



The Role of the Palaeogene Adriatic Carbonate Platform in the Spatial Distribution of Alveolinids

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Abstract: Sediments of the Palaeogene Adriatic carbonate platform, a distinctive palaeogeographic unit, are today exposed along the eastern Adriatic coast for a distance of 800 km and a width of 100–130 km. The large number of identified alveolinid species (69) from the Early Ypresian (Ilerdian) to the Bartonian record the dynamics of their evolution, with emphasis on the following: (1) great species diversity and great abundance in the middle Ilerdian (SBZ 7–8) followed by a sharp decline in occurrences at the Ilerdian/Cuisian transition; (2) a diversity boom in the late Ypresian (late Cuisian, SBZ 11–12) and (3) an abrupt decrease in species numbers after the early Lutetian. This pattern shows a relationship between abundance and diversity and global sea-level changes in TA and AP events. The ‘two peaks’ model in alveolinid occurrence is present also in the ‘Mediterranean assemblage’ in the Pyrenees and within the middle Cuisian assemblages of various Mediterranean areas.

Based on studies of numerous stratigraphic sections from the Palaeogene Adriatic carbonate platform, biosedimentary zones (BioZ 2, BioZ 3.1, BioZ 3.2 and BioZ 4) were determined, and each zone is characterized by specific alveolinid associations. These zones are distributed as belts stretching from NE Italy (Friuli region) to Montenegro. Alveolinid associations served as a base for a palaeogeographic map of the Palaeogene Adriatic carbonate platform from the Thanetian to the Priabonian.

Key Words: Alveolina, Palaeogene Adriatic carbonate platform, Tethys, Cretaceous/Palaeocene–Priabonian, palaeogeography

Alveolinid’lerin Mekan-zaman Dağılımında Paleojen Adriyatik Karbonat Platformu’ nun Rolü

Özet: Paleojen Adriyatik karbonat platform çökelleri paleocoğrafik bir birim olarak Adriyatik doğu kıyısı boyunca 800 km uzunluğunda ve 100–130 km eninde bir kuşak boyunca yüzlek verirler. Bu kuşakta Erken İpreziyen (İlerdiyen)–Bartoniyen aralığında tanımlanan çok sayıda alveolinid türünün (69 tür) ayrıntılı irdelenmesi ile elde edilen sonuçlar şu şekilde sıralanabilir: (1) Orta İlerdiyen’ de (SBZ 7–8) gözlenen zengin tür çeşitliliği ve bolluğu İlerdiyen/Kuiziyen sınırı dolaylarında önemli bir azalma gösterir; (2) geç İpreziyende (geç Kuiziyen, SBZ 11–12) tür çeşitliliğinde önemli bir artış gözlenir ve (3) Erken Lütesiyenden sonra tür sayısı ani olarak azalır. Bu değişimler, TA ve AP olaylarındaki global deniz seviyesi değişimleri, bolluk ve çeşitlilik arasındaki ilişkiyi göstermektedir. Alveolinidlerin dağılımındaki ‘iki zirveli’ model aynı zamanda Pirene’lerdeki ‘Akdeniz toplulukları’ ve Akdeniz bölgesindeki birçok orta Kuiziyen topluluklarında gözlenmektedir. Paleojen Adriyatik karbonat platformunda çalışılan bir çok stratigrafik kesitten elde edilen veriler her biri spesifik alveolinid toplulukları ile temsil edilen biyosedimanter zonların (BioZ 2, BioZ 3.1, BioZ 3.2 ve BioZ 4) tanımlanmasına imkan sağlamıştır. Bu zonlar kuşaklar halinde KD İtalya’dan (Friuli bölgesi) Karadağ’a kadar uzanmakta olup, çalışılan alveolinid toplulukları Paleojen Adriyatik karbonat platformunun Tanesiyen–Priaboniyen aralığında paleocoğrafik haritalarının oluşturulmasında temel oluşturmaktadır.

Anahtar Sözcükler: Alveolina, Paleojen Adriyatik Karbonat Platformu, Tetis, Kretase/Paleosen–Priaboniyen, paleocoğrafya

Introduction

Representatives of the genus *Alveolina* were common larger benthic foraminifera in the late Palaeocene and Early to Middle Eocene Tethyan (Neotethyan)

shallow-water carbonate platforms (Hottinger 1960; Drobne 1977; Hottinger & Drobne 1988; Pignatti 1998; Sirel & Acar 2008). During this timespan, alveolinids represent important sediment

contributors to shallow-water carbonates of the Adriatic carbonate platform. The Palaeogene Adriatic carbonate platform (PgAdCP, named in Drobne *et al.* 2009) developed within the Central Tethys (around 32° N palaeolatitude) from the Palaeocene (Danian) to the late Middle Eocene (Bartonian). During this time, the PgAdCP was elongated in a NW–SE-trending gulf open to the north, west, and east during the early Palaeogene, and later also to the south (Drobne 2003). The shallow water carbonate regime produced various facies types which are defined using the larger benthic foraminiferal associations and sedimentary structures. These facies are grouped into four main biosedimentary units, BiosZ 2, BioZ 3.1, BioZ 3.2 and BiosZ 4 (Drobne 2000; Drobne *et al.* 2008b). These zones followed one another in a step-wise geographic pattern and record the temporal and spatial demise of certain ecological conditions. Sedimentation within each zone started with restricted, marginal marine, paralic and palustrine carbonates that we consider to be the initial onset of full marine conditions (Ćosović *et al.* 2008a). Once the marine regime was established, the shallow water settings supported the development of diverse and abundant foraminiferal assemblages.

A dozen published studies are extant since the first reconnaissance of alveolinids was carried out by d'Orbigny (1826). Alveolinids from European sediments were the first to be described (Checchia-Rispoli 1905), followed by those from northern Africa (Schwager 1883), and later those from the Indo-Pacific region (Somalia, Pakistan and India; Silvestri 1938).

Alveolinids show a diversification at the specific level, *i.e.* involving rapid increase in species diversity, shell size and adult dimorphism. *Alveolina* is known to have developed a large range of shapes induced by reproductive strategies and by environmental factors (light intensity, hydrodynamic characteristics). Alveolinids living in shallow water produced compact, ovate porcelaneous tests with thick walls (flosculinized tests), to prevent photoinhibition of symbiotic algae within the tests under bright sunlight.

This group of larger benthic foraminifera, adapted to a variety of ecological situations, developed many parallel evolutionary lineages (Hottinger & Drobne 1988) and rapid evolutionary changes in

morphology (Drobne 1977; Hottinger & Drobne 1988; Sirel & Acar 2008). Available knowledge on the palaeoecology of alveolinids refers to their mode of life, their palaeobathymetric distribution, and their faunal association. Recent alveolinids occur in a wide range of habitats, from deep lagoons to fore-reef settings, down to a depth of about 60 m (Yordanova & Hohenegger 2002). This fact, together with the fact that alveolinids are miliolines, with a broad tolerance of salinity and temperature fluctuation, makes this group probably less sensitive to smaller sea-level changes. The genus *Alveolina* became extinct at the onset of the Late Eocene, possibly because of numerous and rapid sea-level changes (TA 2.49, TA 3.12, Haq *et al.* 1987; AP10/AP11; Haq & Al-Qahtani 2005) which led to the disappearance of carbonate platforms and lagoonal areas.

For age determination we employ the Shallow Benthic Zonation (SBZ, Serra-Kiel *et al.* 1998), a correlative scheme of platform and pelagic environments in the Tethys.

The present study focuses on alveolinids from the Thanetian to the Bartonian, from numerous sections stretching from the Italian part of the Kras region (Friuli) to Montenegro studied by the senior author since the mid-1970s. The objectives of the study are: (a) to describe the spatial distribution of the alveolinids on the PgAdCP; (b) to discuss the processes that controlled such distribution; (c) to describe the evolution of alveolinid associations within the Palaeocene and Eocene; and (d) to illustrate the role of the studied area in the palaeobiogeographic distribution of alveolinids within the Tethys ocean.

Geological Setting and Studied Sections

The Palaeogene Adriatic Carbonate Platform, from Onset to Demise

Exposed along the eastern Adriatic coast, from the Friuli region in Italy SE to Montenegro, the Palaeogene sediments form a more or less continuous belt up to 800 km long (Ćosović *et al.* 2008a, b) of varying width (100–130 km, Figure 1), due to erosion as a consequence of tectonically induced uplift and thrusting (the important factors controlling changes on the Adria plate are summarized by Korbar 2009).

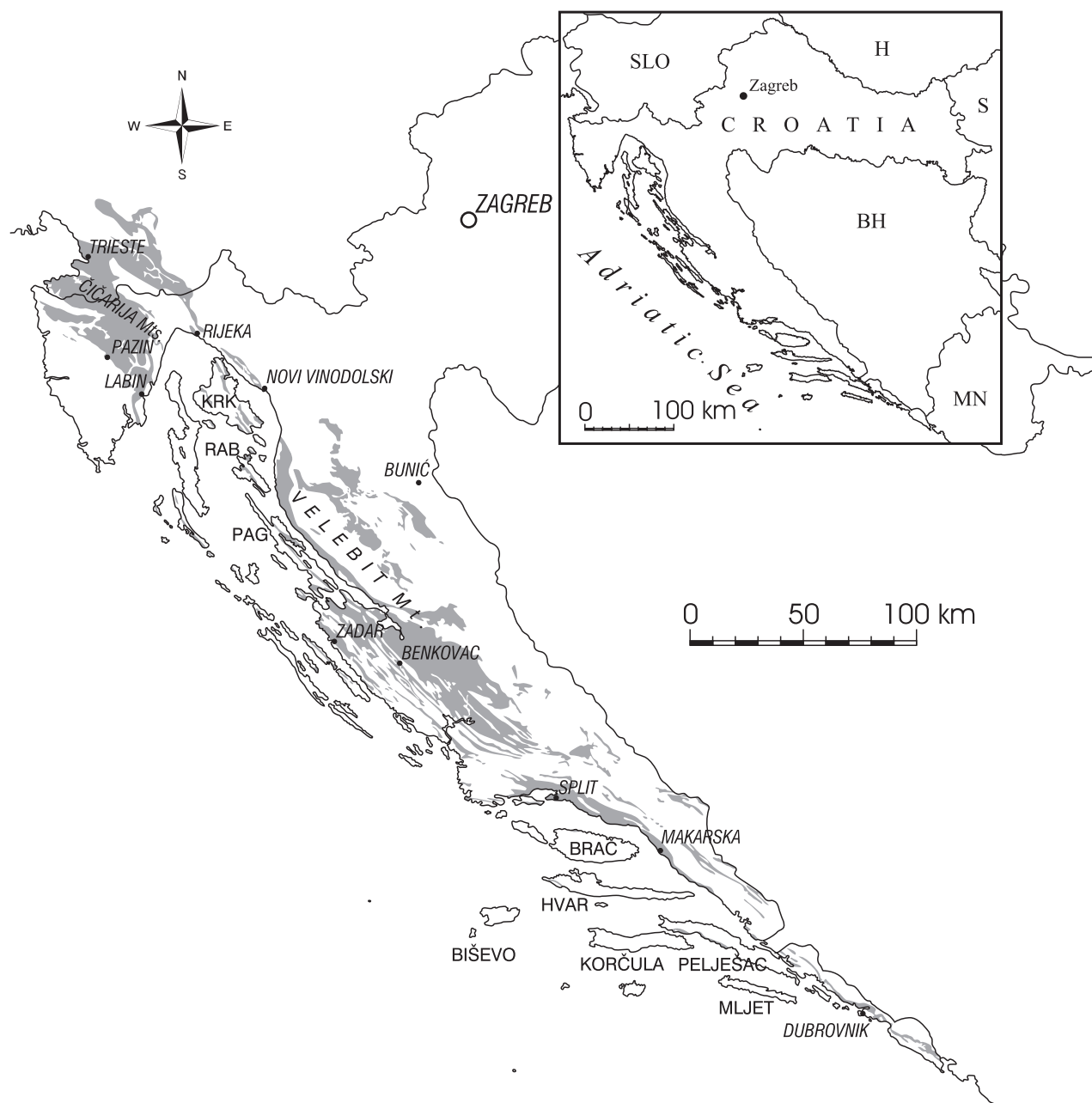


Figure 1. Simplified geological map of the Palaeogene domains, remnants of the Palaeogene Adriatic carbonate platform showing the location of the regions studied in this paper (adapted from Čosović *et al.* 2008b).

These sediments form a succession up to 1000 m thick deposited on the shallow water carbonate platform (PgAdCP). The PgAdCP was part of the shallow shelves within the Central Tethys (Butterlin *et al.* 1993), and developed on the formerly extensive Mesozoic Adriatic Carbonate Platform. A trench existed to the north, and the Ionian – Adriatic-

Belluno basin was situated to the south, where ocean currents flowed from the Indo-Pacific (E Tethys) via W Tethys (Pyrenean and Iberian basins) to the opening Atlantic Ocean (Hottinger 1990; Premru 2005; Premru *et al.* 2006; Drobne *et al.* 2008a). The Late Cretaceous regional regression left the vast area exposed, and the subsequent transgression advanced

from the northwestern and northeastern borders, from the Cretaceous/Palaeocene (K/Pc) boundary throughout the Palaeocene and up to the Middle Eocene (Bartonian). A combination of sea-level fluctuations, variations in the configuration of the sedimentary basins and different rate of subsidence over the vast region resulted in a diachronous onset of the transgression and the development of various shallow water environments (lagoons, shoals, inner ramp, bars). The entire area, from the middle Cuisian onward, was covered by a shallow sea, except for a narrow trench that developed in the Palaeocene and extended westward from eastern Herzegovina (Chorovitz 1975; Marinčić *et al.* 1976; Jelaska *et al.* 2003; Čosović *et al.* 2006).

The PgAdCP is characterized by variations of distinct facies associations from the platform margin to the basin. From the Palaeocene, the facies distribution along the platform-basin transects can be subdivided into two regions: Slovenian Kras (including the Friuli region) and the N and E part of Herzegovina (BioZ 2 and BioZ 3; Drobne 2003) are considered as one sub-region, while Istria, NW, Central and Southern Dalmatia and Western Herzegovina (BioZ 4) belonged to the another sub-region (Drobne *et al.* 2008b).

A generalized stratigraphic column in the Kras region contains 5 superimposed lithostratigraphic units (Stache 1889; Drobne & Pavlovec 1991; Košir 2003). The Liburnian Formation (Maastrichtian to Lower Palaeocene), composed of restricted, marginal marine, paralic and palustrine carbonates, is overlain by the Trstelj Formation (Upper Palaeocene), composed of foraminiferal and coralgall limestones and *Alveolina-Nummulites* limestones (Lower and partly Middle Eocene) dominated by the accumulation of larger benthic foraminifera. The demise of the shallow water regime is marked by the deposition of the so-called Transitional Beds (hemipelagic and pelagic limestones) of Lower and Middle Eocene age and Flysch, a succession of sandstone-dominated turbidites, marls, mudstones and resedimented carbonates more than 1000 m thick (Drobne & Pavlovec 1991; Zamagni *et al.* 2007). In this area (NW part of the PgAdCP) the K/Pc boundary is exposed in several sections and developed in a shallow-marine carbonate facies.

This lithological development is rarely found in the Mediterranean region, where hiatuses, shallow-water terrigenous deposits or deep-water deposits are typical. The section at Dolenja Vas is the most completely documented (for a summary, see e.g., Drobne *et al.* 1988, 1989; Barattolo 1998; Turnšek & Drobne 1998), and sections such as Sopada near Sežana, and Čebulovica (Pugliese *et al.* 1995; Ogorelec *et al.* 2001; Tewari *et al.* 2007; Zamagni *et al.* 2007) are also stratigraphically and sedimentologically well documented. The studied sections from the Kras are characterized by complete Upper Cretaceous to Palaeogene successions in the PgAdCP, including Maastrichtian to Palaeocene restricted inner platform carbonates (SBZ 1; De Castro *et al.* 1994; Drobne *et al.* 2007a; Ogorelec *et al.* 2007; Čosović *et al.* 2008a). The shallow water conditions where inner ramp limestones were deposited lasted until the late Ilerdian (SBZ 9, BioZ 2), whereas outer ramp conditions persisted until the late Cuisian (SBZ 12, BioZ 3).

In Istria and Dalmatia, the beginning of Palaeogene sedimentation is marked by carbonates deposited in marine marginal, brackish to palustrine environments (Drobne 1977; Drobne & Pavlovec 1991; Čosović *et al.* 2004, 2008a, b). They unconformably overlie various Lower or Upper Cretaceous lithostratigraphic units over a major hiatus related to a regional subaerial exposure. The typical Palaeogene succession has been subdivided into the following informal lithostratigraphic units: Liburnian Formation (early Eocene, Cuisian) – restricted to brackish lagoons, ramp interior; Foraminiferal limestones (early to middle Eocene, Cuisian to late Lutetian) – inner to middle ramp, and Transitional beds (middle Lutetian to Bartonian) – middle to outer ramp. The Foraminiferal limestones can be divided into four lithostratigraphic types, which are mostly in superpositional relationship. These are: Miliolidae-, *Alveolina*-, *Nummulitids*- and *Orthophragminae*- limestones. The Transitional Beds illustrate the sedimentological and facies transition from carbonate ramp to the basin environment. The most complete sections are Pićan (in Istria), where a 120-m-thick succession was deposited from SBZ 11 to SBZ 14 (late Cuisian to middle Lutetian; Pavlovec *et al.* 1991), Benkovac in the Ravni kotari region (Drobne *et al.* 1991d) and in Central Dalmatia on

Hvar Island and the Pelješac Peninsula (Marjanac *et al.* 1998).

In SE Herzegovina, on the SE margin of the PgAdCP, Palaeogene sediments crop out west and east of the Neretva River. The most complete section on the eastern side of the Neretva River is the Stolac-Hrgud section, where the beginning of the carbonate sedimentation coincides with the Thanetian (SBZ 3). The Palaeocene deposits overlie the Campanian–Maastrichtian limestones. In this section, the thickness of the whole Palaeogene succession (BioZ 3) does not exceed 120 m (Drobne & Trutin 1997; Drobne *et al.* 2000; Trutin *et al.* 2000). In the Metković–Sjekoše section (Drobne *et al.* 2007a), the Upper Cretaceous sediments are transgressively overlain by the Palaeocene deposits. These deposits pass upward into the Ilerdian to middle Cuisian sediments, which are interpreted to be inner to middle ramp origin and yield a diverse assemblage which includes alveolinids (Foraminiferal limestones). The sea-level rose in the middle Cuisian and for the very first time shallow seas spread over the western part of Herzegovina (west of the Neretva River). The beginning of sedimentation is marked with the bituminous limestones originated in brackish water and in places intercalated with coal beds. The whole succession reaches up to 200 m in thickness (Slišković 1968; Drobne *et al.* 2000; Trutin *et al.* 2000; Jungwirth 2001; Drobne 2003). These deposits, equivalent to the Liburnian Formation, suggest the existence of shallow water conditions similar to those in Istria and Dalmatia (Drobne *et al.* 1991b, d; Pavlovec *et al.* 1991; Čosović & Drobne 1998).

Climate Changes

The evolution of the PgAdCP is partly a climate-dependent process. The early Palaeocene was ice-free and slightly cooler than the Cretaceous. By the Late Palaeocene, temperatures rose with an anomalously warm global climate optimum, known as the Palaeocene Eocene Thermal Maximum (PETM, Zachos *et al.* 2001). This warm period continued through the Eocene (tropical sea-surface temperatures thought to be at least 28–32° C; Pearson *et al.* 2007) and favoured a broad latitudinal distribution of temperature-sensitive organisms (larger benthic foraminifera, including alveolinids).

The overall warming trend was interrupted three times (Zachos *et al.* 2001): from 60–58 Ma (SBZ 2), when a slight cooling occurred, and also two times with exceptional warming at the Pc/E boundary (SBZ 4/SBZ 5 boundary) and around 52–50 Ma (SBZ 10–SBZ 11). The first event is registered only in sediments that are spatially confined to the NW part of the PgAdCP by excursion in the $\delta^{13}\text{C}$ record and changes in associated biota (Ogorelec *et al.* 2007). The second significant event known as the PETM (SBZ 4/SBZ 5, recognized in the Sopada section only, Drobne *et al.* 2006) was characterized by a warm, humid climate (widespread occurrences of bauxite in Istria; Durn *et al.* 2003) and intensive weathering. During this warm interval sea surface temperatures, in the low latitudes, rose by 4–5 °C (Zachos *et al.* 2003; Sluijs *et al.* 2007). The higher rates of physical weathering and denudation initiated eutrophication of shallow-water settings, supporting the development of those larger benthic foraminifera that are more tolerant to enhanced nutrient levels (glomalveolinids; Scheibner & Speijer 2008). The third climate event took place during the early Eocene, referred to as the Early Eocene Climate Optimum (EECO). The EECO featured high global temperatures and marked the end of the pre-glacial stage of the Cenozoic. In the studied area, in shallow water environments, diversification and specimen abundance of particular, competitive groups of larger benthic foraminifera increased (Čosović *et al.* 2009) and their spatial distribution extended (the expansion of hospitable settings coincides with the global sea-level fall close to the transition from Ta 2.49/TA 3.12 (Haq *et al.* 1987) or AP 10/AP 11 cycles (Haq & Al-Qahtani 2005).

Material and Methods

The present alveolinid inventory is based on detailed sampling and microfossil analysis of sediments from various locations along the eastern Adriatic coast, adjacent mainland regions and off-shore wells. A total of 157 sedimentary logs from onshore sections and outcrops and off-shore wells (Tari-Kovačić *et al.* 1998; Drobne *et al.* 2007b) were studied, representing more than 30 years of interest in Palaeogene carbonates from K. Drobne and her colleagues. The dataset is based on a compilation of published data,

and the results of more than 30 papers have been integrated (for reference and details see Drobne *et al.* 2008a, 2009).

Wherever possible, complete sections from the K/Pc boundary up to the Lower or Middle Eocene were logged and sampled. Thousands of thin sections were analyzed for microfossil content, with special emphasis on alveolinids. Identification of species was done with oriented sections. Systematic determinations of alveolinids mainly follow the criteria of Reichel (1937), Hottinger (1960), Drobne (1977), Loeblich & Tappan (1987) and Hottinger & Drobne (1988).

The studied materials are stored at the Ivan Rakovec Institute of Palaeontology of ZRC of the Slovenian Academy of Sciences and Arts in Ljubljana and the Museum of Natural History in Basel.

Results

The regional distribution of sediments with alveolinids is associated with the spatial distribution of shallow water settings since Danian times during the uplift of the Dinarides and Alps. The composition and nature of alveolinid associations are related to interspecies and intraspecies competition, the timing of sea-level changes and the opening or closing of potential migration pathways. The available data on alveolinid distribution in space and time are summarized in Tables 1–3.

Broad regional comparison of the Danian (SBZ 1) of the northwestern and southeastern margins of the PgAdCP (Kras region and E Herzegovina) indicates stratigraphic, lithologic and biofacies similarities and peritidal settings, characterized by unstable environmental conditions with frequent subtidal to supratidal changes. Sporadic opportunistic, r-strategist small-sized miliolids (including rotaliids and larger miliolids), together with discorbids and *Bangiana hanseni* Drobne 2007 (Drobne *et al.* 2007a), thin-shelled ostracods, and gastropods, occurred, all able to tolerate frequent environmental changes. The overlying deposits are of normal marine origin, and contain miliolids, corals (known only from the northwestern margin where they formed local patch reefs; Turnšek & Drobne 1998) and dasycladales (Barattolo 1998), and all indicate establishment

of stable, lasting marine conditions that allowed development and proliferation of K-strategists by the end of SBZ 2.

The first occurrence of the first Palaeocene alveolinid, *Glomalveolina primaeva* (Reichel 1937) corresponds to the base of SBZ 3, with the expansion of normal marine settings, differentiation of the sea-bottoms (sandy to perennially vegetated) and changes in the composition of bottom-dwelling foraminifera. The Thanetian deposits (SBZ 3 and SBZ 4), spatially confined to the Kras region and E Herzegovina (northwestern and southeastern borders of the PgAdCP), contain algae (corallinaceans and dasycladales), corals (massive and encrusting) on the northern platform margin, which built small coral-microbial reef mounds; (Zamagni *et al.* 2009), and moderate K-strategists, *i.e.* larger miliolids, glomalveolinids (*G. dachelensis* (Schwager 1883), *G. ludwigi* (Reichel 1937) and *G. telemetensis* (Hottinger 1960)), and the first nummulitids in the PgAdCP.

In the early Ilerdian (SBZ 5–SBZ 6) moderate sized, spherical and flosculinized alveolinids (*Alveolina aramaea* Hottinger 1960, *A. globosa* (Leymerie) 1846, *A. daniensis* Drobne 1977, *A. solida* Hottinger 1960) and the ovoidal to elongated *A. vredenburgi* Davies & Pinfold 1937 and *A. ellipsoidalis* Schwager 1883 settled on middle ramp sandy to muddy bottoms, from the Pyrenees, to the Northern and Southeastern parts of the PgAdCP, and eastwards to Turkey (Figure 8, Table 1, Plate 1).

Palaeogeographically, during the middle Ilerdian (SBZ 7–SBZ 8, BioZ 2 and BioZ 3.1), a shrinkage of shallow water settings took place in E Herzegovina (Figures 2 & 8), while in the northwest–west, the area suitable for larger benthic foraminifera expanded. At the same time, alveolinids showed greater species diversification and abundance. Medium-sized species with sub-spherical to spherical test morphologies prevailed. Species with elongated, large tests occurred, too. Moderate to heavily flosculinized tests occurred as well as those without thick basal layers. Ovoidal species, *Alveolina aragonensis* Hottinger 1960 and *A. moussoulenensis* Hottinger 1960 and flosculine such as *A. avellana* Hottinger 1960, *A. pisiformis* Hottinger 1960, *A. leupoldi* Hottinger 1960 and *A. parva* Hottinger 1960, known from the Aquitaine and Tresp basins (Pyrenean region:

Table 1. Distribution data for Ilerdian alveolinids (after Hottinger 1960; Drobne 1977; Hottinger & Drobne 1980; Drobne et al. 1991a, b, 2000; Drobne & Trutin 1997; Trutin et al. 2000; Ibrahimpašić 2004; Sameeni & Butt 2004; Vecchio et al. 2007; Sirel & Acar 2008).

Species	Testmorphology (after Hottinger 1960; Drobne 1977; Sirel & Acar 2008)	Geographic Distribution: West-Tethyan	Geographic Distribution: Palaeogene Adriatic Carbonate Platform and NE Italy	Geographic Distribution: East-Tethyan
<i>A. ellipsoidalis</i> Schwager 1883	subglobular to ovoidal	N Spain	Podgorje, Kozina, Ljubinjje-Vlahovići	Egypt, Greece, Turkey
<i>A. moussoulensis</i> Hottinger 1960	ovoidal	Pyrenean basin	Dane, Ritomeće, Podgrad, Dane (Istra), Klana	Turkey
<i>A. anamaea</i> Hottinger 1960	spherical to ovoidal		Fajtin hrib, Dane, Veliko Gradišće, Kozina	Turkey, Iraq, Iran
<i>A. vredenburgi</i> Davies & Pinfold 1937	elongated to ovoidal	S France, N Spain, Pyrenean basin	Dane, Ritomeće, Kozina, Golež, Žbevnica	Pakistan
<i>A. dantensis</i> Drobne 1977	subspherical to spherical		Dane, Veliko Gradišće, Golež	Turkey
<i>A. solida</i> Hottinger 1960	spherical to ovoidal	S France	Fajtin hrib, Dane, Veliko Gradišće, Kozina, Klana	Egypt, Turkey
<i>A. tristina</i> Hottinger 1960	ovoidal (flosculinized)		Veliko Gradišće, Golež, Novi Vinodolski, Ljubinjje-Vlahovići, NE Italy	
<i>A. globosa</i> (Leymerie) 1846	spherical flosculinized	S France, N Spain	Fajtin hrib, Ritomeće, Podgrad, Podgorje	Turkey
<i>A. brassica</i> Drobne 1977	subspherical (flosculinized)		Ritomeće, Veliko Gradišće, Golež, Ljubinjje-Vlahovići	Turkey
<i>A. avellana</i> Hottinger 1960	spherical flosculinized	S France, N Spain, Pyrenean basin	Dane, Kozina, Golež, Podgorje	Turkey
<i>A. pisiformis</i> Hottinger 1960	spherical flosculinized	Pyrenean basin	Fajtin hrib, Dane, Veliko Gradišće, Golež, Žbevnica, Dane (Istra)	Turkey
<i>A. pastillata</i> Schwager 1883	spherical flosculinized	S and N Spain, S France	Fajtin hrib, Dane, Ritomeće, Veliko Gradišće, Podgrad, Kozina, Golež, Novi Vinodolski	Egypt, Greece, Turkey
<i>A. leopoldi</i> Hottinger 1960	spherical to ovoidal flosculinized	S France, Pyrenean basin	Fajtin hrib, Ritomeće, Golež, Dane (Istra), Klana	Turkey
<i>A. parva</i> Hottinger 1960	subspherical flosculinized	N Spain	Ritomeće, Veliko Gradišće, Novi Vinodolski, NE Italy	Turkey, Sicily
<i>A. montanarii</i> Drobne 1977	spherical		Dane, Ritomeće, Veliko Gradišće, Golež, Ljubinjje-Vlahovići	Turkey, Sicily
<i>A. aragonensis</i> Hottinger 1960	subglobular to ovoidal	Pyrenean basin	Ritomeće, Veliko Gradišće, Podgrad, Golež, Žbevnica, Dane (Istra), Ljubinjje-Vlahovići	Turkey
<i>A. fornasinii</i> Cecchia-Rispoli 1909	ovoidal	N Spain	Dane, Ritomeće, Metković-Sjakoše, NE Italy	Sicily
<i>A. deadolia</i> Drobne 1977	ovoidal		Dane, Ritomeće, Veliko Gradišće, Dane (Istra)	Turkey
<i>A. subpyrenatica</i> Leymerie 1846	ovoidal	Pyrenean basin	Fajtin hrib, Dane, Ritomeće, Veliko Gradišće, Žbevnica, Dane (Istra), Ljubinjje-Vlahovići	Turkey, Iran
<i>A. pisella</i> Drobne 1977	ovoidal		Dane, Ritomeće	Turkey
<i>A. laxa</i> Hottinger 1960	ovoidal (flosculinized)	N Spain	Dane, Veliko Gradišće, Podgrad, Kozina, Golež, NE Italy	Turkey
<i>A. citrea</i> Drobne 1977	elongated ovoidal	N Spain	Jelsane	Turkey
<i>A. cylindrata</i> Hottinger 1960	subcylindrical	N Spain	Ritomeće, Veliko Gradišće, Ljubinjje-Vlahovići	
<i>A. guidonis</i> Drobne 1977	subcylindrical to ovoidal		Dane, Ritomeće, Veliko Gradišće, Golež, Ljubinjje-Vlahovići	Turkey
<i>A. decipiens</i> Schwager 1883	ovoid to subcylindrical	N Spain, S France, Pyrenean basin	Ritomeće, Veliko Gradišće, Kozina, Žbevnica, NE Italy	S Italy, Libya, Egypt

Table 2. Distribution data for Cuisian alveolinids (after Hottinger 1960; Montanari 1964b; Drobne 1977; Hottinger & Drobne 1980; Samsó 1988; Samsó *et al.* 1990; Drobne *et al.* 1991d, 2000; Pavlovec *et al.* 1991; Drobne & Trutin 1997; Hottinger *et al.* 1998; Trutin *et al.* 2000; Ibrahimpašić 2004; Čosović *et al.* 2008a, b; Sirel & Acar 2008).

Species	Test-morphology (after Hottinger 1960; Drobne 1977; Sirel & Acar 2008)	Geographic Distribution: West-Tethyan	Geographic Distribution: Palaeogene Adriatic Carbonate Platform and NE Italy	Geographic Distribution: East-Tethyan
<i>A. canavari</i> Checchia-Rispoli 1905	subcylindrical	S Spain	Kozina, Golež, Slavec, NE Italy	Central Italy, Sicily, Turkey
<i>A. oblonga</i> d'Orbigny 1826	cylindrical	NW Spain, Paris basin, W Aquitaine	Slavec, Humac (Stolac), Metković-Sjekoše, NE Italy	Sicily, Turkey, Egypt
<i>A. coutourensis</i> Hottinger 1960	cylindrical	S France, N Spain, Africa (Kilwa)	Boljunsko polje, Klis	
<i>A. rectangularis</i> Drobne 1977	cylindrical		Golež, Šterna, Boljunsko polje, Bunić	
<i>A. histrica</i> Drobne 1977	subcylindrical		Ivartnik (E Alps), Rosandra, Kozina, Slavec, Golež, Podgorje, Bunić, Hrgud-Stolac	
<i>A. septentrionalis</i> Drobne 1977	subcylindrical		Golež, Kozina, Podgorje, Voz, Bunić, Lištica-Dobrinj, Hrgud-Stolac, Metković-Sjekoše	Turkey
<i>A. rakoveci</i> Drobne 1977	subcylindrical		Ivartnik (E Alps), Rosandra, Kozina-Socerb, Golež, Slavec, Podgrad, Voz, Bunić, Lištica-Dobrinj	
<i>A. cosinensis</i> Drobne 1977	ovoidal	N Spain,	Kozina, Slavec	
<i>A. cosigena</i> Drobne 1977	ovoidal		Ivartnik (E Alps), Rosandra, Golež, Slavec, Bunić, Lištica-Dobrinj, Hrgud-Stolac	
<i>A. carantana</i> Drobne 1977	elongated ovoidal		Ivartnik (E Alps)	Turkey
<i>A. colatiensis</i> Drobne 1977	elongated ovoidal		Rosandra, Bunić, Lištica-Dobrinj	Turkey
<i>A. dainelli</i> Hottinger 1960	spherical flosculinized		NE Italy, Vipava	
<i>A. azzarolii</i> Drobne 1977	ovoidal		Golež, Kozina, Slavec, Šterna, Bunić, Lištica-Dobrinj	Somalia
<i>A. minuta</i> Checchia-Rispoli 1907	ovoidal		Slavec, Žbevnica	Sicily, Central Apennines, Turkey
<i>A. decastroi</i> Scotto di Carlo 1966	ovoidal	N Spain	Žbevnica, Podgorje, Slavec, Benkovac, Skradin	Gargano (Southern Apennines)
<i>A. multicanalifera</i> Drobne 1977	cylindrical		Karolja, Šterna, Pićan; Kuk, Benkovac, Skradin	
<i>A. cuspidata</i> Drobne 1977	fusiform		Kozina, Slavec, Golež, Klis	
<i>A. crematae</i> Checchia-Rispoli 1905	ovoidal to fusiform		Kozina, Slavec, Podgorje, Golež, Šterna, Boljunsko polje, Lupoglav, Voz, Bunić, Skradin, Lištica-Dobrinj, Hrgud-Stolac, Metković-Sjekoše, NE Italy	Gargano (Southern Apennines), Greece, Turkey
<i>A. levantina</i> Hottinger 1960	fusiform	S Spain	Šterna, Kuk, Boljunsko polje, Pićan, Karolja, Sv. Tom, Mali Lošinj, Molat, Benkovac, Skradin, Klis	Southern Apennines, Greece, Lebanon, Palestine, Somalia
<i>A. rugosa</i> Hottinger 1960	subcylindrical to fusiform		Kozina, Golež, Slavec, Klis, NE Italy	Turkey, Greece, Sicily
<i>A. croatica</i> Drobne 1977	ovoidal		Šterna, Boljunsko polje, Pićan, Skradin	
<i>A. schwageri</i> Checchia-Rispoli 1905	fusiform	S France, N Spain, Paris basin	Ivartnik (E Alps), Rosandra, Kozina, Golež, Slavec, Žbevnica, Bunić, Metković-Sjekoše, NE Italy	Sicily, Greece
<i>A. distefano</i> Checchia-Rispoli 1905	fusiform to subcylindrical	N Spain	Ivartnik (E Alps), Rosandra, Golež, Podgrad, Kozina, Slavec, Podgorje, Žbevnica, Voz, Bunić, Lištica-Dobrinj, Hrgud-Stolac, NE Italy	Gargano (Southern Apennines), Greece, Sicily, Turkey
<i>A. lehnerti</i> Hottinger 1960	ovoidal to subcylindrical	N Spain	Kozina, Slavec, Voz	Turkey
<i>A. pinguis</i> Hottinger 1960	fusiform to subcylindrical		Kozina, Benkovac, Skradin	Turkey
<i>A. ruetimeyeri</i> Hottinger 1960	subcylindrical to cylindrical	S Spain, N Spain, S France	Ivartnik (E Alps), Rosandra, Kozina, Golež, Slavec, Šterna, Žbevnica, Bunić, Lištica-Dobrinj, Hrgud-Stolac, NE Italy	Sicily, Turkey
<i>A. violae</i> Checchia-Rispoli 1905	subcylindrical		NE Italy, Goriška brda, Šterna	
<i>A. axiample</i> Drobne 1977	subcylindrical		Šterna, Boljunsko polje, Benkovac	

Table 3. Distribution data for Lutetian alveolinids (after Hottinger 1960; Montanari 1964a; Drobne 1977; Hottinger & Drobne 1980; Drobne *et al.* 1991c, d, 2000; Drobne & Trutin 1997; Trutin *et al.* 2000; Ibrahimpašić 2004; Cosović *et al.* 2008a, b; Sirel & Acar 2008, Vecchio *et al.* 2007).

Species	Test-morphology (after Hottinger 1960; Drobne 1977; Sirel & Acar 2008)	Geographic Distribution: West-Tethyan	Palaeogene Adriatic Carbonate Platform and NE Italy	Geographic Distribution: East-Tethyan
<i>A. elliptica nuttalli</i> Davies 1940	ovoidal to subcylindrical		Pićan, Filip Jakov, NE Italy	Sicily, Greece, Somalia, Persian Gulf, Madagascar, Indonesia
<i>A. stercusmuris</i> Mayer-Eymar 1886	ovoidal		Pićan, Ragancini-Lišani, Benkovac, Skradin, NE Italy	Egypt, Turkey
<i>A. obtusa</i> Montanari 1964	cylindrical		Pićan, Benkovac	Sicily
<i>A. boscii</i> (Defrance in Bonn) 1825	fusiform	S France, Paris basin, N Spain	Osp, Rakitovec	Libya
<i>A. frumentiformis</i> Schwager 1886	fusiform to subcylindrical	N Spain	Šterna, Boljunsko polje, Benkovac, NE Italy	Egypt, Libya, Iran
<i>A. hottingeri</i> Drobne 1977	subcylindrical		Kuk, Pićan, Karojba, Sv. Tom, Ragancini-Lišani, Marjan	S Italy
<i>A. croatica</i> Drobne 1977	ovoidal		Kuk, Karojba, Sv. Tom	Gargano (Southern Apennines)
<i>A. gigantea</i> Checchia-Rispoli 1907	cylindrical		Pićan, Benkovac	Sicily, Lebanon
<i>A. callosa</i> Hottinger 1960	cylindrical	N Spain	Šterna, Boljunsko polje, Pićan, Ragancini-Lišani, Sv. Tom, Silba, Benkovac, Skradin	
<i>A. ospiensis</i> Drobne 1977	cylindrical		Šterna, Osp, Benkovac, Skradin	
<i>A. stipes</i> Hottinger 1960	subcylindrical	N Spain	Pićan, Benkovac, NE Italy	Turkey, Lebanon, Libya, Pakistan
<i>A. muniteri</i> Hottinger 1960	cylindrical	Pyrenean basin, SW France, Asturia	Boljunsko polje, Pićan, Karojba, Benkovac, NE Italy	
<i>A. tenuis</i> Hottinger 1960	subcylindrical	Pyrenean basin, S France, N Spain	Šterna, Filip Jakov, Klis	Sicily, Turkey

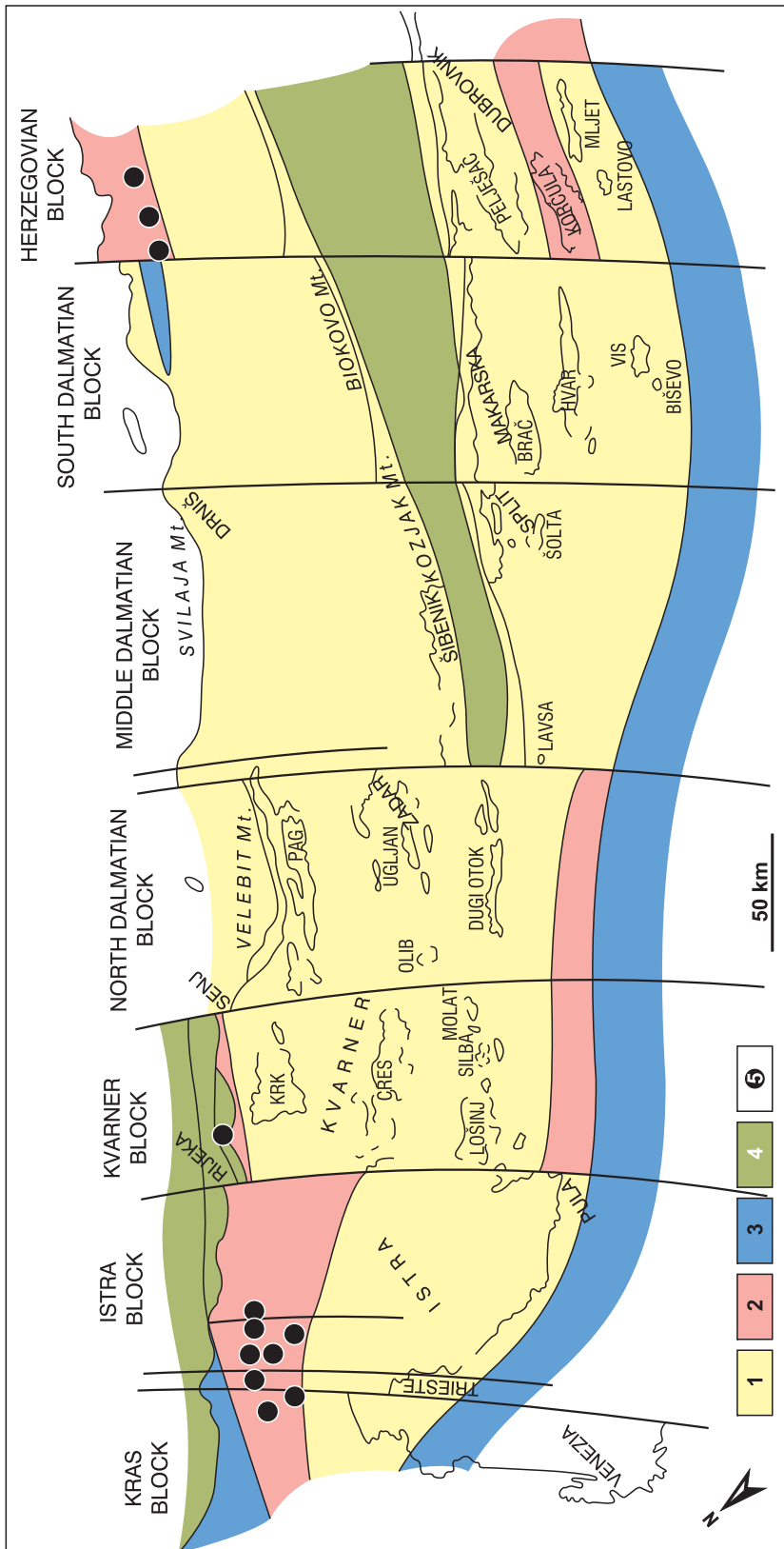


Figure 2. Palaeogeographic sketch of the Palaeogene Adriatic carbonate platform during the Late Ilerdian (SBZ 9) between 53–52.5 Ma (simplified after Premru *et al.* 2006). 1 – land, 2 – carbonate shelf, 3 – trough where flysch was deposited, 4 – basin with flysch and Scaglia-type sediments, 5 – location of sediments with alveolinids.

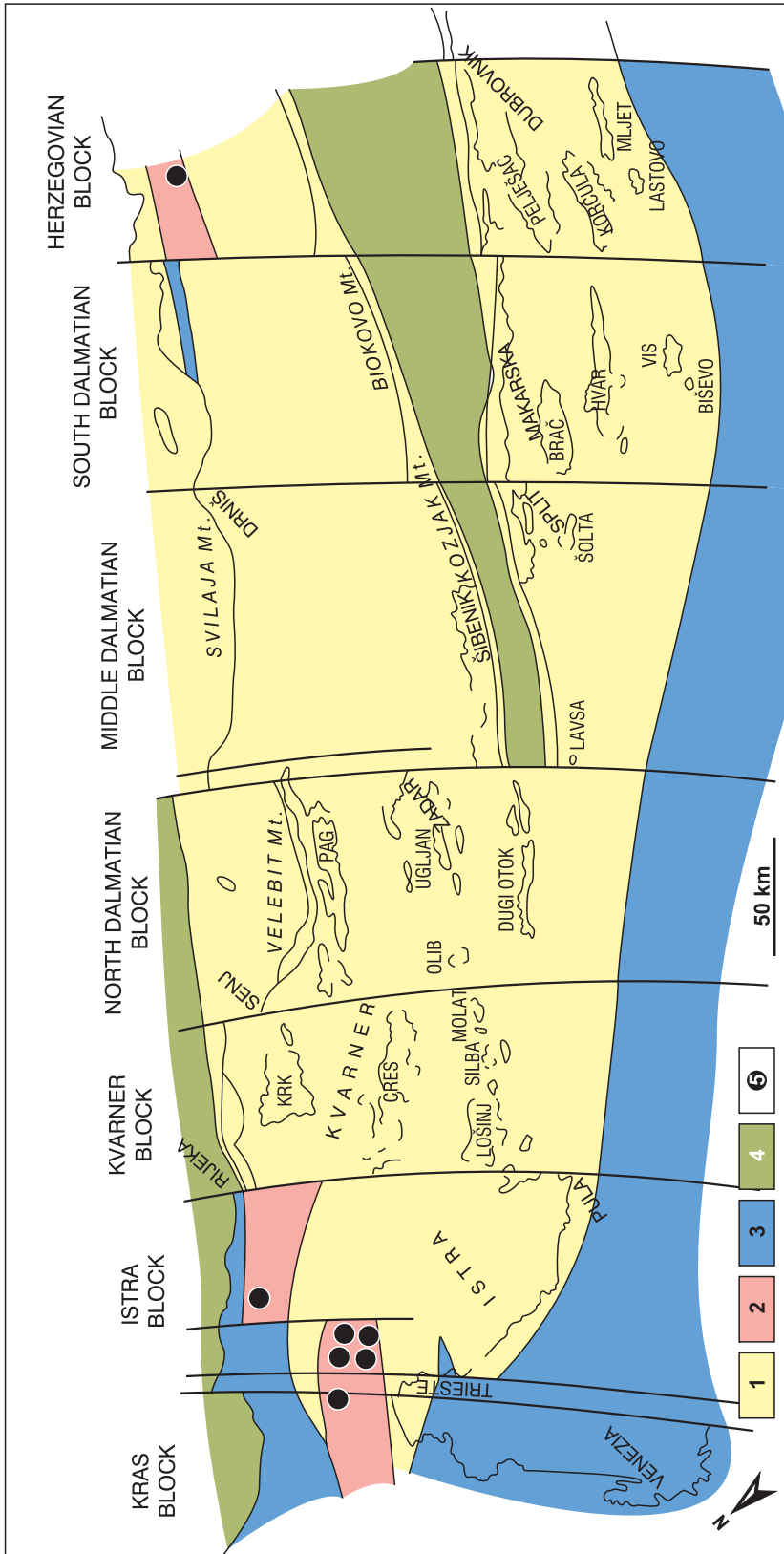


Figure 3. Palinspastic sketch of the Palaeogene Adriatic carbonate platform during the Early Cuisian (SBZ 10) between 52.5–50.5 Ma (simplified after Premru *et al.*, 2006). 1– land, 2– carbonate shelf, 3– trough where flysch and Scaglia-type sediments were deposited, 4– basin with flysch and Scaglia-type sediments, 5– location of sediments with alveolimids.

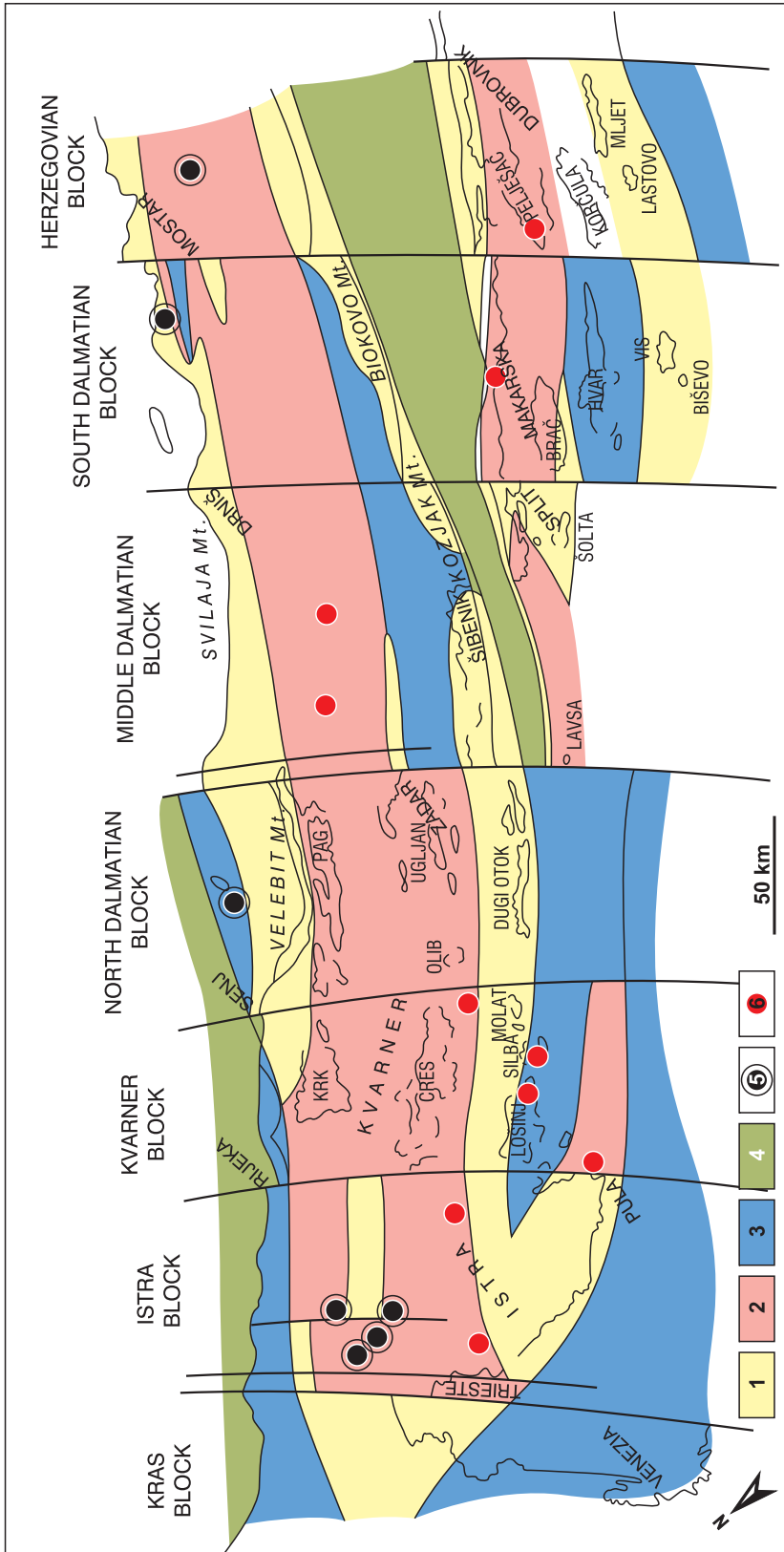


Figure 4. Palimpsestic sketch of the Palaeogene Adriatic carbonate platform during the Middle Cuisian (SBZ 11) between 50.7–49.5 Ma (simplified after Premru *et al.* 2006).
 1 – land, 2 – carbonate shelf, 3 – trough where flysch was deposited, 4 – basin with flysch and Scaglia-type sediments, 5 – location of sediments with alveolinids of the *A. histrica* lineage, 6 – location of sediments with alveolinids of the *A. levantina* lineage.

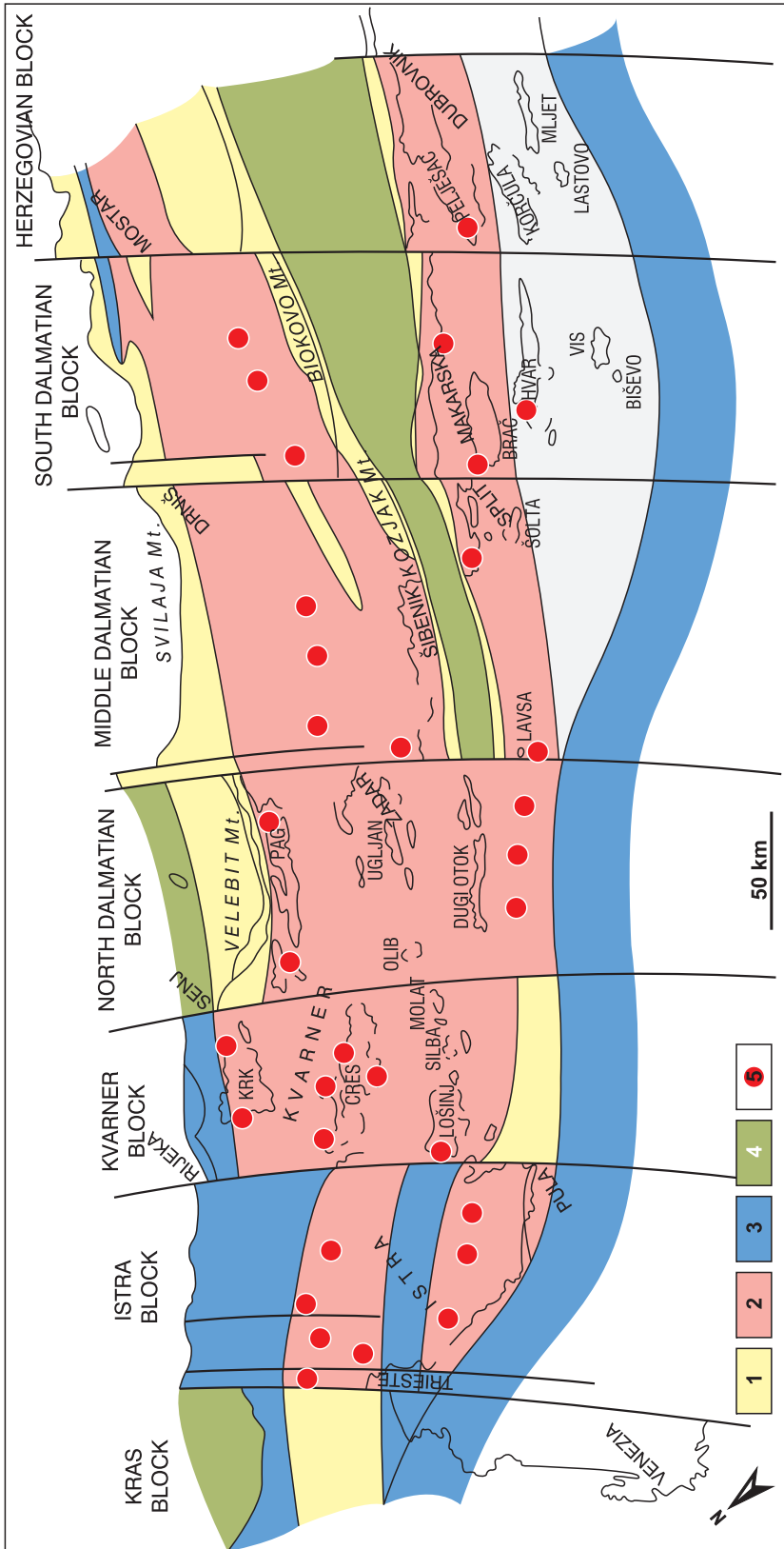


Figure 5. Palinspastic sketch of the Palaeogene Adriatic carbonate platform during the Middle Lutetian (SBZ 13–SBZ 15) between 45.8–41.7 Ma (simplified after Premru *et al.* 2006). 1– land, 2– carbonate shelf, 3– trough where flysch was deposited, 4– basin with flysch and Scaglia-type sediments, 5– location of alveolinites of the *A. levantina* lineage.

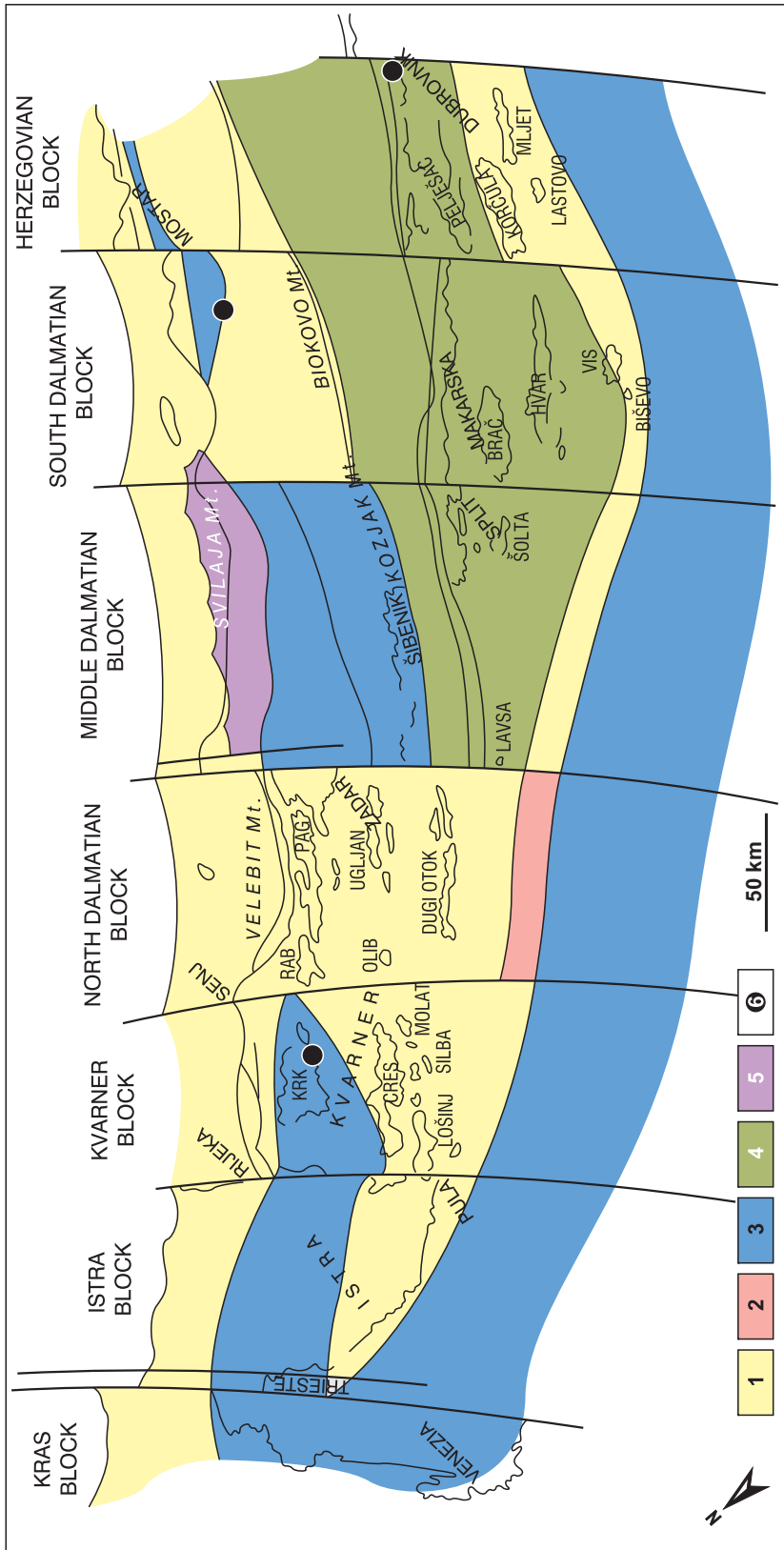


Figure 6. Palinspastic sketch of the Palaeogene Adriatic carbonate platform during the Bartonian (SBZ 17) between 41.5–38.3 Ma (simplified after Premru *et al.* 2006).
 1 – land, 2 – carbonate shelf, 3 – trough where flysch and Scaglia-type sediments were deposited, 4 – basin with flysch and Scaglia-type sediments, 5 – molasse (Promina Fm), 6) – location of sediments with alveolinids.

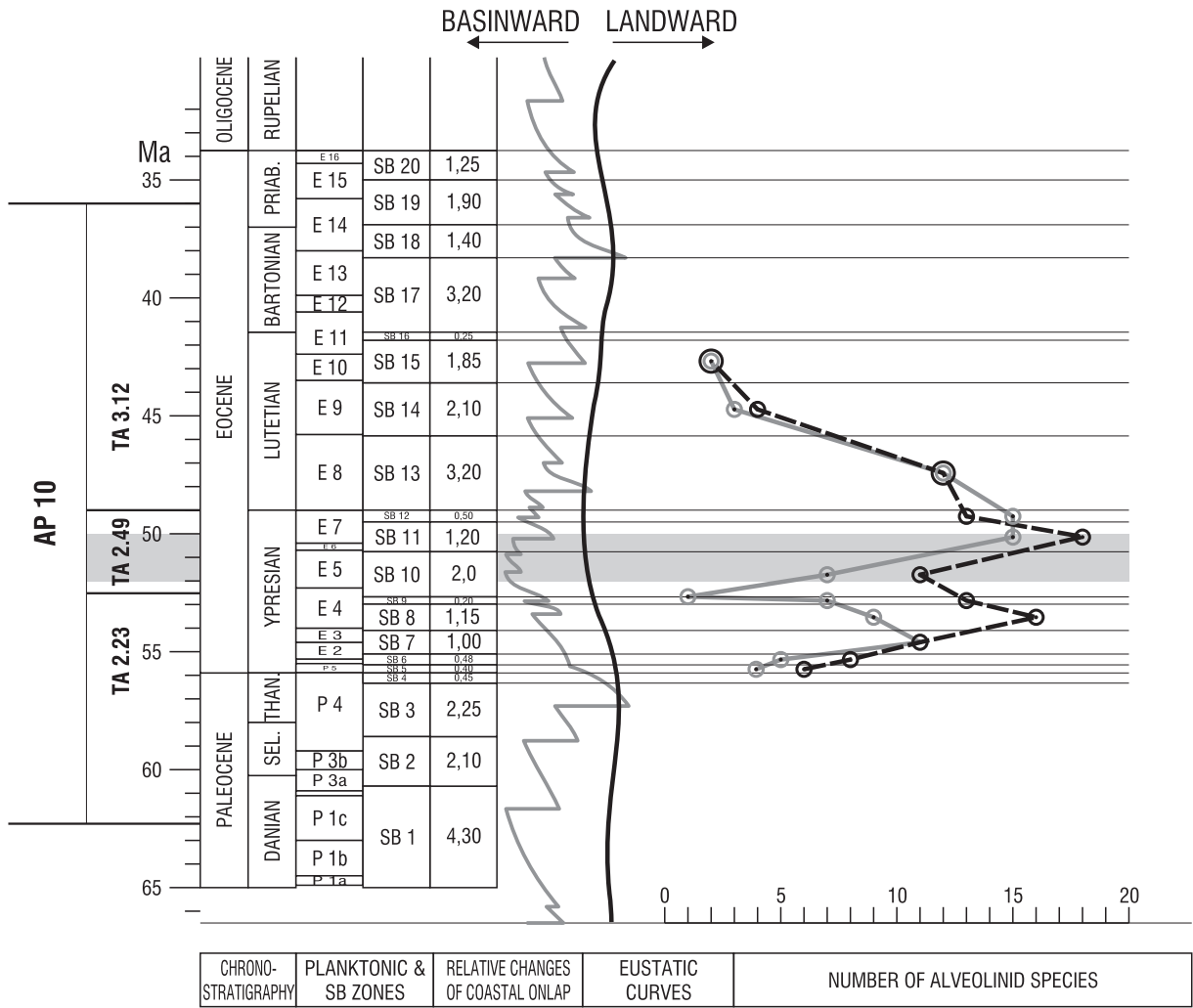


Figure 7. Species diversity of alveolinids within the Palaeogene Adriatic carbonate platform (dotted line= northern sub-region, full-line= southern sub-region; after Drobne 1977; Hottinger & Drobne 1980, 1988), and stratigraphic range. SBZ–Shallow Benthic Zones of Serra-Kiel *et al.* 1998, Pc/E boundary of Luterbacher *et al.* 2004. Eustatic curve (and AP and TA cycles) after Haq *et al.* 1987; Haq & Al-Qahtani 2005. The EECO period is in grey.

Hottinger 1960; Samsó 1988; Samsó *et al.* 1990) have been reported from the sediments collected on the northwestern margin (Table 1). A recent study of alveolinids from Turkey (Sirel & Acar 2008) extends the palaeobiogeographic distribution of these species. The two species *A. pasticillata* Schwager 1883 and *A. subpyrenaica* Leymerie 1846, known from sediments from the Pyrenees to Iran (Table 1, Plate 1), were identified, too. But the most abundant and diversified is an association composed of species, which were recorded in this area for the first time either by Hottinger (1960) or by the senior author:

A. laxa Hottinger 1960, *A. triestina* Hottinger 1960, *A. brassica* Drobne 1977, *A. pisella* Drobne 1977, *A. montanarii* Drobne 1977, and *A. guidonis* Drobne 1977 (Table 1). The largest Ilerdian spherical species, *A. aramaea* Hottinger 1960, *A. daniensis* Drobne 1977, *A. dedolia* Drobne 1977, *A. pisella*, and *A. brassica*, occurred in the eastern (Neo)Tethys (Sirel & Acar 2008). During the late Ilerdian (SBZ 9) areas occupied by alveolinids in the western part of the PgAdCP expanded, while in the east their range diminished. The association is a less diversified grouping of small forms that thrived on the shallow-

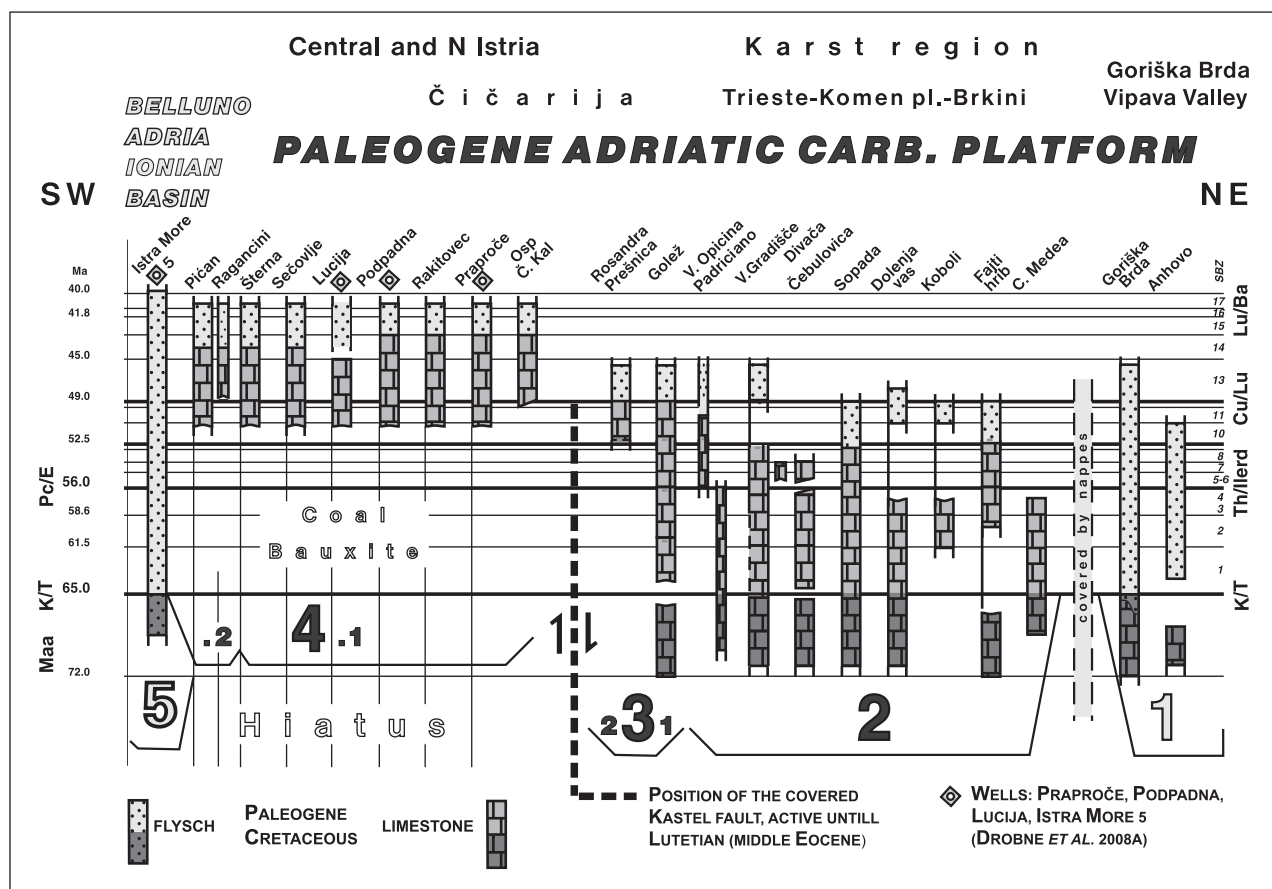


Figure 8. Model of successive biosedimentary zones (BiosZ1–BiosZ4) from the Late Cretaceous/Palaeocene boundary to late Middle Eocene on the Palaeogene Adriatic carbonate platform (Drobne 2003; Drobne *et al.* 2009). Biosedimentary zones BioZ 2, BioZ 3.1 and BioZ 3.2 characterize the northern sub-region, while BioZ 4 is restricted to the southern sub-region.

water platforms from the Pyrenees to Turkey (*A. citrea* Drobne 1977) or from the Pg ADCP and Turkey (*A. guidonis*, *A. montanarii*).

At the beginning of the Cuisian (SBZ 10, BioZ 3.1), a narrow land corridor emerged and split the northwestern margin of the platform into two settings (Figures 3 & 8). On the south-eastern margin the reduction of shallow water settings continued. Cosmopolitan, cylindrical medium-sized morphologies (Table 2) dominated (*Alveolina oblonga* d’Orbigny 1826, *A. schwageri* Checchia-Rispoli 1905 and *A. canavarii* Checchia-Rispoli 1905). The small, flosculine, ovoid *A. cosigena* Drobne 1977 is geographically restricted to the PgAdCP.

In the middle Cuisian (SBZ 11, BioZ 3.1 and BioZ 3.2), shallow water conditions were widespread (Figure 4), permitting the development of the most diverse alveolinid association. The cosmopolitan

species, *Alveolina distefanoi* Checchia-Rispoli 1905 and *A. ruetimeyeri* Hottinger 1960 thrived (Table 2). At the same time, one western Tethys species reached the NW margin of the platform (*A. coudurensis* Hottinger 1960, Boljunsko polje section; Drobne 1977). The most diverse assemblage was that of the eastern Tethys, with *A. cremae* Checchia-Rispoli 1905, *A. decastrói* Scotto di Carlo 1966, *A. dainellii* Hottinger 1960, *A. lehneri* Hottinger 1960, *A. pinguis* Hottinger 1960, *A. rugosa* Hottinger 1960 and *A. minuta* Checchia-Rispoli 1907, making up a significant portion of the shallow water biota in the Kras region (Drobne 1977). Representatives of the Adriatic fauna were separated into two regions: members of the *A. histrica* lineage occupied shallow sea floors in the northern areas (BioZ 3.1 and BioZ 3.2), while species of the *A. levantina* lineage were restricted to the southern part of the platform (BioZ 4; Figures 4

& 8, Table 2). Sediments from the northern region contain the following species: *A. histrica* Drobne 1977, *A. septentrionalis* Drobne 1977, *A. lehneri*, *A. cosigena* Drobne 1977, *A. colatiensis* Drobne 1977 and *A. dainellii*. These species are characterized by ovoidal to subcylindrical outer test morphology. Flosculinization is recorded in *A. dainellii* and *A. cosigena*. Species found in sediments deposited in shelf settings to the south are: *A. levantina* Hottinger 1960, *A. multicanalifera* Drobne 1977 and *A. boljunensis* Drobne 1977 (not cited among the species in Tables 1–3). Tests are elongated and cylindrical (fusiform) and specimens of *A. levantina* have been found further east (Greece, Turkey, Lebanon, Palestine and Somalia) and west (Northern Spain).

The studied sections of the Upper Cuisian (SBZ 12) record the differentiation into two alveolinid assemblages. To the north, Adriatic large, elongated species of the *Alveolina histrica* lineage (*A. rakoveci* Drobne 1977) occurred with *A. azzarolii* Drobne 1977, *A. cuspidata* Drobne 1977 and with the Eastern Tethyan species *A. pinguis* Hottinger 1960. In contrast, representatives of the *A. levantina* lineage dominated in many shallow water settings to the south (Drobne 1977; Pavlovec *et al.* 1991), where they shared habitats with flosculinized *A. flosculina* (Silvestri 1938) (not cited among the species in Tables 1–3; Drobne 1977; Pavlovec *et al.* 1991; Ibrahimpašić 2004). The northern region is characterized by a less diverse alveolinid assemblage in terms of species number and test morphology. Interestingly, the common occurrence of *A. violae* Checchia-Rispoli 1905 (Drobne & Bačar 2003) is recorded in clastic deposits (Flysch). By the late Cuisian, species of the *A. histrica* lineage spread over the PgAdCP, and reached the southeastern shallow-water sub-region (BioZ 3.1 and BioZ 3.2; Krk Island, Lika and E Herzegovina), but become less abundant.

Numerous successions of the Lutetian (SBZ 13–SBZ 16) shallow-water carbonates from Istria to South Dalmatia and W Herzegovina (Pavlovec *et al.* 1986) suggest that over a vast area suitable settings existed for alveolinids (Figures 5 & 8, Table 3). The alveolinid association is composed of a very diverse assemblage of Tethyan species such as *Alveolina boscii* (Defrance, *in* Bronn 1825), *A. frumentiformis* Schwager 1883, *A. tenuis* Hottinger 1960, *A. callosa*

Hottinger 1960, *A. stipes* Hottinger 1960, *A. munieri* Hottinger 1960, Eastern Tethyan species (*A. gigantea* Checchia-Rispoli 1907, *A. obtusa* Montanari 1964a, *A. elliptica nuttalli* Davies 1940 and *A. stercusmuris* Mayer-Eymar 1886), and the ‘Adriatic’ species *A. hottingeri* Drobne 1977, *A. croatica* Drobne 1977, and *A. ospiensis* Drobne 1977. The first two ‘Adriatic’ species have also been found recently in S Italy (Vecchio *et al.* 2007).

The occurrences of *Alveolina fusiformis* Sowerby 1850 indicates a Bartonian (SBZ 17) age for the shallow water sediments found on three geographically isolated sectors (Figure 6) that were left after reduction of platform environments due to uplift of the Dinarides.

Parameters Controlling Alveolinids Distribution

Geographic Distribution of Alveolinids on the PgAdCP

The distribution model of alveolinid associations depicts the Palaeogene Adriatic carbonate Platform evolution. The Thanetian (58 Ma) – Bartonian (37 Ma) time interval corresponds to four platform stages, according to the presence and dominance of different alveolinid species and various test morphologies. The beginning of these four stages coincided with four biosedimentary zones (BioZ 2, BioZ 3.1, BioZ 3.2 and BioZ 4; Figure 8). During the middle Cuisian (SBZ 11), two independent platforms developed simultaneously in the northern (BioZ 3.2) and southern (BioZ 4) areas of the PgAdCP, yielding development of different alveolinid associations. As sea-level rose, the entire area remained in comparatively shallow waters as proved by the occurrences of alveolinids.

The onset of the first platform stage coincides with the most prominent Palaeocene eustatic sea-level fall (58.9 Ma, Hardenbol *et al.* 1998; Figures 7 & 8) and ends very close to the SBZ 3/SBZ 4 boundary. This platform stage (BioZ 2) is characterized by the presence of dasycladales and corals (Barattolo 1998; Turnšek & Drobne 1998; Zamagni *et al.* 2009) that thrived on the margin, while in the inner parts of the shallow-water area charophytes, miliolids (including *Glomalveolina*), rotaliids and cyanobacteria were common (Ogorelec *et al.* 2001; Zamagni *et al.* 2009).

The platform stage II is restricted to the Ilerdian (SBZ 5–SBZ 9, BioZ 3.1; Figure 8) and is characterized by the first occurrence of the alveolinid shoals. The distribution of Ilerdian sediments allows us to reconstruct the position and size of shallow water platform settings, while their facies differences indicate the diversification of environmental conditions (Figure 2). The radiation and proliferation of alveolinids coincided with SBZ 6 and SBZ 7. During this stage alveolinid adaptation to different energy, substrate and palaeobathymetry resulted in a taxonomic radiation: 25 species of varying test morphology can be identified (Table 1), from spherical (7 species), flosculine (8 species), ovoid (8 species) to elongate subcylindrical forms (2 species). The latter morphology, with high values of diameter/thickness ratio, dominated and is interpreted as related to adaptations for avoiding excessive solar radiation.

In the platform stage III (alveolinid-dominated platform, Figures 3, 4 & 8), during the Cuisian (SBZ 10–SBZ 12) the area was covered with shallow water (BioZ 3.1). The transgression in the middle Cuisian progressed in two directions: from the northwest towards the southern margin (BioZ 3.2), and from the south (Ionian-Adriatic-Belluno basin) to the northeast (BioZ 4; Figure 8). The studied sections indicate that the beginning of the marine regime was diachronous, and facies analysis reveals differentiations between shallow water environments. During this platform stage (i.e. in the middle Cuisian), the platform conditions changed. The emergent areas on the northern and southern margins and marine troughs affected the composition of alveolinid assemblages in different ways: availability of suitable settings, changes in trophic regime due to possible weathering, and their role as filters or barriers for foraminiferal migrations. This stage is characterized by the most diverse alveolinid assemblage in terms of species richness (30 species) and test morphology (cylindrical= 6 species, subcylindrical= 8 species, ovoidal= 10 species, spherical= 1 species and fusiform= 5 species), including one flosculine species (Table 2). Separation into two lineages – provinces was caused by the physical barrier, but differences in ecological gradient also played an important role.

The fourth stage (Lutetian to Bartonian, SBZ 13–SBZ 17; Figure 8) is characterized by the further

reduction of the shallow water alveolinid-suitable settings, and consequently diminished species richness (from 14 species during the Lutetian to 1 species in the Bartonian) and limited variety in test morphology (Plate 3, Table 3), from cylindrical (5 species) and subcylindrical (3 species), to ovoidal (4 species) and fusiform (2 species).

The species richness of alveolinids and their suitable settings during the existence of the PgAdCP (69 described species) correlate well, because of the basic assumption that a larger geographic area implies more species and the reverse (Figure 7).

Alveolinids in the PgAdCP and the Role of the PgAdCP in Their Spatial Distribution

Alveolinids, which are K-strategists, require long-term environmental stability. Interruption of stable oligotrophic conditions may cause the disappearance of K-strategists (Hottinger 1983). The Palaeocene–Eocene Thermal Maximum represents such an interruption of stable conditions, but a comparison of the biota before and after (at a limited number of locations) shows minor breaks in the larger benthic foraminiferal (alveolinid) community on the PgAdCP. The EECO, with an overall temperature rise, favoured stable oligotrophic conditions over a vast region, and alveolinids proliferated.

At the same time, alveolinid associations, like other Palaeogene larger foraminiferal associations, changed their composition in accordance with the Global Community Maturation (GCM) cycle (Hottinger 1998, 2001). According to this model, the ecological community matures during intervals of unchanged environmental conditions, while changes affect or disrupt its development. The earliest PgAdCP alveolinids correspond to Phase 2 of the Palaeocene–Eocene GCM (Hottinger 1998, 2001), the appearance of new morphologies and a further increase of genetic diversity. Recolonization of vacant shallow water settings proceeded in the early Ilerdian (SBZ 5 and SBZ 6, BioZ 2 and BioZ 3.1), within the phase 3 of GCM, giving opportunity for species diversification. The beginning of this phase coincides with the PETM, and it marks just a minor change in the overall Palaeogene larger foraminiferal community. The studied alveolinids match phase 4 of

the GMC (SBZ 7 to SBZ 12 and SBZ 11 to SBZ 14/15; BioZ 3.1, BioZ 3.2 and BioZ 4) very well. Alveolinids show size increase, the highest species diversification, and great spatial distribution by colonization of vacant niches due to mainly eastward (Levant) migrations and settlement of species. Within this phase the EECO took place, and rising sea-surface temperature supported the overall oligotrophic conditions and the greatest diversification of alveolinids in the studied region (Figures 7 & 8). This event can be interpreted as the period in which environmental conditions changed considerably. The cycle ended in the late Middle Eocene (late Lutetian to early Bartonian, SBZ 15 and SBZ 16 with phase 5), characterized by a decrease in species diversity.

According to their geographic preferences, alveolinids can be described as Adriatic, East Tethyan, West Tethyan, or cosmopolitan Tethyan species (Plates 1–3, Tables 1–3).

Altogether 25 alveolinid species were identified from the early Ypresian sediments (from early to late Ilerdian; Plate 1). Among them, one species (*A. triestina*) is confined to the Adriatic region and can be considered as an endemic Adriatic species, and sixteen species are known from the Tethys, which we described as cosmopolitan species (*A. ellipsoidalis*, *A. moussoulensis*, *A. vredenburgi*, *A. solida*, *A. globosa*, *A. avellana*, *A. pisiformis*, *A. pasticillata*, *A. leupoldi*, *A. parva*, *A. aragonensis*, *A. fornasinii*, *A. subpyrenaica*, *A. laxa*, *A. citrea*, *A. decipiens*). Due to their occurrence in Turkey (Sirel & Acar 2008), seven species, *A. aramea*, *A. daniensis*, *A. brassica*, *A. montanarii*, *A. pisella*, *A. dedolia* and *A. guidonis* are considered to be East Tethyan (Table 1). The larger number of eastern migrated – Tethyan species in shallow water environments of the PgAdCP suggests open migration routes across the area from east to west. The East Tethyan species migrated to the Kras region (NW margin of the platform) and settled there, while only one Western Tethyan species (*A. cylindrata*) reached the same area. It seems that during the Ilerdian the Kras region was an open corridor that allowed East Tethyan species to migrate further west and vice versa (sixteen cosmopolitan species are present in the area). The trench and basin that surrounded the PgAdCP both north and south of the Kras region did not prevent the further

dispersal of alveolinids towards the western region. If test morphologies are compared, those with ovoidal tests were West-Tethyan and Adriatic species, while East-Tethyan ones were subcylindrical and spherical, and cosmopolitan taxa show greater variability (from ovoid to subcylindrical).

The palaeobiogeographic affinity of the Late Ypresian (Cuisian) species is more complex. 30 species were found (Table 2), four within the early Cuisian, eleven in the middle Cuisian (of which four were present in both the early and middle Cuisian), nine species were limited to the late Cuisian and three to the middle and late Cuisian. The early Cuisian *A. oblonga*, *A. canavarii* and *A. schwageri* were cosmopolitan species and *A. cosinensis* occurred in sediments from the PgAdCP and in northern Spain (Table 2). In the middle Cuisian, the Adriatic shallow water environment split into sub-regions, each region with its specific composition of species. The border between the two sub-regions generally matches the position of a narrow shallow sea (Figures 5 & 8) which remained after reorganization of the region following the regression (Haq *et al.* 1987; Haq & Al-Qahtani 2005) and probably different rates of subsidence. The same trend in species diversity (Figure 7) of alveolinid assemblages from both sub-regions (BioZ 3.1, BioZ 3.2 and BioZ 4; Figure 8) suggests that the same abiotic (temperature and type of sea-bottom) and biotic (intraspecies and interspecies relationships) factors operated.

The emergent area was a physical barrier that allowed the development of assemblages with Adriatic and East-Tethys dominant lineages on either side of the land (Figure 5). The palaeogeographic affinities of the recorded species reveal that eight species were cosmopolitan (*A. oblonga*, *A. canavarii*, *A. distefanoi*, *A. decastroi*, *A. schwageri*, *A. ruetimeyeri*, *A. coudurensis* and *A. cosinensi*). Eight species (*A. septentrionalis*, *A. carantana*, *A. minuta*, *A. azzarolii*, *A. cremae*, *A. dainielli*, *A. rugosa*, *A. pinguis*) are found also in the eastern part of Tethys (Turkey, Greece and further east). Endemism on the PgAdCP reached its maximum with ten species. Alveolinids of the *A. histrica* lineage: *A. histrica*, and *A. rakoveci*, considered as ‘Adriatic’ species, were found in sediments deposited on the northwestern margin in the middle and late Cuisian (Rosandra,

Golež, Voz), in Lika (Bunić, Drobne & Trutin 1997) and also on the SE margin (E Herzegovina, Stolac-Hrgud, Drobne *et al.* 2000). Interestingly, during the late Cuisian, populations of the *A. histrica* lineage thrived, became larger, more abundant and diverse and widely distributed (Plate 2). Their appearance in the northern sub-region (BioZ 3.1, BioZ 3.2) coincided with the end of the warmest period within the Eocene and with regional regression. The representatives of the *A. levantina* lineage were confined to the southern sub-region, from Istria to southern Dalmatia and W Herzegovina during the middle and late Cuisian and the Lutetian (BioZ 4; Figure 8).

The overall palaeogeographic distribution of alveolinids changed considerably during the Lutetian. Clear, shallow water and a warm climate promoted the growth of larger benthic foraminifera. Eventually, some lineages of larger benthic foraminifera (alveolinids of the *A. levantina* lineage) outcompeted the other alveolinids, and by the beginning of the Lutetian, a reduction in alveolinid abundance and species diversity took place (Plate 3). Species diversity decreased considerably, as just 14 species were found, one of them Adriatic (*A. ospiensis*), two (*A. callosa* and *A. munieri*) found in the Pyrenean region, and four had a wide Tethyan distribution (*A. boscii*, *A. tenuis*, *A. frumentiformis* and *A. stipes*). Those that occurred in the region and are also known from Italy and PgAdCP to Turkey are *A. gigantea*, *A. obtusa*, *A. hottingeri*, *A. croatica*, *A. elliptica nuttalli*, and *A. stercusmuris* (Plate 3). Due to an overall transgression, the entire platform was flooded, and shallow water settings inhabited by elongated alveolinids (subcylindrical to cylindrical morphologies) dominate, while spherical *A. palermitana* Hottinger 1960 (not included in the list of identified species of Table 3) occurred sporadically. The low immigration rate was characteristic for this period; two species migrated westward, compared with six spreading eastward.

We found that the average test size of members of the *A. histrica* lineage is generally greater than those of the *A. levantina* (from 1.2 to 6 orders of magnitude variation). Because size influences growth rates, respiration, nutrient uptake, and reproduction in foraminifera, we surmise that size played a

significant role in success and persistence of taxa of the *A. levantina* lineage, by allowing species to survive unfavorable fluctuations in environmental conditions. When the decrease in overall temperature after the EECO and changes in spatial distribution of suitable shallow water settings took place, species of the *A. levantina* lineage spread over the entire PgAdCp (BioZ 4; Figures 7 & 8).

The PgAdCP was a suitable environment for alveolinids: up to now 69 species have been identified from sediments of the PgAdCP from the Ilerdian to the Lutetian. The shallow-water area with a favourable circulation pattern during the Ileridan allowed both westward and eastward migration (16 species were common in shallow seas stretching from the Pyrenees to Turkey). In the Cuisian, a reduced number of species passed through this region (eight cosmopolitan species), while during the Lutetian only four species were able to enlarge their spatial distribution to both the west and east.

Conclusion

The correlation of the Palaeogene Adriatic carbonate platform evolution and composition, and the abundance, and diversity of alveolinid assemblages from many localities along the eastern Adriatic coast, from the Kras region in Italy to Montenegro, indicate that:

1. High species diversity in the Ilerdian (25 species) and in the Cuisian (30 species) was due to the diversification of environmental conditions and additionally stimulated by the EECO.
2. The number of cosmopolitan species that populated shallow seas from the Pyrenees to Turkey reduced through time; sixteen in the Ilerdian, eight in the Cuisian and four in the Lutetian.
3. The highest rate of endemism was in the Cuisian (eleven species), in contrast to one endemic species in the Ilerdian and Lutetian.
4. An abrupt change in composition of alveolinid assemblages took place at the Ilerdian/Cuisian boundary, due to the highest species

diversification and recolonization of vacant shallow water settings created as a result of sea-level rise.

5. The splitting of the platform into two lineage-dominated sub-regions started during the middle Cuisian (SBZ 11): the northern one with the *Alveolina histrica* lineage and the southern one with the *Alveolina levantina* lineage. Their separation is attributed to the emergence of a physical barrier and to different ecological conditions from north to south along the Central Tethys shelves.
6. The dominance of the cosmopolitan species of the *A. levantina* lineage in the early Lutetian over the entire Palaeogene Adriatic carbonate platform.
7. The Mediterranean (two peaks) distribution pattern of species abundances of alveolinids: the first peak in the Ilerdian, SBZ 7–8 and the second one in the Cuisian, SBZ 11.
8. The good correlation between global sea-level changes and abundance/diversity trends.

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Plate 1

Axial sections (all in incident light) of Ilerdian key species discussed in this paper. SBZ 5–SBZ 6: *A. ellipsoidalis* Schwager 1883; *A. aramaea* Hottinger 1960; *A. daniensis* Drobne 1977; *A. solida* Hottinger 1960, *A. avellana* Hottinger 1960. SBZ 7 - SBZ 8: *A. moussoulensis* Hottinger 1960; *A. globosa* (Leymerie) 1846; *A. brassica* Drobne 1977; *A. pasticillata* Schwager 1883; *A. aragonensis* Hottinger 1960; *A. pisella* Drobne 1977; *A. laxa* Hottinger 1960. SBZ 9: *A. guidonis* Drobne 1977. Illustrated specimens are from the following sections: Kozina (sample K 6), Veliko Gradišče (samples VGr 8, 10, 21), Dane (samples Da 12/1, 12/2, 16, 20), Golež (sample Go 23), Gradišče (samples Gr 5, 5/2), Jelšane (sample J1 1) and Košana (sample Koš 9), all located in SW Slovenia.

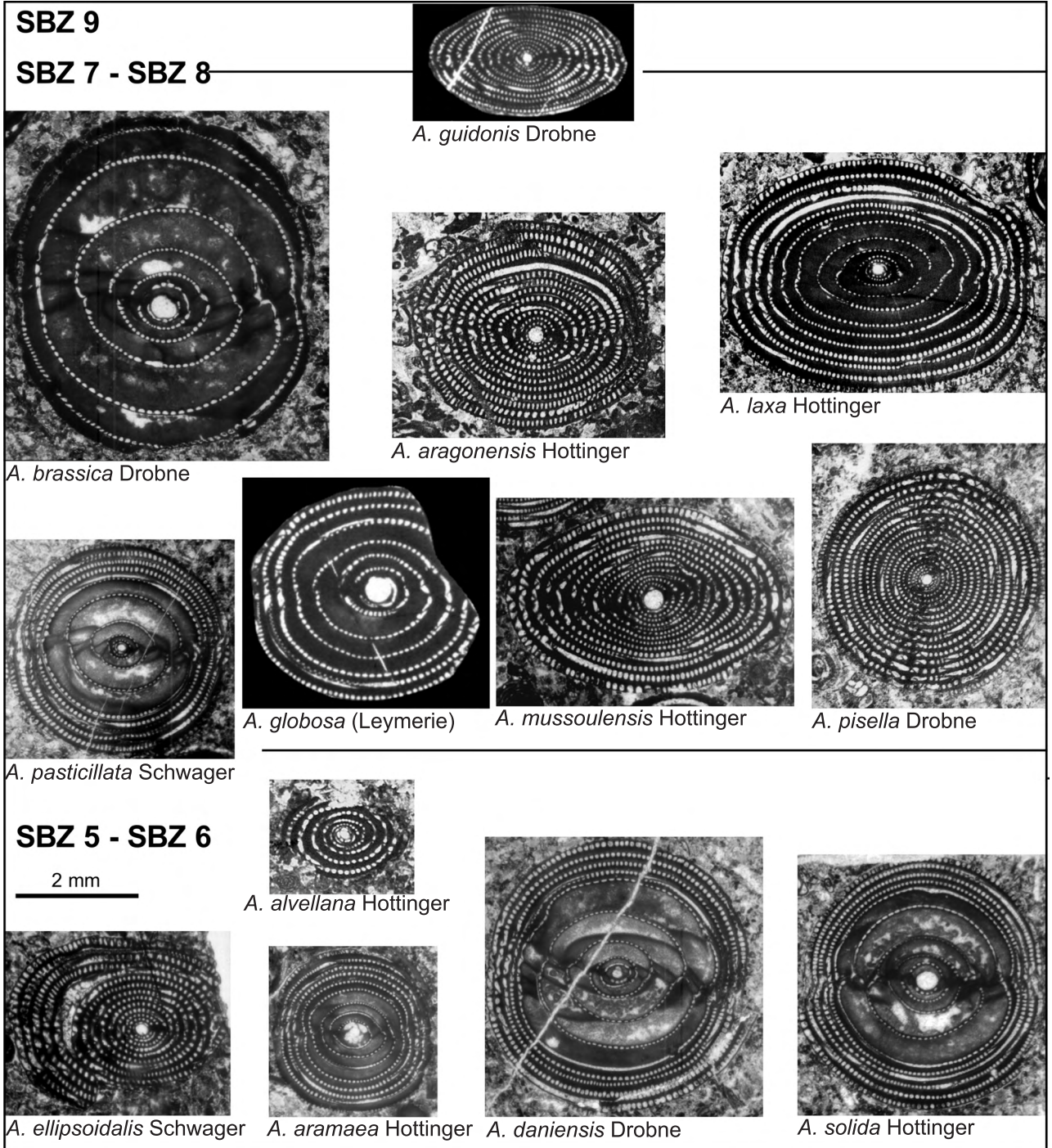


Plate 2

Axial sections (all in incident light) of Cuisian key species discussed in this paper. SBZ 10: *A. canavarii* Checchia-Rispoli 1905; *A. oblonga* d'Orbigny 1826; *A. schwageri* Checchia-Rispoli 1905. SBZ 11: *A. cosigena* Drobne 1977; *A. decastroi* Scotto di Carlo 1966; *A. cremae* Checchia-Rispoli 1905; *A. ruetimeyeri* Hottinger 1960; *A. septentrionalis* Drobne 1977; *A. lehneri* Hottinger 1960. SBZ 12: *A. rakoveci* Drobne 1977; *A. pinguis* Hottinger 1960, *A. cuspidata* Drobne 1977; *A. azzarolii* Drobne 1977. Illustrated specimens are from the following sections: Kozina (samples K 10, 11, 17, 18, 19, 23), Golež (sample Go 97), Slavec (sample Slv 27, 38), Žbevnica (sample Žbv 29), Šterna (sample Štr 23), Močibob - Karojba (sample 507a), Voz (Krk Island; sample Voz 1b), located in SW Slovenia, Istria and Krk Island (Croatia).

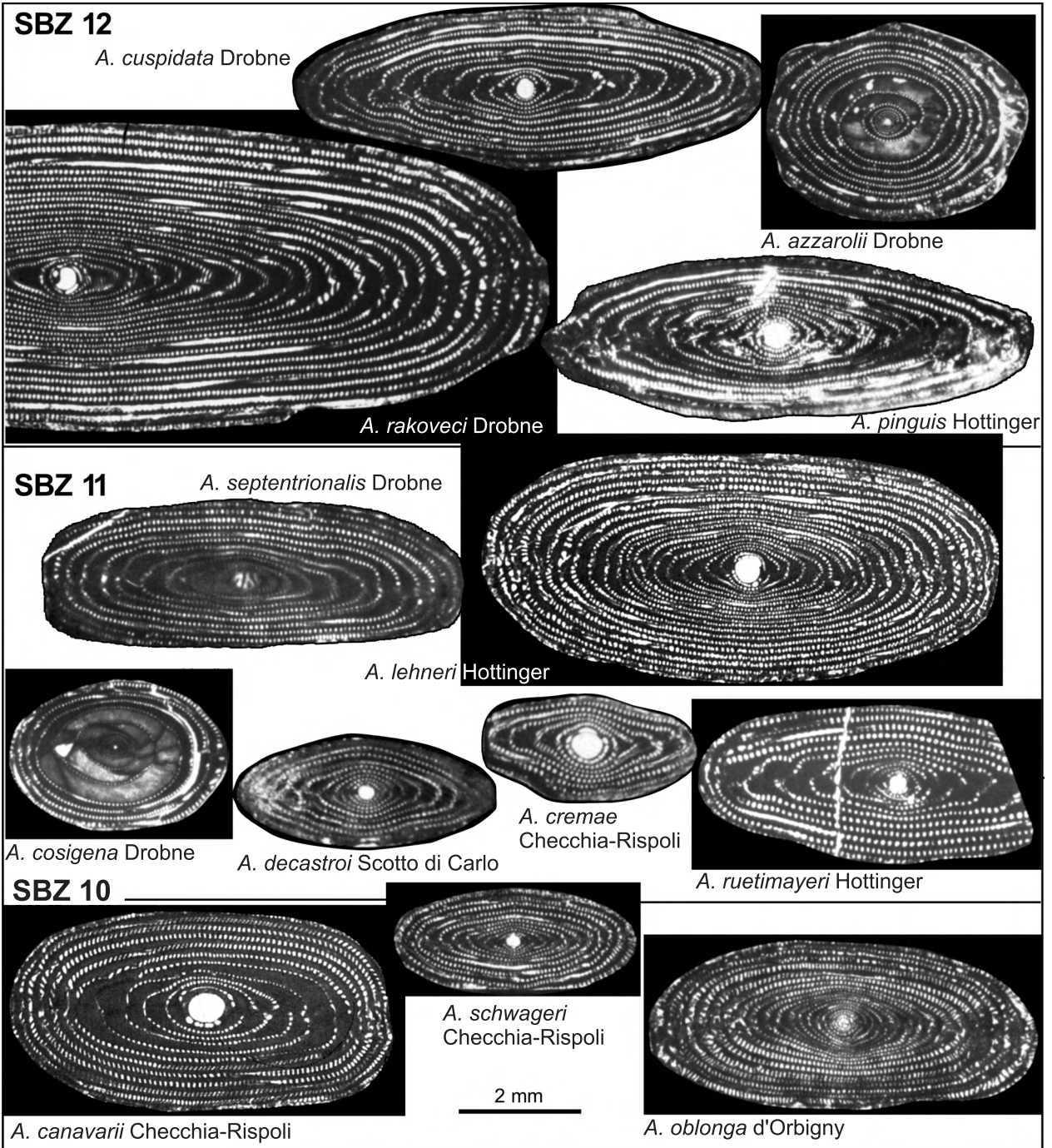
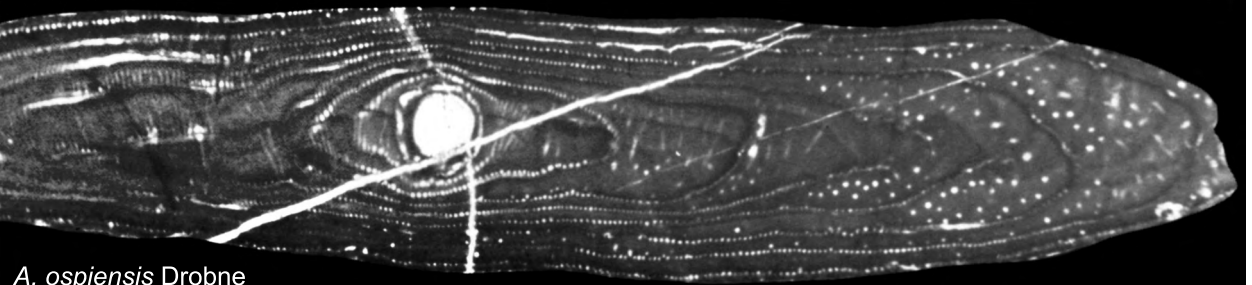


Plate 3

Axial sections (all in incident light) of Lutetian key species discussed in this paper. SBZ 13: *A. stercusmuris* Mayer-Eymar 1886; *A. elliptica nuttalli* Davies 1940; *A. tenuis* Hottinger 1960; *A. levantina* Hottinger 1960; *A. callosa* Hottinger 1960; *A. stipes* Hottinger 1960. SBZ 14: *A. ospiensis* Drobne 1977. Illustrated specimens are from the following sections: Pićan (samples Pć 17, 18, 21), Ragancini – Lišani (sample R-L 8), Boljunsko polje (sample BP 12) and Osp (samples Osp 6, 14), located in Istria (Croatia and Slovenia).

SBZ 14

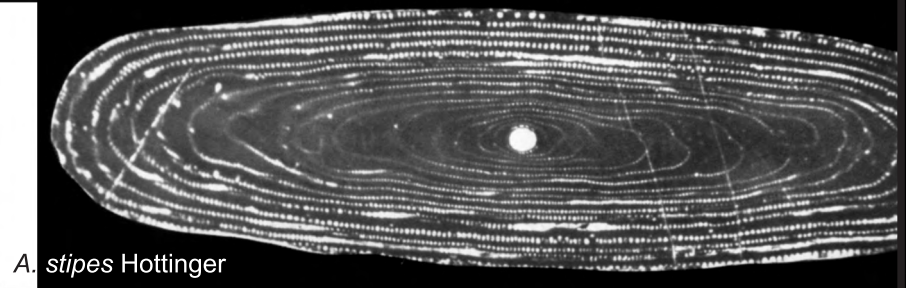


A. ospiensis Drobne

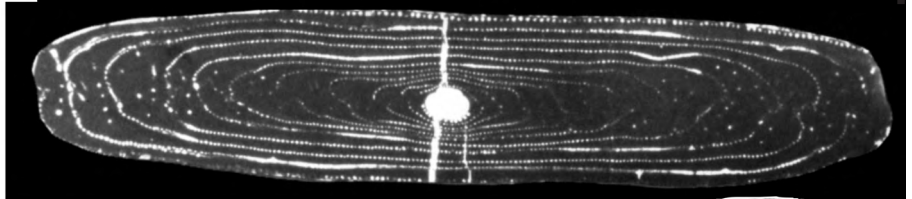
SBZ 13



A. callosa Hottinger, fB



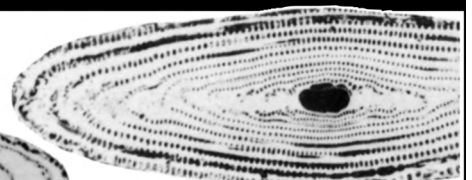
A. stipes Hottinger



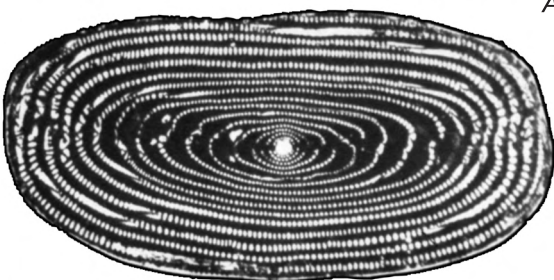
A. callosa Hottinger



A. tenuis Hottinger

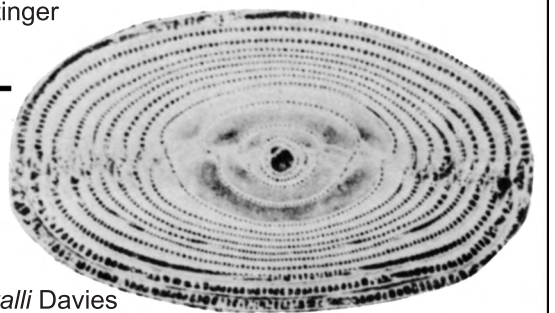


A. levantina Hottinger



A. stercusmuris Mayer Eymar

2 mm



A. elliptica nuttalli Davies