The floral study and the observed vegetational changes during Miocene regarding the palaeoenvironmental evolution of the Messara-Gavdos area in Crete

by

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(Law 5343/1932, article 202)
... to my wife Alexia and my daughters
  Maria, Adamantia and Yakinthie
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ABSTRACT

Based on macro-remains, three fossil plant assemblages are described 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), is mainly documented by leaf imprints, including a fern, a conifer (Tetraclinis cf. salicornioides) and 24 angiosperms. The assemblage is dominated by Daphnogene polymorpha, Myrica lignitum, Podocarpium podocarpum and Salix cf. angusta. Well documented are further Berchemia multinervis, Decodon gibbosus, Fraxinus sp., Populus populina and Ulmus cf. plurinervia.

The plant record from Pitsidia (Messara Basin, Ambelouzos Fm, Lower Tortonian) comprises thousands of specimens. The plant material is preserved as imprints often covered by an inorganic encrustation (replica). One alga, 2 ferns, at least 5 conifers and more than 45 woody angiosperms have been identified. Dominant species are Myrica lignitum and Pinus pitsidiensis sp. nov. documented by vegetative and reproductive organs. Leaves of deciduous oaks (Q. pseudocastanea and Q. cf. kubinyii) and Daphnogene polymorpha as well as twigs of Taxodium dubium are also fairly common. Several further taxa are represented by both vegetative and fertile (fruits/infructescences) organ remains such as Liquidambar europaea, Podocarpium podocarpum, Acer and Ulmus (ZIDIANAKIS et al., 2017). Other well documented taxa are "Pteris" oeningensis, two- and five-needled pines as well as the woody dicots Acer integrilobum, A. tricuspidatum, Carya sp., Fagus gussonii, Mimosites sp., Populus populina, Quercus mediterranea and Ulmus cf. plurinervia.

A unique mass-occurrence of Myrica and Pinus characterises the flora of Pitsidia (ZIDIANAKIS et al., 2014). Myrica remains include leaves, fruits and male catkins. The leaves have been assigned to Myrica lignitum (UNGER) SAPORTA, the fruits, sometimes even attached to their infructescence axis, to M. ceriferiformis KOWNAS, and the male catkins to M. cf. goepertii. Taphonomic evidence indicates that the different plant organs derived from a single species of Myrica. The fruit size, the unbranched male catkins and mainly the fused filaments into a staminal column in the male flower, point towards the sect. Cerophora (sensu CHEVALIER) of the subgen. Morella (ZIDIANAKIS et al., 2015). This reveals a closer affinity to the American, African and Macaronesian species of Myrica than to Asian ones.

Pinus pitsidiensis sp. nov. includes dwarf and long shoots, isolated needles, fascicle bracts and probably pollen cones, winged seeds and isolated scales of male cones. Based on the number of needles per fascicle, the persistence of the basal sheath, the distribution of stoma rows and resin ducts in the needles an assignment to sect. Pinus, subgen. Pinus is proposed for this species (ZIDIANAKIS et al., 2016).

From the palaeoflora of Metochia, which is the youngest (Gavdos Island, Metochia Fm, middle Tortonian), (MANTZOUKA et al., 2015), further taxa are reported, among them are a five-needled pine, Quercus mediterranea, and cf. Ziziphus paradistiaca. Remarkable is the leaf remain of a palm (Sabalites sp.).
The age estimation of the plant-bearing sediments was possible according to previous studies and is based on bio-stratigraphy (Pitsidia, Metochia, and Kassanoi) (e.g. MEULENKAMP et al., 1979; ANTONARAKOU, 2001; ZACHARIASSSE et al., 2011), on Sr-isotope stratigraphy (Pitsidia) (KRÖGER, 2004) and magneto- and cyclo-stratigraphy (Metochia) (HILGEN et al., 1995; KRJGSMAN et al., 1995).

In Pitsidia excavation, a square grid was established in order to record the collected specimens three-dimensionally. The enumeration of the flora has been attempted and the lateral and vertical distribution of the material within the fossiliferous deposits is pictured. Damages on Pitsidia plant material due to biostratonomic and diagenetic processes have been examined. Judging from the frequency of the after-shedding damages, the material underwent severe mechanical stress probably due to transportation.

The studied floras share only a few elements. Differences in composition may be attributed to differences in environmental and mainly depositional settings. Additionally, these floras are compared to the further Neogene record of Crete and the Greek peninsula as well as to the modern flora of the area.

Also, plant/arthropod interactions were analysed to assess further palaeo-synecological signals. The spectrum of traces in Pitsidia comprises external foliage feeding, piercing and sucking, galling, mining and oviposition as main types of leaf damages.

The plant material is evaluated systematically-taxonomically. Vegetation assessment is attempted both empirically-sociologically and by the Integrated Plant Record (IPR) vegetation analysis. The climate is estimated based on the Coexistence Approach (CA). The reconstructed vegetation models are thoroughly presented and discussed in the context of the palaeoenvironmental history of the Messara-Gavdos area. According to the IPR vegetation analysis, the plant assemblages of Pitsidia and Kassanoi were classified to the zonal subtropical, subhumid sclerophyllous or microphyllous forest (ShSF). A mixed mesophytic broad-leaved forest with a small proportion of thermophilic elements resulted for Metochia. The palaeoclimatic datasets from the floras of Pitsidia and Metochia reveal a warm temperate to subtropical climate (13.5 to 18.5 °C for the mean annual temperature and approx. 850–1600 mm for the mean annual precipitation), with a weak seasonal drought that did not coincide with the warmest period of the year. Thus, a Cfa-type sensu KÖPPEN-GEIGER system can be referred for the Messara-Gavdos area.
ΠΕΡΙΛΗΨΗ
Η παρούσα εργασία πραγματεύεται τρεις απολιθωμένες χλωρίδες, η περιγραφή των οποίων βασίστηκε στα φυτικά λείψανα (αποτυπώματα) που συλλέχθηκαν εντός Μειοκαινικών ιζημάτων της Λεκάνης της Μεσσαράς (Νότια Κρήτη) και του γειτονικού νησιού της Γαύδου.

Η παλαιοχλωρίδα των Κασσάνων, η οποία είναι και η παλαιότερη σε ηλικία (Μεσσαρά, Σχηματισμός Βιάννου, Σερραβάλλιο), περιλαμβάνει κυρίως λείψανα φύλλων μεταξύ των οποίων ένα είδος πετριδόφυτου, ένα κονοφόρο (Tetraclinis cf. salicornioides) καθώς και 24 αγγειόσπερμα. Στη συνάθροιση κυριαρχούν τα είδη Daphne polymorpha, Myrica lignitum, Podocarpium podocarpum και Salix cf. angusta. Επίσης αναγνωρίστηκαν τα Berchemia multinervis, Decodon gibbosus, Fraxinus sp., Populus populina και Ulmus cf. plurinervia.

Τα φυτικά λείψανα των Πιτσίδιων (Μεσσαρά, Σχηματισμός Αμπελούζου, κατότερο Τορτόνιο) περιλαμβάνουν χλώδες δείγματα, κυρίως απολιθωμένα φύλλα, καθώς και ποικιλία φυτικών αναπαραγωγικών οργάνων. Στην πλειοψηφία τους έχουν διατηρηθεί ως αποτυπώματα, συχνά συνδεδεμένα από ένα ανόργανη φύσις κάλυμμα (με τη μορφή αντιγράφον του φυτικού οργάνου). Συνολικά, αναγνωρίστηκαν ένα είδος φύκιους, δύο πετριδόφυτα, τουλάχιστον 5 κονοφόρα και περισσότερα από 45 ξυλόδες αγγειόσπερμα. Κυριαρχούν είδα αποτελούν τα Myrica lignitum και Pinus pitsidiensis sp. nov. Οι πολυπληθή χαρακτηρίζονταν λείψανα φύλλων των φυλλοβόλων βελανιδίων (Q. pseudocastanea and Q. cf. kubinyii), του Daphne polymorpha καθώς και τα βραχυκλάδια του Taxodium dubium. Στη συνάθροιση αρκετά τάξα αντιπροσωπεύοντας τόσο από βλαστικά όσο και από αναπαραγωγικά όργανα (καρπού/ταξικαρπίες) όπως η Liquidambar europaea, το Podocarpium podocarpum καθώς και τα γένη Acer και Ulmus (ZIDIANAKIS et al., 2017). Άλλα συχνά εμφανίζονται στη συνάθροιση χλωρίδικα στοιχεία είναι τα "Pteris" oeningensis, δύο είδη πεύκου με βραχυκλάδια που φέρουν δύο και πέντε βελόνες αντίστοιχα καθώς και τα δικότυλα Acer integrilobum, A. tricuspitatedum, Carya sp., Fagus gussonii, Mimosites sp., Populus populina, Quercus mediterranea και Ulmus cf. plurinervia.

Η συνάθροιση των Πιτσίδιων χαρακτηρίζεται από μία μοναδική, μαζική παρουσία των γένη των Myrica και Pinus (ZIDIANAKIS et al., 2014). Τα υπολείμματα του γένους Myrica περιλαμβάνουν εκτός από φύλλα, καρπού και αρασινές ταξικαρπίες (ιουλιόφιλες). Τα φύλλα αναγνωρίστηκαν ως Myrica lignitum (UNGER) SAPORTA, οι καρποί, ενίοτε με μορφή ολόκληρον ταξικαρπίο, ως M. ceriferiformis KOWNAS και οι ίουλοι ως M. cf. goeppertii. Τα ταφονομικά δεδομένα της θέσης, συνηγορούν στο γεγονός ότι τα παραπάνω φυτικά μέρη προέρχονται από ένα και μόνο είδος Myrica. Μάλιστα η εξαιρετική απολιθώμηση ορισμένων δειγμάτων βοήθησε στη διατήρηση σημαντικών μικρο-μορφολογικών και ανατομικών λεπτομερείων ταξινομικής αξίας. Το μέγεθος των καρπών, οι μη διακλαδισμένοι ιουλοί και κυρίως η σύμφωνη των νημάτων των στημών στα αρασινικά ανθίδια επιτρέπουν την κατάταξη του απολιθωμένου είδους στο sect. Cerophora (κατά
CHEVALIER) του υπογένους Morella και τη συσχέτισή του με τα σύγχρονα αμερικάνικα και αφρικάνικα (συμπεριλαμβανομένων των Κανάριων νήσων) παρά με τα ασιατικά είδη του γένους (ZIDIANAKIS et al., 2015). Το αμερικάνικο είδος Myrica cerifera L. προτείνεται ως το εγγύτερο μορφολογικά σύγχρονο είδος με βάση την πυκνότητα των αδένων επί της φυλλικής επιφάνειας καθώς και τη μορφολογία του καρπού και των αρσενικών ταξιανθών.

Τα υπολείμματα του νέου είδους πεύκου Pinus pitsidiensis που βρέθηκαν στα Πιτσίδια περιλαμβάνουν βραχυκλάδια, βλαστούς, μεμονωμένες βελόνες, βράκτια, καθώς και πιθανότατα αρσενικούς κώνους, πτερυγιοφόρους καρπούς και μεμονωμένα λέπια θηλυκών κώνων. Αξιολογώντας μορφο-ανατομικά δεδομένα όπως ο αριθμός βελόνων ανά βραχυκλάδιο, η διατήρηση του περιβλήματος της βάσης του βραχυκλαδίου καθώς και η κατανομή των στομάτων στην επιφάνεια των βελόνων και των βραχυφόρων αδένων στο παρέχεται, προτάθηκε η ταξινόμηση του είδους αυτού στο sect. Pinus του υπογένους Pinus (ZIDIANAKIS et al., 2016).

Οι ηλικίες των ιζημάτων που φιλοξενούν τις υπό εξέταση χλωρίδες έχουν υπολογιστεί με τη βοήθεια κυρίως βιοστρατογραφικών δεδομένων (Πιτσίδια, Κασσάνοι και Μετόχια) (π.χ. MEULENKAMP et al., 1979; ANTONARAKOU, 2001; ZACHARIASSE et al., 2011) καθώς και με τη χρήση ραδιοϊσοτόπων Sr (Πιτσίδια) (KRÖGER, 2004), όπως και μαγνητο- και κυκλοστρωματογραφίας (Μετόχια) (HILGEN et al., 1995; KRIEGSMAN et al., 1995).

Ειδικά στα Πιτσίδια, η ανασκαφή πραγματοποιήθηκε με τη βοήθεια δειγματοληπτικού κάναβου και η θέση κάθε φυτικού λειψάνου καταγράφηκε. Οι πυκνότητες των πιο κοινών χλωριδικών στοιχείων εντός του ιζήματος υπολογίστηκαν και ερευνήθηκε η πλευρική και κατακόρυφη κατανομή τους εντός των απολιθωματοφόρων στρωμάτων. Επιπλέον, στο απολιθωμένο υλικό εξετάστηκαν οι βλάβες από τη δράση βιοστρατογραφικών και διαγενετικών διεργασιών. Κρίνοντας από τα υψηλά ποσοστά που παρατηρήθηκαν, συμπεραίνουμε ότι μεγάλο ποσοστό των φύλλων, μετά την πτώση τους και πριν την εναπόθεση τους, υπέστησαν σημαντική μηχανική καταπόνηση, πιθανότατα κατά την μεταφορά του στο χώρο απολίθωσης. Επίσης, ο τρόπος σχηματισμού των ανόργανων επικαλύψεων επί των απολιθωμάτων στα Πιτσίδια με τη μορφή αντιγράφων συζητείται.

Από τη σύγκριση των τριών χλωρίδων προκύπτει ότι αυτές μοιράζονται λίγες σχετικά τάξει. Η χλωριδική αυτή ανομοιογένεια θα μπορούσε κυρίως να αποδοθεί στις διαφορετικές περιβαλλοντικές συνθήκες και
κυρίως στα διαφορετικά περιβάλλοντα απόθεσης του φυτικού υλικού. Επιπλέον, επιχειρήθηκε μία σύντομη σύγκριση των εξεταζόμενων χλωρίδων με άλλες Νεογενής χλωρίδες της Κρήτης και της Ελληνικής χερσονήσου καθώς και με τη σύγχρονη χλωρίδα της περιοχής.

Η παλαιοοικολογική εξέταση του φυτικού υλικού, και ιδιαίτερα των Πιτσιδίων που παρουσιάζει την υψηλότερη ποιότητα αποθήκευσης, αποκάλυψε ένα ευρύ φάσμα από ιχνή αλληλεπίδρασης φυτών-αρθροπόδων, κυρίως με τη μορφή ζημιών επί του φυλλώματος. Η κατανάλωση μέρους του ελάσματος, η νύξη-μύζηση φυτικού χυμού, η ανάπτυξη κηκιδίων, η ανόρυξη στοών εντός του παρεγχυματικού ιστού καθώς και η εναπόθεση ωνών είναι οι κυριότερες μορφές που καταγράφηκαν.

Το απολιθωμένο υλικό αξιοποιήθηκε για την περιγραφή βασικών στοιχείων της βλάστησης και του κλίματος της ευρύτερης περιοχής κατά το Μειόκαινο. Η φυτο-κοινονιολογική ανασύσταση της βλάστησης που επιχειρήθηκε εξετάστηκε υπό το πρίσμα της παλαιοπεριβαλλοντικής εξέλιξης της περιοχής Μεσσαρά-Γαύδος όπως αυτή προκύπτει από στρωματογραφικές και γεωτεκτονικές εργασίες που έχουν πραγματοποιηθεί στην περιοχή. Εφαρμόζοντας τη μέθοδο IPR (integrated plant record) ανάλυσης της βλάστησης, οι φυτικές συνάθροισης των Πιτσιδίων και των Κασσάνων κατατάχθηκαν στα υποτροπικά, σκληρόφυλλα ή μικρόφυλλα δάση (ShSF) ενώ η χλωρίδα στα Μετόχια βρέθηκε ότι αντιπροσωπεύει ένα μικτό μεσοφυτικό πλατώφυλλο δάσος με μικρό ποσοστό θερμόφιλων στοιχείων. Η χρήση της μεθόδου CA (coexistence approach) για την εκτίμηση του παλαιοκλίματος έδειξε για την ευρύτερη περιοχή της Μεσσαράς-Γαύδου ένα θερμό εύκρατο έως υποτροπικό κλίμα (μέση ετήσια θερμοκρασία 15,5–18,5 °C και μέσο ετήσιο ύψος βροχόπτωσης περίπου 850–1.600 mm), με περιορισμένη εποχική ξηρασία η οποία δε συμπίπτει με την θερμή περίοδο του έτους, πιθανόν τύπο Σfa κατά το σύστημα των KöPPEN-GEIGER.
1. INTRODUCTION
The history of the Islands of Crete and Gavdos begins at the bottom of the ancient ocean of Tethys where huge quantities of marine sediments, that later constituted their pre-Neogene structural basement, were accumulated. At the beginning of Lower Miocene, about 23 Ma, a continuous landmass (Aegeis) emerged as part of the northern coast of the declining Tethys Ocean covering the current Aegean area (DERMITZAKIS and PAPANIKOLAOU, 1981). In the upper Serravallian (late Middle Miocene) to lower Tortonian (early Upper Miocene) (about 12–9 Ma) a fan-like southward expansion of this area took place leading to the break-up of the southern part and eventually since to the formation of a separate island area, Crete (CREUTZBURG, 1963; DERMITZAKIS and PAPANIKOLAOU, 1981). Hence, Crete followed its own course as an Island system, influenced from time to time, by major tectonic events and sea level fluctuations. In this long-term history, the abiotic as well as the biotic environment underwent significant changes mostly unknown to us. Palaeobotany using as a tool the study of ancient plant remains, opens time windows in the past offering an insight to help us decipher such palaeoenvironmental parameters.

1.1. Purpose and scope
This study aspires to enrich our knowledge on the structure and operation of the past terrestrial environments in Cretan area, focusing on the Miocene plant communities of this southernmost part of Europe. For this purpose, two newly discovered plant macro-assemblages in Pitsidia and Kassanoi (Messara Basin) in the northern part of central Crete are studied, using rich material of thousands of specimens (text-fig. 1.1). Also, in the adjacent Gavdos Island, several newly reported taxa are presented from the recently published palaeoflora of Metochia.

Hitherto, the main evidence concerning terrestrial environment for the Messara-Gavdos area has derived by:

i. a Valesian (Late Miocene) fauna of small and large mammals including *Hipparion primigenium* and *Progonomys cathalai* discovered in Kastellios hill near Kasteliana village at the eastern part of the Messara Basin (DE BRUIJN et al., 1971; DE BRUIJN and ZACHARIASSE, 1979) (appendix 22),

ii. two micro-floras provided by the analysis of pollen and spore remains from Kastellios hill and Almiri Panagia (NW Messara) (BENDA et al., 1974; VAN DE WEERD, 1983; SEN et al., 1986),

iii. body remain of an insect (ant, family Formicidae) recovered from the Late Miocene sediments close to Apomarma village in the NW part of Messara Basin (WAPPLER et al., 2009) and

iv. the plant macro-remains from Metochia on the Gavdos Island (MANTZOUKA et al., 2015).

This study aims to:

- record the Middle–Late Miocene flora of the Messara Basin and Gavdos Island as is revealed by the collected fossil material from three different localities, Kassanoi, Pitsidia - which constitutes the principal studied locality and Metochia,
- provide evidence concerning the structure and function of the past ecosystems through the analysis of plant-arthropods interaction as preserved on the fossil plant material,
- reveal taphonomical aspects that influence the deposition and preservation of the fossil material in Pitsidia,
- interpret the floristic, synecological and taphonomical results in an attempt to understand the ancient depositional environment of the fossiliferous localities, reconstruct the vegetation structure and estimate the major palaeoclimatic parameters of the region,
- compare the herein described palaeofloras with contemporary Greek floras providing evidence about past biogeographic relationships and the relative biodiversity. A special comparison with the modern flora and vegetation of the Messara-Gavdos area is also intended.

Text-figure 1.1. The studied area of Messara Basin in Crete and the Gavdos Island (simplified geological map, modified from KRIGSMAN et al., 1994)

1.2. The Palaeobotany in Crete and Gavdos - Historical context

The exploration history of the Cenozoic flora in the Cretan Island, contrary to other parts of Greece such as Alonissos (BRONGNIART, 1833, as “Iliodroma”) and Euboea (e.g. BRONGNIART, 1861; UNGER, 1862, 1867; SAPORTA, 1868), is rather recent. Concerning Neogene plant macro-fossils, the first palaeobotanical data were by VELITZELOS and GREGOR (1990) only in the form of brief notes. In an overview of the Cenozoic floras of Greece, they reported the occurrence of pine cones from the area of Achlia village (appendix 22), in the eastern part of Crete without providing any description or illustration.
One year later, in the pan-European Palaeobotanical conference in Vienna, Mohr et al. (1991) announced the discovery of a diverse plant assemblage of Upper Miocene age close to Makrilia village in eastern Crete (text-fig. 1.2). A comprehensive account of this flora was given in the Ph.D. thesis of Sachse conducted in the ETH of Zurich (Sachse and Mohr, 1996; Sachse, 1997; Sachse et al., 1999; Sachse, 2004). In total, approx. 130 different taxa from this locality were identified based on foliage, diaspore as well as sporomorph remains. Leaves were preserved as poor in quality impressions without epidermal structures, making occasionally their systematic identification quite ambiguous.

At the onset of 21st century, in the western part of the Island, during the construction of stone buildings in the Mediterranean Agronomic Institution of Chania, the personnel noticed the occurrence of leaf impressions in limestone blocks. Fossil collecting from the limestone quarry close to the village of Vrysses (text-fig. 1.2) proved a rather hard task due to the rock-hardness, low abundance and limited exposure of the plant-bearing layers. The Late Miocene assemblage of Vrysses comprises mostly foliage and rarely seed or fruit remains, and as in the case of Makrilia material, the low quality and the lack of epidermal evidences made the identification of several species problematic (Zidianakis et al., 2007).

In the same time period, Kröger during his Ph.D. project on the sedimentary environments of the western Messara Basin noted the occurrence of plant macro-fossils in fine-grained layers near the village Pitsidia (Kröger, 2004; text-fig. 1.2). He reported an outcrop in 1 km (as referred in the caption of fig. 2.3.4.) or 2 Km (as referred in the text, p. 21) SW of the village Pitsidia that yielded a flora comprising, according to Sachse’s identifications, Taxodium Richard, Pinus L., Carpinus betulus fossilis L., Salix L. as well as the families Leguminosae and Lauraceae. He figured a catkin of Myrica goeppertii co-occurring with the leaf base of a Myrica lignitum (fig. 2.3.4.b, as Carpinus betulus), two leaves of M. lignitum (fig. 2.3.4.c, as Lauraceae indet. and Salix sp.) as well as fragmentary needles of Pinus pitsidiensis co-occurring with a M. lignitum leaf fragment, a Taxodium dubium twig and a bud scale of Pinus sp. (fig. 2.3.4.d).

Not long after this study, the plant-bearing layers became easily accessible thanks to extensive earthworks that were carried out by the owner of the land property. In the summer of 2008, during a geological field-trip in the area of Pitsidia, a new outcrop rich in plant fossils is discovered by Zidianakis et al. (2010). In the following two years (2009–2010) the Natural History Museum of Crete made the first fossil collection from Pitsidia. Preliminary results were presented in the 12th conference of the Geological Society of Greece.

In 2014, Velitzelos D. et al. published a comprehensive review of the Cenozoic floras of Greece, providing amended species lists for all the already known Cretan floras mentioned above.

Regarding Gavdos Island, the occurrence of plant macro-remains of terrigenous origin has already been noticed by the first geologists who explored the island the 19th century (e.g. Simonelli, 1894). More recently, several studies referred to the occurrence of plant material in the turbiditic sequences of the Metochia deposits though no descriptions were provided (Postma et al., 1993; Gaudant et al., 2005;
The palaeoflora of Metochia was presented in 2015 by MANTZOUKA et al. based on the plant material that was collected by TSAPARAS (2005). The poor preservation of this material was a critical factor that decreased the potential of accurate identifications.

Text-figure 1.2. Geological map of Crete and Gavdos islands showing the plant macro-remain localities (modified from I.G.M.E., 1993); the herein studied localities are underlined.

Studies on plant sporomorphs from the Neogene sediments of Crete are diverse including the Tortonian (Late Miocene) pollen spectra from Makrilia, Kastellios Hill, Plakias?, Georgioupolis, Viglotopi, Triopetra and Almiri Panagia localities (BENDA et al., 1974; VAN DER WEERD, 1983; SEN et al., 1986), the Messinian (Late Miocene) Perama/Dafnedes and Agia Varvara as well as the Pliocene of Agios Vlassios (BENDA et al., 1974; DRIVALIARY, 1993) (appendix 22).
2. GEOGRAPHICAL AND GEOLOGICAL SETTING - AGES

2.1. The Cretan Island

2.1.1. Geological structure

Crete is the fifth larger island of the Mediterranean Sea with an elongated shape (approx. 260 km in length and 12–60 km in width) crossed by a high mountain range. The geological structure of the Island is characterised by a complex mosaic of pre-Alpine and Alpine rocks composing the pre-Neogene basement and post-Alpine deposits that fill the Neogene-Quaternary sedimentary basins.

The Pre-Neogene basement of the Island is built of a pile of nappes that consists of various rocks from different palaeogeographic zones that could be divided according to their tectonostratigraphic position and tectonometamorphic history into two main sequences: the Lower sequence of high-pressure low-temperature (HP-LT) metamorphic rocks (Plattenkalk, Trypali and Phyllite Quartzite units) and the upper sequence with non-metamorphic rocks (Tripolitza, Pindos and Uppermost units) (e.g. CREUTZBURG and SEIDEL, 1975; SEIDEL et al., 1982; BONNEAU, 1984; PAPANIKOLAOU and VASILAKIS, 2010) (text-fig. 1.2) The tectonic contact of these two units is considered to be an extensional detachment striking E-W, the so called Cretan detachment, acting in the area since the Middle Miocene as a low angle normal fault (FASSOULAS et al., 1994; JOLIVET et al., 1996; RING et al., 2010; VAN HINSBERGEN and MEULENKAMP, 2006; TORTORICI et al., 2010).

**Lower sequence**

Plattenkalk is the lowest unit exposed on the Crete Island, consisting of stromatolitic dolomite, carbonate breccia and a distinctive sequence of platy, well bedded carbonates with chert interbeds. In western Crete, the Plattenkalk unit is overlain by the Trypali nappe of Late Triassic-Early Jurassic well bedded dolomite with peloidal mudstone and detrital carbonate layers. The overlaying Phyllite Quartzite unit constitutes a series of Late Carboniferous to Middle Triassic marine phyllites dominated by quartz-rich siliciclastic sediments with minor limestone, gypsum and volcanic rocks.

**Upper sequence**

Above the Phyllites Quartzites are the shallow-water carbonates of Tripolitza unit, deposited between the Upper Triassic and Middle Eocene. The overlaying Pindos unit is characterised by deep-water sediments, including pelagic limestones, radiolarites, calciturbidites and calc-breccias. The Uppermost unit, of Arvi, Miamou, Vatos, Asteroussia and ophiolites nappes are detected in several small outcrops all over the Crete, with a variety of rocks, including oceanic pillow basalts, gabbros, deep-marine sediments, schists and serpentinite).
The Neogene sedimentary sequence of Crete is subdivided by MEULENKAMP et al. (1979) into six major lithostratigraphic groups, the Prina, Tefelion, Vrysses, Hellenikon, Finikia and Agia Galini Groups (text-fig. 2.1):

1. **Prina group** constitutes the base of the Neogene sequence in several areas, especially in eastern and western Crete. It consists of limestone breccia and breccio-conglomerates, in many cases displaying components embedded in a well-cemented, calcareous matrix. In other places this group occurs as intraformational mappable units within the Tefelion group. Prina group is deposited in non-marine to brackish of shallow-marine environments.

2. **Tefelion group** (Serravallian to Tortonian) consists of poorly consolidated clastic formations and informal rock units that unconformably overlay the pre-Neogene basement or the Prina group and underlay the calcareous successions of the Vrysses group. The formations incorporated in this group are predominantly composed of conglomerates, sands and clays reflecting deposition in fresh-water, brackish and marine environments.

3. **Vrysses group** (upper Tortonian to Messinian) overlies conformably the Tefelion group or unconformably the pre-Neogene basement. It consists of marine bioclastic, often reefal algal-coral limestones or alternations of laminated and homogeneous marls with evaporite intercalations locally.

4. **Hellenikon group** was formed during Messinian salinity crisis and overlies unconformably the Vrysses group, older Neogene strata or the pre-Neogene basement. This group includes reddish, terrestrial conglomerate and lacustrine, fluvial and occasionally brackish and lagoonal fine-grained successions. Locally thin evaporite beds also occur. In the central and eastern Crete, the Hellenikon group is generally absent.

5. **Finikia group** accumulated during the Pliocene and consists of open-marine marls and clays overlying either the Hellenikon and Vrysses group or the pre-Neogene basement. Its basal part frequently contains marl breccia. Finikia Group was initially deposited at deep-marine levels, but displays a quick shoaling upward trend to a depth of approximately 300 m.

6. **The Agia Galini group** represents the highest Neogene rock unit in Crete of upper Pliocene to Pleistocene age. This group overlies the Finikia group and contains terrestrial reddish conglomerates and fluviolacustrine sands and clays.
2.1.2. Geodynamic evolution - Palaeogeography

The Cretan Island constitutes a prominent horst structure of the southern Aegean forearc in the still active Hellenic subduction zone (text-fig. 2.2). Its complex structure has been strongly affected by the Alpine orogenic processes in the Eastern Mediterranean, due to the convergence of 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 evolution of the present day tectonism of the eastern Mediterranean area started in the Upper Cretaceous with the break up of the Pangaea and a counter-clockwise rotation of the Afro-Arabian plate towards the Eurasian plate to the north that caused a continuous subduction process (DERCOURT et al., 1986; FACCENNA et al., 2014). During the Oligo-Miocene phase, the Hellenic subduction zone has been dominated by the southward migration of the Aegean plate due to the rollback of the African lithosphere (MEULENKAMP et al., 1988; McCLUSKY et al., 2000). Since the Upper Miocene or Lower Pliocene, the palaeostress field changes from N-S to NNE-SSW due to the collision of the northward migrating Arabian plate with the Anatolian one. This caused the westward extrusion of the Anatolian plate and changed the pure southward migration of the Aegean plate to a SSW movement (DEWEY et al., 1986; LE PICHON et al., 1995).

<table>
<thead>
<tr>
<th>Epoch</th>
<th>Stage</th>
<th>Planktonic Foraminifera</th>
<th>Calcareous Nanoplankton</th>
<th>Mammal Zones</th>
<th>Sporo- morphs</th>
<th>Litho-strati- graphy</th>
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</thead>
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<tr>
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<td>Globoquadrina continens</td>
<td>Discocyclina divaricata</td>
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<td></td>
<td>Hellenikon</td>
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<tr>
<td>17.5</td>
<td>Langhian</td>
<td>Neogloboquadrina acostaensis</td>
<td>Discocyclina divaricata</td>
<td></td>
<td></td>
<td>Vrysses</td>
</tr>
<tr>
<td>12.5</td>
<td>Serravallian</td>
<td>Neogloboquadrina acostaensis</td>
<td>Discocyclina divaricata</td>
<td></td>
<td></td>
<td>Tefeli</td>
</tr>
<tr>
<td>10.0</td>
<td>Tortonian</td>
<td>Neogloboquadrina acostaensis</td>
<td>Discocyclina divaricata</td>
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<td></td>
<td>Priha</td>
</tr>
<tr>
<td>7.5</td>
<td>Messinian</td>
<td>Globorotalia costata</td>
<td>Discocyclina divaricata</td>
<td></td>
<td></td>
<td>Pre-Neogene rocks</td>
</tr>
</tbody>
</table>

Text-figure 2.1. a. Litho-chronostratigraphy of the Miocene sediments in Crete (FASSOULAS, 2001, after BENDA et al., 1974 and MEULENKAMP et al., 1979)
The first land in the Cretan area emerged at the beginning of Lower Miocene, as continuous landmass covering the current Aegean area (DERMITZAKIS and PAPANIKOLAOU, 1981) (text-fig. 2.3a–b). The Neogene basins on Crete were formed since the Middle Miocene by numerous multi-directional, normal faults as a consequence to the intense crustal extension in the Aegean region caused by this retreatment of the African plate subduction and the lateral extrusion of the Anatolian plate (ANGELIER et al., 1982; FASSOULAS, 2001; MEULENKAMP and SISSINGH, 2003). During the upper Serravallian (uppermost Middle Miocene) a transition in the sedimentation process on the island from terrigenous to marine deposits took place, indicating the inflow of the sea in the southern part (FORTUIN, 1978; MEULENKAMP t al. 1979; PETERS et al., 1985; text-figs 2.3c–e). It was probably the first time during the post-alpine period that the Cretan area was connected directly with an open marine body.

The absence of marine sediments of Serravallian (Middle Miocene) age at the extant Cretan sea suggests the occurrence of a continental area north of Crete (TEN VEEEN and POSTMA, 1999). The Aegean Sea was probably formed later, in upper Tortonian (lower Upper Miocene), by extension forces in the backarc area, and during Tortonian (Upper Miocene) its southern part became gradually deeper forming a separate sea, the Cretan Sea (LYBERIS et al., 1982). Eventually, the connection of the Cretan area with the Greek mainland and Minor Asia was interrupted. During the Upper Miocene and Pliocene pronounced uplifts of blocks composed of pre-Neogene rocks like limestones, sandstones, phyllites, quartzites and ophiolites shaped the present-day mountains of the Island (MEULENKAMP et al. 1994; TEN VEEEN and POSTMA, 1999). Due to significant sea
fluctuations that took place from time to time, these uplifted blocks became Islands forming an archipelago in the Cretan area.

Text-figure 2.3. a–b. Palaeogeographic reconstruction of the Mediterranean sea, a. upper Oligocene, b. Middle Miocene (modified from STEININGER and RÖGL, 1984); c–e. Palaeogeographic reconstruction of the Greek area, c. upper Burdigalian–Langhian), d. uppermost Serravallian), e. upper Tortonian (modified from POULAKAKIS et al., 2005, after CREUTZBURG, 1963; DERMITZAKIS and PAPANIKOLAOU, 1981 and DERMITZAKIS, 1990);

2.2. The Messara Basin

Messara Basin, located at the southern part of central Crete is developed over the hanging wall of the Cretan Detachment forming a supra-detachment Basin with deformed basement and several extensional klippen (VAN HINSBERGEN and MEULENKAMP, 2006) (text-fig. 1.2). Originally, it was formed during the Neogene as part of a larger Basin extending northwards to the area of the present day Heraklion Basin. Tectonic processes during the Lower Pliocene separated these two basins with the development of the east-west central Heraklion Ridge (FASSOULAS, 2001).

Today, Messara Basin extends in an east-west orientation, covering an area of about 360 km², bordered by the Ida (Psiloritis) Mountains and the central Heraklion Ridge to the north, the Asteroussia Mountains to the south and Dicti Mountains to the east (text-figs 1.1, 2.4). Westwards it expands into the Libyan sea.

Sedimentation in the Messara Basin started in the Middle Miocene resulting in the deposition of sequences lying unconformably on the basement and characterised by abrupt lateral and vertical changes in lithology (MEULENKAMP, 1979; ZACHARIASSE et al., 2011; VAFIDIS et al., 2012; MARAVELIS et al., 2013). These
For the Neogene deposits of the Messara Basin, no formal lithostratigraphic scheme has been established so far. The preliminary subdivision for the Crete deposits that has been proposed by Meulenkamp et al. (1979) and has been adopted by the most authors is followed here. According to this scheme the Miocene depositional succession of the Messara Basin could be subdivides into four Formations characterised by a unique combination of lithology, depositional environment and stratigraphic position (Meulenkamp, 1979; Zachariasse et al., 2011):

-Viannos Fm (Serravallian, Tefeli group) constitutes the oldest Neogene unit in the Messara Basin. It overlies unconformably the pre-Neogene basement, and is dominated by alternations of clay, silt and cemented sandstone of fluvio-lacustrine origin, covering a wide range of depositional environments such as channel-belt, overbank and lake deposits. The numerous cross-bedded fines and the decreasing grain-size and increasing roundness indicate between south and west source of sediments. The sandstones constitutes either 2–6 m thick tabular bodies or thinner interbeds within mudstone and silt intervals. Lignitic clays infrequently occur whereas platy weathered limestones are common. In the limestones and clays fresh-water molluscs such as *Theodoxus Montfort*, *Melanopsis Férussac*, *Unio Philipsson* and *Planorbis Müller* are occasionally found. Also, in several layers, plant debris and leaf remains rarely occur. The maximum exposed thickness of this formation is estimated at about 600m (Panagopoulos et al., 2011). Viannos Fm is considered of Serravallian age as the overlying shallow-marine deposits of Skinias Fm dated as lower Tortonian (Zachariasse, 1975). According to Panagopoulos et al. (2011), Viannos Fm exhibit six
coarsening upward cycles, each up to 100m thick, with clays at the base and sand layers at the top of each cycle (text-fig. 2.5).

-Skinias Fm (upper Serravallian–lower Tortonian, Tefeli group) consists of marine clays with interbeded sandstones and occasionally gravels overlying conformably the Viannos Fm. The maximum exposed thickness is about 250 m. The lower part of the Formation is characterised by shallow-marine silty clays with locally abundant *Turritella* LAMARCK while deep-marine clays characterise the middle part. The upper part gradually coarsens upwards from clay-rich to sand-rich deposits.

-Ambelouzos Fm (lower–middle/upper Tortonian, Tefeli group) reaches 350 m in thickness, overlying disconformably the Skinias Fm and comprises a variety of lithologies such as silty clays, sands, conglomerates as well as occasionally travertines, lignites, oyster beds and coral bioherms, 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 and silts and clays rich in *Limnocardium* FISHER, *Terebralia* SWAINSON, *Turritella* LAMARCK, *Murex* L., and *Cerithium* BRUGUIÈRE indicate repeated marine transgressions leading from lagoonal to inner neritic conditions.

-Varvara Fm (middle/upper Tortonian–lower Messinian, Vrysses group) of homogenous and laminated mixed siliciclastic and calcareous marine sequences. It reaches approx. 100 m in thickness and either overlies conformably the Ambelouzos Fm or with an angular unconformity the Viannos/Skinias Fms or the pre-Neogene basement. The basal sediments (lower member) are mostly deposited in inner neritic environments while the upper ones (upper member) in deep-water.

ZACHARIASSE et al. (2011) proposed an upgraded litho-stratigraphic system for the Tortonian–early Messinian deposits of central Crete. According to this, the Miocene sediments of Messara Basin are classified in a sequence of five Formations (subdividing Varvara Fm into Moulia and Agios Miron Fms) and younger ages than MEULENKAMP et al. (1979) has been proposed for most of them:

-Viannos Fm (~10.8 to ~10.4 Ma) (lower Tortonian).
-Skinias Fm (~10.4 to ~9.6 Ma) (lower–middle Tortonian).
-Kasteliana Fm (=Ambelouzos Fm) (~9.6 to ~8.2 Ma) (middle–upper Tortonian), type section Kastellios Hill.
-Moulia Fm (part of Varvara Fm) (basal part ~8.2 Ma) (upper Tortonian–Messinian)
-Agios Miron Fm (part of Varvara Fm) (basal part ~7.4 Ma) (Messinian).
2.3. The Gavdos Island

The island of Gavdos, situating 37 Km south of Crete, forms the southernmost extension of the South Aegean island arc (text-fig. 1.2). It covers an area of about 33 km². 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 Pindos unit (carbonates and flysch) as well as ophiolites (KOPP, 1977; ANASTASAKIS et al., 1995) (text-fig. 2.6). The carbonate part, exceeding in thickness 300 m, consists of crystalline, thin bedded limestones with reddish, rich in iron oxides intercalations of Upper Maastrichtian–Danian age (ANASTASAKIS et al., 1995; VICENTE, 1970). The flysch, having a thickness of approx. 35 m, is arenaceous-pelitic with fragments of greenrocks, limestones and radiolarites, of Eocene age. Towards the NE part of Gavdos Island a volcano-sedimentary series is exposed which is thrusted over the Pindos unit (BONNEAU, 1984).

Neogene sediments are situated at the NE part, covering two thirds of the Island (text-fig. 2.6), with a thickness of up to 150 m, overlain unconformably on the pre-Neogene basement, (VICENTE, 1970; I.G.M.E., 1993; ANASTASAKIS et al., 1995).
For the Miocene deposits of the Island the broad accepted subdivision that has been proposed by ANASTASAKIS et al. (1995) is followed. According to this, two formations, Potamos and Metochia Fm have been identified:

-Potamos Fm (lower/middle Serravallian to lowermost Tortonian) overlies with an angular unconformity the pre-Neogene basement, comprising a variety of rocks such as conglomerate, coral limestone, sandstone alternations of marly limestones or shales with sands and white limestones, with a total thickness of more than 200 m. The depositional environments are mainly marine ranging from shallow to several hundreds or thousands of meters in depth. This Formation it seems to be time-equivalent with the fluvio-lacustrine sediments of the Viannos Fm and possibly the marine Skinias Fm in central Crete (POSTMA et al., 1993; MEULENKAMP et al., 1994; van HINSBERGEN and POSTMA, 2006; ZACHARIASSE et al., 2011).

-Metochia Fm (middle–upper Tortonian) with a maximum thickness of about 50 m overlies unconformably the pre-Neogene basement consisting at the base of conglomerates, paleosol and sandstones rich in Pecten MÜLLER, Clypaster LAMARCK and Heterostegina D’ORBIGNY, followed by an extended cyclothematic alternation of grey marls with brown-grey “sapropels” (containing terrestrial plant remains), and closing with layers of diatomites, marl and limestones. Sedimentological evidences suggest a marine environment for most part of this formation.
2.4. The studied outcrops and their ages

2.4.1. The Kassanoi outcrop

The outcrop of Kassanoi is situated in the NE part of Messara Basin, on a roadcut leading to Viannos province, one Km SW of Kassanoi village (pl. I, fig. 2; pl. II, fig. 2; text-fig. 2.7). The section, comprises a more than 8 meters thick siliclastic succession of sandstone and silt-clay alternations, brownish to gray, occasionally with fresh-water mollusc shells (pl. V, fig. 1; pl. VI, fig. 3; text-fig. 2.8). At the upper part of the sequence a coal seam, a few centimetres thick is present (pl. V, fig. 4). Plant macro-remains, mainly leaf impressions, occur in the fine-grained intercalations below this coal seam, often co-occurring with plant debris (pl. V, figs 2–3; pl. VI, figs 1, 4). About fifteen centimetres below the coal seam a horizon comprising in situ preserved roots was detected (pl. VI, fig. 2). The presence of fresh-water mollusc shells and in situ root remains, as well as the lack of marine macro-fossils suggest a fluvio-lacustrine depositional environment. The first plant remains in this outcrop were discovered by the author during a geological field trip in the summer of 2010.

Outcrop age. According to the 1:25,000 and 1:50,000 geological maps of I.G.M.E. (1994; 2002) (appendix 1a) the Kassanoi outcrop is placed into Viannos Fm (possibly at the lower part of the Fm due to its close proximity to the exposed pre-Neogene flysch and the overall tilt of the sediments in the broader area). The
The age of Viannos Fm and consequently of the plant-bearing sediments is considered as Serravallian (MEULENKAMP et al., 1979). According to ZACHARIASSE et al. (2011) stratigraphic scheme, the age or this Fm is estimated to approx. 10.8–10.4 Ma. Taking into account these estimations, the age of the Kassanoi outcrop should be regarded as Serravallian although a lower Tortonian age could not be excluded so far.

2.4.2. The Pitsidia outcrop

Pitsidia is a typical Cretan village in the SW part of Messara Basin, close to the ancient (Minoan) ports of Komos and Matala, the latter well known for its caves in marly limestone. The plant-bearing outcrop, is situated about 1 Km SW of the Pitsidia village, at an area characterized by dissected low hills (pl. I, fig. 1; pl. II fig. 1; text-fig. 2.7). KRÖGER (2004) was the first who noted the occurrence of plant macro-remains in the area of Pitsidia.

The deposits of this outcrop constitute a thick succession of terrigenous clastics, estuarine and shallow-marine sediments which can be divided into three main litho-stratigraphic units (text-fig. 2.9; appendix 1b):

- **The lower unit** comprises a more than 40 m thick alternation of deltaic to fluvialite conglomerates, sands, clays and silts, originated from the metamorphic rocks of the nearby mountains, with abundant plant macro-remains. This unit is assigned to Ambelouzos Fm and can be well correlated with Kröger’s (2004) LFA1 lithostratigraphic unit.
-The middle unit, 4–6 m thick, consists of siliclastic successions of calcareous sands, sandstones and conglomerates rich in echinoids and mollusks, intercalating with rhodolith rudstones indicating coastal, estuarine and shallow-marine depositional environments (text-fig. 2.10). An interfingering of this unit with the above described has not been observed.

- The upper unit comprises shallow-marine bioclastic limestones, up to 5 m thick.

The middle and the upper units of the outcrop match with KRÖGER’s LFA2a and LFA2c lithostratigraphic units, respectively.

Text-figure 2.9. Pitsidia outcrop, the three lithostratigraphic units are separated by dashed lines

The main fossiliferous layer (briefly MFL) is beige to slightly blue-green, poorly lithified, fine-grained, 3.5–4.0 m thick, lacking pronounced sedimentary structures. Superimposed and for the next 1 m, thin layers occur, some of them bearing plant remains as well (fossiliferous layers 1 to 3, or briefly FL1–3) (text-fig. 2.11).

Outcrop age. The plant-bearing layers of Pitsidia outcrop (lower litho-stratigraphic unit) constitutes part of the Ambelouzos Fm. MEULENKAMP et al. (1979) placed the deposits of this Fm to lower–upper Tortonian mainly on the basis of the obtained sporomorphs and mammal associations as well as of the planktonic foraminifera and calcareous nannoplankton from the adjacent marine Formations of Skinias and Varvara.
KRÖGER (2004), based on Sr-isotope stratigraphy, determined the age of the marine sediments at the base of the LFA2a unit from a section in the Matala area (about one km from the Pitsidia outcrop) as somewhat older than 10.5 Ma. Hence, he assigned the underlying LFA1 unit which includes the herein studied plant-bearing layers to lower Tortonian or even upper Serravallian.

Text-figure 2.10. Fossils from the middle unit of Pitsidia outcrop, a. Clypaster, scale bar 2 cm; b. Pecten, scale bar 1 cm

Text-figure 2.11. Litho-stratigraphic column of the plant-bearing deposits of Pitsidia
ZACHARIASSE et al. (2011) proposed an age span for the Ambelouzos Fm (as Kasteliana Fm) between approx. 9.6–8 Ma. It’s noteworthy to mention that the section of Kastellios Hill (type section of Kasteliana Fm) has been correlated by SEN et al. (1986) using magnetostratigraphic sequences to Chron 5r attributing it to the lower Tortonian, probably older than 10.30 Ma and younger than 11.47 Ma.

Taking into account all the above mentioned estimations, the age of the Pitsidia plant-bearing sediments should be regarded as lower Tortonian, though middle Tortonian or upper Serravallian ages should not be excluded so far.

2.4.3. The Metochia outcrop

The section of Metochia is situated in the northern part of the Gavdos Island, approx. 1.5 km western of Sarakiniko bay (text-fig. 2.6; appendix 1c). It constitutes an extensive sedimentary succession, more than 100 m thick, of Upper Miocene age (POSTMA et al., 1993; HILGEN et al., 1995; KRIJGSMAN et al., 1995) (pl. I fig. 3; pl. II fig. 3). This section provides the most representative sequence of the Metochia Fm (type section) and is separated by a normal fault in two secondary, complementary sections (STIGTER, 1989; POSTMA et al., 1993; ANASTASAKIS et al., 1995; KRIJGSMAN et al., 1995).

The basal part of the succession consists of palaeosol overlain by estuary sediments with oyster banks and shallow-marine sandstones. These horizons upwards are replaced by 96 rhythmic hemi-pelagic alternations of homogenous, bioturbated, light grey-blue marls and poorly to non-bioturbated, brown-grey laminites rich in organic matter (“sapropels”) with bedding planes rich in plant macro-fossils, mostly leaf imprints (text-fig. 2.12; pl. VII, figs 1–4) (POSTMA et al., 1993; KRIJGSMAN et al., 1995; SCHENAU et al., 1999; ANTONARAKOU, 2001; TSAPARAS, 2005; PYLIOTIS et al. 2013). At the lowest part, the “sapropelic” layers are gradually replaced by multi-laminated sandy turbidites, while at the top, the succession passes in stratigraphic continuity to cyclically bedded diatomites of Messinian age (HILGEN et al., 1995; TRIANTAPHYLLOU et al., 1999; POSTMA, 2001; PEREZ-FOLGADO et al., 2003). The section represents marine deposits that were probably supplied by river flooding. The dominant occurrence of fishes such as Bregmaceros albyi SAUVAGE and Lepidopus sp. in the plant-bearing layers indicate a maximum sea depth of 300 m (GAUDANT et al., 2005; TSAPARAS, 2005) (pl. VII, fig. 5).

Outcrop age. The entire Metochia section spans a time interval from 9.7 Ma to 6.6 Ma and constitutes a fundamental component for the development of a rather precise and reliable chrono-stratigraphical framework for the Upper Miocene of the Eastern Mediterranean region (HILGEN et al., 1995; KRIJGSMAN et al., 1995). Metochia deposits allowed the application of a combination of various independent dating methods such as magneto-, bio- and cyclo-stratigraphic as well as the association of this succession with others situated on Crete Island or in the Eastern Mediterranean basin. Especially on the basis of cyclo-
stratigraphy, as the rhythmic depositional character of the Metochia sediments has been correlated with the astronomical curves of the orbital movements of the Earth, every individual “sapropelic” layer corresponds to the minima of a precession cycle (HILGEN et al. 1995).

Text-figure 2.12. Litho-stratigraphic column of the Metochia section (ANTONARAKOU, 2001)

The excavated plant-bearing layers match with the Nrs M16–M26 sedimentary cycles of HILGEN et al. (1995) and KRIEGSMAN et al. (1995) and according to planktonic foraminifera analysis correspond well with the Biozone N16 after BLOW (1969). Especially in the sedimentary cycle Nr. M15, KRIEGSMAN et al. (1995) and ANTONARAKOU (2001) identified the lower common occurrence of Globorotalia menardii form 4 TIALSMA while in Nr. M28 they recorded the first appearance of Globoquadrina dehiscens CHAPMAN, PARR
and Collins. The former author identified within the Metochia section, 17 magnetic polarity reversals that could be correlated to the geomagnetic polarity time scale CK95 (Cande and Kent, 1995). More precisely, the observed normal polarity in the Nrs M14–M15 sedimentary cycles corresponds with the subchron C4Ar.1n (about 9.3 Ma) and similarly another one in the Nrs M40–M41 cycles corresponds with the cryptochron C4r.2r-1 (approx. 8.6 Ma). In the same time, Hilgen et al. (1995) associating the rhythmic deposition of the section with the astronomical parameters of the earth orbit, estimated the age of the “sapropelic” intervals Nrs M16–M26 at about 9.28–9.06 Ma.

Taking into account all the above mentioned data, the age of the excavated plant-bearing layers in Metochia corresponds to the middle Tortonian, approx. 9.0–9.4 Ma. The plant material that was described by Mantzouka et al. (2015) is considered of almost the same age, as it came from the “sapropel layers” of the Nrs M16–M22 sedimentary cycles.
3. MATERIAL AND METHODS

3.1. Material

This study deals with plant fossil material that was collected by the author from three different sites, Pitsidia and Kassanoi (Messara Basin) as well as Metochia (Gavdos Island). The majority of the plant fossils are preserved as imprints, without adhered carbonized substance. Their surface is typically lightly grey, brownish or yellowish colored showing more or less details of the leaf venation. Due to severe oxidation the cuticle on leaf imprints has not generally been preserved. All studied material is housed in the Natural History Museum of Crete (NHMC) under the collection numbers (appendix 9b):

- 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.

**Pitsidia outcrop.** The outcrop of Pitsidia yielded the majority of the herein examined plant remains. Apart from plant impressions the collected material includes:
- isolated fish bones,
- gastropod shells,
- insect imprints,
- a coalified wood fragment
- a few coalified monocot leaf fragments and
- ostracod valves.
Totally, approx. 6500 slabs with more than 9000 macro-fossils were collected mostly from the main fossiliferous layer (MFL) and the three superimposed thinner layers (FL1–3) (text-fig. 2.11). Additionally, the material collected earlier (in 2009–2010) and partly presented in the preliminary results of the Pitsidia palaeoflora by ZIDIANAKIS et al. (2010) is also taken under consideration and commented where it was necessary (Nrs 31.4.2.1–710, NHMC).

Among the plant remains, thick material such as coriaceous or needle-like leaves, shoots, fruits, seeds, and inflorescences is often covered by an inorganic encrustation (replica), yielding significant micro-morphological or even anatomical details. Frequently, even when the plant material was freshly excavated these encrustations appeared weathered, because of sediment fracturing and the action of penetrating water (pl. IV, fig. 3).

**Kassanoi and Metochia outcrops.** Kassanoi material comprises 341 plant macro-fossils that derived from 248 slabs. All of them were collected from the silty intercalations a few centimeters below the coal seam (text-fig. 2.8).
From Metochia “sapropelic” layers of Nrs M16–M26 sedimentary cycles, 64 slabs were collected with 71 fossils on them (text-fig. 2.12). Exceptionally, inorganic encrustations (replica of plant tissue) occurred, mostly on shoot and needle-like leaf impressions.

### 3.2. Methods

#### 3.2.1. Fossil collection

**Pitsidia outcrop.** The bulk amount of the studied material was collected during systematic excavations that were conducted from April 2011 to August 2012. Initially, the loose, weathered material from the excavation area was removed and a 7x13 meters grid was set up on the exposed surface of the layers subdividing them into 1 m squares (pl. III, fig. 5). The main axis of the grid was parallel to the layer tilt. The excavation work mainly concentrated in the rich in plant fossils layers (MFL and the overlain FL1–3). Within the main fossiliferous layer, due to its extensive thickness, 6 levels (I–VI) were defined, each of them 70 cm thick (pl. III, fig. 1; appendix 2a). The use of grid and level division of the MFL were considered essential, basically by the need to record the collected specimens three-dimensionally within the superimposed site grid.

The fossiliferous sediments were already broken in blocks of various sizes by natural fracturing (pl. III, fig. 3) mostly caused by creeping. These blocks were removed by hand excavation tools. The larger ones, of several dm in size, were recorded (layer – grid square number – MFL level), labeled, covered by paper and put into plastic boxes for transportation to the labs of the Natural History Museum of Crete (pl. III, figs 2, 4). There, using hammers and knives the sediment blocks were split carefully seeking for fossils. The smaller blocks were split in the field and the recovered specimens were packed and transported to the labs.

**Kassanoi and Metochia outcrops.** In Kassanoi the plant remains were collected during the period of 2010–2012 using the traditional sampling method i.e., remove sediment blocks from the plant-bearing layers and split them searching for fossils (pl. V, fig. 3). The fossil material from Metochia was recovered in the same way during an expedition to Gavdos Island in September 2010.

All specimens from Pitsidia, Kassanoi and Metochia were fully exposed from the sediment using preparation needles. Afterwards, they were labeled and placed in boxes for storage.

#### 3.2.2. Plant material study

All the collected specimens were examined under a Motic SMZ-168 stereoscope. For the SEM study of selected specimens, the JEOL 6390LV scanning electron microscope of the University of Crete (for the wood fragment and the monocot foliage) and the JEOL 6320 of the University of Patras (for the rest specimens)
were used. Photographs were taken with a Nikon 5100 digital camera. For image adjustments and drawings, the Adobe Photoshop Software version 9.0 was used.

The identification of foliage was based on the macro-morphological features as the absence of organic matter didn’t allow the application of cuticular analysis. In the coriaceous or needle-like leaves and the reproductive organs (inorganic replicas) as well as in the coalified wood and monocot leaf fragments micro-morphological and anatomical structures were evaluated. It hasn’t been possible to identify all the collected specimens to at least the family level, as in many cases they did not present sufficient traits to rely on them. A list of the main leaf characters that have been taken under consideration is given in appendix 3 (text-fig. 3.1). For selected specimens, latex casts were prepared in order to understand better their morphology (e.g. pine long shoots and fertile cone scales).

![Text-figure 3.1. Principal leaf characters taken under consideration in this study](image)

The used morphological terminology for leaf architecture is based on Hickey (1973), Dilcher (1974), Ash et al. (1999) and Ellis et al. (2009) descriptions. The arrangement of Angiosperm taxa is based on the classification proposed by recent molecular phylogenetic studies, mainly REVEAL (2012), which follow the classification of Angiosperm Phylogeny group II (Bremer et al., 2003) and III (Bremer et al., 2009). Gymnosperms and ferns are arranged following the classification scheme of Christenhusz et al. (2011) and Christenhusz and Chase (2014) respectively.
3.2.3. Taphonomical study

**Sedimentological, chemical/geochemical analysis, leaf orientation.** For the grain size analysis of the plant-bearing and adjacent layers in Pitsidia the sieve and pipette methods were applied (FOLK, 1974). The % content of organic carbon was estimated by the titration method (GAUDETTE et al., 1974) and the % content of CaCO$_3$ by the CH$_3$COOH method (VARNAVAS, 1979). For the chemical analysis of the plant bearing sediment and the inorganic encrustation the energy dispersive X-ray spectroscopy was applied (SEM, University of Crete). This technique is based on the principle that each chemical element has a unique atomic structure allowing a different set of peaks on its electromagnetic emission spectrum.

**Mechanical damages on plant remains.** All the collected plant material from Pitsidia has been examined macroscopically tracing for post mortem mechanical damages:

a. after shedding - before burial, due to biostratonomic processes and
b. after burial, due to diagenetic processes.

**Enumeration of the assemblage.** In Pitsidia systematic excavation, in order to accomplish randomness, the collection of the total amount of the recovered fossils from each excavated grid square and level, regardless of their size, fragmentation, quality of preservation, origin and taxonomic value was attempted. This proved impossible because of the abundant and monotonous occurrence of leaf fragments mostly of *Myrica lignitum* and to a lesser degree of the small isolated bones, all a few cm in size, scattered throughout the excavated layers. Hence, in most cases, the collection of dicot leaves smaller than approx. 1/6 of their original size as well as most of the fish remains, mainly disarticulated backbones and opercula, were ignored.

In order to estimate the density of the plant material in the sediment, twelve sediment blocks (block Nrs 1–12) with a total volume of 50.3 dm$^3$ were collected and transferred to the NHMC labs (appendix 4). The volume of each block was estimated individually and all the recovered plant remains, excluding the leaf fragments <1/6, were collected and recorded. Disarticulated fish bones, were occasionally collected.

Technically, due to the mode of preservation of the plant fossils (as imprints) along with their high frequency, it was not possible to recover all the plant remains from the sediment. Exceptionally, for a more accurate estimation of the density of the fossils in the sediment, a fossil-destructive sampling method was employed in block Nr 13 (volume 4.8 dm$^3$). Using a knife, the free surface of the block was scratched looking for fossils. Fossils, when detected, were prepared properly, recorded, illustrated and finally partly or entirely destroyed as the scratching procedure continued to the layers beneath. With this method all the remains of both plant (including leaf fragments <1/6) and animal remains were detected and recorded in detail (appendix 13).
3.2.4. Palaeoenvironmental study

**Palaeovegetation.** For the classification of the assemblages in terms of zonal vegetation type, the integrated plant record (IPR) vegetation analysis, a semi-quantitative method based on taxonomic and ecological evidences, is applied (KOVAR-EDER et al., 2008, TEODORIDIS et al. 2011). The vegetation reconstruction of the three studied plant assemblages (Kassanoi, Pitsidia and Metochia) was undertaken using the phytosociological approach (MAI, 1995).

**Palaeo-syneology.** All the collected plant material has been examined for tracing of pre-mortem plant-arthropod interaction. In order to distinguish the damages caused by arthropod a combination of criteria has been used for each plant specimen (LABANDEIRA, 1998; LABANDEIRA et al., 2002; WILF et al., 2005):

i. the presence of plant reaction tissue,

ii. the occurrence of cuspatate chewed margins or veinal stringers,

iii. stereotyped patterns of leaf modifications, where size, shape and position are similar or almost similar to modern feeding damages and

iv. the targeting of particular plant tissues or host species.

The traces of arthropod action were identified using a series of distinctive features, including size, shape, position and pattern on the plant organ, special external and internal structural features as well as type and degree of plant tissue response. Modifications that were associated with trophic behavior were assigned, according to the mode of feeding, in particular functional feeding groups of terrestrial arthropods (LABANDEIRA et al., 2007). At the same time, for each feeding damage, an attempt was made to determine the degree of host specificity.

To fulfill the needs of this project, recent plant material from the botanical garden of the NHMC, as well as specimens available on line were examined macroscopically for arthropod modifications. At the same time, literature concerning pests and diseases that cause injuries to modern vascular plants was taken into account as well as recent reports on fossil plant-arthropod associations.

**Palaeoclimatic.** For palaeoclimatic estimates the coexistence approach (CA) (MOSBRUGGER and UTESCHER, 1997; UTESCHER et al., 2014) was applied. This method is based on the interpretation of the closest living relatives of the identified fossil taxa. The climatic data for the living relatives were retrieved from the Palaeoflora Database (UTESCHER and MOSBRUGGER, 2013).
4. RESULTS

4.1. Systematic palaeontology

In the following section all reliably identified plant taxa from Pitsidia, Metochia and Kassanoi are presented (appendices 5–8). Taxa with a questionable affinity are included in the “Incertaine sedis” where cumulative terms such as *Dicotylophyllum* spp., *Monocotylophyllum* spp., *Carpolithus* spp. and *Antholites* spp. have been applied. The synonym list includes the basic references as well as all the publications available to us from the Greek Tertiary localities. All studied specimens are referred with the collection numbers of the Natural History Museum of Crete.

4.1.1. The palaeofloras of Pitsidia, Kassanoi and Metochia

I. Algae

| Thallus | Fam. et gen. et sp. indet. | Pl. IX, fig. 1 |

**Material:** Pitsidia, one 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. Its limited preservation quality makes difficult any attempt to trace a more accurate systematic affinity. The sedimentary implications of the Pitsidia outcrop deliver a probable fresh-water or brackish character for this element.

II. Polypodiophyta

**Polypodiales** LINK

Fam. indet.

“*Pteris* oeningensis” UNGER

Pl. VIII, figs 1–13, 26; text-fig. 4.1

**Synonym list**

1847  *Pteris oeningensis* UNGER, p. 124, pl. 37, figs 6–7 (Freyberg)
1855  *Pteris oeningensis* UNGER – HEER, p. 39, pl. 12, fig. 5 (Schweizer Molasse, Upper Miocene)
1859  *Pteris oeningensis* UNGER – HEER, p. 154, pl. 145, figs 5–6 (Schweizer Molasse, Upper Miocene)
1954  *Pteridium oeningense* (UNGER) HANTKE – HANTKE pp. 40–41, pl. 1, figs 6–7 (Schrotzburg, Upper Miocene)

? 1986  *Pteridium aff. aquilinum fossilis* (L.) KUHN – VELITZELOS et KOBLOCH, pl. 12, fig. 6 (Skoura, Peloponnese, Pliocene)
Pteris cf. oeningensis UNGER – KLEINHÖLTER, pl. 14, fig. 8 (Pyrgos and Zacharo basins, Peloponnese, Messinian)

Pteridium aquilinum fossilis (L.) KUHN – BUTZMANN et al., p. 23 (Vegora, W. Macedonia, Messinian) (no figure)

Pteridophyta fam. indet. – ZIDIANAKIS et al., fig. 2a (Pitsidia, central Crete, Tortonian)

Material: Pitsidia, forty seven 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; 31.4.2.2201,ab; 31.4.2.2201aop,2203; 31.4.2.2256; 31.4.2.2387ii; 31.4.2.3142op; 31.4.2.3496aop,iii; 31.4.2.3630; 31.4.2.4082; 31.4.2.4112; 31.4.2.4179op,iv; 31.4.2.4256v; 31.4.2.4302; 31.4.2.4337; 31.4.2.4376; 31.4.2.4384; 31.4.2.4845; 31.4.2.4972; 31.4.2.5027,a,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; 31.4.2.5742ai; 31.4.2.5884aop; 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; 31.4.2.6478a,ii,iii; 31.4.2.6543ii; 31.4.2.6569iii; 31.4.2.6574a,bi; 31.4.2.6665a,b; 31.4.2.8243a,b).

Description: i. Ultimate, lateral pinnatifid segment (text-figure 4.1iv). Petiolulate, petiolule 1 mm long, segment coriaceous, ovate, 11 mm long and 6.5 mm wide, lobed; lateral lobes dense, alternate to sub oppositely 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, more or less enrolled, 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 angles of 45–85° from the midrib, straight or slightly curved, giving birth to numerous fine veinlets, originating at acute angles, once or twice dichotomised, seldom simple (in smaller lobes), first dichotomy at the first ¼ part of the vein, ending to the margin.

ii. Ultimate, lateral simple segment (text-fig. 4.1ii, iii). Mostly densely spaced, alternately to sub-oppositely arranged, lanceolate to oblong, more or less asymmetric, bent upwards, 6–9 mm long and 2.5–3.5 mm wide, apex acute to rounded, margin entire to erose; venation dichotomous, open, primary vein moderate, bent, secondaries fine, dense, in more than 7 pairs, mostly forked two times, first dichotomy at the first ¼ part of the vein, ending to the margin.

iii. Ultimate terminal segment (text-fig. 4.1i). Lanceolate to oblong in shape, slightly asymmetric, up to 11 mm long and 3 mm wide, apex bluntly acute, margin entire, venation similar to that of the lateral simple segments.

Remarks: These remains probably belong to a single fern species (text-fig. 4.1). As a complete frond has not been found yet, the described lateral ultimate segments most likely represent pinnulae or parts of lower division. Thus, the fronds of this fern possibly were bi- or more pinnate/pinnatifid.

On the basis of macro-morphological features of the segments such as shape, venation and especially enrolled margin, this material matches well with specimens that were described by UNGER (1847) from Freyberg (Styria, Austria) as Pteris oeningensis. Fertile structures which are of high systematic value have not been observed in the examined material although the enrolled margin of the segments suggests a possible marginal arrangement for the sporangia.
Polypodiophyta incertae sedis

Frond fragments type 1
Fam. et gen. et sp. indet.
Pl. VIII, figs 14–15

Material: Pitsidia, three incomplete segments (Nrs 31.4.2.1940bop; 31.4.2.2337i; 31.4.2.2337ii).

Description: Isolated segments, fragmentary, chartaceous in texture, shape ovate to lanceolate, more than 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.

Remarks: These specimens differ from “Pteris” oeningensis on the basis of the broader shape of the segment, the thinner texture and the not enrolled margin.
Frond fragments type 2
Fam. et gen. et sp. indet.
Pl. XLIII, figs 1–2

Material: Kassanoi, two fragmentary fronds (Nrs 31.6.2.112; 31.6.2.161aii,bii).

Description: Fronds sterile, probably lanceolate, more than 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 angles of more or less 45°, dichotomising close to the margin.

Remarks: Fern material from Kassanoi is rare and rather fragmentary.

III. Spermatophyta
Gymnospermae

Family CUPRESSACEAE
Genus Tetraclinis MASTERS

*Tetraclinis* cf. *salicornioides* (UNGER) KVAČEK
Pl. VIII, figs 20–23, 27–29; Pl. XLIII, fig. 18; Pl. XLIX, fig. 1

Synonym list

1847 *Thuites salicornioides* UNGER, p. 11, pl. 2, figs 1–4; pl. 20, fig. 8 (Radoboj, 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
1993 *Tetraclinis salicornioides* (UNGER) KVAČEK – VELITZELOS, pl. 2, figs 2–3 (Nea Stira, Euboea, Lower Miocene)
1994* Tetraclinis salicornioides* (UNGER) KVAČEK – KLEINHÖLTER, pl. 1, fig. 3; pl. 15, figs 10–11 (Pyrgos and Zacharo basins, Peloponnesse, Messinian)
1996 *Tetraclinis brachyodon* (BRONNIART) MAI and WALTER – SACHSE and MOHR, fig. 4.11 (Makrilia, E. Crete, Tortonian)
1997 *Tetraclinis* sp. – SACHSE, pl. 8, figs 3, 8 (Makrilia, E. Crete, Tortonian)
? 2002* Tetraclinis salicornioides* (UNGER) KVAČEK – VELITZELOS et al., p. 11 (Kimi, Euboea, Lower Miocene) (no figure)
2007 *Tetraclinis* sp. – ZIDIANAKIS et al., figs 2C–D (Vrysses, W. Crete, Messinian)
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, Lower Miocene) (no figure)
2015 *Tetraclinis salicornioides* (UNGER) KVAČEK – MANTZOUKA et al., figs 3.1–3.3 (Metochia, Gavdos Island, Tortonian)

Material:
Pitsidia, two incomplete leafy twigs and one isolated segment (Nrs 31.4.2.845; 31.4.2.6324ai,b; 31.4.2.6331aopi,6922opiv).
Kassanoi, two twig fragments (Nrs 31.6.2.182iii; 31.6.2.182iv).
Metochia, one leafy twig (Nr. 31.5.2.9).
**Description:** Incomplete twigs 1.5 to 7.5 cm long, broad and flattened; leaves scale-like, dimorphic (facial and lateral), born in four, fused in most of their length forming a flattened cladode-like segment that do not overlap between adjacent nodes; whorls cuneiform or narrow elongate in shape, 2.5–6 mm long and 1–3 mm wide with rounded to truncate base; facial leaves closely appressed with an acute apex, lateral leaves linear overlapping margins of facial leaves, mostly free-tipped, shorter than the facial leaves, apex acute, slightly incurved; three or five veins occur on each whorl according to their position.

**Remarks:** According to KVAČEK et al. (2000) two different species of Tetraclinis can be distinguished in the European Paleogene/Neogene, *T. brachyodon* (BRONGNIART) MAI and WALTHER and *T. salicornioides*, though there are some authors arguing for the existence of a single species (e.g. FERGUSON et al., 1998; MAI, 1998). Morphologically, these species differ mainly in bract morphology of the seed cone, stomata distribution, branching and to a lesser degree segment morphology and leaf fusion completion. In the studied assemblages seed cones were not found, leaf epidermis is not preserved and branching is merely available. The foliage fusion seems to be quite complete and segments are more or less broad, isomorphic. These features allowed us assuming that the material at hand possibly belongs to *T. salicornioides*. In order to verify the species determination, additional material is necessary such as the characteristic broad cuneiform segments or opposite branching twigs which are diagnostic features of this species. MANTZOUKA et al. (2015) reported one foliage twig and 2 detached leafy segments that were assigned to *T. salicornioides* from Metochia. Though not abundant, twigs of *Tetraclinis* are also present in the palaeofloras of Makrilia and Vrysses (SACHSE, 1997; ZIDIANAKIS et al., 2007).

*Tetraclinis salicornioides* was distributed over large parts of Europe and North America since the Lower Eocene (KOVAR-EDER et al., 1994; MEYER and MANCHESTER, 1997; KVAČEK et al., 2000; GÜMBEL and MAI, 2002). Today, this genus is monotypic. The extant representative, *Tetraclinis articulata* (VAHL) MASTERS is endemic in northern Africa, southern Spain and Malta, adapted to warm summer-dry climates. Its autecology seems to differ from that of the fossil species. *T. salicornioides* was a frequent accessory element of sub-tropical to warm-temperate mesophytic forests (KVAČEK, 1989; MAI, 1994; KVAČEK et al., 2000).

**Genus Taxodium L.C. RICHARD**

*Taxodium dubium* (STERNBERG) HEER

Pl. IX, figs 2–20, 22–23

**Synonym list**

1823 Pyllites dubius STERNBERG, p. 37, pl. 36, fig. 3, tentamen and index (Bílina, Lower Miocene)
1853 *Taxodium dubium* (STERNBERG) – HEER, p. 136
1855 *Taxodium dubium* (STERNBERG) HEER – HEER, pp. 49–50, pl.17, figs 5–15 (Hohe Rhonen, Upper Miocene)
Sequoia langsdorfii (BRONGNIART) HEER – UNGER, pl. 2, figs. 22–23 (Kimi, Euboea, Lower Miocene)

Taxodium dubium (STERNBERG) HEER – HEIMANN et al., pl. 14, fig. 4 (Paghi, Corfu Island, Messinian)

Sequoia langsdorfii (BRONGNIART) HEER – VELITZELOS and SCHNEIDER, fig. 4 (Vegora, W. Macedonia, Messinian)

Taxodium vel Sequoia spec. – VELITZELOS, pl. 1, figs 1, 6 (Pappades, Euboea, Upper Miocene)

Taxodium spec. – VELITZELOS, pl. 1, figs 1, 6 (Pappades, Euboea, Upper Miocene)

Material: Pitsidia, eighty two 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; 31.4.2.1021; 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; 31.4.2.2158ab; 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; 31.4.2.2563; 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; 31.4.2.3150aiv,3158; 31.4.2.3223; 31.4.2.3372vii; 31.4.2.3589a; 31.4.2.3614a,b; 31.4.2.3842a,b; 31.4.2.4023a,b; 31.4.2.4137a,bi; 31.4.2.4303a,b; 31.4.2.4455; 31.4.2.4468ai,bi; 31.4.2.4540ai,bi. 31.4.2.4540aai,bi; 31.4.2.4683; 31.4.2.4856; 31.4.2.4861ai,bi; 31.4.2.4864a,bi; 31.4.2.4888; 31.4.2.4906a,b; 31.4.2.4946ii; 31.4.2.4991a,b; 31.4.2.4993a,bi; 31.4.2.5307; 31.4.2.5564; 31.4.2.5687; 31.4.2.5744a,b; 31.4.2.5747; 31.4.2.5788ai,b; 31.4.2.5979; 31.4.2.6093; 31.4.2.6050op; 31.4.2.6123a,bi; 31.4.2.6124a,bi; 31.4.2.6235; 31.4.2.6388a,bi; 31.4.2.6577a,bi; 31.4.2.6782aop; 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 single leaves. They can be separated in three different shoot types according to leaf size and spreading:

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

ii. Shoot more than 30 mm long with flattened, bifacial needle-like leaves, straight, 7–13 mm long and 0.8–1.2 mm wide, originating at angles of 25–40°, spreading in one plane (distichously) despite the helical arrangement as the needles are twisted at their basal part, needle base somewhat decurrent, tapering into an acute apex, margin entire; mid-vein strong, well distinguished; needles longer near the middle part of the short shoot or below, decreasing in length and width towards the apex.
iii. Shoots quite similar to the second type, but needles longer (13–20 mm), occasionally curved, apex sometimes mucronate, originating at more open angles (35–50°).

In cross section, inorganic replicas of the needles are characterized by a prominent vascular bundle, but resin ducts have not been detected. Stomatal structures were not preserved.

**Remarks:** Sterile shoots with needle-like, distichously arranged leaves occur in four different genera of the Cupressaceae family, *Glyptostrobus*, *Sequoia*, *Taxodium* and *Metasequoia*. 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 correspond better to *Taxodium* (KUNZMANN et al., 2009). Since the Lower Oligocene, this genus, was a significant element in back swamps and near-shore riparian forests (MAI and WALTER, 1978; PETRESCU and GIVULESCU, 1986; WALther and EICHLER, 2010), while it is relict conifer taxon today. Most authors distinguish two different species, *T. distichum* (L.) L. C. RICHARD and *T. mucronatum* TENORE distributed in SE North America and Central America respectively (FARJON, 2001). Its populations thrive in swampy or poorly drained areas of subtropical and warm-temperate regimes (URNS and HONKALA, 1990; FARJON, 2005). A few incomplete shoots of *Taxodium dubium* have been also reported from the localities of Makrilia and Metochia (SACHSE, 1997; MANTZOUKA et al., 2015).

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**Family PINACEAE**

**Genus Pinus L.**  
Subgenus: *Pinus* L.

*Pinus pitsidiensis* ZIDIANAKIS, ILIOPoulos, ZEliLIDis and KOVAR-EDER  
Pl. X, figs 1–12; pl. XI, figs 1–12; pl. XVI figs 1–3, 5–8; text-fig. 4.2

**Synonym list**

2010 *Pinus* sp. – ZIDIANAKIS et al., fig. 2c (Pitsidia, central Crete, Tortonian)

2016 *Pinus pitsidiensis* ZIDIANAKIS, ILIOPoulos, ZEliLIDis and KOVAR-EDER – pl. 2, figs 1–12, pl. 3, figs 1–12 (Pitsidia, central Crete, Tortonian)

**Material:** Pitsidia  
**Holotype:** Nr 31.4.2.2013a,b, a long shoot with closely arranged three-needled fascicles, at least one of them physically attached (pl. XI, fig. 10)

**Paratypes:** Dwarf shoots with fragmented needles in fascicles of three, Nrs 31.4.2.3372i; 31.4.2.3873 (four-needled); 31.4.2.3874; 31.4.2.5430ai,bi; 31.4.2.6102i; needles, Nrs 31.4.2.2782; 31.4.2.3498i; 31.4.2.3698ai,bi; 31.4.2.3857i; 31.4.2.5978aiii; 31.4.2.6668ii; long shoots, Nrs 31.4.2.2010a,b; 31.4.2.2141a,b.

**Additional material:** Four hundred ninety two pine dwarf shoots bearing fragmented needles in fascicles of three, fifty fragments of pine long shoots (branchlets), numerous isolated needle fragments (for collection numbers of the specimens see appendix 9a).

**Type locality:** Pitsidia, Messara Basin, central part of southern Crete, Greece.

**Type stratum:** Ampelouzos (sensu MEULENKAMP et al., 1979) or Kasteliana (sensu ZACHARIASSE et al., 2011) Formation.
**Age:** Lower Tortonian.

**Etymology:** From the Greek name of the village Pitsidia located near the fossiliferous outcrop.

**Repository:** Natural History Museum of Crete, Greece

**Diagnosis:** Dwarf shoots with three (exceptionally four) needles per fascicle; basal sheath prominent, persistent; needles typically up to 30 cm long, rather wide; needle in cross-section originally flabellate; margin entire, apex more or less acute; stomata arranged in rows on both sides, usually 7–11 rows adaxially and 7-8 abaxially; usually 7–10 resin ducts per needle, positioned both ventrally and dorsally, most of them externally but also positioned medially; long shoots are characterised by external scars forming a distinctive pattern of more or less complete rhombi.

**Description:** Dwarf shoots with three, exceptionally four needles (less than 1% of all shoot findings); a prominent basal sheath is formed by several spirally-arranged, scaly leaves covering the dwarf shoot and the needle base, always persistent, (3) 10–15 (21) mm (average 12.3 mm) long, and (1.5) 2.5–4 (5) mm (average 3.1 mm) wide, with somewhat swollen, rounded bases. Needles typically up to 30 cm long or even longer, (Nr 31.4.2.3372i 30.5 cm long) never twisted, (0.7) 1.1–1.6 (1.7) mm (average 1.3 mm) wide, about 0.7–0.9 mm thick; needle shape in cross-section originally flabellate, secondarily flattened, apex more or less acute, margin entire; imprint of the adaxial needle surface finely striate, abaxially medial-keeled; needles amphistomatic, stomata in well defined, continuous, irregularly spaced, longitudinally arranged rows, usually 7–11 rows adaxially and 7–8 abaxially, stomata regularly spaced within rows, 10–15 per 1 mm of the row; resin ducts numerous, (4) 7–10 (11) (average 8.8), all in the palisade parenchyma, mainly externally but also medially positioned adaxially and abaxially; almost always an external duct runs along the ventral keel and a medial one on each needle edge; duct about 25–80 μm (average 35 μm) in diameter.

Long shoots. Fragments, mainly defoliated, specimen Nr 31.4.2.2013a,b with at least one three-needled fascicle physically attached; shoot fragments 10–80 mm long and 5–20 mm wide, the longer fragments consisting of two internodes; surface covered by three different types of helically arranged scars: type A dense, elliptic to short rhomboid or even linear scars, forming a ring; type B situated above the type A ring, mainly rhomboid to flabellate or 4- to 5-sided scars, larger than type A; type C consisting of two superimposed scars, the basal one more or less flabellate to cordate or 4- to 5-sided in shape crowned by a circular to slightly elliptical scar, basal scar 1.5–4 mm high (average 2.4 mm) and 2–5.5 mm wide (average 3.3 mm), height/width index 0.6–1 (average 0.7); and type C scars form a characteristic, distinctive pattern on the long shoots of more or less complete, helically-arranged rhombi, rhombus side (2) 2.5–3.5 (4.0) mm long.

**Remarks:** Three-needled fascicles are notably abundant in the Pitsidia outcrop. Only *Myrica* leaves and catkins occur in higher frequencies (ZIDIANAKIS et al., 2015). These fascicles are scattered throughout the fossiliferous sediments and are extremely abundant in a single horizon at the top of the fossiliferous sequence (about 60–80 fascicles per m²) (pl. IV, fig. 4).
All *Pinus pitsidiensis* dwarf shoots bear needles in fascicles of three. Specimens with four-needled fascicles are very rare (pl. X, fig. 3). Their features like the persistent basal sheath, the almost constant number of three needles per fascicle combined with the amphistomatic character of the needles allows to assign this species to the subgen. *Pinus* (table 2 in appendix 10; see also in Discussion). However, the unique features of this material distinguish this species from any other ancient or extant pine and support the description of a new species.

In specimens Nrs 31.4.2.2013a,b (holotype) and 31.4.2.2010 (paratype) long shoot fragments of *Pinus* are in close association with several three-needled fascicles (pl. XI, fig. 10). The orientation of the fascicles indicates that they were originally attached to the long shoots and got disarticulated after their deposition. In the holotype at least one fascicle is physically attached to the long shoot.

Based on comparisons with recent pine material, it is possible to interpret the three different scar types on the surface of the long shoots as follows: type A appears to be the bud scale scars which form the bud scale ring at the base of each branchlet interval (pl. XI, figs 6, 14); type B appears to be the scars left by the “sterile” fascicle bracts, i.e., the bracts that do not bear an axillary dwarf shoot (pl. XI, figs 7, 14); and type C, the scar of a “fertile” fascicle bract accompanied by the scar of its axillary dwarf shoot just above (“fertile” is defined here as a fascicle bract that subtends a dwarf shoot) (pl. XI, figs 8–9, 12–16).

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**Text-figure 4.2.** Line drawings; a. *Pinus* organs explaining the terms used in the text, 1. needle in cross-section; 2. fascicle bract; 3. winged seed; 4. ovulate cone scale, dorsal view; 5. ovulate cone scale, ventral view; 6. pollen cone scale, dorsal view; 7. pollen cone scale, lateral view; 8. bud scale; b. resin duct patterns of *Pinus pitsidiensis* needles in cross-section, the empty spots correspond to external ducts, while the full dots represent medial ones, the number on the right corresponds to the width of the inorganic needle replica.
In the Cretan area three-needled pine remains have been found in Vrysses (a single specimen of a dwarf shoot with very long, entire-margined needles, pl. XV, fig. 18) and in the Early Pleistocene marine deposits of Prassas close to Iraklion, well known for its fish fauna (GAUDANT et al., 1994) (a single specimen of a dwarf shoot with broad, incomplete needles; pl. XV, fig. 17). Both have been preserved as imprints in marls and diatomites respectively. These findings are reported for the first time and are housed in the NHMC under the Nrs 32.1.2.355 (Vrysses) and 30.1.2.181 (Prassas).

*Pinus* sp. – two-needled fascicles
Pl. XV, fig. 16

**Synonym list**

? 1997 *Pinus cf. hepios* (UNGER) HEER – SACHSE, pl. 8, fig. 15 (Makrilia, E. Crete, Tortonian)

? 2007 *Pinus* sp. – ZIDIANAKIS et al., figs 2A–B (Vrysses, W. Crete, Messinian)

2016 *Pinus* sp. – two-needled fascicles – ZIDIANAKIS et al., pl. 7, fig. 16 (Pitsidia, central Crete, Tortonian)

**Material:** Pitsidia, two fragmentary fascicles (Nrs 31.4.2.2871; 31.4.2.8183).

**Description:** Dwarf shoots with two needles, basal sheath 1 mm wide, persistent; needles more than 6.8 cm long and 0.6–0.8 mm wide.

**Remarks:** These fascicles are extremely rare in the assemblage and clearly differ from *Pinus pitsidiensis* in needle size and in the number of needles per fascicle. The persistent basal sheath, along with the two needles per fascicle, suggest an affinity to subgen. *Pinus*.

Two-needled pine remains have been reported from all the known plant-bearing localities of Crete. The material from Pitsidia matches well with that of Vrysses (as *Pinus* sp.) as well as with the *Pinus cf. hepios* (UNGER) HEER from Makrilia in the sense of their slender needles.

*Pinus* sp. – fascicle bracts
Pl. XII, figs 1–25; text-fig. 4.2

**Synonym list**

2016 *Pinus* sp. – fascicle bracts – ZIDIANAKIS et al., pl. 4, figs 1–25 (Pitsidia, central Crete, Tortonian)

**Material:** Pitsidia, four hundred thirty nine isolated fascicle bracts and one specimen with a group of attached fascicle bracts (for collection numbers of the specimens see appendix 9a).

**Description:** Bract scarious, sessile, (8) 10–17 (20) mm (average 14.7 mm) long, (2) 3.5–5 (7) mm (average 4.3 mm) wide, length/width index typically 2–3.8 (average 2.9), lanceolate or subulate to narrow triangular in shape, more or less curved inwards along their length, at the upper third part strongly tapering, apex acute or mostly acuminate; bract margin entire to erose, seldom ciliate; surface on both sides smooth with a well distinguished longitudinal striation; no stomata or resin ducts observed.
Pulvinous thin, (1) 2–4 (7) mm (average 3.1 mm) long, (2) 3–5 (7) mm (average 4.3 mm) wide; shape variable, mainly cordate to flabellate or broad elliptic to rhomboid, less frequently irregularly five- to four-sided or even triangular, all sides more or less curved; base acute to obtuse, apex rounded to reflexed; with an inconspicuous fine striation abaxially. Bract/pulvinous length index about 1.8–9 (average 5).

In specimen Nr. 31.4.2.7032a, b (pl. XII, fig. 18), six fascicle bracts attached on a tiny fragment of a long shoot; spirally arranged.

**Remarks:** The base of fascicle bracts often retain a portion of the external layers of the long shoot, herein referred as the pulvinous, when they fall off (text-fig. 4.2; pl. XI, fig. 16; pl. XII, fig. 26). Fascicle bracts are normally curled (pl. XI, fig. 15; pl. XII, fig. 29). However, they uncurl and flatten out in water so their appearance would be similar to the forms seen in the fossil material (pl. XII, figs 26–27). Judging from specimen Nr. 31.4.2.7032a,b the bract attachment on the long shoot is decurrent (pl. XII, fig. 18). This feature is consistent for the separation of the two subgenera *Pinus* and *Strobus*, although CARVAJAL and McVAUGH (1992) recognized a somewhat intermediate condition in the species of subsect. *Cembroides* (subgen. *Strobus*) (SHAW, 1914; LITTLE and CRITCHFIELD, 1969; PRICE et al., 1998; GERNANDT et al., 2005). In this sense the fascicle bracts are assigned to the subgen. *Pinus*.

Several fascicle bracts are less than 11 mm long, broad ovate to elliptic in shape with an obtuse to more or less rounded apex (pl. XII, figs 20–23). This material either represents strongly weathered (on the tree) forms or derives from a different pine species.

*Pinus* sp. 1 – ovulate cone scales
Pl. XIII, figs 1–7; text-fig. 4.2

**Synonym list**
2016 *Pinus* sp. 1 – ovulate cone scales – ZIDIANAKIS et al., pl. 5, figs 1–7 (Pitsidia, central Crete, Tortonian)

**Material:** Pitsidia, five cone scales; four complete and one fragmentary (Nrs 31.4.2.1262a-c; 31.4.2.7012a,b; 31.4.2.7015; 31.4.2.7016a,b; 31.4.2.7018a,b).

**Description:** Seed scales 20–40 mm long and 12–18 mm wide, obovate to flabellate or rhomboid in shape, apex rounded, base rounded to cuneate; sealing band well defined, apophysis 11–13 mm long and 12–18 mm wide, irregularly hexagonal in shape, smooth, transversally keeled, slightly raised (about 5–6 mm), terminating in a relatively small, dorsally positioned umbo; in the lower field of the apophysis 2–3 weakly-developed, longitudinal keels, running from the umbo towards the sealing band; umbo protuberant, rhomboidal to ovate in shape, about 1.5 mm long, 3.0 mm wide and 1.0 mm high, rather distally located, avallate, always unarmed; mucro not observed; on the ventral side of the seed scales, impressions of winged seeds sometimes visible; seed body area flat, about 3.5–5.0 mm long, 1.5–2.5 mm wide, in specimen Nr 31.4.2.7018a, b (pl. XIII, fig. 4) one seed body ca. 8 mm long and 6 mm wide with a pronounced cavity in
the position of the seed body, the other one with a smaller and flat seed body area ca. 3.5 mm long and 2.5 mm wide; seed wing about 13.5–18 mm long and 4–6 mm wide, triangular to ovate in shape with an obtuse, rounded apex.

**Remarks:** Judging from the size and morphology of the seed body area, the cone scale Nr 31.4.2.7018a, b (pl. XIII, fig. 4) shows two unequally-sized seeds, with only one of them being fully developed (see also the description of isolated seeds below). Due to the small and flat seed body area and the cuneate scale base, the seeds on the other cone scales probably were also not fully developed. All these cone scales are unambiguously assigned to the subgen. *Pinus* based on the presence of the sealing band and the dorsal position of the umbo.

**Subgenus Strobus** LEMMON

*Pinus* sp. 1 – five-needled fascicles
Pl. XI, figs 13–15; text-fig. 4.2

**Synonym list**
2016 *Pinus* sp. 1 – five-needled fascicles – ZIDIANAKIS et al., pl. 7, figs 13–15 (Pitsidia, central Crete, Tortonian)

**Material:** Pitsidia, thirteen fragments of five-needled fascicles, twelve isolated needles (Nrs 31.4.2.838; 31.4.2.839; 31.4.2.1133; 31.4.2.2767a,bi; 31.4.2.2817; 31.4.2.2820a,b; 31.4.2.2911aii,b,c; 31.4.2.2940ai,bi; 31.4.2.3014; 31.4.2.3078i; 31.4.2.3200a,b; 31.4.2.3220; 31.4.2.3262; 31.4.2.3275i; 31.4.2.3349; 31.4.2.3355; 31.4.2.4659ai,bi; 31.4.2.4800; 31.4.2.4921a,b; 31.4.2.6226; 31.4.2.6325ai,b; 31.4.2.6829; 31.4.2.6847aii,bi; 31.4.2.6882; 31.4.2.8223aop).

**Description:** Dwarf shoots with five needles, basal sheath 4.5–8 mm long and 1.5 mm wide, persistent; needles fine, more than 70 mm long and 0.5–0.7 mm wide. In specimen Nr 31.4.2.2820a five external resin ducts are distinguished in the needle parenchyma.

**Remarks:** No fascicle with complete needles has been found in the assemblage. Most needles were fragmented due to their delicate character or broken secondarily as a result of sediment slumping and cracking. The higher number of needles per fascicle (5 versus 3), the more delicate and markedly shorter needles, and the less profound basal sheath clearly differentiate this material from *Pinus pitiadiensis*. Five needles per fascicle and external resin ducts are very common features in subgen. *Strobus* (appendix 10). Contrary to our specimens, in this subgenus the basal sheath is almost always deciduous.

SACHSE (1997) reported one specimen of a five-needled pine in Makrilia, without any illustration. In this study a needle fragment is also described from Metochia that probably belongs to a five-needled pine on the basis of its cross-section shape.
Pinus sp. 2 – five-needled fascicles
Plate XLIX, fig. 2

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

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

Remarks: The original length of this needle is unknown. Its shape in cross-section indicates a five-needled pine species. MANTZOUKA et al. (2015) reported from Metochia the occurrence of wide needles (2.0–2.6 mm) with a preserved length of 8–43 mm, in fascicles of two, without a sheath.

Pinus sp. 2 – ovulate cone scale
Pl. XIII, fig. 8

Synonym list
2016 Pinus sp. 2 – ovulate cone scale – ZIDIANAKIS et al., pl. 5, fig. 8 (Pitsidia, central Crete, Tortonian)

Material: Pitsidia, one cone scale (Nr. 31.4.2.7017).

Description: Scale fragment, 15 mm long and 12 mm wide, obovate or elliptic in shape, apex rounded; without a sealing band; umbo terminal, rhomboidal, 1 mm long, 2.5 mm wide and 1–2 mm high, unarmed.

Remarks: The lack of a sealing band and the terminal position of the umbo differentiate this scale from that of Pinus sp. 1 – ovulate cone scales and indicate affinity with the subgen. Strobus.

Not assignable to a specific subgenus

Pinus sp. 1 – fully developed seeds
Pl. XIII, figs 9–12; text-figs 4.2–4.3

Synonym list
2016 Pinus sp. 1 – fully developed seeds – ZIDIANAKIS et al., pl. 5, figs 9–12 (Pitsidia, central Crete, Tortonian)

Material: Pitsidia, twelve seeds; one complete and eleven fragmentary (Nrs 31.4.2.1203ii; 31.4.2.2571a,b; 31.4.2.3811opi; 31.4.2.4138; 31.4.2.4971i,4956i; 31.4.2.5108a,b; 31.4.2.5109a,b; 31.4.2.5841a,b; 31.4.2.6196; 31.4.2.6249a,b; 31.4.2.6497; 31.4.2.6941aii,b).

Description: Seeds with adnate wing. Seed body large, broadly ellipsoid to slightly ovate (secondarily flattened), 7–11 (average 9.5) mm long, 4–8 (average 6.5) mm wide, apex and base more or less broad, rounded; wing membranous, shape ovate to deltoidal, about 22–23 mm long, 8 mm wide, seed body/wing
ratio about 1:1.5–1:2.5); one side of the seed and the wing surface with distinctly undulate striations running parallel to the long axis, wing surface with more or less perpendicular wrinkles.

**Remarks:** The undulate striations and the perpendicular wrinkles on the wing surface, strongly support a pine affinity of the examined seeds. A further assignment of the isolated pine seeds to the species level is problematic because of wide infra-specific variation and inter-specific overlap. In a few specimens the seed body is lacking and the remaining wing is damaged at the seed body area (pl. XII, fig. 12).

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**Text-figure 4.3. Palaeoflora of Pitsidia, Crete, *Pinus* sp. line drawings,**

1. pulvinous shapes of *Pinus* sp. – fascicle bracts; 2. seed of *Pinus* sp. 1 – fully developed seeds, Nr. 31.4.2.5108a; 3–8. seeds of *Pinus* sp. – underdeveloped seeds; 3. Nr. 31.4.2.5374a; 4. Nr. 31.4.2.2300iii; 5. Nr. 31.4.2.4990; 6. Nr. 31.4.2.3307; 7. Nr. 31.4.2.1586i; 8. Nr. 31.4.2.2183aiii; scale bar 0.5 cm.

**Synonym list**

*Pinus* sp. 2 – fully developed seeds

Pl. XIII, figs 23–24; text-figs 4.2

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**Pinus** sp. 2 – fully developed seeds

Pl. XIII, figs 23–24; text-figs 4.2

**Material:** Pitsidia, four seeds; one complete and three fragmentary (Nrs 31.4.2.4492i; 31.4.2.4537aii,c; 31.4.2.4690; 31.4.2.8241a,b).

**Description:** Isolated seeds with an adnate wing; seed body ovate (secondarily flattened), 4–5 mm long, 3–3.5 mm wide, apex relatively narrow; wing membranous, more than 15 mm long and ca. 8 mm wide, surface with undulate striations and perpendicular wrinkles.

**Remarks:** The undulate striations and the perpendicular wrinkles indicate again a pine affinity for these seeds. They are distinguished from *Pinus* sp. 1 by the remarkably smaller seed body.
**Pinus sp. – underdeveloped seeds**

Pl. XIII, figs 13–18, 20, 22; text-figs 4.2–4.3

**Synonym list**

2010 *Pinus sp.–ZIDIANAKIS et al., fig. 2f (Pitsidia, central Crete, Tortonian)*

2016 *Pinus sp. – underdeveloped seeds – ZIDIANAKIS et al., pl. 5, figs 13–18, 20, 22 (Pitsidia, central Crete, Tortonian)*

**Material:** Pitsidia, ninety seeds; eleven complete and seventy nine fragmentary (Nrs 31.4.2.833,839; 31.4.2.111i; 31.4.2.1129a,b; 31.4.2.1301op; 31.4.2.1582i,1584i; 31.4.2.1586i; 31.4.2.1715aopii; 31.4.2.1985a,bi; 31.4.2.2114; 31.4.2.2138a,b; 31.4.2.2159bopii; 31.4.2.2183a,i,bi;ii; 31.4.2.2288iiii; 31.4.2.2300i; 31.4.2.2307; 31.4.2.2314bop; 31.4.2.2370; 31.4.2.23710; 31.4.2.23729; 31.4.2.2813,2777i; 31.4.2.2960aop; 31.4.2.3027a,bi; 31.4.2.3051,3050op; 31.4.2.3098op; 31.4.2.3126a,b; 31.4.2.31282; 31.4.2.3304op; 31.4.2.3491i,3482bopi; 31.4.2.3486a,b; 31.4.2.3592a,bi; 31.4.2.3637aopiii; 31.4.2.3637a,bi; 31.4.2.3886a,b; 31.4.2.3923a,bi; 31.4.2.4074i; 31.4.2.4101bii; 31.4.2.4133a,b; 31.4.2.4136; 31.4.2.4159,4161ii; 31.4.2.4172; 31.4.2.4181; 31.4.2.4182; 31.4.2.4183; 31.4.2.4250aopii; 31.4.2.4327i; 31.4.2.4329ii; 31.4.2.4338a,bi;ii; 31.4.2.4393a,b; 31.4.2.4482; 31.4.2.4513; 31.4.2.4539aopii; 31.4.2.4545; 31.4.2.4563,4565aop; 31.4.2.4620a,bi; 31.4.2.4622b,ii; 31.4.2.4655a,b; 31.4.2.4694; 31.4.2.4724a,ii; 31.4.2.4814; 31.4.2.4963i; 31.4.2.4990; 31.4.2.5048; 31.4.2.5117ii; 31.4.2.5136a,b; 31.4.2.5142; 31.4.2.5230i; 31.4.2.5374a,b; 31.4.2.5496iii; 31.4.2.6149aopii; 31.4.2.6149aopiii; 31.4.2.6169i; 31.4.2.6230op; 31.4.2.6260i; 31.4.2.6262opiv; 31.4.2.6345opii; 31.4.2.6361bopii; 31.4.2.6394a,b; Nr. 31.4.2.6437aopiii; 31.4.2.6437aopii; 31.4.2.6502op; 31.4.2.6532ii; 31.4.2.6582; 31.4.2.6590; 31.4.2.6667a,b; 31.4.2.6758ii; 31.4.2.6942aop; 31.4.2.6964op; 31.4.2.6981; 31.4.2.8064; 31.4.2.8070; 31.4.2.8102op; 31.4.2.8158; 31.4.2.8184i; 31.4.2.8232ai).

**Description:** Seed body small, not placed terminally, ovate to ellipsoidal, rarely spherical in shape (secondarily flattened), 1.5–4.5 mm long, 1–3 mm wide, apex obtuse or acute, base obtuse, rounded, with undulate striation on the surface of one side. Wing 13–26 mm long and 5–9 mm wide, quite variable in shape, more or less obdeltoidal, ovate to obovate or elliptic, abmedial side mainly concave, admedial side slightly convex, the widest part commonly occurs at the distal half of the wing, apex more or less acute or obtuse, mostly rounded, surface with undulate striations and perpendicular wrinkles; seed body/wing ratio about 1/4 to 1/8.

**Remarks:** In living pines, the basal and apical scales of the ovulate cones commonly are sterile or their ovules are aborted at an early stage of their development. The result is either a bare wing or an underdeveloped seed body, e.g., WOLFE and SCHORN (1990), ERWIN and SCHORN (2006). In the specimens at hand, the position of the seed bodies (not terminally) indicates their incomplete development (pl. XIII, figs 19–22).

*Pinus sp. 1 – pollen cones*

Pl. XIV, figs 1–13; pl. XVI, fig. 4; text-fig. 4.2

**Synonym list**

2016 *Pinus sp. 1 – pollen cones – ZIDIANAKIS et al., pl. 6, figs 1–13 (Pitsidia, central Crete, Tortonian)*

**Material:** Pitsidia, sixty seven pollen cones; eight complete, fifty nine fragmentary and numerous isolated pollen scales (microsporophylls) (Nrs 31.4.2.983; 31.4.2.1180a,b; 31.4.2.1195; 31.4.2.1204,1195; 31.4.2.1277i; 31.4.2.1377; 31.4.2.1615,1597; 31.4.2.1631,1611aop; 31.4.2.1673; 31.4.2.1675a,b; 31.4.2.1729i; 31.4.2.1821a,bi; 31.4.2.1868a,b; 31.4.2.1905i; 31.4.2.2334; 31.4.2.2369a,bi; 31.4.2.2372a,bi; 31.4.2.2457op; 31.4.2.2522a,b; 31.4.2.2524i; 31.4.2.2595,2597a,ii; 31.4.2.2678ii; 31.4.2.2695bi; 31.4.2.2696; 31.4.2.3059;
Description: Pollen cones, 28–32 (average 30.3) mm long, 3.5–8 (average 5.4) mm wide, obovate in shape (secondarily flattened); microsporophylls numerous, helically-arranged; peltum semicircular, about 0.7–1 mm long, 1.5–2 mm wide, margin more or less entire, surface reticulate; a pair of elongated microsporangia attached ventrally, about 1.5–2 mm long, 0.5 mm wide, dehiscent longitudinally; basal bracts of the cones ca. 3–9 mm long.

Remarks: In the examined specimens, microsporophylls are more or less attached to the cone axis. Bare cone axes are rather rare while isolated microsporophylls are quite common but due to their small size they are inconspicuous. In Nrs 31.4.2.5890aop and 31.4.2.8241a, a few isolated microsporophylls are close to a pollen cone seemingly detached after the final deposition of the cone but prior to being covered by sediment (pl. XVI, fig. 4).

**Pinus** sp. 2 – pollen cones

Pl. XIV, figs 14–18; text-fig. 4.2

Synonym list

2016 **Pinus** sp. 2 – pollen cones – ZIDIANAKIS et al., pl. 6, figs 14–18 (Pitsidia, central Crete, Tortonian)

Material: Pitsidia, sixteen complete pollen cones (Nrs 31.4.2.844aop; 31.4.2.959; 31.4.2.1917ii; 31.4.2.3115aii; 31.4.2.5179a,b; 31.4.2.5597; 31.4.2.5778; 31.4.2.5612ai,b; 31.4.2.6140a,b; 31.4.2.6204; 31.4.2.6310; 31.4.2.8120; 31.4.2.8221i; 31.4.2.8222i; 31.4.2.8233; 31.4.2.8236).

Description: Pollen cones 7–14 mm long and 2–3.5 mm wide, elliptic to slightly obovate in shape (secondarily flattened); several microsporophylls helically arranged; peltum semicircular, rather curved, surface reticulate, basal bracts of the cones ca. 1–3 mm long.

Remarks: The cone axis, microsporophylls and basal bracts are smaller in these pollen cones than in the former species, whereas the peltum is more elongated and rather curved (for comparison see pl. XIV, figs 12–13 and pl. XIV, figs 17–18).

**Pinus** sp. – bud scales

Pl. XV, figs 1–12; text-fig. 4.2

Synonym list

2016 **Pinus** sp. – bud scales – ZIDIANAKIS et al., pl. 7, figs 1–12 (Pitsidia, central Crete, Tortonian)

Material: Pitsidia, four hundred forty six isolated bud scales (for collection numbers of the specimens see appendix 9a).
**Description:** Scales membranaceous, sessile, typically (12) 14–20 (24) (average 17.1) mm long, (2.5) 3.5–5.0 (6.5) (average 4.1) mm wide, lanceolate to delta-shaped, more or less curved inwards, apex acuminate; margin mainly conspicuously fringed by numerous densely spaced trichomes, 1–2 mm, occasionally up to 3 mm, long.

**Remarks:** Comparing the bud scales with the fascicle bracts, the bud scales are thinner, with an acuminate apex and dense trichomes at the margin.

Pinaceae, gen. et sp. indet. – coalified wood  
Pl. XVI, figs 9–17

**Material:** Pitsidia, one coalified wood fragment without bark (Nr. 31.4.2.7011).

**Description:** Small wood fragment, coalified; in transverse section growth ring boundaries distinct, composed of axial early and latewood tracheids, earlywood tracheids angular, pentagonal to hexagonal in shape, occasionally rounded, transition from early to latewood gradual, latewood tracheids thick-walled, axial parenchyma not found, normal axial intercellular resin canals are present, epithelial cells are not preserved; in radial section pitting in radial walls of early-wood 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 are present.

**Remarks:** The wood structure of the examined fragment is homogenous, composed of tracheids with distinct growth ring boundaries. In this sense, it belongs to the conifers (WATSON and DALLWITZ, 2008). The presence of resin ducts accounts for the assignment to the Pinaceae (YOUNG and WATSON, 1969). Among the modern members of Pinaceae, both axial and horizontal normal resin ducts occur in the genera of 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. IX, fig. 21

**Material:** Pitsidia, one incomplete leafy shoot (Nr. 31.4.2.4290a,b).

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

**Remarks:** The shape of the attached leaves suggests a gymnosperm affinity for this specimen. The lack of epidermal structures hinders a more accurate determination.
Shoots  
Fam. et gen. et sp. indet.  
Pl. XL, figs 1–3

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

Description: Long shoots 38–53 mm long, nodes surrounded by numerous dense 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. VIII, figs 16–19

Material: Pitsidia, four needle-like leaves; three complete, one almost complete (Nrs 31.4.2.4439aii,bii; 31.4.2.5521; 31.4.2.5603; 31.4.2.5822ii).

Description: Isolated needle-like leaves, sessile, linear to lanceolate, 0.7–11 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 do not seem to be easily identifiable due to the lack of diagnostic features. A Pinaceae or/and Cupressaceae origin is likely. Some of them (e.g. pl. VIII, figs 18–19) might represent juvenile (primary) leaves of *Pinus* because this taxon occurs masswise in this assemblage.

Ovulate cone scale type 1  
Fam. et gen. et sp. indet.  
Pl. VIII, fig. 24

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

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

Remarks: Obviously, this material constitutes an ovulate scale of a conifer. The lack of macroscopically diagnostic features does not allow a more precise systematic determination.

Ovulate cone scale type 2  
Fam. et gen. et sp. indet.  
Pl. VIII, fig. 25

Material: Pitsidia, one ovulate scale of a seed cone, incomplete (Nr. 31.4.2.4538bopiv).
**Description:** Scale broadly ovate in shape, 5 mm long and ca. 9 mm wide (when completed), apex rounded with two seeds placed at the base; seeds oval to elliptic in shape, 2–2.5 mm long and 1–1.5 mm wide.

**Remarks:** This sample could also be of coniferous origin.

**Angiospermae**

*Family LAURACEAE*

*Genus Daphnogene UNGER*

*Daphnogene polymorpha* (A. BRAUN) ETTINGSHAUSEN

Pl. XVII, figs 1–11; Pl. XVIII, fig. 1; Pl. XLIII, figs 3, 6–17; Pl. XLIX, fig. 5

**Synonym list**

<table>
<thead>
<tr>
<th>Year</th>
<th>Synonym</th>
<th>Author</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1845</td>
<td>Ceanothus polymorphus</td>
<td>AL. BRAUN</td>
<td>p. 171 (Öhningen, Upper Miocene)</td>
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<td>1851</td>
<td>Daphnogene polymorpha</td>
<td>(A. BRAUN) ETTINGSHAUSEN – ETTINGSHAUSEN</td>
<td>p. 16, pl. 2, figs 23–25 (Hernals)</td>
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<tr>
<td>1867</td>
<td>Cinnamomum lanceolatum</td>
<td>UNGER – UNGER</td>
<td>pl. 7, figs 1–10 (Kimi, Euboea, Lower Miocene)</td>
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<td>1867</td>
<td>Cinnamomum scheuchzeri</td>
<td>HEER – UNGER</td>
<td>pl. 7, figs 11–24 (Kimi, Euboea, Lower Miocene)</td>
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<td>1867</td>
<td>Cinnamomum subrotundum</td>
<td>HEER – UNGER</td>
<td>pl. 7, figs 25–29, (not 30) (Kimi, Euboea, Lower Miocene)</td>
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<td>1867</td>
<td>Bauhinia olympica</td>
<td>UNGER – UNGER</td>
<td>pl. 15, fig. 36 (Kimi, Euboea, Lower Miocene)</td>
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<td>1873</td>
<td>Litsea Delphica</td>
<td>SAPORTA – SAPORTA</td>
<td>pl. 2, fig. 7b (Kimi, Euboea, Lower Miocene)</td>
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<td>1953</td>
<td>Cinnamomum polymorphum</td>
<td>(A. BRAUN) FRENZT. – BERGER</td>
<td>fig. 6 (Kastron, Lemnos Island, Lower Miocene)</td>
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<td>1953</td>
<td>Daphnogene lanceolata</td>
<td>UNGER – BERGER</td>
<td>figs 7–11 (Kastron, Lemnos Island, Lower Miocene)</td>
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<td>1953</td>
<td>Cinnamomum polymorphum</td>
<td>A. BRAUN – BERGER</td>
<td>fig. 18 (Moudros, Lemnos Island, Lower Miocene)</td>
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<td>1953</td>
<td>Cinnamomum cf. scheuchzeri</td>
<td>(HEER) FRENZT. – BERGER</td>
<td>figs 19–20 (Moudros, Lemnos Island, Lower Miocene)</td>
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<td>1981</td>
<td>Cinnamomum polymorphum</td>
<td>HEER – VELITZELOS and PETRESCU</td>
<td>pl. 2, figs 1–8 (Lesbos Island, Lower Miocene)</td>
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<td>1984</td>
<td>Cinnamomum lanceolatum</td>
<td>HEER – VELITZELOS and GREGOR</td>
<td>p. 242 (Aliveri, Euboea, Lower Miocene) (no figure)</td>
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<td>1985</td>
<td>Cinnamomum polymorphum</td>
<td>HEER – DERMITZAKIS and VELITZELOS</td>
<td>p. 165 (Kato Komi, Chios Island, Serravallian-Tortonian) (no figure)</td>
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<td>1991</td>
<td>Cinnamomum polymorphum</td>
<td>HEER – TSAPARAS</td>
<td>p. 26 (Nea Stira, Euboea, Lower Miocene) (no figure)</td>
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<td>1992</td>
<td>Daphnogene polymorpha</td>
<td>(A. BRAUN) ETTINGSHAUSEN – VELITZELOS et al.</td>
<td>pl. 6, figs 6–7 (Aliveri, Euboea, Lower Miocene)</td>
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<td>1993</td>
<td>Daphnogene polymorpha</td>
<td>(A. BRAUN) ETTINGSHAUSEN – VELITZELOS</td>
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<td>1993–95</td>
<td>Cinnamomum polymorphum</td>
<td>KRÄUSEL and WEYLAND – SCHIMANI and SCHNEIDER</td>
<td>figs 3–4 (not 5) (Platanos-Paliopyrgos, Thessaly, Lower Miocene)</td>
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<td>1994</td>
<td>Cinnamomum polymorphum</td>
<td>HEER – VOUTOS and PAPAGIANNIS</td>
<td>pl. 4, fig. 4 (Kimi, Euboea, Lower Miocene)</td>
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<td>1994a</td>
<td>Daphnogene polymorpha</td>
<td>(A. BRAUN) ETTINGSHAUSEN – KLEINHÖLTER</td>
<td>pl. 1, fig. 8; pl. 18, figs 1–2 (Pyrgos and Zacharo basins, Peloponnesse, Messinian)</td>
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1997 *Daphnogene polymorpha* (A. BRAUN) ETTINGSHAUSEN – ERDEI and KVAČEK, fig. 6 (Kimi, Euboea, Lower Miocene)

1997 fgen. *Cinnamomophyllum* sp. – SACHSE, pl. 11, figs 7–8 (Makrilia, E. Crete, Tortonian)

non 1997 fsp. *Cinnamomophyllum polymorpha* (A. BRAUN) HEER – SACHSE, pl. 11, fig. 12 (Makrilia, E. Crete, Tortonian)

1999 *Daphnogene polymorpha* (A. BRAUN) ETTINGSHAUSEN – VELITZELOS et al., fig. E7 in p. 461 (Kimi, Euboea, Lower Miocene)

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, Lower Miocene)

2014 *Daphnogene polymorpha* (A. BRAUN) ETTINGSHAUSEN – VELITZELOS D. et al., pl. 9, figs 9–10 (Kimi, Euboea, Lower Miocene)

2014 *Daphnogene polymorpha* (A. BRAUN) ETTINGSHAUSEN – VELITZELOS D. et al., pl. 13, figs 1–2 (Lesbos Island, Lower Miocene)

2014 *Daphnogene polymorpha* (A. BRAUN) ETTINGSHAUSEN – VELITZELOS D. et al., pl. 14, fig. 3 (Lemnos Island, Lower 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*, seventy leaves; twelve complete or almost complete and fifty eight fragmentary (Nrs 31.4.2.843; 31.4.2.893a,b; 31.4.2.1380op; 31.4.2.1672; 31.4.2.1863a,b; 31.4.2.1919; 31.4.2.2467a; 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; 31.4.2.3696a,bi; 31.4.2.3737a,b; 31.4.2.3799; 31.4.2.3824,3823op; 31.4.2.4233i,4227op; 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; 31.4.2.5466a,bi; 31.4.2.5499ai,b; 31.4.2.5566op; 31.4.2.5584op; 31.4.2.5630; 31.4.2.5697aopii; 31.4.2.5713; 31.4.2.5791,5743bop; 31.4.2.5806ai,bi; 31.4.2.5811ai,bi; 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; 31.4.2.8208a,aii; 31.4.2.8208aii; 31.4.2.8190).

*Kassanoi*, forty two leaves; five complete or almost complete, thirty seven fragmentary (Nrs 31.6.2.29ii; 31.6.2.113ii; 31.6.2.120v; 31.6.2.122; 31.6.2.123i; 31.6.2.124ii; 31.6.2.125; 31.6.2.126i; 31.6.2.126ii; 31.6.2.128ii,135i; 31.6.2.128ii,135ii; 31.6.2.128ii; 31.6.2.128iv; 31.6.2.129; 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 more than 14 mm long, mostly incompletely preserved; lamina coriaceous in texture, polymorphic in shape, mostly ovate, elliptic to obovate, rarely lanceolate or falcate to ca. 95 mm long and 10–50 mm wide, L/W index 1.7–2.6, base angle acute, rarely obtuse, variable in shape from cuneate to convex or less frequently rounded or decurrent, occasionally slightly asymmetrical, 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, more or less alternately arranged, arising from the central vein at angle of 25–45°, at distances of 2–9 mm from lamina base, extending to the 1/3 upper part of the lamina, main secondary veins in ca. 4–7 pairs at the upper
part of the lamina, quite thinner, originating at angles of 40–70°, initially straight in course, curved close to
the margin forming well developed loops, interior secondaries (between primary veins) closely arranged,
mixed percurrent (opposite to alternate), almost perpendicular to the primaries, minor secondaries
(originating from the 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 on the ground of their gross
morphology. 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, 1997; ZIDIANAKIS et al., 2007).
Mantzouka et al. (2015) also described several leaves of this type from Metochia (as *Daphnogene* sp.).

*Daphnogene polymorpha* is considered as an evergreen element in gallery and mixed mesophytic forests. A
direct correlation to an extant genus of Lauraceae is not possible so far (FERGUSON, 1971; KVAČEK and
WALTHER, 1974). Pingen et al. (1994) described laurel fruit remains from the Miocene deposits of Kreuzau
as *Cinnamonum costatum* (MAI) Pingen, Ferguson and Collinson and proposed that these fruits and the
foliage of *D. polymorpha* belong to the same natural species as both co-occur there.

Genus *Lindera* THUNBERG

*Lindera ovata* KOLAKOVSKY
Pl. XVII, figs 12–14; Pl. XLIX, fig. 6

**Synonym list**

? 1957 *Lindera ovata* KOLAKOVSKY, p. 277, pl. 14, figs 4–5; pl. 15, fig. 1 (Kodor river, Pliocene)
? 1997 *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, three leaves; one complete and two fragmentary (Nrs 31.4.2.3956a,c; 31.4.2.3957a,b; 31.4.2.6925).
Metochia, two incomplete leaves (Nrs 31.5.2.12a,b; 31.5.2.16).

**Description:** Leaves petiolate, petiole fragmentary, more than 7 mm long; lamina possibly chartaceous in
texture, shape ovate to elliptic, 35–50 mm long and 15–30 mm wide, L/W ratio 1.7–2.4, base acute to obtuse,
convex to cuneate, apex widely obtuse to rounded, margin entire; venation almost basal acrodromous, central
primary vein moderately thick, more or less bent, lateral primary veins almost equal in thickness to central,
sub-oppositely arranged, originating at approx. 25°–45°, running close to the margin, sub-parallel, reaching the 1/4 upper part of the lamina, main secondary veins in a few pairs, about 3–5, at the upper part of the lamina, originating at angles of 35°–50°, more delicate, bent, looping along the margin, interior secondaries, dense, almost perpendicular to the primaries, mixed percurrent (opposite to alternate), minor secondaries fine, markedly curved, forming loops at the margin with the adjacent ones, intersecondaries 1–3 per intercostal area, parallel, weak, higher order veins form a regular polygonal network.

**Remarks:** This material differs from *D. polymorpha* foliage in the thinner texture of the lamina, the wider apex, and mainly the almost basal acrodromous venation. Quite similar leaves have been described by KOLAKOVSKY (1957, 1964) from Pliocene sediments of Kodor River. As epidermis anatomy is unknown so far, the assignment of this foliage to the laurel family remains uncertain.

MANTZOUKA et al. (2015) described several leaves of this type from Metochia as *?Lindera ovata* too. In Makrilia flora, judging from the figures and descriptions given by SACHSE (1997) several specimens referred as *Dicotylophyllum* type 3, match well with our material.

**?Lauraceae gen. et sp. indet. – folia**
Pl. XXXVII, fig. 8

**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, a bit undulate; venation brochidodromous, primary vein strong, straight, secondary veins delicate, in approx. 12 pairs, originating at angles of 50°–75°, forming loops with the adjacent ones near to the margin, intersecondaries present, 1–2 per intercostal area, parallel to the secondaries, well developed, tertiary veins reticulate, forming a regular quadrate to pentagonal network with higher order venation.

**Remarks:** This leaf, though its small size, shows affinities to Lauraceae regarding firm texture, entire margin and venation pattern but.

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**Monocotyledonae**

Family ARECACEAE
Sub-family Coryphoideae
Genus Sabalites SAPORTA

* Sabalites sp.  
Pl. XLIX, fig. 7; pl. L, fig. 1

**Synonym list**

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

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

**Remarks:** The costapalmate shape along with the wedge-shaped segments suggests an affinity to the tribes Corypheae or Borasseae of the subfamily Coryphoideae (DRANSFIELD et al., 2008). In the fossil record of Crete the presence of palms has been recently reported by VELITZELOS D. et al. (2014) with some palmate leaf fragments from Makrilia (pl. 27, figs 1–3, as Sabal sp. in page 74).

In the European Paleo/Neogene, such leaf forms are typically assigned to the genus Sabal ADANSON. As the relation of this finding from Metochia to Sabal is not fully documented, the fossil genus Sabalites as introduced by SAPORTA (1865) and emended by READ and HICKEY (1972) is considered as more suitable. Palmate foliage with a more or less extending costa are well known from several Late Cretaceous and Tertiary localities in Europe e.g. BRONGNIART (1822), UNGER (1847, 1850a, 1852), HEER (1855), MAI and WALThER (1978), AKHMETIEV (1993), KVAČEK J. and HERMAN (2004). Today, palm trees are considered typical components of tropical to subtropical habitats. Exceptionally, some species are distributed in warm temperate areas, or thrive in swampy areas while others could stand aridity growing in sandy coastal regions or dry open lands (DRANSFIELD et al., 2008).

**Family** BUXACEAE  
**Genus** Buxus L.

*Buxus pliocenica* SAPORTA and MARION  
Pl. XLIV, figs 1–2

**Synonym list**

1876  
*Buxus ploiosaenica* SAPORTA and MARION, p.144, pl. 32 figs 6–8 (Meximieux)

1994a  
*Buxus sempervirens* L. – KLEinhölTER, pl. 9, fig. 1 (Patra, Rhion, Corinth basins, Peloponnese, Pliocene)

1996  
*Buxus pliocenica* SAPORTA and MARION – SACHSE and MOHR, pl. 3, figs 50–51; pl. 6, figs 6. 9 (Makrilia, E. Crete, Tortonian)

1997  
*Buxus cf. pliocenica* SAPORTA and MARION – SACHSE, pl. 9, figs 2–3; pl. 20, figs 13, 15 (Makrilia, E. Crete, Tortonian)

2007  
*Buxus pliocenica* SAPORTA and MARION – ZIDIANAKIS et al., figs 3E, 5M (Vrysses, W. Crete, Messimian)

**Material:** Kassanoi, three leaves; two complete, one fragmentary (Nrs 31.6.2.102; 31.6.2.119x; 31.6.2.195).
**Description:** Leaves petiolate, petiole moderately thick, about 3 mm long; lamina more or less 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, approx. 15 per cm, arising at angles of 30–45°, running parallel with numerous intersecondaries towards the margin, tertiary veins oblique to secondaries, joining them, straight, higher order venation not visible.

**Remarks:** The above described entire-margined small leaves resemble regarding leaf form and venation architecture the European Late Neogene records of *Buxus plioecenica*. One specimen shows marks of pre-burial arthropod feeding resulting to leaf skeletonization (pl. XLIV, fig. 2). In the Cretan Neogene, remains of this element have been also described from Makrilia (SACHSE, 1997) and Vrysses (ZIDIANAKIS et al., 2007). The occurrence of *B. plioecenica* in Pitsidia (ZIDIANAKIS et al., 2010) is not confirmed.

**SAPORTA** and **MARION** (1876) treated this fossil-species as an ancestor of *Buxus sempervirens* L. Kvaček et al. (1982) considered it to be closely allied to the B. *sempervirens* - B. *colchica* - B. *hyrcana* group. According to these authors this group replaced the large-leaved *Buxus* lineage which became extinct because of climatic deterioration during the Upper Neogene. Today, *Buxus sempervirens* is a typical element of sclerophyllous vegetation in the Mediterranean region while *B. hyrcana* POJARKOVA and *B. colchica* POJARKOVA occur in pure stands or underwood in lowland deciduous broad-leaved mesophytic forests in the Hyrcanian and Colchis regions respectively.

**Family ALTINGIACEAE**
Genus *Liquidambar* L.

*Liquidambar europaea* A. BRAUN (in BUCKLAND)
Pl. XIX, figs 1–10; Pl. XX, figs 1–20; pl. XXI, figs 1–13; text-fig. 4.4

**Synonym list**

<table>
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<tr>
<th>Year</th>
<th>Synonym</th>
</tr>
</thead>
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<tr>
<td>1836</td>
<td>Liquidambar europaeum A. BRAUN (in BUCKLAND), p. 513 (Öhningen, Upper Miocene)</td>
</tr>
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<td>1954</td>
<td>Liquidambar europaea A. BRAUN – HANTKE, p. 63, pl. 8, figs 3–5, 7; pl. 9, fig. 1 (Schrotzburg, Upper Miocene)</td>
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<td>1993</td>
<td>Liquidambar europaea A. BRAUN – VELITZELOS, pl. 2, fig. 1 (Nea Stira, Euboea, Lower Miocene)</td>
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<td>1994a</td>
<td>Liquidambar europaeum A. BRAUN – KLEINHÖLTER, pl. 21, figs 1–4 (Pyrgos and Zacharo basins, Peloponnese, Messinian)</td>
</tr>
<tr>
<td>1994b</td>
<td>Liquidambar europaeum A. BRAUN – KLEINHÖLTER, pl. 3, fig. 1 (Patra, Rion and Corinth basins, Peloponnese, Pliocene)</td>
</tr>
<tr>
<td>1995</td>
<td>Liquidambar europaeum A. BRAUN – KLEINHÖLTER, pl. 2, fig. 6 (Patra, Rion and Corinth basins, Peloponnese, Pliocene)</td>
</tr>
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<td>?2002b</td>
<td>Liquidambar europaea A. BRAUN – VELITZELOS et al., p. 184 (Archangelos, Rhodes Island, Pleistocene) (no figure)</td>
</tr>
<tr>
<td>2010</td>
<td>Liquidambar europaeum A. BRAUN – ZIDIANAKIS et al., fig. 21 (Pitsidia, central Crete, Tortonian)</td>
</tr>
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</table>

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, Pliocene) (no figure)

2007  *Liquidambar europaea* A. BRAUN – MAI and 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) (no figure)

? 2014  *Liquidambar europaea* A. BRAUN – VELITZELOS D. et al., p. 70 (Elassona, Thessaly, Messinian) (no figure)

Material:  Pitsidia, twenty five leaves; two almost complete, twenty three fragmentary (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,bi; 31.4.2.4123a,bi; 31.4.2.4253a,bi; 31.4.2.4769a,bi; 31.4.2.5278; 31.4.2.5358bi,5359i; 31.4.2.5385ai-c; 31.4.2.5601a,bi; 31.4.2.5796a,bi; 31.4.2.5808a,bi; 31.4.2.5908a,b; 31.4.2.6001; 31.4.2.6082ai; 31.4.2.6149a,aii; 31.4.2.6507; 31.4.2.6541; 31.4.2.6962i; 31.4.2.6964i; 31.4.2.8260; 31.4.2.8272),

fifty eight infructescences (fruiting heads), thirty eight almost complete and twenty fragmentary (Nrs 31.4.2.278; 31.4.2.820,821; 31.4.2.881ab; 31.4.2.975; 31.4.2.1034ab; 31.4.2.1052; 31.4.2.1233iii; 31.4.2.1305ab; 31.4.2.1500; 31.4.2.1857; 31.4.2.1928ii; 31.4.2.1997i; 31.4.2.2023; 31.4.2.2034; 31.4.2.2155ab; 31.4.2.2375ab; 31.4.2.2512; 31.4.2.2540ai,bi; 31.4.2.2868a,bi; 31.4.2.3047ai,bi; 31.4.2.3085a,bi; 31.4.2.3145ab; 31.4.2.3203; 31.4.2.3500; 31.4.2.3858; 31.4.2.3997aopii; 31.4.2.4028b,ab; 31.4.2.4037; 31.4.2.4093ii; 31.4.2.4327ii; 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; 31.4.2.5304a,aii; 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; 31.4.2.6184aii; 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,bi; 31.4.2.8160).

Description:  Leaves mostly fragmented, long petiolate, petiole rarely preserved, more than 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; venation actinodromous, 3 or 5 primary veins depending on the number of lobes, in five-lobed leaves the most lateral primary veins originating often supra-basal, central primary vein stout, straight or bent, lateral primary veins thinner, curved, rarely straight, arising at angles of 50–95° from the midrib, secondary veins semicraspedodromous, mostly alternately arranged, curved, arising at rather closed angles, interconnected near the margin, tertiary veins weakly percurrent (alternate), venation of higher order forming an irregular network.

Fructification.  As imprints with well developed inorganic structures of solitary, probably woody, capitale infructescences (fruiting heads), pedunculate, composed of dense clusters of fruits; peduncles in most cases
missing or fragmentarily preserved, more than 12 mm long and ca. 1.5 mm wide, extending into the inner part of the infructescence, as central axis; the main body of the fruiting head is lenticular in shape as a result of compression, original shape spherical or almost spherical, 8–21 mm (average 14.5 mm) in diameter, L/W ratio ranging from 1–1.1, with 30–45 fruits, in most specimens about 10–20 visible; fruits elongate, more or less wedge-shaped, bilocular capsules, 4.5–8 mm long, 2.5–4.5 mm wide, arranged fairly tightly on the central axis, inner pericarp wall thin with fine transverse ridges on the surface, locules elongate, cone- to sack-like; along the outer surface of the infructescence the adjacent fruits form roundish pentagons or hexagons (honeycomb-like structures), the area between the fruits (peripheral rim sensu GREGOR, 1978 and FERGUSON, 1989) is smooth, somewhat thickened, with a fine fusion line; occasionally style remains are preserved, narrow elongate, straight, slightly bent or S-like in shape 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 the base, other extrafloral structures like spines or knobs have not been detected.

**Remarks:** The studied foliage is characteristic of the genus *Liquidambar*. HEER (1856) provided drawings from the rich fossil material of the type locality of Öhningen, which clearly picture the intraspecific leaf variation of this taxon. Since then, foliage of *L. europaea* is well documented in several Early Oligocene and especially Neogene localities in Central Europe (KOVAR-EDER et. al. 1994). According to some authors (e.g. BŮŽEK, 1971; MAI, 1995), three-lobed leaves predominated against five-lobed ones in Europe during the Upper Oligocene and Lower Miocene. The five-lobed leaf forms became more abundant only in the Upper Miocene and Pliocene.

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 for the 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, 1999b), most of the infructescences described from Europe as *L. magniloculata* CZECZOTT and SKIRGIELLO, *L. pliocenica* GEYLARD and KINKELIN or *L. orientalis* fossilis, constitute in fact *L. europaea* which is considered the valid name for all of them. However, in many cases fruiting heads are not well preserved, consisting of compressions without diagnostic features (FERGUSON, 1989). Two different species are broadly recognized in the European Tertiary on the ground of their infructescenses, *L. europaea* and *L. wutzleri* GREGOR. The latter taxon is characterized by wart- to thorn-like radial extensions on the surface polygonals between the capsules (GREGOR, 1993). Such structures are not found in the examined material. *Liquidambar europaea* was widespread throughout the European Neogene until the onset of the Pleistocene (MAI, 1997). Infructescences from the Italian peninsula and Rhodos Island (Dodecanese, Greece) proved a longer persistence of *Liquidambar* populations in southern European regions at least until the Lower Pleistocene (MARTINETTO 2001; MAI and VELITZELOS, 2007). The fossil record shows a continuous occurrence of *Liquidambar* in the Greek area from the Lower Miocene to the Pleistocene (Archangelos, Rhodes Island, approx. 1.6 Ma). BOYD
(2007) referred *Liquidambar* leaves from Kolymbia on Rhodos aged ca. 0.5 Ma but failed to provide a description and figure.

Today, *Liquidambar* exhibits an intercontinental biogeographic disjunction. Two species, *L. formosana* and *L. acalycina*, thrive in eastern Asia, *L. orientalis* in western Asia and *L. styraciflua* in eastern North and Central America (ICKERT-BOND et al., 2005; BOLGE, 1986). Molecular and isozyme studies, along with morphological data, pointed out that *L. orientalis* and *L. styraciflua* are closely related species and constitute a different clade from the two eastern Asia species (HOEY and PARKS, 1991; 1994; LI and DONOGHUE, 1999; ICKERT-BOND et al., 2005). On the base of their morphology, some authors proposed that *L. orientalis* and *L. styraciflua* could be united to one species as their differences can be considered as intraspecific variation (RECHINGER, 1943; MEIKLE, 1977). Based on fruiting head features (mainly the occurrence of extrafloral structures), HARMS (1930) treated the species *L. orientalis* and *L. styraciflua* as members of the section *Liquidambar* and *L. formosana* as the sole member of section *Cathayambar*. CHANG (1959) described *L. acalycina* for the first time and placed it to the section *Liquidambar*.

![Text-figure 4.4. Palaeoflora of Pitsidia, Crete, Liquidambar europaea; a. fructification line drawings, i. fruiting head, Nr. 31.4.2.820, scale bar 5 mm; ii. persistent 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. Max fruits per head, d. Length of style remnants; the data for the modern species are from ICKERT-BOND et al. (2005)
Most palaeobotanists classified *L. europaea* to the modern section *Liquidambar*. On the basis of head macro- and micro-morphological characters some of them related it to modern *L. orientalis* (MAI, 1997; 1999) (contrary to the results from leaf morphology which correlate it with the American *L. styraciflua*), while others placed it between the species *L. orientalis* and *L. styraciflua* (UNGER, 1847; HEER, 1856; GREGOR, 1978). Morphology and biometrics of the material from Pitsidia, e.g. size of heads and carpels, number of capsules per head, morphology and length of persistent styles, smooth thickened areas between adjacent fruits and lack of other extrafloral structures, support a closer relation to the modern species *L. orientalis* (text-fig. 4.4b–d) (ZIDIANAKIS et al., 2017). *L. orientalis* is considered as a Tertiary relict thriving in SW Asia Minor, Syria and Rhodos Island at altitudes of 0–400 m or sometimes higher up to 1000 m (ALAN and KAYA, 2003), while *L. styraciflua* thrives in woodlands, flood plains, swamps, riverbanks at altitudes of 0–800 m in Eastern North America (MEYER, 1997).

In Pitsidia, contrary to foliage, the fruiting heads of *Liquidambar* are quite abundant and well preserved. So far, this element is absent from the palaeofloras of Vrysses, Kassanoi and Metochia. A single infructescence has been reported from Makrilia (this study, pl. LII, fig. 7), while leaf remains lack entirely there.

**Family FABACEAE**

**Genus Leguminosites BOWERBANK emend. SCHIMPER**

*Leguminosites* sp. 1

Pl. XXIII, fig. 9

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

**Description:** Leaflet short petiolulate, petiolule missing, lamina texture chartaceous, shape oblong, 43 mm long, 19 mm wide, L/W ratio 2.3, base obtuse, rounded, a bit asymmetric, apex retuse, margin entire; venation brochidodromous, primary vein strong, straight, secondary veins much finer, in ca. 10 pairs originating at angles of 35–75°, gently bent, looping near the margin, intersecondaries numerous, parallel, hardly visible, higher order venation indistinct.

**Remarks:** The emarginate 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. SACHSE (1997) reported from Makrilia 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. In Vrysses, though several specimens of leguminosoid leaflets are available, none resembles closely the leaflet at hand. MANTZOUKA et al. (2015) described four different taxa of Fabaceae from Metochia. On the ground of descriptions and figures, the leaflets referred as *Leguminosites* sp. 2 are quite close to the material at hand. Fertile material of this family has not been found in Pitsidia till now. Recently, a fragmentary pod was recovered in Makrilia (pl. LII, fig 4).
Leguminosites sp. 2  
Pl. XXIII, fig. 8

**Synonym list**  
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 probably coriaceous, shape obovate, 48 mm long, 23 mm wide, L/W ratio 2.1, base cuneate at one side, convex the other, asymmetric, apex obtuse, retuse, margin entire; venation brochidodromous, midrib prominent, straight, abruptly bent at the base, secondary veins ca. 12 pairs, delicate, originating at angles of 45–75°, irregularly spaced, occasionally dichotomising close to the primary vein, straight, gently curved distally, interconnected in loops with adjacent secondaries or intersecondaries along the margin, intersecondary veins mostly one or even two per intercostal area, well developed, parallel or almost so to the secondaries, tertiary veins conspicuous, randomly reticulate, anastomosing with higher order venation forming an irregular net.

**Remarks:** This well preserved specimen shares several common features with *Leguminosites* sp. 1 (e.g. apex shape, venation) but the thickness of the laminae is profoundly different. Because of this difference, they are handled as different taxa of Leguminosae.

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*?Leguminosites* sp. 3  
Pl. XLV, fig. 1

**Material:** Kassanoi, one fragmentary leaflet (Nr 31.6.2.62).

**Description:** Leaflet subsessile, lamina shape ovate, about 35 mm long (when complete) and 16 mm wide, L/W ratio 2.2, rounded to cordate, strongly asymmetric (basal extension asymmetry), apex missing, margin entire; venation brochidodromous, primary vein moderately thick, straight, slightly bent distally, secondary veins delicate, arising from the midrib at narrow angles (approximately 30–50°), smoothly curved along their length, forming loops close to the margin, higher order venation not visible.

**Remarks:** This specimen shows features that are common among Fabaceae as the base asymmetry, entire margin and brochidodromous venation. This leaflet differs from the others found in Pitsidia and Metochia by the much narrower angle of the secondaries.

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*?Leguminosites* sp. 4  
Pl. XLIX, fig. 11

**Material:** Metochia, two leaflets; one complete and one fragmentary (Nrs 31.5.2.49; 31.5.2.51).
**Description:** Leaflets petiolate, petiole partly preserved, 1.5 mm long; texture coriaceous, shape narrow oblong, approximately 35 mm long and 9–12 mm wide, L/W ratio almost 3, base convex, strongly asymmetry (basal insertion asymmetry), apex rounded, margin entire; venation brochidodromous, primary vein strong, straight, secondary veins ca. 10–14 pairs, diverging from the midrib at angles of 40–75°, straight or smoothly bent, joining in arcs the adjacent secondaries and intersecondaries along the margin, intersecondary veins 1 or rarely 2 per intercostal area, well developed, parallel to the secondaries, tertiary veins reticulate anastomosing at various angles forming an irregular network.

**Remarks:** On the ground of the asymmetric base, the entire margin and the venation architecture, leaf forms like this could be classified to the legume family. The studied specimens do not match with 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. XXII, figs 1–21; Pl. XLIV, figs 3, 5–14; text-fig. 4.5

Syonym list
1845  *Gleditschia podocarpa* A. BRAUN, p. 173 (Öhningen, Upper Miocene)

Folia:
1880  *Podocarpium lyellianum* HEER – STUR in TELLER, (Kap Nenita, Chios Island, Serravallian–Tortonian)
1997  *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, fig. 3 (Kato Komi, Chios Island, Serravallian–Tortonian)

Fructus:

Material:
Pitsidia, thirteen leaflets; seven complete or almost complete and six fragmentary (Nrs 31.4.2.2705aii; 31.4.2.2720ii; 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), twenty fruits, twelve complete or almost complete and eight fragmentary (Nrs 31.4.2.2704a,b; 31.4.2.3597a,b; 31.4.2.3727a;p; 31.4.2.3968a,b; 31.4.2.4134; 31.4.2.4284a;ibi; 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; 31.4.2.6166bop; 31.4.2.6478ai,bi; 31.4.2.6575a,b; 31.4.2.6662a,b; 31.4.2.6931a,b; 31.4.2.8262iii).
Kasannoi, thirty five leaflets; twenty six complete or almost complete and nine fragmentary (Nrs 31.6.2.15iii; 31.6.2.15v; 31.6.2.24ii; 31.6.2.26i; 31.6.2.30ii; 31.6.2.35ii; 31.6.2.37ii; 31.6.2.66ao; ?31.6.2.91ii; 31.6.2.100iii; 31.6.2.119ix; 31.6.2.119xii; 31.6.2.15ii; 31.6.2.166aii; 31.6.2.168ai,bi; 31.6.2.168aii,bi; 31.6.2.168aii,bi; 31.6.2.168aivb; 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;
Description: Leaflets sessile or shortly petiolulate (ca. 0.5 mm long), lamina narrow elliptic to lanceolate, approximately 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 a characteristic pair of prominent basal secondary veins originating at acute angles and running parallel to the leaf margin; midrib strong, straight, secondary veins numerous, densely arranged at distances of 0.5–1.5 mm, arising at acute angles forming angular loops near the margin, intersecondary veins present, simple, parallel to the secondaries, weakly-developed, tertiaries reticulate, 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 about 1 mm wide, slightly swollen at the base with numerous scars; valves thin in texture, 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 a more or less developed projection (style remnant), margin entire, occasionally showing a rather fine marginal line running parallel to the valve edge, being visible from the inner side, distance of valve edge-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 preserved; funiculus in a few specimens discernable, slender, 2–3 mm long, curved, situated in the apical third of the placental suture indicating seed attachment at the apical part of the pod.

Remarks: The morphological features of the leaflets (especially the asymmetric base and the presence of a prominent basal pair of secondaries) and fruits coincide exactly with *P. podocarpum*. Contrary to Pitsidia, in Kassanoi vegetative remains of *P. podocarpum* are more abundant and display a wider range of leaflet variation. On the other hand, *Podocarpium* fruits lack completely from Kassanoi. From Makrilia, SACHSE (1997) has described a few leaflets of this taxon.

This common, well documented Eurasian element, represents an extinct genus of the Leguminosae family (HERENDEEN, 1992a,b; WANG et. al, 2007). HEER (1859) described a specimen with physically connected pinnately compound leaves and fruits. Although morphologically similar fruits occur in several extant legume genera, this species does not conform to any of the extant legume species because no modern species bears the features of both leaves and fruits (HERENDEEN, 1992a,b; WANG et al., 2007). According to HERENDEEN (1992b), *P. podocarpum* is one of the few species in the European Neogene that could be related to modern African taxa, a fact that can be considered biogeographically remarkable. It is generally accepted that it represents a typical mesophytic or riparian element of subtropical and warm-temperate climates occurring in Eurasia from the Lower Oligocene to Upper Pliocene (HERENDEEN, 1992a; LIU et al., 2001;
KOVAR-EDER, 2004). In Central Europe it was abundant, mainly in late Early to Middle Miocene plant assemblages.

Text-figure 4.5. Palaeoflora of Pitsidia, Crete. *Podocarpium podocarpum* fruits (pods), line drawings; a. Nr. 31.4.2.3968a, scale bar 1 cm; b. Nr. 31.4.2.6478ai, scale bar 1 cm; c. Nr. 31.4.2.4833i, scale bar 1 cm; d. shape of the valve apices, scale bar 0.5 cm; e. venation on the valve surface, Nr. 31.4.2.3597a detail, scale bar 3 mm; f. Nr. 31.4.2.3597a, scale bar 0.5 cm

Subfamily Mimosoideae
Genus *Mimosites*

*Mimosites* sp.
Pl. XXXVIII, figs 1–5

**Material:** Pitsidia, fifteen leaflets; thirteen complete and two fragmentary (Nrs 31.4.2.2305ii; 31.4.2.2371; 31.4.2.3075aiii,bi; 31.4.2.3338ii; 31.4.2.4087aii,bi; 31.4.2.4346ai,b; 31.4.2.4389aii,bi; 31.4.2.4398aii,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 ca. 0.5 mm with prominent wrinkled pulvinous, lamina narrow elliptic to oblong, rarely ovate to lanceolate, 5–8 mm long and 2–3.5 mm wide, L/W ratio 1.5–3.5, apex obtuse to rounded often mucronate, base rounded or widely cuneate, strongly asymmetrical, margin entire; venation brochidodromous, primary vein moderate, laminae divided into two strongly unequally broad parts, straight or slightly curved, secondary veins thin, in 5–6 pairs, originating at wide angles, close to the margin forming well developed loops in the wider half of the lamina, the basal secondary is distinct, strongly curved upwards, the further secondaries originating at angles of 50–70°, tertiary veins are reticulate forming an irregular net with higher order venation. Furthermore three leaflets of similar leaf architecture but with longer lamina (9.5–10.5 mm).
Remarks: The venation architecture and especially the strongly asymmetrical base with a wrinkled petiolule indicate a Fabaceae affinity of this foliage (HERENDEEN, 1992). Furthermore, the lamina size and asymmetry are characteristic of ‘mimosoid’ leaflets. A more precise classification is not possible on the ground of leaflet gross morphology. SACHSE (1997) reported a few lanceolate leaflets of possible Mimosoideae origin (as ?Mimosites sp., pl. 12, figs 4, 6; pl. 20, fig. 31) that differ by the rather narrow lamina with acute apex from the material from Pitsidia. Concerning the three longer leaflets, we hesitate to assign them to a separate systematic entity because they differ only in length.

Family ROSACEAE

?Rosa sp. – folia
Pl. XVIII, figs 7–8

Material: Pitsidia, one lateral and one terminal leaflet, complete (Nrs 31.4.2.1500a,b; 31.4.2.6166a,b).

Description: Lateral leaflet (Pl. XVIII, fig. 7) 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 the upper 2/3 part, near the base entire; teeth acute, triangular in shape, distal side convex to straight, rarely flexuous, proximal 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, more or less curved, often forking close to the margin, higher order venation not preserved.

Terminal leaflet (Pl. XVIII, fig. 8) petiolate, petiole 17 mm long; lamina obovate in shape, 33 mm long and 21 wide, L/W ratio 1.9, base cuneate, apex broadly acute, margin as in the lateral leaflet, venation craspedodromous, primary vein stout, straight; secondary veins delicate, in 7–8 pairs, arising at angles of 55–80°, straight, somewhat irregular, forked once or twice, inervating marginal teeth; tertiaries hardly visible.

Remarks: Due to the partly serrate margin and the venation pattern a Rosaceae affinity can be assumed. This family shows high divergence in leaf form. In many cases an identification to the genus level based on the gross morphology of isolated leaflet is difficult. Traditionally, this type of leaflets is classified as Rosa, though a different generic affinity cannot be excluded.

Rosaceae gen. et sp. indet. – folia
Pl. XLIV, figs 15–16

Material: Kassanoi, two leaves; one complete, one fragmentary (Nrs 31.6.2.18ai,bi; 31.6.2.119vi).

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

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

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**Family RHAMNACEAE**

**Genus Berchemia NECKER ex DE CANDOLLE**

*Berchemia multinervis* (A. BRAUN) HEER

*Pl. XLV, figs 2–4, text-fig. 4.12a*

**Synonym list**

<table>
<thead>
<tr>
<th>Year</th>
<th>Name</th>
<th>Authors and Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1836</td>
<td><em>Rhamnus multinervis</em></td>
<td>A. BRAUN (in BUCKLAND, p. 513 (Öhningen, Upper Miocene)</td>
</tr>
<tr>
<td>1859</td>
<td><em>Berchemia multinervis</em></td>
<td>(A. BRAUN) – HEER, p. 77, pl. 128, figs 9–18 (Schweizer Molasse, Upper Miocene)</td>
</tr>
<tr>
<td>1994a</td>
<td><em>Berchemia multinervis</em></td>
<td>(A. BRAUN) HEER – KLEINHÖLTER, pl. 8, fig. 6; pl. 28 figs 7–8 (Pyrgos and Zacharo basins, Peloponnese, Messinian)</td>
</tr>
<tr>
<td>1994b</td>
<td><em>Berchemia multinervis</em></td>
<td>(A. BRAUN) HEER – KLEINHÖLTER, pl. 2, fig. 1 (Pyrgos and Zacharo basins, Peloponnese, Messinian)</td>
</tr>
</tbody>
</table>

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

**Description:** Leaf lamina ovate to broad elliptic, 30 to ca. 37 mm long and 21 to ca. 28 mm wide, L/W ratio ca. 1.5, base rounded to slightly cordate, apex rounded, entire-margined; venation eucamptodromous, primary vein strong, straight, secondary veins in ca. 11–12 pairs, moderate, opposite to alternate, arising at angles of 40–60°, the more acute angles distally, in distances of 2.5–4 mm, parallel, initially straight (basally often weakly S-like), close to the margin abruptly bent upwards, tertiary veins delicate, percurrent, almost perpendicular to the secondaries, dense, ca. 16–20 per cm, slightly S-like to almost straight, higher order venation not visible.

**Remarks:** Leaves with such characteristic venation pattern were classified by A. BRAUN (in BUCKLAND, 1836) to the genus *Rhamnus* L. A few years later they were transferred by A. BRAUN (1845) and UNGER (1847) to the genus *Karwinskia* ZUCCARINI and finally it was HEER (1859) who placed them to *Berchemia*. Although fragmentary, the studied specimens coincide exactly with the material from Öhningen, as figured by HEER (1859: pl. 123, figs 9–18), especially the broader elongate forms. Like in Öhningen, the tertiary veins are almost perpendicular to the secondaries, slightly S-shaped to almost straight [text-fig. 4.12a, compare with Heer (1859): pl. 123, fig. 17b].
The exact systematic position of Berchemia multinervis still remains unresolved. Morphologically similar leaves are observed in the North American modern species B. scandens (HILL) K. KOCH and in several East Asian species such as B. lineata DE CANDOLLE, B. pauciflora MAXIMOWICZ, and B. racemosa SIEBOLD and ZUCCARINI as well as in other genera of the families Rhamnaceae and Cornaceae, especially in Cornus L. (HANTKE, 1954; BŮŽEK, 1971). JONES and DILCHER (1980) proposed for such leaves an extinct genus of Rhamnaceae, Berhamniphyllum (tribe Zizyphoeae).

Genus Ziziphus MILLER
cf. Ziziphus paradisiaca (UNGER) HEER
Pl. LI, figs 9–11

Synonym list

1850b Daphnogene paradisiaca UNGER, p. 167, ?pl. 37, 8–11; pl. 38, figs 1, ?2, ?3, 4–7 (Socka, Eocene)
1859 Zizyphus paradisiaca UNGER – HEER, p. 74
? 1867 Cinnamomum rossmaessleri HEER – UNGER, pl. 7, fig. 32 (Kimi, Euboea, Lower Miocene)
1997 Dicotylrophyllum sp. 3, SACHSE, pl. 14, figs 7, 9, ?11, ?13, 14; pl. 20, figs ?39, 41, ?42 (Makrilia, E. Crete, Torontian)
2007 cf. Ziziphus ziziphoides (UNGER) WĘYLAND – ZIDIANAKIS et al., figs 3N-P (Vrysses, W. Crete, Messinian)

Material: Metochia, three leaves; one almost complete, one incomplete and a fragment (Nrs 31.5.2.13ai,b; ?31.5.2.15; 31.5.2.57).

Description: Leaf petiolate, petiole partly preserved, more than 2 mm long; lamina ovate to broadly elliptic, ca. 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 at least at the lower 1/4 part of the lamina, simply, obtusely serrate to undulate in the further part; teeth few, spaced at intervals of ca. 4–7 mm, proximal side mostly convex and convex to straight distally, proximal/distal side ratio 5–7, apex obtuse to bluntly acute, approx. 1 mm in height, sinuses shallow, narrow, angular to rounded; venation basal acrodromous, central primary vein straight to gently curved, lateral primary veins thinner, arising at angles of 30–50º directly from the petiole-midrib fusion point, running subparallel to the margin, closer to the margin than to the midvein, reaching the apex of the lamina, major secondary veins (at the upper 1/2 part of the lamina) in 5–8 pairs, delicate, originating at angles of 50–60º, more or less straight, forked, forming loops with the adjacent secondaries or intersecondaries or at the apex with the lateral primaries, interior secondary veins (at the basal 1/2 part of the lamina) fine, weakly developed, dense, originating at wide angles (from midrib at ca. 70–80º, from the lateral primaries at ca. 90º) straight, anastomosing with the tertiary veins forming an irregular polygonal network, minor secondaries numerous, hardly visible, originating at broad angles, initially almost straight, close to the margin forked, forming loops with the adjacent secondaries or intersecondaries, sending veinlets to the margin, one of the veinlets inserting the marginal sinus.
Remarks: Tri-veined, basal acrodromous, obtusely serrate to crenate leaves are common in the Cretan Upper Miocene (Makrilia, Vrysses and Metochia). SACHSE and MOHR (1996) initially assigned these leaves from Makrilia to the Rhamnaceae family relating them to the genera *Ziziphus* MILLER, *Paliurus* MILLER, *Ceanothus* L. and *Colubrina* RICHARD ex BRONGNIART (p. 164; table 1; pl. 3, figs 75–77). Later, SACHSE (1997) changed this systematic treatment and transferred them to incertae sedis as *Dicotylophyllum* sp. 3, recognizing more similarities with genera such as *Lonicera* L. (Caprifoliaceae) and *Clematis* L. (Ranunculaceae). In Vrysses, ZIDIANAKIS et al. (2007) compared these tri-veined leaves with *Ziziphus ziziphoides* (UNGER WEYLAND (as cf. *Ziziphus ziziphoides*). The foliage of *Z. ziziphoides* from the type locality of Häring is represented by two slender leaves, with finely serrate to crenate margin, strongly asymmetric base, acuminate apex, with a short petiole forming a wide angle with the midrib (UNGER, 1847: pl. 49, fig. 10, as *Ceanothus ziziphoides*). Although one of them fragmentary, both leaves unambiguously belong to the same species and were compared to several modern genera and especially to *Ziziphus* (WEYLAND, 1943; PETRESCU, 1968).

The material of *Z. paradisiaca* from the type locality of Sotzka (Socka, Slovenia, Eocene) comprises broad ovate, occasionally almost elliptic leaves, coarsely serrate to crenulate, with symmetric, broad base, acuminate, more or less round-tipped apex and long, robust petiole without angle to the midrib (UNGER, 1850b: pl. 38, figs 1, 2, 4, 5, 7, as *Daphnogene paradisiaca*). Occasionally, when the midrib is bent close to the leaf base, the petiole is in oblique position to the leaf axis continuing the midrib course (Unger, 1850b: pl. 38, fig. 6). UNGER also illustrated under this taxon four entire- or almost entire-margined leaves that possibly belong to a different taxon (pl. 37, figs 8–11). The specimen that was figured by Unger on pl. 38, fig. 3 is morphologically closer to Lauraceae.

Both above mentioned species of *Ziziphus* are morphologically very similar. In *Z. paradisiaca* the secondaries (interior, major and minor) as drawn by UNGER are rather weakly developed, almost perpendicular to the primaries (pl. 38 fig. 7a) or oblique (pl. 38, fig. 1a) rapidly anastomosing with tertiaries forming a polygonal network. In UNGER’S (1847) illustration of *Z. ziziphoides* other venation features apart from the primary vein course are not visible. Thus, we are unable to compare and differentiate the type specimens of these two species in the sense of their higher order venation.

In his monograph on the fossil flora of Häring ETTINGSHAUSEN (1853) provided drawings of numerous tri-veined, dentate leaves, under the name *Ceanothus zizyphoides* (pl. 25, figs 9–39) (as *C. ziziphoides* in the caption). Some of them are slender resembling the type specimens of UNGER from the same locality. Others are broader in form and quite similar to *Z. paradisiaca* (pl. 25, figs 14, 18–19, 24–26, 29, 36–38), though none shows the typical symmetric base, strong petiole and round-tipped apex. On the ground of this co-occurrence of both leaf forms (*Z. zizyphoides* and *Z. paradisiaca*), it is reasonable to assume that they possibly constitute part of the leaf variation of a single species. Today, some authors treat them as synonyms or as different leaf forms of a single species, while others separated them into two different species (e.g.
Kvaček and Walther, 2004; Givulescu, 1962). According to Bůžek et al. (1996) they differ mainly in the tertiary vein course, oblique in Z. ziziphoides, horizontal in Z. paradisiaca. Anatomical aspects of the epidermis or related reproductive organs that could be systematically helpful are unknown so far.

Concerning the material from Metochia, the leaves are broad-shaped as Z. paradisiaca. In specimen Nr 31.5.2.13a,b the margin is distinctly serrate, the leaf base is widely convex to rounded, while the petiole is missing (pl. LI, fig. 11). The secondary veins are absent (either not visible or not formed) resembling exactly the specimen figured from Socka by Unger (1850b) in pl. 38, fig., 7. The other leaf from Metochia (Nr. 31.5.2.57) is almost complete with preserved venation details (pl. LI, fig. 10). Although this leaf does not represent the typical leaf form met in Socka, it matches well the small leaf figured in pl. 38, fig., 6 in which the petiole is in oblique position to the leaf axis continuing the midrib course.

The typical leaf form of Z. paradisiaca as described above has been found in Vrysses (Zidianakis et al.: fig. 3P as cf. Z. ziziphoides) as well as in Makrilia (pl. LII, figs 1, 9, in this study). Not necessarily, all tri-veined basal acrodromous specimens with serrate or crenulate margins from these localities belong to the same species. For example, the leaf illustrated in pl. 14, fig. 14 by Sachse (1997) showing a narrow cuneate base is quite different from Z. paradisiaca.

Numerous modern species of different dicot families or even monocots have leaves with a tri-veined acrodromous venation pattern, among them Lauraceae, Fabaceae, Ulmaceae, Menispermaceae, Myrtaceae, Oleaceae, Ranunculaceae, Ericaceae, Caprifoliaceae and Rhamnaceae. In most of them leaves are entire-margined or/and show a supra-basal acrodromous venation, [e.g. Cinnamomum Schäffer, Lindera Thunberg, Litsea Lamarck, Sassafras Presl (Lauraceae), Bauhinia L. (Fabaceae), Myrtus L. (Myrtaceae) and Jasminum L. (Oleaceae)] or/and shows special macro-morphological features that differentiated them from Z. ziziphoides and Z. paradisiaca [e.g. densely, sharply serrate margin in Celtis L. (Ulmaceae)]. The similarities to modern members of Paliurus, Ceanothus and especially of Ziziphus (Rhamnaceae) are obvious, in lamina form, type and arrangement of marginal teeth, apex shape and vein architecture (weakly developed interior secondaries, tertiary course etc; pl. LII, fig. 3). The fact that it is impossible to distinguish the foliage of these genera on the basis of their gross morphology alone makes the generic assignment of fossil material to some degree equivocal.

Concerning the Greek Tertiary, Unger (1867) figured a single leaf of possibly Z. paradisiaca origin from Kimi (Euboea) (pl. 7, fig. 32, as Cinnamomum rossmaessleri Heer; identified as Z. ziziphoides f. paradisiaca by Velitzelos et al. 2002). Z. ziziphoides is well documented in the Oligocene floras of Evros (localities Laguna, Lyra and Fylakton) (Velitzelos D. et al. 2014). In the Cretan area, contrary to the broad leaves of Z. paradisiaca affinities, slender leaf forms of Z. ziziphoides are entirely absent so far. Mantzouka et al. (2015) reported an incomplete leaf of Paliurus tiliifolius (Unger) Bůžek from Metochia and expressed the viewpoint that some of the tri-veined leaves from Vrysses and Makrilia, described as cf. Ziziphus ziziphoides (Zidianakis et al. 2007) and Dicotylophyllum sp. 3 (Sachse, 1997) respectively, match the foliage of
?Lindera ovata from Metochia pointing however that the finely dentate margin might indicates a different origin (Rhamnaceae).

Family ULMACEAE
Genus Ulmus L.

Ulmus cf. plurinervia UNGER
Pl. XXIII, figs 6, 12, 14; Pl. XXXVIII, figs 10–13; Pl. XLV, figs 5–10, 15; text-fig. 4.6b, c, e; text-fig. 4.12e

Synonym list
1847 Ulmus cf. plurinervia UNGER, p. 95, pl. 25, figs 1–4 (Parschlug, Middle Miocene)
1851 Planera ungeri ETTINGSHAUSEN, p. 14, pro parte, pl. 2, figs 11–12 (Wien)

Material:
Pitsidia, thirteen leaves, four complete or almost so leaves and nine fragmentary (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,bi; 31.4.2.6318; 31.4.2.6383; 31.4.2.6935a,b; 31.4.2.8119).
Kassanoi, seven leaves; four complete or almost complete, three fragmentary (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: Leaf, shortly petiolate, petiole 4–5 mm long, thick, broader near the base, slightly curved, in open angle with the 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 more or less asymmetric, rounded to subcordate, margin simply to double, finely serrate, teeth dense, broadly triangular, blunt or occasionally sharp, convex to slight S-like in proximal side, mainly convex to straight or concave in distal; tooth apex bluntly acute, proximal side convex, distal side concave to straight, sinus angular, acute; venation craspedodromous, primary vein strong, straight or gently bent, tapering towards the apex, secondary veins in 6 to more than 12 pairs, arising at angles of 30°–70°, straight or almost so, delicate, subparallel, often forked once, inervating the marginal teeth, tertiary veins percurrent, weakly developed, opposite or alternate, straight or S-like, venation of higher order forming a dense network.

Remarks: For these specimens, the generic position is well documented because of the base asymmetry, the shape and length of the petiole, the simply to double serrate margin and the forked secondaries. Two fossil species are considered as morphologically more close to this material, U. carpinoides GöPPERT (type locality Sośnica) and U. plurinervia UNGER (type locality Parschlug). KVAČEK et al. (2002), examining material from both these type localities, considered that in U. plurinervia the leaf forms tend to be slender, smaller in size and finely serrate while, in U. carpinoides it is pronouncedly asymmetric, broader and double serrate in the margin. In this respect, the examined foliage displays the characters of the former species.
Text fig. 4.6. Palaeoflora of Pitsidia, Crete. *Ulmus* and Betulaceae gen. et sp. indet. foliage, line drawings;

a. Betulaceae gen. et sp. indet., note the symmetric base and the simply to weakly double serrate margin, Nr. 31.4.2.8266, scale bar 1 cm;
b. *Ulmus* cf. *plurinervia*, Nr. 31.4.2.3950ai, scale bar 1 cm;
c. *Ulmus* cf. *plurinervia*, the double serrate margin, Nr. 31.4.2.3950bi detail, scale bar 3 mm;
d. Betulaceae gen. et sp. indet., simply to weakly double serrate margin, Nr. 31.4.2.6206b detail, scale bar 3 mm;
e. *Ulmus* cf. *plurinervia*, margin and venation pattern of the lamina base, Nr. 31.4.2.3950bi detail, scale bar 5 mm

*Ulmus* sp. – fructus
Pl. XXIII, fig. 10

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

**Description:** Samara Shortly stalked, stalk 1 mm long, without any remnant of the calyx; wings quite thin of almost circular 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 the apex of the fruit with fine striation on its surface.

**Remarks:** The overall morphology of this winged fruit, the course of the prominent axial vein and the probably double apices enable the assignment of this specimen to *Ulmus*. The absence of the calyx remnant may be ascribed either to taphonomical factors or to its possibly deciduous nature (not persistent calyx). Similar winged fruits have been described by Göppert (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 quite different from the specimen at hand (broader with more prominent venation).
Genus Zelkova SPACH

Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA
Pl. XXIII, figs 7, 13; Pl. XLV, figs 11–12; text-fig. 4.12b

Synonym list

1843 Ulmus zelkovaefolia UNGER, p. 94, pl. 24, figs 9–13 (non fig. 7) (Parschlug)
? 1862 Fagus chamaephegos UNGER – UNGER, fig. 10 (Kimi, Euboea, Lower Miocene)
1867 Planera ungeri ETTINGSHAUSEN – UNGER, pl. 4, figs 10–16 (Kimi, Euboea, Lower Miocene)
1953 Zelkova praelonga (UNGER) BERGER – BERGER, figs 4–5 (Kastron, Lemnos Island, Lower Miocene)
1985-86 Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA – DERMITZAKIS et al., figs 6.2, 6.4 (Akropotamos, E. Macedonia, Messinian)
1986a Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA – KNOBLOCH and VELITZELOS, pl. 3, fig. 5; pl. 8, fig. 5 (Elassona, Thessaly, Messinian)
1986b Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA – KNOBLOCH and VELITZELOS, pl. 15, figs 5, 8 (Prosilio, W. Macedonia, Messinian)
1963 Zelkova zelkovifolia (UNGER) – BÜZEK and KOTLABA in KOTLABA, p. 59, pl. 3, figs 7–8 (Bory)
1991 Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA – TSAPARAS, two figs in p. 46 (Nea Stira, Euboea, Lower Miocene)
1994a Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA – KLEINHÖLTER, pl. 11, figs 1–3; pl. 30, figs 8–9 (Patra, Rion and Corinthis basins, Peloponnese, Pliocene)
1994b Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA – KLEINHÖLTER, p. 265 (Pyrgos and Zacharo basins, Peloponnese, Messinian) (no figure)
1994 Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA – VOUTOS and PAPAGIANNIS, pl. 3, fig. 1 (Kimi, Euboea, Lower Miocene)
1995 Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA – KLEINHÖLTER, pl. 2, fig. 3 (Patra, Rion and Corinthis basins, Peloponnese, Pliocene)
1996 Zelkova sp. and Ulmaceae – SACHSE, pl. 3, fig. 82; pl. 7, figs 1, 3 (Makrilia, E. Crete, Tortonian)
1997 Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA – SACHSE, pl. 14, figs 1–2; pl. 20, fig. 46 (Makrilia, E. Crete, Tortonian)
1998 Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA – GOUDELLI and LOUMAKI, pl. 11, fig. 1 (Skoura, Peloponnese, Pliocene)
1999 Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA – VELITZELOS et al., fig. D9 in p. 461 (Vegora, W. Macedonia, Messinian)
2002 Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA – KAČEK et al., pl. 20, figs 1–8, 10–11 (Vegora, W. Macedonia, Messinian)
2005 Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA – DENK and GRIMM, figs 35–42 (Vegora, W. Macedonia, Messinian)
2014 Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA – VELITZELOS D. et al., p. 58 (Grevena, W. Macedonia, Lower Miocene) (no figure)
2014 Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA – VELITZELOS D. et al., pl. 26, figs 6–8 (Kato Komi, Chios Island, Serravallian–Tortonian)
2014 Zelkova zelkovifolia (UNGER) BÜZEK and KOTLABA – VELITZELOS D. et al., pl. 27, fig. 6 (Makrilia, E. Crete, Tortonian)

Material:
Pitsidia, one almost complete leaf (Nrs 31.4.2.1663ai,bi).
Kassanoï, two incomplete leaves (Nrs 31.6.2.75; 31.6.2.76a,b).
**Description:** Lamina chartaceous, oblong to ovate, 22–41 mm long and 18–30 mm wide, W/L ratio 0.7–2.3, apex acute to widely acute, base rounded, margin coarsely simply serrate; teeth obtuse to rounded, in both sides convex, 1–2 mm long and 2–3 mm wide, corresponding in number to the secondary veins, sinuses shallow, narrow angular; venation craspedodromous, primary vein straight, moderately thick, more or less bent, secondary veins delicate, in 4–12 pairs, arising at angles of 40–70°, the steeper angles distally, straight or bent upwards, close to the margin sending veinlets to the adjacent sinuses, inervating the marginal tooth, tertiary veins reticulate, forming polygonal meshes with higher order venation.

**Remarks:** On the basis of the characteristic shape of the marginal teeth and the pattern of second and third order venation, these leaves resemble to the foliage of *Z. zelkovifolia*. The high number of marginal teeth and more densely spaced secondary veins of the leaf from Pitsidia and the large size of the lobes and the rather broad cordate base of the leaves from Kassanoi are not consistent with this taxon.


**Family FAGACEAE**

**Genus Quercus L.**

*Quercus pseudocastanea* GÖPPERT emend. WALTHER and ZASTAWNIK
Pl. XXIV, figs 1–20; pl. LVI, figs 6–7, 11; pl. LVII, figs 3, 7; text-fig. 4.7a–b

**Synonym list**

1852 *Quercus pseudocastanea* GÖPPERT, p. 276, pl. 35, fig. 1 (Sośnica, Upper Miocene)
1991 *Quercus pseudocastanea* (GÖPPERT) – WALTHER and ZASTAWNIK, p. 169, pl. 2, figs 2–3, 5–6; pl. 3, figs 1–6; text-fig. 8 (Sośnica, Upper Miocene)
1986 *Quercus pseudocastanea* GÖPPERT – VELITZELOS and KNOBLOCH, pl. 11, figs 2, 4, 7 (Skoura, Peloponnese, Pliocene)
1986b *Quercus pseudocastanea* GÖPPERT – KNOBLOCH and VELITZELOS, pl. 15, figs 1–2 (Prosilio, W. Macedonia, Messinian)
1998 *Quercus pseudocastanea* GÖPPERT – GIUDELLI and LOUMAKI, pl. 4, figs 1–2; pl. 5, figs 1–2; pl. 6, figs 1–2; pl. 7, figs 1–2; pl. 8, figs 1–2 (Skoura, Peloponnese, Pliocene)
1999 *Quercus roburoides* MASSALLONGO – VELITZELOS and KVAČEK, pl. 1, fig. 5 (Vegora, W. Macedonia, Messinian)
1999 *Quercus pseudocastanea* GÖPPERT – VELITZELOS et al., fig. D8 in p. 461 (Vegora, W. Macedonia, Messinian)
2002 *Quercus pseudocastanea* GÖPPERT emend. WALTHER and ZASTAWNIK – 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)
2008 *Quercus pseudocastanea* GÖPPERT – GIASSAKI, E., pl. 8, figs 1–3 (Skoura, Peloponnese, Pliocene)
2010 *Quercus roburoides* MASSALLONGO – ZIDIANAKIS et al., fig. 2j (Pitsidia, central Crete, Tortonian)
2014 *Quercus pseudocastanea* GÖPPERT – VELITZELOS D. et al., pl. 7, figs 5–6, 8 (Grevena, W. Macedonia, Lower Miocene)
2014 *Quercus pseudocastanea* GÖPPERT – VELITZELOS D. et al., pl. 15, fig. 6 (Vegora, W. Macedonia, Messinian)
Material: Pitsidia, one hundred twenty two leaves; eighteen complete or almost complete and one hundred four fragmentary (for collection numbers of the specimens see appendix 9a).

Description: Leaves petiolate, petiole strong, up to 25 mm long (average 9.8 mm); lamina texture chartaceous, shape obovate to elliptic or oblanceolate, 32–84 mm (average 58 mm) long and 13–37 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 the 1/3 basal part; lobes rounded, with more or less convex sides, occasionally with a pointed apex, sinuses shallow, rounded; venation craspedodromous, midvein straight or bent, moderately strong, secondary veins alternate, in 7–13 pairs, originating in angles of mostly 30–60°, interspaced at distances of ca. 4–10 mm, straight or curved, running towards the margin, ending in the lobe apices, tertiary veins fine, percurrent, opposite or alternate, straight or sinuous, almost in right angles to the secondaries, higher venation forming a polygonal net.

Remarks: The leaf variability of this material matches well that of *Q. pseudocastanea* from Sośnica as emended by WALTHER and ZASTAWNIAK (1991) including *Q. pseudorobur* KOVATS and *Q. hispanica* RÉROLLE. *Q. roburoides*, which is common in the European Pliocene is morphologically very close, usually differs in deeper marginal lobes.

Some leaves diverge morphologically from the typical form described from Pitsidia, having an elongated, narrower lamina (pl. XXIV, figs 14–20; Pl. LVI, fig. 7). Because of the wide leaf variation of modern oak species, it is 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 Middle Europe *Q. pseudocastanea* occurs from the Middle Miocene to the Upper Pliocene (KOVAR-EDER et. al. 1994). Among extant oaks, it is considered closely allied to the group of *Quercus petraea* (MATTUSCHKA) LIEBLEIN (BRUGH, 1993; KÜRSCHNER, 1997).
**Quercus cf. kubinyii (KOVÁTS ex ETTINGSHAUSEN) CZECZOTT**
Pl. XXV, figs 1–23; pl. XXXII, figs 5, 10; pl. LVI, fig. 8; text-fig. 4.7c–h

**Synonym list**

1852 *Castanea kubinyii* (KOVÁTS ex ETTINGSHAUSEN), p. 5, pl. 1, fig. 12 (Erdöbenye)
1951 *Quercus kubinyii* (KOVÁTS ex ETTINGSHAUSEN) – CZECZOTT, p. 392, fig. 7 (Zalesce)
? 2010 *Quercus cf. kubinyii* (KOVÁTS ex ETTINGSHAUSEN) CZECZOTT – ZIDIANAKIS et al., fig. 2k (Pitsidia, central Crete, Tortonian)

**Material:** Pitsidia, forty three leaves; sixteen complete or almost complete, twenty seven fragmentary (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; 31.4.2.5177ai,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 ovate, 25 to more than 94 mm long and 11–47 mm wide, L/W ratio 1.7–3.9, base rounded to broadly cuneate, more or less symmetric, apex acute to acuminate, margin simply dentate; teeth narrow, more or less triangular, mostly large in size, proximal side convex less frequently straight to flexuous, distal side concave or occasionally straight to retroflexuous, 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 about 10–15 pairs, originating at angles of 35–80º, angle decreasing distally, 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 sinusuous, usually perpendicular to the secondaries; quaternary veins forming an irregular polygonal network.

**Remarks:** These oak leaves, with sharp triangular teeth resemble also *Q. gigas* GÖPPERT emend. WALTHER and ZASTAWNIK. The affinity to *Q. kubinyii* is more probable on the basis of the relatively smaller and slender leaves and variation in shape.

SACHSE (1997) reported from Makrilia, 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. These facts make the assignment to *Q. kubinyii* ambiguous. In Europe, *Quercus kubinyii* is common, especially during the Upper Miocene and Pliocene demonstrating a remarkable variation in leaf shape (KNOBLOCH and KVAČEK, 1976; HABLY and KVAČEK, 1997; KVAČEK et al., 2002; WOROBIEC, 2003).

Several modern oaks of the section Cerris such as *Quercus libani* OLIVIER are regarded as possible modern analogues of *Quercus kubinyii* (WALTHER and ZASTAWNIK, 1991; KVAČEK et al., 2008). Some authors related such leaves to the genus *Castanea* (ETTINGSHAUSEN, 1854; KOVÁTS, 1856).
**Quercus mediterranea** UNGER

Pl. XXVI, figs 1–3; pl. XXXII, figs 3–4, 9; pl. LI, figs 6–7

**Synonym list**

1847  *Quercus mediterranea* UNGER, p. 114, pl. 32, figs 5–9 ( Parschlug, Middle Miocene)

? 1862  *Quercus mediterranea* UNGER – UNGER, p. 158 (Kimi, Euboea, Lower Miocene) (no figure)

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

? 1921  *Quercus mediterranea* UNGER – UNGER – FRITEL, p. 472 (Oropos, Attica, Lower Miocene) (no figure)

1867  *Quercus mediterranea* UNGER – UNGER – HEIMANN et al., pl. 14, fig. 10 (Paghi, Corfu Island, Messinian)

1883  *Quercus mediterranea* UNGER – VELITZELOS, pl. 1, figs 2, 5–6 (Pappades, Euboea, Lower Miocene)

? 1985  *Quercus mediterranea* UNGER – DERMITZAKIS and VELITZELOS, p. 165 (Kato Komi, Chios Island, Serravallian-Tortonian) (no figure)

1986a  *Quercus mediterranea* UNGER – KNOBLOCH and VELITZELOS, pl. 2, fig. 5 (Elassona, Thessaly, Messinian)

1986b  *Quercus cf. ilex* L. – HEIMANN et al., pl. 1, figs 2, 11; pl. 15, fig. 7 (Prosilio, W. Macedonia, Messinian)

1989  *Quercus mediterranea* UNGER – KVAČEK and 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, Lower 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 and MOHR, pl. 3, figs 9–11; pl. 5, fig. 5 (Makrilia, eastern Crete, Tortonian)

1997  *Quercus mediterranea* UNGER – SACHSE, pl. 10, figs 4–5, 8; pl. 19, figs 10–11 (Makrilia, E. Crete, Tortonian)

1998  *Quercus mediterranea* UNGER – GOUDELLI and LOUMAKI, pl. 11, fig. 2 (Skoura, Peloponnese, Pliocene)

1999  *Quercus mediterranea* UNGER – VELITZELOS and 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)

2007  *Quercus mediterranea* UNGER – ZIDIANAKIS et al., figs 2H–K, 5J (Vrysses, W. Crete, Messinian)

2010  *Quercus mediterranea* 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, nine leaves, four complete or almost complete and five fragmentary (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, two leaves; one complete and one fragmentary (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 more or less rounded, apex obtuse to acute or shortly acuminate, margin entire, irregularly, simply serrate at the upper half of the lamina, teeth small with acute apices, sinuses
shallow, wide, rounded; venation craspedodromous or eucamptodromous (at the lamina part with entire margin), primary vein stout, secondary veins strong, almost opposite to alternate, in 6–9 pairs, originating at angles of 25–85°, angle decreasing distally, irregularly spaced, straight or curved, mostly not parallel, rarely forked, running towards the margin entering the teeth, tertiary veins opposite percurrent, straight or curved.

**Remarks:** These small, simply and irregularly serrate leaves are characteristic of the sclerophyllous oak *Quercus mediterranea*. With the exception of Kassanoi, *Q. mediterranea* has been reported from all the Neogene floras of Crete (SACHSE, 1997; ZIDIANAKIS et al. 2007). Especially in Vrysses, this oak is one of the dominant species. Contrary, in Pitsidia and Metochia its presence is rather limited. *Quercus mediterranea* is considered a sclerophyllous probably evergreen element, similar to the extant *Q. coccifera* L. and its allies (KVAČEK et al., 2002). Based on leaf morphology and cuticle structure of extant and fossil oak taxa, DENK et al. (2017) proposed that this species and *Q. drymeja* are related to *Quercus*, Group *Ilex*. In their opinion, the modern analogues of vegetation types with sclerophyllous oaks of the Group *Ilex* are located in Asia and their growth occurs under humid conditions suggesting more likely a mesophytic than a xerophytic character for these species.

*Quercus* sp. – folia
Pl. XLV, figs 13–14, 16

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

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

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

**Genus Fagus L.**

*Fagus gussonii* MASSALONGO emend. KNOBLOCH and VELITZELOS
Pl. XXVI, fig. 4; pl. XXXII, fig. 2; pl. LI, figs 1–4; text-fig. 4.7j–k

**Synonym list**

<table>
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<th>Year</th>
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<td>1859</td>
<td><em>Fagus gussonii</em> MASSALONGO in MASSALONGO and SCARABELLI</td>
<td>p. 202, pl. 25, figs 2, 5 (Senigallia, Upper Miocene)</td>
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<td>1859</td>
<td><em>Fagus marsilii</em> MASSALONGO in MASSALONGO and SCARABELLI</td>
<td>p. 201, pl. 9, fig. 19; pl. 21, fig. 18 (Senigallia, Upper Miocene)</td>
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<td>1986a</td>
<td><em>Fagus gussonii</em> MASSALONGO – KNOBLOCH and VELITZELOS</td>
<td>p. 9, pl. 2, figs 2–4, 6–8; pl. 5, fig. 11; pl. 6, fig. 5 (Elassona, N. Thessaly, Messinian)</td>
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Text fig. 4.7. Palaeoflora of Pitsidia, Crete, 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–i Quercus cf. kubinyii; c. Nr. 31.4.2.4646b; d. Nr. 31.4.2.3806ai; e. Nr. 31.4.2.1416a; f. Nr. 31.4.2.8176bi; g. lamina apex, Nr. 31.4.2.1420a; h. Nr. 31.4.2.6070a,b synthesis; i. ?Quercus cf. kubinyii, Nr. 31.4.2.4189ai;
j Fagus gussonii, Nr. 31.4.2.7038;
k. ?Fagus gussonii Nr. 31.4.2.6125iii
1986b  *Fagus gussonii* MASSALONGO – KNOBLOCH and VELITZELOS, pl. 14, fig. 2 (Prosilio, W. Macedonia, Messinian)

1987  *Fagus gussonii* MASSALONGO – KNOBLOCH and VELITZELOS, pl. 1, fig. 5 (Elassona, N. Thessaly, Messinian)

1996  *Fagus* sp., aff. *Alnus* sp. – SACHSE and MOHR, pl. 3, figs 1–2, 5 (Makrilia, E. Crete, Tortonian)

1997  *Fagus type gussonii*, *Fagus type attenuata* – SACHSE, pl. 10, figs 1–2, 6, pl. 19, figs 1, 2, 5 (Makrilia, E. Crete, Tortonian)

2002  *Fagus gussonii* MASSALONGO emend. KNOBLOCH and 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 – 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)

? 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)

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 and VELITZELOS – MANTZOUKA et al., figs 4.1–4.3 (Metochia, Gavdos Island, Tortonian)

**Material:**

**Pitsidia,** eleven leaves; two complete or almost complete and nine fragmentary (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,** fourteen leaves; three complete to almost complete, eleven fragmentary (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 strong, more than 6–8 mm long, lamina chartaceous, oblong to ovate or elliptic, about 40 to more than 82 mm long and 20 to more than 62 mm wide, L/W ratio ca. 2–2.4, base cuneate to rounded, apex acute, margin simply dentate, with small, sharp teeth alternating with open, shallow, rounded to S-like sinuses; venation (sub-) craspedodromous, primary vein strong, straight to gently curved, often slightly sinuous near the leaf apex, secondary veins slender, alternate to subopposite, in 10–15 pairs, regularly spaced, parallel or subparallel, arising at angles of 30–80º, interspacing in distances of 2–8 mm angles and distances decreasing towards the apex, unbranched, straight or gently curved, entering the marginal teeth, tertiary veins dense, opposite or alternate percurrent, oblique or perpendicular to the secondaries, sinuous or straight in course, higher order venation forming a polygonal network.

**Remarks:** The marginal serration, the (sub-) craspedodromous venation, the strictly straight and parallel secondary veins with the basal pairs being slightly concave, suggest a *Fagus* origin for these specimens. In most features this material falls into the range of *Fagus gussonii*. SACHSE (1997) and MANTZOUKA et al. (2015) described several leaf remains of this species from Makrilia and Metochia respectively, while in Vrysses and Kassanoi *F. gussonii* it has been absent so far.
*Fagus gussonii* is restricted to the Upper Miocene of southern Europe, Anatolia and Iceland contrary to the widely distributed species in the central and eastern European Neogene, *F. haidingeri* KOVÁTS. It belongs to the Eurasian-North American subgenus of *Fagus* and closely resembles extant *F. sylvatica* L. and *F. longipetiolata* SEEMEN (DENK et al., 2004).

Family Myricaceae
Genus *Myrica* L.

*Myrica lignitum* (UNGER) SAPORTA
Pl. XXVI, figs 5–6, 8; pl. XXVII, figs 1–22; pl. XXXVIII, figs 14–16, 19, 22; pl. XLIV, figs 17–18; pl. XLVI, figs 1–8, 15; pl. XLIX, fig. 12; text-fig. 4.8a–aii, b

**Synonym list**

<table>
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<th>Year</th>
<th>Name</th>
<th>Author</th>
<th>Location</th>
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<td>1847</td>
<td><em>Quercus lignitum</em></td>
<td>UNGER, p.113, pl. 31, figs 5–7 (Parschlug, Middle Miocene)</td>
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<td>1862</td>
<td><em>Laurinastrum dubium</em></td>
<td>UNGER – UNGER, fig. 17 (Kimi, Euboea, Lower Miocene)</td>
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<td>1862</td>
<td><em>Dryandroides lignitum</em></td>
<td>ETTINGSHAUSEN – UNGER, fig. 23 (Kimi, Euboea, Lower Miocene)</td>
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<td>1862</td>
<td><em>Asclepias podalyrii</em></td>
<td>UNGER – UNGER, fig. 27 (Kimi, Euboea, Lower Miocene)</td>
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<td>1865b</td>
<td><em>Myrica lignitum</em></td>
<td>SAPORTA, p. 102, pl. 4, fig. 10 (Armissan-Peyriac, Tertiary)</td>
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<td>1867a</td>
<td><em>Myrica solonis</em></td>
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<td><em>Myrica vindobonensis</em></td>
<td>(ETTINGSHAUSEN) HEER – UNGER, pl. 4, figs 23–27 (Kimi, Euboea, Lower Miocene)</td>
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<td>1867</td>
<td><em>Laurinastrum dubium</em></td>
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<td><em>Banksia solonis</em></td>
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<td>1867</td>
<td><em>Dryandroides hakeaefolia</em></td>
<td>UNGER – UNGER, pl. 9, figs 4–13, 15 (Kimi, Euboea, Lower Miocene)</td>
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<td><em>Olea noti</em></td>
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<td><em>Euclea relicta</em></td>
<td>UNGER – UNGER, pl. 11, fig. 39 (Kimi, Euboea, Lower Miocene)</td>
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<td>1873</td>
<td><em>Myrica oxydonta</em></td>
<td>SAPORTA – SAPORTA, pl. 2, fig. 15 (Kimi, Euboea, Lower Miocene)</td>
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<td>? 1985</td>
<td><em>Myrica lignitum</em></td>
<td>(UNGER) SAPORTA – DEHRITZAKIS and VELITZELOS, p. 165 (Kato Komi, Chios Island, Serravallian-Tortonian) (no figure)</td>
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<td>? 1993</td>
<td><em>Myrica lignitum</em></td>
<td>(UNGER) SAPORTA – VELITZELOS, p. 7 (Iliokomi-Kormitsa, E. Macedonia, Messinian) (no figure)</td>
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<td>1993-95</td>
<td><em>Grevillea kymeana</em></td>
<td>UNGER – SCHIMANI and SCHNEIDER, figs 8–9 (Platanos-Paliopyrgos, Thessaly, Lower Miocene)</td>
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<td>1994a</td>
<td><em>Myrica lignitum</em></td>
<td>(UNGER) SAPORTA – KLEINHÖLTER, pl. 26, fig. 5 (Pyrgos and Zacharo basins, Peloponnese, Messinian)</td>
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<td>1996</td>
<td>Juglandaceae vel Lauraceae, <em>Dicotylyphillum</em> sp. 9 – SCHAESE and MOHR, pl. 3, figs 24, 29 (Makrilia, E. Crete, Tortonian)</td>
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<td>1997</td>
<td><em>Myrica</em> sp. Typ <em>M. cf. lignitum</em> (UNGER) SAPORTA sensu ETTINGSHAUSEN et STANDFEST – SCHAESE, pl. 13, figs. 2, 4–5, 7, 9; pl. 19, figs 24, 29 (Makrilia, E. Crete, Tortonian)</td>
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<td>(UNGER) SAPORTA – ERDEI and KVAČEK, fig. 8. (Kimi, Euboea, Lower Miocene)</td>
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<td>1999</td>
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<td>(UNGER) SAPORTA – VELITZELOS et al., fig. E6 in p. 461 (Kimi, Euboea, Lower Miocene)</td>
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<td>2010</td>
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<td>(UNGER) SAPORTA – ZIDIANAKIS et al., fig. 2g (Pitsidia, central Crete, Tortonian)</td>
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<td>2010</td>
<td><em>Comptonia diformis</em> (STERNBERG) BERRY – ZIDIANAKIS et al., fig. 2h (Pitsidia, central Crete, Tortonian)</td>
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<td>2014</td>
<td><em>Myrica lignitum</em></td>
<td>(UNGER) SAPORTA – VELITZELOS D. et al., pl. 7, fig. 9 (Grevena, W. Macedonia, Lower Miocene)</td>
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Material:

Pitsidia, two thousand seven hundred and sixty two leaves; complete fifty five, fragmentary two thousand seven hundred and seven (for collection numbers of the specimens see appendix 9a).

Kassanoi, twenty eight leaves; eight complete or almost complete, twenty fragmentary (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, two incomplete leaves (Nrs 31.5.2.46; 31.5.2.48at,b).

Description: Leaves simple, petiole (1) 10–16 (34) mm long (average 12.2 mm), base sometimes slightly swollen; lamina texture coriaceous, adaxially and abaxially globose glands occur scattered all over the lamina surface with density on the adaxial surface about 20–40 per mm², abaxially clearly denser; lamina shape variable, lanceolate, linear, elliptic or rarely oblong, size microphyll or less frequently nanophyll, (7) 19–70 (109) mm long (average 46 mm) and (1) 7–15 (29) mm wide (average 9 mm), length/width ratio (1.8) 4–8 (14.5) (average 5.7), base acute, almost always decurrent, apex acute, mainly straight or slightly convex, rarely obtuse, rounded or retuse (the latter probably due to arthropod-mediated damage), margin entire or crenate to simply serrate, rarely lobed, mostly in upper 1/2 of lamina, smaller leaves mainly entire margined; teeth variable in size, shape and spacing, tooth size ranges from tiny to large blunt ones (up to 5 mm), usually small, proximal side convex or retroflexed, less frequently straight, distal side mainly convex or straight, tooth apex acute or less frequently obtuse, sinus between teeth mainly angular in shape, acute or obtuse, tooth spacing mostly irregular, tooth density usually increasing towards leaf apex, number of teeth on each side of lamina mainly less than 8, rarely reaching 15; venation semicraspedodromous when margin is toothed to brochidodromous when is entire, primary vein prominent, straight or more frequently curved (occasionally strongly bent), tapering along its length, secondary veins compared to the midrib very fine, somewhat densely spaced (mainly 5–20 pairs per leaf), opposite or alternately arranged, originating from the primary vein more or less uniformly at angles of 55–80°, decreasing towards leaf base and apex, secondaries spacing decreases distally and proximally, course straight or slightly curved; intersecondary veins present, 1–3 per intercostal area, running almost parallel to the adjacent secondaries; tertiary and quaternary veins weakly reticulate, forming an irregular network; areoles hardly visible; tooth major accessory veins form looping connections to the principal vein.

Remarks: In Pitsidia, the low number of complete leaves compared to the increased number of fragments was caused by mechanical stress prior to deposition as well as by sediment ruptures (secondarily fragmented). On numerous leaf imprints an iron-rich replica is developed, suggesting a coriaceous leaf texture. The large variability in leaf form conforms well to the variability observed in the type locality of
Parschlug in Austria (ETTINGSHAUSEN and STANDFEST, 1888; KOVAR, 1982; KOVAR-EDER et al., 2004). A few specimens are deeply lobed, superficially resembling Comptonia (pl. XXVII, fig. 11). Judging from the venation course and shape of the leaf base, they probably represent extreme forms of M. lignitum. In this sense, the deeply lobed fragment reported as Comptonia difformis (STERNBERG) Berry by ZIDIANAKIS et al. (2010) is assigned here to M. lignitum.

In Pitsidia, we observed neither large leaves with large teeth and dense secondaries arising at almost right angles from the mid vein, typical for M. solonis (UNGER) Saporta, nor short petiolate leaves with sharp teeth as in M. vindobonensis (ETTINGSHAUSEN) Heer. In general, leaves of these species are well distinguished from M. lignitum. Intermediate leaf forms may, however, be difficult to determine with certainty. This fact is obvious in the Early Miocene assemblage of Kimi (UNGER, 1867; VELITZELOS et al., 2002), where M. lignitum co-occurs with these two taxa.

In Kassanoi Myrica lignitum is a dominant floristic element. The broad leaf form figured in pl. XLVI, fig. 6, with prominent secondary veins could represent a second Myrica species, though poor preservation provided limited evidence for such a determination.

Myrica lignitum is quite common in the Upper Miocene of Crete. So far it has been absent only from Vrysses. Stratigraphically, M. lignitum occurs from the Lower Oligocene to the Pliocene with a peak in the Upper Miocene (KNOBLOCH and KVAČEK, 1976; KOVAR, 1982; FISCHER and BUTZMANN, 2000).

Myrica ceriferiformis KOWNAS

Pl. XXVI, figs 5, 7; pl. XXVIII, figs 1–17; text-fig. 4.8aiii

Synonym list

1955 Myrica ceriferiformis KOWNAS, p. 459, figs 8a–b (Dobrzyn)
1964 Myrica ceriferiformis KOWNAS – MAI, p. 60, pl. 7, fig. 5
2003 Myrica ceriferiformis KOWNAS – TEODORIDIS, p. 16, pl. 3, figs 13–21; pl. 4, figs 1, 4 (HRÁDEK)
2012 Myrica ceriferiformis KOWNAS – HOLÝ et al. p. 75, pl. 7, figs 10–11
? 2002a Myrica ceriferiformis KOWNAS – VELITZELOS et al., p. 11 (Kimi, Euboea, Lower Miocene) (no figure)
2015 Myrica lignitum (UNGER) Saporta – ZIDIANAKIS et al. – pl. 1, figs 5–6; pl. 3, figs 1–17 (Pitsidia, central Crete, Tortonian)

Material: Pitsidia, one hundred and seventeen isolated fruits, twenty three fruiting stalks with at least one fruit attached and forty one bare fruiting stalks (for collection numbers of the specimens see appendix 9a).

Description: Fruits small drupes, globose (secondarily flattened), less frequently slightly ovoid, (1.5) 2–3.5 (4) mm in diameter (average 2.7 mm), base of the fruit (area of attachment) often slightly flattened, near the apex a distinct projection is usually developed; exocarp consisting of a mosaic of warty, densely packed protuberances, 8 to 12 warts in the equatorial
plane; protuberances mainly ovoid, about 0.1–0.4 mm long in the main axis (smaller near base of fruit), upper part rounded, lower part rounded to somewhat angular, creating an irregular net on external surface of exocarp, internal structure of protuberances cancellous; exocarp in the equatorial area of the fruit 0.30–0.45 mm thick; mesocarp about 0.25–0.40 mm thick, lacking distinct features; few specimens yielding a replica of the pyrina (hard endocarp with the enclosed seed/s), pyrina ovoid to rounded, secondarily compressed, (1.3) 1.5–2.2 (2.3) mm long (average 1.8 mm) and (1.5) 1.6–2.0 (2.2) mm (average 1.7) broad, occupying most of the internal space of the fruit; base of pyrina rounded, apex obtuse to acute with a distinct tip; external surface of endocarp smooth, in one specimen the seam of dehiscence is well visible.

Fruits spirally arranged in relatively loose clusters (infructescences), attached directly to the axis without pedicel; infructescence axis quite stout, more or less curved or rarely S-like, (10) 11–18 (25) mm long (average 15.8 mm) and 1.2–3 mm wide near the base, narrowing gradually towards the apex, occasionally bearing small bracts; surface of axis rough with numerous compartments in short intervals formed to hold the drupes, base with characteristic scars; each fruiting axis is estimated to hold about 10–20 fruits.

**Remarks:** The preservation of the fossil material enables recognising morphological details fairly well. The distinct tip at the apex of the pyrina is interpreted as the base of the style. The scars at the base of the stalks probably derive from the bracts of the floral buds. Unfortunately, the preservation does not allow any conclusions about pubescence of the fruit wall or protuberances, which would be diagnostically relevant.

Among the fruit remains from Pitsidia, drupes of *Myrica* are the most abundant. About 35% of the yielded female axes bear one or more drupes, indicating that the parent plant shed them before all fruits had dropped. On one slab, several isolated fruits were found close to a fruiting axis: they were apparently detached after the deposition of the catkin in the sediment but prior to sediment coverage (pl. XXVI, fig. 7).

The material from Pitsidia is very similar to *Myrica ceriferiformis* described by KOWNAS (1955) from Dobrzyń. The drupes from Pitsidia and Dobrzyń share the shape, exocarp structure and thickness, protuberance size and density as well as the endocarp shape. The fruits from Dobrzyń are, however, somewhat bigger (2.3–4.3 mm in diameter, average 3.2 mm) and the mesocarp is slightly thicker (about 0.5 mm).

*Myrica ceriferiformis* is a common element in the European Neogene, with highest abundances in the Upper Miocene (KOWNAS, 1955; PALAMAREV, 1968; ŁAŃCUCKA-ŚRODONIOWA et al., 1981; MELLER, 1998; MAI, 1999b, MAI, 2001; GÜMBEL and MAI, 2002;
In Greece a twig with fruits of *Myrica ceriferiformis* has been reported by VelitzeLos et al. (2002a) from Kimi.

**Myrica cf. goeppertii KOHLMAN-ADAMSKA,**
**ZIEMBIŃSKA-TWORZYDŁO and ZASTAWNIAK**

Pl. XXVI, fig. 6; pl. XXIX, figs 1–16; pl. XXX, figs 1–12; text-fig. 4.8aiv

**Material:** Pitsidia, five hundred and eighty-six male inflorescences; complete one hundred twenty-three, fragmentary four hundred sixty-three (for collection numbers of the specimens see appendix 9a).

**Description:** Male inflorescences, staminate catkins without pedicel; catkins simple, more or less loose, (sub)cylindrical, secondarily flattened, (5) 10–25 (32) mm (average 17.2 mm) long and 2–5 mm (average 3.6 mm) wide, with numerous inconspicuous flowers (florets), typically more than 25 per inflorescence, densely crowded; inflorescence axis unbranched. Flowers apetalous, composed typically of 4 stamens attached to the axil of a single bract; bracts prominent, distinctly curved, quite broad, deltoid to ovate, about 1–3.5 mm long and 1–3.5 mm wide, arranged spirally on inflorescence axis, proximally at wide angles (almost 90°), angle gradually decreasing distally and almost parallel to axis near apex of inflorescence; bract apex probably acute, base broad, margin entire or rarely minutely erose, no marginal cilia detected; external surface of bract bearing a smooth, parallel-running striation; no bracteoles detected; immature pollen sacs elongate, slightly C- or S-shaped, paralleling the curved shape of the bract, length/width ratio ranging from 3:1 to 6:1, dehiscing longitudinal; filaments hardly visible, fused into a branched staminal column, shorter than the accompanying floret bract.

**Remarks:** Male catkins of *Myrica* are surprisingly common in Pitsidia, as are leaves and fruits/infructescences. They predominate among flower and inflorescence remains of other taxa. The excellent preservation of this material allows the observation of the floret details (bract and stamens), their number per axis, size and arrangement. Even immature florets and their anthers are extraordinarily well preserved (pl. XXIX, fig. 13; pl. XXX, figs 1–2, 8). Among the numerous staminate catkins from Pitsidia, neither androgynous inflorescences nor catkins with hermaphrodite flowers have been observed, features occurring in some modern *Myrica* species.

The replicas of the florets indicate that the stamen filaments were fused into a branched staminal column (pl. XXX, figs 3–5). This feature constitutes a reliable criterion to distinguish the sections *Faya* and *Cerophora*
from section *Morella* (sensu CHEVALIER, 1901) within the genus *Myrica* (HERBERT, 2005) (appendix 11, see in Discussion). It remains open whether cilia were not developed on the bracts of the studied material or whether their absence is due to a taphonomic bias.

Text-figure 4.8. Palaeoflora of Pitsidia, Crete, *Myrica*

a. vegetative and fertile organs, line drawings, scale bar 2.5mm (unless stated otherwise); i. complete leaf of *M. lignitum*, Nr. 31.4.2.3782bii, scale bar 6mm; ii. leaf fragment, venation and margin details are visible, Nr. 31.4.2.4407i; iii. *M. cf. goeppertii* infructescence with 14 attached fruits, Nr. 31.4.2.8103b; iv. *M. ceriferiformis* male catkin, Nr. 31.4.2.5300bi;
b. localities of *Myrica lignitum* from the Greek Paleogene/Neogene

Male catkins of *Myrica* are rather rare in the European fossil record and usually are determined to the generic level only, e.g., ETTINGSHAUSEN (1853), SAPORTA (1865b), ETTINGSHAUSEN (1888), KOVAR-EDER (1998). GÖPPERT (1855: pl. 14, fig. 22) figured a sole inflorescence as “Amentum Myricae” along with *Myrica* fruits from Sośnica. Recently, KOHLMAN-ADAMSKA et al. (2004) described a new specimen from Sośnica – a small catkin, 25 mm long and 4–5 mm wide with spirally arranged florets, composed of four stamens attached to a sole bract – as a new fossil-species *M. goeppertii*. The material from Pitsidia matches very well this specimen from Sośnica in gross morphology as well as in the number of stamens. Further morphological details of the florets are not available from this specimen. Therefore, the assignment of the catkins from Pitsidia to this fossil species is somewhat ambiguous.
Family JUGLANDACEAE
Genus Carya NUTTALL

Carya sp. – folia
Pl. XXXI, figs 1–13; pl. LVI, figs 9–10

 synonym list
2010  Carya minor SAPORTA and MARION – ZIDIANAKIS et al., figs 2o, 3c (Pitsidia, central Crete, Tortonian)
2014  Carya serrifolia (GÖPPERT) KRÄUSEL – VELITZELOS D. et al., pl. 27, fig. 5 (Makrilia, E. Crete, Tortonian)

material: Pitsidia, sixty three leaflets; twenty complete or almost complete, forty three fragmentary (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; 31.4.2.3827ai,bi; 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; 31.4.2.5267aibi; 31.4.2.5269opi; 31.4.2.5296a,b; 31.4.2.5386a,5385; 31.4.2.5417ai,bi; 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; 31.4.2.6963bbi,ii; 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; 31.4.2.8258a,b)

description: Leaflets subsessile (lateral ones) or petiolulate (terminal ones), lamina chartaceous, lateral leaflets shape elliptic to ovate, 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, decurrent, symmetric in terminal ones; margin sharply simple serrate; teeth dense, fine, more or less irregular in shape, acute, distal side mostly straight, straight to convex or slightly concave proximally, 0.5–1 mm long, 5–7 teeth per cm, sinuses narrow, angular; venation craspedodromous to partly semicraspedodromous, primary vein strong, straight to curved or S-like, secondary veins more delicate, almost opposite to alternate, 6–18 pairs, interspaces 2–7 mm, arising at angles of 50–85°, course slightly irregular, curved, often forked once or more times, sending veinlets into the marginal teeth, intersecondary veins rare, parallel to secondaries, half of the secondary long, tertiary veins dense, percurrent, mostly opposite, oblique or almost perpendicular to the secondaries, straight to sinuous, quaternary veins form an irregular quadrate or pentagon network.

remarks: The overall shape of the studied leaflets, the tooth type and the secondary vein course conform to Juglandaceae and especially to the genera Pterocarya, Carya, Juglans and Cyclocarya. The broad lamina, the craspedodromous course of the secondary veins and the somewhat irregular teeth serration suggest generic affinity to the genus Carya.

The study of modern foliage showed that Carya leaves do not express significant differences among the various species (MANCHESTER, 1987). Concerning fossil material, common species entities such as C. minor SAPORTA and MARION, C. serrifolia (GÖPPERT) KRÄUSEL need re-examination and species delimitation. Therefore the assignment to a particular fossil-species is avoided. Based on fruits, a few different species
have been recognized e.g. *C. angulata* C. and E. M. Reid, *C. askenasyi* (Kinkel) Mai, *C. globosa* (Ludwig) Mädler, suggesting a limited diversity of *Carya*. From Makrilia, Velitzelos D. et al. (2014) figured a fragment of an elongated leaflet as *Carya serrifolia* that resembles the slender leaflet forms of *Pitsidia* in both venation and marginal teeth.

**Genus Pterocarya Kunth**

*Pterocarya* sp. – fructus

Pl. XXXII, fig. 1

**Material:** Pitsidia, one fragmentary fruit (Nr. 31.4.2.3000).

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

**Remarks:** The morphology of this fruit is characteristic of *Pterocarya*, especially the wing features and the occurrence of style remnants. Several fossil species of this genus have been recognized in the European Neogene as *P. limburgensis* C. and E. M. Reid, *P. cf. rhoifolia* Siebold and Zuccarini, *P. cf. stenoptera* Candolle and *P. kireevskiana* Dorofeev (Reid and Reid, 1915; Dorofeev, 1960; Cezzotti and Skirgiello, 1961; Manchester and Dilcher, 1982). The studied specimen lacks diagnostic details for an assignment to the species-level.

**Genus Engelhardia Leschenault ex Blume**

*Engelhardia orsbergensis* (Wessel and Weber) Jähniche, Mai and Walther

Pl. XLIX, figs 13–14

**Synonym list**

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<th>Name</th>
<th>Authors</th>
<th>Reference</th>
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<td>1855</td>
<td>Banksia orsbergensis</td>
<td>Wessel and Weber</td>
<td>p. 146, pl. 25, fig. 9a (Orsberg)</td>
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<td>1977</td>
<td>Engelhardia orsbergensis</td>
<td>Wessel and Weber</td>
<td>– Jähniche et al., p. 326, pls 38–49; text-figs 1–3</td>
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<td>1984</td>
<td>Palaeocarya orsbergensis</td>
<td>Wessel and Weber</td>
<td>– Jähniche et al., p. 109, pls 1–6; text-figs 2–4</td>
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<td>? 1953</td>
<td>cf. Quercus lonchitis</td>
<td>Unger – Berger</td>
<td>figs 2–3 (Kastron, Lemnos Island, Lower Miocene)</td>
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<td>1986b</td>
<td>Palaeocarya orsbergensis</td>
<td>Wessel and Weber</td>
<td>Jähniche, Friedrich and Takáč – Knobloch and Velitzelos, pl. 14, fig. 12 (Prosilio, W. Macedonia, Messinian)</td>
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<td>1996</td>
<td>Palaeocarya sp.</td>
<td>Sachse and Mohr</td>
<td>pl. 3, fig. 12; pl. 5, figs 2, 7–8 (Makrilia, E. Crete, Tortonian)</td>
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<td>1997</td>
<td>cf. Engelhardia orsbergensis</td>
<td>Wessel and Weber</td>
<td>Jähniche, Mai and Walther – Sachse, pl. 11, figs 1–4; pl. 19, fig. 12 (Makrilia, E. Crete, Tortonian)</td>
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<td>? 2002a</td>
<td>Engelhardia orsbergensis</td>
<td>Wessel and Weber</td>
<td>Jähniche, Mai and Walther – Velitzelos et al., p. 12 (Kimi, Euboea, Lower Miocene) (no figure)</td>
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2014  *Engelhardia orsbergensis* (WESSEL and WEBER) JÄHNICHEN, MAI and WALTHER – VELITZELOS D. et al., pl. 13, fig. 4 (Lesbos Island, Lower Miocene)

? 2014  *Engelhardia orsbergensis* (WESSEL and WEBER) JÄHNICHEN, MAI and WALTHER – VELITZELOS D. et al., p. 66 (Kimi-Nea Stira, Euboea, Lower Miocene) (no figure)

? 2014  *Engelhardia orsbergensis* (WESSEL and WEBER) JÄHNICHEN, MAI and WALTHER – VELITZELOS D. et al., p. 69 (Prosilio and Lava, W. Macedonia, Messinian) (no figure)

2015  *Engelhardia orsbergensis* (WESSEL and WEBER) JÄHNICHEN, MAI and WALTHER – MANTZOUKA et al., figs 5.12–5.13 (Metochia, Gavdos Island, Tortonian)

**Material:** Metochia, two complete leaflets (Nrs 31.5.2.3a,b; 31.5.2.5).

**Description:** Leaflets shortly petiolulate, petiolule 2–6 mm long; lamina chartaceous, shape lanceolate, more or less asymmetric, 34–58 mm long and 9–12 wide, L/W ratio 3.7–4.8, base rounded to narrow cuneate, strongly asymmetric in one specimen (pl. L, fig. 13), apex acute, margin widely, simply dentate with small, acute teeth; venation camptodromous to semicraspedodromous, primary vein stout, more or less smoothly curved, secondary veins much thinner, densely spaced, originating at angles of 35–60°, intersecondary veins delicate, parallel to the secondaries, higher order venation not visible.

**Remarks:** The asymmetric lamina with fine marginal teeth and the venation pattern are characteristic of *Engelhardia orsbergensis*, a well documented thermophilous element of the European Tertiary (JÄHNICHEN et al., 1984). In the specimen figured on pl. XLIX, fig. 13 the rather long petiolule is not a characteristic feature of *E. orsbergensis*. This long petiolule could be a result of arthropod damage at the base of the leaflet.

In the Greek Area *E. orsbergensis* was a common element during the Lower Miocene, while in the Upper Miocene it appears mostly in the palaeofloras of Crete. In Makrilia, *E. orsbergensis* co-occurs with the three-lobed samaras of *Engelhardia macroptera* (BRONGNIART) UNGER (SACHSE, 1997). In Metochia, the remains of incomplete leaflets have been described by MANTZOUKA et al. (2015). On the basis of leaf and fruit morphology, the extant *E. roxburghiana* WALlich (eastern Asia) and *Oreomunnea mexicana* (STANDLEY) LEROY (Central America) are considered as closer allies. Both thrive in sub-tropical to paratropical forests or in rather warm-temperate mesophytic forests (JÄHNICHEN et al., 1977).

**Juglandaceae gen. et sp. indet. – folia**

Pl. XXXVII, fig. 13

**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 the apex; venation brochidodromous to craspedodromous (apically), primary vein almost straight, secondary veins distinct, in approx. 12 pairs arising at angles of 45–80°, distances 3–4 mm, initially straight, then curved, forming well developed loops close to the margin, apically inervating the marginal teeth, tertiary veins weakly percurrent.
Remarks: The leaf architecture of this sample, especially margin, course of secondaries, percurrent tertiaries, resembles leaflets of several members of the Juglandaceae.

Family BETULACEAE

Betulaceae gen. et sp. indet. – folia
Pl. XXIII, figs 1–5, 11; text-fig. 4.6a,d

Material: Pitsidia, seven leaves; two almost complete, five fragmentary (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, ca. 5.5 mm long, lamina chartaceous, narrow elliptic to ovate, about 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 not entirely preserved, acute to acuminate, margin finely simple to weakly double serrate, with narrow, acute teeth and angular sinuses, teeth about 1 mm long, proximal side concave, distal 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, less than 45°, straight to gently curved upwards, forked close to the margin, forks unequal, the stronger inervating the first order teeth, the weaker the second order ones, tertiary veins percurrent, opposite or alternate, very fine, deriving almost perpendicular from the secondaries.

Remarks: The above described foliage is characterized by a symmetric lamina base, quite acute angles of secondary veins and a finely serrate margin with delicate teeth. Leaves resembling these specimens can be found in the Betulaceae and especially in the genus Ostrya SCOPOLI.

Family SALICAEAE

Genus Salix L.

Salix cf. angusta A. BRAUN
Pl. XLVI, figs 9–14; pl. XLVIII, fig. 10; text-fig. 4.12c

Synonym list

1836 Salix angustifolia A. BRAUN (in BUCKLAND), p. 512 (Öhningen, Upper Miocene)
1856 Salix angusta A. BRAUN – HEER, p. 30, pl. 69, figs 1–11 (Schweizer Molasse, Upper Miocene)
? 2015 Salix cf. angusta A. BRAUN – MANTZOUKA et al., figs 5.7–5.9 (Metochia, Gavdos Island, Tortonian)

Material: Kassanoi, twenty-one leaves, more or less 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; 31.6.2.37i; 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; 31.6.2.120ii; 31.6.2.120vi).
**Description:** Leaves petiolate, petiole fragmented, more than 5 mm long, lamina texture chartaceous, shape lanceolate to linear with margins subparallel to parallel, 53 to more than 95 mm long, (4) 12–22 (32) mm wide (the greatest width mostly in the lower half part of the lamina), L/W ratio 5–14, base obtuse to acute, convex to slightly cuneate, occasionally asymmetric, apex acuminate, margin entire to slightly crenulate; venation eucamptodromous, primary vein very strong, straight or slightly bent, secondary veins numerous, more than 15 pairs, delicate, subopposite to alternate, arising at wide angles, mostly 40–70°, interspaces 4–8 mm, course initially straight, after uniformly curved upward forming broad arcs, intersecondary veins 1–2 per intercostal area, at wider angles than secondaries, half in length of secondaries, tertiary veins indistinct.

**Remarks:** Willow leaves are very common in the Kassanoi assemblage. Leaves similar in gross-morphology have been described from the type locality of Öhningen as *Salix angusta*, *S. angustifolia* and *S. angustissima* (A. BRAUN in BUCKLAND, 1836; A. BRAUN, 1845; A. BRAUN in BRUCKMANN, 1850). Later they were united as *Salix angusta* HEER (1856). 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 point of view on the existence of transitional forms between these two extremes and the lack of differential features.

The very narrow, linear leaf illustrated on pl. XLVI, fig. 13, probably constitutes an extremely narrow form. From Makrilia, SACHSE (1997) described a number of elongate, entire-margined or probably indistinctly finely serrate leaves under the name *Salix* type 1 (pl. 13, figs 8, 10–11; pl. 19, figs 23, 31) and *Salix* type *purpurea* (pl. 13, fig. 12; pl. 19, fig. 30). The venation of these specimens (as far as is possible to recognise) differs from the herein described material (secondaries from less broad arcs, equal angles of secondary and intersecondary veins, tertiary veins well distinct). As SACHSE noted, some of them, probably represent members of other plant families. In Gavdos, MANTZUKA et al. (2015) identified several elongate, entire-margined leaves of willow and conferred them to the species *Salix angusta*. In gross morphology these leaves are similar to the material from Kassanoi, except for differences in the shape of the apex.

*Salix* sp. – *folia*  
Pl. XXXII, fig. 6

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

**Description:** Leaf fragment elongate, ca. 55 mm long and ca. 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 the midrib at angles of 40–80°, strongly curved along their length, alternating with weak intersecondaries; higher order venation not visible.

**Discussion:** This specimen can be attributed to *Salix* on account of its shape and especially of serrate margin and secondary as well as intersecondary vein course. The determination to the species level remains open.

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Genus *Populus* L.

*Populus populina* (BRONGNIART) KNOBLOCH

Pl XVIII, figs 3–6; pl. XXXIII, figs 1–8; pl. XLVII, fig. 11; pl. LI, fig. 8

**Synonym list**

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<th>Author(s)</th>
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<td>1822</td>
<td><em>Phyllites populina</em></td>
<td>BRONGNIART, p. 237, pl. 14, fig. 14</td>
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<td>1850a</td>
<td><em>Populus latior</em></td>
<td>BRAUN – ÜNGER, p. 416</td>
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<td>1867</td>
<td><em>Populus attenuata</em></td>
<td>BRAUN – ÜNGER, pl. 6, fig. 29 (Kimi, Euboea, Lower Miocene)</td>
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<td>1964</td>
<td><em>Populus populina</em></td>
<td>BRONGNIART – KNOBLOCH, p. 601</td>
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<td>1994a</td>
<td><em>Populus populina</em></td>
<td>KNOBLOCH – KLEIHÖLTER, pl. 9, fig. 10; pl. 31, fig. 5 (Pyrgos and Zacharo basins, Peloponnese, Messinian)</td>
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<tr>
<td>1994b</td>
<td><em>Populus populina</em></td>
<td>KNOBLOCH – KLEIHÖLTER, pl. 2, fig. 5 (Pyrgos and Zacharo basins, Peloponnese, Messinian)</td>
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<td>1995</td>
<td><em>Populus populina</em></td>
<td>KNOBLOCH – KLEIHÖLTER, pl. 31, figs 6–7 (Patra, Rion and Corinth basins, Peloponnese, Pliocene)</td>
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<td>1999</td>
<td><em>Populus</em> sp. – VELITZELOS and KVAČEK</td>
<td>pl. 2, fig. 2 (Vegora, W. Macedonia, Messinian)</td>
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<td>2002</td>
<td><em>Populus populina</em></td>
<td>KNOBLOCH – KVAČEK et al., pl. 21, figs 1–5 (Vegora, W. Macedonia, Messinian)</td>
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<td>2007</td>
<td><em>P. tremula</em> L. foss. – ZIDIANAKIS et al.</td>
<td>fig. 3D (Vrysses, W. Crete, Messinian)</td>
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<td>2010</td>
<td><em>Populus crenata</em></td>
<td>BERGER – ZIDIANAKIS et al., fig. 3b (Pitsidia, central Crete, Tortonian)</td>
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<td>2014</td>
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<td>BRONGNIART – VELITZELOS D. et al., pl. 7, fig. 7 (Grevena, W. Macedonia, Lower Miocene)</td>
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<td>2014</td>
<td><em>Populus populina</em></td>
<td>BRONGNIART – VELITZELOS D. et al., p. 70 (Elissona, Thessaly, Messinian) (no figure)</td>
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<td>2015</td>
<td><em>Populus populina</em></td>
<td>KNOBLOCH – MANTZOUKA et al., figs 5.10–5.11 (Metochia, Gavdos Island, Tortonian)</td>
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**Material:**

Pitsidia, seventeen leaves; five complete or almost complete and twelve fragmentary (Nrs 31.4.2.340a,b; 31.4.2.1140; 31.4.2.1178a,b; 31.4.2.1585ai,bi; 31.4.2.1940a,b; 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, two 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, 10 to ca. 60 mm long and 19 to ca. 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 the tips, teeth occasionally rather large, acute, sinus rounded; venation semicraspedodromous, in specimens pl. XXXIII, fig. 2 and pl. LI, fig. 8 basal actinodromous, tri-veined primary vein stout and almost straight, secondary veins in 4–7 pairs, basal pair rather strong, sub- or almost opposite, ascending towards the middle part of the lamina (in tri-veined specimens towards the apex of the lamina), subopposite to alternate, originating mostly at wide angles of 40–85°, angles decreasing towards the apex, interspaces of 4–18 mm, slightly to strongly bent, intersecondary veins infrequently present, tertiary veins percurrent, opposite or alternate, sinuous in course, 3–5 per cm of secondary, quaternaries reticulate forming a polygonal net with the higher order venation.

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Remarks: The broad ovate shape of the lamina, the broad base and the coarsely dentate margin coincide exactly with the morphology of *P. populina*, a common polar in the European Neogene. *P. populina* probably belongs to sect. *Populus* (former *Leuce* DUBY). Morphological close analogues are the Eurasian *P. tremula* L. and *P. alba* L. (KNOBLOCH and KVAČEK, 1976). The strongly tri-veined poplar leaves figured in pl. XXXIII, fig. 2, and pl. LI, fig. 8 match well *P. populina* from Vegora and Rhineland (BELZ and MOSBRUGGER, 1994; KVAČEK et al., 2002).

SACHSE (1997) reported from Makrilia a capsule of poplar (as *Populus* sp.) and ZIDIANAKIS et al. (2007) from Vrysses two specimens of *P. populina* under the name *P. tremula* L. foss. In Metochia a tri-veined leaf of this species has been described by MANTZOUKA et al. (2015: figs 5.10–5.11 counterparts). Considering the leaf form variability of the species in Pitsidia, specimen on pl. XVIII, figs 3–4 described by Zidianakis et al. (2010) as *P. crenata* BERGER is transferred to this taxon (compare leaf margin with specimen in pl. XXXIII, fig. 5).

*Populus* sp. – folia
Pl. XXXII, figs 7–8

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

Description: Leaf lacking petiole, lamina broadly ovate, about 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 distances of 13–22 mm and at angles of 30–50°, angle decreasing towards the apex, more or less curved, the first pair arising at the base somewhat more prominent than the others, tertiary veins percurent, opposite to alternate, perpendicular to the secondaries, straight or slightly sinuous, 7–8 per cm.

Remarks: This poplar leaf differs from the above described species especially in the laminar shape, the angles of the secondaries and density of tertiary veins. Unfortunately, the poor preservation of the margin prevents the examination of teeth shape and density. Most available features match the variation of *P. balsamoides* GOEPPTERT, a common European poplar.

Family LYTHRACEAE
Genus *Decodon* J. F. Gmelin

*Decodon gibbosus* (E.M. REID) E.M. REID in NIKITIN – folia
Pl. XLVII, figs 3–5; text-fig. 4.12d

Synonym list

? 1856 *Ficus multinervis* HEER, p. 63, pl. 81, figs 6–10; pl. 82, fig. 1 (Schweizer Molasse, Upper Miocene)

? 1859 *Apocynophyllum helveticum* HEER, p. 91, pl. 154, figs 2–3 (Schweizer Molasse, Upper Miocene)
1920  *Diclidocarya gibbosa* E.M. Reid, p. 82, pl. 4, figs 23, 25; text-fig. 1 left
1929  *Decodon gibbosus* (E.M. Reid) E.M. Reid – Nikitin, p. 37, pl. 589, figs 8–9
1999  *Decodon gibbosus* (E.M. Reid) E.M. Reid – Kvaček and Sakala, pl. 1, figs 1–8; pl. 2, figs 1–12; pl. 3, figs 1–5; pl. 4, figs 1–6 (Bílina, Lower Miocene)

**Material:** Kassanoi, three leaves; two complete and one fragmentary (Nrs 31.6.2.35op; 31.6.2.171a,b; 31.6.2.192).

**Description:** Leaves petiolate, petiole moderately thick, more than 7 mm long; lamina probably coriaceous, shape ovate to elliptic, sometimes slightly asymmetrical, ca. 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; venation brochidodromous, primary vein strong, straight or gently bent across its length, secondary veins much thinner, numerous, more than 15 pairs, originating at angles of 60–80°, densely arranged, interspaces 2–3.5 mm, straight to slightly zik-zak, close to the margin joining into an intramarginal vein, intersecondary veins 1–2 per intercostal area, almost parallel to the secondaries, half of the length of the secondaries, occasionally continuing to the intramarginal vein, tertiary veins more or less oblique, interconnecting secondaries and intersecondarys, forming an 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 and Sakala (1999) reported a leafy twig from the Lower Miocene of the Bílina 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 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. XXXIV, figs 1–12; pl. LVI, fig. 13; text-fig. 4.9

**Synonym list**

1838  *Acer tricuspidatum* BRonn, p. 865, pl. 35, figs 10a–b (Salzhausen, Middle Miocene)
1867  *Acer trilobatum* A. Braun – Unger, pl. 12, figs 28–29 (Kimi, Euboea, Lower Miocene)
1953  *Acer trilobatum* A. Braun – Berger, fig. 12 (Kastron, Lemnos Island, Lower Miocene)
1953  *Acer (Palaeo-Spicata) ponziamum* Gaudin – Berger, figs 24–26 (Allatini, Central Macedonia, Pliocene)
1981  *Acer platyphyllum* A. Braun – VelitzeLoS and Petrescu, pl. 3, fig. 3 (Vegora, W. Macedonia, Messinian)
Material: Pitsidia, nineteen leaves; six complete or almost complete and thirteen fragmentary (Nrs 31.4.2.853ai,bi; 31.4.2.998a,b; 31.4.2.1932a,b; 31.4.2.2437a,b; 31.4.2.3496a,bi; 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, ca. 21–65 mm long and 21–80 mm wide, L/W 0.8–1.7, base rounded to subcordate, lobe apices acute to acuminate, margin simple serrate, teeth size variable, tooth blunt (mostly in the basal part of the lamina) to sharp (mainly apically), proximal side mostly concave, convex or flexuous, rarely straight, distal side straight, retroflexed or occasionally convex, 3–5 teeth per cm or less near the lamina base, sinuses between lobes shallow and wide, more or less angular, medial lobe widely triangular, longer and wider than the lateral ones; venation basal actinodromous with 3 main veins, moderately thick and strong, straight or slightly bent, diverging under angles of 35–45° in the unlobed (tricuspidate) and of 32–65° in three-lobed leaves, secondary veins mostly craspedodromous, moderately thick and strong, in 6–9 pairs, position alternate or subopposite, originating in angles of 30–70°, usually irregularly spaced, curved or rarely straight, intersecondary veins absent or one per intercostal area, usually not well developed, less than 1/2 of the length of the secondary, more or less parallel to secondaries, forked; agrophic veins well developed 5–7 on each side of the lamina, tertiary veins very fine, reticulate or very weekly alternate percurrent, about 5–6 per cm of secondary, arising at angles of about 90°, forming a more or less irregular polygonal network; quaternary and quinternary veins
more or less reticulate forming polygonals the former and mostly pentagons the latter; tooth principal vein terminating in the tooth apex, course of accessory tooth veins convex.

**Remarks:** The material of Pitsidia shows a remarkable variability ranging from broad trilobate forms to narrow simple tricuspidate small leaves. This variation matches well to *A. tricuspidatum* a widespread floristic element during the Upper Oligocene and Neogene over Central Europe (KOVAR-EDER et al. 1994).

Because of its morphological variability *A. tricuspidatum* has been ascribed several formas or subspecies (e.g. PROCHÁZKA and BůŽEK, 1975; HUMMEL, 1983), mostly attached to swampy and riparian habitats. According to most researchers *A. tricuspidatum* does not have an unequivocal modern analogue. Possibly it constitutes a member of the section *Rubra* PAX with many similarities to the extant *A. rubrum* L. and *A. saccharinum* L. (WALThER, 1972).

*Acer integrilobum* WEBER sensu WALThER
Pl. XXXV, figs 1–7; pl. LVI, fig. 5; text-fig. 4.10

**Synonym list**

1852 Acer integrilobum WEBER, p. 196, pl. 22, figs 5a–b
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
1986b Acer integrilobum WEBER – KNOBLOCH and VELITZELos, pl. 14, fig. 5 (Prosilio, W. Macedonia, Messinian)
1994a Acer integrilobum WEBER – KLEINHÖLTER, pl. 31, fig. 2 (Pyrgos and Zacharo basins, Peloponnese, Messinian)
1996 Acer decipiens AL. BRAUN – SACHSE and MOHR, pl. 3, figs ?38, 39; pl. 7, fig. 7 (Makrilia, E. Crete, Tortonian)
1997 Acer ser. Monspessulana POJARK – SACHSE, pl. 8, figs 12, ?13, 14; pl. 19, figs ?2, 3 (Makrilia, E. Crete, Tortonian)
2002 Acer integrilobum WEBER – KVAČEK et al., pl. 25, figs 3–5, 7 (Vegora, W. Macedonia, Messinian)
2010 Acer pseudomonspessulanum UNGER – ZIDIANAKIS et al., fig. 3k (Pitsidia, central Crete, Tortonian)

**Material:** Pitsidia, nine leaves; six complete and 3 fragmentary (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, sometimes with small, irregular, teeth, central lobe more prominent and longer than lateral ones, lobe apices mostly acute, narrowing continuously, tip rounded, sinuses between the lobes usually rounded and wide; venation basal actinodromous with three moderately strong primary veins, often bent distally, angles between central primary and lateral veins 40–70° (average 57°), secondary veins
a–d with lobed lamina, scale bar 2 cm; 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, scale bar 2 cm; 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
slender, brochidodromous, originating at angles of 45–90° (average 65°) from the primaries, more or less straight, looping with the adjacent ones close to the margin, intersecondary veins frequent in the central lobe, very fine, tertiary veins random reticulate or very weekly alternate percurrent, forming a more or less irregular polygonal net with 4th and 5th order venation.

**Remarks:** This material is morphologically also similar to *A. pseudomonspessulanum*. It differs, however, by the longer and broader central lobe, wide and rounded sinuses and lateral lobes narrowing continuously. *A. integrilobum* constitutes usually an accessory element in mesophytic forests of the European Paleogene/Neogene. In gross morphology it is very close to the modern *A. cappadocicum* ssp. *sinicum* var. *tricaudatum* (Veitch ex Rehder) Rehder though regarding the cuticular structures there are only a few similarities between both (Ströbitzer-Hermann, 2002). Cuticular similarities exist to the extant Chinese *A. campbellii* spp. *wilsonii* (Rehder) Dejong (Ströbitzer-Hermann, 2002).

In Crete, *A. integrilobum* is represented by a significant number of specimens not only in Pitsidia but also in Makrilia and Vrysses (as *Acer* Ser. *Monspessulana* and *Acer pseudomonspessulanum* Ungär respectively) (Sachse, 1997; Zidianakis et al., 2007).

Text-figure 4.10. Palaeoflora of Pitsidia, Crete, *Acer integrilobum* foliage, line drawings, scale bar 2 cm (unless stated otherwise); a. complete leaf, Nr. 31.4.2.6103ai; b. Nr. 31.4.2.5464ai; c. complete small leaf, Nr. 31.4.2.1030b; d–f venation pattern details of the 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 the lobe apex, Nr. 31.4.2.1030b detail, scale bar 0.75 mm.
Acer aegopodifolium (GÖPPERT) BAJKOVSKAYA ex ILJINSKAYA  
Pl. XXXIX, fig. 2

Synonym list
1855  Rhus aegopodifolia GÖPPERT, p. 37, pl. 25, fig. 10 (Sośnica, Upper Miocene)
1965  Acer aegopodifolium (GÖPPERT) BAJKOVSKAYA – SHVAREVA, p. 953, comb. inval. (L’vov, Middle Miocene)
1968  Acer aegopodifolium (GÖPPERT) BAJKOVSKAYA – ILJINSKAYA, p. 67, pl. 9, figs 12–15; pl. 20, figs 5–6 (Rika, Ignatovskoe, Neogene)
1999  Acer aegopodifolium (UNGER) ILJINSKAYA – VELITZELOS and KVAČEK, pl. 2, fig. 8 (Vegora, W. Macedonia, Messinian)
2002  Acer aegopodifolium (GÖPPERT) BAJKOVSKAYA – KVAČEK et al., pl. 25, fig. 2 (Vegora, W. Macedonia, Messinian)

Material: Pitsidia, one complete leaflet (Nr. 31.4.2.5697a ii,b ii).

Description: Lamina texture chartaceous, shape asymmetrically lanceolate, 20 mm long and 6 mm wide, L/W ratio 3.3, base narrow cuneate, apex acute, margin 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 the apex, lateral primary vein very similar to central one, entering the rather big lower marginal tooth; secondary veins on the toothed side craspedodromous to camptodromous, 3–4 in number, originating at angles of 35–50°, curved, on the entire-margined side indistinct, camptodromous, higher order venation reticulate, forming an irregular network.

Remarks: The asymmetric lamina with marginal teeth on one side suggests that the sample at hand represents a lateral leaflet of A. aegopodifolium. References of this species from the Greek Neogene are very rare, as only one specimen from Vegora has been reported (VELITZELOS and KVAČEK, 1999).

Acer sp. 1 – fructus  
Pl. XXXV, figs 9–12; text-fig. 4.11

Material: Pitsidia, six samaras; two complete and four fragmentary (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: Fruits winged, 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 the proximal margin of the wing and the contact line of the nutlet (attachment angle) 50–58°; wing 18–24 mm long and 8–10 mm wide, proximal side of the wing gently concave, distal one distinctly convex, wing apex widely obtuse to rounded, wing broadest in its middle part, gradually narrowing towards the point of attachment and frequently claps less than the 1/3 of the nutlet, veins numerous, distinct, curved, more than twice dichotomised.
Remarks: SACHSE (1997) reported from Makrilia three different winged fruit types of Acer. The Makrilia specimen referred to Acer sp. type 3 (SACHSE, 1997: pl. 17, fig. 3) shows similarities with the herein described fruits, based on the wing shape and size, as well as in the angle of the nutlet attachment.

*Acer* sp. 2 – fructus  
Pl. XXXV, fig. 8; text-fig. 4.11

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

Description: Fruit winged, 16–21 mm long; nutlet elliptic, 6–8 mm long and 3–4 mm wide, contact line of nutlet ca. 3 mm long; attachment angle about 40–45°; wing partly preserved, rather narrow especially close to the nutlet, the preserved part 4 mm wide, proximal side of the wing S-like, distally concave, wing apex missing; wing veins numerous.

Remarks: The samara of *Acer* sp. 2 differs from *Acer* sp. 1 on the wing shape and its attachment on the nutlet. Probably these two types of samaras are correlated with the maple species described above on the basis of leaves.

Text-figure 4.11. Terminology of winged fruits of *Acer* (from WOLFE and TANAI, 1987)

Family RUTACEAE  
*Chaneya* sp. – fructus  
Pl. XLVIII, fig. 13

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

Description: Winged fruit, fragmented, size 10x8 mm, consisting of a globose nutlet ca. 2.5 mm in diameter encircled by a persistent five-lobed calyx. Sepals partly preserved, equal in size, probably elongate, sinuses between sepals acute, deeply incised; sepal venation consisting of probably five subparallel veins, prominent, more or less equal, arising independently from the base, other veins not visible.

Remarks: Wind-dispersed fruits with persistent five-lobed calyx occur in various extant genera such as *Porana, Dinetus* (Convolvulaceae), *Astronium, Gluta* (Anacardiaceae) and *Monotes* (Dipterocarpaceae) as well in the fossil *Chaneya* WANG and MANCHESTER. In the latter the lobes are entire-margined, more or less
equal, elliptical to obovate with rounded apices and with venation consisting mostly of five longitudinal veins in each lobe, originating independently from the base, and the midvein being slightly stronger (WANG and MANCHESTER, 2000). The preserved features of the calyx lobes of the specimen from Kassanoi are very close in morphology to the fruits of this extinct genus.

Family OLEACEAE
Genus Fraxinus L.

Fraxinus sp. – folia
Pl. XLVII, figs 6–10

Synonym list
? 1994a Fraxinus ungeri (GAUDIN) KNOBLOCH and KVAČEK – KLEINHÖLTER, pl. 32, figs 6–7 (Patra, Rion and Corinth basins, Peloponnese, Pliocene)

Material: Kassanoi, three leaflets; one complete and two fragmentary (Nrs 31.6.2.18a,ii; 31.6.2.159a,b; 31.6.2.160).

Description: Leaflets petiolulate, petiolule strong, more than 2mm long; lamina chartaceous, elongate oblong to lanceolate or falcate, 62 to more than 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 simply, coarsely serrate to crenulate, teeth small, blunt, irregularly spaced, 1.5–2.5 per cm, sinuses shallow, rounded; venation semiperaspedodromous, midrib strong, proximally more or less bent, approx. 12 pairs of thin secondary veins, arising at angles of 50–70°, initially straight, close to the margin bent, forked one branch forming weak loops with the supradjacent secondary, the other giving birth to veinlets, reaching the marginal sinuses, intersecondary veins occasionally present, half the length and parallel to the secondaries, tertiary veins reticulate, forming an irregular network with higher order venation.

Remarks: Based on the laminar shape and the secondary venation pattern these remains represent leaflets of the Juglandaceae (e.g. Carya, Pterocarya) or Oleaceae (e.g. Fraxinus). The irregular serration, the reticulate tertiary venation and the veinlets course (entering the marginal sinuses) suggest Fraxinus. In the European Neogene several species of ash foliage have been reported, distinguished mostly on the basis of the leaf epidermal traits. Among them F. angusta HUMMEL from the Pliocene of Poland, F. ettingshausenii KOVAR-EDER from the Upper Miocene of Austria and Fraxinus bilinica (UNGER) KVAČEK and HURNÍK [also as Fraxinus ungeri (GAUDIN) KNOBLOCH and KVAČEK] from Wackersdorf and Bilina. Their systematic relation to modern species largely remains unresolved. Contrary to foliage, the fruits of ash are rather common in the European Tertiary, probably due to their robustness that increased the potential to become fossilised. Although several species have been established based on fruit remains e.g. F. primigenia UNGER, F. macroptera ETTINGSHAUSEN, gross morphology is not sufficient for an assignment to the species level (KOVAR-EDER et al., 2004). Fruits of ash have also been reported from various Greek Neogene localities as
Makrilia, Vegora, Prosilio, Likoudi (Upper Miocene), N. Peloponnese (Pliocene) (KLEINHÖLTER, 1994a; SACHSE, 1997; VELITZELOS D. et al., 2014). Reports of ash leaves are very rare, possibly because they were misinterpreted as Juglandaceae leaflets and because shed ash foliage rapidly decays. The only record derives from the Pliocene basins of Patra, Rio and Corinth in the North Peloponnese (KLEINHÖLTER, 1994a; pl. 32, figs 6–7).

Family CORNACEAE
Genus *Cornus* L.

*Cornus* sp. – folia
Pl. XLVIII, figs 1, 11

**Synonym list**

? 1953 *Cornus cf. orbifera* HEER – BERGER, fig. 27 (Allatini, central Macedonia, Pliocene)

**Material:** Kassanoi, two leaves; one complete and one fragmentary (Nrs 31.6.2.117; 31.6.2.162).

**Description:** Lamina shape ovate, 36–45 mm long and 23–32 mm wide, L/W ratio 1.4–1.6, base rounded, apex acute to acuminate, margin entire; venation eucamptodromous, primary vein moderately thick, straight, secondary veins in 5 pairs, delicate, originating at angles of 30–60° (angles decreasing distally) interspaces 3.5–13 mm (distances increasing distally), tertiary veins percurrent, perpendicular to the primary vein, 20 per cm, fine, straight or almost so, higher order venation hardly visible.

**Remarks:** The overall gross morphology of these specimens suggests affinities to Cornaceae (e.g. *Cornus*) and Rhamnaceae (e.g. *Rhamnus, Berchemia, Rhamnidium*). Specific features such as the laminar L/W ratio and the lack of secondary veins in the upper third of the lamina (apart from one weak pair close to the apex) indicate a cornel affinity.

From the Paleo/Neogene of Greece, records of Cornaceae are rare. A broad ovate leaf with characteristic eucamptodromous venation was recorded from Allatini (close to Thessaloniki) (BERGER, 1953: fig. 27 as *Cornus cf. orbifera* HEER). This author compared this specimen to the modern Eurasian species *C. sanguinea* L. From Makrilia, an entire-margined leaf with eucamptodromous venation and tertiaries perpendicular to secondaries is assigned to Cornaceae (pl. LII, fig. 10) (GIANNELOU and PSILLAKI, 2009).

Family HYDRANGEACEAE
cf. *Hydrangea* sp. – flower
Pl. XXXIX, fig. 7

**Material:** Pitsidia, part of flower (Nr. 31.4.2.4495aop).

**Description:** Calyx tetramerous with two sepals partly preserved, sepal shape probably broad elliptic to obovate, more than 12 mm long and 8 mm wide, apex missing, venation distinct, with approx. five
longitudinal main veins, more or less equally thick, originating independently from the central part of the flower, subparallel, multiply dichotomized, joining each with delicate veinlets.

**Remarks:** Large-sized sepals with such venation pattern are common in *Hydrangea*. In the European Paleogene/Neogene, remains of this genus as conspicuous sterile flowers are well known (e.g. MAI, 1985; Kvaček, 2002).

**Angiospermae incertae sedis**

**Monocotyledonae**

Apart from the below described specimens (*Monocotylophyllum* sp. 1–10), at least sixty eight leaf fragments from Pitsidia and thirty eight from Kassanoi with parallel primary veins are available. They probably are of monocotyledonous affinity. Their identification is, however, biased by the poor preservation and lack of diagnostic features. All the material of monocotyledons probably represents hydrophilic grass-like herbs.

*Monocotylophyllum* sp. 1
Pl. XXXVI, figs 1–11

**Material:** Pitsidia, eighteen specimens; three incomplete leaves (in groups) and fifteen isolated leaf fragments (Nrs 31.4.2.907i; 31.4.2.1182ai,b; 31.4.2.1576ai,b; 31.4.2.1576a1ii; 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; 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 the base, linear in shape, more than 80 mm long and 5–12 mm wide, entire-margined with numerous, often hardly visible, parallel primary veins of similar thickness interspaced at distances of about 0.2 mm, venation of higher order not visible; leaves frequently mechanically damaged forming a group of strings and belts. Occasionally, at the basal part where the leaves are connected, an accumulation of coarse sand occurs (pl. XXXVI, figs 2, 8–9).

**Remarks:** The preservation of organically connected leaves implies that this monocot thrived in or very close to the water system where it was embedded. Coarse sand grains seem to have been trapped at the base of this herbaceous plant.

*Monocotylophyllum* sp. 2
Pl. XXXVI, Figs 12–15; Pl. XXXVII, figs 1–4; Pl. LVII, fig. 6

**Material:** Pitsidia, sixteen leaf fragments (Nrs 31.4.2.1017bop; 31.4.2.1452; 31.4.2.2872op; 31.4.2.3027a1ii; 31.4.2.3198op; 31.4.2.3939; 31.4.2.3940; 31.4.2.4750i; 31.4.2.4774; 31.4.2.4955; 1.4.2.5949i, 31.4.2.5981opi; 31.4.2.6051bii; 31.4.2.6101a1ii,biii; 31.4.2.6261; 31.4.2.5542).

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**Description:** Leaf fragments, tiny, mostly coalified, of parallel-margined leaves, up to 50 mm long and 10 mm wide, margin inconspicuously serrate; venation parallel with about 14 primary veins, similarly thick, at distances of ca. 0.15 mm, dense almost perpendicular interconnecting veins (15–25 per 5 mm); stomata in rows parallel to primary veins, about 20 stomata per mm, epidermal cells elongated, papillose, ca. 60–80μm long.

**Remarks:** These tiny leaf fragments are quite common in Pitsidia but due to their small size are not easily detected. The original size of the leaves is unknown. The epidermis structure of several specimens are well-preserved (pl. XXXVII, figs 1–4).

*Monocotylophyllum* sp. 3  
Pl. XXXVI, fig. 16

**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 distances of ca. 0.5 mm, interconnected by (almost) perpendicular cross veins, 3–5 per 5mm.

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

*Monocotylophyllum* sp. 4  
Pl. XXXVI, fig. 17

**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, venation parallel, one primary vein, moderate in thickness, secondary veins very thin, hardly visible, 10–12 in number running across the lamina parallel to the primary.

**Remarks:** This leaf differs in V-shape, serrate margin and venation pattern.

*Monocotylophyllum* sp. 5  
Pl. XXXVI, figs 18–20

**Material:** Pitsidia, two leaf fragments (Nrs 31.4.2.4697aiii,bi,ii, 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 ca. 14–18, moderately thick, at distances of ca. 0.5–0.8 mm, secondary veins thin, hardly visible, 10–12 between two primary ones, running parallel to the primaries.

**Remarks:** These leaves are broader than the afore described ones. The main veins are distinct with numerous parallel veins between and without oblique or perpendicular veinlets.

*Monocotylophyllum* sp. 6  
Pl. XLVIII, fig. 2

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

**Description:** Leaf shape probably broad linear, more than 47 mm long and 31 mm wide, entire-margined; venation parallelobothryodromous, primary vein single, strong, forming a prominent keel, secondary veins parallel to the midrib, numerous, delicate, interspacing at distances of 0.4–0.6 mm, higher order venation not visible.

**Remarks:** This leaf is characterised by a prominent primary vein and numerous secondaries.

*Monocotylophyllum* sp. 7  
Pl. XLVIII, fig. 3

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

**Description:** Leaf linear, more than 47 mm long and 16 mm wide, entire-margined; venation parallelobothryodromous, primary veins numerous, delicate, almost indistinct, straight, interspaces 0.5–0.6 mm, no veinlets are present.

**Remarks:** This specimen is morphologically close to *Monocotylophyllum* sp. 5. Distinctive are, however, the delicate primary veins.

*Monocotylophyllum* sp. 8  
Pl. XLVIII, fig. 4

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

**Description:** Leaf probably broad linear, more than 96 mm long and 24 wide, margin not preserved; venation parallelobothryodromous, primary veins numerous, more than 15, moderate in thickness, interspacing at distances of 2 mm, veinlets perpendicular to the primary veins, distinct, interspaces ca. 1.5 mm.

**Remarks:** This fragment recalls the *Monocotylophyllum* sp. 3 but the venation is less dense.
Monocotylophyllum sp. 9
Pl. XLIX, fig. 9

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 moderate in thickness, ca. 10–12, interspaces ca. 1 mm, secondary veins thinner, 8 per intercostal area; transverse veinlets not detected.

Remarks: These leaf fragments resemble Monocotylophyllum sp. 5, however, their venation is less dense.

Monocotylophyllum sp. 10
Pl. XLIX, fig. 8

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

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

Remarks: This specimen is characterised by its thickness accounting for the indistinct venation and by its broad shape.

Dicotyledonae

Dicotylophyllum Saporita

Dicotylophyllum sp. 1
Pl. XXXVII, fig. 6

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

Description: Lamina chartaceous, probably obovate, 28 mm long (incomplete) and 24 mm wide, lacking leaf base, apex emarginate, margin entire; venation eucamptodromous to weakly brochidodromous, primary vein stout, straight, secondary veins fine, almost opposite to alternate, arising at angles of 55–80°, interspaces 5–9 mm, curved, but not really parallel to each other, intersecondary veins 1–2 per intercostal area, parallel to the secondaries, well developed, reaching about half the length of the 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 while the shape of the lamina apex is probably a result of damage. A Lauraceae affinity for this specimen is possible.
Dicotylophyllum sp. 2
Pl. XXXVII, fig. 7

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

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

Remarks: This leaf lacks any diagnostic features.

Dicotylophyllum sp. 3
Pl. XXXVII, fig. 9

Material: Pitsidia, one 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, proximal side convex to flexuous, distal side concave to straight; venation craspedodromous to brochidodromous, primary vein moderately thick, almost straight, secondary veins delicate, vaguely visible, originating at angles of 30–65°, curved, inervating the tooth or forming loops close to the margin.

Remarks: It is difficult to assign this dentate leaf or leaflet to a specific plant family.

Dicotylophyllum sp. 4
Pl. XXXVII, fig. 10

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

Description: Probably leaflets, subsessile, lamina chartaceous, ovate to obovate, 26–36 mm long and 12 mm wide, L/W ratio 2.2–3, base rounded, more or less asymmetric, apex bluntly acute, entire-margined; venation brochidodromous, primary vein strong, gently bent, secondary veins moderate, in approx. 8 pairs, at angles of 45–70°, interspaced at distances of 2–4 mm, course straight to curved, forming loops close to the margin, higher order venation not visible.

Remarks: This entire-margined leaves may represent lateral leaflets of compound leaves. We are unable to find the systematic affinity of these leaves although a legume origin seems possible because of the asymmetry and venation pattern.
**Dicotylodonia sp. 5**  
Pl. XXXVII, fig. 11

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

**Description:** Leaf long petiolate, petiole more than 8 mm long, lamina probably chartaceous, oblong, approx. 30 mm long and 8 mm wide (incomplete), base angle acute, shape convex, asymmetric, apex not preserved, margin entire; primary vein strong, slightly curved, secondaries hardly visible, arising at angles of 40–55°, more or less straight.

**Remarks:** The poor preservation of this long-petiolate leaf biases any further attempt for a more accurate assignment.

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**Dicotylodonia sp. 6**  
Pl. XXXVII, fig. 12

**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 angles of 40–60°, straight, forked close to the margin.

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

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**Dicotylodonia sp. 7**  
Pl. XXXVIII, figs 6–9

**Material:** Pitsidia, four leaves complete or almost (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 the branchlets of adjacent secondaries close to the margin, the first 2 or 3 pairs of secondaries are more prominent, reaching close to the apex, tertiary veins hardly visible, reticulate.

**Remarks:** This foliage is well distinguished by several features as the small, mainly obovate lamina, the dense, steeply ascending and forked secondaries which diverge from the midrib at rather narrow angles. The venation pattern reminds of *Hedera multinervis* KOLAKOVSKY. The material from Pitsidia differs by the small leaf size.
Dicotylyphillum sp. 8  
Pl. XXXVIII, 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, 8–10 mm long and 4–6 mm wide, L/W ratio ca. 1.7–2, base rounded, apex acute to obtuse, margin serrate, teeth sharp, densely spaced, 6 per 0.5 cm, proximal side convex, distal side concave, sinus deep, angular; venation craspedodromous, primary vein thick, almost straight, secondary veins hardly visible.

Remarks: The sharp, large teeth of these specimens are very characteristic resembling Rosaceae. The coriaceous texture prevents the examination of the vein course. The systematic affinity of these leaves should remain open.

Dicotylyphillum sp. 9  
Pl. XXXVIII, fig. 20

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 simply, coarsely serrate at the upper 2/3 part of the lamina, teeth small, sharp, sinuses narrow, angular; primary vein moderately thick, almost straight, secondary veins very fine, initially severely bent, close to the margin indistinct.

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

Dicotylyphillum sp. 10  
Pl. XXXVIII, fig. 21

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

Description: Leaf petiolate, petiole more than 2 mm long, lamina obovate, 12 mm long and 7 mm wide, L/W ratio 1.7, base cuneate, apex obtuse, entire-margined, at the upper quarter of the 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 inervating the marginal teeth, tertiaries reticulate forming an irregular network with higher order venation.

Remarks: The lamina shape as well as the serration are rather characteristic. A Rosaceae affinity (e.g. Crataegus and Rosa) is considered possible for this specimen.
**Dicotylophyllum** sp. 11  
Pl. XXXIX, figs 1–6

**Material:** Pitsidia, seven leaves, five complete and two fragmentary (Nrs. 31.4.2.3163ai,b; 31.4.2.4182ai,b; 31.4.2.4651aii,b; 31.4.2.4782a,b; 31.4.2.4971iii; 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 the upper third of the lamina, secondaries delicate, in 5–10 pairs, originating at angles of 35–70°, straight or almost so, forked close to the margin, forming open loops with the adjacent ones, intersecondary veins rare, parallel to secondaries, weak, tertiaries reticulate.

**Remarks:** The lack of diagnostic features prevents a well supported identification for these specimens.

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**Dicotylophyllum** sp. 12  
Pl. XXXVII, fig. 5

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

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

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

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**Dicotylophyllum** sp. 13  
Pl. XVIII, fig. 2

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

**Description:** Lamina slightly coriaceous, shape elliptic, about 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 in angles of 50–70° from the midrib, irregularly spaced, straight or gently curved, forking near the margin, forming loops with the adjacent one, there are loops formed by higher order venation as
well, single weak intersecondary veins occurring, tertiaries very delicate but distinct, reticulate, higher order venation forming a regular polygonal net.

Remarks: The entire margin, the acuminate apex, the brochidodromous pattern of main veins and regular network of higher order venation suggest a Magnoliaceae or Lauraceae origin of the specimen at hand. This leaf resembles superficially *Dicotylodendron* sp. 2 described by Knobloch and Velitezlos (1986) from Elassona. But the specimen from Elassona bears small marginal teeth and a prominent basal pair of secondaries reaching up to the middle of the lamina.

*Dicotylodendron* sp. 14  
Pl. XLIII, figs. 4–5  

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

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

Remarks: This taxon is characterised by large leaves with coriaceous, conspicuously undulating lamina. Its origin remains unknown.

*Dicotylodendron* sp. 15  
Pl. XLVIII, figs 5–8  

Material: Kassanoi, seventeen 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; 31.6.2.16iii; 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, more than 100 mm long and 22–31 mm wide, L/W ratio ca. 4–5, base decurrent, apex acute to acuminate, margin entire; venation semicraspedodromous, primary veins stout, straight to gently bent proximally, secondary veins much thinner, numerous (more than 12 pairs), interspaces 5–8 mm, arising at angles of 35–80°, slight zik-zak in course, dichotomising close to the margin, one branch reaching the margin, the other often forming weak, angular loops with the 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 the adjacent intersecondaries, higher order venation not preserved.

Remarks: These elongate leaves are rather common in the assemblage. Their large size, and especially the rather irregular appearing venation pattern with delicate, secondaries slightly zig-zag in 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. XLVIII, fig. 9

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

**Description:** Lamina fragmentary, approx. 3.5 cm long (more than 5 cm when complete) and ca. 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, more or less bent, forming loops near the margin, loops sending veinlets towards the margin which either inervate 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 an irregular network.

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

*Dicotylophyllum* sp. 17
Pl. XLVII, figs 1–2

**Material:** Kassanoi, five leaves; two complete or almost and three fragmentary (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 moderate in thickness, 5.5–9 long, lamina chartaceous, lanceolate to oblong or narrow elliptic, 34 to ca. 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 the primary vein at angles of 35–50° proximally and 60–70° distally, interspaces 2–6 mm, gently curved reaching the margin, intersecondary veins one or rarely two per intercostal area, half of the length of the secondaries, tertiary veins percurrent, opposite, perpendicular to oblique to the secondaries, mostly curved or S-like, higher order venation not visible.

**Remarks:** No suggestion can be made to ascribe these remains to a specific taxon of dicots.

*Dicotylophyllum* sp. 18
Pl. XLIX, figs 3–4, 10

**Material:** Metochia, three incomplete leaves (Nrs 31.5.2.30a,b; 31.5.2.35a,b; 31.5.2.42,45).
**Description:** Leaves petiolate, petiole strong, more than 8 mm long; lamina coriaceous, narrow elliptic to lanceolate, more than 60 mm long and 15–25 mm wide, L/W ratio ca. 4, base cuneate, apex acute, margin entire; venation brochidodromous, primary vein strong, straight to smoothly bent, secondary veins much thinner, in more than 8 pairs, arising at an angle of 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 with higher order veins a regular network, areolation 3 to 4 sided.

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

*Dicotylophyllum* sp. 19  
Pl. LI, fig. 12

**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 the upper two third of the lamina, teeth prominent, narrow triangular to hook-like with distinct bristles apically; venation possibly craspedodromous, primary vein strong, gently bent, tapering towards the apex, secondary veins much thinner, in ca. 10 pairs, arising at angles of 40–70°, more or less bent, indistinct close to the 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*. The poor preservation of the venation pattern prevents a further robust identification.

**Male inflorescence**  
Fam. et gen. et sp. indet.  
Pl. XXXIX, figs 10, 16

**Material:** Pitsidia, one incomplete male inflorescence.

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

**Remarks:** From the hundreds of catkins available from Pitsidia, this specimen is the only one that does not belong to *Myrica* because of loosely crowed florets on the axis. Its overall appearance is closer to *Quercus*, however, more and better preserved material is required.
**Antholites sp.**  
Pl. XLVIII, fig. 12

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

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

**Remarks:** This specimen probably represents a dicotyledonous plant taxon with pentameric, flowers. In Makrilia, several isolated flowers have been discovered (SACHSE, 1997: pl. 17, figs. 17–20) but none of them resembles the specimen from Kassanoi. Among them two octameric, that have been identified as *Asterocalyx styriacus* ETTINGSHAUSEN (KOVAR-EDER et al., 2004).

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**Fruits**  
Fam. et. gen. et sp. indet.

**Drupe**  
Pl. XXXIX, fig. 8

**Material:** Pitsidia, one complete fruit (Nr. 31.4.2.1727ii).

**Description:** Globose fruit, 3 mm in diameter, attached to a 4 mm long peduncle, endocarp oval in shape with smooth surface.

**Remarks:** Based on its shape, this specimen probably represents a drupe.

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**?Carpolithus sp.**  
Pl. XXXIX, fig. 9

**Material:** Pitsidia, shoot fragment with an endocarp-like structure (Nr. 31.4.2.7019).

**Description:** Long shoot with an oval-shaped structure attached to a node, about 1 cm long and 7 mm wide, smooth.

**Remarks:** Due to its size and form, the structure on the long shoot may represent part of a persistent fruit.

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**?Septum**  
Pl. XXXIX, figs 11, 17

**Material:** Pitsidia, one complete specimen (Nr. 31.4.2.5215opii).

**Description:** Thin, chartaceous structure, spindle-shaped, about 7 mm long and 3.5 mm wide, base and apex acute, framed with seven main veins originating at the base, running subparallelly across the structure, joining again at the apex.
Remarks: This specimen recalls the septum of a silicula-like dry fruit, dividing it into two chambers.

?Fruit
Fam. et gen. et sp. indet.
Pl. LII, fig. 5

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

Description: ?Fruit fragment, ovate in shape, 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 represents 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. XXXIX, figs 12–13

Material: Pitsidia, fourteen 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,bi; 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, cutting perpendicularly the longitudinal axes of the scale, margin entire, a few subparallel linear scars are visible at the base of the scale, other ornamentation or appendages are 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. XXXIX, fig. 14

Material: Pitsidia, six 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, cutting perpendicularly the longitudinal axes of the scale, margin entire, occasionally subparallel linear scars are visible.
**Remarks:** This type of bud scale is very close in morphology to the previous one. It differs in its more elongate shape and acute apex.

**Bud scale type 3**  
*Pl. XXXIX, fig. 15*

**Material:** Pitsidia, five 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 in shape, ca. 11–13 mm long and 3–7 mm wide, L/W ca. 2.5–3, apex acute, entire-margined, with numerous subparallel, equally strong veins running longitudinally.

**Remarks:** 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).

**Shoots – Wood fragments**  
*Fam. et gen. et sp. indet.*  
*Pl. XL, figs 4–9, 17*

**Material:** Pitsidia, three hundred eight seven long shoots and one hundred thirty three wood fragments, as inorganic replicas (for specimen numbers see appendix 9a).

**Description:** Long shoot fragments, 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.

**Remarks:** 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. XL, fig. 17).

**Rhizom**  
*Fam. et gen. et sp. indet.*  
*Pl. LX, figs 10, 18*

**Material:** Pitsidia, one fragmentary rhizome (Nr. 31.4.2.2574ai).

**Description:** Rhizome 32 mm long and 9 mm wide, with short internodes and numerous characteristic stirs arranged around the central point of the basal disc.

**Remarks:** This sample constitutes the only rhizome that has been found in Pitsidia.
Roots
Fam. et gen. et sp. indet.
Pl. XL, figs 11–16

Material: Pitsidia, twenty four 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).

Description: Root remains either developed from one point in clusters, more or less similarly thick (adventitious roots) or with a primary root and the lateral distinctly thinner (tap) roots.

Remarks: Specimens of roots are uncommon in the assemblage, representing both monocots (adventitious roots, pl. XL, figs 11–12, 14) and dicots (tap roots, pl. XL, fig. 13). In Kassanoi a bedding plane comprising in situ preserved roots occur (pl. VI, fig.2).

Text-figure 4.12. Palaeoflora of Kassanoi, Crete, selected floristic elements, leaf margin and venation are partly lined, scale bar 1 cm; a. Berchemia multinervis, Nr. 31.6.2.158ii; b. ?Zelkova zelkovifolia, Nr. 31.6.2.76a; c. Salix cf. angusta, narrow leaf forma, Nr. 31.6.2.37i; d. Decodon gibbosus, Nr. 31.6.2.171a; e. Ulmus cf. plurinervia, Nr. 31.6.2.78a.
Text-figure 4.13. Palaeoflora of Metochia, Gavdos Island, selected floristic elements, scale bar 1 cm; a. *Fagus gussonii*, foliage, Nr. 31.5.2.29ai; b. *Tetraclinis* cf. *salicornioides*, leafy twig, Nr. 31.5.2.9; c. *Quercus mediterranea*, foliage, Nr. 31.5.2.7; cf. *Ziziphus paradisiaca*, foliage, Nr. 31.5.2.57
4.1.2. The palaeofauna of Pitsidia

The palaeofauna of Pitsidia comprises mainly fish remains and sporadically insect body impressions and gastropod shells. Regarding fish, 277 disarticulated fish bones and bone fragments have been collected mostly operculum, praeoperculum and spinal bones (pl. XLII, figs 1–7, 9–10). Judging from their gross morphology and size, the majority of them, belongs to a single fish taxon. Additionally, nine isolated pharyngeal teeth have been documented, ranging from less than 1 mm and up to 3 mm long, mostly with a characteristic protuberance at their upper part (pl. XLII, figs 12–15) as well as a fragment of jaw with several teeth on it (pl. XLII, figs 8, 11). Most of these pharyngeal teeth belong to the fresh-water family Cyprinidae (identification by A. AGATHAGGELOU, per. com.). Fish scales or otoliths haven’t been detected.

Among insect remains is an imprint of a complete insect body approx. 13 mm long and 4 mm wide with a large head capsule and unconstructed junction between the thorax and the abdomen (pl. XLI, fig. 10). Furthermore, a few remains of isolated wings, sole or in pairs occur. The wings are either chitinised, ornamented with spots in lines at the longitudinal dimension (elytra, Coleoptera) (pl. XLI, figs 1–3) or thin, almost triangular with distinct veins (pl. XLI, fig. 11).

The mollusk fauna comprises seventeen shells, entire or fragmentary, small, with diameter approx. 1–3 mm, poorly preserved (pl. XLI, figs 4–8). Most of them represent fresh-water snails of the family Planorbidae (pl. XLI, figs 4–5, 8).

Concerning microfauna, Ostracod valves elliptically-shaped in side view, approx. 0.6–0.8 mm long, approx. 0.3–0.4 mm wide, without ornamentation in the external surface (family Candonidae), are common in the sediments (pl. XLI, figs 9, 12).

4.2. Taphonomical aspects on the Pitsidia assemblage

4.2.1. Enumeration of the assemblage

During the systematic excavation (grid setting) in Pitsidia, 8131 specimens were collected from the layers MFL and FL1–3 (appendix 2). Leaf fragments of dicots less than 1/6 of the original leaf size regularly were not collected and fish bones were collected occasionally (for excavation details see section 3.2). Specimens representing pine needle fragments have been excluded from this enumeration treatment as they often represent parts of the same twig, due to the exceptionally elongated needles of the dominant P. pitsidiensis. Only needle fragments attached to the twig were taken into account.

From the layer MFL, 7930 specimens were collected. The great majority of them (96.4%) represents plant remains. Fish bones (and rarely fish teeth) constitute about 3% while gastropod shells and insect-body remains are very rare (text-fig. 4.14a).
From the sampling blocks Nrs 1–12, totally 285 specimens were collected (excluding pine needle fragments) (appendix 4). Plant remains predominate with more than 95% and fish bones follow with approx. 2.8% (text-fig. 4.14b).

In sampling block Nr 13, where a fossil-destructive method was applied, 58 specimens were detected (excluding pine needle fragments) (appendix 13). About 72.5% of them represent plant remains (text-fig. 4.14d) and 27.5% fish bones. The abundance of plant remains increased to approx. 86% when dicot leaf fragments less than 1/6 of the original leaf size were taken into account (text-fig. 4.14c).

Based on the sampling blocks Nrs 1–12 and 13, the densities of different fossils in the MFL (fossils per 1 m³ of undamaged sediment) are estimated (table 4.1).

Text-figure 4.14. Abundances of different fossils:

- a. collected from layer MFL in Pitsidia during the systematic excavation, dicot leaf fragments <1/6 of the original leaf size were ignored, fish bones were collected occasionally;
- b. collected from the sediment blocks Nrs 1–12 (MFL, square 6B, level I and square 5C, level IV; total volume 50.3 dm³), leaf fragments <1/6 of the original leaf size ignored, fish bones were collected occasionally;
- c. detected in the sediment block Nr. 13 (MFL, square 7C, level II; volume 4.8 dm³) including leaf fragments <1/6 of the original leaf size;
- d. detected in the sediment block Nr. 13, leaf fragments <1/6 of the original leaf size ignored

Concerning plant material from layer MFL (7644 specimens), foliage remains predominate representing 52.1% (text-fig. 4.15). Shoot fragments, leafy twigs, scales/bracts and catkins are quite common, contrary to
fruits/seeds and pollen cones which are less frequent. Roots and ovulate scales are rare. Based on the sampling blocks Nrs 1–12 and 13, the densities of different plant parts/organs in the MFL are estimated (table 4.1).

Text-figure 4.15. Frequencies (%) of the plant organs/parts collected from MFL during systematic excavation

In layer MFL about 5500 plant remains have been identified, classified into more than 70 different morphotaxa (appendix 5). The frequencies of the most common taxa are provided in text-figs 4.16–4.17. Based on the sampling blocks Nrs 1–12 and 13, the densities of the most common taxa in the MFL are estimated (table 4.1, text-fig. 4.18).

Text-figure 4.16. Frequencies (%) of most common taxa (>0.5%) in MFL layer (systematic excavation)
Within layer MFL, the abundances of the most common plant taxa are very close or even constant in the different grid squares and levels (appendix 12).

<table>
<thead>
<tr>
<th>Fossils</th>
<th>MFL, estimated fossil density per m$^3$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type</td>
<td>Block Nr 13</td>
</tr>
<tr>
<td>plant remains</td>
<td>4375</td>
</tr>
<tr>
<td>fish bones</td>
<td>1670</td>
</tr>
<tr>
<td>plant remains (including leaves &lt;1/6)</td>
<td>10420</td>
</tr>
<tr>
<td>leaves</td>
<td>2292</td>
</tr>
<tr>
<td>leafy twigs</td>
<td>208</td>
</tr>
<tr>
<td>catkins</td>
<td>208</td>
</tr>
<tr>
<td>fruits/seeds</td>
<td>---</td>
</tr>
<tr>
<td>scales/bracts</td>
<td>208</td>
</tr>
<tr>
<td>leaves (including &lt;1/6)</td>
<td>8333</td>
</tr>
<tr>
<td>Identified Plant Remains</td>
<td></td>
</tr>
<tr>
<td>Myrica lignitum</td>
<td>1875</td>
</tr>
<tr>
<td>Pinus pitsidensis (twigs)</td>
<td>208</td>
</tr>
<tr>
<td>Myrica cf. goeppertii</td>
<td>624</td>
</tr>
<tr>
<td>Myrica ceriferiformis</td>
<td>---</td>
</tr>
<tr>
<td>deciduous Quercus</td>
<td>208</td>
</tr>
<tr>
<td>Myrica lignitum (including &lt;1/6)</td>
<td>7500</td>
</tr>
</tbody>
</table>

Table 4.1. Pitsidia, estimated densities of the different fossils in the layer MFL (fossils per m$^3$ of undamaged sediment) based on the findings in sediment blocks Nrs 1–12 and 13.
Text-figure 4.18. The most common taxa in MFL and their estimated densities (specimens per m³ of undamaged sediment) on the basis of the findings in the sediment blocks Nrs 1–12, a. leaf remains; b. reproductive remains; c. other vegetative remains.

The fossil findings in the layers FL1 and FL3 were not treated statistically because their number was too small. Layer FL2 is characterized by the uppermost occurrence of a well distinguished bedding plane rich in pine remains including ovulate cone scales (pl. IV, fig. 4). A figure of the findings in this layer (excluding the findings of this bedding plane, as well as all needle fragments) is given in text-fig. 19. The abundances of the identified plant species are very close to those of the MFL (table 1 in appendix 12).

Summarizing the above results:
- The density of plant remains (excluding dicot leaf <1/6 of their original size) in the main fossiliferous layer (MFL) is estimated to approx. 4500–5500 specimens per m³ of the undamaged sediment while the density of disarticulated fish bones to approx. 1500–2000 specimens.
- Among the different plant parts, leaves are the most abundant (approx. 2.300–2.600 leaves per m³, approx. 50% of the plant remains). The presence of other plant parts such as long shoot fragments, leafy twigs, scales/bracts, catkins and fruits/seeds is also considerable.
- Among identified plant remains, *Myrica* leaves (approx. 1850–1900 per m³)/catkins/fruits and *Pinus* twigs (approx. 200–400 per m³)/scales/bracts/seeds/pollen cones prevail in the assemblage. *Quercus*
*pseudocastanea, D. polymorpha, Carya sp. and Q. cf. kubinyii, as well as T. dubium leafy shoots and “Pteris” oeningensis fronds and L. europaea infructescences are abundant or common (>30 specimens in MFL).

- The abundances of the dominant and abundant plant species are relatively constant in the different levels and squares of MFL, as well as in the FL2.

- Leaf fragments of dicots <1/6 of the original leaf size (heavily fragmented) are abundant in MFL, more than 6000 specimens per m³ of undamaged sediment.

Text-figure 4.19. Frequencies of collected fossil in layer FL2 (systematic excavation; the pine needle fragments and the findings in the *Pinus*-rich bedding plane are excluded): a. fossil types; b. plant organs/parts; c–e. most common taxa; c. leaf remains; d. fertile remains; e. other vegetative remains
4.2.2. Grain size, chemical and geochemical analyses

According to the grain size analysis the plant-bearing and adjacent layers consist mainly of sandy silts and silty sands, whereas coarser lithologies such as muddy sandy gravel and gravelly muds are also observed (text-fig 4.20; table 4.2). Nevertheless, the fossiliferous layers MFL and FL1–3 are classified as sandy silts (text-figs 4.20, 4.21b; table 4.2) and thus these are the sediments that facilitated the preservation of plant and animal remains. The organic carbon and calcium oxide analyses indicate that the plant-bearing layers are very poor in organic C, less than 0.32%, and moderate in CaCO\(_3\), approx. 7–26% (table 4.2). Regarding the chemical composition of the MFL, the elements oxygen (O) and carbon (C) predominate in its chemical composition (about 50% and 20% respectively) while Ca, Si and Al follow with quite lower percentages (text-fig. 4.21a). The percentage of Fe is very low, mostly less than 1%. The elemental analysis of MFL indicates the dominance of the argilic mineral illite.

![Text-figure 4.20. Pitsidia, classification ternary plots after FOLK (1957) for the plant-bearing and the adjacent layers](image1)

![Text-figure 4.21. Pitsidia, a. chemical elements analysis of the plant-bearing deposits (five samples within MFL), Energy Dispersive X-ray Spectroscopy technique; b. General view of the MFL clay mineral grains, under the SEM](image2)
### Table 4.2. Pitsidia, grain size composition and geochemical features of the plant-bearing and adjacent layers

<table>
<thead>
<tr>
<th>LAYER</th>
<th>THICKNESS cm</th>
<th>GRAVE %</th>
<th>SAND %</th>
<th>SILT %</th>
<th>CLAY %</th>
<th>TYPE</th>
<th>Org. C %</th>
<th>CaCO₃ %</th>
</tr>
</thead>
<tbody>
<tr>
<td>P1</td>
<td>40+</td>
<td>---</td>
<td>58.98</td>
<td>29.70</td>
<td>11.32</td>
<td>Silty sand</td>
<td>0.17</td>
<td>2.58</td>
</tr>
<tr>
<td>P2</td>
<td>22</td>
<td>68.21</td>
<td>27.85</td>
<td>3.94</td>
<td>---</td>
<td>Muddy sandy gravel</td>
<td>0.19</td>
<td>3.60</td>
</tr>
<tr>
<td>P3</td>
<td>8</td>
<td>1.42</td>
<td>36.67</td>
<td>61.91</td>
<td>---</td>
<td>Slightly gravelly sandy mud</td>
<td>0.14</td>
<td>2.19</td>
</tr>
<tr>
<td>P4</td>
<td>7</td>
<td>---</td>
<td>27.38</td>
<td>50.63</td>
<td>22.00</td>
<td>Sandy silt</td>
<td>0.26</td>
<td>1.26</td>
</tr>
<tr>
<td>P5 (MFL)</td>
<td>350-400</td>
<td>---</td>
<td>34.60</td>
<td>62.43</td>
<td>2.97</td>
<td>Sandy silt</td>
<td>0.19</td>
<td>26.21</td>
</tr>
<tr>
<td>P6</td>
<td>17</td>
<td>---</td>
<td>21.82</td>
<td>69.27</td>
<td>8.91</td>
<td>Sandy silt</td>
<td>0.06</td>
<td>16.96</td>
</tr>
<tr>
<td>P7</td>
<td>12</td>
<td>---</td>
<td>66.90</td>
<td>23.60</td>
<td>9.50</td>
<td>Silty sand</td>
<td>0.03</td>
<td>1.42</td>
</tr>
<tr>
<td>P8 (FL1)</td>
<td>7</td>
<td>---</td>
<td>47.94</td>
<td>41.82</td>
<td>10.25</td>
<td>Sandy silt</td>
<td>0.12</td>
<td>9.35</td>
</tr>
<tr>
<td>P9</td>
<td>6</td>
<td>---</td>
<td>62.00</td>
<td>29.31</td>
<td>8.69</td>
<td>Silty sand</td>
<td>0.20</td>
<td>23.94</td>
</tr>
<tr>
<td>P10</td>
<td>24</td>
<td>---</td>
<td>33.08</td>
<td>43.76</td>
<td>23.17</td>
<td>Sandy mud</td>
<td>0.12</td>
<td>2.68</td>
</tr>
<tr>
<td>P11 (FL2)</td>
<td>17</td>
<td>---</td>
<td>25.05</td>
<td>68.63</td>
<td>6.32</td>
<td>Sandy silt</td>
<td>0.27</td>
<td>16.10</td>
</tr>
<tr>
<td>P12</td>
<td>16</td>
<td>---</td>
<td>26.44</td>
<td>60.52</td>
<td>13.04</td>
<td>Sandy silt</td>
<td>0.22</td>
<td>5.75</td>
</tr>
<tr>
<td>P13 (FL3)</td>
<td>37</td>
<td>---</td>
<td>41.86</td>
<td>50.26</td>
<td>7.88</td>
<td>Sandy silt</td>
<td>0.32</td>
<td>7.57</td>
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<tr>
<td>P14</td>
<td>6</td>
<td>7.91</td>
<td>37.17</td>
<td>54.91</td>
<td>---</td>
<td>Gravelly mud</td>
<td>0.04</td>
<td>3.84</td>
</tr>
<tr>
<td>P15</td>
<td>125</td>
<td>41.93</td>
<td>51.27</td>
<td>6.80</td>
<td>---</td>
<td>Muddy sandy gravel</td>
<td>0.06</td>
<td>2.34</td>
</tr>
</tbody>
</table>

#### 4.2.3. Inorganic encrustations on plant imprints

The inorganic encrustation (replica) that cover several imprints (especially thick material such as coriaceous or needle-like leaves, shoots, fruits, seeds, and inflorescences) in Pitsidia is mostly built by crystalline microspherules 15–30 μm in diameter, composed by pyramidal crystals 1–5 μm in size, rich in O (approx. 35–50%) and Fe (approx. 10%) (text-figs 4.22–4.23). The chemical composition of the crystals indicates the occurrence of the mineral ferrihydrite (5Fe²⁺O₃•9H₂O), a widespread hydrous ferric oxyhydroxide mineral at the surface of the earth (PENN, 2007).

![Text-figure 4.22. Pitsidia, chemical elements analysis of the crystals of the leaf inorganic encrustation (four leaf samples), energy dispersive X-ray spectroscopy technique (C represents the carbon coating of the samples)](image-url)
4.2.4. Post-mortem damages on plant remains

The examined post-mortem damages on Pitsidia fossil material comprise:

a. Pre-burial damages caused after shedding and before final deposition (biostratonomic processes). The collected dicot leaves seem to have undergone mechanical stress as this type of damages is abundant in the assemblage, exceeding 66% of the examined foliage (MFL, systematic excavation) ((pl. IV, fig. 1; pl. LVII, figs 1–5; text-fig. 4.24). In special cases, leaf damages caused in the limited time period after their deposition and before their final burial have been documented (pl. LVII, figs 6–8; the leaves are separated into 2 or more different parts, distributed in proximity).

b. Post-burial. In Pitsidia, the majority of post-burial damages were caused either due to natural sediment fracturing (diagenetic processes) (pl. XXVI, fig. 8; pl. LVII, figs 9–11, 14–15) or by the collectors during the excavation process and block splitting. In the examined dicot leaves approx. 28% shows damages caused by sediment fracturing and 60% damages caused during the specimen collecting (text-fig. 4.24). Exceptionally, in exposed parts of the fossiliferous deposits post-burial damages related to action of modern plants (roots) and insects (nesting) were also detected (pl. LVII, figs 12–13).
Among the leaves that have been collected from layer MFL, 5.3% were complete (petiole not taken into account), while in approx. 84% the lamina base and in approx. 89% the apex was missing respectively. About 22% of the examined leaves lost their leaf base and 29% their apices respectively due to mechanical stress after shedding and prior to final burial (text-fig. 4.25).

Concerning *Myrica* catkins that were collected from layer MFL during the systematic excavation, approx. 30% were complete, while 27.5% were fragmentary by pre-burial mechanical processes. For the rest specimens, post-burial mechanical damages were identified.

The results on post-mortem damages reveals severe mechanical stress for the Pitsidia plant material, before its burial. Significant are also the mechanical damages caused by diagenetic processes as well as during fossil collection.

Text-figure 4.25. a. Causes of damages in a sample of 3978 leaves collected from the MFL; a. damaged leaf bases, b. damaged leaf apices
4.3. Palaeoenvironment

4.3.1. Plant-arthropod interaction (Palaeo-synecology)

The plant-arthropod interaction referred to pre-mortem (before shedding) damages on plant remains caused by the action of arthropods. In Pitsidia, contrary to Kassanoi and Metochia, the large number of specimens, the favorable preservation and the sampling method which intended to reduce sampling biases, make the material suitable for such investigations. The inorganic encrustations which often occur in Pitsidia maintained well the traces of arthropod activity and made them easily distinguishable. The attempt focuses especially on *Myrica lignitum* and *Pinus pitsidiensis*, the taxa that predominate in the assemblage and their inorganic replicas are frequently preserved.

4.3.1.1. The Pitsidia assemblage

**Damages on *Myrica* remains.** On the leaves of *M. lignitum* eighteen different types of damages have been distinguished (appendix 14, text-fig. 4.26). These damages have been detected in 540 leaves/leaf fragments from the MFL layer (approx. 20.6%). Heavily damaged leaves or leaves showing more than one type of different damage are not common. Damages on *Myrica* male inflorescences and infructescences have not been detected.

A. Foliage damages related to trophic behaviour

**A1. External feeding**

-**Open margin feeding** (pl. LIII, figs 1–5, 7–9, 11, 12, 27–28)
  
  **Description:** Lamina margin excision, variable in shape and size, shallowly or deeply incised, with entire edges, seldom with bite traces.

-**Interveinal margin feeding** (pl. LIII, fig. 6)
  
  **Description:** Lamina excisions with remaining veinal stringers.

-**Extended lamina feeding** (pl. LIII, figs 13–14)
  
  **Description:** Extended excisions expanding often up to the primary vein.

-**Apex feeding** (pl. LIII, figs 15–16)
  
  **Description:** Excision of leaf apex including the primary vein.

-**Closed margin feeding** (pl. LIII, fig. 10)
  
  **Description:** Trenched excision of the lamina that abruptly expands inwardly, deeply incised.

-**Elliptic to circular perforations 2-6 mm long across the long diameter** (pl. LIII, figs 17–21, 27–28)
  
  **Description:** Extensive, elliptic to almost circular or circular perforations, 2–6 mm long across the long diameter, never crossing the midrib, with indistinct reaction tissue.

-**Small circular perforations** (pl. LIII, figs 24–26)
Description: Circular or almost circular perforations, less than 2 mm in diameter, isolated or occasionally found in groups, with a distinct ring of reaction tissue.

-Polylobate perforations (pl. LIII, figs 22–23)

Description: Polylobate perforations never crossing the midrib, reaction tissue indistinct.

Remarks: External foliage feeding is the most abundant damage in the examined fossil material (text-fig. 4.26, appendix 14). When these damages occur in an early stage of leaf growth, they are often followed by lamina distortion (e.g. pl. LIII, fig. 19). All the above-described external feeding damages can be assigned to unspecialized herbivorous arthropods.

A2. Piercing and sucking feeding

Lamina distortion (pl. LIV, figs 1–20)

Description: Leaves with abnormal apex, base or margin, or overall lamina shape without other visible damage that could cause this distortion; deformed margin and base often with characteristic shallow to deep sinuses; deformed apex obtuse, rounded or emarginated; lamina distortion variable, occasionally asymmetrical in shape or resulting in profoundly smaller laminar size, or dwarfing.

Remarks: In contrast to chewing mediated damages, tissue damages caused by piercing and sucking are more or less inconspicuous, lacking the mark of piercing. These damages are mainly expressed by foliage distortion. In the foliage of *M. lignitum* from Pitsidia such deformations are rather frequent exceeding 6% of the specimens derived from layer MFL. Apart from biotic factors, abiotic ones such as mechanical injuries, physical damages, need to be considered for this type of damages. Leaf deformations also co-occur in a few cases with oviposition and margin feeding. Today, similar patterns of deformations are common in various sclerophyllous Mediterranean elements such as *Olea europaea* L. and *Nerium oleander* L. (pl. LIV, figs 21–22).

A3. Mining (pl. LV, fig. 1)

Description: Short serpentine trail with both the entry point and the terminal chamber; the thickness of the trail increases gradually, reaching a width of 1.0 mm ending up in a rounded pupation chamber; in the last third of the course frass remains are visible.

Remarks: In modern habitats, miners are characterized by high specialization to the plant host. The precise trail pattern is often diagnostically valuable to determine the respective insect even to the generic level (LABANDEIRA et al., 2007). Today, the main insect groups performing leaf mining are Diptera, Lepidoptera and Coleoptera.
A4. Galling (pl. LV, figs 2–6)

Description: Isolated galls, circular to polylobate in shape, about 1 mm in diameter, occasionally with core tissue in radiating partitions, leaves with abundant gall structures rare.

Remarks: Gall morphology is usually very specific to the galler (LABANDEIRA et al., 2007). In the examined material, the distortion of these three-dimensional structures, as a result of diagenetic processes, makes the identification of the causing agent difficult.

A5. Other damages

- Removal of surface tissues less than 2 mm in diameter (pl. LV, figs 7–8)

Description: Removal of surface tissues, surrounded by a reaction rim, circular to ellipsoidal in shape, less than 1 mm in diameter, single or in groups.

- Removal of surface tissues more than 2 mm to 4 mm in diameter (pl. LV, fig. 9)

Description: Removal of surface tissues with reaction rim, circular to ellipsoidal in shape, 2–4 mm in diameter, single or in groups.

- Polylobate removed surface tissues (pl. LV, fig. 9)

Description: Removal of surface tissues, polylobate, surrounded by a reaction rim, sole or in groups.

Remarks: These types of marks possibly may be attributed to surface feeding damages.

B. Foliage damages related to reproduction behaviour

- Leaf oviposition (pl. LV, figs 11–12)

Description: Arthropod exophytic oviposition on the foliage surface; eggs preserved as pseudomorphs, oblong in shape, about 0.5 mm long, clustered in groups of 10–20, arranged in an arcuate row along the leaf margin their long axes orientated parallel to sub-parallel.

Remarks: This oviposition is always accompanied by notable leaf deformation.

C. Foliage damages of unknown origin

- Depressed spots (pl. LV, figs 14–16)

Description: Small, circular structures, usually less than 1 mm in diameter, single or in groups, surface roughened, with central depression.

Remarks: The origin of this type of damage remains unknown.

- Spots surrounded by callus (pl. LV, fig. 17)

Description: Spots in groups, less than 1 mm in diameter, surrounded by distinct callus, unpatterned.

Remarks: This type of damage could be of fungal or bacterial origin.

- Curled lamina (pl. LV, fig. 13)
**Description:** Leaf forms smooth curves in and out of the plane of the lamina.

**Remarks:** These damages could have been caused by numerous factors, both biotic and abiotic.

**Leaf damages on** *P. pitsidiensis* (pl. LVI, figs 15–16). Among the hundreds of examined three-needled fascicles of *P. pitsidiensis*, only two damaged specimens were detected: a peculiar needle distortion and a tiny, hole in a needle, less than 1 mm in diameter.

Text-figure 4.26. Frequencies (%) of different types of damages on *M. lignitum* foliage in the MFL; totally 618 damages on 540 leaves/leaf fragments of the 2617 leaves/leaf fragments of this species in the MFL (several leaves have more than one type of damages)

**Leaf damages on other taxa.** Arthropod damages on the foliage of other taxa apart from *M. lignitum* and *P. pitsidiensis*, is biased by low preservation quality (especially in chartaceous leaves) and low abundances. Non-specialised damages such as margin and hole feeding are occasionally present on the leaves of other taxa (pl. LVI, figs 2–8, 11). Specialised damages such as galling structures occur mainly in *Liquidamon europaea*, in the deciduous oaks *Q. pseudocastanea* and *Q. cf. kubinyii*, as well as in *Carya* sp. (pl. LVI, figs 7, 12–14). Leaflets of *Carya* sp. often show a rather typical apex deformation caused probably by piercing and sucking feeding (pl. LVI, figs 9–10). In general, the detected feeding damages are few and in low abundances. Heavily folivorized specimens are very rare.

On wood (preserved as inorganic replica), the only observed damage is tiny borings possibly representing feeding tunnels of xylophagous or sapro-xylophagous insects (pl. LVI, fig. 1).
4.3.1.2. The Kassanoi and Metochia assemblages

Arthropod damages on Kassanoi and Metochia plant remains is biased by poor quality of preservation and limited number of specimens. Damages such as margin and hole feeding were occasionally observed (e.g. pl. XLV, fig. 11; pl. XLVII, fig. 4; pl. XLIX, fig. 14; pl. LI, fig. 11). In the Myrica lignitum material from Kassanoi a severe lamina distortion (pl. XLIV, fig. 18) and an isolated leaf gall (pl. XLVI, figs 5, 8) were detected which are almost identical in morphology to the deformed leaves and galls that have been described in Pitsidia (pl. LIV, fig. 18; pl. LV, figs 2–6).

4.3.2. Vegetation reconstruction

In table 4.3 are presented the results of the integrated plant record (IPR) vegetation analysis that has been applied for the classification of the studied assemblages in terms of zonal vegetation type.

<table>
<thead>
<tr>
<th>Locality</th>
<th>% of BLD</th>
<th>% of BLE</th>
<th>% of SCL + LEG</th>
<th>ZON PALM</th>
<th>% of DRY HERB</th>
<th>% of MESO HERB</th>
<th>% of zonal herbs of zonal taxa</th>
<th>Number of zonal taxa</th>
<th>Number of zonal woody angiosperms</th>
<th>Total Number of taxa</th>
<th>Problematic taxa</th>
<th>Vegetation type sensu Teodoridis et al. (2011)</th>
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</thead>
<tbody>
<tr>
<td>Pitsidia</td>
<td>48.61</td>
<td>25.00</td>
<td>26.39</td>
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<td>0</td>
<td>2.44</td>
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<td>41</td>
<td>36</td>
<td>52</td>
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</tr>
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<td>Kassanoi</td>
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<td>2.63</td>
<td>19</td>
<td>17.5</td>
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<td>ShSF</td>
</tr>
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<td>33</td>
<td>30</td>
<td>38</td>
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Table 4.3. Results and assigning zonal vegetation types derived by IPR vegetation analysis for the studied fossil assemblages (sensu Kovar-Eder et al., 2008; Teodoridis et al., 2011), for Metochia the floristic elements reported by Mantzouka et al. (2015) also taken into account

According to the thresholds of the key components for defining vegetation types, the plant assemblages of Pitsidia and Kassanoi belong to the zonal subtropical, subhumid sclerophyllous or microphyllous forest (ShSF). Based on the preliminary taxa list of Pitsidia published by Zidianakis et al. (2010), Mantzouka et al. (2015) arrived at the same result.

Regarding the Metochia assemblage, Mantzouka et al. (2015) concluded for transitional vegetation between broad-leaved deciduous and mixed mesophytic forests. Including the further taxa, described in our study (6 zonal wood angiosperms), the percentage of broad-leaved deciduous taxa decreases to less than 75% as none of them seems to be broad-leaved deciduous. Thus, the vegetation of Metochia represents more likely mixed mesophytic forests.

4.3.3. Climate proxies

The coexistence approach (CA) was applied for Pitsidia and Metochia palaeofloras. Due to the primarily fluviatile character and low diversity, the Kassanoi flora is inappropriate for climatic analyses. The estimated
values for seven different climatic parameters are presented in table 4.4. For comparison, the results of this method applied by MANTZOUKA et al. (2015) as well as the climatic conditions in Messara plain today (meteorological station of Tympaki) are also given.

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<th>CMMT min</th>
<th>CMMT max</th>
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<th>WMMT max</th>
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<tr>
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<td>18.5</td>
<td>2.5</td>
<td>7.7</td>
<td>23.3</td>
<td>26.4</td>
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<td>9.4</td>
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<tr>
<td>Pitsidia</td>
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<td>19.7</td>
<td>2.5</td>
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Table 4.4. Palaeoclimatic estimates using the coexistence approach; *Tympaki meteorological station, Hellenic National Meteorological Inst., http://www.hnms.gr/emy/el/climatology/climatology_city?perifereia=Crete&poli=Tympaki); MAT: mean annual temperature, CMMT: cold season mean month temperature, WMMT: warm season mean month 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
5. DISCUSSION
5.1. Palaeofloristic analysis

The palaeoflora of Pitsidia comprises an alga, two ferns, at least five conifers and more than forty five taxa of angiosperms, documented mostly by foliage and leafy shoots and secondarily by inflorescences, fruits/seeds, pollen cones and scale remains (appendix 5, text-fig. 4.15). Among them, arboreal elements prevail, while herbs are much less frequent (five morpho-species of monocots). Floristically the assemblage is characterized by the predominance of Arctotertiary elements, whereas thermophilic ones are less common (appendices 5, 15). Pinaceae, Lauraceae, Fabaceae, Ulmaceae, Fagaceae, Salicaceae and Sapindaceae are most diversified.

Two fossil-species clearly predominate, *Myrica lignitum* and *Pinus pitsidiensis*, represented by mass-occurrences of foliage as well as fertile organs (text-figs 4.16–4.18). The leaves of deciduous oaks (*Quercus pseudocastanea* and *Q. cf. kubinyii*), leafy shoots of *Taxodium dubium*, foliage of *Daphogene polymorpha* and *Carya* sp., frond fragments of “*Pteris* oeningensis” and fruiting heads/foliage of *Liquidambar europaea* are also fairly common. Elements such as *Podocarpium podocarpum* (leaflets and pods), *Acer tricuspidatum*, *Mimosites* sp., *Populus populina* and five-needled *Pinus* are well represented. Among accessory elements, documented by just a few specimens, are *Tetraclinis* cf. *salicornoides*, two-needled *Pinus*, *Ulmus* cf. *plurinervia*, *Fagus gussonii*, *Quercus mediterranea*, *Pterocarya* sp., *Populus* sp., *Salix* sp., *Acer integrilobum*, *Acer aegopodifolium*, probably *Zelkova zelkovifolia*, *Rosa* sp., *Hydrangea* sp. and *Lindera ovata*. Deciduous woody elements represent about the 2/3 of the identified dicots. Besides, there are more than fifteen dicot taxa of problematic affinity, including several very small leaves, a few fruits and an inflorescence.

The palaeoflora of Kassanoi includes twenty four taxa of angiosperms based almost exclusively on foliage remains (appendix 6). Polypodiophyta and conifers are far less abundant and diverse than in Pitsidia, represented by a fern species and *Tetraclinis* cf. *salicornoides*. Shrub and tree elements prevail, while herbs (monocots and *Decodon gibbosus*) are less frequent. Fabaceae and Salicaceae are most diversified. *Daphgone polymorpha*, *Podocarpium podocarpum*, *Myrica lignitum* and *Salix cf. angusta* are the dominant species. Further elements are *Ulmus* cf. *plurinervia*, *Berchemia multinervis*, *Fraxinus* sp., *Buxus pliocenica*, a deciduous oak, *Populus populina*, *Chaneya* sp. and *Cornus* sp. Deciduous woody elements represent about the 3/5 of the dicot spectrum. Foliage and flower remains of unknown affinity are identified to 5 different dicot taxa.

The palaeoflora of Metochia on Gavdos Island was firstly described by Mantzouka et al. (2015), reporting thirty taxa. In our study, sixteen plant taxa have been identified from the same outcrop, enriching the already known floristic composition by eight elements (appendices 7, 16).
The palaeoflora (including taxa reported by MANTZOUKA et al., 2015) comprises four conifers and at least thirty four angiosperms based on foliage, leafy shoot and fruit remains. The most diverse families are Lauraceae with four different leaf types (including Daphnogene) and Fabaceae with at least five taxa (Podocarpium is absent) including a pod fragment. Fagus gussonii and Laurophyllum sp. dominate. Daphnogene polymorpha, ?Lindera ovata, Salix cf. angusta and Myrica lignitum are quite common. Among accessory elements, are Tetraclinis salicornioides, Taxodium dubium, two- and five-needled Pinus, Paliurus tilifolius, Betula sp., Engelhardia orsbergensis, Quercus mediterranea, Ailanthus pythii, Sapindus graecus, Acer angustilobum and probably Sassafras sp., Carpinus sp., Populus populina, Ulmus plurinervia and cf. Ziziphus paradisiaca. Monocots are represented by a leaf fragment of the palm Sabalites and by numerous fragments of linear leaves. The latter are the only herbs documented in this flora. Besides, eight leaf morphotaxa of unknown affinity have been recognized.

5.1.1. Myrica and Pinus - the dominant taxa in Pitsidia

5.1.1.1. Myrica fossil material

Whole plant reconstruction. In Pitsidia, Myrica and Pinus are represented by mass-occurrences of different organs, always found close to each other (ZIDIANAKIS et al., 2014). Myrica remains – leaves, infructescences/fruits, male catkins – make up 38 % of all collected fossil specimens and more than 60% of the identified plant remains in MFL (text-fig. 4.16). In several specimens fruits are still attached to the infructescence axis and fragile structures such as stamens occur on the inflorescence remains. Specimen Nr. 31.4.2.4607b suggests that disintegration occurred directly after deposition but prior to sediment coverage (pl. XXVI, fig. 7). All these facts imply close vicinity to the depositional area. Therefore, the detached organs – M. lignitum, M. ceriferiformis and M. cf. goeppertii – obviously derive from one plant species representing a fossil-taxon which lived near the depositional area (ZIDIANAKIS et al., 2015), as it has also been suggested for Pinus (chapter 5.1.1.2 in this study; ZIDIANAKIS et al., 2016). This interpretation is also supported by the occasional co-occurrence of M. lignitum foliage and M. ceriferiformis fruits in other Neogene deposits of Europe, a condition that enabled some authors to draw the same conclusion for leaves and fruits, e.g. KVAČEK et al. (2004).

Fissile sediments in Sośnica yielded a male catkin of M. goeppertii with pollen, a single leaf of M. lignitum and one fruit impression of M. ceriferiformis (GÖPPERT, 1855; ŁANCUCKA-ŚRODONIOWA et al., 1981; KOHLMAN-ADAMSKA et al., 2004). From sieved fruit and seed material, M. ceriferiformis and M. cf. minima NEGRU fruits have been determined (ŁANCUCKA-ŚRODONIOWA et al., 1981). The differences to Pitsidia are evident: no mass-occurrence of Myrica and probably more allochthonous than paraautochthonous deposition of the plant material.
Parschlug is famous for the mass-occurrence of *M. lignitum* leaves associated mainly with vegetative and fertile organs of *Glyptostrobus europaeus* (BRONGNIART) UNGER and *Liquidambar europaeus* A. BRAUN. Fertile parts of *Myrica* are, however, hardly preserved there (KOVAR-EDER et al., 2004).

**Systematic position – comparison to extant *Myrica* species** (appendix 11). On the subgeneric level, the examined material matches well the subgenus *Morella* (LOUREIRO). The subgenus *Gale* (SPACH) differs by the chartaceous leaf texture and nuts that have a smooth surface and are subtended by 2 bracteoles. Regarding the sections (sensu CHEVALIER 1901) of subgen. *Morella*, section *Morella* (LOUREIRO) bears branched male inflorescences, the stamen filaments are free and the drupes are often larger than our fossil ones (approx. 6–8 mm in diameter). In section *Faya* (WEBB) the male florets bear at least 8 stamens and are characterised by fruits of about 4–6 mm in diameter. Our fossil taxon matches well section *Cerophora* (RAFINESQUE), [series *Cerothamnus* (TIDESTROM) sensu WILBUR, 1994], in which the male catkins are simple, the florets bear less than 7 stamens and the filaments are fused into a staminal column. The fruits are ca. 1–5 mm in diameter and bear protuberances. All these features are found in the herein-described fossil material. Among the above referred characters used to distinguish the different sections of subgen. *Morella*, the fusion of the filaments into a staminal column is considered the most constant one and thus the most reliable criterion (HERBERT, 2005).

Consequently, *Myrica* from Pitsidia is assigned to sect. *Cerophora* of the subgen. *Morella*. Traditionally, sect. *Cerophora* is subdivided in subsect. *Americanae* and subsect. *Africanae*. These represent geographically based groups and hitherto no morphological feature has been found to distinguish them.

Already UNGER (1852) observed a great similarity of *Myrica lignitum* foliage to the extant *M. pensylvanica* MIRBEL. ETTINGSHAUSEN and STANDFEST (1888) considered *M. lignitum* as the ancestor of several modern species of the respective genus, pointing out that none of them coincides morphologically exactly with this ancient species. Since then, several authors have shared the opinion of ETTINGSHAUSEN and STANDFEST (1888), while most of them have noticed the profound similarities of *M. lignitum* to the extant *M. cerifera* L., *M. pensylvanica* and *M. heterophylla* RAFINESQUE, all occurring in the Atlantic North and Central America (FERGUSON, 1971; KNOBLOCH and KVAČEK, 1976; KOVAR, 1982; DUNCAN and DUNCAN, 1987). Contrary to *M. pensylvanica* and *M. heterophylla*, leaves of *M. cerifera* are always leathery, sometimes linear in shape and the density of glands is high, especially on the abaxial leaf surface (BORNSTEIN, 1997). In these aspects the material from Pitsidia supports the view that *M. lignitum* leaves could be best compared to *M. cerifera*.

Concerning *M. ceriferiformis*, KOWNAS (1955) considered it to be closer to *M. cerifera*, whereas MAI (1999b) related it to *M. cerifera* and *M. pensylvanica*.

Comparing the infructescence axes of *M. ceriferiformis* from Pitsidia to *M. cerifera* and *M. pensylvanica* reveals that those of *M. ceriferiformis* are longer bearing a higher number of drupes. In fruit size, the material
from Pitsidia is closer to *M. cerifera* than to *M. pensylvanica*, whose fruits are bigger (about 3.5–5.5 mm in diameter) (BORNSTEIN, 1997).

For *M. goeppertii*, no modern analogue has been referred to so far (KOHLMAN-ADAMSKA et al., 2004). In gross morphology, the catkins of *M. cf. goeppertii* from Pitsidia resemble those of *M. cerifera, M. pensylvanica* and *M. heterophylla*, i.e., elongated, unbranched with numerous florets. In all these extant species, the male catkins are 3–18 mm long, the bract of the floret is marginally more or less ciliate and shorter than the branched staminal column (BORNSTEIN, 1997). In contrast, in *M. cf. goeppertii* male catkins are somewhat longer and the bract of the floret is longer than the branched staminal column. The bract lacks marginal cilia, although it remains open whether the absence of cilia is an artefact caused by preservation.

**Nomenclatural aspects.** According to the rules of nomenclature (MCNEILL et al., 2012) it would be appropriate to name *Myrica lignitum* leaves, *M. ceriferiformis* fruits/infructescences, and *M. cf. goeppertii* male catkins from Pitsidia as a fossil-taxon (whole-plant) with a single name (*Myrica lignitum*). Being also in accordance with the nomenclatural rules (MCNEILL et al. 2012: art. 11.1), we prefer the use of different names for different organs for the following reasons: (1) The wide morphological variability, occurrence in different palaeoenvironments and the long stratigraphic range of *Myrica lignitum* foliage lead us to suspect that it includes more than a single natural species. (2) Fertile remains of *Myrica* from Parschlug are extremely rare – a sole fruit of *Myrica* affinity was referred (ETTINGSHAUSEN and STANDFEST, 1888; KOVAR-EDER et al., 2004). It lacks relevant features that could be compared to the material at hand. (3) The fusion of the filaments into a staminal column as recognized in the remains from Pitsidia is open for *M. goeppertii* from Sośnica.

**5.1.1.2. Pinus fossil material**

i. *Pinus pitsidiensis*  

**Whole plant reconstruction.** In the Pitsidia assemblage *Pinus* remains account for approximately 26% of the identified plant remains in MFL (text-fig. 4.16) (ZIDIANAKIS et al., 2016). The dwarf shoots support the occurrence of at least three different pine species, among which *P. pitsidiensis* predominates with hundreds of fascicles. In a particular horizon at the top of the fossiliferous sequence (pl. IV, fig. 4) *P. pitsidiensis* fascicles are fairly abundant and densely spaced, reminiscent of the respective litter that accumulated beneath a *Pinus* stand. In contrast, the other two species of foliage are quite rare, especially the two-needled one. The preservation of *P. pitsidiensis* needles is excellent and a rather low proportion is damaged contrary to the two- and five-needled fascicles.

The needled fascicles and the long shoots of *P. pitsidiensis* have been found physically connected (specimen Nr. 31.4.2.2013a; pl. XI, fig. 10) so their association is unambiguous. Morphometrically, the pulvinus of the fascicle bracts (*Pinus* sp. – fascicle bracts) match the scars of the deciduous fascicle bracts on the long shoots.
of *P. pitsidiensis* and consistently co-occur with them in the assemblage. Hence, we suggest that *Pinus* sp. – fascicle bracts and *P. pitsidiensis* probably constitute parts of the same ancient pine. Pollen cones (including isolated pollen cone scales) of *Pinus* sp. 1, as well as seeds of *Pinus* sp. – underdeveloped seeds, also co-occur with *P. pitsidiensis* fascicles throughout the fossiliferous sediments. All these organs are remarkably abundant, in close proximity to each other raising the possibility that they derived from the same pine species. Additionally, the morphology of the seed imprints on the scales of *Pinus* sp. 1 – ovulate cone scales (especially in specimen Nr. 31.4.2.7018; pl. XIII, fig. 4) are very similar to *Pinus* sp. 1 – fully developed seeds and *Pinus* sp. – underdeveloped seeds suggesting that they are the seeds of *P. pitsidiensis* as well. We therefore propose that these remains constitute reproductive parts of *P. pitsidiensis*.

Furthermore, none of the vegetative and fertile remains included in this putative reconstruction show characters in conflict with the assignment to subgen. *Pinus*.

**Systematic position – comparison to extant pine species** (appendix 10). For the assignment of *Pinus pitsidiensis* to a subgenus the number of needles per fascicle, the persistence of the basal sheath and the distribution of stoma rows on the needle surface is evaluated (appendix 10: table 2).

Number of needles per fascicle: This is a variable feature among the extant species of *Pinus* ranging from one to eight. Most species of subgen. *Pinus* tend to bear needles in fascicles of two or three while in subgen. *Strobus* fascicles of five needles dominate (SHAW, 1914; LITTLE and CRITCHFIELD, 1969; FARJON and STYLES, 1997; PRICE, 1989; GERNANDT et al., 2005). Exceptions are subsect. *Ponderosae* within subgen. *Pinus* (i.e., *P. montezumae* has fascicles of 3 to 5 and *P. durangensis* has 6, rarely 5 or 7) and subsect. *Nelsoniae, Krempfianae, Cembroides and Gerardianae* within subgen. *Strobus* (e.g., *P. nelsonii* with three, *P. krempfii* with two and *P. monophylla* with one and rarely two needles).

Persistence of the basal sheath: All the extant members of subgen. *Pinus* have a persistent basal sheath except for *P. leiophylla* and *P. lumholtzii* (subsect. *Australes*) (SHAW, 1914; LITTLE and CRITCHFIELD, 1969; FARJON and STYLES, 1997; GERNANDT et al., 2005). In subgen. *Strobus* the sheath is deciduous, nevertheless this character has been lost in *P. nelsonii*.

Stoma distribution: In subgen. *Pinus* the needles are always amphistomatic whereas in subgen. *Strobus* stomata occur either ventrally or both dorsally and ventrally (LITTLE and CRITCHFIELD, 1969).

The dwarf shoots of *P. pitsidiensis* are characterised by an almost constant number of three needles per fascicle, persistent basal sheath and amphistomatic needles. The combination of these three criteria definitely suggests for this species a subgen. *Pinus* (*Diploxylon*) affinity. In this subgenus two sections are widely recognised, sect. *Trifoliae* with about 50 species in America and sect. *Pinus* with about 26, mainly Eurasian and Mediterranean species (including the American *P. resinosa* and *P. tropicalis*) (appendix 10: table 1).
In order to assign *P. pitsidiensis* to section level we evaluated the distribution of resin ducts in the needle parenchyma (appendix 10: table 2).

Resin duct distribution: Subgen. *Pinus*, sect. *Trifoliae* is characterised by internal or medial resin ducts, except for *P. leiophylla*, which has medial to external and *P. oocarpa* and *P. pringlei* which have internal to septal ones (Farjon and Styles, 1997). In sect. *Pinus* external or medial resin ducts and rarely septal ones (i.e., *P. tropicalis*) occur. Hence, with the exception of *P. leiophylla*, no pine species of sect. *Trifoliae* possesses external resin ducts contrary to the members of sect. *Pinus* (Shaw, 1914; Price et al., 1998; Gernandt et al. 2005). On this basis, *P. pitsidiensis* is assigned to sect. *Pinus*. Note that the presence of external resin ducts in the needles of modern pines constitutes the most reliable morphological criterion in both vegetative and fertile organs to distinguish the two sections of subgen. *Pinus*.

Within sect. *Pinus* three extant species are comparable with *P. pitsidiensis* based on the consistent number of three needles per fascicle: *P. canariensis* and *P. roxburghii* in subsect. *Pinaster* and *P. kesiya* in subsect. *Pinus* while *P. yunnanensis* has two or three needles (Shaw, 1914; Fu et al., 1999; Ding et al., 2013). *Pinus canariensis* and *P. roxburghii* (together constitute the former sect. *Sula Mayr*) differ from *P. pitsidiensis* in having more slender needles with serrulate margins and in the smaller number of resin ducts and stomatal rows (Shaw, 1914; Frankis, 2009; Earle, 2013; Tiwari et al., 2013). The needles of *P. kesiya* are slightly shorter (about 12–25 cm), more slender, with a serrulate margin, occasionally appearing in fascicles of two (Shaw, 1914, as *P. insularis*; Fu et al., 1999; Frankis, 2009; Ding et al., 2013; Earle, 2013). Based on these differences, no modern pine species matches exactly *P. pitsidiensis*.

**Comparison with the European pine record.** In the European Paleogene and Neogene, pine needles in fascicles of three are quite common and numerous species names have been proposed. We traced in the literature twenty-five pine species, many of them established during the 19th century (appendix 10: table 3). In most cases the type specimens are preserved as impressions providing few diagnostic features and rarely showing any anatomical details. Several of these species have a wide stratigraphic as well as geographic range and many authors regard them as cumulative species representing more than one ancient natural species while other species are handled as synonyms of earlier described ones, e.g., Berger (1951), Mai (1999a), Teodoridis and Sakala (2008). Nonetheless, we compare all of them with *Pinus pitsidiensis* (appendix 10: table 3).

The species *Pinus dolichophylla*, *P. gracilis*, *P. resurgens*, *Pinites rigidus*, *P. cf. rigios*, *P. schiefferdeckeri*, *P. sodalis*, *P. subrigida* and *P. trichophylla*, contrary to *P. pitsidiensis*, have needles with serrulate/scabrous margin. In *P. goethana*, *P. orbicularis*, *P. pretaedaeformis* and *P. vetustior* the needles are very short, notably shorter than those of *P. pitsidiensis*. In *P. divaricata*, *P. diversifolia*, *P. pseudotaeda*, *P. saturnii*, and *P. taedaeformis* the needles are less than 1 mm wide. *Pinus holothana*, *P. kunowii* and *P. rigios* have very broad needles (up to 2 mm or wider). The fascicles of *P. debilis* are in clusters of three and four needles but
their basal sheath is very short. In *P. hellenica*, which is considered synonymous to *P. holothana* (SAPORTA, 1868), the basal sheath is very short as well. Only *P. palaeotaeda* and *P. post-taedeiformis* can be considered morphologically closer to *P. pitsidiensis* regarding needle width and size of the basal sheath. Both produce, however, shorter needles and the micromorphological and anatomical details of their needles are not yet known.

Concerning the Cenozoic deposits in Greece, pine remains with three-needled fascicles have been reported from several localities, i.e., *Pinus* cf. *rigios* in Lyra and Fylakton (Evrus Mountains, Thrace, Rupelian-Chattian volcanic complex), *P. cf. saturnii* in Pyrgos and Zacharo basins (West Peloponnese, southern Greece, Messinian), *P. hellenica* and *P. holothana* in Kimi (Euboea, central Greece, Lower Miocene), *P. kolymbiensis* BOYD in Rhodes Island (Dodecanese islands, middle Pleistocene), (UNGER, 1867; SAPORTA, 1867a; KLEINHÖLTER, 1994; BOYD, 2009; VELITZELOS D. et al., 2014). The three-needled fascicle from Vrysses reported in this study is morphologically very close to *P. pitsidiensis*. For the Prassas specimen any systematic assignment is risky because of its poor preservation.

*Pinus kolymbiensis* from Rhodes Island and the three-needled fascicle from Vrysses are undoubtedly closer to *P. pitsidiensis* than the other European fossil taxa in sharing the long, entire-margined needles in fascicles of three and the prominent persistent sheath. Judging from figures 8c and 9a of BOYD (2009), *P. kolymbiensis* seems to differ in needle width, as *P. pitsidiensis* needles are wider. Additionally, *P. pitsidiensis* needles have a lower number of stomatal rows (7–11 adaxially and 7–8 abaxially versus 10–14 and 10 respectively in *P. kolymbiensis*). Unfortunately, there is no evidence of the resin duct distribution of *P. kolymbiensis* needles. About 20% of *P. kolymbiensis* dwarf shoots bear only two needles per fascicle. According to BOYD (2009), they probably lost a needle during pre-burial transportation. KVÁČEK et al. (2014) assumed that the fascicles of *P. kolymbiensis* may be associated with seed cones of *P. strozzii* GAUDIN (former sect. *Sula*) also recovered from the Pleistocene deposits of Rhodes. Nevertheless, the close relation of *P. pitsidiensis* to the fascicle from Vrysses and *P. kolymbiensis* is obvious indicating that long-needled pines with three-needled fascicles occurred in various areas of SE Greece from the Upper Neogene to middle Pleistocene.

Traditionally, the European fossil record of three-needled pines is interpreted to be related to the extant species of sect. *Trifoliae* in America. This is reasonable since the section comprises numerous three-needled pines with a wide variety of needle forms, while sect. *Pinus* includes just a few species with exclusively three-needled fascicles. In most cases, this assignment is based only on a few macro-morphological features of the needles and the basal sheath. The exceptional preservation of *P. pitsidiensis* showing the resin ducts in the needle parenchyma provides unambiguous evidence for its affinity to sect. *Pinus* rather than to sect. *Trifoliae*. Focusing on the cone morphology of European Paleogene and Neogene pines, MAI (1986) came to two significant conclusions, (a) the pine species from the European Paleogene and Neogene are not conspecific with any extant species. More likely they represent different species; (b) systematically they are
closer to the European, Canarian, Himalayan, and East Asian modern species. Our results based on the examination of *P. pitsidiensis* strongly support these conclusions.

**ii. Taxonomic implications for the remaining pine material in Pitsidia.**

Apart from the fascicles of *Pinus pitsidiensis*, the two- and five-needled dwarf shoots, the fascicle bracts and ovulate cone scales from Pitsidia can also be classified to the subgenus level. For the assignment of dwarf shoots the number of needles per fascicle, the persistence of the basal sheath and the resin duct distribution were used. Accordingly, for the fascicle bracts the mode of their attachment to the long shoots was considered a significant taxonomic feature, and for the cone scales the position of the umbo and the presence of a sealing band.

As documented in the systematic section, *Pinus* sp. – two-needled fascicles, *Pinus* sp. – fascicle bracts and *Pinus* sp. 1 – ovulate cone scales have been assigned to the subgen. *Pinus*, while *Pinus* sp. – five-needled fascicles and *Pinus* sp. 2 – ovulate cone scales are assigned to the subgen. *Strobus*. Thus, the co-occurrence of both subgenera *Pinus* and *Strobus* in the assemblage is documented.

Concerning the described pine seeds from Pitsidia, their classification to the subgenus level is more difficult because the position of the seeds in the cone appears to have a bearing on their development and it depends whether they appear typical or atypical (aborted or underdeveloped). In extant species of the subgen. *Pinus* the wing is articulate or rarely adnate (only in *P. canariensis* and *P. roxburghii*), while in subgen. *Strobus* seed wings are rather polymorphic, articulate, adnate, rudimentary or absent. In Pitsidia, both fully and poorly developed seeds bear an adnate wing. Hence, they can be classified either in subgen. *Strobus* or in the former sect. *Sula* of subgen. *Pinus*.

For the pollen cones and bud scales of the assemblage, the lack of diagnostic features does not allow a more accurate classification.

**5.1.2. Palaeoflora comparisons**

*5.1.2.1. The studied floras in the Cretan Upper Miocene context*

Apart from the herein described palaeofloras, two further Neogene macro floras are known from Crete so far. The oldest, deriving from the surroundings of Makrilia village in the eastern part of the island, is dated to the upper Tortonian, approximately 7.7–8.6 Ma (SACHSE, 1997) (appendix 17). The plant assemblage occurs in a few meter thick silty interval, of an alternation of hemipelagic marls and sand turbiditic layers. The other flora is located close to Vrysses village in the western part of the island and is dated to the Messinian (ZIDIANAKIS et al., 2007) (appendix 18; see also section 1.2). The plant-bearing layers comprise marls and marly limestones deposited in a shallow semi-enclosed marine embayment.
The Middle–Late Miocene floras of Crete (Makrilia, Vrysses, Metochia, Pitsidia and Kassanoi) are not uniform (appendix 19). Differences in composition and frequency of taxa may be related mainly to different depositional environments (text-fig. 5.1) as well as to different habitats reflected in the fossil record, though differences in climate, palaeogeography and time succession of the floras cannot be ruled out completely. The Pitsidia and Kassanoi floras differ distinctly from the other Cretan floras due to their pronounced floodplain/backswamp and fluviatile/lacustrine character respectively. Taxonomically, the floras share some elements, as *T. cf. salicornioides*, *D. polymorpha*, *M. lignitum* (except for Vrysses), *Q. mediterranea* (except for Kassanoi) and *P. populina* (except for Makrilia). Pinaceae, Lauraceae, Fagaceae, Fabaceae, Juglandaceae, Salicaceae and Sapindaceae also are better represented both in species diversity and abundances.

*Tetraclinis* cf. *salicornioides* occurs in all assemblages while *T. dubium* is present in Pitsidia, Makrilia and Metochia but absent in Vrysses and Kassanoi. Pines (two-, three- or five-needled species) are present in almost all localities except for Kassanoi. Lauraceae are always represented by *D. polymorpha* and less frequently by other elements assigned to *Laurophyllum*. *Lindera* possibly occurs in Metochia and Pitsidia but *Sassafras* is recorded only from Metochia. *Buxus pliocenica* is a rare element in the Cretan palaeofloras, missing in Pitsidia and Metochia.

*Liquidambar europaea*, both infructescences and foliage, is common in Pitsidia, very rare in Makrilia and lacks at the other sites. Legumes are always present and rather diverse, mainly documented by isolated leaflets and rarely also by pods. *P. podocarpum* is well documented in Pitsidia, and it is further present in Kassanoi and Makrilia. Members of the Rosaceae family are always present, even in low numbers. Rhamnaceae are documented (apart from Pitsidia) mainly by *cf. Z. paradisiaca* and rarely by *Paliurus* (Metochia) and *Berchemia* (Kassanoi). Ulmaceae are well represented by *Ulmus* (mostly as *U. plurinervia*) and *Zelkova*. This family lacks in Vrysses while *Z. zelkovifolia* has unambiguously been identified only in Makrilia. Elm samaras occasionally occur (Pitsidia and Makrilia).

Fagaceae are represented by *Quercus* and *Fagus*. The sclerophyllous *Q. mediterranea* occurs in all assemblages while deciduous oaks are rare, except for Pitsidia where *Q. pseudocastanea* and *Q. cf. kubinyii* are common. In Gavdos and Makrilia the ecological niche of deciduous oaks possibly was occupied by *F. gussonii*. *M. lignitum* is absent so far only from Vrysses, while it is common to abundant elsewhere. Juglandaceae are represented by *E. orsbergensis* (Makrilia and Metochia), *Carya* (Pitsidia and Makrilia) and *Pterocarya* (Pitsidia). Betulaceae are poorly represented in the Cretan palaeofloras. They are documented by a few samaras of *Carpinus* in Makrilia, *Alnus* and *Betula* foliage in Makrilia and Metochia, respectively, a species in Pitsidia (as Betulaceae gen. et sp. indet.), lacking entirely in Kassanoi and Vrysses. All the palaeofloras share members of the Salicaceae. Most common are *P. populina* and various species of *Salix*. Especially in Kassanoi *S. cf. angusta* is rather abundant. Maples are present in most assemblages (*A. tricuspidatum*, *A. angustilobum*, *A. ?integerrimum*, *A. aegopodifolium* and *A. integrilobum*) except for Kassanoi. Other dicot genera such as *Cornus* (Kassanoi), *Fraxinus* (Kassanoi and Makrilia), *Decodon*
(Kassanoi), *Ailanthus* (Metochia), *“Parrotia”* (Vrysses), *Tilia* (Makrilia) and *Sapindus* (Metochia) occur sporadically.

Text-figure 5.1. The Middle–Late Miocene floras of Crete; estimated ages, depositional environments and dominant types of vegetation

**Comparison with the micro-flora of Kastellios Hill**

In Messara Basin, palynological analyses have been carried out in Kastellios Hill and Panagia Almiri (Benda, 1974; van der Weerd, 1983 and Sen et al., 1986). The microflora of Kastellios Hill is of great interest as it is considered contemporary to the Pitsidia flora.

The two floras, Pitsidia and Kastellios Hill, share some of their dominant elements as *Pinus* and Taxodiaceae and deciduous *Quercus*, *Carya* and Myricaceae (text-fig. 5.2). Both share further some accessory deciduous genera such as *Ulmus*, *Acer*, *Salix* and possibly *Ostrya* (in Pitsidia as Betulaceae gen. et sp. indet.) and *Castanea* (in Pitsidia as *Quercus* cf. *kubinyii*). The pollen flora mostly differs by the presence of the thermophilic taxa *Engelhardia*, *Symplocos* and Areaceae as well as the temperate taxa *Alnus* and *Juglans*, which have not been encountered in Pitsidia. In the pollen spectra diverse conifers such as *Cedrus*, *Tsuga*, *Picea*, *Abies* and *Scaiadopitys* also occur. Non-arboreal elements are mostly Amaranthaceae-Chenopodiaceae, Poaceae, Asteraceae, Caryophyllaceae, Cyperaceae and Typhaceae. The low percentages of herbs and shrubs compared to trees and large shrubs, indicate the extent presence of a mixed forest (Sen et al., 1986).
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5.1.2.2. The studied floras in the Greek Upper Miocene context

In the Cenozoic of Greece, more than 40 floras have been reported so far (appendix 20). Early and Late Miocene floras are better represented than Middle Miocene ones.

Based on floristic composition, the Messinian floras can be divided into two groups. The first one includes Vegora, Ellassona, Prosilio and Lava floras from W. Macedonia and N. Thessaly (Meso-Hellenic Trough) where deciduous woody taxa, especially Fagus gussomii and oaks, are dominant whereas subtropical evergreens are rather rare or absent. The second group includes the Messinian floras of other mainland areas of Greece (e.g. Iliokomi-Kromitsa, Akropotamos, Pyrgos-Zacharo basins) as well as of the Greek islands (Paghi, Vrysses). In the second group, Fagus and deciduous oaks are infrequent while more thermophilic
elements such as Lauraceae, Myrica lignitum, Liquidambar europaea, Podocarpium podocarpum and other legumes are often present.

The most significant Tortonian floras of Greece are the Makrilia, Metochia and Pitsidia (Cretan area) and possibly the kap Nenita and Kato Komi floras (Chios Island, Serravallian–Tortonian). The Tortonian Cretan floras appear to be connected floristically to both above described Messinian groups sharing not only physiognomic aspects but also several important elements. With the first group of Messinian floras the Cretan floras shares both Fagus (Makrilia and Metochia) and lobed oaks (Pitsidia), all abundant or dominant. With the second group have in common Daphnogene polymorpha, Myrica lignitum, Liquidambar europaea and diverse Fabaceae including Podocarpium podocarpum. Based on floristic composition the Pitsidia assemblage is closer to the rich plant assemblage of Pyrgos-Zacharo basins (Messinian, W. Peloponnese) sharing more than 15 elements, among them ferns, conifers and dicots. In both assemblages Pinaceae, Lauraceae, Fabaceae, Fagaceae and Sapindaceae are rather diverse and elements such as M. lignitum, L. europaea and D. polymorpha are well documented. Also, the Messinian floras of Vegora (W. Macedonia) and Elassona (Thessaly), the Serravallian–Tortonian of Kato Komi (Chios Island) and the Burdigalian of Kimi (Euboea) have in common with Pitsidia several elements. Among them several conifers, Fagaceae and Sapindaceae (Vegora and Elassona) as well as M. lignitum, D. polymorpha and P. podocarpum (Kimi and Kato komi).

The Metochia flora could be compared floristically mainly with Vegora and Elassona floras (see also MANTZOUKA et al., 2015), as well as with Pyrgos-Zacharo one (more than 10 species in common). With the former shares among others the dominance of F. gussonii. For the Kassanoi flora, none comparable Greek Neogene flora is founded.

5.1.2.3. Comparison with the modern flora of the area

Today, the vegetation of Messara and Gavdos shows strong adaptations to the Mediterranean climate and human impact (TURLAND et al., 1993; GREUTER, 1975). Phrygana and shrub communities predominate while woodlands, composed mainly of sclerophyllous trees, are rather limited. Seashore and wetland plant associations, along coastlines and streams respectively, are well developed. Most trees, tall shrubs, woody climbers, and ferns occurring in the Messara-Gavdos area today, regarded as part of the natural vegetation, are summarised in appendix 21 (from TURLAND et al., 1993). Out of these, the palaeoflora and the modern flora share six genera (Pinus, Quercus, Acer, Zelkova, Salix and probably Rosa).

Modern gallery forests of the area are formed mainly by Platanus orientalis or its endemic semi-evergreen variety (P. orientalis var. cretica) in association with the undergrowth evergreen shrubs Nerium oleander (Apocynaceae), Laurus nobilis and Myrtus communis as well as the deciduous Vitex agnus-castus. Often, this forest is enriched or replaced by Salix alba and Tamarix parviflora. Genera such as Liquidambar,
Daphnogene, Ulmus, Carya, Podocarpium or Taxodium and Myrica, common in the Upper Miocene of the area have disappeared. Close to the coast, small populations of Phoenix theophrastii occur, one of the scarce European palms. *P. theophrastii* probably constitutes a relict from more diverse palm associations of the Upper Miocene as revealed from the findings of Metochia and Makrilia (in this study; Velitzelos D. et al., 2014).

Along the coast line, *Pinus brutia* and various *Juniperus* species are common in pure stands or associated with sclerophyllous woody taxa as *Pistacia lentiscus* and *Ceratonia siliqua*. In the Upper Miocene, pine diversity was higher (at least 3 species), among them *Pinus pitsidiensis*, possibly an ancestral form of the extant long-needled *P. canariensis*, the Asian *P. roxburghii*, and *P. kesiya*.

Today zonal woods of the Messara-Gavdos area are composed mainly of *Cupressus sempervirens*, *Pinus brutia*, *Quercus coccifera*, *Acer sempervirens*, *Pistacia terebinthus*, *Phillyrea latifolia*, *Ceratonia siliqua*, *Olea europaea* and, less frequently, of *Quercus ilex*. Evergreen climbers as *Smilax aspera*, *Hedera helix* and *Rosa sempervirens* are often present. Sclerophyllous elements present in the Cretan palaeofloras probably are two- and five-needled pines as well as Fabaceae, Rhamnaceae (cf. *Z. paradisiaca* and *P. tiliifolius*) and Fagaceae (*Q. mediterranea*). Contrary broad-leaved deciduous woody taxa are almost absent today. The deciduous oak *Quercus pubescens* is mostly found as sole trees scattered in cultivated areas. *Zelkova abelicea* is rare, thriving in humid stands in the mountains of the area. Both are probably relicts.

5.2. Taphonomy of Pitsidia assemblage

5.2.1. Enumeration of the assemblage
The Pitsidia fossil assemblage comprises almost exclusively of plant parts/organs. Nevertheless a notable number of fish bones has been recovered as well. Gastropod shells and insect bodies (mainly wings) are extremely rare (text-fig. 4.14). Concerning the material collected from the MFL during the systematic excavations, fish bones (mostly as disarticulated vertebrae and opercula) constitute about 3% of the collected specimens, although due to their small size and monotonous type they have not been collected systematically, whereas plant fossils make up the great majority of the findings, about 96%. In block No 13, where all the preserved material has been recorded, the frequency of fossil bones is about 15% when very small leaf fragments of dicots were taken into account and were increased to about 25% when these fragments were ignored (text-fig. 4.14c–d). Accordingly, the frequencies of plant remains is estimated to about 85% and 75% respectively. A number of about 1500–2000 fish bones and 4500–5500 plant remains (when dicot leaf fragments <1/6 of the original size were ignored) is therefore expected to be found per m$^3$ of the original deposits (table 4.1). These estimations confirm the dominance of the plant material in the fossiliferous sediments, but also show the elevated presence of disarticulated fish bones. The lack of entire fish skeletons
or even articulated bones suggests their allochthonous origin, being probably transported from adjacent water bodies into the burial site by water currents.

About 50% of the plant findings from MFL comprise foliage, approx. 2.300–2.600 leaves per m³ (when dicot leaf fragments representing less than 1/6 of the laminar original size are not taken into account) (text-fig. 4.15, table 4.1). Leafy twigs (of Pinus and Taxodium) as well as shoot fragments partly with buds, wood and bark particles, scales/bracts and catkins follow with percentages between 7–13%. Fruits/seeds and pollen cones are less frequent, while roots and ovulate scales are rare. In general, the abundance of fertile organs is much lower than that of vegetative ones not succeeding 15% of the collected plant specimens.

Myrica and Pinus remains, vegetative and fertile, prevail in the assemblage (text-fig. 4.16–4.18, table 4.1). (approx. 1850–1900 Myrica leaves and 200–400 P. pitsidiensis twigs per m³). The vegetative remains of Q. pseudocastanea, T. dubium, D. polymorpha, Carya sp., “Pteris” oeningensis and Q. cf. kubinyii, as well as the infructescences of L. europaea are fairly common (frequencies >0.5% of identified specimens in MFL).

Concerning FL2, the abundances of the most common plant species seem to be close to those of the MFL layer. The difference to MFL is the increased percentages of fruits/seeds and ovulate cone scales and the slight decrease of foliage remains (text-fig. 4.19). Possibly, this indicates slightly increased water transfer energy which is also supported by the slightly coarser sediments. However, the most remarkable difference in FL2 is a pronounced bedding plane rich in pine remains (pl. IV, fig. 4).

5.2.2. Biostratonomic implications

The Pitsidia material comprises vegetative and fertile plant parts that mostly underwent natural shedding. There is no evidence for strong winds, severe infections or animal action that would have caused extensive loss of plant organs/parts. The high abundances of M. lignitum and P. pitsidiensis as well as the diversity of their organs (text-figs 4.16–4.18) indicate that both taxa were probably more abundant than other or even dominating in the closest vicinity of the depositional area. The assemblage is characterised by the strong presence of more or less fragmented leaves. Approx. 65% of the collected leaves shows pre-depositional mechanical damages (text-fig. 4.24; pl LVII, figs 1–5). All these extensive pre-burial mechanical damages reveal that leaves had obviously undergone transportation.

5.2.3. Diagenetic implications - The inorganic encrustations

The great majority of the studied material from Messara and Gavdos has been preserved as imprints, mostly without any organic matter. Generally in imprints, the third dimension is substantially absent as plant remains become more or less flattened under the pressure of the overlying layers (SCHOPF, 1975; REX and CHALONER, 1983). Although being most abundant, this preservation type is less informative as internal
structure or cellular details are usually destroyed. In special cases, when the matrix of the rock is extremely fine, micro-morphological features such as the outline of epidermal cells, the occurrence and distribution pattern of stomata and trichomes may be preserved. Latex replicas of such impressions, examined by SEM, may deliver epidermal structure details (REX et CHALONER, 1983). In Pitsidia, the replicas that were prepared from foliage imprints delivered negative results as it should be expected for a sandy silt matrix.

Despite low quality, several imprints from Pitsidia (and exceptionally in Metochia) are covered by an inorganic encrustation (replica) built by crystalic micro-spherules of Fe-oxides that in special cases has a key role in the preservation of plant tissue structures. However, the relatively large size of the micro-spherules, (15–30 μm in diameter) prevented preservation in cell-level.

Although they have not been thoroughly studied, inorganic encrustations are known even from the early history of palaeobotany. KRYSTOFOVICH (1944) observed that plant material entering into stagnant fresh-water was gradually covered by a thin encrustation of inorganic material even before burial which increased its preservation potential. He was suspecting that in this encrustation carbon dioxide participated, produced by the decaying organic matter. Later, SPIKER (1975, 1977) noted that foliage was encrusted with a film of inorganic material rich in Fe within a few weeks after entering into a fresh-water fluvial/lacustrine environment. This crust was so strongly coherent to the leaf surface that it could not be removed even during violent transport. He considered that this could be the result of the activity of iron bacteria on the surfaces of plant remains during the early taphonomic stages. He did not exclude the possibility that the formation or the enrichment of this iron-rich encrustation occurred in the early stage of diagenesis.

Today, the formation of inorganic-encrusted impressions in the fossil record has been attributed to the development of biofilm on the original plant organ/part (DUNN et al., 1997). Hence, a thin biofilm coat can be formed as a result of the continuous colonization and growth of microorganisms on the organ/part surface (COSTERTON et al., 1995; DUNN et al., 1997). Biofilms are a dominant mode of microbial growth in natural environments associated with processes such as plant tissue decomposition. The colonization concerns a variety of different microorganisms that have the ability to develop to various substrates of hydrophobic or hydrophilic character (VAN LOOSDRECHT et al., 1997). As bacterial cell surfaces and extracellular polymers within biofilms are largely anionic, biofilms quickly alter the chemistry of the substrate surface and enable it to interact with metal cations forming minerals (MCLEAN et al., 1999).

Consequently, once a plant part is removed from the parent plant and entered into an aquatic environment, a variety of bacteria [not only iron-bacteria as initially reported by SPIKER (1977)] quickly colonize its surface forming a biofilm (MORRIS et al. 1997). The hydrophobic surface of most plant organs (e.g. waxy cuticle on leaves) is transformed into metal-receptive. In case that the plant remains are exposed in an environment of elevated concentration of metal ions such as Fe^{2+}, they rapidly get encrusted with cementing minerals. This metal binding onto their surface is beneficial to fossilisation as it inhibits further microbial decomposition.
and constitutes the initial step in the formation of an accurate replica of the respective plant organ. In this way considerable details, even at the microscopic level can be preserved.

A series of factors such as sediment type, pH, availability of microbes and metals and anoxic conditions are crucial for the time needed and the type of the final mineral product, with iron-oxides being more often responsible for replicating delicate tissues during diagenesis (CHEN and ERDTMANN, 1991; JIN et al., 1991).

Regarding the Pitsidia assemblage, the sources of iron that participated in the formation of such abundant iron-rich replicas is to debate. The analysis of the main fossiliferous layer reveals the absence or limited concentration of iron minerals in the sediments (text-fig. 4.21a). Probably, this is an indication of early diagenetic mineralization. This is also supported by the excellent preservation of the plant tissues. In an aquatic environment, iron precipitates as a result of the decomposition of the organic matter which contains quantities of iron as, e.g. part of the vital protein ferritin (CHASTEEN and HARRISON, 1999; SCOTT and COLLISON, 2003; MASUDA et al., 2010).

5.2.4. The depositional environment of the Pitsidia assemblage

At Pitsidia and the adjacent area, the geological and sedimentological setting imply a transitional marine landscape where estuarine palaeoenvironments were interfingering with backswamp, floodplain, riverbank and bog habitats that were located close to the coast (KRÖGER, 2004). The almost absent organic matter and the medium CaCO₃ content in the fossiliferous sequence reflects a depositional Basin with good oxygen circulation where oxidising conditions prevailed. The grain-size of the plant-bearing layers suggests that the plant material was deposited in calm or stagnant waters of low depth. Disarticulated bones, mostly of a single fish taxon, are common in the studied deposits but the lack of fish skeletons and scales indicate transportation of this material. The identified animal remains reveal a fresh-water ecological preference for the fishes (Cyprinidae), molluscs (Planorbidae) and ostracods (Candonidae).

5.2.5. Evaluation of the excavation method

In the systematic excavation of Pitsidia, the fossil collecting method of sediment splitting was employed. The results of the fossil-destructive sampling in sediment block Nr. 13 reveal that traditional collecting method of sediment splitting is quite effective since the estimated densities of plant remains in the sediment from block Nr. 13 are close to those from blocks Nrs 1–12 (table 4.1). Although effective, splitting proved rather destructive. A profoundly elevated portion of the collected leaves were mechanically damaged during fossil extraction (text-fig. 4.24).
5.3. Palaeoenvironmental analysis

5.3.1. Evolution of the Messara-Gavdos area

After the main orogenetic movements had ended and the continuous landmass of Aegeis (including Cretan area) has been emerged, uplift and erosion processes prevailed (Meulenkamp et al., 1979). Since Middle Miocene, the Neogene sedimentary basins of Crete were formed in response to the extensional geodynamic processes in the Aegean region (Angelier et al., 1982; Ten Veen and Postma, 1999; Fassoulas, 2001; Meulenkamp and Sissingh, 2003). Among them the Messara Basin, originally as part of a larger Basin extending northwards to the present day Heraklion Basin. During the Lower Pliocene tectonic processes separated the two basins with the development of the east-west central Heraklion Ridge (Fassoulas, 2001).

Based on the available structural, sedimentological and stratigraphical data obtained from the Neogene sediments of Crete and Gavdos Islands most authors subdivide the Neogene depositional history of the Messara-Gavdos area into several tectonostratigraphic intervals, each with its own style of rock deformation and basin fill architecture (e.g. Meulenkamp et al., 1979; Anastasakis et al., 1995; Ten Veen and Postma, 1999; Van Hinsbergen and Meulenkamp, 2006; Zachariasse et al., 2011). Van Hinsbergen and Postma (2006) provided schematic palaeogeographic maps presenting an approach of the possible geologic history of the Cretan area. These maps are used in our analysis in order to provide a general outline of the palaeoenvironment of Messara and Gavdos during the deposition of the three herein studied plant assemblages:

1st tectonostratigraphic interval. Middle–upper Serravallian (Viannos and Potamos Fms – Kassanoi flora).

The base of the stratigraphic sequence in Messara Basin is formed by the extensive fluvo-lacustrine deposits of Viannos Fm. The lateral equivalent in the adjacent Ierapetra Basin is considered to be Males Fm consisting of alternations of well-sorted conglomerates, intercalated with fine-grained deposits and is interpreted as a braided to meandering river system feeding the lacustrine Viannos Fm (Fortuin, 1977) (text-fig. 5.3). The numerous cross-beded fine sediments and the decreasing grain size and increasing roundness indicate flow directions between south and west. The Males-Viannos sedimentary system is probably a lateral equivalent of the marine sediments of Potamos Fm on Gavdos Island (Meulenkamp et al., 1994). The few meters of coral limestones at the base of Potamos Fm are followed by deep-water mudrocks and sapropels (around 500–600 m) indicating a late Serravallian subsidence in the Gavdos area.
Text-figure 5.3. Schematic palaeogeographic map of the Crete-Gavdos area in the 1st tectonostratigraphic interval (middle–upper Serravallian), an east to west running longitudinal sedimentary system connects the river sediments of Males Fm in Ierapetra area with the lacustrine sediments of Viannos Fm in central Crete and the deep-marine sediments of Potamos Fm in Gavdos (VAN HINSBERGEN and MEULENKAMP, 2006).

2nd tectonostratigraphic interval. Upper Serravallian–lower Tortonian (Skinias Fm). The Viannos Fm underlies conformably the marine deposits of Skinias Fm reflecting a marine transgression with which the Messara Basin from the upper Serravallian to lower Tortonian was submerged. The initial drowning of the Basin is represented by shallow-marine deposits with intercalated reefs which is followed by a rapid deepening (MEULENKAMP et al., 1979) (text-fig. 5.4). In Gavdos area, the deep-marine mudstones and sapropels of Potamos Fm are overlain by shallow-marine sands, reflecting an uplift episode during the upper Serravallian/lower Tortonian time.

Text-figure 5.4. Schematic palaeogeographic map of the Crete-Gavdos area in the 2nd tectonostratigraphic interval (upper Serravallian–lower Tortonian), a marine transgression submerged the Messara Basin from the upper Serravallian to lower Tortonian (modified from VAN HINSBERGEN and MEULENKAMP, 2006).
3rd tectonostratigraphic interval. Lower–middle/upper Tortonian (Ambelouzos and Metochia Fms – Pitsidia and Metochia florases). The lower Tortonian transgressive sedimentary succession in Messara Basin is interrupted by a short episode of tectonic uplift. The action of N–S and E–W oriented faults formed a high number of relatively small intermontane basins with variable facies distribution (MEULENKAMP et al., 1979; TEN VEEEN and POSTMA, 1999) (text-figs 5.5–5.6). The accumulated deposits represent different facies of fluvial, brackish and shallow-marine environments. The occurrence of the fluvial to shallow-marine facies is rather patchy pointing to several local-scale transgression and regression cycles. Especially in the western part of the Messara Basin, floodplain deposits dissected by braided river channels are well documented, while marine transgressions repeatedly submerged the area leading to lagoonal or inner neritic environments (KRÖGER, 2004). The deposits of Metochia Fm suggest a marine environment for Gavdos during the middle to upper Tortonian. The containing plant macro-remains (Metochia palaeoflora) in the “sapropel” layers (Metochia palaeoflora) obviously represent terrigenous supplies from the adjacent land of Palaeocrete.
4th tectonostratigraphic interval. Middle/upper Tortonian–lower Messinian (Ag. Varvara Fm). In the upper Tortonian, large parts of the Cretan region subsided, as shown by the sharp transition from shallow-marine into deep-marine facies (text-fig. 5.7). Later, in the lower Messinian a drop in siliciclastics and a shift toward carbonate accumulation took place.

![Text-figure 5.7. Schematic palaeogeographic map of the Crete-Gavdos area in the 4th tectonostratigraphic interval (Middle/upper Tortonian–lower Messinian) (modified from VAN HINSBERGEN and MEULENKAMP, 2006); antiform](image)

5.3.2. Vegetation reconstruction - Phytosociological approach

Kassanoi assemblage. The stratigraphic position of the Kassanoi assemblage corresponds to the 1st tectonostratigraphic interval. In accordance with the fluvio-lacustrine environment, the Kassanoi flora comprises elements mostly of moist habitats (appendices 6, 15; text-fig. 5.9a). Along the fluvial-lacustrine systems a gallery forest was possibly formed by S. cf. angusta, P. podocarpum, D. polymorpha, U. cf. plurinervia, P. populina, and Fraxinus sp. A herb layer with ferns and monocots probably occurred. The shrubs of M. lignitum either constituted part of the riparian association or thrived in a swampy environment close to the depositional site. D. gibbosus is interpreted as a rooted plant with stems floating on the surface of calm waters comparable to the extant D. verticillatus. It was a constituent of aquatic and wetland communities.

Contrary to the wetland vegetation, zonal plant associations are under-represented with a limited number of taxa and low abundances. In the adjacent plains and low hills, a forest of deciduous oaks and T. cf. salicornioides may be expected. Considering its resemblance to modern analogue allies (see appendix 15), B. multinervis, probably, either represented a climbing plant or was part of the understory. In drier substrates elements like Leguminosae, Cornus sp. and ?B. pliocenica possibly occurred.
**Pitsidia assemblage.** The stratigraphic position of Pitsidia assemblage corresponds to the 3rd tectonostratigraphic internal. This assemblage probably was deposited in an estuarine palaeoenvironment, interfingering with costal backswamp, floodplain, riverbank and bog habitats (see section 5.2.4; text-fig. 5.6). Phytosociologically the taxa of the Pitsidia assemblage are assigned to five different habitat types. Swampy and lowland forest on waterlogged substrates, coastal and mixed forests on well drained soils and xerophytic woodlands on drier substrates (appendices 5, 15; text-fig. 5.8). More specifically:

Within the deltaic plain, typical backswamp systems with *T. dubium* occurred. This could be either the sole canopy component or it was associated with broad-leaved deciduous arboreal elements such as *A. tricuspidatum* and possibly *L. europaea*. In the forest understorey *M. lignitum* was very common.

Modern *Myrica* species are usually considered as early succession elements requiring strong light conditions and exhibiting a nitrogen-fixing root symbiosis which enables *Myrica* to survive in nutrient-poor substrates (Dawson, 1990; Swensen, 1996). Taking into account these physiological characteristics along with the extreme abundances of *Myrica* remains in the fossil assemblage, the occurrence of bog-like habitats with *M. lignitum* shrubs may be expected with low nutrient supply and ground water level near or above the soil surface.

The active river channels and the allied oxbow ponds may have been lined by a gallery forest with deciduous taxa such as *P. populina, Salix, U. cf. plurinervia, Carya, Pterocarya, A. tricuspidatum, L. europaea*, and possibly *P. podocarpum* and *A. aegopodifolium* as well as *D. polymorpha*. The occurrence of *M. lignitum* in the understory is likely, while ferns and monocots seem to constitute a usual element in the herb layer.

At the coastline *P. pitsidiensis* probably was a dominant taxon associated mainly with *M. lignitum*. Both may represent elements of early successional stages. The pine forests along the coastal flatlands of SE North America could be considered a modern analogue, where *P. palustris* forests are broadly distributed and *M. cerifera* is one of the differential understory species in these forests (Miyawaki et al., 1994).

On the slopes of the adjacent hills, beyond the influence of flooding, the zonal vegetation was quite diverse but not uniform, depending on moisture and fertility of the soil as well as on sun exposure. On moderately moist substrates mixed forest probably occurred, composed mainly of broad-leaved deciduous trees and a low proportion of evergreen elements. The deciduous oaks *Q. pseudocastanea* and *Q. cf. kubinii*, possibly were predominating in the forest canopy, *D. polymorpha* and ?*L. ovata*, as well as *T. cf. salicornioides, Q. mediterranea, A. integrilobum, A. aegopodifolium, F. gussonii, Pterocarya,* ?*Z. zelkovifolia* and possibly *P. podocarpum, Leguminosites* and *Mimosites* represented accessory elements in the assemblage. The shrub layer was probably poorly developed consisting of deciduous elements such as ?*Rosa* sp. and ?*Hydrangea*. On drier substrates, this association may have been replaced by more sclerophyllous woodlands with two- and five-needled pines possibly co-occurring with Leguminosae (*Mimosites, Leguminosites*) and the
evergreen oak of *Q. mediterranea*. On the southern slopes and in areas with poor substrates, the pine trees were probably forming pure stands.

Text-figure 5.8. Vegetation reconstruction model of the Messara area based on Pitsidia palaeoflora, a. azonal vegetation; b. zonal vegetation

**Metochia assemblage** can also be positioned to the 3rd interval. The plant macro-remains are deposited in a deep-marine environment and their source should be considered the neighboring land of the Palaeocrete area. In this assemblage the zonal taxa are better represented (appendices 15–16; text-fig. 5.9b). The upland areas probably were occupied by mesophytic to sclerophyllous forests with a relatively high percentage of broad-leaved deciduous taxa such as *F. gussonii, A. angustilobum, S. graecus, E. orsbergensis, A. pythii, Betula* and *Sassafras*. Evergreen taxa and conifers such as *Laurophyllum, Daphnogene polymorpha* and *T.*
salicornioides were limited. Sclerophyllous taxa are represented by Q. mediterranea, various Pinus species, Fabaceae, P. tiliifolius and cf. Z. paradisiaca.

Regarding intrazonal vegetation, T. dubium and M. lignitum as well as Sabalites sp. are scarcely found. The gallery forests consisted of U. plurinervia, P. populina, Salix and D. polymorpha, different monocot herbs and possibly M. lignitum.

5.3.3. Palaeo-synecology

The record of terrestrial plants from Kassanoi, Pitsidia and Metochia yields direct evidences of other contemporaneous organisms which were related to the plants ecologically, such as feeding damages and oviposition marks of invertebrate herbivores. Taking into account the fact that in modern terrestrial habitats, plants and arthropods constitute two ecologically dominant clades of macroscopic organisms comprising most of recent biodiversity, the value of such data is apparent (STORK, 1987; SCHOONHOVEN, et al., 2005; PRICE P., 2002). Moreover, the investigation of arthropod mediated feeding damages on plant remains adds a new supplementary approach in order to follow past climatic fluctuations and detect prominent changes (WILF and LABANDEIRA 1999; WILF et al., 2001; SMITH, 2008; CURRANO et al., 2010; KNOR et al., 2012).

Pitsidia assemblage. The plant assemblage of Pitsidia provides evidence of two different functions in macro-invertebrate physiology, feeding and reproduction. The feeding traces comprise mainly arthropod mediated damages on angiosperm foliage and are categorized in four main functional feeding groups: i. external
feeding, ii. piercing and sucking, iii. mining and iv. galling. The reproduction traces can be referred exclusively to arthropod oviposition on the foliage substrate. Abundance and diversity of the feeding damages on leaf remains appear not to have reached particularly high levels and heavily folivorized specimens are rather rare. Among damages, external feeding (especially leaf perforation and margin excision) and piercing-sucking predominate in the assemblage. Leaf galling holds an elevated richness in the assemblage as at least 5 different gall types are presented in an equal number of different plant taxa, while mining is very rare.

Concerning the two dominant taxa of the assemblage, in M. lignitum the damaged leaves exceed 20% of all specimens, while in P. pitsidiensis, only two damaged needles have been detected (less than 0.5%).

For Myrica lignitum in particular (appendix 14, text-fig. 4.26):
-external foliage feeding is the most abundant and diverse damage including 8 different types of perforation and margin excision. The majority of them, on the basis of their morphological features, can be assigned to unspecialized herbivorous host insects.

-lamina deformations are quite frequent, regularly not accompanied by other visible leaf marks or damages. Today, similar patterns of leaf distortion can be observed in several evergreen Mediterranean taxa such as Olea europaea L. and Nerium oleander L. They are caused by small-sized insect feeding, e.g. Thysanoptera, Homoptera (pl. LIV, figs 21–22; I.N.R.A., 1998; own observations). These insects penetrate the living tissues with their piercing mouthparts, causing asymmetric tissue growth and finally they shape the deformations of young leaves in particular. This type of leaf damage is also well known in modern Myrica species (MARKIN et al., 1995; Herbarium specimens e.g. Nrs 118300, 232471, 231970 in WUNDERLIN et al., 2017).

-leaf mining, only one type has been recognized which is restricted to leaves of M. lignitum. Leaf mines are produced by insect larvae that typically feed on the parenchyma of the mesophyll, leaving the epidermis untouched.

-galls are frequent in M. lignitum but low in diversity. Galls are formed by abnormal plant tissue growth and constitute excellent microhabitats for the affecting organisms. They are characterized by high host specialization. In modern ecosystems, the formation of galls is mainly induced by arthropods but it is also quite common among nematodes, fungi, bacteria or viruses (STONE and SCHÖNROGGE, 2003). In dry climates they are considerably diverse and abundant (FERNANDES and PRICE, 1988, 1991; PRICE P. et al., 1998; WRIGHT and SAMWAYS, 1998).

-arthropod exophytic oviposition has been observed exclusively on leaves of M. lignitum. It is accompanied by notable leaf deformation probably due to the female preference of attaching eggs on immature foliage that had not yet completed their growth. In recent ecosystems oviposition on foliage surface is a common behaviour where the females deposit eggs in a precise microhabitat on or near the required food sources.
Considering all these observations in Pitsidia plant material it is obvious that through the examination of the preserved trace fossils, the plant-arthropod dynamic interactions and their trophic associations in the ancient habitats are well illustrated.

As referred above, leaf galling in Pitsidia is well-documented (five types in different plant species, approx. 15% of the damaged leaves in *M. lignitum*). The ecological investigations on modern and fossil plant-insect interaction indicate that leaf galling is negatively correlated with moisture contrary to extensive folivory (Coley and Barone, 1996; Smith, 2008; Currano et al., 2010; Wappler, 2010; Knor et al., 2012). Nevertheless, more evidence such as the leaf palatability of the plants to herbivores, the defence strategies and the stage of vegetation succession must be also taken into account (Coley and Barone, 1996; Royer et al., 2007). Such research is, however, beyond the scopes of this study.

In contrast to the indisputable presence of ichnofossils, Pitsidia excavation yielded poor evidence of arthropod body fossils comprising basically of imprints of a complete insect body and a few isolated insect wings. These findings along with the sole Formicidae specimen recovered from the Late Miocene sediments near Apomarma village (Wappler et al., 2009) constitute the only terrestrial arthropod body fossils that have been recovered from the Messara Basin to date.

**Kassanoi and Metochia assemblages.** Regarding Kassanoi and Metochia assemblages, the limited number of specimens and the poor quality of preservation prevent a thorough study of the plant-arthropod interactions and the expression of any specific conclusion. However, it is of high interest the fact that a few frequently encountered damages on *M. lignitum* leaves in Pitsidia occur also in a much older assemblage such as Kassanoi (compare pl. LIV, fig. 18 and pl. LV, figs 2, 6 in Pitsidia to pl. XLIV, fig. 18 and pl. XLVI, figs 5, 8 in Kassanoi respectively). Moreover, such characteristic damages caused by highly specialized arthropods can be used as a supplementary tool in plant species systematic identifications e.g., in *M. lignitum* the above referred distinct type of lamina deformation and gall shape and in *Carya* sp. leaflets with the specific apex deformation (pl. LVI, figs 9–10).

### 5.3.4. Climate proxies

The results of the coexistence approach (CA), applied for Pitsidia and Metochia palaeofloras, indicate a warm temperate to subtropical climate in the lower–middle Tortonian, probably Cfa-type sensu Köppen-Geiger system with a mean annual temperature (MAT) between 13.5 to 18.5 °C, warm season mean month temperature (WMMT) between 23.3 to 26.4 °C, cold season mean month temperatures (CMMT) > 2.5 °C and
mean annual precipitation (MAP) of 843–1613 mm (table 4.4). The climatic analysis implies seasonal drought [mean precipitation of the driest month (MPdry) 17–63 mm] that did not coincide with the warmest period of the year as illustrated by the mean precipitation of the warmest month (MPwarm) 80–89 mm.

The temperature seasonality of the Tortonian climate in Crete is also supported by the stable isotope records ($\delta^{18}O$, $\delta^{13}C$) in coral skeletons (BRACHERT et al., 2006). Exceptionally well preserved corals (Porites LINK) from Ambelouzos Fm indicate probable seasonal changes in sea surface temperature.

MANTZOUKA et al. (2015) assessed climate proxies from the Late Miocene floras of Crete [Makrilia, Vrysses, Pitsidia (using ZIDIANAKIS et al., 2010 taxa list) and Metochia] applying the coexistence approach (CA), the leaf margin analysis (LMA) (WOLFE, 1979; SU et al., 2010) and the climate leaf analysis multivariate program (CLAMP) (WOLFE and SPICER, 1999; SPICER et al., 2009). The results of MANTZOUKA et al. (2015) are close to ours (table 4.4). Differences to mention are the lower MATmin (Metochia) and a divergence in MAPmax and MPdrymin-max (Metochia and Pitsidia) in MANTZOUKA et al. (2015) estimations. Concerning Metochia, the differences in the results can be explained by the here-reported taxa, especially Sabalites (increasing minimum temperatures) and cf. Ziziphus paradisiaca (decreasing precipitation values). For Pitsidia, the differences may be explained by the erroneous identification of Buxus pliocenica and Acer pseudomonspessulanum by ZIDIANAKIS et al. (2010), account for lower MAPmax and MPdrymin-max values.

Today, the climate in the Messara-Gavdos area is slightly warmer and much drier, and the warm period of the year coincide with the driest; type CSA sensu KÖPPEN-GEIGER system (table 4.4).
6. CONCLUSIONS

- Three Miocene floras of different ages from the Messara Basin (Crete) and Gavdos have been studied.

- The palaeoflora of Kassanoi which is the oldest (Messara Basin, Serravallian) is mainly documented by foliage and includes a fern, a conifer (Tetraclinis cf. salicornioides) and 24 angiosperms.
  - The assemblage is dominated by Daphnogene polymorpha, Myrica lignitum, Podocarpium podocarpum and Salix cf. angust. Other well documented taxa are Berchemia multinervis, Decodon gibbosus, Fraxinus sp., Populus populina and Ulmus cf. plurinervia.

- The palaeoflora of Pitsidia (Messara Basin, Lower Tortonian) is rich in plant material and diverse in fossil taxa, delivering one alga, 2 ferns, at least 5 conifers and more than 45 angiosperms, mostly identified on the basis of imprints.
  - Dominant species are Myrica lignitum and Pinus pitsidiensis and the foliage of deciduous oaks, whereas Taxodium dubium and Daphnogene polymorpha are the most common.
  - Further well documented taxa are ”Pteris” oeningensis, two- and five-needled pines as well as Acer integrilobum, Acer tricuspidatum, Carya sp., Fagus gussonii, Liquidambar europaea, Mimosites sp., Podocarpium podocarpum, Populus populina, Quercus mediterranea, and Ulmus cf. plurinervia.
  - A new pine species with long needles in fascicles of three, Pinus pitsidiensis, was identified on the basis of morphological and anatomical features of its vegetative organs (twigs, isolated needles and long shoots) showing affinity to sect. Pinus of the subgen. Pinus. Pinus pitsidiensis shares vegetative and reproductive characteristics with P. canariensis and P. roxburghii (former sect. Sula) of subsect. Pinaster and P. kesiya of subsect. Pinus.
  - The mass-occurrence of vegetative and fertile remains of Myrica (leaves, fruits, infructescences and male catkins) allowed for the whole plant reconstruction. It remains disputable whether Myrica lignitum leaves represent a natural species or a cluster of Myrica species with similar leaves.
  - The morphological features of Myrica fertile organs point towards a relationship to the sect. Cerophora (sensu CHEVALIER, 1901) of subgen. Morella. A closer relationship to modern M. cerifera was proposed.

- For the palaeoflora of Metochia (Gavdos Island, middle Tortonian), eight taxa are recorded for the first time, among them are a five-needled pine, Quercus mediterranea, cf. Ziziphus paradisiaca and the leaf remain of a palm (Sabalites sp.).

- The significant differences in floristic composition of the studied assemblages may be attributed to differences in environmental and especially depositional settings.
• In Pitsidia a taphonomical analysis for the fossil material is attempted:
  o The majority of the plant material has undergone after-shedding mechanical stress probably due to transportation of the plant material prior to deposition.
  o Sedimentological and geochemical analysis of the plant-bearing layers as well as the autoecology of the hosted palaeofauna indicate a fresh-water depositional environment, in calm conditions, with good oxygen circulation.
  o The plant remains (imprints) are occasionally covered by an inorganic encrustation, rich in iron (ferrihydrite) which represent a plant organ replica. The low proportion of Fe in the fossiliferous sediment indicate early diagenetic mineralization.

• A palaeoenvironmental analysis has derived from the studied floras:
  o The palaeo-synecological studies reveal a dynamic interaction between plants and arthropods in Pitsidia which is expressed by a wide spectrum of distinctive damages of two different arthropod functions, feeding and reproduction.
  o Based on the IPR vegetation analysis, the floras of Pitsidia and Kassanoi are assigned to subtropical, subhumid sclerophyllous or microphyllous forest (ShSF) and for Metochia a mixed mesophytic broad-leaved forest with a small proportion of thermophilic elements is indicated.
  o The floristic composition and the sociologically reconstructed vegetation models of the assemblages are in accordance to the Neogene palaeoenvironmental evolution of the Messara-Gavdos area as it has been revealed by the numerous stratigraphic and tectonic studies in the area.
  o The coexistence approach delivers a warm temperate to subtropical climate (MAT 13.5–18.5 °C and MAP approx. 850–1600 mm), with seasonality in precipitation, probably a type Cfa (sensu KÖPPEN-GEIGER) for Pitsidia and Metochia floras.
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OTHER LITRATURE


PLATES
PLATE I
Figs 1–3 General view of the studied areas, the arrows shows the location to the plant-bearing outcrops
Fig. 1. Pitsidia, western Messara Basin, Crete Island
Fig. 2. Kassanoi, eastern Messara Basin, Crete Island
Fig. 3. Metochia, Gavdos Island
PLATE II
Figs 1–3 The studied plant-bearing outcrops, the arrows indicate the sampling layers
Fig. 1. Pitsidia, western Messara Basin, Crete Island
Fig. 2. Kassanoi, eastern Messara Basin, Crete Island, for scale notice the lug
Fig. 3. Metochia, Gavdos Island, partly view of the marl- laminites sequence, for scale notice the colleagues at the upper part
PLATE III
Figs 1–5 Pitsidia, the excavation of fossil plant material
Fig. 1. the MFL is divided in 6 levels, 70 cm thick; the flag indicates the position of the datum and the arrow the uppermost part of the MFL
Fig. 2. the grid and the larger in size removed sediment blocks
Fig. 3. natural fracturing of the plant-bearing deposits, ruler 10 cm long
Fig. 4. working at the 5C grid square, IV level of the MFL
Fig. 5. general view of the area, the red lines represents the grid, the black ones define the main exposure of the studied fossiliferous sediment, the arrow indicates the North and the flag the position of the datum; the excavated squares are given in green color, the Latin numbers shows the excavated levels of the MFL
PLATE IV

Figs 1–4 The Pitsidia assemblage, Crete

Fig. 1. slab with various plants remains, the arrows indicate their orientation, (M, *Myrica lignitum* leaf; P, *Pinus pitsidiensis* needles; F, *Myrica* cf. *goeppertii* male catkin); Nr. 31.4.2.3543b, scale bar 5 cm

Fig. 2. two fragmentary leaves of *Myrica lignitum* syn-deposited with a three-needled twig of *Pinus pitsidiensis* (white arrow), note the fracture that cross the *Myrica* leaves (black arrow), Nr. 31.4.2.4179, scale bar 1 cm

Fig. 3. a complete leaf of *Myrica lignitum* damaged by sediment fracturing and weathered, in E–W orientation, in situ

Fig. 4. bedding plane with numerous three-needled fascicles of *Pinus pitsidiensis*, in situ, scale bar 10 cm
PLATE V
Fig. 1–4 Kassanoi, fossil collection process
Fig. 1. the fossiliferous deposits, the hammer for scale (arrow)
Fig. 2. bedding plane with an isolated leaf impression of *Daphnogene polymorpha* (arrow)
Fig. 3. collecting fossils
Fig. 4. the coal seam at the upper part of the section (arrow)
PLATE VI

Figs 1–4 The Kassanoi assemblage, Crete, scale bar 2cm
Fig. 1. fragmentary leaves and plant debris, Nr. 31.6.2.15
Fig. 2. in situ root remains
Fig. 3. mollusk shell accumulation
Fig. 4. complete leaves co-occurring with abundant leaf fragments, Nr. 31.6.2.120
PLATE VII

Figs 1–3 Metochia, fossil collection process
Fig. 1. excavated layers, the hammer for scale
Fig. 2. *Engelhardia orsbergensis* foliage, the plant fossils are mostly founded as isolated impressions in the bedding planes,
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Figs 4–5 The Metochia assemblage, Gavdos
Fig. 4. imprint of a costapalmate leaf fragment
Fig. 5. fish skeletons occasionally occur in the fossiliferous layers
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Palaeoflora of Pitsidia, Crete, scale bar 5 mm
Figs 1–13 “Pteris” oeniegensis
Fig. 1. pinnatifid segment, Nr. 31.4.2.6268a
Fig. 2. fragment of pinnatifid segment, Nr. 31.4.2.5218
Fig. 3. isolated terminal lobe, Nr. 31.4.2.5884aop
Fig. 4. isolated lateral lobe, Nr. 31.4.2.2201a
Fig. 5. isolated lateral lobe, Nr. 31.4.2.8243a
Fig. 6. two fragmentary lateral lobes, Nr. 31.4.2.6194ii
Fig. 7. isolated lateral lobe, Nr. 31.4.2.5894i
Fig. 8. fragment with simple lateral segments, Nr. 31.4.2.979bi
Fig. 9. terminal lobe with a partly preserved lateral lobe at the base, Nr. 31.4.2.2197i
Fig. 10. fragment of pinnatifid segment with lateral lobes, Nr. 31.4.2.4112
Fig. 11. isolated lateral lobe, Nr. 31.4.2.4972
Fig. 12. isolated lateral lobe”, Nr. 31.4.2.4846
Fig. 13. fragment with two simple lateral segments loosely arranged on the costa, Nr. 31.4.2.6574b
Figs 14–15 Polypodiophyta fam. gen et sp. indet., frond segments
Fig. 14. Nr. 31.4.2.1940bop
Fig. 15. two, close to each other, Nr. 31.4.2.2337
Figs 16–19 Gymnospermae fam. et gen. et sp. indet., isolated needle-like leaves
Fig. 16. Nr. 31.4.2.5822ii
Fig. 17. Nr. 31.4.2.5521
Fig. 18. Nr. 31.4.2.5603
Fig. 19. Nr. 31.4.2.4439aii
Figs 20–23 Tetraclimis cf. salicornioides
Fig. 20. twig, Nr. 31.4.2.6324b
Fig. 21. twig, Nr. 31.4.2.6324ai (counterpart of fig. 20)
Fig. 22. twig, Nr. 31.4.2.6331aopi
Fig. 23. solitary segment, Nr. 31.4.2.845
Fig. 24. Gymnospermae fam. et gen. et sp. indet., ovulate scale with two seeds,
Nr. 31.4.2.1421aopi
Fig. 25. fam. et gen. et sp. indet., ovulate scale with two seeds, Nr. 31.4.2.4538bopivy
Figs 26–30 Close up, scale bar 1.75 mm
Fig. 26. “Pteris” oeniegensis, isolated lateral lobe, Nr. 31.4.2.2201a
Fig. 27. Tetraclimis cf. salicornioides, segment, Nr. 31.4.2.6324ai detail
Fig. 28. Tetraclimis cf. salicornioides, segment (counterpart), Nr. 31.4.2.6324b detail
Fig. 29. Tetraclimis cf. salicornioides, segment, Nr. 31.4.2.6331aopi detail
Fig. 30. Gymnospermae fam. et gen. et sp. indet., isolated needle, Nr. 31.4.2. 5822
PLATE IX
Palaeoflora of Pitsidia, Crete, scale bar 1 cm (unless stated otherwise)

Fig. 1. Algae, thallus fragment, Nr. 31.4.2.1517b
Figs 2–10 Taxodium dubium, foliage twigs with acicular leaves
Fig. 2. Nr. 31.4.2.6577a
Fig. 3. almost complete, Nr. 31.4.2.3137a
Fig. 4. complete Nr. 31.4.2.1217i
Fig. 5. three attached twigs, Nr. 31.4.2.6123b
Fig. 6. dichotomised twig, Nr. 31.4.2.1135a
Fig. 7. mechanically damaged, Nr. 31.4.2.2670
Fig. 8. mechanically damaged, Nr. 31.4.2.4886a
Fig. 9. Nr. 31.4.2.5788ai
Fig. 10. Nr. 31.4.2.4861aii
Figs 11–18 Taxodium dubium, incomplete foliage twigs with broad needle-like leaves
Fig. 11. Nr. 31.4.2.2158b
Fig. 12. Nr. 31.4.2.2204a
Fig. 13. Nr. 31.4.2.1263
Fig. 14. Nr. 31.4.2.4023a
Fig. 15. Nr. 31.4.2.4303a
Fig. 16. Nr. 31.4.2.1260
Fig. 17. upper part with a prominent bud Nr. 31.4.2.5687
Fig. 18. Nr. 31.4.2.2944
Figs 19–20 Taxodium dubium, foliage twigs with slender needle-like leaves
Fig. 19. complete, Nr. 31.4.2.4137a
Fig. 20. Nr. 31.4.2.1865b
Fig. 21. Gymnospermae, fam. et gen. et sp. indet. leafy shoot, Nr. 31.4.2.4290b
Fig. 22. Taxodium dubium, close up of needle-like inorganic replica, SEM, Nr. 31.4.2.2204a detail
Fig. 23. Taxodium dubium, close up, Nr. 31.4.2.5687 detail
PLATE X
Palaeoflora of Pitsidia, Crete

Figs 1–12 *Pinus pitsidiensis* sp. nov., dwarf shoots and needles

Fig. 1. fragments of three-needled fascicles co-occurring with an infructescence of *Liquidambar*, Nr. 31.4.2.5430a, scale bar 2 cm

Fig. 2. fragment of a three-needled fascicle, Nr. 31.4.2.6441, scale bar 1 cm

Fig. 3. fragment of a four-needled fascicle, Nr. 31.4.2.3873, scale bar 1 cm

Fig. 4. accumulation of needles, Nr. 31.4.2.2000bi, scale bar 1 cm

Fig. 5. two entire three-needled fascicles, Nr. 31.4.2.3372i,ii, paratype, scale bar 5 cm

Fig. 6. needle apices, Nr. 31.4.2.6082b detail, scale bar 2 mm

Fig. 7. replica of the dwarf shoot, Nr. 31.4.2.3997aii, scale bar 2.5 mm

Fig. 8. replica of the dwarf shoot covered by the basal sheath, Nr. 31.4.2.5329, scale bar 2.5 mm

Fig. 9. adaxial surface of a needle replica, arrows indicate the rows of stomata, Nr. 31.4.2.3698aii detail, paratype, scale bar 0.5 mm

Fig. 10. abaxial surface of a needle replica, the arrows indicate some of the rows of stomata, Nr. 31.4.2.3698aii detail, paratype, scale bar 0.5 mm

Fig. 11. imprint of the keeled abaxial surface of the needle, Nr. 31.4.2.1389 detail, scale bar 1 mm

Fig. 12. imprint of the adaxial surface of the needle, Nr. 31.4.2.1399 detail, scale bar 1 mm
PLATE XI
Palaeoflora of Pitsidia, Crete

Figs 1–5 *Pinus pitsidiensis* sp. nov., needles
Fig. 1. anatomical and epidermal details, resin ducts (black arrows) and rows of stomata (white arrows) are visible, Nr. 31.4.2.5978aiii detail, paratype, SEM, scale bar 0.5 mm
Fig. 2. medial resin duct near the lateral edge (arrow), Nr. 31.4.2.4837b detail, SEM, scale bar 100 μm
Fig. 3. anatomical details, the palisade (white arrows) and the transfusion parenchyma (black-white arrow) are visible, Nr. 31.4.2.3589aii detail, scale bar 0.5 mm
Fig. 4. anatomical details, the epidermis, the palisade parenchyma and three resin ducts (arrows) are visible, Nr. 31.4.2.3698aii detail, paratype, scale bar 0.5 mm
Fig. 5. anatomical details, the epidermis, the palisade parenchyma and three resin ducts are visible (arrows), Nr. 31.4.2.3589aii detail, scale bar 0.5 mm

Figs 6–12 *Pinus pitsidiensis* sp. nov., long shoots
Fig. 6. external surface, scars of the bud scales (type A), Nr. 31.4.2.4191, scale bar 2.5 mm
Fig. 7. external surface, scars of the “sterile” fascicle bracts (type B), Nr. 31.4.2.3146a, scale bar 2.5 mm
Fig. 8. external surface, scars of type C, Nr. 31.4.2.4925a, scale 2.5 mm
Fig. 9. external surface, scars of type C, Nr. 31.4.2.2151i, scale 2.5 mm
Fig. 10. long shoot with three-needled fascicles, some details are lined, the black arrow shows the physically attached fascicle, the black-white arrows show the bud rings, Nr. 31.4.2.2013a, holotype, scale bar 2 cm
Fig. 11. imprint of the internal surface, the needle position is visible (arrows), Nr. 31.4.2.2141b, scale bar 0.5 cm
Fig. 12. external surface, type C scars, the pattern of the spirally arranged rhombi is well distinguished, Nr. 31.4.2.2141a, paratype, scale bar 0.5 cm

Figs 13–16 Long shoots of extant *Pinus* species for comparison
Fig. 13. scars type C on the external surface of *Pinus canariensis*, scale bar 0.5 cm
Fig. 14. scars on the external surface of *Pinus pinea*, black arrows indicating the bud rings (type A scars), black-white arrows the type B scars and white arrows the type C scars, scale bar 0.5 cm
Fig. 15. *Pinus canariensis*, three-needled fascicle with the subtended “fertile” fascicle bract, scale bar 2.5 mm
Fig. 16. *Pinus canariensis* scar of type C, the scar of the “fertile” fascicle bract below and the scar of the three-needled fascicle above, scale bar 2.5 mm
PLATE XII

Palaeoflora of Pitsidia, Crete

Figs 1–25 *Pinus* sp. – fascicle bracts, scale bar 0.5 cm (unless stated otherwise)

Fig. 1. abaxial side, Nr. 31.4.2.4130
Fig. 2. abaxial side, Nr. 31.4.2.6128a
Fig. 3. abaxial side, Nr. 31.4.2.1432
Fig. 4. abaxial side, Nr. 31.4.2.4654bi
Fig. 5. abaxial side, Nr. 31.4.2.2398i
Fig. 6. abaxial side, arrow indicating the ciliate margin, Nr. 31.4.2.5065
Fig. 7. abaxial side, Nr. 31.4.2.5906
Fig. 8. abaxial side, Nr. 31.4.2.4205
Fig. 9. abaxial side, arrow indicating the co-occurrence with a *Pinus* sp. 1 – pollen cone microsporophyll, Nr. 31.4.2.3718
Fig. 10. abaxial side, Nr. 31.4.2.3482bii
Fig. 11. abaxial side, folded, Nr. 31.4.2.1610, scale bar 2.5 mm
Fig. 12. abaxial side, folded, Nr. 31.4.2.3979i, scale bar 2.5 mm
Fig. 13. abaxial side, folded, Nr. 31.4.2.1466, scale bar 2.5 mm
Fig. 14. lateral view, Nr. 31.4.2.5759a
Fig. 15. lateral view, Nr. 31.4.2.6406op
Fig. 16. lateral view, Nr. 31.4.2.4919
Fig. 17. lateral view, Nr. 31.4.2.6215i
Fig. 18. six fascicle bracts spirally attached on a fragment of a long shoot, Nr. 31.4.2.7032a, scale bar 2.5 mm
Fig. 19. cross-section of a bract replica, Nr. 31.4.2.2496opii detail
Fig. 20. bract with rounded apex, Nr. 31.4.2.6598, scale bar 2.5 mm
Fig. 21. bract with rounded apex, Nr. 31.4.2.8054, scale bar 2.5 mm
Fig. 22. bract with rounded apex, Nr. 31.4.2.5064, scale bar 2.5 mm
Fig. 23. bract with rounded apex, Nr. 31.4.2.5030, scale bar 2.5 mm
Fig. 24. bract replica, adaxial view, note the fine longitudinal striation, Nr. 31.4.2.1234, scale bar 2.5 mm
Fig. 25. pulvinous abaxial surface with inconspicuous fine striation, Nr. 31.4.2.5455 detail, scale bar 1 mm

Figs 26–29 Fascicle bracts of extant *Pinus*

Fig. 26. bract of *Pinus canariensis*, adaxial side, scale bar 0.5 cm
Fig. 27. gradual extension of *Pinus canariensis* bract in the water body, scale bar 0.5 cm
Fig. 28. long shoot of *Pinus brutia* with the remaining bases of the bracts, scale bar 1 cm
Fig. 29. long shoot of *Pinus canariensis* with curled “sterile” and “fertile” bracts, arrow indicating the bud ring, scale bar 1 cm
PLATE XIII
Palaeoflora of Pitsidia, Crete

Figs 1–7 *Pinus* sp. 1 (subgen. *Pinus*) – ovulate cone scales, scale bar 1 cm (unless stated otherwise)

Fig. 1. dorsal side, Nr. 31.4.2.7012a
Fig. 2. Ventral side with traces of two winged seeds, Nr. 31.4.2.7012b
Fig. 3. dorsal side, the margins of the scale, the apophysis and umbo as well as the keels are lined, Nr. 31.4.2.7016b
Fig. 4. ventral side, the traces of two winged seeds, a fully developed on the left and an underdeveloped one on the right, are lined, Nr. 31.4.2.7018a
Fig. 5. entire replica, dorsal view, Nr. 31.4.2.1262c, scale bar 0.5 cm
Fig. 6. ventral side, traces of two winged seeds hardly visible, Nr. 31.4.2.1262b, scale bar 0.5 cm
Fig. 7. silicon replica of the apophysis area, margins of the apophysis and umbo are lined, Nr. 31.4.2.7012a, scale bar 2.5 mm

Figs 8–11 *Pinus* sp. 2 (subgen. *Strobus*) – ovulate cone scales, Nr. 31.4.2.7017, scale bar 0.5 cm.

Figs 9–12 *Pinus* sp. 1 – fully developed seeds, scale bar 0.5 cm
Fig. 9. entire, Nr. 31.4.2.5108a
Fig. 10. Nr. 31.4.2.4138
Fig. 11. Nr. 31.4.2.5109a
Fig. 12. with damage at the seed body area, Nr. 31.4.2.6249a

Figs 13–18 *Pinus* sp. – underdeveloped seeds, scale bar 2.5 mm (unless stated otherwise)
Fig. 13. entire, Nr. 31.4.2.3307, scale bar 0.5 cm
Fig. 14. Nr. 31.4.2.2183a
Fig. 15. Nr. 31.4.2.1715a
Fig. 16. Nr. 31.4.2.1586i
Fig. 17. Nr. 31.4.2.6590
Fig. 18. Nr. 31.4.2.3886b

Figs 19–20 Comparison of an underdeveloped seeds, scale bar 2.5 mm
Fig. 19. *Pinus canariensis*, underdeveloped seed
Fig. 20. *Pinus* sp. – underdeveloped seed, Nr. 31.4.2.2183a detail

Figs 21–22 Comparison of an underdeveloped seeds, scale bar 2.5 mm
Fig. 21. *Pinus brutia*, underdeveloped seed
Fig. 22. *Pinus* sp. – underdeveloped seed, Nr. 31.4.2.1584i detail

Figs 23–24 *Pinus* sp. 2 – fully developed seeds, scale bar 2.5 mm
Fig. 23. Nr. 31.4.2.4537a
Fig. 24. Nr. 31.4.2.8241ai

Fig. 25. winged seed of *Pinus canariensis*; scale bar 5 mm
PLATE XIV
Palaeoflora of Pitsidia, Crete

Figs 1–13 Pinus sp. 1 – pollen cones, scale bar 0.5 cm (unless stated otherwise)
Fig. 1. entire, Nr. 31.4.2.1274bi
Fig. 2. entire, Nr. 31.4.2.8234
Fig. 3. entire, Nr. 31.4.2.5308bi
Fig. 4. entire, Nr. 31.4.2.2369ai
Fig. 5. almost entire, Nr. 31.4.2.6185a
Fig. 6. bare axis with sterile bracts proximally, Nr. 31.4.2.2524ii
Fig. 7. fragment, Nr. 31.4.2.1821bi
Fig. 8. close up on the vein course of the peltum surface, Nr. 31.4.2.4626bi detail, scale bar 0.1 mm
Fig. 9. microsporophyll, dorsal view, Nr. 31.4.2.8241a detail, scale bar 1 mm
Fig. 10. microsporophyll, ventral view, Nr. 31.4.2.3074b detail, scale bar 1 mm
Fig. 11. Peltum of the microsporophyll, Nr. 31.4.2.2678ii detail
Fig. 12. close up on the sterile bracts of the cone axis, Nr. 31.4.2.1274bi detail, scale bar 1 mm
Fig. 13. attached microsporophylls, close up, Nr. 31.4.2.8241a detail, scale bar 1 mm
Figs 14–18 Pinus sp. 2 – pollen cones, scale bar 2.5 mm (unless stated otherwise)
Fig. 14. entire, Nr. 31.4.2.8236
Fig. 15. entire, Nr. 31.4.2.5179b
Fig. 16. entire, Nr. 31.4.2.323
Fig. 17. close up on the sterile bracts of the cone axis, Nr. 31.4.2.6204 detail, scale bar 1 mm
Fig. 18. attached microsporophylls, close up, Nr. 31.4.2.6204 detail, scale bar 1 mm
PLATE XV
Palaeoflora of Pitsidia, Crete
Figs 1–12 Pinus sp. – bud scales, scale bar 0.5 cm
Fig. 1. two, closely spaced, Nr. 31.4.2.5425
Fig. 2. Nr. 31.4.2.2966
Fig. 3. Nr. 31.4.2.5583
Fig. 4. Nr. 31.4.2.4375
Fig. 5. Nr. 31.4.2.5061b
Fig. 6. Nr. 31.4.2.5146i
Fig. 7. Nr. 31.4.2.6246
Fig. 8. Nr. 31.4.2.4117
Fig. 9. lateral view, Nr. 31.4.2.6338
Fig. 10. Nr. 31.4.2.5538a
Fig. 11. Nr. 31.4.2.4247
Fig. 12. Nr. 31.4.2.1551i
Figs 13–15 Pinus sp., five-needled fascicles, scale bar 2 cm
Fig. 13. Nr. 31.4.2.4659ai
Fig. 14. co-occurring with a needle fragment of P. pitsidiensis (arrow), Nr. 31.4.2.2940ai
Fig. 15. Nr. 31.4.2.2820a
Fig. 16. Pinus sp. – two-needled fascicle, Nr. 31.4.2.2871, scale bar 2 cm
Fig. 17. three-needled fascicle of Pinus from Prassas (northern part of central Crete, Lower Pleistocene), Nr. 30.1.2.181, scale bar 2 cm
Fig. 18. three-needled fascicle of Pinus from Vrysses (west Crete, Upper Miocene), Nr. 32.1.2.355a, scale bar 3 cm
PLATE XVI
Palaeoflora of Pitsidia, Crete

Figs 1–8 Pine co-occurring parts/organs, scale bar 0.5 cm (unless stated otherwise)
Fig. 1. needles of *Pinus pitsidiensis* secondarily fragmented by sediment slumping, arrows indicate the relative movement, Nr. 31.4.2.3247i detail, scale bar 2.5 mm
Fig. 2. three-needled fascicle of *Pinus pitsidiensis* co-occurring with a leaf fragment of *Myrica lignitum*, Nr. 31.4.2.6106a, scale bar 2 cm
Fig. 3. three-needled fascicle of *Pinus pitsidiensis* co-occurring with a leaf base of *Myrica lignitum*, Nr. 31.4.2.1153, scale bar 2 cm
Fig. 4. pollen cone of *Pinus* sp. 1 accompanied by isolated cone scales (arrows), Nr. 31.4.2.8241a
Fig. 5. co-occurrence of winged seed of *Pinus* and three-needled fascicle of *Pinus pitsidiensis*, Nr. 31.4.2.1584
Fig. 6. co-occurring fragments of needle and branchlet of *Pinus pitsidiensis* (a, b), winged seed (c) and fascicle bract (d), Nr. 31.4.2.6437aop
Fig. 7. needles of *Pinus pitsidiensis* co-occurring with a fascicle bract (black arrow) and a bud scale of *Pinus* (black-white arrow), Nr. 31.4.2.4198
Fig. 8. three-needled fascicle of *Pinus pitsidiensis* and bud scale of *Pinus* co-occurrence, Nr. 31.4.2.3705a

Figs 9–17 Anatomy of coalified wood fragment, SEM, Nr. 31.4.2.7011
Fig. 9. growth ring and axial resin canals, transverse section
Fig. 10. gradual transition from early to latewood, transverse section
Fig. 11. normal axial intercellular resin canals, transverse section
Fig. 12. latewood axial tracheids and radial parenchyma, transverse section
Fig. 13. cross field of radial parenchyma and axial tracheids, radial section
Fig. 14. pitting in radial walls of earlywood tracheids, radial section
Fig. 15. cross-field pitting, radial section
Fig. 16. uniseriate rays, tangential section
Fig. 17. horizontal resin canal, tangential section
PLATE XVII
Palaeoflora of Pitsidia, Crete, scale bar 2 cm (unless stated otherwise)

Figs 1–11 Daphnogene polymorpha, foliage
Fig. 1. complete, Nr. 31.4.2.5806ai
Fig. 2. complete, Nr. 31.4.2.5466aiv
Fig. 3. Nr. 31.4.2.4538ai
Fig. 4. Nr. 31.4.2.1863b
Fig. 5. almost complete, Nr. 31.4.2.8208bi
Fig. 6. almost complete, Nr. 31.4.2.4102b
Fig. 7. Nr. 31.4.2.3737b
Fig. 8. Nr. 31.4.2.4364a
Fig. 9. Nr. 31.4.2.5785biv
Fig. 10. course of inner and minor secondary veins, Nr. 31.4.2.6537 detail, scale bar 8 mm
Fig. 11. inner secondaries and regular network of higher order veins, Nr. 31.4.2.1166 detail, scale bar 3 mm
Fig. 12–14 Lindera ovata, foliage
Fig. 12. complete, Nr. 31.4.2.3957b
Fig. 13. almost complete, Nr. 31.4.2.6925
Fig. 14. almost complete with well preserved venation pattern, Nr. 31.4.2.3956a
PLATE XVIII
Palaeoflora of Pitsidia, Crete, scale bar 2 cm
Fig. 1. *Daphnogene polymorpha*, foliage, large incomplete leaf, Nr. 31.4.2.5811ai
Fig. 2. *Dicotylophyllum* sp. 13, foliage, Nr. 31.4.2.4250a
Figs 3–6 *Populus populina*, foliage
Fig. 3. almost complete leaf, Nr. 31.4.2.349b
Fig. 4. counterpart of the sample above, published in ZIDIANAKIS et al. 2010, Nr. 31.4.2.349a
Fig. 5. almost complete small leaf, Nr. 31.4.2.340b
Fig. 6. incomplete leaf, Nr. 31.4.2.1140
Figs 7–8 *Rosa* sp., foliage
Fig. 7. lateral leaflet, Nr. 31.4.2.6166a
Fig. 8. terminal leaflet, Nr. 31.4.2.1500a
PLATE XIX
Palaeoflora of Pitsidia, Crete, scale bar 1 cm (unless stated otherwise)

Figs 1–10 *Liquidambar europaea*, foliage
Fig. 1. almost complete, Nr. 31.4.2.6001
Fig. 2. incomplete, Nr. 31.4.2.5796a
Fig. 3. leaf fragment, Nr. 31.4.2.8260
Fig. 4. leaf fragment, Nr. 31.4.2.5808a
Fig. 5. incomplete with well preserved margin and venation details, Nr. 31.4.2.3747
Fig. 6. with well developed lobes, Nr. 31.4.2.6507
Fig. 7. leaf fragment, Nr. 31.4.2.5278
Fig. 8. leaf lobe, Nr. 31.4.2.6962i
Fig. 9. with prominent galls, Nr. 31.4.2.276
Fig. 10. close up, showing marginal teeth and venation pattern, Nr. 31.4.2.3747 detail,
scale bar 3 mm
PLATE X
Palaeoflora of Pitsidia, Crete, scale bar 1cm (unless stated otherwise)
Figs 1–14 Liquidambar europaea, fruiting heads
Fig. 1. with bilocular capsules arranged densely, Nr. 31.4.2.820
Fig. 2. honeycomb-like structures, on the external surface, Nr. 31.4.2.2868a
Fig. 3. numerous styles crowning the fructification, Nr. 31.4.2.6184a
Fig. 4. with long peduncle, Nr. 31.4.2.3500
Fig. 5. two fruiting heads closely arranged, Nr. 31.4.2.4028ci
Fig. 6. honeycomb-like structures, Nr. 31.4.2.2375b
Fig. 7. with well preserved central axis, Nr. 31.4.2.2155a
Fig. 8. honeycomb-like structures, Nr. 31.4.2.2155b
Fig. 9. impression, preserved in coarser sediments, Nr. 31.4.2.1034b
Fig. 10. fragmentary head, Nr. 31.4.2.3047bi
Fig. 11. fragmentary head with well preserved capsules, Nr. 31.4.2.5610
Fig. 12. with complete styles, Nr. 31.4.2.5798
Fig. 13. with broken styles, close up, Nr. 31.4.2.6184a detail, scale bar 4 mm
Fig. 14. with numerous complete styles, Nr. 31.4.2.5935bi, scale bar 4 mm
PLATE XXI

Palaeoflora of Pitsidia, Crete, scale bar 1 cm (unless stated otherwise)

Figs 1–13 *Liquidambar europaea*, details of fruiting heads

Fig. 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

Fig. 2. capsule, the two carpels (black arrows), ventral seem (black-white arrow), locules (white arrows) are lined, Nr. 31.4.2.5610 detail, scale bar 2.5 mm

Fig. 3. basal part of carpel, notice the carpel wall with fine transverse ridges (black arrow) and the seed (white arrow), Nr. 31.4.2.820 detail, scale bar 1 mm

Fig. 4. two adjacent persistent styles, Nr. 31.4.2.5935ai detail, scale bar 1.5 mm

Fig. 5. persistent style, Nr. 31.4.2.5935bi, scale bar 1.5 mm

Fig. 6. Persistent style, Nr. 31.4.2.6184a detail, scale bar 1.5 mm

Fig. 7. Persistent style, Nr. 31.4.2.5798 detail, scale bar 1.5 mm

Fig. 8. Persistent style, Nr. 31.4.2.5798 detail, scale bar 1.5 mm

Fig. 9. smooth, slight thickened area between capsules (peripheral rim), close up, Nr. 31.4.2.278 detail, scale bar 1 mm

Fig. 10. scars of the capsule bases on the central axis of the infructescence, Nr. 31.4.2.4573 detail, scale bar 2 mm

Fig. 11. fine transverse ridges structure of the carpel wall, Nr. 31.4.2.4573 detail, scale bar 0.5 mm

Fig. 12. isolated ?styles detected in the sediment, Nr. 31.4.2.881a, scale bar 4 mm

Fig. 13. isolated capsule detected in the sediment, Nr. 31.4.2.6209, scale bar 3 mm
PLATE XXII

Palaeoflora of Pitsidia, Crete

Figs 1–9 Podocarpium podocarpum, foliage (leaflets), scale bar 1.25 cm
Fig. 1. complete, Nr. 31.4.2.4016
Fig. 2. complete, Nr. 31.4.2.5215opi
Fig. 3. complete, Nr. 31.4.2.8180op
Fig. 4. lamina base, Nr. 31.4.2.2705aii
Fig. 5. lamina base, Nr. 31.4.2.8244iii
Fig. 6. lamina base, Nr. 31.4.2.4543bi
Fig. 7. complete, Nr. 31.4.2.5552i
Fig. 8. complete, Nr. 31.4.2.3801a
Fig. 9. counterpart of the above, Nr. 31.4.2.3801b,
Figs 10–21 Podocarpium podocarpum, fruits (pods), scale bar 2 cm (unless stated otherwise)
Fig. 10. complete, Nr. 31.4.2. 6478ai
Fig. 11. complete, Nr. 31.4.2.4833i
Fig. 12. complete, Nr. 31.4.2.3968a
Fig. 13. complete, Nr. 31.4.2.4495a
Fig. 14. Nr. 31.4.2.5600b
Fig. 15. Nr. 31.4.2.5884ai
Fig. 16. Nr. 31.4.2.3597a
Fig. 17. close up, suture (black arrow), style remnant (white arrow), funiculus (black-white arrow) are visible, Nr. 31.4.2.6662a detail, scale bar 1 cm
Fig. 18. close up, suture (black arrow), style remnant (white arrow), (black-white arrow) funiculus are visible, Nr. 31.4.2.5600a detail, scale bar 1 cm
Fig. 19. double seemed margin of the valve, Nr 31.4.2.4706a detail, scale bar 2 mm
Fig. 20. swollen base of the stipe, Nr. 31.4.2.3968a detail, scale bar 4 mm
Fig. 21. mechanical damage at the stipe-valve connection, Nr. 31.4.2.4833i detail, scale bar 7 mm
PLATE XXIII  
Palaeoflora of Pitsidia, Crete, scale bar 2 cm (unless stated otherwise)

Figs 1–5 Betulaceae gen. et sp. indet., foliage:
   Fig. 1. Nr. 31.4.2.5261
   Fig. 2. with symmetric base and simply serrate margin, Nr. 31.4.2.8266
   Fig. 3. Nr. 31.4.2.6591
   Fig. 4. with weakly double serrate margin Nr .31.4.2.6206b
   Fig. 5. Nr. 31.4.2.6965b
   Fig. 6. *Ulmus* cf. *plurinervia* with strongly asymmetric base and double serrate margin, Nr. 31.4.2.3950ai
   Fig. 7. *Zelkova zelkovifolia* foliage, Nr. 31.4.2.1663bi
   Fig. 8. *Leguminosites* sp. 2, leaflet, Nr. 31.4.2.207 (Fig. 3j in ZIDIANAKIS et al. 2010)
   Fig. 9. *Leguminosites* sp. 1, leaflet, Nr. 31.4.2.5295a
   Fig. 10. *Ulmus* sp., samara, Nr. 31.4.2.4150a, the seed, wing margin and preserved venation are lined, scale bar 5 mm
   Fig. 11. Betulaceae gen. et sp. indet., simply serrate margin, Nr. 31.4.2.6206b detail, scale bar 5 mm
   Fig. 12. *Ulmus* cf. *plurinervia*, double serrate margin, Nr. 31.4.2.3950b detail, scale bar 5 mm
   Fig. 13. *Zelkova zelkovifolia* the tooth shape and the 2nd, 3rd and 4th order venation pattern are visible, Nr. 31.4.2.1663ai detail, scale bar 5 mm
   Fig. 14. *Ulmus* cf. *plurinervia*, double serrate margin, close up, Nr. 31.4.2.3950bi detail, scale bar 2.5 mm
PLATE XXIV

Palaeoflora of Pitsidia, Crete, scale bar 2 cm:

Figs 1–13 *Quercus pseudocastanea*, foliage, typical leaf form
Fig. 1. complete, Nr. 31.4.2.4786a
Fig. 2. almost complete, Nr. 31.4.2.4820ai
Fig. 3. almost complete, Nr. 31.4.2.8191a
Fig. 4. almost complete, Nr. 31.4.2.4280ai
Fig. 5. Nr. 31.4.2.8244i
Fig. 6. damaged by sediment fracturing, Nr. 31.4.2.4011
Fig. 7. complete, Nr. 31.4.2.5785bi
Fig. 8. small, Nr. 31.4.2.5945i
Fig. 9. Nr. 31.4.2.4980ai
Fig. 10. leaf base, Nr. 31.4.2.6933a
Fig. 11. leaf base, Nr. 31.4.2.1139
Fig. 12. complete, Nr. 31.4.2.322i (Fig. 2j in ZIDIANAKIS et al., 2010)
Fig. 13. complete, Nr. 31.4.2.1419α

Figs 14–20 *Quercus pseudocastanea*, foliage, “narrow leaf form”
Fig. 14. complete leaf, Nr 31.4.2.4641b
Fig. 15. Nr. 31.4.2.5948a
Fig. 16. Nr. 31.4.2.5681ai
Fig. 17. Nr. 31.4.2.4564b
Fig. 18. Nr. 31.4.2.1138i
Fig. 19. Nr. 31.4.2.2137
Fig. 20. co-occurring with a *M. lignitum* leaf, Nr. 31.4.2.1405ii
PLATE XXV

Palaeoflora of Pitsidia, Crete

Figs 1–23 Quercus cf. kubinyii, foliage, scale bar 2 cm (unless stated otherwise)

Fig. 1. Nr. 31.4.2.646a
Fig. 2. Nr. 31.4.2.6070a
Fig. 3. Nr. 31.4.2.2705aop
Fig. 4. Nr. 31.4.2.2426a
Fig. 5. Nr. 31.4.2.4360bi
Fig. 6. Nr. 31.4.2.3806ai
Fig. 7. Nr. 31.4.2.18176bi
Fig. 8. complete, Nr. 31.4.2.6938ai
Fig. 9. Nr. 31.4.2.007
Fig. 10. Nr. 31.4.2.971a
Fig. 11. Nr. 31.4.2.2926b
Fig. 12. Nr. 31.4.2.7037a
Fig. 13. complete, Nr. 31.4.2.1416a
Fig. 14. ?extreme leaf form, Nr. 31.4.2.8238
Fig. 15. Nr. 31.4.2.8197
Fig. 16. complete, Nr. 31.4.2.8265
Fig. 17. Nr. 31.4.2.2914b
Fig. 18. with bristle teeth, Nr. 31.4.2.3828
Fig. 19. note the bristle-tipped tooth at the upper part of the lamina (arrow), Nr. 31.4.2.1420a
Fig. 20. sharp triangular teeth, Nr. 31.4.2.6070 detail, scale bar 5 mm
Fig. 21. sharp triangular teeth, Nr. 31.4.2.4646a detail, scale bar 5 mm
Fig. 22. bristle teeth, Nr. 31.4.2.3828 detail, scale bar 5 mm
Fig. 23. pattern of third and fourth order venation, Nr. 31.4.2.1420a detail, scale bar 5 mm
PLATE XXVI
Palaeoflora of Pitsidia, Crete, scale bar 1.5 cm

Figs 1–3 *Quercus mediterranea*, foliage
Fig. 1. ?Nr. 31.4.2.271a
Fig. 2. Nr. 31.4.2.272 (Fig. 2m in ZIDIANAKIS et al., 2010)
Fig. 3. small leaf, Nr. 31.4.2.5183a

Fig. 4. *Fagus gussoni*, foliage Nr. 31.4.2.7038

Figs 5–8 *Myrica* vegetative and fertile remains
Fig. 5. *Myrica* fruit (arrow) - leaf co-occurrence, Nr. 31.4.2.2149a
Fig. 6. *Myrica* male catkin - leaf co-occurrence, Nr. 31.4.2.5694

Fig. 7. infructescence fragment with fruits of *Myrica ceriferiformis* and closely spaced isolated fruits, Nr. 31.4.2.4607b

Fig. 8. *Myrica* leaf and *Pinus* needle damaged by sediment fracturing, Nr. 31.4.2.3810
PLATE XXVII

Palaeoflora of Pitsidia, Crete

Figs 1–11 Leaf form variation of *Myrica lignitum*, scale bar 2 cm
Fig. 1. Nr. 31.4.2.6031i
Fig. 2. Nr. 31.4.2.2350
Fig. 3. Nr. 31.4.2.803a, 31.4.2.803bi (counterparts, synthesis)
Fig. 4. Nr. 31.4.2.5447ai
Fig. 5. Nr. 31.4.2.2705ai
Fig. 6. Nr. 31.4.2.8126i
Fig. 7. Nr. 31.4.2.6928b
Fig. 8. Nr. 31.4.2.6942b
Fig. 9. Nr. 31.4.2.2113
Fig. 10. Nr. 31.4.2.4606ai
Fig. 11. deeply lobed margin, Nr. 31.4.2.8240

Fig. 12. fragment of an inorganic leaf replica of *M. lignitum*, adaxial surface, Nr. 31.4.2.3525op, scale bar 7 mm

Figs 13–14 Petioles of *M. lignitum*, scale bar 2.5 mm
Fig. 13. Nr. 31.4.2.4164bv detail
Fig. 14. Nr. 31.4.2.2661ii detail

Figs 15–17 Tooth venation of *M. lignitum*, scale bar 2.5 mm
Fig. 15. small acute tooth, Nr. 31.4.2.4407i detail
Fig. 16. obtuse tooth, Nr. 31.4.2.3826 detail
Fig. 17. obtuse tooth, Nr. 31.4.2.3741ai detail

Figs 18–22 Surface of *M. lignitum* leaf with glands
Fig. 18. adaxial side with 24 glands in 1 mm$^2$ near the apex of the lamina, the glands are marked with black spots, Nr. 31.4.2.4320b detail, scale bar 0.65 mm
Fig. 19. abaxial side with 33 glands in 1 mm$^2$ near the apex of the lamina, the glands are marked with black spots, Nr. 31.4.2.4320a detail, scale bar 0.65 mm
Fig. 20. adaxial side with 119 glands in 4 mm$^2$ (light green square), the glands are marked with green spots, Nr. 31.4.2.3955 detail, scale bar 1 mm
Fig. 21. fine venation and glands, adaxial side, SEM, Nr. 31.4.2.3955 detail, scale bar 400 μm
Fig. 22. gland, adaxial side, SEM, Nr. 31.4.2.3955 detail, scale bar 100 μm
PLATE XXVIII
Palaeoflora of Pitsidia, Crete
Figs 1–9 Fruits of *Myrica ceriferiformis*, scale bar 2 mm (unless stated otherwise)
Fig. 1. imprint, Nr. 31.4.2.5889
Fig. 2. replica, Nr. 31.4.2.2912a
Fig. 3. cross section showing exocarp, mesocarp and central pyrina, Nr. 31.4.2.4273bi
Fig. 4. cross section showing exocarp, mesocarp and central rather broad pyrina, Nr. 31.4.2.7035
Fig. 5. cross section, the arrow indicates the dehiscence seam on the pyrina surface, Nr. 31.4.2.4617
Fig. 6. attached to the infructescence axis, the arrow indicates the projection at the fruit apex, Nr. 31.4.2.5977ii detail
Fig. 7. drupe with a distinct hole which is the cast of the connection tissue of the fruit with the infructescence axis, Nr. 31.4.2.3476opi
Fig. 8. irregular net formed on the fruit surface by the external protuberances, Nr. 31.4.2.8049
Fig. 9. external surface of the fruit, the internal cancellous structure of the protuberances is visible, Nr. 31.4.2.4607avi detail, scale bar 0.5 mm
Figs 10–17 Infructescence remains with *M. ceriferiformis* fruits, scale bar 5 mm
Fig. 10. basal part of an infructescence with attached fruits, Nr. 31.4.2.4148ai
Fig. 11. entire, extreme form (curled) of an infructescence, Nr. 31.4.2.8103b
Fig. 12. cross view, the hole in the centre constitutes the cast of the axis, Nr. 31.4.2.5745a
Fig. 13. basal part of an axis with attached fruits, Nr. 31.4.2.7033a
Fig. 14. basal part of an axis with two fruits attached, Nr. 31.4.2.6619
Fig. 15. basal part of an infructescence with attached fruits, a bract (arrow) and the scars of detached fruits are well visible, Nr. 31.4.2.5977ii
Fig. 16. counterpart, Nr. 31.4.2.5976aopii
Fig. 17. complete axis with a few tiny (probably incomplete) fruits, Nr. 31.4.2.3617i
PLATE XXIX
Palaeoflora of Pitsidia, Crete

Figs 1–9 Myrica cf. goeppertii entire or almost entire male catkins, scale bar 5 mm
Fig. 1. Nr. 31.4.2.1934
Fig. 2. severely bent, Nr. 31.4.2.2860a
Fig. 3. Nr. 31.4.2.2342
Fig. 4. Nr. 31.4.2.2549b
Fig. 5. Nr. 31.4.2.5694ii
Fig. 6. Nr. 31.4.2.8112i
Fig. 7. Nr. 31.4.2.6623b
Fig. 8. very small, Nr. 31.4.2.3896a
Fig. 9. very small, Nr. 31.4.2.2599

Figs 10–16. M. cf. goeppertii male catkins, close-up, scale bar 2 mm
Fig. 10. ross section, adaxial side of the bracts, Nr. 31.4.2.5028i
Fig. 11. cross section, arrangement of the anthers, Nr. 31.4.2.5315b
Fig. 12. arrangement of the florets at the apical part, Nr. 31.4.2.1304 detail
Fig. 13. immature fragment, Nr. 31.4.2.2917i
Fig. 14. mature fragment, Nr. 31.4.2.5970
Fig. 15. mature fragment, Nr. 31.4.2.5363bii
Fig. 16. mature fragment, Nr. 31.4.2.5300bi
PLATE XXX
Palaeoflora of Pitsidia, Crete

Figs 1–6 *M. cf. goeppertii* florets, scale bar 1 mm
Fig. 1. immature floret, adaxial view, Nr. 31.4.2.6305ii detail
Fig. 2. immature floret, anther arrangement below the floret bract, Nr. 31.4.2.6811 detail
Fig. 3. mature floret (lateral view) consisting of a prominent floret bract (arrowhead) and the axillary stamens, the branched staminal column (arrow) is clearly shorter than the floret bract, Nr. 31.4.2.4416 detail
Fig. 4. mature stamens, their filaments are fused into a branched staminal column (arrow), Nr. 31.4.2.5363bii detail
Fig. 5. mature stamens, their filaments are fused into a branched staminal column (arrow), Nr. 31.4.2.5363aii detail
Fig. 6. floret bract, no marginal cilia are visible, Nr. 31.4.2.5028i detail
Fig. 7. a floret of the extant *M. cerifera* L., the branched staminal column (arrow) is clearly longer than the floret bract (arrowhead), the marginal cilia of the bract are visible, scale bar 1 mm
Fig. 8. immature floret of *M. cf. goeppertii*, lateral view, Nr. 31.4.2.5970 detail, scale bar 0.5 mm
Figs 9–12 Pollen sacs of *M. cf. goeppertii* florets, scale bar 0.5 mm (unless stated otherwise)
Fig. 9. dehiscent sacs, external surface (epidermis), Nr. 31.4.2.5944b detail
Fig. 10. dehiscent sacs, internal surface, Nr. 31.4.2.1664 detail
Fig. 11. structure of the pollen sac. The arrow indicates the external layer (epidermis), SEM, Nr. 31.4.2.8191aopii detail, scale bar 0.2 mm
Fig. 12. pattern on the external surface of the pollen sac, close-up, SEM, Nr. 31.4.2.8191aopii detail, scale bar 40 μm
PLATE XXXI
Palaeoflora of Pitsidia, Crete, scale bar 2 cm (unless stated otherwise)

Figs 1–2 Carya sp. terminal leaflets
Fig. 1. physically attached on the leaf rachis, Nr. 31.4.2.6615a
Fig. 2. Nr. 31.4.2.471 (Fig. 3c in ZIDIANAKIS et al., 2010)

Figs 3–13 Carya sp. lateral leaflets
Fig. 3. Nr. 31.4.2.972b
Fig. 4. Nr. 31.4.2.6972
Fig. 5. Nr. 31.4.2.4149bi
Fig. 6. Nr. 31.4.2.206 (Fig. 2o in ZIDIANAKIS et al., 2010)
Fig. 7. Nr. 31.4.2.5466cvi
Fig. 8. Nr. 31.4.2.5741a
Fig. 9. Nr. 31.4.2.6479i
Fig. 10. asymmetric lamina base, Nr. 31.4.2.5267b
Fig. 11. two leaflets, Nr. 31.4.2.8257i
Fig. 12. Nr. 31.4.2.5900ai
Fig. 13. venation pattern close to the margin, Nr. 31.4.2.5741a detail, scale bar 1 cm
PLATE XXXII
Palaeoflora of Pitsidia, Crete, scale bar 2 cm (unless stated otherwise)

Fig. 1. *Pterocarya* sp. winged fruit, Nr. 31.4.2.3000, scale bar 7.5 mm
Fig. 2. *Fagus gussonii*, foliage, Nr. 31.4.2.6125iii
Figs 3–4 *Quercus mediterranea*, foliage
Fig. 3. Nr. 31.4.2.2159bii
Fig. 4. Nr. 31.4.2.5812a
Fig. 5. *Quercus cf. kubinyii*, foliage, Nr. 31.4.2.4189ai
Fig. 6. *Salix* sp., foliage, Nr. 31.4.2.1125aiv
Figs 7–8 *Populus* sp. foliage
Fig. 7. Nr. 31.4.2.8198i
Fig. 8. venation details, Nr. 31.4.2.8198i detail, scale bar 1 cm
Fig. 9. *Quercus mediterranea*, marginal tooth, Nr. 31.4.2.5812a detail, scale bar 2 mm
Fig. 10. *Quercus cf. kubinyii*, marginal teeth, Nr. 31.4.2.4189b detail, scale bar 5 mm
PLATE XXXIII
Palaeoflora of Pitsidia, Crete, scale bar 2 cm (unless stated otherwise)

Figs 1–8 *Populus populina* foliage

Fig. 1. typical leaf type, Nr. 31.4.2.6131a
Fig. 2. three-veined, Nr. 31.4.2.3027ai
Fig. 3. Nr. 31.4.2.1178b
Fig. 4. Nr. 31.4.2.6948ai
Fig. 5. Nr. 31.4.2.6111a
Fig. 6. Nr. 31.4.2.2489a
Fig. 7. venation close to the margin, Nr. 31.4.2.3027b detail, scale bar 1 cm
Fig. 8. venation texture, Nr. 31.4.2.6111b detail, scale bar 1 cm
PLATE XXXIV
Palaeoflora of Pitsidia, Crete, scale bar 2 cm
Figs 1–9 *Acer tricuspidatum*, foliage, lobed lamina
Fig. 1. Nr. 31.4.2.4345ai
Fig. 2. Nr. 31.4.2.853bi
Fig. 3. Nr. 31.4.2.6922ai
Fig. 4. ?Nr. 31.4.2.4361
Fig. 5. Nr. 31.4.2.2437a
Fig. 6. Nr. 31.4.2.4129
Fig. 7. Nr. 31.4.2.998a
Fig. 8. Nr. 31.4.2.4099
Fig. 9. Nr. 31.4.2.8247
Figs 10–12 *Acer tricuspidatum*, foliage, tricuspidate lamina
Fig. 10. Nr. 31.4.2.8262i
Fig. 11. Nr. 31.4.2.3496bi
Fig. 12. Nr. 31.4.2.5112ai
PLATE XXXV
Palaeoflora of Pitsidia, Crete

Figs 1–7 Acer integrilobum, foliage, scale bar 2 cm
Fig. 1. complete leaf, Nr. 31.4.2.6103ai
Fig. 2. Nr. 31.4.2.5464ai
Fig. 3. Nr. 31.4.2.211b
Fig. 4. small leaf, Nr. 31.4.2.3627aop
Fig. 5. small leaf, Nr. 31.4.2.1030b
Fig. 6. Nr. 31.4.2.851a
Fig. 7. Nr. 31.4.2.4537ai
Fig. 8. Acer sp. 2, winged fruits, Nr. 31.4.2.1653b, scale bar 1 cm
Figs 9–12 Acer sp. 1, winged fruits, scale bar 1 cm
Fig. 9. Nr. 31.4.2.4390a
Fig. 10. Nr. 31.4.2.5545a
Fig. 11. Nr. 31.4.2.8263
Fig. 12. Nr. 31.4.2.3949ai
PLATE XXXVI
Palaeoflora of Pitsidia, Crete

Figs 1–11 Monocotylophyllum sp. 1, foliage, scale bar 2 cm (unless stated otherwise)
Fig. 1. two basically connected linear leaves, Nr. 31.4.2.1182ai
Fig. 2. linear leaf with sand accumulation close to the base, Nr. 31.4.2.2425a
Fig. 3. mechanically damaged leaf, Nr. 31.4.2.1576ai
Fig. 4. mechanically damaged leaf, Nr. 31.4.2.1748a
Fig. 5. mechanically damaged leaf, Nr. 31.4.2.4959a
Fig. 6. mechanically damaged leaf, Nr. 31.4.2.2368b
Fig. 7. mechanically damaged leaf, Nr. 31.4.2.6576
Fig. 8. sand accumulation, Nr. 31.4.2.2425b detail, scale bar 7.5 mm
Fig. 9. sand accumulation, close up, Nr. 31.4.2.2425b detail, scale bar 3 mm
Fig. 10. damaged leaf, probably by microorganism infection, Nr. 31.4.2.4334a detail, scale bar 1 mm
Fig. 11. globose structures in the mesophyll of the infected leaf, close up, Nr. 31.4.2.4334a detail, scale bar 0.4 mm

Figs 12–15 Monocotylophyllum sp. 2, foliage, scale bar 2 mm
Fig. 12. Nr. 31.4.2.4750i
Fig. 13. Nr. 31.4.2.4955
Fig. 14. Nr. 31.4.2.3198op
Fig. 15. Nr. 31.4.2.4750i detail, scale bar 0.5 mm

Fig. 16. Monocotylophyllum sp. 3, foliage, Nr. 31.4.2.8254, scale bar 2 mm
Fig. 17. Monocotylophyllum sp. 4, foliage, Nr. 31.4.2.1562ai, scale bar 1 cm

Figs 18–20 Monocotylophyllum sp. 5, foliage, scale bar 1 cm
Fig. 18. Nr. 31.4.2.4697biii
Fig. 19. Nr. 31.4.2.4904
Fig. 20. Nr. 31.4.2.4697biii detail, scale bar 0.75 mm
PLATE XXXVII
Palaeoflora of Pitsidia, Crete
Figs 1–4 Monocotylophyllum sp. 2, foliage, coalified, close up, SEM, stomatal rows, substomatal chambers (white arrows) and epidermal elongate, papillose cells (black arrows) are visible, Nr. 31.4.2.4955 detail
Figs 5–13 Dicotylophyllum, foliage, scale bar 1 cm
Fig. 5. Dicotylophyllum sp. 12, Nr. 31.4.2.6987a
Fig. 6. Dicotylophyllum sp. 1, co-occurring with a Myrica lignitum leaf, Nr. 31.4.2.5216
Fig. 7. Dicotylophyllum sp. 2, Nr. 31.4.2.5902b
Fig. 8. ?Lauraceae gen. et sp. indet., Nr. 31.4.2.8115
Fig. 9. Dicotylophyllum sp. 3, Nr. 31.4.2.8255
Fig. 10. Dicotylophyllum sp. 4, Nr. 31.4.2.6997
Fig. 11. Dicotylophyllum sp. 5, Nr. 31.4.2.5306
Fig. 12. Dicotylophyllum sp. 6, Nr. 31.4.2.5929i
Fig. 13. Juglandaceae gen. et sp. indet., Nr. 31.4.2.5901a
PLATE XXXVIII
Palaeoflora of Pitsidia, Crete, scale bar 0.5 cm

Figs 1–5 *Mimosites* sp. leaflets
Fig. 1. Nr. 31.4.2.4389aii
Fig. 2. Nr. 31.4.2.4087bi
Fig. 3. Nr. 31.4.2.4398ai
Fig. 4. Nr. 31.4.2.2371
Fig. 5. with longer lamina, Nr. 31.4.2.5324

Figs 6–9 *Dicotylophyllum* sp. 7, foliage
Fig. 6. Nr. 31.4.2.4699a
Fig. 7. Nr. 31.4.2.4283ii
Fig. 8. Nr. 31.4.2.5650
Fig. 9. Nr. 31.4.2.4502a

Figs 10–13 *Ulmus* cf. *plurinervia*, foliage
Fig. 10. Nr. 31.4.2.8119
Fig. 11. Nr. 31.4.2.5830a
Fig. 12. Nr. 31.4.2.2148a
Fig. 13. Nr. 31.4.2.4557b

Figs 14–16 *Myrica lignitum*, small leaves
Fig. 14. Nr 31.4.2.1273
Fig. 15. Nr 31.4.2.5208
Fig. 16. Nr 31.4.2.1589

Figs 17–18 *Dicotylophyllum* sp. 8, foliage
Fig. 17. Nr. 31.4.2.1269i
Fig. 18. Nr. 31.4.2.4283i

Fig. 19. *Myrica lignitum*, fragment, Nr. 31.4.2.2202

Fig. 20. *Dicotylophyllum* sp. 9, Nr. 31.4.2.3592ii

Fig. 21. *Dicotylophyllum* sp. 10, Nr. 31.4.2.1922

Fig. 22. *Myrica lignitum*, small leaf, Nr. 31.4.2.2136
PLATE XXXIX
Palaeoflora of Pitsidia, Crete, scale bar 1 cm (unless stated otherwise)

Fig. 1. *Dicotylophyllum* sp. 11, foliage, Nr. 31.4.2.5215
Fig. 2. *Acer aegopodifolium*, foliage, Nr. 31.4.2.5697bii
Figs 3–6 *Dicotylophyllum* sp. 11, foliage
Fig. 3. Nr. 31.4.2.8109
Fig. 4. Nr. 31.4.2.4182ai
Fig. 5. Nr. 31.4.2.4651aii
Fig. 6. Nr. 31.4.2.3163b
Fig. 7. cf. *Hydrangea* sp., flower, Nr. 31.4.2.4495aop
Fig. 8. drupe, fam. et. gen. et sp. indet., Nr. 31.4.2.1727ii
Fig. 9. ?*Carpolithus* sp., Nr. 31.4.2.7019
Fig. 10. male inflorescence, fam. et gen. et sp. indet., Nr. 31.4.2.6891
Fig. 11. ?septum of dry fruit, Nr. 31.4.2.5215opii
Figs 12–15 Bud scales, fam. et. gen. et sp. indet.
Fig. 12. type 1, Nr. 31.4.2.8185
Fig. 13. type 1, Nr. 31.4.2.4389aiii
Fig. 14. type 2, Nr. 31.4.2.5823
Fig. 15. type 3, Nr. 31.4.2.3768ai
Fig. 16. male inflorescence close up, Nr. 31.4.2.6891detail, scale bar 4 mm
Fig. 17. ?septum of dry fruit, close up, with subparallel venation, Nr. 31.4.2.5215opii,
scale bar 4 mm
PLATE XL
Palaeoflora of Pitsidia, Crete, scale bar 1 cm (unless stated otherwise)

Figs 1–3 Shoots of gymnosperm origin, fam. et. gen. et sp. indet.
Fig. 1. Nr. 31.4.2.5186
Fig. 2. Nr. 31.4.2.5049ai
Fig. 3. Nr. 31.4.2.6463a

Figs 4–8 Shoots of angiosperm origin, fam. et. gen. et sp. indet.
Fig. 4. alternately arranged scars, Nr. 31.4.2.1163
Fig. 5. with well preserved buds, Nr. 31.4.2.5373b
Fig. 6. alternately arranged scars, Nr. 31.4.2.2283i
Fig. 7. Nr. 31.4.2.4602i
Fig. 8. Nr. 31.4.2.5884ai

Fig. 9. Fragment of wood as inorganic replica, Nr. 31.4.2.1835
Fig. 10. Rhizome, Nr. 31.4.2.2574ai

Figs 11–16 Root remains, fam. et. gen. et sp. indet.
Fig. 11. adventitious system, Nr. 31.4.2.1127
Fig. 12. adventitious system, Nr. 31.4.2.2957
Fig. 13. tap system, Nr. 31.4.2.6666a
Fig. 14. adventitious system, Nr. 31.4.2.3073
Fig. 15. woody fragment, Nr. 31.4.2.2178opii
Fig. 16. woody fragment, Nr. 31.4.2.5472aii

Fig. 17. shoot cross section, pith (p), cork (c) and epidermis (e), Nr. 31.4.2.3295, scale bar 0.75 mm
Fig. 18. Rhizom base with characteristic stirs, Nr. 31.4.2.2574ai detail, scale bar 0.5 cm
PLATE XLI
Palaeofauna of Pitsidia, Crete, scale bar 1 mm (unless stated otherwise)

Figs 1–3 Insect wings, elytra
Fig. 1. in pair, Nr. 31.4.2.5276opi
Fig. 2. in pair, Nr. 31.4.2.1428op
Fig. 3. sole, Nr. 31.4.2.4802ii

Figs 4–8 Mollusc shell remains
Fig. 4. Planorbidae, Nr. 31.4.2.4763
Fig. 5. Planorbidae, Nr. 31.4.2.991ii
Fig. 6. Nr. 31.4.2.5480ii
Fig. 7. Nr. 31.4.2.4164bi

Figs 10–11 Insect remains, scale bar 3.5 mm
Fig. 10. entire insect, Nr. 31.4.2.5487
Fig. 11. isolated wing, Nr. 31.4.2.6536ii

Fig. 12. Ostracod, family Candonidae, Nr. 31.4.2.5536aii, scale bar 0.5 mm
PLATE XLII
Palaeofauna of Pitsidia, Crete

Figs 1–11 Fish bones, scale bar 5 mm (unless stated otherwise)
Fig. 1. operculum, Nr. 31.4.2.2725
Fig. 2. praeperculum, Nr. 31.4.2.2126
Fig. 3. spinal bone, Nr. 31.4.2.6919bop
Fig. 4. Nr. 31.4.2.2041
Fig. 5. Nr .31.4.2.5047
Fig. 6. praeperculum, Nr 31.4.2.4373
Fig. 7. Nr. 31.4.2.886
Fig. 8. jaw with teeth, Nr. 31.4.2.963aiii
Fig. 9. large spinal bone, Nr. 31.4.2.8264
Fig. 10. large spinal bone, lateral view, Nr. 31.4.2.8264
Fig. 11. jaw with teeth, close up, Nr. 31.4.2.963aiii, detail, scale bar 1 mm
Figs 12–15 Fish pharyngeal teeth, family Cyprinidae, scale bar 3 mm (unless stated otherwise)
Fig. 12. Nr. 31.4.2.3624
Fig. 13. Nr. 31.4.2.5227
Fig. 14. Nr. 31.4.2.3805
Fig. 15. Nr. 31.4.2.3306ii, scale bar 1 mm
PLATE XLIII
Palaeoflora of Kassanoi, Crete, scale bar 2 cm (unless stated otherwise)

Figs 1–2 Polypodiophyta fam., gen. et sp. indet., frond fragments
Fig. 1. apical part, Nr. 31.6.2.161bii
Fig. 2. basal part, Nr. 31.6.2.112
Fig. 3. Daphnogene polymorpha, foliage, Nr. 31.6.2.174
Figs 4–5 Dicotylrophyllum sp. 14, foliage, foliage
Fig. 4. Nr. 31.6.2.165i
Fig. 5. almost complete leaf, Nr. 31.6.2.5
Figs 6–17 Daphnogene polymorpha, foliage
Fig. 6. Nr. 31.6.2.122
Fig. 7. Nr. 31.6.2.170i
Fig. 8. Nr. 31.6.2.123
Fig. 9. Nr. 31.6.2.131
Fig. 10. leaf base, Nr. 31.6.2.138i
Fig. 11. Nr. 31.6.2.125
Fig. 12. small leaf, Nr. 31.6.2.147
Fig. 13. Nr. 31.6.2.145
Fig. 14. Nr. 31.6.2.136
Fig. 15. slab with four closely arranged leaves of D. polymorpha (arrows), Nr. 31.6.2.128
Fig. 16. slab with two D. polymorpha leaves (arrows), Nr. 31.6.2.126
Fig. 17. close up on leaf venation, Nr. 31.6.2.128i, detail, scale bar 0.4 mm
Fig. 18. Tetraclinis cf. salicornioides, twig with a simple elongate segment giving rise to two similar in shape lateral segments, Nr. 31.6.2.182iii, scale bar 0.4 mm
PLATE XLIV
Palaeoflora of Kassanoi, Crete, scale bar 1 cm

Figs 1–2 *Buxus pliocenica*, foliage
Fig. 1. Nr. 31.6.2.195
Fig. 2. with skeletonization duo to arthropod feeding, Nr. 31.6.2.119x

Fig. 3. *Podocarpium podocarpum* small leaflet, Nr. 31.6.2.91ii
Fig. 4. *Podocarpium podocarpum* small leaflet, Nr. 31.6.2.210

Figs 5–14 *Podocarpium podocarpum*, foliage
Fig. 5. slab with five leaflets closely arranged, Nr. 31.6.2.168
Fig. 6. note the acuminate apex (arrow), Nr. 31.6.2.205
Fig. 7. Nr. 31.6.2.228
Fig. 8. Nr. 31.6.2.214
Fig. 9. Nr. 31.6.2.169
Fig. 10. Nr. 31.6.2.180i
Fig. 11. Nr. 31.6.2.66aop
Fig. 12. Nr. 31.6.2.218
Fig. 13. Nr. 31.6.2.15v
Fig. 14. leaflet, closely arranged with a Poaceae leaf fragment, Nr. 31.6.2.196

Fig. 15–16 Rosaceae gen. et sp. indet., foliage
Fig. 15. Nr. 31.6.2.18ai
Fig. 16. Nr. 31.6.2.119vi

Figs 17–18 *Myrica lignitum*, not typical foliage
Fig. 17. small, falcate leaf, Nr. 31.6.2.119viii
Fig. 18. small, deformed leaf, Nr. 31.6.2.217
PLATE XLV
Palaeoflora of Kassanoi, Crete, scale bar 1 cm (unless stated otherwise)

Fig. 1. *Leguminosites* sp. 3, leaflet, Nr. 31.6.2.62
Figs 2–4 *Berchemia multinervis*, foliage
Fig. 2. Nr. 31.6.2.170iii
Fig. 3. Nr. 31.6.2.158ii
Fig. 4. apical part, Nr. 31.6.2.163
Figs 5–10 *Ulmus* cf. *plurinervia*, foliage
Fig. 5. Nr. 31.6.2.78a
Fig. 6. Nr. 31.6.2.79
Fig. 7. basal part, Nr. 31.6.2.68
Fig. 8. Nr. 31.6.2.119v
Fig. 9. Nr. 31.6.2.71
Fig. 10. Nr. 31.6.2.119iv
Figs 11–12 *Zelkova zelkovifolia*, foliage
Fig. 11. Nr. 31.6.2.76b
Fig. 12. Nr. 31.6.2.75
Figs 13–14 *Quercus* sp., foliage
Fig. 13. Nr. 31.6.2.166ai
Fig. 14. Nr. 31.6.2.113i
Fig. 15. *Ulmus* cf. *plurinervia* close up on marginal teeth, Nr. 31.6.2.71, detail, scale bar 4 mm
Fig. 16. *Quercus* sp., close up on venation details, Nr. 31.6.2.166b, detail, scale bar 4 mm
PLATE XLVI

Palaeoflora of Kassanoi, Crete, scale bar 1 cm (unless stated otherwise)

Figs 1–8 Myrica lignitum, foliage
Fig. 1. complete, Nr. 31.6.2.120i
Fig. 2. complete, Nr. 31.6.2.40
Fig. 3. Nr. 31.6.2.80i
Fig. 4. Nr. 31.6.2.69ii
Fig. 5. with an isolated gall (arrow), Nr. 31.6.2.245opii
Fig. 6. Myrica ?lignitum, Nr. 31.6.2.95
Fig. 7. Nr. 31.6.2.33ii
Fig. 8. leaf gall, close up, Nr. 31.6.2.245opii detail, scale bar 2 mm

Figs 9–14 Salix cf. angusta, foliage
Fig. 9. Nr. 31.6.2.49i
Fig. 10. Nr. 31.6.2.32
Fig. 11. Nr. 31.6.2.51i
Fig. 12. apex, Nr. 31.6.2.35i
Fig. 13. narrow forma, closely arranged with a Podocarpium podocarpum leaflet, Nr. 31.6.2.37
Fig. 14. venation pattern, close up, Nr. 31.6.2.32 detail, scale bar 5 mm
Fig. 15. Myrica lignitum, leaf venation pattern, close up, Nr. 31.6.2.88 detail, scale bar 5 mm
PLATE XLVII
Palaeoflora of Kassanoi, Crete, scale bar 1 cm (unless stated otherwise)
Figs 1–2 *Dicotylophyllum* sp. 17, foliage
Fig. 1. Nr. 31.6.2.33i
Fig. 2. Nr. 31.6.2.31
Figs 3–5 *Decodon gibbosus*, foliage
Fig. 3. synthesis of the counterparts, Nr. 31.6.2.171a,b
Fig. 4. Nr. 31.6.2.35op
Fig. 5. Nr. 31.6.2.192
Figs 6–10 *Fraxinus* sp., foliage
Fig. 6. Nr. 31.6.2.159a
Fig. 7. Nr. 31.6.2.18aii
Fig. 8. Nr. 31.6.2.160
Fig. 9. venation pattern, close up, Nr. 31.6.2. 159b detail, scale bar 5 mm
Fig. 10. marginal teeth and venation pattern, close up, Nr. 31.6.2. 18aii detail, scale bar 5 mm
Fig. 11. *Populus populina*, foliage, Nr. 31.6.2.69i
PLATE XLVIII

Palaeoflora of Kassanoi, Crete, scale bar 2 cm (unless stated otherwise)

Fig. 1. *Cornus* sp., foliage, Nr. 31.6.2.117
Fig. 2. *Monocotylophyllum* sp. 6, Nr. 31.6.2.83op
Fig. 3. *Monocotylophyllum* sp. 7, Nr. 31.6.2.203
Fig. 4. *Monocotylophyllum* sp. 8, Nr. 31.6.2.184
Figs 5–8 *Dicotylophyllum* sp. 15, foliage
Fig. 5. Nr. 31.6.2.20
Fig. 6. Nr. 31.6.2.15i
Fig. 7. Nr. 31.6.2.17
Fig. 8. Nr. 31.6.2.16i
Fig. 9. *Dicotylophyllum* sp. 16, foliage, Nr. 31.6.2.70
Fig. 10. *Salix cf. angusta*, foliage, Nr. 31.6.2.45
Fig. 11. *Cornus* sp., tertiary venation pattern, close up, Nr. 31.6.2.117 detail, scale bar 4 mm
Fig. 12. *Antholites* sp., calyx, Nr. 31.6.2.118i, scale bar 8 mm
Fig. 13. *Chaneya* sp., winged fruit, Nr. 31.6.2.80ii, scale bar 8 mm
PLATE XLIX
Palaeoflora of Metochia, Gavdos island, scale bar 1 cm (unless stated otherwise)

Fig. 1. *Tetraclinis* cf. *salicornioides*, leafy twig, Nr. 31.5.2.9
Fig. 2. *Pinus* sp. 2, five-needled, isolated needle fragment, Nr. 31.5.2.14
Figs 3–4 *Dicotylophyllum* sp. 18, foliage
Fig. 3. Nr. 31.5.2.35a
Fig. 4. Nr. 31.5.2.30a
Fig. 5. *Daphnogene polymorpha*, foliage, the petiole, lamina margin and venation are partly lined, Nr. 31.5.2.31a
Fig. 6. *?Lindera ovata*, foliage, Nr. 31.5.2.12a
Fig. 7. *Sabalites* sp., leaf fragment, Nr. 31.5.2.44b
Fig. 8. *Monocotylophyllum* sp. 10, incomplete broad leaf, Nr. 31.5.2.40a
Fig. 9. *Monocotylophyllum* sp. 9, fragment of narrow linear leaf, Nr. 31.5.2.41aii
Fig. 10. *Dicotylophyllum* sp. 18, leaf venation close up, Nr. 31.5.2.30b detail, scale bar 6mm
Fig. 11. *?Leguminosites* sp. 4, complete leaflet, Nr. 31.5.2.49
Fig. 12. *Myrica lignitum*, leaf base, Nr. 31.5.2.46
Fig. 13. *?Engelhardia orsbergensis*, complete leaflet Nr. 31.5.3.5
Fig. 14. *Engelhardia orsbergensis*, complete leaflet Nr. 31.5.2.3a
PLATE L
Palaeoflora of Metochia, Gavdos island, scale bar 1 cm
Fig. 1. Sabalites sp., costapalmate leaf fragment, Nr. 31.5.2.44a
PLATE LI

Palaeoflora of Metochia, Gavdos island, scale bar 1 cm

Figs 1–4 *Fagus gussonii*, foliage
Fig. 1. Nr. 31.5.2.21a
Fig. 2. Nr. 31.5.2.18
Fig. 3. with sub-crasspedodromous venation (arrow), Nr. 31.5.2.29ai,
Fig. 4. Nr. 31.5.2.2

Fig. 5. ?fruit fragment, fam. et gen. et sp. indet., Nr. 31.5.2.63
Figs 6–7 *Quercus mediterranea*, foliage
Fig. 6. Nr. 31.5.2.59

Fig. 7. Nr. 31.5.2.7
Fig. 8. ?*Populus populina*, three-veined leaf forma, Nr. 31.5.2.4
Figs 9–11 cf. *Ziziphus paradisiaca*, three-veined leaves
Fig. 9. ?Nr. 31.5.2.15
Fig. 10. Nr. 31.5.2.57
Fig. 11. Nr. 31.5.2.13a
Fig. 12. *Dicotylophyllum* sp. 19, serrate leaf with bristle-tipped teeth, Nr. 31.5.2.1a
PLATE LII
Palaeoflora of Makrilia, Crete, scale bar 1 cm (unless stated otherwise)

Fig. 1. *cf. Ziziphus paradisiaca*, three-veined leaf, Nr. 31.3.2.223a

Fig. 2. *Mahonia* sp., leaf fragment, Nr. 31.3.2.319

Fig. 3. *Ziziphus jujuba* MILLER, modern leaf, for comparison

Fig. 4. *Leguminocarpon* sp., fruit fragment (pod) (from GIANNELOU and PSILLAKI, 2009), Nr. 31.3.2.318

Fig. 5. Pinaceae gen. et sp. indet. (excluding *Pinus*), winged seed (from GIANNELOU and PSILLAKI, 2009), Nr. 31.3.2.316

Fig. 6. *Acer* cf. *integerrimum*, five-lobed leaf (from GIANNELOU and PSILLAKI, 2009), Nr. 31.3.2.320

Fig. 7. *Liquidambar europaea*, fructification, Nr. 31.3.2.317, scale bar 0.6 cm

Fig. 8. Cupressaceae gen. et sp. indet., leafy shoot, Nr. 31.3.2.315, scale bar 0.6 cm

Fig. 9. *cf. Ziziphus paradisiaca*, venation pattern close up, Nr. 31.3.2.223b, scale bar 0.6 cm

Fig. 10. Cornaceae foliage (from GIANNELOU and PSILLAKI, 2009), Nr. 31.3.2.321, scale bar 0.6 cm

Fig. 11. *Myrica lignitum*, leaf fragment with characteristic venation pattern, Nr. 31.3.2.322, scale bar 0.6 cm
PLATE LIII
Palaeoflora of Pitsidia, Crete, arthropod action on plant macro-fossils

Figs 1–28 Myrica lignitum, external feeding

Fig. 1. margin feeding, open arc with entire edges, up to primary, Nr. 31.4.2.6844bi, scale bar 2 cm

Fig. 2. margin feeding, open arc with entire edges, shallowly to deeply incised, co-occurring with a medium in size, almost circular perforation, Nr. 31.4.2.4698, scale bar 2 cm

Fig. 3. several margin arcs along the lamina margin with entire edges (arrows), Nr. 31.4.2.4454ai, scale bar 2 cm

Fig. 4. four margin arcs with edges characterised by bite traces, Nr. 31.4.2.3978ai, scale bar 2 cm

Fig. 5. shallow, open arc of margin excision with edge characterised by bite traces, Nr. 31.4.2.6104i, scale bar 2 cm

Fig. 6. severe margin feeding with veinal stringers presence (arrows), Nr. 31.4.2.6104i, scale bar 2 cm

Fig. 7. margin excision with entire edge, close up, Nr. 31.4.2.6844bi detail, scale bar 5 mm

Fig. 8. margin excision with bite traces, close up, Nr. 31.4.2.39788bi detail, scale bar 5 mm

Fig. 9. Margin excision with bite traces, close up, Nr. 31.4.2.6104i detail, scale bar 5 mm

Fig. 10. closed, small excision of the leaf lamina that abruptly expands inwardly, extended to the primary vein, Nr. 31.4.2.4358iii detail, scale bar 5 mm

Fig. 11. open, irregular margin feeding (arrow), Nr. 31.4.2.5116iii detail, scale bar 1 cm

Fig. 12. open irregular margin excision, up to primary vein (arrow), Nr. 31.4.2.1430, scale bar 1 cm

Fig. 13. extended margin feeding, near the base, Nr. 31.4.2.1982, scale bar 2 cm

Fig. 14. extended margin feeding, Nr. 31.4.2.3959ai, scale bar 1 cm

Fig. 15. excision of leaf apex, including primary vein, Nr. 31.4.2.1415, scale bar 5 mm

Fig. 16. excision of leaf apex, including primary vein, Nr. 31.4.2.1716, scale bar 5 mm

Fig. 17. four elliptic or almost perforations, >2 mm in long diameter, their edges are outlined, Nr. 31.4.2.6918a, scale bar 2 cm

Fig. 18. isolated elliptic perforation, >2 mm in long diameter, its edge is outlined, Nr. 31.4.2.1912, scale bar 1 cm

Fig. 19. elliptic perforation, >2 mm in long diameter, accompanied by lamina deformation, Nr. 31.4.2.1646, scale bar 2 cm

Fig. 20. isolated almost circular perforation, >2 mm in diameter, with not easily detected reaction tissue, Nr. 31.4.2.6060, scale bar 1 cm

Fig. 21. two almost circular perforations near the lamina margin, >2 mm in diameter, their edges are outlined, Nr. 31.4.2.6975, scale bar 2 cm

Fig. 22. isolated polylobate perforation, Nr. 31.4.2.4408, scale bar 5 mm

Fig. 23. isolated polylobate perforation, Nr. 31.4.2.5560, scale bar 1 cm

Fig. 24. leaf fragment with three small sized perforations, less than 2 mm in diameter, that characterized by circular shape and well developed reaction rim, Nr. 31.4.2.3591, scale bar 5 mm

Fig. 25. isolated perforation, almost circular in shape, less than 2 mm in diameter and well developed reaction rim, Nr. 31.4.2.5344a, scale bar 1 cm

Fig. 26. isolated small perforation, close up, Nr. 31.4.2.5344a detail, scale bar 5 mm

Fig. 27. entire leaf with open arc margin excision, isolated circular perforation and severe apex distortion, Nr. 31.4.2.4181i, scale bar 2 cm

Fig. 28. leaf fragment with margin excision, isolated circular perforation and typical margin distortion, Nr. 31.4.2.3480, scale bar 5 mm
PLATE LIV
Palaeoflora of Pitsidia, Crete, arthropod action on plant macro-fossils

Figs 1–20 Myrica lignitum, lamina distortion.

Fig. 1. marginal (arrow), Nr. 31.4.2.5815aii, scale bar 2 cm
Fig. 2. marginal (arrow), Nr. 31.4.2.2573ai, scale bar 2 cm
Fig. 3. marginal (arrow), Nr. 31.4.2.1013, scale bar 1 cm
Fig. 4. marginal (arrow), Nr. 31.4.2.5800i, scale bar 2 cm
Fig. 5. marginal (arrow) and lamina shape, Nr. 31.4.2.5422, scale bar 2 cm
Fig. 6. marginal, Nr. 31.4.2.6358i, scale bar 2 cm
Fig. 7. lamina shape deformation, Nr. 31.4.2.6559b, scale bar 1 cm
Fig. 8. lamina shape deformation, Nr. 31.4.2.1254ai, scale bar 1 cm
Fig. 9. marginal (arrow), Nr. 31.4.2.8990pi, scale bar 2 cm
Fig. 10. basal (arrow), Nr. 31.4.2.2870op, scale bar 2 cm
Fig. 11. basal (arrow), Nr. 31.4.2.1770, scale bar 2 cm
Fig. 12. marginal (arrows) and lamina shape deformation, Nr. 31.4.2.1161, scale bar 2 cm
Fig. 13. lamina shape deformation, Nr. 31.4.2.4472b, scale bar 1 cm
Fig. 14. marginal (arrow), the leaf margin is outlined, Nr. 31.4.2.5693i, scale bar 1 cm
Fig. 15. marginal with lamina perforation (arrow), Nr. 31.4.2.5751aii, scale bar 1 cm
Fig. 16. marginal (arrow), close up, the leaf margin is outlined, Nr. 31.4.2.5751aii detail, scale bar 2.5 mm
Fig. 17. apex deformation, Nr. 31.4.2.5890aiii detail, scale bar 5 mm
Fig. 18. severe distortion in lamina shape along with extended margin feeding, Nr 31.4.2.3347op, scale bar 5 mm
Fig. 19. apex deformation, Nr. 31.4.2.6251b detail, scale bar 5 mm
Fig. 20. apex deformation, Nr. 31.4.2.4300aii, scale bar 5 mm
Fig. 21. extant Olea europaea, lamina distortions by Liothrips oleae COSTA, scale bar 3 cm
Fig. 22. extant Nerium oleander, lamina distortions, scale bar 2 cm
PLATE LV
Palaeoflora of Pitsidia, Crete, arthropod action on plant macro-fossils

Figs 1–17 *Myrica lignitum*, various leaf damages

Fig. 1. mine of serpentine type, the trail is outlined, Nr. 31.4.2.2700b, scale bar 5 mm
Fig. 2. group of galls, Nr. 31.4.2.913, scale bar 1 cm
Fig. 3. abundant galls, Nr. 31.4.2.5272, scale bar 1 cm
Fig. 4. scattered small galls (arrows), Nr. 31.4.2.5891a, scale bar 2 cm
Fig. 5. dense group of galls on a small leaf fragment, Nr. 31.4.2.6450, scale bar 5 mm
Fig. 6. galls in close up, the arrows indicate the preserved inorganic replica inside, Nr. 31.4.2.913 detail, scale bar 2.5 mm
Fig. 7. spots of removed surface tissue < 2 mm, Nr. 31.4.2.2867, scale bar 5 mm
Fig. 8. removed surface tissue < 2 mm in close up, Nr. 31.4.2.2867 detail, scale bar 2.5 mm
Fig. 9. spots of removed surface tissue 2–4 mm, Nr. 31.4.2.1862b, scale bar 5 mm
Fig. 10. polylobate removed surface tissue, Nr. 31.4.2.3283, scale bar 5 mm
Fig. 11. arcuate row of 18 eggs and egg scars on the deformed margin of the lamina, arrow indicates the egg position, Nr. 31.4.2.6042, scale bar 1 cm
Fig. 12. egg replicas in an elongate row, close up, Nr. 31.4.2.6042 detail, scale bar 1 mm
Fig. 13. curled lamina, Nr. 31.4.2.1995a, scale bar 2 cm
Fig. 14. numerous depressed spots, Nr. 31.4.2.1151, scale bar 1 cm
Fig. 15. group of depressed spots, Nr. 31.4.2.987b, scale bar 1 cm
Fig. 16. depressed spots, close up, Nr. 31.4.2.987b detail, scale bar 2.5 mm
Fig. 17. numerous spots surrounded by callus, Nr. 31.4.2.4458b, scale bar 1 cm
PLATE LVI
Palaeoflora of Pitsidia, Crete, arthropod action on plant macro-fossils

Figs 1–16 Leaf damages of other plant taxa
Fig. 1. wood fragment preserved as inorganic replica, with easily distinguished vessels and arthropod mediated borings, Nr. 31.4.2.4256opiv, scale bar 1 mm
Fig. 2. ?Quercus, feeding of lamina apex, Nr. 31.4.2.5353, scale bar 1 cm
Fig. 3. Populus populina, extensive margin excision of tissue between secondary veins with veinal stringer remains (arrows), Nr. 31.4.2.6131a, scale bar 1 cm
Fig. 4. Liquidambar europaea leaf margin feeding (arrow), Nr. 31.4.2.5358a, scale bar 1 cm
Fig. 5. Acer integrilobum, basal feeding (black arrow) and lamina perforation (white arrow), Nr. 31.4.2.2581ai, scale bar 1 cm
Fig. 6. Quercus pseudocastanea, spot with callus, Nr. 31.4.2.3462a, scale bar 1 mm
Fig. 7. Quercus pseudocastanea, closed margin feeding (black arrow) and a group of galls (white arrow), Nr. 31.4.2.4135, scale bar 1 cm
Fig. 8. Quercus cf. kubinyii, lamina perforation (arrows), Nr. 31.4.2.6938bi detail, scale bar 1 cm
Fig. 9. Carya sp., typical apex distortion, Nr. 31.4.2.5226a, scale bar 1 cm
Fig. 10. Carya sp., typical apex distortion, Nr. 31.4.2.5447c, scale bar 1 cm
Fig. 11. Quercus pseudocastanea, numerous spots of removed surface tissue <1 mm, Nr. 31.4.2.5313, scale bar 1 cm
Fig. 12. Liquidambar europaea, galls, Nr. 31.4.2.5908a, scale bar 1 cm
Fig. 13. ?Acer tricuspidatum, numerous gall-like structures, Nr. 31.4.2.4361 detail, scale bar 1 cm
Fig. 14. Carya sp., galls (arrows), Nr. 31.4.2.990b detail, scale bar 1 cm
Fig. 15. Pinus pitsidiensis, perforation on a needle inorganic replica of, Nr. 31.4.2.3698b detail, scale bar 0.5 mm
Fig. 16. Pinus pitsidiensis, needle distortion, Nr. 31.4.2.6082b, scale bar 1 cm
PLATE LVII
Palaeoflora of Pitsidia, Crete, after shedding damages on plant remains, scale bar 2 cm (unless stated otherwise)

Figs 1–5 Pre-depositional mechanical damages
Fig. 1. Myrica lignitum, leaf fragments, Nr. 31.4.2.3809
Fig. 2. Myrica lignitum, leaf, Nr. 31.4.2.4013b,
Fig. 3. Quercus pseudocastanea, leaf, Nr. 31.4.2.1421ai,
Fig. 4. Pinus pitsidiensis, needle, Nr. 31.4.2.4559
Fig. 5. Myrica lignitum, incomplete leaf, Nr. 31.4.2.3551a

Figs 6–8 After deposition, pre-burial damages
Fig. 6. Monocotylophyllum sp. 2, leaf fragment, Nr. 31.4.2.5981opi
Fig. 7. Quercus pseudocastanea, leaf, Nr. 31.4.2.2266b
Fig. 8. Myrica lignitum, leaf, Nr. 31.4.2.1635a

Figs 9–15 Post-burial damages
Fig. 9. Myrica lignitum, leaf base damaged by sediment fracturing, Nr. 31.4.2.4251i
Fig. 10. Myrica lignitum, leaf base damaged by sediment fracturing, Nr. 31.4.2.3558i
Fig. 11. Myrica lignitum, leaf apex damaged by sediment fracturing, Nr. 31.4.2.3270
Fig. 12. Myrica lignitum, leaf damaged by nesting of extant insects, Nr. 31.4.2.5802a
Fig. 13. Pinus pitsidiensis, needles penetrated by modern rootlets, Nr. 31.4.2.3951
Fig. 14. block with three fracturing surfaces, damaging a leaf of Quercus pseudocastanea,
    Nr. 31.4.2.4011, scale bar 5 cm
Fig. 15. fracturing (line) damaging plant remains, Nr. 31.4.2.3496b
APPENDICES
APPENDIX 1

a. Geological map of NE Messara Basin (from I.G.M.E., 1989, 2002; sheets Ano Viannos and Mochos; synthesis); Kassanoi outcrop

Talus cones and scree
Varvara Fm
Skinias Fm
Flysch

Alluvial deposits
Ambelouzos Fm
Viannos Fm
Limestones
b. Geological map of western Messara Bassin (from I.G.M.E., 1984, 1985, 1985; sheets Timbakion, Andiskarion and Melames; synthesis); Pitsidia outcrop

- Conglom., sands and clays (Quaternary)
- Conglom., sands and clays (Pleist-Pliocene)
- Marine deposits (Lower Pliocene)
- Marine, brack. and fresh-water dep. (Tortonian)
- Marls (Messinian)
- Clay-sand alternations (Middle Miocene)
- Vatos unit
- Kroussonas series
c. Geological map of Gavdos (I.G.M.E., 1993; sheet Gavdos); Metochia outcrop
APPENDIX 2

a. Pitsidia, the collected specimens per level and square grid in systematic excavation

<table>
<thead>
<tr>
<th>Excavated layer</th>
<th>Number of grid square</th>
<th>Specimens*</th>
<th>Total specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td>MFL level I 0.00–0.70m</td>
<td>8B</td>
<td>8</td>
<td>787</td>
</tr>
<tr>
<td></td>
<td>8C</td>
<td>450</td>
<td></td>
</tr>
<tr>
<td></td>
<td>8D</td>
<td>33</td>
<td></td>
</tr>
<tr>
<td></td>
<td>8E</td>
<td>71</td>
<td></td>
</tr>
<tr>
<td></td>
<td>9C</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td></td>
<td>9E</td>
<td>54</td>
<td></td>
</tr>
<tr>
<td></td>
<td>10D</td>
<td>118</td>
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<tr>
<td></td>
<td>11D</td>
<td>2</td>
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<tr>
<td></td>
<td>11E</td>
<td>1</td>
<td></td>
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<tr>
<td>MFL level II 0.70–1.40m</td>
<td>6C</td>
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<td>7C</td>
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<tr>
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<td>8B</td>
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<tr>
<td>MFL level III 1.40–2.10m</td>
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<td></td>
<td>8B</td>
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<td>MFL level IV 2.10–2.80m</td>
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<tr>
<td>MFL level V 2.80–3.50m</td>
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<td>788</td>
</tr>
<tr>
<td>MFL level VI 3.50–ca. 4.00m</td>
<td>2A</td>
<td>104</td>
<td>330</td>
</tr>
<tr>
<td></td>
<td>4A</td>
<td>226</td>
<td></td>
</tr>
<tr>
<td>FL1 (7cm)</td>
<td>4A</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>3A</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3-A</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1-A</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>FL2 (17cm)</td>
<td>4A</td>
<td>135</td>
<td>155</td>
</tr>
<tr>
<td></td>
<td>3A</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3-A</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1-A</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>FL3 (37cm)</td>
<td>3A</td>
<td>3</td>
<td>59</td>
</tr>
<tr>
<td></td>
<td>1A</td>
<td>54</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1-A</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Other</td>
<td>diverse</td>
<td>92</td>
<td>92</td>
</tr>
<tr>
<td>TOTAL</td>
<td>8812</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* including pine needle fragments; the different abundances of collected specimen among the grid squares and levels reflect mainly the scale of destruction of the excavated sediments due to weathering
b. The collected specimens in Pitsidia

- collected and examined specimens
- by systematic excavation (grid setting) from all sediment layers
- from MFL and FL1-3 layers
- excluding pine needle fragments
- i. from MFL layer
- ii. from FL2 layer
- plant remains
- identified plant remains

Leaves and leafy twigs
F.: Fertile organs/parts
V.: Vegetative organs/parts
APPENDIX 3

Principal morphological leaf characters that taken under consideration in this study

1. Petiole characters
   1.1 Petiolate
   1.2 Sessile
   1.3 Petiole length
   1.4 Special petiole features

2. Lamina general characters
   2.1 Texture
   2.2 Length
   2.3 Width
   2.4 L/W Ratio
   2.5 Shape
   2.6 Lamina symmetry
   2.7 Apex shape/angle
   2.8 Base shape/angle
   2.9 Base symmetry
   2.10 Margin type
   2.11 Lobation
   2.12 Special margin features

3. Vein characters
   3.1 Primary vein framework
   3.2 Major secondary vein framework
   3.3 Major secondary vein spacing
   3.4 Major secondary vein angle to midvein
   3.5 Interior secondary veins
   3.6 Minor secondary veins
   3.7 Marginal/Intramarginal secondary veins
   3.8 Agrophic veins
   3.9 Intersecondary veins
   3.10 Tertiary vein course
   3.11 Tertiary vein spacing
   3.12 Tertiary vein angle to secondaries
   3.13 Quaternary vein course
   3.14 Areolation
   3.15 Marginal ultimate venation

4. Tooth characters
   4.1 Number of tooth order
   4.2 Tooth size
   4.3 Tooth shape
   4.4 Tooth apex shape/angle
   4.5 Special features of tooth apex
   4.6 Tooth spacing
   4.7 Sinus shape/angle
   4.8 Principal vein course
   4.9 Major accessory vein course
   4.10 Special features of the tooth
APPENDIX 4

Pitsidia, the sediment blocks Nrs 1–12 and 13

<table>
<thead>
<tr>
<th>Block Nr.</th>
<th>Slab Nrs</th>
<th>Volume (dm$^3$)</th>
<th>Grid Square</th>
<th>Level</th>
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<tbody>
<tr>
<td>1</td>
<td>31.4.2.4787–31.4.2.4798</td>
<td>3.20</td>
<td>6C</td>
<td>II</td>
</tr>
<tr>
<td>2</td>
<td>31.4.2.4799–31.4.2.4814</td>
<td>5.04</td>
<td>6C</td>
<td>II</td>
</tr>
<tr>
<td>3</td>
<td>31.4.2.4815–31.4.2.4824</td>
<td>1.65</td>
<td>6C</td>
<td>II</td>
</tr>
<tr>
<td>4</td>
<td>31.4.2.4825–31.4.2.4832</td>
<td>1.28</td>
<td>6C</td>
<td>II</td>
</tr>
<tr>
<td>5</td>
<td>31.4.2.4833–31.4.2.4844</td>
<td>4.34</td>
<td>6C</td>
<td>II</td>
</tr>
<tr>
<td>6</td>
<td>31.4.2.4845–31.4.2.4852</td>
<td>1.68</td>
<td>6C</td>
<td>II</td>
</tr>
<tr>
<td>7</td>
<td>31.4.2.5357–31.4.2.5365</td>
<td>1.78</td>
<td>5C</td>
<td>IV</td>
</tr>
<tr>
<td>8</td>
<td>31.4.2.5385–31.4.2.5409</td>
<td>5.75</td>
<td>5C</td>
<td>IV</td>
</tr>
<tr>
<td>9</td>
<td>31.4.2.5410–31.4.2.5422</td>
<td>6.86</td>
<td>5C</td>
<td>IV</td>
</tr>
<tr>
<td>10</td>
<td>31.4.2.5430–31.4.2.5446</td>
<td>4.05</td>
<td>5C</td>
<td>IV</td>
</tr>
<tr>
<td>11</td>
<td>31.4.2.5447–31.4.2.5465</td>
<td>7.02</td>
<td>5C</td>
<td>IV</td>
</tr>
<tr>
<td>12</td>
<td>31.4.2.5466–31.4.2.5485</td>
<td>7.68</td>
<td>5C</td>
<td>IV</td>
</tr>
<tr>
<td>SUM</td>
<td>294 specimens$^\wedge$</td>
<td>50.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>31.4.2.3372–31.4.2.3436*</td>
<td>4.80</td>
<td>7C</td>
<td>II</td>
</tr>
<tr>
<td>SUM</td>
<td>64 (not destroyed) + 22 (destroyed during collection) = 86 specimens</td>
<td>4.80</td>
<td></td>
<td></td>
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</tbody>
</table>

$^\wedge$ including pine needle fragments

*not destroyed specimens during collection
### APPENDIX 5

Plant assemblage of Pitsidia, floristic composition

<table>
<thead>
<tr>
<th>Nr.</th>
<th>Family</th>
<th>Taxon</th>
<th>Plant Part/Organ</th>
<th>Sample Frequency*</th>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Abundance description</td>
</tr>
<tr>
<td>1</td>
<td>Algae</td>
<td>indet.</td>
<td>gen. et sp. indet.</td>
<td>thallus</td>
</tr>
<tr>
<td>2</td>
<td>Polypodiophyta</td>
<td>indet.</td>
<td>&quot;Pteris&quot; oeningtensis</td>
<td>frond fragments</td>
</tr>
<tr>
<td>3</td>
<td>Polypodiophyta</td>
<td>indet.</td>
<td>gen. et sp. indet.</td>
<td>frond fragments</td>
</tr>
<tr>
<td>4</td>
<td>Gymnospermae</td>
<td>Cupressaceae</td>
<td>Tretaciltis cf. salicornoides</td>
<td>leafy twigs</td>
</tr>
<tr>
<td>5</td>
<td>Gymnospermae</td>
<td>Taxodium dubium</td>
<td>leafy twigs</td>
<td>common</td>
</tr>
<tr>
<td>6</td>
<td>Gymnospermae</td>
<td>Pinus pitisidensis</td>
<td>dwarf shoots</td>
<td>dominant</td>
</tr>
<tr>
<td>7</td>
<td>Gymnospermae</td>
<td>Pinus pitisidensis</td>
<td>branchlets</td>
<td>common</td>
</tr>
<tr>
<td>8</td>
<td>Gymnospermae</td>
<td>Pinus sp. 1, 2-needled, subgen. Pinus</td>
<td>dwarf shoots</td>
<td>very rare</td>
</tr>
<tr>
<td>9</td>
<td>Gymnospermae</td>
<td>Pinus sp. 5-needled, subgen. Strobus</td>
<td>dwarf shoots</td>
<td>rare</td>
</tr>
<tr>
<td>10</td>
<td>Gymnospermae</td>
<td>Pinus sp., subgen. Pinus</td>
<td>fascicle bracts</td>
<td>dominant</td>
</tr>
<tr>
<td>11</td>
<td>Gymnospermae</td>
<td>Pinus sp., subgen. Pinus</td>
<td>ovulate cone scales</td>
<td>very rare</td>
</tr>
<tr>
<td>12</td>
<td>Gymnospermae</td>
<td>Pinus sp., subgen. Strobus</td>
<td>ovulate cone scale</td>
<td>very rare</td>
</tr>
<tr>
<td>13</td>
<td>Gymnospermae</td>
<td>Pinus sp. 1</td>
<td>seeds</td>
<td>rare</td>
</tr>
<tr>
<td>14</td>
<td>Gymnospermae</td>
<td>Pinus sp. 2</td>
<td>seeds</td>
<td>very rare</td>
</tr>
<tr>
<td>15</td>
<td>Gymnospermae</td>
<td>Pinus sp.</td>
<td>underdeveloped seeds</td>
<td>common</td>
</tr>
<tr>
<td>16</td>
<td>Gymnospermae</td>
<td>Pinus sp. 1</td>
<td>pollen cones</td>
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<tr>
<td>17</td>
<td>Gymnospermae</td>
<td>Pinus sp. 2</td>
<td>pollen cones</td>
<td>rare</td>
</tr>
<tr>
<td>18</td>
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<td>Pinus sp.</td>
<td>bud scales</td>
<td>dominant</td>
</tr>
<tr>
<td>19</td>
<td>Angiospermae</td>
<td>gen. et sp. indet.</td>
<td>wood</td>
<td>very rare</td>
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<tr>
<td>20</td>
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<td>gen. et sp. indet.</td>
<td>leafy twig</td>
<td>very rare</td>
</tr>
<tr>
<td>21</td>
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<td>gen. et sp. indet.</td>
<td>long shoots</td>
<td>very rare</td>
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<tr>
<td>22</td>
<td>Angiospermae</td>
<td>gen. et sp. indet., diverse</td>
<td>needles</td>
<td>very rare</td>
</tr>
<tr>
<td>23</td>
<td>Angiospermae</td>
<td>gen. et sp. indet.</td>
<td>ovulate cone scale</td>
<td>very rare</td>
</tr>
<tr>
<td>24</td>
<td>Angiospermae</td>
<td>gen. et sp. indet.</td>
<td>ovulate cone scale</td>
<td>very rare</td>
</tr>
<tr>
<td>25</td>
<td>Angiospermae</td>
<td>Lauraceae</td>
<td>Daphnogene polymorpha</td>
<td>leaves</td>
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<tr>
<td>26</td>
<td>Angiospermae</td>
<td>Lauraceae gen. et sp. indet.</td>
<td>leaf</td>
<td>very rare</td>
</tr>
<tr>
<td>27</td>
<td>Angiospermae</td>
<td>Lauraceae gen. et sp. indet.</td>
<td>leaf</td>
<td>very rare</td>
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<tr>
<td>28</td>
<td>Angiospermae</td>
<td>Altingiaceae</td>
<td>Liquidambur europaea</td>
<td>leaves</td>
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<tr>
<td>29</td>
<td>Angiospermae</td>
<td>Liquidambur europaea</td>
<td>infructescences</td>
<td>common</td>
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<td>Fabaceae</td>
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<td>leaflet</td>
</tr>
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<td>Angiospermae</td>
<td>Leguminosites sp. 2</td>
<td>leaflet</td>
<td>very rare</td>
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<td>33</td>
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<td>Podocarpium podocarpum</td>
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<td>rare</td>
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<td>34</td>
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<td>Mimosites sp.</td>
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<td>rare</td>
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<td></td>
<td>Family</td>
<td>Genus/Species</td>
<td>Part/Structure</td>
<td>Frequency</td>
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<td>------------</td>
<td>---------------------</td>
<td>---------------</td>
<td>-------------</td>
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<tr>
<td>35</td>
<td>Rosaceae</td>
<td>?Rosa sp.</td>
<td>leaflets</td>
<td>very rare</td>
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<tr>
<td>36</td>
<td>Ulmaceae</td>
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<td>rare</td>
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<tr>
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<td>Ulmaceae</td>
<td>Ulmus sp.</td>
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</tr>
<tr>
<td>38</td>
<td>?Zelkova</td>
<td>zelkowskii</td>
<td>leaves</td>
<td>very rare</td>
</tr>
<tr>
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<td>Fagaceae</td>
<td>Quercus pseudocastanea</td>
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<td>very rare</td>
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<td>Fagus gussoni</td>
<td>leaves</td>
<td>rare</td>
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<td>fruits+infructescenses</td>
<td>abundant</td>
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<td>Myrica cf. goeppertii</td>
<td>catkins</td>
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<td>Juglandaceae</td>
<td>Carusa sp.</td>
<td>leaflets</td>
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<td>Pterocarya sp.</td>
<td>fruit</td>
<td>very rare</td>
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<td>48</td>
<td>Juglandaceae</td>
<td>Juglandaceae gen. et sp. indet.</td>
<td>leaflet</td>
<td>very rare</td>
</tr>
<tr>
<td>49</td>
<td>Betulaceae</td>
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<td>leaves</td>
<td>very rare</td>
</tr>
<tr>
<td>50</td>
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<td>Salix sp.</td>
<td>leaves</td>
<td>very rare</td>
</tr>
<tr>
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<td>Salicaceae</td>
<td>Populus populinia</td>
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<td>rare</td>
</tr>
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<td>52</td>
<td>Salicaceae</td>
<td>Populus sp.</td>
<td>leaf</td>
<td>very rare</td>
</tr>
<tr>
<td>53</td>
<td>Sapindaceae</td>
<td>Acer tricuspidatum</td>
<td>leaves</td>
<td>rare</td>
</tr>
<tr>
<td>54</td>
<td>Sapindaceae</td>
<td>Acer integriobum</td>
<td>leaves</td>
<td>very rare</td>
</tr>
<tr>
<td>55</td>
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<td>Acer aegopodifolium</td>
<td>leaflet</td>
<td>very rare</td>
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<tr>
<td>56</td>
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<td>Acer sp. 1</td>
<td>fruits</td>
<td>very rare</td>
</tr>
<tr>
<td>57</td>
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<td>Acer sp. 2</td>
<td>fruits</td>
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</tr>
<tr>
<td>58</td>
<td>Hydrangeaceae</td>
<td>cf. Hydrangea sp.</td>
<td>flower</td>
<td>very rare</td>
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<tr>
<td>59</td>
<td>indet.</td>
<td>Monocotylophyllum sp. 1</td>
<td>leaves</td>
<td>rare</td>
</tr>
<tr>
<td>60</td>
<td>indet.</td>
<td>Monocotylophyllum sp. 2</td>
<td>leaves</td>
<td>rare</td>
</tr>
<tr>
<td>61</td>
<td>indet.</td>
<td>Monocotylophyllum sp. 3</td>
<td>leaf</td>
<td>very rare</td>
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<tr>
<td>62</td>
<td>indet.</td>
<td>Monocotylophyllum sp. 4</td>
<td>leaf</td>
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</tr>
<tr>
<td>63</td>
<td>indet.</td>
<td>Monocotylophyllum sp. 5</td>
<td>leaves</td>
<td>very rare</td>
</tr>
<tr>
<td>64</td>
<td>indet.</td>
<td>Dicotylophyllum sp. 1</td>
<td>leaf</td>
<td>very rare</td>
</tr>
<tr>
<td>65</td>
<td>indet.</td>
<td>Dicotylophyllum sp. 2</td>
<td>leaves</td>
<td>very rare</td>
</tr>
<tr>
<td>66</td>
<td>indet.</td>
<td>Dicotylophyllum sp. 3</td>
<td>leaf/leaflet</td>
<td>very rare</td>
</tr>
<tr>
<td>67</td>
<td>indet.</td>
<td>Dicotylophyllum sp. 4</td>
<td>leaflets</td>
<td>very rare</td>
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<tr>
<td>68</td>
<td>indet.</td>
<td>Dicotylophyllum sp. 5</td>
<td>leaf</td>
<td>very rare</td>
</tr>
<tr>
<td>69</td>
<td>indet.</td>
<td>Dicotylophyllum sp. 6</td>
<td>leaf/leaflet</td>
<td>very rare</td>
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<tr>
<td>70</td>
<td>indet.</td>
<td>Dicotylophyllum sp. 7</td>
<td>leaves</td>
<td>very rare</td>
</tr>
<tr>
<td>71</td>
<td>indet.</td>
<td>Dicotylophyllum sp. 8</td>
<td>leaves/leaflets</td>
<td>very rare</td>
</tr>
<tr>
<td>72</td>
<td>indet.</td>
<td>Dicotylophyllum sp. 9</td>
<td>leaf</td>
<td>very rare</td>
</tr>
<tr>
<td>73</td>
<td>indet.</td>
<td>Dicotylophyllum sp. 10</td>
<td>leaf</td>
<td>very rare</td>
</tr>
<tr>
<td>74</td>
<td>indet.</td>
<td>Dicotylophyllum sp. 11</td>
<td>leaves</td>
<td>very rare</td>
</tr>
<tr>
<td>75</td>
<td>indet.</td>
<td>Dicotylophyllum sp. 12</td>
<td>leaf</td>
<td>very rare</td>
</tr>
<tr>
<td>76</td>
<td>indet.</td>
<td>Dicotylophyllum sp. 13</td>
<td>leaf</td>
<td>very rare</td>
</tr>
</tbody>
</table>

314
<table>
<thead>
<tr>
<th>No.</th>
<th>Genus et Species</th>
<th>Type</th>
<th>Description</th>
<th>Abundance</th>
<th>1</th>
<th>10–29</th>
<th>30–99</th>
<th>100–299</th>
<th>≥300</th>
</tr>
</thead>
<tbody>
<tr>
<td>77</td>
<td>gen. et sp. indet.</td>
<td>inflorescence</td>
<td>very rare</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>---</td>
<td></td>
<td></td>
</tr>
<tr>
<td>78</td>
<td>drape</td>
<td>fruit</td>
<td>very rare</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>---</td>
<td></td>
<td></td>
</tr>
<tr>
<td>79</td>
<td>?Carpolithus sp.</td>
<td>?fruit</td>
<td>very rare</td>
<td>1</td>
<td>1</td>
<td>---</td>
<td>---</td>
<td></td>
<td></td>
</tr>
<tr>
<td>80</td>
<td>?septum</td>
<td>fruit</td>
<td>very rare</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>---</td>
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</tr>
<tr>
<td>81</td>
<td>type 1</td>
<td>bud scales</td>
<td>rare</td>
<td>14</td>
<td>9</td>
<td>9</td>
<td>---</td>
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<tr>
<td>82</td>
<td>type 2</td>
<td>bud scales</td>
<td>very rare</td>
<td>6</td>
<td>6</td>
<td>6</td>
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<tr>
<td>83</td>
<td>type 3</td>
<td>bud scales</td>
<td>very rare</td>
<td>5</td>
<td>4</td>
<td>4</td>
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<tr>
<td>84</td>
<td>gen. et sp. indet., diverse</td>
<td>shoots</td>
<td>---</td>
<td>387</td>
<td>374</td>
<td>365</td>
<td>---</td>
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<td>85</td>
<td>gen. et sp. indet., diverse</td>
<td>wood fragments (inorganic)</td>
<td>---</td>
<td>133</td>
<td>130</td>
<td>116</td>
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<tr>
<td>86</td>
<td>gen. et sp. indet.</td>
<td>rhizomes</td>
<td>very rare</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>---</td>
<td></td>
<td></td>
</tr>
<tr>
<td>87</td>
<td>gen. et sp. indet., diverse</td>
<td>roots</td>
<td>---</td>
<td>24</td>
<td>24</td>
<td>20</td>
<td>---</td>
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</tr>
</tbody>
</table>

*very rare ≤9, rare 10–29, common 30–99, abundant 100–299, dominant ≥300
## APPENDIX 6

Plant assemblage of Kassanoi, floristic composition

<table>
<thead>
<tr>
<th>Nr.</th>
<th>Family</th>
<th>Taxon</th>
<th>Plant Part/Organ</th>
<th>Frequency*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><strong>Polypodiophyta</strong></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>1</td>
<td>Fam. indet.</td>
<td>gen. et sp. indet.</td>
<td>fronds</td>
<td>rare</td>
</tr>
<tr>
<td>2</td>
<td><strong>Gymnospermae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Cupressaceae</td>
<td><em>Tetraclinis cf. salicornioides</em></td>
<td>leafy twigs</td>
<td>rare</td>
</tr>
<tr>
<td></td>
<td><strong>Angiospermae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Lauraceae</td>
<td><em>Daphnogene polymorpha</em></td>
<td>leaves</td>
<td>abundant</td>
</tr>
<tr>
<td>4</td>
<td>Buxaceae</td>
<td><em>Buxus pliocentica</em></td>
<td>leaves</td>
<td>rare</td>
</tr>
<tr>
<td>5</td>
<td>Fabaceae</td>
<td><em>Leguminosites sp. 3</em></td>
<td>leaflet</td>
<td>rare</td>
</tr>
<tr>
<td>6</td>
<td></td>
<td><em>Podocarpium podocarpum</em></td>
<td>leaflets</td>
<td>abundant</td>
</tr>
<tr>
<td>7</td>
<td>Rosaceae</td>
<td>gen. et sp. indet.</td>
<td>leaves</td>
<td>rare</td>
</tr>
<tr>
<td>8</td>
<td>Rhamnaceae</td>
<td><em>Berberis multiverticis</em></td>
<td>leaves</td>
<td>rare</td>
</tr>
<tr>
<td>9</td>
<td>Ulmaceae</td>
<td><em>Ulmus cf. plurinervis</em></td>
<td>leaves</td>
<td>common</td>
</tr>
<tr>
<td>10</td>
<td></td>
<td><em>Zelkova zelkovifolia</em></td>
<td>leaves</td>
<td>rare</td>
</tr>
<tr>
<td>11</td>
<td>Fagaceae</td>
<td><em>Quercus sp.</em></td>
<td>leaves</td>
<td>rare</td>
</tr>
<tr>
<td>12</td>
<td>Myricaceae</td>
<td><em>Myrica lignitum</em></td>
<td>leaves</td>
<td>abundant</td>
</tr>
<tr>
<td>14</td>
<td>Salicaceae</td>
<td><em>Salix cf. angustia</em></td>
<td>leaves</td>
<td>abundant</td>
</tr>
<tr>
<td>15</td>
<td></td>
<td><em>Populus populina</em></td>
<td>leaves</td>
<td>rare</td>
</tr>
<tr>
<td>16</td>
<td>Lithraceae</td>
<td><em>Decodon gibbosus</em></td>
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<td>rare</td>
</tr>
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<td><em>Chameya sp.</em></td>
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<td>rare</td>
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<tr>
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<td>Oleaceae</td>
<td><em>Fraxinus sp.</em></td>
<td>leaflets</td>
<td>rare</td>
</tr>
<tr>
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<td>Cornaceae</td>
<td><em>Cornus sp.</em></td>
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<td>rare</td>
</tr>
<tr>
<td>20</td>
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<td>rare</td>
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<td>21</td>
<td></td>
<td><em>Monocotylophyllum sp. 7</em></td>
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<td>22</td>
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<td><em>Monocotylophyllum sp. 8</em></td>
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<tr>
<td>23</td>
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<td><em>Dicotylophyllum sp. 14</em></td>
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<td>rare</td>
</tr>
<tr>
<td>24</td>
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<td><em>Dicotylophyllum sp. 15</em></td>
<td>leaf</td>
<td>abundant</td>
</tr>
<tr>
<td>25</td>
<td></td>
<td><em>Dicotylophyllum sp. 16</em></td>
<td>leaf</td>
<td>rare</td>
</tr>
<tr>
<td>26</td>
<td></td>
<td><em>Dicotylophyllum sp. 17</em></td>
<td>leaves</td>
<td>common</td>
</tr>
<tr>
<td>27</td>
<td></td>
<td><em>Antholites sp.</em></td>
<td>flower</td>
<td>rare</td>
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</table>

*Rare 1–4, Common 5–15, abundant ≥16*
## APPENDIX 7

Plant assemblage of Metochia, the floristic elements that were identified in this study (newly described taxa in bold)

<table>
<thead>
<tr>
<th>Nr.</th>
<th>Family</th>
<th>Taxon</th>
<th>Plant part/Organ</th>
<th>Frequency*</th>
<th>Abundance description</th>
<th>Samples</th>
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<tr>
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<td></td>
</tr>
<tr>
<td></td>
<td>Gymnospermae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Cupressaceae</td>
<td><em>Tetraclinis cf. salicornioides</em></td>
<td>leafy twig</td>
<td>rare</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Pinaceae</td>
<td><em>Pinus sp. 2, 5-needled</em></td>
<td>needle</td>
<td>rare</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Lauraceae</td>
<td><em>Daphne gen. polymorpha</em></td>
<td>leaf</td>
<td>rare</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>4</td>
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<td><em>Lindera ovata</em></td>
<td>leaves</td>
<td>rare</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Arecales</td>
<td><em>Sabalites sp.</em></td>
<td>leaf</td>
<td>rare</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Fabaceae</td>
<td><em>?Leguminosites sp. 4</em></td>
<td>leaf</td>
<td>rare</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Rhamnaceae</td>
<td><em>cf. Ziziphus paradisiaca</em></td>
<td>leaves</td>
<td>rare</td>
<td>3</td>
<td></td>
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<tr>
<td>8</td>
<td>Fagaceae</td>
<td><em>Quercus mediterranea</em></td>
<td>leaves</td>
<td>rare</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td></td>
<td><em>Fagus gussoni</em></td>
<td>leaves</td>
<td>common</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>Myricaceae</td>
<td><em>Myrica lignitum</em></td>
<td>leaves</td>
<td>rare</td>
<td>2</td>
<td></td>
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<tr>
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<td>Juglandaceae</td>
<td><em>Engelhardia orsbergensis</em></td>
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<td>rare</td>
<td>2</td>
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<tr>
<td>12</td>
<td>Salicaceae</td>
<td><em>Populus populina</em></td>
<td>leaf</td>
<td>rare</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td></td>
<td><em>Monocotylophyllum sp. 9</em></td>
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<td>rare</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>14</td>
<td></td>
<td><em>Monocotylophyllum sp. 10</em></td>
<td>leaf</td>
<td>rare</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td></td>
<td><em>Dicotylophyllum sp. 18</em></td>
<td>leaves</td>
<td>rare</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>16</td>
<td></td>
<td><em>Dicotylophyllum sp. 19</em></td>
<td>leaf</td>
<td>rare</td>
<td>1</td>
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</table>

*rare 1–5, common ≥6
## APPENDIX 8

Identified taxa in the three studied assemblages (Pitsidia, Kassanoi and Metochia)

<table>
<thead>
<tr>
<th>Nr.</th>
<th>Taxon</th>
<th>Pitsidia</th>
<th>Kassanoi</th>
<th>Metochia</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>Thallus, fam. et gen. et sp. indet.</td>
<td></td>
<td></td>
<td>√</td>
</tr>
<tr>
<td>2</td>
<td>“Pteris” oeningensis</td>
<td>√</td>
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<td>Frond fragments type 1, fam. et gen. et sp. indet.</td>
<td></td>
<td>√</td>
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<tr>
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<td></td>
<td>√</td>
</tr>
<tr>
<td>5</td>
<td><em>Tetraclinis</em> cf. <em>salicornioides</em></td>
<td>√</td>
<td>√</td>
<td>√</td>
</tr>
<tr>
<td>6</td>
<td><em>Taxodium</em> dubium</td>
<td></td>
<td></td>
<td>√</td>
</tr>
<tr>
<td>7</td>
<td><em>Pinus</em> <em>pitsidiensis</em></td>
<td></td>
<td></td>
<td>√</td>
</tr>
<tr>
<td>8</td>
<td><em>Pinus</em> sp. – two-needled fascicles</td>
<td></td>
<td></td>
<td>√</td>
</tr>
<tr>
<td>9</td>
<td><em>Pinus</em> sp. – fascicles bracts</td>
<td></td>
<td></td>
<td>√</td>
</tr>
<tr>
<td>10</td>
<td><em>Pinus</em> sp. 1 – ovulate cone scales</td>
<td></td>
<td></td>
<td>√</td>
</tr>
<tr>
<td>11</td>
<td><em>Pinus</em> sp. 1 – five-needled fascicles</td>
<td></td>
<td></td>
<td>√</td>
</tr>
<tr>
<td>12</td>
<td><em>Pinus</em> sp. 2 – five-needled fascicles</td>
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<td></td>
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<tr>
<td>13</td>
<td><em>Pinus</em> sp. 2 – ovulate cone scale</td>
<td></td>
<td></td>
<td>√</td>
</tr>
<tr>
<td>14</td>
<td><em>Pinus</em> sp. 1 – fully developed seeds</td>
<td></td>
<td></td>
<td>√</td>
</tr>
<tr>
<td>15</td>
<td><em>Pinus</em> sp. 2 – fully developed seeds</td>
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</tr>
<tr>
<td>16</td>
<td><em>Pinus</em> sp. 1 – undeveloped seeds</td>
<td></td>
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<tr>
<td>17</td>
<td><em>Pinus</em> sp. 1 – pollen cones</td>
<td></td>
<td></td>
<td>√</td>
</tr>
<tr>
<td>18</td>
<td><em>Pinus</em> sp. 1 – pollen cones</td>
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</tr>
<tr>
<td>19</td>
<td><em>Pinus</em> sp. – bud scales</td>
<td></td>
<td></td>
<td>√</td>
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<td>20</td>
<td>Pinaceae, gen. et sp. indet. – coalified wood</td>
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<tr>
<td>21</td>
<td>Leafy shoot, fam. et gen. et sp. indet.</td>
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<td>Long shoots, fam. et gen. et sp. indet.</td>
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<td>Needle-like leaves, fam. et gen. et sp. indet.</td>
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<td>Ovulate cone scale type 1, fam. et gen. et sp. indet.</td>
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<td>Ovulate cone scale type 2, fam. et gen. et sp. indet.</td>
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<td><em>Daphnogene polymorpha</em></td>
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<td>√</td>
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<tr>
<td>27</td>
<td>?<em>Lindera ovata</em></td>
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<tr>
<td>28</td>
<td>?<em>Lauraceae</em>, gen. et sp. indet. – folia</td>
<td></td>
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</tr>
<tr>
<td>29</td>
<td><em>Sabalites</em> sp.</td>
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<tr>
<td>30</td>
<td>?<em>Buxus pliocenica</em></td>
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<tr>
<td>31</td>
<td><em>Liquidambar europaea</em> – folia</td>
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<tr>
<td>32</td>
<td><em>Liquidambar europaea</em> – fructus</td>
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<td>33</td>
<td><em>Leguminosites</em> sp. 1</td>
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<td>34</td>
<td><em>Leguminosites</em> sp. 2</td>
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<td>?<em>Leguminosites</em> sp. 3</td>
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<td>36</td>
<td>?<em>Leguminosites</em> sp. 4</td>
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<td>37</td>
<td><em>Podocarpium podocarpum</em> – folia</td>
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<td>Species/Monocotylophyllum/Dicotylophyllum</td>
<td>Status</td>
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<tr>
<td>38</td>
<td><em>Podocarpium podocarpum</em> – fructus</td>
<td>✓</td>
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<tr>
<td>39</td>
<td><em>Mimosites</em> sp.</td>
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<td></td>
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<tr>
<td>40</td>
<td>?<em>Rosa</em> sp. – folia</td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td>41</td>
<td>Rosaceae, gen. et sp. indet. – folia</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>42</td>
<td><em>Berhemia multinervis</em></td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td>43</td>
<td>cf. <em>Ziziphus paradisiaca</em></td>
<td></td>
<td></td>
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<tr>
<td>44</td>
<td><em>Ulmus</em> cf. <em>plurinervia</em></td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td>45</td>
<td><em>Ulmus</em> sp. – fructus</td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td>46</td>
<td>?<em>Zelkova zelkoviifolia</em></td>
<td>✓</td>
<td></td>
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<td>47</td>
<td><em>Quercus pseudocastanea</em></td>
<td>✓</td>
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<td>48</td>
<td><em>Quercus</em> cf. <em>kubinyii</em></td>
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<td><em>Quercus mediterranea</em></td>
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<td>50</td>
<td><em>Quercus</em> sp. – folia</td>
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<tr>
<td>51</td>
<td><em>Fagus gussonii</em></td>
<td>✓</td>
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<td>106</td>
<td>?Carpolithus sp.</td>
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<td>107</td>
<td>?Septum</td>
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<td>Shoots – Wood fragments, fam. et gen. et sp. indet.</td>
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<td>Rhizom, fam. et gen. et sp. indet.</td>
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<td>114</td>
<td>Roots, fam. et gen. et sp. indet.</td>
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APPENDIX 9
a. Pitsidia, collection numbers for the most abundant taxa (>100 specimens)

Pinus pitsidiensis ZIDIANAKIS, ILIOPOULOS, ZELILIDIS and KOVAR-EDER
Long shoots (branchlets)
Material: Nrs 31.4.2.1730; 31.4.2.1892i; 31.4.2.1905ii; 31.4.2.1916; 31.4.2.1977i; 31.4.2.2007ii; 31.4.2.2010a,b;
31.4.2.2012; 31.4.2.2013a,b; 31.4.2.2014a,b; 31.4.2.2110; 31.4.2.2141a,b; 31.4.2.2151i,2147i; 31.4.2.2274;
31.4.2.2304i; 31.4.2.2365a,b; 31.4.2.2640a,b; 31.4.2.2968; 31.4.2.3065ai-c; 31.4.2.3065biii; 31.4.2.3110,3156;
31.4.2.3146a,bi; 31.4.2.3698ai,bi; 31.4.2.3748a,b; 31.4.2.3853i; 31.4.2.3853ii; 31.4.2.3986i; 31.4.2.3988ai,b;
31.4.2.3990ai,b; 31.4.2.3992; 31.4.2.4008ii; 31.4.2.4057; 31.4.2.4191,4194ii; 31.4.2.4288; 31.4.2.4461aiii; 31.4.2.4560;
31.4.2.4625ii; 31.4.2.4658a,bi; 31.4.2.4660; 31.4.2.4836i; 31.4.2.4925a,b; 31.4.2.4970i; 31.4.2.4970iii; 31.4.2.4994i;
31.4.2.5149; 31.4.2.5288aiv,biv; 31.4.2.5393; 31.4.2.5919; 31.4.2.5976a,bi; 31.4.2.5996ii; 31.4.2.6346a,b;
31.4.2.6437aopi; 31.4.2.6984; 31.4.2.7024. Additionally, the holotype and the paratypes.

Dwarf shoots
Material: Nrs 31.4.2.896a,b; 31.4.2.963ai,bi; 31.4.2.972aii; 31.4.2.1019i; 31.4.2.1041aiii,biii; 31.4.2.1132;
31.4.2.1134i; 31.4.2.1153i; 31.4.2.1171; 31.4.2.1175; 31.4.2.1209; 31.4.2.1212; 31.4.2.1214; 31.4.2.1270op;
31.4.2.1290i; 31.4.2.1313; 31.4.2.1314i; 31.4.2.1314ii; 31.4.2.1323i; 31.4.2.1333; 31.4.2.1335; 31.4.2.1359;
31.4.2.1368ii; 31.4.2.1385; 31.4.2.1437op; 31.4.2.1453; 31.4.2.1458i; 31.4.2.1482,1481op; 31.4.2.1492a,b; 31.4.2.1514;
31.4.2.1517aop; 31.4.2.1563bii; 31.4.2.1564; 31.4.2.1565; 31.4.2.1568; 31.4.2.1576aopi; 31.4.2.1576aopii;
31.4.2.1584ii,1582v; 31.4.2.1585aii,bii; 31.4.2.1621; 31.4.2.1635aopi,1643i; 31.4.2.1638i; 31.4.2.1641i,1648opi;
31.4.2.1649; 31.4.2.1652; 31.4.2.1658,1654i; 31.4.2.1663bopii; 31.4.2.1669aop; 31.4.2.1686; 31.4.2.1700; 31.4.2.1702;
31.4.2.1703i; 31.4.2.1715aii,bii; 31.4.2.1727i; 31.4.2.1732; 31.4.2.1769; 31.4.2.1786; 31.4.2.1823i,1817opi;
31.4.2.1855; 31.4.2.1859; 31.4.2.1870i; 31.4.2.1876; 31.4.2.1885; 31.4.2.1892ii; 31.4.2.1917i; 31.4.2.1995opii;
31.4.2.2010ai,bi; 31.4.2.2018aii; 31.4.2.2064; 31.4.2.2066aopi; 31.4.2.2068; 31.4.2.2076; 31.4.2.2093ii; 31.4.2.2097i;
31.4.2.2101; 31.4.2.2102; 31.4.2.2105ii; 31.4.2.2109; 31.4.2.2125i; 31.4.2.2183aiv,biv; 31.4.2.2208; 31.4.2.2217;
31.4.2.2218i; 31.4.2.2221; 31.4.2.2224; 31.4.2.2237a,b; 31.4.2.2239op; 31.4.2.2252; 31.4.2.2287bop; 31.4.2.2288i;
31.4.2.2299; 31.4.2.2300ii; 31.4.2.2306; 31.4.2.2327a,b; 31.4.2.2330; 31.4.2.2351; 31.4.2.2354; 31.4.2.2357i;
31.4.2.2364; 31.4.2.2383; 31.4.2.2402; 31.4.2.2407; 31.4.2.2410a,b; 31.4.2.2416ai,bi; 31.4.2.2440aii,bii;
31.4.2.2461a,bi; 31.4.2.2466; 31.4.2.2503; 31.4.2.2518; 31.4.2.2526i; 31.4.2.2526ii; 31.4.2.2537; 31.4.2.2560;
31.4.2.2562; 31.4.2.2574aop,b; 31.4.2.2577; 31.4.2.2587a-c; 31.4.2.2590bop; 31.4.2.2610; 31.4.2.2613; 31.4.2.2660;
31.4.2.2679ai-d; 31.4.2.2689a,b; 31.4.2.2690; 31.4.2.2701; 31.4.2.2723b; 31.4.2.2724a,b; 31.4.2.2738opi; 31.4.2.2742;
31.4.2.2784; 31.4.2.2791a,b; 31.4.2.2802; 31.4.2.2853aiii,ciii; 31.4.2.2853aiv,civ; 31.4.2.2913i; 31.4.2.2939,2907aii;
31.4.2.2948i; 31.4.2.3029; 31.4.2.3048fii; 31.4.2.3053; 31.4.2.3054ai,bi; 31.4.2.3054aii,bii; 31.4.2.3095a,b;
31.4.2.3117ai,b; 31.4.2.3131; 31.4.2.3137aop; 31.4.2.3160; 31.4.2.3174i; 31.4.2.3175i; 31.4.2.3206; 31.4.2.3227;
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31.4.2.3372iv; 31.4.2.3456a,b; 31.4.2.3460; 31.4.2.3465i; 31.4.2.3466; 31.4.2.3467i; 31.4.2.3468; 31.4.2.3472;
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31.4.2.3571; 31.4.2.3609bop; 31.4.2.3620; 31.4.2.3635opi; 31.4.2.3642ai,bi; 31.4.2.3651; 31.4.2.3655; 31.4.2.3660;
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31.4.2.4268ai,b; 31.4.2.4301; 31.4.2.4316ai; 31.4.2.4316aop; 31.4.2.4331; 31.4.2.4332; 31.4.2.4338ai,bi;
31.4.2.4339aii; 31.4.2.4340aii; 31.4.2.4355; 31.4.2.4358i; 31.4.2.4362opi; 31.4.2.4381; 31.4.2.4394i; 31.4.2.4399;
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31.4.2.4651ai; 31.4.2.4693; 31.4.2.4695; 31.4.2.4728ii; 31.4.2.4730; 31.4.2.4770; 31.4.2.4789; 31.4.2.4806i,4799i;
31.4.2.4837a,b; 31.4.2.4894; 31.4.2.4895; 31.4.2.4934; 31.4.2.5054; 31.4.2.5110ai; 31.4.2.5115op; 31.4.2.5117i;
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Additionally, the paratypes.
Pinus sp. – fascicle bracts

Material: Nrs 31.4.2.810op; 31.4.2.829; 31.4.2.907ii; 31.4.2.963biv; 31.4.2.972aop; 31.4.2.979biii; 31.4.2.1103; 31.4.2.1131; 31.4.2.1148a,b; 31.4.2.1234; 31.4.2.1256ii;i; 31.4.2.1269ii; 31.4.2.1279op; 31.4.2.1324v; 31.4.2.1328i; 31.4.2.1332ii; 31.4.2.1562op; 31.4.2.1409; 31.4.2.1419bop; 31.4.2.1421a;ii; 31.4.2.1432; 31.4.2.1433op;i; 31.4.2.1445i; 31.4.2.1446; 31.4.2.1447; 31.4.2.1448ii; 31.4.2.1452op; 31.4.2.1458ii; 31.4.2.1466; 31.4.2.1467; 31.4.2.1470ai;b; 31.4.2.1470aii;i; 31.4.2.1478bop; 31.4.2.1486; 31.4.2.1489; 31.4.2.1497ai;ibi; 31.4.2.1521; 31.4.2.1543ii; 31.4.2.1552i; 31.4.2.1554; 31.4.2.1555i; 31.4.2.1582ii; 31.4.2.1591vii; 31.4.2.1601,1605; 31.4.2.1610; 31.4.2.1617i; 31.4.2.1643ii,1635aopvii; 31.4.2.1662; 31.4.2.1715aiv; 31.4.2.1721; 31.4.2.1739; 31.4.2.1756op; 31.4.2.1785ii; 31.4.2.1832ii,1817opii; 31.4.2.1900; 31.4.2.1915,1893ii; 31.4.2.1929; 31.4.2.1935; 31.4.2.1944ii; 31.4.2.2020ii; 31.4.2.2029; 31.4.2.2038; 31.4.2.2070; 31.4.2.2085op; 31.4.2.2092; 31.4.2.2096; 31.4.2.2118; 31.4.2.2122op; 31.4.2.2130; 31.4.2.2148biii;219i;ii; 31.4.2.2197ii; 31.4.2.2197op; 31.4.2.2216; 31.4.2.2228; 31.4.2.2253; 31.4.2.2257; 31.4.2.2264; 31.4.2.2266aii; 31.4.2.2276aoppi; 31.4.2.2323; 31.4.2.2326aoppi; 31.4.2.2326aopvi; 31.4.2.2349; 31.4.2.2353; 31.4.2.2370ai;ibi;ii; 31.4.2.2398ii; 31.4.2.2403ii; 31.4.2.2419; 31.4.2.2421ii; 31.4.2.2422ii; 31.4.2.2452op; 31.4.2.2461bii; 31.4.2.2461bop; 31.4.2.2489aop; 31.4.2.2496opii; 31.4.2.2522aop; 31.4.2.2646; 31.4.2.2668; 31.4.2.2717ii; 31.4.2.2721bop;
Material: 

Nrs 31.4.2.818biii; 31.4.2.1030a;i; 31.4.2.1109; 31.4.2.1111i; 31.4.2.121i; 31.4.2.121ii; 31.4.2.1223aop; 31.4.2.1276; 31.4.2.1289ii; 31.4.2.1293ii; 31.4.2.1320ii; 31.4.2.1323iii; 31.4.2.1324; 31.4.2.1339ii; 31.4.2.1346ii; 31.4.2.1371opiii; 31.4.2.1373ii; 31.4.2.1423ai; 31.4.2.1449; 31.4.2.1455; 31.4.2.1474i; 31.4.2.1550; 31.4.2.1551i; 31.4.2.1552ii; 31.4.2.1553; 31.4.2.1556aop; 31.4.2.1562bii; 31.4.2.1576aopii; 31.4.2.1578ii; 31.4.2.1581; 31.4.2.1582iv; 31.4.2.1588ii; 31.4.2.1591vii; 31.4.2.15959ii; 31.4.2.1602aii; 31.4.2.1611aivi; 31.4.2.1641iii; 1635aopix; 31.4.2.1645ii; 31.4.2.1659; 31.4.2.1682; 31.4.2.1709aii; 31.4.2.1715aiii; 31.4.2.1727ii; 31.4.2.1728opii; 31.4.2.1752; 31.4.2.1775; 31.4.2.1817i; 31.4.2.1851; 31.4.2.1861; 31.4.2.1870ii; 31.4.2.1889; 31.4.2.1976ii; 31.4.2.1976iv; 31.4.2.1990opii; 31.4.2.2066aiv; 31.4.2.2075; 31.4.2.2080; 31.4.2.2089; 31.4.2.2103aop; 31.4.2.2122ii; 31.4.2.2125ii; 31.4.2.2172; 31.4.2.2179op; 31.4.2.2218s; 31.4.2.2211ii; 31.4.2.2281ii; 31.4.2.2223; 31.4.2.2226ii; 31.4.2.2244; 31.4.2.2267bopii; 31.4.2.2283ii; 31.4.2.2290; 31.4.2.2298bii; 31.4.2.2326bv; 31.4.2.2328; 31.4.2.2344i;

Pinus sp. – bud scales
Isolated fruits

**Material:** Nrs 31.4.2.815aiii,bi; 31.4.2.1020ao; 31.4.2.1156ao; 31.4.2.1307bo; 31.4.2.1562ai,bi; 31.4.2.1598; 31.4.2.1715vi; 31.4.2.2140ai; 31.4.2.2149ai,bi; 31.4.2.2276aoop; 31.4.2.2289aii; 31.4.2.2507a,bi; 31.4.2.2825; 31.4.2.2912a; 31.4.2.2917ii; 31.4.2.3044,3041; 31.4.2.3048avii; 31.4.2.3189op; 31.4.2.3257ii; 31.4.2.3341a,bi; 31.4.2.3476ao; 31.4.2.3476op; 31.4.2.3482bo; 31.4.2.3490,3495ao; 31.4.2.3491iv; 31.4.2.3525ii; 31.4.2.3582ii; 31.4.2.3585aii; 31.4.2.3586; 31.4.2.3599; 31.4.2.3627biv; 31.4.2.3741ao; 31.4.2.3742ii; 31.4.2.3755; 31.4.2.3807bop; 31.4.2.3827bop; 31.4.2.3925ii; 31.4.2.3935; 31.4.2.3948; 31.4.2.3958ao; 31.4.2.3958avi; 31.4.2.4028ai; 31.4.2.4121aiii,bi; 31.4.2.4164bi; 31.4.2.4222; 31.4.2.4273ai; 31.4.2.4284ao; 31.4.2.4329i; 31.4.2.4333; 31.4.2.4360aii; 31.4.2.4456bo; 31.4.2.4462ao; 31.4.2.4464; 31.4.2.4474i; 31.4.2.4537ao; 31.4.2.4551; 31.4.2.4604op; 31.4.2.4607avo; 31.4.2.4617; 31.4.2.4616i; 31.4.2.4641ai; 31.4.2.4646; 31.4.2.4976ii; 31.4.2.5036a,bi; 31.4.2.5085i; 31.4.2.5181ii; 31.4.2.5212bop; 31.4.2.5254a,bi; 31.4.2.5286; 31.4.2.530hai,bi; 31.4.2.5477ii; 31.4.2.5492ii; 31.4.2.5512i; 31.4.2.5525; 31.4.2.5526; 31.4.2.5580; 31.4.2.5652; 31.4.2.5656i; 31.4.2.5699op; 31.4.2.5847ai; 31.4.2.5889; 31.4.2.5908ao; 31.4.2.5962i; 31.4.2.5973; 31.4.2.5981op; 31.4.2.6081iv; 31.4.2.6160i; 31.4.2.6161,6167; 31.4.2.6176; 31.4.2.6211; 31.4.2.6217ai; 31.4.2.6256a,bi; 31.4.2.6311; 31.4.2.6336; 31.4.2.6374i; 31.4.2.6423; 31.4.2.6444iv; 31.4.2.6447i; 31.4.2.6461ai,bi; 31.4.2.6478biv; 31.4.2.6493ao; 31.4.2.6637a,b; 31.4.2.6712aiii; 31.4.2.6835ii; 31.4.2.6871opb; 31.4.2.6942aio; 31.4.2.6957; 31.4.2.6967op; 31.4.2.6985; 31.4.2.7013ii; 31.4.2.7013ii; 31.4.2.7035; 31.4.2.8030,8049.

Fruiting stalks with at least one fruit attached

**Material:** Nrs 31.4.2.2066ao; 31.4.2.2762a,bi; 31.4.2.3671ii; 31.4.2.4148ai,bi; 31.4.2.4214ai,bi; 31.4.2.4325; 31.4.2.4474i; 31.4.2.4541ao; 31.4.2.4607ai; 31.4.2.4541; 31.4.2.4545; 31.4.2.5609,31.4.2.565a,bi; 31.4.2.5785avii; 31.4.2.5863a,bi; 31.4.2.5977ii,5976ao; 31.4.2.6162ii; 31.4.2.6266; 31.4.2.6619; 31.4.2.7033a,bi; 31.4.2.8071; 31.4.2.8074op; 31.4.2.8103a,bi; 31.4.2.8228op.

Fruiting stalks

**Material:** Nrs 31.4.2.2906; 31.4.2.1259,1223opiv; 31.4.2.1730op; 31.4.2.2494ai,bi; 31.4.2.261,12647ii; 31.4.2.2853avi; 31.4.2.2891; 31.4.2.2959a,b; 31.4.2.3013ao; 31.4.2.3032; 31.4.2.3525ii; 31.4.2.3841i; 31.4.2.3988a; 31.4.2.4236a,bi; 31.4.2.4357ai,bi; 31.4.2.4466,4458ao; 31.4.2.4467a,bi; 31.4.2.4643a,bi; 31.4.2.5077a,bi; 31.4.2.5078a,b; 31.4.2.5207a,bi; 31.4.2.5376; 31.4.2.5471ai,bi; 31.4.2.5520; 31.4.2.5533; 31.4.2.5578; 31.4.2.5658; 31.4.2.5672; 31.4.2.5728; 31.4.2.5786ii; 31.4.2.5787ai; 31.4.2.6142iv; 31.4.2.6159; 31.4.2.6277av; 31.4.2.6390ii; 31.4.2.6437a,bi; 31.4.2.6438; 31.4.2.6680; 31.4.2.6886; 31.4.2.8067; 31.4.2.8251.
b. Explanation of the fossil collection numbers

Wood fragments (as inorganic replicas)
APPENDIX 10 Table 1. Simplified systematic scheme of genus *Pinus* sensu GERNANDT et al. (2005)

<table>
<thead>
<tr>
<th>Subgenus</th>
<th>Section</th>
<th>Subsection</th>
<th>Number of species (aprox.)</th>
<th>Distribution</th>
<th>Selected species (common or referred in the text)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pinus</em></td>
<td><em>Pinus</em></td>
<td><em>Pinus</em> L.</td>
<td>17</td>
<td>Eurasia and two North and Central America species*</td>
<td><em>P. kesiya</em> ROYLE ex GORDON, <em>P. massoniana LAMBERT, <em>P. resinosa AITON</em>, <em>P. sylvestris</em> L., <em>P. tropicalis</em> MORELET</em>, <em>P. yunnanensis</em> FRANCHET P. brutia TENORE, <em>P. canariensis</em> C. SMITH, <em>P. halepensis</em> MILLER, <em>P. pinaster</em> AITON, <em>P. roxburghii</em> SARGENT, <em>P. pinea</em> L.</td>
</tr>
</tbody>
</table>
|                    | Trifoliae       | *Contortae LITTLE et CRICHFIELD* | 4                          | America                                               | *P. banksiana* LAMBERT, *P. condorta* DOUGLAS  
|                 | *Australis* LOUDON|                             | 26                         | Eastern North America, Central America                | *P. banksiana* LAMBERT, *P. condorta* DOUGLAS  
|                 | *Ponderosae* LOUDON|                             | 17                         | Western North America, Central America, Caribbean     | *P. banksiana* LAMBERT, *P. condorta* DOUGLAS  
| *Strobus*       | *Parrya*         | *Balfourianae* ENGELMANN    | 3                          | North and Central America                             | *P. banksiana* BALFOUR  
*P. cembroides* ZUCCARINI, *P. culminicola ANDERSEN and BEAMAN, *P. monophylla TORREY et FREMONT                                                                                                                                   |
|                 |                  | *Cembroides* ENGELMANN      | 11                         | North and Central America                             | *P. banksiana* BALFOUR  
*P. cembroides* ZUCCARINI, *P. culminicola ANDERSEN and BEAMAN, *P. monophylla TORREY et FREMONT                                                                                                                                   |
|                 |                  | *Nelsoniae* VAN DER BURGH   | 1                          | Central (Northeastern Mexico) America                 | *P. nelsonii* SHAW  
*P. banksiana* BALFOUR  
*P. cembroides* ZUCCARINI, *P. culminicola ANDERSEN and BEAMAN, *P. monophylla TORREY et FREMONT                                                                                                                                   |
|                 | *Quinquefoliae*  | *Gerardianae* LOUDON        | 3                          | Asia                                                   | *P. banksiana* BALFOUR  
*P. cembroides* ZUCCARINI, *P. culminicola ANDERSEN and BEAMAN, *P. monophylla TORREY et FREMONT                                                                                                                                   |
|                 |                  | *Krempfianae* LITTLE et CRICHFIELD | 1                          | Asia (Vietnam)                                        | *P. banksiana* BALFOUR  
*P. cembroides* ZUCCARINI, *P. culminicola ANDERSEN and BEAMAN, *P. monophylla TORREY et FREMONT                                                                                                                                   |
|                 | *Strobus* LOUDON |                             | 21                         | North and Central America, Eurasia                    | *P. banksiana* BALFOUR  
*P. cembroides* ZUCCARINI, *P. culminicola ANDERSEN and BEAMAN, *P. monophylla TORREY et FREMONT                                                                                                                                   |
Table 2. Relevant foliage features that differentiate the genus *Pinus* at the sub-sectional level (composed from Shaw, 1914; Little et Critchfield, 1969; Price et al., 1998; Farjon, 2005; Gernandt et al., 2005); with grey the features that appear in *P. pitsidiensis*

<table>
<thead>
<tr>
<th>Subgenus</th>
<th>Pinus</th>
<th>Trifoliae</th>
<th>Parrya</th>
<th>Quinquefoliae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Section</td>
<td>Pinus</td>
<td>Pinaster</td>
<td>Contortae</td>
<td>Australes</td>
</tr>
<tr>
<td>Subsect.</td>
<td>Pinus</td>
<td>Pinaster</td>
<td>Contortae</td>
<td>Australes</td>
</tr>
<tr>
<td>Needle vascular bundles</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fascicle bract attachment</td>
<td>mostly decurrent</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal fascicle sheath</td>
<td>Persistent</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stoma distribution</td>
<td>amphistomatic</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Num. of needles per fascicle</td>
<td>2 (3)</td>
<td>2 (3)</td>
<td>2</td>
<td>2-5 mainly 3</td>
</tr>
<tr>
<td>Resin ducts</td>
<td>medial, external (septal)</td>
<td>medial</td>
<td>medial</td>
<td>septal, internal, medial</td>
</tr>
</tbody>
</table>

337
Table 3. The three-needled pine fossil species that are compared in this study to *P. pitzidiensis*

<table>
<thead>
<tr>
<th>Nr.</th>
<th>Species</th>
<th>Length (cm)</th>
<th>Width (mm)</th>
<th>Margin</th>
<th>Other</th>
<th>Sheath Length (mm)</th>
<th>Width</th>
<th>Other</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>P. debilis</em></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>very short</td>
<td>–</td>
<td>3 or 4-needled</td>
<td>SAPORTA, 1867&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>2</td>
<td><em>P. divaricata</em></td>
<td>moderate / about 15</td>
<td>thin / less than 1</td>
<td>–</td>
<td>–</td>
<td>short</td>
<td>–</td>
<td>–</td>
<td>SAPORTA, 1865&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>3</td>
<td><em>P. diversifolia</em></td>
<td>c.a. 15–20</td>
<td>thin / less than 1</td>
<td>–</td>
<td>–</td>
<td>short</td>
<td>–</td>
<td>2 or 3-needled</td>
<td>SAPORTA, 1862</td>
</tr>
<tr>
<td>4</td>
<td><em>P. dolichophylla</em></td>
<td>–</td>
<td>2.5</td>
<td>serrulate</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>CASPARY and KLEBS, 1907</td>
</tr>
<tr>
<td>5</td>
<td><em>P. goethana</em></td>
<td>c.a. 2.5</td>
<td>thin</td>
<td>–</td>
<td>slightly curved</td>
<td>short</td>
<td>–</td>
<td>–</td>
<td>UNGER, 1850&lt;sup&gt;a&lt;/sup&gt;; 1852; A. BRAUN, 1851</td>
</tr>
<tr>
<td>6</td>
<td><em>P. gracilis</em></td>
<td>elongate / about 10</td>
<td>very thin / less than 1</td>
<td>scabrous–serrulate</td>
<td>–</td>
<td>very short</td>
<td>–</td>
<td>always 3-needled</td>
<td>SAPORTA, 1862</td>
</tr>
<tr>
<td>7</td>
<td><em>P. hellenica</em></td>
<td>more than 15 cm / 16–20</td>
<td>c.a. 1</td>
<td>–</td>
<td>–</td>
<td>short</td>
<td>–</td>
<td>–</td>
<td>SAPORTA, 1867&lt;sup&gt;a&lt;/sup&gt;; 1868</td>
</tr>
<tr>
<td>8</td>
<td><em>P. holothana</em></td>
<td>15.5</td>
<td>2</td>
<td>–</td>
<td>rigid, sharply keeled</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>UNGER, 1867</td>
</tr>
<tr>
<td>9</td>
<td><em>P. kunowii</em></td>
<td>–</td>
<td>2</td>
<td>entire</td>
<td>stomata rows 6 adax. and 10 abax.</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>CASPARY and KLEBS, 1907</td>
</tr>
<tr>
<td>10</td>
<td><em>P. orbicularis</em></td>
<td>4</td>
<td>1</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>LUDWIG, 1860</td>
</tr>
<tr>
<td>11</td>
<td><em>P. palaeotaeda</em></td>
<td>6–14</td>
<td>1.0–1.2</td>
<td>–</td>
<td>–</td>
<td>extended</td>
<td>narrow</td>
<td>–</td>
<td>ETTINGSHAUSEN, 1872 as <em>P. palaeotaeda</em></td>
</tr>
<tr>
<td>12</td>
<td><em>P. posttaedaeforis</em></td>
<td>more than 10.5–13</td>
<td>up to 1.3</td>
<td>–</td>
<td>–</td>
<td>more than 14</td>
<td>–</td>
<td>–</td>
<td>ETTINGSHAUSEN, 1878, 1890</td>
</tr>
<tr>
<td>13</td>
<td><em>P. pretaedaeforis</em></td>
<td>short</td>
<td>thin</td>
<td>–</td>
<td>–</td>
<td>short</td>
<td>–</td>
<td>–</td>
<td>ETTINGSHAUSEN, 1878, 1890 as <em>pre-taedaeforis</em></td>
</tr>
<tr>
<td>14</td>
<td><em>P. pseudotaeda</em></td>
<td>10</td>
<td>thin</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>3 or 4-needled</td>
<td>SAPORTA, 1865&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
**Horizontal Table:**

<table>
<thead>
<tr>
<th>#</th>
<th>Species</th>
<th>Category</th>
<th>Characteristics</th>
<th>Measurements</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td><em>P. resurgens</em></td>
<td>c.a. 12</td>
<td>broad / c.a. 2</td>
<td>serrulate</td>
<td>erect 6–7</td>
</tr>
<tr>
<td>16</td>
<td><em>Pinites rigidus</em></td>
<td>short&lt;sup&gt;*&lt;/sup&gt;</td>
<td>thin&lt;sup&gt;*&lt;/sup&gt;</td>
<td>serrulate</td>
<td>rigid, keeled</td>
</tr>
<tr>
<td>17</td>
<td><em>P. rigios</em></td>
<td>more than 6.6, 12.5–15</td>
<td>broad, 2–3</td>
<td>entire</td>
<td>rigid, occasionally bended extended, 13</td>
</tr>
<tr>
<td>18</td>
<td><em>P. cf. rigios</em></td>
<td>more than 14</td>
<td>up to 1.8</td>
<td>serrulate</td>
<td>stomata rows 6–10 adax. and 4–6 abax. up to 10</td>
</tr>
<tr>
<td>19</td>
<td><em>P. saturni</em></td>
<td>c.a. 18</td>
<td>up to 0.55</td>
<td>–</td>
<td>rigid or basically curved extended, 15.5</td>
</tr>
<tr>
<td>20</td>
<td><em>P. schiefferdeckeri</em></td>
<td>–</td>
<td>0.5</td>
<td>serrulate</td>
<td>–</td>
</tr>
<tr>
<td>21</td>
<td><em>P. sodalis</em></td>
<td>10–11</td>
<td>c.a. 1</td>
<td>scabrous</td>
<td>slightly flexus</td>
</tr>
<tr>
<td>22</td>
<td><em>P. subrigida</em></td>
<td>7.5–10</td>
<td>–</td>
<td>serrulate</td>
<td>–</td>
</tr>
<tr>
<td>23</td>
<td><em>P. taedaeformis</em></td>
<td>10.5–13</td>
<td>thin / less than 1&lt;sup&gt;*&lt;/sup&gt;</td>
<td>–</td>
<td>extended narrow</td>
</tr>
<tr>
<td>24</td>
<td><em>P. trichophylla</em></td>
<td>17–20</td>
<td>very thin / ca. 1</td>
<td>serrulate</td>
<td>erect, sub-flexous moderate</td>
</tr>
<tr>
<td>25</td>
<td><em>P. vetustior</em></td>
<td>4</td>
<td>moderate / c.a. 1&lt;sup&gt;*&lt;/sup&gt;</td>
<td>erect, close stand, keeled</td>
<td>moderate</td>
</tr>
</tbody>
</table>

<sup>*</sup> measurements derived from the drawings
APPENDIX 11

Relevant features to differentiate the genus *Myrica* at the subgeneric level (composed from *Chevalier*, 1901; *Baird*, 1968; *Chourey*, 1974; *Wilbur*, 1994; *Herbert*, 2005), *a* sensu *Chevalier* 1901; *b* sensu *Wilbur*, 1994.

<table>
<thead>
<tr>
<th></th>
<th><em>Myrica subgen. Gale</em></th>
<th><em>Myrica subgen. Morella</em></th>
<th><em>sect. Morella</em></th>
<th><em>sect. Faya</em></th>
<th><em>sect. Cerophora</em> or series <em>Cerothamnus</em></th>
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<tr>
<td><strong>leaf</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>texture</td>
<td>chartaceous, deciduous</td>
<td>coriaceous, usually evergreen</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>margin</td>
<td>entire or toothed</td>
<td>entire or toothed</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stipules</td>
<td>absent</td>
<td>absent</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stomata</td>
<td>sunken</td>
<td>not sunken</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>glands</td>
<td>-</td>
<td>balloon with two-celled stalk base</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Male flower</strong></td>
<td>3–6 (9) usually 4</td>
<td>8 or more</td>
<td>fused into a branched staminal column</td>
<td>fused into a branched staminal column</td>
<td>less than 7</td>
</tr>
<tr>
<td>stamens</td>
<td>free</td>
<td>free</td>
<td>fused into a branched staminal column</td>
<td>fused into a branched staminal column</td>
<td>less than 7</td>
</tr>
<tr>
<td>filaments</td>
<td>free</td>
<td>free</td>
<td>fused into a branched staminal column</td>
<td>fused into a branched staminal column</td>
<td>less than 7</td>
</tr>
<tr>
<td>anthers</td>
<td>-</td>
<td>2 per staminal column branch</td>
<td>one per staminal column branch</td>
<td></td>
<td></td>
</tr>
<tr>
<td>bracteoles</td>
<td>4</td>
<td>2–6</td>
<td>0–3</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Male catkin</strong></td>
<td>form</td>
<td>simple</td>
<td>branched</td>
<td>simple or branched</td>
<td>usually simple</td>
</tr>
<tr>
<td><strong>Female flower</strong></td>
<td>pistils</td>
<td>-</td>
<td>1–3 in the axil of each bract</td>
<td>one in the axil of each bract</td>
<td></td>
</tr>
<tr>
<td><strong>Fruit</strong></td>
<td>form</td>
<td>smooth nut subtended by 2 bracteoles</td>
<td>drupe</td>
<td>drupe</td>
<td>drupe</td>
</tr>
<tr>
<td>form</td>
<td>smooth nut covered by protuberances</td>
<td>6–8 mm in diam. covered by protuberances</td>
<td>4–6 mm in diam. covered by protuberances</td>
<td>1–5 mm in diam. covered by protuberances</td>
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<tr>
<td>exocarp</td>
<td>thin</td>
<td>thin</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Infructescence</strong></td>
<td>form</td>
<td>in dense subcylindrical spikes</td>
<td>in loose clusters</td>
<td></td>
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</tr>
</tbody>
</table>

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APPENDIX 12

Table 1. Pitsidia assemblage, abundances of the most common taxa in the different levels within layer MFL and in layer FL2

<table>
<thead>
<tr>
<th>Layer</th>
<th>Level</th>
<th>Myrica lignitum</th>
<th>Myrica cf. goeppertii</th>
<th>Pinus pitsidiensis</th>
<th>Pinus sp. fascicle bracts</th>
<th>Quercus pseudocastanea</th>
<th>Taxodium dubium</th>
<th>Daphnogene polymorpha</th>
</tr>
</thead>
<tbody>
<tr>
<td>MFL Level 1</td>
<td>41.75</td>
<td>6.31</td>
<td>7.75</td>
<td>2.15</td>
<td>2.15</td>
<td>2.58</td>
<td>1.43</td>
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<tr>
<td>Level 2</td>
<td>34.21</td>
<td>6.04</td>
<td>15.79</td>
<td>6.10</td>
<td>1.46</td>
<td>1.18</td>
<td>0.32</td>
<td></td>
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<tr>
<td>Level 3</td>
<td>30.72</td>
<td>7.83</td>
<td>13.38</td>
<td>5.78</td>
<td>1.17</td>
<td>0.47</td>
<td>1.23</td>
<td></td>
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<tr>
<td>Level 4</td>
<td>32.82</td>
<td>7.77</td>
<td>6.81</td>
<td>5.18</td>
<td>1.25</td>
<td>0.58</td>
<td>1.54</td>
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<tr>
<td>Level 5</td>
<td>34.99</td>
<td>9.92</td>
<td>10.86</td>
<td>3.89</td>
<td>1.88</td>
<td>0.67</td>
<td>0.54</td>
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<tr>
<td>Level 6</td>
<td>39.87</td>
<td>8.64</td>
<td>10.96</td>
<td>6.64</td>
<td>0.33</td>
<td>1.00</td>
<td>0.33</td>
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<tr>
<td>FL 2 (17cm)</td>
<td>27.97</td>
<td>4.90</td>
<td>6.99</td>
<td>7.69</td>
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<td>0.00</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td></td>
<td>34.62</td>
<td>7.34</td>
<td>10.36</td>
<td>5.35</td>
<td>1.18</td>
<td>0.92</td>
<td>0.77</td>
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Table 2. Pitsidia assemblage, abundances of the most common taxa in six different grid squares within layer MFL

<table>
<thead>
<tr>
<th>Grid square</th>
<th>Myrica lignitum</th>
<th>Myrica cf. goeppertii</th>
<th>Pinus pitsidiensis</th>
<th>Pinus sp. fascicle bracts</th>
<th>Quercus pseudocastanea</th>
<th>Taxodium dubium</th>
<th>Daphnogene polymorpha</th>
</tr>
</thead>
<tbody>
<tr>
<td>5B</td>
<td>34.75</td>
<td>9.82</td>
<td>10.72</td>
<td>3.75</td>
<td>1.94</td>
<td>0.65</td>
<td>0.52</td>
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<tr>
<td>5C</td>
<td>32.12</td>
<td>7.71</td>
<td>6.62</td>
<td>0.45</td>
<td>1.18</td>
<td>0.64</td>
<td>1.72</td>
</tr>
<tr>
<td>6C</td>
<td>27.63</td>
<td>7.21</td>
<td>10.21</td>
<td>3.73</td>
<td>1.34</td>
<td>0.81</td>
<td>0.65</td>
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<tr>
<td>7C</td>
<td>44.50</td>
<td>5.05</td>
<td>18.79</td>
<td>2.75</td>
<td>0.62</td>
<td>1.60</td>
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<tr>
<td>8B</td>
<td>35.20</td>
<td>7.06</td>
<td>23.08</td>
<td>6.24</td>
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<tr>
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<td>44.63</td>
<td>6.10</td>
<td>6.10</td>
<td>2.20</td>
<td>2.93</td>
<td>2.93</td>
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<td>7.16</td>
<td>12.59</td>
<td>3.19</td>
<td>1.68</td>
<td>1.21</td>
<td>0.78</td>
</tr>
</tbody>
</table>

Average
### APPENDIX 13

Pitsidia systematic excavation, detected fossils in the sediment block Nr. 13

<table>
<thead>
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<th>Nr.</th>
<th>Identification</th>
<th>Organ/Part</th>
<th>Fragmentation</th>
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<td>?</td>
<td>bone</td>
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</tr>
<tr>
<td>2</td>
<td>?</td>
<td>bone</td>
<td>-</td>
</tr>
<tr>
<td>3</td>
<td>?</td>
<td>bone</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>?</td>
<td>bone</td>
<td>-</td>
</tr>
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<td>5</td>
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<tr>
<td>6</td>
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<td>bone</td>
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<tr>
<td>7</td>
<td>?</td>
<td>bone</td>
<td>-</td>
</tr>
<tr>
<td>8</td>
<td>?</td>
<td>bone</td>
<td>-</td>
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<td>9</td>
<td>Myrica cf. goeppertii</td>
<td>catkin</td>
<td>almost entire</td>
</tr>
<tr>
<td>10</td>
<td>Myrica cf. goeppertii</td>
<td>catkin</td>
<td>almost entire?</td>
</tr>
<tr>
<td>11</td>
<td>Myrica cf. goeppertii</td>
<td>catkin</td>
<td>almost entire?</td>
</tr>
<tr>
<td>12</td>
<td>Pinus sp.</td>
<td>fascicle bract</td>
<td>complete</td>
</tr>
<tr>
<td>13</td>
<td>?</td>
<td>leaf</td>
<td>complete, small</td>
</tr>
<tr>
<td>14</td>
<td>?</td>
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<td>fragment&lt;1/6</td>
</tr>
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<td>?Carya sp.</td>
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<td>fragment&lt;1/6</td>
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<tr>
<td>16</td>
<td>Myrica lignitum</td>
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</tr>
<tr>
<td>81</td>
<td>Pinus pitsidiensis</td>
<td>needle 1</td>
<td>fragment</td>
</tr>
<tr>
<td>82</td>
<td>Pinus pitsidiensis</td>
<td>needle 1</td>
<td>fragment</td>
</tr>
<tr>
<td>83</td>
<td>Pinus pitsidiensis</td>
<td>needle 1</td>
<td>fragment</td>
</tr>
<tr>
<td>84</td>
<td>Pinus pitsidiensis</td>
<td>needle 1</td>
<td>fragment</td>
</tr>
<tr>
<td>85</td>
<td>Pinus pitsidiensis</td>
<td>needle 1</td>
<td>fragment</td>
</tr>
<tr>
<td>86</td>
<td>Pinus pitsidiensis</td>
<td>needle 1</td>
<td>fragment</td>
</tr>
</tbody>
</table>
APPENDIX 14

Pitsidia assemblage, type of damages and their frequency on *M. lignitum* foliage in MFL; 618 damages were detected on 540 leaves/leaf fragments of the totally 2617 collected leaf specimens of *M. lignitum* (several leaves have more than one type of damages)

<table>
<thead>
<tr>
<th>Type of behaviour</th>
<th>Type of feeding</th>
<th>Type of damage</th>
<th>Specimens</th>
<th>Frequency*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feeding behaviour</td>
<td>External feeding</td>
<td>Open margin feeding</td>
<td>123</td>
<td>abundant</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Interveinal margin feeding</td>
<td>1</td>
<td>very rare</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Extended lamina feeding</td>
<td>21</td>
<td>rare</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Apex feeding</td>
<td>17</td>
<td>rare</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Closed margin feeding</td>
<td>3</td>
<td>very rare</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Elliptic to circular holes 2–6 mm in diameter</td>
<td>38</td>
<td>rare</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Circular holes &lt; 2 mm in diameter</td>
<td>32</td>
<td>rare</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Polylobate holes</td>
<td>10</td>
<td>rare</td>
</tr>
<tr>
<td></td>
<td>Piercing and sucking feeding</td>
<td>Foliage distortion</td>
<td>169</td>
<td>abundant</td>
</tr>
<tr>
<td>Mining</td>
<td>Short serpentine trail</td>
<td>3</td>
<td>very rare</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Galls</td>
<td>95</td>
<td>common</td>
<td></td>
</tr>
<tr>
<td>Unknown</td>
<td>Removal of surface tissue &lt;2 mm in diameter</td>
<td>66</td>
<td>common</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Removal of surface tissue &gt;2 mm in diameter</td>
<td>6</td>
<td>very rare</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Polylobate removed surface tissue</td>
<td>26</td>
<td>rare</td>
<td></td>
</tr>
<tr>
<td>Reproduction behaviour</td>
<td>Oviposition</td>
<td>External positioned eggs</td>
<td>2</td>
<td>very rare</td>
</tr>
<tr>
<td>Damages of unknown causes</td>
<td>Depressed spots</td>
<td>3</td>
<td>very rare</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spots surrounded by callus</td>
<td>1</td>
<td>very rare</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Curled lamina</td>
<td>2</td>
<td>very rare</td>
<td></td>
</tr>
</tbody>
</table>

*very rare 1–5 specimens, rare 6–50, common 51–100, very common, abundant >100
APPENDIX 15
Origin, ecological preferences and modern analogue allies for the described in Kassanoi, Pitsidia and Metochia floristic elements

<table>
<thead>
<tr>
<th>Nr.</th>
<th>Fossil taxon</th>
<th>Origin</th>
<th>Ecological preferences</th>
<th>Modern analogue allies</th>
<th>Distribution of modern allies</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>&quot;Pteris&quot; oeningensis</td>
<td>Arctotertiary</td>
<td>Riparian, Swampy</td>
<td>Pteridium aquilinum</td>
<td>Temperate and subtropical regions in both hemispheres</td>
</tr>
<tr>
<td>2</td>
<td>Tetraclinis cf. salicornioides</td>
<td>Palaeotropic</td>
<td>Mesophytic</td>
<td>Tetraclinis articulata</td>
<td>N. Africa, S. Spain, Malta</td>
</tr>
<tr>
<td>3</td>
<td>Taxodium distichum</td>
<td>Arctotertiary</td>
<td>Swampy</td>
<td>Taxodium distichum</td>
<td>S.E. North America</td>
</tr>
<tr>
<td>4</td>
<td>Pinus pitsidiensis</td>
<td>Arctotertiary</td>
<td>Costal, Xerophytic</td>
<td>Pinus canariensis, Pinus roxburghii, Pinus keisiya</td>
<td>Asia, Canary Islands</td>
</tr>
<tr>
<td>5</td>
<td>Pinus sp., 2-needled</td>
<td>Arctotertiary</td>
<td>Xerophytic</td>
<td>Pinus subgen. Pinus</td>
<td>N. Hemisphere</td>
</tr>
<tr>
<td>6</td>
<td>Pinus spp., 5-needled</td>
<td>Arctotertiary</td>
<td>Xerophytic</td>
<td>Pinus subgen. Strobus</td>
<td>N. Hemisphere</td>
</tr>
<tr>
<td>7</td>
<td>Daphnogene polymorpha</td>
<td>Palaeotropic</td>
<td>Mesophytic, Riparian</td>
<td>Lauraceae</td>
<td>Cosmopolitan, absent from northern temperate regions</td>
</tr>
<tr>
<td>8</td>
<td>?Lindera ovata</td>
<td>Palaeotropic</td>
<td>Mesophytic</td>
<td>Lauraceae</td>
<td>Cosmopolitan, absent from northern temperate regions</td>
</tr>
<tr>
<td>9</td>
<td>?Lauraceae, gen. et sp. indet.</td>
<td>Palaeotropic</td>
<td>Mesophytic</td>
<td>Lauraceae</td>
<td>Cosmopolitan, absent from northern temperate regions</td>
</tr>
<tr>
<td>10</td>
<td>Sabalites sp.</td>
<td>Palaeotropic</td>
<td>?Costal swamps</td>
<td>Sub-family Coryphoideae</td>
<td>Cosmopolitan, absent from northern temperate regions</td>
</tr>
<tr>
<td>11</td>
<td>?Baxus pliocenica</td>
<td>Palaeotropic</td>
<td>Mesophytic, Xerophytic</td>
<td>Buxus sempervirens, Buxus colchica, Buxus hircana</td>
<td>Mediterranean Basin, Euxinian area, Hycranian area</td>
</tr>
<tr>
<td>12</td>
<td>Liquidambur europaea</td>
<td>Arctotertiary</td>
<td>Riparian, Swampy</td>
<td>Liquidambur styraciflua, Liquidambur orientalis</td>
<td>E. North America, Minor Asia and Rhodes island</td>
</tr>
<tr>
<td>13</td>
<td>Leguminosites spp.</td>
<td>Palaeotropic</td>
<td>Mesophytic, Xerophytic</td>
<td>Fabaceae</td>
<td>Cosmopolitan</td>
</tr>
<tr>
<td>14</td>
<td>Podocarpium podocarpm</td>
<td>Palaeotropic</td>
<td>Riparian, Mesophytic</td>
<td>Detariaceae-Ampherstieae complex of Casalpinioideae subfamily</td>
<td>Africa</td>
</tr>
<tr>
<td>15</td>
<td>Mimosites sp.</td>
<td>Palaeotropic</td>
<td>Xerophytic, Mesophytic</td>
<td>Mimosoideae</td>
<td>Cosmopolitan, absent from northern temperate regions</td>
</tr>
<tr>
<td>16</td>
<td>?Rosa sp.</td>
<td>Arctotertiary</td>
<td>Mesophytic</td>
<td>Rosaceae</td>
<td>Cosmopolitan</td>
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<tr>
<td>17</td>
<td>Rosacea, gen. et sp. indet.</td>
<td>Arctotertiary</td>
<td>Mesophytic</td>
<td>Rosaceae</td>
<td>Cosmopolitan</td>
</tr>
<tr>
<td>18</td>
<td>Berhemia multinervis</td>
<td>Palaeotropic</td>
<td>?Mesophytic</td>
<td>Berhemia scandens, Berhemia lineata, Berhemia pauciflora, Berhemia racemosa</td>
<td>North America, East Asia</td>
</tr>
<tr>
<td>19</td>
<td>cf. Ziziphus paradisiaca</td>
<td>Palaeotropic</td>
<td>Mesophytic, Xerophytic</td>
<td>Rhamnaceae</td>
<td>Cosmopolitan</td>
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<td>20</td>
<td>Ulmus cf. plurinervia</td>
<td>Arctotertiary</td>
<td>Riparian</td>
<td>Ulmus parvifolia</td>
<td>Asia</td>
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<td>21</td>
<td>Ulmus sp.</td>
<td>Arctotertiary</td>
<td>Riparian</td>
<td>Ulmaceae</td>
<td>N. Hemisphere</td>
</tr>
<tr>
<td>22</td>
<td>?Zelkova zelkovifolia</td>
<td>Arctotertiary</td>
<td>Mesophytic, Riparian</td>
<td>Zelkova carpinifolia</td>
<td>Euxinian area, Hycranian area</td>
</tr>
<tr>
<td>23</td>
<td>Quercus pseudocastanea</td>
<td>Arctotertiary</td>
<td>Mesophytic</td>
<td>Quercus group petraea</td>
<td>Eurasia</td>
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<tr>
<td>24</td>
<td>Quercus cf. kubinii</td>
<td>Arctotertiary</td>
<td>Mesophytic</td>
<td>Quercus section Cerris, Castanea</td>
<td>Eurasia, N. Africa</td>
</tr>
<tr>
<td>25</td>
<td>Quercus mediterranea</td>
<td>Arctotertiary</td>
<td>Mesophytic, Xerophytic</td>
<td>Quercus group Ilex</td>
<td>Eurasia</td>
</tr>
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<td>No.</td>
<td>Species</td>
<td>Age Group</td>
<td>Life Form</td>
<td>Sub-Families</td>
<td>Geographical Region</td>
</tr>
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<td>------------</td>
<td>---------------</td>
<td>--------------</td>
<td>------------------------------</td>
</tr>
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<td>26</td>
<td>Quercus sp.</td>
<td>Arctotertiary</td>
<td>Mesophytic</td>
<td>Quercus spp.</td>
<td>N. Hemisphere</td>
</tr>
<tr>
<td>27</td>
<td>Fagus gussonii</td>
<td>Arctotertiary</td>
<td>Mesophytic</td>
<td>Fagus sytiva, Fagus longipetiolata</td>
<td>Eurasia</td>
</tr>
<tr>
<td>28</td>
<td>Myrica lignitum</td>
<td>Palaeotropic</td>
<td>Swampy, Costal, Riparian</td>
<td>M. cerifera, M. pensylvanica, M. heterophylla</td>
<td>North and Central America</td>
</tr>
<tr>
<td>29</td>
<td>Carya sp.</td>
<td>Arctotertiary</td>
<td>Riparian</td>
<td>Carya spp.</td>
<td>Asia, N. America</td>
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<tr>
<td>30</td>
<td>Pterocarya sp.</td>
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<td>Riparian, Mesophytic</td>
<td>Pterocarya spp.</td>
<td>Asia</td>
</tr>
<tr>
<td>31</td>
<td>Engelhardia orsbergensis</td>
<td>Palaeotropic</td>
<td>Mesophytic</td>
<td>Engelhardia roxburghiana, Oreo mannea mexicana</td>
<td>E. Asia, Central America</td>
</tr>
<tr>
<td>32</td>
<td>Juglandaceae, gen. et sp. indet.</td>
<td>Arctotertiary</td>
<td>---</td>
<td>Juglandaceae</td>
<td>Eurasia, America</td>
</tr>
<tr>
<td>33</td>
<td>Betulaceae, gen. et sp. Indet.</td>
<td>Arctotertiary</td>
<td>Mesophytic</td>
<td>Betulaceae</td>
<td>Eurasia, America</td>
</tr>
<tr>
<td>34</td>
<td>Salix cf. angusta</td>
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<td>Riparian</td>
<td>Salix viminalis L.</td>
<td>Eurasia</td>
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<td>35</td>
<td>Salix sp.</td>
<td>Arctotertiary</td>
<td>Riparian</td>
<td>Salix spp.</td>
<td>N. Hemisphere</td>
</tr>
<tr>
<td>36</td>
<td>Populus populina</td>
<td>Arctotertiary</td>
<td>Riparian</td>
<td>Populus tremula, Populus alba</td>
<td>Eurasia</td>
</tr>
<tr>
<td>37</td>
<td>Populus sp.</td>
<td>Arctotertiary</td>
<td>Riparian</td>
<td>Populus spp.</td>
<td>N. Hemisphere</td>
</tr>
<tr>
<td>38</td>
<td>Decodon gibbosus</td>
<td>---</td>
<td>Aquatic, Swampy</td>
<td>Decodon verticillatus</td>
<td>North America</td>
</tr>
<tr>
<td>39</td>
<td>Acer tricuspidatum</td>
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<td>Swampy, Riparian</td>
<td>A. saccharinum, Acer rubrum</td>
<td>North America</td>
</tr>
<tr>
<td>40</td>
<td>Acer integrilobum</td>
<td>Arctotertiary</td>
<td>Mesophytic</td>
<td>Acer cappadocicum, Acer campbellii</td>
<td>Asia</td>
</tr>
<tr>
<td>41</td>
<td>Acer aegopodifolium</td>
<td>Arctotertiary</td>
<td>Mesophytic</td>
<td>Acer griseum, A. trifolium</td>
<td>Asia</td>
</tr>
<tr>
<td>42</td>
<td>Acer spp.</td>
<td>Arctotertiary</td>
<td>Mesophytic</td>
<td>Acer spp.</td>
<td>N. Hemisphere</td>
</tr>
<tr>
<td>43</td>
<td>Chaneya sp.</td>
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<td>Mesophytic</td>
<td>Rutaceae</td>
<td>Worldwide</td>
</tr>
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<td>44</td>
<td>Fraxinus sp.</td>
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<td>Riparian</td>
<td>Fraxinus spp.</td>
<td>N. Hemisphere</td>
</tr>
<tr>
<td>45</td>
<td>Cornus sp.</td>
<td>Arctotertiary</td>
<td>Mesophytic</td>
<td>Cornus spp.</td>
<td>N. Hemisphere</td>
</tr>
<tr>
<td>46</td>
<td>Hydrangea sp.</td>
<td>Palaeotropic</td>
<td>Mesophytic</td>
<td>Hydrangeaceae</td>
<td>N. Hemisphere</td>
</tr>
</tbody>
</table>
### APPENDIX 16

The Metochia palaeoflora (MANTZOUKA et al., 2015), amended floral list taking into account the herein described findings

---

<table>
<thead>
<tr>
<th>Nr.</th>
<th>Family</th>
<th>Taxon</th>
<th>Remarks</th>
<th>Plant Part/Organ</th>
<th>Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Cupressaceae</td>
<td><em>Tetraclinis salicornioides</em></td>
<td>foliage shoot, leafy segments</td>
<td>1+2 (+ 1 in this study)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(UNG ER) KVACEK</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td></td>
<td><em>Taxodium dubium</em></td>
<td>foliage shoots</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(STERNBERG) HEER</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Pinaceae</td>
<td><em>Pinus</em> sp.</td>
<td>needle fragments</td>
<td>2-4</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>2-needled</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td></td>
<td><em>Pinus</em> sp. 5-needled</td>
<td>in this study</td>
<td>needle fragment</td>
<td>1</td>
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</table>

### Gymnospermae

#### Angiospermae

<table>
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<th>Nr.</th>
<th>Family</th>
<th>Taxon</th>
<th>Remarks</th>
<th>Plant Part/Organ</th>
<th>Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>Lauraceae</td>
<td><em>Daphnogene polymorpha</em></td>
<td>leaves</td>
<td></td>
<td>7* (+ 1 in this study)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td></td>
<td><em>Laurophyllum</em> sp.</td>
<td>leaves</td>
<td></td>
<td>11* (+ 3 in this study)</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td></td>
<td><em>?Lindera ovata</em> KOLAKOVSKY</td>
<td>leaves</td>
<td></td>
<td>6* (+ 2 in this study)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td></td>
<td><em>?Sassafras</em> sp.</td>
<td>leaves</td>
<td></td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>9</td>
<td>Arecaceae</td>
<td><em>Sabalites</em> sp.</td>
<td>in this study</td>
<td>leaf</td>
<td>1</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>Fabaceae</td>
<td><em>Leguminocarpon</em> sp.</td>
<td>one taxon in this study</td>
<td>leaflets</td>
<td>10*</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td></td>
<td><em>Leguminocarpon</em> sp.</td>
<td>pod</td>
<td></td>
<td>1</td>
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<tr>
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<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>12</td>
<td>Rhamnaceae</td>
<td><em>Paliurus tilitifolius</em></td>
<td>leaf</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(UNG ER) BUZEK</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>13</td>
<td></td>
<td><em>cf. Ziziphus paradisata</em></td>
<td>in this study</td>
<td>leaves</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(UNG ER) HEER</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>14</td>
<td>Ulmaceae</td>
<td><em>Fagus</em> sp.</td>
<td>leaf</td>
<td></td>
<td>1</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>15</td>
<td>Fagaceae</td>
<td><em>Fagus</em> sp.</td>
<td>leaves</td>
<td>6-7* (+ 15 in this study)</td>
<td></td>
</tr>
<tr>
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<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>16</td>
<td></td>
<td><em>Quercus mediterranea</em> UNGER</td>
<td>in this study</td>
<td>leaves</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
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<tr>
<td>17</td>
<td>Myricaceae</td>
<td><em>Myrica lignitum</em></td>
<td>leaves</td>
<td>8* (+ 2 in this study)</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>(UNG ER) SAPIORTA</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>18</td>
<td>Juglandaceae</td>
<td><em>Engelhardia orsbergensis</em></td>
<td>leaflets</td>
<td>4* (+ 2 in this study)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(WESSEL et WEBER)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>JAHNICHEN, MAI and WALThER</td>
<td></td>
<td></td>
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<tr>
<td>19</td>
<td>Betulaceae</td>
<td><em>Betula</em> sp.</td>
<td>leaves</td>
<td></td>
<td>2</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>20</td>
<td></td>
<td><em>?Carpinus</em> sp.</td>
<td>leaf</td>
<td></td>
<td>1</td>
</tr>
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<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>21</td>
<td>Salicaceae</td>
<td><em>Salix</em> cf. angusta</td>
<td>leaves</td>
<td>9*</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>A. BRAUN</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td></td>
<td><em>Populus</em> sp.</td>
<td>leaf</td>
<td>1 (+ 1 in this study)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>23</td>
<td>Sapindaceae</td>
<td><em>Sapindus</em> urceus UNGER</td>
<td>leaflets</td>
<td>3*</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>24</td>
<td></td>
<td><em>Acer angustilobum</em> HEER</td>
<td>leaf</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
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<tr>
<td>25</td>
<td>Simaroubaceae</td>
<td><em>Akanthus pythii</em></td>
<td>leaflet</td>
<td></td>
<td>1</td>
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<tr>
<td></td>
<td></td>
<td>(UNG ER) KOVAR-EDER and KVAČEK</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>26</td>
<td>Monocotyledonae</td>
<td>fam. et gen. et sp. indet.</td>
<td>one new taxon in this study</td>
<td>leaf fragments</td>
<td>6*</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>27</td>
<td>---</td>
<td><em>Dicotylophyllum</em> spp. (8 different types)</td>
<td>two new taxa in this study</td>
<td>leaves/leaflets</td>
<td>10</td>
</tr>
</tbody>
</table>

*it is not clear if some of the referred in MANTZOUKA et al. (2015) code numbers represents the counterparts of the same specimens and thus counted twice*
APPENDIX 17

The Makrilia palaeoflora (SACHSE, 1997), amended floral list taking into account the herein described findings

<table>
<thead>
<tr>
<th>Nr.</th>
<th>Family</th>
<th>Taxon</th>
<th>Remarks</th>
<th>Plant Part/Organ</th>
<th>Frequency</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Polipodiophyta</td>
<td>Equisetum sp.</td>
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<td>stem</td>
<td>1</td>
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<tr>
<td>2</td>
<td>Cupressaceae</td>
<td><em>Tetraclinis salicornoides</em> as <em>Tetraclinis salicornoides</em> and <em>Tetraclinis</em> sp.</td>
<td>MANTZOUKA et al., 2015</td>
<td>foliage shoots, leafy segments, cone</td>
<td>2/2/1</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td><em>Taxodium dubium</em> (STERNBERG) HEER</td>
<td></td>
<td>leafy shoot</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td>gen. et sp. indet.</td>
<td>in this study</td>
<td>leafy shoot</td>
<td>1</td>
</tr>
<tr>
<td>5</td>
<td>Pinaceae</td>
<td>cf. Cathaya vel Keletaria vel Cedrus sp.</td>
<td></td>
<td>cone scale</td>
<td>1</td>
</tr>
<tr>
<td>6</td>
<td></td>
<td>gen. et sp. indet. (not <em>Pinus</em>)</td>
<td>in this study</td>
<td>winged seed</td>
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<tr>
<td>7</td>
<td></td>
<td><em>Pinus</em> cf. heptis (UNGIER) HEER</td>
<td></td>
<td>2-needled twig</td>
<td>1</td>
</tr>
<tr>
<td>8</td>
<td></td>
<td><em>Pinus</em> sp.</td>
<td></td>
<td>2-needled twig with very short needles</td>
<td>1</td>
</tr>
<tr>
<td>9</td>
<td></td>
<td><em>Pinus</em> sp. 5-needled</td>
<td></td>
<td>twig</td>
<td>1</td>
</tr>
<tr>
<td>10</td>
<td></td>
<td><em>Pinus</em> sp.</td>
<td></td>
<td>needle fragments</td>
<td>5</td>
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<td>11</td>
<td>Angiospermae</td>
<td><em>Daphnogene polymorpha</em> as fgen. <em>Cinnamomophyllum</em> sp.</td>
<td>VELITZELOS D. et al., 2014; in this study</td>
<td>leaves</td>
<td>2</td>
</tr>
<tr>
<td>12</td>
<td></td>
<td><em>Laurephyllum</em> spp. (4 different types)</td>
<td></td>
<td>leaves</td>
<td>10</td>
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<tr>
<td>13</td>
<td></td>
<td><em>Cymodocea</em> vel <em>Posidonia</em> sp.</td>
<td></td>
<td>rhizomes, leaves</td>
<td>5</td>
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<tr>
<td>14</td>
<td>Ruppiaceae</td>
<td>cf. <em>Ruppiya</em> sp.</td>
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<td>seed</td>
<td>1</td>
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<td>15</td>
<td>Smilacaceae</td>
<td><em>Smilax</em> cf. <em>petiolata</em> (WEBER) WELYAND</td>
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<td>leaves</td>
<td>2</td>
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<tr>
<td>17</td>
<td></td>
<td><em>Mahonia</em> sp.</td>
<td>in this study</td>
<td>leaf</td>
<td>1</td>
</tr>
<tr>
<td>18</td>
<td>Buxaceae</td>
<td><em>Buxus</em> cf. <em>egertiana</em> KVAČEK, BŮŽEK and HOLÝ</td>
<td></td>
<td>leaves</td>
<td>2</td>
</tr>
<tr>
<td>19</td>
<td></td>
<td><em>Buxus</em> pliocenica SÁPORTA and MARION</td>
<td></td>
<td>leaves</td>
<td>3</td>
</tr>
<tr>
<td>20</td>
<td>Altingiaceae</td>
<td><em>Liquidambar</em> sp.</td>
<td>in this study</td>
<td>infructescence</td>
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<td>21</td>
<td>Vitaceae</td>
<td>cf. <em>Ampelopsis vel Vitis</em> sp.</td>
<td></td>
<td>seed</td>
<td>1</td>
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<tr>
<td>22</td>
<td>Fabaceae</td>
<td><em>Leguminosae</em> spp. (7 different types)</td>
<td></td>
<td>leaflets/leaf</td>
<td>14/1</td>
</tr>
<tr>
<td>23</td>
<td></td>
<td><em>Podocarpum podocarpum</em> (A. BRAUN) HERENDEEN</td>
<td></td>
<td>leaflets</td>
<td>4</td>
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<tr>
<td>24</td>
<td></td>
<td><em>Mimosites</em> sp.</td>
<td></td>
<td>leaflet, leaf frag.</td>
<td>1/1</td>
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<tr>
<td>25</td>
<td></td>
<td><em>Leguminosae</em> gen. et sp. indet. (heterogenous leaflets)</td>
<td></td>
<td>leaflets</td>
<td>10</td>
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<tr>
<td>26</td>
<td></td>
<td>cf. <em>Leguminosites</em> sp.</td>
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<td>seed</td>
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</tr>
<tr>
<td>27</td>
<td></td>
<td><em>Leguminocarpus</em> sp.</td>
<td>in this study</td>
<td>fruit</td>
<td>1</td>
</tr>
<tr>
<td>28</td>
<td>Rhamnaceae</td>
<td>cf. <em>Ziziphus paradisiaca</em> (UNGIER) HEER as fgen. <em>Dicotylophyllum</em> type 9</td>
<td>in this study</td>
<td>leaves</td>
<td>3</td>
</tr>
<tr>
<td>No.</td>
<td>Family</td>
<td>Genus/Species/Comments</td>
<td>Refs.</td>
<td>Examples</td>
<td></td>
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<td>-----</td>
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<td>------------------------</td>
<td>-------</td>
<td>----------</td>
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<tr>
<td>29</td>
<td>Ulmaceae</td>
<td>cf. Ulmus plurinervia UNGER</td>
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<td>leaf</td>
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<td>30</td>
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<td>Ulmus sp.</td>
<td></td>
<td>fruit</td>
<td></td>
</tr>
<tr>
<td>31</td>
<td></td>
<td>Zelkova zelkowskii (UNGER) BÜZEK and KOTLABA</td>
<td></td>
<td>leaf, twig with 3 leaves</td>
<td></td>
</tr>
<tr>
<td>32</td>
<td>Fagaceae</td>
<td>Fagus gussonii MASSALONGO emend. KNOBLOCH and VELITZELOS</td>
<td>DENK et al., 2004; VELITZELOS et al., 2014; MANTZOUKA et al., 2015; in this study</td>
<td>leaves</td>
<td></td>
</tr>
<tr>
<td>33</td>
<td></td>
<td>Quercus kubinii (KOVÁTS ex ETTINGSHAUSEN) BERGER</td>
<td></td>
<td>leaf</td>
<td></td>
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<td>34</td>
<td></td>
<td>Quercus mediterranea UNGER</td>
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<td>leaves 4</td>
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<td>35</td>
<td></td>
<td>Quercus drymeja UNGER</td>
<td></td>
<td>leaf 1</td>
<td></td>
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<tr>
<td>36</td>
<td></td>
<td>Quercus sp.</td>
<td></td>
<td>acorn 1</td>
<td></td>
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<tr>
<td>37</td>
<td>Myricaceae</td>
<td>Myrica lignitum (UNGER) SAPORTA</td>
<td>VELITZELOS D. et al., 2014; in this study</td>
<td>leaves 8</td>
<td></td>
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<tr>
<td>38</td>
<td>Juglandaceae</td>
<td>Engelhardia orsbergensis (WEISSEL and WEBER) JÄHNIKEN, MAI and WALTHER</td>
<td>MANTZOUKA et al., 2015; in this study</td>
<td>leaflets 6</td>
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<td>39</td>
<td></td>
<td>Engelhardia macroptera (BRONGIART) UNGER</td>
<td>VELITZELOS D. et al., 2014; in this study</td>
<td>samara 1</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td></td>
<td>Carya serrifolia (GÖPPERT) KRÄUSEL</td>
<td>VELITZELOS D. et al., 2014</td>
<td>leaf 1</td>
<td></td>
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<tr>
<td>41</td>
<td></td>
<td>Jugians vel Carya sp.</td>
<td></td>
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<td></td>
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<tr>
<td>42</td>
<td>Betulaeae</td>
<td>cf. Alnus gaudini (HEIR) KNOBLOCH and KVAŽEK</td>
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<td>leaf 1</td>
<td></td>
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<tr>
<td>43</td>
<td></td>
<td>Carpinus sp.</td>
<td></td>
<td>leaves 8</td>
<td></td>
</tr>
<tr>
<td>44</td>
<td></td>
<td>Carpinus type orientalis</td>
<td></td>
<td>fruits 2</td>
<td></td>
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<td>45</td>
<td>Salicaceae</td>
<td>Salix type purpurea</td>
<td></td>
<td>leaf 1</td>
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<td>46</td>
<td></td>
<td>Salix type 1</td>
<td></td>
<td>leaves 7</td>
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<tr>
<td>47</td>
<td></td>
<td>Populus sp.</td>
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<td>fruit 1</td>
<td></td>
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<tr>
<td>48</td>
<td>Sapindaceae</td>
<td>Acer sp. (5-lobed)</td>
<td>VELITZELOS et al. (2014) listed as Acer integerrimum (VIVIANI) MASSALONGO</td>
<td>leaves 2</td>
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<td>49</td>
<td></td>
<td>Acer integrilobum WEBER</td>
<td>as Acer ser. Monspessulana</td>
<td>leaves 14</td>
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<tr>
<td>50</td>
<td></td>
<td>Acer angustilobum HEER</td>
<td>as cf. Ampelopsis vel Vitis sp.</td>
<td>leaves 1</td>
<td></td>
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<tr>
<td>51</td>
<td></td>
<td>Acer &quot;integerrimum (VIVIANI) MASSALONGO&quot;</td>
<td>MANTZOUKA et al. 2015</td>
<td>leaf 1</td>
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<td>52</td>
<td></td>
<td>Acer spp. (3 different types)</td>
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<td>53</td>
<td>Rutaceae</td>
<td>cf. Toddaia sp.</td>
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<td>seed 1</td>
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<td>54</td>
<td>Thymelaeaceae</td>
<td>Aquilaria sp.</td>
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<td>Tiliaceae</td>
<td>cf. Tilia sp.</td>
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<td>bracts 2</td>
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<td>56</td>
<td>Symplacaceae</td>
<td>Symplocos cf. minutula (STERNBERG) KIRCHHEIMER</td>
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<td>seed 1</td>
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<td>57</td>
<td>Oleaceae</td>
<td>Praxinus sp.</td>
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<td>fruit 1</td>
<td></td>
</tr>
<tr>
<td>58</td>
<td></td>
<td>Monocotylodium spp.</td>
<td></td>
<td>leaf fragments</td>
<td></td>
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<tr>
<td>59</td>
<td></td>
<td>Asterocalyx styracius ETTINGSHAUSEN</td>
<td>KOVAR-EDER et al. 2004</td>
<td>flower 1</td>
<td></td>
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<tr>
<td>60</td>
<td></td>
<td>Dicotylodium spp. (20 different types, we exclude D. type 3 as cf. Ziziphus paradoxiaca and D. type 9 as Berberidaceae)</td>
<td>leaves/leaflets</td>
<td>46-2-8=38</td>
<td></td>
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<tr>
<td>61</td>
<td></td>
<td>Carpolithus spp. (3 different types)</td>
<td></td>
<td>fruits/seeds 4</td>
<td></td>
</tr>
</tbody>
</table>

Revised taxa list of Makrilia palaeoflora (SACHSE, 1997), taking into account the findings of this study (pl. LII, figs 1–2, 4–11) and of VELITZELOS D. et al. (2014), as well as the comments of MANTZOUKA et al. (2015). Ambiguous identified floristic elements: ?Magnolia sp. ?Illicium rhenanum KRÄUSEL and WEYLAND

349
fsp. *Cinnamomophyllum polymorphum* (A. BRAUN) HEER (see MANTZOUKA et al., 2015)

?*Cladastris* sp.

?*Machaerium* spp. (2 types)

?*Swartzia* sp.

cf. *Quercus rhenana* (KRÄUSEL et WEYLAND) KNOBLOCH and KVAČEK

?*Pistacia lentiscus*

?*Ilex* type *aquifolium*

cf. Myrtaceae gen. et sp. indet.

?*Lonicera* type *etrusca*

VELITZELLOS D. et al. (2014) reported abundant frond fragments of *Sabal* sp. (Arecaceae) from Makrilia. The outcrop and its stratigraphy haven’t been published.
APPENDIX 18
The Vrysses palaeoflora (ZIDIANAKIS et al., 2007), amended floral list taking into account the herein described findings

<table>
<thead>
<tr>
<th>Nr.</th>
<th>Family</th>
<th>Taxon</th>
<th>Remarks</th>
<th>Plant Part/Organ</th>
<th>Frequency</th>
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</thead>
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<td>Cupressaceae</td>
<td>Tetraclinis cf. salicornioides (UNGER) KVAČEK</td>
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<td>foliage shoots</td>
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<td>2</td>
<td>Pinaceae</td>
<td>Pinus sp. 2-needled</td>
<td>Twigs and needle fragments</td>
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<td>17</td>
</tr>
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<td>Pinaceae</td>
<td>Pinus sp. 3-needled</td>
<td>in this study</td>
<td>3-needled twig</td>
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<tr>
<td>4</td>
<td>Lauraceae</td>
<td>Daphnogene polymorpha (A. BRAUN) ETTINGSHAUSEN</td>
<td>leaves</td>
<td></td>
<td>2</td>
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<tr>
<td>5</td>
<td>Buxaceae</td>
<td>Buxus pliocenica SAPORTA and MARION</td>
<td>leaf</td>
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<td>1</td>
</tr>
<tr>
<td>6</td>
<td>Fabaceae</td>
<td>gen. et sp. indet. (2 different types)</td>
<td>leafletets</td>
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<td></td>
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<td>Rosaceae</td>
<td>gen. et sp. indet.</td>
<td>leaves/leaflets</td>
<td>3</td>
<td></td>
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<tr>
<td>8</td>
<td>Hamamelidaceae</td>
<td>&quot;Parrotia&quot; pristina (ETTINGSHAUSEN) STUR</td>
<td>leaf</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>9</td>
<td>Rhamnaceae</td>
<td>cf. Ziziphus paradisica (UNGER) HEER</td>
<td>as ?Ziziphus ziziphoides (UNGER) WEYLAND</td>
<td>leaves</td>
<td>8</td>
</tr>
<tr>
<td>10</td>
<td>Fagaceae</td>
<td>Quercus mediterranea UNGER</td>
<td>leaves</td>
<td></td>
<td>12</td>
</tr>
<tr>
<td>11</td>
<td></td>
<td>Quercus sp.</td>
<td>leaves</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>Juglandaceae</td>
<td>?Juglans acuminata A. BRAUN ex UNGER</td>
<td>leaflets</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>Salicaceae</td>
<td>?Salix sp.</td>
<td>leaves</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>14</td>
<td></td>
<td>Populus populina (BRONGINIART) KNOBLOCH</td>
<td>as Populas tremula floss.</td>
<td>leaves</td>
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<td>15</td>
<td>Sapindaceae</td>
<td>Acer integrolobum WEBER sensu WALTER</td>
<td>as A. pseudomonos pessulanum UNGER</td>
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<td>Acer cf. integerrimum (VIVIANI and MASSALONGO)</td>
<td>as Acer sp.</td>
<td>VELITZELO S et al., 2014</td>
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<td>Monocotylophyllum spp. (2 different types)</td>
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<td>Dicotylophyllum spp. (12 different types)</td>
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### APPENDIX 19

Comparison of the Cretan palaeofloras

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<th>Taxon</th>
<th>Makrilia</th>
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<td>Thallus, Fam. et gen. et sp. indet.</td>
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<td>Equisetum sp.</td>
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<td>Polypodiophyta fam. et gen. et sp. indet. – frond</td>
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<td>Tetracnemis cf. salicornioides</td>
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<td>Pinus sp. – 2-needled fascicles</td>
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<td>Pinus sp. – 5-needled fascicles</td>
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<td>cf. Cathaya vel Keleteria vel Cedrus sp. – cone scale</td>
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<td>Lindera ovata</td>
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<td>cf. Rupphia sp. – seed</td>
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<td>27</td>
<td>cf. Amelopsis vel Vitis sp. – seed</td>
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<td>+++</td>
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<td>?+</td>
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<td>?+</td>
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<td>Quercus sp. deciduous – folia</td>
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<td>+</td>
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<td>57</td>
<td><em>cf. Alnus gaudinii</em></td>
<td>+</td>
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<tr>
<td>58</td>
<td><em>Carpinus</em> sp. – <em>folia</em></td>
<td>++</td>
<td></td>
<td></td>
<td>?+</td>
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<td>59</td>
<td><em>Carpinus</em> type <em>orientalis</em> – <em>fructus</em></td>
<td>+</td>
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<td><em>Betulaceae</em> gen. et sp. indet. – <em>folia</em></td>
<td>+</td>
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<td>62</td>
<td><em>Salix</em> cf. angusta</td>
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<td>+++</td>
<td>+++</td>
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<td><em>Salix</em> type purpurea</td>
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<td><em>Salix</em> sp. – <em>folia</em></td>
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<td>?+ (1 type)</td>
<td>+ (1 type)</td>
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<td><em>Populus populina</em></td>
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<td>+</td>
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<td><em>Decodon gibbosus</em></td>
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<td>71</td>
<td><em>Acer integerrimum</em></td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
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<td><em>Acer aegopodifolium</em></td>
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<td>73</td>
<td><em>Acer</em> cf. integerrimum</td>
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<td>74</td>
<td><em>Acer truncatum</em></td>
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<td>75</td>
<td><em>Acer</em> sp. – <em>fructus</em></td>
<td>+ (3 types)</td>
<td>+ (2 types)</td>
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<td>76</td>
<td><em>cf. Toddalia</em> sp. – <em>seed</em></td>
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<td><em>Chamaecyparis</em> sp. – <em>fructus</em></td>
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<td><em>Ailanthus pythii</em></td>
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<td><em>Aquilaria</em> sp. – <em>folia</em></td>
<td>+</td>
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<td>80</td>
<td><em>cf. Tilia</em> sp. – <em>bracts</em></td>
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<td><em>Cornus</em> sp. – <em>folia</em></td>
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<td>82</td>
<td><em>cf. Hydrangea</em> sp. – <em>flower</em></td>
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<td>83</td>
<td><em>Symlocos</em> cf. <em>minutula</em></td>
<td>?+</td>
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<td>84</td>
<td><em>Fraxinus</em> sp. – <em>folia</em></td>
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<td><em>Fraxinus</em> sp. – <em>fructus</em></td>
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<td>86</td>
<td><em>Asterocalyx styriacus</em></td>
<td>+</td>
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<td>87</td>
<td><em>Monocotylodonthyllum</em> sp.</td>
<td>+</td>
<td>+ (2 types)</td>
<td>+ (5 types)</td>
<td>+ (3 types)</td>
<td>+ (&gt;2 types)</td>
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<td>88</td>
<td><em>Dicotylodonthyllum</em> sp.</td>
<td>+ (20 types)</td>
<td>+ (12 types)</td>
<td>+ (13 types)</td>
<td>+ (4 types)</td>
<td>+ (8 types)</td>
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<td><em>Carpoldis</em> sp.</td>
<td>+ (3 types)</td>
<td>?+ (2 types)</td>
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<td>90</td>
<td><em>Antholites</em> sp.</td>
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<td>+ (1 type)</td>
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APPENDIX 20

Main Cenozoic localities with plant macro-fossils in the Greek area:

**Oligocene:** 1. Lagina, 2. Lyra, 3. Fylakton, 4. Aetochori, 5. Lykovi;


**Early Miocene:**

**Oligocene:**

**Early Miocene:**

**Pliocene:**

**PlIOCene:**

**Pleistocene:**


* in the original publication dated as Pliocene; possibly Pleistocene
APPENDIX 21

Most extant trees, tall shrubs, woody climbers and ferns from the Messara-Gavdos area; the extant families and genera that represented in the palaeofloras of the area are coloured (extracted from TURLAND et al., 1993)

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<th>Family</th>
<th>Species</th>
<th>Remarks</th>
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<td>Pteridophyta</td>
<td>Adiantiaceae</td>
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<tr>
<td></td>
<td>Adiantum capillus-veneris</td>
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APPENDIX 22

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