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Responses of a shallow-water ecosystem to the early Paleogene greenhouse environmental conditions

Evolution of Larger Foraminifera and coral communities from the Northern Tethys

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Si fermò; e, guardandomi come per esser sicuro che capivo e che magari condividevo, si mise a elencare quelle idee:

"Questo non è il solo mondo", disse, indicando con un ampio gesto del braccio l´intero orizzonte.

"Questo non è il solo tempo", e puntò il dito contro il mio orologio.

"Questa non è la sola vita", e indicò se stesso, Angela, me, il cane e tutto quel che c´era attorno.

Si fermò come per farci riflettere.

"E questa non è la sola coscienza." Toccandomi il petto concluse: "Ciò che è fuori è anche dentro; e ciò che non è dentro non è da nessuna parte".

Poi, come volesse allergerire l´atmosfera, scoppiò in una bella risata e, rivolto a me, aggiunse: "Per questo viaggiare non serve. Se uno non ha niente dentro, non troverà mai niente fuori. È inutile andare a cercare nel mondo quel che non si riesce a trovare dentro di sé".

Mi sentii colpito. Aveva ragione.

Tiziano Terzani, "Un altro giro di giostra"

ABSTRACT

Modern anthropogenic forcing of atmospheric chemistry poses the question of how the Earth System will respond as thousands of gigatons of greenhouse gas are rapidly added to the atmosphere. A similar, albeit nonanthropogenic, situation occurred during the early Paleogene, when catastrophic release of carbon to the atmosphere triggered abrupt increase in global temperatures. The best documented of these events is the Paleocene-Eocene Thermal Maximum (PETM, ~55 Ma) when the magnitude of carbon addition to the oceans and atmosphere was similar to those expected for the future. This event initiated global warming, changes in hydrological cycles, biotic extinction and migrations. A recently proposed hypothesis concerning changes in marine ecosystems suggests that this global warming strongly influenced the shallow-water biosphere, triggering extinctions and turnover in the Larger Foraminifera (LF) community and the demise of corals.

The successions from the Adriatic Carbonate Platform (SW Slovenia) represent an ideal location to test the hypothesis of a possible causal link between the PETM and evolution of shallow-water organisms because they record continuous sedimentation from the Late Paleocene to the Early Eocene and are characterized by a rich biota, especially LF, fundamental for detailed biostratigraphic studies. In order to reconstruct paleoenvironmental conditions during deposition, I focused on sedimentological analysis and paleoecological study of benthic assemblages. During the Late Paleocene-earliest Eocene, sedimentation occurred on a shallow-water carbonate ramp system characterized by enhanced nutrient levels. LF represent the common constituent of the benthic assemblages that thrived in this setting throughout the Late Paleocene to the Early Eocene. With detailed biostratigraphic and chemostratigraphic analyses documenting the most complete record to date available for the PETM event in a shallow-water marine environment, I correlated chemostratigraphically for the first time the evolution of LF with the δ^{13}C curves. This correlation demonstrated that no major turnover in the LF communities occurred synchronous with the PETM; thus the evolution of LF was mainly controlled by endogenous biotic forces.

The study of Late Thanetian metric-sized microbialite-coral mounds which developed in the middle part of the ramp, documented the first Cenozoic occurrence of microbially-cemented mounds. The development of these mounds, with temporary dominance of microbial communities over corals, suggest environmentally-triggered “phase shifts” related to frequent fluctuations of nutrient/turbidity levels during recurrent wet phases which preceding the extreme greenhouse conditions of the PETM. The paleoecological study of the coral community in the microbialites-coral mounds, the study of corals from Early Eocene platform from SW France, and a critical, extensive literature research of Late Paleocene – Early Eocene coral occurrences from the Tethys, the Atlantic, the Caribbean realms suggested that these corals types, even if not forming extensive reefs, are common in the biofacies as small isolated colonies, piles of rubble or small patch-reefs. These corals might have developed ‘alternative’ life strategies to cope with harsh conditions (high/fluctuating nutrients/turbidity, extreme temperatures, perturbation of aragonite saturation state) during the greenhouse times of the early Paleogene, representing a good fossil analogue to modern corals thriving close to their thresholds for survival.

These results demonstrate the complexity of the biological responses to extreme conditions, not only in terms of temperature but also nutrient supply, physical disturbance and their temporal variability and oscillating character.

ZUSAMMENFASSUNG

Die anthropogene Beeinflussung der Chemie der Atmosphäre in der modernen Zeit wirft die Frage nach dem Schicksal des Systems Erde auf, wenn tausende von Tonnen an Treibhausgasen in kurzer Zeit in die Atmosphäre einströmen. Im Känozoikum trat bereits eine ähnliche Situation während des frühen Paläogens auf, als eine katastrophale Freisetzung von Kohlenstoff in die Atmosphäre einen plötzlichen Anstieg der globalen Temperatur hervorrief. Das am besten dokumentierte dieser Ereignisse stellt das Paläozän-Eozäne Temperatur Maximum (PETM, ~55 Ma) dar, bei welchem die Größenordnung der Kohlenstoffzufuhr in Ozeanen und Atmosphäre jener ähnelte, die in der Zukunft zu erwarten ist. Das damalige Ereignis initiierte eine globale Erwärmung, Veränderungen hydrologischer Kreisläufe, biotische Auslöschung und Abwanderungen. Eine kürzlich veröffentlichte Hypothese zu Veränderungen in marinen Ökosystemen postuliert, dass diese globale Erwärmung die Biosphäre der Flachwässer stark beeinflusste, indem sie Aussterben und Fluktuation innerhalb der Gemeinschaft der Großforaminiferen (GF) sowie den Niedergang einiger Korallen bewirkte.

Die Abfolgen der Adriatischen Karbonatplattform (SW-Slovenien) stellen einen idealen Ort dar, um die Hypothese des kausalen Zusammenhangs zwischen dem PETM und der Evolution der Flachwasserorganismen zu überprüfen, da sie aufgrund ihrer kontinuierlichen Sedimentation vom Spätpaläozän bis zum Früheozän und ihres Reichtums an Biota, insbesondere an GF, fundamentale Voraussetzungen für eine detaillierte biostratigraphische Studie erfüllen. Um die Paläoumweltbedingungen während der Sedimentablagerung zu rekonstruieren, wurde der Schwerpunkt dieser Arbeit auf eine sedimentologische Analyse und eine paäoökologische Studie benthischer Vergesellschaftungen gesetzt. Während dem Spätpaläozan bis zum frühesten Eozän fand die Sedimentation auf einem Flachwasser-Rampensystem statt, welches durch ein erhöhtes Nährstoffangebot gekennzeichnet war. GF stellen jenen häufigen und verbreiteten Bestandteil der benthischen Vergesellschaftungen dar, welcher in dieser Umgebung durch das Spätpaläozän hindurch bis ins Früheozän gedeihen konnte. Mit den in dieser Arbeit vorgestellten detaillierten bio- und chemostratigraphischen Analysen, deren Dokumentation den zur Zeit vollständigsten Datensatz für das PETM-Ereignis in einem flachmarinen Milieu repräsentieren, wurde die Evolution der GF zum ersten Mal mit $\delta^{13}C$ -Kurven chemostratigraphisch korreliert. Diese Korrelation zeigte, dass in den GF-Gemeinschaften keine großmaßstäbliche Fluktuation zeitgleich mit dem PETM auftrat, und dass daher die Evolution der GF hauptsächlich durch endogene biotische Einflüsse kontrolliert worden sein muss.

Die Studie mikrobiell-überkrustete Korallenhügel im Größenbereich zwischen einigen Metern und einigen Zehnermetern, die sich im Spätthanetium im mittleren Teil der Rampe entwickelten, dokumentiert das erste Auftreten mikrobiell-zementierter Erhebungen während des Känozoikums. Die Entwicklung dieser Erhebungen, mit einer zeitweiligen Dominanz der mikrobiellen Gemeinschaften gegenüber den Korallen, spricht für ein Auftreten Umwelt-gesteuerter "Phasenverschiebungen" im Zusammenhang mit häufigen Wechseln von Nahrungsangebot und Trübung während wiederkehrender nasser Phasen, welche dem extremen Treibhaus der PETM vorausgingen. Die paläoökologische Studie der Korallen-Gemeinschaften in den mikrobiell-überkrusteten Korallenhügeln, die Studie der Korallen der früheozänen Plattform in SW-Frankreich sowie eine kritische, ausgedehnte Literaturrecherche zum Auftreten spätpaläozäner bis früheozäner Korallen in der Tethys, im Atlantik und in der Karibik sprechen dafür, dass diese Korallentypen – selbst wenn sie nicht ausgedehnte Riffe formen – in der Biofazies häufig als kleine isolierte Kolonien, Berge von Geröll

oder kleine Kuppelriffe auftreten. Diese Korallen könnten 'alternative' Überlebensstrategien entwickelt haben, um mit den rauen Bedingungen (hohes/wechselndes Nahrungsangebot, schwache/starke Trübung, schwankende Temperaturen, häufige physikalische Störungen) fertig zu werden, die während den Zeiten des paläogenen Treibhauses vorherrschten, und stellen damit ein gutes fossiles Analog zu modernen Korallen dar, welche nahe an ihrer Überlebensgrenze gedeihen.

Diese Ergebnisse zeigen die Komplexität der biologischen Reaktionen auf extreme Bedingungen, nicht nur im Hinblick auf Temperaturen, sondern auch hinsichtlich Nahrungsangebot, physikalische Beeinträchtigungen sowie deren zeitliche Schwankungen und deren oszillierenden Charakter.

CONTENTS

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1. INTRODUCTION

È bello raccontare i guai passati.

Primo Levi, “Il sistema periodico”

The increasing concern about climatic change and the discussion about possible consequences for the Earth system have stimulated an increasing interest in climatic variations in the geological record. In particular, the mechanisms involved and the responses of the Earth System during times characterized by significant global warming, such as the early Paleogene, have become objects of intense study. During the Paleogene (65 to 23 Ma) the Earth experienced climatic variations from a warm “greenhouse” during the early Paleogene, when the Earth was generally much warmer than today, to a cooler “Icehouse” world starting from the Oligocene, through extreme transient climatic perturbations (*Zachos et al.*, 2001, fig.1.1). The most extreme hyperthermal event is known as the Paleocene-Eocene Thermal Maximum (PETM) or the Late Paleocene Thermal Maximum (LPTM~55 Ma). This transient warming event, one of the best geological analogues for modern anthropogenic climate change, was superimposed on a long-term warming trend which started in the Late Paleocene (~59 Ma) and culminated with the Early Eocene Climatic Optimum (EECO ~51 Ma). During the PETM, sea surface temperature (SST°) increased by 5°C in the tropics to 8°C at mid-latitudes, and up to 9°C at high latitudes. This hyperthermal event is globally recognized in marine and continental sedimentary rocks using the Carbon Isotopic Excursion (CIE), a prominent 2-3‰ negative carbon isotopic shift at the onset of the Eocene which provides a distinctive geochemical marker for the PETM (*Kennett and Stott,* 1991).

During the last decades, data obtained by the Ocean Drilling Program has provided many insights into the characteristics of Paleogene oceans. Pelagic organisms show rapid diversification in surface waters (e.g., *Crouch et al.,* 2001*; Kelly et al.,* 1996) but also dramatic extinction concomitant to the PETM, as in the case of deep benthic foraminifera which experienced the most severe extinction of the last 90 Ma (*Thomas,* 2000). However, only recently the response of shallow-water marine ecosystems to this rapid warming event has been studied in successions from the Atlantic coast (Spain; *Orue-Etxebarria et al*., 2001; *Pujalte et al*., 2003; *Scheibner et al*., 2007; *Pujalte et al*., 2009a) and the Southern Tethys (Egypt; *Scheibner et al*., 2005; *Scheibner and Speijer*, 2009). These studies have suggested a direct causal link between the PETM and biotic events in the platform, but due to the limited occurrences of biostratigraphic markers, the common occurrence of stratigraphic gaps in shelfal areas, and the low resolution of the $\delta^{13}C$ curves acquired, these correlations remain speculative.

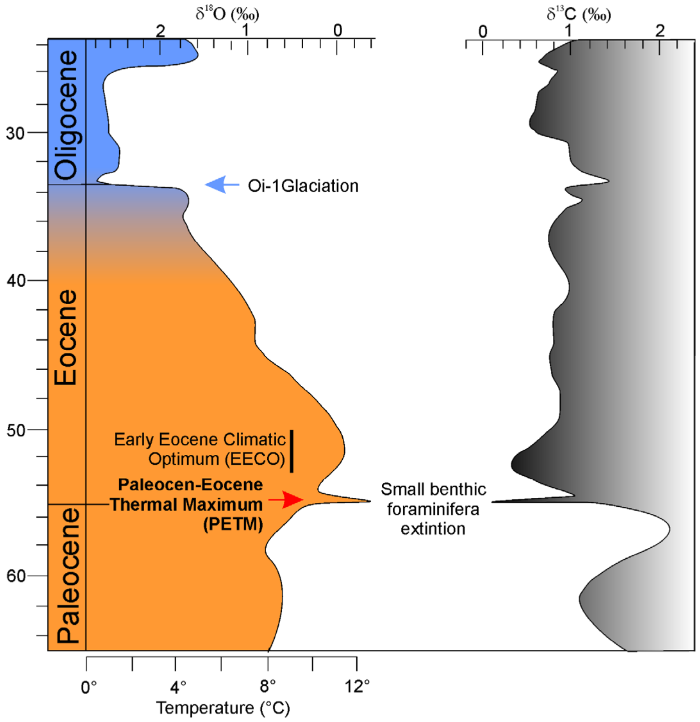

Figure 1.1: Global deep-sea oxygen and carbon isotope records for the Paleogene, modified from *Zachos et al.*, 2001.

I have studied the possible effects of Early Paleogene rapid variations in climate and associated feedbacks on shallow-water ecosystems in sub-tropical setting from the Central Tethys by utilizing facies and paleoecological analysis, and chemostratigraphy. I especially focused on larger foraminifera and corals, the most important biocalcifiers in tropical and sub-tropic platforms. These organisms are highly sensitive to short-term environmental changes. As the possible consequences of the recent warming on reef corals and symbiont-bearing foraminifera remain widely debated in recent literature, studies on geological scale will provide some insights to the fate of these organisms.

In order to test the hypothesis of possible causal link between the PETM and evolution of shallow-water organisms, I have studied carbonate successions from the Adriatic Carbonate Platform (SW Slovenia), a wide, sub-tropical, isolated platform located along the northern margin of the Central Tethys. Here, Paleocene and Early Eocene marine carbonates are well exposed and have been the object of paleontological studies since the 1970s due to their rich biota, especially larger benthic foraminifera, which are fundamental for detailed biostratigraphic studies.

I reconstructed a depositional model and the paleoenvironmental conditions in terms of light levels, nutrients, depth, and substrate nature, focusing on the composition of benthic assemblages and the sedimentological analysis of two sections spanning the Late Paleocene to the earliest Eocene (Chapter 2). Both facies and benthic assemblage analyses suggest enhanced nutrient levels in shallow-water, with nutrients transported and redistributed along the coastal surface by bottom currents and storms. Larger foraminifera (LF) represent the common constituent of the latest Paleocene-earliest Eocene benthic assemblages, showing a good tolerance to enhanced/fluctuating nutrient levels, and thus probably not confined to nutrient-depleted environments, as previously argued by other researchers. At the transition from the Paleocene to the Eocene, larger foraminifera assemblages seem to be mainly marked by changes in morphotypes rather than major faunal turnover.

Tackling the issue of the possible responses of shallow-water ecosystem to the PETM is pivotal to reconstructing a precise and continuous carbon isotope curve for the shallow-water carbonates to achieve the highest possible temporal resolution and to compare the sections of this work with the reference curves from the pelagic realm. This establishes a correlation between well studied paleoceanographic events and major biotic changes as observed in shallower-water platforms. Thus, I performed detailed biostratigraphic and chemostratigraphic analyses which demonstrate that the successions from the Adriatic Carbonate Platform represent the one the most detailed record currently available for the PETM event in a shallow-water marine environment (Chapter 3). I correlated for the first time in detail the evolution of larger foraminifera with the $\delta^{13}C$ curve. This correlation shows that the appearance of the *Alveolina* genus coincided with the onset that the PETM; however, no clear evidence of major turnover in the LF communities have been observed.

With the detailed sedimentological and paleoecological study of the Late Thanetian microbialite-coral mounds, I documented the first occurrence of Cenozoic microbially-cemented mounds (Chapter 4). Paleoecological relationships among the main bioconstructors, with temporary dominance of microbial communities over corals, suggest environmentally-triggered “phase shifts” in the dominant mound-biota. Frequent environmental perturbations in terms of fluctuating nutrient and turbidity levels related to recurrent wet phases are suggested to be likely mechanisms favoring alternatively heterotrophic/oligophotic microbes and meso-oligotrophic/mesophotic corals. This study sheds new light on the understanding of paleoenvironmental conditions in shallow water preceding the extreme climatic conditions of the PETM.

The presence of a diversified community of corals in the mid-ramp microbialites-coral mounds poses the problem of the paleoecology of the Early Paleogene corals. At this time corals did not formed extensive reefs and, based on the classical "optimal" model of coral occurrence in clear, oligotrophic water, the Early Paleogene warm tropical coral reefs have been interpreted as a phase of crisis for corals. Nonetheless corals occurred frequently in the shallow-water carbonates as small isolated colonies, piles of rubble or small patch-reefs. Thus, in order to understand this unusual coral record and to gather new information about paleoenvironmental conditions in shallow water, I performed an extensive, critical review of available literature from the Tethys, the Atlantic, and the Caribbean realms and combined it with two of my own datasets from the Adriatic Carbonate Platform and the Minervois platform (SW France) (Chapter 5), focusing on coral facies sedimentology, coral reef-building capacity, and diversity. I suggest a new working hypothesis, considering that Early Paleogene corals might have represented fossil analogues of modern coral communities living on marginal conditions in terms of nutrients, temperatures, and aragonite saturate state characterized by the reduced capacity to create permanent, extensive reefs. The development of an "alternative", adapted state for corals might have been the response to the establishment in neritic settings of increased nutrient levels coupled with extremely high temperatures and perturbation of the aragonite saturation state related to high pCO_2 levels, during the Late Paleocene – Early Eocene greenhouse times.

With the exception of this chapter and Chapter 6 (Conclusions), the chapters of this thesis have either been published in peer-reviewed journals or will soon be submitted. Chapter 2 ("Evolution of shallow benthic communities during the Late Paleocene – earliest Eocene transition in the Northern Tethys (SW Slovenia)" by Jessica Zamagni, Maria Mutti and Adrijan Košir) was published in 2008 in *Facies*. Chapter 3 ("The Paleocene – Eocene Thermal Maximum (PETM) in shallow-water successions (Adriatic Carbonate Platform): implication for larger foraminifera evolution" by Jessica Zamagni, Maria Mutti, Adrijan Košir) is going to be submitted to *Paleoceanography* Chapter 4 ("The first microbialite-coral mounds in the Cenozoic (Uppermost Paleocene) from the Northern Tethys (Slovenia): environmentally-triggered phase shifts preceding the PETM?" by Jessica Zamagni, Adrijan Košir, Maria Mutti) was published in 2009 in *Palaeogeography, Palaeoclimatology, Palaeoecology*. Chapter 5 ("Evolution of Late Paleocene - Early Eocene coral communities: queer fellows or non-reef building corals adapted to rapid climate changes?" by Jessica Zamagni, Adrijan Košir, Maria Mutti) is going to be submitted to *Geology*.

2. EVOLUTION OF SHALLOW BENTHIC COMMUNITIES DURING THE LATE PALEOCENE–EARLIEST EOCENE TRANSITION IN THE NORTHERN TETHYS, NW AdCP (SW SLOVENIA)

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Abstract

A paleoecological and sedimentological study has been carried out on shallow-water carbonates of the Kras Plateau (SW Slovenia) with the goal of reconstructing paleoenvironmental conditions and evolution of foraminiferal communities on the north-western Adriatic Carbonate Platform (AdCP) during the Late Paleocene - earliest Eocene. Three facies have been recognized and summarized in a carbonate ramp model. Within these facies, six foraminiferal assemblages, representing different ramp sub-environments, have been defined: during the Late Paleocene sedimentation took place in a protected innermost ramp with (1) smaller miliolids- and (2) small benthic foraminifera-dominated assemblages thriving on partly vegetated, soft substrates. In the uppermost Paleocene sedimentation primarily occurred along a mid ramp. The upper mid-ramp was sporadically influenced by storms/currents and occupied by (3) *Assilina*-dominated assemblage occurring on a soft sandy substrate. The deeper mid-ramp was characterized by (4) 'bioconstructors'- and (5) orthophragminids-dominated assemblages, colonizing biotopes with substrates of different nature. During the earliest Eocene deposition occurred in an inner-ramp setting with (6) alveolinids-nummulitids assemblage thriving on muddy and sandy substrate, partly covered or close to seagrass beds. The Late Paleocene - earliest Eocene environmental conditions, coupled with the long-term evolution of Larger Foraminifera (LF), seem to have favored this group as common sediment contributors, showing tolerance to relatively high nutrient levels. By comparing the evolution of the shallow-water biota from the Adriatic area with data from the Pyrenees and Egypt, a latitudinal trend can be recognized. However, on a smaller geographical scale, local conditions are likely to have played some role in promoting the evolution of biota characterized by peculiar features as the development of microbial mounds during the Late Thanetian.

2.1 Introduction

A distinct period of extreme global warming occurred close to the boundary between the Paleocene and Eocene, approximately 55.5 Ma ago (e.g. *Zachos et al.,* 2001). This event, termed the Paleocene - Eocene Thermal Maximum (PETM), coincided with a time of generally warm, “greenhouse” climate conditions representing a short-lived event in global warm temperatures. The PETM was characterized by a globally quasi-uniform 5-8°C warming in less in than 10 ka (e.g. *Röhl et al.,* 2000). The biotic responses to this event in the oceans were largely investigated. These studies documented heterogeneity in nature and severity of responses, including radiations, extinctions and migrations (e.g. deep benthic foraminifera extinction, *Pak and Miller,* 1992; planktonic foraminifera and calcareous nannofossil diversifications, e.g. *Thomas,* 1998*; Kelly et al.,* 2005*; Bralower,* 2002). Conversely, how and to which extent shallow-water ecosystems reacted to these paleoenvironmental changes has been almost neglected.

Larger Foraminifera (LF) were the most common constituents of Upper Paleocene–Lower Eocene shallow-water carbonates. Especially Eocene LF were used extensively as a tool for reconstructing paleoenvironments due to their great diversity and abundance in the photic zone of tropical and subtropical settings. In the late Early Eocene - Middle Eocene, LF experienced their highest diversification marking the climax of the Eocene Global Community Maturation (GCM) cycle (see *Hottinger,* 1997, 1998). In the frame of this general reorganization after the crisis at the Cretaceous - Paleocene boundary, a first turnover occurred during the Thanetian (*Hottinger,* 1998) with a diversification of LF at the genus level. Starting from the Eocene a specific diversification of a restricted number of successful genera occurred. This second event is placed between the top of Thanetian and the base of Ilerdian (*Hottinger,* 1998) marking the Paleocene - Eocene boundary. At this time LF modified their life strategy and the specific diversification was mainly linked to the development of adult dimorphism and a large shell size (*Hottinger,* 1998).

In recent studies from northern Spain (*Orue-Etxebarria et al.,* 2001*; Pujalte et al.,* 2003*; Baceta et al.,* 2005*; Rasser et al.,* 2005*; Scheibner et al.,* 2007) and Egypt (*Scheibner et al.,* 2005), the LF evolution was correlated to the PETM climatic changes. These authors proposed a synchronicity and a causal relation between the environmental changes (i.e. warmer sea temperatures and changes in the trophic regimes) and the general turnover in the LF communities at the P-E transition. *Scheibner et al.* (2007) analyzed and compared the shallow-water benthic communities from Spain and Egypt, especially their evolution during the Thanetian and the Ilerdian. They suggested that a latitudinal effect determined differences in the biotic composition, with the PETM and the long-term warming during the Early Eocene affecting the low-latitude southern Tethys (Egypt) more severely than the mid-latitude Atlantic realm (Pyrenees).

Paleontological and biostratigraphical studies on carbonate platform successions from SW Slovenia documented a great diversity of shallow-water benthic foraminifera during the Late Paleocene - Early Eocene (e.g. *Drobne,* 1977, 1979; *Drobne et al.,* 1988). Within this frame the study of the Slovenian (northern Tethys) sedimentary successions is of great interest in order to verify the latitudinal effects on shallow-water benthic communities. In fact, during the Early Paleogene the Adriatic and the Pyrenean carbonate platforms were located approximately at the same paleolatitudes (around 35°N).

Here we present data on two continuously exposed shallow-water carbonate successions from the Kras region (SW Slovenia). The study of these successions allows us to track down the evolution of the LF assemblages across the P-E transition by documenting their major features during the pre-climax phase of the Eocene. A carbonate ramp facies model is reconstructed by combining the depth gradient with the nature of the substrate. Based on our findings we describe three phases of evolution for the Slovenian successions. These phases have different features respect to those described for Spain and Egypt by *Scheibner et al.* (2007). We suggest that local effects (i.e. paleogeography and differences in depositional settings) are the main sources for the differences in the evolution of shallow-water biota between the results from Spain and Egypt and our findings in SW Slovenia.

2.2 Geological setting and stratigraphy

The studied carbonate successions crop out in the southern part of the Kras (Karst) Plateau in SW Slovenia (Fig. 2.1). Structurally, the Kras Plateau corresponds to the Komen Thrust Unit of the NW External Dinarides fold-and-thrust belt (*Placer,* 1981). The latest Cretaceous to Early Paleogene paleogeography of the NW External Dinarides and the Dinaric foreland (Istrian Peninsula) was characterized by a vast subaerially exposed central area of the Adriatic Carbonate Platform (AdCP) and significantly reduced extent of shallow-water carbonate depositional environments on the marginal parts of the formerly extensive Mesozoic carbonate platform (*Vlahović et al.,* 2005). Towards the north/northeast, a deep-water basin was contiguous to a south-westward-verging advancing orogenic wedge (*Otoničar,* 2007 and references therein). The uppermost Cretaceous and Early Paleogene shallow-water carbonate successions represent a terminal, synorogenic megasequence of the AdCP. The megasequence, together with the overlying siliciclastic successions, exhibits a typical stratigraphic pattern of underfilled foreland basins (*Sinclair,* 1997). This pattern comprises three units, superimposed during basin migration (*Košir and Otoničar*, 2001), which reflect deposition during major tectonic events when the AdCP was subaerially exposed, subsequently re-established, then drowned, and finally buried by prograding deep-water clastics (flysch).

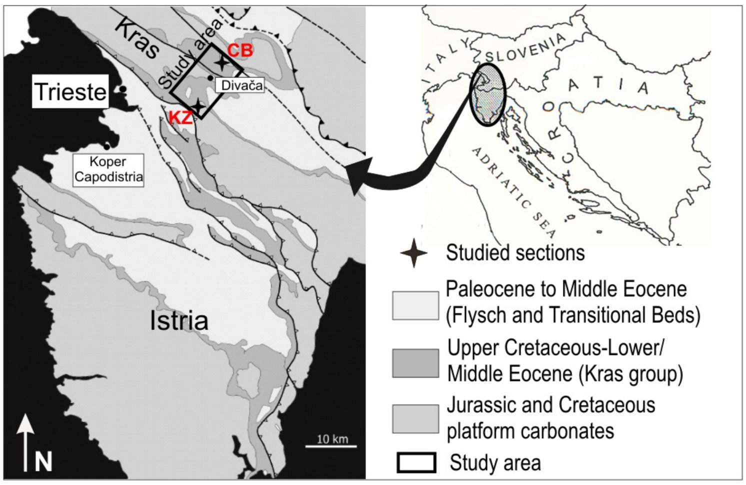


Figure 2.1: Simplified geological map of SW Slovenia and NE Croatia showing location of the study area and the stratigraphic sections. Adapted from *Košir* (2003). KZ: Kozina section, CB: Čebulovica section

A generalized stratigraphic column of the Upper Cretaceous, Paleocene, and Eocene deposits in the Kras region is shown in figure 2.2. The lower unit (the Kras Group; *Košir,* 2003) overlies the forebulge unconformity and comprises three formations: 1) Liburnian Formation (Upper Maastrichtian to Lower Paleocene) characterized by restricted, marginal marine, paralic and palustrine carbonates; 2) Trstelj Formation (Upper Paleocene) composed of foraminiferal and coralgal limestones deposited in shallow-water environments; and 3) Alveolina-Nummulites Limestone (Lower Eocene) dominated by accumulations of larger benthic foraminifera. The total thickness of the Kras Group ranges from several tens of meters to more than 450 m. The middle unit (Transitional Beds; Lower Eocene) consists of up to 50 m of pelagic and hemipelagic limestones and marls. The upper unit (Flysch; Lower Eocene) is composed of a succession (>1.000 m thick) of sandstone-dominated turbidites, marls, mudstones, and resedimented carbonates (debrites and calciturbidites). All of the three units occur diachronously along the regional profile, corresponding to the platform and basin migration from NE towards SW. This lasted from the Campanian/Maastrichtian to the Middle Eocene (*Bignot,* 1972; *Drobne,* 1977; *Cousin,* 1981; *Košir and Otoničar*, 2001). Age assignments noted above correspond to overall time-spans of the lithostratigraphic units in the Kras region (see *Drobne,* 1977; *Jurkovšek et al.,* 1996). Relatively consistent NE-SW regional stratigraphic trends (*Košir and Otoničar*, 2001; *Otoničar*, 2007) indicate that the platform and basin stratigraphies were largely controlled by the flexural deformation and/or tilting of the foreland. Local variations in stratigraphy, especially of carbonates onlapping the forebulge unconformity and of platform-to-basin successions, most likely resulted from non-flexural deformations, e.g., reactivation of antecedent pre-orogenic structures.

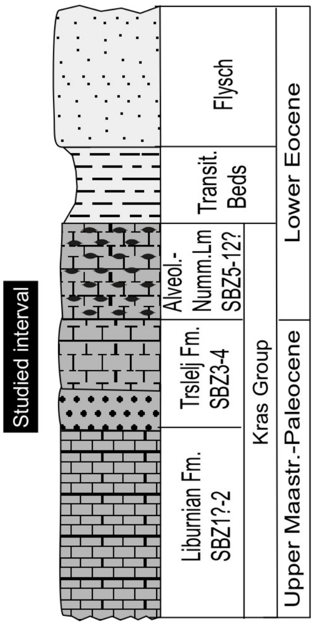


Figure 2.2: Generalized stratigraphic column of the uppermost Cretaceous-Eocene succession in the Kras region, SW Slovenia (*Košir*, 2003) and the studied interval.

A reliable reconstruction of the architecture and size of the Early Paleogene carbonate platform in the studied area is difficult because of the complex thrust-nappe structure of NW Dinarides and the intensive post-orogenic tectonic deformation. However, the platform geometry inferred from regional facies relationships (*Drobne,* 1977; *Jurkovšek et al.*, 1996, 1997) corresponds to a carbonate ramp depositional system characterized by roughly parallel NW-SE trending facies belts. This is in agreement with the paleotransport patterns recorded in the siliciclastic turbidites of the flysch foredeep successions in the NW Dinarides (*Orehek*, 1991; *Babić and Zupanič*, 1997), which have predominantly NW and SE-oriented axial paleocurrent directions, whereas a general paleotransport pattern in resedimented carbonates shows that carbonate debris derived from south-southwestern source areas (*Turnšek and Košir*, 2004; *Babić and Zupanič*, 1997).

Vertical facies successions of Paleocene and Lower Eocene shallow-marine carbonates (Trstelj Formation and Alveolina-Nummulites Limestone) generally exhibit a retrogradational pattern. This reflects a deepening trend and final drowning of the carbonate ramp by pelagic and hemipelagic deposits (*Košir*, 1997).

The Late Paleocene – Early Eocene width of the carbonate ramp and the foredeep basin can only be inferred from a rough palinspastic restoration *(Placer*, 1981) based on a combination of published maps and structural mapping of SW Slovenia. The width of the Early Paleogene shallow-water carbonate depositional area probably did not exceed 50 km, whilst the maximum width of the contemporaneous foredeep basin, estimated from the north-easternmost outcrops of Upper Paleocene flysch, supposedly deposited in inner foredeep settings, was probably less than 100 km. It is important to note, however, that the position of the front of the orogenic wedge during the Early Paleogene cannot be precisely established. Indeed, the Periadriatic Fault cuts the nappe structure of western Slovenia from its "root zone" on the NNE side (*Otoničar*, 2007 and references therein).

2.3 Material and methods

Two continuously outcropping stratigraphic sections (Čebulovica and Kozina) were studied at road cuts along the highway between Ljubljana and Koper (Figs. 2.1 and 2.3). The Čebulovica section is located 4 km northwest of the town of Divača. The section is ~200 m thick and covers the complete Trstelj Formation and the lower part of the Alveolina-Nummulites Limestone. The basal part of the section includes the contact with the underlying Liburnian Formation.

The Kozina section is located near the town of Kozina, about 12 km southwest of the Čebulovica section. The section (100 m thick) comprises the upper part of the Trstelj Formation and the lower part of the Alveolina-Nummulites Limestone. The lower part of the Trstelj Formation and the contact with the Liburnian Formation are not exposed. The sections have been logged, sampled, and described with respect to the sedimentary structures, textures and biotic components, with special attention to the distribution of foraminifera. Textural and compositional characteristics of the investigated lithologies were based on transmitted-light microscopy of 350 thin sections. The textural descriptions follow *Dunham* (1962) and *Embry and Klovan* (1971) classifications. The Shallow Benthic Zones of *Serra-Kiel et al.* (1998) have been adopted for the present study.

The paleoenvironmental distribution of foraminiferal assemblages and depositional conditions has been reconstructed, combining comparison with Recent counterparts and with the distribution of fossils forms from known facies models. Since many of the Early Paleogene LF became extinct at the Eocene - Oligocene boundary, the comparisons between distribution of fossil and living foraminifera have been conducted mainly considering similarities in the foraminiferal shell structures between extant and extinct forms. Hence, the ecology of living LF has been applied for paleobathymetric interpretation at a qualitative level. Since the depth signal produced by foraminiferal is strictly dependent on the age of the studied association (*Hottinger*, 1997), only Late Paleocene - Early Eocene foraminiferal occurrences have been considered for paleoecological interpretation. Additional ecological considerations on some of the main biotic components (calcareous algae and scleractinian corals) have been used to implement paleoenvironmental reconstruction.

2.4 Facies and foraminiferal assemblages: description and interpretation

Based on field observations, fossil contents, textural and sedimentological features, both successions have been subdivided into three facies (Fig. 2.3; Table 2.1 at the end of the chapter): Foraminiferal limestones (F), corresponding to the lower part of the Trstelj Formation (SBZ3, Early Thanetian); the For-Algal limestones (FA), covering the upper part of the Trstelj Formation (SBZ4, Late Thanetian); and the Bio-Peloidal limestones (BP), which corresponds to the lower part of the Alveolina-Nummulites Limestones (SBZ5-SBZ8, Early to Late Ilerdian). Each facies is characterized by distinct foraminiferal assemblages (Table 2.1). In particular, two foraminiferal assemblages dominated by small benthic foraminifera have been described from the facies F, three foraminiferal assemblages in the facies FA dominated by *Assilina*, orthophragminids, and encrusting foraminifera respectively, and one assemblage dominated by alveolinids and nummulitids in the facies BP.

2.4.1 Foraminiferal limestones (F)

Facies description – The facies occurs at the base of the two studied sections with a thickness of 30 m in the Kozina and 65 m in the Čebulovica, respectively (Fig. 3.3). In the Kozina section the basal contact with the Liburnian Formation is not exposed, therefore 30 m should be considered a minimum thickness. These dark limestones consist of a heterogeneous group of alternating lithologies dominated by thick-bedded packstones, wackestones, and rare grainstones. Wackestones with millimetric-sized fenestral porosity are occasionally present.

The biota consists of abundant and diversified benthic foraminifera (mainly miliolids associated with small rotaliids, conical agglutinated foraminifera and lituolids) and subordinate calcareous green algae (dasycladaleans). *Miscellanea* and small *Ranikothalia* are rarely present. Locally small dendritic-ramose coral colonies (mainly *Dendrophyllia* and *Oculina*) are scattered in the sediments to form small patches of bafflestone. Additional biogenic components are ostracods, echinoids, gastropods and bryozoans. Micritized foraminifera and fecal pellets are abundant. Reworked *Microcodium* occurs in the basal parts of grainstone/packstone beds or *in situ* in packstones, representing subaerial exposure surfaces in poorly developed shoaling sequences.

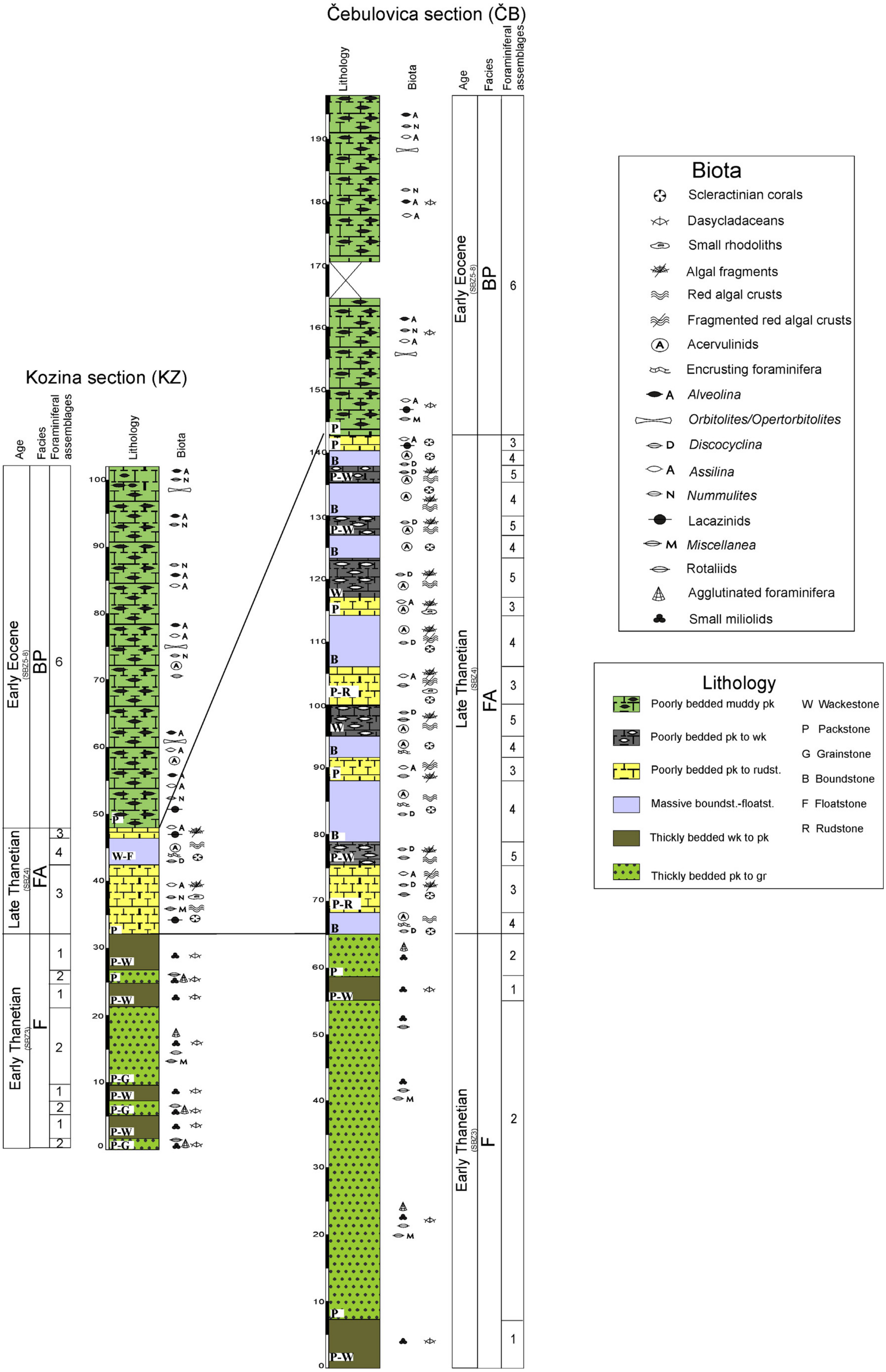
Among benthic foraminifera, the most valuable for biostratigraphical purpose are *Coskinon rajkae, Fallotella alavensis, Cribrobulimina carniolica, Haymanella paleocenica* and *Miscellanea juliettae*, the occurrence of which indicates early Thanetian age (SBZ3) for the Foraminiferal limestones.

Foraminiferal assemblages - This facies is characterized by two foraminiferal assemblages (Fig. 2.3, Table 2.1): smaller miliolids-dominated assemblage and small benthic foraminifera-dominated assemblage.

Assemblage 1: Smaller miliolids-dominated assemblage

This assemblage occurs in fine-grained packstones to wackestones representing an oligotypic community dominated by small miliolids and discorbids (Fig. 2.4a). Dasycladaleans and ostracods are associated with foraminifera. Recent miliolids are euryhaline forms living in shallow, restricted/lagoonal environments with low turbulence thriving on soft substrates. They were observed to proliferate also within seagrasses as epifaunal benthos (*Davies*, 1970) and as epiphytes on vegetated sediments (*Brasier*, 1975a). When present in great abundance they may indicate nutrient-enriched conditions and/or extreme salinities (*Geel*, 2000). Therefore, the low diversity of this foraminiferal assemblage might be indicative of a shallow, locally restricted environment, most likely characterized by enhanced nutrients, and development of algal meadows.

Figure 2.3: Stratigraphic columns of the Kozina and Čebulovica sections with distribution of the foraminiferal assemblages (1-6) and facies (F, FA, BP). (1) Smaller miliolids-dominated assemblage; (2) small benthic foraminifera dominated assemblage; (3) *Assilina*-dominated assemblage; (4) ‘bioconstructors’-dominated assemblage; (5) orthophragminids-dominated assemblage; (6) alveolinids-nummulitids assemblage. SBZ: Shallow Benthic Zones (*Serra-Kiel et al.*, 1998).


Čebulovica section (ČB)
Kozina section (KZ)
Lithology
Biota
Age
Facies
Foraminiferal assemblages
Early Eocene (SBZ5-8)
BP
6
Late Thanetian (SBZ4)
FA
Early Thanetian (SBZ3)
F
P
B
P-W
W
P-R
W-F
P-G
Biota
Scleractinian corals
Dasycladaceans
Small rhodoliths
Algal fragments
Red algal crusts
Fragmented red algal crusts
Acervulinids
Encrusting foraminifera
A Alveolina
Orbitolites/Opertorbitolites
D Discocyclina
A Assilina
N Nummulites
Lacazinids
M Miscellanea
Rotaliids
Agglutinated foraminifera
Small miliolids
Lithology
Poorly bedded muddy pk
Poorly bedded pk to wk
Poorly bedded pk to rudst.
Massive boundst.-floatst.
Thickly bedded wk to pk
Thickly bedded pk to gr
W Wackestone
P Packstone
G Grainstone
B Boundstone
F Floatstone
R Rudstone

Assemblage 2: Small benthic foraminifera-dominated assemblage

This assemblage usually occurs in fine-grained, bioturbated packstones and very rare grainstones. It is composed of miliolids (e.g. *Idalina*, *Periloculina*), small rotaliids (e.g. *Kathina*, *Smoutina*), agglutinated foraminifera (*Coskinon rajkae*, *Fallotella alavensis*), lituolids (*Haymanella paleocenica*), *Miscellanea* (Fig. 2.4c), the latter locally common in the Čebulovica section as well as very rare and small *Ranikothalia.* Foraminifera of this assemblage are associated with peloids, dasycladaleans, and subordinate echinoid remains, bryozoans, gastropods and isolated corals.

This assemblage has a high diversity of small, r-strategist foraminifera. It is worth remembering that the r-strategy (where “r” is the intrinsic growth rate of the population) applies to small-sized organisms, with high rate of fecundity, short generation times and rapid growths of populations. These traits are advantageous in unstable and/or unpredictable environments where resources have to be exploited in the quickest possible manner as soon as they become available. On the other hand, K-strategists (where “K” indicates the carrying capacity of the environment) have large body sizes, long life spans and produce fewer, but nurtured offspring. These organisms usually colonize temporally stable environments and their population sizes are very near to the carrying capacity to stretch limiting sources by mechanism of nutrient recycling (like symbiontic relationship in LF; *Hottinger*, 1983). Small rotaliids and agglutinated foraminifera are generally considered to be shallow-water dwellers living in lagoonal and open marine waters (e.g. *Geel*, 2000; *Ghose*, 1977). Rotaliids have been found on seagrass leaves in eastern Shark Bay (*Davies*, 1970). The development of ventral ornamentation characterizes Paleocene rotaliids (i.e. *Kathina*). *Hottinger* (2006) proposed that they use these ventral structures to maintain a proper position on soft, fine-grained substrate. *Miscellanea* is a common component in the shallow-water biota of the Thanetian. Based on the observation of Periadriatic platforms, *Pignatti* (1994) suggested that small forms of *Miscellanea* are reef dwellers, while larger forms should be typical of deeper waters, associated with nummulitids and *Discocyclina.* In our surveys, *Miscellanea* has always a small size and is associated with small rotaliids in fine-grained packstones with relatively abundant carbonate mud. Thanetian foraminiferal assemblages from Turkey, dominated by small rotaliids and miscellanids, have been interpreted by *Özgen-Erdem et al.* (2005) as thriving in lagoonal open environment.

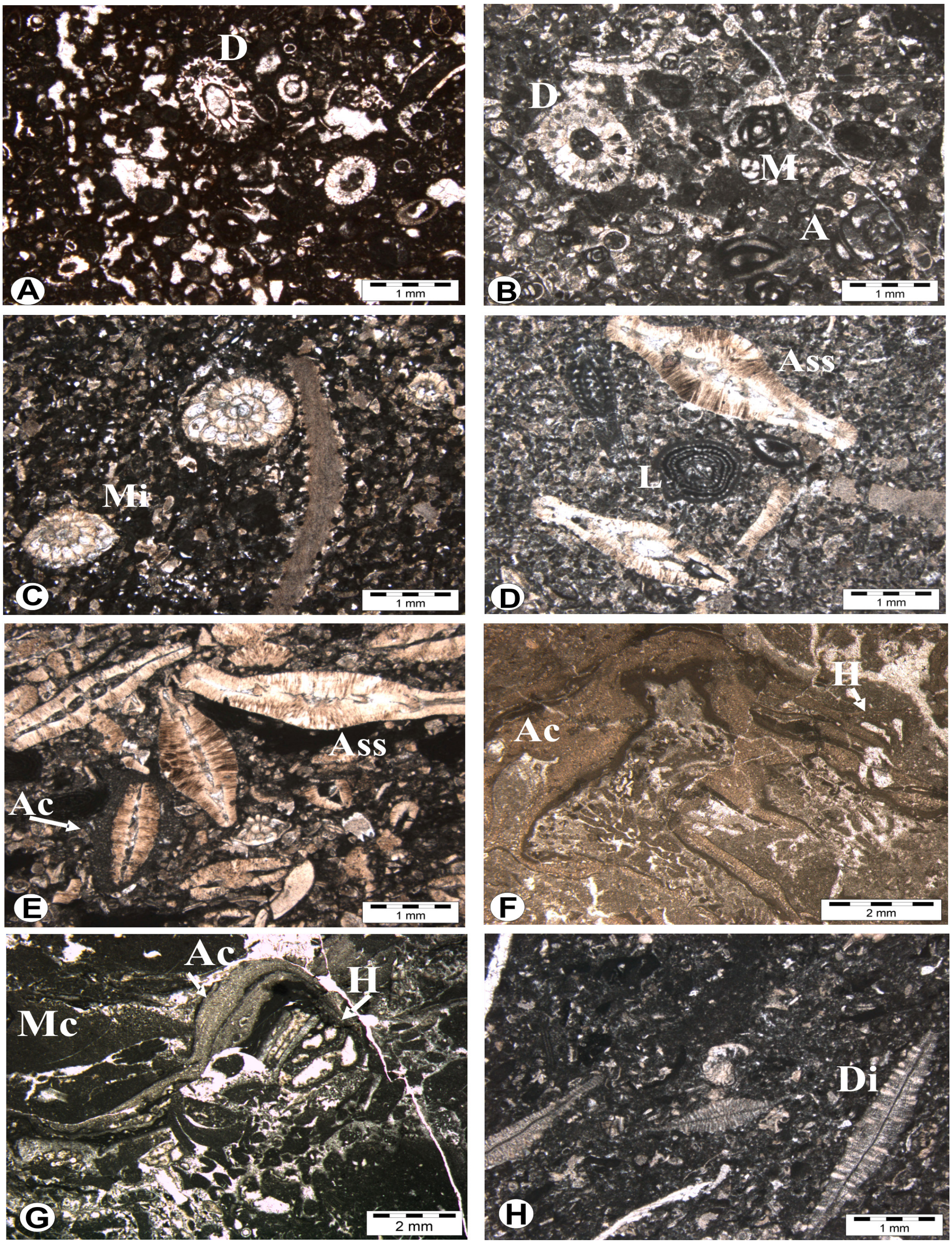


Figure 2.4: Photomicrographs of Thanetian foraminiferal assemblages from innermost ramp facies (F) and mid-ramp facies (FA): **a** Assemblage 1: fenestral packstone/wackestone with dasycladalean algae (*D*) and almost completely micritized miliolids; **b** Assemblage 2: packstone with dasycladaleans (*D*), miliolids (*M*) and agglutinated foraminifera (*A*, *Cribrobulimina carniolica*); **c** Assemblage 2: fine-grained packstone with *Miscellanea* (*Mi*), echinoid fragments and micritized foraminifera; **d** Assemblage 3: bioclastic packstone with *Assilina* (*Ass*) and lacazinids (*L*); **e** Assemblage 3: bioclastic packstone with *Assilina* (*Ass*), note acervulinid (*Ac*) encrusting *Assilina*; **f, g** Assemblage 4: boundstone with acervulinids (*Ac*) and haddonids (*H*) associated with red algae encrusting corals; **h** Assemblage 5: fine bioclastic wackestone with orthophragminids (*Di*).

Accordi et al. (1998) described a similar Thanetian association from Greece with abundant small benthic foraminifera associated with dasycladaleans as deposited in a shallow protected subtidal setting with algal meadows. The relatively high diversity of foraminiferal assemblage 2 might also be related to the existence of seagrasses beds. *Brasier* (1975b) concluded that ancient seagrass assemblages might be expected to show increased diversity compared to adjacent biofacies due to the higher nutrient levels within and adjacent to seagrass beds.

Summarizing, the small benthic foraminifera-dominated assemblage likely represents a community thriving on soft, sandy to muddy, locally vegetated substrate, in a low energy, very shallow subtidal setting.

Facies interpretation – The Early Thanetian deposits of the first facies are dominated by mud-supported lithologies. Evidence for periodical subaerial exposure is indicated by the occurrence of levels enriched in *Microcodium.* Reworked *Microcodium* and *in situ* colonies in almost unaltered limestones indicate early stages of soil formation during periodical subaerial exposure (*Košir*, 2004). The facies was probably deposited in a very shallow protected environment with a lateral gradient in degree of restriction as testified by the alternation with thin strata dominated by oligotypic fauna (smaller miliolids-dominated assemblage). The common occurrence of bivalves, gastropods and echinoids associated with a diversified community of benthic foraminifera likely suggests the presence of some algal or seagrass cover. The relatively high percentage of dasycladaleans supports this hypothesis. Moreover, fecal pellets, locally forming linear accumulations, suggest the occurrence of sedentary organisms (e.g. annelids). These usually burrow close to the seagrass roots and deposit fecal pellets in the tunnel that they dug (e.g. *Beavington-Penney et al.*, 2004). The presence of seagrass beds could have favored the high diversity of small benthic foraminifera in this facies.

2.4.2 Foralgal limestones (FA)

Facies description - The facies occurs in the middle part of the studied successions and has a thickness of 15 m in the Kozina section and 75 m in the Čebulovica section (Fig. 2. 3, Table 2. 1). The bulk of this facies consists of massive, white coral-microbialite mud mounds (*Zamagni et al.*, 2006) alternating with poorly stratified bioclastic packstones (dominated by *Assilina* spp.) and massive wackestones (with flattened orthophragminids and small rotaliids). Miliolines, represented by lacazinids and small miliolids, are usually scarce throughout this facies. The diversity and abundances of larger benthic foraminifera are generally low and rarely exceeds the 10% of the rock volume.

Associated with larger foraminifera are mainly calcareous red algae. The algal assemblage is dominated by corallinaceans (mainly melobesioids such as *Mesophyllum* and *Lithothamnion*), *Sporolithon, Distichoplax biserialis* (usually as small fragments) and peyssonneliaceans (*Polystrata alba*). Calcareous red algae form crusts (associated with bryozoans and encrusting foraminifera) and small aggregates (rodoliths) with sediments or other organisms like bryozoans as nuclei. In more muddy lithologies the algae form thin, irregularly distributed crusts. Scleractinian corals occur throughout the facies with diversity and abundance changing in different lithotypes. In packstones and wackestones they are present as rubbles and small colonies with domal-bulbous or laminar-tabular encrusting morphologies. The diversity is low with *Actinacis* and *Goniopora* as common genera, frequently found encrusting bivalves. In the coral-microbialite mud mounds the coral community is quite diverse and dominated by small colonies of ramose-dendritic and encrusting morphotypes commonly associated with microbialitic crusts and encrusting foraminifera. Algae are reduced to thin crusts occasionally coating corals.

Macrofauna in this facies is mainly represented by echinoid remains, bryozoans and bivalves (mainly oysters). Rare planktonic foraminifera are also present.

Bioerosion is a common feature affecting all the components and producing abundant sandy to silty debris (common coral, algal and foraminiferal fragments) and mud. Macroborings affecting foralgal encrustations, coral-microbialites and single components (mainly bivalves and foraminifera) are a common feature throughout this facies. Micritization is pervasive: foraminifera often show destructive micritic envelopes (see *Perry*, 1999). Rare biofabrics, such as tubular tempestite, can be also observed (*Tedesco and Wanless*, 1991). No wave-produced fabrics are identified so far and the amount of carbonate mud is high. Only occasionally beds occur enriched in abraded and fragmented grains, where foraminifera are preferentially orientated parallel to bedding. The packing degree is usually medium to low with micrite partially filling the inter-skeletal voids between the foraminiferal tests.

The most important biostratigraphic markers in FA limestones are represented by the nummulitids *Assilina yvettae*, *Assilina azilensis*, the miliolines *Lacazina blumenthali*, *Glomalveolina dachalensis* and *Glomalveolina levi*. Among calcareous algae the most valuable biostratigraphical indicator is *Distichoplax biserialis*. This fossil content indicates SBZ4 (Late Thanetian).

Foraminiferal assemblages - The FA limestones are characterized by three, alternating assemblages of benthic foraminifera (Fig. 2.3, Table 2.1). Nummulitids (*Assilina*-dominated assemblage), encrusting foraminifera (‘bioconstructors’-dominated assemblage) and orthophragminids (orthophragminids-dominated assemblage) are dominant.

Assemblage 3: Assilina-dominated assemblage

The *Assilina*-dominated assemblage consists of common flattened *Assilina* (*Assilina yvettae* and *Assilina azilensis*) (Fig. 2.4d-e), associated with small rotaliids, rare *Miscellanea* spp., rare small miliolids, lacazinids (*Lacazina* sp. and *Pseudolacazina* sp.), alveolinids (*Glomalveolina* spp.), rare *Ranikothalia* sp. and very rare robust/lenticular *Discocyclina. Haddonia* and acervulinids are present, locally encrusting larger foraminifera (Fig. 2.4e). Associated with foraminifera are calcareous red algae and isolated coral colonies. This assemblage occurs in poorly stratified packstones with abundant skeletal debris and carbonate mud.

Nowadays *Assilina* thrives in the lower photic zone on soft, muddy sediments, with *Assilina ammonoides* being one of the few larger benthic foraminifera able to tolerate a certain degree of eutrophication (e.g. Lacadive Islands; *Langer and Hottinger*, 2000). Fossil, large, flat form of *Assilina* were interpreted as living in the deeper parts of the photic zone (e.g. Oman; *Racey*, 1994) but also as shallow-water dwellers in turbid fore- and back-reef environments (e.g. Early Eocene forms from the South Pyrenean foreland; *Gilham and Bristow*, 1998; *Ghose*, 1977). The paleoecology of the other larger foraminifera found in the assemblage is here only tentatively inferred because extant counterparts do not exist. Lacazinids represented a widespread group of miliolines during the Early Paleogene; they were completely replaced by the ecologically vicariant alveolinids during the Early Eocene (*Drobne and Hottinger*, 2004). Their occurrence in this assemblage likely indicates preference for a soft substrate.

Data on the Central Western Tethys foraminiferal associations (e.g. Turkey; *Özgen-Erdem et al.*, 2005; Greece; *Accordi et al.*, 1998) show the simultaneous occurrence of *Assilina* along with small rotaliids and *Discocyclina.* Such an assemblage once again indicates preference for a soft substrate (both muddy and sandy) in low water energy and close to the lower photic zone. *Scheibner et al.* (2007) described a similar assemblage in an inner platform of the Pyrenean realm.

Summarizing, the *Assilina*-dominated assemblage was likely developed on a soft sandy substrate composed of foraminifera and other bioclastic fragments, in the shallow part of the mid-ramp. The flattened shape of *Assilina* suggests reduced light conditions.

Assemblage 4: 'Bioconstructors'-dominated assemblage

The 'bioconstructors'-dominated assemblage is composed of a diverse community of encrusting foraminifera, mainly acervulinids, associated with textulariids (*Placopsilina* and *Haddonia,* Fig. 2.4f-g), *Planorbulina* and *Miniacina*. Other foraminifera are less frequent and represented by small flattened *Discocyclina* and small rotaliids. Rare planktonic foraminifera are observed. Encrusting foraminifera are associated with scleractinian corals, microbial crusts, encrusting algae and branching bryozoans to form complex encrustations. Together with algae and/or bryozoans, encrusting foraminifera form thin crusts or aggregates and play a primary role in the bioconstructions of coral-microbialite mud mounds and acervulinid floatstones/boundstones.

At present, the distribution of encrusting foraminifera is primarily controlled by light intensity, water energy and competition for space (e.g. *Perrin*, 1992). Modern acervulinids occur commonly from shallow water down to 130 m, with a cryptic habitat in very shallow settings (e.g. Gulf of Aqaba; *Reiss and Hottinger*, 1984). *Perrin* (1992) described acervulinids as adapted to low-light conditions where competition with other encrusting organisms as calcareous algae is reduced. This would allow foraminifera to spread laterally, enhancing their role as primary builders. During the Early Eocene the acervulinid *Solenomeris* has been able to build monospecific reefs substituting corals as the main reef builder in relatively deep-water settings of the Tethyan realm (*Plaziat and Perrin*, 1992). The encrusting textulariid *Haddonia* and *Placopsilina* genera are widespread in this association occurring with *in situ* specimens. Modern *Haddonia* from the Somali Coast and Java (*Matteucci*, 1996) thrive in low light, low energy environments, being highly susceptible to detachment and destruction by high-water energy. The association of encrusting foraminifera with few flattened *Discocyclina* and small rotaliids points to the existence of limiting conditions like low light intensity and relatively high nutrients, which favor extensive microbial crusts development. This scenario would explain the low abundance and diversity of the LF.

In conclusion, the ‘bioconstructors’-dominated assemblage represent a benthic community adapted to live in a low-energy environment (deep mid-ramp setting), on primary soft, muddy substrate and secondary hard biogenetic substrate (corals and microbial crusts), likely characterized by enhanced nutrient level and reduced light intensity.

Assemblage 5: Orthophragminids-dominated assemblage

This foraminiferal assemblage only occurs in the Čebulovica section, usually in massive fine-grained wackestones. It is dominated by flattened orthophragminids, which constitute most part of a scarce and low-diverse community. Orthophragminids are usually represented by few specimens, associated with rare fragmented *Assilina* and small rotaliids (Fig. 2.4h). Calcareous red algae are common component associated with foraminifera.

The paleoecological interpretation of this assemblage is difficult because orthophragminids became extinct at the Eocene - Oligocene boundary. Therefore, a direct comparison to phylogenetically close extant taxa is not possible. Based on the morpho-functional characteristics, orthophragminids are considered homeomorph to *Cycloclypeus* (e.g. *Ćosović et al.*, 2004). Today most of the species belonging to this genus colonize the deep environments, down to the lower limit of the photic zone (*Langer and Hottinger*, 2000). Fossil orthophragminids have been described from a diverse array of environments within the photic zone including shallow back- and fore-reef/shoal environments (e.g. *Anketell and Mriheel*, 2000; *Ghose*, 1977) to deeper, outer ramp environments (e.g. *Gilham and Bristow*, 1998). Their test morphologies were proposed as feature to differentiate inner-ramp environments above the FWWB (ovate form) from mid- to outer-ramp areas (flattened forms; e.g. Eocene from Tunisia; *Loucks et al.*, 1998). In our assemblage, orthophragminids have quite flat tests and lateral chamberlets with a low shape. They occur in a micritic matrix together with thin, delicate algal and foralgal crusts. These features indicate deposition in a somehow deep, low-energy setting with reduced light conditions.

Therefore, the orthophragminids-assemblage thrived in a deep mid-ramp setting characterized by a soft muddy substrate.

Facies interpretation – The facies FA is characterized by foraminiferal assemblages and sedimentological features which indicate a change in depositional conditions with respect to the underlying Foraminiferal limestones (F). The boundary between facies F and FA is marked by an increase in the amount of micrite, an increase in diversity (but only moderately in abundance) of larger foraminifera and the common occurrence in the FA of encrusters (mainly foraminifera associated with red calcareous algae, corals and microbial crust). The high amount of micrite and the absence of wave-related sedimentary structures likely reflect deposition in a relatively low-energy environment.

The diversity of larger foraminifera in this facies indicates the existence of ecological niches with different features. However, their moderate abundance, especially in the more muddy lithologies, might be due to limiting ecological conditions likely low light intensity and/or relatively high nutrient levels. Considering the calcareous red algae assemblage, corallines are dominant, represented by Melobesioideae, Sporolithaceae and Peyssonneliaceae. In more bioclastic lithologies they occur as small rodoliths and subordinate thick crusts, commonly associated with *Assilina*. When the mud content is higher they form thin, irregular crusts and occur together with small orthophragminids and small rotaliids. Nowadays, Sporolithaceae and Melobesioideae occur in carbonate environments of subtropical and tropical areas occupying deep-water habitats with variable nutrient conditions (*Aguirre et al.*, 2000). Peyssonneliaceans show a broad latitudinal distribution ranging from the tropics to the poles in waters of normal marine salinity at depths of few meters, although they were observed down to depths of 120 m (*Bassi*, 1997).

Therefore, this facies is interpreted as deposited below the FWWB, in a mid-ramp setting. The presence of abraded and fragmented bioclasts occurring in specific beds, points to occasional reworking by storms and/or bottom currents. In this mid-ramp, the upper part was dominated by LF (mainly *Assilina*) commonly associated with calcareous red algae and small coral colonies and rubbles. The deeper mid-ramp, close to the lower limit of the photic zone, had few LF (mainly flattened orthophragminids) and encrusting biota forming coral-microbialite mud mounds and wackestones with thin foralgal crusts. The occurrence of these thin delicate crusts, the presence of a diversified community of encrusting foraminifera and the morphological features of corals occurring as dendritic-ramose and encrusting colonies suggest reduced light conditions (*Bassi*, 2005; *Bosellini and Papazzoni*, 2003). Moreover, possible high nutrient values could have favored the growth of microbial crusts (*Zamagni et al*., 2006) associated with encrusting foraminifera.

2.4.3 Bio-Peloidal limestones (BP)

Facies description - This facies occurs in the uppermost part of the studied sections with a thickness of 55 m (Fig. 2.3, Table 2.1). It is represented by poorly stratified, dark grey packstones with a relatively high amount of carbonate mud, dominated by larger foraminifera and other skeletal remains mixed with variable percentage of fecal pellets and micritic grains (mainly micritized bioclasts) acting as a matrix to larger bioclasts (e.g. alveolinids). The most abundant larger foraminifera are represented by the alveolinids, nummulitids and subordinate soritids associated with other benthic foraminifera (mainly small rotaliids and miliolids), encrusting foraminifera, and rare small, robust/ovate orthophragminids. The associated macrofauna is composed of abundant echinoid fragments and rare complete skeletons with spines clustered around their tests, common bryozoans and few mollusks (mainly gastropods). Calcareous algae are rare, mostly represented by dasycladaleans and very rare small fragments of red algae.

Micritization and bioerosion strongly affect the bioclasts in this assemblage producing a bimodal grain-size distribution with abundant mud and sand-size fragments (mainly foraminifera and echinoids). Foraminifera are usually abraded and affected by micritization, especially nummulitids and small rotaliids with development of thin destructive micritic coatings. Constructive micrite envelopes with no clear evidence of microborings are locally developed on foraminiferal outer walls. Alveolinid shells are frequently encrusted by acervulinids and/or thin constructive coatings and are affected by macroborings. Peloids are the second most abundant component in this facies. They mostly represent micritized bioclasts and fecal pellets, which form elongated clusters.

The appearance of *Alveolina* spp. (*A. aramaea aramaea*) at the base of PB limestones indicates Ilerdian age (SBZ5) for this facies, ranging until SBZ8 (middle Ilerdian).

Foraminiferal assemblages - One larger foraminiferal assemblage was identified in this facies, the alveolinids-nummulitids assemblage (ass. 6).

Assemblage 6: Alveolinids-Nummulitids assemblage

The most abundant larger foraminifera in this assemblage are represented by *Alveolina*, *Assilina*, *Nummulites* and subordinate soritids (Fig. 2.5). Other common foraminifera are small rotaliids (e.g. *Smoutina* sp., *Kathina* sp.), encrusting foraminifera (acervulinids and *Haddonia*), miliolines (small miliolids, lacazinids), agglutinated foraminifera (*Vania, Thomasella*), and rare small and robust *Discocyclina* sp. The alveolinids-nummulitids assemblage is dominated by alveolinid in the lower portion of the facies and *Nummulites*, occurring throughout the facies but with variable concentration. To a general extent they are more abundant in the upper part of the successions. *Nummulites* are 'robust', ovate, macrospheric forms whereas B-forms are rarely present. *Assilina* is present throughout the facies with few, small specimens. Soritids are concentrated in beds and are represented by *Orbitolites* (Fig. 2.5b) and *Opertorbitolites*.

Encrusting foraminifera occur with acervulinids, which encrust and bond larger foraminifera or as scattered fragment with circular and hooked shapes (Fig. 2.5c). *Haddonia* is also present, encrusting foraminiferal shells.

Living and fossil alveolinids are shown to occur in a variety of shallow-marine settings with distributions independent of the substrate. Living forms, such as *Borelis* sp. and *Alveolinella quoyi*, proliferate to depths less than 35 m (*Langer and Hottinger*, 2000). In Papua New Guinea, *Alveolinella quoyi* has been observed to live as epibiont on both algal-covered hard substrates in protected, shallow (3-5 m) environments, or on stable substrates covered with organic detritus in 20-30 m of water (*Severin and Lipps*, 1989). Alveolinids have been described from the Eocene of Oman, associated with *Nummulites* and *Assilina* as living on protected, inner ramp setting with sparsely vegetated sand substrates close to seagrass beds (*Beavington-Penney et al.*, 2006).

Extant *Nummulites* have never been described as seagrass dwellers. However, the occurrence in this foraminiferal assemblage of robust/ovate, A-form-dominated population with rare or absent B-forms suggests a shallow-marine environment affected by limiting conditions, such as slightly elevated nutrient levels, favoring the development of a community of 'r-selection' strategists (*Beavington-Penney and Racey*, 2004; *Hohenegger*, 1999). Since *Orbitolites* and *Opertorbitolites* are extinct since the Late Eocene, ecological considerations must be based on living homeomorphs. Based on structural similarities (e.g. *Ghose*, 1977), a general agreement exists to consider living larger soritids such as *Marginopora*, *Sorites* and *Amphisorus* as the closest genera to *Orbitolites.*

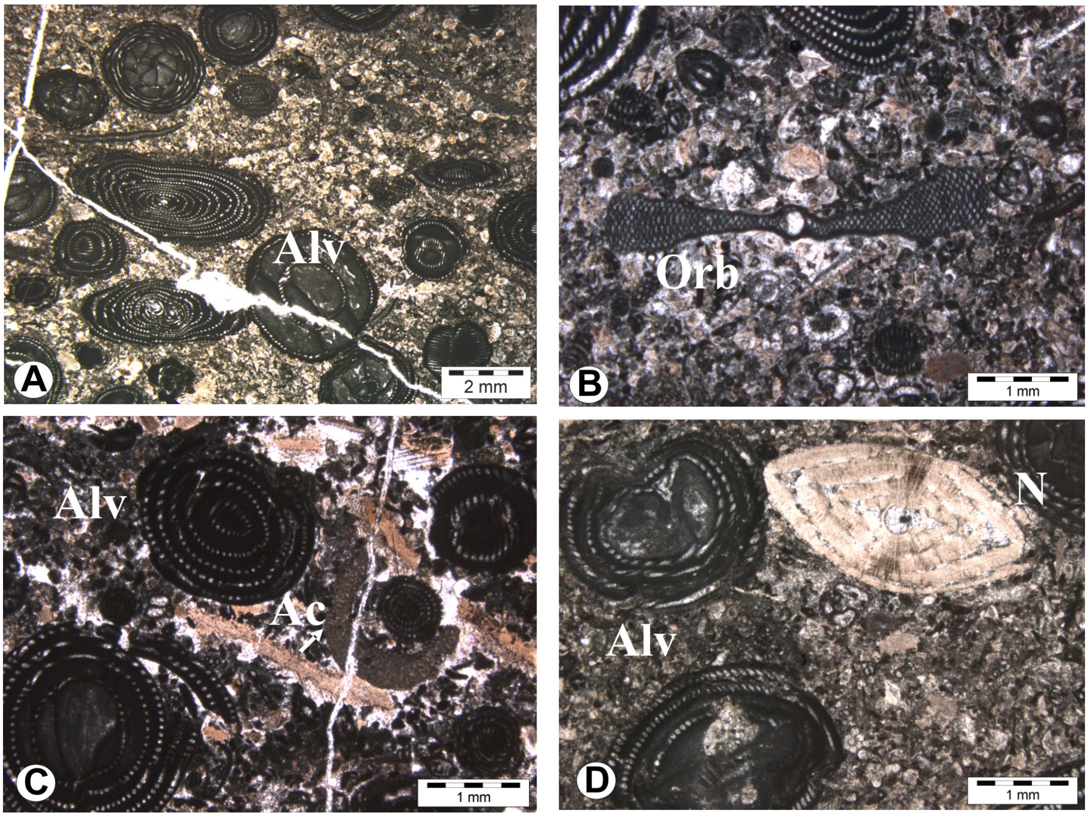


Figure 2.5: Photomicrographs of Ilerdian foraminiferal assemblages of the inner ramp Bio-Peloidal facies (BP): **a** Assemblage 6: packstone with *Alveolina* (*Alv*); **b** Assemblage 6: packstone with *Orbitolites* (*Orb*); **c** Assemblage 6: packstone with *Alveolina* (*Alv*), echinoid fragments and hooked-shape acervulinids (*Ac*); **d** Assemblage 6: packstone with *Alveolina* (*Alv*) and *Nummulites* (*N*), note bioerosion of the alveolinids.

Living soritids are commonly described as epiphytes thriving in shallow lagoonal environments, although none appear to be restricted to seagrass leaves. *Amphisorus* and *Marginopora* have been observed in the NW Pacific (*Hohenegger*, 2004) to settle on rounded boulders and unstructured carbonate rocks, where they strongly attach with organic glue to numerous fine algal filaments *(Langer*, 1993). Today, the closest analogue of Paleogene *Haddonia* and acervulinids represent important stabilizing encrusters of tropical bioclastic bottom with a wide depth range of distribution (e.g. 40-90 m in the Gulf of Elat; *Hottinger*, 1983). Modern analogue of Paleogene *Haddonia heissigi* have been found to live in low intertidal and subtidal environments on bioclastic sand forming the substrate for seagrass covers (e.g. Southern Somalia; *Matteucci*, 1996).

A similar foraminiferal assemblage from Greece have been interpreted by *Accordi et al.* (1998) as deposited at the boundary between inner and mid ramp, representing stabilized sandy shoals in a protected coastal embayment. Similarly, *Beavington-Penney et al.* (2006) described a foraminiferal community from Oman dominated by *Alveolina* likely thriving on the patchily vegetated muddy sands of a protected lagoon or embayment. *Özgen-Erdem et al.* (2005) interpreted alveolinids, nummulitids, and orbitolitids dominated assemblage from Turkey as deposited in a lagoonal environment. In Spain (Scheibner et al. 2007) and in France (*Rasser et al.*, 2005) *Alveolina*-dominated assemblages have been considered as thriving in inner platform, influenced by siliciclastic input.

To summarize, foraminifera of the assemblage 6 thrived in a protected inner ramp, likely a lagoon or embayment, characterized by muddy and sandy substrate, mainly represented by foraminiferal test and echinoids fragments and carbonate mud. The substrate was probably sparsely vegetated by seagrass and/or stabilized by algal films as indicated by the occurrence of the ephiphytic *Orbitolite*s and *Opertorbitolites*.

Facies Interpretation – Based on their biotic components and sedimentological features, facies of the Ilerdian BP limestones have been interpreted as deposits of an inner ramp setting. The common occurrence of carbonate mud and absence of structures indicative of high-energy events support this interpretation. However, in the field no evidence of shoals or bioconstructions that would allow the development of a protected lagoon has been found. The protection could have derived from an embayed nature of the depositional setting as well as from the existence of seagrass or algal cover. The occurrence of constructive micrite envelopes on larger foraminifera indicates the presence of a vegetated substrate; in fact such structures have been described from modern seagrass beds (*Perry*, 1999). The patchy distribution of encrusting epiphytes (*Orbitolites* and *Opertorbitolites*) and dasycladaleans indicate the existence of algal meadows. Their distribution in specific beds could be the result of storm-induced winnowing from close seagrass with consequent transport of seagrass leaf and respective encrusters or alternatively due to a low seagrass cover. However, large distribution of epiphytic foraminifera was described from Istrian Eocene Alveolina-Nummulites Limestone (*Drobne,* 1977, 1979). Moreover, the biofabrics and poorly developed bedding in facies BP most probably reflect intensive bioturbation and abundant remains of infaunal echinoids support this interpretation. Widespread bioerosion and micritized bioclasts indicate low sedimentation rate likely coupled with enhanced nutrient conditions (*Hallock*, 1988).

2.5 Discussion and paleoenvironmental interpretation

The distribution of the studied benthic assemblages in the shallow-water carbonates from SW Slovenia has been controlled mostly by a combination of depth gradient and substrate nature. Based on sedimentological and paleontological data a generalized facies model and foraminiferal assemblage distribution has been reconstructed (Fig. 2.6).

The facies model presented here shows a depth gradient from the inner ramp to the mid ramp with distribution of foraminifera and other important components (scleractinian corals and calcareous algae) reflecting the presence of different depositional biotopes depending mainly on the nature of the substrate. In fact, substrate nature and water depth are key parameters in controlling biosystems inhabited by different genera or species of larger foraminifera (*Hottinger*, 1983).

In the Thanetian, the studied successions exhibit a deepening trend with Foraminiferal limestones (facies F) deposited in a protected, locally restricted, patchily vegetated innermost ramp. In this setting the two foraminiferal assemblages (assemblages 1 and 2) are dominated by agglutinated foraminifera, small rotaliines and miliolines with local enrichment of *Miscellanea* and small *Ranikothalia*. The presence of beds with oligotypic fauna (smaller miliolids-dominated assemblage) indicates locally restricted conditions. The Foralgal limestones (facies FA) are interpreted as deposited in a mid-ramp setting. The three foraminiferal assemblages that characterize this facies, alternate with one another suggesting close depositional depths. However, some major ecological and compositional gradients can be identified between the *Assilina*-dominated assemblage (assemblage 3) on one side and the ‘bioconstructors’-dominated assemblage (assemblage 4) / orthophragminids-dominated assemblage (assemblage 5) on the other side. These gradients are expressed by: (1) an increase in encrusting biota (foraminifera, calcareous red algae and microbialite crusts); (2) decrease in abundances and diversity of larger foraminifera; (3) increase in carbonate mud; and (4) decrease in coarse bioclasts. These features indicate a decrease in the hydrodynamic energy with *Assilina*-dominated assemblage thriving in storm/current influenced environments, just below the FWWB, passing to the orthophragminids and the ‘bioconstructors’-dominated assemblages colonizing a deeper, lower energy setting along the mid ramp. Additionally, the substrate nature shows a differentiation as consequence of changing water energy. The *Assilina*-dominated assemblage thrived on sandy, unstable substrates; the orthophragminids-dominated assemblage lived on muddy substrates, and the ‘bioconstructors’-dominated assemblage flourished on secondary hard biogenic substrate represented by coral-microbial encrustations. Deposition of the Ilerdian Bio-Peloidal limestones (facies BP) marks a shallowing trend with deposition on a protected inner ramp with muddy and sandy substrates, partly covered or close to seagrass beds. *Alveolina*, *Nummulites* and locally *Orbitolites* (assemblage 6) thrived in this setting.

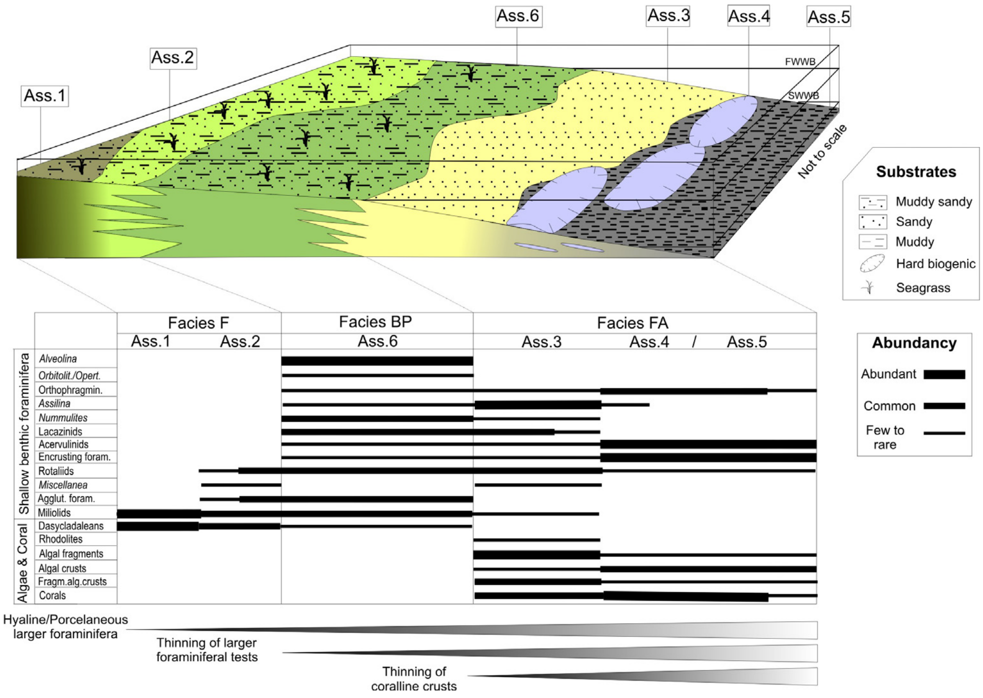


Figure 2.6: Schematic reconstruction of Late Paleocene-earliest Eocene foraminiferal assemblage distributions in respect to depth, substrate nature, water energy and nutrients along a ramp transect.

The quality of the paleo-depth signal is the highest when a foraminiferal community reaches its greatest diversification. The consequence of higher diversification is the restriction of each group to specific niches (*Hottinger*, 1997). In fact, paleoenvironmental models of foraminiferal distribution during the Early Paleogene are mainly based on Eocene assemblages (e.g. *Arni*, 1965; *Luterbacher*, 1984), since that was the time of higher diversification. These models usually involve “bank” of larger foraminifera (especially made up of *Nummulites* and *Alveolina*), which forms significant relief on the sea floor producing a range of linked sub-environments within the photic zone. In the present study we focus on a pre-Eocene climax, when the diversification of foraminifera was still quite low.

This model differs from the Eocene ones mainly for the absence of foraminiferal shoals and banks, which have been not found in the studied area.

Light intensity

Changes in the foraminiferal test composition, shape, and dimensions express environmental changes nonlinearly correlated with water depth gradients, most likely light intensity and water energy (*Hottinger*, 1983). Thanetian assemblages are characterized by a taxonomic transition from small imperforate porcelaneous and robust lamellar-perforate hyaline forms in the lower facies (Facies F) to larger, flatter hyaline forms (including orthophragminids and *Assilina*) and encrusting foraminifera in the facies FA. Such a shift suggests a decrease of light intensity. In fact, LF typical of shallow waters produce ovate tests with thick wall, like lamellar-perforate foraminifera, and/or porcelaneous, imperforate wall structures. These features allow preventing photoinhibition of symbiontic algae within the test in high intensity light conditions. On the other hand, the shift to flattened, hyaline foraminifera are usually found at increasing water depths where the light intensity is strongly reduced (e.g. *Hohenegger*, 1999). An increase in light intensity in shallower-water settings most likely characterizes the deposition of the Ilerdian facies BP, as attested by the presence of large porcelaneous forms (lacazinids, alveolinids and *Orbitolites*) associated in variable proportions with lenticular/ovate hyaline forms (small *Nummulites* and *Assilina*).

Water energy

All of the facies analyzed in the present study have a low energy index. Carbonate mud is generally abundant and cements are reduced to syntaxial overgrowth on echinoid fragments. These evidences combined with the absence of high-energy structures in the inner-ramp facies F and PB, indicate deposition of Čebulovica and Kozina successions in a protected environment, like an embayment, as a local feature characterizing the studied part of the AdCP. Alternatively or additionally, sedimentological and compositional evidence suggests the existence of a vegetation cover, which could explain the low energy index.

Nutrients

The protected nature of the depositional setting, possibly affected by tectonically confined physiography of the NW Dinaric foreland basin during the Early Paleogene, would explain the development of high nutrient content in an otherwise oligotrophic region as the Central Tethys (*Hottinger*, 1990). In the studied sections, both facies and foraminiferal assemblages show evidence of an elevated trophic regime. In particular, the facies F, deposited in shallow subtidal setting, hosts foraminiferal assemblages dominated by small miliolids and rotaliids, usually micritized. Miliolids and small rotaliines commonly replace larger symbiont-bearing rotaliines when trophic resources increase (*Hallock and Glenn*, 1986). Additionally, bioeroders, such as endolithic algae and fungi, clionid sponges, boring bivalves and echinoids, may flourish in moderately oligotrophic to mesotrophic settings, with highly effective micritization processes (*Hallock*, 1988; *Peterhänsel and Pratt*, 2001).

LF became common in the facies FA. These are mainly large, flat rotaliines with moderate diversity and abundance, mainly associated with echinoids, encrusting foraminifera and encrusting calcareous red algae. The common occurrence of encrusting biota in assemblages 4 and 5 suggests enhanced trophic levels (i.e. mesotrophic conditions), with competition for the substrate as the main limiting factor (*Mutti and Hallock*, 2003). The presence of scleractinian corals as small encrusting colonies, rubbles and/or colonies encrusted by microbialite to form mud mounds support this interpretation. Indeed, bioerosion may reduce or halt reef development as a consequence of an excess of nutrients. These nutrification processes would in turn account for the cyanobacterial and algal blooms (*Hallock*, 2005), as suggested by the development of microbialites overgrowing corals in the mid-ramp setting. This pattern could be interpreted as the result of occasional storms creating bottom currents responsible for transportation and redistribution of nutrients in deeper waters (e.g. *Bassi*, 2005).

Facies BP also shows evidence of enhanced nutrient levels, possibly due to the proximity of seagrass beds. Porcelaneous foraminifera (alveolinids, *Orbitolites*) and robust, small hyaline foraminifera (*Nummulites*) strongly affected by micro- and macrobioerosion are dominant in this facies. Additionally, abundance of detritivores (echinoids) and filter-feeders (bryozoans) agrees with this interpretation.

Mechanisms for changes in nutrient supply

High nutrient concentration is a limiting factor in the flourishing of symbiont-bearing foraminifera that are considered forms highly adapted to stable, oligotrophic, nutrient-deficient conditions of tropical and subtropical settings (e.g. *Hallock*, 1985). Nevertheless, studies performed on shallow-water carbonate sediments in SE Asia (e.g. *Wilson and Vecsei*, 2005) demonstrated that low light-dependant organisms, like LF, can form abundant and extensive facies in humid tropical settings affected by local upwelling and/or intense run off. During the Late Paleocene - Early Eocene, sedimentation along the AdCP took place in the subtropical climate zone. The hot humid climate of this area during the Early Paleogene is indicated by the widespread occurrence of bauxites in Istria (*Durn et al.*, 2003). These bauxites are associated with a regional paleokarstic unconformity and occur in an apparent stratigraphic gap of about 30-50 Ma between the Lower to Upper Cretaceous and Lower to Middle Eocene carbonate deposits. The Early Eocene age of the paralic/palustrine Liburnian deposits overlying the bauxite-filled karst relief in northern Istria (*Drobne*, 1977) indicates hot and humid climatic conditions, contemporaneous to the deposition of the studied Upper Paleocene/lowermost Eocene carbonates. In fact, these conditions are fundamental for ferrallitic weathering and bauxite formation.

The deposition of facies FA and BP coincided with the incursion of the warmest period of the Cenozoic (*Zachos et al.*, 2001). This thermal perturbation should not have had direct effects on distribution of larger foraminifera. Extant symbiont-bearing foraminifera are usually distributed within the 25°C summer isotherms, with selected larger foraminifera (i.e. alveolinids and nummulitids) tolerating temperature around 30°C and more (*Langer and Hottinger*, 2001). However, high temperature could have also promoted secondary effects such as the intensification of tropical cyclones/storms (*Huber*, 2006) and/or of the weathering processes. Increased nutrient input by rivers is consistent with results from general circulation models predicting an intensified hydrological cycle at elevated greenhouse gas concentrations (*Pierrehumbert*, 2002; *Huber et al.*, 2003; *Caballero and Langen*, 2005), like during the PETM. These processes could have modulated nutrient delivery to the shallow-water realm coupled with bottom currents responsible for transportation of nutrients along the coastal surface water and the ramp.

2.6 Facies changes across the Paleocene - Eocene boundary

The studied successions in the north-western AdCP show a certain differentiation in facies and foraminiferal assemblages from the Paleocene to the Eocene. Small benthic foraminifera dominate the Upper Paleocene (SBZ3) facies. Corals are almost entirely absent except for rare and small patches. LF become common in the benthic communities of the uppermost Paleocene (SBZ4), with *Assilina* and orthophragminids being the most abundant forms often associated with red calcareous algae and corals. The Eocene is still dominated by different groups of LF. The dominance of larger benthic foraminifera in the whole Tethyan realm during the latest Paleocene to earliest Eocene is a well-known phenomenon. However, a major difference emerges by comparing the distribution of the shallow-water biota presented in this study with those described for North Spain and Egypt by *Scheibner et al.* (2007). The authors proposed a three-stage evolution for shallow-water carbonates from Spain relatively similar to that identified in Egypt (*Scheibner et al.*, 2005). They found persistent corals in the Pyrenees throughout the entire period under study. This does not hold for Egypt, where coralgal associations disappeared in the uppermost Paleocene. At this time LF became common in both regions, with *Assilina* dominant in the Pyrenees (*Assilina* beds, *Baceta et al.,* 2005), *Ranikothalia* and *Miscellanea* forming shoals in Egypt (*Scheibner et al.*, 2003). *Scheibner et al.* (2007) interpreted this evolution in terms of temperature gradients, with extreme values developed during the PETM and the long-term Eocene warming, affecting in a stronger way the low-latitude communities. Instead, the middle-latitude assemblages suffered a less intense effect with foraminifera experiencing only changes in morphotypes. Thus, the two middle-latitude carbonate platforms (AdCP and Pyrenees) were more similar to each other that each of them was to Egypt. Similarly to what observed in Spain, during the Latest Paleocene-earliest Eocene the LF of the north-western AdCP adapted to different depths, but no dramatic changes occurred in the assemblage composition. Similarities between these areas might suggest the existence of a latitudinal effect on the evolution of shallow-water benthic communities. However, during the Late Paleocene, the shallow-water biota of the AdCP was dominated by orthophragminids and coral-microbialite mud-mounds. This represents an unusual association if compared to other Tethyan localities. These dissimilarities could be, at least partially, explained in terms of differences in the local conditions exerting a control in the development of the shallow-water carbonate assemblages.

2.7 Conclusions

During the Late Paleocene-earliest Eocene sedimentation in the north-western AdCP (SW Slovenia) took place along a shallow-water carbonate ramp depositional system. This carbonate system was dominated by foraminiferal and foralgal deposits during the Thanetian. Agglutinated foraminifera, small rotaliids and miliolids dominated the Lower Thanetian innermost ramp assemblages. *Assilina*, *Discocyclina*, lacazinids and encrusting foraminifera associated with red algae and corals characterized the Upper Thanetian communities colonizing the middle-ramp setting. During the Ilerdian *Alveolina*, *Nummulites* and *Orbitolites* thrived in a protected and vegetated inner ramp. In the studied sections the predominance of mud-supported lithologies, packstones with relatively abundant carbonate mud and the lack of wave-related fabrics indicate that deposition occurred along a protected carbonate ramp. The widespread microbial activity, indicated by strong micritization and growth of microbial mud mounds, has been interpreted as the consequence of increased concentration of nutrients. The intense weathering in the humid, hot climate of the Late Paleocene-Early Eocene most probably played an important role delivering nutrients to the basin. In these conditions LF (*Alveolina*, *Nummulites*, *Assilina* and orthophragminids) thrived as dominant components showing unexpected tolerance to enhanced nutrients levels. The extreme climatic conditions at the Paleocene-Eocene transition might have caused environmental changes in the shallow-water settings. However, at the passage from the Paleocene to the Eocene larger foraminifera assemblages seem to be mainly marked by changes in morphotypes rather than major faunal turnover. On a more geographically restricted scale, local conditions might have controlled the development and evolution of shallow-water biota. When compared the studied LF assemblages to those from other mid-latitude (Atlantic realm, Pyrenees) and low-latitude areas (southern Tethys, Egypt), the existence of a latitudinal gradient in the benthic community composition might have had some effects to promote differences in the composition of the shallow-water benthic composition.

2.8 Acknowledgments

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Facies	Textures	Sedimentary structures	Taphonomic and early diagenetic features	F.A.	Benthic foraminifera	Other biota	Occurrences	Dep. setting
F	Wackestones to packstones	Thick bedded	Bioturbation Micritization	1	Miliolids, discorbids	dasycladaleans, ostracodes	KZ, ČB	Innermost ramp with restricted conditions
	Packstones, rarely grainstones			2	miliolids, agglutinated foraminifera, rotaliids, *Miscellanea,* small *Ranikhotalia*	dasycladaleans, echinoids, bryozoans	KZ, ČB	Innermost ramp
FA	Packstones to rudstones	Poorly bedded	Micritization Encrustation Bioerosion	3	*Assilina,* lacazinids, small/ovate *Discocyclina,* small/ovate *Nummulites, Miscellanea,* acervulinids, *Haddonia*, small rotaliids, miliolids, textulariids	peyssonneliaceans, corallinaceans (melobesioids, sporolithaceans, *Distichoplax biserialis*), scleractinian corals, echinoids, bryozoans, oysters	KZ, ČB	Upper mid-ramp
	Boundstones to floatstones	Massive		4	acervulinids, *Haddonia, Planorbulina*, *Miniacina*, *Plocopsilina*, *Discocyclina,* small rotaliids	scleractinian corals, encrusting red algae, microbial crusts, bryozoans, bivalves, ostracodes, planktonic foraminifera	KZ, ČB	Deeper mid-ramp
	Wackestone to packstones	Poorly bedded to massive		5	flatted orthophragminids, *Assilina*, acervulinids, *Haddonia*, small rotaliids	corallinaceans, peyssonneliaceans, bryozoans, echinoids, crinoids, bivalves	ČB	Deeper mid ramp
BP	Packstones	Poorly bedded with wave bedding surfaces	Micritization Encrustation Bioturbation Bioerosion	6	*Alveolina, Assilina Nummulites,* soritids *(Orbitolites, Opertorbitolites)*, *small Discocyclina,* acervulinids, *Haddonia*, lituolids, agglutinated foraminifera (*Thomasella labyrinthica, Vania anatolica*), miliolids, small rotaliids	dasycladaleans, echinoids, bryozoans, gastropods, bivalves, ostracodes	KZ, ČB	Inner ramp

Table 2.1: Relationship among facies, foraminiferal assemblages, textural and sedimentological features and major components. Benthic foraminifera and other biota are listed in order of decreasing abundance. F.A.: foraminiferal assemblages. KZ: Kozina section; ČB: Čebulovica section.

3. THE PALEOCENE – EOCENE THERMAL MAXIMUM (PETM) IN SHALLOW-WATER SUCCESSIONS (ADRIATIC CARBONATE PLATFORM): IMPLICATION FOR LARGER FORAMINIFERA EVOLUTION

Abstract

The effects on the biosphere of the environmental changes associated with the Paleocene-Eocene Thermal Maximum (PETM) (~55 Ma), one of the most rapid and extreme warming events in Earth history, are well characterized in open marine and terrestrial records but less is known from shallow-water settings, a major carbon sink. Here, we present δ^{13}C curves recording the full PETM event in shallow-water setting from carbonate successions of the Adriatic Carbonate Platform (SW Slovenia). The carbon isotope excursion (CIE), recorded in bulk-rock and foraminifera δ^{13}C records, is represented by a pronounced negative shift at the onset of the event followed by CIE-peak and a gradual recovery. The CIE coincides with the appearance of the first Eocene *Alveolina aramaea aramaea* marking the P-E boundary. The combined results from biostratigraphic and chemostratigraphic records show any synchronicity between the Early Eocene LF Turnover and the PETM. The turnover was probably a gradual replacement culminated with radiation of first large-sized LF occurring well after the PETM recovery during the Early Eocene, a fact suggesting that no direct causal link existed between the two events with the PETM exerting almost no influence on this long-term evolutionary history.

3.1 Introduction

The Paleocene - Eocene Thermal Maximum (PETM) was a rapid, transient warming event that occurred ~55.5 Ma ago (*Röhl et al.,* 2000; *Lourens et al*., 2005). During the PETM, sea surface temperature (SST°) increased by 5°C in the tropics to 8°C at mid-latitudes, and up to 9°C at high latitudes (*Sluijs et al*., 2008 and references therein). This hyperthermal event is globally recognized in marine and continental sedimentary rocks with the Carbon Isotopic Excursion (CIE), a prominent negative carbon isotopic shift at the onset of the Eocene, which provides a distinctive geochemical marker for the PETM (e.g., *Kennett and Stott*, 1991; *Thomas et al*., 2002). The CIE has been related to a geologically instantaneous (< 10 k.y.) injection of ^{13}C-depleted carbon in the form of CO_2 and/or CH_4, into the global exogenic carbon pool (*Dickens et al*., 1995; 1997), although the mechanism for this release remains controversial (*Sluijs et al*., 2007a). The rise of these greenhouse gases in the atmosphere promoted biogeochemical feedback processes, primarily increase of chemical weathering (*Ravizza et al*., 2001; *Crouch et al*., 2003) as consequence of a more effective hydrogeological cycle, recorded widely at middle and high latitudes (*Pagani et al.*, 2006). Studies for the Tethyan region (e.g., *Bolle and Adatte*, 2001; *Schmitz and Pujalte*, 2007; *Egger et al.*, 2009) indicated that during the Late Paleocene – earliest Eocene a seasonal climate, characterized by enhanced intra-annual humidity gradients, was established at intermediate latitudes.

Despite an abundance of studies on the effects of this abrupt climatic event on open marine systems, documenting heterogeneous responses from dramatic extinction (deep benthic foraminifera extinction e.g., *Thomas*, 2007) to rapid spreading (global acme of the heterotrophic dinocyst *Apectodinium*, *Crouch et al.*, 2001, 2003; *Egger et al.*, 2003; *Sluijs et al.*, 2007b), the information on the extent of this event on shallow-water marine organisms are still few (*Orue-Etxebarria et al.*, 2001; *Pujalte et al.*, 2003; *Scheibner et al.*, 2005; *Scheibner et al.*, 2007; *Pujalte et al.*, 2009a; *Scheibner and Speijer*, 2009). In these works the authors suggested a synchronicity between a major turnover in the Larger Foraminifera (LF) community ("Larger Foraminifera Turnover", hereafter LFT, *Orue-Etxebarria et al.*, 2001), with the rise of forms adapted to stable environmental conditions in warm, nutrient-depleted settings (extreme K-strategists), and the PETM event. Nonetheless, due to the limited occurrences of biostratigraphic markers, the common occurrence of stratigraphic gaps in shelfal areas, and the low resolution of the $\delta^{13}C$ curves acquired, these correlations remain speculative. Specifically, if the PETM induced such dramatic environmental perturbations (e.g., higher temperatures and precipitations, elevated fluxes of sediments and dissolved ions, eutrophication of marginal seas), how could have been coincident with the full recovery of K-strategy of life in the LF community?

In this work we focus on the study of shallow-water marine successions from the Adriatic Carbonate Platform (SW Slovenia), a wide, sub-tropical, isolated platform located along the northern margin of the Tethys. Here, continuous Paleocene to Lower Eocene marine carbonates are well exposed (*Zamagni et al.*, 2008). Tackling the issue of the possible effects of the PETM on the evolution of LF we reconstruct precise and continuous $\delta^{13}C$ curves for the shallow-water carbonates with two major aims: 1) to achieve the highest possible temporal resolution for the PETM on carbonate platform setting; 2) to compare the curves of this work with the reference curves from the pelagic realm. This establishes a detailed correlation between well studied paleoceanographic events and major biotic changes as observed in shallow-water platforms. We performed detailed biostratigraphic and chemostratigraphic analyses of two successions. This correlation shows that the appearance of the *Alveolina* genus coincided with the onset that the PETM; however, no clear evidence of major turnover in the LF communities have been observed. The new data for the PETM interval on the Adriatic Carbonate Platform provided in this study represent one of the most complete such records in shallow-water settings.

3.2 Geological and stratigraphical setting

The studied carbonate successions are exposed in the southern part of the Kras (Karst) Plateau in SW Slovenia (Fig. 3.1A), corresponding to the Komen Thrust Unit of the NW External Dinarides fold and thrust belt (*Placer*, 1981). The Kras region has been since long time a key area for biostratigraphic study of the LF, especially alveolinids (*Drobne*, 1977), due to their widespread occurrences and abundances in shallow-water successions. During the latest Cretaceous - Early Paleogene the paleogeography of this area (~32°N paleolatitudes) was characterized by a vast subaerially exposed, isolated carbonate platform, the Adriatic Carbonate Platform (AdCP, *Vlahović et al*. 2005), with shallow-water carbonate sequences deposited in marginal areas (Fig. 3.1B). Towards the north/northeast, a deep-water basin was contiguous to the SW-verging Dinaric orogenic wedge (*Otoničar*, 2007).

A tectonically southwest-ward driven platform-basin migration occurred from the uppermost Cretaceous to the Lower Paleogene (*Bignot*, 1972; *Drobne*, 1977; *Košir and Otoničar*, 2001) and was recorded by the diachronous deposition of three superimposed units (Kras Group, Transitional Beds, and Flysch). Consistent NE-SW regional stratigraphic trends (*Košir and Otoničar*, 2001; *Otoničar*, 2007) indicate that the stratigraphic patterns of the platform and basin were largely controlled by flexural subsidence. A generalized stratigraphic column of the Upper Cretaceous, Paleocene, and Eocene deposits in the Kras region is shown in figure 3.1C. The lower unit (the Kras Group; Košir 2003) overlies the forebulge in unconformity (*Otoničar*, 2007 and references therein) and comprises three formations: 1) Liburnian Formation (Upper Maastrichtian to Lower Paleocene), an alternation of restricted, marginal marine, paralic and palustrine carbonates (*Ogorelec et al*., 2001); 2) Trstelj Formation (Upper Paleocene), shallow subtidal limestones composed of a lower member dominated by foraminiferal limestones and an upper member including foralgal limestones and microbialite-coral mounds (*Zamagni et al*., 2008, 2009); and 3) Alveolina-Nummulites Limestone (Lower Eocene), shallow subtidal limestones characterized by accumulations of larger foraminifera (*Drobne*, 1977; *Jurkovšek et al*., 1996; *Zamagni et al*., 2008).

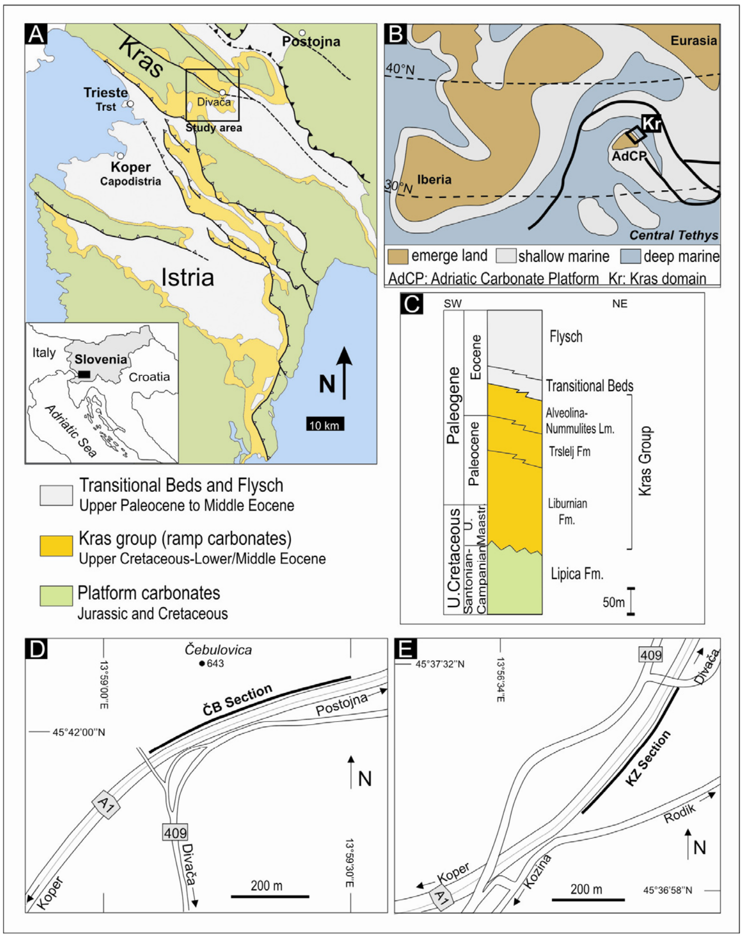

Figure 3.1: Geographic and geological context of the study area. A) Simplified geological map of the SW Slovenia and NW Croatia modified from *Košir* (2003). B) Early Paleogene paleogeographic reconstruction based on *Ziegler* (1990) with the approximated location of the Kras region (Kr). C) Generalized stratigraphic column of the Uppermost Cretaceous – Eocene succession in the Kras region (based on *Košir*, 2003). D) Location of the Čebulovica section. E) Location of the Kozina section.

The total thickness of the Kras Group ranges from several tens of meters to more than 450 m. The middle unit (Transitional Beds; Lower Eocene) consists of up to 50 m of pelagic and hemipelagic limestones and marls. The upper unit (Flysch; Lower Eocene) is composed of a thick succession of sandstone-dominated turbidites, marls, mudstones, and resedimented carbonates. Local variations of the stratigraphic patterns most likely resulted from reactivation of antecedent pre-orogenic structures.

A reliable reconstruction of architecture and size of the Early Paleogene carbonate platform in the studied area is difficult because of the complex thrust-nappe structure of the NW Dinarides. However, the platform geometry inferred from regional facies relationships (*Drobne*, 1977; *Jurkovšek et al.*, 1996; *Ćosović et al.*, 2004) corresponds to a carbonate ramp depositional system characterized by roughly parallel NW-SE trending facies belts, as suggested also by paleotransport patterns (*Orehek*, 1991; *Babić and Zupanič,* 1996; *Turnšek and Košir,* 2004).

3.3 Material and methods

3.3.1 Sections

The studied sections are exposed along the motorway between Postojna and Koper (Fig. 3.1). Two sections were sampled in detail, Čebulovica and Kozina, to perform biostratigraphic and chemostratigraphic studies. Other sections, Divača (D), Divača-Kozina East (DKE), and Divača-Kozina West (DKW) were sampled to refine the facies interpretation and the depositional model, initially based only on the study of first two sections (*Zamagni et al.*, 2008). All the sections show negligible or moderate tectonic deformation and almost continuous exposure. The sections were logged, sampled, and described with respect to sedimentary structures and components.

The Čebulovica section (ČB) is located 4 km northwest of the town of Divača (starting point 45°42’1’’N - 13°59’19’’E). The logged succession is ~200 m thick (Fig. 3.1D), and is composed of ~155 m of poorly bedded to massive limestones (Trstelj Formation, Upper Paleocene), followed by ~45 m of wavy-bedded Alveolina-Nummulites Limestones (lowermost Eocene). The base of the section does not cover the contact with the rhythmically-organized, dark limestones of the Liburnian Formation (Uppermost Cretaceous – Lower Paleocene, *Jurkovšek et al.*, 1996; *Ogorelec et al.*, 2001). The Kozina section (KZ) is located close the town of Kozina (starting point 45°37’22’’N - 13°57’19’’E), ~10 km southwest of the Čebulovica section (Fig. 3.1E). The contact with the Liburnian Formation is not exposed. The succession, ~100 m thick, comprises ~50 m of thickly-bedded to massive limestones of the Trstelj Formation overlying by ~50-m-thick succession of Alveolina-Nummulites Limestones. Sections Divača (D), Divača-Kozina East (DKE), and Divača-Kozina West (DKW) are located between the ČB and KZ sections along the motorway, covering the upper member of the Trstelj Formation (DKE and D) and, in the case of DKW, also the P-E boundary. Meter-scale microbialite-coral mounds are exposed in the DKW section, which were identified as latest Paleocene in age (*Zamagni et al.*, 2009). Section D is ~130 m thick, with 75 m of thickly-bedded and nodular limestones (lower member of the Trstelj Formation) at the base overlain by 55 m of massive to strongly nodular limestones (upper member of the Trstelj Formation).

3.3.2 Stable isotopes

Carbon and oxygen stable isotopes were measured on bulk rock for the Čebulovica and Kozina sections. Samples for isotope stratigraphy were taken at an average spacing of ~1 m, except close to the P-E boundary where the sampling space was ~30 cm in Čebulovica, and ~50 cm in Kozina. Samples were drilled from freshly cut rock slabs avoiding sparry cements and vein material. In addition, in the Čebulovica section fine-grained texturally uniform matrix micrite, large miliolids/alveolinids, and nummulitids were also sampled for stable isotope analysis close to the P-E boundary. The bulk sample powder was analyzed on a DELTA plus XL Thermo-Fischer Finnigan GasBench II mass spectrometer at the GFZ in Potsdam. The micrite and foraminifera samples were analyzed on a MAT 253 Thermo-Fischer Finnigan GasBench II at the ETH in Zurich. Stable isotope values are reported in the δ (per mil) notation relative to the Vienna Pee Dee belemnite standard (vPDB). External analytical precision based on replicate analysis of standards (NBS19, CO1, CO8) was <0.1‰ and +/- 0.1‰ for O and C isotopes, respectively.

3.3.3 Biostratigraphic framework

The biostratigraphic study of Larger Foraminifera (LF) is based on randomly oriented thin-sections of cemented carbonate rocks. The taxonomic frameworks used for LF identification are *Drobne* (1977), *Hottinger* (1960), *Schaub* (1981), and *Hottinger and Drobne* (1980).

The zonal scheme used in this study follows the shallow benthic standard zonation (SBZ) of *Serra-Kiel et al.* (1998), with the amendments regarding the position of the P-E boundary placed at the SBZ4-SBZ5 limit according to the new calibration proposed by *Scheibner and Speijer* (2009) and the position of this limit coincident with the base of the Ilerdian stage (*Pujalte et al*., 2009b), an informal stage introduced for marine deposits of the Tethyan realm (*Hottinger and Schaub*, 1960). The base of the Ilerdian stage correlates in the *Scheibner and Speijer* (2009) scheme with the base of the Ypresian Stage, which represents the Early Eocene (*Gradstein et al*., 2004; *Pujalte et al*., 2009b) and hereafter used intending earliest Eocene.

3.4 Results

3.4.1 Sedimentological analysis and biostratigraphic correlations

Upper Paleocene – Lower Eocene facies associations and foraminiferal assemblages

Three Upper Paleocene – Lower Eocene facies associations characterized by different foraminiferal assemblages were recognized (see *Zamagni et al*., 2008 for paleoecological interpretation of the foraminiferal assemblages). Main compositional and textural features of the facies associations are summarized in table 3.1; their stratigraphic distribution and correlation are represented in figure 3.2. The Paleocene deposits (Trstelj Formation) comprise facies association A, the Foraminiferal Limestones (SBZ3, early Thanetian, *Zamagni et al*., 2008), and facies association B, the Foralgal Limestones (SBZ4, late Thanetian, *Zamagni et al*., 2008). The facies association A is composed of a suite of facies deposited in a shallow inner ramp with lagoonal environments and shoals, dominated by small-sized benthic foraminifera and dasycladacean algae. Sedimentary structures are almost absent due to intense bioturbation. Locally, levels with *in situ* and reworked *Microcodium* and rhizoliths-indicate short episodes of subaerial exposure and early stages of calcrete formation (*Košir,* 2004). The passage to the facies association B is marked by a shift to lime mud-dominated lithologies, associated with a change of foraminiferal assemblages. The bulk of the Foralgal Limestones consists of deposits dominated by orthophragminids and crustose coralline algae (forming algal pavements) alternating with microbialite-coral mounds. These facies were interpreted as deposited on a distal mid-ramp to outer ramp, under the influence of storms and bottom currents. The lower Eocene limestones (Alveolina-Nummulites Limestone), corresponding to facies association C (Biopeloidal Limestones, early - middle Ilerdian, SBZ5 to SBZ8, *Zamagni et al*., 2008), were deposited in a protected inner ramp, dominated by *Alveolina*, associated with mollusks, micritized grains, echinoid fragments, and few dasycladaceans. More open marine settings are indicated in beds where *Nummulites* and *Assilina* occur together with abundant echinoid fragments and nummulitid debris.

Based on this facies analyses it has been concluded that a first increase in accommodation space took place at the transition from facies association A to B. With the deposition of the uppermost Thanetian facies, characterized by the increase of imperforate foraminifera, a reduction in the accumulation space occurred with the transition from proximal mid ramp to inner ramp of facies association C.

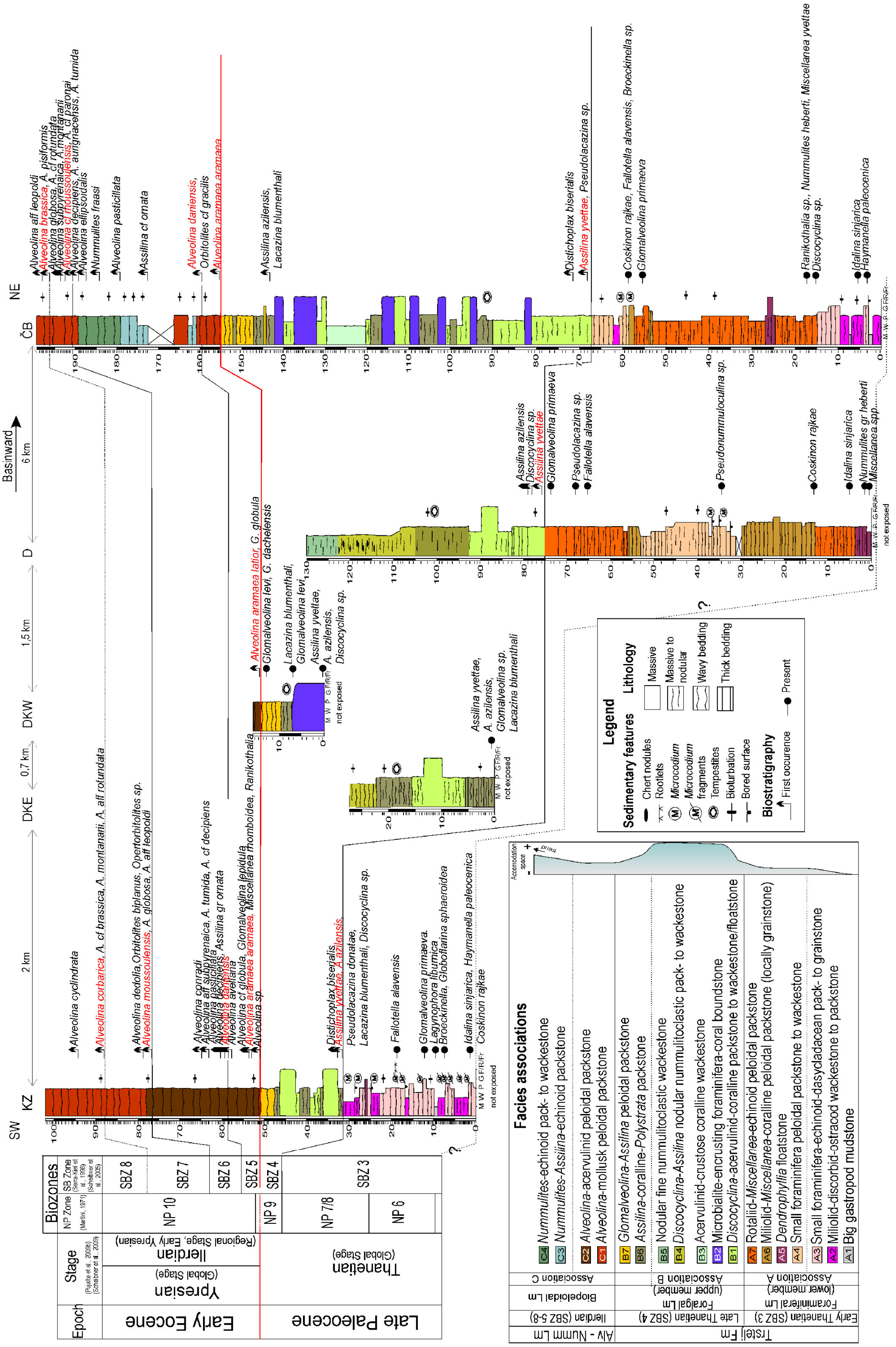

Figure 3.2: Facies associations (after *Zamagni et al.*, 2008), stratigraphy, and biostratigraphic markers in the studied sections. The position of the P-E boundary for the AdCP shallow-water successions is at the SBZ4-SBZ5 boundary according to *Pujalte et al.* (2009b) and *Scheibner and Speijer* (2009). See text for further explanation.

Biostratigraphic correlations and Larger Foraminifera biozonation

All the species used for the biostratigraphic correlation of the studied sections represent index fossils according to *Serra-Kiel at al.* (1998). The common occurrences of *Coskinon rajkae, Fallotella alavensis*, *Glomalveolina primaeva, Miscellanea yvettae*, and *Nummulites heberti* were used to make correlations within the SBZ3 (Fig. 3.2). The base of SBZ3 is not well defined in our sections mainly due to a lack of index taxa marking the SBZ2–SBZ3 boundary.

In contrast to this, the transition from SBZ3 (early Thanetian) to SBZ4 (late Thanetian) is well constrained (Fig. 3.2). The base of the SBZ4 is identified by the first occurrences (FOs) of *Assilina yvettae*, together with *Assilina azilensis*. *Glomalveolina levi*, another fossil index for the SBZ4, occurs only at the top of the facies association B, in shallower facies compared to those dominated by *Assilina,* together with *Lacazina blumenthali*. The latter enters also in the SBZ5. Other index fossils for the SBZ4 occurring together with assilinids are *Miscellanea miscella* and other miscellanids, and *Ranikothalia* sp. *Miscellanea rhomboidea* and *Ranikothalia* sp. occur also above the SBZ4. The base of the Ilerdian (SBZ5) is marked by the FOs of the *Alveolina aramaea aramaea*, *Alveolina avellana, Alveolina globula*, and *Glomalveolina lepidula* (Fig. 3.2). The absence of *Alveolina vredenburgi,* a common fossil index for the SBZ5*,* in the studied sections might be related to a reduced development of this species in the AdCP compared to other localities as the Pyrenees (*Pujalte et al*., 2009b). In fact, *Drobne* (1977) described rare specimens of this species in association with common *Alveolina aramaea* from outcrops close to Kozina. The base of SBZ6 is marked by the FO of *Alveolina daniensis* together with *Alveolina pasticillata*; the FO of *Alveolina moussoulensis* marks the base for the SBZ7, while the base of SBZ8 is marked by the FOs of *Alveolina corbarica* and *Alveolina brassica*.

3.4.2 Stable isotope data for the AdCP sections

The Kozina section: $\delta^{13}C$ - $\delta^{18}O_{bulk\ rock}$ curves

The 100-m-thick Kozina section represents the most proximal of the studied sections (Figs. 3.2-3.3). Facies association A (early Thanetian) covers the first 31.5 m of the section, with deposition of restricted lagoonal facies, with local development of brackish conditions, and bioclastic shoals. Evidences of subaerial exposure with *Microcodium* accumulation and pseudomicrokarsts are common in this facies. Facies association B (late Thanetian, 31.5-51 m) consists of mid-ramp deposits with development of foralgal pavements alternated with bioclastic *Assilina*-dominated packstones. Facies association C (early - middle Ilerdian, 51-102 m) consists of bioturbated packstones deposited in a protected inner ramp setting.

The $\delta^{13}C_{\text{bulk rock}}$ data collected for the Kozina section can be subdivided into four intervals (1-4 in fig. 3.3). Interval 1 (0-31.5 m), corresponding to facies association A, shows a first decrease from 2 to 0‰ followed by an increase up to 2 - 3‰, locally punctuated by negative spikes (-1‰ at 5, 12.5 and 23 m). A more pronounced negative excursion occurs at the top of this interval starting from 27 m, where values of -4‰ are reached. This negative excursion and the previous spikes broadly correlate with the occurrences of *Microcodium* levels, thus interpreted as representing short emersions. In the interval 2 (31.5-55.5 m), corresponding to facies association B, the $\delta^{13}C_{\text{bulk rock}}$ values are fairly homogeneous, with a long-term decrease from 2‰ to 0.5‰ at the transition to the following interval. This third interval (51-58.5 m) covers the base of facies association C and is characterized by a first negative spike (-0.2‰) followed by stable values around 0‰ and a further shift towards 2‰ in the uppermost part. This negative excursion is concomitant with the appearance of *Alveolina* sp., and immediately above *Alveolina aramaea aramaea* (Fig. 3.3), the biostratigraphic marker for the base of the Eocene (SBZ5, early Ilerdian, *Serra-Kiel et al.*, 1998), therefore is here interpreted as the onset of the CIE. In the fourth interval (58.5-102 m) $\delta^{13}C_{\text{bulk rock}}$ values remain rather stable around 2‰.

The $\delta^{18}O_{\text{bulk rock}}$ curve can be subdivided into four intervals roughly corresponding to those of the $\delta^{18}C_{\text{bulk rock}}$ curve. From 0 to 31.5 m (first interval) most of the values oscillate between -3 and -4‰, punctuated by negative spikes up to -6‰ at 5, 12.5, and 23 m. The uppermost part shows more negative values oscillating between -5 and -3‰. These negative spikes broadly correlate with negative spikes of the $\delta^{13}C_{\text{bulk rock}}$. In the second and third intervals the $\delta^{18}O_{\text{bulk rock}}$ values fluctuate widely between -3‰ and -5‰. In the forth interval the $\delta^{18}O_{\text{bulk rock}}$ values remain quite stable around -3‰.

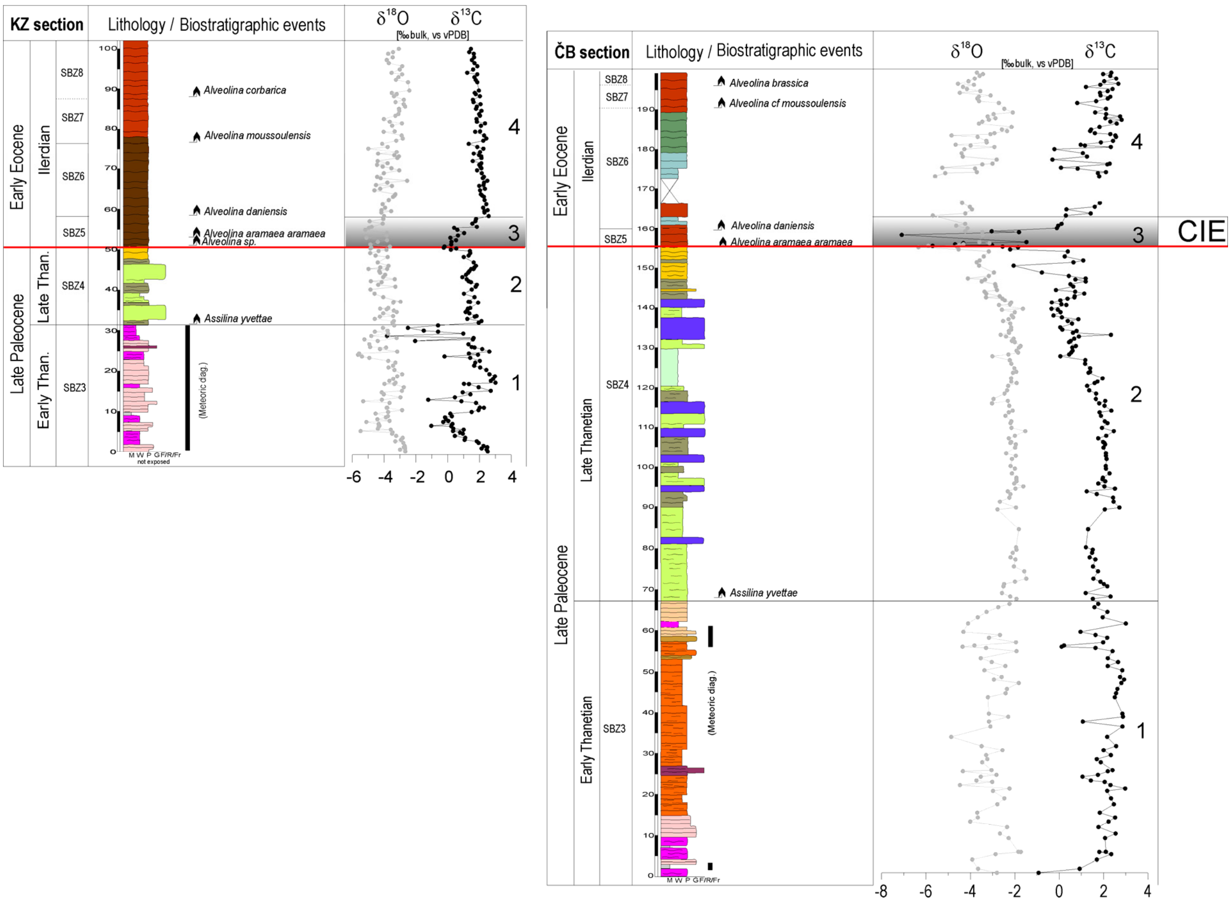

Figure 3.3: Biostratigraphic markers and stable isotope curves from bulk-rock samples of Kozina section and Čebulovica section. See text for further explanation.

The Čebulovica sections: δ^{13}C-δ^{18}O $_{\text{bulk rock}}$, and δ^{13}C-δ^{18}O $_{\text{micrite, alveolinids, nummulitids}}$ curves

The Čebulovica facies associations (Figs. 3.2-3.3) reflect deposition in a more distal position of the ramp compared to the Kozina section. Facies association A, corresponding to the first part of the section (0-67.5 m, early Thanetian), is characterized at the base by lagoonal and brackish facies alternated to foraminiferal shoals. The remainder interval is dominated by inner-ramp deposits with occasional emersions as indicated by thin levels with *Microcodium* towards the top of the interval. Facies association B (67.5-155 m, late Thanetian) is composed of mid-ramp deposits, characterized by the presence of metric microbialite-coral mounds associated with foralgal packstones and wackestones, in the more distal part of the mid ramp. Facies association C (155-198 m, early-middle Ilerdian) is characterized at the base by bioturbated packstones of protected lagoon with *Alveolina*, passing towards the top to deeper and more open marine facies dominated by nummulitids and echinoid fragments.

The isotope curves of the Čebulovica section are subdivided into four intervals (1-4 in fig. 3.3). The first interval (0-67.5 m) corresponds to the development of facies association A. The $\delta^{13}C_{\text{bulk rock}}$ curve is characterized by values oscillating around 2‰ except for two negative spikes at 56 m (0‰) and 60 m (1‰) correlating with the occurrence of *Microcodium*. The $\delta^{18}O_{\text{bulk rock}}$ curve is characterized by high-amplitude fluctuations between -2 and -4‰. The second interval (67.5-155 m), corresponding to the facies association B, is marked by a slow long-term decrease in the $\delta^{13}C_{\text{bulk rock}}$ values from 2‰ to 0‰, ending with a more pronounced oscillation and two abrupt negative shifts. The first occurs at 150 m (-2‰), followed by an increase to 1‰, and the second is at the top of the interval (154.5 m) with $\delta^{13}C_{\text{bulk rock}}$ values of -2.2‰. In this interval $\delta^{18}O_{\text{bulk rock}}$ is stable around -2‰ until 142 m, where the values decrease with a negative spike at 150 m (-3.5‰). This negative value correlates with the negative spike of the $\delta^{13}C_{\text{bulk rock}}$, and a second abrupt negative shift at the contact with the third interval (-6.3‰). The third interval (155-163 m) corresponds to the base of the Eocene (first occurrence of the *Alveolina aramaea aramaea*, fig. 3.3), and is marked by a sharp negative shift of the $\delta^{13}C_{\text{bulk rock}}$ values, from -1.8‰ at the passage between the second and the third interval to -5.7‰, just above the contact. This negative shift is interpreted here as the onset of the CIE. This negative spike is followed by a second more negative peak (-7‰) and an abrupt return to 0‰ at the top of the interval. Over this interval the $\delta^{13}C_{\text{bulk rock}}$ and $\delta^{18}O_{\text{bulk rock}}$ curves seem to be inversely correlated. In fact, the $\delta^{18}O_{\text{bulk rock}}$ curve shows a positive shift from -5.5 to -3.5‰ at the base of the interval, and remains around this value in correspondence of the negative peaks of the $\delta^{13}C_{\text{bulk rock}}$ curve. At the top of the interval $\delta^{18}O_{\text{bulk rock}}$ curve shows a slight negative shift to -4‰ when $\delta^{13}C_{\text{bulk rock}}$ curve shows a positive shift. In the fourth interval (163-198 m) $\delta^{13}C_{\text{bulk rock}}$ values oscillate, with high-amplitude fluctuations, around 2‰, with the $\delta^{18}O_{\text{bulk rock}}$ ranging between -5‰ and -2‰.

In order to further verify the quality of the isotopic data, the $\delta^{13}C$- $\delta^{18}O_{\text{bulk rock}}$ curves are compared with the $\delta^{18}O$ and the $\delta^{13}C$ curves from micrite (as the matrix of grainy bioclastic facies), alveolinids (in the Ilerdian deposits)/big miliolids (in the uppermost Paleocene deposits), and nummulitids (only for the Ilerdian deposits). The $\delta^{13}C_{\text{micrite, alveolinids, nummulitids}}$ curves show remarkable similarities in the trend comparable with that of $\delta^{13}C_{\text{bulk rock}}$ (Fig. 3.4). These similar trends with $\delta^{13}C$-$\delta^{18}O_{\text{bulk rock}}$ might account for the presence of diagenetic calcite, within the shell chambers, to screw the $\delta^{13}C_{\text{big miliolids/alveolinids}}$ towards very low values, as well as the microspar within the matrix, which might have modified the $\delta^{13}C_{\text{matrix}}$ in the same direction of the $\delta^{13}C_{\text{bulk rock}}$. Nonetheless, all the $\delta^{13}C$ curves for the three rock components record the abrupt negative shift, at 155 m just at the base of the Ilerdian, representing the onset of the CIE.

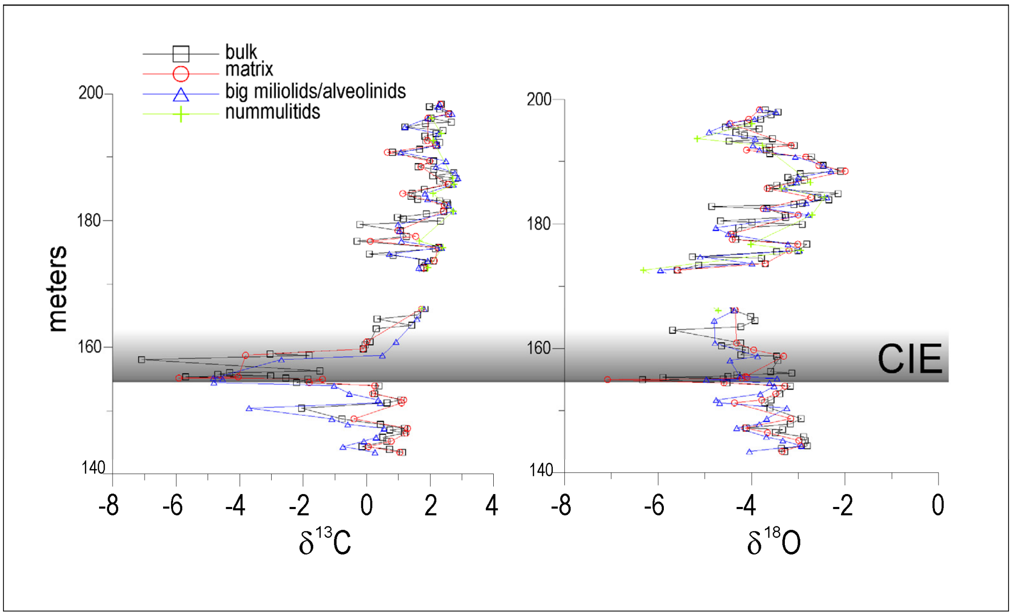

Figure 3.4: Isotopic curves of micrite, bulk, alveolinids, and nummulitids from Čebulovica section across the P - E interval and above.

3.5 Discussion

3.5.1 The AdCP $\delta^{13}C_{\text{bulk rock}}$ curves and the Carbon Isotopic Excursion

The primary sea-water stable isotope composition of shallow-marine carbonates can be influenced by regionally distinct water masses in lagoonal environments (e.g., *Patterson and Walter*, 1994; *Holmden et al*., 1998). Other possible causes for deviation of isotopic values from normal marine composition include the “vital effect” of skeletal grains that may exhibit non-equilibrium isotopic fractionation during biocalcification linked mainly to photosynthetic processes, as in the symbiont-bearing Larger Foraminifera (e.g., *Erez*, 1978). Nonetheless, under favorable conditions it has been demonstrated that major excursions and trends related to global paleoceanographic and paleoenvironmental changes can impact and be recorded in shallow-water carbonates (e.g. *Mutti et al.*, 1997; *Ferreri et al.*, 1997; *Jenkyns et al.*, 1999; *Mutti et al.*, 2006; *Parente et al.*, 2007; *Parente et al.*, 2008). In order to evaluate the reliability of the Kozina and Čebulovica isotopic curves with respect to the global $\delta^{13}C$ curve, we discuss correlations between $\delta^{13}C_{bulk\ rock}$, and sedimentological evidences of diagenesis, subaerial exposures, and facies changes, as well as comparing the AdCP curves with reference curves for the CIE.

Sedimentological and petrographic evidences of subaerial exposure and meteoric diagenesis are restricted to the first interval of the Kozina section (0-35 m) and to two *Microcodium*-enriched levels (at 56 and 60 m) in the Čebulovica section (Fig. 3.3). Negative peaks in $\delta^{13}C$ - $\delta^{18}O_{bulk\ rock}$ values correspond stratigraphically to the development of *Microcodium* levels indicating that marine values have been overprinted by meteoric diagenesis. The second interval in both sections is characterized by jagged long-term decline interrupted by an abrupt negative excursion corresponding to the CIE onset at the base of the third interval. In the Čebulovica section the magnitude of the CIE based on $\delta^{13}C_{bulk\ rock}$ is 3.85‰ (from -1.85‰ to -5.70‰), while in the Kozina section is ~1‰ (from 0.54‰ to -0.21‰). Although the shape of the CIE is largely dependant by substrate-specific differences (*Sluijs et al.*, 2007a), it is generally characterized by an onset marked by an abrupt, negative shift in $\delta^{13}C$ values, followed by a phase of relatively stable, low values, termed the 'body' of the CIE, and a subsequent recovery to higher $\delta^{13}C$ (*Bowen et al.*, 2006). This pattern is well reproduced in the Čebulovica and Kozina $\delta^{13}C$ curves, with the first negative shift and the following low values representing the initiation and main body of the CIE followed by the gradual return to values of 2‰ representing the recovery interval.

Concerning the amplitudes of the CIE excursion, the Čebulovica excursion is comparable to the average of 2.5‰ to 4‰ observed in mid-latitude continental shelf successions (e.g., *John et al.*, 2008). In the Kozina section, the magnitude of the excursion is comparatively smaller (~1‰) than records from literature and compared to the Čebulovica excursion. This might be related to a possible incomplete record of the CIE onset in the more proximal Kozina section due to sedimentary hiatus. However, no sedimentological and petrographic evidences of subaerial exposure have been observed at this interval. Additionally, biostratigraphic data indicate the presence of all the SBZs across the P-E boundary, thus possible hiatus are below the resolution of this study. Alternatively, the lower resolution sampling of the Kozina section compared to the Čebulovica section might account for this difference in the intensity of the negative shift at the CIE onset.

However, it must be considered that in normal deep-sea marine sediments the values for the CIE oscillate between -1 and 3‰ (*Zachos et al.*, 2001; *Giusberti et al.*, 2007), up to -3.5‰ for benthic foraminifera on the New Jersey margin shelf (*John et al.*, 2008). Thus, the significance of the very negative values at the onset (-5.7‰) and peak of the CIE (-7.0‰) in the Čebulovica section needs to be discussed. Shallow-water carbonates can be particularly susceptible to meteoric-water diagenesis, affecting the behaviour of carbon and oxygen isotopes. Periodic emergences usually introduce fluids with low $\delta^{18}O$ and $\delta^{13}C$ values derived from rain water (e.g., *Hudson*, 1977; *Swart and Eberli*, 2005). Horizons affected by such processes would have relatively low carbon-isotope and oxygen-isotope ratios compared with typical marine values. However, the absence of any sedimentological and petrographic evidences of emersion combined with the low percentage of aragonitic grains in the facies association C lead to exclude the hypothesis of meteoric effects overprinting the CIE negative shift. In correspondence of the third and fourth intervals in the Čebulovica section, corresponding to whole facies association C, petrographic observations show a frequent alternation of well cemented and less cemented layers affected by mechanical and chemical compaction. Cemented layers contain microspar and syntaxial cements growing on echinoid fragments. Bioclasts, especially *Alveolina* tests, are not deformed or broken. Conversely, in the poorly cemented layers almost no cements are present, with highly deformed *Alveolina* shells (to form sort of dissolution seems), and fragmented nummulitids (usually with the last chamber or the alar structures broken but still in the original position). This diagenetic pattern characterizes the whole facies assemblage C in the Čebulovica section, being not restricted to the third interval of the $\delta^{13}C_{\text{bulk rock}}$ curve spanning the CIE. This suggests firstly that cementation initiated before burial and secondly the whole Ilerdian deposits have been subject to a similar diagenetic history, thus excluding specific overprint affecting only the interval corresponding to the CIE. On the base of these evidences we suggest that no diagenetic event was responsible for the quite negative values recorded in correspondence of the CIE in the Čebulovica section rather than we interpret them as related to depositional condition during the PETM event. We are aware that this hypothesis deserves more studies to be tested in other successions, in order to get a better picture of the impact that the PETM event exerted in the carbon cycle of shallow-water realm.

In the AdCP sections the CIE onset occurs at the SBZ4-SBZ5 boundary, and roughly spans the SBZ5 and the base of the SBZ6. This result has two important implications; the first is to confirm the position of the P-E boundary between the SBZ4 and SBZ5 in shallow-water successions in agreement with *Pujalte et al.* (2009b) and *Scheibner and Speijer* (2009) results, the second is to estimate for the first time, even roughly, the duration of the CIE in shallow-water settings. On the basis of the biostratigraphic data the entire CIE seems to have lasted <400 k.y. These results are comparable with the estimated duration of the $\delta^{13}C$ excursion of ~250 k.y. calculated at Forada (*Giusberti et al*., 2007), and 200 to 400 k.y. from hemipelagic section of Zumaia (Northern Spain) (*Schmidt et al*., 1997). The age models for the PETM and CIE, based on various and independent approaches, suggest that the whole event lasted between 170 and 250 k.y. (*Sluijs et al*., 2007a) up to 280-320 k.y. (*Cohen et al*., 2007).

3.5.2 The AdCP $\delta^{13}C_{\text{bulk rock}}$ profiles and the reference section of Forada (E-Alps)

An important record of the CIE from middle latitude in a hemipelagic setting of the Northern Tethys (Forada section) was recently published (*Giusberti et al*., 2007). The authors correlated the Forada $\delta^{13}C$ profile with other reference sections for the CIE and PETM, from deep marine and continental settings demonstrating its applicability as reference section for the CIE in this region. Thus, due to the close geographical location, the $\delta^{13}C_{\text{bulk rock}}$ curves from the AdCP are tentatively correlated with the Forada $\delta^{13}C$ reference curve (Fig. 3.5A). In Forada the initial $\delta^{13}C$ values decrease followed by a build-up (NP5-6) and culminating with the onset of the mid-Paleocene maximum (NP7-8). This trend is well recorded in the first interval of the Kozina $\delta^{13}C_{\text{bulk rock}}$ curve, superimposed by diagenetically-related spikes, but it is less obvious in the Čebulovica section. In agreement with the global trend expressed in Forada, after this maximum, both studied sections show a long-term $\delta^{13}C$ decrease (covering the NP9 in the Forada corresponding to the SBZ4 in the Čebulovica and Kozina sections). The onset of the CIE is similar in the three sections, with the body of the CIE excursion followed by the recovery interval with values gradually returning to new stable averages. Thus, the good correlation of Čebulovica and Kozina $\delta^{13}C_{\text{bulk rock}}$ profiles with this reference curve for the global $\delta^{13}C$ history further indicate that diagenetic processes did not mask the original marine chemostratigraphic trend.

3.5.3 Biostratigraphy of the Larger Foraminifera (LF) in relation to the PETM

The record of the PETM in shallow-water successions from the AdCP and the richness of biostratigraphic markers, offer the outstanding opportunity to investigate the relationship between LF biostratigraphic distributions with respect to the PETM event, hence the possible effects of PETM on the evolution of LF (next section). Here, we combine data from the AdCP sections and data from literature (mainly the distribution chart of *Serra-Kiel et al*., 1998 based on the critical survey of biostratigraphic data from the whole Tethys) then correlated with δ^{13}C curves (Fig. 3.5B). We identified three groups of LF showing different temporal distributions with respect to the PETM:

1. *Glomalveolina-Discocyclina-Assilina* group. These are common genera in the foraminiferal assemblage of the uppermost Thanetian (SBZ4), persisting in the lower Eocene deposits of the AdCP sections. *Glomalveolina* is particularly common in the shallower facies of the Thanetian and in the Ilerdian assemblages in the AdCP sections as well as in the whole Tethys (*Hottinger*, 1960). *Discocyclina,* associated to other orthophragminids, is represented by small-sized species in the AdCP sections, locally abundant especially in the SBZ4 (Orthophragminids-dominated assemblage, *Zamagni et al*., 2008). They become rare in the Ilerdian due to a shallowing of the depositional setting. The small-sized *Assilina* appeared during the Latest Thanetian (SBZ4) with two species (*A. yvettae* and *A. azilensis*) dominating the open marine assemblages around the Tethys (e.g., in the AdCP *Assilina*-dominated assemblage, *Zamagni et al*., 2008; Spain, *Baceta et al*., 2005; Egypt, *Scheibner et al*., 2005; Oman, *White*, 1994; Turkey, *Özgen-Erdem et al*., 2005; Pakistan, *Afzal et al*., 2005). *Assilina* genus as well as orthophragminids diversified in the whole Tethys later in the Early Eocene, with pronounced increase in size starting from the middle Ilerdian (~SBZ7). Thus, *Glomalveolina-Discocyclina-Assilina* group started to evolve at the passage between zones SBZ3 (early Thanetian) and SBZ4 (late Thanetian), and thrived later during the Eocene, apparently unaffected by any perturbation associated with the PETM.

2. *Lacazina-Miscellanea-Ranikothalia* group. In the AdCP sections, these LF represent common components of the foraminiferal assemblages during the late Thanetian (starting from SBZ3) and, even subordinated, during the early Ilerdian (up to SBZ6), disappearing approximately during the middle Ilerdian (~SBZ7). Thus, the biostratigraphic distribution of lacazinids, *Ranikothalia* and *Miscellanea* genera covers the decline of δ^{13}C values (SBZ4), the PETM and afterward (SBZ5-6-7?). *Lacazina blumenthali* together with other big miliolids (e.g., *Periloculina*, *Idalina sjniarica*, and

Pseudolacazina) occurred commonly during the Late Paleocene in the AdCP areas and in the whole Central Tethyan, with complex form like *Lacazina* thriving during the latest Thanetian. Starting from the lowermost Eocene they declined probably overwhelmed by the competition with alveolinids (*Drobne and Hottinger*, 2004). *Miscellanea* and *Ranikothalia*, common during the Late Thanetian, persist during the early Ilerdian in the AdCP sections, with *M. rhomboidea* in zone SBZ5, and *Ranikothalia* sp. up to zone SBZ6 and maybe SBZ7. Similarly, they were common components of the foraminiferal assemblages of the latest Thanetian in the entire Tethys (e.g., Turkey, *Sirel*, 1998; Northern Calcareous Alps, *Moussavian*, 1984; Pyrenees, *Baceta et al*., 2005; Majella, *Moussavian and Vecsei*, 1995; Oman, *White*, 1994; *Racey*, 1994; Egypt, *Scheibner et al*., 2005; Iran, *Rahaghi*, 1983; Yemen, *Pignatti et al*., 1998; NW India – Pakistan, *Butt*, 1991; *Akhtar & Butt*, 1999; *Afzal et al*., 2005; NE India, *Jauhri*, 1996, 1998). In the Eastern Tethys *Miscellanea* and *Ranikothalia* occur together with *Alveolina vredenburgi* (*Hottinger*, 1971, *Jauhri*, 1994, 1996, 1998; *Jauhri et al*., 2006), the marker fossil of SBZ5. In NW India *Ranikothalia* persisted during the early Ilerdian, replace only later in the Eocene by *Nummulites* (*Jauhri*, 1998). In the Northern Calcareous Alps, *Ranikothalia spp.*, together with *Discocyclina*, thrived on the open shelf during the early Ilerdian, substituted during the middle Ilerdian by *Assilina* and *Nummulites* (*Moussavian*, 1984). *Miscellanea* were found associated with *Alveolina*, in horizons equivalent to the SBZ5, in Turkey (*Hottinger*, 1960; *Sirel*, 1997), Iran (*Rahaghi*, 1983), Iraq (*Hottinger*, 1960), and Afghanistan (*Kaever*, 1970, reported in *Jahuri*, 1998). It might be possible that *Miscellanea* and *Ranikothalia* disappearances were related to strong ecological competition with better adapted *Assilina* and *Nummulites* from the middle Ilerdian onward (*Lepping*, 1988). Also this group apparently evolved unaffected by any perturbation directly associated with the PETM.

3. small-sized *Alveolina-Nummulites* group, with small, globular *Alveolina* (e.g., *A. aramaea, A. avellana, A. globula, A. pasticillata*) and small *Nummulites* (e.g., *N. fraasi*) appearing at the P-E boundary, dominating the assemblages with high specific diversity during the early Ilerdian (Alveolina-Nummulites dominated assemblages, *Zamagni et al*., 2008). The appearance and spreading of the first small-sized globular *Alveolina* and small *Nummulites* coincide with the PETM onset. The first big, elongated forms appeared from the middle Ilerdian (~SBZ7, *Alveolina aff rotundata*) onwards, well after the CIE recovery.

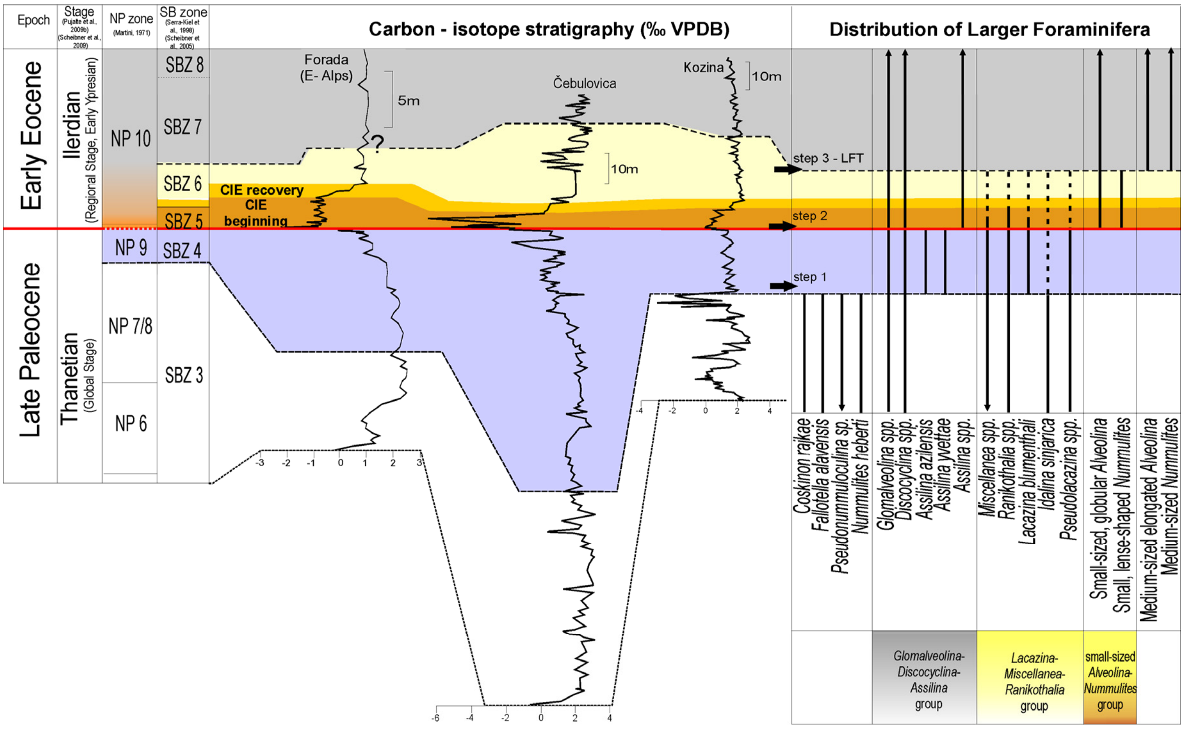

Figure 3.5: Correlation between $\delta^{13}C$ curves and the biostratigraphic distributions of LF. $\delta^{13}C$ bulk record from the Upper Paleocene to the Early Eocene, through the Carbon Isotopic Excursion (CIE) at Čebulovica and Kozina sections correlated with $\delta^{13}C$ bulk record of the hemipelagic section of Forada (*Giusberti et al*., 2007). Forada curve is considered starting from the base of NP5, which roughly corresponds to the boundary between SBZ2 and SBZ3 according to the *Serra-Kiel et al.* (1998) biostratigraphic correlation. In Forada the CIE covers the uppermost part of zone NP9-base of zone NP10 (*Giusberti et al*., 2007). The P-E boundary is located somewhere in the uppermost zone NP9 and correlated in the shallow-water successions with the SBZ4-SBZ5 boundary. Biostratigraphic distribution of LF based on their occurrences in the studied sections (continuous line) and literature (dashed line). CIE: carbon isotope excursion; LFT: Larger Foraminifera Turnover; VPDB: Vienna Peedee belemnite standard.

3.5.4 Implications of the PETM for the Larger Foraminifera evolution

The evolution of LF during the Early Paleogene was primarily a long-term process of reorganization of this group after the K-T crisis (*Hottinger*, 1998) characterized by the progressive recovery of a K-strategy of life. K-strategists are organisms characterized by long life cycle and low reproductive potential, expressed by large-sized shell and adult dimorphism (*Hottinger*, 1983). They are highly dependent on the long-term stability of the environments and attain the highest diversity and greatest dimensions in region of low primary productivity (*Hottinger*, 1983), where algal symbiosis offer great advantages (*Hallock*, 1985). Within this long-term evolution, it has been suggested (*Orue-Etxebarria et al*., 2001; *Pujalte et al*., 2003; *Scheibner et al*., 2005; *Pujalte et al*., 2009b; *Scheibner and Speijer*, 2009) that the PETM trigged major changes in the composition of the LF community, causing the some extinctions

(*Ranikothalia* and *Miscellanea*), and the spreading of other genera (*Alveolina, Nummulites*, *Assilina*). This interpretation poses the problem how the appearance of *Alveolina,* considered a proof of the LFT accomplishment and thus the full recovery of the K-strategy, can be interpreted in relation to the PETM event.

Based on the biostratigraphic and chemostratigraphic data presented in this study, we propose that the PETM represented a short perturbation within the Early Paleogene long-term evolution of the LF, coeval to provisional adaptations, but that did not hit this group dramatically (as in the case of the small calcareous benthic foraminifera, with 35-50% of the deep-sea species rapidly extinct during this event, e.g., *Thomas*, 1998) apparently without provoking any extinctions as indicated by biostratigraphic distribution of LF. Actually the major groups of LF cross the P-E boundary, with *Miscellanea* and *Ranikothalia* disappearing during the middle Ilerdian. In this scenario, the LFT was not an instantaneous event but a gradual replacement, mainly controlled by endogenous biotic forces, culminated approximately during the middle Ilerdian, well after the end of the PETM event, as reveled by the correlation with the δ^{13}C curve and. The replacement ('turnover') in the LF community across the Latest Paleocene - earliest Eocene proceeded through a three-step process (Fig. 3.6).

During the Latest Paleocene (step 1 pre-PETM, fig. 3.6B) the LF assemblages were dominated by *Miscellanea*, *Ranikothalia*, *Glomalveolina* and small-sized *Assilina* and *Discocyclina.* Even characterized by all features which distinguish these foraminifera from the "smaller" benthic foraminifera (complex body plan, adult dimorphism), the small size (shell diameter ~1.5 mm), and the weak dimorphism of generations points to a relatively short life and frequent reproductions, all useful adaptations to exploit fluctuating availability of resources (r-mode tendency). In these associations most of the genera were mono- or oligospecific, likely as consequence of these fluctuating conditions in the shallow-water realm, limiting the efficient partitioning of available resources, thus reducing the specific diversity. Studies of living representatives and feeding experiments demonstrated that Recent larger symbiont-bearing foraminifera have taxon-specific tolerance limits to environmental perturbation in terms of nutrient and turbidity pressures (*Langer and Hottinger*, 2000; *Langer and Lipps*, 2003; *Hallock et al*., 2003; *Renema*, 2008). These results suggest the possibility that LF may have developed some adaptations to apparently unfavorable environmental conditions. In the Tethys, an increase in continental run-off, related to intensified weathering, started before the CIE (*Speijer and Wagner*, 2002; *Gavrilov et al.,* 2003) promoting an enhanced productivity in surface waters (*Egger et al.*, 2003) and occasional blooms of the heterotrophic, organic-walled dynocist *Apectodinium* preceding the CIE by several k.y. (*Sluijs et al.*, 2007b). All together, these data from pelagic settings, the development of microbialite-coral mounds in this sector of the AdCP (*Zamagni et al.,* 2009), and the characteristics of the LF assemblages, point to environmental perturbations in shallow-water settings before the CIE.

The climatic conditions at the onset of the PETM became more extreme with enhanced humidity and an intensified hydrologic cycle (*Bolle and Adatte*, 2001; *Ravizza et al*., 2001). This promoted increased runoff and nutrient input into marginal basins, as suggested by biogeochemical proxies (increase in the rate of hemipelagic sedimentation in the northern Tethys, *Egger et al*., 2003; *Giusberti et al*., 2007; organic-rich deposits and black shale deposits in the Tethys, *Bolle and Adatte*, 2001; *Speijer and Wagner*, 2002; *Gavrilov et al*., 2003; increased biogenic barium values, *Schmitz et al*., 1997; *Bains et al*., 2000; *Schmitz*, 2000; *Giusberti et al*., 2007; widespread bloom of the dinoflagellate *Apectodinium*; *Crouch et al*., 2001, 2003; *Crouch and Brinkhuis*, 2005; increased abundance of siliceous plankton and dinoflagellates in the north-western Tethys, *Egger et al*., 2003, 2005). These data indicate that productivity in coastal surface waters increased considerably close to the P/E boundary. In the case of the NW AdCP, the geochemical study of a flysch sequence covering the P-E boundary (Goriška Brda area, W Slovenia, *Dolenec et al*., 2000) evidenced the development of anoxic conditions in the basin adjacent to the studied ramp. Thus, a strong stratification was developed in the basin, likely related to differential density of the water masses with relatively fresh, nutrient-rich waters sitting on top of denser, more saline water masses.

Within this framework, the appearance of the small-sized *Alveolina-Nummulites* group coincident with the PETM onset (step 2 PETM and afterward, fig. 3.6C) can be interpreted either as the shallow waters having been insignificantly affected by increased nutrients or other perturbations related to the PETM event, or the first Ilerdian (SBZ5-6) alveolinids and nummulitids having been sufficiently adapted to exploit the enhanced nutrient levels without adverse effects. Because eutrophic, anoxic waters would have promoted the substitution of LF with small opportunistic forms, as observed in field studies of nutrient-polluted habitats of LF (*Hallock,* 2000, *Hallock et al*., 2003) and in the geological record (e.g., during the Cenomanian–Turonian OAE, *Parente et al*., 2008), the widespread occurrences of LF suggest that shallow-waters were not so affected by dramatic increase of nutrients. Nonetheless, the early Ilerdian alveolinids and nummulitids appear different from the counterpart that evolved afterward. The early globular to ovoid *Alveolina* are characterized by diameters less than 4 mm (similar to dimensions reported by *Drobne*, 1977), and the *Nummulites* have diameters less than 5 mm, pointing to a relatively short life cycle. The existence of asexual alveolinid clones in the form of small embryos (<200µm) is related to high fecundity under unstable conditions (*Hallock*, 1985). Adult dimorphism in these early forms was still weak at this time. Even if these LF already showed the pre-adaptations to thrive in stable environmental conditions (complex shell morphology, large-sized shell, and adult dimorphism), they fully evolved these features only later in the Early Eocene. During the early Ilerdian they were likely able to tolerate relatively high or frequently fluctuating nutrient levels. Hence, it took some time to fully evolve the k-strategy in these LF and this process was unrelated to the PETM since the big, elongated alveolinids started at least from the middle Ilerdian, well after (~400 k.y.) the PETM event (step 3, fig. 3.6D).

Considering all these evidences, did the PETM exert any direct effects on the evolutionary history of the Early Paleogene LF? The PETM may have stimulated specific diversification at the P-E boundary. Records from middle latitude, near-shore marine sediments provided evidence for 8°C warming of mean sea surface temperatures (SST°) during the PETM with maximum temperatures up to 35°C (*Zachos et al.*, 2006). Such warming might have affected the metabolic rates of LF favoring the diversification observed in the LF concomitant with the PETM. LF, like all foraminifera, are ectotherm organisms, with body temperatures that tend to equilibrate with ambient temperatures. Because the kinetics of chemical reactions associated with metabolism is a function of temperature changes (*Hallock et al.*, 1991), increased temperatures would have a major effect on life processes in LF. Recent studies on diversity patterns have demonstrated that diversity is directly correlated with speciation rate and that both phenomena seem to be causally linked to increased temperature (*Escarguel et al.*, 2008). Increase in phenotypic diversification has also been linked to acceleration of mutation rates due to repairs of DNA damaged by extreme environmental conditions, like high salinity (*Hebert et al.*, 2002) or increase of UV-B radiations (e.g., morphological variability on Recent *Amphistegina* offsprings, *Hallock,* 2000). Interestingly, in this scenario, the appearance of the *Alveolina* genus is concomitant with the PETM and the rapid speciation experienced by this genus during the Early Eocene Climatic Optimum, the hottest time in the Cenozoic (SST° reached the 34°C, *Tripati et al.*, 2003). Nowadays, the alveolinid *Alveolinella quoyi* d´Orbigny

1826 thrives under the highest SST° observed in modern oceans (*Langer and Hottinger*, 2000; *Langer and Lipps*, 2003).

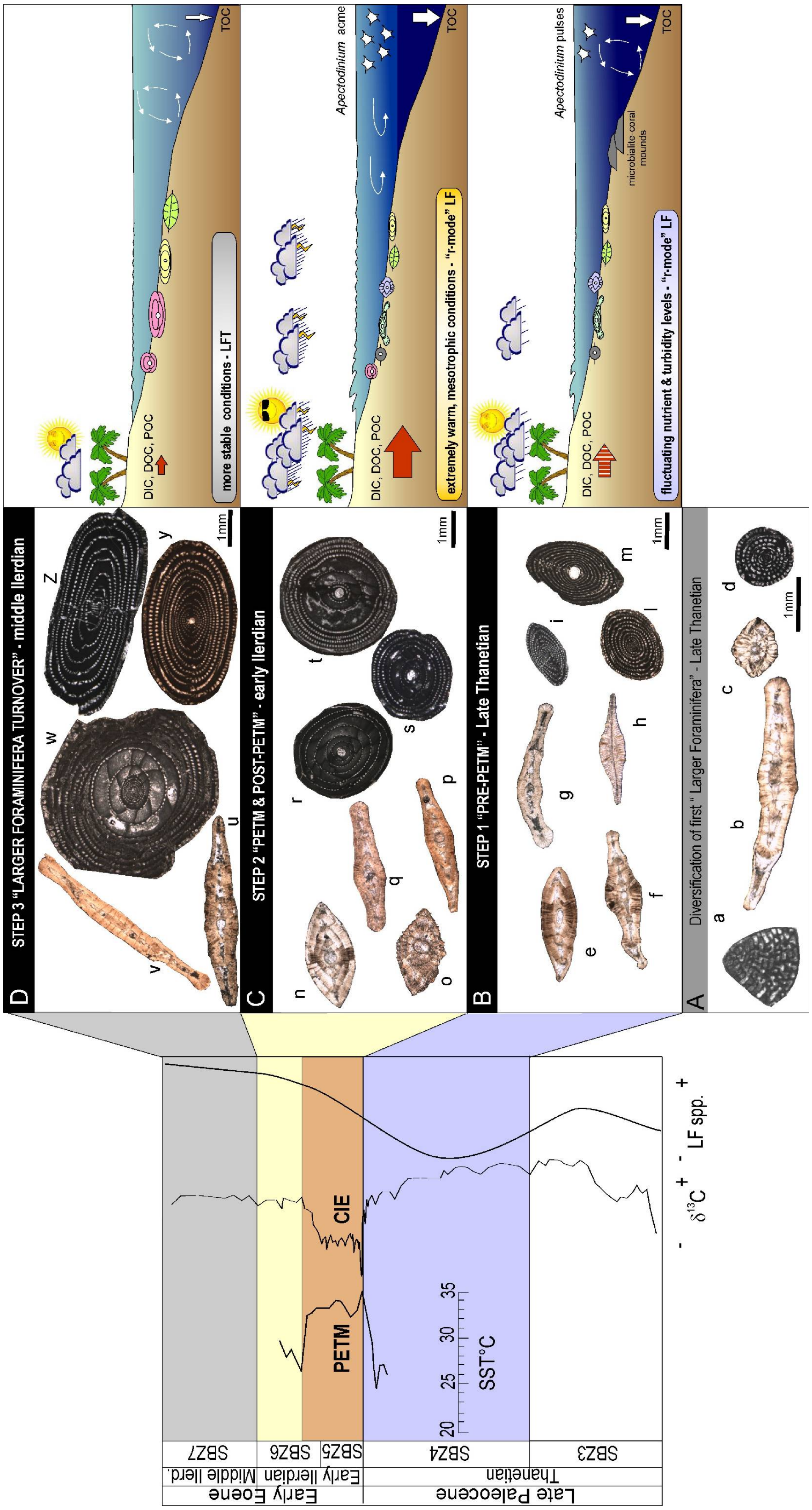

Figure 3.6: Evolution of LF from the AdCP in relation to environmental changes during the PETM. $\delta^{13}C$ curve from Forada (*Giusberti et al*., 2007). SST° curve for the PETM from *Zachos et al*. (2006). LF specific diversity from *Hottinger* (1998). LF from the AdCP successions: a. *Coskinon rajkae*; b. *Nummulites cf heberti*; c. *Miscellanea yvettae*; d. *Glomalveolina primaeva*; e. *Assilina yvettae*; f. *Assilina azilensis*; g. *Ranikothalia sp.*; h. *Discocyclina seunesi*; i. *Glomalveolina levi*; l. *Glomalveolina sp.*; m. *Lacazina blumenthali*; n. *Nummulites sp.*; o. *Miscellanea rhomboidea*; p. *Nummulites* cf *fraasi*; q. *Ranikothalia* sp.; r. *Alveolina aramaea aramaea*; s. *Alveolina avellana*; t. *Alveolina daniensis*; u. *Assilina* cf *ornata*; v. *Ranikothalia* sp.; w. *Alveolina montanarii*; y. *Alveolina moussoulensis*; z. *Alveolina* cf *rotundata*. Note change of scale from A to B. See text for further explanation.

3.5.5 Ocean acidification during the PETM; an overview from the shallow-water realm

Results from the study of several open marine records indicate that for a brief period of time coincident with the PETM, much of the ocean beneath the thermocline was highly undersaturated with respect to calcite (*Zachos et al.,* 2005, *Giusberti et al.*, 2007). This promoted intense sea floor carbonate dissolution and partly affected biocalcification processes in deep-sea benthic fauna (*Steineck and Thomas*, 1996; *Thomas*, 1998; *Zachos et al*., 2005; *Kaiho et al*., 2006) and planktonic biota (e.g., *Kelly et al.*, 1998; *Bralower*, 2002). What was, if any, the response of the shallow-water biocalcifiers to this rapid ocean acidification during the PETM in the AdCP?

Biofacies from the AdCP corresponding to the PETM are dominated by alveolinids, echinoids, nummulitids (mainly *Nummulites*), small benthic foraminifera (miliolids, rotaliids), and a few other associated components (bryozoans, bivalves, dasycladaceans). Alveolinids and nummulitids show high variability in the taphonomic state, with intense bioerosion, shell breakage, recrystallisation, deformation, and encrustation. These taphonomic features are common throughout the facies association C, thus not limited to the interval coeval to the PETM. The deposition in a protected inner ramp might have favored syndepositional chemical dissolution (due to organic matter oxidation, e.g., see *Sanders*, 2003 and references therein). At the same time, low sedimentation rate combined with a relatively high nutrient pressure might have enhanced the infestation and encrustation processes (*Hallock*, 1988). No evidence of morphological abnormalities, like brakeage and repair or distorted shell, have been observed, which might suggest problems during biomineralization processes (*Toler and Hallock*, 1998). So, apparently no clear evidence of biocalcification problems have been observed affecting LF during the PETM. *John et al.* (2008) found that on both the Atlantic and Pacific coasts of the continental U.S., carbonate preservation increases on siliciclastic shelves at the onset of the CIE. These results are in line with the observation from the AdCP, suggesting that in both carbonatic and siliciclastic shallow-water systems, there was no response to the acidification affecting deep-sea waters. However, LF are sophisticated biomineralizers, upon which experimental studies have demonstrated the existence of a strong biological control in the biomineralisation processes (*Erez*, 2003; *Bentov and Erez*, 2006), with seawater chemistry exerting a relatively weak effect.

3.6 Summary

The study of $\delta^{13}C$ records of shallow-water carbonate successions from the Adriatic Carbonate Platform (SW Slovenia) document a detailed record for the Paleocene-Eocene Thermal Maximum (PETM) in this shallow-water paleodepositional setting. The onset of the CIE is clearly defined by a sudden decrease of $\delta^{13}C$ values that coincides with the appearance of the first Eocene *Alveolina aramaea aramaea*, marking the P-E boundary. The more distal section records a ~3.5‰ CIE; this is a typical value for mid-latitude continental shelves during this time interval. In the more proximal section we document a ~1‰ CIE; this low value may be related to a biostratigraphically-unresolved sedimentary hiatus or to lower sampling resolution compared to the distal section. We suggest, based on petrographic and sedimentological observations, that no diagenetic event was responsible for the strongly negative values recorded corresponding to the CIE in the Čebulovica section. Instead, we interpret them as related to depositional conditions during the PETM event. We are aware that this hypothesis deserves more studies to be tested in other successions, in order to get a better picture of the impact that the PETM event exerted in the carbon cycle of the shallow-water realm.

Biostratigraphic studies constrain the duration of the whole event to the SBZ5 and part of the SBZ6. The combined results from biostratigraphic and chemostratigraphic records do not show any synchronicity between the Early Eocene LF Turnover and the PETM, suggesting that there is not a direct causal link between the two events. The temporal distribution of the major groups of LF covers the Late Paleocene-earliest Eocene time interval; no extinctions have been recorded coeval with the PETM. Hence, the suggested turnover at the P-E boundary was probably a gradual replacement that culminated during the middle Ilerdian (~SBZ7), well after the PETM recovery. At this time, the final disappearance of *Ranikothalia*, *Miscellanea,* and the spreading of large *Alveolina* and *Nummulites* took place. The evolution of LF therefore seems to have been driven by endogenous biotic forces, with the PETM exerting almost no influence on this long-term evolutionary history.

3.7 Acknowledgements

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Facies associations	**Facies (occurrence)**		**Sedimentary and Post-depositional features**	**Foram. Ass.**[1]	**Main components**	**Subordinated components**	**Depositional setting**	
Association A Foraminiferal Limestones	A1	Big gastropod mudstone (KZ -ČB)	borrowing	1	big gastropods (F)	miliolids (R) *Lagynophora* (VR)	Restricted lagoon to Inner ramp	Restricted /brackish lagoon
	A2	Miliolid-discorbid-ostracod wackestone to packstone (KZ -ČB)	bioturbation, borrowing, dissolution (millimetric-size fenestrae and *Microcodium*-enriched levels)		miliolids (C), discorbids (C), ostracods (C)	conical foraminifera (F)		Restricted lagoon , periodically emerged
	A3	Small foraminifera-echinoid-dasycladacean packstone (locally grainstone) (KZ -ČB)	bioturbation, dissolution (*Microcodium*-enriched levels), root-related structures, micritization	2	miliolids (C), conical foraminifera (C), echinoids (C/A), dasycladaceans (C/F), micritised grains and peloids (A)	rotaliids (F)		Innermost shoals periodically emerged and vegetated
	A4	Small foraminifera peloidal packstone to wackestone (D-ČB)	bioturbation, borrowing, dissolution (*Microcodium*-enriched levels), micritization		miliolids (F /C), rotaliids and conical foraminifera (F /C), ostracods (C), micritised grains and peloids (A)	echinoid and coralline fragments (F), solitary corals (R), faecal pellets (R), intraclasts of mudstone with *Microcodium* (VR)		Open lagoon
	A5	*Dendrophyllia* floatstone (KZ - D -ČB)	bioturbation		dendroid corals (F), crustose corallines and acervulinids (F), rotaliids (F), *Miscellanea* (F), dasycladaceans (F)	miliolids and conical foraminifera (R), gastropods (R), bryozoans (R), faecal pellets (R)		Open lagoonal small coral patches
	A6	Miliolid-*Miscellanea*-coralline peloidal packstone to grainstone (D - ČB)	thick bedding, gradation from medium to fine at metric scale		miliolids (C/A), abraded coralline debris (C), ostracods (F), *Miscellanea* (F), echinoid fragments (A), micritized grains and peloids (A), fine debris (C)	conical foraminifera (F), rotaliids (R), acervulinids (R), dasycladaceans (R), dendroid corals (VR), intraclasts of mudstone with *Microcodium* (VR)		Open marine shoals
	A7	Rotaliid-*Miscellanea*-echinoid peloidal packstone (D - ČB)			rotaliids (C), *Miscellanea* (F), micritized grains and peloids (A), echinoid fragments and fine debris (C/A)	bryozoans and coralline debris (F/R), conical foraminifera, miliolids and *Glomalveolina* (F/R), *Nummulites gr heberti*, *Ranikothalia*, and *Discocyclina* (VR)		Open marine, fore-shoal deposits
Association B Foralgal Limestones	B1	*Discocyclina*-acervulinid-crustose algae packstone to wackestone/floatstone (KZ - DKE - D - ČB)	bioturbation, encrustation, bioerosion	5a	acervulinids (C), encrusting foraminifera (F/C, mainly *Haddonia*), peyssonneliaceans and thin crustose corallines (C), small flattened *Discocyclina* (F to C), rotaliids (F), bryozoans, echinoderm and bivalve debris (F)	*Assilina* (R/F), small massive corals and debris (R) locally encrusted by millimetric-thick microbial crusts, calcareous sponges (R), miliolids and *Glomalveolina* (VR)	Distal mid ramp with development of mounds and algal pavements	Algal pavements

Facies associations	Facies (occurrence)		Sedimentary and Post-depositional features	Foram. Ass.[1]	Main components	Subordinated components	Depositional setting	
Association B Foralgal Limestones	B2	Microbialite-encrusting foraminifera-coral boundstone (KZ - DKW - D - ČB)	encrustation, bioerosion	4	microbialitic crusts (C), colonial corals (F), small rotaliids (F), encrusting foraminifera (F), bryozoans (F), *Discocyclina* (F/R)	calcareous sponges (R), thin crustose corallines and peyssonneliaceans (R), echinoid spines and bivalve fragments (R)	Distal mid ramp with development of mounds and algal pavements	Microbialite-coral mounds
	B3	Microbialite-encrusting foraminifera-coral boundstone (KZ - DKW - D - ČB)	encrustation, bioerosion	4	thin acervulinid-crustose coralline crusts (C), bivalve fragments (C/F), bryozoans (F), fine debris (C)	coral debris (R), *Discocyclina* (R)		
	B4	*Assilina-Discocyclina* nodular nummulitoclastic packstone to wackestone (locally with chert nodules) (DKE - D)	bioturbation, levels with small benthic foraminifera and matrix oxidized	5b	nummulitid debris (C/A), small rotaliids (C/F), big flattened *Assilina* (F/C), big flattened *Discocyclina*(F/C)	small benthic foraminifera stained with oxides (F), planktonic foraminifera (VR)	Distal mid ramp/upper outer ramp	Algal pavements
	B5	Nodular fine nummulitoclastic wackestone (D)	bioturbation	5b	fine nummulitoclastic debris (C)	*Discocyclina* and *Assilina* (VR)		Fine-grained distal storm/current deposits
	B6	*Assilina*-coralline-*Polystrata* packstone (locally rudstone) (KZ - DKE - DKW - D - ČB)	bioturbation, micritization, storm-related structures (concentric orientation of *Assilina* tests), encrustation	3	*Assilina* (C), nummulitoclastic debris (C), peyssonneliaceans, corallines and acervulinids as crusts and fragments (C/F)	Small ovate *Discocyclina* (F /R), *Miscellanea* (R), small rodoliths (R), miliolids, lacazinids and *Glomalveolina* (F/R), coral debris and small massive colonies (R), bryozoans (F), oysters (F/R), encrusting foraminifera (F/R, mainly *Haddonia*)	Proximal mid ramp to inner ramp	Proximal mid ramp storm-reworked deposits
	B7	*Glomalveolina-Assilina* peloidal packstone (KZ - DKW - ČB)	bioturbation, micritization		miliolids, lacazinids and *Glomalveolina* (C), *Assilina* (F), peloids and micritised grains (C)	rotaliids (F/R)		Proximal mid to inner ramp
Association C Bio-Peloidal Limestones	C1	*Alveolina*-mollusk peloidal packstone (KZ - ČB)	bioturbation, micritization, bioerosion,	6a	*Alveolina* (C), *Nummulites* (F), dasycladaleans (F) gastropods and bivalves (C), echinoids (C), micritised grains and peloids (C)	*Assilina* (F), *Orbitolites* and *Opertorbitolites* (F/R), acervulinids (R)	Inner ramp to proximal mid ramp	Protected inner ramp, small or seasonal sea-grasses
	C2	*Alveolina*-acervulinid peloidal packstone (KZ)	bioturbation, micritization, bioerosion encrustation	6a	miliolids and *Glomalveolina* (C), *Alveolina spp.* (C), acervulinids (F), peloids (C)	*Assilina* (R), *Orbitolites* and *Opertorbitolites* (R)		
	C3	*Nummulites-Assilina*-echinoid packstone (ČB)	bioturbation, locally with reddish matrix,	6b	small ovate *Nummulites* and *Assilina* (C), nummulitid debris (C), echinoid fragments (A)	*Discocyclina* (VR) *Alveolina* (VR)		Open marine
	C4	*Nummulites*-echinoid packstone to wackestone (ČB)	bioturbation, micritization, bioerosion	6b	*Nummulites* (C), echinoids (A), fine debris (C)	*Alveolina* (F/R)		

Table 3.1: relationship among facies associations, foraminiferal assemblages (1), sedimentological features and major components. Section labels: KZ-Kozina; ČB-Čebulovica; D-Divača; DKE-Divača-Kozina East; DKW-Divača-Kozina West.

4. THE FIRST MICROBIALITE - CORAL MOUNDS IN THE CENOZOIC (UPPERMOST PALEOCENE) FROM THE NORTHERN TETHYS (SLOVENIA): ENVIRONMENTALLY-TRIGGERED PHASE SHIFTS PRECEDING THE PETM?

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Abstract

Upper Thanetian microbialite-coral mounds from the Adriatic Carbonate Platform (SW Slovenia) are described herein for the first time, representing an important case study of extensively microbially-cemented boundstones in the Early Paleogene. The mounds are constructed primarily by microbialites associated to small-sized coral colonies, forming metric bioconstructions in a mid-ramp setting.

Detailed macroscopic and microscopic studies show that microbes are the major framework builders, playing a prominent role in the stabilization and growth of the mounds, with corals being the second most important component. Microbial carbonates represent up to 70% of the mounds, forming centimetric-thick crusts alternating with coral colonies. The microbial nature of the crusts is demonstrated by their growth form and internal microfabrics, showing accretionary, binding, and encrusting growth fabrics, often with gravity-defying geometries. Thin sections and polished slabs reveal a broad range of mesofabrics, with dense, structureless micrite (leiolite), laminated crusts (stromatolites), and clotted micritic masses (thrombolites). A first layer of micro-encrusters, including leiolites and thrombolites, occurs in cryptic habitats, whereas discontinuous stromatolites encrust the upper surface of corals. A second encrustation, the major mound construction phase, follows and is dominated by thrombolites, encrusting corals and other micro-encrusters. This sequence represents the basic constructional unit horizontally and vertically interlocked, in an irregular pattern, to form the mounds. The processes, which favored the deposition of these microbial carbonates, were mainly related to *in situ* precipitation, with minor evidences for grain agglutination and trapping processes. Scleractinian corals comprise moderately diversified community of small (centimetric) colonial, massive, platy encrusting, and branching forms. Coral colonies are distributed uniformly throughout the mounds without developing any ecological zonation. These features indicate that coral development remained at the pioneer stage throughout the mound growth.

The spatial relationships between corals and microbialites, as well as the characteristics of microbial crusts and coral colonies, indicate a strong ecological competition between corals and microbes. A model for the evolution of the trophic structures during the mound growth is proposed, with changes in the paleoecology of the main bioconstructors triggered by frequent environmental perturbations. Turbidity and nutrient pressure, interpreted here as related to frequent recurrences of wet phases during the warm, humid climate of the Uppermost Thanetian, might have promoted temporary dominance of microbes over corals, causing rapid environmentally-driven "phase shifts" in the dominant biota.

4.1 Introduction

Microbial carbonates waxed and waned in the in Earth History (*Webb*, 2001). Especially the Cenozoic was characterized by a drastic decline of microbialites. No microbial-dominated reefs were so far reported from the Early Paleogene (e.g., *Perrin*, 2002) and only few examples were described for the Neogene (Late Miocene, SE Spain; *Riding et al.*, 1991; *Braga et al.*, 1995). Thus, the study of the microbialite-coral mounds, object of this work, provides insights into the development of patch reef facies in the Late Thanetian, including previously unexpected microbially-cemented facies.

Starting from the 'mid' Danian, environmental conditions in (sub)tropical zones of the Tethys and Atlantic coasts were favorable for the expansion of coralgal communities to form buildups, for example in the Pyrenean basin (*Baceta et al.*, 2005), in the Majella platform (*Vecsei and Moussavian*, 1997), and Egypt (*Schuster*, 1996). During the Thanetian smaller bioconstructions, mainly composed of calcareous algae associated with moderately diversified communities of small corals, were developed especially in mid-latitude settings both in the Tethys (*Terry and Williams*, 1969; *Bebout and Pendexter*, 1975; *Vecsei and Moussavian*, 1997) and in the Atlantic realm (*Bryan*, 1991; *Baceta et al*., 2005). Within these Paleocene bioconstructions, the occurrences of microbialites were until now neglected. However, a number of these studies reported the occurrence of micritic and peloids fabrics without attributing it specifically to a microbial origin (*Bebout and Pendexter*, 1975; *Bryan*, 1991; *Vecsei and Moussavian*, 1997). This holds true also for the Adriatic Carbonate Platform (AdCP, *Vlahović et al*., 2005) where small Danian and Thanetian coral-algal buildups (SW Slovenia) were described, but no microbial-related structures were reported (*Drobne et al.*, 1988; *Turnšek and Drobne*, 1998). Only reworked clasts, likely Thanetian in age and described as "mud-mound" type buildups, were found (*Turnšek and Košir*, 2004).

The microbialite-coral mounds described here represent the first *in situ*, microbially-cemented bioconstructions described from the AdCP, and hitherto from the Tethyan realm. Located on the southern part of the Kras region, some road-cuts near to Divača village (SW Slovenia) reveal the existence of meter-size microbialite-coral mounds, latest Paleocene (Latest Thanetian) in age. These well-exposed bioconstructions are characterized by an exceptional development and preservation of microbial crusts, associated with a diverse coral community. Objectives of this work are: (1) describe for the first time these Upper Paleocene microbialite-coral mounds and their variety of fabrics, through field observations and petrographic analysis; (2)

propose a model for the development of these microbial-coral mounds, interpreting the factors which determined the settlement, morphology, growth, and ecological relationships of microbial and coral communities.

4.2 Stratigraphical and geological settings

The carbonate succession investigated in this study crops out in the southern part of the Kras Plateau in SW Slovenia (Fig. 4.1). This area during the latest Cretaceous to Early Paleogene was characterized by shallow-water depositional environments, developed on the marginal parts of the formerly extensive Mesozoic Adriatic Carbonate Platform (AdCP). Towards the north/northeast, a deep-water basin was forming in a foreland basin associated with the growing southwestward-verging Dinarides orogenic wedge (*Otoničar*, 2007 and references therein). Vertical facies successions of Paleocene and Lower Eocene shallow-marine carbonates generally exhibit a retrogradational pattern, reflecting a deepening trend and final drowning of the carbonate platform by pelagic and hemipelagic deposits (*Košir*, 1997).

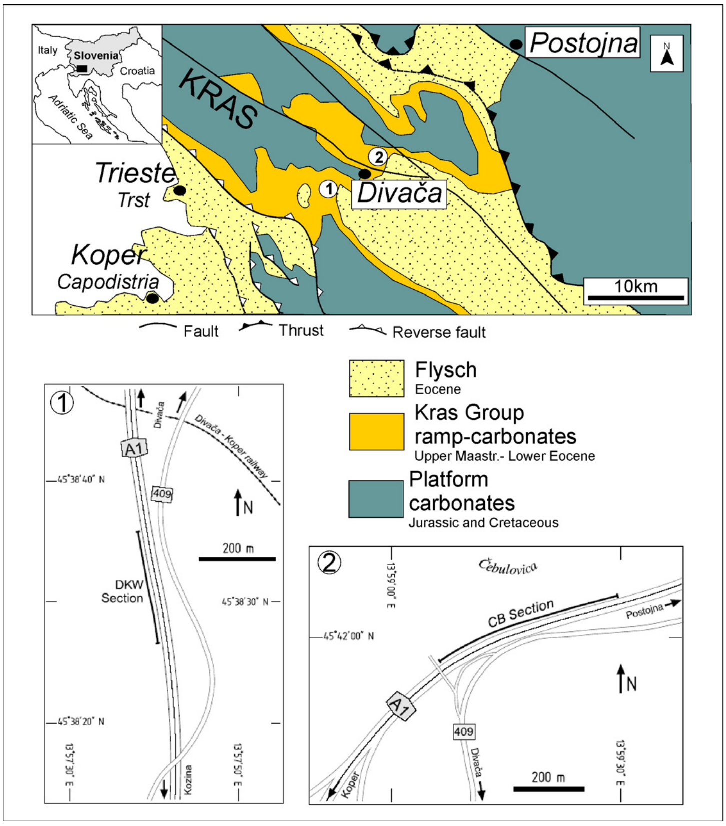


Figure 4.1: Simplified geological map of the Kras region (SW Slovenia) modified from *Košir* (2003), with location of the studied sections: (1) Divača; (2) Čebulovica.

A reliable, detailed reconstruction of the architecture and size of the Early Paleogene carbonate platform is difficult due to the complex thrust-nappe structure of NW Dinarides. However, the platform geometry inferred from regional facies relationships (*Drobne*, 1977; *Jurkovšek et al*., 1996, 1997) corresponds to a carbonate ramp depositional system characterized by roughly parallel NW-SE trending facies belts. The width of the carbonate ramp, only inferred from a rough palinspastic restoration (*Placer*, 1981), probably did not exceed 50 km, while the maximum width of the contemporaneous fore-deep basin was probably less than 200 km. It is important to note, however, that the position of the front of the orogenic wedge during the Early Paleogene cannot be established with precision.

A general stratigraphic column of the Upper Cretaceous, Paleocene, and Eocene deposits in the Kras region is shown in figure 4.2. The Cretaceous and Early Paleogene carbonate successions, together with the overlying siliciclastic successions, exhibit a stratigraphic pattern typical for underfilled foreland basins (*Sinclair*, 1997). This pattern reflects deposition during major tectonic events when the AdCP was subaerially exposed, subsequently re-established with deposition of the Uppermost Cretaceous – Early Paleogene carbonate sequence, then drowned, and finally buried by prograding deep-water clastics (flysch) (*Otoničar*, 2007).

The Uppermost Cretaceous – Early Paleogene succession is composed by a lower unit (the Kras Group; *Košir*, 2003), that overlies the forebulge unconformity (*Otoničar*, 2007 and references therein), and comprises three formations: 1) Liburnian Formation (Upper Maastrichtian to Lower Paleocene) characterized by restricted, marginal marine, paralic and palustrine carbonates (*Ogorelec et al*., 2001); 2) Trstelj Formation (Upper Paleocene) composed of a lower member dominated by foraminiferal limestones and an upper member with foralgal limestones and buildups (*Zamagni et al*., 2008), deposited in shallow-water setting; and 3) *Alveolina-Nummulites* Limestone (Lower Eocene) dominated by larger benthic foraminifera (*Drobne*, 1977; *Jurkovšek et al*., 1996; *Zamagni et al*., 2008).

The mounds, object of this work, belong to the upper member of the Trstelj Formation (Fig. 4.2), covering the SBZ4 (Upper Thanetian, according to the zonal scheme of *Serra-Kiel et al*., 1998). In the studied area this member, which contains the microbialite-coral mounds, consists of middle-ramp facies (*Zamagni et al*., 2008).

This interpretation is supported by the presence in the mounds of corals with platy morphologies, typical for low light environments, the presence of thin foralgal crusts of corallines and peyssonneliaceans, the absence of lagoonal and very shallow-water biota, and the dominance of fine-grained wackestones and packstones associated to the mounds, indicating deposition under low energy regime.

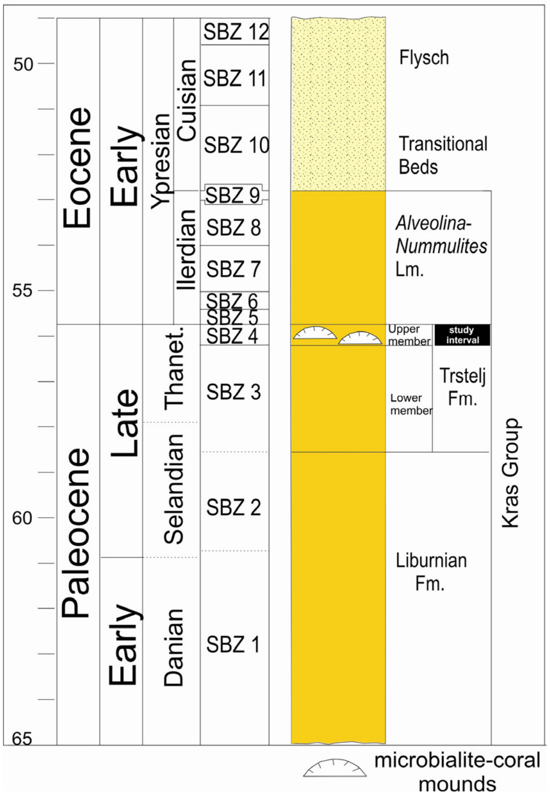


Figure 4.2: Stratigraphic framework for the Kras region during the Early Paleogene. Shallow marine biozonation (Shallow Benthic Zone, SBZ) and time scale based on *Serra-Kiel et al.* (1998), with the Paleocene – Eocene boundary placed at the SBZ 4 – SBZ 5 limit.

Turnšek and Drobne (1998) described coral assemblages from several localities in the Kras regions, occurring in different levels of Paleocene carbonates from the Selandian (SBZ2) up to the latest Thanetian (SBZ4). These coral-bearing limestones were interpreted as small coral-algal patch-reefs (*Drobne et al*., 1988; *Turnšek and Drobne*, 1998), but no microbially-cemented frameworks were described so far.

4.3 Materials and Methods

The microbialite-coral mounds are exposed in road-cuts between Postojna and Koper where two localities have been studied in detail, Čebulovica and Divača (Fig. 4.1). In the case of the Divača mound a two-dimensional reconstruction of component distribution has been performed based on a combination of field observations, macroscopic study on slabs, and microscopic data from thin sections (Fig. 4.3A - B). In the case of the Čebulovica, difficult accessibility and the intense fracturing, limited a detailed mapping of the mounds. Nonetheless, the combined study of the Čebulovica and Divača mounds permits to understand the relationship between the bioconstructed facies and the associated bioclastic deposits. The Divača mound has a lenticular shape and it is exposed over a length of about 240 m, and a maximum thickness of 10 m (Fig. 4.3A - B). The base of the mound is not exposed; therefore these thicknesses measured must to be considered as minimum values.

For the high-resolution paleoecological and sedimentological analysis a total of 165 samples were collected along the mound and vertical transects covering the whole exposed bioconstruction and the overlying deposits. In the Čebulovica section the microbial carbonates form massive metric-thick mounds (up to 6 m thick) exposed over a length of 70 m, alternated with foralgal packstones and wackestones (Fig. 4.3C) (Foralgal Facies, *Assilina*-dominated assemblage and Orthophragminids-dominated assemblage, cf. *Zamagni et al*., 2008). In total 100 samples were collected from the Čebulovica mounds. Samples have been studied on polished, etched slabs, and in thin sections to investigate the patterns of microbialite growth and relation with other skeletal (mainly corals) and encrusting components. For optical-microscope analysis about 80 large thin sections (5.0 x 7.5 cm) and 50 small thin sections (2.8 x 4.6 cm) from the Divača mound and 30 large thin sections from the Čebulovica mounds have been prepared.

The taxonomic study of corals is based on randomly oriented thin-sections of cemented carbonate rocks. The taxonomic framework used to identify species is based on the work of *Turnšek and Drobne* (1998), and revision of *Baron-Szabo* (2006). All the samples used for systematic study of the corals are stored in the Institute of Geosciences at the University of Potsdam.

The biostratigraphic scheme used in this work follows the shallow benthic foraminifera biozones (SBZs) of *Serra-Kiel et al*. (1998; Fig. 3). The Paleocene–Eocene boundary is located in this study between SBZ 4 and SBZ 5. The absolute time scale is adopted from *Berggren et al*. (1995).

4.4 General patterns of encrustation within the mounds

The mounds are complex bioconstructions, mainly composed by sheetstone facies (dominated by sheet-like massive corals, based on classification of *Insalaco*, 1998) associated with bafflestones, and rudstones. They are composed by microbialites, colonial corals, micro-encrusters, macrofauna, mound matrix, and cements. The distribution of the components within the mounds is quite heterogeneous (Fig. 4.3).

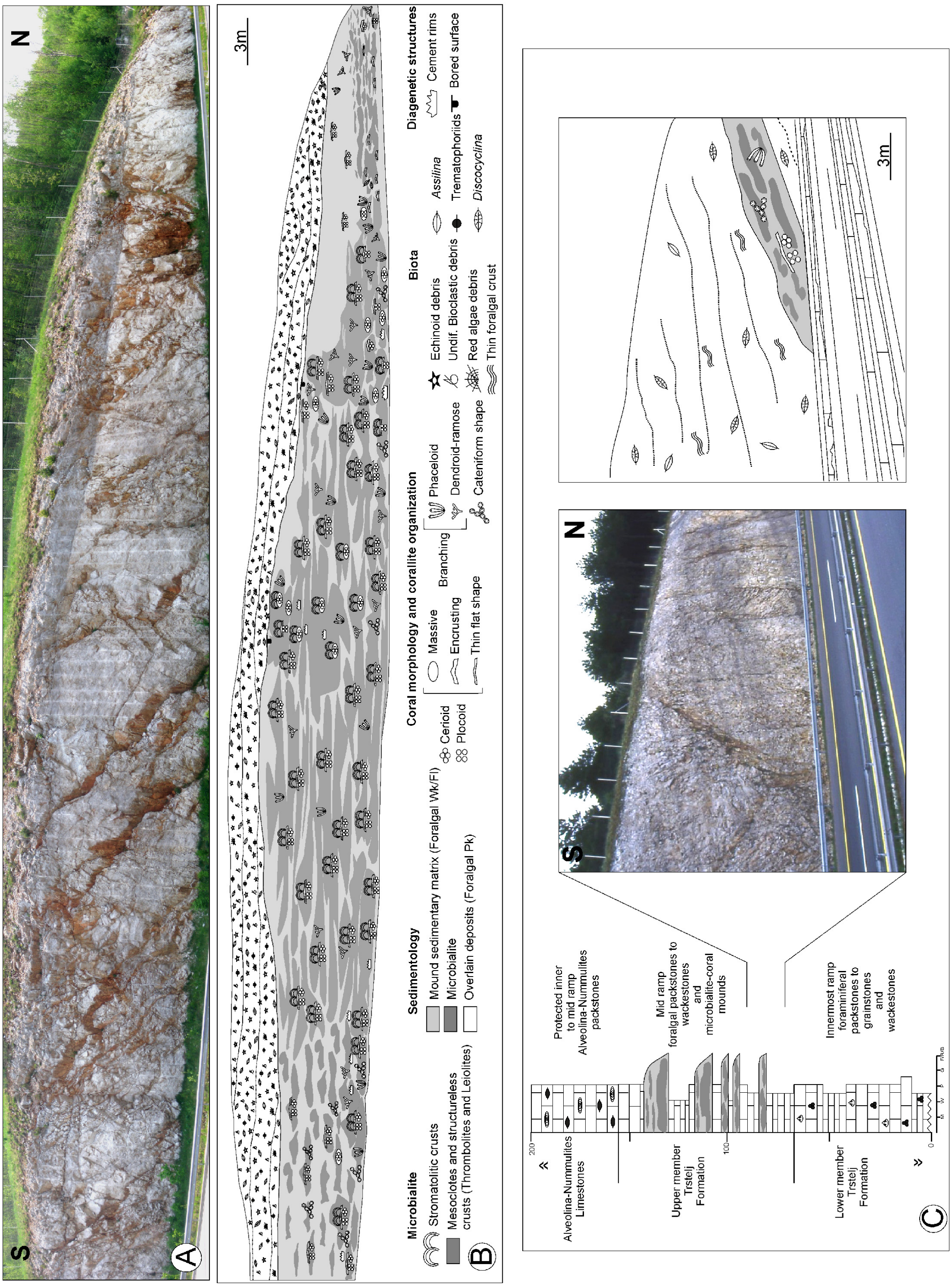
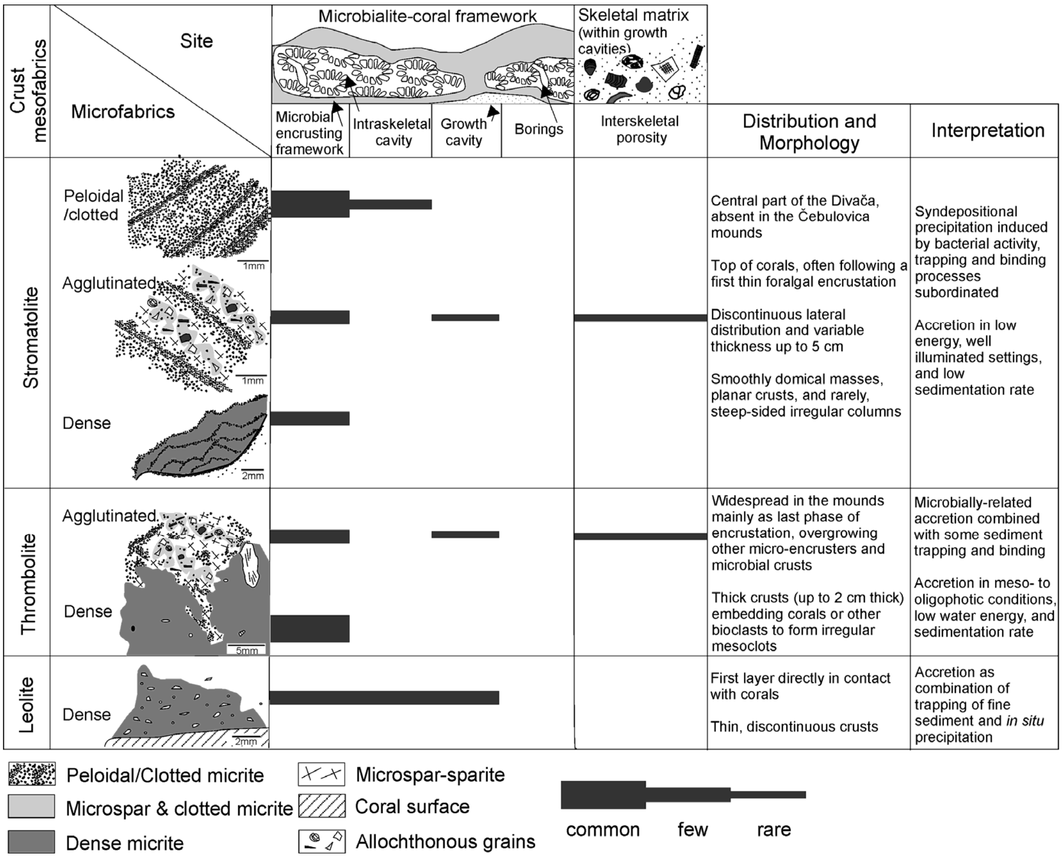


Figure 4.3: (A) First part of the Divača mound. (B) General distribution of the microbial carbonates and coral morphologies compared to the mound matrix. The foralgal packstones overlay the bioconstruction. (C) Stratigraphy of the Late Paleocene – Ilerdian (Eocene) Čebulovica section and outcrop photo of one of the mounds.

An overview of the relationship between these components indicates that in a first phase corals and micro-encrusters, including discontinuous stromatolitic crusts on top of coral surfaces and cryptic microbialites form a first loose, microbially-cemented framework. In a second phase benthic thrombolites, occurring as centimetric-thick crusts, become the dominant constructors excluding other encrusting biota. This pattern represents, in a simplified reconstruction, the basic constructional unit horizontally and vertically interlocked, in an irregular pattern, to form the mounds. No isochronous surfaces dominated either by corals or microbialites can be traced within the mounds. In the following section the diagnostic features of the microbialites are treated in detail, and the other components are described in the section 4.6.

4.5 Microbialite morphologies and fabrics

The microbialites volumetrically dominate the mounds, being the major framework constructor and stabilizer. The term “microbialite” is used according to the broad definition of *Burne and Moore* (1987, p. 241-242) as organosedimentary deposits that have accreted by combination of trapping and binding of detrital sediments by a benthic microbial community and/or mineral precipitation. Microbial carbonates form up to 70% of the Divača mound and around 50% in the Čebulovica mounds and are characterized by a range of mesofabrics (scale of description according to *Shapiro*, 2000) that can be attributed to: stromatolites, thrombolites, and leiolites (definitions according to *Riding*, 2000). Often the three types grade into one another even within the same thin section, indicating a complex construction of the framework. Macroscopically, the microbialites have a structureless, massive aspect, which makes difficult to distinguish the different morphotypes in the field. As a coarse rule, usually the microbialites are darker than the adjacent cavity-filling sediment. Microscopically, a range of fabrics has been observed and described in detail in the following paragraphs. For an overview, a simplified sketch of the meso-/microfabrics spatial distribution within the mound microenvironments together with a qualitative evaluation of their abundances, their major morphological features, and interpretation are illustrated and summarized in figure 4.4.



Crust mesofabrics	Distribution and Morphology	Interpretation
Stromatolite	Central part of the Divača, absent in the Čebulovica mounds Top of corals, often following a first thin foralgal encrustation Discontinuous lateral distribution and variable thickness up to 5 cm Smoothly domical masses, planar crusts, and rarely, steep-sided irregular columns	Syndepositional precipitation induced by bacterial activity, trapping and binding processes subordinated Accretion in low energy, well illuminated settings, and low sedimentation rate
Thrombolite	Widespread in the mounds mainly as last phase of encrustation, overgrowing other micro-encrusters and microbial crusts Thick crusts (up to 2 cm thick) embedding corals or other bioclasts to form irregular mesoclots	Microbially-related accretion combined with some sediment trapping and binding Accretion in meso- to oligophotic conditions, low water energy, and sedimentation rate
Leolite	First layer directly in contact with corals Thin, discontinuous crusts	Accretion as combination of trapping of fine sediment and *in situ* precipitation

Figure 4.4: Types of microbial carbonate fabrics distributed in different microenvironments of the mounds, main features, and interpretation.

4.5.1 Stromatolitic fabric

Characteristics

Stromatolitic fabrics are best developed in the central part of the Divača mound; whereas they are almost absent in the Čebulovica mounds.

Typically they occur on top of corals, often following a first thin foralgal encrustation, showing discontinuous lateral distribution and a variable thickness up to 5 cm. They form smoothly domal masses, planar crusts, and rarely, steep-sided irregular columns. The stromatolitic fabric consists of dense to peloidal/clotted micrite, commonly with scarce fine-grained allochthonous material embedded. The lamination is largely defined by changes in peloidal packing and differential compaction (Fig. 4.5A - B). The peloids in the stromatolites have a wide range of size but often they are ~50 μm wide, with margins both well-defined with simple outlines and more irregular to form aggregates creating a clotted fabric. In both cases, the remaining cavities between peloids and aggregates are filled by sparry calcite (Fig. 4.5C). A third fabric occurs, the agglutinated fabric, that can be described as peloidal packstone to grainstone with fine sand to silt-sized bioclasts (mainly small foraminifera and angular algal fragments, both micritized) and patches of silt-sized peloids floating in a sparry calcite (Fig. 4.5D).

In thin section, lamination ranges from wavy to smooth and it is usually best developed on planar and low domal crusts (Fig. 4.6), instead it is more irregular and poorly developed on steep-side crusts. Where sediment supply increases, laminae are weakly developed or absent and gradually pass to agglutinated microbialites or to detrital carbonate sediment. The stromatolites show both abrupt and gradual contacts with the detrital carbonate sediment, acting as matrix in the mound. When detrital sediment becomes more abundant, the matrix can be incorporated into the crust, coarsening the texture, or forming distinct separated laminae. Locally, stromatolites overlay the dense thrombolitic mesoclots (Fig. 4.6E).

Crusts composed by dense micrite with a crude lamination can be observed as first layer directly on top of corals, to form a discontinuous, thin (<1 mm) layer (Fig. 4.6F).

Interpretation

The stromatolitic fabric is clearly a syndepositionally lithified feature, as indicated by the gravity-independent accretion and the nature of the lamination, with discontinuous and reduced lateral persistence. Additionally, the floating habit of peloids and peloidal clusters within the sparry cement indicates an early mechanical stabilization and a biologically-induced accretion of the crusts. These microfabrics are widely distributed in modern (e.g., *Dupraz et al.*, 2004) and fossil stromatolites (e.g., *Riding and Tomás*, 2006), where they have been interpreted as produced by the micrite nucleation within biofilms embedding microbial communities (e.g., *Sprachta et al.*, 2001; *Dupraz et al.*, 2004).

Hence, the stromatolitic fabrics in the studied mounds are interpreted as having formed by syndepositional precipitation induced by bacterial activity, with additional trapping and binding playing a minor role. Nevertheless, the local occurrence of stromatolites with agglutinated fabrics and crude lamination points to episodes of higher bioclastic input, probably due to storms and bottom currents, with enhanced trapping and binding of allochthonous grains by the microbial mats. The agglutinated stromatolites likely were produced by microbial colonization of the interskeletal space, stabilizing the sediment and producing the peloidal packstone and grainstone fabrics.

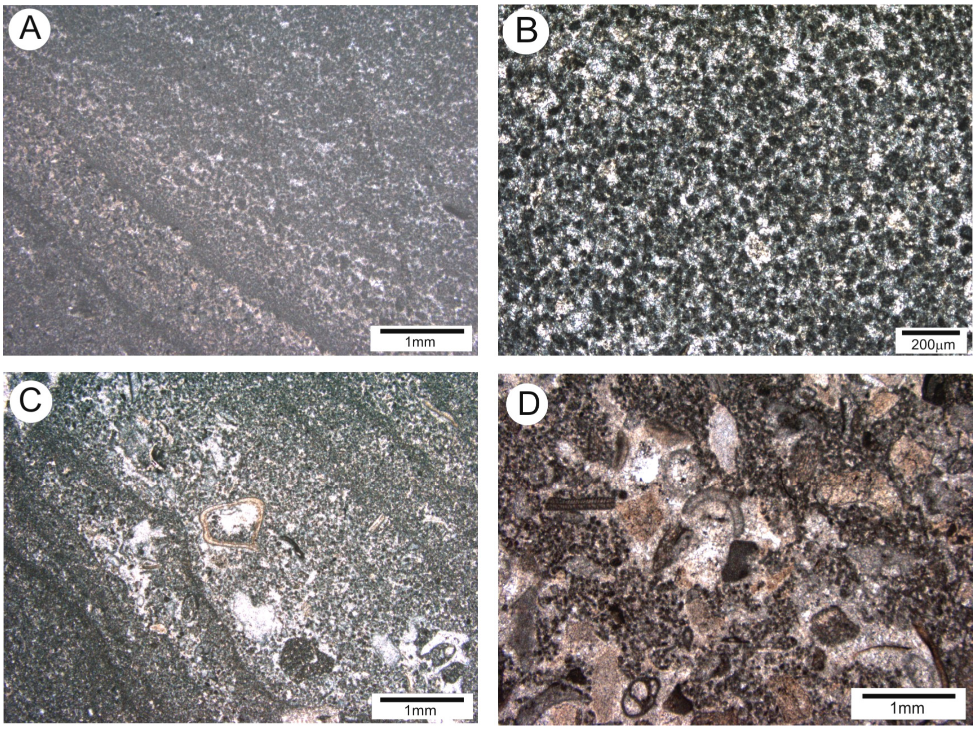
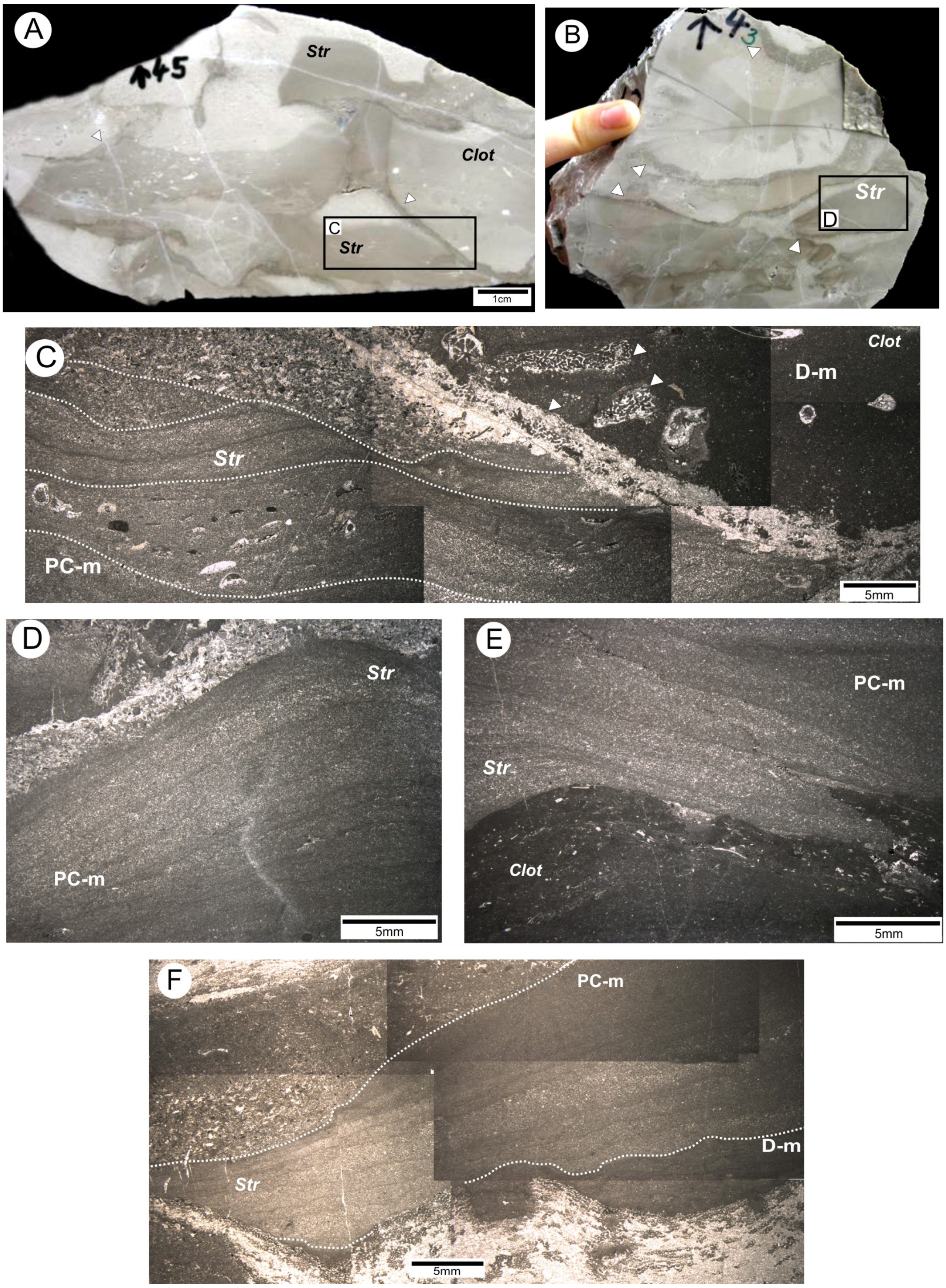


Figure 4.5: Microfabrics. (A) Lamination with darker layers produced by fine-grained closely packed peloids alternated with laminae with coarser, less-compacted peloids within microsparite. (B) Peloidal microfabric. (C-D) Detail of agglutinated microfabrics. (C) Peloidal grainstone with crude lamination. Lamination with coarsening upward sequence due to agglutination of allochthonous material embedded into spar and microspar, alternated with clotted/dense layers. (D) Agglutinated fabric with the bioclasts embedded into sparry calcite with patches of peloids, forming a peloidal grainstone.

The distribution of stromatolitic crusts mainly on the upper surface of corals points to a prominent role of photophile microbes, responsible for their accretion. The discontinuous distribution of these crusts on the coral surfaces might be related to a development confined to dead part of coral colonies. Moreover, this accretion was probably quite fast and continuous as testified by the almost complete absence of any other micro-encrusters associated with these crusts. The dominance of planar and low domal morphologies over columnar structures and the general development of well-defined lamination are interpreted as linked to a generally low to moderate sedimentation rate (*Dupraz et al*., 2006).

Figure 4.6 (next page): Divača mound. Stromatolitic mesofabric. Arrows indicate upward direction. (A-B) Polished surface with corals indicated by white arrows. (C) Thin-section photomicrograph detail of panel A (rectangle). Laminated crust on the left side of the coral colony (white arrows) with wavy accretionary style. The crust is composed of clotted micrite, passing abruptly to sedimentary matrix. Dense structureless micritic mass on the right side, with embedded coral fragments (white arrows). (D) Thin-section photomicrograph detail of panel B (rectangles) with domical, laminated microbial crust. (E) Stromatolite with crude lamination overlain dense mesoclot. (F) Thin-section photomicrograph of a crust with domal shape on top of coral, with crude lamination. The crust follows a first discontinuous layer of dense, irregularly laminated stromatolite and passes upward to fine detrital wackestone. *Str*: Stromatolite. PC-m: Peloidal/Clotted micrite; D-m: Dense micrite.



4.5.2 Thrombolitic fabric

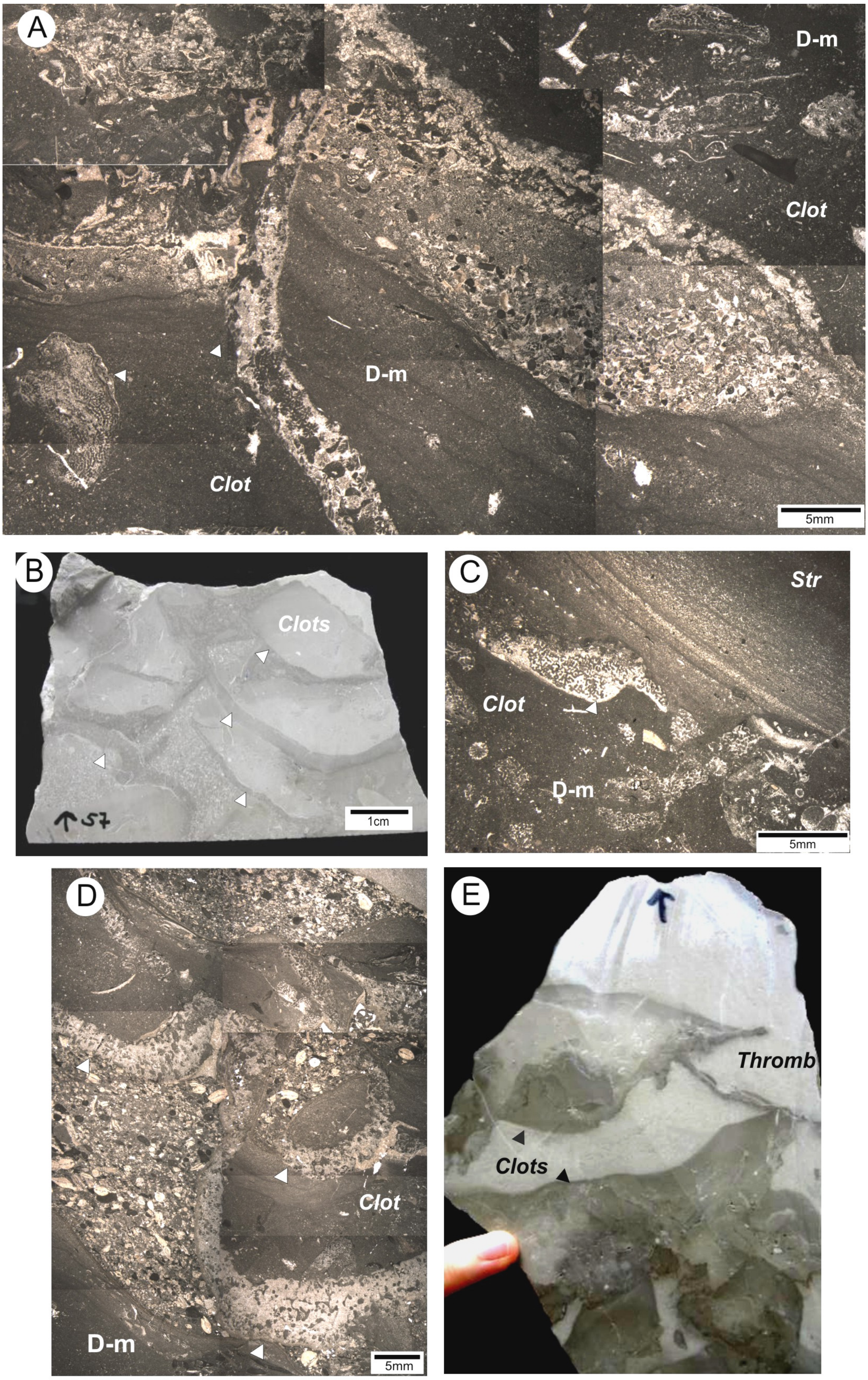
Characteristics

Microbialitic crusts showing clotted mesostructure characteristic of thrombolites (*Aitken*, 1967; *Kennard and James*, 1986; *Shapiro*, 2000) are commonly present in the mounds. Thrombolites have been observed within cavities, but they mainly occur as the last phase of encrustation, overgrowing other micro-encrusters and microbial crusts, filling the growth cavities, and encrusting the first coral-microbialite framework. Thick thrombolitic crusts (up to 2 cm thick) develop on the upper surface of corals as well as embedding them or other bioclasts to form an irregular clotted fabric (Fig. 4.7). Macro- and mesoscopically, these microbialites show a clotted aspect (Fig. 4.7B - E) and consist of millimeter to centimeter-sized dark, dense micritic clots passing to lighter areas enriched in allochthonous grains. The clots have an irregular shape with sharp as well as “fuzzier” margins grading to agglutinated microbialites or sedimentary matrix. Thrombolites have been also observed associated with clasts of stromatolitic crusts and coral debris to form a chaotic, breccia-like fabric (Fig. 4.8A - B), which hints for a complex growth history of the mounds.

Interpretation

The thrombolites show some of the typical features described by *Kennard and James* (1986), with dense mesoclots with little debris inside separated by patches of micrite, sediments and cements. The dense to peloidal/clotted nature of the microfabrics has been interpreted as the result of carbonate precipitation induced by the metabolic activity of heterotrophic coccoid or coccoid-dominated microbial communities (e.g., *Kennard and James*, 1986; *Leinfelder et al.*, 1996; *Dupraz and Strasser*, 1999). The studied thrombolites have a broad distribution irrespective of exposure to light, forming encrustations on both sides of corals and in cryptic habitats. This points to a formation linked to the activity of sciaphile bacteria, using heterotrophic metabolisms, in settings with low energy and low sedimentation rate (e.g., *Leinfelder et al.*, 1993; *Leinfelder et al.*, 1996; *Camoin and Montaggioni*, 1994; *Camoin et al.*, 1997; *Camoin et al.*, 1999; *Dupraz and Strasser*, 1999, 2002). Apart from *in-situ* precipitation and trapping and binding, the major processes leading to the development of thrombolites, other processes also might have played a role in the formation of the thrombolitic mesofabric.

Figure 4.7 (next page): Divača mound. Thrombolitic mesofabrics. Arrow indicates upward direction. (A) Thrombolite with dark micritic clots embedding corals (white arrows). (B-D) Polished surface and thin-section photomicrograph with thick crusts of structureless micrite as clots on top of corals (white arrows), passing to bioclastic deposits filling the inter-clot space. (C) Passage from thrombolitic dense crust with embedded coral debris to laminated stromatolite overlying the mesoclot. (E) Polished surface. Mesoclots with darker aspect and irregular shape (black arrows), passing abruptly to lighter areas. *Thromb*: Thrombolite; *Str*: Stromatolite. D-m: Dense micrite.


A
D-m
Clot
D-m
Clot
5mm
B
Clots
↑57
1cm
C
Str
Clot
D-m
5mm
D
Clot
D-m
5mm
E
Thromb
Clots

The common presence of borings in the thrombolites as well as the co-occurrence and transition to stromatolite crusts, forming locally chaotic texture resembling a breccia, seem to point to syndepositional reworking (e.g., storms and bioturbation) responsible for enhancing the clotted fabric. *Braga et al*. (1995) described Miocene thrombolites from Spain, produced by multiple processes with the calcification of microfossils associated with a complex interaction of irregular agglutination, skeletal encrustation, erosional processes and bioturbation.

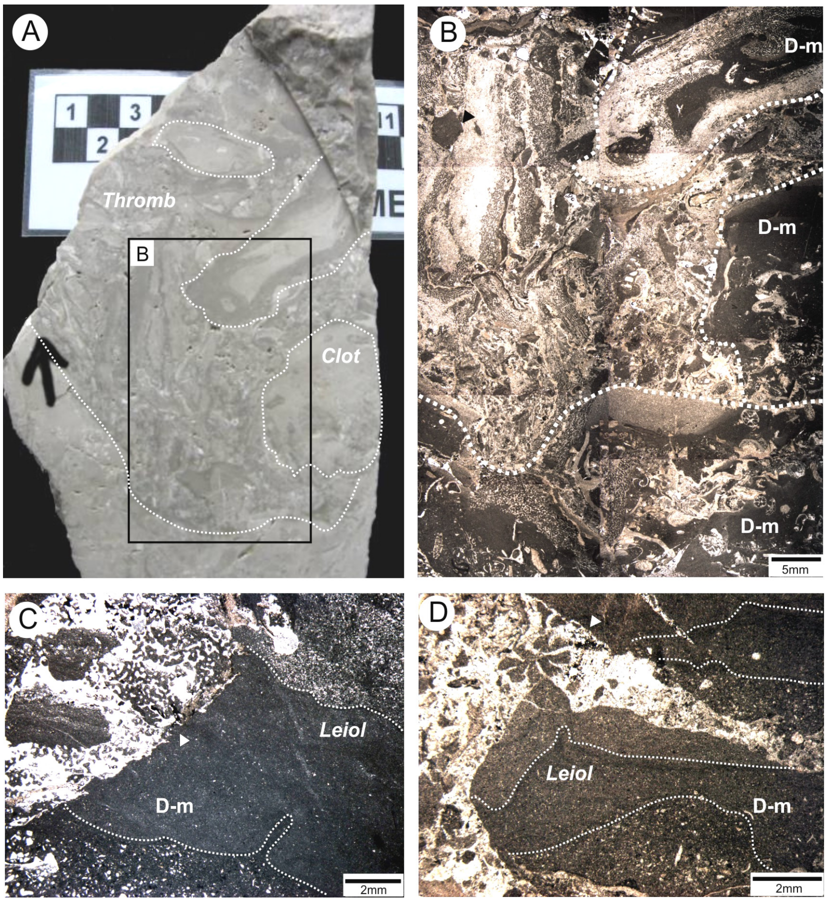


Figure 4.8: Divača mound. Thrombolitic meso- and microfabrics. (A-B) Polished surface and thin-section photomicrographs. Clotted mesofabric with chaotic association of coral debris and dense clots. Leiolites. (C-D) Corals (white arrows) encrusted by thin dense micrite with fine debris inside passing to dense, debris-free micritic crusts. *Thromb*: Thrombolite; *Leiol*: Leiolite. D-m: Dense micrite; PC-m: Peloidal/Clotted micrite.

4.5.3 Leiolitic fabric

Description

Leiolitic fabric occurs in both the Divača and the Čebulovica bioconstructions, but is better developed in the first, where it is widespread throughout the mound even volumetrically quite subordinated compared to thrombolites and stromatolites. Macroscopically, leiolites are difficult to distinguish due to the general aphanitic aspect of the mound limestones. They form thin discontinuous crusts.

In thin section, they are usually composed of dense micrite with well-sorted, very fine-grained debris embedded. The contact with the surrounding deposits is usually sharp and their crustose nature is inferred from the development of knobs and protuberances (Fig. 4.8C - D). Commonly these crusts form a first layer directly in contact with corals as well as in interskeletal and growth cavities, being followed by stromatolite and/or thrombolite crusts, and the mound matrix.

Interpretation

The common presence of allochthonous fine sand-sized debris embedded in the leiolitic crusts seems to indicate accretion resulting from the combination of trapping of fine sediment and microbially-induced precipitation of micrite. Their occurrence on the upper surface of corals as well as cryptic habitats points to an origin from microbial communities with variable light requirements.

4.6 Other components of the microbialite-coral mounds

4.6.1 Coral assemblage

The coral colonies occur in the mounds without a clear growth direction and without a defined ecological zonation throughout the bioconstructions, showing a heterogeneous distribution of morphotypes. They do not form coral-dominated levels within the mounds, rather they are randomly distributed. The corals and associated micro-encrusters are usually welded by thick microbial crusts (stromatolites and to a less extend leiolites) and surrounded by thrombolites. The microbial crusts develop over corals in growth position and coral clasts. Alternations between encrusting coral and microbial crusts are observed at centimetric scale to form a first loose framework (sheetstone growth fabric). Coral skeletons are commonly affected by bioerosion. In the Divača mound corals might represent up to ~ 30% of the bioconstruction. Colonies are small, centimetric in width (less than 10 cm) and corals have moderate generic/low specific diversities (13 genera, 15 species) (Fig. 4.9). The dominant morphologies are represented by plocoid and cerioid encrusting, thin platy and massive low-relief colonies. Dendroid and phaceloid forms are less abundant but widespread throughout the bioconstruction. Some of the most common species are the massive *Goniopora elegans* (Leymerie 1846) and *Astrocoenia gibbosa* Duncan 1880*,* the encrusting *Astreopora esperanzae* Frost & Langenheim 1974*, Stylocoenia neutra* Barta-Camus 1973*,* and *Actinacis cognata* Oppenheim 1901.

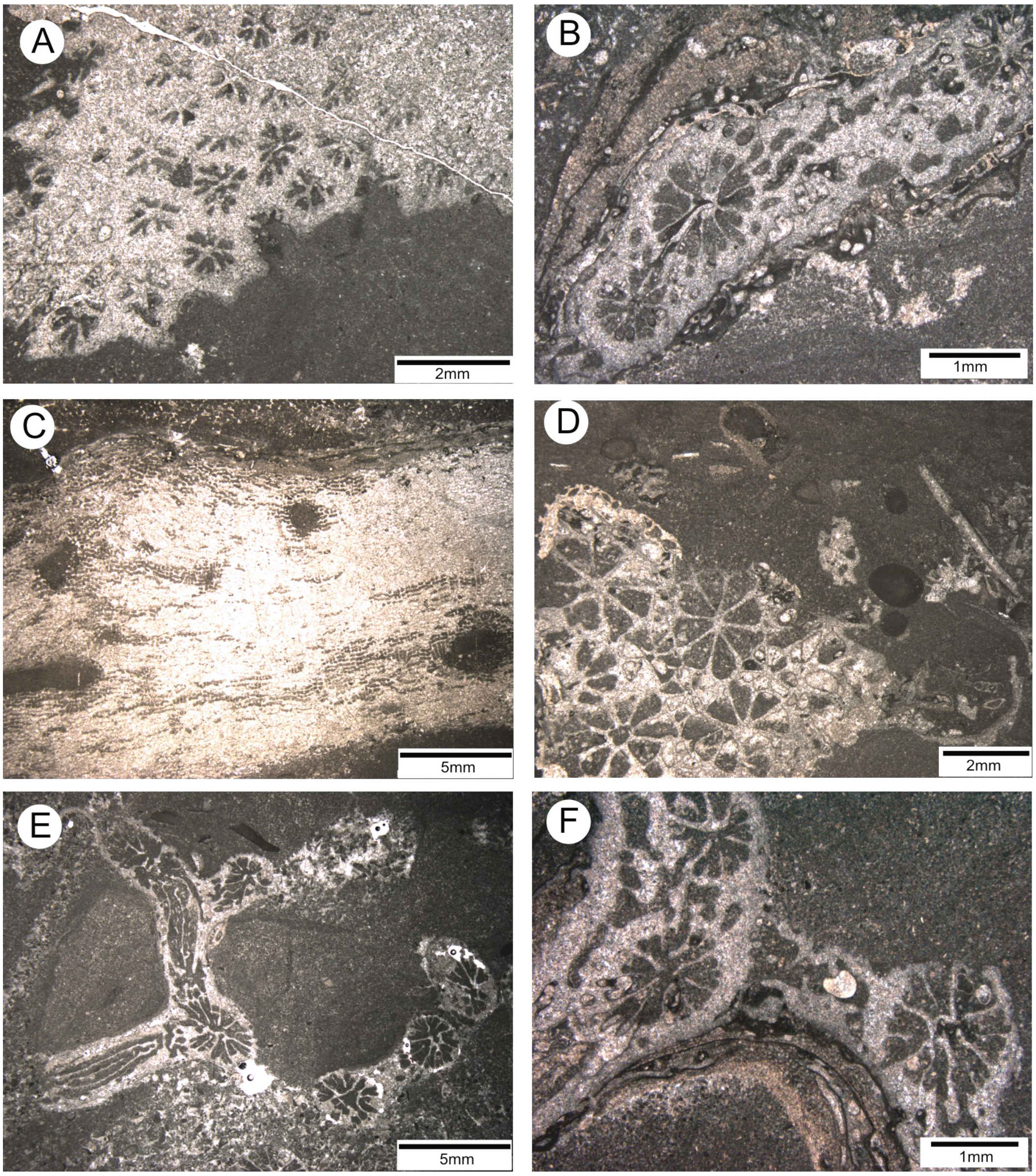


Figure 4.9: Coral assemblage. (A) *Stylocoenia neutra* Berta-Calmus 1973. (B) *Astreopora esperanzae* Frost & Langenheim 1974. Note the acervulinid encrustation. (C) *Actinacis cognata* Oppenheim 1901. Note macroborings. (D) *Astrocoenia gibbosa* Duncan 1880. *Planorbulina* specimen on the top left of the coral colony. (E) *Oculina becki* (Nielsen 1922). (F) *Rhizangia padricensis* Tunšek, 1998.

Other very common encrusting forms include the tiny, cateniform *Bacarella vipavica* Turnšek 2004, described for the first time in *Turnšek and Košir* (2004), and the reptoid

Rhizangia padricensis Turnšek 1998, described firstly in *Turnšek and Drobne* (1998). Dendroid and phaceloid colonies are mainly represented by *Dendrophyllia candelabrum* Hennig 1899, and *Oculina conferta* Milne Edwards & Haime 1850. Colonies and fragments of *Madracis sp*. Milne Edwards & Haime 1849, *Oculina becki* (Nielsen 1922)*, Pachygyra savii* (D'Achiardi 1866), *Plocophyllia carstica* Turnšek 1988, and *Litharaea sp*. Milne Edwards & Haime 1851 have been also observed. In the Čebulovica mounds corals seem to be less abundant, and less diverse, compared to the Divača mound, even if these features might be artifacts due to a more spaced sampling. Corals represent ~ 20% of the mounds and are mainly represented by the *Actinacis cognata, Astreopora esperanzae, Bacarella vipavica, Rhizangia padricensis*, and *Stylocoenia neutra* associated with *Dendrophyllia* spp., and *Oculina conferta*.

4.6.2 Micro-encrusters

Micro-encrusters, mainly foraminifera, directly encrust the coral surfaces forming discontinuous coatings, up to 2 cm thick, complex encrustations, with *Acervulina* and *Haddonia* associated with *Miniacina, Planorbulina*, and nubeculariids as the most common forms (Fig. 4.9B - D - F). Calcareous red algae, subordinated compared to the foraminifera, are represented by melobesioids, which form very thin (less than 500µm), discontinuous veneer around corals. These encrustations are usually not bored pointing to a rapid overgrowth by microbialites. Other, less frequent micro-encrusters are bryozoans, calcareous sponges and serpulids. Encrusters are generally excluded during the prominent microbialite growth.

4.6.3 Macrofauna

The macrofaunal biota (excluded corals) is generally a subordinated component (an average of ~10%) represented by small calcareous sponges, delicate branching bryozoans, thin shelled bivalves, small gastropods, and echinoderms (rare skeletal elements of crinoids and more commonly echinoid spines and fragments). Locally, tiny spicules of sponges have been observed. Small benthic foraminifera are few and represented by rotaliids associated with very rare miliolids and textulariids. Larger benthic foraminifera are scarce and represented by small, flattened specimens of *Discocyclina* and *Assilina*.

4.6.4 Mound matrix

The microbialites, corals, and micro-encrusters together contribute to form a sort of mound framework. Primary growth cavities in the mounds are filled, together with microbialites, by allochthonous and reworked sediments forming the mound matrix. This matrix is represented by wackestones to packstones with fine, abraded fragments of calcareous red algae (corallines, peyssonneliaceans and fragments of *Distichoplax biseralis* (Dietrich) Pia), micritized grains, small foraminifera, and fine debris. Locally larger benthic foraminifera (*Assilina azilensis* Tambareau, *Assilina yvettae* Schaub, and *Discocyclina seunesi* Douvillé) and other small benthic foraminifera can be also accumulated (Fig. 4.7D). This mound matrix passes to the microbial crusts through sharp contacts, although often it seems to grade and be incorporated into the microbial crusts, forming agglutinated fabrics.

4.6.5 Cements

Locally, millimetric to centimetric-thick, isopachous rims of brownish, inclusion-rich radiaxial-fibrous calcite have been observed to fill cavities of irregular shape, growth cavities or to alternate with microbial crusts. The transition from the peloidal micrite of the microbialites to the radiaxial-fibrous calcite rims can be gradual, with peloids embedded in the calcite crystals (Fig. 4.10A) or sharp, marked by an undulate surface (Fig. 4.10B). This relationship provides a further argument for the early lithification of the microbialites.

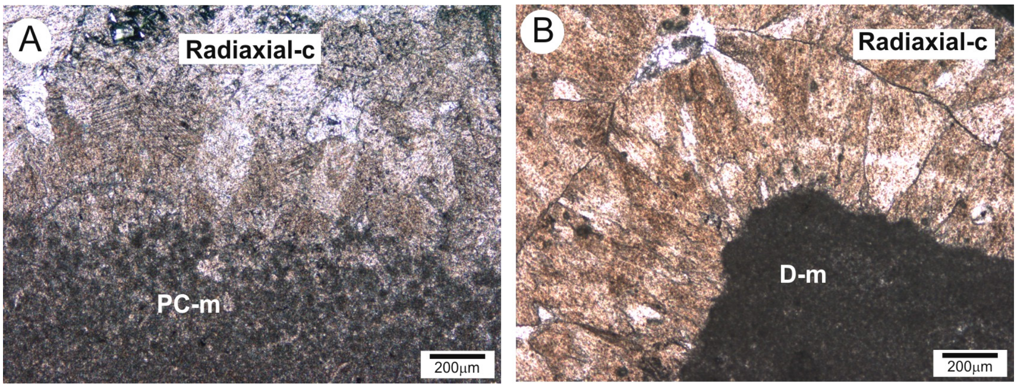


Figure 4.10: (A) Radiaxial-fibrous calcite embedding peloids and nucleated directly on the microbial substrate with peloidal microfabric. (B) Isopachous rim of radiaxial-fibrous calcite nucleated directly on dense microbial substrate. D-m: Dense micrite; PC-m: Peloidal/Clotted micrite; Radiaxial-c; radiaxial calcite.

4.7 Lateral and overlying skeletal deposits associated with the mounds

The Divača mound grades laterally into wackestones/floatstones. These are characterized by fine bioclastic debris and thin foralgal crusts, mainly of peyssonneliacean algae *Polystrata alba* (Pfender) Denizot associated with acervulinids and bryozoans. Coral fragments can occur, often encrusted by acervulinids. Small benthic foraminifera (mainly rotaliids) and rare larger foraminifera (small/flattened *Discocyclina* specimens) form an assemblage comparable to the Orthophragminids-dominated assemblage in the Čebulovica section (cf. *Zamagni et al.*, 2008). Locally, angular fragments of microbial crusts are resedimented.

The Divača mound is abruptly overlain by stratified foralgal packstones (Fig. 4.3A - B), which rest over a hardground surface marking the top of the mound. This surface is characterized by borings filled by the overlying deposits, indicating an early lithification for the mound. These deposits belong to the upper member of the Trstelj Fm. (Foralgal Facies, *Assilina*-dominated assemblage, cf. *Zamagni et al.*, 2008), Latest Thanetian in age (SBZ4). The packstones are dominated by perforate foraminifera, mainly *Assilina*, associated with less common small/ovate *Discocyclina* and rare big miliolids. Calcareous red algae occur as fragments, crusts and nodules with melobesioids and peyssonneliaceans as dominant forms. Echinoid fragments are abundant.

The Čebulovica mounds are vertically alternated with the packstones and wackestones of the Foralgal Facies of the Trstelj Fm. (*Zamagni et al.*, 2008) (Fig. 4.3C). The comparison with the Divača mound suggests that the Čebulovica mounds represent either a superposition of several incipient mounds overlain by the foralgal facies or a lateral mound facies representing a transition between the mound core and the lateral deposits. The packstones and wackestones alternating with the incipient mound facies contain bioclasts that are generally angular and associated with abundant and irregularly distributed micrite. The bioclasts show widespread micritization and the development of constructive micrite envelopes (see *Perry*, 1999) pointing to an intense colonization by microbial organisms, promoting the stabilization of these sediments (*Hillgärtner et al.*, 2001). Locally, the isoorientation of the foraminiferal tests and their distribution resemble tubular tempestites (see *Tedesco and Wanless*, 1991). These structures have been observed especially in the bioclastic packstones dominated by *Assilina*.

These features would suggest that the skeletal deposits on top of the Divača mound and the packstones alternating in the Čebulovica mounds accumulated under the influence of periodical storms or bottom currents affecting the mid-ramp and redistributing material from the inner/upper-mid-ramp towards the distal part of the ramp (*Zamagni et al*., 2008).

4.8 Discussion

4.8.1 Coral and microbialite growth rates and their roles in the mound development

Microbial growth rates are relatively low in comparison to that of Recent colonial corals, with microbialite largely restricted to cryptic habitats in modern reefs (e.g. *Webb*, 2001). Microbial precipitates can become prominent components of a bioconstruction where environmental conditions produce a slower coral growth rate, like in the case of deep-water reef mounds (e.g., *Sun and Wright*, 1989). Considering the microbial carbonate accretion rates reported in literature from marine settings, it is possible to establish a range from 1-2 mm/yr for the stromatolite/thrombolite complex on Stocking Island, Bahamas (*Macintyre et al*., 1996) up to 8 mm/yr calculated by *Montaggioni and Camoin* (1993) for stromatolitic crusts within a coralgal reef in Tahiti. These accretion rate estimates slightly overlap the growth rate of scleractinians living in moderately deep waters, even if they are on average slower. Growth rates of some modern zooxanthellate scleractinian corals from the Caribbean, reported by *Dullo* (2005), clearly show a decrease with increasing water depth. The Caribbean *Porites* shows an annual growth rate in the order of 10 mm/yr in shallow-water regions, dropping to 4 mm/y in deeper-water settings and 2.3 mm/yr at 30 m depth in Jamaica. *Montastrea* from deep water (45 m depth) of Jamaica is characterized by a very slow growth rate of 1.6 mm/yr.

In addition to water depth, changes in water quality may further decrease coral growth rates. Episodic increases of nutrient/turbidity levels might reduce the coral growth rates and directly or indirectly favoring partial to complete mortality by bacterial infestation, disease and suffocation (*Hallock*, 1987, 2005; *Thacker and Paul*, 2001; *Ritson-Williams et al*., 2005; *Smith et al*., 2006; *Smith et al*., in press). The development of discontinuous stromatolitic crusts on the upper surface of platy corals might be an indication for the presence of local bacterial infestation affecting living corals; alternatively microbes could have used only dead part of the colonies as substrate. In both cases the deterioration of water quality in terms of coral requirements might have been the cause of coral demise with the microbe spreading as consequence. This change of dominant bioconstructors from corals to microbes could be interpreted in terms of “phase shift” (see *Done et al*., 1992 for definition) related to environmental degradation. Today the rapid overgrowth of degraded reef corals by algae (e.g., *McCook*, 1999) and other cnidarians (e.g., *Work et al*., 2008) is a phenomenon observed in regions where a combination of factors related to human activity (e.g., overfishing, eutrophication) strongly reduces the cover of living corals. Nonetheless, it remains an intriguing issue whether the new invaders are responsible for coral death or if they just colonize dead coral surface. In the case of the studied mounds, the widespread bioerosion affecting coral skeleton, prior to major thrombolite encrustation points to nutrient pressure (e.g., *Hallock*, 1988) already affecting corals, and likely limiting their growth capacity.

The widespread development of microbialitic crusts in open, not confined environments, associated with complex intergrowth with corals, indicates that the microbialites and corals might have had comparable growth rates, thus competing for space. The dominance of encrusting, flat forms and low-relief massive coral colonies suggests the necessity to optimize light catchment. This would point to growth in the oligophotic zone, implying a general slow coral growth rate due to a less vigorous photosynthetic activity. Additionally, the coral assemblage shows features which indicate a general tolerance to turbidity pressure with small corallites and plocoid- (e.g. *Actinacis*) cerioid (e.g., *Goniopora*) colonies common (*Sanders and Baron-Szabo*, 2005). Nonetheless, episodic increases in turbidity/nutrient levels might have affected these corals strongly reducing their growth rates, and promoting the thrombolite development.

Further observations suggest that environmental “disturbances” were rather episodic than continuous. Based on the dimensions of the coral colonies (max. 6/7 cm) we can speculate that their growth periods might have duration of few decades assuming slow growth rate of 1-2mm/yr. This would explain the pioneer stage of the coral community in these mounds. They occur as disoriented and more-or-less fragmented colonies, with any ecological zonation within the bioconstructions, possibly as consequence of a shorter time interval of disturbance compared to the time needed for full community recovery. Actually, both in fossil and recent records frequently disturbed coral communities appear as rubble piles and/or mounds instead of coral reefs (*Sanders and Baron-Szabo*, 2005 and therein references).

4.8.2 Micro-encruster assemblage and macrofauna

The study of the encruster assemblages combined with their association to specific microbialite types has been used largely and successfully applied for paleoenvironmental reconstructions (e.g., Upper Jurassic reefs: *Leinfelder et al.*, 1993; *Dupraz and Strasser*, 1999). Two major groups of encrusters provide useful hints for a general discussion: encrusting foraminifera and coralline algae. Both encrusting foraminifera, and to a less extend red algae, are common in the coral-microbial phases and absent in the thrombolite-dominated growth phases.

Foraminifera include common opportunist forms with acervulinids and nubeculariids dominant, often overgrown by *Haddonia*. Modern counterparts of these encrusters are not associated with photosymbiotic endosymbionts (*Reiss and Hottinger*, 1984). Recent acervulinids are common in very shallow water, as cryptobionts, up to lower limit of the photic zone, likely due to the disappearance with depth of benthic diatoms, their food source (*Reiss and Hottinger*, 1984). Their constructional role is enhanced where light conditions reduce competition for substrate encrustation (*Perrin*, 1992). Modern species of the genus *Haddonia* live in shaded areas, indicating a sciaphile affinity (*Matteucci*, 1996). The widespread occurrence of these heterotrophic encrusters indicates suitable conditions in terms of food availability. The exclusion of encrusting foraminifera from the benthic thrombolites would suggest that conditions promoting fast microbial growth were preventing the development of other encrusters.

Coralline algae are present but clearly were not successful with respect to corals, microbialites, and encrusting foraminifera with a minimal binding function of in the framework construction. Coralline algae were important framework bioconstructors during the Late Paleocene (e.g. in the Pyrenees, *Baceta et al.*, 2005) and experienced a diversification at that time (*Aguirre et al.*, 2000). These facts exclude the possibility that the reduced presence of coralline algae was related to evolutionary processes. The presence of organisms adapted to normal marine-water conditions, first of all corals, precludes the possibility that the environment had not normal salinity or oxygen levels. Therefore, the reasons for the development of microbial and foraminiferal encrustations instead of corallines need to be further investigated. A similar, enigmatic situation occurred also in Upper Miocene coral-microbialite reefs from Southern Spain (e.g. *Riding et al.*, 1991), where corallines have been excluded from the frame building and substituted by thick microbial crusts.

Among the macrofaunal components, the larger benthic foraminifera are few and represented by *Assilina* and *Discocyclina* genera. At present, *Assilina* thrives in the lower photic zone on soft, muddy sediments, with *Assilina ammonoides* able to tolerate eutrophication events (e.g. Lacadive Islands; *Langer and Hottinger*, 2000). Macrofaunal elements other than larger foraminifera and corals are represented by grazers and filter-feeders (echinoids, gastropods, bivalves, bryozoans, and calcareous sponges). Their presence indicates adequate nutrient concentrations to sustain this fauna. Bioerosion is quite well developed as testified by the widespread occurrence of macroborings in coral skeletons.

Based on the weight of these evidences it is possible to reconstruct environmental conditions, during the growth of micro-encrusters and macrofauna, as characterized by oligophotic and mesotrophic nature. Thus, the exclusion of micro-encrusters during the massive growth of thrombolites might indicate enhanced concentration of nutrients to high mesotrophic to eutrophic levels promoting the fast microbial bloom.

4.8.3 Microbialite growth history

Repeated episodes of shifts from corals to microbialites produced the vertical superposition of several microbialite-coral growth units. The microbial crusts were lithified early, as revealed by the common occurrence of encrusting corals using microbialites as stable substrates, the presence in the lateral deposits of resedimented fragments of microbial crusts and the bored surface of the Divača mound at the contact with the overlain foralgal packstones. The presence of macroborings in thrombolites, further confirms an early lithification. The shift from one microbialite morphotype to another could have resulted from episodes of enhanced microbial calcification, changes in the morphology of microorganisms, fluctuations in the relative importance of microbial calcification respect to trapping of sediment. Furthermore, environmental changes related to nutrient/turbidity pressure might have promote changes in the trophic structure, leading to a shift from phototrophic to heterotrophic nutritional modes (*Hallock and Schlager*, 1986; *Dupraz and Strasser*, 2002; *Mutti and Hallock*, 2003), associated with a change in microbe community and, thus microbialite fabrics.

Based on the geometric relationship between corals, microbial crusts, mound matrix, and bioclastic deposits associated with the mounds, and despite the complex growth pattern and transition between the different microbialite morphologies, a simplified model of development for the microbial crusts and for the mound bodies is tentatively reconstructed (Fig. 4.11):

(1) A first stage for the mound evolution was the development of a stable substrate. The bioclastic sediments occurring laterally to the Divača mound and vertically alternated with the Čebulovica mounds were deposited in the distal mid ramp under the periodical influence of storms and bottom currents. The widespread micritization of the bioclasts and the development of constructive micrite envelopes suggest an intense activity of microendolithic organisms immediately after deposition of the bioclastic deposits. In conditions of low accumulation rate, as likely was during the deposition of these limestones, this process could have initiated the stabilization of the bioclastic deposits (*Hillgärtner et al.*, 2001), thus proving an initial substrate for coral colonization (Fig. 4.11a).

(2) After the early stabilization of the substrate, the mound growth initiated with coral colonization and a first generation of micro-encrusters. During this phase, first structureless, cryptic microbialites (leiolitic and thrombolitic crusts) and planar to domal stromatolites were growing. The growth of these crusts probably started on platy corals, from which they extend laterally to connect coral colonies contributing to the formation of a first framework (Fig. 4.11b-c). At this time the coral and microbialite growth rates were comparable, with corals being slightly faster. The development of the microbial crusts during this phase was confined to cavities within the framework and likely dead part of the coral colonies, as suggested by the later discontinuity of the stromatolitic crusts. The environmental conditions at this time were of low-moderate turbidity, low mesotrophic condition and low sedimentation rate, as inferred by stromatolite crust morphologies, mainly planar and domal, with steep-sided form almost absent (*Dupraz et al.*, 2006) and flat encrusting and low-surface relief massive coral colonies dominant (*Sanders and Baron-Szabo*, 2005).

(3) Changes in the environmental parameters, with temporal increase of nutrient availability and turbidity caused a shift to high mesotrophic-eutrophic conditions, with thrombolites taking on the building role (Fig. 4.11d). The sediment accumulation was probably still low, and did not prevent the thrombolite growth, with sediments likely by-passing the mounds (e.g., *Larcombe et al.*, 2001), but still causing increase of nutrient levels and high turbidity. The state of preservation of the corals, with widespread macroborings, and common coral fragments embedded into thrombolites, indicates a shift to heterotrophic nutritional mode, with high bioerosion rate, coupled with reduced coral growth rates in highly turbiditic conditions, which favored the thrombolite growth.

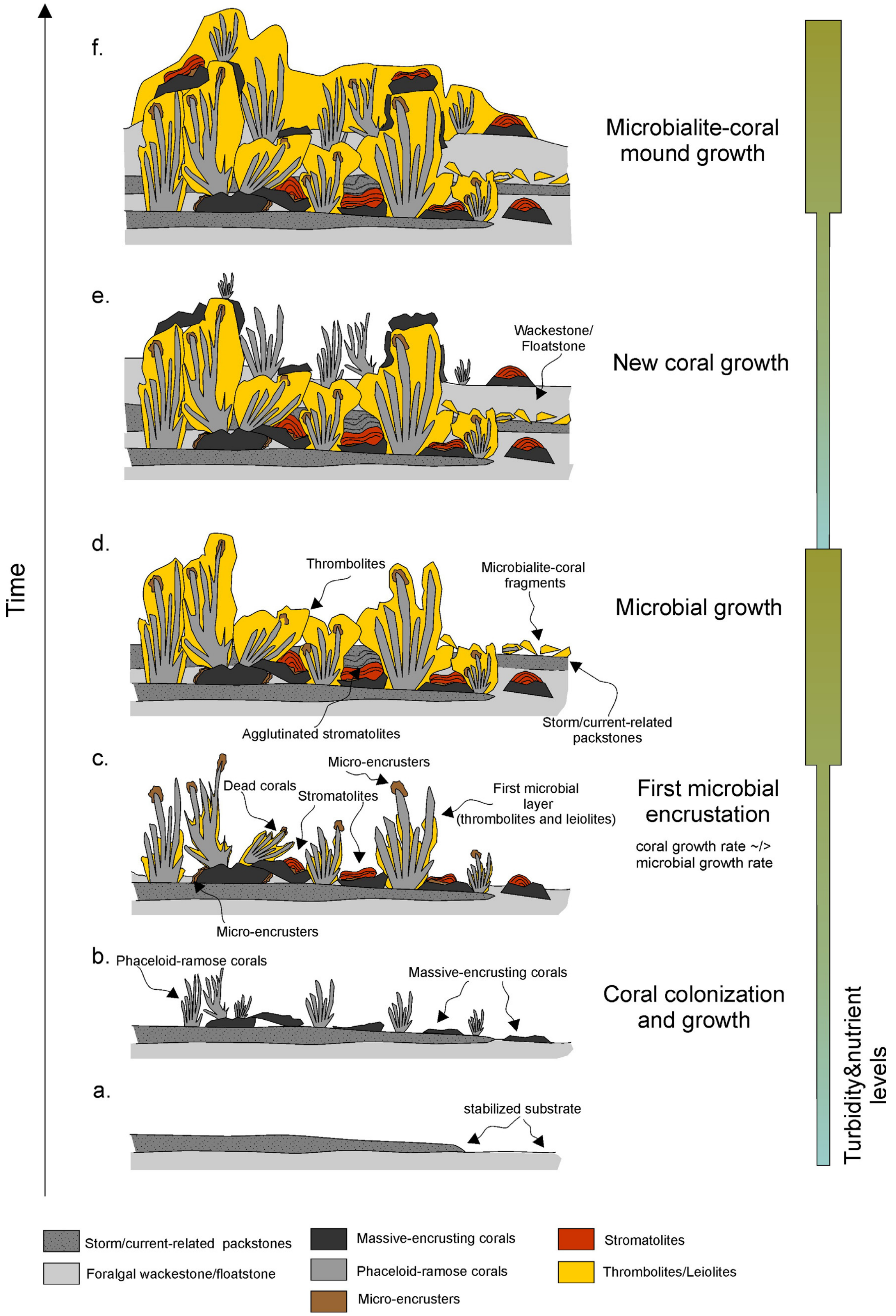


Figure 4.11: Simplified model for the evolution in time of the mounds. See text for explanation.

Thus, the blooming of microbialites was probably not the cause of the coral demise, but the consequence, with corals likely dead at the time of thrombolitic encrustation. The shift from corals to thrombolites was therefore an environmentally-driven process, resulting in change of the trophic structure at micro- and macroscale from phototrophic to heterotrophic, with demise of corals and stromatolites substituted by thrombolites.

(4) After a period of recovery with lowering of turbidity/nutrient levels, during which bioeroders are still active producing macroborings on the thrombolites, a new colonization of the lithified microbialite substrate by corals and micro-encrusters occurred (Fig. 3.11e) leading to the further growth of the mound (Fig. 4.11f).

4.8.4 Main factors controlling microbialite-coral growth and mound development as related to local and global climatic events

Physico-chemical properties of the environment control and eventually promote microbial accretion processes (e.g., *Neuweiler*, 1993; *Riding*, 2000). Thus, climate, paleogeographic configuration, and their impact on water physico-chemical features such as alkalinity, pO_2, salinity, nutrient/terrigenous influx, and sedimentation rate are the most important extrinsic factors controlling the development of microbially-induced precipitates. The studied carbonates were deposited along the marginal areas of the large, isolated Adriatic Carbonate Platform (paleolatitudes ~32°N), locally subaerially exposed since the Late Cretaceous (*Vlahović et al.*, 2005). During the Thanetian, the Tethyan realm was affected by a general warm, humid, subtropical climate (*Pearson et al.*, 2007; *Lourens et al.*, 2005; *Bolle and Adatte*, 2001). At mid-latitudes, a more pronounced seasonality was developed, with warm climate characterized by alternation of wet and dry seasons (*Bolle et al.*, 2000, *Schmitz and Andreasson*, 2001; *Egger et al.*, 2002; *Schmidt and Pujalte*, 2007). *Durn et al.* (2003) have reported from Istria bauxites as well as paleokarsts indicating prevailing humid conditions which favored laterization processes.

Repeated brackish incursions are characteristic throughout the Thanetian in NW AdCP as testified by the presence of levels rich in ostracods, gastropods, characeans, and locally coal, alternated with fully marine deposits (*Bignot*, 1972). These evidences suggest the occurrence of wet periods, with increased runoff and development of brackish conditions. Dissolved compounds from rivers and groundwater discharges were likely mechanisms of nutrient delivery to the ramp during this time. The nutrients and particulates might have been redistributed along the ramp by currents promoting high mesotrophic conditions also at intermediate depths (mid ramp). Locally, intense phosphatization in the more proximal ramp was described (*Jurkovšek et al.*, 1996).

Thus, fluctuating runoff due to repeated wet seasons could have been responsible for creating environmental instability inducing periodic changes in the nutrient pressure, turbidity level and delivery of alkaline waters (from the weathered AdCP). These conditions might have favored the growth of small coral colonies alternated to that of benthic microbialites, causing a shift in the nutritional mode from phototrophic to heterotrophic favoring a phase shift of dominant mound biota.

The inferred intensification of wet periods during the Late Thanetian, based on the study of these microbialite-coral mounds, would fit with the general climatic evolution in the Tethys. In fact, based on clay mineral studies (e.g., *Bolle et al*., 2000), seasonal and drier conditions during the Early Paleocene shifted to extreme humid and warm climate at the Paleocene-Eocene boundary concomitant with the Paleocene-Eocene Thermal Maximum (PETM, *Zachos et al*., 2001). A global eutrophication of surface waters in marginal seas, close to this event was recognized (e.g., *Crouch et al*., 2001), with the *Apectodinium* dinoflagellate acme coinciding with the PETM (*Crouch et al*., 2003), and occasional *Apectodinium* pulses just before the PETM (*Sluijs et al*., 2007). Geochemical proxies further sustain an increase of sea-surface productivity (sapropelitic sediments, *Speijer et al*., 1997, *Gavrilov et al*., 2003; biogenic barium, *Schmitz et al*., 1997; *Bains et al*., 2000). Concerning the northern margin of Tethys, *Egger et al*. (2002) suggested that well before the Paleocene-Eocene boundary, the high rates of precipitation caused an increase in continental runoff and associated nutrients delivery favoring enhanced productivity in surface waters.

The growth of these microbially-cemented bioconstructions, considered until now to be virtually absent during the Early Paleogene (*Webb*, 1996), shed new light for the interpretation of paleoenvironmental conditions in shallow-water realms, during a time of rapidly changing climate, leading to the extreme, super-greenhouse conditions of the PETM.

4.9 Conclusions

- The study of the microbialite-coral mounds, from the NE margin of the AdCP (SW Slovenia, 32°N paleolatitudes), offers a unique opportunity to document extensive microbially-cemented bioconstructions, developed during the Latest Thanetian (Latest Paleocene).

- The mounds are mainly composed of: (a) microbially-precipitated micrite, sparite and microsparite forming early lithified crusts with accretionary, binding and encrusting growth forms, and gravity-defying morphologies (up to 70% of the mounds); (b) moderately diversified coral community (15 species; usually small plate-shaped colonies); (c) micro-encrusters (especially encrusting foraminifera); (d) mound matrix composed by foralgal wackestones to packstones.
- Microbialites show different mesofabric types with common, centimetric-thick stromatolites, usually occurring on top of platy corals; and leiolites forming discontinuous veneers on top of corals and cryptic sites and thrombolites encrusting coral colonies and other mound components. Corals and micro-encrusters, including cryptic leiolite/thrombolites and stromatolites on top of corals, form the first framework. A second encrustation with the development of thick thrombolites marks the phase shift in dominant biota, from phototrophic to heterotrophic dominated nutritional mode. This shift is interpreted as environmentally-driven, with increase of nutrient pressure and turbidity weakening the coral growth and turning microbes as main bioconstructors.
- Combination of extrinsic parameters (favorable physico-chemical properties of the seawater related to warm, subtropical climate), worked together with intrinsic factors, (coral autoecology and biostrategic interrelationship between the microbial and coral communities), to form these microbialite-coral mounds. Repeated increases of nutrients/turbidity, and input of alkaline waters linked to enhanced weathering and runoff during the wet periods generated environmental instability reducing the growth rate of corals and turning microbial accretion as the prominent process responsible for the mound construction and stabilization. The occurrence of repeated wet periods during the Late Thanetian in this part of the Tethys might have represented the prelude to the extremely humid and warm conditions developed during the PETM event.

4.10 Acknowledgements

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5. EVOLUTION OF LATE PALEOCENE - EARLY EOCENE CORAL COMMUNITIES: QUEER FELLOWS OR NON-REEF BUILDING CORALS ADAPTED TO RAPID CLIMATE CHANGES?

Abstract

Today coral assemblages, often taxonomically similar to coral reefs, form ephemeral patch-reefs or occur as coral carpets and knobs. These corals are adapted to tolerate a wide range of environmental conditions exceeding commonly accepted thresholds for their survival (marginal settings). Might have been possible that fossil records characterized by no coral reef development but widespread occurrence of coral-bearing carbonates represented the fossil analogue of these non-frame-building coral community? If so they could be extremely valuable proxies for paleoenvironmental reconstruction. We explore this new working hypothesis considering the Early Paleogene coral assemblages (late Danian -Ypresian) a perfect fossil target during time of extreme global warming. A general shift can traced from middle Paleocene coral-dominated patch reefs in nearshore shallow-water settings to Upper Paleocene coral-bearing mounds dominated by groups tolerant to higher levels of trophic resources (calcareous red algae, encrusting foraminifera, microbes, sponges) as main producers together with corals, and finally to massive corals forming knobs in detrital, turbid settings during the earliest Eocene. This change points for expansion in shallow-water settings of marginal conditions, likely increased nutrient levels and low aragonite saturation state. The adaptation of these corals to live under stressed conditions, promoted by the climate changes with increased weathering rate, and thus nutrient loads, and high pCO_2 allowed to grow and being locally important carbonate sediment producers. Nonetheless, these conditions limited their chances of preservation and reef construction due to reduced calcification rates and *in situ* carbonate accretion under increasing bioerosion and ecological competition.

5.1 Introduction

Spatially and bathymetrically significant reef structures are most commonly built by corals in low-latitude, warm, clear-water settings. Nonetheless, today non-framework coral communities, often taxonomically comparable to coral reefs, but unable to produce extensive framework structures, occur in a broad range of marine settings, considered ‘marginal’ (e.g., *Perry and Larcombe*, 2003; *Halfar et al.*, 2005 and reference therein). In these settings the range of temperatures, nutrients, light levels, and aragonite saturation are fluctuating or close to what are considered thresholds for coral survival. The widespread occurrences of these corals in marginal settings emphasize the capacity of adaptation of colonial, zooxanthellated coral to conditions other than that of clear, warm-water settings, offering a new prospective to interpret non-reef building coral communities in the fossil record at times of prominent climate changes.

In this frame the Early Paleogene coral record characterized by no extensive coral reefs, although coral facies have been reported commonly in shallow neritic facies, represents a perfect target. The absence of extensive coral reefs has been interpreted as a crisis in the coral communities and frequently discussed in the frame of comparison with the modern "optimal" coral reef systems, as related to the adverse effects of Early Paleogene global warming (e.g., *Scheibner and Speijer*, 2008b). Nonetheless, this "actulialist" approach is not convincing given the difference in global greenhouse climatic conditions during the Early Paleogene and the present climate/warming events, their different temporal/spatial scale, and the great differences between the modern and Early Paleogene coral assemblages. For instance, *Acropora*-dominated communities that greatly promotes the rate of modern reef growth, is a relatively recent "invention" (*Veron*, 2000) which can be hardly compared with any of the Early Paleogene coral communities. Hence, why colonial corals were able to growth but not to produce extensive reefs? Which mechanisms limit these communities from forming frameworks? Were they incipient reefs, reefs that have given-up, switched-of or simply never switched-on?

In this study we screened the current literature performing a critical and extensive synthesis with the aim to get information about Early Paleogene coral communities. We discuss possible causes for the decoupling between coral proliferation and framework building capacity. We suggest that the expansion of non-reef building coral facies can be the results of an 'alternative' state of ecological adaptations of corals to multiple stressors related to the effects of acidification of shallow-water oceans combined with high nutrient loads as climate feedback mechanisms.

5.2 Coral assemblages during the Late Paleocene – Early Eocene

Occurrences of coral assemblages characterized by colonial forms typical of zooxanthellated corals have been reported from many Early Paleogene settings (e.g., *Schuster*, 1996). Several of the subsequently important reef-building genera were already present since the mid Danian (*Rosen*, 2000). Nonetheless, the coral reefs are quite rare in terms of absolute recorded numbers during this time with globally preserved volume peaks in the Paleocene, followed by drop in the earliest Eocene (*Kiessling and Baron-Szabo*, 2004). The diversity was increasing throughout the

Paleogene (*Rosen*, 2000), with the survivors of the end-Cretaceous extinction proliferating into a diverse cosmopolitan fauna (*Veron*, 2000).

This state has prompted us to investigate these occurrences of corals from low to mid latitude carbonate settings. Hence, to tackle the issue of non-reef building coral community's development during the Early Paleogene we created a broad database from the Tethys, the Atlantic, and the Caribbean realms. We screened the available literature ending with 25 middle Paleocene-lowermost Eocene studies (Table 5.1). The stratigraphic ranges of the investigated cases are plotted (Fig. 5.1), together with their global distribution (Fig. 5.2). In compiling such a data set it becomes evident that even though coral facies are important components in a particular locality, they often are poorly described, in terms of morphology and systematic, compared for instance to foraminiferal assemblages. On the other hand, some studies describe reef complexes, whereas the biofacies clearly indicates a low percentage of corals and a predominance of foralgal facies. An additional problem in constructing Figure 5.1 regards the accuracy in the age determination and the timing of the coral assemblages. Unless biostratigraphic markers are well preserved or other kinds of age assignments are available, precise stratigraphic positioning of coral facies remains problematic as well as chronostratigraphic correlations. Therefore, to construct the Figure 5.1 we had to critically tune the age, depositional settings, coral frame-building capacity, morphology, and interaction with other bioconstructors often based on own biostratigraphic, sedimentological and paleoecological evaluations.

However, even with the uncertainties of the stratigraphic resolution, Figure 5.1 indicates that the middle Paleocene was a time when coral dominate the reef factory even if producing mainly small patch reefs. Moderately to highly diversified assemblages of small (centimetric) encrusting colonies (common are the genera *Actinacis, Goniopora,* and astrocoeniids) associated with branching forms (e.g., *Dendrophyllia*, *Oculina*, and *Cladocora*) formed framework in euphotic settings from around the Tethys and along the Atlantic coasts. In the Pyrenees corals even formed exceptionally extended barrier reefs with high generic diversity although even in this case the vertical and horizontal dimensions of colonies did not excided 50 cm (*Baceta et al.*, 2005). The passage to the Upper Paleocene marks a general decrease of frame-building capacity by corals now subordinated to calcareous red algae forming mounds. This transition on bioconstructors from corals to algae (and to a less extent microbes and foraminifera) is observed both at low (e.g., W. Egypt, 9) and middle latitudes (Spanish Pyrenees, 23) and in a range of depositional settings (both at shallow and moderate water depths). Nonetheless, in these mounds coral assemblages show a diversity comparable to that of the middle Paleocene, with laminar/encrusting corals and branching forms common (*Actinacis, Goniopora,* and astrocoeniids still dominant together with *Stylocoenia*, *Rhizangia*, *Dendrophyllia*, *Oculina*, and *Cladocora*) thickly encrusted by algae (W. Desert, Egypt, 9; Majella, 4; Spanish Pyrenees, 23; Alabama, 21 and Java, 16, resenting the fist coral assemblage from the Caribbean region and the SE Pacific respectively) or microbes and foraminifera (SW Slovenia, *Zamagni et al*., 2009). In the N Calcareous Alps rodolith facies substitute completely coral facies (*Moussavian*, 1985) even if colonial corals have been described by *Tragelehn, H.* (1996). Similarly in W. Egypt, *Schuster* (1996) described a shift from coral patch reefs to algal mounds and rodolith beds with very rare encrusted coral fragments. This expansion of calcareous red algae during the Late Paleocene might indicate an important biotic community replacement rather than a simple facies shift, with coral still able to growth but forced to struggle with other organisms and increasing bioerosion (*Perrin*, 2002). This competition seems to continue in the earliest Eocene associated with a general reduction of coral occurrences and diversity. Colonial corals remains subordinated to algae and foraminifera within mounds at both shallow and intermediate water depths. In the Pyrenees *Actinacis* patch reefs are replaced by the encrusting foraminifera *Solenomeris* reefs (*Plaziat and Perrin*, 1992). In other localities corals still occur within algal mounds (e.g., Oman, 10; NE India, 14). Most interestingly, massive coral assemblages (with few specie, often resistant to high turbidity, *Goniopora* is typical) become common as knobs within shallow-water detrital, high energy settings (e.g., Pyrenees, 23; Oman, 10; Ionian Island; 5), locally associated to glauconitic sand (Pyrenees, 22), and muddy lagoonal deposits (e.g., W. Egypt, 9). The appearance of these coral assemblages in highly unstable and unfavorable settings might represent a further shift in the ecology of these earliest Eocene corals.

5.3 Diversity trends in other Early Paleogene biocalcifiers

In parallel to the development of these peculiar coral assemblages other groups of phototrophic marine organisms, adapted to low-light level conditions underwent rapid radiations during the middle Paleocene-earliest Eocene time. The Paleocene shallow-water communities where characterized by the rapid diversification of calcareous algae. Starting form the Maastrichtian across the whole Paleocene and the Early Eocene calcareous coralline algae (CCR) rapidly expanded, with a peak during the

Early Eocene followed by a temporary decline during the Middle Eocene (*Aguirre et al.*, 2000).

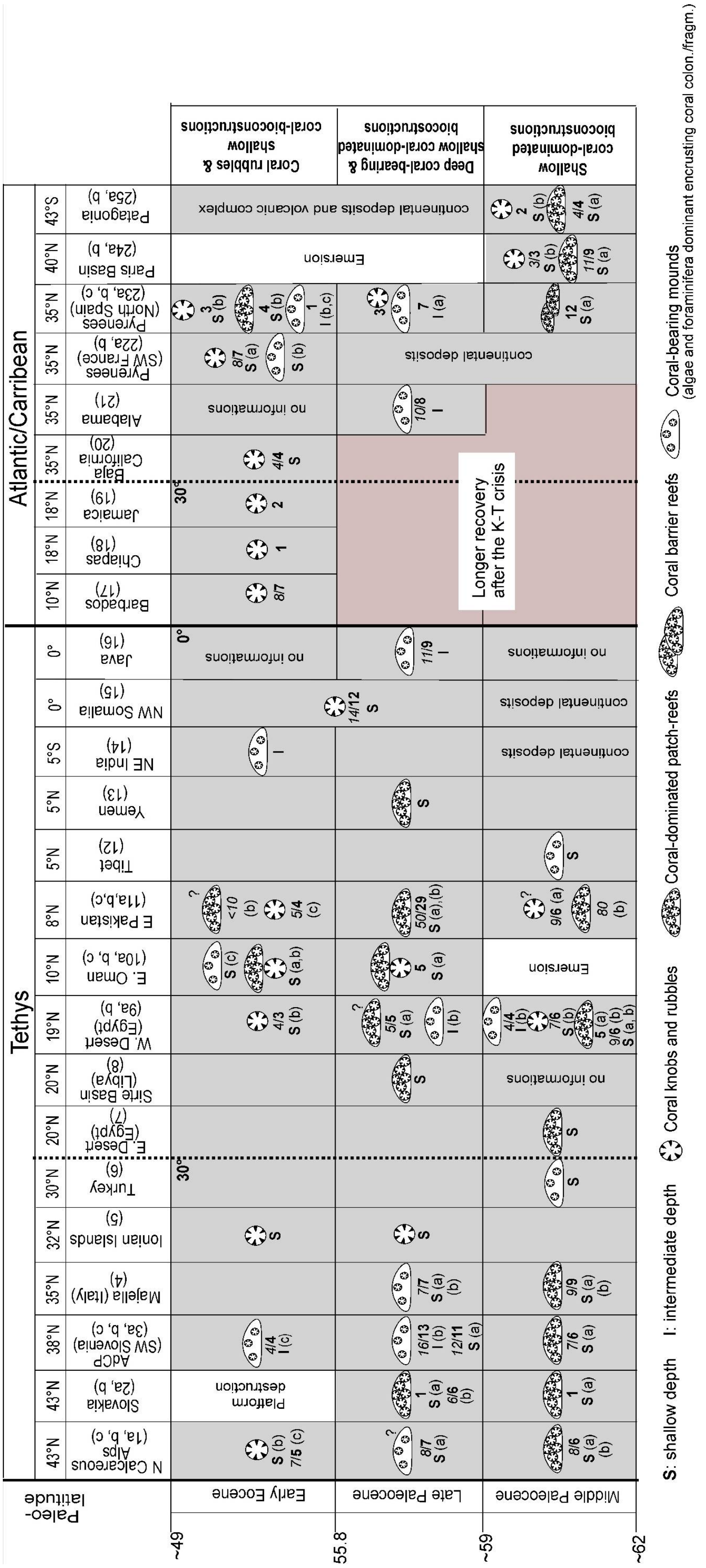

Figure 5.1: Stratigraphical and paleogeographic distribution of corals at low and mid latitudes, and their bioconstructional capacity. Note depositional depths (S shallow; I intermediate depth) defined by the authors or here inferred by associated fauna and facies description. Generic diversity in bold, specific diversity in italics. Numbers refer to Table 5.1.

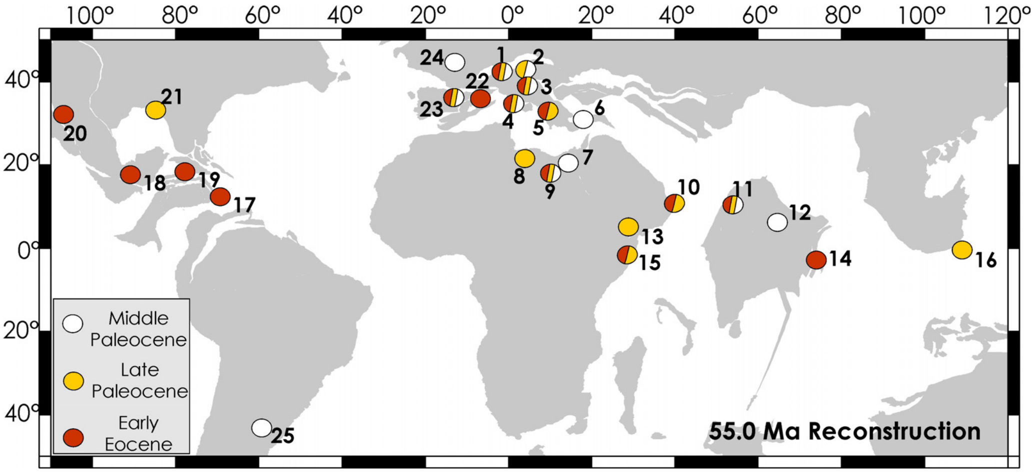

Figure 5.2: Global distribution of late-early Paleocene – Early Eocene corals displayed on paleogeographic reconstruction at 55 Ma map (Ocean Drilling Stratigraphic Network online; plate reconstruction data from *Hay et al*., 1999 and references therein). Numbers refer to those in figure 5.1 and Table 5.1.

This expansion, especially of melobesioids, seems to exclude the adverse effect of missing encrusters in the reduced formation of framework during this time (*Kiessling and Szabo*, 2004). Moreover, modern biofacies dominated by coralline red algae are known to develop extensively either under low temperatures or in nutrient-rich mesotrophic, reduced-light conditions (e.g., Gulf of California, *Halfar et al*., 2004; SE Asia platforms, *Wilson and Vecsei*, 2005). Thus, the expansion of rhodalgal facies was likely related to nutrient enrichment in shallow waters. At the same time, calcified green algae (dasycladaleans) experienced the most rapid diversification in their evolutionary history, culminated in the highest number of genera for the Cenozoic during the Thanetian, followed by a decline during the Early Eocene. This was likely a consequence of the high temperature promoting growth and calcification of these aragonitic algae (*Aguirre and Riding*, 2005). Larger foraminifera, protists with photosymbionts adapted to oligo- to mesotrophic conditions (*Renema*, 2008) increased progressively in diversity and size starting from the Late Paleocene and culminating during the Middle Eocene (*Hottinger*, 1998). Thus, biotic assemblages characterized by low-light dependent larger foraminifera and calcareous algae occurred commonly, as today on many platforms in the humid equatorial belt, or in tropical areas associated with nutrient upwelling or high land-derived nutrient loads (*Wilson and Vecsei*, 2005).

5.4 Occurrence of non-reef-building corals and oceanographic changes

The lost of reef-building capacity by the coral communities throughout the Paleocene-Early Eocene has been repetitively discussed as related to global high sea-surface temperatures (SST) (e.g., *Scheibner and Speijer*, 2008b). Elevated sea surface temperatures (Fig. 5.3), up to 33°C–34°C during the hyperthermal Paleocene-Eocene Thermal Maximum (~55 Ma, PETM, *Zachos et al.*, 2006) and the Early Eocene Climatic Optimum (*Pearson et al.*, 2007), might have being detrimental for reef development. Nonetheless, throughout the Early Paleogene colonial corals continued to colonize both shallow and relatively deep settings, both at low and middle latitudes, without clear biased towards deep water and high latitude settings, as possible refugia against high SST° and high solar irradiance. *Kiessling and Baron-Szabo* (2004) found high concentration of new Paleocene coral genera in low latitudes, suggesting that the tropics formed a source of evolutionary novelty in the recovery phase after the K-T crisis. Thus, even if thermal stress might have had some detrimental effects on reef development, high temperatures alone are not convincing.

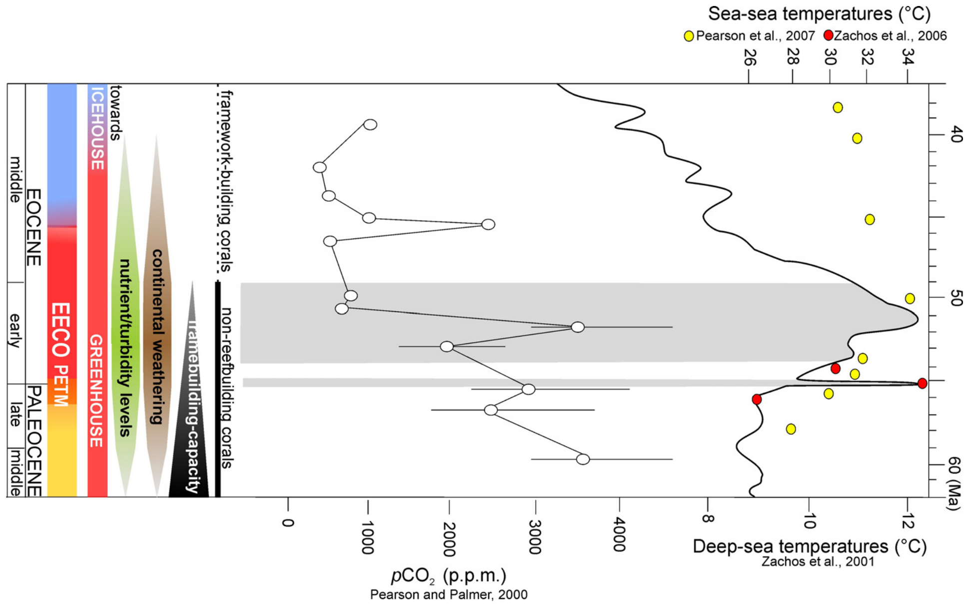

Figure 5.3: Key Early Paleogene climatic events (Early Eocene Climatic Optimum, EECO; Paleocene – Eocene Thermal Maximum, PETM) in relation to paleoceanographic changes in shallow waters. The evolution of adapted, non-reef building coral communities correlates with increase of nutrient delivery and CO_2 buildup, with maximum reduction in frame-building capacity concomitant with to the EECO.

Although high concentrations of nutrients and fluctuation in nutrient loading (*Smith and Buddemeier*, 1992) have long been known to affect coral growth (e.g., *Hallock and Schlager*, 1986) and coral-reef development (*Hallock*, 1988) they have been somewhat neglected in the study of Early Paleogene coral history. A progressive increase of warmth and humidity in the middle Paleocene to Early Eocene mainly related to CO_2 buildup (*Pearson and Palmer*, 2000), promoted intensification of continental weathering as evidenced by Os-isotopic studies (*Ravizza et al*., 2001) and increased sedimentation rate during the PETM (e.g., *Egger et al*., 2003; *John et al*., 2008) and the EECO (*Smith et al*., 2008). A consequent increase in discharge by rivers of sediment and nutrients to fertilize the coastal oceans, promoted the acmes of heterotrophic dinoflagellates during the latest Paleocene and the PETM (e.g., *Crouch et al*., 2003; *Sluijs et al*., 2007b) and increase of primary productivity (*Egger et al.,* 2003; *Speijer and Wagner*, 2002) and biogenic barium (*Bains et al*., 2000). Evidences for increased nutrient availability in shallow-water environments throughout the Upper Paleocene-earliest Eocene are represented by the increasing bioerosion (*Perrin*, 2002) but mostly by the community shift with corals forced to compete with faster-growing organisms as coralline algae and encrusting foraminifera, loosing importance as reef producers (Fig. 5.2). Under these conditions coral reef formation was strongly limited. However, small colonial corals likely with zooxanthellae are widespread in the Paleocene and Early Eocene, mainly *Goniopora* (both branching and massive forms) and *Actinacis* (encrusting, platy form) together with astrocoeniids and faviids (*Baron-Szabo*, 2006). *Goniopora* and *Actinacis* are pioneer species able to live in muddy, mesotrophic settings (*Schuster*, 1996; *Rosen*, 2000). Adaptations to nutrient-stress conditions, similar to those of modern non-framework corals living on mesotrophic conditions (*Halfar et al*., 2005) can be found in these corals. Especially, the dominance of colonies with growth forms suitable for low light conditions and high turbidity (e.g., encrusting forms as result of reduced water quality), and reduced growth rate strongly limiting the dimensions of coral colonies, likely related to high phosphate content inhibiting or slowing calcification (*Hallock and Schlager,* 1986). Additionally, the common co-occurrence in the same associations of these corals with dendroid, azooxanthellated forms as *Dendrophyllia*, *Oculina* and *Cladocora* (e.g., *Schuster*, 1996; *Turnšek and Drobne*, 1998; *Baceta et al*., 2005) further demonstrate the mesotrophic nature of the shallow waters in the middle Paleocene to earliest Eocene coastal oceans. A slow or poor calcification rates with development of fragile skeleton prone to fragmentation, and thus producing coral rubbles, might have been also related to changes of surface seawater chemistry related to increasing atmospheric carbon dioxide during the Early Paleogene when CO_2 levels were at least 3-4 times those of today (e.g., *Pearson and Palmer*, 2000). A perturbation of aragonite saturation state in shallow waters would explain the common fate of colonial corals (mainly zooxanthellated) and solitary corals (mainly azooxanthellated) both groups affected by peaks of extinction at the P-E boundary (*W. Kiessling, pers. comm.*) corresponding with peaks in CO_2 emissions (Fig. 5.3). Hence, progressive changes in water chemistry, significantly affected the rate at which the corals grow, although without limiting their existence and diversification, lowering their resistance to predators and the possibility to outgrow their competitors restraining their capacity to make three-dimensional, permanent structures.

5.5 Conclusions

The evolution in nearshore shallow-water carbonate producers to groups tolerant to higher levels of nutrients included adapted, non-reefal coral communities might be related to progressive increased nutrient levels in the middle Paleocene to earliest Eocene coastal oceans. These changes might be related to Early Paleogene global changes. We suggest that coral reef accretion was limited by enhancement of trophic resources during the Late Paleocene-Early Eocene. At this time nutrient availability was promoted by weathering-related nutrient input into coastal systems. The nutrient increases, together with reduced aragonite saturation state following the CO_2 buildup during the PETM and EECO triggered a strong ecological competition with faster-growing organisms and bioeroders, inhibiting the growth of extensive coral reefs but not the proliferation of diversified coral communities.

5.6 Acknowledgements

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Location	Formation	Reference
1a) N Calcareous Alps	Kambühelkalkes	Tragelehn, H., 1996. Maastricht und Paläozän am Südrand der Nördlichen Kalkalpen (Niederösterreich, Steiermark) - Fazies, Stratigraphie und Fossilführung des 'Kambühelkalkes' und assoziierter Sedimente. PhD Thesis, Erlangen, 216 p.
1b) N Calcareous Alps	Angerber Beds	Moussavian, E., 1984. Die Gosau- und Alttertiär-Gerölle der Angerberg-Schichten (Höheres Oligozän, Unterinntal, Nördliche Kalkalpen). *Facies, 10*, 1-86.
1c) N Calcareous Alps	\	Baron-Szabo, R., 2004. Austrian Scleractinian corals from the K/T-boundary to the Miocene. *Ber. Inst. Erdwiss.K-F.-Univ. Graz, 9*, 63-66.
1a) Slovakia	\	Köhler, E., Salaj, J., and Bucek, S., 1993. Paleogeographical development of the Myjava sedimentary area (western Slovakia) during the existance of the Paleocene reef complex. *Geologica Carpathica, 44*, 373-380.
1b) Slovakia	Kambühelkalkes	Tragelehn, H., 1996. Maastricht und Paläozän am Südrand der Nördlichen Kalkalpen (Niederösterreich, Steiermark) - Fazies, Stratigraphie und Fossilführung des 'Kambühelkalkes' und assoziierter Sedimente. PhD Thesis, Erlangen, 216 p.
3a) Adriatic Carbonate Platform (SW Slovenia)	\	Turnšek, D., and Drobne, K., 1998. Paleocene corals from the northern Adriatic platform. *Dela Opera SAZU 4, 34/2*, 129-154.
3b) Adriatic Carbonate Platform (SW Slovenia)	Trstelj Formation	Zamagni, J., Košir, A., Mutti, M., 2009. The first microbialite – coral mounds in the Cenozoic (Uppermost Paleocene) from the Northern Tethys (Slovenia): Environmentally-triggered phase shifts preceding the PETM? *Palaeogeography, Palaeoclimatology, Palaeoecology, 247*, 1-17
3c) Adriatic Carbonate Platform (SW Slovenia)	Alveolina-Nummulites Limestones	Košir, A., 1997. Eocenski talozni slijed prijelaza karbonatne platforme u bazeen na podrucju JZ Slvoenije. *Magistrarski red. Sveuciliste u Zagrebu* 1-130. Košir, A., pers. Comm.., 2008
4) Majella (Italy)	S.Spirito and Avella Formations	Vecsei, A., and Moussavian, E., 1995. Paleocene reefs from the Maiella Carbonate Platform, Italy. *Facies, 32*, 213-222.
5) Ionian Islands	\	Accordi, G., Carbone, F., and Pignatti, J., 1998. Depositional history of a Paleogene carbonate ramp (Western Cephalonia, Ionian Islands, Greece): *Geologica Romana, 34*, 131-205.
6) Turkey	\	Özgen-Erdem N., İnan N., Akyazi M., and Tunoğlu, C., 2005. Benthic foraminiferal assemblages and microfacies analysis of Paleocene-Eocene carbonate rocks in the Kastamonu region, Northern Turkey. *Journal of Asian Earth Science, 25*, 403-417.
7) Eastern Desert (Egypt)	\	Scheibner, C., Reijmer, J. J. G., Marzouk, A. M., Speijer, R. P., and Kuss, J., 2003. From platform to basin: the evolution of a Paleocene carbonate margin (Eastern Desert, Egypt). *Journal of Earth Science, 92*, 624-640.
8) Sirte Basin (Libya)	\	Terry, C., and Willians, J.J., 1969. The Idris "A" bioherm and oilfield, Syrte basin, Libya: its commercial development, regional Paleocene geologic setting and stratigraphy. The Exploration for Petroleum in Europe and North Africa. Institute of Petroleum, London, 31-48.
9a) Western Desert (Egypt)	\	Barthel, K.W., and Herrmann-Degen, W., 1981. Late Cretaceous and Early Tertiary stratigraphy in the Great Sand Sea and its margins (Farafra and Dakhla Oases), SW Desert, Egypt. *Mittelungen der Bayerischen Staatssamlung für Paläontologie und historische Geologie, 21*, 141-182.
9b) Western Desert (Egypt)	Kurkur, Abu Tartur, Dakhla, and Esna Formations (Paleocene)/Farafra Formation (Eocene)	Schuster, F., 1996. Paleoecology of Paleocene and Eocene corals from the Kharga and Farafra oases (western Desert, Egypt) and the depositional history of the Paleocene Abu Tartur carbonate platform, Kharga oasis: Tübinger Geowissenschaftiche Arbeiten 31, 96 p.
10a) Oman	Jafnayn Formation	Bernecker, M., 2005. Biotic response to sea-level fluctuations and climate change: a case study from the Paleogene shelf of Oman, in Proceedings, 24th IAS Meeting of Sedimentology, Muscat, Oman, 33.
10b) Oman	Jafnayn Formation	Racey, A., Siddiq Al-Sayigh, A.R., and Hanna, S.S., 2005. Biostratigraphy and microfacies of the Jafnayn Formation (Late Paleocene-Lower Eocene) of Northern Oman, in Proceedings, 24thIAS Meeting of Sedimentology, Muscat, Oman, 131.
10c) Oman	Umm Er Radhuma Formation	Racz, L., 1979, Paleocene carbonate development of Ras al Hamra, Oman. Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine, v. 3, p. 767-779.
11a) Eastern Pakistan	\	Duncan P. M., 1880. Sind fossil corals and Alcyonaria. Memoirs of the Geological Survey of India. *Palaeontologica Indica, Ser. 7 and 14*, 1-110.
11b) Eastern Pakistan	Ranikot and Laki Series	Sahni, A., and Kumar, V., 1974. Palaeogene palaeobiogeography of the Indian subcontinent. *Palaeogeography, Palaeoclimatology, Palaeoecology, 15*, 209-226.
11c) Eastern Pakistan	Ranikot Series	Nuttall D.F.C., 1932. The stratigraphy of the upper Ranikot Series (Lower Eocene) of Sind, India. *Records of the Geological Society of India, 35*, 306-313.
12) Southern Tibet	Zhepure Shan Formation	Zhicheng Z., Willems H., and Binggao Z. 1997. Marine Cretaceous-Paleogene biofacies and ichnofacies in southern Tibet, China, and their sedimentary significance. *Marine Micropaleontology, 32*, 3-29.
13) Yemen	Ummer Radhuma Formation	Pignatti, J., Matteucci, R., Parlow, T., and Fantozzi, P.L., 1998. Larger foraminifera biostratigraphy of the Maastrichtian – Ypresian Wadi Mashid succession (Southern Hadramawt Arch, SE Yemen). *Zeitschrift fürGeologische Wissenschaften, 26*, 609-635.

14) NE India	Lakadong Formation	Jauhri A.K., Misra, P.K., Kishore, S., and Singh, S.K., 2006. Larger foraminifera and calcareous algal facies in the Lakadong Formation on the Southern Shillong Plateau, NE India. *Journal of the Paleontological Society of India, 51*, 51-61.
15) NW Somalia	Auradu Limestone Formation	Carbone, F., Matteucci, R., Pignatti, J. S., and Russo, A. 1993. Facies analysis and biostratigraphy of the Auradu Limestone Formation in the Berbera-Sheikh Area, northwestern Somalia. *Geologica Romana, 29*, 213-235.
16) Java	\	Pignatti J.S., pers.comms, 2008.
17) Barbados	\	Frost, S.H., 1977. Cenozoic reef systems of the Caribbean - prospects for paleoecologic synthesis, in Frost, S.H. Et al., eds., Reefs and related carbonates - ecology and sedimentology. *AAPG Studies in Geology, 4*, 93-110.
18) Chiapas	\	Frost, S.H., and Langenheim, R.L., 1974. *Cenozoic reef biofacies*. No Illinois University Press, DeKalb, 388 p.
19) Jamaica	\	Wells, J.W., 1934. Some fossil corals from the West Indies. *Proceeding U.S. Natural Museum, 83*, 71-110.
20) Baja California	Bateque Formation	Squires R. L., and Demetrion R. A., 1992. Paleontology of the Eocene Bateque Formation, Baja California Sur, Mexico. *Natural History Museum of Los Angeles County, Contributions in Science, 434*, 1-55.
21) Alabama	Salt Mountain Limestone	Bryan, J. R., 1991. A Paleocene coral-algal-sponge reef from southwestern Alabama and the ecology of Early Tertiary reefs. *Lethaia, 24*, 423-4438; Bryan J. R., Carter B. C., Flugeman R. J. Jr., Krumm D. K., and Stemann T. A., 1997. The Salt Mountain Limestone of Alabama. *Tulane Studies in Geology and Paleontology, 30*, 2-60.
22a) Pyrenees (SW France)	equivalent of Serraduy Formation	Zamagni J., personal observations.
22b) Pyrenees (SW France)	Calcaires à Alvéolines and Calcaires à Alvéolines et à Algues	Plaziat, J.-C., and Perrin, C., 1992. Multikilometer-sized reefs built by foraminifera (*Solenomeris*) from the early Eocene of the Pyrenean domain (S. France, N. Spain): paleoecologic relations with coral reefs. *Palaeogeography, Palaeoclimatology, Palaeoecology, 96*, 195-231.
23a) Pyrenees (Northern Spain)	\	Baceta, J. I., Pujalte, V., and Bernaola, G., 2005. Paleocene coralgal reefs of the western Pyrenean basin, northern Spain: New evidence supporting an earliest Paleogene recovery of reefal systems. *Palaeogeography, Palaeoclimatology, Palaeoecology, 224*, 117-143.
23b) Pyrenees (Northern Spain)	Ager, Llmiana, Alinya sequences	Eichenseer, H., and Luterbacher, H., 1992. The marine Paleogene of the Tremp region (NE Spain) - depositional sequences, facies history, biostratigraphy and controlling factors. *Facies, 27*, 119-152.
23c) Pyrenees (Northern Spain)	\	Plaziat, J.-C., Perrin, C., 1992. Multikilometer-siyed reefs built by foraminifera (*Solenomeris*) from the early Eocene of the Pyrenean domain (S. France, N. Spain): paleoecologic relations with coral reefs. *Palaeogeography, Palaeoclimatology, Palaeoecology, 96*, 195-231.
24a) Paris Basin	Vichy Limestones	Meyer, J.C., 1987. Le récif danien de Vigny. *Saga Informations, 26*, 1-72.
24b) Paris Basin	Vichy Limestones	Montenat, C., Barrier, P., and d' Estevou, P.O., 2002. The Vigny limestones: a record of Palaeocene (Danian) tectonic-sedimentary events in the Paris Basin. *Sedimentology, 49*, 421-440.
25a) Patagonia	\	Baron-Szabo, R.C., Casadio, S., and Parros, A., 2003. First shallow water scleractinian coral reef from the Danian, northern Patagonia, Argentina. *Ameghiniana, 40*, 79.
25b) Patagonia	Lefipán Formation	Kiessling W., Aragón E., Scasso R.,·Aberhan M.,·Jürgen K.,·Medina F., and Fracchia D., 2005. Massive corals in Paleocene siliciclastic sediments of Chubut (Argentina). *Facies, 51*, 233-241.

Table 5.1: Occurrences of Early Paleogene coral facies (numbers refer to those in Figs. 1 and 2).

6. CONCLUSIONS

To investigate the biotic response of shallow-water ecosystems to rapid extreme global warming during the Late Paleocene-Early Eocene, especially across the Paleocene-Eocene Thermal Maximum (PETM), I have combined sedimentological and paleoecological studies with biostratigraphic and chemostratigraphic analyses of shallow-water carbonatic successions from the Central Tethys.

During the Late Paleocene-earliest Eocene, sedimentation in the NW Adriatic Carbonate Platform (AdCP, SW Slovenia) took place on a shallow-water carbonate ramp system. The studied successions are composed of three major facies: Late Paleocene (Thanetian) Foraminiferal and Foralgal limestones (F and FA facies), and earliest Eocene (Ilerdian) Biopeloidal limestones (BP facies). Within these facies, six foraminiferal assemblages, representing different sub-environments, were recognized: early Thanetian (1) smaller miliolids- and (2) small benthic foraminifera-dominated assemblages thriving on partly vegetated, soft substrates in a protected innermost ramp; late Thanetian (3) *Assilina*-dominated assemblage living on soft sandy substrate in the upper mid ramp affected by storm and current activity, (4) 'bioconstructors'- and (5) orthophragminids-dominated assemblages, occurring respectively within microbialite-coral mounds and laterally on hard substrate in deeper mid-ramp setting; earliest Eocene (6) alveolinids-nummulitids assemblage thriving on muddy and sandy substrate in an inner-ramp setting.

The intense weathering and runoff in the humid, hot climate of the Late Paleocene-Early Eocene might have caused environmental changes in the shallow-water settings delivering nutrients to the basin. This could favor widespread microbial activity, explaining growth of microbial mounds and strong micritization of macrofauna. In these conditions, the dominance of benthic communities by Larger Foraminifera (LF) indicates an unexpected tolerance of this group to enhanced/fluctuating nutrient levels. At the passage from the Paleocene to the Eocene, LF assemblages seem to be mainly marked by changes in morphotypes rather than major faunal turnover.

To constrain the possible link between the PETM and the evolution of LF in the AdCP shallow-water system, I have reconstructed detailed $\delta^{13}C$ records of two successions documenting the most complete and detailed records currently available for the Paleocene-Eocene Thermal Maximum (PETM) for shallow-water settings. The onset of the CIE is clearly defined by a very rapid decrease of $\delta^{13}C$ values that coincides with the appearance of the first Eocene *Alveolina aramaea aramaea*, marking the P-E boundary. The more distal section records a ~3.5‰ CIE; this is a typical value for mid-latitude continental shelves during this time interval. In the more proximal section we document a ~1‰ CIE; this low value may be related to a biostratigraphically-unresolved sedimentary hiatus.

Biostratigraphic studies constrain the extension of the whole event to the SBZ5 and part of the SBZ6. The combined results from biostratigraphic and chemostratigraphic records do not show any synchronicity between the Early Eocene LF Turnover and the PETM, suggesting that there is not a direct causal link between the two events. The temporal distribution of the major groups of LF covers the Late Paleocene-earliest Eocene time interval; no extinctions have been recorded coeval with the PETM. Hence, the suggested turnover at the P-E boundary was probably a gradual replacement culminated during the middle Ilerdian (~SBZ7), well after the PETM recovery. At this time the final disappearance of *Ranikothalia*, *Miscellanea* and the spreading of large *Alveolina* and *Nummulites* took place. Hence, the evolution of LF seems to have been driven by endogenous biotic forces, with the PETM exerting almost no influence on this long-term evolutionary history.

Detailed sedimentological and paleoecological studies of the Late Thanetian microbialite-coral mounds from the AdCP document the first occurrence of Cenozoic microbially-cemented mounds. In this work I have gathered new information about paleoenvironmental conditions in shallow-water realms preceding the PETM. Detailed macroscopic and microscopic studies documented that the mounds are primarily composed of microbially-precipitated micrite, sparite and microsparite (up to 70% of the mounds), forming early lithified crusts with accretionary, binding and encrusting growth forms, and gravity-defying morphologies. Coral colonies represent the second component of the mounds (moderately diversified community with 15 species; usually small plate-shaped, encrusting colonies) associated with micro-encrusters (especially encrusting foraminifera) and mound matrix, composed by foralgal wackestones to packstones. A first layer of micro-encrusters, including leiolites and thrombolites, occurs in cryptic habitats, whereas discontinuous stromatolites encrust the upper surface of corals. A second encrustation, the major mound construction phase, follows and is dominated by thrombolites, encrusting corals and other micro-encrusters, marking the phase shift in dominant biota from phototrophic- to heterotrophic-dominated nutritional mode. This sequence represents the basic constructional unit which by horizontal and vertical interlocking, in an irregular pattern, forms the mounds.

The shift in dominant biota is interpreted as an environmentally-driven perturbation in the benthic community. Repeated increases of nutrients/turbidity, and input of alkaline waters linked to enhanced weathering and runoff during wet periods likely generated environmental instability which weakened the coral growth and turned microbes into the main bioconstructors. The occurrence of repeated wet phases during the Late Thanetian might have represented the prelude to the extremely humid and warm conditions that developed during the PETM event.

The combined study of coral communities from the AdCP microbialites-coral mound, coral facies from the earliest Eocene ramp system from SW France (Minervois region), and an extensive synthesis of coral occurrences during the Late Paleocene to Early Eocene, further hint at the existence of marginal environmental conditions (high/fluctuating nutrient/turbidity levels, perturbation of aragonite saturation state) in shallow-water settings. At this time, corals did not form extensive reefs; nonetheless they occurred frequently in the shallow-water to deeper facies as coral carpets, piles of rubble or small patch-reefs often characterized by high specific diversity. These peculiar features resemble those of modern coral community that have adapted to thrive in conditions considered thresholds for coral survival, making of the Early Paleogene the best fossil analogue for these still poorly understood communities.

The relationship between the evolution of shallow-water biota and global warming events underscores the complexity of the biological responses to environmental perturbations, especially for corals and LF, which are highly sensitive organisms. Their persistence during the warmest time in the Cenozoic hints at possibility to evolve some adaptations, which deserve more studies in order to understand future scenarios.

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