




The paleo-community of the Sciacca red coral

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Abstract

The sub-fossil red coral deposits of Sciacca (Sicily Channel) have attracted scientific attention for nearly 150 years. Their origin and formation have been long questioned and investigated, given the fact that they represent one of the most intriguing geobiological events ever to occur in the Mediterranean basin. Less attention was given to the paleo-community associated with the sub-fossil coral. Radiocarbon age determinations, in particular, were provided only for red coral, neglecting the possibility of understanding which species were simultaneously present in the coralline paleo-community and which was their role. The study of cemented coral rubble pieces revealed that *Corallium rubrum* covered the largest time interval (more than 3000 years) and was contemporary to many secondary epibionts over two millennia and to *Madrepora oculata* for about 500 years; this last finding suggested that an uncommon co-dominance between the two structuring species occurred in the nearby living communities. The lack of Fe–Mg deposits on the cemented coral rubbles coupled with the low bioerosion rate of the red coral skeletons by the demosponge *Siphonodictyon coralliirubri* (assessed through the analysis of the erosive paleo-scars) suggested that the deposits met with a rapid sediment cover-up. Moreover, for the first time, the analysis of a piece of cemented coral rubble of sub-fossil red coral coming from Sardinian waters confirmed that, albeit to a lesser extent, the conditions favouring the preservation of dead corals can occur also in different localities far from Sciacca.

Keywords *Corallium rubrum* · Sicily channel · Sardinia · Sub-fossil coral · Radiocarbon dating · Associated fauna

Introduction

In the Mediterranean Sea, the Sicily Channel has long been one of the most famous precious coral [*Corallium rubrum* (Linnaeus, 1758)] fishing grounds (Cattaneo-Vietti et al. 2016, 2017) since it hosts the largest sub-fossil red coral deposit ever found in the basin (Di Geronimo et al. 1993; Lodolo et al. 2017; Bavestrello et al. 2021). These accumulations were discovered in the late nineteenth century, between 1875 and 1878, off Sciacca, a small town in the South of

Sicily (Mazzarelli 1915a, b). The amount of accumulated red coral can be evaluated by the evidence that, between 1875 and 1914, 18,000 tons of raw material scattered on the muddy/detritic bottom were harvested (Liverino 1998; Rajola 2012; Cattaneo-Vietti et al. 2016).

A few years after their discovery, scientific studies and oceanographic campaigns were conducted to unveil the mystery behind the origin and formation of the deposits. Canestrini and Canestrini (1883) suggested that the Sciacca coral deposits could have been formed in 1831, during the eruption generating the ephemeral Ferdinanda Island (Coltelli et al. 2016; Cavallaro and Coltelli 2019). Mazzarelli 1915a, b), building on this hypothesis, suggested that periodic earthquakes, underwater storms, and strong sea currents could have gradually accumulated the deposits. Holocene submarine eruptions in the area have indeed been proven recently by dating the oldest coralligenous encrustations on volcanic pyroclastic material (Lodolo et al. 2021). Nowadays, a problem to face in the study of Sciacca deposits is that neither the exact depth nor coordinates of the banks are known. Nevertheless, the actual occurrence of coral-bearing

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deposits has been constrained in previous works to three sites with a common narrow depth range between 180 and 250 m (Di Geronimo et al. 1993; Lodolo et al. 2017; Bavestrello et al. 2021).

Di Geronimo et al. (1993) proposed that rich living coral populations, developing on nearby particularly friable tuffaceous rocks (Caparezza et al. 1979), could have been broken off and accumulated at the base of the volcanos throughout periodic earthquakes. The same opinion was more recently shared by Lodolo et al. (2017), studying the living populations on the volcanic edifices of the Graham Bank. Additionally, small deposits of red coral fragments were reported in the area by remotely operated vehicles (ROV) (Toma et al. 2022a) and cold-water coral rubble talus deposits (including red coral) were reported at the foot of a nearby volcanic bank (Titschack et al. 2016). Bavestrello et al. (2021) supplied a morphometric description of the red coral paleo-population, studying colonies and fragments to extrapolate the annual growth rate (about 0.3 mm/year) and the average population age (about 33.5 years). Ultimately, the radiocarbon age estimation of the red coral branches suggested that the deposits were not the result of a single event, but they accumulated over a long period of time, ranging from about 9000 years BP to the present (Lodolo et al. 2017; Bavestrello et al. 2021).

Despite the interest in the origin of the sub-fossil red coral deposits, very few data were provided regarding the associated paleo-community. On material dredged in the putative location of the deposits, Di Geronimo et al. (1993) provided a list of species belonging to two separate paleo-communities: one, more ancient, typical of a deep circalittoral hard bottom and a second, characterizing a bathyal soft bottom. The first included red coral together with different species of scleractinians, particularly *Dendrophyllia cornigera* (Lamarck, 1816) and *Lophelia pertusa* (= *Desmophyllum pertusum*) (Linnaeus, 1758) and, rarer, *Caryophyllia* (*Caryophyllia*) *smithii* Stokes and Broderip, 1828 and *Madrepora oculata* Linnaeus, 1758. The authors stated that this community was settled on the flanks of submerged volcanic edifices, while the bathyal community laid down on the soft sediments at their base.

Although this accurate description, radiocarbon age determinations were provided only for red coral, avoiding the possibility to understanding which species were simultaneously present in the coralline paleo-community.

Here, we present data obtained by the taxonomic study of cemented remains of calcareous organisms intermixed with red coral branches coming from the Sciacca Banks, accompanied by a radiocarbon age determination of their most frequent elements. A specific focus was made on the boring sponges excavating the branches of the sub-fossil red coral studying the shape and ornamentation of the erosion scars present on the wall of the boring chambers. It was already

pointed out by Di Geronimo et al. (1993) and Lodolo et al. (2017) that the intense three decades-long coral harvesting activity disturbed and mixed the original Sciacca taphocenoses. Hence, the study of cemented coral rubble samples gave the unique chance to work on the original community composition.

To now, the Sciacca beds are the main known sites where sub-fossil red coral can be profusely found; nevertheless, new information was also taken into consideration. Basilio Liverino, owner of one of the oldest and most important coral factories in Torre del Greco (Italy), in its famous book dedicated to red coral (1983), published a photo of a large block of cemented red coral branches intermixed with micritic matrix coming from Sardinia Island. Thanks to the courtesy of Enzo Liverino, the current owner of the factory, we could study this unusual sample and use a coral fragment for radiocarbon age determination.

Materials and methods

Taxonomic and morphometric analyses

The examined material included photographs taken from three cemented coral rubble pieces (SC1, SC2, SC3), courtesy of the coral factories of the *Consorzio Corallo Sciacca* (Sicily) (Fig. 1A–C), and two specimens (SC4, SC5) present in the authors' collection (Fig. 1D, E). All the specimens came from the Sciacca deposits. The depth and date of collection are unknown. In addition, several photographs were taken of a large piece of cemented coral rubbles (SR1) coming from Sardinian waters (Fig. 2A, B) and present in the collection of Mr Enzo Liverino; also in this case, locality, depth, and date of collection are unknown. Due to its size and weight, it was probably collected by a trawling net.

For each piece, the diameter (in mm) of 100 coral branches was measured by a calliper and used to provide size-frequency distributions. All the recognizable carbonatic organisms were identified at the lower possible taxonomic level through direct examination of the cemented coral rubble samples, optical microscopy, and through photographs.

A morphological study of the sponge erosions was conducted on two cemented coral rubbles (SC4, SC5) coming from the Sciacca deposits. Portions of the etched coral branches were cleaned from organic tissue by boiling in hydrogen peroxide (120 vol) and then mounted on stubs and coated with gold for Scanning Electron Microscope (SEM) analysis (Vega 3_TESCAN microscope type LMU, Microscopy Laboratory, University of Genoa). Pit dimensions were obtained with the ImageJ software. The axes of 50 pits per species were measured. Non-perpendicular and irregular surfaces were avoided when taking SEM pictures.

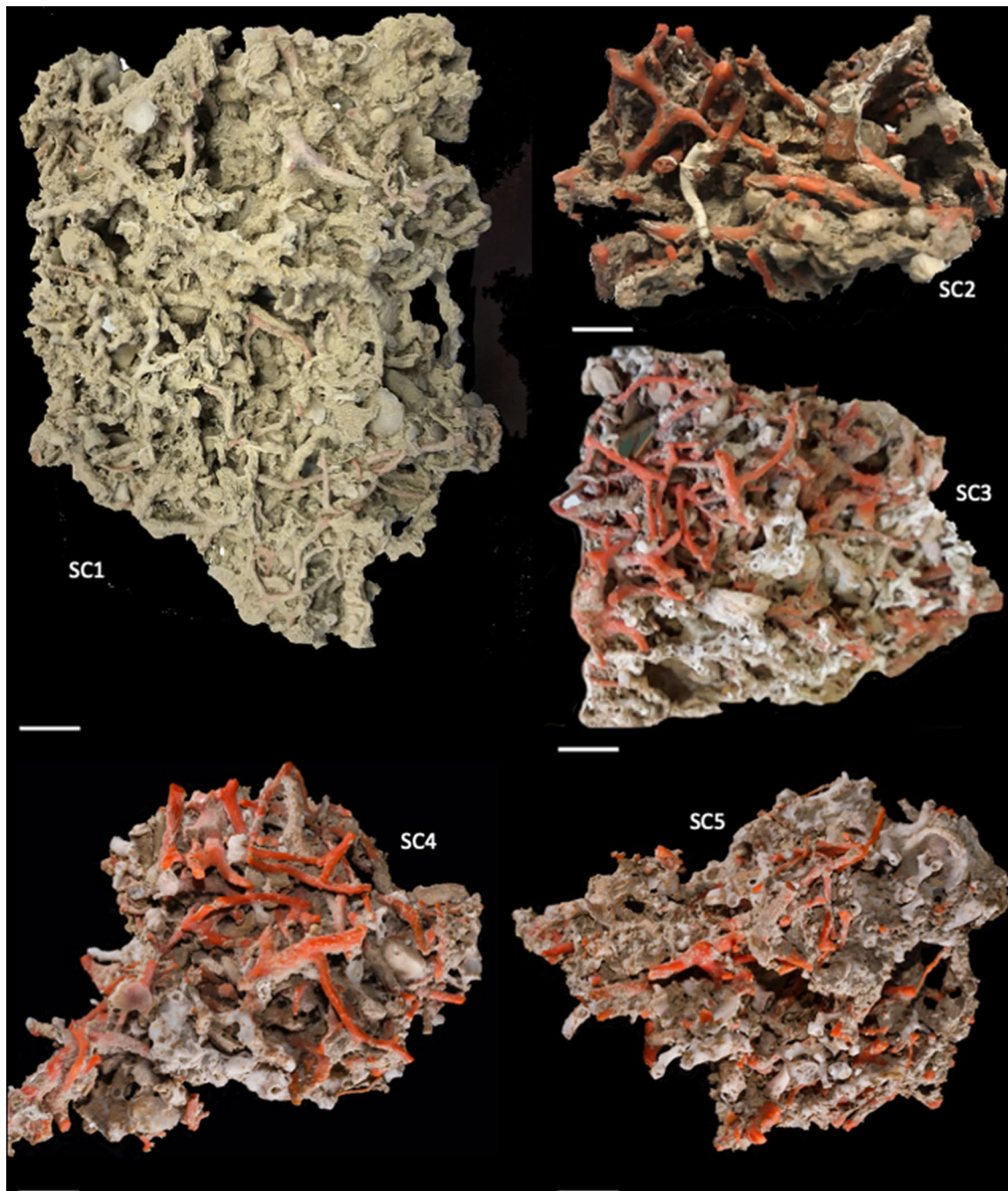


Fig. 1 Sciacca red coral. Lithified coral rubbles analyzed in this study. Scale bar: 1 cm. Labels as in Table 1

Radiocarbon dating

For radiocarbon age determination, 18 specimens of red coral, branched and solitary scleractinians, bivalves and brachiopods were selected from the samples SC4 and SC5 together with one red coral fragment from the Sardinian sample (SR1). For radiocarbon dating, an Accelerator Mass Spectrometry (AMS) at the Center of Dating and Diagnostic (CEDAD) of the University of Salento (Calcagnile et al.

2005, 2019) was employed. Samples were converted to carbon dioxide by acid hydrolysis (H_3PO_4), and the extracted CO_2 was converted to graphite after cryogenic purification (D'Elia et al. 2004). Conventional radiocarbon ages were then calculated from the $^{14}\text{C}/^{12}\text{C}$ isotopic ratios measured with the AMS system after correcting for isotopic fractionation, chemical processing and machine background.

Conventional radiocarbon ages were then calibrated in calendar years, expressed as years before 1950 CE (years

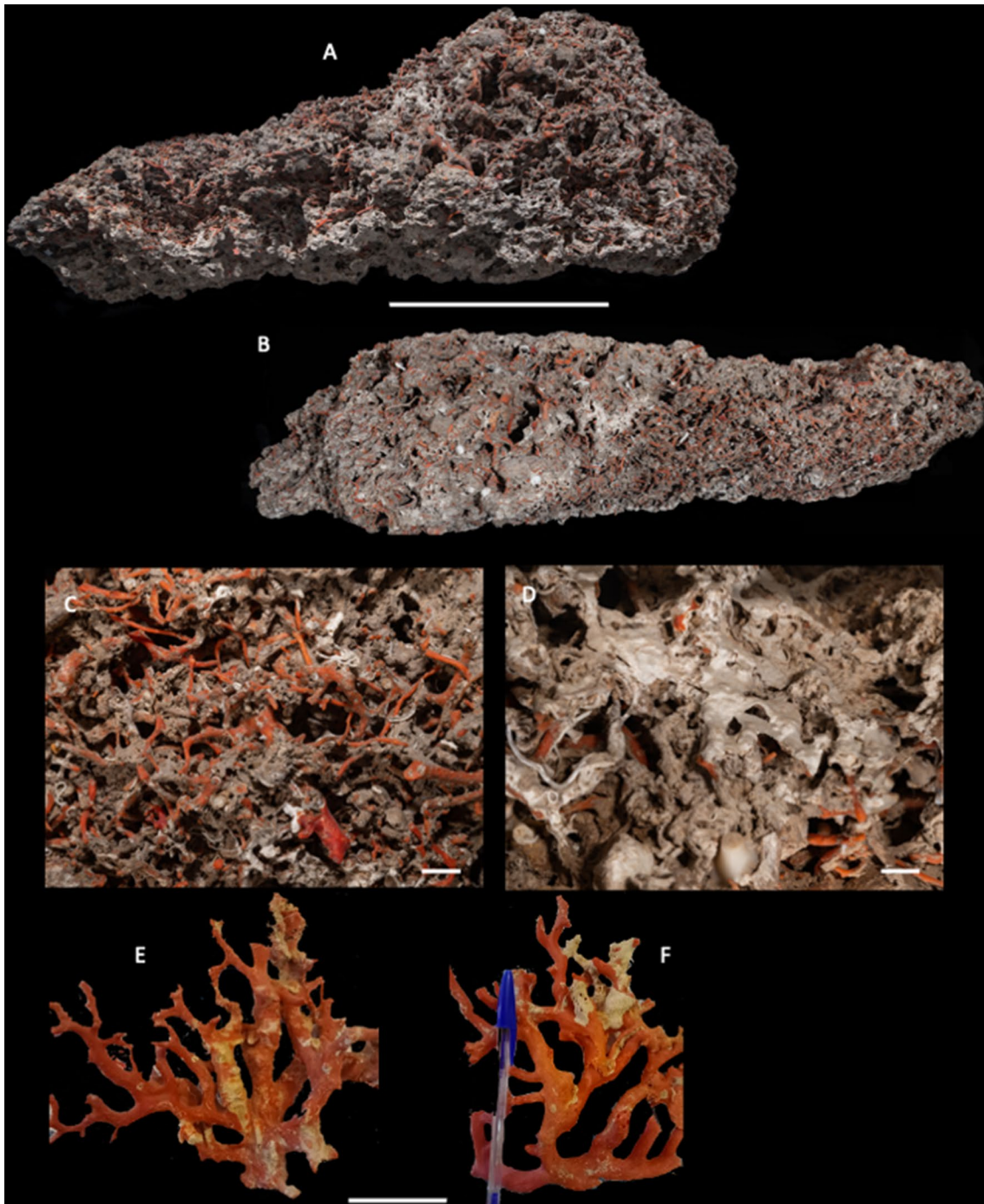


Fig. 2 Sardinian lithified coral rubble (SR1) and associate paleo-community. **A, B** Frontal and back view of the Liverino block (the arrow indicates the coralline algae crust on the putative upper side of the conglomerate). **C** Close-up view of the scaffold showing a large number of coral branches joined together by micritic cement. **D**

Close-up view of the upper side of the block showing the thick coat of coralline algae. **E, F** Scleraxis of two large colonies of red coral collected inside the sediments in Sardinia waters (courtesy of Massimo Scarpat (i)). Scale bar: **A, B**, 30 cm; **C, D**, 1 cm; **E, F**, 5 cm

BP), by using the MARINE20 curve (Heaton et al. 2020; Quarta et al. 2021)) and a $\Delta R = -88 \pm 50$, as the average value for the Mediterranean Sea (Siani et al. 2000).

Results

In the area of the Sciacca deposits, red coral was collected as fragments free in the sediments or as cemented rubbles of different sizes, the latter being the target of this study (Fig. 1). The studied samples ranged from 7 to 11 cm in maximum length, while the sample coming from Sardinia was a large block, 120 cm-long, weighing about 200 kg (Fig. 2A, B). The study of the diversity of the Sciacca samples (Table 1) indicated that they were quite homogeneous, all being mainly composed of broken branches of *Corallium rubrum* (Fig. 3A) and fragments of the colonial cold-water scleractinian *Madrepora oculata* (Fig. 3B) associated with the tubiculous polychaete *Eunice norvegica* (Linnaeus, 1767). Fragments were cemented together by a micritic matrix (Fig. 1). On this scaffold were settled corallites of the scleractinians *Caryophyllia* sp. (Fig. 3C, D) and *Polycyathus muelleriae* (Abel, 1959) (Fig. 3E, F). The barnacles *Adna anglica* Sowerby, 1823 were recorded on the corallites (Fig. 3F). In some cases, colonies of red coral were found settled on branches of *M. oculata* (Fig. 3A). Shells of the bivalve *Spondylus gussonii* Costa, 1830 (Fig. 3G), fragments of an unidentified pectinid, the brachiopods *Megerlia truncata* (Linnaeus, 1767) (Fig. 3H) and *Terebratulina retusa* (Linnaeus, 1758)

(Fig. 3I), tubes (*Serpula* spp.) (Fig. 3J), and an unidentified bryozoan were also observed although less frequently.

Regarding the Sardinian block, red coral branches were the main component together with small scleractinians, serpulids tubes and brachiopods, all cemented together by a large amount of micritic matrix (Table 1; Fig. 2C). An important difference with the Sciacca specimens was the total absence of *M. oculata*. It is relevant to note that on one side of the sample, a thick, almost continuous sheet of coralline algae was present (Table 1; Fig. 2B, D). Among the accompanying species, the most abundant were the serpulids *Protula* sp. (Fig. 4A), *Serpula* sp. (Fig. 4B), and *Vermiliopsis* sp. (Fig. 4C), the brachiopod *M. truncata* (Fig. 4D), the bivalves *S. gussonii* (Fig. 4E), fragments of small pectinids (Fig. 4F) also recorded in the Sciacca specimens. On the contrary, the gastropod *Calliostoma* sp. (Fig. 4G, H), the bryozoan *Copidozoum* sp. (Fig. 4I), the scleractinians *Thalamophyllia gasti* (Döderlein, 1913) (Fig. 4J), *Ceratotrochus magnaghii* Cecchini, 1914 (Fig. 4K), and *Coenocyathus cylindricus* Milne Edwards & Haime, 1848 (Fig. 4L) were exclusively observed in the Sardinian block (Table 1).

Generally, the diameter of the red coral fragments was very variable: the maximal recorded value was 9 mm and 8.8 mm for Sciacca and Sardinia, respectively, but, in both cases, numerous remarkably thin branches (<2 mm) were present. On average, the diameter was 2.9 ± 0.21 mm and 2.5 ± 0.18 mm, respectively, for Sciacca and Sardinia red coral. The two size-frequency distributions are similar and show the same modal class peak at <2 mm (Fig. 5).

Table 1 Diversity of the studied cemented coral-rubble pieces from Sciacca (SC) and Sardinia (SR)

	SC1	SC2	SC3	SC4	SC5	SR1
<i>Corallium rubrum</i>	X	X	X	X*	X*	X*
<i>Madrepora oculata</i>	X	X	X	X*	X*	
<i>Caryophyllia</i> sp.	X	X	X	X*	X*	
<i>Polycyathus muelleriae</i>	X		X		X	
<i>Thalamophyllia gasti</i>						X
<i>Coenocyathus cylindricus</i>						X
<i>Eunice norvegica</i>	X	X	X	X	X	
<i>Serpula</i> spp.	X	X	X	X	X	X
<i>Protula</i> sp.						X
<i>Vermiliopsis</i> sp.						X
<i>Spondylus gussonii</i>		X		X*	X	X
<i>Calliostoma</i> sp.						X
<i>Ceratotrochus magnaghii</i>						X
<i>Megerlia truncata</i>	X	X	X	X*	X*	X
<i>Terebratulina retusa</i>	X	X	X	X	X	
<i>Copidozoum</i> sp.						X
<i>Adna anglica</i>	X		X	X	X	
Coralline algae						X

Asterisk (*) indicates the piece to which dated specimens belong



Fig. 3 Close-up pictures of the main components of the lithified coral rubbles from Sciacca. **A** Red coral branches showing typical longitudinal stripes. This specimen was observed overgrowing a dead fragment of *Madrepora oculata*. **B** Fragment of *Madrepora oculata* encrusted with lithified micrite. **C, D** corallites of the solitary scleractinian *Caryophyllia* sp. settled on the red coral branches. **E, F** Corallites of the scleractinian *Polycyathus muelleriae* sometimes epibionted by the barnacle *Adna anglica* (arrow) (**F**). **G** The bivalve *Spondylus gussonii* settled on a red coral branch. **H, I** The brachiopods *Megerlia truncata* (**H**) and *Terebratulina retusa* (**I**). **J** The serpulid *Serpula* sp. on a red coral branch. Scale bar: 5 mm

The radiocarbon age of the main components of the Sciacca cemented coral rubble pieces was estimated (Table 2). Red coral showed the widest age range, from 3430 to 132 years BP. The age range of *M. oculata* was more limited, from 2880 to 2252 years BP, while that of the accompanying species (*Caryophyllia* sp., *S. gussonii*, *M. truncata*) ranged from 3779 to 1124 years BP. The estimated radiocarbon age of a Sardinian red coral branch was 119 years BP (Fig. 6). All ages fall in the Mid-Late Holocene epoch.

Finally, in the Sciacca samples, traces of sponge erosion were rare and mainly recorded in the red coral branches. Boring chambers were subspherical or elongated, 1–3 mm in their maximal diameter, interconnected by channels 0.5–1 mm in diameter (Fig. 7A–D). In some cases, the boring chambers completely invaded the coral scleraxis leaving only a thin external layer (Fig. 7E). The walls of the boring chambers (Fig. 7F) were covered by subcircular erosion scars, 20–40 µm in diameter, characterized by deep grooves extending to the pit centre (Fig. 7G, H).

Discussion

Thanatocoenoses are made of exposed fossil or sub-fossil remains and may build, especially when consolidated, conspicuous secondary hardgrounds in the deep Mediterranean Sea from the shelf edge to the lower bathyal realm, also in offshore locations (Di Geronimo et al. 2001; Remia and Taviani 2005; Rosso et al. 2010; Bo et al. 2020). The most studied thanatocoenoses in the basin are those constituted by cold-water corals in the form of reef-like bioherms or unconsolidated rubble (Taviani et al. 2011; Enrichetti et al. 2023), although others have been investigated, dominated by remains of bivalves, polychaetes, and sponges (Rosso et al. 2010; Maldonado et al. 2015; Taviani et al. 2019), some of which associated to a living counterpart. Various studies also targeted the taxonomic identification of the fauna, both living and dead, associated with these frameworks in order to give a better overview of the paleo-communities (Taviani and Colantoni 1984; Zibrowius and Taviani 2005; Rosso et al. 2010; Nasto et al. 2018; Taviani et al. 2011).

The Sciacca coral represents a unique case of Mediterranean thanatocoenosis for many reasons: (i) its origin, not related to the end of the Plio-Pleistocene glacial episodes (Lodolo et al. 2017; Bavestrello et al. 2021), (ii) its current position, different from the area in which the living colonies are settled (Di Geronimo et al. 2001; Lodolo et al. 2017), (iii) its geographic localization, limited to a distinct area of the Sicily Channel, (iv) its composition (the only two other known octocoral-dominated thanatofacies are those of *Isidella elongata* (Esper, 1788) and *Keratoisis* sp.) (Zibrowius 1989; Rosso et al. 2010), (v) its vertical extension (a deep, partially consolidated, accumulation in the sediments as a result of multiple formation events), and finally, (vi) the fact that, unlikely any other known thanatofacies, it has been widely exploited, and probably completely removed, for economic purposes. In this latter regard, it has been calculated that in 34 years of exploitation (1875–1888 and 1893–1914), 18,000 tons of raw material were collected in the Sciacca deposits, the so-called “Coral Valley” (Cattaneo-Vietti et al. 2016). The deep perturbation of the Sciacca thanatocoenosis, due to the anthropogenic impact of trawlers, resulted in extreme difficulty in the reconstruction of the paleo-community and formation events (Di Geronimo et al. 1993; Lodolo et al. 2017). The present paper took advantage of working on cemented coral-rubble samples, which partially preserved the original species composition allowing, for the first time, the description of the paleo-community.

The *Corallium rubrum* and *Madrepora oculata* thanatofacies of Sciacca

The five samples from Sciacca are all characterized by the same benthic components, with a dominance of red coral and *Madrepora oculata* fragments. This homogeneity among different samples suggests that the reported species composition is representative of the investigated benthic community. Given the co-occurrence of the two dominant species in the same framework, with also a few cases of overgrowth of red coral on white coral, it is plausible that, at that time, the nearby hardgrounds hosted a peculiar biocoenosis, co-dominated by *C. rubrum* and *M. oculata*. This is no longer the case in the present assemblage.

Nowadays, flourishing red coral populations are present at mesophotic depths in the Sciacca area (specifically the Graham Bank) (Altobelli et al. 2017; Lodolo et al. 2017; Consoli et al. 2021; Toma et al. 2022b) as well as in nearby sites of the Sicily Channel, such as Ragusa, where the dense colonies have been subjected to illegal exploitation by trawling gears (Cattaneo-Vietti et al. 2017).

Madrepora oculata and *Lophelia pertusa* were more prolific during colder and more eutrophic settings like the Younger Dryas (McCulloch et al. 2010), while nowadays are constrained to canyon heads (Taviani et al. 2019) and

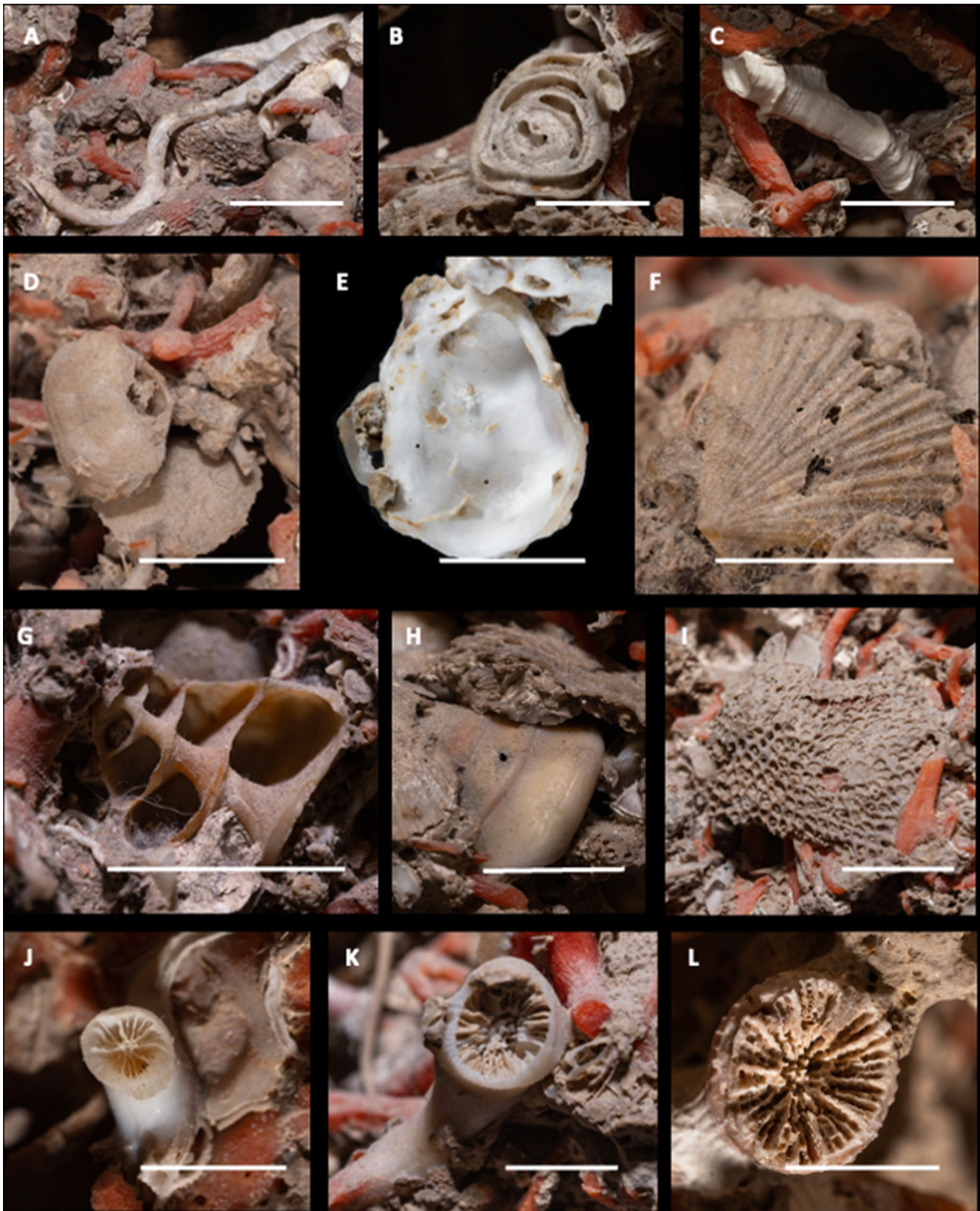


Fig. 4 Close-up pictures of the main components of the Sardinian cemented coral rubble. The serpulids *Protula* sp. (A), *Serpula* sp. (B) and *Vermiliopsis* sp. (C); the brachiopod *Megerlia truncata* (D); the bivalves *Spondylus gussonii* (E) and an unidentified small pectinids

(F); the gastropod *Calliostoma* sp. (G, H); the bryozoan *Copidozoum* sp. (I); the scleractinians *Thalamophyllia gastii* (J), *Ceratotrochus magnaghii* (K) and *Coenocyathus cylindricus* (L). Scale bars: A, C, D, F, G, H, I=1 cm; B, E, J, K, L=0.5 cm

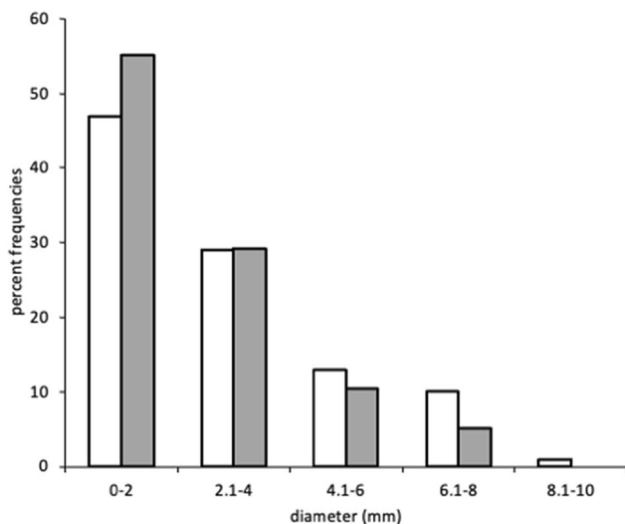


Fig. 5 Percentage size-frequency distribution of the diameter of red coral branches. White bars, Sciacca; grey bars, Sardinia

current-dominated banks and cliffs, in particular in the Sicily Channel. Here, living occurrences of these species are only known in the bathyal depth range between 400 and 700 m off Malta, Linosa, south of Pantelleria, and the Nameless Bank (also known as Urania Bank) (Zibrowius and Taviani 2005; Schembri et al. 2007; Freiwald et al. 2009; Martorelli et al. 2011; Titschack et al. 2016; Chimienti et al. 2019), this latter being the closest site to the Sciacca area.

Despite being relatively common species, the co-occurrence of *C. rubrum* and *M. oculata* in a combined facies, as observed in the studied thanatocoenosis, is a rarity also in the present fauna with only three records so far. The extensive ROV surveys of the METEOR M70-1 cruise reported the two species (together with *L. pertusa*) south of Malta at a depth of 458 m and along the Linosa Trough (Freiwald et al. 2009). In this latter site were discovered the spectacular "Hanging gardens of Linosa", where living *C. rubrum*, *M. oculata*, and *L. pertusa* abundantly colonized steep rock cliffs and extensive overhangs at 673 m (Freiwald et al. 2009). Additionally, cold-water coral rubble talus deposits formed by white and red corals were reported at the foot of the volcanic Urania bank (Titschack et al. 2016). The only example of co-occurrence of *M. oculata* and *C. rubrum* in a depth range similar to the Sciacca one is the Cassidaigne Canyon in the Gulf of Lion, at 180–200 m (Fabri et al. 2014). The factors driving this combined facies, both in shallow and deep waters, remain unclear. The absence of *L. pertusa* in the studied cemented coral rubbles is in agreement with the current known Mediterranean bathymetric distribution of this species, usually present below 300 m and becoming more common deeper than 600 m (Freiwald et al. 2009; Chimienti et al. 2019).

Table 2 Radiocarbon age of the main components of the cemented coral-rubble pieces

Sample	Lab code	Conventional ^{14}C age (BP)	Calibrated age (Years BP = before 1950 AD) (Probability 95.4%)
<i>Corallium rubrum</i>			
Scr1 (SC4)	LTL20603	549 ± 45	132 ± 135
Scr2 (SC4)	LTL20604	3350 ± 45	3165 ± 110
Scr3(SC4)	LTL20605	3576 ± 45	3430 ± 207
Scr4(SC5)	LTL20606	2158 ± 45	1704 ± 203
Scr5(SC5)	LTL20607	2730 ± 45	2425 ± 232
Srcr1 (SR1)	LTL21886	469 ± 45	119 ± 117
<i>Madrepora oculata</i>			
Smo1(SC4)	LTL20608	2781 ± 45	2495 ± 208
Smo2(SC4)	LTL20609	2912 ± 45	2619 ± 212
Smo3(SC5)	LTL20610	2667 ± 45	2337 ± 234
Smo4(SC5)	LTL20611	2609 ± 45	2252 ± 220
Smo5(SC5)	LTL20612	3110 ± 45	2880 ± 195
<i>Caryophyllia</i> sp.			
Sca1(SC4)	LTL20613	1637 ± 45	1124 ± 172
Sca2(SC4)	LTL20614	2472 ± 45	2090 ± 215
Sca3(SC4)	LTL20615	2114 ± 45	1637 ± 208
Sca4(SC5)	LTL20616	3179 ± 45	2950 ± 203
Sca5(SC5)	LTL20617	2706 ± 45	2388 ± 237
<i>Spondylus gussonii</i>			
Ssg1(SC4)	LTL20618	3699 ± 45	3595 ± 212
<i>Megerlia truncata</i>			
Smt1(SC4)	LTL20620	3857 ± 45	3779 ± 227
Smt2(SC5)	LTL20621	2391 ± 45	1972 ± 224

In brackets, the number of the sample according to Table 1. Data calibrated by using the MARINE20 curve and a $\Delta R = -88 \pm 50$ as measured for Sicily

The past and present benthic community of Sciacca

The unusual combined thanatofacies between red coral and *M. oculata* was accompanied by a relatively low number of species, considering the taxa potentially feasible to remain in the fossil record. Similar coral framestones, but dominated only by white corals, were shown to host a larger number of species (Remia and Taviani 2005). The scarcity of species may be related to the fact that the source population was not as tridimensional as the frameworks of the bathyal white corals but also to the fossilization dynamics of the rubble, which may have limited the secondary settling of slow-growing species.

Most of the observed secondary components of the holocene facies are species also known in the Mediterranean's recent cold-water coral fauna (Taviani et al. 2005; Mastro-totaro et al. 2010; Rueda et al. 2019). Among these, the

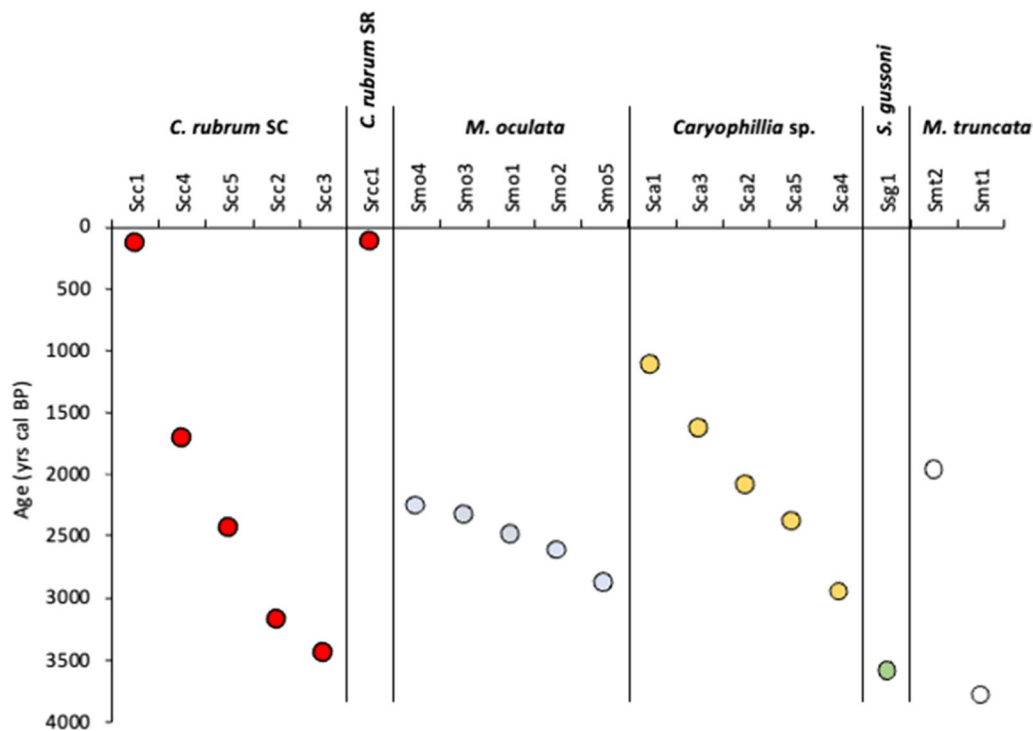


Fig. 6 Radiocarbon age estimation (expressed as years cal BP) of the analyzed specimens corresponding to the dominant species forming the sub-fossil coral rubbles

commensal polychaete *Eunice norvegica* is known as a common symbiont of *M. oculata* and *L. pertusa*, where it induces the formation of a tubular extra-calcification inside which it lives (Oppelt et al. 2017). Given the close association with the scleractinians, it is not surprising the occurrence of tubes' remains in the sub-fossil framework. The bivalve *Spondylus gussonii* has been frequently found on living cold-water coral frameworks (Mastrototaro et al. 2010) and within coral rubble thanatofacies (Rosso et al. 2010). In the Sicily Channel, this bivalve is nowadays commonly recorded at a depth greater than that of the Sciacca rubble, in association with the cold-water coral assemblages (Schembri et al. 2007). No other bivalves, now commonly reported as associated with white coral habitats [e.g., *Asperarca nodulosa* (Müller, 1776)] (Taviani et al. 2005), have been found, even if this could probably partially be related to the shallower depths of the Sciacca source population and the absence of a reef tridimensionality attracting a higher diversity of associated macrofauna (Rueda et al. 2019). The recorded brachiopod species, *Megerlia truncata* and *Terebratulina retusa*, are known both from mesophotic depths and cold-water coral environments (Mastrototaro et al. 2010; Toma et al. 2022c). Their occurrence is well documented from Pleistocene white coral framestones (Remia and Taviani 2005). A recent study describing the distribution of large brachiopod species in the Ligurian Sea, Tyrrhenian Sea and the Sicily Channel indicates that *M. truncata* is today very abundant in the area

of the Sciacca Banks, while *T. retusa* has a more northern distribution (Toma et al. 2022c).

The colonial scleractinian *Polycyathus muelleriae* and the parasitic barnacle *Adna anglica*, differently from the other associated species reported in the facies, are typically found in shallow-water and mesophotic environments (Koukourou and Matsa 1998; Corriero et al. 2019). Their occurrence in the thanatofacies suggests that the original source population was represented by a combined circalittoral and bathyal fauna not only for the main structuring species but also for the associated components. *P. muelleriae* is known from cave environments and sciaphilous coralligenous habitats, but it also holds a habitat-forming role in some mesophotic sites of the south Adriatic Sea (Corriero et al. 2019). *A. anglica* is a cold-affinity species known to parasitize caryophyllids (present in the assemblage) and is among the Mediterranean cirripedes with the longest history, having survived in the basin since the early Pleistocene (Chan et al. 2020; Gale et al. 2021).

Temporal formation dynamics of the Sciacca thanatocoenosis

This study provides, for the first time, the radiocarbon age determination of the dominant and accompanying species of the Sciacca thanatocoenosis, providing insights into the dynamics of the formation events. Based on the radiocarbon

ages and the position of all the species remains in the cemented rubbles, it is possible to affirm that the studied frameworks are the result of multiple settling events of the different biological components over a long span of time, specifically millennia, in the late Holocene. Not all species co-existed for the entire time period. The red coral branches, the corallites of the solitary *Caryophyllia* sp., and presumably the other major secondary epibionts, like *S. gussonii* and brachiopods, gathered in the cemented pieces across a period ranging from 3800 to 1100 years BP or less. On the contrary, *M. oculata* became part of the cemented coral rubbles in a more restricted range, from 2800 to 2252 years BP. The Sciacca red coral samples analyzed until today date from the early Holocene to the present. Nevertheless, the highest frequency of specimens falls in a range comprised between 3900 and 1700 years BP: of 19 specimens tested in three studies (Lodolo et al. 2017; Bavestrello et al. 2021, this study), 13 (68.5%) were recorded in that range. Also, data obtained for *M. oculata* and most of the epibiontic organisms coincides with this interval. This bulk of data suggests a particularly prolific growth in the community in this time frame.

A study conducted on the calcareous nanofossil assemblages obtained from a drilling program in the area demonstrated various productivity variations in the Sicily Channel during Holocene. In particular, four main intervals of productivity increases were identified between about 8.7–8.2, 6.2–5.3, 3.2–2.3, and 1.8–1.0 ka BP (Incarbona et al. 2008). The third interval is overlapped with the period of putative flourishing of the coral community. It is interesting to note that the disappearance of *M. oculata* from the Sciacca Banks overlapped with a similar phenomenon that occurred in the Alboran Sea (Trias-Navarro et al. 2021), where it is correlated to a time of increased agriculture activities in Morocco, causing enhanced fluvial sediment supply (McGregor et al. 2009). A sudden remarkable increase in the sedimentation rate (Fink et al. 2013) may have hampered coral growth at a local scale.

The prolific growth of *M. oculata* in the area could also be related to the paleoceanographic settings of the region, favouring its occurrence at particularly shallow depths. In this regard, it is interesting that, at present, a continuous convective motion supports a seasonally homogenous vertical structure of the water column with low temperatures and high availability of nutrients extending in the photic zone (Incarbona et al. 2008; Montagna et al. 2022). Additionally, upwelling events are supported by the summer cyclonic gyre (ABV, Adventure Bank Vortex) moving over the Adventure Bank topographic feature (Incarbona et al. 2008). This situation may have also favoured in the past a local vertical mixing of water masses, in particular an upwelling of the Levantine Intermediate Water. In this regard, a water flow coming from the easternmost coral sites (Santa Maria di Leuca or South Adriatic Sea) may have supplied an input

of *M. oculata* larvae to the area of Graham. In support of this hypothesis, there is an overlap in the radiocarbon age of *M. oculata* from Santa Maria di Leuca (2748 years BP) (Malinverno et al. 2010) with the prolific period highlighted in this study.

The general absence of Fe–Mg deposits on the coral remains suggests that the branches have been covered by mud, preventing the formation of the encrustations, which usually occur on bathyal hardgrounds. At the same time, however, a prolonged exposition to anoxic conditions as those found in the mud should have turned the skeletons dark grey, and this is not the case observed in Sciacca. A certain degree of sediment covering could have promoted the micritisation process and the formation of cemented coral rubbles. Sediment covering, coupled with exposure to hydrothermal emissions, has been identified as responsible for the chemical processes turning red coral branches from this area in their typical light orange colouration (Rajola 2012; Lodolo et al. 2017). The ecological succession of the species overgrowing others, therefore, could be identified either in the pristine community or shortly after its accumulation on the seafloor or following a mixing event, which exposed part of the deposits.

The Sardinian sub-fossil cemented coral rubble

The discovery of sub-fossil deposits of red coral in Sardinian waters was examined here for the first time. The main difference between the large sample studied here and the Sciacca cemented rubble is the complete absence of *M. oculata*. This fact suggests that probably, the depth of formation was lower, as also testified by the wide presence of coralline algae on the upper side of the block. These algal formations are very rarely recorded deeper than 150 m depth (Toma et al. 2022b). The other accompanying species found in the lithified coral rubble are also indicative of a mesophotic environment, despite two scleractinian species, *Coenocyathus cylindricus* and *Ceratotrochus magnaghii*, being known from a larger bathymetric range since the Late Pleistocene (Taviani et al. 2011; Altuna and López González 2015).

Both in the Sardinian and Sciacca thanatofacies, the size-frequency distribution of the red coral branches, characterized by a modal class in the smaller diameters and by a regularly decreasing distribution pattern, is in agreement with the low number of entire colonies and the dominance of branches and branch fragments in the thanatocoenoses. Therefore, these data are not representative of the size structure of the past source populations.

The traditionally invoked hypothesis explaining the formation of the Sciacca deposits is based on recurring earthquakes in a volcanic area hosting large populations of red coral (Rajola 2012; Lodolo et al. 2017, 2021). On the contrary, it is not easy to formulate a hypothesis for the

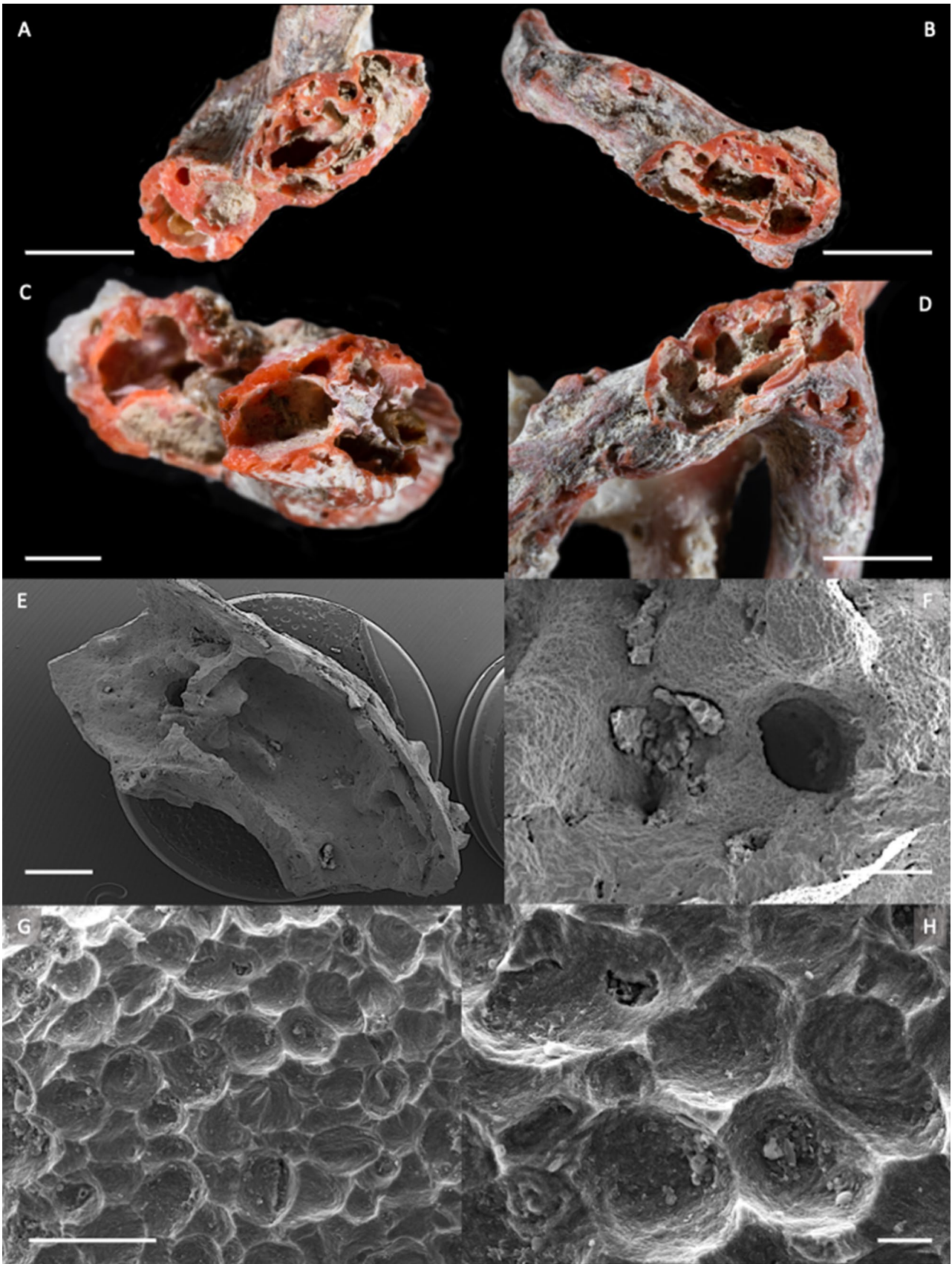


Fig. 7 Microscopic analyses of the sponge erosion on Sciacca red coral. **A–D** View of the boring channels as seen from the stereomicroscope. **E–H** SEM pictures of the boring chambers in longitudinal view with pit scars in evidence. **A, C, D**=5 mm; **C, E**=2 mm; **F**=0.5 mm; **G**=50 µm; **H**=10 µm

formation of the Sardinian sample. In this region, red coral populations settle on granite substrates in a non-volcanic area. Nevertheless, ROV explorations have recently recorded numerous dead mesophotic red coral populations in different Sardinian localities, still in place by the time of the observations, as well as a few small deposits of fragments (Carugati et al. 2022; Toma et al. 2022a). It is possible that, at least locally, a series of mass mortality events, of unknown origin, triggered the accumulation of coral skeletons that successively lithified at the foot of the rocky terraces. Deep mass mortality events of red coral have been indeed documented in other Mediterranean areas related to pollution or hot water masses linked to seismic events (Rivoire 1987, 1991; Bavestrello et al. 2014). Recent ROV surveys have never detected cemented coral rubbles at the base of offshore rocky reliefs, but they can be masked by a sediment layer or by encrusting algae. The occurrence of large coral branches in the detritic under overhanging rocks hosting red coral populations has indeed been reported by Sardinian fishermen (Scarpati M., pers. comm) (Fig. 2E, F).

Sponge erosion in the sub-fossil red coral

Precious red coral colonies are characterized by a scleraxis composed of Mg-calcite organized in an extremely compact structure of acicular to lamellar calcite crystals, forming fan-like structures (Cortesogno et al. 1999; Vielzeuf et al. 2008). This carbonatic matrix is frequently bored by sponges that expand their choanosomal tissue in chambers of different shapes, interconnected by tunnels. Boring sponges have developed a unique cellular means to penetrate the substrate (see Bergquist 1978; Pomponi 1980). The sponges bore using etching cells that separate chips from the substrate (Rützler and Rieger 1973; Zundevich et al. 2007; Benedetti et al. 2016; 2020). The study of the ultrastructure of the wall of the perforation chambers has put evidence that the erosion scars resulting from the etching process have morphological features that are genus-specific (Vacelet 1999; Calcinai et al. 2003, 2004).

Although the different micro-etching characteristics are particularly useful for distinguishing the generic identity of ichnotaxa in the paleontological study of macro-boring communities (Budd and Perkins 1980) until now, no attempt was conducted in this direction for the Sciacca red coral. According to the findings of Calcinai et al. (2003, 2004), it is possible to attribute the boring agent of the Sciacca red coral to a species of the genus *Siphonodictyon* based on the

micro-layered concentric pattern reaching the centre of the pits. In the Mediterranean Sea, two species of *Siphonodictyon*, *Siphonodictyon insidiosa* (Johnson, 1899) and *Siphonodictyon coralliirubri* Calcinai, Cerrano and Bavestrello, 2007, are recognized (Calcinai et al. 2007). The average size of the pits suggests that, very likely, *S. coralliirubri* is responsible for the bioerosion recorded in the Sciacca red coral.

It is important to underline that sponge erosion is a rare event in the studied Sciacca material, as already reported by Bavestrello et al. (2021). This situation seems unusual: in fact, in other places, dead red coral colonies have always been recorded as deeply etched by sponge borers (Bavestrello et al. 1996). This observation would be in accordance with a catastrophic mass mortality event followed by a rapid sediment cover-up of the deposits coupled with additional chemical processes preventing the boring activity of sponges.

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Data availability The authors confirm that the data supporting the findings of this study are available within the article.

Declarations

Conflict of interest No potential competing interest was reported by the authors.

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