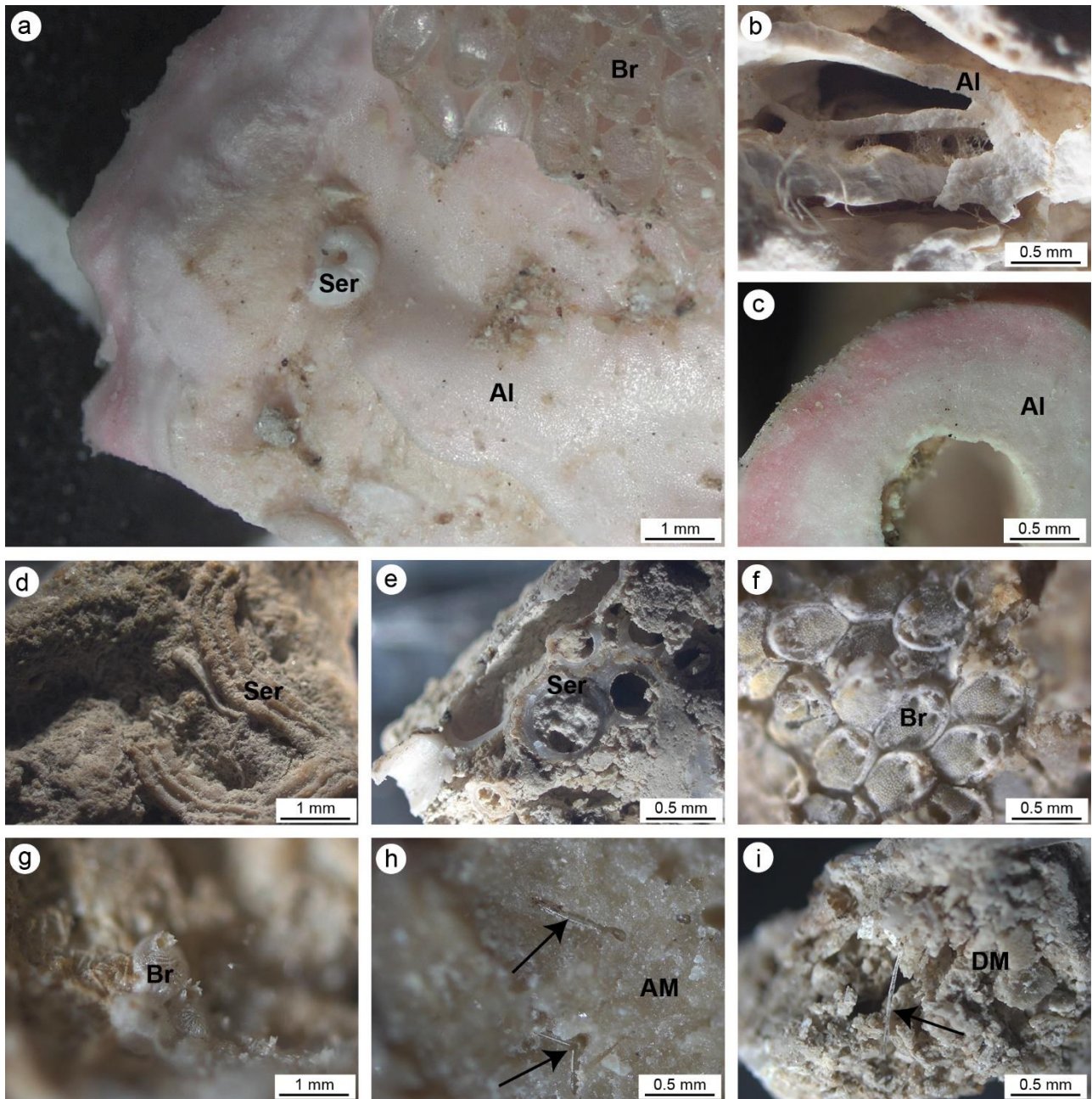
Figure 5 (**a** and **b**) Main carbonate components of the small fragments collected on the cut surfaces of the build-ups. (**a**) Pink crustose coralline algae (Al) encrusted by serpulids (Ser) and bryozoans (Br). (**b**) Different generations of crustose coralline algae encrusted one on top of the others. (**c**) Cross section of a crustose coralline alga. (**d**) Serpulid tube encrusting cemented micrite. (**e**) Section of serpulid tubes intermingled with micritic sediments. (**f** and **g**) Bryozoan colonies. (**h**) Dense and homogeneous autochthonous micrite (AM) engulfing sponge spicules. (**i**) Heterogeneous and loose, detrital micrite sediment (DM) engulfing sponge spicules. In (**h**) and (**i**) black arrows point to sponge spicules engulfed in the micrite sediments.

Two types of sediments (micrite) have been observed: homogeneous or autochthonous (compact and dense; Fig. 5h) that emits a bright fluorescence when excited by UV-light, and heterogeneous or detrital (less cemented and rich of fine bioclasts; Fig. 5i) that does not emit fluorescence (Fig. 6). Both types of micrites engulf sponge spicules.

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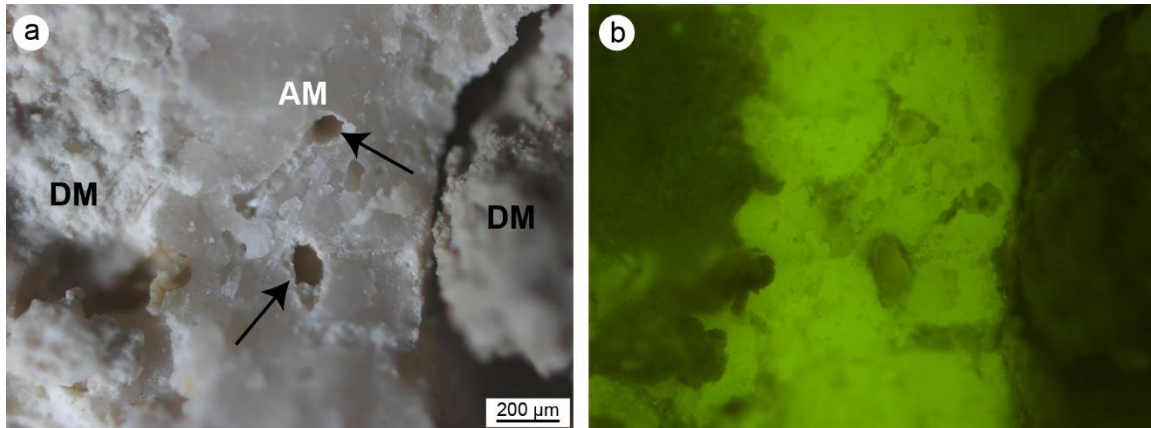
Figure 6 Micrite sediments from CBR2_4_21c build-up observed in reflected light (**a**) and ultraviolet light (**b**). The bright fluorescence indicates a high content in organic matter of the autochthonous micrite, whereas the absence of fluorescence of the detrital micrite denotes an inorganic origin. Note the microcavities left by sponge spicules (black arrows). AM: autochthonous micrite; DM: detrital micrite.

3.3 Microfacies characterization

Thin sections observation confirms the main role of skeletonized organisms in forming the carbonate framework of the Coralligenous (Fig. 7). CCA are the main builders through successive generations of specimens encrusted one on top of the others (Fig. 7). Bryozoans and serpulids play a subordinate bio-constructional role. Sponges are abundant and their amorphous remains are widely distributed in cavities and microcavities, often associated to loose sediment, engulfed in cemented micrite. Numerous other bioclasts, produced by organisms that do not participate directly to build the bioconstructions were detected in the cavities together with muddy material. Non-skeletal carbonate material was also detected (see below).
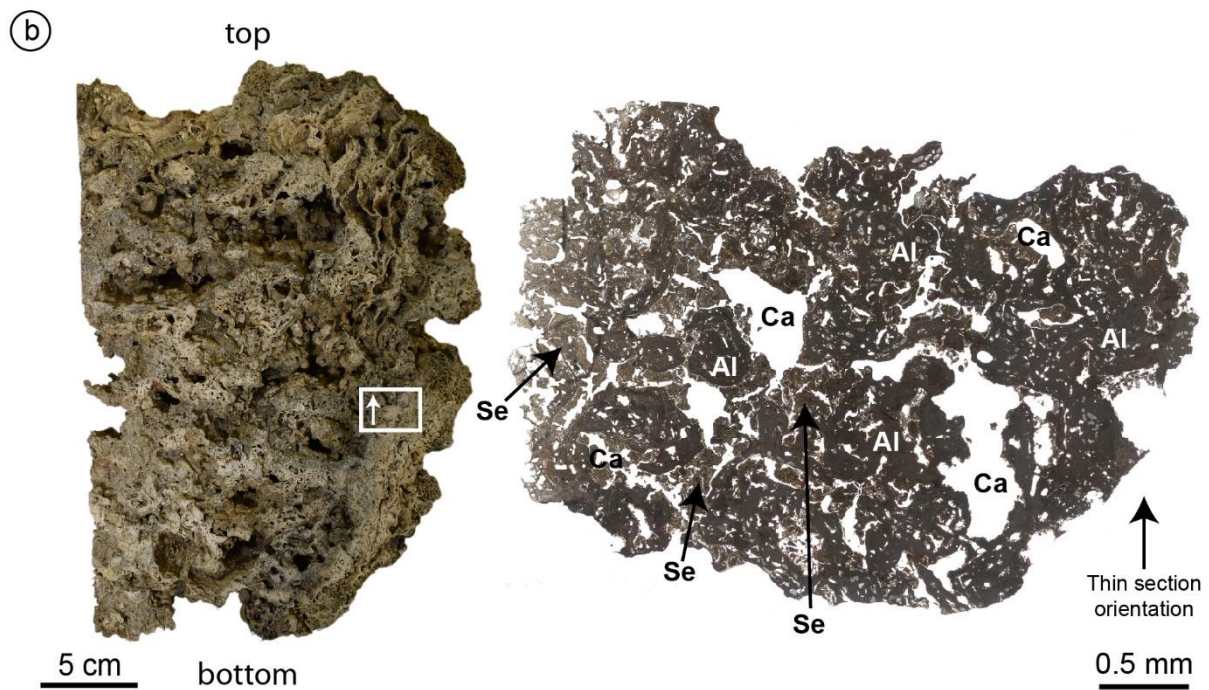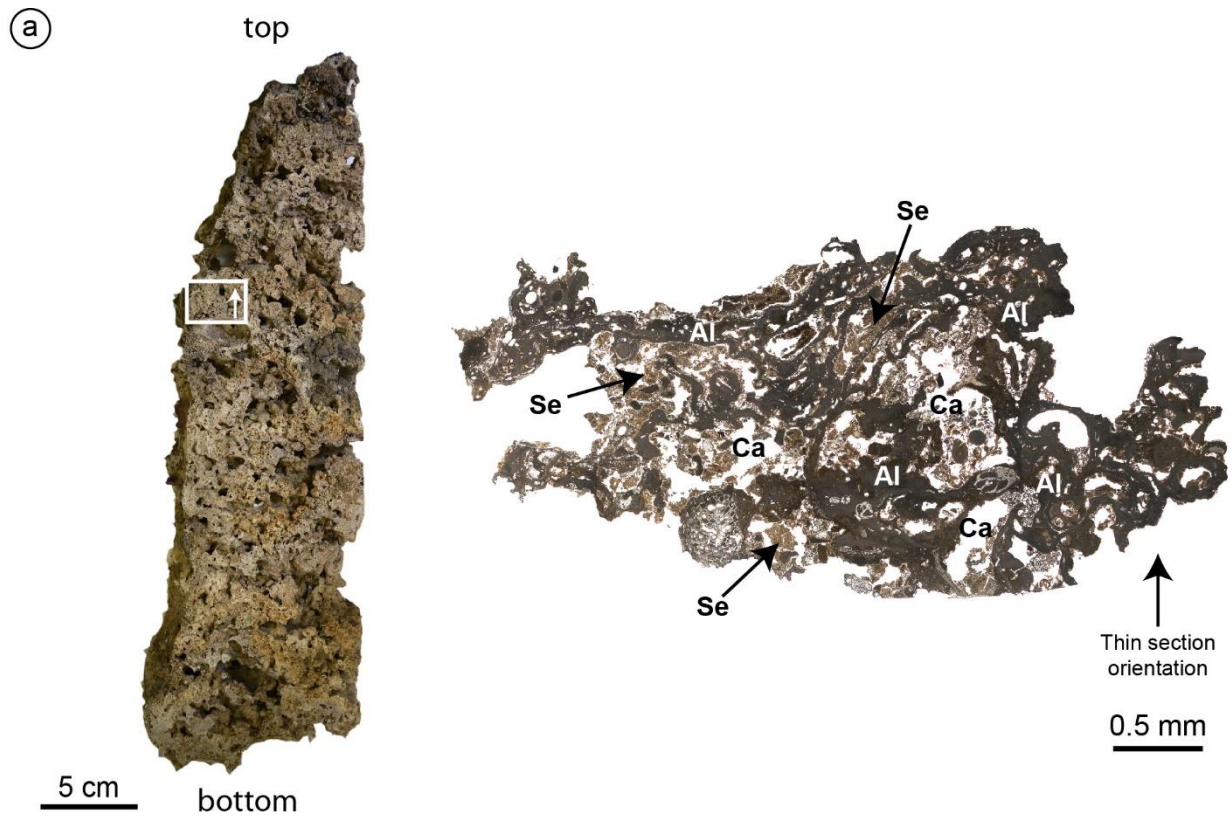
Figure 7 Cutting planes (left) and optical microscope photocomposition of representative thin sections (right) of the build-ups CBR2_3_7c (**a**) and CBR2_4_21c (**b**). Note the primary role of the coralline algae (Al) as major constituent of both build-ups and the presence of cavities (Ca) empty or filled with micrite sediment (Se). White rectangles and the arrows within them indicate the location and the orientation of the thin sections.

3.3.1 Skeletal components

Articulate and crustose coralline red algae are the main skeletal components detected in all thin sections (Fig. 8). The skeletons of the algae clearly form a continuous framework at the mesoscale (Fig. 7) but at the microscale, laminae are

rarely continuous, often showing traces of bioerosion (Fig. 8a-c, f). Two main types of bioturbations are distinguishable: (i) irregular borings and (ii) tube-like micro-borings. Borings, showing sizes from a few microns to a few millimeters are mainly formed by endolithic sponges that corrode and perforate skeletons. These cavities could be: a) empty due the decaying of the sponge's organic tissue (Fig. 8b); b) filled with detrital sediment (Fig. 8b); or c) filled with spicules and remains of organic matter deriving from soft tissue decay of the boring sponge *Cliona* sp. (Fig. 8f). The skeletons often show also micritization phenomena contributing to the alteration of the original microstructures together with bioerosion.
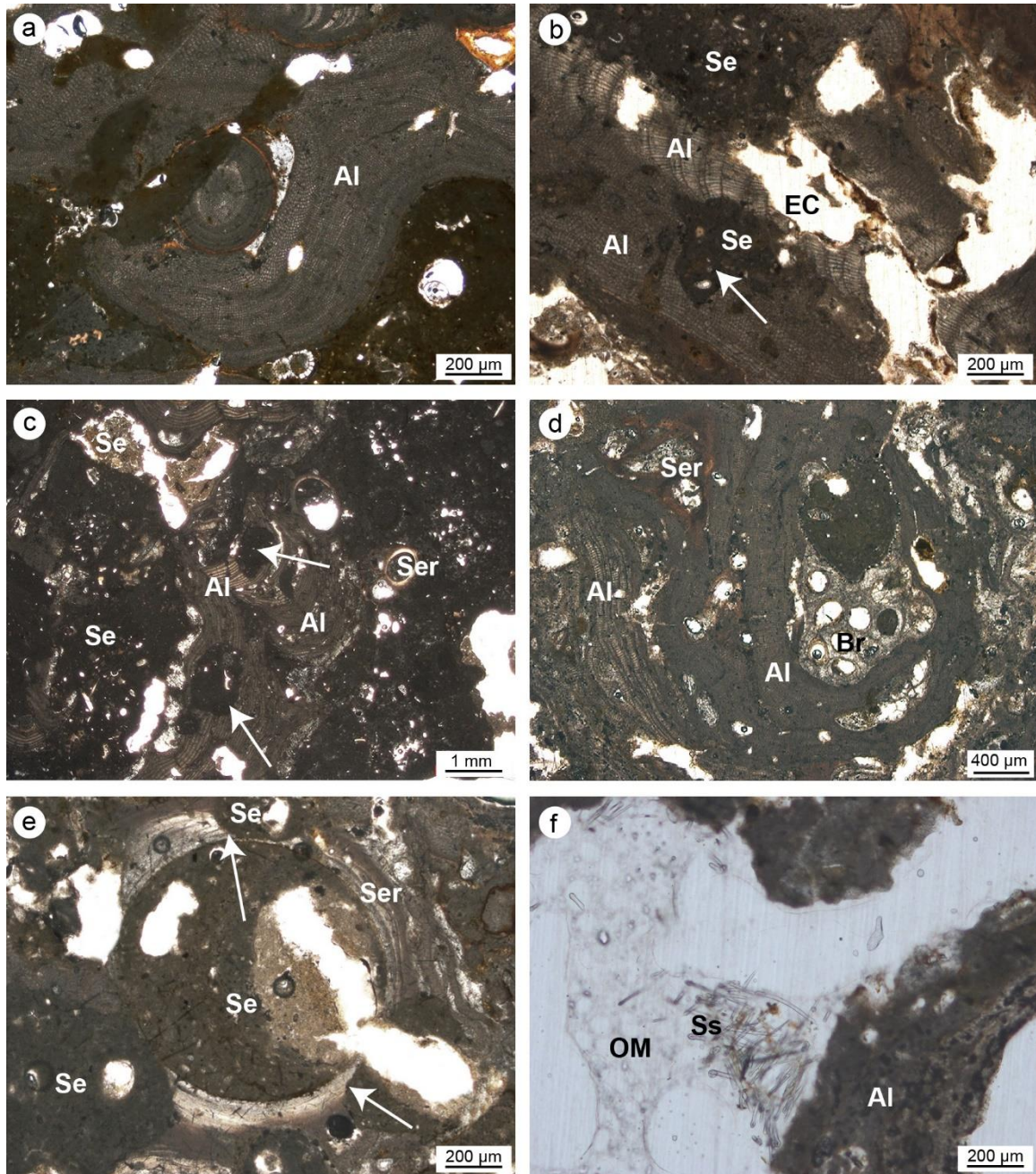
Figure 8 (**a-c**) Skeletal tissues of algae (Al) showing microcavities due to bioturbations (white arrows); the cavities are empty (EC) or filled with sediment (Se). (**d**) Strict interconnection among the main builders of the studied coralligenous build-ups (Al: algae; Ser: serpulids; Br: ? bryozoans). (**e**) Bioeroded serpulid skeleton (Ser); note the borings (white arrows) filled with sediment (Se). (**f**) Bioerosion cavity in algae (Al) with remains of organic matter (OM) and spicules (Ss) derived from sponge's decay (*Cliona* sp.). [**a-b**, **e-f**: CBR_2_3_7c; **c-d**: CBR_2_4_21c].

236   The biological activity involved in these bioerosional processes was not investigated but could represent a further step in

237   the reconstruction of the complex biological relationships which develop in these coralligenous ecosystem. The erosive

238   action of sponges is clearly visible where remains of amorphous material and spicules are associated with corroded

239   substrates (Fig. 9).

240   The sponge spicules, mainly belonging to species of the genus *Jaspis*, also fill the algae's conceptacles and often, small

241   spherical corpuscles are recognizable among spicules in UV-epifluorescence.

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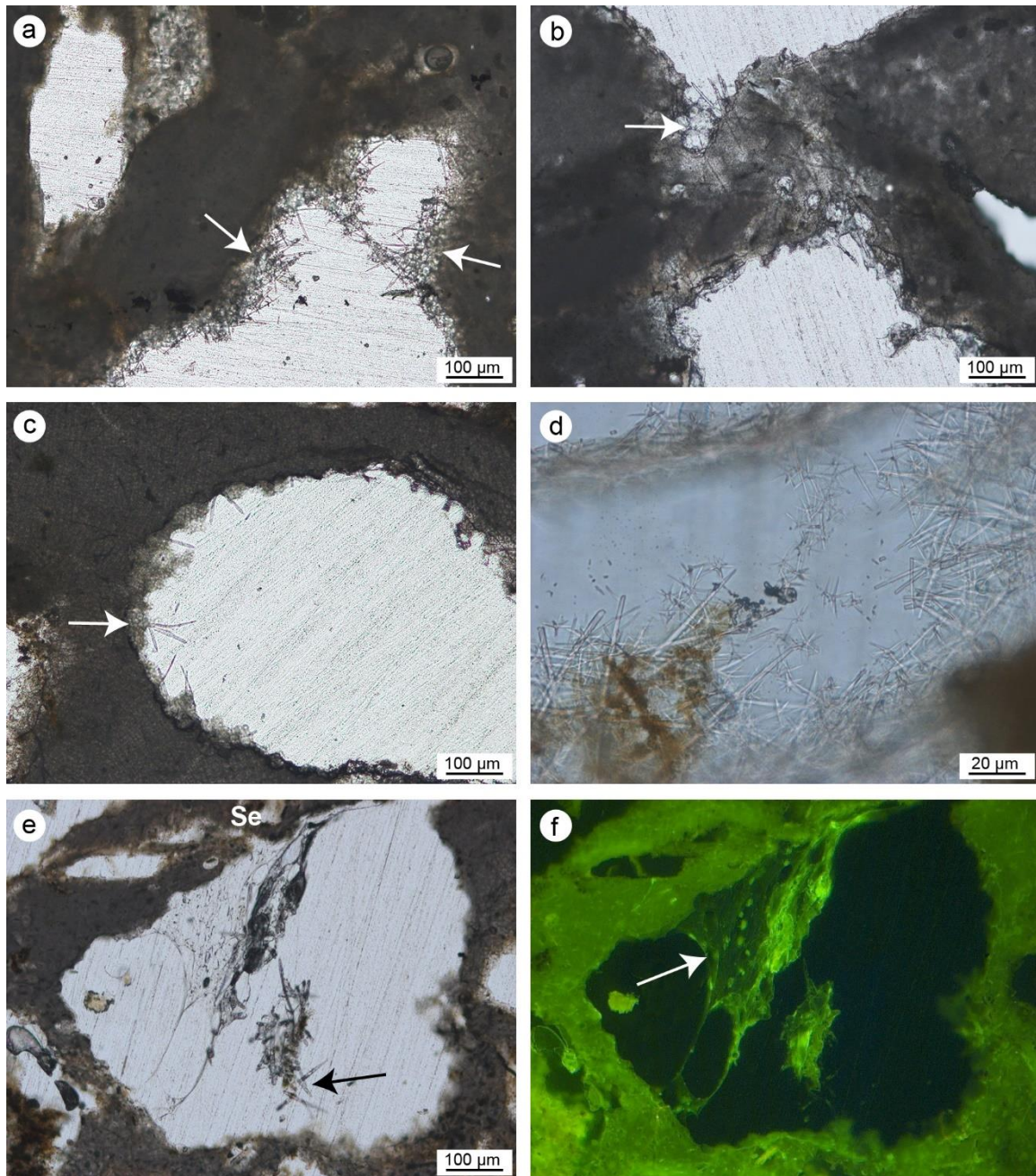
Figure 9 (**a**-**c**) Microcavities inside the skeletal framework of the coralligenous build-ups showing sponge spicules (plurispicular tracts) associated with the corroded substrates (white arrows). (**d**-**f**) Details of sponge spicules of *Jaspis* sp. (**d**) and *Cliona* sp. (**e**) observed in transmitted light, and UV-epifluorescence (**f**); the non-fluorescent siliceous spicules are engulfed in remains of organic matter (**f**) deriving from sponge soft tissue decay. [**a**-**c**: CBR_2_4_21c; **d**-**f**: CBR_2_3_7c].

248   Serpulids are common in the microfacies of both build-ups. They occur as isolated or grouped tubes with outer diameters

249   ranging from 200 µm to 1 mm. The number of clustered tubes usually increases with decreasing of their size. They are

empty, or filled with sediment, or sometimes occupied by endolytic sponges (Fig. 4b). Serpulids are often encrusted or encrust bryozoans and/or algae (Fig. 8d). Serpulids show different degrees of preservation and their original microstructure is observable in the bigger tubes, while dissolution, recrystallization and/or micritization often alter the smaller ones. Serpulids also suffer bioerosion by endolytic organisms (Fig. 8e).

Remains of amorphous material and spicules inside the skeletons of bryozoans may derive from insinuating and/or bioeroding sponges, as observed for other skeletonised taxa.

3.3.3 Non-skeletal carbonate components: autochthonous and allochthonous (detrital) micrite

The cavities of the skeletal framework are filled with different micrite types distinguished under light microscope examination and UV-epifluorescence. The texture and organic matter content allowed to distinguish an autochthonous and an allochthonous (detrital) micrite.

The autochthonous micrite consists of very fine-grained calcite and shows aphanitic (Fig. 10a-f) or peloidal to clotted peloidal textures (Fig. 10g-h). The autochthonous aphanitic micrite displays a light brown colour and shows a structureless mud-supported texture with rare bioclasts. Autochthonous peloidal micrite displays a darker colour, does not exhibit grain-supported textures and shows interclot areas indicating a not gravitational genesis. Peloidal micrite fills microcavities or coats serpulid tubes or other bioclasts. Peloids aggregate often in clots separated by calcite microspar (euhedral Mg–calcite crystals), forming a clotted texture or, less commonly, a compact texture through the coalescence of several clots. Peloidal and aphanitic microfabric derive from mineralization mediated indirectly by organic processes and represent *in situ* precipitation of the micrite, whose syndepositional cementation contributes to stabilize the skeletal structures of the build-ups.

Aphanitic and peloidal micrites show a bright autofluorescence under UV-light indicating a high content of organic matter relics, most likely related to the bio-induced crystal precipitation. Aphanitic micrite is widely associated with the presence of sponge spicules (Fig. 10a-f), and generally fills bioeroded cavities inside the skeletal framework. On the contrary, peloidal micrite, is not associated with sponge spicules and often occludes serpulid tubes and spaces within adjacent individuals, contributing at cementing the skeletons together. Small terebellid tubes are often associated with this micrite type (Fig. 10g-h).

The amount of the autochthonous micrite is variable in the thin sections but always represents a minor component in comparison to the skeletal framework, and shows a different distribution along the bottom-top direction of each build-up, with the major content in the column CBR_2_4_21c.

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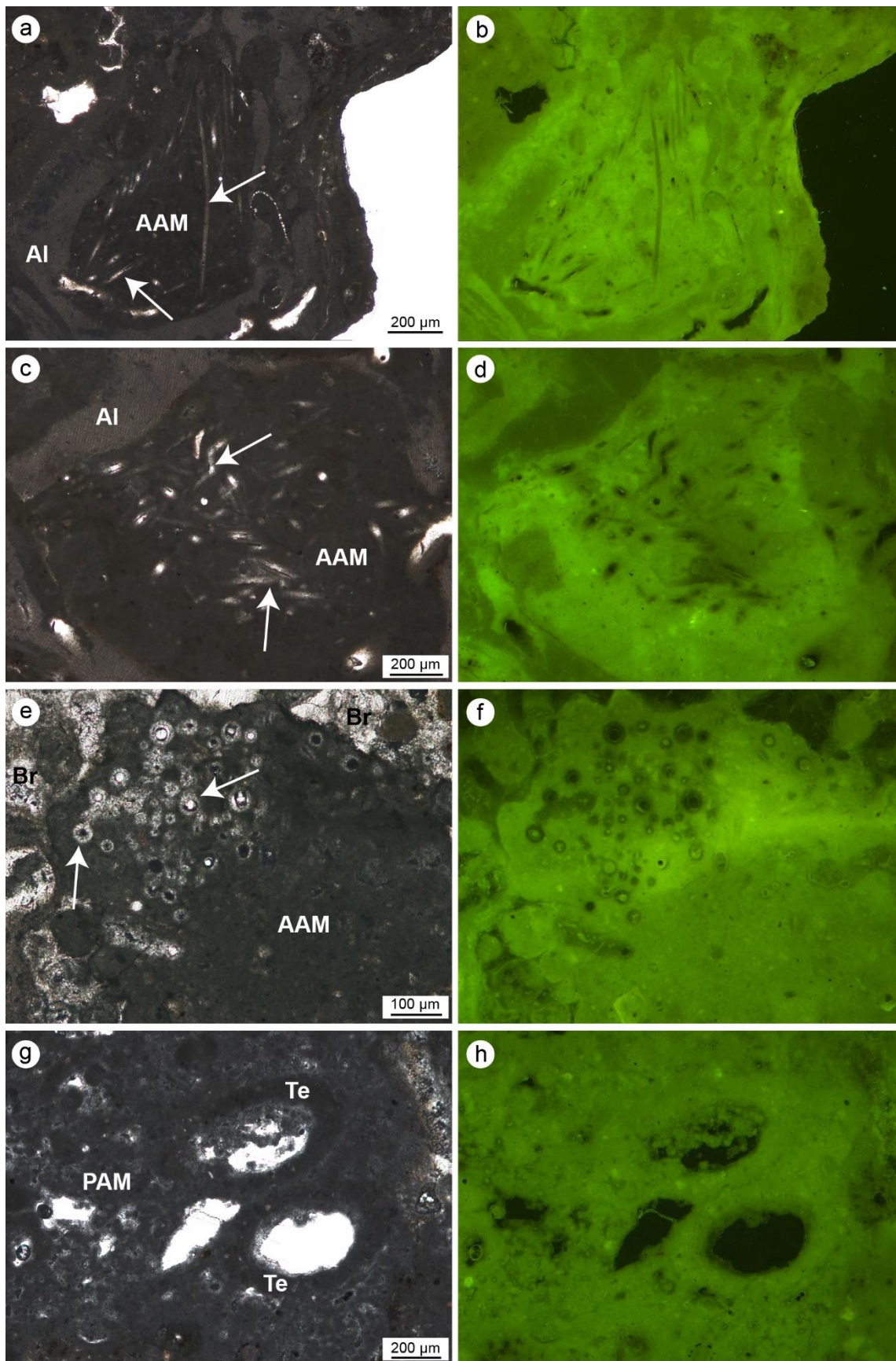


Figure 10 (**a-f**) Aphanitic autochthonous micrite (AAM) engulfing sponge spicules (white arrows) observed in transmitted light (left) and UV-epifluorescence (right); the bright epifluorescence of the AAM indicates the presence of organic matter relics closely related to the bioinduced crystals. (**g-h**) Peloidal autochthonous micrite (PAM) engulfing some agglutinated skeletons of terebellids (Te) observed in transmitted light (left) and UV-epifluorescence (right); even

283 in this case the bright epifluorescence of the PAM indicates the presence of organic matter relics closely related to the
284 bioinduced crystals. [**a-b**, **e-h**: CBR_2_4_21c; **c-d**: CBR_2_3_7c].

285 The detrital micrite shows a light brownish colour and is characterized by a texture with variable density (Fig. 11). Two

286 types of detrital micrite with different textures have been tentatively recognised: organic and inorganic. Organic detrital

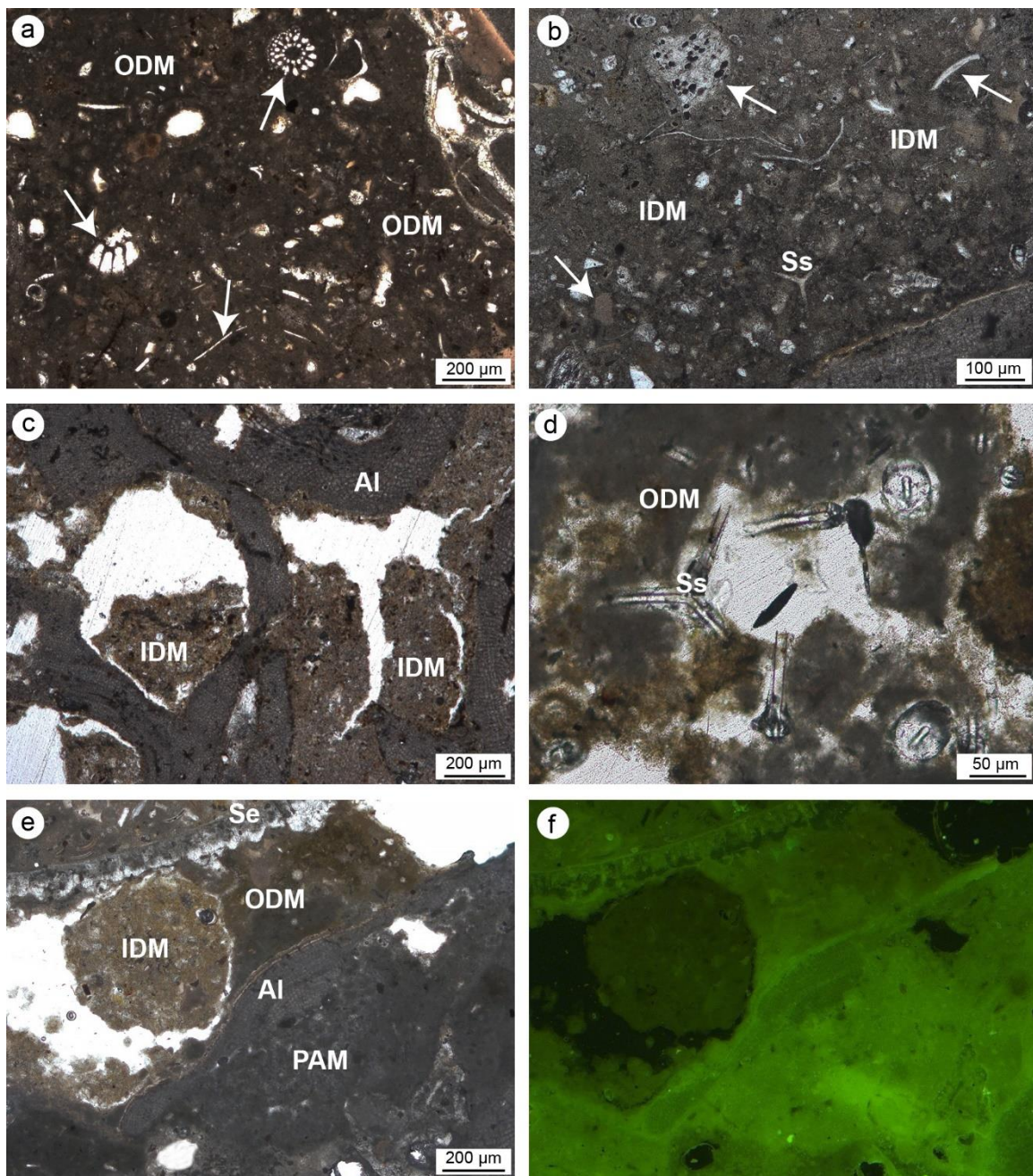
287 micrite shows a denser muddy texture and it is enriched in bioclasts, intraclasts and sponge spicules (Fig. 11a, d, e). It

288 shows a very faint to scarce epifluorescence (Fig. 11f). The inorganic detrital micrite is made up of particles with larger

289 sizes (in the silty range) and includes a minor amount of bioclasts. Due to the absence of epifluorescence under UV-light

290 an inorganic nature of these components is assumed. Detrital micrites represent the main non-biomineralized component

291 of both build-ups, and fill primary, inter- and intra-skeletal cavities, and secondary micro-cavities generated by boring

292 organisms.

293

294 **Figure 11** Detrital micrite textures. (**a**) Organic detrital micrite (ODM) with a dense muddy texture enriched in bioclasts
295 (white arrows), intraclasts and sponge spicules. (**b**) Inorganic detrital micrite (IDM) consists of particles with larger sizes
296 incorporating a minor amount of bioclasts (white arrows). (**c**) Microcavities in bioeroded algae (Al) filled with IDM. (**d**)

297 ODM engulfing sponge spicules (Ss). (**e-f**) Relationship between IDM (light brown), ODM (dark brown), algae (Al) and
298 peloidal autochthonous micrite (PAM) observed in transmitted light (left) and UV-epifluorescence (right); faint and scarce
299 fluorescence of the detrital micrite denotes an inorganic nature of this component. [**a-b**, **d-f**: CBR_2_4_21c; **c**:
300 CBR_2_3_7c].

3.3.4 Cements

302 Cement only sporadically fills cavities representing a subordinate component of the build-ups. Two types of cement have
303 been recognised: primary (syndepositional) and secondary (diagenetic) cement. Syndepositional cement shows
304 isopachous, botryoidal and peloidal microcrystalline fabric. Isopachous cements develop with homogeneous fringes on
305 the surface of intra- and inter-skeletal microcavities. Botryoids consist of dome-shaped hemispheres built by radiating
306 fibrous calcite crystals and crystal fans filling the primary cavities and voids created by bioerosion processes. Peloidal
307 microcrystalline cement is composed of tiny peloids within a microcrystalline calcite matrix; it was mainly detected in
308 small intra-skeletal cavities. Secondary cement is rare and fills residual microcavities with drusy micro-textures.

3.3.5 Point counting analyses

310 Seven structural and non-structural components have been counted: carbonate framework builders, bioclasts,
311 autochthonous micrite, organic and inorganic detrital micrite, boring sponges and empty cavities. Bioclasts include all
312 skeletal remains of organisms that do not participate to the formation of the skeletal framework but were trapped inside
313 the cavities either first living in association with the build-up or transported by neighbouring habitats. Among these,
314 bivalves, gastropods, foraminifers, ostracods, echinoid plates and spines, and algal fragments have been recognized. The
315 boring sponges counting class includes perforations interpreted as originally occupied by sponges, because infilled with
316 amorphous organic remains rich in spicules. It is worth to note that this component could be underestimated due to the
317 cutting procedures and the preparation of the thin sections which could have washed away the residues of the sponge
318 tissue that originally occupied the cavities. The analysis shows the following average percentages for the CBR_2_3_7c
319 and CBR_2_4_21c build-up respectively: 46.2 % and 47.1 % carbonate framework builders (algae, serpulids, bryozoans);
320 4.4 % and 3.6 % other bioclasts (planktonic and benthic foraminifer shells, ostracods, molluscs, echinoid plates and spines
321 and, small fragments of coralline algae); 3.6 % and 9.2 % autochthonous micrite, 16.4 % and 14.3 % organic detrital
322 micrite, 13.6 % and 9.3 % inorganic detrital micrite, 14.8 % and 15.4 % empty cavities and, 1 % and 1.1 % boring sponges
323 (Tables 1-2).

Table 1. Quantitative percentage of the main components recognised in the thin section samples from CBR_2_3_7c build-up.

Samples Name	Carbonate framework builders (%)	Other bioclasts (%)	Autochthonous micrite (%)	Organic detrital micrite (%)	Inorganic detrital micrite (%)	Empty cavities (%)	Boring sponges (%)
A5	60.9	4.2	2.4	1.7	20.7	10.1	0
A7	35.2	5.4	3.2	17.8	17.2	20.2	1
A11	42.9	5.5	1.2	31	11.5	6.7	1.2
A13	49.6	2.7	2.9	11	16.6	17.2	0
A19	36.7	4.8	8.9	30.5	8.6	9.7	0.8
B4	41.7	4	3.5	7.5	10.3	28.3	4.7
B10	60.7	4.3	1.4	8.4	10.5	14.5	0.2
B16	54	6	0	14.3	7.6	16.9	1.2
B19	32.7	2.1	7.6	28.5	15.5	13.6	0
C8	51	3.6	0.9	11.5	16.6	15.8	0.6
C15	45.6	3.1	0.9	15.9	15.3	19.1	0.1
C13	38.1	4.4	9.3	18.1	13.9	12.8	3.3
C18	50.7	7	4	16.6	12.6	8.6	0.5
Av. (%)	46.2	4.4	3.6	16.4	13.6	14.8	1

Table 2. Quantitative percentage of the main components recognised in the thin section samples from CBR_2_4_21c build-up.

Samples Name	Carbonate framework builders (%)	Other bioclasts (%)	Autochthonous micrite (%)	Organic detrital micrite (%)	Inorganic detrital micrite (%)	Empty cavities (%)	Boring sponges (%)
A7	40.8	5.3	9.6	22.2	10.3	11.5	0.3
B5	55.9	2.2	9.7	3.1	9.9	19	0.2
B8	59.4	3	3	6.2	10.9	15.8	1.7
B11	58.1	2.9	5.1	5.9	6.9	20.4	0.7
C2	28.9	4.4	14.7	20.7	8.7	21.4	1.2
C7	57.8	1.2	7.6	9.3	5.3	15	3.8
C10	42.7	2.5	7.3	25.5	2.7	18.3	1
C12	49.1	3.3	6	3	13.3	24.3	1.1
D3	48.1	1.6	8	22.2	8.6	11.1	0.4
D8	42.2	5.2	15.5	13.6	12.7	10.7	0.1
D10	54.6	2.8	7.8	11.9	11.2	11.7	0
E2	32	10.2	19.7	13.1	9.7	14	1.3
E6	37	1.6	10.1	27.2	11.5	12.6	0
E10	53.8	4	5.3	16.4	8.8	10	1.7
Av. (%)	47.1	3.6	9.2	14.3	9.3	15.4	1.1

Among the non-skeletal carbonate components, the allochthonous (detrital) micrites is definitively more abundant in comparison to the component directly mineralized (autochthonous micrite) in the cavities of the build-ups. Noteworthy, the percentage of autochthonous micrite, whose early cementation contributes to reinforce the coralline algae framework, is higher in the CBR_2_4_21c build-up than in the CBR_2_3_7c build-up. The average percentages of total cavities, *i.e.* the sum of empty cavities and cavities filled with detrital sediment, are similar in the two build-ups.

3.4 Characterization of micromorphology and geochemistry with electron microscopy

SEM observations and EDS microanalyses allowed us to detect the micro/nano-morphologies and the composition of the main skeletal and non-skeletal components. The presence of pristine micro- and nano-morphology and original mineralogy of skeletons (high Mg-calcite or aragonite of algae and serpulids) testify that the carbonate components of the build-ups have not undergone neomorphic processes, like recrystallization, polymorphic transformation or aggrading neomorphism. In some cases, the skeletal components display evidence of the dissolution process.

Microcavities are filled with sponge spicules and remains of carbonaceous amorphous substances (Fig. 12). Spicules are mainly oxeas and (sub-) tylostyles, which may be associated with species of the *Cliona* genus, but there are also triactines and rare tetractines. Spicules are closely intermingled with organic matter and are often well visible cleats with sterrasters and oxyasters, typical of species of the genus *Erylus* (Fig. 12e and f). Areas close to the corroded boundaries of some microcavities containing spicules (Fig. 12g-h) also include small carbonate chips (Fig. 12i) seemingly detached from the encasing skeleton due to mechanical boring activity of the sponges. The substrate of the bioeroded cavities shows the typical erosion scars (pits) left by the perforating activity of sponges of the Clionaidae family (Fig. 12d). Spicules often show circular erosion marks and an enlarged axial canal (Fig. 13a-e) due to silica dissolution caused by high pH values of the porewater inside the crevices of the coralligenous build-up.

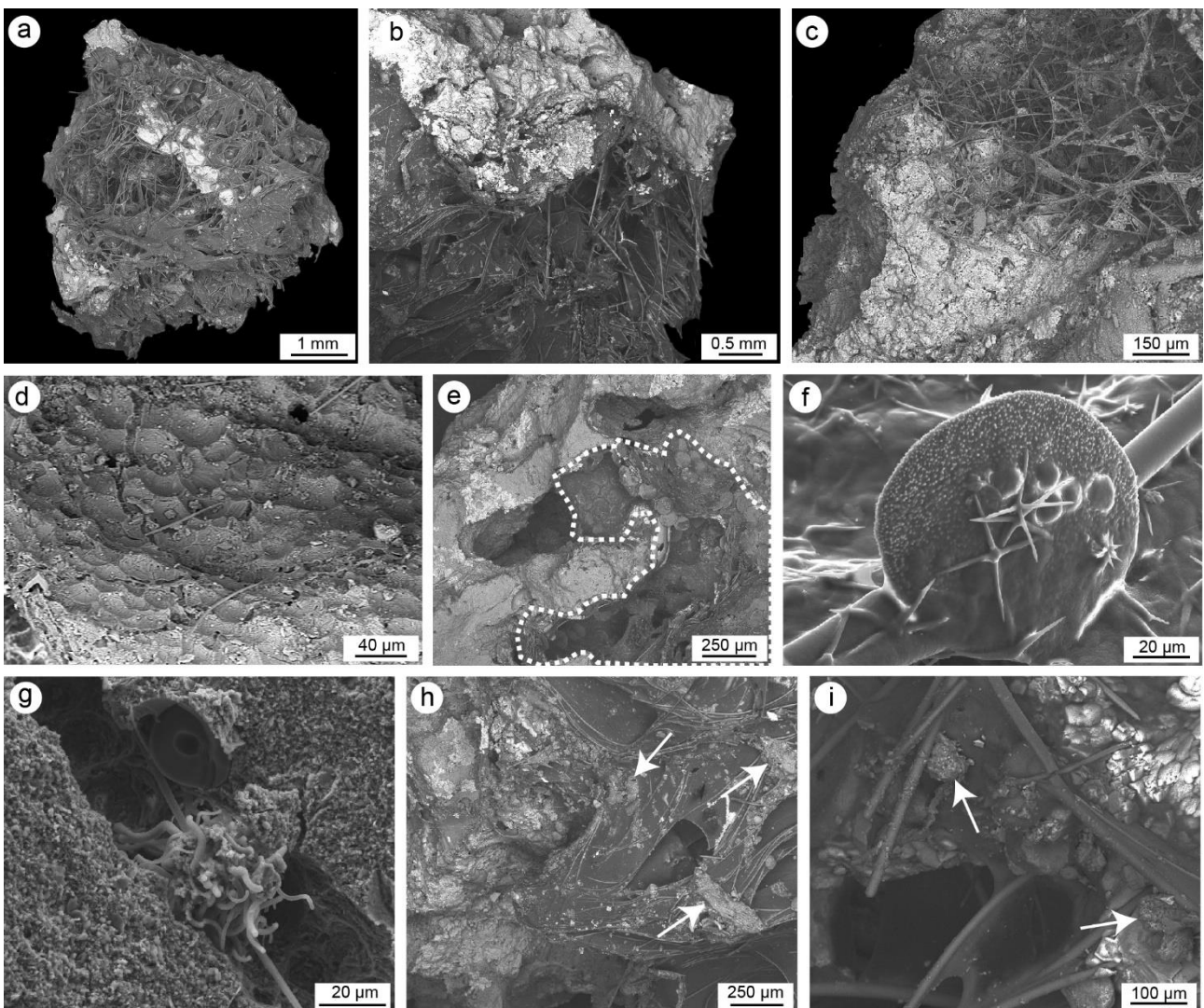



Figure 12 SEM images of sponge spicules and remains of carbonaceous amorphous substances. (**a-c**) Coralligenous fragments whit pervasive colonization of sponges both on external surface and internal microcavities. (**d**) Sponge erosion

371 scars (pits) on a skeletal substrate. (**e**) Endolithic sponge (dotted line) inside a microcavity of the skeletal framework. (**f**)
372 Detail of sterraster and oxyaster of *Erylus* sp. (**g**) *Cliona vermifera* spiraster associated with a bioeroded cavity. (**h**)
373 Spicules and amorphous organic matter in an internal microcavity. (**i**) Detail of spicules and amorphous organic matter
374 englobing small carbonate chips (white arrows) detached through sponge bioerosion activity. [**a**, **d-f**, **g-i**: CBR_2_3_7c;
375 **b-c**: CBR_2_4_21c].

376 A high amount of siliceous and rare calcareous sponge spicules (still under study: Bertolino et al. in prep.) has been

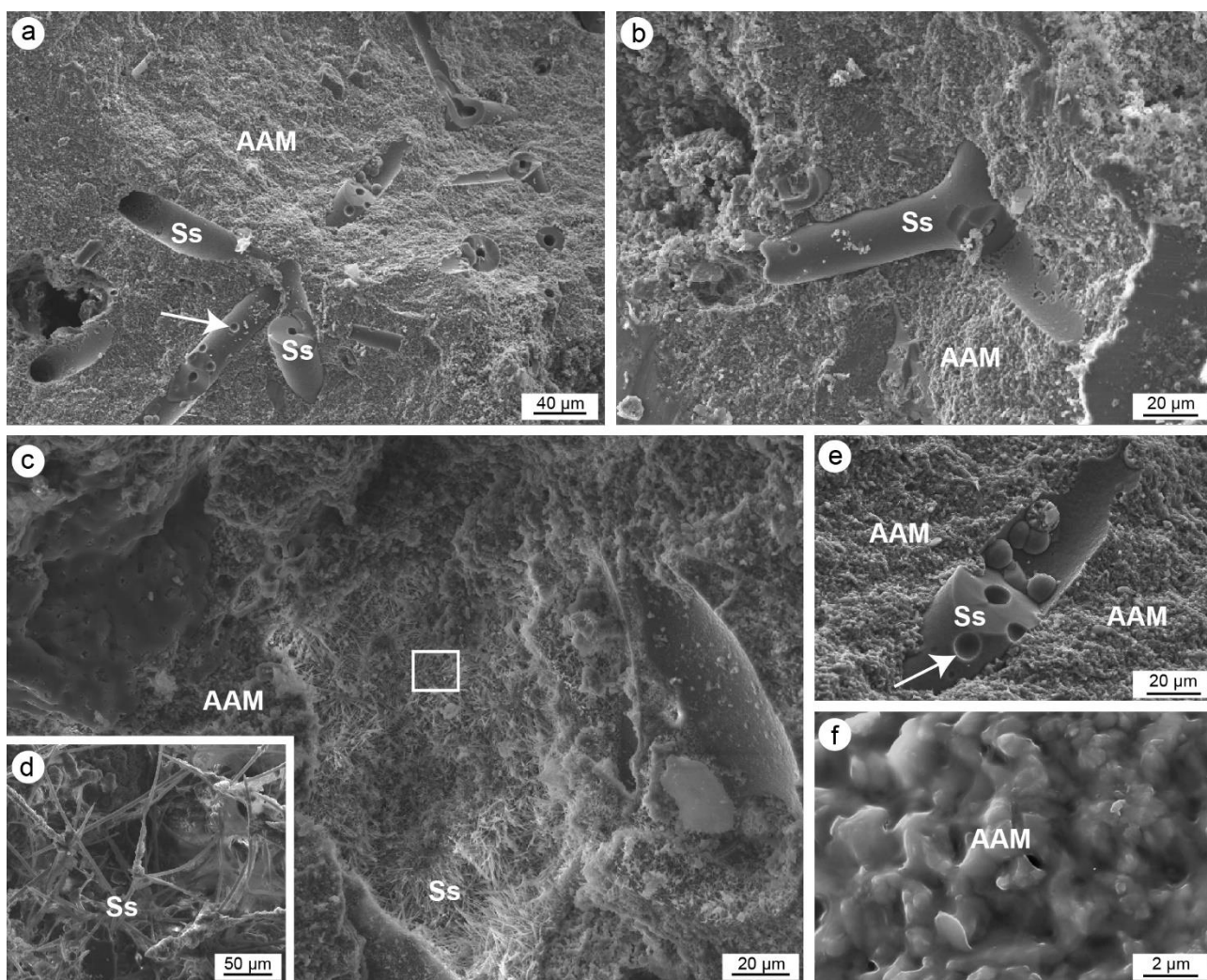
377 recognised in both autochthonous (Fig. 13) and detrital (Fig. 14) micrite pointing to a considerable diversity.

378 Autochthonous micrite shows micro- to nano-meter anhedral to sub-euhedral crystals engulfed in amorphous organic

379 material (Fig. 13f) and has a high magnesium calcite (Ca ~91 wt%; Mg ~6.5 wt%) composition with minor terrigenous

380 components (<2 wt%). Micrite engulfing spicules is well cemented (Fig. 13a, b and e). Peloidal micrite passes to aphanitic

381 textures when cavities become filled. In comparison to the detrital micrite, the autochthonous micrite engulfing sponge

382 spicules lacks skeleton fragments or allochthonous components like planktonic foraminifers or coccoliths.

383

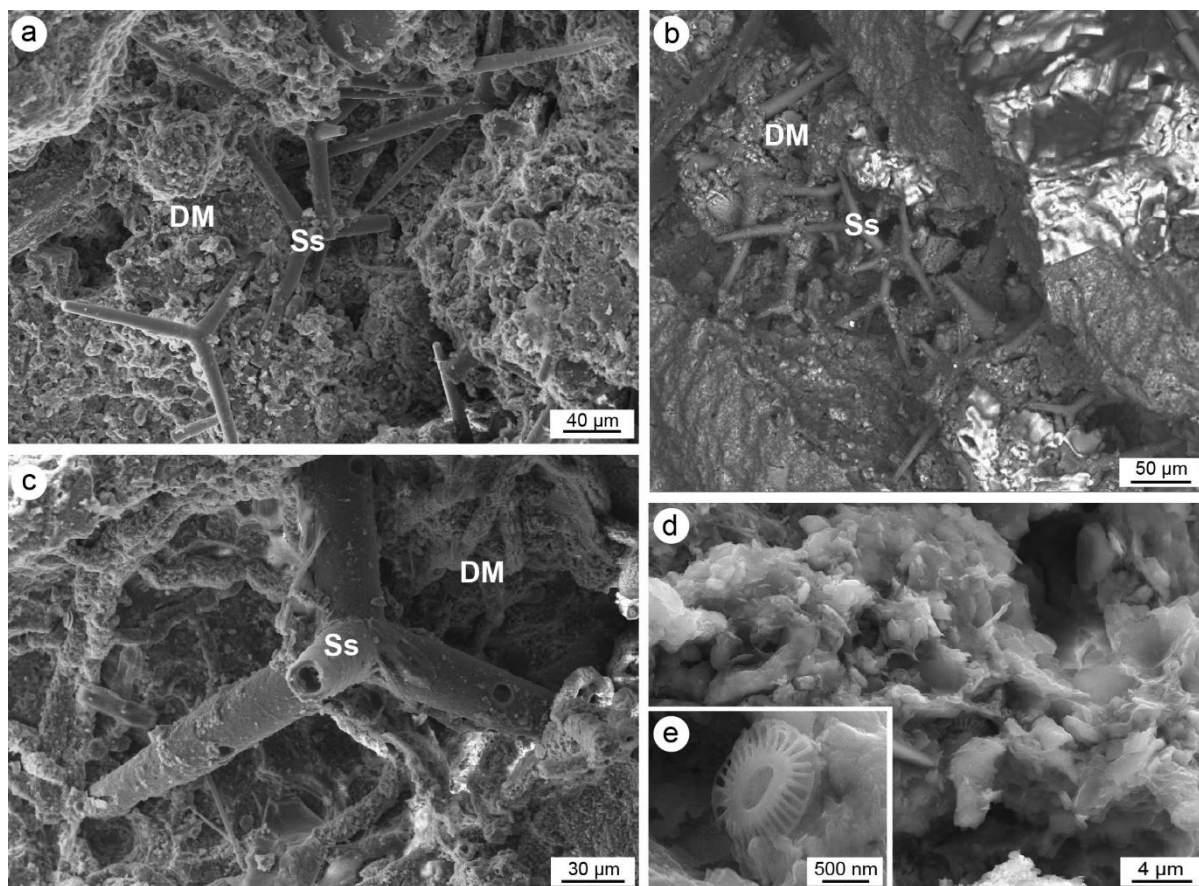
384 **Figure 13** (**a-f**) SEM images of aphanitic autochthonous micrite (AAM) engulfing sponge spicules (Ss). In (**a**) and (**e**)
385 note the well-defined circular boreholes (white arrows) and enlarged axial canal of the spicules. (**d**) Magnification of the
386 spicules in (**c**). (**f**) Detail of the aphanitic autochthonous micrite showing the micrometer sub-euhedral crystals engulfed
387 in amorphous organic material. [**a**, **e-f**: CBR_2_3_7c; **b-d**: CBR_2_4_21c].

388 Detrital micrite shows a heterogeneous composition (Fig. 14), in terms of type and size of the grains, has a magnesium

389 calcite composition and a high percentage of terrigenous components. It is composed of Ca (~46 wt%), Mg (~3 wt%), Fe

390 (~6 wt%), K (~3 wt%), a discrete quantity of Si (~26 wt%), Al (~12 wt%) and a lower amount of other elements (S, Na,

391 Cl <2 wt% each). Detrital micrite constantly incorporates sponge spicules (Fig. 14), but occasionally also small intraclasts

392 and several bioclasts of benthic and planktonic organisms. At the microscale, detrital micrites denote a high amount of
393 nannoplankton plates (*e.g., Emiliania huxleyi*) (Fig. 14e).

394
395 **Figure 14** (**a-c**) SEM photos of detrital micrite (DM) engulfing fine intraclasts, bioclasts and sponge spicules (Ss). (**d**)
396 Details of the detrital micrite and (**e**) a nannoplankton plate of *Emiliana huxley*. [**a**, **c-e**: CBR_2_3_7c; **b**: CBR_2_4_21c)].

4. Discussion

398 The analysed coralligenous build-ups from the Ionian Sea are mainly constituted of skeletonized organisms with dominant
399 coralline algae and subordinate bryozoans and serpulids. CCA forms a porous self-sustaining framework whose
400 stabilization is reinforced by bryozoans and serpulids. The role of foraminifers and corals is negligible. Morphological
401 growth is influenced by sponges. These organisms are highly diversified and play a triple role: locally affect the direction
402 of encrustations of the skeletonised builders, weaken the framework through bioerosion processes and induce
403 precipitation of autochthonous sediments (autochthonous micrite). An important role is also played by the micrite which
404 could be subdivided into two types: autochthonous, directly produced in the build-ups by organic-induced
405 biomineralization processes, and allochthonous (or detrital), derived by the accumulation of loose fine particles in the
406 cavities of the build-ups.

4.1 Skeletal builders and framework density

408 The two build-ups are characterized by a high porous skeletal framework, showing primary and secondary cavities, from
409 a few mm to ten cm large. Primary cavities represent the interspaces generated during the superimposition of skeletonized
410 encrusting organisms, whereas secondary cavities could derive from the necrolysis of soft-body organisms sandwiched
411 between the skeletonised ones or from the bioerosion produced by endolytic organisms, mainly sponges and subordinately
412 bivalves.

413 Quantitative counting of the microfacies components demonstrates the role of algae, serpulids and bryozoans as builders
414 of the two build-ups (see Table 1 and Table 2). These data agree with the indirect quantification obtained through image
415 analysis and computerized axial tomography by Bracchi et al. (2022) on the same build-ups analysed in this paper. Bracchi
416 et al. (2022) correlated four density classes with the framework cementation degree and distinguished the different
417 components, identifying the CCA as dominant. This is because computerized axial tomography does not provide a direct
418 association between skeletal and non-skeletal components and the variation of density. In contrast, and despite referring
419 to only one surface for each build-up, the microfacies characterization at microscale confirmed that the density is not
420 directly correlated to specific components but it is linked to the degree of packing of the skeletons (mainly CCA) and to
421 the degree of cementation of non-skeletal carbonate components. Furthermore, it is worth to note that the presence of
422 autochthonous micrite, which cement syndepositionally, contributes to increase the build-ups density, regardless of the
423 nature of the components with which it is associated.

424 **4.2 Role of the sponges in the coralligenous growth**

425 Coralligenous growth is the result of the interplay between building activity and the physical and biological demolition
426 (erosion and dissolution) processes (Garrabou and Ballesteros, 2000; Bressan et al., 2001; Cerrano et al., 2001; Ingrosso
427 et al., 2018; Turicchia et al., 2022). Like for biocontructions in the Mediterranean Sea and worldwide (Rosell and Uriz,
428 2002; Evcen and Çınar, 2015; Glynn and Manzello, 2015; Achlatis et al., 2017; Turicchia et al., 2022), boring sponges
429 represent the main cause of bioerosion for the coralligenous build-ups of Marzamemi. The colonization, amount and
430 bioerosion processes of sponges is influenced by temperature, nutrients, turbidity, depth, light, and pH (Schönberg, 2008;
431 Calcinai et al., 2011; Nava and Carballo, 2013; Marlow et al., 2018). Bioerosion has a direct influence on the coralligenous
432 build-ups due to the erosion of the substrate and the skeletal framework, which reduces the mechanical stability of the
433 build-ups (Scott et al., 1988), but at the same time it creates new space and shelter for other organisms (Cerrano et al.,
434 2001; Calcinai et al., 2015).
435 The main boring taxa belong to the family Clionaidae, and especially *Cliona celata, C. schmidtii* and *C. viridis*. Boring
436 and insinuating, cavity-dwelling endolithic sponges, constitute a considerable proportion of the total biomass, even higher
437 than that of the epibenthic layer, both in coralligenous build-ups (Calcinai et al., 2015) and marine caves (Corriero et al.,
438 2000). The contribution of cryptic fauna should be taken into consideration on Coralligenous studies, considering that the
439 number of sponges occurring outside these build-ups is lower than the number of taxa identified inside them (Calcinai et
440 al., 2015).
441 The high amount of sponges and their expected diversity fits well with results by Bertolino et al. (2013) revealing the
442 occurrence of 53 insinuating and 10 boring species inside the coralligenous build-ups. Among them, not-perforating
443 encrusting or massive species occupy cavities of the bioconstructions previously formed by boring sponges (Bertolino et
444 al., 2013).
445 When sponges die, their spicules remain trapped in the cavities of the coralligenous framework, offering the opportunity
446 to recognize the spongofauna over a very long time (Bertolino et al., 2014; 2017a; 2017b; 2019). Spicules of non-eroding
447 sponges from the build-up surfaces may be mixed with spicules of boring and insinuating species in the cavities of the
448 build-ups (Calcinai et al., 2019). In the studied coralligenous build-ups, the pervasive colonization of sponges is testified
449 by the high amount of spicules occurring on the surface and within cavities. Oxeas and tylostyles sponge spicules were
450 observed mixed or grouped by type. It is unclear if the oxeas and other spicules derive from insinuating sponges or from
451 species (*e.g.* haplosclerids) which encrust the external hard surfaces of the build-ups. Spicules associated with amorphous
452 organic matter (spongin remains) in empty cavities testify the presence of recently dead endolithic sponges, possibly even

after the collection of the samples. Among these, boring sponges are recorded by spicules associated with small chips detached from the substrate in cavities showing irregular edges and corroded surfaces. Most of the spicules are mixed with fine detrital sediment and other bioclasts filling intra- and inter-skeletal holes. These spicules may originate from sponges thriving on the build-up surfaces or their internal niches, and together with those preserved in the autochthonous micrite, they represent the record of past Coralligenous sponges. The characterization and dating of these components may reveal the ecological evolution and functional role of the sponge associations during the growth of the build-ups. Sponges also seem to influence the morphological development of build-ups. They can be often bioimmurated by encrusting organisms (mainly crustose algae) thus affecting the local growth direction of the carbonate crusts, that follow the morphologies of the sponges.

4.3 Origin and role of the micrite sediments in the coralligenous framework

The micromorphological observations allowed us to recognize and investigate the role of the sediment in the Coralligenous. Of the two main types of sediments detected, *i.e.* autochthonous and allochthonous (detrital) micrite, the former is produced *in situ* through biomineralization processes. Biomineralization involves organisms, processes and products and includes controlled, induced and influenced mineral precipitation (Lowenstam and Weiner, 1989; Riding, 2000, 2011; Benzerara et al., 2011; Phillips et al., 2013; Anbu et al., 2016; Riding and Virgone, 2020). These different pathways of biomineral precipitation depend also on the chemical and physical conditions of the environment (Riding, 2011; Riding and Liang, 2005; Deias et al., 2023). The recognition of biominerals, especially those not biologically controlled (like skeletons) but precipitated via organic mediation in equilibrium with the water medium, can be considered as a remarkable archive, documenting the presence of non-fossilizable associations as well as their relations with environmental conditions. In the Coralligenous, the presence of autochthonous micrite ("automicrite" *sensu* Wolf, 1965) whose precipitation could be linked to microbial metabolic activity (biologically induced mineralization, mediated by living organic substrates, *sensu* Dupraz et al., 2009) or decaying organic matter mediation (biologically influenced, mediated by non-living organic substrates, *sensu* Trichet and Défarge, 1995), documents communities with low preservation potential but heavily affecting the development of the build-ups.

The autochthonous micrites detected in the studied coralligenous build-ups show two fabrics: 1) structureless (aphanitic) and 2) peloidal to clotted peloidal. Both types consist of Mg–calcite and show an intense fluorescence when excited by UV-light, suggesting a high content in organic matter. Despite these similarities, the two fabrics may have different origins. The massive presence of spicules engulfed in the aphanitic micrite could indicate a carbonate precipitation in association with decaying organic substrates of sponges as repeatedly suggested in literature (Leinfelder and Keupp, 1995; Reitner and Neuweiler, 1995; Reitner et al., 1995; Trichet and Défarge, 1995; Pickard, 1996; Pratt., 2000; Neuweiler et al., 2000, 2003, 2023; Reolid, 2007, 2010). This organic mineralization (organomineralization, *sensu* Trichet and Défarge, 1995) is supposed to form via Ca^{2+}-binding ability of humic and fulvic amino acids, derived from organic matter degraded metazoan during early diagenesis (Braga et al., 1995; Neuweiler et al., 1999, 2007; Wood, 2001; Dupraz et al., 2009). This micrite type is usually darker than the allochthonous micrite, due to the organic matter content (Warnkle, 1995; Delecat et al., 2001; Delecat and Reitner, 2005). Shen and Neuweiler (2018) suggested an organomineralization (produced by induced or supported processes), rather than microbial mediation for the deposition of the autochthonous micrite in the Ordovician carbonate mounds, formed mainly of calathid–demosponge (north-west China). A similar process was proposed for the autochthonous micrite mineralized in the biotic crust of submarine caves of Lesvos (Guido et al., 2019a, 2019b).

The peloidal and clotted peloidal micrite have commonly been linked to anaerobic bacteria activity and represent the main component of the microfacies recognised in modern and ancient microbialites (Monty, 1976; Chafetz, 1986; Kennard and James, 1986; Buczynski and Chafetz, 1991; Reitner 1993; Kazmierczak et al., 1996; Dupraz and Strasser, 1999; Folk and Chafetz, 2000; Riding, 2002; Riding and Tomás 2006; Dupraz et al., 2009; Guido et al., 2013, 2016; Riding et al., 2014). The microorganisms and metabolic pathways responsible for the formation of clotted and peloidal micrites still remain unknown in most instances. In the studied build-ups, the scarce peloidal fabric is mainly confined to framework microcavities, particularly the interior of serpulid tubes and spaces between skeletons. In these suboxic/anoxic confined microenvironments anaerobic heterotrophic bacterial communities can flourish, as observed in several submarine caves by Guido et al. (2017a, 2017b, 2019a, 2022). In the Coralligenous, the clotted peloidal micrite is very subordinate in comparison to aphanitic micrite, and generally it is not associated with sponge spicules, but includes terebellid polychaetes often intermingled with the autochthonous peloidal micrite. The presence of terebellids associated with peloidal micrite suggests a close association between these polychaetes and microbial communities. A symbiotic relationship between terebellids and sulphate-reducing bacteria has been described in confined environments of submarine caves (Guido et al., 2014, 2022). These authors proposed that in pendant bioconstructions terebellids use the peloids produced by microbial activity to form their skeletons and the bacteria flourish on the biomass produced by the terebellids and other metazoans. The occurrence of a similar association in the coralligenous build-ups seems to suggest that this symbiosis is not habitat-specific, but develops in different marine settings, from open to confined habitats, where conditions of cryptic micro-environments in the framework of bioconstructions may promote the development of carbonatogenic microbial communities.

An early lithification of autochthonous micrite has been suggested by many authors (*e.g.*, Grotzinger and Knoll, 1999; Reid et al., 2000) as an explanation for the modes of accretion and textures of various types of bioconstructions. The accretion of the Sicilian Coralligenous was clearly produced by the superposition of different generations of skeletonized organisms, but early lithification of autochthonous micrite, inside primary and secondary cavities, further contributes to cementation and stabilization of the skeletal framework.

The detrital micrite generally derives from degradation and transport of organism's skeletons, transported from neighbouring areas, or from erosion of pre-existing bioclastic rocks (Stockman et al., 1967; Tucker and Wright 1990). The two different types of detrital micrite observed in the studied Coralligenous (*i.e.* organic and inorganic) differ by the occurrence or absence of organic material trapped in the muddy sediment, the different degree of fluorescence under UV-light and the bioclast content. The common loose state of these sediments in the studied build-ups seems to point that their lithification rate is generally lower in comparison to the autochthonous micrite, and may take place some time after the formation of the primary framework. The different amount of organic matter, however, may have a role in the lithification processes. Further knowledge is needed to help the comprehension of the diagenetic dynamic of the detrital micrite helping to clarify the general growth and morphological development of the coralligenous build-ups.

4.4 Coralligenous build-ups *vs* Biostalactites: comparison between recent bioconstructions of different marine settings

Knowledge of the compositional and morphological characterization of the coralligenous build-ups forming along the open marine sectors of the Mediterranean Sea shelf, allows their comparison with bioconstructions forming in confined marine settings, such as blind submarine dark and semi-dark caves. These confined environments have been recently utilized as natural laboratories to study the role of metazoan and microbial communities in forming unusual bioconstructions (Guido et al., 2013; Gischler et al., 2017a). Due to the peculiar conditions of cave environments, notably

low water circulation, reduced or null light intensity, oxygen depletion and remarkable oligotrophy, caves are colonized mainly by cryptic organisms like serpulids, bryozoans, sponges and corals (Harmelin, 1985; Fichez, 1990, 1991). These organisms may be involved in the formation of small biogenic crusts or larger bioconstructions named biostalactites that develop under suitable conditions (Onorato et al., 2003; Belmonte et al., 2009, 2020; Guido et al., 2013, 2017b, 2019a, 2022; Sanfilippo et al., 2015; Gischler et al., 2017a, 2017b; Onorato and Belmonte, 2017; Kazanidis et al., 2022). Serpulids and bryozoans are the main skeletal builders of the biostalactites that are further stabilized by the early cementation induced by the precipitation of autochthonous peloidal and aphanitic micrites mediated by microbial activity (Guido et al., 2013; Gischler et al., 2017a, 2017b). Despite the difference in size (from some cm up to 1-2 m), biostalactites forming in submarine caves of Sicily, Cyprus and Apulia show a uniform style of growth (Guido et al., 2013, 2017b, 2022). In contrast, the biotic crusts forming in the caves from Lesvos island of the Aegean Sea (Fara and Agios Vasilios caves), show a rich sponge association, widely present both on the surface and in the framework microcavities. There, the pervasive presence of sponges in almost all the micro-niches of the bioconstructions, play a limiting role in the development of heterotrophic bacteria (like sulfate reducing bacteria) involved in carbonate precipitation (Guido et al., 2013, 2019a, 2019b, 2022). The competition for space between sponges and carbonatogenic bacteria has been used to explain the morphological differences between large biostalactites and biogenic crusts common in the Mediterranean caves (Guido et al., 2019a, 2019b). In the biotic crusts from Lesvos, sponge spicules are mainly concentrated in detrital micrite that fills primary cavities. Only sporadically, they are associated with autochthonous micrite, suggesting that organomineralization linked to soft sponge tissue decay is a relatively minor process in the in-situ production of micrite (Guido et al., 2019a).

A very similar competition could be suggested for the coralligenous build-ups. Despite the different environmental conditions, size and morphologies characterizing the centimetre sized biotic crust of Lesvos caves *versus* the some decimetres to meter-sized coralligenous build-ups of Marzameni, sponges pervasively cover the surfaces and the internal cavities of both types of bioconstructions. The coralligenous framework is produced by encrusting red algae but the primary inter-skeletal porosity derived from the superposition of different generations of skeletons is enhanced by the bioerosive activity of endolithic organisms. Though cavities could be a site for the settlement of anaerobic bacterial communities (Guido et al., 2013), they are occupied by insinuating and/or perforating endolithic sponges that reduce the availability of micro-niches favourable for the development of sulfate reducing bacteria, hampering the precipitation of autochthonous micrite through their metabolic activity.

The decaying of the soft sponge tissue produces a huge amount of spicules that are trapped in cavities together with fine detrital material. Occasionally, the spicules are engulfed in aphanitic micrite rich in organic matter that do not enclose detrital fragments. This material presumably results from induced and/or supported organomineralization of the soft tissue, like observed in the biotic crusts of Lesvos caves (Guido et al., 2019a). The same process has been suggested also for the Ordovician calathid-demosponge carbonate mounds of north-west China (Shen and Neuweiler, 2018).

5. Conclusions

The study of the build-ups from the Ionian Sea (Marzamemi area) offered the opportunity to investigate the relationship between skeletal builders and associated sediments. These components influence the general morphology and internal framework of the Coralligenous and allow the development of a unique ecosystem where peculiar geobiological processes occur, making these build-ups natural laboratories useful for the palaeoecological reconstruction of the fossil record. The studied build-ups are formed mainly of crustose coralline algae, which constitute a self-sustaining skeletal framework further stabilized by bryozoans and serpulids. The superposition of different generations of builders forms a high porous

structure. The porosity is further enhanced by bio-erosive activity of perforating organisms. These discontinuities in the skeletal framework represent ideal niches for the colonization of cryptic organisms like sponges, bryozoans, serpulids and microbial communities. Among these, sponges are especially common both with insinuating and perforating taxa. After decaying of soft tissue, the spicules of these organisms accumulate in the cavities together with allochthonous micrite and other bioclasts.

Muddy to silty sediments represent the main non-skeletal carbonate component. Sediments consist mainly of allochthonous (detrital) components derived from external sources or from (bio)erosive processes of the build-up components. The autochthonous micrite, mineralized directly inside the build-up through organomineralization processes, represents a minor component. It shows mainly structureless textures and it is associated with sponge spicules. The microbial derived micrite, showing peloidal to clotted peloidal texture, is rare and fills small intra- or inter-skeletal microcavities. Actually, sponges colonize the cryptic micro-niches which are ideal microenvironments for the growth of carbonatogenic bacteria, and the small quantities of autochthonous micrite engulfing the spicules probably results from induced- and supported- organomineralization of the soft tissue of sponges, rather than from microbial mediation. Despite the subordinate abundance in comparison to the skeletonized organisms, the occurrence of autochthonous micrite suggests a possible contribution of this component in cementing and strengthening the skeletal framework due to the early cementation of this type of micrite.

The formation of microbialites seems to be prevented by the competition between sponges and microbial communities colonizing the same cryptic spaces. The similar competition among these organisms in the biotic crusts of confined submarine caves suggests that this relationship is not habitat specific. It may develop in similar microhabitats of different open to cryptic environments, and could be used for palaeoecological reconstructions and for interpreting the role of metazoans and microbialite in the fossil build-ups.

Data availability. All raw data can be provided by the corresponding authors upon request.

Author contributions. Daniela Basso, Antonietta Rosso and Maurizio Muzzupappa designed the project and allowed the collection of the samples; Adriano Guido and Mara Cipriani conducted the study and prepared the first draft. All authors contributed with ideas and in reviewing the manuscript.

Competing interests. The authors declare that they have no conflict of interest.

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