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EXCEPTIONALLY PRESERVED CORAL BANK AND SEAGRASS MEADOW FROM THE LOWER PLEISTOCENE OF FAUGLIA (TUSCANY, ITALY).

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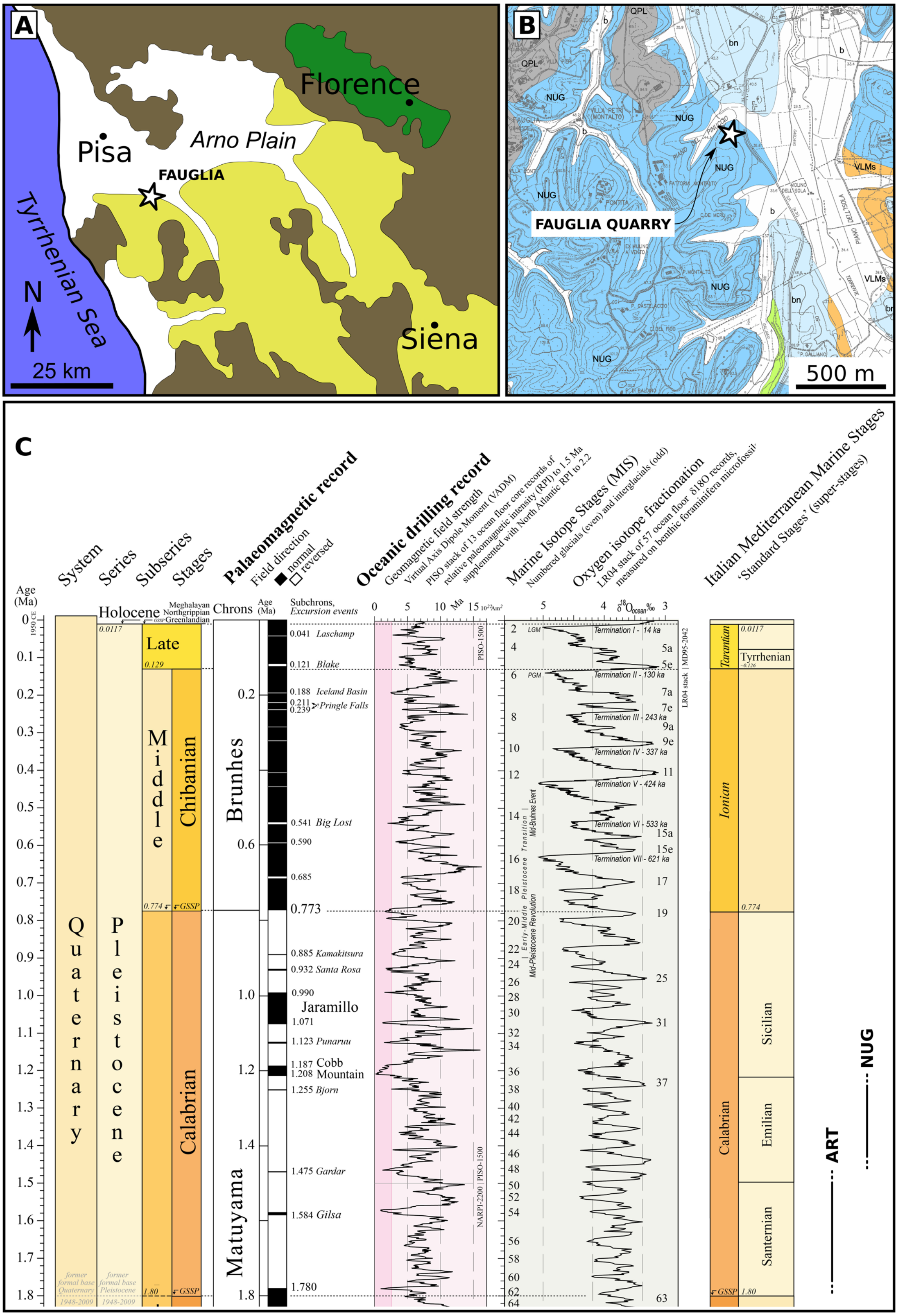
ABSTRACT: Near the Fauglia village (Tuscany, Italy), a Calabrian (lower Pleistocene) stratigraphic succession crops out in a sand quarry. This succession is comprised of an alternation of sands and silts featuring an exceptionally preserved *Posidonia oceanica* meadow (preserving *in situ* rhyzomes and loose leaves) and an abundant and diverse assemblage of fossil invertebrates that also includes the zooxanthellate coral *Cladocora caespitosa*. The latter forms a rare example of a *Cladocora* bank, exhibiting peculiar fossilization modes that range from compound molds to recrystallized corallites, overlain by an oyster reef. Paleoenvironmental considerations, based on a comparison with analogue environments from the present-day Mediterranean region, indicate a shallow-water, protected marine environment characterized through time by a seagrass meadow (ranging in water depth from 10 to 35 m), a subsequent coral bank (5 to 20 m water depth), and finally by an oyster reef in water shallower than 5-10 m. Throughout the 6-m-thick stratigraphic section, five taphofacies are recognized, showing different diagenetic signatures. Subsequent stages of aragonite dissolution and calcite re-precipitation are thus hypothesized, revealing a complex and unusual diagenetic history for this remarkable find of exceptionally preserved Pleistocene coral bank and seagrass meadow.

Keywords**:** *Cladocora caespitosa*, *Posidonia oceanica*, Calabrian, fossil diagenesis, taphofacies.

1. INTRODUCTION

Throughout the Cenozoic Era, the Mediterranean region has been characterized by the presence of coral reefs (Esteban, 1996, Bosellini & Perrin, 2008; Perrin & Bosellini, 2012; Vertino et al., 2014). In particular, the Mediterranean can presently boast its own and unique kind of coral bioconstructions: the *Cladocora caespitosa* (Linnaeus, 1767) banks. *Cladocora caespitosa*, also known as "cushion coral", is the largest and most common species of symbiont-bearing, colonial scleractinian coral of the Mediterranean (e.g., Peirano et al., 2004). Although scattered colonies of *C. caespitosa* are relatively common, large banks (i.e., more than a meter high and several meters wide) consisting of a large number of coalescent colonies are relatively rare, with only about ten of these structures being currently known basinwide (Peirano et al., 2001; Kersting & Linares, 2012; El Kateb et al., 2016; Chefaoui et al., 2017). These banks do not grow up to the water surface like their tropical counterparts and usually develop in relatively protected settings (with the two largest banks occurring in a marine lake and in an extinct volcanic caldera, respectively), where they are sheltered by violent storm waves (Kružić & Benković, 2008; Kersting & Linares, 2012; Hadjioannou et al., 2016; Chefaoui et al., 2017). Similar to their living counterparts, large fossil *C. caespitosa* banks are also rare (El Kateb et al., 2016; Coletti et al., 2018b). In the present-day scenario of climate warming, *C. caespitosa* is severely threatened by heat waves, pollution and human coastal activities (Rodolfo-Metalpa et al., 2006; Kružić & Benković, 2008; Peirano et al., 2009; Kružić et al., 2012; El Kateb et al., 2016). As a consequence of that, *C. caespitosa* is listed as a protected species and its banks are regarded as protected habitats (European Community, 1992; Casado-Amezúa et al., 2015). Because of the rarity of *C. caespitosa* banks, the environmental conditions favorable to their development as well as the associated fauna are relatively poorly known and loosely constrained, with only few studies existing for both recent and fossil occurrences (e.g., Conato & Dai Pra, 1980; Fornós et al., 1996; Bernasconi et al., 1997; Aguirre & Jiménez , 1998; Koukouras et al., 1998; Drinia et al., 2010; Amorosi et al., 2014; Pitacco et al., 2014; Chefaoui et al., 2017; Monnier et al., 2021). The investigation of fossil examples poses further difficulties since diagenetic processes have the potential to skew fossil assemblages via the


A
Florence
Pisa
Arno Plain
FAUGLIA
Tyrrhenian Sea
N
25 km
Siena
B
QPL
bn
b
NUG
VLMs
FAUGLIA QUARRY
500 m
C
System
Series
Subseries
Stages
Palaeomagnetic record
Field direction
◆ normal
◇ reversed
Oceanic drilling record
Geomagnetic field strength
Virtual Axis Dipole Moment (VADM)
PISO stack of 13 ocean floor core records of relative paleomagnetic intensity (RPI) to 1.5 Ma supplemented with North Atlantic RPI to 2.2
Marine Isotope Stages (MIS)
Numbered glacials (even) and interglacials (odd)
Oxygen isotope fractionation
LR04 stack of 57 ocean floor δ18O records, measured on benthic foraminifera microfossil
Italian Mediterranean Marine Stages
'Standard Stages' (super-stages)
Age (Ma)
Holocene
Meghalayan
Northgrippian
Greenlandian
Chrons
Subchrons, Excursion events
0.0117
Late
0.129
Middle
Chibanian
0.774
GSSP
Quaternary
Pleistocene
Calabrian
1.80
former formal base Quaternary 1948-2009
former formal base Pleistocene 1948-2009
Brunhes
Matuyama
0.041 Laschamp
0.121 Blake
0.188 Iceland Basin
0.211
0.239 Pringle Falls
0.541 Big Lost
0.590
0.685
0.773
0.885 Kamakitsura
0.932 Santa Rosa
0.990
Jaramillo
1.071
1.123 Punaruu
1.187 Cobb
1.208 Mountain
1.255 Bjorn
1.475 Gardar
1.584 Gilsa
1.780
10²²Am²
PISO-1500
NARPI-2200 | PISO-1500
δ18Oocean‰
LGM
PGM
Termination I - 14 ka
Termination II - 130 ka
Termination III - 243 ka
Termination IV - 337 ka
Termination V - 424 ka
Termination VI - 533 ka
Termination VII - 621 ka
Mid-Brunhes Event
Early-Middle Pleistocene Transition
Mid-Pleistocene Revolution
LR04 stack | MD95-2042
Tarantian
Tyrrhenian
~0.126
Ionian
Sicilian
Emilian
Santernian
ART
NUG

preferential dissolution of the aragonitic remains (e.g., Cherns & Wright, 2000; Cherns et al., 2011), and this is quite unfortunate as both *C. caespitosa* and many of the reef-associated shell-bearing invertebrates feature skeletal parts that consist of aragonite (Koukouras et al., 1998; Pitacco et al., 2014).

Similar to *C. caespitosa*, *Posidonia oceanica* (Linnaeus) Delile, 1813 is a shallow-water Mediterranean endemic species. The meadows formed by this seagrass species comprise one of the most biologically diverse and ecologically relevant ecosystems of the Mediterranean Sea (Duarte & Chiscano, 1999; Guidetti, 2000; Short et al., 2007). Further recalling *C. caespitosa*, *P. oceanica* is an ecosystem engineer: the meadow stabilizes the seafloor through its roots and rhizomes network, while the leaves baffle floating particles, thus favoring local sedimentation (Boudouresque & Jeudy de Grissac, 1983; Moriarty & Boon, 1989; De Falco et al., 2000; Gacia & Duarte, 2001). Among its roots and canopy, *P. oceanica* hosts large communities of epiphytes that remarkably contribute to the local production of bioclastic sediment (Mazzella et al., 1989; Langer, 1993; De Falco et al., 2008; Mateu-Vicens et al., 2014). In addition, by sustaining and providing shelter to a broad variety of large-sized animals, the seagrass meadow comprises a key element of the Mediterranean biodiversity (Francour, 1997; Guidetti, 2000). Similar to the *Cladocora* banks, the *Posidonia* meadows are also endangered by human activities and climate change (European Community, 1992; Francour et al., 1999; Burkholder et al., 2007; Balata et al., 2010; Hendriks et al., 2017; Sanchez-Vidal et al., 2021). However, while living seagrass meadows can cover tens of thousands of square kilometers, very few indisputable fossil examples of such ecosystems are known as the seagrass organic materials are rarely featured in the fossil record due to their poor preservation potential (Brasier, 1975; Brunetti & Vecchi, 2005; Moissette et al., 2007; Reich et al., 2015; Koskeridou et al., 2019).

Here, we report on a Pleistocene outcrop in Tuscany (central Italy) that features the exceptional occurrence of both a fossil seagrass meadow and a *C. caespitosa* bank. Moving from sedimentological, taxonomic and taphonomic observations, our preliminary characterization of this outcrop reveals spectacularly preserved examples of both these important Mediterranean biocoenoses. This paper aims at documenting the sedimentological features and paleontological content of the outcrop in order to reconstruct the paleoenvironmental and depositional conditions. Taphonomic features of the outcrop are also examined and different taphofacies recognized to gain insights into the different styles of preservation and into the fossilization paths behind the preservation of the *Cladocora* bank and the *Posidonia* meadow. The paleoenvironmental reconstruction and taphonomic observations carried out in this study have the common goal of promoting this remarkable paleontological site.

2. GEOLOGICAL SETTING

The fossiliferous deposits studied herein are exposed at an active sand quarry located near the Fauglia village (Pisa Province, Tuscany, Italy), along the left bank of the Isola stream (geographic coordinates: 43° 33'52" N, 10°31'56" E). The succession exposed at the Fauglia quarry (also known as Montalto quarry) takes its place in the northern sector of the Tora-Fine Basin, a post-collisional basin of the Northern Apennine chain (Mazzanti, 2016). Comprising one of the most external basins of mainland Tuscany, the Tora-Fine Basin was filled by upper Miocene to Pliocene sediments under extensional control (Bossio et al., 1999). During the subsequent early Pleistocene, a changing tectonic regime caused a substantial restructuring of the basin borders as well as significant latitudinal differences in deposition, with the surroundings of Fauglia acting as the location of conspicuous marine sedimentation (Bossio et al., 1999) (Fig. 1A). In the study area, the Pleistocene units overlie Pliocene marine deposits (Marroni et al., 1990) and include, in ascending stratigraphic order, the Morrona Formation, the Sabbie di Nugola Vecchia Fm and the Casa Poggio ai Lecci Fm (Mazzanti, 2016) (Fig. 1B), all of which have sometimes been mapped as comprising a single lithostratigraphic unit, namely, the Sabbie e Argille ad *Arctica islandica* Fm (e.g., Bossio et al., 1999).

The Morrona Fm (hereinafter, ART) includes infralittoral and upper circalittoral sands and clays that have been referred to the lower Calabrian (i.e., “Santernian” according to the ‘Italian Marine Stages’ regional scheme; Gibbard & Cohen, 2008), although the top of the formation might belong to the mid-Calabrian (i.e., “Emilian”) (Boschian et al., 2006; Catanzariti & Da Prato, 2020). These deposits are rich in fossil remains of macro-invertebrates, including bivalves, gastropods, brachiopods, echinids, corals, crustaceans and annelids. Furthermore, “northern guests” such as *Arctica islandica* (Linnaeus, 1767) (whose first occurrence in the Mediterranean Basin occurs around the base of the Calabrian; Gibbard & Head, 2010; Crippa et al., 2019) are typically present (Mazzanti, 2016). In the study area, the maximum thickness of the ART is estimated at about 50 m (Mazzanti, 2016).

The Sabbie di Nugola Vecchia Fm (hereinafter,

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Fig. 1 - A) Simplified geological map of Tuscany, showing the areas of Mio-Pleistocene outcrop, and the location of the study area (modified from Carnevale et al., 2008). White: alluvial deposits; yellow: Neogene and Quaternary marine deposits; green: Quaternary continental deposits; brown: substratum; star: study site. B) Schematic geological map of the study area, showing the location of the investigated quarry (after Regione Toscana, 2006-2009). Orange; Villamagna Fm (= VLMs; Pliocene); green: Morrona Formation (= ART; lower Pleistocene); blue: Sabbie di Nugola Vecchia Fm (= NUG; lower Pleistocene); gray: Casa Poggio ai Lecci Fm (= QPL; Middle Pleistocene); white: alluvial and fluvioglacial deposits (= b; Recent), and alluvial terraces (= bn; Recent); star: study site. C) Chronostratigraphic assignment of the lower Pleistocene sedimentary units exposed in the vicinities of Fauglia (right corner) in the framework of the 2020-updated version of the "Global chronostratigraphical correlation table for the last 2.7 million years" (modified from https://stratigraphy.org/ICSchart/QuaternaryChart.pdf) (Cohen & Gibbard, 2019). See the main text for further details and data sources.

NUG) consists of fine-grained, ochre-colored sands punctuated by conglomerates and calcarenite lenses. Referred by Mazzanti (2016) to the mid-Calabrian (i.e., Emilian), these infralittoral and upper circalittoral deposits are typically poor in macroscopic fossils, although rare bivalves (ostreids and pectinids) are locally present. The NUG reaches a maximum thickness of more than 100 m (Mazzanti, 2016).

The Casa Poggio ai Lecci Fm (hereinafter, QPL) consists of conglomerates with subordinate sands and silts that deposited in a transitional environment (including deltaic, limnic and lagoonal settings; Barsotti et al., 1974) during the Chibanian (middle Pleistocene). Macro-invertebrates from these strata are very scarce and include rare bivalves and gastropods. The thickness of the QPL ranges between 1 and ca. 30 m (Mazzanti, 2016).

Fig. 2 - Outcrop views of the Lower Pleistocene deposits cropping out at the Fauglia quarry. A) Eastward panoramic view of the analyzed outcrop exposed at the Fauglia quarry. B) Northward panoramic view of the analyzed outcrop exposed at the Fauglia quarry. The red arrow indicates a bluish-grayish sediment lens. Note people for scale.

According to Bossio et al. (1993) and Tani & Gazzerro (1999), the ART and NUG would respectively represent the transgressive and regressive portions of a single depositional cycle. However, Sarti et al. (2007, 2008) argued that these formations represent two distinct depositional cycles. In turn, there is consensus that the overlying QPL represents a subsequent transgression (e.g., Bossio et al., 1993; Sarti et al., 2008; Mazzanti, 2016).

The national (Mazzanti, 2016), regional (Regione Toscana, 2006-2009), and local (Marroni et al., 1990) geological cartographies agree in indicating that the fossiliferous deposits cropping out at the Fauglia quarry belong to the NUG (Fig. 1B), and such an assignment is embraced herein. However, the abundance of fossils at the study site is not typical for NUG and might suggest a different attribution of the strata cropping out therein. In other nearby Tuscan basins, *C. caespitosa* bioconstructions have been observed in deposits that are stratigraphically congruent with the ART (Sarti et al., 2007), but not in NUG-equivalent strata. That said, the co-occurrence of exceptionally preserved coral bank and seagrass meadow at the Fauglia quarry is, to the best of our knowledge, unique among the Pleistocene outcrops of western Tuscany; furthermore, correlations with previously established sections are further hindered by the lateral facies variability that characterizes the aforementioned deposits (see e.g. discussion on the stratigraphic position of the Argille e limi di Vigna Nuova di Peccioli in Mazzanti, 2016). Up to date, published works on the paleontological aspects of the Fauglia quarry have assigned the stratigraphic succession cropping out at the Fauglia quarry to unnamed lower Pleistocene deposits (Brunetti et al., 2008; Chirli & Forli, 2017; Cresti & Forli, 2020) or to the NUG (Berta et al., 2015).

3. METHODS

The outcrop studied in the present paper is 6 m high and can be followed along a 66-m-long subvertical surface at the Fauglia quarry (Figs. 1, 2). A stratigraphic log was measured by using a Jacob's staff and later refined with the support of laser grain-size analyses (see below). In the field, strata were described through observations on their lateral continuity, thickness, color, grain-size, vertical grading, boundaries, sedimentary structures and fossil content. Ten sediment samples were collected at different stratigraphic heights (see Fig. 3), with a particular attention to the lateral variability of the stratigraphic layers (e.g., the thickness of the *C. caespitosa* bank varies horizontally from a minimum of 10 cm to a maximum of 200 cm, see Fig. 2A).

Sediment samples were analyzed with a Malvern Mastersizer 2000E™ Laser Granulometer at the Università degli Studi di Milano-Bicocca for gathering grain-size data. From each sample, three subsamples were obtained, and each subsample was measured three times. Grain-size data were processed with the Grain Size Analysis Program GRADISTAT (Blott & Pye, 2001). This software provides a physical description of the textural group which the sample belongs to, with the term “mud” referring to silt and clay indifferently, and the sediment name after Folk (1954) (see Table 1).

In the field, invertebrate and plant fossil specimens were described according to their stratigraphic position, distribution, orientation, articulation degree, and style of preservation; some macrofossils were also carefully sampled from each stratigraphic horizon. Ca. 300 fossil specimens were collected from the field with hammers, chisels and awls. They were subsequently cleaned from the sediment by using a scalpel and a small brush, after which they were stored in the laboratories and collections of the G.A.M.P.S. (Gruppo A.V.I.S. Mineralogia Paleontologia Scandicci) permanent exhibition.

For paleoecological and paleoenvironmental purposes, we compared our data with known occurrences of invertebrates and plants in modern marine environments (e.g., Duarte, 1991; Campbell et al., 1998; Luckenbach et al., 1999; Kružić & Benković, 2008; Infantes et al., 2009; Kersting & Linares, 2012; Chefaoui et al., 2017; Kersting et al., 2017; Christianen et al., 2018).

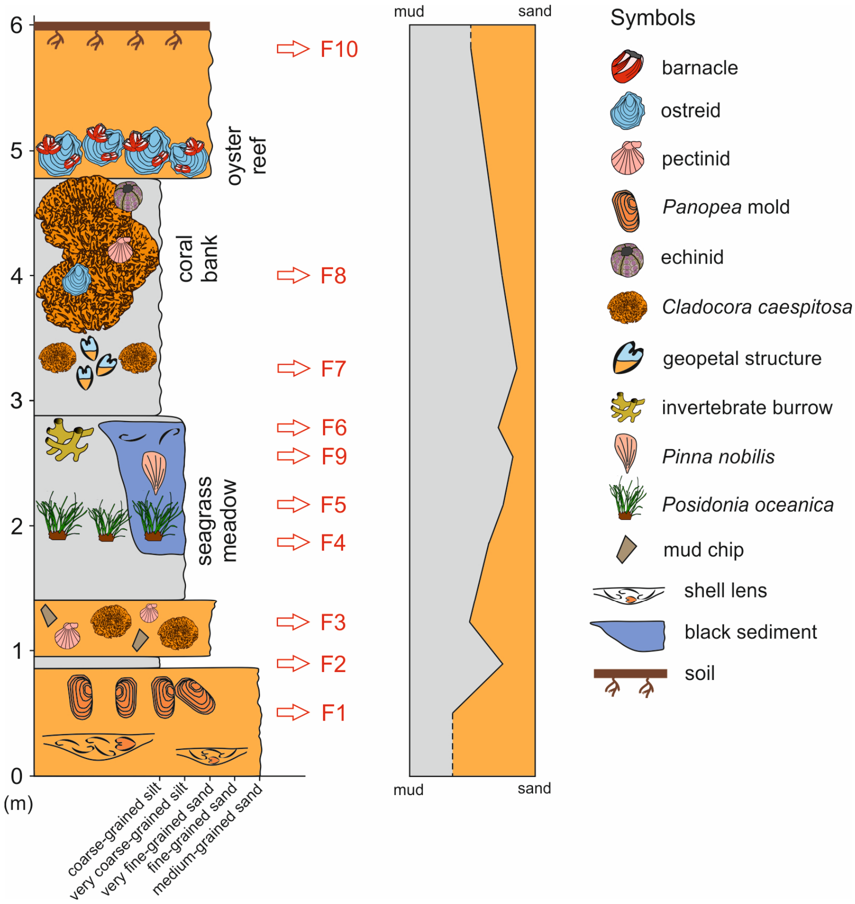

Fig. 3 - Stratigraphic log measured at the Fauglia quarry, with indication of the lithology and fossil content, and associated sand/mud grain-size diagram based on laser granulometer analyses. The stratigraphic position of the collected samples is also indicated.

For taphonomic investigations, fossil invertebrates and plants were examined under standard optical stereomicroscopes at the Università degli Studi di Milano-Bicocca and Università di Pisa. Two thin sections were also prepared from two articulated bivalve specimens featuring internal geopetal structures. Bivalves were first embedded in epoxy resin and then cut orthogonal to the hinge and parallel to the shell height. The thin sections were thus observed under a Leica Leitz Laborlux S transmitted light optical microscope at the Università degli Studi di Milano-Bicocca for petrographic and microtextural analyses. Finally, ca. 100 fossil specimens were also exposed under the long wavelength (300-400 nm) ultraviolet (UV) light of a Wood lamp in the G.A.M.P.S. darkroom for studying the phosphorescence phenomena of the calcite shells as well as for enhancing the exhibition impact of the fossil collection.

4. RESULTS

4.1. Sedimentological description

The stratigraphic section measured at Fauglia features an alternation of silty sands and sandy silts, devoid of sedimentary structures, and rich of macrofossils (Fig. 3). The lateral variability of the exposed deposits is high, which makes the sedimentological characterization of the outcrop difficult. A detailed stratigraphic log was built on the basis of the laser grain-size analyses, which indicate poorly to very poorly sorted sandy mud and muddy sand, usually displaying a polymodal distribution (Table 1). In particular, the percentage of sand varies between 14.8% and 64.8%, with sand being dominant at the bottom and top of the section. The percentage of mud ranges from 35.2% to 85.2%, that is, mud is generally more abundant than the sand-grained sediment. The abundance of mud peaks between 200 and 330 cm above the base of the measured section (hereinafter, abs) (Fig. 3, Table 1). The sand component decreases through the section up to ca. 330 cm abs, then increases upwards until the top of the stratigraphic log.

Up to 85 cm abs, the stratigraphic succession consists of yellowish brown sands comprised of coarse-silty medium sand. These sands host decimeter-sized shell lenses with disarticulated bivalves, and a laterally continuous shell bed characterized by articulated infaunal bivalves (Fig. 3). Following 10 centimeters of a muddier and more cemented deposit, another 44-cm-thick laterally continuous sandy interval is recognized. This is characterized by very-coarse-silty very-fine sand with abundant disarticulated bivalves and common mud chips (Fig. 3). Up to 287 cm abs, the dominant sediment is a grayish brown very-fine-sandy very-coarse silt; the sand percentage decreases upwards. This interval hosts abundant plant remains that are found ca. 200 cm abs. Moving laterally, this sediment is characterized by dark, bluish-grayish, laterally discontinuous lenses. These lenses span from few to few tens of meters of lateral extension (Fig. 2B) and are characterized by the presence of common shell material and rare vertical invertebrate burrows (Fig. 3). Above this deposit, a laterally continuous, 190-cm-thick layer occurs. It consists of yellowish-brownish, coarse silts that become more sandy upwards. These silts host several bivalve specimens, featuring internal geopetal structures, as well as a conspicuous coral bank, up to ca. 200 cm in thickness (Fig. 3). The stratigraphic log is topped by a 120-cm-thick layer with a sharp base consisting of very-coarse-silty very-fine yellowish sand. This interval is characterized by the presence of clusters of bivalve shells that comprise a true oyster reef (*sensu* Puffer & Emerson, 1953).

4.2. Faunal assemblage

As also observed with respect to the sedimentological traits, the lateral variability of the paleontological content of the studied outcrop is high; nonetheless, different fossil assemblages can be recognized throughout the stratigraphic section. Up to 2 m abs, below the seagrass meadow layer, the macrofossil assemblage is dominated by mollusks (mostly bivalves) (Fig. 3). At the bottom, the sandy deposit is characterized by decimeter -sized lenses of common disarticulated pectinid valves together with common gastropod, venerid and cardiid specimens preserved as internal molds. The latter belong to the genera *Chama*, *Pelecyora*, and *Procardium* (Fig. 4). The overlying sediment hosts a horizon with abundant *Panopea* specimens preserved as both internal and external molds in life position (Fig. 4). Above this shell bed, the sandy sediment is characterized by abundant bivalve shells, mainly pectinids, and by common isolated, fasciculate, centimeter- to decimeter-sized patches of *C. caespitosa* corallites. Ca. 2 m abs, a continuous layer characterized by exquisitely preserved, abundant brownish remains of *P. oceanica* is present (Fig. 5A, B). Few large specimens of *Pinna nobilis* Linnaeus, 1758 (Fig. 5C) and abundant benthic foraminifera were found associated with the *Posidonia* meadow. Moving laterally, the sediment changes to dark gray, organic-rich lenses (Fig. 3), where few representatives of the genera *Solen*, *Pinna*, and small infaunal bivalves occur. In the overlying silts, abundant mollusk specimens are preserved as completely recrystallized shells or contain geopetal structures. These include rare remains of *Lutraria oblonga* (Gmelin, 1791), abundant specimens of *Pelecyora* sp., common mitiloids (among which the genus *Modiolus* has been recognized), and rare gastropods of the families Turritelidae and Naticidae. A few centimeters above, isolated colonies of *C. caespitosa* start to crop out (Fig. 3), and they are overlain by the *Cladocora* bank, which displays a thickness variable between ca. 10 and 200 cm (Fig. 5D-F). The coral bank is associated with abundant pectinids, including specimens of *Pecten*, *Flexopecten*, *Mimachlamys, Anomia* (Fig. 6A-C) and common ostreids (e.g., *Ostrea edulis* Linnaeus, 1758, Fig. 6D) that are mostly preserved in life position. Regular echinoids also occur in the coral bank. Above the bank, a discontinuous oyster reef (*sensu* Puffer and Emerson, 1953) is present, being dominated by abundant specimens of *O. edulis* that are pervasively encrusted by balanid barnacles and vermetid gastropods (Figs. 3, 6E, F). During laboratory analyses, benthic and planktonic foraminifera, ostracods, and erect bryozoans were also detected within

Sample	Stratigraphic height (cm)	Sample type	Sorting	Sediment name	Textural group	Gravel %	Sand %	Mud %
F10	590	Unimodal	Poorly sorted	Very coarse silty very fine sand	Muddy sand	0	51.4	48.6
F8	ca. 400	Trimodal	Very poorly sorted	Coarse sandy coarse silt	Sandy mud	0	26.0	74.0
F7	330	Bimodal	Very poorly sorted	Very fine sandy coarse silt	Sandy mud	0	14.8	85.2
F6	280	Trimodal	Very poorly sorted	Very fine sandy very coarse silt	Sandy mud	0	29.0	71.0
F9	260	Trimodal	Very poorly sorted	Very fine sandy very coarse silt	Sandy mud	0	17.3	82.7
F5	220	Trimodal	Very poorly sorted	Very fine sandy very coarse silt	Sandy mud	0	25.0	75.0
F4	190	Trimodal	Very poorly sorted	Very fine sandy very coarse silt	Sandy mud	0	36.6	63.4
F3	120	Unimodal	Poorly sorted	Very coarse silty very fine sand	Muddy sand	0	51.9	48.1
F2	90	Polymodal	Very poorly sorted	Medium sandy coarse silt	Sandy mud	0	24.9	75.1
F1	ca. 50	Bimodal	Very poorly sorted	Coarse silty medium sand	Muddy sand	0	64.8	35.2

Tab. 1 - Grain-size characterization of the collected sediment samples.

samples from the whole succession. Further micropaleontological analyses are definitively needed for providing a comprehensive description of the microscopical fossil assemblage.

It is worth noting that “northern guests” such as e.g. *Arctica islandica* were not detected among the Fauglia fossil invertebrates, in contrast with previous reports by Chirli & Forli (2017). Although this observation may prove of some litho- and chronostratigraphical significance (see e.g. the distribution of the finds of northern guests across the lower Pleistocene formations mentioned by Mazzanti, 2016), it could also reflect taphonomic or sampling biases as well as the local establishment of unfavourable paleoenvironmental conditions (see e.g. Crippa et al., 2019 for an overview of the varying habitat preferences of *A. islandica* across the Italian Pleistocene localities). Thus, for the moment being, we refrain from discussing the apparent absence of northern guests at the Fauglia quarry.

A few elasmobranchs teeth are also known from the Fauglia quarry. Including a carcharhine (*Carcharhinus plumbeus* (Nardo, 1827)) and an eagle ray (Myliobatidae indet.), these specimens come from displaced quarry debris; therefore, their stratigraphic whereabouts are unfortunately unknown. Another vertebrate fossil, consisting of an isolated pinniped calcaneum assigned to an indeterminate genus and species of Monachini (monk seals and relatives), was also described from the Fauglia quarry by Berta et al. (2015).

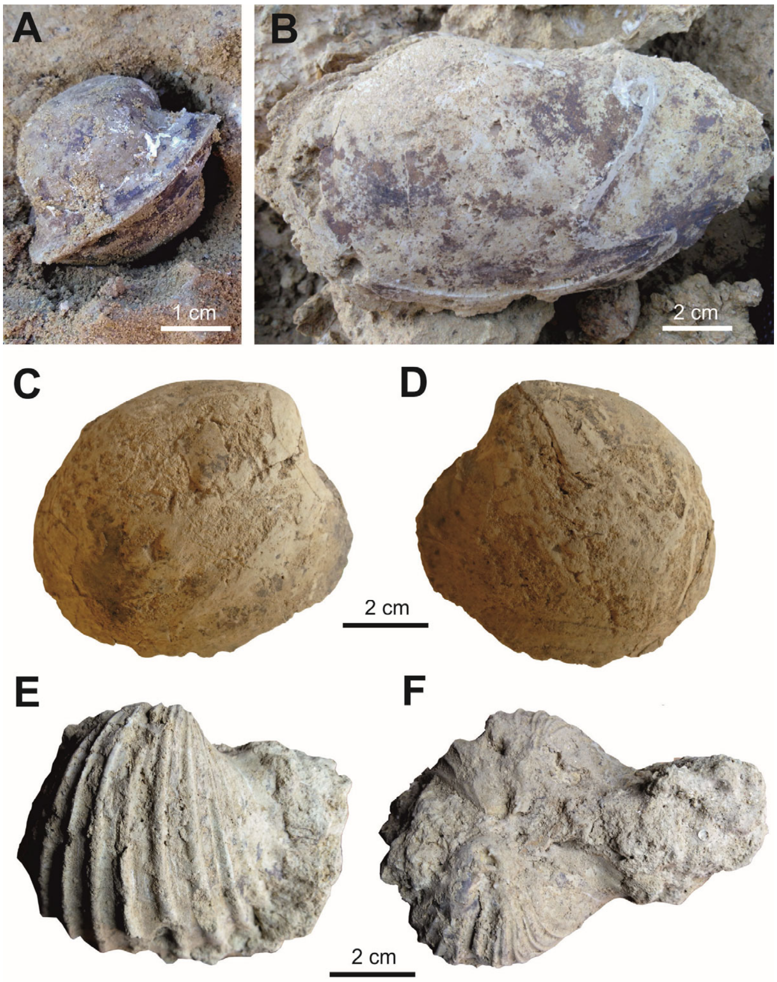

Fig. 4 - Examples of the faunal assemblage from below the *Posidonia*-rich interval. A) Internal mold of *Chama* sp. B) Internal mold of *Panopea* sp. C, D) External views of an internal mold of *Pelecyora* sp. E, F) External and umbonal views of an internal mold of *Procardium* sp.

4.3. Taphonomy

In ascending stratigraphic order, five different taphofacies (i.e., facies defined on the basis of diagnostic taphonomic traits; Speyer & Brett, 1986) have been recognized. Individuation of the taphofacies followed the criteria proposed by Gonçalves Garcia et al. (2021), based on biostratinomic observations (regarding e.g. the degrees of articulation, orientation and fragmentation), the presence or absence of encrusting episkeletozoans, and especially the macro- and microscopic evidence for the action of diagenetic mechanisms such as dissolution, cementation, recrystallization, neomorphism and cavity filling.

Taphofacies 1. Found at the base of the studied succession, this taphofacies consists of accumulations of disarticulated, usually fragmented, randomly disposed pectinid shells and calcite internal molds of articulated bivalve shells. Fully articulated specimens of the infaunal bivalves *Panopea* are preserved in life position as calcite internal molds and, less abundantly, as external molds (Fig. 7A). The internal molds are formed by sediment cemented by calcite. Aragonitic shells are not preserved, whereas the calcite ones retain their original mineralogical composition. Shells do not exhibit encrusting organisms, nor traces thereof. This taphofacies also includes isolated, reworked blocks of *C. caespitosa* preserved as external molds. The associated sediment is constituted by medium- to very fine-grained sands.

Taphofacies 2. This taphofacies hosts several exceptionally preserved plant remains in form of brownish mineralized remains of *P. oceanica*, including both rhizomes and leaves (Fig. 7B). Rhizomes are usually rather complete and preserved *in situ*, whereas leaves are detached, generally fragmented, and randomly oriented. They do not show any encrusted organisms or traces of encrustation. This taphofacies occurs in very coarse-grained brownish silt and is heteropic with Taphofacies 3.

Taphofacies 3. This facies is characterized by black peaty remains of *P. oceanica* as well as finely preserved aragonitic shells (Fig. 7C). Infaunal and semi-infaunal bivalves such as *P. nobilis* exhibit a well pre-

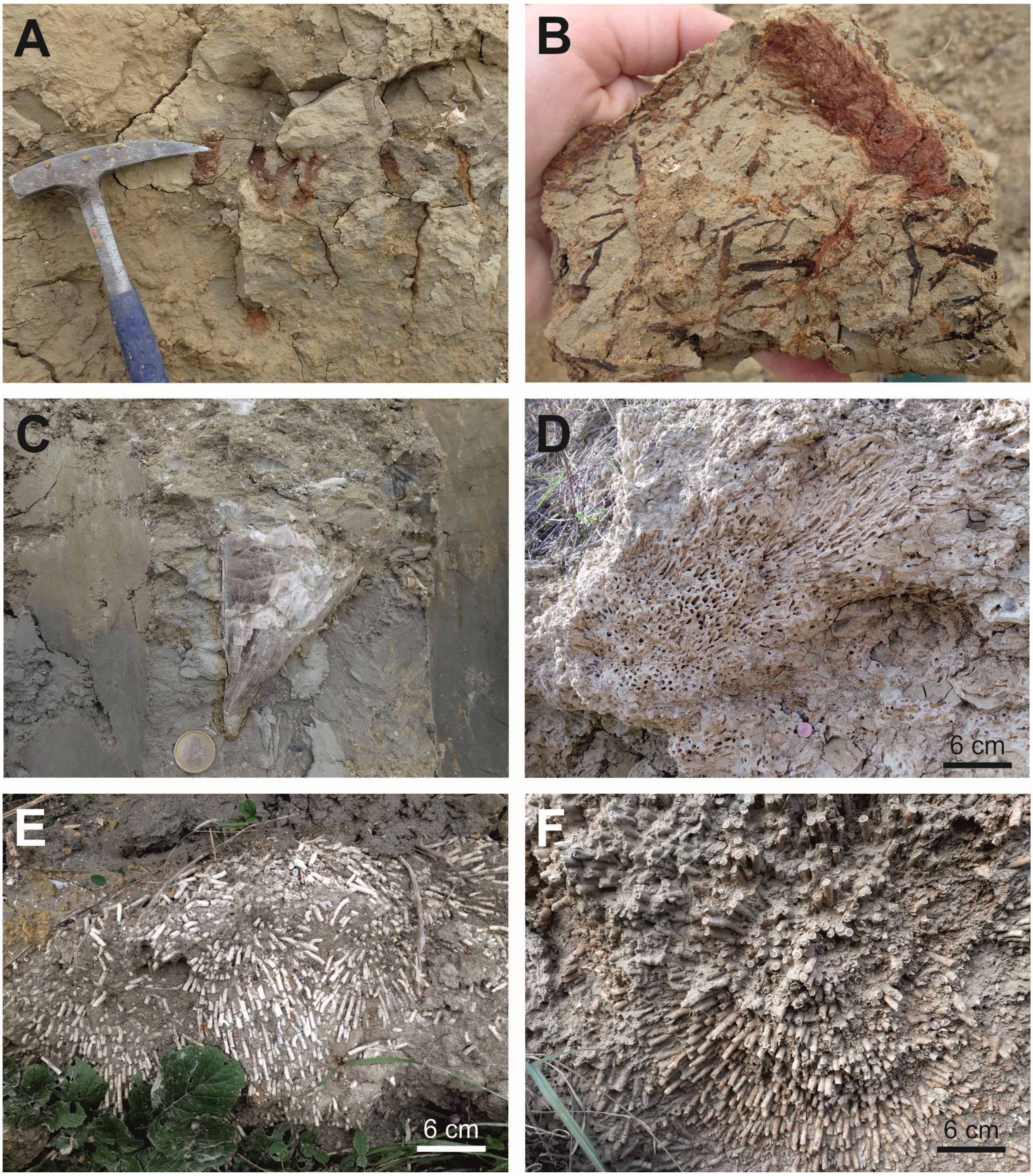

Fig. 5 - Field photos of the *Posidonia*-rich interval and *Cladocora caespitosa* bank. A) *Posidonia oceanica* rhyzomes in life position. B) Detail of *Posidonia oceanica* rhyzome and leaves. C) *Pinna nobilis* specimen in life position from a *Posidonia*-rich interval. D) *Cladocora caespitosa* bank preserved as external molds. E, F) *Cladocora caespitosa* clusters preserved with shells found *ex situ*.

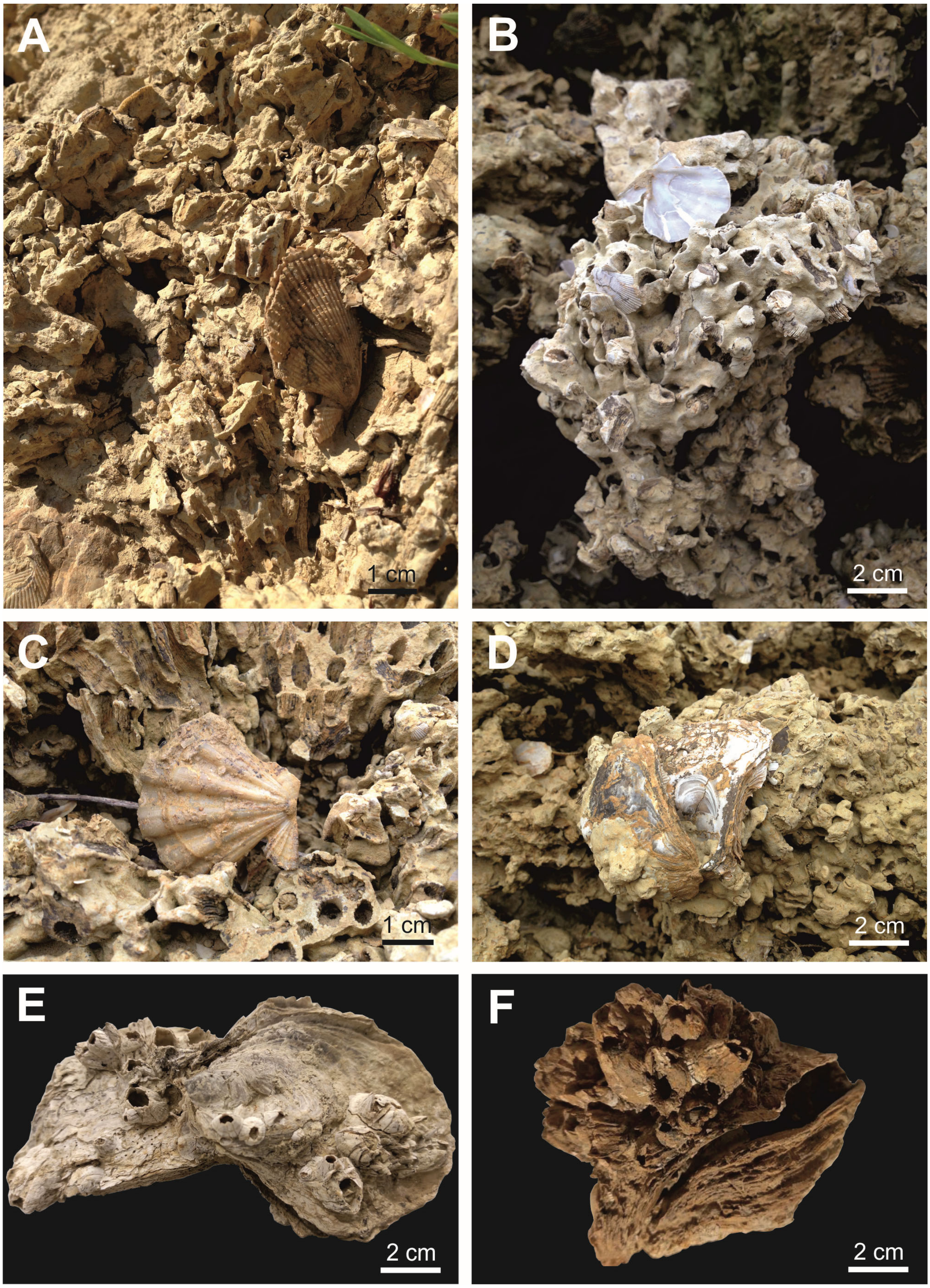

Fig. 6 - Field photos of the faunal assemblage associated to the *Cladocora caespitosa* bank and specimens from the oyster reef. A) Articulated specimen of *Mimachlamys* sp. preserved *in situ* in the coral bank. B, C) Disarticulated specimens of *Flexopecten* sp. D) Articulated ostreid specimen preserved *in situ* in the coral bank. E, F) Balanid barnacles encrusting *Ostrea edulis* specimens from the oyster reef.

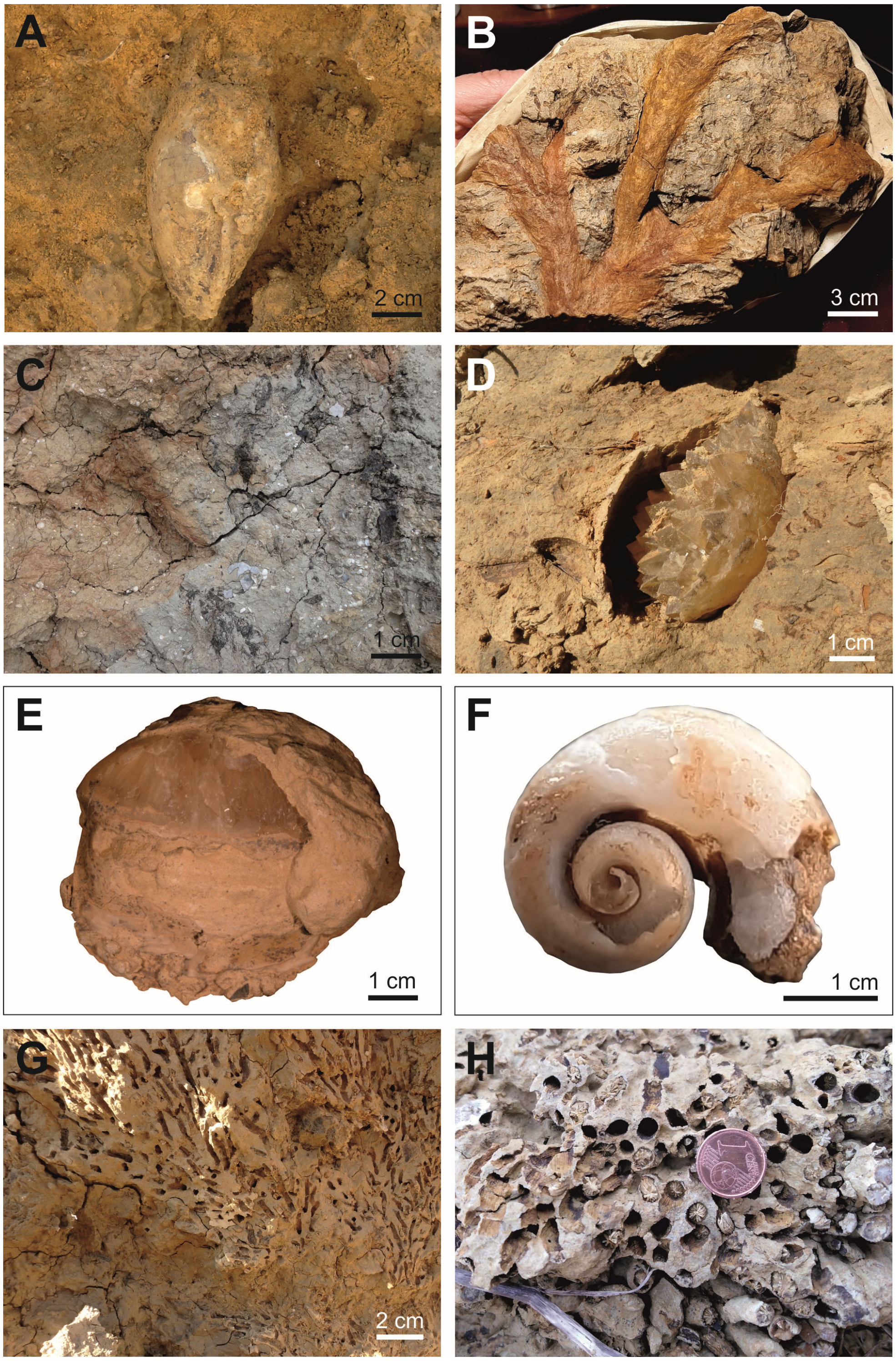

Fig. 7 - Different preservation styles from the five Fauglia taphofacies. A) Internal mold of *Panopea* specimen preserved in life position from Taphofacies 1. B) Exceptionally preserved, brownish *Posidonia oceanica* rhyzomes from Taphofacies 2. C) Brownish *Posidonia oceanica* remains from Taphofacies 2 and adjacent black peaty *Posidonia oceanica* remains in dark gray sediments from the Taphofacies 3. D) Geopetal calcite filling of a bivalve found in life position from Taphofacies 4 (note the large-sized euhedral crystals). E) Geopetal structure of a bivalve showing different generations of calcite cements from Taphofacies 4. F) Fully recrystallized naticid gastropod from Taphofacies 4. G) External molds of *Cladocora caespitosa* corallites from Taphofacies 5. H) Compound molds of the *Cladocora caespitosa* bank from Taphofacies 5.

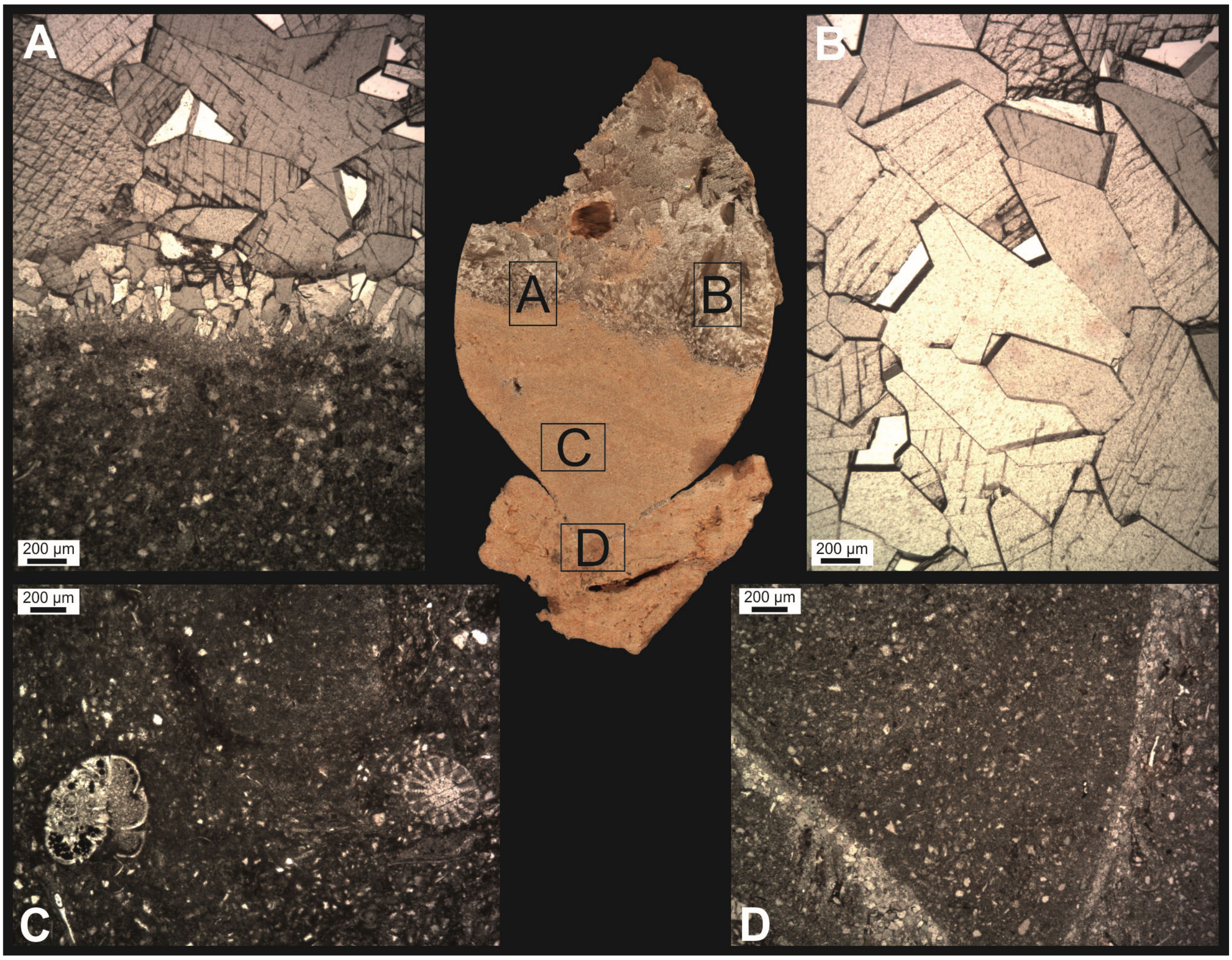

Fig. 8 - Thin section and microphotographs of the geopetal structure of a bivalve from Taphofacies 4. Note the laminated sediment infill. The microphotographs show a benthic foraminifer and a echinoid spine within the sediment (C), different calcite generations (A, B) and the substitution of the original shell by big calcite crystals (D).

served nacreous aragonitic shell and are fully articulated, in life position. The *P. nobilis* specimens usually display an incomplete upper portion, probably due to the low preservation potential of the fragile nacreous shell exposed to seawater (e.g. Bracchi et al., 2020). The surrounding sediment, a very coarse-grained silt, is dark-colored, probably as a consequence of the high amount of organic matter it hosts.

Taphofacies 4. In this taphofacies, mollusks are partially or completely recrystallized. They often exhibit geopetal structures that are recognizable in both bivalves and gastropods (Fig. 7D, E). Bivalves are preserved as fully articulated shells, usually in life position, and do not display any evidence of encrustation. *Cladocora caespitosa*, usually preserved in form of isolated *in situ* patches, is also represented by completely recrystallized corallites. Thin sections of the geopetal structures of infaunal bivalves (Fig. 8A-D) show at least four stages of mineral precipitation: the cementation of the terrigenous infill; the recrystallization of the shell following aragonite dissolution; and two steps of precipitation of large-sized calcite crystals filling the remaining voids. Petrographic analyses and reaction to 5%-diluted HCl reveal a calcite composition for all these phases. All the sampled materials coming from this taphofacies become luminescent under UV light excitation; the light emission fades in a few seconds after cessation of the UV exposition (Fig. 9A-E). This taphofacies is associated with coarse-grained silt.

Taphofacies 5. This taphofacies is dominated by a conspicuous, 66-m-long *C. caespitosa* bank in which the corallites are only preserved as compound molds or as recrystallized shells (Fig. 7G, H). Internal molds of articulated infaunal bivalves are also found. No aragonitic skeletons are observed, whereas calcite invertebrates such as pectinids, oysters and barnacles preserve their original shells and are found in life position, with fully articulated valves and mural plates, both in the coral bank and in the oyster reef (see Fig. 6). No fragmentation is observed in this facies. The disposition of encrusting organisms, such as balanid barnacles and vermetid gastropods, on the upper outer surface of the oyster shells positively indicates an *in-vivo* colonization of the latter (Luci and Lazo, 2014). This taphofacies is associated with coarse-grained silt and, in case of the oyster reef, with very fine-grained sand.

5. DISCUSSION

5.1. Paleoenvironmental reconstruction

The Fauglia succession features a high diversity of marine invertebrates (including bivalves, gastropods, barnacles, echinoids, corals, foraminifera, ostracods and erect bryozoans) and well-preserved marine plants. This fossil association can be related to three important coastal biotopes, namely: the *Cladocora* bank, the *Posidonia* meadow, and the oyster reef (Fig. 10). The latter, although presently extinct along the European coasts due to overfishing, is known to have been a common feature of coastal areas until one century ago (Airoldi & Beck, 2007; Christianen et al., 2018). The lowermost 1.5 m of the succession are characterized by transported shell fragments and *Cladocora* small clusters, but also feature *in situ* bivalves, mostly represented by sand-dwelling *Panopea* clams. Nowadays, *Panopea* clams (geoducks), the largest burrowing bivalves of the world, are found in a broad spectrum of unconsolidated substrates (from clay to gravel), down to a depth of 1 m below the sediment surface. They range in distribution from the intertidal zone to depths greater than 110 m, but concentrate between 3 m and 20-24 m of water depth (Campbell et al., 1998; Bureau et al., 2002). Therefore, considering the high density of *Panopea* specimens in the lowermost part of the Fauglia outcrop, a subtidal seafloor shallower than 24 m is here hypothesized.

Posidonia oceanica meadows are a major feature of the Mediterranean biota, covering a remarkable percentage of the shallow coastal areas (Vacchi et al., 2017). They usually extend from 0 to 50 m water depth, but mostly occur between 10 and 35 m, with the upper and lower limits being controlled by hydrodynamic energy and light penetration, respectively (Duarte, 1991; Piazzi et al., 2000; Infantes et al., 2009; Vacchi et al., 2017). The well-preserved *in situ* rhyzomes and the specimens of *P. nobilis* preserved in life position (a powerful seagrass meadow indicator; Vázquez-Luis et al., 2014; Reich et al., 2015), unambiguously indicate that the *Posidonia*-rich layer developed at less than 50 m water depth, and most likely between 10 and 35 m. Although the grain-size distribution of the sediment associated with the *Posidonia* remains could be related to the baffling effect of the plant leaves (Boudouresque & Jeudy de Grissac, 1983; Moriarty & Boon, 1989; De Falco et al., 2000; Gacia & Duarte, 2001; Reich et al., 2015), the grain-size of the sediment and the high content of organic matter (witnessed by the dark color of the deposit) might suggest a moderate to low-energy environment where the sedimentation rate was moderately high. Actually, marine sediments deposited under oxic conditions are generally characterized by a positive correlation between organic carbon content and sedimentation rate, with moderate amounts of organic carbon (i.e., 0.1-2%) being usually associated with moderately rapid sedimentation rates (i.e., 1-10 cm per 1000 yr.) (Müller & Suess, 1979; Stein, 1990).

Nowadays, *C. caespitosa* occurs between 5 and 35 m water depth; however, the largest majority of large-sized banks and beds with high densities of colonies occur between 5 and 20 m, and especially between 10 and 15 m (Kružić & Požar-Domac, 2003; Kružić & Benković, 2008; Kersting & Linares, 2012; El Kateb et al., 2016; Kersting et al., 2017; Mačić et al., 2019). The development of these bioconstructions seems to be related to a delicate balance between three environmental parameters, namely: i) water circulation and nutrient availability (which must be enough to feed the polyps), ii) adequate sheltering from storm waves that might destroy the delicate structure of *Cladocora* colonies, and iii) conditions of water clarity (necessary for the symbionts of the coral to thrive) (Kružić & Benković, 2008; Kersting & Linares, 2012; Chefaoui et al., 2017). These requirements are usually attained along coastlines with complex physiographies and sheltered bays characterized by fine-grained sedimentation; this pattern can be observed in both modern and fossil *Cladocora* banks (Chefaoui et al., 2017; Coletti et al., 2018b). The bank of Fauglia is remarkably similar to the large banks that currently occur along the eastern Adriatic coast (Kružić

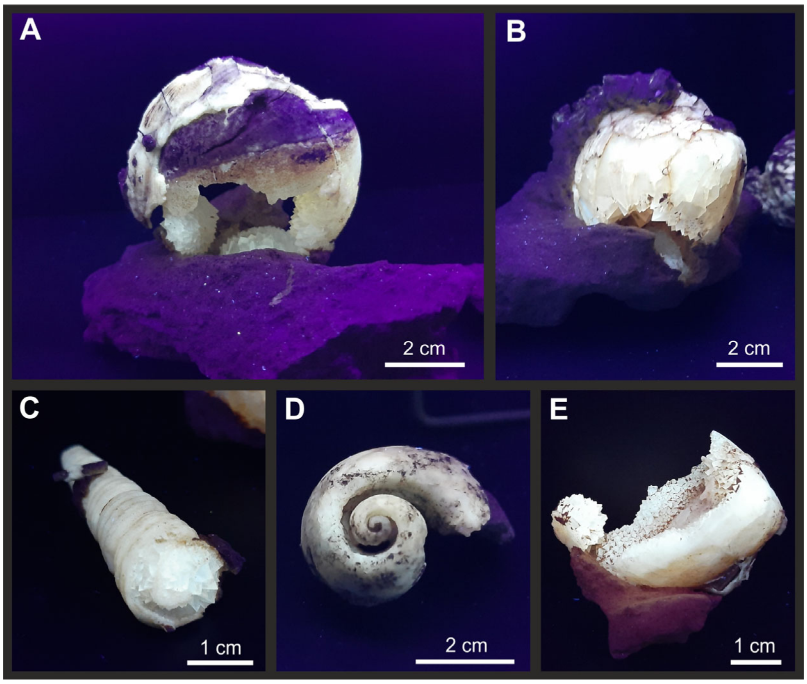

Fig. 9 - Recrystallized calcite specimens from Taphofacies 4 showing phosphorescence under UV light. A, B. Recrystallized bivalve specimen. C. Recrystallized turritellid gastropod. D. Recrystallized naticid gastropod. E. Recrystallized bivalve specimen showing large euhedral crystals.

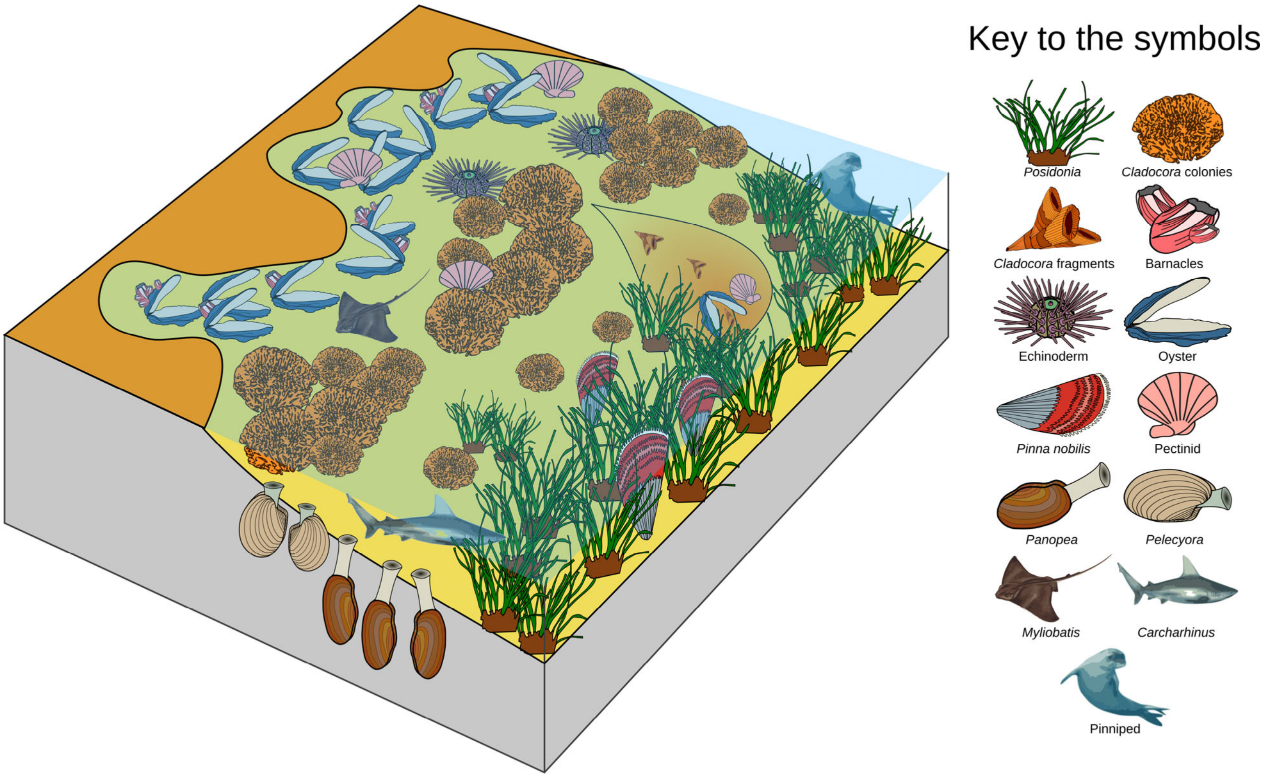

Fig. 10 - Schematic paleoenvironmental reconstruction of the Early Pleistocene Fauglia paleoecosystem.

& Benković, 2008), as it is characterized by a remarkable thickness and especially lateral continuity. Further recalling the present-day *Cladocora* banks (Koukouras et al., 1998; Pitacco et al., 2014, 2017), the Fauglia bank occurs associated with a molluscan assemblage dominated by hard-substrate taxa such as *Pecten*, *Flexopecten*, *Mimachlamys*, *O. edulis* and *Anomia*. For summarizing, in light of the distribution of modern *Cladocora* banks, we suggest that the Fauglia bank developed between 5 and 20 m water depth (and possibly between 10 and 15 m), in a relatively sheltered setting. Similar conditions were probably common along the Pleistocene coastline of central Italy, as witnessed by the abundance of *C. caespitosa* remains in both lower (Bonadonna, 1967; Conato & Dai Pra, 1980; Sarti et al., 2007; Bizzarri & Baldanza, 2020) and middle to upper Pleistocene deposits (Romano et al., 1994; Zanchetta et al., 2019).

The oyster reef that characterizes the uppermost part of Fauglia succession consists of small clusters of shells of *O. edulis* encrusted by abundant balanid barnacles and less vermetid gastropods. These shell clusters recall the small bioconstructions currently developed by *O. edulis* along the northern coasts of Europe in waters shallower than 5 m (Christianen et al., 2018; Kregting et al., 2020). More generally, oyster reefs usually occur in very shallow settings, from the intertidal zone up to 10 m of water depth (Puffer & Emerson, 1953; Haven & Whitcomb, 1983; Luckenbach et al., 1999; Boudreaux et al., 2006; La Peyre et al., 2014; Gain et al., 2017; Toscano et al., 2018). Oysters can also build reef into deeper waters (e.g., Angeletti & Taviani, 2020); however, such bioconstructions do not display abundant barnacles like the shallow-water ones (e.g., Boudreaux et al., 2006; Barnes et al., 2010; Lunt et al., 2017). Oyster reefs are usually favored by gently sloping, complex coastlines; hydrodynamic energy must be low enough to favor larval pooling (and as such, the clustering of subsequent generations of individuals) while also providing suitable shallow-water settlement substrate (Kregting et al., 2020). Thus, similar to its modern counterparts, the Fauglia oyster reef probably developed in very shallow water (less than 5-10 m) and, possibly, in a shallow bay. The abundant presence of barnacles might suggest elevated nutrient availability, as barnacles are particularly enhanced by plankton abundance (Sanford & Menge, 2001; Coletti et al., 2018a; Coletti et al., 2021).

Overall, the studied succession illustrates a progressive shallowing of the depositional environment. This shallowing-upward trend favored the development of the *Cladocora* bank over an area that was previously colonized by the *Posidonia* meadow. As observed by Monnier et al. (2021), large concentrations of *C. caespitosa* colonies might coexist alongside seagrass meadows, but the former develops near the upper bathymetric limit of the meadows, suggesting that decreasing water depth might induce a shift from a *Posidonia*-dominated environment to a *C. caespitosa*-dominated environment. Further shallowing might have fostered the development of the oyster reef that could have taken advantage from the hard substrate provided by the *C. caespitosa* bank. The well-preserved, organic-rich, seagrass meadow, the *C. caespitosa* bank, and the oyster reef are all indicative of a relatively protected setting, not exposed to large storm-waves.

As already mentioned, the stratigraphic whereabouts of the vertebrate finds from Fauglia are unfortunately unknown. However, eagle rays such as the widespread *Myliobatis* are nearshore durophagous fishes (e.g., Jardas et al., 2004) that might have fed upon the hard-shelled invertebrates of the coral bank and oyster reef. The sandbar shark, *C. plumbeus*, is also a largely coastal fish. Interestingly, in the present-day Mediterranean Sea, conspicuous numbers of sandbar sharks have been observed in the Gulf of Gabes, Tunisia, in occurrence of the largest *Posidonia* meadow worldwide (Enajjar et al., 2015); interestingly, until recent environmental degradation, this area was also characterized by *Cladocora* banks (El Kateb et al., 2016). Finally, the only living Mediterranean pinniped, the monachine monk seal *Monachus monachus* (Hermann, 1779), is thought to occasionally include *P. oceanica* in its diet (Salman et al., 2001; Pierce et al., 2011).

5.2. A complex taphonomic history

What is remarkable of the Fauglia fossil site is the co-occurrence of several different preservation modes (Fig. 7) that have been used for defining the five aforementioned taphofacies. Although taphofacies were originally developed for Paleozoic fossil invertebrate associations (Brett & Baird, 1986; Speyer & Brett, 1986, 1988), this concept has also been employed for the study of invertebrate- and vertebrate-bearing successions of the Neogene (e.g., Yesares-García & Aguirre, 2004; Hendy et al., 2006; Rico-García et al., 2008; Boessenecker et al., 2014) and of the Quaternary (e.g., Meldahl & Flessa, 1990; Kowalewski et al., 1994; Parsons-Hubbard, 2005). The five taphofacies recognized at Fauglia take their place at different stratigraphic heights along the studied succession, but in some cases they also show significant lateral variations (e.g. taphofacies 2 and 3 are heteropic).

Taphofacies 2 and 3 are characterized by the presence of shells retaining their pristine aragonitic composition, such as specimens of *P. nobilis* (Fig. 5C), as well as by spectacular fossil remains of *P. oceanica* (Figs. 5A, B, 7B). Since seagrass has a very low preservation potential, the (rarely reported) discovery of seagrass meadows in the fossil record is puzzling. Seagrass remains from fossil meadow settings are very rare and only few examples have been reported worldwide (Reich et al., 2015). Pleistocene remains of *P. oceanica* are only known from Rhodes, Greece (Moissette et al., 2007; Koskeridou et al., 2019) and Emilia, Italy (Raffi & Serpagli, 1993; Brunetti & Vecchi, 2005, 2012). *Posidonia oceanica* specimens are mostly represented by *in situ* rhyzomes buried in life position (Fig. 5A). Abundant leaves do also occur besides the rhyzomes, and this is quite remarkable as *Posidonia* leaves are usually too fragile to be preserved as fossils. The reddish color exhibited by the rhyzomes preserved in Taphofacies 2 (Fig. 5B) is possibly provided by iron oxides (Moissette et al., 2007), whereas the rhyzomes from Taphofacies 3 are black and display a peaty consistence as typical of coalified compressions (*sensu* Schopf, 1975) (Fig. 7C). The dark gray color of the sediment of this taphofacies indicates abundance of organic material, suggesting oxygen deficiency within the sediment.

Taphofacies 1, 4 and 5 can be grouped together by virtue of the lack of aragonitic shells, which were subject to preferential dissolution (e.g., Cherns & Wright, 2000; Cherns et al., 2011). These taphofacies are characterized by pristine calcite invertebrate remains (e.g., ostreids and pectinids; Fig. 6), fossils preserved as compound molds (Fig. 7A, G, H), and geopetal calcite fillings of the voids (Fig. 7D, E, F). These diagenetic traits lead to hypothesize a complex taphonomic history for the studied succession, similar to that of other fossil invertebrate assemblages for which different stages of diagenetic mineral precipitation and dissolution are suggested (Fernández-López, 1997; Gioncada et al., 2018; Bosio et al., 2021). In addition, all the fossil materials coming from the upper portion of the section and constituted by secondary diagenetic calcite become luminescent under UV light exposition, which suggests a high content of elements that comprise luminescent centers such as manganese (Fonda, 1940; Aguilar & Osendi, 1982).

A handful of *C. caespitosa* banks are known from the Quaternary geological record of the Mediterranean area (El Kateb et al., 2016; Coletti et al., 2018b), and an even lower number of fossil *Posidonia* meadows is known (Reich et al., 2015). The peculiar setting reconstructed herein for the Fauglia paleo-area, consisting of a shallow bay protected from strong storm waves, might have favored the preservation of these structures, similar to what has been hypothesized for the exceptional preservation of bioconstructions such as the cirratulid and reefs that characterize the Miocene strata of the East Pisco Basin of Peru (Kočí et al., 2021). Low turbulence likely inhibited post-burial reworking of the invertebrate remains, thus promoting the *in situ* preservation of mollusks (e.g., *P. nobilis*, *Panopea* sp. and *Pelecyora* sp.), phanerogams (i.e., *P. oceanica*) and corals (*C. caespitosa* bioconstructions), for which a rapid and undisturbed burial must be hypothesized in case of high-quality fossilization and lack of encrusting organisms (Aguirre & Jiménez, 1998). In particular, the presence of fine-grained sediments, the abundance of organic matter at the seafloor, and the lack of primary porosity could explain both the preservation of aragonitic shells and that of phanerogam remains in Taphofacies 2 and 3. In fact, nacreous aragonitic shells, which have a low preservation potential, can be preserved in organic-rich sediments (Hall et al., 1967; Janiszewska et al., 2018), and unmineralized remains have higher preservation potentials when entombed in fine-grained sediments such as clays (e.g., Butterfield, 1995; McCoy et al., 2015). On the contrary, in highly porous sediments, such as sands and/or anywhere primary textural voids occur, aragonitic remains are usually poorly preserved or absent (e.g., Cherns & Wright 2000; Cherns et al., 2011), reflecting their relatively low resistance to changes in the chemical environment introduced by diagenesis (e.g., Brand & Veizer, 1980, 1981; Brett & Baird, 1986). In Taphofacies 1, 4 and 5, high porosity (both primary and secondary) allowed for a pervasive fluid circulation that greatly impacted on fossil preservation by dissolving aragonite (which should have been very abundant in a coral bank of such dimensions). As a consequence of this, carbonate supersaturation occurred in the diagenetic environment, leading to the re-precipitation of calcite in subsequent stages (e.g., Fernández-López, 1997 and references therein; McCoy et al., 2015). Thus, different generations of cements recognizable in the compound molds and geopetal structures testify to the complex taphonomic history of these remarkable fossil-bearing facies.

6. CONCLUSION

Exceptionally preserved *C. caespitosa* bank and *P. oceanica* meadow are found in the proximities of the Fauglia village (Tuscany, central Italy). This is the only Pleistocene succession in which a *C. caespitosa* bank occur within a vertical distance of a few meters from a *P. oceanica* meadow. The studied fossil assemblage allows to reconstruct biotopes that have extant analogues in the present-day Mediterranean region. Sedimentological and paleontological observations concur in suggesting a relatively protected setting, not exposed to large storm-waves, suitable for the development of a seagrass meadow, a *C. caespitosa* bank, and an oyster reef. The paleontological content of the studied succession also suggests a shallowing-upward trend. The extraordinary nature of this site is to be found in the peculiar fossilization history of this succession, characterized by a rapid burial and the lack of post-burial reworking. Taphonomic features allow to recognize five distinct taphofacies, exhibiting peculiar preservation styles and diagenetic imprints. Organisms with original calcite shells are usually preserved, whereas aragonitic shells are preserved only in fine-grained, non-porous, *Posidonia*-associated sediments, where plant remains are exquisitely preserved *in situ*. On the other hand, the high degree of carbonate dissolution that occurred in the highly porous *Cladocora*-bearing sediments was followed by a widespread calcite re-precipitation that allowed the preservation of invertebrates as internal, external and compound molds. The exceptional discovery of body fossils organisms characterized by a low-preservation potential such as *P. oceanica* qualify the Fauglia outcrop as a remarkable fossiliferous site that undoubtedly merits an adequate geoconservation effort.

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