

Commensal symbiosis between agglutinated polychaetes and sulfate-reducing bacteria

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ABSTRACT

Pendant bioconstructions occur within submerged caves in the Plemmirio Marine Protected Area in SE Sicily, Italy. These rigid structures, here termed biostalactites, were syngenerally lithified by clotted-peloidal microbial carbonate that has a high bacterial lipid biomarker content with abundant compounds derived from sulfate-reducing bacteria. The main framework builders are polychaete serpulid worms, mainly *Protula* with subordinate *Semivermilia* and *Josephella*. These polychaetes have lamellar and/or fibrillar wall structure. In contrast, small agglutinated terebellid tubes, which are a minor component of the biostalactites, are discontinuous and irregular with a peloidal micritic microfabric. The peloids, formed by bacterial sulfate reduction, appear to have been utilized by terebellids to construct tubes in an environment where other particulate sediment is scarce. We suggest that the bacteria obtained food from the worms in the form of fecal material and/or from the decaying tissue of surrounding organisms and that the worms obtained peloidal micrite with which to construct their tubes, either as grains and/or as tube encompassing biofilm. Peloidal worm tubes have rarely been reported in the recent but closely resemble examples in the geological record that extend back at least to the early Carboniferous. This suggests a long-lived commensal relationship between some polychaete worms and heterotrophic, especially sulfate-reducing, bacteria.

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INTRODUCTION

Serpulids can tolerate low-oxygen conditions (Sageman *et al.*, 1991) and can be the main constituent of build-ups affected by oxygen or salinity stress, as well as by eutrophic conditions, in both present-day (Fornós *et al.*, 1997) and ancient environments (Palma & Angeleri, 1992; Friebe, 1994; Cirilli *et al.*, 1999). Serpulids are locally dominant components of the macrobenthos in Holocene marine caves in the Mediterranean, usually as isolated to clustered individuals or forming thin-to-thick crusts (Harmelin, 1985; Zabala *et al.*, 1989; Bianchi & Sanfilippo, 2003; Bussotti *et al.*, 2006; Rosso *et al.*, 2013). Serpulid bioconstructions resembling stalactites in shape, in a submerged cave near Columbus Cay on the Belize Barrier Reef, were termed pseudostalactites (Macintyre & Videtich, 1979;

Macintyre, 1984). They consist of worm tubes together with peloidal 'cements' that strengthen the structure. Similar concretions in submarine caves at Capo d'Otranto in Apulia, Italy, were named biostalactites (Onorato *et al.*, 2003; Belmonte *et al.*, 2008). Somewhat similar concretions of coralline algae with peloidal and laminated micrite in cavities within Pleistocene bioherms in Greece, described as 'pendant coralline dripstones' (Kershaw & Guo, 2006; Kershaw *et al.*, 2007), can include serpulids (Kershaw *et al.*, 2005). A few examples of similar communities have been documented in the Mesozoic (Mišik & Aubrecht, 2004; Schlögl *et al.*, 2008). Preferential colonization of cryptic environments by serpulids has been suggested to possibly reflect photophobic behavior and/or a response to competition or predation (Reolid & Molina, 2010). In sea caves in Sicily, freshwater seeps occur (Leonardi, 1994;

Pitruzzello & Russo, 2008). Nutrient input from them might favor growth of the dense serpulid aggregates and associated suspension feeding organisms (bryozoans, corals, sponges and ascidians) that occur in the biostalactites (Guido *et al.*, 2012a, 2013c). The accumulation and decay of this biomass, together with continuous fecal production by these metazoans, is likely to have promoted low-oxygen microenvironments within the biostalactites, allowing anaerobic heterotrophic bacterial communities to thrive (Guido *et al.*, 2013c).

Here, we also recognize small agglutinated terebellid polychaetes as a minor component of Sicilian biostalactites. Until now, terebellids appear to have remained unrecorded in present-day submarine caves. We investigated their presence in these confined environments and their possible symbiotic relationship with heterotrophic bacteria.

The discontinuous fossil record of terebellids goes back at least to the Triassic (Campbell & Campbell, 1970). They are widespread in microbial carbonate crusts in cavities of Jurassic coral reefs at several localities in Europe, often associated with sponges, serpulids, bryozoans and foraminifers (Leinfelder *et al.*, 1993; Dupraz & Strasser, 1999; Olivier *et al.*, 2003; Reolid *et al.*, 2005; Olchowy, 2011). Also in the Jurassic, along the northern shelf of Western Tethys, a ‘*Tubiphytes*-*Terebella*’ facies developed in association with siliceous sponges in carbonate platform talus in deep-water low-energy environments (Brachert, 1986; Nose, 1995; Schlagintweit & Ebli, 1999; Schlagintweit & Gawlick, 2008), probably reflecting dysaerobic conditions (Leinfelder *et al.*, 1993). *Terebella* occurs commensally with lyssakine sponges in slope mud mounds and sponge-algal build-ups in Liassic carbonate platforms in Morocco (Neuweiler *et al.*, 2001), and terebellid worms are also recorded in *Halimeda* beds and slope environments from the Mediterranean Messinian (Brachert *et al.*, 2007).

At the present-day, terebellid worms occur worldwide in mostly shallow marine environments, particularly mudflats (Harman, 1969) and littoral substrates. They are common infaunal elements of sea-grass beds (Pérès, 1982) and also occur in tropical coral reef environments (João *et al.*, 2003), especially in sediments between coral colonies and in rubble, or in ‘spongiferous’ sandy bottoms near coral reefs (Walton-Smith, 1954; Pérès, 1982). In Mediterranean bathyal environments, mainly upper slope muddy substrates (Rowe, 1971; Pérès, 1982), they occur as dense populations and isolated individuals associated with deep-water corals (Mastrototaro *et al.*, 2010; Sanfilippo *et al.*, 2013).

Granchi submerged cave and its biostalactites

Biostalactites were sampled in the Granchi submarine cave (Fig. 1), in the Plemmirio Marine Protected Area of SE Sicily, on the eastern side of the Maddalena Peninsula, 8 km SSE of Syracuse. Bedrock in the area is mainly Middle Miocene and Pleistocene limestones that unconformably overlie Cretaceous volcanics (Grasso & Lentini, 1982). The caves developed in Miocene biocalcarenes and biocalcirudites of the Burdigalian–Serravallian Monti Climiti Formation that are commonly thick bedded, intensely faulted and karstified. They formed mostly in less resistant layers of these gently dipping limestones during Quaternary lowstands and were further enlarged by marine abrasion during Holocene sea-level rise. According to Dutton *et al.* (2009), the caves were completely flooded about 8000 years before the present. Granchi is a blind cave whose entrance is currently about 20 m below sea level on the steep rocky coastline (Leonardi, 1994). It extends nearly horizontally with a flat floor from an entrance resembling a twinned lancet window, 8 m wide and 2.5 m

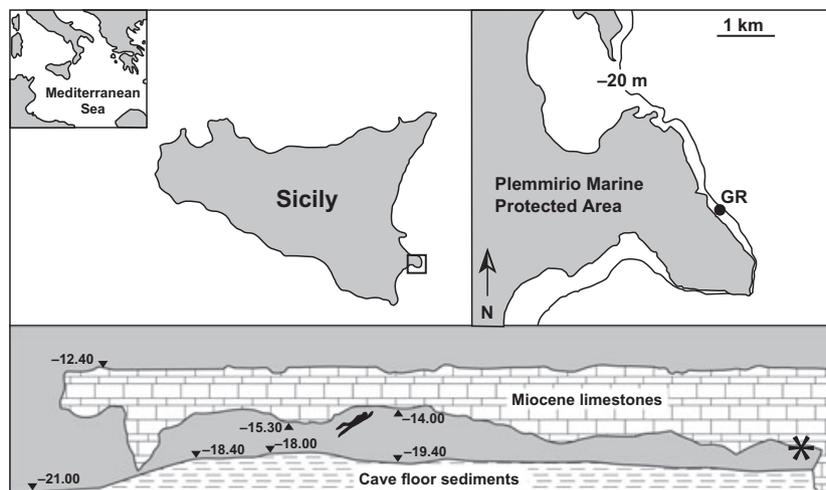


Fig. 1 Plemmirio Marine Protected Area, showing the location and longitudinal section of Granchi Cave (GR). Asterisk indicates location of the biostalactites described here (modified from Guido *et al.*, 2013c).

high. The cave is 53 m long and consists of three chambers. The ceiling is 3.5 m high in the first two chambers and 2.5 m high in the third chamber. Biogenic crusts are formed by a diverse, largely skeletal, fauna dominated by sponges, serpulids and bryozoans, with occasional scleractinian corals (Pitruzzello & Russo, 2008; Rosso *et al.*, 2012). Nodular to pillar-like biostalactites project obliquely from the walls and perpendicularly from the roof toward the cave floor. They range from a few to 20 cm in length and up to 10 cm in diameter. They are scattered and scarce near the cave entrance and become more abundant, larger and closely spaced toward the interior. Guido *et al.* (2012a, 2013c) described their morphological characteristics and biotic nature, as well as the importance of microbial micrite in building and strengthening these structures.

Study material

We examined a biostalactite, named GR5v, collected in September 2009 from the ceiling in the innermost cave recess about 53 m from the entrance (Fig. 1). It is 11 cm long and subcylindrical with a diameter of about 6 cm (Fig. 2). It grew downward and has surface digitations that are cylindrical, flabelliform, crest-shaped and separated by furrows up to 2–3 cm deep. The surface is largely coated by manganese- and iron-oxy-hydroxides and colonized by encrusting organisms.



Fig. 2 Longitudinal section showing the porous structure of a Granchi biostalactite. Note the polychaete tubes surrounded by autochthonous micrite.

Serpulids, including *Protula tubularia*, *Semivermilia crenata* and *Josephella marenzelleri*, are abundant and particularly common on prominent protuberances where the living worms are associated with whitish tubes of dead specimens. The dominant species, *Semivermilia crenata* and the microserpulid *Josephella marenzelleri*, build their tubes via controlled biomineralization with well-ordered microstructures (see Fig. 3). Small agglutinated tubes, attributed to terebellids, also occur and are closely associated with the microbial clotted-peloidal micrite. The walls of these polychaetes are made of peloidal micrite that

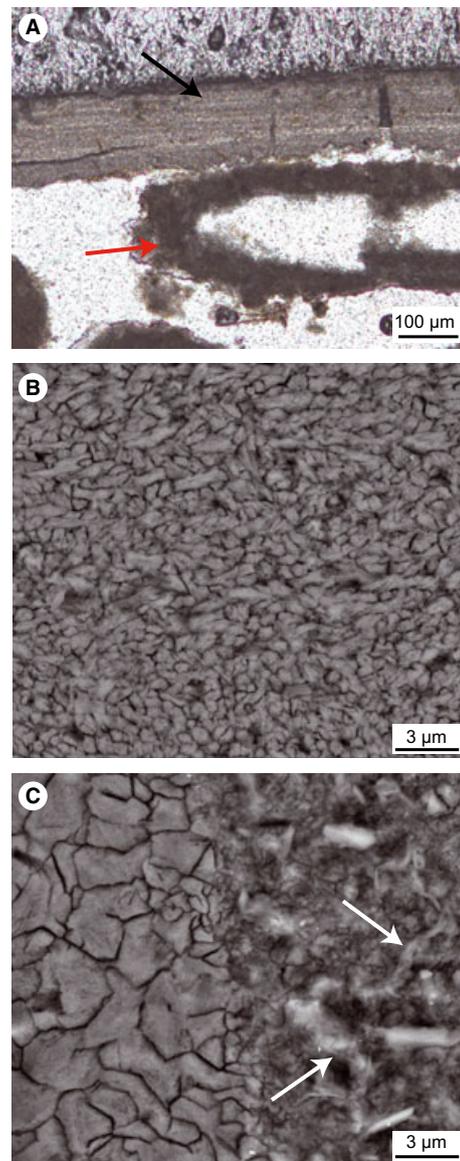


Fig. 3 (A) Serpulid (black arrow) and terebellid (red arrow) skeletons. (B) Magnification of serpulid skeleton (*Protula tubularia*) showing the organization of the biocontrolled small calcite crystals. (C) Detail of the boundary between microsparite (left) and the terebellid skeleton (right). Note the very small grains agglutinated by mucoprotein substances (white arrow).

closely resembles peloids in the surrounding matrix (see Fig. 3). Bryozoans such as *Onychocella marioni*, *Puellina* (*Glabrilaria*) *pedunculata*, *Annectocyma indistinta* and *Crisia pyrula* are subordinate components. Sponges and hydrozoans also occur; bivalves and brachiopods are rare.

METHODS

Micro- and nano-fabrics of the carbonates were characterized by optical and scanning electron microscopy (SEM) on uncovered and weak-acid etched thin-sections (48 × 28 mm). Uncovered thin-sections were examined by fluorescence to reveal the organic matter distribution. Residual organic matters together with Mn²⁺ are significant activators of fluorescence in calcite and dolomite and organically activated luminescence appears to be caused mainly by aromatic and conjugated organic molecules (Dravis & Yurewicz, 1985; Machel *et al.*, 1991; Neuweiler & Reitner, 1995; Russo *et al.*, 1997; Guido *et al.*, 2011, 2012b, 2013a,b; Mastandrea *et al.*, 2011; Tosti *et al.*, 2011). Fluorescence was induced by a Hg vapor lamp linked to an Axioplan II imaging microscope (Zeiss)

equipped with high-performance wide bandpass filters (BP 436/10 nm/LP 470 nm for green light; BP 450–490 nm/LP 520 nm for yellow light).

Chemical composition was determined using a Genesis 4000 energy-dispersive X-ray spectrometer linked to a FEI-Philips ESEM-FEG Quanta 200F SEM. The samples analyzed were polished with 0.25- μ m diamond-impregnated surfaces, then etched and carbon coated (about 250 Å). Working conditions and detector constants were as follows: voltage 15 kV, tilt angle 0°, take-off angle 36.01°. To confirm the reliability of the data collected from thin-sections, the same observations were also performed on freshly broken surfaces.

RESULTS

Optical microscopy and UV epifluorescence

The biostalactite (Fig. 2) is mainly composed of serpulid tubes. Subordinate small agglutinated terebellid tubes composed of peloidal micrite have an average diameter of 250 μ m (Fig. 4). They are nearly similar in size to *Josephella*

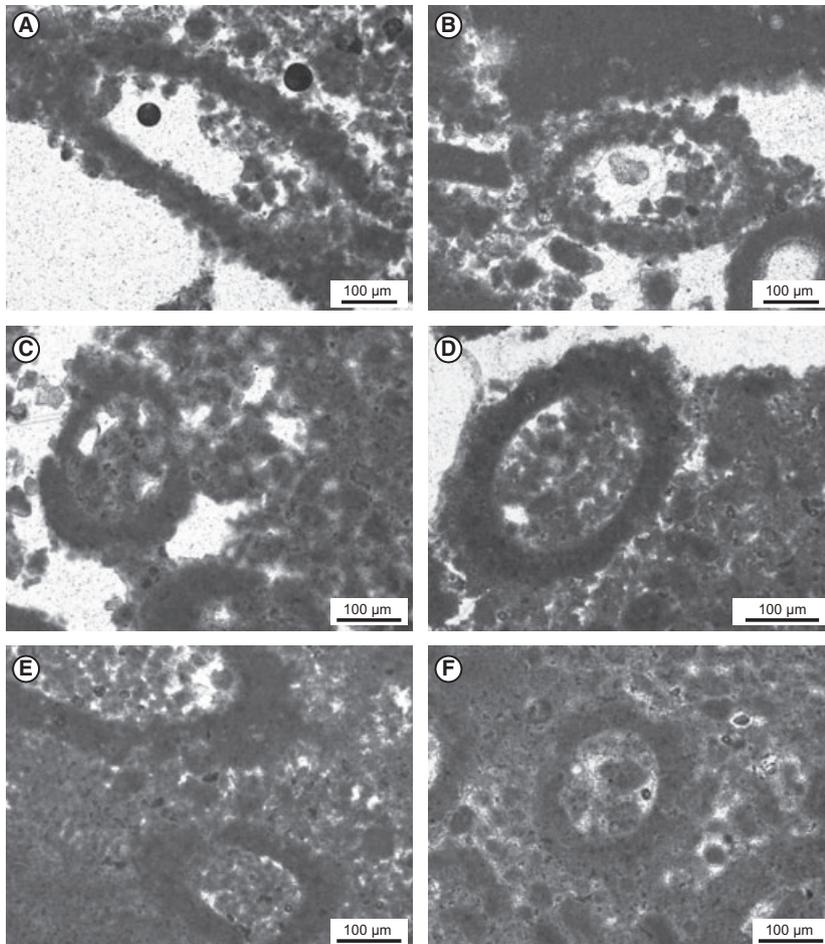


Fig. 4 Micritic agglutinated terebellid tubes that variously appear either peloidal (A–B) or dense and homogeneous (C–F).

marenzelleri, but differ in being agglutinated and dark in appearance. Their compact to flocculent walls are locally peloidal (Fig. 4A–B), but can also be densely micritic (Fig. 4C–D), and commonly contain small clasts and foraminifer tests, plus rare siliciclastic grains. No living specimens have been observed and the tubes are empty or partly filled by either clotted-peloidal micrite or, less commonly, detrital micrite. Both the peloidal to clotted-peloidal micrite matrix and the micritic terebellid skeletons show bright fluorescence under UV light, indicating a higher organic matter content than the associated allochthonous micrite and calcite spar (Fig. 5).

Spaces between the skeletons are filled by clotted and peloidal micrite with micritic aggregates 15–150 μm in diameter that form clotted masses frequently rimmed by small euhedral Mg-calcite crystals. Less commonly, coalesced clots form more uniform compact texture (Fig. 4) in which individual clots are difficult to recognize.

Electron microscopy

High content of organic matter disturbs the secondary electron signal under the SEM, creating a fuzzy image that makes it difficult to accurately estimate the morphology and size of the calcite crystals. We therefore used backscattered electron images that, at lower resolution, give sharper pictures that also reflect the chemical composition of the sample. The peloidal, clotted peloidal, and micritic tubes are all composed of 1–4 μm CaCO_3 crystals (Fig. 6). Coalesced peloids form the tube walls and patchily fill areas between the tubes (Fig. 6). Clay minerals are present in both the micritic tubes and in the clotted-peloidal micrite between the tubes, but are absent from the peloidal micrite inside the tubes (Fig. 7). Energy-dispersive X-ray analyses confirm the similarity of the micrite of the peloids and the micritic tubes. Elemental composition data show differences between the peloidal micrite external to the tubes and that inside them (Table 1). The values for the peloidal micrite external to the tubes are: calcium (Ca) 79.2–83.5 wt%, magnesium (Mg) 10.2–10.7 wt%, silicon (Si) 3.3–6.4 wt%, aluminum (Al) 1.7–3.5 wt%, and sulfur (S) 0.6–0.7 wt%. The values for the peloidal micrite within the tubes are as follows: Ca 87.5–88.0 wt%, Mg 10.6–11.2 wt%

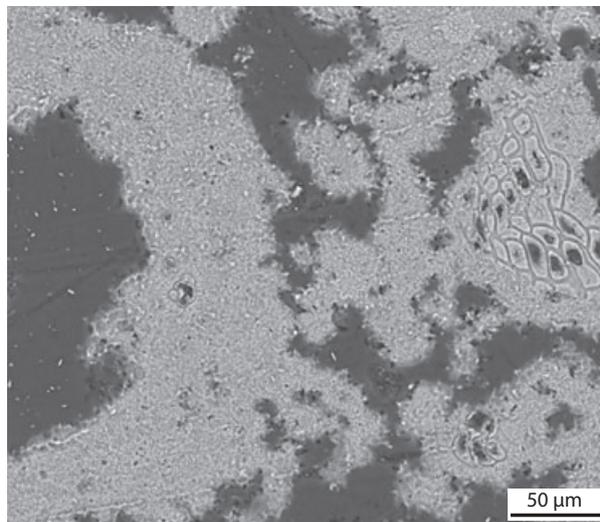


Fig. 6 Backscattered SEM image of a polished thin-section showing randomly arranged calcite crystallites forming both the clotted-peloidal micrite and the terebellid tubes. Note the agglutinated nature of the tube revealed by the presence of incorporated microforaminifer tests and other small inclusions.

, S 0.7–0.9 wt%, with Al and Si being present only as traces. Values for the micritic tubes are the following: Ca 73.4–79.7 wt%, Mg 9.6–10.1 wt%, Si 6.0–9.7 wt%, Al 3.5–5.2 wt%, and S 0.7 wt% to 0.9 wt%. Iron (Fe) is absent from the peloidal micrite within the tubes and is only present patchily and in small amounts in the external areas and in the tube walls.

DISCUSSION

Biostalactites in marine caves from Sicily are the result of the interaction between skeletal metazoans and microbial activity (Guido *et al.*, 2012a, 2013c). Their distinctive vertical or oblique downward growth from the roof and walls of the caves reflects syndepositional encrustation of the metazoan skeletal framework by autochthonous, microbially induced micrite (Guido *et al.*, 2013c). The agglutinated polychaetes assigned to terebellids are minor components of these biostalactites but are significant for their tube microstructure and ecology.

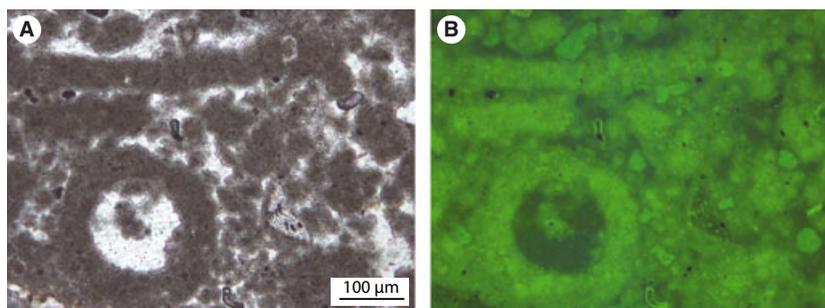


Fig. 5 Transmitted light (left) and epifluorescence (right) images of the clotted-peloidal micrite and agglutinated tubes. The intense fluorescence indicates high organic matter content.

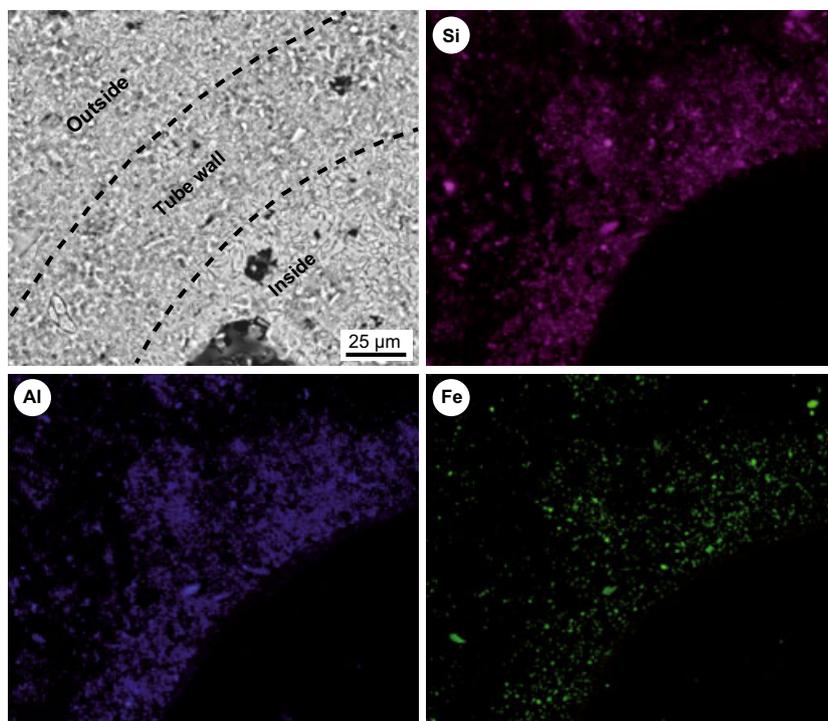


Fig. 7 Map of the main siliciclastic elements in the terebellid agglutinated walls, where they are relatively common, and in the clotted-peloidal micrite outside the tubes.

Table 1 Elemental weight percentage based on EDX spectroscopy

Elements	Peloidal micrite outside the tubes				Terebellid tube walls				Peloidal micrite inside the tubes			
	Area 1	Area 2	Area 3	Area 4	Area 1	Area 2	Area 3	Area 4	Area 1	Area 2	Area 3	Area 4
Ca	82.06	81.47	79.21	83.51	73.41	79.75	77.14	74.81	87.98	87.54	88.03	87.67
Mg	10.75	10.58	10.23	10.61	9.69	9.84	10.08	9.63	10.89	11.17	10.63	10.69
Si	3.32	4.62	6.38	3.44	8.79	5.97	7.22	9.66	0.21	0.18	0.45	0.55
Al	1.89	2.63	3.49	1.71	4.71	3.55	4.79	5.2	0	0.2	0	0.35
Fe	1.33	0	0	0	2.58	0	0	0	0	0	0	0
S	0.65	0.7	0.69	0.73	0.82	0.89	0.77	0.7	0.92	0.91	0.89	0.74

Terebellid-clotted-peloidal micrite association

In contrast to serpulids, terebellids build tubes by agglutinating and cementing sediment particles together (Posey *et al.*, 1984; Grémare, 1988; Vovelle & Grasset, 1990; Stewart *et al.*, 2004; Fournier *et al.*, 2010). Žitň & Vodrážka (2013) described Cretaceous phosphatic crusts with terebellid tubes made of agglutinated phosphatic particles, mostly fecal pellets. Many authors have reported fossil terebellids associated with clotted-peloidal micrite fabrics (Dupraz & Strasser, 1999; Olivier *et al.*, 2003, 2006; Reolid, 2007; Schlagintweit & Gawlick, 2008; Bucur *et al.*, 2010). Webb (2005) described massive peloidal fabrics with terebellid tubes in Early Mississippian microbial reefs in Australia. Olivier *et al.* (2003) recognized peloidal thrombolitic crusts associated with *Terebella* as well as corals, bivalves, and bioclasts, in upper Jurassic reefs in western France. Although the micritic nature of the terebellid tubes is evident in these

examples, their origin and relationship with the associated microbial clotted micrite do not appear to have been discussed.

Fischer *et al.* (2000), studying mineralization in the cirratulids *Diplochaetetes* and *Dodecaceria*, recognized a phase of microbial induced precipitation. The tubes are composed of micritic peloidal lamellae with a concentric pattern showing stromatolitic fabric alternating with fibrous calcite/aragonite lenses and peloids. Fischer *et al.* (2000) suggested that two processes were involved in the tube formation. In the first, the worm produces an acidic organic mucus that temporarily inhibits mineralization and then binds Ca^{2+} , producing the controlled lamellar stromatolitic fabric. The second process is not controlled by the worm itself and takes place within the spaces between the primary lamellae, where non-specific exopolymeric substance (EPS)-rich mucus is abundant. In this phase, the formation of fibrous aragonitic crystals

and peloidal micrite fabric suggest the involvement of bacteria in the mineralization processes.

The role of microbial mediation in the formation of peloidal/clotted-peloidal microfabric has long been suggested (Monty, 1976; Chafetz, 1986; Buczynski & Chafetz, 1991; Reitner, 1993; Pratt, 1995; Reitner & Neuweiler, 1995; Kazmierczak *et al.*, 1996; Folk & Chafetz, 2000; Riding, 2000; Riding & Tomás, 2006; Guido *et al.*, 2007, 2012c; Vescogni *et al.*, 2008, 2011) and is confirmed in the Granchi biostalactite by the presence of biomarkers for sulfate reducing bacteria (Guido *et al.*, 2012a, 2013c). The organic matter composition in the biostalactite is remarkably similar to that in post-glacial reefal microbialites which also are peloidal (Heindel *et al.*, 2010, 2012; Guido *et al.*, 2013c).

Increase in alkalinity induced by microbial metabolism, including degradation of EPS by heterotrophic bacteria, can promote autochthonous micrite precipitation (Reitner, 1993; Trichet & Défarge, 1995; Reid *et al.*, 2000, 2003; Reitner *et al.*, 2000; Dupraz *et al.*, 2004; Decho *et al.*, 2005; Dupraz & Visscher, 2005; Hendry *et al.*, 2006), and this process may be linked to the calcium-binding capacity of EPS (Dupraz *et al.*, 2004, 2009; Braissant *et al.*, 2007, 2009; Heindel *et al.*, 2010).

We propose that sulfate-reducing bacteria, occupying suboxic/anoxic microenvironments of the skeletal framework of the biostalactites in the Granchi cave, promoted the formation of peloidal micrite in close association with the terebellids. This is similar to the suggestion by Dupraz & Strasser (1999) that association of terebellids and *Shamovella* (*Tubiphytes*) in Oxfordian shallow coral bioherms in the Swiss Jura Mountains indicates dysoxic/anoxic conditions.

Commensal symbiosis between terebellids and sulfate-reducing bacteria in the Granchi cave

Terebellids have not previously been reported from biostalactites. Agglutinated polychaetes are unexpected in this situation because pendant accretion within sea caves seems likely to limit the availability of the sediment grains necessary to form their skeletons (Fauchald & Jumars, 1979; Rouse & Pleijel, 2001). Terebellids are highly adapted surface deposit feeders, mostly living in burrows inside the sediment or attached to shelly material (Rouse & Pleijel, 2001), or in crevices of hard bottoms (Hutchings, 2000). Terebellid tentacles produce mucus that incorporates particles extracted from the surrounding sediment. These particles include sand and silt grains, shell fragments, sponge spicules, and even sea-grass roots. Tubes of the various species are delicate and vary in mucus production, as well as in the nature, size and shape of the particles (Grémare, 1988).

The Granchi micritic agglutinated worm tubes (Fig. 6) consist of peloidal micrite and locally exhibit irregular lumpy external surfaces that appear to be produced by the agglutination of micritic clots (Fig. 3). The micrite in both the tube walls and between the tubes has a similar homogeneous composition, consisting of high-magnesian calcite with minor amounts of siliciclastic material (Fig. 7). During the formation of the micritic clots *via* bacterial sulfate reduction, it appears that clay mineral particles were incorporated within the calcite crystals. In contrast, the peloids that were mineralized inside the tubes consist of magnesian calcite, presumably because this microenvironment where mineralization occurred was isolated from external sources (Fig. 7).

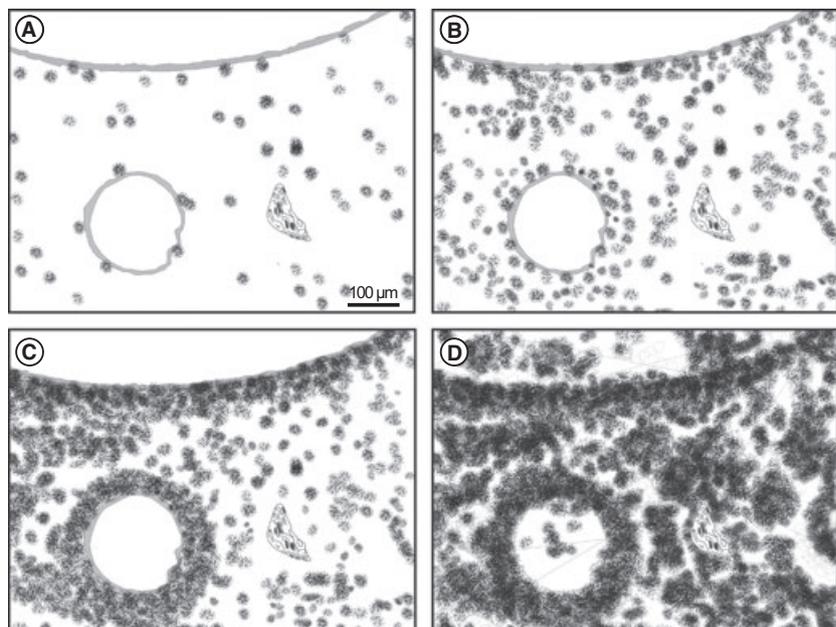


Fig. 8 Schematic representation of the evolution of the clotted-peloidal fabric and development of the agglutinated worm-tube wall. (A) Initial microbial peloid deposition; note the inferred terebellid mucoprotein tubes. (B) Inception of peloid agglutination in the tube walls. (C) Late stage of tube development. (D) Very early diagenetic phase following death of the worm. Note deposition of microbial peloids inside the tube cavities and the encrustation of small grains such as microforaminifer tests. Based on Fig. 5.

The similarities in composition and micro-nanomorphology between the agglutinated worm-tube walls and the intimately associated autochthonous microbially induced micrite suggest a commensal relationship between terebellids and sulfate-reducing bacteria (Fig. 8) in which terebellids utilized microbially induced peloids to form their tubes and the sulfate-reducing bacteria thrived on the biomass derived from the terebellids and other associated metazoans. In this way, bacterial peloids provided particles that could be agglutinated by the terebellids, allowing them to survive and build tubes in an environment where the availability of siliciclastic and/or skeletal particles was very limited (Fig. 8). It is likely that these terebellids used their mucus-rich tentacles to capture the micritic grains and fix them to their mucoproteic tubes.

It is also possible, but perhaps less likely, that the bacterial mat that developed on the tube walls induced peloid mineralization directly on the worms' surfaces. We addressed this question by comparing our terebellid specimens with the cirratulid tubes studied by Fischer *et al.* (2000). In both cases, the tubes are characterized by an uncontrolled mineralization phase. The main difference between mineralization in terebellids and cirratulids lies in the site of precipitation and the micromorphology of the mineralization products. Cirratulid tubes are composed of stromatolitic lamellae (controlled phase) and interlaminar fibrous cements and sparse peloids (induced phase), whereas terebellid tubes consist only of more or less clotted peloids.

In our case study, the precipitation of peloids that are subspherical in shape and are widespread throughout the bioconstruction, even in cavities and in areas without terebellids, is not consistent with mineralization that is linked to organic templates. The post-mortem filling of terebellid tubes by peloidal micrite is, however, consistent with this interpretation and suggests that peloid mineralization occurs independently of the terebellid organic envelopes. Moreover, the presence of foraminifer tests and other fine skeletal grains in the walls indicates phases of agglutination processes during growth (Fig. 8).

CONCLUSIONS

Agglutinated polychaetes, attributed to terebellids, are reported here for the first time in distinctive bioconstructions that grow downward from the walls and ceilings of a submerged Mediterranean cave. The tubes are micritic and occur in close association with microbial clotted-peloidal micrite. We infer that the bacteria obtained nutrients for growth from decaying metazoan organic matter and fecal material, and that the worms utilized microbially induced peloids to form their skeletons. This direct link between sulfate-reducing bacteria and agglutinated polychaetes suggests a novel symbiotic relationship between invertebrates and bacteria.

This commensal symbiosis may not be restricted to grain-poor environments but, as suggested by the widespread occurrence of *Terebella*-like tubes in the geological record, might be a favored mechanism of tube construction, considering the close physical and ecological relationship of worms and sulfate-reducing bacteria in these bioconstructions.

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