Hanging coral gardens of a Tyrrhenian submarine cave from Sicily (Italy)

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ABSTRACT - An exceptionally well-preserved cave palaeocommunity is described from the Capo Milazzo Peninsula (NE Sicily). The Fulco Cave formed within a layer of breccia including metamorphic and Miocene limestone blocks together with rare clasts of isidid-bearing lithified bathyal sediments. This new breccia type points to a still undescribed deposition event in the early Pleistocene. The fossil association inside the cave is relatively diversified and dominated by the dendrophyllid coral Astroides calcycularis *whose colonies encrusted the cavity ceiling and grew in an upside-down position, forming spectacular "hanging gardens". The warm climate affinity of* Astroides *indicates that colonisation took place during an interglacial period, possibly during the Tyrrhenian. The palaeocommunity indicates a semi-dark cave open toward the sea in a shallow water setting. The elongation of* Astroides *corallites was possibly driven by a low level of water motion and/or competition for space and food. The common constrictions point to slow or no growth phases possibly related to environmental fluctuations, periodically leading to mass mortality events.*

RIASSUNTO - [Giardini di coralli pendenti in una grotta sottomarina di età tirreniana della Sicilia (Italia)] - La Grotta Fulco si trova in un livello di brecce che includono blocchi metamorfici e di calcari miocenici oltre a rari clasti di sedimenti batiali litificati contenenti internodi di isididi. Per la natura dei clasti costituenti, questo nuovo tipo di breccia testimonierebbe un evento deposizionale non ancora descritto nell'area, avvenuto all'inizio del Pleistocene inferiore. L'associazione fossile all'interno della grotta è relativamente diversificata ma dominata dal corallo dendrofillide Astroides calcycularis *le cui colonie incrostarono la volta della grotta accrescendosi dall'alto verso il basso e formando spettacolari giardini sospesi. Considerata l'affinità calda di* Astroides*, la colonizzazione avvenne durante una fase interglaciale e, presumibilmente, durante il Tirreniano. La paleocomunità nel suo insieme indica una grotta con condizioni di semi-oscurità, ma aperta e situata a debole profondità. L'allungamento dei coralliti di* Astroides *è stato probabilmente causato da un idrodinamismo relativamente basso e/o da una possibile competizione per lo spazio e per il nutrimento. Le comuni strozzature presenti lungo i coralliti indicherebbero stasi più o meno prolungate nella crescita correlate a possibili fluttuazioni ambientali, con alcuni eventi di maggiore entità che potevano causare periodiche mortalità di massa.*

INTRODUCTION

Present-day submarine caves and their biota have received special attention in the last decades because they provide an excellent opportunity to study community structure and zonation on a relatively small spatial scale. Moreover, caves permit to investigate colonisation successions over millennial scales and deep-water conditions at shallow depths (e.g., Zibrowius, 1971; Harmelin et al., 1985; Bianchi & Morri, 1994; Harmelin, 2000; Denitto et al., 2007; Rosso et al., 2013a). More recently, studies have also focused on the biodiversity of these peculiar habitats for conservation purposes (e.g., MSFD, 2008; Gerovasileiou et al., 2015).

Nevertheless, little is presently known about species diversity and community structure of Pleistocene submarine cave communities (Rosso et al., 2015). Information mostly relates to the mere presence of cave biota, which are employed to reconstruct the uplift history of the regions where the caves open (Zibrowius, 1995; Morhange et al., 1999; Rosso et al., 2015 for a review), with the only exception of Barrier et al. (1989) describing the cavity fossil community of a palaeocliff. Rosso et al. (2015) demonstrated that exceptional and diverse submarine cave communities existed in the

Pleistocene of the Central Mediterranean. A first effort to make palaeontologists aware of this topic has been the organisation of the international meeting on cave habitats: "Cave environments: present and past, 2015" held in Custonaci (Trapani) in May 2015. This event highlighted the existence of further fossil submarine caves hosting hard-surface sessile palaeocommunities of particular interest for their peculiarity and because they document complex colonisation histories (Guido et al., 2016; M. Steinthorsdottir & E. Håkansson, pers. comm.; RS, AR and Laura Bonfiglio, pers. obs.). Here we record an upper Pleistocene assemblage encrusting the ceiling of a shallow-water cave, recently discovered in the Milazzo Peninsula (North-Eastern Sicily) and brought to our attention by the amateur palaeontologist Carmelo Fulco, after whom the cave is named.

The fossil community of the cave consists of very dense hanging colonies with exceptionally elongated corallites of *Astroides calcycularis* (Pallas, 1766), a scleractinian coral widely recorded from present-day submarine overhangs and caves, and as a component of fossil cave communities (Zibrowius, 1978, 1995; Morhange et al., 1999).

The aims of this work are to: 1) describe the cave and its location; 2) describe the hanging bioconstruction

formed by the fossil community of the cave; 3) provide some information about the cave-encasing rock; 4) discuss the particular morphology of the corals in the frame of the palaeo-habitat reconstruction; 5) infer the colonisation history of the cave.

MATERIAL AND METHODS

In order to preserve the Fulco Cave outcrop as much as possible, careful observation was made in the field and through photographic documentation. Large pieces of encrusting material, already detached from the ceiling of the cave and fallen down on the soil presently infilling the cavity, were collected for closer inspection. The uppermost 2-3 cm of sediment were scraped from the available surface to retrieve small fragments of the organogenous crust. The collected material was routinely washed using a 63 μm mesh to retain microfossils in the Palaeoecological Laboratory of the University of Catania.

Taxonomic identification was made on this collected material using a Zeiss V8 stereomicroscope. Selected fragments and specimens were examined through Scanning Electron Microscopy (SEM) using a Tescan VEGA 2 equipped with a medium-sized low vacuum chamber at the Microscopy Laboratory of the University of Catania. Images were produced using back-scattered electrons of cleaned uncoated specimens. Material is housed in the Palaeontological Museum of the University of Catania, under the collective code PMC. Fulco Cave Collection, Tyrrhenian.

GEOLOGICAL SETTING

The Fulco Cave is located in the north-western sector of the Capo Milazzo Peninsula, in an area referred to as "Contrada Paradiso", at 53 m above the present-day sea level, along the trench of the road running roughly parallel to the coast (Figs 1-2).

In the Capo Milazzo Peninsula, the erosional surface on the Palaeozoic metamorphic basement constitutes the substrate for Tortonian to lower Messinian carbonates formed in shallow-water settings and including *Porites*-dominated coral reefs (Fois, 1990a, b; Lentini et al., 2000). Poorly cemented limestone follows, which was deposited in small topographic depressions during the Pliocene-early Pleistocene interval, starting after the reflooding of the Mediterranean Sea, and whose rich fossil content points to bathyal palaeoenvironments (e.g., Gaetani & Saccà, 1984; Violanti, 1988; Fois, 1990a, b; Rosso, 2005; Sciuto, 2012; Rosso & Di Martino, 2015). These deposits are transgressively overlain by shallow-water sandstone and cobblestone of Tyrrhenian age, and subsequent volcanic ashes emplaced after eruptions from the Aeolian Arc. Ashes even previous topographic roughness and crop out widely in the Capo Milazzo Peninsula. Holocene sediments, including rock debris and emerged beaches, are present mostly along the coast (Fig. 1c). A general uplift raising the Tyrrhenian terrace at an elevation of 50-85 m above the present-day sea level and to the emersion at about 4 m of Holocene tidal notches and
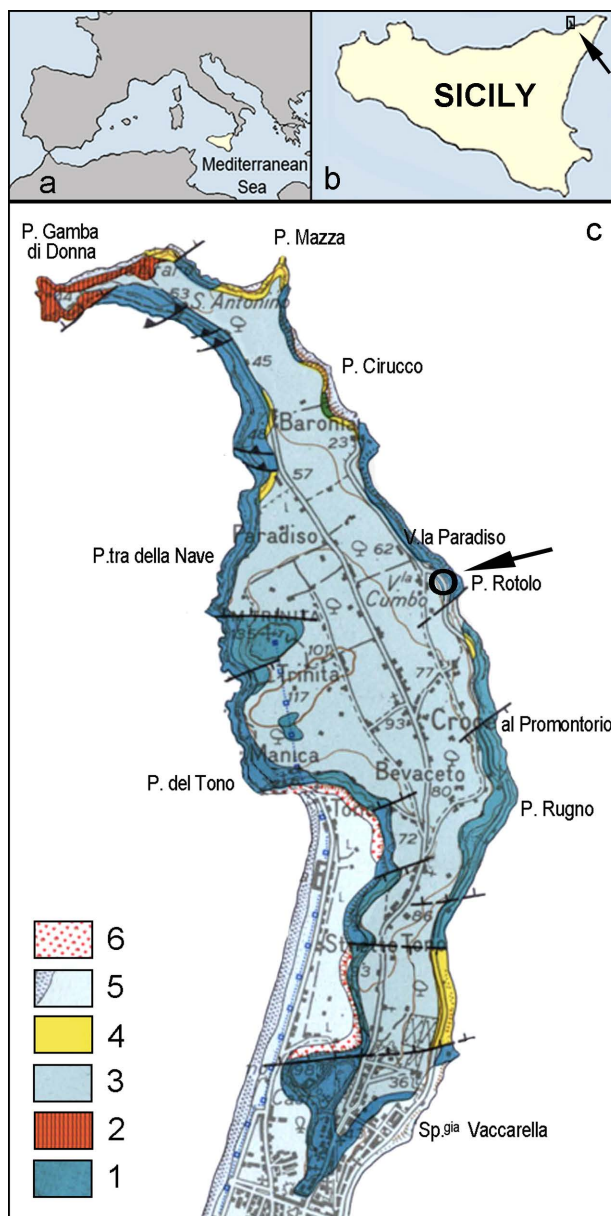

Fig. 1 - (Color online) Location of the study cave in: a) the Central Mediterranean. b) The north-eastern corner of Sicily. c) The north-eastern side of the Capo Milazzo Peninsula (redrawn and adapted from Lentini et al., 2000). 1: metamorphic basement; 2: upper Miocene shallow-water and reefal carbonates; 3: Plio-Pleistocene bathyal sediments; 4: upper Pleistocene volcanic ashes and discontinuous underlying sandy-to-gravelly coastal deposits; 5: Recent and present-day alluvial sediments and beaches; 6: present-day rock-debris.

coastal encrustations, has been demonstrated by several studies (Rust & Kershaw, 2000; Gringeri et al., 2004; Antonioli et al., 2006).

RESULTS

The cave can be observed in a layer of coarse clast-supported breccia (Fig. 2). Locally, the breccia directly lays upon the metamorphic basement, which discontinuously crops out at different heights along the base of the road trench. The breccia's thickness is difficult

Fig. 2 - (Color online) The Fulco Cave along the road trench. a) General appearance showing the development of the nearly 10 m long and 2 m high cave; scale bar corresponds to 1 m. b) Detail of the exposed eastern termination (left frame in a) of the cave with ceiling formed by large angular blocks encrusted by corals, sometimes also along their vertical surfaces corresponding to original crevices; scale bar corresponds to 20 cm. c) The exposed western termination (right frame in a) showing polygenic rounded blocks irregularly piled-up to form the ceiling; scale bar corresponds to 10 cm. d) Close-up of the frame in c, showing the ceiling of the cave heavily coated by a thick organogenous crust, largely consisting of *Astroides calycularis* (Pallas, 1766) corallites. The arrow points to a *Gastrochaenolites* trace; scale bar corresponds to 20 cm. e) Detail of the arrowed sector in c, with a succession of at least three superimposed layers of elongated downward-facing corallites. Further organisms are visible, including the boring bivalve *Lithophaga* (short white arrow), the encrusting bivalve *Chama* (short black arrow) and serpulids (long white arrow); scale bar corresponds to 10 cm. f) Corals hanging from the isidid-rich wackestone block, indicated by an arrow in c. A *Gastrochaenolites* borehole is arrowed; scale bar corresponds to 10 cm.

to measure because of the cover of soil and detritus, but it probably does not exceed 2-3 m.

This deposit is mostly formed by large polymictic elements, including boulders large up to 70 cm, made up of metamorphic basement, Miocene reef limestone,

Pleistocene wackestone as well as blocks of cemented polymictic breccia composed of cm- to dm-sized clasts. Some wackestone boulders are rich in internodes of octocoral isidids (Fig. 2c, f) and because of their lithology and fossil content are comparable to lower Pleistocene

deep-water deposits cropping out some hundreds of metres north of Contrada Paradiso. Matrix infilling has been locally observed, formed of light-coloured silt-sized carbonate sediment, but most spaces between blocks are empty or filled by soil.

Only the ceiling of the cave can be examined, extending for about 10 m in length; it is not fully exposed in its mid part (Fig. 2a). The cavity is almost entirely filled of Tyrrhenian polygenic marine conglomerates, which are widespread along the peninsula, and of a large amount of present-day soil, whose presence hampers detailed observation. The height of the cave varies and could not be measured due unfavourable exposure, however a maximum height of 2 m can be roughly estimated.

The cave ceiling is irregular and formed of stacked polymictic boulders covered by a coral-dominated carbonate crust (Fig. 2b-f). The crust is better developed and exposed in the western side of the cave where it is more than 30 cm thick (Fig. 2d-f) but becomes discontinuous and thinner towards the eastern termination of the cave (Fig. 2b). Thin encrustations can be locally observed also on some blocks from the cave ceiling, along subvertical surfaces for up to 30 cm, pointing to the occurrence of possible large crevices in the original cave's roof (Fig. 2b). This biogenic carbonate layer is a bioconstruction almost entirely built up by the scleractinian coral *Astroides calycularis* (Fig. 3). The coral grew downwards, forming densely-packed phaceloid colonies characterised by very elongate (up to 8 cm), cylindrical and subparallel corallites (Figs 2d-f; 3a, d-e). The corallites are generally interconnected in their basal part through little developed coenosteum (Fig. 3a), but are separate and spaced up to 4 mm apart for most of their length (Fig. 3a-b, d-e). However, anastomosis is frequent and long corallites may fuse their walls even in the distal part of the colony (Fig. 3b, f). Subordinately to elongate phaceloid forms, plocoid colonial portions with stout corallites, up to 1.5 cm in height (Fig. 3f), immersed in the coenosteum, occur, without any apparent distribution pattern. The corallite calices of both phaceloid and plocoid growth forms are typically circular and less than 1 cm in diameter, commonly ranging between 0.7 to 0.9 cm in adult specimens. In the largest corallites septa are regularly arranged in four cycles and do not show any Pourtalés Plan (Fig. 3b) that is instead visible in transversally broken large corallite portions or in calices of smaller corallites. Septa cycles S1 and S2 are commonly indistinguishable, S3 are slightly narrower (> 2/3 of S1-2), though commonly reaching the spongy columella, whereas S4 are much smaller and not exceeding 1/3 of S1-2 width. Well-preserved septa show coarse granulations and concave distal edges (Fig. 3b); horizontal plates are common. The spongy and free-standing columella is typically about 1/3 of the calice in diameter (Fig. 3b) and extends in height up to 2-3 mm from the calicular edge. The outer wall of the corallites is variable even within the same colony. It can be mostly coarsely granulated along longitudinal hispid costae (Fig. 3c) or epithecate with marked transversal corrugations. In the latter case corallites may show constrictions corresponding to growth stases (Fig. 3a, d). Very often initial corallite stages, up to 2 mm high, are found within the calice of other corallites (Fig. 3a-b). In some cases these corallites grow merging their basal walls with corallites that served as substrate. Due to the similar diameter between the two subsequent corallites, they may appear as a single, very long individual (Fig. 3a, d). As typical in *A. calycularis,* budding is extracalicular. Interestingly, newly budded corallites may show peculiar "ceratoid" shapes, probably due to overcrusting of unpreserved soft organisms (e.g., sponges?) (Fig. 3e). The preservation state is variable and mostly related to the differential exposure of the corallites to subaerial degradation. Submarine degradation is common and there are diverse borings (not studied in detail in the present paper), locally pervasive on corals and on other bioclastic remains as well as on some exposed boulders forming the cave ceiling. Locally, mostly in the southern part of the cave, calices and interspaces between corallites of *A. calycularis* are filled with lithified fine sediment. Coral skeletons may be heavily recrystallised.

As a whole, the coral crust thickness appears to reflect a step-like superimposition of subsequent colonies. Although several constrictions can be observed along the walls of single or connected corallites, three main coral growth phases separated by intervening stases can be inferred from the discontinuity surfaces observed in the outcrop (Fig. 2e). These surfaces correspond to preferential breakage surfaces, as in the case of a detached block (about 3x2x1 dm large) collected for the present study.

Other sessile invertebrates occur only subordinately (Figs 2e-f, 4). Few cemented valves of the large-sized bivalve *Spondylus gaederopus* Linnaeus, 1758, slightly exceeding 10 cm in length, have been observed encrusting clusters of corallites that appear truncated nearly at the same height. The lamellar expansions forming the typical ornamentation of this bivalve, which are usually not particularly prominent on the encrusting valve, are conspicuous in these specimens, pervading the free spaces in between corallites, often for 1-2 cm (Fig. 4i-j). The internal surfaces of these valves are the substrate for new hanging coral colonies as well as for low young corallites which occur also on the external surfaces. These valves show bioerosion traces produced mostly by clionaid sponges and by further unidentified borers. *Gastrochaenolites japonicum* Hatai et al., 1974 (= *G. torpedo* Kelly & Bromley, 1984) borings are common within the coral bioconstruction (Fig. 2f). Some of them still host the skeletal remains of their producer, the bivalve *Lithophaga lithophaga* (Linnaeus, 1758), whose valves are often well preserved and empty (Figs 2e, 4h), although sporadically encrusted on their internal sides by bryozoans and serpulids, among which is *Vermiliopsis labiata* (O.G. Costa, 1861) (Fig. 4d). Corallites are encrusted by rare bivalves, among which is *Chama* sp., as well as large-sized serpulids and vermetid gastropods. Serpulids are relatively common, mostly represented by *Semivermilia crenata* (O.G. Costa, 1861) (Fig. 4a), *Protula* sp. (Figs 2e, 4e) and *V. labiata*, followed by *Filogranula gracilis* Langerhans, 1844 and *Metavermilia multicristata* (Philippi, 1844). The large tubes of *Protula* sp., together with *V. labiata* and *M. multicristata*, contribute to strengthen the coral frame reducing voids and bridging adjacent corallites. At places, also the vermetid gastropod *Petaloconchus intortus* (Lamarck, 1818) is common occurring in clusters of superimposed specimens (Fig. 4f-g) near calices
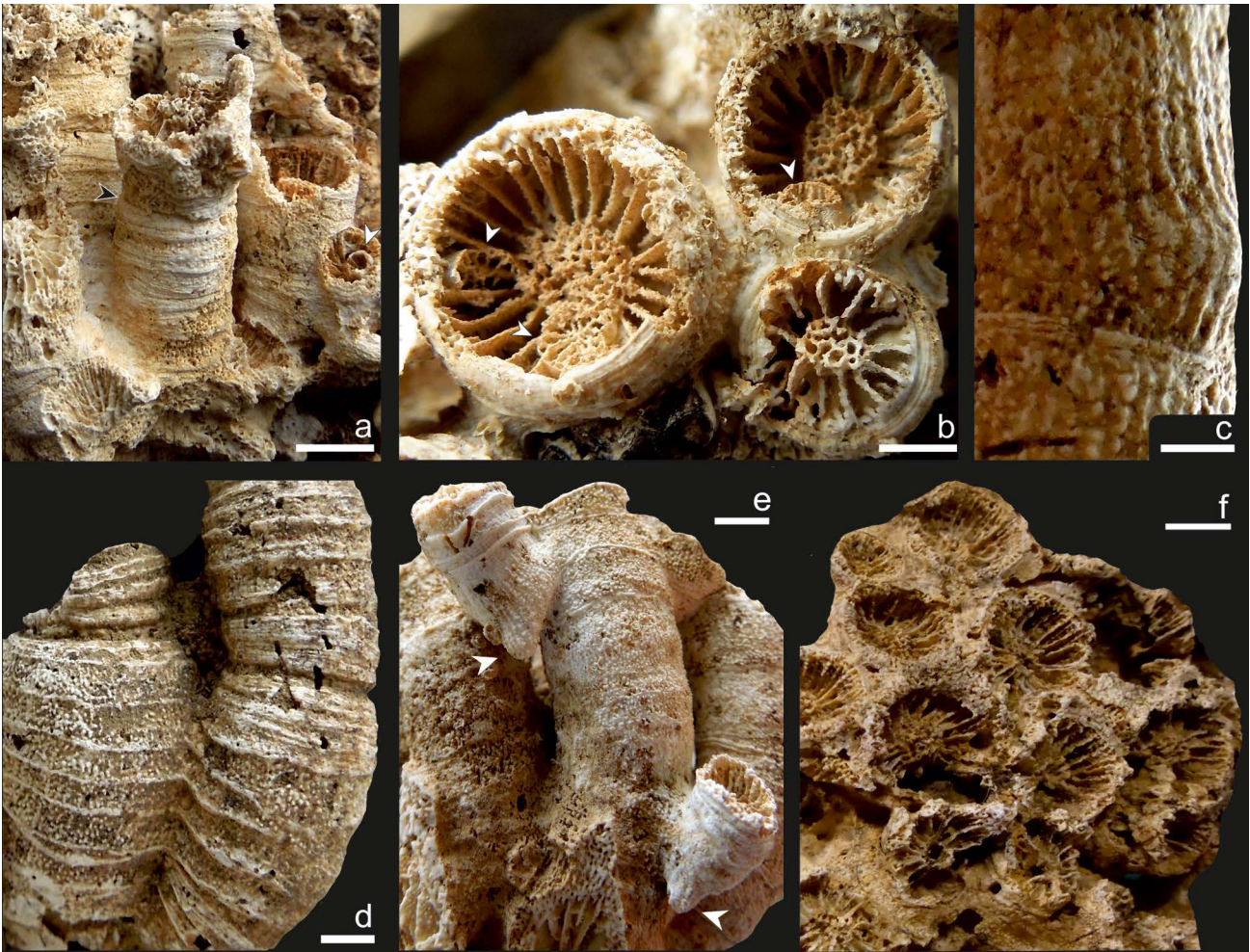
Fig. 3 - (Color online) *Astroides calycularis* (Pallas, 1766) from the Fulco Cave. a-e) Phaceloid colony fragments. a) Elongate, subcylindrical and epithecate corallites connected in their basal part; white arrow indicates a juvenile corallite settled within the calice of a dead individual; black arrow indicates the boundary between two distinct corallites growing on each other; scale bar corresponds to 5 mm. b) Distal view showing the well-preserved skeletal features of three circular calices; note juvenile corallites settled within the calices (arrowed); scale bar corresponds to 2 mm. c) Detail of longitudinal costae of a corallite outer wall; scale bar corresponds to 1 mm. d) Two cylindrical corallites with connected corrugate epitheca and synchronous main growth stasis; scale bar corresponds to 2 mm. e) Peculiar "ceratoid" shape of juvenile corallites (white arrows); scale bar corresponds to 2 mm. f) Plocoid colony fragment; scale bar corresponds to 5 mm.

of *Astroides* corallites, partly filling interspaces and occasionally growing within calices.

Further species, which are smaller-sized or rare and hidden between corallites, have been identified only after close inspection at the microscope. Additional species and taxonomic groups include spirorbids and bryozoans as well as some serpulids (Tab. 1). The latter include sparse *Josephella marenzelleri* (Caullery & Mesnil, 1897) and *Spiraserpula massiliensis* (Zibrowius, 1968). The spirorbids *Janua* (*Dexiospira*) *pagenstecheri* (Quatrefages, 1866) (Fig. 4b) and *Vinearia koehleri* (Caullery & Mesnil, 1897) (Fig. 4c) are particularly abundant, although volumetrically subordinate, on corallites. Bryozoans are rare and exclusively represented by encrusting colonies, mostly belonging to the anascan *Crassimarginatella crassimarginata* (Hincks, 1880) (Fig. 5b-c). Rare specimens of *Haplopoma graniferum* (Johnston, 1847) (Fig. 5d-f) were found, and a single specimen each for *Crassimarginatella solidula* (Hincks, 1860) (Fig. 5a) and *Celleporina caminata* (Waters, 1879). Undeterminable, poorly-preserved encrusting cyclostomes

are rare. Foraminifers are also present with *Miniacina miniacea* (Pallas, 1766) and encrusting agglutinated species. Small patches of encrusting coralline algae were also detected.

DISCUSSION

The cave encasing breccia

The cave is excavated in a small-sized lens consisting of a breccia, whose clast composition differs from that of any other coarse deposits as yet described from Capo Milazzo. Indeed, conglomerates and breccias that crop out discontinuously throughout the peninsula are known to include metamorphic rocks from the basement and Tortonian-Messinian reefal and peri-reefal carbonates (Fois, 1990a, b). These conglomerates and breccias formed in different marine and subaerial settings, from the late Miocene (Tortonian) to the Pliocene and in the Tyrrhenian (Fois, 1990a, b). The cave-encasing rock includes both blocks of cemented polymictic breccia composed of cm-

ENCRUSTERS	**Calcareous algae**	*
	Foraminifers	
	Miniacina miniacea (Pallas, 1766)	*
	Undetermined agglutinated species	*
	Scleractinians	
	Astroides calycularis (Pallas, 1766)	***
	Gastropods	
	Petaloconchus intortus (Lamarck, 1818)	*
	Bivalves	
	Arcidae sp.	*
	Spondylus gaederopus Linnaeus, 1758	*
	Cardita sp.	*
	Chama sp.	*
	Serpulids	
	Spiraserpula massiliensis (Zibrowius, 1974)	*
	Vermiliopsis labiata (O.G. Costa, 1861)	*
	Filogranula gracilis Langerhans, 1844	*
	Spirobranchus sp.	*
	Semivermilia crenata (O.G. Costa, 1861)	**
	Metavermilia multicristata (Philippi, 1844)	*
	Josephella marenzelleri Caullery & Mesnill, 1896	*
	Protula sp.	**
	Spirorbids	
	Vinearia koehleri (Caullery & Mesnil, 1897)	**
	Janua (Dexiospira) pagenstecheri (Quatrefages, 1866)	**
	Bryozoans	
	Haplopoma graniferum (Johnston, 1847)	*
	Crassimarginatella crassimarginata (Hincks, 1880)	**
	Crassimarginatella solidula (Hincks, 1860)	*
	Celleporina caminata (Waters, 1879)	*
	Undetermined cyclostomatids	*
BORERS	**Sponges**	
	Undetermined Clionaidae species	**
	Bivalves	
	Lithophaga lithophaga (Linnaeus, 1758)	**
	Polychaetes	
	Undetermined spionid species	*
	Barnacles	*
	Undetermined boring species	*

Tab. 1 - List of the organisms found in the palaeocommunity of the Fulco Cave. Asterisks refer to rough estimated abundance of each taxon in the analysed material: * < 5 specimens; ** 5-50 specimens; *** > 50 specimens.

to dm-sized rocks, and wackestone boulders with isidid internodes. The former clasts may correspond to the B2C facies of Fois (1990a), recorded from the neighbouring Punta Mazza area. This facies has been interpreted as the product of a landslide in an outer shelf setting (Fois, 1990a), or as linked to intraformational autoclastic processes (Barrier, 1984), before or contemporaneous to the early deposition of the "yellow calcareous marls" (sensu Violanti, 1988) of Capo Milazzo. The isidid wackestone boulders are remnants of the lower Pleistocene "yellow calcareous marls". The co-occurrence of both

types of clasts points to a still undescribed depositional event, that presumably took place in the early Pleistocene, during or soon after the deposition of the so-called "bathyal marls", possibly as the result of local addition from neighbouring elevated areas, as described for some older breccia bodies capped by the Plio-Pleistocene succession. This event, in addition to those reported by Fois (1990a), possibly affected a larger area, as breccias including clasts of lower Pleistocene rocks formed in bathyal environments have been discovered in several other localities surrounding the city of Messina (Vertino, 2003).

The cave community

All species recognised in the Fulco Cave, excluding *P. intortus*, still thrive in the present-day Mediterranean. These species have been reported from present-day submarine caves (e.g., Harmelin, 1969, 1985, 1986; Zibrowius, 1978; Balduzzi & Rosso, 2003; Bianchi & Sanfilippo, 2003; Rosso et al., 2013a, b, and references therein) and most of them can be considered to be indicative of cave environments. According to Rosso et al. (2013b), the serpulid *S. massiliensis* and the bryozoans *C. crassimarginata* and *C. solidula* can be considered as typical cave species, whereas the serpulids *S. crenata* and *J. marenzelleri* along with the spirorbid *J. koehleri* and the bryozoan *C. caminata* are particularly schiaphilic species, found in caves and crevices, overhangs and coralligenous habitats. Further species, such as the spirorbid *J. (D.) pagenstecheri*, appear to be more tolerant to higher light levels and usually thrive in shallow shelf environments (Knight-Jones & Knight-Jones, 1977). The bivalve *S. gaederopus*, usually considered as indicative of the Infralittoral Algae biocoenosis (see Pérès, 1982) and often found on vertical walls and overhangs in both recent and upper Pleistocene communities (Barrier et al., 1989), has been recorded from caves (Radolović et al., 2015), where it is a subordinate constituent. The boring bivalve *L. lithophaga* has a somewhat similar distribution, although it shows a more marked preference for shallower depths, forming denser populations in a few metres wide superficial belt and usually above 6 m (Devescovi & Ivecša, 2008 and references therein). Finally, the bryozoan *H. graniferum* is a species overall rarely reported and only occasionally from caves in the Mediterranean (V. Gerovaliseiou & AR, pers. obs.).

Taking into account the distributional information derived from these species and that on *A. calycularis* (Madonna et al., 2015) (see below), the fossil association of the Fulco outcrop consistently points to a submarine cave environment characterised by semi-dark conditions, possibly in a shallow setting. This inference is also supported by the absence of species strictly indicative of dark-cave conditions or biocoenosis of Grottes Obscures sensu Pérès & Picard (1964), except for *S. massiliensis*, and of particularly sciaphilic taxonomic groups, such as brachiopods and sponges. Interestingly, the association from the Fulco Cave shares only a restricted number of taxa (the spirorbid *V. koehleri* and the serpulids *V. labiata, J. marenzelleri* and *S. massiliensis*, the last, characterised by a completely different relative dominance) with the only fossil cave well documented from Sicily, i.e. the Rumena Cave, which is relatively more ancient (Rosso et al., 2015).
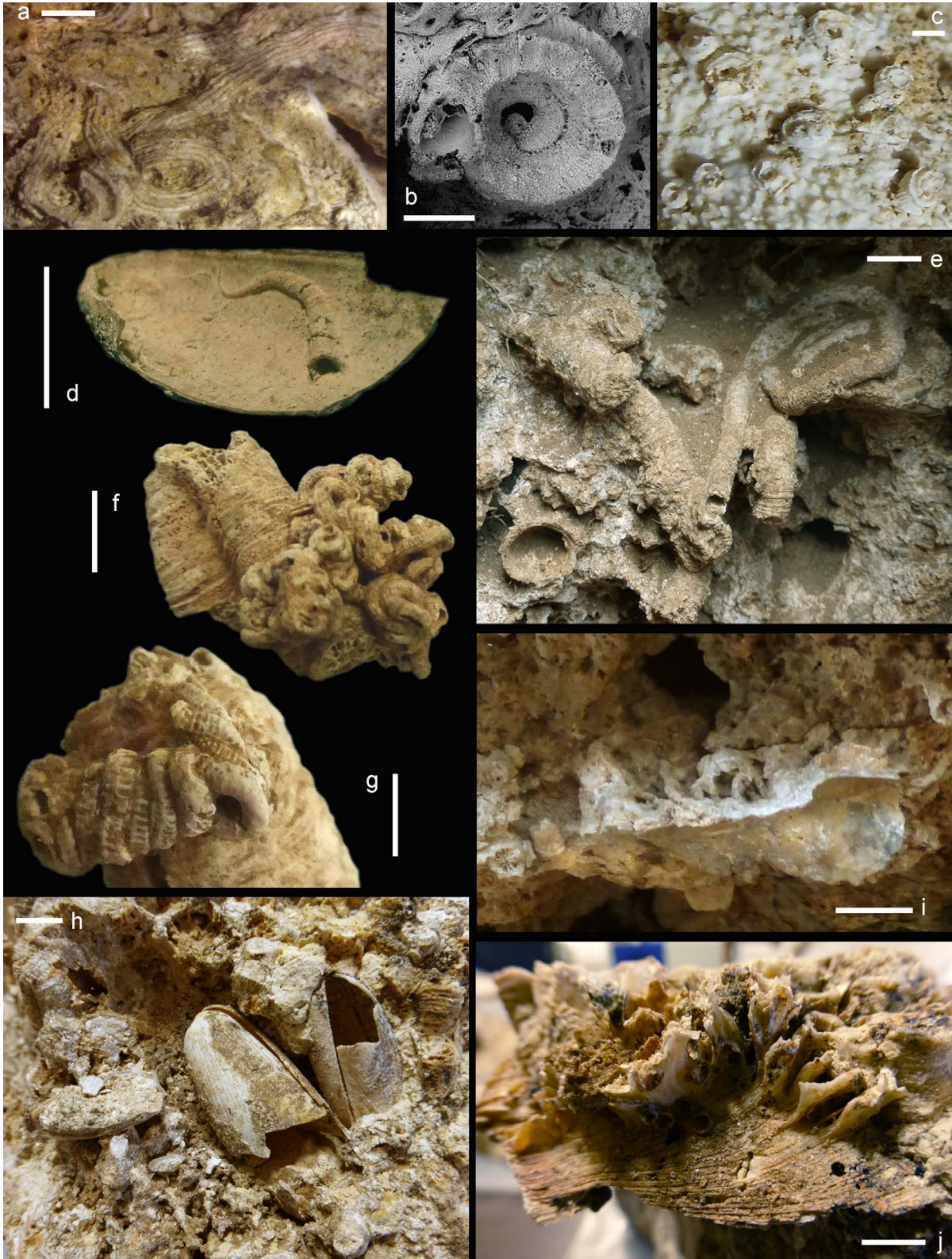
Fig. 4 - (Color online) Invertebrate skeletonised biota associated with the hanging corals of the Fulco Cave. a) Tubes of the serpulid *Semivermilia crenata* (O.G. Costa, 1861); scale bar corresponds to 1 mm. b) The spirorbid *Janua* (*Dexiospira*) *pagenstecheri* (Quatrefages, 1866), scale bar corresponds to 200 µm. c) Spirorbid cluster including *Vinearia koehleri* (Caullery & Mesnil, 1897) on the external surface of a corallite; scale bar corresponds to 2 mm. d) The serpulid *Vermiliopsis labiata* (O.G. Costa, 1861) encrusting the inner side of a *Lithophaga lithophaga* (Linnaeus, 1758) valve; scale bar corresponds to 5 mm. e) Cemented valve of the bivalve *Chama* sp. (bottom left) and a large tube of the serpulid *Protula* sp. (right), bridging together some hanging-down *Astroides* corallites. It is noteworthy that also the adult serpulid tube grew downwards; scale bar corresponds to 5 mm. f-g) The vermetid *Petaloconchus intortus* (Lamarck, 1818). f) Cluster of specimens within intracorallite spaces; scale bar corresponds to 5 mm. g) An enlarged specimen; scale bar corresponds to 2 mm. h) Specimens of *Lithophaga lithophaga* (Linnaeus, 1758) still preserved inside their borings; scale bar corresponds to 1 cm. i-j) valves of *Spondylus gaederopus* Linnaeus, 1758: i) still cemented in place; scale bar corresponds to 2 cm; j) detached, showing well developed ornamentation and bioerosion; scale bar corresponds to 1 cm.
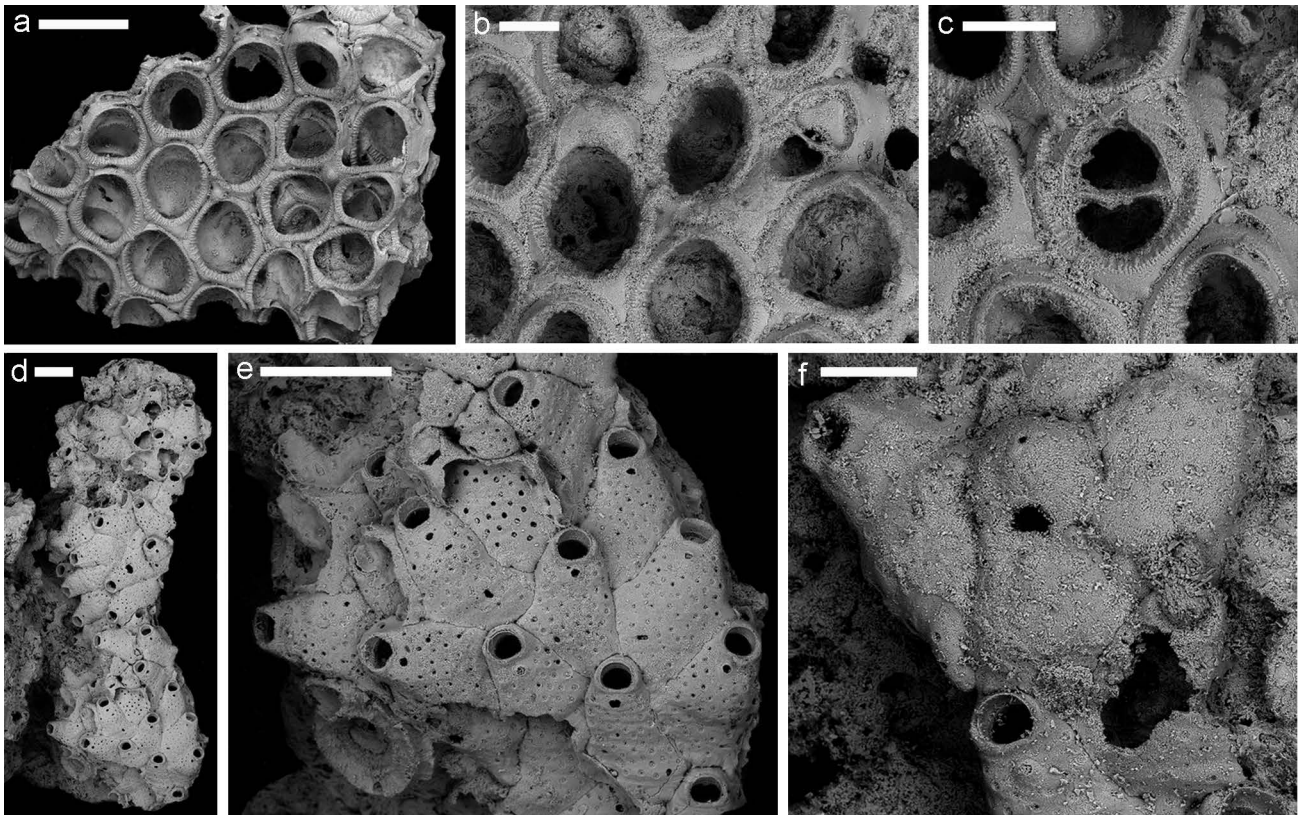
Fig. 5 - Scanning Electron Microscope (SEM) photos of bryozoans associated with the corals of the Fulco Cave. a) *Crassimarginatella solidula* (Hincks, 1860); scale bar corresponds to 500 μm. b-c) *C. crassimarginata* (Hincks, 1880): b) group of zooids; scale bar corresponds to 200 μm; c) close-up of the diagnostic interzooidal avicularia; scale bar corresponds to 200 μm. d-f) *Haplopoma graniferum* (Johnston, 1847): d) a large colony, scale bar corresponds to 500 μm; e) close-up of some sterile zooids in d; scale bar corresponds to 500 μm; f) an ooecium from another poorly preserved colony; scale bar corresponds to 200 μm.

Unique dense build-up of elongate Astroides

The dendrophylliid *A. calycularis* is a typical Mediterranean colonial azooxantellate scleractinian. It is rather common in the south-western and central part of this basin (Zibrowius, 1980, 1983, 1995; Ocaña et al., 2000; Cebrián & Ballesteros, 2004; Alvarez-Pérez et al., 2005; Bianchi, 2007; Terrón-Sigler et al., 2016 and references therein) and has been recently reported also from the eastern (Kružic et al., 2002; Grubeli et al., 2004; Bianchi, 2007) and northern (Casellato et al., 2007) Adriatic Sea. Rare occurrences are also known in Atlantic waters, immediately west to the Gibraltar Strait (Espartel Cape, Morocco, and La Caleta, Cadiz, Spain) (Zibrowius, 1980, 1983, 1995; Terrón-Sigler et al., 2016 and references therein). Its brightly, orange to yellow, pigmented polyps typically live in the upper 20 m of the sea-water column, along vertical walls, overhangs and entrance of caves (Rossi, 1971; Zibrowius, 1980, 1995; Terrón-Sigler et al., 2016 and references therein) and preferentially under moderate to strong water movement (Zibrowius, 1980, 1995; Kružic et al., 2002; Grubelić et al., 2004). The species has been rarely found below 40 m water depth (Ocaña et al., 2000; Kružic et al., 2002). As in most scleractinian species, colony shape in *A. calycularis* has a very high intraspecific variability. Zibrowius (1980) recognised two "extreme" morphotypes and related them to different environmental conditions: 1) plocoid, massive-shaped colonies with circular to polygonal calices and porous coenosteum, typical of very shallow environments and strong hydrodynamism; 2) phaceloid, bush-shaped colonies with separated and elongate subcylindrical corallites, more common in deeper and/or sheltered environments (such as entrance of caves).

The elongate, subcylindrical and independent corallites (Fig. 3) of the Fulco outcrop clearly correspond to the second morphotype described by Zibrowius (1980) and are therefore consistent with the interpretation of the outcrop as the entrance of a marine cave. The extreme elongation of the corallites hints at relatively low hydrodynamic conditions; moreover it could also be explained as a result of competition for space and food. Indeed, polyps may tend to extend as far as possible from the substrate in order to increase their living space and reach better water circulation (i.e., greater amounts of food particles and oxygen) in the more open parts of the cavity. This hypothesis would also explain the preferential settlement of new coral larvae in the distalmost portion of dead corallites and within their calices (Fig. 3 a-b).

Comparable downward elongations of dense frame-building organisms have been observed in both fossil and modern sheltered and cave environments. They involve corals and several animal groups and species sometimes growing as isolated but contiguous hanging individuals. A representative example is given by the hanging bioconstructions formed by exceptionally long specimens of the gregarious solitary scleractinian *Desmophyllum*

dianthus (Esper, 1794) on overhangs of the Chilean fjords (Försterra et al., 2005; Fillinger & Richter, 2013) and of the much deeper Porcupine Seabight (Wheeler et al., 2016; AV, pers. obs.). Typically, these overhanging *Desmophyllum* "pseudocolonies" are formed by the settlement of new coral larvae on pre-existing corallites and within their calices. This growth habit has been also observed by Jakubowicz et al. (2014) in Devonian cave communities from Morocco dominated by rugose corals and in Pleistocene caves near Taormina dominated by vermetid gastropods (RS, AR and Laura Bonfiglio, pers. obs.). In other cases, the overhanging bioconstructions are made of elevated nodular- to crest-like structures such as some bryozoans (Harmelin, 1985, 1986; Rosso et al., 2013b; AR, pers. obs.) and even intergrowing to form pendant stalactite-like hanging structures mostly constructed by serpulid polychaetes (Belmonte et al., 2009; Sanfilippo et al., 2015, 2017), usually associated with microbial communities (Guido et al., 2013, 2017). The downward growth of these bioconstructions can be considered as a mere consequence of the available space and their particular elongation may be explained as a special adaptation to compete for space and food. This could be particularly true in restricted habitats, such as caves, characterised by rapidly increasing confinement and food depletion (Bianchi & Morri, 1994).

The occurrence of calicular restrictions placed at the same height in neighbouring corallites from the same colony (Fig. 3d), can be interpreted as the response of *Astroides* to temporary unfavourable conditions. More severe stress and related longer periods of growth stasis could explain the formation of the observed surfaces of separation between the, at least three (Figs 2e, 6), superimposed "layers" of *Astroides* colonies of the Fulco Cave. These growth crises are locally marked by the presence of serpulid and mostly *Petalochonchus* tubes, covering some *A. calycularis* calices or forming clusters at their edge (Fig. 4f-g), overgrowing corallites with senescent or dead polyps. This is also the case of *S. gaederopus* specimens, whose encrusting valves growing in a horizontal position perfectly transversal to the corallites they cover, and developing lamellar ornamentation in the intercalicular spaces (Fig. 4i-j), clearly point to a growth stasis of the coral at their emplacement time. Because *Astroides* corallites increment their length at a comparable growth rate, *Spondylus* shells would become inclined during growth with juvenile shell portions covering corallites shorter than those overgrown by the peripheral shell portions. This is because corallites below peripheral portions were able to increment, even if slightly, their length during the *Spondylus* life span. In this hypothesis, and taking into account that the largest specimens of *S. gaederopus* found in the Fulco Cave do not exceed 12 cm in length, we can hypothesize that coral growth ceased locally at least for one or two decades. Indeed, Galinou-Mitsoudi et al. (2012) observed that the growth rate of *S. gaederopus* is relatively variable, although faster in the first 2-3 years, and that 6-17 years are needed to reach 6-10 cm in length, without any strong correlation between total length and life span.

Possible causes of iterative temporary growth stases of *Astroides* colonies, and even of their mortality, could be the reduction in food supply from outside the cave and also climate and temperature changes. In particular, changes in type and quantity of food input inside the cave could have affected the corals, causing temporary size reduction of corallites, but seemingly not other organisms such as serpulids, vermetid gastropods and bivalves, which may have benefitted from the decreasing in competition for substratum surface. In contrast, temperature changes could have caused local, nearly contemporaneous demise of all coral colonies in the cave. Several studies indicate a high sensitivity of *A. calycularis* to temperature changes. For instance, Gambi et al. (2010) reported that in summer 2008 persisting high temperatures (28-29 °C at the surface and 25-26 °C at 30 m depth) in a cave of Southern Italy (Grotta Azzurra, Palinuro, Campania), led to at least 20% of mortality in an *A. calycularis* population. Indeed the geographic distribution of *A. calycularis*, almost exclusively limited to the southern part of the Mediterranean Sea, hints at a narrow temperature tolerance of this species and its preference for relatively warm sea waters (Zibrowius, 1995). The records of few colonies beyond the "normal" northern limit of this species near Naples has been explained as an exceptional event (Bianchi & Morri, 1994) or, in the case of the Adriatic Sea, as an "ongoing northward shift" of the species due to increased temperature of the surface marine layer (Grubelić et al., 2004). According to Zibrowius (1995), transplanted specimens, collected near Naples, survived 11 years in the northern Mediterranean but did not produce any new colonies, probably due to inhibition of lower sea-water temperature on the reproduction cycle of *A. calycularis*. Recent studies confirm the influence of temperature variations on regulating the reproductive cycle of this azooxanthellate coral species (Goffredo et al., 2010, 2011; Casado-Amezúa et al., 2013).

Interestingly, the mortality event described by Gambi et al. (2010) for the Palinuro cave affected also specimens of *S. gaederopus* that underwent death and disarticulation contemporaneously to corals. However this did not happen in the Fulco Cave, where *Spondylus* colonisation followed the coral demise, and *Spondylus* apparently grew for several years (see above). As only its encrusting valves are presently found lining the surfaces of the inferred coral growth stases, a recovery of the *A. calycularis* population followed the death and the rapid disarticulation of the bivalves.

CONCLUSIONS

The present study allows us to put forward some hypotheses about the inception, development and demise of the spectacular hanging coral gardens formed by *A. calycularis* and the biota of the cave community of the Fulco Cave.

1. The Fulco Cave, elongated parallel to the present-day and presumed past coastline, can be interpreted as a submarine coastal cave. It presumably formed through the erosional action of sea-water partly dismantling the weakly cemented, matrix-lacking, heterometric, polymictic breccia in which it opens, displacing and removing some less cemented cobbles, pebbles and boulders.
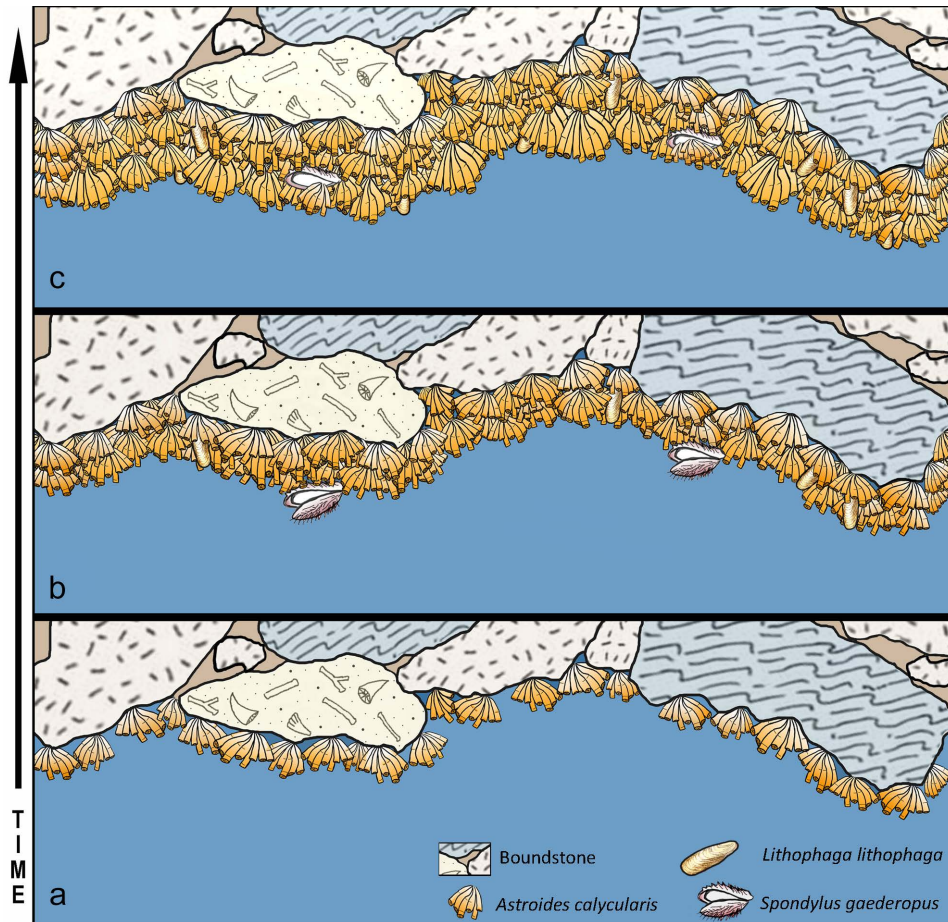
Fig. 6 - (Color online) Inferred colonisation history of the Fulco Cave. a) A first generation of conspicuous *Astroides calycularis* (Pallas, 1766) colonies developed, hanging down from the blocks forming the cave ceiling and reaching large sizes, before decreasing or temporarily stopping their growth. b) The crust thickened through the superimposition of a new generation of *Astroides* colonies, terminated by a further growth slowdown or a stasis, marked by the encrustation of large specimens of *Spondylus gaederopus* Linnaeus, 1758 on the corallites. c) Further thickening took place with a third (last?) generation of corals, which grew on previous populations and locally colonised the internal side of the encrusting valves of *Spondylus* after their death and disarticulation. *Lithophaga lithophaga* (Linnaeus, 1758) repeatedly exploited the carbonate substrate of the coral crust. Scale is approximate.

2. The cave possibly formed after the early Pleistocene, because the excavated breccia includes boulders of lower Pleistocene rocks. It is possible that excavation happened shortly before the cave colonisation and even as the result of the same sea level raise with erosion acting when the breccia was at the sea surface and/or just below it. Colonisation occurred when the cave was flooded, presumably during an interglacial period, because *A. calycularis* is considered as a warm-temperate species. This colonisation presumably took place during the Tyrrhenian.

3. The preserved skeletonised biota indicates a semi-dark cave association, which lived in a cavity presumably located near the sea surface, possibly relatively open to the sea.

4. The remarkable elongation of the corallites of *A. calycularis* may reflect the combined effect of low water movement and competition for space and food, driving the polyps to extend as far as possible from the cave ceiling in order to reach more oxygenated and food-rich waters.

5. Periodic corallite constrictions, corresponding to slow or no coral growth phases, and the distribution of associated biota, suggest short-time fluctuations in environmental conditions presumably linked to temporary rapid changes in temperature (at least near the sea surface) and/or food supply. Three major growth stases of the bioconstruction, likely corresponding to coral mass mortality, are marked by superimposed "layers" of *Astroides* colonies (Fig. 6). Bioconstruction ultimately ceased with the relative sea level fall, possibly as a result of the combined sea level fall consequent to the intervening Glacial and the general uplift of the promontory. The cave was sealed by the deposition of the Tyrrhenian conglomerates widespread all along the Capo Milazzo Peninsula.

to R. Sanfilippo and A. Rosso. Catania Palaeontological Research Group: contribution n.427.

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