A late Miocene leaf assemblage from Vrysses, western Crete, Greece, and its paleoenvironmental and paleoclimatic interpretation

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Zidianakis G., Mohr B. A. R. & Fassoulas C. 2007. — A late Miocene leaf assemblage from Vrysses, western Crete, Greece, and its paleoenvironmental and paleoclimatic interpretation. *Geodiversitas* 29 (3): 351-377.

ABSTRACT
A new leaf impression flora is described from late Miocene marly sediments (6-7.5 Ma) near the village of Vrysses in northwestern Crete, Greece. The studied plant remains represent more than 30 taxa of conifers and angiosperms. Deciduous broad-leaved woody plants such as *Acer pseudomonspessulanum*, 5-lobed *Acer*, *Ziziphus ziziphoides*, "*Parrotia*" *pristina*, *Populus tremula*, *Salix* sp. and Juglandaceae, prevail in this leaf assemblage. These plants are associated with sclerophyllous, evergreen taxa (*Quercus mediterranea*, *Quercus* sp., *Buxus pliocenica* and *Pinus* sp.) and a few subtropical Miocene elements (*Daphnogene polymorpha*, *Tetraclinis* sp.). A regional vegetation reconstruction is developed based on the ecological affinities of the nearest living relatives. The climate conditions are deduced from the physiognomy and composition of the Vrysses plant assemblage. They indicate a warm-humid climate possibly with a weakly developed dry period during the summer months.

KEY WORDS
Late Miocene,
Crete,
Greece,
leaves,
paleovegetation,
paleoclimate.

RÉSUMÉ

Une paléoflore du Miocène supérieur de Vrysses, Crète occidentale (Grèce) et son interprétation paléoenvironnementale et paléoclimatique.

Une nouvelle flore constituée d'empreintes foliaires a été découverte dans des sédiments du Miocène supérieur (6-7,5 Ma) près du village de Vrysses au nord de la Crète (Grèce). L'étude des restes de plantes concerne plus de 30 taxa de conifères et d'angiospermes. Des arbres feuillus décidus, tels qu'*Acer pseudomonspessulanum*, *Acer* à cinq lobes, *Ziziphus ziziphoides*, "*Parrotia*" *pristina*, *Populus tremula*, *Salix* sp. et Juglandaceae, dominent cette paléoflore. Ces plantes sont associées à des taxa sclérophylles (*Quercus mediterranea*, *Quercus* sp., *Buxus pliocenica* et *Pinus* sp.) et à quelques éléments subtropicaux du Miocène (*Daphnogene polymorpha*, *Tetraclinis* sp.). Un modèle de végétation régionale est développé sur la base des affinités écologiques des plus proches parents vivants. Les conditions climatiques sont déduites de la physiognomie et de la composition de la paléoflore de Vrysses et elles indiquent la présence d'un climat chaud et humide avec peut-être une légère période sèche pendant les mois d'été.

MOTS CLÉS
Miocène supérieur,
Crète,
Grèce,
feuilles,
paléovégétation,
paléoclimat.

INTRODUCTION

During the last decades progress had been made in understanding Late Neogene eastern Mediterranean vegetation and climate. For many years the results of paleoclimatic studies were highly controversial and often hampered by the lack of precise dating of plant bearing strata. Therefore paleoclimatic reconstructions for Miocene climates differed, ranging from humid climates with maximum precipitation during summer (e.g., Gregor 1990) to strongly seasonal climates with minimum precipitation during summer (e.g., Palamarev 1989). Recent climate reconstructions for the European Tertiary using the Coexistence Approach revealed that spatial temperature gradients became more strongly developed during the early late Miocene and must have become even more differentiated towards the end of the Miocene (Bruch *et al.* 2004). Studies on a well dated late Tortonian plant assemblage from eastern Crete near the village Makrilia confirmed that besides laurophyllous and deciduous taxa, the sclerophyllous Mediterranean component was more pronounced than in central European floras of similar age (Sachse *et al.* 1999) indicating possibly a seasonal climate with a (weakly developed) summer drought.

In western Crete plant megafossils have never been collected systematically so far. Meulenkamp *et al.* (1979) were the first who recognized plant macro-fossils in the laminated marls of the Vrysses basin. During the last decades more fossils came to light in small quarries where Neogene limestone is worked for building purposes. In order to study Neogene vegetation and climate of this part of the island, a survey on Neogene sedimentary rocks all over western Crete was undertaken (Zidianakis 2002) for new outcrops containing plant macro-remains.

Although stratigraphy and fauna of Cretan Neogene strata are well studied (Meulenkamp *et al.* 1979; Kuss 1980; Dermitzakis & Papanikolaou 1981; Peters 1985; Frydas & Keupp 1996; ten Veen 1998), vegetation studies are rare and mainly focused on eastern Crete (Mohr *et al.* 1991; Sachse & Mohr 1996; Sachse 1997; Sachse *et al.* 1999).

The discovery and study of the Vrysses plant assemblage offers the opportunity for a comparison

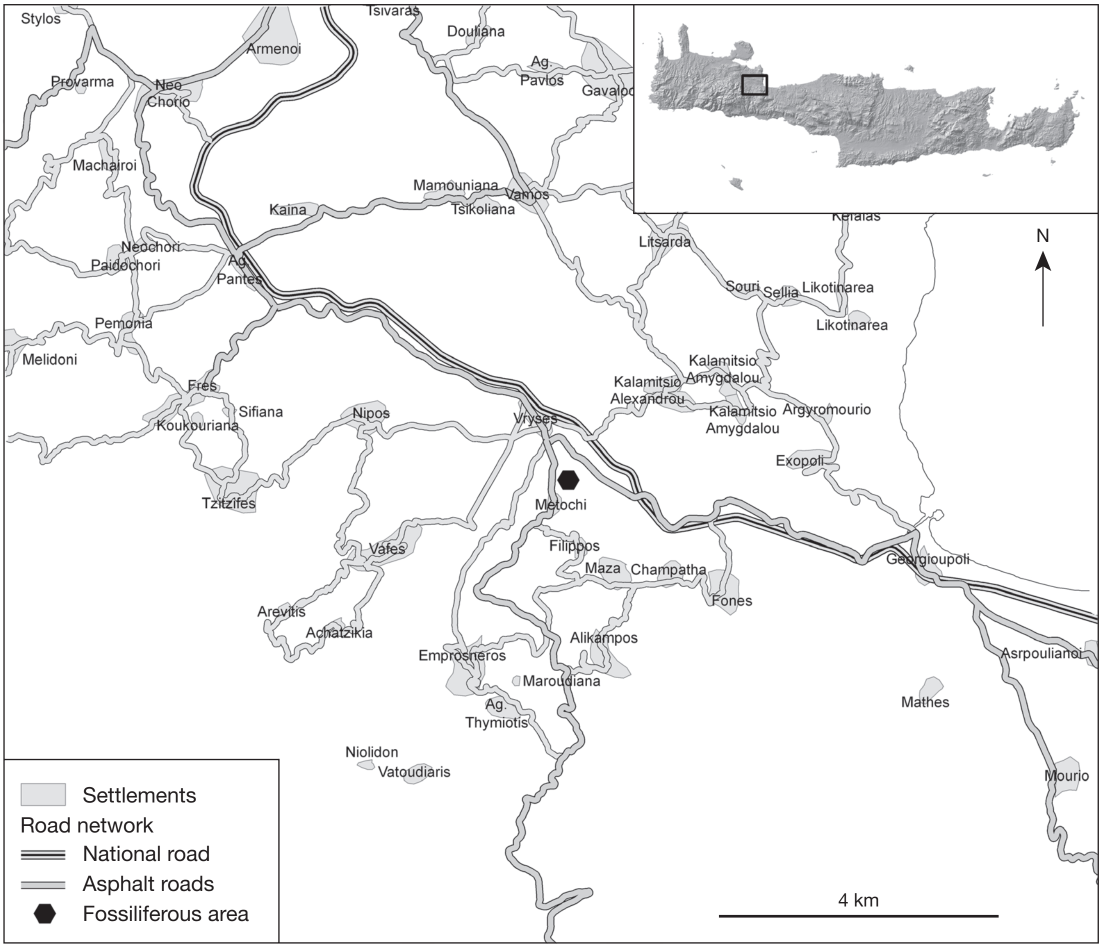

Fig. 1. — Generalized map of the fossiliferous locations in Vrysses basin, western Crete (Greece).

with the slightly older eastern Cretan Makrilia plant assemblage, and thus enables us to reconstruct temporal and spatial differences of the Cretan paleovegetation and climate change and more importantly to shed light on the Miocene paleoenvironment of southern Greece and the eastern Mediterranean region.

GEOLOGICAL SETTING

The macroflora was discovered near the village of Vrysses, located 15 km southeast of the town of Chania close to the road leading to the Sfakia area (Fig. 1). The material was collected at two fossiliferous outcrops, two quarries located 150 m from each other, just a few hundred meters south of Vrysses.

The island Crete is located in the southernmost part of the Helenides orogene and has experienced complicated geologic processes throughout the Neogene (Fassoulas 2001). Thick sedimentary units comprise the basement rocks, while large, tectonically controlled basins occur all over the island. The study area crops out at the eastern part of an elongated, east-west trending Neogene basin, the so-called Vrysses-Kalives basin. It is an area of low relief that is gradually passing southwards to the

Lefka Ori Mountains, the largest mountain area of the island with many summits over 2000 m. The basin develops in a graben structure inclined towards the sea that fragments the same Mesozoic carbonate rocks that build the Lefka Ori Mountains (Vidakis *et al.* 1983).

The Vrysses Formation, that rests unconformably on Mesozoic crystalline limestone and dolomites of the Plattenkalk and Tripali units (Vidakis *et al.* 1983), covers most of the area around Vrysses. According to Meulenkamp *et al.* (1979), the Vrysses Formation is mainly composed of bioclastic and reefal, light-colored limestones and alternations of laminated shallow water, white to grayish marls. A rich fauna represented by molluscs (mainly *Ostrea*) occurs in the limestone beds, whereas molluscs, echinoderms and remnants of fish and plants are found in the marls. Based on planktonic foraminifera Meulenkamp *et al.* (1979) correlated the formation to the *Globorotalia conomiozea* biozone which traces the Tortonian/Messinian boundary in the Mediterranean basin (Negri & Villa 2000). According to the mammal bio-stratigraphy the formation is placed between the MN12 and MN13 biozones. The age of the formation is thus regarded to be late Tortonian-Messinian (6-7.5 ma). In lignite layers of the Vrysses basin of about the same age, Benda *et al.* (1968) found fragments of a mastodon tooth. No younger sediments, except of Holocene riverbed deposits, are cropping out in the area.

The Vrysses beds are almost horizontal or slightly inclined to the northeast. In the study area limestone and marls can be approached in naturally eroded outcrops or in active quarries. The typical section in the study area can be lithologically subdivided into five distinct horizons. The lowermost (M1) is formed by massive white limestone, normally very competent, that shows irregular and angular fracture. Its thickness is at least 1 m and it is poor in fossils which are well preserved. The next horizon (M2) is constituted of well laminated yellowish to grayish marls and marly limestone of an overall thickness of 50 cm. Most of the plant remains are found in the marly limestone. In these strata animal remains are limited to a few insect wings and fish scales. The third horizon (M3) is made of a thin bed of yellow, well stratified marl with few fossils and high organic component. The M4 horizon comprises a whitish sandy to marly limestone of an average thickness up to 1 m. This horizon is full of mollusks, mainly gastropods and ostracodes and has a moderate competency and hardness. Finally, the uppermost horizon (M5) is formed by a stratified white sandy limestone that is partly covered by soil. A few leaf fossils have been found in this horizon too.

Paleogeographic studies of Crete (Meulenkamp *et al.* 1979; Dermitzakis & Papanikolaou 1981) suggest that during the Miocene, Crete was fragmented into smaller and larger islands, some of them located at the present mountain areas. The Lefka Ori area was at that times a hilly area, surrounded by shallow marine, lagoonal and delta environments. During the late Miocene tectonic activity formed an elongated marine realm at the northern flanks of the Lefka Ori Mountains that was extending eastwards to the Rethimnon area and was characterized by shallow bays, reefs and small islands. During this period and prior to the Messinian salinity crisis the light-colored limestone and marls of the Vrysses Formation were deposited.

MATERIAL AND METHODS

More than 250 specimens of plant macro-remains were excavated from the two quarries mentioned above. In addition, 12 specimens were collected from stone walls in the Mediterranean Agronomic Institute of Chania that originated from the Vrysses quarries. All studied plant fossils are preserved as leaf impressions. The specimens were studied after careful cleaning and in a few cases mechanical preparation was applied. Unfortunately, the leaves were in most cases fragmented, very rarely complete. The lack of organic material on nearly all of the leaf specimens did not allow any cuticular analysis. However, the fine-grained marls maintained many leaf characteristics for a large number of specimens. A Leica MZ8 stereoscope was used to observe details of the leaf morphology and a Canon digital camera (Powershot G4) for the photographs. Transparent tracing paper was used for drawings of the leaves. The majority of the material is stored in the Palaeontological Department of the Natural History

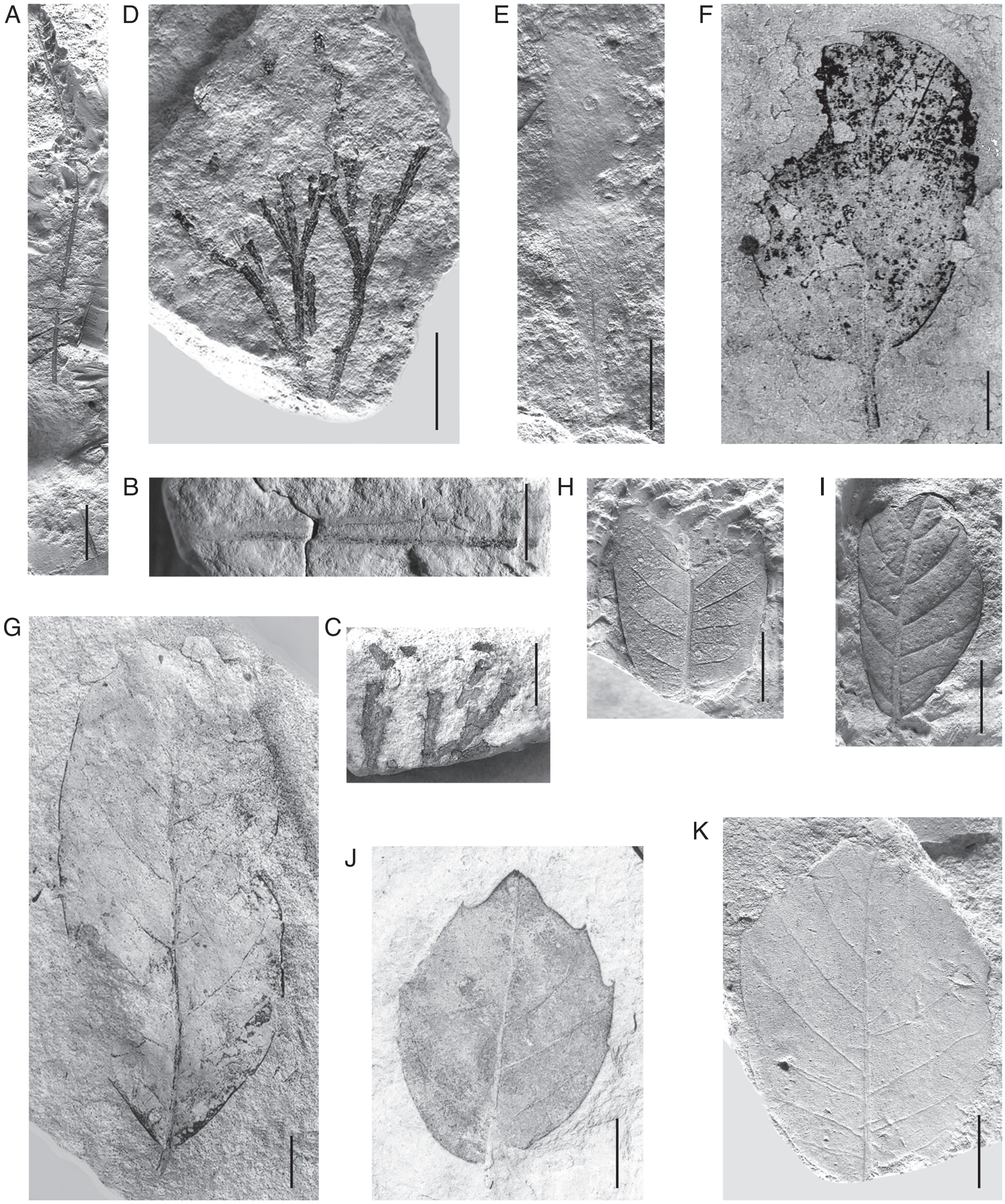

FIG. 2. — Photographs of fossil leaves from the Vrysses outcrops (western Crete): **A**, **B**, *Pinus* sp., needles nos. 32.1.2.168 and 32.1.2.48; **C**, **D**, *Tetraclinis* sp., twig fragments nos. 32.1.2.126 and 32.1.2.141; **E**, *Daphnogene polymorpha* (A.Braun) Ettingsh., no. 32.1.2.20; **F**, cf. "*Parrotia*" *pristina* (Ettingsh.) Stur, no. 32.1.3.5; **G**, cf. *Juglans acuminata* Braun ex Unger, no. 32.1.3.1; **H**-**K**, *Quercus mediterranea* Unger, nos. 32.1.2.24, 32.1.2.155, 32.1.3.2 and 32.1.2.79. Scale bars: 1 cm.

Museum of Crete in Irakleio while the 12 specimens from stone walls are housed in the Mediterranean Agronomic Institute of Chania.

The determination and systematic affinities of the Vrysses specimens is based on morphological characteristics of the leaves (shape and size of lamina, margin type, leaf venation, etc.) through studies of herbarium specimens of the Natural History Museum of Crete as well as published descriptions and illustrations of Neogene plant assemblages of Europe and modern regional floras.

In order to estimate climatic parameters of the Vrysses area during the Late Neogene, we applied two different methods that fit Vrysses material characteristics and preservation conditions:

– 1) leaf margin analysis (after Bailey & Sinnott 1915, 1916; Roth & Dilcher 1978; Wolfe 1979, 1985). This method correlates leaf margin shape with mean annual temperatures (MAT). In tropic forests most canopy species are entire-margined in order to conserve water. Moving to the temperate zone, the amount of transpiration is generally less critical and the number of woody species with toothed leaves tends to increase. So the percentage of entire-margined species can be used as an approach to reconstruct the temperature regime. Studies on humid to mesic broad-leaved forests of eastern Asia have shown that the percentage of species with entire-margined leaves is in direct proportion to the mean annual temperature of the particular forest (Wolfe 1979);

– 2) co-existence approach (Mosbrugger & Utescher 1997; Gastaldo & Ferguson 1998). This method uses nearest living relatives of the fossil taxa in order to estimate several of the main parameters of paleoclimate. It is based on the assumption that Neogene plant taxa had similar climatic requirements as their modern nearest relatives in order to determine the climatic interval in which all relatives of the assemblage can co-exist.

SYSTEMATICS

All leaf taxa found in the Vrysses outcrops are briefly described below, along with some notes on possible systematic relationships as well as geographic and stratigraphic occurrences. They comprise remains of gymnosperms, such as Pinaceae (Fig. 2A, B) and Cupressaceae (Fig. 2C, D), dicotyledonous (Figs 2E-K; 3; 4A-J; 5) and monocotyledonous angiosperms (Fig. 4K-L). The material is listed with the collection numbers of Natural History Museum of Crete. The terminology of leaf architecture is based on Hickey (1973).

Division GYMNOSPERMAE
Family PINACEAE
Genus *Pinus* L.

Pinus sp.
(Fig. 2A, B)

MATERIAL EXAMINED. — Specimens nos. 32.1.2.23; 32.1.2.48; 32.1.2.71; 32.1.2.100; 32.1.2.129; 32.1.2.154; 32.1.2.156; 32.1.2.162; 32.1.2.163; 32.1.2.168; 32.1.2.170; 32.1.2.183; 32.1.2.185; 32.1.2.201; 32.1.2.212; 32.1.2.213; 32.1.2.239.

DESCRIPTION

Seventeen fascicles of two leaves or isolated leaf fragments have been recovered, linear in outline, quite thin. Some of these pine needles are more than 12 cm long.

REMARKS

The taxon described above is possibly related to the modern Mediterranean long leaf species *Pinus halepensis* Mill. or *Pinus pinaster* Aiton because of the unusual leaf length.

Family CUPRESSACEAE
Genus *Tetraclinis* Mast.

Tetraclinis sp.
(Fig. 2C, D)

MATERIAL EXAMINED. — Twigs nos. 32.1.2.73; 32.1.2.125; 32.1.2.126; 32.1.2.141.

DESCRIPTION

Four twig segments of the genus *Tetraclinis* composed of small, closely attached leaves fused in veticles of four. Lengths of specimens varying from 0.5 to 3 cm.

REMARKS

Because of poor preservation these samples are not identifiable to the species level. *Tetraclinis* is a common element in Oligocene and Miocene strata of Europe. During the Miocene existed possibly two species (Kvaček 1989; Kovar-Eder & Kvaček 1995), *Tetraclinis salicornioides* (Unger) Kvaček and *Tetraclinis brachyodon* (Brongn.) Mai & Walter. Both differed mainly in epidermal structure of their leaves. *Tetraclinis salicornioides* is considered to have been a thermophilous element of the undergrowth of mixed evergreen and deciduous forests (Kovar-Eder *et al.* 1996), though *T. brachyodon* was most likely a more xeromorphic element growing mainly in lowland forest along sea coasts (Kvaček 1989). Today, a single species exists, *Tetraclinis articulata* Mast., which thrives in the Atlas Mountains (Morocco) and is well adapted to the Mediterranean climate (Achhal *et al.* 1980; Kovar-Eder *et al.* 1996).

Division ANGIOSPERMAE
Class DICOTYLEDONAE
Family LAURACEAE
Genus *Daphnogene* Unger

Daphnogene polymorpha (A.Braun) Ettingsh.
(Figs 2E; 5D)

MATERIAL EXAMINED. — Complete leaf no. 32.1.2.20; fragmentary leaf no. 32.1.2.26.

DESCRIPTION

One complete leaf and one fragmentary specimen. Leaves petiolate, about 4 to 4.5 cm long and 1 to 1.2 cm wide with entire margin. Shape of lamina narrowly elliptic or oblanceolate, obtuse at the apex, cuneate at the base. Venation acrodromous, triveined. Midvein thin, straight, lateral primary veins sub-basal, slender, running in convergent arches toward the leaf apex. No additional details of the venation visible.

REMARKS

These narrow triveined leaves are comparable to foliage of fossil *Daphnogene polymorpha*. Such leaves were formerly described under the generic name *Cinnamomum* Schaeff. However neither morphology nor anatomy allowed to obtain an exact correlation of this leaf type to the modern taxa of Lauraceae family (Kvaček & Walter 1974). Thus the name of the fossil genus *Daphnogene* is preferred. *Daphnogene polymorpha* is a common species in European Neogene deposits, with remarkable variability in leaf forms. The plant is considered to represent a paleotropical element of riparian forests along rivers and mixed mesophytic forests (Belz & Mosbrugger 1994) where it survived in this southerly area till Late Neogene.

Family HAMAMELIDACEAE
Genus *Parrotia* C.A.Mey.

cf. "***Parrotia*" *pristina*** (Ettingsh.) Stur
(Fig. 2F)

MATERIAL EXAMINED. — Complete leaf no. 32.1.3.5.

DESCRIPTION

One long petiolate, broadly obovate complete leaf (*c.* 5.5 cm long, 3.5 cm wide). Base rounded, slightly asymmetrical, apex broadly rounded. Margin dentate, with a few wide, obtuse teeth mainly at the upper part of lamina. Venation craspedodromous, primary vein slightly curved. Five pairs of secondary veins, straight or slightly curved, branching from the midvein at an angle of 30 to 40°. The basal pair of secondaries runs to the upper third of the lamina.

REMARKS

Leaf shape and venation are similar to the fossil species "*Parrotia*" *pristina.* However, leaves of this fossil species usually show an acute or even acuminate apex. In the specimen of Vrysses, the apex is broadly rounded thus the identification remains somewhat uncertain. "*Parrotia*" *pristina* leaves have been found in numerous Miocene and Pliocene outcrops throughout Europe (Shatilova & Stuchlik 2001). Due to the considerable similarity of these leaves in morphology and anatomical features to the recent genera *Fothergilla* L. and *Parrotia*, Kovar-Eder (1988) proposed to use the genus name *Parrotia* with quotation marks. Extant *Parrotia* is monotypic. The only species, *Parrotia persica* (DC.) C.A.Mey. is a deciduous mesic woody plant, restricted in its distribution. It occurs in the coastal area south of the Caspian Sea and to the Caucasus up to 1500 m altitude.

Family Juglandaceae
Genus *Juglans* L.

cf. ***Juglans acuminata*** Braun ex Unger
(Figs 2G; 5F)

Material examined. — Complete leaf no. 32.1.3.1; fragmentary leaves nos. 32.1.2.72; 32.1.2.158.

Description
One almost complete and two incomplete leaves; broadly oval to elongate, slightly asymmetric in shape; at least 10 cm long and 4.5 cm wide. Margin entire, base widely cuneate to rounded, apex not preserved. Petiole *c.* 0.5 cm long. Primary vein stout, slightly bent. Venation brochidodromous, 8-10 pairs of curved secondary veins arising at 35-60° from the midvein, regularly and widely spaced, joined together in a series of arches along the margin. Tertiary veins percurrent, straight or irregularly branched. Leaf texture possibly leathery.

Remarks
Size, shape and venation pattern of these specimens seems to fit the description of the fossil species *Juglans acuminata.* This taxon is present in many European Neogene deposits. Leaflets of *Juglans* sect. *Juglans* show entire margins (e.g., *J. regia* L.). Therefore, *Juglans acuminata* may be related to modern *Juglans regia* that grows in mixed mesophytic forests in southeast Europe and North Asia. However, Knobloch & Kvaček (1976) had studied the epidermal anatomy, and considered *Juglans acuminata* to be related to the North American species *Juglans rupestris* Engelm.

Since several species of *Pterocarya* Kunth also have leaves with entire margins, it can not be completely ruled out that the Vrysses leaves belong to this taxon. In the Makrilia plant assemblages from eastern Crete pollen of *Pterocarya* was a common element (Sachse & Mohr 1996).

Family Fagaceae
Genus *Quercus* L.

Quercus mediterranea Unger
(Figs 2H-K; 5J)

Material examined. — Complete leaves nos. 32.1.2.6; 32.1.2.17; 32.1.2.79; 32.1.2.155; 32.1.3.2; fragmentary leaves nos. 32.1.2.24; 32.1.2.43; 32.1.2.147; 32.1.2.229; 32.1.2.233; 32.1.2.248; 32.1.3.4.

Description
Five complete leaves very variable in shape, 3.3 to 6.9 cm long and 1.8 to 4.7 cm wide. Shape broadly oval to ovate or obovate. Base acute or rounded, rarely cordate and apex acute, obtuse or slightly emarginate. Leaf margin simple serrate at least in the upper half of the lamina, occasionally entire or undulate. Teeth widely spaced, rather small, more or less sharply pointed. Venation craspedodromous, midvein stout, in the upper part more slender and in some cases slightly sinuous. Secondary veins distinct, in 5 to 9 pairs, arising at an angle of 30 to 80° from the primary vein, irregularly spaced, rarely forked, running straight or bent towards the leaf margin entering the teeth. Tertiary veins poorly visible, irregular, simple or branched. Leaf texture rather chartaceous or coriaceous. Also, 7 fragmentary leaves are assigned to this fossil species.

Remarks
Quercus mediterranea is a characteristic common element in Neogene deposits especially in southern Europe. In Greece, this species is represented in numerous Miocene and Pliocene plant assemblages of mainland and islands (Knobloch & Velitzelos 1987; Velitzelos & Gregor 1990). Leaf remains of *Quercus mediterranea* from the Vrysses outcrops correspond much better to the records from Vegora (late Miocene, N Greece) and Kymi (early Miocene Evia Island, central Greece) on the basis of gross-morphology (Velitzelos *et al.* 2002; Kvaček *et al.* 2002; Kvaček & Walter 1989) while leaves assigned to *Q. mediterranea* from Makrilia (late Miocene,

eastern Crete, S Greece) seem to differ slightly. At the latter locality oaks are represented by a few leaves, which are rather small. They hardly reach a length of 2.5 cm (Sachse 1997).

Based on studies of leaf epidermis tissue from Lava (North Greece) that indicated an extremely thin cuticle, it was suggested that *Q. mediterranea* was a mesophytic deciduous oak (Kvaček & Walter 1989). However newly obtained epidermal characteristics show that in spite of the thin cuticle, the epidermis of either leaf side is sclerenchymatous underlain by a hypodermis (Kvaček *et al.* 2002). Thus *Q. mediterranea* probably was a sclerophyllous element able to survive short dry periods.

Quercus mediterranea is perhaps ancestral to the modern evergreen species *Quercus ilex* L. and *Quercus coccifera* L., although both do not correspond in all details of leaf anatomy and morphology to the fossils. Today these oaks are present throughout the Mediterranean basin and on coastal slopes towards the Atlantic (South France) and Black Sea, on relatively dry soils.

According to Barbero *et al.* (1992), *Q. ilex* thrives in a wide climatic range (from warm-temperate to subtropical and from medium humid to semi-arid) due to numerous morphological adaptations. In the northern Mediterranean realm, *Q. ilex* forms woodland with several laurophyllus elements such as *Arbutus* L., *Hedera* L., *Ilex* L. and *Viburnum* L., while in south it thrives together with more xerothermic taxa such as *Juniperus* L., *Phillyrea* Tourn. ex Adans., *Genista*, *Ephedra* L. and *Buxus*. In the eastern Mediteranean basin *Q. ilex* is replaced by *Q. coccifera*.

Quercus sp.
(Figs 3A; 5Q)

MATERIAL EXAMINED. — Fragmentary leaves nos. 32.1.2.19; 32.1.2.95; 32.1.2.142.

DESCRIPTION
Three leaf fragments, long petiolate (up to 1.5 cm). Complete leaf length estimated at 7 to 9 cm or perhaps more, width about 2.5 to 3.2 cm. Shape of lamina ovate to broadly elliptic, leaf margin undulate or simply serrate with small widely spaced teeth, serration starting in the lower third of the lamina. Base cordate, apex acute maybe acuminate. Venation craspedodromous. Midvein prominent more or less curved, slightly zig-zag at the upper part. Secondary veins more than 10 pairs, regularly disposed, quite dense, diverging at angles of 40 to 80° and running straight, parallel to each other, across lamina, entering marginal teeth. Higher order venation poorly preserved.

REMARKS
Such leaves may be assigned to the genus *Quercus*, representing probably an evergreen oak quite different from *Q. mediterranea* especially in leaf size and shape and secondary veins pattern. Leaf remains from early Miocene plant assemblage of Kymi figured by Unger (1867: taf. VI, figs 23-27) and identified as *Quercus drymeja* Unger by Velitzelos *et al.* 2002 (revised list of Kymi material), are very close in morphology to Vrysses specimens. However more and better preserved material is necessary to elucidate the systematic relationships of these specimens.

Family ULMACEAE

Ulmaceae gen. et sp. indet.
(Fig. 3B)

MATERIAL EXAMINED. — Complete leaf no. 32.1.2.70.

DESCRIPTION
One small, broadly elliptic leaf, about 1.8 cm long and 1 cm wide. Apex incomplete, probably acute to acuminate, base rounded, strongly asymmetrical. Leaf margin serrate at the upper half part of lamina with several wide, simple teeth. Venation craspedodromous. Midvein prominent, quite thick and strongly curved. From the primary vein arise four pairs of secondaries at angles of 35 to 55°, rather strong, more or less curved, running into the tooth apices. No other details of the venation preserved.

REMARKS
Such a leaf shape (leaf margin, asymmetrical base, laminar shape) suggests a relationship with the

family Ulmaceae. However this specimen lacks further diagnostic features for a determination to genus level. The Ulmaceae is a family of tropical and mainly temperate trees and shrubs, with 16 genera (Heywood *et al.* 1993). Due to very small size (nanophyll) and simple dentate margin, the Vrysses specimen may represent a slightly xeromorphic element.

Family Salicaceae
Genus *Salix* L.

cf. ***Salix*** sp.
(Fig. 3C)

Material examined. — Fragmentary leaf no. 32.1.2.39.

Description
Basal half of a probably narrow elliptic, slightly asymmetrical leaf (3.9 cm long and 1.7 cm wide); entire leaf possibly twice that long. Leaf base acute, margin finely serrate with simple acuminate teeth, regularly spaced. Midvein medium, thick, well developed and curved. Higher order venation not visible.

Remarks
Shape and margin of this leaf show resemblance to those of extant *Salix* L. However, because the upper part of the leaf is missing, as well as higher order venation, a definite identification is not possible.

Genus *Populus* L.

Populus tremula L., foss.
(Fig. 3D)

Material examined. — Complete leaf no. 32.1.3.7; fragmentary leaf no. 32.1.2.160.

Description
One complete and one fragmentary leaf. Lamina broadly ovate, 4.5 to 4.8 cm long and about 5.5 to 5.7 cm wide. Apex probably obtuse, base rounded, margin dentate with obtuse teeth. Petiole not preserved. Venation actinodromous with three primary veins. Midvein slightly bent, laterals curved and forked. Four or five pairs of curved secondary veins arising from the midvein at 30-55°, looping with the laterals and the adjacent secondaries near the margin. Tertiary veins oblique forming meshes between secondaries.

Remarks
Shape, teeth at the leaf margin and venation of these specimens are similar to lamina of the modern species *Populus tremula*. Leaf remains of this poplar have been found in several European Neogene deposits. Today *Populus tremula* trees grow in open mesophilous forests up to 1000 m of altitude in Europe, North Africa, Asia Minor and Siberia (Leroy & Roiron 1996).

Family Buxaceae
Genus *Buxus* L.

Buxus pliocenica Saporta & Marion
(Figs 3E; 5M)

Material examined. — Complete leaf no. 32.1.2.140.

Description
One complete leaf, narrowly elliptic, with short petiole, 3.6 cm long and 1.2 cm wide. Leaf margins entire, apex acute, base cuneate. Primary vein thin and almost straight. Secondary veins fine, arising at an angle of 30 to 70°, closely spaced, parallel to each other, branched once to many times in acute angles without higher order veins rejoining secondaries.

Remarks
Buxus pliocenica fossils have been known in Miocene and Pliocene deposits of Eurasia, mostly in the form of leaf impression and compression, rarely as pollen or fossil fruits. Saporta & Marion (1876) treat *Buxus pliocenica* as an ancestor of *Buxus sempervirens* L. However, Kvaček *et al.* (1982) consider *Buxus pliocenica* closely allied to the *B. sempervirens*-

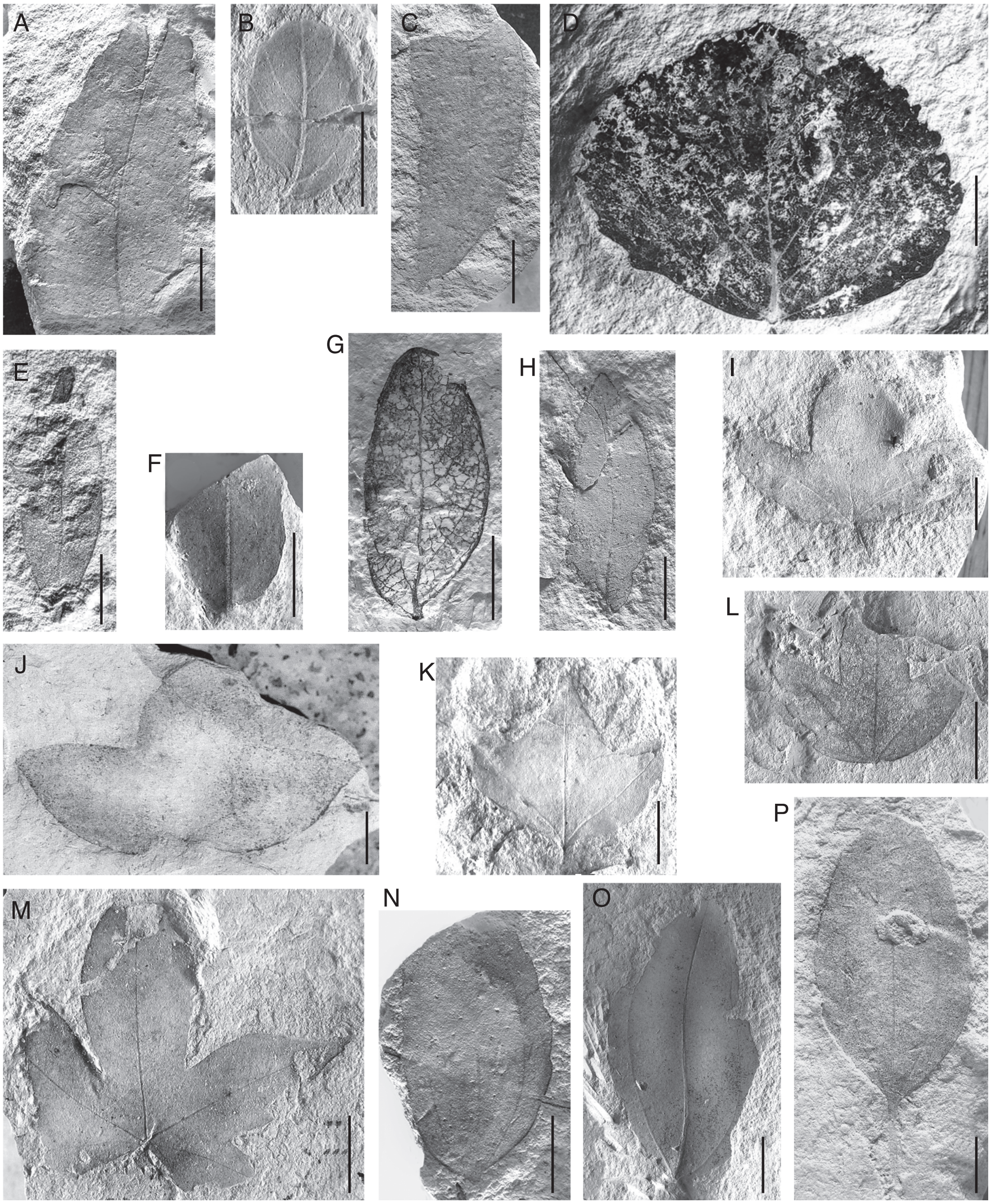

FIG. 3. — Photographs of fossil leaves from the Vrysses outcrops (western Crete): **A**, *Quercus* sp., no. 32.1.2.142; **B**, Ulmaceae gen. et sp. indet., no. 32.1.2.70; **C**, cf. *Salix* sp., no. 32.1.2.39; **D**, *Populus tremula* L., foss., no. 32.1.3.7; **E**, *Buxus pliocenica* Saporta & Marion, no. 32.1.2.140; **F**, Rosaceae gen. et sp. indet., no. 32.1.2.55; **G**, Fabaceae type 1, no. 32.1.2.161; **H**, Fabaceae type 2, no. 32.1.2.78; **I**-**L**, *Acer pseudomonspessulanum* Unger, nos. 32.1.2.61, 32.1.3.8, 32.1.2.46 and 32.1.2.67; **M**, *Acer* sp., no. 32.1.2.12; **N**-**P**, cf. *Ziziphus ziziphoides* (Unger) Weyland, nos. 32.1.2.3, 32.1.2.180 and 32.1.2.5. Scale bars: 1 cm.

B. colchica-B. hyrcana group. According to these authors this group replaced the large-leaved *Buxus* lineage which became extinct because of the climatic deterioration during the late Miocene. Extant *Buxus sempervirens* is a typical element of sclerophyllous vegetation in Mediterranean basin while *Buxus hyrcana* Pojark. and *Buxus colchica* Pojark. occur in pure stands or in underwood in lowland deciduous broad-leaved mesophilous forests in the Hyrcanian region (between the southern shores of the Caspian Sea and the Elburz Mountains) and in the Colchis (Western Georgia).

Family Rosaceae

Rosaceae gen. et sp. indet. (Figs 3F; 5G, S)

Material examined. — Complete leaf no. 32.1.2.41; fragmentary leaves nos. 32.1.2.8; 32.1.2.55.

Description

One complete and two fragmentary leaves with short petiole. Leaf length 2.7 to 3.5 cm (may be more) and width 1.3 to 2 cm. Shape of lamina ovate or oval, rounded at the base acute at the apex. Margin finely serrate with small, simple and sharp teeth. Primary vein well developed and straight. Higher order veins not visible.

Remarks

The features observed in these fossils and especially leaf margin suggest an affinity to the family Rosaceae. Today this large family comprises about 3300 species. It is cosmopolitan with maximum diversity in the northern temperate area (Heywood *et al.* 1993).

Family Fabaceae

Fabaceae type 1 (Fig. 3G)

Material examined. — Complete leaflet no. 32.1.2.161.

Description

One complete, very well preserved leaflet; 3.3 cm long and 1.5 cm wide, with oval outline. Margin of lamina entire, rounded at the apex and quite asymmetrical at the base. Texture chartaceous, petiolule missing. Venation brochidodromous. Primary vein thin, running irregularly (zig-zag) to the apex of leaflet. Five pairs of secondaries arising at an angle of 30 to 80° from the midvein, running more or less sinuous, joining each other by loops near the margin. The lateral secondary at one leaflet side is prominent, extending to the upper third of the middle of the leaflet. Intersecondary veins two or three, weakly developed. Higher order venation branching out and joining the secondaries to form a network of rather large, irregularly shaped areoles.

Remarks

This type of leaflets is related to the subfamily Caesalpinioideae and especially to the artificial genera *Cassiophyllum* and *Caesalpinites* by the asymmetrical form, the size and the venation pattern. These genera occur in European deposits from the Oligocene to Miocene. The determination of modern equivalents is difficult because the leaflets of many species have a similar morphology, as for instance *Scohtia humboltioides* Oliv., *Wagetia spicata* Daez and some *Cassia* species (Shakryl 1992).

Fabaceae type 2 (Fig. 3H)

Material examined. — Almost complete leaflet no. 32.1.2.78.

Description

One leaflet 3.8 cm long (complete about 4 cm) and 1.5 cm wide, narrow elliptic to lanceolate, slightly asymmetrical, entire-margined. Apex of lamina acute, base obtuse or rounded, asymmetrical (part of the base is missing). Primary vein strong, S-like curved. Higher order venation fine, hardly visible.

Remarks

Entire margins and asymmetry of this specimen are features that suggest a relationship with the

Fabaceae. Unfortunately, poor preservation of the leaflet does not allow a more precise determination. Fabaceae is a very large plant family (approximately 17000 species) with great variety of habitat and a cosmopolitan distribution in tropical, subtropical and temperate zones (Heywood *et al.* 1993). The small-sized leaflet of Vrysses may belong to a more or less xeric element.

Family ACERACEAE
Genus *Acer* L.

Acer pseudomonspessulanum Unger
(Figs 3I-L; 5L, P, R)

MATERIAL EXAMINED. — Complete leaves nos. 32.1.2.46; 32.1.2.61; 32.1.2.67; 32.1.3.8; fragmentary leaves nos. 32.1.2.28; 32.1.2.29; 32.1.2.31; 32.1.2.37; 32.1.2.40; 32.1.2.45; 32.1.2.58; 32.1.2.62; 32.1.2.91; 32.1.2.244; 32.1.3.9; 32.1.3.10.

DESCRIPTION
Four complete and 12 incomplete leaves, are assigned to this fossil species. Lamina deeply trilobate, 2.1 to 4 cm (or somewhat more) long and 3 to 6.3 cm wide, with short petiole. Leaf texture coriaceous. Base of lamina rounded or cordate, margin entire. The median lobe more or less broader than the lateral lobes. Apices of lobes acute to obtuse. Venation actinodromous with three primary veins, straight to slightly bent. Secondary veins fine, dense, arising at an angle of 60 to 80° from the primaries, branching near the margin. Higher order veins poorly preserved.

REMARKS
Most of these fossil leaves (the larger specimens) are most likely related to *Acer monspessulanum* L. but some of them, with sharper sinuses and less broad lobes with acuminate apices which stretch upwards, are related to *Acer sempervirens* L. In fact, remains of *Acer pseudomonspessulanum* from Vrysses do not differ in gross-morphology from the records in Makrilia, from where this leaf type was described as *Acer* series Monspessulana Pojark. Material from Vegora that is also similar in its variability has been determined as *A. pseudomonspessulanum* and *A. integrilobum* Weber. The name *Acer pseudomonspessulanum* is used as the Neogene ancestors of the modern species of the series Monspessulana Pojark., especially *A. monspessulanum* and *A. sempervirens* and their intermediate forms (Leroy & Roiron 1996). Leaf and fruit remains of *Acer pseudomonspessulanum* are known from several Neogene deposits in Europe. Today *Acer monspessulanum* extends from central, south Europe and northwest Africa to north Iran (south shores of the Caspian Sea), while *A. sempervirens* occurs at the east Mediterranean basin. *Acer monspessulanum* is a deciduous element while *A. sempervirens* is considered as deciduous or semi-evergreen element. Both of these maples are trees or shrubs and common elements of more or less xerothermic mixed evergreen and deciduous forests. Today *Acer sempervirens* grows on Crete at mountain slopes between 300 and 1700 m (Turland *et al.* 1993).

Acer sp.
(Figs 3M; 5K)

MATERIAL EXAMINED. — Almost complete leaves nos. 32.1.2.12; 32.1.2.56; fragmentary leaves nos. 32.1.2.14; 32.1.2.49; 32.1.2.75.

DESCRIPTION
Two almost complete leaves and 3 fragments, 5-lobed, 3.1 cm to 3.9 cm (possibly more) long and 4.4 to 5.8 cm wide. Margins entire with acuminate apex. Leaf base cordate, venation actinodromous with five primary veins. Lateral primaries arising under angles of 40 to 55° from the midvein, while basal primaries arise under angles of 80 to 110°. Five to seven pairs of hardly visible secondary veins, arise at 30 to 55° from primary veins and run in curves towards the leaf margin.

REMARKS
Some of these specimens are comparable to *Acer integerrinum*, a common element of European Neogene deposits. In Greece, *A. integerrinum* is represented in the late Miocene fossiliferous deposits of Licudi, central Greece (Velitzelos & Gregor 1990).

Acer laetum C.A.Mey. and *Acer pictum* Thunb. are considered to be the possible analogue among extant maples on the basis of their gross-morphology (Leroy & Roiron 1996). *Acer laetum* thrives from the Caucasus to the Himalayas and the mountains of central China while *A. pictum* grows on the slopes of northern China and Japan.

Family Rhamnaceae
Genus *Ziziphus* Mill.

cf. ***Ziziphus ziziphoides*** (Unger) Weyland
(Fig. 3N-P)

Material examined. — Almost complete leaves nos. 32.1.2.3; 32.1.2.5; 32.1.2.22; 32.1.2.180; fragmentary leaves nos. 32.1.2.10; 32.1.2.32; 32.1.2.106; 32.1.2.209.

Description
Four almost complete leaves and four fragments. Lamina broad oval to ovate 3.2-5.8 cm long (maybe more) and 1.9-4.1 cm wide, simply dentate at the upper two thirds of the leaf margin. Apex acute to obtuse, base partly asymmetric. Venation acrodromous with three stout primary veins running in convergent arches toward the leaf apex. Higher order veins very fine, hardly visible, vertical to midvein.

Remarks
The specimens described above probably belong to the species *Ziziphus ziziphoides*, a common element in the European Paleogene and Neogene. The genus *Ziziphus* consists of about 100 species of deciduous or evergreen trees and shrubs distributed in the tropical and subtropical regions of the world (Johnston 1963). This leaf form may be related to a non-sclerophyllous species of *Ziziphus* not identical with recent species of the Mediterranean area and the Near East. The nearest extant relatives of *Ziziphus ziziphoides* considered to be the deciduous *Z. sinensis* and *Z. glabrata* both thrive in Asia (Givulescu 1962). However, this leaf type may also represent a completely different family (see Sachse 1997; *Dicotylophyllum* type 3).

Family *incertae sedis*
Genus *Dicotylophyllum* Saporta

Dicotylophyllum sp. 1
(Fig. 4A)

Material examined. — Complete leaf no. 32.1.2.1.

Description
One entire leaf, reniform, 2.4 cm long and about 3.2 cm wide, stalked, entire-margined. Leaf texture evidently fine. Venation actinodromous with seven primary veins. Midvein straight, stronger than the lateral primaries. All primary veins forked before reaching leaf margin. Secondary veins on the medial primary vein widely and irregularly spaced in four pairs, also forked. Higher order venation not visible.

Remarks
A very interesting leaf form. In morphology (venation, margin, shape), it is comparable with the foliage of modern *Cercis silliquastrum* L. (Fabaceae), differing mainly by having smaller leaf size than living element. *Cercis silliquastrum* is a Mediterranean, deciduous tree.

Dicotylophyllum sp. 2
(Figs 4B; 5H)

Material examined. — Almost complete leaf no. 32.1.2.92.

Description
One almost complete (only a small part of its apex is missing) leaf, narrow oblanceolate 6.2 cm long (complete leaf somewhat more) and 2.2 cm wide. Lamina with entire margin, gradually narrowing towards the base. Primary vein straight, very strong and thick. Leaf texture coriaceous. Secondary veins fine, hardly visible, arising at 30 to 50° from the midvein.

Remarks
This leaf with poorly preserved venation cannot be reliably assigned to any specific genus. The general shape of this specimen suggests that it represented a broad-leaved humid or mesic element.

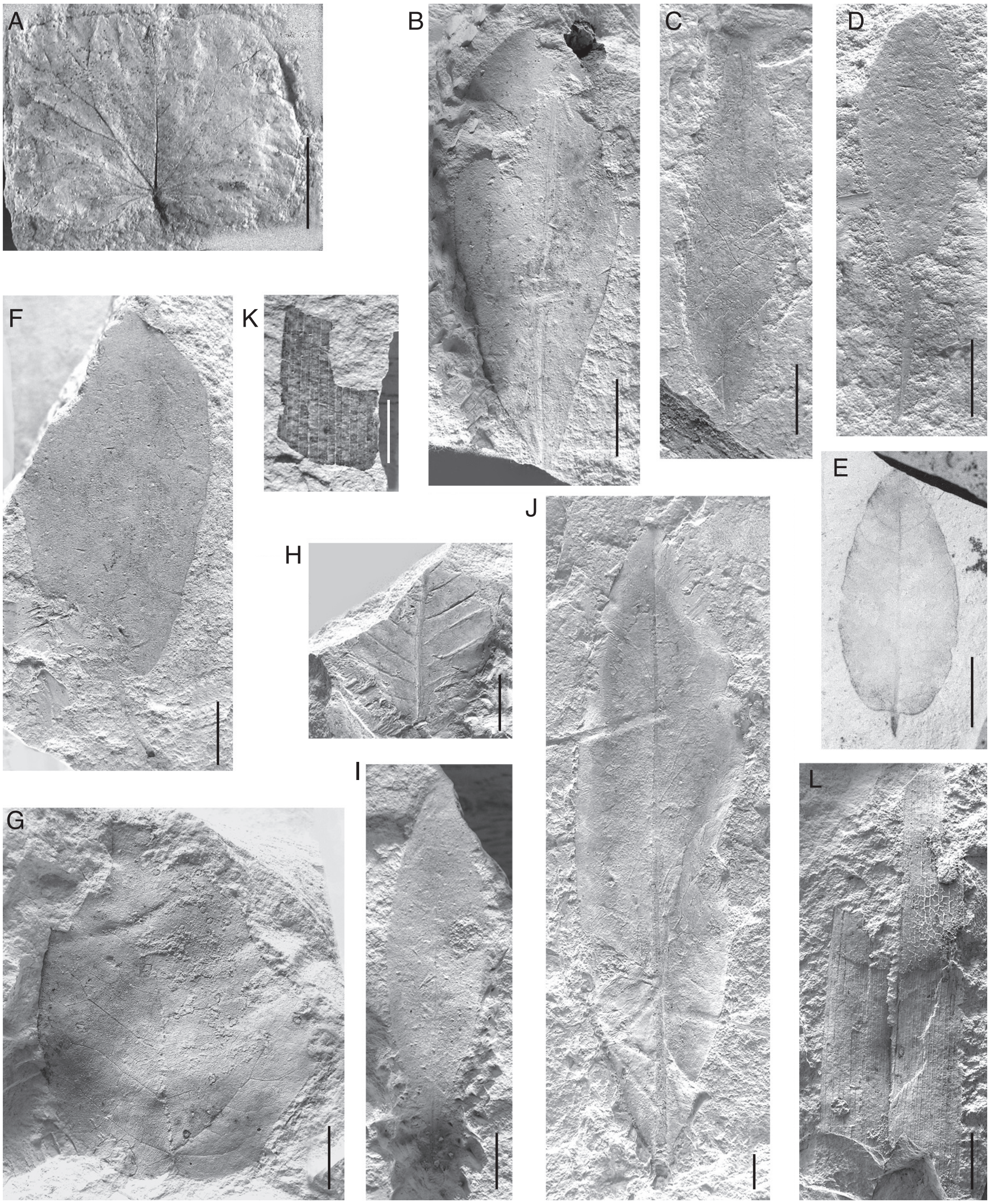

FIG. 4. — Photographs of fossil leaves identified in Vrysses outcrops (western Crete): **A**, *Dicotylophyllum* sp. 1, no. 32.1.2.1; **B**, *Dicotylophyllum* sp. 2, no. 32.1.2.92; **C**, *Dicotylophyllum* sp. 3, no. 32.1.2.16; **D**, *Dicotylophyllum* sp. 4, no. 32.1.2.33; **E**, *Dicotylophyllum* sp. 5, no. 32.1.3.6; **F**, *Dicotylophyllum* sp. 6, no. 32.1.2.9; **G**, *Dicotylophyllum* sp. 8, no. 32.1.2.223; **H**, *Dicotylophyllum* sp. 9, no. 32.1.2.30; **I**, *Dicotylophyllum* sp. 10, no. 32.1.2.93; **J**, *Dicotylophyllum* sp. 11, no. 32.1.2.159; **K**, Poaceae/Cyperaceae type 1, no. 32.1.2.191; **L**, Poaceae/Cyperaceae type 2, no. 32.1.2.54. Scale bars: 1 cm.

Dicotylophyllum sp. 3
(Fig. 4C)

Material examined. — Complete leaf no. 32.1.2.16.

Description
One complete leaf (only petiole missing), narrowly elliptic, slightly asymmetrical leaf; 5 cm long and 1.2 cm wide. Apex rounded, base obtuse, somewhat asymmetrical, leaf margin entire. Primary vein stout, S-like curved. Secondary veins fine, rather dense, hardly visible.

Remarks
It has not been possible to determine the affinity of this leaf due to poor preservation.

Dicotylophyllum sp. 4
(Figs 4D; 5O)

Material examined. — Complete leaves nos. 32.1.2.27; 32.1.2.33; 32.1.2.60; 32.1.2.144.

Description
Four complete leaves, small, long petiolate, oblanceolate to obovate leaves, 4 to 5.5 cm long and 1 to 1.5 cm wide. Leaf apex obtuse or rounded, base attenuate and leaf margin entire. Texture coriaceous. Primary vein strong, more or less curved. No other details of the venation visible.

Remarks
The affinity of these specimens is unknown and much better preserved material is necessary for a reliable identification.

Dicotylophyllum sp. 5
(Figs 4E; 5B, N)

Material examined. — Complete leaves no. 32.1.3.4; 32.1.3.6; fragmentary leaves nos. 32.1.2.34; 32.1.2.35.

Description
Two almost complete petiolate leaves. Length of the lamina 2.5 to 3.9 cm and width 1.7 to 1.9 cm. Leaf broadly lanceolate to obovate, apex acute to obtuse and base obtuse to slightly cordate. Margin slightly wavy or dentate with small simple teeth. Venation semicraspedodromous. Primary vein prominent, somewhat straight. Secondary veins thin, densely spaced at angles of 45 to 80°, running almost straight, parallel to each other across the lamina, dichotomised near the margin before entering teeth. Tertiary veins percurrent or simply forked forming irregular meshes with quaternary veins. Also two fragmentary leaves are assigned to this form.

Remarks
This fossil leaf taxon is similar in gross-morphology to numerous genera in different families such as Rhamnaceae and Fagaceae.

Dicotylophyllum sp. 6
(Figs 4F; 5I)

Material examined. — Fragmentary leaves nos. 32.1.2.9; 32.1.2.107.

Description
Two fragmentary leaves with broad obovate outline, 5 to 5.7 cm long (perhaps more) and 2.2 to 3.2 cm wide. Petiole rather slender, up to 1.2 cm long. Base of lamina heart-shaped, apex absent, with undulate or finely, simply dentate margin. Midvein fine, hardly visible, straight or slightly bend. Higher order venation invisible. Leaf texture coriaceous.

Remarks
The poor preservation makes it difficult to clarify the systematic relationship of these specimens.

Dicotylophyllum sp. 7
(Fig. 5T)

Material examined. — Complete leaf no. 32.1.2.44.

Description
One complete, petiolate, slightly asymmetrical, broadly oval leaf with entire margin. Leaf length

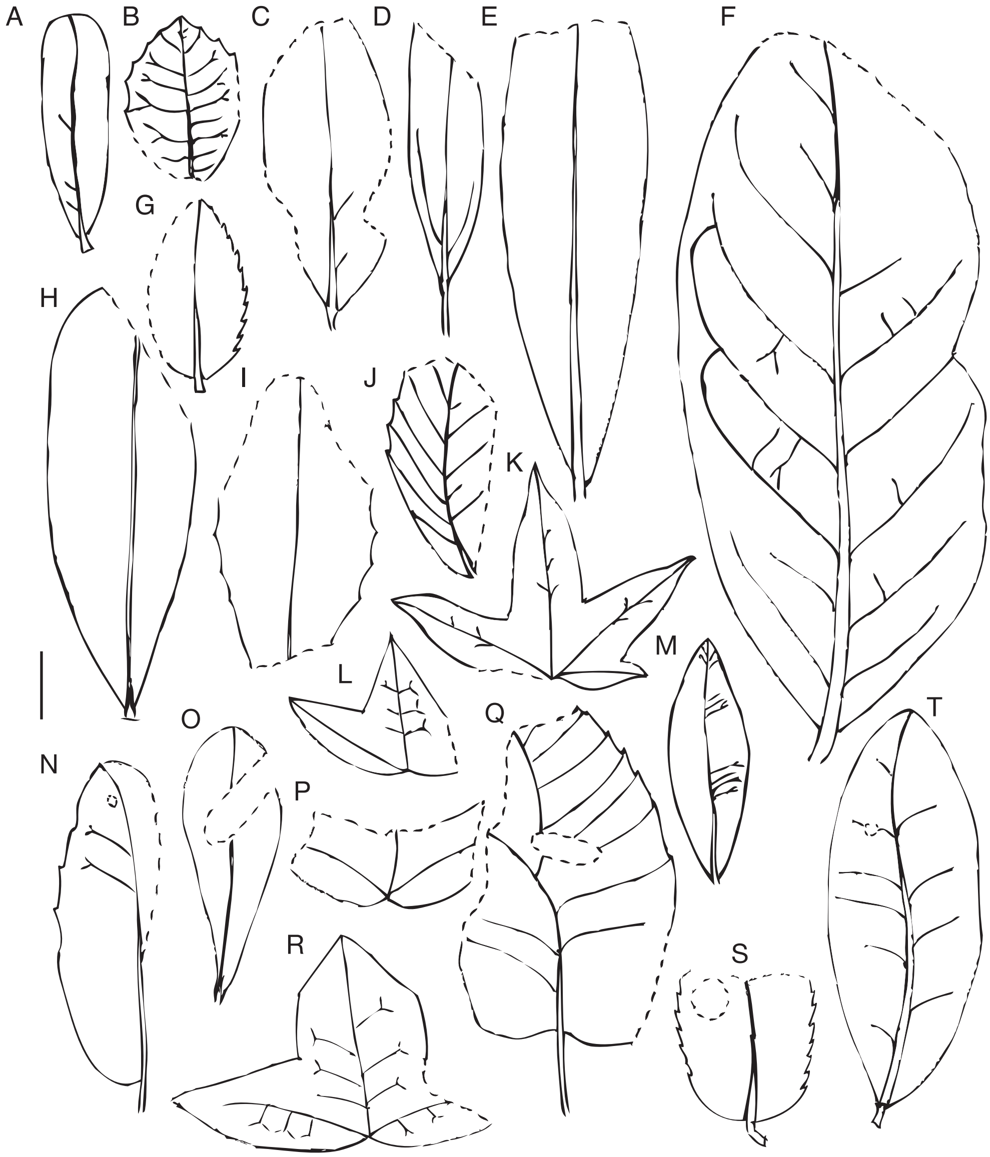

FIG. 5. — Drawings of selected fossil leaves from Vrysses (western Crete): **A**, *Dicotylophyllum* sp. 12, no. 32.1.2.42; **B**, **N**, *Dicotylophyllum* sp. 5, nos. 32.1.3.4 and 32.1.2.34; **C**, *Dicotylophyllum* sp. 10, no. 32.1.2.4; **D**, *Daphnogene polymorpha* (A.Braun) Ettingsh., no. 32.1.2.26; **E**, *Dicotylophyllum* sp. 11, no. 32.1.2.98; **F**, cf. *Juglans acuminata* Braun ex Unger, no. 32.1.3.1; **G**, **S**, Rosaceae gen. et sp. indet., nos. 32.1.2.41 and 32.1.2.8; **H**, *Dicotylophyllum* sp. 2, no. 32.1.2.92; **I**, *Dicotylophyllum* sp. 6, no. 32.1.2.107; **J**, *Quercus mediterranea* Unger, no. 32.1.2.147; **K**, *Acer* sp., no. 32.1.2.56; **L**, **P**, **R**, *Acer pseudomonspessulanum* Unger, nos. 32.1.3.9, 32.1.2.37 and 32.1.2.31; **M**, *Buxus pliocenica* Saporta & Marion, no. 32.1.2.140; **O**, *Dicotylophyllum* sp. 4, no. 32.1.2.144; **Q**, *Quercus* sp., no. 32.1.2.95; **T**, *Dicotylophyllum* sp. 7, no. 32.1.2.44. Scale bar: 1 cm.

5.9 cm, width 2.2 cm. Leaf base obtuse, apex rounded. Venation probably semicraspedodromous. Primary vein quite strong, S-like curved. Secondary veins at least seven pairs, hardly visible, very delicate, rather widely spaced, arising at angles of 55 to 80° from the midvein, running nearly straight to somewhat bent towards the margin. Probably secondaries forking near the margin. Further venation pattern not preserved.

REMARKS
The systematic affinity of this leaf taxon remains unclear.

Dicotylophyllum sp. 8
(Fig. 4G)

MATERIAL EXAMINED. — Almost complete leaf no. 32.1.2.223.

DESCRIPTION
One leaf almost complete (only a small part of apex missing), broadly ovate, quite asymmetrical, 5.7 cm long (complete leaf about 6 cm) and 4.3 cm wide. Apex of lamina acute or acuminate and base heart-shaped. Margin simply dentate with moderately large and acute teeth, irregularly spaced. Venation actinodromous with five primary veins. Primary vein rather stout, S-like. Basal primaries quite weak, arising from the midvein at angles of 100 to 120° while lateral primaries stronger, arising at angles of 60 to 80°. Four pairs of curved secondary veins arising from the midvein, widely spaced, dichotomised near the margin. Tertiary veins usually simple forked forming polygonal meshes with quaternary veins.

REMARKS
Crucial characters are missing and thus it is impossible to determine the systematic affinity of this specimen.

Dicotylophyllum sp. 9
(Fig. 4H)

MATERIAL EXAMINED. — Fragmentary leaf no. 32.1.2.30.

DESCRIPTION
One fragmentary leaf, broadly elliptic or obovate, 2.6 cm long and 2.5 cm wide (entire leaf about 3.6 long and 3 cm wide). Leaf apex not preserved, base obtuse, margin hardly visible, undulate. Leaf texture coriaceous. Venation craspedodromous, primary vein stout, S-like curved. Secondaries at least seven pairs, strong, parallel, regularly spaced, more or less straight, directed towards the margin. Higher order veins not visible.

REMARKS
Such leaves may be related to the genus *Fagus* L., but such affinity cannot be proved. More and much better preserved material is necessary to elucidate the position of this specimen.

Dicotylophyllum sp. 10
(Figs 4I; 5C)

MATERIAL EXAMINED. — Complete leaf no. 32.1.2.93; fragmentary leaves nos. 32.1.2.4; 32.1.2.94.

DESCRIPTION
One complete and two fragmentary leaves, petiolate, with elliptic outline. Their length is 5 to 6.2 cm (maybe somewhat more) and their width 1.7 to 1.9 cm. Leaf margin entire, acute at the apex and cuneate at the base. Primary vein prominent and straight. Secondary veins fine, hardly visible. Higher order venation not preserved.

REMARKS
The systematic affinity of these three specimens is unclear.

Dicotylophyllum sp. 11
(Figs 4J; 5E)

MATERIAL EXAMINED. — Complete leaf no. 32.1.2.159; fragmentary leaves nos. 32.1.2.98; 32.1.2.131.

DESCRIPTION
One complete leaf, the largest in the Vrysses assemblage, 17 cm long and 4 cm wide (size of lamina more than 4.500 mm^2). Also two fragmentary leaves, smaller, up to 12 cm long and 2 to 2.5 cm wide. Leaf apex obtuse or acute, base cuneate, entire-

margined, with broad elliptic outline. Primary vein characteristically thick and strong, straight or slightly bent. Higher order venation not visible probably duo to thick coriaceous texture.

Remarks

Such leaf specimens are usually considered to belong to magnoliid families, such as Magnoliaceae or Lauraceae. However a relationship with other families cannot be excluded.

Dicotylophyllum sp. 12
(Fig. 5A)

Material examined. — Complete leaf no. 32.1.2.42.

Description

A small complete leaf, short petiolate, 3.2 cm long and 1 cm wide. Lamina narrow obovate, with apex rounded, base acute and entire margin. Primary vein quite strong and thick, S-like curved. Secondary veins poorly preserved, arise from the midvein at angles of 30 to 50°. Leaf texture chartaceous.

Remarks

This leaf lacks diagnostic features.

Class MONOCOTYLEDONAE
Families Poaceae/Cyperaceae

Poaceae/Cyperaceae type 1
(Fig. 4K)

Material examined. — Fragmentary leaves nos. 32.1.2.57; 32.1.2.63; 32.1.2.151; 32.1.2.169; 32.1.2.186; 32.1.2.189; 32.1.2.190; 32.1.2.191; 32.1.2.192; 32.1.2.199; 32.1.2.203; 32.1.2.208; 32.1.2.224; 32.1.2.228; 32.1.2.236; 32.1.2.245.

Description

Sixteen fragments of narrow strap-like leaves about 1 to 1.5 cm wide, that bear parallel venation.

Remarks

These fossil leaves are similar in gross-morphology to numerous genera mainly in Poaceae and Cyperaceae. The Poaceae and Cyperaceae are two large families of monocotyledons, cosmopolitan. Only few ecological plant formations lack Poaceae, while many formations are dominated by them (Heywood *et al.* 1993).

Poaceae/Cyperaceae type 2
(Fig. 4L)

Material examined. — Fragmentary leaves nos. 32.1.2.54; 32.1.2.198.

Description

Two fragments of broad linear leaves, wide, more than 2 cm wide, with parallel venation.

Remarks

These specimens probably also represent leaves of Poaceae or Cyperaceae.

FLORISTIC COMPOSITION

The Vrysses plant assemblage is documented by foliage. More than 260 specimens of leaf megafossils, in many cases very fragmentary, were examined. A total of 31 taxa of vascular plants have been described based on their macro morphological features (Table 1). Nineteen of them were relatively well preserved and identified at least to family level. Two genera of conifers and 29 taxa of angiosperms, shrubs, trees and, rarely herbs have been documented.

Conifers are represented in the assemblage by *Tetraclinis* and *Pinus* shoots and leaves. Fertile parts, such as cones, cone scales or seeds were not found.

Angiosperm taxa make up approximately 95% of the total flora. Among the angiosperms, Aceraceae and Fagaceae are most common. Fagaceae is represented by the genus *Quercus*, mainly by the probably evergreen oak *Quercus mediterranea*, which predominates and *Quercus* sp. considered also to belong to evergreen oaks. Two leaf-types belong to Aceraceae; a small 3-lobed leaf identified as *Acer pseudomonspessulanum*, considered to be more or

TABLE 1. — Summary of the taxa of the Vrysses flora (western Crete), their dispersal mechanisms and physiognomic signatures. Note: **a**, taxa which cannot be restricted to one single category, are included in all assigned categories. Percentage of entire-margined taxa: 48.1% (13 taxa). Percentages of notophyll, microphill and nanophyll taxa: notophyll 7.4% (2 taxa), microphyll 85.2% (23 taxa) and nanophyll 7.4% (2 taxa). Percentages related to deciduous, laurophyllous and sclerophyllous taxa: deciduous 37-59% (10-16 taxa), laurophyllous 11-30% (3-8 taxa) and sclerophyllous 15-52% (4-14 taxa). Abbreviations: **D**, deciduous; **L**, laurophyllous; **S**, sclerophyllous.

Family	Genus	Species/ type series	Leaves/ needles shoots	Leaf margin entire	Maximum leaf size class	D, L, S [a]	Dispersal mechanism
GYMNOSPERMAE							
Pinaceae	*Pinus*	sp.	17 needles	-	-	-	wind
Cupressaceae	*Tetraclinis*	sp.	4 twig fragments	-	-	-	wind
ANGIOSPERMAE							
Dicotyledonae							
Lauraceae	*Daphnogene*	*polymorpha*	2	yes	microphyll	L	endozoochory
Hamamelidaceae	?"*Parrotia*"	*pristina*	1	no	microphyll	D	autochory
Juglandaceae	?*Juglans*	*acuminata*	3 leaflets	yes	notophyll	D	dyschory
Fagaceae	*Quercus*	*mediterranea*	12	no	microphyll	S	dyschory
	Quercus	sp.	3	no	microphyll	S	dyschory
Ulmaceae	gen. indet.	-	1	no	nanophyll	D/S	wind
Salicaceae	?*Salix*	sp.	1	no	microphyll	D	wind
	Populus	*tremula*, foss.	2	no	microphyll	D	wind
Buxaceae	*Buxus*	*pliocenica*	1	yes	microphyll	L/S	autochory/ myrmecochory
Rosaceae	gen. indet.	-	3	no	microphyll	D	wind/ exozoo-/endo-zoochory
Fabaceae	gen. indet.	type 1	1 leaflet	yes	microphyll	D/S	-
	gen. indet.	type 2	1 leaflet	yes	microphyll	D/S	-
Aceraceae	*Acer*	*pseudomonspessulanum*	16	no	microphyll	D/S	wind
	Acer	sp.	5	no	microphyll	D	wind
Rhamnaceae	?*Ziziphus*	*ziziphoides*	8	no	microphyll	D	endozoochory
Family *incertae sedis*	*Dicotylophyllum*	sp. 1	1	yes	microphyll	D/L/S	-
	Dicotylophyllum	sp. 2	1	yes	microphyll	L	-
	Dicotylophyllum	sp. 3	1	yes	microphyll	S	-
	Dicotylophyllum	sp. 4	4	yes	microphyll	L/S	-
	Dicotylophyllum	sp. 5	4	no	microphyll	D/S	-
	Dicotylophyllum	sp. 6	2	no	microphyll	D	-
	Dicotylophyllum	sp. 7	1	yes	microphyll	L/S	-
	Dicotylophyllum	sp. 8	1	no	microphyll	D	-
	Dicotylophyllum	sp. 9	1	no	microphyll	D	-
	Dicotylophyllum	sp. 10	3	yes	microphyll	L/S	-
	Dicotylophyllum	sp. 11	3	yes	notophyll	L	-
	Dicotylophyllum	sp. 12	1	yes	nanophyll	S	-
Monocotyledonae							
Poaceae/ Cyperaceae	gen. indet.	type 1	16	-	-	-	wind/ nautochory/ exozoo-/ endozoochory
	gen. indet.	type 2	2	-	-	-	wind/ nautochory/ exozoo-/ endozoochory

less xeromorphic and a 5-lobed leaf represents most likely a mesophytic deciduous species.

Fabaceae are represented by a few leaflets that have been subdivided into two morphotypes (Fabaceae type 1 and type 2). Juglandaceae seem to be also present. The leaflets of the Vrysses plant assemblage may belong to *Juglans acuminata*. The family Rhamnaceae may be represented by irregularly dentate, 3-veined leaves that are close in appearance to the Neogene species *Ziziphus ziziphoides*. Leaves of Lauraceae seem to have been present in the assemblage as well by the narrow leaf type of *Daphnogene polymorpha*. Imprints of *Populus tremula*, foss., *Salix* sp. and possibly "*Parrotia*" *pristina* occur rarely. One leaf of *Buxus* sp. has been identified. Rosaceae and Ulmaceae may have been present as well. Monocots are represented by numerous specimens of the families Poaceae and Cyperaceae. However many leaf impressions of the Vrysses plant assemblage have doubtful affinities. They are considered to belong to 12 taxa of angiosperms, and classified as *Dicotylophyllum*.

Considering the number of specimens, four woody taxa are most common in the assemblage: *Pinus* sp., *Acer pseudomonspessulanum*, *Quercus mediterranea* and *Ziziphus ziziphoides* (Table 1). *Tetraclinis* sp. and *Acer* 5-lobed are found also more frequently. More than one species may have existed among Aceraceae, Fagaceae Salicaceae and Fabaceae (all two taxa).

The majority of the genera identified at Vrysses are related to elements now growing in the Northern Hemisphere. The modern living relatives of *Buxus pliocenica*, *Populus tremula*, foss., *Acer pseudomonspessulanum* and *Juglans acuminata* thrives in Eurasia while *Daphnogene polymorpha* has its closest counterparts in Asia and America and *Ziziphus ziziphoides* in Asia. A few taxa have affinities to living Mediterranean species such as *Tetraclinis* and *Quercus mediterranea* while extant *Parrotia* is a relic found in Iran (Zohary 1947; Wang 1961; Zohary & Orshan 1966; Meusel *et al.* 1965, 1978; Strahler & Strahler 1992; Achhal *et al.* 1980; Quezel 1988; Barbero *et al.* 1992; Turland *et al.* 1993; Arabatzis 1998, 2001). The core of the nearest living relatives of the fossil taxa grows today in the temperate to subtropical zone, whereas only a few taxa extend to the tropical zone (Lauraceae) (Walter & Lieth 1967; Browics 1982; Klötzli 1988).

TAPHONOMY AND VEGETATION ANALYSIS

The Vrysses Formation was most likely deposited in a shallow, semi-enclosed marine embayment, bordered by islands and shoals (Meulenkamp *et al.* 1979). The fossil assemblage contains autochthonous and a large proportion of allochthonous elements. This is confirmed mainly by the composition of the taphocoenosis that consists of a mixture of plant remains from different habitats and the high percentage of small-sized leaves (Ferguson 1985; Spicer 1991). More than 85% of the taxa identified in Vrysses outcrops are classified as microphyll (225-2.025 mm^2), while 7.4% as nanophyll (25-225 mm^2) (Table 1). The allochthonous nature of the assemblage is also reflected by the absence of different organs, such as seeds and fruits of the same taxon in the assemblage and by the high percentage of heavily fragmented leaves that reach 64% of the examined specimens.

Plant debris have probably been transported by river floods into their offshore burial site. Alternatively, plant remains may have drifted on the sea surface and reached the locality of sedimentation after having been blown by strong winds from high coastal cliffs.

According to its composition, the Vrysses plant assemblage is a heterogeneous mixture of higher plants with different ecology. Considering the specific features of the modern associations (Wolfe 1979; Klötzli 1988; Song 1983, 1988) that can be related to the Vrysses fossil leaves, the outline of a regional vegetation reconstruction has been developed, that is characterized by a floristic differentiation based on water efficiency and altitude (Gastaldo & Ferguson 1998).

– a) Riparian paleocoenoses composed of representatives of the wood elements *Salix* sp. and perhaps *Populus tremula* and Juglandaceae, as well as Poaceae and Cyperaceae herbs. These elements were forming a belt of a riparian forest along the banks of inflowing streams. Subtropical, partly evergreen elements, such as *Daphnogene polymorpha* may have played also a certain role in these lowland forests.

– b) Sclerophyll forest paleocoenoses consisted in general of microphyllous, broad-leaved taxa (such as *Quercus mediterranea*, *Quercus* sp., possibly *Buxus pliocenica*, *Acer pseudomonspessulanum*, Ulmaceae and several Fabaceae) and conifers (*Pinus*, possibly *Tetraclinis*) forming woodland at dry lowland areas.

– c) Mixed-Mesophytic forest coenoses. Sclerophyllous evergreen forests of lowlands were gradually replaced by mixed mesophytic forests of higher elevations along an altitude gradient. The canopy of these forests was dominated by deciduous representatives

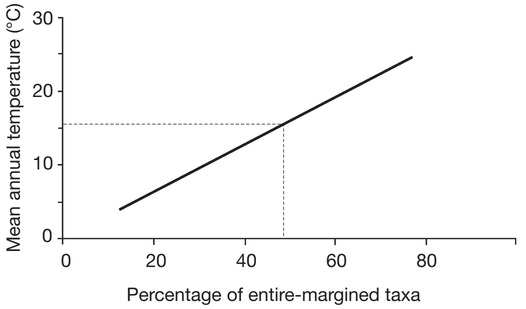

FIG. 6. — Correlation of percentage of species with entire-margined leaves in the humid and mesic broad-leaved forests of eastern Asia with mean annual temperature, after Wolfe (1979). ---, percentage of entire-margined taxa in the Vrysses (western Crete) plant assemblage.

of *Acer* 5-lobed, *Populus tremula*, *Ziziphus ziziphoides*, Juglandaceae and probably *Acer pseudomonspessulanum* and Ulmaceae. In the stratum of lower trees and shrubs a mixture of evergreen (*Buxus pliocenica* and *Daphnogene polymorpha*), as well as deciduous elements ("*Parrotia*" *pristina*, Rosaceae) and conifers (*Tetraclinis* sp.) seem to have existed.

It is also interesting to consider dispersal mechanisms of the recorded taxa. About 23% of the identified plant taxa were dispersed either endo- or exozoochorously by birds or mammals (see Table 1) that implies also a diverse paleofauna.

PALEOCLIMATE RECONSTRUCTION

Analyses of Neogene plant assemblages are in general a very useful tool to extract proxy data for paleoclimatic reconstructions. We tried to apply two different methods in order to estimate climatic parameters of the broader Vrysses area during the late Miocene: the leaf margin analysis and the coexistence approach. However because of the limited number of taxa and the unresolved taxonomic problems due to poor preservation of the material only rough estimations were possible.

– a) Leaf margin analysis. The proportion of taxa with entire-margined species in the Vrysses plant assemblage reaches 48% (Table 1), suggesting a mean annual temperature of 15-16°C (Zidianakis *et al.* 2004) (Fig. 6). The relatively high percentage of sclerophyllous elements (about 15-52%) reduces the accuracy of this correlation.

– b) Co-existence approach. Table 2 shows the modern taxon analog of the species recognized in the Vrysses plant assemblage and their mean annual temperature requirements. A range of 15-16°C for mean annual temperature is also estimated.

Several of the Vrysses taxa seem to have their natural habitat today in the Euxino-Hyrcanian Province. These taxa comprise *Parrotia*, *Buxus*, *Juglans* and *Acer*. The average annual temperature of the Hyrcanian region varies from 15°C in the west to 17.5°C in the east. The temperature of the warmest month ranges between 28-35°C while that of the coldest month ranges from 1.5 to 4°C.

Rainfall varies substantially from 530 mm in the east to 1350 mm in the west. In most areas of this region precipitation is all year round with maxima in spring, late fall and winter, the eastern parts experience three months of summer drought (see www.rifr-ac.ir/index_eng.htm). If we take this region as model for the Neogene climate, a range of 15-17.5°C for mean annual temperature (MAT), and more than 800 mm for mean annual precipitation (MAP) is estimated.

The average small leaf size of the assemblage (microphyllous flora) may be not only caused by taphonomic processes but also by climatic factors, such as periodic drought. The relatively high proportion of sclerophyllous xeromorphic elements in the plant assemblage may confirm the latter hypothesis.

On the basis of physiognomic features, leaf remains of Vrysses are divided in three main categories: 1) a broad-leaved deciduous component which predominates with approximately 37-59%; 2) broad-leaved evergreens (laurophyllous taxa) reach about 11-30%; and 3) the sclerophyllous component with the relatively high proportion of 15-52% (Table 1). The broad-leaved deciduous elements are characteristic for humid, temperate climatic conditions, while the broad-leaved evergreen taxa for humid, subtropical and sclerophyllous taxa for sub-humid, subtropical conditions (Berger 1954; Kovar-Eder *et al.* 2006).

Thus, the Vrysses plant assemblage may indicate a warm-temperate, humid climate for the late

TABLE 2. — Mean annual temperature (MAT) requirements for nearest living relatives (NLR) of taxa of the Vrysses (western Crete) assemblage. Data are taken from Palaeoflora Database (Utescher & Mosbrugger 1999).

Taxa	NLR	MAT of NLR (°C)
Tetraclinis sp.	*Tetraclinis articulata*	15.60-19.90
"*Parrotia*" *pristina*	*Parrotia persica*	13.60-15.80
Juglans acuminata	*Juglans regia*	10.10-17.30
Quercus mediterranea	*Quercus ilex*, *Quercus coccifera*	11.70-19.50
Populus tremula, foss.	*Populus tremula*	1.60-19.00
Buxus pliocenica	*Buxus sempervirens*	9.70-17.30
Acer pseudomonspessulamum	*Acer pseudomonspessulanum*, *Acer sempervirens*	9.60-20.50
Ziziphus ziziphoides	*Ziziphus sinensis*	7.30-27.60

Miocene. The existence of a dry period during the year is probable, although this seasonality was clearly not yet as pronounced as today. Using the climatic classification of Köppen (1931), the Vrysses paleoclimate is most likely ranging between Cfa (warm temperate with warm, humid summers) and Csa (warm temperate with warm, arid summers) climates. The climatic change from pre-late Miocene summer wet climates to summer dry climates was possibly caused by the successive westward retreat of the Paratethys between the Oligocene and the middle Miocene (Popov *et al.* 2004) and the changing topography of eastern Asia (Sachse 1997).

DISCUSSION

The discovery of a new Miocene leaf assemblage in the eastern Mediterranean realm offers the opportunity for a better understanding of the floristic and climatic development of this region. Neogene floras occur in central and northern Greece, as well as in several Aegean islands including Crete (Knobloch & Velitzelos 1987; Velitzelos & Gregor 1990; Sachse & Mohr 1996, Velitzelos *et al.* 2001). If the Vrysses plant assemblage is compared with the known Greek plant assemblages on the basis of physiognomy and floristic composition, the closest match seems to be with the late Miocene assemblage of Makrilia, eastern Crete (Sachse 1997, 2004).

The plant macro-remains of Makrilia occur in semi-pelagic silty layers and represent a plant assemblage of which 94% of the leaf taxa are microphyll or nanophyll (Sachse 1997). The age of the Makrilia flora was determined using nannoplankton and dinoflagellate cysts as late Miocene (7.7-8.6 Ma; Sachse & Mohr 1996) and is thus slightly older than the Vrysses flora. As it was expected, the Makrilia assemblage shares many arboreal taxa with the Vrysses flora. More than 70% of the taxa identified in Vrysses exist also in Makrilia. Subtropical laurophyllous elements, such as *Daphnogene polymorpha*, deciduous elements, such as *Acer* 5-lobed, *Populus*, *Salix* and *Ziziphus*, conifers, such as *Tetraclinis*, *Pinus* and xeromorphic taxa, such as *Quercus mediterranea*, *Acer pseudomonspessulanum* and *Buxus pliocenica* are common in both floras. However, the Makrilia assemblage is more diverse than the one from Vrysses. Considering the composition of the Makrilia flora it clearly contains relatively more deciduous taxa than the Vrysses plant assemblage. However, it is not clear whether this is a real signal or the result of taphonomic processes or in the nearby hinterland of the Vrysses area floras of high elevations might have simply not existed.

The late Miocene floras of continental Greece (Vegora, Likudi, Prosilion, Lava) and other islands (Chios, Kerkyra) consist mainly of conifers and deciduous broad-leaved elements, such as *Ginkgo*, Taxodiaceae, Pinaceae, *Sassafras*, *Alnus*, *Fagus*, deciduous *Quercus*, *Populus*, *Zelkova*, *Ulmus* and *Acer* (Velitzelos *et al.* 2001). Obviously, not only on Crete but in entire Greece, the exotic elements of the early Miocene were gradually replaced by deciduous broad-leaved trees and shrubs, forming forests that resembled modern mixed mesophytic woods of Eastern Asia, the Colchis and the Caspian area. This change most likely indicates a decrease of mean annual temperature during the Miocene in Greece, as it seems to have happened in all the other Tethys and Paratethys areas (Gregor 1990; Kovar-Eder 1987).

Furthermore, the relative increase of xeromorphic taxa, such as evergreen oaks (*Quercus drymeja* Unger, *Q. mediterranea* and *Q. sosnowskyi* Kolakovskii), as well as *Acer pseudomonspessulanum* and *Chamaerops humilis* (Velitzelos & Schneider 1978; Velitzelos *et al.* 2001; Kvaček *et al.* 2002) may indicate the beginning of weak drought periods during the last Miocene in Greece and the onset of the Csa climate type *sensu* Köppen (1931) (warm temperate with arid summers). The existence of summer drought may be more obvious in the plant assemblage of Vrysses indicating already the beginning Messinian salinity crisis (Hsu *et al.* 1973).

CONCLUSIONS

The upper Tortonian (6-7.5 Ma) Vrysses plant assemblage consists of a mixture of leaf taxa that had most likely originally grown in riparian to possibly mid altitude forests.

The Vrysses assemblage represents a microphyll flora consisting of 31 taxa. Remains of *Acer pseudomonspessulanum*, *Pinus* sp., *Quercus mediterranea* and *Ziziphus ziziphoides* predominate. The assemblage contains deciduous mesophytic elements (approximately 37-59%), thermophilous evergreens (appr. 11-30%) and xerophytic elements (appr. 15-52%).

A comparison of the Vrysses plant remains with recent taxa and their ecological needs leads to the following reconstruction: riparian forests with various taxa of *Salix* sp. and possibly *Populus tremula*, Juglandaceae existed, including possibly several thermophilous evergreens, such as *Daphnogene polymorpha*. Sclerophyllous vegetation comprising possibly *Quercus mediterranea*, *Quercus* sp., maybe *Buxus pliocenica*, *Acer pseudomonspessulanum*, Ulmaceae and several legumes stood most likely on dry lowland soils. Mixed mesophytic deciduous trees, such as *Acer* sp., *Populus tremula*, *Juglans acuminata*, *Ziziphus ziziphoides* and possibly *Acer pseudomonspessulanum* and Ulmaceae, with evergreen (*Buxus pliocenica* and *Daphnogene polymorpha*), deciduous ("*Parrotia*" *pristina*, Rosaceae) and conifers (*Tetraclinis* sp.) occurred in the lower strata.

The floristic composition and physiognomy of the assemblage, as well as a comparison with published Miocene Greek assemblages indicate a warm-temperate, humid climate for this period, possibly with not very pronounced dry periods for the end of the Tortonian in the eastern Mediterranean area.

Acknowledgements

We would like to thank Prof. M. Mylonas, director of the Natural History Museum of Crete, for his helpful suggestions, and Dr. A. Nikolaidis, director of the Mediterranean Agronomic Institute of Chania, for providing samples from this institution. For the free access to the Berlin Herbarium of the Botanic Garden for comparative studies we thank Dr. R. Vogt. This work would not have been possible without the help of the staff of the Natural History Museum of Crete, A. Kagiambaki, M. Trikali, G. Iliopoulos, E. Nikolakakis and P. Lyberakis. Also, comments of Dr. D. Franceschii, Dr. S. Sen and of an anonymous reviewer greatly improved this paper.

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Submitted on 23 December 2005;
accepted on 17 April 2007.