

HIGH CORAL DIVERSITY IS COUPLED WITH REEF-BUILDING CAPACITY DURING THE LATE OLIGOCENE WARMING EVENT (CASTRO LIMESTONE, SALENTO PENINSULA, S ITALY)

FRANCESCA R. BOSELLINI*¹, ALESSANDRO VESCOGNI¹, ANN F. BUDD² & CESARE A. PAPAZZONI¹

¹Dipartimento di Scienze Chimiche e Geologiche, Università di Modena e Reggio Emilia, via Campi 103, 41125 Modena, Italy. E-mail: francesca.bosellini@unimore.it, alessandro.vescogni@unimore.it, papazzoni@unimore.it

²Department of Earth & Environmental Sciences, 115TH, University of Iowa, Iowa City, IA 52242, USA. E-mail: ann-budd@uiowa.edu

*Corresponding Author.

To cite this article: 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 event (Castro Limestone, Salento Peninsula, S Italy). *Riv. It. Paleontol. Strat.*, 127(3): 515-538.

Keywords: Scleractinia; facies analysis; systematics; Apulia Platform; Chattian.

Abstract. The Oligocene, well known as the apex of Cenozoic reef growth, is a crucial period of time to investigate the mutual relationship between coral reef construction and coral diversity and their link with palaeoclimate and palaeoenvironmental changes. Here we provide a complete characterization of the Upper Oligocene reef complex of the Castro Limestone (Salento Peninsula, S Italy), which is one of the best-preserved Oligocene coral reefs of the Mediterranean region. By combining facies analysis with the first detailed characterization of its coral fauna, we show that the Castro Limestone has both a rich scleractinian coral fauna (25 genera and 41 species) and a large reef volume, and it represents a luxuriant fringing reef formed within the euphotic zone in clear water conditions facing the open sea. The coral fauna differs both in its composition and in its proportions among reef palaeoenvironments, ranging from the shallow back reef to the fore reef slope, and its stratigraphic and palaeogeographic distribution testifies to the persistence of a cosmopolitan Tethyan fauna in Oligocene time, with the Mediterranean and Indo-Pacific provinces being more closely connected than the Mediterranean and the Caribbean. The age of the Castro Limestone is here reassigned to the middle-late Chattian, which coincides with the Late Oligocene Warming Event (LOWE) when atmospheric CO₂ values declined. We suggest that the strong reef-building capacity of the Castro Limestone, coupled with high coral diversity, was not hampered by warming conditions but most probably promoted by the reduced pCO₂ and a suitable local/regional physiographic setting.

INTRODUCTION

During the Cenozoic, reef environments have experienced significant changes in the carbonate-producing biotas and in the structure of coral buildups (Perrin 2002; Pomar et al. 2017). They have been subjected to a variety of climate boundary conditions that represent the transition from a greenhouse to an icehouse Earth (Zachos et al.

2001, 2008). Within this framework, the Oligocene, well known as the apex of Cenozoic reef growth, is a crucial period for understanding the response of coral reef environments to palaeoenvironmental stressors that are in various ways linked to palaeoclimatic and palaeoceanographic changes. The isolation of Antarctica and the establishment of a circum-Antarctic surface current caused a cooling event at the Eocene/Oligocene transition (EOT), followed by a warmer phase culminating in the Late Oligocene Warming Event (LOWE) that characterized the late Chattian stage (Zachos et al. 2001).

Received: January 20, 2021; accepted: June 25, 2021



Fig. 1 - a) Schematic map of the southern Salento Peninsula showing the location of the study area (red square). b) Overview of the study area with the location of the selected stratigraphic sections; a NW/SE oriented transect (blue dashed line) is drawn perpendicular to the Castro Limestone reef margin (white solid and dashed line) displaying the orientation of the reef depositional system, from its landward portion (NW) towards the open sea (SE).

Extensive coral reefs, characterized by moderate to high diversity of scleractinian corals, have been recorded in particular in the Oligocene of the Caribbean and Mediterranean regions (Frost 1981; Budd 2000; Perrin 2002; Perrin & Bosellini 2012), which at that time were both interconnected with the Indo-Pacific province by the westward flowing Tethyan seaway (Berggren & Hollister 1974; Perrin 2002). Diversity at the genus level and palaeobiogeographic patterns of Oligocene-Miocene Mediterranean reef corals have been recently revised by Bosellini & Perrin (2008) and Perrin & Bosellini (2012) through analysis of a rich database. The results show that reef corals reached the highest generic richness during the Chattian and were widely distributed across the circum-Mediterranean from the Eastern

Atlantic to the Eastern Mediterranean (Perrin & Bosellini 2012). A review of Cenozoic reef building evolution and carbonate production has been recently published for the west-central Tethys by Pomar et al. (2017). According to these authors, all pre-late Tortonian coral buildups developed in mesophotic conditions and increased in volume during times of global cooling (i.e. late Danian, Bartonian-Priabonian, early Chattian, Late Miocene) (Pomar et al. 2017). The relationship between reef development and reef coral diversity is not discussed in these recent review papers, although a decoupling between these two main features has been documented during the Cenozoic (Kiessling & Baron-Szabo 2004; Johnson et al. 2008; Zamagni et al. 2012; Perrin & Bosellini 2013), suggesting control by different parameters

involving the strong influence of evolutionary and palaeogeographic patterns. A reef coral hotspot in fact does not imply the presence of a massive reef framework or vice versa.

The Upper Oligocene Castro Limestone (hereafter CL), outcropping along the eastern coastline of the Salento Peninsula (S Italy) (Fig. 1a), is one of the best-preserved coral reefs in the Mediterranean palaeo-biogeographic province. It has both a rich coral fauna and a large reef volume, and has been interpreted both as a fringing reef complex with facies and related palaeoenvironments extending from the back reef to the fore reef slope (Bosellini & Russo 1992; Bosellini 2006) and alternatively as a mesophotic reef developed along a distally steepened ramp (Pomar et al. 2014).

The aim of this paper is to characterize in detail the composition and distribution of the coral fauna of the CL. For the first time, we combine results from the taxonomic identification of a coral collection at the genus and species levels, with quantitative data obtained directly in the field. This characterization of the coral fauna is coupled with a revision of the CL stratigraphic setting, facies pattern and age determination that are crucial for placing the CL coral reef within the palaeoclimatic and palaeogeographic context of the Late Oligocene.

GEOLOGICAL SETTING

The Salento area, located at the southeastern corner of the Italian Peninsula (Fig. 1a), belongs to the Apulia Platform, a major structural element of the Adria Plate. Since the Late Triassic, this margin acted as a shallow-water carbonate platform, and since the Late Cretaceous, the collision between the African and the European blocks has led to a further shallowing and partial emersion, in connection to the formation of the Hellenide chain on the east and of the Apennines on the west (Bosellini et al. 1999; Ricchetti & Ciaranfi 2013 and references therein). This led to the formation of a wide, isolated carbonate platform, where the sedimentation was mainly controlled by sea-level oscillations of a moderate amount, resulting in the production of a very reduced accommodation space. As a consequence, a unique stratigraphic architecture developed in the Salento area, which is well exposed along its eastern coastal strip from Otranto to Leuca (Fig. 1a). It is

characterized by a series of relatively thin, superimposed sequences developed over an Upper Cretaceous basement, which are mainly concentrated on the distal portion of the platform and separated by major unconformities (Fig. 2) (Bosellini et al. 1999). The first post-Cretaceous units are of Eocene age, represented by clinostratified bioclastic sediments (Torre Tiggiano Limestone, Lutetian/Bartonian) and by reef slope deposits (Torre Specchialaguardia Limestone, Priabonian), and are characterized by relatively small, discontinuous outcrops along the coastline (Bosellini & Russo 1992; Parente 1994; Russo 2006). The Eocene sequences are overlain by the Chattian coral-rich Castro Limestone (CL) and by the uppermost Chattian Porto Badisco Calcarenite, which is represented by poorly cemented bioclastic deposits with a basal accumulation of large rhodoliths (Bosellini & Russo 1992; Brandano et al. 2010; Pomar et al. 2014; Parente & Less 2019). During the Middle Miocene, the Salento area suffered a rapid subsidence, related to the emplacement of two thrust loads on both margins of the Adriatic Sea (Bosellini et al. 1999). As a consequence, sedimentation reached the internal areas of the platform with the deposition of a thin, condensed hardground (*Aturia* level, Serravallian/Tortonian) (Föllmi et al. 2015; Vescogni et al. 2018) and of a well-developed coral reef complex (Novaglie Formation and Andrano Calcarenites, lower Messinian) (Bosellini et al. 2001, 2002; Bosellini 2006; Brachert et al. 2007; Vescogni et al. 2008, 2011; Braga et al. 2009; Guido et al. 2012). On the top of the Novaglie Fm. lies the Leuca Breccia Formation, consisting of etherometric clasts derived from the dismantling of the underlying Messinian carbonates and related to a major lowstand phase during the late Messinian salinity crisis (Bosellini et al. 1999). The Leuca Breccia is followed by some decimeter thick levels of greenish marls of Early Pliocene age (Bossio et al. 2002) on the top of which lies the Upper Pliocene Uggiano la Chiesa Formation, which consists of some tens of meters thick calcarenites with breccia deposits at the base (Bosellini et al. 1999). The Uggiano la Chiesa Fm. indicates the start of the last shallowing phase in the Salento Peninsula, which ultimately led to the deposition of the lower Pleistocene Salento and Gravina Calcarenites, which are the most recent sedimentary units in the area, usually cropping out within embayments along the coastline (Bosellini et al. 1999; Ricchetti & Ciaranfi 2013).

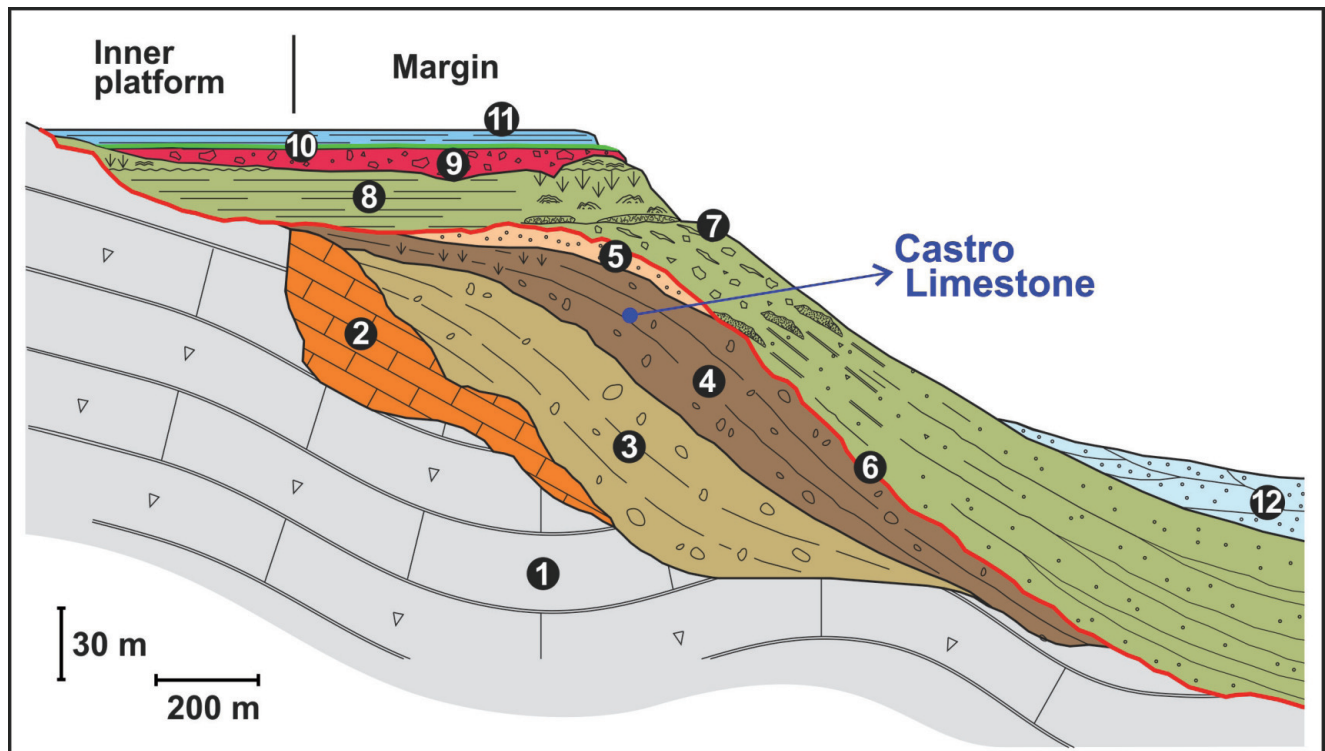


Fig. 2 - Stratigraphic architecture of the eastern Salento Peninsula: 1- Upper Cretaceous substrate, 2- Torre Tiggiano Limestone (Lutetian/Bartonian), 3- Torre Specchialaguardia Limestone (Priabonian), 4- Castro Limestone (middle-upper Chattian), 5- Porto Badisco Calcarenites (uppermost Chattian), 6- *Aturia* level (Serravallian/Tortonian), 7- Novaglie Formation (lower Messinian), 8- Andrano Calcarenites (lower Messinian), 9- Leuca Breccia (upper Messinian), 10- Lower Pliocene marls, 11- Uggiano la Chiesa Formation (Middle Pliocene), 12- Salento Calcarenites (Lower Pleistocene) (modified after Bosellini et al. 1999).

MATERIAL AND METHODS

Stratigraphy and facies analysis

The present study is based on data collected along five main stratigraphic sections, selected for their degree of preservation and located in the surroundings of the small towns of S. Cesarea, Castro and Vitigliano (Fig. 1b). Four of these outcrops (i.e. la Scogliera, $40^{\circ}01'35.62''\text{N} / 18^{\circ}25'56.77''\text{E}$; S. Cesarea, $40^{\circ}02'23.61''\text{N} / 18^{\circ}26'49.58''\text{E}$; Porto Miggiano, $40^{\circ}02'5.49''\text{N} / 18^{\circ}26'42.4\text{E}$; Zinzulusa, $40^{\circ}00'45.68''\text{N} / 18^{\circ}26'0.33''\text{E}$) can be directly correlated in the field, while the Vitigliano section ($40^{\circ}02'25.69''\text{N} / 18^{\circ}25'1.83''\text{E}$) has been ascribed to the CL depositional system by facies analysis and biostratigraphic correlation. Despite the good preservation, these outcrops present a relatively small lateral extension and recognizable reef-top and reef-crest beds that can be seen to pass continuously down into reef palaeoslope at the same survey site are absent. This prevented a precise, geometric reconstruction of the original palaeobathymetry, further hampered by quite variable dip values of the slope strata. For this reason, the palaeobathymetry of each facies has been estimated mainly on the basis of biotic assemblages and sedimentary features. From all these localities, data on stratigraphy, facies types and fossil associations have been acquired by means of macroscopic observations, coupled with microfacies analysis performed on a total of 175 thin sections ($60 \times 45 \text{ mm}$). In the characterization of soft sediments (Vitigliano and la Scogliera sections), 12 additional samples have been dissolved in water and sieved (1-0.5-0.25-0.125 mm) before microscopic observation. Rock textures have been identified following Dunham (1962) and Embry & Klovan (1971). Terms for coralline algae growth forms follow Woelkerling et al. (1993), Beavington-Penney et al. (2004), Sola et al. (2013).

The larger foraminifera used for determining the biozones were examined in thin sections, by searching the best-oriented sections for specimens that could be identified at least at the genus level. To determine the age, we refer to the Shallow Benthic (SB) Zones of Cahuzac & Poignant (1997).

Coral fauna

After the original study of Bosellini & Russo (1992), with a preliminary identification of the main coral genera in the field, the study of the CL coral fauna has been carried out following two different but parallel approaches: 1) a quantitative survey at the genus level directly in the field; 2) a collection of specimens to be used for species identification and for systematic revisions.

Quantitative approach. In order to characterize the coral assemblages of the different facies across the composite reef profile of the CL, a quantitative approach has been initially tested by Bosellini & Perrin (1994) in the back reef tract represented by the Vitigliano section. Here, three types of quantitative methods have been used in the field: 1) count of coral colonies in growth position on a subvertical measured surface; 2) line-intercept transect; 3) photomosaic and coral mapping within quadrats placed on a subvertical outcrop surface. Using these methods, corals have been directly identified in the field at the genus level. Poorly preserved corals have been grouped into families or recorded as "Scleractinia-undefined" if the preservation is very bad. The results provided information about the composition of the coral fauna based on relative abundance of genera, and about the coral cover expressed as the % of corals preserved in growth position vs the % of inter-coral sediment (from linear and areal measurements) (Bosellini & Perrin 1994).

These methods have been subsequently applied in the other sections of the CL (in collaboration with C. Perrin) and recently

improved and updated. However, as constraints imposed by outcrop conditions and preservation of corals strongly control the choice of the method, it has not been possible to apply the same method in all the sections. The coral count was found to be the most suitable method for characterizing the composition of the coral fauna, and line transects for characterizing coral cover. Quadrats have been applied only in two sections (Vitigliano, S. Cesarea). Growth forms and size of the coral colonies in growth position have also been documented. Length (L) and height (H) were measured on colonies at five localities: Vitigliano, la Scogliera, S. Cesarea, Porto Miggiano, Zinzulusa. Colony size (L, H) and shape (H/L) were compared among localities using two nonparametric statistical tests (Kruskal-Wallis, Median) and Tukey HSD.

Coral collection. Before and during quantitative studies, many coral specimens have been collected in the different sections and facies, with the aim of making a complete collection and integrating the quantitative data obtained at the genus level. Sampling was carried out in different periods, covering a time interval of about 20 years, and was also biased by outcrop conditions and accessibility and by state of coral preservation thus leading to an uneven distribution of specimens collected from different sections.

The collection is represented by a total of 223 specimens (and 146 thin sections) and is housed at the Department of Chemical and Geological Sciences of the University of Modena and Reggio Emilia (IPUM: Inventario Paleontologico Università di Modena).

Since the beginning of the coral collection, several specimens have been used for systematic revisions of various genera: *Actinacis* (Bosellini & Russo 1995), with recognition of *A. rollei* for the CL; *Tarbellastraea* (Budd et al. 1996), with recognition of *T. russoi* and *T. salentinensis* for the CL; *Hydnophora* (Bosellini 1999), with recognition of *H. pulchra* for the CL; *Acropora* (Wallace & Bosellini 2015), with recognition of *A. salentina* and *A. astroites* for the CL; meandroid corals (Budd & Bosellini 2016), with recognition of *Hydnophyllia costata* and *H. scalaria* for the CL.

The classification system adopted herein takes into consideration the systematics based on recent molecular analysis and phylogenetic relationships between traditional families (Fukami et al. 2004, 2008), together with macro-morphological characters used in recent systematic revisions (Budd & Stolarski 2009; Budd et al. 2012): colony shape, colony organization, budding, corallite, septa, internal lobes, columella, dissepiments, wall, coenosteum, CD (corallite diameter), VW (valley width), CCD (distance between corallite centers), CS (corallite spacing), NS (number of septa). Observations were mostly made on transverse thin sections using transmitted light, although some calical surfaces have also been observed using a stereoscope. A table with all identified species and their diagnostic characters is provided in the supplementary material, together with six plates (Tab. 1, Pl. 1-6).

THE CASTRO LIMESTONE REEF SYSTEM

Previous Studies

First briefly described by Rossi (1969) and considered as one of the best-preserved Upper Oligocene coral reefs in the Mediterranean, the CL is a carbonate sequence that runs parallel to the Salento southeastern coastline, from S. Cesarea to the Leuca cape (Fig. 1a), with a total length of 28 km, a maximum width of about 3 km and a thickness ranging from 5 up to 100 m (Bosellini & Russo 1992). The

studies of Bosellini & Russo (1992) and Bosellini (2006) provided important information on the CL stratigraphic setting and facies pattern, together with a preliminary characterization of the coral assemblages. In particular, these authors interpreted this unit as a fringing reef complex, with a well-developed E-W oriented palaeobathymetric profile including a back reef environment, a bioconstructed coral margin and clinostratified slope deposits. Bosellini & Perrin (1994) provided a further description of the CL coral assemblage by means of qualitative and quantitative analyses focusing on the back reef environment. More recently, the fringing reef depositional model has been questioned by Pomar et al. (2014), who interpreted the CL as a meso-oligophotic, distally steepened ramp. In their study, the coral fauna was interpreted as mainly confined to the mesophotic belt, forming scattered mounds but with no evidence of a wave-resistant framework. In addition, these authors did not recognize the presence of a coral-rich, back reef environment along the palaeobathymetric profile (Vitigliano section), ascribing this facies to the uppermost Chattian Porto Badisco Calcarene (Fig. 3).

Refining the age

The CL was originally assigned to the “middle Chattian” *Cyclochypus droogeri*-*C. mediterraneus* zone by Bosellini & Russo (1992), on the basis of the identification of *Nephrolepidina praemarginata* “very close to the transition to *N. morgani*” using the biozonation scheme of Drooger & Laagland (1986).

Parente (1994) ascribed the CL to the “lower Chattian” according to the presence of *Eulepidina dilatata* and *Nephrolepidina praemarginata* and using the biozonation scheme of Laagland (1990). In the framework of the Shallow Benthic (SB) Zones successively defined by Cahuzac & Poignant (1997), this corresponds with the SB 22B Zone (lower Chattian).

More recently, Pomar et al. (2014) reaffirmed the CL as lower Chattian referring to the taxonomic determinations reported by Bosellini & Russo (1992) and Parente (1994) and mentioning the “absence of Miogypsinidae”. In contrast, they report that the overlying Porto Badisco Calcarene can be assigned to the “late Chattian” *Miogypsinoides* zone of Drooger & Laagland (1986), corresponding with the SBZ 23 of Cahuzac & Poignant (1997), because it contains among others “*Miogypsinoides ex interc.*

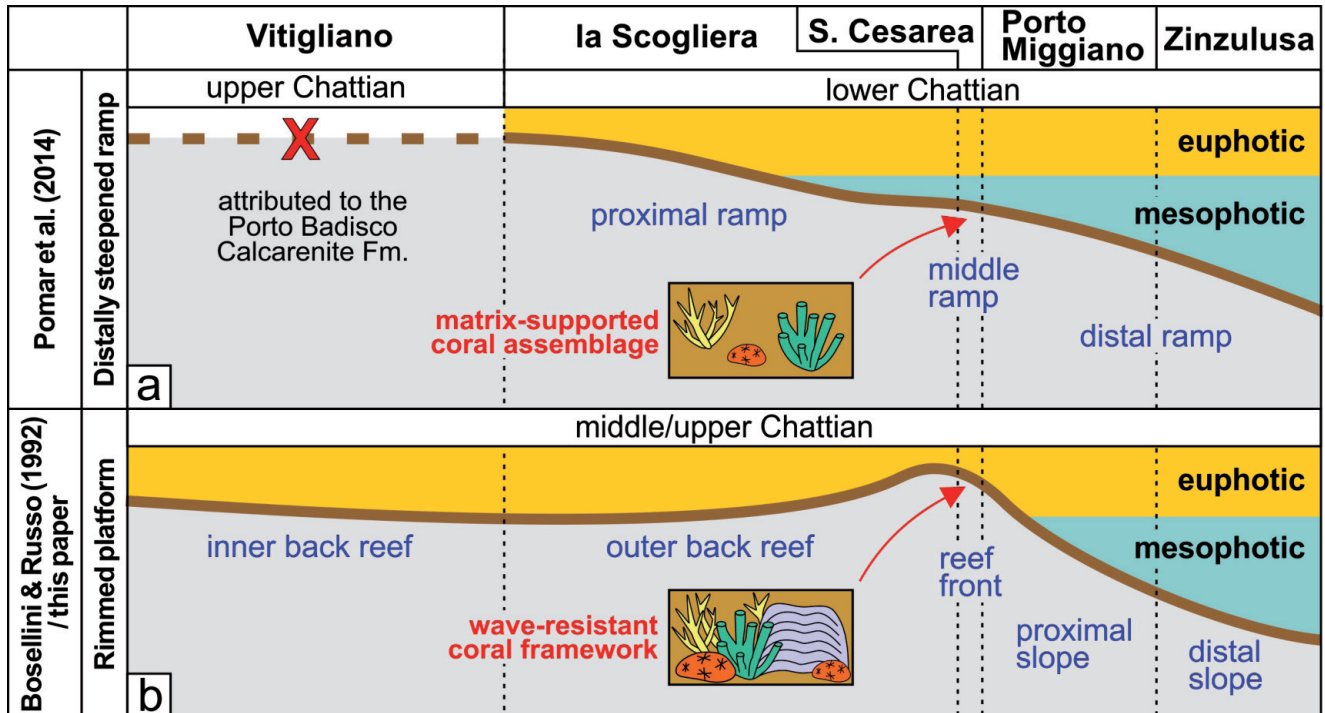


Fig. 3 - Comparison between the main features and age determinations of the two Castro Limestone depositional models: a) Pomar et al. (2014). b) Bosellini & Russo (1992), this paper.

complanata-formosensis?. Moreover, on the basis of the occurrence of *Miogypsinoides*, Pomar et al. (2014) reassigned the Vitigliano section (formerly ascribed to the CL) to the Porto Badisco Calcarenite and therefore to the middle-upper Chattian SBZ 23.

Parente & Less (2019) analyzed the Porto Badisco Calcarenite by means of Sr isotope stratigraphy, giving an absolute age of 23.6 ± 0.5 Ma for the lower part of this formation, which corresponds with the latest part of the Chattian, quite close to the Oligocene-Miocene boundary, 23.03 Ma according to the International Chronostratigraphic Chart v2021/07 (see stratigraphy.org/chart).

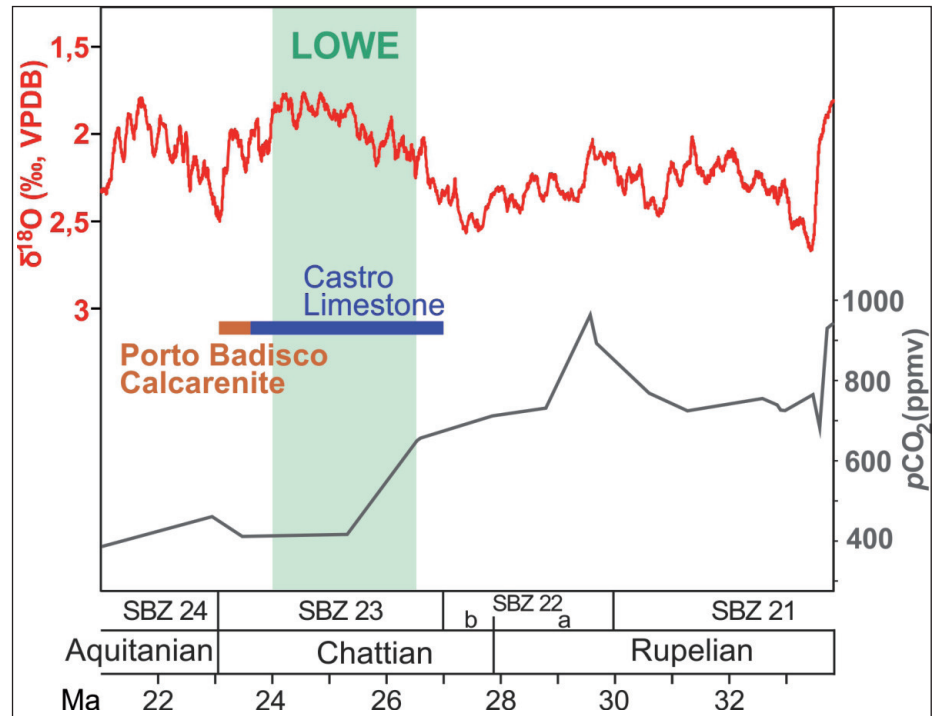
Herein, we examined thin sections from the CL and found the presence of *Miogypsinoides* sp. in three localities, namely Vitigliano, la Scogliera and Santa Cesarea (Fig. 1b). The specimens are rare but uniformly distributed in all the mentioned localities.

Because the genus *Miogypsinoides* appeared at the base of the SB 23 Zone (Cahuzac & Poignant, 1997), we can confidently assign all these samples to this interval and correct the age of the CL as belonging to the same biozone as the Porto Badisco Calcarenite. However, the stratigraphic relationships suggest that the two formations are superposed, with the CL below the Porto Badisco Calcarenite (Fig. 4).

Redefining the reef profile

The projection along a NW/SE oriented transect (Fig. 1b) of the positions, geometries and stratigraphic features of the five studied sections, coupled with sedimentary data and the palaeoecological constraints of the biotic assemblages, are used to reconstruct a palaeobathymetric profile of the CL depositional system (Fig. 5a). Over a distance of about 2.4 km the succession of five different palaeoenvironments and related facies has been identified similarly to the previous interpretation of Bosellini & Russo (1992), and represented by inner and outer back reef, reef front, proximal and distal slope. In particular, in the study area, the reef front is recognizable as a distinct, SW/NE oriented ridge largely coincident with the eastern border of the present-day Salento plateau (Fig. 1b), whereas the slope deposits develop southeastward and are well exposed along the present-day coastal strip. An overview of this setting is depicted in Fig. 5b, corresponding with the northeastern quadrant of the study area: there the massive, elevated structure of the reef front (eastern side of la Scogliera section, S. Cesarea section) directly passes into the clinostratified deposits of the proximal slope, excellently exposed along the roadcut of the Porto Miggiano section.

Fig. 4 - Age of the Castro Limestone Fm. relative to the Shallow Benthic Zones (SBZ, Cahuzac & Poignant 1997) and to the onset of the uppermost Chattian Porto Badisco Calcarenite (Parente & Less 2019). This time interval is plotted against the period corresponding with the Late Oligocene Warming Event (LOWE, according to O'Brien et al. 2020) and compared with the climate and atmospheric CO₂ global trends (Zhang et al. 2013).



REEF FACIES AND CORAL ASSEMBLAGES

Inner back reef

The inner back reef can be recognized along the NW/SE oriented roadcut located east from the town of Vitigliano (Fig. 1b). The CL is up to 5 m thick and characterized by massive to weakly stratified deposits (Fig. 5c) consisting of a coarse, structureless packstone/grainstone. Together with corals, the main bioclastic components are abundant benthic foraminifera (mainly lepidocyclinids, rotaliids, miliolids, nummulitids and miogypsinids) and coralline algae (mainly small nodules and fragments of non-geniculated taxa, with prevailing Melobesioideae, Sporolithoideae and with a lesser amount of Mastophoroideae) (Fig. 6a). Fragments of coralline algae include abundant foliose morphologies, associated with scattered hooked and hollow growth-forms. Fragments of echinoderms, corals, molluscs, encrusting foraminifera, geniculate algae, bryozoans and serpulids are also present.

Coral assemblage. A quantitative survey has been previously applied in this section, and the results are published in Bosellini & Perrin (1994). The coral fauna is represented by quite scattered colonies in growth position (Fig. 6b-e), even though some aggregates and clusters may also be present. Colonies usually exhibit a large size (20 to 130 cm in length, 10 to 70 cm in height) and

have massive-globose to tabular growth forms. Bioerosion is clearly visible in several corals and it is mainly testified by *Lithophaga* borings (Fig. 6c). The coral cover, measured along a transect line of 30 m, is about 20% (Fig. 6f). About 13 genera have been identified in the field from a coral count of 310 colonies in growth position on a surface of 375 m², with the most common being *Porites* (30%), *Favites* (16%), *Tarbellastraea* (13%) and *Pavona* (11%) (Fig. 6g).

Outer back reef

The outer back reef is exposed at the la Scogliera section, along the E/W oriented roadcut about 2.3 km NE from the town of Castro towards the eastern margin of the present-day Salento plateau (Fig. 1b). With a thickness of few meters, the reef deposits are subdivided into two units by a clear discontinuity characterized by a landward dip of about 20°: a lower one (unit I in Fig. 5d-e) with a compact, stratified organization, and an upper one (unit II in Fig. 5d), characterized by poorly cemented deposits with massive appearance. Both of these units consist of packstone and grainstone with benthic foraminifera (mainly miliolids, rotaliids, nummulitids and rare lepidocyclinids) and non-geniculate coralline algae (prevailing are Melobesioideae and Sporolithoideae with fewer Mastophoroideae) (Fig. 7a). Coralline algal taxa



Fig. 5 - a) Palaeobathymetric profile of the Castro Limestone reef system derived from the projection along a NW/SE oriented transect (see Fig. 1b) of the different reef facies. b) Overview of the coastal tract between the sections of la Scogliera and S. Cesarea (see Fig. 1b): the massive reef front on the top of the Salento plateau passes SE into the clinostратified deposits of the proximal reef slope. c) Massive inner back reef deposits, Vitigliano section. d) Weakly stratified outer back reef deposits separated into two superimposed units, la Scogliera section. e) Overview of the uppermost outer back reef unit, next to its transition into the reef front, eastern portion of la Scogliera section. f) Massive reef front, S. Cesarea section. g) Clinostратified proximal slope deposits, Porto Miggiano section. h) Clinostратified distal slope deposits, Zinzulusa section.

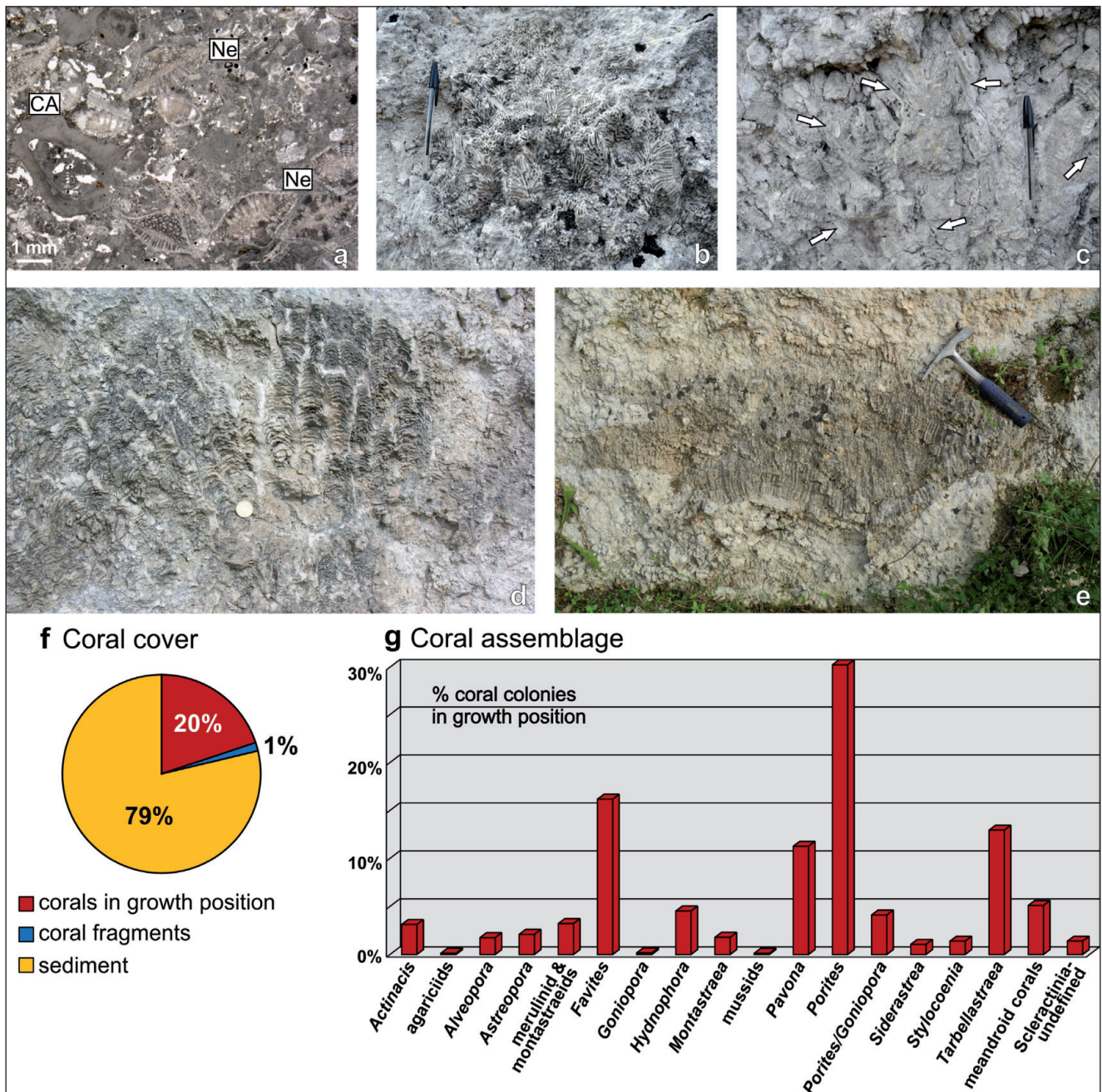


Fig. 6 - Inner back reef, Vitigliano section: a) Foraminifera and coralline algae packstone containing coral colonies (CA: coralline algae; Ne: *Nephrolepidina*). b) *Tarbellastrea*, c) *Stylocoenia* (arrows indicate *Lithobaga* traces), d) *Porites* and e) *Favites* are some of the main coral genera in growth position. f) Percentage of coral cover derived from quantitative linear measurements. g) Evaluation of the coral assemblage at the genus level expressed by the percentage of colonies in growth position and derived from coral counts on the outcrop surface.

are present as small nodules and fragments, the latter with foliose or irregular shapes, less frequently with hooked and hollow growth-forms. Other bioclasts are fragments of echinoderms, encrusting foraminifera, geniculate red algae, bryozoans, molluscs and serpulids.

Coral assemblage. Corals are represented by scattered colonies, sometimes with a large size (e.g. 20 to 270 cm in length, 10 to 100 cm in height),

and with massive to tabular growth forms (Fig. 7b-d). The coral cover measured along a transect line of 122 m is very low, about 4% (Fig. 7e). About 12 different genera have been identified in the field from a coral count of 34 colonies in growth position on a surface of 330 m², with the most common being the clearly dominant *Actinacis* (30%) together with *Alveopora* (12%) and *Astreopora* (9%) (Fig. 7f).

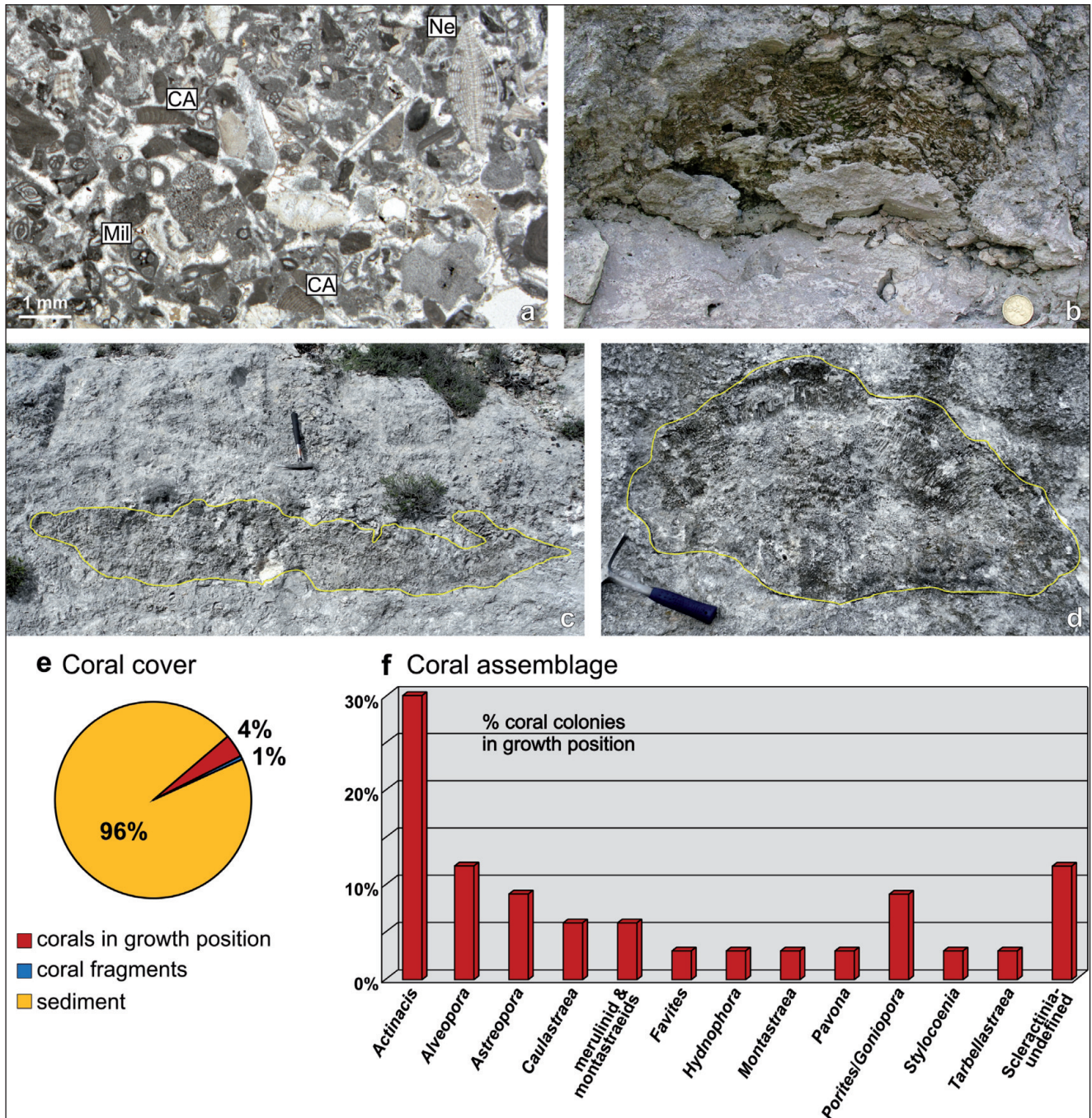


Fig. 7 - Outer back reef, la Scogliera section: a) Foraminifera and coralline algae grainstone (CA: coralline algae; Ne: *Nephrolepidina*; Mil: miliolid). b, c) *Actinacis* and d) *Favites* are some of the main coral genera in growth position. e) Percentage of coral cover derived from quantitative linear measurements. f) Evaluation of the coral assemblage at the genus level expressed as the percentage of colonies in growth position and derived from coral counts on the outcrop surface.

Reef front

The CL reef front runs parallel to the present-day coastline between Castro and S. Cesarea (Fig. 1b) and it is exemplarily exposed along the S. Cesarea section, a E/W oriented roadcut located NW from S. Cesarea (Fig. 5f). Here the CL unconformably lies on the calcirudite deposits of the Torre Tiggiano Limestone (Lutetian) and, with a thickness of about eight meters, it shows the superimposition of two

main subfacies with different sedimentological and palaeontological features:

- Basal coral rubble (2.5 m thick). Well sorted grainstone where etherometric coral fragments and reworked colonies are associated with benthic foraminifera (abundant rotaliids, lepidocyclinids, miliolids, nummulitids, associated with less frequent alveolinids), coralline red algae, echinoderms, molluscs, encrusting foraminifera, serpulids, geniculate

algae and bryozoans (Fig. 8a, b). Coralline algae are mainly non-geniculate (Melobesioideae, Sporolithoideae, sparse Mastophoroideae and rare *Polystrata*), represented by irregular fragments as well as by foliose, hooked and hollow growth-forms. Some spheroidal rhodoliths, a few cm in diameter, may also occur. The amount of removed corals tends to increase towards the top of the facies, associated with a progressive appearance of sparse colonies in growth position.

- Coral framework (5.7 m). Massive unit characterized by the dominance of coral colonies in growth position associated with coral fragments and scattered removed colonies. Coral colonies become particularly abundant towards the top of the section, frequently in close contact and forming a dense, three-dimensional framework (Fig. 8c). Inter-coral sediment is a prevailing grainstone similar to the one described for the underlying coral rubble, but with scattered areas with variable amounts of micrite.

Coral assemblage. The coral assemblage is largely dominated by massive and globose colonies, with subordinate tabular and platy colonies (20 to 180 cm in length, 8 to 130 cm in height) (Fig. 8c-f). The coral cover, measured along a transect line of 30 m in the dense area is about 64% (Fig. 8g). About 13 different genera have been identified in the field from a coral count of 321 colonies in growth position on a surface of 153 m², with the dominant corals represented by poritids (about 57% including indistinguishable poritids, *Porites* and *Goniopora*) and merulinid & montastraeids (about 24% including indistinguishable merulinid & montastraeids, *Caulastraea*, *Favites*, *Hydnophora*, *Hydnophyllia*, *Montastraea* and *Tarbellastraea*) (Fig. 8h).

Proximal reef slope

The proximal portion of the reef slope can be observed along the Porto Miggiano section, a 150 m long roadcut southeast from S. Cesarea (Fig. 1b), where a 30 m thick succession shows the superimposition of some meters thick clinobeds with a 20°–30° E/SE dip (Fig. 5g).

The prevailing lithology is a compact limestone rich in large coral fragments (Fig. 9c, d) and whole colonies, most of which are upturned (Fig. 9e) although some are preserved in growth position. Coral fragments can be irregularly scattered or concentrated into discontinuous deposits, forming floatstone to rudstone levels parallel to the stratifica-

tion. Their amount generally increases towards the top of the outcrop. The matrix surrounding the corals consists of two types of sediment that cyclically alternate along the section: 1) coral grainstone rich of coral fragments associated with abundant benthic foraminifera (rotaliids, miliolids, nummulitids and sparse alveolinids) and non-geniculate coralline algae (mainly Melobesioideae and Sporolithoideae) with small, irregular to rounded fragments and rare foliose growth-forms, together with echinoderms, molluscs, geniculate algae, serpulids and bryozoans (Fig. 9a); 2) coral packstone having a bioclastic fraction very similar to that of the coral grainstone, but with additional scattered, large *Nephrolepidina* and *Eulepidina* tests and sparse planktonic foraminifera (Fig. 9b).

Typical of this facies is also the abundance of a fine-grained, geopetally laminated glauconitic sand, filling intercoral cavities and small fractures. Microfacies analysis of this sediment revealed its close similarity to the phosphatic deposits of the *Aturia* level (Vescogni et al. 2018), a Serravallian/Tortonian hardground from which this material could have filtered by a series of fractures and through the primary porosity of the CL reef slope.

Coral assemblage. The coral assemblage is characterized by a coral count made along the section within an area approximately of 345 m² and where the percentage of coral fragments and overturned colonies (68%) and that of coral colonies in growth position (32%) have been calculated (Fig. 9f). The coral cover has not been assessed in this facies because outcrop conditions and the detrital nature of the deposits hampered the measurement of transect lines of enough length parallel to stratification.

As regards the corals in growth position (153 in total), about 11 genera have been identified with the most common, similarly to the reef front facies, represented by colonies of poritids (*Porites* and *Goniopora*: about 34%) and merulinid & montastraeids (indistinguishable merulinid & montastraeids, *Antiguastrea*, *Caulastraea*, *Hydnophora*, *Hydnophyllia*, *Montastraea*, *Tarbellastraea*: about 33%) (Fig. 9f). The size of corals in growth position varies from 8 to 100 cm in length and 6 to 50 cm in height.

The occurrence of massive beds consisting of a rubble (chaotic assemblage of tiny broken coral branches) rich in fragments of thin branching corals, mainly *Stylophora* with some *Acropora*, is typical and unique for this facies (Fig. 9d).

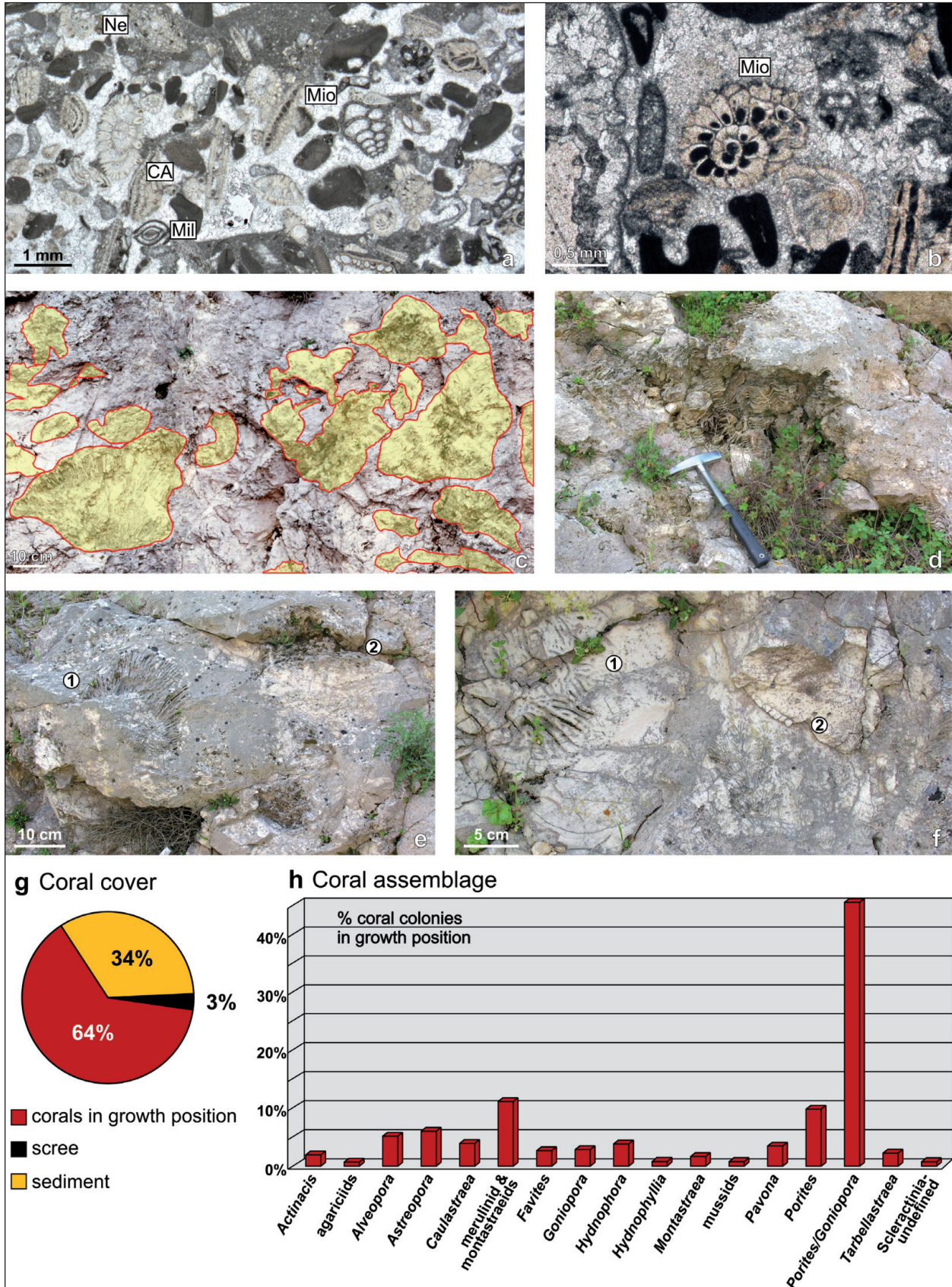


Fig. 8 - Reef front, S. Cesarea section: a) Foraminifera and coralline algae grainstone among the coral colonies (CA: coralline algae; Ne: *Nephrolepidina*; Mil: miliolid; Mio: *Miogypsinoides*). b) Close-up of a *Miogypsinoides* test (Mio). c) The coral framework, in yellow the coral colonies in growth position. d) Poritid, e1) *Hydnophora*, e2) Poritid, f1) *Hydnophora* and f2) *Tarbellastraea* are some of the main coral taxa in growth position. g) Percentage of coral cover derived from quantitative linear measurements. h) Evaluation of the coral assemblage at the genus level expressed as the percentage of colonies in growth position and derived from coral counts on the outcrop surface.

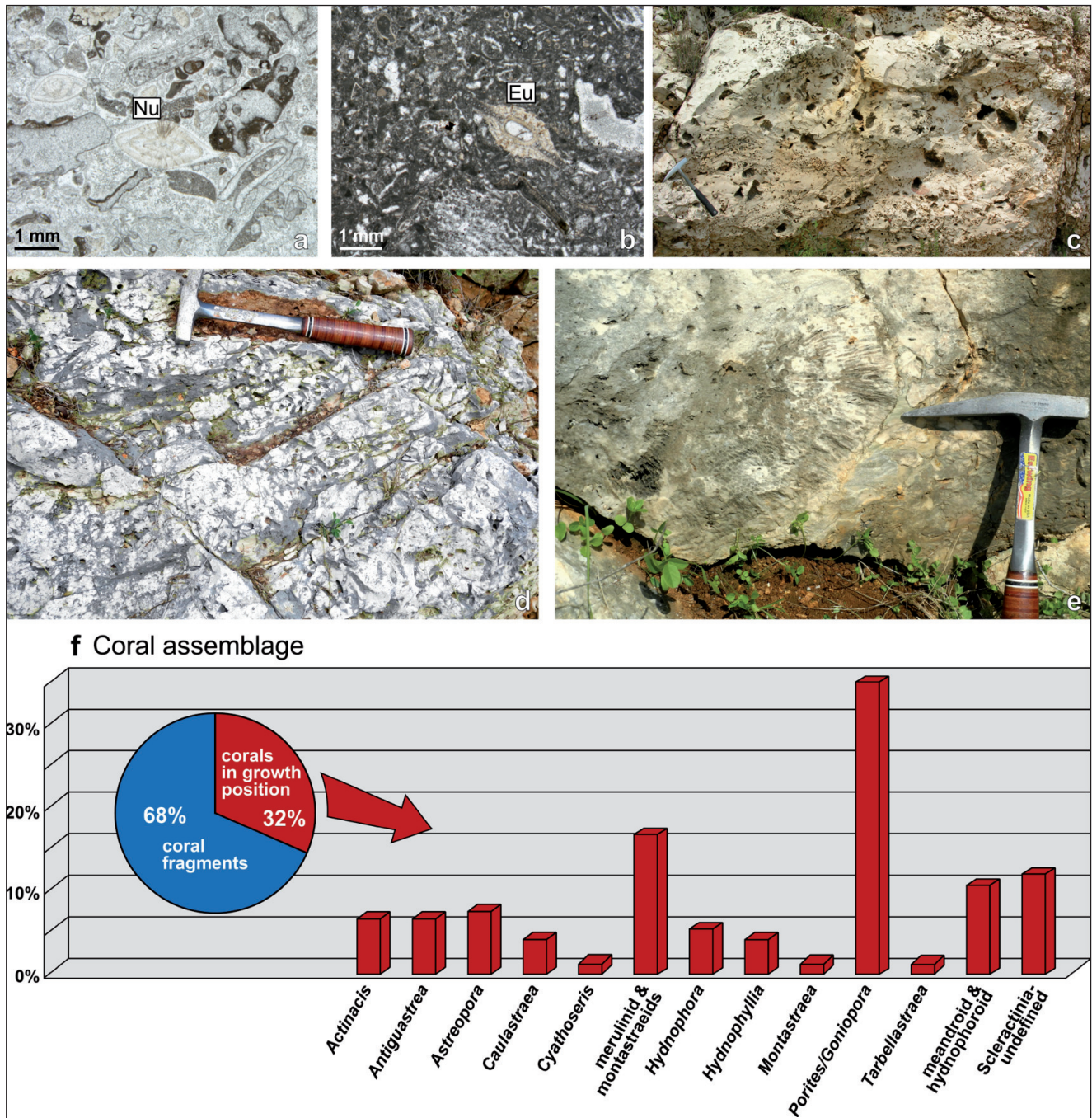


Fig. 9 - Proximal reef slope, Miggiano section: a) Coral and foraminifera grainstone (Nu: *Nummulites*). b) Coral and foraminifera packstone with *Eulepidina* test (Eu). c) Clinostratified coral debris rudstones and floatstones. d) Close-up of coral rubble consisting of fragmented branching colonies of *Stylophora* and subordinate *Acropora*. e) Upturned *Favites* colony. f) Percentage of corals in growth position vs. coral fragments and evaluation of the coral assemblage at the genus level expressed as the percentage of colonies in growth position; both derived from coral counts on the outcrop surface.

Distal reef slope

The distal slope is clearly visible along the present-day coastline at the Zinzulusa outcrop (Fig. 1b), a 400 m long palaeoembayment originally cut in the Cretaceous substrate and subsequently filled with CL clinostratified deposits. The section measures up to 12 m in thickness, with strata characterized by a E/SE dip between 20° and 30°

(Fig. 5h). As in the proximal slope, the most significant characteristic is the abundance of corals, represented by large fragments and whole colonies, sometimes in growth position, and forming discontinuous rudstone and floatstone accumulations. As in the Porto Miggiano section, the prevailing textures are grainstone and packstone (Fig. 10a-b) with abundant fragments of corals, larger foraminifera

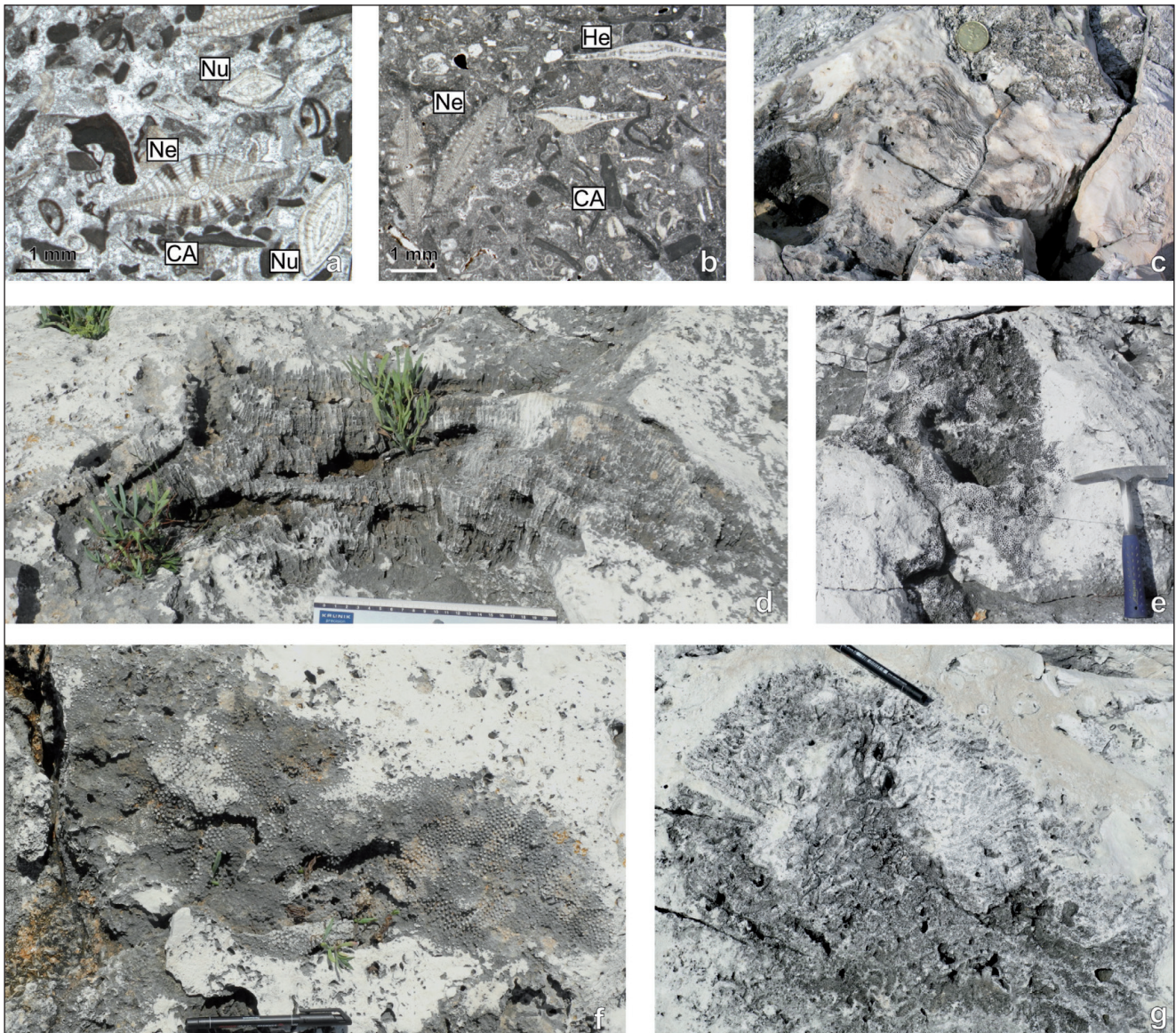


Fig. 10 - Distal reef slope, Zinzulusa section: a) Foraminifera and coralline algae grainstone (CA: coralline algae; Ne: *Nephrolepidina*; Nu: *Nummulites*) and b) Foraminifera and coralline algae packstone (CA: coralline algae; He: *Heterostegina*; Ne: *Nephrolepidina*); note in both sediments the occurrence of large *Nephrolepidina* specimens. c) *Actinacis*, d) *Montastraea*, e) *Antiguastrea*, f) *Astreopora* and g) *Hydnophora* are some of the main coral genera in growth position.

(large *Nephrolepidina* tests associated with *Heterostegina*, some rotaliids, small nummulitids, rare miliolids and alveolinids) and coralline red algae (mostly small fragments with irregular shape). Planktonic foraminifera are also common together with fragments of echinoderms, molluscs and bryozoans. As in the proximal slope, small deposits of greenish, fine-grained sediment are present among the coral rudstones and floatstones.

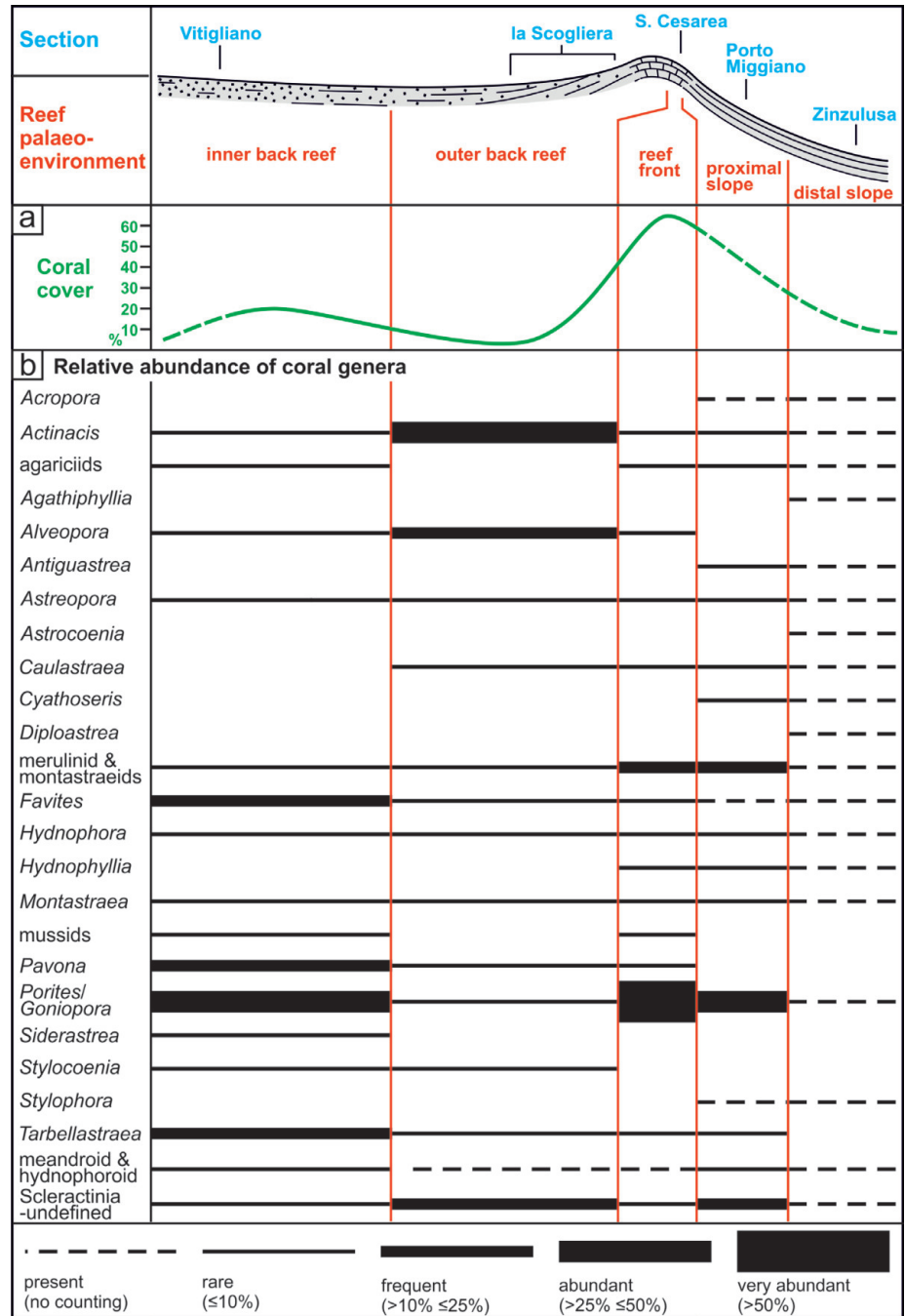
Coral assemblage. Quantitative measurements were not carried out at the Zinzulusa outcrop because the rocks are directly exposed to sea water action (karstic dissolution and wave erosion), and

are not easily accessible and difficult to sample. In a field-survey, about 15 coral genera have been identified with the most common represented by colonies of *Actinacis*, *Antiguastrea*, *Astreopora*, *Goniopora*, *Porites*, *Hydnophora*, *Favites*, *Astrocoenia*, *Agathiphyllia*, and *Stylophora* (Fig. 10c-g). Several solitary corals are also present. Very few coral sizes have been measured, and range from 30 to 85 cm in length to 20 to 80 cm in height.

Synthesis of coral data

In order to have a complete picture across the reef profile, the relative abundance of genera recog-

Fig. 11 - a) Variations in the coral cover, and b) distribution of the Castro Limestone coral genera, along the reconstructed palaeobathymetric reef profile. The relative abundance of colonies in growth position is indicated by frequency categories.



nized in the field by coral counts has been subdivided into frequency categories: rare ($\leq 10\%$), frequent ($> 10\% - \leq 25\%$), abundant ($> 25\% - \leq 50\%$), very abundant ($> 50\%$). To these categories, we also added the occurrence of corals identified in the coral collection but not included in the counts (Fig. 11b).

The most significant traits include: the ubiquitous abundance of poritids (*Porites* and *Goniopora*) in all the facies, the increasing abundance of merulinid & montastraeids towards the margin and slope of the reef, the relative high abundance in the inner back reef of *Favites*, *Pavona* and *Tarbellastraea*, the

striking dominance of *Actinacis* in the outer back reef, the occurrence of delicate branching corals such as *Stylophora* and *Acropora* (although in rubble deposits), together with *Cyathoseris*, in the slope facies (Fig. 11b).

Coral cover, expressed as the % of corals preserved in growth position vs the % of inter-coral sediment (from linear measurements), shows a very clear variation across the reef profile from 4-20% in the back reef up to 64% of the reef front facies, followed by a decrease towards the reef slope (Fig. 11a).

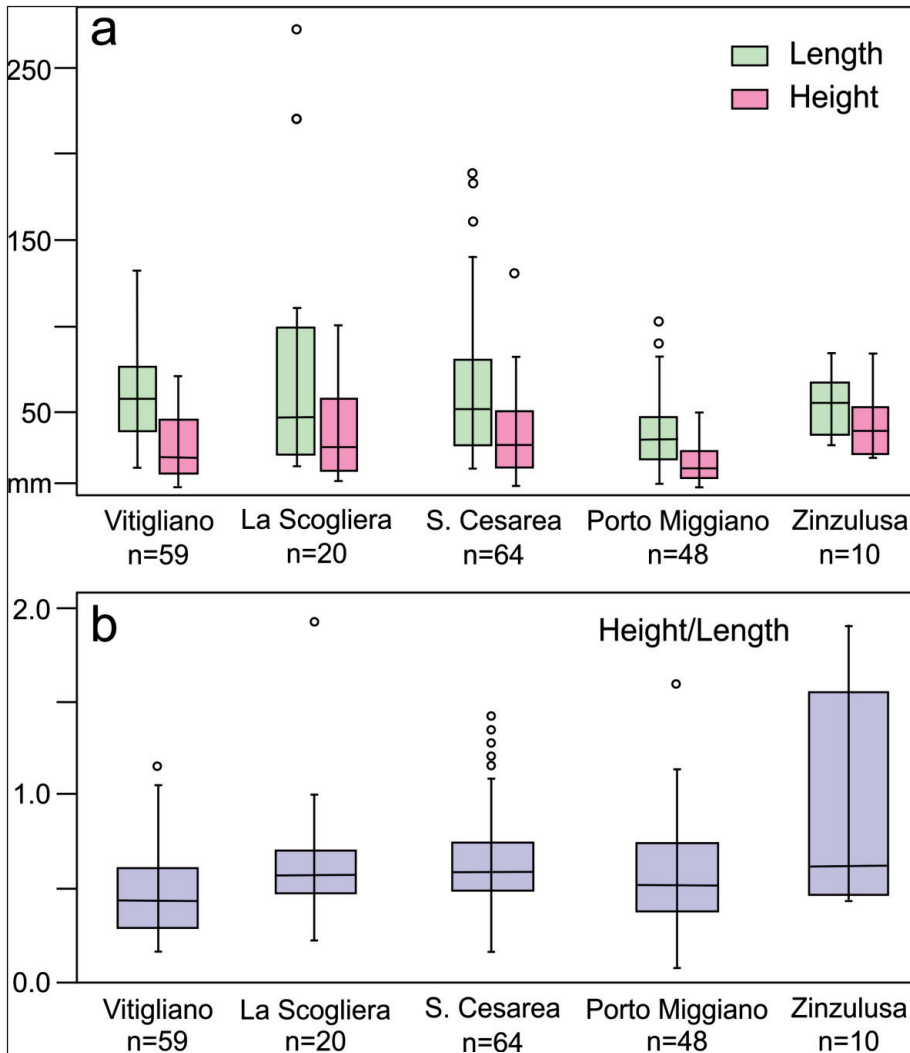


Fig. 12 - Box and whisker plots comparing: a) colony size (length, height), and b) shape (height/length) among localities and reef facies. Boxes enclose 50% of the measurements, lines within each box are medians, whiskers above and below each box are maximums and minimums, and points above whiskers are outliers. Localities are arranged from nearshore to offshore.

As regards colony size and shape, colony lengths, heights, and height/length overlap considerably among localities. Kruskal Wallis and Median tests indicate, however, that significant differences do exist for: length (Kruskal Wallis $H=21.7$, $df=4$, $p<.000$; Median=48, chi-square=19.7, $df=4$, $p=.001$), height (Kruskal Wallis $H=23.2$, $df=4$, $p<.000$; Median=26, chi-square=10.9, $df=4$, $p=.028$), and height/length (Kruskal Wallis $H=17.4$, $df=4$, $p<.000$; Median=0.53, chi-square=10.8, $df=4$, $p=.029$).

Tukey HSD tests for length show that [Porto Miggiano \leq (Zinzulusa = Vitigliano = Santa Cesarea) \leq la Scogliera] (Fig. 12a), indicating that colonies at Porto Miggiano are generally shorter in length. Tukey HSD tests for height show that [(Porto Miggiano = Vitigliano) \leq (la Scogliera = Santa Cesarea = Zinzulusa)] (Fig. 12a), indicating that colony height is variable across the reef but generally lower at Porto Miggiano and Vitigliano.

Tukey HSD tests for height/length show that [(Vitigliano = Porto Miggiano = Santa Cesarea = la Scogliera) \leq Zinzulusa] (Fig. 12b), suggesting that colonies in deeper water, more distant from shore, are more equidimensional but not tabular or platy.

DISCUSSION

Depositional model and palaeoecological traits

The most important element of the CL depositional system is the occurrence of a bioconstructed, wave-resistant margin that raised above the sea-floor allowing the formation of a shallow shoreward back reef (Fig. 5a). The bioconstructed nature of the CL reef margin is supported by the coral assemblage in the S. Cesarea reef front facies, where a large number of massive coral colonies

grew in close contact, forming up to the 64% of the whole lithology (Fig. 8c, g). This robust framework, particularly dense towards the upper part of the section, prograded over the basal coral rubble, forming a raised structure that during the late Chattian ran more or less parallel to the present-day coastline (Fig. 1b). The original topographic relief of this margin is determined by the geometries at the eastern side of the la Scogliera section, where the coral framework passes into the bioclastic unit I of the outer back reef, forming a landward flank with a 15° westward dip (Fig. 5d-e). In this position the top layers of unit I overlay the reef margin, probably passing into a reef crest facies now completely eroded. The back reef was later filled by the sediments of the unit II (Fig. 5d), representing a successive sequence in the depositional history of the CL.

In the facies analysis, the recognition of some important palaeoenvironmental indicators is crucial to interpreting depositional conditions. Among benthic foraminifera, miliolids, whose large amount is usually correlated with extremely shallow-water settings, are abundant in the proximal portion of the depositional system, from the inner shoreward back reef to the reef margin (reef front) but are especially concentrated within the outer back reef. A similar distribution is observed also for the coralline algae assemblage, in particular for fragments with foliose, hooked and hollow growth-forms. These types of crusts are interpreted as the product of coralline algae growth as epiphytes on seagrass vegetation with their morphology adapted to the surface of stems and leaves, and thus considered as reliable markers of euphotic conditions (Beavington-Penney et al. 2004; Perry & Beavington-Penney 2005; Sola et al. 2013). This evidence, associated also with the coarse packstone and grainstone textures of the back reef deposits and with the dominant grainstone of the reef front, indicates that all of these facies developed under high-energy, shallow-water conditions, well within the euphotic range. The occurrence in the reef front of scattered, micrite-rich deposits can be related to the presence of sheltered areas within the coral framework.

Starting from the massive alignment of the reef front, clinostratified slope deposits develop E/SE, with a 20°/30° dip (Fig. 5b). Both proximal and distal slope are characterized by abundant corals, mainly represented by fragments and whole reworked colonies, with a smaller amount preserved in

growth position. The coral deposits show two main types of matrix cyclically alternated: (1) a grainstone dominated by foraminifera and coralline algae, with an assemblage very similar to that of the reef margin; and (2) a packstone, where large *Nephrolepidina* and *Eulepidina*, planktonic foraminifera are also present and more abundant within the distal slope succession. This pattern can be interpreted as a result of a moderate sea-level cyclicity. Coral-rich accumulations with grainstone matrix can be associated with relatively low sea-level phases, during which the slope deposits accumulated under high-energy hydrodynamic conditions, at a short distance from the euphotic coral margin (Esteban 1996; Flügel 2004; Bosellini 2006). On the contrary, coral deposits with packstone matrix can be associated with transgression phases, with a landward shift of the bioconstructed margin, the establishment of moderate hydrodynamic conditions and the appearance of markers of relatively deeper, mesophotic settings, such as *Nephrolepidina* and planktonic foraminifera (Bosellini et al. 1987; Hottinger 1997). However, the moderate lateral extension of the studied outcrops hampers the exhaustive characterization of these cycles over long distances. Therefore, the superimposition within the slope of sediments from different palaeobathymetric settings could be alternatively explained by periodic episodes of offbank shedding. In this way, relatively deep sediments would be interspersed with deposits of shallower origin, coming from the margin and mobilized during storms or by gravity, facilitated by the steep inclination of the slope (Mulder et al. 2017).

What does the composition and distribution of the coral fauna tell us about the CL reef system? Although some traits appear constant all along the CL reef profile, such as the dominance of massive poritids and merulinid & montastraeids (with the latter increasing towards the margin and slope of the reef) and, in general, the diversity in terms of number of genera recognized in the different facies, quantitative data from field surveys show that the coral assemblages vary along the reef profile both in their composition and in their proportions (relative abundance of genera).

A distinct coral zonation has not been observed, however, several features characterize the different facies and provide useful information for their palaeoenvironmental interpretation. The coral cover clearly fluctuates across the reef profile and

reaches its maximum value in the reef front facies, where corals occur in the most suitable conditions for a dense colonization. The most distinct facies is the so called “outer back reef facies”: the number of colonies in growth position per measured area is very low (34 in 330 m²), as also documented by the very reduced coral cover (4%). It is dominated by the genus *Actinacis* which is known to be one of the most plastic and resilient genera of the Paleogene (Bosellini & Stemmann 1996; Sanders & Baron-Szabo 2005). This evidence points to a degree of ecostress much higher than in the other facies, suggesting that this was most probably a part of the reef quite close to sea-level and to the reef crest (not preserved), and most subjected to the wave action.

In general, a zonation of growth forms is not visible, but most colonies are massive-globose, with some tabular ones. Platy corals are extremely rare (some *Cyathoseris* in the slope facies) and branching colonies are poorly represented, except for the occurrence of massive layers consisting of the rubble of delicate branching *Stylophora* and subordinate *Acropora* in the proximal slope facies, which not having been recognized in the shallower facies, suggests some luxuriant colonization in this part of the reef. Totally absent are the typical branching growth forms that the same CL genera (i.e. *Actinacis*, *Porites*, *Goniopora*) exhibit in many turbid-water Cenozoic reef settings partly controlled by terrigenous input (Bosellini & Trevisani 1992; Sanders & Baron Szabo 2005; Silvestri et al. 2011; Santodomingo et al. 2016; Baron-Szabo & Sanders 2020).

The combination of all these traits depicts a luxuriant fringing reef formed in clear water conditions and facing the open sea, thus mostly controlled by wave energy, which varied along a palaeobathymetric gradient reconstructed by stratigraphic relationships, microfacies and distribution and composition of the coral fauna. Based on these traits, the CL represents an almost unique case in the Oligocene of the peri-Mediterranean region, as most other examples show a reduced thickness and extension and/or developed in turbid and mixed carbonate-siliciclastic settings (Perrin & Bosellini 2012 and references therein; Baron-Szabo & Sanders 2020; Bosellini et al. 2020).

The diversity of the CL coral fauna and its spatiotemporal significance

Coral reefs increased in abundance, size, and

biotic diversity during the Oligocene, especially in the Caribbean and western Tethys/Mediterranean regions, with buildups often represented by framework reefs, characterized by moderate to high diversity and dominated by scleractinian corals (Budd 2000; Perrin 2002; Johnson 2007; Bosellini & Perrin 2008; Perrin & Bosellini 2012).

Of all Oligocene scleractinian faunas, those of the lower Oligocene (Rupelian) of the Mediterranean region have been exceptionally documented since the 19th century (Baron-Szabo & Sanders 2020 and references therein). In contrast, despite the highest genus level diversity for the whole region recorded during the Late Oligocene (Chattian) (Bosellini & Perrin 2008), for this time interval most papers contain lists of taxa (Pfister 1985; Hladil et al. 1991; Cahuzac & Chaix 1993, 1994, 1996; Yazdi et al. 2012) and few provide a detailed taxonomic characterization (Chaix & Cahuzac 2001; Schuster 2002 a, b).

The CL coral fauna, is herein described and illustrated (supplementary material: Tab. 1 and Pl. 1-6), confirming the high taxonomic richness that has been recognized in Chattian Mediterranean reefs (Bosellini & Perrin, 2008). Most genera comprise one to two species, except *Goniopora*, *Montastrea* and *Stylophora* which have three to four species. The collection is deposited at the Department of Chemical and Geological Sciences of the University of Modena and Reggio Emilia and is represented by 212 specimens consisting of 25 genera and 41 species.

The stratigraphic distribution of the identified species shows that 17 species (about 41%) were already present during the Eocene, 12 species (29%) are strictly Oligocene and 10 species (about 24%) cross the Oligocene/Miocene boundary (Fig. 13). Their palaeobiogeographic distribution is mainly Mediterranean, but with some occurrences in Sulawesi, Iran, United Arab Emirates, Pakistan and Tanzania (Reuter et al. 2019), thus highlighting an Indo-Pacific affinity due to the marine gateway to the Indian Ocean that closed completely only in the Middle Miocene (Rögl 1999; Reuter et al. 2009). The CL pool of coral species reaches the largest geographic distribution during the Oligocene, and the widely distributed species are also those with the longest stratigraphic ranges. Only two endemic species have been recognized (*Acropora salentina* and *Tarbellastraea salentinensis*).

Bosellini 2016). Including coral taxa typical of both the Eocene-Rupelian and Miocene times, the upper Chattian fauna of the CL also documents a phase of transition between the Oligocene and the Miocene.

Regional vs global drivers

Three different coral reef episodes have been recognized in the Salento Peninsula: during the Priabonian (Torre Specchialaguardia Limestone) (Russo 2006), during the Chattian (Castro Limestone) and during the Messinian (Novaglie Formation) (Bosellini et al. 2001, 2002; Bosellini 2006). These reefs grew at different times in the same depositional setting, i.e. the stable margin of the pure carbonate Apulia Platform, which maintained the same geometry during the Cenozoic (Bosellini & Parente 1994; Bosellini et al. 1999) and clearly offered suitable physiographic conditions for the settlement of coral reefs at the local/regional scale.

At the global scale, the herein refined age places the CL in the middle-late Chattian and within 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 characterized by an unexpected inverse correlation between global sea-surface temperature and $p\text{CO}_2$. In fact, after a period of gradual cooling following the onset of Antarctic glaciation near the Eocene/Oligocene boundary, global $\delta^{18}\text{O}$ values indicate a period of substantial warming and/or deglaciation during the Late Oligocene that is coincident with declining atmospheric CO_2 (Zhang et al. 2013; O'Brien et al. 2020) (Fig. 4).

A direct link between global sea-surface temperature and reef coral richness (at the genus level), as postulated by the Energy Hypothesis (Fraser & Currie 1996), has been explored for the Oligocene-Miocene circum-Mediterranean regions (Rosen 1999; Bosellini & Perrin 2008), showing that variation in genus richness broadly parallels global temperatures inferred by independent methods.

More complex and controversial seems to be the relationship between climate change and capacity of corals to build massive reefs, also considering that reef development and coral diversity were often unrelated (Kiessling & Baron-Szabo 2004; Johnson et al. 2008; Zamagni et al. 2012; Perrin & Bosellini 2013).

In this regard, it is worth emphasizing that Pomar et al. (2014), by interpreting the CL as a mesophotic distally steepened ramp and ascribing it to the early Chattian when both global SST and $\delta^{13}\text{C}$ were represented by low values, corroborated the theory that coral buildups increased in volume during times of global cooling and that before the late Tortonian they were all mesophotic and not able to build rigid framework close to the sea level (Pomar & Hallock 2008; Pomar et al. 2014, 2017).

Although the discussion of the major drivers of climate change during the Cenozoic, and in particular during the Oligocene, are beyond the aim of this paper, it is clear that the results herein presented depict a different scenario, where the massive reef complex of the CL not only shows euphotic palaeoenvironments, but it developed during a warming period that paralleled a declining atmospheric CO_2 . The CL, which is not an exception as regards coral reefs formed within euphotic conditions in pre-late Tortonian times (Perrin 2000; Vescogni et al. 2014, 2016; Bosellini et al. 2020), shows that its massive development and the high reef-building capacity of its corals were not hampered by warming conditions, but most probably promoted by the reduced $p\text{CO}_2$ conditions and by a local/regional suitable physiographic setting.

As a last consideration, our results about the CL highlight that temperature and atmospheric CO_2 may act and impact coral reefs in different ways if their effect is not combined. The increase of temperature alone is not a driver for coral demise, but high temperature in synergy with high CO_2 levels can significantly affect coral reef construction, as we are witnessing nowadays in the “Anthropocene”.

CONCLUSIONS

By revisiting the Castro Limestone (CL) and combining facies analysis with the first detailed characterization of its coral fauna, we aimed to provide a complete picture of one of the best-preserved Oligocene coral reefs of the Mediterranean region and to discuss the mutual relationship between coral reef construction and coral diversity during the Oligocene, the epoch of the Cenozoic that witnessed the apex of coral reef growth. Our main findings can be summarized as follows:

A careful field survey and facies analysis confirm the previous interpretation of the CL as a fringing reef complex (Bosellini & Russo 1992), whose profile is reconstructed and subdivided in different palaeoenvironments and related facies ranging from the shallow back reef to the fore reef slope.

By the study of the larger foraminifera association (Fig. 8b), the age of the CL is revised and assigned to the lower part of the Shallow Benthic (SB) Zone 23 of middle-late Chattian age, thus within the Late Oligocene Warming Event (LOWE) phase.

The CL coral fauna is here described and illustrated for the first time at both the genus and species level, and clearly shows a high diversity with the recognition of 25 genera and 41 species. Quantitative data from field surveys show that the coral assemblages of the reef palaeoenvironments differ both in their composition and in their proportions.

The stratigraphic and palaeogeographic distribution of the identified taxa make the CL coral fauna a very good example of a coral assemblage at the transition between the typical Oligocene and Miocene assemblages, and an excellent example of the persistence of a cosmopolitan Tethyan fauna in the Oligocene time, with the Mediterranean and Indo-Pacific provinces being more closely connected than the Mediterranean and the Caribbean.

The high diversity is here coupled with a strong reef-building capacity of the corals, which were able to form an extensive and massive reef within the euphotic zone in a clear-water setting and during a warming period coincident with declining atmospheric CO₂ values. Reef-building capacity was not hampered by warming conditions, but was most probably promoted by the reduced pCO₂ conditions and by a suitable local/regional physiographic setting.

Acknowledgments: The authors wish to thank the two reviewers Diethard Sanders and Nadia Santodomingo for their valuable comments and helpful suggestions.

This study was funded by the Italian Ministry of Education and Research (MIUR), funds PRIN 2017: project “Biota resilience to global change: biomineralization of planktic and benthic calcifiers in the past, present and future” (prot. 2017RX9XXY).

REFERENCES

- Baron-Szabo R.C. & Sanders D. (2020) - Scleractinian corals (Anthozoa) from the lower Oligocene (Rupelian) of the Eastern Alps, Austria. *Bollettino della Società Paleontologica Italiana*, 59(3): 319-336.
- Beavington-Penney S.J., Wright V.P. & Woelkerling W.J. (2004) - Recognising macrophyte-vegetated environments in the rock record: a new criterion using “hooked” forms of crustose coralline red algae. *Sedimentary Geology*, 166: 1-9.
- Berggren W.A. & Hollister C.D. (1974) - Paleogeography, paleobiogeography and the history of circulation in the Atlantic Ocean. *SEPM Special Publication*, 20: 12-186.
- Bosellini A. & Parente M. (1994) - The Apulia Platform margin in the Salento Peninsula (southern Italy). *Giornale di Geologia*, 56:167-177.
- Bosellini A., Russo A., Arush M.A. & Cabdulqadir M.M. (1987) - The Oligo-Miocene of Eil (NE Somalia): a prograding coral-*Lepidocyclus* system. *Journal of African Earth Sciences*, 6: 583-593.
- Bosellini A., Bosellini F.R., Colalongo M.L., Parente M., Russo A. & Vescogni A. (1999) - Stratigraphic architecture of the Salento coast from Capo d'Otranto to S. Maria di Leuca (Apulia, southern Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 105: 397-416.
- Bosellini F.R. (1999) - The scleractinian genus *Hydnophora* (revision of Tertiary species). *Paläontologische Zeitschrift*, 73: 217-240.
- Bosellini F.R. (2006) - Biotic changes and their control on Oligocene–Miocene reefs: a case study from the Apulia Platform margin (southern Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 241: 393-409.
- Bosellini F.R. & Perrin C. (1994) - The coral fauna of Vitigliano: qualitative and quantitative analysis in a backreef environment (Castro Limestone, Late Oligocene, Salento Peninsula, southern Italy). *Bollettino della Società Paleontologica Italiana*, 33: 171-181.
- Bosellini F.R. & Perrin C. (2008) - Estimating Mediterranean Oligocene - Miocene sea-surface palaeotemperatures: an approach based on coral taxonomic richness. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 258: 71-88.
- 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. & Russo A. (1995) - The Scleractinian genus *Actinacis*. Systematic revision and stratigraphic record of the Tertiary species with special regard to Italian occurrences. *Rivista Italiana di Paleontologia e Stratigrafia*, 101: 215-230.
- Bosellini F.R., Russo A. & Vescogni A. (2001) - Messinian reef-building assemblages of the Salento Peninsula (southern Italy): palaeobathymetric and palaeoclimatic significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 175: 7-26.
- Bosellini F.R., Russo A. & Vescogni A. (2002) - The Messinian reef complex of the Salento Peninsula (Southern Italy): stratigraphy, facies and paleoenvironmental interpretation. *Facies*, 47: 91-112.
- Bosellini F.R. & Stemann T. (1996) - Autecological significance of growth form in the scleractinian *Actinacis rollei* Reuss (Oligocene, Lessini Mountains, Northern Italy). In: Cherchi A. (Ed.) - Autecology of selected fossil or-

- ganisms: Achievements and problems. *Bollettino della Società Paleontologica Italiana*, spec. vol. 3: 31-43.
- Bosellini F.R. & Trevisani E. (1992) - Coral facies and cyclicity in the Castelmongiberto Limestone (early Oligocene, eastern Lessini Mountains, northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 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). *Bollettino della Società Paleontologica Italiana*, 59(3): 337-348.
- Bossio A., Mazzei R., Monteforti B. & Salvatorini G. (2002) - Note illustrative alla carta geologica della zona di S. Maria di Leuca. *Atti della Società Toscana di Scienze Naturali, Memorie*, 107: 97-163.
- Brachert T.C., Vescogni A., Bosellini F.R., Reuter M. & Mertz-Kraus R. (2007) - High salinity variability during the early Messinian revealed by stable isotope signatures from vermetid and *Halimoda* reefs of the Mediterranean region. *Geologica Romana*, 40: 51-66.
- Braga J.C., Vescogni A., Bosellini F.R. & Aguirre J. (2009) - Coralline algae (Corallinales, Rhodophyta) in western and central Mediterranean Messinian reefs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 275: 113-128.
- Brandano M., Morsilli M., Vannucci G., Parente M., Bosellini F.R. & Mateu-Vicens G. (2010) - Rhodolith-rich lithofacies of the Porto Badisco Calcarenes (upper Chattian, Salento, southern Italy). *Bollettino della Società Geologica Italiana*, 129(1): 119-131.
- Budd A.F. (2000) - Diversity and extinction in the Cenozoic history of Caribbean reefs. *Coral Reefs*, 19: 25-35.
- Budd A.F., Bosellini F.R. & Stemann T. (1996) - Systematics of the Oligocene to Miocene reef coral *Tarbellastraea* in the Northern Mediterranean. *Palaeontology*, 39: 515-560.
- Budd A.F. & Bosellini F.R. (2016) - Revision of Oligocene Mediterranean meandroid corals in the scleractinian families Mussidae, Merulinidae, and Lobophylliidae. *Journal of Systematic Palaeontology*, 14: 771-798.
- Budd A.F., Fukami H., Smith N.D. & Knowlton N. (2012) - Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). *Zoological Journal of the Linnean Society*, 166: 465-529.
- 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 Zoologica*, 90: 142-165.
- Cahuzac B. & Chaix C. (1993) - Les faunes de coraux (Anthozoaires Scléactiniaires) de la façade atlantique française au Chattien et au Miocène. *Ciências da Terra*, 12: 57-69.
- Cahuzac B. & Chaix C. (1994) - La faune de coraux de l'Oligocène supérieur de la Téalère (Peyrehorade, Landes). *Bulletin de la Société de Borda*, 436(4): 463-484.
- Cahuzac B. & Chaix C. (1996) - Structural and faunal evolution of Chattian-Miocene reefs and corals in western France and the northeastern Atlantic Ocean. In: Franseen E.K., Esteban M., Ward W.C. & Rouchy J.-M. (Eds.) - Models for Carbonate Stratigraphy from Miocene Reef Complexes of the Mediterranean regions. *Concepts in Sedimentology and Paleontology, SEPM*, 5: 105-127.
- Cahuzac B. & Poignant A. (1997) - Essai de biozonation de l'Oligo-Miocène dans les bassins européens à l'aide des grands foraminifères néritiques. *Bulletin de la Société Géologique de France*, 168: 155-169.
- Chaix C. & Cahuzac B. (2001) - Une faune inédite de coraux scléactiniaires dans le gisement chattien d'Escornebéou (Landes, SW France): stratigraphie, systématique et paléocologie. *Annales de Paléontologie*, 87(1): 3-47.
- Drooger C.W. & Laagland H. (1986) - Larger foraminiferal zonation of the European Mediterranean Oligocene. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B*, 89: 135-148.
- Dunham R.J. (1962) - Classification of carbonate rocks according to depositional texture. In: Hamm W.E. (Ed.) - Classification of carbonate rocks, a symposium. *American Association of Petroleum Geologists Memoir*, 1: 108-121.
- Embry A.F. & Klovan J.E. (1971) - A Late Devonian reef tract on Northeastern Banks Island, N.W.T. *Bulletin of Canadian Petroleum Geology*, 19: 730-781.
- Esteban M. (1996) - An Overview Of Miocene Reefs From Mediterranean Areas: General Trend And Facies Models. In: Franseen E.K., Esteban M., Ward W.C. & Rouchy J.-M. (Eds.) - Models for Carbonate Stratigraphy from Miocene Reef Complexes of the Mediterranean regions. *Concepts in Sedimentology and Paleontology, SEPM*, 5: 3-53.
- Flügel E. (2004) - Microfacies of carbonate rocks. Springer, Berlin, 976 pp.
- Föllmi K.B., Hofmann H., Chiaradia M., de Kaenel E., Frijia G. & Parente M. (2015) - Miocene phosphate-rich sediment in Salento (southern Italy). *Sedimentary Geology*, 327: 55-71.
- Fraser R.H. & Currie D.J. (1996) - The species richness-energy hypothesis in a system where historical factors are thought to prevail: coral reefs. *The American Naturalist*, 148: 138-159.
- Frost S.H. (1981) - Oligocene reef coral biofacies of the Vicentin, northeast Italy. In: Toomey D.F. (Ed.) - European fossil reef model. *S.E.P.M. Special Publication*, 30: 483-539.
- Fukami H., Budd A.F., Paulay G., Sole-Cava A.M., Chen C.A., Iwao K. & Knowlton N. (2004) - Conventional taxonomy obscures deep divergence between Pacific and Atlantic corals. *Nature*, 427: 832-835.
- 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.
- Guido A., Vescogni A., Mastandrea A., Demasi F., Tosti F., Naccarato A., Tagarelli A. & Russo F. (2012) - Characterization of the micrites in the Late Miocene vermetid carbonate bioconstructions, Salento Peninsula, Italy: record of a microbial/metazoan association. *Sedimentary Geology*, 263-264: 133-143.

- Hladil J., Otava J. & Galle A. (1991) - Oligocene carbonate buildups of the Sirt Basin, Libya. In: Salem M.J., Hamuda O.S. & Eliagoubi B.A. (Eds.) - *The Geology of Libya*, Elsevier, 4: 1401-1420.
- Hottinger L. (1997) - Shallow benthic foraminiferal assemblages as signals for depth of their deposition and their limitations. *Bulletin de la Société Géologique de France*, 168: 491-505.
- Johnson K.G. (2007) - Reef-coral diversity in the Late Oligocene Antigua Formation and temporal variation of local diversity on Caribbean Cenozoic Reefs. In: Hubmann B. & Piller W.E. (Eds.) - *Fossil Corals and Sponges. Proceedings of the 9th International Symposium on Fossil Cnidaria and Porifera. Österreichische Akademie der Wissenschaften, Schriftenreihe der Erdwissenschaftlichen Kommission*, 17: 471-491.
- Johnson K.G., Jackson J.B.C. & Budd A.F. (2008) - Caribbean reef development was independent of coral diversity over 28 million years. *Science*, 319: 1521-1523.
- Kiessling W. & Baron-Szabo R. (2004) - Extinction and recovery patterns of scleractinian corals at the Cretaceous–Tertiary boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 214: 195-223.
- Laagland H. (1990) - *Cyclochypus* in the Mediterranean Oligocene. *Utrecht Micropaleontological Bulletins*, 39: 1-171.
- Mulder T., Joumes M., Hanquez V., Gillet H., Reijmer J.J.G., Tournadour E., Chabaud L., Principaud M., Schnyder J.S.D., Borgomano J., Fauquembergue K., Ducassou E. & Busson J. (2017) - Carbonate slope morphology revealing sediment transfer from bank to-slope (Little Bahama Bank, Bahamas). *Marine and Petroleum Geology*, 83: 26-34.
- O'Brien C.L., Huber M., Thomas E., Pagani M., Super J.R., Elder L.E. & Hull P.C. (2020) - The enigma of Oligocene climate and global surface temperature evolution. *PNAS*, 117 (41): 25302-25309.
- Parente M. (1994) - A revised stratigraphy of the Upper Cretaceous to Oligocene units from southeastern Salento (Apulia, southern Italy). *Bollettino della Società Paleontologica Italiana*, 33: 155-170.
- Parente M. & Less G. (2019) - Nummulitids, Lepidocyclinids and strontium isotope stratigraphy of the Porto Badisco Calcarene (Salento Peninsula, southern Italy). Implications for the biostratigraphy and paleobiogeography of Oligocene Larger Benthic Foraminifera. *Italian Journal of Geosciences*, 138(2): 1-23.
- Perrin C. (2000) - Changes of palaeozonation patterns within Miocene coral reefs, Gebel Abu Shaar, Gulf of Suez, Egypt. *Lethaia*, 33: 253-268.
- Perrin C. (2002) - Tertiary: The emergence of modern reef ecosystems. In: Kiessling W., Flügel E. & Golonka J. (Eds.) - *Phanerozoic Reef Patterns. SEPM Special Publication*, 72: 587-621.
- Perrin C. & Bosellini F.R. (2012) - Paleobiogeography of scleractinian reef corals: changing patterns during the Oligocene-Miocene climatic transition in the Mediterranean. *Earth-Science Reviews*, 111: 1-24.
- Perrin C. & Bosellini F. R. (2013) -The Late Miocene coldspot of z-coral diversity in the Mediterranean: patterns and causes. *Comptes Rendus Palevol*, 12: 245-255.
- Perry C.T. & Beavington-Penney S.J. (2005) - Epiphytic calcium carbonate production and facies development within sub-tropical seagrass beds, Inhaca Island, Mozambique. *Sedimentary Geology*, 174: 161-176.
- Pfister T. (1985) - Coral fauna and facies of the Oligocene fringing reef near Cairo Montenotte (Liguria, northern Italy). *Facies*, 13: 175-226.
- Pomar L., Baceta J.I., Hallock P., Mateu-Vicens G. & Basso D. (2017) - Reef building and carbonate production modes in the west-central Tethys during the Cenozoic. *Marine and Petroleum Geology*, 83: 261-304.
- Pomar L. & Hallock P. (2008) - Carbonate factories: a conundrum in sedimentary geology. *Earth Science Reviews*, 87: 134-169.
- Pomar L., Mateu-Vicens G., Morsilli M. & Brandano M. (2014) - Carbonate ramp evolution during the Late Oligocene (Chattian), Salento Peninsula, southern Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 404: 109-132.
- Reuter M., Bosellini F.R., Budd A.F., Coric S., Piller W.E. & Harzhauser M. (2019) - High coral reef connectivity across the Indian Ocean is revealed 6-7 Ma ago by a turbid-water scleractinian assemblage from Tanzania (Eastern Africa). *Coral Reefs*, 38: 1023-1037.
- Reuter M., Piller W.E., Harzhauser M., Mandic O., Berning B., Rögl F., Kroh A., Aubry M.P., Wielandt-Schuster U. & Hamedani A. (2009) - The Oligo-/Miocene Qom Formation (Iran): evidence for an early Burdigalian restriction of the Tethyan Seaway and closure of its Iranian gateways. *International Journal of Earth Sciences*, 98: 627-650.
- Ricchetti G. & Ciaranfi N. (2013) - Note illustrative della Carta Geologica d'Italia alla scala 1:50.000 – foglio 537 Capo Santa Maria di Leuca. ISPRA – Servizio Geologico d'Italia, Litografia Artistica Cartografica, Firenze.
- Rögl F. (1999) - Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). *Geologica Carpathica*, 50(4): 339-349.
- Rosen B.R. (1999) - Paleoclimatic implications of the energy hypothesis from Neogene corals of the Mediterranean region. In: Agusti J., Rook L. & Andrews P. (Eds.) - *The evolution of Neogene terrestrial ecosystems in Europe*. Cambridge University Press: 309-327.
- Rossi D. (1969) - Foglio 215. Otranto. Note Illustrative Carta Geologica Italia. Servizio Geologico Italiano, 31 pp.
- Russo A. (2006) - The upper Eocene reef deposits of Torre Specchialaguardia Limestone (S. Cesarea Terme, Salento Peninsula, southern Italy). In: Buccheri G. & Di Stefano P. (Eds.) - *Celebrazioni di G.G. Gemmellaro ad un secolo dalla scomparsa. Atti del Convegno, Palermo 9-12 Settembre 2004. Quaderni del Museo Geologico "G.G. Gemmellaro" 9*: 96-109.
- Sanders D. & Baron-Szabo R.C. (2005) - Scleractinian assemblages under sediment input: their characteristics and relation to the nutrient input concept. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 216: 139-181.
- Santodomingo N., Renema W. & Johnson K.G. (2016) - Un-

- derstanding the murky history of the Coral Triangle: Miocene corals and reef habitats in East Kalimantan (Indonesia). *Coral Reefs*, 35: 765-781.
- Schuster F. (2002a) - Scleractinian corals from the Oligocene of the Qom formation (Esfahan-Sirjan fore-arc basin, Iran). *Courier Forschungsinstitut Senckenberg*, 239: 5-55.
- Schuster F. (2002b) - Oligocene scleractinian corals from Doutsiko (Mesohellenic Basin, northwestern Greece). *Courier Forschungsinstitut Senckenberg*, 239: 83-127.
- Silvestri G., Bosellini F.R. & Nebelsick J.H. (2011) - Microtaphofacies analysis of Lower Oligocene turbid-water coral assemblages. *Palaios*, 26: 805-820.
- Sola F., Braga J.C. & Aguirre J. (2013) - Hooked and tubular coralline algae indicate seagrass beds associated to Mediterranean Messinian reefs (Poniente Basin, Almería, SE Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 374: 218-229.
- Vescogni A., Bosellini F.R., Cipriani A., Gürlér 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. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 410: 213-232.
- Vescogni A., Bosellini F.R., Papazzoni C.A., Giusberti L., Roghi G., Fornaciari E., Dominici S. & Zorzin R. (2016) - Coralgall buildups associated with the Bolca Fossil-Lagerstätten: new evidence from the Ypresian of Monte Postale (NE Italy). *Facies*, 62: 21.
- Vescogni A., Bosellini F.R., Reuter M. & Brachert T.C. (2008) - Vermetid reefs and their use as palaeobathymetric markers: new insights from the Late Miocene of the Mediterranean (Southern Italy, Crete). *Palaeogeography, Palaeoclimatology Palaeoecology*, 267: 89-101.
- Vescogni A., Guido A., Mastandrea A. & Russo F. (2011) - Microbialite-Vermetid Community Salento Peninsula (southern Italy): a Late Miocene Example of Automicrite Deposition. *Lecture Notes in Earth Sciences*, 131: 301-310.
- Vescogni A., Vertino A., Bosellini F.R., Harzhauser M. & Mandic O. (2018) - New paleoenvironmental insights on the Miocene condensed phosphatic layer of Salento (southern Italy) unlocked by the coral-mollusc fossil archive. *Facies*, 64: 7.
- Wallace C.C. & Bosellini F.R. (2015) - *Acropora* (Scleractinia) from the Oligocene and Miocene of Europe: species longevity, origination and turnover following the Eocene–Oligocene transition. *Journal of Systematic Palaeontology*, 13(6): 447-469.
- Woelkerling W.J., Irvine L.M. & Harvey A. (1993) - Growth-forms in nongeniculate coralline red algae (Corallinales, Rhodophyta). *Australian Systematic Botany*, 6: 277-293.
- Yazdi M., Shirazi M.P., Rahiminejad A.H. & Motavalipour R. (2012) - Paleobathymetry and paleoecology of colonial corals from the Oligocene-early Miocene (?) Qom Formation (Dizlu area, central Iran). *Carbonates Evaporites*, 27 (3-4): 395-405.
- Zachos J.C., Pagani M., Sloan L., Thomas E. & Billups K. (2001) - Trends, rhythms and aberrations in global climate 65 Ma to present. *Science*, 292: 686-693.
- Zachos J.C., Dickens G.R. & Zeebe R.E. (2008) - An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature*, 451: 279-283.
- Zamagni J., Mutti M. & Košir A. (2012) - The evolution of mid Paleocene–early Eocene coral communities: how to survive during rapid global warming. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 317-318: 48-65.
- Zhang Y.G., Pagani M., Zhonghui L., Bohaty S.M. & DeConto R. (2018) - A 40-million-year history of atmospheric CO₂. *Philosophical Transactions of the Royal Society A*, 371: 20130096.