

# Evolution of shallow benthic communities during the Late Paleocene–earliest Eocene transition in the Northern Tethys (SW Slovenia)

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**Abstract** A paleoecological and sedimentological study was 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 northwestern 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) ortho-phragminids-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 benthic foraminifera (LBF), seem to have favored this

low-light dependent group as common sediment contributors. By comparing the evolution of the shallow-water biota from the Adriatic area with data from the Pyrenees and Egypt, a general latitudinal trend can be recognized. However, on a smaller geographical scale, local conditions are likely to have played a pivotal role in promoting the evolution of biota characterized by suites of unique features.

**Keywords** Shallow-water carbonates · Larger benthic foraminifera · Paleoecology · Facies analysis · SW Slovenia · Late Paleocene–earliest Eocene

## 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 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 benthic foraminifera (LBF) were the most common constituents of Upper Paleocene–Lower Eocene

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shallow-water carbonates. Especially Eocene LBF 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, LBF 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 LBF 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, LBF 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 LBF 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 LBF 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).

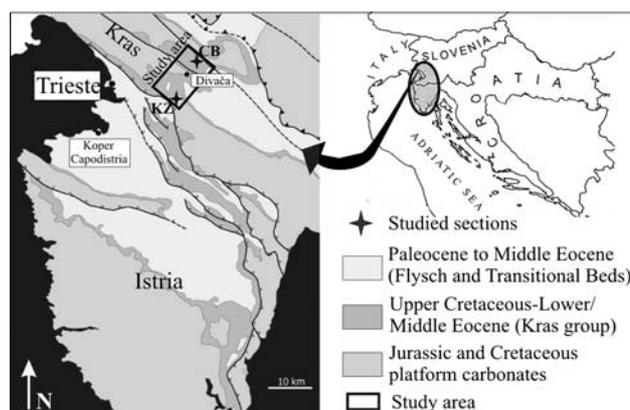
Here we present data on two continuously exposed shallow-water carbonate successions from the Kras region (SW Slovenia). The study of these successions allows us to track down the evolution of the LBF assemblages across the P–E transition by documenting their major features during the pre-climax phase 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 relative 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.

### Geologic setting and stratigraphy

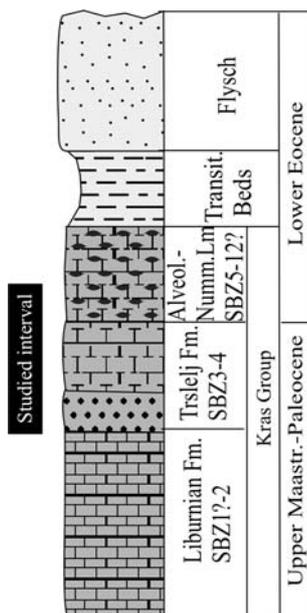
The studied carbonate successions crop out in the southern part of the Kras (Karst) Plateau in SW Slovenia (Fig. 1). Structurally, the Kras Plateau corresponds to the Komen Thrust Unit of the NW External Dinarides fold-and-thrust belt (Placer 1981). The latest Cretaceous to Early Paleogene paleogeography 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 southwestward-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),



**Fig. 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

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). A generalized stratigraphic column of the Upper Cretaceous, Paleocene, and Eocene deposits in the Kras region is shown in Fig. 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 coralgall 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 three of the 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).



**Fig. 2** Generalized stratigraphic column of the uppermost Cretaceous-Eocene succession in the Kras region, SW Slovenia (Košir 2003) and the studied interval

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.

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 paleo-transport patterns recorded in the siliciclastic turbidites of the flysch foredeep successions in the NW Dinarides (Orehek 1991; Babić and Zupanić 1996), which have predominantly NW and SE-oriented axial paleocurrent directions, whereas a general paleo-transport pattern in resedimented carbonates shows that carbonate debris derived from south-southwestern source areas (Turnšek and Košir 2004; Babić and Zupanić 1996). Vertical facies successions of Paleocene and Lower Eocene shallow-marine carbonates (Trstelj Formation and Alveolina-Nummulites Limestone) generally exhibit a retrogradational (backstepping) 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).

## Materials and methods

Two continuously outcropping stratigraphic sections (Čebulovica and Kozina) were studied at road cuts along the highway between Ljubljana and Koper (Figs. 1, 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 have been reconstructed, combining comparison with Recent counterparts and with the distribution of fossils forms from known facies models. Since many of the early Paleogene LBF 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 LBF 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.

### 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. 3, Table 1): Foraminiferal limestones (F), corresponding to the lower part of the Trstelj Formation (SBZ3, Early Thanetian); the Foralgal limestones (FA), covering the upper part of the Trstelj

**Fig. 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)

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 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.

#### 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, (Fig. 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 rotalids, conical agglutinated foraminifera and litulids) 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*, *Cribrbulimina carniolica*, *Haymanella paleocenica* and *Miscellanea juliettae*, the occurrence of which indicates Early Thanetian age (SBZ3) for the Foraminiferal limestones.



**Table 1** Relationship among facies, foraminiferal assemblages, textural and sedimentological features and major components

Facies	Textures	Sedimentary structures	Taphonomic and early diagenetic features	FA Benthic foraminifera	Other biota	Occurrences	Interpreted setting
F	Wackestones to packstones	Thick bedded	Bioturbation micritisation	1 Miliolids, discorbids	Dasycladaleans, ostracodes	KZ, CB	Innermost ramp with restricted conditions
	Packstones, rarely grainstones			2 Miliolids, agglutinated foraminifera, rotaliids, <i>Miscellanea</i> , small <i>Ramkothalia</i>	dasycladaleans, echinoids, bryozoans	KZ, CB	Innermost ramp
FA	Packstones to rudstones	Poorly bedded	Micritisation Encrustation Bioerosion	3 <i>Assilina</i> , lacazinids, small/ovate <i>Discocyclina</i> , small/ovate <i>Nummulites</i> , <i>Miscellanea</i> , acervulinids, <i>Haddonia</i> , small rotaliids, miliolids, textulariids	Peyssonneliaceans, corallineans (melobesioids, sporolithaceans, <i>Distichoplax biserialis</i> ), scleractinian corals, echinoids, bryozoans, ostreids	KZ, CB	Upper mid ramp
	Boundstones to floatstones	Massive		4 Acervulinids, <i>Haddonia</i> , <i>Planorbulina</i> , <i>Miniacina</i> , <i>Plocopsilina</i> , <i>Discocyclina</i> , small rotaliids	Scleractinian corals, encrusting red algae, microbial crusts, bryozoans, bivalves, ostracodes, planktonic foraminifera	KZ, CB	Deeper mid ramp
	Wackestone to packstones	Poorly bedded to massive		5 Flattened orthoheragminids, <i>Assilina</i> , acervulinids, <i>Haddonia</i> , small rotaliids	Corallineans, peyssonneliaceans, bryozoans, echinoids, crinoids, bivalves	CB	Deeper mid ramp
BP	Packstones	Poorly bedded with wave bedding surfaces	Micritisation Encrustation Bioturbation Bioerosion	6 <i>Alveolina</i> , <i>Assilina</i> , <i>Nummulites</i> , sortids ( <i>Orbitolites</i> , <i>Opertorbitolites</i> ), small <i>Discocyclina</i> , acervulinids, <i>Haddonia</i> , litooids, agglutinated foraminifera ( <i>Thomasella labyrinthica</i> , <i>Vania anatolica</i> ), miliolids, small rotaliids	Dasycladaleans, echinoids, bryozoans, gastropods, bivalves, ostracodes	KZ, CB	Inner ramp

Benthic foraminifera and other biota are listed in order of decreasing abundance

FA foraminiferal assemblages, KZ Kozina section, CB Čebulovica section

### Foraminiferal assemblages

This facies is characterized by two foraminiferal assemblages (Fig. 3, Table 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. 4a). Dasycladaleans and ostracods are associated to 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.

#### 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*), litiolids (*Haymanella paleocenica*), *Miscellanea* (Fig. 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 (Fig. 4b) 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 a high rate of fecundity, short generation times, and rapid growth 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 the mechanism of nutrient recycling (like symbiotic relationship in LBF; Hottinger 1983).

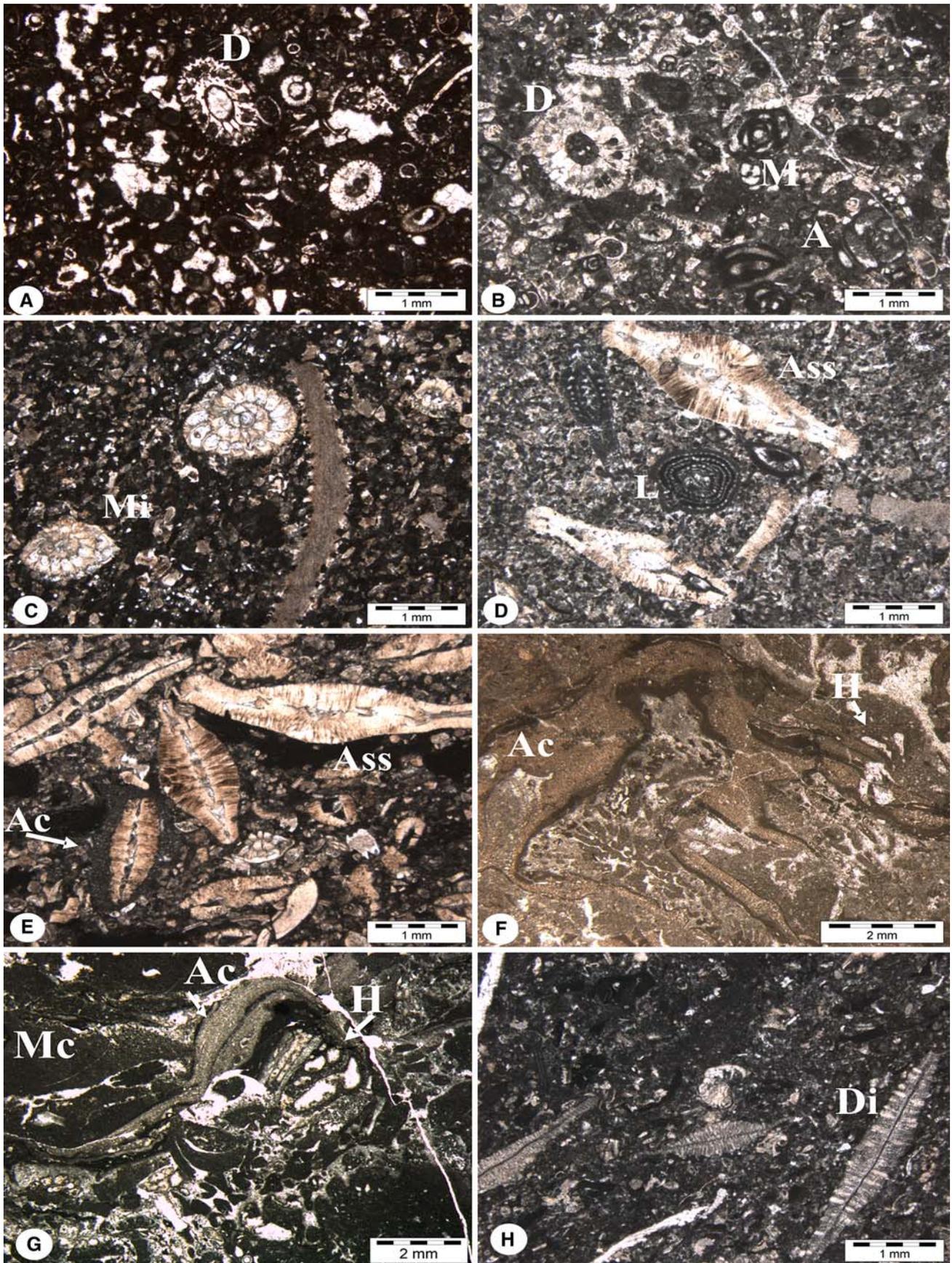
Small rotaliids and agglutinated foraminifera are generally considered to be shallow-water dwellers living in lagoonal and open marine waters (e.g., Geel 2000; Ghose 1977). Rotaliids have been found on seagrass leaves in eastern Shark Bay (Davies 1970). The development of ventral ornamentation characterizes 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 environments. 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 seagrass 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 presence of 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



◀ **Fig. 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 and microbial crusts (*Mc*) encrusting corals. **h** Assemblage 5: fine bioclastic wackestone with orthophragminids (*Di*)

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). They usually burrow close to the seagrass roots and deposit fecal pellets in the tunnel that they dig (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.

#### 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. 3, Table 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 coral-linaceans (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 (rhodoliths) 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 ostreids). 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 also be 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. 3, Table 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. 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*. *Haddonina* and acervulinids are present, locally encrusting larger foraminifera (Fig. 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, the 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 a 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. 4f, g), *Planorbulina* and *Miniacina*. Other foraminifera are less frequent and are 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 LBF.

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. 4h). Calcareous red algae are a 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., Čosović 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 a 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 crusts). 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 Peyssoneliaceae. In more bioclastic lithologies they occur as small rhodoliths 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). Peyssoneliaceans 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

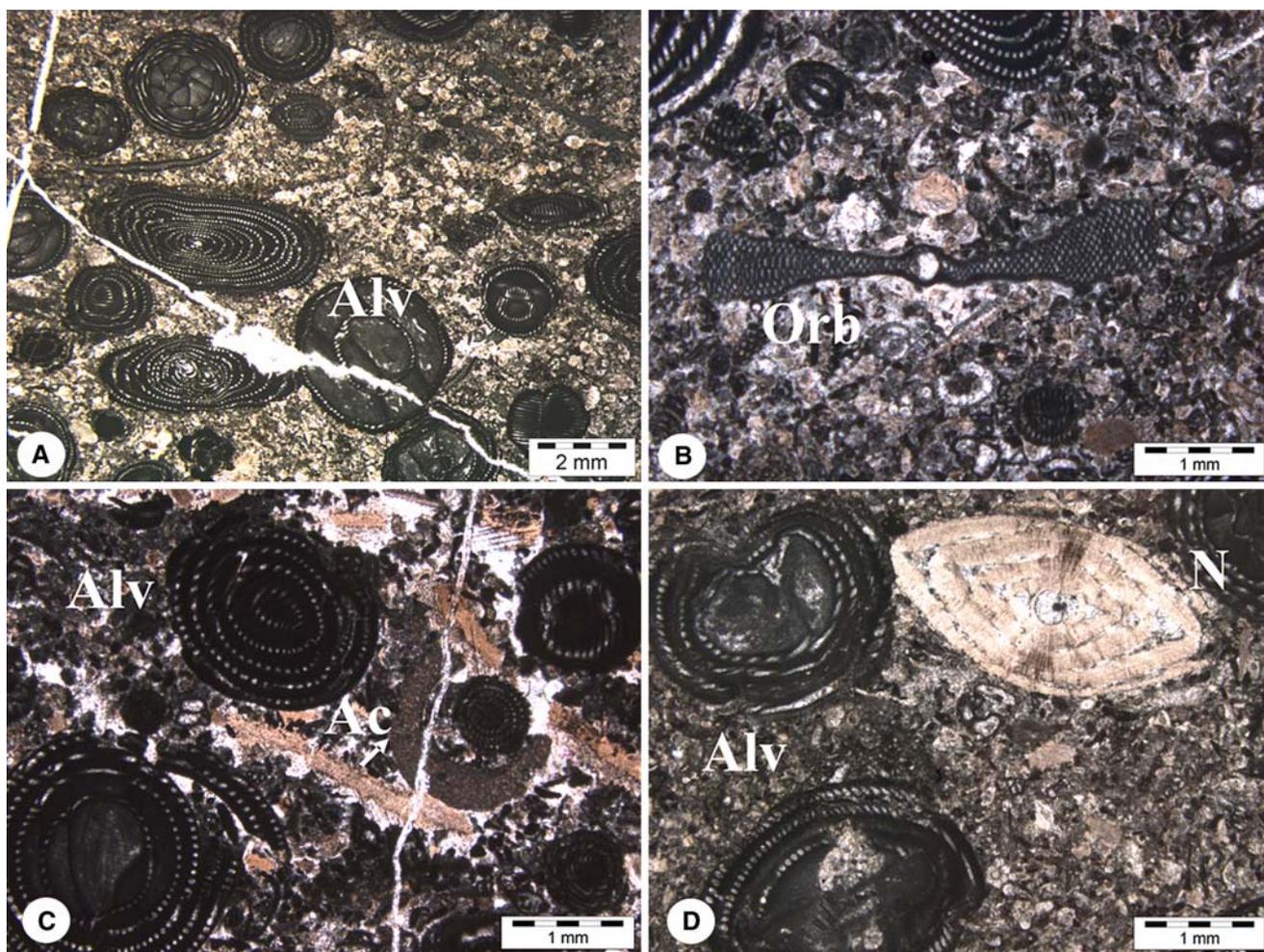
to occasional reworking by storms and/or bottom currents. In this mid-ramp, the upper part was dominated by LBF (mainly *Assilina*) commonly associated with calcareous red algae and small coral colonies and rubbles. The deeper mid-ramp, close to the lower limit of the photic zone, had few LBF (mainly 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.

#### Bio-Peloidal limestones (BP)

##### *Facies description*

This facies occurs in the uppermost part of the studied sections with a thickness of 55 m (Fig. 3, Table 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 molluscs (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 (Fig. 5d). Peloids are the second most abundant component in this facies. They mostly represent micritized bioclasts and fecal pellets, which form elongated clusters.



**Fig. 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

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 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. 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 *Discocyclusina* 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. 5b) and *Opertorbitolites*. Encrusting foraminifera occur with acervulinids, which encrust and bond larger foraminifera or as scattered fragment with circular and hooked shapes (Fig. 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*. 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, 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 silicoclastic 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 epiphytic *Orbitolites* 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 leaves 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 a low sedimentation rate likely coupled with enhanced nutrient conditions (Hallock 1988).

#### **Discussion and paleoenvironmental interpretation**

The distribution of the studied benthic assemblages in the shallow-water carbonates from SW Slovenia have 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. 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



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.

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, LBF 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 symbiotic 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 (Iacazinids, 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. Such low-energy conditions would explain the lack of hard substrates. 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 during the late Paleocene—early Eocene. 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).

LBF 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 nitrification 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 macro-bioerosion are dominant in this facies. Additionally, abundance of detritivores (echinoids) and suspensivores (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 LBF, 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 2000). 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.

#### Facies changes across the Paleocene–Eocene boundary

The studied successions in the northwestern 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. LBF 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 LBF. 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 LBF became common in both regions, with *Assilina* dominant in the Pyrenees (*Assilina* beds, Bacceta 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 than each of them was to Egypt. Similarly to what observed in Spain, during the latest Paleocene–earliest Eocene the LBF of the northwestern AdCP adapted to different depths, but no dramatic changes occurred in the assemblage composition. Similarities between these areas 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 *Assilina*, orthophragminids and coral-microbialite mud-mounds. This represents an unusual association if compared to other Tethyan localities. Moreover, the Early Eocene biota shows transitional features compared to Egypt and Spain, with LBF still dominant and with corals and red algae being completely absent.

These dissimilarities could be, at least partially, explained in terms of differences in the local conditions

exerting a strong control in the development of the shallow-water carbonate assemblages.

## Conclusions

During the late Paleocene–earliest Eocene the sedimentation in the northwestern 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*, *Discocyclusina*, 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. These environmental conditions promoted the development of specific low-light dependent communities, with LBF (*Alveolina*, *Nummulites*, *Assilina* and orthophragminids) showing tolerance to enhanced nutrients levels.

The hypothesized ecological changes in the shallow-water realms of the AdCP at the Paleocene–Eocene transition were most probably linked to drastic climatic changes coupled with the peculiar paleogeography of the area. Overall, when comparing the studied LBF 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 is evident. The present study demonstrates, however, that on a more geographically restricted scale, local conditions were predominant in controlling the development and evolution of shallow-water biota.

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