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THE MAKRILIA-FLORA (CRETE, GREECE) – A CONTRIBUTION TO THE NEOGENE HISTORY OF THE CLIMATE AND VEGETATION OF THE EASTERN MEDITERRANEAN

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ABSTRACT. The combined interpretation of marine and terrigeneous macro- and microfossils from the marine Late Miocene Makrilia Formation near Ierapetra, south-eastern Crete was used for the reconstruction of the palaeoenvironment and palaeoclimatic conditions. The continental derived material in this near shore environment includes leaves, fruits/seeds and pollen grains. For climatic interpretation the climatic requirements of the nearest living relatives of the Makrilia-Flora have been considered and leaf margin analyses have been applied. In combiantion with the present distribution of coral reefs, a fish taxon and distinct dinocyst assemblages, these data suggest a subtropical climate with temperatures similar to those of today but with higher precipitation. The terrestrial vegetation represented in the fossil assemblage indicates a subtropical to transitional subtropical/tropical vegetation (sensu Song 1983, 1988) with arid seasons. Recently published computer simulations suggest that this may have been expressed as weakly developed summer dryness. A palaeovegetational interpretation has been attempted, taking into consideration potential transport and sorting of leaves and pollen and plant-biome distributions in present-day environments.

KEY WORDS: Eastern Mediterranean, palaeoclimate, palaeovegetation, Crete, Late Miocene, macroflora, pollen, dinocysts

INTRODUCTION

In the south-eastern part of Crete a palaeobotanical and palynological investigation (Sachse & Mohr 1996, Sachse 1997) in the type locality of the Late Miocene Makrilia Formation allowed us to carry out an integrated investigation of both continental and marine fossils. The locality is situated in a curve of the road from Ierapetra to the village of Makrilia, some 100 m SE of Makrilia and 8 km north of Ierapetra. For the palynological record 9 samples from the type locality as well as 4 samples from a section some 100 m above have been used. About 130 taxa of macroscopic plant remains (only impressions), pollen grains and spores (Tab. 1), as well as about 60 taxa of dinocysts, acritarchs, Prasinophyceae, and fresh water algae have been identified. A detailed taxonomical treatment will be published later. An overview of the terrigeneous fossils is given in Table 1, the leaf taxa are presented in Figs 1, 2. For pollen grain identifications, the modern botanical nomenclature (mainly at the genus level) has been preferred to the artificial palynological nomenclature. Indeed, it has been demonstrated that most of the European Neogene pollen grains belong to modern botanical genera (Suc & Bessais 1981).

The marine Makrilia Formation represents an alternation of hemipelagic marls and sandy turbiditic layers. The plant remains analysed here are contained in a short interval of silty layers of a few meters thickness. These are interpreted as deriving from river floods during high precipitation events. The Makrilia Formation was deposited in an active half-graben system of the Ierapetra basin which formed in the subduction zone south of Crete (Fortuin 1977). Integrated biostratigraphy of dinocysts and nannoplankton yields an age of 7.7–8.6 Ma (Late Tortonian). The unusual combination in the investigated beds of marine and terrigeneous macro- and microfossils allow an interdisciplinary palaeoclimatic interpretation and contributes to a better understanding of Neogene climate and vegetation in Greece and the entire Mediterranean. Present conceptions still range from mixed-mesophytic forests correlated with a humidity balanced Cfa-Climate (e.g. Gregor 1990; Velitzelos & Gregor 1990) to a lateral and altitudinal diversified pattern including semi-arid open landscapes (e.g. Pons *et al*. 1995, Suc *et al.* 1995).

PALAEOCLIMATE

To reduce the large uncertainties related to taphonomy, taxonomy and evolutionary adaptation, all available terrestrial plant remains (e.g. pollen grains, leaves,

Table 1. Composition of the Makrilia flora. Large fields indicate taxa, that cannot be separated

Family	Genus, Species	Leaves	other	Pollen(%)
Cupr., Taxac., Taxod.	indet.			< 1
Cupressaceae	*Tetraclinis salicornoides*		1 twig	
Cupressaceae	*Tetraclinis*		1 seed, 1 cone	
			3 twig segments	
Taxodiaceae	*Taxodium dubium*		1 twig pits	< 1
Pinaceae	indet.			53
Pinaceae	*Abies*			2.4
Pinaceae	*Cathaya*			15.2
Pinaceae	*Cedrus*			4.3
Pinaceae	*Picea*			1.9
Pinaceae	*Pinus* cf. *hampeana*	1x two needled		
Pinaceae	*Pinus* cf. *hepios*	1x two needled		
Pinaceae	*Pinus* spp.	1x five-, 2x two-, 3x simple-needled		22.4
Pinaceae	indet.		1 cone scale	
Pinaceae	*Tsuga*			< 1
Pinidae fam.	indet.		1 cone	
Ephedraceae	*Ephedra* spp.			< 1
Monocotyledonae	indet.		20 sprout fragm.	
Cyperaceae	indet.		4 sprout fragm.	0 – 3
Liliaceae	indet.			< 1
Liliaceae	*Dipcadi*			< 1
Palmae	*Nypa*			? <1
Poaceae	indet.			0.2 – 7
Potamogetonaceae	*Potamogeton*			0 – 5
Potamogetonaceae	*Potamogeton* type *lucens*			< 1
Potamogetonaceae	*Cymodocea* vel *Posidonia*		2 rhizoms	
Ruppiaceae	cf. *Ruppia*		1 seed	
Smilacaceae	cf. *Smilax*	2		
Sparganiaceae	indet.			< 1
Typhaceae	*Typha*			< 1
Acanthaceae	type *Peristophe*			< 1
Aceraceae	*Acer* spp.		3 winged seeds	< 1
Aceraceae	*Acer decipiens*	14		< 1
Anacardiaceae	*Pistacia* type *lentiscus*	? 1 leaflet		
Apiaceae	fsp. *Umbelliferoipollenites ovatus*			< 1
Apiaceae	*Molospermum*			< 1
Aquifoliaceae	*Ilex* type *aquifolium*	? 1		< 1
Aquifoliaceae	fsp. *Ilexpollenites margaritatus*			< 1
Araliaceae	*Araliaceoipollenites euphorii*			< 1
Araliaceae	*Hedera*			< 1
Asteraceae	Asteroideae			1 – 2
Asteraceae	type *Centaurea*			< 1
Asteraceae	fsp. *Cichoriaearumpollenites gracilis*			0 – 2
Berberidaceae	*Berberis, Mahonia*	? 2		
Betulaceae	cf. *Alnus*	1		0 – 2
Brassiacaceae	indet.			< 1
Buxaceae	*Buxus* cf. *egeriana*/*B.* type *myrica*	2		< 1
Buxaceae	*Buxus pliocenica*/*B.* type *balearica*	2		< 1
Buxaceae	*Buxus* type *bahamensis*			< 1
Caprifoliaceae	*Lonicera* type *etrusca*/fsp. *Lonicerapollis gallwitzi*	1		< 1

Table 1. Continued

Family	Genus, Species	Leaves	other	Pollen(%)
Caprifoliaceae	*Sambucus*			< 1
Caryophyllaceae	indet.			< 1
Celastraceae	indet.			< 1
Celastraceae	*Celastrus*			< 1
Celastraceae	*Microtropis* cf. *fallax*			0 – 5
Chenopodiaceae	indet.			< 1
Cistaceae	*Helianthemum*			< 1
Cistaceae	*Cistus*			< 1
Convolvulaceae	*Convolvulus* spp.			< 1
Corylaceae	*Carpinus*	3 – 8		0 – 3
Corylaceae	*Carpinus* type *orientalis*		2 seeds	
Cyrillaceae	type *Cyrilla*			<1
Dipsacaceae	*Scabiosa*			<1
Ericaceae vel Myrtaceae	indet.	1		
Ericaceae, Empetraceae	indet.			<1
Fagaceae	*Fagus* type *attenuata*	3		0 – 2
Fagaceae	*Fagus* type *gussonii*	10		
Fagaceae	*Quercus*, deciduous			<1
Fagaceae	*Quercus kubinyi*	1		
Fagaceae	*Quercus* cf. *mediterranea*	4		1 – 4
Fagaceae	cf. *Quercus rhenana*	1		
Fagaceae	*Quercus*		1fruit	0 3
Flacourtiaceae	*Homalium* vel Styracaceae		? 1 flower	
Juglandaceae	Engelhardieae	6	1 seed	3 – 11
Juglandaceae	*Carya*		1 fruit	4 – 16
Juglandaceae	*Juglans*			0 – 2
Juglandaceae	*Pterocarya*			0 – 5
Labiaceae	indet.			<1
Lauraceae	*Laurophyllum* spp.	6 – 10		
Lauraceae	*Cinnamomophyllum* spp.	3		
Leguminoseae	cf. *Leguminosites* spp.	15 leaflets	1 winged seed	
Leguminoseae/Caes.	*P. podocarpum*/fsp. *T. sibiricum*	4 leaflets		<1
Leguminoseae/Caes.	type *Dalbergia*	5 leaflets, 1 leaf		
Leguminoseae/Mim.	fgen. *Acaciapollenites*		1	<1
Leguminoseae/Mim.	fgen. *Polyadopollenites multipartitus*			<1
Leguminoseae/Papil.	indet.			<1
Leguminoseae/Papil.	*Cladastris*	? 1, twig (5 leaflets)		
Leguminoseae/Papil.	*Machaerium* spp.	? 2		
Leguminoseae/Papil.	*Swartzia*	? 1		
Linaceae	*Linum* spp.			<1
Magnoliaceae	*Magnolia*	? 1		
Magnoliaceae	*Illicum rhenanum*	? 1		
Moraceae	*Morus* type *nigra*			<1
Myricaceae	*Myrica* type *lignitum*	8		0 – 3
Myristicaceae	indet.			<1
Myrtaceae	indet.	3		
Nyssaceae	indet.			<1
Oleaceae	*Fraxinus*		1 fruit	
Oleaceae	*Phillyrea*	? 1		
Oleaceae	cf. *Osmanthus*			0 – 8
Oleaceae	*Olea* type *europaea*			<1

(cont.)

Table 1. Continued

Family	Genus, Species	Leaves	other	Pollen(%)
Plantaginaceae	*indet.*			<1
Polygonaceae	*indet.*			<1
Ranunculaceae	*indet.*		? 1 seed	<1
Rosaceae	*Sanguisorba*			<1
Rutaceae	*Ruta, Dictamus*			? <1
Rutaceae	cf. *Toddalia*		1 seed	
Salicaceae	*Populus*		1 fruit	
Salicaceae	*Salix* spp.	7		<1
Salicaceae	*Salix* type *purpurea*	1		
Sapotaceae	indet.			0 – 9
Simaroubaceae	*Ailanthus* vel *Chenopodiaceae*		1 seed	
Symplocaceae	*Symplocos*			<1
Symplocaceae	*Symplocos* cf. *minutula*	? 1		
Thymeliaceae	*Aquilaria*	1		<1
Tiliaceae	*Tilia*		2 bracts	<1
Tiliaceae	indet.			<1
Ulmaceae	*Celtis*			<1
Ulmaceae	*Ulmus plurinerva*	cf. 3		
Ulmaceae	aff. *Ulmus*		1 winged seed	0 – 4
Ulmaceae	*Zelkova davidii*			<1
Ulmaceae	*Zelkova zelkovaefolia*	1, twig (3 leaves)		1 – 7
Vitaceae	*Ampelopsis* vel *Vitis*	1		
Vitaceae	*Leea*			cf. <1
indet.	fsp. *T. longiplicatus*			<1

fruits) were analysed. Two different methods have been applied:

a) Leaf margin analysis (after Wolfe 1979)

Abundance of leaf shapes have been correlated with mean annual temperatures (MAT), mean temperatures of the coldest month (CMMT) and warmest month (WMMT). The proportion of taxa with entire-margined leaves (60%) in the Makrilia flora suggests a mean annual temperature of 18–19°C. The generally small leaf sizes (microphyllous flora) could either be due to climatic (dryness) or – more likely – taphonomic processes.

b) Modern taxon analog

Alternative approaches rely on the use of climate parameters of the nearest living relatives of the fossil taxa. Using the nearest living relatives of the Makrilia terrestrial macro- and microremains, a range of 14–20°C for MAT (Engelhardieae for lower, *Carpinus orientalis* for upper limit), 5–12°C for CMMT (*Carya* for lower, *Fagus* for upper limit) and 800–1600 mm for the mean annual precipitation (*Zelkova* for lower, *Carya* for upper limit) is estimated.

Marine dinocysts (*Polysphaeridium zoharyi, Operculodinium israelianum)*, corals (*Porites*) and fishes (*Bregmaceros*) may be used as indicators of the palaeoclimate. Varying abundances of dinocyst-, prasinophyte- and freshwater associations of normal marine, lagoonal, and brackish water origin indicate seasonally fluctuating sa-

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Fig. 1. Leaf assemblage from the Makrilia flora. **1** – *Fagus* Typ *gussonii.* No. 96.27; **2** – *Fagus* Typ *attenuata.* No. 96.28; **3** – *Laurophyllum* Typ 1. No. 96.45; **4** – *Carpinus* sp. No. 96.25; **5** – *Fagus* Typ *gussonii.* No. 96.144; **6** – *Dicotylophyllum* Typ 11. No. 96.112; **7** – *Dicotylophyllum* Typ 18. No. 96.145; **8** – *Dicotylophyllum* Typ 22. No. 96.28; **9** – ? *Ilex* Typ *aquifolium.* No. 96.22; **10, 11** – *Quercus mediterranea.* No. 96.30, 96.31; **12** – *Engelhardia orsbergensis.* No. 96.39; **13** – ? Juglandaceae. No. 96.146; **14** – ? *Quercus kubinyi.* No. 96.29; **15** – Dicotylophyllum Typ 12. No. 96.147; **16** – cf. *Quercus rhenana.* No. 96.35; **17** – *Dicotylophyllum* Typ 18. No. 96.148; **18** – *Myrica* sp. Typ *M.* cf. *lignitum.* No. 96.72; **19** – cf. *Salix* sp. No. 96.76; **20** – *Dicotylophyllum* Typ 19. No. 96.149; **21** – *Dicotylophyllum* Typ 18. No. 96.150; **22** – *Dicotylophyllum* Typ 12. No. 96.110; **23** – ? *Salix* sp. 1 vel Oleaceae. No. 96.151; **24** – *Myrica* sp. Typ *M.* cf. *lignitum.* No. 96.68; **25** – *Dicotylophyllum* Typ 5. No. 96.96; **26** – *Myrica* sp. Typ *M.* cf. *lignitum*. No. 96.69; **27** – *Dicotylophyllum* Typ 14. No. 96.111; **28** – ? fgen. *Laurophyllum* Typ 1. No. 96.152; **29** – *Myrica* sp. Typ *M.* cf. *lignitum*. No. 96.75; **30** – *Salix* Typ *purpurea*. No. 96.78; **31** – ? *Salix* sp. 1 vel Oleaceae. No. 96.153; **32** – fsp. *Laurophyllum princeps*. No. 96.40; **33** – ? fgen. *Laurophyllum* Typ 1. No. 96.41; **34** – *Dicotylophyllum* Typ 17. No. 96.102; **35, 36** – *Dicotylophyllum* Typ 18. No. 96.154, No. 96.155. Enlargement: × 1


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linities. Occasionally high concentrations of the neritic cyst taxa *Polysphaeridium zoharyi* (11%) and *Operculodinium israelianum* (5%) suggest sea-surface temperatures of at least 28°C in summer and at least 16°C in winter (Edwards & Andrle 1992).

These temperatures are in agreement with those which may be deduced from the the U.S. Navy Climatic Atlas of the world (1968) for the modern distribution of *Bregmaceros* (Landini & Menesini 1988) and coral reefs (Franseen *et al*. 1996).

Although in Makrilia only *Porites* was found, the presence of contemporary reef deposits, characterized by a low diversity and *Porites* as the dominating taxon, is known from Crete (Chaix & Delrieux 1994) and in nearby Turkey (Tuzcu *et al.* 1997).

Comparable modern coral reefs (e.g. Persian Gulf, Southern Japanese coast) are restricted to areas with a lower limit of 17°C for the mean annual temperature and 10°C for the mean temperature of the coldest month of the coastal continental areas (Walter & Lieth 1967). Using the previously mentioned sources for temperatures in the marine and the nearby coastal continental realm, we found a general correlation in the middle latitudes. The difference of the temperature never exceeds 6°C in winter time, because the relatively warmer ocean water acts as a buffer for the coastal continental temperatures. Therefore the results from the marine record may be used also for the palaeoclimatic reconstruction of the terrestrial realm. The resulting palaeoclimatic parameters indicate that the Tortonian continental and water temperatures were similar to those of today but that precipitation was higher:

1. terrestrial realm
   mean annual temperature: 17–20°C (presumably about 18°C)
   mean temperature of the coldest month: 10–12°C
   annual precipitation: 800–1600 mm/a (presumably about 1000–1200 mm/a)
2. marine realm
   temperatures in wintertime: ≥16°C
   temperatures in summertime: ≥28°C.

PALAEOVEGETATION

The majority of the Makrilia flora indicates a subtropical to warm temperate affinity. However the possible presence of a few taxa pointing to subtropical/tropical influence (see below) is in full agreement with the above mentioned palaeoclimatic data.

The plant remains indicating the warmest temperatures are exclusively preserved as pollen in the Makrilia Formation. Since the leaves of such plants are often shed continuously throughout the year, a storm event will not as easily concentrate and transport them to a marine burial site as is the case with the subtropical plants which often have more distinct vegetation periods. Because of the taphonomical influences, proportional changes in taxonomic composition need to be interpreted with utmost caution.

Comparing the macro- and micro-remains of the Makrilia plant assemblage with the biogeography of recent biomes (e.g. Kloetzli 1988, Song 1983, 1988, Wolfe 1979), the following model is postulated:

A lowland flora consisted of coastal vegetation, riparian forests and subtropical laurophyllous evergreen forest (e.g. *Cinnamomophyllum*, *Taxodium*). The canopy of these forests was dominated by subtropical trees. In the lower tree and shrub strata, taxa comparable to those, that today live under subtropical/tropical conditions (e.g. *Buxus* type *bahamensis*, perhaps *Microtropis fallax*) also existed – like today in the southern subtropical vegetation of China (Song 1988). However, the Makrilia assemblage also contains sclerophyllous elements (e.g. *Cistus*, *Quercus* sect. *Ilex*, *Olea europaea* type). These are found today especially in areas with lower groundwater table or hydric contrasted seasons (e.g. the Mediterranean, Western China). Summergreen plants generally localized at higher elevations (e.g. *Carpinus*, *Fagus, Ulmus, Zelkova*) could also have grown on dryer or immature soils or as secondary vegetation. The Makrilia assemblage also contains pollen of plants which are found today mostly at higher elevations (e.g. *Cedrus*, *Abies*, *Picea*, *Tsuga*), suggesting a considerable topography in the hinterland. The evergreen forests of the lowlands may

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Fig. 2. Leaf assemblage from the Makrilia flora. **1** – cf. *Ampelopsis* vel *Vitis*. No. 96.87; **2, 3** – *Acer* ser. *Monspessulanum*. No. 96.14, No. 96.156; **4** – ? *Acer* Blatt-Typ 1. No. 96.157; **5, 12** – fgen. *Leguminosites* Typ 2. No. 96.61, No. 96.53; **6** – *Dicotylophyllum* Typ 12. No. 96.105; **7** – *Dicotylophyllum* Typ 20. No. 96.158; **8** – ? Leguminosae fam., gen. et sp. indet. No. 96.159; **9** – *Dicotylophyllum* Typ 15. No. 96.160; **10** – *Smilax* cf. *petiolata*. No. 96.16; **11** – ? *Lonicera* Typ *etrusca*. No. 96.23; **12** – cf. Myrtaceae gen. et spec. indet. No. 96.161; **13–15** – *Buxus* cf. *pliocenica*. No. 96.20, No. 96.19, No. 96.162; **16** – ? Leguminosae fam., gen. et sp. indet. vel Typ *Pistacia lentiscus*. No. 96.163; **17** – *Dicotylophyllum* Typ 12. No. 96.164; **18** – *Dicotylophyllum* Typ 16. No. 96.165; **19** – ? Leguminosae fam., gen. et sp. indet. vel Typ *Pistacia lentiscus*. No. 96.66; **20** – *Dicotylophyllum* Typ 1. No. 96.91; **21** – *Dicotylophyllum* Typ 21. No. 96.166; **22** – *Dicotylophyllum* Typ 20. No. 96.167; **23, 25, 26** – ? Leguminosae fam., gen. et sp. indet. No. 96.55, No. 96.168, No. 96.169; **24** – ? fgen. *Leguminosites* Typ 3 (*Dalbergia*-Typ). No. 96.57; **27** – gen. *Leguminosites* Typ 3 (*Dalbergia*-Typ). No. 96.170; **28** – *Dicotylophyllum* Typ 12. No. 96.171; **30** – *Dicotylophyllum* Typ 16. No. 96.108; **31** – ? *Mimosites*. No. 96.152; **32** – cf. Myrtaceae gen. et spec. indet. No. 96.79; **34** – ? *Dicotylophyllum*. No. 96.172; **33, 35** – cf. *Ulmus plurinerva*. No. 96.173, No. 96.84; **36** – *Dicotylophyllum* Typ 7. No. 96.98; **37** – cf. *Alnus gaudinii*. No. 96.18; **38** – *Dicotylophyllum* Typ 12. No. 96.174; **39, 41, 42** – *Dicotylophyllum* Typ 3. No. 96.90; **40** – *Dicotylophyllum* Typ 4. No. 96.95; **43** – fgen. *Laurophyllum* Typ 2. No. 96.46; **44** – Juglandaceae vel Lauraceae. No. 96.175; **45** – *Dicotylophyllum* Typ 23. No. 96.176; **46** – *Zelkova zelkovaefolia*. No. 96.81. Enlargement: × 1


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have changed gradually into humid mixed mesophytic and deciduous forests at mid-altitudes. Slopes with southern exposure would have been covered by mesoxerophytic to xerophytic assemblages. Even higher a mountain vegetation dominated by conifers was situated.

The plant remains may have been transported by river floods and turbidity currents into their offshore burial site. Alternatively, the plant remains might have drifted on the sea surface to the locality of sedimentation, after having been blown by exceptionally strong winds from high coastal cliffs. This hypothesis would also account for the large number of leaves of deciduous taxa, which would have dominated at higher elevations.

The plant association of the Makrilia flora is in full agreement with several proposed climate reconstructions for the Mediterranean Neogene done by computer simulations (e.g. Kutzbach *et al*. 1993, Ramstein *et al*. 1997). Summer dryness had already set in and most of the yearly precipitation took place in winter time, although moisture seasonality was clearly not yet as pronounced as today. Such a gradual summer drying in the eastern Mediterranean area may have been caused by the diminishing moisture supply from Paratethys in the NE and the orogenesis of major mountain belts.

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