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Three (middle to) late Miocene plant macroremain assemblages (Pitsidia, Kassanoi and Metochia) from the Messara–Gavdos region, southern Crete

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ABSTRACT. Based on macroremains, we describe three fossil plant assemblages from the Miocene of the Messara Basin (southern Crete) and the adjacent Gavdos Island. The palaeoflora of Kassanoi, which is the oldest (Messara Basin, Viannos Fm, Serravallian/early Tortonian), is documented mainly by leaf imprints, including a fern, a conifer (*Tetraclinis* cf. *salicornioides*) and 23 angiosperms. The assemblage is dominated by *Daphnogene polymorpha*, *Podocarpium podocarpum* and *Myrica lignitum*. The plant record from Pitsidia (Messara Basin, Ambelouzos Fm, early Tortonian) comprises thousands of specimens. The plant fossils are preserved as imprints often covered by an inorganic encrustation (replica). One alga, 2 ferns, at least 5 conifers and more than 45 woody angiosperms were identified. Dominant taxa are *Myrica* and *Pinus pitsidiensis*, documented by numerous vegetative and reproductive organs (Zidianakis et al., 2015, 2016). Leaves of oaks (*Q. pseudocastanea*, *Q. kubinyii*) and *Daphogene polymorpha* as well as twigs of *Taxodium dubium* are also fairly common. From the palaeoflora of Metochia, which is the youngest (Gavdos Island, Metochia Fm, middle Tortonian), (Mantzouka et al., 2015), we report further taxa, including *Quercus mediterranea*, *Ziziphus paradisiaca* and a palm (*Sabalites* sp.).

The vegetation is assessed both empirically (phytosociologically) and by Integrated Plant Record (IPR) Vegetation Analysis. The reconstructed vegetation models are presented in detail and discussed in the context of the geological and palaeontological settings of the area. The climate is assessed based on the Coexistence Approach (CA) and the Climate Leaf Analysis Multivariate Program (CLAMP). The palaeoclimatic datasets reveal a warm temperate to subtropical climate, probably with a weak seasonal drought.

KEYWORDS: plant macroremains, Miocene, Crete, plant systematics, palaeovegetation, palaeoclimate

INTRODUCTION

In the early Miocene, a continuous landmass, Aegeis, emerged as part of the northern coast of the declining Tethys Ocean covering the current Aegean and Cretan Sea area (Dermitzakis and Papanikolaou, 1981). During the transition period from the middle to the late Miocene, a fan-like southward expansion took place, leading to the break-up of the southern part of Aegeis and ultimately to the formation of numerous separate islands (Dermitzakis and Papanikolaou, 1981; Meulenkamp and Sissingh, 2003). In such a dynamic tectonic system, the plant fossil record opens time windows into the past, offering insights into the major environment changes.

Contrary to other parts of Greece, the exploration history of the Cenozoic floras in Crete is rather recent. Velitzelos and Gregor (1990)

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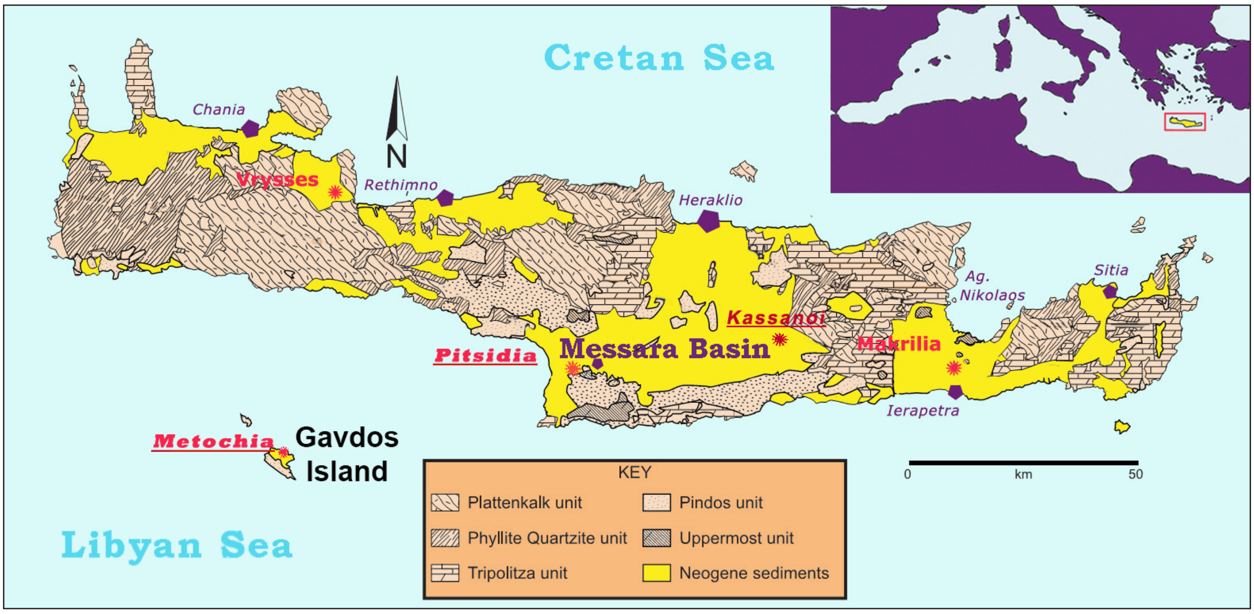

Fig. 1. Geological map of Crete and Gavdos islands, showing the localities bearing plant macroremains (modified from I.G.M.E., 1993); the localities studied herein are underlined

reported pine cones from the area of Achlia village (Appx. 1) in the eastern part of Crete, without providing a description or illustration. Later, Mohr et al. (1991) discovered a late Miocene plant assemblage close to Makrilia village in eastern Crete (Fig. 1). Approximately 130 taxa were identified based on foliage and diaspores as well as palynomorph remains (Sachse and Mohr, 1996; Sachse, 1997, 2004; Sachse et al., 1999). In the early 21st century, leaf impressions in limestone blocks were encountered in Vrysses, northwestern Crete (Zidianakis et al., 2007) (Fig. 1). This late Miocene assemblage comprises mostly poorly preserved foliage and rarely seed or fruit remains. Kröger (2004) studied the sedimentary environments of the western Messara Basin, noting the occurrence of plant macrofossils in fine-grained layers near Pitsidia village. He reported an outcrop 1–2 km SW of this village that yielded a florula. Because of extensive earthworks, the plant-bearing layers became easily accessible, and in 2008 a new outcrop rich in plant fossils was discovered (Zidianakis et al., 2010).

Recently, Velitzelos D. et al. (2014) published a review of the Cenozoic floras of Greece, illustrating a few new findings from Makrilia and providing amended species lists for the Cretan palaeofloras. From Pitsidia, Zidianakis et al. (2015, 2016) described mass occurrences of *Myrica* and *Pinus pitsidiensis* Zidianakis, Iliopoulos, Zelilidis, Kovar-Eder, including vegetative and reproductive organs. Plant–arthropod interactions were studied by Zidianakis et al. (2020), whereby the leaves of *Myrica lignitum* provide evidence of arthropod physiology, feeding and reproduction, with several types of damage.

Studies on plant sporomorphs from Neogene sediments of Crete are quite diverse, including Tortonian pollen spectra from Makrilia, Kastellios Hill, Plakias, Georgioupolis, Viglotopi, Triopetra and Almiri Panagia localities, the Messinian Perama/Dafnedes and Agia Varvara, as well as from the Pliocene of Agios Vlassios (Benda et al., 1974; van der Weerd, 1983; Sen et al., 1986; Drivaliari, 1993) (Appx. 1).

Unlike for Crete, the occurrence of terrestrial plant macroremains from the adjacent Gavdos Island was noticed by geologists already in the 19th century (Simonelli, 1894). More recently, several studies referred to the occurrence of plant material lacking descriptions from turbiditic sequences of the Metochia deposits (Postma et al., 1993; Gaudant et al., 2005; Tsaparas, 2005; Fig. 1). Mantzouka et al. (2015) described such plant material collected by Tsaparas (2005).

In this study we present a very rich plant macro-assemblage from Pitsidia and that of Kassanoi (Fig. 1), recently discovered, both situated in the southern part of central Crete. Also, several yet-unrecorded taxa are reported from the published palaeoflora of Metochia, Gavdos Island (Mantzouka et al., 2015).

GEOGRAPHICAL AND GEOLOGICAL SETTINGS

CRETE ISLAND

Crete constitutes a prominent horst structure of the southern Aegean Forearc in the still-active Hellenic subduction zone (Fig. 2). Its complex structure has been strongly affected by Alpine orogenic processes in the Eastern Mediterranean, due to the convergence of the Eurasian and African plates and the subduction of the Tethyan oceanic crust (Bonneau, 1984; Lister et al., 1984; Mountrakis et al., 2006; Ring et al., 2010; Maravelis et al., 2015). The geological structure of the island is a complex mosaic of pre-Alpine and Alpine rock comprising the pre-Neogene basement and post-Alpine deposits that fill the Neogene–Quaternary sedimentary basins. The basement is built of a pile of nappes that consist of various rocks from different palaeogeographic zones. Based on tectonostratigraphic position and tectonometamorphic history it is subdivided into two main sequences: the lower one consisting of metamorphic rocks, and the upper one of nonmetamorphic rocks (e.g. Creutzburg and Seidel, 1975; Seidel et al., 1982; Bonneau, 1984; Papanikolaou and Vassilakis, 2010). The Neogene sedimentary sequence of Crete comprises a variety of lithologies reflecting deposition in freshwater, brackish and marine environments, and is subdivided into six major lithostratigraphic groups (Meulenkamp et al., 1979) (Fig. 3).

THE MESSARA BASIN

Located in the southern part of central Crete, the Messara Basin is developed over the hanging wall of the Cretan Detachment (the tectonic contact of the two main nappe sequences of the Cretan basement), forming a supradetachment basin with deformed basement and several extensional klippen (van Hinsbergen, Meulenkamp; 2006) (Fig. 4). This basin was formed in the Neogene as part of

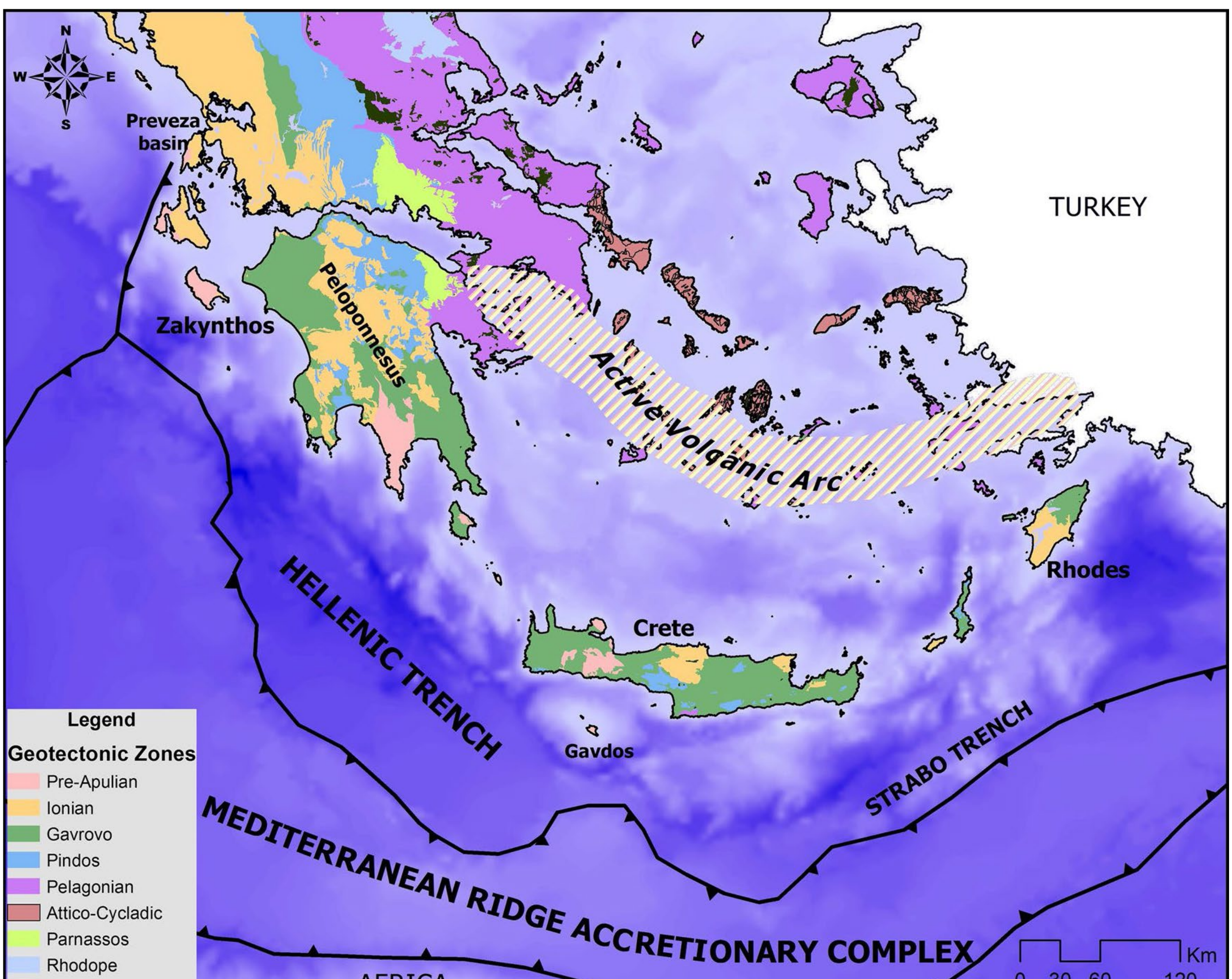

Fig. 2. Geotectonic map of SE Aegean and Crete region (Zelilidis et al., 2016, after Maravelis et al., 2015)

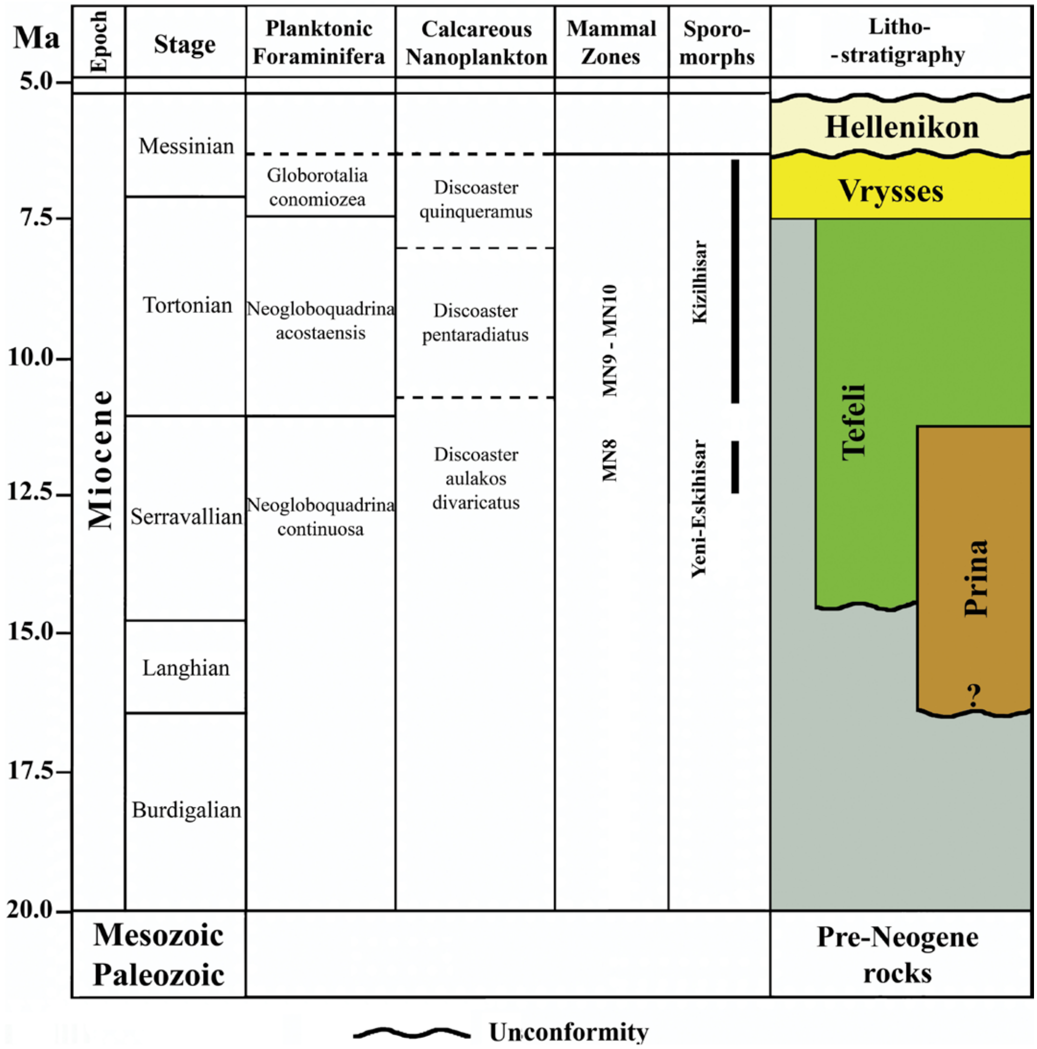

Fig. 3. Litho-chronostratigraphy of the Miocene sediments in Crete (Fassoulas, 2001, after Benda et al., 1974 and Meulenkamp et al., 1979)

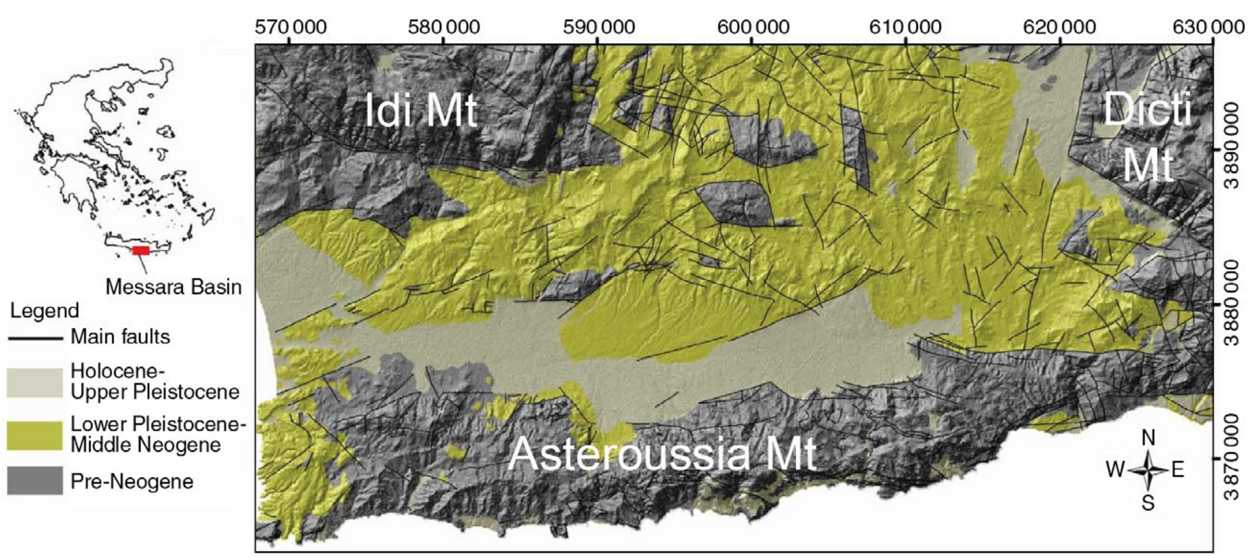

Fig. 4. Neogene deposits and main faults in the Messara Basin (Vafidis et al., 2012, after I.G.M.E., 1993)

a larger one extending northwards to the area of the present-day Heraklion Basin. During the early Pliocene, tectonic processes separated these two basins by the development of the east–west central Heraklion ridge (Fassoulas, 2001). The sedimentation started during the middle Miocene, resulting in the deposition of sequences lying unconformably upon the basement, characterised by abrupt lateral and vertical changes in lithology (Meulenkamp et al., 1979; Zachariasse et al., 2011; Vafidis et al., 2012). These sequences have undergone multidirectional extensional as well as compressional tectonic events (ten Veen and Postma 1999; van Hinsbergen and Meulenkamp, 2006; Chatzaras et al., 2006).

No formal lithostratigraphic scheme has been established yet for the Neogene deposits of the Messara Basin. According to the preliminary subdivision proposed by Meulenkamp et al. (1979), the Miocene depositional succession of the Basin could be subdivided into four formations characterised by a unique combination of lithology, depositional environment and stratigraphic position:

The Viannos Formation (Serravallian, Tefeli group) constitutes the oldest Neogene unit in the Messara Basin and is dominated by alternations of clay, silt and cemented sandstone of fluvio-lacustrine origin. This formation covers a wide range of depositional environments such as channel-belt, overbank and lacustrine settings. Platy weathered limestones are common, while lignitic clays are infrequent. According to Meulenkamp et al. (1979), the Viannos Fm is considered to be of Serravallian age because the overlying shallow-marine deposits of the Skinias Fm are dated to the early Tortonian (Zachariasse, 1975).

The Skinias Formation (upper Serravallian–lower Tortonian, Tefeli group) consists of marine clays with interbedded sandstones and occasionally gravels conformably overlying the Viannos Fm.

The Ambelouzos Formation (lower–middle/upper Tortonian, Tefeli group) reaches 350 m in thickness and disconformably overlies the Skinias Fm. It comprises a variety of lithologies representing fluvial-lacustrine, lagoonal and inner neritic environments. The poorly sorted conglomerates and their associated silty clays, lignites and travertines are interpreted as floodplain deposits dissected by braided channels. The massive oyster beds, silts and clays indicate repeated marine transgressions leading from lagoonal to inner neritic conditions.

The Varvara Formation (middle/upper Tortonian–lower Messinian, Vrysses group) consists of homogeneous to laminated mixed siliciclastic/calcareous marine sequences overlying either conformably the Ambelouzos Fm or with an angular unconformity the Viannos/Skinias Fms or the pre-Neogene basement.

Zachariasse et al. (2011) proposed an upgraded lithostratigtraphic system for the Tortonian–lower Messinian deposits of central Crete. Accordingly, the Miocene sediments of the Messara Basin are classified into a sequence of five formations (subdividing the Varvara Fm into the Moulia and Agios Miron Fms), and ages slightly younger than those proposed by Meulenkamp et al. (1979) were suggested.

GAVDOS ISLAND

Gavdos Island, situated 37 km south of Crete, forms the southernmost extension of the South Aegean Island Arc. It covers ~33 km^2. The pre-Neogene basement of the island consists of a series of NW–SE-striking thrust units, similar to that of Crete mostly represented by the Pindos unit (carbonates and flysch) as well as ophiolites (Kopp, 1977; Anastasakis et al., 1995) (Fig. 5). Neogene sediments up to 150 m thick cover two thirds of the island and unconformably overlie the pre-Neogene basement (Vicente, 1970; I.G.M.E., 1993; Anastasakis et al., 1995). These sediments are subdivided into two formations, the Potamos Fm and Metochia Fm (Anastasakis et al., 1995). The mainly marine Potamos Fm (lower/middle Serravallian–lowermost Tortonian) overlies the pre-Neogene basement with an angular unconformity and is considered as a possible time-equivalent to the fluvio-lacustrine sediments of the Viannos Fm and to the marine Skinias Fm in central Crete (Postma et al., 1993; Meulenkamp et al., 1994; van Hinsbergen and Meulenkamp, 2006; Zachariasse et al., 2011). The Metochia Fm (middle–upper Tortonian), up to 50 m thick, unconformably overlies the pre-Neogene basement, representing mostly marine environments. Starting from the base, it consists of conglomerates, paleosoils and sandstones, followed by an extended cyclothematic alternation of grey marls with brown-grey “sapropels”, finally followed by layers of diatomites, marls and limestones.

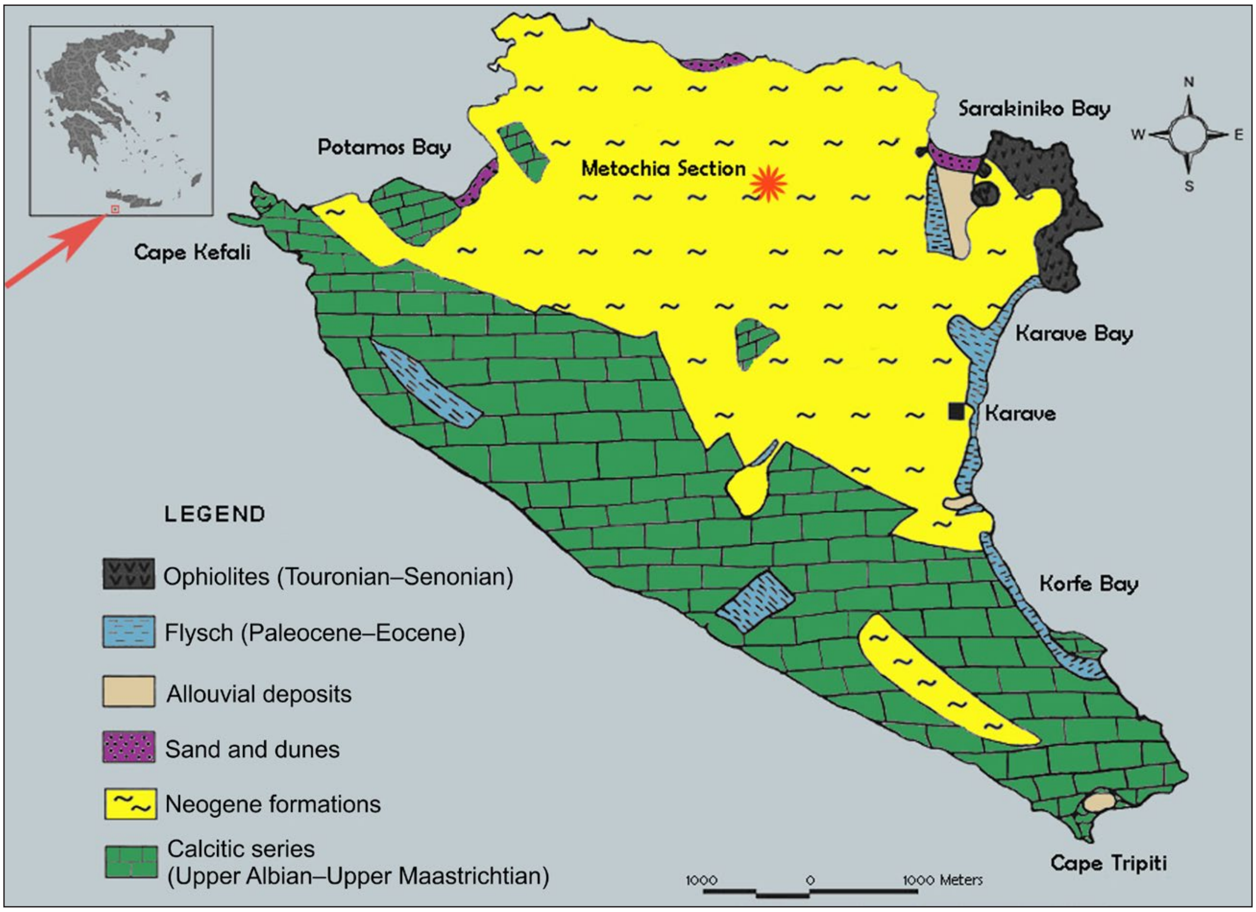

Fig. 5. Simplified geological map of Gavdos Island (Tsaparas, 2005, after I.G.M.E., 1993); the position of the Metochia section is asterisked

THE STUDIED OUTCROPS

The plant-bearing outcrop of Pitsidia is situated in the southwestern part of the Messara Basin ~1 km southwest of Pitsidia village (Fig. 1; Pl. 1, fig. 1). The deposits constitute a thick succession of terrigenous clastics, estuarine and shallow-marine sediments of the Ambelouzos Fm, which can be divided into three main lithostratigraphic units (Fig. 6). The main fossiliferous layer (abbreviated here MFL) is 3.5–4.0 m thick, beige to slightly blue-green, fine-grained and poorly lithified. Thin layers are superimposed for the next 1 m, some of them bearing plant remains as well (fossiliferous layers 1 to 3, abbreviated FL1–3) (Fig. 7). Apart from plant macrofossils, the fossiliferous layers further include isolated fish bones (mainly opercula, praeopercula and spinal bones), fish pharyngeal teeth (Cyprinidae) and sporadic gastropod shells (Planorbidae), ostracod valves (Candonidae) and insect imprints (mostly Coleoptera) (Fig. 8a). Based on Sr-isotope stratigraphy, the plant-bearing layers are dated somewhat older than 10.5 Ma, in the early Tortonian (Kröger, 2004).

The outcrop of Kassanoi is situated in the northeastern part of the Messara Basin, on a roadcut leading to Viannos Province, 1 km southwest of Kassanoi village (Fig. 1; Pl. 1, fig. 2). The section comprises a siliclastic succession of sandstone and silt-clay alternations more than 8 m thick, brownish to gray, occasionally with freshwater mollusc shells (Fig. 9). In the upper part of the sequence, a coal seam a few cm thick is developed. Plant remains, mainly leaf impressions, occur in the fine-grained intercalations below this coal seam, often co-occurring with plant debris. A horizon with roots preserved in situ is present ~15 cm below the coal seam (Pl. 2, fig. 5). The presence of in situ root remains and freshwater mollusc shells suggest a fluvio-lacustrine depositional environment for the outcrop. According to the 1:25,000 and 1:50,000 geological maps of IGME (1994; 2002), the outcrop is part of the Viannos Fm, considered of Serravallian age sensu Meulenkamp et al. (1979) or early Tortonian sensu Zachariasse et al. (2011).

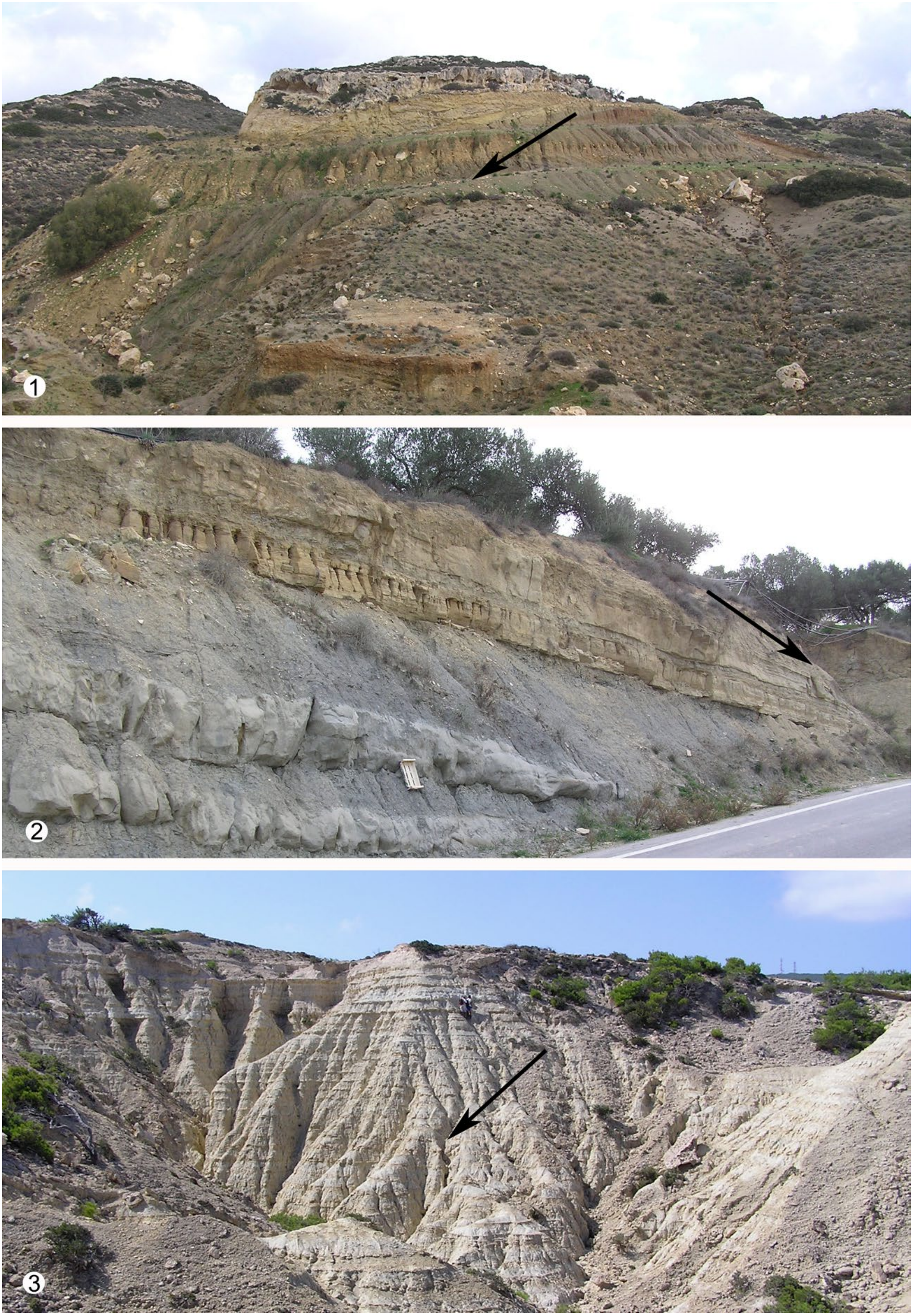

Plate 1. **1–3**. General view of the studied areas (arrows indicate plant-bearing outcrops); **1**. Pitsidia, western Messara Basin, Crete Island; **2**. Kassanoi, eastern Messara Basin, Crete Island; **3**. Metochia, Gavdos Island

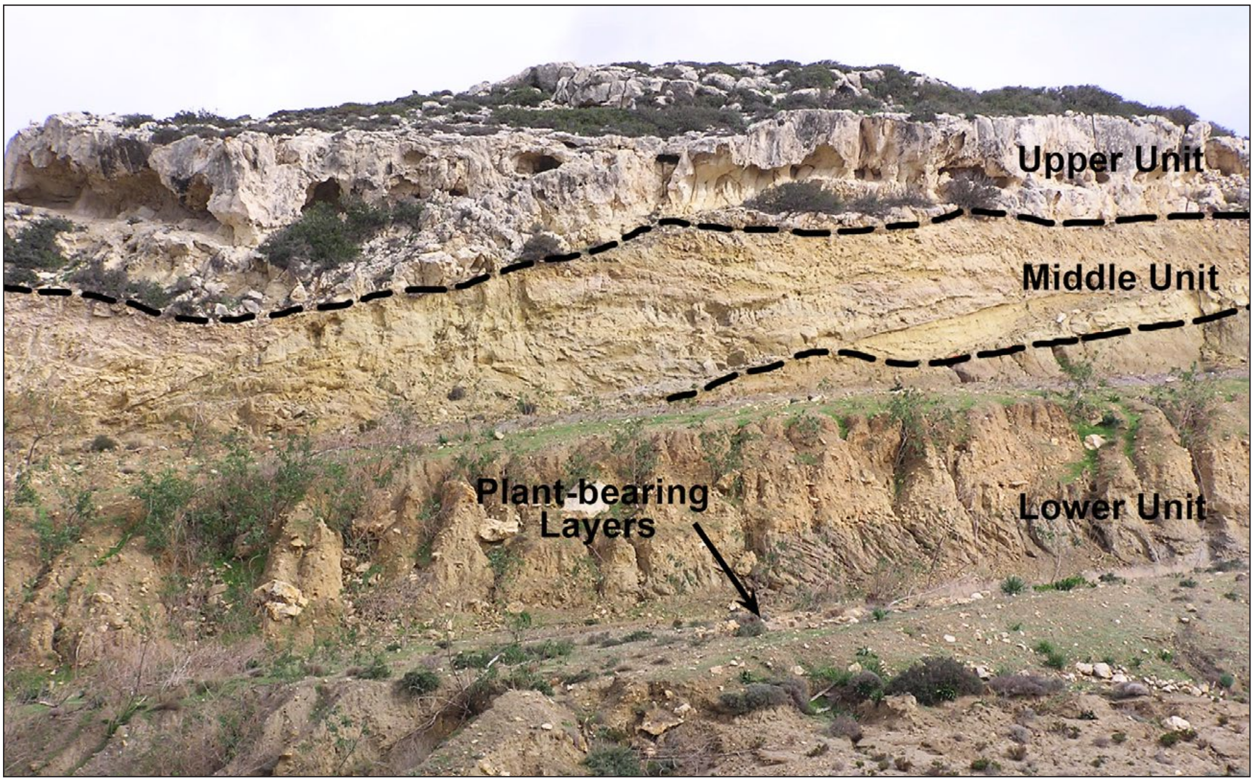

Fig. 6. Pitsidia outcrop; the three litho-stratigraphic units are separated by dashed lines

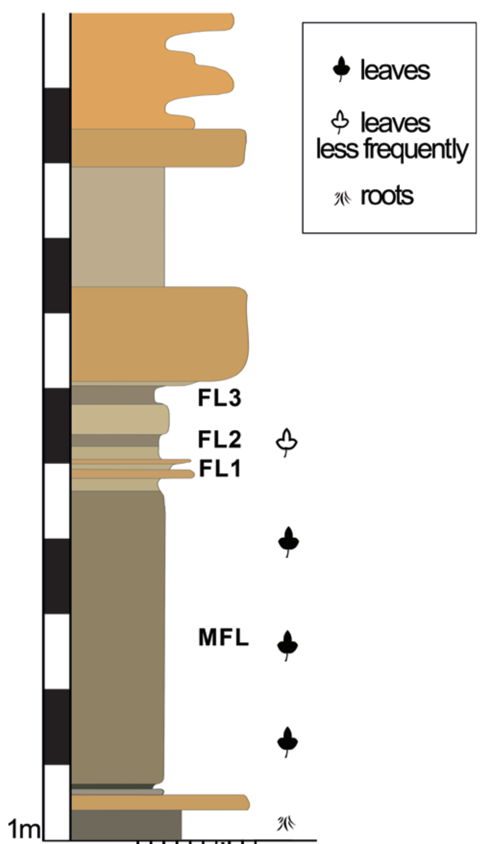

Fig. 7. Litho-stratigraphic sequence of the plant-bearing deposits of Pitsidia

The Metochia outcrop is situated in the northern part of Gavdos Island, ~1.5 km west of Sarakiniko Bay; it is the type section of the Metochia Fm (Figs 5, 10; Pl. 1, fig. 3). The poorly to non-bioturbated laminites (sapropels) of this outcrop are rich in plant macrofossils, mostly leaf imprints. The sediments represent a marine depositional environment which probably was supplied by river flooding. Based on magneto-, bio- and cyclostratigraphic data, the entire Metochia section spans a time interval from 9.7 to 6.6 Ma (Hilgen et al., 1995; Krijgsman et al., 1995). The excavated plant-bearing layers match with the Nrs M16–M26 sedimentary cycles corresponding to the middle Tortonian, approximately 9.0–9.4 Ma. The plant material described by Mantzouka et al. (2015) is considered to be of almost the same age because it came from the Nrs M16–M22 "sapropel" layers.

MATERIALS AND METHODS

From Pitsidia, ~6500 slabs with more than 9000 macrofossils were studied, collected from the main fossiliferous layer (MFL) and three superimposed thinner layers (FL1–3) (Fig. 7). Additionally, the material presented preliminarily by Zidianakis et al. (2010) is included herein and commented where necessary

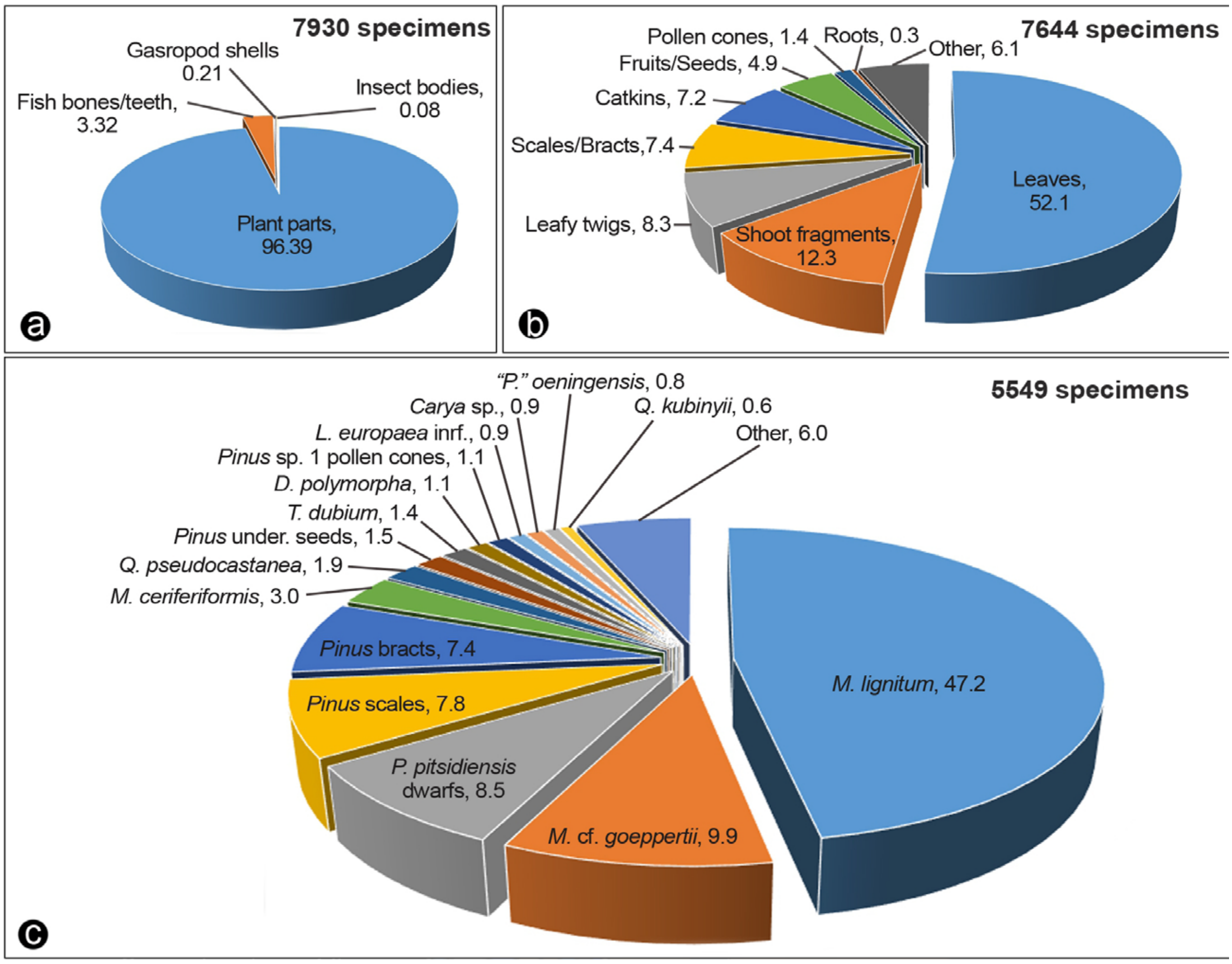

Fig. 8. Palaeoflora of Pitsidia. Frequencies (%) of different fossils collected from the main fossiliferous layer (MFL) during systematic excavation; a. fossil types (dicot leaf fragments < 1/6 of the original leaf size were ignored, and fish bones were collected only occasionally); b. plant organs/parts; c. plant taxa (frequency >0.5%)

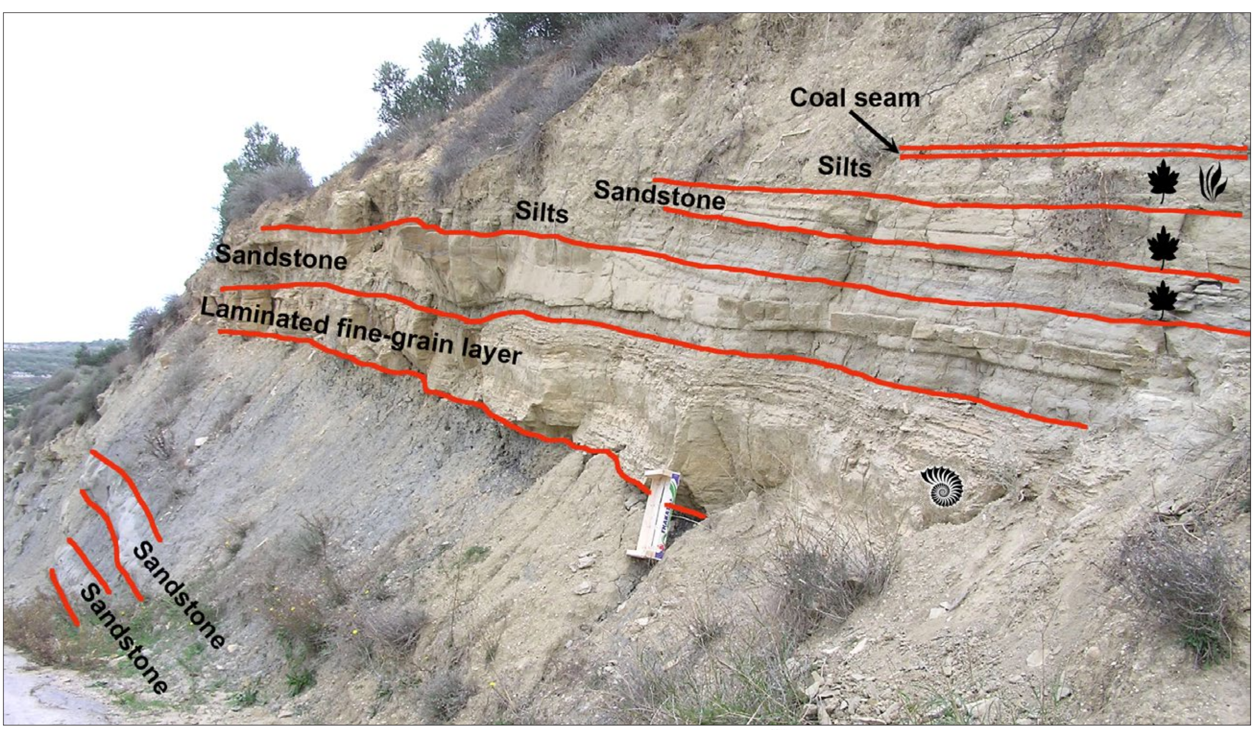

Fig. 9. Stratigraphic succession of the fossiliferous outcrop of Kassanoi; plant macroremains, in situ plant roots, freshwater mollusk shells

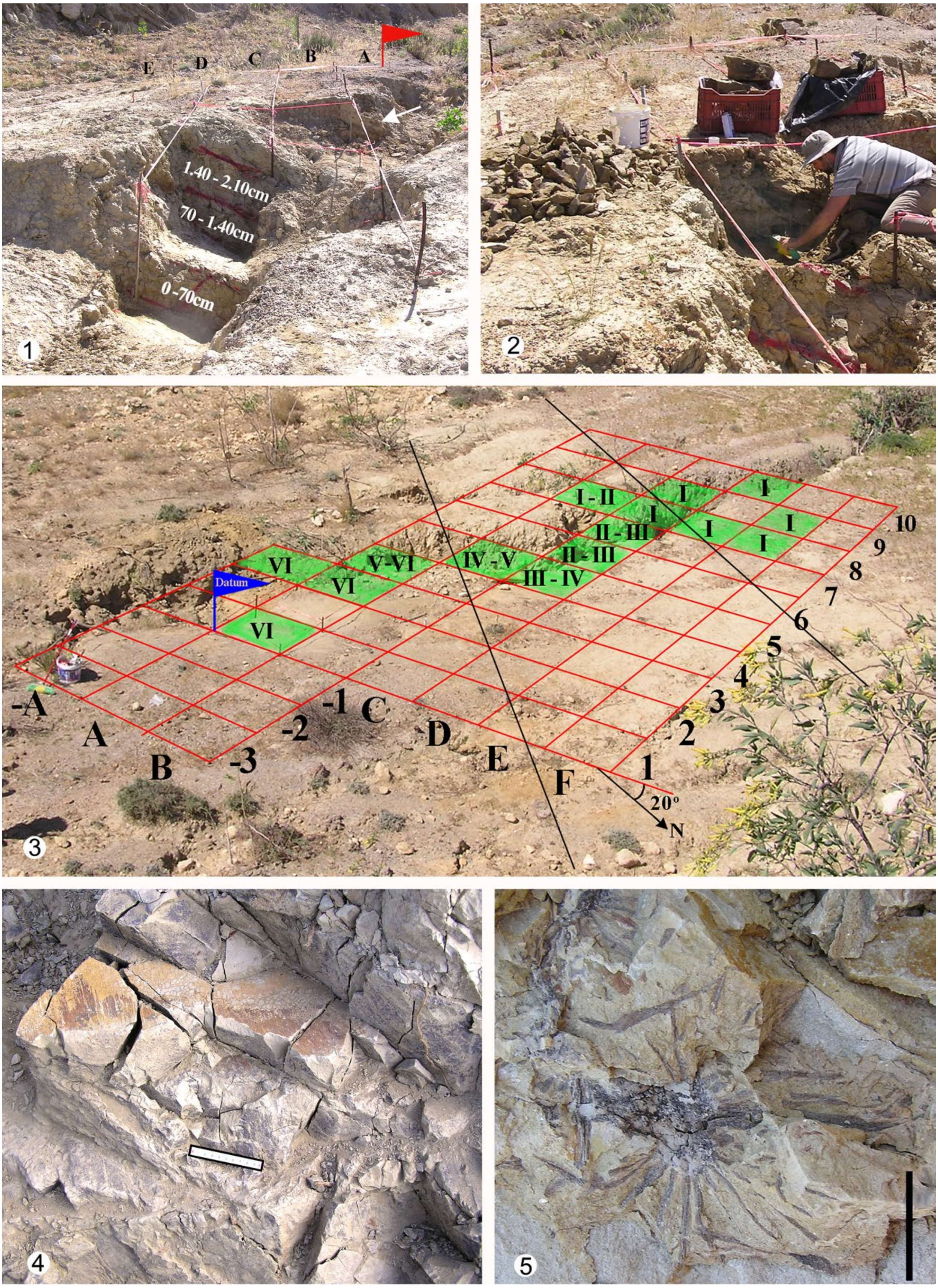

Plate 2. **1–4**. Pitsidia, excavation and collection of fossil plant material; **1**. the MFL is divided into 6 levels, 70 cm thick (flag indicates datum point, arrow indicates uppermost part of the MFL); **2**. working at grid square 5C, IV level of the MFL; **3**. general view of the excavation area (red lines mark the 7×13 m grid, black lines the main exposure of the studied fossiliferous sediment, arrow indicates North and flag datum point, green the mainly excavated squares, Roman numerals show the excavated levels in each square); **4**. natural fracturing of the plant-bearing deposits, scale bar = 10 cm; **5**. Kassanoi, bedding plane with in situ root remains, scale bar = 2 cm

(Nrs 31.4.2.1–710, Natural History Museum of Crete). Beyond a few coalified fragments (wood and monocot foliage), the majority of the plant fossils are leaf imprints, typically of light grey, brownish or yellowish colour, showing more or less detailed leaf venation. Inflorescences and scales/bracts are common as well (Fig. 8b). Coriaceous or needle-like leaves, shoots, fruits, seeds and inflorescences are often covered by an inorganic encrustation (replica of plant tissue), showing significant micromorphological and in some cases anatomical details. Even when the plant material was freshly excavated, these encrustations often appeared weathered due to cracks in the sediment and water penetration (Pl. 2, fig. 4).

In order to record the collected specimens three-dimensionally in the main fossiliferous layer, a grid of 1×1 m squares was established, and 6 levels (I–VI), each 70 cm thick, were delineated (Pl. 2, figs 1–3). All recovered fossils, regardless of their size, fragmentation, quality of preservation and taxonomic value, were collected and evaluated. Only fragments of dicot leaves smaller than ~1/6 their original size were ignored. The density of the plant remains (excluding dicot leaves < 1/6 their original size) in the main fossiliferous layer (MFL) is estimated at ~5500 specimens per m^3 of undamaged sediment. The dominant taxa in the assemblage, *Myrica lignitum* and *Pinus pitsidiensis*, are estimated to occur at density of ~1700 leaves and 400 dwarf shoots per m^3, respectively.

The material from Kassanoi comprises 341 plant imprints on 248 slabs. They were collected from silty intercalations a few centimetres underneath the coal seam (Fig. 9). From the Metochia “sapropelic” layers, in M16–M26 sedimentary cycles, 64 slabs with 71 plant fossils (imprints) on them were collected (Fig. 10). Inorganic encrustations occurred exceptionally, mostly on defoliated shoots and needle-like leaves.

All studied material is housed in the Natural History Museum of Crete (NHMC) under collection numbers 31.4.2.800–7038 and 31.4.2.8000–8273 for Pitsidia, 31.6.2.1–248 for Kassanoi, and 31.5.2.1–64 for Metochia.

The collected specimens were examined under a Motic SMZ-168 stereoscope. Selected specimens were studied by SEM at the University of Crete (JEOL

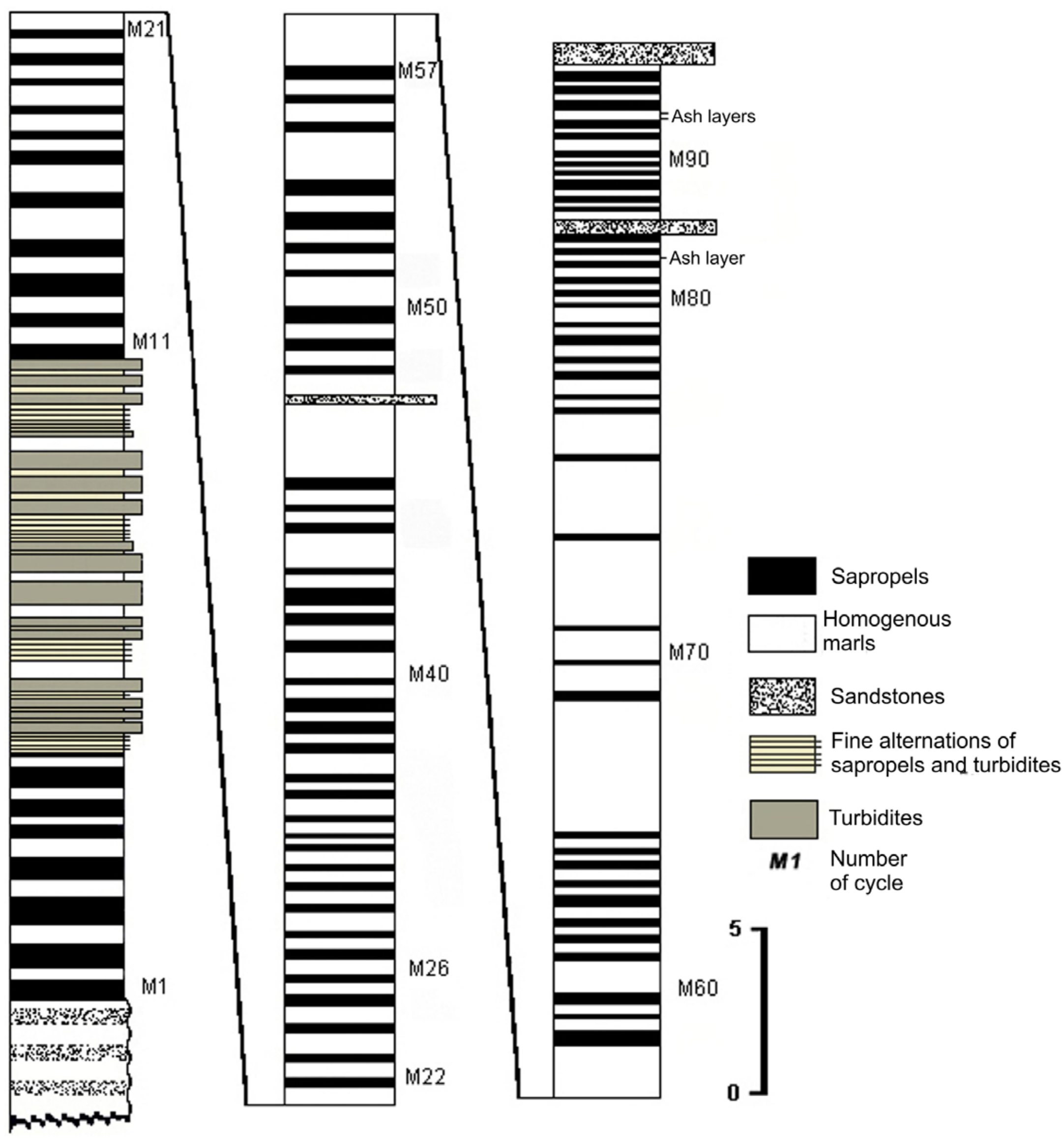

Fig. 10. Litho-stratigraphic sequence of the Metochia section (after Antonarakou, 2001)

6390LV) and the University of Patras (JEOL 6320). Photographs were taken with a Nikon 5100 digital camera. Image adjustment and drawings employed Adobe Photoshop Software version 9.0. Identification of foliage is based on macromorphological features. For coriaceous or needle-like leaves and reproductive organs with inorganic replicas, as well as for coalified wood and monocot leaf fragments, we include micromorphological and anatomical structures. Morphological terminology for leaf architecture is based on Hickey (1973), Dilcher (1974), Ash et al. (1999) and Ellis et al. (2009). Angiosperm systematics is based on Reveal (2012), which follows the classification of APG II (Bremer et al., 2003) and III (Bremer et al., 2009). Gymnosperm and fern systematics follow Christenhusz et al. (2011) and Christenhusz, Chase (2014).

Vegetation reconstruction of the three studied plant assemblages (Kassanoi, Pitsidia and Metochia) is based on the phytosociological approach (Mai, 1995; Denk, 2016). For classification of the assemblages in terms of zonal vegetation type, we applied the Integrated Plant Record (IPR) Vegetation Analysis (Kovar-Eder, Kvaček 2007; Kovar-Eder et al., 2008; Teodoridis et al., 2011). For palaeoclimatic estimates we used two techniques: the Coexistence Approach (CA) based on interpretation of the nearest living relatives (NLR) of woody dicots (Mosbrugger and Utescher 1997; Utescher et al., 2014) and the Climate Leaf Analysis Multivariate Program (CLAMP) based on leaf physiognomy (Wolfe and Spicer, 1999; Spicer et al., 2009; Yang et al., 2011). In CA, climatic data of living relatives were retrieved from the Palaeoflora Database (Utescher and Mosbrugger, 2015). Application of CLAMP follows the procedure explained on the CLAMP website (http://clamp.ibcas.ac.cn, accessed September 2020). Datasets of physiognomic and gridded meteorological calibration collected from 189 sites were selected.

SYSTEMATICS

Due to poor preservation, the affinities of several morphotypes could not be resolved, so open nomenclature has been applied. Taxa of questionable affinity are included in "Incertae sedis", where cumulative terms such as *Dicotylophyllum* spp., *Monocotylophyllum* spp. and *Antholites* spp. have been used. The synonym list includes the basic references and records from Greece.

Algae

Thallus

Fam. et gen. et sp. indet.

Pl. 4, fig. 1

Material. Pitsidia, a thallus fragment (Nr. 31.4.2.1517a,b).

Description. Thallus filamentous, stipe (stem-like axis) 24 mm long and 3.5 mm wide, dichotomised twice.

Remarks. This specimen possibly belongs to an alga. A more accurate systematic assignment is hampered by the poor preservation. The sedimentary context implies freshwater or brackish character of this element.

Polypodiophyta

Polypodiales Link

Fam. indet.

"Pteris" oeningensis Unger

Pl. 3, figs 1–12; Fig. 11

1847 *Pteris oeningensis* Unger, p. 124, pl. 37, figs 6, 7 (Freiberg, Austria, Miocene).

? 1986 *Pteridium* aff. *aquilinum fossilis* (L.) Kuhn; Velitzelos, Knobloch, pl. 12, fig. 6 (Skoura, Peloponnese, Pliocene).

? 1994a *Pteris* cf. *oeningensis* Unger; Kleinhölter, pl. 14, fig. 8 (Pyrgos and Zacharo basins, Peloponnese, Messinian).

? 2007a *Pteridium aquilinum fossilis* (L.) Kuhn; Butzmann et al., p. 23 (Vegora, W. Macedonia, Messinian) (no figure).

2010 Pteridophyta fam. indet.; Zidianakis et al., fig. 2a (Pitsidia, central Crete, Tortonian).

? 2014 cf. *Pteris oeningensis* Unger; Velitzelos D. et al., p. 69 (Prosilio and Lava, W. Macedonia, Messinian) (no figure).

Material. Pitsidia, 47 fragments of probably bi-pinnate/pinnatifid or more divided fronds (Nrs 31.4.2.828ii; 31.4.2.979ai,bi; 31.4.2.1938; 31.4.2.1958; 31.4.2.2197i; 31.4.2.2201a,b; 31.4.2.2201aop, 2203; 31.4.2.2256; 31.4.2.2387ii; 31.4.2.3142op; 31.4.2.3496aopiii; 31.4.2.3630; 31.4.2.4082; 31.4.2.4112; 31.4.2.4179opiv; 31.4.2.4256v; 31.4.2.4302; 31.4.2.4337; 31.4.2.4376; 31.4.2.4845; 31.4.2.4846; 31.4.2.4972; 31.4.2.5027a,b; 31.4.2.5050ii; 31.4.2.5218; 31.4.2.5258a,b; 31.4.2.5372ai,bi; 31.4.2.5502; 31.4.2.5594; 31.4.2.5638; 31.4.2.5742ai; 31.4.2.5884aop; 31.4.2.5894i; 31.4.2.6079; 31.4.2.6194ii; 31.4.2.6205a,b; 31.4.2.6213; 31.4.2.6268a,bi; 31.4.2.6407iii; 31.4.2.6427bop; 31.4.2.6478aii,bii; 31.4.2.6543iii; 31.4.2.6569iii; 31.4.2.6574a,b; 31.4.2.6639; 31.4.2.6665a,b; 31.4.2.8243a,b).

Description. (i). Ultimate lateral segments, pinnatifid (Fig. 11c). Petiolulate, petiolule 1 mm

Plate 3. Cretan palaeofloras, scale bar = 5 mm; **1–12**. "*Pteris*" *oeningensis* Unger, segments, Pitsidia; **1**. pinnatifid segment, Nr. 31.4.2.6268a; **2**. two lateral, simple segments loosely arranged on costa, Nr. 31.4.2.6574b; **3**. lateral, simple segments, Nr. 31.4.2.979bi; **4**. fragment of pinnatifid segment, Nr. 31.4.2.4112; **5**. fragment of pinnatifid segment, Nr. 31.4.2.5218; **6**. fragment of pinnatifid segment, Nr. 31.4.2.6194ii; **7**. isolated lateral lobe, Nr. 31.4.2.8243a; **8**. isolated terminal segement, Nr. 31.4.2.2197i; **9**. isolated terminal segment, Nr. 31.4.2.5884aop; **10**. isolated lateral lobe, Nr. 31.4.2.5894i; **11**. isolated lateral lobe, Nr. 31.4.2.4846; **12**. isolated lateral lobe, Nr. 31.4.2.4972; **13**. Polypodiophyta fam. gen et sp. indet., two frond segments close to each other, Pitsidia, Nr. 31.4.2.2337; **14–19**. *Tetraclinis* cf. *salicornioides* (Unger) Kvaček, leafy twigs; **14**. Pitsidia, Nr. 31.4.2.6324b; **15**. Pitsidia, Nr. 31.4.2.6324ai (counterpart of Pl. 3, fig. 14); **16**. Pitsidia, Nr. 31.4.2.6331aopi; **17**. solitary segment, Pitsidia, Nr. 31.4.2.845; **18**. Metochia, Nr. 31.5.2.9; **19**. Kassanoi, Nr. 31.6.2.182iii; **20**. Gymnospermae fam. et gen. et sp. indet., ovulate scale type 2 with two seeds, Pitsidia, Nr. 31.4.2.4538bopiv; **21**. Gymnospermae fam. et gen. et sp. indet., ovulate scale type 1 with scars of two seeds, Pitsidia, Nr. 31.4.2.1421aopii; **22–25**. Gymnospermae fam. et gen. et sp. indet., isolated needle-like leaves, Pitsidia; **22**. Nr. 31.4.2.5822ii; **23**. Nr. 31.4.2.5521; **24**. Nr. 31.4.2.5603; **25**. Nr. 31.4.2.4439aii

long, segment coriaceous, ovate, 11 mm long and 6.5 mm wide, lobed; lateral lobes dense, alternate to suboppositely arranged, ovate to triangular, 2–5.5 mm long and 1.5–2.5 mm wide, lobe sides convex to straight, apex acute to rounded, margin entire, ± involute sinuses narrow, mainly angular; terminal lobe lanceolate to linear, up to 6 mm long and 1–2 mm wide; venation dichotomous, open, every lobe with a main vein arising at 45–85° from midrib, straight or slightly curved, producing numerous fine veinlets, originating at acute angles, dichotomised once or twice, seldom simple (in smaller lobes), first dichotomy at the first 1/4 part of vein, ending at margin; (ii). Ultimate lateral or terminal segments, simple (Fig. 11a–b). Densely spaced, alternately to sub-oppositely arranged, lanceolate to oblong, ± asymmetric, ultimate lateral ones bent upwards, 6–11 mm long and 2.5–3.5 mm wide, apex (bluntly) acute to rounded, margin entire to erose; venation dichotomous, open, primary vein moderate, bent, secondaries fine, dense, in >7 pairs, mostly forked twice,

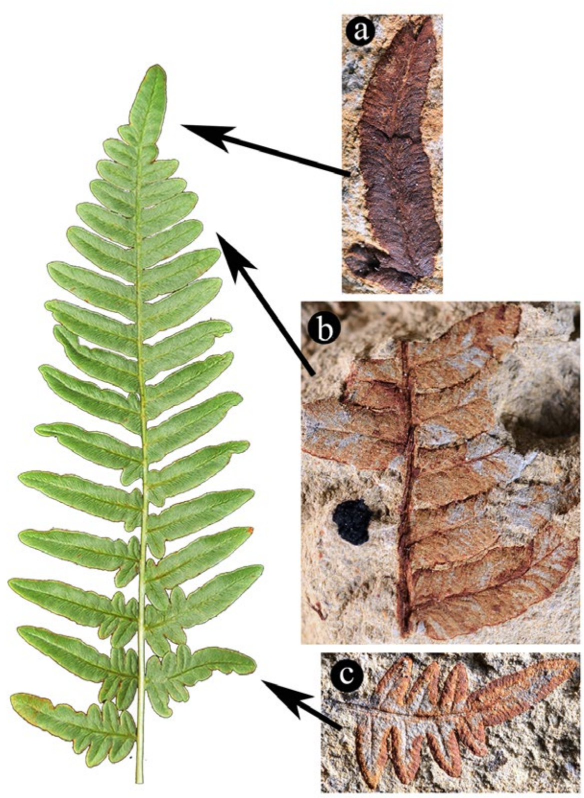

Fig. 11. Palaeoflora of Pitsidia. Schematic correlation of a pinnula of modern *Pteridium aquilinum* with material of "*Pteris*" *oeningensis* recovered from Pitsidia; **a**. ultimate terminal segment, Nr. 31.4.2.2197i; **b**. ultimate, lateral simple segments, Nr. 31.4.2.979bi; **c**. ultimate, lateral pinnatifid segment, Nr. 31.4.2.6268a

first dichotomy at the first 1/4 part of vein, ending at margin.

R e m a r k s. These remains probably belong to a single fern species. As no complete frond was found, the described lateral segments most likely represent pinnulae or parts of lower division. Thus, the fronds of this fern possibly were bi- or more pinnate/pinnatifid. No fertile structures were observed, although the involute margin of the segments suggests a possible marginal arrangement for sporangia.

Polypodiophyta incertae sedis

Frond fragments type 1

Fam. et gen. et sp. indet.

Pl. 3, fig. 13

M a t e r i a l. Pitsidia, 3 fragmentary segments (Nrs 31.4.2.1940bop; 31.4.2.2337i; 31.4.2.2337ii).

D e s c r i p t i o n. Isolated, fragmentary segments, texture chartaceous, shape ovate to lanceolate, >8 mm long and 3 mm wide, apex missing, margin entire, primary vein stout, straight, secondaries dense, originating at acute angles, bent, forked once or twice, reaching the segment margin.

R e m a r k s. These specimens differ from "*Pteris*" *oeningensis* by the broader shape of the segment, the thinner texture, and margin which is not involute.

Frond fragments type 2

Fam. et gen. et sp. indet.

Pl. 4, figs 2, 3

M a t e r i a l. Kassanoi, 2 fragmentary fronds (Nrs 31.6.2.112; 31.6.2.161aii,bii).

D e s c r i p t i o n. Fronds sterile, probably lanceolate, >38 mm long and 22 mm wide, apex acute, entire-margined; venation dichotomous, open, primary vein strong, straight, secondary veins numerous, delicate, densely arranged, parallel, arising at ~45°, dichotomising close to margin.

R e m a r k s. This fern material is rare and rather fragmentary.

Plate 4. Cretan palaeofloras, scale bar = 1 cm; **1**. Algae, thallus fragment, Pitsidia, Nr. 31.4.2.1517b; **2, 3**. Polypodiophyta fam., gen. et sp. indet., frond fragments, Kassanoi; **2**. apical part, Nr. 31.6.2.161bii; **3**. basal part, Nr. 31.6.2.112; **4–12**. *Taxodium dubium* (Sternberg) Heer, foliage shoots with acicular leaves (type i), Pitsidia; **4**. Nr. 31.4.2.4861aii; **5**. Nr. 31.4.2.3137a; **6**. Nr. 31.4.2.1217i; **7**. three attached twigs, Nr. 31.4.2.6123b; **8**. Nr. 31.4.2.5788ai; **9**. mechanically damaged, Nr. 31.4.2.2670; **10**. Nr. 31.4.2.6577a; **11**. mechanically damaged, Nr. 31.4.2.4886aii; **12**. dichotomised twig, Nr. 31.4.2.1135a; **13–20**. *Taxodium dubium* (Sternberg) Heer, incomplete foliage shoots with broad needle-like leaves (type ii), Pitsidia; **13**. upper part with prominent bud Nr. 31.4.2.5687; **14**. Nr. 31.4.2.2158b; **15**. Nr. 31.4.2.2944; **16**. Nr. 31.4.2.1263; **17**. Nr. 31.4.2.1260; **18**. Nr. 31.4.2.4023a; **19**. Nr. 31.4.2.4303a; **20**. Nr. 31.4.2.2204a; **21, 22**. *Taxodium dubium* (Sternberg) Heer, foliage shoots with slender needle-like leaves (type iii), Pitsidia; **21**. Nr. 31.4.2.4137a; **22**. Nr. 31.4.2.1865b; **23**. Gymnospermae, fam. et gen. et sp. indet. leafy shoot, Pitsidia, Nr. 31.4.2.4290b; **24**. *Pinus* sp. 2, five-needled, isolated needle fragment, Metochia, Nr. 31.5.2.14; **25–27**. defoliated long shoots of gymnosperm origin, fam. et. gen. et sp. indet., Pitsidia; **25**. Nr. 31.4.2.5049ai; **26**. Nr. 31.4.2.5186; **27**. Nr. 31.4.2.6463a

Spermatophyta

Gymnospermae

Family Cupressaceae

Genus *Tetraclinis* Masters

Tetraclinis* cf. *salicornioides (Unger) Kvaček

Pl. 3, figs 14–19

? 1847 *Thuites salicornioides* Unger, p. 11, pl. 2, figs 1–4; pl. 20, fig. 8 (Radoboj, Croatia, Miocene).
1975 *Libocedrites salicornioides* (Unger) Endlicher; Heimann et al., pl. 14, fig. 6 (Paghi, Corfu Island, Messinian).
1989 *Tetraclinis salicornioides* (Unger); Kvaček, p. 48, pl. 1, fig. 11; pl. 2, figs 2–14; pl. 3, figs 1–4; text-fig. 1 (European Tertiary).
1993 *Tetraclinis salicornioides* (Unger) Kvaček; Velitzelos, pl. 2, figs 2, 3 (Nea Stira, Euboea, early Miocene).
1994a *Tetraclinis salicornioides* (Unger) Kvaček; Kleinhölter, pl. 1, fig. 3; pl. 15, figs 10, 11 (Pyrgos and Zacharo basins, Peloponnese, Messinian).
1996 *Tetraclinis brachyodon* (Brongniart) Mai et Walter; Sachse and Mohr, fig. 4.11 (Makrilia, E. Crete, Tortonian).
? 2002a *Tetraclinis salicornioides* (Unger) Kvaček; Velitzelos et al., p. 11 (Kimi, Euboea, early Miocene) (no figure).
2004 *Tetraclinis* sp.; Sachse, pl. 8, figs 3, 8 (Makrilia, E. Crete, Tortonian).
2014 *Tetraclinis salicornioides* (Unger) Kvaček; Velitzelos D. et al., pl. 19, figs 6–8 (Elassona, N. Thessaly, Messinian).
? 2014 *Tetraclinis salicornioides* (Unger) Kvaček; Velitzelos D. et al., p. 67 (Megalonissi, Lesbos Island, early Miocene) (no figure).
2015 *Tetraclinis salicornioides* (Unger) Kvaček; Mantzouka et al., figs 3.1–3.3 (Metochia, Gavdos Island, Tortonian).

M a t e r i a l. Pitsidia, 2 fragmentary leafy twigs and a single isolated segment (Nrs 31.4.2.845; 31.4.2.6324ai,b; 31.4.2.6331aopi,6922opiv). Kassanoi, 2 leafy twig fragments (Nrs 31.6.2.182iii; 31.6.2.182iv). Metochia, a leafy twig (Nr. 31.5.2.9).

D e s c r i p t i o n. Incomplete twigs 7 to 17 mm long, broad and flattened; leaves scale-like, dimorphic (facial and lateral), borne in four, fused along most of their length, forming a flattened cladode-like segment that does not overlap with adjacent ones; whorls cuneiform or narrow elongate, 2.0–7.5 mm long and 1–3 mm wide, with rounded to truncate base; facial leaves closely appressed with acute apex, lateral leaves linear, overlapping margins of facial leaves, mostly free-tipped, shorter than facial leaves, apex acute, slightly incurved; three or five veins occur on each whorl according to their position.

R e m a r k s. According to Kvaček et al. (2000), two different species of *Tetraclinis* can be distinguished in the European Paleogene/Neogene, *T. brachyodon* (Brongniart) Mai et Walther and *T. salicornioides*, though some authors argue for the existence of a single species (e.g. Ferguson et al., 1998; Mai, 1998). Morphologically, these species differ mainly in the bract morphology of the seed cone, stomata distribution, branching, and to a lesser degree segment morphology and leaf fusion completion. Only the segment morphology is available in the material studied here. In Pitsidia and Metochia, the foliage fusion seems to be quite complete and the segments are more or less broad, isomorphic. These features allowed the assignment to *T. salicornioides*. Mantzouka et al. (2015) reported 1 twig and 2 detached leafy segments of *T. salicornioides* from Metochia. Vrysses is the only Cretan locality where *T. brachyodon* has been documented (Zidianakis et al., 2007, as *Tetraclinis* sp.). *T. salicornioides* is regarded as a frequent accessory element of subtropical to warm-temperate mesophytic forests (Kvaček, 1989; Mai, 1994; Kvaček et al., 2000).

Genus *Taxodium* L.C. Richard

Taxodium dubium (Sternberg) Heer

Pl. 4, figs 4–22

1823 *Pyllites dubius* Sternberg, p. 37, pl. 36, fig. 3, tentamen and index (Bílina, Czech Republic, early Miocene).
1855 *Taxodium dubium* (Sternberg) Heer; Heer, pp. 49–50, pl. 17, figs 5–15 (Hohe Rhonen, Switzerland, late Miocene).
? 1867 *Sequoia langsdorfii* (Brongniart) Heer; Unger, pl. 2, figs 22, 23 (Kimi, Euboea, early Miocene).
1975 *Taxodium dubium* (Sternberg) Heer; Heimann et al., pl. 14, fig. 4 (Paghi, Corfu Island, Messinian).
? 1977 *Sequoia langsdorfii* (Brongniart) Heer; Velitzelos, Schneider, fig. 4 (Vegora, W. Macedonia, Messinian).
? 1983 *Taxodium* vel. *Sequoia* spec.; Velitzelos, pl. 1, figs 1, 6 (Pappades, Euboea, late Miocene).
? 1994a *Taxodium* sp.; Kleinhölter, pl. 1, fig. 4; pl. 15, fig. 13 (Pyrgos and Zacharo basins, Peloponnese, Messinian).

1996 *Taxodium dubium* (Sternberg) Heer; Sachse, Mohr, fig. 4.10 (Makrilia, E. Crete, Tortonian).

1998 *Taxodium dubium* (Sternberg) Heer; Velitzelos et al., pl. 7, fig. 1 (Vegora, W. Macedonia, Messinian).

2002 *Taxodium dubium* (Sternberg) Heer; Kvaček et al., pl. 1, figs 7, 8; pl. 27, fig. 4 (Vegora, W. Macedonia, Messinian).

2004 *Taxodium dubium* (Sternberg) Heer; Sachse, pl. 8, fig. 7 (Makrilia, E. Crete, Tortonian).

?2007b *Taxodium dubium* (Sternberg) Heer; Butzmann et al., p. 25 (Fylakton, Thrace, Oligocene) (no figure).

2010 *Taxodium* sp.; Zidianakis et al., fig. 2d (Pitsidia, central Crete, Tortonian).

2014 *Taxodium dubium* (Sternberg) Heer; Velitzelos D. et al., p. 69, pl. 16, figs 3–5 (Prosilio and Lava, W. Macedonia, Messinian).

?2014 *Taxodium* vel *Sequoia*; Velitzelos D. et al., pl. 8, fig. 2 (Kimi, Euboea, early Miocene).

2015 *Taxodium dubium* (Sternberg) Heer, Mantzouka et al., fig. 3.4 (Metochia, Gavdos Island, Tortonian).

Material. Pitsidia, 82 leafy shoots or shoot fragments (Nrs 31.4.2.832a,b; 31.4.2.974; 31.4.2.988ii; 31.4.2.988iv; 31.4.2.1020ai,bi; 31.4.2.1021; 31.4.2.1106; 31.4.2.1121a,b; 31.4.2.1135a,b; 31.4.2.1217i; 31.4.2.1222ai,bi; 31.4.2.1230; 31.4.2.1260; 31.4.2.1263,6884i; 31.4.2.1265; 31.4.2.1408opii; 31.4.2.1865a,b; 31.4.2.1930a,b; 31.4.2.2158a,b; 31.4.2.2204a,b; 31.4.2.2281ai,bi; 31.4.2.2314a,b; 31.4.2.2442a,b; 31.4.2.2446a,b; 31.4.2.2636; 31.4.2.2647i; 31.4.2.2670; 31.4.2.2709; 31.4.2.2717op; 31.4.2.2727,2714op; 31.4.2.2739aiv; 31.4.2.2753; 31.4.2.2818; 31.4.2.2944; 31.4.2.2963a,b; 31.4.2.3036; 31.4.2.3137a,b; 31.4.2.3150avi,3158; 31.4.2.3223; 31.4.2.3372vii; 31.4.2.3589aiii; 31.4.2.3614a,b; 31.4.2.3842a,b; 31.4.2.3907a,b; 31.4.2.4023a,b; 31.4.2.4137a,bi; 31.4.2.4303a,b; 31.4.2.4455; 31.4.2.4468ai,b; 31.4.2.4540ai,bi; 31.4.2.4540aii,bii; 31.4.2.4683; 31.4.2.4856; 31.4.2.4861aii,bii; 31.4.2.4886aii,b; 31.4.2.4888; 31.4.2.4906a,b; 31.4.2.4946iii; 31.4.2.4991a,b; 31.4.2.4993a,b; 31.4.2.5307; 31.4.2.5640; 31.4.2.5687; 31.4.2.5744a,b; 31.4.2.5747; 31.4.2.5788ai,b; 31.4.2.5979; 31.4.2.6059i,6050op; 31.4.2.6123a,b; 31.4.2.6124a,b; 31.4.2.6235; 31.4.2.6388a,b; 31.4.2.6577a,b; 31.4.2.6872aop; 31.4.2.6881; 31.4.2.6885; 31.4.2.6955; 31.4.2.8139iii; 31.4.2.8156aiii; 31.4.2.8223a,b; 31.4.2.8224i; 31.4.2.8235ai,bi).

Description. Leafy shoots with helically arranged leaves. They can be separated into three different shoot types according to leaf size and spreading:

Type (i). shoots ~45–55 mm long, with short, acicular to slightly subulate, bifacial leaves, ± appressed, 3–7 mm long and ~0.5 mm wide, spreading three-dimensionally, angles between shoot and leaf axes ~25–40° (this type of shoot prevails in the assemblage),

Type (ii). shoots >30 mm long, with flattened, bifacial needle-like leaves, straight, 7–13 mm long and 0.8–1.2 mm wide, originating at 25–40°, spreading in one plane (distichously), needle base twisted, somewhat decurrent, needle tapering into an acute needle apex, margin entire; mid-vein strong, distinct; needles longer near the middle part of the short shoot or below, decreasing in length and width towards apex.

Type (iii). Shoots quite similar to second type but needles slender, somewhat longer, occasionally curved, originating at more open angles (35–50°), apex sometimes mucronate.

In cross section, inorganic replicas of the needles show a prominent vascular bundle but no resin ducts were detected. Stomatal structures are not preserved.

Remarks. Sterile shoots with needle-like, helically inserted and distichously arranged leaves occur in three genera of the Cupressaceae, in *Glyptostrobus*, *Sequoia* and *Taxodium*. The narrow shape of the needles, tapering towards the apex, and the position of the longest needles at the middle part of the short shoots are features that match better with *Taxodium* (Kunzmann et al., 2009) than with the other taxa. Remarkably, no fertile structures of *Taxodium dubium* were encountered in Pitsidia, although twig fragments are rather common. This may indicate parautochthonous to allochthonous origin. From Crete, a few incomplete shoots of *T. dubium* have also been reported from Makrilia and Metochia (Sachse, 2004; Mantzouka et al., 2015).

Family Pinaceae

Genus *Pinus* L.

Subgenus: *Pinus* L.

For *Pinus pitsidiensis* Zidianakis, Iliopoulos, Zelilidis et Kovar-Eder, *Pinus* sp. – two-needled fascicles, *Pinus* sp. – fascicle bracts, and *Pinus* sp. 1 – ovulate cone scales we refer to Zidianakis et al. (2016).

Subgenus *Strobus* Lemmon

For *Pinus* sp. 1 – five-needled fascicles we refer to Zidianakis et al. (2016).

Pinus sp. 2 – five-needled fascicle

Pl. 4, fig. 24

Material. Metochia, one needle fragment (Nr. 31.5.2.14).

Description. Needle fragment, 31 mm long, 0.7–0.8 mm wide, ~0.3–0.4 mm high, needle shape narrow flabellate in cross-section, abaxially profoundly medial-keeled, margin entire; amphistomatic, stomata in well-defined longitudinally arranged rows; rows six abaxially, irregularly spaced, stomata regularly spaced within rows, ~14–16 per 1 mm.

Remarks. The original length of this needle is unknown. The flabellate shape in cross section indicates a five-needled pine species.

Pinus sp. 2 – ovulate cone scale, see Zidianakis et al. (2016)

Not assignable to a specific subgenus: *Pinus* sp. 1 – fully developed seeds, *Pinus* sp. 2 – fully developed seeds, *Pinus* sp. – underdeveloped seeds, *Pinus* sp. 1 – pollen cones, *Pinus* sp. 2 – pollen cones, *Pinus* sp. – bud scales, see all in Zidianakis et al. (2016).

Pinaceae, gen. et sp. indet. – coalified wood

Fig. 12

Material. Pitsidia, one wood fragment (Nr. 31.4.2.7011).

Description. Small fragment of wood, coalified; in transverse section, growth ring boundaries distinct, composed of axial early- and latewood tracheids, earlywood tracheids angular, pentagonal to hexagonal, occasionally roundish, transition from early- to latewood

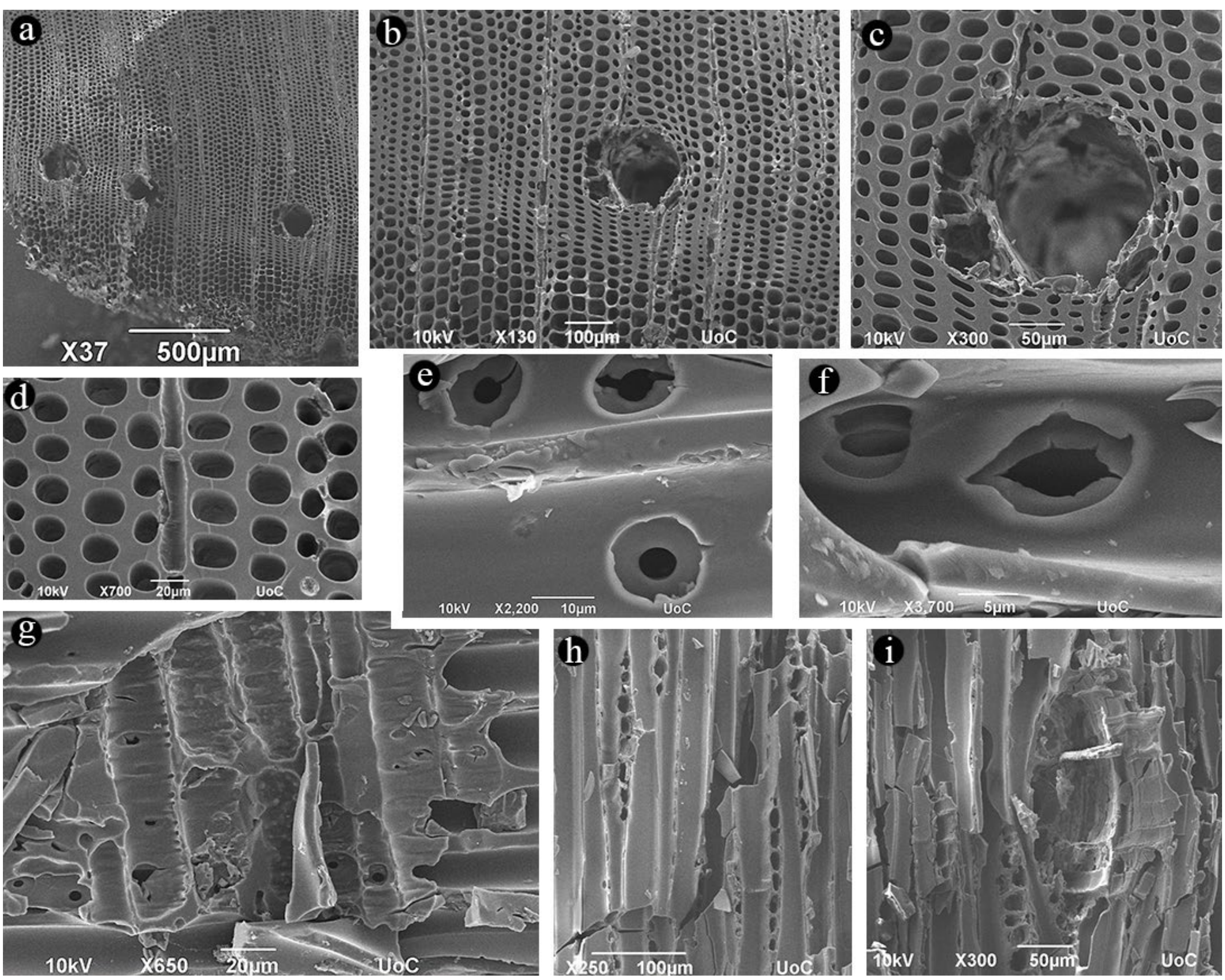

Fig. 12. Palaeoflora of Pitsidia. Anatomy of a coalified wood fragment, SEM, Nr. 31.4.2.7011; **a**. growth ring and axial resin canals, transverse section; **b**. gradual transition from earlywood to latewood, transverse section; **c**. normal axial intercellular resin canals, transverse section; **d**. latewood axial tracheids and radial parenchyma, transverse section; **e**. cross field of radial parenchyma and axial tracheids, radial section; **f**. pitting in radial walls of earlywood tracheids, radial section; **g**. cross-field pitting, radial section; **h**. uniseriate rays, tangential section; **i**. horizontal resin canal, tangential section

gradual, latewood tracheids thick-walled, axial parenchyma not found, normal axial intercellular resin canals present, epithelial cells not preserved; in radial section, pitting in radial walls of earlywood tracheids predominantly uni-seriate, cross-field pitting pinoid to cupressoid; in tangential section, rays exclusively uni-seriate, ray height medium (9–10 cells), horizontal intercellular resin canals present.

Remarks. The wood structure is homogeneous, composed of tracheids with distinct growth ring boundaries. It is therefore assigned to the conifers (Watson and Dallwitz, 2008). The presence of resin ducts accounts for the assignment to the Pinaceae (Young and Watson, 1969). Among modern members of Pinaceae, both axial and horizontal normal resin ducts occur in the genera *Cathaya*, *Larix*, *Picea*, *Pinus* and *Pseudotsuga* (Lin et al., 2000; Estenban and De Palacios, 2009).

Gymnospermae incertae sedis

Leafy shoot

Fam. et gen. et sp. indet.

Pl. 4, fig. 23

Material. Pitsidia, a fragmentary leafy shoot (Nr. 31.4.2.4290a,b).

Description. Isolated shoot 30 mm long, attached leaves linear, ~15 mm long, incomplete, and 2 mm wide, helically arranged, originating at acute angles, severely twisted basally, forming a pseudo-petiole, leaf apex missing, margin entire, mid-vein moderately thick.

Remarks. The shape of the attached leaves suggests a gymnosperm affinity for this specimen. It is not included in *Taxodium dubium* because of the broader needles.

Defoliated long shoots

Fam. et gen. et sp. indet.

Pl. 4, figs 25–27

Material. Pitsidia, at least 4 fragmentary long shoots (Nrs 31.4.2.5049ai,b; 31.4.2.5186; 31.4.2.6270i,6243ii; 31.4.2.6463a,b).

Description. Defoliated shoots 38–54 mm long, nodes surrounded by numerous densely spaced scars of bud scales, internodes with helically arranged large scars of abscised leaves.

Remarks. The type of scars and their arrangement on the shoots suggest a gymnosperm origin for these specimens.

Needle-like leaves

Fam. et gen. et sp. indet.

Pl. 3, figs 22–25

Material. Pitsidia, 3 complete needle-like leaves and an almost complete one (Nrs 31.4.2.4439aii,bii; 31.4.2.5521; 31.4.2.5603; 31.4.2.5822ii).

Description. Isolated needle-like leaves, sessile (no petiole), linear to lanceolate, 7–11 mm long and 1–2 mm wide, apex acute, base rounded to truncate, margin entire, mid-vein strong and straight.

Remarks. This material comprises various kinds of needles that are not easily identifiable due to the lack of diagnostic features. A Pinaceae or/and Cupressaceae origin is likely. Some of them (e.g., Pl. 3, figs 24, 25) may represent juvenile (primary) leaves of *Pinus*, because pine needles occur massively in the assemblage of Pitsidia.

Ovulate cone scale type 1

Fam. et gen. et sp. indet.

Pl. 3, fig. 21

Material. Pitsidia, a complete ovulate scale of a seed cone (Nr. 31.4.2.1421aopii).

Description. Isolated cup-like scale, 5 mm long and 5 mm wide, base asymmetric, rounded, apex shortly acuminate, with two seeds positioned proximally; seeds elliptic, 2.5 mm long and 1.0 mm wide, with rounded ends.

Remarks. The lack of diagnostic features prevents a more precise systematic assignment.

Ovulate cone scale type 2

Fam. et gen. et sp. indet.

Pl. 3, fig. 20

Material. Pitsidia, one incomplete ovulate scale of a seed cone (Nr. 31.4.2.4538bopiv).

Description. Scale broadly ovate, 5 mm long and ~9 mm wide (when completed), apex rounded, with two seeds at base; seeds oval to elliptic, 2–2.5 mm long and 1–1.5 mm wide.

Remarks. This specimen could be of coniferous origin.

Angiospermae

Family Lauraceae

Genus *Daphnogene* Unger

Daphnogene polymorpha
(A. Braun) Ettingshausen
Pl. 5, figs 1–15

1845 *Ceanothus polymorphus* A. Braun, p. 171 (Öhningen, Germany, middle Miocene).

1851 *Daphnogene polymorpha* (A. Braun) Ettingshausen; Ettingshausen, p. 16, pl. 2, figs 23–25 (Hernals, Austria, middle Miocene).

1867 *Cinnamomum lanceolatum* Unger; Unger, pl. 7, figs 1–10 (Kimi, Euboea, early Miocene).

1867 *Cinnamomum scheuchzeri* Heer; Unger, pl. 7, figs 11–24 (Kimi, Euboea, early Miocene).

1867 *Cinnamomum subrotundum* Heer; Unger, pl. 7, figs 25–29, (not 30) (Kimi, Euboea, early Miocene).

1867 *Bauhinia olympica* Unger; Unger, pl. 15, fig. 36 (Kimi, Euboea, early Miocene).

? 1873 *Litsea Delphica* Saporta; Saporta, pl. 2, fig. 7b (Kimi, Euboea, early Miocene).

1953 *Cinnamomum polymorphum* (A. Braun) Frentz.; Berger, fig. 6 (Kastron, Lemnos Island, early Miocene).

1953 *Daphnogene lanceolata* Unger; Berger, figs 7–11 (Kastron, Lemnos Island, early Miocene).

1953 *Cinnamomum polymorphum* A. Braun; Berger, fig. 18 (Moudros, Lemnos Island, early Miocene).

1953 *Cinnamomum* cf. *scheuchzeri* (Heer) Frentz.; Berger, figs 19, 20 (Moudros, Lemnos Island, early Miocene).

1981 *Cinnamomum polymorphum* Heer; Velitzelos, Petrescu pl. 2, figs 1–8 (Lesbos Island, early Miocene).

? 1984 *Cinnamomum lanceolatum* Heer; Velitzelos, Gregor, p. 242 (Aliveri, Euboea, early Miocene) (no figure).

? 1985 *Cinnamomum polymorphum* Heer; Dermitzakis, Velitzelos, p. 165 (Kato Komi, Chios Island, Serravallian–Tortonian) (no figure).

1992 *Daphnogene polymorpha* (A. Braun) Ettingshausen; Velitzelos et al., pl. 6, figs 6, 7(Aliveri, Euboea, early Miocene).

1993 *Daphnogene polymorpha* (A. Braun) Ettingshausen; Velitzelos, pl. 3, fig. 1 (Moudros, Lemnos Island, early Miocene).

1993–95 *Cinnamomum polymorphum* Kräusel, Weyland; Schimani, Schneider, figs 3, 4 (not 5) (Platanos-Paliopyrgos, Thessaly, early Miocene).

1994a *Daphnogene polymorpha* (A. Braun) Ettingshausen, Kleinhölter, pl. 1, fig. 8; pl. 18, figs 1, 2 (Pyrgos and Zacharo basins, Peloponnese, Messinian).

1997 *Daphnogene polymorpha* (A. Braun) Ettingshausen; Erdei, Kvaček, fig. 6 (Kimi, Euboea, early Miocene).

1999 *Daphnogene polymorpha* (A. Braun) Ettingshausen; Velitzelos et al., fig. E7 in p. 461 (Kimi, Euboea, early Miocene).

2004 fgen. *Cinnamomophyllum* sp.; Sachse, pl. 11, figs 7, 8 (Makrilia, E. Crete, Tortonian).

Non 2004 fsp. *Cinnamomophyllum polymorphum* (A. Braun) Heer; Sachse, pl. 11, fig. 12 (Makrilia, E. Crete, Tortonian).

2007 *Daphnogene polymorpha* (A. Braun) Ettingshausen; Zidianakis et al., figs 2E, 5D (Vrysses, W. Crete, Messinian).

2010 *Daphnogene polymorpha* (A. Braun) Ettingshausen; Zidianakis et al., fig. 3a (Pitsidia, central Crete, Tortonian).

2014 *Daphnogene polymorpha* (A. Braun) Ettingshausen; Velitzelos D. et al., pl. 7, fig. 3 (Grevena, W. Macedonia, early Miocene).

2014 *Daphnogene polymorpha* (A. Braun) Ettingshausen; Velitzelos D. et al., pl. 9, figs 9–?10 (Kimi, Euboea, early Miocene).

2014 *Daphnogene polymorpha* (A. Braun) Ettingshausen; Velitzelos D. et al., pl. 13, figs 1, 2 (Lesbos Island, early Miocene).

2014 *Daphnogene polymorpha* (A. Braun) Ettingshausen; Velitzelos D. et al., pl. 14, fig. 3 (Lemnos Island, early Miocene).

? 2014 *Daphnogene polymorpha* (A. Braun) Ettingshausen; Velitzelos D. et al., p. 73 (Zyfia, Chios Island, middle Miocene) (no figure).

2015 *Daphnogene* sp.; Mantzouka et al., figs 3.10–3.12 (Metochia, Gavdos Island, Tortonian).

Material. Pitsidia, 11 complete or almost complete leaves and 58 fragmentary leaves (Nrs 31.4.2.843; 31.4.2.893a,b; 31.4.2.978i; 31.4.2.1096; 31.4.2.1105a,b; 31.4.2.1146a,b; 31.4.2.1166; 31.4.2.1286iii; 31.4.2.1303; 31.4.2.1380op; 31.4.2.1672; 31.4.2.1863a,b; 31.4.2.1919; 31.4.2.2467aii,c; 31.4.2.2718; 31.4.2.3100a,b; 31.4.2.3280; 31.4.2.3572aopii,3558ii; 31.4.2.3627ai,bi; 31.4.2.3652; 31.4.2.3670; 31.4.2.3696aii,bii; 31.4.2.3737a,b; 31.4.2.3799; 31.4.2.3824,3823op; 31.4.2.4102ai,b; 31.4.2.4233i,4227opi; 31.4.2.4246; 31.4.2.4364a,b; 31.4.2.4538ai,b; 31.4.2.4740a,b; 31.4.2.5131bii; 31.4.2.5180; 31.4.2.5255; 31.4.2.5444; 31.4.2.5466aiv,biv; 31.4.2.5499ai,b; 31.4.2.5566op; 31.4.2.5584op; 31.4.2.5630; 31.4.2.5697aopiii; 31.4.2.5713; 31.4.2.5785aiv,biv; 31.4.2.5791,5743bop; 31.4.2.5806bopii; 31.4.2.5811ai,bi;

Plate 5. Cretan palaeofloras, scale bar = 2 cm; **1–15**. *Daphnogene polymorpha* (A. Braun) Ettingshausen, foliage; **1**. Pitsidia, Nr. 31.4.2.5466aiv; **2**. Pitsidia, Nr. 31.4.2.4538ai; **3**. Pitsidia, Nr. 31.4.2.1863b; **4**. leaf base, Pitsidia, Nr. 31.4.2.4364a; **5**. leaf base, Pitsidia, Nr. 31.4.2.5785biv; **6**. Pitsidia, Nr. 31.4.2.3737b; **7**. Pitsidia, Nr. 31.4.2.4102b; **8**. small leaf, Kassanoi, Nr. 31.6.2.147; **9**. Kassanoi, Nr. 31.6.2.136; **10**. Kassanoi, Nr. 31.6.2.122; **11**. Kassanoi, Nr. 31.6.2.125; **12**. leaf base, Kassanoi, Nr. 31.6.2.138i; **13**. Kassanoi, Nr. 31.6.2.131; **14**. slab with two leaves (arrows), Kassanoi, Nr. 31.6.2.126; **15**. petiole, lamina margin and venation are partly lined, Metochia, Nr. 31.5.2.31a

31.4.2.5845a,b; 31.4.2.6260ii; 31.4.2.6270ii,6243iii; 31.4.2.6306; 31.4.2.6317; 31.4.2.6496; 31.4.2.6519; 31.4.2.6537; 31.4.2.6718; 31.4.2.6789; 31.4.2.6790; 31.4.2.6794; 31.4.2.6940i; 31.4.2.6944a,b; 31.4.2.6988; 31.4.2.6951a,bi; 31.4.2.8108; 31.4.2.8161; 31.4.2.8180; 31.4.2.8215; 31.4.2.8208ai,bi; 31.4.2.8208aii; 31.4.2.8190).

Kassanoi, 5 complete or almost complete leaves and 37 fragmentary ones (Nrs 31.6.2.29ii; 31.6.2.113ii; 31.6.2.120v; 31.6.2.122; 31.6.2.123i; 31.6.2.124i; 31.6.2.125; 31.6.2.126i; 31.6.2.126ii; 31.6.2.128i,135i; 31.6.2.128ii,135ii; 31.6.2.128iii; 31.6.2.128iv; 31.6.2.129; 31.6.2.130i; 31.6.2.130ii; 31.6.2.131; 31.6.2.132; 31.6.2.133; 31.6.2.136; 31.6.2.137a,b; 31.6.2.138i,155; 31.6.2.139; 31.6.2.140; 31.6.2.142; 31.6.2.143; 31.6.2.144; 31.6.2.145; 31.6.2.146; 31.6.2.147; 31.6.2.148; 31.6.2.149; 31.6.2.150; 31.6.2.151i; 31.6.2.152i; 31.6.2.153; 31.6.2.154; 31.6.2.156; 31.6.2.170i; 31.6.2.174; 31.6.2.180ii; 31.6.2.221). Metochia, one complete leaf (Nr. 31.5.2.31a,b).

Description. Leaves petiolate, petiole robust, 8 mm to >14 mm long, mostly incompletely preserved; lamina polymorphic in shape, coriaceous, mostly ovate, elliptic to obovate, rarely lanceolate 24–95 mm long and 10–50 mm wide, L/W ratio 1.7–2.6, base angle acute, rarely obtuse, variable in shape from cuneate to convex or less frequently rounded or decurrent, occasionally slightly asymmetric, apex acute to acuminate, margin entire; venation suprabasal acrodromous, central primary vein stout, usually gently curved apically or throughout its length, lateral primary veins thinner, ± alternately arranged, arising from central vein at 25–45°, at distances of 2–9 mm from lamina base, extending to upper third of lamina, main secondary veins in ~4–7 pairs at upper part of lamina, rather delicate, originating at 40–70°, initially straight, curved close to margin, forming well-developed loops, interior secondaries (between primary veins) closely arranged, mixed percurrent (opposite to alternate), almost perpendicular to primaries, minor secondaries (originating from lateral primaries outwards) arising at 30–50°, thin, course similar to main secondaries, tertiary veins weakly percurrent, higher-order veins forming a regular polygonal net.

Remarks. The affinity of these remains to *D. polymorpha* is obvious. This species is a dominant element in the flora of Kassanoi, with leaves typically broader and probably more leathery than those of Pitsidia and Metochia, suggesting either different ecological growth conditions or proximity to the depositional area. In the Greek Neogene, *Daphnogene* is quite common, with the exception of the Messinian floras of N Thessaly and W Macedonia. In Crete it has been documented in Makrilia (two specimens, as *Cinnamomophyllum* sp.) and Vrysses (two slender leaves) (Sachse, 2004; Zidianakis et al., 2007). Mantzouka et al. (2015) also described several leaves of this type from Metochia (as *Daphnogene* sp.). Pingen et al. (1994) described laurel fruit remains from the Miocene deposits of Kreuzau as *Cinnamomum costatum* (Mai) Pingen, Ferguson et Collinson, and proposed that these fruits and the foliage of *D. polymorpha* belong to the same natural species because both co-occur there.

Genus *Lindera* Thunberg

?***Lindera ovata*** Kolakovsky

Pl. 7, figs 1–3

?1957 *Lindera ovata* Kolakovsky, p. 277, pl. 14, figs 4, 5; pl. 15, fig. 1 (Kodor River, Abkhazia, Pliocene)

?2004 *Dicotylophyllum* type 3; Sachse, pl. 14, figs 11, 13, pl. 20, figs 39, 42 (Makrilia, E. Crete, Tortonian).

2015 ?*Lindera ovata* Kolakovsky; Mantzouka et al., figs 3.13–3.16 (Metochia, Gavdos Island, Tortonian).

Material. Pitsidia, two complete and two fragmentary leaves (Nrs 31.4.2.3956a,c; 31.4.2.3957a,b; 31.4.2.6925; 31.4.2.5806ai,bi). Metochia, two incomplete leaves (Nrs 31.5.2.12a,b; 31.5.2.16).

Description. Leaves petiolate, petiole fragmentary, >7 mm long; lamina ovate to elliptic, possibly chartaceous, 35–52 mm long and 15–35 mm wide, L/W ratio 1.7–2.4, base acute to obtuse, convex to cuneate, apex widely obtuse to rounded, rarely acute, margin entire; venation almost basal acrodromous, central primary vein moderately thick, ± bent, lateral primary veins almost equal in thickness to central, suboppositely arranged, originating at ~25–45°, running close to margin, sub-parallel, reaching upper quarter of lamina, main secondary veins in a few pairs, ~3–5, at upper part of lamina, delicate, originating at 35–50°, bent, looping along margin, interior secondaries dense, almost perpendicular to primaries, mixed percurrent (opposite to alternate), minor secondaries fine, markedly curved, forming loops at margin with adjacent ones, intersecondaries 1–3 per intercostal area, parallel, weak, higher-order veins forming a regular polygonal network.

Remarks. This material differs from *D. polymorpha* foliage mainly by the almost basal acrodromous venation and the wider apex. Quite similar leaves have been described by Kolakovsky (1957, 1964) from Kodor River. From Metochia, Mantzouka et al. (2015) assigned similar leaves to ?*Lindera ovata* as well, and, from Makrilia, Sachse (2004) referred several specimens to *Dicotylophyllum* type 3, which possibly matches our material.

?Lauraceae gen. et sp. indet. – folia

Pl. 7, fig. 4

Material. Pitsidia, one complete leaf (Nr. 31.4.2.8115).

Description. Leaf shortly petiolate, petiole thick, 1.5 mm long, complete, lamina coriaceous, shape oblong, 27 mm long and 8 mm wide, L/W ratio 3.4, base almost cuneate, apex acute, margin entire, somewhat undulate; venation brochidodromous, primary vein strong, straight, secondary veins delicate, in ~12 pairs, originating at 50–75°, forming loops with adjacent ones near margin, intersecondaries present, 1–2 per intercostal area, parallel to secondaries, well developed, tertiary veins reticulate, forming a regular quadrangular to pentagonal network with higher-order venation.

Remarks. Though small, this leaf resembles Lauraceae by its firm texture, entire margin and venation pattern.

Monocotyledonae

Family Arecaceae

Sub-family Coryphoideae

Genus *Sabalites* Saporta

Sabalites sp.

Pl. 6, fig. 1

?1999 *Sabal major* Heer; Velitzelos et al., fig. B in p. 461 (Vatera, Lesbos Island, Pliocene)

Material. Metochia, one incomplete leaf (Nr. 31.5.2.44a,b).

Plate 6. Palaeoflora of Metochia; **1**. *Sabalites* sp., costapalmate leaf fragment, Nr. 31.5.2.44a. Scale bar = 2 cm

Description. Leaf palmate, 13 cm long (incomplete) and 10 cm wide; petiole partly preserved, 1.4 cm long and 2.8 cm wide, robust, probably unarmed, extending into blade, forming a short costa (2.5 cm long) tapering rapidly towards apex; leaf segments ~50, emerging from costa in obtuse angles at basal part and in acute ones distally, fused, shape elongate, ~5–8 mm wide in preserved part, wedge-shaped in transverse section; venation of segments parallelodromous, hardly visible.

Remarks. The costapalmate shape, along with the wedge-shaped segments, suggests an affinity to the tribes Corypheae or Borasseae of subfamily Coryphoideae (Dransfield et al., 2008). The relation of this specimen to *Sabal* is uncertain. Therefore, the fossil genus *Sabalites*, as introduced by Saporta (1865) and emended by Read and Hickey (1972), is considered more suitable. From the Miocene of Crete, the presence of fan palms has been recently reported from Makrilia (Velitzelos D. et al., 2014).

Family Altingiaceae

Genus *Liquidambar* L.

Liquidambar europaea
A. Braun (in Buckland)

Pl. 7, figs 5–12; Pl. 8, figs 1–14; Pl. 9, figs 1–12; Fig. 13

1836 *Liquidambar europaeum* A. Braun (in Buckland), p. 513 (Öhningen, Germany, middle Miocene).
1954 *Liquidambar europaea* A. Braun; Hantke, p. 63, pl. 8, figs 3–5, ?6; pl. 9, fig. 1 (Schrotzburg, Germany, Middle Miocene).

Folia:
1993 *Liquidambar europaea* A. Braun; Velitzelos, pl. 2, fig. 1 (Nea Stira, Euboea, early Miocene).
1994a *Liquidambar europaeum* A. Braun; Kleinhölter, pl. 21, figs 1–4 (Pyrgos and Zacharo basins, Peloponnese, Messinian).
1994b *Liquidambar europaeum* A. Braun; Kleinhölter, pl. 3, fig. 1 (Patra, Rion and Corinth basins, Peloponnese, Pliocene).
1995 *Liquidambar europaeum* A. Braun; Kleinhölter, pl. 2, fig. 6 (Patra, Rion and Corinth basins, Peloponnese, Pliocene).
?2002b *Liquidambar europaea* A. Braun; Velitzelos et al., p. 184 (Archangelos, Rhodes Island, Pleistocene) (no figure).
2010 *Liquidambar europaea* A. Braun; Zidianakis et al., fig. 2l (Pitsidia, central Crete, Tortonian).
2014 *Liquidambar europaea* A. Braun; Velitzelos D. et al., pl. 33, figs 3, 4 (Archangelos, Rhodes Island, Pleistocene).

Fructification:
1994a *Liquidambar europaeum* A. Braun; Kleinhölter, pl. 21, fig. 5 (Pyrgos and Zacharo basins, Peloponnese, Messinian).
1994a *Liquidambar europaeum* A. Braun; Kleinhölter, pl. 21, figs 6, 7 (Patra, Rion and Corinth basins, Peloponnese, Pliocene).
?1994a *Liquidambar europaeum* A. Braun; Kleinhölter, p. 197 (Skoura, Peloponnese, Pliocene) (no figure).
?2002b *Liquidambar europaea* A. Braun; Velitzelos et al., p. 184 (Archangelos, Rhodes Island, Pleistocene) (no figure).
2007 *Liquidambar europaea* A. Braun; Mai, Velitzelos, pl. 5, figs 17–19 (Kallithea, Rhodes Island, Pliocene/Pleistocene boundary).
2010 *Liquidambar* sp.; Zidianakis et al., fig. 2n (Pitsidia, central Crete, Tortonian).
2014 *Liquidambar europaea* A. Braun; Velitzelos D. et al., pl. 33, fig. 5 (Archangelos, Rhodes Island, Pleistocene).
2014 *Liquidambar europaea* A. Braun; Velitzelos D. et al., pl. 31, fig. 4 (Skoura, Peloponnese, Pliocene).
?2014 *Liquidambar europaea* A. Braun; Velitzelos D. et al., p. 70 (Elassona, Thessaly, Messinian) (no figure).

Material. Pitsidia, 2 almost complete leaves and 23 fragmentary ones (Nrs 31.4.2.276; 31.4.2.848ai,bi; 31.4.2.1487i; 31.4.2.2827a-d; 31.4.2.3747; 31.4.2.4014aii,bii; 31.4.2.4123a,b; 31.4.2.4253a,b; 31.4.2.4769a,b; 31.4.2.5278; 31.4.2.5358bi,5359i; 31.4.2.5385ai-c; 31.4.2.5601a,b; 31.4.2.5796a,b; 31.4.2.5808a,b; 31.4.2.5908a,b; 31.4.2.6001; 31.4.2.6082ai; 31.4.2.6149aopii; 31.4.2.6507; 31.4.2.6541; 31.4.2.6962i; 31.4.2.6964i; 31.4.2.8260; 31.4.2.8272); 38 almost complete fruiting heads and 20 fragmentary ones (Nrs 31.4.2.278; 31.4.2.820,821; ?31.4.2.881a,b; 31.4.2.975; 31.4.2.1034a,b; 31.4.2.1052; 31.4.2.1223iii; 31.4.2.1305a,b; 31.4.2.1600; 31.4.2.1857; 31.4.2.1928i; 31.4.2.1997; 31.4.2.2023; 31.4.2.2034; 31.4.2.2155a,b; 31.4.2.2375a,b; 31.4.2.2512; 31.4.2.2540ai,b; 31.4.2.2868a,b; 31.4.2.3047ai,bi; 31.4.2.3085a,b; 31.4.2.3145a,b; 31.4.2.3203; 31.4.2.3500; 31.4.2.3858; 31.4.2.3997aopii; 31.4.2.3997b; 31.4.2.4028bviii; 31.4.2.4028ci; 31.4.2.4028cii; 31.4.2.4037; 31.4.2.4093iii; 31.4.2.4327i; 31.4.2.4573; 31.4.2.4665; 31.4.2.4692; 31.4.2.4761; 31.4.2.4860; 31.4.2.4877,4865aii; 31.4.2.5096; 31.4.2.5181i; 31.4.2.5256; 31.4.2.5430aiv,bi; 31.4.2.5610; 31.4.2.5719; 31.4.2.5798; 31.4.2.5935ai,bi; 31.4.2.6026bi; 31.4.2.6039,6026bi; 31.4.2.6184a,b; 31.4.2.6209; 31.4.2.6809; 31.4.2.6813i; 31.4.2.6963aii,bi; 31.4.2.6980; 31.4.2.6982; 31.4.2.6989a,b; 31.4.2.8160).

Description. Leaves mostly fragmented, long petiolate, petiole rarely preserved, >39 mm long; lamina palmate, three- or five-lobed, 27–50 mm long, 44–58 mm wide, L/W ratio 0.63–0.85, base mostly cordate, apex of lobes acute to acuminate, margin regularly crenulate, lobes oblong to lanceolate or triangular, central lobe broader than lateral ones, sinuses angular, acute to obtuse, teeth small, rounded or rarely acute, with glanduliferous apices; venation actinodromous, 3 or 5 primary veins, depending on number of lobes, in five-lobed leaves the lateral-most primary veins often originating supra-basally, central primary vein stout, straight or bent, lateral primary veins thinner, curved, rarely straight, arising at 50–95° from midrib, secondary veins semicraspedodromous, mostly alternately arranged, curved, arising at rather acute angles, interconnected near margin, tertiary veins weakly percurrent (alternate), venation of higher orders forming an irregular network.

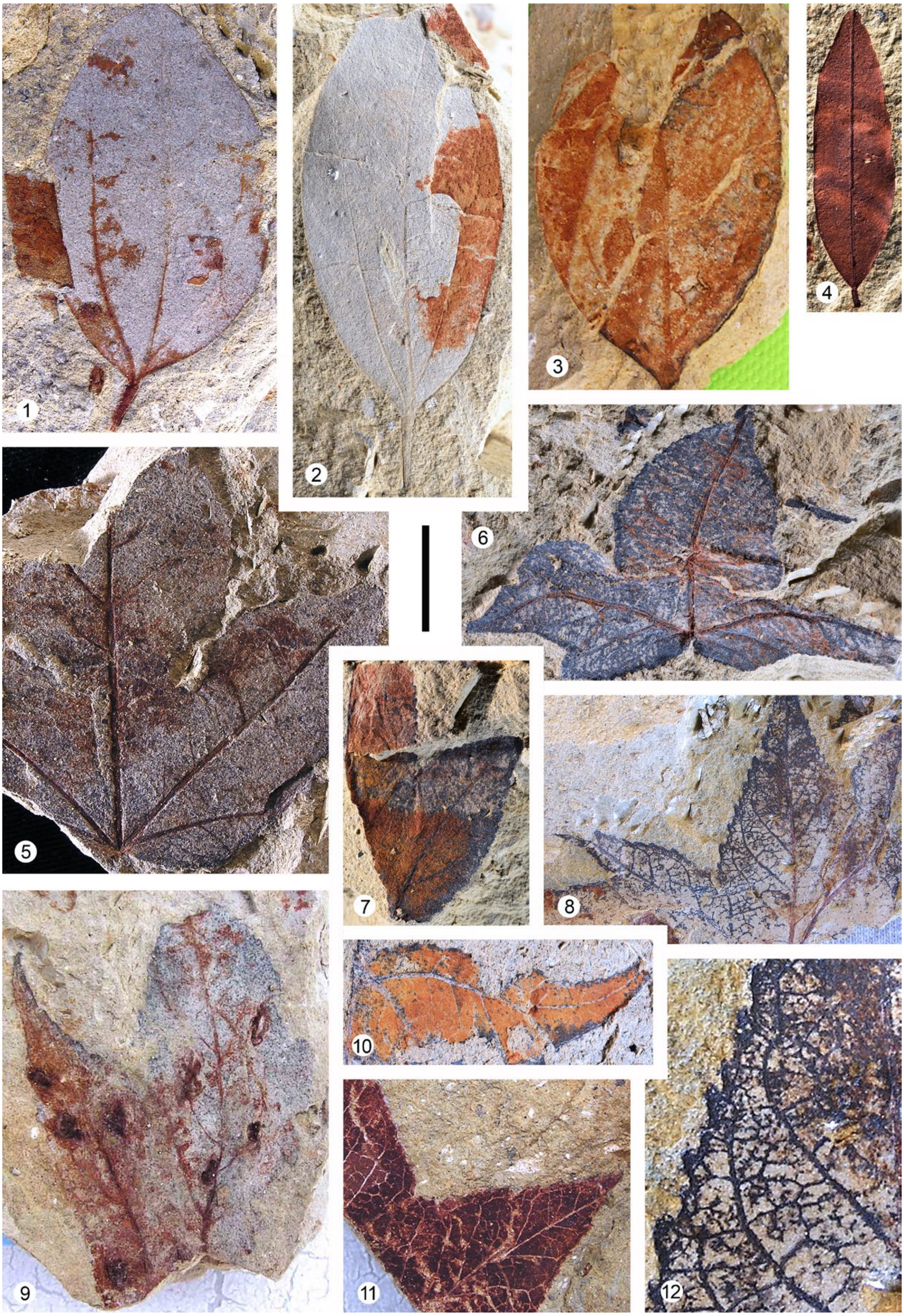

Plate 7. Cretan palaeofloras, scale bar = 1 cm (unless otherwise stated); **1–3**. ?*Lindera ovata* Kolakovsky, foliage; **1**. Pitsidia, Nr. 31.4.2.3957b; **2**. Pitsidia, Nr. 31.4.2.6925; **3**. Metochia, Nr. 31.5.2.12a; **4**. ?Lauraceae gen. et sp. indet., foliage, Pitsidia, Nr. 31.4.2.8115; **5–12**. *Liquidambar europaea* A. Braun, foliage, Pitsidia; **5**. Nr. 31.4.2.5796a; **6**. Nr. 31.4.2.6001; **7**. Nr. 31.4.2.5808a; **8**. well-preserved margin and venation details, Nr. 31.4.2.3747; **9**. with prominent galls, Nr. 31.4.2.276; **10**. leaf lobe, Nr. 31.4.2.6962i; **11**. leaf fragment, Nr. 31.4.2.8260; **12**. close-up, showing marginal teeth and venation pattern, Nr. 31.4.2.3747 detail, scale bar = 3 mm

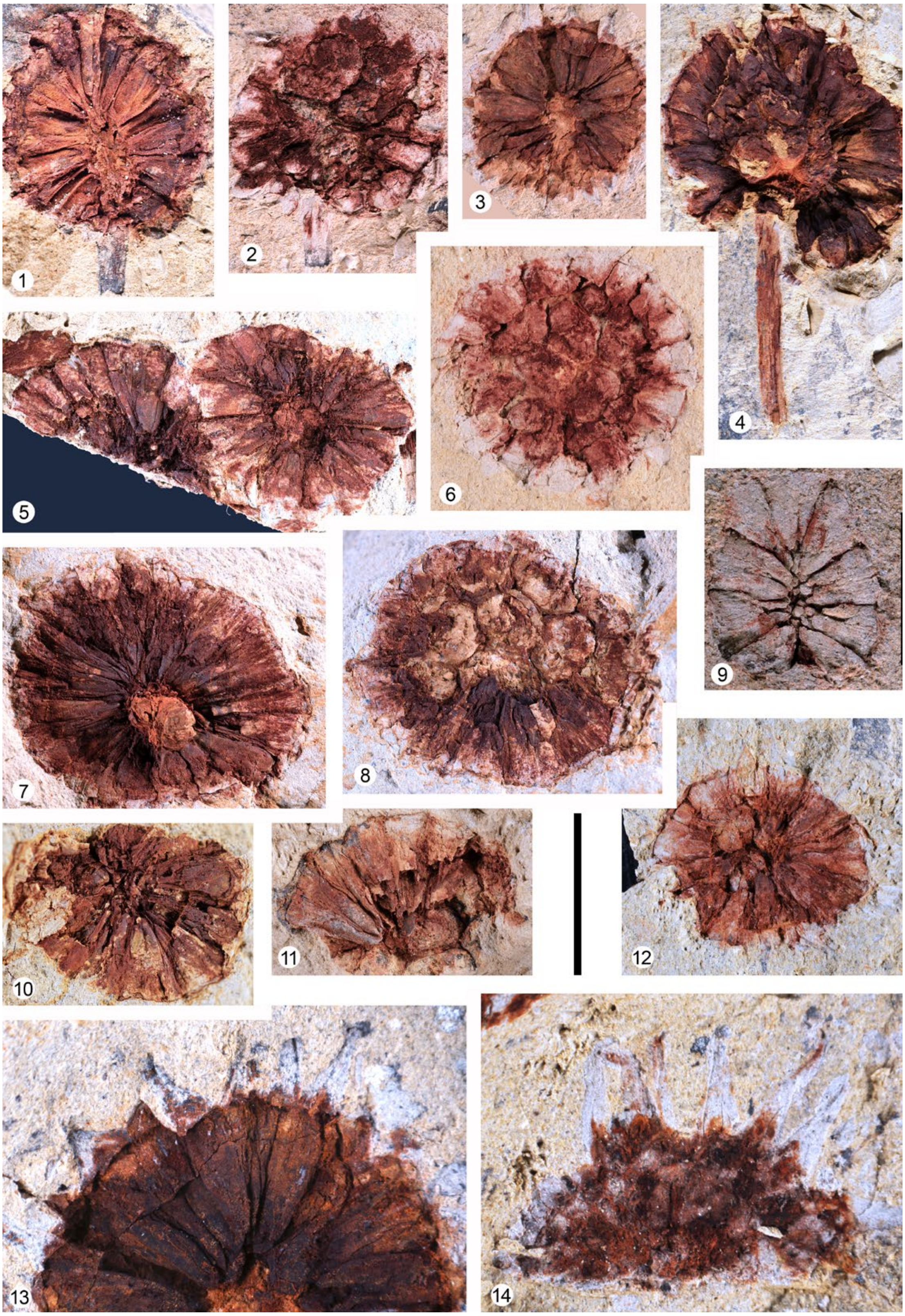

Plate 8. Palaeoflora of Pitsidia, scale bar = 1 cm (unless otherwise stated); **1–14**. *Liquidambar europaea* A. Braun, fruiting heads; **1**. note densely arranged bilocular capsules, Nr. 31.4.2.820; **2**. Nr. 31.4.2.2868a; **3**. numerous styles crowning the fructification, Nr. 31.4.2.6184a; **4**. with long peduncle, Nr. 31.4.2.3500; **5**. two fruiting heads closely arranged, Nr. 31.4.2.4028c; **6**. Nr. 31.4.2.2375b; **7**. central axis well-preserved, Nr. 31.4.2.2155a; **8**. note honeycomb-like structure, Nr. 31.4.2.2155b; **9**. impression, preserved in coarser sediment, Nr. 31.4.2.1034b; **10**. Nr. 31.4.2.3047bi; **11**. fragmentary head with well-preserved capsules, Nr. 31.4.2.5610; **12**. complete styles crowning the fructification, Nr. 31.4.2.5798; **13**. broken styles, close-up, Nr. 31.4.2.6184a detail, scale bar = 4 mm; **14**. complete styles, Nr. 31.4.2.5935bi, scale bar = 4 mm

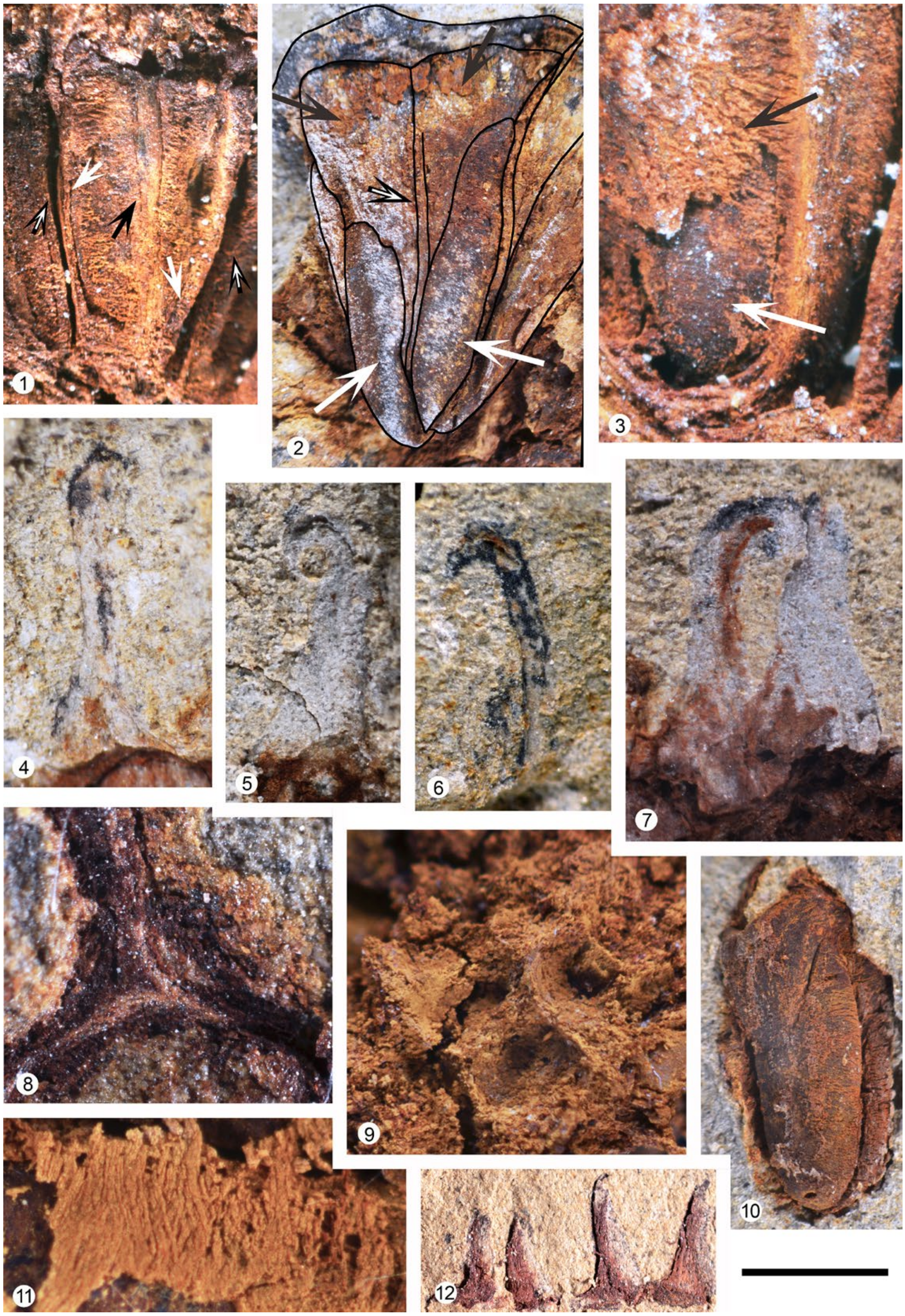

Plate 9. Palaeoflora of Pitsidia, scale bar = 1.5 mm (unless otherwise stated); **1–12** *Liquidambar europaea* A. Braun, details of fruiting heads; **1**. capsule with two carpels, carpel fusion (ventral seem) (black arrow), dorsal seems (white arrows), gap between capsules (black-white arrow), Nr. 31.4.2.820 detail, scale bar = 2 mm; **2**. capsule, the two carpels (black arrows), ventral seam (black-white arrow), locules (white arrows) are lined, Nr. 31.4.2.5610 detail, scale bar 2.5 mm; **3**. basal part of carpel, note carpel wall characterised with fine transverse ridges (black arrow) and the seed (white arrow), Nr. 31.4.2.820 detail, scale bar = 1 mm; **4**. persistent style, Nr. 31.4.2.5798 detail; **5**. persistent style, Nr. 31.4.2.5935bi; **6**. persistent style, Nr. 31.4.2.5798 detail; **7**. two adjacent persistent styles, Nr. 31.4.2.5935ai detail; **8**. smooth, slightly thickened area between capsules (peripheral rim), close-up, Nr. 31.4.2.278 detail, scale bar = 1 mm; **9**. scars of capsule bases on central axis of infructescence, Nr. 31.4.2.4573 detail, scale bar = 2 mm; **10**. isolated capsule detected in sediment, Nr. 31.4.2.6209, scale bar = 3 mm; **11**. fine transverse ridges of carpel wall, close-up, Nr. 31.4.2.4573 detail, scale bar = 0.5 mm; **12**. isolated styles detected in sediment, Nr. 31.4.2.881a, scale bar = 4 mm

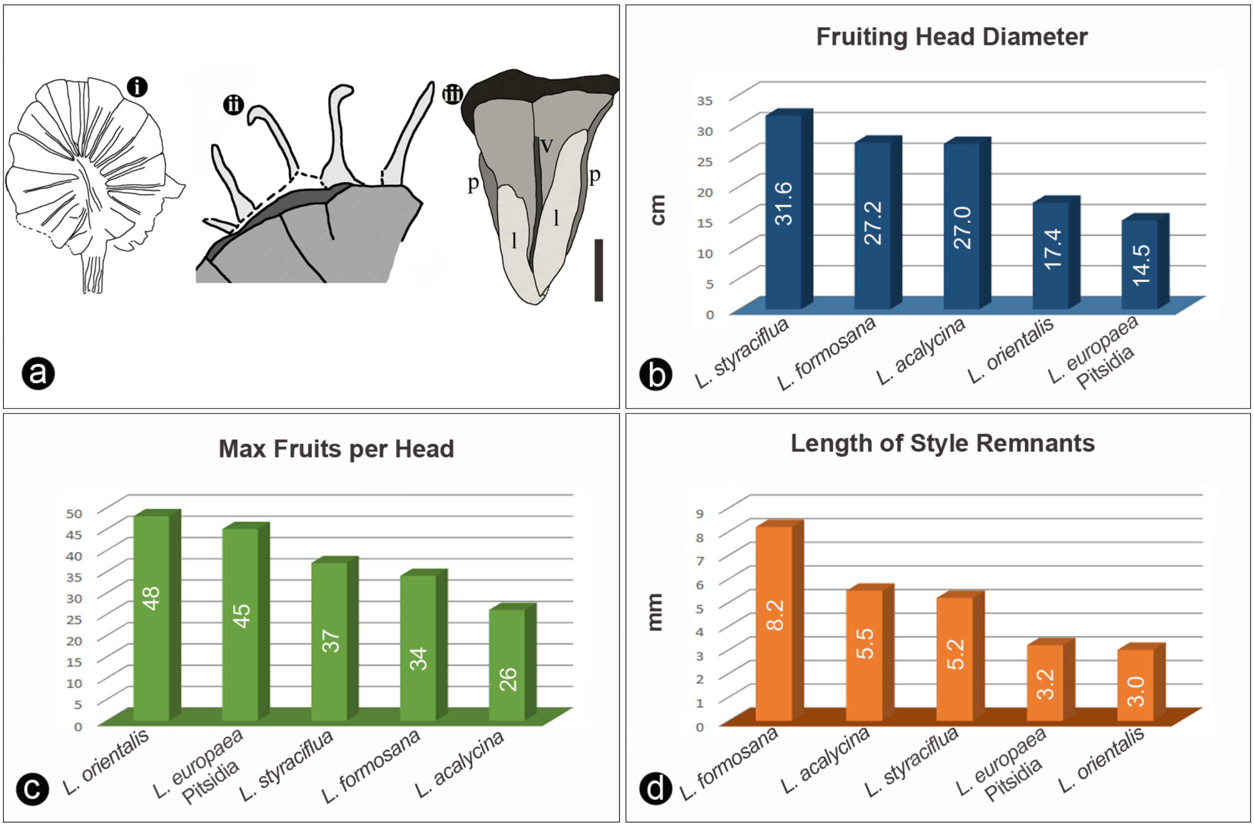

Fig. 13. Palaeoflora of Pitsidia. *Liquidambar europaea*; **a**. i–iii. fructification line drawings; i. fruiting head, Nr. 31.4.2.820, scale bar = 5 mm; ii. pesistent styles of fruiting head with curved tips and triangular-shaped bases, Nr. 31.4.2.5798 detail, scale bar = 2 mm; iii. capsule with two carpels (s. ventral seem, l. locules, p. pericarp), Nr. 31.4.2.5610 detail, scale bar = 2 mm; **b–d**. biometric fructification comparisons with the extant species of *Liquidambar*; b. diameter of fruiting head; c. maximum fruits per head; d. length of style remnants; data for modern species are from Ickert-Bond et al. (2005)

Fructifications. Imprints with well-developed inorganic structures of solitary, probably woody, capitate infructescences (fruiting heads), pedunculate, composed of dense clusters of fruits; peduncles in most cases missing or fragmentarily preserved, >12 mm long and ~1.5 mm wide, extending into inner part of infructescence, as central axis; shape of fruiting head lenticular as a result of compression, original shape probably spherical or almost spherical, 8–21 mm (average 14.5 mm) in diameter, L/W ratio 1–1.1, with 30–45 fruits; fruits elongate, ± wedge-shaped, bilocular capsules, 4.5–8 mm long, 2.5–4.5 mm wide, arranged fairly tightly on central axis, inner pericarp wall thin with fine transverse ridges on surface, locules elongate, cone- to sack-like; along outer surface of infructescence the adjacent fruits form roundish pentagons or hexagons (honeycomb-like structures), area between fruits – peripheral rim sensu Gregor (1978) and Ferguson (1989) – smooth, somewhat thickened, with a fine fusion line; style remains occasionally preserved, narrow elongate, straight, slightly bent or S-like, with triangular-shaped bases and curved to hook-like tips, 2.5–4.0 mm (average 3.2 mm) long and 1–2 mm wide at base, no other extrafloral structures such as spines or knobs detected.

Remarks. Unlike the foliage, the fruiting heads are quite abundant and well-preserved in Pitsidia. Several members of the Altingiaceae bear their fruits in a capitulum (head) at the end of a long peduncle. Specific features such as the capsule shape and the occurrence of persistent styles allowed an assignment to *Liquidambar* sensu stricto (Bolge, 1986; Ferguson, 1989; Ickert-Bond et al., 2005; Ickert-Bond and Wen 2006, 2013). According to Gregor (1978) and Mai (1997, 1999), most of the infructescences described from Europe as *L. magniloculata* Czeczott et Skirgiello, *L. pliocenica* Geylard et Kinkelin or *L. orientalis fossilis* constitute in fact *L. europaea*, which is considered the valid name for all of them. In many cases, however, fruiting heads are not well preserved, consisting of compressions without diagnostic features (Ferguson, 1989). *L. wutzleri* Gregor differs from *L. europaea* by the wart- to thorn-like radial extensions on the surface polygonals between the capsules (Gregor, 1993). Such structures are lacking in the examined material from Pitsidia.

Most palaeobotanists have classifed *L. europaea* to the modern section *Liquidambar*. Based on head macro- and micromorphological characters, some authors related it to modern *L. orientalis* (Mai, 1997, 1999) (contrary to the results from leaf morphology, which suggest a closer relationship to *L. styraciflua*), while earlier it was placed between *L. orientalis* and *L. styraciflua* (Unger, 1847; Heer, 1856; Gregor, 1978). The morphology and biometrics of the material from Pitsidia, such as size of heads and carpels, number of capsules per head, morphology and length of persistent styles, smooth thickened areas between adjacent fruits and the lack of other extrafloral structures, support a closer relation to the modern species *L. orientalis* (Fig. 13b–d). So far, this element is absent from the palaeofloras of Vrysses, Kassanoi and Metochia. A single infructescence has been reported from Makrilia (Zidianakis, 2018: Pl. 52, fig. 7), whereas leaf remains are entirely lacking there.

Family Fabaceae

Genus *Leguminosites*
Bowerbank emend. Schimper

Leguminosites sp. 1

Pl. 10, fig. 1

Material. Pitsidia, one almost complete leaflet (Nr. 31.4.2.5295a,b).

Description. Probably a leaflet, petiolule missing, shape oblong to broad elliptic, 42 mm long, 19 mm wide, L/W ratio 2.3, base obtuse, rounded but acute at the very base, somewhat asymmetric, apex retuse, margin entire; venation brochidodromous, primary vein strong, straight, secondary veins much more delicate, in ~10 pairs originating at 35–75°, almost straight, looping at different distances from margin, intersecondaries numerous, parallel, indistinct, higher-order venation hardly preserved.

Remarks. The retuse apex, the slightly asymmetric base, the entire margin and the brochidodromous venation pattern, with several intersecondaries, are features that often occur in the family Fabaceae. From Makrilia, Sachse (2004) reported diverse leaflets of Fabaceae affinity. He classified most of them in eight different taxa. Some of them and especially ?*Swartzia* sp. show similarities to the specimen from Pitsidia. Although several specimens of leguminosoid leaflets are available from Vrysses, none closely resembles the leaflet at hand. Mantzouka et al. (2015) described four taxa of Fabaceae from Metochia. Judging from the descriptions and figures, *Leguminosites* sp. 2 resembles the here-described leaflet.

Leguminosites sp. 2

Pl. 10, fig. 2

2010 Leguminosae gen. indet., Zidianakis et al., fig. 3j (Pitsidia, central Crete, Tortonian).

Material. Pitsidia, one complete leaflet (Nr. 31.4.2.207).

Description. Leaflet shortly petiolulate, petiolule 5 mm long, texture coriaceous, shape slightly obovate, 51 mm long, 23 mm wide, L/W ratio 2.1, base cuneate at one side, convex at the other, asymmetric, apex obtuse, retuse, margin entire to slightly crenate apically; venation brochidodromous, midrib prominent, straight, abruptly bent at base, secondary veins ~12 pairs, delicate, originating at 45–75°, irregularly spaced, occasionally dichotomising close to primary vein, straight, gently curved distally, interconnected in loops with adjacent secondaries or intersecondaries along margin, intersecondary veins mostly one or even two per intercostal area, well developed, quite similar to secondaries, tertiary veins conspicuous, anastomosing with higher-order venation and forming an irregular net.

Remarks. This well-preserved specimen shares only a few features with *Leguminosites* sp. 1, such as apex shape and brochidodromous venation pattern. They are therefore treated as different taxa.

?***Leguminosites*** sp. 3

Pl. 10, fig. 3

Material. Metochia, one complete and one fragmentary leaflet (Nrs 31.5.2.49; 31.5.2.51).

Description. Leaflets petiolulate, petiolule partly preserved, 1.5 mm long; texture coriaceous, shape narrow oblong, ~35 mm long and 9–12 mm wide, L/W ratio almost 3, base convex but concave near the very base, strongly asymmetric (basal insertion asymmetry), apex

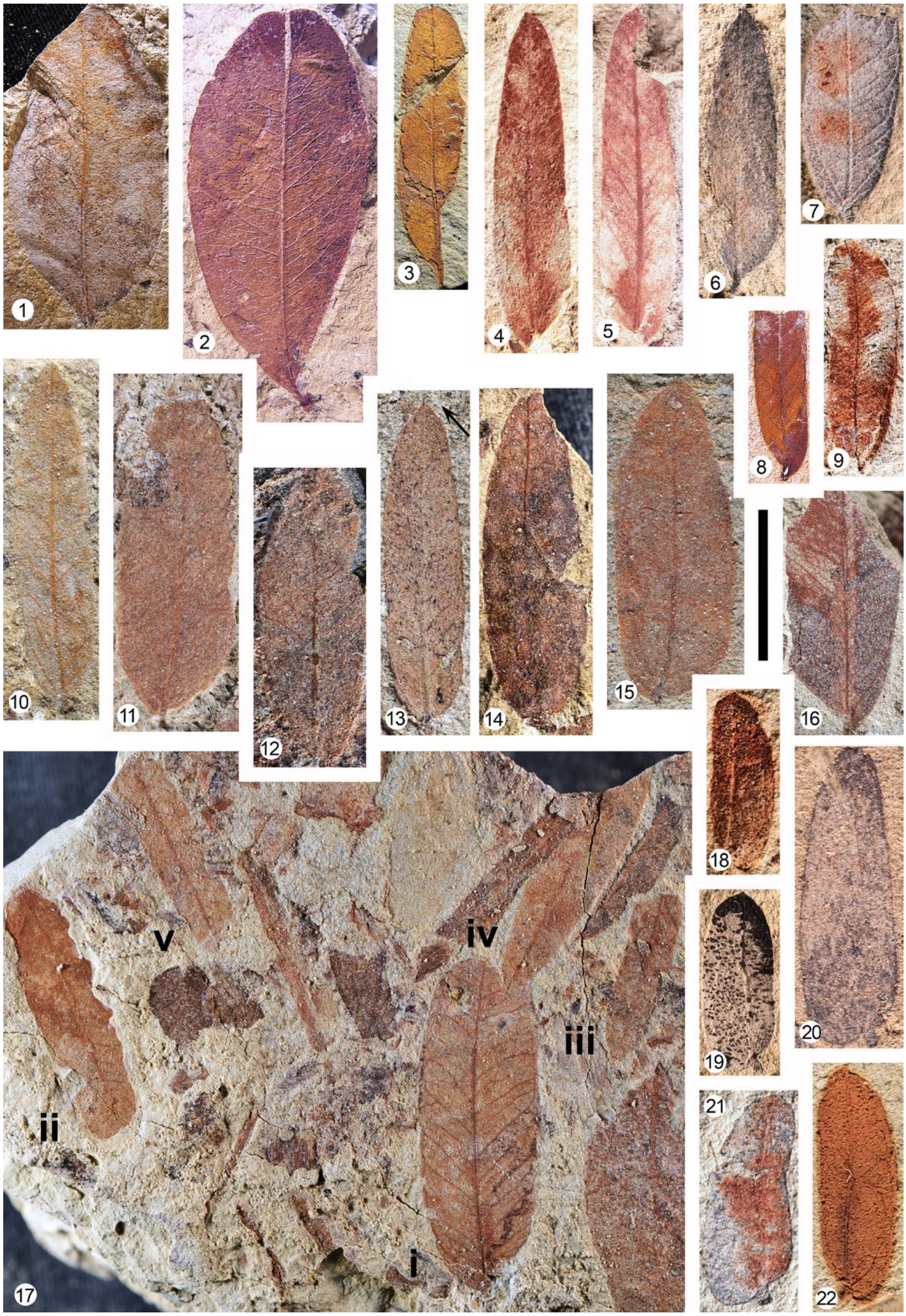

Plate 10. Cretan palaeofloras; **1–3**. *Leguminosites* Bowerbank emend. Schimper, leaflets, scale bar = 2 cm; **1**. *Leguminosites* sp. 1, Pitsidia, Nr. 31.4.2.5295a; **2**. *Leguminosites* sp. 2, Pisidia, Nr. 31.4.2.207 (Fig. 3j in Zidianakis et al., 2010); **3**. ?*Leguminosites* sp. 3, Metochia, Nr. 31.5.2.49; **4–17**. *Podocarpium podocarpum* (A. Braun) Herendeen, leaflets, scale bar = 1 cm; **4**. Pitsidia, Nr. 31.4.2.3801a; **5**. Pitsidia, (counterpart of Pl. 10, fig. 4), Nr. 31.4.2.3801b; **6**. Pitsidia, Nr. 31.4.2.5552i; **7**. Pitsidia, Nr. 31.4.2.8244iii; **8**. Pitsidia, Nr. 31.4.2.2705aii; **9**. Pitsidia, Nr. 31.4.2.5215opi; **10**. Kassanoi, Nr. 31.6.2.228; **11**. Kassanoi, Nr. 31.6.2.15v; **12**. Kassanoi, Nr. 31.6.2.180i; **13**. note acuminate apex (arrow), Kassanoi, Nr. 31.6.2.205; **14**. Kassanoi, Nr. 31.6.2.218; **15**. Kassanoi, Nr. 31.6.2.169; **16**. Kassanoi, Nr. 31.6.2.66aop; **17**. slab with five leaflets closely arranged, Kassanoi, Nr. 31.6.2.168; **18–22**. *Mimosites* sp., leaflets, Pitsidia, scale bar = 5 mm; **18**. Nr. 31.4.2.2371; **19**. Nr. 31.4.2.4398ai; **20**. Nr. 31.4.2.5324; **21**. Nr. 31.4.2.4087bi; **22**. Nr. 31.4.2.4389aii

rounded, slightly mucronate, margin entire; venation brochidodromous, primary vein strong, straight, tapering along length, secondary veins ~10–14 pairs, distinctly weaker than midvein, diverging from midrib at 40–75°, straight or smoothly bent upwards, near apex slightly recurved, joining in arcs the adjacent secondaries and intersecondaries at some distance from margin, intersecondary veins 1 or rarely 2 per intercostal area, well developed, parallel to secondaries, tertiary veins reticulate, anastomosing at various angles and forming an irregular network.

Remarks. The strongly asymmetric base, the entire margin, apex shape and venation architecture point towards the legume family. The studied specimens do not match any of the leaf morphotypes within Fabaceae described by Mantzouka et al. (2015).

Subfamily Caesalpinioideae

Genus *Podocarpium*
A. Braun ex Stizenberger

Podocarpium podocarpum
(A. Braun) Herendeen

Pl. 10, figs 4–17; Pl. 11, figs 1–11; Fig. 14

1845 *Gleditschia podocarpa* A. Braun, p. 173 (Öhningen, Germany, middle Miocene)

1859 *Podogonium knorrii* (Braun) Heer, Heer pl. 134, figs 22–26a; pl. 135, figs 1–18, 20–26; pl. 136, figs 1–9 (Öhningen, Germany, middle Miocene)

1992a *Podocarpium podocarpum* (A. Braun); Herendeen, p. 732 (European Tertiary)

1880 *Podocarpium lyellianum* Heer; Stur in Teller, (Kap Nenita, Chios Island, Serravallian–Tortonian)

2004 *Podocarpium podocarpum* (A. Braun) Herendeen; Sachse, pl. 12, fig. 16 (Makrilia, E. Crete, Tortonian)

2010 *Podocarpium podocarpum* (A. Braun) Herendeen; Zidianakis et al., fig. 3e (Pitsidia, central Crete, Tortonian)

2014 *Podocarpium podocarpum* (A. Braun) Herendeen; Velitzelos D. et al., pl. 25, figs 3–5 (Kato Komi, Chios Island, Serravallian–Tortonian)

Material. Pitsidia, 7 complete or almost complete leaflets and 6 fragmentary ones (Nrs 31.4.2.2705aii; 31.4.2.2720i; 31.4.2.3801a,b; 31.4.2.3933; 31.4.2.4016; 31.4.2.4183a,b; 31.4.2.4543ai,bi; 31.4.2.5215opi; 31.4.2.5552i; 31.4.2.5629a,b; 31.4.2.6297,6294op; 31.4.2.8180op; 31.4.2.8244iii); 12 complete or almost complete fruits and 8 fragmentary ones (Nrs 31.4.2.2704a,b; 31.4.2.3597a,b; 31.4.2.3727aopi; 31.4.2.3968a,b; 31.4.2.4134; 31.4.2.4284aii,b; 31.4.2.4396; 31.4.2.4495a,b; 31.4.2.4672; 31.4.2.4706a,b; 31.4.2.4833i; 31.4.2.5600ai,b; 31.4.2.5827; 31.4.2.5884ai,bi; 31.4.2.6166bopi; 31.4.2.6478ai,bi; 31.4.2.6575a,b; 31.4.2.6662a,b; 31.4.2.6931a,b; 31.4.2.8262iii).
Kassanoi, 26 complete or almost complete leaflets and 9 fragmentary ones (Nrs 31.6.2.15iii; 31.6.2.15v; 31.6.2.24ii; 31.6.2.26ii; 31.6.2.30ii; 31.6.2.35iii; 31.6.2.37ii; 31.6.2.66aop; ?31.6.2.91ii; 31.6.2.100iii; 31.6.2.119ix; 31.6.2.119xii; 31.6.2.152ii; 31.6.2.166aii; 31.6.2.168ai,bi; 31.6.2.168aii,bii; 31.6.2.168aiii,biii; 31.6.2.168aiv,biv; 31.6.2.168av,bv; 31.6.2.169; 31.6.2.177i; 31.6.2.178; 31.6.2.180i; 31.6.2.182i; 31.6.2.185; 31.6.2.187; 31.6.2.188; 31.6.2.196i; 31.6.2.205; 31.6.2.206; ?31.6.2.210; 31.6.2.214; 31.6.2.216; 31.6.2.218; 31.6.2.228).

Description. Leaflets sessile or shortly petiolulate (~0.5 mm long), lamina narrow elliptic to lanceolate, ~7–24 mm long and 2–8 mm wide, L/W ratio 2.0–4.8, base obtuse to acute, convex, occasionally cuneate, asymmetric, apex acute to obtuse or rounded, emarginate, seldom mucronate, margin entire; venation brochidodromous with characteristic pair of prominent asymmetric basal secondary veins originating at acute angles and running parallel to leaf margin; midrib strong, straight, secondary veins numerous, much weaker than midrib, arranged 0.5–1.5 mm apart, arising at acute angles and forming angular loops near margin, intersecondary veins present, simple, parallel to secondaries, weakly developed, tertiaries forming a dense, irregular, polygonal network.

Fruits. Long-stipitate one-seeded pods consisting of two valves, dehiscent along both sutures; stipe straight or slightly bent, 25–38 mm (average 31.5 mm) long and ~1 mm wide, slightly swollen at base; valves elliptic, 21–29 mm (average 24.6) long and 7–11 mm (average 9 mm) wide, base acute, slightly oblique, apex acute, rounded or frequently with ± developed projection (style remnant), margin entire, occasionally showing rather fine marginal line running parallel to valve edge, visible from inner side, distance of valve edge to marginal line 0.1–0.2 mm, possibly representing the width of the suture, venation indistinct, oblique, with numerous anastomoses, forming a polygonal network; seeds not

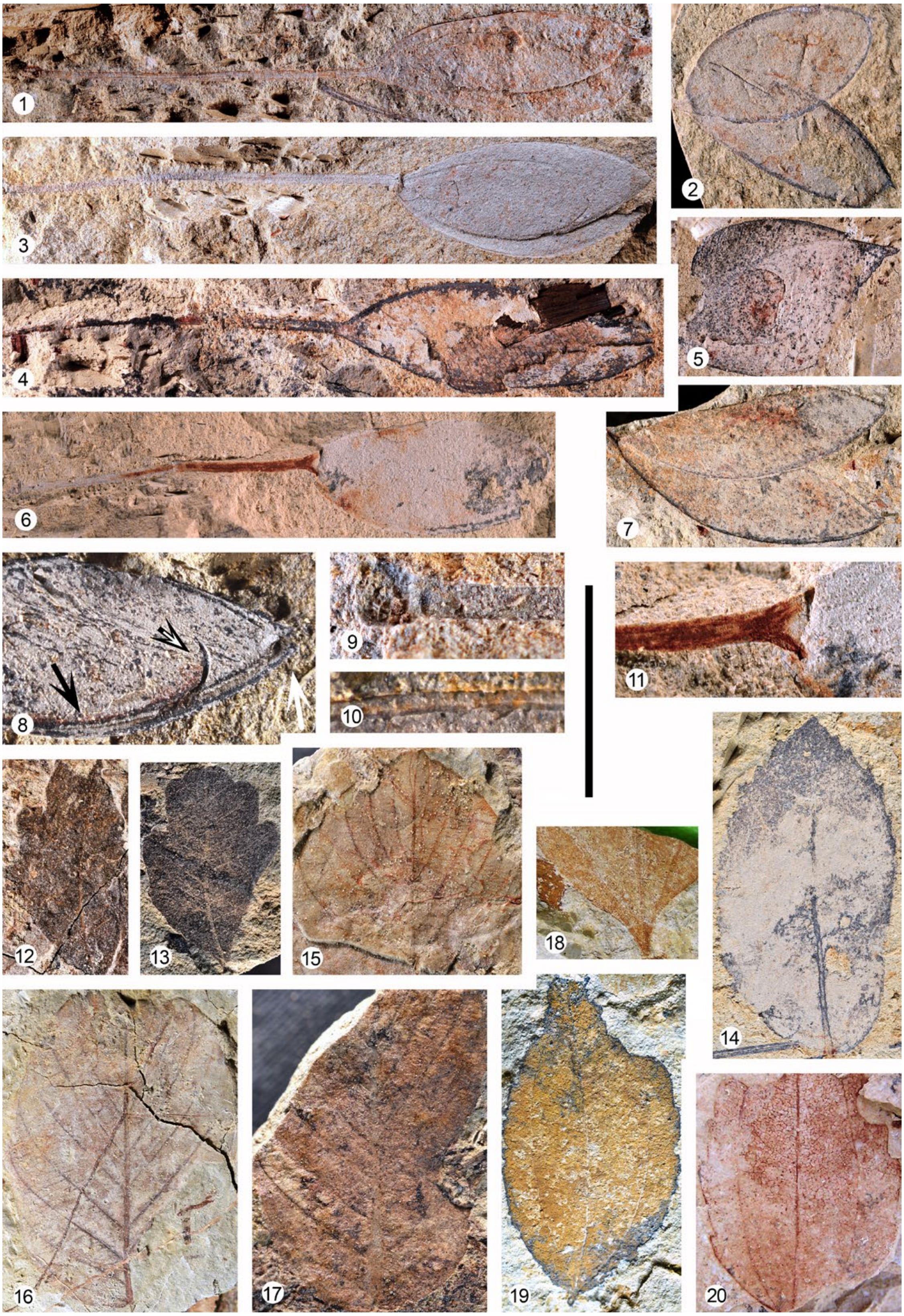

Plate 11. Cretan palaeofloras, scale bar = 2 cm (unless otherwise stated); **1–11**. *Podocarpium podocarpum* (A. Braun) Herendeen, fruits (pods), Pitsidia; **1**. Nr. 31.4.2. 6478ai; **2**. Nr. 31.4.2.5884ai; **3**. Nr. 31.4.2.3968a; **4**. Nr. 31.4.2.4495a; **5**. Nr. 31.4.2.3597a; **6**. Nr. 31.4.2.4833i; **7**. Nr. 31.4.2.5600b; **8**. note suture (black arrow), style remnant (white arrow), funiculus (black-white arrow), valve close-up, Nr. 31.4.2.6662a detail, scale bar = 1 cm; **9**. swollen base of stipe, Nr. 31.4.2.3968a detail, scale bar = 4 mm; **10**. double-seamed margin of valve, Nr 31.4.2.4706a detail, scale bar = 2 mm; **11**. mechanical damage at stipe-valve connection, Nr. 31.4.2.4833i detail, scale bar = 6 mm; **12, 13**. Rosaceae gen. et sp. indet. type 2, foliage, Kassanoi; **12**. Nr. 31.6.2.119vi; **13**. Nr. 31.6.2.18ai; **14**. Rosaceae gen. et sp. indet. type 1, lateral leaflet, Pitsidia, Nr. 31.4.2.6166a; **15–17**. *Berchemia multinervis* (A. Braun) Heer*,* foliage, Kassanoi; **15**. apical part, Nr. 31.6.2.163; **16**. Nr. 31.6.2.158ii; **17**. Nr. 31.6.2.170iii; **18–20**. *Ziziphus paradisiaca* (Unger) Heer, foliage. Metochia; **18**. basal part, Nr. 31.5.2.15; **19**. Nr. 31.5.2.57; **20**. Nr. 31.5.2.13ai

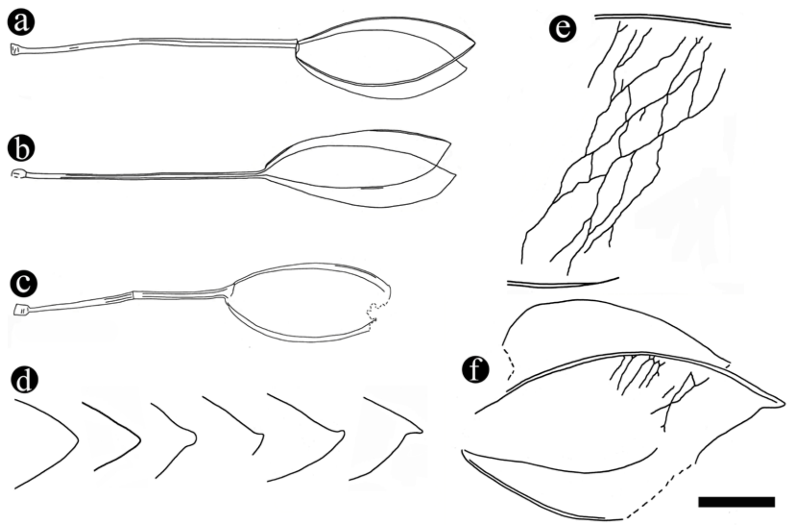

Fig. 14. Palaeoflora of Pitsidia. *Podocarpium podocarpum* fruits (pods), line drawings, scale bar = 1 cm (unless otherwise stated); **a**. Nr. 31.4.2.3968a; **b**. Nr. 31.4.2. 6478ai; **c**. Nr. 31.4.2.4833i; **d**. shape of valve apices, scale bar = 5 mm; e. venation on valve surface, Nr. 31.4.2.3597a detail, scale bar = 3 mm; f. Nr. 31.4.2.3597a, scale bar = 5 mm

preserved; funiculus discernable in a few specimens, slender, 2–3 mm long, curved, situated in apical third of placental suture, indicating seed attachment at apical part of pod.

Remarks. The features of both leaflets (especially the asymmetric base and the presence of a prominent basal pair of secondaries) and fruits match *P. podocarpum* very well. Although the remains of pods are numerous, no seeds were detected. Contrary to Pitsidia, in Kassanoi the vegetative remains of *P. podocarpum* are more abundant and display a wider range of leaflet variation, whereas pods are lacking completely. From Makrilia, Sachse (2004) described a few leaflets of this taxon. *Podocarpium podocarpum* is an extinct genus of the Leguminosae family (Herendeen, 1992a, b; Wang et. al, 2007). According to Herendeen (1992a), it is one of the few species in the European Neogene that possibly is related to modern African taxa, which would be biogeographically remarkable. In Central Europe it was abundant, mainly in late early to middle Miocene plant assemblages.

Subfamily Mimosoideae

Genus *Mimosites* Bowerbank

Mimosites sp.

Pl. 10, figs 18–22

Material. Pitsidia, 13 complete leaflets and 2 fragmentary (Nrs 31.4.2.2305ii; 31.4.2.2371; 31.4.2.3075aiii,biii; 31.4.2.3338ii; 31.4.2.4087aii,bi; 31.4.2.4346ai,b; 31.4.2.4389aii,bii; 31.4.2.4398ai,b; 31.4.2.4417; 31.4.2.4574; 31.4.2.4750ii; 31.4.2.5324; 31.4.2.5505; 31.4.2.6006op; 31.4.2.6946).

Description. Leaflets, small, short-petiolulate, petiolule ~0.5 mm long and 0.3–0.5 mm wide, with prominent wrinkled pulvinus, lamina strongly asymmetric, elliptic to oblong, rarely ovate to lanceolate, 5–10.5 mm long and 2–3.5 mm wide, L/W ratio 1.5–3.5, apex obtuse to rounded, often mucronate, base rounded or slightly cordate, asymmetric, margin entire; venation brochidodromous, primary vein thick, dividing the lamina into two distinctly unequally broad, straight or slightly curved parts; secondary veins thin, 5–6 pairs poorly visible except for basal secondaries, which are strongly curved upwards; secondaries originating at wide angles, looping near margin, tertiary veins reticulate.

Remarks. The venation architecture and especially the strongly asymmetric lamina with a wrinkled petiolule indicate a Fabaceae affinity of this foliage (Herendeen, 1992b). Furthermore, the size of the lamina and its asymmetry are characteristic of "mimosoid" leaflets. A more precise classification is not possible currently. From Makrilia, Sachse (2004) reported a few lanceolate leaflets of possible Mimosoideae origin (?*Mimosites* sp., Pl. 12, figs 4, 6; Pl. 20, fig. 31) which differ from the material at hand by the rather narrow lamina with an acute apex.

Family Rosaceae

Rosaceae gen. et sp. indet. type 1 – folia

Pl. 11, fig. 14

Material. Pitsidia, one lateral leaflet, complete (Nr. 31.4.2.6166a,b).

Description. Lateral leaflet, subsessile, lamina somewhat asymmetric, elliptic to obovate, 32 mm long and 17 mm wide, L/W ratio 1.9, base rounded, apex widely acute, margin simple serrate in upper 2/3, entire near base; teeth acute, triangular, basal side convex to straight, rarely flexuous, apical side concave to straight, tooth spacing regular, 3–5 per cm, sinus between teeth mostly angular, very narrow; venation craspedodromous, primary vein stout, slightly bent; secondary veins delicate, in 7–8 pairs, ± curved, often forked close to margin, higher-order venation not preserved.

Remarks. The serrate margin and the venation pattern point to a Rosaceae affinity. This family shows high diversity in leaf form. An identification to genus level is difficult when based solely on the gross morphology of isolated leaflets.

Rosaceae gen. et sp. indet. type 2 – folia

Pl. 11, figs 12, 13

Material. Kassanoi, one complete and one fragmentary leaf (Nrs 31.6.2.18ai,bi; 31.6.2.119vi).

Description. Leaf shortly petiolate, petiole 1 mm long, lamina chartaceous, obovate, 19 to >20 mm long and 11–13 mm wide, L/W ratio ~1.5, base cuneate, apex obtuse, margin apically lobed, with two prominent lobes on each side, lobes convex on both sides, apex rounded; venation brochidodromous to craspedodromous, primary vein moderate, curved, secondary veins fine, in 9–10 pairs, straight or slightly bent, reaching apex of lobes or forming loops with adjacent secondaries, higher-order venation not visible.

Remarks. These small leaves with characteristic rounded lobes are morphologically close to various genera of the Rosaceae, such as *Ribes* L. and *Crataegus* Tournefort ex L.

Family Rhamnaceae

Genus *Berchemia* Necker ex de Candolle

Berchemia multinervis (A. Braun) Heer

Pl. 11, figs 15–17

1836 *Rhamnus multinervis* A. Braun (in Buckland), p. 513 (Öhningen, Germany, middle Miocene).

1859 *Berchemia multinervis* (A. Braun); Heer, p. 77, pl. 128, figs 9–18 (Swiss Molasse, Switzerland, late Miocene).

1994a *Berchemia multinervis* (A. Braun) Heer; Kleinhölter, pl. 8, fig. 6; pl. 28 figs 7, 8 (Pyrgos and Zacharo basins, Peloponnese, Messinian).

1994b *Berchemia multinervis* (A. Braun) Heer; Kleinhölter, pl. 2, fig. 1 (Pyrgos and Zacharo basins, Peloponnese, Messinian).

Material. Kassanoi, one almost complete and three fragmentary leaves (Nrs 31.6.2.158ii; 31.6.2.163; 31.6.2.170iii; 31.6.2.173).

Description. Lamina ovate to broad elliptic, 30 to ~37 mm long and 21 to ~28 mm wide, L/W ratio ~1.5, base rounded to slightly cordate, margin entire; venation eucamptodromous, primary vein strong, straight, secondary veins in ~11–12 moderately thick pairs, arising at 40–60°, more acute angles distally, opposite to alternate, interspaced 2.5–4 mm, parallel, initially straight (near base of lamina often weakly S-like) to gently curved, close to margin abruptly bent upwards, tertiary veins delicate, opposite percurrent, straight, ~16–20 per cm, slightly S-like to almost straight, higher-order venation not visible.

Remarks. Leaves with such a characteristic venation pattern were classified by A. Braun (in Buckland, 1836) to the genus *Rhamnus* L. Later they were transferred by A. Braun (1845) and Unger (1847) to the genus *Karwinskia* Zuccarini and, finally, Heer (1859) placed them in *Berchemia*. The exact systematic position of *Berchemia multinervis* remains unresolved, however, as its venation type occurs in different genera in Rhamnaceae. For such leaves, Jones, Dilcher (1980) proposed an extinct genus of Rhamnaceae, *Berhamniphyllum* (tribe Zizypheae).

Genus *Ziziphus* Miller

Ziziphus paradisiaca (Unger) Heer

Pl. 11, figs 18–20

1850b *Daphnogene paradisiaca* Unger, p. 167, ?pl. 37, 8–11; pl. 38, figs 1, ?2, ?3, 4–7 (Socka, Slovenia, Eocene).

1859 *Zizyphus paradisiaca* Unger; Heer, p. 74 (Socka, Slovenia, Eocene).

? 1867 *Cinnamomum rossmaessleri* Heer; Unger, pl. 7, fig. 32 (Kimi, Euboea, early Miocene).

? 2002a *Ziziphus ziziphoides* f. *paradisiaca* (Unger) Weyland; Velitzelos et al., pl. 7, fig. 32 (Kimi, Euboea, early Miocene).

2004 *Dicotylophyllum* sp. 3, Sachse, pl. 14, figs 7, 9, ?11, ?13, 14; pl. 20, figs ?39, 41, ?42 (Makrilia, E. Crete, Tortonian).

2007 cf. *Ziziphus ziziphoides* (Unger) Weyland; Zidianakis et al., figs 3N-P (Vrysses, W. Crete, Messinian).

Material. Metochia, one almost complete leaf, one incomplete, and one fragment (Nrs 31.5.2.13ai,b; 31.5.2.15; 31.5.2.57).

Description. Leaf petiolate, petiole partly preserved, >2 mm long; lamina ovate to broadly elliptic, ~30–33 mm long (when complete) and 16–19 mm wide, L/W ratio 1.7–1.9, base widely convex to almost rounded, apex acuminate, entire-margined in lower 1/4 of lamina, simply, obtusely serrate to undulate in further part; teeth few, spaced at intervals of ~4–7 mm, basal side mostly convex, apical side convex to straight, apex obtuse to bluntly acute, tooth height ~1 mm, sinus shallow, narrow, angular to rounded; venation basal acrodromous, central primary vein straight to gently curved, lateral primary veins thinner, arising directly from the petiole-midrib fusion point at 30–50° from central vein, running subparallel to margin, closer to margin than to midvein, reaching apex of lamina, interior secondary veins delicate, weakly developed, dense, originating at wide angles, straight, anastomosing with tertiary veins and forming an irregular polygonal network; minor secondaries numerous, hardly visible, originating at wide angles, initially almost straight, close to margin forked, forming loops with adjacent secondaries or intersecondaries, sending veinlets to margin, one of the veinlets inserting the tooth sinus.

Remarks. The shape and arrangement of the marginal teeth and especially the vein architecture (weakly developed interior secondaries merging with tertiaries) point towards Rhamnaceae affinity (*Paliurus*, *Ceanothus* and especially *Ziziphus*). The figured specimens show the leaf form characteristic of *Z. paradisiaca*, well known as an accessory element at several European localities and dominant in only a few floras such as Mecsek (Hungary) and Radoboj (Croatia) (Heer, 1859; Hably, 2020). Such leaves are common in the Cretan late Miocene. From Makrilia, Sachse, Mohr (1996: p. 164, Tab. 1, Pl. 3, figs 75–77) initially assigned such leaves to the Rhamnaceae, relating them to *Ziziphus* Miller, *Paliurus* Miller, *Ceanothus* L. and *Colubrina* Richard ex Brongniart. Sachse (2004) transferred them to incertae sedis as *Dicotylophyllum* sp. 3, recognizing more similarities with genera such as *Lonicera* L. (Caprifoliaceae) and *Clematis* L. (Ranunculaceae). Zidianakis et al. (2007) compared them to *Ziziphus ziziphoides*. All three-veined basal acrodromous specimens with a serrate or crenulate margin from these localities do not necessarily belong to a single species. For example, the leaf illustrated by Sachse (2004) on Pl. 14, fig. 14, showing a narrow cuneate base, is quite different from *Z. paradisiaca*.

Family Ulmaceae

Genus *Ulmus* L.

***Ulmus* cf. *plurinervia* Unger**

Pl. 16, figs 1–4, 20; Fig. 15b, c, e

1847 *Ulmus plurinervia* Unger, p. 95, pl. 25, figs 1–4 (Parschlug, middle Miocene)

Material. Pitsidia, 4 complete or rather complete leaves and 9 fragmentary ones (Nrs 31.4.2.2148a,bi; 31.4.2.2899; 31.4.2.3781i; 31.4.2.3950ai,bi; 31.4.2.4304a,b; 31.4.2.4557a,b; 31.4.2.4818; 31.4.2.5830a,b; 31.4.2.6277ai,b; 31.4.2.6318; 31.4.2.6383; 31.4.2.6935a,b; 31.4.2.8119). Kassanoi, 4 complete or almost complete leaves and 3 fragmentary ones (Nrs 31.6.2.68; 31.6.2.71; 31.6.2.78a,b; 31.6.2.79; 31.6.2.119iv; 31.6.2.119v; 31.6.2.237).

Description. Leaves shortly petiolate, petiole 4–5 mm long, thick, broader near base, slightly curved, in open angle with primary vein; lamina ovate to broad elliptic, 6–34 mm long and 4–23 mm wide, L/W ratio 0.7–2.8; apex bluntly acute to acuminate, base ± asymmetric, rounded to subcordate, margin simple to double, finely serrate, teeth dense, broadly triangular, blunt or occasionally sharp, basal side mainly convex to straight or concave, apical side convex to slightly S-like; tooth apex bluntly acute, sinus angular, acute; venation craspedodromous, primary vein strong, straight or gently bent, tapering towards apex, secondary veins in 6 to >12 pairs, arising at 30–70°, straight or almost so, delicate, subparallel, often forked once, innervating the marginal teeth, tertiary veins percurrent, weakly developed, opposite or alternate, straight or S-like.

Remarks. For these specimens the generic position is evident by the asymmetric base, the shape and length of the petiole, the simple to double serrate margin and the forked secondaries. Morphologically similar taxa are *U. carpinoides* Goeppert and *U. plurinervia* Unger. Kvaček et al. (2002) examined material from both type localities (Sośnica and Parschlug). They considered more slender leaf forms, smaller size and fine serration to be characteristic of *U. plurinervia* as compared to *U. carpinoides*, which is usually larger, strongly asymmetric and broader, with a double serrate margin. Consequently, the examined foliage is closer morphologically to *U. plurinervia*.

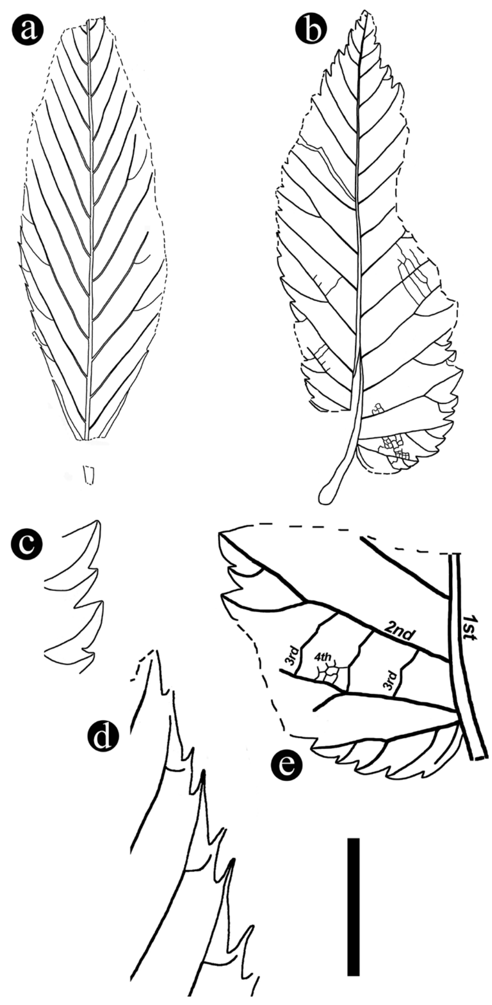

Fig. 15. Palaeoflora of Pitsidia. *Ulmus* and cf. *Ostrya* sp. foliage, line drawings, scale bar = 1 cm (unless otherwise stated); **a**. cf. *Ostrya* sp., note symmetric base and serrate margin, Nr. 31.4.2.8266; **b**. *Ulmus* cf. *plurinervia*, Nr. 31.4.2.3950ai; **c**. *Ulmus* cf. *plurinervia*, double serrate margin, Nr. 31.4.2.3950bi detail, scale bar = 3 mm; **d**. cf. *Ostrya* sp., simple serrate margin, Nr. 31.4.2.6206b detail, scale bar = 3 mm; **e**. *Ulmus* cf. *plurinervia*, margin and venation pattern of lamina base, Nr. 31.4.2.3950bi detail, scale bar = 5 mm

Ulmus sp. – fructus

Pl. 16, fig. 5

Material. Pitsidia, one almost complete samara (Nr. 31.4.2.4150a,b).

Description. Samara shortly stalked, stalk 1 mm long, lacking any remnant of calyx; wings quite thin, almost circular in shape, 5.5 mm long and 5.0 mm wide, base broadly cuneate, apex indistinct, probably with double-apex termination, marginal vein moderately strong, higher-order venation delicate, vaguely visible; endocarp broad elliptic, 4.0 mm long and 2.5 mm wide, seed slightly ovate, 1.7 mm long and 0.9 mm wide, positioned close to apex of fruit, with fine surface striation.

Remarks. The overall morphology of this winged fruit, the course of the prominent axial vein and the apex point towards *Ulmus*. The absence of the calyx remnant may be ascribed either to taphonomic factors or to its possibly deciduous nature (not persistent calyx). Similar winged fruits have been described by Goeppert (1855) from Sośnica, the type locality of *Ulmus carpinoides* (Pl. 14, figs 18–20). The winged fruit/seed from Makrilia which Sachse (2004) figured as *Ulmus* sp. (Pl. 17, fig. 24) is broader and bears more prominent venation.

Genus *Zelkova* Spach

?***Zelkova zelkovifolia***
(Unger) Bůžek et Kotlaba

Pl. 16, figs 6, 19

Material. Pitsidia, one almost complete leaf (Nr. 31.4.2.1663ai,bi).

Description. Lamina chartaceous, oblong to ovate, 41 mm long and 18 mm wide, W/L ratio 2.3, apex acute, base rounded, margin coarsely simple serrate; teeth, basal and apical sides convex, 1–2 mm long and wide, corresponding in number to secondary veins, sinus narrow angular; venation craspedodromous, primary vein slightly bent, moderately thick, secondaries delicate, arising at 40–70°, the steeper angles distally, straight or bent upwards, innervating the marginal tooth apex, close to the margin each secondary sending a veinlet to the apically adjacent sinus, tertiaries reticulate.

Remarks. The characteristic shape of the teeth and the pattern of second- and third-order venation point towards *Zelkova zelkovifolia*. The high number of teeth and more densely spaced secondary veins explain the hesitation to assign these remains unambiguously. In Crete, Sachse (2004) and Velitzelos D. et al. (2014) reported *Z. zelkovifolia* from Makrilia.

Family Fagaceae

Genus *Quercus* L.

Quercus pseudocastanea
Goeppert emend. Walther et Zastawniak

Pl. 12, figs 1–17; Fig. 16a–b

1852 *Quercus pseudocastanea* Goeppert, p. 276, pl. 35, fig. 1 (Sośnica, Poland, late Miocene).

1991 *Quercus pseudocastanea* (Goeppert); Walther, Zastawniak, p. 169, pl. 2, figs 2, 3, 5, 6; pl. 3, figs 1–6; text-fig. 8 (Sośnica, Poland, late Miocene).

1986 *Quercus pseudocastanea* Goeppert; Velitzelos, Knobloch, pl. 11, figs 2, 4, 7 (Skoura, Peloponnese, Pliocene).

1986b *Quercus pseudocastanea* Goeppert, Knobloch, Velitzelos, pl. 15, figs 1, 2 (Prosilio, W. Macedonia, Messinian).

1999 *Quercus roburoides* Massalongo; Velitzelos, Kvaček, pl. 1, fig. 5 (Vegora, W. Macedonia, Messinian).

1999 *Quercus pseudocastanea* Goeppert; Velitzelos et al., fig. D8 in p. 461 (Vegora, W. Macedonia, Messinian).

2002 *Quercus pseudocastanea* Goeppert emend. Walther et Zastawniak; Kvaček et al., pl. 13, figs 3–5; pl. 14, figs 1, 2, 4–6; pl. 15, figs 1, 4, 6; pl. 30, fig. 4 (Vegora, W. Macedonia, Messinian).

2010 *Quercus roburoides* Massalongo; Zidianakis et al., fig. 2j (Pitsidia, central Crete, Tortonian).

2014 *Quercus pseudocastanea* Goeppert; Velitzelos D. et al., pl. 7, figs 5, 6, 8 (Grevena, W. Macedonia, early Miocene).

2014 *Quercus pseudocastanea* Goeppert; Velitzelos D. et al., pl. 15, fig. 6 (Vegora, W. Macedonia, Messinian).

2014 *Quercus pseudocastanea* Goeppert; Velitzelos D. et al., pl. 18, fig. 4 (Prosilio, W. Macedonia, Messinian).

2014 *Quercus pseudocastanea* Goeppert; Velitzelos D. et al., pl. 22, figs 5, 6 (Elassona, Thessaly, Messinian).

2014 *Quercus pseudocastanea* Goeppert emend. Walther et Zastawniak; Velitzelos D. et al., pl. 29, fig. 4 (Zeli, central Greece, Pliocene).

2014 *Quercus pseudocastanea* Goeppert; Velitzelos D. et al., pl. 30, figs 2, 3 (Skoura, Peloponnese, Pliocene).

2014 *Quercus pseudocastanea* Goeppert; Velitzelos D. et al., pl. 33, fig. 6 (Archangelos, Rhodes Island, Pleistocene).

Material. Pitsidia, 18 complete or almost complete leaves and 104 fragmentary ones (Nrs 31.4.2.322i; 31.4.2.824i; 31.4.2.853aii,bii; 31.4.2.874; 31.4.2.900; 31.4.2.918; 31.4.2.953i; 31.4.2.955; 31.4.2.1036a,b; 31.4.2.1138i; 31.4.2.1139; 31.4.2.1280a,b; 31.4.2.1405ii; 31.4.2.1419a,b; 31.4.2.1421ai,b; 31.4.2.1437i; 31.4.2.1578i; 31.4.2.1663aii,bii; 31.4.2.1663aiii,biii; 31.4.2.1709ai,b; 31.4.2.1715bviii; 31.4.2.1728; 31.4.2.1848; 31.4.2.1858; 31.4.2.1860; 31.4.2.1877; 31.4.2.2133i; 31.4.2.2135a,bi; 31.4.2.2135bop; 31.4.2.2137; 31.4.2.2159aiii,cii; 31.4.2.2164; 31.4.2.2266ai,b; 31.4.2.2276a,b; 31.4.2.2326ai,bi; 31.4.2.2431; 31.4.2.2756; 31.4.2.2834; 31.4.2.2941; 31.4.2.2960a,b; 31.4.2.3030ai,b; 31.4.2.3324; 31.4.2.3462a,b; 31.4.2.3636i; 31.4.2.3736ai,bi; 31.4.2.3807aii,bii; 31.4.2.3839; 31.4.2.3958ai,bi; 31.4.2.4010a,b; 31.4.2.4011; 31.4.2.4046; 31.4.2.4083bi; 31.4.2.4127a,b; 31.4.2.4135,4133aop; 31.4.2.4147ai,b; 31.4.2.4252; 31.4.2.4275ai,b; 31.4.2.4280ai,b; 31.4.2.4367a,b; 31.4.2.4457a,b; 31.4.2.4564a,b; 31.4.2.4641aiii,b; 31.4.2.4676; 31.4.2.4679; 31.4.2.4680; 31.4.2.4734a,b; 31.4.2.4735ai,bi; 31.4.2.4786a,b; 31.4.2.4820ai,b; 31.4.2.4852a,b; 31.4.2.4900a,bi; 31.4.2.4980ai,bi; 31.4.2.5021a,b; 31.4.2.5088a,b; 31.4.2.5092ai,b; 31.4.2.5217a,bi; 31.4.2.5313; 31.4.2.5357aop; 31.4.2.5446a,b; 31.4.2.5546; 31.4.2.5550; 31.4.2.5621,5620aop; 31.4.2.5681ai,bi; 31.4.2.5785ai,bi; 31.4.2.5817; 31.4.2.5883; 31.4.2.5945i; 31.4.2.5948a,b; 31.4.2.6003a,b; 31.4.2.6086; 31.4.2.6104ii; 31.4.2.6116i; 31.4.2.6123bop; 31.4.2.6152a,bi; 31.4.2.6152bii; 31.4.2.6178i; 31.4.2.6216aii,b; 31.4.2.6217ai,b; 31.4.2.6229a,b; 31.4.2.6494a,b; 31.4.2.6540i; 31.4.2.6617; 31.4.2.6802a,b; 31.4.2.6805; 31.4.2.6844aii,bii; 31.4.2.6866a,6873; 31.4.2.6867,6871b; 31.4.2.6933a,b; 31.4.2.6967; 31.4.2.8014opii; 31.4.2.8156ai,bi; 31.4.2.8157a,b; 31.4.2.8164; 31.4.2.8191a,b; 31.4.2.8193i; 31.4.2.8198ii; 31.4.2.8198iii; 31.4.2.8205; 31.4.2.8242ai,bi; 31.4.2.8242aii,bii; 31.4.2.8244i; 31.4.2.8271).

Description. Leaves petiolate, petiole slender, up to 25 mm long; lamina texture probably chartaceous, shape obovate to elliptic

Plate 12. Palaeoflora of Pitsidia, scale bar = 2 cm; **1–13**. *Quercus pseudocastanea* Goeppert emend. Walther et Zastawniak, foliage, typical form; **1**. Nr. 31.4.2.4786a; **2**. Nr. 31.4.2.4820ai; **3**. Nr. 31.4.2.4280ai; **4**. Nr. 31.4.2.322i (Fig. 2j in Zidianakis et al., 2010); **5**. Nr. 31.4.2.8191a; **6**. small leaf, Nr. 31.4.2.5945i; **7**. leaf base, Nr. 31.4.2.1139; **8**. Nr. 31.4.2.1419α; **9**. Nr. 31.4.2.8244i; **10**. Nr. 31.4.2.5785bi; **11**. leaf apex, Nr. 31.4.2.2137; **12**. leaf base, Nr. 31.4.2.6933a; **13**. damaged by sediment fracturing, Nr. 31.4.2.4011; **14–17**. *Quercus pseudocastanea* Goeppert emend. Walther et Zastawniak, foliage, narrow form; **14**. Nr 31.4.2.4641b; **15**. Nr. 31.4.2.5681ai; **16**. Nr. 31.4.2.4564b; **17**. Nr. 31.4.2.1138i

or oblanceolate, 32–92 mm (average 58 mm) long and 13–51 mm (average 24.2 mm) broad, L/W ratio 1.5–3.4, base symmetric to asymmetric, mostly acute, cuneate to rounded, rarely subcordate, apex acute to acuminate, margin coarsely simply lobate, often entire in basal third; lobes rounded, basal side flexuous to convex, apical side ± convex, lobe apex occasionally pointed, sinuses shallow, rounded; venation craspedodromous, midvein straight or bent, moderately strong, secondary veins mainly alternate to more rarely subopposite, near their origin narrowing the midvein then curving outwards, diverging and further running straight or curved towards margin, ending in the lobe apices, in 7–13 pairs, originating mostly at 30–60°, interspaced ~4–10 mm, tertiary veins fine, percurrent, opposite or alternate, straight or sinuous, almost at right angles to secondaries, higher venation forming a polygonal net.

Remarks. The leaf variability well matches that of *Q. pseudocastanea* from Sośnica as emended by Walther, Zastawniak (1991), including *Q. pseudorobur* Kováts and *Q. hispanica* Rérolle, although the leaves are smaller. *Q. roburoides*, which is common in the European Pliocene, is morphologically very similar, usually differing in having deeper marginal lobes. Some leaves diverge morphologically from the typical form described from Pitsidia, having an elongated, narrower lamina (Pl. 12, figs 14–17). Because of the wide leaf variation of modern oak species, these leaves are included in *Q. pseudocastanea* as a distinct narrow leaf form. In modern oaks it is difficult to differentiate leaf species based on gross morphology. Therefore *Q. pseudocastanea* should better be considered as a species complex. In Central Europe, *Q. pseudocastanea* occurs from the middle Miocene to late Pliocene (Kovar-Eder et. al., 1994).

Quercus kubinyii
(Kováts ex Ettingshausen) Czeczott

Pl. 13, figs 1–18; Fig. 16c–g

1852 *Castanea kubinyii* (Kováts ex Ettingshausen), p. 5, pl. 1, fig. 12 (Erdőbénye, Hungary, middle Miocene).

1951 *Quercus kubinyii* (Kováts ex Ettingshausen); Czeczott, p. 392, fig. 7 (Zalesce, Poland, middle Miocene).

?2010 *Quercus* cf. *kubinyii* (Kováts ex Ettingshausen) Czeczott; Zidianakis et al., fig. 2k (Pitsidia, central Crete, Tortonian).

Material. Pitsidia, 16 complete or almost complete leaves and 27 fragmentary ones (Nrs 31.4.2.007; 31.4.2.831; 31.4.2.850a,b; 31.4.2.852; 31.4.2.870a,b; 31.4.2.956; 31.4.2.971a,b; 31.4.2.1087; 31.4.2.1094; 31.4.2.1416a,b; 31.4.2.1420a,b; 31.4.2.2200a,b; 31.4.2.2426a,b; 31.4.2.2705aop,b; 31.4.2.2914a,b; 31.4.2.2926a,b; 31.4.2.3374a,b; 31.4.2.3534a,3543aopi; 31.4.2.3806ai,bi; 31.4.2.3828,3516; 31.4.2.3922i; 31.4.2.3922ii; 31.4.2.4124; 31.4.2.4140a,b; 31.4.2.4161opi,4147opai; ?31.4.2.4189ai,b; 31.4.2.4360ai,bi; 31.4.2.4621a,b; 31.4.2.4646a,b; 31.4.2.5112aiop; 31.4.2.5177a,bi; 31.4.2.5462a,b; 31.4.2.6070,6141ii; 31.4.2.6938ai,bi; 31.4.2.6986ai,bi; 31.4.2.7037a,b; 31.4.2.8176ai,bi; 31.4.2.8192a,b; 31.4.2.8197; 31.4.2.8238; 31.4.2.8265; 31.4.2.8267; 31.4.2.8270).

Description. Leaves petiolate, petiole moderately thick, 10–27 mm long; lamina oblong to lanceolate or somewhat ovate, 25 to > 94 mm long and 11–47 mm wide, L/W ratio 1.7–3.9, base rounded, slightly cordate to broadly cuneate, ± symmetric, apex acute to acuminate, margin simply dentate; teeth narrow, ± triangular and mostly large, basal side concave or occasionally straight to retroflexuous, apical side convex, less frequently straight to flexuous, tooth apex acute to mucronate, sinus mainly deep, rounded to subangular; venation craspedodromous, primary vein stout, straight or smoothly curved basically or apically, secondary veins alternate to almost opposite, in ~10–15 pairs, originating at 35–80°, angle decreasing towards apex, interspaces regular, distances 3–9 mm, course subparallel, unbranched, straight, occasionally bent along their length exmedially, tertiary veins dense, percurrent, opposite or alternate, straight to sinuous, usually perpendicular to secondaries; quaternary veins forming a polygonal network.

Remarks. These oak leaves, with sharp triangular teeth, also resemble *Q. gigas* Goeppert emend. Walther et Zastawniak. The affinity to *Q. kubinyii* is more probable, based on the relatively smaller and slender leaves and variation in shape. From Makrilia, Sachse (2004) reported a narrow, coarsely dentate leaf fragment as ?*Quercus kubinyii*. The arced secondary veins of this specimen are not parallel and their course close to the margin is unknown.

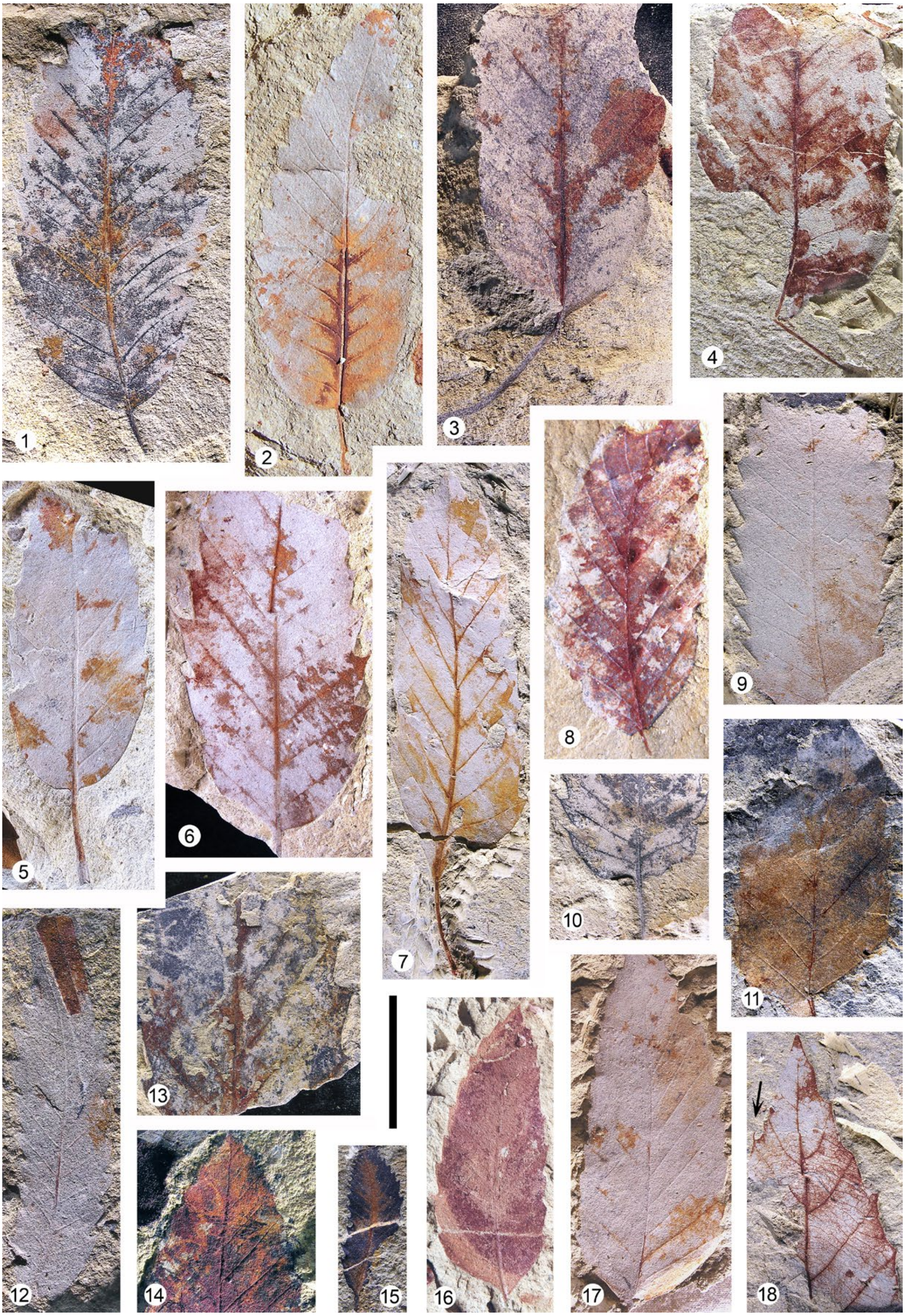

Plate 13. Palaeoflora of Pitsidia; **1–18**. *Quercus kubinyii* (Kováts ex Ettingshausen) Czeczott, foliage, scale bar = 2 cm; **1**. Nr. 31.4.2.4646a; **2**. Nr. 31.4.2.8265; **3**. Nr. 31.4.2.971a; **4**. Nr. 31.4.2.4360bi; **5**. Nr. 31.4.2.3806ai; **6**. Nr. 31.4.2.2705aop; **7**. Nr. 31.4.2.6938ai; **8**. Nr. 31.4.2.007; **9**. Nr. 31.4.2.6070; **10**. Nr. 31.4.2.3828; **11**. Nr. 31.4.2.2926b; **12**. Nr. 31.4.2.8176bi; **13**. Nr. 31.4.2.2426a; **14**. Nr. 31.4.2.8197; **15**. ?extreme leaf form, Nr. 31.4.2.8238; **16**. Nr. 31.4.2.1416a; **17**. Nr. 31.4.2.7037a; **18**. note bristle-tipped tooth at upper part of lamina (arrow), Nr. 31.4.2.1420a

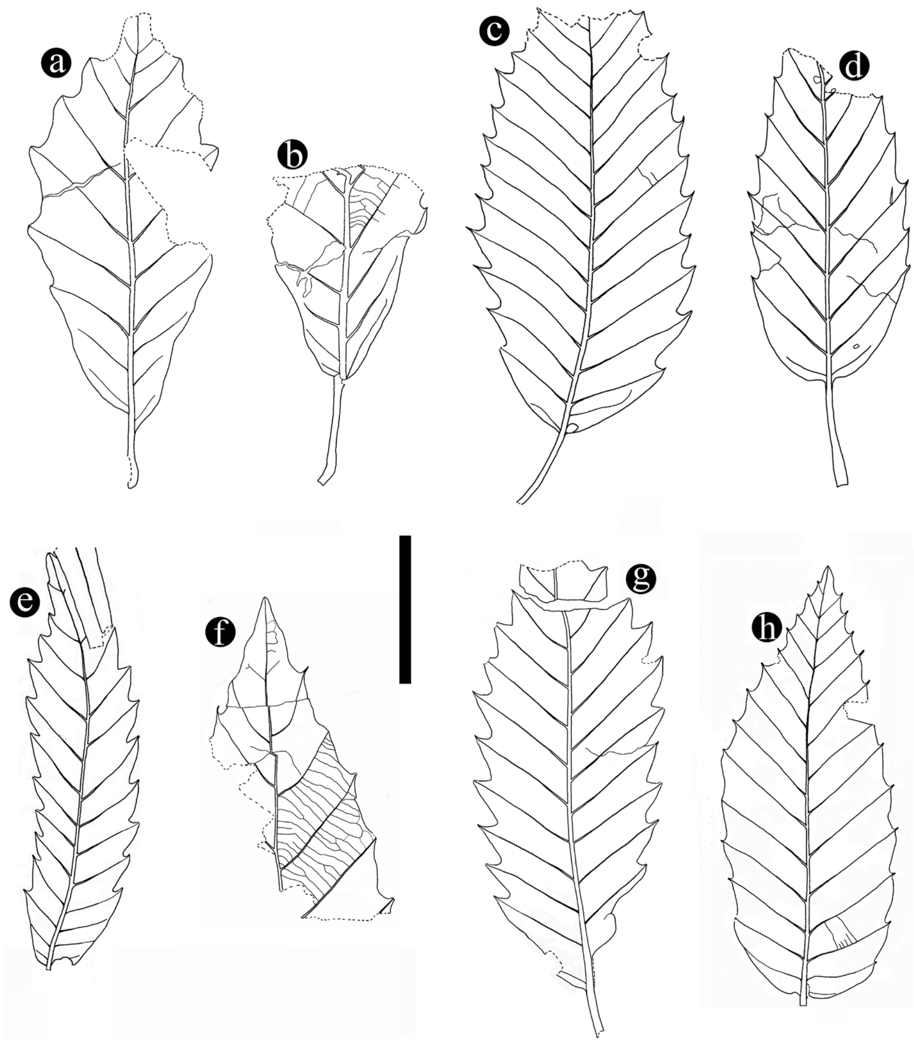

Fig. 16. Palaeoflora of Pitsidia. Fagaceae foliage, line drawings, scale bar = 2 cm; **a–b**. *Quercus pseudocastanea*; **a**. Nr. 31.4.2.5785ai; **b**. leaf base, Nr. 31.4.2.1139; **c–g**. *Quercus kubinyii*; **c**. Nr. 31.4.2.4646b; **d**. Nr. 31.4.2.3806ai; **e**. Nr. 31.4.2.8176bi; **f**. lamina apex, Nr. 31.4.2.1420a; **g**. Nr. 31.4.2.6070,6141ii synthesis; **h**. *Fagus gussonii*, Nr. 31.4.2.7038

The assignment to *Q. kubinyii* is therefore uncertain. Especially during the late Miocene and Pliocene, *Quercus kubinyii* is known from numerous European sites and shows remarkable variation in leaf shape (Knobloch and Kvaček, 1976; Hably and Kvaček, 1997; Kvaček et al., 2002; Worobiec, 2003). However, records from the Greek peninsula and adjacent islands are restricted to Pitsidia and possibly Makrilia.

Quercus mediterranea Unger

Pl. 14, figs 1–5

1847 *Quercus mediterranea* Unger, p. 114, pl. 32, figs 5–9 (Parschlug, Austria, middle Miocene).

? 1862 *Quercus mediterranea* Unger; Unger, p. 158 (Kimi, Euboea, early Miocene) (no figure).

1867 *Quercus mediterranea* Unger; Unger, pl. 6, figs 1–22, pl. 13, figs 7–9 (Kimi, Euboea, early Miocene).

? 1921 *Quercus mediterranea* Unger; Fritel, p. 472 (Oropos, Attica, early Miocene) (no figure).

1975 *Quercus* cf. *ilex* L.; Heimann et al., pl. 14, fig. 10 (Paghi, Corfu Island, Messinian).

1983 *Quercus mediterranea* Unger; Velitzelos, pl. 1, figs 2, 5, 6 (Pappades, Euboea, early Miocene).

? 1985 *Quercus mediterranea* Unger; Dermitzakis, Velitzelos, p. 165 (Kato Komi, Chios Island, Serravallian–Tortonian) (no figure).

1985-86 *Quercus mediterranea* Unger; Dermitzakis et al., fig. 6.1 (Akropotamos, E. Macedonia, Messinian).

1986a *Quercus* cf. *mediterranea* Unger; Knobloch, Velitzelos, pl. 2, fig. 5 (Elassona, Thessaly, Messinian).

1986b *Quercus* cf. *mediterranea* Unger; Knobloch, Velitzelos, pl. 14, figs 4, 11; pl. 15, fig. 7 (Prosilio, W. Macedonia, Messinian).

1989 *Quercus mediterranea* Unger; Kvaček, Walther, text-figs 5a–b (Lava, W. Macedonia, Messinian).

1992 *Quercus mediterranea* Unger; Velitzelos et al., pl. 5, figs 1–15; pl. 7, figs 5–7; text-figs 5–7 (Aliveri, Euboea, early Miocene).

1994a *Quercus mediterranea* Unger; Kleinhölter, pl. 6, fig. 1; pl. 23, figs 3, 6 (Pyrgos and Zacharo basins, Peloponnese, Messinian).
1996 *Quercus mediterranea* Unger; Sachse, Mohr, pl. 3, figs 9–11; pl. 5, fig. 5 (Makrilia, eastern Crete, Tortonian).
1999 *Quercus mediterranea* Unger; Velitzelos, Kvaček, pl. 1, fig. 7 (Vegora, W. Macedonia, Messinian).
2002 *Quercus mediterranea* Unger; Kvaček et al., pl. 10, figs 7, 9–11; pl. 31, figs 1, 2 (Vegora, W. Macedonia, Messinian).
2004 *Quercus mediterranea* Unger; Sachse, pl. 10, figs 4, 5, 8; pl. 19, figs 10, 11 (Makrilia, E. Crete, Tortonian).
2007 *Quercus mediterranea* Unger; Zidianakis et al., figs 2H–K, 5J (Vrysses, W. Crete, Messinian).
2010 *Quercus mediterra.nea* Unger; Zidianakis et al., fig. 2m (Pitsidia, central Crete, Tortonian).
2014 *Quercus mediterranea* Unger; Velitzelos D. et al., pl. 18, fig. 3 (Prosilio, W. Macedonia, Messinian).

Material. Pitsidia, 4 complete or almost complete leaves and 5 fragmentary ones (Nrs ?31.4.2.271a,b; 31.4.2.272; 31.4.2.2159bii; 31.4.2.3732ai,bi; 31.4.2.4230; 31.4.2.4565a,b; 31.4.2.5183a,b; 31.4.2.5812a,b; 31.4.2.5813a,b). Metochia, one complete and one fragmentary leaf (Nrs 31.5.2.7; 31.5.2.59).

Description. Leaves short petiolate, petiole 0.5–4 mm long, lamina broad elliptic to obovate, 13–35 mm long and 9–20 mm wide, L/W ratio 1.4–2.2, base ± rounded, apex obtuse to acute or shortly acuminate, margin entire near base, irregularly simpe serrate in upper half of lamina, teeth small with acute apices, sinuses wide, rounded; venation craspedodromous or eucamptodromous (in entire-margined part), primary vein stout, secondary veins strong, almost opposite to alternate, in 6–9 pairs, originating at 25–85°, angle decreasing distally, irregularly spaced, straight or curved, mostly not parallel, occasionally forked, running towards margin, entering teeth, tertiary veins opposite percurrent, straight or curved.

Remarks. These irregularly simple serrate leaves, which are smaller than the afore-described oaks, are characteristic of *Quercus mediterranea*. Based on leaf morphology, Denk et al. (2017) proposed a relation to *Quercus*, Group *Ilex*. Except for Kassanoi, *Q. mediterranea* has been reported from all Neogene floras of Crete (Sachse, 2004; Zidianakis et al., 2007). Especially in Vrysses, this oak is one of the dominant species. In contrast, in Pitsidia and Metochia it is rather rare.

Quercus sp. – folia

Pl. 14, figs 6, 7

Material. Kassanoi, three leaf fragments (Nrs 31.6.2.113i; 31.6.2.166ai,b; 31.6.2.167).

Description. Lamina probably obovate, >46 mm long and >31 wide, base and apex missing, margin lobed; venation craspedodromous, primary vein strong, secondary veins moderately thick, originating at 45–55°, bent, innervating the lobes, tertiary veins dense, perpendicular to secondaries, percurrent, ± opposite, curved or S-like, higher-order venation not preserved.

Remarks. The gross morphology of these specimens suggests a deciduous oak.

Genus *Fagus* L.

Fagus gussonii Massalongo emend. Knobloch et Velitzelos

Pl. 14, figs 8–10; Fig. 16h

1859 *Fagus gussonii* Massalongo in Massalongo, Scarabelli, p. 202, pl. 25, figs 2, 5 (Senigallia, Italy, late Miocene).
1859 *Fagus marsilii* Massalongo in Massalongo, Scarabelli, p. 201, pl. 9, fig. 19; pl. 21, fig. 18 (Senigallia, Italy, late Miocene).
1986a *Fagus gussonii* Massalongo; Knobloch, Velitzelos, p. 9, pl. 2, figs 2–4, 6–8; pl. 5, fig. 11; pl. 6, fig. 5 (Elassona, N. Thessaly, Messinian).
1986b *Fagus gussonii* Massalongo; Knobloch, Velitzelos, pl. 14, fig. 2 (Prosilio, W. Macedonia, Messinian).
1987 *Fagus gussonii* Massalongo; Knobloch, Velitzelos, pl. 1, fig. 5 (Elassona, N. Thessaly, Messinian).
1996 *Fagus* sp., aff. *Alnus* sp.; Sachse, Mohr, pl. 3, figs 1, 2, 5 (Makrilia, E. Crete, Tortonian).
2002 *Fagus gussonii* Massalongo emend. Knobloch et Velitzelos; Kvaček et al., pl. 5, figs 3–9; pl. 6, figs 1–7; pl. 7, figs 1–5; pl. 29, figs 3, 4 (Vegora, W. Macedonia, Messinian).
2004 *Fagus gussonii* Massalongo emend. Knobloch et Velitzelos; Denk, pl. 12, figs B–F, I, K (Vegora, W. Macedonia, Messinian).
2004 *Fagus gussonii* Massalongo; Denk, pl. 12, figs G–H (Elassona, N. Thessaly, Messinian).
2004 *Fagus gussonii* Massalongo; Denk, pl. 12, fig. L (Makrilia, E. Crete, Tortonian).
2004 *Fagus* type *gussonii*, *Fagus* type *attenuata*; Sachse, pl. 10, figs 1, 2, 6, pl. 19, figs 1, 2, 5 (Makrilia, E. Crete, Tortonian).
?2010 *Fagus* type *attenuata*; Zidianakis et al., fig. 2i (Pitsidia, central Crete, Tortonian).
2014 *Fagus gussonii* Massalongo; Velitzelos D. et al., pl. 15, fig. 4 (Vegora, W. Macedonia, Messinian).

Plate 14. Cretan palaeofloras, scale bar = 2 cm (unless otherwise stated); **1–5**. *Quercus mediterranea* Unger, foliage; **1**. Pitsidia, Nr. 31.4.2.2159bii; **2**. Pitsidia, Nr. 31.4.2.5812a; **3**. Metochia, Nr. 31.5.2.59; **4**. small leaf, Pitsidia, Nr. 31.4.2.5183a, scale bar = 1.5 cm; **5**. small leaf, Metochia, Nr. 31.5.2.7, scale bar = 1.5 cm; **6, 7**. *Quercus* sp., foliage, Kassanoi; **6**. Nr. 31.6.2.166ai; **7**. Nr. 31.6.2.113i; **8–10**. *Fagus gussonii* Massalongo emend. Knobloch et Velitzelos, foliage, **8**. Pitsidia, Nr. 31.4.2.7038; **9**. Metochia, Nr. 31.5.2.2; **10**. Metochia, Nr. 31.5.2.21a; **11–16**. *Myrica lignitum* (Unger) Saporta*,* foliage; **11**. Kassanoi, Nr. 31.6.2.40; **12**. *Myrica ?lignitum* (Unger) Saporta, Kassanoi, Nr. 31.6.2.95; **13**. Kassanoi, Nr. 31.6.2.80i; **14**. leaf base, Kassanoi, Nr. 31.6.2.69ii; **15**. leaf base, Metochia, Nr. 31.5.2.46; **16**. Kassanoi, Nr. 31.6.2.33ii

2014 *Fagus gussonii* Massalongo; Velitzelos D. et al., pl. 17, fig. 7 (Prosilio, W. Macedonia, Messinian).

2014 *Fagus gussonii* Massalongo; Velitzelos D. et al., pl. 21, fig. 11 (Elassona, N. Thessaly, Messinian).

2015 *Fagus gussonii* Massalongo emend. Knobloch et Velitzelo; Mantzouka et al., figs 4.1–4.3 (Metochia, Gavdos Island, Tortonian).

Material. Pitsidia, 2 complete or almost complete leaves and 9 fragmentary ones (Nrs 31.4.2.1176ai,bi; 31.4.2.2316; 31.4.2.3870a,b; 31.4.2.3960; 31.4.2.4153a,b; 31.4.2.4339aiii; 31.4.2.4340ai,b; ?31.4.2.6125iii; 31.4.2.6241ai,b; 31.4.2.6387a,b; 31.4.2.7038). Metochia, 3 complete to almost complete leaves and 11 fragmentary ones (Nrs 31.5.2.2; 31.5.2.17; 31.5.2.18; 31.5.2.20; 31.5.2.21a,b; 31.5.2.22; 31.5.2.23; 31.5.2.24; 31.5.2.25; 31.5.2.26; 31.5.2.27a,b; 31.5.2.28a,b; 31.5.2.29ai,b; 31.5.2.32a,b).

Description. Leaves petiolate, petiole >6–8 mm long, lamina probably chartaceous, oblong to ovate or elliptic, ~40 to >82 mm long and 20 to >62 mm wide, L/W ratio ~2–2.4, base cuneate to rounded, apex acute, margin simple dentate, with small, sharp teeth alternating with open, shallow, rounded to S-like sinuses; venation craspedodromous, primary vein strong, straight to gently curved, often slightly sinuous near leaf apex, secondary veins delicate, alternate to subopposite, in 10–15 pairs, regularly spaced, arising at 30–80°, interspacing 2–8 mm, angles and distances decreasing towards apex, course parallel to subparallel, straight, unbranched, entering marginal teeth, tertiary veins dense, opposite or alternate percurrent, oblique or perpendicular to secondaries, sinuous or straight.

Remarks. The marginal serration, craspedodromous venation, strictly straight and parallel secondary veins and the size of the lamina correspond with *Fagus gussonii*. This species is distributed mainly in southern Europe and Anatolia (Denk, 2004). It is very common especially in the late Miocene floras of Italy and northern Greece and in the middle Miocene floras of the Yatağan Basin in Turkey (Massalongo and Scarabelli, 1859; Knobloch and Velitzelos, 1986, Güner et al., 2017). From Crete, Sachse (2004) and Mantzouka et al. (2015) described several leaf remains of *F. gussonii* from Makrilia and Metochia. In Vrysses and Kassanoi this element has not yet been detected.

Family Myricaceae

Genus *Myrica* L.

Myrica lignitum (Unger) Saporta

Pl. 14, figs 11–16; Fig. 17a,b

Material. Pitsidia, (in Zidianakis, 2018). Kassanoi, 8 complete or almost complete leaves and 20 fragmentary ones (Nrs 31.6.2.16v; 31.6.2.33ii; 31.6.2.40; 31.6.2.41; 31.6.2.46; 31.6.2.47; 31.6.2.50; 31.6.2.69ii; 31.6.2.80i; 31.6.2.82; 31.6.2.88; 31.6.2.89; 31.6.2.91iii; 31.6.2.94; ?31.6.2.95; 31.6.2.99; 31.6.2.106; 31.6.2.107i; 31.6.2.107ii; 31.6.2.109; 31.6.2.119viii; 31.6.2.120i; 31.6.2.120ii; 31.6.2.123ii; 31.6.2.123iii; 31.6.2.124ii; 31.6.2.217; 31.6.2.245opii). Metochia, 2 incomplete leaves (Nrs 31.5.2.46; 31.5.2.48ai,b).

Description. See Zidianakis et al. (2015)

Remarks. From Pitsidia the evidence of *Myrica* comprises not only leaves but also catkins, fruits and infructescences in a remarkable state of preservation; they have already

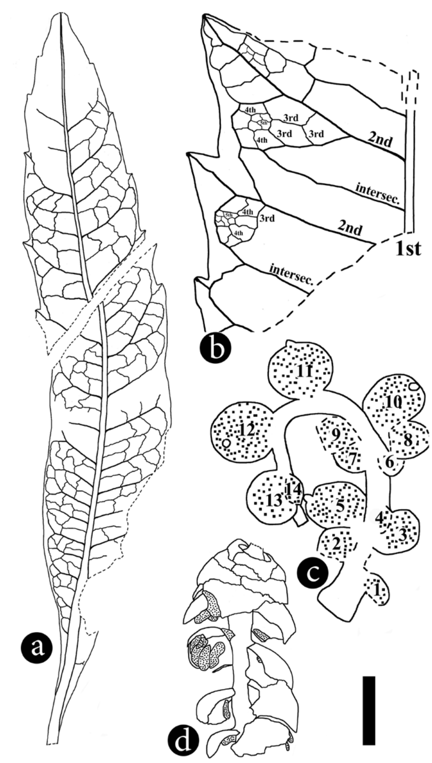

Fig. 17. Palaeoflora of Pitsidia. *Myrica* vegetative and fertile organs, line drawings, scale bar = 2.5 mm (unless otherwise stated); **a**. complete leaf of *M. lignitum*, Nr. 31.4.2.3782bii, scale bar = 6 mm; **b**. leaf fragment, venation and margin details visible, Nr. 31.4.2.4407i; **c**. *M.* cf. *goeppertii* infructescence with 14 attached fruits, Nr. 31.4.2.8103b; **d**. *M. ceriferiformis* male catkin, Nr. 31.4.2.5300bi

been dealt with separately (Zidianakis et al., 2015). In Kassanoi, *Myrica lignitum* is a dominant element, as it is in Pitsidia. The specimen figured in Pl. 14, fig. 12, with its broad leaf form and prominent secondary veins, may represent another *Myrica* species, but poor preservation prevents a diagnosis. The examination of the vegetative and reproductive organs of a single *Myrica* species (*Myrica lignitum* leaves, *M. ceriferiformis* fruits and *M*. cf. *goeppertii* male catkins) from Pitsidia suggests a relationship to section *Cerophora* (sensu Chevalier, 1901) of subgenus *Morella* and a closer affinity to the American, African and Macaronesian modern species of *Myrica* than to Eurasian ones (Zidianakis et al., 2015).

Myrica ceriferiformis Kownas

Fig. 17c

See Zidianakis et al. (2015)

A shoot remain reported as Cupressaceae gen. indet. by Zidianakis et al. (2010) is part of a bare infructescence axis of this taxon.

Myrica cf. ***goeppertii*** Kohlman-Adamska, Ziembińska-Tworzydło et Zastawniak

Fig. 17d

See Zidianakis et al. (2015). The inflorescence figured by Kröger (2004: fig. 2.3.4.b, as *Carpinus betulus fossilis* L.) is a catkin of this taxon.

Family Juglandaceae

Genus *Carya* Nuttall

Carya sp. – folia

Pl. 15, figs 1–11

2010 *Carya minor* Saporta et Marion; Zidianakis et al., figs 2o, 3c (Pitsidia, central Crete, Tortonian).

2014 *Carya serrifolia* (Goeppert) Kräusel; Velitzelos D. et al., pl. 27, fig. 5 (Makrilia, E. Crete, Tortonian).

Material. Pitsidia, 20 complete or almost complete leaflets and 43 fragmentary ones (Nrs 31.4.2.206; 31.4.2.471; 31.4.2.971aop,973; 31.4.2.972ai,b; 31.4.2.990a,b; 31.4.2.1232i,1222aop; 31.4.2.1256i; 31.4.2.1684aiii; 31.4.2.1694a,b; 31.4.2.1808; 31.4.2.1920a,b; 31.4.2.2428a,b; 31.4.2.2439a,b; 31.4.2.2656ai,bi; 31.4.2.3359ai,bi; 31.4.2.3520op; 31.4.2.3572ai,bi; 31.4.2.3676,3635opiii; 31.4.2.3827aiv,biv; 31.4.2.3919bop; 31.4.2.3937a,b; 31.4.2.4149ai,bi; 31.4.2.4285; 31.4.2.4321a,b; 31.4.2.4422a,b; 31.4.2.4439ai,bi; 31.4.2.4442a,b; 31.4.2.4704; 31.4.2.4980aopiii; 31.4.2.5068; 31.4.2.5213ai,b; 31.4.2.5224,5551; 31.4.2.5226a,b; 31.4.2.5267aii,b; 31.4.2.5269opi; 31.4.2.5296a,b; 31.4.2.5386a,5385; 31.4.2.5417ai,b; 31.4.2.5447c,5447aii; 31.4.2.5466avii,5466cvi; 31.4.2.5472ai,bi; 31.4.2.5741a,b; 31.4.2.5900ai,bi; 31.4.2.5990a,b; 31.4.2.6192; 31.4.2.6479i,6464op; 31.4.2.6615a,b; 31.4.2.6661a,b; 31.4.2.6714a,b; 31.4.2.6715ii; 31.4.2.6719; 31.4.2.6722; 31.4.2.6949; 31.4.2.6963bbii; 31.4.2.6972; 31.4.2.8010i; 31.4.2.8102; 31.4.2.8212a,b; 31.4.2.8253; 31.4.2.8257i; 31.4.2.8257ii; 31.4.2.8258ai,b; 31.4.2.8259a,b).

Description. Leaflets subsessile (lateral ones) or petiolulate (terminal ones), lamina chartaceous, shape of lateral leaflets elliptic to ovate, shape of terminal ones obovate, 19–71 (average 47.5) mm long and 11–35 (average 25.5) mm wide, L/W ratio 1.4–2.5 (average 1.9), apex acute to acuminate, occasionally characteristically deformed by arthropod feeding, base rounded to widely cuneate, asymmetric in lateral leaflets, symmetric and decurrent in terminal ones; margin sharply simple serrate; teeth dense, fine, ± irregular in shape, acute, basal side mostly straight, apical side straight to convex or slightly concave, 0.5–1 mm long, 5–7 teeth per cm, sinuses narrow, angular; primary vein strong, straight to curved or S-like, secondary venation semicraspedodromous to partly craspedodromous, secondaries delicate, almost opposite to alternate, 6–18 pairs, interspaces 2–7 mm, arising at 50–85°, course curved, slightly irregular, often forked once or more times, sending veinlets into marginal teeth, intersecondaries rare, parallel to secondaries, up to half of the secondary long, tertiary veins dense, percurrent, almost opposite, oblique or almost perpendicular to secondaries, straight to sinuous, quaternary veins forming an irregular square or pentagonal network.

Remarks. The gross morphological traits of these remains clearly suggest an affinity to *Carya*. Modern foliage of *Carya* does not show significant differences among the various species (Manchester, 1987). Delimitation of fossil species such as *C. minor* Saporta et Marion or

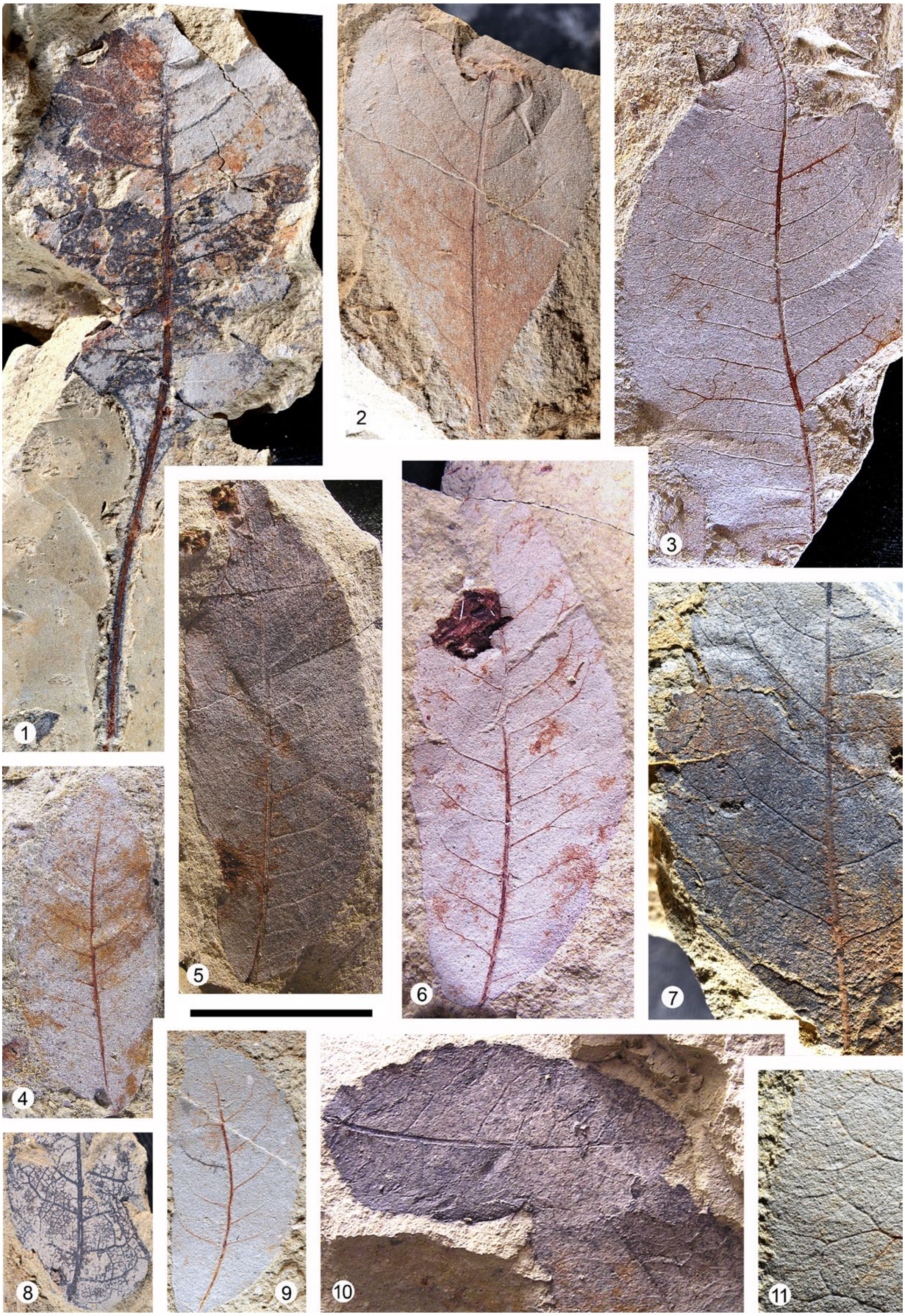

Plate 15. Palaeoflora of Pitsidia, Crete, scale bar = 2 cm (unless otherwise stated); **1, 2**. *Carya* sp. terminal leaflets; **1**. physically attached on leaf rachis, Nr. 31.4.2.6615a; **2**. Nr. 31.4.2.471 (Fig. 3c in Zidianakis et al., 2010); **3–11**. *Carya* sp. lateral leaflets; **3**. Nr. 31.4.2.5741a; **4**. Nr. 31.4.2.6479i; **5**. Nr. 31.4.2.5466cvi; **6**. Nr. 31.4.2.206 (Fig. 2o in Zidianakis et al., 2010); **7**. Nr. 31.4.2.6972; **8**. asymmetric lamina base, Nr. 31.4.2.5267b; **9**. Nr. 31.4.2.972b; **10**. two leaflets, Nr. 31.4.2.8257i; **11**. venation pattern close to margin, Nr. 31.4.2.5741a detail, scale bar = 1 cm

C. serrifolia (Goeppert) Kräusel is also problematic. Therefore, assignment to a particular fossil species is avoided here. Based on fruits, a few different fossil species have been recognized, for example *C. angulata* C. Reid et E.M. Reid, *C. askenasyi* (Kinkelin) Mai and *C. globosa* (Ludwig) Mädler, suggesting some species diversity in *Carya*. From Makrilia, Velitzelos D. et al. (2014) figured a fragment of an elongated leaflet as *Carya serrifolia*, which resembles the slender leaflet forms of Pitsidia both in venation and in marginal teeth. A leaf reported as *Quercus drymeja* by Zidianakis et al. (2010) actually is a leaflet of this genus.

Genus *Pterocarya* Kunth

Pterocarya sp. – fructus

Pl. 16, fig. 10

Material. Pitsidia, a single fragmentary fruit (Nr. 31.4.2.3000).

Description. Two-winged nutlet, wings oriented parallel to main axis of nutlet, wings broad elliptic, 11 mm long and 8 mm wide, margin entire to undulate, with no differential thickenings; wing veins fine, continuous from edge of nutlet to wing margin, bifurcating and occasionally anastomosing; nutlet compressed globose, 3 mm in diameter, with two remnants of styles diverging from apex.

Remarks. The morphology of this fruit is characteristic of *Pterocarya*, especially the wing features and the occurrence of style remnants. This is the first report of a fruit of this genus from the fossil record of Greece; foliage of *Pterocarya paradisiaca* (Unger) Iljinskaya is well represented in the Neogene of continental Greece.

Genus *Engelhardia* Leschenault ex Blume

Engelhardia orsbergensis
(Wessel et Weber) Jähnichen, Mai et Walther

Pl. 16, figs 8, ?9

1855 *Banksia orsbergensis* Wessel et Weber, p. 146, pl. 25, fig. 9a (Orsberg, Germany, late Oligocene).

1977 *Engelhardia orsbergensis* (Wessel et Weber); Jähnichen et al., p. 326, pls 38–49; text-figs 1–3 (European Tertiary).

1984 *Palaeocarya orsbergensis* (Wessel et Weber); Jähnichen et al., p. 109, pls 1–6; text-figs 2–4 (European Tertiary).

?1953 cf. *Quercus lonchitis* Unger; Berger, figs 2, 3 (Kastron, Lemnos Island, early Miocene).

1986b *Palaeocarya orsbergensis* (Wessel et Weber) Jähnichen, Friedrich, Takáč; Knobloch, Velitzelos, pl. 14, fig. 12 (Prosilio, W. Macedonia, Messinian).

1996 *Palaeocarya* sp., Sachse, Mohr, pl. 3, fig. 12; pl. 5, figs 2, 7, 8 (Makrilia, E. Crete, Tortonian).

?2002a *Engelhardia orsbergensis* (Wessel et Weber) Jähnichen, Mai et Walther; Velitzelos et al., p. 12 (Kimi, Euboea, early Miocene) (no figure).

2004 cf. *Engelhardia orsbergensis* (Wessel et Weber) Jähnichen, Mai et Walther; Sachse, pl. 11, figs 1–4; pl. 19, fig. 12 (Makrilia, E. Crete, Tortonian).

2014 *Engelhardia orsbergensis* (Wessel et Weber) Jähnichen, Mai et Walther; Velitzelos D. et al., pl. 13, fig. 4 (Lesbos Island, early Miocene).

?2014 *Engelhardia orsbergensis* (Wessel et Weber) Jähnichen, Mai et Walther; Velitzelos D. et al., p. 66 (Kimi-Nea Stira, Euboea, early Miocene) (no figure).

?2014 *Engelhardia orsbergensis* (Wessel et Weber) Jähnichen, Mai et Walther; Velitzelos D. et al., p. 69 (Prosilio and Lava, W. Macedonia, Messinian) (no figure).

2015 *Engelhardia orsbergensis* (Wessel et Weber) Jähnichen, Mai et Walther; Mantzouka et al., figs 5.12–5.13 (Metochia, Gavdos Island, Tortonian).

Material. Metochia, 2 complete leaflets (Nrs 31.5.2.3a,b; 31.5.2.5).

Description. Leaflets shortly petiolulate, petiolule 2 and 6 mm long; lamina chartaceous, shape lanceolate, asymmetric, 34 and 58 mm long, 9 and 12 mm wide, L/W ratio 3.7 and 4.8, base rounded to narrow cuneate, strongly asymmetric in one specimen (Pl. 16, fig. 9), apex acute, margin widely, simply dentate, teeth small, possibly with glands apically, basal side concave to straight, apically concave, sinuses open and shallow; venation camptodromous to semicraspedodromous, primary vein stout, ± smoothly curved, secondary veins much more delicate, densely spaced, originating at 35–60°, intersecondary veins delicate, parallel to secondaries, higher-order venation not visible.

Remarks. The asymmetric lamina with fine, widely spaced marginal teeth and the venation pattern are characteristic of *Engelhardia orsbergensis* (Jähnichen et al., 1984). The specimen figured on Pl. 16, fig. 9 shows a rather long petiolule uncharacteristic for *E. orsbergensis*. Its assignment therefore remains somewhat uncertain. In the floras of the Greek peninsula, *E. orsbergensis* was a common element during the early Miocene, whereas in the late Miocene it appears mainly in the palaeofloras of Crete. In Makrilia, *E. orsbergensis* co-occurs with samaras of *Engelhardia macroptera* (Brongniart) Unger (Sachse, 2004). From Metochia, Mantzouka et al. (2015) described remains of incomplete leaflets.

Juglandaceae gen. et sp. indet. – folia

Pl. 16, fig. 7

Material. Pitsidia: one complete leaflet (Nr. 31.4.2.5901a,b).

Description. Leaflet possibly sessile, lamina elliptic, 44 mm long and 15 mm wide, L/W ratio 2.9, base rounded, apex bluntly acute, entire-margined with one or two pairs of blunt, inconspicuous teeth close to apex; venation brochidodromous to craspedodromous (apically), primary vein almost straight, secondary veins distinct, in ~12 pairs arising at 45–80°, intervals 3–4 mm, initially straight, then curved, forming well-developed loops close to margin, apically innervating the marginal teeth, tertiary veins percurrent, almost perpendicular to secondaries.

Remarks. This leaf, especially its margin, the course of secondaries and percurrent tertiaries, rather resembles *Juglans* leaflets.

Family Betulaceae

Genus *Ostrya* Scopoli

cf. ***Ostrya*** sp. – folia

Pl. 16, figs 11–14, 21; Fig. 15a, d

Material. Pitsidia, 2 almost complete leaves and 5 fragmentary ones (Nrs 31.4.2.1923; 31.4.2.5261; 31.4.2.6206a,b; 31.4.2.6591; 31.4.2.6965a,b; 31.4.2.7036; 31.4.2.8266).

Description. Leaves short petiolate, petiole delicate, up to 5.5 mm long, lamina chartaceous, narrow elliptic to ovate, ~35–47 mm long (average 39.5 mm) and 11–18 mm wide (average 14 mm), L/W ratio 2.2–3, base acute, cuneate to convex, symmetric, apex acute to acuminate, not entirely preserved, margin finely simple to weakly double serrate, with narrow, acute teeth and angular sinuses, teeth ~1 mm long, basal side concave, apical side straight to concave, with acute to acuminate tooth apex; venation craspedodromous, primary vein stout, moderately thick, straight, secondary veins in 12–14 pairs, delicate, densely arranged, interspaces 2.5–4 mm, straight, originating at acute angles of less than 45°, straight to gently curved upwards, forked occasionally at variable distances from margin, forks mostly unequal, innervating the marginal teeth, tertiary veins percurrent, opposite or alternate, very fine, originating almost perpendicularly from secondaries.

Remarks. These leaves have a symmetric leaf base, densely spaced seconduries and a finely double serrate margin with delicate teeth. Such leaves often occur in the genus *Ostrya*.

Family Salicaceae

Genus *Salix* L.

Salix angusta A. Braun

Pl. 16, fig. 15

1836 *Salix angustifolia* A. Braun (in Buckland), p. 512 (Öhningen, Germany, middle Miocene).

1856 *Salix angusta* A. Braun; Heer, p. 30, pl. 69, figs 1–11 (Swiss Molasse, Switzerland, late Miocene).

?2015 *Salix* cf. *angusta* A. Braun; Mantzouka et al., figs 5.7–5.9 (Metochia, Gavdos Island, Tortonian).

Material. Kassanoi, single leaf, almost entire (Nr. 31.6.2.37i).

Description. Leaf lamina linear in shape with parallel margins, >52 mm long and 4 mm wide, L/W ratio 13, base cuneate, apex attenuate, margin entire to slightly crenulate; venation eucamptodromous, primary vein very strong, slightly bent, secondary veins numerous, >15 pairs, delicate, subopposite to alternate, arising at 40–70°, curved upward, forming broad arcs close to margin, intersecondary veins arising at wider angles than secondaries, reaching about half the length of secondaries, tertiary veins indistinct.

Remarks. Examining fossil material from the North Bohemian Basin, Bůžek (1971) combined the entire-margined leaf form, usually described as *Salix angusta*, with the finely serrate one of *Salix lavateri* Al. Brown as *Salix haidingeri* Ettingshausen. He based his viewpoint on the existence of transitional forms between the two extremes, and the lack of differential features. From Gavdos, Mantzouka

Plate 16. Cretan palaeofloras, scale bar = 2 cm (unless otherwise stated); **1–4**. *Ulmus* cf. *plurinervia* Unger, foliage; **1**. with strongly asymmetric base, Pitsidia, Nr. 31.4.2.3950ai; **2**. Kassanoi, Nr. 31.6.2.119v; **3**. Kassanoi, Nr. 31.6.2.79; **4**. Kassanoi, Nr. 31.6.2.78a; **5**. *Ulmus* sp., samara, seed, wing margin and preserved venation are lined, Pitsidia, Nr. 31.4.2.4150a, scale bar = 1 cm; **6**. ?*Zelkova zelkovifolia* (Unger) Bůžek et Kotlaba foliage, Pitsidia, Nr. 31.4.2.1663bi; **7**. Juglandaceae gen. et sp. indet., leaflet, Pitsidia, Nr. 31.4.2.5901a; **8**. *Engelhardia orsbergensis* (Wessel et Weber) Jähnichen, Mai et Walther, leaflet, Metochia, Nr. 31.5.2.3a; **9**. ?*Engelhardia orsbergensis* (Wessel et Weber) Jähnichen, Mai et Walther, leaflet, Metochia, Nr. 31.5.2.5; **10**. *Pterocarya* sp. winged fruit, Pitsidia, Nr. 31.4.2.3000, scale bar = 7.5 mm; **11–14**. cf. *Ostrya* sp., foliage, Pitsidia; **11**. with simple serrate margin, Nr. 31.4.2.8266; **12**. with weakly double-serrate margin, Nr. 31.4.2.6206b; **13**. Nr. 31.4.2.6591; **14**. Nr. 31.4.2.5261; **15**. *Salix angusta* A. Braun, foliage, closely arranged with *Podocarpium podocarpum* (A. Braun) Herendeen leaflet, Kassanoi, Nr. 31.6.2.37; **16**. *Salix* sp., foliage, Pitsidia, Nr. 31.4.2.1125aiv; **17, 18**. ?*Salix* sp., foliage, Kassanoi; **17**. Nr. 31.6.2.49i; **18**. Nr. 31.6.2.32; **19–21**. leaf margin close-up, Pitsidia; **19**. ?*Zelkova zelkovifolia* (Unger) Bůžek et Kotlaba, simple serrate, Nr. 31.4.2.1663ai detail, scale bar = 4 mm; **20**. *Ulmus* cf. *plurinervia* Unger, double serrate, Nr. 31.4.2.3950bi detail, scale bar = 2 mm; **21**. cf. *Ostrya* sp., simple serrate, Nr. 31.4.2.6206b detail, scale bar = 2.5 mm

et al. (2015) identified several elongate, entire-margined leaves of willow and assigned them to *Salix angusta*. These leaves well match the gross morphology of the specimen from Kassanoi. From Makrilia, Sachse (2004) described a number of elongate, entire-margined or probably indistinctly finely serrate leaves under the name *Salix* type 1 and ?*Salix* type *purpurea*. The venation of those specimens (as far as can be recognised) differs from the herein-described material by having secondaries that form less broad arcs and equal angles of the secondary and intersecondary veins. Sachse suggested that some of them probably are members of other plant families.

Salix sp. – folia

Pl. 16, fig. 16

Material. Pitsidia, one fragmentary leaf (Nr. 31.4.2.1125aiv).

Description. Leaf fragment elongate, ~55 mm long and 18 mm wide, L/W ratio >3, base and apex missing, margin finely simple serrate; venation eucamptodromous, midvein moderate, gently curved, secondary veins numerous, rather thin, densely spaced, diverging from midrib at 40–80°, strongly curved along their length, alternating with weak intersecondaries; higher-order venation not visible.

Remarks. This specimen is attributed to *Salix* based on its laminar shape, the serrate margin, and the secondary as well as intersecondary venation. The determination to species level remains open.

?***Salix*** sp. – folia

Pl. 16, figs 17, 18

Material. Kassanoi: 20 leaves, rather fragmented (Nrs 31.6.2.16iii; 31.6.2.23; 31.6.2.25; 31.6.2.30i; 31.6.2.32; 31.6.2.35i; 31.6.2.43; 31.6.2.44; 31.6.2.45; 31.6.2.49i; 31.6.2.51i; 31.6.2.52i; 31.6.2.53; 31.6.2.57; 31.6.2.59; 31.6.2.60; 31.6.2.118ii; 31.6.2.119vii; 31.6.2.120iii; 31.6.2.120vi;).

Description. Leaves petiolate, petiole fragmented, >5 mm long, lamina texture chartaceous, shape lanceolate to linear with subparallel margins, 53 to >95 mm long, 12–32 mm wide (widest in lower half of lamina), L/W ratio 5–6, base convex to slightly cuneate, occasionally ± asymmetric, apex attenuate, margin entire to crenulate; venation eucamptodromous, primary vein very stout, straight or slightly bent, secondary veins numerous, fine, subopposite to alternate, arising at wide angles, mostly 40–70°, interspaces 4–8 mm, course initially straight, then uniformly curved upward, forming broad arcs, intersecondary veins arising at wider angles than secondaries, reaching about half the length of secondaries, tertiary veins invisible.

Remarks. Such leaves are common in the Kassanoi assemblage. They share a few morphological features with *Salix* but this assignment remains uncertain.

Genus *Populus* L.

Populus latior A. Braun

Pl. 17, figs 1–9

1845 *Populus latior* A. Braun, p. 169 (Öhningen, Germany, middle Miocene).

1850a *Populus latior* A. Braun; Unger, p. 416 (Öhningen, Germany, middle Miocene).

1867 *Populus attenuata* A. Braun; Unger, pl. 6, fig. 29 (Kimi, Euboea, early Miocene).

1994a *Populus populina* (Brongniart) Knobloch; Kleinhölter, pl. 9, fig. 10; pl. 31, fig. 5 (Pyrgos and Zacharo basins, Peloponnese, Messinian).

1994b *Populus populina* (Brongniart) Knobloch; Kleinhölter, pl. 2, fig. 5 (Pyrgos and Zacharo basins, Peloponnese, Messinian).

1995 *Populus populina* (Brongniart) Knobloch; Kleinhölter, pl. 31, figs 6, 7 (Patra, Rion and Corinth basins, Peloponnese, Pliocene).

1999 *Populus* sp.; Velitzelos, Kvaček, pl. 2, fig. 2 (Vegora, W. Macedonia, Messinian).

2002 *Populus populina* (Brongniart) Knobloch; Kvaček et al., pl. 21, figs 1–5 (Vegora, W. Macedonia, Messinian).

2007 *P. tremula* L. foss.; Zidianakis et al., fig. 3D (Vrysses, W. Crete, Messinian).

2010 *Populus crenata* Berger; Zidianakis et al., fig. 3b (Pitsidia, central Crete, Tortonian).

2014 *Populus populina* (Brongniart) Knobloch; Velitzelos D. et al., pl. 7, fig. 7 (Grevena, W. Macedonia, early Miocene).

?2014 *Populus populina* (Brongniart) Knobloch; Velitzelos D. et al., p. 70 (Elassona, Thessaly, Messinian) (no figure).

2015 *Populus populina* (Brongniart) Knobloch; Mantzouka et al., figs 5.10–5.11 (Metochia, Gavdos Island, Tortonian).

Material. Pitsidia, 5 complete or almost complete leaves and 12 fragmentary ones (Nrs 31.4.2.340a,b; 31.4.2.349a,b; 31.4.2.1140; 31.4.2.1178a,b; 31.4.2.1585ai,bi; 31.4.2.1940a,b;

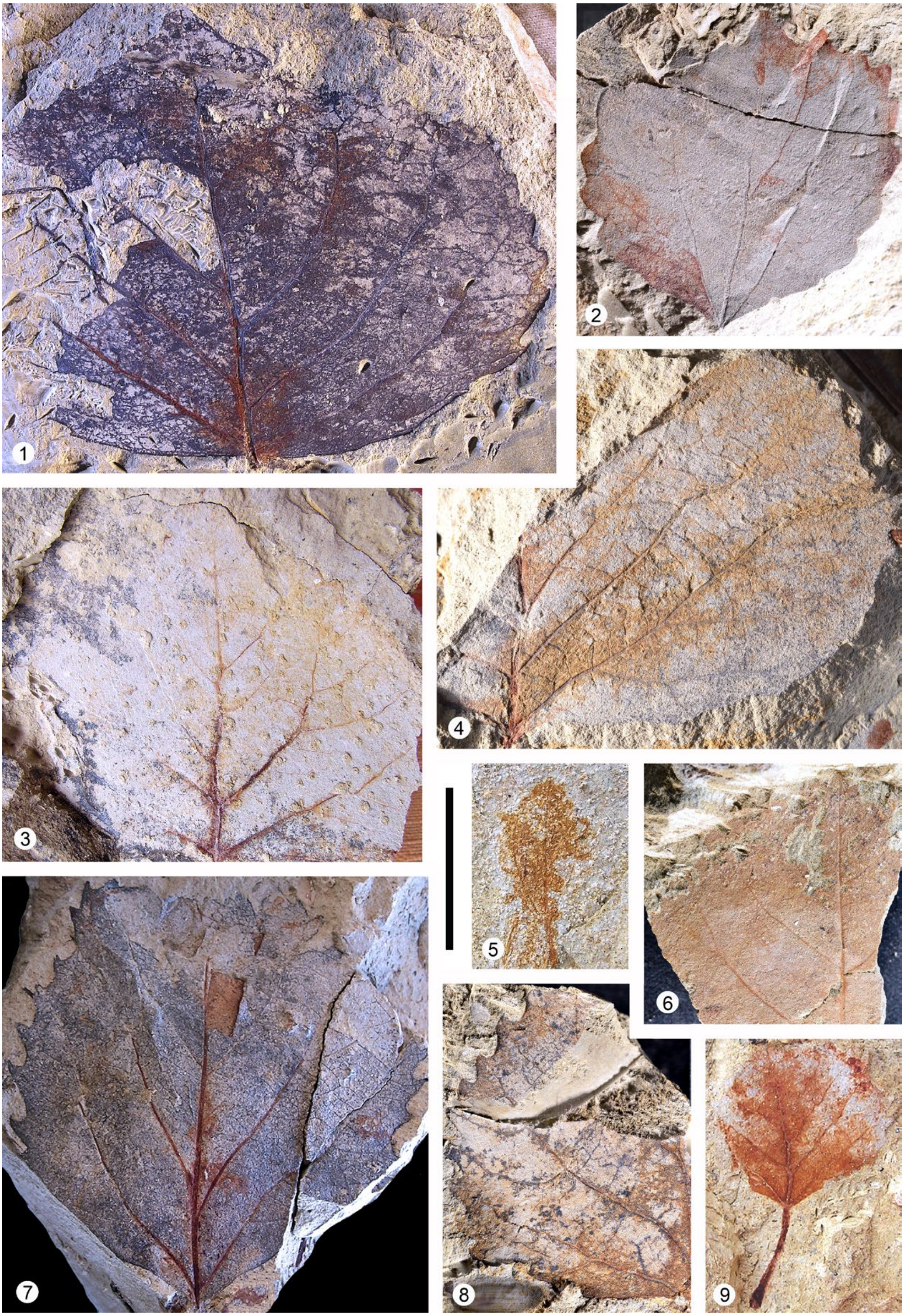

Plate 17. Cretan palaeofloras, scale bar = 2 cm; **1–9**. *Populus latior* A. Braun foliage; **1**. typical form, Pitsidia, Nr. 31.4.2.6131a; **2**. three-veined form, Pitsidia, Nr. 31.4.2.3027ai; **3**. Pitsidia, Nr. 31.4.2.1178b; **4**. Pitsidia, Nr. 31.4.2.6948ai; **5**. small three-veined leaf, Metochia, Nr. 31.5.2.4; **6**. Kassanoi, Nr. 31.6.2.69i; **7**. with prominent marginal teeth, Pitsidia, Nr. 31.4.2.349a (Fig. 3b in Zidianakis et al., 2010); **8**. with prominent marginal teeth, Pitsidia, Nr. 31.4.2.6111a; **9**. small leaf, Pitsidia, Nr. 31.4.2.340b

31.4.2.2489a,b; 31.4.2.3027ai,b; 31.4.2.3958aii-,bii; 31.4.2.4857; 31.4.2.5511aiii; 31.4.2.5933; 31.4.2.6111a,b; 31.4.2.6131a,b; 31.4.2.6934; 31.4.2.6948ai,b; 31.4.2.6999). Kassanoi, 2 fragmentary leaves (Nrs 31.6.2.69i,63; 31.6.2.77). Metochia, one complete leaf (Nr. 31.5.2.4).

Description. Leaves petiolate, petiole up to 63 mm long; laminar shape ovate to widely elliptic, 20 to ~60 mm long and 16 to ~80 mm wide, L/W ratio 0.8–1, base truncate to broadly rounded, apex broadly acute to acuminate, margin coarsely dentate to crenate with blunt, rounded teeth, sometimes glandular at tips, teeth occasionally rather large, acute, sinus rounded; venation semicraspedodromous to basal tri-veined actinodromous (Pl. 17, figs 2, 5), primary vein stout and almost straight, secondary veins in 4–7 pairs, basal pair rather stout, sub- or almost opposite, ascending towards middle part of lamina (in tri-veined specimens towards apex of lamina), secondaries otherwise subopposite to alternate, originating mostly at wide angles of 40–85°, angles decreasing towards apex, interspaces of 4–18 mm, slightly to strongly curved, sending veinlets towards next apical teeth, intersecondaries infrequently present, tertiary veins percurrent, opposite or alternate, sinuous, 3–5 per cm of secondary vein, quaternaries forming a polygonal net with further-order venation.

Remarks. The broad ovate shape of the lamina, the broad base and the coarsely dentate margin coincide exactly with the morphology of *P. populina* (Brongniart) Knobloch, which was used until recently and now is considered an illegitimate synonym of *Populus latior* (Doweld, 2017). The strongly tri-veined leaves (Pl. 17, figs 2, 5) well match *P. populina* from Vegora and Rhineland (Belz and Mosbrugger, 1994; Kvaček et al., 2002). In Metochia a similar tri-veined leaf has been described by Mantzouka et al. (2015: Figs 5.10–5.11 counterparts).

Populus sp. – folia

Pl. 20, fig. 8

Material. Pitsidia, one almost complete leaf (Nr. 31.4.2.8198i).

Description. Leaf lacking petiole, lamina broadly ovate, ~82 mm long and 62 mm wide, base widely rounded, apex not preserved, margin poorly preserved, probably regularly dentate to serrate; venation semicraspedodromous, primary vein strong, almost straight, bent apically, secondary veins thinner, arising at 30–50°, angle decreasing towards apex, interspaced 13–22 mm, course ± curved, first pair arising at the base somewhat more prominent than the others, tertiary veins percurrent, opposite to alternate, perpendicular to secondaries, straight or slightly sinuous, 7–8 per cm.

Remarks. This leaf differs from the above-described species especially by the laminar shape, angles of secondaries and density of tertiary veins. The poor preservation of the margin prevents an examination of tooth shape and density. The available features match the variation of *P. balsamoides* Goeppert.

Family Lythraceae

Genus *Decodon* J.F. Gmelin

Decodon gibbosus
(E.M. Reid) E.M. Reid (in Nikitin) – folia

Pl. 20, figs 1–3

? 1856 *Ficus multinervis* Heer, p. 63, pl. 81, figs 6–10; pl. 82, fig. 1 (Swiss Molasse, Switzerland, late Miocene).

? 1859 *Apocynophyllum helveticum* Heer, p. 91, pl. 154, figs 2, 3 (Swiss Molasse, Switzerland, late Miocene).

1920 *Diclidocarya gibbosa* E.M. Reid, p. 82, pl. 4, figs 23, 25; text-fig. 1 left (Pont de Gail, France, Pliocene).

1929 *Decodon gibbosus* (E.M. Reid) E.M. Reid in Nikitin, p. 37, pl. 589, figs 8, 9 (Krivoborye, Russia, Pliocene).

1999 *Decodon gibbosus* (E.M. Reid) E.M. Reid; Kvaček, Sakala, pl. 1, figs 1–8; pl. 2, figs 1–12; pl. 3, figs 1–5; pl. 4, figs 1–6 (Bílina, Czech Republic, early Miocene).

Material. Kassanoi, 2 complete leaves and one fragmentary one (Nrs 31.6.2.35op; 31.6.2.171a,b; 31.6.2.192).

Description. Leaves petiolate, petiole moderately thick, preserved in one specimen, >7 mm long; lamina shape ovate to elliptic, symmetric to slightly asymmetric, ~20–55 mm long and 8.5–24 mm wide, L/W ratio 2.2–2.6, base cuneate to long cuneate or rounded, apex acuminate, entire-margined to undulate; venation brochidodromous, primary vein strong, straight or gently bent across its length, secondary veins much thinner, numerous, >15 pairs, originating at 60–80°, densely arranged, interspaces 2–3.5 mm, straight to slightly zigzag, close to margin joining into an intramarginal vein, intersecondary veins 1–2 per intercostal area, almost parallel to secondaries, reaching about half the length of secondaries, connecting with them and forming elongated, irregularly shaped meshes, only intersecondaries occasionally continuing to intramarginal vein, tertiary veins ± oblique, interconnecting secondaries and intersecondaries, forming irregular network with higher-order venation.

Remarks. Leaves with this characteristic venation pattern and intramarginal vein are found in several families of modern angiosperms, (e.g. Moraceae, Lythraceae, Rutaceae, Apocynaceae, Asclepiadaceae). Kvaček, Sakala (1999) reported a leafy twig from the early Miocene of the Bilina mine with leaves of similar venation, bearing capsules with intact seeds of *Decodon gibbosus* (E.M. Reid) E.M. Reid. Some of the detached co-occurring leaves of this species are almost identical to the material from Kassanoi (Kvaček and Sakala, 1999: Pl. 2, figs 9, 11). The plant fossil assemblages associated with *Decodon gibbosus* as well as the extant relative *Decodon verticillatus* (L.) Elliott (from North America) suggest a shallow-water to swampy habitat for this element.

Family Sapindaceae

Genus *Acer* L.

Acer tricuspidatum Bronn

Pl. 18, figs 1–12; Fig. 18

1838 *Acer tricuspidatum* Bronn, p. 865, pl. 35, figs 10a–b (Salzhausen, Germany, middle Miocene).
1867 *Acer trilobatum* A. Braun; Unger, pl. 12, figs 28–29 (Kimi, Euboea, early Miocene).
1953 *Acer trilobatum* A. Braun; Berger, fig. 12 (Kastron, Lemnos Island, early Miocene).
1953 *Acer (Palaeo-Spicata) ponzianum* Gaudin; Berger, figs 24–26 (Allatini, Central Macedonia, Pliocene).
1981 *Acer platyphyllum* A. Braun; Velitzelos, Petrescu, pl. 3, fig. 3 (Vegora, W. Macedonia, Messinian).
?1985 *Acer tricuspidatum* Bronn; Dermitzakis et al., p. 165 (Kato Komi, Chios Island, Serravallian–Tortonian) (no figure).
1986a *Acer tricuspidatum* Bronn; Knobloch, Velitzelos, pl. 5, fig. 9 (Elassona, Thessaly, Messinian).
1986b *Acer* cf. *tricuspidatum* Bronn; Knobloch, Velitzelos, pl. 14, figs 1, 7 (Prosilio, W. Macedonia, Messinian).
?1987 *Acer tricuspidatum* Bronn; Knobloch, Velitzelos p. 160 (Lava, W. Macedonia, Messinian) (no figure).
?1993 *Acer tricuspidatum* Bronn; Velitzelos, p. 7 (Iliokomi-Kormitsa, E. Macedonia, Messinian) (no figure).
1994a *Acer tricuspidatum* Bronn; Kleinhölter, pl. 7, fig. 1; pl. 8, fig. 1; pl. 29 figs 6–8 (Pyrgos and Zacharo basins, Peloponnese, Messinian).
1999 *Acer tricuspidatum* Bronn; Velitzelos et al., fig. F3 in p. 461(Kastron, Lemnos Island, early Miocene).
2002 *Acer tricuspidatum* Bronn; Kvaček et al., pl. 23, figs 1–3, 6, 7; pl. 32, fig. 6 (Vegora, W. Macedonia, Messinian).
2014 *Acer tricuspidatum* Bronn; Velitzelos D. et al., pl. 7, fig. 10 (Grevena, W. Macedonia, early Miocene).
2014 *Acer tricuspidatum* Bronn; Velitzelos D. et al., pl. 18, figs 13, 14 (Prosilio, W. Macedonia, Messinian).
?2014 *Acer tricuspidatum* Bronn, Velitzelos D. et al., p. 70 (Paghi, Corfu Island, Messinian) (no figure).
2014 *Acer tricuspidatum* Bronn, Velitzelos D. et al., pl. 26, fig. 3 (Kato Komi, Chios Island, Serravallian–Tortonian).
?2014 *Acer tricuspidatum* Bronn, Velitzelos D. et al., p. 77 (Makrision, Peloponnese, Pliocene) (no figure).

Material. Pitsidia, 6 complete or almost complete leaves and 13 fragmentary ones (Nrs 31.4.2.853ai,bi; 31.4.2.998a,b; 31.4.2.1932a,b; 31.4.2.2139a,b; 31.4.2.2437a,b; 31.4.2.3496a,bi; 31.4.2.3985i; 31.4.2.4099; 31.4.2.4129; 31.4.2.4251ii; 31.4.2.4345ai,b; ?31.4.2.4361; 31.4.2.5112ai,b; 31.4.2.6327ii; 31.4.2.6922ai,b; 31.4.2.8195; 31.4.2.8203; 31.4.2.8247; 31.4.2.8262i).

Description. Leaves lacking petiole, lamina chartaceous, shape trilobate to simple tricuspidate, ~21–65 mm long and 13–80 mm wide, L/W 0.8–1.7, base rounded to subcordate, lobe apices acute to acuminate, margin simple serrate, tooth size variable, teeth blunt (mostly in basal part of lamina) to sharp (mainly in apical part of lamina), basal side mostly concave, convex or flexuous, rarely straight, apical side straight, retroflexed or occasionally convex, 3–5 teeth per cm, or less near lamina base, sinuses between lobes shallow and wide, ± angular, lobes widely triangular, medial lobe 10–21 mm long and 20–35 mm wide, lateral lobes shorter and narrower; venation basal actinodromous with 3 main veins, moderately thick and strong, straight or slightly bent, diverging at 35–45° in unlobed (tricuspidate) and at 32–65° in three-lobed leaves, secondary

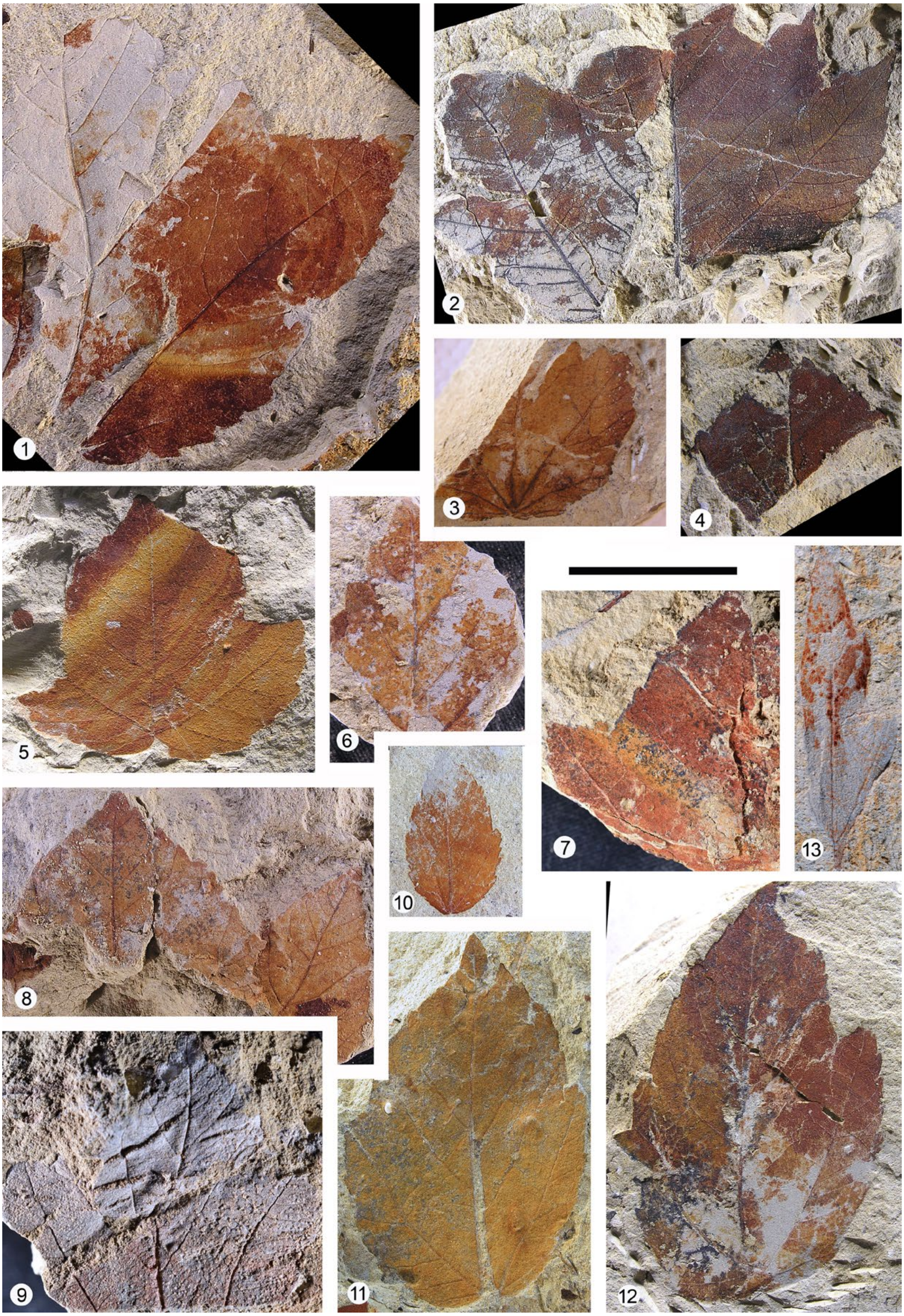

Plate 18. Palaeoflora of Pitsidia, scale bar = 2 cm (unless otherwise stated); **1–9**. *Acer tricuspidatum* Bronn, foliage, lobed form; **1**. Nr. 31.4.2.4345ai; **2**. Nr. 31.4.2.853bi; **3**. Nr. 31.4.2.998a; **4**. Nr. 31.4.2.4099; **5**. Nr. 31.4.2.6922ai; **6**. Nr. 31.4.2.4361; **7**. Nr. 31.4.2.4129; **8**. Nr. 31.4.2.2437a; **9**. Nr. 31.4.2.8247; **10–12**. *Acer tricuspidatum* Bronn, foliage, tricuspidate form; **10**. small leaf, Nr. 31.4.2.8262i; **11**. Nr. 31.4.2.3496bi; **12**. Nr. 31.4.2.5112ai; **13**. ?*Acer aegopodifolium* (Goeppert) Bajkovskaya ex Iljinskaya, leaflet, Nr. 31.4.2.5697bii, scale bar = 1 cm

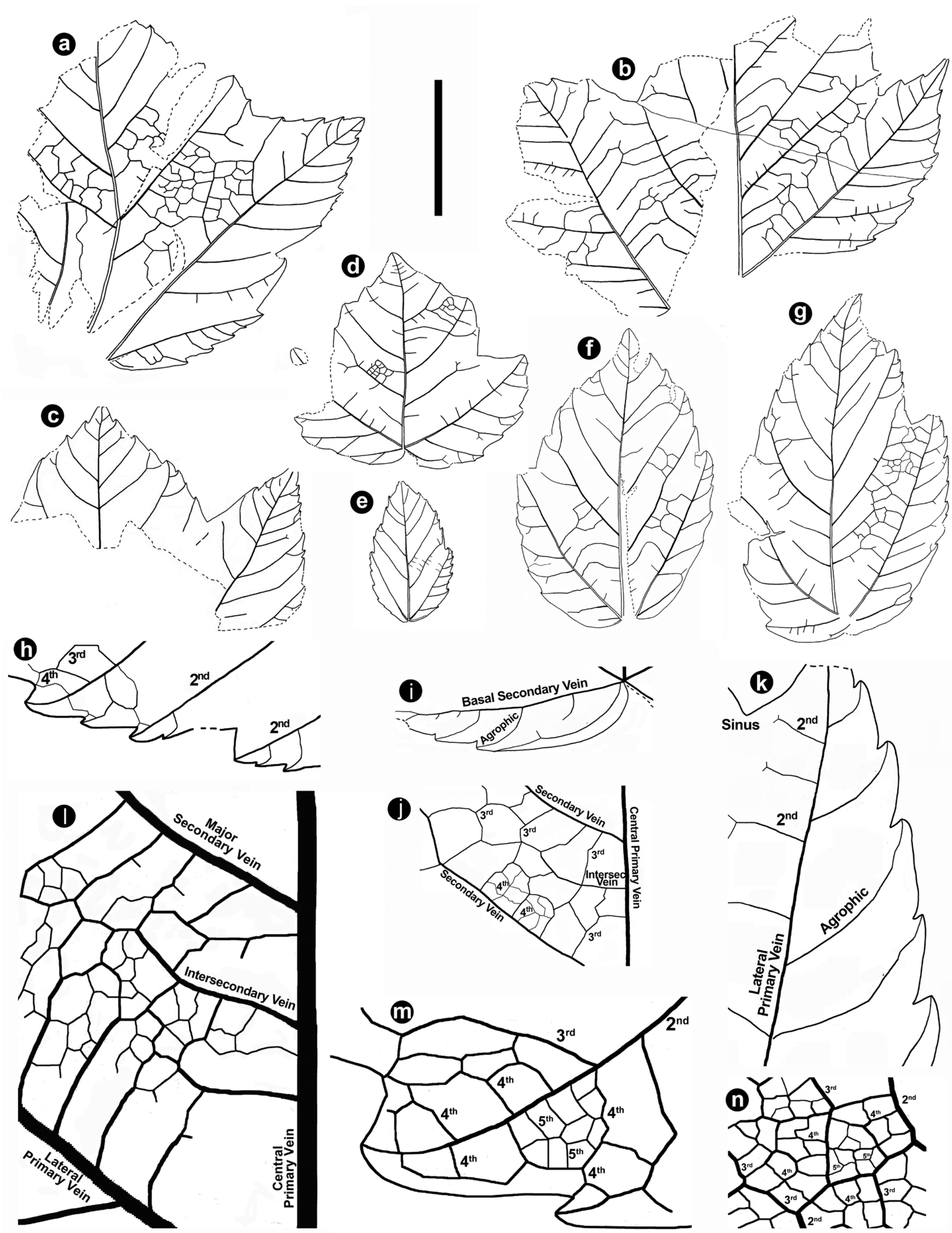

Fig. 18. Palaeoflora of Pitsidia. *Acer tricuspidatum*, foliage, line drawings, scale bar = 2 cm (unless otherwise stated); **a–d** with lobed lamina; **a**. Nr. 31.4.2.4345ai; **b**. Nr. 31.4.2.853bi; **c**. Nr. 31.4.2.2437a; **d**. Nr. 31.4.2.6922ai; **e–g**. with tricuspidate lamina; **e**. Nr. 31.4.2.8262i; **f**. Nr. 31.4.2.3496bi; **g**. Nr. 31.4.2.5112ai; **h–k**. margin and venation details, scale bar = 5 mm; **h**. Nr. 31.4.2.853ai detail; **i**. Nr. 31.4.2.6922ai detail; **j**. Nr. 31.4.2.6922ai detail; **k**. Nr. 31.4.2.5112ai detail; **l–n**. margin and venation details, scale bar = 1.25 mm; **l**. Nr. 31.4.2.853ai detail; **m**. Nr. 31.4.2.853ai detail; **n**. Nr. 31.4.2.5112ai detail

veins mostly craspedodromous, in 6–9 pairs, position alternate or subopposite, originating at 30–70°, usually irregularly spaced, curved or rarely straight, intersecondary veins absent or one per intercostal area, usually not well developed, less than half the length of secondary, ± parallel to secondaries, forked; agrophic veins in basal part of lamina well developed, 5–7 on each side of lamina, tertiary veins very fine, reticulate or very weakly alternate percurrent, ~5–6 per cm of secondary, arising at ~90°, forming ± irregular polygonal network; 4^{th}- and 5^{th}-order veins ± reticulate, forming polygons in the former and mostly pentagons in the latter; tooth principal vein terminating in tooth apex, course of accessory tooth veins convex.

Remarks. The material of Pitsidia shows remarkable variability, ranging from broad trilobate forms to small, narrow, simple, tricuspidate leaves. This variation well matches *A. tricuspidatum*, a widespread floristic element during the late Oligocene and Neogene across Central Europe (Kovar-Eder et al., 1994). Because of its morphological variability, *A. tricuspidatum* has been ascribed several forms or subspecies (e.g. Procházka and Bůžek, 1975; Hummel, 1983; Ströbitzer-Hermann, 2002), mostly related to swampy and riparian habitats. Among them, *A. tricuspidatum* forma *pyrenaicum* Rérolle sensu Ströbitzer-Hermann is closer to the Pitsidia material.

Acer integrilobum Weber *sensu* Walther

Pl. 19, figs 1–7; Fig. 19

1852 *Acer integrilobum* Weber, p. 196, pl. 22, figs 5a–b (Rott, Germany, Oligocene).

1972 *Acer integrilobum* Weber; Walther, p. 111, pl. 25, figs 1–7, 9, ?10; pl. 26, figs 1, 2, 4–7, ?8, 9, 10; pl. 56, figs 6, 7 (European Tertiary).

1986b *Acer integrilobum* Weber; Knobloch, Velitzelos, pl. 14, fig. 5 (Prosilio, W. Macedonia, Messinian).

1994b *Acer integrilobum* Weber, Kleinhölter, pl. 31, fig. 2 (Pyrgos and Zacharo basins, Peloponnese, Messinian).

1996 *Acer decipiens* A. Braun, Sachse, Mohr, pl. 3, figs ?38, 39; pl. 7, fig. 7 (Makrilia, E. Crete, Tortonian).

2002 *Acer integrilobum* Weber; Kvaček et al., pl. 25, figs 3–5, 7 (Vegora, W. Macedonia, Messinian).

2004 *Acer* ser. *Monspessulana* Pojark; Sachse, pl. 8, figs 12, ?13, 14; pl. 20, figs ?2, 3 (Makrilia, E. Crete, Tortonian).

2007 *Acer pseudomonspessulanum* Unger; Zidianakis et al., figs 3I–L, 5L, P, R (Vrysses, W. Crete, Messinian).

2010 *Acer pseudomonspessulanum* Unger; Zidianakis et al., fig. 3k (Pitsidia, central Crete, Tortonian).

Material. Pitsidia, 6 complete and 3 fragmentary leaves (Nrs 31.4.2.211a,b; 31.4.2.851a,bi; 31.4.2.1030ai,b; 31.4.2.2581ai,b; 31.4.2.3627aop,3610; 31.4.2.4537ai,b; 31.4.2.5464ai,c; 31.4.2.5494a,b; 31.4.2.6103ai,b).

Description. Palmately three-lobed leaves lacking petiole, lamina chartaceous, shape broad ovate, 23–48 (average 34) mm long and 26–54 (average 42) mm wide, lamina L/W ratio 0.8–1 (average 0.9), base subcordate to rounded, margin entire, central lobe more prominent, abruptly narrowing, longer than lateral ones, lobe apices mostly acute, tip rounded, sinuses between lobes usually rounded and wide; venation basal actinodromous with three moderately strong primary veins, often bent apically, angles between central primary and lateral veins 40–70° (average 57°), secondary veins slender, brochidodromous, originating at 45–90° (average 65°) from primaries, ± straight, looping with adjacent ones close to margin, intersecondary veins frequent in central lobe, very fine, tertiary veins random reticulate or very weakly alternate percurrent, forming ± irregular polygonal net with 4^{th}- and 5^{th}-order venation.

Remarks. This material differs from *A. pseudomonspessulanum* Unger by the longer and broader, abruptly narrowing central lobe, wide and rounded sinuses, and lateral lobes narrowing continuously. *Acer integrilobum* usually constitutes an accessory element in mesophytic forests of the European Paleogene/Neogene. In Crete, *A. integrilobum* is represented by several specimens, not only in Pitsidia but also in Makrilia and Vrysses (Sachse, 2004; Zidianakis et al., 2007).

?***Acer aegopodifolium***
(Goeppert) Bajkovskaya ex Iljinskaya

Pl. 18, fig. 13

?1855 *Rhus aegopodifolia* Goeppert, p. 37, pl. 25, fig. 10 (Sośnica, Poland, late Miocene).

?1968 *Acer aegopodifolium* (Goeppert) Bajkovskaya–Iljinskaya, p. 67, pl. 9, figs 12–15; pl. 20, figs 5, 6 (Rika, Ignatovskoe, Russia, Neogene).

Material. Pitsidia, a single complete leaflet (Nr. 31.4.2.5697aii,bii).

Description. Lamina texture probably chartaceous, shape asymmetrically lanceolate, 20 mm long and 6 mm wide, L/W ratio 3.3, base narrow cuneate, apex acute, margin probably entire on one side, two teeth on the other; teeth prominent with acute apices, sinuses rounded; venation suprabasal actinodromous with two primary veins, central primary vein stout, smoothly curved near apex, lateral primary vein very similar to central one, entering rather large lower marginal tooth; secondary veins on toothed side craspedodromous to camptodromous, 3–4 in number, originating at 35–50°, curved, on entire-margined side indistinct, camptodromous, higher-order venation reticulate, forming irregular network.

Remarks. This sample possibly is a lateral leaflet of *A. aegopodifolium*. However, its identification should remain open because it is

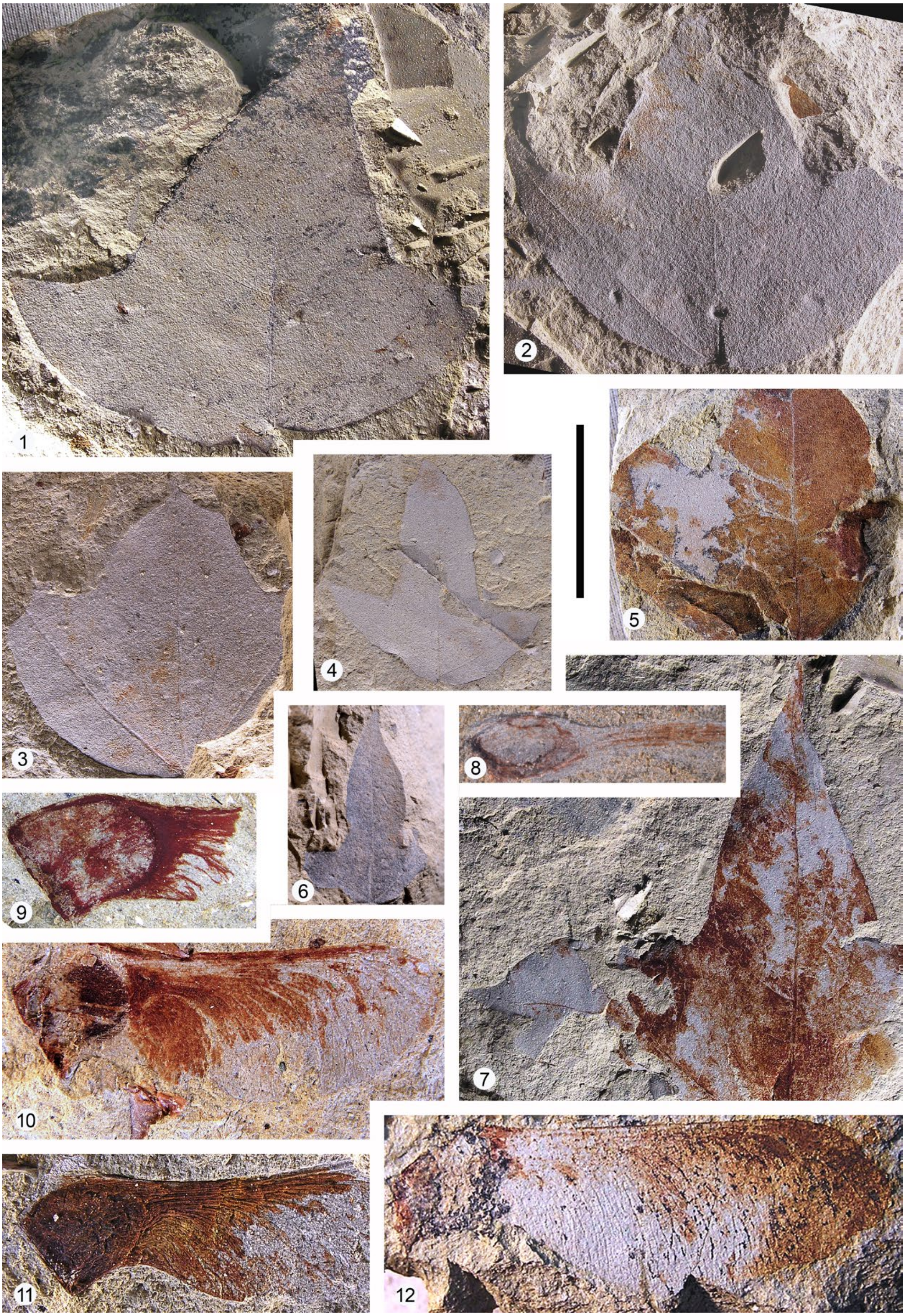

Plate 19. Palaeoflora of Pitsidia; **1–7**. *Acer integrilobum* Weber *sensu* Walther, foliage, scale bar = 2 cm; **1**. Nr. 31.4.2.6103ai; **2**. Nr. 31.4.2.5464ai; **3**. Nr. 31.4.2.211b; **4**. small leaf, Nr. 31.4.2.1030b; **5**. Nr. 31.4.2.851a; **6**. small leaf, Nr. 31.4.2.3627aop; **7**. Nr. 31.4.2.4537ai; **8**. *Acer* sp. 2, winged fruit, Nr. 31.4.2.1653b, scale bar = 1 cm; **9–12**. *Acer* sp. 1, winged fruits, scale bar = 1 cm; **9**. Nr. 31.4.2.4390a; **10**. Nr. 31.4.2.3949ai; **11**. Nr. 31.4.2.5545a; **12**. Nr. 31.4.2.8263

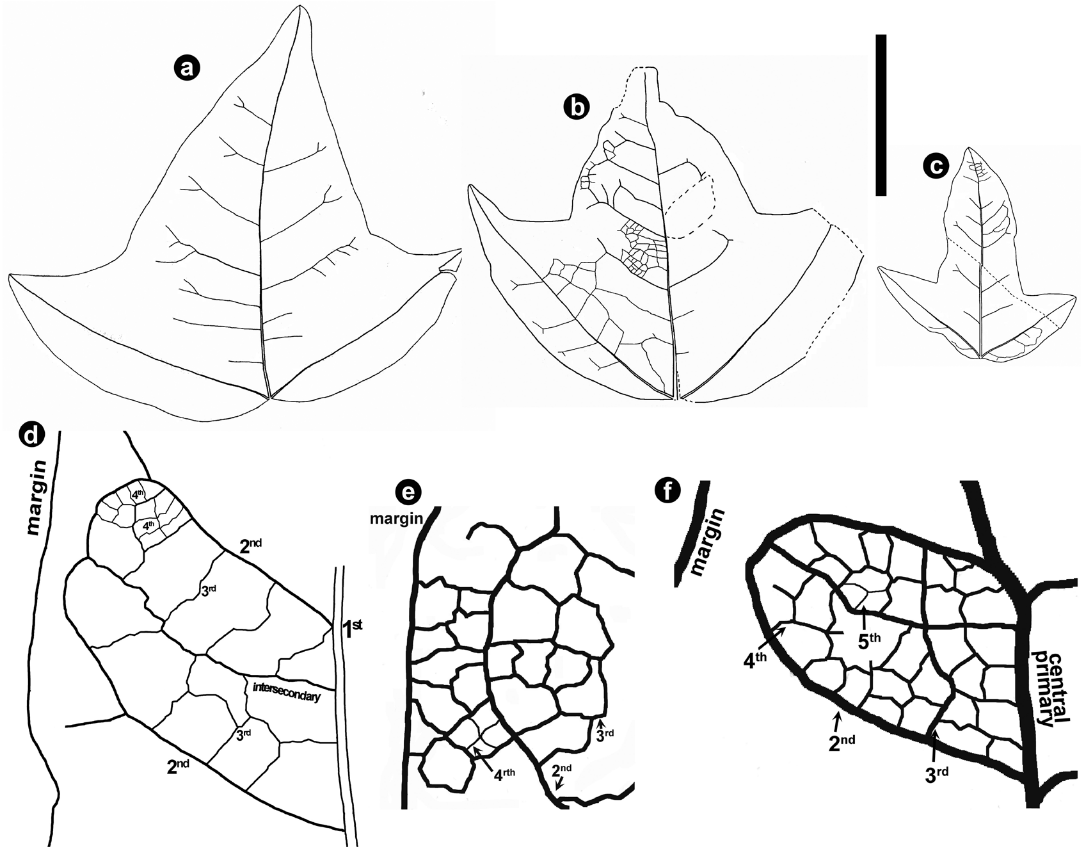

Fig. 19. Palaeoflora of Pitsidia. *Acer integrilobum* foliage, line drawings, scale bar = 2 cm (unless otherwise stated); **a**. complete leaf, Nr. 31.4.2.6103ai; **b**. almost complete leaf, Nr. 31.4.2.5464ai; **c**. small leaf, Nr. 31.4.2.1030b; **d–f**. venation pattern details of central lobe; **d**. Nr. 31.4.2.1030ai detail, scale bar = 2.5 mm; **e**. Nr. 31.4.2.1030ai detail, scale bar = 0.75 mm; **f**. close to lobe apex, Nr. 31.4.2.1030b detail, scale bar = 0.75 mm

difficult to clarify whether the entire margin on the left side represents the original leaf shape or is a taphonomic distortion. References to this species from the Greek Neogene are very rare: only one specimen from Vegora has been reported (Velitzelos and Kvaček, 1999).

Acer sp. 1 – fructus

Pl. 19, figs 9–12; Fig. 20

Material. Pitsidia, 2 complete and 4 fragmentary samaras (Nrs 31.4.2.3949ai,bi; 31.4.2.4289; 31.4.2.4390a,b; 31.4.2.4453a,b; 31.4.2.5545a,b; 31.4.2.8263)

Description (for terminology see Fig. 20). Winged fruits, 25–31 mm long, nutlet flat, broad elliptic to oval, 6–9 mm long and 4–6 mm wide, contact line of nutlet 5–7 mm long; angle between proximal margin of wing and contact line of nutlet (attachment angle) 50–58°; wing 18–24 mm long and 8–10 mm wide, proximal side of wing gently concave, distal one distinctly convex, wing apex widely obtuse to rounded, wing broadest in its middle part, gradually narrowing towards point of attachment and frequently clasping less than 1/3 of nutlet, veins numerous, distinct, curved, dichotomised more than twice.

Remarks. Sachse (2004) reported from Makrilia three different winged fruit types of *Acer*. The Makrilia specimen referred to *Acer* sp. type 3 (Sachse, 2004: Pl. 17, fig. 3) shows similarities with the herein described fruits based on wing shape and size as well as nutlet attachment angle.

Acer sp. 2 – fructus

Pl. 19, fig. 8; Fig. 20

Material. Pitsidia: two incomplete samaras (Nrs 31.4.2.1653a,b; 31.4.2.8080).

Description. Fruit winged, >21 mm long; nutlet elliptic, 6–8 mm long and 3–4 mm wide, contact line of nutlet ~3 mm long; attachment angle ~40–45°; wing partly preserved, rather narrow especially close to nutlet, the preserved part 4 mm wide, proximal side of wing S-like, distal side concave, wing apex not preserved; wing veins numerous.

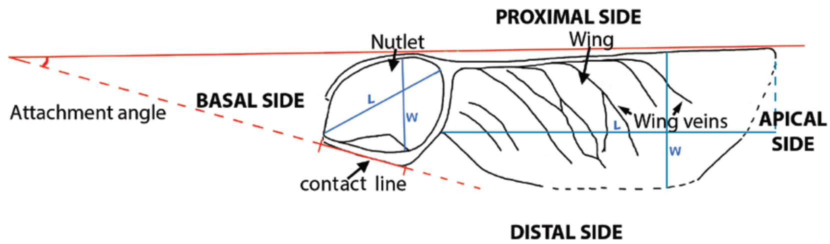

Fig. 20. Terminology of winged fruits of *Acer* (from Wolfe and Tanai, 1987)

Remarks. *Acer* sp. 2 differs from *Acer* sp. 1 by the shape of the nutlet, the short wing attachment, and wing shape. These two types of samaras probably belong to the maple species described above on the basis of leaves.

Family Oleaceae

Genus *Fraxinus* L.

Fraxinus sp. – folia

Pl. 20, figs 4–7

? 1994a *Fraxinus ungeri* (Gaudin) Knobloch et Kvaček – Kleinhölter, pl. 32, figs 6, 7 (Patra, Rion and Corinth basins, Peloponnese, Pliocene)

Material. Kassanoi, a complete leaflet and two fragmentary ones (Nrs 31.6.2.18aii,bii; 31.6.2.159a,b; 31.6.2.160).

Description. Leaflets petiolulate, petiolule strong, >2 mm long; lamina probably chartaceous, elongate oblong to lanceolate or falcate, 62 to >75 mm long and 17–26 mm wide, L/W ratio 3.2–3.5, base cuneate, strongly asymmetric, apex widely acute to acuminate, margin coarsely serrate to crenulate, teeth small, blunt, irregularly spaced, 1.5–2.5 per cm, sinuses shallow, rounded; venation semicraspedodromous, midrib strong, proximally ± bent, ~12 pairs of thin secondary veins, arising at 50–70°, initially straight, close to margin bent, forked, one branch forming weak loops with supradjacent secondary, the other giving rise to veinlets, reaching marginal sinuses, intersecondary veins occasionally present, half the length of and parallel to secondaries, tertiary veins reticulate, forming irregular network with higher-order venation.

Remarks. Based on the laminar shape and the secondary and tertiary venation pattern, these remains resemble leaflets of *Fraxinus*. Contrary to Juglandaceae, in which the tertiary venation is mainly percurrent, in *Fraxinus* it is reticulate. Reports of ash leaflets are generally not common, possibly because shed ash foliage rapidly decays. The cuticle preservation, which enables distinction from Juglandaceae, is even rarer (Kovar-Eder and Krainer, 1991). The only records from the Greek region derive from the Pliocene basins of Patra, Rio and Corinth in the North Peloponnese (Kleinhölter, 1994a). Unlike foliage, ash fruits are rather common, probably due to their robustness. Although several fossil species have been established, gross morphology is not sufficient for an assignment to species level (Kovar-Eder et al., 2004). Fruits of ash have also been reported from various Greek Neogene localities such as Makrilia, Vegora, Prosilio, Likoudi (late Miocene) and N. Peloponnese (Pliocene) (Kleinhölter, 1994a; Sachse, 2004; Velitzelos D. et al., 2014).

Angiospermae incertae sedis

Monocotyledonae

Apart from the below-described specimens (*Monocotylophyllum* sp. 1–10), at least 68 leaf fragments from Pitsidia and 38 from Kassanoi with parallel primary veins are available. All of them are of monocotyledonous affinity. Their identification is biased, however, by poor preservation and a lack of diagnostic features. These monocotyledons probably represent hydrophilic grass-like herbs or reeds and sedges.

Genus *Monocotylophyllum* E.M. Reid et Chandler

Monocotylophyllum sp. 1

Pl. 22, figs 1, 2, 17

Material. Pitsidia, 3 incomplete leaves (in groups) and 15 isolated leaf fragments (Nrs 31.4.2.907i; 31.4.2.1182ai,b; 31.4.2.1576ai,b; 31.4.2.1576aii; 31.4.2.1588i; 31.4.2.1595a,bi; 31.4.2.1748a,b; 31.4.2.2313a,b; 31.4.2.2315a,b; 31.4.2.2368a,b; 31.4.2.2425a,b; 31.4.2.4334a-d;

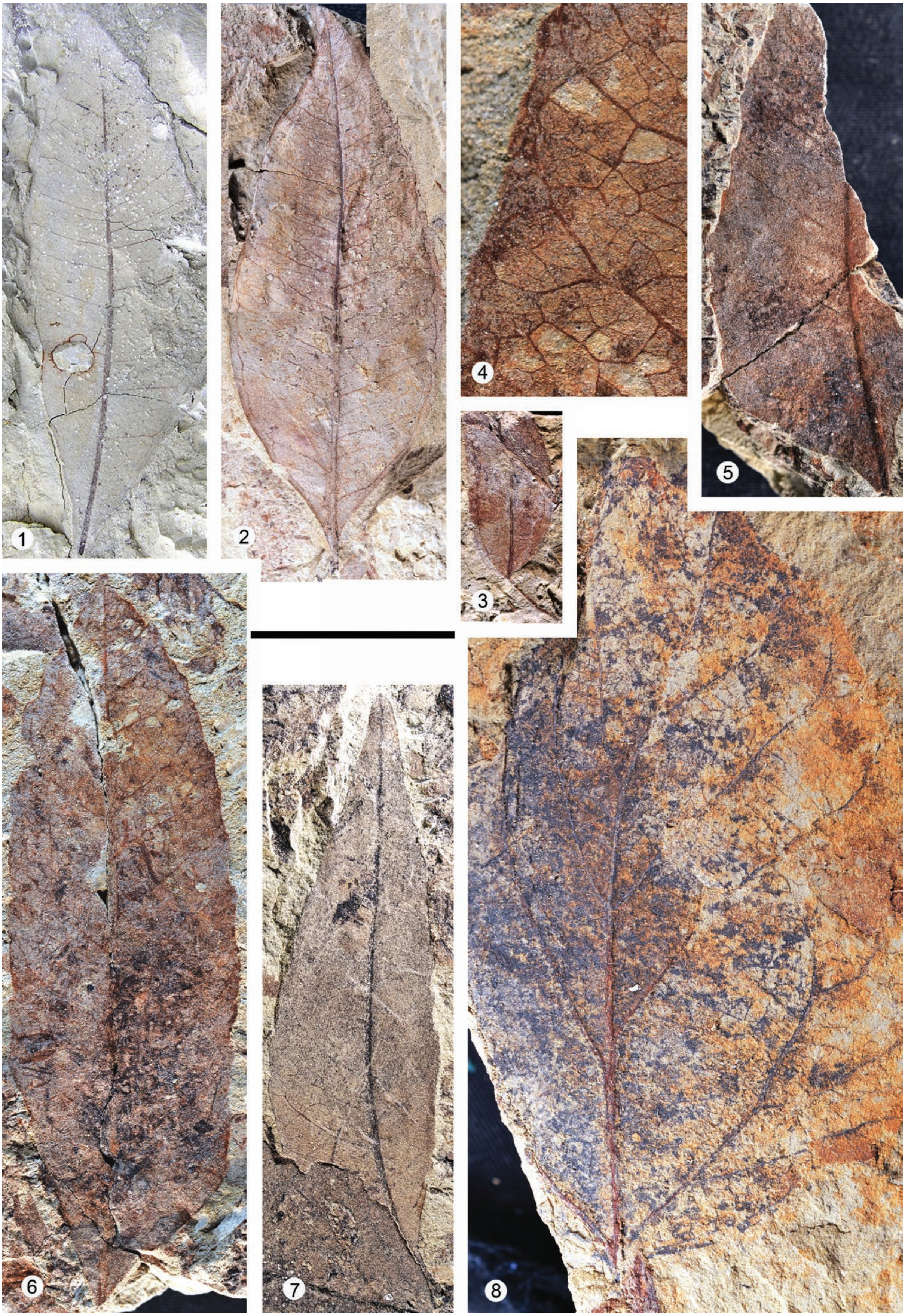

Plate 20. Cretan palaeofloras, scale bar = 2 cm (unless otherwise stated); **1–3**. *Decodon gibbosus* (E.M. Reid) E.M. Reid, foliage, Kassanoi; **1**. Nr. 31.6.2.35op; **2**. synthesis of counterparts, Nr. 31.6.2.171a,b; **3**. small leaf, Nr. 31.6.2.192; **4–7**. *Fraxinus* sp., leaflets, Kassanoi; **4**. venation pattern, close-up, Nr. 31.6.2. 159b detail, scale bar = 7.5 mm; **5**. Nr. 31.6.2.160; **6**. Nr. 31.6.2.159a; **7**. Nr. 31.6.2.18aii; **8**. *Populus* sp., foliage, Pitsidia; Nr. 31.4.2.8198i

31.4.2.4359; 31.4.2.4959a,b; 31.4.2.5571a,b; 31.4.2.6321; 31.4.2.6576; 31.4.2.8082).

Description. Fragmentary leaves, single or in groups of 2–3, connected at base, linear in shape, >80 mm long and 5–12 mm wide, entire-margined with numerous, often hardly visible, parallel primary veins of similar thickness interspaced ~0.2 mm, higher-order venation not visible; leaves frequently mechanically damaged, forming a group of strings and belts. Occasionally, coarse sand is accumulated at the basal part where the leaves are fused (Pl. 22, figs 2, 17).

Remarks. The preservation of organically connected leaves implies that this monocot thrived in or very close to the waterbody where it was embedded. Coarse sand grains apparently were trapped at the base of these herbaceous plants.

Monocotylophyllum sp. 2

Pl. 21, figs 10, 11; Fig. 21

Material. Pitsidia, 16 leaf fragments (Nrs 31.4.2.1017bop; 31.4.2.1452; 31.4.2.2872op; 31.4.2.3027aiii; 31.4.2.3198op; 31.4.2.3939; 31.4.2.3940; 31.4.2.4750i; 31.4.2.4774; 31.4.2.4955; 1.4.2.5949iii; 31.4.2.5981opi; 31.4.2.6051biii; 31.4.2.6101aiii,biii; 31.4.2.6261; 31.4.2.5542).

Description. Parallel-margined leaf fragments, mostly tiny and carbonized, up to 50 mm long and 10 mm wide, margin inconspicuously serrate; venation parallel, with numerous similarly thick primary veins, interspaced ~0.15 mm, dense, almost perpendicular interconnecting veins (15–25 per 5 mm); stomata in rows parallel to primary veins, ~20 stomata per mm, epidermal cells elongated, papillose, ~60–80 µm long.

Remarks. These tiny leaf fragments are quite common in Pitsidia, but due to their small size they are not easily detected. The original size of the leaves is unknown. The epidermis structure of several specimens is well-preserved (Fig. 21).

Monocotylophyllum sp. 3

Pl. 21, fig. 12

Material. Pitsidia, one leaf fragment (Nr. 31.4.2.8254).

Description. Tiny leaf fragment of a probably linear leaf, 7 mm long and 4 mm wide, venation parallel, with numerous veins of similar thickness at intervals of ~0.5 mm, interconnected by (almost) perpendicular cross veins, 3–5 per 5 mm.

Remarks. This fragment closely resembles *Monocotylophyllum* sp. 2 but the venation is less dense.

Monocotylophyllum sp. 4

Pl. 21, fig. 1

Material. Pitsidia, one leaf fragment (Nr. 31.4.2.1562ai,bi).

Description. Leaf fragment probably linear in shape, 33 mm long and 3.5 mm wide, slightly V-shaped in cross section, margin probably serrate with inconspicuous teeth, one primary vein, moderately thick, 10–12 very thin secondaries, hardly visible, running across lamina and paralleling the primary vein.

Remarks. This leaf differs from the other monocotyledon remains by the V-shape, the serrate margin and the venation pattern.

Monocotylophyllum sp. 5

Pl. 21, fig. 2; Pl. 22, fig. 3

Material. Pitsidia, two leaf fragments (Nrs 31.4.2.4697aiii,biii, 31.4.2.4904).

Description. Parallel-sided leaf fragments, 22 and 40 mm long, 8 and 15 mm wide, entire-margined; venation parallel, primary veins ~14–18, interspaced ~0.5–0.8 mm, secondary veins thin, hardly visible, running parallel to primaries.

Remarks. These leaves are broader than the afore-described ones. The main veins are distinct, with numerous parallel veins between them but without oblique or perpendicular veinlets.

Monocotylophyllum sp. 6

Pl. 22, fig. 4

Material. Kassanoi, three leaf fragments (Nrs 31.6.2.15vi; 31.6.2.83op; 31.6.2.199).

Description. Leaf shape probably broad linear, >47 mm long and 31 mm wide, entire-margined; venation parallelodromous, primary vein single, strong, forming prominent keel,

Plate 21. Cretan palaeofloras, scale bar = 1 cm (unless otherwise stated); **1**. *Monocotylophyllum* sp. 4, Pitsidia, Nr. 31.4.2.1562ai; **2**. *Monocotylophyllum* sp. 5, Pitsidia, Nr. 31.4.2.4697biii; **3**. *Monocotylophyllum* sp. 9, leaf fragment, Metochia, Nr. 31.5.2.41aii; **4**. *Dicotylophyllum* sp. 2, Pitsidia, Nr. 31.4.2.5902b; **5**. *Dicotylophyllum* sp. 3, Pitsidia, Nr. 31.4.2.8255; **6**. *Dicotylophyllum* sp. 4, Pitsidia, Nr. 31.4.2.6997; **7**. *Dicotylophyllum* sp. 5, Pitsidia, Nr. 31.4.2.5306; **8**. *Dicotylophyllum* sp. 6, Pitsidia, Nr. 31.4.2.5929i; **9**. *Dicotylophyllum* sp. 12, Pitsidia, Nr. 31.4.2.6987a; **10, 11**. *Monocotylophyllum* sp. 2, Pitsidia, scale bar = 2 mm; **10**. tiny leaf framgment, Nr. 31.4.2.4955; **11**. tiny leaf framgment, Nr. 31.4.2.3198op; **12**. *Monocotylophyllum* sp. 3, tiny leaf framgment, Pitsidia, Nr. 31.4.2.8254, scale bar = 2 mm; **13–16**. *Dicotylophyllum* sp. 7, Pitsidia, scale bar = 5 mm; **13**. Nr. 31.4.2.4699a; **14**. Nr. 31.4.2.5650; **15**. Nr. 31.4.2.4283ii; **16**. Nr. 31.4.2.4502a; **17, 18**. *Dicotylophyllum* sp. 8, Pitsidia, scale bar = 5 mm; **17**. Nr. 31.4.2.1269i; **18**. Nr. 31.4.2.4283i; **19**. *Dicotylophyllum* sp. 9, Pitsidia, Nr. 31.4.2.3592ii, scale bar = 5 mm; **20**. *Dicotylophyllum* sp. 10, Pitsidia, Nr. 31.4.2.1922, scale bar = 5 mm; **21–23**. *Dicotylophyllum* sp. 11, Pitsidia, scale bar = 5 mm; **21**. Nr. 31.4.2.4182ai; **22**. Nr. 31.4.2.4651aii; **23**. Nr. 31.4.2.8109

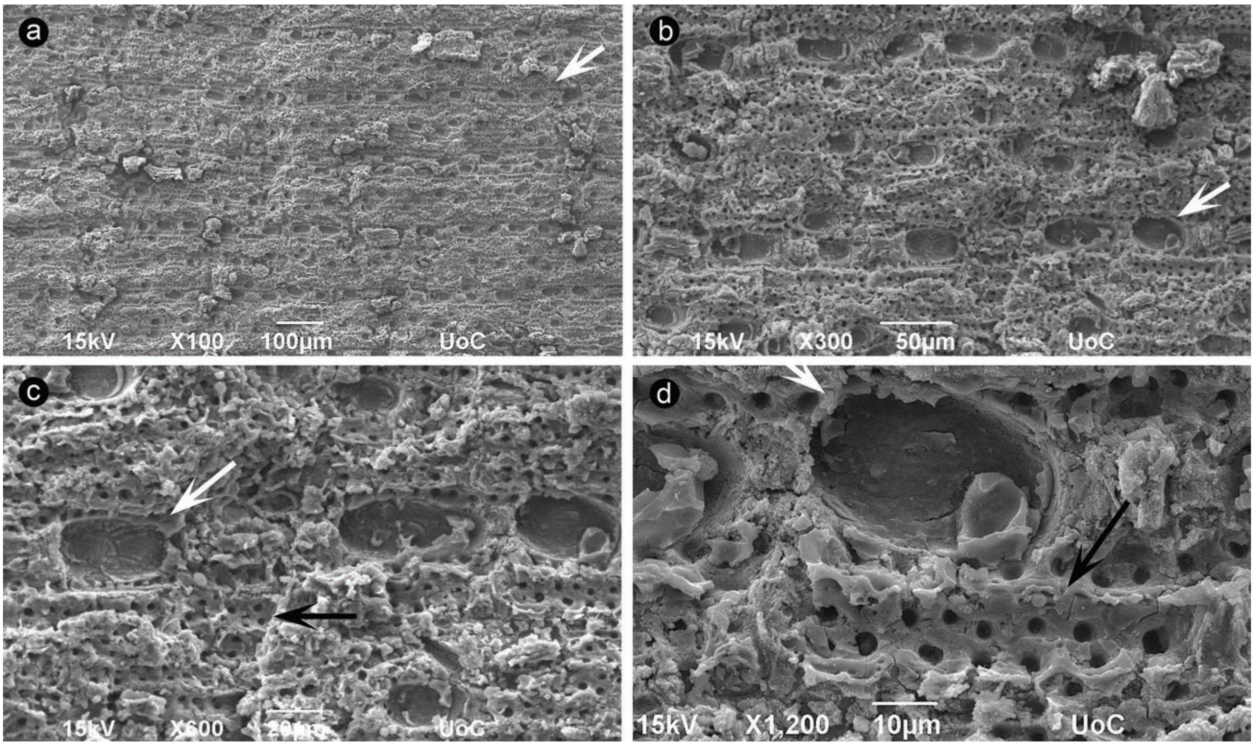

Fig. 21. Palaeoflora of Pitsidia. **a–d**. *Monocotylophyllum* sp. 2, coalified leaf fragment; stoma rows, substomatal chambers (white arrows) and elongated, papillose epidermal cells (black arrows) visible, SEM, Nr. 31.4.2.4955 detail

secondary veins parallel to midrib, numerous, delicate, interspaced 0.4–0.6 mm, higher-order venation not visible.

Remarks. This leaf shows a prominent primary vein and numerous secondaries.

Monocotylophyllum sp. 7

Pl. 22, fig. 5

Material. Kassanoi, one leaf fragment (Nr. 31.6.2.203).

Description. Leaf fragment linear, >57 mm long and 16 mm wide, entire-margined; venation parallelodromous, primary veins numerous, delicate, indistinct, straight, interspaces 0.5–0.6 mm, no veinlets present.

Remarks. This specimen is morphologically close to *Monocotylophyllum* sp. 5 but is distinguished by its delicate primary veins.

Monocotylophyllum sp. 8

Pl. 22, fig. 6

Material. Kassanoi, one leaf fragment (Nr. 31.6.2.184).

Description. Leaf probably broad linear, >96 mm long and 24 wide, margin not preserved; venation parallelodromous, primary veins numerous, >15, moderately thick, interspaced 2 mm, veinlets perpendicular to primary veins, distinct, interspaces ~1.5 mm.

Remarks. This fragment somewhat resembles *Monocotylophyllum* sp. 3 but the venation is less dense.

Monocotylophyllum sp. 9

Pl. 21, fig. 3

Material. Metochia, two leaf fragments (Nrs 31.5.2.10; 31.5.2.41aii).

Description. Leaf fragments probably linear, 11–26 mm long and 8–9 mm wide, entire-margined; venation parallelodromous, primary veins numerous, interspaced ~1 mm, secondary veins thinner than primaries; transverse veinlets not detected.

Remarks. Such leaf fragments of monocotyledonous affinity are very rare in Metochia. They resemble *Monocotylophyllum* sp. 5 but their venation is less dense.

Monocotylophyllum sp. 10

Pl. 22, fig. 8

Material. Metochia, one incomplete leaf (Nr. 31.5.2.40a,b).

Plate 22. Cretan palaeofloras, scale bar = 2 cm (unless otherwise stated); **1, 2**. *Monocotylophyllum* sp. 1, Pitsidia; **1**. two basically connected linear leaves, Nr. 31.4.2.1182ai; **2**. linear leaf with sand accumulation close to base (arrow), Nr. 31.4.2.2425a; **3**. *Monocotylophyllum* sp. 5, Pitsidia, Nr. 31.4.2.4904; **4**. *Monocotylophyllum* sp. 6, Kassanoi, Nr. 31.6.2.83op; **5**. *Monocotylophyllum* sp. 7, Kassanoi, Nr. 31.6.2.203; **6**. *Monocotylophyllum* sp. 8, Kassanoi, Nr. 31.6.2.184; **7**. *Dicotylophyllum* sp. 1, Pitsidia, Nr. 31.4.2.5216i; **8**. *Monocotylophyllum* sp. 10, incomplete broad leaf, Metochia, Nr. 31.5.2.40a; **9**. *Dicotylophyllum* sp. 13, Pitsidia, Nr. 31.4.2.4250a; **10, 11**. *Dicotylophyllum* sp. 14, Kassanoi; **10**. Nr. 31.6.2.5; **11**. Nr. 31.6.2.165i; **12–15**. *Dicotylophyllum* sp. 15, Kassanoi; **12**. Nr. 31.6.2.16i; **13**. Nr. 31.6.2.20; **14**. fragment of large leaf, Nr. 31.6.2.15i; **15**. Nr. 31.6.2.17; **16**. *Dicotylophyllum* sp. 16, Kassanoi, Nr. 31.6.2.70; **17**. *Monocotylophyllum* sp. 1, sand accumulation, close-up, Pitsidia, Nr. 31.4.2.2425b detail, scale bar = 3 mm

Description. Lamina coriaceous, shape broad, not parallel-sided, 115 mm long and 35 mm wide, fragmentary, entire-margined, venation indistinct, parallelodromous, primary veins numerous, 3–5 delicate secondary veins between two primary ones.

Remarks. This specimen is well distinguished by its broad shape. Its thickness explains its indistinct venation.

Dicotyledonae

Genus *Dicotylophyllum* Saporta

Dicotylophyllum sp. 1

Pl. 22, fig. 7

Material. Pitsidia, one leaf, fragmentary (Nr. 31.4.2.5216i).

Description. Upper part of a probably obovate leaf, lamina 28 mm long (incomplete) and 24 mm wide, apex emarginate, margin entire; venation eucamptodromous to weakly brochidodromous, primary vein stout, straight, secondary veins almost opposite to alternate, arising at 55–80°, interspaced 5–9 mm, curved, not entirely parallel to each other, intersecondary veins 1–2 per intercostal area, parallel to secondaries, well developed, reaching more than half the length of secondaries, tertiary veins weakly percurrent, opposite to alternate, higher-order veins regular quadrangular or pentagonal.

Remarks. Although fragmentary, the venation of this leaf is rather distinct. The emarginate shape of the apex probably is a result of damage. A Lauraceae affinity for this specimen is possible.

Dicotylophyllum sp. 2

Pl. 21, fig. 4

Material. Pitsidia, two incomplete leaves (Nrs 31.4.2.5471ai,bi; 31.4.2.5902a,b).

Description. Leaf petiolate, coriaceous, petiole 3.5 mm long, complete, lamina elliptic, ~25–30 mm long and 12–14 mm wide, L/W ratio ~2.1, slightly asymmetric, base obtuse, apex not preserved, margin entire; venation brochidodromous, midvein thick, almost straight, secondary veins numerous, rather indistinct, arising at 50–80°, straight, intersecondaries present, weak, tertiary veins reticulate, quaternary veins forming irregular quadrangular to pentagonal network.

Remarks. This leaf appears rather coriaceous, indicating evergreen origin.

Dicotylophyllum sp. 3

Pl. 21, fig. 5

Material. Pitsidia, one almost complete leaf/leaflet (Nr. 31.4.2.8255).

Description. Lamina lanceolate, 29 mm long and 9 mm wide, L/W ratio 3.2, base rounded, apex acute, margin coarsely, simply dentate, teeth unequal in size, irregularly spaced, sinus shallow, mostly rounded, teeth blunt, basal side convex to flexuous, apical side concave to straight; venation craspedodromous to brochidodromous, primary vein moderately thick, almost straight, secondary veins delicate, vaguely visible, originating at 30–65°, curved, innervating the tooth or forming loops close to margin.

Remarks. The affinity of this leaf or leaflet is unknown.

Dicotylophyllum sp. 4

Pl. 21, fig. 6

Material. Pitsidia, two complete leaves or leaflets (Nrs 31.4.2.1879; 31.4.2.6997).

Description. Probably subsessile leaves or leaflets, lamina chartaceous, elliptic to obovate, 26 and 36 mm long and 12 mm wide, L/W ratio 2.2–3, base rounded, slightly asymmetric, apex bluntly acute, entire-margined; venation brochidodromous, primary vein strong, gently bent, secondary veins moderately strong, in ~8 mainly subopposite pairs, arising at 45–70°, interspaced 2–4 mm, course straight to curved, forming loops close to margin, higher-order venation not visible.

Remarks. These remains likely are lateral leaflets of compound leaves.

Dicotylophyllum sp. 5

Pl. 21, fig. 7

Material. Pitsidia, one complete leaf (Nr. 31.4.2.5306).

Description. Leaf long-petiolate, petiole >8 mm long, lamina oblong, ~30 mm long (incomplete) and 8 mm wide, base acute, asymmetric, apex not preserved, margin entire; primary vein strong, slightly curved, secondaries hardly visible, arising at 40–55°, ± straight, higher-order veins not visible.

Remarks. The poor preservation of this long-petiolate, entire-margined leaf hinders any further assignment.

Dicotylophyllum sp. 6

Pl. 21, fig. 8

Material. Pitsidia, one complete leaf/leaflet (Nr. 31.4.2.5929i).

Description. Lamina probably coriaceous, elliptic, somewhat asymmetric, 33 mm long and 10 mm wide, L/W ratio 3.3, base rounded, apex acute, entire-margined; primary vein moderately thick, S-like, secondary veins very delicate, arising at 40–60°, straight, forked close to margin.

Remarks. This specimen lacks diagnostic features for a more accurate determination.

Dicotylophyllum sp. 7

Pl. 21, figs 13–16

Material. Pitsidia, 4 complete or almost complete leaves (Nrs 31.4.2.4283ii; 31.4.2.4502a,b; 31.4.2.4699a,b; 31.4.2.5650).

Description. Small leaves, lamina obovate to spatulate or elliptic, 6.5–10 mm long and 4–5 mm wide, L/W ratio 1.3–2.5, base narrow cuneate, apex acute to shortly acuminate or obtuse, entire-margined, venation brochidodromous, primary vein moderately thick and straight, secondary veins almost equally thick as midrib, originating at acute angles of 25–45°, in 5–6 pairs, ascending steeply, straight, once- to multi-forked, forming weak, angular loops with branchlets of adjacent secondaries close to margin, the first 2 or 3 pairs of secondaries more prominent, reaching close to apex, tertiary veins hardly visible, reticulate.

Remarks. This foliage is well distinguished by several features such as the small, mainly obovate lamina as well as the dense, steeply ascending and forked secondaries which diverge from the midrib at rather narrow angles. The venation pattern resembles *Hedera multinervis* Kolakovsky. The material from Pitsidia differs by the small leaf size.

Dicotylophyllum sp. 8

Pl. 21, figs 17, 18

Material. Pitsidia, two incomplete leaves/leaflets (Nrs 31.4.2.1269i; 31.4.2.4283i).

Description. Small leaves/leaflets, lamina coriaceous, ovate, 8–9 mm long and 4–6 mm wide, L/W ratio ~1.7–2, base rounded, apex acute to obtuse, margin serrate, teeth sharp, densely spaced, 6 per 0.5 cm, basal side convex, apical side concave, sinus deep, angular; venation craspedodromous, primary vein thick, almost straight, secondary veins hardly visible.

Remarks. The large, sharp teeth of these specimens are very characteristic, resembling Rosaceae. The systematic affinity of these leaves should remain open.

Dicotylophyllum sp. 9

Pl. 21, fig. 19

Material. Pitsidia, one complete leaf (Nr. 31.4.2.3592ii).

Description. Leaf short petiolate, lamina chartaceous, elliptic, 10 mm long and 4 mm wide, L/W ratio 2.5, base cuneate, apex damaged, margin coarsely serrate at upper 2/3 part of lamina, teeth small, sharp, sinuses narrow, angular; primary vein moderately thick, almost straight, secondary veins very fine, initially severely bent, close to margin indistinct.

Remarks. The size of this leaf, its subsessile character and the type of the marginal teeth resemble the extant Mediterranean shrub *Phillyrea latifolia* L. (Oleaceae).

Dicotylophyllum sp. 10

Pl. 21, fig. 20

Material. Pitsidia, one complete leaf (Nr. 31.4.2.1922).

Description. Leaf petiolate, petiole >2 mm long, lamina obovate, 12 mm long and 7 mm wide, L/W ratio 1.7, base cuneate, apex not preserved, entire-margined, at upper quarter of lamina serrate, teeth densely spaced, triangular, sharp; venation mostly craspedodromous, primary vein strong, straight, secondary veins in 9–10 pairs, originating at narrow angles, straight or gently curved, the upper pairs innervating the marginal teeth, tertiaries reticulate, forming an irregular network with higher-order venation.

Remarks. The lamina shape as well as the serration are characteristic. A Rosaceae affinity (e.g. *Crataegus* or *Rosa*) is possible for this specimen.

Dicotylophyllum sp. 11

Pl. 21, figs 21–23

Material. Pitsidia, 5 complete and 2 fragmentary leaves (Nrs. 31.4.2.3163ai,b; 31.4.2.4182ai,b; 31.4.2.4651aii,b; 31.4.2.4782a,b; 31.4.2.4971ii; 31.4.2.5215; 31.4.2.8109).

Description. Lamina obovate to broadly elliptic, 6–22 mm long and 2.5–11 mm wide, L/W ratio 2, apex emarginate to obtuse, base narrow cuneate to decurrent, entire-margined; venation brochidodromous, primary vein strong, initially straight or slightly bent, zig-zag at upper third of lamina, secondaries delicate, in 5–10 pairs, originating at 35–70°, straight or almost so, forked close to margin, forming open loops with adjacent ones, intersecondary veins rare, parallel to secondaries, weak, tertiaries reticulate.

Remarks. The systematic affinity of this unusual foliage is unclear.

Dicotylophyllum sp. 12

Pl. 21, fig. 9

Material. Pitsidia, one complete leaf (Nr. 31.4.2.6987a,b).

Description. Leaf petiolate, petiole ~3 mm long, lamina chartaceous, ovate to almost elliptic, 29 mm long and 17.5 mm wide, L/W ratio 1.7, apex acute, base widely rounded, margin entire or with inconspicuous teeth in apical part; venation ?eucamptodromous, primary vein stout, straight, secondary veins in ~6 pairs, delicate, sub-oppositely positioned, arising at 30–50°, angles decreasing distally, interspaces 3–5 mm increasing distally, running uniformly in wide arcs over their whole length towards margin, intersecondaries not observed, tertiary veins hardly visible.

Remarks. This small leaf shows affinities to *Alnus* (Betulaceae), especially in the lamina shape, the secondary vein course and the possible occurrence of tiny marginal teeth. Nevertheless, a different systematic position cannot be ruled out.

Dicotylophyllum sp. 13

Pl. 22, fig. 9

Material. Pitsidia, one almost complete leaf (Nr. 31.4.2.4250a).

Description. Lamina possibly slightly coriaceous, shape elliptic, ~65 mm long and 31 mm wide, L/W ratio 2.1; base convex to slightly rounded, somewhat asymmetric; apex acuminate, margin entire; venation brochidodromous, primary vein stout, straight, secondary veins distinctly weaker, in 8 pairs, alternate, originating at 50–70° from midrib, irregularly spaced, straight or gently curved, forking at some distance from margin, forming loops with adjacent one, additonal loops formed by higher-order venation as well, single weak intersecondary veins present, tertiaries very delicate but distinct, reticulate, higher-order venation forming regular polygonal network.

Remarks: The entire margin, the acuminate apex, the brochidodromous pattern of the main veins and the regular network of higher-order venation suggest a *Nyssa* origin of this specimen. This leaf superficially resembles *Dicotylophyllum* sp. 2 described by Knobloch and Velitzelos (1986a) from Elassona, but that specimen bears small marginal teeth and a prominent basal pair of secondaries reaching up to the middle of the lamina.

Dicotylophyllum sp. 14

Pl. 22, figs 10, 11

Material. Kassanoi, two leaves, incomplete (Nrs 31.6.2.5; 31.6.2.165i).

Description. Lamina likely coriaceous, shape oblong to lanceolate, >95 mm long and 21–30 mm wide, L/W ratio ~3.8, apex bluntly acute, base missing, entire-margined; venation brochidodromous, primary vein stout, straight or bent, secondary veins in >15 pairs, rather strong, undulating the lamina, originating at 55–80° at intervals of 4–8 mm, higher-order venation hardly visible.

Remarks. This taxon has large leaves with coriaceous, conspicuously undulating lamina. Its origin remains unknown.

Dicotylophyllum sp. 15

Pl. 22, figs 12–15

Material. Kassanoi, 17 fragmentary leaves (Nrs 31.6.2.4; 31.6.2.8; 31.6.2.10; 31.6.2.11; 31.6.2.12; 31.6.2.120iv; 31.6.2.13; 31.6.2.14; 31.6.2.158iii; 31.6.2.15i; 31.6.2.16i; 31.6.2.16ii; 31.6.2.17; 31.6.2.171aop; 31.6.2.19; 31.6.2.20; 31.6.2.21).

Description. Lamina texture probably coriaceous, shape oblong to elliptic, >100 mm long and 22–31 mm wide, L/W ratio ~4–5, base decurrent, apex acute to acuminate, margin entire; venation semicraspedodromous, primary vein stout, straight to gently bent basally, secondary veins much thinner, numerous (>12 pairs), interspaces 5–8 mm, arising at 35–80°, slightly zig-zag in course, dichotomising close to margin, one branch reaching margin, the other often forming weak, angular loops with supradjacent secondary, intersecondary veins 1–2 per intercostal area, parallel or almost so, more than half of the secondary long, tertiary veins delicate, oblique to perpendicular to secondaries, bent or S-like, joining secondaries with adjacent intersecondaries, higher-order venation not preserved.

Remarks. These elongate leaves are common in the assemblage. Their large size, and especially the rather irregular venation pattern, with delicate secondaries showing a slight zig-zag in their course, and intersecondaries, are very characteristic and make them easily distinguishable from other elongate, entire-margined leaf forms in this assemblage.

Dicotylophyllum sp. 16

Pl. 22, fig. 16

Material. Kassanoi, one leaf fragment (Nr. 31.6.2.70).

Description. Lamina fragmentary, ~3.5 cm long (>5 cm when complete) and ~3 cm wide, base missing, apex acute, margin coarsely, sharply dentate, teeth triangular with straight to concave sides and acute apex, sinus shallow, broad rounded; venation brochidodromous, secondary veins delicate, originating at wide angles, ± bent, forming loops near margin, loops sending veinlets towards margin which either innervate the teeth or form smaller loops with adjacent veinlets, intersecondary veins one per intercostal area, half of the secondary long, parallel to secondaries, tertiary veins reticulate, forming irregular network.

Remarks. This fragment of a broad, toothed leaf resembles *Mahonia* L. and *Ilex* L. based on the margin and secondary venation pattern.

Dicotylophyllum sp. 17

Pl. 23, figs 1, 2

Material. Kassanoi, 2 complete or almost complete leaves and 3 fragmentary ones (Nrs 31.6.2.22; 31.6.2.27; 31.6.2.31,39; 31.6.2.33i; 31.6.2.38).

Description. Leaves petiolate, petiole moderately thick, 5.5–9 long, lamina chartaceous, lanceolate to oblong or narrow elliptic, 33 to ~42 mm long and 10–16 mm wide, L/W ratio 3–4, base obtuse convex, apex acute or occasionally obtuse, margin entire; venation eucamptodromous, primary vein moderate, slightly curved, secondary veins very delicate, mostly in 10–12 pairs, alternate to subopposite, arising from primary vein at 35–50° proximally and 60–70° distally, interspaced 2–6 mm, gently curved, reaching margin, intersecondary veins one or rarely two per intercostal area, half the length of secondaries, tertiary veins percurrent, opposite, perpendicular to oblique to secondaries, mostly curved or S-like, higher-order venation not visible.

Remarks. No assignment of these remains to a specific taxon of dicots is possible.

Dicotylophyllum sp. 18

Pl. 23, fig. 3

Material. Kassanoi, a complete leaf and one fragment (Nrs 31.6.2.117; 31.6.2.162).

Description. Lamina shape broad elliptic, 36–45 mm long and 23–32 mm wide, L/W ratio 1.4–1.6, base rounded, apex bluntly acute, margin entire to somewhat undulate; venation eucamptodromous, primary vein moderately thick, straight, secondary veins alternate, originating at 30–60° (angles decreasing distally), interspaces wide, 3.5–13 mm (distances increasing distally), course curved, tertiary veins distinctly more delicate than secondaries, very dense, 20 per cm, percurrent, ± straight, perpendicular to widely acute to the primary vein, higher-order venation hardly visible.

Remarks. The overall gross morphology of these specimens suggests affinities to Cornaceae (e.g. *Cornus*) or Rhamnaceae (e.g. *Rhamnus*, *Berchemia*, *Rhamnidium*).

Dicotylophyllum sp. 19

Pl. 23, figs 4, 5

Material. Kassanoi, 2 complete and one fragmentary leaf (Nrs 31.6.2.102; 31.6.2.119x; 31.6.2.195).

Description. Leaf petiolate, petiole moderately thick, ~2 mm long; lamina ± coriaceous, obovate, 12–16 mm long, 6–9 mm wide, L/W ratio 1.8–2.7, base narrow cuneate to decurrent, apex emarginate, margin entire; venation camptodromous, primary vein strong, almost straight, secondary veins numerous, fine, densely arranged, ~15 per cm, arising at 30–45°, running parallel, interspacing with numerous intersecondaries towards margin, tertiary veins oblique to secondaries, joining them, straight, higher-order venation not visible.

Remarks. The systematic position of these leaves remains unknown.

Dicotylophyllum sp. 20

Pl. 23, fig. 7

Material. Metochia, 3 incomplete leaves (Nrs 31.5.2.30a,b; 31.5.2.35a,b; 31.5.2.42,45).

Description. Leaves petiolate, petiole strong, >8 mm long; lamina coriaceous, narrow elliptic to lanceolate, >60 mm long and 15–25 mm wide, L/W ratio ~4, base cuneate, apex acute, margin entire; venation brochidodromous, primary vein strong, straight to smoothly bent, secondary veins much thinner, in >8 pairs, arising at 30–80° (the most acute proximally), looping along margin, intersecondary veins mostly one per intercostal area, of the same course but shorter than secondaries, tertiary veins reticulate, almost perpendicular to secondaries, forming regular network with higher-order veins, areolation 3–4-sided.

Remarks: The gross morphology of these specimens and especially the venation architecture indicate a lauraceous origin.

Dicotylophyllum sp. 21

Pl. 23, fig. 6

Material. Metochia, one complete leaf (Nr. 31.5.2.1a,b).

Description. Lamina elliptic, 30 mm long, 15 mm wide, L/W ratio 2, base rounded, apex acuminate, margin simply, regularly serrate in upper two thirds of lamina, teeth prominent, narrow triangular to hook-like, ending in distinct bristles apically; venation possibly craspedodromous, primary vein strong, gently bent, tapering towards apex, secondary veins much thinner, in ~10 pairs, arising at 40–70°, ± bent, indistinct close to margin.

Remarks. A Fagaceae affinity of this leaf with characteristic bristle-tipped marginal teeth is probable. It could represent an extreme form of *Quercus mediterranea*.

Male inflorescence

Fam. et gen. et sp. indet.

Pl. 23, fig. 24

Material. Pitsidia, one incomplete male inflorescence (Nr. 31.4.2.6891).

Description. Staminate catkin, simple, (sub) cylindrical, secondarily flattened, 15 mm long and 3 mm wide, with numerous inconspicuous flowers (>20), loosely crowded, inflorescence axis unbranched; florets poorly preserved, 1–1.5 mm long, probably spirally arranged on axis.

Remarks. From the hundreds of catkins available from Pitsidia, this specimen is the only one that does not belong to *Myrica*, because of the loosely crowded florets on the axis. Its overall appearance is closer to *Quercus*, but more and better-preserved material is required.

Genus *Antholithes* Brongniart

Antholithes sp.

Pl. 23, fig. 19

Material. Kassanoi, a part of a flower (Nr. 31.6.2.118i).

Description. Flower remain, probably calyx, actinomorphic to slightly zygomorphic, with five, almost free sepals; sepals 2 mm long and 1–1.5 mm wide, with slender primary vein.

Remarks. This specimen probably belongs to a dicotyledonous plant taxon with pentameric flowers. In Makrilia, several isolated flowers have been discovered (Sachse, 2004: Pl. 17, figs 17–19) but none of them resembles the specimen from Kassanoi. Among them, two are octameric and have been identified as *Asterocalyx styriacus* Ettingshausen (Kovar-Eder et al., 2004).

Fruit

Fam. et gen. et sp. indet.

Pl. 23, fig. 18

Material. Kassanoi, one fragmentary fruit (Nr. 31.6.2.80ii).

Description. Winged fruit, incomplete, size 11 × 8 mm, consisting possibly of a nutlet ~2.5 mm in diameter encircled by a persistent, thick, five-lobed calyx. Sepals partly preserved, elongate, sinuses between sepals acute, deeply incised; sepal venation consisting of subparallel veins, prominent, ± equal, arising independently from the base, other veins not visible.

Remarks. Wind-dispersed fruits with a persistent five-lobed calyx occur in various extant genera (e.g. *Porana*, *Dinetus*, *Astronium*, *Gluta*, *Monotes*) as well as in the fossil *Chaneya* Wang et Manchester. In the latter the lobes are entire-margined, elliptic to obovate with rounded apices, and with venation consisting mostly of five longitudinal veins in each lobe, originating independently from the base (Wang and Manchester, 2000). The preserved features of the calyx lobes of the specimen from Kassanoi are morphologically close to this extinct genus.

?Fruit

Fam. et gen. et sp. indet.

Pl. 23, fig. 14

Material. Metochia, one fragment (Nr. 31.5.2.63).

Description. Possibly a fruit fragment, ovate, 11 mm long and 11 mm wide, with two distinct lateral extensions, pedicel 6 mm long, special features on the external surface absent.

Remarks. This specimen possibly was part of a fertile organ (e.g. exocarp or cup). Its systematic position remains uncertain.

Bud scales

Fam. et gen. et sp. indet.

Bud scale type 1

Pl. 23, fig. 23

Material. Pitsidia, 14 isolated bud scales (Nrs 31.4.2.1275; 31.4.2.3621ai,b; 31.4.2.3702i; 31.4.2.4292; 31.4.2.4389aiii,biii; 31.4.2.5143i; 31.4.2.5692ii; 31.4.2.6151ii; 31.4.2.6171op; 31.4.2.8044; 31.4.2.8050, 8034; 31.4.2.8124a,b; 31.4.2.8185; 31.4.2.8258aiii).

Description. Bud scales broad ovate, 5–11.5 (average 7.2) mm long and 6.5–13 (average 9.5) mm wide, L/W ratio 0.7–0.9, apex obtuse, rounded, base almost straight or slightly irregular, perpendicularly cutting longitudinal axes of scale, margin entire, a few subparallel linear scars visible at base of scale, other ornamentation or appendages absent.

Remarks. Bud scales are not frequent in Pitsidia. This type of scale is the most abundant one in the assemblage.

Bud scale type 2

Pl. 23, fig. 21

Material. Pitsidia, 6 isolated bud scales (Nrs 31.4.2.1629; 31.4.2.3600; 31.4.2.4172i; 31.4.2.4298; 31.4.2.4950,4952; 31.4.2.5823,5815bopi).

Description. Bud scales ovate, 8–13 mm long and 5–9 mm wide, L/W ratio 1.4–1.7, apex obtuse, base almost straight or slightly irregular, perpendicularly cutting longitudinal axis of scale, margin entire, occasionally subparallel linear scars visible.

Remarks. This type of bud scale is morphologically very close to the previous one. It differs in its more elongate shape and acute apex.

Bud scale type 3

Pl. 23, fig. 22

Material. Pitsidia, 5 isolated bud scales (Nrs 31.4.2.1751iii; 31.4.2.2183bopii; 31.4.2.3030aopiii; 31.4.2.3768ai,bi; 31.4.2.8217).

Description. Bud scales elongated, elliptic to ovate, ~11–13 mm long and 3–7 mm wide, L/W ratio ~2.5–3, apex acute, entire-margined,

Plate 23. Cretan palaeofloras, scale bar = 1 cm (unless otherwise stated); **1, 2**. *Dicotylophyllum* sp. 17*,* Kassanoi; **1**. Nr. 31.6.2.33i; **2**. Nr. 31.6.2.31; 3. *Dicotylophyllum* sp. 18*,* Kassanoi, Nr. 31.6.2.117; **4, 5**. *Dicotylophyllum* sp. 19, Kassanoi; **4**. Nr. 31.6.2.195; **5**. lamina skeletonization due to arthropod feeding, Nr. 31.6.2.119x; **6**. *Dicotylophyllum* sp. 21, serrate margin with bristle-tipped teeth, Metochia, Nr. 31.5.2.1a; **7**. *Dicotylophyllum* sp. 20, Metochia, Nr. 31.5.2.30a; **8–12**. Defoliated long shoots of woody dicots, fam. et. gen. et sp. indet., Pitsidia; **8**. Nr. 31.4.2.1163; **9**. Nr. 31.4.2.2283i; **10**. with well-preserved buds, Nr. 31.4.2.5373b; **11**. Nr. 31.4.2.4602i; 12. Nr. 31.4.2.5884aii; **13**. ?Rhizome, Nr. 31.4.2.2574ai, Pitsidia; **14**. ?Fruit fragment, fam. et gen. et sp. indet., Metochia, Nr. 31.5.2.63; **15, 16**. Root remains, fam. et. gen. et sp. indet., Pitsidia; **15**. adventitious system, Nr. 31.4.2.1127; **16**. adventitious system, Nr. 31.4.2.2957; **17**. Fragment of wood as inorganic replica, Pitsidia, Nr. 31.4.2.1835; **18**. Winged fruit, fam. et gen. et sp. indet., Kassanoi, Nr. 31.6.2.80ii, scale bar = 5 mm; **19**. *Antholithes* sp.*,* calyx, Kassanoi, Nr. 31.6.2.118i, scale bar = 5 mm; **20**. ?Rhizome base with characteristic stirs, Pitsidia, Nr. 31.4.2.2574ai detail, scale bar = 5 mm; **21–23**. Bud scales, fam. et. gen. et sp. indet., Pitsidia, scale bar = 5 mm; **21**. type 2, Nr. 31.4.2.5823; **22**. type 3, Nr. 31.4.2.3768ai; **23**. type 1, Nr. 31.4.2.4389aiii; **24**. Male inflorescence, fam. et gen. et sp. indet., Pitsidia, Nr. 31.4.2.6891, scale bar = 5 mm; **25**. Defoliated shoot of woody dicot, cross section, pith (p), cork (c) and epidermis (e), Pitsidia, Nr. 31.4.2.3295, scale bar = 0.75 mm

with numerous subparallel, equally strong veins running longitudinally.

R e m a r k s. The overall shape of this material and its venation pattern are close to the buds produced by the genus *Acer* (Gabrielyan and Kovar-Eder, 2011: Pl. 6 figs 9–41).

Defoliated long shoots / Wood fragments

Fam. et gen. et sp. indet.

Pl. 23, figs 8–12, 17, 25

M a t e r i a l. Pitsidia, 387 fragments of long shoots of woody dicots and 133 small fragments of wood, as inorganic replicas or impressions (see collection numbers in Appendix 2).

D e s c r i p t i o n. Defoliated shoots, mostly fragmentary, diverse in length and diameter, mostly with scars of leaf and buds alternately arranged; also, wood fragments preserved as inorganic replicas, cell-level structures not preserved.

R e m a r k s. Due to the lack of any diagnostic features, these vegetative remains cannot be assigned to a specific plant group. In several specimens the quality of the replica preservation is high (Pl. 23, fig. 25).

? Rhizome

Fam. et gen. et sp. indet.

Pl. 23, figs 13, 20

M a t e r i a l. Pitsidia, one fragment (Nr. 31.4.2.2574ai).

D e s c r i p t i o n. Possibly a rhizome fragment, 32 mm long and 9 mm wide, with short internodes and numerous characteristic stirs arranged around central point of basal disc.

R e m a r k s. Such specimens are very rare in Pitsidia. They may be rhizome fragments.

Roots

Fam. et gen. et sp. indet.

Pl. 23, figs 15, 16

M a t e r i a l. Pitsidia, 24 root remains, mainly fragmentary (Nrs 31.4.2.1127; 31.4.2.1223iv; 31.4.2.1440; 31.4.2.2066aiii,b; 31.4.2.2178opii; 31.4.2.2279op; 31.4.2.2957; 31.4.2.3073; 31.4.2.3406; 31.4.2.4100a,b; 31.4.2.4643biii; 31.4.2.4725iii; 31.4.2.5010; 31.4.2.5105; 31.4.2.5168; 31.4.2.5472aii; 31.4.2.5609i; 31.4.2.5916; 31.4.2.6666a,b; 31.4.2.6792iii; 31.4.2.7001; 31.4.2.7002; 31.4.2.7003; 31.4.2.7004).

D e s c r i p t i o n. Root remains, either developed from one point in clusters, ± similarly thick (adventitious), or with a primary root and the lateral ones distinctly thinner (tap).

R e m a r k s. Specimens of roots are uncommon in the assemblage and represent both monocots and dicots.

FLORA, TAPHONOMY AND VEGETATION RECONSTRUCTION

PITSIDIA

The palaeoflora of Pitsidia comprises an alga, two ferns, at least five conifers and more than 45 angiosperms (Tab. 1). Conifers are documented mostly by needle-like leaves and needle shoots, and secondarily by ovulate scales, pollen cones and bracts (Fig. 8b). Dicots are represented by leaves and leaflets as well as inflorescences, fruits/seeds and infructescences, whereas monocots are documented only by fragmentary foliage. Most of the examined fertile remains are associated with taxa identified based on foliage such as *Pinus*, *Liquidambar*, *Podocarpium*, *Myrica* and *Acer*. The only exception is *Pterocarya,* represented exclusively by a winged fruit. Arboreal elements prevail in the assemblage, while remains of herbs are less frequent, i.e. five morpho-species of monocots. Floristically the assemblage shows the predominance of deciduous elements comprising ~2/3 of the identified dicots, whereas thermophilic taxa are less common. Regarding leaf size, the highest number of leaves represent microphyll foliage.

The assemblage is characterised by the mass occurrence of two fossil taxa, *Myrica* and *Pinus pitsidiensis*, represented by hundreds of vegetative and fertile remains (Tab. 1, Fig. 8c). This allows the first reconstruction of *M. lignitum* whole plant and the identification of a new pine species (Zidianakis et al., 2015, 2016). Among the plant families, Pinaceae, Lauraceae, Fabaceae, Ulmaceae, Fagaceae, Salicaceae and Sapindaceae are the most common and diversified. Remarkably, Pitsidia lacks Betulaceae components except for some ambiguous remains (cf. *Ostrya* sp., *Dicotylophyllum* sp. 12), although this family is well-known from several other Miocene European and Cretan floras (i.e. *Alnus, Betula, Carpinus*). Fagaceae are fairly diverse, with four different species including *Fagus* as well as lobed and toothed oaks. The leaves of *Quercus pseudocastanea* and *Q. kubinyii* are most abundant, while *Q. mediterranea* and *Fagus gussonii*, two common elements in the Cretan fossil record, are represented by just a few leaf remains. Other well-represented woody plants are *Daphnogene polymorpha*, *Liquidambar europaea*, *Carya* sp., *Acer tricuspidatum*, *Populus latior* and the legumes *Podocarpium podocarpum* and *Mimosites* sp. Conifers are mostly represented by various pine species and *Taxodium dubium*. "*Pteris*" *oeningensis* is the only identified fern. The occurrence of *Equistum* sp., *Buxus pliocenica*, *Quercus drymeja* and *Comptonia difformis* (Zidianakis et al., 2010) was not confirmed.

At Pitsidia and in the adjacent area, the geological and sedimentological settings imply a transitional marine landscape where estuarine palaeoenvironments interfingered with backswamp, floodplain, riverbank and bog habitats located close to the coast (Kröger, 2004). The almost complete absence of organic matter and the medium $CaCO_3$ content in the fossiliferous sequence of Pitsidia reflect a depositional environment with good oxygen circulation, where oxidising conditions prevailed (Zidianakis, 2018). The grain-size of the plant-bearing layers suggests that the plant material was deposited in calm or stagnant waters of shallow depth. Disarticulated bones, mostly of a single fish taxon, are common in the studied deposits. The identified faunal elements reveal freshwater ecological preferences for fishes (Cyprinidae), molluscs (Planorbidae) and ostracods (Candonidae) (Zidianakis, 2018). The lack of entire fish skeletons or articulated bones suggests their allochthonous origin, probably having been transported by water currents.

The assemblage has many rather fragmented leaves; this condition applies to ~65% of them, implying pre-depositional mechanical damage. The extensive pre-burial mechanical damage reveals that most leaves had clearly undergone transport.

We estimate that about half of the plant findings in Pitsidia comprise foliage, mostly *Myrica lignitum*, ~1700 leaves per m^3 sediment (Fig. 8b). Leafy twigs, mostly of *Pinus* and *Taxodium*, as well as shoot fragments and scales/bracts, are very common. All these vegetative remains co-occur with fertile plant organs, mostly catkins, fruits/seeds and pollen cones, in considerable numbers that total ~15% of the collected material (Fig. 8b). Especially for *Myrica* and *P. pitsidiensis*, their extreme abundance, along with high organ diversity, probably reflect growth close to the depositional area, and parautochthonous deposition.

According to most authors, the breakup of the Aegeis landmass began in the middle to the late Miocene (Dermitzakis and Papanikolaou, 1981; Dermitzakis, 1990; Meulenkamp and Sissingh, 2003). As a consequence, differently oriented faults in the Messara Basin formed several relatively small intermontane basins in which deposits of variable facies (fluvial, brackish, shallow-marine) accumulated (ten Veen and Postma, 1999; Zachariasse et al., 2011). Understanding the landscape's heterogeneity, vegetation structure and plant associations in the Pitsidia area, the geological, sedimentological and taphonomic evidence, along with leaf physiognomy and putative plant autecology (Appx. 3) are taken into account. For the present phytosociological approach, we applied the vegetation units proposed by Denk (2016: VU 0–7). Apart from the Pitsidia macro-assemblage, we also supplementarily evaluated the time-equivalent pollen and spore flora of Kastellios Hill, located in the eastern part of the Messara Basin (Appx. 1, 3). The pollen record from Kastellios Hill yields a diverse conifer as well angiosperm spectrum of taxa (Sen et al., 1986) (Appx. 4). Although both floras share several taxa, including the dominant Taxodioideae, Myricaceae, *Quercus* and *Carya*, Kastellios Hill yields taxa that have not been recorded in Pitsidia. Among them, non-arboreal elements, high-altitude conifers, thermophilic taxa (*Engelhardia*, *Symplocos*, Arecaceae) and deciduous mesophytic woody plants such as *Carpinus*, *Corylus*, *Betula*, *Juglans*, *Ilex* and *Tilia* reflect habitats of a wider range.

Two typical floristic elements of swamp vegetation, the conifer *Taxodium dubium* and the dicot shrub *Myrica lignitum*, were well documented in both the Pitsidia and Kastellios Hill floras (VU 3). These elements probably were

Table 1. Plant assemblage of Pitsidia, floristic composition

Nr.	Family	Taxon	Plant part/organ	Frequency*
Algae				
1	fam. indet	gen. et sp. indet.	thallus	very rare
Polypodiophyta				
2	fam. indet	*"Pteris" oeningensis*	fronds	common
3	fam. indet	gen. et sp. indet. type 1	fronds	very rare
Gymnospermae				
4	Cupressaceae	*Tetraclinis* cf. *salicornioides*	leafy twigs/segments	very rare
5		*Taxodium dubium*	leafy shoots	common
6	Pinaceae	*Pinus pitsidiensis*	dwarf shoots/branchlets	dominant
7		*Pinus* sp. 1, 2-needled, subgen. *Pinus*	dwarf shoots	very rare
8		*Pinus* sp. 1, 5-needled, subgen. *Strobus*	dwarf shoots	rare
9		*Pinus* sp., subgen. *Pinus*	fascicle bracts	dominant
10		*Pinus* sp., subgen. *Pinus*	ovulate cone scales	very rare
11		*Pinus* sp., subgen. *Strobus*	ovulate cone scales	very rare
12		*Pinus* sp. 1	seeds	rare
13		*Pinus* sp. 2	seeds	very rare
14		*Pinus* sp.	underdeveloped seeds	common
15		*Pinus* sp. 1	pollen cones	common
16		*Pinus* sp. 2	pollen cones	rare
17		*Pinus* sp.	bud scales	dominant
18		gen. et sp. indet.	coalified woods	very rare
19	fam. indet.	gen. et sp. indet.	leafy shoots	very rare
20		gen. et sp. indet.	long shoots	very rare
21		gen. et sp. indet., diverse	needles	very rare
22		gen. et sp. indet. type 1	ovulate cone scales	very rare
23		gen. et sp. indet. type 2	ovulate cone scales	very rare
Angiospermae				
24	Lauraceae	*Daphnogene polymorpha*	leaves	common
25		?*Lindera ovata*	leaves	very rare
26		?Lauraceae gen. et sp. indet.	leaves	very rare
27	Altingiaceae	*Liquidambar europaea*	leaves/ infructescences	common
28	Fabaceae	*Leguminosites* sp. 1	leaflets	very rare
29		*Leguminosites* sp. 2	leaflets	very rare
30		*Podocarpium podocarpum*	leaflets/fruits	common
31		*Mimosites* sp.	leaflets	rare
32	Rosaceae	gen. et sp. indet. type 1	leaflets	very rare
33	Ulmaceae	*Ulmus* cf. *plurinervia*	leaves	rare
34		*Ulmus* sp.	fruits	very rare
35		?*Zelkova zelkovifolia*	leaves	very rare
36	Fagaceae	*Quercus pseudocastanea*	leaves	abundant
37		*Quercus kubinyii*	leaves	common
38		*Quercus mediterranea*	leaves	very rare
39		*Fagus gussonii*	leaves	rare
40	Myricaceae	*Myrica lignitum*	leaves	dominant
41		*Myrica ceriferiformis*	fruits/infructescences	abundant
42		*Myrica* cf. *goeppertii*	catkins	dominant
43	Juglandaceae	*Carya* sp.	leaflets	common
44		*Pterocarya* sp.	fruits	very rare
45		gen. et sp. indet.	leaflets	very rare
46	Betulaceae	cf. *Ostrya* sp.	leaves	very rare
47	Salicaceae	*Salix* sp.	leaves	very rare
48		*Populus latior*	leaves	rare
49		*Populus* sp.	leaves	very rare
50	Sapindaceae	*Acer tricuspidatum*	leaves	rare
51		*Acer integrilobum*	leaves	very rare
52		?*Acer aegopodifolium*	leaflets	very rare
53		*Acer* sp. 1	fruits	very rare
54		*Acer* sp. 2	fruits	very rare

Table 1. Continued

Nr.	Family	Taxon	Plant part/organ	Frequency*
55	fam. indet.	*Monocotylophyllum* sp. 1	leaves	rare
56		*Monocotylophyllum* sp. 2	leaves	rare
57		*Monocotylophyllum* sp. 3	leaves	very rare
58		*Monocotylophyllum* sp. 4	leaves	very rare
59		*Monocotylophyllum* sp. 5	leaves	very rare
60		*Dicotylophyllum* sp. 1	leaves	very rare
61		*Dicotylophyllum* sp. 2	leaves	very rare
62		*Dicotylophyllum* sp. 3	leaves/leaflets	very rare
63		*Dicotylophyllum* sp. 4	leaves/leaflets	very rare
64		*Dicotylophyllum* sp. 5	leaves	very rare
65		*Dicotylophyllum* sp. 6	leaves/leaflets	very rare
66		*Dicotylophyllum* sp. 7	leaves	very rare
67		*Dicotylophyllum* sp. 8	leaves/leaflets	very rare
68		*Dicotylophyllum* sp. 9	leaves	very rare
69		*Dicotylophyllum* sp. 10	leaves	very rare
70		*Dicotylophyllum* sp. 11	leaves	very rare
71		*Dicotylophyllum* sp. 12	leaves	very rare
72		*Dicotylophyllum* sp. 13	leaves	very rare
73		gen. et sp. indet.	inflorescences	very rare
74		gen. et sp. indet. type 1	bud scales	rare
75		gen. et sp. indet. type 2	bud scales	very rare
76		gen. et sp. indet. type 3	bud scales	very rare
77		gen. et sp. indet., diverse	defoliated long shoots of woody dicots/ wood fragments (inorganic)	dominant
78		gen. et sp. indet.	?rhizoms	very rare
79		gen. et sp. indet., diverse	roots	rare

* very rare ≤9, rare 10–29, common 30–99, abundant 100–299, dominant ≥300

associated in swamp habitats with several broad-leaved deciduous arboreal elements such as *Liquidambar europaea, Acer tricuspidatum*, *Alnus* and *Nyssa*, and possibly Palmae. Modern swamp forests of southeastern North America can serve as the modern equivalent to the expected setting in the Pitisidia region during the Tortonian.

The wet alluvial forest in better-drained areas and along the canals probably included *Carya*, polars (*Populus latior*, *Populus* sp.), *Salix*, *Ulmus*, *Alnus*, *Liquidambar europaea* and *Daphnogene polymorpha* (UV4). The occurrence of *M. lignitum* in the understory is likely, whereas ferns such as "*Pteris*" *oeningensis* and monocots would be expected as herb layer components.

Based on the abundance of individual taxa in the assemblage, the long-needled *Pinus pitsidiensis* was probably widespread in the lowlands, forming coastline woodlands potentially associated with *M. lignitum.* Both represent likely elements of early successional stages. The pine forests along the coastal flatlands in southeastern North America serve as a modern analogue, where *P. palustris* forests are widely distributed and *M. cerifera* is one of the understory species (Miyawaki et al., 1994). Due to parautochthonous deposition, we cannot exclude the possibility that *P. pitsidiensis* thrived on sites with higher soil fertility and moisture close to the wetland, like extant *Pinus elliottii* Engelmann in Everglades pinelands.

Farther from the deposition area, in the adjacent surroundings, well-drained lowland forests probably comprised deciduous and to a lesser extent broad-leaved evergreen taxa (VU5). *Quercus pseudocastanea* and *Quercus kubinyii* in the macrorecord, and Fagaceae in the microflora, are well represented. *Daphnogene polymorpha* may have been common. Different maples, *Carya* sp., *Tetraclinis* cf. *salicornioides* and several other taxa better captured in the palynological record of Kastellios Hill (*Engelhardia*, *Juglans*, *Ostrya* and other Betulaceae) complement the composition of this zonal vegetation as accessory elements.

Upland forests may have included a *Fagus* mesic forest (VU6). A number of conifers represented in the microflora, mostly *Cedrus*, *Tsuga*, *Picea* and *Abies*, along with some broad-leaved deciduous trees such as maples and Betulaceae, may have contributed to these upland forests or formed pure conifer forests.

The ecological signal of several identified taxa in the macrorecord is difficult to assess. The degree to which some of them (e.g., *Dicotylophyllum* sp. 2, 7, 8 and 10, several Fabaceae, *Quercus mediterranea*, two- and five-needled *Pinus*) represent "sclerophyllous" components remains open (Denk, 2016; Denk, et al. 2017). For instance, modern Fabaceae occur in a wide range of environments and not only in dry areas. The occurrence of sclerophyllous woodlands in lowland areas with less favorable conditions for plants (shallow and relatively dry soils, south-exposed slopes) may be assumed in the surroundings of Pitsidia.

Ephedra and *Artemisia*, along with Amarathaceae/Chenopodiaceae and Asteraceae pollen, indicate more open habitats (VU0). Taxa with possibly wide ecological ranges such as *Zelkova*, *Ostrya*, Palmae and Fabaceae are expected in such open landscapes.

Integrated Plant Record (IPR) Vegetation Analysis (Kovar-Eder and Kvaček, 2007; Kovar-Eder et al., 2008; Teodoridis et al., 2011) was applied to the flora of Pitsidia (Tab. 2, Appx. 5a). This semiquantitaive method serves to determine major zonal vegetation types based on assignment of the taxa to a suite of defined components reflecting the leaf physiognomy and autecology of the taxa. The major vegetation types are defined by the proportions of key components (i.e. zonal taxa). For the palaeoflora of Pitsidia, this approach yielded a subhumid sclerophyllous forest (ShSF) as the most likely zonal vegetation type.

KASSANOI

The palaeoflora of Kassanoi includes 23 taxa of angiosperms based almost exclusively on leaf remains (Tab. 3). Arboreal elements – trees and shrubs – prevail, while herbs (monocots and *Decodon gibbosus*) are less frequent. Deciduous woody elements comprise about three fifths of the dicot spectrum. *Daphnogene polymorpha*, *Podocarpium podocarpum*, *Myrica lignitum,* ?*Salix* and *Dicotylophyllum* sp. 15 are the dominant ones. In this flora, not a single pine remain has been reported and other conifers are scarce, among them a few leafy twigs of *Tetraclinis* cf. *salicornioides*. *Quercus* and *Acer*, two of the most common genera in the Cretan late Miocene, are represented in Kassanoi by only a few leaves of *Quercus* sp., while maples are entirely absent.

Based on the alternation of sandy and silty/clay beds and the presence of freshwater molluscs and in situ root remains, Kassanoi could reflect a fluvio-lacustrine environment. The plant material possibly accumulated at overbank, freshwater reservoirs with fluctuations in water flow that temporarily held rooted plants. The frequent occurrence of plant debris in bedding planes and the high fragmentation rate of the leaf material indicate higher water flow and that some time had passed before the plant material was finally embedded. Wind transport apparently played a minor role, because winged fruits and flower remains are scarce.

In Kassanoi the depositional setting agrees well with the autecology of the reported taxa. Most of them such as *Salix* cf. *angusta*, *Populus latior*, *Fraxinus*, *Daphnogene polymorpha* and *Myrica lignitum* likely belonged to moist broad-leaved gallery forests. This association corresponds to VU4 of Denk (2016). Apart from *M. lignitum* and possibly *Decodon gibbosus*, typical swamp elements are absent (VU3). *D. verticillatus*, which is considered the modern analogue of the latter, is an aquatic plant inhabiting stream shores and shallow water at the edges of lakes and swamps (Miyawaki et al., 1994). In the surroundings, outside the influence of flooding, a mixed broad-leaved forest probably developed, with deciduous and evergreen taxa such as deciduous oaks, *Podocarpium podocarpum*

Table 2. Results derived by IPR Vegetation Analysis (sensu Kovar-Eder et al., 2008; Teodoridis et al., 2011) for the studied fossil assemblages; regarding Metochia, the floristic elements reported by Mantzouka et al. (2015) are also taken into account

Locality	% of BLD	% of BLE	% of SCL + LEG	ZONAL PALM	% of DRY HERB	% of MESO HERB	% of zonal herbs of zonal taxa	Number of zonal taxa	Number of zonal woody angiosperms	Problematic taxa	Total number of taxa	Vegetation type sensu Teodoridis et al. (2011)
Pitsidia	61.40	12.40	26.20	0	0	1.26	1.26	39.72	36.22	0	52.97	**ShSF**
Kassanoi	50.00	29.63	20.37	0	0	3.33	3.33	15	13.5	0	23	**ShSF**
Metochia	58.62	18.97	20.69	1.72	0	0	0	32	29	0	38	**ShSF**

Table 3. Plant assemblage of Kassanoi, floristic composition

Nr.	Family	Taxon	Plant part/organ	Frequency*
Polypodiophyta				
1	fam. indet.	gen. et sp. indet. type 2	fronds	rare
Gymnospermae				
2	Cupressaceae	*Tetraclinis* cf. *salicornioides*	leafy twigs	rare
Angiospermae				
3	Lauraceae	*Daphnogene polymorpha*	leaves	abundant
4	Fabaceae	*Podocarpium podocarpum*	leaflets	abundant
5	Rosaceae	gen. et sp. indet. type 2	leaves	rare
6	Rhamnaceae	*Berchemia multinervis*	leaves	rare
7	Ulmaceae	*Ulmus* cf. *plurinervia*	leaves	common
8	Fagaceae	*Quercus* sp.	leaves	rare
9	Myricaceae	*Myrica lignitum*	leaves	abundant
10	Salicaceae	*Salix angusta*	leaves	rare
11		?*Salix* sp.	leaves	abundant
12		*Populus latior*	leaves	rare
13	Lythraceae	*Decodon gibbosus*	leaves	rare
14	Oleaceae	*Fraxinus* sp.	leaflets	rare
15	fam. indet.	*Monocotylophyllum* sp. 6	leaves	rare
16		*Monocotylophyllum* sp. 7	leaves	rare
17		*Monocotylophyllum* sp. 8	leaves	rare
18		*Dicotylophyllum* sp. 14	leaves	rare
19		*Dicotylophyllum* sp. 15	leaves	abundant
20		*Dicotylophyllum* sp. 16	leaves	rare
21		*Dicotylophyllum* sp. 17	leaves	common
22		*Dicotylophyllum* sp. 18	leaves	rare
23		*Dicotylophyllum* sp. 19	leaves	rare
24		*Antholithes* sp.	flowers	rare
25		gen. et sp. indet.	?fruits	rare

* rare 1–4, common 5–15, abundant ≥16

and *D. polymorpha*. *Berchemia multinervis* either represented a climber or was part of the understory. *Ulmus* cf. *plurinervia*, *Tetraclinis* cf. *salicornioides*, *Fraxinus*, Rosaceae and Salicaceae could also have been part of this association (VU5).

For Kassanoi the application of IPR Vegetation Analysis is hampered by the limited number of zonal taxa and the poor preservation of the leaf material, which makes it difficult to assign the components. The zonal vegetation type deduced by IPR Vegetation Analysis is subhumid sclerophyllous forest (ShSF) (Tab 2; Appx. 5b).

METOCHIA

For the palaeoflora of Metochia on Gavdos Island, eight further taxa were identified in this study, enriching the record reported by Mantzouka et al. (2015). (Tab. 4; Appx. 6). Among them are *Sabalites*, *Quercus mediterranea*, *Ziziphus paradisiaca* and a 5-needled pine.

The Metochia assemblage originated in a marine environment supplied by river flooding (Antonarakou, 2001; Tsaparas, 2005). The delta plain possibly was located in the southern parts of central and western Crete (e.g., Meulenkamp et al., 1988; Postma et al., 1993). The occurrence of fishes such as *Bregmaceros albyi* Sauvage and *Lepidopus* sp. in the plant-bearing layers indicates a maximum sea depth of 300 m (Gaudant et al., 2005; Tsaparas, 2005).

Similar to Pitsidia and Kassanoi, application of IPR Vegetation Analysis for the plant assemblage of Metochia indicates a subhumid sclerophyllous forest (ShSF) (Tab. 2; Appx. 5c). Due to differences in scoring some taxa such as *Daphnogene* and *Leguminosites* div. sp., our results stand in contrast to those of Mantzouka et al. (2015), who assumed transitional vegetation between broad-leaved deciduous (BLDF) and mixed mesophytic forests (MMF).

THE STUDIED FLORAS IN THE MIOCENE CONTEXT OF CRETE

Apart from the herein-described floras, two more macro-assemblages – Makrilia in the eastern part of the island (late Tortonian,

Table 4. Plant assemblage of Metochia, floristic elements identified in this study

Nr.	Family	Taxon	Plant part/organ	Frequency*
Gymnospermae				
1	Cupressaceae	*Tetraclinis* cf. *salicornioides*	leafy twigs	rare
2	Pinaceae	*Pinus* sp. 2, 5-needled, subgen. *Strobus*	needles	rare
Angiospermae				
3	Lauraceae	*Daphnogene polymorpha*	leaves	rare
4		?*Lindera ovata*	leaves	rare
5	Arecaceae	*Sabalites* sp.	leaves	rare
6	Fabaceae	?*Leguminosites* sp. 3	leaflets	rare
7	Rhamnaceae	*Ziziphus paradisiaca*	leaves	rare
8	Fagaceae	*Quercus mediterranea*	leaves	rare
9		*Fagus gussonii*	leaves	common
10	Myricaceae	*Myrica lignitum*	leaves	rare
11	Juglandaceae	*Engelhardia orsbergensis*	leaflets	rare
12	Salicaceae	*Populus latior*	leaves	rare
13	fam. indet.	*Monocotylophyllum* sp. 9	leaves	rare
14		*Monocotylophyllum* sp. 10	leaves	rare
15		*Dicotylophyllum* sp. 20	leaves	rare
16		*Dicotylophyllum* sp. 21	leaves	rare
17		gen. et sp. indet.	?fruits	rare

*rare 1–5, common ≥6

Sachse, 2004) and Vrysses in western Crete (Messinian, Zidianakis et al., 2007) – have been reported previously (Fig. 1). The Makrilia plant assemblage occurs in a silty layer a few meters thick, being part of alternating series of hemipelagic marls and sand turbiditic layers. In Vrysses the plant-bearing layers comprise marls and marly limestones deposited in a shallow semi-enclosed marine embayment. The present study revises the original floristic lists of these assemblages, taking into account the newly described findings (Velitzelos D. et al., 2014; Zidianakis et al., 2016; Zidianakis, 2018) and a re-examination of the available material (Appx. 7, 8).

Due to their spatial and temporal proximity, the Cretan palaeofloras (Makrilia, Vrysses, Metochia, Pitsidia, Kassanoi) are quite similar floristically. In most of them (except for Kassanoi), Pinaceae, Lauraceae, Fagaceae, Fabaceae, Juglandaceae, Salicaceae and Sapindaceae are well represented in terms of species diversity and abundance (Tab. 5). They share *Daphnogene polymorpha*, *Myrica lignitum*, *Quercus mediterranea*, two-needled *Pinus* (except for Kassanoi) and *Populus latior* (except for Makrilia).

The Makrilia and Metochia plant-bearing sediments were deposited in an open marine environment, Vrysses in a shallow semi-enclosed marine embayment, and Pitsidia and Kassanoi in freshwater reservoirs. For the taphocoenoses of Makrilia and Metochia a more regional character may be assumed; this is expressed by the higher diversity of taxa and smaller leaf size, especially in Makrilia. Pitsidia and Kassanoi seem to depict a more local origin which better expresses the adjacent habitats. In this context, the swampy and riparian elements are better represented in Pitsidia and Kassanoi than the other floras are. The occurrence of zonal broad-leaved taxa and especially beech is more distinct in Makrilia and Metochia, implying a stronger representation of taxa from the hinterland. In Pitsidia the dominant lobed oak *Quercus pseudocastanea*, which is entirely absent from the other assemblages, is likely related to its local occurrence in the surroundings of the deposition area. Alternatively, this oak may be azonal. Thermophilic elements (e.g. *Sabalites*, Lauraceae, *Asteroxylon*, *Engelhardia*) are more frequent in Makrilia and Metochia. This may be related to the higher floristic diversity of these sites or to a climatic shift towards warmer conditions. Contrary to the other floras, in Vrysses, *Tetraclinis* is represented by twig fragments of the type *T. brachyodon*, which may be considered more xerophytic than *T. salicornioides* occurring in the other floras. Apart from *T. brachyodon*, the dominance of several sclerophyllous elements in Vrysses (e.g. 2-needled pine, *Quercus metiderranea*, *Ziziphus paradisiaca*) is evident.

Table 5. Floristic comparison of the Cretan palaeofloras

Nr.	Taxon	Kassanoi	Pitsidia	Metochia	Makrilia	Vrysses
Algae						
1	Fam. et gen. et sp. indet. – thallus		+			
Polypodiophyta						
2	*Equisetum* sp.				+	
3	*“Pteris” oeningensis*		++			
4	Polypodiophyta fam. et gen. et sp. indet. – frond	+ (1 type)	+ (1 type)			
Gymnospermae						
5	*Tetraclinis salicornioides*	cf. +	cf. +	++	+	
7	*Tetraclinis brachyodon*					+
8	*Taxodium dubium*		++	+	+	
9	Cupressaceae gen. et sp. indet. – leafy shoot				+	
10	*Pinus pitsidiensis*		+++			+
11	*Pinus* sp. – 2-needled fascicles		+	+	+	+++
12	*Pinus* sp. – 5-needled fascicles		+	+	+	
13	*Cathaya* vel *Keleteria* vel *Cedrus* sp. – cone scale				cf.+	
14	Pinaceae gen. et sp. indet. (not *Pinus*) – seed				+	
Angiospermae						
15	*Daphnogene polymorpha*	+++	++	++	+	+
16	*Laurophyllum* sp.			+++	+ (4 types)	
17	*Lindera ovata*		?+	?++		
18	*Sassafras* sp. – folia			?+		
19	Lauraceae gen. et sp. indet.		?+			
20	*Cymodocea* vel *Posidonia* sp. – rhizome				++	
21	*Ruppia* sp. – seed				cf.+	
22	*Smilax* cf. *petiolata*				+	
23	*Sabalites* sp.			+		
24	*Berberis* vel *Mahonia*				cf.+	
25	*Mahonia* sp.				+	
26	*Buxus pliocenica*				+	+
25	*Buxus* cf. *egeriana*				+	
27	*Liquidambar europaea*		++		+	
28	*Ampelopsis* vel *Vitis* sp. – seed				cf.+	
29	*Podocarpium podocarpum*	+++	++		++	
30	*Mimosites* sp.		+		?+	
31	*Leguminosites* sp.		+ (2 types)	+ (?5 types)	+ (?7 types)	+ (2 types)
32	*Leguminosites* sp. – seed				cf.+	
33	*Leguminocarpon* sp.			+ (1 type)	+ (1 type)	
34	Rosaceae gen. et sp. indet. type 1 – folia		+			
35	Rosaceae gen. et sp. indet. type 2 – folia	+				+
36	*“Parrotia” pristina*					?+
37	*Berchemia multinervis*	+				
38	*Paliurus tiliifolius*			+		
39	*Ziziphus paradisiaca*			+	+	++
40	*Ulmus* cf. *plurinervia*	++	+	+	+	
41	*Ulmus* sp. – fructus		+		+	
42	*Zelkova zelkovifolia*		?+		+	
43	*Quercus pseudocastanea*		+++			
44	*Quercus kubinyii*		++		?+	
45	*Quercus mediterranea*		+	+	++	+++
46	*Quercus* sp. deciduous – folia	+				
47	*Quercus* sp. evergreen – folia					+
48	*Quercus* sp. – fructus				+	
49	*Fagus gussonii*		+	+++	+++	
50	*Myrica lignitum*	+++	+++	+++	++	+
51	*Juglans acuminata*					?+
52	*Carya serrifolia*				+	
53	*Carya* sp. – folia		++			

Table 5. Continued

Nr.	Taxon	Kassanoi	Pitsidia	Metochia	Makrilia	Vrysses
54	*Pterocarya* sp. – fructus		+			
55	*Engelhardia orsbergensis*			++	++	
56	*Juglans* vel *Carya* sp. – fructus				+	
57	Juglandaceae gen. et sp. indet. – folia		+			
58	*Alnus gaudinii*				cf.+	
59	*Carpinus* sp. – folia			?+	++	
60	*Carpinus* type *orientalis* – fructus				+	
61	*Betula* sp.			+		
62	*Ostrya* sp. – folia		cf.+			
63	*Salix angusta*	+		cf. +++		
64	*Salix* type *purpurea*				?+	
65	*Salix* sp. – folia	?+++	+ (1 type)		++ (1 type)	?+ (1 type)
66	*Populus latior*	+	+	+		+
67	*Populus* sp. – folia		+			
68	*Populus* sp. – fructus				+	
69	*Decodon gibbosus*	+				
70	*Sapindus graecus*			+		
71	*Acer tricuspidatum*		+			
72	*Acer integrilobum* and/or *A. pseudomonspessulanum*		+		+++	+++
73	*Acer aegopodifolium*		?+			
74	*Acer* cf. *integerrimum*				+	+
75	*Acer angustilobum*			+	+	
76	*Acer* sp. – fructus		+ (2 types)		+ (3 types)	
77	*Toddalia* sp. – seed				cf.+	
78	*Ailanthus pythii*			+		
79	*Aquilaria* sp. – folia				+	
80	*Tilia* sp. – bracts				cf.+	
81	*Symplocos* cf. *minutula*				?+	
82	*Fraxinus* sp. – folia	+				
83	*Fraxinus* sp. – fructus				+	
84	*Asterocalyx styriacus*				+	
85	*Monocotylophyllum* sp.	+ (3 types)	+ (5 types)	+ (>2 types)	+ +	++ (2 types)
86	*Dicotylophyllum* sp.	+++ (6 types)	+ (13 types)	+ (8 types)	+ (20 types)	+ (12 types)
87	*Carpolithus* sp.				+ (3 types)	
88	*Antholithes* sp.	+ (1 type)				

THE FLORAS OF PITISIDIA, KASSANOI AND METOCHIA IN THE CONTEXT OF VEGETATION DEVELOPMENT IN EUROPE

During the Neogene, North Mediterranean plant ecosystems underwent considerable changes. Humid and thermophilous taxa successively became extinct, and more open landscapes frequently replaced dense forest vegetation. Although typical Mediterranean sclerophyllous plants such as *Olea*, *Ceratonia*, *Phillyrea* and *Quercus ilex*-type have been documented in the pollen record since the early Miocene, modern-type sclerophyllous Mediterranean ecosystems probably did not develop prior to the beginning of the late Pliocene (Suc et al., 2018). Studies focused on vegetation in South and Southeast Europe show a progressive reduction in thermophilous plants and those with high water requirements during the Miocene, and an increase in (warm-) temperate deciduous and seasonally adapted taxa during the late Miocene and Pliocene (Bertini, 2003; Kovar-Eder et al., 2006; Jiménez-Moreno et al., 2007; Utescher et al., 2007; Ivanov et al., 2011; Suc et al., 2018). Reconstructions based on macrofloras generally indicate forest vegetation in the northern Mediterranean realm for the Tortonian. Palynological records, however, point to more open, sclerophyllous woodlands, especially in northern Spain and central Anatolia (Bertini, 2003; Suc et al., 2018). A more or less drought-adapted vegetation is inferred for the southern part of the Balkan Peninsula (Kovar-Eder et al., 2006; Utescher et al., 2007). Climate reconstructions for European low latitudes show conditions too dry for fully humid vegetation, indicating open woodlands (François et al., 2011). Large-mammal data support the presence of open landscape in South Europe since the early late Miocene (Agustí et al., 1999; Fortelius et al., 2006). Note, however, that Denk et al. (2018) reconstructed the vegetation in the Eastern Mediterranean, including Pitsidia, Metochia, Makrilia and Vrysses floras, pointing to mesic forests for the late Miocene. According to Denk et al. (2018) the only exceptions were two pollen floras from the Serres Basin in northern Greece, where, along with a mesic forest, a steppe forest with Pinaceae probably existed.

According to Kovar-Eder et al. (2008), in the time interval around 12–8.5 Ma, the Central European vegetation was characterised by broad-leaved deciduous forests (BLDF) which had replaced early Miocene evergreen forests (BLEF) and mixed mesophytic forests (MMF) as well as Middle Miocene subhumid sclerophyllous forests (ShSF) (Kovar-Eder and Teodoridis, 2018). In the late Miocene and early Pliocene, warmth- and humidity-requiring forests (BLEF and MMF) were still present in some refugia such as the northern Balkan and Italian peninsulas. At the same time, the first records of xeric grasslands were recognised near the northern margin of the Black Sea region (Kovar-Eder et al., 2008). Subhumid sclerophyllous forests (ShSF) were largely restricted to southern parts of Europe. The assignment of Pitsidia, Metochia and Kassanoi to subhumid sclerophyllous forests (ShSF) and the high percentages of the sclerophyllous and legume-like component agree with and confirm the occurrence of this vegetation type in these southern parts of Europe at that time (Tab. 2).

From the Messinian to the middle Zanclean, open woodlands gradually appeared in the central and southern parts of the Italian and Greek peninsulas (Kovar-Eder et al., 2008). IPR Vegetation Analysis of the Messinian floras of Vrysses in Crete and of Vegora in northern Greece resulted in ShSF as the most likely zonal vegetation type. Here the sclerophyllous and legume-like component accounts for 34% and 26% at the two sites, respectively (Kovar-Eder et al., 2008; Mantzouka et al., 2015).

CLIMATE PROXIES

We applied the Coexistence Approach (CA) for the palaeofloras from Pitsidia and Metochia, and the Climate Leaf Analysis Multivariate Program (CLAMP) for Pitsidia. The results of CLAMP for Metochia in Mantzouka et al. (2015) are also taken into consideration. Because of its low diversity, Kassanoi is considered inappropriate for application because the precision of climatic calculations is strongly related to the diversity of taxa (Mosbrugger and Utescher, 1997; Wolfe and Spicer, 1999).

The Coexistence Approach estimates quantitative climatic data from fossil floras using the climate tolerance of the nearest living

Table 6. **a**. Estimated ranges of 7 palaeoclimatic parameters for Pitsidia and Metochia assessed by the Coexistence Approach (CA): MAT (mean annual temperature), CMT (coldest month mean temperature), WMT (warmest month mean temperature), MAP (mean annual precipitation), MPwet (mean precipitation of the wettest month), MPdry (mean precipitation of the driest month), MPwarm (mean precipitation of the warmest month); **b**. Estimated ranges for 5 palaeoclimatic parameters for Pitsidia and Metochia assessed by CLAMP (physiognomic and gridded meteorological calibration datasets from 189 sites); MAT (mean annual temperature), WMT (warmest month mean temperature), CMT (coldest month mean temperature), 3-WET (precipitation during 3 consecutive wettest months), 3-DRY (precipitation during 3 consecutive driest months)

a	Locality	MATmin	MATmax	CMTmin	CMTmax	WMTmin	WMTmax	MAPmin	MAPmax	MPwet min	MPwet max	MPdry min	MPdry max	MPwarm min	MPwarm max
This study	Pitsidia	13.5	18.5	2.5	7.7	23.3	28.1	897	1613	167	195	20	64	78	80
	Metochia	13.8	18.5	3.1	9.4	22.8	26.4	843	1741	170	195	17	70	73	80
Mantzouka et al., 2015	Pitsidia	13.5	19.7	2.5	9.4	19.6	27.5	897	1333	160	191	8	56	84	100
	Metochia	13.8	18.5	3.1	9.4	22.5	26.4	843	1741	170	195	17	70	73	80

b	Locality	MAT (°C)	CMT (°C)	WMT (°C)	3-WET (mm)	3-DRY (mm)
This study	Pitsidia	14.7	4.0	25.9	643	227
Mantzouka et al., 2015	Metochia	15.2	7.5	24.9	736	185

relatives (Mosbrugger and Utescher, 1997; Utescher et al., 2014). The results indicate a warm temperate to subtropical climate for Pitsidia, with mean annual temperature (MAT) between 13.5°C and 18.5°C, warmest month mean temperature (WMT) between 23.3°C and 28.1°C, coldest month mean temperature (CMT) >2.5°C and mean annual precipitation (MAP) of 897–1613 mm (Tab. 6a; Appx. 9a). This climatic analysis implies weak dry-season conditions [mean precipitation of the driest month (MPdry) of 20–64 mm] that may not have coincided with the warmest period of the year, as illustrated by the mean precipitation of the warmest month (MPwarm) of 78–80 mm. CA results for Metochia indicate climatic conditions very close to those of Pitsidia (Tab. 6a; Appx. 9b). The CA results for Pitsidia and Metochia differ only slightly from those derived by Mantzouka et al. (2015), although the floristic spectrum has been enriched considerably by our study.

CLAMP is based on a multivariate statistical technique to quantitatively determine palaeoclimatic parameters, using the leaf physiognomy of woody dicots (Wolfe and Spicer, 1999; Spicer et al., 2009). The application of CLAMP provides estimations for three temperature (MAT, CMT, WMT) and two precipitation variables (3-WET: precipitation during the 3 consecutive wettest months; 3-DRY: precipitation during the 3 consecutive driest months). In both palaeofloras, Pitsidia and Metochia, the estimated CLAMP temperature values fall into the ranges suggested by CA (Tab. 6b; Appx. 10). Regarding precipitation, CLAMP and CA reconstruct different parameters not allowing direct comparison. Similar to the CA results, CLAMP values indicate seasonality in precipitation, somewhat more pronounced in Metochia.

In the Messara Basin, climatic data derived from shallow-water coral carpets dated as early Tortonian suggest surface sea temperatures above 18°C (Brachert et al., 2006). Based on stable isotope records of $\delta^{18}O$ and $\delta^{13}C$ in coral skeletons, annual seasonality and interannual fluctuations in sea surface temperature at a time-scale of 2 to 5 years are well expressed. Based on the analysis of non-lattice-bound element concentrations within the coral skeletons (Mertz-Klaus et al., 2009), strong seasonality in precipitation has been proposed, with higher values in the winter.

In a wider climatic context, the mean $\delta^{18}O$ values from planktonic foraminifera increased gently through the late Miocene until the Pliocene, indicating cooling related to the onset of Arctic glaciation, although several short-time warming events took place (Thiede et al., 1998; Zachos et al., 2001; Winkler et al., 2002; Lear et al., 2003). Climate data for western Eurasia derived from fossil floras and faunas mostly correlated well with the marine records (e.g. Böhme, 2003; Mosbrugger et al., 2005; Bruch et al., 2007; Fauquette et al., 2007; Jiménez-Moreno, Suc, 2007). According to these data, a general cooling trend took place from the middle to late Miocene in Europe, characterised by a weak increase in both latitudinal and seasonal differentiation for temperature parameters and to a lesser degree in the latitudinal precipitation gradient (Mosbrugger et al., 2005; Bruch et al., 2006, 2007, 2011; Utescher et al., 2011). A warm and humid climate within a Cfa-type climate sensu Köppen-Geiger is documented during the Tortonian, with high latitudes being significantly warmer than today, while the low latitudes ranged at about the same level. Suc et al. (2018) argue that the climatic pattern indicates a north–south climatic gradient during the Tortonian, with increasing temperature and decreasing precipitation.

Using CA, Bruch et al. (2006) estimated MAT of ~14–18°C, mean temperature of the warmest month (WMT) of 24–27°C, and mean temperature of the coldest month (CMT) of 2–9°C in the Tortonian for Central and South Europe, with warmer values at lower latitudes. The temperature parameters we calculated for Pitsidia and Metochia are consistent with these data.

The precipitation rate in western Eurasia was generally higher during the Tortonian than today, and slightly wetter as compared to the Messinian and the Serravallian (Mosbrugger et al., 2005; Bruch et al., 2006, 2011). MAP mostly exceeded 1000 mm, and according to Mosbrugger et al. (2005) this value did not change drastically until the Pliocene. Bruch et al. (2006, 2011) reconstructed MAP for Central and South Europe in the range ~750–1400 mm, representing humid conditions. Spatial differentiation is mostly expressed by lower precipitation in the south, especially in southern Greece. The calculated values of MAP coexistence intervals from Pitsidia and Metochia fall into the range estimated by Bruch et al. (2006, 2011).

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Appendix 1. Simplified geological map of Crete and Gavdos Islands, showing the localities referred to in the text (modified from Krijgsman et al., 1994)

Appendix 2. Pitsidia, collection numbers for defoliated long shoots and wood fragments

Fragments of defoliated long shoots

Material: Nrs 31.4.2.812aopi; 31.4.2.812opii; 31.4.2.819ai,bi; 31.4.2.835; 31.4.2.847; 31.4.2.927; 31.4.2.940; 31.4.2.952; 31.4.2.1042; 31.4.2.1097; 31.4.2.1098; 31.4.2.1119; 31.4.2.1163,1158a,b; 31.4.2.1182aii; 31.4.2.1187; 31.4.2.1193ii; 31.4.2.1202,1185op; 31.4.2.1246; 31.4.2.1297; 31.4.2.1301ii; 31.4.2.1476; 31.4.2.1479; 31.4.2.1501a,b; 31.4.2.1510; 31.4.2.1516; 31.4.2.1637,1635aiii; 31.4.2.1648opi; 31.4.2.1708,1698; 31.4.2.1725; 31.4.2.1729ii; 31.4.2.1751i; 31.4.2.1751op; 31.4.2.1782; 31.4.2.1792; 31.4.2.1804; 31.4.2.1806; 31.4.2.1839,1807; 31.4.2.1871a,b; 31.4.2.1881; 31.4.2.1924; 31.4.2.1928ii; 31.4.2.2017i; 31.4.2.2084; 31.4.2.2098; 31.4.2.2169; 31.4.2.2180; 31.4.2.2185ii; 31.4.2.2188; 31.4.2.2199; 31.4.2.2215; 31.4.2.2270; 31.4.2.2283i; 31.4.2.2333; 31.4.2.2395; 31.4.2.2451; 31.4.2.2489bop; 31.4.2.2500; 31.4.2.2535; 31.4.2.2567; 31.4.2.2575; 31.4.2.2593; 31.4.2.2618ai,bi; 31.4.2.2632i; 31.4.2.2658a,b; 31.4.2.2666; 31.4.2.2702; 31.4.2.2712a,b; 31.4.2.2778; 31.4.2.2792; 31.4.2.2816; 31.4.2.2856; 31.4.2.2862; 31.4.2.2865; 31.4.2.2943iii; 31.4.2.2972i; 31.4.2.2989; 31.4.2.3004i; 31.4.2.3022; 31.4.2.3030aopii; 31.4.2.3035ii; 31.4.2.3039; 31.4.2.3063aop; 31.4.2.3065bii; 31.4.2.3066a,b; 31.4.2.3067bii; 31.4.2.3070; 31.4.2.3104op; 31.4.2.3109; 31.4.2.3112; 31.4.2.3115ai; 31.4.2.3128ai,bi; 31.4.2.3139ai,bi; 31.4.2.3139aii; 31.4.2.3139aiii; 31.4.2.3146bii; 31.4.2.3150bopii; 31.4.2.3161; 31.4.2.3162; 31.4.2.3163aii; 31.4.2.3168; 31.4.2.3169a,b; 31.4.2.3169a,bii; 31.4.2.3174ii; 31.4.2.3198iii; 31.4.2.3216; 31.4.2.3219; 31.4.2.3238i; 31.4.2.3238iil 31.4.2.3238iii; 31.4.2.3247ii; 31.4.2.3295; 31.4.2.3306opi; 31.4.2.3338i; 31.4.2.3345iii; 31.4.2.3401; 31.4.2.3449a,b; 31.4.2.3452v; 31.4.2.3458a,bi; 31.4.2.3461; 31.4.2.3483; 31.4.2.3484; 31.4.2.3496aopii; 31.4.2.3500op; 31.4.2.3504ii; 31.4.2.3526a,b; 31.4.2.3533ii; 31.4.2.3539; 31.4.2.3543bopv; 31.4.2.3543bopvi; 31.4.2.3560op; 31.4.2.3573ai,b; 31.4.2.3581; 31.4.2.3584a,b; 31.4.2.3590aii; 31.4.2.3602; 31.4.2.3613; 31.4.2.3621bii; 31.4.2.3622; 31.4.2.3625; 31.4.2.3627bop; 31.4.2.3627c; 31.4.2.3629i; 31.4.2.3633; 31.4.2.3635ii; 31.4.2.3645; 31.4.2.3658; 31.4.2.3673; 31.4.2.3682; 31.4.2.3684; 31.4.2.3701iii; 31.4.2.3706opii; 31.4.2.3707aii,bii; 31.4.2.3710ai,bi; 31.4.2.3716ii; 31.4.2.3732aii,bii; 31.4.2.3736aiii; 31.4.2.3740b; 31.4.2.3741aii,biv; 31.4.2.3744bopii; 31.4.2.3744bopiii; 31.4.2.3750,3748aop; 31.4.2.3751; 31.4.2.3753; 31.4.2.3765a,b; 31.4.2.3769; 31.4.2.3772i; 31.4.2.3774; 31.4.2.3776; 31.4.2.3780; 31.4.2.3781ii; 31.4.2.3797; 31.4.2.3806aopii; 31.4.2.3810i; 31.4.2.3811opiii; 31.4.2.3819; 31.4.2.3822; 31.4.2.3843; 31.4.2.3847i; 31.4.2.3854; 31.4.2.3855; 31.4.2.3863i; 31.4.2.3863ii; 31.4.2.3893; 31.4.2.3894a,b; 31.4.2.3897; 31.4.2.3904aii,bii; 31.4.2.3914iii; 31.4.2.3917ii; 31.4.2.3924i; 31.4.2.3924ii; 31.4.2.3953a,b; 31.4.2.3984i; 31.4.2.3989; 31.4.2.3994ii; 31.4.2.3997aopi; 31.4.2.4003i; 31.4.2.4004i; 31.4.2.4012a,b; 31.4.2.4021i; 31.4.2.4030i; 31.4.2.4031i; 31.4.2.4044iii; 31.4.2.4051ii; 31.4.2.4053; 31.4.2.4063aii,bii; 31.4.2.4068i; 31.4.2.4083bopii; 31.4.2.4115; 31.4.2.4116; 31.4.2.4125; 31.4.2.4169; 31.4.2.4170; 31.4.2.4221; 31.4.2.4235i; 31.4.2.4240ii; 31.4.2.4240iii; 31.4.2.4241; 31.4.2.4256ii; 31.4.2.4262; 31.4.2.4263ii; 31.4.2.4269; 31.4.2.4276; 31.4.2.4281; 31.4.2.4309ii; 31.4.2.4339bii; 31.4.2.4347aii,bii; 31.4.2.4357; 31.4.2.4393bii; 31.4.2.4411iii; 31.4.2.4418; 31.4.2.4421bii; 31.4.2.4433aii; 31.4.2.4434; 31.4.2.4440; 31.4.2.4469a,b; 31.4.2.4499ii; 31.4.2.4500i; 31.4.2.4501; 31.4.2.4538aiv; 31.4.2.4539aopii; 31.4.2.4562aii,bii; 31.4.2.4572ii; 31.4.2.4575; 31.4.2.4581i; 31.4.2.4602i; 31.4.2.4606av,bv; 31.4.2.4610; 31.4.2.4614; 31.4.2.4616; 31.4.2.4641ai; 31.4.2.4696aiii,biii; 31.4.2.4739ai,bi; 31.4.2.4754; 31.4.2.4758a,b; 31.4.2.4771; 31.4.2.4779a,b; 31.4.2.4827ii; 31.4.2.4851ai,bi; 31.4.2.4874; 31.4.2.4958; 31.4.2.4978a,b; 31.4.2.4981aiii; 31.4.2.4984; 31.4.2.4986; 31.4.2.5005; 31.4.2.5013; 31.4.2.5066op; 31.4.2.5093; 31.4.2.5094a,b; 31.4.2.5097opii; 31.4.2.5138; 31.4.2.5200; 31.4.2.5231op; 31.4.2.5233ii; 31.4.2.5264; 31.4.2.5292; 31.4.2.5293; 31.4.2.5358biii; 31.4.2.5361aii; 31.4.2.5361b; 31.4.2.5362ai; 31.4.2.5373a,b; 31.4.2.5404; 31.4.2.5466aopi; 31.4.2.5466aopii; 31.4.2.5468; 31.4.2.5496ii; 31.4.2.5514; 31.4.2.5575; 31.4.2.5599; 31.4.2.5607; 31.4.2.5635; 31.4.2.5643i; 31.4.2.5649a,b; 31.4.2.5657; 31.4.2.5676opii; 31.4.2.5703ii; 31.4.2.5720; 31.4.2.5725; 31.4.2.5730; 31.4.2.5765; 31.4.2.5768i; 31.4.2.5770; 31.4.2.5806bopi; 31.4.2.5815aopi,5824; 31.4.2.5831; 31.4.2.5884aii,bii; 31.4.2.5890av,bv; 31.4.2.5928ai,bi; 31.4.2.5935aiii; 31.4.2.5962i; 31.4.2.5966; 31.4.2.5974ii; 31.4.2.5985; 31.4.2.6067aii; 31.4.2.6067aiv;

Appendix 2. Continued

31.4.2.6068opi; 31.4.2.6185ai,bi; 31.4.2.6186i; 31.4.2.6186ii; 31.4.2.6189aii; 31.4.2.6203; 31.4.2.6232op; 31.4.2.6271; 31.4.2.6276i; 31.4.2.6277aii; 31.4.2.6277aiii; 31.4.2.6278i; 31.4.2.6283opi; 31.4.2.6287; 31.4.2.6290; 31.4.2.6308; 31.4.2.6325aiii; 31.4.2.6326; 31.4.2.6345iii; 31.4.2.6369; 31.4.2.6378; 31.4.2.6389a,b; 31.4.2.6447ii; 31.4.2.6473i; 31.4.2.6479opi; 31.4.2.6513; 31.4.2.6516; 31.4.2.6532ii; 31.4.2.6556aop; 31.4.2.6562,6556aop; 31.4.2.6567opi; 31.4.2.6584; 31.4.2.6589; 31.4.2.6593; 31.4.2.6605; 31.4.2.6626op; 31.4.2.6669; 31.4.2.6679; 31.4.2.6706i; 31.4.2.6706ii; 31.4.2.6723; 31.4.2.6729; 31.4.2.6731; 31.4.2.6765op; 31.4.2.6772op; 31.4.2.6780op; 31.4.2.6834; 31.4.2.6834op; 31.4.2.6835; 31.4.2.6836; 31.4.2.6837; 31.4.2.6850; 31.4.2.6856; 31.4.2.6869op; 31.4.2.6899,6866aop; 31.4.2.6948aiv; 31.4.2.6951aop; 31.4.2.2842a,b; 31.4.2.8019; 31.4.2.8033; 31.4.2.8056; 31.4.2.8057; 31.4.2.8061,8079; 31.4.2.8062,8063i; 31.4.2.8072; 31.4.2.8075; 31.4.2.8076; 31.4.2.8077,8058; 31.4.2.8083; 31.4.2.8166a,b; 31.4.2.8167iii.

Wood fragments

Material: Nrs 31.4.2.818bii; 31.4.2.1056; 31.4.2.1058ii; 31.4.2.1080a,b; 31.4.2.1269op; 31.4.2.1270; 31.4.2.1290ii; 31.4.2.1311ii; 31.4.2.1341ii; 31.4.2.1356; 31.4.2.1361ii; 31.4.2.1590; 31.4.2.1591vi; 31.4.2.1835; 31.4.2.1917v; 31.4.2.1917vi; 31.4.2.1950; 31.4.2.1951; 31.4.2.2000aii,bii; 31.4.2.2020i; 31.4.2.2037; 31.4.2.2078i; 31.4.2.2194; 31.4.2.2255; 31.4.2.2321; 31.4.2.2331; 31.4.2.2376; 31.4.2.2393; 31.4.2.2554ii; 31.4.2.2629; 31.4.2.2631i; 31.4.2.2632ii; 31.4.2.2638; 31.4.2.2661i; 31.4.2.2674; 31.4.2.2706a,b; 31.4.2.2734; 31.4.2.2739aop; 31.4.2.2793; 31.4.2.2797; 31.4.2.2823,2824; 31.4.2.2882; 31.4.2.2894; 31.4.2.2898; 31.4.2.2923; 31.4.2.2932; 31.4.2.2970; 31.4.2.3005; 31.4.2.3007; 31.4.2.3076; 31.4.2.3077aop; 31.4.2.3315op; 31.4.2.3382; 31.4.2.3413; 31.4.2.3414; 31.4.2.4256opiv; 31.4.2.4584aiii,biii; 31.4.2.4682ii; 31.4.2.4688; 31.4.2.4697ai,bi; 31.4.2.4700cii; 31.4.2.4703ii; 31.4.2.4718; 31.4.2.4762a,b; 31.4.2.4825ii; 31.4.2.4834ai,b; 31.4.2.4853ii; 31.4.2.4869a,bi; 31.4.2.4871; 31.4.2.4882aii,bii; 31.4.2.4883; 31.4.2.4885a,b; 31.4.2.4899; 31.4.2.4911; 31.4.2.4916ii; 31.4.2.4954; 31.4.2.4968; 31.4.2.4980bopii; 31.4.2.4994ii,4985op; 31.4.2.5197; 31.4.2.5219ai,bi; 31.4.2.5243; 31.4.2.5421; 31.4.2.5466aopviii; 31.4.2.5511aii,bii; 31.4.2.5523; 31.4.2.5527; 31.4.2.5613; 31.4.2.5767; 31.4.2.5785aviii,bvii; 31.4.2.5815aiii; 31.4.2.5815aopiii; 31.4.2.5840; 31.4.2.5898ii; 31.4.2.5915; 31.4.2.5936; 31.4.2.5937; 31.4.2.5947op; 31.4.2.5948opii; 31.4.2.5959; 31.4.2.5978aop; 31.4.2.5981opiii; 31.4.2.5998ii; 31.4.2.6125ii; 31.4.2.6171iii; 31.4.2.6191aiii; 31.4.2.6216aopii; 31.4.2.6274; 31.4.2.6305i; 31.4.2.6357opiv; 31.4.2.6364ii; 31.4.2.6441op; 31.4.2.6442; 31.4.2.6446; 31.4.2.6449a,b; 31.4.2.6457; 31.4.2.6478aiv; 31.4.2.6479opii; 31.4.2.6493aopii; 31.4.2.6512; 31.4.2.6520ii; 31.4.2.6521; 31.4.2.6586; 31.4.2.6707iii; 31.4.2.6721; 31.4.2.6833a,b; 31.4.2.6839; 31.4.2.6893; 31.4.2.6990; 31.4.2.7025; 31.4.2.8224opiii; 31.4.2.8224opiv; 31.4.2.8230op.

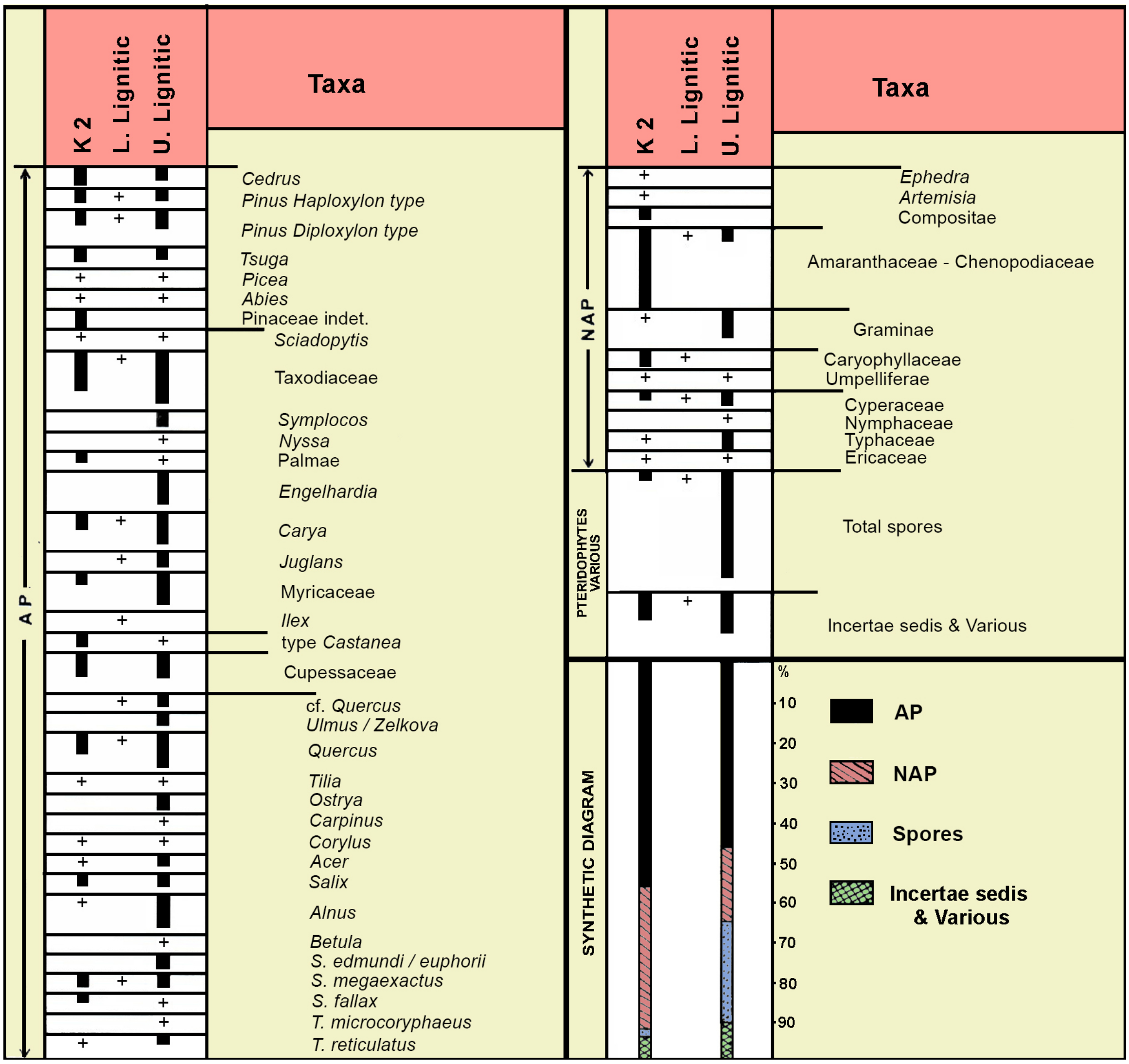
Appendix 3. Growth form, ecological preferences, vegetation units sensu Denk (2016) and modern morphologically analoguous allies for the floristic elements described from Kassanoi, Pitsidia, Metochia and Kastellios Hill

Taxon	Growth form	Ecology	Vegetation units (sensu Denk, 2016)	Modern morphologically analogue allies
Pitsidia – Kassanoi – Metochia (macro) floristic elements				
"Pteris" oeningensis	Fern	Indifferent		Polypodiophyta
Tetraclinis cf. *salicornioides*	Shrub$_{gym}$	Well-drained lowland and upland forests or scrubs	VU5, VU6	*Tetraclinis articulata*
Taxodium dubium	Tree$_{gym}$	Swamp	VU3	*Taxodium* spp.
Pinus pitsidiensis	Tree$_{gym}$	Indifferent		*Pinus canariensis*, *P. roxburghii*, *P. kesiya*
Pinus sp., 2-needled	Tree$_{gym}$	Indifferent		*Pinus* subgen. *Pinus*
Pinus spp., 5-needled	Tree$_{gym}$	Indifferent		*Pinus* subgen. *Strobus*
Daphnogene polymorpha	Tree$_{ang}$	Riparian, well-drained lowland forest	VU4, VU5	*Cinnamomum camphora*
?*Lindera ovata*	Tree$_{ang}$	Well-drained lowland and upland forests	VU5, VU6	Lauraceae
?Lauraceae, gen. et sp. indet.	Tree$_{ang}$	Well-drained lowland and upland forests	VU5, VU6	Lauraceae
Sabalites sp.	Tree, shrub$_{ang}$	Swamp, well-drained lowland forest	VU0, VU3, VU5	Coryphoideae
Monocotylophyllum spp.	Herb	Indifferent		
Liquidambar europaea	Tree$_{ang}$	Swamp, riparian, well-drained lowland forest	VU3, VU4, VU5	*Liquidambar styraciflua*, *L. orientalis*
Leguminosites spp.	Tree$_{ang}$	Indifferent		Fabaceae
Podocarpium podocarpum	Tree$_{ang}$	Well-drained lowland and upland forests	VU5, VU6	Detarieae-Ampherstieae complex of Caesalpinioideae
Mimosites sp.	Tree, shrub$_{ang}$	Step-like midowes	VU0	Mimosoideae
Rosaceae, gen. et sp. indet.	Tree, shrub$_{ang}$	well-drained lowland and upland forests	VU5, VU6	Rosaceae
Berchemia multinervis	Climbing, shrub$_{ang}$	Well-drained lowland forest	VU5	*Berhemia scandens*, *B. lineata*, *B. pauciflora*, *B. racemosa*
Ziziphus paradisiaca	Tree, shrub$_{ang}$	Well-drained lowland and upland forests or scrubs	VU5, VU6	Rhamnaceae
Ulmus cf. *plurinervia*	Tree$_{ang}$	well-drained lowland forest	VU5	*Ulmus* spp.
Ulmus sp.	Tree$_{ang}$	Riparian, well-drained lowland forest	VU4, VU5	*Ulmus* spp.
?*Zelkova zelkovifolia*	Tree, shrub$_{ang}$	well-drained lowland forest	VU0, VU5	*Zelkova* spp.
Quercus pseudocastanea	Tree$_{ang}$	Well-drained lowland forest	VU5	*Quercus* section *Quercus* group *petraea*
Quercus kubinyii	Tree$_{ang}$	Well-drained lowland forest	VU5	*Quercus* section *Cerris*
Quercus mediterranea	Tree$_{ang}$	Well-drained lowland and upland forests	VU5, VU6	*Quercus* section *Cerris* group *Ilex*
Quercus sp.	Tree$_{ang}$	Indifferent		*Quercus* spp.
Fagus gussonii	Tree$_{ang}$	Well-drained lowland and upland forests	VU 5, VU6	*Fagus sylvatica*
Myrica lignitum	Shrub$_{ang}$	Swamp, riparian	VU3, VU4	*M. cerifera, M. pensylvanica*, *M. heterophylla*
Carya sp.	Tree$_{ang}$	Riparian, well-drained lowland forest	VU4, VU5	*Carya* spp.
Pterocarya sp.	Tree$_{ang}$	Well-drained lowland forest	VU5	*Pterocarya* spp.
Engelhardia orsbergensis	Tree$_{ang}$	Well-drained lowland forest	VU5	*Engelhardia roxburghiana*, *Oreomunnea mexicana*
Juglandaceae, gen. et sp. indet.	Tree$_{ang}$	Indifferent		Juglandaceae
cf. *Ostrya* sp.	Tree$_{ang}$	Well-drained lowland forest	VU0, VU5	*Ostrya*
Salix angusta	Tree, shrub$_{ang}$	Riparian, well-drained lowland forest	VU4, VU5	*Salix viminalis* L.
Salix spp.	Tree, shrub$_{ang}$	Riparian, well-drained lowland forest	VU4, VU5	*Salix* spp.
Populus latior	Tree$_{ang}$	Riparian, well-drained lowland forest	VU4, VU5	*Populus alba*
Populus sp.	Tree$_{ang}$	Riparian, well-drained lowland forest	VU4, VU5	*Populus* spp.
Decodon gibbosus	Shrub$_{ang}$	Aquatic, swamp	VU1, VU3	*Decodon verticillatus*
Acer tricuspidatum	Tree$_{ang}$	Swamp, well-drained lowland and upland forests	VU3, VU5, VU6	*Acer* section *Rubra*

Appendix 3. Continued

Taxon	Growth form	Ecology	Vegetation units (sensu Denk, 2016)	Modern morphologically analogue allies
Acer integrilobum	$Tree_{ang}$	Well-drained lowland and upland forests	VU5, VU6	*Acer* section *Palmata*
?*Acer aegopodifolium*	$Tree_{ang}$	Well-drained lowland and upland forests	VU5, VU6	*Acer* section *Trifolia*
Fraxinus sp.	$Tree_{ang}$	Riparian, well-drained lowland forest	VU4, VU5	*Fraxinus* spp.
Kastellios Hill (diaspores) floristic elements				
Cedrus	$Tree_{gym}$	Well-drained lowland and upland forests	VU7	
Pinus Haploxylon type	$Tree_{gym}$	Indifferent		
Pinus Diploxylon type	$Tree_{gym}$	Indifferent		
Tsuga	$Tree_{gym}$	Well-drained lowland and upland forests	VU7	
Picea	$Tree_{gym}$	Well-drained lowland and upland forests	VU7	
Abies	$Tree_{gym}$	Well-drained lowland and upland forests	VU7	
Pinaceae gen. at sp. indet.	$Tree_{gym}$	Indifferent		
Sciadopytis	$Tree_{gym}$	Well-drained lowland and upland forests	VU7	
Taxodiaceae	$Tree_{gym}$	Swamp	VU3	
Cupressaceae	$Tree_{gym}$, $shrub_{gym}$	Well-drained lowland and upland forests	VU5, VU6	
Symplocos	$Shrub_{ang}$	Swamp, riparian, well-drained low-land and upland forests	VU3–VU6	
Nyssa	$Tree_{ang}$	Swamp, well-drained lowland forest	VU3, VU5	
Palmae	$Tree_{ang}$, $shrub_{ang}$	Swamp, well-drained lowland forest	VU0, VU3, VU5	
Engelhardia	$Tree_{ang}$	Well-drained lowland forest	VU5	
Carya	$Tree_{ang}$	Riparian, well-drained lowland forest	U4, VU5	
Juglans	$Tree_{ang}$	Well-drained lowland forest	VU5	
Myricaceae	$Tree_{ang}$, $shrub_{ang}$	Swamp, riparian, well-drained low-land forest	VU3, VU4, VU5	
Ilex	$Tree_{ang}$, $shrub_{ang}$	Well-drained lowland and upland forests	VU5, VU6	
Castanea type	$Tree_{ang}$	Well-drained lowland forest	VU5	
cf. *Quercus*	$Tree_{ang}$	Indifferent		
Ulmus/Zelkova	$Tree_{ang}$	Swamp, riparian, well-drained low-land forest	VU0, VU3, VU4, VU5	
Quercus	$Tree_{ang}$	Indifferent		
Tilia	$Tree_{ang}$	Well-drained lowland forest	VU5	
Ostrya	$Tree_{ang}$	Well-drained lowland forest	VU0, VU5	
Carpinus	$Tree_{ang}$	well-drained lowland forest	VU5	
Corylus	$Tree_{ang}$, $shrub_{ang}$	Well-drained lowland and upland forests	VU5, VU6	
Acer	$Tree_{ang}$	Indifferent		
Salix	$Tree_{ang}$, $shrub_{ang}$	Riparian, well-drained lowland forest	U4, VU5	
Alnus	$Tree_{ang}$, $shrub_{ang}$	Swamp, riparian	VU3, VU4	
Betula	$Tree_{ang}$	Well-drained lowland and upland forests	VU5, VU6	
Ephedra	$shrub_{ang}$	Open, light forest	VU0	
Artemisia	Herb dry	Open, dry meadows	VU0	
Asteraceae	Herb	Wet and dry meadows	VU0, VU2	
Amaranthaceae/ Chenopodiaceae	Herb dry	Open, dry meadows, salty soils	VU0	
Poaceae	Herb	Indifferent		
Caryophyllaceae/ Apiaceae	Herb	Indifferent		
Cyperaceae	Herb wet	Bogs, wet meadows	VU2	
Nymphaceae	Aquatic herb	Aquatic	VU1	
Typhaceae	Herb wet	Bogs, wet meadows	VU2	
Ericaceae	Herb, shrub	Indifferent		

Appendix 4. Pollen diagram from Kastellios Hill in Messara Basin, Crete; sediment layers: K2, upper lignitic clay and lower lignite clay (modified from Sen et al., 1986).



Appendix 5. IPR Vegetation Analysis, scoring sheets for a. Pitisidia, b. Kassanoi and c. Metochia

a. Pitsidia (Messara)	ZONAL								AZONAL			PROBLEMATIC taxa
Taxa	CONIFER	BLD	BLE	SCL	LEG	ZON PALM	ARB FERN	DRY HERB	MESO HERB	AZONAL WOODY	AZNW	AQUATIC	
Thallus												1.00	
“*Pteris*” *oeningensis*									0.50		0.50		
Tetraclinis cf. *salicornioides*	1.00												
Taxodium dubium										1.00			
Pinus pitsidiensis										1.00			
Pinus sp. 1, subgen, *Pinus*, 2-needled	1.00												
Pinus sp. 2. subgen. *Strobus*, 5-needled	1.00												
Pinus sp. fascicle bracts													
ovulate cone scales subgen. *Pinus*													
ovulate cone scales subgen. *Strobus*													
Pinus seeds 2 types													
Pinus pollen cones 2 types													
Pinus bud scales													
Daphnogene polymorpha			0.50							0.50			
?*Lindera ovata*		1.00											
?Lauraceae			1.00										
Liqudambar europaea		0.50								0.50			
Leguminosites sp. 1					1.00								
Leguminosites sp. 2					1.00								
Podocarpium podocarpum					1.00								
Mimosites sp.					1.00								
Rosaceae type 1		1.00											
Ulmus cf. *plurinervia*		0.75		0.25									
Ulmus sp.		0.50		0.25						0.25			
?*Zelkova zelkovifolia*		0.50		0.50									
Quercus pseudocastanea		1.00											
Quercus kubinyii		0.50		0.50									
Quercus mediterranea			0.50	0.50									
Fagus gussonii		1.00											
Myrica lignitum										1.00			
Myrica ceriferiformis													
Myrica cf. *goeppertii*													
Carya sp.		0.50								0.50			
Pterocarya sp.		1.00											
Juglandaceae		1.00											
cf. *Ostrya* sp.		1.00											
Salix sp.		0.50								0.50			
Populus latior		0.50								0.50			
Populus sp		0.50								0.50			
Acer tricuspidatum		0.50								0.50			
Acer integrilobum		1.00											
?*Acer aegopodifolium*		1.00											
Monocotylophyllum sp. 1–5											5.00		
Dicotylophyllum sp. 1		0.33	0.33	0.33									
Dicotylophyllum sp. 2				1.00									
Dicotylophyllum sp. 3		1.00											
Dicotylophyllum sp. 4		1.00											
Dicotylophyllum sp. 5		0.33	0.33	0.33									
Dicotylophyllum sp. 6			1.00										
Dicotylophyllum sp. 7			0.50	0.50									
Dicotylophyllum sp. 8		0.50		0.50									
Dicotylophyllum sp. 9		1.00											
Dicotylophyllum sp. 10		0.50		0.50									

Appendix 5. Continued

a. Pitsidia (Messara)	ZONAL									AZONAL			PROBLEMATIC taxa
Taxa	CONIFER	BLD	BLE	SCL	LEG	ZON PALM	ARB FERN	DRY HERB	MESO HERB	AZONAL WOODY	AZNW	AQUATIC	
Dicotylophyllum sp. 11		0.33	0.33	0.33									
Dicotylophyllum sp. 12		1.00											
Dicotylophyllum sp. 13		1.00											
Sum of taxa (51)	3.00	22.24	4.49	5.49	4.00	0.00	0.00	0.00	0.50	6.75	5.50	1.00	0.00
Percentage of zonal taxa	7.55	55.99	11.30	13.82	10.07	0.00	0.00	0.00	1.26				
percentage of zonal woody angiosperms		61.40	12.40	15.16	11.04	0.00							

Sum of % SCL+ LEG	26.20
Sum of % DRY HERB + MESO HERB (ZONAL HERB)	1.26

b. Kassanoi (Messara)	ZONAL									AZONAL			PROBLEMATIC taxa
Taxa	CONIFER	BLD	BLE	SCL	LEG	ZON PALM	ARB FERN	DRY HERB	MESO HERB	AZONAL WOODY	AZNW	AQUATIC	
Polypodiophyta									0,50		0.50		
Tetraclinis cf. *salicornioides*	1.00												
Daphnogene polymorpha			0.50							0.50			
Podocarpium podocarpum					1.00								
Rosaceae type 2		1.00											
Berchemia multnervis		0.50		0.50									
Ulmus cf. *plurinervia*		0.75		0.25									
Quercus sp.		1.00											
Myrica lignitum										1.00			
Salix angusta		0.50								0.50			
?*Salix* sp.		0.50								0.50			
Populus latior		0.50								0.50			
Decodon gibbosus										0.50		0.50	
Fraxinus sp.		0.50								0.50			
Monocotylophyllum sp. 6–8											3.00		
Dicotylophyllum sp. 14			1.00										
Dicotylophyllum sp. 15			1.00										
Dicotylophyllum sp. 16		0.50	0.50										
Dicotylophyllum sp. 17		0.50	0.50										
Dicotylophyllum sp. 18		0.50	0.50										
Dicotylophyllum sp. 19				1.00									
Sum of taxa (23)	1.00	6.75	4.00	1.75	1.00	0.00	0.00	0.00	0.50	4.00	3.50	0.50	0.00
Percentage of zonal taxa	6.67	45.00	26.67	11.67	6.67	0.00	0.00	0.00	3.33				
percentage of zonal woody angiosperms		50.00	29.63	12.96	7.41	0.00							

Sum of % SCL+ LEG	20.37
Sum of % DRY HERB + MESO HERB (ZONAL HERB)	3.33

Appendix 5. Continued

c. Metochia (Gavdos)	ZONAL									AZONAL			PROBLEMATIC taxa
Taxa	CONIFER	BLD	BLE	SCL	LEG	ZON PALM	ARB FERN	DRY HERB	MESO HERB	AZONAL WOODY	AZNW	AQUATIC	
Tetraclinis salicornioides	1.00												
Taxodium dubium										1.00			
Pinus sp. 1, subgen, *Pinus*, 2-needled	1.00												
Pinus sp. 2. subgen. *Strobus*, 5-needled (in this study)	1.00												
Daphnogene sp.			0.50							0.50			
Laurophyllum sp.			1.00										
?*Lindera ovata*		1.00											
?*Sassafras* sp.		1.00											
Sabalites sp (in this study)						0.50				0.50			
Leguminosites sp. 1/ *Leguminocarpon* sp.					1.00								
Leguminosites sp. 2		0.50			0.50								
Leguminosites sp. 3		0.50			0.50								
Leguminosites sp. 4		0.50			0.50								
?*Leguminosites* sp. 3 (in this study)					1.00								
Paliurus tiliifolius		0.50		0.50									
Ziziphus paradisiaca (in this study)		0.50		0.50									
Ulmus ?*plurinervia*		0.75		0.25									
Quercus mediterranea (in this study)			0.50	0.50									
Fagus gussonii		1.00											
Myrica lignitum										1.00			
Engelhardia orsbergensis		0.50	0.50										
Betula sp.		1.00											
?*Carpinus*		1.00											
Salix cf. *angusta*		0.50								0.50			
Populus latior		0.50								0.50			
Sapindus graecus		1.00											
Acer angustilobum		1.00											
Ailanthus pythii		1.00											
Monocotyledonae indet.											1.00		
Monocotylophyllum sp. 10 (in this study)											1.00		
Dicotylophyllum sp. 1		1.00											
Dicotylophyllum sp. 2		1.00											
Dicotylophyllum sp. 3		0.50	0.50										
Dicotylophyllum sp. 4		0.50	0.50										
Dicotylophyllum sp. 5		1.00											
Dicotylophyllum sp. 6			1.00										
Dicotylophyllum sp. 20 (in this study)			1.00										
Dicotylophyllum sp. 21 (in this study)		0.50		0.50									
Sum of taxa (38)	3.00	17.00	5.50	2.50	3.50	0.50	0.00	0.00	0.00	4.00	2.00	0.00	0.00
Percentage of zonal taxa	9.38	53.13	17.19	7.81	10.94	1.56	0.00	0.00	0.00				
percentage of zonal woody angiosperms		58.62	18.97	8.62	12.07	1.72							

Sum of % SCL+ LEG	20.69
Sum of % DRY HERB + MESO HERB (ZONAL HERB)	0.00

Appendix 6. Metochia palaeoflora (Mantzouka et al., 2015), amended floristic list including the herein-described findings

Nr	Family	Taxon	Remarks	Plant part/organ	Samples
Gymnospermae					
1	Cupressaceae	*Tetraclinis salicornioides*		leafy twig/ segments	1/2 +1 in this study
2		*Taxodium dubium*		foliage shoots	2
3	Pinaceae	*Pinus* sp., 2-needled		needle fragments	4
4		*Pinus* sp., 5-needled	in this study	needle fragment	1
Angiospermae					
5	Lauraceae	*Daphnogene polymorpha*		leaves	7 +1 in this study
6		*Laurophyllum* sp.		leaves	11
7		?*Lindera ovata*		leaves	6 +2 in this study
8		?*Sassafras* sp.		leaves	2
9	Arecaceae	*Sabalites* sp.	in this study	leaf	1
10	Fabaceae	*Leguminosites* spp. (5 different types)	(one newly reported taxon) in this study	leaflets	9 +2 in this study
11		*Leguminocarpon* sp.		pod	1
12	Rhamnaceae	*Paliurus tiliifolius* (Unger) Bůžek		leaf	1
13		*Ziziphus paradisiaca*	in this study	leaves	3
14	Ulmaceae	*Ulmus* ?*plurinervia*		leaf	1
15	Fagaceae	*Quercus mediterranea*	in this study	leaves	2
16		*Fagus gussonii*		leaves	7 +14 in this study
17	Myricaceae	*Myrica lignitum*		leaves	8 +2 in this study
18	Juglandaceae	*Engelhardia orsbergensis*		leaflets	4 +2 in this study
19	Betulaceae	*Betula* sp.		leaves	2
20		?*Carpinus* sp.		leaf	1
21	Salicaceae	*Salix* cf. *angusta*		leaves	9
22		*Populus latior*		leaf	1 +1 in this study
23	Sapindaceae	*Sapindus graecus* Unger		leaflets	3
24		*Acer angustilobum* Heer		leaf	1
25	Simaroubaceae	*Ailanthus pythii* (Unger) Kovar-Eder et Kvaček		leaflet	1
26	fam. indet. Monocotyledonae	gen. et sp. indet.		leaves	5
27	fam. indet. Monocotyledonae	*Monocotyllophyllum* sp. (2 different types)	in this study	leaves	3
28	fam. indet. Dicotyledonae	*Dicotylophyllum* spp. (8 different types)	(two newly reported taxa) in this study	leaves/leaflets	9 +4 in this study

Appendix 7. Makrilia palaeoflora (Sachse, 2004), amended floristic list including the newly described findings in Velitzelos D. et al. (2014) and Zidianakis (2018). Velitzelos D. et al. (2014) reported frond fragments of *Sabal* sp. (Arecaceae) from the Makrilia area. The location of the outcrop and its stratigraphic position have not been published yet

Nr.	Family	Taxon (Sachse, 2004)	Remarks for revised or further taxa		Plant part/organ	Samples
			Original identification in Sachse (2004)	Reference for revision		
Polipodiophyta						
1	Equisetaceae	*Equisetum* sp.			stem	1
Gymnospermae						
2	Cupressaceae	*Tetraclinis salicornioides*			leafy twigs, segments, cone	2/2/1
3		*Taxodium dubium*			leafy shoot	1
4		gen. et sp. indet.	Zidianakis, 2018		leafy shoot	1
5	Pinaceae	cf. *Cathaya* vel *Keleteria* vel *Cedrus* sp.			cone scale	1
6		gen. et sp. indet. (not *Pinus*)	Zidianakis, 2018		winged seed	1
7		*Pinus* cf. *hepios* (Unger) Heer			2-needled dwarf shoot	1
8		*Pinus* cf. *hampeana* (Unger) Heer			2-needled dwarf shoot with short needles	1
9		*Pinus* sp. 5-needled			dwarf shoot	1
10		*Pinus* sp.			needle fragments	5
Angiospermae						
11	Magnoliaceae	?*Magnolia* sp.	problematic record		leaf	1
12		?*Illicum rhenanum* Kräusel et Weyland	problematic record		leaf	1
13	Lauraceae	*Daphnogene polymorpha*	*Cinnamomophyllum* sp.	Velitzelos D. et al., (2014) and in this study	leaves	2
14		*Laurophyllum* spp. (4 different types)			leaves	10
15		*Cinnamomophyllum polymorphum* (A. Braun) Heer	problematic record		leaf	1
16	Potamogetonaceae s.l.	*Cymodocea* vel *Posidonia* sp.			rhizomes, eaves	5
17	Ruppiaceae	cf. *Ruppia* sp.			seed	1
18	Smilacaceae	*Smilax* cf. *petiolata* (Weber) Weyland			leaves	2
19	Berberidaceae	cf. *Berberis* vel *Mahonia*	*Dicotylophyllum* type 9	Velitzelos D. et al., (2014) listed this element as cf. *Berberis*	leaflets	2
20		*Mahonia* sp.	Zidianakis, 2018		leaflet	1
21	Buxaceae	*Buxus* cf. *egeriana* Kvaček, Bůžek et Holý			leaves	2
22		*Buxus pliocenica* Saporta et Marion			leaves	3
23	Altingiaceae	*Liquidambar* sp.	Zidianakis, 2018		infructescence	1
24	Vitaceae	cf. *Ampelopsis* vel *Vitis* sp.			seed	1
25	Fabaceae	*Leguminosites* spp. (7 different types)			leaflets/leaf	14/1
26		*Podocarpium podocarpum*			leaflets	4
27		?*Mimosites* sp.			leaflet, leaf frag.	1/1
28		?Leguminosae gen. et sp. indet. (heterogenous leaflets)			leaflets	10
29		cf. *Leguminosites* sp.			seed	1
30		*Leguminocarpon* sp.	Zidianakis, 2018		fruit	1
31		?*Cladastris* sp.	problematic record		leaflet, leaf frag.	1/1
32		?*Machaerium* spp. (2 different types)	problematic record		leaflets	2
33		?*Swartzia* sp.	problematic record		leaflet	1
34	Rhamnaceae	*Ziziphus paradisiaca*	*Dicotylophyllum* type. 3	Zidianakis, 2018	leaves	3
35	Ulmaceae	cf. *Ulmus plurinervia*			leaf	3
36		*Ulmus* sp.			fruit	1
37		*Zelkova zelkovifolia*			leaf, twig with 3 leaves	1/1

Appendix 7. Continued

Nr.	Family	Taxon (Sachse, 2004)	Remarks for revised or further taxa		Plant part/organ	Samples
			Original identification in Sachse (2004)	Reference for revision		
38	Fagaceae	*Fagus gussonii*	*Fagus* type *gussonii* and *Fagus* type *attenuata*	Denk et al., 2004; Velitzelos et al., 2014; Mantzouka et al., 2015 and in this study	leaves	13
39		?*Quercus kubinyii*			leaf	1
40		*Quercus mediterranea*			leaves	4
41		*Quercus* sp.			acorn	1
42		cf. *Quercus rhenana* (Kräusel et Weyland) Knobloch et Kvaček	problematic record		leaf	1
43	Myricaceae	*Myrica lignitum*	*Myrica* sp. type *M.* cf. *lignitum*	Velitzelos D. et al., 2014 and in this study	leaves	8
44	Juglandaceae	*Engelhardia orsbergensis*	cf. *Engelhardia orsbergensis*	Mantzouka et al., 2015 and in this study	leaflets	6
45		*Engelhardia macroptera* (Brongniart) Unger	cf. *Palaeocarya macroptera*	Velitzelos D. et al., 2014 and in this study	samara	1
46		*Carya serrifolia* (Goeppert) Kräusel	Velitzelos D. et al., 2014		leaf	1
47		*Juglans* vel *Carya* sp.			fruit	1
48	Betulaceae	cf. *Alnus gaudinii* (Heer) Knobloch et Kvažek			leaf	1
49		*Carpinus* sp.			leaves	8
50		*Carpinus* type *orientalis*			fruits	2
51	Salicaceae	?*Salix* type *purpurea*			leaf	1
52		*Salix* type 1			leaves	7
53		*Populus* sp.			fruit	1
54	cf. Myrtaceae	gen. et sp. indet.	problematic record		leaves	3
55	Anacardiaceae	?type *Pistacia lentiscus*	problematic record		leaflets	2
56	Sapindaceae	?*Acer* sp. (5-lobed)	Velitzelos et al. (2014) listed as *Acer integerrimum*		leaves	2
57		*Acer integrilobum* and/or *A. pseudomonspessulanum* Unger	*Acer* ser. *Monspessulana*	in this study	leaves	14
58		*Acer angustilobum* Heer	cf. *Ampelopsis* vel *Vitis* sp.	Mantzouka et al., 2015	leaf	1
59		*Acer* ?*integerrimum* (Viviani) Massalongo	Zidianakis, 2018		leaf	1
60		*Acer* spp. (3 different types)			samaras	3
61	Rutaceae	cf. *Toddalia* sp.			seed	1
62	Thymelaeaceae	*Aquilaria* sp.			leaf	1
63	Tiliaceae	cf. *Tilia* sp.			bracts	2
64	Symplocaceae	?*Symplocos* cf. *minutula* (Sternberg) Kirchheimer			seed	1
65	Oleaceae	*Fraxinus* sp.			fruit	1
66	Aquifoliaceae	?*Ilex* type *aquifolium*	problematic record		leaf	1
67	Caprifoliaceae	?*Lonicera* type *etrusca*	problematic record		leaf	1
68	---	*Monocotylophyllum* spp.		leaf fragments	leaves	numerous
69	---	*Asterocalyx styriacus* Ettingshausen	as Blütenreste	Kovar-Eder et al., 2004	flower	1
70	---	*Dicotylophyllum* spp. (20 different types, we exclude *D.* type 3 as cf. *Ziziphus paradisiaca* and *D.* type 9 as Berberidaceae)			leaves/leaflets	38
71	---	*Carpolithus* spp. (3 different types)			fruits/seeds	4

Appendix 8. Vrysses palaeoflora (Zidianakis et al., 2007), amended floristic list taking into account the newly described findings in Zidianakis et al. (2016) and unpublished data

Nr.	Family	Taxon (Zidianakis et al., 2007)	Remarks for revised or further taxa		Plant part/ organ	Samples
			Original identification in Zidianakis et al. (2007)	Reference for revision		
Gymnospermae						
1	Cupressaceae	*Tetraclinis brachyodon* (Brongniart) Mai et Walther	*Tetraclinis* sp.	in this study	leafy twigs	4
2	Pinaceae	*Pinus* sp. 2-needled			dwarf shoots/ needle fragments	17
3		*Pinus pitsidiensis*	Zidianakis et al., 2016		dwarf shoot	1
Angiospermae						
4	Lauraceae	*Daphnogene polymorpha*			leaves	2
5	Buxaceae	*Buxus pliocenica* Saporta et Marion			leaf	1
6	Fabaceae	gen. et sp. indet. (2 different types)			leaflets	2
7	Rosaceae	gen. et sp. indet.			leaves/leaflets	3
8	Ulmaceae	gen. et sp. indet.	problematic record		leaf	1
9	Hamamelidaceae	?*"Parrotia" pristina* (Ettingshausen) Stur			leaf	1
10	Rhamnaceae	*Ziziphus paradisiaca*	?*Ziziphus ziziphoides* (Unger) Weyland	in this study	leaves	8
11	Fagaceae	*Quercus mediterranea*			leaves	12
12		*Quercus* sp.			leaves	3
13	Myricaceae	*Myrica lignitum*	unpublished data		leaves	
14	Juglandaceae	?*Juglans acuminata A.* Braun ex Unger			leaflets	3
15	Salicaceae	?*Salix* sp.			leaf	1
16		*Populus latior*	*Populus tremula* foss.	in this study	leaves	2
17	Sapindaceae	*Acer integrilobum* and/or *A. pseudomonspessulanum* Unger	*A. pseudomonspessulanum* Unger	in this study	leaves	16
18		*Acer* cf. *integerrimum* (Viviani) Massalongo	*Acer* sp.	Velitzelos et al., 2014	leaves	5
19	---	*Monocotylophyllum* spp. (2 different types)			leaf fragments	18
20	---	*Dicotylophyllum* spp. (12 different types)			leaves	23

Appendix 9. Coexistence Approach, scoring sheets for a. Pitsidia and b. Metochia

a. Pitsidia (Messara)

Fossil taxon	Reference taxa	MATmin	MATmax	CMTmin	CMTmax	WMTmin	WMTmax	MAPmin	MAPmax	MPwet min	MPwet max	MPdry min	MPdry max	MPwarm min	MPwarm max
Polypodiophyta	Polypodiophyta	unspecific													
"Pteris" oeningensis	Polypodiophyta	unspecific													
Tetraclinis cf. *salicornioides*	*Tetraclinis articulata*	relict													
Taxodium dubium	*Taxodium* sp.	13.3	25	−0.1	19.8	18.9	31.2	290	2615	60	265	0	93	19	227
Pinus pitsidiensis	*Pinus* sp.	−9.2	25.5	−36.8	21.4	7.1	32.9	180	10798	28	2446	0	94	0	1100
Pinus 2-needled	*Pinus* sp.	−9.2	25.5	−36.8	21.4	7.1	32.9	180	10798	28	2446	0	94	0	1100
Pinus 5-needled	*Pinus* sp.	−9.2	25.5	−36.8	21.4	7.1	32.9	180	10798	28	2446	0	94	0	1100
Daphnogene polymorpha	*Cinnamomum camphora*	13.5	27.2	2.5	26.1	18.6	31.7	828	10798	160	2446	3	135	30	1100
?*Lindera ovata*	Lauraceae	4.4	28.1	−16.8	27	19.3	30.1	191	10798	56	2446	0	165	0	1100
?Lauraceae	Lauraceae	4.4	28.1	−16.8	27	19.3	30.1	191	10798	56	2446	0	165	0	1100
Liquidambar europaea	*Liquidambar styraciflua*, *L. orientalis*	12.5	21.3	−0.1	16.3	19.6	28.6	897	1613	106	265	2	93	84	195
Leguminosites sp. 1	Fabaceae	−7.7	27.7	−22.7	25.9	10.5	28.1	224	3905	46	610	0	196	1	221
Leguminosites sp. 2	Fabaceae	−7.7	27.7	−22.7	25.9	10.5	28.1	224	3905	46	610	0	196	1	221
Podocarpium podocarpum	Fabaceae	−7.7	27.7	−22.7	25.9	10.5	28.1	224	3905	46	610	0	196	1	221
Mimosites sp.	Fabaceae	−7.7	27.7	−22.7	25.9	10.5	28.1	224	3905	46	610	0	196	1	221
Rosaceae	Rosaceae	−15	27.7	−41	26.5	3.6	32.9	122	10798	22	2446	0	229	0	1100
Ulmus cf. *purinervia*	*Ulmus* sp.	−4.9	26.6	−25.8	26.1	16	29.4	201	3285	33	569	0	100	0	239
?*Zelkova zelkovaefolia*	*Zelkova* sp.	6.2	21.9	−12.8	13.6	19.4	29.7	246	2648	46	370	3	67	3	344
Quercus pseudocastanea	*Quercus* sp.	−1.4	27	−25.1	25.9	8.4	28.3	201	10798	33	2446	0	180	5	1100
Quercus kubinyii	*Quercus* sect. *Cerris*	4.7	22.2	−8.7	15.6	11.7	28.6	470	3000	48	2695	0	85	0	1781
Quercus mediterranea	*Quercus* sect. *Cerris*	4.7	22.2	−8.7	15.6	11.7	28.6	470	3000	48	2695	0	85	0	1781
Fagus gussonii	*Fagus* sp. (Europe)	5.9	19.7	−5	9.4	17.1	31.7	376	2115	46	195	5	94	5	195
Myrica lignitum	*Myrica* sp.	−8.9	28.1	−29	27	8.9	33.9	233	3151	34	508	0	165	0	221
Carya sp.	*Carya* sp.	4.4	21.3	−11.5	18.2	19.3	30.6	373	1724	68	434	8	93	45	258
Pterocarya sp.	*Pterocarya* sp.	3.9	24.2	−12.8	17	15.3	31.6	246	2648	46	424	1	64	2	424
Juglandaceae	Juglandaceae	0	27.5	−22.7	25	13.7	31.2	210	3172	44	582	1	152	2	189
cf. *Ostrya* sp.	*Ostrya*	2.5	21.9	−17.7	19.3	18.9	28.1	279	1355	74	237	0	72	0	228
Salix sp.	*Salix* sp.	−17	27.7	−50.1	26.5	7.6	32.9	122	2399	22	448	0	108	0	252
Populus latior	*Populus alba*	2.5	18.5	−14.6	12.5	17.9	26.4	419	1741	57	254	1	109	3	80
Populus sp.	*Populus* sp.	−16	26	−49	13.6	9.8	35.6	25	2559	8	358	0	93	0	224
Acer tricuspidatum	*Acer* sectio *Rubra*	3.4	23.9	−12.9	19.4	18.8	29.4	735	1613	102	241	20	94	49	177
Acer integrilobum	*Acer* sect. *Palmata*	6.2	24	−8.1	20.6	16.7	29.3	529	10798	116	2446	0	135	26	1100
?*Acer aegopodifolium*	*Acer* sectio *Trifolia*	3.3	18.5	−20.1	7.7	23.3	29.3	577	1724	167	358	4	64	78	258
Monocotylophyllum sp. 1–5	Monocotyledonae	unspecific													
Taxa with climatic data	30														
Coexistence intervals		13,5	18.5	2.5	7.7	23.3	28.1	897	1613	167	195	20	64	78	80
Coexisting taxa (%)			100		100		100		100		100		100		96.7

Appendix 9. Continued

b. Metochia (Gavdos)

Fossil taxon	Reference taxa	MATmin	MATmax	CMTmin	CMTmax	WMTmin	WMTmax	MAPmin	MAPmax	MPwet min	MPwet max	MPdry min	MPdry max	MPwarm min	MPwarm max
Tetraclinis cf. *salicornioides*	*Tetraclinis articulata*	relict													
Taxodium dubium	*Taxodium* sp.	13.3	25	−0.1	19.8	18.9	31.2	290	2615	60	265	0	93	19	227
Pinus 2-needled	*Pinus* sp.	−9.2	25.5	−36.8	21.4	7.1	32.9	180	10798	28	2446	0	94	0	1100
Pinus 5-needled	*Pinus* sp.	−9.2	25.5	−36.8	21.4	7.1	32.9	180	10798	28	2446	0	94	0	1100
Daphnogene sp.	Lauraceae	4.4	28.1	−16.8	27	19.3	30.1	191	10798	56	2446	0	165	0	1100
Laurophyllum sp.	Lauraceae	4.4	28.1	−16.8	27	19.3	30.1	191	10798	56	2446	0	165	0	1100
?*Lindera ovata*	Lauraceae	4.4	28.1	−16.8	27	19.3	30.1	191	10798	56	2446	0	165	0	1100
?*Sassafras* sp.	*Sassafras* sp.	6.5	22.8	−7.9	14.7	19.6	30.1	843	1864	71	295	17	93	64	195
Sabalites sp.	Arecaceae	13.3	27.7	−0.1	27	22.8	33.1	37	3151	8	389	0	165	0	225
Leguminosites spp. (5 types)	Fabaceae	−7.7	27.7	−22.7	25.9	10.5	28.1	224	3905	46	610	0	196	1	221
Paliurus tiliifolius	*Paliurus* sp.	10	23.1	−7.3	17	22.5	28.8	396	1958	68	448	2	70	2	431
Ziziphus paradisiaca	Rhamnaceae	1.6	27.7	−14.1	27	16.3	33.1	37	3151	8	389	0	165	0	221
Ulmus cf. *purinervia*	*Ulmus* sp.	−4.9	26.6	−25.8	26.1	16	29.4	201	3285	33	569	0	100	0	239
Quercus mediterranea	*Quercus* sect. *Cerris*	4.7	22.2	−8.7	15.6	11.7	28.6	470	3000	48	2695	0	85	0	1781
Fagus gussonii	*Fagus* sp. (Europe)	5.9	19.7	−5	9.4	17.1	31.7	376	2115	46	195	5	94	5	195
Myrica lignitum	*Myrica* sp.	−8.9	28.1	−29	27	8.9	33.9	233	3151	34	508	0	165	0	221
Engelhardia orsbergensis	*Engelhardia*, *Oreomunea*, *Alfaroa*	13.8	27.4	3.1	26.1	18.9	33.6	748	10798	170	2446	0	152	48	1100
Betula sp.	*Betula* sp.	−15	25.8	−41	21.1	1.3	28.7	110	10798	23	2446	0	135	2	1100
?*Carpinus* sp.	*Carpinus* sp.	0	25.8	−22.7	21.1	16.8	28.7	164	10798	20	2446	0	130	2	1100
Salix cf. *angusta*	*Salix* sp.	−17	27.7	−50.1	26.5	7.6	32.9	122	2399	22	448	0	108	0	252
Populus latior	*Populus alba*	2.5	18.5	−14.6	12.5	17.9	26.4	419	1741	57	254	1	109	3	80
Sapindus graecus	*Sapindus* sp.	10	27.7	−7.3	27	20.2	32.9	184	3151	22	389	2	165	20	304
Acer angustilobum	*Acer* sect. *Acer*	2.7	24	−15.6	20.6	16.2	28.6	115	2559	19	370	1	135	1	366
Ailanthus pythii	*Ailanthus* sp.	6.9	26.7	−8.1	25.3	18.3	28.9	376	3459	92	638	1	119	73	304
Monocotyledonae	Monocotyledonae	unspecific													
Taxa with climatic data	23														
Coexistence intervals		13,8	18.5	3.1	9.4	22.8	26.4	843	1741	170	195	17	70	73	80
Coexisting taxa (%)			100		100		100		100		100		100		95.7

Appendix 10. Percentages of foliar physiognomic characters derived by CLAMP for Pitsidia and Metochia

Foliar physiognomic character		Pitsidia (in this study)	Metochia (Mantzouka et al., 2015)
Margin character states	Lobed	6,757	7.69
	No teeth	45,946	59.62
	Teeth regular	35,811	21.15
	Teeth close	29,730	18.27
	Teeth round	24,324	20.15
	Teeth acute	28,378	23.08
	Teeth compound	0,000	7.69
Size character states	Nanophyll	0,000	0.00
	Leptophyll I	2,703	0.00
	Leptophyll II	14,405	0.00
	Microphyll I	25,189	0.00
	Microphyll II	38,676	41.62
	Microphyll III	12,108	29.42
	Mesophyll I	6,730	27.50
	Mesophyll II	0,000	1.27
	Mesophyll III	0,000	0.00
Apex character states	Apex emarginated	9,375	0.00
	Apex round	18,219	34.23
	Apex acute	61,969	55.96
	Apex attenuate	16,656	9.81
Base character states	Base cordate	10,000	1.92
	Base round	51,429	40.38
	Base acute	38,571	57.96
Length to width character states	L:W < 1:1	10,351	0.00
	L:W = 1–2:1	29,243	18.58
	L:W = 2–3:1	36,892	26.27
	L:W = 3–4:1	17,081	44.54
	L:W > 4:1	6,297	10.58
Shape character states	Obovate	18,865	4.62
	Elliptic	49,946	39.23
	Ovate	31,027	56.15