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Serpulid build-up from Miocene last tropical ecosystems in SE Sicily☆

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ABSTRACT

A small carbonate bioconstruction, consisting of serpulids (Annelida, Polychaeta) of the genus *Spirobranchus* and micrite, is described from the Upper Miocene of the Monte Carrubba Formation at Faro Santa Croce, Augusta (southeastern Sicily). The build-up is lens-shaped and consists of serpulids forming roughly alternating layers of tubes with erect distal ends subparallel to one another, and layers with irregularly coiled tubes. Fine micrite sediment partly detrital (*i.e.*, likely derived from physical processes) and partly autochthonous (*i.e.*, putatively induced by *in situ* heterotrophic microbial activity) fills the inter-tube spaces. The build-up presumably formed in a shallow-water intertidal/subtidal palaeoenvironment, where scattered hard substrates within predominantly soft bottoms were colonised by serpulids. The tubes were subsequently encrusted by conspecifics and other epibionts, including coralline algae and bryozoans.

Rapid micritic infilling stabilized the 3D skeletal structure of the serpulid tubes, preventing total collapse despite significant fragmentation. Post-depositional processes locally caused tube dissolution and pervasive diagenetic recrystallization.

The occurrence of this serpulid build-up highlights local habitat heterogeneity in the Mediterranean during the Late Miocene, a critical interval of environmental change that remains poorly understood. It also represents the first documented Upper Miocene serpulid-dominated build-up from the Mediterranean and other open-marine settings, complementing the Middle Miocene record of serpulids-microbialite bioherms known from the Paratethys.

1. Introduction

Serpulids (Serpulidae Rafinesque, 1815) are a group of polychaete worms with a mineralised exoskeleton composed of calcite, aragonite or a mixture of both polymorphs (Vinn et al., 2008), that frequently occur in marine habitats, encrusting a wide range of hard substrates, such as rocks, shells (Rosso and Sanfilippo, 2005), corals (Sanfilippo et al., 2013; Rosso et al., 2015) and coralligenous concretions (Sanfilippo et al., 2025), at all depths, in both fossil and present-day habitats (Kupriyanova et al., 2014).

In some extreme environments like intertidal/subtidal coasts, lagoons (Bosence, 1979; Minchin, 1987; Hughes et al., 2008; Dodd et al., 2009; Sandonnini et al., 2021; Nishi et al., 2022; Bastida-Zavala et al., 2025) and submerged caves (Guido et al., 2013; Sanfilippo et al., 2013), affected by stressful chemical/physical conditions, serpulids can evolve the ability to aggregate their tubes to construct biogenic build-ups (see ten Hove, 1979; ten Hove and Van den Hurk, 1993; ten Hove and Kupriyanova, 2009).

Serpulid build-ups mostly grow in unstable environments and are favoured by a complex set of parameters, including salinity, competition for food and space, larval retention, and high primary production (Bosence, 1979; ten Hove, 1979). On soft bottoms the presence of scattered small hard substrates (such as shells) may favour serpulid aggregation, with tubes initially settling on these isolated elements and subsequently growing on each other. Biological trait of the worm itself, such as larval gregariousness, is also a contributing factor to mass occurrence (ten Hove, 1979) through chemical stimuli (Scheltema et al., 1981), as well as asexual reproduction by scissiparity, which leads to bifurcating adjacent tubes, and/or the combination of both processes (Hoeksema and ten Hove, 2011).

The formation of reef-like serpulid build-ups has been studied in

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several localities worldwide, both in the geological past (Fagerstrom, 1987; Palma and Angeleri, 1992; Friebe, 1994; Cirilli et al., 1999; Georgieva et al., 2019; ten Hove and Van den Hurk, 1993) and in the present day (Bianchi et al., 1995; Bosence, 1979; Bianchi and Morri, 2001; Hoeksema and ten Hove, 2011; Sandonnini et al., 2021; Montefalcone et al., 2022). According to ten Hove (1979), the formation of build-ups occurs in unstable environments and is restricted to some euryecious serpulid species. These environments were distinguished by ten Hove and Van den Hurk (1993) into three groups, occurring in different environmental settings: 1) intertidal zone of open coasts; 2) quiet, enclosed embayments of normal salinity; and 3) brackish estuaries and lagoons. Among euryecious serpulids, the otherwise solitary genus *Spirobranchus* forms aggregates under type 1 environmental conditions. Similarly, among the seven types of serpulid reefs recognised by Montefalcone et al. (2022), based on their building modality and the habitats they colonize, *Spirobranchus* is reported to form aggregates in "littoral belts" and "subtidal reefs".

Nowadays, the genus *Spirobranchus* is often associated with warm and tropical marine environments, such as coral reefs (ten Hove, 1973). In the fossil record, serpulids are similarly found associated with tropical coral reefs, where they functioned as primary or secondary framework builders, as, for example, in the Jurassic-Cretaceous of Europe (Kemper, 1988; Kubiatowicz and Matyja, 1977: Kočí and Jäger, 2015; Cox and Sumbler, 1989) and North Africa (Vinn et al., 2025), and in the Middle Miocene of the Parathetys (ten Hove and Van den Hurk, 1993; Harzhauser and Mandic, 2023; Piller and Harzhauser, 2023, for a review).

This study focuses on a monospecific serpulid bioconstruction constituted by individuals of the genus *Spirobranchus* from a Miocene pre-evaporitic carbonate succession from SE Sicily.

The aims of this paper are to: 1) describe the serpulid framework and its relationships with the embedding micrites; 2) elucidate the micrite origin (autochthonous *vs* detrital) and identify possible evidence of *in situ* microbial biomineralization; 3) reconstruct the processes leading to the formation of this peculiar serpulid-micrite bioconstruction; and 4) discuss the depositional and palaeoenvironmental context in the frame of the Late Miocene crisis of the Mediterranean basin.

2. Geographical and geological setting

The study area, known as Faro Santa Croce (FSC), is located north of the Augusta town in southeastern Sicily (37°14′38.48" N; 15°15′18.61″ E), where a sedimentary succession belonging to the basal part of the Monte Carrubba Formation is well exposed near the coastline (Fig. 1).

In this eastern margin of the Hyblean Plateau (Fig. 2), the Monte Carrubba Formation is represented by Upper Miocene carbonate deposits, sandwiched between lower Oligocene to Miocene carbonates and Pliocene to Pleistocene volcanics (Pedley et al., 2007). The formation was deposited on the inner sector of a distally steepened carbonate ramp, developed onto the tectonically stable foreland margin of the Pelagian Block during the late Tortonian to early Messinian (Grasso et al., 1982; Pedley et al., 2007). It is clearly differentiated in two units, separated by an erosional surface indicating subaerial exposure: a basal "open marine unit" characterised by matrix-rich limestones with pectinids and coral patch reefs, and an overlying "restricted marine unit" with oolitic shoals and lagoonal mudstones with low diversity cardiid-veneriid-mactrid bivalve assemblages. Based on molluscan assemblages, Harzhauser et al. (2013) recognised that oolitic grainstones underlying lagoonal mudstones of the upper "restricted marine unit", indicate deposition in normal marine to slightly hypersaline shallow waters under high hydrodynamic conditions.

The FSC succession (Fig. 2B) begins with coastal marine bioclastic calcarenites exhibiting upwards wave-ripple cross-lamination. These layers contain mainly pectinids (*Pecten aduncus* Eichwald, 1830) and other bivalves such as *Loripes lucinalis* (Lamarck, 1818), often with articulated valves, *Acanthocardia turonica* (Hornes, 1862), *Callista italica* (Defrance, 1818) and well-preserved *Pinna*-like bivalves in life position. Overlying these deposits are pale-yellow limestones that contain an *in situ* coral reef, approximately 5 m wide and 2 m thick, mainly built by *Porites*, locally associated with crustose coralline algae. The reef is capped by numerous oyster shells and truncated by an erosional surface that may also affect the surrounding limestones. Above this surface, the upper "restricted marine unit" of Pedley et al. (2007) and Harzhauser et al. (2013) was deposited, starting with fossiliferous marlstones that

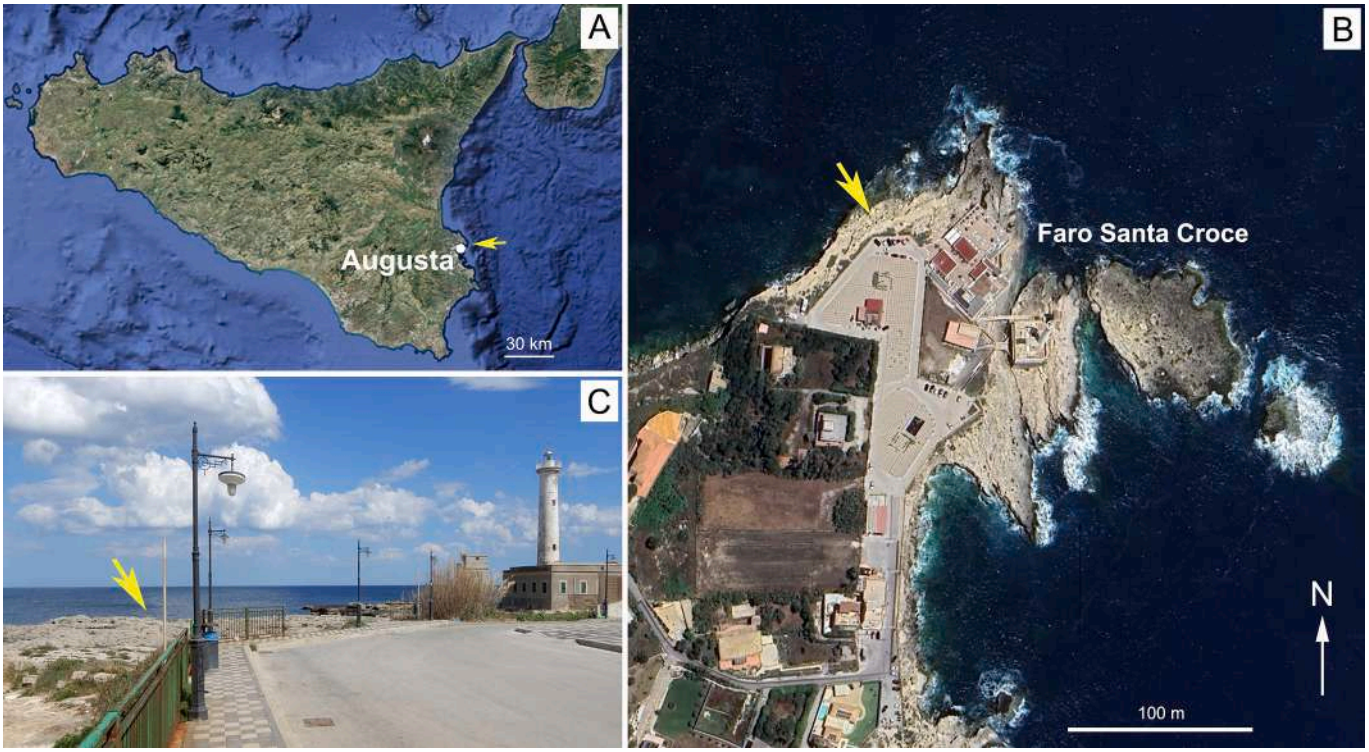

Fig. 1. Location of the study area in SE Sicily (Italy), north of the Augusta town (A) at the Faro Santa Croce locality (B), along the rocky coastline (C).

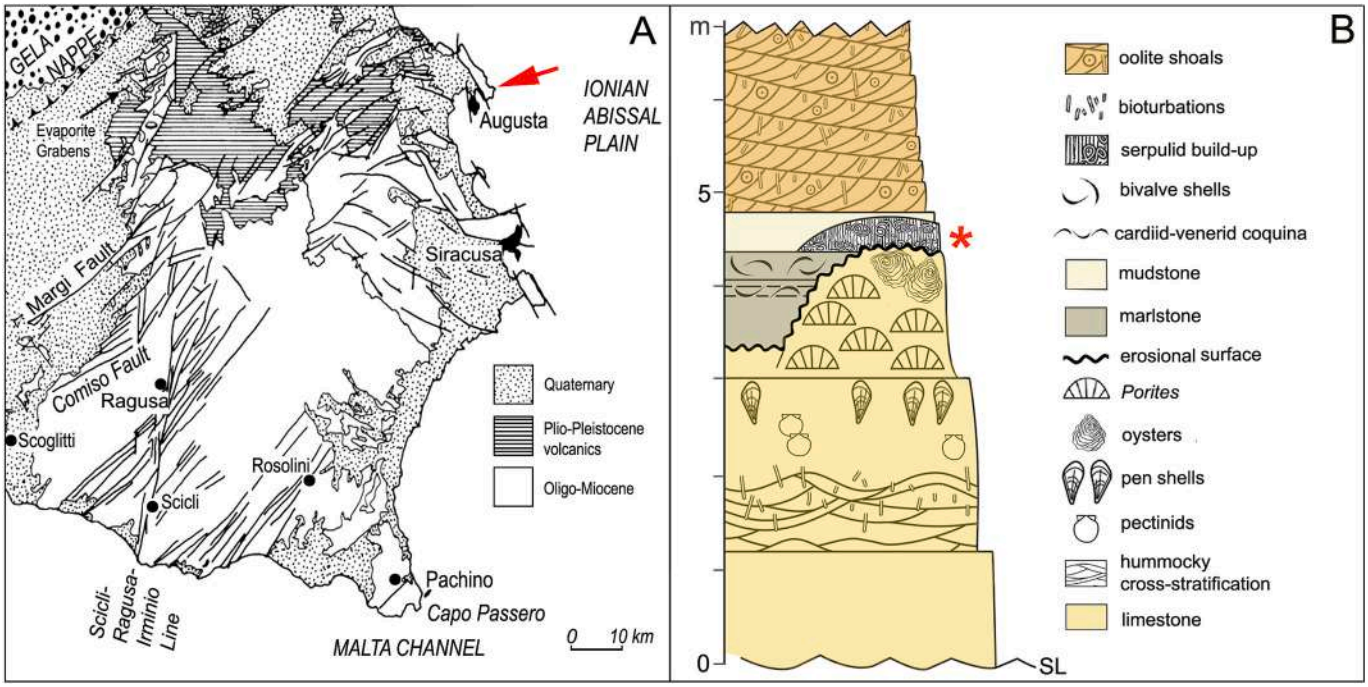

Fig. 2. A. Simplified geological map of the Hyblean region and location of the Faro Santa Croce section (arrow). The Monte Carrubba Formation mainly occupy the northern half of the 'Oligo-Miocene' outcrop. B. Lower part of the geological section cropping out at FSC, drawn combining literature data (Pedley et al., 2007; Harzhauser et al., 2013) and personal field observations. The asterisk marks the position of the serpulid build-up.

display a cardiid-venerid (*Acanthocardia-Polititapes*) coquina, with scattered batillariid and cerithiids gastropods. These sediments likely deposited in depressions lateral to the reef.

The serpulid build-up developed at the base of the upper "restricted marine unit", apparently initiating on the truncation surface above the coral-oyster reef and expanding laterally over the coquina layer. The build-up is lens-shaped and composed of carbonate serpulid tubes and micrite sediment filling inter-tube spaces.

Oolite-rich sediments, forming inclined tabular bodies and containing rare pectinids, follow upwards, interpreted as shoals foresets.

Further details on the geology of the area and on the FSC section can be found in Grasso et al. (1982), Pedley et al. (2007), Harzhauser et al. (2013) and Tomassetti et al. (2022).

The serpulid build-up is only briefly mentioned in these studies, whereas it is described here for the first time in detail from a systematic, palaeoecological, and taphonomic perspective.

3. Material and methods

Specimens from small samples of the build-up were documented and identified under a Zeiss Discovery 8 stereomicroscope equipped with the imaging software ZEN 3.1 at the Palaeoecology laboratory of the Department of Biological, Geological and Environmental Sciences, University of Catania. Further observations and photo-documentation were performed in the same laboratory, using a Tescan Vega 2 LMU, Low Vacuum Scanning Electron Microscope (SEM) at the Microscopical Laboratory.

Two polished slabs were cut transversely and longitudinally with respect to the growth direction of the tube aggregates and observed under an Axioplan II imaging Zeiss stereomicroscope. Microfacies were identified on thin sections following the classifications of Dunham (1962), modified by Embry and Klovan (1971) and expanded for reef rocks by Cuffey (2016).

A large part of the examined material is housed in the Palaeontological Museum of the University of Catania under the collective code "PMC. Faro Santa Croce Sanfilippo Serpulid Collection".

Further small subsamples and thin sections of the serpulid bioconstruction are housed at the Department of Biology, Ecology and Earth Sciences of the University of Calabria, where photo-documentation, as well as taxonomical and minero-petrographic analyses, were performed.

Fragments of the build-up and thin sections, cut both transversely and longitudinally relative to the growth direction of the tube aggregates, were examined using optical microscope, Scanning Electron Microscopy (SEM) and Energy-Dispersive X-ray Spectroscopy (EDS).

Optical microscopy was conducted using a Zeiss Axioplan 2 Imaging microscope at magnifications of 2.5×, 5×, 10×, 20×, and 40×. Fluorescence was analysed under incident light using a high-pressure Hg vapour lamp and high-performance wide bandpass filters (436/10 nm) combined with a long-pass filter (470 nm, no. 488006) for the green channel, and bandpass filters (450–490 nm) combined with a long-pass filter (515 nm, no. 488009) for the yellow channel. UV epifluorescence was employed to detect organic material (Neuweiler et al., 2000, 2003; Cipriani et al., 2023, 2024).

SEM observations were carried out on carbon-coated thin sections and fragments with an ultra-high-resolution (UHR-SEM) ZEISS Crossbeam 350 operated at 10 keV accelerating voltage, 100 pA probe current, 11 mm working distance and 123 eV resolution.

Mineralogical and chemical compositions were determined using an EDAX Octane Elite Plus silicon drift detector with Si_3N_4 window, under 15 keV accelerating voltage, probe current 60 mm, 12 mm working distance, 40° take-off angle and 30 s live time. Standardless quantitative analyses were checked against the SPI standard no. 02757-AB (serial 4 AK) and processed using the AMETEK APEX software suite V2.

4. Results

4.1. Description of the serpulid reef

The build-up is lens-shaped, about 1.5 m wide and up to 0.7 m thick (Fig. 3), and is composed of a monospecific serpulid aggregation. Tubes are arranged with subparallel, undulated distal ends that rise from the

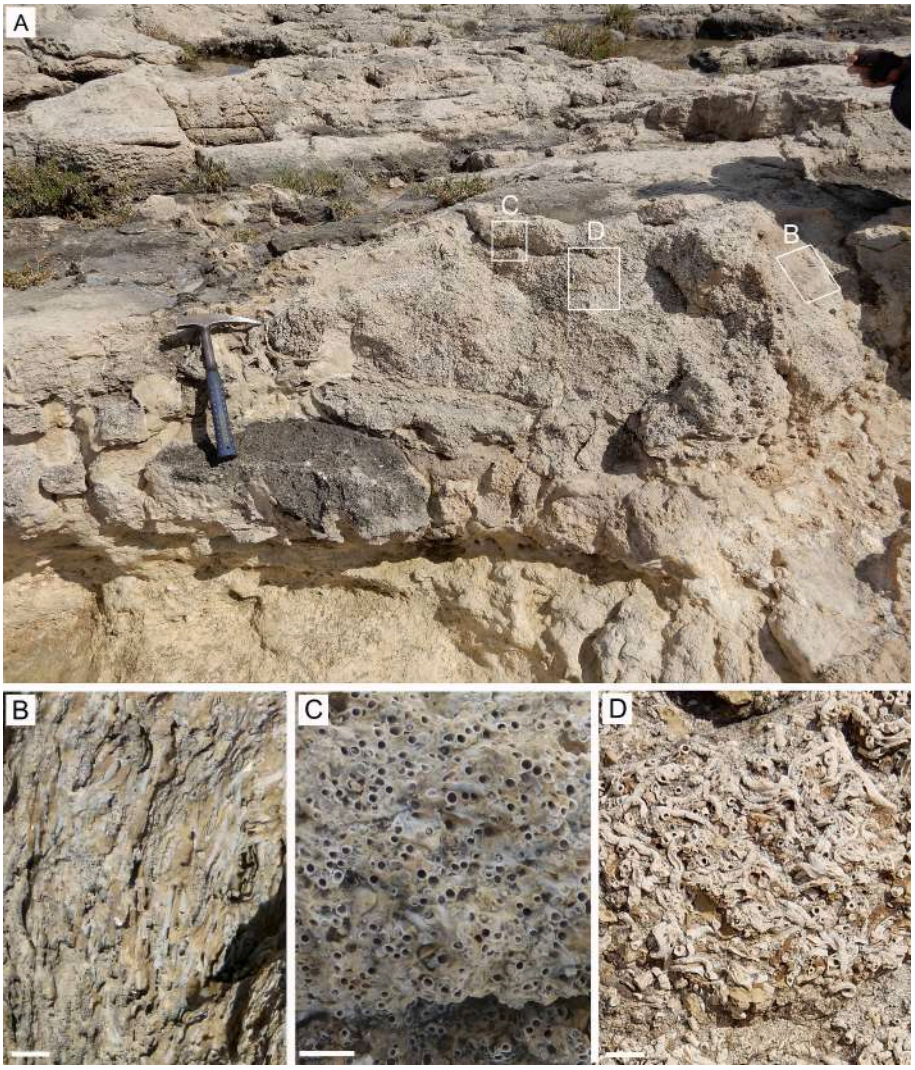

Fig. 3. A. The lens-shaped serpulid tube aggregation in the field, above marlstones and below the oolitic cross laminated grainstones. B. Main framework consisting of subparallel tubes that grew upwards with distal ends raised from the substratum. C. Outer surface of the build-up showing widely spaced tubes in cross section, and spaces between tubes filled with yellow ochre micrite. D. Intermingled tubes from a lateral outer part of the build-up. Scale bars 5 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

substratum (Fig. 3B). Growth increments, approximately 6 cm thick, are evident and reflect the overgrowth of successive generations (Fig. 4C). In the peripheral part of the build-up, a few layers consisting of convoluted, disorderly arranged tubes, 5–6 cm thick, occur (Figs. 3D, 4A) and are locally interlayered with levels formed by subparallel tubes (Fig. 4B).

The skeletal framework is relatively open, with tubes generally widely spaced and only rarely in close contact (Fig. 3C). Voids between them account for ~50% of the total build-up volume and are filled with fine yellow-ochre micritic sediment. Diagnostic characters are commonly poorly preserved because of frequent fracturing and external corrosion, which partly obliterates the original ornamentation. Nevertheless, overall morphology can be reconstructed: the proximal portion is triangular in cross section, whereas the erect distal part is subcircular. The exterior is smooth and dorsally keeled, and basal flanges bear peripheral areoles. This combination of characters supports assignment to the genus *Spirobranchus* de Blainville, 1818 (= *Pomatoceros,* Philippi, 1844; = *Pomatoleois* Pixell, 1913) (Fig. 5A-C). Ribs and peristomes slightly concave towards the aperture are obvious in some erect distal ends of tubes (Fig. 5A, B). Diameter is relatively constant throughout growth (mean outer diameter 0.8 mm, range 0.5–1.2 mm; mean lumen diameter 0.4 mm, range 0.2–0.5 mm), and wall thickness is ~0.2 mm.

Preservation is generally poor and diagenetic overprint is strong. Internal moulds locally alternate with the more frequent preserved portions of the tubes, whose walls are heavily recrystallised, nearly obliterating internal structure. Fracturing is widespread (Figs. 5F, 6C), and compression commonly causes collapse. In these cases, the wall around the lumen breaks into several closely adjoining fragments. Despite this local damage, the three-dimensional fabric is largely maintained by micrite infilling the intervening spaces. Diagenesis is further indicated by dissolution of the outer wall (partially in some cases: Fig. 5D; completely in others, leaving only internal moulds: Fig. 5A). Recrystallization also affects the yellow interstitial sediment, which locally becomes indistinguishable from the skeletal framework (Fig. 6A). Cross sections commonly display a dark outer tube layer, possibly secondary and diagenetic, consistently with the presence in some specimens of shiny crystals growing into the lumen.

Locally, along the periphery of the build-up, coralline algal crusts, 1–2 cm thick, co-occur with scarce celleporiform bryozoans and other bryozoan taxa (Fig. 6A, B), while in the overlying oolitic grainstones, a pectinid shell is encrusted by *Hydroides* tubes that adhere to it for their entire length (Fig. 5E).

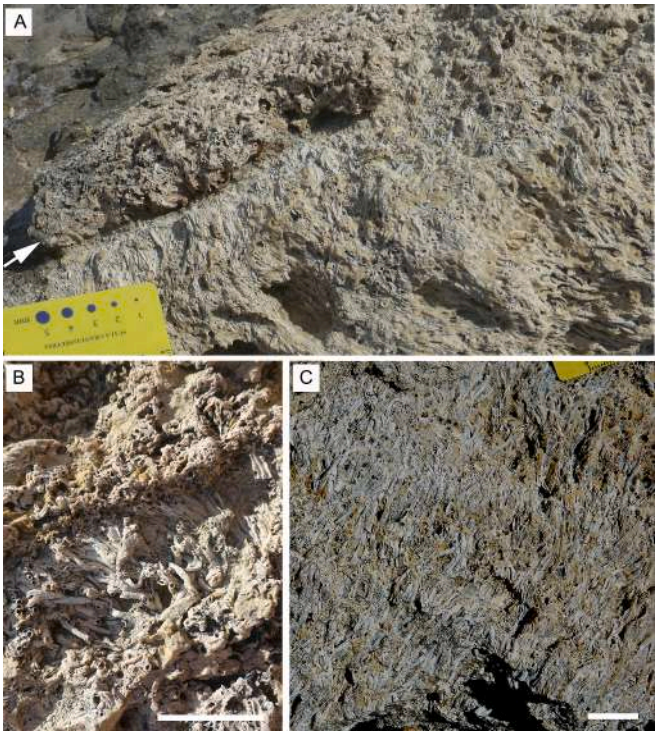

Fig. 4. A. Outer part of the build-up showing a 6 cm thick layer of convoluted disorderly arranged tubes (arrowed), above the main framework made by subparallel tubes. B. Portion close to the external surface of the build-up, showing two layers with twisted and disorderly arranged tubes alternating with layers with raised and ordered tubes (scale bar = 3 cm). C. Structure of the internal framework with subparallel tubes showing subsequent growth increments.

4.2. Microfacies characterization and geochemical signatures of the serpulid-dominated framework

Optical and SEM observations reveal that the investigated samples consist of a serpulid-dominated (monospecific) limestone displaying a bafflestone texture (Embry and Klovan, 1971).

Microscopic observations are consistent with the macroscopic features of the build-up and allow a detail framework components characterization.

The skeletal framework is formed by serpulid tubes (Fig. 7A), preserved either intact or fractured, whereas the non-skeletal fraction consists of detrital and autochthonous micrite (Fig. 7B). Both components are clearly distinguishable under optical microscopy and SEM, allowing their microstructural features to be readily identified (Fig. 7F).

Detrital micrite is light-brown, heterogeneous, and contains abundant siliciclastic components. It occurs as an infill within inter-skeletal spaces and, locally, within tube lumina, often forming geopetal structures. Under UV light, it shows no fluorescence (Fig. 7C).

Autochthonous micrite shows aphanitic or peloidal textures. The homogeneous aphanitic fabric is dark brown in colour and occurs in cryptic cavities of the framework, mainly between skeletal components and sometimes in contact with detrital micrite. On the other hand, peloidal micrite displays a well-preserved clotted texture (Fig. 7D) and predominantly occupies intraskeletal cavities within tubes. Under UV light, the aphanitic micrite shows a strong fluorescence (Fig. 7C), whereas the peloidal micrite displays an intermediate fluorescence intensity (Fig. 7E), which is locally attenuated and, in some areas, becomes comparable to the non-fluorescent behaviour of detrital micrite. This apparent similarity might reflect a minor diagenetic overprint affecting the less compact texture of the peloidal micrite.

Some samples show *Frutexites*-like structures (Fig. 8A), which commonly occur at the contact between fractured serpulid tubes, and locally overgrow the detrital micrite. Under transmitted light, they are dark brown to black, forming a sharp contrast with the surrounding light-coloured micrite, whereas under UV light, they display intense fluorescence (Fig. 8B), clearly contrasting with the non-fluorescent detrital micrite.

EDS analyses confirmed that the detrital micrite is compositionally heterogeneous and enriched in siliciclastic component, whereas the aphanitic micrite (low-Mg calcite) is more compact and homogeneous.

The different compositions of skeletal and non-skeletal components are showed in Fig. 9, where EDS-based elemental distribution maps highlight spatial variability within the framework. Detrital micrite is enriched in Si and Al and shows comparatively lower Ca. In contrast, the aphanitic micrite is more Ca-rich and compositionally homogeneous. The peloidal micrite, showing weaker fluorescence in comparison do the aphanitic one, displays locally lower Ca signal in the mapped areas (Fig. 9C). Iron oxides are mainly associated with detrital micrite, whereas pyrite is preferentially concentrated in the autochthonous micrite. Moreover, EDS maps indicate that serpulid tubes are presently composed of low-Mg calcite in contrast to values of 10–15 mol% $MgCO_3$ measured in present day *Pomatoceros* tubes from the British Isles (Buckman 2015).

5. Discussion

5.1. Serpulid build-up formation

The progressive tube accretion by gregarious serpulids produced a three-dimensional rigid framework that created cavities suitable for microbial colonization and acted as an efficient trap for fine-grained sediment. The coexistence of skeletal and non-skeletal components, with the latter systematically occupying framework spaces, indicates a close relationship among bioconstruction, sediment trapping and early diagenetic cementation. These processes were therefore not independent, but mutually connected during the development of the serpulid build-up.

Detrital micrite records the input and trapping of fine material within and around the serpulid framework. The absence of fluorescence is consistent with a low content of preserved organic matter, either because detrital micrite was originally depleted in organics or because organic matter was largely degraded during early taphonomic processes. In contrast, the autochthonous micrite, occurring as compact aphanitic textures as well-defined peloids in cryptic cavities, shows discrete fluorescence, indicating an enrichment in organic matter.

The variable fluorescence between the two textures of the autochthonous micrite, together with the locally lower Ca signal observed in the mapped areas (Figs. 7E, 9C), is attributed to diagenetic overprint (*e.g.*, recrystallization and degradation/removal of fluorescent organic compounds) rather than to siliciclastic input. Accordingly, UV fluorescence is treated as a qualitative indicator that may be altered by diagenesis and does not directly track microbial activity or organic-matter abundance (Neuweiler et al., 2000, 2003). The similarity in fluorescence intensity between the peloidal micrite and the detrital micrite is therefore interpreted as the result of convergent diagenetic modification of the fluorescence signal rather than an allochthonous origin.

The overall architecture of the build-up suggests that more open, better-flushed parts of the framework were dominated by passive trapping of externally supplied mud, whereas sheltered, low-energy cavities within and between tubes, in the internal part of the skeletal framework, provided favourable microhabitats for microbial communities (living in cryptic cavities and low-energy conditions) capable of inducing or influencing *in situ* carbonate precipitation. As a result, small-scale redox and nutrient gradients likely developed in cavities among serpulid tubes. These conditions sustained localised microbial activity and promoted the accumulation of organic-rich micrite.

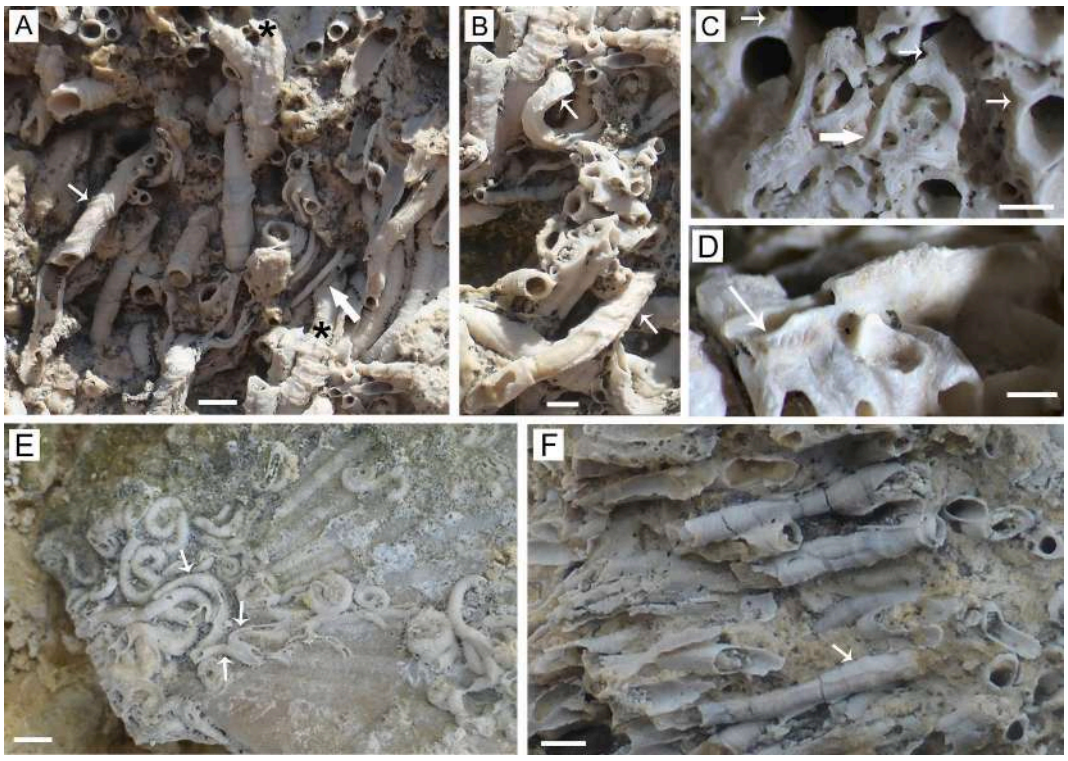

Fig. 5. *Spirobranchus* mass occurrence from the Late Miocene of Faro Santa Croce, SE Sicily. A. Distal ends of aggregated tubes subcircular in cross section bearing peristomes (small white arrow). Partial dissolution is obvious on the outer surfaces of some tubes (asterisks); total dissolution sometimes occurs leading to the preservation of internal tube moulds (large white arrow). B. Portion with irregularly arranged, partly preserved tubes showing a longitudinal dorsal keel (arrows). C. Proximal parts of tubes subtriangular in cross-section: the bold arrow indicates an areola inside the lateral basal flange of the wall while thin arrows indicate dorsal keels. D. Partially dissolved tube exposing some areoles aligned inside the basal flange and filled with cemented micrite. E. Three individuals (arrows), with some *Hydroides* tubes encrusting them along their entire length, on a pectinid shell overlying the oolitic grainstones. F. Subparallel distal ends of tubes, subcircular in cross-section and with a faint dorsal keel (arrowed). Note the intense breakage. Scale bars 1 mm (A, B, E, F); 0.5 mm (C, D).

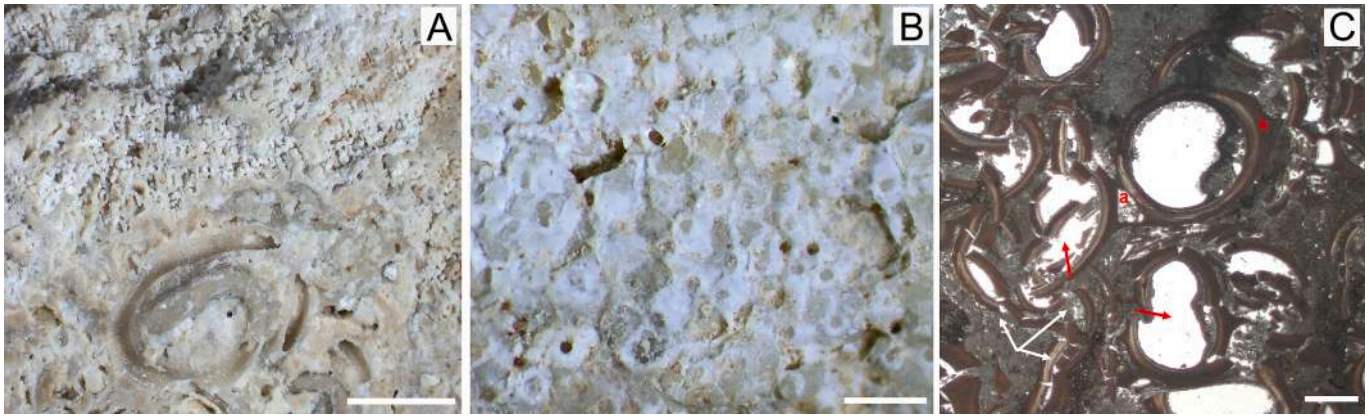

Fig. 6. Detail of peripheral parts of the build-up, which appears extremely diagenised (A, B) and fractured (c). A. Complete skeletal dissolution of coralline algae and the tubes themselves, both preserved as only internal moulds. Heavy recrystallization affects the sediment within the inter-tube spaces. Scale bar 1 mm. B. Partially preserved colony of a celleporiform bryozoan (scale bar 0.5 mm). C. Microfacies of the serpulid bafflestone lithofacies. Tubes range from lightly (red arrows) to severely crushed (white arrows). Where compression is stronger, tube walls are pressed together, coming into contact and locally occluding the lumen. Inter-tube space is filled with micrite and abundant, slightly displaced small tube fragments; dorsal keel (k); a: areola from the basal flange of tube encrusting on an unbroken tube. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The elemental distribution maps further reinforce the distinction between the different micrite types and help constraining the redox and diagenetic conditions within the framework. Detrital micrite shows higher Si and Al contents, in line with its allochthonous and siliciclastic-rich character, and hosts most of the detected iron oxides, suggesting stronger exposure to more oxidizing conditions in more open microenvironments. In contrast, autochthonous micrite is relatively enriched in Ca and contains most of the pyrite, implying localised reducing conditions within cryptic cavities where organic matter accumulation was enhanced and led to anaerobic heterotrophic microbial activity.

This geochemical signature indicates that the serpulid framework functioned as a small-scale environmental filter, separating more oxygenated, sediment-laden waters circulating through open pores, from more stagnant, reducing microenvironments confined within

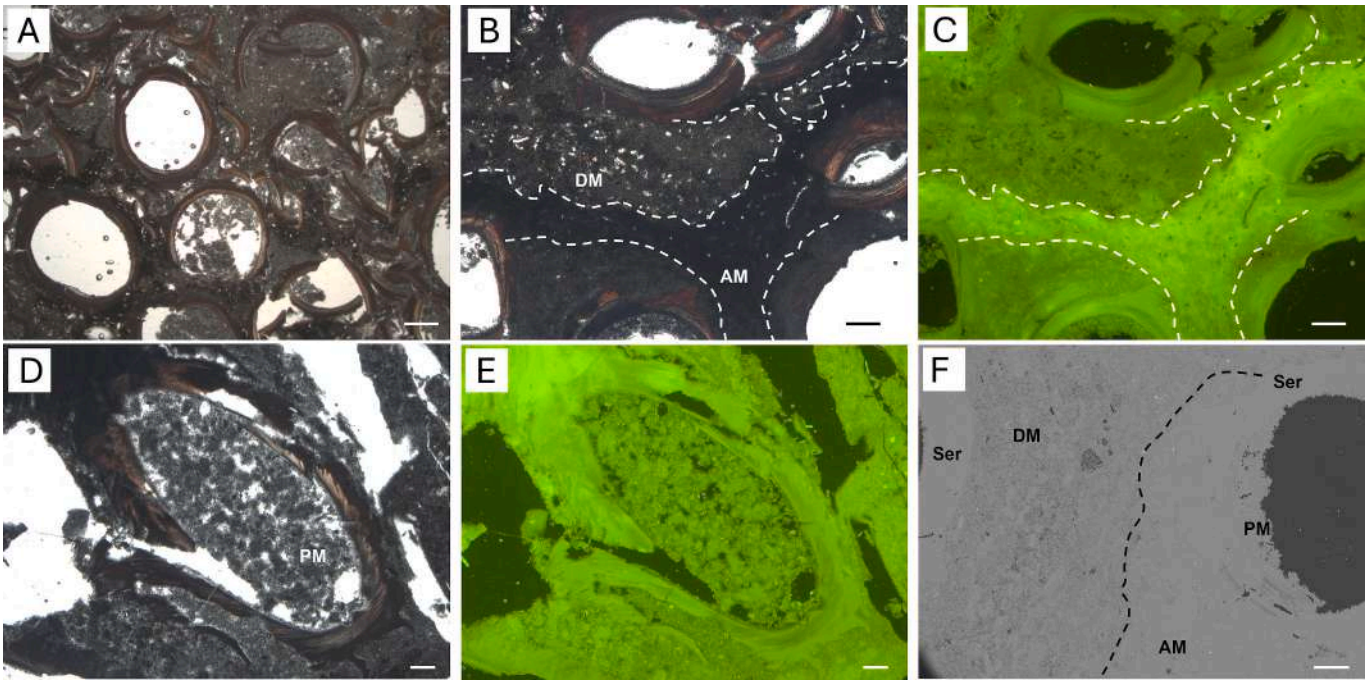

Fig. 7. Optical (A–E) and SEM (F) images of the investigated samples. (A) serpulid-dominated framework cemented by micrite. (B and C) Detail of detrital (rich in siliciclastic materials) and autochthonous micrite showing respectively scarce and high fluorescence under UV-light. (D, E) Peloidal micrite infilling intraskeletal cavities displays fluorescence. (F) Sem image showing all skeletal (serpulids) and non-skeletal components (detrital, autochthonous and peloidal micrite). Scale bars 200 μm (A, D, E and F); 100 μm (B and C). Ser = serpulids; DM = detrital micrite; AM = autochthonous micrite; PM = peloidal micrite. Dotted lines indicate the boundary between the autochthonous micrite (AM) and detrital micrite (DM).

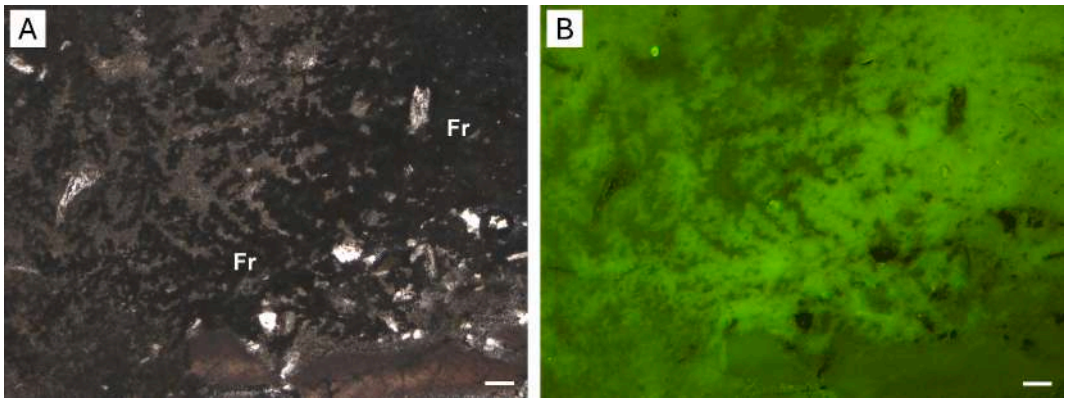

Fig. 8. (A and B) *Frutexites*-like structures appearing dark under transmitted light and intensely fluorescent under UV.

sheltered cavities.

The microfacies documented in the studied build-up closely resemble those described from Upper Miocene micrite-vermetid bioconstructions of the Salento Peninsula (Guido et al., 2012). Similar relationships among micrite fabrics, organic-matter distribution, and redox conditions have also been reported from Mid to Upper Triassic reefs in the Dolomites (Tosti et al., 2014). Comparable associations are further documented in metazoan-microbial biostalactites from Mediterranean and tropical submarine caves, where autochthonous clotted-peloidal to aphanitic micrite has been linked to sulfate-reducing bacteria (SRB) (Guido et al., 2013, 2014, 2017a, 2017b; Gischler et al., 2017). Similar autochthonous micrites have also been described in biotic crusts from Pleistocene marine caves (Sicily) and in cryptic microbialites from the Aegean Sea, where they are interpreted as products of heterotrophic SRB inhabiting low-oxygen microhabitats (Guido et al., 2017a, 2017b, 2019a, 2019b, 2022). The occurrence of *Frutexites*-like structures provides additional insights into the late diagenetic overprint affecting the serpulid framework. These structures preferentially develop within detrital micrite and form dendritic aggregates of micro columnar branches that spread laterally as thin, planar coatings draping the underlying micrite, rather than building three-dimensional bodies. Their geometry, strictly confined to sub-parallel surfaces above micritic layers, is more consistent with surface-bound mineral growth during late-stage diagenetic processes than with cavity-filling or fracture-controlled mineralization.

The UV-induced fluorescence of the *Frutexites*-like aggregates is interpreted primarily as a diagenetic signal. It does not necessarily indicate organic-matter enrichment, because Mn-bearing phases formed during late diagenesis can produce a similarly strong UV response. In these samples, the combination of planar, surface-following morphologies with fluorescence compatible with Mn-rich compositions, suggest a predominantly abiotic, late-diagenetic origin, with mineral growth concentrated along micrite-lined surfaces. Consequently, unlike the *Frutexites*-type fabrics described in confined marine bioconstructions,

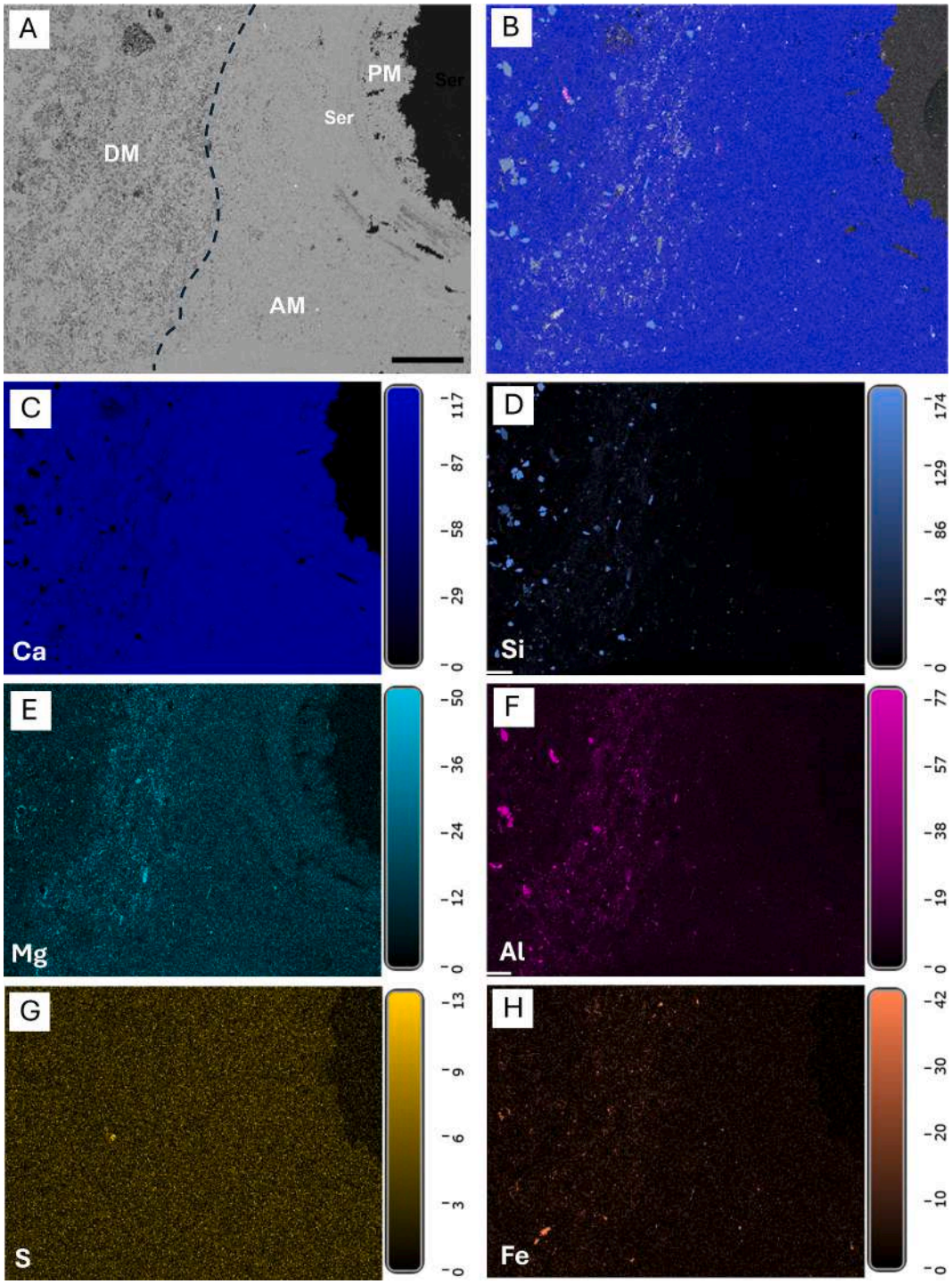

Fig. 9. SEM-EDS elemental distribution maps highlighting the spatial variability of the main elements (magnesium, aluminium, silicon, calcium and iron) within the framework. (A) SEM backscattered-electron image (scale bar = 200 μm) showing detrital micrite (DM), autochthonous micrite (AM), peloidal micrite (PM) and serpulid tube wall (Ser); the dashed line marks the contact between DM and AM; (B) Composite EDS map of all elements investigated. (C–H) Single-element distribution maps: (C) Ca, (D) Si, (E) Mg, (F) Al, (G) S, and (H) Fe. The vertical colour bars show the EDS X-ray signal intensity for each element, scaled from 0 to the maximum value measured in the corresponding map (note that each element has its own scale).

where dendritic Fe—Mn accumulations are linked to focused fluid circulation (Guido et al., 2022), the structures documented here are interpreted as thin, late-diagenetic coatings.

5.2. Depositional environment

The serpulid build-up of FSC formed along the inner belt of a distally steepened carbonate ramp that evolved from open-marine coral patch reefs to restricted lagoonal deposits during the late Tortonian-early Messinian, immediately before the onset of the Messinian Salinity Crisis. The vertical transition from a coral-algal-oyster reef to a serpulid-algal-bryozoan build-up and, finally, to oolitic shoals and lagoonal mudstones of the upper restricted marine unit, captures a shift from fully marine, high-diversity conditions to a more marginal, hydrodynamically

variable and salinity fluctuating setting.

The serpulid build-up likely formed under environmentally stressful conditions in intertidal to shallow-subtidal open coasts. These settings can foster the development of euryecious taxa such as *Spirobranchus*. The presence of a serpulid bafflestone facies denotes low hydrodynamic energy, consistent with the sheltered microenvironments identified within inter-tube spaces in similar shallow-water fossil reefs (ten Hove, 1979; Cirilli et al., 1999; Bianchi and Morri, 2001; Piller and Harzhauser, 2024).

Comparable depositional conditions are recorded in other Miocene metazoan-microbial bioconstructions of the Salento Peninsula, where microbial micrite associated with vermetid frameworks reflects the rise in opportunistic, stress-tolerant builders under fluctuating salinity and trophic conditions in the run-up to the MSC (Guido et al., 2012). The upper Messinian, Salento microbialites of the Terminal Carbonate Complex represent an end member of this process, with metazoan frameworks largely replaced by microbial build-ups developed in highly restricted, evaporitic lagoons (Vescogni et al., 2022, 2025; Vescogni and Guido, 2026). Similar shifts in carbonate producing assemblages in upper Tortonian-lower Messinian ramps, with coral frameworks progressively replaced by coralline algae, oysters, vermetids, serpulids, and microbial communities are documented in nearby Mediterranean outcrops (Esteban, 1979; Riding, 1991; Pedley, 1998; Pedley et al., 2007; Vescogni et al., 2022). At Acquabona (Tuscany), early Messinian coral reefs of the Calcare di Rosignano Formation show repeated shifts between coral-rich and coral-poor facies accompanied by an increased algal component; these changes have been interpreted as pre-evaporitic oscillations driven by variations in circulation, nutrient availability, and salinity (Coletti et al., 2024). In this context, the FSC succession may represent a coeval but more proximal expression of the same pre-evaporitic stress regime, linked to progressive restriction of the Mediterranean-Atlantic gateways during the late Tortonian-early Messinian (Grasso et al., 1982; Flecker et al., 2015).

The FSC serpulid build-up also fits into a broader trend of microbial colonization and ecological filtering recognised in Upper Miocene shallow-water carbonates of the Mediterranean. The almost exclusive occurrence of serpulids in the build-up points to environmental conditions that favoured eurytopic serpulids and microbial communities over other carbonate producer taxa. Particularly, the presence of *Spirobranchus* specimens in isolated tubes on shells of the upper oolitic sands, may not be merely indicative of brackish waters, but rather of episodes of variable conditions, from hypo- to hypersaline, associated with variable hydrodynamics.

Sea-level oscillations in the Mediterranean basin are evidenced by a subaerial erosional surface immediately below the serpulid build-up (Fig. 2B). Additional support comes from the internal architecture of the build-up, which shows layers with sub-parallel, upward-oriented tubes alternating with layers of intermingled, convoluted tubes. This alternation suggests shifts in hydrodynamic conditions, possibly related to minor changes in water depth.

The erosional surface has been correlated with the first global low stand within the lower part of the TB3.3 cycle, at the top of the *Globorotalia mediterranea* Subzone. This correlation allows the serpulid build-up to be dated to the early Messinian at 6.8 Ma (Di Grande and Romeo, 1975, 1980; Grasso et al., 1982). The FSC serpulid-micrite build-up can be interpreted as a transitional stage during the Late Miocene evolution of shallow-water system, from coral-dominated tropical reefs to mixed metazoan-microbial bioconstructions and, finally, to nearly purely microbial systems. In this context, the emergence and local dominance of serpulids act as a sensitive proxy for pre-evaporitic environmental stress in the central Mediterranean (Flecker et al., 2015).

5.3. Taphonomy

The preservation status of the serpulid tubes, which include both fractured and fully intact specimens, indicates post-burial deformation. This pattern is consistent with differential stress induced by early diagenetic compaction of the sediment. Variability in tube preservation likely reflects difference in the mechanical behaviour of the micrite matrix: detrital micrite, unconsolidated at deposition, was susceptible to compaction-induced fracturing of the tubes, whereas autochthonous micrite, cemented during early diagenesis, contributing to maintaining tube structural integrity. The *in situ* disposition of fractured fragments further supports a diagenetic origin for the observed breakage, rather than transport or pre-burial biostratinomic processes.

The build-up underwent intense post-depositional alteration. Partial to complete dissolution of tube walls leading to local preservetion of internal moulds, indicates selective removal of skeletal carbonate during early diagenesis. Pervasive recrystallization of micritic sediment infilling the inter-tube spaces, which in places becomes indistinguishable from the skeletal framework, points to extensive neomorphism processes. Tube cross-sections exhibit a dark outer layer, accompanied by shiny crystals growing into the lumen, indicating a secondary diagenetic origin, potentially linked to fluid circulation and mineral precipitation during burial.

6. Conclusions

The analysed build-up cropping out at Faro Santa Croce consists of aggregated serpulids stabilized by the early lithification of autochthonous micrite, with only minor contributions from coralline algae and bryozoan in its final phase.

The framework is composed exclusively of serpulid tubes assigned to the eurytopic genus *Spirobranchus*, whose species can be stress-tolerant and able to form aggregates and low diversity bioconstructions in marginal environmental settings worldwide.

The studied serpulid build-up likely developed in an intertidal-subtidal environment, within a succession that records progressive upward-shallowing and increasingly restricted water circulation, most likely related to the progressive restriction of the Mediterranean circulation during the Late Miocene. Such conditions may have led to instability in nutrient supply, salinity fluctuations, or a combination of these factors, supporting the interpretation of serpulid proliferation as a proxy for environmental stress within the basin.

Episodes of environmental instability are also suggested by layers with differently arranged tubes within the serpulid framework, possibly owing to slight variations in the hydrodynamic regime in the exposed coastal setting. Likewise, the erosional surface immediately below the serpulid build-up testifies a phase of subaerial exposure and relative sea-level fall resulting from the interplay between sea-level oscillations and local tectonic movements.

The distribution and textural organisation of the serpulid tubes, together with the different types of micrite, support a multi-phases history, in which successive generations of serpulids developed and produced cavities filled either by loose siliciclastic-rich detrital micrite, or by syndepositionally cemented autochthonous micrite. This alternating pattern reflects a pulsed sedimentary regime, where periods of reduced siliciclastic influx allowed microbial communities to thrive within the framework, driving the *in situ* carbonate precipitation that ultimately stabilized the reef architecture.

Credit authorship contribution statement

Rossana Sanfilippo: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Mara Cipriani:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Emanuela Di Martino:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Gemma Donato:** Writing – review & editing, Methodology, Investigation, Data curation. **Giuseppe Maruca:**

Writing – review & editing, Methodology, Formal analysis, Data curation. **Gianmarco Minniti:** Writing – review & editing, Methodology, Investigation, Data curation. **Antonietta Rosso:** Writing – review & editing, Validation, Investigation, Formal analysis, Data curation, Conceptualization. **Adriano Guido:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

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