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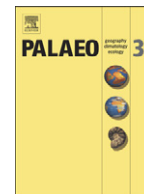
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The evolution of mid Paleocene-early Eocene coral communities: How to survive during rapid global warming

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ABSTRACT

Today, diverse communities of zooxanthellate corals thrive, but do not build reef, under a wide range of environmental conditions. In these settings they inhabit natural bottom communities, sometimes forming patch-reefs, coral carpets and knobs. Episodes in the fossil record, characterized by limited coral-reef development but widespread occurrence of coral-bearing carbonates, may represent the fossil analogs of these non-reef building, zooxanthellate coral communities. If so, the study of these corals could have valuable implications for paleoenvironmental reconstructions. Here we focus on the evolution of early Paleogene corals as a fossil example of coral communities mainly composed by zooxanthellate corals (or likely zooxanthellate), commonly occurring within carbonate biofacies and with relatively high diversity but with a limited bioconstructional potential as testified by the reduced record of coral reefs. We correlate changes of bioconstructional potential and community compositions of these fossil corals with the main ecological/environmental conditions at that time. The early Paleogene greenhouse climate was characterized by relatively short pulses of warming with the most prominent occurring at the Paleocene-Eocene boundary (PETM event), associated with high weathering rates, nutrient fluxes, and pCO₂ levels. A synthesis of coral occurrences integrated with our data from the Adriatic Carbonate Platform (SW Slovenia) and the Minervois region (SW France), provides evidence for temporal changes in the reef-building capacity of corals associated with a shift in community composition toward forms adapted to tolerate deteriorating sea-water conditions. During the middle Paleocene coral-algal patch reefs and barrier reefs occurred from shallow-water settings, locally with reef-crest structures. A first shift can be traced from middle Paleocene to late Paleocene, with small coral-algal patch reefs and coral-bearing mounds development in shallow to intermediate water depths. In these mounds corals were highly subordinated as bioconstructors to other groups tolerant to higher levels of trophic resources (calcareous red algae, encrusting foraminifera, microbes, and sponges). A second shift occurred at the onset of the early Eocene with a further reduction of coral framework-building capacity. These coral communities mainly formed knobs in shallow-water, turbid settings associated with abundant foraminiferal deposits. We suggest that environmental conditions other than high temperature determined a combination of interrelated stressors that limited the coral-reef construction. A continuous enhancement of sediment load/nutrients combined with geochemical changes of ocean waters likely displaced corals as the main bioconstructors during the late Paleocene-early Eocene times. Nonetheless, these conditions did not affect the capacity of some corals to colonize the substrate, maintain biodiversity, and act as locally important carbonate-sediment producers, suggesting broad environmental tolerance limits of various species of corals. The implications of this study include clues as to how both ancient and modern zooxanthellate corals could respond to changing climate.

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1. Introduction

Diverse coral communities dominated by different kinds of zooxanthellate, colonial forms, occur today in a broad range of marine settings where temperature, nutrients, light levels, and aragonite

saturation fluctuate or remain close to what are considered thresholds for coral survival (e.g., Kleypas et al., 1999). In these sites zooxanthellate coral assemblages with constructional potential are developed with a composition comparable to that of coral reefs, however, they do not form a framework. These assemblages are often characterized by high species richness and represent localized sites of carbonate sediment production and accumulation (e.g., Benzoni et al., 2003; Moyer et al., 2003; Perry, 2003; Perry and Larcombe, 2003; Riegl, 2003; Halfar et al., 2005; Thomson and Frisch, 2010).

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These examples highlight the necessity for a distinction between reef-building versus non reef-building corals as compared with symbiont bearing (zooxanthellate, z-corals) and non-symbiont bearing (azooxanthellate corals, az-corals). Corals are traditionally categorized as either hermatypic (reef building) or ahermatypic (non reef building), which is often treated as being equivalent to zooxanthellate versus azooxanthellate. However, many kinds of both z- and az-corals can build reefs only if the environment supports minimal deposition (e.g., Hallock, 1988). Therefore, reef-building capacity is not necessary correlated to algal symbiosis. Hosting zooxanthellae does not translate into reef building if the environmental conditions do not support hypercalcification and/or if the nutrient regime supports bioerosion rates that exceed deposition rates (e.g., Pomar and Hallock, 2008). Similarly, diversity and reef-building capacity are not necessary correlated (as demonstrated for example by Johnson et al., 2008). If environmental conditions are conducive to either hypercalcification or to minimal deposition, just a few species or even a single species can build a carbonate mound or even a reef (e.g., *Porites*-reefs during the Miocene, Pomar, 1991; modern *Porites* reefs in east-central tropical Pacific, e.g., Cortés, 1997).

In this study we focus on the evolution of early Paleogene zooxanthellate corals (or zooxanthellate-like corals, for forms resembling modern zooxanthellate corals see Rosen and Turnšek, 1989), as a possible fossil analogs of these modern non-reef building, zooxanthellate coral communities. The early Paleogene fossil record is characterized by a lack of extensive coral reefs, although coral facies, dominated by z- and z-like forms, have been reported commonly in shallow neritic facies (e.g., Drobne et al., 1988; Schuster, 1996; Baceta et al., 2005; Zamagni et al., 2009). These coral assemblages were characterized by constructional potential but a general limited reef-building capacity.

The early Paleogene experienced the most pronounced long-term warming of the Cenozoic, starting in the late Paleocene (~59 Ma) and culminating in the early Eocene (~51 Ma) with the Early Eocene Climatic Optimum (EECO; Zachos et al., 2001). Short-term warming events, known as hyperthermals, were superimposed on this long-term warming trend, including most notably the Paleocene-Eocene Thermal Maximum (PETM or ETM-1, Kennett and Stott, 1991), the ETM-2 or “Elmo” event, (Lourens et al., 2005), and the ETM-3 or “X” event (Agnini et al., 2009). These hyperthermals are characterized by carbonate dissolution horizons and negative carbon isotope excursions (CIE) (Lourens et al., 2005; Zachos et al., 2005; Nicolo et al., 2007; Zachos et al., 2010). They are likely related to abrupt and massive releases of ¹³C-depleted carbon into the ocean-atmosphere system (Dickens et al., 1995). The onset of the PETM was characterized by rapid changes in terrestrial and marine biota, including the largest extinction of benthic foraminifera (~40% of the species, e.g., Thomas, 2007) recorded during the Cenozoic. Pelagic ecosystems showed rapid diversification with high origination and extinction levels in planktonic foraminifera and calcareous nannofossils (e.g. Kelly et al., 1998; Kelly, 2002; Bralower, 2002; Gibbs et al., 2006). On shallow-water carbonate platforms, the rapid diversification of larger benthic foraminifera has been related to the PETM (Orue-Etxebarria et al., 2001; Scheibner et al., 2005). A causal link between the decreased volume of coral reefs and the global warming events of the late Paleocene-early Eocene time interval, particularly the PETM, has been frequently suggested (Scheibner and Speijer, 2008a, b), based on comparison with modern coral reef system responses to ongoing increase of sea-water temperature. Such an actualistic approach is not fully convincing, because what is happening today is much more than bleaching, and includes increasing temperature, ocean acidification, nutrient loading, increased (and increased variability in) short-wavelength radiation caused by stratospheric ozone depletion and coastal development (i.e., fluctuating delivery of photo-protective tannins to coastal waters), transport of microbes worldwide (e.g., Hallock, 2005 and references therein). A major difference is that modern perturbations are not occurring in an ocean with

high calcium concentrations (e.g., Pomar and Hallock, 2008). Finally, there are great differences between modern and early Paleogene coral assemblages. For instance, *Acropora*-dominated communities that greatly promote the rate of modern reef growth are a relatively recent “invention” (Veron, 2000) with *Acropora*-dominated assemblages virtually absent until the end of the Early Miocene (McCall et al., 1994). These assemblages can be hardly compared with any of the early Paleogene coral communities. However, since the 1970s, acroporid species in the Caribbean have experienced extreme and accelerating declines estimated at 90–98% (e.g., Aronson and Precht, 2001). Modern Caribbean might represent a relatively good model for the Tethys in the early Paleogene.

The reduced reef-building potential of early Paleogene z-corals (Scheibner and Speijer, 2008b), not mirrored by a decline of diversity (e.g., Rosen, 2000), and the nature of these communities that survived the most intense global warming event of the last 50 My, deserve a more detailed study. To tackle this issue we critically screened and synthesized the published literature with the aim to document the main features and changes characterizing the coral assemblages throughout the mid Paleocene-early Eocene time span and to investigate the possible responses to rapid and frequent environmental changes. These questions have been addressed during our study of coral communities from the Adriatic Carbonate Platform (SW Slovenia), where unexpected diverse coral assemblages characterized late Paleocene microbialite-coral mounds (Zamagni et al., 2009), and from the Minervois region (SW France), where early Eocene diverse non-reef building coral assemblages thrived in deltaic, turbiditic shallow-water settings (Zamagni and Mutti, 2007). Based on the present study, we suggest that the evolution of these early Paleogene corals was a multi-step process triggered by the progressive expansion of shallow-water settings characterized by enhanced nutrients and sediment load associated with unfavorable seawater composition (mainly acidification of shallow waters). These conditions might have reduced coral calcification rates limiting their possibility to build permanent reef structures. Nonetheless, coral assemblages maintained relatively high diversity and shifted toward assemblages dominated by sediment/nutrient tolerant forms.

2. Terminologies

Numerous definitions of coral reefs, reef frameworks, reef communities exist in the literature (for a review of terminology see, for example, Riegl and Piller, 2000). According to Riegl and Piller (2000), the term reef is used in this work to describe the development of three-dimensional, biologically influenced buildups of coral framework and carbonate sediments. The use of the term framework follows Fagerstrom (1987) as denoting a mass of colonial, intergrown skeletal organisms. A further distinction is between coral-algal patch-reefs as small buildups of coral-algal framework, ecologically uniform in contrast to coral reefs which are biogenic complex characterized by a distinct vertical zonation displayed by the reef-building organisms. Coral-bearing mound is used here to define carbonate bodies consisting of mud (biolastic and/or precipitated in situ) with minor accounts of organic binding and skeletal organism, usually developed in deeper water setting. In these buildups corals are highly subordinated to other skeletal organisms (mainly red algae, microbes, encrusting foraminifera, sponges). The term coral-bearing mound is used here as counterparts of coral reefs. Coral carpets are defined according to Riegl and Piller (2000) as laterally more or less continuous veneers of coral communities, which do not create a distinct three-dimensionality and are ecologically uniform.

3. The early Paleogene and the late Cretaceous corals: something in common

The long-term comparison between coral-reef accretion and coral diversity based on the data from Kiessling and Baron-Szabo (2004) shows that two parameters are closely correlated for all epochs except for the late Cretaceous to late Paleocene-early Eocene interval. During

that interval this relationship appears to be reversed, with a clear decoupling between diversification of corals and coral-reef construction (Fig. 1). After the K–T crisis, which caused ~30% generic extinction of corals (Kiessling and Baron-Szabo, 2004), several important genera with reef-building potential occurred during the mid Danian (Rosen, 2000), with the Paleocene corals being more prolific reef builders than their latest Cretaceous counterparts (Kiessling and Baron-Szabo, 2004). Although coral reefs remained rare for most of the Paleogene in terms of absolute recorded numbers, the volume of reefs produced by corals increased during the Paleocene (Kiessling and Baron-Szabo, 2004). The volume dropped dramatically in the early Eocene, and climbed again sharply in the late Oligocene (Kiessling and Baron-Szabo, 2004; Kiessling and Simpson, 2011) (Fig. 1). This sharp decline during the early Eocene, however, was associated with a continuous increase of the coral community diversity throughout the Paleogene (Rosen, 2000; Kiessling and Baron-Szabo, 2004) (Fig. 1). The evolution of late Cretaceous reef systems is not a focus of this work, however, a brief consideration of that time period helps to highlight some aspects in the evolution of the early Paleogene corals. Late Cretaceous shallow tropical shelves were mainly dominated by rudist bivalves as reef-builders, with corals that rarely achieved rock-forming abundance (e.g., Johnson et al., 2002). Despite this dominance, many studies showed that diverse coral assemblages (often dominated by forms tolerant to low-light levels and high sedimentation rates such as *Actinacis*, Bosellini, 1998) and rudists coexisted in the same bioconstructions (e.g., Sanders and Baron-Szabo, 1997; Skelton et al., 1997; Grötz, 2003) with both groups often showing benefits from this coexistence. Ecological competition between corals and rudists existed (e.g., Kaufmann and Johnson, 1988). Physicochemical environmental conditions (e.g., seawater chemistry, sedimentation and resuspension rates; Sanders and Baron-Szabo, 1997; Skelton et al., 1997; Stanley and Hardie, 1998), favored the dominance of rudists in the reef development.

Studying the early Paleogene coral communities, which seem to share characteristics with the Late Cretaceous coral communities, might help to elucidate the ecological requirements of fossil coral communities developed in warm oceans of a greenhouse world.

4. Material and methods

To tackle the issue of the evolution of the early Paleogene coral fossil community, we collected a broad database from the Tethys, the Atlantic, and the Caribbean realms from low- to mid-latitude carbonate settings. The earliest Paleocene is characterized by a gap in the

fossil record of coral reefs, with the occurrences of early Danian corals represented by azooxanthellate forms from high latitudes (Kiessling and Baron-Szabo, 2004), and thus is not included in this work. After screening the available literature we collected data from 27 localities (Tables 1 and 2) with early Paleogene coral occurrences spanning the interval from the middle Paleocene to the early Eocene. This list of studies represents the sum of current knowledge and it was integrated with our new data from SW France (Minervois region) and published data from SW Slovenia (Zamagni et al., 2009). The stratigraphic ranges of these studies are plotted in Fig. 2 together with their paleogeographic positions shown in Fig. 3. In Tables 1 and 2 the main information for each locality is summarized. Composite data sets are especially susceptible to biases created by uneven sampling, inadequate systematic, reduced morphological and/or sedimentological descriptions. In addition, sampling and identification of fossil taxa are often linked to coral preservation and diagenesis. This is partly related to the relatively poor preservation potential associated with coral aragonite skeletons. In compiling such a database it becomes evident that even though coral facies are important components in a particular locality, they are often poorly described in terms of morphology and systematic, compared for instance to foraminiferal assemblages. Additionally, the age of coral-bearing facies is often difficult to constrain due to the lack of stratigraphical biomarkers within these facies. Unless biostratigraphic markers are well preserved (mainly larger benthic foraminifera) or other kinds of age constraints are available, precise stratigraphic positioning of coral facies and chronostratigraphic correlations remain problematic. Therefore, to construct Fig. 2 we had to critically tune the age, depositional settings, coral frame-building capacity, coral morphology, and interaction with other bioconstructors. The age assessment was mainly based on determination of larger benthic foraminifera index species. In most studies a more precise age assessment is possible but in others the exact time frame is less certain. In the Tethyan realm the biostratigraphic scheme of Serra-Kiel et al. (1998) has been used, with the regional Ilerdian stage representing the lowermost Eocene according to Scheibner et al. (2005). This stage was introduced for marine deposits of the Tethyan realm for which no marine time equivalent in northern Europe exists (Hottinger and Schaub, 1960).

For the compilation of the different studies a uniform time frame had to be established, as the studies adopt various age/epoch definitions. For example, the Paleocene is in some instances only subdivided into Danian and Thanetian and in other studies the Paleocene also includes the Ilerdian, or no subdivision into shallow benthic zones exists

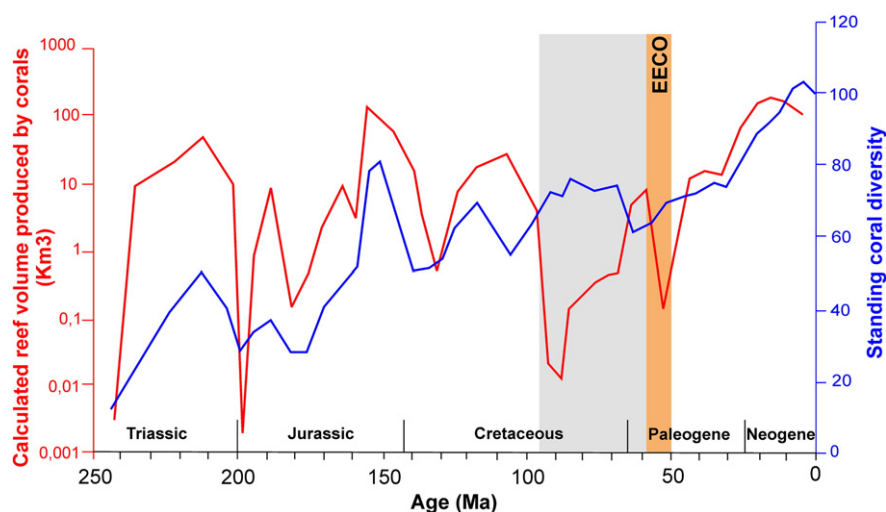


Fig. 1. Comparison between the global preserved reef volume constructed by corals (red line, note logarithmic scale) and the standing diversity of scleractinian coral genera (blue line) during the Mesozoic and Cenozoic. EECO: Early Eocene Climatic Optimum, marked by orange field. The gray field marks the time interval when the relationship between diversity and reef productivity appears reversed. Modified from Kiessling and Baron-Szabo (2004).

Table 1
Mid-late Paleocene coral occurrences (numbers refer to those in Figs. 2 and 3a, b).

Tethyan realm						
Locations (paleolatitude)	Coral time span/Formation	Coral diversity and morphology	Associated biota	Coral occurrences and depositional settings	Notes	References
1) N Calcareous Alps (43°N)	Thanetian/Angerber Beds	No information	Encrusting red algae and encrusting foraminifera	Shallow-water coral–algal reef complex (Alpine–Carpathian reef belt) forming a fringing-reef	No subdivision into SBZ. Thanetian is considered mid Paleocene. Ilerdian is considered late Paleocene. Thanetian age (SBZ3–4 likely) is indicated by LF occurrences (<i>Glomalveolina primaeva</i> and <i>Glomalveolina levis</i>). Taxonomy of Austrian scleractinian corals from K–T boundary to the Miocene. Paleocene corals, no major information about the age	a) Moussavian (1984) b) Baron-Szabo (2004)
2) West Carpathians, W Slovakia (43°N)	Paleocene	<i>Actinacis reussi</i> , <i>Heterocoenia bacellaris</i> , <i>Multicolunmastraea cyathiformis</i> , <i>Stylocoenia montium</i> , <i>Acropora</i> sp., <i>Astrotopora auvertiaca</i> , <i>A. hexaphylla</i> , <i>Goniatrea tenera</i> , <i>Paraplacocoenia orbignyana</i> , <i>Haimesastraea conferta</i> , <i>Oculina becki</i> , <i>Falksephyllia</i> , <i>Alveopora</i> sp., <i>Pachygyra savii</i> , <i>Agathiphyllia cf. blaviensis</i> genus <i>Actinacis</i> dominant in the reef, branching corals in the lagoon	Encrusting red algae, encrusting foraminifera, bryozoans	Shallow-water coral–algal reef complex (Alpine–Carpathian reef belt) forming a fringing-reef, small patch reefs in the lagoon	LF indicate Danian (small <i>Miscellanea</i>) up to Thanetian (<i>Glomalveolina primaeva</i> and <i>Miscellanea juliettae</i> prove SBZ3; <i>Operculina azilensis</i> prove SBZ4)	Köhler et al. (1993)
3) Adriatic Carbonate Platform (SW Slovenia) (38°N)	Danian/Selandian	<i>Dendrophyllia dendrophyllodes</i> , <i>Rhizangia</i> sp., <i>Siderastraea</i> sp., <i>Haimesastraea peruviana</i> , <i>Dendrophyllia candelabrum</i> , <i>Stylocoenia montium</i> , <i>Actinacis cognata</i> , <i>Goniopora elegans</i> , <i>Litharaea subepithecata</i> , <i>Plocophyllia carstica</i>	Red algae, benthic foraminifera	Small shallow-water coral–algal patch-reefs dominated by dendroid and phaceloid corals	Danian/Selandian correspond to SBZ1–2	a) Turnšek and Drobne (1998); Drobne et al. (1988); Jurkovešek et al. (1996)
	Thanetian	<i>Dendrophyllia</i> sp., <i>Goniopora</i> sp., <i>Stylocoenia neutra</i> , <i>Rhizangia padricensis</i> , <i>Pironastrea discoides</i> , <i>Astraeopora pseudopanticea</i> , <i>Astrocoenia bistellata</i> , <i>Oculina conferta</i> , <i>Orbignygyra</i> sp., <i>Goniopora hpeljensis</i> , <i>Litharaea websteri</i> , <i>Mesomorpha</i> sp.	Red algae, larger benthic foraminifera	Shallow-water coral–algal patch-reefs dominated by massive corals	Thanetian corresponds to SBZ3–4	a) Turnšek and Drobne (1998); Drobne et al. (1988); Jurkovešek et al. (1996); Jurkovešek (2008)
	Late Thanetian/Trstelj Formation	Mainly massive and encrusting forms together with branching and ramose forms. <i>Astrocoenia gibbosa</i> , <i>Stylocoenia neutra</i> , <i>Madracis</i> , <i>Astrotopora esperanzae</i> , <i>Bacarella vipavica</i> , <i>Dendrophyllia candelabrum</i> , <i>Rhizangia padricensis</i> , <i>Oculina becki</i> , <i>O. conferta</i> , <i>Pachygyra savii</i> , <i>Plocophyllia carstica</i> , <i>Actinacis cognata</i> , <i>Goniopora elegans</i> , <i>Goniopora</i> sp., <i>Litharaea</i> sp.	Microbes, encrusting red algae, encrusting foraminifera, bryozoans	Coral-microbialite mounds developed at intermediate water depth (mid ramp). Corals thickly encrusted by microbialites	Age defined by the association with larger benthic foraminifera typical the SBZ4 (<i>Assilina azilensis</i> , <i>A. yettae</i>)	b) Zamagni et al. (2009)
		Coral dimensions ranging between few centimeters and less than 30 cm				

(continued on next page)

Table 1 (continued)

Tethyan realm												
Locations (paleolatitude)	Coral time span/Formation	Coral diversity and morphology	Associated biota	Coral occurrences and depositional settings	Notes	References						
4) Pyrenees (Spain) (38°N)	Danian	Up to 19 coral taxa with variable morphologies (domal, laminar, branching, and encrusting). Common corals in the reef core: <i>Actinacis cognata</i> , <i>Rhabdophyllopsis alloiteani</i> , <i>Placocoeniopsis kazi</i> , <i>Cladocora</i> sp., <i>Oculina</i> sp., <i>Dendrophyllia</i> sp., <i>Astrocoenia</i> , <i>Goniopora</i> , <i>Astreopora</i> , <i>Agathiphyllia</i> , <i>Mesomorpha</i> , <i>Montastrea</i> . Fore reef with <i>Actinacis cognata</i> , reef crest with <i>A. cognata</i> , <i>Goniopora</i> , <i>Pachygyra</i> , <i>Astrocoenia</i> . Coral dimensions ranging between few centimeters and 50 cm. Occasionally up to 1.5 m in diameter Mainly tabular–laminar and branching corals. Reef core: <i>A. cognata</i> , <i>Goniopora</i> , <i>Litharaca</i> , <i>Rhizangia</i> , <i>Dendrophyllia</i> , <i>Cladocora</i> , <i>Agathiphyllia</i> . Inter-reef facies and reef crest/back reef with isolated knobs of <i>A. cognata</i> , <i>Goniopora</i> , <i>Agathiphyllia</i> Colonial corals	Encrusting red algae and foraminifera	Three reef growth phases. First two phases (Da-1 sequence, lower-middle Danian) characterized by small coral–algal patch-reefs dominated by corals (inner platform). The third phase (Da-2 sequence, upper Danian) characterized by barrier reef formation		a) Baceta et al. (2005)						
6) Majella (Italy) (35°N)	Danian–Early Thanetian/S.Spirito Formation	<i>Actinacis cf. cognata</i> , <i>Actinacis</i> sp., <i>Actinacis cognata</i> , <i>Goniopora</i> sp., <i>G. elegans</i> , <i>Cladocora</i> sp., <i>Polytrema</i> sp., <i>Dendrophyllia candabrum</i> , <i>Stylocoenia montium</i> , <i>Rhizangia</i> sp. <i>Actinacis cf. cognata</i> , <i>A. barretti</i> , <i>Actinacis</i> sp., <i>Goniopora</i> sp., <i>Cladocora</i> sp., <i>Polytrema</i> sp., <i>Stylocoenia</i> sp., <i>Stylocoenia neutra</i> , <i>Rhizangia padricensis</i> , <i>Alveopora</i> sp.	Dominant encrusting red algae, common bryozoans and encrusting foraminifera	Two main reef growth phases (Th-1 sequence, early to middle Thanetian in age, SBZ3) with development of low-relief algal–coral banks. Deeper part of the photic zone		a) Baceta et al. (2005)						
	Late Thanetian	Colonial corals	Dominant encrusting red algae, common bryozoans and encrusting foraminifera	Coral–algal boundstone–rudstone, with corals encrusted by red algae and foraminifera deposited at intermediate water depth (deeper part of the photic zone) Small shallow-water coral–algal patch-reefs dominated by crustose, dendroid, and columnar corals	Coral occurrence in the Campo section corresponds to Th-2 sequence in Baceta et al. (2005), with a depositional age corresponding to SBZ4 Studies based on redeposited reefal blocks	b) Scheibner et al., 2007						
7) Ionian Islands (32°N)	Thanetian	No information	Red algae, larger foraminifera	Shallow-water coral–algal patch-reefs likely forming a small barrier	Studies based on redeposited reefal blocks. Larger foraminifera described by the authors indicate deposition during SBZ3 (<i>Cribrulimitina carniolica</i> , <i>Fallotella alavensis</i> , <i>Idalina syriarica</i>) and SBZ4 (<i>Ramkothalia cf. sindensis</i>) Deposition during the SBZ3 and SBZ4 which are not differentiated	a) Moussavian and Vecsei (1995) b) Vecsei and Moussavian (1997)						
8) North to central Turkey (30°N)	Selandian–Thanetian	No information	Larger benthic foraminifera, red algae	Corals boundstones together with red algae	Biostratigraphy and systematic of foraminifera	Özgen-Erdem et al. (2005)						
9) North Iraq (Kurdistan) (22°N)	Late Paleocene/Sinjar Formation	Dendroid corals, no information about diversity	Encrusting red algae, larger benthic foraminifera	Algal–coral bank reefs dominated by red algae, corals subordinated to form framework. Intermediate depth, below the fair-weather wave base	The occurrence at the base of the succession (spanning the late Paleocene–early Eocene interval) points to a Late Paleocene age (likely SBZ3)	Daod (2009)						
10) Eastern Desert (Galala Mountains, Egypt) (20°N)	Late Selandian–early Thanetian	Dendroid, meandroid, and ceroid corals	Encrusting red algae	Coral–algal patch-reefs at the platform margin	Deposition during the SBZ3	Scheibner et al. (2003)						

11) Sirte Basin (Libya) (20°N)	Late Paleocene	No information	No information	Shallow-water coral–algal bioconstructions	It is impossible to establish a more precise age for the reef construction since larger foraminifera index species are not mentioned. Large nummulitids associated to the reefal facies are mentioned which might indicate SBZ3/SBZ4 as depositional age. Reefal age formation might correlate with the SBZ3 and SBZ4	Terry and Williams (1969)
12) Western Desert (Egypt) (19°N)	Thanetian/Dakhla Formation	<i>Siderastrea</i> sp., <i>Caulastrea</i> sp., <i>Favia</i> sp., <i>Platygrya</i> sp., <i>Actinastrea</i> sp.	Massive and ramose morphologies. <i>Astrocoenia spongilla</i> , <i>A. aff. decaphylla</i> , <i>A. kurkurensis</i> , <i>Astrocoenia</i> sp., <i>Siderastrea</i> sp., <i>Dimorphastrea iradians</i> , <i>Leptoria laxa</i> . L. cf. <i>paucis</i> , <i>Monastrea</i> sp., <i>Pachygyra savii</i> morphologies. <i>Astrocoenia spongilla</i> , <i>A. Kurkurensis</i> , <i>Cyathoseris</i> sp., <i>Siderastrea scotica</i> , <i>Actinacis cognata</i> , <i>Cladocora tenuis</i> , <i>Agathiphyllia</i> sp.	Chain of small shallow-water patch-reefs	Reefal age formation might correlate with the SBZ3 and SBZ4	a) Data from http://paleodb.org Original reference: Barthel and Herrmann-Degen (1981) b) Schuster (1996)
	Late Danian/"Abu Tartur" Formation	No information	Encrusting red algae and serpulids common	Shallow-water small coral patch-reefs (less than 20 m water depth)		b) Schuster (1996)
	Thanetian/Kurkur Formation	Massive, ramose and encrusting morphologies. <i>Astrocoenia spongilla</i> , <i>A. Kurkurensis</i> , <i>Cyathoseris</i> sp., <i>Siderastrea scotica</i> , <i>Actinacis cognata</i> , <i>Cladocora tenuis</i> , <i>Agathiphyllia</i> sp.	Corals encrusted by red algae, serpulids and bryozoans	Coral knobs in high turbidity/nutrient near-shore setting		b) Schuster (1996)
	Thanetian/"Abu Tartur" Formation	<i>Oculina</i> sp., <i>Cladocora prolifera</i> , <i>Madracis densa</i> , <i>Dendrophyllia</i> sp., few fragments of massive ceratoids and meandroid species	Corals encrusted by diverse red algal association	Dendroid coral patch-reefs in shallow-water, high nutrient setting		b) Schuster (1996)
13) SW Iran (Zagron Basin) (18°N)	Thanetian/Garra Formation	No information	Corals encrusted by diverse red algal association	Algal buildups with rare coral fragments and rodolith beds	These buildups follow the dendroid coral facies	b) Schuster (1996)
	Early Thanetian/ Taleh Zang Formation	Colonial, massive corals	Encrusting red algae and foraminifera	Coral–algal bioconstructions in a mid ramp setting	Corals occur during the SBZ 3 based on distribution of larger benthic foraminifera	Bagherpoura and Vaziria (2011)
15) NW India/East Pakistan (5°N)	Danian	<i>Rhabdophyllia barkii</i> , <i>Litharaea epithecata</i>	No information	No information		a) Data from http://paleodb.org Original reference: Duncan P. M. (1880)
	Selandian to Thanetian/Ranikot Formation	<i>Trichosmita medicotti</i> , <i>Stylocoenia maxima</i> , <i>S. vicaryi</i> , <i>S. ranikoti</i> , <i>Montivaltia granti</i> , <i>Trichosmita cristata</i> , <i>Plocophyllia sindiana</i> , <i>P. flabelata</i> , <i>Dictyophyllia hydrorhoroidea</i> , <i>Stephanocoenia micratuberculata</i> , <i>Astrocoenia blanfordi</i> , <i>A. cellulata</i> , <i>A. nana</i> , <i>A. gibbosa</i> , <i>A. ramosa</i> , <i>Siderastrea morloti</i> , <i>Pironastrea indica</i> , <i>Goniopora grandis</i> , <i>G. microscopica</i> , <i>Porites superposita</i> , <i>Pachygyra princeps</i>	No information	Coral reefs	Age assignment based on stratigraphic correlation with NE India (Jauhi and Agarwal, 2001).	a) Data from http://paleodb.org Original reference: Duncan P. M. (1880)
	Paleocene/ Ranikot Formation	Coral diversity high with about 80 species, no information about taxonomy	No information	Coral reefs	Corals thrived during the Paleocene along the western border of the Indian subcontinent. No descriptions of these reefs are given by the authors	b) Sahni and Kumar (1974)
15) Pakistan (Indus Basin) (5°N)	Selandian–Thanetian/ Lockhart and Dungan Formations	Laminar–tabular corals form the framework. No information about coral taxonomy	Green algae, red algae	Shallow-water coral–algal patch-reefs (open lagoon)	Corals thrived during the Paleocene along the western border of the Indian subcontinent. No descriptions of these reefs are given by the authors	c) Afzal et al. (2011)

(continued on next page)

Table 1 (continued)

Tethyan realm						
Locations (paleolatitude)	Coral time span/Formation	Coral diversity and morphology	Associated biota	Coral occurrences and depositional settings	Notes	References
16) Tibet (5°N)	Danian/Zhepure Shan Formation	Pocilloporidae, Poritidae: <i>Goniopora</i> , <i>Alveopora</i>		Coral mainly as nuclei of rhodoids (rhodoids bars) or forming small patch-reefs in shallow subtidal settings	Age of the horizons with corals poorly constrained. Corals occur in the first two members of the Zhepure Shan formation with an approximate age corresponding to SBZ2 and SBZ3	Zhicheng et al. (1997)
17) SE Yemen (5°N)	Late Thanetian-early Ilherdian/Ummer Radhuma Formation	No information		Small patch-reefs	Coral beds occur in correspondence of foraminiferal assemblages pointing to a deposition within the SBZ4 (<i>Ranikothalia</i> sp., <i>Miscellanea</i> spp.) and the early Ilherdian SBZ5/6 (<i>Alveolina</i> spp.)	Pignatti et al. (1998)
18) NW Somalia (0°)	Thanetian/Auradu Limestone Formation	Small subspherical massive or phaceloid coral colonies. <i>Acropora tergestina</i> , <i>Aplophyllia barkai</i> , <i>Astrocoenia gregoryi</i> , <i>A. immersa</i> , <i>Cerepiphyllia tenuis</i> , <i>Cladocora rosicensis</i> , <i>Cycloseris striata</i> , <i>Dendracis</i> sp., <i>Dendrophyllia candelebrum</i> , <i>Paracryathus altus</i> , <i>Stephanocoenia tricononata</i> , <i>Stratogyra savii</i> , <i>Stylococenia ranikoti</i> , <i>Tubicocora ayimeri</i>	Larger and smaller benthic foraminifera, dasycladalean algae	Coral patches scattered in the sediment of a shallow-water low energy inner ramp setting. No biogenic framework	Precise age of the coral facies not defined by the authors. The majority of corals occur in the lower part of the studied section likely pointing to deposition during the SBZ3 and maybe SBZ4	Carbone et al. (1993)
19) Java (0°)	Thanetian/Karangasambung Olistostrome	Colonial corals, 11 species belonging to 9 genera. No more information about coral taxonomy.	Red algae abundant mainly <i>Distichopanax biserialis</i> forming small buildups	Coral-algal buildups likely developed in the deeper part of the photic zone	Jatibungkus limestone olistolith can be broadly considered as Thanetian in age (SBZ3/SBZ4) based on larger benthic foraminifera distributions (<i>Ranikothalia</i> , <i>Miscellanea</i> , rotaliids, and orthophragmines)	Pignatti J.S., pers.comm. (2008); Accordi et al. (2010)
Atlantic/Caribbean realm						
24) Alabama (35°N)	Thanetian/Salt Mountain Limestone	<i>Madracis</i> sp., <i>M. herricki</i> , <i>Cyathoseris valmondasiaca</i> , <i>Oculina</i> sp., <i>Anitilia</i> sp., <i>Cyathoseris eocenica</i> , <i>Actinacis barretti</i> , <i>Dendrophyllia dendrophyllodes</i> , <i>Sideroseris durhami</i> , <i>Stylophora ponderosa</i>	Encrusting red algae, sponges, larger benthic foraminifera, bryozoans	Coral-algal-sponge reef (abundant micritic matrix) with development of different biotic zones. Deposition at intermediate depth	Paleocene is divided into Danian and Selandian corresponding to earliest Paleocene and mid-late Paleocene, respectively	Bryan (1991); Bryan et al. (1997)
25) Paris Basin (40°N)	Danian/Calcaire de Vigny Formation	Reefal limestones built of laminar, encrusting, and bulbous corals (<i>Actinacis</i> sp.), " <i>Dermosmilia</i> " sp., <i>Calamophylloopsis</i> sp.	Encrusting red algae	Coral-algal reefs	Reef limestones occur as olistolith. The authors suggest the existence of a reef complex with internal zonation	Montenat et al. (2002)
26) Patagonia (43°S)	Late Danian/Lefipán Formation	<i>Haimestraea conferta</i> (massive, domal, hemispherical, irregular growth forms)		Coral colonies developed on top of an hardground within conglomerates	Age poorly constrained	Kiessling et al. (2005)

Table 2
Early Eocene coral occurrences (numbers refer to those in Figs. 2 and 3c).

Locations (paleolatitude)	Coral time span/Formation	Coral diversity and morphology	Associated biota	Coral occurrences and depositional settings	Notes	References
1) N Calcareous Alps (43°N)	Early Eocene	No information about coral diversity	Red algae, bryozoans, and encrusting foraminifera dominant forming algal-foraminiferal boundstones and rodolith beds	Isolated colonial corals in shallow-waters together with larger benthic foraminifera (mainly <i>Alveolina</i> spp.) and green algae	Late Ilerdian based on <i>Alveolina</i> species	a) Moussavian (1984)
3) Adriatic Carbonate Platform (SW Slovenia) (38°N)	Ypresian Earliest Eocene (Ilerdian)/Alveolina-Nummulites Limestone Early Eocene?	<i>Stylocoenia bistellata</i> , <i>Actinacis</i> sp., <i>Favia costata</i> , <i>Meandrina angigyrta</i> , <i>M. reticulata</i> , <i>Montastrrea rudis</i> , <i>M. imperatoris</i> <i>Goniopora</i> sp., <i>Coscinaraea</i> sp., ? <i>Rhizangia</i> sp., <i>Astreopora</i> sp. <i>Bacarella vipavica</i> , <i>Actinacis</i> sp., <i>Goniopora</i> sp., <i>Rhizangia</i> sp., <i>Astreopora</i> sp., <i>Alveopora</i> sp., <i>Stratogyra</i> sp., <i>Agathiphyllia</i> sp., <i>Dendrophyllia</i> sp., <i>Glyphastraea</i> sp., <i>Plocophyllia</i> sp. No information	Red algae	Patches of algal-coral bindstones within a succession of nummulite packstones and wackestones Reef-mound/mud mound buildups with corals encrusted by coralline algae and foraminifera crusts and micritic crusts Coral wacke- to boundstones with corals thickly encrusted by acervulinid foraminifera. Deposited in the inner platform setting Coral-algal patch-reefs along carbonate bank margins; reef mounds deeper front of the carbonate bank margins, with red algae dominant; <i>Solenomeris</i> reef mounds	No major information about the age	b) Baron-Szabo (2004) c) Košir (1997)
4) Pyrenees (Spain) (38°N)	Earliest Eocene (Ilerdian)	No information	Larger benthic foraminifera	Coral wacke- to boundstones with corals thickly encrusted by acervulinid foraminifera. Deposited in the inner platform setting	Early Eocene and/or Paleocene clasts in Early Eocene flysch deposits	d) Turnšek and Košir (2004)
5) Pyrenees (SW France) (38°N)	Earliest Eocene (Ilerdian)/Ager, Limiana, Alinya sequences	Coral-algal patch-reef association: <i>Actinacis</i> , <i>Leptoria</i> , favoids, montastreids, <i>Cladocora</i> , siderastreids, <i>Goniopora</i> , <i>Antiguastrea</i> . Coral knobs within bioclastic grain flats: platy <i>Actinacis</i> , siderastreids, <i>Caulastrea</i> , <i>Stylocoenia</i> . Coral mounds: platy <i>Actinacis</i> , siderastreids. <i>Solenomeris</i> reef mounds: platy <i>Actinacis</i> Mainly massive and encrusting forms. <i>Astrocoenia gibbosa</i> , <i>Stylocoenia neutra</i> , <i>Madracis</i> , <i>Astreopora esperanzae</i> , <i>A. auvertiaca</i> , <i>Actinacis cognata</i> , <i>Goniopora</i> sp., <i>Litharrea</i> sp., <i>Porites</i> sp. Coral dimensions ranging between few centimeters and less than 50 cm Coral assemblage dominated by poritids	Larger benthic foraminifera, encrusting foraminifera, encrusting red algae	Coral knobs within high energy inner ramp deposits (mixed carbonate-siliciclastic shoals)	Coral bed within the IL-2 sequence corresponding to SBZ5/6	b) Scheibner et al. (2007)
6) Majella (Italy) (35°N)	Earliest Eocene (Ilerdian)/Calcaires à Alvéolines and Calcaires à Alvéolines et à Algues	No information	No information	<i>Solenomeris</i> reefs (km-sized) and small coral patch-reefs developed in muddy lagoon and inner platform settings. Coral reefs and coral-rich facies represent the substratum for the <i>Solenomeris</i> reefs Coral-algal reef?	Félines-Minervois section. Age based on co-occurrence of coral-bearing limestones and <i>Alveolina</i> limestones (SBZ5–6)	a) Zamagni, J. unpublished data. b) Plaziat and Perrin (1992)
7) Ionian Islands (32°N)	Early to middle Eocene Earliest Eocene	Massive colonial corals	Larger benthic foraminifera	Sparse coral colonies found frequently within the subtidal zone of the inner ramp associated to foraminiferal shoals	Lower to middle Eocene coral-algal reef sediments from displaced boulders within slope limestones of the same age SBZ5-6 are considered Thanetian rather than Ilerdian. Marine sedimentation followed by emersion during the Ypresian	b) Vecsei and Moussavian (1997) Accordi et al. (1998)

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Table 2 (continued)

Locations (paleolatitude)	Coral time span/Formation	Coral diversity and morphology	Associated biota	Coral occurrences and depositional settings	Notes	References
12) Western Desert (Egypt) (19°N)	Earliest Eocene/Esna Formation	Laminar, encrusting and foliaceous corals. <i>Leptoseris</i> sp., <i>Sylocoenia epithecata</i> , <i>Goniopora farafraensis</i>	Larger benthic foraminifera	Coral beds, one on top of foraminiferal accumulations (<i>Nummulites</i> -bank) in turbid/muddy shallow waters	Probably SBZ6 based on larger foraminifera distributions (alveolinitids and nummulitids)	b) Schuster (1996); Wielandt (1996)
	Earliest Eocene/Farafra Formation	Branching and laminar corals. <i>Goniopora elegans</i> , <i>Goniopora farafraensis</i>	Larger benthic foraminifera	Coral biostromes lateral to facies interpreted as seagrasses in restricted muddy lagoonal setting	Probably SBZ6 based on larger benthic foraminifera distributions (alveolinitids and nummulitids)	b) Schuster (1996); Wielandt (1996)
14) Oman (12°N)	Late Paleocene/Early Eocene	<i>Astrocoenia</i> , <i>Siderastraea</i> , <i>Pachygyra</i> , <i>Dendrophyllia</i> , <i>Polytremacis</i>	Coralline algae nodules, larger benthic foraminifera (alveolinitids)	Isolated corals and coral banks in shallow shelf environment	The age of these coral–algal facies is likely early Eocene as suggested by the co-occurrence with abundant alveolinitids	a) Bernecker (2005)
	Mid early Eocene/Jafnayn Formation	Coral debris	Red algae	Coral and red algal-rich nodular packstones–grainstones. Existence of shallow-water patch-reefs providing coral debris is suggested	Age defined as post-Alveolina <i>temprina</i> zone (late Ilerdian)	b) Racey et al. (2005)
15) NW India/Pakistan (5°N)	Early Eocene/Umm Er Radhuma Formation	Coral debris	Red algae dominant to form the “reef” facies (mainly constructed by accumulation of oncoids)		Age for the coral-bearing limestones defined by the co-occurrence of <i>Alveolina</i> and <i>Nummulites</i>	c) Racz (1979)
17) SE Yemen (5°N)	Late Thanetian-early Ilerdian/Ummir Radhuma Formation	No information	Larger benthic foraminifera (alveolinitids), rodoliths	Inner platform		d) Nolan et al. (1990)
20) NE India (5°S)	Earliest Eocene (Ilerdian)/Lakadong Formation	No information	Encrusting red algae and foraminifera, larger benthic foraminifera	Small patch-reefs	Coral reefs retreated during the Eocene to the north	b) Sahni and Kumar (1974)
					Coralline algae and encrusting foraminifera are the dominant bioconstructors	Pignatti et al. (1998)
					Encrusting red algae (corallines) - corals-encrusting foraminifera boundstones developed in deeper mid-uppermost outer ramp setting.	Jauhri et al. (2006)
					Within the Lakadong Formation corals have been found in beds of the <i>Discocyclusina</i> – <i>Ramikoithalia</i> foraminiferal association which correlates with the lower Ilerdian (SBZ5–SBZ6?) identified by the presence <i>A. vredenburgi</i> , the marker fossil of SBZ5. In NE India <i>A. vredenburgi</i> co-occurs with <i>Miscellanea miscella</i> and <i>Ramikoithalia nuttalli</i> . The Lakadong Formation correlates with the Ranikot Formation in Pakistan	
Atlantic/Caribbean realm	21) Barbados (10°N)	<i>Astrocoenia</i> , <i>Favia</i> , <i>Goniopora</i> , <i>Montastraea</i> , <i>Siderastraea</i> , <i>Stylophora</i>	No information	No information		Budd (2000)
	22) Chiapas (18°N)	Early Eocene/Lecheria Limestone Formation	No information	Shallow subtidal depositional setting		Frost and Langenheim (1974)
	23) Jamaica	Early Eocene/Richmond Formation	No information	No information		Budd (2000)

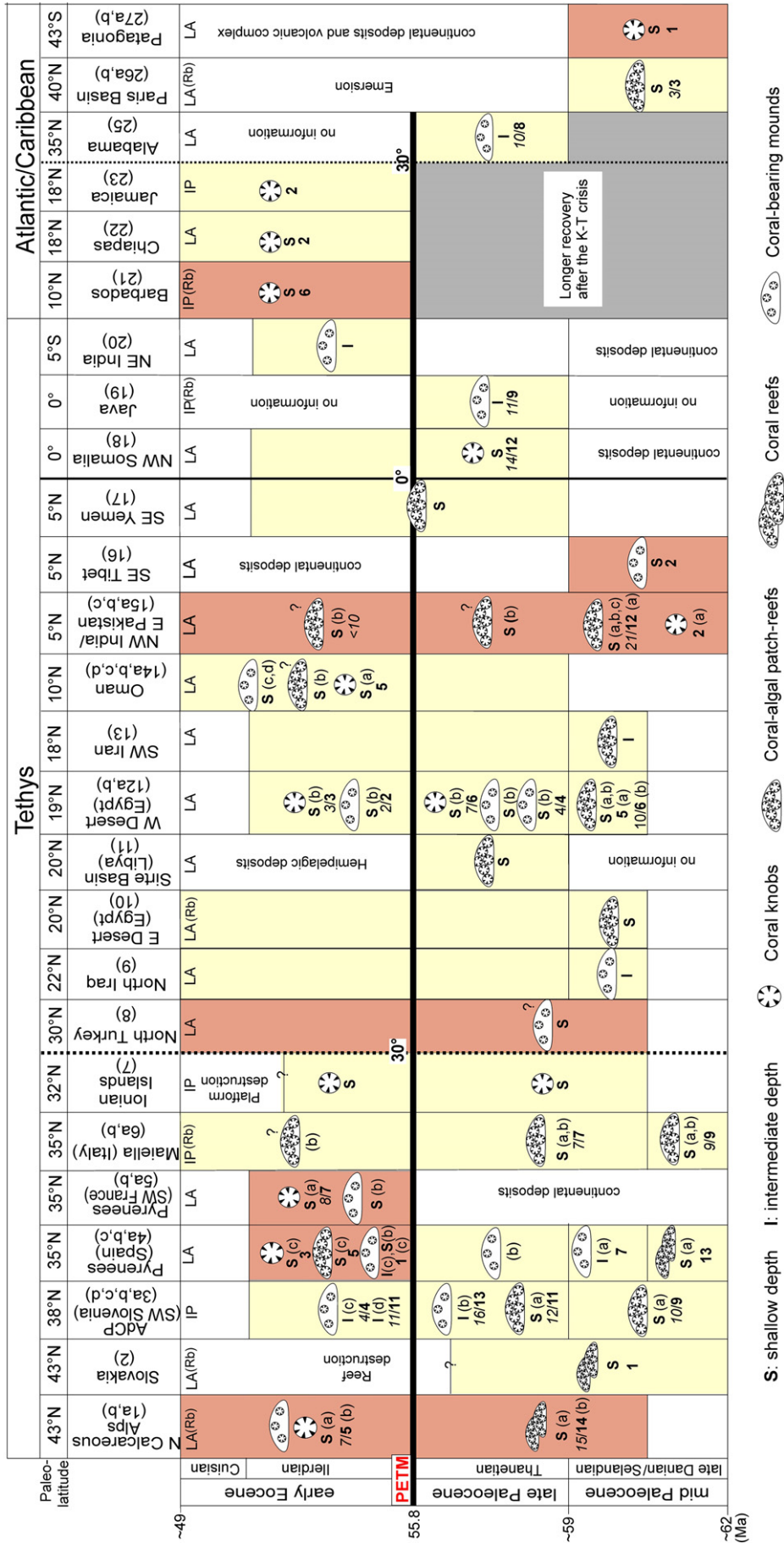


Fig. 2. Stratigraphical and paleogeographic distribution of corals at low and mid latitudes, and their bioconstrucational capacity. Note depositional capacity. Note depositional depths (S shallow; I intermediate depth) defined by the authors or inferred in this study by associated fauna and facies description. Field colors refer to coral-bearing rock composition (yellow: pure carbonate systems, brown: mixed carbonate-siliclastic systems). Coral generic diversity in bold, specific diversity in italics. IP: Isolated Platforms, LA: Land-attached Platforms, Rb: Resedimented blocks. Location numbers refer to those in Fig. 3 and Tables 1 and 2.

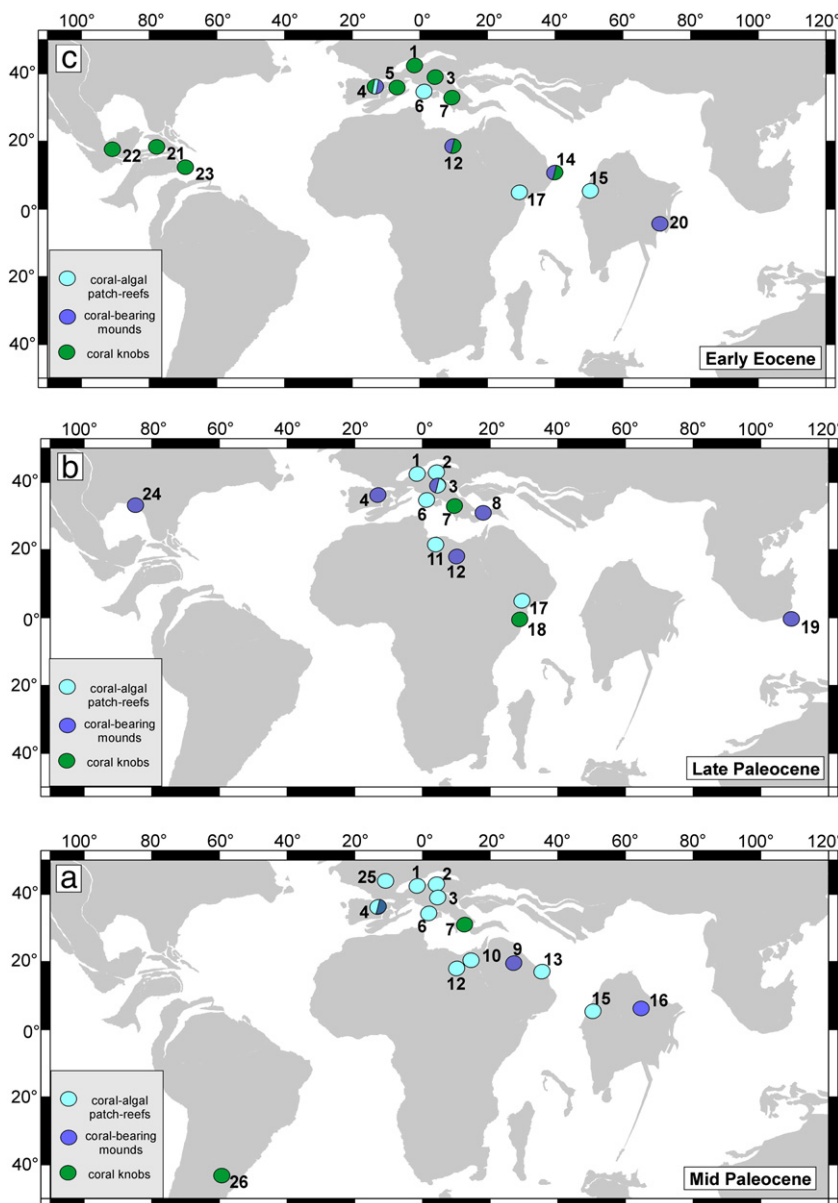


Fig. 3. Global distributions of: a) mid Paleocene, b) late Paleocene, and c) early Eocene coral occurrences, displayed on paleogeographic reconstructions at 55 Ma map (Ocean Drilling Stratigraphic Network online; plate reconstruction data from Hay et al. (1999) and references therein. Numbers refer to those in Fig. 2 and Tables 1 and 2.

or larger foraminifera were not identified. Despite these potential biases important information about coral diversity and change in community compositions can be tracked as shown in this study. Sedimentological and paleoecological evaluations concerning depositional settings (water depths, water energy, and light intensity) were inferred from the combination of hydrodynamic energy estimates (textures) and depth-related components (e.g., algae, foraminifera). We defined as shallow-water depth the inner ramp (above the fair-weather wave base)/inner platform depositional settings as well as the euphotic zone (as defined by Pomar, 2001, commonly corresponding to 20–30 m water depth). Intermediate water depth is usually referred to the mid ramp (above the storm-wave base) setting and/or the meso-oligophotic zone (as defined by Pomar, 2001, lower limit in the 50–100 m depth range).

5. Results: evolution of mid Paleocene-early Eocene coral communities

Even with the uncertainties described above, Fig. 2 highlights some trends in the evolution of early Paleogene coral assemblages (Table 3).

The middle Paleocene (Table 1) was a time when corals dominated the reef community (67% of the coral occurrences, Table 3), producing mainly patch-reefs in shallow-water settings but also reef complexes (Fig. 3a). In the frame of the low-level diversity of earliest Paleogene corals, the middle Paleocene coral assemblages can be considered moderately diverse (up to 14 genera), also according to the criteria developed by Kiessling and Flügel (2002) (those having between 5 and 25 species of corals). Massive, encrusting, and laminar (or platy) forms were common (e.g., *Actinacis*, *Goniopora*, and astrocoeniids) associated with branching forms (e.g., *Dendrophyllia*, *Oculina*, and *Cladocora*)

Table 3
Percentages of various categories of coral occurrences for each time interval.

	Coral-algal patch reefs/barrier reefs	Coral-bearing mounds	Coral knobs
Early Eocene	4 (22%)	4 (22%)	10 (56%)
Late Paleocene	6 (43%)	6 (43%)	2 (14%)
Mid Paleocene	10 (67%)	3 (20%)	2 (13%)

within bioconstructions in euphotic settings around the Tethys. Along the margins of the central Tethys corals formed the Alpine–Carpathian reef belt (loc. 1–2) with development of fringing reefs, while coral–algal patch-reefs occurred in the AdCP (loc. 3), in the Apulian platform (Maiella, loc. 6), and Egypt (loc. 10–12). In the eastern Tethys coral–algal patch-reefs with high diversity occurred in NW India/E Pakistan (loc. 15). In the Pyrenees (Spain, loc. 4), corals formed extended barrier reefs during the late Danian with high generic diversity (Baceta et al., 2005). In other localities corals are present as subordinate components within mounds dominated by calcareous red algae as in N Iraq (loc. 9) and SE Tibet (loc. 16). Interestingly, in high latitude regions such as the Paris basin (40°N, loc. 25) and Patagonia (43°N, loc. 26), corals occurred within coral–algal patch-reef and as coral knobs, respectively.

The transition to the late Paleocene marked a general decrease of frame-building capacity by corals (coral–algal patch-reefs decline to 43% of the coral occurrences, Table 3), which became subordinate to calcareous red algae in forming mounds (coral-bearing mounds in Figs. 2 and 3b and Table 1, 43% of the coral occurrences versus 20% during the mid Paleocene, Table 3). This shift from corals to other framework builders (mainly red algae and to a less extent microbes and foraminifera) is well documented at low (e.g., W Desert, Egypt, loc. 12) and middle latitudes (AdCP, loc. 3; Pyrenees, loc. 4, in this area it occurs a bit earlier than the other localities), both in shallow and moderate water depths. At middle latitudes coral–algal patch-reefs and reef complex were still present (e.g., Alpine–Carpathian reef belt, loc.1–2; Maiella, loc. 6). At low latitudes coral assemblages with moderate diversity (up to 12 genera) occurred as knobs (e.g., W Desert, Egypt, loc. 12; NW Somalia, loc. 18) or associated to other organisms within mounds (Java, loc. 19; Alabama, loc. 25). In some cases coral assemblages show diversity comparable to that of the middle Paleocene (up to 13 genera in the AdCP, Zamagni et al., 2009), while in other localities a decline of diversity is observed (W. Desert, Egypt, loc. 12; Pyrenees, loc. 4; Maiella, loc. 6). Coral fossils are usually thickly encrusted by red algae, encrusting foraminifera, and microbes (AdCP, loc. 3; Pyrenees, loc. 4; W Desert, Egypt, loc. 12; Java, loc. 19; Alabama, loc. 25). In Egypt, for examples, Schuster (1996) described a shift from coral–algal patch-reefs to algal mounds and rhodolith beds with rare, encrusted coral fragments. In these late Paleocene assemblages, laminar and encrusting corals were common, including *Actinacis*, *Goniopora*, and astrocoeniids as dominant forms, together with branching forms (*Stylocoenia*, *Rhizangia*, *Dendrophyllia*, *Oculina*, and *Cladocora*).

In the earliest Eocene coral occurrences and diversity declined (Figs. 2 and 3c, Table 2), representing a short-term reversal within a long-term trend toward increasing diversity (Fig. 1). Corals remained subordinate to red algae and foraminifera within mounds in both shallow and intermediate water depths. In the N Calcareous Alps (loc. 1), coral facies were almost completely replaced by rhodolith facies (Moussavian, 1984). In the Pyrenees (loc. 4–5), *Actinacis* patch reefs were replaced by reefs made by the encrusting foraminifera *Solenomeris* (Plaziat and Perrin, 1992). In other localities corals still occurred within algal mounds (e.g., Oman, loc. 14; NE India, loc. 20). Importantly, a shift toward coral assemblages dominated by few species resistant to high turbidity can be observed. *Goniopora* is a typical representative (both branching and massive morphologies depending from the depositional settings), together with *Actinacis* (mainly as laminar-plate forms). These genera became dominant forming knobs (56% of the coral occurrences) within very shallow-water, high-energy settings (e.g., Pyrenees, loc. 4–5; Oman, loc. 14; Ionian Island, loc. 7), or within muddy lagoonal deposits (e.g., W Desert, Egypt, loc. 12). Interestingly, z- or z-like corals occurred for the first time in the Cenozoic in the Caribbean realm as isolated knobs (loc. 21–22–23). The distributions of mid Paleocene–early Eocene corals point to colonization of broad range of habitats. In association with this habitat expansion, a progressive reduction in capacity to form framework occurred. As shown in Table 3, this process is

reflected in the shift from mid Paleocene occurrences mainly represented by coral–algal patch reefs to coral-bearing mounds common during the late Paleocene and finally to early Eocene coral knobs typical of very shallow-water settings. A general feature which characterizes the corals throughout the early Paleogene time is the reduce colony dimensions usually in the range of centimeters (e.g., AdCP, loc. 3; Pyrenees, loc. 4–5).

6. Discussion

6.1. Diversity trends in early Paleogene shallow-water biocalcifiers

During the late Paleocene to early Eocene, other groups of phototrophic marine organisms underwent rapid radiations. An overview of the evolution of these biocalcifiers can help to better understand the paleoecology of the early Paleogene coral communities. The Paleocene shallow-water benthic communities where characterized by a rapid diversification of calcareous algae (Fig. 4). Starting from the Maastrichtian across the whole Paleocene and the early Eocene, calcareous coralline algae expanded rapidly, with a peak during the early Eocene, followed by a temporary decline during the middle Eocene (Aguirre et al., 2000). This expansion contradicts the hypothesis that framework building was reduced due to lack of binders. Modern biofacies dominated by coralline red algae are known to develop extensively under lower temperature, nutrient-rich, reduced-light conditions (e.g., Gulf of California, Halfar et al., 2004; SE Asian platforms, Wilson and Vecsei, 2005), and large depth range (from very shallow, high water energy environments up to 270 m, e.g., Littler et al., 1986). The expansion of calcareous red algae, starting from the late Paleocene, could have been related to a biotic community replacement driven by changes in sediment/nutrient load, rather than a simple facies shift related to a change in relative sea level. Short-term pulses of relative sea level rise cannot be excluded at that time (e.g., Sluijs et al., 2008a). However, rapid and high amplitude sea-level fluctuations are not expected because the polar regions are considered to have been mostly ice-free. We suggest that during the late Paleocene–early Eocene, a general increase, as well as frequent fluctuations, of nutrients forced corals to compete for substrate with more nutrient-opportunistic sessile organisms, mainly red algae but also encrusting foraminifera and microbes (e.g., *Solenomeris* reefs in the Pyrenees, Plaziat and Perrin, 1992; coral-microbialite mounds in the AdCP, Zamagni et al., 2009). The increase of nutrients, likely in the range of mesotrophic conditions, combined with heavy grazing, suggested by progressive increase of bioerosion during the early Paleogene (Perrin, 2002), might have favored the coralline algae expansion. Elevated nutrients without heavy grazing would have promoted filamentous and macroalgal takeover of the substratum to the detriment of both coral and coralline algal communities (e.g., coral–macroalgal phase shift in the Caribbean, Hughes, 1994). We do not have clear evidence that where algae have replaced corals, algal bloom were the cause, and not simply the consequence, of coral mortality due to changes of water quality (see McCook et al., 2001 for a review about competition between corals and algae). In Egypt, however, Schuster (1996) described enhanced bioerosion and overgrowth of corals by red algae occurring prior to the main shift from coral growth to rhodoliths and algal-mound accretion, suggesting that algal spreading might have been the consequence of declining condition favorable to coral growth. Similarly, in the AdCP fluctuation in nutrients and turbidity promoted repeated shift from corals to microbialite/encrusting foraminifera. This processes lead to the accretion of microbialite–coral mounds, with corals probably declining prior to microbial encrustation (Zamagni et al., 2009).

Calcified green algae (dasycladaleans) experienced the most rapid diversification in their evolutionary history, culminating with the highest number of genera for the Cenozoic during the late Paleocene, followed by a decline during the early Eocene (Aguirre and Riding, 2005). This decline coincided with the highest levels of pCO₂ in the

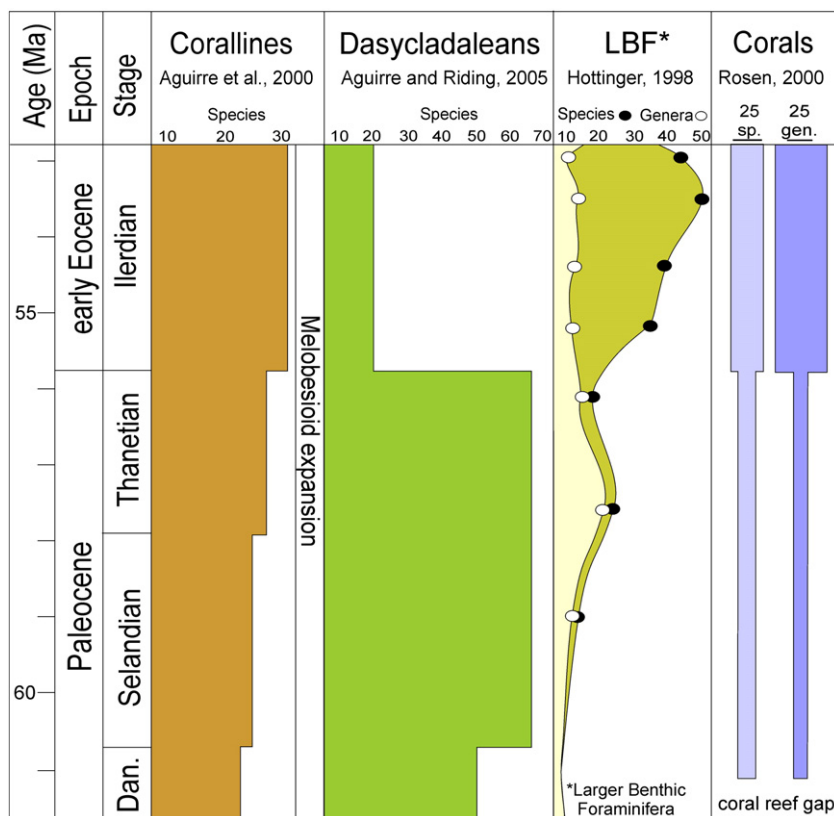


Fig. 4. Diversity trends of calcareous algae (corallines and dasycladaleans), larger benthic foraminifera and corals during the early Paleogene.

Cenozoic, and might be related to a biocalcification crisis induced by perturbation of the aragonitic saturation state of sea water (e.g., Kleypas and Yates, 2009).

Larger benthic foraminifera increased progressively in diversity and size starting from the late Paleocene throughout the early and middle Eocene (Hottinger, 1997, 1998). Scheibner et al. (2005) suggested that the competition between larger benthic foraminifera and corals might have found the foraminifera winner, being better adapted to extreme high temperatures. Hallock and Pomar (2009) interpreted the Paleogene diversification of larger benthic foraminifera as a response to warmer deep sea water combined to minimal temperature gradient between the thermocline and the deep sea. Alternatively, the early Paleogene larger benthic foraminifera might have been better adapted to thrive under frequent fluctuations of nutrients, as suggested by studies of living representatives and feeding experiments (e.g., Langer and Hottinger, 2000; Hallock et al., 2003; Renema, 2008). Additionally, larger benthic foraminifera secrete calcite shells and recent studies have demonstrated that they were not impacted adversely by the ocean acidification that might have characterized the PETM (Robinson, 2011). However, experimental studies on benthic foraminifera have demonstrated the existence of a strong biological control in their biomineralisation processes, with seawater chemistry exerting a relatively weak effect (e.g., Erez, 2003; Bentov and Erez, 2006).

6.2. Distribution of reef coral communities and paleoceanographic changes

6.2.1. Sea-surface temperatures

The progressive loss of reef-building capacity by the corals throughout the mid Paleocene-early Eocene has been repeatedly discussed as mainly related to global high sea-surface temperatures (SST) (e.g., Scheibner and Speijer, 2008a, b; Kiessling and Simpson, 2011). Elevated SST (Fig. 5), up to 33 °C–34 °C during the PETM

(Zachos et al., 2006) and the EECO (Pearson et al., 2007), might have been detrimental for reef development. Nonetheless, this study shows that throughout the early Paleogene corals continued to colonize a broad range of settings, without clear bias toward deep waters and high latitudes, as possible refugia against high SST and high solar irradiance (Figs. 2 and 3). Bleaching (loss of symbionts or chlorophyll pigments, Brown, 1997) can be induced by a diverse range of stress factors such as low salinity, low temperature, high sedimentation, aerial exposure, and cyanide exposure. At present, the combination of high irradiance and anomalously warm sea surface temperatures seems to be the primary triggering condition for large-scale mass bleaching events (reviewed by Hoegh-Guldberg, 1999). However, modern bleached and unbleached corals are often encountered side by side (e.g., Loya et al., 2001; Hughes et al., 2003), with different species responding quite differently to bleaching (e.g., Marshall and Baird, 2000; Jokiel and Brown, 2004). Even the same species can respond differently, depending upon its symbionts, or the same colony, depending upon symbiont distributions and exposure to light (Rowan, 2004; Berkelmans and van Oppen, 2006; Abrego et al., 2008). Bleaching susceptibilities may have changed over time as a result of ongoing adaptation to adverse environmental conditions (e.g., evolution of temperature tolerance, Hughes et al., 2003) with the development of alternative life strategies at times of prominent climate changes, as suggested by recent work on the effects of thermally fluctuating environments on coral thermal tolerance (e.g., Jones et al., 2008; Oliver and Palumbi, 2011). Two main mechanisms may occur to shift the thermal tolerances of corals and their endosymbionts: 1) coral adaptation via natural selection for heat-tolerant lineages of the coral leading to a community compositional shift toward a more thermally-tolerant suite of coral species; 2) natural selection for heat-tolerant lineages of the algal endosymbiont harbored by the coral host. Concerning the first mechanism, the common occurrences in the early Paleogene, especially in the early Eocene fossil record, of massive corals belonging to the family Poritidae (especially

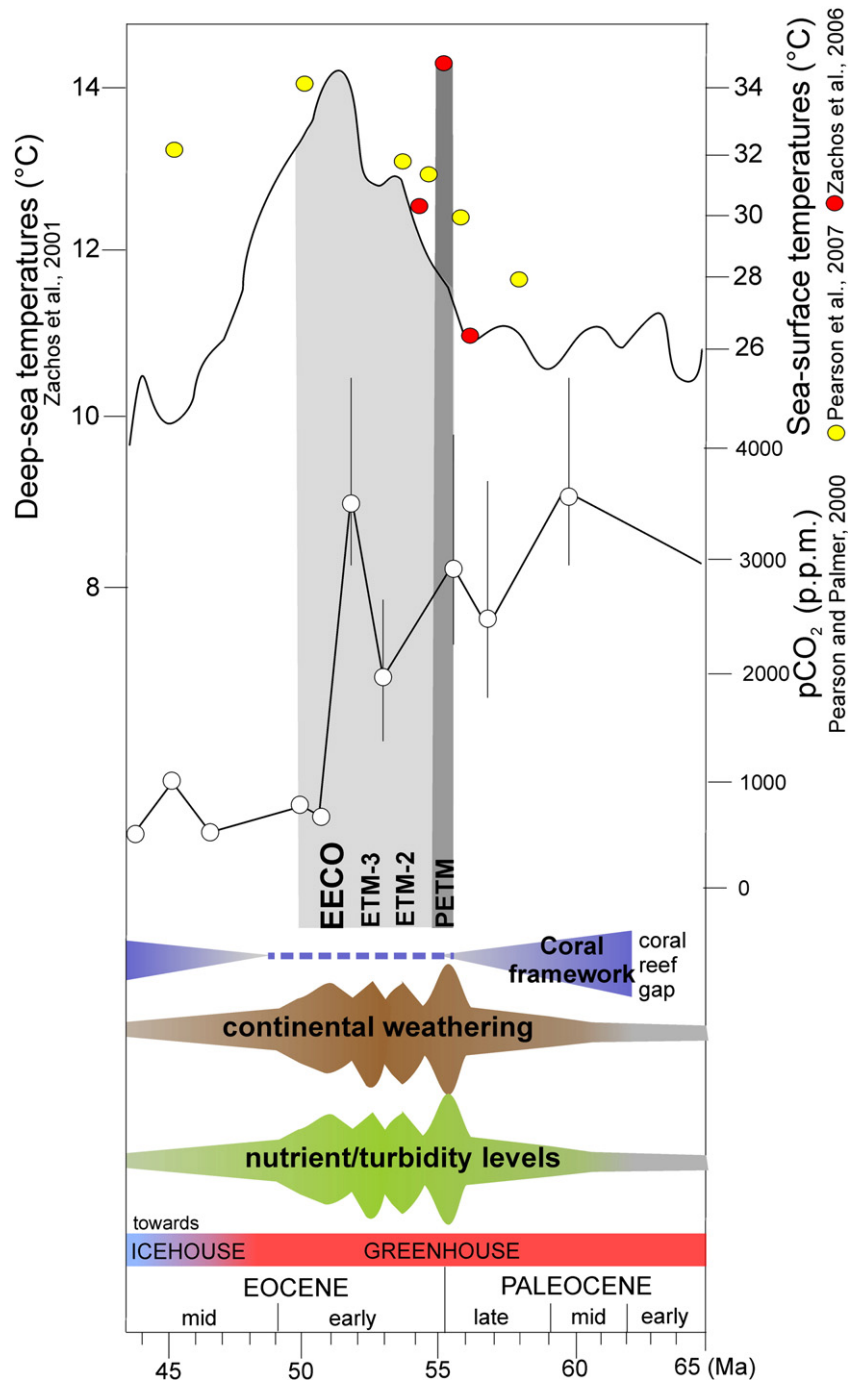


Fig. 5. Key early Paleogene climatic events (Early Eocene Climatic Optimum, EECO, culminating at ~51 Ma; ETM-2/Elmo event at ~53.6 Ma, ETM-3/X event at ~52.5 Ma, Paleocene-Eocene Thermal Maximum, PETM, at ~55.5 Ma) in relation to paleoceanographic changes in shallow waters. In this model the evolution of coral communities is correlated with increase of nutrient/sediment delivery and CO₂ buildup, with maximum reduction in frame-building capacity during the early Eocene. The fluctuating nature of continental weathering rate and nutrient levels are predicted consequences of the model presented in this work.

Goniopora and *Actinacis*) point to a selection toward heat-tolerant communities at this time. Today, corals of the family Poritidae appear as the less susceptible to bleaching with *Goniopora* being one of the most resistant taxa to thermal stress (e.g., Marshall and Baird, 2000). The second mechanism was likely not so important in the evolution of some thermal tolerance in the early Paleogene corals. According to the diversification of *Symbiodinium* zooxanthellae clades reported by Pochon et al. (2006), at this time the diversity of the algal endosymbionts was low.

Thermal stress alone, however, does not account for the evolution of corals during the early Paleogene and does not resolve the

controversy concerning the dramatic drop of coral-reef production close to the P–E boundary and during the early Eocene concomitant with the long-term increase in coral diversity.

6.2.2. Surface productivity and sediment load

Although fluctuations in nutrient loading have long been known to affect coral growth (e.g., Hallock and Schlager, 1986) and coral-reef development (Hallock, 1988), these factors have been neglected in the study of the early Paleogene coral evolution. In addition to these factors, it has recently been demonstrated (Wooldridge, 2009; Wooldridge and Done, 2009) that corals which regularly experience poor water quality

conditions (elevated concentrations of dissolved inorganic nitrogen) are less 'resistant' to thermal stress and display higher bleaching sensitivity (per unit increase in SST). A progressive increase of warmth and humidity during the middle Paleocene to early Eocene, mainly related to CO₂ buildup (Pearson and Palmer, 2000), intensified the continental weathering with increasing/fluctuating runoff and nutrient delivery to the oceans (e.g., Crouch et al., 2003; Pagani et al., 2006; Zachos et al., 2006; Giusberti et al., 2007; Nicolo et al., 2007; Sluijs et al., 2008b; Smith et al., 2008; Agnini et al., 2009; Sluijs and Brinkhuis, 2009). The shallow waters were probably not subject to extreme peaks in nutrients, as indicated by the nature of the biotic assemblage dominated by larger benthic foraminifera rather than small opportunist benthic foraminifera and other heterotrophic organisms (e.g., Hallock, 1988; Hallock et al., 2003). Based on our study, however, we suggest an increase/fluctuation in nutrient availability in the mesotrophic range. This change in the trophic conditions was likely related to the cumulative impact of repeated pulses that occurred over tens of thousands of years. A long-term chronic increase of nutrient levels over millions of years would have probably caused a major shift in the benthic communities with heterotrophic organism dominant (e.g., Mutti and Hallock, 2003).

This trophic conditions likely enhanced competition, as reflected by the shift in the sessile community from the middle to the late Paleocene-early Eocene. Corals were forced to compete with other faster-growing, nutrient-opportunist sessile organisms, mainly coral-line algae and encrusting foraminifera. Additionally, bioerosion increased during the early Paleogene (Perrin, 2002) suggesting an increase of surface productivity. Under such conditions, the corals of the late Paleocene and early Eocene developed adaptations to nutrient replete conditions, similar to those of modern zooxanthellate corals living under mesotrophic conditions (Halfar et al., 2005). Coral morphologies changed throughout the mid Paleocene to the early Eocene time span, with a clear shift from more variable morphologies during the mid Paleocene (massive, laminar/platy, encrusting, and branching forms) toward earliest Eocene assemblages dominated by growth forms suitable for low-light conditions (e.g., massive and encrusting forms in nearshore settings with reduced water quality combined with high water energy, and laminar/platy forms in mesophotic settings). The general limited dimension of the coral colony size (range of centimeters, but the number of detailed studies is limited) might result from rapid population dynamics (e.g., high recruitment rates and mortality at young age) as response to frequent environmental perturbations (e.g., changes of sediment/nutrients load, Te, 1992). The early Paleogene coral assemblages are dominated by *Goniopora* (both branching and massive forms) and *Actinacis* (platy form) along with massive astrocoeniids and faviids (Baron-Szabo, 2006). *Goniopora* and *Actinacis* are pioneer genera tolerant to both turbidity and high nutrients (Schuster, 1996; Bosellini, 1998; Rosen, 2000). Additionally, the common co-occurrence in the same assemblages of dendroid, mainly azooxanthellate forms as *Dendrophyllia*, *Oculina*, and *Cladocora* (e.g., Schuster, 1996; Turnšek and Drobne, 1998; Baceta et al., 2005) further supports the hypothesis of an increase of surface productivity. Increased nutrients might have caused slower coral growth rates, resulting in regional decline in reef-building capacity. Similar processes have been suggested to explain "reef gap" in the Caribbean during the Miocene (Johnson and Pérez, 2006) and the Oligocene/Miocene transition (Edinger and Risk, 1994). Growth rate of adult corals, however, might remain high as nutrient flux increase, with a decline of net framework production due to coral cover decline and bioerosion rate increase converting framework to sediments (Hallock, 2001). Similar processes might account for the progressive increase of mounds with abundant carbonate mud during the late Paleocene. Unfortunately, no studies exist concerning the coral growth rates in fossil corals of early Paleogene. Therefore, this is a hypothesis that remains to be tested. The perturbation of the nutrient cycle may have been a major cause of

regional decline in coral reef production, especially in partly land-locked regions of the Tethys. This mechanism alone, however, fails to explain the progressive shift observed from reef-building to non-reef building coral communities during the early Paleogene.

6.2.3. Ocean chemistry

The late Paleocene-earliest Eocene global warming events are all associated with sea floor carbonate dissolution and negative carbon excursions (Zachos et al., 2010 and references therein). Changes in surface sea-water chemistry, due to rapid accumulation of atmospheric CO₂ (Fig. 5) and consequent ocean acidification, has been suggested as important factor in reduced reef production at the Paleocene-Eocene boundary (e.g., Kiessling and Simpson, 2011). Experiments in artificial seawaters demonstrated that scleractinian corals calcified at slower rate under unfavorable seawater chemistry (e.g., Langdon et al., 2000; Ries et al., 2006) as they would have done during the early Paleogene. We suggest that slow calcification rates resulting from the production of aragonitic skeletons in chemically unfavorable seawater of the early Paleogene (ocean Mg/Ca ratio < 2), probably contributed to the generally limited capacity of corals to build extensive reefs. Additionally, slow calcification rates would have reduced the ability of corals to outgrow their fast-growing competitors, and their associated fragile skeletons would have left the corals prone to fragmentation and bioerosion. As well as the chance of preservation might have been reduced due to a less effective calcification (e.g., reduced calcification of *Porites* in high latitude settings, Halfar et al., 2005; Lough and Barnes, 2000). So far, there is no convincing evidence for surface-water acidification during the PETM (e.g., Kump et al., 2009 and reference therein). PETM carbon release, and hence acidification, was likely too slow limiting the magnitude of surface water acidification (e.g., Zachos et al., 2008; Ridgwell and Schmidt, 2010). The results from these recent studies (e.g., Gibbs et al., 2006, 2010; Ridgwell and Schmidt, 2010; Robinson, 2011) all suggest that the PETM may only provide a minimum estimate of the response of marine calcifiers to future surface water ocean acidification. Interestingly, Cai et al. (2011) observed that acidification of coastal waters can be enhanced by eutrophication, thus it might be possible that similar processes observed today in the northern Gulf of Mexico and in the East China Sea have affected the coastal waters during the PETM and other early Paleogene hyperthermal events. Thus, further studies to test the hypothesis that coral calcification rates were slower as a response to a possible shallow-water ocean acidification associated to the PETM would add useful information to this debate.

Today Caribbean is characterized by a decline of reefs (e.g., Porter et al., 2002), a persistence of patch reefs with significantly high coral cover, richness, and habitat complexity (e.g., Dupont et al., 2008), and zooxanthellate coral communities thriving in deeper depths in the Gulf of Mexico (e.g., Jarrett et al., 2005). This situation suggests that selected z-coral assemblages may adapt to the ongoing climate changes and associated feedback processes evolving alternative strategy of life, preserving diversity and continuing to contribute to the carbonate sediment production. The early Paleogene fossil examples give positive clues to support this hypothesis.

7. Conclusions

- Analysis of coral occurrences during the early Paleogene show that the evolution of these coral communities was characterized by a progressive reduction of reef-building potential. In particular, 1) the mid Paleocene record was dominated by shallow-water coral-algal patch-reefs/reef complexes (67%), 2) the late Paleocene record was characterized by small shallow-water coral-algal patch-reefs (43%) together with coral-bearing mounds at shallow and intermediate depths (43%) where corals are subordinated to other bioconstructors (mainly calcareous red algae and foraminifera), 3) the early Eocene record was

dominated by isolated coral knobs mainly in shallow-water settings (56%).

- Coral diversity slightly decreased across the mid Paleocene-early Eocene in association with a shift toward communities dominated by forms tolerant to thermal stress and high turbidity/nutrients levels (mainly *Actinacis*, *Goniopora*), especially during the early Eocene. These changes document the capacity of corals to colonize a broad range of settings as result of adaptations to adverse environmental conditions.
- We suggest that the progressive expansion of coral communities that did not build reefs from the middle Paleocene to the early Eocene was likely related to perturbation of the ocean chemistry due to high atmospheric pCO₂ levels, combined with moderately high nutrient loads. These stressors might have strongly affected the coral reef-framework production limiting the grow rates of coral colonies, and lowering their capacity to compete with faster-growing, nutrient-opportunistic organisms and bioeroders.
- The hypothesis that coral calcification rates were slower during the early Paleogene especially as a consequence of ocean acidification affecting shallow-water settings during the PETM and other early Paleogene hyperthermal events deserve further studies in order to add useful information to the debate whether there was a significant acidification affecting shallow-water settings.

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