

## Stratigraphic and Palaeoenvironmental Significance of Bartonian–Priabonian (Middle–Late Eocene) Microfossils from the Başçeşme Formation, Denizli Province, Western Anatolia

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**Abstract:** This study explains the stratigraphical and palaeoenvironmental significance of Bartonian–Priabonian (Middle–Late Eocene) fossils, the fauna and flora obtained from the Başçeşme formation of the Çardak–Tokça basin (western Anatolia). The studied sequence is an outcrop from the Başçeşme formation, deposited in a shallow-marine to coastal environment without stratigraphic breaks. Forty genera and 58 species have been recognized in the palynological assemblage of the Başçeşme formation. A well-preserved diverse palynomorph and foraminiferal assemblages yield the Middle–Late Eocene age for the Başçeşme formation. In western Anatolia, mangrove elements *Nypa* and *Pelliciera* have been first recorded in this study. The pollen of *Mauritia* and *Acrostichum* occur in the back-mangrove environment. Lowland–Riparian and montane elements are characterized by dominance of Myricaceae, Betulaceae, *Engelhardia*, Fagaceae, Myrtaceae, Anacardiaceae and Taxodiaceae, *Pinus*, *Abies*, *Picea*, *Cathaya*, *Quercus* and *Castanea*, respectively. Fresh-water elements are represented by Sparganiaceae, *Pediastrum* sp. and *Aglaoreidia cyclops*.

The palynological data for samples taken from the lower part of the section of the Başçeşme formation indicate a back-mangrove environment. The presence of poorly preserved dinoflagellate cysts suggest that sedimentation occurred in a mangrove environment in the upper part of the section. The well-preserved foraminiferal data, along with corals, bivalves and gastropods, indicate that sedimentation ceased in the shallow-marine environment. In this paper, terrestrial climatic conditions of the Başçeşme formation are also discussed on the basis of the coexistence approach.

**Key Words:** Middle–Late Eocene, mangrove, western Anatolia, benthic foraminifer, palynomorph, palaeoenvironment, palaeoclimate

### Denizli Yöresindeki Bartoniyen–Priaboniyen (Orta–Geç Eosen) Mikrofosilleri İçeren Başçeşme Formasyonu'nun Stratigrafik ve Ortamsal Önemi, Batı Anadolu

**Özet:** Bu çalışma, Çardak–Tokça havzasının (Batı Anadolu) Başçeşme formasyonundan elde edilen Bartoniyen–Priaboniyen (Orta–Geç Eosen) yaşlı, fauna ve floranın stratigrafik ve paleoortamsal önemini açıklar. Çalışılan istif, stratigrafik kesiklik olmaksızın, sığ deniz, kıyı ortamında çökelmiş Başçeşme formasyonundan bir yüzlektir. Başçeşme formasyonunun palinolojik topluluğunda 40 cins ve 58 tür tanımlanmıştır. İyi korunmuş çeşitli palinomorf ve foraminifer toplulukları, Başçeşme formasyonunun yaşını Orta–Geç Eosen olarak vermektedir. Batı Anadolu'da, mangrove elementleri olan *Nypa* ve *Pelliciera* ilk kez bu çalışmada kaydedilmiştir. Mangrov gerisindeki ortamda *Mauritia* ve *Acrostichum* polenleri mevcuttur. Alçak alan–Irmak kenarı elemanları, Myricaceae, Betulaceae, *Engelhardia*, Fagaceae, Myrtaceae, Anacardiaceae ve Taxodiaceae, dağ elemanları ise *Pinus*, *Abies*, *Picea*, *Cathaya*, *Quercus* ve *Castanea* ile karakterize edilir. Tatlısu elemanları Sparganiaceae, *Pediastrum* sp. ve *Aglaoreidia cyclops* ile temsil edilir.

Elde edilen palinolojik veriler, Başçeşme formasyonunun alt kesimlerinden alınan örneklerin mangrov gerisi ortamı belirttiğini göstermektedir. İstifin üst kesimlerinde kötü korunmuş dinoflagellatların varlığı tortullaşmanın

mangrove ortamında gerçekleştiğini göstermektedir. Mercan, bivalvia ve gastropodlu iyi korunmuş foraminifer verileri, tortulaşmanın sığ denizel ortamda son bulunduğunu göstermektedir. Bu makalede, 'coexistence approach' yöntemine dayalı, Başçeşme formasyonunun karasal iklimsel koşulları da tartışılmıştır.

**Anahtar Sözcükler:** Orta-Geç Eosen, mangrov, Batı Anadolu, bentik foraminifer, palinomorf, paleoortam, paleoiklim

## Introduction

The Palaeocene–Eocene sedimentary successions of western Anatolia are claimed to have developed on the different tectonostratigraphic units, such as the Lycian Nappes (Poisson 1976; Yalçınkaya *et al.* 1986; Göktaş *et al.* 1989; Özkaya 1991; Şenel 1991, 1997; Collins & Robertson 1997, 1998, 1999; Bozkurt & Park 1999; Sözbilir *et al.* 2001; Sözbilir 2002), the Menderes Massif (e.g., Poisson 1976; Özkaya 1990, 1991; Bozkurt & Park 1994; Özer *et al.* 2001; Koralay *et al.* 2004) and the Bey Dağları carbonate platform (Özkaya 1991; Collins & Robertson 1998; Sarı & Özer 2002) (Figure 1a, b). The non-metamorphosed Palaeocene–Eocene sedimentary successions of western Anatolia generally consist of conglomerate, sandstone, turbiditic sandstone–mudstone alternations, bioclastic limestone lenses, blocks of limestones and volcanic rocks, and these have been interpreted to be of the supra-allochthonous basin type, and to have developed over the Lycian Nappe package (Sözbilir 2002). Limited coal-bearing Eocene outcrops have been observed in western Anatolia. The coal-bearing Eocene sediments of the Çardak-Tokça basin, which stratigraphically overlie the Lycian Nappes, are exposed 35 km east of Denizli (Figure 1a, b).

Micropalaeontological and stratigraphical studies on the Eocene formations of the Çardak-Tokça basin have been either neglected or carried out by Mineral Research of Exploration Institute (M.T.A.). The unpublished report of Göktaş *et al.* (1989) was the first comprehensive stratigraphic and palaeontological study of the Tertiary sediments of the Çardak-Tokça basin. The Başçeşme formation was formerly subdivided into four members (from bottom to top), the Dazlak, Beşparmak reef, Maden and Asar members. That study reported that the age of the Başçeşme formation is Late Eocene (Priabonian) on the basis of unillustrated benthic foraminifers, mollusks and corals. Şahbaz & Görmüş (1992) examined the stratigraphic and sedimentological properties of the conglomerates that crop out as the Çardak-Tokça basin fill and recognized three different

types of conglomerates, these belonging to the Eocene, Lower Oligocene and Oligocene, respectively. Şenel (1997) collected the findings of Göktaş *et al.* (1989) and reinterpreted the age of the Başçeşme formation as Late Lutetian–Priabonian. Sözbilir *et al.* (2001) studied the stratigraphic and tectonic properties of the Eocene in the Baklan succession, located 10 km from the study area, (Figure 1b) and reported a well-preserved marine fauna which yields a Bartonian (Middle Eocene) age.

This study focuses on the Başçeşme formation, composed of both marine and coal-bearing lacustrine sediments. The objective of this paper is to provide for the first time palynological and foraminiferal evidence from the Maden and the Asar members of the Başçeşme formation, to obtain precise ages, to ascertain depositional environments, to begin to understand qualitative palaeoclimatic conditions for these units, and also to analyze the similarities to and differences from correlative Eocene basins in Turkey.

## Stratigraphy

In the area, pre-Eocene basement consists of the Triassic–Lower Eocene Lycian Nappes and generally comprises metaconglomerate, metasandstone, recrystallized limestone, metavolcanites, dolomite, dolomitic limestones, and ophiolitic-rock matrix and blocks (Göktaş *et al.* 1989). The Başçeşme formation unconformably overlies the Lycian Nappes and is made up of four different members which are terrestrial and shallow marine in character; these are (from bottom to top) the Dazlak, Beşparmak reef, Maden and Asar members (Göktaş *et al.* 1989; Şenel 1997) (Figures 1b & 2). In the study area, the Dazlak, Maden and Asar members occur the sequence (Figure 2). Here, their lithological properties are described briefly, in ascending order.

The Dazlak member, which is barren of microfossils, generally comprises a reddish conglomerate and sandstone alternation of transgressive character. The

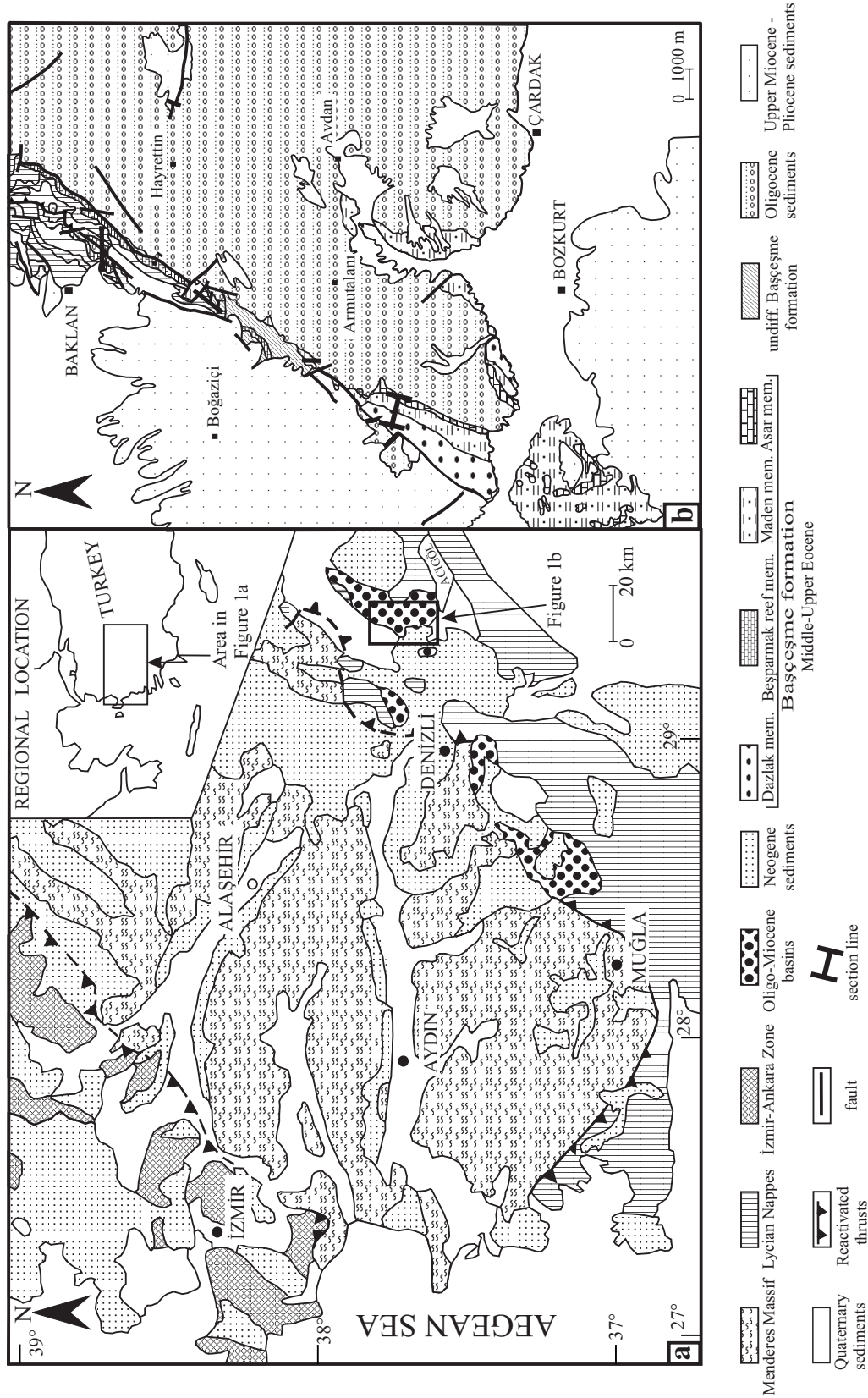


Figure 1. (a) Simplified geological map of western Anatolia (Şengör & Yılmaz 1981; Şengör et al. 1985; Konak et al. 1987; Seyitoğlu & Scott 1996). (b) Geological map of the Çardak-Tokça basin (modified from Cöktaş et al. 1989).

MIDDLE-LATE EOCENE MICROFOSSILS FROM DENİZLİ AREA

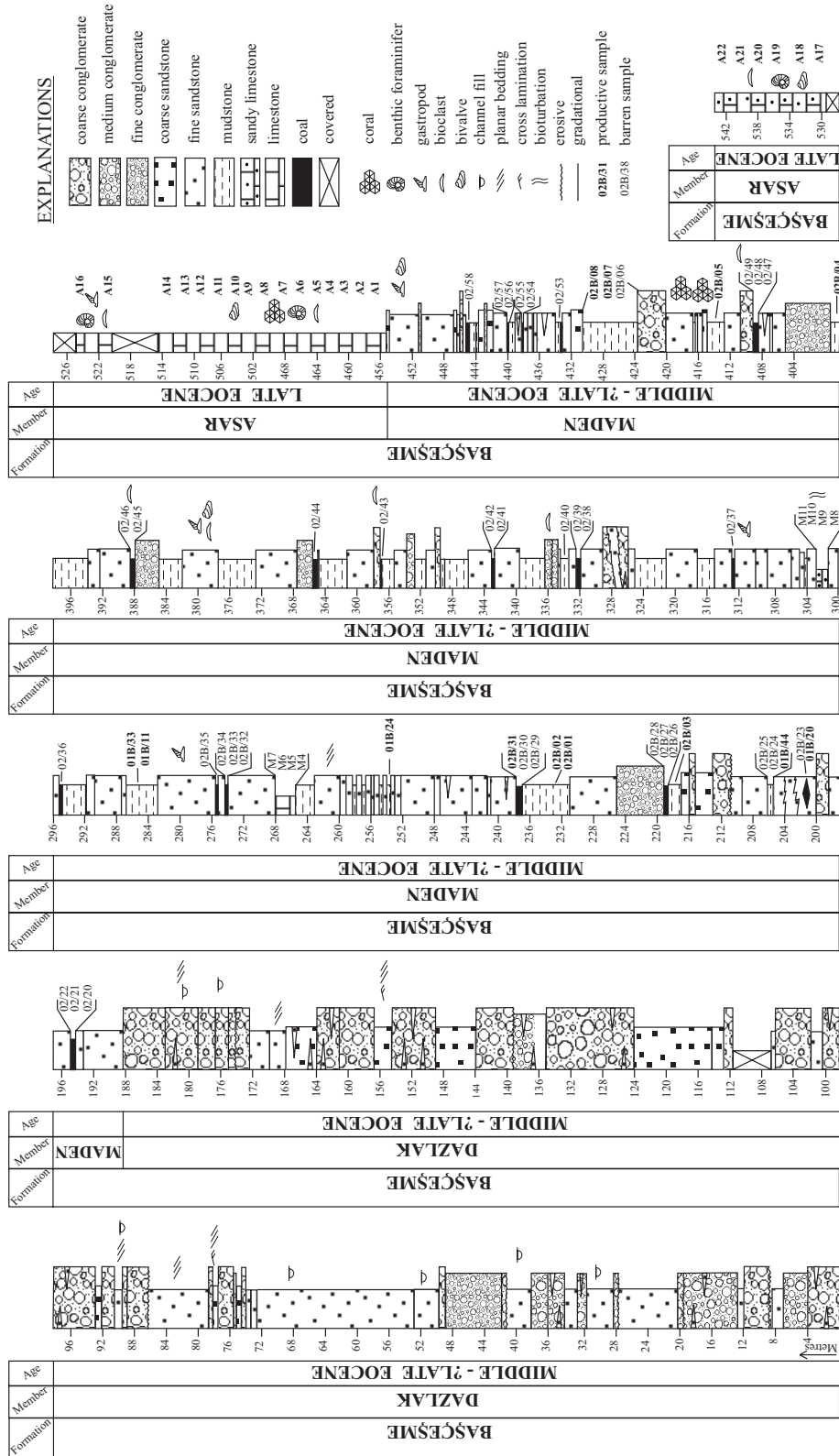


Figure 2. Detailed measured stratigraphic section from the Başçeşme formation. See Figure 1 for the location of the section.

conglomerates are coarse-grained and poorly sorted. Channel fills occur at some levels in the sandstones (Figure 2). The Dazlak member was interpreted as alluvial-fan deposits by Şahbaz & Görmüş (1992).

The Maden member, transitional with the underlying Dazlak member, generally consists of yellowish sandstone and mudstone alternations and includes conglomerate and reefal limestone lenses (Figure 2). The Maden member, deposited in intertidal environment, also contains coal seams and lenses. Moreover, shallow-marine macrofossils – such as gastropods and bivalves – are abundant in the sandstones (Figure 2).

The last member of the Eocene transgressive sequence is the Asar member, which generally comprises cream-coloured reefal limestones (Figures 1b & 2). In some places, the member includes conglomerate, sandstone, sandy limestone and mudstone (Figure 2). It has abundant macrofossils and microfossils, such as coral, benthic foraminifers, gastropods and bivalves. It was deposited in an intertidal environment, including an ecologic reef complex (Göktaş *et al.* 1989). Lower–“Middle” Oligocene formations unconformably overlie the Asar member in the study area (Göktaş *et al.* 1989; Şenel 1997; Şahbaz & Görmüş 1992; Sözbilir 2002; Akkiraz & Akgün 2005). All of these units are overlain by Miocene to Quaternary continental deposits (Koçyiğit 2005; Westaway *et al.* 2005; Sözbilir 2005).

## Materials and Methods

A detailed stratigraphic section was measured in the Başçeşme formation; it contained the Dazlak, Maden and Asar members (Figures 1b & 2). A total of 49 clay, carbonaceous clay and lignite samples were collected from the Maden member, the only suitable lithology with respect to palynological study (Figure 2). Thirty samples were also taken from the section for foraminiferal investigation, from both the Maden and Asar members (Figure 2). Ten grams of each sample were treated with HCL, HF and HNO<sub>3</sub> for palynological preparation. The organic residue was screened through an 8 µm mesh screen and 2 and 6 slides per sample of the >8 µm fraction were prepared for transmitted light microscopy. Pollen counts were carried out at 400X using an Olympus microscope. Palynological counts range between 94 and 253 grains/specimen (Table 1). To reconstruct the palaeoenvironment of the Başçeşme formation in western

Anatolia, statistical analyses were done using the PAST programme developed by Ryan *et al.* (1995). Non-metric multidimensional scaling (MDS), using the Hamming distance and Raup-Crick index of unweighted pair-group average (UPGMA) cluster analysis have been applied (Figures 3 & 4). Thin sections were prepared in order to analyze the foraminifers.

In addition, the palynoflora has also been analyzed quantitatively using the coexistence approach proposed by Mosbrugger & Utescher (1997) for climatic analysis. The aim of the coexistence approach is to find the intervals of various climate parameters for a given fossil flora in which a maximal number of nearest living relatives (NLR) of this flora may coexist. These coexistence intervals are considered the best description of the palaeoclimatic situation under which the fossil flora lived. The application of the coexistence approach is facilitated by use of a computer programme, ClimStat, and the Palaeoflora database. Here, mean annual temperature (MAT) was calculated using this method.

## Palynological Data

In this section, the age of the palynological assemblage of the Maden member is discussed. There is no fossil record in the Dazlak member because of its coarse-grained, clastic nature. All palynological outcrop samples were obtained from the Maden member (Figure 2). Thirteen of 49 samples investigated for their pollen content contain spores and gymnosperm and angiosperm pollen grains, which are fairly well preserved. The flora is characterized by 58 taxa and is here recorded (Table 1). The angiosperm pollen count is always higher in than spores and gymnosperms. In addition, *Pediastrum* spp. and poorly preserved dinoflagellate cysts were also observed.

Statistical analyses yield a long list of stratigraphically unimportant, long-ranging taxa, but with a few index taxa, for which stratigraphic ranges are given in Table 2. In addition, selected palynomorphs recorded in this study are also illustrated in Plates I–III.

Some of the characteristic Early Eocene taxa of Normapolles, such as *Basapollis*, *Interpollis* and *Urkutipollenites*, are poorly represented in the Lower Eocene and do not occur in the Middle Eocene at Hungarian localities (Kedves 1986). These pollen have never been recorded in the samples of the Maden member. The stratigraphic distributions of

Table 1. Counting results (quantitative) of palynomorphs encountered in the Başçeşme formation of the Çardak-Tokça basin.

SAMPLES	MADEN MEMBER												
	01B/20	01B/44	02B/03	02B/01	02B/02	02B/31	01B/24	01B/11	01B/33	02B/04	02B/05	02B/07	02B/08
TAXA													
SPORES													
<i>Retriletes</i> sp.													
<i>Leiotriletes adriennis</i>			2		1	1		1		3			
<i>Leiotriletes minor</i>	6	2								1			5
<i>Leiotriletes wolffii</i>			1		1					2			
<i>Leiotriletes microadriennis</i>		1				1				19			
<i>Leiotriletes</i> sp.	2		3	9	29	2			1	36	7	34	1
<i>Triplanosporites microsinuosus</i>			1										
<i>Baculatisporis ovalis</i>			1										
<i>Baculatisporites nanus</i>			4										
<i>Baculatisporis</i> sp.													
<i>Cicatricosporites</i> sp.		1			1				1	3			
<i>Polypodiaceoisporites microconcaus</i>						1							
<i>Polypodiaceoisporites kedvesii</i>						1							
<i>Polypodiaceoisporites muricunguliformis</i>	2							2		2			2
<i>Polypodiaceoisporites</i> sp.	1					2	3	2		2	1		1
<i>Echinatisporis</i> sp.			1										
<i>Laevigatosporites haardti</i>	2		5		1				2	1			1
GYMNOSPERMOUS													
<i>Abiespollenites</i> cf. <i>absolutus</i>			10										
<i>Abiespollenites</i> sp.					1								
<i>Pitysoporites microalatus</i>			47	2	27					9			1
<i>Pitysoporites labdacus</i>			2			3							
<i>Pitysoporites</i> sp.			51	1	40	2		1	1	23	3	1	1
<i>Piceapollenites</i> sp.			1										
<i>Cathayapollis pulaiensis</i>			1							1			
<i>Cathayapollis</i> sp.													
<i>Inaperturopollenites dubius</i>										12			
<i>Inaperturopollenites concaedipites</i>					1								
<i>Inaperturopollenites magnus</i>					1						1		
<i>Inaperturopollenites</i> sp.			7		2					2			
ANGIOSPERMOUS													
MONOCOTYLEDONEAE													
<i>Cycadopites gracilis</i>						2	2		1				
<i>Cycadopites instaructus</i>									1				
<i>Cycadopites ?minimus</i>	1					2	2						
<i>Cycadopites</i> sp.	6				1	4	1	1	1	2	5	1	
<i>Areolites</i> sp.													2
<i>Sequoiapollenites polyformosus</i>													
<i>Sparganiaceoisporites polygonalis</i>	1	1											
<i>Longaperites discoidis</i>										2			
<i>Longaperites</i> sp.	2									1			

Table 1. (continued)

SAMPLES	MADEN MEMBER												
	01B/20	01B/44	02B/03	02B/01	02B/02	02B/31	01B/24	01B/11	01B/33	02B/04	02B/05	02B/07	02B/08
<i>Spinizonocolpites</i> sp.								1					2
<i>Kopekipollenites transdanubicus</i>													
DICOTYLEDONEAE													
<i>Triatriopollenites nurensis</i>	2						1	1		1			
<i>Triatriopollenites bituitus</i>	1	1					1	1		1			
<i>Triatriopollenites excelsus</i> ssp. <i>minor</i>	16	14				2	5	2	4	1		1	
<i>Triatriopollenites excelsus</i> ssp. <i>typicus</i>	7	7	1			2	5	3	3	4			
<i>Plicatopollis lunatus</i>	3	3	6			1	1	1	1				
<i>Plicatopollis plicatus</i>		5					2						1
<i>Plicapollis</i> sp.						2		1					
<i>Momipites punctatus</i>	9	6	5	1		3		1	1				
<i>Momipites quietus</i>	2					1	1	1	1				
<i>Momipites</i> sp.		3				4		5					
<i>Tripoporollenites robustus</i>	3	2	5							4	2		
<i>Labrapollis labraferus</i>	1												
<i>Tripoporollenites</i> sp.							1		2				2
<i>Trivestibulopollenites betuloides</i>	3	6		2			2	2		3			
<i>Subtripoporollenites anulatus</i> ssp. <i>nanus</i>	1	2						1					
<i>Subtripoporollenites constans</i>	1												
<i>Intratripoporollenites indubitabilis</i>													
<i>Mauritidites francisci</i>			1				1						
<i>Olaxipollis mathressii</i>	1												
<i>Polyporopollenites undulosus</i>		2			1		1	1					
<i>Polyporopollenites carpinoides</i>			1			2	1	1					
<i>Polyporopollenites</i> cf. <i>stellatus</i>					1								
<i>Polyvestibulopollenites verus</i>						1							
<i>Pentapollenites pentangulus</i>		1	2										
<i>Chenopodipollis multiplex</i>	1							1					
<i>Tricopopollenites retiformis</i>	2					1	1	1					
<i>Tricopopollenites microhemici</i>	4						4	12	5		1		
<i>Tricopopollenites asper</i>	1						1	3	2				
<i>Tricopopollenites liblarensis</i> ssp. <i>fallax</i>	1	1				1	1	3	2				
<i>Tricopopollenites</i> sp.	2						3				1		1
<i>Polycolpites</i> sp.							1						
<i>Myrtacidites mesonesus</i>								1					
<i>Tricopopollenites cingulum oviformis</i>	1	6					1	1	1				
<i>Tricopopollenites cingulum fuscus</i>		3					1						
<i>Tricopopollenites cingulum pusillus</i>							1	1			1		
<i>Tricopopollenites megaexactus</i>							1						
<i>Tricopopollenites pseudocingulum</i>	1							1					
<i>Tricopopollenites microreticulatus</i>							1						
<i>Tricopopollenites</i> sp.	9								2				
<i>Psilatricolporites crassus</i>	111	142	5	185	87	102	204	152	170	48	171	161	76
<i>Psilatricolporites</i> cf. <i>costatus</i>			5				2						
<i>Nowemproctectus tumanganicus</i>			3							2	1		
<i>Pediastrum</i> spp.													
INCERTAE CEDIS													
Dinoflagellate cysts										1	1	1	6
Total	206	210	182	200	194	139	253	203	201	183	204	205	94

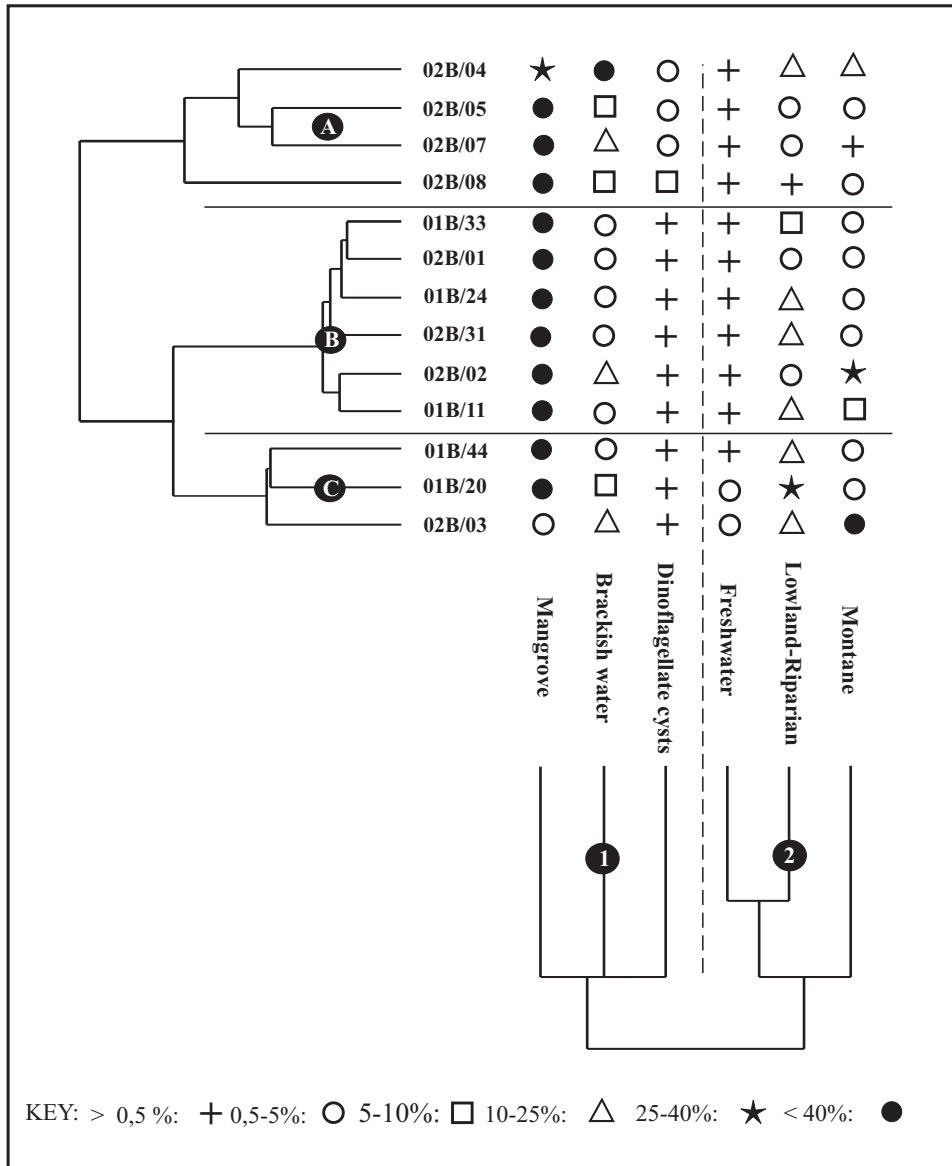


Figure 3. Dendograms for UPGMA cluster analysis of palaeocommunities (bottom) and samples (side), using the Raup-Crick Index. See Figure 2 for the locations of the samples.

*Triatriopollenites excelsus*, *Subtriporopollenites anulatus* ssp. *nanus*, *Subtriporopollenites constans*, *Plicatopollis lunatus* and *Nowemprojetus tumanganicus* are restricted to the Palaeocene and Eocene the world over (Table 2). *Nowemprojetus tumanganicus* is here recorded for the first time from the Eocene sediments of Turkey. Additionally, *Aglareidia cyclops* appears in the Middle Eocene and seems have its last occurrence within or at the top of the 'Middle' Oligocene. Thus, this species is not

recorded in sediments older than the Middle Eocene (Nickel 1996; Chateauneuf 1980; Hochuli 1978; Vinken 1988).

In addition to the taxa mentioned above, mangrove and back-mangrove elements such as *Psilatricolporites crassus* (*Pelliciera*), *Spinizonocolpites* group (*Nypa*) and *Leiotriletes adriennis* (*Acrostichum*) and *Mauritiidites franciscoi* (*Mauritia*) were first recorded in western Anatolia. According to Rull (1998a, 1999), the Early



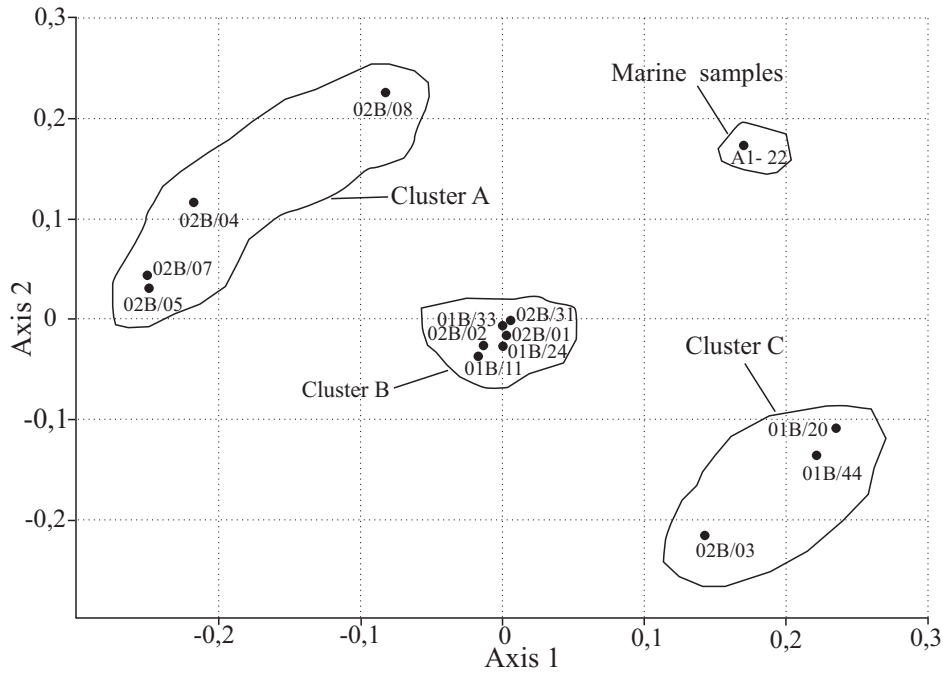


Figure 4. Scattergram of taxa ordination, from a two-dimensional MDS using the Hamming distance. Stress = 0.3028.

Eocene occurrence of *Psilatricolporites crassus* (*Pelliciera*) and *Spinizonocolpites echinatus* (*Nypa*) is always sparse as compared to the Middle Eocene of the Venezuelan Maracibo basin; that observation is consistent with the data of this study. Most European *Nypa* pollen appearances are in Ypresian–Cuisian deposits of France (Gruas-Cavagnetto 1977), except for Spanish occurrences that range from Cuisian to Early Lutetian (Haseldonckx 1972) in age. Cavagnetto & Anadón (1996) describe complex mangrove-swamp elements, such as *Nypa*, *Avicennia* and *Pelliciera* from the Middle Bartonian of the eastern Ebro basin (northern Spain). According to Riegel *et al.* (1999), the mangrove association is widespread and diverse in the Middle Eocene seam group relative to the Lower Eocene seam group at Helmstedt, northern Germany. The oldest biodiversification age of the mangroves on the European sea-shores is Middle Eocene (Plaziat *et al.* 2001). Based on the palynological data, the Maden member should have been deposited during the Middle–?Late Eocene period (Figure 2).

#### Comparison of Palynological Data with Other Coeval Basins in Turkey

To date, only limited palynological studies on the Eocene units have been made in the Yozgat and Çorum areas of central Anatolia (Nakoman 1966; Akyol 1980; Akgün *et al.* 2002; Akgün 2002). The Turkish Eocene microflora was first examined by Nakoman (1966). That author accepted that the age of the sediments in the Yozgat area (Sorgun lignites) was Early Eocene based on the presence of important biostratigraphic forms such as *Triatriopollenites excelsus*, *Tetracolporopollenites biconus*, *Inaperturopollenites echinatus* and *Monocolpopollenites granulatus*.

Akyol (1980) studied the palynological aspects of the Bayat lignites (nearby Çorum area of central Anatolia). That author determined a rich flora, including some forms that have biostratigraphic significance (see Akgün *et al.* 2002 for discussion). A Middle–Late Eocene age is suggested on the basis of palynological and foraminiferal data. Although Nakoman (1966) and Akyol (1980) recognized some biostratigraphically significant species

**Table 2.** Stratigraphic distribution of selected taxa encountered in the Başçeşme formation.

Fossil	Age	References
<i>Leiotriletes adriennis</i>	Middle Eocene–Middle Miocene	Stuchlik <i>et al.</i> 2001
<i>Leiotriletes wolffii</i>	Late Eocene–Pliocene	Nickel 1996; Stuchlik <i>et al.</i> 2001
<i>Aglaoreidia cyclops</i>	Middle Eocene–Middle Oligocene Early–Middle Oligocene	Nickel 1996 Roche 1988; Hochuli 1978; Ollivier-Pierre <i>et al.</i> 1993
<i>Spinizonocolpites</i> Group	Eocene Middle Eocene–Early Oligocene	Vinken 1988 Elsik 1974; Frederiksen 1973
<i>Triatriopollenites excelsus</i>	Paleocene–Late Eocene	Thomson & Pflug 1953; Kedves 1969, 1982; Akyol 1978; Gruas-Cavagnetto 1978; Nickel 1996
<i>Plicatopollis lunatus</i>	Eocene–Middle Oligocene Paleocene–Early Eocene Middle Eocene Late Paleocene–Eocene	Nickel 1996 Frederiksen 1980a Thiele-Pfeiffer 1988 Akgün 2002
<i>Subtriporopollenites anulatus</i> ssp. <i>nanus</i>	Late Palaeocene–Late Eocene	Thomson & Pflug 1953; Krutzsch 1957, 1970; Krutzsch & Vanhoorne 1977
<i>Subtriporopollenites constans</i>	Palaeocene–Early Eocene Middle Eocene Middle Eocene–Middle Oligocene Palaeocene–Early Oligocene	Kedves 1970; Krutzsch & Vanhoorne 1977 Thiele-Pfeiffer 1988 Krutzsch 1970 Gruas-Cavagnetto 1978
<i>Nowemprojectus tumanganicus</i>	Paleocene–Middle Eocene Eocene	Bolotnikova (1979) Frederiksen <i>et al.</i> (2002)

for the Turkish Eocene, they did not document any of the mangrove species which have been determined in the present study.

After those palynological studies at different localities in central Anatolia, Akgün *et al.* (2002) and Akgün (2002) obtained a rich species diversification. They also obtained new Eocene palynological data and suggested the presence of different kinds of mangrove and back-mangrove elements, such as *Avicennia*, *Psilatricolporites* (*Pelliciera*), *Spinizonocolpites* (*Nypa*), *Mauritiidites franciscoi* (*Mauritia*) and *Leiotriletes adriennis* (*Acrostichum*) from the Middle–?Upper Eocene Yoncalı formation in central Anatolia (Yozgat and Amasya areas). The species *Spinizonocolpites echinatus*, *S. prominatus*, *S. baculatus*, *S. gemmatus*, *S. microgemmatus*, *S. bulbospinosus* *S. cf. wodehousei*, *S. indicus*, *S. cf. adamanteus* and *Spinizonocolpites* spp. were abundantly recorded in samples of the Yoncalı formation (central Anatolia). In contrast, *Spinizonocolpites* spp. has been

determined as individual grains from the Maden member (western Anatolia) (sample O2B/O7). Diversification of pteridophytic spores, tricolpate and tricolporate pollen grains is high in samples from the Yoncalı formation (central Anatolia) compared to the Maden member (western Anatolia). The species *Nowemprojectus tumanganicus* has been determined in samples of the Maden member (Table 1) but does not occur in the Yoncalı formation. The mangrove element *Psilatricolporites crassus* (*Pelliciera*) is abundant in almost all samples from the Maden member (54–90%) (Table 1), but is less abundant in samples from the Yoncalı formation. Although the percentages of mangrove elements are different in central and western Anatolian samples, the Middle–?Upper Eocene coal occurrences of central Anatolia can be correlated with the data of this study on the basis of the presence of mangrove elements. The difference in relative frequencies of the species is likely related to the palaeoecological factors which persisted during the deposition of these coals.

### Foraminiferal Data and Age Determination

Thirty samples were collected from both the Maden and Asar members of the Başçeşme formation along the section (Figure 2). However, only 22 samples were found to be micropalaeontologically productive; samples from the limestones of the Maden member are barren (the samples of M4–M11) (Figure 2).

However, Sözbilir *et al.* (2001) studied the microfauna of the Eocene sediments cropping out in the southeastern part of the Baklan area, located 10 km northeastern of the study area (Figure 1b). Those authors obtained well-preserved foraminiferal data from the Beşparmak reef member, which is conformably overlain by the Maden member. The well-preserved fauna comprises *Asterigerina rotula*, *Nummulites perforatus*, *Nummulites beaumonti*, *Fabiania cassis*, *Europertia magna*, *Chapmanina gassinensis*, *Halkardia minima*, *Silvestrialla tetraedra*, *Rotalia* sp., *Globigerina* sp., *Operculina* sp., *Heterostegina* sp., *Assilina* sp., *Gypsina* sp., *Planorbulina* sp., *Textularia* sp., *Discocyclus* sp., *Hauerinidae*, *Rotaliidae* and *algae*. A Bartonian age was suggested by those authors, and is in agreement with our palynological data for the Maden member.

In this study, samples (A1–A22) collected from the Asar member are rich in benthic foraminifers (Figure 2). A *Nummulites* assemblage, including *Nummulites fabianii* and *Nummulites striatus*, has been determined. In addition, *Fabiania cassis*, *Eorupertia magna*, *Halkyardia minima*, *Baculogypsinoidea tetraedra*, *Asterigerina rotula*, *Quinqueloculina* sp., *Asterigerina* sp., *Discocyclus* sp., *Heterostegina* sp., *Eponides* sp., *Alveolina* sp., *Praealveolina* sp., *Nealveolina* sp., *Anomalina* sp., *Mississippina* sp., *Pararotalia* sp., *Pyrgo* sp. and *Orbitolites* sp. have also been recorded in the samples. Rotaliidae, Textulariidae, Miliolidae, algae, bivalves, gastropods and echinoderms have been documented as well. The foraminiferal fauna suggests a Late Eocene (Priabonian) age, indicating a carbonate-shelf depositional environment for the Asar member.

On the basis of foraminiferal data, Sözbilir *et al.* (2001) suggested that the age of the Beşparmak reef member is Bartonian. In addition, a Bartonian–?Priabonian age has been suggested for the Maden member on the basis of palynostratigraphic data. Also, a Priabonian age is assigned on the basis of well-constrained foraminiferal data from the Asar member. In

summary, the Beşparmak reef, Maden and Asar members were deposited during Bartonian–Priabonian time in the study area. However, it is difficult to interpret the age of the Dazlak member, which is located at the base of the Başçeşme formation, due to the lack of fossils. According to Şenel (1997), Eocene sedimentation in the Çardak-Tokça basin began in the Late Lutetian, an age which may be accepted doubtfully for the Dazlak member (Figure 2).

### Reconstruction of the Palaeoenvironment

The palynological assemblage of the Başçeşme formation in the Çardak-Tokça basin is limited due to conditions of sedimentation, and exhibits some differences in the frequency of the same taxa in different samples (Table 1). To reconstruct the palaeoenvironment during the deposition of the Başçeşme formation, definite ecological marker taxa have been selected from the published literature. The ecological characteristics of species have been grouped under generic headings, such as “mangroves” (*Nypa* and *Pelliciera*) and “fresh-water elements” (*Aglaoreidia cyclops*, *Sparganiaceae* and *Pediastrum* spp.). The rhizomatic palm *Nypa* is an ecological marker of mangrove vegetation (Germeraad *et al.* 1968; Jiménez 1984; Frederiksen 1985; Thanikaimoni 1987; Westgate & Gee 1990; Srivastava & Binda 1991; Graham 1995; Rull 1998a; Lenz & Riegel 2001). *Pelliciera* is another mangrove element (Jiménez 1984; Rull 1998a). According to Frederiksen (1985), *Aglaoreidia cyclops* was found to favour fresh-water habitats; e.g., *Azolla*, *Pediastrum*, *Botryococcus*, *Potamegaton*, *Sparganium* and *Typha*. Thus, the species was thought to have been produced by fresh-water habitats (Fowler 1971; Frederiksen 1985; Riegel *et al.* 1999).

From the palaeovegetational point of view, the palaeocommunities and samples can be divided into two or three assemblages (Figure 3). In the palaeocommunities dendrogram, assemblage 1 consists of mangroves, brackish-water elements and dinoflagellate cysts. Assemblage 2 includes fresh-water, lowland-riparian and montane elements (Figure 3).

In the sample dendrogram, assemblage A is characterized by a dominance of mangroves, brackish-water elements and low frequencies of dinoflagellate cysts and montane elements, corresponding to the palaeocommunity cluster 1 (Figure 3). The samples of

cluster A coincide with samples taken from the upper part of the section (Figure 2). The presence of poorly preserved dinoflagellate cysts and the abundance of mangrove elements in these samples indicate close proximity to a marine environment (Figures 3 & 5). The samples taken from the lower part of the section lack dinoflagellate cysts (Figures 2, 3 & 5).

Sample cluster B is represented by the dominance of mangrove and the absence of fresh-water elements and dinoflagellate cysts. The lowland-riparian and montane elements in sample cluster B are higher than in cluster A (Figures 3 & 5).

The samples of cluster C were taken from the lowest part of the section (Figure 2) and are represented by the presence of fresh-water elements, high frequencies of mangrove, lowland-riparian and montane elements, and the absence of dinoflagellate cysts (Figures 3 & 5), corresponding to cluster 2 in the palaeocommunity dendrogram (Figure 3). There are low numbers of mangrove elements in sample cluster C as compared to clusters A and B (Figure 5).

All micropalaeontological samples have also been subjected to non-metric multidimensional scaling (MDS) using the Hamming distance method (Figure 4). The MDS shows results similar to those of the cluster analysis. The MDS of the samples (Figure 4) shows that groups identified in the cluster analysis have also been recognized in this plot. The samples, which are situated at the positive part of the second axis, show a close proximity to the marine environment based on the presence of marine samples (A1–A22); also, cluster A includes dinoflagellate cysts, mangroves and brackish-water elements (Figures 3 & 4). The samples at the negative part of the second axis indicate relatively terrestrial conditions.

Mangrove element *Pelliciera* (*Psilatricolporites crassus*) is found in abundance in all samples (Table 1). According to Jiménez (1984), *Pelliciera* is more sensitive to high soil salinities than other more widespread neotropical mangroves. It develops best on wet soils, shallowly inundated at high tides (Collins *et al.* 1977). It also thrives on firm, sandy slightly elevated soils which are located in inter-channel areas (Fuch 1970; Jiménez 1984). *Nypa*, pollen of which is observed as individual grains in sample 02B/07, occurs in permanently brackish humid soil on the proximal fringes of mangrove fronts (Blasco 1977; Chapman 1976; Srivastava & Binda 1991)

(Table 1). The combination of *Psilamonocolpites* sp., *Mauritiidites franciscoi* (*Mauritia*) and *Leiotriletes adriennis* (*Acrostichum*), which are back-mangrove swamps, have been observed as individual grains in some samples. Their presence in the Tertiary of Venezuela has been interpreted as representative of the wetlands behind mangroves near the limit of tidal influence (Rull 1992, 1997a, b, 1998a, b). A *Mauritia* palm forest associated with ferns indicates a zone of fresh-water (to locally brackish) swamps and marshes in the Eocene of Colombia (González-Guzmán 1967). The pollen of *Mauritia* grew back of the coastline (Van Der Hammen & Wijmstra 1964); its presence in the sediments is a reliable indicator of a warm tropical lowland environment flooded by fresh (sometimes oligohaline) waters (Rull 1998b). In addition, *Mauritiidites* may also be observed in more inland associations. The scarce presence of *Nowemprojetus tumanganicus* in samples 02B/03, 2B/04 and 02B/05 should be indicative of peaty substrates (Frederiksen *et al.* 2002) (Table 1). The pollen of Chenopodiaceae may endure droughts in salt marshes (Figure 5).

Pteridophytic spores of Polyodiaceae, Schizaceae, Selaginellaceae, Lygodiaceae and *Osmunda* are dispersed in the samples indicating the prevalence of perennial water in the brackish-water palaeocommunity (Figure 5). The presence of *Sparganiaceapollenites* (*Sparganiaceae*), *Pediastrum* spp. and *Aglaoreidia cyclops* in samples 02B/03, 01B/20 and 01B/44 correspond to sample cluster C and may be considered as the fresh-water palaeocommunity (Figures 3 & 5). Almost all samples include lowland-riparian elements such as Juglandaceae, Betulaceae, *Engelhardia*, Fagaceae and Myrtaceae. Montane elements are represented by *Pinus*, *Abies*, *Picea*, *Cathaya*, *Quercus* and *Castanea* (Figure 5). The frequencies of lowland-riparian and montane elements and also the presence of fresh-water elements in palaeocommunity cluster 2 (which corresponds to the sample cluster C) may indicate low sea levels (Figures 3, 4 & 5). The deposition of these samples in cluster C may have occurred in a non-marine, back-mangrove environment. The abundance of mangrove brackish-water elements and the presence of poorly preserved dinoflagellate cysts in sample cluster A indicate high sea levels (Figures 3 & 5). Samples of clusters A and B must have been deposited in a mangrove environment (Figure 5).

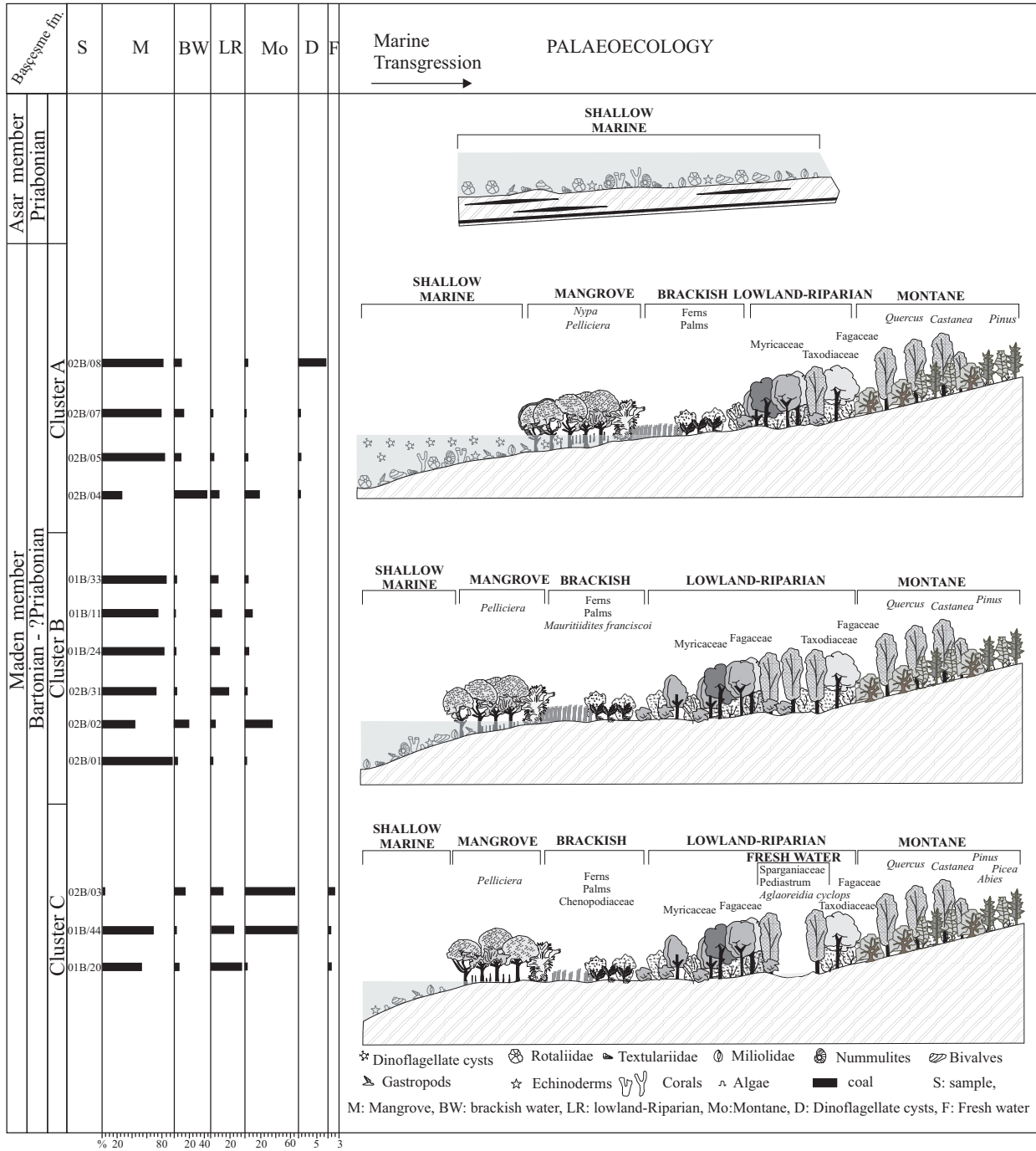


Figure 5. Relative abundance of ecological groups obtained from the Maden member and palaeoenvironmental reconstruction of the Çardak-Tokça basin (western Anatolia) during the deposition of the coal-bearing Middle–Upper Eocene Başçesme formation (Maden and Asar members).

In summary, it is clear that Middle–Late Eocene transgression is recorded from cluster C to cluster A (Figure 5). The presence of marine limestones in the study area indicates that maximum sea-level conditions

were attained during deposition of the Asar member (Figure 5). The marine transgression is also well documented by the presence of reefal limestones containing rich marine fossils, such as coral reefs, benthic

foraminifers and echinoderms (Figure 5). In western Anatolia, there has been no study focused on the Bartonian–Priabonian transgression. However, on a regional scale, the Palaeocene–Eocene successions of western Anatolia were probably associated with depressions (Sözbilir 2002).

**Palaeoclimate**

Quantitative terrestrial palaeoclimatic analysis based on the palynological assemblage of the Maden member (Başçeşme formation) was carried out using the coexistence approach proposed by Mosbrugger & Utescher (1997); this technique is based on the ‘nearest living relative’ philosophy, the assumption that climatic requirements of Tertiary plant taxa are similar to those of their living relatives (Mosbrugger & Utescher 1997). The palaeoclimatic reconstruction of the palynoflora of the Başçeşme formation is based on a total of 19 taxa (Figure

6). The calculated coexistence intervals result in a mean annual temperature (MAT) range mainly between 24.8 and 25 °C, but intervals between 17.2 and 21.1 °C also occur (Figure 6). Thus, two different mean annual temperatures (24.8–25 °C and 17.2–21.1 °C) have been obtained by applying the coexistence approach proposed by Mosbrugger & Utescher (1997). For this reason, Nix’s (1982) terms *megatherm* and *mesotherm* are quite relevant. Nix (1982) recognized plant groups for characteristic temperature response models for Australia and New Guinea. The megatherm element is dominant where the mean annual air temperature exceeds 24 °C and corresponds to the environment of the mangrove association. The mesotherm element is dominant where mean annual air temperature ranges between 14 °C and 21 °C and coincides with the slope and montane-forest association. An intermediate zone is indicated as an area where the mean annual temperatures are less than 24 °C but greater than 21 °C. The obtained climatic values

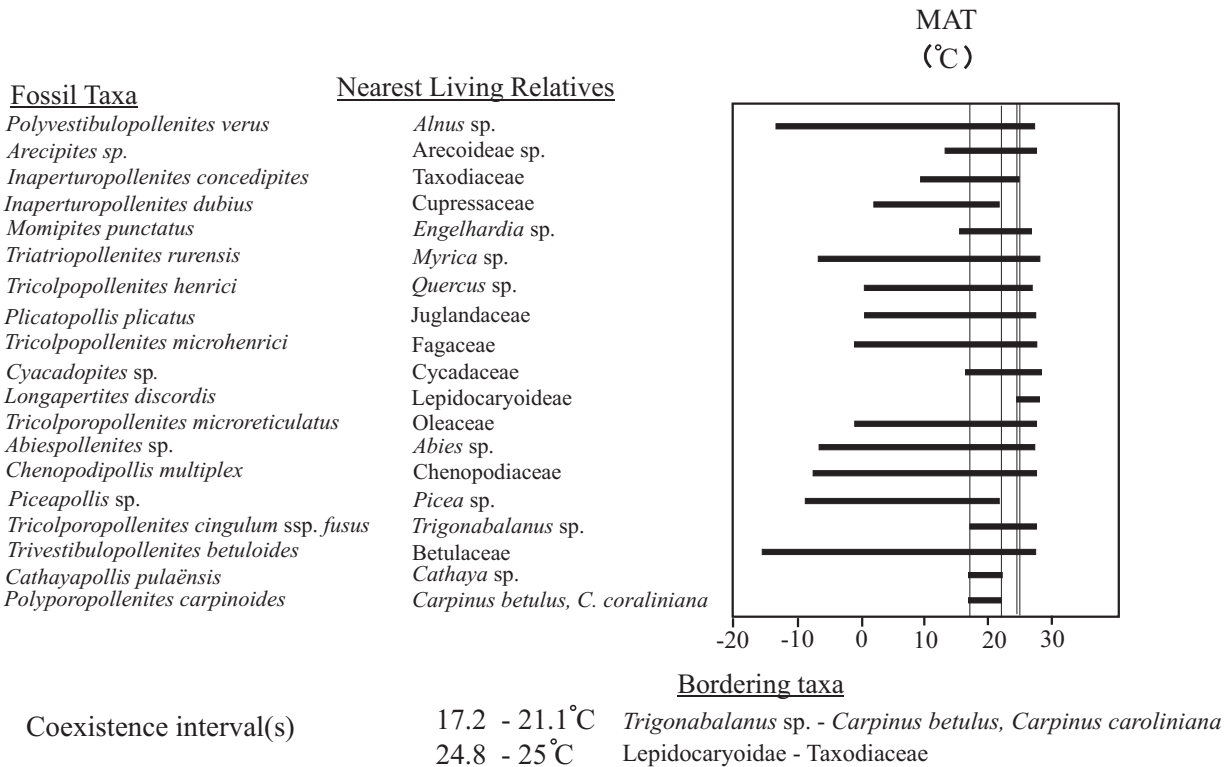


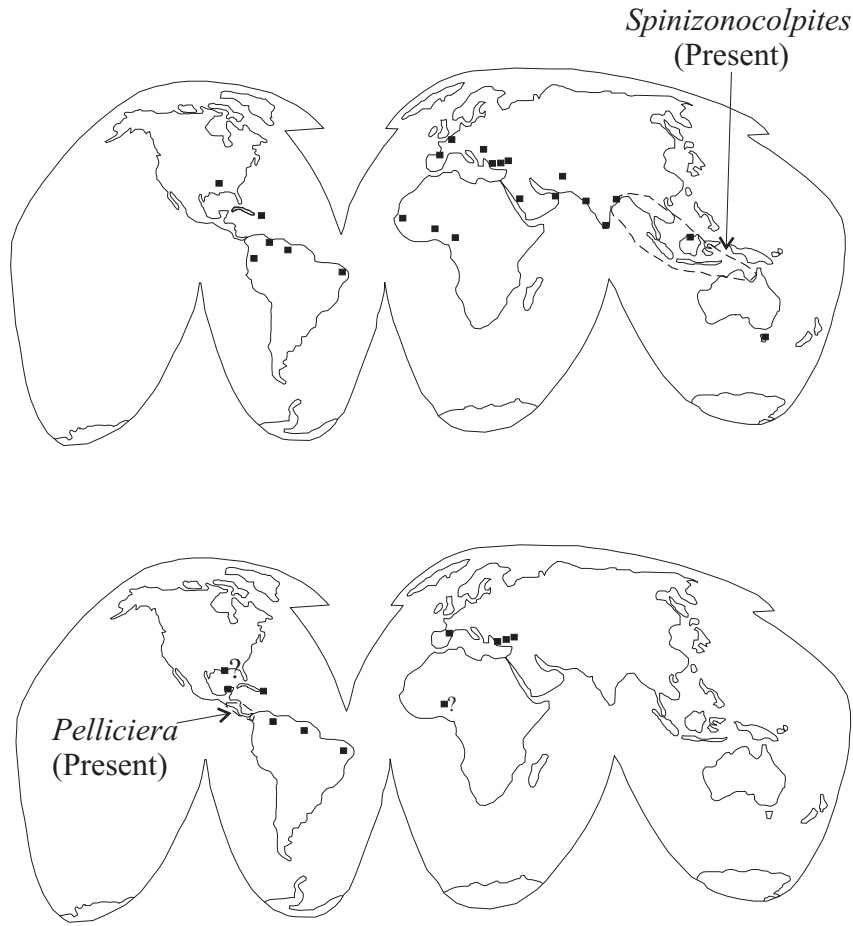
Figure 6. Application of the coexistence approach to the palynoflora of the Maden member in the Çardak-Tokça basin (western Anatolia). The shaded boxes mark the climatic requirements of the taxa, the vertical lines delimit the widths of coexistence intervals (MAT: mean annual temperature).

correspond to the terminology of Nix (1982). Climatic conditions should be 24.8–25 °C near the coast, including the megathermal elements (mangrove association). The second MAT value (17.2–21.1 °C) corresponds to Nix's mesotherm zone. The intermediate zone is characterized by a temperature of 21.1–24.8 °C. Nix (1982) used these terms to do away with the confusion that is usually associated with the use of tropical, subtropical and temperate, since these have both geographic and thermal connotations. On the other hand, according to Wolfe (1979), the moist tropical forests have an MAT higher than 25 °C; the 20–25 °C isotherms lie in the region of development for the paratropical forest; broad-leaf evergreen forests grow in a subtropical climate (13–20 °C). The occurrence of *Nypa* pollen suggests that tropical to subtropical climatic conditions existed during deposition of the Başçeşme formation. If the habitat requirements of *Nypa* during the Eocene were similar to those of extant *Nypa*, water temperatures must have been warmer than 24 °C. *Nypa* cannot survive in temperatures less than 20 °C (Fechner 1988). The species of *Nypa*, *Avicennia* and *Pelliciera* are among the megathermal taxa (Cavagnetto & Anadón 1995, 1996). *Psilatricolporites crassus* (*Pelliciera*) in particular has been recorded with great frequency in our samples as a megathermal species. The mangroves need the tropical and humid climate to develop (Frederiksen 1985; Westgate & Gee 1990). In addition, the presence of the zooxanthellate coral fauna with larger foraminifera in the carbonate rocks indicates the tropical temperatures of the Tethys Sea. The zooxanthellate coral fauna and reef growth with larger foraminifera control the minimum sea-surface temperature (Schmiedl *et al.* 2002). Ediger *et al.* (1990) studied the palynological properties of the Tertiary of the northern Thrace Basin (northwestern Turkey), and discussed the palaeoclimate of the Eocene period. According to those authors, the increased percentages of thermophilous elements, such as *Cycadapites*, *Monocolpopollenites* and *Dicolpopollenites kalewensis*, indicate that the temperature was higher in the Oligocene than in the Eocene, probably resulting in a temperate climate in the Eocene and a subtropical climate in the Oligo–Miocene. However, they also noted that the Eocene part of the climate curve should be drawn with caution on the basis of previous palaeoclimatic studies (Wolfe 1978; Hochuli 1984). Throughout the Eocene epoch, the climate of the Mediterranean region underwent fluctuations (Aleksandrova *et al.* 1987). The

Early Eocene is marked by some decrease in the mean annual temperatures in what is present-day Belgium, Germany and the East European platform, later succeeded in Europe by a warm tropical and subtropical climate (Buchardt 1978; Yasamanov 1982). Palaeobotanical determinations of the Middle Eocene palaeoclimate (Gray 1960; Dilcher 1973; Wolfe 1978; Upchurch & Wolfe 1987; Greenwood & Wing 1995) and of the Late Eocene palaeoclimate (Frederiksen 1980b; Wolfe 1992) for the northern Gulf Coast, U.S.A. are all winter-dry tropical to humid paratropical climates on lowlands, and most infer no freezing. Frederiksen (1980a, b) suggested a regime of winter-dry tropical climate on lowlands adjacent to the coastline and a marginal humid paratropical climate on the upper coastal plain. In conclusion, we have identified the presence of a mixture of subtropical/paratropical climatic zones, corresponding to an interval having mean annual temperatures 17.2° and 25 °C, and from coast to montane environments. This climatic discrepancy is related to the effects of the tropical Tethys Sea on terrestrial environments.

#### Palaeogeographic Data

On the basis of previous studies and the data of the present study, the present-day and Eocene geographic distributions of mangrove elements *Nypa* and *Pelliciera* have been plotted on maps (Figure 7). The pollen of *Nypa* (*Spinizonocolpites*) and *Pelliciera* (*Psilatricolporites crassus*), which were first recorded from Middle–?Upper Eocene deposits in central Anatolia (Yozgat and Amasya areas) by Akgün (2002) and Akgün *et al.* (2002), have been cited in the section on palynological data. *Nypa* was present on all continents during the Eocene but, at present, only occurs in the Indo-Malaysian region (Figure 7). Conversely, *Pelliciera* (*Psilatricolporites crassus*) occurred in the Caribbean area and on the Atlantic coasts of Guyana and Brazil during Eocene–Oligocene time (Rull 1998a); it was also recorded from the Middle–Late Eocene sediments of the Ebro basin (northeast Spain) by Cavagnetto & Anadón (1995, 1996). Although its presence in Africa is uncertain during Eocene time, it has been reported from Middle–Upper Eocene sediments in both central (Yoncalı formation) and western Anatolia (Başçeşme formation) (Figure 7). It was also reported from the Tertiary of the Guiana basin (Van Der Hammen & Wijmstra 1964), and from Early Miocene sediments of



**Figure 7.** Present (dashed areas) and Eocene (black squares) geographic distributions of *Spinizonocolpites* spp. (*Nypa*) and *Psilatricolporites crassus* (*Pelliciera*). After Germeraad *et al.* (1968), Müller (1980, 1981), Thanikaimoni *et al.* (1984), Frederiksen (1980a, 1985, 1988, 1994), Thanikaimoni (1987), Westgate & Gee (1990), Srivastava & Binda (1991), Cavagnetto & Anadón (1995), Graham (1995), Nickel (1996), Pole & Macphail (1996), Rull (1998a, 1999), El Beialy (1998), Riegel *et al.* (1999), Akgün (2002), Akgün *et al.* (2002).

Panama (Graham 1977). According to Graham (1995), its presence persisted into the Quaternary Gulf/Caribbean region (Mexico, the Antilles, Central America, and northern South America). However, at present, *Pelliciera* (*Psilatricolporites crassus*) is observed in a restricted area of central and northern South America (Figure 7). In this study, the present Atlantic mangrove (*Pelliciera*) and present Indo-Pacific mangrove (*Nypa*) elements have not been reported as fossils from western Anatolia. Their presence in Middle–Upper Eocene sediments of western and central Anatolian implies warm mid-latitude Tethys

waters. At the global scale, since the tropical Tethys free seaway connected the Palaeo-Atlantic and Indian oceans, the mangroves should have invaded southeastern Asian, African, North and South American and European shores.

### General Conclusions

The results of this study are as follows: (1) Palynological and benthic foraminiferal assemblages indicate a Bartonian–Priabonian age for the Maden and Asar members of the Başıçeşme formation. (2) An overall rise



in sea level from the Bartonian to the Priabonian is indicated by the distribution of both microfaunal and palynological associations from the back-mangrove to shallow-marine environment. The lower part of the Maden member was deposited in a non-marine, back-mangrove environment. The palaeoenvironment changed from back-mangrove to mangrove or front-mangrove environment in the upper part of the Maden member and also to a shallow-marine environment in the Asar member, which contains marine fossils. Based on the palynological and microforaminiferal data, sea-level rise likely was related to basin subsidence as a result of tectonic development. (3) The mangrove taxa and coral fauna with larger foraminifera in the carbonate strata of the Başçeşme formation indicate tropical water temperatures during the Bartonian–Priabonian interval. Palaeoclimatic conditions are characterized by 24.8–25 °C MAT values in the mangrove environment, whereas there was a mean annual temperature of 21.1–24.8 °C in the megatherm/mesotherm intermediate zone and of

17.2–21.1 °C in the mesotherm zone. These climatic intervals indicate subtropical/paratropical climatic conditions during deposition of the Başçeşme formation. (4) The circulation of warm Tethys waters was probably responsible for the growth of mangroves in both central and western Anatolia during the Middle–Late Eocene.

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### References

- AKGÜN, F. 2002. Stratigraphic and paleoenvironmental significance of Eocene palynomorphs of the Çorum-Amasya area in the central Anatolia, Turkey. *Acta Palaeontologica Sinica* **41**, 576–591.
- AKGÜN, F., AKAY, E. & ERDOĞAN, B. 2002. Terrestrial to shallow marine deposition in central Anatolia: a palynological approach. *Turkish Journal of Earth Sciences* **11**, 1–27.
- AKKIRAZ, M.S. & AKGÜN, F. 2005. Palynology and age of the Early Oligocene units in Çardak-Tokça basin, southwest Anatolia: paleoecological implications. *Geobios* **38**, 283–299.
- AKYOL, E. 1978. Stratigrafik palinoloji, kömür işletmeciliği ve bir örnek [Stratigraphic palynology, coal mining and a case study]. *Jeoloji Mühendisliği Dergisi* **6**, 31–38 [in Turkish with English abstract].
- AKYOL, E. 1980. Etude palynologique de l'Eocene de Bayat (Çorum-Turquie) et essai de corrélation entre Karakaya et Emirşah. *Mineral Research and Exploration Institute of Turkey (MTA) Bulletin* **91**, 39–53.
- ALEKSANDROVA, A.N., PROZOROV, Y.I. & YASAMANOV, N.A. 1987. Climatic and floristic zonation of the Mediterranean region during the Early Cenozoic time. *International Geology Review* **29**, 503–514.
- BLASCO, F. 1977. Outlines of ecology, botany and forestry of the mangals of the Indian subcontinent. In: CHAPMAN, V.J. (ed), *Ecosystems of the World. Wet Coastal Ecosystems* **1**, 241–260.
- BOLOTNIKOVA, M.D. 1979. *Spore-Pollen Complexes of Tertiary Deposits of the Western Coast of the Sea of Japan*. "Science" Publishing House, Moscow.
- BOZKURT, E. & PARK, R.G. 1994. Southern Menderes Massif: an incipient metamorphic core complex in western Anatolia, Turkey. *Journal of the Geological Society, London* **151**, 213–216.
- BOZKURT, E. & PARK, R.G. 1999. The structure of the Palaeozoic schists in the southern Menderes Massif, western Turkey: a new approach to the origin of the main Menderes metamorphism and its relation to the Lycian Nappes. *Geodinamica Acta* **12**, 25–42.
- BUCHARDT, B. 1978. Oxygen isotope paleotemperatures from the Tertiary period in the North Sea area. *Nature* **275**, 121–123.
- CAVAGNETTO, C. & ANADÓN, P. 1995. Uno mangrove complexe dans le Bartonien du bassin de le l'Ebre (Ne de l'Espagne). *Palaeontographica Abteilung B Ionnides* **236**, 147–165.
- CAVAGNETTO, C. & ANADÓN, P. 1996. Preliminary palynological data on floristic and climatic changes during the Middle Eocene- Early Oligocene of the eastern Ebro Basin, northeast Spain. *Review of Palaeobotany and Palynology* **92**, 281–305.
- CHAPMAN, V.J. 1976. *Mangrove Vegetation*. J. Cramer, FL-9490 Vaduz, 447 p.
- CHATEAUNEUF, J.J. 1980. Palynostratigraphie et Paléoclimatologie de l'Eocène Supérieur et de l'Oligocène du Bassin de Paris. Mémoire du Bureau de Recherches Géologiques et Minières **116**, 1–360.
- COLLINS, J., BERKELHAMER, R.C. & MESLER, M. 1977. Notes on the natural history of the mangrove *Pelliciera rhizophorae* Tr. & Pl., (Theaceae). *Bresnia* **10/11**, 17–29.
- COLLINS, A.S. & ROBERTSON, A.H.F. 1997. The Lycian Mélange, southwest Turkey: an emplaced accretionary complex. *Geology* **25**, 255–258.
- COLLINS, A.S. & ROBERTSON, A.H.F. 1998. Processes of Late Cretaceous to Late Miocene episodic thrust sheet translation in the Lycian Taurides, SW Turkey. *Journal of the Geological Society, London* **155**, 759–772.

- COLLINS, A.S. & ROBERTSON, A.H.F. 1999. Evolution of the Lycian allochthon, western Turkey, as a north-facing Late Palaeozoic to Mesozoic rift and passive continental margin. *Geological Journal* **34**, 107–138.
- DILCHER, D.L. 1973. A palaeoclimatic interpretation of the Eocene floras southeastern North America. In: GRAHAM, A. (ed), *Vegetation and Vegetational History of Northern Latin America*. Elsevier Publishing Company, 39–59.
- EDIGER, V.Ş., BATI, Z. & ALIŞAN, C. 1990. Paleopalynology and paleoecology of *Calamus* like disulcate pollen grains. *Review of Palaeobotany and Palynology* **62**, 97–105.
- EL BEIALY, S.Y. 1998. Stratigraphic and palaeoenvironmental significance of Eocene palynomorphs from the Rusayl Shale Formation, Al Khawd, northern Oman. *Review of Palaeobotany and Palynology* **102**, 249–258.
- ELSIK, W.C. 1974. Characteristic Eocene palynomorphs of the Gulf Coast, U.S.A. *Palaeontographica Abteilung B Ionnides* **149**, 90–111.
- FECHNER, G.G. 1988. Selected palynomorphs from the Lower to Middle Eocene of the South Atlas Border Zone (Morocco) and their environmental significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* **65**, 73–79.
- FOWLER, K. 1971. A new species of *Aglaoreidia* from the Eocene of southern England. *Pollen et Spores* **13**, 135–147.
- FREDERIKSEN, N.O. 1973. New mid-Tertiary spores and pollen grains from Mississippi and Alabama. *Tulane Studies in Geology and Paleontology* **10**, 65–86.
- FREDERIKSEN, N.O. 1980a. Sporomorphs from the Jackson Group (Upper Eocene) and adjacent strata of Mississippi and western Alabama. *Geological Survey Professional Paper* **1084**, 1–75.
- FREDERIKSEN, N.O. 1980b. Mid-Tertiary climate of southeastern United States: the sporomorph evidence. *Journal of Paleontology* **54**, 728–739.
- FREDERIKSEN, N.O. 1985. Review of early Tertiary sporomorph palaeoecology. *American Association of Stratigraphical Palynologists Contribution Series* **19**, 1–92.
- FREDERIKSEN, N.O. 1988. Sporomorph biostratigraphy, floral changes, and paleoclimatology, Eocene and earliest Oligocene of the eastern Gulf Coast. *United States Geological Survey Professional Paper* **1448**, 1–68.
- FREDERIKSEN, N.O. 1994. Middle and Late Paleocene angiosperm pollen from Pakistan. *Palynology* **18**, 91–137.
- FREDERIKSEN, N.O., EDWARDS, L.E., AGER, T.A. & SHEEHAN, T.P. 2002. Palynology of Eocene strata in the Sagavanirktok and Canning formations on the north slope of Alaska. *Palynology* **26**, 59–93.
- FUCH, J.R. 1970. Ecological and palynological notes on *Pelliciera rhizophorae*. *Acta Botanica Neerlandica* **19**, 884–894.
- GERMERAAD, J.H., HOPPING, C.A. & MÜLLER, J. 1968. Palynology of Tertiary sediments from tropical areas. *Review of Palaeobotany and Palynology* **6**, 189–348.
- GONZÁLEZ-GUZMÁN, A.E. 1967. *A Palynological Study on the Upper Los Cuervos and Mirador Formations (Lower and Middle Eocene, Tibu Area, Colombia)*. E.J. Brill, Leiden.
- GÖKTAŞ, F., ÇAKMAKOĞLU, A., TARI, E., SÜTÇÜ, Y. F. & SARIKAYA, H. 1989. *Çivril-Çardak Arasının Jeolojisi [Geology of Çivril-Çardak Region]*. Mineral Research and Exploration Institute of Turkey (MTA) Report **8701**, 107 p [in Turkish, unpublished].
- GRAHAM, A. 1977. New records of *Pelliciera* (Theaceae/Pelliceriaceae) in the Tertiary of the Caribbean. *Biotropica* **9**, 48–52.
- GRAHAM, A. 1995. Diversification of Gula/Caribbean mangrove communities through Cenozoic time. *Biotropica* **27**, 20–27.
- GRAY, J. 1960. Temperate pollen genera in the Eocene (Claiborne) flora, Alabama. *Science* **132**, 808–810.
- GREENWOOD, D.R. & WING, S.L. 1995. Eocene continental climates and latitudinal temperature gradients. *Geology* **23**, 1044–1048.
- GRUAS-CAVAGNETTO, C. 1977. Étude palynologique de l'Eocène du Bassin Anglo-Parisien. Thèse de Doctorat d'État es Sciences Naturelles, Université de Pierre Marie Curie **VI**, 287 p.
- GRUAS-CAVAGNETTO, C. 1978. Étude palynologique de l'Eocène du Bassin Anglo-Parisien. *Mémoire de la Société Géologique de France* **131**, 1–64.
- HASELDONCKX, P. 1972. The presence of *Nypa* palm in Europe: a solved problem. *Geologie en Mijnbouw* **51**, 645–650.
- HOCHULI, P.A. 1978. Palynologische Untersuchungen im Oligozän und Untermiozän der Zentralen und Westlichen Paratethys. *Beiträge Paläontologie Österreich* **4**, 1–132.
- HOCHULI, P.A. 1984. Correlation of the Middle and Late Tertiary sporomorph assemblage. *Paléobiologie continentale* **14**, 301–314.
- JIMÉNEZ, J.A. 1984. A hypothesis to explain the reduced distribution of the mangrove *Pelliciera rhizophorae* Tr. & Pl. *Biotropica* **16**, 304–308.
- KEDVES, M. 1969. Etudes palynologiques des couches du Tertiaire inférieur de la région Parisienne. IV. Pollens des Normapolles. *Pollen et Spores* **11**, 385–396.
- KEDVES, M. 1970. Etudes palynologiques des couches du Tertiaire inférieur de la région Parisienne. *Pollen et Spores* **12**, 83–97.
- KEDVES, M. 1982. Palynology of the Thanetian layers of Ménat. *Palaeontographica Abteilung B Ionnides* **182**, 87–150.
- KEDVES, M. 1986. Paleogene fossil sporomorphs of the Bakony Mountains IV. *Studia Biologica Hungarica* **21**, 1–120.
- KOÇYİĞİT, A. 2005. The Denizli graben-horst system and the eastern limit of western Anatolian continental extension: basin fill, structure, deformational mode, throw amount and episodic evolutionary history, SW Turkey. *Geodinamica Acta* **18**, 167–208.
- KONAK, N., AKDENİZ, N. & ÖZTÜRK, E.M. 1987. *Geology of the South of Menderes Massif*. Guide Book for the Field Excursion Along Western Anatolia, IGCP Project No. **5**, 42–53.
- KORALAY, O.E., DORA, O.Ö., CHEN, F., SATIR, M. & CANDAN, O. 2004. Geochemistry and geochronology of orthogneisses in the Derbent (Ağşehir) area, eastern part of the Ödemiş-Kiraz submassif, Menderes Massif: Pan-African magmatic activity. *Turkish Journal of Earth Sciences* **13**, 37–61.

- KRUTZSCH, W. 1957. Sporen- und Pollengruppen aus der Oberkreide und dem Tertiär Mitteleuropas und ihre stratigraphische Verteilung. *Zeitschrift für Angewandte Geologie* **3**, 509–548.
- KRUTZSCH, W. 1970. *Atlas der mittel- und jungtertiären dispersen Sporen- und Pollen- sowie der Mikroplanktonformen des nördlichen Mitteleuropas*. Lieferung VII, VEB Gustav Fischer Verlag, Jena, 175 p.
- KRUTZSCH, W. & VANHOORNE, R. 1977. Die pollen flora von Epinois und Loksbergen in Belgien. *Palaeontographica Abteilung B Ionnides* **163**, 1–110.
- LENZ, O.K. & RIEGEL, W. 2001. Isopollen maps as a tool for the reconstruction of a coastal swamp from the Middle Eocene at Helmstedt (northern Germany). *Facies* **45**, 177–194.
- MOSBRUGGER, V. & UTESCHER, T. 1997. The coexistence approach – a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using the plant fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* **134**, 61–86.
- MÜLLER, J. 1980. Fossil pollen records of extant angiosperms. *Botanical Review* **47**, 1–142.
- MÜLLER, J. 1981. Palynological evidence for Paleogene climatic changes. *Mémoires du Museum National d'Histoire Naturelle, Nouvelle Série*, B Botanique **XXVII**, 211–218.
- NAKOMAN, E. 1966. Analyse sporopollinique des lignites eocenes de Sorgun (Yozgat–Turquie). *Mineral Research and Exploration Institute of Turkey (MTA) Bulletin* **67**, 68–88.
- NICKEL, B. 1996. Palynofazies und Palynostratigraphie der Pechelbronn Schichten im nördlichen oberrhein talgraben. *Palaeontographica Abteilung B Ionnides* **240**, 1–151.
- NIX, H.A. 1982. Environmental determinations of biogeography and evolution in Terra Australis. In: BARKER, W.S. & GREENSLADE, P.J.M. (eds), *Evolution of the Flora and Fauna of Arid Australia*. Peacock Publication, Adelaide, 47–66.
- OLLIVIER-PIERRE, M.F., MAUPIN, C., ESTÉOULE-CHOUX, J. & SITTNER, C. 1993. Transgression et paleoenvironnement à l' Oligocène en Bretagne. Sédimentologie, micropaléontologie palynologie et palynofaciés du Rupélien du Bassin de Rennes. *Palaeogeography, Palaeoclimatology, Palaeoecology* **103**, 223–250.
- ÖZER, S., SÖZBİLİR, H., ÖZKAR, İ., TOKER, V. & SARI, B. 2001. Stratigraphy of Upper Cretaceous-Palaeogene sequences in the southern and eastern Menderes Massif (western Turkey). *International Journal of Earth Sciences* **89**, 852–866.
- ÖZKAYA, İ. 1990. Origin of Lycian Nappes, SW Turkey. *Tectonophysics* **177**, 367–379.
- ÖZKAYA, İ. 1991. Evolution of a Tertiary volcanogenic trough in SW Turkey – the Alakaya basin of the Lycian belt. *Geologische Rundschau* **80**, 657–668.
- PLAZIAT, J.C., CAVAGNETTO, C., KOENIGUER, J.C. & BALTZER, F. 2001. History and biogeography of the mangrove ecosystem, based on a critical reassessment of the paleontological record. *Wetlands Ecology and Management* **9**, 161–179.
- POISSON, A. 1976. Essai d'interprétation d'une transversale Korkuteli–Denizli (Taurus ouest-anatolien-Turquie). *Bulletin of the Geological Society of France* **2**, 499–509.
- POLE, M.S. & MACPHAIL, M.K. 1996. Eocene *Nypa* from Regatta Point, Tasmania. *Review of Palaeobotany and Palynology* **92**, 55–67.
- RIEGEL, W., BODE, T., HAMMER, J., HAMMER-SCHLIMMANN, G., LENZ, O. & WILDE, V. 1999. The palaeoecology of the Lower and Middle Eocene at Helmstedt, northern Germany – a study in contrasts. *Acta Palaeobotanica Supplement* **2**, 349–358.
- ROCHE, E. 1988. Pollen and spores (compilation). In: VINKEN, R. (ed), *The Northwest European Tertiary Basin*. Geologisches Jahrbuch (Hannover), Reihe A **100**, 288–320.
- RULL, V. 1992. Paleoecología y análisis secuencial de una sección deltaica Terciaria en la Cuenca de Maracaibo. *Boletín Sociedad Venezolana Geólogos* **46**, 16–26.
- RULL, V. 1997a. Sequence analysis of western Venezuelan Cretaceous to Eocene sediments using palynology; chrono-paleoenvironmental and paleovegetational approaches. *Palynology* **21**, 79–90.
- RULL, V. 1997b. Oligo–Miocene palynology of the Rio Chama sequence (western Venezuela), with comments on fossil algae as paleoenvironmental indicators. *Palynology* **21**, 213–229.
- RULL, V. 1998a. Middle Eocene mangroves and vegetation changes in the Maracibo Basin. *Palaios* **13**, 287–296.
- RULL, V. 1998b. Biogeographical and evolutionary considerations of *Mauritia* (Arecaceae), based on palynological evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* **100**, 109–122.
- RULL, V. 1999. Paleofloristic and paleovegetational changes across the Paleocene–Eocene boundary in northern South America. *Palaeogeography, Palaeoclimatology, Palaeoecology* **107**, 83–95.
- RYAN, P.D., HARPER, D.A.T. & WHALLEY, J.S. 1995. *PALSTAT, Statistics for palaeontologists*. Chapman & Hall, London (now Kluwer Academic Publishers).
- ŞAHBAZ, A. & GÖRMÜŞ, S. 1992. Çardak (Denizli) kuzeyindeki Eosen ve Oligosen yaşlı konglomeraların stratigrafik ve sedimentolojik incelenmesi. [Stratigraphic and sedimentological investigation of Eocene and Oligocene conglomerates in the north of Çardak (Denizli)] *9th Petroleum Congress of Turkey* **2**, 62–74 [in Turkish with English abstract].
- SARI, B. & ÖZER, S. 2002. Upper Cretaceous stratigraphy of the Bey Dağları carbonate platform, Korkuteli area (Western Turides, Turkey). *Turkish Journal of Earth Sciences* **11**, 39–59.
- SCHMIEDL, G., SCHERBACHER, M., BRUCH, A.A., JELEN, B., NEBELSICK, J.H., HEMLEBEN, C., MOSBRUGGER, V. & RIFELJ, H. 2002. Palaeoenvironmental evolution of the Paratethys in the Slovenian Basin during the Late Paleogene. *International Journal of Earth Sciences* **91**, 123–132.
- ŞENEL, M. 1991. Palaeocene-Eocene sediments interbedded with volcanics within the Lycian Nappes: Faralya formation. *Mineral Research and Exploration Institute of Turkey Bulletin* **113**, 1–14.
- ŞENEL, M. 1997. *Denizli–J9 Quadrangle, 1:100,000 Scale Geological Map and Explanatory Text*. Mineral Research and Exploration Institute of Turkey (MTA) Publications, Ankara.

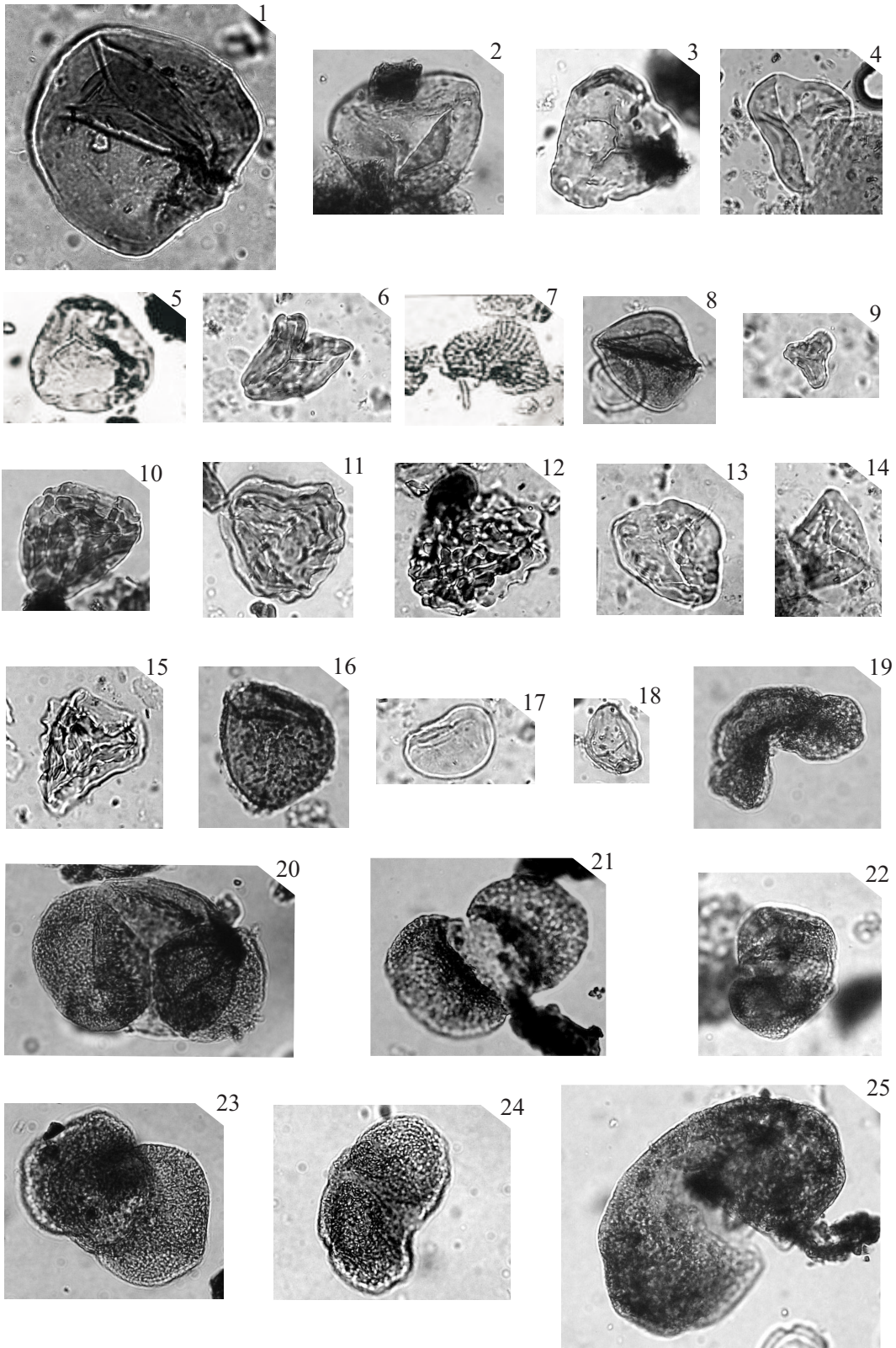
- ŞENGÖR, A.M.C. & YILMAZ, Y. 1981. Tethyan evolution of Turkey: a plate tectonic approach. *Tectonophysics* **75**, 181–241.
- ŞENGÖR, A.M.C., GÖRÜR, N. & ŞAROĞLU, F. 1985. Strike-slip deformation, basin formation and sedimentation: Strike-slip faulting and related basin formation in zones of tectonic escape: Turkey as a case study. In: BIDDLE, K.T. & CHRISTIE-BUCK, N. (eds), *Strike-slip Faulting and Basin Formation*. Society of Economic Paleontologists and Mineralogist, Special Publications **37**, 227–264.
- SEYİTOĞLU, G. & SCOTT, B. 1996. The cause of N-S extensional tectonics in western Turkey: tectonic escape vs back-arc spreading vs orogenic collapse. *Journal of Geodynamics* **22**, 145–153.
- SÖZBİLİR, H. 2002. Revised stratigraphy and facies analysis of Palaeocene–Eocene supra-allochthonous sediments (Denizli, SW Turkey) and their tectonic significance. *Turkish Journal of Earth Sciences* **11**, 87–112.
- SÖZBİLİR, H. 2005. Oligo–Miocene extension in the Lycian orogen: evidence from the Lycian molasse basin, SW Turkey. *Geodinamica Acta* **18**, 255–282.
- SÖZBİLİR, H., ÖZER, S., SARI, B. & AVŞAR, N. 2001. Supra-allochthon sedimentary succession in western Anatolia: new stratigraphic data and tectonic results. *Fourth International Turkish Geology Symposium*, Abstracts, 36.
- SRIVASTAVA, S.K. & BINDA, P.L. 1991. Depositional History of the Early Eocene Shumaysi Formation, Saudi Arabia. *Palynology* **15**, 47–61.
- STUCHLIK, L., ZIEMBIŃSKA-TWORZYDŁO, M., KOHLMAN-ADAMSKA, A., GRABOWSKA, I., WAŻYŃSKA, H., SŁODKOWSKA, B. & SADOWSKA, A. 2001. Atlas of pollen and spores of Polish Neogene. W. Szafer Institute of Botany, *Polish Academy Sciences* **1**, 1–69.
- THANIKAIMONI, G. 1987. Mangrove palynology. Institut français de Pondichéry, *Travaux de la Section Scientifique et Technique XXIV*, 1–100.
- THANIKAIMONI, G., CARATINI, C., VENKATACHALA, B.S., RAMANUJHAM, C.G.K. & KAR, R.K. 1984. Selected Tertiary angiosperms pollen from India and their relationship with African Tertiary pollens. Institut français de Pondichéry, *Travaux de la Section Scientifique et Technique XIX*, 1–192.
- THIELE-PFEIFFER, H. 1988. Die Mikroflora aus dem mitteloazänen ölschiefers von Messel bei Darmstadt. *Palaeontographica Abteilung B Ionnides* **211**, 1–86.
- THOMSON, P.W. & PFLUG, H. 1953. Pollen und Sporen des mitteleuropäischen Tertiärs. *Palaeontographica Abteilung B Ionnides* **94**, 1–138.
- UPCHURCH, G.R. & WOLFE, J. A. 1987. Mid-Cretaceous to early Tertiary vegetation and climate: evidence from fossil leaves and woods. In: FRIIS, E.M., CHALONER, W.G. & CRANE, P.H. (eds), *The Origins of Angiosperms and Their Biological Consequences*. Cambridge University Press, 75–105.
- VAN DER HAMMEN, T. & WIJMSTRA, T.A. 1964. A palynological study on the Tertiary and Upper Cretaceous of British Guiana. *Leidse Geologische Mededelingen* **30**, 183–241.
- VINKEN, R. 1988. *The Northwest European Tertiary Basin*. (IGCP 124). Geologisches Jahrbuch (Hannover) Reihe A **100**, 1–508.
- WESTAWAY, R., GUILLOU, H., YURTMEN, S., DEMİR, T., SCAILLET, S. & ROWBOTHAM, G. 2005. Constraints on the timing and regional conditions at the start of the presence phase of crustal extension in western Turkey, from observations in and around the Denizli region. *Geodinamica Acta* **18**, 209–238.
- WESTGATE, J.W. & GEE, C.T. 1990. Palaeoecology of a Middle Eocene mangrove biota (vertebrates, plants and invertebrates) from southwest Texas. *Palaeogeography, Palaeoclimatology, Palaeoecology* **78**, 163–177.
- WOLFE, J.A. 1978. A paleobotanical interpretation of Tertiary climates in northern hemisphere. *American Scientist* **66**, 694–703.
- WOLFE, J.A. 1979. Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the Northern Hemisphere and Australasia. *United States Geological Survey Professional Paper* **1106**, 37 p.
- WOLFE, J.A. 1992. Climatic, floristic and vegetational changes near the Eocene/Oligocene boundary in North America. In: PROTHERO, D.R. & BERGGREN, W.A. (eds), *Eocene–Oligocene Climatic and Biotic Evolution*. Princeton University Press, 421–436.
- YALÇINKAYA, S., ENGIN, A., TANER, K., AŞAR, Ö.P., DALKILIÇ, H. & ÖZGÖNÜL, E. 1986. *Bati Torosların Jeolojisi [Geology of Western Taurides]*. Mineral Research and Exploration Institute of Turkey (MTA) Report **7898**, 132 p [in Turkish, unpublished].
- YASAMANOV, N.A. 1982. The problem of global changes in temperature regime of the earth's surface during Cenozoic time. *Izvestiya AN SSSR, seriya geologicheskaya* **10**, 106–110.

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**Plate I**

**(all photomicrographs x 500)**

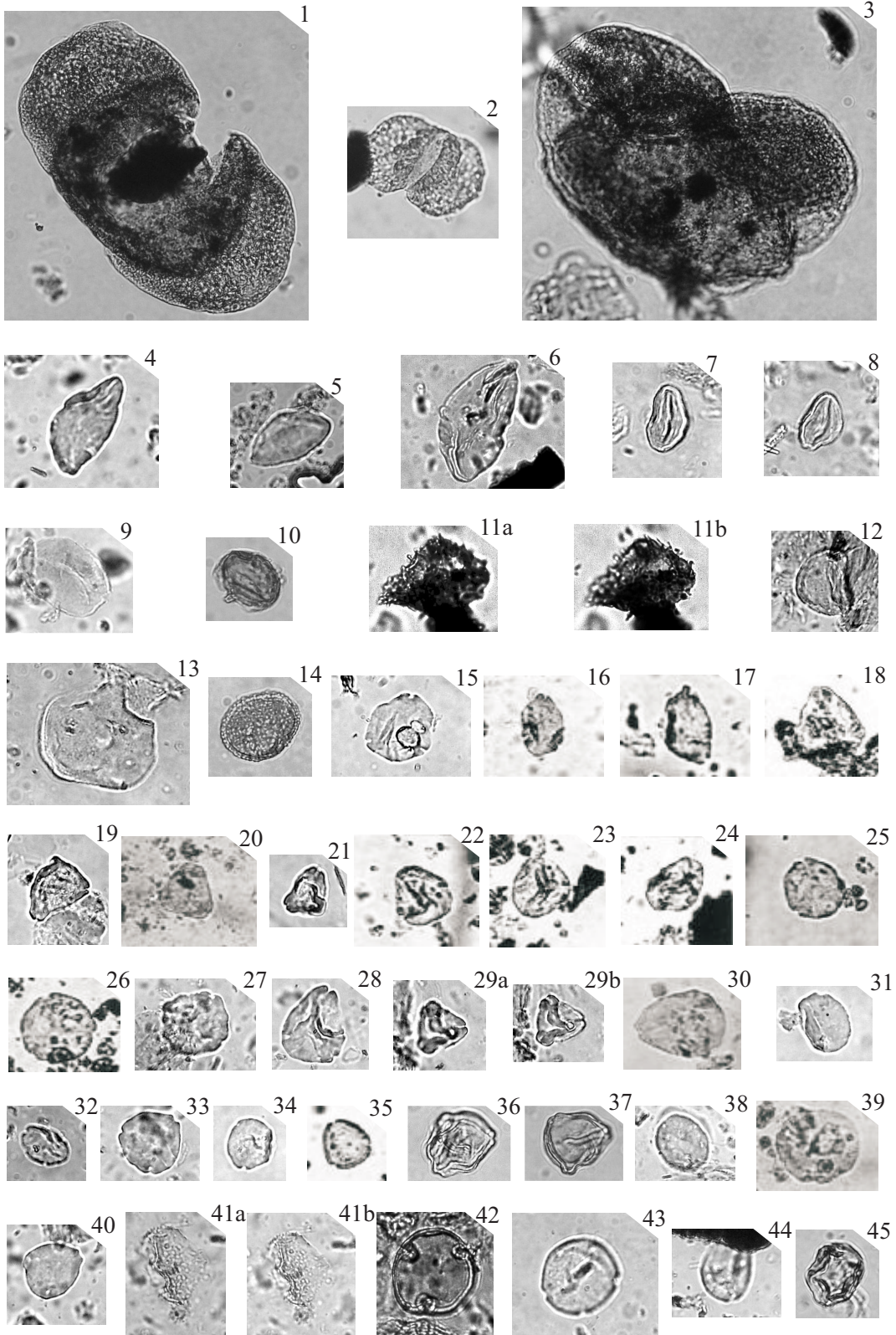
- Figure
- 1, 2 *Leiotriletes adriennis* (R. Potonié and Gelletich) Krutzsch
  - 3 *Leiotriletes minoris* (Krutzsch) Ziemińska-Tworzydło
  - 4 *Leiotriletes wolffii* Krutzsch
  - 5 *Leiotriletes microadriennis* Krutzsch
  - 6 *Leiotriletes* sp.
  - 7 *Cicatricosisporites* sp.
  - 8 *Triplanosporites microsinuosus* Pflanzl
  - 9 *Polypodiaceosporites microconcaus* Krutzsch
  - 10 *Polypodiaceosporites kedvesii* Stuchlik
  - 11 *Polypodiaceosporites muricinguliformis* Nagy
  - 12-15 *Polypodiaceosporites* sp.
  - 16 *Retitriletes* sp.
  - 17, 18 *Laevigatosporites haardti* (R. Potonié & Venkatachala) Thomson & Pflug
  - 19, 20 *Pityosporites labdacus* (R. Potonié) Thomson & Pflug
  - 21-24 *Pityosporites microalatus* (R. Potonié) Thomson & Pflug
  - 25 *Abiespollenites* cf. *absolutus* Thiergart



**Plate II**

**(all photomicrographs x 500)**

- Figure
- 1 *Abiespollenites* cf. *absolutus* Thiergart
  - 2 *Cathayapollis pulaënsis* (Nagy) Ziemińska-Tworzydło
  - 3 *Cathayapollis* sp.
  - 4,5 *Cycadopites gracilis* (Wodehouse) Krutzsch
  - 6 *Cycadopites intrasructus* Krutzsch
  - 7,8 *Cycadopites* cf. *minimus* Krutzsch
  - 9 *Psilamonocolpites* sp.
  - 10 *Sequoiapollenites polyformosus* Thiergart
  - 11a, b *Spinizonocolpites* sp.
  - 12 *Longapertites* sp.
  - 13 *Kopekipollenites transdanubicus* Kedves
  - 14 *Sparganiaceapollenites polygonalis* Theiergart
  - 15 *Triatriopollenites bituitus* (R. Potonié) Thomson & Pflug
  - 16-19 *Triatriopollenites excelsus* (R. Potonié) Thomson & Pflug ssp. *typicus* Pflug
  - 20, 21 *Triatriopollenites excelsus* (R. Potonié) Thomson & Pflug ssp. *minor* Pflug
  - 22-24 *Plicatopollis plicatus* (R. Potonié) Krutzsch
  - 25-29 *Plicatopollis lunatus* Kedves
  - 30 *Tripoporopollenites robustus* (Pflug) Thomson & Pflug
  - 31 *Tripoporopollenites* sp.
  - 32-35 *Momipites quietus* (R. Potonié) Nichols
  - 36, 37 *Trivestibulopollenites betuloides* Pflug in Thomson & Pflug
  - 38 *Subtripoporopollenites anulatus* (Pflug) ssp. *nanus* Pflug & Thomson in Thomson & Pflug
  - 39 *Subtripoporopollenites constans* (Pflug) Thomson & Pflug
  - 40 *Olaxipollis matthesii* Krutzsch
  - 41a,b *Mauritiidites franciscoi* (Van Der Hammen) Van Der Hammen & Garcia de Mutis
  - 42 *Intratripoporopollenites indubitalibis* (R. Potonié) Pflug & Thomson in Thomson & Pflug
  - 43, 44 *Polypoporopollenites undulosus* (Wolff) Thomson & Pflug
  - 45 *Polyvestibulopollenites verus* (R. Potonié) Thomson & Pflug





**Plate III**

**(all photomicrographs x 500)**

- Figure
- 1 *Myrtaceidites mesonesus* Cookson & Pike
  - 2 *Pentapollenites pentangulus* (Pflug in Thomson & Pflug) Krutzsch
  - 3, 4 *Tricolpopollenites microhenrici* (R. Potonié) Thomson & Pflug
  - 5 *Tricolpopollenites liblarensis* (Thomson) Thomson & Pflug ssp. *fallax* (R. Potonié) Thomson & Pflug
  - 6 *Tricolpopollenites liblarensis* (Thomson) Thomson & Pflug spp. *liblarensis* (Thomson) Thomson & Pflug
  - 7 *Tricolpopollenites parmularius* (R. Potonié) Thomson & Pflug
  - 8 *Tricolpopollenites retiformis* (Pflug & Thomson) Thomson & Pflug
  - 9, 10 *Tricolporopollenites cingulum* (R. Potonié) Thomson & Pflug ssp. *fuscus* (R. Potonié) Thomson & Pflug
  - 11 *Tricolporopollenites cingulum* (R. Potonié) Thomson & Pflug ssp. *pusillus* (R. Potonié) Thomson & Pflug
  - 12, 13 *Tricolporopollenites megaexactus* (R. Potonié) Thomson & Pflug ssp. *brühlensis*  
(Thomson in Potonié) Thomson & Thiergart
  - 14 *Tricolporopollenites* cf. *pseudocingulum* (R. Potonié) Thomson & Pflug
  - 15-19 *Psilatricolpites crassus* Van Der Hammen & Wymstra
  - 20 *Psilatricolporites* cf. *costatus* Dueñas
  - 21 *Chenopodipollis multiplex* (Weyland & Pflug) Krutzsch
  - 22-24 *Nowemproctus tumanganicus* (Bolotnikova) Frederiksen
  - 25, 26 undifferentiated dinoflagellate cysts
  - 27, 28 *Pediastrum* spp.

