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Resilient coral reef ecosystems: The case study of turbid-mesophotic coral buildups during the Late Oligocene Warming Event (Tertiary Piedmont Basin, NW Italy)

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A R T I C L E I N F O

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A B S T R A C T

Nowadays, but also in the geological record, coral communities living in marginal conditions (i.e. low light, high turbidity, extreme temperatures, high nutrients and sediment input) are quite common and there is evidence that some of these reefs, often associated with mesophotic environments, may be more resilient to the current global warming trend, thus serving as possible ecological refugia.

As an attempt to understand the response and resilience to past warming events of marine calcifying organisms, such as zooxanthellate corals of marginal reefs, herein we reconstruct the palaeoenvironment of an Oligocene mixed siliciclastic-carbonate system in the Tertiary Piedmont Basin (NW Italy), where a suite of coral assemblages formed small buildups at the edge of a coarse-grained delta system. Geochronological dating by strontium isotope stratigraphy places the coral buildups in the middle Chattian, thus within the Late Oligocene Warming Event (LOWE): a crucial climatic event for coral reefs as characterised by substantial warming coincident with declining atmospheric CO_2.

The depositional model that we propose is ascribed to a fan-delta system, deposited within a narrow valley cutting through the metamorphic basement, where small and laterally discontinuous coral buildups grow-up in the prodelta setting, thus suggesting a mesophotic environment. In this context, the coral buildups appear to have been intermittently deactivated or smothered by fine-grained terrigenous input during flood phases or shifts in distributary channels until their final suffocation by fluvial sediments input.

Within the coral buildups, the four distinguished coral facies (branching *Stylophora* floatstone, *Acropora-Stylophora* floatstone/rudstone, *Goniopora/Caulastraea* pillarstone, and mixed-coral domestone) are characterised in general by sediment-resistant corals and by specific taphonomic features.

These coral facies shifted in time and space during the LOWE, highlighting the noteworthy adaptability and resilience of Oligocene corals to a complex interplay of environmental stressors such as turbidity, hydrodynamic energy, sediment and nutrient supply within a mesophotic setting.

1. Introduction

The Oligocene epoch corresponds to the apex of Cenozoic coral reef growth and represents a crucial period for understanding the response of corals reef ecosystems to palaeoenvironmental stressors. Numerous Oligocene coral reefs occur worldwide (e.g. Michel et al., 2020) including the Mediterranean region (Perrin and Bosellini, 2012), and especially in Italy, where a broad spectrum of reef types and depositional settings is recorded: i.e. the Rupelian barrier reef/lagoon system of the Lessini Shelf in northeastern Italy (Bosellini and Trevisani, 1992; Bosellini et al., 2020), the pure carbonate Chattian fringing reef complex of the Castro Limestone in southern Italy (Bosellini and Russo, 1992; Bosellini, 2006; Bosellini et al., 2021), and the various upper Rupelian-Chattian coral assemblages and reefs of the Tertiary Piedmont Basin

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(TPB) that crop out in Liguria and Piedmont (NW Italy) and that are associated with mixed carbonate-siliciclastic settings and turbid-water conditions (Pfister, 1980, 1985; Fravega et al., 1987, 1994; Quaranta et al., 2009; Briguglio et al., 2021a, 2021b).

Quite recently, coral reefs exposed to relatively high turbidity, reduced light penetration and a significant sedimentary input have gained a considerable scientific attention (see Zweifler et al., 2021 for a review), debunking the paradigm that clear, warm and oligotrophic waters are necessary for an optimal coral reef growth. In modern oceans there is evidence that turbid-water reefs may be more resilient to climate change impacts, especially to prolonged period of high sea-surface temperature that usually causes severe bleaching events (Morgan et al., 2017; Sully and van Woesik, 2020; Rosedy et al., 2023), thus serving as possible ecological refugia (Smith et al., 2014; Assis et al., 2016; Cacciapaglia and van Woesik, 2016).

Looking at the geological record, many coral reefs and coral assemblages are associated to marly and mixed carbonate-siliciclastic sediments (Wilson and Lokier, 2002; Sanders and Baron-Szabo, 2005 for a review; Morsilli et al., 2012; Santodomingo et al., 2015, 2016; Reuter et al., 2019) and their frequency increases throughout the Phanerozoic (Kiessling, 2002).

These types of marginal-turbid coral reef environments have been called "coastal low light reefs" (Renema, 2019) or "brown mesophotic reefs" (Zapalski et al., 2021; Majchrzyk et al., 2022) in order to underline that low light conditions (i.e. mesophotic) may also occur at shallow depths under the control of turbidity and sedimentation rate. In these settings, the coral assemblage is usually dominated by massive and branching morphotypes. In contrast, terms such "oceanic low light reefs" (Renema, 2019) or "blue mesophotic reefs" (Zapalski et al., 2021; Majchrzyk et al., 2022) indicate relatively deep conditions in clear-water settings, typically characterised by the occurrence of platy corals.

Herein we present a study focused on the coral assemblages of a mixed siliciclastic-carbonate system from the TPB which is well exposed at the locality named Gelati (about 20 km south of Acqui Terme, Piedmont, NW Italy) (Fig. 1a, b). The TPB is known for its rich coral localities since the 19th century, some of which represented by true reefs, while others are characterised by scattered coral occurrences (Quaranta et al., 2009). So far, however, the TPB coral assemblages have been described mainly with respect to their coralline algae associations (Fravega et al., 1987, 1994; Vannucci et al., 2003, 2010) and only few localities have been investigated with special attention to corals and providing coral facies (Pfister, 1980, 1985; Fravega et al., 1987; Briguglio et al., 2021b). As a result, detailed palaeoecological reconstructions and depositional models have yet to be proposed.

By a detailed facies analysis and characterization of the coral assemblages we aim: 1) to reconstruct the ecosystem dynamics depicted by a first colonization event, the development of small coral buildups and their final demise; 2) to evaluate the changes in the composition of the coral assemblage and associated biota, such as coralline red algae, in order to assess the mutual effects of environmental factors such as turbidity, hydrodynamic energy, sediment and nutrient supply; and 3) to propose a detailed depositional model.

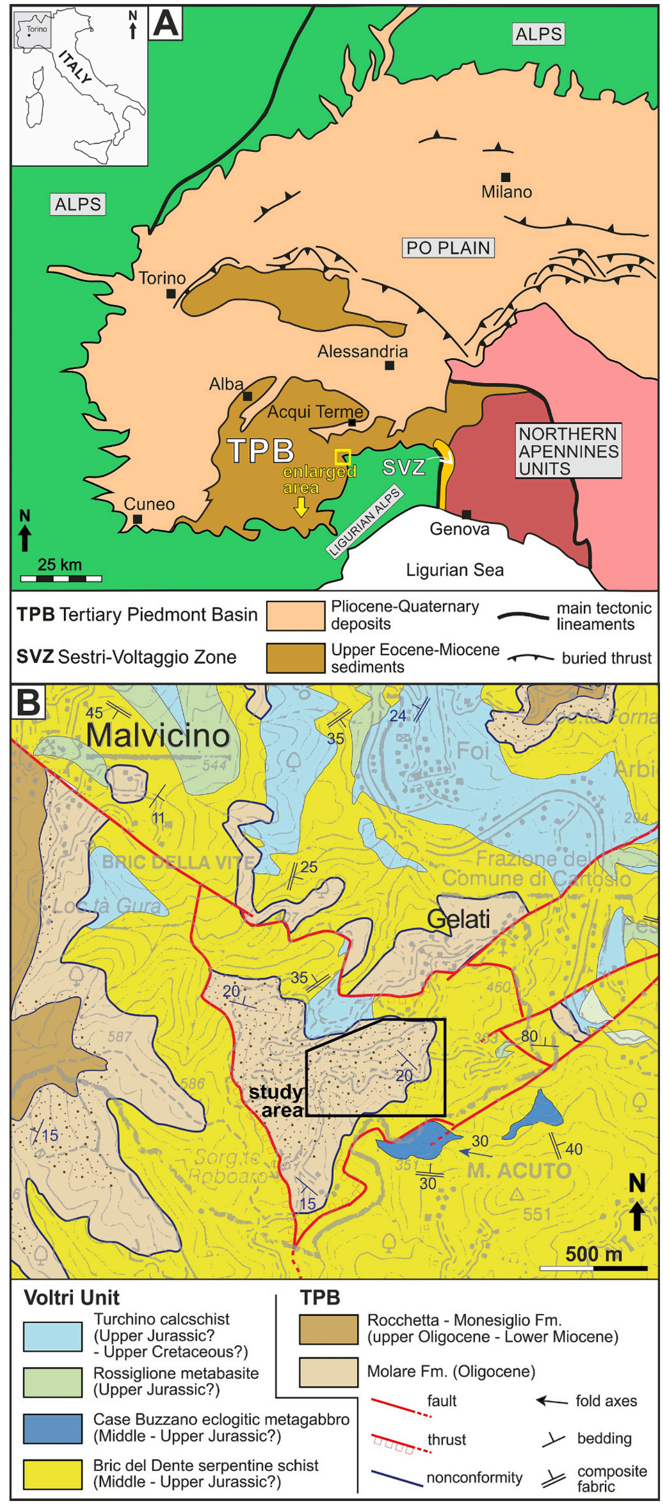

Fig. 1. A. Simplified structural map of north-west Italy (modified from Dela Pierre et al., 2010). B. Geological map of the Gelati surroundings and location of the study area (modified from Federico et al., 2022).

2. Geological setting

The TPB is a sedimentary basin outcropping along the Liguria-Piedmont border (NW Italy) and is considered as a late- to post-orogenic basin that evolved in a piggy-back position on the Monferrato Complex thrust belt. Its depositional history is strongly controlled by tectonic and eustatic events (a.o.: Gelati and Gnaccolini, 1988; Capponi et al., 2009). The basin deposits unconformably overlie the Ligurian Alps, Sestri-Voltaggio Zone, and NW termination of the Northern Apennine and include non-marine to marine sediments (upper Eocene? - upper Miocene) (Lorenz, 1969; Quaranta et al., 2009; Federico et al., 2016, 2022; and reference therein) (Fig. 1a).

The study area (Fig. 1b) is located in the southwestern portion of this thrust-top basin, that during the Oligocene recorded a general marine transgression, from NE to SW with respect to the present orientation. The progressive flooding happened over an articulated continental substrate, with high reliefs and deep valleys carved on metaophiolithes and related metasediments of the Voltri Unit (Capponi et al., 2016; Federico et al., 2016, 2022; and references therein). On this substrate the basal basin-fill sedimentation accumulated up to 150 m of siliciclastic non-marine to shallow marine sandstones and conglomerates (Molare Formation, Oligocene). These deposits were related to sandy and gravelly beaches and to a fan-delta to prodelta system fed by the erosion of the underlying Voltri Unit. The Molare Fm. also contains coral-rich bodies such as biostrome and bioherms, grading upwards to sandstones, siltstones and marly siltstones. The coral assemblages can be found directly on the metamorphic substrate or embedded within the clastic deposits, as those investigated in the present study (Lorenz, 1969; Gnaccolini, 1981; Pfister, 1980, 1985; Fravega et al., 1987; Vannucci et al., 1997, 2003).

The Molare Fm. is followed by silty sandstones, siltstones and marls, with sandstone and conglomerate thick lenses interbedding (Rocchetta - Monesiglio Formation, upper Oligocene - lower Miocene) (Ghibaudo et al., 2014; Briguglio et al., 2021a, 2021b; and reference therein).

3. Materials and methods

3.1. Stratigraphy and lithology

To characterise the stratigraphic architecture and sedimentological features of the Molare Fm. extensive fieldwork was carried out in a study area about 14 km south from Aqui Terme, in the province of Alessandria. Traditional mapping techniques were used to identify and map different lithofacies (Fig. 2). GPS position was carefully recorded during the mapping process to facilitate the creation of accurate digital maps. In addition, photogrammetric surveys were conducted using a DJI Mavic Pro UAV equipped with a high-resolution camera capable of capturing images with a resolution of up to 12 megapixels. The images were processed using Agisoft Metashape software to create 3D point clouds, digital elevation models (DEMs), orthomosaics and a digital outcrop models (DOMs). These photogrammetric data were integrated with the field data and inserted in QGIS software for a geometrically correct lithofacies map distribution.

Based on the thickness and degree of preservation, three carbonate, coral-rich outcrops were selected for detailed description and measurement of stratigraphic logs (Fig. 2).

- Cascine section (Fig. 3): 36.5 m in thickness; start 44°32′52.112" N - 8°26′10.793″ E.
- Valletta section (Fig. 4): 12.7 m in thickness; start 44°32′45.819" N - 8°26′5.071″ E.
- Streghe section (Fig. 5): 14.7 m in thickness; 44°32′43.130" N - 8°26′3.987″ E.

3.2. Coral facies analysis

The coral-rich facies have been defined on the basis of their dominant coral genera and type of colonies growth fabric. Coral taxa have been identified directly in the field or through analysis of thin and polished sections, both at the generic and species level. Growth forms have been described through the bidimensional measurement of colony size: maximum diameter and maximum height of colonies in growth position, mean diameter of coral branches when preserved as rubble. Coral growth fabrics have been named according to the terminology proposed by Insalaco (1998).

The occurrence of coral genera and growth forms has been semi-quantitatively evaluated, leading to the distinction of three categories: 1) absent/rare, 2) common, and 3) abundant. Estimation of coral cover has been provided using the line-intercept transect method (Perrin et al., 1995; Bosellini et al., 2021) along some well exposed surfaces. Microfacies analysis of the sediments within the coral facies has been performed on a total of 130 thin sections, with identification of rock textures and skeletal components. Carbonate textures have been named following Dunham (1962), whereas the textural classification of Embry and Klovan (1971) and Insalaco (1998) have been used for a general description in the field. The percentage of carbonate content of the inter-coral sediment has been determined through gasometric measurements using a Dietrich–Frühling calcimeter and the siliciclastic content consequently calculated and examined by X-ray diffraction analysis (Bragg-Brentano Philips diffractometer). According to Wilson (2005), based on the siliciclastic amount, inter-coral sediments can be separated into "mixed carbonate-siliciclastic facies" (36–90% siliciclastic) and "carbonate facies" (6–35% siliciclastic).

Along with the microfacies analysis, a study of primary taphonomic

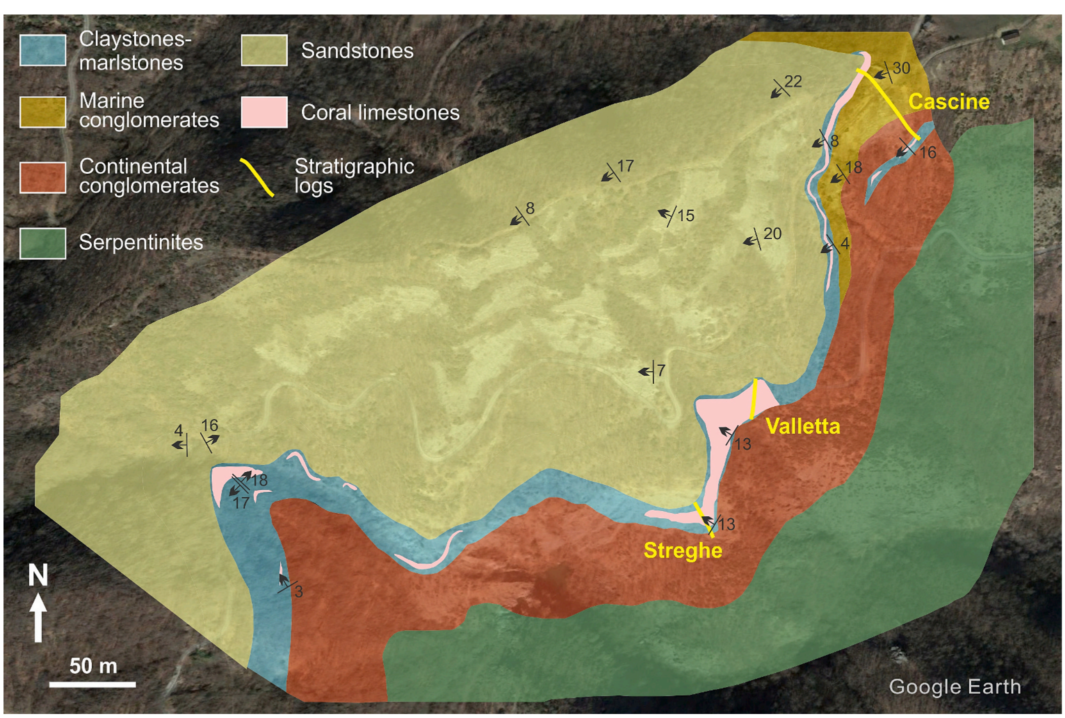

Fig. 2. Detailed geological map of the study area with indication of the three measured stratigraphic sections.

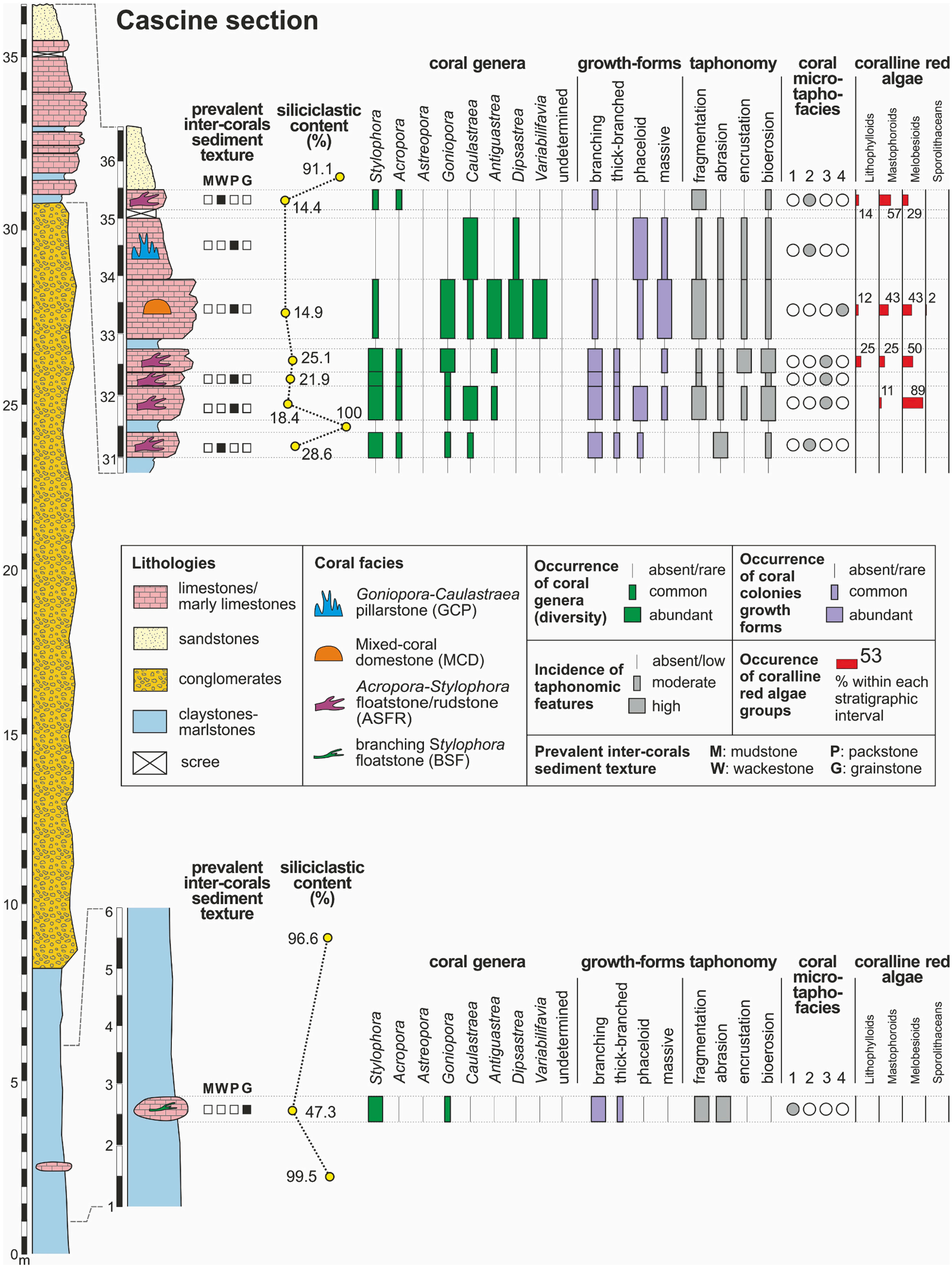

Fig. 3. Cascine section with the stratigraphic position of the identified coral facies coupled with vertical changes in inter-corals sediment texture, carbonate content, semi-quantitative estimation of coral diversity, inferred growth forms, taphonomic signatures and quantitative evaluation of coralline red algae palaeoecological informal groups. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

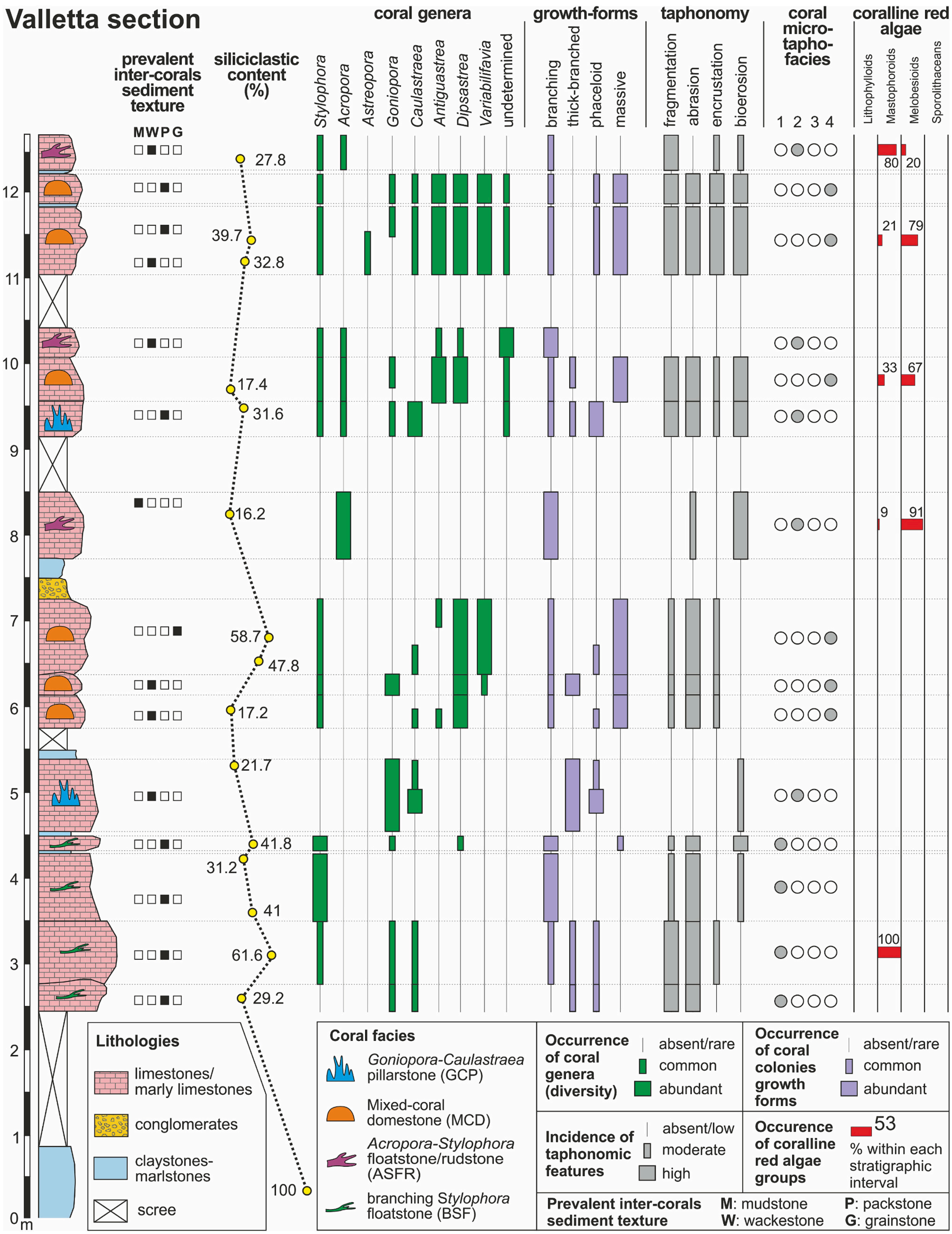

Fig. 4. Valletta section with the stratigraphic position of the identified coral facies coupled with vertical changes in inter-corals sediment texture, carbonate content, semi-quantitative estimation of coral diversity, inferred growth forms, taphonomic signatures and quantitative evaluation of coralline red algae palaeoecological informal groups. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

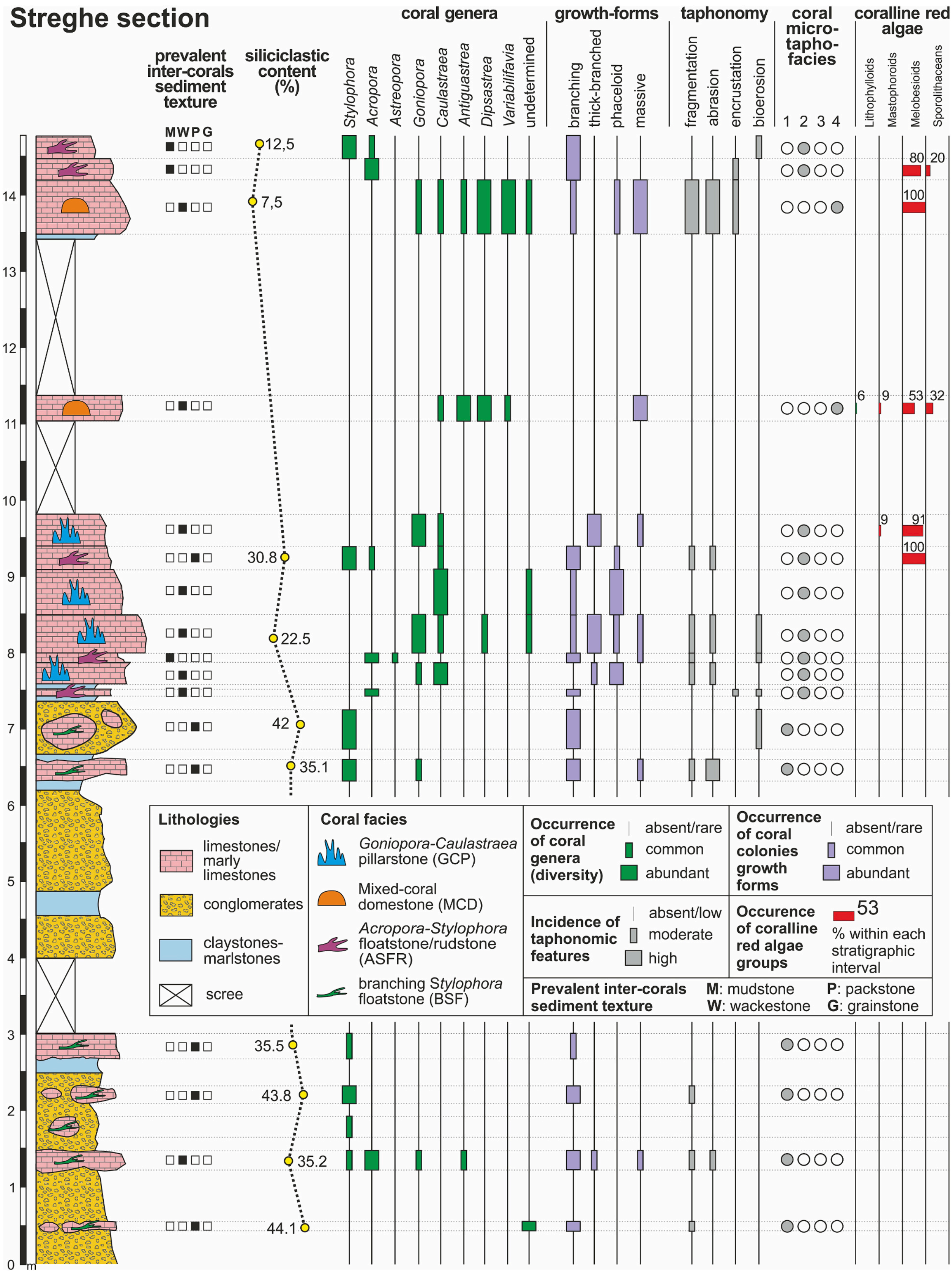

Fig. 5. Streghe section with the stratigraphic position of the identified coral facies coupled with vertical changes in inter-corals sediment texture, carbonate content, semi-quantitative estimation of coral diversity, inferred growth forms, taphonomic signatures and quantitative evaluation of coralline red algae palaeoecological informal groups. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

processes affecting coral skeletons has been performed. Taphonomic signatures that we considered are fragmentation, abrasion, encrustation, and bioerosion. Their degree of incidence has been semi-quantitatively estimated according to three categories: 1) absent/low, 2) moderate, 3) high. We refer to Silvestri et al. (2011) for detailed description of taphonomic processes and signatures recognized in fossil corals. Semi-quantitative estimation of the incidence of taphonomic processes have been integrated with data obtained from traditional microfacies analysis, thus concurring to identify a suite of coral microtaphofacies (MTFs) along the measured stratigraphic sections.

As regards scleractinian corals, the classification system adopted herein takes into consideration the systematics based on recent molecular analysis and phylogenetic relationships between traditional families (Fukami et al., 2008), together with macro-morphological characters used in recent systematic revisions (Budd and Stolarski, 2009; Budd et al., 2012).

As regards calcareous red algae, recent studies on modern specimens based on multigene analyses have led to a deep revision of their classification, also affecting the subdivision of fossil taxa. For a detailed summary of these aspects readers can refer to Briguglio et al. (2021b). The present study follows the classifications of Rösler et al. (2016) and Peña et al. (2020), but for the palaeoecological interpretation we use the informal groups of lithophylloids (including *Lithophyllum*), mastophoroids (*Lithoporella* and *Spongites*), melobesioids (*Lithothamnion* and *Mesophyllum*), and sporolithaceans (*Sporolithon*). Even if they have no more a taxonomic value, these groups are still useful as they bring together taxa with comparable palaeoenvironmental requirements (see for example Adey and Macintyre, 1973; Bosence, 1991; Aguirre et al., 2000; Kroeger et al., 2006; Vannucci et al., 2010; Singh et al., 2020; Briguglio et al., 2021b). A first study of the red calcareous algae assemblage of the study area was made by Pastorino (1994), in this paper those original data were completely revised and reprocessed focusing only on their palaeoecological meaning. Along the three selected logs a total of 199 thalli has been analysed and identified in thin section. The presence in percentage of the recognized groups is reported along the stratigraphic logs together with the other main coral facies features (Figs. 3,4,5).

3.3. Age determination

Very few and broken oyster shells were recovered during sampling and they were used to perform a geochronological calibration of the succession by measuring their strontium isotope content. The Sr isotope curve of the last 590 Ma is kept consistently updated (McArthur and Howarth, 2004; McArthur et al., 2012, 2020) and thus accurate chronostratigraphic dating may be achieved in time-intervals with especially steep trends in the Sr isotope curve, such as the transition from the Oligocene towards the Miocene (Vescogni et al., 2014; Kocsis et al., 2018). Oyster shells used herein to run this analysis are also considered among the most accurate specimens for SIS: their low-Mg calcite ensures a high resistance to diagenetic alteration (McArthur, 1994; Ullmann and Korte, 2015). Within the study area, a total of five samples has been collected. Two samples came from several broken pieces of undetermined oysters, recovered from the uppermost part of the section Streghe, and three more fragments of oysters were recovered from the sandstones almost 30 m above the top of Streghe section (Fig. 2).

The selected specimens were checked for signs of recrystallization or crystal overgrowthsand only well preserved, microlaminated portions of the shells were chosen for the analyses. These were cleaned in an ultrasonic bath to remove any adherent sediment and the external part was shaved off with a microdrill to avoid sampling any altered parts that may have come in contact with diagenetic fluid. Unfortunately, the retrieved material was too small to make a thin section and check the preservation on a cathodoluminescence microscope, and only a stereoscopical inspection was feasible, and gave positive results. All the geochemical analyses were performed at the Institute for Geology, Mineralogy and Geophysics of the Ruhr-University (Bochum, Germany). Strontium element was separated using a standard cation exchange process, and then the isotopic ratios were analysed on a Finnigan MAT 262 thermal-ionization mass spectrometer. The USGS EN-1 measured at the laboratory at the time when the samples were analysed was 0.709161 ± 0.000005 (2 s.e., $n = 451$). The mean value of the USGS EN-1 standards run together with the samples analysed for this study is 0.709200 ± 0.000005. The $^{87}Sr/^{86}Sr$ ratios of the samples were corrected for interlaboratory bias, using the long-term Bochum value of this standard, to a value of 0.709161 for the USGS EN-1 standard to be consistent with the normalization used in the compilation of the "look-up" table of McArthur et al. (2001; version 4: 08/04). This table, which is tied to the Geological Time Scale of Gradstein et al. (2004) (GTS2004), was used to derive numerical ages from the studied samples. Minimum and maximum ages were obtained by combining the statistical uncertainty (2 s.e.) of the mean values of the Sr-isotope ratios of the samples with the uncertainty of the seawater curve. The numerical ages were then translated into chronostratigraphic ages and corresponding standard biozones by reference to the GTS2004. An attempt to correlate the GTS2004 with the new GTS2020 was also made.

4. Geochronological dating

The isotopic data retrieved from the oyster shells collected from the top of Streghe section gave $^{87}Sr/^{86}Sr$ values of 0.708165 and 0.708151, which indicate a geochronological age comprised between 25.34 and 24.53 Ma, and thus corresponding to the late middle Chattian according to all version of GTS previously mentioned. This time interval, included within the SB 23 Zone (Cahuzac and Poignant, 1997), coincides with the Late Oligocene Warming Event (LOWE) (Zachos et al., 2001; Zhang et al., 2013): a still poorly known and enigmatic interval of time which, according to the most recent reconstruction, occurred between ~26.5 to 24 Ma and was characterised by an unexpected inverse correlation between global sea-surface temperature and pCO_2.

The isotopic data retrieved from the oyster shells collected 35 m above Streghe section gave $^{87}Sr/^{86}Sr$ values of 0.708329 and 0.708360, which indicate a geochronological age comprised between 21.94 and 21.27 Ma, and thus corresponding to the middle Aquitanian according to all version of GTS previously mentioned.

5. Lithofacies and measured logs

The study area displays sedimentary lithofacies that encompass conglomerates, claystones-marlstones, coral limestones and fining-upward marine siliciclastic sandstones (Fig. 2). While the clastic-terrigenous lithologies are briefly described in this section, the coral-dominated carbonates will be discussed in more depth throughout chapter 6.

5.1. Conglomerates

This facies is characterised by an up to 30 m thick sequence of coarse to medium-sized orthoconglomerates that exhibit a fining-upward trend. These conglomerates rest on the metamorphic basement and are primarily composed of serpentinite, with a minor amount of metabasite, metasediment and quartz pebbles/cobbles (grain size variable to 40–50 cm to less than 5 cm) embedded within a reddish sandy matrix (Fig. 6a). The conglomerates themselves are typically thick-bedded with erosional bedding planes. The pebbles within the conglomerates tend to be discoidal and rounded and display a preferential orientation parallel to the stratification. At the Cascine section (Fig. 3), the conglomeratic interval presents a general dip towards SW with a variable angle along dip-direction from 30° to 8°. In the upper-middle part (between 22 and 29 m) cross-bedding stratification with marked foreset is clearly visible. Towards the Valletta section, this lithofacies passes laterally into a mix of clay and fine-grained conglomerate. It should be noted that the fossil content within this lithofacies is poorly preserved, with only

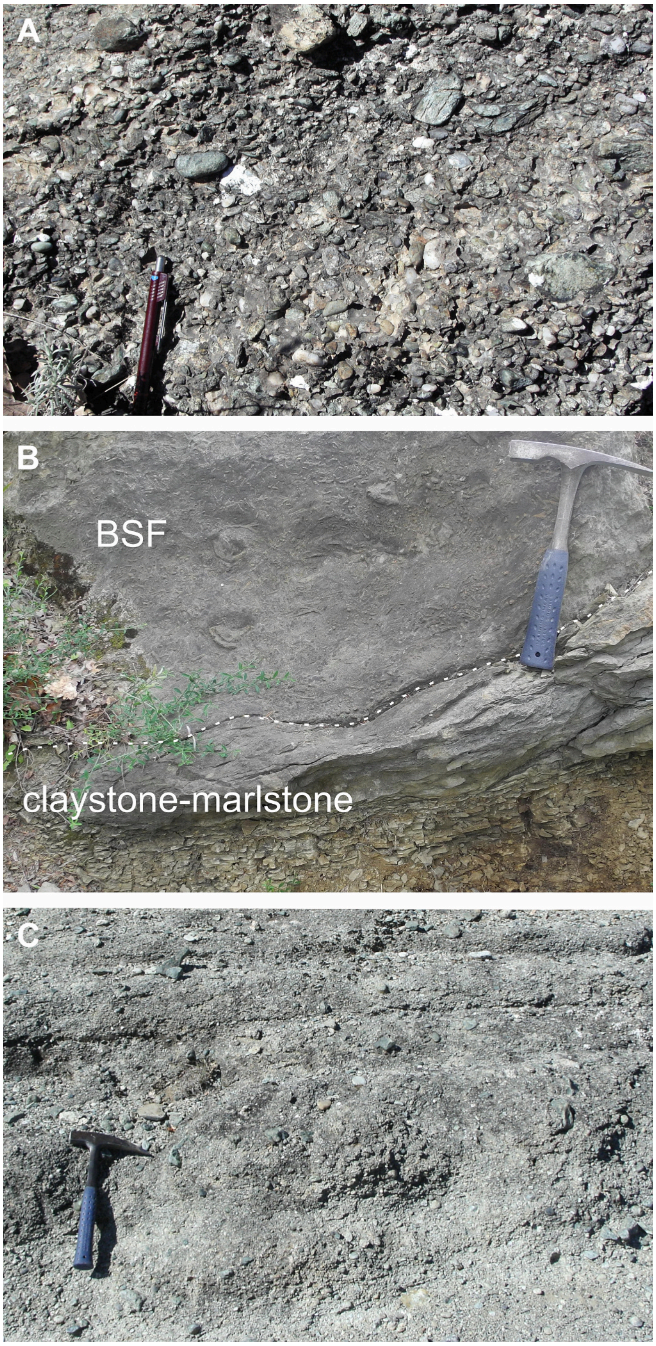

Fig. 6. Main lithofacies of the study area. A. Conglomerates. B. Claystones-marlstones passing into the BSF coral facies. C. Marine sandstones with scattered pebbles.

resedimented coral fragments, bivalves, and a small number of benthic foraminifera.

5.2. Claystones-marlstones

This lithofacies crops out for about 8 m and primarily consists of claystone-marlstone deposits with rare sandstone beds. The carbonate content is notably low and ranges between 0 and 8%, but in localized areas towards the top of the succession, it can increase up to 60%. Claystone-marlstone deposits either overlap the metamorphic basement moving towards NE, or located directly above the conglomeratic horizons moving towards SW. The layers within this lithofacies are typically between 0.5 and 7 m thick, although in some cases, they can occur as thin intercalations within the coral beds (Fig. 6b). It is noteworthy that the fossil content within this lithofacies is limited to scattered small undetermined leaf remains.

5.3. Marine siliciclastic sandstones

This facies crops out extensively in the upper part of the study area (Fig. 2), with an overall thickness of about 35 m. In the Cascine section coral limestones are overlapped by 4 m of cross-bedded fining upwards marine siliciclastic sandstones. These sandstones have a carbonate content of 9% and exhibit a fining-upward texture, passing from coarse to medium, and are interspersed with pebbles/cobbles (Fig. 6c) sometimes arranged in discontinuous beds. More upwards, the medium to fine-grained sandstones become increasingly well-stratified, displaying hummocky cross stratification (HCS). The fossil content of this particular facies is relatively sparse and limited to a few fragments of bivalves used for Sr dating.

5.4. Measured logs

The stratigraphic logs have been measured in order to intercept the three most representative coral outcrops, but other smaller and scattered coral levels crop out in the area (Fig. 2). In particular the total thickness of coral limestones ranges about from 3 m to 15 m and it thins out laterally. The measured sections show limited variations in respect to lithology and biogenic content.

1) The Cascine log (Figs. 2, 3) is located in the north-eastern part of the study area. The profile consists in a well-bedded succession composed at the base of claystone-marlstone strata containing only a thin (40 cm maximum) lensoidal marly limestone with coral fragments. This unit is followed by 22 m of cross-bedded deltaic conglomerates and siltstones. A 4.8 m thick succession of coral limestone beds (from 30 to 100 cm in thickness), separated by thin clay-rich intervals, covers directly the coarse-grained conglomeratic deposits. After the demise of coral growth, the succession continues with cross-bedded sandstones (through cross-lamination to HCS) alternated with conglomerate beds in the lower part.
2) The Valletta log (Figs. 2, 4) is located in the central-eastern part of the study area. Coral limestones crop out for about 10.5 m overlying a marly level. Coral-rich beds are alternated with usually thin terrigenous intervals; a relatively thick level (about 50 cm) composed of conglomerates and clays is also present around 7.5 m from the base.
3) The Streghe log (Figs. 2, 5) is located in the south-central part of the study area, about 70 m westward from the Valletta log. In the lower part of the succession the first coral levels (up to 40 cm thick) are alternated with deltaic conglomeratic and silty beds. In the upper part of the log coral limestone beds are more continuously developed, with an overall thickness of about 7.5 m.

6. Coral facies

Coral-bearing beds are in general alternated with clay-rich horizons and along the measured sections they display a variable overall thickness, from about 4.5 m (Cascine section) up to 10.5 m (Valletta section). Four different coral facies have been identified: branching *Stylophora* floatstone (BSF), *Acropora*-*Stylophora* floatstone/rudstone (ASFR), *Goniopora*/*Caulastraea* pillarstone (GCP), mixed-coral domestone (MCD); their descriptions and interpretation are reported below and summarized in Table 1.

6.1. Branching *Stylophora* floatstone (BSF)

This facies is characterised by branching coral fragments included in a prevalent packstone matrix (occasionally wackestone and grainstone).

Table 1
Comparative table summarizing the main palaeontological and sedimentological features of the four coral facies.

Coral facies	Type of coral assemblage	Coral fabric	Coral growth forms	Main coral genera	Secondary coral genera	Micro-taphofacies	Inter-coral sediment type	Inter-coral sediment texture
BSF Branching *Stylophora* floatstone	rubble deposits	floatstone	fine-branched (massive, phaceloid)	*Stylophora*	*Acropora, Goniopora, Antiguastrea, Dipsastraea, Caulastraea*	MTF1	mixed carbonate siliciclastic	packstone (wackestone, grainstone)
ASFR *Acropora-Stylophora* floatstone/ rudstone	rubble deposits	floatstone to rudstone	thick-branched (phaceloid, massive)	*Stylophora, Acropora*	*Caulastraea, Goniopora, Astreopora, Antiguastrea, Dipsastraea*	MTF2 MTF3	carbonate	mudstone to packstone
GCP *Goniopora/ Caulastraea* pillarstone	in situ bioherms	pillarstone	thick-branched, phaceloid, (massive)	*Goniopora, Caulastraea*	*Dipsastraea, Stylophora, Acropora*	MTF2	carbonate	wackestone to packstone
MCD Mixed-coral domestone	in situ bioherms	domestone	massive, (phaceloid, thick-branched)	*Dipsastraea, Antiguastrea, Variabilifavia*	*Astreopora, Goniopora, Caulastraea, Stylophora, Acropora*	MTF4	carbonate / mixed carbonate siliciclastic	wackestone to packstone (grainstone)

The occurrence of BSF is restricted to the basal part of the studied sections (Figs. 3–5) and is represented by coral beds from 30 to 75 cm thick; their lateral continuity is usually limited and they may alternate with clay levels and conglomerate deposits.

The coral fauna is mainly composed of fine-branching *Stylophora thirsiformis* (Michelotti, 1874) (Fig. 7a) and more rarely of *Acropora haidingeri* (Reuss, 1864). *Stylophora* branches are here particularly thin (average diameter 3–4 mm), and some specimens exhibit a preserved secondary order of branching. *Acropora* is conversely preserved as single branches up to 7 cm long. Isolated sticks of *Goniopora nummulitica* (Reuss, 1864) (average diameter of branches 3–4 cm), few small massive knobby colonies of *Antiguastrea lucasiana* (Defrance, 1826) and *Dipsastraea subdenticulata* (Catullo, 1856) together with phaceloid *Caulastraea pseudoflabellum* (Catullo, 1852) in growth position sparsely occur (Fig. 7b).

The intra-coral matrix contains few other biotic components, represented by some plant remains, small benthic foraminifera, fragments of coralline algae, very rare fragments of bivalves, gastropods and serpulids.

Microtaphofacies associated to BSF has been named as MTF1. Fragmentation and abrasion are scored as scarce-moderate (Fig. 8a) to high. Encrustation is nearly absent or represented by thin, sparse, dishomogenous, crusts made by coralline algae exclusively of the mastophoroids group or by foraminifera. Although some traces of boring worms (*Trypanites*) occur on corals (Fig. 8b), bioerosion is scored as low. In all the three examined sections intra-coral sediment has a relatively abundant siliciclastic content (varying from a minimum of 31.2% to a maximum of 61.6%). It is in fact the only coral facies whose sediments can be classified for the most part as “mixed carbonate-siliciclastic”. This siliciclastic component consists of grains of serpentinite, quartz, clay minerals (chlorite, illite and kaolinite) and subordinate feldspar. Authigenic metal oxides and pyrite are also common.

6.2. *Acropora-Stylophora* floatstone/rudstone (ASFR)

This facies is represented by coral floatstones to rudstones with mudstone to packstone matrix. ASFR is quite common all along the three stratigraphic sections (Figs. 3–5), representing also the last coral facies before the overlapping sandstones at the top of the succession. Beds range from 15 to 75 cm in thickness and are in general horizontally continuous, although significant lateral variations of the coral diversity and coral cover commonly occur. ASFR deposits are frequently alternated with thin clay levels devoid of biogenic components.

Fragments of branching *Stylophora thirsiformis* and *Acropora haidingeri* dominate this facies, mainly forming monospecific layers (Figs. 7c-f); their diameter (average 5.5 mm) is larger than in the BSF and are often isooriented, forming in this case floatstone deposits. In places, fragments of *Stylophora* and *Acropora* are also associated to other corals, such as phaceloid colonies of *Caulastrea pseudoflabellum*, both as fragments and in growth position, isolated *Goniopora* sticks, or to some massive colonies tilted or in growth position (*Astreopora*, *Antiguastrea*, *Dipsastrea*).

Inter-coral matrix contains highly fragmented remains of coralline algae, small bivalves and gastropods, small benthic foraminifera (namely miliolids and rotaliids), serpulids, ostracods, fragments of barnacles, sponges and very rare echinoids.

Two different microtaphofacies, indicated as MTF2 and MTF3, have been distinguished within ASFR. MTF2 is the most common, it is associated to floatstones where coral branches seem to be locally isooriented parallel to bedding planes and *Acropora* is dominant (Fig. 8c), and occurs in all the three sections. The inter-coral matrix has usually a wackestone texture. MTF2 exhibits low fragmentation and abrasion, with thin branching corals preserving their delicate morphological structures. *Acropora* seems on the whole less fragmented and abraded than *Stylophora.* Bioinfestation is weakly developed and typically sparse, especially as concerning bioerosion, which leaves most corals nearly unaffected. Both traces referred to *Entobia* and *Trypanites* can be distinguished. Encrustation mostly occurs as sparse, occasionally fragmented, with crusts formed by foraminifera (namely *Miniacina* and *Planorbulina*) (Fig. 8d) and coralline red algae. In order of importance the latter are represented by melobesioids, mastophoroids, lithophylloids and sporolithaceans. MTF3 is less common, recognized only in the Cascine section, but clearly different from MTF2. It can be found within coral rudstones and the most diagnostic taphonomic signature is the generally high level of fragmentation, which affects not only the most delicate morphologies but also the more resistant ones (i.e. massive) and is as well documented by the abundant fine biogenic detritus dispersed in the inter-coral matrix (Fig. 8e). MTF3 is also characterised by a high level of bioerosion; most traces are referred to *Trypanites* (Fig. 8f), although several traces of *Entobia* are also present. Abrasion is scored as moderate, as well as encrustation, which consists of few sparse monotaxon crusts related to encrusting foraminifera or coralline algae, difficult to identify because of their fragmentation degree. The siliciclastic content, mainly represented by serpentinite, quartz and clay minerals, is variable (from 12.5% to 30.8%), but always lower than the 35% threshold that defines carbonate sediments.

6.3. *Goniopora-Caulastraea* pillarstone (GCP)

This facies is less common and mainly present along the Streghe

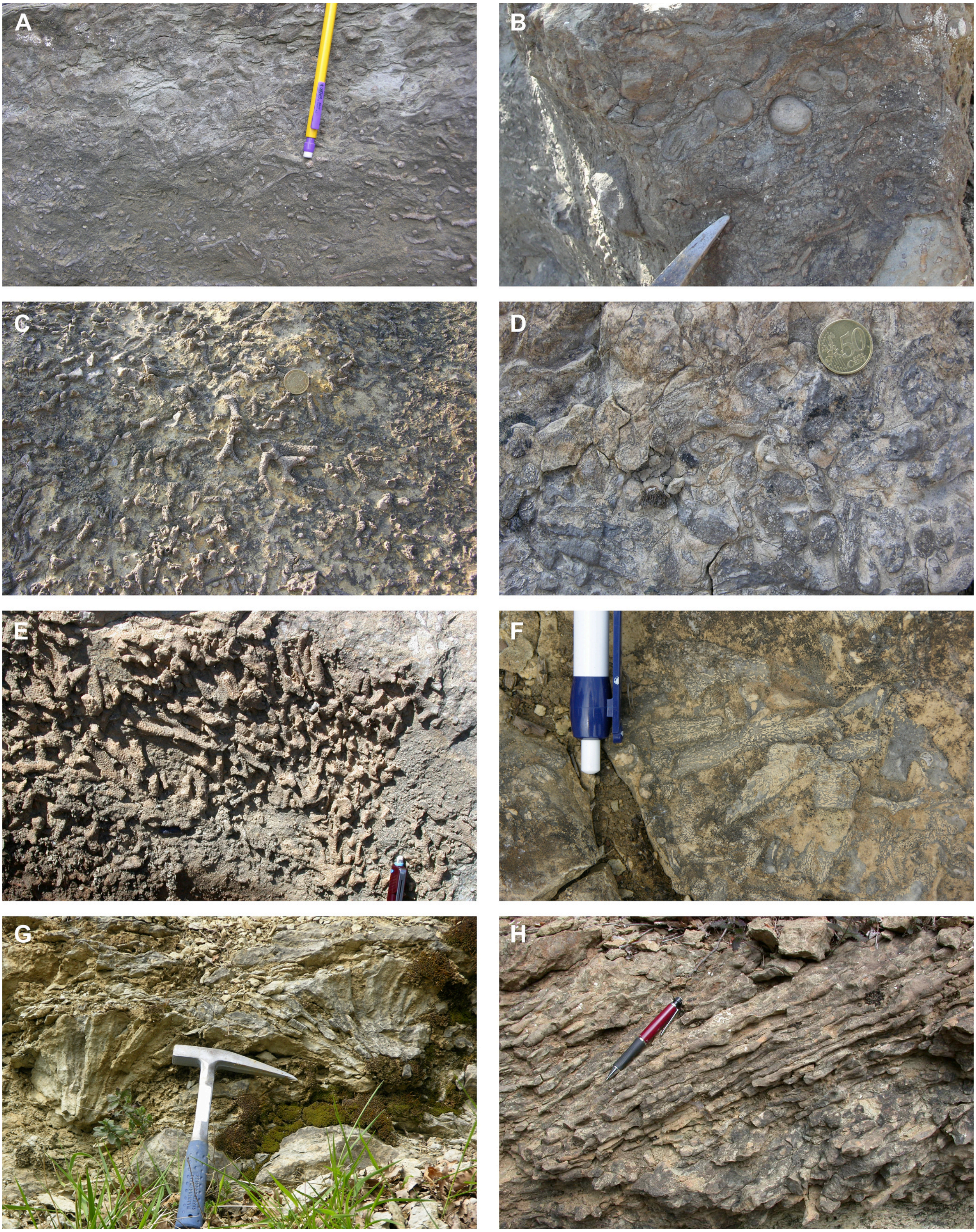

Fig. 7. Coral facies. A. BSF: floatstone with rubble of branching *Stylophora thirsiformis* (base of the Cascine section). B. BSF: floatstone dominated by thin-branching fragments of *Stylophora thirsiformis*, with sticks of branching *Goniopora nummulitica* in the upper part (Cascine section). C. ASFR: rudstone dominated by thin-branching fragments of *Stylophora thirsiformis* (Cascine section). D. ASFR: rudstone dominated by branching fragments of *Acropora haidingeri* (Cascine section). E. ASFR: *Stylophora thirsiformis* in growth position (Cascine section). F. ASFR: floatstone-rudstone with branching *Acropora haidingeri* (Streghe section). G. GCP: phaceloid colonies of *Caulastraea pseudoflabellum* in growth position (Valletta section). H. GCP: densely-packed and tilted pillars of *Goniopora nummulitica* (Streghe section).

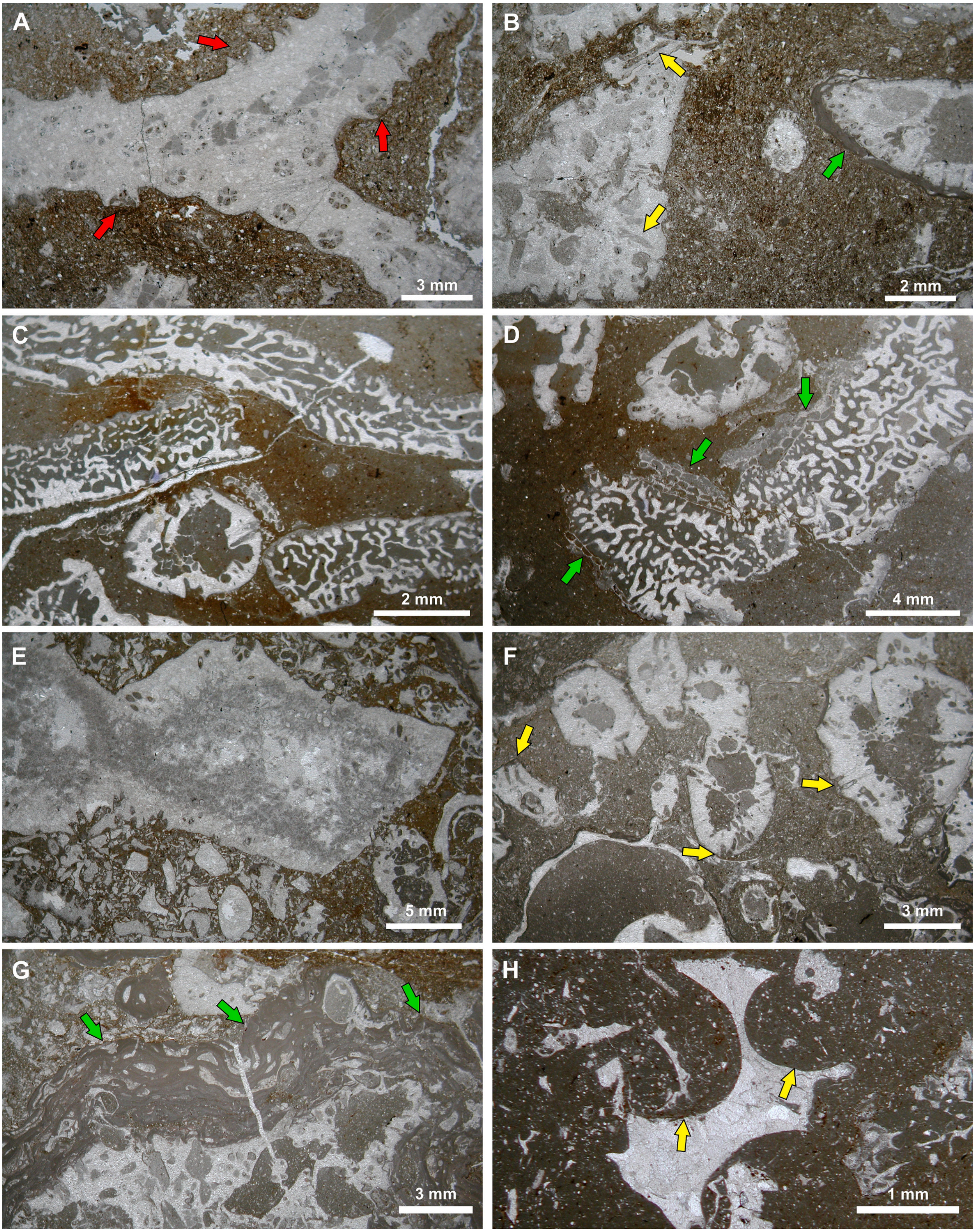

Fig. 8. Coral microtaphofacies. A. MTF1: well preserved corallites (red arrows) on the surface of a thin *Stylophora* double branch (Streghe section). B. MTF1: coralline algae crust (green arrow) and *Trypanites* perforations on coral fragments (yellow arrows) (Streghe section). C. MTF2: isooriented *Acropora* branches (Streghe section). D. MTF2: *Planorbulina* crusts on *Acropora* (green arrows) (Streghe section). E. MTF3: inter-coral matrix with abundant biogenic fragments (Cascine section). F. MTF3: extensive bioperforation by *Trypanites* (yellow arrows) on coral fragments (Cascine section). G. MTF4: thick coralline algal crust (green arrows) on a fragment of *Stylophora* (Cascine section). H. MTF4: large traces of bioperforation on a coral fragment (yellow arrows) (Cascine section). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

section (Fig. 5), with beds 50–100 cm in thickness. GCP consists of low diversity pillarstones of thick-branched or phaceloid coral colonies respectively belonging to *Goniopora nummulitica* and *Caulastraea pseudoflabellum*, in growth position or preserved as dense, tilted assemblages (Figs. 7g-h and 9a-b). Pillarstones are typically densely packed but laterally very limited and sometimes interfingering into branching coral rudstones and floatstones, which often constitute also their substrate (Fig. 9b). *Goniopora* sticks are up to 80 cm high, whereas *Caulastraea* colonies have a maximum diameter of 70 cm and a thickness of 40 cm. Some massive colonies such as *Dipsastraea subdenticulata* may occur, and fragments of highly recrystallized *Stylophora* and *Acropora* are dispersed in the matrix as well.

Corals are embedded in a lime-mud matrix with a wackestone-packstone texture and a reduced amount of other biogenic components. The microtaphofacies associated to this facies fits the MTF2, already described above for the SAFR facies. Coralline red algae are rare in the GCP and mainly represented by melobesioids with a lesser amount of mastophoroids. The siliciclastic content spans from 21.7 to 31.6%, thus indicating fully carbonate sediments.

6.4. Mixed-coral domestone (MCD)

This facies consists of mostly massive coral colonies in growth position embedded in a fine wackestone/packstone (rarely grainstone) matrix. MCD is mainly restricted to the middle-upper portion of the studied sections (Figs. 3–5), forming beds 50 to 120 cm in thickness. Coral colonies are usually not densely packed (Fig. 9g), but in some cases a coral cover of 50–60% has been estimated by the line-intercept transect method. The coral assemblage is composed of a dominant suite of coral taxa, basically *Dipsastraea subdenticulata, Antiguastrea lucasiana* and *Variabilifavia confertissima* (Reuss, 1868), associated to less common *Astreopora meneghiniana* (d'Achiardi, 1866) and *Goniopora nummulitica*. Colony size is variable, with some corals ranging from 10 to 20 cm in diameter and some others considerably larger (50–70 cm in diameter). The growth form can be considered massive in a broad sense; there are some domal and globous colonies together with some fungiform and tabular habits and most of them are much more developed in width than in height (Fig. 9c-h). Several colonies show ragged margins (Fig. 9d) and evidence of stress bands. Several phaceloid colonies of *Caulastraea pseudoflabellum* occur as well, both in growth position and resedimented. Some rubble of branching corals (namely *Stylophora* with some *Acropora*) is present as well.

Microtaphofacies associated to MCD has been named MTF4. The most diagnostic taphonomic signature is the high encrustation, often represented by widely distributed crusts of coralline algae (Fig. 8g). In order of importance they are melobesioids, mastophoroids, sporolithaceans and lithophylloids. The occurrence of small rhodoliths, usually composed of monospecific encrusting thalli of *Lithothamnion* and *Sporolithon* formed around fragments of branching corals or small metamorphic pebbles, is a typical feature of this MTF. Sparse crusts made by encrusting foraminifera (*Planorbulina* and *Placoxylina*) have been also recognized. Fragmentation and abrasion are scored as high, as they affect also resistant coral morphotypes (i.e. massive). Bioerosion is on the whole moderately developed as well, although boring traces (Fig. 8h) are usually difficult to identify because of intense abrasion of the coral remains.

The intra-coral matrix contains few small benthic foraminifera and fragments of bivalves and gastropods. This sediment shows a highly variable siliciclastic content (7.5 / 58.7%), thus ranging from carbonate to mixed carbonate-siliciclastic.

7. Discussion

This study shows that the coral-bearing beds are composed of different facies, each with their unique sedimentological, palaeontological and taphonomical features. Their analysis and interpretation, together with detailed stratigraphic and sedimentological reconstructions, depicts a complex mixed carbonate-siliciclastic sedimentary environment where depositional conditions and environmental factors changed in time and space. These changes may have controlled life, composition and preservation of the coral assemblages.

The depositional model that we present here for the Gelati outcrops (Fig. 10) is the first detailed reconstruction ever proposed for the TPB coral localities and derives from the combination of the sedimentological features with the palaeoecological interpretation of the coral facies as described in the two following paragraphs.

7.1. Depositional model

Based on the lithofacies occurrences and their vertical and lateral organization, a detailed depositional model for the Gelati area has been reconstructed (Fig. 10). The sedimentary succession in this study area exhibits a general transgressive trend, which influenced the entire TPB (Federico et al., 2022 and references therein). At certain intervals, this trend was interrupted by varying terrigenous inputs, ranging from marine to continental conglomerates, particularly evident in the marginal areas, along with the sporadic occurrence of coral-rich facies. In contrast to the broader regional distribution of the Molare Formation, the stratigraphic architecture in this confined area displays high-frequency transgressive/regressive cycles with a facies pattern of the depositional systems passing from retrogradational to progradational.

The sedimentary succession is stratigraphically and spatially organized within a valley carved on the metamorphic basement, gradually infilled by continental alluvial deposits passing into marine facies. This erosional feature is attributed to continental exposure associated with deformation and uplift of the Alpine chain during the Eocene and early Oligocene (Capponi et al., 2009; Ghibaudo et al., 2014; Federico et al., 2022; Morelli et al., 2022, and references therein). The palaeovalley initiated its progressive infilling with a sequence of fining-upward conglomerates. In the Streghe area, these conglomerates, approximately 30 m thick, are interpreted as alluvial coarse-grained sediments deposited in a braided river setting during the initial phase of transgression or late lowstand. In terms of sequence stratigraphy, they represent the typical incised valley fill deposits. These continental deposits gradually fill the lowest part of the palaeovalley and onlap the present eastern flank, as depicted in the geological map (Fig. 2). Subsequently, they change abruptly to an interval containing fine-grained conglomerates, clay, and very coarse sandstones, prominently observed at the base of the Streghe and Cascine sections. Despite the dominance of terrigenous input, these lithofacies are distinctly deposited within a marine environment, as testified by scattered and resedimented lenticular coral-rich beds (BSF coral facies). The lithofacies of this interval are interpreted as the distal portion of a fan-delta system or coarse-grained delta (Gilbert-type), specifically representing the initial bottomset part, corresponding to the prodelta setting.

These lithofacies also indicate a rapid transgression over the preceding continental facies, characterised by a retrogradational trend and onlap termination against the upper part of eastern flank of the palaeovalley (Fig. 2). In fact, along this eastern flank (Cascine section), marine clays and conglomerates are gradually overlain by a 20 m thick conglomeratic body with steep foreset that can be interpreted as a small fan-delta, that starts to prograde over the former prodelta clay setting. Towards the upper part of this conglomeratic unit, the presence of high-angle cross-bedding suggests the existence of fluvial bars within the topset of the fan-delta. Fan-deltas or Gilbert-type deltas are commonly recognized in various areas where the Molare Formation is exposed (Gnaccolini, 1981; Fravega et al., 1987; Rossi and Craig, 2016; Federico et al., 2022). The conglomeratic foreset to topset beds are confined to a small eastern area (Cascine section), indicating an increase in terrigenous input, which can be interpreted as a short-term regressive phase (Fig. 2). This fan-delta system undergoes abrupt deactivation, with the conglomeratic interval initially overlain by a thin clay layer and

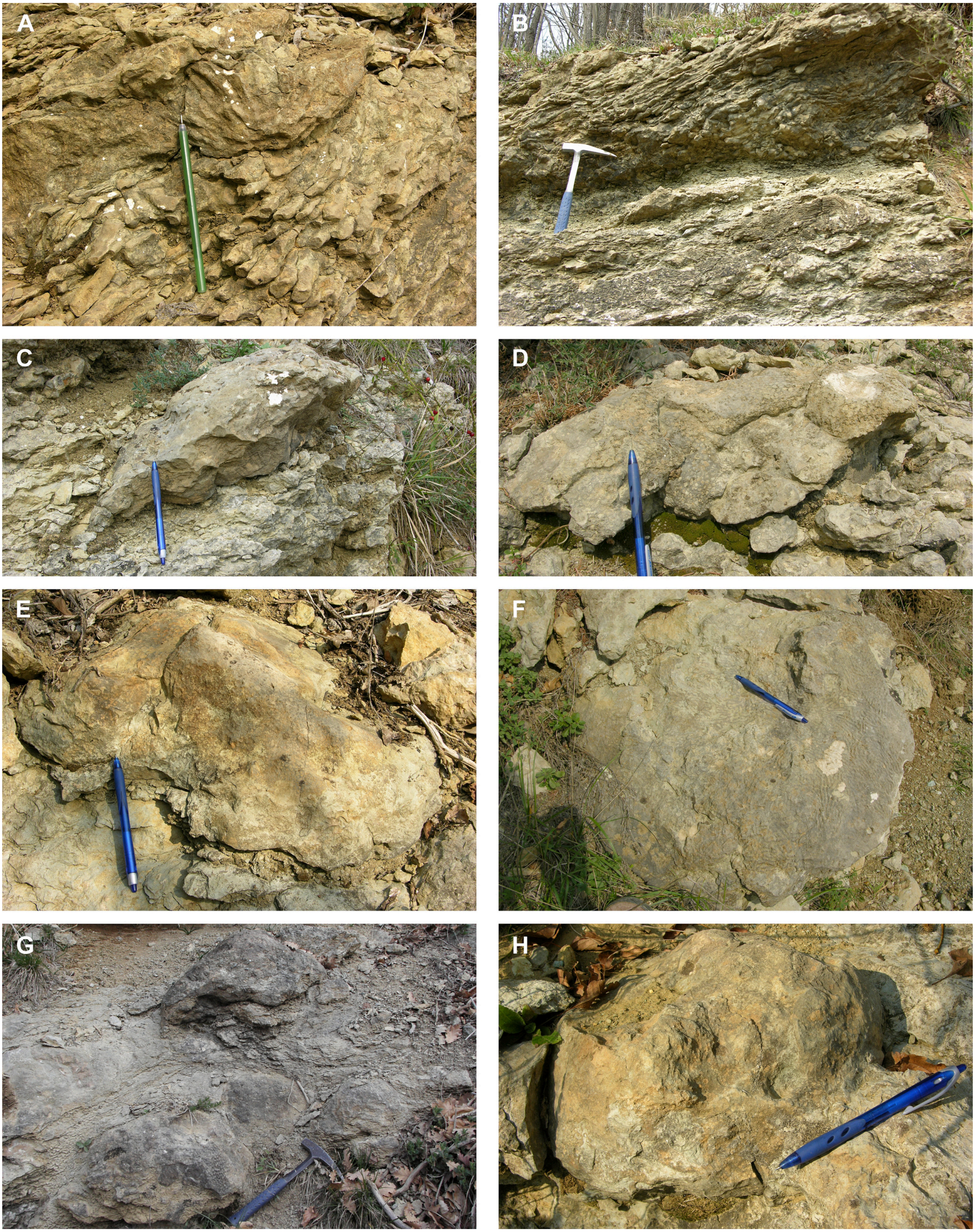

Fig. 9. Coral facies. A. GCP: colony of *Caulastraea pseudoflabellum* settled directly on the top of tilted columnar branches of *Goniopora nummulitica* (Streghe section). B. GCP: Tilted columnar colony of *Goniopora nummulitica* on the top of the *Acropora-Stylophora* floatstone-rudstone (Streghe section). C. MCD: globous-domal colony of *Goniopora mummulitica* (Cascine section). D. MCD: large fungiform colony of *Dipsastrea subdenticulata* (Cascine section). E. MCD: domal colony with a flat lower surface of *Antiguastrea lucasiana* (Cascine section). F. MCD: domal colony of *Variabilifavia confertissima* (Cascine section). G. MCD: globous-domal colonies engulfed in the marly sediments (Valletta section). H. MCD: massive colony of *Astreopora* sp. (Cascine section).

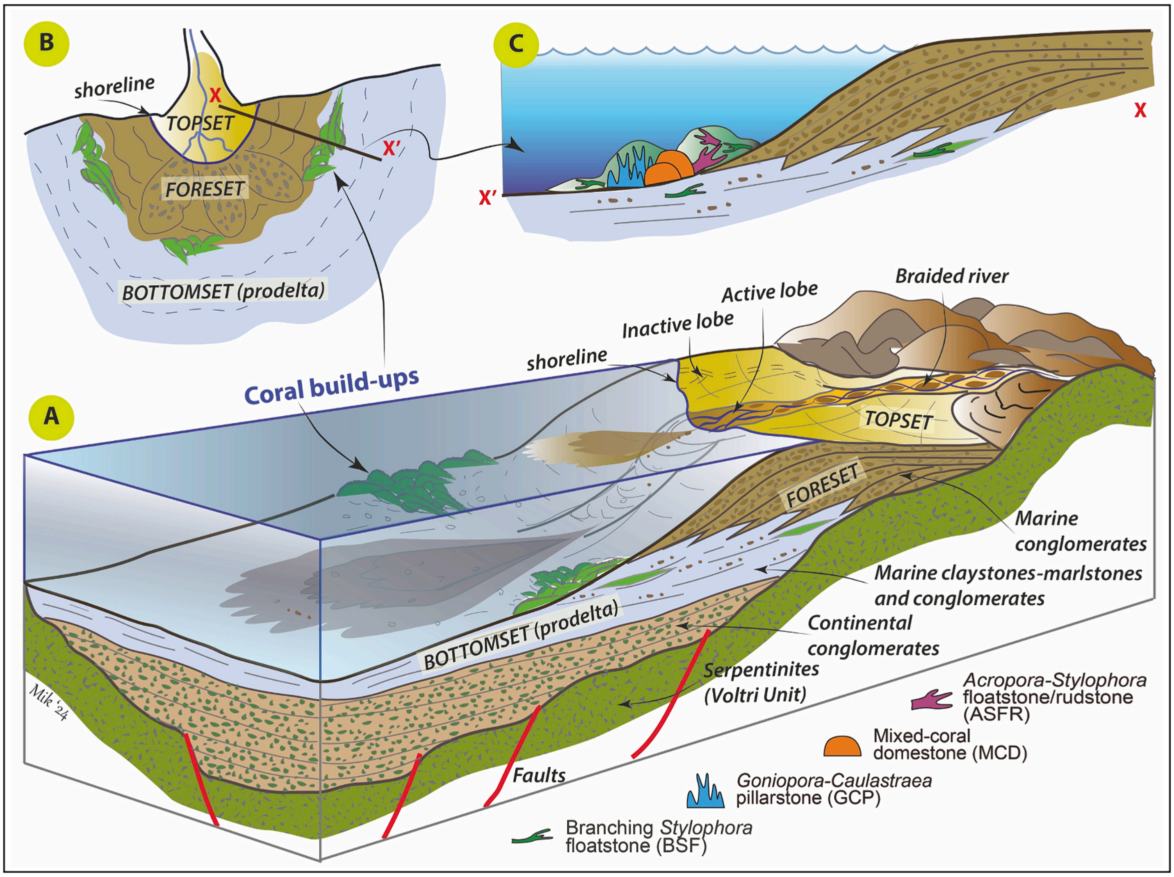

Fig. 10. Schematic representation of a fan-delta depositional system with associated coral buildups. A. Three-dimensional view of the depositional system infilling an incised valley. It highlights the distribution of active and inactive lobes with a braided river system and delineates a classic fan-delta including topset, foreset, and bottomset strata. Coral buildups are notably situated along the transition between the prodelta (bottomset) and the clinostratified foreset beds. B. Plan view of the fan-delta system, showing both the emerged topset and the submerged parts of the delta front (foreset) and the prodelta (bottomset). C. Cross-section view (X-X') of a single coral buildup, reconstructing its relative growth position within the sedimentary depositional model.

subsequently by slightly resedimented and in situ coral-rich beds (as observed in the Cascine section). This sharp transition is interpreted as a high-frequency transgressive pulse, accompanied by a significant increase in water depth and a transition to a prodelta setting. The coral-rich beds of the Cascine section, limited in thickness and lateral extension, are contemporaneous with other carbonate intervals documented in the Streghe and Valletta sections (Figs. 4, 5). In these sections, the conglomeratic foreset beds are absent, and the coral-rich beds form laterally discontinuous small buildups directly overlying the prodelta clay and conglomerates. Finally, the succession in both sectors is overlain by thick sandstones deposited in a shoreface to offshore transition setting. The demise of the coral carbonate factory is attributed to the substantial influx of these sandstones and rare conglomerates, indicating a massive input of siliciclastic sediments.

The lithofacies types and their architecture and spatial distribution enable the reconstruction of the depositional model for the Gelati area (Fig. 10). Additionally, they suggest that the coral buildups are laterally discontinuous and confined to the prodelta setting, likely in a lateral position with respect to the active fan-delta lobes. These buildups appear to have been intermittently deactivated or smothered by fine-grained terrigenous input during flood phases or shifts in distributary channels.

7.2. Palaeoecological interpretation of coral facies

Along the measured sections, coral facies are interdigitated with conglomerates and claystones-marlstones and, according to the above reconstructed physiographic and depositional setting, they indicate a colonization in a deltaic environment at the depositional boundary between these lithologies, thus in a relatively deep setting and under "brown mesophotic" conditions (sensu Zapalski et al., 2021; Majchrzyk et al., 2022) Fig. 10). The measured sections also show the occurrence of two main colonization phases: the first is recorded only in the lower part of the Cascine section, while the second is detected in the upper part of the Cascine section and in all carbonate levels of Streghe and Valletta sections.

The first colonization by corals is represented at the base of the Cascine section by the "branching *Stylophora* floatstone" (BSF). This coral assemblage, embedded mostly in a micritic sandstone where the non-carbonate component is abundant (up to 60%), is dominated by a rubble of branching *Stylophora thirsiformis* deposited in the distal part of the fan-delta (close to the transition between foreset and bottomset). The microtaphofacies MTF1 associated to these corals shows in general a relatively high level of fragmentation and abrasion but is by far the less affected by bioinfestation suggesting a fast transport and a relatively short surface residence time of coral remains before burial. Thus, the duration of these coral assemblages is here assumed as very short, mainly controlled by periodic episodes of more abundant sedimentary run-off determined by higher fluvial activity. Although it is not possible to establish exactly the original growth environment of these corals, the ecological requirements of their present-day counterparts suggest growth at shallower depths where they probably formed small and ephemeral carpets (sensu Riegl and Piller, 1999). Fast-growing branching corals belonging to the pioneer and highly plastic genus *Stylophora* (Loya, 1976; Shaish et al., 2007) are retained as particularly suitable to cope with strong sediment accumulation and possibly with high nutrient supply. Such branching growth forms are by far the most effective with respect to sediment clearance by passive removal (Stafford-Smith, 1993) and *Stylophora* has been in fact reported even in the upwelling-influenced high-nutrient environment of the Gulf of Aden (Yemen) (Benzoni et al., 2003). Fragments of branching corals, mostly dominated by *Stylophora*, are reported from the mesophotic deltaic palaeoenvironment recorded in Friuli (NE Italy) during the early Eocene (Bosellini et al., 2022).

The BSF, documenting the initial stages of coral colonization also of the second phase, may be also related to a low stand phase of fluvial activity, during which rivers exerted a strong erosion and discharged great amount of siliciclastic sediments.

The second phase of colonization, represented in all the three measured sections, continues with a complex alternation of the three facies ASFR, GCP, and MCD. Although some zonation is illustrated in the static model of Fig. 10, ecosystem dynamics is actually represented by the interdigitation of these facies and is strictly connected to the extreme instability of the depositional environment. The periodic migration of river mouths may have caused changes in substrate type, hydrodynamics, turbidity (brightness), nutrients, etc., leading to rapid changes in coral facies in space and time.

The "*Goniopora-Caulastraea* pillarstone" (GCP) facies, associated to microtaphofacies MTF2, is embedded in a muddy micrite mostly exhibiting a wackestone texture, which is consistent with a fine-grained sedimentation and generally low hydrodynamic conditions, fitting with a depositional setting coincident with the distal part of the fan-delta where reduced light penetration and turbid-waters are also inferred. Phaceloid corals and thick-branched corals, which compose the monogeneric coral pillarstones, have been interpreted as reflecting high turbidity conditions possibly alternated to phases of fine-grained sediment accumulation that likely forced corals to a partial shifting to heterotrophy and to a high tolerance to sediment veneer (Sanders and Baron-Szabo, 2005).

Phaceloid corals, such as *Caulastraea*, are reported as able to change their way of feeding in response to high-turbidity phases (Dryer and Logan, 1978; Dupraz and Strasser, 2002) and also as representing an adaptation to muddy substrate and high sedimentation rates (Dryer and Logan, 1978). Some small-polyped corals belonging to the family Poritidae, like *Goniopora*, are known to be highly tolerant to sediment being able to settle their larvae even into mobile substrates and their juvenile forms to develop in spite of constant rain of sediment (Rogers, 1983; Stafford-Smith, 1993). In the Cenozoic fossil record, and especially in the Oligocene, phaceloid corals like *Caulastraea* and *Goniopora/Actinacis* paucispecific thickets, known as well as "pioneer" assemblages (Bosellini and Stemann, 1996; Sanders and Baron-Szabo, 2005) colonized the muddy and turbid lagoon of the barrier reef/lagoon system of the Castelgomberto Limestone in northern Italy (Bosellini and Trevisani, 1992; Bosellini et al., 2020).

The "mixed-coral domestone" facies (MCD), associated to microtaphofacies MTF3–4, is instead interpreted as a coral assemblage thriving in a relatively shallower and exposed setting, but also periodically affected by sedimentary input connected to fluctuations of fluvial activity. Water energy was probably quite high, favoring sediment clearance on corals and relative water transparency. Within these environmental conditions, small coral patches dominated by massive morphotypes were able to develop.

Massive corals, in particular those with large corallites, are retained as most effective in active sediment rejection, whereas branching forms are known to face sediment accumulation mostly through passive removal (Bak and Elgershuizen, 1976; Stafford-Smith, 1993). The ragged margins exhibited by several massive-tabular colonies, together with evidences of growth anomalies and irregular knobby surfaces document events of sediment coverage and partial mortality followed by phases of recovery (Sanders and Baron-Szabo, 2005; Reuter et al., 2019).

Inter-coral matrix exhibits a packstone texture and MTF3–4 is the most affected by fragmentation (52%) and abrasion (59%). This signature may be explained both as an effect of bioerosion-induced fragmentation, reflected by the analogously higher bioerosion index (65%), or as an effect of more intense resedimentation due to water movement and/or transport. Relatively higher hydrodynamic conditions are also inferred by the occurrence of quite large massive growth forms and the thicker diameter of the associated branching corals. The high bioerosion degree may be interpreted as indicative of a long resilience of both living and death corals before complete burial. Although the occurrence of traces due to worms is widespread, traces referred to boring sponges are remarkably frequent within this MTF. This taphonomic signature may be indicative of a setting where suspended mud was kept at low levels or possibly absent. Bioerosion due to boring sponges is known to produce large amount of biogenic debris, which is a typical feature of this MTF, being up to 98% of bored substrate deposited as fine sediment "chips" (Hutchings, 1986; Perry and Hepburn, 2008). The occurrence within the inter-coral matrix of frequent pebbles of metamorphic rocks is consistent with a relatively proximal setting and/or with occasional episodes of coarse-grained run-off, which likely contributed to rubble formation, as documented in other similar contexts (Tomassetti et al., 2013).

The "*Acropora-Stylophora* floatstone/rudstone" (ASFR) is quite interdigitated with both GCP and MCD, with this rubble often forming a suitable substrate for the settlement of corals such as the phaceloid and thick-branched colonies of the GCP facies (Fig. 8b). The periodic sediment burial and re-exposure of older coral rubble, suitable for new coral recruitment, is in fact reported as a process characterizing most sediment-influenced coral communities (Perry, 2005).

As regards in particular the *Acropora*-dominated floatstones, associated with microtaphofacies MTF2 (the same of GCP facies), the preferential orientation of coral branches parallel to the bedding plane is consistent with some transport by unidirectional currents. Significantly different degrees of taphonomic alteration occur between the dominant components (namely *Acropora*) and the associated scattered fragments of *Stylophora*, with these latter more affected by fragmentation, abrasion and bioerosion. The general better preservation of *Acropora* allows thus to assume that these corals have been affected by a lesser transport than *Stylophora* and that probably their original life environment was not far away from where they have been deposited. The higher incidence of bioerosion on *Stylophora* may depend both on intrinsic factors, such as the higher skeleton density of *Stylophora* which is thus retained more attractive for borers (Highsmith, 1981), and on environmental causes. It is hence realistic to suppose that *Stylophora* originally colonized settings more suitable for flourishing of a macroboring community and that bioerosion on these corals was thus mostly pre-depositional.

It is important to underline that *Acropora*, which is known in the present-day oceans as a genus typical of shallow, well-lit agitated waters (Wallace, 1999), displayed in the geological record different ecological requirements, with these corals often found associated to deeper, low energy and possibly turbid-water settings (Schuster, 2002; El-Azabi, 2023), also together with a strong resilience to major ocean chemistry changes (Stolarski et al., 2016). To increase light catchment, it is here supposed that *Acropora* adopted a shape consisting of straight simple branches and lacking of secondary branches, being vertical trend of shape and orientation a strategy to optimize light capture (Graus and Macintyre, 1976). Reduced light penetration likely determined a decrease of calcification (Rogers, 1990; MacDonald and Perry, 2003), responsible of weakening corals and making them more vulnerable to some episodes of higher energy and definitely to breakage with consequent rubble formation.

7.3. Palaeoecological interpretation of red algae associations

The four main informal groups considered herein (lithophylloids, mastophoroids, melobesioids and sporolithaceans) have been traditionally used as reliable palaeobathymetric (in relation to brightness conditions) and palaeoclimatic markers (Adey, 1979; Bosence, 1991; Aguirre et al., 2000; Braga and Aguirre, 2004; Kroeger et al., 2006;

Vannucci et al., 2010; Sarkar, 2017; Singh et al., 2020 and reference therein). In particular lithophylloids, here represented only by the heliophilic genus *Lithophyllum*, are typical of cool to warm shallow-waters. Mastophoroids are dominant taxa in very shallow tropical waters. Melobesioids taxa commonly dominate tropical environments below 20 m water depth and down to 110–120 m, and in modern reefal environments are relevant components below 10–15 m. Sporolithaceans algae exhibit ecological characteristics similar to those of the melobesioids.

The corallinacean algae association retrieved along the three examined logs confirms the palaeoenvironment conditions indicated by the coral assemblages. The considerable amount of mastophoroids along the Valletta and Cascine sections, also coupled in Cascine to *Lithophyllum,* indicate shallow-water, marine tropical conditions. The general abundance of melobesioids and the occurrence of sporolithaceans, which are among the deepest dwelling taxa retrieved, are here rather interpreted as indicators of poor seafloor irradiation, possibly related to an increased water turbidity. This could be enhanced by increased runoff of the riverine-deltaic system reacting to the active tectonic but also to the deteriorating climatic condition of the uppermost Oligocene. This is particularly visible along the Streghe section, where the dominant melobesioids are associated with sporolithaceans, thus indicating a higher turbidity level than in the other two successions.

The general dominance of melobesioids, coupled to abrupt changes in the percentage of the other three coralline algae groups even in samples which are stratigraphically close, also supports the idea of a quite unstable environment. Sudden variations in light conditions could have occurred, possibly related to sharp variations of the sedimentary input in space and time.

7.4. Coral buildups in fan-delta systems: palaeodepth and main controlling factors

The depositional model reconstructed for the Gelati area sheds light on the intricate relationship between sedimentary processes and the development of coral buildups within fan-delta systems. Coral development along fan-delta or nearshore turbid-water setting is not uncommon in modern environments as well as in the fossil record. Starting from the seminal works of Roy and Smith (1971) and Mount (1984) many authors have worked on these mixed carbonate-siliciclastic systems (Wilson and Lokier, 2002; Wilson, 2005; Perry and Smithers, 2006, 2010; Browne et al., 2012, 2019; Morsilli et al., 2012; Perry et al., 2012; Santodomingo et al., 2015; Moura et al., 2016 among others). However, in turbid-water contexts like these, inferring the palaeodepth of coral growth presents challenges compared to oligotrophic and clear seawater settings (Fabricius et al., 2016). The real water depth of the prodelta, though potentially shallow, can be difficult to ascertain accurately due to the persistent turbidity influencing visibility and sedimentation rates. In this context the presence of light-dependent organisms cannot help the palaeoecological reconstruction, considering that corals or other reef-building organisms can thrive and flourish also in the mesophotic setting (e.g. Lesser et al., 2009, 2018; Pérez-Castro et al., 2022).

Fan-delta systems, characterised by dynamic sedimentary processes and variable terrigenous input, often provide a complex yet conducive environment for coral growth. Similar to the findings in the Gelati area, various studies have documented coral buildups within fan-delta settings worldwide. For instance, in the Borneo area, coral reefs have a high resilience where terrigenous sediment discharge is high (Browne et al., 2019). These reefs demonstrate resilience to sedimentation stress, adapting to fluctuating conditions by adjusting growth rates and morphology (Morgan et al., 2017). Other examples are known in the fossil record such as in the Eocene of the Pyrenees, where an extensive coral buildup, up to 50 m thick, developed inside a prodelta mud-rich setting (Morsilli et al., 2012). As well as the patch reef developed in the Miocene of the eastern Borneo along the Mahakam Delta (Wilson, 2005) and along the eastern Kalimantan in Indonesia (Novak et al., 2013; Santodomingo et al., 2015), where branching corals can be dominant (Kusworo et al., 2015). In these environments, like in the Gelati area, typical deep mesophotic platy corals may be absent as the polyps on their upper surface would be easily "suffocated" and buried.

In the context of fan-delta systems, coral buildups may exhibit lateral discontinuity due to periodic smothering by sediment influx during flood events or shifts in channel patterns. Such dynamics are evident in the Gelati area, where coral-rich beds intermittently alternate with fine-grained terrigenous deposits. This pattern suggests that coral growth is influenced by the interplay between sedimentation rates and hydrodynamic conditions within the deltaic environment.

According to Wilson (2005), nutrient supply is often associated to siliciclastic input and is here supposed to represent a major environmental constraint for coral fauna. Turbidity entails a complex interaction between sedimentary input, mean grain-size of the sediment eventually suspended in the water column and water energy. A certain degree of water movement (i.e. hydrodynamic conditions) is supposed to be necessary to maintain mud particles in suspension for a long time (Woolfe and Larcombe, 1999), thus possibly determining higher turbidity conditions in the most proximal part of the bottomset (prodelta) where the combination of fine-grained sedimentation and the still active effect of water movement favoured nearly chronic mud suspension.

8. Conclusions

In the face of rising global temperatures, coral reefs are one of the ecosystems most threatened and for which a global severe decline is expected even if global warming is limited to 1.5 °C, as recently indicated by the IPCC report 2022. It is, however, emerging the evidence that coral reefs living in marginal settings provide better and suitable conditions to escape the effects of the current global warming trend with respect to shallow, euphotic coral reefs, and thus acting as potential ecological refugia.

Deltaic palaeoenvironments hosting reef coral assemblages, in particular thoseshallow and turbid mesophotic ("brown mesophotic reefs"), show a good record throughout the Cenozoic, also during climate warming events, thus becoming extremely useful to understand the dynamics and durability of these coral ecosystems and to provide empirical evidence of their long-term response and resilience to climatic perturbations.

In this study we have characterised coral buildups that formed at the edge of a fan-delta system during the middle Chattian, and thus in coincidence with the Late Oligocene Warming Event (LOWE). The main outputs are the following:

- By an accurate field-work and facies analysis we provide a detailed depositional model of an Oligocene coral reef associated to a fan-delta system. Despite the Tertiary Piedmont Basin (TPB) is quite rich of coral outcrops that attracted the interest of geologists and palaeontologist since the 19th century, our model is the first proposed so far.
- We document that coral growth took place in the prodelta setting, and thus within a mesophotic environment. We depict here a complex mixed carbonate-siliciclastic sedimentary environment where depositional conditions and environmental factors changed in time and space, controlling life, composition and preservation of the coral assemblages. The reef colonial corals formed small buildups, laterally discontinuous and intermittently deactivated or smothered by fine-grained terrigenous input during flood phases or shifts in distributary channels.
- The ecosystem dynamics depicted by the first colonization event by branching *Stylophora* corals, the development of the small coral buildups and their final demise, clearly occurred under strong fluviatile control. Final suffocation is attributed to the substantial

influx of sandstones and rare conglomerates, indicating a massive input of siliciclastic sediments.

- We define four different types of coral facies (branching *Stylophora* floatstone, *Acropora-Stylophora* floatstone/rudstone, *Goniopora-Caulastraea* pillarstone, mixed-coral domestone). Their coral assemblages are characterised according to coral taxonomic composition, growth forms (branching, phaceloid and massive) and taphonomic features. Coral facies appear quite interdigitated as strictly connected to the extreme instability of the depositional environment.
- All coral assemblages are represented by sediment-resistant taxa and look quite resilient, adapting and shifting in time and space according to the changes of stressors like turbidity, hydrodynamic energy, sediment and nutrient supply, in turn imposed by river activity.
- Our results shed a light on the fossil record of Oligocene mesophotic reefs and provide useful data for better understanding the long-term resilience of these ecosystems and their capacity to support diversity and ecological functions.

CRediT authorship contribution statement

Francesca R. Bosellini: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Alessandro Vescogni:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Data curation, Conceptualization. **Antonino Briguglio:** Writing – review & editing, Investigation, Funding acquisition. **Michele Piazza:** Writing – review & editing, Investigation. **Cesare A. Papazzoni:** Investigation. **Giulia Silvestri:** Writing – review & editing, Investigation, Data curation. **Michele Morsilli:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Francesca R. Bosellini reports financial support was provided by Italian Ministry of Education and Merit. Francesca R. Bosellini reports financial support was provided by European Union. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data are reported in the article

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References

Adey, W.H., 1979. Crustose coralline algae as microenvironmental indicators in the Tertiary. In: Gray, J., Boucot, A.J. (Eds.), Historical Biogeography, Plate Tectonics and the Changing Environment. Oregon University Press, Corvallis, pp. 459–464.

Adey, W.H., Macintyre, I.G., 1973. Crustose coralline algae: a re-evaluation in the geological sciences. Geol. Soc. Am. Bull. 84, 883–904.

Aguirre, J., Riding, R., Braga, J.C., 2000. Diversity of coralline red algae: origination and extinction patterns from the early cretaceous to the Pleistocene. Paleobiology 26, 651–667.

Assis, J., Coelho, N.C., Lamy, T., Valero, M., Alberto, F., Serrão, E.Á., 2016. Deep reefs are climatic refugia for genetic diversity of marine forests. J. Biogeogr. 43, 833–844.

Bak, R.P.M., Elgershuizen, J.H.B.W., 1976. Patterns of oil-sediment rejection in corals. Mar. Biol. 37, 105–113.

Benzoni, F., Bianchi, C.N., Morri, C., 2003. Coral communities of the North-western Gulf of Aden (Yemen): variation in framework building related to environmental factors and biotic conditions. Coral Reefs 22 (4), 475–497.

Bosellini, F.R., 2006. Biotic changes and their control on Oligocene–Miocene reefs: a case study from the Apulia Platform margin (southern Italy). Palaeogeogr. Palaeoclimatol. Palaeoecol. 241, 393–409.

Bosellini, F.R., Russo, A., 1992. Stratigraphy and facies of an Oligocene fringing reef (Castro Limestone, Salento Peninsula, southern Italy). Facies 26, 146–166.

Bosellini, F.R., Stemann, T.A., 1996. Autoecological significance of growth form in the scleractinian coral *Actinacis rollei* Reuss (Oligocene, Lessini Mountains, Northern Italy). In: Cherchi, A. (Ed.), Autoecology of Selected Fossil Organisms: Achievements and Problems, Boll. Soc. Paleontol. Ital. spec. vol, vol. 3, pp. 31–43.

Bosellini, F.R., Trevisani, E., 1992. Coral facies and cyclicity in the Castelgomberto Limestone (early Oligocene, eastern Lessini Mountains, northern Italy). Riv. Ital. Paleontol. Stratigr. 98 (3), 339–352.

Bosellini, F.R., Vescogni, A., Kiessling, W., Zoboli, A., Di Giuseppe, D., Papazzoni, C.A., 2020. Revisiting reef models in the Oligocene of northern Italy (venetian Southern Alps). Boll. Soc. Paleontol. Ital. 59 (3), 337–348.

Bosellini, F.R., Vescogni, A., Budd, A.F., Papazzoni, C.A., 2021. High coral diversity is coupled with reef-building capacity during the late Oligocene Warming (Castro Limestone, Salento Peninsula, S. Italy). Riv. Ital. Paleontol. Stratigr. 127 (3), 515–538.

Bosellini, F.R., Benedetti, A., Budd, A.F., Papazzoni, C.A., 2022. A coral hotspot from a hot past: the EECO and post-EECO rich reef coral fauna from Friuli (Eocene, NE Italy). Palaeogeogr. Palaeoclimatol. Palaeoecol. 607, 111284.

Bosence, D.W.J., 1991. Coralline algae: Mineralization, taxonomy, and palaeoecology. In: Riding, R. (Ed.), Calcareous Algae and Stromatolites. Springer-Verlag, pp. 98–113.

Braga, J.C., Aguirre, J., 2004. Coralline algae indicate Pleistocene evolution from deep, open platform to outer barrier reef environments in the northern great barrier reef margin. Coral Reefs 23, 547–558.

Briguglio, A., Crobu, S., Lutaj, E., Piazza, M., 2021a. Integrated stratigraphy from a transgressive upper Oligocene section in NW Italy. Stratigraphy 18 (2), 123–137.

Briguglio, A., Vannucci, G., Bruzzone, C., Piazza, M., 2021b. Stratigraphic development of a late Oligocene Reef complex under strong fluviatile influence in the Tertiary Piedmont Basin (Liguria, NW Italy). Micropaleontology 67 (4), 315–339.

Browne, N.K., Smithers, S.G., Perry, C.T., 2012. Coral reefs of the turbid inner-shelf of the Great Barrier Reef, Australia: an environmental and geomorphic perspective on their occurrence, composition and growth. Earth-Sci. Rev. 115 (1–2), 1–20.

Browne, N., Braoun, C., McIlwain, J., Nagarajan, R., Zinke, J., 2019. Borneo coral reefs subject to high sediment loads show evidence of resilience to various environmental stressors. PeerJ 7 (8), e7382.

Budd, A.F., Stolarski, J., 2009. Searching for new morphological characters in the systematics of scleractinian reef corals: comparison of septal teeth and granules between Atlantic and Pacific Mussidae. Acta Zool. 90, 142–165.

Budd, A.F., Fukami, H., Smith, N.D., Knowlton, N., 2012. Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). Zool. J. Linnean Soc. 166, 465–529.

Cacciapaglia, C., van Woesik, R., 2016. Climate-change refugia: shading reef corals by turbidity. Glob. Chang. Biol. 22, 1145–1154.

Cahuzac, B., Poignant, A., 1997. Essai de biozonation de l'Oligo-Miocène dans les bassins européens à l'aide des grands foraminifères néritiques. Bull. Soc. Géol. France 168, 155–169.

Capponi, G., Crispini, L., Federico, L., Piazza, M., Fabbri, B., 2009. Late Alpine tectonics in the Ligurian Alps: constraints from the Tertiary Piedmont Basin conglomerates. Geol. J. 44, 211–224.

Capponi, G., Crispini, L., Federico, L., Malatesta, C., 2016. Geology of the Eastern Ligurian Alps: a review of the tectonic units. Ital. J. Geosci. 135 (1), 157–169.

Dela Pierre, F., Martire, L., Natalicchio, M., Clari, P., Petrea, C., 2010. Authigenic carbonates in Upper Miocene sediments of the Tertiary Piedmont Basin (NW Italy): Vestiges of an ancient gas hydrate stability zone? GSA Bull 122 (7/8), 994–1010.

Dryer, S., Logan, A., 1978. Holocene reefs and sediments of Castle Harbour, Bermuda. J. Mar. Res. 36, 399–425.

Dunham, R.J., 1962. Classification of carbonate rocks according to depositional texture. In: Hamm, W.E. (Ed.), Classification of Carbonate Rocks, a Symposium, AAPG Mem, vol. 1, pp. 108–121.

Dupraz, C., Strasser, A., 2002. Nutritional modes in coral-microbialite reefs (Jurassic, Oxfordian, Switzerland): evolution of trophic structure as a response to environmental change. Palaios 17, 449–471.

El-Azabi, M.H., 2023. Sedimentary facies and stratal architecture of the Middle Eocene Acropora-dominated succession in a storm-influenced ramp system, El-Ramliya area, north Eastern Desert, Egypt. Sediment. Geol. 447, 106368.

Embry, A.F., Klovan, J.E., 1971. A late Devonian reef tract on Northeastern Banks Island. N.W.T. Bull. Can. Petrol. Geol. 19, 730–781.

Fabricius, K.E., Logan, M., Weeks, S.J., Lewis, S.E., Brodie, J., 2016. Changes in water clarity in response to river discharges on the Great Barrier Reef continental shelf: 2002-2013. Estuar. Coast. Shelf Sci. 173, A1–A15.

Federico, L., Crispini, L., Dabove, G.M., Piazza, M., Capponi, G., 2016. Stratigraphic vs structural contacts in a late orogenic basin: the case of the Tertiary Piedmont Basin in the Sassello area (Ligurian Alps, Italy). J. Maps 12 (5), 959–967.
Federico, L., Crispini, L., Scarsi, M., Capponi, G., Piazza, M., 2022. Late orogenic tectonics in the Ligurian Alps (Italy): constraints from syntectonic sedimentary deposits at the top of an exhumed plate interface. J. Maps 18 (2), 178–189.
Fravega, P., Giammarino, S., Piazza, M., Russo, A., Vannucci, G., 1987. Significato paleoecologico degli episodi coralgali a nord di Sassello. Nuovi dati per una ricostruzione paleogeografico-evolutiva del margine meridionale del Bacino Terziario del Piemonte. Atti Soc. Tosc. Sci. Nat. 94, 19–76.
Fravega, P., Piazza, M., Stockar, R., Vannucci, G., 1994. Oligocene coral and algal reef and related facies of Valzemola (Savona, NW Italy). Riv. Ital. Paleontol. Stratigr. 100 (3), 423–456.
Fukami, H., Chen, C.A., Budd, A.F., Collins, A.G., Wallace, C.C., Chuang, Y.-Y., Chen, C. A., Dai, C.-F., Iwao, K., Sheppard, C., Knowlton, N., 2008. Mitochondrial and Nuclear Genes suggest that stony corals are monophyletic but most families of stony corals are not (Order Scleractinia, Class Anthozoa, Phylum Cnidaria). PLoS One 3, e3222.
Gelati, R., Gnaccolini, M., 1988. Sequenze deposizionali in un bacino episuturale, nella zona di raccordo tra Alpi ed Appennino Settentrionale. Atti Tic. Sci. Terra 31, 340–350.
Ghibaudo, G., Massari, F., Chiambretti, I., 2014. Oligo-Miocene tectono-sedimentary evolution of the Langhe sub-basin: from continental to basinal setting (Tertiary Piedmont Basin – Northwestern Italy). J. Med. Earth Sci. 6, 53–144.
Gnaccolini, M., 1981. Oligocene fan-delta deposits in northern Italy: a summary. Riv. Ital. Paleontol. Stratigr. 87 (4), 627–636.
Gradstein, F.M., Ogg, J.G., Smith, A.G., 2004. A Geologic Time Scale 2004. Cambridge University Press, 589 pp.
Graus, R.R., Macintyre, I.G., 1976. Light control of growth form in colonial reef corals: computer simulation. Science 193, 895–897.
Highsmith, R.C., 1981. Coral bioerosion: damage relative to skeletal density. Am. Nat. 117, 193–198.
Hutchings, P.A., 1986. Biological destruction of coral reefs: a review. Coral Reefs 4, 239–242.
Insalaco, E., 1998. The descriprive nomenclature and classification of growth fabrics in fossil scleractinian reefs. Palaeogeogr. Palaeoclimatol. Palaeoecol. 121, 169–194.
IPCC, 2022. In: Pörtner, H.-O., Roberts, D.C., Tignor, M., Poloczanska, E.S., Mintenbeck, K., Alegría, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A., Rama, B. (Eds.), Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, 3056 pp.
Kiessling, W., 2002. Secular variations in the Phanerozoic reef ecosystems. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), Phanerozoic Reef Patterns. Spec. Publ. 72. SEPM, pp. 625–690.
Kocsis, L., Briguglio, A., Roslim, A., Razak, H., Coraie, S., Frijia, G., 2018. Stratigraphy and age estimate of Neogene shallow marine fossiliferous deposits in Brunei Darussalam (Ambug Hill, Tutong district). J. Asian Earth Sci. 158, 200–209.
Kroeger, K.F., Reuter, M., Brachert, T.C., 2006. Palaeoenvironmental reconstruction based on non-geniculate coralline red algal assemblages in Miocene limestone of Central Crete. Facies 52, 381–409.
Kusworo, A., Reich, S., Wesselingh, F.P., Santodomingo, N., Johnson, K., Todd, J.A., Renema, W., 2015. Diversity and paleoecology of Miocene corals-associated mollusks from East Kalimantan (Indonesia). Palaios 30, 116–127.
Lesser, M.P., Slattery, M., Leichter, J.J., 2009. Ecology of mesophotic coral reefs. J. Exp. Mar. Biol. Ecol. 375 (1–2), 1–8.
Lesser, M.P., Slattery, M., Mobley, C.D., 2018. Biodiversity and functional ecology of mesophotic coral reefs. Ann. Rev. Ecol. Evol. Syst. 49, 49–71.
Lorenz, C., 1969. Contribution à l'étude stratigraphique de l'Oligocène inférieur des confins Liguro-Piémontais (Italie). Atti Ist. Geol. Univ. Genova 6 (2), 888.
Loya, Y., 1976. The Red Sea coral *Stylophora pistillata* is an r strategist. Nature 259, 478–480.
MacDonald, I.A., Perry, C.T., 2003. Biological degradation of coral framework in a turbid lagoon environment, Discovery Bay, North Jamaica. Coral Reefs 22, 523–535.
Majchrzyk, A., Jakubowicz, M., Berkowski, B., Bongaerts, P., Zapalski, M., 2022. In the shadow of a giant reef: palaeoecology of mesophotic coral communities from the Givetian of Anti-Atlas (Morocco). Palaeogeogr. Palaeoclimatol. Palaeoecol. 602, 111177.
McArthur, J.M., 1994. Recent trends in Strontium isotope stratigraphy. Terra Nova 6, 331–358.
McArthur, J.M., Howarth, R.J., 2004. Sr-isotope stratigraphy: the Phanerozoic $^{87}Sr/^{86}Sr$-curve and explanatory notes. In: Gradstein, F.M., Ogg, J.G., Smith, A.G. (Eds.), A Geological Timescale 2004, 7. Cambridge University Press, pp. 96–102.
McArthur, J.M., Howarth, R.J., Bailey, T.R., 2001. Strontium isotope stratigraphy: LOWESS version 3: best fit to the marine Sr-isotope curve for 0–509 Ma and accompanying look-up table for deriving numerical age. J. Geol. 109, 155–169.
McArthur, J.M., Howarth, R.J., Shields, G.A., 2012. Strontium isotope stratigraphy. In: Gradstein, F.M., Ogg, J.G., Smith, A.G. (Eds.), A Geological Timescale 2004. Cambridge University Press, pp. 127–144.
McArthur, J.M., Howarth, R.J., Shields, G.A., Zhou, Y., 2020. Chapter 7 - Strontium Isotope Stratigraphy. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), Geologic Time Scale 2020. Elsevier, pp. 211–238.
Michel, J., Lanteaume, C., Lettéron, A., Kenter, J., Morsilli, M., Borgomano, J., 2020. Oligocene and Miocene global spatial trends of shallow-marine carbonate architecture. J. Geol. 128, 563–570.
Morelli, D., Locatelli, M., Corradi, N., Cianfarra, P., Crispini, L., Federico, L., Migeon, S., 2022. Morpho-Structural setting of the Ligurian Sea: the Role of Structural Heritage and Neotectonic Inversion. J. Mar. Sci. Engin. 10 (9), 1176.
Morgan, K.M., Perry, C.T., Johnson, J.A., Smithers, S.G., 2017. Nearshore turbid-zone corals exhibit high bleaching tolerance on the Great Barrier Reef following the 2016 ocean warming event. Front. Mar. Sci. 4, 224.
Morsilli, M., Bosellini, F.R., Pomar, L., Hallock, P., Aurell, M., Papazzoni, C.A., 2012. Mesophotic coral buildups in a prodelta setting (late Eocene, southern Pyrenees, Spain): a mixed carbonate–siliciclastic system. Sedimentology 59 (3), 766–794.
Mount, J.F., 1984. Mixing of siliciclastic and carbonate sediments in shallow shelf environments. Geology 12 (7), 432–435.
Moura, R.L., Amado-Filho, G.M., Moraes, F.C., Brasileiro, P.S., Salomon, P.S., Mahiques, M.M., Bastos, A.C., Almeida, M.G., Silva, J.M., Araujo, B.F., Brito, F.P., Rangel, T.P., Oliveira, B.C.V.V., Bahia, R.G., et al., 2016. An extensive reef system at the Amazon River mouth. Sci. Adv. 2 (4) e1501252.
Novak, V., Santodomingo, N., Rösler, A., Di Martino, E., Braga, J.C., Taylor, P.D., Johnson, K.G., Renema, W., 2013. Environmental reconstruction of a late Burdigalian (Miocene) patch reef in deltaic deposits (East Kalimantan, Indonesia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 374, 110–122.
Pastorino, P., 1994. La trasgressione oligocenica in un settore nord-occidentale del Gruppo di Voltri: l'insediamento recifale di Cascine. Università di Genova, Tesi di Laurea, 178 pp.
Peña, V., Vieira, C., Braga, J.C., Aguirre, J., Rösler, A., Baele, G., De Clerck, O., Le Gall, L., 2020. Radiation of the coralline red algae (Corallinophycidae, Rhodophyta) crowngroup as inferred from a multilocus time-calibrated phylogeny. Molec. Phylogen. Evol. 150, 106845.
Pérez-Castro, M.Á., Schubert, N., Ang-Montes de Oca, G., Leyte-Morales, G.E., Eyal, G., Hinojosa-Arango, G., 2022. Mesophotic Coral Ecosystems in the Eastern Tropical Pacific: the current state of knowledge and the spatial variability of their depth boundaries. Sci. Total Environ. 806, 150576.
Perrin, C., Bosellini, F.R., 2012. Palaeobiogeography of scleractinian corals: changing patterns during the Oligocene-Miocene climatic transition in the Mediterranean. Earth Sci. Rev. 111, 1–24.
Perrin, C., Bosence, D.W., Rosen, B., 1995. Quantitative approaches to palaeozonation and palaeobathimetry of corals and coralline algae in Cenozoic reefs. In: Bosence, D. W., Allison, P.A. (Eds.), Marine Palaeoenvironmental Analisys from Fossils. Spec. Publ. 83. The Geological Society, London, pp. 181–229.
Perry, C.T., 2005. Structure and development of detrital reef deposits in turbid nearshore environments, Inhaca Island, Mozambique. Mar. Geol. 214, 143–161.
Perry, C.T., Hepburn, L.H., 2008. Syn-depositional alteration of coral reef framework through bioerosion, encrustation and cementation: Taphonomic signatures of reef accretion and reef depositional events. Earth Sci. Rev. 86, 106–144.
Perry, C.T., Smithers, S.G., 2006. Taphonomic signatures of turbid-zone reef development: examples from Paluma Shoals and Lugger Shoal, inshore central Great Barrier Reef, Australia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 242, 1–20.
Perry, C.T., Smithers, S.G., 2010. Evidence for the episodic "turn on" and "turn off" of turbid-zone coral reefs during the late Holocene Sea-level highstand. Geology 38 (2), 119–122.
Perry, C.T., Smithers, S.G., Gulliver, P., Browne, N.K., 2012. Evidence of very rapid reef accretion and reef growth under high turbidity and terrigenous sedimentation. Geology 40 (8), 719–722.
Pfister, T., 1980. Paläoökologie des oligozänen Korallenvorkommens von Cascine südlich Acqui (Piemont, Norditalien). Jb. Naturhist. Mus. Bern 7, 247–262.
Pfister, T., 1985. Coral fauna and facies of the Oligocene fringing reef near Cairo Montenotte (Liguria, Northern Italy). Facies 13, 175–226.
Quaranta, F., Piazza, M., Vannucci, G., 2009. Cliamtic and tectonic control on the distribution of the Oligocene reefs of the Tertiary Piedmont Basin (NW Italy). Ital. J. Geosci. 128 (2), 587–591.
Renema, W., 2019. Large benthic foraminifera in low-light environments. In: Loya, Y., Puglise, K., Bridge, T. (Eds.), Mesophotic Coral Ecosystems, vol. 12. Springer, Cham, pp. 553–561.
Reuter, M., Bosellini, F.R., Budd, A.F., Coric, S., Piller, W., Harzhauser, M., 2019. High coral reef connectivity across the Indian Ocean is revealed 6-7 Ma ago by a turbid-water scleractinain assemblage from Tanzania (Eastern Africa). Coral Reefs 38, 1023–1037.
Riegl, B., Piller, W.E., 1999. Coral frameworks revisited-reefs and coral carpets in the northern Red Sea. Coral Reefs 18, 241–253.
Rogers, C.S., 1983. Sublethal and lethal effects of sediments applied to common Caribbean reef corals in the field. Mar. Pollut. Bull. 14, 378–382.
Rogers, C.S., 1990. Response of coral reef and reef organisms to sedimentation. Mar. Ecol. Prog. Ser. 62, 185–202.
Rosedy, A., Ives, I., Waheed, Z., Syed Hussein, M.A., Sosdian, S., Johnson, K., Santodomingo, N., 2023. Turbid reefs experience lower coral bleaching effects in NE Borneo (Sabah, Malaysia). Reg. Stud. Mar. Sci. 68, 103268.
Rösler, A., Peefectti, F., Pena, V., Braga, J.C., 2016. Phylogenetic relationships of corallinaceae (corallinales, Rhodophyta): taxonomic implications for reef-building corallines. J. Phycol. 52, 412–431.
Rossi, M., Craig, J., 2016. A new perspective on sequence stratigraphy of syn-orogenic basins: insights from the Tertiary Piedmont Basin (Italy) and implications for play concepts and reservoir heterogeneity. Geol. Soc. London Spec. Publ. 436 (1), 93–133.
Roy, K.J., Smith, S., 1971. Sedimentation and coral reef development in turbid water: Fanning Lagoon. Pac. Sci. 25, 234–248.
Sanders, D., Baron-Szabo, R.C., 2005. Scleractinian assemblages under sediment input: their characteristics and relation to the nutrient input concept. Palaeogeogr. Palaeoclimatol. Palaeoecol. 216, 139–181.

Santodomingo, N., Novak, V., Pretkovic, V., Marshall, N., Di Martino, E., Lo Giudice Capelli, E., Rösler, A., Reich, S., Braga, J.C., Renema, W., Johnson, K.G., 2015. A diverse patch reef from turbid habitats in the Middle Miocene (East Kalimantan, Indonesia). Palaios 30, 128–149.
Santodomingo, N., Renema, W., Johnson, K.G., 2016. Understanding the murky history of the Coral Triangle: Miocene corals and reef habitats in East Kalimantan (Indonesia). Coral Reefs 35, 765–781.
Sarkar, S., 2017. Ecology of coralline red algae: fossil evidences from India. Thalassas 33, 15–28.
Schuster, F., 2002. Oligocene and Miocene examples of Acropora-dominated palaeoenvironments: Mesohellenic Basin (NW Greece) and northern Gulf of Suez (Egypt). In: Proc. 9th Int. Coral Reef Symp., Bali, Vol. 1, pp. 199–204.
Shaish, L., Abelson, A., Rinkevich, B., 2007. How plastic can phenotypic plasticity be? The branching coral *Stylophora pistillata* as a model system. PLoS One 2 (7), e644.
Silvestri, G., Bosellini, F.R., Nebelsick, J.H., 2011. Microtaphofacies analysis of lower Oligocene turbid-water coral assemblages. Palaios 26, 805–820.
Singh, S.K., Kishore, S., Jauhri, A.K., Misra, P.K., 2020. Palaeoenvironmental reconstruction based on coralline algal assemblages in the Oligocene of Kachchh, Gujarat, western India. J. Palaeontol. Soc. India 65, 55–63.
Smith, T.B., Glynn, P.W., Maté, J.L., Toth, L.T., Gyory, J., 2014. A depth refugium from catastrophic coral bleaching prevents regional extinction. Ecology 95, 1663–1673.
Stafford-Smith, M.G., 1993. Sediment-rejection efficiency of 22 species of Australian scleractinian corals. Mar. Biol. 115, 229–243.
Stolarski, J., Bosellini, F.R., Wallace, C.C., Gothmann, A., Mazur, M., Domart-Coulon, I., Gutner-Hoch, E., Neuser, R.D., Levy, O., Shemesh, A., Meibom, A., 2016. A unique coral biomineralization pattern has resisted 40 million years of major ocean chemistry change. Sci. Rep. 6, 27579.
Sully, S., van Woesik, R., 2020. Turbid reefs moderate coral bleaching under climate-related temperature stress. Glob. Chang. Biol. 26, 1367–1373.
Tomassetti, L., Bosellini, F.R., Brandano, M., 2013. Growth and demise of a Burdigalian coral bioconstruction on a granite rocky substrate (Bonifacio Basin, South Corsica). Facies 59 (4), 703–716.
Ullmann, C., Korte, C., 2015. Diagenetic alteration in low-Mg calcite from macrofossils: a review. Geol. Q. 59, 3–20.
Vannucci, G., Piazza, M., Pastorino, P., Fravega, P., 1997. Le facies a coralli coloniali e rodoficee calcaree di alcune sezioni basali della Formazione di Molare (Oligocene del Bacino Terziario del Piemonte, Italia nord-occidentale). Atti Soc. Tosc. Sci. Nat. Mem. Ser. A 104, 1–27.
Vannucci, G., Quaranta, F., Piazza, M., Fravega, P., 2003. The Oligocene reefal facies of Bric San Bernardino (Millesimo, Italia Nord-occidentale). Atti Tic. Sci. Terra 44, 35–44.
Vannucci, G., Testa, M., Piazza, M., Pastorino, P., 2010. *Subterraniphyllum* and free-living *neogoniolithon* (coralline algae) from the Oligocene reef facies of Costa d'Ovada (Tertiary Piedmont Basin, Alessandria, NW Italy). Ital. J. Geosci. 129, 4–14.
Vescogni, A., Bosellini, F.R., Cipriani, A., Gürler, G., Ilgar, A., Paganelli, E., 2014. The Dağpazarı carbonate platform (Mut Basin, Southern Turkey): facies and environmental reconstruction of a coral reef system during the Middle Miocene Climatic Optimum. Palaeogeogr. Palaeoclimatol. Palaeoecol. 410, 213–232.
Wallace, C.C., 1999. Staghorn Corals of the World; a Revision of the Genus *Acropora*. CSIRO Press, Melbourne, p. 422.
Wilson, M.E.J., 2005. Equatorial delta-front patch reef development during the Neogene, Borneo. J. Sediment. Res. 75, 116–134.
Wilson, M.E.J., Lokier, S.W., 2002. Siliciclastic and volcaniclastic influences on equatorial carbonates: insights from the Neogene of Indonesia. Sedimentology 49 (3), 583–601.
Woolfe, K.J., Larcombe, P., 1999. Terrigenous sedimentation and coral reef growth: a conceptual framework. Mar. Geol. 155, 331–345.
Zachos, J.C., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rythms and aberrations in global climate 65 Ma to present. Science 292, 686–693.
Zapalski, M.K., Baird, A.H., Bridge, T., Jakubowicz, M., Daniell, J., 2021. Unusual shallow water Devonian coral community from Queensland and its recent analogues from the inshore Great Barrier Reef. Coral Reefs 40, 417–431.
Zhang, Y.G., Pagani, M., Zhonghui, L., Bohaty, S.M., DeConto, R., 2013. A 40-million-year history of atmospheric CO_2. Philos. Trans. R. Soc. A 371, 20130096.
Zweifler, A., O'Leary, M., Morgan, K., Browne, N.K., 2021. Turbid coral reefs: past, present and future – a review. Diversity 13, 251.