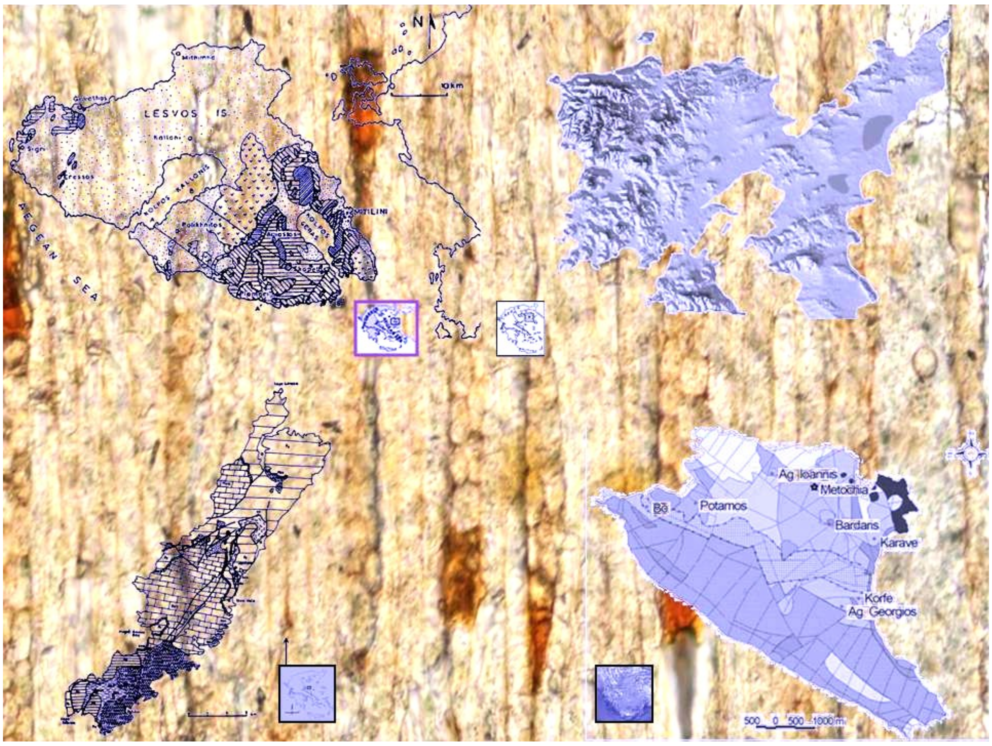
NATIONAL AND KAPODISTRIAN UNIVERSITY OF ATHENS

SCHOOL OF SCIENCES
DEPARTMENT OF GEOLOGY AND GEOENVIRONMENT
SECTION OF HISTORICAL GEOLOGY - PALAEONTOLOGY

PhD THESIS

Research of the Cenophytic Palaeoflora of the Eastern Mediterranean (Lesbos, Lemnos, Alonissos, Gavdos Islands)

DIMITRA V. MANTZOUKA



Supervisor: Professor Dr. Vasileios Karakitsios

ATHENS
JUNE 2016

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Professor Dr. Vasileios Karakitsios (Supervisor)
Professor Emeritus Dr. Evangelos Velitzelos
Professor Dr. Nikolaos Christodoulakis

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ΤΟΜΕΑΣ ΙΣΤΟΡΙΚΗΣ ΓΕΩΛΟΓΙΑΣ - ΠΑΛΑΙΟΝΤΟΛΟΓΙΑΣ

ΔΙΔΑΚΤΟΡΙΚΗ ΔΙΑΤΡΙΒΗ

Έρευνα της παλαιοχλωρίδας του Καινοφυτικού στην Ανατολική Μεσόγειο (Νήσοι: Λέσβος, Λήμνος, Αλόννησος, Γαύδος)

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Καθηγητής Δρ. Νικόλαος Χριστοδουλάκης

ΑΘΗΝΑ

ΙΟΥΝΙΟΣ 2016

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Dimitra V. Mantzouka
ID: 143

SUPERVISOR: Vasileios Karakitsios, Professor UoA

ADVISORY COMMITTEE:

Professor Dr. Vasileios Karakitsios(Head of Advisory Committee)
National and Kapodistrian University of Athens, Faculty of Geology & Geoenvironment,Director of the Department of Historical Geology-Palaeontology

Professor Emeritus Dr. Evangelos Velitzelos
National and Kapodistrian University of Athens, Faculty of Geology & Geoenvironment, Department of Historical Geology-Palaeontology

Professor Dr. Nikolaos Christodoulakis
National and Kapodistrian University of Athens, Faculty of Biology, Department of Botany

EXAMINATION COMMITTEE

Professor Dr. George Theodorou
National and Kapodistrian University of Athens, Faculty of Geology & Geoenvironment, Department of Historical Geology-Palaeontology, Director of the Museum of Palaeontology & Geology of the University of Athens

Professor Dr. Zlatko Kvaček
Charles University of Prague, Institute of Geology and Palaeontology, Faculty of Science

Professor Dr. Nikolaos Zouros
University of the Aegean, Geography Department, Director of the Natural History Museum of the Lesvos Petrified Forest

Assistant Professor Dr. Jakub Sakala
Charles University of Prague, Institute of Geology and Palaeontology, Faculty of Science

ATHENS
2016

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Δήμητρα Β. Μαντζούκα
Α.Μ.: 143

ΕΠΙΒΛΕΠΩΝ ΚΑΘΗΓΗΤΗΣ: ΒΑΣΙΛΕΙΟΣ ΚΑΡΑΚΙΤΣΙΟΣ, Καθηγητής ΕΚΠΑ

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Εθνικό και Καποδιστριακό Πανεπιστήμιο Αθηνών, Τμήμα Γεωλογίας και Γεωπεριβάλλοντος, Διευθυντής του Τομέα Ιστορικής Γεωλογίας-Παλαιοντολογίας

Ομότιμος Καθηγητής Δρ. Ευάγγελος Βελιτζέλος
Εθνικό και Καποδιστριακό Πανεπιστήμιο Αθηνών, Τμήμα Γεωλογίας και Γεωπεριβάλλοντος, Τομέας Ιστορικής Γεωλογίας-Παλαιοντολογίας

Καθηγητής Δρ. Νικόλαος Χριστοδουλάκης
Εθνικό και Καποδιστριακό Πανεπιστήμιο Αθηνών, Τμήμα Βιολογίας, Τομέας Βοτανικής

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Καθηγητής Δρ. Γεώργιος Θεοδώρου
Εθνικό και Καποδιστριακό Πανεπιστήμιο Αθηνών, Τμήμα Γεωλογίας και Γεωπεριβάλλοντος, Τομέας Ιστορικής Γεωλογίας-Παλαιοντολογίας, Διευθυντής Μουσείου Παλαιοντολογίας & Γεωλογίας του Πανεπιστημίου Αθηνών

Καθηγητής Δρ. Zlatko Kvaček
Πανεπιστήμιο του Καρόλου (Πράγα), Ινστιτούτο Γεωλογίας και Παλαιοντολογίας, Τμήμα Επιστημών

Καθηγητής Δρ. Νικόλαος Ζούρος
Πανεπιστήμιο Αιγαίου, Τμήμα Γεωγραφίας, Διευθυντής του Μουσείου Φυσικής Ιστορίας Απολιθωμένου Δάσους Λέσβου

Επίκουρος Καθηγητής Δρ. Jakub Sakala
Πανεπιστήμιο του Καρόλου (Πράγα), Ινστιτούτο Γεωλογίας και Παλαιοντολογίας, Τμήμα Επιστημών

ΑΘΗΝΑ
2016

ABSTRACT

The presence of plant (macro) fossils in Greece is known since ancient times and is of high significance by the Greek and International scientific community because of: their age, the species and plant organs diversity and the information about the palaeoenvironment and paleoclimate which can be excluded. The present work is dealing with: the research for new plant fossiliferous localities of Cenophytic age at the Eastern Mediterranean (Lesbos, Lemnos, Alonissos, Gavdos Islands), the study of the new findings under the perspective of palaeobotanical analysis (petrified wood anatomy with the usage of microscope, study of leaves imprints) and use of older (method of the Nearest Living Relative) and new methodologies (e.g., CLAMP, IPR) in order to export significant conclusions about the geological history of the Eastern Mediterranean and of Greece.

SUBJECT AREA: Eastern Mediterranean (Lesbos, Lemnos, Alonissos, Gavdos Islands).
KEYWORDS: Palaeobotany, plant macrofossils, Lesbos, Lemnos, Alonissos, Gavdos, Eastern Mediterranean, Neogene, Miocene, fossil plants, fossil wood anatomy, modern wood anatomy, leaves' imprints, Lauraceae, *Laurinoxylon* types, *Laurinoxylon* aff. *czechense, Laurinoxylon* cf. *daberi, Laurinoxylon* aff. *diluviale, Laurinoxylon* cf. *ehrendorferi, Cinnamomoxylon seemannianum*, *Cryptocaryoxylon*, *Quercoxylon*, *Cedroxylon lesbium*, *Cedrus*, *Taxodioxylon*, *Sequoia abietina*, *Glyptostrobus europaeus*, *Pinuxylon, Fagus gussonii, Sapindus graecus, Ailanthus pythii,* plant taphonomy, lignites, xylites.

ΠΕΡΙΛΗΨΗ

Η ύπαρξη φυτικών (μακρο)απολιθωμάτων στον ελλαδικό χώρο είναι γνωστή από την αρχαιότητα και χαίρει ιδιαίτερης σπουδαιότητας από την ελληνική και παγκόσμια επιστημονική κοινότητα λόγω της ηλικίας, της ποικιλότητας ειδών και οργάνων και των πληροφοριών για το παλαιοπεριβάλλον και το παλαιοκλίμα. Μέσα από την παρούσα εργασία πραγματοποιείται: έρευνα νέων θέσεων εύρεσης φυτικών απολιθωμάτων Καινοφυτικής ηλικίας στην Ανατολική Μεσόγειο (νήσος Λέσβος, Λήμνος, Αλόννησος, Γαύδος), προσπάθεια προσέγγισης των νέων ευρημάτων από τη σκοπιά της παλαιοβοτανικής ανάλυσης με ό,τι αυτή περιλαμβάνει (ανατομία απολιθωμένου ξύλου με χρήση μικροσκοπίου, μελέτη αποτυπωμάτων φύλλων) αλλά και χρήση παλαιότερων (μέθοδος του Πλησιέστερου Σημερινού Συγγενή) και νέων μεθοδολογιών (π.χ. CLAMP, IPR) με στόχο την εξαγωγή σημαντικών συμπερασμάτων για τη γεωλογική ιστορία της Ανατολικής Μεσογείου και γενικότερα του ελλαδικού χώρου.

ΘΕΜΑΤΙΚΗ ΠΕΡΙΟΧΗ: Ανατολική Μεσόγειος (Νήσοι: Λέσβος, Λήμνος, Αλόννησος, Γαύδος).

ΛΕΞΕΙΣ ΚΛΕΙΔΙΑ: Παλαιοβοτανική, φυτικά μακροαπολιθώματα, Λέσβος, Λήμνος, Αλόννησος, Γαύδος, Ανατολική Μεσόγειος, Νεογενές, Μειόκαινο, απολιθωμένα φυτά, ανατομία απολιθωμένου ξύλου, ανατομία σύγχρονου ξύλου, αποτυπώματα φύλλων, απολιθωμένες Δαφνίδες, τύποι *Laurinoxylon, Laurinoxylon* aff. *czechense, Laurinoxylon* cf. *daberi, Laurinoxylon* aff. *diluviale, Laurinoxylon* cf. *ehrendorferi, Cinnamomoxylon seemannianum*, *Cryptocaryoxylon*, *Quercoxylon*, *Cedroxylon lesbium*, *Cedrus*, *Taxodioxylon*, *Sequoia abietina*, *Glyptostrobus europaeus*, *Pinuxylon, Fagus gussonii, Sapindus graecus, Ailanthus pythii,*ταφονομία φυτών, λιγνίτες, ξυλίτες.

To

Alexandros,

Vaios & Rika,

Antonia

and my parents

Vaios & Despina

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List of Publications

Published papers and abstracts:

1) Mantzouka D., Karakitsios V., Sakala J. & Wheeler E. in press. Using idioblasts to group *Laurinoxylon* species – Case study from the Oligo-Miocene of Europe. IAWA Journal, Volume: xx, pages: 1-59.

2) Mantzouka D., Karakitsios V., Sakala J. & Kvaček Z. in press. Fossil forest of Lesbos Island (Greece): A palaeobotanical puzzle of a unique Geopark and the new discoveries. Cabridge Scholars Publishing, Volume: xx, pages: 1-15.

3) Mantzouka D., Kvaček Z., Teodoridis V., Utescher T., Tsaparas N. & Karakitsios V. 2015. A new late Miocene (Tortonian) flora from Gavdos Island in southernmost Greece evaluated in the context of vegetation and climate in the Eastern Mediterranean. Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen. 01/2015; 275(1):47-81.

4) Mantzouka D., Kvaček Z., Teodoridis V., Utescher T., Tsaparas N. & Karakitsios V. 2014. Gavdos Island Palaeoflora: A newly recovered late Neogene flora of the Eastern Mediterranean (Greece). 9th European Palaeobotany-Palynology Conference, August 26-31 2014, Padova, Italy, Volume: 1, page: 154.

5) Mantzouka D., Sakala J. & Karakitsios V. 2014. A new methodological approach on *Laurinoxylon* and the importance of the oil and/or mucilage cells. 9th European Palaeobotany-Palynology Conference, August 26-31 2014, Padova, Italy, Volume: 1, page: 154.

6) Mantzouka D., Sakala J., Kvaček Z. & Karakitsios V. 2013a. Palaeobotanical study of Polichnitos region, Southern part of Lesbos island, Greece (Preliminary results on angiosperm wood). Bulletin of the Geological Society of Greece, vol. XLVII: 204-215. 13th International Congress of the Geological Society of Greece, September 5-8 2013, Chania, Crete, Greece.

7) Mantzouka D. V, Sakala J, Rapprich V & Karakitsios V. 2013b. Plant fossils and taphonomical processes from Lesbos island, Greece. Proceedings of the 22nd International Workshop on Plant Taphonomy in Pilsen and Radnice, p. 6-7.

Participations in conferences:

1) Mantzouka D., Christodoulakis N. & Karakitsios V. 2015. Revealing *Peuce lesbia* Unger (=*Cedroxylon lesbium* Kraus) from the Petrified Forest area (Sigri, Lesbos Island): The first diagnosis after the 19th century. 2nd International Geo-Cultural Symposium “Sigri 2015”, Mytilene, 4th-6th June 2015.

2) Mantzouka D , Kvaček Z., Teodoridis V., Utescher T., Tsaparas N. & Karakitsios V. 2014. Gavdos Island Palaeoflora: A newly recovered late Neogene flora of the Eastern Mediterranean (Greece). 9th European Palaeobotany-Palynology Conference, August 26-31 2014, Padova, Italy, Volume: 1, page: 154

3) Mantzouka D., Sakala J. & Karakitsios V. 2014. A new methodological approach on *Laurinoxylon* and the importance of the oil and/or mucilage cells. 9th European Palaeobotany-Palynology Conference, August 26-31 2014, Padova, Italy, Volume: 1, page: 154

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5) Mantzouka D., Sakala J., Kvaček Z., Karakitsios V. 2013. Fossil lauraceous wood with special reference to the Petrified Forest of Lesbos Island (early Miocene, Greece). 1st International workshop of the NECLIME working group on "fossil wood", June 5-8 2013, Brno, Czech Republic.

6) Mantzouka D., Sakala J., Rapprich V. & Karakitsios V. 2013. Plant fossils and Taphonomical processes from Lesbos Island, Greece. Abstracts volume of 22nd International Workshop on Plant Taphonomy in Pilsen and Radnice, Czech Republic pp. 6-7.

DECLARATION OF AUTHORSHIP

Dimitra V. Mantzouka declares that the thesis entitled:

RESEARCH OF THE CENOPHYTIC PALAEOFLORA OF THE EASTERN MEDITERRANEAN (LESBOS, LEMNOS, ALONISSOS, GAVDOS ISLANDS)

and the work presented in the thesis are both my own, and have been generated by me as the result of my own original research.

I confirm that:

1. This work was done mainly at the National and Kapodistrian University of Athens and at the Charles University of Prague, Institute of Geology and Palaeontology, Faculty of Science through a bilateral collaboration.
2. Any part of this thesis has not been submitted in any previous application for a higher degree or any other qualification at this University or any other Institution.
3. Where I have consulted the published work of others, this is always clearly attributed.
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work.
5. I have acknowledged all main sources of help.
6. A full bibliographic reference is made to the original source.
7. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself,
8. The datasets presented in the thesis are available upon request to the corresponding author,
9. Parts of this work are (as it is stated above) or will be published as separate papers in peer-reviewed scientific journals and conference proceedings.

Signed:

Date:

ΣΥΝΟΠΤΙΚΗ ΠΑΡΟΥΣΙΑΣΗ ΤΗΣ ΔΙΑΤΡΙΒΗΣ (στα ελληνικά)

Η παρούσα μελέτη επικεντρώνεται στην έρευνα του παλαιοβοτανικού αρχείου της Ανατολικής Μεσογείου (Νήσοι: Λέσβος, Λήμνος, Αλόννησος και Γαύδος) κατά τη διάρκεια του Καινοφυτικού.

Η πλειονότητα των συλλεχθέντων δειγμάτων (με μόνη εξαίρεση όσων προέρχονταν από τη νήσο Γαύδο) ανήκει σε τμήματα απολιθωμένου ξύλου (από τη Λέσβο, τη Λήμνο και την Αλόννησο).

Για το λόγο αυτό, **το πρώτο κεφάλαιο που αποτελεί το εισαγωγικό τμήμα** της παρούσας διατριβής πραγματεύεται την αποσαφήνιση των όρων «ξύλο» ή «ξύλημα», «ξυλώδης ιστός» και «ανατομία κορμού ή ξύλου», την εξέλιξη του ξύλου κατά το πέρας των γεωλογικών περιόδων, τη διάκριση μεταξύ αγγειόσπερμων και κωνοφόρων με βάση την ανατομία του ξύλου. Για την πληρέστερη κατανόηση του κειμένου της εισαγωγής έχουν χρησιμοποιηθεί επιλεγμένες εικόνες και τρισδιάστατες απεικονίσεις που παρουσιάζουν τις τρεις τομές (εγκάρσια, ακτινική και εφαπτομενική) που απαιτούνται για τη μελέτη και τον προσδιορισμό των απολιθωμένων και σύγχρονων αντιπροσώπων με ξυλώδη ιστό. Εν συνεχεία (στα κεφάλαια 2 έως 5) αναλύονται λεπτομερώς οι περιπτωσιολογικές μελέτες.

Στο δεύτερο κεφάλαιο παρουσιάζεται η έρευνα που πραγματοποιήθηκε στη Νήσο Λέσβο. Στο τμήμα αυτό της διατριβής αποκαλύπτεται αρχικά το ιστορικό της αναγνώρισης και της ταυτοποίησης του παλαιοχλωριδικού θησαυρού της Λέσβου. Ακολούθως δίδονται τα αποτελέσματα της μελέτης του προσδιορισμού των νέων απολιθωμένων ευρημάτων καθώς και η περίληψη της νέας προτεινόμενης μεθοδολογίας για τον προσδιορισμό των απολιθωμένων Δαφνίδων και το συσχετισμό τους με τα σημερινά είδη, η οποία βασίστηκε σε νεοσυλλεχθέντα πολυάριθμα δείγματα από τις έρευνες που πραγματοποιήθηκαν στο νησί το 2011 για τις ανάγκες εκπόνησης της παρούσας διατριβής και εκδόθηκε πρόσφατα σε σημαντικό επιστημονικό περιοδικό (IAWA Journal) του Διεθνούς Οργανισμού των Ανατόμων Ξύλου (International Association of Wood Anatomists-IAWA), ενώ υπογραμμίζονται και οι υπολειπόμενες ανακολουθίες σχετικά με προσδιορισμένα είδη και προτείνονται πιθανές λύσεις στα παρατηρηθέντα προβλήματα.

Πιο αναλυτικά, νέες απολιθωματοφόρες θέσεις ηλικίας Κατωτέρου Μειοκαίνου ανακαλύφθηκαν στο νότιο τμήμα της Νήσου Λέσβου, στις περιοχές Αλωνέλια, Χονδροκούκι, Ρογκάδα, Δαμάνδρι, Πλάκες και Μεσότοπος. Κάποια από τα νέα ευρήματα των ως άνω αναφερθέντων περιοχών προσδιορίστηκαν να ανήκουν στο γένος *Laurinoxylon*. Το γεγονός αυτό σε συνδυασμό με την εκ νέου μικροσκοπική μελέτη απολιθωμένου ξύλου τριών ολότυπων από τις περιοχές της Τσεχίας και της

Ουγγαρίας (= *Laurinoxylon diluviale*, *L. czechense* και *L. müller–stolli*), οδήγησε στη γένεση μιας νέας προτεινόμενης παγκόσμιας κλείδας προσδιορισμού για το απολιθωμένο ξύλο των Δαφνίδων.

Το *Laurinoxylon* είναι ένα απολιθωμένο γένος που χρησιμοποιείτο κατά κόρον για τα απολιθωμένα γένη και είδη Δαφνίδων (ξύλου πάντα) που δεν θα μπορούσαν να δώσουν συσχετισμούς με σημερινά γένη Δαφνίδων. Η προτεινόμενη ταξινόμηση του γένους *Laurinoxylon* είναι παγκόσμια και παρέχει άμεση σύνδεση με τη σύγχρονη βοτανική. Χάρη στην αφθονία των ευρημάτων του γένους *Laurinoxylon* στο αρχείο απολιθωμάτων, αυτή η νέα μεθοδολογία μπορεί να χρησιμοποιηθεί απευθείας τόσο από παλαιοβοτανικούς/παλαιοντολόγους όσο και από γεωλόγους ως ένα καλό εργαλείο για περαιτέρω μελέτες στη συστηματική, τη στρωματογραφία και το παλαιοκλίμα.

Η διαφορετικότητα της μελέτης αυτής συγκριτικά με αντίστοιχες παλαιότερες σχετίζεται με την εξέταση της ακριβούς θέσης και της κατανομής των ιδιόβλαστων κυττάρων (ελαιοφόρων ή βλεννοφόρων) και των συνδυασμών τους ως το τελευταίο στάδιο της προτεινόμενης μεθοδολογίας (και όχι μεμονωμένα όπως γινόταν σε αρκετές προγενέστερες δημοσιευμένες μελέτες) μιας σειράς «φίλτρων» (κριτηρίων/χαρακτηριστικών αποκλεισμού) τα οποία ο Richter (1981a) είχε ορίσει ως «χαρακτηριστικά υψηλότατης σπουδαιότητας».

Η ευρεία αυτή μελέτη για την εξέταση της σημασίας των ιδιόβλαστων κυττάρων ως ενός απαραίτητου εργαλείου για την εύρεση των σημερινών βοτανικών συγγενειών των απολιθωμένων αντιπροσώπων της οικογένειας των Δαφνίδων (και ειδικά του γένους *Laurinoxylon*) βασίστηκε α) στην εργασία των Richter (1981a) και van der Werff & Richter (1996) για τα σύγχρονα γένη των Δαφνίδων, β) στις νέες λεπτομερείς περιγραφές της ανατομίας ξύλου πολυάριθμων δειγμάτων προερχόμενων από τέσσερις περιοχές της Νοτιο-Ανατολικής και Κεντρικής Ευρώπης από το Ολιγόκαινο έως το Μειόκαινο και γ) σε δημοσιευμένα δεδομένα και ανατομικές περιγραφές που αφορούν σε απολιθωμένους και σύγχρονους αντιπροσώπους της οικογένειας των Δαφνίδων όπως αναφέρονται σε πολυάριθμες δημοσιεύσεις και όπως συγκεντρώνονται στη βάση δεδομένων του InsideWood Database.

Σύμφωνα με τους Metcalfe & Chalk (1957, σ. 111) το πιο ξεχωριστό χαρακτηριστικό του ξύλου, τα ελαιοφόρα ή βλεννώδη (= ιδιόβλαστα) κύτταρα των ακτίνων και του παρεγχύματος, συνήθως υποδηλώνουν συσχετισμό με τις οικογένειες των Μαγνολιίδων (Magnoliaceae) και των Δαφνίδων (Lauraceae). Είναι επίσης σημαντικό να υπογραμμιστεί πως οι περισσότερες διαφορές ανάμεσα στις οικογένειες των Κανελλίδων (Canellaceae) και των Δαφνίδων (Lauraceae) θα μπορούσαν να ερμηνευτούν ότι οφείλονται στα διαφορετικά επίπεδα εξειδίκευσης. Το μήκος των αγγείων και κάποια άλλα χαρακτηριστικά καταδεικνύουν ότι η οικογένεια των Κανελλίδων (Εικ. 11) είναι λιγότερο εξειδικευμένη σε σχέση με αυτή των Δαφνίδων (η οποία περιλαμβάνει ίνες που χωρίζονται με διαφράγματα και απλές και πολλαπλές/κλιμακωτές πλάκες διάτρησης, εικ. 10) που με τη σειρά της είναι λιγότερο εξειδικευμένη σε σχέση με αυτή των Μαγνολιίδων (που περιλαμβάνει μόνο κλιμακωτές πλάκες διάτρησης, εικ. 12).

Η αναθεωρημένη διάγνωση του γένους *Laurinoxylon* (Dupéron *et al.* 2008) επέτρεψε τη συγκεκριμενοποίηση των χαρακτηριστικών που προσδιορίζουν ποιοι απολιθωμένοι ξυλώδεις αντιπρόσωποι δεν μπορούν να αντιστοιχούν στο *Laurinoxylon.* Τα χαρακτηριστικά αυτά περιγράφονται ακολούθως:

A. Χαρακτηριστικά αξονικού παρεγχύματος (αποτραχειακού - παρατραχειακού): A1. Περιθωριακό αξονικό παρέγχυμα, A2. Πτερυγιοειδές έως πτερυγιοειδές-συρρέον παρατραχειακό παρέγχυμα,

B. Χαρακτηριστικά ακτίνων: B1. Ακτίνες ψηλότερες από 1 mm, B2. Αποκλειστικά ομογενείς/ομοκυτταρικές ακτίνες, B3. Ακτίνες με περισσότερα από 5 κύτταρα κατά πλάτος, B4. Ακτίνες «δεσμιδωτές» ή «σε στρώσεις» (=storied rays).

C. Πορώδες: Τύπου «δακτυλίου» ή «δακτυλιόπορου»,

D. Ιδιόβλαστα κύτταρα: Απουσία των ιδιόβλαστων κυττάρων.

Η εφαρμογή των ανωτέρω αναφερθέντων τεσσάρων κριτηρίων αποκλεισμού (A1+2, B1+2+3+4, C και D) έδωσε ως αποτέλεσμα τους σημερινούς βοτανικούς συγγενείς του *Laurinoxylon*. Το απολιθωμένο γένος *Laurinoxylon* πλησιάζει περισσότερο τα σύγχρονα γένη των ταξονομικών κατηγοριών α) Laureae (*Lindera* A και B, North American *Persea*, *Litsea, Actinodaphne, Laurus, Neolitsea*) και β) Perseae (*Persea*, *Cinnamomum*, *Nothaphoebe*, *Phoebe, Dicypellium*, *Urbanodendron, Dehaasia, Systemonodaphne, Aiouea, Pleurithyrium, Nectandra, Ocotea, Aniba, Licaria* και *Cryptocarya* Μαδαγασκάρης), που αντιπροσωπεύουν το Βόρειο Ημισφαίριο και την Νεοτροπική (= περιλαμβάνει την Κεντρική και Νότια Αμερική με το τροπικό νότιο τμήμα του Μεξικού και της Καραϊβικής) ή τη Νεοτροπική/Ασιατική ζώνη, καθώς επίσης και γ) τα γένη *Apollonias* και *Iteadaphne.*

Η παρατήρηση της ακριβούς θέσης των ιδιόβλαστων κυττάρων μας επέτρεψε να αναγνωρίσουμε τέσσερις ομάδες ειδών του γένους *Laurinoxylon*:

- Τύπος 1 με ιδιόβλαστα κύτταρα που σχετίζονται μόνο με τα ακτινικά παρεγχυματικά κύτταρα,
- Τύπος 2a με ιδιόβλαστα κύτταρα που σχετίζονται με δύο τύπους παρεγχυματικών στοιχείων: με το ακτινικό και το αξονικό παρέγχυμα,

- Τύπος 2b με ιδιόβλαστα κύτταρα που σχετίζονται με δύο διαφορετικούς τύπους στοιχείων: τις ακτίνες και τις ίνες, και
- Τύπος 3 με ιδιόβλαστα κύτταρα που σχετίζονται με τρεις τύπους στοιχείων: με το ακτινικό και αξονικό παρέγχυμα και με τις ίνες.

Το επόμενο βήμα ήταν η εύρεση των συσχετισμών που θα συνέδεαν τους απολιθωμένους αντιπροσώπους των κατηγοριών του *Laurinoxylon* με τα σύγχρονα γένη των Δαφνίδων. Τα αποτελέσματα της μελέτης έδειξαν ότι τα σύγχρονα γένη που πλησιάζουν περισσότερο στον Τύπο 1 του *Laurinoxylon* είναι τα ακόλουθα: *Dicypellium, Systemonodaphne, Urbanodendron, Persea* Βορείου Αμερικής, *Litsea chinensis* group, *Laurus.* Από αυτά, τα γένη που εμφανίζουν μεγάλο ποσοστό ειδών με κρυστάλλους είναι τα: *Laurus*, *Litsea chinensis* group & *Systemonodaphne, ενώ τα γένη χωρίς κρυστάλλους είναι τα: Dicypellium, North American Persea & Urbanodendron.*

Τα απολιθωμένα είδη που ανήκουν στον τύπο 2a του *Laurinoxylon* είναι πλησιέστερα στα σύγχρονα γένη: *Aniba, Licaria, Aiouea, Pleurothyrium, Cryptocarya* Μαδαγασκάρης, *Dehaasia, Nothaphoebe, Phoebe, Persea, Apollonias, Lindera* group A. Από αυτά, τα γένη με υψηλό ποσοστό ειδών με κρυστάλλους είναι τα: *Aniba, Apollonias, Dehaasia, Phoebe, Licaria* & *Pleurothyrium,* ενώ τα γένη χωρίς κρυστάλλους είναι τα: *Cryptocarya* Μαδαγασκάρης, *Nothaphoebe*, καθώς και το 70% των ειδών των: *Aiouea, Persea* & *Lindera* group A.

Τα είδη του τύπου 2b του *Laurinoxylon* είναι πιο κοντά στα σημερινά γένη: *Actinodaphne* p.p., *Neolitsea* p.p. και *Nectandra* p.p. Το 25% των ειδών της *Actinodaphne*, το 40% των ειδών της *Nectandra* και το 50 % των ειδών της *Neolitsea* δεν περιέχουν κρυστάλλους (επίσης, το 90% των ειδών της *Actinodaphne* & *Neolitsea* και το 84% της *Nectandra* δεν περιλαμβάνουν ιδιόβλαστα κύτταρα στις ίνες, παρά μόνο στο ακτινικό και αξονικό παρέγχυμα και ανήκουν σε αυτήν την κατηγορία).

Τέλος τα είδη του τύπου 3 του *Laurinoxylon* (συνώνυμο: *Cinnamomoxylon*) είναι πλησιέστερα στα σύγχρονα γένη: *Actinodaphne* p.p., *Nectandra* p.p., *Ocotea, Endlicheria, Cinnamomum, Neolitsea* p.p. Από τα προαναφερθέντα γένη αυτά που εμφανίζουν μεγάλο ποσοστό ειδών με κρυστάλλους είναι τα: *Actinodaphne* p.p., *Endlicheria, Nectandra* p.p. & *Neolitsea* p.p. (για την ακρίβεια, μόνο το 10% των ειδών της *Actinodaphne* & *Neolitsea* και το 16% των ειδών της *Nectandra* περιλαμβάνουν ιδιόβλαστα κύτταρα και στις ίνες και ανήκουν σε αυτήν την κατηγορία). Τα γένη *Cinnamomum* & *Ocotea* δεν εμφανίζουν κρυστάλλους.

Η μετονομασία και η εκ νέου μελέτη κάποιων ειδών του γένους *Laurinoxylon* που έχουν ήδη περιγραφεί (και λανθασμένα θεωρήθηκε ότι ανήκουν στο εν λόγω γένος) από άλλους συγγραφείς αποτελεί ένα ακόμη από τα αποτελέσματα της παρούσας μελέτης.

Στο ίδιο κεφάλαιο δίδονται και οι συστηματικές περιγραφές αρκετών «τύπων ξύλου» (="wood types") (Wiemann *et al.* 1988) νέων ευρημάτων αγγειόσπερμων και κωνοφόρων από το νησί της Λέσβου. Μεταξύ των ευρημάτων περιγράφονται τουλάχιστον 13 «τύποι ξύλου» αγγειόσπερμων και 5 «τύποι ξύλου» κωνοφόρων.

Ανάμεσα στα μελετηθέντα αγγειόσπερμα που αναγνωρίστηκαν είναι τα ακόλουθα: *Laurinoxylon* aff. *czechense* Prakash, Březinová & Bůžek, *Laurinoxylon* cf. *daberi* Greguss, *Laurinoxylon* aff. *diluviale* (Unger) Felix emend. Dupéron *et al.*, *Cinnamomoxylon seemannianum* Mädel. Τα είδη αυτά του γένους *Laurinoxylon* & *Cinnamomoxylon* εμφανίζονται για πρώτη φορά στην Ελλάδα. Επιπλέον έχει προσδιοριστεί το γένος *Quercoxylon* Kräusel και *Cryptocaryoxylon* Leisman. Όσον αφορά το τελευταίο απολιθωμένο γένος, κατά την εκπόνηση της παρούσας μελέτης προσδιορίστηκε και σε ευρήματα της νήσου Λήμνου και αντιπροσωπεύει την πρώτη εμφάνιση του γένους για το Νεογενές της Ευρασίας.

Μεταξύ των μελετηθέντων κωνοφόρων ήταν και το *Cedroxylon lesbium* Kräusel (*Peuce lesbia* Unger) το οποίο ανακαλύφθηκε σε συλλογή μουσείου του εξωτερικού, μελετήθηκε στο μικροσκόπιο, περιγράφηκε λεπτομερώς και φωτογραφήθηκε για πρώτη φορά σχεδόν 2 αιώνες μετά από τον πρώτο προσδιορισμό του.

Το τρίτο κεφάλαιο πραγματεύεται τη μελέτη περίπτωσης της νήσου Λήμνου. Το ιστορικό της παλαιοχλωρίδας της νήσου Λήμνου έχει δοθεί λεπτομερώς στο κεφάλαιο αυτό. 30 νέα δείγματα από νέες απολιθωματοφόρες θέσεις από τις περιοχές του Μούδρου, του Βάρους και του Θάνους βρέθηκαν και μελετήθηκαν. Παράλληλα μελετήθηκαν 44 δείγματα απολιθωμένου ξύλου που φυλάσσονται στο Δημαρχείο του Μούδρου.

Μεταξύ των μελετηθέντων αγγειόσπερμων είναι το είδος *Laurinoxylon* cf. *ehrendorferi* Berger το οποίο βρέθηκε και μελετήθηκε 63 χρόνια μετά την πρώτη του αναγνώριση καθώς επίσης και το γένος *Cryptocaryoxylon* Leisman, το οποίο (μαζί με το δείγμα που βρέθηκε στη Λέσβο, η μελέτη του οποίου έδειξε ότι ανήκει στο εν λόγω γένος) αποτελεί την πρώτη εύρεση και ταυτοποίηση του συγκεκριμένου γένους για το Νεογενές της Ευρασίας.

Ο προσδιορισμός των απολιθωμένων κωνοφόρων από τη νήσο Λήμνο περιλαμβάνει τουλάχιστον τρεις τύπους του γένους *Taxodioxylon* Hartig emend. Gothan. Πρόκειται για την πρώτη αναφορά του συγκεκριμένου γένους στη νήσο Λήμνο.

Το τέταρτο κεφάλαιο έχει ως θέμα την μελέτη περίπτωσης της νήσου Αλοννήσου. Στο εν λόγω κεφάλαιο, εκτός από το ιστορικό κομμάτι που σχετίζεται με την αναγνώριση και τον προσδιορισμό των φυτικών απολιθωμάτων στο νησί, ένα μεγάλο τμήμα είναι αφιερωμένο στην (επιτυχή) προσπάθεια ανακάλυψης της ακριβούς θέσης όπου πριν από σχεδόν 2 αιώνες βρέθηκε και προσδιορίστηκε για πρώτη φορά το είδος *Taxodium europaeum (*Brongniart) Unger. Μεταξύ των νεοσυλλεχθέντων ευρημάτων είναι και ένα ιδιαίτερο ξυλιτικό δείγμα που προσδιορίστηκε ότι ανήκει στο γένος *Pinuxylon* Gothan.

Το πέμπτο κεφάλαιο ασχολείται με τη νήσο Γαύδο. Περισσότερα από 100 αποτυπώματα φύλλων από τη θέση Μετόχια στο Βόρειο τμήμα του νησιού μελετήθηκαν και προσδιορίστηκαν. Ανάμεσα στα είδη που προσδιορίστηκαν περιλαμβάνονται και οι εμφανίσεις των: *Fagus gussonii* (η νοτιότερη εμφάνιση του είδους), *Sapindus graecus* (επιβεβαίωση της περιορισμένης εξάπλωσής του μόνο στη ΝΑ Ευρώπη)*, Ailanthus pythii* (πρώτη εμφάνιση για τη Μεσόγειο) Η αναγνώριση μεγάλου αριθμού αγγειόσπερμων επέτρεψε τη χρήση αρκετών τεχνικών σχετικών με την ανασύσταση της παλαιοβλάστησης [π.χ. Φυτοκοινωνιολογική προσέγγιση (=Phytosociological approach) και Ανάλυση βλάστησης του ολοκληρωμένου φυτικού αρχείου (=Integrated Plant Record vegetation analysis – IPR vegetation analysis)], και του παλαιοκλίματος [π.χ. Ανάλυση του περιθωρίου των φύλλων (=Leaf Margin Analysis), Πολυπαραγοντικό πρόγραμμα ανάλυσης κλίματος-φύλλων (=Climate Leaf Analysis Multivariate Program – CLAMP) και η μέθοδος του πλησιέστερου σημερινού συγγενή (Coexistence Approach)].

Στο έκτο κεφάλαιο παρουσιάζονται τα αποτελέσματα της διατριβής με συζητήσεις σχετικά με τα πιο ενδιαφέροντα νέα ευρήματα από τις νήσους Λέσβο, Λήμνο, Αλόννησο και Γαύδο και η σπουδαιότητά τους.

Το κείμενο συνοδεύεται από δύο παραρτήματα: το πρώτο αφορά στα φυτικά (μακρο-) απολιθώματα ξύλου και φύλλων (φτέρες, κωνοφόρα και αγγειόσπερμα) από τη νήσο Λέσβο και το δεύτερο πραγματεύεται τα έως τώρα απολιθωμένα φυτικά (μακρο- και μικρο-) ευρήματα ξύλου, φύλλων και γύρης που ανήκουν σε κωνοφόρα και αγγειόσπερμα από το νησί της Λήμνου.

Πολυάριθμα σχήματα και 41 πίνακες με πληθώρα μακροσκοπικών και (κυρίως) φωτογραφιών οπτικού και ηλεκτρονικού μικροσκοπίου έχουν δημιουργηθεί. Για περαιτέρω λεπτομέρειες αναφορικά με συγκεκριμένα κεφάλαια της διατριβής (π.χ. ανάπτυξη της νέας μεθοδολογίας για τον προσδιορισμό του *Laurinoxylon* και των σημερινών γενών στα οποία αντιστοιχεί με βάση τα ιδιόβλαστα κύτταρα, ή σχετικά με τη μελέτη της παλαιοχλωρίδας της νήσου Γαύδου) ο αναγνώστης καλείται να συμβουλευτεί τα συνημμένα παραρτήματα στο τέλος του κειμένου που αποτελούν τμήματα της παρούσας διατριβής δημοσιευμένα σε επιστημονικά περιοδικά μετά από αξιολόγηση κριτών.

CONTENTS

CASE STUDIES

INSTEAD OF A PREFACE

“…The real voyage of discovery consists not in seeking new landscapes, but in having new eyes”

Marcel Proust

1. INTRODUCTION

The research of the palaeobotanical record of specific regions at the eastern Meditteranean (Lesbos, Lemnos, Alonissos and Gavdos Islands) during the Cenophytic is a demanding issue.

The Cenophytic era is composed by the palaeo- (Late Cretaceous-Neogene) and neo-cenophytic (Quaternary) floras (Meyen 1987). The age of the findings the present study deals with is mainly Miocene. Popov *et al.* (2004, Map 4–Map 9) have visualized the palaeogeography of the early, middle and late Miocene.

The structure of the study includes an “introduction” chapter, four “case study areas” chapters (Lesbos, Lemnos, Alonissos and Gavdos) with the typical order (introduction-localities and geology-material and methods-historical part of the plant fossil findings-systematic descriptions with comparisons and discussion-fossil flora appendix for each area) followed on the development of each research area and at the end a “discussion and conclusions” chapter. This order has been chosen as the most appropriate for the purposes of this research and the most convenient to be followed by the readers.

New plant fossiliferous localities with hundreds new specimens have been revealed. Leaves’ imprints have been studied only from Gavdos Island. The majority of the collected samples (from Lesbos, Lemnos and Alonissos Islands) belong to fossil wood remnants therefore this study has been focused primarily on the fossil wood anatomy. For the purposes of the examination of possible nearest living relatives of the fossil species there were special references to modern wood anatomy (e.g. *Cedrus*). An introduction to the wonderful world of the fossil wood seems to be necessary and is given below.

1.1 Wood definition

The term ‘wood’ or ‘xylem’ is used for plants with secondary radial thickening (Carlquist, 2001) as also for the lignified specimens. Schweingruber & Büntgen (2013) have recommended the botanically more neutral term ‘stem anatomy’ instead of ‘wood anatomy’, which further implies integration of the xylem and bark of all terrestrial plants.

The distinction among wood, stem and roots is also a matter of several studies concerning the identification of fossil representatives. Regarding to the evolution, the fossil record shows that wood evolved in small stature plants prior to the evolution of a distinctive leaf-stem-root organography (Strullu-Derrien *et al.* 2013).

1.2 Distinction concerning the wood

The main wood categories include angiosperms (or hard woods) and conifers (or soft woods). The latter wood categories are discussed in detail by Baas *et al.* (2004, p. 275).

1.3 Identification of angiosperm wood

Concerning the history of the angiosperms, pollen grains from the Valanginian (ca 135 mya) of Israel, are considered as the oldest record of angiosperm (Singh 2009). *Archaefructus* from Upper Cretaceous (nearly 124 mya) of China, a follicle with clearly defined spirally arranged conduplicate carpels enclosing ovules without petals and sepals and with 3 species up to now (*Archaefructus liaoningensis*, *A. sinensis* and *A. eoflora*), is regarded as the oldest record of angiosperm flower (Sun *et al.* 2002, Qiang *et al.* 2004, Singh 2009). Undoubtedly, the knowledge on the evolution of stem-group angiosperms is still very poor.

The phyllogeny of the "flowering plant families" (Fig. 1) is continuously revisited and updated by Stevens (Angiosperm Phylogeny Website, 2001-onwards), and a different visualization of the seed plant universe is available also from the Botanical Chart website (http://www.botanicalchart.org.uk).

The angiosperms have as their synonym the term "hardwood" because of their anatomy (= the density of the cells, the amount of lignin in the cell walls, and the percentage of tiny air spaces or pores within the cell walls) which confers to the wood weight and hardness (also known as the 'specific gravity', a scale method invented thousands years ago by Archimedes based on the comparison measures using 1.0 for pure water).

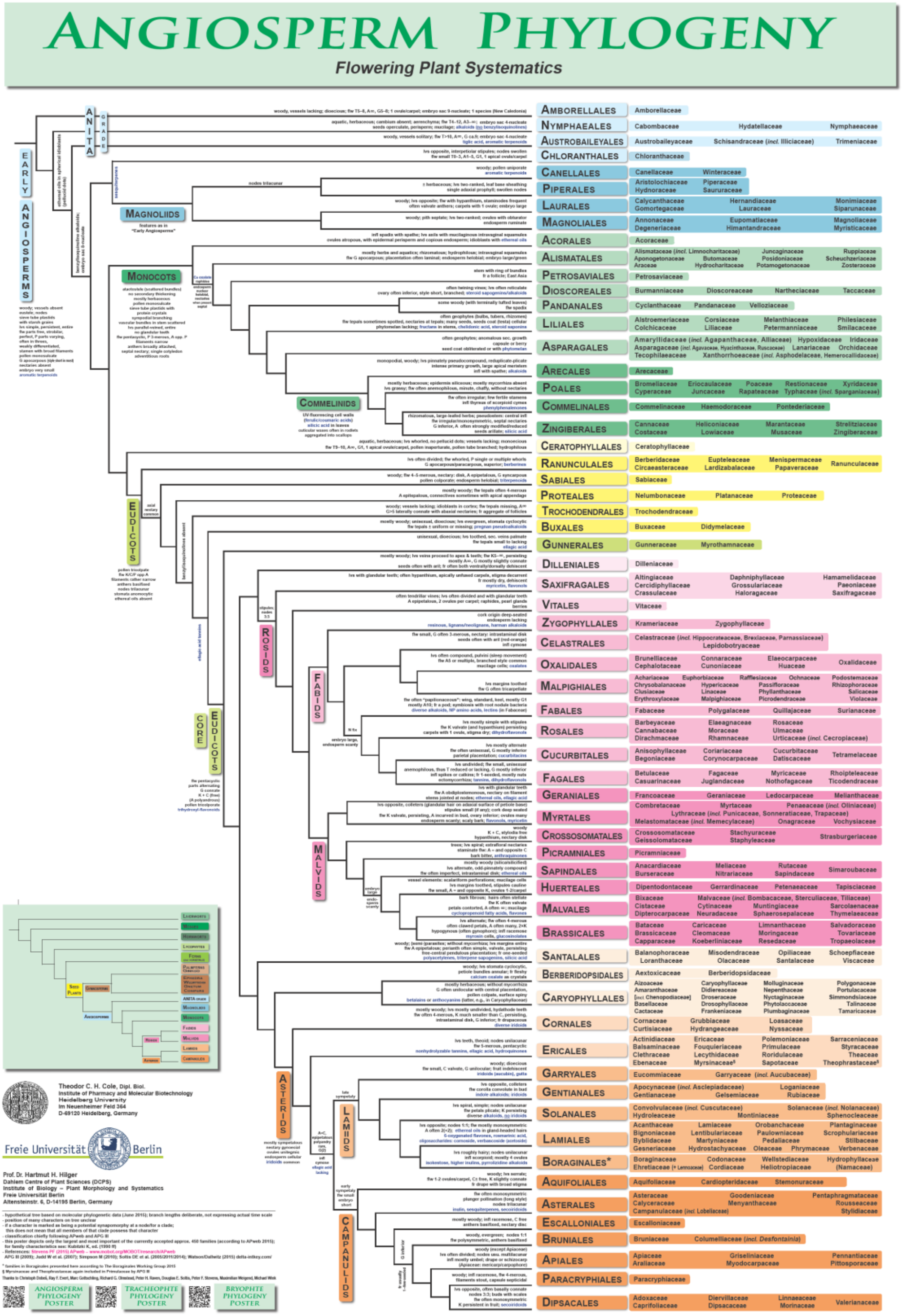


Fig. 1: The “flowering plant families” (=Angiosperms) phyllogeny (Stevens, Angiosperm Phylogeny Website, 2001-onwards).

The characteristic of the angiosperm wood concerning its anatomy is the occurrence of vessels (Fig. 2), although they are absent in some angiosperms (Winteraceae) and on the contrary they are present in some gymnosperms (Gnetales) (Singh, 2009). If one could search through time in order to explore the diversity of the angiosperms (= flowering plants), he could be astonished. Magallón & Castillo (2009) have examined angiosperms diversification since the Lower Cretaceous noting, at their introduction, that even Charles Darwin has been wondering about the diversification of the angiosperm concerning its rhythm through time (constant or not) and the start point which lead to modern species whole image.

The identification of angiosperm woods based on their anatomical characteristics (Fig. 2) is a really demanding process. According to IAWA (1989) several anatomical features must be identified and measured for the identification of a hardwood, concerning the growth ring (boundaries), the vessels (porosity, arrangement and grouping, outline, the perforation plates, the intervessel pits arrangement and size, the vestured pits, the vessel-ray pitting, the helical thickenings, the tangential diameter of the vessel lumina, the number of the vessels per square millimeter, the mean vessel element length, the occurrence of tyloses and deposits inside them), the tracheids and fibres, the axial parenchyma (apotracheal, paratracheal, banded, storied structures), the rays (width, height, cellular composition, size, number per millimetre, aggregate or not, with sheath or tile cells, perforated) the secretory elements and cambial variants (oil and mucilage cells, intercellular canals, tubes), the mineral inclusions (prismatic crystals, druses and other crystal types), etc. The Inside Wood Database (InsideWood. 2004-onwards) uses the same features for search through the fossil and modern record.

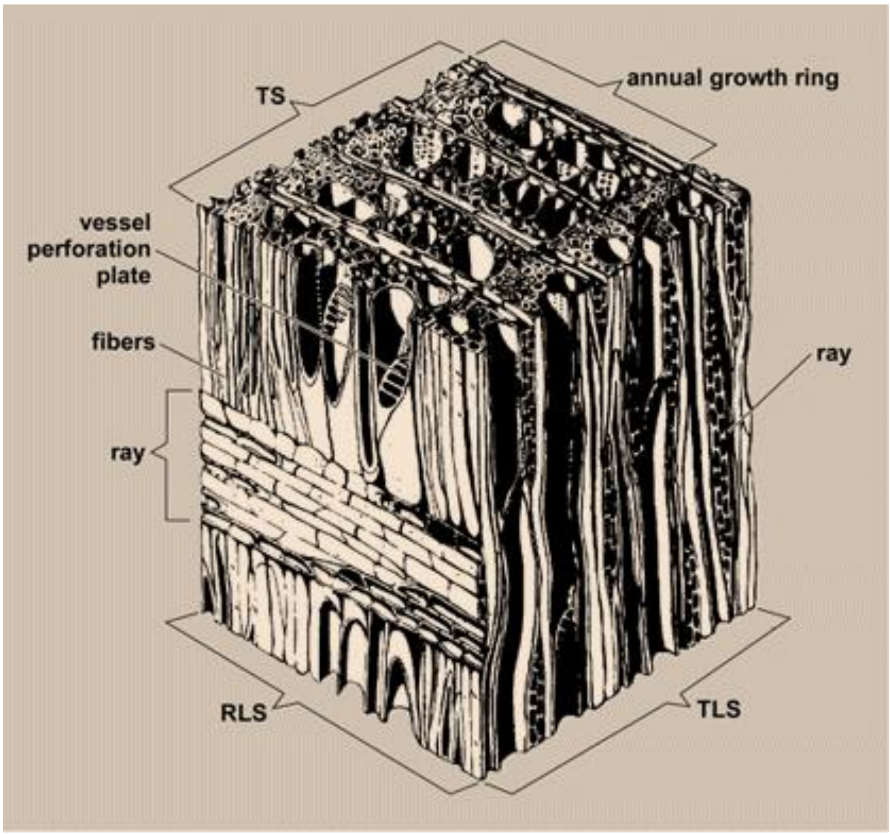


Fig. 2: 3D interpretation of the xylem anatomy showing the three planes needed for the identification of a fossil and modern angiosperm wood specimen. TS = Transverse, RLS= Radial and TLS= Tangential Section. Photo by the courtesy of U.S. Forest Service, modified.

1.4 Identification of conifers

The wood of the conifers have as their synonym the term “softwood” because according to their anatomy, their wood is composed mainly of tracheids (= water-conducting cells) without fibre cells. According to Farjon (2001) the families which belong to the softwoods (Fig. 3) include the Pinopsida (Coniferales) and Ginkgoopsida [Araucariaceae, Cephalotaxaceae, Cupressaceae (including Taxodiaceae), Ginkgoaceae, Phyllocladaceae, Pinaceae, Podocarpaceae, Sciadopityaceae and Taxaceae]. The University of Berlin has presented the tracheophyte and gymnosperms (conifers) phylogeny as shown below (Fig. 3).

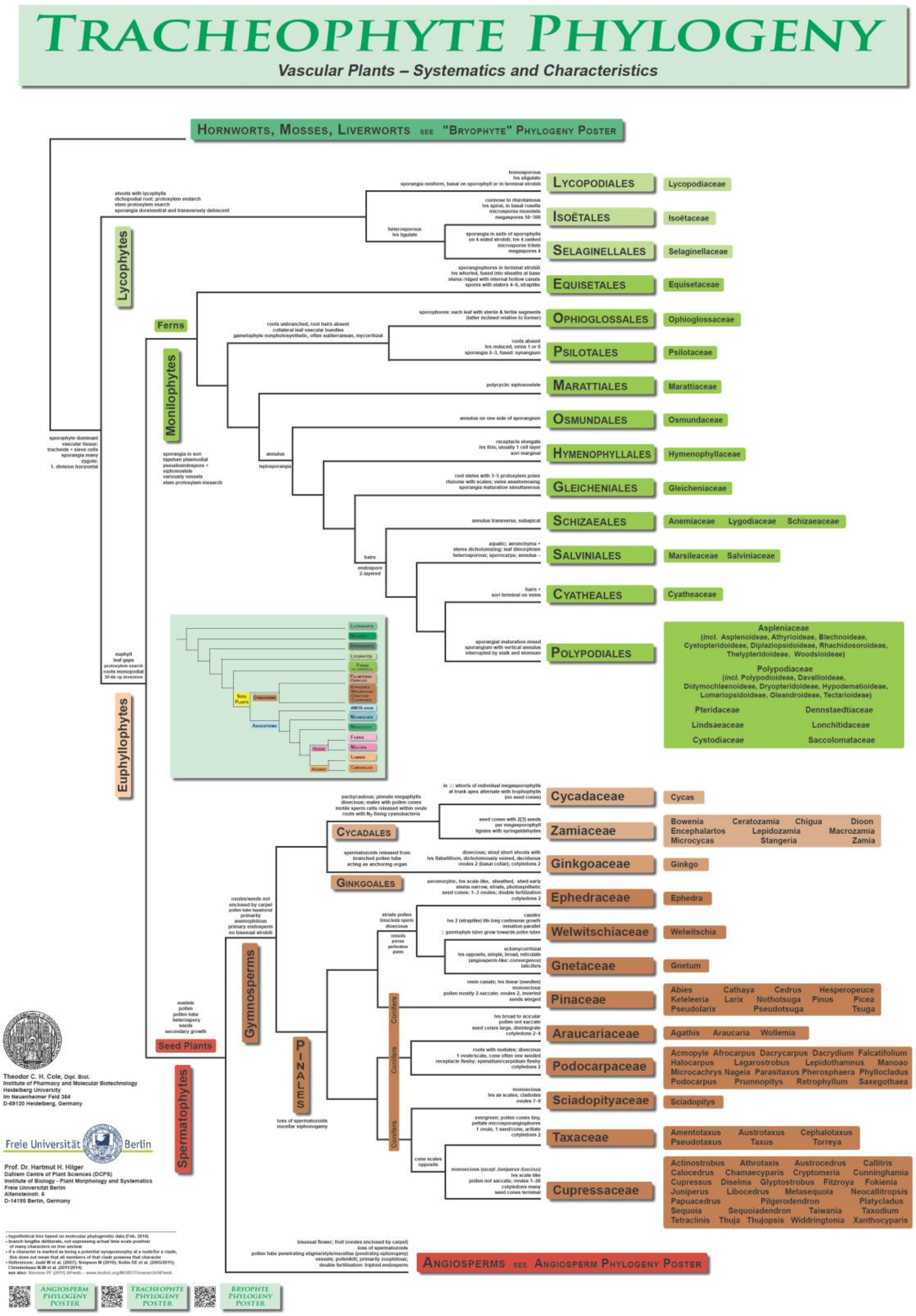


Fig.3: Systematics and characteristics of the vascular plants presented by the University of Berlin. The gymnosperms (conifers) phylogeny is shown in brown colour.

The identification of “gymnosperm” woods (= conifers) follows the “Softwood identification” terminology based on their anatomical characteristics by IAWA (2004). The anatomical features which must be identified and measured for the identification of a softwood (Fig. 4) concern the growth rings (boundaries and transition from early- to late-wood), the tracheids (pitting in radial walls, arrangement, organic deposits, average length, intercellular spaces throughout the wood, latewood tracheid wall thickness, torus, torus extensions, pits with notched borders, warty layer), helical and other wall thickenings (e.g. in tracheids), axial parenchyma (arrangement, transverse end walls), ray composition (ray tracheids, cell walls of ray tracheids, pit borders, end walls, horizontal walls, indentures), cross-field pitting categories (and number of pits per cross-field), ray size (height, width), intercellular canals (axial, radial, traumatic, average diameter of the canals, epithelial cells), mineral inclusions (crystals, their type and location).

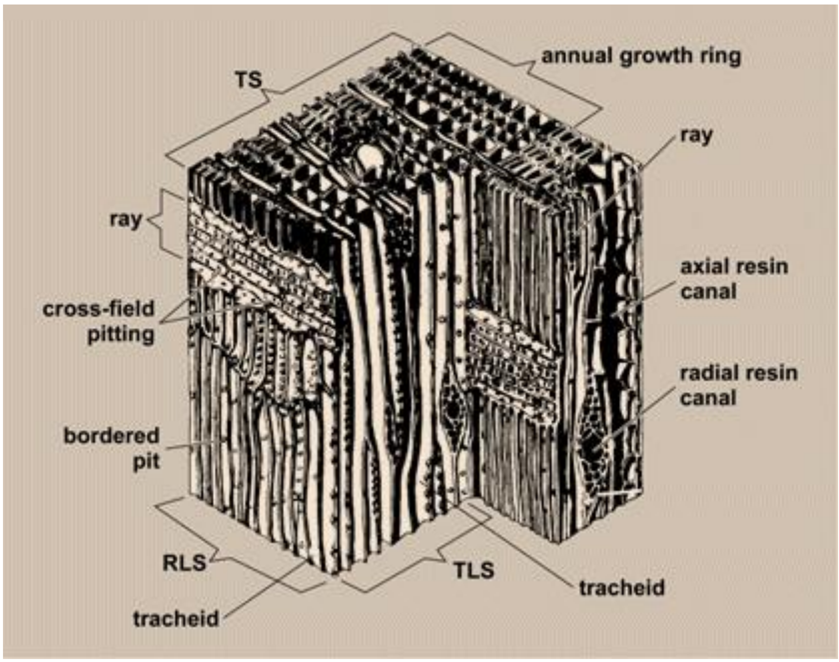


Fig. 4: 3D interpretation of the xylem anatomy showing the three planes needed for the identification of a fossil and modern conifer wood specimen. TS = Transverse, RLS= Radial and TLS= Tangential Section. Photo by the courtesy of U.S. Forest Service, modified.

2. LESBOS ISLAND

2.1.1 Introduction

In 2012 Lesbos Island has faced the ultimate recognition as one of Unesco's Global Geoparks, an honor for its geological treasure as revealed by the variety of its geosites. This unique geological and palaeobotanical heritage, focused on the occurrence of the Petrified Forest at the Western part of the Island has been notified since the 3rd century B.C. by the famous Greek botanist Theophrastus from Eressos (Lesbos Island, Greece).

The scientific research and identification of the plant fossils of the western peninsula of the Island started at the 19th century by F. Unger (1845, 1847, 1850) and P. Fliche (1898). More intensive efforts were made the last decades of the 20th century by the University of Athens and by the Natural History Museum of the Lesvos Petrified Forest (e.g., Velitzelos & Zouros 2008). The research during the last two centuries has revealed 25 species of conifers and 5 species of angiosperms concerning the wood occurrences while the foliage findings certify the opposite (Mantzouka *et al.* 2013a, Annex 1).

The main focus of this study is: 1) to reveal the historical part of Lesbos palaeofloristic treasure, 2) to draw the new fossil–wood identification results of a new research started in 2011 and 3) to underline the remaining inconsistencies and propose solutions.

The discovery of new Lower Miocene fossiliferous localities (Fig. 5) since 2011 at the Southern part of the Island (Mantzouka *et al.* 2013a) along with the new results originated from the new studies and also based on the new and previous data allow to apply the Whole Plant Concept (Sakala 2004, Teodoridis & Sakala 2008) and a new proposed methodology on Lauraceae (Mantzouka *et al.* in press) with interesting results for the Oligo–Miocene palaeoflora of Europe.

The study of the xylotomical anatomy of the fossil tree–remnants – with the preparation of thin slides for each and every one of the decades of the newly discovered fossils – revealed various coniferous samples along with numerous angiosperms among the findings.

Not only the new evidence on the palaeofloristic catalogue but also the variety of the fossilization (taphonomical processes with several parameters strongly connected to volcanism) and preservation types (leaf impressions, molds and casts, permineralized, silicified and lignified trunks, fossiliferous block assemblages, lignitic horizons) interpreted for each fossiliferous locality and also the extension of the plant fossil assemblages with – not only sporadic occurrences but – numerous fossil plants at the Southern part of the Island are of great importance (Mantzouka *et al.* 2013b).

2.1.2 Localities and Geology

Lesbos Island is highly appreciated by the scientific community because of the occurrence of the famous Miocene Petrified Forest at the western peninsula of the Island.

Since 2012 the whole Island of Lesbos (and not only the area of the Petrified Forest) has been declared as a European and Global Geopark under the auspices of UNESCO (belonging to the EGN and GGN) and on November 2015 Lesbos Island has received the ultimate recognition of its international significance honored as a UNESCO Geopark. Geoparks represent the holistic approach of unique and important territories which combine the protection and promotion of geological heritage with sustainable local development (Zouros 2004).

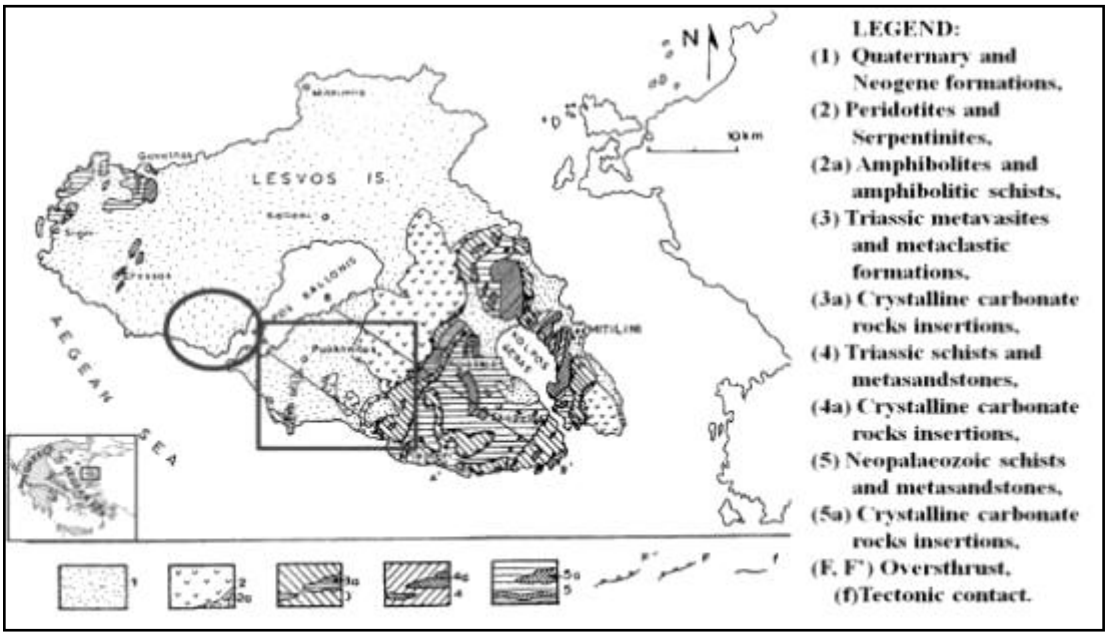


Fig. 5: Geological map of Lesbos Island by Katsikatsos *et al.* (1986), modified. The region of Polichnitos and Mesotopos, which represent our study areas, are included in the rectangular and inside the circle respectively.

Lesbos Island is located at the NE part of Aegean and it belongs to the Pelagonian geotectonic zone of Greece which represents a fragment of the

Cimmerian Continent (Mountrakis 1983; 1986) with the bending of the geotectonic zones to the E / NE to the Sakaraya zone of Asia minor (Thomaidou 2009) or to the Lesbos geotectonic zone (and in three different terrains) according to Papanikolaou *et al.* (2004).

The geology of Lesbos has been described by several scientists, for instance: Fytikas *et al.* (1984), Hecht (1971; 1974; 1975), Katsikatsos *et al.* (1982; 1986), Mountrakis *et al.* (1983; 2001), Pe–Piper (1978), Thomaidou (2009), as well as its palaeogeographical evolution through time (Dermitzakis 1996, Dermitzakis & Drinia 1999, Drinia *et al.* 2002). Hecht (1971; 1974) presented the geological map of the Island (1: 50.000 scale). The geology of Lesbos Island consists of:

- An autochthonous unit of Permo–Triassic age, including mica schists, quartzites, metasandstones and phyllites. A carbonate sequence, often more than 400m thick, occurs in the upper part of this unit. These rocks extend widely in the south–eastern part of the Island, while in the north–western part they have a rather smaller extension. Although the origin of this autochthonous unit remains undocumented, it is considered a probable remnant of the Cimmerian continent (Katsikatsos *et al.* 1986, Mountrakis *et al.* 1983, Papanikolalou 1999).
- Two allochthonous units representing the volcanosedimentary nappe and the ophiolite nappe. The first one consists of metabasites and metamorphic sedimentary rocks such as crystalline limestones, amphibolitic schists, metapellites and meta–cherts of Triassic age. The ophiolite nappe consists mainly of serpentinized peridotites and dunites, as well as metamorphic rocks, amphibolites and amphibole schists – parts of the metamorphic sole. The initial placement of both allochthonous units took place during Jurassic times (Papanikolaou 1999) and they represent remnants of an old Tethyan oceanic crust (Mountrakis *et al.* 2001) that was obducted (= overthrusted) over the Eurasian continental margin.

The central and western part of the Island is covered by Neogene volcanic rocks (of calcium–alkaline and shoshonitic composition) originating from the volcanic activity which took place at the Central–Northern Aegean area (volcanic arc) and ended at the Western Anatolia during the Upper Oligocene – Middle Miocene. (Fytikas *et al.* 1984).

Plate 1

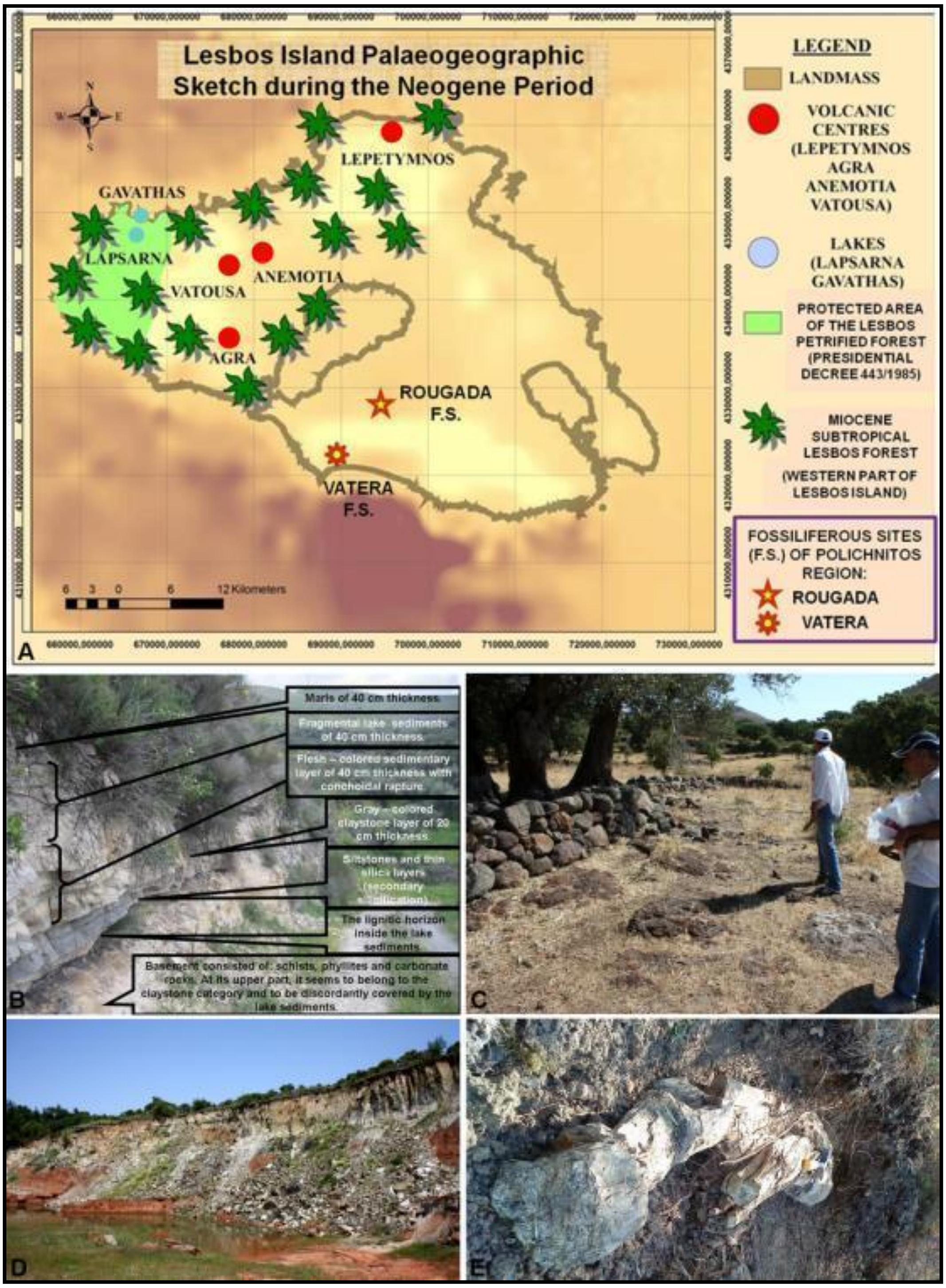


Plate 1.

A: Lesbos Island palaeogeographic sketch during the Neogene period with the volcanic centres, palaeolakes and the fossiliferous localities of the Island pointed. **B:** Lapsarna lignitic horizon and the stratigraphic column of the section. **C:** Mesotopos limonitic block assemblage filled with plant fossil remnants on the ground surface. **D:** New fossiliferous site: Alonelia section. **E:** New fossiliferous site: Rogkada section.

The specimens described herein are from new fossiliferous localities of the Southern part of Lesbos Island from Aegean Sea in northeastern Greece, namely Alonelia (Fig. 6, 7), Hondrokouki, Rogkada, Damandri, Plakes, Mesotopos (Plate 1). Rogkada new fossiliferous site is close to the locality found in 1994 by Professor E. Velitzelos.

Fig. 6: An example of the outcrops of the localities in Polichnitos region (Locality: Alonelia, date: 21/08/11).

Fig. 7: An example of the outcrops of the localities in Polichnitos region. The car as a scale. (Locality: Alonelia, date: 21/08/11).

The stratigraphic sequence of our section fits almost perfectly with the one presented by Katsikatsos *et al.* (1982) for Polichnitos area, with the difference of a tephra horizon (formation ‘e.i’ in Fig.8) – which can be attributed to the ‘volcanic rocks (+) formation’ – under Polichnitos ignimbrite (formation ‘c’ in Fig.8) as it is shown in Figure 8.

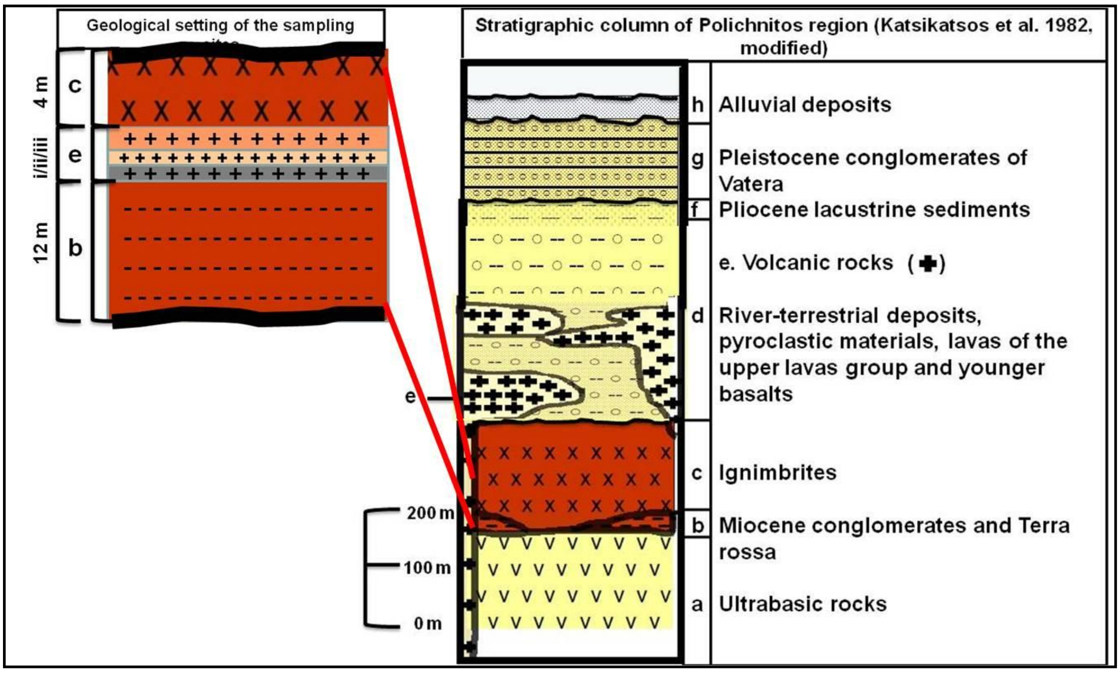


Fig. 8: “Polichnitos – Vatera” area stratigraphic column (from the bottom to the top layer) according to Katsikatsos *et al.* (1982), modified (right) and correlated with the geological setting of the new fossiliferous sites (left). The geology and the stratigraphic sequence of the newly discovered localities have been studied and described in detail recently (Mantzouka *et al.* 2013a).

According to our studies the plant fossiliferous outcrops (from the bottom to the top layer) consist of:

– Miocene Terra rossa with a thickness of approximately 12 m (formation ‘b’ in Fig.8). This is the layer which has the same stratigraphic position with the thick deposits of conglomerates and pyroclastic materials of the area of Sigri – Antissa, which are also lying under the ignimbrites and have at their lower part (and mainly at their basis) marly layers which host small lignitic deposits (Katsikatsos *et al.*, 1986). According to Lamera (2004) it might represent a ‘lahar’ formation. The basement / underlying layer is not seen at the outcrop but the general view of the area shows that the basement consists of ultrabasic rocks which belong to the allocthonous unit of the ophiolite tectonic nappe with pyroxenic peridotites, dunites, serpentinite peridotites and serpentinites**.**

– Over the Terra rossa there is a tephra horizon of 1,5 m thickness (formation ‘e. i’ in Fig.8, left column) and over this there are volcanics of beige color – consisting of 2 horizons, one of 0,4 m (‘e. ii’ formation in Fig.8, left column) and one of 2 m thickness (‘e. iii’ formation in Fig.8, left column) – with a total thickness of 2.4 m which are underlying the

– Ignimbrite of Polichnitos with a thickness of 4 m (formation ‘c’ in Fig.8). According to Pe–Piper & Piper, 1993 the only radiometric date of Polichnitos ignimbrite in 17.2 ± 0.5 Ma ‘was made by Borsi *et al.* (1972) with the geological dating method of K40/Ar40 based on the biotite of the ignimbrites corrected to the Steiger & Jäger, (1977) decay constant’.

Polichnitos ignimbrite formation belongs to the magnetic epoch 17 (Fig. 9) with an age of ~ 18.4 – 17.2 Ma (Pe–Piper, 1980; Pe–Piper & Piper, 1993 while, according to the proposed categorization of Lesbos ignimbrites by Lamera (2004), it represents the PU unit. The fossil plants of this study come from the layers which are underlying Polichnitos ignimbrite and especially from the upper and lower part of the tephra horizon (ei, eii, b in Fig. 8, left column).

The new plant fossiliferous localities of Polichnitos region, Southern part of Lesbos Island, have been discovered inside a volcanic layer that underlies the ignimbrite of Polichnitos (PU unit), the age of which is 17.2 Ma (early Miocene) and it belongs to the magnetic epoch 17 (Borsi *et al.* 1972; Pe–Piper 1980; Pe–Piper and Piper 1993; Lamera 2004; Lamera *et al.* 2004).

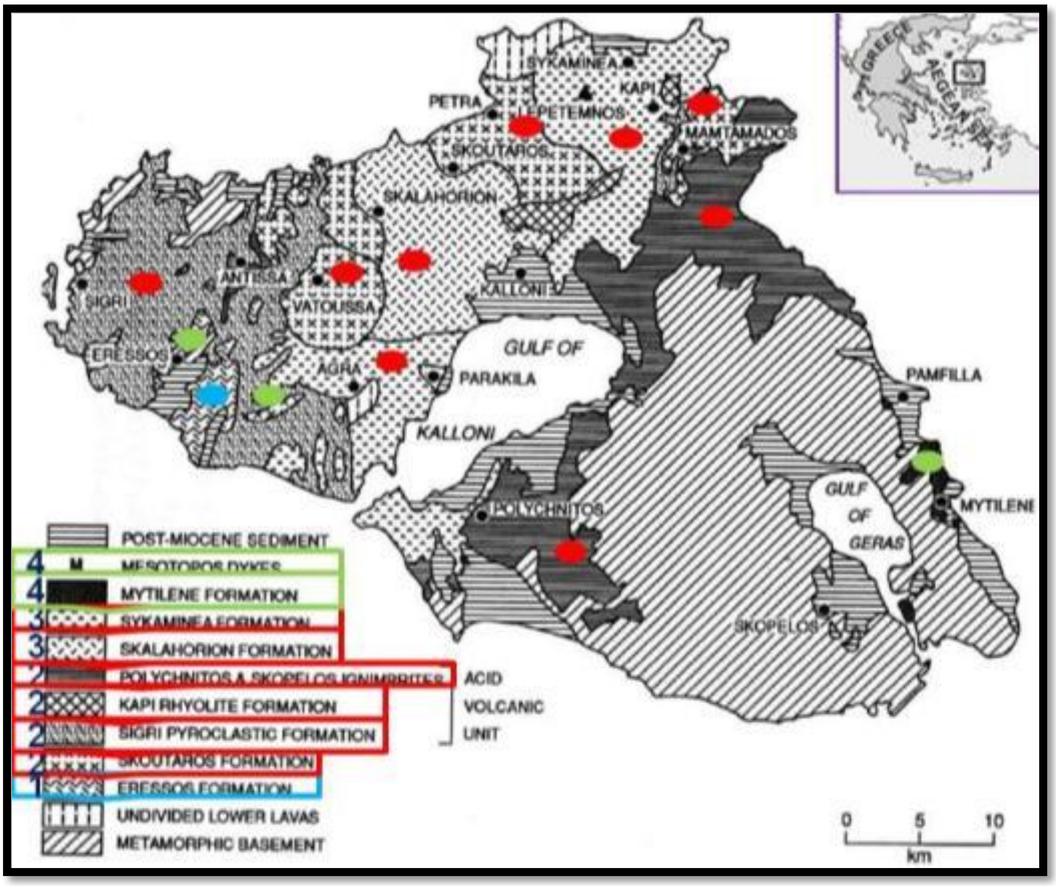


Fig. 9: Lesbos Island geological map according Pe–Piper & Piper (1993), modified. The magnetic epochs are represented with different colours as follows: 1) in red colour: the vigorous volcanic activity restricted to about one million years (18.4–17.3 Ma: Magnetic epoch 17) which included the Skoutaros, Sigri, Kapi formations & Polichnitos & Skopelos ignimbrites, 2) in blue colour: an earlier minor volcanic phase (21.5±0.5 Ma: Magnetic epoch 19) with the occurrence of Eressos formation and 3) in green colour: a younger minor volcanic phase (16.5–16.2 Ma: Magnetic epoch 16) which includes the formation of Mytilene and the dykes of Mesotopos.

This sequence of ours in the general geological setting of Polichnitos region is followed by the formations shown below:

- River–terrestrial and pyroclastic materials' horizon with volcanic rocks: They are water–permeable formations of terrestrial, river and volcanic origin interchangeable in the vertical and the horizontal which consist of conglomerates, small to large and of great consistency, clay–sandy materials, red clay with scattered conglomerate breccia, cohesive pyroclastic breccia and tuff materials having a thickness from a few to 100m. Inside these formations, in many localities and mainly in the form of veins, there is the occurence of masses of volcanic rocks.

- Volcanic rocks: They are mainly basalts, dacites and andesites belonging to the upper lava system of Lesbos occuring mainly in the form of spills into the horizon of river–terrestrial and pyroclastic formations above. In some localities (as at “Plakes” region which is located at the SW part of Polichnitos region), the basalts are under the river–terrestrial and the pyroclastic formations of the area, while in others the basaltic bodies are over the river–terrestrial and pyroclastics formation (as at ‘Monastiraki’ region which is located at the western part of Polichnitos region). In some other localities they are inside the river–terrestrial – pyroclastic formations while sometimes penetrate even into the base of the marly lake layers of the Pliocene.
- Pliocene lacustrine sediments: These are tight non water – permeable formations consist of marls and marly limestones with sandstones and conglomerates interference, with a thickness of more than 100 meters in some cases. In many places these formations are strongly opalised. The lacustrine formations of the area of Polichnitos host a great amount of macrofossils, mainly *Planorbis* sp., as well as thin lignitic appearances of Upper Pliocene age.
- Pleistocene conglomerates: They consist of conglomerates and breccias with diversity in lithological content and size, while in some localities there are also some interference of clays, marls and sands of river–terrestrial origin.

Among the new fossiliferous sites there is a limonitic site (M: Mesotopos) with material not proper for identification but with information about the occurrence of hydrothermal source in the area (Plate 2). This site contains mixed fragments of branches and roots not well preserved (Plate 2: B, C, E, F). We were only able to identify a fragmented remnant of a *Quercus* type leaf (Plate 2: D).

Plate 2

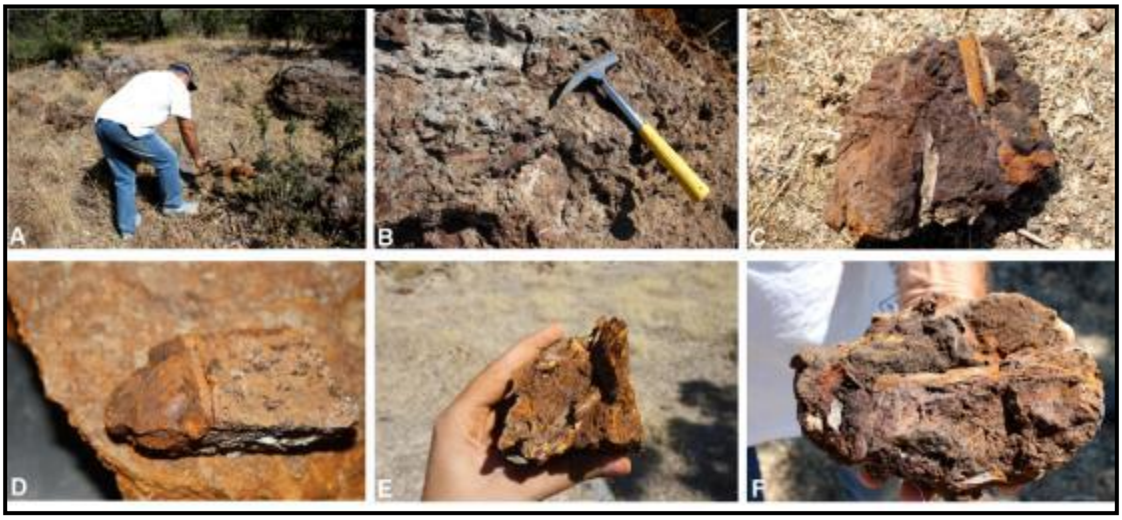


Plate 2. Close to Mesotopos village a new fossiliferous locality has been found in 2011. The hydrothermal origin of the material is clearly seen if one notices the limonitic mass which includes plant fossil remnants.

A: The basement of the area represents the limonitic fossiliferous block assemblage.

B: A closer photo of the limonitic fossiliferous block assemblage.

C, E, F: Mixed plant fossil remnants (branches and roots).

D: Fragment of *Quercus* type leaf.

2.1.3 Material and Methods

During 2011 and 2012 almost 400 specimens were collected from six new localities in Polichnitos region (Southern Lesbos Island). The specimens are stored at the Natural History Collection of Vrisa–Cultural, Research and Education Center (annex of the Museum of Palaeontology and Geology of the National and Kapodistrian University of Athens, hosted by the Faculty of Geology and Geoenvironment), Lesbos Island, Greece. After their collection, the dimensions of the fossil woods from Lesbos were measured and photographed (with a Canon EOS 1000D) and then they were catalogued. Thin slides for more than 70 samples were prepared (three for each sample: transversal, radial and tangential) in order to study their anatomical features with the light microscope. The thin slides' preparation took place at the Laboratory of the Department of Historical Geology & Paleontology, Faculty of Geology & Geoenvironment, National and Kapodistrian University of Athens.

The thin sections were observed with: 1) an Olympus BX51 microscope with an Olympus DP73 camera and QuickPHOTO MICRO 3.0 image analysis software, in the facilities of the Institute of Geology and Paleontology, Faculty of Science, Charles University in Prague, 2) at the facilities of the Department of Historical Geology & Paleontology, Faculty of Geology & Geoenvironment (with a Leitz Ortholux II Pol–MK and a Leica DM LP microscope) and 3) at the Faculty of Botany, Department of Biology (with an Olympus CX41 optical microscope, Nikon D5000, 12.3 megapixel camera), National and Kapodistrian University of Athens, 4) at the National Museum in Prague and 5) at the Agricultural University of Athens. Data tables were subsequently created using the Microsoft Office Excel. The anatomical descriptions of the recently found fossil wood samples are in accordance with the IAWA Hardwood List (IAWA Committee 1989), Wheeler (1986) and Crivellaro & Schweingruber (2013) for angiosperms and the IAWA Softwood List (IAWA Committee 2004) for conifers. Concerning the angiosperm fossil woods each vessel was counted separately, both for density and vessel grouping percentage, as proposed by Wheeler (1986). Identifications were made with reference to the InsideWood Web site (InsideWood 2004–onwards; Wheeler 2011). Due to the preservation, for the identification of the pits we have followed Gerards *et al.* (2007) (IAWA Journal, Vol. 28 (1):49–60). In several steps of the study the ArcMap – ArcGIS Program was used, in order to have the already existing knowledge and the new data of the palaeogeographical history of Lesbos Island portrayed.

For the purposes of species comparison and for the creation of a new methodology on *Laurinoxylon* (Lauraceae) thin slides of important (and unique) Czech and Hungarian material have been prepared at the facilities of the Czech Geological Survey in Prague.

As far as the study on fossil Lauraceae is concerned, the counting of idioblasts has been made in cross section only for the efficiency of comparison reasons with – and among – the already described species. Concerning Lesbos wood, some values of the vessel elements lengths seem low because they come from small axes which might have such short vessel elements. Some of the *Laurinoxylon* types photos are the result of the synthesis of almost 40 pictures of each specimen taken by an Olympus BX51 microscope, Olympus DP73 camera and QuickPHOTO MICRO 3.0 image analysis software (provided by the Charles University of Prague, Czech Republic).

The study of *Peuce lesbia* (= *Cedroxylon lesbium*) was efficient, thanks to the original material and slides provided by the Natural History Museum of Vienna.

The following abbreviations were used throughout the manuscript: NHMW: Natural History Museum of Vienna, NHMLPF: Natural History Museum of the Lesvos Petrified Forest, A: Alonelia, H: Hondrokouki, R: Rogkada, D: Damandri, P: Plakes, M: Mesotopos.

2.1.4 History of the recognition and identification of the plant fossils in Lesbos

Investigating the first traces of Palaeobotany in Lesbos Island we evaluated several references from the ancient philosophers about the existence of the fossiliferous localities and fossil plants. The original descriptions of the past provided unique information about the studied material and they were also used as sources for highlighting important inconsistencies. The same procedure has been followed also for the references of the 20th century and led to a collection of the most important of them presented bellow.

The first palaeobotanical research and study of the fossil flora of Lesbos and of Greece in general took place at the 3rd century B.C. by Theophrastus (372–287 B.C.) from Eressos, Lesbos Island, Greece.

Among the works ascribed to Theophrastus by Diogenes Laertius is a treatise On Petrifactions in two books. This lost work probably contained a systematic treatment of the fossil trees of Lesbos. What is also interesting in the references on the lost book is the recognition of different types of fossilization with the usage of different words (e.g., for describing petrification, carbonization, lignites of several kinds, petrified Indian reed).

Inside his book “On Stones” there are indications about fossil trees while there are also some references for the book “On Petrifactions”. More specifically taking into account the work by Caley & Richards, (1956, p. 45, 66–67), supplying critical notes on the original text of Theophrastus book “On Stones”, there is a reference of the verb ‘petrify’ [«απολιθώνω»] at the first chapter, at the 4th paragraph: “And some show a number of differences in the actual process of being set on fire and burnt, and some, like the smaragdos can make the color of water the same as their own, whereas others can turn what is placed on them entirely into stone”.

In the second chapter (Caley & Richards 1956, p. 47), in the 12th paragraph there is a reference of the ‘carbonization’ and of ‘lignites’: “Some of those that can be broken are like hot coals when they burn, and remain like this for some time, such as those found in the mine at Binai which are brought down by the river; for when they are covered with charcoal they burn as long as air is blown onto them, then they die down and afterwards can be kindled again, so that they can be used for a long time, but their odor is very harsh and disagreeable”. According to the historians analysts the text refers to lignite or non–asphaltic pyrobitumen from Bina or solid bitumen from Thrace.

Also, in the same chapter (2nd) and in the 16th and 17th paragraphs (Caley & Richards 1956, p. 48, 85–90) there is a reference for the co–existence of carbonised plants and amber: “Among the substances that are dug up because they are useful, those known simply as coals are made of earth, and they are set on fire and burnt like charcoal. They are found in Liguria, where amber also occurs, and in Elis as one goes by the mountain road to Olympia; and they are actually used by workers in metals. In the mines at Scapte Hyle a stone was once found which was like rotten wood in appearance. Whenever oil was poured on it, it burnt, but when the oil had been used up, the stone stopped burning, as if it were itself unaffected. These are roughly the differences in the stones that burn”. The comments from the specialists are focused on the use of lignite (which typically is found in Liguria as well as in other places in Greece) and the fact that apart from Antigonus of Carystus – who says that according to Theopompus coals were dug up for use in the neighborhood of the Thesprotians – Theophrastus appears to be the only ancient writer who touches on the subject. Scapte Hyle of the 17th paragraph was a mining district in Thrace opposite Thasos Island in the Northern Aegean. The reference on “rotten wood” most probably refers to brown fibrous lignite. Theophrastus uses also, as well as Aristotle – and the Peripatetic philosophers – the word “anthrax” with which he describes a transparent incombustible precious stone of a deep red color.

The most important and clear reference of his work on the fossil plants can be noticed in the 38th paragraph of the 6th chapter (Caley & Richards 1956, p. 53, 140–142):“Coral, which is like a stone, is red in color and rounded like a root, and it grows in the sea. And in a way the petrified Indian reed is not very different in its nature from coral. But this is a subject for another inquiry“. Theophrastus has described the Indian reed in his History of Plants as a species of bamboo. The "petrified Indian reed" according the analysts could be a bamboo or some other reed incrusted with calcareous sinter or a true plant fossil. The final sentence of this section may be an indication that his treatise, “On Petrifactions”, was written after the work “On Stones”.

Almost 2000 years after the very first recording of Lesbos plant fossils, the scientific interest returns on Lesbos. In 1842 during the annual fossils’ exhibition at the Landesmuseum Joanneum in Austria some samples of fossil plants from Lesbos, which have been collected by the Archduke Johann are also exposed. What should be underlined is the fact that the Professor of Botany and Director of the famous Botanical garden of this institution from 1835 until 1849 was Franz Unger.

The Austrian botanist Franz Unger was the expert who started to describe the fossil plants from Lesbos in several works of him (Unger 1845, 1847, 1862): *Thujoxylum peucinum*, *Taxoxylum priscum* (= *Taxoxylon priseum* Ung.), *Peuce lesbia* (= *Cedroxylon lesbium* Kr.), *Juglandinium mediterraneum* (= *Juglandoxylon mediterraneum* Ung.), *Mirbellites lesbius* (=*Juglandoxylon mediterraneum* Ung.), *Brongniartites graecus*.

Prokesch–Osten (1852) knowing already the publication of F. Unger about the plant fossils of Lesbos Island publishes his notes from the visit that he had made in Lesbos in 1829 in which he was describing the images that he was seeing from the port of Sigri from where he could see hundreds of petrified tree trunks. He was describing a trunk of 3 m (10 ⅓ feet) in diameter and 2,7 m (9 feet) in length with three branches, trunks of 0,6 m to 1 m (24 to 40 inches) thick and 5,5 m to 7 m (3 to 4 fathoms) long, a trunk of 0,5 m (1 ½ feet) in diameter and more than 4,5 m (15 feet) high and some very close and under the sea, while he seemed to be sure that some of them should belong to pine trees because of their growth rings and their barks, and thinking of some olive trees as well.

In 1898 Fliche, a professor at the Forestry School of Nancy was giving the determination of fossilized and silicified trees from the region of Ordymnos Mountain (western peninsula) with references to the fossil plants *Cedroxylon*, *Palmoxylon* and *Ebenoxylon* from the Island of Lesbos.

It seems that he was also the first who noticed the existence of fossilized trees not only at Ordymnos (and at its NE part along with Sigri) but also at the islet of Nissiopi, while he believed that the majority of the fossils belonged to the genus *Cedroxylon* and *Pityoxylon* and he was giving to the lignite of Ordymnos a Pontian age (7.246 ± 0.005 to 5.332 ± 0.005 mya) similar to the fauna fossiliferous areas of Kumi (Euboea) and Attique (Megara, Markopoulo) which had been described by Fuchs. The lignites of Ordymnos most probably are the lignites of Lapsarna area which have been studied the last years with combined results on palaeobotany and geochemistry–mineralogy (Kelepertsis & Velitzelos 1992) and on the palaeolake's inhabitants and age (Mantzouka 2009a; 2009b, Vasileiadou & Zouros 2012).

The significance of this unique monument was first underlined by Richard Kräusel (1965) who was comparing the scientific value of the Lesbos Petrified Forest with the one of Gilboa (N.Y., U.S.), Chemnitz (Germany) and Yellowstone (Wyoming, U.S.)

Sixteen years later, a great effort for the promotion of Lesbos palaeofloristic evidence started with the initiative of Greek scientists. The first results were published by Velitzelos, Petrescu and Symeonidis (1981a, 1981b) (and revised by Velitzelos *et al.* 2014) focused on the composition of the palaeoflora, the identification of leaf imprints [*Cinnamomum polymorphum* (= *Daphnogene polymorpha* (A. Braun) Ettingshausen), *Laurus* sp. (=Lauraceae vel Fagaceae gen. et spec. indet.), *Litsea primigenia* (=Lauraceae vel Fagaceae gen. et spec. indet.), *Lindera ovata* (= *Dicotylophyllum* sp. 2), *Oreodaphne heeri* (=*Laurophyllum* sp.), *Lauraceae* (= Lauraceae vel Fagaceae gen. et spec. indet.), *Quercus apocynophyllum* (= Lauraceae vel Fagaceae gen. et spec. indet.), *Carpinus pliofaurei* forma *helladae, Carpinus uniserrata, Alnus cycladum, Populus balsamoides, Populus* sp*., Tilia* sp*., Diospyros brachysepala* (= *Laurophyllum* sp. and Lauraceae vel Fagaceae aff. *Castanopsis bavarica* Knobloch et Kvaček), *Myrsinites sp.* (= *Dicotylophyllum* sp. 1 – aff. *Cedrela attica* (Unger) Palamarev), *Rhus* sp., Sapotaceae (= *Dicotylophyllum* sp. 3)] and the determination of the palaeoclimatic conditions (subtropical climate relative to the continental subtropical zone of SE Asia and N America) and the forest's relative age (Upper Oligocene – Middle Miocene).

The protection of the important floristic fossiliferous sites of Greece was another issue which had to be developed in parallel with the scientific identification and promotion. Two Academics from the University of Athens, Velitzelos & Symeonidis (1984) started the attempt of awareness rising of the scientists, politicians and inhabitants of the areas of interest through a paper connecting the fossilized woods of the petrified forests of Greece (Lesbos, Thrace and N. Euboea) with suggestions for their preservation.

Since then there has been interest at the Western peninsula of Lesbos which has been declared as a Protected Natural Monument since 1985 with a special Presidential Decree (No 443/1985) and mainly at the localities of the five petrified forest parks: Petrified Forest park or Bali Alonia; Nissiopi park; Sigri park; Plaka park; Skamiouda park.

Later on, a fossil wood of approximately 600 years old trunk from the area of the petrified forest of Lesbos was studied and described as a new species: *Taxaceoxylon biseriatum*. More publications followed with the descriptions of *Pinoxylon paradoxum* and *Pinoxylon pseudoparadoxum*, *Taxodioxylon gypsaceum,* the first occurrence of *T. albertense, T. pseudoalbertense* in Greece which was also the first for the Tertiary of Europe, the identification of Dicotyledonous wood (mainly Lauraceae and Fagaceae) and of new species: *Taxodioxylon megalonissum*, *Glyptostroboxylon microtracheidae*, *Tetraclinoxylon velitzelosi, Thujoxylon antissum, Chimairoidoxylon lesboense, Podocarpoxylon articulatum*, *P. graciliradiatum*, *Chimairoidoxylon conspicum*, *Ginkgoxylon lesboense*, *G. diversicellulatum*, *Lesbosoxylon* (*Pinoxylon) diversiradiatum*, *Lesbosoxylon* (*Pinoxylon) graciliradiatum*, *L. ventricosuradiatum*, along with the identification of leaves' imprints: *Pronephrium stiriacum, Tetraclinis* sp.*, Pungiphyllum crutiatum* (= *Quercus cruciata*)*, Phoenix* sp. *(=Phoenicites* sp.*), Platanus* sp.*, Acer* sp., *Laurus primigenia* (= vel Fagaceae gen. et spec. indet.), *Daphnogene polymorpha, Quercus* sp., *Pinus* sp., *Sequoia abietina (= Sequoia abietina* (Brongniart) Knobloch vel *Taxodium* sp.), *Tetraclinis salicornoides, Rubus* sp., *Engelhardia orsbergensis, Rubus niacensis* (partly *Alnus cycladum*)*, Sabal major* (Süss & Velitzelos 1994a; 1994b; 1997; 1998; 2000; 2001; 2009; 2010, Süss 1997; 2003, Selmeier & Velitzelos 2000, Velitzelos 1993, Velitzelos *et al.* 1999, Velitzelos & Zouros 2008, revisions by Velitzelos *et al.* 2014).

2.2 New suggested methodology

2.2.1 A New Proposed Identification Key for Fossil Lauraceous Wood

Studies for more than three years on lauraceous wood anatomy for the purposes of the description of the new findings from Lesbos Island gave birth to a new proposed identification key for fossil lauraceous wood published recently (Mantzouka *et al.* 2014; Mantzouka *et al.* in press, Annex 2).

Based on anatomical description of new fossil woods from Lesbos (Greece) as well as re–investigation of three holotype specimens from the Czech Republic and Hungary (= *Laurinoxylon diluviale*, *L*. *czechense* and *L*. *müller–stolli*), a more natural classification of the large and rather artificial fossil genus *Laurinoxylon* and its linking with relative groups of modern lauraceous genera has been proposed.

The suggested classification of *Laurinoxylon* of this study is universal and directly linked to modern botany. Thanks to the abundance of *Laurinoxylon* in the fossil record, it can be directly used both by palaebotanists/palaeontologists and geologists as a good tool for further systematic, stratigraphic and paleoclimatic studies.

The fossil woods studied microscopically for the establishment of this methodology cover time interval from early Oligocene to early Miocene and the numerous published descriptions studied in detail cover the Tertiary. Two of the described sites, i.e., Lesbos in Greece and Ipolytarnóc in Hungary, are famous as they are both members of the European and UNESCO Global Geoparks Network (EGN and GGN).

Moreover, another fossil wood, described for the purposes of this study, came from mineralogically famous locality Jáchymov in the Czech Republic which represents the worldwide oldest (historically) plant fossil ever found and mentioned (already in 16th century) and mainly the nomenclatoric type of the whole genus *Laurinoxylon*, which is, re–discovered now.

The significance of the present study is related with the examination of the exact occurrence and distribution of the idioblasts (oil &/or mucilage cells) and their combinations only as the last step of the proposed methodology (and not separately as in several previously published studies), after the application of a number of ‘filters’ (= excluding criteria/features) which Richter (1981a) had defined as “characters with the highest significance”.

This broader study on the examination of the importance of idioblasts as an essential tool for botanical affinities of the Lauraceae (and especially *Laurinoxylon*) was based on the work of extant lauraceous genera by Richter (1981a) and van der Werff and Richter (1996), and the new detailed anatomical descriptions of several wood samples from four different areas of South–Eastern and Central Europe from Oligocene to Miocene age, along with the published descriptions and data from the InsideWood Database, both modern and fossil.

Lauraceae is a family distributed worldwide with about 50 genera (van der Werff and Richter 1996; Stevens 2001; Schweingruber *et al.* 2011; Johansson 2013) and more than 2500 species of mainly evergreen woods and shrubs with the great majority of the genera of tropical and subtropical distribution (Fig. 10). In Europe today this family is represented only by the genus *Laurus* L. (Mai 1995).

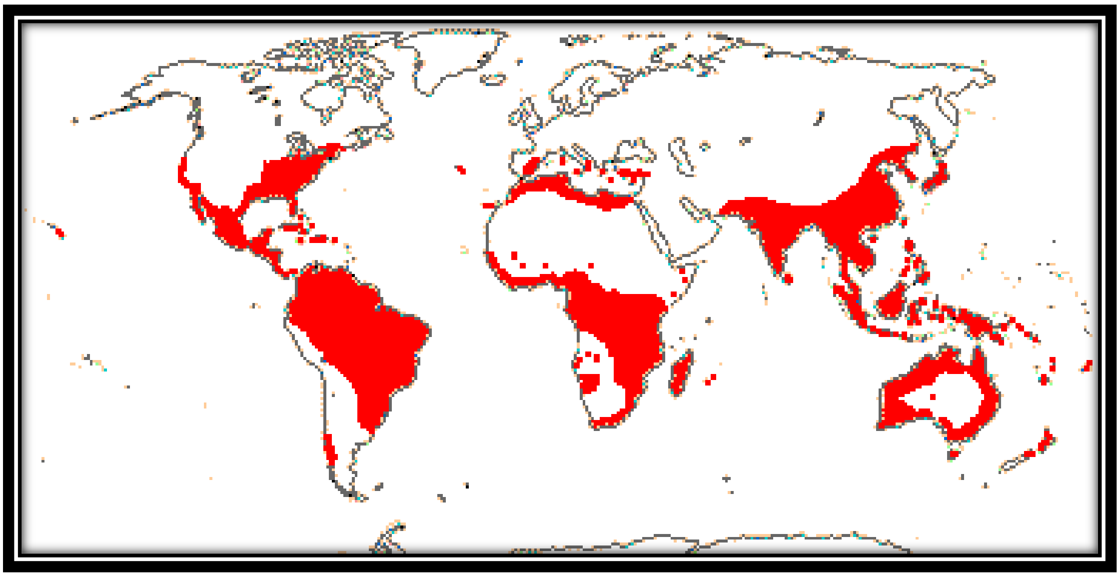


Fig. 10: Lauraceae present day distribution (Stevens 2001 onwards).

According to Mai (1995), the fossil Lauraceae of Europe – which phytogenetically belong to the palaeotropical elements – are important because they are the most common trees among the Cenozoic wood formations and are generally indicators of warm climate with high humidity at the atmosphere even during the coolest season. The categorization of this family contains various widely defined fossil genera based on fossil leaves (e.g., *Laurophyllum* Göppert or *Laurophyllites* Weyland & Kilpper) or wood anatomy (e.g., *Ulminium* Unger in Endlicher or *Laurinoxylon* Felix emend. Dupéron *et al.*). The abundance of Lauraceae in the fossil record is explained if one considers that Lauraceous woods are easily recognizable by the anatomists due to the occurrence of the idioblasts and also because their heartwood has a serious possibility becoming silicified being resistant to decay (Wheeler & Manchester 2002).

Precise botanical affinities of fossil lauraceous stems have always been difficult to determine. *Laurinoxylon* is a fossil genus for fossil lauraceous wood genera or species that are impossible to be directly related to a botanical genus. The diagnosis of *Laurinoxylon* was recently emended by Dupéron *et al.* (2008) as follows: heteroxylous fossil wood with average solitary vessels or in radial groups; perforation plates simple and sometimes scalariform; intervascular pits alternate and moderately large; tyloses present; paratracheal parenchyma; uni– to 5-seriate rays, slightly heterocellular and less than 1mm high; ray–vessel pits large, sometimes stretched; fibres libriform or pits on radial walls; oil or mucilage (idioblasts) cells present. The term “average” represents the English translation of the “vaisseaux moyens” which according to Boureau (1957, p. 542) is used for vessels with a diameter from 100 to 200 μm.

The presence of the oil &/or mucilage cells, hereafter referred to as idioblasts, is not common through plant families. Idioblasts occur only in the Lauraceae and other Magnoliid families – Annonaceae, Canellaceae, Hernandiaceae, Magnoliaceae (p. 1347–1354 in Metcalfe & Chalk 1950; Carlquist 2001).

According to Metcalfe & Chalk (1950) the most outstanding feature of the wood, the oil or mucilage cells of the rays and wood parenchyma, usually suggests affinity with the Magnoliaceae and the Lauraceae. What is important is that most of the points of difference between the Canellaceae and the Lauraceae, might be explained as due to different levels of specialization. Vessel member length and some other characters suggest that the Canellaceae (Fig. 11) are less specialized than the Lauraceae (which have septate fibres and simple and scalariform perforation plates) and are even less specialized than the Magnoliaceae (Fig. 12) (which have scalariform perforation plates).

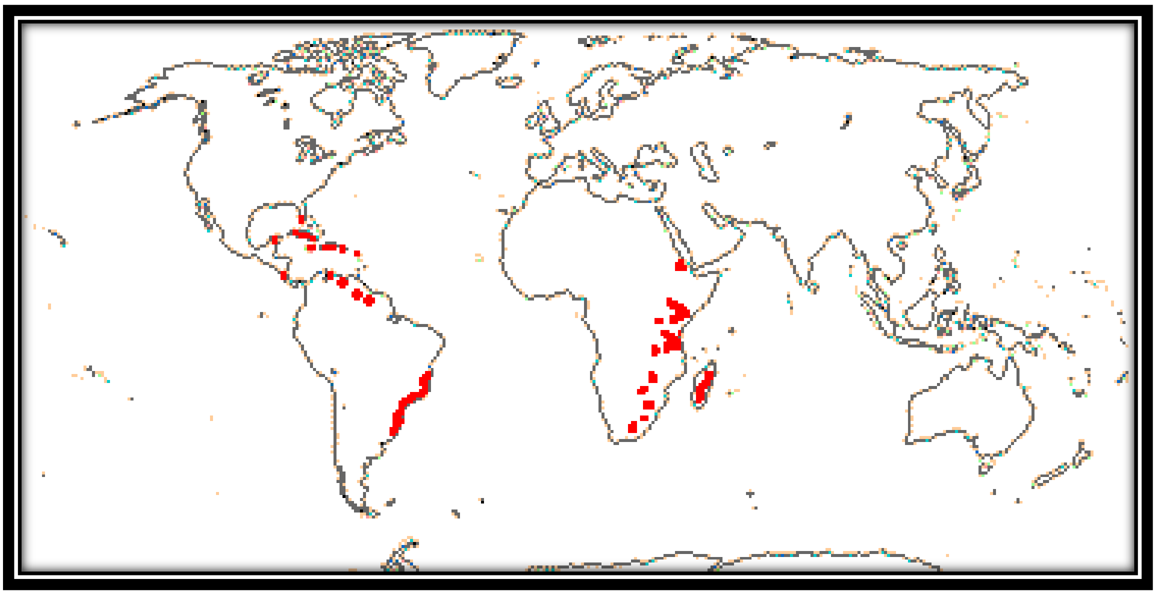


Fig. 11: Canellaceae present day distribution (Stevens 2001 onwards).

Fig. 12: Magnoliaceae present day distribution (Stevens 2001 onwards).

The idioblasts cells, as suggested by their name, can be recognized due to their size and colour – they are usually bigger and different in colour than the surrounding cells of the tissue in which they are embedded. The first idioblasts' observation took place in a lauraceous wood in 1676 by Antoni van Leeuwenhoek (Fig. 13), so the observations on idioblasts are connected to the Lauraceae (Baas and Gregory 1985). This, in collaboration with the fact that the first fossil wood ever found and described in a scientific way – *Ulminium diluviale* Unger [*Laurinoxylon diluviale* (Unger) Felix] from Jáchymov, Czech Republic (Dupéron *et al.*, 2008) – has also idioblasts, shows that the Lauraceae are among the families which have played a very important role for the observation of the idioblasts.

The revised diagnosis of the genus (Dupéron *et al.* 2008) allowed us to suggest that the features indicating that a fossil wood should not be assigned to *Laurinoxylon* are the following:

A. Axial parenchyma features*: A1. Marginal axial parenchyma, A2. Aliform to aliform–confluent paratracheal parenchyma,

B. Ray features: B1. Rays higher than 1 mm, B2. Exclusively homocellular rays, B3. Rays with more than 5 cells in width, B4. Rays storied.

C. Porosity: Ring–porous wood,

D. Idioblasts: Absence of idioblasts

Fig. 13: Antoni van Leeuwenhoek, the father of microbiology. In 1676 he was the researcher who made the first idioblasts observation ever described in Lauraceae. Photo from the room dedicated to the microscopic scientific research in the National History Museum of Vienna (NHMW) (photo by D. Mantzouka 11/5/2014).

What has to be also mentioned is the fact that taking into account Richter's observations on vessels size (as well as older publications on this subject) has been avoided by prudence because his monograph was published in 1981 and most probably his measurements didn't follow Wheeler's proposal (1986).

The application of the above mentioned four excluding criteria (A1+2, B1+2+3+4, C and D) has given as a result the botanical affinities of *Laurinoxylon* (Fig. 14). *Laurinoxylon* is closer to modern genera of the Laureae (*Actinodaphne, Laurus, Lindera* A and B, *Litsea, Neolitsea,* North American *Persea*) and Perseae tribes (*Aiouea, Aniba, Cinnamomum*, *Cryptocarya* of Madagascar, *Dehaasia, Dicypellium*, *Endlicheria*, *Licaria, Nectandra, Nothaphoebe*, *Ocotea, Persea* with the North American species, *Phoebe, Pleurithyrium, Systemonodaphne, Urbanodendron*), which are representatives of the Northern Hemisphere and of the Neotropical or Neotropical/Asian zone, and also to *Apollonias* and *Iteadaphne* (Mantzouka *et al.* in press).

*The decision for using as first criterion the axial parenchyma type was based on the observation of the correlation between the type of the parenchyma and its occurrence in specific lauraceous genera (Richter 1981a, 1990). Richter (1981a, 1990) reported the existence of axial paratracheal and marginal parenchyma by describing the occurrence of paratracheal mostly abundant vasicentric to aliform, often confluent with multiseriate bands (2–6(–10)) cell wide (Richter 1981a, Abb. 17a) in *Beilschmiedia*, *Endiandra*, *Potameia/Syndiclis* and *Triadodaphne*, the existence of paratracheal mostly sparse to slightly vasicentric multi–seriate bands 2–4(–8) cell wide (Richter 1981a, Abb. 17b) in *Cryptocarya* and *Ravensara* and the occurrence of paratracheal incomplete to closed vasicentric bands of exclusively one–cell wide line in *Licaria wilhelminensis* as also marginal (or seemingly marginal), fine, up to three cell wide bands in *L. subbullata* Kosterm. (Richter & Dallwitz 2000–onwards); the latter two species are apparently synonyms according to The Plant List (2013).

The observation of the exact occurrence of the idioblasts allowed us to recognized four groups of *Laurinoxylon* species:

- Type 1 with idioblasts associated only with ray parenchyma cells;
- Type 2a with idioblasts associated with two types of parenchyma elements, i.e., with rays and axial parenchyma;
- Type 2b with idioblasts associated with two different elements, with rays and present among the fibres; and
- Type 3 with idioblasts associated with three types of elements, i.e., with ray and axial parenchyma cells and present among the fibres.

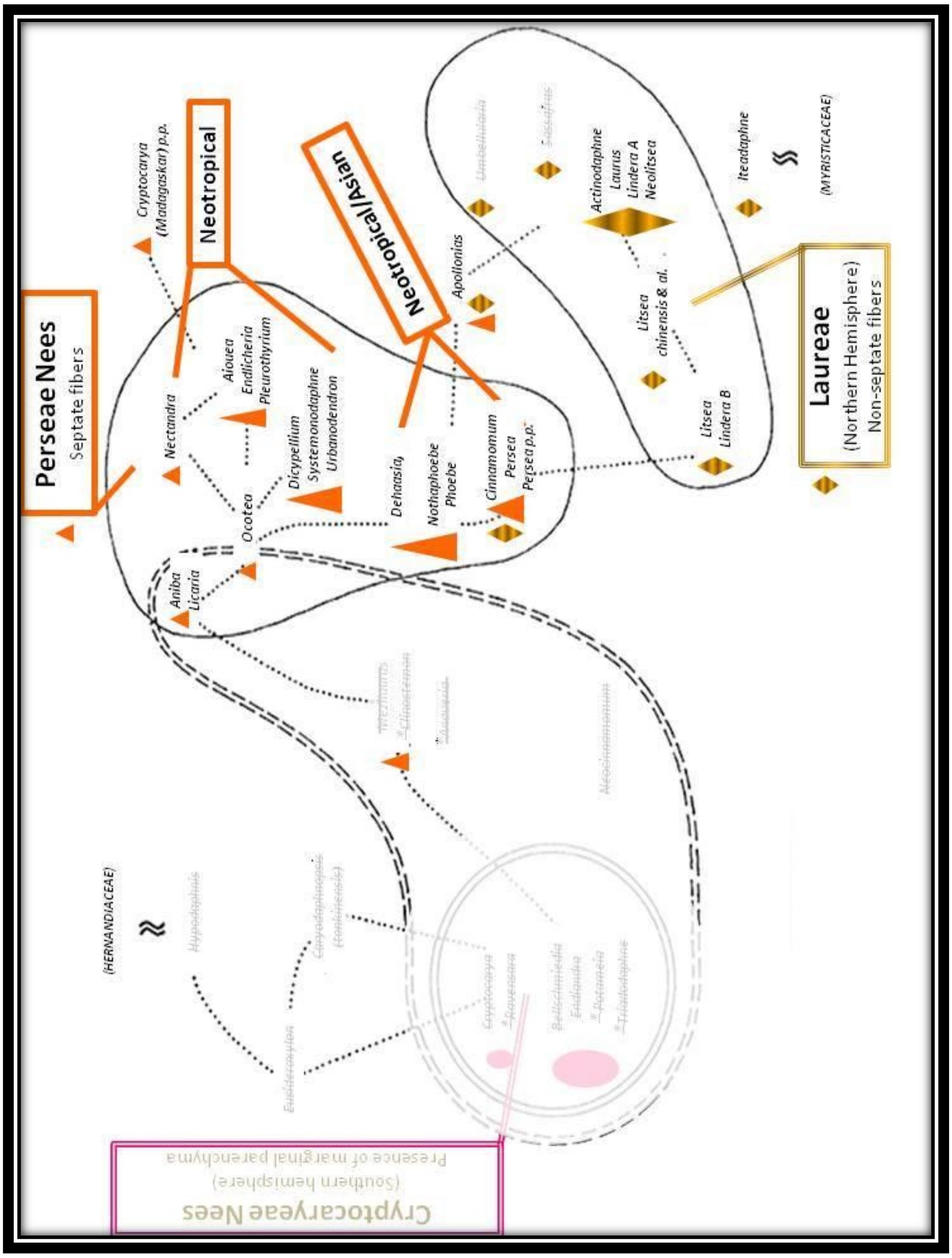


Fig. 14: *Laurinoxylon* botanical affinities concerning wood anatomy. (Richter 1981a, van der Werff and Richter 1996 modified).

The description of new fossil woods from Lesbos (Types 1, 2b and 3) and Ipolytarnóc (Type 2a) as well as the re–interpretation of the original slides of the type species of *L. czechense* from Kadaň–Zadní Vrch Hill (Type 1) and *L. diluviale* from Jáchymov (Type 2b) which represents the type species of the fossil genus *Laurinoxylon*, where only some of the important species on which our new proposed methodology was applied, showing that the taxonomical importance of *Laurinoxylon* in the Cenozoic fossil wood record had been underestimated (Table 1). More

Laurinoxylon fossil species were discussed in the published paper (see Annex 2, Mantzouka *et al.* in press) and linked to the *Laurinoxylon* Types 1–3.

The renaming – or at least the introduction of further discussion – and the new investigation of some already described *Laurinoxylon* species has been also one of the results of our recent published paper (Mantzouka *et al.* in press) as follows :

- ❖ From *Laurinoxylon* type 1 species (with idioblasts associated only with ray parenchyma cells):
- *Laurinoxylon intermedium* Huard has only scalariform perforation plates, abudant axial (vasicentric–confluent) parenchyma forming concentric bands of 4–12 cells and seemingly terminal bands (Huard 1967). Therefore, it cannot be attributed to Cryptocaryeae tribe and moreover it cannot be attributed to Lauraceae). The hypothesis of its assignment to Magnoliaceae is supported. The sample needs to be examined to determine to which magnoliaceous genus it belongs. Moreover, according to Kvaček *et al.* (2011) the leaf flora of this area includes one species of Magnoliaceae, *Magnolia liblarensis* (Kräusel et Weyland) Kvaček. A possible correlation between this wood and *Magnolia liblarensis* leaves needs investigation.
- *Laurinoxylon microtracheale* Süss has almost homocellular rays (Süss 1958), so it seems more possible that it belongs to *Umbellularia*.

More fossil species from the InsideWood Database (InsideWood 2004–onwards), which could be included in this category based on their anatomical description are *Laurinoxylon perseamimatus* Petrescu, *L. namsangensis* Lakhanpal *et al.* and *L. neagui* S. Iamandei et E. Iamandei.

- ❖ From *Laurinoxylon* type 2a species (with idioblasts associated with ray and axial parenchyma):
- *Laurinoxylon nectandrioides* Kräusel & Schönfeld has confluent parenchyma (and at least seemingly marginal bands) and it has also septate fibres and crystals (Kräusel & Schönfeld 1924; van der Burgh 1964, 1973). Consequently, it could belong to Perseae tribe, although more study should be provided for its identification.
- *Laurinoxylon endiandroides* Süss has aliform to confluent axial parenchyma (Süss 1958), which is not in accordance with the emended diagnosis of *Laurinoxylon*. Maybe it could be closer to *Cinnamomoxylon*, although its possible attribution to Cryptocaryeae Nees tribe should be also investigated.

- *Laurinoxylon annularis* Gottwald should be also observed since it is a ring porous wood and there is a strong possibility that its parenchyma is not simply (scanty) paratracheal vasicentric but confluent–aliform (Gottwald 1997). It should belong to *Sassafrasoxylon* Brezinová & Süss.
- *Laurinoxylon hasenbergense* Süss has rays up to 1–2 mm height, crystals and only simple perforation plates (Süss 1958) recommending a possible assignment to *Licaria*.
- *L. aniboides* Greguss emend. Süss & Mädel has rays up to 1.23 mm height, crystals and only scalariform perforation plates (Süss & Mädel 1958). Therefore it should be excluded from Lauraceae and its possible assignment to Magnoliaceae family (or to specific species of Canellaceae) could be investigated.

This category could also include *Laurinoxylon* sp. from Karlovy Vary, Czech Republic (Březinová 1981) and *Laurinoxylon stickai* Boonchai & Manchester from the Eocene of Wyoming, USA (Boonchai and Manchester 2012).

- ❖ From *Laurinoxylon* type 2b species (with idioblasts associated with rays and present among the fibres):
- *Laurinoxylon compressum* Huard has ring porous and short rays (Huard 1967), so maybe it could belong to *Sassafrasoxylon* Březinová & Süss.
- *Laurinoxylon perfectum* Huard has scanty paratracheal parenchyma which in some cases has a trend to be aliform with 1–3 rows of cells (Huard 1967). This is a characteristic not in accordance with the emended diagnosis of *Laurinoxylon*. Therefore the specimen should be re–studied.

A search of InsideWood (2004–onwards), suggests also some non–European species which could be included in Type 2b such us: *Laurinoxylon siwalicus* Prasad, *L. varkalaensis* Awasthi & Ahuja, *L. naginimariense* Awasthi & Mehrota, *L. deccanensis* Bande & Prakash and *L. deomaliensis* Lakhanpal *et al.*

Through this study it has been supported, with arguments, our suggestion according which the *Laurinoxylon* type 3 species having idioblasts in ray and axial parenchyma and among the fibres along with aliform–confluent parenchyma should be transferred to the fossil genus *Cinnamomoxylon.*

- ❖ From *Laurinoxylon* type 3 species (with idioblasts associated with ray and axial parenchyma and present among the fibres):

- *Laurinoxylon* cf. *seemannianum* described by Selmeier (1967, 1969, 1984) and Gottwald (1992) has idioblasts associated only with the ray parenchyma. I believe that *Laurinoxylon* cf. *seemannianum* specimens require a re–examination in order to be compared with the fossil *Laurinoxylon* species of Type 1 group.
- *Laurinoxylon variabile* Privé–Gill & Pelletier has aliform–confluent axial parenchyma forming oblique or tangential bands (Privé–Gill & Pelletier 1981) and that's why it should be transferred to *Cinnamomoxylon*. We propose the new combination *Cinnamomoxylon variabile* (Privé-Gill & Pelletier) Mantzouka, Karakitsios, Sakala, & Wheeler.

A search of InsideWood (2004–onwards) suggests including *Laurinoxylon tertiarum* Prakash & Tripathi in this category.

The next step was to find the botanical affinities of the *Laurinoxylon* wood categories by linking the fossil species with the modern wood. According to our study the representatives of *Laurinoxylon* Type 1 are closer to the extant genera: *Dicypellium, Laurus, Litsea chinensis group, North American Persea, Systemonodaphne, Urbanodendron* (Fig. 15).

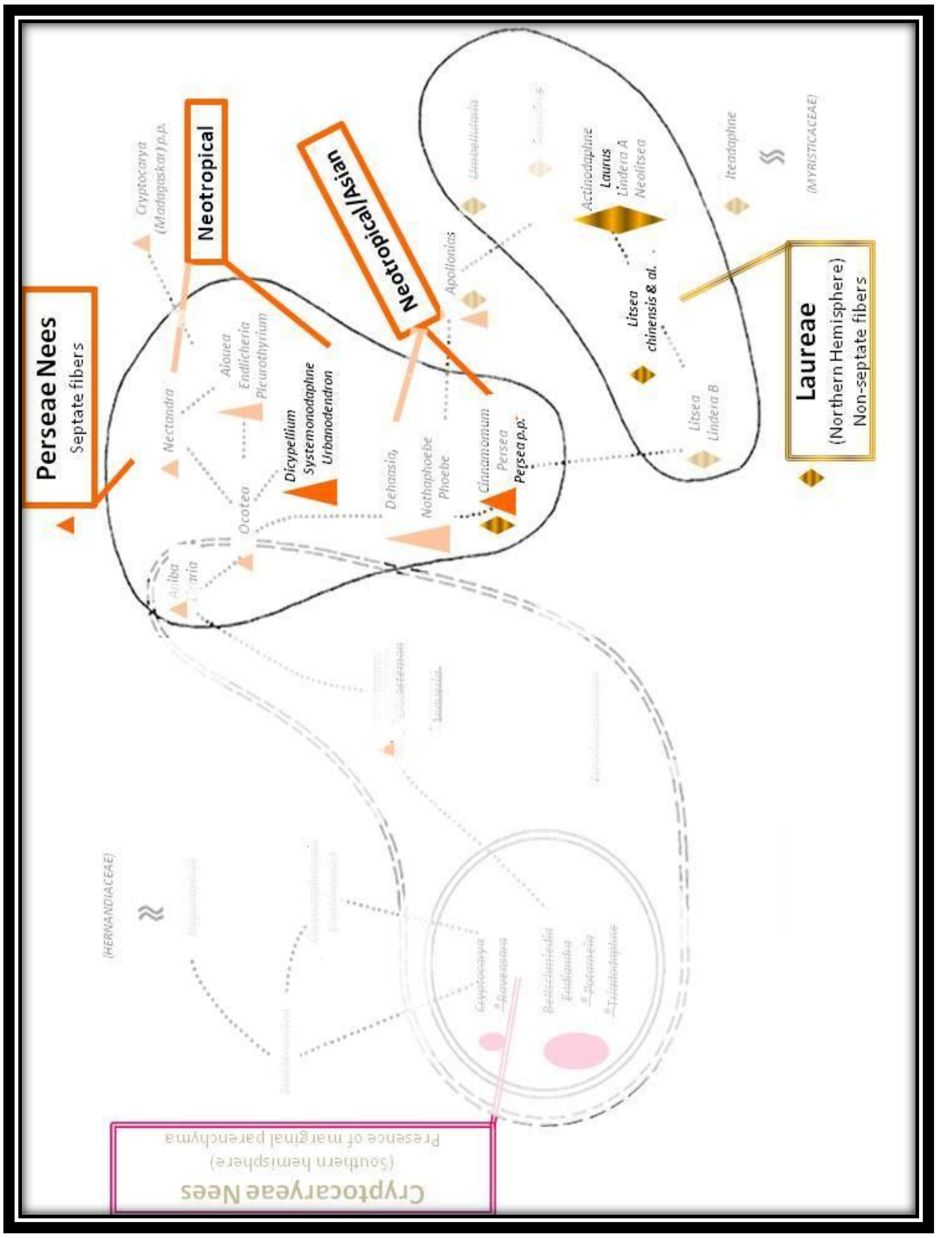


Fig. 15: *Laurinoxylon* Type 1 (with idioblasts associated only with ray parenchyma cells) botanical affinities concerning wood anatomy. (Richter 1981a, van der Werff and Richter 1996 modified).

Laurinoxylon Type 2a fossil species are closer to modern *Aiouea, Aniba, Apollonias, Cryptocarya from Madagascar, Dehaasia, Licaria, Lindera group A, Nothaphoebe, Persea, Phoebe* and *Pleurothyrium* (Fig. 16).

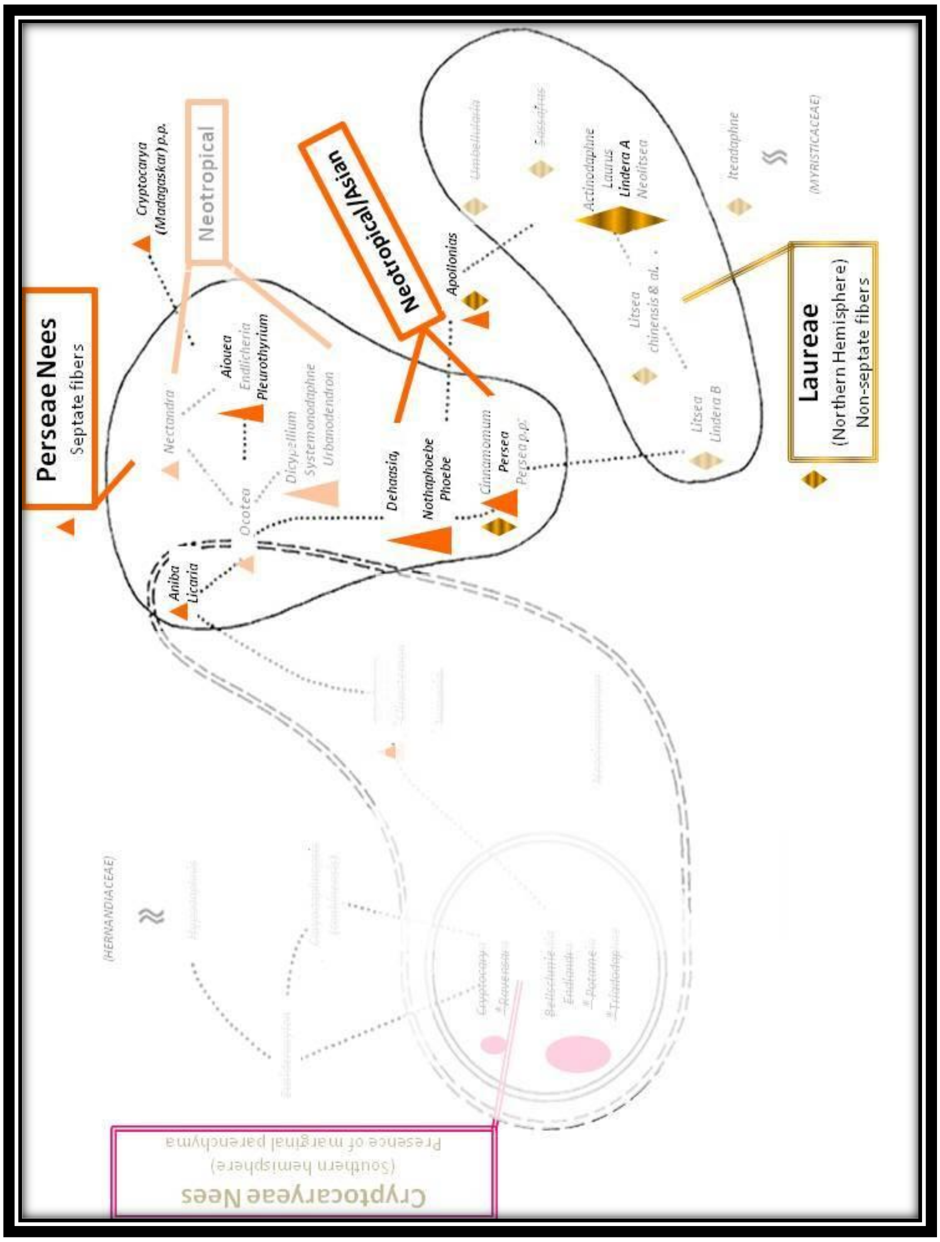


Fig. 16: *Laurinoxylon* Type 2a (with idioblasts associated with two types of parenchyma elements, i.e., with rays and axial parenchyma) botanical affinities concerning wood anatomy. (Richter 1981a, van der Werff and Richter 1996 modified).

The species of *Laurinoxylon* Type 2b are closer to modern *Actinodaphne p.p., Nectandra p.p. and Neolitsea p.p.* Crystals are present in 75% of *Actinodaphne* species, 60% of *Nectandra* species, and 50% of *Neolitsea* species (Fig. 17). Crystals are absent in 25% of *Actinodaphne* species, 40% of *Nectandra* species, and 50% of *Neolitsea* species. (90% of *Actinodaphne* and *Neolitsea* species, and 84% of Nectandra don’t contain idioblasts among the fibres – only in rays and axial parenchyma – and belong in this category).

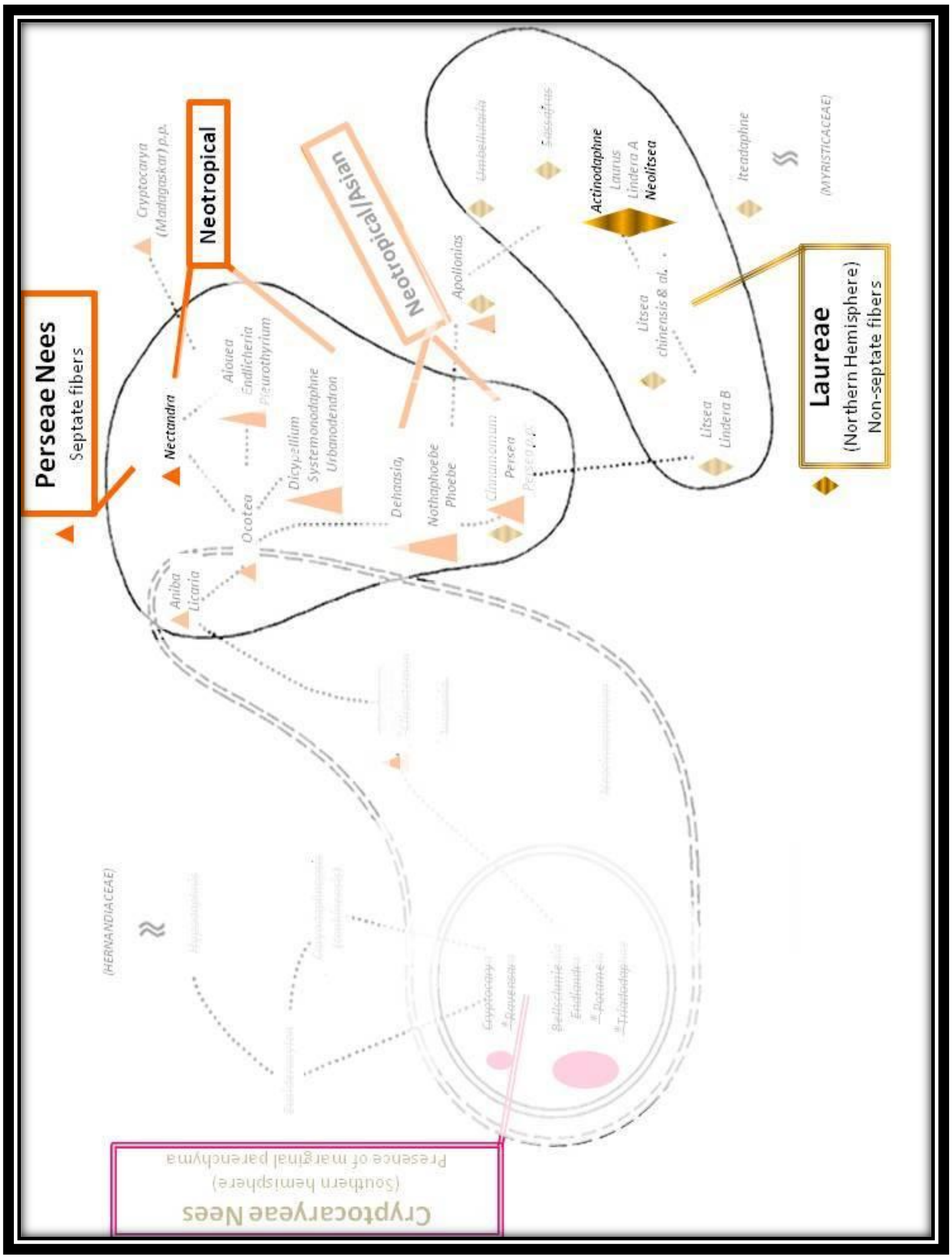


Fig. 17: *Laurinoxylon* Type 2b (with idioblasts associated with two different elements, with rays and present among the fibres) botanical affinities concerning wood anatomy. (Richter 1981a, van der Werff and Richter 1996 modified).

Finally, the species of *Laurinoxylon* Type 3 (syn. *Cinnamomoxylon*) are closer to the extant genera*: Actinodaphne p.p., Cinnamomum, Endlicheria, Nectandra p.p., Neolitsea p.p. and Ocotea* (Fig. 18). From the genera mentioned above *Cinnamomum* and *Ocotea* don't have crystals and *Actinodaphne* p.p., *Endlicheria, Nectandra* p.p. and *Neolitsea* p.p. have a high percentage of crystals (in fact only

10% of *Actinodaphne* and *Neolitsea* species, and 16% of Nectandra contain idioblasts also among the fibres and belong in this category).

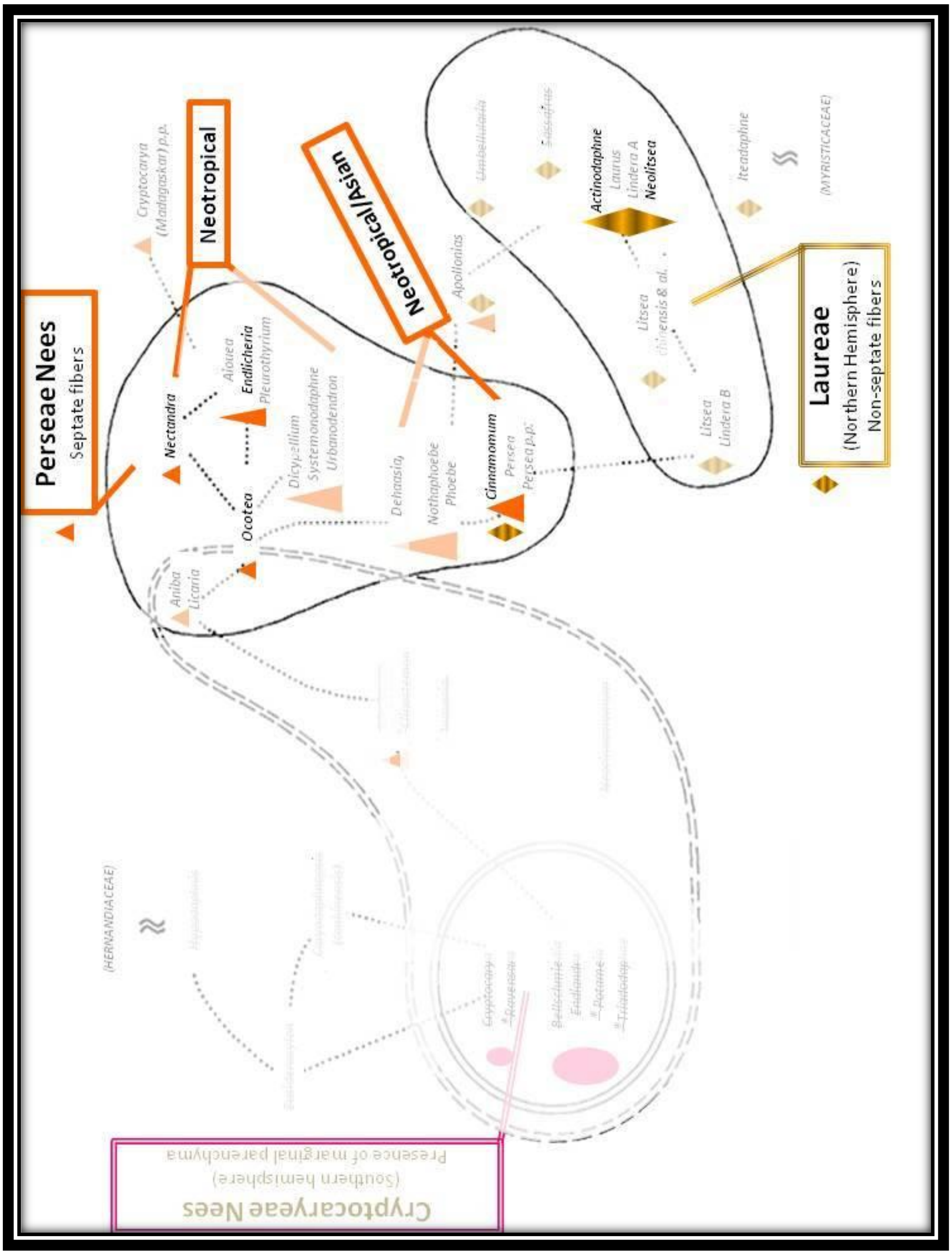


Fig. 18: *Laurinoxylon* Type 3 (with idioblasts associated with three types of elements, i.e., with ray and axial parenchyma cells and present among the fibres) botanical affinities concerning wood anatomy. (Richter 1981a, van der Werff and Richter 1996 modified).

The existence of idioblasts in four unique combinations (Type 1, 2a, 2b and 3) together with the preceding application of four excluding criteria or ‘filters’ (A1+2, B1+2+3+4, C and D) allowed a more natural classification of the large and rather artificial fossil genus *Laurinoxylon* where the fossil species can be linked to the group of modern lauraceous genera.

The observation on the existence of crystals and crystalliferous masses and septa in fibres along with the application of the Whole–Plant concept (e.g., Sakala 2004) for the co–occurring leaves and other organs, can make possible the depiction of only one modern genus, which would correspond to a concrete fossil *Laurinoxylon* species.

As far as the Whole Plant concept is concerned, in order to achieve the best possible inferences for our studies we have theoretically consult whole plant reconstruction approaches – which are usually based on co–occurrence, anatomical similarities, and taxonomic affinities – because their importance has been underlined from the earliest days of paleobotanical research up to now. A great number of recent studies focused especially on fossil angiosperms and the contribution to a more complete understanding of angiosperm evolution with interpretations in palaeoecology, climatology, phytostratigraphy, paleobiogeography, phylogenetics, systematics, evolution, distribution, diversification (Kvaček 2008; Manchester *et al.* 2014). We decided to apply, finally the Whole Plant Concept (Sakala 2004) because it uses as the main discipline palaeoxylology on condition that "it should respect the results based on other palaeobotanical remains such as foliage, seeds, fruits, pollen, etc."

In this point it would be prudent to give some explanations reasoning why in the fossil wood record of *Laurinoxylon* there are no representatives with idioblasts associated only with fibres or only with axial parenchyma or associated with fibres and axial parenchyma. Richter (1981a; p.78; Table 11) has found that a) the genera (or species) which have idioblasts only associated with fibres ("Is" in the original text) are: 10% of *Actinodaphne* species, 10% of *Endiandra* species, 50% of *Neolitsea* species, 1 species of *Ravensara, Triadodaphne, Beilschmiedia, Endiandra, Potameia, Triadodaphne*, b) the genera (or species) which have idioblasts only in axial parenchyma ("Sp" in the original text) are: 5% of *Litsea* species, 25% of *Nothaphoebe* species, *Caryodaphnopsis, Eusideroxylon melagangai/E. zwageri, Hypodaphnis* (it has no idioblasts but oily contents in the parenchyma), *Umbellularia, Litsea, Lindera B, Anaueria, Clinostemon, Neocinnamomum* and c) the genera (or species) which have idioblasts in fibres ("Is") and in axial parenchyma ("Sp") are: 10% of *Beilschmiedia* species, 10% of *Cinnamomum,* 10% of *Cryptocarya,* 50% of *Endlicheria,* 15% of *Ocotea,* 90% of *Beilschmiedia,* 100% of *Endiandra,* 80% of *Potameia,* 75% of *Cryptocarya* (although at the 20% there are also in rays), 90% of *Ravensara* (although at the 30% there are also in rays). One could advice Richter's

Table 11 (1981a) for further information complementary to the text (p. 78) having in mind the meaning of the symbols he used: x = when the feature generally exists, xx = when the feature is especially pronounced, o = when the feature in only part of the species exists, (_) = when the feature is weakly pronounced. From all the genera listed above, only 10% of *Actinodaphne* species, 50% of *Neolitsea* species, 5% of *Litsea* species, 25% of *Nothaphoebe* species, *Lindera B,* 10% of *Cinnamomum,* 50% of *Endlicheria,* 15% of *Ocotea* could be found (scarced) in the future in the fossil record of *Laurinoxylon* representing the previously undescribed categories.

Plate 3 *Laurinoxylon* and its types associated with modern genera of Lauraceae subdivided into three tribes based on wood anatomy (Richter 1981; Van der Werff & Richter 1996, modified). The erased genera have been excluded from being attributed to *Laurinoxylon* after the usage of specific features described in Mantzouka *et al.* (in press).

A: *Laurinoxylon* botanical affinities among Lauraceae corresponding to its emended diagnosis, after the usage of four features.

B: Botanical affinities of *Laurinoxylon* Type 1 species with idioblasts associated only with ray parenchyma cells.

C: Botanical affinities of *Laurinoxylon* Type 2a species with idioblasts associated with ray and axial parenchyma.

D: Botanical affinities of *Laurinoxylon* Type 2b species with idioblasts associated with rays and present among the fibres.

E: Botanical affinities of *Laurinoxylon* Type 3 (syn. *Cinnamomoxylon*) species with idioblasts associated with ray and axial parenchyma and present among the fibres.

Plate 3

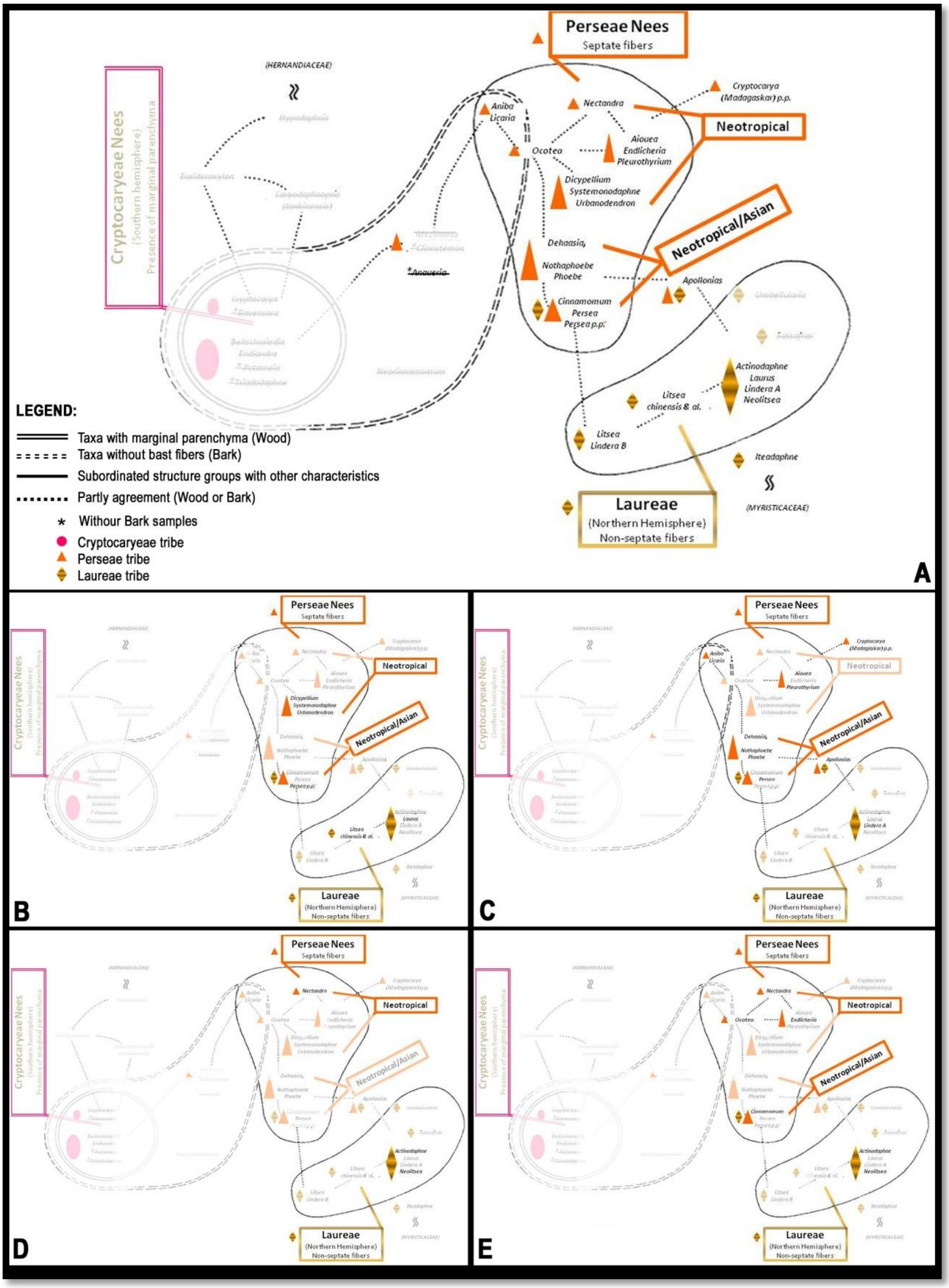

Perseae Nees
Septate fibers
(HERNANDIACEAE)
Hypodaphnis
Cryptocaryeae Nees
(Southern hemisphere)
Presence of marginal parenchyma
Eusideroxylon
Caryodaphnopsis
(tonkinensis)
Aniba
Licaria
Nectandra
Cryptocarya
(Madagaskar) p.p.
Neotropical
Ocotea
Aiouea
Endlicheria
Pleurothyrium
Dicypellium
Systemonodaphne
Urbanodendron
Neotropical/Asian
Dehaasia,
Nothaphoebe
Phoebe
Apollonias
Cinnamomum
Persea
Persea p.p.
Umbellularia
Sassafras
*Mezilaurus
*Clinostemon
*Anaueria
Cryptocarya
*Ravensara
Beilschmiedia
Endiandra
*Potameia
*Triadodaphne
Neocinnamomum
Actinodaphne
Laurus
Lindera A
Neolitsea
Litsea
chinensis & al.
Litsea
Lindera B
Iteadaphne
(MYRISTICACEAE)
Laureae
(Northern Hemisphere)
Non-septate fibers
LEGEND:
Taxa with marginal parenchyma (Wood)
Taxa without bast fibers (Bark)
Subordinated structure groups with other characteristics
Partly agreement (Wood or Bark)
* Withour Bark samples
Cryptocaryeae tribe
Perseae tribe
Laureae tribe
A
B
C
D
E

Table 1

	Laurinoxylon aff. *czechense*	*Laurinoxylon czechense* (type)	*Laurinoxylon mueller-stolli* (?type)	*Laurinoxylon* aff. *diluviale*	*Laurinoxylon diluviale* (type)	*Laurinoxylon* cf. *seemannianum*
	Laurinoxylon Type 1		*Laurinoxylon* Type 2a	*Laurinoxylon* Type 2b		*Laurinoxylon* Type 3
Locality	Southeastern Lesbos, Greece	Kadaň-Zadní vrch Hill, Czech Republic	Ipolytarnóc (Hungary) and Wiesa at Kamenz (Germany)	Southeastern Lesbos, Greece	Jachymov (Boheme) Czech Republic	Southeastern Lesbos, Greece
Age	Early Miocene	Early Oligocene	Early Miocene (A. Burdigalian)	Early Miocene	?Oligocene	Early Miocene
Growth ring boundaries	Distinct	Distinct	Distinct	Distinct	Distinct	Distinct
Wood porosity	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse
Vessel density (per mm²)	52-74	15–25	12-18	20-100	9-33	40-100
Vessel grouping	often solitary (18%) and clusters (21%), mainly in radial multiples of 2 (50%), sometimes in radial multiples of 3 (7,5%), rarely in radial multiples of 4 (3,5%)	Mainly solitary, sometimes in radial multiples of 2–4 and clusters	mainly solitary (56%), often in radial multiples of 2 (25%) and 3-4 (19%)	Often solitary (29%) and in radial multiples of 3 (17%), mainly in radial multiples of 2 (50%),rarely in radial multiples of 4 (4%)	mainly solitary (75%), often in radial multiples of 2 (20%), rarely in clusters (3%) and in radial multiples of 3-4 (2%)	Mostly in radial multiples of 2 (32.5%), often solitary (17.3%), and in radial multiples of 3 (14.1%), of 4 (14.8%) and clusters (21.3%)
Mean (range) vessel tangential diameter (µm)	60 (40-85)	100 (50–150)	160	40-110	100-154 (early wood), 44-72 (late wood)	45-50
Mean (range) vessel element length (µm)	73 (50-110)	125 (60–195)	175 (85-240)	50-150	300-550	60-110
Tyloses	Present	Present	Present	Present	Present	Present
Solitary vessel outline (in transversal section)	Rounded to oval	Rounded to oval	Rounded to oval	Rounded to oval	Rounded but sometimes angular	Mainly angular
Perforation plates simple/scalariform	Yes/No	Yes/Yes (10–15 bars, rarely in narrow vessels)	Yes/Yes	Yes/Yes (6-12 bars)	Yes/Yes (6-12 bars)	Yes/No
Intervessel pits, size (µm)	Alternate polygonal, 10 in DM 13.1	Oval to polygonal with lenticular apertures, 8–12	Alternate, 10-15 (large)	Alternate/Small to medium (but also in some cases large)	Bordered, Alternate, round or elliptical/3 x 7-10 (small?) 7–10 (medium) & 10–15 × 7–10 (large)	Alternate
Vessel-ray pitting	Not preserved	Not preserved	with distinct or much reduced borders; similar to intervessel pits in size and shape throughout the ray cell (100 - 200 µm)	?	Yes	?
Axial parenchyma	(scanty?) paratracheal vasicentric	Scanty paratracheal to vasicentric	scanty paratracheal vasicentric	(scanty?) paratracheal, vasicentric	paratracheal, vasicentric (1-2 cells wide rows)	(scanty?) paratracheal, vasicentric
Ray seriation	1-3, mostly 2-3	1–3, mostly 3	1-3, mostly 2	1-4 (mostly 2-3)	1-5 [mostly 3 (51%) and 4 (29%)]	1-5
Rays density (per mm)	(15) 9-24		5-8	11-16	6-9 (transversal) (or 12-18 tangential)	7-14 (mostly 9)
Ray width (µm)	25-30	12–40	25-30	20-60		50-60
Ray height (µm)	280-520	80–900	260-500	160-650	60-820 (frequently: 220-420	300 – 500
Fibers	Probably non-septate	Non-septate	Septate	Probably septate	Probably septate	Possibly septate
Idioblasts density (per mm²)	35-65	**37**	35–65	in general 35-70	0-18 (with big dimensions)	15-33
Idioblasts size (µm)	Radial: 15-45, tangential: 10-36	Radial: 20-25, Tangential: 40-50	tangential height: 40–75 µm, width: 30–50 µm	radial: 25-70, tangential: 15-40 (in transversal)	At the edges of the rays: radial: 50-80, tangential: 27-60 µm. Inside the rays: 37(rd)x27(tg)	Radially: 30-50, tangential: 90-175

Table 1. Comparison of the anatomical characteristics for the four *Laurinoxylon* types from the Cenozoic of southern part of Lesbos Island (Greece), Kadaň-Zadní Vrch Hill and Jáchymov (Czech Republic) and Ipolytarnóc (Hungary), as categorised by the occurrence of the idioblasts.The last column is renamed as *Cinnamomoxylon seemannianum*.

2.3 Systematic Descriptions

Wiemann *et al.* (1988) had introduced the usage of “**wood type**” as the taxonomic unit (most often a genus and occasionally a species or group of species) because isolated wood can rarely be identified to individual species. Great effort has been done in this PhD for the identification of the species of fossil specimens. When this wasn’t feasible wood types were identified based on the anatomical characteristics of the fossil woods, allowing a first level grouping according to the observed features and an evaluation on how these identifications’ results should be better used in the future.

When it was possible by the wood anatomy, additional information was given concerning the “wood structure and palaeoenvironment” because in most angiosperms, the anatomical structure reflects morphological adaptations (Baas and Schweingruber 1987), or the possible identification of climatic region (e.g., woods of tropical rain forests trees contain big vessels accompanied by groups of parenchyma cells instead of dry sites where the trees have small vessels and apotracheal and paratracheal parenchyma, Schweingruber *et al.* 2008), even of drought (or flooded) and drainage periods (Schweingruber 2007) and the correlations of anatomical features with the ecology (still not absolutely proven if they are constant or varied over time, Wheeler & Baas 1993).

Moreover the “dwarfism” of some of the studied specimen could be another possible explanation concerning some strange anatomical characteristics, interpreted as stress effects, especially in conifers (e.g., vessel frequency is higher and vessel diameter lower in dwarfs, Baas 1984).

2.3.1 Identification of angiosperm wood from Lesbos Island

2.3.1.1

Family—Lauraceae Juss.

Fossil Genus—*Laurinoxylon* Felix emend. Dupéron, Dupéron–Laudoueneix, Sakala & De Franceschi

***Laurinoxylon* Type 1**

Fossil Species—*Laurinoxylon* aff*. czechense* Prakash, Březinová & Bůžek

(Plate 4*A*–4*E*, Plate 10*M*; Table 1, Annex 2, Lesbos Island Fossil Flora Appendix)

Material: DM 10 (2 slides), DMDA 13.1 (3 slides)
Locality: Hondrokouki and Damandri (Southeastern Lesbos Island), Greece
Stratigraphic horizon: Under Polichnitos Ignimbrite (PU unit), inside volcanics
Age: early Miocene

Macroscopic description. The specimens are from small stems of a diameter of 2.5 cm that were enclosed in volcanic material (Pl. 4*A*), they are silicified, light, porous, whitish red–brown with distinct growth ring boundaries that can be seen with naked eye. There is also a strange colouration type of circles (due to fossilization processes).

Microscopic description. Growth rings: distinct (Pl. 4*A*). — Wood: diffuse–porous (Pl. 4*A*). — Vessels: 40–100 (52–74) vessels/sq. mm., 18% solitary, 50% groups of two, 7.5% in groups of 3, 3.5% in groups of 4 and 21% clusters; tangential diameter 40 to 85 µm, mean: 60 µm; radial diameter of the solitary vessels 50 to 110 µm, mean: 73 µm; outline of solitary vessels round to oval (Pl. 4*A,* 4*B,* 4*D*); vessel walls thin; perforation plates exclusively simple; tyloses common (Pl. 4*C*); intervessel pits alternate and polygonal in shape, about 10 µm across. — Rays: heterocellular (Pl. 4*E*) up to 3 cells wide (25–30 µm) (Pl. 4*B*–4*D*), commonly 2–3–seriate and 280–520 µm high, body of multiseriate rays composed of procumbent cells with one row of upright cells (Pl. 4*E*); no crystals observed; 9–24 (mean 15) rays per tangential millimeter.— Axial parenchyma: scanty paratracheal (Pl. 4*D*) with a tangential width of 15–20 µm. — Fibres: most probably (due to the bad preservation) non–septate. — Idioblasts: associated with the ray parenchyma cells only (Pl. 4*B*–4*E*). Mean radial x tangential diameter of the idioblasts in transverse section: 15–22 × 26–36 µm; Number of idioblasts per sq. mm (transverse section): 35–65.

***Comparison among Laurinoxylon species with similar type of idioblasts** – only associated with the ray parenchyma* (Table 1). The two specimens from Lesbos have wood diffuse porous, growth ring boundaries distinct, vessels solitary, in radial multiples of 2–3 or sometimes in clusters with simple perforation plates and alternate pitting, scanty paratracheal (vasicentric) axial parenchyma, heterocellular 2–3–seriate rays, tyloses (common) and idioblasts associated only with the ray parenchyma cells. These features are characteristic of *Laurinoxylon* Type 1 and there are several similar previously described fossil species that would fit this type as well.

Laurinoxylon czechense Prakash, Březinová & Bůžek, appears the most similar to the Lesbos material based on microscopic examination of the holotype slides G 4036, G 4037, G 4038, G 4063, G 4064 of the specimen CNB–2 (Mantzouka *et al.* in press). It has idioblasts associated only with the ray parenchyma cells occurring in the body of the rays as well as at the margins. It differs from the Lesbos wood in having slightly bigger vessel diameters, occasional presence of scalariform perforation plates, and slightly higher rays. Therefore, we refer to these Lesbos fossil woods as *Laurinoxylon* aff. *czechense* Prakash, Březinová & Bůžek.

Botanical affinities. Based on the work of Richter 1981a and van der Werff & Richter 1996, and excluding those which have crystals in great percentages of their species, Mantzouka *et al.* (in press) have found that the modern genera closest to *Laurinoxylon* type 1: are: *Dicypellium*, *Urbanodendron* and North American *Persea* (Pl. 3*B*).

Concerning the material from Lesbos and because most probably it doesn’t have septate fibres it seems more closely related to North American *Persea* (which, in contrary with other *Persea* species is close to Laureae tribe which has non–septate fibres). Velitzelos *et al.* (1981a,b; 1999) described numerous leaf findings related to the Lauraceae from Lesbos (appendix in Mantzouka *et al.* 2013a-Annex 1), so there will be a possible correlation with the fossil wood.

Plate 4

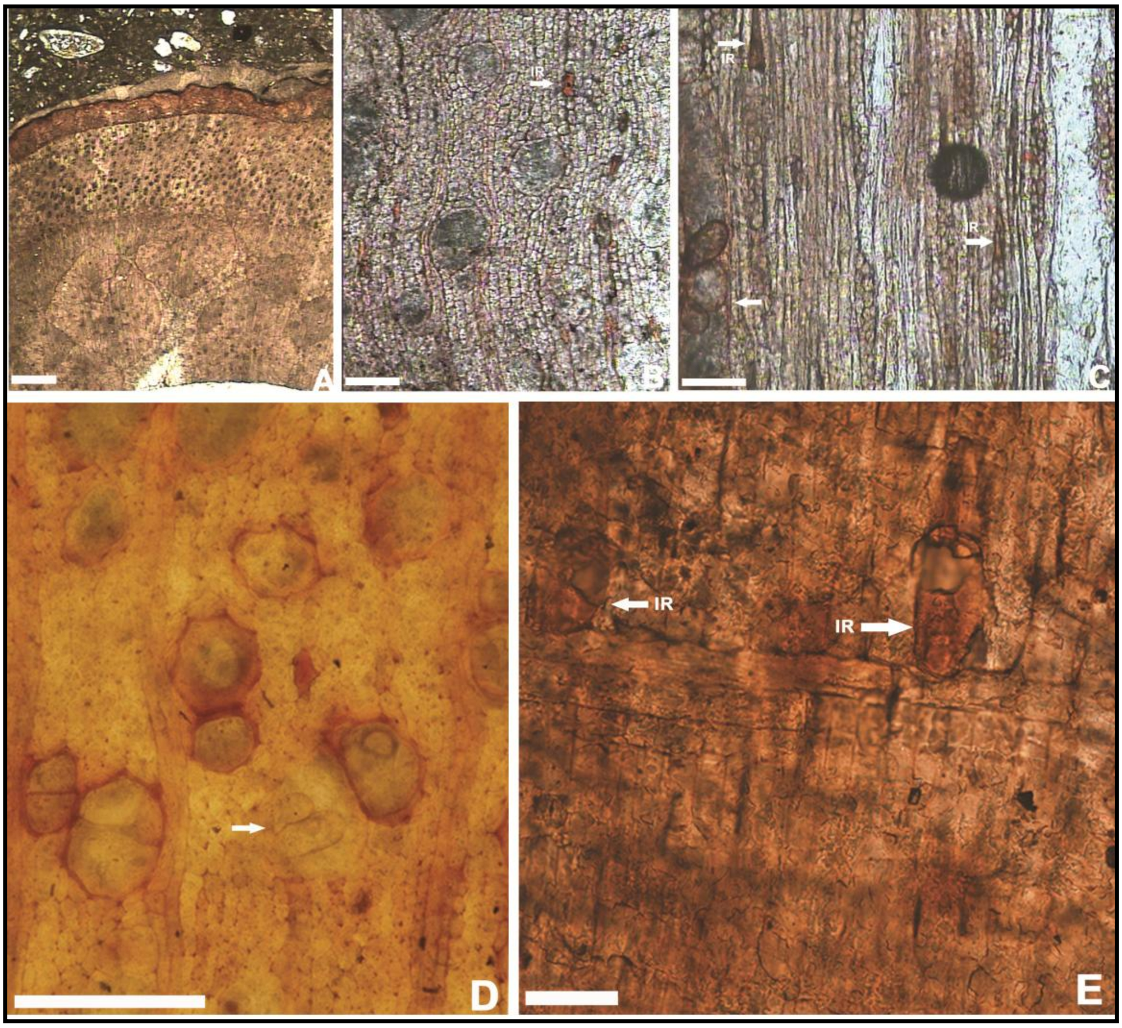


Plate 4 *Laurinoxylon* Type 1: PL. 4A–4E *Laurinoxylon* aff. *czechense* Prakash *et al.* (Lesbos) (DM13.1: Pl. 4A, 4B, 4C, 4D, 4E)

A: Silicified small stem of a diameter of 2.5 cm, enclosed by volcanic material, Growth rings distinct, diffuse-porous wood. **B:** Outline of solitary vessels round to oval; idioblasts: associated with the ray parenchyma cells. **C:** Tyloses, rays up to 3-seriate, idioblasts: associated with the ray parenchyma cells, mainly at the margins and less commonly in the body of the rays. The bottom left arrow shows tyloses. **D:** Outline of solitary vessels round to oval, vasicentric (scanty paratracheal) parenchyma, tyloses (indicated by the arrow), idioblasts associated with the ray parenchyma cells. **E:** Rays heterocellular, body of multiseriate rays composed of procumbent cells with one row of upright cells, Idioblasts: associated with the ray parenchyma cells. Scale bar = 50 µm in E; 100 µm in B, C; 250 µm in D ; 1000 µm in A. A, B, D = TS; C = TLS; E = RLS.

2.3.1.2
Laurinoxylon Type 2a
Fossil Species—Laurinoxylon cf. *daberi* Greguss
(Plate 5*A*–5*I*, Table 1, Lesbos Island Fossil Flora Appendix)

Material: DM 05 (5 slides)
Locality: Damandri, Southeastern Lesbos Island, Greece
Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics
Age: early Miocene

Macroscopic description. Part of a small branch (stem) of 4 cm diameter. The pith is preserved and well seen (Pl.5*A*).

Microscopic description. Growth rings: distinct (Pl. 5*B*). — Wood: diffuse–porous — Vessels: mainly solitary, but also in groups of two and in clusters; outline of solitary vessels round to oval (Pl. 5*B*); perforation plates simple (Pl. 5*E*, 5*G*); tyloses common (Pl. 5*B*), intervessel pits alternate, polygonal, small in size, about 5–7 μm, most probably vessel–ray pits with much reduced borders to apparently simple (Pl. 5*D*, 5*E*, 5*G*, 5*H*). — Rays: heterocellular, up to 3 cells wide, commonly 2–seriate (Pl. 5*B*, 5*C*), body of multiseriate rays composed of procumbent cells with one row of upright and/or square marginal cells (Pl. 5*F*), crystals observed inside the axial parenchyma idioblastic cells (Pl. 5*C*, 5*D*, 5*G*, 5*H*, 5*I*) — Axial parenchyma: vasicentric paratracheal (Pl. 5*B*, 5*C*), fibres septate (Pl. 5*C*) — Idioblasts: associated with the ray and axial parenchyma (Pl. 5*B*, 5*C*) — Crystals: present with the form of prisms, especially inside the axial (and ray) parenchyma idioblasts (Pl. 5*D*, 5*F*, 5*G*, 5*H*, 5*I*). Possibility of crystalliferous masses inside the fibres (Pl. 5*F*, 5*G*, 5*H*).

Comparison among Laurinoxylon species with similar type of idioblasts *– associated with the ray and axial parenchyma* (Table 1)*:* DM05 sample from Lesbos Island has been compared with *Laurinoxylon mueller–stolli* Greguss emend. Süss & Mädel of Lower Miocene (A. Burdigalian) age from Ipolytarnóc (Hungary), with *Laurinoxylon hasenbergense* Süss (Süss 1958) and *Laurinoxylon* cf. *hasenbergense* (Greguss 1969), *Laurinoxylon endiandroides* Süss, *Laurinoxylon annularis* Gottwald, *Laurinoxylon aniboides* Greguss emend. Süss & Mädel, *Laurinoxylon nectandrioides* Kräusel & Schönfeld and *Laurinoxylon ehrendorferi* Berger.

Our specimen (DM05) from the southern part of Lesbos Island has a lot of similarities with *Laurinoxylon* cf. *hasenbergense* (Greguss 1969) basically due to the occurrence of the crystals–prisms related especially to the axial parenchyma idioblasts, as also Greguss had observed. Süss (1958) had noticed that the shape of the oil cells in *L. hasenbergense* was never conical. What is quite interesting in Greguss's (1969) description is the observation of granular content (probably residues of extractives in parenchyma cells), possibly of starch grains, inside the ray and axial parenchyma cells and also the occurrence of frequent diamond–shaped, pentagonal or hexagonal crystals inside the idioblasts and axial parenchyma cells. In this point we should notice that the occurrence of crystals is not clearly defined at the emended diagnosis of *Laurinoxylon* sensu Duperón *et al.* 2008. On the other hand, *Laurinoxylon hasenbergense* Süss (Süss 1958) and *Laurinoxylon* cf. *hasenbergense* (Greguss 1969) have rays up to 1200 µm. This problematic characteristic is discussed in detail in Mantzouka *et al.* (in press) where the hypothesis of the assignment of the latter two species in *Licaria* is supported.

DM05 sample could be very close to *L. nectandrioides* Kräusel & Schonfeld, but not in the sense of van der Burgh (1964, 1973) (because he describes also the presence of tracheids). The main problem is the type of parenchyma which is confluent with seemingly marginal bands in *L. nectandrioides*. This characteristic is problematic for the assignment of this species to *Laurinoxylon* (see in Mantzouka *et al.* in press).

Laurinoxylon ehrendorferi Berger has no crystals. *Laurinoxylon endiandroides* Süss, *Laurinoxylon annularis* Gottwald and *Laurinoxylon aniboides* Greguss emend. Süss & Mädel, are discussed in detail in Mantzouka *et al.* (in press) where there are all the evidence proving that the latter species should not belong to *Laurinoxylon* and *L. aniboides* shouldn't belong even to the Lauraceae.

Greguss (1969) had described *Laurinoxylon daberi* giving the following diagnosis: "there is a remarkable great amount of diffuse axial parenchyma, seen in cross–section as white dots within brown ground substance, idioblasts both in rays and parenchyma (= directly connected with *Laurinoxylon* type 2a of our studies), however those in rays are not so pronounced and remarkable numerous crystals (e.g. the photo below)". This diagnosis of *Laurinoxylon daberi* has been also confirmed by J. Sakala in his last scientific visit at the Natural History Museum of Budapest (Sakala pers. com. 08/2015). Our sample (DM05) from Lesbos Island could be assigned to *L. daberi* from Ipolytarnóc (Fig. 19).

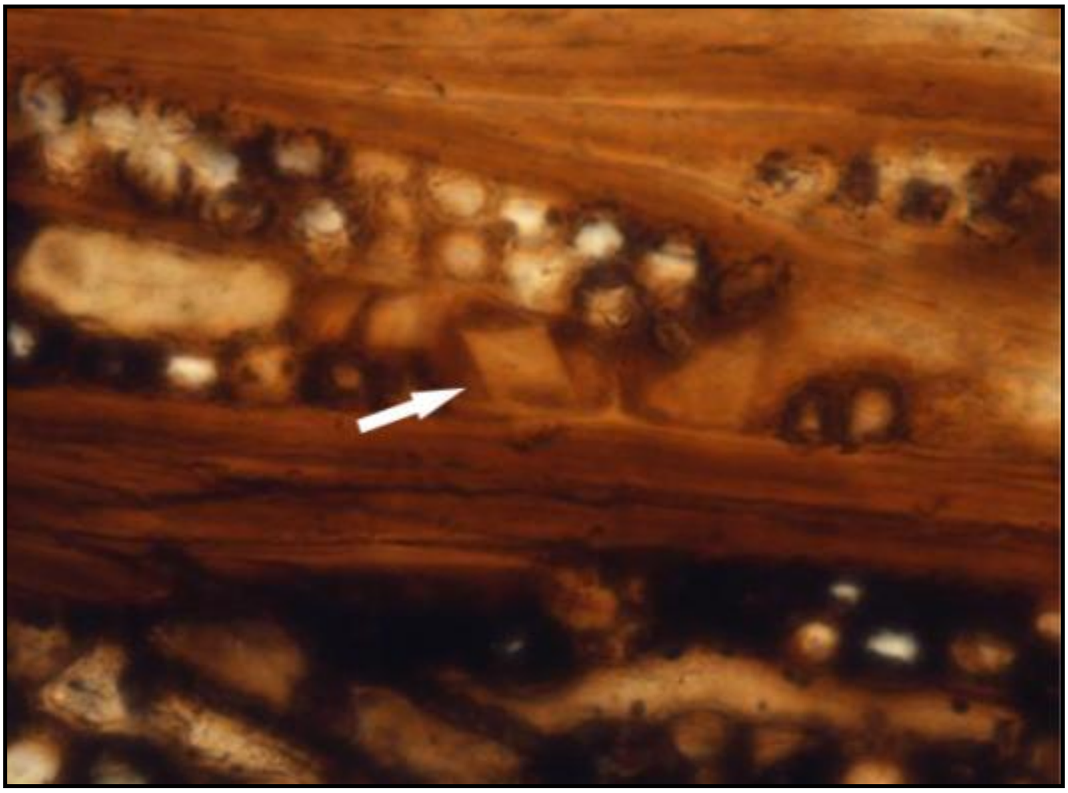


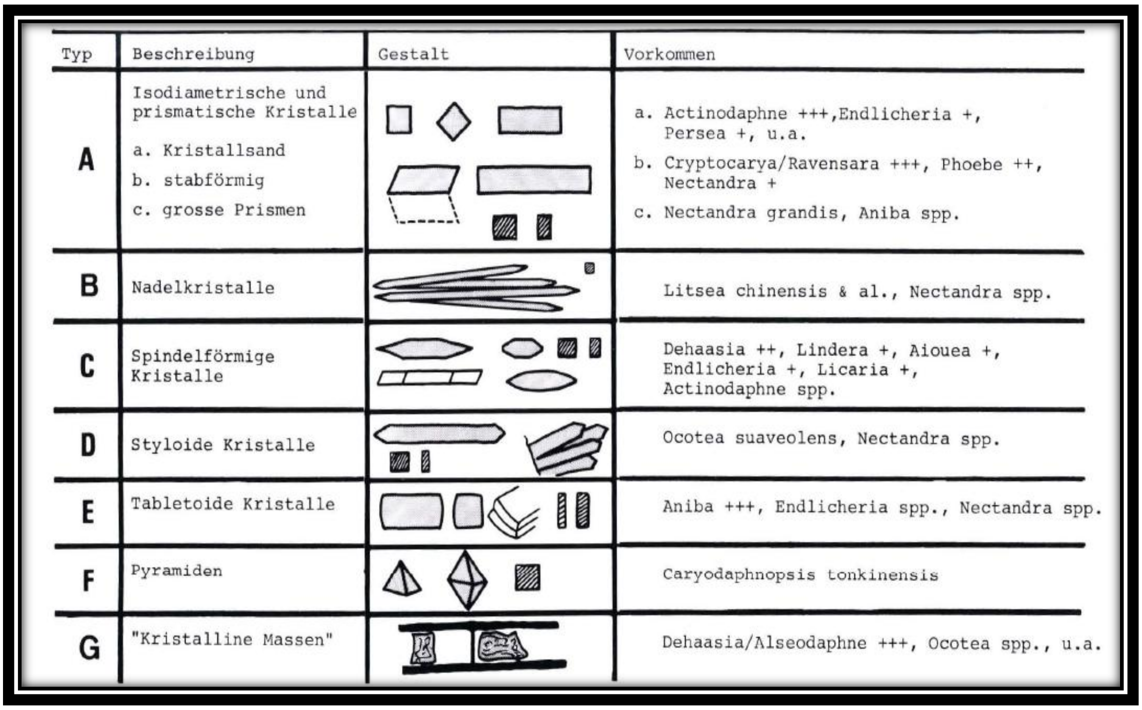
Fig. 19: *Laurinoxylon daberi* Greguss: A crystal (arrow) inside the axial parenchyma idioblast. Photo by J. Sakala (published with permission).

Botanical affinities. According to Mantzouka *et al.* (in press), the list of the genera to which *Laurinoxylon* Type 2a corresponds (Pl. 3*C*) is the following: *Aniba, Licaria, Aiouea, Pleurothyrium, Cryptocarya* from Madagaskar*, Dehaasia, Nothaphoebe, Phoebe, Persea, Apollonias, Lindera A*. DM05 sample is closer to the sub–group which includes the genera with the high percentage of crystals (*Aniba, Licaria, Pleurothyrium, Dehaasia, Phoebe, Apollonias*).

We could exclude from this list *Pleurothyrium* because it has simple and scalariform perforation plates. In case our sample had terminal bands then we could assign it to *Licaria wilhelminensis*.

Finally, it seems that *Licaria*, *Phoebe*, *Apollonias*, *Aniba* and *Dehaasia* (which has simple or simple and scalariform perforation plates but not so pronounced) are the most possible modern analogues of our sample. All the latter are Neotropical / Neotropical–Asian genera belonging to Perseae Nees tribe.

Discussion. In some cases, at the radial section there is an impression of crystals because of the existence of vessel–ray parenchyma pits the occurrence of which is connected with tyloses. Wood forms tyloses when vessels become air–filled. The occurrence of tyloses (as also of gums) generally is related to the size of the interconnections (pits) between vessels and ray parenchyma (Chattaway 1949, Bonsen & Kučera 1990, Saitoh *et al.* 1993).



Typ	Beschreibung	Gestalt	Vorkommen
A	Isodiametrische und prismatische Kristalle a. Kristallsand b. stabförmig c. grosse Prismen		a. Actinodaphne +++,Endlicheria +, Persea +, u.a. b. Cryptocarya/Ravensara +++, Phoebe ++, Nectandra + c. Nectandra grandis, Aniba spp.
B	Nadelkristalle		Litsea chinensis & al., Nectandra spp.
C	Spindelförmige Kristalle		Dehaasia ++, Lindera +, Aiouea +, Endlicheria +, Licaria +, Actinodaphne spp.
D	Styloide Kristalle		Ocotea suaveolens, Nectandra spp.
E	Tabletoide Kristalle		Aniba +++, Endlicheria spp., Nectandra spp.
F	Pyramiden		Caryodaphnopsis tonkinensis
G	"Kristalline Massen"		Dehaasia/Alseodaphne +++, Ocotea spp., u.a.

Fig. 20: Crystals types observed in Lauraceae (Richter 1981a).

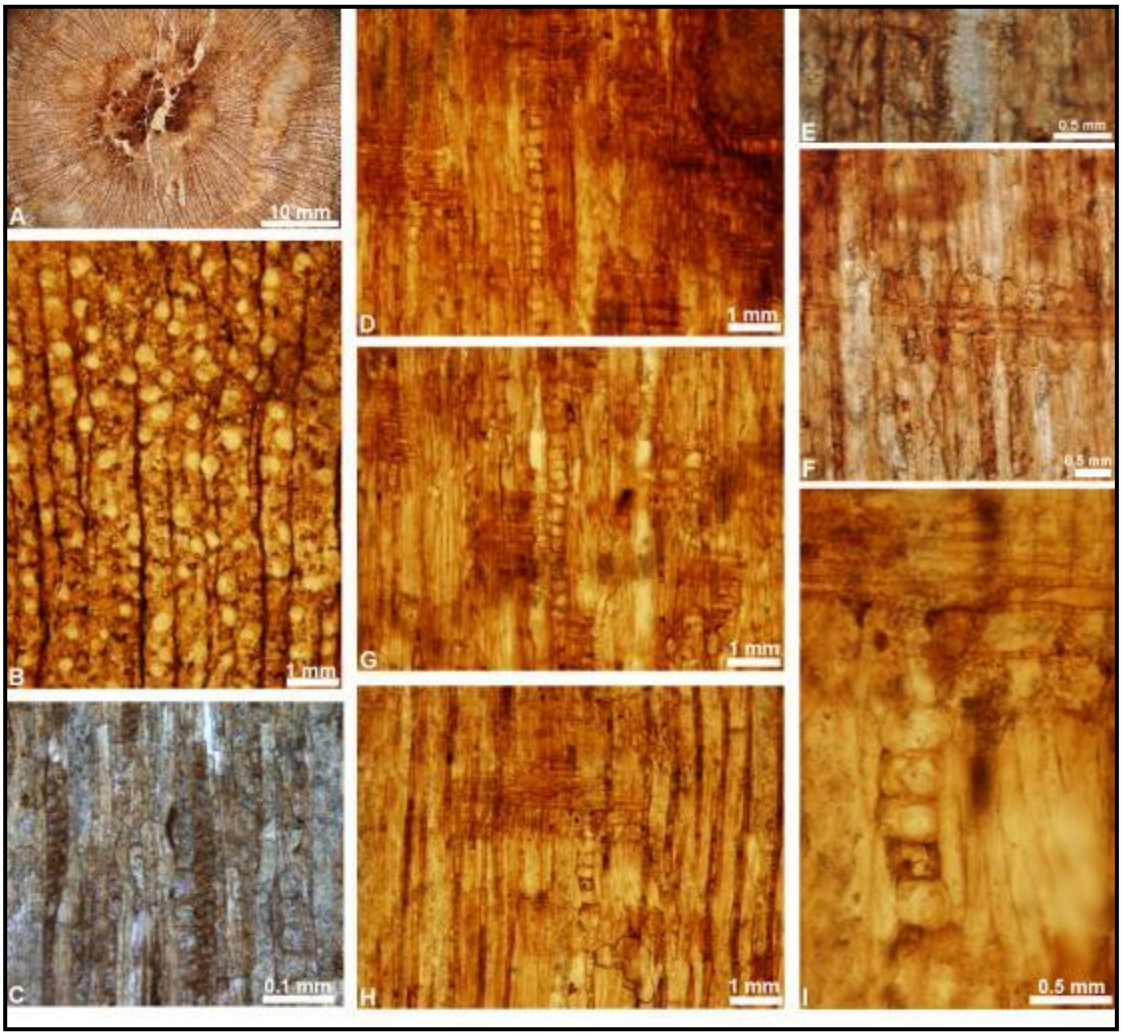
Crystals in form of quadratic prisms (or table–like) are obvious inside parenchyma cells at the radial section (also Greguss had commented for *Laurinoxylon aniboides* and Süss did so in the original diagnosis of *Laurinoxylon endiandroides)*. Rough silica bodies in rays can be seen at the radial section.

Taking into account the work by Richter (1981a) and the figure 20 (above) the genus *Licaria* has crystals of the categories A, C ,E, *Phoebe* has crystals of A category, *Apollonias* has crystals of A and C categories, *Pleurothyrium* has crystals of C category, *Aniba* has crystals belonging to the categories Ac, D and E and *Dehaasia* has crystals of A and C category, SiO_2 of B category and crystalliferous masses inside the fibres. In our sample DM05 from Damandri, Polichnitos area (Lesbos Island) there is the occurrence of big quadratic prisms which are shown in Ac and E categories of Richter's sketch as also a possible occurrence of silica bodies (maybe it could be more similar to *Dehaasia*).

Plate 5 *Laurinoxylon* Type 2a: Pl. 5A–5I *Laurinoxylon* cf. *daberi* Greguss (Lesbos) (DM05: Pl. 5A –5I)

A: Preserved pith, distinct growth rings. **B:** Round outline of solitary vessels, tyloses, vasicentric parenchyma, idioblasts associated with the ray and axial parenchyma, rays up to 3 cells wide. **C:** Rays up to 3 cells wide, Idioblasts associated with the ray and axial parenchyma, crystals observed inside the axial parenchyma idioblastic cells, fibres septate. **D:** Intervessel pits alternate, polygonal, small in size, about 5-7 μm, most probably vessel-ray pits with much reduced borders to apparently simple, crystals present with the form of prisms observed inside the axial (and ray) parenchyma idioblastic cells. **E:** Perforation plates simple, intervessel pits alternate, polygonal, small in size, about 5-7 μm, most probably vessel-ray pits with much reduced borders to apparently simple. **F:** Body of multiseriate rays composed of procumbent cells with one row of upright and/or square marginal cells, crystals: present with the form of prisms, especially inside the axial (and ray) parenchyma idioblasts, possibility of crystalliferous masses inside the fibres. **G:** Perforation plates simple, intervessel pits alternate, polygonal, small in size, about 5-7 μm, most probably vessel-ray pits with much reduced borders to apparently simple, crystals observed inside the axial (and ray) parenchyma idioblastic cells, possibility of crystalliferous masses inside the fibres. **H:** Intervessel pits alternate, polygonal, small in size, about 5-7 μm, most probably vessel-ray pits with much reduced borders to apparently simple, crystals observed inside the axial (and ray) parenchyma idioblastic cells, possibility of crystalliferous masses inside the fibres. **I:** Enlarged detail of Pl. 5H showing the crystals inside the axial parenchyma idioblastic cells. A, B = TS; C = TLS; D, E, F, G, H, I = RLS.

Plate 5



2.3.1.3

Laurinoxylon Type 2b

Fossil Species—*Laurinoxylon* aff. *diluviale* (Unger) Felix emend. Dupéron *et al.* (Plate 6*A*–6*J*, Plate 10*B*, 10*G*; Table 1, Annex 2, Lesbos Island Fossil Flora Appendix)

Material: DMKO 1 (3 slides), DMDA 2 (4 slides), DMDA 7 (5 slides)
Locality: Damandri *(*Southeastern Lesbos Island) Greece
Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics
Age: early Miocene

Macroscopic description. The two specimens are from small stems (the pith is preserved) which are enclosed to the surrounding volcanic material with the following dimensions (in cm): 18 × 9 × 4, 12 × 3.5 × 2 and from a part of a stem with knots (the pith wasn't observed), which is silicified, heavy, red–brown with the dimension of: 31 × 21 × 11 cm. They are silicified, light, whitish brown with distinct growth ring boundaries that can be seen with naked eye. There is a strange colouration type of circles, due to fossilization processes (Pl. 6*A*).

Microscopic description. *Growth rings:* distinct. — *Wood:* diffuse–porous. — *Vessels:* 20–100 vessels/sq.mm, 29% solitary, 50% in groups of two, 17% in groups of 3, and 4% in groups of 4; tangential diameter 40–110 μm, mean: 70 μm; radial diameter 50–150 μm, mean: 90 μm; outline of solitary vessels round to oval (Pl. 6*A, 6B*); vessel walls thin; perforation plates simple (Pl. 6*C*, 6*D*) and scalariform with 6–12 bars (Pl. 6*D*); tyloses common (Pl. 6*A,* 6*B*), — *Rays:* heterocellular up to 3 cells wide (extremely rare of 4 cells), (20–60 μm), and 160–650 μm high (Pl. 6*C*), body of multiseriate rays composed of procumbent and upright cells, marginal rows of 1–4 upright cells; no crystalliferous elements observed; Rays per millimetre: 11–16 — *Axial parenchyma:* scanty paratracheal (Pl. 6*B*), cells with a tangential width of 15–30 μm— *Fibres:* probably septate— *Idioblasts*: associated with the ray parenchyma cells and among the fibres (Pl. 6*C*–6*D*), idioblasts in transverse section with radial diameter × tangential diameter (in μm) from 25 × 15 up to 70 × 40; Number of idioblasts per sq. mm in transverse section: in general 35–70/sq. mm.

Comparison among Laurinoxylon species with similar type of idioblasts *– only associated with the ray parenchyma and among the fibres* (Table 1). The material from Lesbos has been compared with *Laurinoxylon compressum* Huard, *Laurinoxylon perfectum* Huard, *Laurinoxylon diluviale* Unger and has been identified as *Laurinoxylon* aff*. diluviale* because is similar to *Laurinoxylon diluviale* from

Jáchymov. In Mantzouka *et al.* (in press) there are the details about the comparison as well as the discussion about the problematic *Laurinoxylon* species (*Laurinoxylon compressum* Huard and *Laurinoxylon perfectum* Huard) and the proposals for their new assignment.

What should be also discussed in this category is the observation at the tangential slides of some idioblastic cells (which used to be the edges of the rays) looking as if they had been dragged some distance away from the rays' bodies (as if the idioblast's edge was detached from the rest of the ray).

Botanical affinities. The modern genera which belong to *Laurinoxylon* Type 2b according to Mantzouka *et al.* (in press) are: *Nectandra*, *Actinodaphne* and *Neolitsea* (Pl. 3*D*) and they are characterised by the occurrence of crystals. According to Richter (1981a) crystals occur in 60% of *Nectandra* species, in 75% of *Actinodaphne* species and in 50% of *Neolitsea* species. The absence of crystals in *Laurinoxylon* aff. *diluviale* from Lesbos (and in *Laurinoxylon diluviale* from Jachymov), allows us to suggest that it could be close to the species of these three modern genera which do not have crystals. However, leaves of these genera have not been found in the area of the Petrified Forest of Lesbos (Velitzelos *et al.* 1981a,b; 1999, appendix in Mantzouka *et al.* 2013a) so we cannot combine the wood with other organs. The observation of septate fibres in this material allows the hypothesis that *Laurinoxylon* aff. *diluviale* is more closely related to *Nectandra*, and especially to the 40% of *Nectandra* species which do not have crystals.

Plate 6

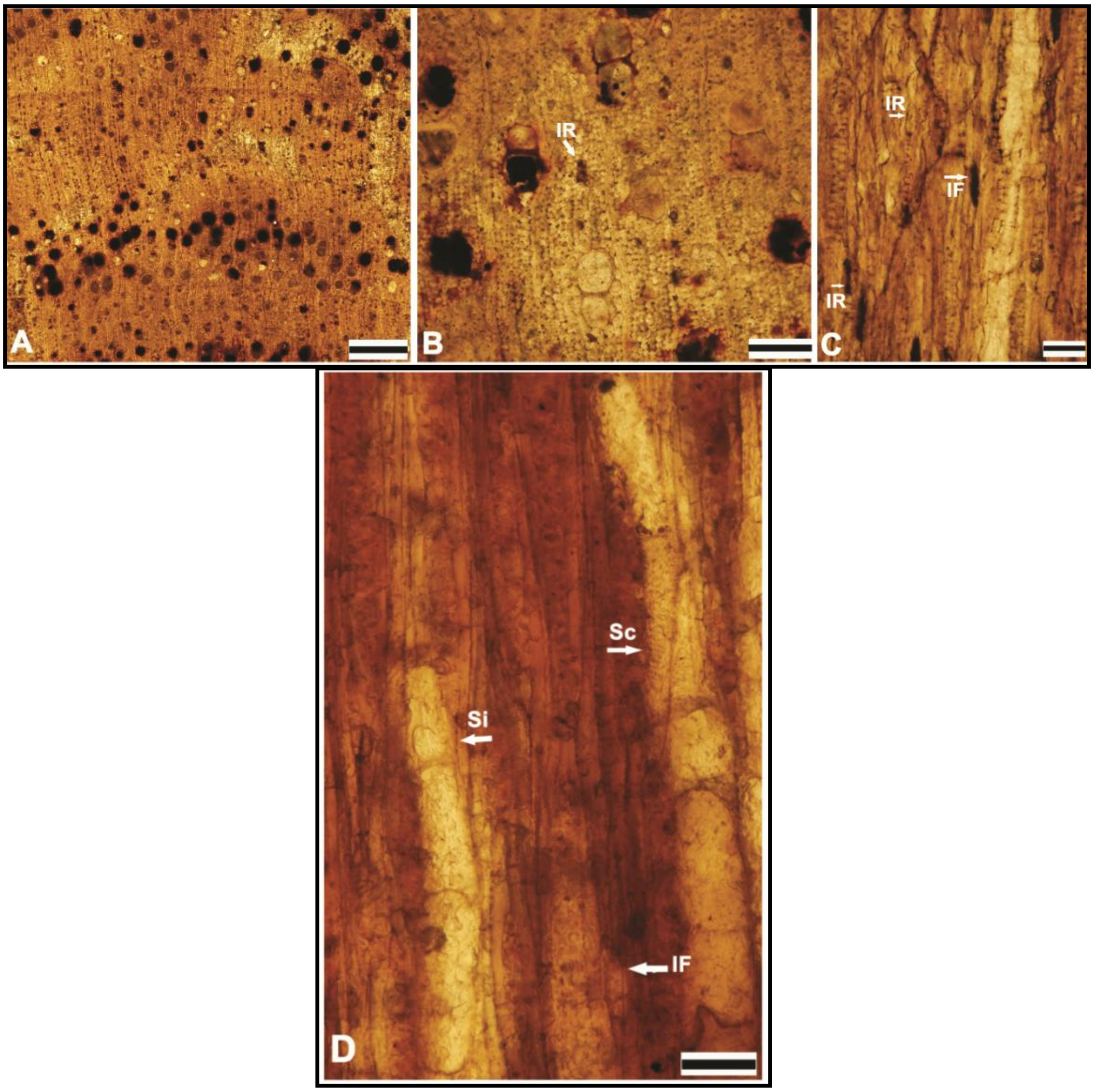


Plate 6 *Laurinoxylon* Type 2b: Pl. 6*A*–6*D* *Laurinoxylon* aff. *diluviale* (Unger) Felix emend. Dupéron *et al.* (DMDA7: Pl. 6A, B; DMDA2: Pl. 6C; DMKO1: Pl. 6D).

A: Distinct growth ring boundaries, diffuse porous, circular regions with strange coloration, due to fossilization processes (?), outline of solitary vessels round to oval, tyloses, scanty paratracheal parenchyma, idioblasts: associated with the ray parenchyma cells and among the fibres. **B:** axial parenchyma: scanty paratracheal, tyloses, idioblasts associated with the ray parenchyma cells and among the fibres. **C:** Idioblasts: associated with the ray parenchyma cells and among the fibres. **D:** Idioblasts: associated with the ray parenchyma cells and among the fibres, perforation plates simple (Si) and scalariform (Sc). Scale bar = 50 µm in B, C, D; 500 µm in A. A, B = TS; C, D = TLS.

2.3.1.4
Cinnamomoxylon Gottwald (= *Laurinoxylon* Type 3)
*Fossil Species—Cinnamomoxylon seemannianum (*Mädel) Gottwald
(Plate 7*A*–7*G*, Plate 10*F*; Table 1, Annex 2, Lesbos Island Fossil Flora Appendix)

Material: DMDA 6 (7 slides)
Locality: Damandri *(*Southeastern Lesbos Island) Greece
Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics
Age: early Miocene

Macroscopic description. The specimen belongs to one of three small stems found enclosed in volcanic material with the following dimensions (in cm): 4.5 × 2 × 2. This stem and the other two are silicified, light, whitish brown with distinct growth ring boundaries that can be seen with naked eye.

Microscopic description. *Growth rings:* distinct. — *Wood:* diffuse–porous. — *Vessels:* 40–100 vessels/sq.mm, 17% solitary, 33% groups of two, 14% in groups of 3, 15% in groups of 4 and 21% in clusters; mean tangential diameter 47 μm; radial diameter 60–110 μm (mean 90 μm); outline of solitary vessels mainly angular (Pl. 7*B*); vessel walls thin; perforation plates simple (Pl. 7*D, 7E*); tyloses common (Pl. 7*A*); intervessel pits alternate — *Rays:* heterocellular up to 5–seriate (mostly 2–3–seriate) (50–60 μm), and 300–500 μm high, body of multiseriate rays composed of procumbent body ray cells with one row of upright and/or square marginal cells (Pl. 7*F*, 7*G*); no crystalliferous elements observed; Rays per tangential millimetre typically 9 (7–14). — *Axial parenchyma:* scanty paratracheal with a tangential width of 15–40 μm (Pl. 7*A*, 7*B*, 7*D*, 7*E*). The parenchyma tends to form bands being slightly confluent (Pl. 7*A*). — *Fibres:* probably non–septate. — *Idioblasts*: associated with the ray and axial parenchyma cells and among the fibres (Pl. 7*A*–*G*). Measurements of the idioblasts in the transverse view radial × tangential diameter in μm) from 30 × 135 to 50 × 160; Number of idioblasts per sq. mm in transverse (mean): 15–33/sq. mm.

***Comparison among Laurinoxylon species with similar type of idioblasts** –associated with the ray and axial parenchyma and among the fibres* (Table 1). What has been discovered during this study is that the more 'delicate' type of parenchyma (= tending to aliform/confluent) in combination with the existence of idioblasts associated with ray and axial parenchyma and distributed among the fibres – which represent the main characteristics of *Laurinoxylon* type 3 – correspond better to the genus *Cinnamomoxylon* (or even to modern *Cinnamomum*).

The features characteristic of *Laurinoxylon* Type 3 and the reason for which *Cinnamomoxylon* sensu Gottwald (1997) would be the most appropriate genus for this category are discussed in detail in Mantzouka *et al.* (in press).

The description of *Cinnamomoxylon* sensu Gottwald (1997) includes the following wood anatomical characteristics: "Vessels diffuse porous to slightly semi–ring, in short radial chains and solitary, diameter >80μ; perforation plates simple or scalariform; pits alternate, diameter 8 to 12; often with thin–walled tyloses, rays heterogeneous predominantly weak, diameter 2 to 4 cells, height 250 to 450; cross fields type I/II (after Richter 1981a); idioblast secretory cells (oil cells) with different frequencies at the edges, parenchyma vasicentric to aliform also limited confluent; secretory cells vary frequently and vary in size, supporting tissue of fibres, thin to moderately thick–walled, septa interspersed mostly absent or only very occasionally; idioblastic secretory cells vary frequently between the fibres".

Something also important is the fact that the diagnosis of *Cinnamomoxylon* Gottwald as it is – if one takes into account the work by Richter 1981a on Lauraceae – comes to the conclusion that the description of the fossil genus refers to the characteristics of the present day genera *Cinnamomum* and *Ocotea*. Therefore there is the proposal (in Mantzouka *et al.* in press) of the addendum of the following feature: "the rays' width of *Cinnamomoxylon* should be 2–5 cells" (as also described in for the present day genus *Cinnamomum*) and not only 2–4 cells (in order to be used as a diagnostic feature separating *Cinnamomum* from *Ocotea* and consequently *Cinnamomoxylon* from *Ocoteoxylon* – the latter being invalid although maybe it shouldn't)

Lesbos material has been compared with *Laurinoxylon variabile* Privé–Gill & Pelletier, *Cinnamomoxylon limagnese* (Privé–Gill & Pelletier) Gottwald, *Laurinoxylon bergeri* Süss and *Cinnamomoxylon seemannianum* (Mädel) Gottwald. We are referring to the specimen from Lesbos as *Cinnamomoxylon seemannianum*, because it is very close to *Cinnamomoxylon seemannianum* (Mädel) Gottwald. In Mantzouka *et al.* (in press) there is also the proposal of the combination *Cinnamomoxylon variabile* (Privé-Gill & Pelletier) Mantzouka, Karakitsios, Sakala, & Wheeler.

Botanical affinities. Of the extant genera we focus on the ones which are similar to *Laurinoxylon* Type 3 (Pl. 3E) and don't have crystals &/or crystalline masses inside their fibres in great percentages of their species: *Ocotea* and *Cinnamomum*. Taking into account the work by Mantzouka *et al.* (in press) a fossil wood remnant is attributed to *Cinnamomoxylon* and consequently to the present day genus *Cinnamomum* when: the axial parenchyma is vasicentric to confluent or aliform to confluent, it has 2–5–seriate rays and septate or not fibres and on the other hand we can refer to a fossil as a representative of the present day genus *Ocotea* when its wood anatomy has the following characteristics: (scanty?) vasicentric paratracheal parenchyma (up to confluent), 2–4–seriate rays with a height up to 1.2 μm, septate fibres and possible crystal masses and SiO_2 occurrences inside the fibres.

Lesbos wood is assigned to *Cinnamomoxylon* and to the present day *Cinnamomum* having up to 5 ray cells and vasicentric to confluent axial parenchyma. Velitzelos *et al.* (1981 b) had described leaves of *Cinnamomum polymorphum* Heer sensu Grangeon at the area of the Petrified Forest of Lesbos (appendix in Mantzouka *et al.* 2013a). Therefore, the suggestion that this wood may correspond to *Cinnamomum* is being reinforced.

Plate 7

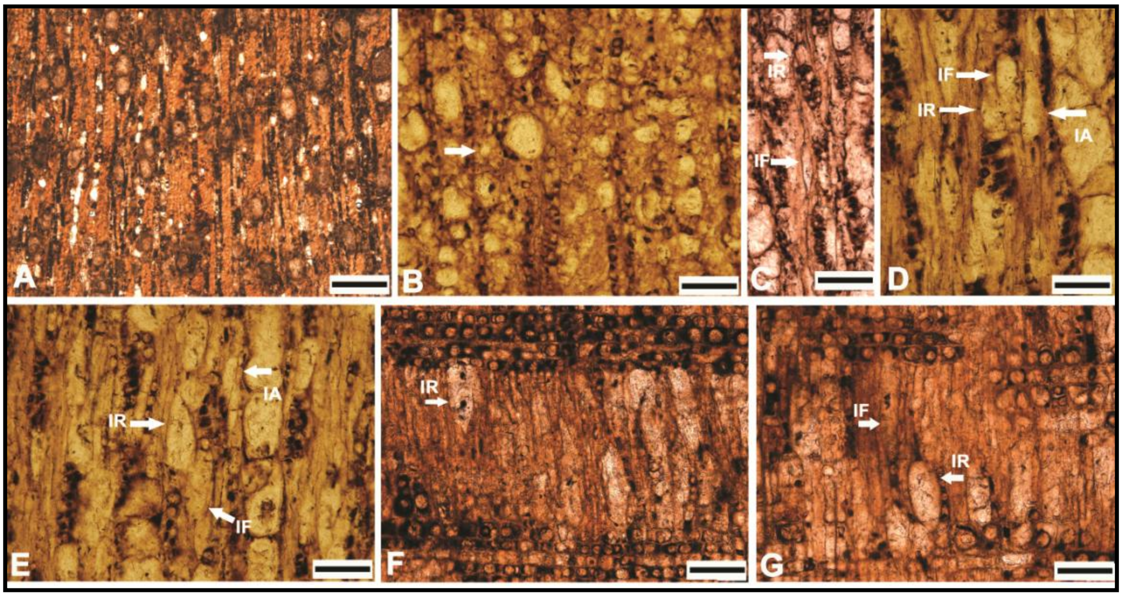


Plate 7 ***Cinnamomoxylon*** **Gottwald (=** ***Laurinoxylon*** **Type 3)*:* Pl. 7A–7G**. ***Cinnamomoxylon seemannianum*** **(Mädel) Gottwald (DMDA6a, DMDA6b, DMDA6c)**

A: Vasicentric paratracheal parenchyma, slightly confluent forming bands, rays up to 5- seriate, idioblasts: associated with the ray and axial parenchyma cells and among the fibres. **B:** Outline of solitary vessels mainly angular, axial parenchyma: (scanty) vasicentric paratracheal, idioblasts: associated with the ray and axial parenchyma cells and among the fibres. **C:** Idioblasts: associated with the ray parenchyma cells and among the fibres. **D:** Idioblasts: associated with the axial and ray parenchyma cells and among the fibres. **E:** Axial parenchyma: scanty paratracheal with a thickness of 15-40 µm, Idioblasts: associated with the ray and axial parenchyma cells and among the fibres. **F:** Heterocellular rays, body ray cells procumbent with one row of upright and/or square marginal cells, idioblasts associated with ray parenchyma cells. **G:** Heterocellular rays, body ray cells procumbent with one row of upright and/or square marginal cells, idioblasts associated with ray parenchyma cells and among the fibres. Scale bar = 50 µm in B; 100 µm in D, E, F, G; 200 µm in A, C. A, B = TS; C, D, E = TLS; F, G = RLS.

2.3.1.5

Fossil genus: *Cryptocaryoxylon* Leisman

(Plate 8*A*–8D, Lesbos Island Fossil Flora Appendix)

Material: DM 17 (3 slides)

Locality: Damandri *(*Southeastern Lesbos Island) Greece

Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics

Age: early Miocene

Macroscopic description. This sample belongs to a small stem of a diameter of 2.5 cm which is enclosed to the surrounding volcanic material. It is silicified, light, porous, whitish red–brown with distinct growth ring boundaries that can be seen with naked eye. The pith of square/rectangular or polygonal shape with cell contents (terminology sensu Crivellaro & Schweingruber 2013) is preserved (Fig. 21).

Microscopic description. *Pith and bark preserved. — Growth rings:* distinct (Pl. 8*A*), 6 at least in number. — *Wood:* diffuse–porous. — *Vessels:* 60–70 vessels/sq.mm, 19% solitary, 50% groups of two, 13% in groups of 3, 2% in groups of 4 and 16% in clusters; mean tangential diameter 70 (50–90) μm; radial diameter 80 (50–110) μm; outline of solitary vessels rounded to oval; vessel walls thin; perforation plates simple; tyloses common (Pl. 8*D*); intervessel pits alternate, polygonal, medium to large in size — *Rays:* heterocellular up to 3–seriate (mostly 2–3–seriate) (25–30 μm), and 180–550 μm high, body of multiseriate rays composed of procumbent body ray cells with one of upright and/or square marginal cell; no crystalliferous elements observed; Rays per tangential millimetre: 13–20. — *Axial parenchyma:* scanty paratracheal with a tangential width of 15–25 μm; axial parenchyma in marginal bands with 1–3 celled width (Pl. 8B). — *Fibres:* non–septate (although there are some artificial cracks). — *Idioblasts*: associated with the ray parenchyma cells (Pl. 8*C*). Measurements of the idioblasts in the transverse view radial × tangential diameter in μm) from 12.5 × 25 to 30 × 50; Number of idioblasts per sq. mm in transverse (mean): 35–45/sq. mm.

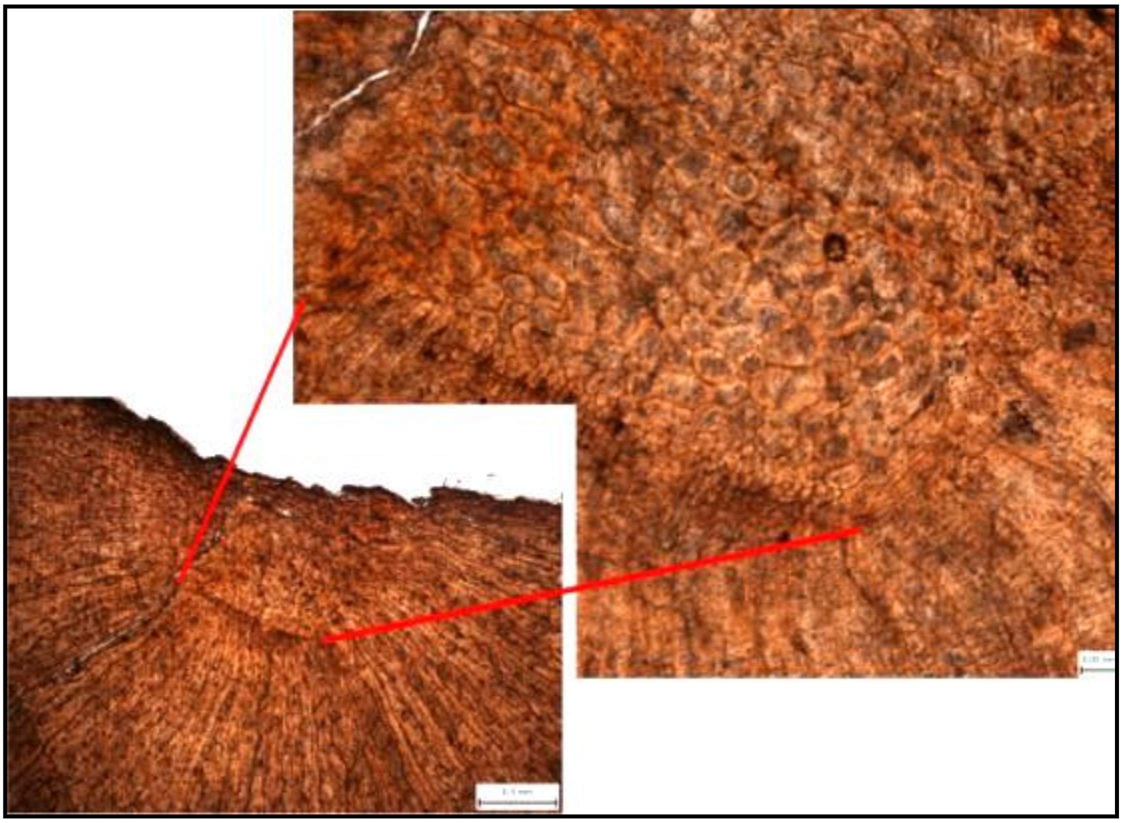


Fig. 21: Preserved pith of square/rectangular or polygonal shape with cell contents present (following the terminology proposed by Crivellaro & Schweingruber 2013) of DM 17 sample. The details of the pith are enlarged.

Comparison with fossil wood. The characteristics of the anatomical study of DM17 sample could "describe" *Laurinoxylon* genus of Type 1, with idioblasts associated only with the ray parenchyma cells. The only feature not in accordance with the emended diagnosis of this genus was the existence of axial parenchyma in marginal bands. This is the main characteristic of the tribe Cryptocaryeae Nees. Searching fossil Lauraceae we found out that the fossil genus *Cryptocaryoxylon* could be close to our sample.

Botanical Affinities.The occurrence of axial parenchyma in marginal bands of up to 3–celled width is a characteristic not so common. After searching through Lauraceae we found that this characteristic in lauraceous genera usually occurs in combination with the existence of aliform to aliform confluent paratracheal parenchyma (e.g. *Beilschmiedia*, *Triadodaphne*, *Eusideroxylon* and *Potoxylon*, *Hypodaphnis*). *Ravensara* could be also a possible match but there are crystals in 100% of its species (crystals were not observed in our sample).Taking into account the anatomical characteristics of our sample and the work by Richter (1981a) we come to the conclusion that this fossil wood could be the fossil representative of *Potameia/Syndiclis* or *Cryptocarya* or *Licaria wilhelminensis* or *Caryodaphnopsis tonkinensis*. It seems more possible that this wood is close to the present day genus *Cryptocarya* because the 20% species of this genus have idioblasts in rays and the 25% of the species of this genus have no crystals.

Discussion. This genus has been found during this study also in Lemnos Island. The material from Lemnos is better preserved and therefore the reader is kindly advised to consult the pages 135-142 where the detailed description, comparison and discussion of Lemnos material are presented.

Plate 8

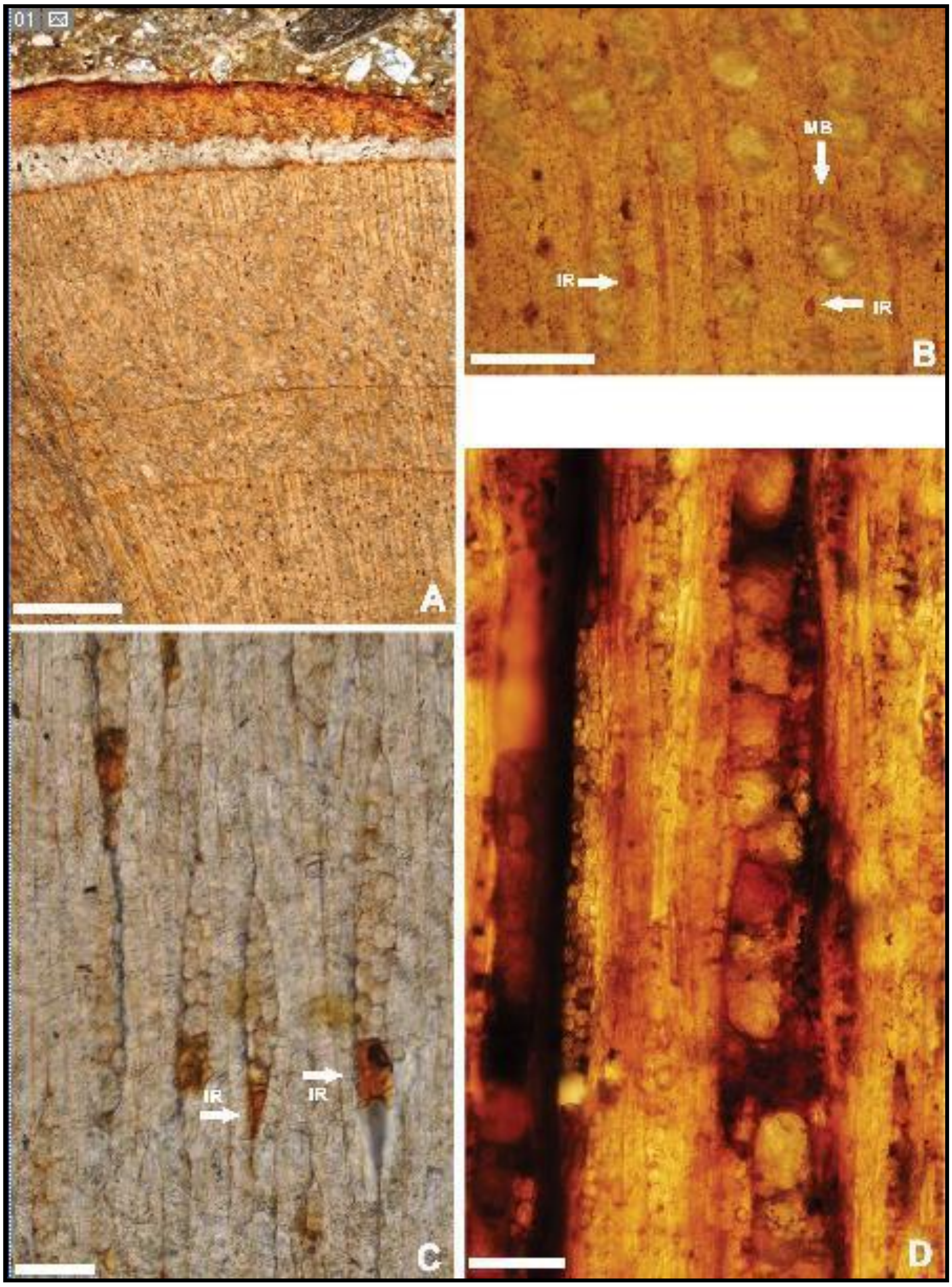


Plate 8. ***Cryptocaryoxylon*** **Leisman (DM17: Pl. 8A, 8B, 8C, 8D)**

A: Growth rings distinct, diffuse-porous wood. **B:** Growth rings distinct, wood diffuse-porous, outline of solitary vessels round to oval, rays up to 3-seriate, idioblasts: associated with the ray parenchyma cells, axial parenchyma in marginal bands (MB). **C:** Idioblasts: associated with the ray parenchyma cells (usually at the edges of the rays, but also inside their body). **D:** Vessels with common tyloses. Scale bar = 50 µm in C; 100 µm in B, D; 1000 µm in A. A, B = TS; C, D = TLS. TS, TLS, and RLS denote transversal, tangential longitudinal and radial longitudinal sections, respectively. Also, IR denotes Idioblasts associated with Rays (IR). MB denotes Axial Parenchyma in Marginal Bands (MB).

2.3.1.6

Family—Fagaceae Dumortier

Fossil Genus—*Quercoxylon* Kräusel (Plate 9, Lesbos Island Fossil Flora Appendix)

Material: DM 16 (4 slides)
Locality: Southeastern Lesbos Island, Greece (Plakes, Polichnitos region)
Stratigraphic horizon: Under Polichnitos Ignimbrite (PU unit), inside volcanics
Age: early Miocene

Macroscopic description. The specimen comes from a small stem of a few centimeters diameter.

Microscopic description. Growth rings: distinct. — Wood: Semi–ring to diffuse–porous (gradual porosity) (Pl. 9*A*). — Vessels: exclusively solitary with more than 90% solitary vessels/sq. mm. (Pl. 9*A–C*), 14– 26 vessels/sq.mm; tangential diameter 55 to 150 μm, mean: 100 μm; radial diameter of the solitary vessels 80 to 170 μm, mean: 120 μm; outline of solitary vessels round to oval (Pl. 9*A–F*); in some cases the vessels' arrangement: seems diagonal to dendritic (Pl. 9*B*); perforation plates exclusively simple; tyloses common (Pl. 9*A–F*) intervessel pits alternate about 2.5–5 μm across. — Rays: of two distinct sizes a) uni/bi–seriate and b) multiseriate: aggregate, compact and compact–compound (Pl. 9*G*, 9*H*) up to 320 μm wide (Pl. 9*A–C*) and more than 1 mm high (2–11 mm) (Pl. 9*G*). — Axial parenchyma: apotracheal diffuse in aggregates (Pl. 9*A–F*), vasicentric, scanty paratracheal (Pl. 9*D–F*) with a tangential width of 15–20 μm and even confluent (but not in large bands – the bands in our specimen are of 1 cell wide) (Pl. 9*D–F*) — Fibres: vasicentric tracheids present with simple to minutely/distictly bordered pits of 2.5–5 μm diameter.

Comparison with other fagaceous wood – Discussion. The gradual porosity of the vessels, the existence of two types of rays (uni–seriate and multiseriate) along with the oval shape of the solitary vessels outline allow as to believe that the sample belongs to oak trees.

Privé (1975) had described different types of the fossil genus *Quercoxylon* Kräusel (1939) emend. Müller–Stoll & Mädel (1957), having botanical affinities with the modern genera *Quercus* L. and *Lithocarpus* BL. (= *Pasania*) occurring at the warm temperate regions of the Northern Hemisphere and of East Indies (= Southeast Asia and India including the Islands) with the following characteristics: oak trees with simple perforation and vessels of radial up to dendritic pattern, rays of two types: multiseriate and very long and narrow uni– &/or bi–seriate. The diffuse porosity characterizes the evergreen species of these two genera (*Quercus* and *Lithocarpus*); the ring porosity is represented at the deciduous species of *Quercus* and at the Northern (septentrionales) species of *Lithocarpus*. At the root wood of deciduous species, the vessels have a tendency often to lose their disposal inside the growth rings, showing a more "diffuse porosity" as at the evergreen species. Concerning the large multiseriate rays sometimes are made of aggregate rays (individual rays very closely associated looking as a single large ray). This characteristic is noted at the evergreen species and at the root wood of the deciduous species Privé (1975).

Generally, there are 3 types of oaks (e.g. see in Hadziev & Mädel 1962, Privé 1975, Gros 1983, Selmeier 1992):

a) "white oak–type": with ring porous, closely spaced latewood vessels with thin walls, usually angular in cross–section, numerous between two rays, with abrupt transition from early to latewood (logs of the mostly deciduous species of *Lepidobalanus* section as also of the section *Macrobalanus* of the genus *Quercus*,

b) "red oak type": with ring porous, latewood vessels relatively large, rounded and thick walled (woods from the deciduous section of *Erythrobalanus* and some species of the section *Lepidobalanus*),

c) "evergreen oaks" of the genera *Quercus* (section *Cyclobalanopsis*) and *Lithocarpus* (section *Lepidobalanus*) species of "sempervirent type" with diffuse or semi–ring porous, scanty and relatively close spaced vessels with radial pattern (radially oriented) with tendency to form aggregate rays (false rays). A similar character can be seen in root wood with diffuse porosity, numerous large vessels, indistinct growth rings and tendency to form false rays (aggregate rays).

Unger in 1842 presented a generic diagnosis for *Quercinium*, revised by Felix. The genus *Quercoxylon* was created by Hofmann in 1929 (although without a type species was considered *nomen nudum*), and defined by Kräusel in 1939. The history of this genus has been given in detail by Iamandei *et al.* (2011, 2012).

According to Petrescu (1976) and Petrescu *et al.* (1980) the key of the generic identification of fagaceous fossil woods is mainly focused on two levels: the first one includes the perforation plates with the vessels' groupings and the second one is dealing with the rays' category, as it is shown in the Key for fagaceous fossil woods given below (Fig.22).

Type A	**Structures with solitary vessels or grouped (2–3 or more), with simple and scalariform perforations.**	**Fine rays (1–3–seriate) and multiseriate compact.**	***Fagoxylon* *Nothofagoxylon***
Type B	**Structures with solitary vessels, simple perforated, sometimes some scalariform, with few bars.**	**Exclusively uniseriate rays.**	***Castanoxylon***
		Uniseriate and multiseriate compact, sometimes compact–composed or partially aggregate rays.	***Quercoxylon***
		Uniseriate and multiseriate aggregate rays.	***Lithocarpoxylon***

Fig. 22: Key of generic identification of fagaceous fossil woods (Petrescu, 1976).

Petrescu *et al.* (1980) have given the definition of compact, compound, aggregate rays and their combinations for the Type B of the fagaceous fossil woods (Fig. 22). The existence of aggregate rays occurs in few taxonomic groups, i.e. in Fagaceae: *Castanopsis, Lithocarpus, Quercus*–evergreen species (IAWA 1989).

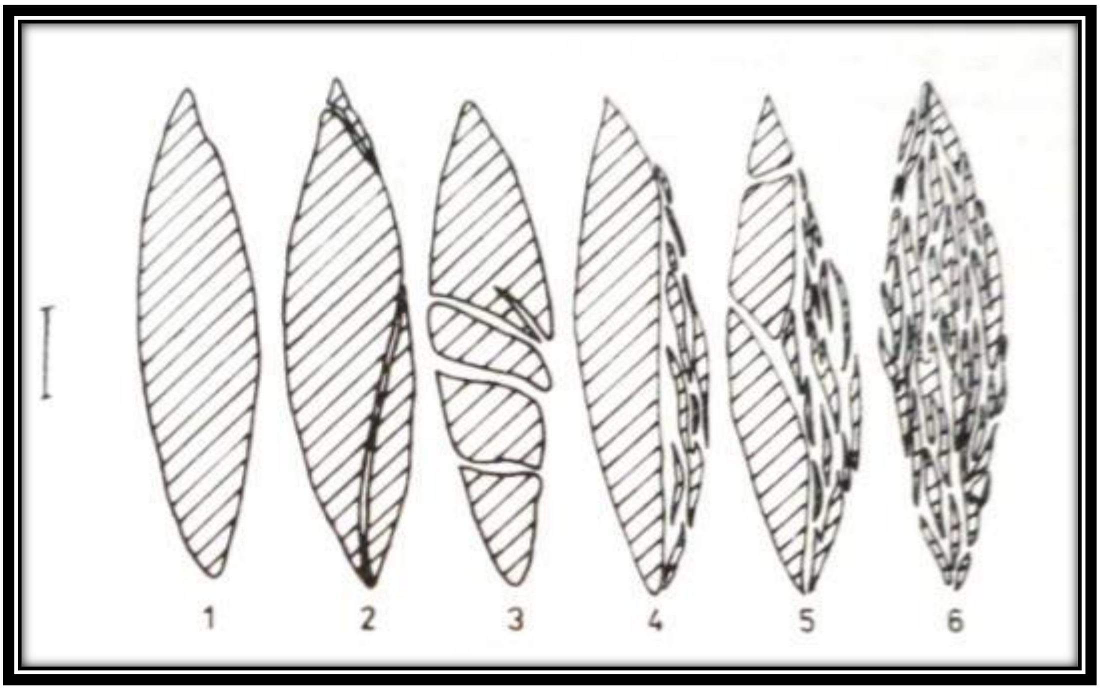


Fig. 23: Types of multiseriate rays in Quercineae in tangential section (after Petrescu *et al.* 1980): 1. Compact, 2. Compact–Compound, 3. Compound, 4. Compact–Aggregate, 5. Compound–Aggregate, 6. Aggregate rays.

The microscopic study of the specimen from Plakes, Polichnitos region (Southern Lesbos Island) as is described above, with the recognition of more than 90% solitary vessels, simple perforation and uni– (and bi–seriate in some cases) and multi–seriate aggregate rays allowed its identification as *Quercoxylon*.

A further detailed anatomical study of the specimen and especially of the tangential section shows the occurrence of compact–compound aggregate rays (as they are shown in Fig. 23), a characteristic which is typical for *Quercoxylon* as is shown in Fig 22. Taking into account the work by Müller–Stoll & Mädel (1957) we compared our fossil with several *Quercoxylon* species and found out that Polichnitos *Quercoxylon* is different from *Q. densum*, *Q. staubii* and *Q. böckhiannum* since it is diffuse up to semi–ring porous and not ring porous as these species. It differs from *Q. viticulosum* in the dimensions of the vessels and of the rest of the characteristics and it is close to *Quercoxylon helictoxyloides* from the Pontian (upper Miocene) of Austria (with an exception of the growth rings boundaries which in *Q. helictoxyloides* are indistinct but in our sample are distinct).

Species of fossil oaks (in Oligocene)	Growth ring type	Ø mean vessel diameter (at the transversal section)		Wood rays	
		Early wood	Late wood	Uni–seriate (height)	Multi–seriate (width)
Quercoxylon praehelictoxyloides	Ring–porous Diffuse–porous	Ø R 165–225 µm Ø Tg 120–180 µm	Ø R 120–180 µm Ø Tg 75–120 µm	(1)–4–12(20) cells	300–700 µm
Q. justiniani	Diffuse–porous	Ø R 150–225 µm Ø Tg 120–150 µm		(1)6–20 (32) cells	200–600 µm
Q. mixtum	Ring–porous	Ø R 200–330 µm Ø Tg 150–225 µm	Ø R 100–180 µm Ø Tg 75–125 µm	(2)4–18(30) cells	180–1200 µm
Q. intermedium	Diffuse–porous Ring–porous	Ø R 200–320 µm Ø Tg 145–240 µm	Ø R 95–220 µm Ø Tg 75–160 µm	(2)8–22(30) cells	300–500 µm

Fig. 24: Comparison of the anatomical elements from several fossil oaks from the Oligocene of Moldavia (*Q. praehelictoxyloides, Q. mixtum*), Romania (*Q. justiniani*) and Thrace–NE Greece (*Q. intermedium*) (Petrescu & Velitzelos 1981, modified).

Among Greek species of *Quercoxylon* (Petrescu & Velitzelos 1981) our specimen seems to be closer to *Quercoxylon praehelictoxyloides* and *Q. intermedium* but not identical (Fig. 24). *Quercoxylon praehelictoxyloides, Q. justiniani,* along with *Q. mixtum* were found in the north–western Transylvania and *Q. intermedium* was identified at the fossil forest of Thrace, Northeastern Greece (Fig. 24). *Quercoxylon praehelictoxyloides* Petrescu has as a synonym *Lithocarpoxylon praehelictoxyloides* (Petrescu) Suzuki & Ohba. Although we have studied in detail *Lithocarpoxylon* genus as well, we don't believe that DM16 belongs to that genus but to *Quercoxylon*.

Botanical affinities. The specimen from the Southern part of Lesbos Island is identified as *Quercoxylon.*

The studied sample has similarities with *Q. intermedium*, which according to Petrescu & Velitzelos (1981) must have descendants (living relatives) among the exotic tropical and subtropical Oaks of Southeast Asia (in the subgenus *Cyclobalanopsis*). In the Oligocene of Thrace, as in several European countries (Roumania, Austria, Czech Republic, Slovakia, Bulgaria), *Quercoxylon* is found in association with wood specimens (trunks) of *Lithocarpoxylon* and *Laurinoxylon*. Taking into account the fact that there are several findings of different *Laurinoxylon* types from Polichnitos region (Southeastern Lesbos Island, Greece) the existence of fagaceous representatives like *Quercoxylon* and *Lithocarpoxylon* is expected.

According to Selmeier (1986) who identified the first occurence of evergreen *Quercus* trees of the Upper Tertiary in Southern Bavaria, the modern species of *Cyclobalanopsis* and *Lithocarpus* are represented in the mountainous areas of Indo–Malaysian and Sino–Japanese floras, while a kind of *Lithocarpus* is common in California (Fig. 25).

According to Privé (1975) the modern representatives of *Quercus* L. and *Lithocarpus* BL. are found in temperate regions of the North Hemisphere and of East Indies (= Southeast Asia including India and the Islands) (Fig. 25).

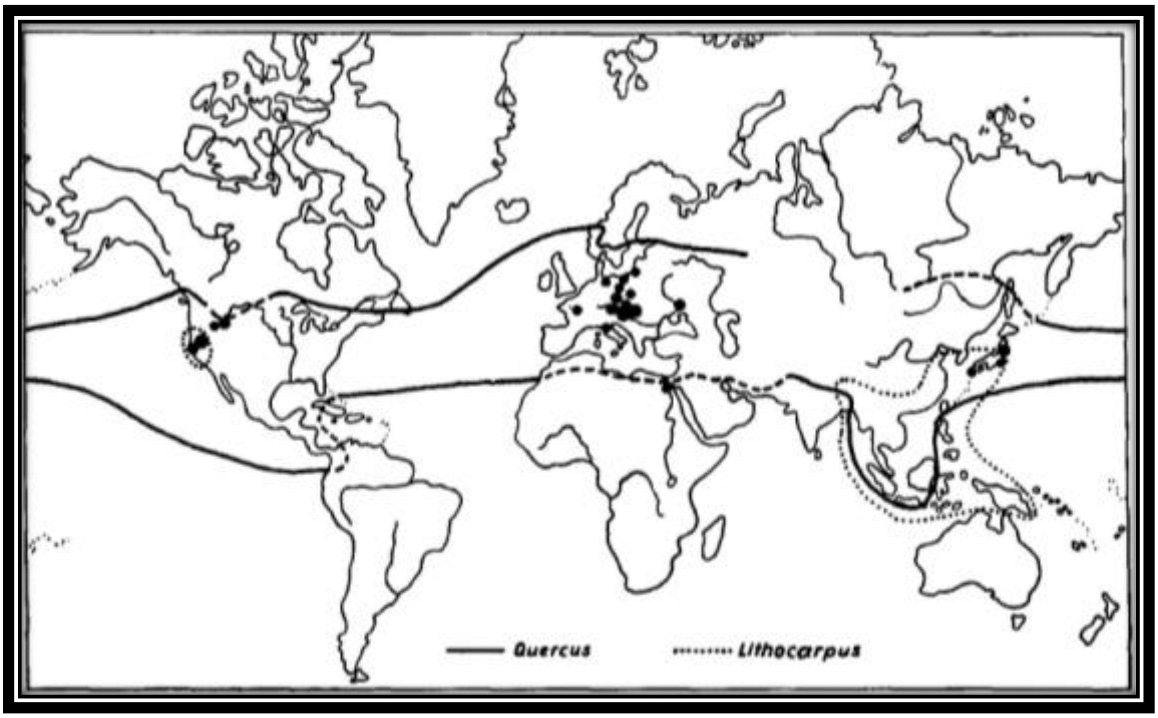


Fig. 25: *Quercus* and *Lithocarpus* distribution (in Müller–Stoll & Mädel 1957).

Fagaceous leaves have been found at the western peninsula of Lesbos [*Quercus* sp., *Quercus apocynophyllum* Ett, *Pungiphyllum crutiatum* (Al. Braun) Frankenhäuser et Wilde (= *Quercus cruciata* Al. Braun) referred by Velitzelos 1993, Velitzelos *et al.* 1981, 1999]. According to Selmeier & Velitzelos 2000 there were possible fagaceous findings (? *Fagus*, ? *Quercus*) in the western part of Lesbos (Eressos, Mesotopos. Tab. 1, p. 218]. In the same paper (Selmeier & Velitzelos 2000) there is the identification from fossil trunks from Mesotopos (Lesbos Island) belonging to *Quercoxylon* or to "evergreen *Quercus*" type and a proposal of grouping the findings belonging to *Quercoxylon* and *Lithocarpoxylon* as the fossil trunks of *Eotrigonobalanus furcinervis*.

This study supports the opinion of the latter scientists stating that the specimen DM 16 from Polichnitos belongs to a "*Quercoxylon*" of the "evergreen *Quercus* type" representing a possible part of a trunk of *Eotrigonobalanus furcinervis*. The identification of *E. furcinervis* leaves from this area in the future is possible and could establish the previously mentioned theory and contribute to the upgrade of our knowledge on the "evergreen oaks–type" evolution and distribution (Fig. 25).

The new finding of a fagaceous wood representative in the Island along with its description supports the hypothesis by Selmeier & Velitzelos (2000).

Plate 9

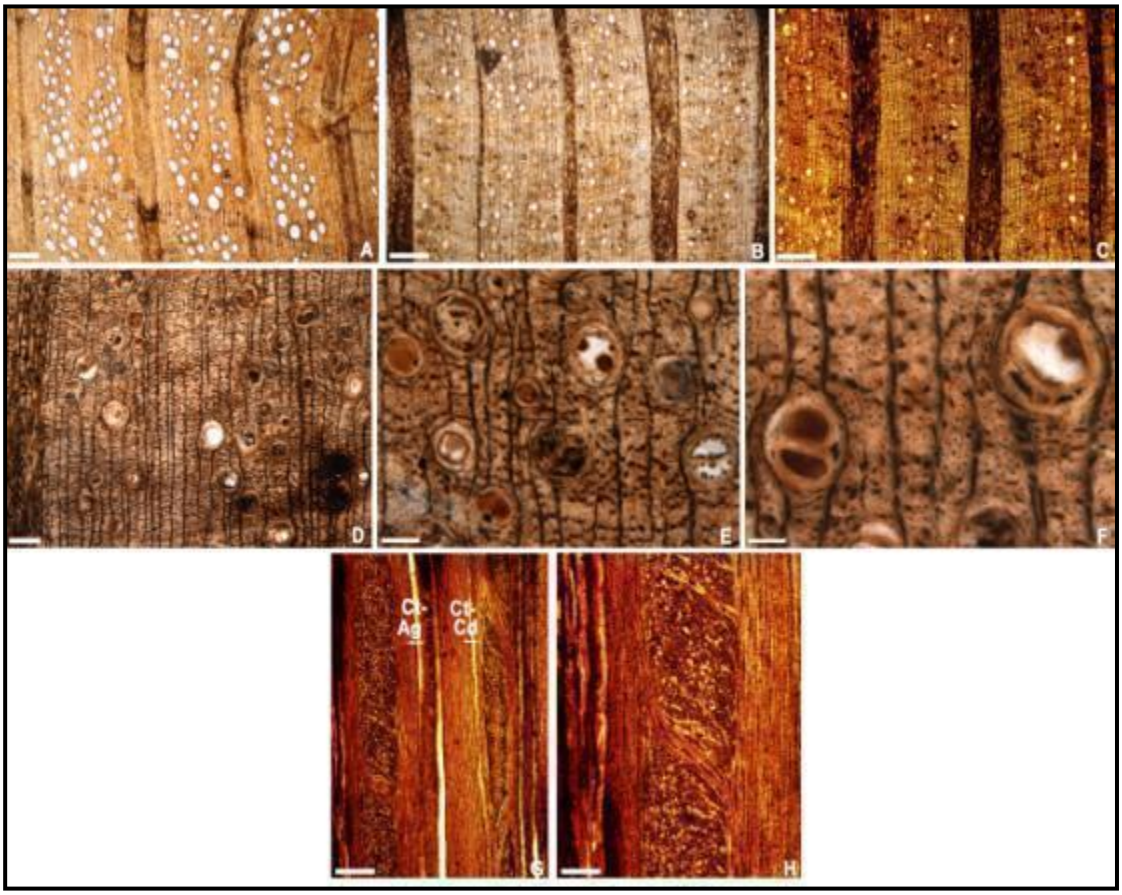


Plate 9 *Quercoxylon* Kräusel (DM 16: Pl. 9A–9H)

A, B, C: Distinct growth ring boundaries, semi-ring to diffuse porous, vessels exclusively solitary with more than 90% solitary vessels/sq. mm, outline of solitary vessels round to oval, vessels' arrangement: seems diagonal to dendritic (but it is not), tyloses, rays of two distinct sizes (uni/bi-seriate and multiseriate), axial parenchyma: apotracheal diffuse – in – aggregates. **D, E, F:** outline of solitary vessels round to oval, 55 to 150 µm, mean: 100 µm; radial diameter of the solitary vessels 80 to 170 µm, mean: 120 µm, tyloses, axial parenchyma: apotracheal diffuse – in – aggregates, vasicentric, scanty paratracheal and even confluent. **G:** Rays: aggregate (Ag), compact (Ct) and compact-compound (Cd) with a width of up to 320 µm and with a height of more than 1 mm (2000-11000 µm). **H:** Enlarged detail from Pl. 9G.

Scale bar = 50 µm in F; 100 µm in E; 250 µm in A, B, C, D, H; 500 µm in G. A, B, C, D ,E, F = TS; G, H = TLS. TS and TLS denote transversal and tangential longitudinal sections, respectively. Also, Ct denotes Compact, Cd denotes Compound and Ag denotes Aggregate rays.

2.3.1.7

Xylotype 5: DMDA 1 (7 slides), DMDA 9 (3 slides), DM 04 (3 slides), DM 09 (4 slides).

(Plate 10*A*, 10*I*)

Locality: Damandri *(*Southeastern Lesbos Island), Greece

Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics

Age: early Miocene

Macroscopic description. The dimensions of the dicotyledonous specimens from Damandri (in cm) are the following:

DMDA 1: 15 x 4 x 2 , DMDA 9: 22 x 18 x 10. Specimen DM 09 represents a very impressive fossil: is a branch enclosed inside the volcanic material. Unfortunately, we didn’t expect that it could be well preserved because even with naked eyes one can see cubes of volcanic material having replaced the internal structure of the branch.

Microscopic description. DMDA 1, DMDA 9: very bad preserved wood, which used to be an angiosperm.

DM 04: Bad preserved wood. Only vessels groupings, homocellular rays and all ray cells procubent could be seen. More slides are needed for its identification.

DM 09: Radial groups of vessels, heterocellular rays with long uniseriate extremities. More slides are needed for its identification.

Plate 10: Studied specimens from Damandri area and their dimensions (in cm).

A: DMDA 1: 15 x 4 x 2. Angiosperm. **B:** DMDA 2: 18 x 9 x 4. Angiosperm. **C:** DMDA 3: 11 x 3 x 2. **D:** DMDA 4: 11 x 3 x 2. **E:** DMDA 5: 9 x 7 x 3. **F:** DMDA 6 represented by three pieces: 6 x 7 x 3, 7 x 4 x 2, 4.5 x 2 x 2. Angiosperm. **G:** DMDA 7: 12 x 3.5 x 2. Angiosperm. **H:** DMDA 8 represented by four pieces: 11 x 3 x 2, 4 x 7 x 9, 10 x 7 x 3.5, 10 x 5 x 3. Conifer. **I:** DMDA 9: 22 x 18 x 10. Angiosperm. **J:** DMDA 10: 6 x 3 x 2. **K:** DMDA 11 represented by three pieces: DMDA 11.1: 15 x 8 x 5, DMDA 11.2: 9 x 6 x 5, DMDA 11.3: 10 x 6.5 x 5. Conifers. **L:** DMDA 12: 9 x 3 x 1.5. **M:** DMDA 13: 9 x 3 x 1.6. Angiosperm.

Plate 10


A
B
C
DMDA 3
D
DMDA 4
E
F
G
H
I
DMDA 9
J
DMDA 10
K
L
DMDA 12
M
DMDA 13
N
DMDA 14

2.3.1.8

Xylotype 6: DMPL 6 (5 slides).

(Plate 11*A*–11*F*)

Locality: Plakes *(*Southeastern Lesbos Island), Greece
Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics
Age: early Miocene

Macroscopic description. The dimensions of DMPL 6 specimen from Plakes area (in cm) are the following: 9 x 4 x 2.5.

Microscopic description. Numerous narrow growth rings, ring porous wood with big vessels and clusters (especially in latewood), vessels with tyloses (Plate 11*A*–11*C*), occurrence of sheath or tile cells connected to the rays (Plate 11*E*), rays not typically homogenous or heterogenous, coalescent apertures of alternate intervessel pits mimicking helical thickenings (Plate 11*D*, 11*E*).

What we could also note about this wood is the fact that the great number of the vessels along with the fact that there are so many narrow growth rings very close to one another can give us some details about the palaeoenvironment. This is an image of “flooded woods” according Schweingruber (2007, p. 93-96). It could also belong to a shrub or a branchwood of tree (Wheeler & Baas 1993).This is a very important specimen that requires more slides and study for its identification.

Plate 11

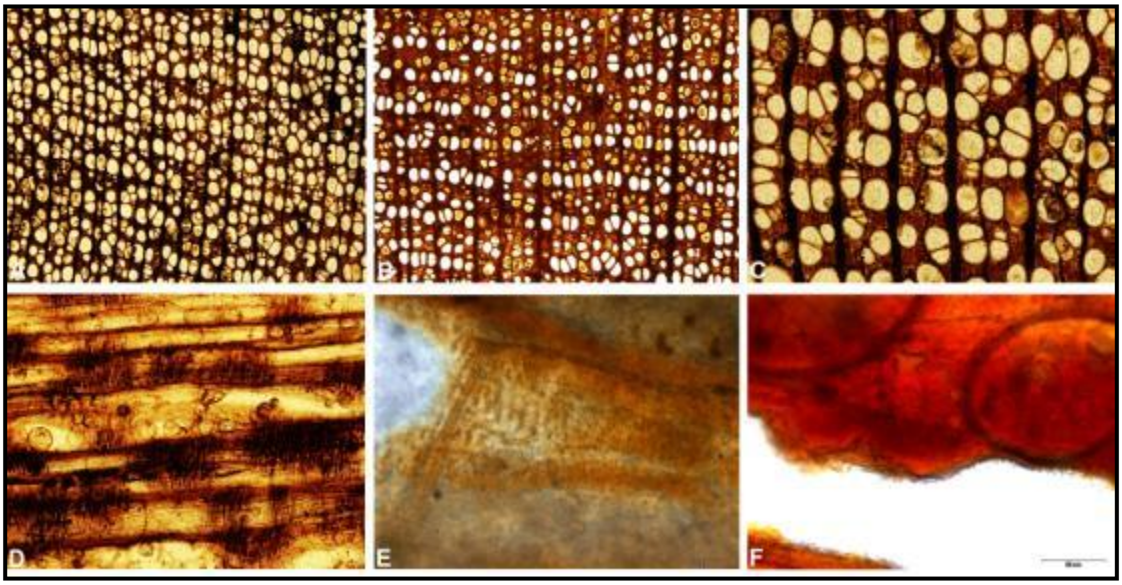


Plate 11 Angiosperm (DMPL 6).

A, B, C: Numerous narrow growth rings, ring porous wood with big vessels and clusters, tyloses. **D, E:** Coalescent apertures of alternate intervessel pits mimicking helical thickenings. **F:** Occurrence of sheath or tile cells connected to the rays.

The intension of this plate was to show the observed features, therefore the scale bar wasn't used in the majority of the figures. A, B, C = TS; D, E = RLS; F = TLS. TS, TLS, and RLS denote transversal, tangential longitudinal and radial longitudinal sections, respectively.

2.3.1.9

Xylotype 7: DM 15 (3 slides)

(Plate 12*A*–12*F*)

Locality: Plakes *(*Southeastern Lesbos Island), Greece

Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics

Age: early Miocene

Microscopic description. This specimen has distinct growth ring boundaries, marginal parenchyma, vessels solitary in dendritic pattern (or diagonal vessel aggregations) (Pl.12*A*–12*C*), simple and scalariform perforation plates, vascular tracheids (Pl. 12*D*–12*F*).

Plate 12

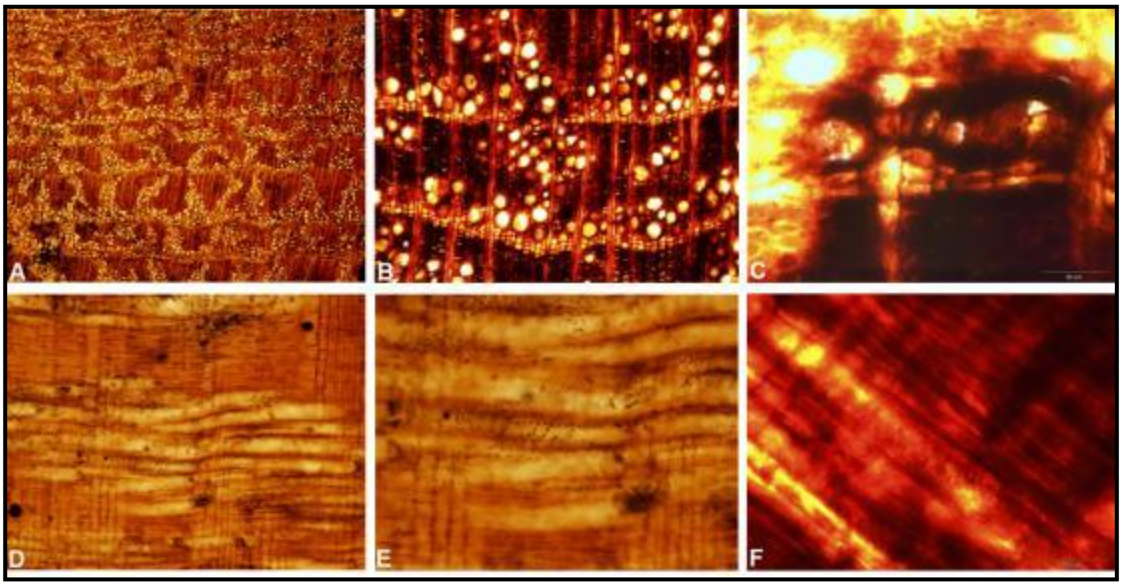


Plate 12 Angiosperm (DM 15)

A: Distinct growth ring boundaries, vessels in dendritic pattern. **B:** Distinct growth ring boundaries, marginal parenchyma, vessels solitary in dendritic pattern, tyloses and vascular tracheids. **C:** Marginal parenchyma and vascular tracheids. **D, E:** Simple and scalariform perforation plates and vascular tracheids. **F:** Scalariform perforation plates and vascular tracheids. The intension of this plate was to show the observed features, therefore the scale bar wasn't used in the majority of the figures. A, B, C = TS; D, E, F = RLS. TS, and RLS denote transversal and radial longitudinal sections, respectively.

2.3.1.10

Xylotype 8: **DM 08.1 (4 slides), DM 11 (4 slides), DM 11.1 (4 slides).**
(Plate 13*A*–13*F*).

Locality: Plakes *(*Southeastern Lesbos Island), Greece
Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics
Age: early Miocene

Macroscopic description. These specimens have a few centimeters size.

Microscopic description.
DM 08.1: Growth ring boundaries distinct, vessels' porosity: wood ring–porous to wood–semi–ring–porous, vessels solitary, in groups of 1–5 and rarely in clusters (Pl. 13*A*), solitary vessel outline rounded/oval, tyloses. Angiosperm with 2 kinds of rays (6–seriate and uni–biseriate and 15 μm width of paratracheal parenchyma. Intervessel pits alternate (Pl. 13*B*). Presence of filaments (Pl. 13*C*). Its detailed description requires better and more slides.

DM 11: Growth ring boundaries distinct, wood semi–ring porous with gradual transition between early–late wood, vessels usually in radial multiples up to 4 or more and some clusters (Pl. 13*D*), up to 4–seriate rays, vasicentric paratracheal parenchyma, intervessel pits alternate, minute to small (1.5–5 μm) (Pl. 13*E*), 1–3 cells ray width (spinkle like rays), simple perforation plates

DM 11.1: Growth ring boundaries distinct with a width of 12–22 μm, semi– ring–porous, early wood vessels' tangential diameter: 142 to 117 μm, tangential diameter of late wood vessels 64 – 77.1 μm, 27 vessels per mm^2, vessels groupings in radial multiples of 2–3 generally, with a variable proportion of solitary vessels and the presence of a few clusters, solitary vessel outline rounded to oval (Pl. 13*F*), tyloses (Pl. 13*G*). Polygonal alternate pits with reduced borders. Scalariform perforation plates with up to 10 bars. Intervessel pit size medium: 7–10 μm. Although a lot of features have been observed, more are required for a detailed identification of this sample.

Plate 13

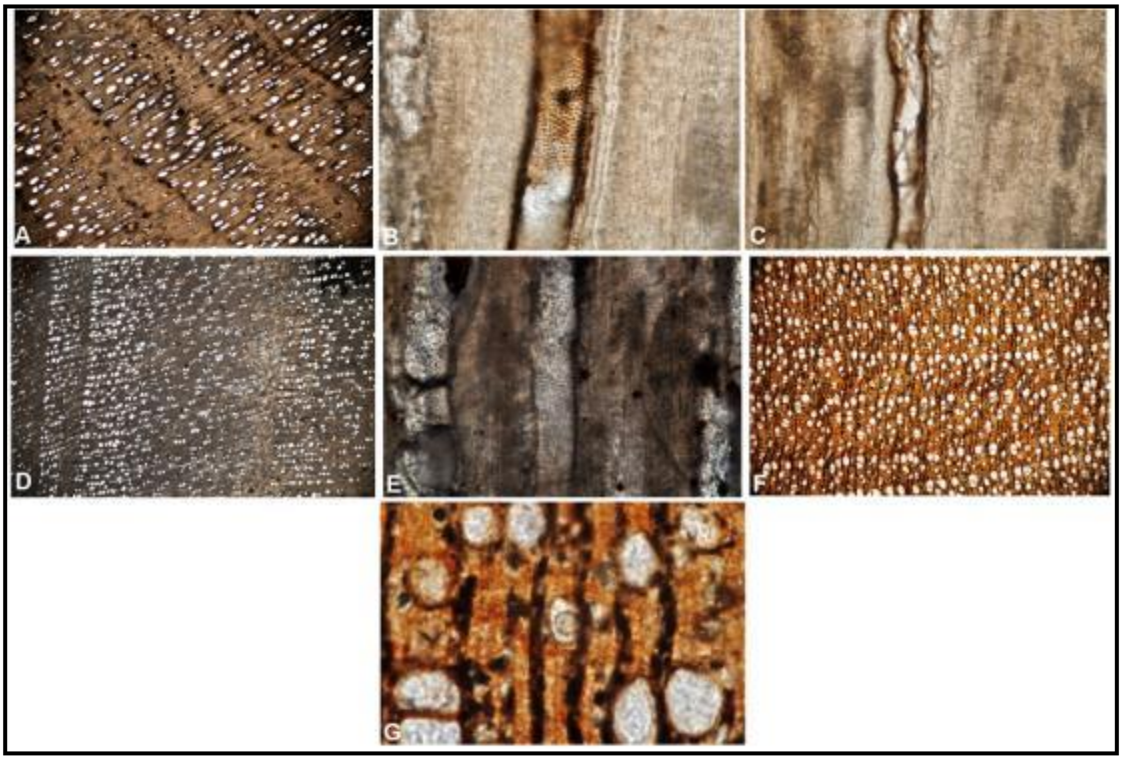


Plate 13 Angiosperm (DM 08.1: Pl. 13A, 13B, 13C; DM 11: Pl. 13D, 13E; DM 11.1: Pl. 13F, 13G)

A: Specimen DM 08.1: Distinct growth ring boundaries, vessels in multiples of up to 5, tyloses. **B:** Specimen DM 08.1: Alternate intervessel pits. **C:** Specimen DM 08.1: Occurrence of filaments. **D:** Specimen DM 11: Growth ring boundaries distinct, wood semi-ring porous, vessels usually in radial multiples up to 4 or more and some clusters. **E:** Specimen DM 11: Alternate intervessel pits. **F:** Specimen DM 11.1: Growth ring boundaries distinct, wood semi-ring porous, vessels groupings in radial multiples of 2-3 generally, with a variable proportion of solitary vessels and the presence of a few clusters. **G**: Specimen DM 11.1: Vessel tyloses.

The intension of this plate was to show the observed features, therefore the scale bar wasn't used in the majority of the figures. A, D, F, G = TS; E, = RLS; B, C = TLS. TS, RLS and TLS denote transversal, radial and tangential longitudinal sections, respectively.

Plate 14 Angiosperm (DM 02, DM 04).

A: Specimen DM 02: Distinct growth ring boundaries, vessels in multiples of up to 4. **B:** Specimen DM 02: Rays b-c-seriate. **C:** Specimen DM 02: body ray cells procumbent with up to 4 rows of upright and / or square marginal cells. The intension of this plate was to show the observed features; therefore the scale bar wasn't used in the majority of the figures. A = TS; C, = RLS; B = TLS. TS, RLS and TLS denote transversal, radial and tangential longitudinal sections, respectively.

2.3.1.11

Xylotype 9: DM 02 (5 slides), DM 04 (3 slides).

(Plate 14*A*–14*C*)

Locality: Hondrokouki *(*Southeastern Lesbos Island), Greece

Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics

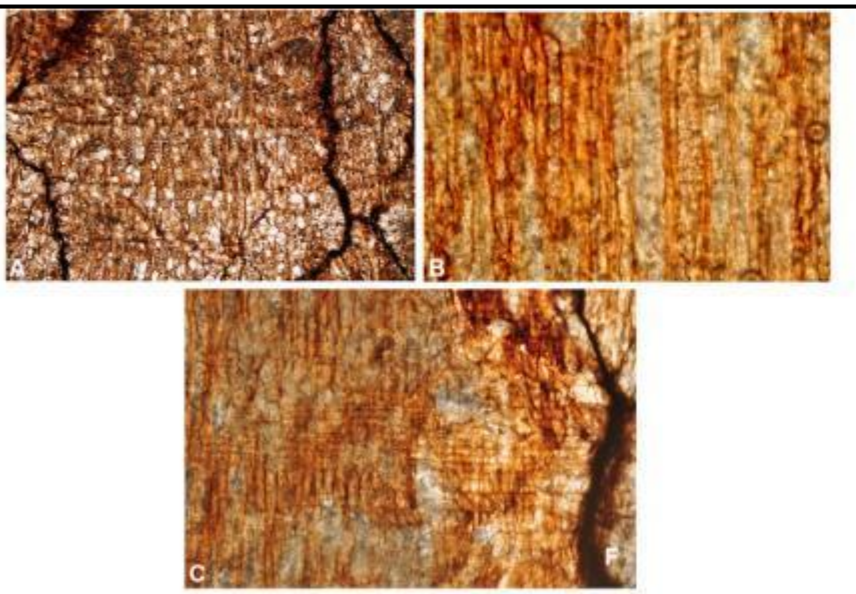
Age: early Miocene

Macroscopic description. Specimen DM 02 represents a very impressive fossil: is a branch enclosed inside the volcanic material. The dimensions of the dicotyledonous specimens from Hondrokouki are of some centimeters.

Microscopic description.

DM 02, DM 04: Wood semi–ring to diffuse porous, vessels solitary, in groups of 2–4 and in clusters (Pl. 14*A*), solitary vessel outline angular (maybe because of the preservation), rays up to 3–seriate (commonly biseriate) (Pl. 14*B*), septate fibres (?), body ray cells procumbent with mostly 1–2 to 2–4 rows of upright and / or square marginal cells (Pl. 14*C*), minute alternate vessel ray pits. Not well preserved for identification.

Plate 14



2.3.1.12

Xylotype 10: DMRO 28 (2 slides), DMRO 29 (3 slides), DM 14 (2 slides). (Plate 15*A*–15*E*)

Locality: Rogkada *(*Southeastern Lesbos Island), Greece

Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics

Age: early Miocene

Microscopic description.

DMRO 28: Diffuse porous wood, heterocellular rays, idioblasts in rays. Unfortunately this wood is not well preserved so the observation of the exact occurrence of idioblasts along with several anatomical features in infeasible and so is its identification.

DMRO 29: So badly preserved that it can only after hard work considered as an angiosperm.

DM 14: Distinct growth ring boundaries, axial parenchyma in marginal bands (Plate 15*A*), wood diffuse porous, vessels not in a particular pattern, in radial multiples of 3 or more, vessels' outline mostly oval but in some cases angular, scanty vasicentric paratracheal axial parenchyma, tyloses in vessels, idioblasts (oil &/or mucilage cells) of great size (Plate 15*A*–*E*) related to rays and to fibres, alternate ray pitting, body ray cells procumbent with 1–2 rows of upright and/or square marginal cells (Plate 15*B*, 15*D*, 15*E*), perforation plates simple and possibly reticulate or scalariform (Plate 15*C*–*E*). More slides are needed in order to be described in detail. The reason for which it wasn't related with the fossil Lauraceous findings is the great size of its idioblasts and the fact that more and better slides were needed.

Plate 15

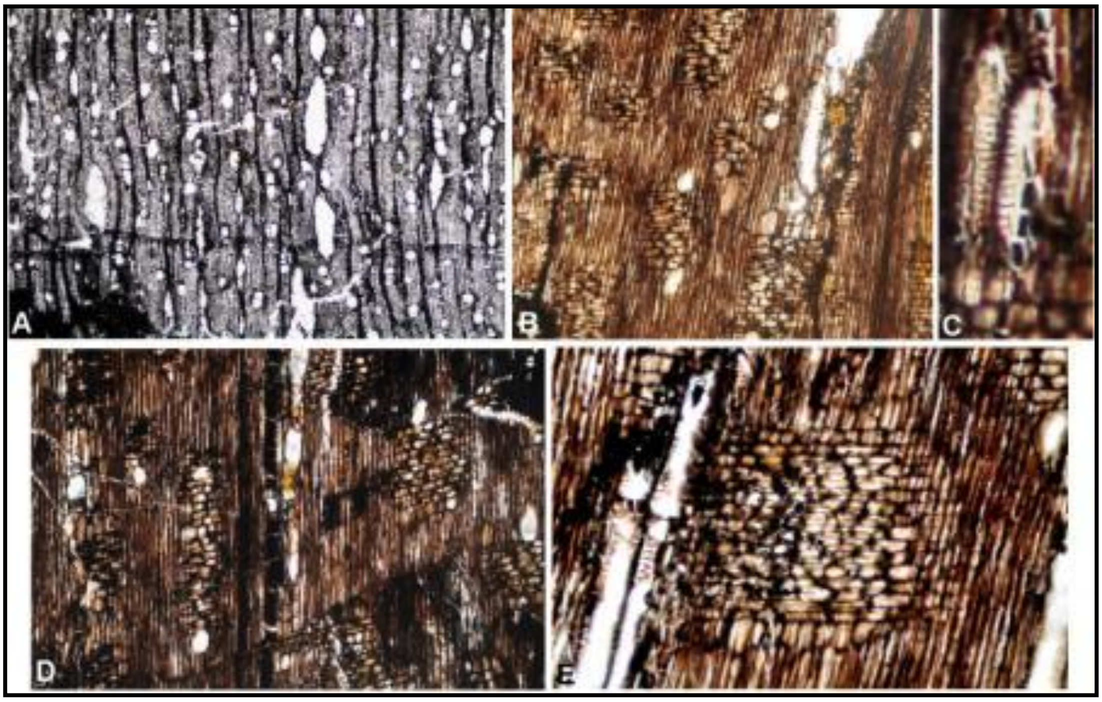


Plate 15 Angiosperm (DMRO 28, DMRO 29, DM 14).

A: Specimen DM 14: Distinct growth ring boundaries, axial parenchyma in marginal bands, idioblasts (oil &/or mucilage cells) of great size. **B:** Specimen DM 14: Body ray cells procumbent with 1-2 rows of upright and/or square marginal cells, idioblasts related to rays and possibly to fibers. **C:** Specimen DM 14: perforation plates reticulate or scalariform. **D:** Specimen DM 14: Body ray cells procumbent with 1-2 rows of upright and/or square marginal cells, idioblasts related to rays and possibly to fibers, perforation plates simple and possibly reticulate or scalariform. **E:** Specimen DM 14: Body ray cells procumbent with 1-2 rows of upright and/or square marginal cells, idioblasts related to rays and possibly to fibers, perforation plates simple and possibly reticulate or scalariform.

The intension of this plate was to show the observed features; therefore the scale bar wasn't used in the majority of the figures. A = TS; B, C, D, E = RLS. TS and RLS denote transversal and radial longitudinal sections, respectively.

Plate 16 Angiosperm (DMAL 16: Pl. 16A; DMAL 27: Pl 16B; DMAL 31: Pl. 16C, 16D)

A: DMAL 16: Distinct growth ring boundaries, vessels in dendritic pattern. **B:** DMAL 27: Distinct growth ring boundaries, vessels in dendritic pattern. **C:** DMAL 31: Distinct growth ring boundaries, vessels in dendritic pattern. **D:** DMAL 31: Idioblasts at the edges of the body ray cells. The intension of this plate was to show the observed features, therefore the scale bar wasn't used. A, B, C = TS; D = RLS. TS and RLS denote transversal and radial longitudinal sections, respectively.

2.3.1.13

Xylotype 11: DMAL 16 (2 slides), DMAL 27 (3 slides), DMAL 31 (3 slides), DM 13 (4 slides).

(Plate 28*P*, 28*AA*, Plate 29*C*, Plate 16*A*–16*D*)

Locality: Alonelia *(*Southeastern Lesbos Island), Greece

Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics

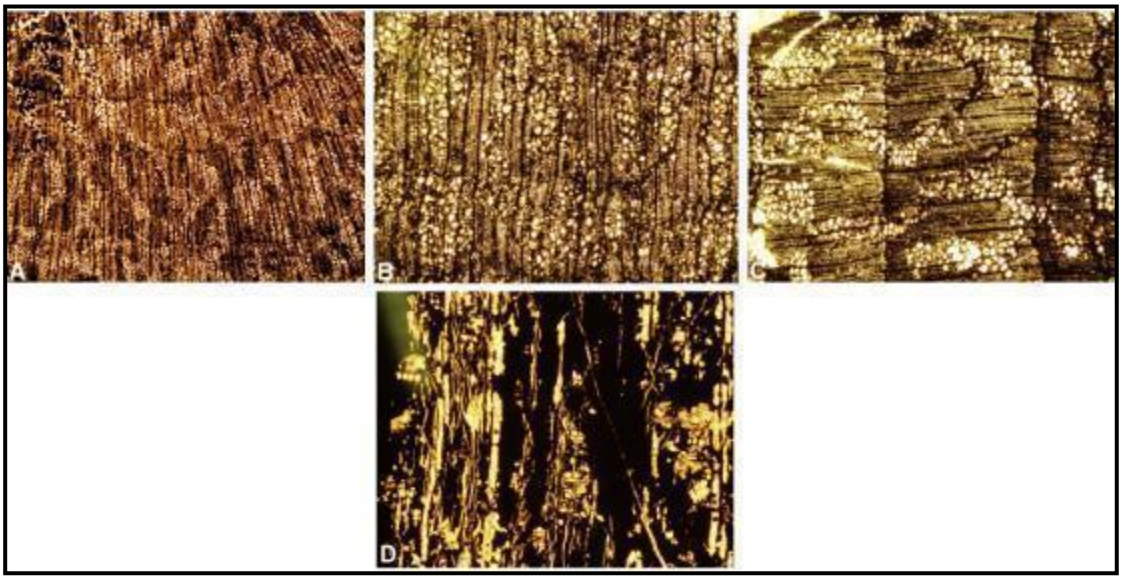
Age: early Miocene

Macroscopic description. The dimensions of the dicotyledonous specimens from Alonelia (in cm) are the following: DMAL 16: 11 x 7.5 x 3.5, DMAL 27: 8 x 8 x 3.8, DMAL 31: 15 x 4 x 2. The specimens are black in color and carbonized. DMAL 16 is medium heavy (in weight); DMAL 27 and DMAL 31 are very heavy.

Microscopic description: DMAL 16 (Pl. 16*A*), DMAL 27 (Pl. 16*B*) and DMAL 31 (Pl. 16*C*) have distinct growth ring boundaries, vessels in dendritic pattern and they contain idioblasts (oil &/or mucilage cells) (Pl. 16*D*). The latter characteristic occurs only in specific families. Most probably they are lauraceous representatives but the preservation was poor for a more specific identification.

DM 13 slides were problematic. New slides are needed for its identification.

Plate 16



2.3.2 Identification of coniferous wood ("Gymnosperm") from Lesbos Island

2.3.2.1

Family Pinaceae Lindley (1836)
Genus: *Cedroxylon* Kraus 1870
***Fossil Species: Cedroxylon lesbium* Kräusel 1919 (=*Peuce lesbia* Unger 1844)**
(4 slides)
(Plate 17*A–H,* Lesbos Island Fossil Flora Appendix)

Basionym:
1844 *Peuce lesbia* Unger

Nomenclature synonyms:
1848 *Pinites lesbius* Göpp. *in* Bronn, Band III, p. 976.

Description:

Transverse section: Nine distinct growth ring boundaries with a width from 0.4–1.2mm (mean: 0.8mm), transition from earlywood to latewood abrupt. The latewood is relatively wide and composed of eleven to nineteen cells, with a mean of fourteen cells. The standard deviation is 2.4. False rings are absent. Latewood tracheids thin–walled, torus well–defined disc–shaped (Pl. 17*A*, 17*B*), axial parenchyma in diffuse (and in some cases looks like in tangentially zonate) arrangement (Pl. 17*A*, 17*B*), resin canals absent.

Tangential section: axial parenchyma is present, transverse end walls smooth (Pl. 17*H*), the rays are very high, with more than 30 cells (Pl. 17*F*–17*H*) and up to biseriate in width (Pl. 17*F*–17*H*).

Radial section: Bordered pits in tracheids (Pl. 17*C*, 17*E*). The tracheids can be uniseriate but mainly they have 2 rows of (bi–seriate) bordered pits (tracheid pitting in radial walls biseriate), arrangement of tracheid pitting in radial walls opposite (occasionally seems alternate but it is due to the crowded pits), crassulae present, circular pits outline (Pl. 17*C*, 17*E*) of a diameter of 18 (15–20) μm, cross–field pitting piceoid up to taxodioid in between two growth rings (Pl. 17*D*) commonly arranged in horizontal rows of two pits per cross–field (but in some cases even 4, e.g. Pl. 17*D*). The uniseriate pits have a diameter of 20–27 μm (with the majority of them at 25 μm) and the biseriate pits have a diameter of 17–20 μm.

Microscopic study results: Coniferous trees from temperate and boreal regions usually have distinct growth ring boundaries and taxa from subtropical or higher altitude tropical regions may have more or less distinct growth ring boundaries (IAWA 2004). The fact that the ring series have a mean ring–width of 0.8mm indicates limited_seasonal growth (Fritts 1976). In general, the relative width of the growth rings is more–or–less equivalent to the number of cells per ring.

The standard deviation is low. This fact indicates that the data points tend to be very close to the mean, also called expected value. The standard deviation of ring width measurements is one method of deducing the variability of growing conditions during the life–time of a tree (Morgans 1999).

The presence of distinct growth rings in the studied specimen indicates that the climate in which the tree grew was seasonal. Measurements of the radial diameter of cells across individual rings show that the cells decrease in size quite rapidly towards the end of each ring, and the latewood may in some cases comprise up to nineteen cells (calculated using the method described by Creber and Chaloner 1984). The regional / local climatic conditions seem that had a dominant affect on the length of the growing season (ring width, latewood growth).

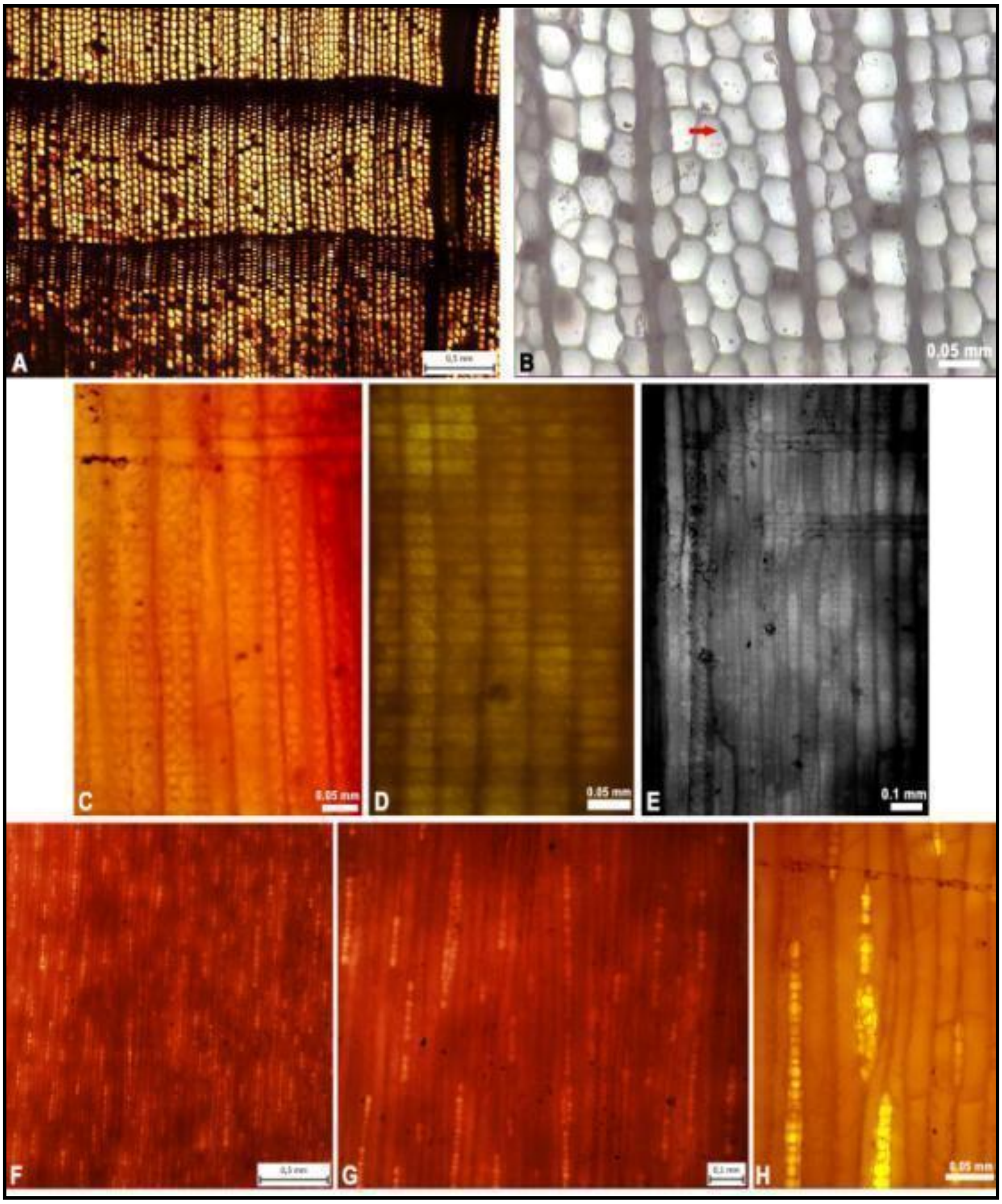
False rings are absent, so there weren't any water shortages during the growing seasons. Also, although this is a character with limited diagnostic value, an abrupt transition (within the same growth ring) as the one of the studied specimen, is characteristic for *Larix* spp., species of the "hard pines" group (*Pinus* spp., sect. Taeda), *Pseudotsuga* spp., and *Keteleeria* davidiana, IAWA 2004, p. 18].

Axial parenchyma is a regular feature of Cephalotaxaceae, Cupressaceae, and most Podocarpaceae (IAWA 2004) and not of Pinaceae.

History of the studied species: According to Unger's original description (1844, "Chloris protogaea", p. 37) *Peuce lesbia* had "growth rings of 0.5–2 mm distance, uni–biseriate pits, medullary rays consisted of 1–40 cells and no resin ducts". The only stratigraphic information which was given is that probably the specimen comes from a tertiary formation of Lesbos Island.

Our description is in accordance with Unger's since the distance between the growth rings is about 1 mm, the rays are up to biseriate and very high (with even more than 30 cells) and there are also no resin ducts.

Plate 17



The synonym *Cedroxylon lesbium* given to our fossil specimen leads us to investigate the similarities and differences with the genus *Cedroxylon*. According to Kraus (1870 in W.P.Schimper, A., p. 370) *Cedroxylon* is the abietineous wood without resin ducts and without parenchyma, with radial tracheids and abietineous pitting with two small pits on the cross field. It is similar with *Cupressinoxylon* in the arrangement of the pits on the tracheids and in the absence of resin–canals but differing in the occurrence of xylem–parenchyma. He underlined the fact that the identification of *Cedrus* nearest living relatives cannot be decided with certainty.

The synonym *Cedroxylon* for Lesbos wood was first used for the study of specimens from Lesbos by Fliche (1898) who had two samples in hand, only one of which was well preserved. According to his descriptions the width of the growth rings was about 2.5 mm at the first and 0.75–1.5mm at the second specimen, with rays' height consisting of 7–11 at the first and 5–13 cells at the second sample, and with the characteristics of *Cedroxylon*. He also observed that the disarrangement of the ray tracheids. This observation could indicate high compression during the fossilization, a characteristic for the not well preserved specimen.

Plate 17 *Cedroxylon lesbium* Kräusel

A: Distinct growth ring boundaries with a mean width of 0.8mm, transition from early- to late-wood abrupt, the latewood is wide and composed of eleven to nineteen cells, with a mean of fourteen cells, axial parenchyma in diffuse arrangement, no intercellular or traumatic canals or epithelial cells of wound ducts. **B:** Axial parenchyma in diffuse arrangement, no intercellular or traumatic canals or epithelial cells of wound ducts, latewood tracheids thin-walled, torus well-defined of disc-shaped (indicated by an arrow). **C:** Bordered pits in tracheids with tori preserved, biseriate tracheid pitting in radial walls, opposite arrangement of tracheid pitting in radial walls, crassulae present, circular pits outline. **D:** Taxodioid pits commonly arranged in horizontal rows of two pits per cross-field. **E:** Bordered pits in tracheids with tori preserved, biseriate tracheid pitting in radial walls, opposite arrangement of tracheid pitting in radial walls, crassulae present, circular pits outline. **F:** Rays very high, with more than 30 cells and up to biseriate in width. **G:** Uni- and biseriate rays very high (with even more than 30 cells). **H:** Transverse end walls of axial parenchyma smooth, uni- to biseriate rays.
A, B = TS; C-E = RLS, F-H = TLS. TS, TLS, and RLS denote transversal, tangential longitudinal and radial longitudinal sections, respectively.

Remarks on *Cedroxylon*: According to Schimper & Schenk (1890, p. 862) and Seward (1919) parenchyma is mostly representative at the latewood of *Cedroxylon* while in *Cupressinoxylon* is not limited. In Harland *et al.* (2007) there is a discussion about *Cedroxylon* and its first representatives: "*Cedroxylon* is the coniferous wood without either resin canals or conspicuous storage parenchyma. On the contrary, woods which are provided with abundant storage parenchyma are designated *Cupressinoxylon*. The pitting in both categories is opposite", in Jeffrey (1866, p. 349). In the same publication is stated that the xylem parenchyma can be in great amounts or completely absent depending on the *Cedroxylon* species and abietineous pitting. Seward (1919) believed that the character of the rays (instead of parenchyma) provides a more satisfactory distinction between *Cedroxylon* and *Cupressinoxylon*. Other characteristics of *Cedroxylon* include circular and separate (and if in more than one row, opposite) bordered pits (Seward 1919; Kräusel 1949; Morgans 1999). This characteristic is also seen in our specimen.

Seward (1919) summarizes the description of *Cedroxylon* giving the following characteristics: "Annual rings well marked, bordered pits on the radial walls of the tracheids usually circular and separate and if in more than one row, opposite, but in some species the Araucarian type of pitting also occurs, the pits being contiguous and alternate or sometimes arranged in stellate clusters. Xylem–parenchyma typically confined to the end of an annual ring, but sometimes absent; Medullary rays generally uniseriate and composed exclusively of parenchyma though horizontal tracheids may occur; Pits on all the walls of medullary–ray cells as in the Abietineae; On the radial walls there may be 1–6 apparently simple circular pits in the field. There are no resin–canals except as the result of injury".

According to Kräusel (1949) *Cedroxylon* has the following characteristics: pits on radial walls of tracheids circular and, where multiseriate, oppositely arranged, never typically araucarioid, normal wood without resin canals, spiral thickenings absent and abietineous ray pitting present.

In Lemoigne (1988, t.2, p. 157) there is a discussion on the distinction among *Brachyoxylon* Jeffrey, *Araucarioxylon* Kraus and *Cedroxylon* Kraus based on their wood anatomical features. According to Bamford & Philippe (2001) the latter three genera have been in many cases identified wrongly, so the occurrence of the genus *Cedroxylon* in Mesozoic is considered problematic.

The affinity of *Cedroxylon* by Nishida & Nishida (1986) with wood parenchyma absent (although in Nishida & Nishida 1986, fig. 7, the occurrence of parenchyma is clearly seen) is not in accordance with our our specimen.

Discussion about the generic name: Even if the generic name of our species is *Peuce* (it should have priority because it was the first one) or if it is *Cedroxylon* (probably it is more appropriate because of the ending –xylon referring to a fossil wood part) the problem remains the same. As it is stated with arguments in Philippe & Bamford (2008) and Bamford & Philippe (2001) both *Peuce* Lindley et Hutton (1832) and *Cedroxylon* Kraus (1870) would be better not to be used for Mesozoic woods.

Reconstruction of the habit & habitat: General Information from stratigraphy: Unfortunately the exact locality from where the fossil was found remains unknown. Fliche (1898) describes without giving further details 4 types of Cedroxyla among his findings from Ordymnos area (*Cedroxylon* type 1: samples No. 4, 31, *Cedroxylon* type 2: samples No 13–16, 23, *Cedroxylon* type 3: samples No 3, 18, 24–30, *Cedroxylon* type 4: sample No 8). From these only one is permineralized (*Cedroxylon* type 4: sample No 8) and the rest are lignitic. Taking into account that the lignitic horizon is located in Lapsarna we come to the hypothesis that he did 2 samplings. One was at the Lapsarna area which some millions years ago (most probably in Ottnangian stage, Mantzouka 2009, Vasileiadou & Zouros 2012) hosted a palaeolake with a general low palaeoaltitude and the other one, hosting the permineralized tree trunks, was at the higher altitudes of Ordymnos mountain where the Petrified Forest Park (Bali Alonia) is located. The fossils Franz Unger (Unger 1844) had in his disposal come very possibly from Sigri area (or from Sigri until Ordymnos area) because this area was easily accessible by boat and the fossils in hand are permineralized.

Comparisons with fossil species: In Unger's Chloris protogae (Unger, 1844, P.34, 37) apart from the brief wood anatomical description of *Cedroxylon lesbium* (= *Peuce lesbia*) there are descriptions also of other *Peuce* species which differ from *P. lesbia* because they don't have biseriate rays and in some of them there are also crystals. In other publications this species is described as the "strange conifer without resin ducts".

The fact that *Cedroxylon lesbium* (= *Peuce lesbia*) is identical with no other known fossil species is strange (at least up to now) but considering that there are already a lot of unique fossil woods in Lesbos {e.g. *Lesbosoxylon paradoxum* Süss & Velitzelos, *Lesbosoxylon pseudoparadoxum* Süss & Velitzelos, *Lesbosoxylon* *graciliradiatum* Süss & Velitzelos, *Lesbosoxylon diversiradiatum* Süss & Velitzelos, *Lesbosoxylon ventricosuradiatum* Süss & Velitzelos, *Taxodioxylon megalonissum* Süss & Velitzelos, *Tetraclinoxylon velitzelosi* Süss, *Thujoxylon antissum* Süss & Velitzelos, *Chimairoidoxylon lesboense* Süss & Velitzelos, *Ginkgoxylon lesboense* Süss, *Mirbellites lesbius* Unger [= *Juglandinium mediterraneum* (Unger 1850; Fliche 1898; Dupéron 1988) = *Juglandoxylon mediterraneum* (Unger) Kraus], *Brongniartites graecus* Unger} we can conclude that the existence of another “unique” wood of the lower Miocene wouldn’t be something extraordinary.

Comparison with the present day genus *Cedrus*:

According to Seward (1919) and as defined by Schimper and Schenk, *Cedroxylon* stands for fossil wood agreeing generally with that of recent species of *Cedrus*, *Abies* and *Tsuga* with or without vertical tracheids. The comparison between *Cedroxylon* and *Cupressinoxylon* has shown that in *Cedroxylon* the parenchyma is confined to the end of each year’s wood whereas in *Cupressinoxylon* the parenchyma is not so limited in its distribution, but a closer examination of different types of wood included in *Cedroxylon* had shown that the xylem parenchyma is an unsafe guide.

For the purposes of this PhD we had compared – not only via the published studies but also – under the microscope our fossil with the modern *Cedrus*, in order to check if this is its modern analogue. The aim of the comparison is to see clearly the similarities and the differences between *Cedroxylon* and *Cedrus* and investigate their possible relationship.

The reason for which we did this research was a paper by Qiao *et al.* (2007) according to which the divergence between *C. atlantica* (North African species) and *C. libani* and *C. brevifolia* (eastern Mediterranean species) happened between 23.49+3.55 to 18.81+1.25 Myr led Qiao *et al.* (2007) (Fig. 26) supported the hypothesis that the ancestor of Mediterranean cedars most probably reached South Europe during the Lower Miocene. The age that this paper referred to was pretty much the same with the age of the Petrified Forest of Lesbos. So, a possible “lost link” in *Cedrus* chain should be investigated.

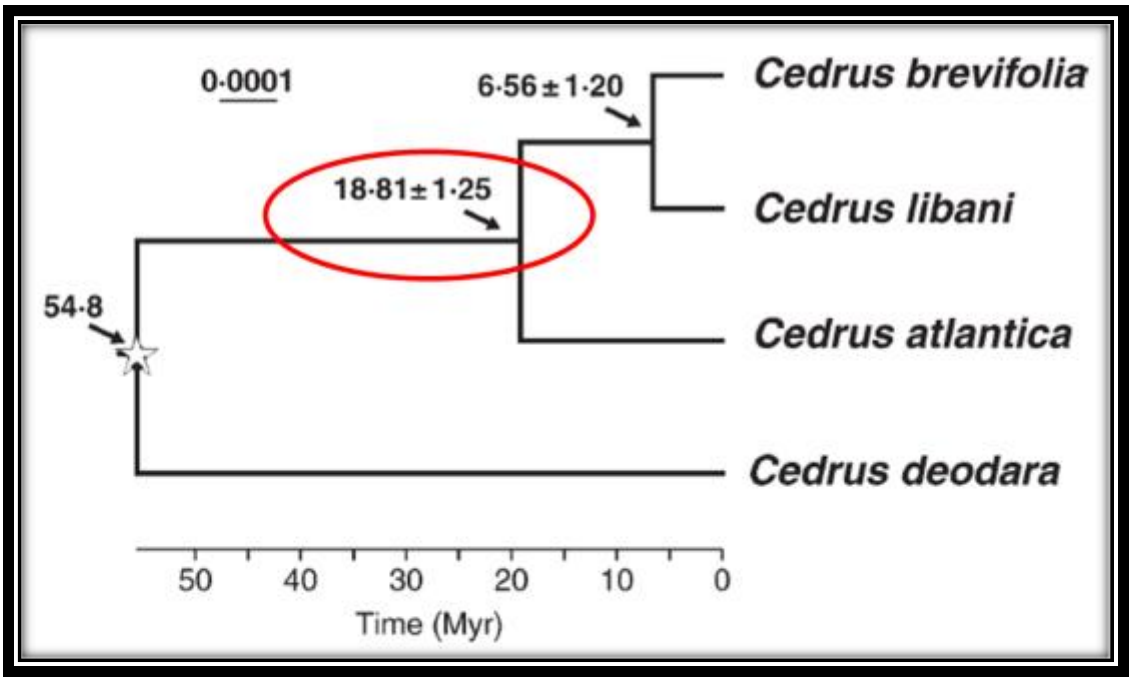


Fig. 26: A reconstructed *Cedrus* phylogeny (molecular clock) places the divergence between *C. atlantica* and the couple *C. libani*–*C. brevifolia* at about 19 Ma, significantly after that with *C. deodara* (ca. 55 Ma) and prior to that within the couple *C. libani*–*C. brevifolia* (ca. 7 Ma) (Qiao *et al.*, 2007).

According to Esteban & de Palacios (2009) *Cedrus* has: distinct growth rings, transition from early– to late wood abrupt or semi–abrupt or gradual, no resin canals, but both axial and radial traumatic resin canals (some authors have placed *Cedrus* in an intermediate position between *Pinus* and *Abies*), distinctly pitted horizontal walls of the ray parenchyma cells and nodular end walls, with not obvious indentures, partially biseriate rays are relatively frequent in species of Abietoideae but do not exceed 10% of the total, frequent ray tracheids, taxodioid or piceoid pitting, although cupressoid pitting has also been observed, alternate tracheid pitting, well defined disc–shaped tori in earlywood pitting, scalloped tori, some species have a warty layer in the inner layer of the secondary wall, frequent but sparse axial parenchyma, normally distributed along the growth ring boundaries in single cells in the first row of earlywood or in the last row of latewood, nodular transverse end walls of axial parenchyma, calcium oxalate crystals, ray tracheids (but without resin canals), occurrence of degenerated cells, ray parenchyma cells with horizontal walls with simple pits, tracheid pitting in radial walls normally uniseriate and when biseriate with opposite and rarely alternate arrangement. Unfortunately, the height of the rays of *Cedrus* was not a matter of discussion in this paper.

From Pinaceae *Cedrus*, *Abies* and *Tsuga* do not have normal vertical and horizontal resin ducts (Phillips 1941, Greguss 1955). *Keteleeria* and *Pseudolarix* do not produce normal resin ducts, only occasional traumatic cysts (Phillips 1941).

With the help of karyotype analysis Bou Dagher–Kharrat *et al.* (2001) subdivide the genus into three species, *C.atlantica*, *C. deodara* and *C. libani*, considering *C. brevifolia* as a variety of *C. libani.* According to Bou Dagher–Kharrat *et al.* (2007) *C. brevifolia*, the endemic taxon from the Island of Cyprus that is found in small and fragmented populations has showed one of the highest levels of diversity. This unexpected pattern of diversity and differentiation observed for *C. brevifolia* suggests a recent divergence rather than a relictual, declining population.

The fossil material in hand had been compared with the modern species of *Cedrus* under the microscope and with a species described by Crivellaro & Schweingruber (2013). The main difference with both the modern species described in Crivellaro & Schweingruber (2013) is the fact that in the fossil one there is axial parenchyma, but in the modern wood there is not. The present day *Cedrus* species have also scalloped tori and the fossil one doesn't seem so. The problem with the modern genus is the fact that there is not a study concerning the wood anatomy of its species (only for *C. libani–brevifolia*).

After deciding a further comparison with the modern cedars we got samples from small branches of *Cedrus deodara* (Plate 18: 1a, 1b), *Cedrus atlantica* (Plate 18: 2a, 2b, 2c), and *Cedrus libani* (Plate 18: 3a, 3b) from the trees growing in "Julia & Alexander N. Diomedes" Botanical Garden of the University of Athens.

Plate 18

Plate 18. Extant *Cedrus* species

1a: *Cedrus deodara* tree (trunk-branches) in its growth position. **1b:** *Cedrus deodara* branch with needles. **2a:** *Cedrus atlantica* tree (trunk-branches) in its growth position. **2b, c:** *Cedrus atlantica* branch with needles. **3a:** *Cedrus libani* tree (trunk-branches) in its growth position. **3b:** *Cedrus libani* branch with needles.

Observing their wood anatomy under the light and electron microscope we have found the following anatomical details:

1. *Cedrus deodara* (Roxburgh ex D. Don) G. Don (Himalayan Cedar): Transverse section: Growth ring boundaries distinct, transition from early wood to latewood abrupt, no axial parenchyma, no resin/traumatic canals observed(Pl. 19*A*); b. Radial section: Pitting in radial walls of earlywood tracheids is predominantly uniseriate (Pl. 19*B*–19*D,* 19*F*)*,* the pits are circular (outline), crassulae present (Pl. 19*D*), torus in earlywood tracheids' pits scalloped, (Pl. 19*A*–19*E*), cross–field pitting taxodioid and cupressoid (Pl. 19*F–19H*), even piceoid (Pl. 19*I*), number of pits per cross–field in earlywood 1–4 in perpendicular arrangement of up to 2 rows (Pl. 19*F*–19*H*). Unfortunately we didn't have a tangential section.

2. *Cedrus atlantica* (Endl.) G.Manetti ex Carrière: a. Transverse section: Pith preserved (Pl. 20*A*–20*B*). Growth ring boundaries distinct, transition from early wood to latewood abrupt (Pl. 20*A*–20*C*). No resin/traumatic canals. No axial parenchyma (Pl. 20*A*–20*D*). Latewood tracheids thick–walled (Pl. 20*D*); b. Radial section: Pitting in radial walls of earlywood tracheids is predominantly uniseriate, the pits are circular (Pl. 20*E*), torus in earlywood tracheids' pits scalloped, crassulae present (Pl. 20*F,* 20*G,* 20*J*), nodular end walls and well pitted horizontal walls, ray tracheids present (Pl. 20*K*), cross–field pitting taxodioid and cupressoid (Pl. 20*H,* 20*I,* 20*K*), number of pits per cross–field in earlywood 1–4 in perpendicular arrangement of up to 3 rows (Pl. 20*H,* 20*I,* 20*K*); c. Tangential section: rays exclusively uniseriate of up to 10–15 cells, no axial parenchyma observed (Pl. 20*L*–20*N*).

3. *Cedrus libani* A. Rich.(Lebanese/Asia Minor Cedar): a. Transverse section: Pith preserved (Pl. 21*A*), growth ring boundaries distinct, abrupt transition from early to latewood, latewood tracheids thick–walled, no axial parenchyma, no resin/traumatic canals observed (Pl. 21*A*–21*C*); b. Radial section: Pitting in radial walls of earlywood tracheids is uniseriate (in some cases seems to be bi–seriate), short tracheids, crassulae (Pl. 21*D,* 21*E*), torus in earlywood tracheids' pits scalloped (Pl. 21*F,* 21*G*), cross–field pitting taxodioid, number of pits per cross–field in earlywood 1–3 in perpendicular arrangement of two rows (Pl. 21*E,* 21*H,* 21*I*). Unfortunately we didn't have a tangential section.

Plate 19

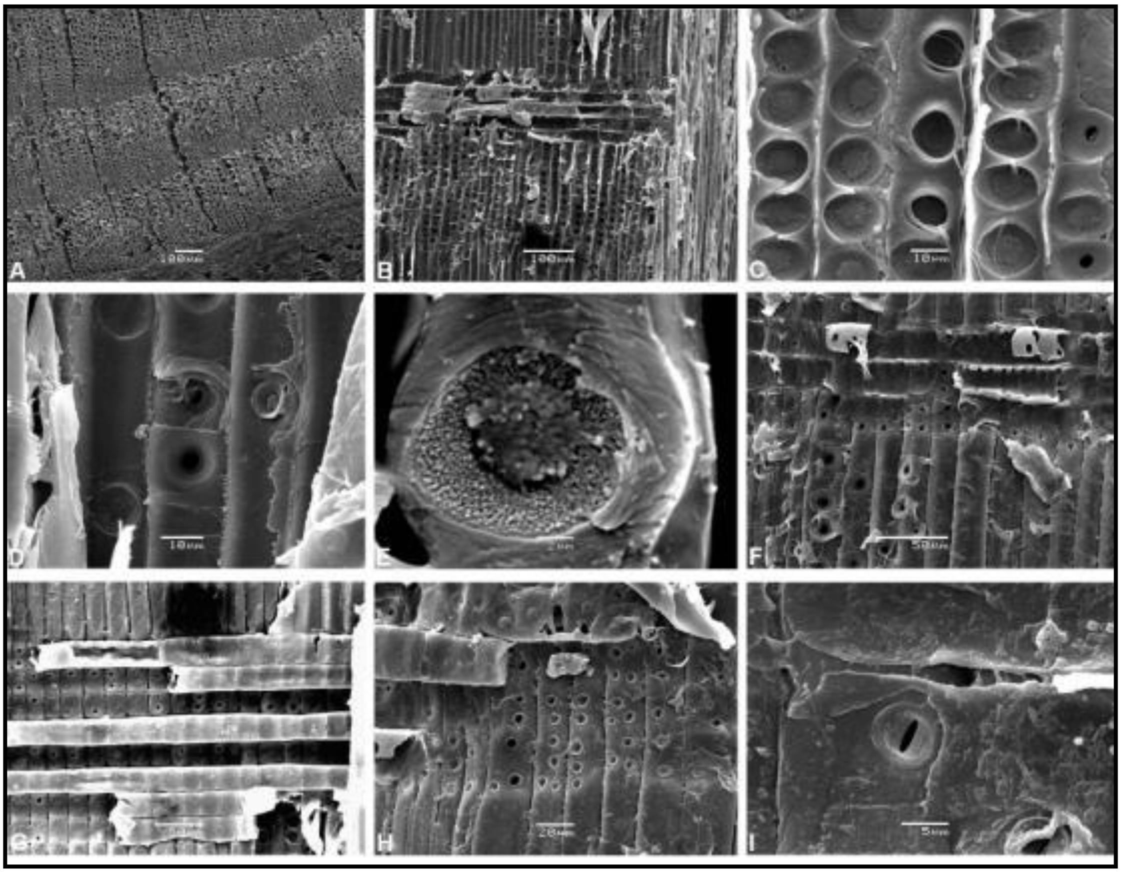
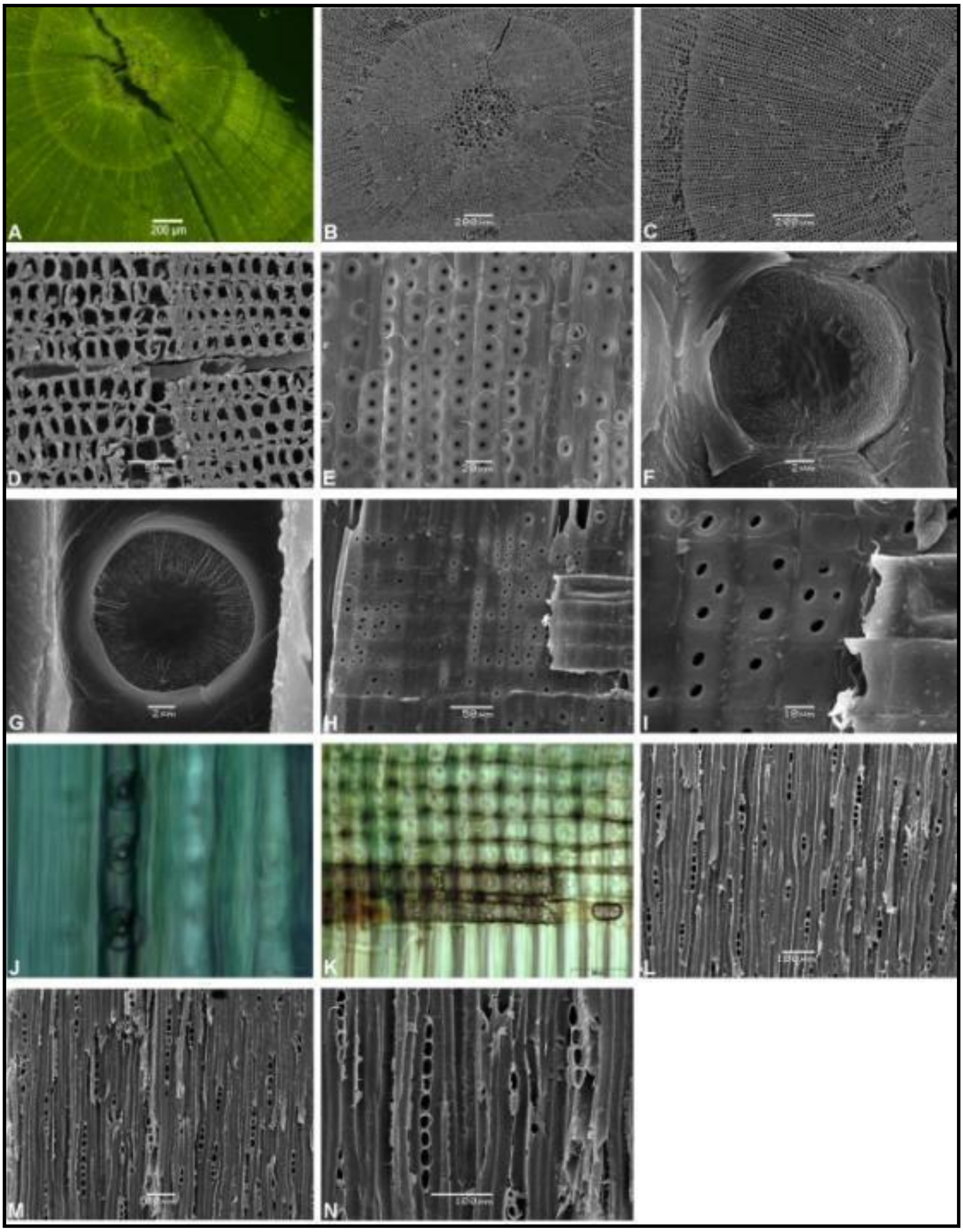


Plate 19 ***Cedrus deodara*** **(Roxburgh ex D. Don) G. Don (electron microscope images):**

A: Distinct growth ring boundaries, no axial parenchyma or resin/traumatic canals, transition from early wood to latewood abrupt. **B:** uniseriate pitting in radial walls of earlywood tracheids. **C:** uniseriate pitting in radial walls of earlywood tracheids, scalloped torus in earlywood tracheids' pits. **D:** uniseriate pitting in radial walls of earlywood tracheids, circular outline of pits, crassulae present, scalloped torus in earlywood tracheids' pits. **E:** Scalloped torus in earlywood tracheids' pits. **F:** uniseriate pitting in radial walls of earlywood tracheids, taxodioid and cupressoid cross-field pitting, 1-4 number of pits per cross-field in earlywood in perpendicular arrangement of up to 2 rows. **G:** Taxodioid and cupressoid cross-field pitting, 1-4 number of pits per cross-field in earlywood in perpendicular arrangement of up to 2 rows. **H:** Taxodioid and cupressoid cross-field pitting, 1-4 number of pits per cross-field in earlywood in perpendicular arrangement of up to 2 rows. **I:** Piceoid cross-field pitting. A = TS; B-I = RLS. TS, and RLS denote transversal and radial longitudinal sections, respectively.

Plate 20


A
200 µm
B
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C
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D
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100 µm

Plate 20 ***Cedrus atlantica*** **(Endl.) G.Manetti ex Carrière (electron and light microscope images):**

A: (Light microscope image): Pith preserved, distinct growth ring boundaries, no axial parenchyma or resin/traumatic canals, transition from early wood to latewood abrupt. **B:** (Electron microscope image): Pith preserved, distinct growth ring boundaries, no axial parenchyma or resin/traumatic canals, transition from early wood to latewood abrupt. **C:** (Electron microscope image): Pith preserved, distinct growth ring boundaries, no axial parenchyma or resin/traumatic canals, transition from early wood to latewood abrupt. **D:** (Electron microscope image): Pith preserved, distinct growth ring boundaries, no axial parenchyma or resin/traumatic canals, thick-walled latewood tracheids. **E:** (Electron microscope image): Uniseriate pitting of earlywood tracheids is predominantly, outline of tracheid pits circular, crassulae present. **F:** (Electron microscope image): Scalloped (= festooned) torus in earlywood tracheids' pits, crassulae present. **G:** (Electron microscope image): Scalloped (= festooned) torus in earlywood tracheids' pits. **H:** (Electron microscope image): Taxodioid and cupressoid cross-field pitting, 1-4 number of pits per cross-field in earlywood, the arrangement is perpendicular in up to 3 rows. **I:** (Electron microscope image): Taxodioid and cupressoid cross-field pitting, 1-4 number of pits per cross-field in earlywood, the arrangement is perpendicular in up to 3 rows. **J:** (Light microscope image): Scalloped (= festooned) torus in earlywood tracheids' pits. **K:** (Light microscope image): Taxodioid and cupressoid cross-field pitting, 1-4 number of pits per cross-field in earlywood, the arrangement is perpendicular in up to 3 rows, nodular end walls and well pitted horizontal walls, ray tracheids present. **L:** (Electron microscope image): Exclusively uniseriate rays of medium height (up to 10-15 cells), no axial parenchyma. **M:** (Electron microscope image): Exclusively uniseriate rays of medium height (up to 10-15 cells), no axial parenchyma. **N:** (Electron microscope image): Exclusively uniseriate rays of medium height (up to 10-15 cells), no axial parenchyma.

A-D = TS; E-K = RLS, L-N = TLS. TS, TLS, and RLS denote transversal, tangential longitudinal and radial longitudinal sections, respectively.

Plate 21

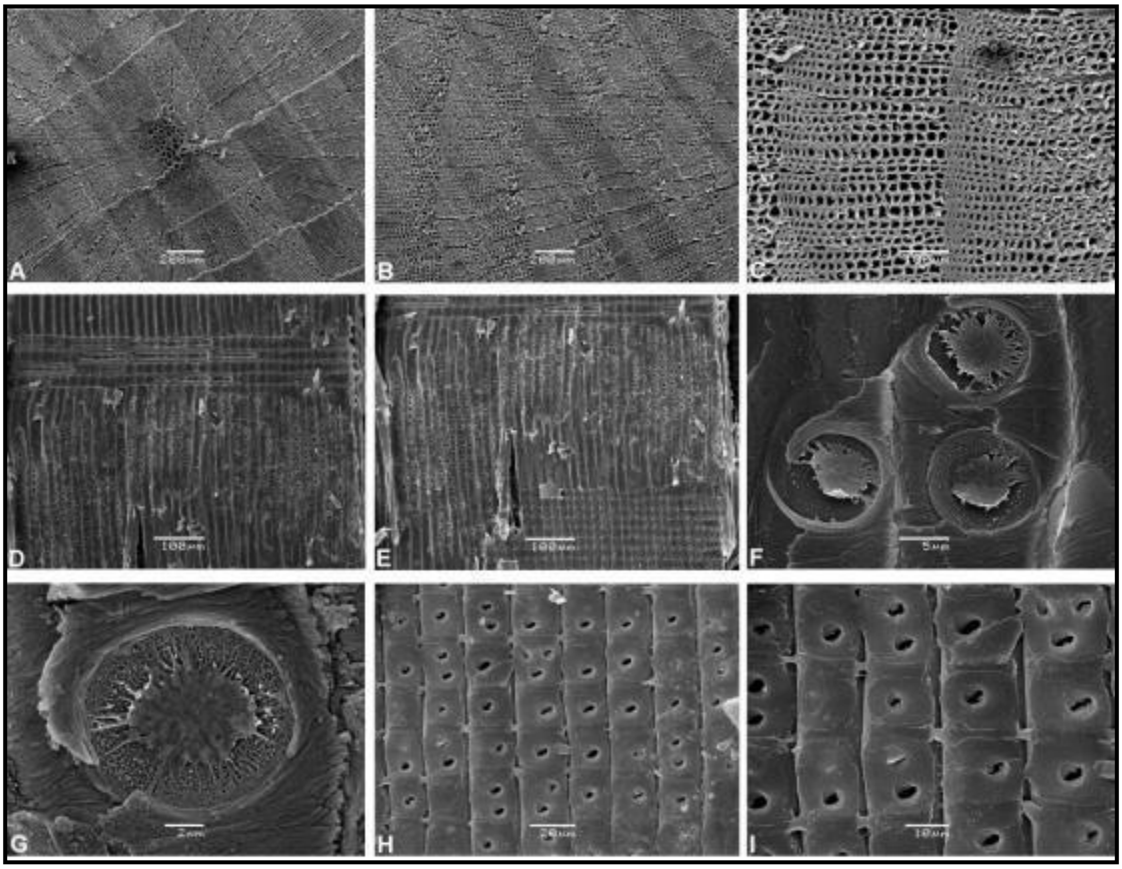


Plate 21 ***Cedrus libani*** **A. Rich. (electron microscope image):**

A: Preserved pith, distinct growth ring boundaries, no axial parenchyma or resin/traumatic canals, transition from early wood to latewood abrupt. **B:** Distinct growth ring boundaries, no axial parenchyma or resin/traumatic canals, transition from early wood to latewood abrupt, latewood tracheids thick-walled. **C:** Distinct growth ring boundaries, no axial parenchyma or resin/traumatic canals, transition from early wood to latewood abrupt, latewood tracheids thick-walled. **D, E:** Uniseriate (in some cases seems also biseriate) pitting in radial walls of earlywood tracheids, short tracheids, crassulae, cross-field pitting taxodioid, number of pits per cross-field in earlywood 1-3 in perpendicular arrangement of two rows. **F, G:** Scalloped (= festooned) tori in earlywood tracheids' pits. **H, I:** Cross-field pitting taxodioid, number of pits per cross-field in earlywood 1-3 in perpendicular arrangement of two rows.

A -C= TS; D-I = RLS. TS, and RLS denote transversal and radial longitudinal sections, respectively.

Results: Correlating the present day species of *Cedrus* with our fossil specimen we can see that there are differences concerning the axial parenchyma, the scalloped (= festooned) tori, the existence of ray tracheids (they are observed by Crivellaro & Schweingruber 2013), the end walls of the tracheids and the arrangement of the tracheid pits (uni– or biseriate) and of the bordered pits (in 1 up to 3 rows perpedicularly). These are the main characteristics which most probably lead us to the conclusion that *Peuce lesbia* is not related to modern *Cedrus* species.

Discussion: The studied sample represents a holotype or a part of the holotype hosted at the Natural History Museum of Vienna (Naturhistorisches Museum Wien) with the code: D 38 (Plate 22*A*–22*C*), and belongs to the Lesbos samples studied and identified by Franz Unger. Unger had identified and published his observations on the material from Lesbos Island in his Chloris protogaea (Unger, 1844, P.34, 37). In this publication there is also the original brief wood anatomical description of *Peuce lesbia*, with no illustration of its anatomy. The information about the locality is unknown, probably Sigri (Mpali Alonia) and there are no anatomical details and measurements. The fact that there is no illustration accompanying the description of the species is problematic (Kvaček, 2008a). No illustration and anatomy accompanied the renaming of the species as *Pinites lesbius* by Göppert in Bronn (1848). In 1898 Fliche studies and describes *Cedroxylon* sp. (nobody knows if they belonged to the same specimens that Unger had studied) lignitic and permineralized samples from the western part of Lesbos Island and more specific from Ordymnos seashore and NE part of Ordymnos (Fliche 1898, p.143, 148). Unfortunately there is no extended description of the specimen and no illustration of its anatomy again. Kräusel (1919, p. 191) gives the synonym of *Cedroxylon lesbium* KRAUS for *Peuce lesbia* UNGER for trees without parenchyma and resin ducts, quoted *Peuce lesbia* as the basionym The specimen that we examine doesn’t have resin ducts but it has parenchyma.

Until a further study and re–identification on all *Peuce lesbia* (= *Cedroxylon lesbium*) samples hosted by several museums throughout Europe is made, and although the basionym [=the legitimate, previously published name on which a new combination or name at new rank is based. ... (Art. 6.10) according to the International Code of Nomenclature for algae, fungi, and plants] *Peuce lesbia* Unger should be the official name for this fossil, we would like to keep the name *Cedroxylon lesbium* mainly because of the ending –xylon which is appropriate for the fossil wood genera.

Plate 22

Plate 22

A–C: The original material and the slides of *Peuce lesbia* (= *Cedroxylon lesbium*) hosted at the Natural History Museum of Vienna (Naturhistorisches Museum Wien) with the code: D 38.

2.3.2.2

***Xylotype 1:* DMDA 8 (3 slides), DMDA 11.1 (4 slides), DMDA 11.2 (4 slides).**
(Plate 10*H*, 10*K*; Plate 23*A*, 23*B*)

Locality: Southeastern Lesbos Island, Greece

Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics

Age: early Miocene

Macroscopic description. The dimensions of the coniferous specimens from Damandri (in cm) are the following:
DMDA 8: 11 x 3 x 2, 4 x 7 x 9, 10 x 7 x 3.5, 10 x 5 x 3, DMDA 11.1: 15 x 8 x 5, 9 x 6 x 5, 10 x 6.5 x 5, DMDA 11.2: 15 x 8 x 5, 9 x 6 x 5, 10 x 6.5 x 5.

Microscopic description. DMDA 8, DMDA 11.1, DMDA 11.2: Growth ring boundaries distinct, vessel groupings in radial multiples of up to 4, with almost absent clusters, no axial parenchyma and no pitting is observed. There are horizontal canals (ducts) very big, inside the rays (Pl. 23*B*). Axial and radial intercellular canals present (Pl. 23*A*).

Discussion: The occurrence of axial and radial intercellular canals should recall Pinaceae and most probably *Pinus*, but better slides from this specimen are required for a more precise identification.

Plate 23

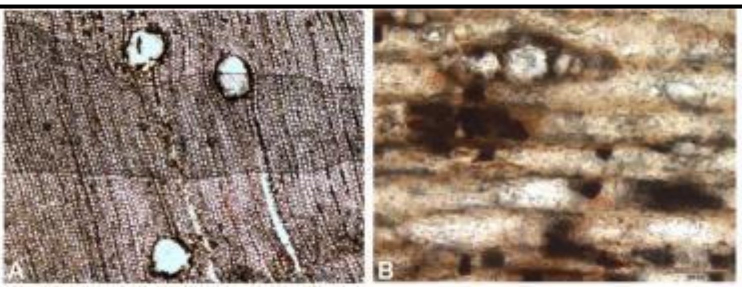


Plate 23 Conifer. **[Xylotype 1: DMDA 8 (3 slides), DMDA 11.1 (4 slides), DMDA 11.2 (4 slides)]**

A: Distinct growth ring boundaries, occurrence of intercellular canals. **B:** Horizontal canals inside the rays. A = TS; B = TLS. TS and TLS denote transversal and tangential longitudinal sections, respectively.

2.3.2.3

Xylotype 2: **DMPL 3 (3 slides), DM 08 (3 slides).**

(Plate 24*A*–24*C;* Plate 25*A*)

Locality: Plakes *(*Southeastern Lesbos Island), Greece

Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics

Age: early Miocene

Macroscopic description. The dimensions of the coniferous specimens from Plakes (in cm) are the following: DMPL 3: 6 x 10 x 5, 12 x 9.5 x 5, 11 x 3.5 x 5. These stems are silicified, light, whitish brown with distinct growth ring boundaries that can be seen with naked eye.

Microscopic description. DMPL 3 and DM 08 specimens have distinct growth ring boundaries, hypertrophic cells which give at least the impression that it belongs to a root (Pl. 24*A*, 24*B*), no axial parenchyma, no unusual cells, and no canals (horizontal ones).Rays uniseriate of a few cells height (Pl. 24*A*, 24*C*). It seems that it could have placqued resin canals (vertical axial normal) (Pl. 24*A, 24B*).

***Discussion*.** According their anatomical features, the samples DMPL 3, DM 08 most probably are related to Pinaceae. Such a hypothesis requires more slides in order to be proved.

Plate 24

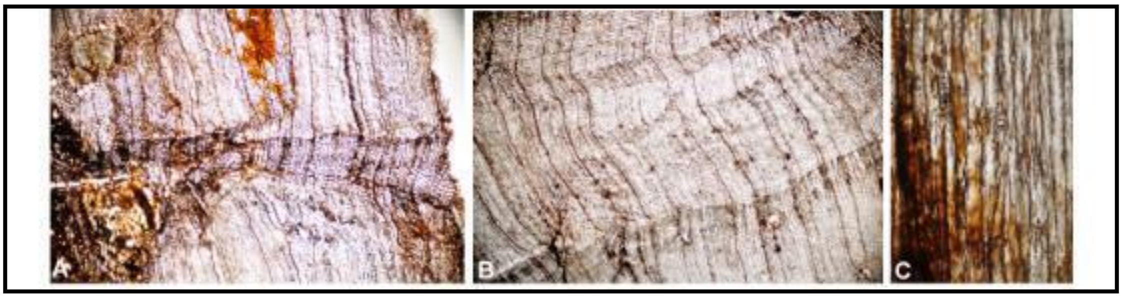


Plate 24 Conifer. [Xylotype 2: DMPL 3 (3 slides), DM 08 (3 slides)]

A, B: Specimen DM 08: Distinct growth ring boundaries, vertical resin canals. This specimen probably belongs to a root. **C:** Specimen DM 08: Rays uniseriate of a few cells height. The intension of this plate was to show the observed features; therefore the scale bar wasn't used in the majority of the figures. A, B = TS; C = TLS. TS and TLS denote transversal and tangential longitudinal sections, respectively.

Plate 25

Plate 25. Specimens from Plakes area.

A: Specimen DMPL 3 with the following dimensions (in cm): 6 x 10 x 5, 12 x 9.5 x 5, 11 x 3.5 x 5. Conifer. **B:** Specimen DMPL 4 represents several fragments of angiosperms. **C:** Specimen DMPL 5 represents a characteristic rock sample from the locality. **D:** Specimen DMPL 6 with the following dimensions (in cm): 9 x 4 x 2.5. Angiosperm. **E:** Specimen DMPL 7. Angiosperms.

2.3.2.4

Xylotype 3: DMRO 1 (3 slides), DMRO 2 (4 slides), DMRO 3.1 (1 slide), DMRO 3.2 (3 slides), DMRO 4 (4 slide), DMRO 5 (2 slides),DMRO 5.1 (1 slide), DMRO 6 (5 slides), DMRO 7 (3 slides), DMRO 8 (4 slides), DMRO 9 (4 slides), DMRO 10 (3 slides), DMRO 11 (3 slides), DMRO 12 (3 slides), DMRO 13 (3 slides), DMRO 14 (3 slides), DMRO 15 (3 slide), DMRO 16.1 (2 slides), DMRO 16.2 (5 slides), DMRO 17 (3 slides), DMRO 18 (2 slides), DMRO 18.1 (3 slides), DMRO 18.2 (1 slide), DMRO 19.1 (3 slides), DMRO 19.2 (3 slides), DMRO 20 (3 slides), DMRO 22 (4 slide), DMRO 23 (3 slides), DMRO 24 (2 slide), DMRO 25 (3 slides), DMRO 26 (3 slides), DMRO 27 (3 slides),DMRO 30 (3 slides), DM 03 (2 slides), DM 06 (1 slide), DM 06.1 (5 slides), DM 07 (2 slides), DM 14.1 (1 slide).

(Plate 26*A*–26*Q*; Plate 27*A*–27*J*)

Locality: Rogkada *(*Southeastern Lesbos Island), Greece

Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics

Age: early Miocene

Macroscopic description. The dimensions of the coniferous specimens from Rogkada (in cm) are the following:

DMRO 1: 23 x 17 x 13, DMRO 2: 20 x 18 x 18, DMRO 3.1: 21 x 9 x 8, DMRO 3.2: 6.5 x 3.5 x 3, DMRO 4: 27 x 22 x 8.5, DMRO 5: 25 x 16 x 9, DMRO 6: 23 x 18 x 14, DMRO 7: 29 x 15 x 6, DMRO 8: 27 x 19 x 13, DMRO 9: 23 x 14 x 6, 19 x 9 x 6, 13 x 12 x 9, DMRO 10: 23 x 12 x 6, 29 x 9.5 x 4.5, DMRO 11: 26 x 5 x 11, DMRO 12: 24 x 14 x 9, DMRO 13: 30 x 12 x 9, 31 x 12 x 5.5, DMRO 14: 19 x 10 x 6, 18 x 7.5 x 5, 16 x 7 x 10, 18 x 7 x 5.5, 18 x 10 x 5.5, DMRO 15: 12 x 11 x 5, 11 x 5.5 x 6, DMRO 16.1: 23 x 10 x 7, DMRO 22: 25 x 12 x 4, 18 x 6 x 8, 17 x 7.5 x 5, 19.5 x 5 x 2.5, 18 x 7 x 5, DMRO 26: 230 x 100.

Microscopic description.

DMRO 14: Numerous growth ring boundaries distinct (seen with naked eye as well). Abrupt transition between early and latewood tracheids. Nothing more could be seen. Although the identification is infeasible this sample provides as with information about the palaeoenvironment. Most probably this specimen belongs to a root or to a conifer from a flooded area because of the numerous transitions of its growth (Schweingruber 2007, p. 93-96) or even to a dwarf conifer (Baas 1984).

DMRO 26: This is the fossil tree which is hosted at the church of Ampeliko village. From the same area (Rogkada or Rougada) in 1994 by Professor E.

Velitzelos, found a fossil trunk. This trunk was studied by Süss & Velitzelos and identified as *Taxaceoxylon biseriatum*. According to the latter authors (Süss & Velitzelos 1994a) *Taxaceoxylon* Kräusel & Jain (1963) fossil woods have simple (homogeneous) rays, tracheids with spiral thickenings and mostly round, bordered pits arranged in ane or two rows, as the present day Taxaceae representatives.

Our observations on DMRO 26 sample include the following features: Growth ring boundaries distinct, transition from earlywood to latewood abrupt, latewood tracheids thin–walled, axial parenchyma diffuse, transverse end walls of axial parenchyma cells smooth, no resin canals, rays uni– and partly b–c– seriate multi–celled (with 15 cells), bordered pits diameter: 0,2–0,3 mm, there are no callitroid (spiral) thickenings. The cross field pits, their arrangement along with the rays and the rest of the anatomical features of this wood are representatives of *Taxodioxylon* wood type

DMRO 27: Growth ring boundaries distinct. Most probably no resin canals. Rays uniseriate short (usually 5-cell high). Nothing more could be seen.

DMRO 30: Numerous growth ring boundaries distinct. Abrupt transition between early and latewood tracheids. Nothing more could be seen.

DM 03: very bad preserved wood. Distinct growth ring boundaries, very high rays, axial parenchyma, but nothing more could be seen.

DM 06: Growth ring boundaries distinct, but not well preserved sample.

DM 06.1: very bad preserved sample. The only features observed are: axial parenchyma and rays.

DM 07: Distinct growth ring boundaries, existence of abundant axial parenchyma, intermediate (opposite–alternate) pitting which recalls protopinoid pitting (= this term was used for a transitional type of radial pitting: between Araucarioid and Abietoid) by Süss, b–seriate tracheid pitting, cross field pitting Taxoidioid and Cupressoid. More and better slides are required for a detailed identification of this specimen.

More and better slides are required for the detailed description of the rest of the specimens from Rougkada area.

Plate 26. Specimens from Rogkada area.

A: Specimen DMKO 1 with the following dimensions (in cm): 31 x 21 x 11. Angiosperm. **B:** Specimen DMRO 1 with the following dimensions (in cm): 23 x 17 x 13. Conifer. **C:** Specimen DMRO 2 with the following dimensions (in cm): 20 x 18 x 18. Conifer. **D:** Specimen DMRO 3 represents two samples with the following dimensions (in cm): 21 x 9 x 8, 6.5 x 3.5 x 3. Conifer. **E:** Specimen DMRO 4 with the following dimensions (in cm): 27 x 22 x 8.5. Conifer. **F:** Specimen DMRO 5 with the following dimensions (in cm): 25 x 16 x 9. Conifer. **G:** Specimen DMRO 6 with the following dimensions (in cm): 23 x 18 x 14. Conifer. **H:** Specimen DMRO 7 with the following dimensions (in cm): 29 x 15 x 6. Conifer. **I:** Specimen DMRO 8 with the following dimensions (in cm): 27 x 19 x 13. Conifer. **J:** Specimen DMRO 9 represents three remnants with the following dimensions (in cm): 23 x 14 x 6, 19 x 9 x 6, 13 x 12 x 9. Conifer. **K:** Specimen DMRO 10 represents three remnants with the following dimensions (in cm): 23 x 12 x 6, 29 x 9.5 x 4.5, 26 x 5 x 11. Conifer. **L:** Specimen DMRO 11. Conifers. **M:** Specimen DMRO 12 with the following dimensions (in cm): 24 x 14 x 9. Conifer. **N:** Specimen DMRO 13 represents two remnants with the following dimensions (in cm): 30 x 12 x 9, 31 x 12 x 5.5. Conifer. **O:** Specimen DMRO 14 represents five remnants with the following dimensions (in cm): 19 x 10 x 6, 18 x 7.5 x 5, 16 x 7 x 10, 18 x 7 x 5.5, 18 x 10 x 5.5. Conifer. **P:** Specimen DMRO 15 represents two remnants with the following dimensions (in cm): 12 x 11 x 5, 11 x 5.5 x 6. Conifer. **Q:** Specimen DMRO 16 with the following dimensions (in cm): 23 x 10 x 7. Conifer.

Plate 26

Plate 27

Plate 27 Specimens from Rogkada area.

A: Specimen DMRO 17. 6 pieces of Conifer fragments. **B:** Specimen DMRO 18. 14 pieces of Conifer fragments. **C:** Specimen DMRO 19. 36 pieces of Conifer fragments. **D:** Specimen DMRO 20. 16 pieces of Conifer fragments. **E:** Specimen DMRO 21. 14 pieces of Conifer fragments. The one examined has the following dimensions (in cm): 30 x 16 x 7. **F:** Specimen DMRO 22 with the following dimensions (in cm): 25 x 12 x 4, 18 x 6 x 8, 17 x 7.5 x 5, 19.5 x 5 x 2.5, 18 x 7 x 5. Conifer. **G:** Specimen DMRO 23. 5 pieces of Conifer fragments. **H:** Specimen DMRO 24. 16 pieces of Conifer fragments. **I:** Specimen DMRO 25 with the following dimensions (in cm): 160 x 85. Conifer. **J:** Specimen DMRO 26 represents a tree trunk found in Rogkada twenty years ago by Prof. E. Velitzelos and hosted at the church of the village Ampelikon. The dimensions (in cm) of this stump are the following: 230 x 100. Conifer.

2.3.2.5

Xylotype 4: DMAL 1 (4 slides), DMAL 2 (3 slides), DMAL 3 (3 slides), DMAL 4 (4 slides), DMAL 5.1 (3 Slides), DMAL 5.2 (3 slides), DMAL 6 (3 slides), DMAL 7 (3 slides), DMAL 11 (3 slides), DMAL 13 (3 slides), DMAL 18 (3 slides), DMAL 19 (3 slides), DMAL 20 (3 slides), DMAL 21 (2 slides), DMAL 22 (2 slides), DMAL 25 (2 slides), DMAL 26 (2 slide), DMAL 28 (3 slides), DMAL 32 (2 slides), DMAL 34 (5 slides), DMAL 35 (2 slides), DMAL 37 (3 slides), DMAL 40 (3 slides), DM 01 (4 slides), DM 12 (2 slides), DM 13.1 (3 slides).

(Plate 28*A*–28*G*, 28*K*, 28*M*, 28*R*–28*V*, 28*Y*–28*Z*, 28*BB*; Plate 29*D*, 29*F*, 29*G*, 29*I*, 29*L*)

Locality: Alonelia *(*Southeastern Lesbos Island), Greece

Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics

Age: early Miocene

Macroscopic description. The dimensions of the coniferous specimens from Alonelia (in cm) are the following:

DMAL 1: 25 x 15 x 9, DMAL 2: 19 x 18 x 12, DMAL 3: 20 x 15.5 x 12, DMAL 4: 24 x 19 x 13, DMAL 5: 28 x 18 x 11.5, DMAL 6: 28 x 18 x 11.5, DMAL 7: 43 x 37 x 25, DMAL 11: 25 x 12 x 13, DMAL 13: 12.5 x 11 x 7.5, DMAL 18: 9.5 x 7 x 5.5, DMAL 19: 5.5 x 3 x 3.5, DMAL 20: 6.5 x 4 x 2.5, DMAL 21: 19 x 10 x 9, DMAL 22: 10 x 10 x 9, DMAL 25: 10 small pieces, DMAL 26: 24 x 14 x 10, DMAL 28: 23 x 20 x 11, DMAL 32: 23 x 15 x 9.5, DMAL 34: 11 x 8.5 x 6, DMAL 35: 11.5 x 6.5 x 9. DMAL 37: 7 x 7.5 x 6, DMAL 40: 17.5 x 15 x 12.

Microscopic description. More and better slides are required for the detailed description and identification of the specimens of Alonelia fossiliferous site.

DM 01: not well preserved. Conifer with uniseriate rays.

DM 12: Occurrence of pinoid–fenestroid cross field pits, ray tracheids and horizontal intercellular canals, dentation of radidal tracheids can be seen. It represents most probably a Pine tree (Pinus) with pinoid pits.

DM 13.1: cupressoid cross–field pits, probably no axial parenchyma.

Plate 28. Specimens from Alonelia area.

A: Specimen DMAL 1 with the following dimensions (in cm): 25 x 15 x 9. Conifer. **B:** Specimen DMAL 2 with the following dimensions (in cm): 19 x 18 x 12. Conifer. **C:** Specimen DMAL 3 with the following dimensions (in cm): 20 x 15.5 x 12. Conifer. **D:** Specimen DMAL 4 with the following dimensions (in cm): 24 x 19 x 13. Conifer. **E:** Specimen DMAL 5 with the following dimensions (in cm): 28 x 18 x 11.5. Conifer. **F:** Specimen DMAL 6 with the following dimensions (in cm): 28 x 18 x 11.5. Conifer. **G:** Specimen DMAL 7 with the following dimensions (in cm): 43 x 37 x 25. Conifer. **H:** Specimen DMAL 8 with the following dimensions (in cm): 45 x 40 x 26. Conifer. It represented the same tree with DMAL 6 that’s why it wasn’t studied microscopically. **I:** Specimen DMAL 9 with the following dimensions (in cm): 15 x 12 x 7. Conifer. **J:** Specimen DMAL 10 with the following dimensions (in cm): 12 x 7 x 9.5. Conifer. It represented the same tree with DMAL 13 that’s why it wasn’t studied microscopically. **K:** Specimen DMAL 11 with the following dimensions (in cm): 25 x 12 x 13. Conifer. **L:** Specimen DMAL 12 with the following dimensions (in cm): 20 x 14 x 10. Conifer. It represented the same tree with DMAL 13 that’s why it wasn’t studied microscopically. **M:** Specimen DMAL 13 with the following dimensions (in cm): 12.5 x 11 x 7.5. Conifer. **N:** Specimen DMAL 14 with the following dimensions (in cm): 13 x 9.5 x 13. Conifer. It wasn’t cut for microscopical study because of its preservation. **O:** Specimen DMAL 15 with the following dimensions (in cm): 23 x 8 x 9. Conifer. It wasn’t cut for microscopical study because of its preservation. **P:** Specimen DMAL 16 with the following dimensions (in cm): 11 x 7.5 x 3.5. Angiosperm. **Q:** Specimen DMAL 17 with the following dimensions (in cm): 7 x 8 x 7.5. Conifer. **R:** Specimen DMAL 18 with the following dimensions (in cm): 9.5 x 7 x 5.5. Conifer. **S:** Specimen DMAL 19 with the following dimensions (in cm): 5.5 x 3 x 3.5. Conifer. **T:** Specimen DMAL 20 with the following dimensions (in cm): 6.5 x 4 x 2.5. Conifer. **U:** Specimen DMAL 21 with the following dimensions (in cm): 19 x 10 x 9. Conifer. **V:** Specimen DMAL 22 with the following dimensions (in cm): 10 x 10 x 9. Conifer. **W:** Specimen DMAL 23 with the following dimensions (in cm): 12 x 5 x 5. Conifer. **X:** Specimen DMAL 24 with the following dimensions (in cm): 9 x 5 x 5. Conifer. **Y:** Specimen DMAL 25 with 10 small pieces. Conifer. **Z:** Specimen DMAL 26 with the following dimensions (in cm): 24 x 14 x 10. Conifer. **AA:** Specimen DMAL 27 with the following dimensions (in cm): 8 x 8 x 3.8. Angiosperm. **BB:** Specimen DMAL 28 with the following dimensions (in cm): 23 x 20 x 11. Conifer.

Plate 28


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
DMAL 16
Q
DMAL 17
R
DMAL 18
S
DMAL 19
T
U
V
W
DMAL 23
X
DMAL 24
Y
Z
AA
DMAL 27
BB

Plate 29

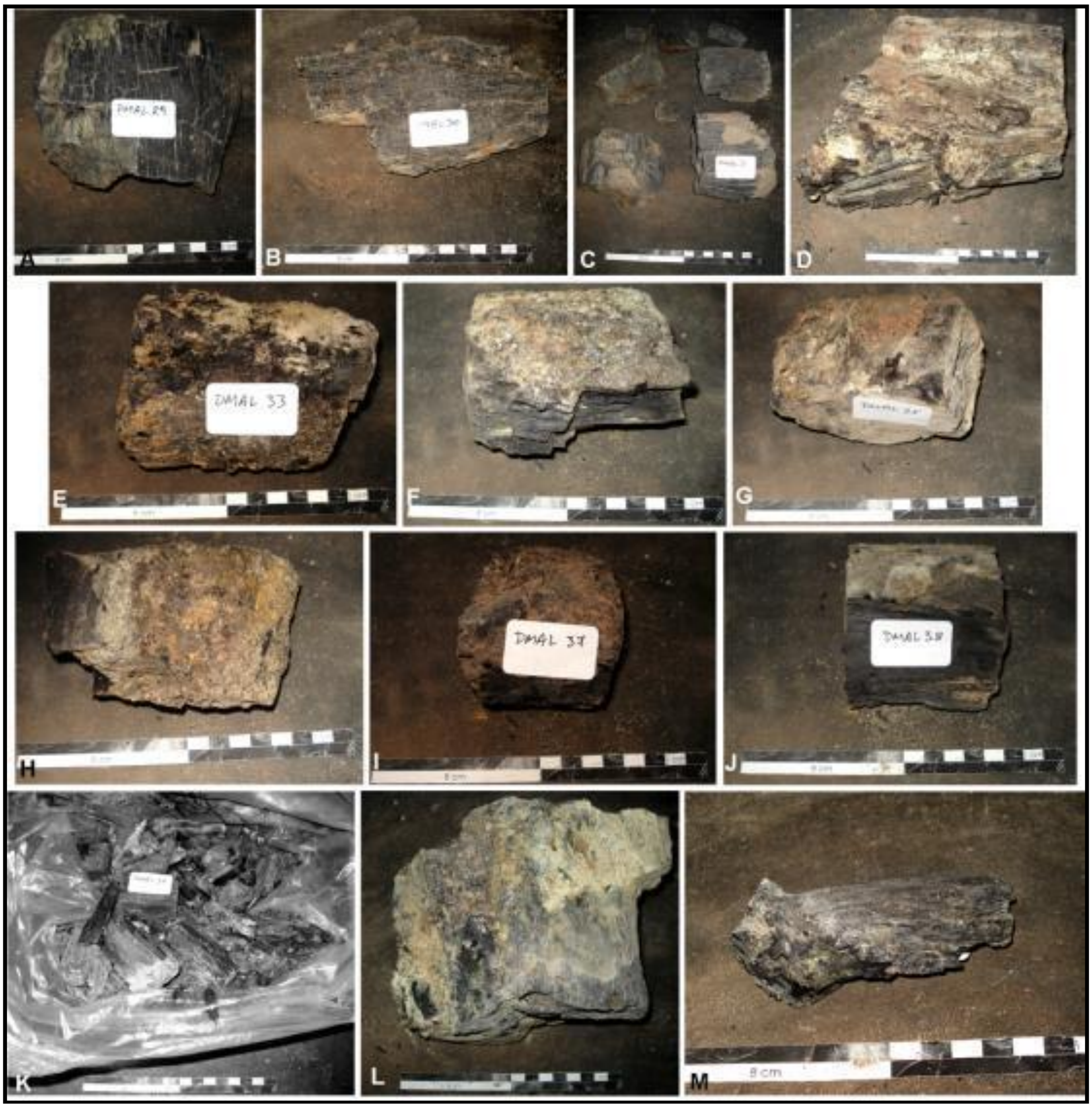


Plate 29. Specimens from Alonelia area.
A: Specimen DMAL 29 with the following dimensions (in cm): 13 x 10 x 5.5. Conifer. **B:** Specimen DMAL 30 with the following dimensions (in cm): 18 x 12 x 4.5. Conifer. **C:** Specimen DMAL 31 represents 8 small pieces with the dimension of some centimeters. Angiosperm. **D:** Specimen DMAL 32 with the following dimensions (in cm): 23 x 15 x 9.5. Conifer. **E:** Specimen DMAL 33 with the following dimensions (in cm): 11 x 7.5 x 7. Conifer. **F:** Specimen DMAL 34 with the following dimensions (in cm): 11 x 8.5 x 6. Conifer. **G:** Specimen DMAL 35 with the following dimensions (in cm): 11.5 x 6.5 x 9. Conifer. **H:** Specimen DMAL 36 with the following dimensions (in cm): 12 x 8 x 7. Conifer. **I:** Specimen DMAL 37 with the following dimensions (in cm): 7 x 7.5 x 6. Conifer. **J:** Specimen DMAL 38 with the following dimensions (in cm): 8 x 7.5 x 6. Conifer. **K:** Specimen DMAL 39 represents many small pieces with the dimension of some centimeters. Conifer. **L:** Specimen DMAL 40 with the following dimensions (in cm): 17.5 x 15 x 12. Conifer. **M:** Specimen DMAL 41 with the following dimensions (in cm): 9.5 x 3.5 x 2.5. Conifer.

2.4 LESBOS ISLAND FOSSIL FLORA APPENDIX (Mantzouka *et al.* 2013a, Velitzelos *et al.* 2014, modified). The new findings and the re-studied samples are shown in bold:

GYMNOSPERM WOOD

Thujoxylum peucinum Unger emend. Süss & Velitzelos [Lesbos unknown locality: ?Sigri described by Unger (1847, p.31, 32). The genus has been emended by Süss & Velitzelos (1998)].

Taxoxylum priscum Unger [Lesbos unknown locality: ?Sigri described by Unger (1847, p.33, 34). Revised as *Taxoxylon priseum* by Unger (1850, p.390, 391)].

***Peuce lesbia* Unger (= *Cedroxylon lesbium* Kraus)** [Lesbos unknown locality: ?Sigri described by Unger (1844, p. 34, 37, Tab. X), photographed and restudied by D. Mantzouka].

Cedroxylon sp. [Lesbos – western part: Ordymnos seashore and NE part of Ordymnos described by Fliche (1898, p. 143, 148) (lignitic and permineralized samples)].

Pityoxylon sp. [Lesbos – western part: NE part of Ordymnos described by Fliche (1898, p. 149) (permineralized sample)].

Taxaceoxylon biseriatum Süss & Velitzelos [Lesbos: Rogkada – Polichnitos region, described by Süss & Velitzelos (1994, p. 259, Taf. I, II)].

Pinoxylon paradoxum (Süss & Velitzelos) Süss & Velitzelos [Lesbos – western part: Bali Alonia, described by Süss & Velitzelos (1994, p. 407, Taf. I, II, III, IV). In 2010 it was revised as *Lesbosoxylon paradoxum* by Süss & Velitzelos].

Pinoxylon pseudoparadoxum (Süss & Velitzelos) Süss & Velitzelos [Lesbos – western part: Bali Alonia, described by Süss & Velitzelos (1994, p. 409, Taf. V). In 2010 it was revised as *Lesbosoxylon pseudoparadoxum* by Süss & Velitzelos].

Taxodioxylon gypsaceum (Goeppert) Kräusel [Lesbos – western part: Sarakina, Molyvos, Bali Alonia and Lapsarna–Gavathas (Antissa) described by Süss & Velitzelos (1997, p. 5, Taf. I)].

Taxodioxylon albertense (Penhallow) Shimakura [Lesbos – western part: Bali Alonia and Sarakina, described by Süss & Velitzelos (1997, p. 7, Taf. II, III)].

Taxodioxylon pseudoalbertense M. Nishida & H. Nishida [Lesbos – western part: Sarakina, described by Süss & Velitzelos (1997, p. 11, Taf. IV)].

Taxodioxylon megalonissum Süss & Velitzelos [Lesbos – western part: Nisiopi (Megalonissi) described by Süss & Velitzelos (1997, p. 12, Taf. V)].

Taxodioxylon sp. [Lesbos – western part described by Süss & Velitzelos (1997, p. 14)].

Glyptostroboxylon microtracheidae Süss & Velitzelos [Lesbos – western part described by Süss & Velitzelos (1997, p. 16, 18, 19, Taf. VI, VII)].

Tetraclinoxylon velitzelosi Süss [Lesbos – western part: Bali Alonia, Sarakina, Sigri, Gavathas described by Süss (1997, p. 290, 294, 295, Taf. I, II)].

Thujoxylon antissum Süss & Velitzelos [Lesbos – western part: Lapsarna (Antissa) described by Süss & Velitzelos (1998)].

Chimairoidoxylon lesboense Süss & Velitzelos [Lesbos – western part: Nissiopi (Megalonissi) and Gavathas described by Süss & Velitzelos (1999, p. 330–334, Taf. I, II, III)].

Podocarpoxylon articulatum Süss & Velitzelos [Lesbos – western part: Bali Alonia (main Petrified Forest Park) described by Süss & Velitzelos (2000, p. 138, Taf. I, II)].

Podocarpoxylon graciliradiatum Süss & Velitzelos [Lesbos – western part: Bali Alonia (main Petrified Forest Park), found lying next to *Taxodioxylon* sp. Süss & Velitzelos (1994) described by Süss & Velitzelos (2000, p. 140, Taf. III, IV)].

Chimairoidoxylon conspicum Süss & Velitzelos [Lesbos – western part: Gavathas, Bali Alonia and Eressos described by Süss & Velitzelos (2001, p. 151, Taf. I, II)].

Ginkgoxylon lesboense Süss [Lesbos – western part described by Süss (2003, p. 304–307, Taf. I, II)].

Ginkgoxylon diversicellulatum Süss [Lesbos – western part described by Süss (2003, p. 307–310, Taf. III, IV)].

Pinoxylon diversiradiatum Süss & Velitzelos [Lesbos – western part: Eressos, described by Süss & Velitzelos (2009, p. 4, Taf. I, II). In 2010 it was revised as *Lesbosoxylon diversiradiatum* by Süss & Velitzelos].

Pinoxylon graciliradiatum Süss & Velitzelos [Lesbos – western part: Eressos, described by Süss & Velitzelos (2009, p. 6, Taf. III, IV). In 2010 it was revised as *Lesbosoxylon graciliradiatum* by Süss & Velitzelos].

Lesbosoxylon diversiradiatum (Süss & Velitzelos) Süss & Velitzelos [Lesbos – western part: Eressos. Revision of the originally described *Pinoxylon diversiradiatum* by Süss & Velitzelos (2009, 2010, p. 22)].

Lesbosoxylon graciliradiatum (Süss & Velitzelos) Süss & Velitzelos [Lesbos – western part: Eressos. Revision of the originally described *Pinoxylon graciliradiatum* by Süss & Velitzelos (2009, 2010, p. 22)].

Lesbosoxylon ventricosuradiatum Süss & Velitzelos [Lesbos – western part: Eressos, described by Süss & Velitzelos (2010, p. 19, Taf I, II)].

Lesbosoxylon paradoxum (Süss & Velitzelos) Süss & Velitzelos [Lesbos – western part: Bali Alonia main Petrified Forest Park. Revision of the originally described *Pinoxylon paradoxum* by Süss & Velitzelos (1994, 2010 p. 22)].

Lesbosoxylon pseudoparadoxum (Süss & Velitzelos) Süss & Velitzelos [Lesbos – western part: Chamandroula. Revision of the originally described *Pinoxylon pseudoparadoxum* by Süss & Velitzelos (1994, 2010, p. 22)].

ANGIOSPERM **WOOD**

Juglandinium mediterraneum (Unger) [Lesbos unknown locality: ?Sigri described by Unger (1845, p. 241). Syn: *Juglandoxylon mediterraneum* (Unger) (Kraus 1882 a,b)].

Mirbellites lesbius (Unger) [Lesbos unknown locality: ?Sigri described by Unger (1845, p. 241, 242). Syn: *Juglandinium mediterraneum* (Unger 1850; Fliche 1898; Dupéron 1988) Syn: *Juglandoxylon mediterraneum* (Unger) (Kraus 1882 a,b)].

Brongniartites graecus Unger [Lesbos unknown locality: ?Sigri described by Unger (1845, p. 264)].

Palmoxylon sp. [Lesbos – western part: Ordymnos seashore described by Fliche (1898, p. 144) (lignitic sample, it looked also like *Sabal* or *Chamaerops*)].

Ebenoxylon sp. [Lesbos – western part: Ordymnos seashore described by Fliche (1898, p. 146) and related to modern *Diospyros* (lignitic sample). Note: Süss 1987 said ?Eben.].

Betulaceae (? *Alnus*), Euphorbiaceae (?), Fagaceae (? *Fagus*, ? *Quercus*), Lauraceae (? *Laurus*, ? *Cinnamomum*, ?), Leguminosae (? *Robinia*), Monimiaceae (?), Myrtaceae (?), Platanaceae (? *Platanus*) [Lesbos – western part: Eressos, Mesotopos. Tab. 1, p. 218 in Selmeier & Velitzelos 2000].

***Laurinoxylon* aff. *czechense* Prakash, Březinová & Bůžek** [Lesbos – southern part: Polichnitos region described by Mantzouka *et al.* (in press)].

***Laurinoxylon* cf. *daberi* Greguss** [Lesbos – southern part: Polichnitos region described by D. Mantzouka].

Laurinoxylon* aff. *diluviale* (Unger) Felix emend. Dupéron *et al. [Lesbos – southern part: Polichnitos region described by Mantzouka *et al.* (in press)].

***Cinnamomoxylon seemannianum* (Mädel) Gottwald** [Lesbos – southern part: Polichnitos region described by Mantzouka *et al.* (in press)].

***Cryptocaryoxylon* Leisman** [Lesbos – southern part: Polichnitos region described by D. Mantzouka].

***Quercoxylon* Kräusel** [Lesbos – southern part: Polichnitos region described by D. Mantzouka].

LEAVES

FERNS

Pronefrium stiriacum (Unger) Knobloch & Kvaček [Lesbos – western part: Eressos described by Velitzelos (1993)].

CONIFERS

Tetraclinis sp. [Lesbos – western part described by Velitzelos (1993)]

Pinus sp. [Lesbos – western part. Referred by Velitzelos & Zouros (2008)].

Cunninghamia miocenica Ettingshausen [Lesbos – western part. Referred by Velitzelos & Zouros (2008)] (*Cunninghamia miocaenica* Ettingshausen as revised by Velitzelos *et al.* 2014).

Sequoia abietina (Brong.) Knobloch [Lesbos – western part. Referred by Velitzelos & Zouros (2008)] (*Sequoia abietina* (Brongniart) Erw. Knobloch vel *Taxodium sp*. as revised by Velitzelos *et al.* 2014).

Tetraclinis salicornoides (Unger) Kvaček [Lesbos – western part. Referred by Velitzelos & Zouros (2008), Megalonisi islet as referred by Velitzelos *et al.* 2014].

ANGIOSPERMS

Cinnamomum polymorphum Heer sensu Grangeon [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)] [(*Daphnogene polymorpha* (A. Braun) Ettingshausen. as revised by Velitzelos *et al.* 2014)].

Laurus sp. [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)] [Lauraceae vel Fagaceae gen. et spec. indet., as revised by Velitzelos *et al.* 2014].

Laurus primigenia Unger [Lesbos – western part. Referred by Velitzelos *et al.* (1999)] [Lauraceae vel Fagaceae gen. et spec. indet., as revised by Velitzelos *et al.* 2014].

Litsea primigenia (Unger) Takht. [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)] [Lauraceae vel Fagaceae gen. et spec. indet., as revised by Velitzelos *et al.* 2014].

Lindera ovata Kolak. [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)] [*Dicotylophyllum* sp. 2, as revised by Velitzelos *et al.* 2014)].

Oreodaphne heeri Gaudin [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)] [*Laurophyllum* sp., as revised by Velitzelos *et al.* 2014].

Lauraceae [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)] [Lauraceae vel Fagaceae gen. et spec. indet., as revised by Velitzelos *et al.* 2014].

Daphnogene polymorpha Al.Braun Ett. [Lesbos – western part. Referred by Velitzelos *et al.* (1999)].

Quercus sp. [Lesbos – western part. Referred by Velitzelos *et al.* (1999)].

Quercus apocynophyllum Ett. [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)] [Lauraceae vel Fagaceae gen. et spec. indet., as revised by Velitzelos *et al.* 2014].

Pungiphyllum crutiatum (Al. Braun) Frankenhäuser et Wilde (= *Quercus cruciata* Al. Braun) [Lesbos – western part described by Velitzelos (1993) as *Quercus cruciata*].

Pungiphyllum crutiatum (Al. Braun.) Frankenhäuser et Wilde [Lesbos – western part. Referred by Velitzelos *et al.* (1999)].

Carpinus pliofaurei Ratiani forma *helladae* Velitzelos *et al.* [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)].

Carpinus uniserrata (Kolakovski) Ratiani (?) [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)].

Alnus cycladum Unger forma *parvifolia* Velitzelos *et al.* [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)].

Alnus cycladum Unger [Lesbos – western part. Referred by Velitzelos *et al.* (1999)].

Populus balsamoides Goepp. [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)].

Populus sp. [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)].

Tilia sp. [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)].

Diospyros brachysepala Al. Braun. [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)] [Lauraceae vel Fagaceae aff. *Castanopsis bavarica* Erw. Knobloch et Kvaček, or *Laurophyllum* sp., as revised by Velitzelos *et al.* 2014].

Myrsinites sp. [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)] [*Dicotylophyllum* sp. 1 (aff. *Cedrela attica* (Unger) Palamarev), as revised by Velitzelos *et al.* 2014)].

Rhus sp. [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)].

Sapotaceae (?) [Lesbos – western part: at the outcrop of the road Antissa–Sigri described by Velitzelos *et al.* (1981)] [*Dicotylophyllum* sp. 3, as revised by Velitzelos *et al.* 2014)].

Rubus sp. [Lesbos – western part. Referred by Velitzelos & Zouros (2008)].

Engelhardia sp. [Lesbos – western part. Referred by Velitzelos *et al.* (1999)] [*Engelhardia orsbergensis* (Weber) Jähnichen, Mai etWalter, as revised by Velitzelos *et al.* 2014)]

Engelhardia orsbergensis (Wessel et Weber) Jähnichen *et al.* [Lesbos – western part. Referred by Velitzelos & Zouros (2008)].

Phoenix sp. [Lesbos – western part described by Velitzelos (1993)] [*Phoenicites* sp., as revised by Velitzelos *et al.* 2014].

Platanus sp. [Lesbos – western part described by Velitzelos (1993)]

Acer sp. [Lesbos – western part described by Velitzelos (1993)]

“*Rubus niacensis*” Marty [Same; partly *Alnus cycladum* Unger, as revised by Velitzelos *et al.* 2014].

Sabal sp. [*Sabal major* (Unger) Heer, as revised by Velitzelos *et al.* 2014].

3. LEMNOS ISLAND

3.1.1 Introduction

Lemnos Island is situated at the North-East part of the Aegean Sea and covers an area of 476 Km^2.

The present contribution brings new scientific data for the palaeoflora of Lemnos Island based on the discovery and study of new and old collections of plant fossils which were found in 2012 from six localities. This new palaeobotanical study with numerous new samples of fossilized wood from the Miocene tuffs of Lemnos Island gives new information about the palaeobotanical and palaeontological content of this area.

Regarding the protection frame of the Island, Lemnos has been characterized by the Hellenic Constitution as a Landscape of Outstanding Natural Beauty (1278/20–10–2000) and it is protected by the Biodiversity Law (3937/2011), while the necessity of being protected also for its geodiversity (following the example of Lesbos western peninsula, Presidential Decree No 443/1985) and even its declaration as a Geopark seems essential.

The importance of the fossils of Lemnos Island – regarding the palaeofauna – has been referred in the work by Philostratus (3rd century B.C.), the ancient Greek philosopher from Lemnos Island. Philostratus wrote down all his observations for the ‘giantic skull’ of Lemnos in his book “On Heroes” (Higgins and Higgins 1996). Inside his book there is the description of a giant skeleton of a vertebrate found by Menecrates of Steira after an earthquake. This fossil looked as if it was allochthonous while its dimensions where similar to the Miocene mammal skulls from Samos and Lesbos Islands (“held more than two Cretan wine amphoras” = 40–48 liters).

The main occurrences of the plant fossils on Lemnos Island have been found at the area of Moudros. This study focuses on the new findings – of both conifers and angiosperms – from new plant fossiliferous localities of Moundros and Thanos regions (Fig. 29), while it includes also the xyloanatomical studies of the findings which were hosted at the Municipality of Moudros.

3.1.2 Localities and Geology

De Launay (1895) was the first who referred to the geology of the island with the creation of a geological map (Fig. 27) by giving a brief legend of the formations, identifying – in parallel – the existence of 2 layers: a sedimentary one (with sandstone and dark colored shale – brown to green – and even conglomerates) rich in leaves' imprints – probably belonging to a lake or a shallow estuary – and a formation of tertiary age including igneous rocks. In his descriptions he noticed that in Varos and Kotsinos are hosted the latest reminants of the volcanic material (tuff).

De Launay (1898) believed that Lemnos could host hydro carbonates because it consists of volcanics with a great quantity of decomposed plant remnants. Later on, there was another opinion on this matter by Partsch & Neumann (1885) who believed (without giving proofs, unfortunately) that the myths about the existence of the 'Lemnian flames' could be a result of the hydrocarbons' escape.

Papp had made geological and palaeontological research through the Aegean islands during the period 1938–1943. It seems that he was the one who collected the plant fossiliferous material from Lemnos Island which was studied later on by Berger (1953a).

According to Tranos (2009) "Papp and Davis studied the geology of Lemnos Island, but Roussos and Innocenti *et al.*, gave the most detailed stratigraphic and geological information for the rocks exposed on the island".

The geological structure of the island consists of a sequence of Middle Eocene to Lower Oligocene flyschtype sediments, overlain by Upper Oligocene to Lower Miocene sandstone, after which a low–angle unconformity signifies a temporary pause in sedimentation, which continues after this event with marl of Middle Miocene age. This sequence is intruded by a variety of volcanic domes and dykes, while pyroclastic deposits and lahars locally cover all underlying formations (Roussos, 1993).

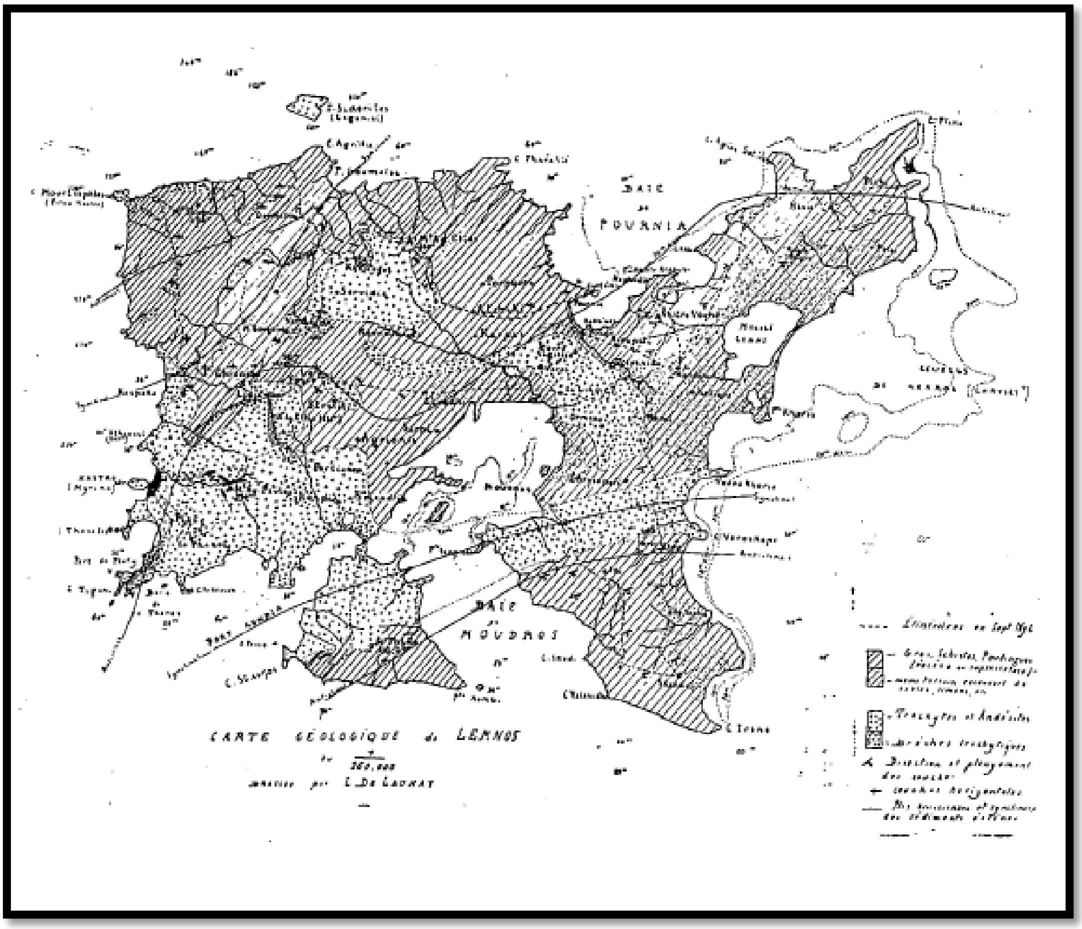


Fig. 27: The first geological map of the Lemnos Island by De Launay (1895).

Roussos (1993) distinguished the sedimentary basement rocks into two units, the Upper (early? Oligocene) and the Lower (late Eocene to early Oligocene) one (Fig. 28). Towards its top, the Upper Unit is composed of terrestrial fluvial sediments, including conglomerates and sandstones. Roughly half of the sedimentary basement on Lemnos Island is unconformably overlain by Lower Miocene volcanic rocks of the Hellenides orogeny, which consists of subvolcanic intrusions, lava flows, and pyroclastic deposits (Innocenti *et al.* 1994; Pe–Piper and Piper 2002; Pe–Piper *et al.* 2009). The volcanic centers are located in the western and southwestern portions of Lemnos Island, and are delineated by domes and lava flows that are accompanied by agglomerates. The sedimentary basement is increasingly exposed at the surface in the east and northeast of the island, distal to the volcanic centers.

Roussos (1993) noted that the Tertiary sediments exposed on the island can be subdivided into a Lower and Upper Unit (Fig. 28). The Lower Unit dated in Late Eocene–Early Oligocene covers the largest part of the island and consists of continental slope deposits such as thick–bedded to massive sandstones and conglomerates, turbidites or interbeds of claystones and sandstones, mudstones with thin interbeds of mudstones–sandstones. The Upper Unit dated as Oligocene is of more limited extent and consists of shallow marine to brackish deltaic sediments at the base such as alternations of claystones and fine–grained sandstones, claystones, sandstones and sandy marlstones. Upwards, in the Upper Unit fluvio–terrestrial deposits (medium– to coarse–grained sandstones and sandy conglomerates) prevail.

The roof of the whole sequence according to Innocenti *et al.* (1994) is an erosional unconformity capped by the Lower Miocene volcanic rocks. The sequence was interrupted in the Early Miocene by intense volcanic activity (Fytikas *et al.*, 1984; Innocenti *et al.*, 1994), which might be the continuation of the extensive magmatism of NW Anatolia (Yilmaz *et al.*, 2001). The volcanic products were high potassium andesitic to dacitic volcanic rocks that form lava domes, dikes and sills exposed in the western part of the island, and associated with a few isolated small intrusive granitic to quartz dioritic stocks. Also, whitish to light grey pyroclastic rocks such as ignimbrites and volcanic breccia are exposed capping the Tertiary sediments, mainly in the central part of the island. K–Ar radiometric ages indicate that these rocks formed between 21 and 18 Ma (Innocenti *et al.*, 1994). This Early Miocene magmatic activity exposed in the North Aegean Trough has been considered either as the result of the back–arc extension and subduction roll–back (Fytikas *et al.*, 1984; Kilias and Mountrakis, 1998) or the crustal thickening due to continental collision (Yilmaz, 1990). Miocene lacustrine sediments such as marls, conglomerates, and marlstones have been reported, but they are of very limited extent on the island. Younger Plio–Quaternary superficial deposits include very shallow marine limestones to calcarenites and Holocene alluvial and coastal deposits.

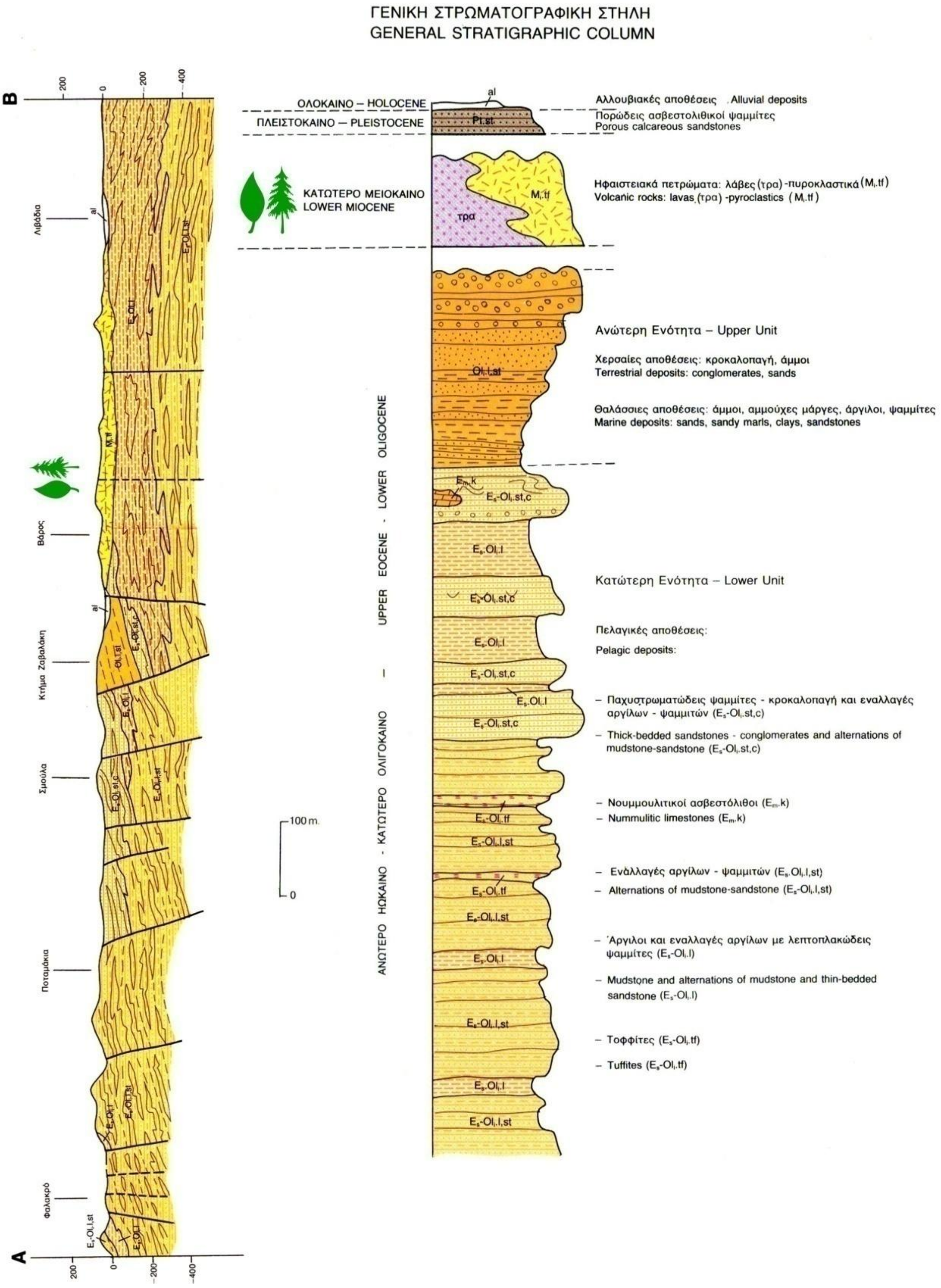


Fig. 28: Stratigraphic column of Lemnos Island and cross section including Varos village by Roussos (1993, I.G.M.E.), modified. The signs of the green leaf and tree indicate the plant fossiliferous horizon.

The Miocene igneous rocks of the island are considered to belong to the one high–K province along the Aegean–Anatolian–Frontier, the Northern one, the ‘Shoshonitic Province’ of Pe–Piper *et al.* (2009) that includes the islands of Samothrace, Lemnos and Lesvos and runs 200 km into Western Anatolia and the Northern part of Chios and İzmir (Smyrna). These high–K rocks, mostly of intermediate composition, indicate ensuing calc–alkaline orogenic volcanism, emitted from large volcanic centres (Fig. 29). Upwelling of asthenospheric mantle has been invoked to account for their genesis (Pe–Piper *et al.* 2009). The end of the Miocene is characterized by the deposition of conglomerates, marls and calcareous sandstones. Local Pleistocene porous calcareous and locally oolitic limestones and Holocene alluvial, coastal deposits and dunes are sparse in Lemnos (Maravelis & Zelilidis, 2012).

Numerous scientists have underlined the proximity of Lemnos Island to the North Aegean Trough – with a 2 km depth – due to its morphology and faulting pattern (Chatzipetros *et al.*, 2013; Koukouvelas and Aydin, 2002; Pavlides and Tranos, 1991; Pavlides *et al.*, 1990; Roussos, 1993; Tranos, 1998, 2009). According to Tranos (2009) “Lemnos Island is subjected to the Late Oligocene–Middle Miocene D1, D2 and D3 events. These events haven’t any genetic relationship with the North Anatolian Fault as also the formation and widening at least of the NE–SW trending Sporades basin of the North Aegean Trough, but to the late collisional processes between Apulia and Eurasia plates that took place in Late Oligocene–Middle Miocene time. The recent deformation of the North Aegean Trough could be attributed not to the propagation of the North Anatolian Fault into the North Aegean Sea, but to the back–arc extension related to the Hellenic subduction zone”.

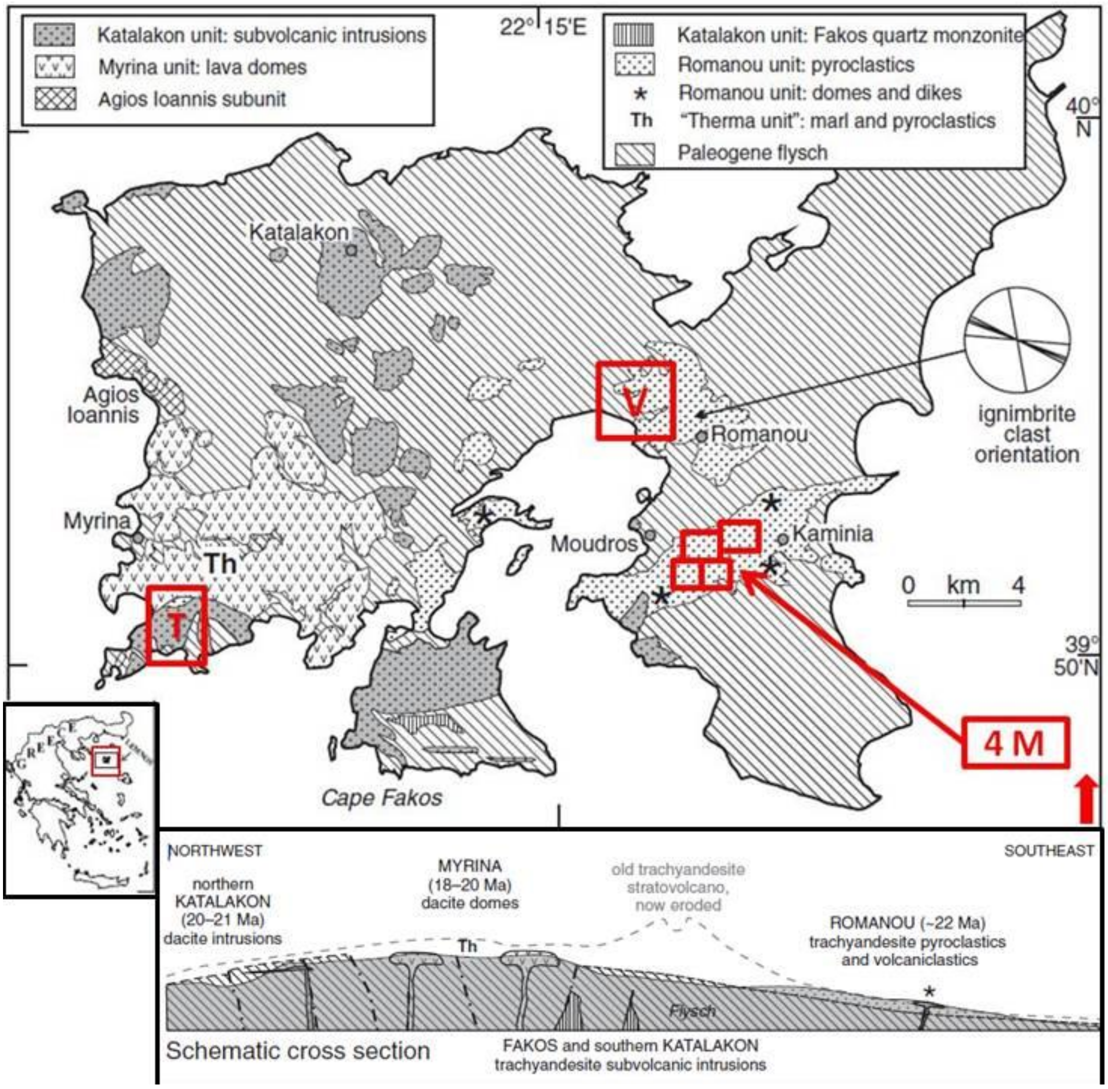


Fig. 29: Geological map and schematic cross section of Lemnos Island by Pe–Piper *et al.* (2009), modified. The fossiliferous sites which have been studied are included in the rectangulars.

3.1.3 The stratigraphy of the fossiliferous sites

According to Innocenti *et al.* (1994) and Fytikas *et al.* (1984) the magmatic rocks of Lemnos are of Lower Miocene age (21–18.2 Ma). The Lower Miocene of Lemnos is divided into three units on the basis of lithology, age, and geographic location: a) the Katalakon, b) Romanou and c) Myrina unit (Innocenti *et al.*, 1994). Romanou is the fossiliferous unit consisting of stratified pyroclastic and volcaniclastic deposits up to 160 m thick. Several ignimbrite horizons are interbedded with flow tuffs which interfinger with five chert beds containing plant fossils which are overlain over these deposits. Romanou unit includes Therma subunit consisting of interbedded marl and volcanic tuff with early Miocene plant fossils in tectonic contact with the apparently overlying Myrina unit (Panagopoulos *et al.* 2011). The same age for Therma was also suggested by Papp (1953) on the basis of fossil plants. (Innocenti *et al.* 2009). According to Pe–Piper *et al.* (2009) the Romanou Unit has an age of 22.3 ± 0.7 Ma – after a new K–Ar date on phlogopite from a lava block of this formation – and is older than the northern Katalakon Unit, which was dated at ca. 20–21 Ma by Innocenti *et al.* (1994) and Fytikas *et al.* (1984). The Myrina Unit is the younger one with an age of 18–20 Ma.

The total age range from Lemnos is similar to Samothraki and Lesbos Islands (Pe–Piper and Piper, 2002), and to central western Anatolia (Dilek and Altunkaynak, 2007). The cherts of the Romanou Unit resemble hot–spring deposits described by De Wet and Hubert (1989).

According to studies focused in mineralogy and silicification (Voudouris *et al.* 2007) the fossiliferous sites of Lemnos Island occur within weakly altered pyroclastics and/or associated to several horizons of sinters interbedded within the pyroclastics, especially in an area which seems to belong to the periphery of an eroded volcanic edifice exposed at Fakos peninsula, including the fossiliferous sites of Portianou, Varos–Roussopouli and Moudros–Roussopouli.

In Roussopouli, Varos, Rapanidi and Moudros, Sealy (1918), Fragkopoulos *et al.* (1964) and Tourptsoglou (1986) had observed the existence of silicified trees inside volcanic tuffs. The latter researchers referred that the specimens' diameter was up to 0.5m, their color was variable from white to black and they probably belonged to conifers.

According to Voudouris *et al.* (2007) the silicified wood occurs in two distinct environments: a) in slightly argillic altered pyroclastics (e.g., Portianou, Varos), b) in several layers of opaline, ‘silica sinter’ – at least six silica sinter horizons have been recognized –. (e.g., from Moudros to Roussopouli), which according to Papp (1953) have a thickness of up to 3m and represent thin bedded lacustrine–fluviatile intercalations in between the pyroclastic formations and were deposited during erosional periods in between the volcanic activity phases. One of the results of the study by Voudouris *et al.* (2007) was the strong relationship between the silicic–alunitic alteration zones and the fossiliferous silica layers. The description of the latter authors is representational: “in some places the fossiliferous horizons overly an alunitic alteration zone whereas the wood occurs as breccia fragments”.

The maps and cross–sections on Lemnos Island made by Roussos (1993) are accompanied with a detailed legend according to which the Lower Miocene deposits of conglomerates, marls and marly limestones have light brown colour and include leaves’ imprints. The small lacustrine occurrences at Agia Paraskevi, close to the road connecting Myrina to Therma include the following spores and pollen: Pinaceae, Palmae, *Engelhardtia*, *Symplocos*, *Liquidambar*, *Carya*, *Quercus*, type–*Castanea*, *Tricolporopollenites dolium*, *T*. *rillensis*, *T*. *fallax*, Graminae, Amaranthaceae–Chenopodiaceae, Polypodiaceae, Osmundaceae (identified by Chrysanthi Ioakeim in Roussos 1993).

About the fossilization: As Voudouris *et al.* (2007) have observed, usually the opaline horizon is intercalated between fresh rocks. Perfectly preserved leaves indicate quiescent conditions during the fossilization procedure. The fossiliferous silicified horizons are crosscut by later chalcedony veins. Silicification in both the "silica sinter", as well as within the wood material, varies from red and white, to black colour, due to the oxides. There is a lateral transition and evolution of the above mentioned alteration zones laterally and upwards in stratiform fossiliferous silicification.

Recent studies confirm that the silicification of wood begins as a process of open space filling and not as a replacement of organic material by SiO_2 (Rößler 2001). It seems to be controlled by diffusion of microscopic particles of $Si(OH)_4$, (molecules of silicic acid) within the wood structure. Under this aspect the deposition of SiO_2 could be resulted without destruction of the organic structure of the wood. However in advanced stages of silicification a removal of organic material is also possible (Rößler 2001).

3.1.4 Materials and Methods

During 2012 almost 30 new specimens were collected from six new localities in Moudros, Varos and Thanos regions (Plate 30A–30G; Plate 33: A_1–A_2).

The fossil plants were photographed, their dimensions were measured and they were catalogued. Apart from the new findings, the same work has been done for 44 wood specimens stored inside Moudros city hall. Small pieces from this material have been taken for thin slides' preparation. Thin slides for the majority of the samples mentioned above were prepared (three for each sample: transversal, radial and tangential) in order to study their anatomical features under the microscope.

The preparation of the thin sections is the same with the one described in page 19-20 referred to Lesbos material.

Among the material that was collected there were also carbonized, or permineralised or fossils inside opal.

What should be also mentioned is the finding of traditional sliding wooden tools used by the farmers until the first half of the past century for threshing the grains, chopping the cereals and separating the grain of the wheat inside the Folklore Museum at Portianou village. These tools have the name "volosyroi or xyloportes" in Greek and their finding is important because in plant fossiliferous localities carved fossil wood remnants (flint) were used due to their toughness as the most appropriate gravels for this work (Plate 30F, 30G).

The following abbreviations were used throughout the manuscript: V: Varos region, T: Thanos region, M: Moudros region, MCH: Moudros City Hall.

3.1.5 Historical research of the fossil plants of Lemnos Island

De Launay had travelled to Aegean sea in 1887 and 1894. He was the first who referred to the amounts of leaves imprints of Lemnos island (De Launay 1897a, p. 1049–1050), while he also found the most important fossiliferous sites (De Launay 1898, p. 55–56) at the Tigani cape at the SW of the island, at the area Fakos and at the cape Plaka at the NE part of the island. He believed that the majority of his findings belonged to conifers while the plant fossils from Gomati (from the NW side of the island) collected by Papp, belonged to Miocene assemblages, same as the material from Moudros and Varos.

Plate 30

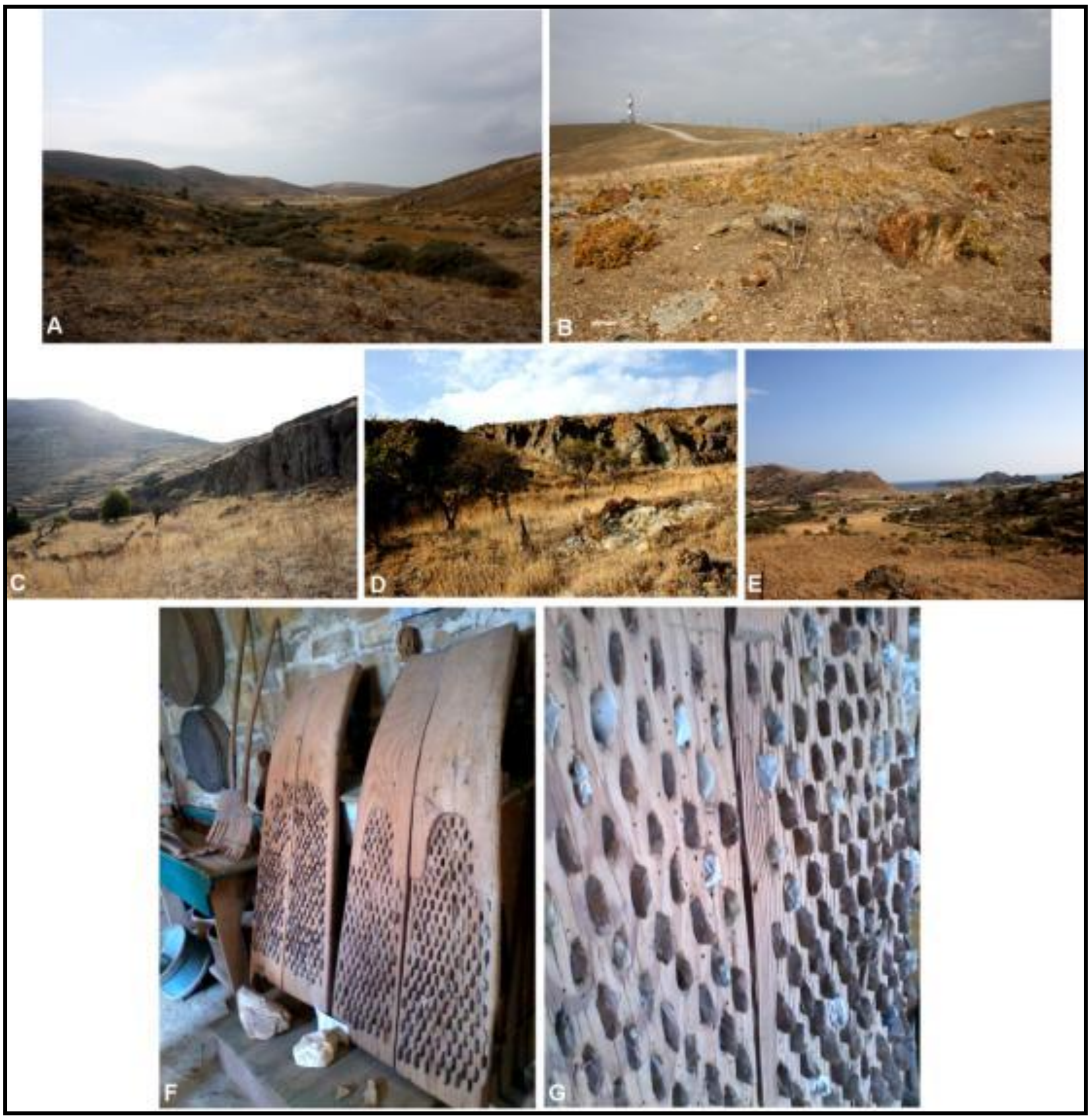


Plate 30

A, B: Moudros fossiliferous localities.

C, D, E: New fossiliferous localities from Thanos village (Southern Lemnos Island).

F, G: Fossil wood remnants used as “tough gravels” of “volosyroi or xyloportes”, the wooden tools for threshing the grains found at the Folklore Museum of Portianou village.

De Launay has given also the stratigraphic column of the island underlying the existence of the plant fossils inside two horizons of pink sandstone. Saporta had studied some of those samples and he related them with some monocots and some conifers, too. “At SW of Goulmatos site (at the NE part of the island) inside the formation of pink sandstone there were wide leaves” imprints which, according to M. de Saporta, could represent remnants of palms’.

According to Berger (1953a) 2 Km SE of Moudros site (as described by Papp) there were findings of fossilised wood which probably belong to the same stratum with the findings of Moudros. The wood findings belong to three (3) categories of silicification: a) chalcedony, b) opal and c) carbon. At the second one the identification is almost not feasible. All the findings studied by Berger (1953a) were collected by Papp since 1938 from three localities: 1) NE of Kastro at the West coast (marls with leaves’ imprints of *Myrica kymeana* (Ung.), cf. *Quercus lonchitis* (Ung.), *Zelkova praelonga* (Ung.) Berger, *Cinnamomum polymorphum* (A. Br.) Frentz., *Daphnogene lanceolata* Ung., *Acer* (Palaeo–Rubra) *trilobatum* A. Br., cf. *Eriolaena* sp., 2) At the South part of the eastern coast of Moudros gulf (quartzites with leaves, fruits, roots, wood of *Goniopteris styriaca* (Ung.) Heer, *Glyptostrobus europaeus* Brong. *Cinnamomum polymorphum* (A. Br.) Frentz. *Cinnamomum* cf. *scheuchzeri* (Heer) Frentz, *Andromeda saportana* Heer, cf. *Phragmites* sp. and 3) At the SE part of Moudros (opal assemblages with wood of *Cedroxylon* sp., *Laurinoxylon ehrendorferi* and *Cornoxylon pappi* and plant remnants, determined by Berger 1953a). All these findings belong to the same stratigraphic position of lake–river (limnic–fluvial) assemblages in between tuff (volcanic material) with a Lower–Middle Miocene age.

As a conclusion, Berger (1953a) underlines the fact that the most dominant family is the one of Lauraceae (*Cinnamomum*, *Daphnogene*, *Laurinoxylon*) with the species which are characteristic for the highlands of tropical–subtropical forests (*Daphnogene lanceolata* and *Cinnamomum scheuchzeri*), while the leaves which refer to *Cinnamomum*, probably belong to *Neolitsea–Tetradenia*. He believed that the fossil flora of Lemnos Island is similar to the one from Kumi (Euboea) and Oropos (Attiki) from Greece and with the one from Skopia (FYROM) with a warm subtropical character. He also believed that there are differences with the floras from Chios and Kos, because the climate to which the plant fossiliferous assemblages of the latter islands refer to is temperate, while there must be a difference in the age, too.

Süss & Velitzelos (1993) reported the occurrence of two remains of wood fossils belonging to the species *Pinoxylon parenchymatosum* (Protopinaceae) of

Upper Oligocene – Lower Miocene age, 2 Km SE of Fergani (to Paradeissi), close to Moudros. From this area there were numerous plant fossils such as leaf imprints, branches and roots of trees and conifers cones. The colour of this horizon is white to reddish brown and its thickness varies between 0,5 and 2 m. Professor Velitzelos E. had discovered the fossiliferous site which contained also roots of palm trees. According to Velitzelos (1990) and Velitzelos & Gregor (1990) “the fossil flora of Lemnos represents an extension of the Petrified Forest of Lesbos”. The authors believed also that the fossils were representing a mesophytic, subtropical–tropical flora developed in a seasonal climate.

From 1887 till 1993, only 2 species of gymnosperm wood (*Cedroxylon* sp. and *Pinoxylon parenchymatosum*) and 3 species of angiosperm wood (*Cornoxylon pappi, Laurinoxylon ehrendorferi* and *Rhizopalmoxylon* sp.) have been identified in the Neogene palaeoflora of Lemnos Island. On the contrary, plenty leaves imprints have been recognized including 3 conifers and 24 angiosperms (Lemnos Island Fossil Flora Appendix).

3.2 Systematic Descriptions

Both conifers and angiosperms have been identified in the samples collected from the new fossiliferous sites and from the material kept at the facilities of Moudros city hall.

Among the newly discovered angiosperm woods we were able to identify species with anatomical characteristics resembling Lauraceae family (*Laurinoxylon* and *Cryptocaryoxylon*). As long as conifers are concerned several Taxodiaceae representatives have been found.

3.2.1 Identification of Angiosperm wood from Lemnos Island

3.2.1.1

Angiosperms

Lauraceae

***Laurinoxylon* Type 2a**
***Fossil Species—Laurinoxylon* cf. *ehrendorferi* Berger**
***Material:* DMLHM24 (2 slides)**
(Plate 31A, 31B, 31C, Lemnos Island Fossil Flora Appendix)

Locality: Moudros, Central–Eastern Lemnos Island, Greece
Stratigraphic horizon: Inside volcanic tuff
Age: early Miocene

Macroscopic description. Part of a specimen with the following dimensions: 42x29x19 cm hosted at the Municipality of Moudros region. (Pl. 31*A*).

Microscopic description. Growth rings: distinct (Pl. 31*B*). — Wood: diffuse–porous — Vessels: mainly solitary, but also in groups of two and in clusters; outline of solitary vessels round to oval (Pl. 31*B*); perforation plates simple; tyloses common (Pl. 31*B*), intervessel pits alternate, polygonal, medium and large in size, about 10 μm, vessel–ray pits with much reduced borders to apparently simple — Rays:

heterocellular, up to 3 cells wide, commonly 2–seriate, body of multiseriate rays composed of procumbent cells with one row of upright and/or square marginal cells (Pl. 31*C*). — Axial parenchyma: vasicentric paratracheal (Pl. 31*B*), fibres septate — Idioblasts: associated with the ray and axial parenchyma — Crystals: not present.

Plate 31

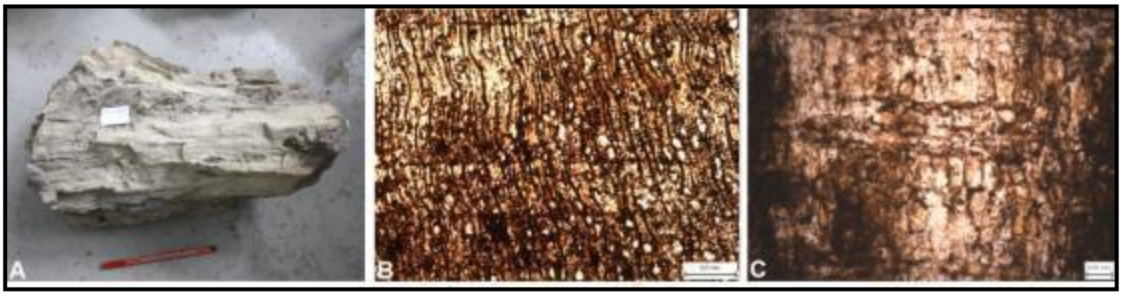


Plate 31 *Laurinoxylon* Type 2a: Pl. 31A–31C *Laurinoxylon* cf. *ehrendorferi* Berger (Lemnos) (DMLHM 24: Pl. 31A–31C).

A: Part of a specimen with the following dimensions: 42x29x19 cm hosted at the Municipality of Moudros. **B:** Growth rings boundaries distinct, diffuse-porous wood, vessels solitary, in groups of two and in clusters; outline of solitary vessels round to oval, tyloses, axial parenchyma vasicentric paratracheal, idioblasts associated with the ray and axial parenchyma. **C:** Body of multiseriate rays composed of procumbent cells with one row of upright and/or square marginal cells, idioblasts associated with the ray and axial parenchyma.

B = TS; C = RLS. TS and RLS denote transversal and radial longitudinal sections, respectively.

Comparison among Laurinoxylon species with similar type of idioblasts *– only associated with the ray and axial parenchyma* (Table 1)*:* DMLHM24 sample from Lesbos Island has been compared with *Laurinoxylon mueller–stolli* Greguss emend. Süss & Mädel, *Laurinoxylon hasenbergense* Süss (Süss 1958), *Laurinoxylon* cf. *hasenbergense* (Greguss 1969), *Laurinoxylon endiandroides* Süss, *Laurinoxylon annularis* Gottwald, *Laurinoxylon aniboides* Greguss emend. Süss & Mädel, *Laurinoxylon nectandrioides* Kräusel & Schönfeld and *Laurinoxylon ehrendorferi* Berger.

Our specimen (DMLHM24) from Moudros area (Central–Eastern part of Lesbos Island) has a lot of similarities with *Laurinoxylon ehrendorferi* Berger. They come from exactly the same locality (Lemnos island, 2 km SSE of Moudros), they both belong to the same category (*Laurinoxylon* type 2a due to the occurrence of the idioblasts related to rays and axial parenchyma) according our studies (Mantzouka *et al.* in press) and it seems that they have as the only difference the existence of vessel ray pits with much reduced borders to apparently simple (pits outline rounded) instead of vessel–ray pits with distinct borders, similar to intervessel pits as described by Berger (1953a), although the preservation of our specimen (DMLHM24) is not so good.

According to our recent study on fossil Lauraceae (Mantzouka *et al.* in press), DMLHM24 sample belongs to *Laurinoxylon* Type 2a (because it has idioblasts associated with the ray and axial parenchyma). The characteristics the species of this group have in common are the following: distinct growth ring boundaries, diffuse porous wood, tyloses, vessels mainly (but not exclusively) solitary, but also in pairs and in radial multiples of 3–4 and rarely in clusters, round to oval vessels (with the exception of the species *Laurinoxylon aniboides*), simple and in some cases scalariform perforation plates (with the exception of *Laurinoxylon aniboides*) , mostly 2–3 seriate rays, septate fibres (with the exception of *Laurinoxylon annularis* which has non–septate and *Laurinoxylon aniboides* from the description of which is not clear), the idioblasts’ size.

Botanical affinities. The list of the genera to which *Laurinoxylon* Type 2a corresponds according to Mantzouka *et al.* (in press) is the following: *Aniba, Licaria, Aiouea, Pleurothyrium, Cryptocarya* from Madagaskar*, Dehaasia, Nothaphoebe, Phoebe, Persea, Apollonias, Lindera A*.

From this list we exclude: the genera which have crystals, in great percentages of their species. The remaining genera – the most similar to *Laurinoxylon* Type 2a – are: *Cryptocarya* from Madagaskar, *Nothaphoebe*, and the species of *Aiouea, Persea* and *Lindera* A, which don’t have crystals (should be true for 70% species of each of these three genera). From the above mentioned genera we can further exclude: 1) *Lindera A* because it has non–septate fibres, 2) *Persea* because it has weakly expressed septate fibres and vessels in radial chains, 3) *Cryptocarya* from Madagascar because it has storied rays (although it has no crystals).

Finally, it seems that *Nothaphoebe* and *Aiouea* could be the most possible modern analogues of our sample. Both genera are Neotropical / Neotropical–Asian belonging to Perseae tribe.

3.2.1.2

Lauraceae
***Cryptocaryoxylon* Leisman**
(Plate 32*A*–32*O*, Lemnos Island Fossil Flora Appendix)

Material: DMLHM11 (3 slides)
Locality: Moudros, Central–Eastern Lemnos Island, Greece
Stratigraphic horizon: Inside volcanic tuff
Age: early Miocene

Macroscopic description. The slides come from a specimen with the following dimensions: 15x10x8 in cm (Pl. 32*A*).

Microscopic description. *Growth rings:* distinct. — *Wood:* semi–ring/diffuse–porous (Pl. 32*B*). — *Vessels:* 14–16 vessels/sq.mm, 30% solitary, 50% in groups of two, 10% in groups of 3, and 10% in clusters; tangential diameter 90–120 μm, mean: 100 μm; radial diameter 100–150 μm, mean: 120 μm; outline of solitary vessels round to oval (Pl. 32*B–32D*); vessel walls thin; perforation plates simple (Pl. 32*G,* 32*L,* 32*N*); tyloses common (Pl. 32*B,* 32*C,* 32*E*), intervessel pits: polygonal alternate and medium (8–10 μm) in size (Pl. 32*G*), — *Rays:* heterocellular up to 5 cells wide, (20–60 μm) (Pl. 32*E*), and 200–600 μm high (mean: 350 μm) (Pl. 32*F*–32*H*), body of multiseriate rays composed of procumbent with one row of upright and/or square marginal cells (Pl. 32*J–32M, 32O*), Silica bodies (crystalliferous elements) observed inside the rays' idioblasts (Pl. 32*F*–32*H,* 32*J*–32*M,* 32*O*); Rays per millimeter: 7–9 (Pl. 32*B*) — *Axial parenchyma:* vasicentric paratracheal to aliform, with up to 3–celled rows (Pl. 32*B–32E*), seemingly marginal bands of parenchyma (Pl. 32*B, 32E*), — *Fibres:* most probably non septate— *Idioblasts*: associated with the ray parenchyma cells and among the fibres (Pl. 32*C*–32*M,* 32*O*), idioblasts in transverse section with radial diameter × tangential diameter (in μm) from 20 × 13 up to 50 × 43; Number of idioblasts per sq. mm in transverse section: in general 15–23/sq. mm.

Plate 32

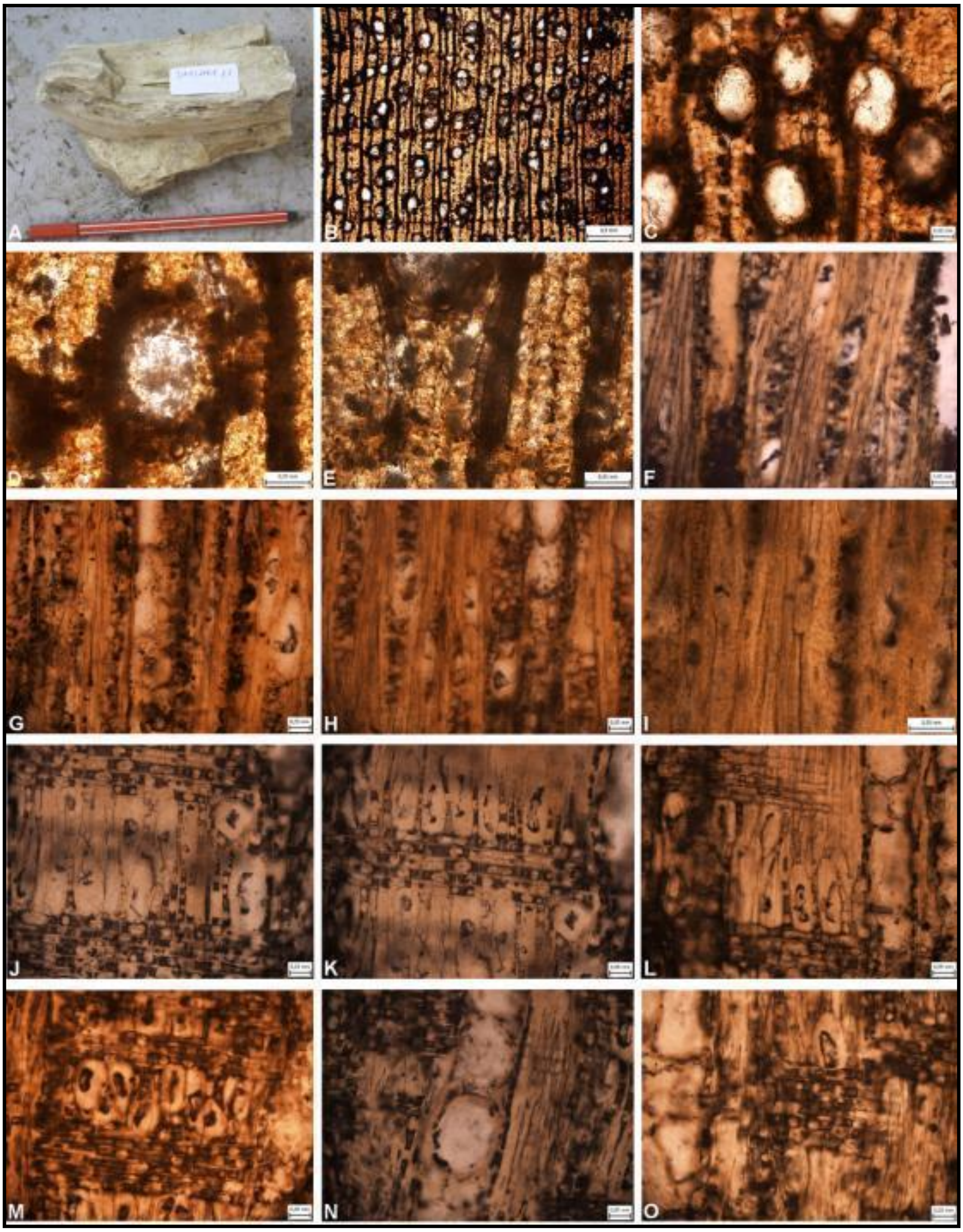


Plate 32 *Cryptocaryoxylon* Leisman (DMLHM11: Pl. 32A–32O)

A: The dimensions of the specimen are: 15x10x8 cm. **B:** Growth rings boundaries distinct, semi-ring/diffuse-porous wood, vessels in multiple groups of up to 3 and in clusters, solitary vessels' outline round to oval, tyloses common, 7-9 rays per millimeter, vasicentric paratracheal to aliform parenchyma, with up to 3-celled rows, seemingly marginal bands of parenchyma. **C:** Vessels in multiple groups of up to 3 and in clusters, solitary vessels' outline round to oval, tyloses common, vasicentric paratracheal to aliform parenchyma, with up to 3-celled rows, seemingly marginal bands of parenchyma, idioblasts associated with the ray parenchyma cells and among the fibres. **D:** Vessels in multiple groups of up to 3 and in clusters, solitary vessels' outline round to oval, vasicentric paratracheal to aliform parenchyma, with up to 3-celled rows, seemingly marginal bands of parenchyma, idioblasts associated with the ray parenchyma cells and among the fibres. **E:** Tyloses common, rays heterocellular up to 5 cells wide, vasicentric paratracheal to aliform parenchyma, with up to 3-celled rows, seemingly marginal bands of parenchyma, idioblasts associated with the ray parenchyma cells and among the fibres. **F:** Rays of 200–600 μm high, idioblasts associated with the ray parenchyma cells and among the fibres, silica bodies (crystalliferous elements) observed inside the rays' idioblasts. **G:** Perforation plates simple, intervessel pits: polygonal alternate and medium, rays of 200–600 μm high, idioblasts associated with the ray parenchyma cells and among the fibres, silica bodies (crystalliferous elements) observed inside the rays' idioblasts. **H:** Rays of 200–600 μm high, idioblasts associated with the ray parenchyma cells and among the fibres, silica bodies (crystalliferous elements) observed inside the rays' idioblasts. **I:** Idioblasts associated with the ray parenchyma cells and among the fibres. **J:** Body of multiseriate rays composed of procumbent with one row of upright and/or square marginal cells, idioblasts associated with the ray parenchyma cells and among the fibres, silica bodies (crystalliferous elements) observed inside the rays' idioblasts. **K:** Body of multiseriate rays composed of procumbent with one row of upright and/or square marginal cells, idioblasts associated with the ray parenchyma cells and among the fibres, silica bodies (crystalliferous elements) observed inside the rays' idioblasts. **L:** Perforation plates simple, body of multiseriate rays composed of procumbent with one row of upright and/or square marginal cells, idioblasts associated with the ray parenchyma cells and among the fibres, silica bodies (crystalliferous elements) observed inside the rays' idioblasts. **M:** Body of multiseriate rays composed of procumbent with one row of upright and/or square marginal cells, idioblasts associated with the ray parenchyma cells and among the fibres, silica bodies (crystalliferous elements) observed inside the rays' idioblasts. **N:** Perforation plates simple. **O:** Body of multiseriate rays composed of procumbent with one row of upright and/or square marginal cells, idioblasts associated with the ray parenchyma cells and among the fibres, silica bodies (crystalliferous elements) observed inside the rays' idioblasts.

B, C, D, E = TS; J, K, L, M, N, O = RLS; F, G, H, I = TLS. TS, RLS and TLS denote transversal, radial and tangential longitudinal sections, respectively. **Note:** Figures 32J-32M & 32O have been knowingly presented in order to show that the occurrence of silica bodies is not artifact but an important characteristic of our specimen which has been observed and should be discussed.

***Comparison among Laurinoxylon species with similar type of idioblasts** – only associated with the ray parenchyma and among the fibres* (Table 1). At the beginning, DMLHM11 specimen from Lemnos was identified as a *Laurinoxylon* Type 2b species because it has wood semi ring–diffuse porous, growth ring boundaries distinct, vessels mainly in radial multiples of 2–3, often solitary and rarely in clusters, simple perforation plates and polygonal alternate intervessel pits medium (8–10 μm), tyloses common, paratracheal axial parenchyma vasicentric (to aliform), rays up to 5–seriate (mainly 2–seriate), heterocellular, body of multiseriate rays composed of procumbent with one row of upright and/or square marginal cells, silica bodies (crystalliferous elements) observed inside the rays' idioblasts and idioblasts associated with ray parenchyma and among the fibres. It had been compared with*:* *Laurinoxylon diluviale* from Jáchymov*,* *Laurinoxylon* aff. *diluviale* from Lesbos, *Laurinoxylon perfectum* and *Laurinoxylon compressum* from South France. From the characteristics mentioned above the occurrence of vasicentric to aliform paratracheal parenchyma and of silica bodies are for sure not so common features for *Laurinoxylon* and not clearly in accordance with its emended diagnosis.

Comparison among fossil Lauraceae. Our specimen DMLHM11 has the characteristics of *Laurinoxylon* with the exception of: a) the type of axial parenchyma which is paratracheal vasicentric–aliform of up to 3–seriate bands wide, b) the apotracheal parenchyma being seemingly in marginal bands and c) the occurrence of idioblasts in rays (abundant) and in fibres (sporadic).

Richter (1981a, 1990) clarifies the existence of axial paratracheal and marginal parenchyma by describing the occurrence of paratracheal mostly abundant vasicentric to aliform, often confluent with multiseriate bands (2–6(–10)) cell wide (Richter 1981a, Abb. 17a) in *Beilschmiedia*, *Endiandra*, *Potameia/Syndiclis* and *Triadodaphne*, the existence of paratracheal mostly sparse to slightly vasicentric multi–seriate bands 2–4(–8) cell wide (Richter 1981a, Abb. 17b) in *Cryptocarya* and *Ravensara* and the occurrence of paratracheal incomplete to closed vasicentric bands of exclusively one–line in *Licaria wilhelminensis* as also marginal (or seemingly marginal), fine, up to three cells wide bands in *L. subbullata* Kosterm*.* (Richter & Dallwitz 2000–onwards); the latter two species are apparently synonyms according to The Plant List (2013). The occurrence of aliform to aliform–confluent paratracheal parenchyma has been observed in *Hypodaphnis* and *Eusideroxylon (+/or Potoxylon,* since some *Eusideroxylon* species have been moved to *Potoxylon,* and possibly *Litsea garciae* and *L. sandakanensis)*.

What is also important is the fact that studying the wood anatomy of DMLHM11 we have recognized the occurrence of crystals (of A and E type sensu

Richter 1981a) along with SiO_2 (mainly of “agglomerate” type C sensu Richter 1981a) inside the rays’ idioblasts. This diagnosis leads us to assign our specimen to *Cryptocaryoxylon*. The result is again the same if we take into account the classification by Richter (1981a, 1987) based on the vessel–ray parenchyma pits correlated with diameter classes of intervessel pits, according to which our sample DMLHM11 belongs to the class b (with intervessel pits 8–12 μm, with vessel–ray pits variable in shape, round to oval, to elongate horizontally, vertically or diagonally).

Leisman (1986) has based the diagnosis of *Cryptocaryoxylon* (by describing the species *Cryptocaryoxylon gippslandicum)* on the characteristics of the extant genus *Cryptocarya* the wood anatomy of which has been fully described by Richter (1981a).

DMLHM11 has been compared with *Cryptocaryoxylon gippslandicum* Leisman (1986) from the Tertiary of eastern Victoria but is wan’t so close to it.

In Wheeler & Manchester 2002 there is a chapter on fossil Lauraceae findings from the Middle Eocene Nut Beds. There one can find the discussion on the fossil lauraceous genera – apart from *Laurinoxylon* or *Ulminium* – which have been identified as: *Caryodaphnoxylon* Gottwald (1992), *Cinnamomoxylon* Gottwald (1997), *Cryptocaryoxylon* Leisman (1986) and *Sassafrasoxylon* Brezinova et Süss (1988). Dupéron–Laudoueneix & Dupéron (2005) had identified another fossil lauraceous genus (*Beilchmiedioxylon*) based on the wood anatomical characteristics of the modern Lauraceae described by Richter 1981 [NB: adopting Richter observations on the quantity of vessels per mm^2 could lead one to wrong results because Richter’s study was published in 1981 and all the recent publications follow the concept by Wheeler (1986) on the way of counting the vessels].

Although the age of the findings in Nut Beds (Middle Eocene) is not so close to ours (Early Miocene) we have compared our specimen with *Cryptocaryoxylon hancockii*, *C. radiporosum* and *C. meeksii* and although there are a lot of similarities it seems that DMLHM11 is not identical with any of the latter species. What should be also underlined is the existence of silica bodies inside the rays’ idioblasts of *Cryptocaryoxylon radiporosum* as well, most probably of C or even B type sensu Richter (1981a) inside the rays’ idioblasts (Fig. 30), although it is not mentioned by the authors.

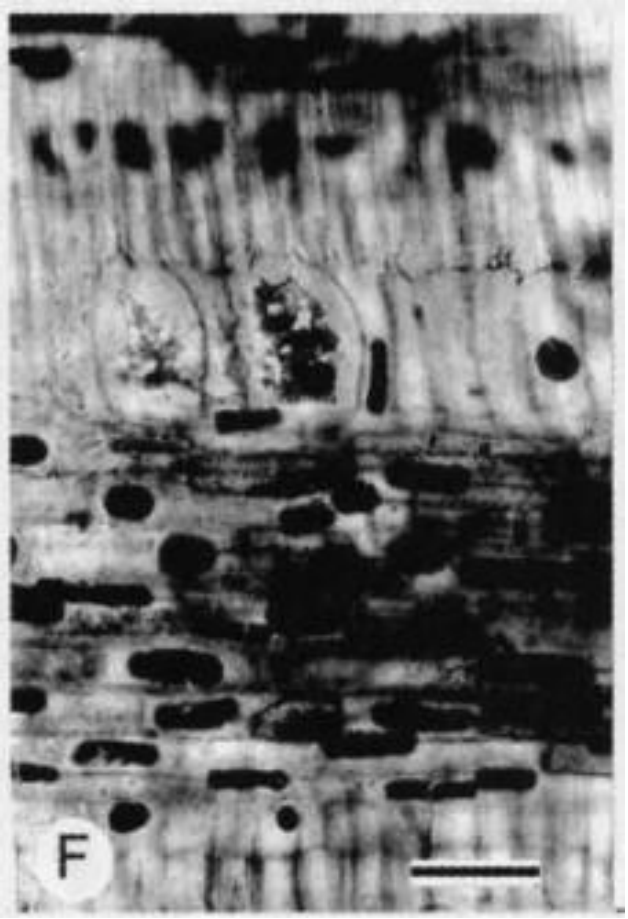
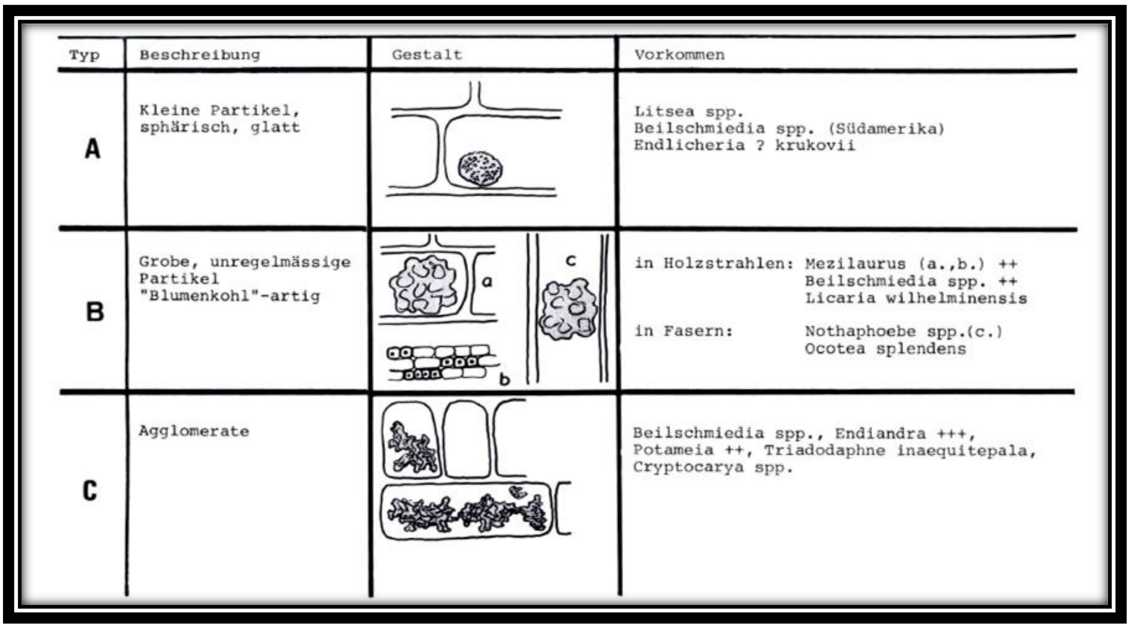


Fig. 30: Inflated cells (?oil cells) in marginal row of ray of *Cryptocaryoxylon radiporosum*, RLS. Scale bar: 50 μm (Wheeler & Manchester 2002, p.71, Fig. 19–F).

Botanical affinities. Taking into account the latter characteristics along with the fact that SiO_2 is observed in *Beilschmiedia*, *Endiandra*, *Potameia*, *Triadodaphne inaequitepala*, *Cryptocarya*, *Mezilaurus*, *Licaria wilhelminensis*, *Litsea*, *Dehaasia*, *Endlicheria*, *Anaueria* and *Clinostemon* (Richter 1981a, table 11) and the occurrence of crystals of A type is seen only in some genera we come to the conclusion that the most close modern genus is *Cryptocarya* which has the following characteristics: simple perforation plates, pits of 9–11 μm diameter, large distinct bordered pits in fibres which are horizontally layered, paratracheal vasicentric to aliform to confluent parenchyma, terminal bands, (–2)3–5(–7)–celled rays, rays with maximum height of 0.4–0.75–1.5 mm with mainly idioblasts in rays and fibres, crystals of A type (Fig. 20) and SiO_2 of “agglomerate” type C (Fig. 31).

Our specimen DMLHM11 belongs to *Cryptocaryoxylon*. *Cryptocarya* is a genus of Cryptocaryeae Nees tribe which includes genera of the Southern hemisphere according to Richter (1981a).



Typ	Beschreibung	Gestalt	Vorkommen
A	Kleine Partikel, sphärisch, glatt		Litsea spp. Beilschmiedia spp. (Südamerika) Endlicheria ? krukovii
B	Grobe, unregelmässige Partikel "Blumenkohl"-artig	a b c	in Holzstrahlen: Mezilaurus (a.,b.) ++ Beilschmiedia spp. ++ Licaria wilhelminensis in Fasern: Nothaphoebe spp.(c.) Ocotea splendens
C	Agglomerate		Beilschmiedia spp., Endiandra +++, Potameia ++, Triadodaphne inaequitepala, Cryptocarya spp.

Fig. 31: Types of silica bodies which can be found in specific genera of Lauraceae described by Richter (1981a).

What is also important is the occurrence of silica bodies and its function. According to Carlquist (2001) the existence of SiO_2 (silica bodies) is of interest to wood anatomists because the presence of silica is often of diagnostic value because only a minority of dicotyledonous woods contain visible silica accumulations while also within families, the generic distribution can be of importance. The representatives of Lauraceae which contain silica according the latter author are: *Cryptocarya, Licaria, Mezilaurus, Ocotea.*

Typical strengthening elements are dead sclerenchyma cells, wood or bast fibres and rarely even living collenchyma cells, silica bodies or druses may function as load–bearing structures. The silica or sclereid bodies have a relatively large surface and apparently serve to increase the strength of the ground parenchyma by increasing the friction energy in bending. From the comparison of the various tree types it is evident that in nearly all trees stability and stiffness of trunks are mainly due to woody fibrous elements (tracheids, sclerenchyma or bast fibres), whereas pneumatic systems, sclereids or silica bodies play a minor role. Compared to fibres, spherical strengthening elements are generally less relevant to the stiffness of trunks. Silica bodies and sclereids help to increase the Young's modulus (= a measure of the stiffness of a solid material) of the ground–parenchyma (Mosbrugger 1990).

Silicon is considered an essential element for *Equisetum* growth, whilst for other higher plants, it is considered only a beneficial element. A likely general consequence of in–life deposition of silicon is to increase plant preservation potential. (Channing & Edwards 2013).

Discussion. This is the first occurrence of the genus *Cryptocaryoxylon* for the Cenozoic of Eurasia. Until now *Cryptocaryoxylon* has been reported only three times: a) with the species *Cryptocaryoxylon gippslandicum* Leisman (1986) from the Upper Eocene–Oligocene (39 Mya) of Australia, b) with the species *C. hancockii*, *C. meeksii* and *C. radiporosum* Wheeler & Manchester (2002) from the middle Eocene of North America and c) with the species *Cryptocaryoxylon oleiferum* which has been found recently belonging in the late Pleistocene of Argentina (Ramos *et al.* 2015).

The modern genus *Cryptocarya* belongs to Cryptocaryeae Nees tribe (Pl. 3) which is related to the Southern hemisphere contrary to *Laurinoxylon* species already described which are related to the North hemisphere and to the Asian/Neotropics genera. This seems to be important information on the evolution of the woods consist the Miocene Forest of Lesbos and Lemnos and on the distribution of their present day representatives.

3.2.2 Identification of Coniferous wood ("Gymnosperm") from Lemnos Island

3.2.2.1

Cupressaceae Gray sensu Farjon 2005b

Cupressales

Taxodiaceae Warming

***Taxodioxylon* Hartig emend. Gothan 1905**

***Taxodioxylon* sp.1**

(Plate 33A_1–33*O,* Lemnos Island Fossil Flora Appendix)

Material: DMLHBA1 (3 slides)
Locality: Varos, Central Lemnos Island, Greece
Stratigraphic horizon: Inside volcanic tuff
Age: early Miocene

Macroscopic description. The slides come from a specimen exposed at the surface only a few meters away from the central road connecting Mirina with Moudros at Varos village (unfortunately the exposed part has marks which prove that it has been treated as a "souvenir"). The specimen belongs to a permineralised tree trunk (stump) the main part of which is still covered under the volcanic material (although this fact doesn't allow us to have a complete image about the dimensions of the finding, is important to remain like this until the specimen's protection will be guaranteed by the authorities, e.g. hosted in a museum or under a special kiosk accompanied with a presidential decree respectively). According to our estimations the diameter of the trunk is at least 1 meter and its length is at least 2 meters. (Pl. 33A_1–33A_2).

Microscopic description**: Transversal (cross) section:** Distinct growth ring boundaries with a width from 0.4–2 mm (mean: 1 mm), transition from earlywood to latewood gradual (Pl. 33*B*–33*C*). False rings are absent. Latewood tracheids thin–walled, axial parenchyma in diffuse (and in some cases looks in tangentially zonate) arrangement (Pl. 33*B*–33*C*) no intercellular spaces, no intercellular or traumatic canals or epithelial cells of wound ducts.

Tangential section: The rays are very high, with more than 30 cells (even with 60 cells), usually uniseriate and up to 3–seriate in width (Pl. 33*D*), the existence of axial parenchyma is also seen in tangential, transverse end walls of axial parenchyma smooth (Pl. 33*E*–33*F*).

Radial section: Absence of ray tracheids, the tracheids are uniseriate but they have also 2 rows of (bi–seriate) bordered pits (tracheid pitting in radial walls biseriate), arrangement of tracheid pitting in radial walls opposite (occasionally seems alternate but it is due to the crowded pits), circular pits outline of a diameter of 20 (15–25) μm (depending on their situation: the uniseriate had a diameter of approximately 25 μm and the biseriate of around 18–20 μm), crassulae observed, well defined tori with sporadic torus extensions (= thickening bars “margo straps” in the pit membrane radiating from the torus to the margo periphery) (Pl. 33*I*–33*J*), up to 3 pits per cross field commonly arranged in one row of 2–3 pits per cross field, cupressoid (when there is compression) (Pl. 33*G*–33*O*) and taxodioid pits (Pl. 33*G*–33*H*), towards the latewood (at the high compression) the pits tend to become piceoid from cupressoid (Pl. 33*N*–33*O*), pit borders: angular, smooth (Pl. 33*H*) and nodular (Pl. 33*G,* 33*J*) end walls of ray parenchyma cells. Smooth horizontal walls of ray parenchyma cells (Pl. 33*G,* 33*H,* 33*J*–33*O*). Possibility of ray tracheids (Pl. 33*M, 33N*).

***Discussion*:** The predominance of taxodioid cross-field pits together with the occurrence of parenchyma characterizes the described wood as a representative of the morphogenus *Taxodioxylon* (Kräusel 1949, p. 168). Our sample has been compared with the *Taxodioxylon* species described from Lesbos Island: *Taxodioxylon albertense* (Penhallow) Shimakura, *T. pseudoalbertense* M. Nishida & H. Nishida, *T. gypsaceum* (Göppert) Kräusel and *T. megalonissum* Süss & Velitzelos. It has no traumatic resin canals so it is neither close to *Taxodioxylon albertense* (Penhallow) Shimakura nor to *T. pseudoalbertense* M. Nishida & H. Nishida. The internal structure of this sample seems to be close to *Taxodioxylon gypsaceum* (Göppert) Kräusel but not identical. Therefore some more comparisons with the published *Taxodioxylon* species from Europe (and not only from the Greek material) are needed.

The study of the fossil has shown a gradual transition from earlywood to latewood which is not characteristic for Pinaceae (but only for *Picea*). There are no resin canals so this specimen cannot belong to *Pinus*, *Picea*, *Larix* and *Pseudotsuga*. DMLHBA 1 specimen has abundant parenchyma so it could belong to Podocarpaceae (*Podocarpus*, *Phyllocladus* and *Dacrydium*), to Cupressaceae

(*Cupressus*, *Chamaecyparis*, *Juniperus*, *Sequoia* and *Taxodium*) and *Ginkgo* (Ginkgoales). From the latter genera the ones belonging to Podocarpaceae are excluded because of the absence of podocarpoid bordered pits, *Taxus* is excluded because it has spirals and our specimen doesn't, *Ginkgo* is excluded because it has araucarioid to cupressoid bordered pits, which is not the case for our sample. The radial tracheid pitting of our sample is not only uniseriate, so it belongs to Sequoia or *Taxodium*.

Plate 33

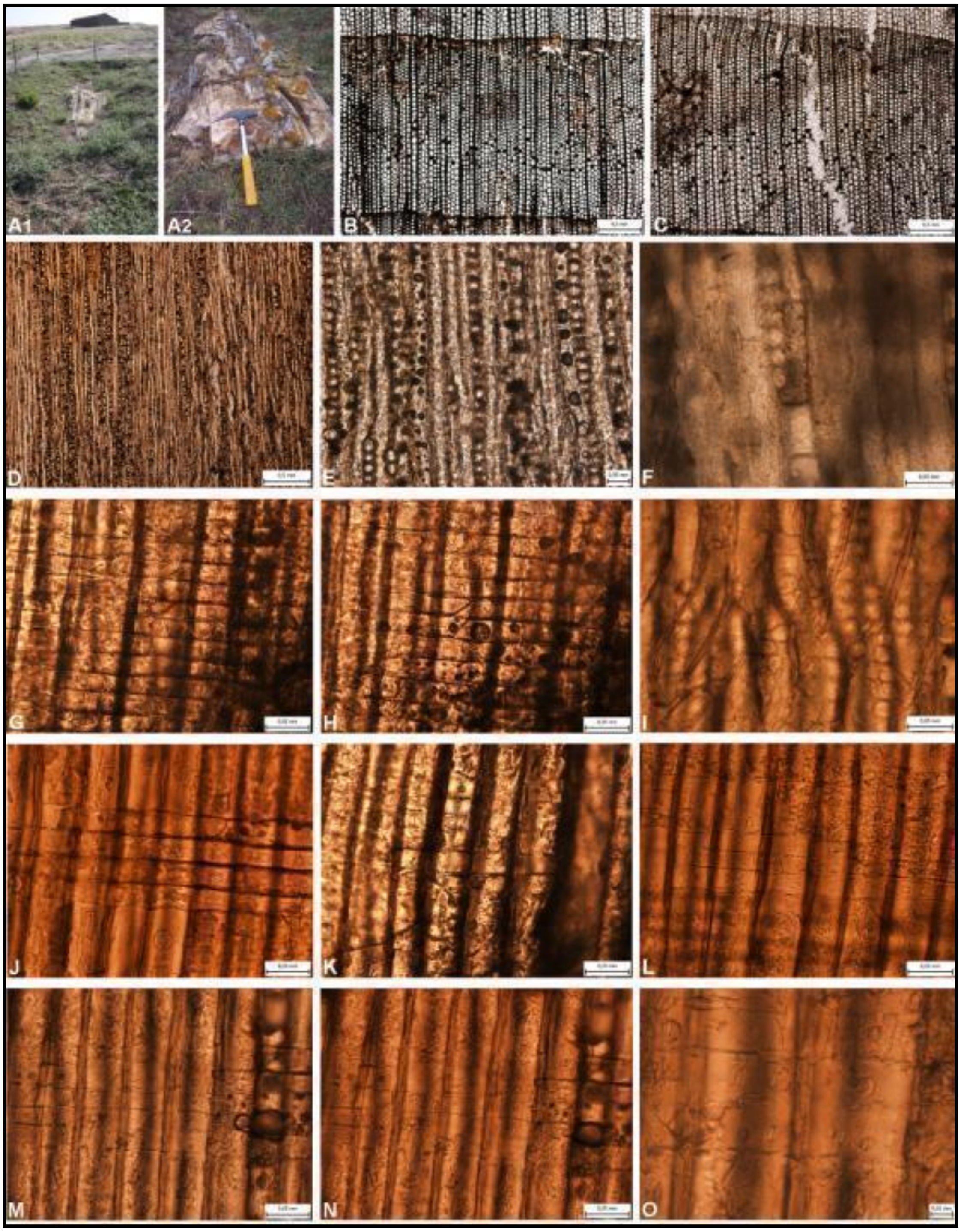


Plate 33 *Taxodioxylon* (sp. 1) Hartig emend. Gothan (DMLHBA 1)

A_1-A_2: DMLHBA1 specimen is exposed at the surface only a few meters away from the central road connecting Mirina with Moudros at Varos village. **B, C:** Distinct growth ring boundaries with a width from 0.4-2 mm, transition from earlywood to latewood gradual, latewood tracheids thin-walled, axial parenchyma in diffuse arrangement. **D:** Rays very high, with more than 30 cells, uni-c-seriate in width. **E, F:** Transverse end walls of axial parenchyma smooth. **G:** Up to 3 pits per cross field commonly arranged in one row of 2-3 pits per cross field, cupressoid (because of compression) and taxodioid pits, nodular walls of ray parenchyma cells, smooth horizontal walls of ray parenchyma cells. **H:** Up to 3 pits per cross field commonly arranged in one row of 2-3 pits per cross field, cupressoid (because of compression) and taxodioid pits, pit borders angular, smooth walls of ray parenchyma cells, smooth horizontal walls of ray parenchyma cells. **I:** Uniseriate and biseriate tracheid pitting, arrangement of tracheid pitting in radial walls opposite, up to 3 pits per cross field commonly arranged in one row of 2-3 pits per cross field, cupressoid (because of compression). **J:** Uniseriate and biseriate tracheid pitting, arrangement of tracheid pitting in radial walls opposite, circular pits outline, up to 3 pits per cross field commonly arranged in one row of 2-3 pits per cross field, cupressoid (because of compression), nodular walls of ray parenchyma cells, smooth horizontal walls of ray parenchyma cells. **K:** Up to 3 pits per cross field commonly arranged in one row of 2-3 pits per cross field, cupressoid (because of compression), smooth horizontal walls of ray parenchyma cells. **L:** Up to 3 pits per cross field commonly arranged in one row of 2-3 pits per cross field, cupressoid (because of compression), smooth horizontal walls of ray parenchyma cells. **M:** Up to 3 pits per cross field commonly arranged in one row of 2-3 pits per cross field, cupressoid (because of compression), smooth horizontal walls of ray parenchyma cells, possibility of ray tracheids. **N:** Up to 3 pits per cross field commonly arranged in one row of 2-3 pits per cross field, cupressoid (because of compression), towards the latewood (at the high compression) the pits tend to become piceoid from cupressoid, smooth horizontal walls of ray parenchyma cells, possibility of ray tracheids. **O:** Up to 3 pits per cross field commonly arranged in one row of 2-3 pits per cross field, cupressoid (because of compression), towards the latewood (at the high compression) the pits tend to become piceoid from cupressoid, smooth horizontal walls of ray parenchyma cells.

3.2.2.2

Cupressaceae Gray sensu Farjon 2005b

Cupressales

Taxodiaceae Warming

Taxodioxylon Hartig emend. Gothan 1905

Taxodioxylon sp.2

(Plate 34*A*–34*F*, Lemnos Island Fossil Flora Appendix)

Material: DMLHM 27 (3 slides)
Locality: Moudros *(*Central–Eastern Lemnos Island), Greece
Stratigraphic horizon: inside volcanic tuff
Age: early Miocene

Macroscopic description. The dimensions of the coniferous specimen DMLHM 27 from Moudros (in cm) are the following: 32 x 25 x 8, (Plate 34*A*).

Microscopic description: Biseriate opposite tracheid pitting (Plate 34*C*), bordered pits torus, crassulae not observed, rays uniseriate and short b–seriate (Plate 34*B*), taxodioid cross–field pits up to 5 per cross–field (Plate 34*D*, 34*E*, 34*F*). Although more slides are required for the determination of this sample the observation from the slides in hand show that DMLHM 27 is a part of a *Taxodioxylon* representative.

Discussion: The predominance of taxodioid cross-field pits together with the occurrence of parenchyma characterizes the described wood as a representative of the morphogenus *Taxodioxylon* (Kräusel 1949, p. 168). Our sample has been compared with the *Taxodioxylon* species described from Lesbos Island: *Taxodioxylon albertense* (Penhallow) Shimakura, *T. pseudoalbertense* M. Nishida & H. Nishida, *T. gypsaceum* (Göppert) Kräusel and *T. megalonissum* Süss & Velitzelos. It has no traumatic resin canals so it is not close to *Taxodioxylon albertense* (Penhallow) Shimakura or to *T. pseudoalbertense* M. Nishida & H. Nishida. The internal structure of this sample seems to be close but not identical to *Taxodioxylon megalonissum* Süss & Velitzelos, because of the short rays and the number and shape of the taxodioid cross field pits.

Plate 34

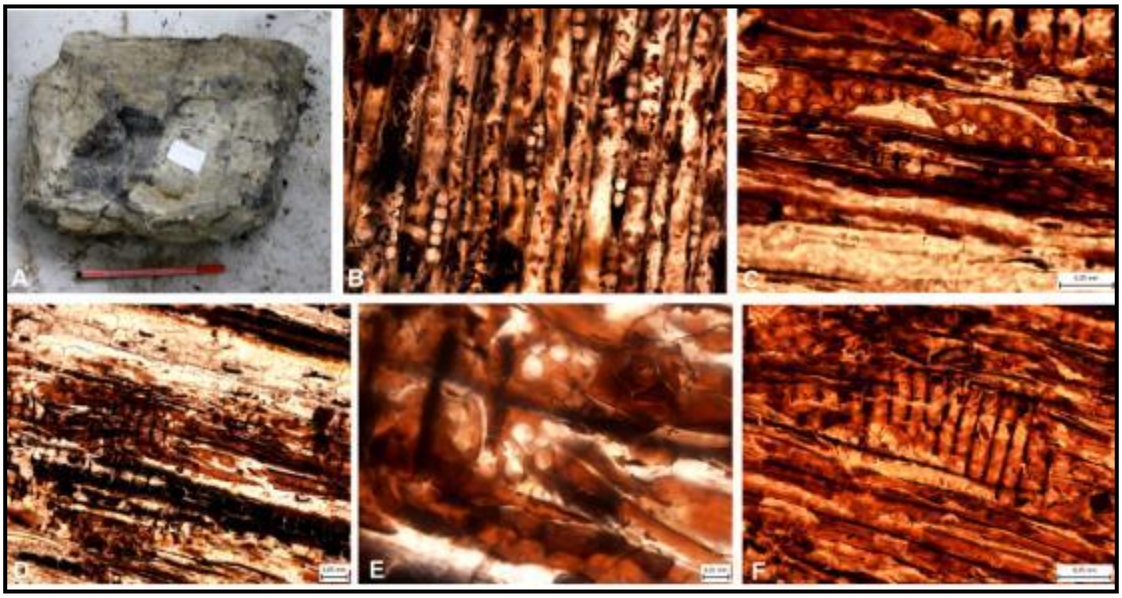


Plate 34 ***Taxodioxylon*** **(sp. 2) Hartig emend. Gothan (DMLHM27)**

A: Specimen DMLHM 27 with the following dimensions in cm: 32 x 25 x 8. Conifer. **B:** Short rays uni- and b-seriate. **C:** Biseriate opposite tracheid pitting. **D, E, F:** Taxodioid cross-field pits in 2 rows, up to 5 per cross-field.

C, D, E, F = RLS; B = TLS. TS, RLS and TLS denote transversal, radial and tangential longitudinal sections, respectively.

3.2.2.3

Cupressaceae Gray sensu Farjon 2005b

Cupressales

Taxodiaceae Warming

***Taxodioxylon* Hartig emend. Gothan 1905**

***Taxodioxylon* sp.3**

(Plate 35*A*–35*L*)

Material: DMLHM 10 (3 slides)
Locality: Moudros *(*Central–Eastern Lemnos Island), Greece
Stratigraphic horizon: inside volcanic tuff
Age: early Miocene

Macroscopic description. The dimensions of the coniferous specimen DMLHM 10 from Moudros (in cm) are the following: 25 x 17 x 7 (Pl. 35*A*).

Microscopic description. Growth ring boundaries distinct, wavy ring boundaries probably caused by buttressed form of trunks, most probably lack of resin ducts/canals, transition from early to latewood abrupt (with a thick zone of almost 15 cells of latewood tracheids with reduced radial diameters), (Pl. 35*B*), axial parenchyma cells with dark contents (resin substance) in diffuse arrangement (Pl. 35*B*, 35*G*), late wood tracheids thickwalled (Pl. 35*L*), associated intercellular spaces between the early wood tracheids (Pl. 35*C*), uniseriate opposite tracheid pitting (Pl. 35 *D*) with notched borders (Pl. 35*E*, 35*F*), tracheid pits torus, infrequent presence of crassulae (Pl. 35*F*), transverse end walls of axial parenchyma smooth (Pl. 35*G*) and probably irregularly thickened (Pl. 35*H*), rays uniseriate with a height up to 30 cells and partly short b–c–seriate (Pl. 35*G*, 35*I*), taxodioid cross–field pits up to 2 in a row and up to5 per cross–field (Pl. 35*J*, 35*K*).

***Discussion*:** Our sample has been compared with the *Taxodioxylon* species described from Lesbos Island: *Taxodioxylon albertense* (Penhallow) Shimakura, *T. pseudoalbertense* M. Nishida & H. Nishida, *T. gypsaceum* (Göppert) Kräusel and *T. megalonissum* Süss & Velitzelos. It has no traumatic resin canals so it is not close to *Taxodioxylon albertense* (Penhallow) Shimakura nor to *T. pseudoalbertense* M. Nishida & H. Nishida. More comparisons with the *Taxodioxylon* species from Europe are needed.

Parenchyma is frequent and consistent in *Sequoia* and *Taxodium* and absent or infrequent in *Pinus*, *Taxus*, *Torreya* and *Larix* (Panshin & DeZeeuw 1980). As indicated by Panshin & DeZeeuw (1980), maximum tangential tracheid diameter may have diagnostic value, especially for species with unusually large (as in *Sequoia*) diameters (and also in accordance with the identifications of Visscher & Jagels 2003).

Taxodioid cross–field pitting, relatively wide tracheids, abundant axial parenchyma distributing in diffuse or tangential zonate, entirely parenchymatous rays with smooth, thin or slightly thickened but un–pitted horizontal walls and absence of normal resin ducts are feautures of Taxodiaceae (Phillips, 1948; Yi *et al.* 2003).

The conifer family Taxodiaceae was widespread in recent geological history where for instance they were often the dominant floristic component such as in lowland swamp forests of North America, Europe and Asia during the Late Cretaceous and into the Middle Tertiary (Chaney, 1951; Florin, 1963). The Taxodiaceae then declined and ultimately disappeared from Europe during the Pliocene and Early Pleistocene (Michaux *et al.*, 1979).

Species of taxodiaceous wood are difficult to distinguish from each other because of their overlapping characters (e.g., Fairon–Demaret *et al.*, 2003). Usually the determination of taxodiaceous fossil or extant secondary xylem relies heavily on the cross–field pits (Peirce, 1936; Krausel, 1949) and the morphology of the horizontal wall of the secondary xylem parenchyma cells (Greguss, 1955). Taxodiaceous woods generally lack true resin canals, lack indentures in horizontal walls of the ray parenchyma, and have taxodioid type cross–field pits (Greguss 1955; Panshin & DeZeeuw 1980).

The Taxodiaceae is represented by 9 genera and 12 species with a restricted geographical distribution in humid, temperate to subtropical regions of Asia, North America and Tasmania (Wu and Raven, 1999). Taxodiaceae has more recently been incorporated into the Cupressaceae family (Eckenwalder 1976; Butala & Cridland 1978; Judd *et al.* 2002; Visscher & Jagels 2003).

According to descriptions of Phillips (1948), Greguss (1972), Gromyko (1982) and Zhou and Jiang (1994), our woods are separated from *Athrotaxis* by absence of nodular end walls in axial parenchyma and from *Taiwania* and *Taxodium* by taxodioid cross–field pitting rather than cupressoid (Yi *et al.*, 2003).

The abundance of axial parenchyma, uniseriate or oppositely paired bi–seriate, circular pits on the radial walls of tracheids, and large taxodioid cross–field pits, description here of fossil woods agrees in all characteristics with *Taxodioxylon* (Gothan, 1905).

Plate 35

Plate 35 *Taxodioxylon* (sp. 3) Hartig emend. Gothan (DMLHM10)

A: DMLHM 1O: 25 x 17 x 7 cm. Conifer. **B:** Growth ring boundaries distinct, occurrence of axial parenchyma cells with dark contents (resin substance), transition from early to latewood abrupt. **C:** Associated intercellular spaces between the early wood tracheids. **D:** Uniseriate opposite tracheid pitting. **E, F:** Bordered pits with notched borders, torus and crassulae. **G:** Transverse end walls of axial parenchyma smooth, rays up to c-seriate. **H:** Transverse end walls of axial parenchyma irregularly thickened. **I:** Short rays uni-b-c-seriate. **J, K:** Taxodioid cross-field pits up to 2 in a row per cross-field. **L:** Late wood tracheids thickwalled. B, C, L = TS; D, E, F, J, K = RLS; G, H, I = TLS. TS, RLS and TLS denote transversal, radial and tangential longitudinal sections, respectively.

3.2.2.4 (More) Studied specimens from Moudros area

Material: DMLHM 1 (3 slides), DMLHM 2 (3 slides), DMLHM 3 (3 slides), DMLHM 4 (7 slides), DMLHM 7 (3 slides), DMLHM 8 (3 slides), DMLHM 9 (3 slides), DMLHM 12.1 (3 slides), DMLHM 12.2 (3 slides), DMLHM 13 (3 slides), DMLHM 14 (4 slides), DMLHM 15, DMLHM 16 (2 slides), DMLHM 17 (2 slides), DMLHM 18, DMLHM 19 (3 slides), DMLHM 20 (3 slides), DMLHM 21, DMLHM 22 (3 slides), DMLHM 23 (3 slides), DMLHM 25, DMLHM 26, DMLHM 36 (3 slides), DMLHM 38 (3 slides), DMLHM 39, DMLHM 40, DMLHM 41, DMLHM 42, DMLHM 43, DMLHM 44.

(Plate 36*A*–36*D*, 36*F*–36*U*; Plate 37*A*–37*C*, 37*E*–37*H*)
Locality: Moudros *(*Central–Eastern Lemnos Island), Greece
Stratigraphic horizon: inside volcanic tuff
Age: early Miocene

Macroscopic description. The dimensions of the coniferous specimens from Moudros (in cm) are the following:
DMLHM 1: 38 x 26 x 16, DMLHM 2: 28 x 26 x 15, DMLHM 3: 27 x 16 x 15, DMLHM 4: 32 x 14 x 22, DMLHM 7: 17 x 15 x 7, DMLHM 8: 21 x 12 x 5, DMLHM 9: 13 x 11 x 6, DMLHM 12: 21 x 20 x 11, DMLHM 13: 30 x 19 x 12, DMLHM 14: 20 x 17 x 11, DMLHM 15: 24 x 18 x 15, DMLHM 16: 14 x 15 x 9, DMLHM 17: 17 x 8 x 5, DMLHM 18: 15 x 16 x 13 , DMLHM 19: 17 x 15 x 13, DMLHM 20: 25 x 20 x 12, DMLHM 21: 24 x 16 x 8, DMLHM 22: 17 x 11 x 6, DMLHM 23: 15 x 12 x 7, DMLHM 25: 22 x 16 x 11, DMLHM 26: 32 x 27 x 19, DMLHM 36: 43 x 24 x 22, DMLHM 38: 40 x 29 x 14, DMLHM 39: 40 x 29 x 16, DMLHM 40: 42 x 37 x 25, DMLHM 41: 43 x 37 x 25, DMLHM 42: 47 x 46 x 23, DMLHM 43: 64 x 40 x 25, DMLHM 44: 58 x 33 x 25.

Microscopic description. The preservation of this material was not that good. More and better slides are required for the full description and identification of the specimens.

Plate 36

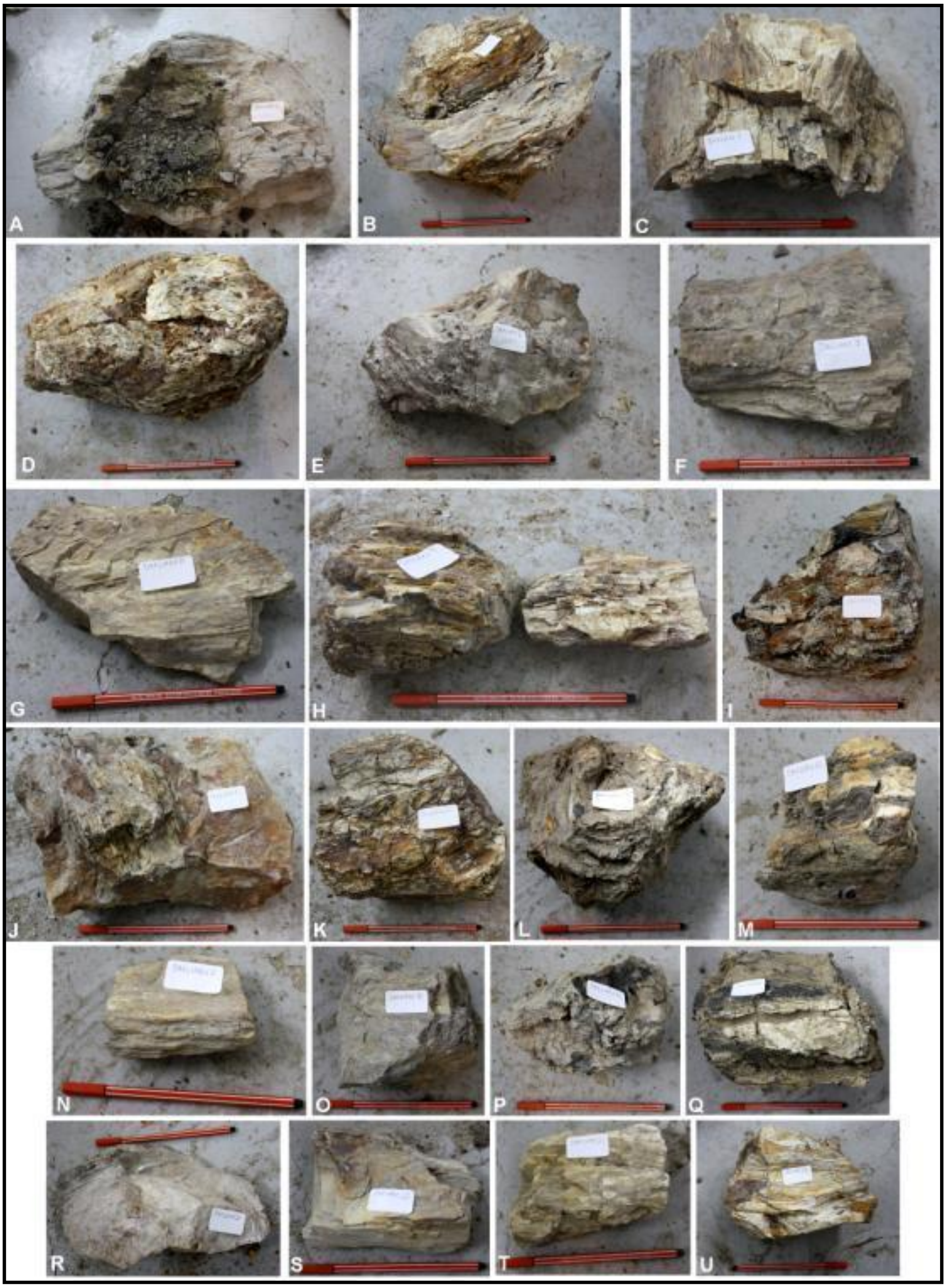


Plate 37

Plate 37. Studied specimens from Moudros area with their dimensions in cm.

A: DMLHM 26: 32 x 27 x 19 cm. Conifer. **B:** DMLHM 36: 43 x 24 x 22 cm. Conifer. **C:** DMLHM 38: 40 x 29 x 14 cm. Conifer. **D:** DMLHM 39: 40 x 29 x 16 cm. *Rhizopalmoxylon*. **E:** DMLHM 40: 42 x 37 x 25 cm. Conifer. **F:** DMLHM 41: 43 x 37 x 25 cm. Conifer. **G:** DMLHM 42: 47 x 46 x 23 cm. Conifer. **H:** DMLHM 43: 64 x 40 x 25 cm. Conifer. **I:** DMLHM 44: 58 x 33 x 25 cm. *Rhizopalmoxylon*.

Plate 36. Studied specimens from Moudros area with their dimensions in cm.

A: DMLHM 1: 38 x 26 x 16 cm. Conifer. **B:** DMLHM 2: 28 x 26 x 15 cm. Conifer. **C:** DMLHM 3: 27 x 16 x 15 cm. Conifer. **D:** DMLHM 4: 32 x 14 x 22 cm. Conifer. **E:** DMLHM 6: 28 x 19 x 13 cm. Angiosperm. **F:** DMLHM 7: 17 x 15 x 7 cm. Conifer. **G:** DMLHM 8: 21 x 12 x 5 cm. Conifer. **H:** DMLHM 9: 13 x 11 x 6 cm. Conifer. **I:** DMLHM 12: 21 x 20 x 11 cm. Conifer. **J:** DMLHM 13: 30 x 19 x 12 cm. Conifer. **K:** DMLHM 14: 20 x 17 x 11 cm. Conifer. **L:** DMLHM 15: 24 x 18 x 15 cm. Conifer. **M:** DMLHM 16: 14 x 15 x 9 cm. Conifer. **N:** DMLHM 17: 17 x 8 x 5 cm. Conifer. **O:** DMLHM 18: 15 x 16 x 13 cm. Conifer. **P:** DMLHM 19: 17 x 15 x 13 cm. Conifer. **Q:** DMLHM 20: 25 x 20 x 12 cm. Conifer. **R:** DMLHM 21: 24 x 16 x 8 cm. Conifer. **S:** DMLHM 22: 17 x 11 x 6 cm. Conifer. **T:** DMLHM 23: 15 x 12 x 7 cm. Conifer. **U:** DMLHM 25: 22 x 16 x 11 cm. Conifer.

3.2.2.5 (More) Studied specimens from Thanos and New Moudros site

Material*:* DMLHNM 1 (3 slides), DMLHNM 2 (3 slides), DMLHNM 3 (3 slides), DMLHNM 4 (7 slides), DMLHNM 5 (3 slides), DMLHNM 6 (4 slides), DMLHNM 7 (3 slides), DMLHNM 8 (3 slides), DMLHNM 9 (3 slides), DMLHNM 10 (3 slides), DMLHNM 11 (3 slides), DMLHTH 1 (3 slides).

(Plate 38*A*–38*F*)

Locality: Moudros New Site *(*Central–Eastern Lemnos Island), Thanos *(*Western Lemnos Island), Greece
Stratigraphic horizon: inside volcanic tuff
Age: early Miocene

Microscopic description: Among the findings there are not only conifers (e.g., DMLHNM 1, Plate 38*F*) and coniferous roots (Plate 38*E*) but also *Rhizopalmoxylon* remnants (Plate 38*F*) is a sample with imprints of *Sequoia abietina* (Brongniart) Knobloch cones (Plate 38*A*). This fossil has been compared with the present day *Sequoia* cones found in Bulgaria (Plate 38*B*, 38*C*).

The specimen DMLHTH 1 represents a part of a fossil coniferous wood from Thanos village. This is the first time ever that the occurrence of plant fossils is referred from this area.

Plate 38

Plate 38. New Moudros Site.

A: Imprints of the cone of *Sequoia abietina* (Brongniart) Knobloch in opal. **B:** Foliage and cones of the present day *Sequoia*. The samples of the modern *Sequoia* were taken in Bulgaria. **C:** Cone of the present day *Sequoia*. The sample is used for comparison with the fossil imprint found in Lemnos Island. **D:** *Rhizopalmoxylon* from Moudros area. **E:** Fossil root from Moudros area. **F:** Specimen DMLHNM 1 internal structure.

3.3 LEMNOS ISLAND FOSSIL FLORA APPENDIX (Berger 1953a, Roussos 1993, Süss & Velitzelos 1993, Velitzelos *et al.* 2014, modified). The new findings and the re-studied samples are shown in bold:

GYMNOSPERM WOOD

Cedroxylon sp. (found in Moudros, Central – Eastern Lemnos Island, described by Berger 1953a).

Pinoxylon parenchymatosum Süss & Velitzelos (found in Moudros, Central – Eastern Lemnos Island, described by Süss & Velitzelos 1993).

***Taxodioxylon* (sp.1) Hartig emend. Gothan** (found in Varos, Central – Eastern Lemnos Island, described by D. Mantzouka).

***Taxodioxylon* (sp.2) Hartig emend. Gothan** (found in Moudros, Central – Eastern Lemnos Island, hosted at the Municipality of Moudros, described by D. Mantzouka).

***Taxodioxylon* (sp.3) Hartig emend. Gothan** (found in Moudros, Central – Eastern Lemnos Island, hosted at the Municipality of Moudros, described by D. Mantzouka).

***ANGIOSPERM* WOOD**

Cornoxylon pappi W. Berger (found in Moudros, Central – Eastern Lemnos Island, described by Berger 1953a).

Laurinoxylon ehrendorferi W. Berger (found in Moudros, Central – Eastern Lemnos Island, described by Berger 1953a).

***Laurinoxylon* cf. *ehrendorferi* Berger** (found in Moudros, Central – Eastern Lemnos Island, hosted at the Municipality of Moudros, described by D. Mantzouka).

***Cryptocaryoxylon* Leisman** (found in Moudros, Central – Eastern Lemnos Island, hosted at the Municipality of Moudros, described by D. Mantzouka).

Rhizopalmoxylon sp. (hosted at the Municipality of Moudros, Central – Eastern Lemnos Island, found and identified by E. Velitzelos)

LEAVES

PTERYDOPHYTES

Pronephrium stiriacum (Unger) Erw. Knobloch et Kvaček (as *Goniopteris styriaca* Heer, found in Moudros, Central – Eastern Lemnos Island, described by Berger 1953a. The species has been emended by Velitzelos *et al.* 2014).

Cyclosorus stiriaca (Unger) Ching & Takhtajan (hosted at the Municipality of Moudros, Central – Eastern Lemnos Island, found and identified by E. Velitzelos)

GYMNOSPERMS

Glyptostrobus europaeus (Brongniart) Unger (found in Moudros, Central – Eastern Lemnos Island, described by Berger 1953a).

Sequoia abietina (Brongniart) Erw. Knobloch (cones found in Moudros, Central – Eastern Lemnos Island, described by Berger 1953a, referred by Süss & Velitzelos 1993).

***Sequoia abietina* (Brongniart) Erw. Knobloch** (cones found in Moudros, Central – Eastern Lemnos Island by D. Mantzouka).

Doliostrobus sp. (hosted at the Municipality of Moudros, Central – Eastern Lemnos Island, found and identified by E. Velitzelos).

ANGIOSPERMS

Acer tricuspidatum Bronn [as *A. trilobatum* A. Braun found in Myrina (“Kastron”), Western Lemnos Island, described by Berger 1953a. The species has been emended by Velitzelos *et al.* 2014].

cf. *Quercus drymeja* Unger [as *Quercus lonchitis* Unger [found in Myrina (“Kastron”), Western Lemnos Island, described by Berger 1953a. The species has been emended by Velitzelos *et al.* 2014].

Cinnamomum polymorphum (A. Braun) Kräusel et Weyland (found in Moudros, Central – Eastern Lemnos Island, referred by Süss & Velitzelos 1993).

Daphnogene polymorpha (A. Braun) Ettingshausen (as *Cinnamomum* cf. *scheuchzeri* Heer, found in Moudros, Central – Eastern Lemnos Island, described by Berger 1953a. The species has been emended by Velitzelos *et al.* 2014).

Daphnogene polymorpha (A. Braun) Ettingshausen [as *Cinnamomum polymorphum* (A. Braun) Kräusel et Weyland found in Myrina (“Kastron”), Western Lemnos Island, described by Berger 1953a. The species has been emended by Velitzelos *et al.* 2014].

Daphnogene polymorpha (A. Braun) Ettingshausen [as *Cinnamomum polymorphum* (A. Braun) Kräusel et Weyland, found in Moudros, Central – Eastern Lemnos Island, described by Berger 1953a. The species has been emended by Velitzelos *et al.* 2014].

*Daphnogene polymorpha (*A. Braun) Ettingshausen [as *Daphnogene lanceolata* Unger found in Myrina (“Kastron”), Western Lemnos Island, described by Berger 1953a. The species has been emended by Velitzelos *et al.* 2014].

Dicotyledoneae fam., gen. et spec. indet. [aff. *Myrica,* Fagaceae, Lauraceae found in Myrina (“Kastron”), Western Lemnos Island, described by Berger 1953a. The family has been emended by Velitzelos *et al.* 2014].

Engelhardia vel *Q. drymeja* Unger [as *Myrica kymeana* (Unger) W. Berger found in Myrina (“Kastron”), Western Lemnos Island, described by Berger 1953a. The species has been emended by Velitzelos *et al.* 2014].

Eriolaena sp*.* [found in Myrina (“Kastron”), Western Lemnos Island, described by Berger 1953a].

Fagaceae vel *Lauraceae* (as *Andromeda saportana* Heer, found in Moudros, Central – Eastern Lemnos Island, described by Berger 1953a. The species has been emended by Velitzelos *et al.* 2014).

Lauraceae vel Fagaceae [as *“Laurus” princeps* Heer found in Myrina (“Kastron”), Western Lemnos Island, described by Berger 1953a. The species has been emended by Velitzelos *et al.* 2014].

Monocotyledoneae fam., gen. et spec. indet. (aff. Cyperaceae) [found in Myrina (“Kastron”), Western Lemnos Island, described by Berger 1953a].

palm roots, palm seeds, palm leaves (found in Moudros, Central – Eastern Lemnos Island, referred by Süss & Velitzelos 1993).

Phragmites sp. (found in Moudros, Central – Eastern Lemnos Island, described by Berger 1953a).

Sabal sp. (found in Moudros, Central – Eastern Lemnos Island, described by Velitzelos *et al.* 2014).

Zelkova zelkovifolia (Unger) Bůžek, Kotlaba [as *Z. praelonga* (Unger) W. Berger found in Myrina ("Kastron"), Western Lemnos Island, described by Berger 1953a. The species has been emended by Velitzelos *et al.* 2014].

Eotrigonobalanus furcinervis (Rossmassler) Walther & Kvaček (hosted at the Municipality of Moudros, Central – Eastern Lemnos Island, found and identified by E. Velitzelos).

Daphnogene cinnamomea (Rossmassler) Knobloch (hosted at the Municipality of Moudros, Central – Eastern Lemnos Island, found and identified by E. Velitzelos).

Sabal raphifolia (Sternberg) Knobloch & Kvaček (hosted at the Municipality of Moudros, Central – Eastern Lemnos Island, found and identified by E. Velitzelos).

Pterocarya sp. (hosted at the Municipality of Moudros, Central – Eastern Lemnos Island, found and identified by E. Velitzelos).

Rhodomyrtophyllum reticulosum (Rossmassler) Knobloch & Kvaček (hosted at the Municipality of Moudros, Central – Eastern Lemnos Island, found and identified by E. Velitzelos).

Salix sp. (hosted at the Municipality of Moudros, Central – Eastern Lemnos Island, found and identified by E. Velitzelos).

Neolitsea sp. (hosted at the Municipality of Moudros, Central – Eastern Lemnos Island, found and identified by E. Velitzelos).

SPORES AND POLLEN

PTERYDOPHYTES

Polypodiaceae (Agia Paraskevi, close to the road connecting Myrina to Therma, Western Lemnos Island, identified by Chr. Ioakeim in Roussos 1993).

ANGIOSPERMS

Palmae, (Agia Paraskevi, close to the road connecting Myrina to Therma, Western Lemnos Island, identified by Chr. Ioakeim in Roussos 1993).

Engelhardtia (Agia Paraskevi, close to the road connecting Myrina to Therma, Western Lemnos Island, identified by Chr. Ioakeim in Roussos 1993).

Symplocos (Agia Paraskevi, close to the road connecting Myrina to Therma, Western Lemnos Island, identified by Chr. Ioakeim in Roussos 1993).

Liquidambar (Agia Paraskevi, close to the road connecting Myrina to Therma, Western Lemnos Island, identified by Chr. Ioakeim in Roussos 1993).

Carya (Agia Paraskevi, close to the road connecting Myrina to Therma, Western Lemnos Island, identified by Chr. Ioakeim in Roussos 1993).

Quercus (Agia Paraskevi, close to the road connecting Myrina to Therma, Western Lemnos Island, identified by Chr. Ioakeim in Roussos 1993).

type-*Castanea* (Agia Paraskevi, close to the road connecting Myrina to Therma, Western Lemnos Island, identified by Chr. Ioakeim in Roussos 1993).

Tricolporopollenites dolium (Agia Paraskevi, close to the road connecting Myrina to Therma, Western Lemnos Island, identified by Chr. Ioakeim in Roussos 1993).

Tricolporopollenites rillensis (Agia Paraskevi, close to the road connecting Myrina to Therma, Western Lemnos Island, identified by Chr. Ioakeim in Roussos 1993).

Tricolporopollenites fallax (Agia Paraskevi, close to the road connecting Myrina to Therma, Western Lemnos Island, identified by Chr. Ioakeim in Roussos 1993).

Osmundaceae (Agia Paraskevi, close to the road connecting Myrina to Therma, Western Lemnos Island, identified by Chr. Ioakeim in Roussos 1993).

Graminae (Agia Paraskevi, close to the road connecting Myrina to Therma, Western Lemnos Island, identified by Chr. Ioakeim in Roussos 1993).

Amaranthaceae-Chenopodiaceae (Agia Paraskevi, close to the road connecting Myrina to Therma, Western Lemnos Island, identified by Chr. Ioakeim in Roussos 1993).

CONIFERS

Pinaceae (Agia Paraskevi, close to the road connecting Myrina to Therma, Western Lemnos Island, identified by Chr. Ioakeim in Roussos 1993).

4. ALONISSOS ISLAND

4.1.1 Introduction

Alonissos Island belongs to the Northern Sporades. It covers an area of 64.5 Km^2 and it has been a geological attraction from the 3rd century B.C. with the findings of giant skeletons accompanied by myths. During the 19th century the explorations for mineral resources had lead the famous geologists of the time to visit the Island. The discovery of lignite had also generated the interest of the palaeobotanists for the palaeoflora of the island. Among the palaeofloristic findings was the first occurrence (the holotype) of *Taxodium europaeum*. During this study there was an effort of revealing the exact locality where this species had been found almost 200 years ago and presenting new information concerning the palaeobotany of Alonissos Island.

4.1.2 Localities and Geology

Alonissos (or Iliodroma or Chilidromia) is a long, narrow, mountainous island belonging to the North Sporades, situated close to the Magnesian peninsula (Thessaly – Volos) at the South–eastern of Euboea Island (Fig. 32).

The geology of the island is studied by several scientists (e.g. I.G.M.E. 1975, Pe–Piper *et al.* 1996, Poulimenos & Karkanas 1998, Papanikolaou *et al.* 2002, Evelpidou *et al.* 2013) and extensively discussed in Jacobshagen & Matarangas (2004), from the bottom to the top consists of (Fig. 33):

- A Pelagonian unit: composed of meta–carbonates of up to 500m thickness (light grayish color, thin– to medium–bedded dolomitic in the bottom of Triasso–Jurassic age and calcitic marbles nearly unbedded at the top). According to Kelepertsis (1975) the age of the upper part of the succession is Kimmeridgian (Upper Jurassic) as proved by the following fossils: *Cladocoropsis* sp., *Clypeina* sp., *Ellipsactinia*, *Pseudocyclammina* sp., *Trocholina* sp., *Nerinea*.
- Eohellenic nappe relics: composed of grayish phyllites and calcschists, with intercalations of thin–bedded black marbles and quartzites (metaturbidites).
- Mesoautochthonous complex : with an 8–meters unit of Basal Conglomerates of Albian or Cenomanian age resting upon a karstic relief (which contains relics of metabauxite filling in places) and the overlying Rudist Limestones with thickbedded

  to massive, roughly recrystallised grayish marbles of several hundred meters thickness of Cenomanian–Turonian age.

- Palouki formation: overlies the Pelagonian marbles or the Eohellenic metabasites, respectively, with tectonical contacts and includes an alternation of marbles, metasandstones, and schists.
- Neogene deposits: consisting of conglomerates, limestones and marls, lignitic formation and reddish clastics.

In I.G.M.E. study (1975, made by Kelepertzis), the Neogene formations of Alonissos Island include Pontian red clays and continental conglomerates overly the formation of the marls, clays and limestones interbedded by thin layers of lignite. Pontian some decades ago was treated as a part of Pleiocene but today this concept has been revised and Pontian stage belongs to the late Miocene period (upper Tortonian–Messinian, see in Popov *et al.* 2006, Fig.1). Inside these red clays (Fig. 34) mammal remains have been found [e.g., Schneider (1972) had found the upper jaw of *Hipparion*]. Consequently the plant fossiliferous layer is early–middle Miocene in age, although the age of the plant fossiliferous layer as proposed by Mai (1995) and LePage (2007) is Burdigalian, early Miocene. This latter layer includes also *Planorbis* sp., *Helix* cf. *vermiculata*, *Melanopsis buccinoides* and fresh water ostracodes (identifications by Dr. Kauffmann, Dr. Risch & Dr. Tsaila–Monopoli in I.G.M.E. 1975).

Virlet (1835) had described the geological formations of Alonissos Island (from the bottom to the top) with a detailed description of the Neogene as follows: 1. Mica–slate, clay–slate and limestone, 2. Blue and grey limestone, 3. A fresh water tertiary formation containing lignites which occupies half of the surface of the island, and was mistaken for coal. The lower part of the last formation is situated 200 or 300 meters above the sea, and is constituted of blue or green marls with a great deposit of fresh water and land shells belonging chiefly to the genera *Planorbis, Paludina, Helix*. Over these marls lie thin strata of marly limestone without fossils, containing a lignite layer of about 0.6 meters, intermixed with clay and shells. Above the lignite grey marls occur, filled with the debris of fossil plants. The whole succession is about 58 meters in thickness. Among the fossils obtained from this formation, the most numerous belonged to a species examined by Adolphe Théodore Brongniart and named by him as *Taxodium europaeum*.

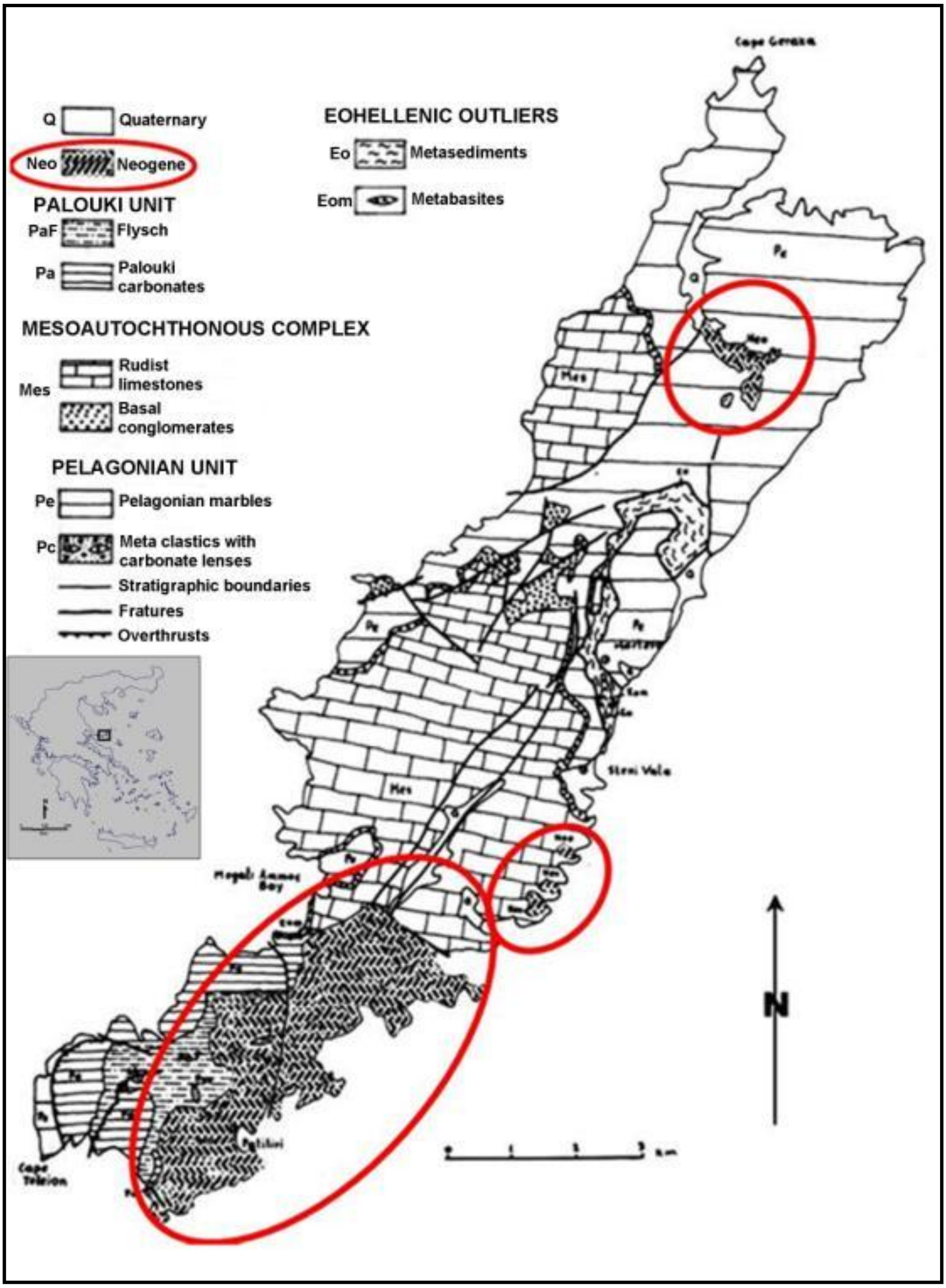


Fig. 32: Geological sketch– map of Alonnisos island, by Jacobshagen & Matarangas (2004) based on Kelepertsis (1975), modified. The Neogene formations are included by the red circles.

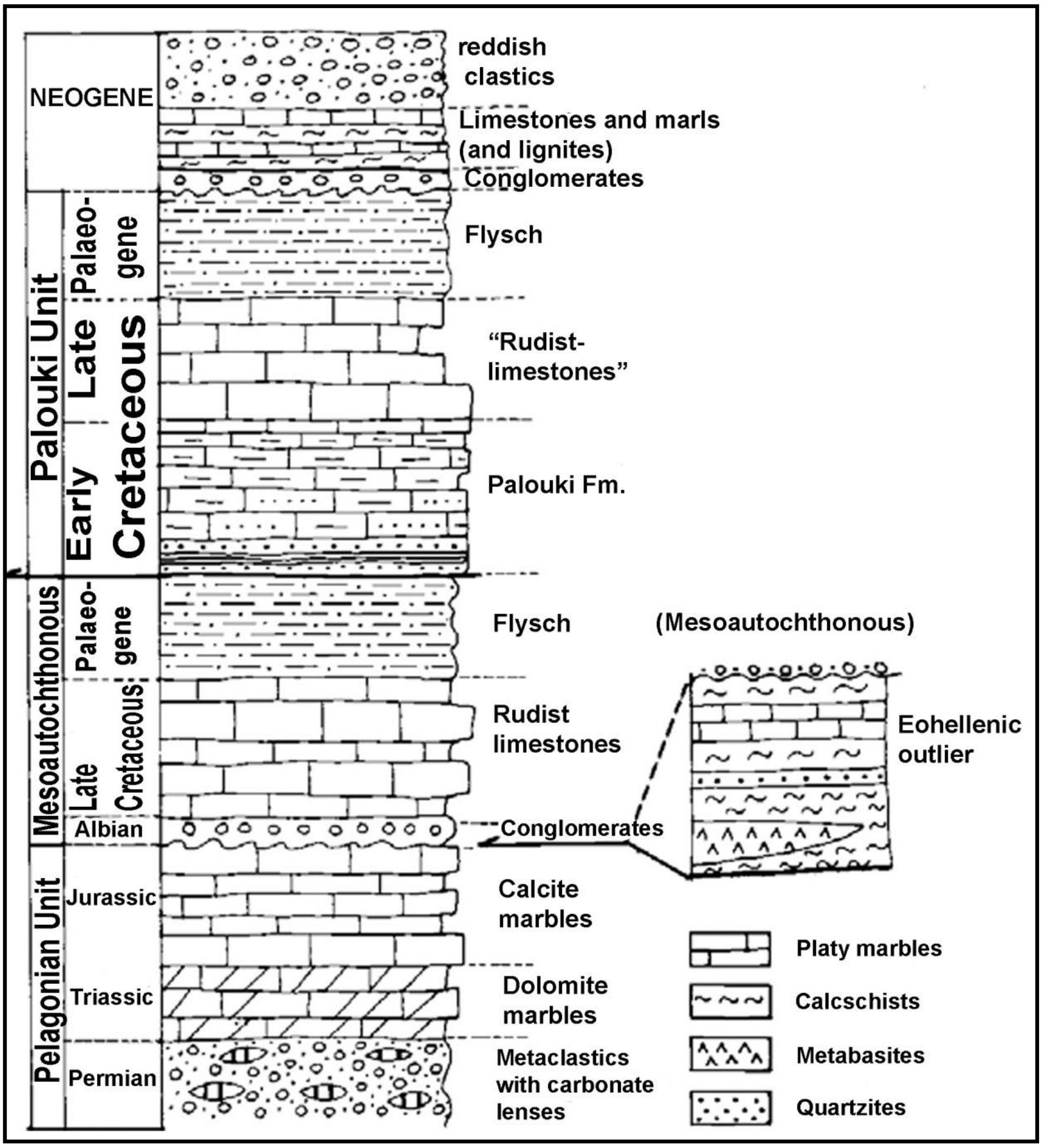


Fig. 33: Tectonostratigraphic column of Alonnisos island (according to Jacobshagen & Matarangas 2004, modified).

Almost 200 years after the first reference about the lignitic horizon and *Taxodium europaeum* finding and taking into account the publication of the 19th century (e.g., Brongniart 1832, 1833, 1834, 1861; Virlet 1833, 1834, 1835; Gaudry 1860) we found the locality where the lignite and the plant fossils were hosted, in a close distance of Votsi village (Plate 39).

Fig. 34: Red clays close to “Kokkino Kastron” locality.

4.1.3 Material and Methods

More than 80 specimens with gastropods, plant remnants and lignite samples have been collected from this locality (Plate 39). Unfortunately we were not able to find again *Taxodium europaeum* or leaves’ imprints because the area had been an active mine until some decades ago and the plant fossiliferous material situated on the top of the lignite has been disappeared (removed).

After a research we found that the holotype of *Taxodium europaeum* from Alonissos Island is hosted at the Muséum national d'Histoire naturelle in Paris (MNHN). Therefore we asked for photos of the sample in order to include them at this study.

The specimens we collected from the field have mainly fossil gastropods (intact and fragments) and fossil plant remnants which unfortunately cannot be determined (bad preserved and mainly belonging to mixed horizons). The material collected is hosted at the Faculty of Geology and Geoenvironment, UOA for future studies. Among the lignite elements we collected for pollen examination in the future there was a part of a xylite.

Plate 39. Alonissos plant fossiliferous site.

A: The abandoned quarry where the lignite was exported from. **B:** The section with the fossil gastropods layer (bottom), the lignite and the plant fossiliferous marls (top). **C, E, G-V, Z-AE:** Undetermined plant fossiliferous specimens. **K** is an enlargement of a detail of **J. AA** is an enlargement of a detail of **Z**. **D, X, Y:** Lignite samples. **X** is a photo from the lignite sample studied microscopically and identified as *Pinuxylon*. **F, AF, AG:** Gastropod fossiliferous samples.

Plate 39

This fossil sample has been boiled in water to become softer, then cut with razor blades and mounted in glycerine jelly (e.g. Gryc & Sakala 2010). This procedure was followed for its preparation for thin sections in order to be photographed. This process took place at the Faculty of Forestry and Wood Technology, Department of Wood Science, Mendel University in Brno in order to be studied microscopically.

4.1.4 History of the recognition and identification of the plant fossils in Alonissos Island

Philostratus (3rd century B.C.), the ancient Greek philosopher from Lemnos Island, has given two descriptions about a giant skeleton of a mammal in Alonissos island, Greece (of about 5.5 m long) declared as one of the giants of the Gigantomachy, and in Imbros island (Imroz), Turkey (the last one has been found and identified as a Miocene mastodon) (Philostratus: On Heroes in Higgins and Higgins 1996).

According to Mayor (2000) if someone follows the descriptions of Philostratus there are also “gigantic skeletons” (Fig. 35) in Kos island, in Phrygia, in Thessaly, in Pallene: Kassandra Peninsula, Chalkidiki, northern Greece, which have been found and identified as deinotheres, mastodons, cave bears, woolly rhinos (e.g. Tsoukala & Melentis 1994). Gigantic skeletons from Crete (the “Cretan giants”) have been also described by Pliny, Philodemus and Solinus.

The observations of this philosopher (Philostratus) have been highly evaluated by us because they give as information about the Neogene formations and moreover the possible plant fossiliferous sites.

During the 19th century the research for the discovery of energy sources (e.g. coal) in Greece was widespread. Virlet had visited Greece soon after the coal was said to have been observed. He visited the Sporades Septentrionales or Devil’s Archipelago, situated at the mouth of the Gulfs of Volo and Salonica, near the coasts of Thessaly and Macedonia, where it was incorrectly said coal existed.

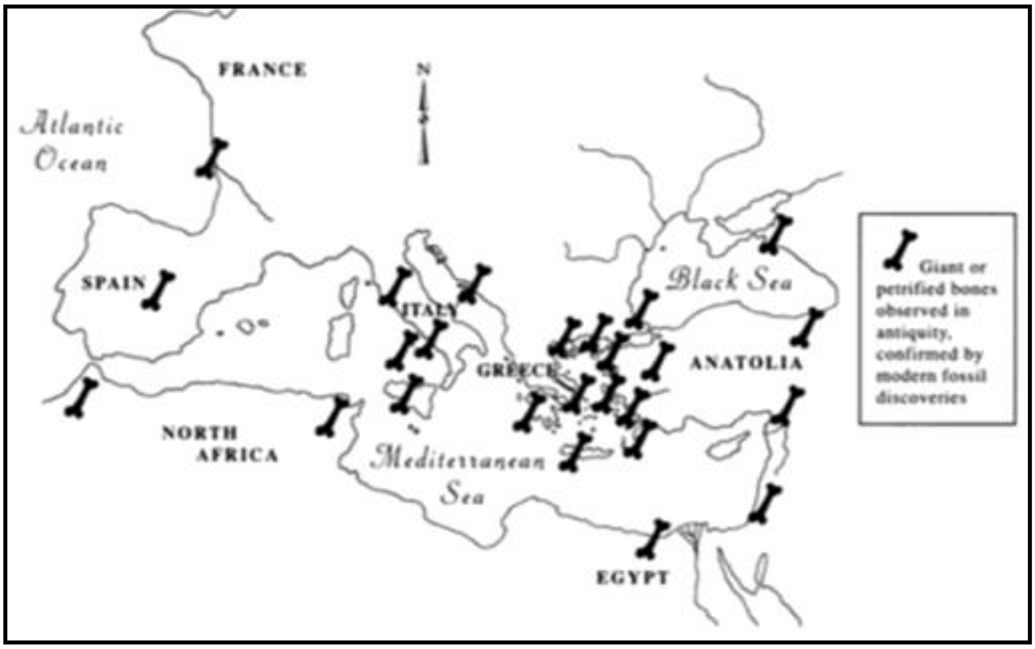


Fig. 35: The "Gigantic skeletons" according the ancient sources compared with modern vertebrate fossil discoveries (map by Mayor 2000).

According to Brongniart (1832, 1833, 1834), Virlet had collected a lot of plant fossils (especially leaf imprints) in a site not far from Kymi (Euboea) and because of the quantity of the findings he presented it as the analogue of Pikermi for the plants.

M. Gaudry (1860) in his letters to M. Elie de Beaumont reports the existence of *Taxodium europaeum* in Kymi underlying the fact that this species was described by Brongniart from his work on Morea (Greece) and it was reported by M. Virlet at Iliodroma island, close to Euboea.

Unger (1862) in his work 'Reise in Griechenland' has a reference on the fossil plants from Chelidhromi (= Alonissos) Island found inside the same 'freshwater formation' – according to Spratt, 1847 – with the one of Kymi, Euboea. Unger had studied the work by Virlet (1833) and Gaudry (1860) who believed that the age of the fossiliferous formation is the same with the one of Kymi, Kalamos, Markopoulo and Oropos and not older than Miocene.

In 1971 the archaeological research has revealed the skeletons of Miocene *Hipparion* and *Rhinoceros* close to the ancient village Ikos (Aupert 1976). Schneider (1972) refers to a Pontian mammal fauna of the Island including *Hipparion* indicative of a late Messinian age.

4.2 Systematic descriptions

Alonissos (Iliodroma) Island is really famous to the palaeobotanists because of the first report of *Glyptostrobus europaeus* (Brongniart) Unger. The holotype of the fossil today is preserved on a marly limestone slab of the following dimensions (in cm): 15x10, from Alonissos Island, Greece and is hosted at the collections of the MNHN with the code F1744 (Plate 40). The fossil was recognised, described and named as *Taxodium europaeum* (basionym) by Brongniart (1832).

Glyptostrobus europaeus represents a species found in several localities in Greece. According to LePage (2007, p. 393) the geographical distribution of this species in Greece includes *Glyptostrobus europaeus* findings from Kymi (Euboea Island) and Alonissos Island of Burdigalian age (Early Miocene) and from Vegora (Macedonia) of Messinian age (Upper Miocene). In Velitzelos *et al.* (2014) there are additional localities in Greece where this species has been found, such as: Iliokomi–Kormitsa (Thrace) of Miocene age, Aliveri (Euboea Island) and Moudros (Lemnos Island) of Burdigalian age, Prosilio and Lava (eastern West Macedonia) and Likoudi and Drymos (Elassona) of Messinian age, Platana (Western Peloponnese) of Upper Miocene age, Pikermi–Chomateri (Attica) of Upper Miocene–Early Pliocene age and Skoura (Sparti) of Pliocene age.

Recent studies (Dolezych and Van der Burgh, 2004) had correlated for the first time *Glyptostrobus europaeus* with *Glyptostroboxylon rudolphii* Dolezych and Van der Burgh. Numerous information for the “whole–plant” reconstruction of the species providing by the connection between fossil stumps, trunks and twigs of the taxon are also given in Vassio *et al.* (2008).

Among the newly collected specimens we were able to identify a xylitic remnant with anatomical characteristics resembling a conifer. Its microscopical study is presented below.

Plate 40

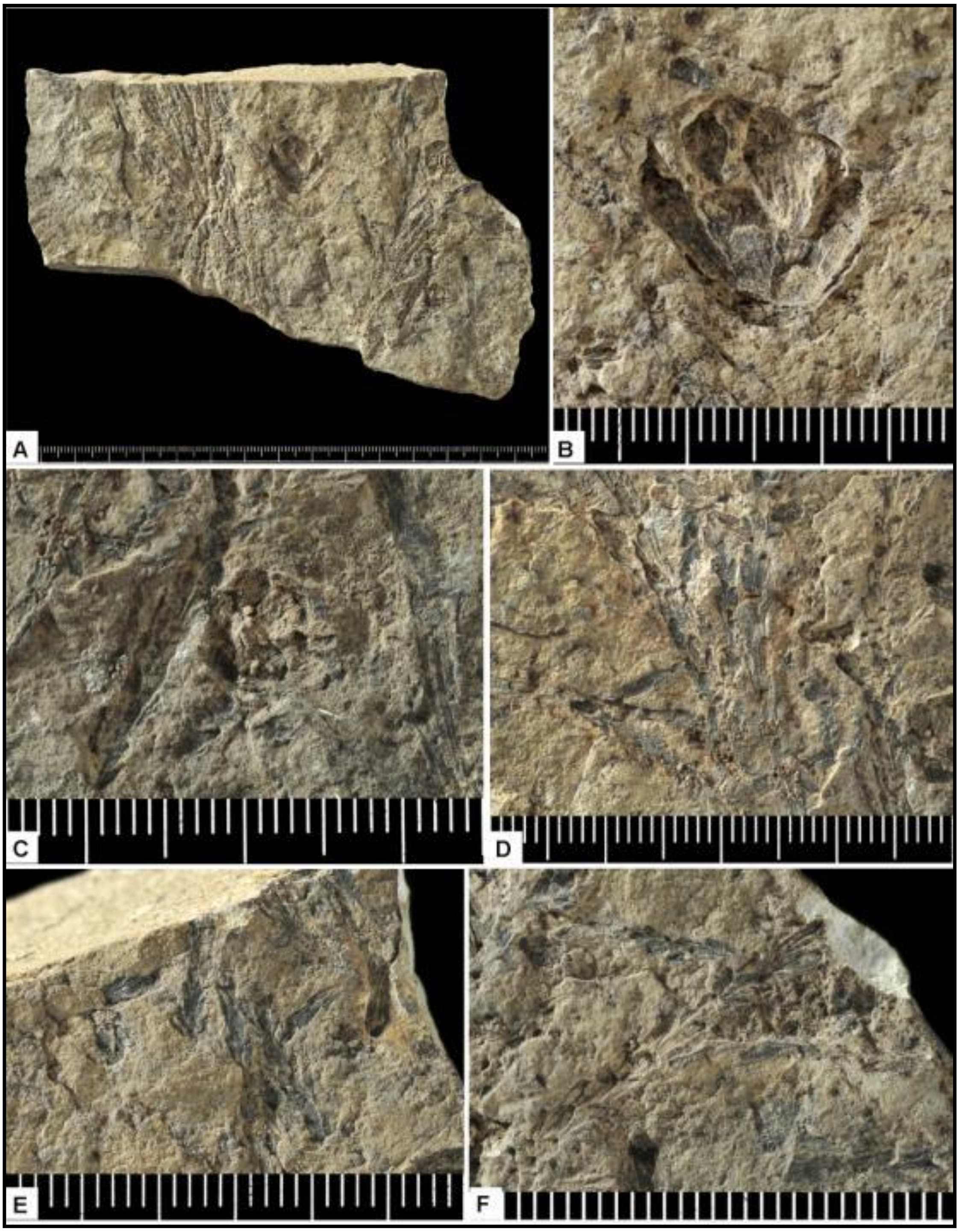


Plate 40 ***Glyptostrobus europaeus*** **(Brongniart) Unger**

A-F: Taxodium europaeum holotype, hosted in the collections of the MNHN in Paris with the code F1744. **B-F** represent details of the fossil magnified.

4.2.1 Identification of Coniferous wood ("Gymnosperm") from Alonissos Island

4.2.1.1

Conifers
Pinaceae L.
***Pinuxylon* Gothan**
(Plate 41A–41O)

Microscopic description.

Transverse section: Growth ring boundaries distinct, transition from early – to latewood gradual (Pl. 41*A*, 41*B*, 41*D*), latewood tracheids thin walled (Pl. 41*A*, 41*B*, 41*C*, 41*D*), large resin canals (axial and radial distributed but mainly at the latewood) with thin–walled epithelial cells (Pl. 41*A*, 41*B*, 41*C*), bordered pits in radial walls with well–defined disc–shaped torus (Pl. 41*D*), no axial parenchyma observed.

Tangential section: Exclusively uniseriate rays (fusiform because they contain radial intercellular canals and have a specific shape), average height of rays 4–12 cells (mostly "medium"sized but they can be up to 20 cells). Resin canals in rays with thin–walled epithelial cells (Pl. 41*L*–41*O*).

Radial section: Tracheid pits uniseriate. Ray tracheids present with up to four rows of cells (Pl. 41*G*, 41*H*, 41*K*), cell walls of ray tracheids smooth (Pl. 41*G*, 41*K*) and dentate (Plate Pl. 41*H*, 41*I*), ray tracheid pit borders with dentate thickenings (Pl. 41*I*). End walls of ray parenchyma cells smooth (Pl. 41*J,* 41*K*). Horizontal walls of ray parenchyma cells smooth (Pl. 41*J,* 41*K*)., no indentures were observed, cross–field pitting pinoid in 2 rows of usually 1–2 pits per cross–field but up to 6 (Pl. 41*E*, 41*G*, 41*H*, 41*J*, 41*K*).

Comparison among greek fossil pine woods. Our specimen has been compared with the fossil pine woods from Greece and has been found to have a lot of differences with them: *Pinoxylon parenchymatosum* (Suss & Velitzelos 1993) from Lemnos Island is characterised by the occurrence of axial parenchyma, a feature not in accordance with our fossil. *P. paradoxum* (Suss & Velitzelos 1994) from Lesbos Island is characterised by the existence of spirals and *P. pseudoparadoxum* (Suss & Velitzelos 1994, Lesbos Island) has very large rays – up to 50–cells.

Plate 41

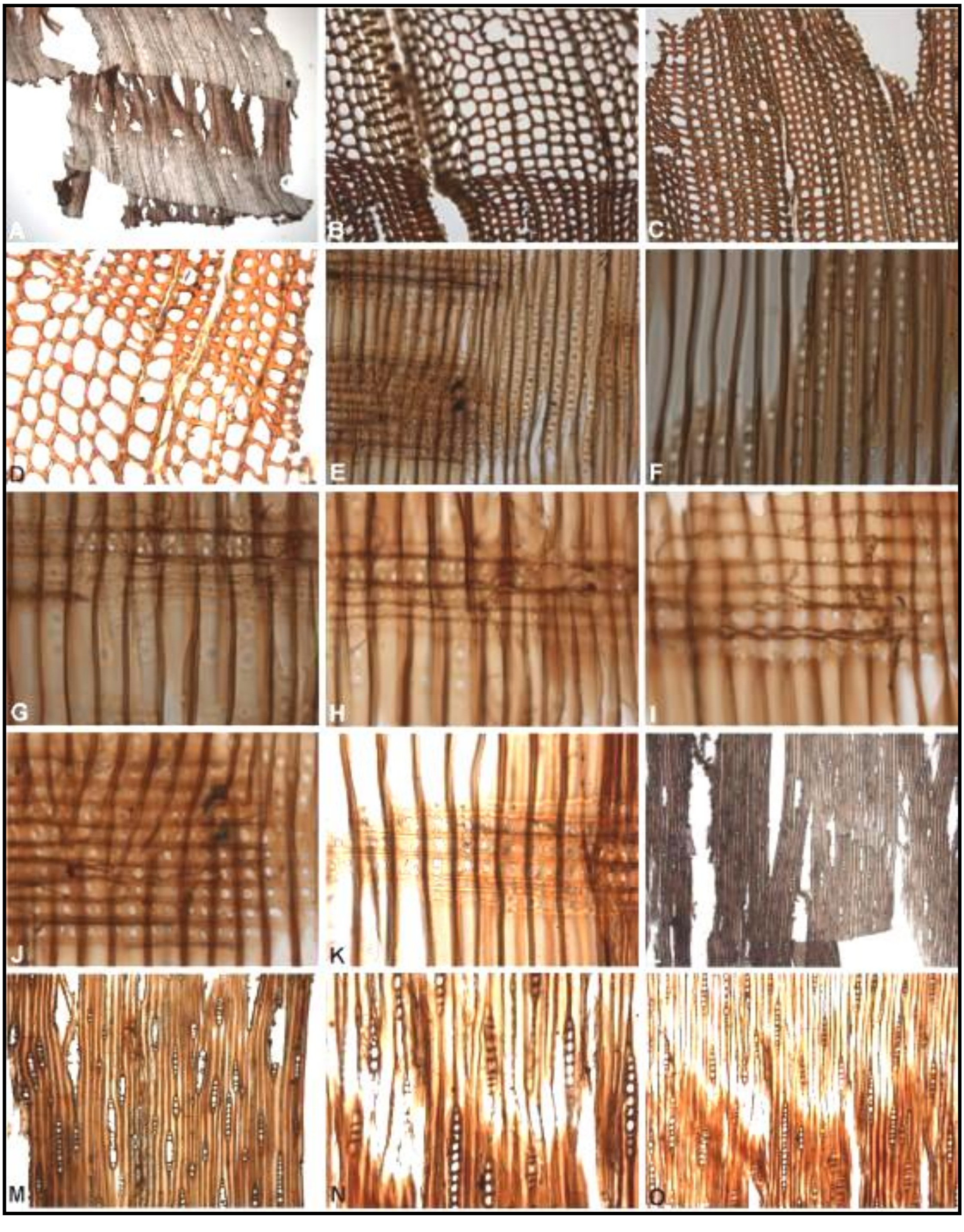


Plate 41 ***Pinuxylon*** **Gothan**

A: Growth ring boundaries distinct, transition from early - to latewood gradual, latewood tracheids thin walled, large resin canals with thin-walled epithelial cells (2.5x). **B:** Growth ring boundaries distinct, transition from early - to latewood gradual, latewood tracheids thin walled, large resin canals (axial and radial) with thin-walled epithelial cells (20x). **C:** Latewood tracheids thin walled, large resin canals with thin-walled epithelial cells (20x). **D:** Growth ring boundaries distinct, transition from early - to latewood gradual, latewood tracheids thin walled, bordered pits in radial walls with well-defined disc-shaped torus. **E:** cross-field pitting pinoid in horizontal 2 rows of usually 1-2 pits per cross-field but up to 6 (20x). **F:** Bordered pits in radial tracheid walls uniseriate (40x). **G:** Tracheid pits uniseriate. Ray tracheids with up to four rows of cells, cell walls of ray tracheids smooth, cross-field pitting pinoid in 2 rows of usually 1-2 pits per cross-field but up to 6 (40x). **H:** Tracheid pits uniseriate. Ray tracheids with up to four rows of cells, cell walls of ray tracheids dentate, cross-field pitting pinoid in 2 horizontal rows of usually 1-2 pits per cross-field but up to 6 (40x). **I:** Cell walls of ray tracheids dentate, ray tracheid pit borders with dentate thickenings (40x). **J:** End walls of ray parenchyma cells smooth, horizontal walls of ray parenchyma cells smooth, cross-field pitting pinoid in 2 rows of usually 1-2 pits per cross-field but up to 6 (40x). **K:** Tracheid pits uniseriate. Ray tracheids with up to four rows of cells, cell walls of ray tracheids smooth, end walls of ray parenchyma cells smooth, horizontal walls of ray parenchyma cells smooth, cross-field pitting pinoid in 2 rows of usually 1-2 pits per cross-field but up to 6. **L-O:** Exclusively uniseriate rays (fusiform because they contain radial intercellular canals and have a specific shape), average height of rays 4-12 cells (mostly “medium”sized but they can be up to 20 cells). Resin canals in rays with thin-walled epithelial cells. (L: 5x, M: 10x).

A, B, C, D = TS; E–K = RLS; L–O = TLS. TS, TLS, and RLS denote transversal, tangential longitudinal and radial longitudinal sections, respectively. The intension of this plate was to show the observed features, therefore the scale bar wasn’t used.

Our specimen differs also from 2 more species from Lesbos Island identified by Suss & Velitzelos (2009): from *Lesbosoxylon* (= *Pinoxylon) diversiradiatum* because it has bi–seriate rays and from *L.* (= *Pinoxylon) graciliradiatum* which has large rays with “idioblast–like” cells. There are also differences with *Lesbosoxylon* (= *Pinoxylon*) *ventricosuradiatum* (e.g. rays with “idioblast–like” cells and pits in the cross–field and ray tracheids not ascertainable) (Suss & Velitzelos 2010, Lesbos Island). A further study on the *Pinuxylon* material studied by van der Burgh (1973) could help in finding affinities with already described fossil pine woods.

Discussion: The occurrence of thin walled resin canals (axial and radial), the absence of parenchyma cells, the uniseriate tracheid pitting, the pinoid cross–field pitting, the existence of ray tracheids and the smooth horizontal end walls of ray parenchyma indicate that our fossil belongs to Pinaceae and more precisely to the genus *Pinus*.

The existence of axial and radial distributed large resin canals characterizes a subtropical taxon, and their presence mainly at the latewood is a feature showing a pronounced seasonal climate.

Botanical affinities: The occurrence of ray tracheid pit borders with dentate thickenings is characteristic only of Diploxylon *Pinus* (e.g. Williams *et al.* 2008). Diploxylon or hard pines have two fibrovascular bundles. The pines belonging to this category are warmth–tolerant. According to a study by Gernandt *et al.* (2005) based on DNA evidence, the Subgenus *Pinus* (the Diploxylon, or hard pines) is divided into the predominantly Eurasian and Mediterranean section *Pinus*, composed of subsections *Pinus* and *Pinaster*, and the strictly North American section *Trifoliae*, composed of subsections *Australes*, *Ponderosae*, and *Contortae*. The Section *Pinus,* Subsection *Pinus* (Eurasia, Mediterranean, E North America, Cuba) includes the following species: *P. densata*, *densiflora*, *hwangshanensis*, *kesiya*, *luchuensis*, *massoniana*, *merkusii*, *mugo*, *nigra*, *resinosa*, *sylvestris*, *tabuliformis*, *taiwanensis*, *thunbergii*, *tropicalis*, *uncinata*, *yunnanensis*; the Subsection *Pinaster* (Canary Islands, Mediterranean, Himalayas) includes: *P. brutia*, *canariensis*, *halepensis*, *heldreichii*, *pinaster*, *pinea*, *roxburghii.* Further studies on our fossil material could help in identifying more precisely the modern relative of our *Pinuxylon*.

5. GAVDOS ISLAND

5.1.1 Introduction

The study of more than 100 leaf impressions of the Metochia section, Gavdos Island, Greece, revealed a recently recovered late Miocene (Tortonian) palaeoflora from the southernmost part of Europe. The detailed study of the Gavdos megaflora contributes to expanding knowledge about the late Neogene floras of the Mediterranean and about the palaeoclimate conditions during the late Miocene for the lower latitudes at the Eastern Mediterranean. This study has been published recently (Mantzouka *et al.* 2014, 2015). The reader is kindly asked to advice Annex 3 for the details of this study.

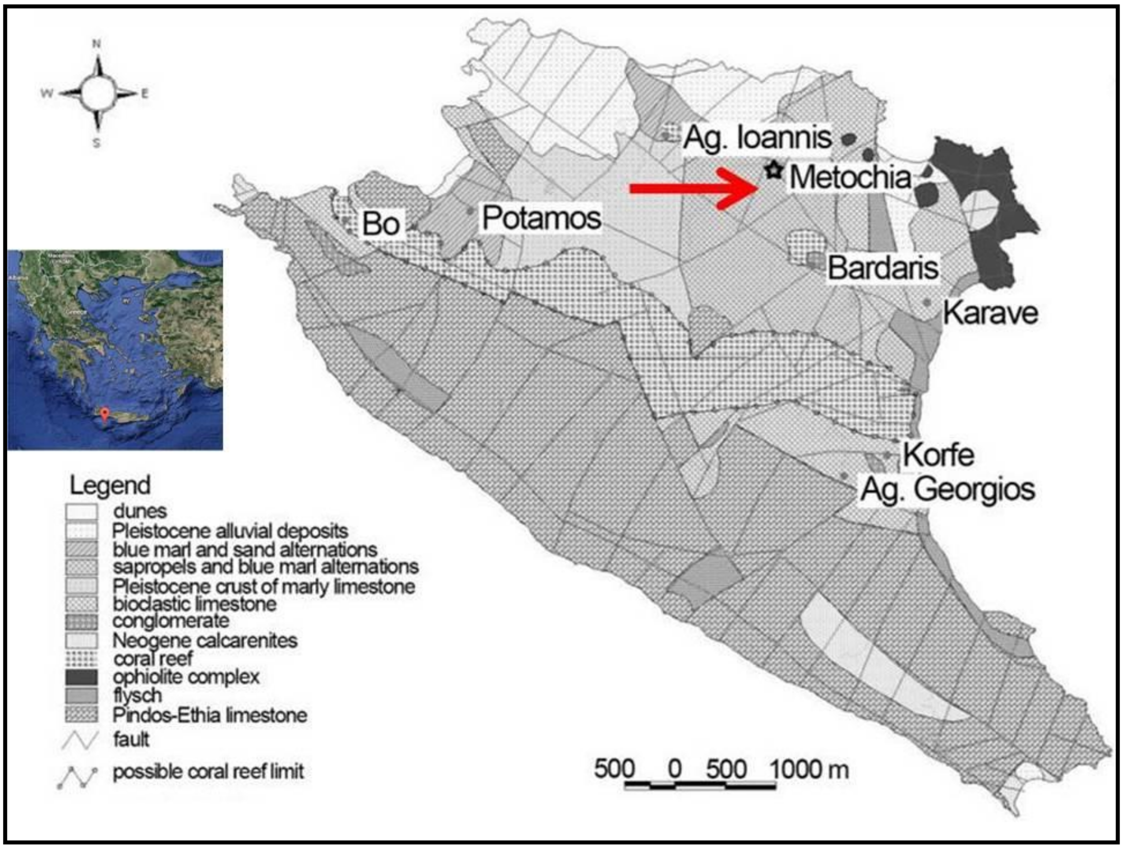


Fig. 36: Gavdos Island is located at the southernmost part of Greece and Europe. The plant fossils investigated for the present study were collected at the Metochia locality (NE Gavdos) which is shown in the geological map of the Island (arrow).

5.1.2 Geology and palaeontology of the studied area

Gavdos island is situated in the southern part of Greece south of Crete (34° 50′ 0″ N, 24° 5′ 0″ E) and covers an area of 33 Km^2 (Fig. 36). The plant fossils investigated for the present study were collected at the Metochia locality (NE Gavdos, Fig. 37).

The plant fossiliferous strata are related to L16–L22 sapropels (Tsaparas 2005) which have a thickness of 5.26 m and an age of 9.4 – 9.1 Ma as has been concluded from the study of the palaeomagnetism (orbital cycles according to periodic oscillations of excentricity) and the foraminifera (Hilgen *et al.* 1995, Antonarakou 2001).

5.1.3 Materials and methods

The number of the determined angiosperms was sufficient enough to allow the application of several techniques concerning the palaeovegetation (Phytosociological approach and IPR-vegetation analysis), and the palaeoclimate (Leaf Margin Analysis, CLAMP and Coexistence Approach).

Fig. 37: Metochia outcrop panoramic photo. The plant fossil site of the Metochia section is hard to be reached because it is situated inside a gorge (arrow).

5.1.4 Systematic descriptions

Among the recovered specimens, three conifers (*Tetraclinis salicornioides*, *Taxodium dubium*, *Pinus* sp.) and 27 fossil species/morphotypes of angiosperms have been recognized (Plates 42-44 in present study and Plates 3-6 in Annex 3). Among them, some represent subtropical, partly evergreen woody elements (e.g. *Daphnogene* sp., *Laurophyllum* sp., *Myrica lignitum*), some others (e.g. ? *Sassafras* sp., *Fagus gussonii*, *Ulmus*, *Acer angustilobum*, *Populus populina*, *Ailanthus pythii*, *Paliurus tiliifolius* and several legumes) belong to deciduous shrubs or trees. Attempts to prepare cuticles failed because of the poor preservation and the high degree of oxidation.

Concerning *Myrica lignitum*, new studies based on numerous fossil findings such as leaves, fruits, infructescences, male catkins mostly preserved as imprints (mainly fragmented and some complete) found in Pitsidia, Messara basin (Crete Island, Greece) have shown that the different plant organs found derived from a single species of *Myrica,* close to the present day species *M. cerifera* (Zidianakis *et al.* 2015).

Plate 42.

1. *Tetraclinis salicornioides* (Unger) Kvaček, segments of ultimate branches, GAVMT 620, scale bar 5 mm; **2.** *Tetraclinis salicornioides* (Unger) Kvaček, segments of ultimate branches, GAVMT 472, scale bar 10 mm; **3.** *Taxodium dubium* (Sternberg) Heer, foliage shoots, GAVMT 653, scale bar 10 mm; **4.** *Taxodium dubium* (Sternberg) Heer, foliage shoots, GAVMT 629, scale bar 5 mm; **5.** *Pinus* sp., needle fascicle, GAVMT 603, scale bar 10 mm; **6.** *Pinus* sp., needle fascicle, GAVMT 446, scale bar 10 mm; **7.** *Laurophyllum* sp., petiolate leaf, GAVMT 481, scale bar 10 mm; **8.** *Laurophyllum* sp., petiolate leaf, GAVMT 327, scale bar 10 mm; **9.** *Daphnogene* sp., leaf petiolate with suprabasal acrodromous venation, GAVMT 391, scale bar 10 mm; **10.** *Daphnogene* sp., leaf petiolate with suprabasal acrodromous venation, GAVMT 440, scale bar 10 mm; **11.** ?*Lindera ovata* Kolakovsky, leaf petiolate with basal acrodromous venation, GAVMT 383, scale bar 10 mm; **12.** *Daphnogene* sp., leaf petiolate with suprabasal acrodromous venation, GAVMT 500, scale bar 10 mm; **13.** ?*Lindera ovata* Kolakovsky, leaf petiolate with basal acrodromous venation, GAVMT 496, scale bar 10 mm; **14.** leaf counter-impression of 13, GAVMT 617, scale bar 10 mm.

Plate 42

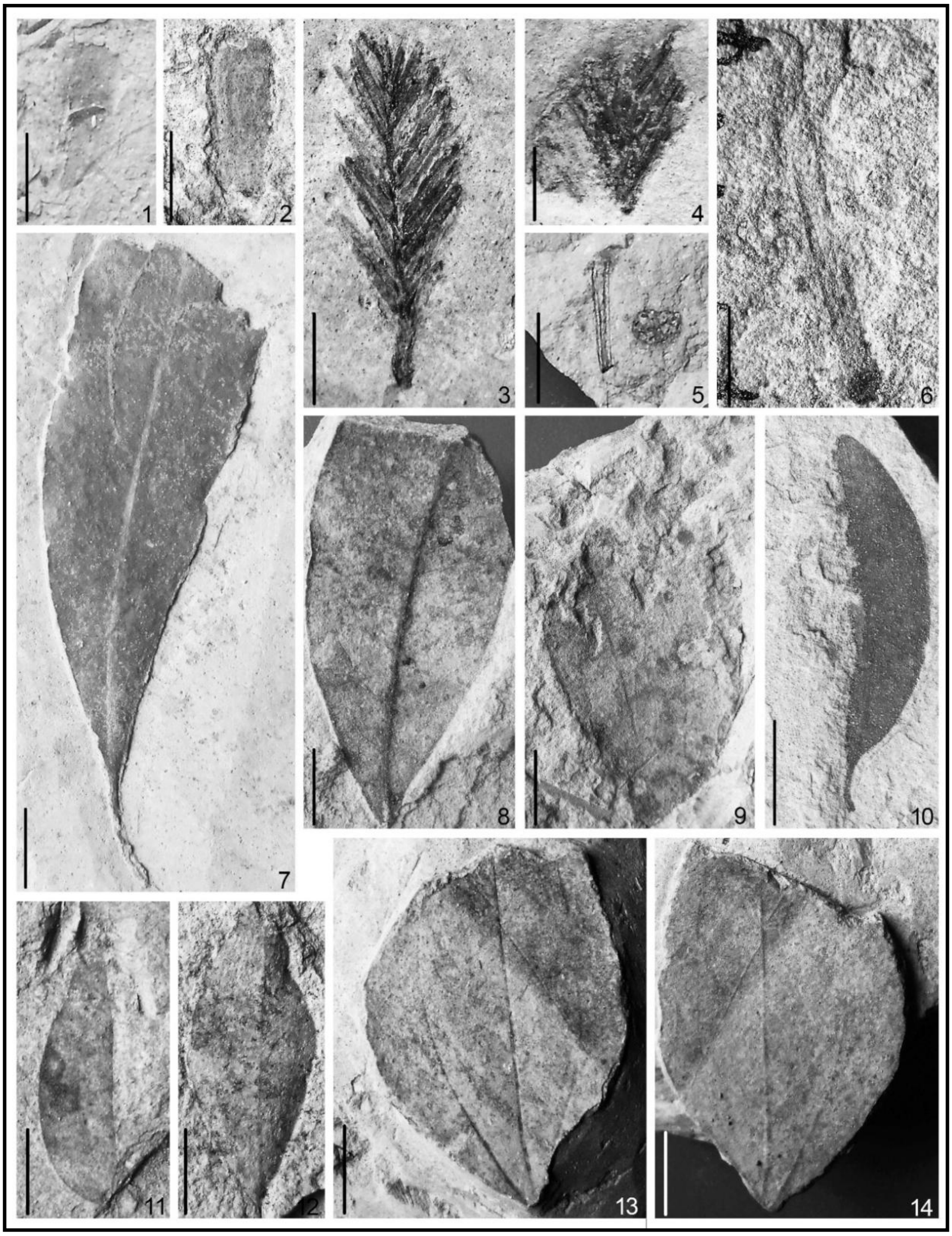


Plate 43

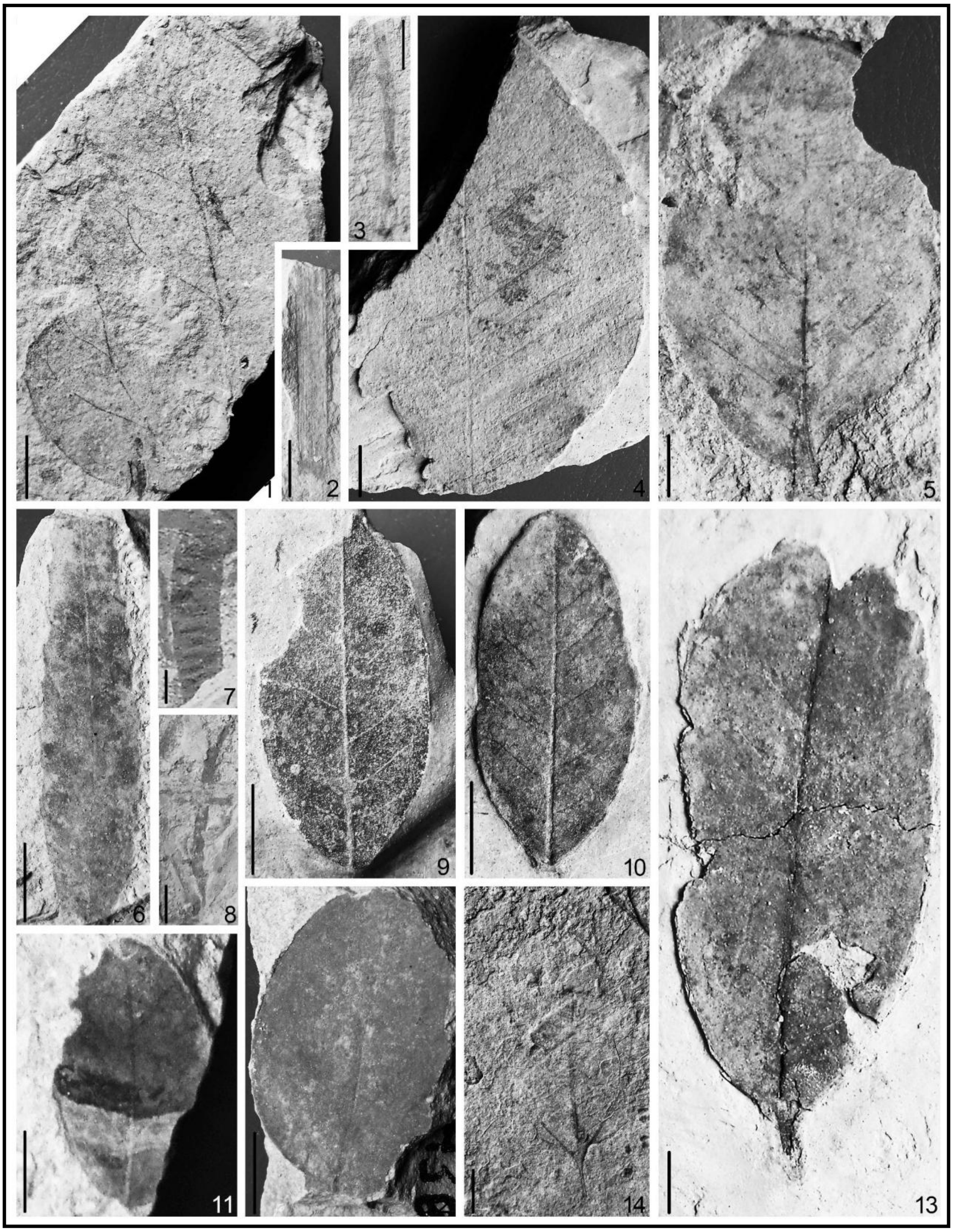


Plate 43.

1. *Sassafras* sp. Fragment of large lobed leaf, GAVMT 433, scale bar 10 mm; **2.** Monocotyledonae, leaf fragment with parallel venation, GAVMT 588, scale bar 10 mm; **3.** Monocotyledonae, leaf fragment with parallel venation, GAVMT 349, scale bar 10 mm; **4.** *Fagus gussonii* Massalongo emend. E. Knobloch & Velitzelos, leaf, GAVMT 534 scale bar 10 mm; **5.** *Fagus gussonii* Massalongo emend. E. Knobloch & Velitzelos, leaf, GAVMT 492, scale bar 10 mm; **6.** *Engelhardia orsbergensis* (Wessel & Weber) Jähninchen, Mai & Walther, leaflet, GAVMT 595, scale bar 5 mm; **7.** *Leguminocarpon* sp., fragment of a pod with large seeds, GAVMT 567, scale bar 5 mm; **8.** ?*Leguminocarpon* sp., pod (?), GAVMT 567, scale bar 5 mm; **9.** *Leguminosites* sp. 2, leaflet of narrow and elliptic shape, GAVMT 551, scale bar 10 mm; **10.** *Leguminosites* sp. 2, leaflet of narrow and elliptic shape, GAVMT 552, scale bar 10 mm; **11.** *Leguminosites* sp. 1, leaflet of broad and elliptic shape, GAVMT 321, scale bar 10 mm; **12.** *Leguminosites* sp. 1, leaflet of broad and elliptic shape, GAVMT 504, scale bar 10 mm; **13.** *Leguminosites* sp. 3, large leaflet with petiolule, GAVMT 525, scale bar 10 mm; **14.** *Paliurus tiliifolius* (Unger) Bůžek, incomplete leaf base, GAVMT 521, scale bar 10 mm.

Plate 44.

1. *Acer angustilobum* Heer, trilobed leaf bluntly dentate on the margin, GAVMT 515, scale bar 10 mm; **2.** *Betula* sp., fragmentary cuneate leaf base, GAVMT 543, scale bar 10 mm; **3.** *Carpinus* sp., complete leaf with bluntly serrate margin, GAVMT 478, scale bar 10 mm; **4.** *Sapindus graecus* Unger, emarginated apex of an incomplete leaflet, GAVMT 572, scale bar 10 mm; **5.** *Ulmus plurinervia* Unger, long petiolate asymmetric leaf base, GAVMT 438, scale bar 5 mm; **6.** *Populus populina* (Brongniart) E. Knobloch, complete petiolate leaf with five basal veins, GAVMT 491, scale bar 5 mm; **7.** *Dicotylophyllum* sp.1, leaf base with serrate margin. GAVMT 584, scale bar 5 mm; **8.** *Dicotylophyllum* sp. 5, leaf, GAVMT 582, scale bar 10 mm; **9.** *Dicotylophyllum* sp. 5, incomplete leaf, GAVMT 483, scale bar 5 mm; **10.** *Dicotylophyllum* sp. 4, leaflet, GAVMT 386, scale bar 10 mm; **11.** *Ailanthus pythii* (Unger) Kovar-Eder & Kvaček, strongly asymmetrical leaflet base, GAVMT 572, scale bar 10 mm; **12.** *Dicotylophyllum* sp. [? *Camellia abchasica* (Kolakovsky) Kolakovsky], shortly petiolate leaf, GAVMT 649, scale bar 10 mm; **13.** *Myrica lignitum* (Unger) Saporta, leaf with entire margin, GAVMT 375, scale bar 10 mm; **14.** *Myrica lignitum* (Unger) Saporta, leaf with dentate margin, GAVMT 643, scale bar 10 mm; **15.** *Salix* cf. *angusta* A. Braun, narrow elongate leaf, GAVMT 576, scale bar 10 mm; **16.** *Salix* cf. *angusta* A. Braun, narrow elongate leaf, GAVMT 650, scale bar 10 mm; **17.** detail of 16, leaf venation, scale bar 5 mm; **18.** *Dicotylophyllum* sp.3, leaf or leaflet, GAVMT 452, scale bar 10 mm; **19.** Detail of 18, detail of leaf/leaflet margin, scale bar 5 mm; **20.** ?*Apocynophyllum* sp., cuneate leaf base, GAVMT 397, scale bar 10 mm; **21.** *Dicotylophyllum* sp. [?*Cotoneaster palaeobacillaris* Kolakovsky], incomplete leaf, GAVMT 405, scale bar 10 mm; **22.** *Leguminosites* sp.4, leaflet base, GAVMT 562, scale bar 10 mm; **23.** Monocotyledonae fam. et gen. indet., extremely narrow leaf with parallelodromous venation, GAVMT 428, scale bar 5 mm.

Plate 44

5.1.5 Comparison of related fossil floras in Europe

The Gavdos palaeoflora has been compared with the late Miocene floristic assemblages of Likudi and Vegora (Macedonia, Greece) (Knobloch & Velitzelos 1986, Kvaček *et al.* 2002), since it belongs to the Mediterranean-Tethys Bioprovince (Mai 1995) and with the late Miocene flora of Kodor (Caucasus area, Paratethys Bioprovince). The newly described plant fossiliferous localities from Crete (Kovar-Eder *et al.* 2006, Sachse & Mohr 1996, Sachse *et al.* 1999, Sachse 2004, Zidianakis 2002, Zidianakis *et al.* 2007, 2010), such as Vrysses (latest Tortonian-early Messinian age, 7.5 – 6.0 Ma) and Pitsidia (Early Tortonian age, 10.5 Ma) were also correlated with Metochia (Gavdos) plant fossils. According to our study the most similar flora, also close in the geographical position and age, is that of Makrilia, Crete of late Tortonian age (8.6 – 7.7 Ma) sharing not only physiognomic aspects but also several important elements.

5.2 Palaeoenvironmental Analysis:

5.2.1 Palaeovegetation. Three specific plant assemblages are distingushed based on the Phytosociological Approach: a) a mixed-swamp forest, b) a riparian assemblage and c) a zonal mesophytic to sclerophyllous vegetation. According to IPR-vegetation analysis (Kovar-Eder *et al.* 2008, Teodoridis *et al.* 2011a), Gavdos belongs to transition (ecotone) between the broad-leaved deciduous forest (BLDF) and the mixed mesophytic forest (MMF) and shows close affinities with BLDF of Mt. Emei, Meili Snow Mt., Mt. Fuji (in China) and the Shirakami Sanchi area (in Japan).

5.2.2 Palaeoclimate. The palaeoclimate data derived for Gavdos, using LMA, CLAMP and CA techniques, are summarized as follows: MAT 13.8 – 20 °C, WMMT 22.5 – 26.4 °C, CMMT 3.1 – 9. °C, MAP 843 – 1741 mm, MPwet 170 – 195 mm, MPdry 17 – 70 mm, MPwarm 73 – 80 mm, 3-WET 735.8 mm (only CLAMP) and 3-DRY 184.8 mm (only CLAMP). The Tortonian paleoclimatic datasets from Gavdos and Crete represent a humid subtropical climate without any dry season during the warmest period (Cfa). At present, the Cfa climate type is restricted to relatively small regions of Europe.

6. DISCUSSION AND CONCLUSIONS

6.1 LESBOS ISLAND

On November 2015 Lesbos Island has received the ultimate recognition of its international significance honored as a UNESCO Geopark. Geoparks represent the holistic approach of unique and important territories which combine the protection and promotion of geological heritage with sustainable local development (Zouros 2004).

The research on the palaeobotanical treasure of Lesbos Island by several scientists (Unger 1845, 1847, 1850; Fliche 1898; Velitzelos *et al.* 1981a, b; Velitzelos & Zouros 2008) during the last two centuries has revealed 25 species of conifers and 5 species of angiosperms concerning the wood occurrences while the foliage findings certify the opposite (Mantzouka *et al.* 2013a).

During this study **new fossiliferous localities have been found** from the Southern part of the Island (A: Alonelia, H: Hondrokouki, R: Rogkada, D: Damandri, P: Plakes, M: Mesotopos).

Hundreds of specimens have been collected from the new fossiliferous sites, stored, cut for slides and studied.

Among these new specimens, **27 angiosperms were studied and described in detail. For their study 101 slides were prepared.**

Regarding the conifers findings, **69 conifers were studied and described. For their study 205 slides were prepared.**

For the comparison with the present day material, 9 slides were prepared for the optical microscope and more than 30 preparations were made for modern *Cedrus* species study under SEM.

Among the new fossiliferous sites there is a limonitic site (M: Mesotopos) with plant fossiliferous material not proper for identification but with information about the occurrence of hydrothermal source in the area.

The variety of the fossilization (taphonomical processes with several parameters strongly connected to volcanism) and preservation types (leaf impressions, molds and casts, permineralized, silicified and lignified trunks, fossiliferous block assemblages, lignitic horizons) interpreted for each fossiliferous locality can supply us with details for the palaeoenvironment. For example the lignitic horizon of Lapsarna (Plate 1), from where a lot of fossils have been collected and studied more than a hundred years ago (Fliche 1898) and has been revealed and studied recently

(Mantzouka 2009a, b; Vassileiadou & Zouros 2012) from a micropalaeontological point of view, represents a palaeolake of a lower palaeoaltitude.

Information on palaeoaltitude of the fossiliferous localities connected with the specimens found and studied in time. In A: Alonelia and R: Rogkada sites, the majority of the trees preserved were conifers which probably represent a higher palaeoaltitude and in H: Hondrokouki, D: Damandri and P: Plakes fossiliferous sites the majority were angiosperms and especially Lauraceae which represent a lower palaeoaltitude.

A new international methodology on fossil Lauraceae has been established recently (Mantzouka *et al.* in press) and it was based on Lesbos material. The suggested classification of *Laurinoxylon* of this study is universal and directly linked to modern botany. Thanks to the abundance of *Laurinoxylon* in the fossil record, it can be directly used both by palaebotanists/palaeontologists and geologists as a good tool for further systematic, stratigraphic and paleoclimatic studies. The fossil woods used for the establishment of this methodology cover time interval from early Oligocene to early Miocene.

This new proposed identification key for fossil lauraceous wood was based on the examination of the importance of oil &/or mucilage cells (= idioblasts) distribution as an essential tool for botanical affinities of the Lauraceae (and especially *Laurinoxylon*) using both the work on extant lauraceous genera by Richter (1981a) and van der Werff and Richter (1996) and new detailed anatomical descriptions of several wood samples from four different areas of South-Eastern and Central Europe from Oligocene to Miocene age. The exact occurrence and distribution of the idioblasts and their combinations was used for the purposes of this study only as the last step of the proposed methodology (and not separately as in several previously published studies), after the application of a number of ‘filters’ (= excluding criteria/features) which Richter (1981a) had defined as “characters with the highest significance”.

The observation of the exact occurrence of the idioblasts allowed the recognition of four groups of *Laurinoxylon* species:

- Type 1 with idioblasts associated only with ray parenchyma cells;
- Type 2a with idioblasts associated with two types of parenchyma elements, i.e., with rays and axial parenchyma;
- Type 2b with idioblasts associated with two different elements, with rays and present among the fibres; and

- Type 3 with idioblasts associated with three types of elements, i.e., with ray and axial parenchyma cells and present among the fibres.

The next step was to find the botanical affinities of the *Laurinoxylon* wood categories by linking the fossil species with the modern wood:

1) the representatives of *Laurinoxylon* Type 1 are closer to: *Dicypellium, Systemonodaphne, Urbanodendron,* North American *Persea*, *Litsea chinensis* group, *Laurus*,
2) *Laurinoxylon* Type 2a fossil species are closer to modern *Aniba, Licaria, Aiouea, Pleurothyrium, Cryptocarya* from Madagascar*, Dehaasia, Nothaphoebe, Phoebe, Persea, Apollonias, Lindera* A,
3) The species of *Laurinoxylon* Type 2b are closer to modern *Actinodaphne, Neolitsea* and *Nectandra* under the supposition that they belong to the percentage of species which don't include crystals,
4) Finally, the species of *Laurinoxylon* Type 3 (syn. *Cinnamomoxylon*) are closer to *Actinodaphne, Neolitsea, Nectandra, Ocotea, Endlicheria, Cinnamomum.*

The observation on the existence of crystals and crystalliferous masses and septa in fibres along with the combination with other co-occurring leaves and other organs, can make possible the depiction of only one modern genus, which would correspond to a concrete fossil *Laurinoxylon* species.

Concerning the lauraceous representatives during this study the identification of the following species for the first time in Lesbos and in Greece was efficient:

1) ***Laurinoxylon* aff. *czechense* Prakash, Březinová & Bůžek** (representative of the Northern hemisphere), a *Laurinoxylon* Type 1 most probably related to the present day genus of the North American *Persea.*
2) ***Laurinoxylon* cf. *daberi* Greguss** (Neotropical / Asian representative), a *Laurinoxylon* Type 2a with big quadratic prisms (Ac and E in Richter's categories) and silica bodies inside the idioblasts.
3) ***Laurinoxylon* aff. *diluviale* (Unger) Felix emend. Dupéron *et al.*** (Neotropical representative), a *Laurinoxylon* Type 2b most probably related to the 40% of the present day *Nectandra* species which do not have crystals*.*

4) ***Cinnamomoxylon seemannianum (*****Mädel) Gottwald** (Neotropical / Asian representative), a *Laurinoxylon* Type 3 (= *Cinnamomoxylon*) most probably related to the present day genus *Cinnamomum*.
5) Another unique lauraceous finding was ***Cryptocaryoxylon* Leisman** (Southern hemisphere representative). This is the first identification of the genus *Cryptocaryoxylon* for the Neogene of Eurasia (during this study the finding of this genus was also made from the Miocene of Lemnos Island). Until now *Cryptocaryoxylon* has been reported only three times: a) with the species *Cryptocaryoxylon gippslandicum* Leisman (1986) from the Upper Eocene-Oligocene (39 Mya) of Australia, b) with the species *C. hancockii*, *C. meeksii* and *C. radiporosum* Wheeler & Manchester (2002) from the middle Eocene of North America and c) with the species *Cryptocaryoxylon oleiferum* which has been found recently belonging in the late Pleistocene of Argentina (Ramos *et al.* 2015).

This study has revealed also *Quercoxylon* (Kräusel) Gros from Lesbos Island. The nearest living relatives of *Quercoxylon* consider to be *Quercus* and *Lithocarpus* which are native in the warm temperate regions of the Northern Hemisphere and of East Indies: Southeast Asia and India including the islands. Additionally, the hypothesis that this evergreen oak type belongs to the extinct genus *Eotrigonobalanus* as stated in Selmeier & Velitzelos (2000) is supported.

The study of *Cedroxylon lesbium* Kraus (*Peuce lesbia* Unger) was another important part of this PhD. The studied sample represents a holotype or a part of the holotype hosted at the Natural History Museum of Vienna (Naturhistorisches Museum Wien) with the code: D 38 (Plate 29*A*-29*C*), and belongs to the Lesbos samples studied and identified by Franz Unger. Unger had identified and published his observations on the material from Lesbos Island in his Chloris protogae (Unger, 1844: p.34, 37). In the latter publication there is also the original brief wood anatomical description of *Peuce lesbia*, with no illustration of its anatomy. The information about the locality is unknown, probably Sigri (Mpali Alonia) and there are no anatomical details and measurements. The fact that there is no illustration accompanying the description of the species is problematic (Kvaček, 2008a). No illustration and anatomy accompanied the renaming of the species as *Pinites lesbius* by Göppert in Bronn (1848). In 1898 Fliche studies and describes *Cedroxylon* sp. lignitic and permineralized samples from the western part of Lesbos Island and more specific from Ordymnos seashore and NE part of Ordymnos (Fliche 1898: p.143, 148). Unfortunately there is no extended description of the specimen and no illustration of its anatomy again. Kräusel (1919, p. 191) gives the synonym of *Cedroxylon lesbium* Kraus for *Peuce lesbia* Unger for trees without parenchyma and resin ducts, quoted *Peuce lesbia* as the basionym The specimen that we examine doesn't have resin ducts but it has parenchyma.

Until a further study and re-identification on all *Peuce lesbia* samples hosted by several museums throughout Europe is made we propose *Cedroxylon lesbium* Kräusel [and not *Peuce lesbia* Unger, the basionym =the legitimate, previously published name on which a new combination or name at new rank is based. ... (Art. 6.10) according to the International Code of Nomenclature for algae, fungi, and plant,] should be the official name for this fossil.

Correlating the present day species of *Cedrus* with *Cedroxylon lesbium* we can see that there are differences concerning the axial parenchyma, the scalloped (= festooned) tori, the existence of ray tracheids (they are observed by Crivellaro & Schweingruber 2013), the end walls of the tracheids and the arrangement of the tracheid pits (uni- or biseriate) and of the bordered pits (in 1 up to 3 rows perpendicularly). These are the main characteristics which most probably lead us to the conclusion that *Cedroxylon lesbium* is not related to modern *Cedrus* species.

A question that has been raised observing the alternant plant fossiliferous layers of the Petrified Forest of Lesbos is: ***"How has the forest been recreated several times after the catastrophic volcanic eruptions?"***

A new possible answer on the subject could be related to the study by Harrison *et al.* (2015), on modern ecosystems. According to this paper the plant communities living in infertile soils, such as serpentine or ultramafic soils (high in Mg and low in Ca and primary nutrients) are more resistant and less sensitive to climatic changes.

6.2 LEMNOS ISLAND

According to Velitzelos *et al.* (2014) the fossil plant assemblages of Lemnos Island are not rich in species, representing mostly riparian communities (*Pronephrium, Daphnogene, Myrica*, palms and monocots) and well-drained areas (*Quercus drymeja* and *Zelkova*). Another fossil genus (in the form of leaf imprint) found in Lemnos was *Eriolaena* which has been identified by Berger (1953a) and the present day genus is native in India, South East Asia and southern China.

We agree with the latter opinions considering additionally that further studies should be done, especially concerning the fossil wood findings, because the unrevealed material is numerous and the new scientific data that we could get are really important and could lead to new conclusions, as it is proved by our study.

From 1887 till 1993, only 2 species of gymnosperm wood [*Cedroxylon* sp. (Berger 1953a) and *Pinoxylon parenchymatosum* (Süss & Velitzelos 1993)] and 3 species of angiosperm wood [*Cornoxylon pappi (*Berger 1953a)*, Laurinoxylon ehrendorferi* (Berger 1953a) and *Rhizopalmoxylon* sp. (found and identified by E. Velitzelos)] have been identified in the Neogene palaeoflora of Lemnos Island. On the contrary, plenty leaves imprints have been recognized including 3 conifers and 24 angiosperms (*see* Lemnos Island Fossil Flora Appendix).

Our study is a new important contribution concerning the palaeobotanical treasure of Lemnos Island. The **study of more than 60 wood samples (12 angiosperms and 48 conifers) with 121 slides (11 for the angiosperms and 110 for the conifers) from new and old fossiliferous localities** resulted to the identification for the first time in Greece: of *Cryptocaryoxylon* as well as first identification of *Laurinoxylon ehrendorferi* since 1953 and the description of several coniferous woods related to *Taxodioxylon*.

New efforts should be done correlating everything already known, leaves and wood findings, older and new identifications.

The present study revealed the first occurrences of the following species for Lemnos Island and for Greece in general:

1) ***Cryptocaryoxylon* Leisman** (Southern hemisphere). This is the first identification of this genus for the Neogene of Eurasia.
2) Revealing ***Laurinoxylon* cf. *ehrendorferi* Berger** (Neotropical / Asian) for the first time after 1953. *Laurinoxylon* cf. *ehrendorferi* belongs to *Laurinoxylon* Type 2a most probably related to the present day genera

Nothaphoebe and *Aiouea.* Both genera are Neotropical / Neotropical-Asian belonging to Perseae Nees tribe.

3) **First descriptions of taxodiaceous wood (*Taxodioxylon* Hartig emend. Gothan) from this island.**

The occurrence of *Cryptocaryoxylon* from the Miocene of Lesbos and Lemnos Islands reveals also useful information on the palaeogegraphy. The modern genus *Cryptocarya* belongs to Cryptocaryeae Nees tribe (Plate 3) which is related to the Southern hemisphere contrary to the nearest living relatives of *Laurinoxylon* species and *Quercoxylon* findings already described which are related to the North hemisphere and to the Asian/Neotropics genera. This seems to be important information on the evolution of the woods consist the Miocene Forest of Lesbos and Lemnos and on the distribution of their present day representatives.

Among several thoughts during our studies one specific question has been plagued us: ***"Why there are numerous Taxodioxylon representatives in Lesbos and Lemnos Petrified forests?"***

We believe that the answer is the following: *Taxodioxylon* was a wood type with characters of *Taxodium distichum* and *Sequoia sempervirens* (Kräusel, 1949) but also with botanical affinities of more genera and species, i.e. *Cryptomeria* (*Dolezych 2005*) depending on the species of the studied fossil material. The species in the key of *Taxodioxylon* are separated on the number of cross-field pits, the nature of the axial parenchyma, and the presence or absence of horizontal and vertical resin ducts (Van der Burgh & Meijer, 1996). In several studies the nearest living relative of *Taxodioxylon* was *Sequoia* (e.g., Gryc & Sakala 2010, Erdei *et al.* 2009). *Sequoia* has a long fossil history and common elements existed in the forests of Europe, Asia, and America forming a subcosmopolitan distribution up to about 5 million years ago (Akkemik *et al.* 2009). Interestingly, the monospecific *Sequoia* (as also *Sequoiadendron*), which today is restricted to a narrow range along the central and northern coast of California, is one of the few conifers that can vegetatively reproduce. Low-intensity fires are necessary for the regeneration of this vulnerable in the list of IUCN genus (Thomas & LePage 2011). Following a major environmental disturbance (e.g. fire), regeneration can occur from the stump, or even roots, and thus allowing it to survive and maintain dominance in an ecologically dynamic habitat (Akkemik *et al.* 2009). This ability may explain the dominance of *Sequoia* in the volcanic environment of Çamlıdere (west Central Anatolia, 18.2-16.9 mya), Lesbos and Lemnos petrified forests.

Another legitimate question that has been raised is the following: ***“Why there are so many different types of Taxodioxylon representatives in Lesbos and Lemnos petrified forests?”***

Studying the material and the publications on the subject we have come to the conclusion that *Taxodioxylon* is a much diversified genus. According to Bailey & Faull (1934) *Sequoia sempervirens* (Redwood) shows a great variability of anatomical characters even related to the different parts of a single tree. Therefore extra care should be taken for the identification of *Taxodioxylon* species (when they come from fragments and not from autochthonous – in situ – stumps) because the differentiation of the features (qualitative ones like the form and orientation of pits and pit apertures and quantitative as the width of the growth rings, the dimensions of the cells and the number of rays per unit area) could be related not with the differentiation of the species but with the trees’ growth under markedly different environmental conditions and with the part of the tree the sample is taken from (e.g., huge old stems, young or immature stems, dwarfed or suppressed stems, roots, branches, etc.). At the same publication there is also the statement that the range of variability tends to be greater in different parts of a single, large mature tree than in homologous parts of different trees and that the cells of the roots and of the outer parts of the clear lengths of huge old stems tend to be larger than those of young stems, of physiologically dwarfed stems, or of branches. The most important conclusion is the necessity of assembled the authentic specimens’ collections with different genera, species and varieties as with different parts of mature trees and of trees growing under different environmental conditions.

By conducting this study we would like to contribute by showing that the occurrences of the plant fossils of Lemnos Island (wood, leaves, and cones) are of high importance for the international scientific community. With the right support, protection and scientific study the fossiliferous localities can become geomorphosites/geosites of global interest and Lemnos Island can be declared as a protected UNESCO European and Global Geopark following the successful example of Lesbos Island representing an important attraction based on the promotion of the palaeobotanical, palaeontological and geological heritage of Greece.

6.3 ALONISSOS ISLAND

The effort of **revealing the exact locality where the holotype of *Glyptostrobus europaeus* had been found almost 200 years ago** was one of the goals of this study. The locality was found and **numerous fossiliferous specimens (including fossil gastropods, plant remnants and lignite samples) have been collected**. Unfortunately imprints were not among the collected material. **One of the lignite samples has been studied microscopically and its anatomy has revealed a *Pinuxylon* remnant.** Regarding the **palaeogeography**, it seems that during the early – Middle Miocene in Alonissos Island there was a lake assemblage, as it is proven by the gastropods findings from the new collected material, e.g. Planorbidae, which represent a lacustrine, shallow environment with a good oxygenation usually (Professor E. Koskeridou pers.com. 2015). Later on this lacustrine environment turned into a swamp palaeo–ecosystem as indicated by the numerous (according the references) findings of *Glyptostrobus europaeus* and by the occurrence of the lignite formations under the plant fossiliferous stratum and above the gastropods fossiliferous layer. Most probably in a close distance of the swamp there was a lowland trees community or forest where the pine wood we examined grew up before falling into the swamp. A future study based on the collected material from this type locality can provide more information concerning the palaeovegetation (based mainly on the fossil pollen) and the palaeoenvironment (based on the fossil molluscs).

6.4 GAVDOS ISLAND

The **study of more than 100 leaf impressions** of the Metochia section, Gavdos Island, Greece, revealed a recently recovered **late Miocene (Tortonian) palaeoflora from the southernmost part of Europe.** The number of the determined angiosperms (with 27 fossil species/morphotypes) allowed the application of several techniques concerning the palaeovegetation (Phytosociological approach and IPR-vegetation analysis), and the palaeoclimate (Leaf Margin Analysis, CLAMP and Coexistence Approach).

The present study places the southernmost limit of the distribution of ***Fagus gussonii*** in Gavdos, confirms the limited distribution of ***Sapindus graecus*** only on the territory of southeast Europe and gives the first evidence of ***Ailanthus pythii*** in the Mediterranean.

The results of the study of the Gavdos flora expand our knowledge about the late Neogene floras of the Mediterranean. According to our study, **palaeogeographical settings rather than climatic oscillations affected the floristic differentiation in the area of SE Europe at about 8 Ma.** Climate data reconstructed for the Gavdos flora and the other Greek localities show no signs of distinct aridization of climate and changes towards a summer-dry ("etesian") regime. Tortonian temperatures estimated from a total of four megafloras of Southern Greece were about at the present-day level or even slightly below. This indicates that the global temperature decline during the Late Neogene affected the study area much less, compared to the middle to higher latitudinal regions of Western Eurasia.

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The reader is kindly requested to read the following published papers (annexes) which represent parts of the present study:

Annex 1: Mantzouka D., Sakala J., Kvaček Z. & Karakitsios V. 2013a. Palaeobotanical study of Polichnitos region, Southern part of Lesbos island, Greece (Preliminary results on angiosperm wood). Bulletin of the Geological Society of Greece, vol. XLVII: 204-215.

Annex 2: Mantzouka D., Karakitsios V., Sakala J. & Wheeler E. in press. Using idioblasts to group *Laurinoxylon* species – Case study from the Oligo-Miocene of Europe. IAWA Journal, xx: 1-59.

Annex3: Mantzouka D., Kvaček Z., Teodoridis V., Utescher T., Tsaparas N. & Karakitsios V. 2015. A new late Miocene (Tortonian) flora from Gavdos Island in southernmost Greece evaluated in the context of vegetation and climate in the Eastern Mediterranean. Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen. 01/2015; 275(1):47-81.

Annex 4: Mantzouka D., Kvaček Z., Teodoridis V., Utescher T., Tsaparas N. & Karakitsios V. 2014. Gavdos Island Palaeoflora: A newly recovered late Neogene flora of the Eastern Mediterranean (Greece). 9th European Palaeobotany-Palynology Conference, August 26-31 2014, Padova, Italy, vol.: 1, page: 154.

Annex 5: Mantzouka D., Sakala J. & Karakitsios V. 2014. A new methodological approach on *Laurinoxylon* and the importance of the oil and/or mucilage cells. 9th European Palaeobotany-Palynology Conference, August 26-31 2014, Padova, Italy, vol.: 1, page: 154.

Annex 6: Mantzouka D. V, Sakala J, Rapprich V & Karakitsios V. 2013b. Plant fossils and taphonomical processes from Lesbos island, Greece. Proceedings of the 22nd International Workshop on Plant Taphonomy in Pilsen and Radnice, p. 6-7.

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PALAEOBOTANICAL STUDY OF POLICHNITOS REGION, SOUTHERN PART OF LESBOS ISLAND, GREECE (PRELIMINARY RESULTS ON ANGIOSPERM WOOD)

Mantzouka D.[1], Sakala J.[2], Kvaček Z.[2] and Karakitsios V.[1]

[1] National and Kapodistrian University of Athens, Faculty of Geology and Geoenvironment, Department of Hist. Geology - Paleontology, dmantzouka@geol.uoa.gr , vkarak@geol.uoa.gr

[2] Charles University of Prague, Czech Republic, Institute of Geology and Palaeontology, Albertov 6, 12843, Prague 2, rade@natur.cuni.cz, kvacek@natur.cuni.cz

Abstract

The present contribution brings new scientific data for the palaeoflora of Lesbos based on new collections of plant fossils which were discovered in 2011 at six new localities from the southern part of Lesbos Island. This study resumes the published data both on the palaeovegetation of the Petrified Forest and the palaeogeography of Lesbos Island during the Neogene.

The new palaeobotanical study with more than seventy new samples of fossilized wood from the broader area of Polichnitos region gives new information about the palaeobotanical and palaeontological content of this area.

It is reported for the first time here the existence of a diversified fossil wood assemblage from the southern part of the Island as long as the identification of three types of lauraceous wood according to their idioblasts characteristics.

Key words: *plant fossil anatomy, Lauraceae, idioblasts, Petrified Forest of Lesbos.*

Περίληψη

Η εν λόγω εργασία φέρνει στο φως νέα επιστημονικά δεδομένα για την παλαιοχλωρίδα της Λέσβου που βασίζονται σε νεοσυλλεχθέντα φυτικά απολιθώματα τα οποία ήρθαν στο φως το 2011και προέρχονται από έξι νέες θέσεις από το νότιο τμήμα της νήσου Λέσβου. Η συγκεκριμένη μελέτη ανακεφαλαιώνει τα ήδη δημοσιευμένα δεδομένα αναφορικά με την σύνθεση της παλαιοβλάστησης του Απολιθωμένου Δάσους καθώς και με την παλαιογεωγραφία της νήσου Λέσβου κατά το Νεογενές.

Η νέα παλαιοβοτανική μελέτη με περισσότερα από εβδομήντα νέα δείγματα απολιθωμένων δέντρων από την ευρύτερη περιοχή του Πολυχνίτου δίνει νέες πληροφορίες σχετικά με το παλαιοβοτανικό και παλαιοντολογικό περιεχόμενο της συγκεκριμένης περιοχής.

Στην εν λόγω εργασία γίνεται για πρώτη φορά αναφορά στην ύπαρξη ποικίλων συγκεντρώσεων απολιθωμένου ξύλου από το νότιο τμήμα του νησιού, καθώς και ο προσδιορισμός τριών τύπων της οικογένειας των Δαφνίδων σύμφωνα με τα χαρακτηριστικά των ιδιόβλαστων κυττάρων τους.

Λέξεις κλειδιά: *Ανατομία απολιθωμένου ξύλου, Οικογένεια Δαφνίδων, ιδιόβλαστα κύτταρα, Απολιθωμένο Δάσος Λέσβου.*

1. Introduction

The importance of the plant fossils of Lesbos Island has been underlined having also the privilege to be the first place of the world where the palaeobotanical research took place by Theophrastus from Eressos, Lesbos Island (372-287 B.C.) at the 3rd century B.C. Theophrastus wrote down all his observations for the fossil trees of Lesbos in his book 'On Petrifactions' ('Περί Λιθουμένων'), which, unfortunately is not saved, although there are some references about the fossil trees inside his book 'On Stones' ('Περί Λίθων') (Theophrastus, *Complete Works* 8. 1. 4; 8. 2. 12; 8. 2. 16; 8. 2. 17; 8. 6. 38). The main occurrences of the plant fossils have been found at the western peninsula of the Island (Petrified Forest park; Nissiopi park; Sigri park; Plaka park; Skamiouda park) which has been declared as a Protected Natural Monument since 1985 with a special Presidential Decree (No 443/1985, in Velitzelos et al., 1999). Up to now the great majority of the studied woods were attributed to "gymnosperms" (especially conifers), while the described leaves belong rather to angiosperms (Velitzelos & Zouros, 2008).

This study focuses on the new findings – of both conifers and angiosperms – from new plant fossiliferous localities from Polichnitos region (which is rather distant from the protected area of the Petrified Forest-Western Peninsula).

2. Geological Setting

Lesbos Island is located at the NE part of Aegean and it belongs to the Pelagonian geotectonic zone of Greece which represents a fragment of the Cimmerian Continent (Mountrakis, 1983; 1986).

According to previously published data (Hecht, 1972b; 1974, Katsikatsos et al. 1982; 1986, Fytikas et al., 1984, Mountrakis et al., 1983; 2001, Thomaidou, 2009) the geology of Lesbos is documented in Figure 1 and it consists of an autochnthonous and two allochthonous units.

Polichnitos – Vatera area is located at the southern part of the Lesbos Island (Figure 1). In this area there are six different localities from where samples of fossil wood were obtained. The stratigraphic sequence is presented in Figure 2.

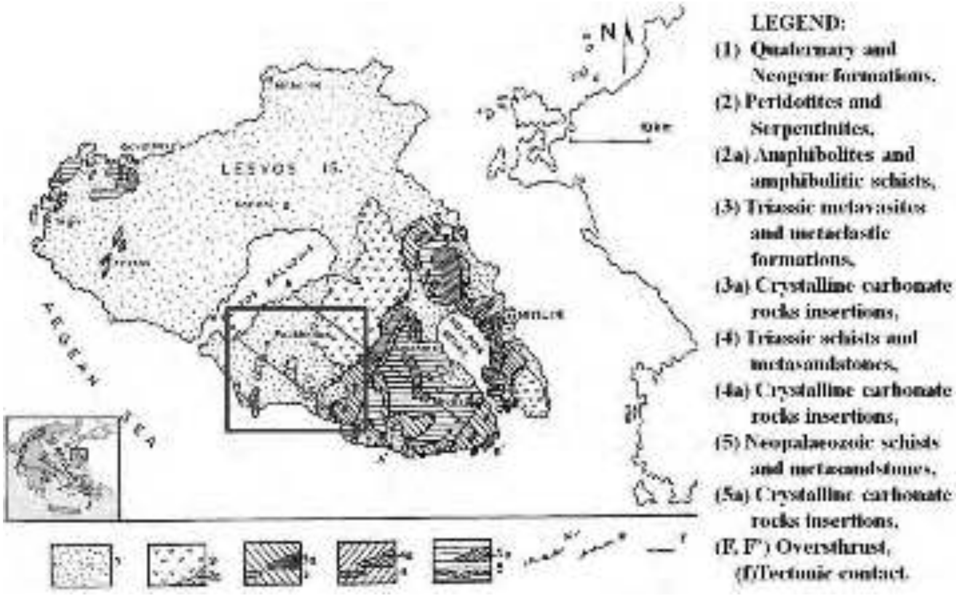

Figure 1 - Geological map by Katsikatsos et al. (1986), modified. Polichnitos-Vatera study area is included in the rectangular.

The stratigraphic sequence of our section fits almost perfectly with the one presented by Katsikatsos et al. (1982) for Polichnitos area, with the difference of a tephra horizon (formation 'e.i' in Fig.2) – which can be attributed to the 'volcanic rocks (+) formation' – under Polichnitos ignimbrite (formation 'c' in Fig.2) as it is shown in Figure 2.

Our outcrops (from the bottom to the top layer) consist of:

- Miocene Terra rossa with a thickness of approximately 12 m (formation 'b' in Fig.2). This is the layer which has the same stratigraphic position with the thick deposits of conglomerates and pyroclastic materials of the area of Sigri - Antisa, which are also lying under the ignimbrites and have at their lower part (and mainly at their basis) marly layers which host small lignitic deposits (Katsikatsos et al., 1986). According to Lamera (2004) it might represent a 'lahar' formation. The basement / underlying layer is not seen at the outcrop but the general view of the area shows that the basement consists of ultrabasic rocks.

- Over the Terra rossa there is a tephra horizon of 1,5 m thickness (formation 'e. i' in Fig.2, left column) and over this there are volcanics of beige color – consisting of 2 horizons, one of 0,4 m ('e. ii' formation in Fig.2, left column) and one of 2 m thickness ('e. iii' formation in Fig.2, left column) – with a total thickness of 2.4 m which are underlying the

- Ignimbrite of Polichnitos with a thickness of 4 m (formation 'c' in Fig.2). According to Pe-Piper & Piper, 1993 the only radiometric date of Polichnitos ignimbrite in 17.2 ± 0.5 Ma 'was made by Borsi et al. (1972) corrected to the Steiger & Jäger, (1977) decay constant'. Polichnitos ignimbrite formation belongs to the magnetic epoch 17 with an age of ~ 18.4 – 17.2 Ma (Pe-Piper, 1980; Pe-Piper & Piper, 1993 while, according to the proposed categorization of Lesbos ignimbrites by Lamera (2004), it represents the PU unit. The fossil plants of our study come from the layers which are underlying Polichnitos ignimbrite and especially from the upper and lower part of the tephra horizon (ei, eii, b in Fig. 2, left column).

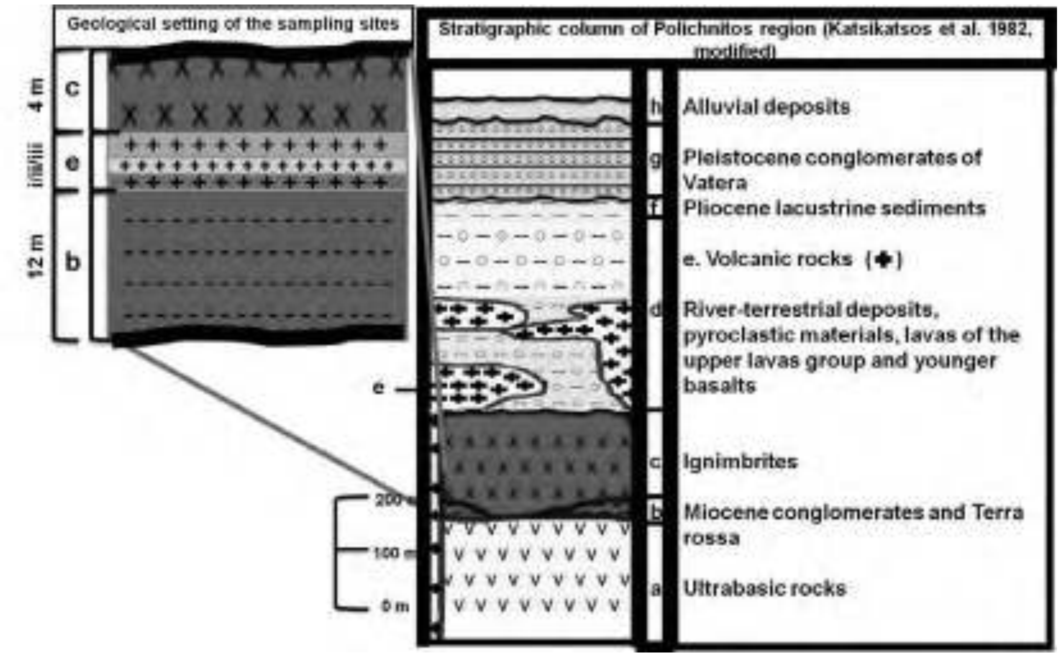

Figure 2 - "Polichnitos – Vatera" area stratigraphic column (from the bottom to the top layer) according to Katsikatsos et al. (1982), modified and the geological setting of the new fossiliferous sites.

Figure 3 - An example of the outcrops of the localities in Polichnitos region (Locality: DMAL, date: 21/08/11).

3. Materials and Methods

During 2011 and 2012 almost 400 specimens were collected by one of us (DM) from six new localities in Polichnitos region. The fossil plants were photographed, their dimensions were measured and they were catalogued. Thin slides for more than 70 samples were prepared (three for each sample: transversal, radial and tangential) in order to study their anatomical features under the microscope.

The thin sections were observed under an Olympus BX51 microscope, in the facilities of Charles University, Prague. Data tables were subsequently created using the Microsoft Office Excel. The anatomical description is in accordance with the IAWA Hardwood List (IAWA Committee 1989) and Wheeler (1986) for angiosperms and the IAWA Softwood List (IAWA Committee 2004) for conifers. In several steps of the study the ArcMap - ArcGIS Program was used, in order to have the already existing knowledge and the new data of the palaeogeographical history of Lesbos Island portrayed.

In Polichnitos region two fossiliferous sites are known (Figure 4):

1. Rougada from which one fossil trunk had been found [*Taxaceoxylon biseriatum* SÜSS & VELITZELOS]. The tree trunk is ash-gray color, is 12.5 m long with a diameter ranging from 80 to 95 cm and was embedded in an ignimbrite layer (Süss & Velitzelos, 1994a).
2. Vatera where the Pliocene vertebrate fauna was discovered and studied by the University of Athens (Dermitzakis, 2002).

Among the material that was collected there were also carbonized fossils (Fig. 5a), or permineralised (Fig. 5b) with the great majority of them having the wood, the bark and the extraxylary tissues preserved in a detailed way.

4. Systematical Part

4.1 Historical Research of the Fossil Plants of Lesbos Island

From 1845 till 2012, 25 species of gymnosperm wood and only 5 species of angiosperm wood have been identified in the Neogene palaeoflora of Lesbos Island, while in some of them there is also information about their preservation. This information is of great value for the taphonomic processes (Appendix). Moreover the references concerning the angiosperm wood species come from the 19th century. The opposite phenomenon – with 5 gymnosperms and 29 angiosperms – occurs at leaves' findings.

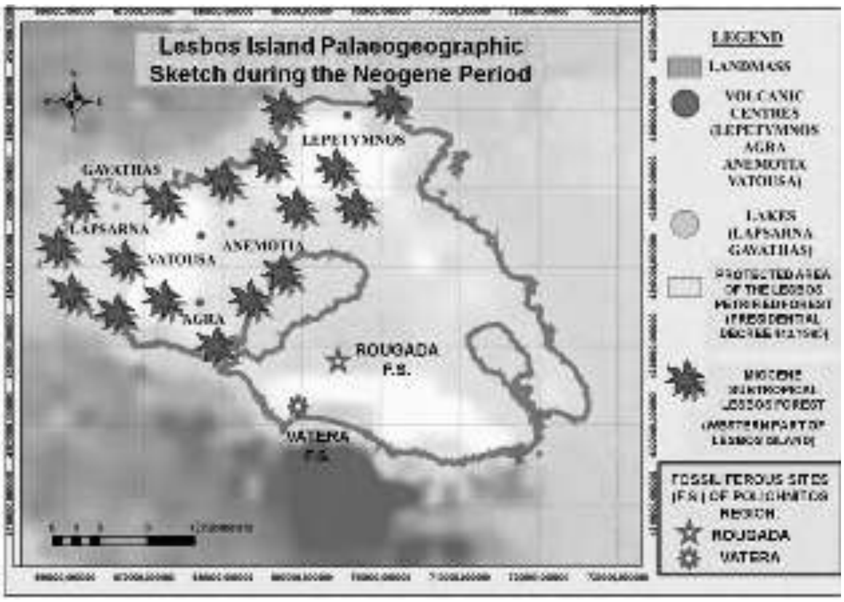

Figure 4 - Palaeogeographic sketch of Lesbos Island during the Neogene Period (Mantzouka 2009a, b, modified).

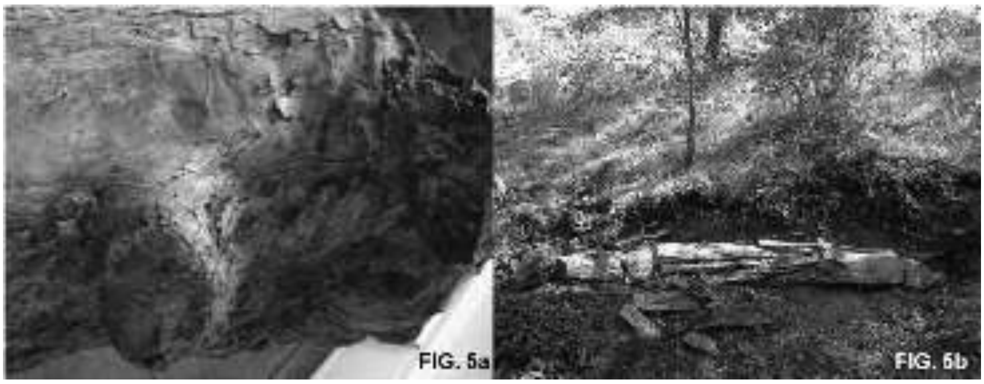

Figure 5 - a. Detail of the external structure of a fossil trunk: the knots and even the bark are preserved (Sample: DMAL 6, date: 21/8/11); b. Among the specimens there is also a lying trunk 2 meters long (Locality: DMRO, date: 17/09/11).

4.2 Preliminary Results

Both conifers and angiosperms have been identified in the samples collected from Polichnitos area. Some of the sampling localities contain only one of these two groups; the others have both of them. However, in this paper only the results from the angiosperms are reported.

Among the newly discovered angiosperm woods we were able to identify anatomical characteristics resembling *Quercus*, *Rhamnus* and Lauraceae family. So far, we recognize seven wood specimens which are similar to the later family according to their typical features as described by Richter in Metcalfe (1987): wood with frequently diffuse porous, vessel solitary or in radial multiples (never exclusively solitary), alternate intervessel pits and tyloses, paratracheal parenchyma, rays 1–3–(5)-seriate, and heterocellular fibers with pitting on radial walls only. Such a fossil wood can be attributed to the morphogenus *Laurinoxylon* FELIX.

Concerning lauraceous woods, they were categorized in different groups, based on their oil cells characteristics. According to Richter (1981) the oil and/or mucilage cells can be of potential diagnostic value, since the difference in their shape and distribution can lead to different taxonomic groups. There are three different groups of idioblasts connected to: a. the ray parenchyma, and b. the vertical strand parenchyma or c. isolated from parenchyma tissues, embedded among the fibers). Three types of lauraceous woods were observed: 1) three samples (Fig. 6b, 7) with oil and/or mucilage cells (idioblasts) connected only to the ray cells, 2) three samples with idioblasts connected to the ray cells and among the fibers and 3) one sample with oil and/or mucilage cells in rays, axial parenchyma and among the fibers. However, a more detailed study is required to obtain solid conclusion.

The samples that have been attributed to the Lauraceae, have some macroscopic characteristics in common: they belong to small stems, which are enclosed to volcanic material (Fig. 6a, b), they are silicified, light, porous, whitish red-brown with distinct growth ring boundaries that can be seen with naked eye, while, most of the times, there is a strange coloration type of circles (possible because of inclusions, of an insect impact or due to mineralization).

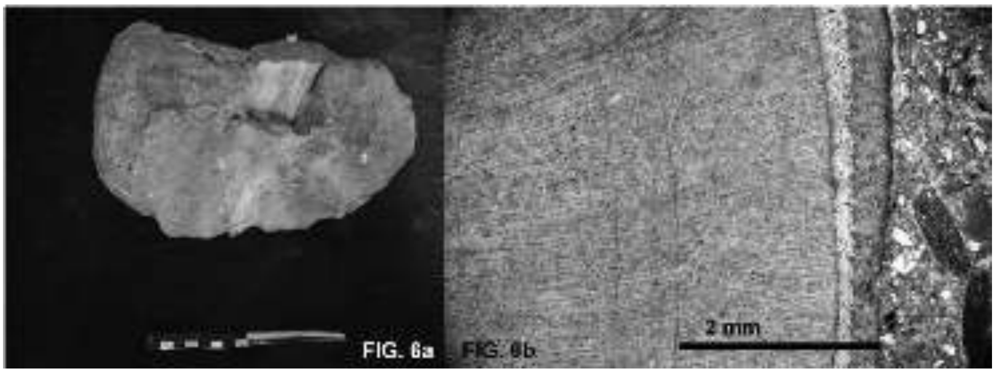

Figure 6 - a. The stem of *Laurinoxylon* type enclosed in volcanic material (sample DMDA 2, dimensions in cm: 18x9x4); b. A stem/branch of type 1 of *Laurinoxylon* (sample DM 17) enclosed in volcanic material (transversal section No. DM17a). The occurrence of the growth ring boundaries is also shown.

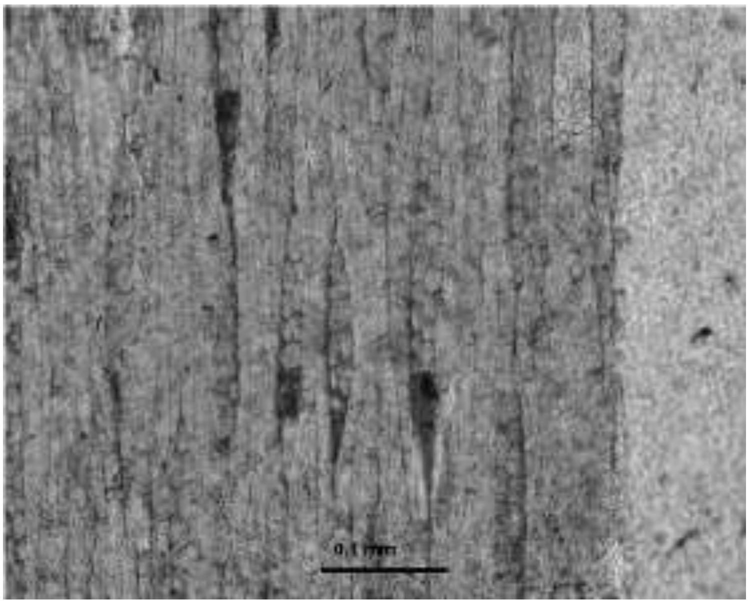

Figure 7 - The oil and/or mucilage cells associated only with the ray parenchyma cells from the same sample DM17 (tangential section No. DM17c).

5. Conclusions

This paper presents preliminary results of a study during which new localities of palaeobotanical interest were discovered in the region of Polichnitos (Vatera) in Lesbos Island; an area that was already well known for its palaeofauna findings. The microscopical study of the collected samples brings new data to the Neogene palaeobotanical record of the Island. Through the study of the new samples there is going to be an effort for collecting as much data as possible in order to follow the 'whole – plant' concept (Sakala 2004) and put together the pieces of the puzzle of reconstructing Lesbos palaeoflora species. Since September of 2012, the whole Island of Lesbos belongs to the Global Geoparks Network of Unesco, which is a recognition of the diversified and many geosites of the Island. By conducting this study we would like to contribute by showing that the occurrences of the petrified trees in other parts of the Island (i.e. apart from the Western peninsula) are not just sporadic but with the right support, protection and scientific study can become geomorphosites/geosites of great importance for the palaeontological heritage of Greece (Zouros & Valiakos 2007).

As far as the stratigraphy is concerned further studies could be conducted by volcanologists and petrologists, since there are localities among the plant fossiliferous ones where the fossils are enclosed inside the volcanic material and others where it seems that the fossiliferous horizon is hosted within the ignimbrite or within lahar deposits. This kind of differentiation of the lithological setting could have a different reflection to the process of silicification, to the palaeoenvirmonment (e.g. the silicification is faster in volcanic lahars) and also could provide more information about the preservation of fossils (Ballhaus et al. 2012). Furthermore, future radiometric dating of specific volcanic layers in the sampling areas will enable the characterization of a biozone and of an exact age.

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APPENDIX:

GYMNOSPERM WOOD

Thujoxylum peucinum UNGER emend. SÜSS & VELITZELOS [Lesbos unknown locality: ?Sigri described by Unger (1847, p.31, 32). The genus has been emended by Süss & Velitzelos (1998)].

Taxoxylum priscum UNGER [Lesbos unknown locality: ?Sigri described by Unger (1847, p.33, 34). Revised as *Taxoxylon priseum* by Unger (1850, p.390, 391)].

Peuce lesbia UNGER (= *Cedroxylon lesbium* KRAUS) [Lesbos unknown locality: ?Sigri described by Unger (1844, p. 34, 37, Tab. X)].

Cedroxylon sp. [Lesbos – western part: Ordymnos seashore and NE part of Ordymnos described by Fliche (1898, p. 143, 148) (lignitic and permineralized samples)].

Pityoxylon sp. [Lesbos – western part: NE part of Ordymnos described by Fliche (1898, p. 149) (permineralized sample)].

Taxaceoxylon biseriatum SÜSS & VELITZELOS [Lesbos: Rougada - Polichnitos region, described by Süss & Velitzelos (1994, p. 259, Taf. I, II)].

Pinoxylon paradoxum (SÜSS & VELITZELOS) SÜSS & VELITZELOS [Lesbos – western part: Bali Alonia, described by Süss & Velitzelos (1994, p. 407, Taf. I, II, III, IV). In 2010 it was revised as *Lesbosoxylon paradoxum* by SÜSS & VELITZELOS].

Pinoxylon pseudoparadoxum (SÜSS & VELITZELOS) SÜSS & VELITZELOS [Lesbos – western part: Bali Alonia, described by Süss & Velitzelos (1994, p. 409, Taf. V). In 2010 it was revised as *Lesbosoxylon pseudoparadoxum* by SÜSS & VELITZELOS].

Taxodioxylon gypsaceum (GOEPPERT) KRÄUSEL [Lesbos – western part: Sarakina, Molyvos, Bali Alonia and Lapsarna-Gavathas (Antissa) described by Süss & Velitzelos (1997, p. 5, Taf. I)].

Taxodioxylon albertense (PENHALLOW) SHIM*A*KURA [Lesbos – western part: Bali Alonia and Sarakina, described by Süss & Velitzelos (1997, p. 7, Taf. II, III)].

Taxodioxylon pseudoalbertense M. NISHIDA & H. NISHIDA [Lesbos – western part: Sarakina, described by Süss & Velitzelos (1997, p. 11, Taf. IV)].

Taxodioxylon megalonissum SÜSS & VELITZELOS [Lesbos – western part: Nisiopi (Megalonissi) described by Süss & Velitzelos (1997, p. 12, Taf. V)].

Taxodioxylon sp. [Lesbos – western part described by Süss & Velitzelos (1997, p. 14)].

Glyptostroboxylon microtracheidae SÜSS & VELITZELOS [Lesbos – western part described by Süss & Velitzelos (1997, p. 16, 18, 19, Taf. VI, VII)].

Tetraclinoxylon velitzelosi SÜSS [Lesbos – western part: Bali Alonia, Sarakina, Sigri, Gavathas described by SÜSS (1997, p. 290, 294, 295, Taf. I, II)].

Thujoxylon antissum SÜSS & VELITZELOS [Lesbos – western part: Lapsarna (Antissa) described by Süss & Velitzelos (1998)].

Chimairoidoxylon lesboense SÜSS & VELITZELOS [Lesbos – western part: Nissiopi (Megalonissi) and Gavathas described by Süss & Velitzelos (1999, p. 330-334, Taf. I, II, III)].

Podocarpoxylon articulatum SÜSS & VELITZELOS [Lesbos – western part: Bali Alonia (main Petrified Forest Park) described by Süss & Velitzelos (2000, p. 138, Taf. I, II)].

Podocarpoxylon graciliradiatum SÜSS & VELITZ*E*LOS [Lesbos – western part: Bali Alonia (main Petrified Forest Park), found lying next to *Taxodioxylon* sp. SÜSS & VELITZELOS (1994) described by Süss & Velitzelos (2000, p. 140, Taf. III, IV)].

Chimairoidoxylon conspicum SÜSS & VELITZELOS [Lesbos – western part: Gavathas, Bali Alonia and Eressos described by Süss & Velitzelos (2001, p. 151, Taf. I, II)].

Ginkgoxylon lesboense SÜSS [Lesbos – western part described by Süss (2003, p. 304-307, Taf. I, II)].

Ginkgoxylon diversicellulatum SÜSS [Lesbos – western part described by Süss (2003, p. 307-310, Taf. III, IV)].

Pinoxylon diversiradiatum SÜSS & VELITZELOS [Lesbos – western part: Eressos, described by Süss & Velitzelos (2009, p. 4, Taf. I, II). In 2010 it was revised as *Lesbosoxylon diversiradiatum* by SÜSS & VELITZELOS].

Pinoxylon graciliradiatum SÜSS & VELITZELOS [Lesbos – western part: Eressos, described by Süss & Velitzelos (2009, p. 6, Taf. III, IV). In 2010 it was revised as *Lesbosoxylon graciliradiatum* by SÜSS & VELITZELOS].

Lesbosoxylon diversiradiatum (SÜSS & VELITZELOS) SÜSS & VELITZELOS [Lesbos – western part: Eressos. Revision of the originally described *Pinoxylon diversiradiatum* by Süss & Velitzelos (2009, 2010, p. 22)].

Lesbosoxylon graciliradiatum (SÜSS & VELITZELOS) SÜSS & VELITZELO*S* [Lesbos – western part: Eressos Revision of the originally described *Pinoxylon graciliradiatum* by Süss & Velitzelos (2009, 2010, p. 22)].

Lesbosoxylon ventricosuradiatum SÜSS & VELITZELOS [Lesbos – western part: Eressos, described by Süss & Velitzelos (2010, p. 19, Taf I, II)].

Lesbosoxylon paradoxum (SÜSS & VELITZELOS) SÜSS *&* VELITZELOS [Lesbos – western part: Bali Alonia main Petrified Forest Park. Revision of the originally described *Pinoxylon paradoxum* by Süss & Velitzelos (1994, 2010 p. 22)].

Lesbosoxylon pseudoparadoxum (SÜSS & VELITZELOS) SÜSS & VELITZELOS [Lesbos – western part: Chamandroula. Revision of the originally described *Pinoxylon pseudoparadoxum* by Süss & Velitzelos (1994, 2010, p. 22)].

ANGIOSPERM WOOD

Juglandinium mediterraneum (UNGER) [Lesbos unknown locality: ?Sigri described by Unger (1845, p. 241). Syn: *Juglandoxylon mediterraneum* (UNGER) (KRAUS 1882 a,b)].

Mirbellites lesbius (UNGER) [Lesbos unknown locality: ?Sigri described by Unger (1845, p.. 241, 242). Syn: *Juglandinium mediterraneum* (Unger 1850; Fliche 1898; Duperon 1988) Syn: *Juglandoxylon mediterraneum* (UNGER) (KRAUS 1882 a,b)].

Brongniartites graecus UNGER [Lesbos unknown locality: ?Sigri described by Unger (1845, p. 264)].

Palmoxylon sp. [Lesbos – western part: Ordymnos seashore described by Fliche (1898, p. 144) (lignitic sample, it looked also like *Sabal* or *Chamaerops*)].

Ebenoxylon sp. [Lesbos – western part: Ordymnos seashore described by Fliche (1898, p. 146) and related to modern *Diospyros* (lignitic sample). Note: Süss 1987 said ?Eben.].

Betulaceae (? *Alnus*), Euphorbiaceae (?), Fagaceae (? *Fagus*, ? *Quercus*), Lauraceae (? *Laurus*, ? *Cinnamomum*, ?), Leguminosae (? *Robinia*), Monimiaceae (?), Myrtaceae (?), Platanaceae (? *Platanus*) [Lesbos – western part: Eressos, Mesotopos. Tab. 1, p. 218 in Selmeier & Velitzelos 2000]

LEAVES

PTERYDOPHYTES

Pronefrium stiriacum (UNGER) KNOBLOCH & KVACEK [Lesbos – western part: Eressos described by Velitzelos (1993)]

GYMNOSPERMS

Tetraclinis sp. [Lesbos – western part described by Velitzelos (1993)]

Pinus sp. [Lesbos – western part. Referred by Velitzelos & Zouros (2008)]

Cunninghamia miocenica ETTINGS HAUSEN [Lesbos – western part. Referred by Velitzelos & Zouros (2008)]

Sequoia abietina (BRONG.) KNOBLOCH [Lesbos – western part. Referred by Velitzelos & Zouros (2008)]

Tetraclinis salicornoides (UNGER) KVAČEK [Lesbos – western part. Referred by Velitzelos & Zouros (2008)]

ANGIOSPERMS

Cinnamomum polymorphum HEER sensu GRANGEON [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]

Laurus sp. [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]

Laurus primigenia UNGER [Lesbos – western part. Referred by Velitzelos et al. (1999)]

Litsea primigenia (UNGER) TAKHT. [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]

Lindera ovata KOLAK. [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]

Oreodaphne heeri GAUDIN [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]

Lauraceae [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]

Daphnogene polymorpha AL.BRAUN ETT. [Lesbos – western part. Referred by Velitzelos et al. (1999)]

Quercus sp. [Lesbos – western part. Referred by Velitzelos et al. (1999)]

Quercus apocynophyllum ETT. [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]

Pungiphyllum crutiatum (AL. BRAUN) FRANKENHÄUSER et WILDE (= *Quercus cruciata* AL. BRAUN) [Lesbos – western part described by Velitzelos (1993) as *Quercus cruciata*]
Pungiphyllum crutiatum (AL. BR.) FRANKENHÄUSER et WILDE [Lesbos – western part. Referred by Velitzelos et al. (1999)]
Carpinus pliofaurei RATIANI forma *helladae* VELITZELOS et al.n. f. [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]
Carpinus uniserrata (KOLAKOVSKI) RATIANI (?) [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]
Alnus cycladum UNGER forma *parvifolia* VELITZELOS et al. n. f. [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]
Alnus cycladum UNGER [Lesbos – western part. Referred by Velitzelos et al. (1999)]
Populus balsamoides GOEPP. [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]
Populus sp. [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]
Tilia sp. [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]
Diospyros brachysepala AL. BRAUN. [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]
Myrsinites sp. [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]
Rhus sp. [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]
Sapotaceae (?) [Lesbos – western part: at the outcrop of the road Antissa-Sigri described by Velitzelos et al. (1981)]
Rubus sp. [Lesbos – western part. Referred by Velitzelos & Zouros (2008)]
Engelhardia sp. [Lesbos – western part. Referred by Velitzelos et al. (1999)]
Engelhardia orsbergensis (WESSEL et WEBER) JÄHNICHEN et al. [Lesbos – western part. Referred by Velitzelos & Zouros (2008)]
Phoenix sp. [Lesbos – western part described by Velitzelos (1993)]
Platanus sp. [Lesbos – western part described by Velitzelos (1993)]
Acer sp. [Lesbos – western part described by Velitzelos (1993)]

USING IDIOBLASTS TO GROUP *LAURINOXYLON* SPECIES – CASE STUDY FROM THE OLIGO-MIOCENE OF EUROPE

Dimitra Mantzouka[1,*], Vasileios Karakitsios[*], Jakub Sakala[†] and Elisabeth Wheeler[††]

*National and Kapodistrian University of Athens, Faculty of Geology and Geoenvironment, Department of Hist. Geology - Paleontology, Panepistimioupoli Zographou, 157 84 Athens, Greece; †Charles University in Prague, Faculty of Science, Institute of Geology and Palaeontology, Albertov 6, 128 43 Prague 2, Czech Republic and ††NC State University, Department of Forest Biomaterials, Campus Box 8005, Raleigh, NC 27695, USA

[1] Corresponding author; e-mail: dmantzouka@yahoo.gr

ABSTRACT

Several specimens of Lauraceae fossil wood from the Cenozoic of Greece (southern part of Lesbos), the Czech Republic (Kadaň-Zadní Vrch Hill and Jáchymov), and Hungary (Ipolytarnóc) were studied. When considering whether they belonged to the speciose fossil wood genus *Laurinoxylon,* we reviewed the literature and data from InsideWood on fossil and modern woods. As a result, we propose criteria for excluding a fossil Lauraceae wood from *Laurinoxylon* and list the species that should be excluded from this genus. The criteria (filters) proposed to exclude a genus from having relationships with *Laurinoxylon* are: A. Axial parenchyma features: A1. Marginal axial parenchyma, A2. Aliform to aliform-confluent paratracheal parenchyma; B. Ray features: B1. Rays higher than 1 mm, B2. Exclusively homocellular rays, B3. Rays more than 5 cells wide, B4. Rays storied; C. Porosity features: Ring-porous; D. Idioblasts: Absence of idioblasts.

Based on the distribution of idioblasts, we recognize four groups in *Laurinoxylon* (*Type 1* –with idioblasts associated only with ray parenchyma cells, *Type 2a* - with idioblasts associated with both ray and axial parenchyma, *Type 2b* - with idioblasts associated both with rays and present among the fibres and *Type 3* - with idioblasts associated with ray and axial parenchyma and also among the fibres) and list the extant genera with features of those groups. Such grouping helps with interpreting the relationships of fossil lauraceous woods with extant genera. We discuss the Oligocene – Miocene European species that belong to these *Laurinoxylon* groups, noting that some warrant reassignment to different genera or even families. Future studies are needed to determine whether new genera should be established to accommodate these species. We propose the new combination *Cinnamomoxylon variabile* (Privé-Gill & Pelletier) Mantzouka, Karakitsios, Sakala & Wheeler.

Keywords: Lauraceae; fossil wood anatomy; oil &/or mucilage cells; *Cinnamomoxylon;* Lesbos Island (Greece); UNESCO Global Geoparks; Czech Republic; Hungary.

INTRODUCTION

Lauraceae is a family distributed worldwide with about 50 genera (van der Werff and Richter 1996; Stevens 2001; Schweingruber *et al.* 2011; Johansson 2013) and more than 2500 species of mainly evergreen trees and shrubs. The great majority of the genera are tropical and subtropical. In present-day Europe, this family is represented only by the genus *Laurus* L. (Mai 1995).

According to Mai (1995), Lauraceae woods are the most common fossil woods in the Cenozoic of Europe and indicate a relatively warm climate. Lauraceous fossil woods occur on all continents, including Antarctica (Gregory *et al.* 2009). The abundance of

Lauraceae in the fossil record is probably due to lauraceous woods being likely to be reported because they are easily recognizable by their idioblasts, and they are likely to enter the fossil record because many have decay resistant heartwood (Wheeler & Manchester 2002).

The relationship of fossil Lauraceae woods to extant genera is difficult to determine because many extant lauraceous woods have similar combinations of features or the fossil is not well enough preserved to observe important diagnostic features (e.g., vessel-ray parenchyma pits or presence/absence of septate fibres). *Laurinoxylon* is a genus name for fossil lauraceous woods that are impossible to assign to a single present-day genus. The diagnosis of *Laurinoxylon* was recently emended by Dupéron *et al.* (2008) as follows: "heteroxylous fossil wood with average vessels, solitary or in radial groups; perforation plates simple and sometimes scalariform; intervessel pits alternate and moderately large; tyloses present; paratracheal parenchyma; uni- to 5-seriate rays, slightly heterocellular and less than 1 mm high; ray-vessel pits large, sometimes stretched; fibres libriform or pits on radial walls; oil or mucilage (idioblasts) cells present". The term "average vessels" is a translation from "vaisseaux moyens" which according to Boureau (1957, p. 542) refers to vessels with a diameter from 100 to 200 μm. Based on the description of the type species *Laurinoxylon diluviale*, the pits on the radial walls of the fibres are not distinctly bordered, and are inconspicuous.

Oil or mucilage cells in wood, hereafter referred to as idioblasts, essentially are restricted to the Lauraceae and other Magnoliid families - Annonaceae, Canellaceae, Hernandiaceae, Magnoliaceae (Metcalfe & Chalk 1950: p. 1347, 1354; Carlquist 2001). As suggested by their name, idioblasts are usually larger than surrounding cells; they often have colored contents. Idioblasts in Lauraceae have been known since 1676, with the first report made by Antoni van Leeuwenhoek (Baas & Gregory 1985).

Our objectives are: 1) to investigate whether idioblasts can help in relating fossil Lauraceae wood to extant genera, 2) to describe fossil Lauraceae woods from four different areas of South-Eastern and Central Europe of Oligocene to Miocene age, 3) to propose a classification scheme for *Laurinoxylon* species, in part based on idioblast distribution, and 4) to suggest which *Laurinoxylon* species do not fit the emended diagnosis of the *Laurinoxylon* and probably should be transferred to another genus.

LOCALITIES AND GEOLOGY

The specimens described herein are from Kadaň-Zadní Vrch Hill and Jáchymov in northwestern Bohemia, Czech Republic; Ipolytarnóc in northern Hungary; and three new localities in the Southern part of the island of Lesbos in the Aegean Sea in northeastern Greece (fig.1).

The three new localities in the Polichnitos region, in the southern part of Lesbos, were discovered by the first author (DM) in 2011. They are in a volcanic layer that underlies the ignimbrite of Polichnitos (PU unit), dated at 17.2 Ma (early Miocene) and belonging to the magnetic epoch 17 (Borsi *et al.* 1972; Pe-Piper 1980; Pe-Piper & Piper 1993; Lamera 2004; Lamera *et al.* 2004). The geology of the area and the stratigraphic sequences of these localities have recently been studied and described in detail (Mantzouka *et al.* 2013). Lesbos is known for its Miocene Petrified Forest at its western peninsula. In 2012, the whole Island of Lesbos, not only the area of the Petrified Forest, was declared a European and Global Geopark. Geoparks combine the protection and promotion of geological heritage in combination with sustainable local development (Zouros 2004). At a meeting in Paris on 17th November 2015, the 195 Member States of UNESCO ratified the creation of the UNESCO Global Geoparks.

The holotype of *Laurinoxylon czechense* Prakash *et al.* (N^{o} CNB-2 with 5 slides: G 4063, G 4064, G 4036, G 4037, G 4038), housed in the National Museum in Prague, comes from the yellowish and greenish tuffites of Kadaň-Zadní Vrch Hill in the Doupovské hory Mountains. The depositional environment is interpreted as a debris flow – lahar, and its age is considered Late Ruppelian (early Oligocene) by Sakala *et al.* (2010). The whole area is the richest site for fossil angiosperm wood in the Czech Republic (Prakash *et al.* 1971; Sakala & Privé-Gill 2004; Sakala *et al.* 2010).

The holotype of *Laurinoxylon diluviale* (Unger) Felix emend. Dupéron *et al.* (4 slides N^{os} 8652–8655), housed in the Muséum National d'Histoire Naturelle in Paris, comes from Jáchymov and was recently described in detail by Dupéron *et al.* (2008). We refer mainly to this recent description, but also discuss a recently discovered part of the original Holotype sample (IGP Jáchymov No. 08 with 2 slides: No. 08/A, No. 08/B now housed in the Institute of Geology and Palaeontology, Charles University, Prague), provided by R. Roessler. The fossiliferous rock, which is volcanic breccias, is probably related to the volcanics of Loučná and estimated to be Oligocene in age (Rapprich pers. comm. 2012).

The sample from Ipolytarnóc (IGP Ipolytarnóc No. 05 with 3 slides: No. 05/A, No. 05/B, No. 05/C, Institute of Geology and Palaeontology, Charles University Prague) was collected by the third author (J.S.) at Ipolytarnóc Fossils Nature Reserve in Hungary from a trunk embedded in the outcrop on the official pathway. Ipolytarnóc is in the European and Global Geoparks Network of UNESCO (as is Lesbos), attesting to its international significance. According to I. Szarvas (pers. comm. 2014), it is plausible that the trunk represents the type species of *Laurinoxylon mueller-stollii* Greguss (1954) emend. Süss and Mädel (1958). Consequently, we consider this sample as a potential part of the holotype of *L. mueller-stollii*. The fossiliferous sediment, which is mainly formed of a combination of sandstone and rhyolite tuff, contains plant and animal fossils as well as fossil tracks (Szarvas 2007). The site was recently radio-isotopically dated to the Ottnangian regional stage of the Central Paratethys (early Miocene) by Pálfy *et al.* (2007).

MATERIALS AND METHODS

Thin sections of the Greek material were prepared at the Laboratory of the Department of Historical Geology & Paleontology, Faculty of Geology & Geoenvironment, National and Kapodistrian University of Athens; thin sections of the Czech and Hungarian material were prepared at the Czech Geological Survey in Prague. Microscopic observations were made with an Olympus BX51 microscope, Olympus DP73 camera and QuickPHOTO MICRO 3.0 image analysis software. Anatomical descriptions follow the IAWA Hardwood List (IAWA Committee 1989). Each vessel was counted separately, both for density and vessel grouping percentage, as proposed by Wheeler (1986). Identifications were made with reference to the InsideWood Web site (InsideWood 2004–onwards; Wheeler 2011). Idioblast frequency was determined from transverse sections.

APPROACH

The distinctions between oil and mucilage cells in structure and chemistry were reviewed by Baas and Gregory (1985), Gregory and Baas (1989), and Carlquist (2001). It is impossible to distinguish between the two in fossil woods, so throughout this paper we use the term idioblasts. Idioblasts in Lauraceae wood may occur: a) associated with the ray parenchyma; b) associated with axial parenchyma strands and / or c) amongst the fibres as individual cells.

First, we determined which extant genera differ from Dupéron *et al.*'s (2008) emended diagnosis. We relied on publications dealing with extant Lauraceae wood anatomy, especially Richter's (1981a) monograph. Other references used were: Callado and Costa (1997), Loutfy (2009), Richter and Van Wyk (1990), Richter (1981b, 1985, 1990), Rohwer *et al.* (2014), van der Werff and Richter (1985, 1996). The following features (A—D) were used as criteria (or filters) to *exclude* a genus from having relationships with *Laurinoxylon*. Lauraceous genera *without* these features possibly may be related to *Laurinoxylon*:

A. Axial parenchyma features *not* in the emended diagnosis: A1. Marginal axial parenchyma, A2. Aliform to aliform-confluent paratracheal parenchyma.

B. Ray features *not* in the emended diagnosis: B1. Rays higher than 1 mm, B2. Exclusively homocellular rays, B3. Rays more than 5 cells wide, B4. Rays storied.

C. Porosity features *not* in the emended diagnosis: Ring-porous.

D. Idioblasts: Absence of idioblasts.

There are two features known to be useful for present-day Lauraceae wood that we choose not to use because they are difficult to determine unless a fossil wood is well-preserved: presence / absence of septate fibres and vessel-parenchyma pit type. Septate fibres characterize the genera of the tribe Perseae, which occur mainly in the Northern Hemisphere, but with some occurrences in Asian tropics, Australia, Africa and Madagascar (Richter 1981a; van der Werff & Richter 1996). Non-septate fibres are reported for the Northern Hemisphere tribe Laureae. Vessel-ray parenchyma pit types are considered to have considerable systematic importance (Richter 1987, in Metcalfe 1987).

According to Richter (1981a), van der Werff and Richter (1996) and Chanderbali *et al.* (2001), Lauraceae have three tribes: Laureae, Perseae, and Cryptocaryeae, plus some genera not assigned to a tribe, e.g., *Iteadaphne* and *Neocinnamomum*. In this paper, we use wood anatomical characteristics of the tribes and their genera given by Richter (1981a) and van der Werff and Richter (1996). They treated 42 genera of Lauraceae. The status of three genera has changed since their work. *Anaueria* is considered a synonym of *Beilschmiedia*, *Clinostemon* is an unresolved name, and *Triadodaphne* is a synonym of *Endiandra* (The Plant List 2013).

RESULTS

Application of features A-D to exclude extant genera as matches for *Laurinoxylon*

A. Axial Parenchyma - Genera differing from *Laurinoxylon* because they have marginal parenchyma (Feature A1) occur in the Cryptocaryeae (a primarily Southern Hemisphere group) and include *Beilschmiedia, Cryptocarya, Endiandra, Potameia,* and *Ravensara*. Marginal parenchyma was one of the characters used to support recognition of the Cryptocaryeae tribe (Richter 1981a; van der Werff & Richter 1996).

However, not all Cryptocaryeae sensu Chanderbali *et al.* (2001, Rohwer *et al.* 2014) can be excluded because some do not have marginal parenchyma, e.g., *Dahlgrenodendron, Syndiclis* (P. Détienne pers. observation for *Syndiclis lotungensis*), but Sun *et al.* (2015) reported that *S. marlipoensis* has marginal parenchyma. Moreover, the wood anatomy of some genera of Cryptocaryeae (*Sinopora*, *Yasunia*) is unknown.

Extant genera excluded from relationships to *Laurinoxylon* because they have aliform to aliform-confluent paratracheal parenchyma (feature A2) are: *Eusideroxylon, Hypodaphnis,* and the *Potoxylon* species once assigned to *Eusideroxylon*.

B. *Ray Features* - The occurrence of rays higher than 1 mm (feature B1) excludes *Caryodaphnopsis* and *Clinostemon.*

Feature B2 (rays homocellular) excludes *Umbellularia* (NB: rays with a single marginal row with some square cells also are present in this genus).

Feature B3 (rays > 5 cells wide) excludes *Dahlgrenodendron* (Richter & van Wyk 1990: p. 177).

Storied rays (feature B4) are rare in Lauraceae, reported only for *Aspidostemon;* some species of *Mezilaurus* have irregularly storied rays, but that is not a consistent feature of the genus (Richter 1990).

C. *Porosity* - The presence of ring porosity excludes *Sassafras* as a candidate for nearest living relative of *Laurinoxylon.*

D. *Idioblasts* - To date, no species of *Neocinnamomum* are known to have idioblasts, so it is excluded.

Modern Genera with Features of Laurinoxylon

After using the "filters" discussed above, this leaves several extant genera with features of the emended diagnosis of *Laurinoxylon.* They are given below using Richter's (1981a) and van der Werff and Richter's (1996) grouping:

Tribe Laureae: *Actinodaphne, Laurus, Lindera* [both groups A & B], *Litsea, Neolitsea;*

Tribe Perseae Nees: *Aiouea, Aniba, Cinnamomum, Dehaasia, Dicypellium, Endlicheria, Licaria, Nectandra, Nothaphoebe, Ocotea, Persea, Phoebe, Pleurothyrium, Systemonodaphne,* and *Urbanodendron.*

Apollonias, Cryptocarya (species from Madagascar) and *Iteadaphne* have not been assigned to a tribe.

Grouping of Laurinoxylon Species and Possible Matching Extant Genera

We used idioblast location to create four groups of *Laurinoxylon* (Tables 1-3). Below we list those groups and the extant genera with similar idioblast location. We fully acknowledge that it may not always be possible to determine presence / absence of crystals in fossil wood. Nonetheless, we use crystal presence / absence to create two subgroups within the extant generic groups below because Richter (1981a) considered crystal occurrence a useful feature.

Type 1 – Laurinoxylon species with idioblasts associated only with ray parenchyma cells (Table 1); extant genera *Dicypellium, Laurus, Litsea chinensis* group, North American *Persea, Systemonodaphne,* and *Urbanodendron*.

Subgroup 1. Genera with a high percentage of species with crystals: *Laurus, Litsea chinensis* group, *Systemonodaphne*.

Subgroup 2. Genera without crystals: *Dicypellium*, North American *Persea*, and *Urbanodendron*.

Type 2a - *Laurinoxylon* species with idioblasts associated with both ray and axial parenchyma (Table 2a); extant genera: *Aiouea, Aniba, Apollonias, Cryptocarya* from Madagascar, *Dehaasia, Licaria, Lindera* group A, *Nothaphoebe, Persea, Phoebe, Pleurothyrium*.

Subgroup 1. Genera with a high percentage of species with crystals: *Aniba, Apollonias, Dehaasia, Phoebe, Licaria, Pleurothyrium.*

Subgroup 2. Genera without crystals: *Cryptocarya* from Madagascar, *Nothaphoebe*, and, according to Richter (1981a), 70% of the species of these three genera lack crystals - *Aiouea, Persea* and *Lindera* group A.

Type 2b - *Laurinoxylon* species with idioblasts associated both with rays and present among the fibres (Table 2b); extant genera: *Actinodaphne* p.p., *Nectandra* p.p., *Neolitsea* p.p.

Crystals are present in 75% of *Actinodaphne* species, 60% of *Nectandra* species, and 50% of *Neolitsea* species. Crystals are absent in 25% of *Actinodaphne* species, 40% of *Nectandra* species, and 50% of *Neolitsea* species. (90% of *Actinodaphne* and *Neolitsea* species, and 84% of Nectandra don't contain idioblasts among the fibres – only in rays and axial parenchyma – and belong in this category).

If crystals are observed in a fossil, this could be useful for assigning *Laurinoxylon* Type 2b specimens to a group of modern genera, using the information on crystal types within the Lauraceae provided by Richter (1981a: p. 68-70).

Type 3 - *Laurinoxylon* species with idioblasts associated with ray and axial parenchyma and also among the fibres (Table 3); matching extant genera: *Actinodaphne* p.p., *Cinnamomum, Endlicheria, Nectandra* p.p., *Neolitsea* p.p. and *Ocotea.*

Subgroup 1. Genera with a high percentage of crystals: *Actinodaphne* p.p., *Endlicheria, Nectandra* p.p. and *Neolitsea* p.p. (10% of *Actinodaphne* and *Neolitsea* species, and 16% of Nectandra contain idioblasts also among the fibres and belong in this category).

Subgroup 2. Genera without crystals. *Cinnamomum* and *Ocotea.*

Table 4 compares some of the salient features of *Laurinoxylon* Types 1, 2a, 2b, and 3. In addition to differences in idioblast location, there are some differences between the groups in range of intervessel pit size, whether there are any scalariform perforation plates, and incidence of septate fibres. The range of the values for vessels per mm^2 for *Laurinoxylon* Types 1, 2b and 3 might in part be due to differences in counting vessels per unit area (Wheeler 1986).

There are some *Laurinoxylon* species that are not discussed in detail in this paper for reasons related to their age, or geographic location or lack of a detailed description. However, the descriptions in the literature and in InsideWood suggest some might be assigned to a group; these are mentioned below.

Possible *Laurinoxylon* Type 1 are *L. namsangensis* Lakhanpal, Prakash & Awasthi (1978, iss. 1981), *L. neagui* S. Iamandei & E. Iamandei (1997), and *L. perseamimatus* Petrescu (1978).

Possible *Laurinoxylon* Type 2a are: *Laurinoxylon* sp. from Karlovy Vary, Czech Republic (Březinová 1981) and *Laurinoxylon stickai* Boonchai & Manchester from the Eocene of Wyoming, USA (Boonchai & Manchester 2012).

Possible *Laurinoxylon* Type 2b species are these Indian species: *L. deomaliensis* Lakhanpal Prakash & Awasthi (1978, iss. 1981), *L. naginimariense* Awasthi & Mehrota (1989, iss. 1990), *L. siwalicus* Prasad (1989, iss. 1990), and *L. varkalaensis* Awasthi & Ahuja (1982).

One possible *Laurinoxylon* Type 3 / *Cinnamomoxylon* is *Laurinoxylon tertiarum* Prakash & Tripathi.

Systematic Descriptions - New Material

Family—Lauraceae Juss.

Fossil Genus—*Laurinoxylon* Felix emend. Dupéron, Dupéron-Laudoueneix, Sakala & De Franceschi

Laurinoxylon Type 1

Fossil Species—*Laurinoxylon* aff. *czechense* Prakash, Březinová & Bůžek

(fig. 2*A*–2*F*, Table 1)

Material: DM 10 (2 slides), DMDA 13.1 (3 slides)

Locality: Southeastern Lesbos, Greece

Stratigraphic horizon: Under Polichnitos Ignimbrite (PU unit), inside volcanics

Age: early Miocene

Macroscopic description. These two specimens are from small stems with a diameter of 2.5 cm that were enclosed in volcanic material (fig. 2*A*), they are silicified, light, porous, whitish red-brown with distinct growth ring boundaries that can be seen with the naked eye. There are also strangely coloured circles.

Microscopic description. Growth rings: distinct (fig. 2*A*). — Wood: diffuse-porous (fig. 2*A*). — Vessels: 40-100 (52-74) vessels/sq. mm.; 18% solitary, 50% groups of two, 7.5% in groups of 3, 3.5% in groups of 4 and 21% clusters; tangential diameter 40 to 85 µm, mean: 60 µm; radial diameter of the solitary vessels 50 to 110 µm, mean: 73 µm; outline of solitary vessels round to oval (fig. 2*A*, 2*B*, 2*E*); vessel walls thin; perforation plates exclusively simple; tyloses common (fig. 2*C*); intervessel pits alternate and polygonal in outline, about 10 µm across. — Rays: heterocellular (fig. 2*F*) up to 3 cells wide (25–30 µm) (fig. 2*B*–2*E*), commonly 2–3-seriate and 280–520 µm high, body of multiseriate rays composed of procumbent cells with one row of upright cells (fig. 2*F*); no crystals observed; 9–24 (mean 15) rays per mm. — Axial parenchyma: scanty paratracheal (fig. 2*E*). — Fibres: most probably non-septate (difficult to determine due to the bad preservation). — Idioblasts: associated with the ray parenchyma cells only (fig. 2*B*–2*F*). Mean radial x tangential diameter of the idioblasts in transverse section: 15–22 × 26–36 µm; Number of idioblasts per sq. mm (transverse section): 35–65.

Comparison with Laurinoxylon I species (Table 1). The two specimens from Lesbos have diffuse porous wood, distinct growth ring boundaries, vessels solitary and in radial multiples of 2–3 or sometimes in clusters, simple perforation plates, alternate pitting, scanty paratracheal axial parenchyma, heterocellular 2–3-seriate rays, tyloses (common) and idioblasts associated only with the ray parenchyma cells. These features are characteristic of *Laurinoxylon* Type 1. There are several previously described fossil species that fit this type.

According to the results of our search through the Inside Wood Database and the literature, some of the *Laurinoxylon* species that belong to Type 1 and warrant comparison with our new material are: *L. czechense* Prakash, Březinová & Bůžek, *L. intermedium* Huard, *L. litseoides* Süss, *L. microtracheale* Süss, and *L. oligocenicum* Prakash, Březinová & Awasthi.

Süss (1958) stated that *Laurinoxylon litseoides* Süss is similar to modern *Litsea chinensis* L. and *L. citrata* Blume. The Lesbos woods described above are similar to *Laurinoxylon litseoides,* differing in vessel diameter (in *L. litseoides* slightly wider), ray seriation (1-4 in *L. litseoides* – 1-3 in Lesbos woods), idioblast density (few in *L. litseoides* – numerous in Lesbos woods) and intervessel pit size (small-medium in *L. litseoides* – large in Lesbos woods). It is probable that the difference in the vessel diameters is likely due to the Lesbos samples being small axes. We were not able to examine the original material of *L. litseoides*.

The original material of *Laurinoxylon oligocenicum* Prakash, Březinová & Awasthi (1974) was considered for a long time lost, but small fragments were recently rediscovered and new slides were cut from them. However, their quality did not allow any detailed revision, so we based our comparison on the original description. Prakash *et al.* (1974) suggested that *L. oligocenicum* was similar to *Persea pubescens*. *Laurinoxylon oligocenicum* differs from the Lesbos wood in vessel diameter and density, number of rays per mm and presence of septate fibres.

Laurinoxylon czechense Prakash, Březinová & Bůžek (1971) appears the most similar to the Lesbos material based on microscopic examination of the holotype slides G 4036, G 4037, G 4038, G 4063, G 4064 of the specimen CNB-2 (fig. 2*G*-2*I*). It has idioblasts associated only with the ray parenchyma cells, as confirmed by Sakala *et al.* (2010). It differs from the Lesbos wood in having slightly wider vessels, occasional scalariform perforation plates, and slightly higher rays. Its idioblasts occur in the body of the rays as well as at the margins. Because of these differences, we refer these Lesbos fossil woods to *Laurinoxylon* aff. *czechense* Prakash, Březinová & Bůžek.

We think that *Laurinoxylon intermedium* Huard and *Laurinoxylon microtracheale* Süss should not be treated as species of *Laurinoxylon* (see below for discussion).

Problems and proposals. According to Huard (1967), *Laurinoxylon intermedium* has characteristics of both Persoideae and Lauroideae. The location described for its idioblasts might suggest placement in *Laurinoxylon* Type 1. However, *Laurinoxylon intermedium* Huard has only scalariform perforation plates, scalariform intervessel pits, and seemingly marginal and concentric parenchyma bands of 4–12 cells. Because of the exclusively scalariform perforation plates and scalariform intervessel pits, it should be excluded from the Lauraceae. The combination of idioblasts, exclusively scalariform perforation plates, and marginal parenchyma indicates it belongs to the Magnoliaceae. The sample needs to be examined to determine to which magnoliaceous genus it belongs. Kvaček *et al.* (2011) recently revised the leaf flora of this area. The leaf flora includes one species of Magnoliaceae, *Magnolia liblarensis* (Kräusel et Weyland) Kvaček. It might be possible that Huard's wood and the *Magnolia liblarensis* leaves represent the same plant.

According to Süss (1958), *Laurinoxylon microtracheale* Süss is similar to *L. nectandrioides* Kräusel & Schönfeld. However, *L. microtracheale* has predominantly homocellular rays, which does not agree with the diagnosis of *Laurinoxylon*. Homocellular rays are rare in the Lauraceae. *Umbellularia* is the one lauraceous genus known to have homocellular rays and idioblasts only associated with the rays. The type material of *L. microtracheale* needs to be examined to determine if its combination of features is consistent with *Umbellularia,* which today is a California endemic.

Botanical affinities. The Lesbos *Laurinoxylon* aff. *czechense* has no crystals. Therefore, we believe it is possibly related to *Dicypellium*, *Urbanodendron* or the North American *Persea*. Because it does not have septate fibres it seems more closely related to North American *Persea*; this group of *Persea* species is close to Laureae tribe, which has non-septate fibres. Leaves of Lauraceae are known from Lesbos (Velitzelos *et al.* 1981a, b, 1999; Mantzouka *et al.* 2013).

Laurinoxylon Type 2a

Fossil Species— *Laurinoxylon mueller-stolli* Greguss emend. Süss & Mädel

(Fig. 3*A*-3*D*, Table 2a)

Material: specimen IGP Ipolytarnóc No. 05 + 3 slides: No. 05/A, 05/B & 05/C (potential part of the holotype of *L. mueller-stolli*)

Locality: Ipolytarnóc Fossils Nature Reserve, Hungary

Stratigraphic horizon: rhyolite tuff

Age: early Miocene

Macroscopic description. Slightly flattened trunk, 50 × 35 cm in diameter, directly embedded in rock with only a part of transverse surface exposed.

Microscopic description. Growth rings: distinct (fig. 3*A*, 3*B*). — Wood: diffuse-porous (fig. 3*A*, 3*B*). — Vessels: 12-18 vessels/sq. mm.; 56% solitary, 25% groups of two, 19% in groups of 3-4; tangential diameter of the solitary vessels 85 to 200 µm, mean 160 µm; radial diameter of the solitary vessels 85 to 240 µm, mean: 175 µm; outline of solitary vessels round to oval (fig. 3*A*, 3*B*); perforation plates simple and scalariform (fig. 3*D*); tyloses common (fig. 3*A*-3*D*), intervessel pits alternate about 10-15 µm, vessel-ray pits with distinct or much reduced borders, similar to intervessel pits in size and shape. — Rays: heterocellular (fig. 3*D*) up to 3 cells wide (25–30 µm) (fig. 3*A*– 3*D*), commonly 2-seriate and 10-15 cells high, body of multiseriate rays composed of procumbent cells with 1–4 or more (mostly 2–4) rows of upright and/or square marginal cells (fig. 3*D*); no crystals observed; 5–8 rays per mm. — Axial parenchyma: vasicentric (fig. 3*A* – 3*C*) 15–20 µm wide circle around the vessel — Fibres: with simple to minutely bordered pits, probably septate (fig. 3*C*-3*D*). — Idioblasts: associated with the ray and axial parenchyma, tangential height: 40–75 µm, width: 30–50 µm (fig. 3*C*–3*D*). Number of idioblasts per sq. mm (transverse section): 35–65.

Comparison with Laurinoxylon Type 2a *species* (Table 2a). – *IGP* Ipolytarnóc No. 05, potential part of the holotype of *Laurinoxylon mueller-stolli* Greguss emend. Süss & Mädel of Lower Miocene (A. Burdigalian) age from Ipolytarnóc (Hungary) was examined and assigned to *Laurinoxylon* Type 2a because it has idioblasts associated with the ray and axial parenchyma (fig. 3*A*–3*D*). In the original description by Süss and Mädel (1958), 'cells as upright prisms of 20–75 µm height and 7–22 µm width' are mentioned, and we believe this refers to the idioblasts associated with the axial parenchyma cells. The values for idioblast size are new observations (Table 2a).

Our search of the Inside Wood Database and the literature suggests the Type 2a *Laurinoxylon* species that should be compared with our material are: *L. aniboides* Greguss emend. Süss & Mädel*, L. annularis* Gottwald*, L. endiandroides* Süss, *L. ehrendorferi* Berger, *L. hasenbergense* Süss, *L.* cf. *hasenbergense*, and *L. nectandrioides* Kräusel & Schönfeld.

Laurinoxylon aniboides Greguss emend. Süss & Mädel (1958) differs in dimensions of idioblasts and vessels and it has only scalariform perforation plates (a characteristic which excludes this species from the Lauraceae, see discussion below).

Laurinoxylon annularis Gottwald (1997) differs in porosity (is a ring-porous wood), vessel diameter, intervessel pit size, and the presence of parenchyma bands up to 3-cells wide (characteristics not in accordance with the emended diagnosis for *Laurinoxylon*).

Berger (1953) suggested *L. ehrendorferi* was closely related to *L. nectandrioides*, based on idioblast characteristics, and was similar to the extant lauraceous genera *Acrodiclidium*, *Aiouea*, *Cinnamomum*, *Cryptocarya*, *Persea* and *Phoebe*. We agree that *Laurinoxylon ehrendorferi* Berger is similar to *L. nectandrioides*, except for more frequently grouped vessels in *L. ehrendorferi* and more abundant axial parenchyma in *L.*

nectandrioides. There are differences between *L. ehrendorferi* and *L. mueller-stollii* in mean radial vessel diameter, the size of the intervessel pits, ray height, and occurrence of some scalariform perforation plates (Table 2a).

Süss (1958) described *Laurinoxylon endiandroides* as having idioblasts associated with both ray and axial parenchyma. However, this species has aliform to confluent parenchyma and thus does not fit the emended description of *Laurinoxylon* (see also the “Problems and proposals” paragraph below). There are additional differences between the Hungarian material we studied and *L. mueller-stolli*, such as the vessel density, vessel diameter, the occurrence of scalariform perforation plates, and the size of the intervessel pits (Table 2a).

Laurinoxylon hasenbergense Süss (Süss 1958) and *L.* cf. *hasenbergense* (Greguss 1969) differ from this Hungarian sample in having exclusively simple perforation plates, narrower vessels, parenchyma bands up to 3-cells wide and no conical idioblasts (Table 2a). The presence of rays up to 1200 μm tall does not agree with the emended diagnosis of *Laurinoxylon*. This “problematic characteristic” is discussed in “Problems and proposals” paragraph below. The description of *Laurinoxylon nectandrioides* Kräusel & Schönfeld (Kräusel & Schönfeld 1924; van der Burgh 1964, 1973) is not clear about the occurrence of idioblasts among the fibres; it deserves re-examination. We also found some differences in tangential (but also in radial) vessel diameter, occurrence of scalariform perforation plates, size of the intervessel pits, ray width and presence of tracheids (observed in *Laurinoxylon nectandrioides* Kräusel & Schönfeld according to van der Burgh 1973, p. 166). The main difference is the presence of aliform – confluent vasicentric paratracheal parenchyma and seemingly marginal bands in *Laurinoxylon nectandrioides*, features not mentioned in the generic diagnosis of *Laurinoxylon.*

The vessel element lengths reported for five of the seven Type 2a lauraceous woods (Table 2a) are very low (means < 250 µm) compared with modern lauraceous woods (typically means > 350 µm). Possible explanations are that distances between tyloses walls were measured instead of between vessel element end walls. Another factor is that the studied samples were from very near the pith and vessel elements are expected to be shorter in juvenile wood than in mature wood.

Problems and proposals -- Laurinoxylon aniboides Greguss emend. Süss & Mädel has rays higher than 1mm and only scalariform perforation plates. Because of the exclusively scalariform perforation plates, it should be excluded from the Lauraceae. Further investigation is needed to determine whether it belongs to the Magnoliaceae or Canellaceae (e.g., *Warburgia stuhlmannii*), two families in which idioblasts and exclusively scalariform perforation plates co-occur.

Laurinoxylon annularis Gottwald has aliform-confluent parenchyma and 3-cell wide parenchyma bands and is ring-porous. This is not typical for *Laurinoxylon*; therefore, we recommend excluding it from this genus and that it be assigned to *Sassafrasoxylon* Brezinová & Süss. This wood needs further study to determine whether it is conspecific with *Sassafrasoxylon gottwaldii* Poole, Richter & Francis or *S. lipnicense* Březinová & Süss or whether if differs enough from those two species so that a new combination be proposed.

For the three species listed below, study of the type material is needed to determine whether their characteristics fit any existing genus for fossil lauraceous woods or if new genera should be created.

Laurinoxylon endiandroides Süss has aliform to confluent axial parenchyma, a characteristic not in accordance with the emended diagnosis of *Laurinoxylon*. We propose that the type be examined to determine whether there are idioblasts associated with the fibres as alluded to by Süss (1958, p.32, “einige scheinbar in der Holzmasse verstreut”). If idioblasts amongst the fibres are present, this species might be assigned to *Cinnamomoxylon*. On the other hand, if there are no idioblasts among the fibres, then it might be assigned to the Cryptocaryeae Nees tribe (because of its axial parenchyma type).

Laurinoxylon hasenbergense Süss and *Laurinoxylon* cf. *hasenbergense* have idioblast distribution that places them in our *Laurinoxylon* Type 2a. However, their published descriptions indicate that they have some characteristics not in accordance with the emended diagnosis of *Laurinoxylon*, e.g., the 3-cell wide parenchyma bands and the rays up to 1.2 mm high. Rays 1.2 mm high in combination with presence of crystals and exclusively simple perforation plates suggest that a relationship with *Licaria* needs investigation.

Laurinoxylon nectandrioides Kräusel & Schönfeld has confluent parenchyma (and seemingly marginal bands), septate fibres and crystals. The parenchyma distribution suggests relationships with genera of the Cryptocaryeae tribe, but the occurrence of septate fibres suggests relationships with the Perseae tribe. Further study is required for determining its placement within the Lauraceae.

Botanical affinities. *Laurinoxylon mueller-stolli* has septate fibres and no crystals, so it could be related to the extant genera with features of *Laurinoxylon* Type 2a that don’t have crystals and belong to the Tribe Perseae Nees: *Aiouea*, *Cryptocarya* from Madagascar, *Nothaphoebe* and *Persea*. Fossil lauraceous leaves also occur at Ipolytarnóc

(Hably 1983) (e.g., *Persea braunii* Heer or *Persea speciosa* Heer in Hably 1983, p. 140), so there may be a correlation between *Laurinoxylon mueller-stolli* and those *Persea* leaves.

Laurinoxylon Type 2b

Fossil Species—*Laurinoxylon* aff. *diluviale* (Unger) Felix emend. Dupéron *et al.*

(fig. 4*A*–4*J*, Table 2b)

Material: DMKO 1 (3 slides), DMDA 2 (4 slides), DMDA 7 (5 slides)

Locality: Southeastern Lesbos, Greece

Stratigraphic horizon: Under Polichnitos Ignimbrite (PU unit), inside volcanics

Age: early Miocene

Macroscopic description. Two specimens are from small stems (the pith is preserved) which are enclosed in the surrounding volcanic material with the following dimensions (in cm): 18 × 9 × 4, 12 × 3.5 × 2 and one is from a part of a stem with knots (the pith wasn't preserved), which is silicified, heavy, red-brown with the dimension of: 31 × 21 × 11 cm. They are silicified, light, whitish brown with distinct growth ring boundaries that can be seen with the naked eye. There is a strange colouration type of circles, due to fossilization processes (fig. 4*A*).

Microscopic description. Growth rings: distinct. — *Wood:* diffuse-porous. — *Vessels:* 20–100 vessels/sq.mm; 29% solitary, 50% in groups of two, 17% in groups of 3, and 4% in groups of 4; tangential diameter 40–110 μm, mean: 70 μm; radial diameter of solitary vessels 50–150 μm, mean: 90 μm; outline of solitary vessels round to oval (fig. 4*A*, 4*B*);

vessel walls thin; perforation plates mostly simple (fig. 4*C*, 4*D*) some scalariform with 6–12 bars; polygonal alternate intervessel pits small (5 µm) to medium (7.5 µm), tyloses common (fig. 4*A*, 4*B*). — *Rays:* heterocellular up to 3 cells wide (extremely rarely 4 cells), (20–60 µm), and 160–650 µm high (fig. 4*C*); body of multiseriate rays composed of procumbent and upright cells, marginal rows of 1–4 upright cells; crystals not seen; Rays per mm: 11-16. — *Axial parenchyma:* scanty paratracheal (fig. 4*B*). — *Fibres:* probably septate. — *Idioblasts*: associated with the ray parenchyma cells and among the fibres (fig. 4*C*–4*D*), idioblasts in transverse section with radial diameter × tangential diameter from 25 × 15 up to 70 × 40 µm; number of idioblasts per sq. mm in transverse section: in general, 35–70/sq. mm.

Comparison with Laurinoxylon Type 2b species (Table 2b) -- These three specimens from Lesbos have features characteristic of *Laurinoxylon* Type 2b. According to the results of our search through the Inside Wood Database and the literature, *Laurinoxylon* species that belong to our Type 2b and that warrant comparison with our new material are: *Laurinoxylon compressum* Huard, *L. perfectum* Huard and *L. diluviale* Unger.

Laurinoxylon compressum Huard was described as ring-porous to semi-ring-porous (closely related to *Ocotea* and *Sassafras* according to Huard 1967), so it is not similar to the samples from Lesbos. *Laurinoxylon perfectum* Huard differs from the Lesbos wood because its parenchyma tends to be aliform, it has 1–3-seriate rays, lower vessel frequency and fewer rays per mm. Both *L. compressum* and *L. perfectum* should be excluded from *Laurinoxylon* (for explanation see “Problems and proposals” paragraph).

Laurinoxylon diluviale from Jáchymov appears the most similar to the Lesbos material. It has been studied by Unger (1842), Felix (1883), and, most recently, Dupéron *et al.* (2008), who made a detailed re-examination of the original type slides. We examined new slides from the newly re-discovered part of the holotype given to us by R. Roessler (holotype specimen IGP Jáchymov No. 08, 2 slides, Fig. 4*E*-*J*). We observed the following features: wood diffuse porous; vessels rounded to slightly angular; 9–33 vessels per sq. mm; 6—9 rays per mm, fibres possibly septate, and tyloses common (fig. 4*F*). Our observations of quantitative features generally agree with Dupéron *et al.* (2008), but we found idioblasts to be larger and associated with ray parenchyma and also dispersed among the fibres (fig. 4*E*-4*J*). We also observed in tangential sections some idioblasts that looked as if they had been shifted some microns away from the rays' bodies (as if the idioblast's edge was detached from the rest of the ray). They can appear to be idioblasts among the fibres, but we believe that they were originally associated with the rays. This strange phenomenon also occurs in the Lesbos material. The Lesbos wood is similar to *Laurinoxylon diluviale* (Table 2b), because it has simple and scalariform perforation plates and 1–5-seriate rays, but differs in vessel diameter and idioblast size and abundance. These differences (Table 2b) may be in fact related to the individual variability as the samples probably come from different parts of the tree.

Problems and proposals. Laurinoxylon compressum Huard is ring-porous. This characteristic is not in accordance with the emended diagnosis of *Laurinoxylon*. We believe that its ring-porosity and low rays indicate it should be assigned to *Sassafrasoxylon* Březinová & Süss. Additional study is needed to determine if it is conspecific with *Sassafrasoxylon lipnicense*.

Laurinoxylon perfectum Huard tends to have some aliform parenchyma. This type of parenchyma is not typical for *Laurinoxylon*. A re-examination of the specimen is recommended for better assessing its affinities.

Botanical affinities - We did not observe crystals in *Laurinoxylon* aff. *diluviale* from Lesbos or in *Laurinoxylon diluviale* from Jáchymov, so our material belongs to the Subgroup 2 of *Laurinoxylon* Type 2b. We observed septate fibres in this material. Septate fibres occur in *Nectandra*, a genus belonging to the Perseae Nees tribe, therefore we suggest that *Laurinoxylon* aff. *diluviale* might have affinities with the group of *Nectandra* species without crystals.

Laurinoxylon Type 3 / *Cinnamomoxylon* Gottwald

Fossil Species—Cinnamomoxylon seemannianum (Mädel) Gottwald (fig. 5*A*–5*G*, Table 3)

Material: DMDA 6 (7 slides)

Locality: Southeastern Lesbos, Greece

Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics

Age: early Miocene

Macroscopic description. The specimen belongs to one of three small stems found enclosed in volcanic material with the following dimensions: 4.5 × 2 × 2 cm. This stem and the other two are silicified, light, whitish brown with distinct growth ring boundaries that can be seen with naked eye.

Microscopic description. Growth rings: distinct. — *Wood:* diffuse-porous. — *Vessels:* 40–100 vessels/sq.mm; 17% solitary, 33% groups of two, 14% in groups of 3, 15% in groups of 4 and 21% in clusters; tangential diameter 45-50 µm (mean 47 µm); radial diameter 60–110 µm (mean 90 µm); outline of solitary vessels mainly round to oval (sometimes the vessels' outline seems angular because the sample is contorted and compressed) (fig. 5B); vessel walls thin; perforation plates simple (fig. 5*D*, 5*E*); tyloses common (fig. 5*A*); intervessel pits alternate.— *Rays:* heterocellular, up to 5-seriate (mostly 2–3-seriate) (50–60 μm), and 300–500 μm high, body of multiseriate rays composed of procumbent body ray cells with one row of upright and/or square marginal cells (fig. 5*F*, 5*G*); crystals not seen; rays 9 (7-14) per mm. — *Axial parenchyma:* scanty paratracheal, vasicentric to confluent (fig. 5*A*, 5*B*, 5*D*, 5*E*). — *Fibres:* probably non-septate. — *Idioblasts*: associated with the ray and axial parenchyma cells and among the fibres (fig. 5*A*–*G*). Idioblasts in the transverse view radial × tangential diameter in μm from 30 × 135 to 50 × 160 and per sq. mm 15–33.

Comparison with Laurinoxylon Type 3 *Species and Cinnamomoxylon* (Table 3) - As indicated by the description above, this specimen from Lesbos has characteristics of *Laurinoxylon* Type 3. The revised diagnosis of *Laurinoxylon* is not clear about how abundant axial parenchyma can be within the genus. We think that the new Lesbos material with the idioblast distribution of the *Laurinoxylon* Type 3 group should be assigned to *Cinnamomoxylon* sensu Gottwald (1997). As implied by its name, this fossil genus has features seen in present-day *Cinnamomum*, which according to Richter (1981a) also has features seen in some species of *Lindera*, *Litsea* and *Persea*.

We think that the diagnosis of *Cinnamomoxylon* Gottwald should be modified to include rays up to 5-seriate (as described in Richter 1981a for extant *Cinnamomum*), rather than 2-4 cells.

According to the results of our search through the Inside Wood Database and the literature, fossil species belonging to Type 3 warranting comparison with our new Lesbos material are: *Cinnamomoxylon limagnense* (Privé-Gill & Pelletier) Gottwald, *Laurinoxylon bergeri* Süss, *Cinnamomoxylon seemannianum* (Mädel) Gottwald, and *Laurinoxylon variabile* Privé-Gill & Pelletier.

Cinnamomoxylon limagnense (Privé-Gill & Pelletier) Gottwald differs from DMDA 6 in vessel grouping, mean vessel diameter, sporadic occurrence of scalariform perforation plates, vessel density and parenchyma arrangement (Privé-Gill & Pelletier 1981) (Table 3).

Süss (1958) suggested that *Laurinoxylon bergeri* resembled extant *Lindera polyantha* and *Aniba ovalifolia.* Later, Gottwald (1997) suggested it had similarities with the modern tropical Asian species of *Actinodaphne*, *Cinnamomum*, *Litsea* and *Persea*. Süss also suggested that *Laurinoxylon bergeri* was similar to *Laurinoxylon aromaticum* Felix, *L. bakeri* Berry, *L. ehrendorferi* Berger, *L. hasenbergense* Schönfeld, *L. linderoides* Schönfeld, and *L. nectandroides* Kräusel.

The Lesbos specimen differs from *Laurinoxylon variabile* in vessel grouping, mean vessel diameter, vessel density, and septate fibre occurrence (Table 3). The most important difference is the occurrence of aliform-confluent parenchyma forming oblique or tangential bands in *Laurinoxylon variabile* (Privé-Gill & Pelletier 1981). There are also differences in rays: *L. variabile* has an extremely low number of rays per mm. Idioblast dimensions of *L. variabile* and Lesbos wood samples are similar.

Süss and Mädel (1958) described *Laurinoxylon seemannianum* Mädel, now *Cinnamomoxylon seemannianum* (Mädel) Gottwald, as having idioblasts associated with ray and axial parenchyma and among the fibres. Their description indicates that the idioblasts of *L. seemannianum* Mädel have similar dimensions as the Lesbos Type 3 wood. The only differences between the Lesbos wood and *Cinnamomoxylon seemannianum* are in dimensions of vessels and rays. Differences are likely to be ontogenetic. Most recently, *Cinnamomoxylon seemannianum* was described by Koutecký & Sakala (2015) from the Oligocene of the Czech Republic.

Laurinoxylon cf. *seemannianum* described by Selmeier (1967, 1969, 1984) and Gottwald (1992) seems problematic (see “Problems and proposals” paragraph) because these two authors have reported idioblasts associated only with the ray parenchyma. Therefore, DMDA6 was compared only with *Laurinoxylon seemannianum* Mädel and not with *Laurinoxylon* cf. *seemannianum*.

We have named the specimen from Lesbos as *Cinnamomoxylon seemannianum* (Mädel) Gottwald (syn. *Laurinoxylon seemannianum* Mädel). There are only minor differences between the Lesbos wood and *Laurinoxylon seemannianum* Mädel which are of the type seen within a single tree, i.e. differences between trunk and branch wood. Unfortunately, our species is not well enough preserved to observe some important details, such as type of vessel-ray parenchyma pits.

Problems and proposals. The parenchyma distribution of *Laurinoxylon variabile* Privé-Gill & Pelletier is aliform-confluent forming oblique or tangential bands differing from the emended diagnosis of *Laurinoxylon*. The occurrence of this type of parenchyma and its other features recommends its assignment to *Cinnamomoxylon*.

We propose the new combination *Cinnamomoxylon variabile* (Privé-Gill & Pelletier) Mantzouka, Karakitsios, Sakala & Wheeler.

Laurinoxylon cf. *seemannianum* was described by Selmeier (1967, 1969, 1984) and Gottwald (1992) as having idioblasts associated only with the ray parenchyma. This description is not in accordance with the one by Süss and Mädel (1958). Because there are no idioblasts in axial parenchyma and amongst the fibres, *Laurinoxylon* cf. *seemannianum* is not comparable to *L. seemannianum*, but with the representatives of *Laurinoxylon* Type 1 group. Consequently, we suggest that *Laurinoxylon* cf. *seemannianum* specimens be re-examined and compared with the *Laurinoxylon* species of Type 1 group. Based on that re-examination they might be assigned to a species in that group or named as a new species.

Botanical affinities. The material from Lesbos has no crystals and it has septate fibres as do *Cinnamomum* and *Ocotea* (Tribe Perseae Nees).

We suggest that fossil woods should be assigned to *Cinnamomoxylon*, rather than *Laurinoxylon,* when their axial parenchyma is vasicentric to confluent or aliform to confluent and rays are 2-5 seriate. This has already been done for two other species: *Cinnamomoxylon limagnense* (Privé-Gill & Pelletier) Gottwald (1987) and *Cinnamomoxylon seemannianum* (Mädel) Gottwald (1987), and we propose the new combination *Cinnamomoxylon variabile* (Privé-Gill & Pelletier) Mantzouka, Karakitsios, Sakala & Wheeler.

Velitzelos *et al.* (1981b) described leaves of *Cinnamomum polymorphum* Heer sensu Grangeon from the area of the Petrified Forest of Lesbos (appendix in Mantzouka *et al.* 2013). It is possible that the wood described here is related to these leaves.

CONCLUSION

Laurinoxylon is a large fossil genus (Gregory *et al.* 2009), which generally has functioned as a catch-all for fossil lauraceous woods. Based on the revised diagnosis of the genus (Dupéron *et al.* 2008), we suggest that the following features indicate that a fossil wood should *no*t be assigned to *Laurinoxylon*:

A. Axial parenchyma features *not* characteristic of *Laurinoxylon*: A1. Occurrence of marginal bands, A2. Aliform to aliform-confluent paratracheal parenchyma;

B. Ray features *not* characteristic of *Laurinoxylon*: B1. Rays higher than 1 mm, B2. Exclusively homocellular rays, B3. Rays more than 5 cells wide, B4. Rays storied;

C. Porosity *not* characteristic of *Laurinoxylon*: Ring-porous wood;

D. The absence of idioblasts (oil &/or mucilage cells).

We found that *Laurinoxylon* has features that occur in some extant genera of the tribes Laureae (*Actinodaphne, Laurus, Lindera* A and B, *Litsea, Neolitsea*) and Perseae (*Aiouea, Aniba, Cinnamomum, Dehaasia, Dicypellium, Endlicheria, Licaria, Nectandra, Nothaphoebe, Ocotea, Persea* - North American species, *Phoebe, Pleurothyrium, Systemonodaphne, Urbanodendron,*), and also in genera whose tribal affinities are as yet unclear: *Apollonias*, *Cryptocarya* of Madagascar and *Iteadaphne*.

We recognized four groups of *Laurinoxylon* species based on the location of the idioblasts:

Type 1 with idioblasts associated only with ray parenchyma cells, as seen in extant *Dicypellium, Laurus, Litsea chinensis* group, North American *Persea, Systemonodaphne, Urbanodendron*;

Type 2a with idioblasts associated with both rays and axial parenchyma, as seen in extant *Aiouea, Aniba, Apollonias, Cryptocarya* from Madagascar*, Dehaasia, Licaria, Lindera* group A, *Nothaphoebe, Persea, Phoebe, Pleurothyrium*;

Type 2b with idioblasts associated with rays and present among the fibres; as seen in extant *Actinodaphne* p.p., *Nectandra* p.p. and *Neolitsea* p.p.*;*

Type 3 with idioblasts associated with ray and axial parenchyma cells and present among the fibres, as seen in *Actinodaphne* p.p.*, Cinnamomum, Endlicheria, Nectandra* p.p., *Neolitsea* p.p. and *Ocotea*.

We described new fossil woods from the Lesbos (Types 1, 2b and 3) and Ipolytarnóc (Type 2a) UNESCO Global Geoparks and added information from the original slides of the types of *L. czechense* from Kadaň-Zadní Vrch Hill (Type 1) and *L. diluviale* from

Jáchymov (Type 2b). Characteristics of *Laurinoxylon* species described earlier were discussed with regard to placing them in one of the groups we propose.

We suggest that using criteria or filters (A – axial parenchyma features, B – ray features, C – ring porosity, D – absence of idioblasts) that preclude assigning a fossil wood to *Laurinoxylon* and idioblast location is useful for relating fossil lauraceous woods to groups of extant lauraceous genera. Further study of the co-occurrence of fossil lauraceous wood, leaves, and reproductive organs may allow doing ‘Whole Plant’ reconstructions (Sakala 2004; Kvaček 2008, Manchester *et al.* 2014), as was done for an extinct Eocene tree belonging to the Platanaceae (Manchester 1986).

During this study, we found evidence suggesting that some *Laurinoxylon* species deserve further study and, in some cases, assignment to another genus. We proposed the new combination *Cinnamomoxylon variabile* (Privé-Gill & Pelletier) Mantzouka, Karakitsios, Sakala, & Wheeler. There are some species that should be excluded from the Lauraceae: *Laurinoxylon intermedium* Huard with features of the Magnoliaceae and *Laurinoxylon aniboides*, which possibly is Magnoliaceae or Canellaceae.

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Table 1

	Laurinoxylon microtracheale *	*Laurinoxylon litseoides*	*Laurinoxylon oligocenicum*	*Laurinoxylon intermedium* *	*Laurinoxylon czechense Prakash, Brezinova & Buzek*	*Laurinoxylon czechense [new observations]*
Laurinoxylon Type 1						
Locality	**Hasenberg bei Wiesa unweit Kamenz (Sachsen)**	**Hasenberg bei Wiesa unweit Kamenz (Sachsen)**	**South Bohemian basin, Czech Republic**	**Landes, S. France**	**Kadan (Zadni vrch Hill), Doupovske hory Mountains, Czech Republic**	**Kadan (Zadni vrch Hill), Doupovske hory Mountains, Czech Republic**
Age	**Middle – Upper Oligocene**	**Middle – Upper Oligocene**	**Oligocene?**	**Miocene**	**Oligocene**	**Oligocene**
GR	**Distinct**	**Distinct**	**Distinct**	**weak with seemingly terminal bands**	**Distinct**	**Distinct**
Porosity	**Diffuse**	**Diffuse**	**Diffuse**	**Diffuse**	**Diffuse**	**Semi-Ring/Diffuse**
V Grps	**mainly sol & in rms of 2, rarely of 3-6**	**mainly sol & in rms of 2, rarely of 3-6 and clusters**	**sol & in RMs of 2-4**	**sol (48%), in rms of 2 (31%), of 3-5 (21%)**	**mainly sol, often in radial or oblique multiples of 2-3 or more**	**mainly sol (76%), in rms of 2 (12%), rarely in rms of 3-4 (6%) and cls (6%)**
VTD: Mean (range) µm	**45 (35-60)**	**70 (30-125)**	**(70-190)**	**(80-100) / (70-130)**	**(50 - 150)**	**100**
V /mm²	**35**	**35**	**10-14**	**15-27**	**15-25**	**24**
VEL: Mean (range) µm	**55 (40-65)**	**95 (40-150)**	**(60-225)**	**(90-150) / (20-90)**	**(60-195)**	**125**
Tyloses	**Present**	**Present**	**Present**	**Present?**	**Absent**	**Present**
PP simple / PP scalariform	**Yes/No**	**Yes/No**	**Yes/No**	**No/Yes: 10 (15)-20 bars**	**Yes/Yes (10-15 bars)**	**Yes/No**
IVP size (µm)		**sm - med., 6-7.5 x 5-6**	**med - lrg, 8-10**		**med - lrg, 8-12**	
AP	**vc**	**scp, vc**	**scp, vc, tending to aliform**	**marginal? & concentric bands of 4-12 cells**	**scp**	**scp. vc**
RW (cell no.)	**1-5, mostly 3-4**	**1-4, mostly 2-3**	**1-3, mostly 2-3**	**1-5, mostly 3-4**	**1-3, mostly 3**	**1-3, mostly 2-3**
RW (µm)	**12-57**	**15-40**		**15-55**	**12-40**	
RH (µm)	**50-320**	**100-470**		**120-700**	**80 - 900**	
SepFib	**Yes**	**Yes**	**Yes**	**No**	**Yes**	**Yes**
Idioblasts per mm²	**Numerous**	**Few**		**8-22**		**37**
Idioblasts size (µm); radial, tangential, height	**R: 35 (25-47), Tl: 21 (12-30), ? Ht: 65 (35-100)**	**R: 45 (27-60), T: 28 (22-42), Ht 75 (37-105)**				**Rl: 20-25, T: 40-50**

Laurinoxylon* aff. *czechense
Southeastern Lesbos, Greece
Early Miocene
Distinct
Diffuse
sol (18%) and clusters (21%), mainly in rms of 2 (50%), sometimes rms of 3 (7,5%), rarely in rms of 4 (3.5%)
60 (40-85)
52-74
73 (50-110)
Present
Yes/No
lrg (10 in DM 13.1)
scp?. vc
1-3, mostly 2-3
25-30
280-520
Probably non-septate
35-65
R: 15-45, T: 10-36

Table 2a

	Laurinoxylon endiandroides*	**Laurinoxylon aniboides***	**Laurinoxylon nectandrioides***	**Laurinoxylon annularis***	***Laurinoxylon* (+ cf.) *hasenbergense***	***Laurinoxylon ehrendorferi***
***Laurinoxylon* Type 2a**						
Locality	Hasenberg at Wiesa close to Kamenz (Saxony-Germany)	Ipolytarnoc, Komitat Nograd (Hungary)	Netherlands, Holland, Germany	East Bavarian Molasse near Ortenburg close to Paasau	Hasenberg, Wiesa, Saxony (Germany)	Lemnos island (2 km SSE of Mudros), Greece
Age	Middle-Upper Oligocene	Early Miocene	Miocene	Allochthonous from Lower Eocene age inside Lower Miocene fluvial sediments	Middle-Upper Oligocene (Süss), Early Miocene (Greguss)	Early or Middle Miocene
GR	Distinct	Distinct	Weak (Berger),Distinct (K-S) or indistinct-absent (van der Burgh)	Distinct	Distinct (but "Blurred")	Weakly distinct
Porosity	Diffuse	Diffuse	Semi-ring or diffuse	Ring porous	Diffuse	Diffuse
V Grps	sol, rms of 2, rarely in rms of 3-6	sol , rms of 2, often in rms of 3-4, rarely cls	mainly sol, rarely in rms of 2-3	sol, rms 2-4	sol, rms of 2, rarely rms of 3-4	sol, rms of 2, rarely in rms of 3
VTD: Mean (range) µm	67 (30-90)	133 (55-220)	(50-180)	80-95	60-95 (25-130)	up to 200
V / mm²	10	25	10-20		10-25, 30-45	12
VEL: Mean (range) µm	90 (30-135)	180 (65-280)	250-400	110-135	70-100 (30-170), 105-140 (30-230)	500
Tyloses	Present	Present	Present	Probably Present	Present	
PP simple/scalariform	Yes/No	No/Yes	Yes/No	Yes/Yes	Yes/No	Yes / ?
IVP size, µm	sm - med, 7.5 x 6-7.5	med - lrg, 7-10 x 7-15,	sm - med, 6 - 7	sm, 4-6	sm - lrg, 5-10 (-12)	lrg
VRP			red		sim	sim, red
AP	alf to cfl	vc	scp. vc, alf, cfl. Marg	vc (riing 3 cells width)	vc (ring 1-3 cells wide)	scp, vc
RW (cell no.)	1-3 (mostly 2, rarely 4)	1-4 (mostly 2-3, rarely 5)	1-4, mostly 2-3	1-3	1-3	2-4
RW (µm)	28 (10-60)	37 (20-60)	12-16		12-52	
R / mm	9-11	7-8			6-11	5
RH (µm)	270 (85-620)	460 (110-1230)	50-100		250-390 (60-1200)	up to 800
SepFib	Yes	No	Yes	No	Yes	Yes
Idioblasts per mm²	very numerous	numerous				
Idioblast size (µm)	R: 48 (35-67), T: 33 (25-52), Ht: 130 (55-310)	R: 56 (30-75), T: 47 (25-70), Ht: 120 (60-320)	R: 40-75, T: 30-50		R: 40-50 (15-100), T: 25-32 (10-65), Ht: 85-130 (30-300)	Height: 200, Width: 80 in TLS

Prismatic crystals	Yes	Yes	Yes	Not observed	Yes	Not observed

Laurinoxylon müller-stolli
Ipolytarnoc (Hungary) and Wiesa at Kamenz (Germany)
Early Miocene (A. Burdigalian)
Distinct
Diffuse
sol (56%), rms of 2 (25%) and 3-4 (19%)
160 (85-200)
12-18
175 (85-240)
Present
Yes /Yes
lrg
sim, red
scp, vc
1-3, mostly 2
25-30
5-8
260-500
35–65
T height: 40–75 µm, width: 30–50 µm

Not observed

Table 2b

	Laurinoxylon (Ulminium) diluviale	***Laurinoxylon perfectum****	***Laurinoxylon compressum****	***Laurinoxylon* aff. *diluviale*** (n=3)
***Laurinoxylon* Type 2b**				
Locality	Jachymov (Boheme) Czech Republic	Landes, S. France	Landes, S. France	Southeastern Lesbos
Age	?Oligocene	Miocene	Miocene	Lower Miocene
GR	Distinct	Distinct	Distinct	Distinct
Porosity	Diffuse	Diffuse	Ring	Diffuse
V Grp	sol (75%), rms of 2 (20%), of 3-4 (2%), and in cls (3%)	sol, (35%), rms of 2 (36%) and 3-4 (29%)	mostly sol, rarely in rms of 2-3	sol (29%) and in rms of 2 (50%), 3 (17%), and 4 (4%)
VTD: mean (range) µm	ew: 100-154; lw: 44-72	ew:100 (75-140), lw: 55 (40-70),	ew: 110-150, lw: 70-95	40-110
V/ mm²	9-33	10-15		20-100
VEL Mean (range) µm	300-550	lw: 57 (48-80), ew: 125 (65-160)	ew: 180-240, lw: 110-150	50-150
Tyloses	Present	Present	Present	Present
PP simple / PP scalariform	Yes/Yes (6-12 bars)	Yes/No	Yes/No	Yes/Yes (6-12 bars)
IVP size (µm)	Med - Lrg (7-15)	Lrg (10-15)		Sm - Med (occ. Lrg)
VRP		red	red-sim	
AP	scp, vc (1-2 cells wide rows)	scp, sometimes tends to alf	scp, vc	scp?, vc
RW (cell no.)	1-5 (3s -51%, 4s 29%	1-3 (mostly 2)	1-3 (mostly 2)	1-4 (mostly 2-3)
RW (µm)		20-48		20-60
R / mm	6-9	16		11-16
RH µm	60-820 (frequently: 220-420	1s: 170 (60-370), 2s: 290 (220-420), 3s: 390 (250-500)	avg: 270 (150-500)	160-650
SepFib	Probably	Yes	No	Probably
Idioblasts per mm²	0-18	Abundant	25-33	usually 35-70
Idioblasts size (µm)	At ray edges: R: 50-80, Tl: 27-60 µm. Inside the rays: R: 37, T: 27	large (max ht: 300)	tangential: height: 115 (65-180), width: 64 (55-80) or transversal: 35-60 µ and radial diameter: 50-90	R: 25-70, T: 15-40 (in TS)
Prismatic crystalls	No	No	No	No

Table 3

	Cinnamomoxylon limagnense* [syn. Laurinoxylon limagnense]	**_Laurinoxylon variabile*_**	**_Laurinoxylon bergeri_**	**_Cinnamomoxylon seemannianum* [syn. Laurinoxylon seemannianum]_**	**_Cinnamomoxylon seemannianum [syn. Laurinoxylon seemannianum] DMDA6_**
Laurinoxylon Type 3					
Locality	d'Aigueperse (Puy-de-Dome), France	d'Aigueperse (Puy-de-Dome), France	Hasenberg at Wiesa close to Kamenz (Saxony-Germany)	Randecker Maar (SW Germany)	Southeastern Lesbos, Greece
Age	Oligocene	Oligocene	Middle-Upper Oligocene	Upper Miocene (Tortonian?)	Early Miocene
GR	Distinct	Distinct	Distinct	Distinct	Distinct
Porosity	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse
V Grps	sol (66%), rms of 2 (28%), 3 (6%) and 4 (1%)	sol (52%), rms of 2 (36%), 3 (9%), 4 (2%) and 5 (1%)	sol, rms of 2, rarely of 3-4	sol & rms of 2-3.	sol (17%), rms of 2 (33%), 3 (14 %), and 4 (15%) and cls (21 %)
VTD: Mean (range) µm	93 (60-140)	164 (65-225)	80-87 (30-135)	99 (25-150)	45-50
V /mm²	12-15	3-5	5-40	20 (13-29)	40-100
VEL: Mean (range) µm	187	295	105-110 (30-180)	115 (45-180)	60-110
Tyloses	Present		Present	Present	Present
PP simple / PP scalariform	Yes/Occasionally (5-8 bars)	Yes/No	Yes/No	Yes/No	Yes/No
IVP size (µm)	9- 12 µm	6- 7 µm			
VRP	Elliptic (4-7x7-15 µm) or circular (6-10 µm)	6- 7 µm	sim		
AP	vc, conf	ali – conf	scp, vc	scp, vc	scp, vc
RW (cell no.)	1-4	1-3 (-4) seriate	1-3	1-3 (2-3)	1-5
RW (µm)	60		25 (7-40)	15-35	50-60
R / mm	7-8	3-8	9-11	5-10	7-14 (mostly 9)
RH (µm)	620	50 – 225	200-230 (25-800)	100-400	300 – 500
SepFib	Possibly	No	No	Some	Possibly
Idioblasts per mm²	very numerous		very numerous	numerous	15-33
Idioblast size (µm)	20-75 X 40-170	26-70 x 30-150 (in TS)	R: 50 (25-75), T: 25 (15-40), H: 110 (50-250)/70 (55-120)	R: 53 (20-95), T: 38 (20-50), Ht: 130 (50-150)	R: 30-50, T: 90-175
Prismatic crystals	No	No	No	No	No

Table 4

	TYPE 1	TYPE 2a	TYPE 2b	TYPE 3
Idioblast location	Rays	Rays & Axial Parenchyma	Rays & Among fibers	Rays & Axial Parenchyma & Among Fibers
Growth ring boundaries	Distinct	Distinct	Distinct	Distinct
Vessel grouping	Solitary, RMs 2 - 4	> 50% solitary, RMs 2-4	Solitary, mostly RMs 2-4	Solitary, RMs 2 - 4
MVTD µm	50-150	60-160	50-160	45 - 164
Vessels / mm²	20 -100	10-45	9 - 100	5 -100
Tyloses	Present	Present	Present	Present
Perforation Plates	Si, Si + Sc	Si, Si + Sc	Si, Si + Sc	Si, Si + Sc
IV pits size	Large	Medium - Large	Small - Large	
Tyloses	Present	Present	Present	Present
Axial parenchyma	scanty paratracheal, vasicentric	scanty paratracheal, vasicentric	scanty paratracheal, vasicentric	scanty paratracheal, vasicentric
Ray seriation	1-3	1 - 3 (-4)	1-5	1-5
Septate fibers present	Yes and No	Yes	Yes and No	Yes

3
2
4
1

Figure 2

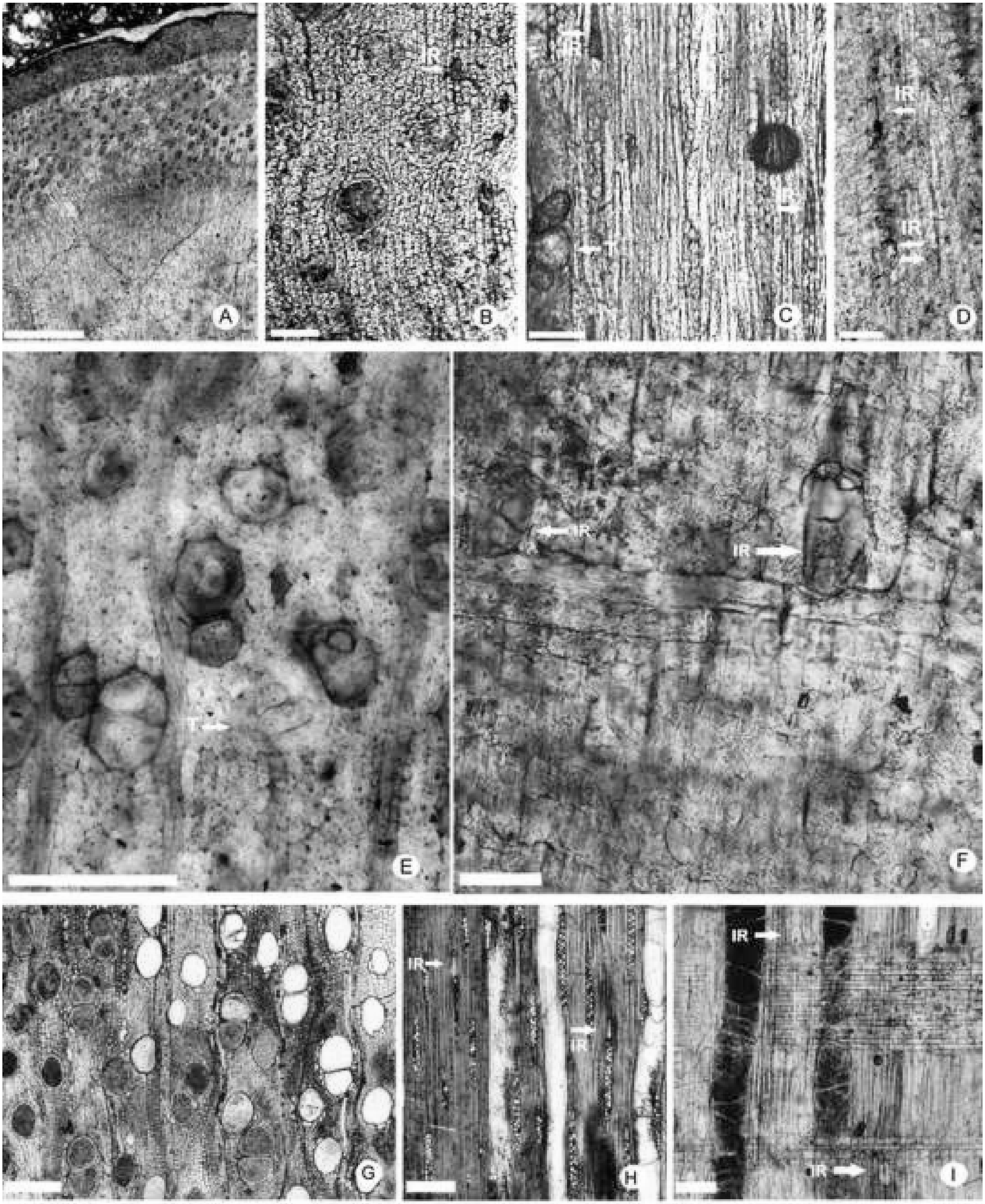


Figure 3

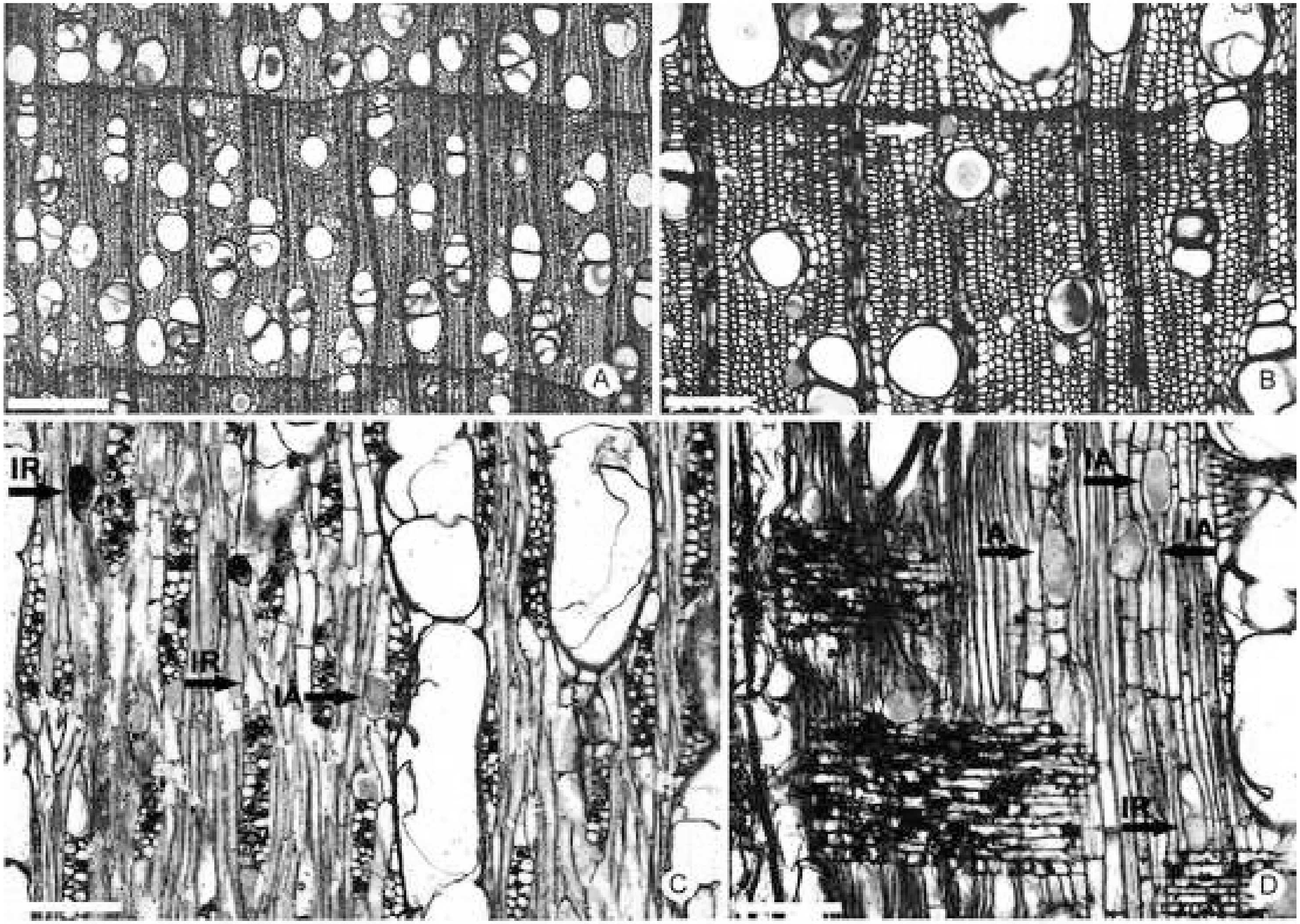
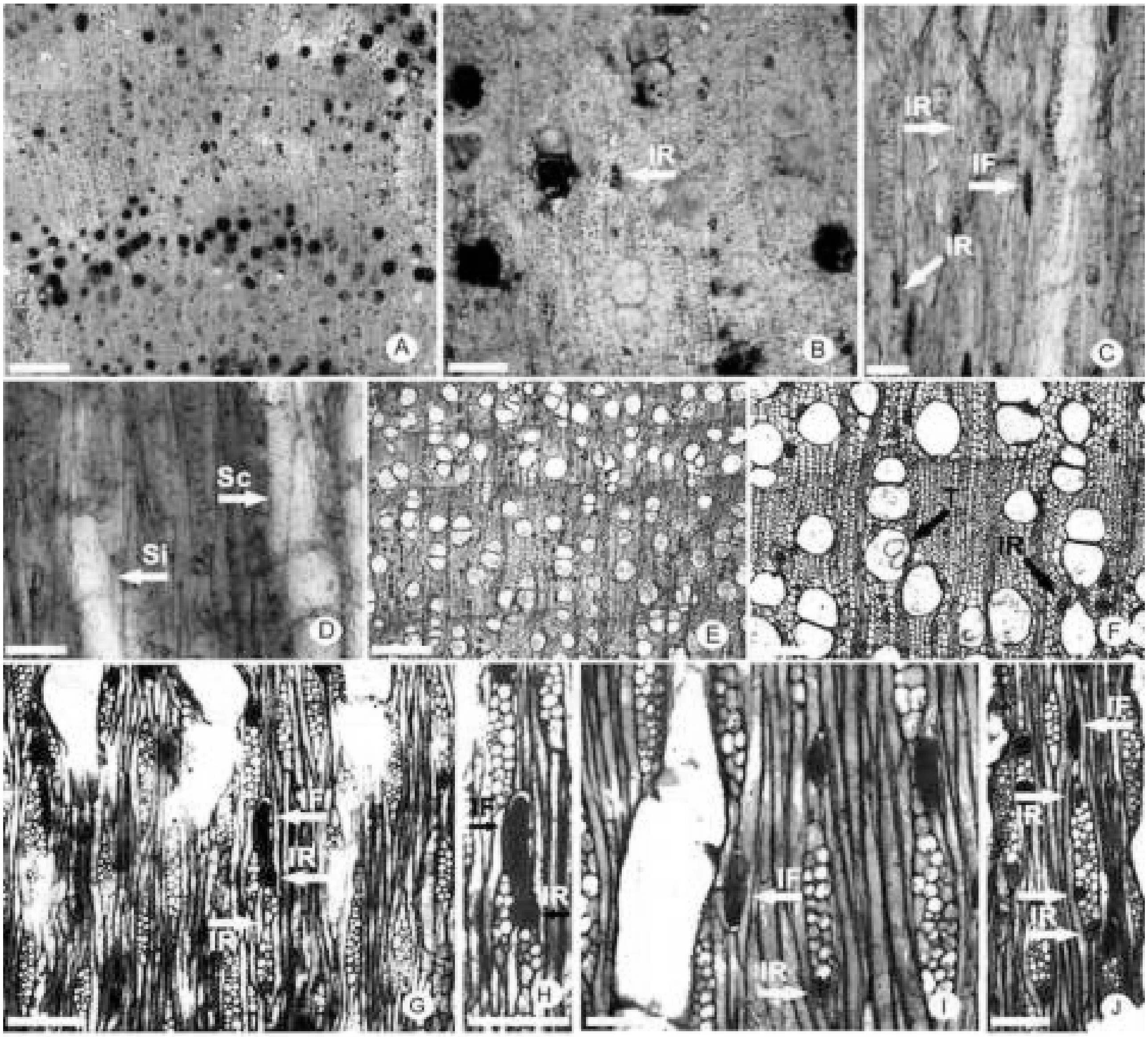
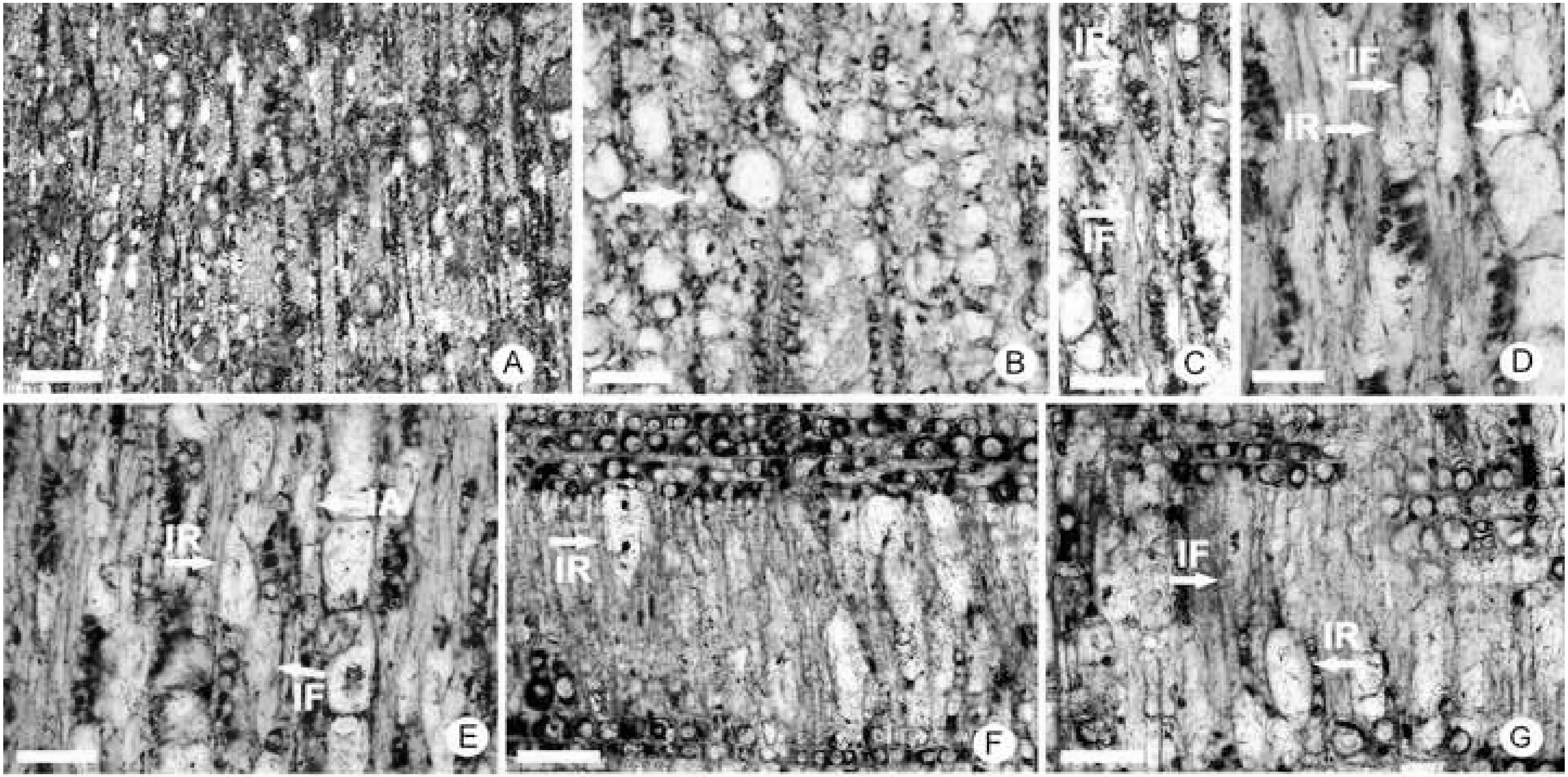


Figure 4




A
B
IR
IF
C
IF
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D
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F
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IR
G

Captions for Tables and Figures

Table 1. Comparison of the anatomical characteristics among *Laurinoxylon* type 1 species. (* is used for the species that we suggest are excluded from *Laurinoxylon*). Regarding the idioblasts, it is not easy to interpret the comparison between descriptions (e.g. numerous or few) and numbers (e.g. 8-22 or 37). We believe that this connection will be feasible only when the previously described species will be re-studied.

The following abbreviations were used in Tables 1, 2a, 2b, 3 & 4:

GR: Growth ring boundaries, V Grp: Vessel groupings (sol: solitary, rms: in radial multiples, cls: in clusters), VTD: mean (range) μm: Mean tangential diameter of vessel lumina (ew: in earlywood, lw: in latewood), V/ mm²: vessels per square millimeter, VEL: vessel element length, PP simple / PP scalariform: Perforation plates simple -/- scalariform, IVP size (μm): Intervessel pits size (sm: small, med: medium, lrg: large), VRP: Vessel-ray pitting (sim: with distinct borders; similar to intervessel pits in size and shape throughout the ray cell, red: with much reduced borders to apparently simple), AP: Axial parenchyma (scp: scanty paratracheal, vc: vasicentric, alf: aliform), RW (cell no.): Ray width (no of cells), RW (μm): Ray width (in μm), R / mm: Rays per millimeter, RH μm: Ray height, SepFib: Septate fibres.

Table 2a. Comparison of the anatomical characteristics among *Laurinoxylon* type 2a species.

Table 2b. Comparison of the anatomical characteristics among *Laurinoxylon* type 2b species. (* is used by the species that we suggest are excluded from *Laurinoxylon*).

Table 3. Comparison of the anatomical characteristics among *Laurinoxylon* type 3 species. (* is used by the species that we suggest are excluded from *Laurinoxylon*).

Table 4. Comparison of the anatomical characteristics among *Laurinoxylon* Types.

Fig.1. Map of Europe with the geographical position of the studied localities indicated: -- 1: Lesbos, Greece (early Miocene), -- 2: Kadaň-Zadní Vrch Hill, Czech Republic (early Oligocene), -- 3: Jáchymov, Czech Republic (?Oligocene), -- 4: Ipolytarnóc, Hungary (early Miocene).

Fig. 2 *Laurinoxylon* Type 1. A--E *Laurinoxylon* aff. *czechense* Prakash *et al.* (Lesbos) (DMDA13.1: Fig. 2A--E). --A, B: Silicified stem with a diameter of 2.5 cm, enclosed by volcanic material, growth rings distinct, diffuse-porous wood, idioblasts associated with the ray parenchyma cells (= IR),TS. --C, D: Tyloses (T), rays up to 3-seriate, idioblasts IR, mainly at the margins and less commonly in the body of the rays, TLS. -- E: Outline of solitary vessels round to oval, vasicentric (scanty) paratracheal parenchyma, tyloses (T), idioblasts IR, TS. -- F: Rays heterocellular, body of multiseriate rays composed of procumbent cells with one row of upright cells, idioblasts IR, RLS. -- G--I. *Laurinoxylon czechense* Prakash *et al.* (part of holotype specimen CNB-2). -- G: Outline of solitary vessels round to oval, vasicentric (scanty paratracheal) parenchyma, tyloses, rays up to 3-seriate, idioblasts IR, slide G 4036, TS. -- H: Simple perforation plates, tyloses, idioblasts IR (at their edges and inside the ray bodies), slide G 4037, TLS. -- I: Rays heterocellular, body of multiseriate rays composed of procumbent with marginal rows 1–4 of upright cells, idioblasts IR, RD. -- Scale bar = 50 μm in D, F, G; -- 100 μm in B, C, H, I; -- 250 μm in E; -- 1000 μm in A.

Fig. 3 *Laurinoxylon* Type 2a, *Laurinoxylon mueller-stolli* Greguss emend. Süss & Mädel (IGP Ipolytarnóc No. 05, potential part of the holotype of *L. mueller-stolli*: Fig. 3A--3D, slide IGP Ipolytarnóc No. 05/A: Fig. 3A, 3B, slide IGP Ipolytarnóc No. 05/C: Fig. 3C, slide IGP Ipolytarnóc No. 05/B: Fig. 3D). -- A, B: Distinct growth rings, diffuse-porous wood, vessels solitary and in multiples of 2-4 with round outline, tyloses, vasicentric parenchyma, idioblasts associated with the ray and axial parenchyma (= IR, IA), TS. -- C: Idioblasts IR and IA, vasicentric parenchyma, abundant tyloses, fibres probably septate, TLS. -- D: Heterocellular rays with procumbent body cells and one row of upright and/or square marginal cells, idioblasts IR and IA, RLS. -- Scale bar = 200 µm in B, C, D; -- 500 µm in A.

Fig. 4 *Laurinoxylon* Type 2b, *Laurinoxylon* aff. *diluviale* (Unger) Felix emend. Dupéron *et al.* (DMDA7: Fig. 4A, B; DMDA2: Fig. 4C; DMKO1: Fig. 4D). --A, B: Distinct growth ring boundaries, diffuse porous, circular regions with strange colouration, outline of solitary vessels round to oval, tyloses, scanty paratracheal parenchyma, idioblasts associated with the ray parenchyma cells and among the fibres (= IR, IF), TS. -- C: Idioblasts IR and IF, TLS. -- D: Idioblasts IR and IF, perforation plates simple (Si) and scalariform (Sc), TLS. -- E--J. *Laurinoxylon diluviale* Unger (Felix) emend. Dupéron *et al.* (part of the holotype specimen IGP Jáchymov No. 08: Fig. 4H--J, slide IGP Jáchymov No. 08/B: Fig. 4E, 4F, slide IGP Jáchymov No. 08/A: 4G--5J). -- E, F: Distinct growth ring boundaries; diffuse porous, tyloses (T), scanty paratracheal parenchyma, idioblasts IR and IF, TS. – G, I, J: Idioblasts IR (at the edges of the rays and in their bodies) and IF, septate fibres (SF), TLS. -- H: Detail from 4G, in black & white for better separation of the IR idioblast from the IF idioblast, septate fibres, TLS. -- Scale bar = 50 µm in B, C, D; -- 100 µm in I, J; -- 200 µm in F, G, H; -- 500 µm in A, E.

Fig. 5 *Cinnamomoxylon* Gottwald (= *Laurinoxylon* Type 3), *Cinnamomoxylon seemannianum* (Mädel) Gottwald (DMDA6a, DMDA6b, DMDA6c). – A, B: (Scanty) vasicentric paratracheal parenchyma, slightly confluent forming bands, outline of solitary vessels mainly angular, idioblasts associated with the ray (= IR) and axial (= IA) parenchyma cells and among the fibres (= IF), TS. -- C, D: Idioblasts IR, IA and IF, TLS. -- E: Axial parenchyma: scanty paratracheal with a thickness of 15-40 µm, idioblasts IR, IA and IF, TLS. – F, G: Heterocellular rays, body ray cells procumbent with one row of upright and/or square marginal cells, idioblasts IR and IF, RLS. -- Scale bar = 50 µm in B; -- 100 µm in D, E, F, G; -- 200 µm in A, C.

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Article

A new late Miocene (Tortonian) flora from Gavdos Island in southernmost Greece evaluated in the context of vegetation and climate in the Eastern Mediterranean

Dimitra Mantzouka, Zlatko Kvaček, Vasilis Teodoridis, Torsten Utescher, Nicolaos Tsaparas, and Vasileios Karakitsios

With 8 figures, 3 tables and 2 appendices

Abstract: A new late Miocene (Tortonian) leaf flora has recently been recovered in the southernmost part of Europe on the island of Gavdos, Greece. So far, three conifers (*Tetraclinis salicornioides, Taxodium dubium* and *Pinus* sp.) and 27 fossil species/morphotypes of angiosperms have been recognized. Among them, some represent subtropical, partly evergreen woody elements (e.g. *Daphnogene* sp., *Laurophyllum* sp., *Myrica lignitum*), some others (e.g., ?*Sassafras, Fagus gussonii*, *Ulmus*, *Acer angustilobum, Populus populina, Ailanthus pythii, Paliurus tiliifolius,* several legumes) belong to deciduous shrubs or trees. The number of the determined angiosperms is sufficient for using statistical techniques to estimate palaeoclimate (LMA, CLAMP, CA) and to reconstruct the palaeovegetation (phytosociological approach, IPR-vegetation analysis).The Gavdos flora is based on leaf impressions and allows correlations with other Greek floras of almost the same age, namely from Crete – Vrysses (latest Tortonian to Messinian, ca. 7.5-6.0 Ma), Makrilia (late Tortonian, ca. 8.6-7.7 Ma) and Pitsidia, Messara Basin (early Tortonian, ca. 10.5 Ma), while that from Vegora, Macedonia (Messinian, ca. 7-6 Ma) may document further trends in the late Miocene.

Key words: Leaf flora, palaeovegetation, palaeoclimate, late Miocene, Mediterranean, Greece.

1. Introduction

While climate evolution during the late Miocene and spatial gradients have been intensely studied for the mid-latitudes of western Eurasia (e.g., Mosbrugger et al. 2005; Bruch et al. 2006, 2011; Utescher et al. 2007; Ivanov et al. 2012) comparatively few detailed studies are available for the lower latitudes of the Eastern Mediterranean. It is still a matter of debate on how humid/dry and seasonal climate was during the late Miocene period in that area. Based on the analysis of anomalies with respect to Present it has been assumed that the southeastern Mediterranean realm had about the same temperatures in the late Miocene as today (Utescher et al. 2011) and therefore would have experienced no drastic cooling during the later Neogene. The newly recovered Gavdos megaflora, together with the availability of revised flora lists of coeval, neighbouring sites allows addressing these questions concerning the palaeoclimate conditions. Besides the documentation of the Gavdos flora, also comparisons are made with related floras and palaeoenvironments are reconstructed based on the recovered macrofossils. Eventually, additional information about the climate before the "Messinian salinity crisis" based on palaeobotanical proxies can reinforce the previous studies (e.g., Kovar-Eder et al. 2006).

The present paper gives a short overview of the so far recognized plant taxa including palaeoenvironmental interpretations based on quantitative meth-

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0077-7749/2015/0448 $ 8.75

Fig. 1. **A** – Metochia outcrop panoramic photo. The arrow shows the position (inside the gorge) of the plant fossiliferous level consisting of sapropels and blue marls alternations (fossil-bearing site, September 2013), **B** – The alternations of blue marls and sands are underlying the plant fossiliferous sapropels. The arrow shows the position (inside the gorge) of the plant fossiliferous level consisting of sapropels and blue marls alternations (Metochia outcrop, September 2013).

ods, and thus contributes to expanding our knowledge about the late Neogene floras of the Mediterranean. It complements previous studies recently accomplished in southernmost Greece, namely in Crete – Makrilia (Sachse & Mohr 1996; Sachse et al. 1999; Sachse 2004), Vrysses (Zidianakis 2002; Zidianakis et al. 2007) and Pitsidia, Messara Basin (Zidianakis et al. 2010).

2. Geology and palaeontology of the study area

The island of Gavdos is situated in the southern part of Greece south of Crete (34°50’0” N, 24°5’0” E) and covers an area of 33 km^2 (Fig. 2A-B). The plant fossils investigated for the present study were collected at the Metochia locality (NE Gavdos), from which also the sapropels (Postma et al. 1993), the calcareous nannoplankton (Raffi et al. 2003; Anastasakis et al. 1995), the echinoid fauna (Tsaparas et al. 2007) and fishes (Gaudant et al. 2005, 2006) have been studied (Fig. 1A). Also benthic foraminifera have been investigated as indicators of the palaeoenvironmental conditions of the Messinian Salinity Crisis (Drinia et al. 2007), as well as planktonic foraminifera and geochemistry (Schenau et al. 1999; Antonarakou & Drinia 2003; Antonarakou et al. 2007).

The first stratigraphic description and interpretation of the island was by Simonelli (1894a, b). According to him the basement consists of limestones with *Clypeaster altus* Klein, *Ostrea crassissima* Lamarck and Heterosteginids, overlain by a layer of brown marls with fossil fish and plant remains (e.g., *Laurus*, *Cinnamomum*, *Callitris*). The next layer consists of blue marls with *Cleodora*, bryozoans and crystals of selenite. Almost 80 years later, in 1970, the first detailed geological exploration of the island took place by Vicente (1970). In 2005 Tsaparas following the stratigraphic and geological notifications discussed above observed an overlying final layer of brown sandy marl containing further plant fossil remains (Tsaparas 2005; Figs. 1B, 2C).

The Alpine substratum comprises a calcareous sequence of late Maastrichtian – Danian age and deposits of the flysch of Eocene age, which are developed in the S-SW part of the island while an ophiolithic complex consisting of a metamorphic volcano-sedimentary series (metamorphosis of Early Jurassic age) is developed towards the NE part of the island. The Mesozoic strata in the NE part of the island are overlain unconformably by Neogene sediments that are up to 150 m thick (Vicente 1970; I.G.M.E. 1993). The geodynamic evolution of the island since the late Cenozoic has been studied in detail (Anastasakis 1987) and the Neogene deposits of the island were divided into two formations: Potamos and Metochia formations (Anastasakis et al. 1995).

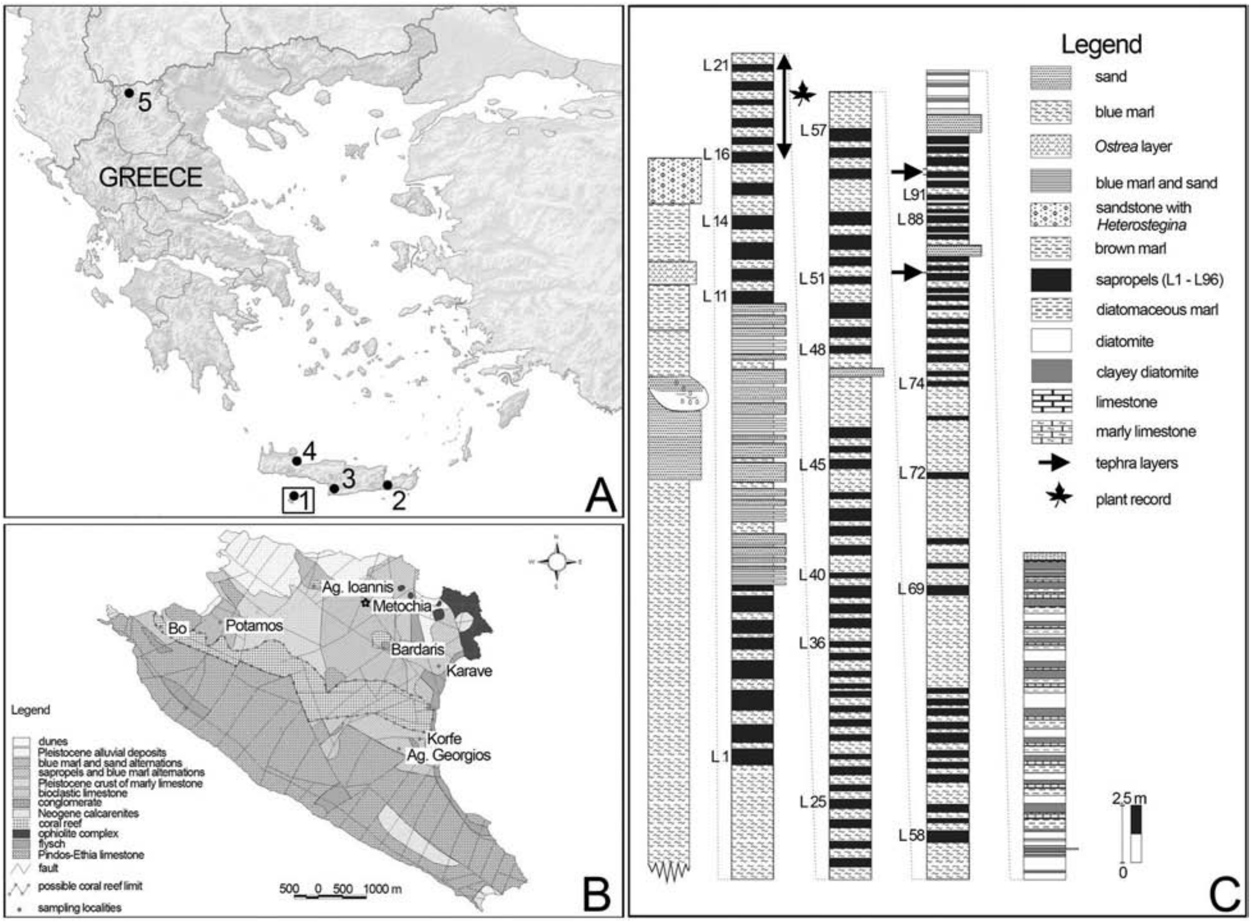

Fig. 2. A – Location of the studied floras in Greece. Floras/sites: 1. Gavdos, 2. Makrilia, 3. Pitsidia, 4. Vrysses, 5. Vegora. **B** – Geological map of the Gavdos Island (modified by Tsaparas 2005). C. Geological profile of Metochia (modified by Tsaparas 2005).

The fossil plant remains studied were collected by N. Tsaparas in 2005 from the Metochia section in the N-NE part of the island from the 'sapropels' L16 to L22 of early to middle Tortonian age (Figs. 1A, B, 2C). The term 'sapropels' is used for the thinly and faintly laminated reddish layers that mark the transition from the clayey diatomites to genuine diatomites of the Metochia section, although according to Gaudant et al. (2006) the 'true sapropels' are the diatomaceous laminated marls. In this section the formations have a lot more than 2% organic material and according to Postma et al. (1993) they represent sapropel episodes.

Studies on various other fossiliferous localities of this island, which are stratigraphically correlated to the site of Metochia have been carried out for the purposes of palaeoenviromental reconstructions using foraminifera (Drinia et al. 2004; Drinia 2009), bryozoan faunas (Drinia et al. 2009), corals and microfacies analyses (Drinia et al. 2010), fish otoliths (Tsaparas & Marcopoulou-Diakantoni 2005) and sedimentological analyses (Pomoni et al. 2013). According to Tsaparas (2005) the predominant occurrence of the fish species *Bregmaceros albyi* Sauvage and *Lepidopus* sp. along with the co-occurrence of plant remains in the sapropels L16 – L22 suggests a maximum water depth of 300 m.

The Metochia section (Figs. 1A, B, 2C) has been sampled in detail by Tsaparas (2005) in order to study several perspectives and to clear it up from a stratigraphical point of view. 96 samples of sapropels (Postma et al. 1993) were taken from the outcrop (L1-L96). Hilgen et al. (1995) and Krijgsman et al. (1995)

conclude that the age of the section is 9.7-6.6 million years, including the plant fossiliferous strata related to L16-L22 sapropels (Fig. 2C) which have a thickness of 5.26 m and an age of 9.4-9.1 million years (Hilgen et al. 1995, Antonarakou 2001) as has been concluded from the study of the palaeomagnetism (orbital cycles according to periodic oscillations of eccentricity) and the foraminifera. The whole section has also been dated through the study of nannofossils (Triantaphyllou et al. 1999), planktonic foraminifera (Antonarakou 2001), and mollusks (Dermitzakis & Georgiades 1987). The access to Metochia section and especially to the plant fossil-bearing site is not easy – due to the general topography and geomorphology of the area – since it is situated inside a gorge (Fig. 1A, B). Two of us (NT and VK) revisited Metochia fossiliferous site on September 2013 for scientific purposes and since there was nothing changed at the already studied section they made new detail samplings collecting a lot of material for further palaeontological and stratigraphical studies.

3. Material and methods

The over 100 specimens of plant fossils studied here were collected by Nicolaos Tsaparas in 2005 from the Metochia section in the N-NE part of the island (Fig. 1A, B). Among the recovered specimens leaf impressions, mostly fragmented, besides twig fragments and a few fruits, prevail. The high degree of oxidation of the fossil-bearing rocks and the resulting poor preservation of most samples prevents the study of leaf anatomy and detailed morphology of the leaf lamina. Attempts to prepare cuticles from the most promising samples failed. Dark-coloured remains on the leaf lamina did not dissolve at routine maceration in Schulze solution followed by rinsing in 5% KOH and obviously represent mineral coatings. Some of the studied leaf material is probably affected by fungi and/or insects as it is shown from their lamina distortions (e.g., Figs. 3.7, 5.6, 5.10, 6.9, 6.10). These observations might be the subject of a future study.

The studied plant material is housed in the collection of the Department of Historical Geology-Palaeontology, Faculty of Geology and Geoenvironment, University of Athens. The specimens are numbered and the frontal letters of their codes (GAVMT) refer to the island of Gavdos and the Metochia section.

Several techniques were used to distinguish palaeoenvironmental characters of the studied flora of Gavdos and other coeval floras from Greece. The phytosociological approach (Mai 1995) and Integrated Plant Record vegetation analysis (IPR vegetation analysis sensu Kovar-Eder et al. 2008; Teodoridis et al. 2011a) are used to evaluate the studied plant assemblages. The phytosociological approach classifies the palaeofloras with the usage of the following symbols for distinguishing vegetative storeys: E1 (herbs and vines), E2 (shrubs and lianas), E3 (trees under 25 m high) and E4 (trees over 25 m high). The IPR vegetation analysis is a semi-quantitative (based on taxonomic and ecological expertise and quantitative evaluation), fossil-based evaluation method which has previously been applied to Neogene and Paleogene leaf, fruit and pollen floras, with a validation based on modern vegetation sites (e.g., Kovar-Eder & Kvaček 2003, 2007; Kovar-Eder et al. 2008; Jacques et al. 2011; Teodoridis et al. 2011a, 2012). The method is used for the classification of fossil floras in terms of zonal vegetation type. For more details the reader is referred to the original description of the method (Kovar-Eder et al. 2008).

Palaeoclimatic estimates were made using three techniques: approaches based on Leaf physiognomy, namely Leaf Margin Analysis (LMA) and Climate Leaf Analysis Multivariate Program (CLAMP), approaches based on taxonomy, and the Coexistence Approach (CA) which is based on interpretation of the Nearest Living Relative (NLR). LMA, which only estimates mean annual temperature (MAT), has been applied on all four leaf floras while CLAMP only on three.The flora of Pitsidia was excluded from the CLAMP analysis because of the low number

Fig. 3. 1. *Tetraclinis salicornioides* (Unger) Kvaček, incomplete foliage twig; GAVMT 420, scale bar 10 mm segments; 2. *Tetraclinis salicornioides* (Unger) Kvaček, detached leafy segment, GAVMT 416, scale bar 5 mm; 3. *Tetraclinis salicornioides* (Unger) Kvaček, detached leafy segment, GAVMT 619, scale bar 3 mm; 4. *Taxodium dubium* (Sternberg) Heer, foliage shoot, GAVMT 652, scale bar 10 mm; 5. *Pinus* sp., needle fragment, GAVMT 602, scale bar 3 mm; 6. *Pinus* sp., needle fascicle, GAVMT 446, scale bar 5 mm; 7. *Laurophyllum* sp., incomplete leaf, GAVMT 327, scale bar 10 mm; 8. *Laurophyllum* sp., petiolate leaf base, GAVMT 555, scale bar 10 mm; 9. *Laurophyllum* sp., incomplete petiolate leaf, GAVMT 481, scale bar 10 mm; 10. *Daphnogene* sp., leaf with suprabasal acrodromous venation, GAVMT 391, scale bar 10 mm; 11. *Daphnogene* sp., leaf petiolate with suprabasal acrodromous venation, GAVMT 485, scale bar 10 mm; 12. *Daphnogene* sp., obovate leaf, GAVMT 479, scale bar 5 mm; 13. ?*Lindera ovata* Kolakovsky, leaf petiolate with basal acrodromous venation, GAVMT 338, scale bar 10 mm; 14. ?*Lindera ovata* Kolakovsky, incomplete leaf petiolate with basal acrodromous venation, GAVMT 383, scale bar 5 mm; 15. ?*Lindera ovata* Kolakovsky, leaf with basal acrodromous venation, GAVMT 496, scale bar 10 mm; 16. leaf counter-impression of Fig. 3.15, GAVMT 617, scale bar 10 mm; 17. ?*Sassafras* sp., fragment of large lobed leaf, GAVMT 432, scale bar 10 mm; 18. Monocotyledonae fam. et gen. indet., leaf fragments with parallel venation, GAVMT 349, scale bar 10 mm; 19. Monocotyledonae fam. et gen. indet., leaf fragment with parallel venation, GAVMT 610, scale bar 10 mm.

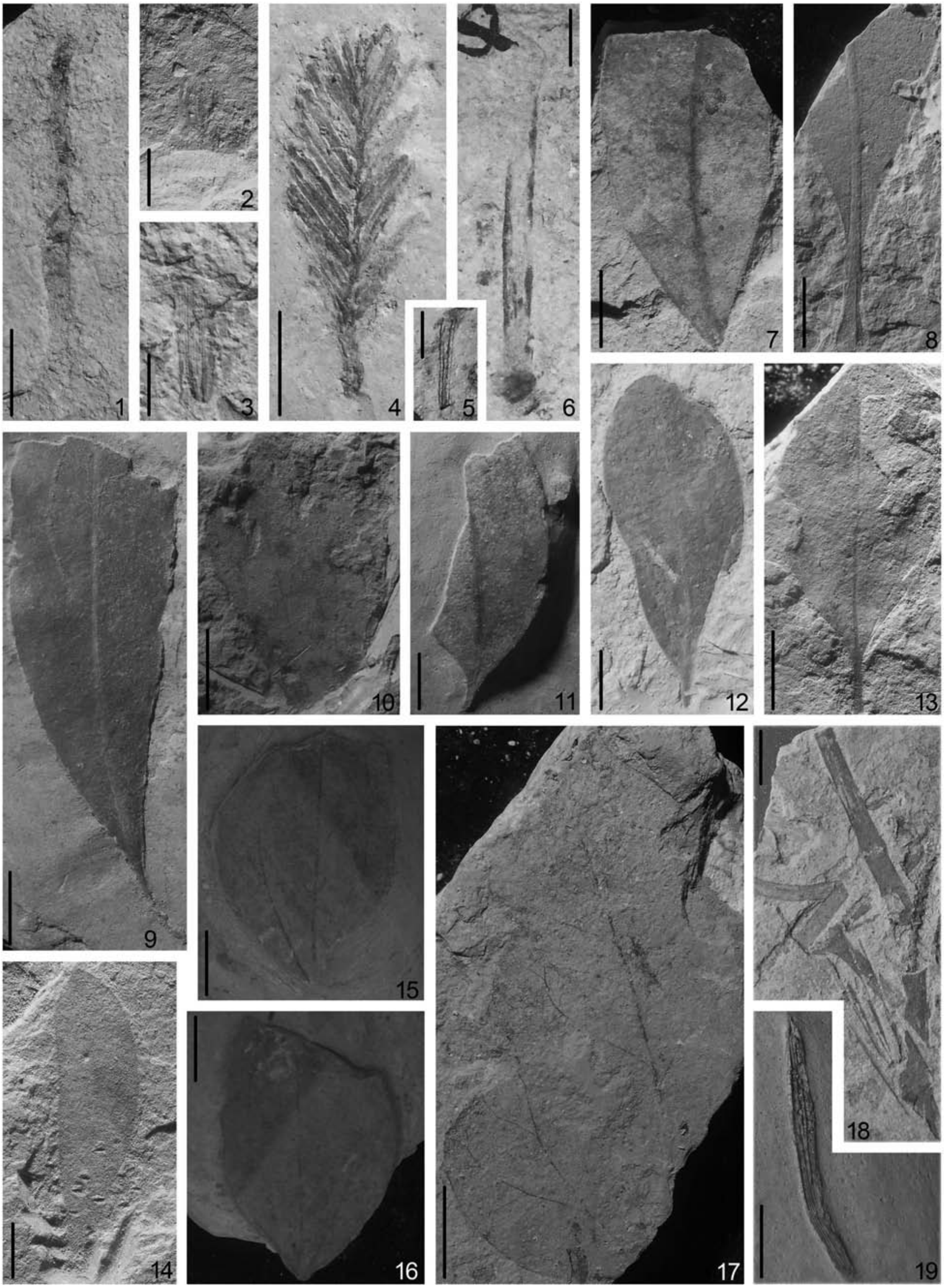

Fig. 3.

of woody dicots. The LMA technique (LMA_{1-3}) uses linear equations published by Wolfe (1979), Su et al. (2010) providing a linear regression equation for East Asian vegetation, and Traiser et al. (2005), based on European vegetation, together with an equation of the sampling error according to Miller et al. (2006). The CLAMP method uses physiognomic characteristics of the studied plant assemblage presented in Appendix 1, and the physiognomic and gridded meteorological calibration datasets from 144 sites (for Vrysses and Makrilia sites) and from 189 sites (for Gavdos site) – see Spicer (2013) selected by a statistical tool published by Teodoridis et al. (2011b) and recently modified by Teodoridis et al. (2012). The application of CLAMP follows the procedure explained on the CLAMP website (http://clamp.ibcas.ac.cn/) (cf. also Wolfe & Spicer 1999; Spicer et al. 2009). CLAMP provides estimates for 3 temperature (MAT, WMMT – warmest month mean temperature, CMMT – coldest month mean temperature) and 2 precipitation variables (3-WET – precipitation during 3 consecutive wettest months, 3-DRY – precipitation during 3 consecutive driest months).

The application of the Coexistence Approach follows the description of the method provided by Mosbrugger & Utescher (1997) and Utescher et al. (2014). Climate data for the Nearest Living Relatives identified for the fossil taxa were retrieved from the current version Palaeoflora Database (Utescher & Mosbrugger, 2013). According to the standard of the method, 3 temperature (MAT, WMMT, CMMT) and 4 precipitation variables (MAP – mean annual precipitation, MPwet – wettest month precipitation, MPdry – driest month precipitation, MPwarm – warmest month precipitation) are reconstructed. The CA can be applied to all fossil taxa based on various organs allowing systematic assessment.

4. Systematic descriptions

In the systematic descriptions angiosperm taxa are arranged according to the classification suggested by recent molecular phylogenetic studies (see Judd et al. 2002; Christenhusz et al. 2011; Reveal 2012) which follow the classification of Angiosperm Phylogeny Group II (2003) and III (2009). Leaf architecture in general is described following current terminology published by Ash et al. (1999) and Ellis et al. (2009). Leaf lamina size categories follow the leaf size template of CLAMP (Spicer 2013), which is based on the original concept of Webb (1959), where microphyll 3 and mesophyll 1 categories are equal to notophyll leaf size and mesophyll 2 and 3 to macrophyll leaves.

Only most relevant synonyms are quoted in a way currently used in the palaeobotanical literature.

Conifers
Cupressaceae
Tetraclinis Masters

Tetraclinis salicornioides (Unger) Kvaček
Figs. 3.1-3.3

1847 *Thuites salicornioides* Unger, p. 11, pl. 2, figs. 1-4, pl. 20, fig. 8.
1989 *Tetraclinis salicornioides* (Unger). – Kvaček, p. 48, pl. 1, fig. 11, pl. 2, figs. 2-14, pl. 3, figs. 1-4, text-fig. 1.
(For further synonyms see Kvaček 1989)

Material: Detached leafy segments and one incomplete foliage twig (GAVMT 416, GAVMT 420, GAVMT 619).

Description: Incomplete foliage twig, 38 mm long, detached leafy segments corresponding to pseudowhorls, 10 and 18 mm long, 3 and 8 mm wide, composed of pairs of dimorphic facial and lateral leaves, at base rounded to truncate, apically obtuse in simple segments or bluntly mucronate in obovate segments from the middle of the foliage sprays, 3 to 5 prominent longitudinal lines seen on surface.

Discussion: According to Kvaček et al. (2000), until being recognized as *Tetraclinis* by attached cones and associated seeds (Kvaček 1989), this conifer was considered to belong to an extinct genus, for which the invalidly published name *Hellia* Unger [see Bůžek et al. 1976] (e.g., Mai 1963; Friis 1977) and recently rejected *Libocedrites* Endlicher [see Zijlstra & Kvaček 2010] (e.g., Knobloch & Kvaček 1976; Mai & Walther 1978; Palamarev et al. 1991; Wilde & Frankenhäuser 1998) were applied. The term cladode-like is used in reference to the foliar branch segments which are distinguished from true cladodes (derived from branches without leaves) by their derivation from fully merged leaves with the branch. Theses segments consist of mutually fused dimorphic scale leaves borne in pseudowhorls. The complete fusion of lateral and facial leaves does not occur among extant Cupressaceae (not even in the extant species of *Tetraclinis*) but does occur in both the European and North American populations of *T. salicornioides*.

According to Kvaček et al. (2000) the foliage segments of *T. salicornioides* are broader and more flattened than those of another fossil representative of this genus, *T. brachyodon* (Brongniart) Mai & Walther and appear to be adapted to more mesic conditions. The same morphology of foliage segments is developed in another extinct conifer *Ditaxocladus* S.X. Guo & Z.H. Sun from the Upper Cretaceous and Palaeocene (Guo et al. 2012).

Tetraclinis Masters has a single extant species, *Tetraclinis articulata* (Vahl) Masters, that is native to warm, summer-dry climates (Cs) of northern Africa, Malta, and southern Spain. This living representative does not reflect the autecology of the fossil *Tetraclinis salicornioides* (Kvaček 2007) and should not be used for palaeoenvironmental considerations. *T. salicornioides* was formerly distributed over large parts of Europe since the Eocene (Meyer & Manchester 1997; Kvaček et al. 2000), having been always connected with humid subtropical to warm-temperate vegetation. It is also represented in the Makrilia outcrop by twigs, a seed and a seed cone partly identified as *Tetraclinis* sp., ?*Tetraclinis* (Sachse 2004) or *Tetraclinis brachyodon* (Sachse et al. 1999; Sachse & Mohr 1996), and in the Vrysses outcrop (Zidianakis et al. 2007).

Taxodium L. C. Richard

Taxodium dubium (Sternberg) Heer
Fig. 3.4

1823 *Phyllites dubius* Sternberg, p. 37, pl. 36, fig. 3; 1825, tentamen & index.
1853 *Taxodium dubium* Sternberg. – Heer, p. 136.
1976 *Taxodium dubium* (Sternberg) Heer. – Kvaček, p. 290, text-figs. 5-6.
1977 *Sequoia langsdorfii* (Brongniart) Heer. – Velitzelos & Schneider, p. 174, pro parte, fig. 6 (? non fig. 5).
(For full synonymy see Kunzmann et al. 2009).

Material: Incomplete foliage shoots (GAVMT 629, GAVMT 652).

Description: Foliage shoots with flattened needles, lanceolate in outline, 13 and 39 mm long, 15 mm wide, needles linear to lanceolate, apex acute, base shortly petiolate and rounded, distichously arranged, alternate at unequal distances, univeined with strong and distinct midrib.

Discussion: The sterile foliage shoots of *Taxodium* and *Sequoia* are difficult to distinguish without the aid of epidermal structure. Nevertheless, the shoots of the *Sequoia sempervirens* type are usually not narrowing to the shoot apex and the length of the needles is approximately uniform. *Taxodium dubium* fossils have been found also in other localities of Greece, such as in Vegora (Kvaček et al. 2002), in the Makrilia outcrop (Sachse & Mohr 1996; Sachse et al. 1999; Sachse 2004) and the Pitsidia outcrop (Zidianakis et al. 2010). The nearest living relatives of this taxon are *T. distichum* and *T. mucronatum*, representatives of swamp vegetation in subtropical and warm temperate climates as deciduous and hygrophilic trees, native in the SE USA and Mexico to Guatemala, respectively (Kvaček et al. 2002; Kunzmann et al. 2009).

Pinaceae
Pinus L.

Pinus sp. (folia)
Figs. 3.5-3.6

Material: Needle leaf fragments (?GAVMT 345, GAVMT 446, ?GAVMT 570, GAVMT 602).

Description: Double-needled fascicles, rounded at base, sheath and apex not preserved, needles partly isolated, fragmentary, in preserved length of 8 to 43 mm, 2 to 2.6 mm wide, straight or slightly curved, univeined, margin entire.

Discussion: The recovered pine needles belong to subgenus *Pinus* (Diploxylon pines), although typical persistent sheaths are not preserved on fascicles due to transportation. Among the findings from the Makrilia outcrop in Crete, 2- and 5-needle fascicles of *Pinus* spp. are known (Sachse & Mohr 1996; Sachse et al. 1999; Sachse 2004). In the Vrysses outcrop, fossil pine foliage also occurs (Zidianakis et al. 2007), partly in fascicles of two, usually thinner than in Gavdos. The pine needles in the Pitsidia outcrop are in fascicles of three and co-occur with winged seeds (Zidianakis et al. 2010).

Angiosperms
Lauraceae
Laurophyllum Göppert

Laurophyllum sp.
Figs. 3.7-3.9

Material: Incomplete leaves and fragments (GAVMT 327, GAVMT 412, GAVMT 418, GAVMT 458, GAVMT 465, GAVMT 481, GAVMT 505, GAVMT 555, GAVMT 592, GAVMT 604, GAVMT 644).

Description: Leaves simple, petiolate, lamina elliptic to obovate, 40 to 85 mm long, 18 to 30 mm wide, base cuneate, narrowed into petiole (up to 12 mm long), apex not preserved, margin entire; venation brochidodromous, midrib strong, straight or slightly curved, secondary veins at an angle of 45 to 60°, looping near margin, alternate, intersecondaries thinner and parallel, tertiary veins perpendicular, straight to sinuous, venation of the higher orders poorly preserved, regular polygonal reticulate, areolation well developed, 3 or 4 sided, veinlets not preserved.

Discussion: Similar leaves of the *Laurophyllum*-type are among the findings from the Makrilia outcrop (Sachse & Mohr 1996; Sachse et al. 1999; Sachse 2004, as *Laurophyllum princeps*, *Laurophyllum bournense* and ?*Laurophyllum* Typ 1, 2). The lack of leaf anatomical structure prevents an exact identification and comparisons.

Daphnogene Unger

Daphnogene sp.
Figs. 3.10-3.12

Material: Incomplete leaves and fragments (GAVMT 355, GAVMT 391, GAVMT 392, GAVMT 440, GAVMT 479, GAVMT 485, GAVMT 500).

Description: Leaves simple, petiolate, lamina widely elliptic to obovate, 40 to 90 mm long, 18 to 27 mm wide, base rarely asymmetric, cuneate with petiole up to 6 mm long, apex shortly acuminate to blunt, margin entire, venation suprabasal acrodromous, midrib strong, moderate, straight or slightly curved in apical part, lateral veins thinner, alternate or opposite, at an angle of 20 to 40°, running along margin, usually connecting secondaries in 2/3 of the blade length, secondary veins thinner, alternate, at an angle of 40 to 50°, curved and looping along margin or straight between midrib and lateral veins, venation of the higher orders poorly preserved.

Discussion: The fossils at hand are not assignable to a species without the cuticle structure. Similar leaf fossils from the Vegora flora were assigned to *Daphnogene pannonica* Kvaček & Knobloch (Kvaček et al. 2002), which differs in thinly cutinized leaf epidermis from *Cinnamomum polymorphum,* widely distributed in the European early-middle Miocene. Among the findings from the Makrilia outcrop are two similar leaves (Sachse 2004) assigned to *Cinnamomophyllum* sp. The leaf fragment assigned to *Cinnamomophyllum polymorphum* by Sachse (2004, pl. 11, fig. 12) was obviously misidentified because of major differences in the venation. The material of *Daphnogene* similar to the Gavdos specimens was recorded in the Vrysses (Zidianakis et al. 2007) as well as in the Pitsidia outcrops (Zidianakis et al. 2010).

Lindera Thunb.

? *Lindera ovata* Kolakovsky
Figs. 3.13-3.16

? 1957 *Lindera ovata* Kolakovsky, p. 277, pl. 14, figs. 4-5; pl. 15, fig. 1.
? 1964 *Lindera ovata* Kolakovsky. – Kolakovsky, p. 106-107, pl. 40, figs. 1-5.
? 1967 *Lindera* cf. *L. ovata* Kolakovsky. – Petkova, p. 142, pl. 5, fig. 6, pl. 12, fig. 4.
? 1984 *Lindera ovata* Kolakovsky. – Kitanov, p. 51, pl. 7, fig.1.

Material: Incomplete leaves and fragments (GAVMT 338, GAVMT 369, GAVMT 383, GAVMT 448, GAVMT 496, GAVMT 539, GAVMT 617).

Description: Leaves simple, petiolate, lamina widely elliptic to ovate, 40 to 60 mm long, 20 to 32 mm wide, base symmetric or rarely slightly asymmetric, widely cuneate to rounded, with petiole up to 5 mm long, apex not preserved, margin entire, venation basal acrodromous, midrib strong, straight to curved, lateral veins thinner, alternate or opposite, at an angle of 20 to 30°, running along margin, secondary veins thinner, alternate, curved and looping at margin or straight steeply ascending between midrib and lateral veins, venation of the higher orders poorly preserved.

Discussion: Kolakovsky (1957, 1964, pl. 40, figs 1-5) described this species from the Kodor River palaeoflora assemblages without the cuticle structure or any other leaf anatomical character. Thus the affinity to the Lauraceae is not well supported, being based entirely on gross morphology. The assignment to the genus *Lindera* is also equivocal.

Similar fossils were described from the Bulgarian palaeoflora by Palamarev et al. (2005, pl. 4, fig. 4) as *Matudaea palaeobalcanica* (Hamamelidaceae). In Zidianakis et al. (2007, fig. 3N-P) both morphotypes are noted as cf. *Ziziphus ziziphoides*, while in Sachse (1997, 2004) they are referred to as *Dicotylophyllum* type 3. Kvaček & Hably (1991: 81, pl. 9, fig. 4) described different morphotypes from the Hungarian Oligocene as *Ziziphus* cf. *ziziphoides* (Unger) Weyland. Among the findings from the Makrilia outcrop, similar leaves are referred to as ?Rhamnaceae (Sachse & Mohr 1996), or *Dicotylophyllum* Typ 3 (Sachse et al. 1999, Sachse 2004) matching the *Lindera ovata* specimens of the current study. In the Vrysses outcrop such leaves, similar to our *Lindera ovata,* also occur and have been assigned to cf. *Ziziphus ziziphoides* (Unger) Weyland (Zidianakis et al. 2007). Because of finely dentate margin (Zidianakis et al. 2007, fig. 3N, P), this material may belong to the Rhamnaceae.

The diagnostic tertiary venation is not well preserved in our material, but the tertiary veins are steep and not dense and at wide angles contrary to the fossil foliage of *Ziziphus* (Rhamnaceae), which differs also in mostly finely serrate margins (e.g., Kvaček & Hably 1991).

Sassafras T. Nees

? *Sassafras* sp.
Fig. 3.17

Material: Incomplete simple leaves (GAVMT 432, GAVMT 505).

Fig. 4. 1. *Fagus gussonii* Massalongo emend. Knobloch & Velitzelos, leaf, GAVMT 473 scale bar 10 mm; 2. *Fagus gussonii* Massalongo emend. Knobloch & Velitzelos, leaf, GAVMT 492, scale bar 10 mm; 3. *Fagus gussonii* Massalongo emend. Knobloch & Velitzelos, leaf, GAVMT 534, scale bar 10 mm; 4. *Leguminocarpon* sp., fragment of a pod with large seeds, GAVMT 567, scale bar 5 mm; 5. *Leguminosites* sp. 1, leaflet of broad and elliptic shape, GAVMT 321, scale bar 5 mm; 6. *Leguminosites* sp. 1, leaflet of broad and elliptic shape, GAVMT 503, scale bar 10 mm; 7. *Leguminosites* sp. 2, leaflet of narrow and elliptic shape, GAVMT 550, scale bar 5 mm; 8. *Leguminosites* sp. 2, leaflet of narrow and elliptic shape, GAVMT 552, scale bar 5 mm; 9. *Leguminosites* sp. 3, large leaflet with petiolule, GAVMT 524, scale bar 10 mm; 10. Leaflet venation of Fig. 4.9, scale bar 10mm; 11. *Leguminosites* sp. 4, basal part of elliptic leaflet, GAVMT 532, scale bar 10 mm; 12. *Leguminosites* sp. 4, basal part of ovate leaflet, GAVMT 562, scale bar 10 mm; 13. *Paliurus tiliifolius* (Unger) Bůžek, incomplete leaf base, GAVMT 520, scale bar 10 mm; 14. *Sapindus graecus* Unger, incomplete leaflet, GAVMT 567 left, scale bar 10 mm; 15. Detail of leaflet venation, GAVMT 567 left, scale bar 5 mm;

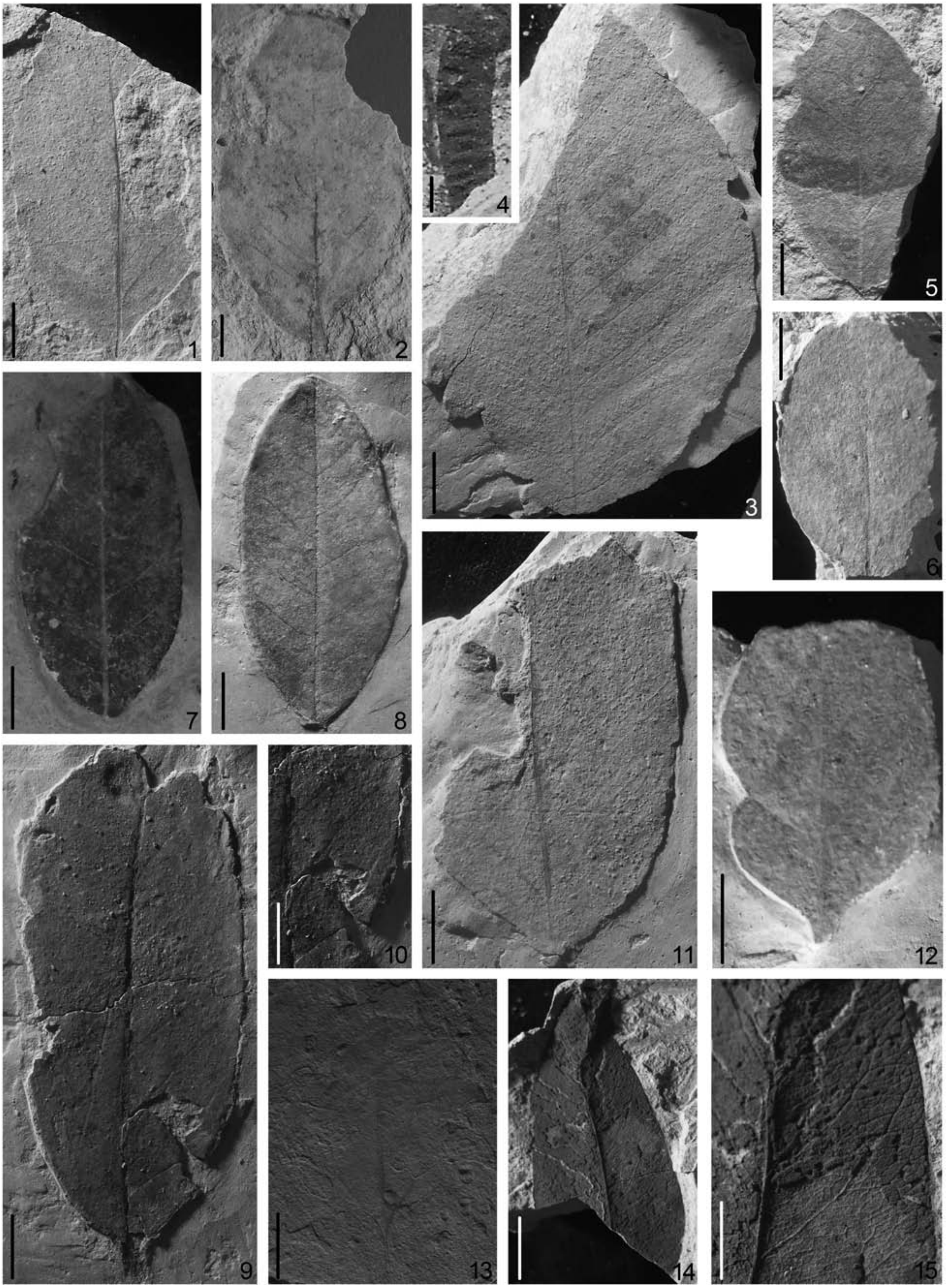

Fig. 4.

Description: Leaves simple, lamina widely elliptic, 32 and 65 mm long, 23 and 35 mm wide, base incomplete, rounded, apex blunt, margin entire, with one large lobe preserved; venation brochidodromous, midrib strong, straight, suprabasal veins slightly thicker, curved, alternate, higher secondary veins thinner, curved, looping along margin, alternate, at angles of 30 to 50°, tertiary veins perpendicular, straight to sinuous, often forked, venation of the higher orders poorly preserved, regular polygonal reticulate, areolation well developed, mainly 4-sided, small glands in axiles of secondaries indistinct.

Discussion: One of the specimens at hand may represent a trilobed leaf, which is similar to *Sassafras ferretianum* Massalongo (see Kvaček et al. 2002: 116 f., pl. 3, fig. 6, pl. 4). The possible misidentification of these specimens with, e.g., *Acer tricuspidatum* Bronn (cf. Hably 1992, pl. 4, fig. 3), cannot be ruled out, but in our opinion it is improbable due to the marginal venation. The lobed leaves of the modern representatives of the Moraceae (e.g., *Morus*) differ in the toothed margin. On the other hand, the described incomplete leaves may resemble also foliage of *Liriodendron* L.

Monocotyledonae

Monocotyledonae fam. et gen. indet.

Figs. 3.18-3.19

Material: Fragments of leaves (GAVMT 323, GAVMT 349, GAVMT 428, GAVMT 588, GAVMT 610).

Description: Leaves strap-like, variable in sizes, with parallel venation, margin entire.

Discussion: These leaf remains may belong to sedges bordering the water. Their exact identification remains open. According to Kvaček et al. (2002) the nearest living relatives of this aggregate taxon probably correspond to hygrophyllic (?) representatives of grass-like monocots. Similar remains of Monocotyledonae recovered in the Vrysses and Pitsidia outcrops have been assigned to two types of Poaceae/Cyperaceae (Zidianakis et al. 2007, 2010).

Fagaceae

Fagus L.

Fagus gussonii Massalongo emend. Knobloch & Velitzelos

Figs. 4.1-4.3

1858 *Fagus gussonii* Massalongo, p. 37.
1859 *Fagus gussonii* Massalongo. – Massalongo & Scarabelli, p. 202, pl. 25, figs. 2, 5.
1979 ? *Fagus attenuata* Göppert. – Mädler & Steffens, p. 15, pl. 4, fig. 2.
1986 *Fagus gussonii* Massalongo emend. Knobloch & Velitzelos, p. 9, pl. 2, figs. 2-4, 6-8, pl. 5, fig. 11, pl. 6, fig. 5.
1994 *Fagus gussonii* Massalongo. – Barrón & Diéguez, p. 23, text-fig. 2.1, 2.2, 3.1-3.3, 4.
1994 *Fagus pristina* Saporta. – Barrón & Diéguez, p. 23, text-figs. 2.3, 2.4, 3.4, 3.5, 5.
1996 *Fagus* sp. – Sachse & Mohr, p. 162, text-fig. 3.2, 3.5.
1999 *Fagus gussonii* Massalongo. – Velitzelos & Kvaček, p. 420, pl. 1, fig. 1.
1999 *Fagus* type *gussonii* Massalongo. – Sachse et al., pp. 367, 370, fig. 1.1, 1.5.
2002 *Fagus gussonii* Massalongo. – Kvaček, Velitzelos & Velitzelos, p. 61, pl. 6, figs. 1-7, pl. 7, figs. 1-5, pl. 29, figs. 3-4.
2004 *Fagus gussonii* Massalongo. – Denk, pp. 9-11, fig. 12.
(For further synonyms see Denk 2004)

Material: Incomplete leaves and fragments (GAVMT 334, ?GAVMT 460, GAVMT 473, GAVMT 492, GAVMT 513, GAVMT 534, GAVMT 596).

Description: Leaves simple, petiolate, lamina widely elliptic to ovate, 36 to 85 mm long and 28 to 55 mm wide, apex acute to shortly acuminate, base mostly symmetric, cuneate to widely cuneate, with fragmentary petiole up to 5 mm long, margin simple widely serrate, teeth acute, poorly preserved, venation craspedodromous, midrib moderately strong, straight, secondary veins thin, numerous, regularly spaced, straight, alternate, at an angle of 30 to 60°, tertiary veins alternate percurrent, straight to convex, venation of the higher orders regular, polygonal reticulate; areolation well developed, 3- or 4-sided; veinlets dichotomous.

Discussion: In Kolakovsky (1964, pl. 26, figs. 5-6) this fossil morphotype was assigned to *F. orientalis* Lipsky *fossilis*. However, even this material belongs in our opinion to *Fagus gussonii* Massalongo emend. Knobloch & Velitzelos (see Kvaček et al. 2002: 61, 62, 96, pl. 5, figs. 1-9, pl. 6, figs. 1-7, pl. 7, figs. 1-5). Sachse et al. (1999) and Sachse (2004) found ten fragments of the *Fagus gussonii* type (partly as *Fagus* Typ *attenuata*) in the Makrilia outcrop. Zidianakis et al. (2007) recovered impressions assigned to *Dicotylophyllum* sp. 9, which might be related to the genus *Fagus* L., but more and better preserved material is needed in order to prove such a hypothesis. In Zidianakis et al. (2010) the same morphotype is noted as *Fagus* type *attenuata*. According to Denk (2004) among the three taxa of *Fagus* recognized for the Cenozoic of Europe [a) *Fagus castaneifolia* Unger 1847; b) *Fagus gussonii* Massalongo 1858 emend. Knobloch & Velitzelos 1986; c) *Fagus haidingeri* Kováts 1856 sensu Knobloch 1969] *Fagus gussonii* is the only straightly comparable to a few modern species and the one which is geographically and stratigraphically most restricted. The distribution of *Fagus gussonii* has been reported in Denk et al. (2011), with its southeasternmost limit in the flora of Makrilia (Crete Island, Greece), and its northwesternmost limit in Iceland. The nearest living relative of this taxon is *Fagus sylvatica* L. subsp. *orientalis* (Lipsky) Greuter & Burdet (= *F. orientalis* L.) – a deciduous and mesic tree, a representative of warm-temperate climates of SE Europe and the Near East (see Kvaček et al. 2002; Denk & Grimm 2009) which comprises several leaf morphotypes (Denk, 1999a, b; Denk et al. 2002). This is also the case with *F. gussonii*.

Fabaceae
Leguminocarpon Göppert

Leguminocarpon sp.
Fig. 4.4

Material: Incomplete pod (GAVMT 567 right).

Description: Pod flat, oblong in outline, indehiscent, 12 mm long and 3 mm wide, apical and basal parts not preserved, 8 prominent outlines of oval seed chambers transversally oriented to the length of the fruit, ca. 2.5 mm long and 0.5 mm wide, fruit wall membranous, structure of upper surface not preserved.

Discussion: Similar morphotypes are referred to as *Leguminocarpon* sp. in Kvaček & Hably (1991, pl. 10, figs. 1-3) or *Leguminosites palaeogaea* or *L. hesperidum* (Unger) Kovar-Eder & Kvaček (Kovar-Eder et al 2004, pl. 9, figs. 1-4). Such fruits were assigned to the genus *Senna* Mill. among the Eocene legumes of North America (Herendeen 1992: 96, 97, 102, fig. 57).

Leguminosites Bowerbank emend. Schimper

Leguminosites sp. 1
Figs. 4.5-4.6

Material: Complete leaflets (GAVMT 321, GAVMT 503).

Description: Leaflets elliptic, 30 and 43 mm long, 17 and 24 mm wide, base slightly asymmetric, rounded, petiolule fragmentary, short and thick, apex rounded, margin entire, venation brochidodromous, midrib strong, straight, secondary veins thinner, looping, alternate, at angles of 30 to 50°, irregularly spaced, tertiary veins alternate percurrent, straight to curved, venation of the higher orders poorly preserved.

Discussion: Among the findings from the Makrilia outcrop nine various genera of legumes have been listed (Sachse & Mohr 1996; Sachse et al. 1999; Sachse 2004) and some may partly correspond to our records. According to Kvaček et al. (2002) such legumes are difficult to identify but may belong to deciduous representatives typical of drier climate. Leaflets assigned to Leguminosae gen. indet. and *Podocarpium podocarpum* have also been reported from the Pitsidia outcrop of the Messara Basin (Zidianakis et al. 2010).

Leguminosites sp. 2
Figs. 4.7-4.8

Material: Incomplete leaflets (GAVMT 494, GAVMT 550, GAVMT 552).

Description: Leaflets elliptic to obovate, 37 to 50 mm long and 14 to 23 mm wide, base symmetric, widely cunate to rounded with fragmentary, up to 4 mm long petiolule, apex rounded, margin entire, venation brochidodromous, midrib strong, straight, secondary veins thinner, looping, alternate, at angles of 45 to 65°, intersecondaries vaguely seen, thinner, parallel, tertiary veins alternate percurrent, straight to curved, venation of the higher orders regular polygonal reticulate, areolation well developed, areoles 3 or 4 sided.

Discussion: This legume differs in a more elongate form of leaflets from *Leguminosites* sp. 1. Also in this case, this taxon may belong to some of Leguminosae with deciduous foliage. Similar material of legumes has been also referred from the Pitsidia outcrop (Zidianakis et al. 2010).

Leguminosites sp. 3
Figs. 4.9-4.10

Material: Incomplete leaflet (GAVMT 524).

Description: Leaflet elliptic, 105 mm long and 42 mm wide, base symmetric, widely cunate with fragmentary 6 mm long petiolule, apex incomplete, probably rounded, margin entire, venation brochidodromous, midrib strong, straight, secondary veins thinner, relatively numerous, regularly spaced, alternate, at angles of 45 to 60°, looping, intersecondaries indistinct, thinner, parallel, tertiary veins alternate percurrent, straight to curved, venation of the higher order not preserved.

Discussion: This single leaflet differs from the previously described morphotypes by its larger size. Such leaflets of legume foliage are not common. In the Makrilia outcrop, similar morphotypes are referred to as *Dicotylophyllum* typ 12 or Juglandaceae vel Lauraceae (Sachse et al. 1999, text-figs. 2.38, 2.44). Leguminosae gen. indet. has been also referred from the Pitsidia outcrop (Zidianakis et al. 2010). Some foliage ascribed to *Dicotylophyllum* sp. 5 (Zidianakis et al. 2007) from Vrysses may belong to a similar morphotype.

Leguminosites sp. 4
Figs. 4.11-4.12

Material: Incomplete leaflets and fragment (GAVMT 349, GAVMT 532, GAVMT 562).

Description: Leaflets elliptic to ovate, 25 to 65 mm long, 27 to 37 mm wide, base symmetrical, cuneate, apex not preserved, margin entire, venation brochidodromous, midrib strong, secondary veins much thinner, densely arranged, straight, rarely curved, looping along margin, alternate, at angles of 30-60°, intersecondary veins thinner, parallel, venation of the higher orders poorly preserved.

Discussion: Our specimens are similar to the material ascribed to *Leguminosites* sp. 3 (Pl. 3, fig. 13) but differs in much more dense venation. It matches foliage from the Kodor Upper Miocene assigned to *Salix integra* Göpp. ? (Kolakovsky 1964, pl. 52, fig. 4) or ?*Dalbergia bella* Heer sensu Kolakovsky (1964, pl. 43, fig. 1).

Rhamnaceae
Paliurus Mill.

Paliurus tiliifolius (Unger) Bůžek
Fig. 4.13

1847 *Paliurus favonii* Unger, p. 147, pro parte, pl. 50, figs. 7-8 (non fig. 6 left).
1847 *Ceanothus tiliaefolius* Unger, p. 143, pl. 49, figs. 1-6.
1850 *Paliurus favonii* Unger, p. 463, pro parte.
1864 *Ziziphus tremula* Unger, p. 16, pl. 3, fig. 39.
1864 *Ziziphus renata* Unger, p. 16, pl. 3, figs. 40, 41.
? 1864 *Ziziphus protolotus* Unger, p. 17, pl. 3, fig. 43.
1971 *Paliurus tiliaefolius* (Unger). – Bůžek, p. 74, pl. 33, figs. 1-21; pl. 34, figs. 1-17.

Material: Incomplete leaf (GAVMT 520).

Description: Leaf simple, lamina widely ovate, 55 mm long and 30 mm wide, base slightly truncate with a 10 mm long petiole, apex not preserved, margin entire to undulate, venation tri-veined, midrib strong, straight, basal lateral veins originating at 30 to 50°, secondary veins due to fragmentary preservation hardly observable, thinner, opposite, curved, venation of the higher orders poorly preserved.

Discussion: Similar fossil material has been described in Kovar-Eder et al. (2004, pl. 11, fig. 1) as *Paliurus tiliifolius* while Palamarev et al. (2005) interpreted such a morphotype as *Cercidiphyllum macrophyllum* (Palamarev et al. 2005, pl. 2, fig. 2). The basal venation of the specimen at hand is similar to the leaf assigned to cf. *'Parrotia' pristina* from Vrysses (Zidianakis et al. 2007, fig. 2-F), which differs in the lower position of the first pair of the secondaries and is clearly coarsely dentate. In Bozukov & Tsenov (2012), a similar morphotype from the Pontian of Bulgaria is also referred to *Parrotia pristina* (Ettingsh.) Stur. Among the findings from the Makrilia outcrop six leaves are referred to the Rhamnaceae as *Paliurus* sp. vel *Zizyphus* sp. vel *Ceanothus* sp. (Sachse & Mohr 1996) but they are clearly different from our material (see above under *Lindera ovata*).

Sapindaceae
Sapindus Tourn. ex L.

Sapindus graecus Unger
Figs. 4.14-4.15

1867 *Sapindus graecus* Unger, p. 73, pl. 12, figs. 1-23.

Material: Incomplete leaflets and fragments (GAVMT 567 left, GAVMT 572 left, GAVMT 580).

Description: Leaflets with lamina asymmetric, elliptic to ovate, 45 to 68 mm long and 28 to 48 mm wide, base not always preserved, decurrent into petiolule, apex acute, margin entire; venation brochidodromous, primary vein distinct, straight, secondary veins thinner, numerous, alternate and slightly curved, at angles of 30 to 60°, looping several times well within the margin, tertiary veins alternate, very oblique to secondaries, sinuous, venation of the higher orders polygonal reticulate, veinlets dichotomous branching.

Discussion: This material is similar to the one described by Unger (1867) (see also Kottis et al. 2002) from the Kymi palaeoflora as *Sapindus graecus* (Unger 1867, pl. 12, figs. 3, 12). Besides the type material, foliage from the same locality ascribed to *Laurus primigenia* (Unger 1867, pl. 8, fig. 5), *Nephelium jovis* or *Eucalyptus agaea* (Unger 1867, pl. 15, fig. 1), or identified as *Trigonobalanopsis rhamnoides* (Unger 1867, pl. 2, fig. 27) is hardly distinguishable. *Sapindus graecus* was also mentioned in Bozukov & Tsenov (2012) for the Bulgarian palaeoflora. Thus its stratigraphic span is the Oligocene – late Miocene, while its geographic area has so far comprised the island of Euboea (Unger 1867), Armenia and Georgia (Palibin 1937, 1939). This finding confirms the limited distribution of this species only on the territory of southeast Europe. Unger (1867) suggested a probable recent analogue of this fossil species to be looked for among the South African representatives of the genus but so far no

Fig. 5. 1. *Acer angustilobum* Heer, trilobed leaf bluntly dentate on the margin, GAVMT 515, scale bar 10 mm; 2. Detail of medial leaf lobe's margin and venation, GAVMT 515, scale bar 5 mm; 3. *Betula* sp., fragmentary cuneate leaf base, GAVMT 541, scale bar 10 mm; 4. *Betula* sp., incomplete leaf, GAVMT 640, scale bar 10 mm; 5. ? *Carpinus* sp., complete leaf with bluntly serrate margin, GAVMT 477, scale bar 10 mm; 6. *Ulmus plurinervia* Unger, long petiolate asymmetric leaf base, GAVMT 438, scale bar 5 mm; 7. *Salix* cf. *angusta* A. Br., basal part of incomplete linear leaf, GAVMT 650, scale bar 10 mm; 8. detail of leaf venation and margin, GAVMT 650, scale bar 5 mm; 9. *Salix* cf. *angusta* A. Br., incomplete elliptic leaf with coarsely simply serrate margin, GAVMT 564, scale bar 10 mm; 10. *Populus populina* (Brongniart) Knobloch, complete petiolate leaf with five basal veins, GAVMT 487, scale bar 5 mm; 11. counter-impression of Fig. 5.10, GAVMT 490, scale bar 5 mm; 12. *Engelhardia orsbergensis* (Wessel & Weber) Jähnichen, Mai & Walther, leaflet, GAVMT 594, scale bar 5 mm; 13. *Engelhardia orsbergensis* (Wessel & Weber) Jähnichen, Mai & Walther, leaflet, GAVMT 544, scale bar 5 mm.

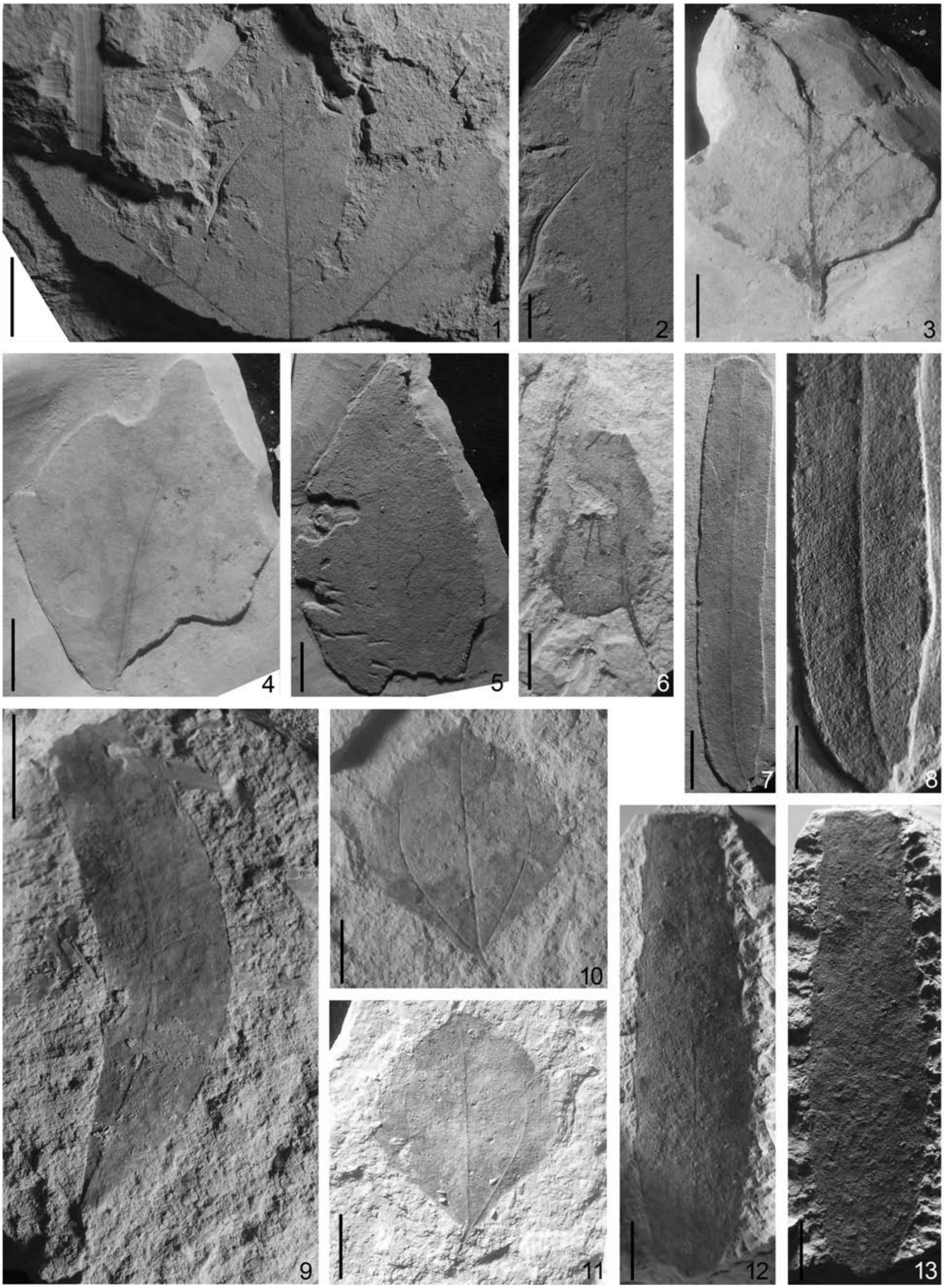

Fig. 5.

detailed morphological study and leaf epidermal data may support this assumption.

Acer L.

Acer angustilobum Heer
Figs. 5.1-5.2

1859 *Acer angustilobum* Heer, p. 57, pl. 118, figs. 4-5, 7. (For further synonymy see Walther 1972: 40)

Material: Incomplete leaf (GAVMT 515).

Description: Only the upper part of the lamina preserved, leaf widely elliptic, palmately sub- 3-lobed, 70 mm long and 84 mm wide, lobes oblong, unevenly widely dentate at margin, apices acute to shortly accuminate, base incomplete; tooth apices acute, venation basal actinodromous, 3 primary veins, lateral veins at an angle of 30° and 40°, straight, strong, moderately thick, secondary veins thinner, alternate, straight to curved , at angles of 30 to 50°, tertiary veins alternate to opposite percurrent, curved to sinuous, venation of the higher orders regular polygonal reticulate, areolation well developed, 3 to 4 sided, veinlets not visible.

Discussion: The maple foliage of such a form has been assigned to *Acer angustilobum* and characterized anatomically (Walther 1972, pl. 35, figs. 1, 9). *A. palaeosaccharinum* Stur is another similar fossil species, which differs mainly in its epidermal structure. Both fossil species are connected with transitional forms (Procházka & Bůžek 1975, as *A. dasycarpoides*). A fragment of the same morphotype was ascribed to the Vitaceae from the Makrilia flora (Sachse & Mohr 1996, pl. 3, fig, 37; Sachse 2004, pl. 20, fig. 1), where foliage of *Acer pseudomonspessulanum* (~ *decipiens*) prevails. Similar more complete maple foliage from the Vegora flora was identified as *A. subcampestre* Göppert (Kvaček et al. 2002, pl. 24, fig. 6). Our material is too fragmentary and lacking epidermal characters. According to T. Denk (pers. comm. 2013) the preserved morphological features suggest *Acer palaeosaccharinum* rather than *A. angustilobum* as the most likely possibility. The Nearest Living Species of both fossil species were determined by Procházka (in Procházka & Bůžek 1975) as *A. saccharum* Marsh. and *A. saccharinum* L., both native in the warm temperate Atlantic USA.

Betulaceae
Betula L.

Betula sp.
Figs. 5.3-5.4

? 1964 *Betula subpubescens* Göppert; Kolakovsky, p. 62 f., pl. 18, fig. 6.

Material: Incomplete leaves (GAVMT 541, GAVMT 640).

Description: Leaves simple, lamina widely elliptic to ovate (?), 45 mm and 52 mm long, 35 mm and 39 mm wide, apex not preserved, base asymmetrical, cuneate with fragmentary 5 mm long petiole, margin entire basally, higher irregularly simple serrate, venation craspedodromous, midrib straight, strong, secondaries alternate, thin, regularly and coarsely spaced, at angles of 40 to 50°, curved, tertiary veins alternate percurrent, straight or curved, venation of the higher orders regular polygonal reticulate, poorly preserved.

Discussion: These specimens are similar to the record from the late Miocene locality Kodor in Abchasia identified as *Betula subpubescens* Göppert (Kolakovsky 1964, pl. 18, fig. 6). The available fragments are insufficient for an exact identification or indication of related living species.

Carpinus L.

? *Carpinus* sp.
Fig. 5.5

Material: Incomplete leaf (GAVMT 477).

Description: Leaf simple, lamina ovate, 76 mm long and 38 mm wide, base incomplete, probably widely cuneate to rounded, apex acute, margin damaged by preparation, probably irregularly simple serrate, venation craspedodromous, midrib straight, strong, secondaries alternate, thin, slightly curved, regularly spaced, at angles of 45 to 60°, tertiary veins alternate percurrent, straight or curved, rarely forked, venation of the higher orders not well preserved, probably regular polygonal reticulate.

Discussion: The single poorly preserved recovered specimen matches in overall leaf morphology foliage of *Carpinus grandis* Unger, which occurs also in the flora of Vegora (Kvaček et al. 2002, pl. 19, fig. 3). The margin is less distinctly toothed than in the better preserved material. *Carpinus betulus* L. is usually considered as the nearest living relative but the morphology of fruits is needed to resolve true specific affinities.

Ulmaceae

Ulmus L.

Ulmus ? *plurinervia* Unger
Fig. 5.6

? 1847 *Ulmus plurinervia* Unger, p. 95, pl. 25, figs. 1-4.
? 1851 *Planera ungeri* Ettingshausen, p. 14, pro parte, pl. 2, figs. 11-12.
(For further synonymy see Kovar-Eder et al. 2004).

Material: Incomplete leaf (GAVMT 438).

Description: Leaf simple, petiolate, lamina ovate, 30 mm long and 14 mm wide, base asymmetric, slightly cordate, with 5 mm long petiole, apex incomplete, margin double serrate, primary teeth triangular, secondary teeth finer, venation craspedodromous, midrib strong, straight, secondary veins thinner, straight or forked, distinct, alternate, opposite at the basal part, parallel, numerous, at an angle of 30 to 50° (basal pair 80°), tertiary veins alternate percurrent, straight to sinuous, venation of the higher orders regular polygonal reticulate, areolation well developed, areoles 3- or 4-sided.

Discussion: This leaf fragment is similar to *Ulmus plurinervia* Unger as characterized by Kovar-Eder et al. (2004, pl. 6, fig. 21) and in Kvaček et al. (2002: 150 f., pl. 20, fig. 12). A similar leaf identified as *Fagus orientalis* Lipsky *fossilis* by Kolakovsky (1964: 26, fig. 6) differs in the larger size and the dentation, which seems to go close to the base. Similar fossil leaves are also ascribed to *Betula subpubescens* Göppert (Kolakovsky 1964, pl. 18, figs. 5-6) or *Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba (Telles Antunes et al. 1999, pl. 1, fig. 5). Among the findings from the Makrilia outcrop three leaves of cf. *Ulmus plurinervia* were described (Sachse et al. 1999; Sachse 2004), not quite matching our material.

Salicaceae

Salix L.

Salix cf. *angusta* A. Braun

Figs. 5.7-5.9

Material: Incomplete leaves and fragments (GAVMT 363, GAVMT 498, GAVMT 528, GAVMT 537, GAVMT 564, GAVMT 576, GAVMT 606, GAVMT 646, GAVMT 650).

Description: Incomplete simple leaves and fragments, linear to narrow oblong, 28 to 90 mm long, 8 to 23 mm wide, base cuneate, rarely asymmetrical, apex rounded, margin entire, venation eucamptodromous, midrib strong, straight, secondary veins dense, alternate, regularly spaced, looping near margin, at angles of 40 to 80°, intersecondaries thin, parallel, tertiary veins alternate percurrent, straight or curved, venation of the higher orders poorly preserved, probably regular polygonal reticulate.

Discussion: Similar leaf forms are usually assigned to *Salix angusta* A. Br. (see Hantke 1954: 58, pl. 6, figs. 1-4). Most of these specimens are also similar to *Apocynophyllum* sp. in sense of Kolakovsky (1964, pl. 7, figs. 9-12, pl. 8, fig. 1) and the others (e.g., GAVMT 537) might be similar to *Nerium* sp. sensu Kovar-Eder et al. (2004, pl. 11, fig. 17) but the intramarginal vein characteristic of both cases is lacking in our material. We suspect that the same morphotype from the Makrilia flora was identified as cf. *Salix* sp. or *Myrica* sp. type *M.* cf. *lignitum* by Sachse et al. (1999, text-figs. 1.19, 1.29). Of the living willows *S. viminalis* L. is usually suggested as NLR although no detailed study has been undertaken to prove this relationship.

Populus L.

Populus populina (Brongniart) E. Knobloch

Figs. 5.10-5.11

1822 *Phyllites populina* Brongniart, p. 237, pl. 14, fig. 4.
1850 *Populus latior* A. Braun. – Unger, p. 416.
1932 *Populus latior* A. Braun. – Konjaroff, p. 54, pl. 16, pl. 17, fig. 2; text-fig 3.
1964 *Populus populina* (Brongniart). – Knobloch, p. 601.

Material: Complete leaf and counter-impression (GAVMT 487, GAVMT 490).

Description: Leaf simple, petiolate, petiole up to 5 mm long, lamina widely elliptic, 28 mm long and 17 mm wide, base widely cuneate, apex widely acute to obtuse; margin regularly coarsely dentate to crenulate, teeth blunt, rounded, venation basal actinodromous, tri-veined, midrib strong, straight, lateral veins thinner, distinct, opposite, ascending towards the upper third of the lamina, at angles of 40-60°, higher secondaries alternate to sub-opposite originating also at angles of 40 to 60°, secondary veins thin, opposite to alternate, venation of the higher orders poorly preserved.

Discussion: This material showing five primary veins matches a leaf illustrated in Kvaček et al. (2002: 152 f., pl. 21, fig.1) from the Vegora flora and assigned to *Populus populina*. The typical form of this species differs by the larger and broader laminae coarsely undulate at margin (Heer 1856, as *Populus latior* A. Braun). The existence of *Populus* is suggested by Zidianakis et al. (2010) in the Pitsidia flora but the morphotype assigned to *P. crenata* Berger differs from our material in coarser dentation and more numerous secondaries. In the Makrilia outcrop there are only fruits of *Populus* sp. among the findings (Sachse & Mohr 1996). According to Kvaček et al. (2002) the Nearest Living Relative of typical *Populus populina* is *P. alba*, which represents a group of elements related to warm-temperate and temperate climatic conditions. *P. alba* is a deciduous and mesic species native to Eurasia. The recovered morphotype is also similar in leaf morphology to *P. pruinosa* Schrenk. from Turkestan and NW Siberia, but no leaf epidermal evidence is available to prove this relationship.

Juglandaceae

Engelhardia Leschen. ex Blume

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

Figs. 5.12-5.13

1856 *Banksia orsbergensis* Wessel & Weber, p. 146, pl. 25, fig. 9a-d.
1977 *Engelhardia orsbergensis* (Wessel & Weber). – Jähnichen, Mai & Walther, pp. 326-346, pls. 38-49, text-figs. 1-3.

1984 *Palaeocarya orsbergensis* (Wessel & Weber). – Jähnichen et al., p. 110.

Material: Incomplete leaflets and fragments (GAVMT 385, GAVMT 544, GAVMT 590, GAVMT 594).

Description: Isolated sessile leaflets, elongate to narrow ovate, 36 to 45 mm long, 8 to 9 mm wide, apex acute to obtuse, base mostly slightly to strongly asymmetric, rounded to widely cuneate, margin in the lower part entire, higher up simply widely serrate, teeth acute, partly S-shaped, venation camptodromous to semicraspedodromous, midrib strong, straight to slightly curved, secondary veins distinctly thinner, numerous and dense, mostly straight, alternate, at 40 to 60°, looping along margin, intersecondaries thinner, parallel, venation of the higher orders poorly preserved.

Discussion: This material belongs to *Engelhardia orsbergensis* (Wessel & Weber) Jähnichen, Mai & Walther (1977), also separated from the genus *Engelhardia* as *Palaeocarya orsbergensis* (in Jähnichen et al. 1984 – for the nomenclature see Winterscheid & Kvaček 2014). Among the findings from the Makrilia outcrop are similar leaflets assigned also to *Palaeocarya* spp. vel *Myrica* (Sachse & Mohr 1996, pl. 3, figs. 12, 17-18, 26, pl. 5, figs. 2, 7-8) or *Engelhardia orsbergensis* (Sachse et al. 1999, text-figs. 1.12-1.13) matching well the Gavdos record.

Simaroubaceae
Ailanthus Desf.

Ailanthus pythii (Unger) Kovar-Eder & Kvaček
Fig. 6.1

1850 *Sapindus pythii* Unger, p. 457 (basionym)
2004 *Ailanthus pythii* (Unger). – Kovar-Eder & Kvaček in Kovar-Eder et al., p. 81, pl. 14, figs. 2-5.

Material: Incomplete basal part of a leaflet (GAVMT 572 right).

Description: Leaflet petiolulate, strongly asymmetrical, elliptic to ovate, base cuneate with 10 mm long petiolule, apex not preserved, margin in the lower part entire, higher up simply serrate, teeth acute, venation semicraspedodromous, midrib strong, curved, secondary veins thinner, curved, alternate, originating at 50° to 70°, tertiary veins percurrent straight to sinuous, venation of the higher orders regular poorly preserved.

Discussion: This morphotype is common in the early-middle Miocene flora of Parschlug but so far not recognized in the late Miocene floras. It is the first evidence of *Ailanthus* in the Mediterranean area assigned to foliage. Among the findings from the Makrilia outcrop a fruit of *Ailanthus* sp. vel Chenopodiaceae has been described (Sachse & Mohr 1996), which may relate to our record.

Myricaceae
Myrica L.

Myrica lignitum (Unger) Saporta
Figs. 6.2-6.4

1847 *Quercus lignitum* Unger, p. 113, pl. 31, figs. 5-7.
1865 *Myrica lignitum* (Unger) Saporta, p. 102.
1982 *Myrica lignitum* (Unger) Saporta. – Kovar, p. 80, pl. 12, figs. 1-8.
1999 *Myrica lignitum* (Unger) Saporta. – Sachse et al., p. 367, pl. 1, figs. 1.18, 1.24, 1.26, 1.29.
(For further synonymy see Kovar 1982)

Material: Incomplete leaves and fragments (GAVMT 323, GAVMT 361, GAVMT 375, GAVMT 408, GAVMT 422, GAVMT 450, GAVMT 454, GAVMT 642).

Description: Leaves simple, petiolate, mostly incomplete, lamina oblong to elliptic or slightly obovate, 23 to 75 mm long and 8 to 23 mm wide, base often asymmetrical cuneate, rarely with up to 7 mm long petiole, apex incomplete probably blunt, acuminate to obtuse, margin entire or coarsely simply serrate, teeth closely spaced, blunt, venation eucamptodromous, in toothed specimens semicraspedodromous, midrib strong, straight, secondary veins thinner, looping along margin, alternate, at angles of 30 to 60°, rare intersecondaries thinner and parallel, venation of the higher orders poorly preserved.

Fig. 6. 1. *Ailanthus pythii* (Unger) Kovar-Eder & Kvaček, strongly asymmetrical leaflet base, GAVMT 572 right, scale bar 10 mm; 2. *Myrica lignitum* (Unger) Saporta, leaf with dentate margin, GAVMT 642, scale bar 5 mm; 3. *Myrica lignitum* (Unger) Saporta, leaf with entire margin, GAVMT 323, scale bar 10 mm; 4. *Myrica lignitum* (Unger) Saporta, leaf with entire margin, GAVMT 619, scale bar 10 mm; 5. *Dicotylophyllum* sp. 1, leaf base with serrate margin, GAVMT 584, scale bar 5 mm; 6. *Dicotylophyllum* sp. 2, shortly petiolate incomplete leaf, GAVMT 648, scale bar 10 mm; 7. *Dicotylophyllum* sp. 2, shortly petiolate leaf, GAVMT 353, scale bar 10 mm; 8. *Dicotylophyllum* sp. 3, leaf or leaflet, GAVMT 452, scale bar 10 mm; 9. *Dicotylophyllum* sp. 4, incomplete leaf with brochidodromous venation, GAVMT 336, scale bar 10 mm; 10. *Dicotylophyllum* sp. 4, incomplete leaf, GAVMT 404, scale bar 10 mm; 11. *Dicotylophyllum* sp. 5, incomplete leaf, GAVMT 483, scale bar 10 mm; 12. *Dicotylophyllum* sp. 5, leaf, GAVMT 582, scale bar 10 mm; 13. *Dicotylophyllum* sp. 6, cuneate leaf base, GAVMT 396, scale bar 10 mm.

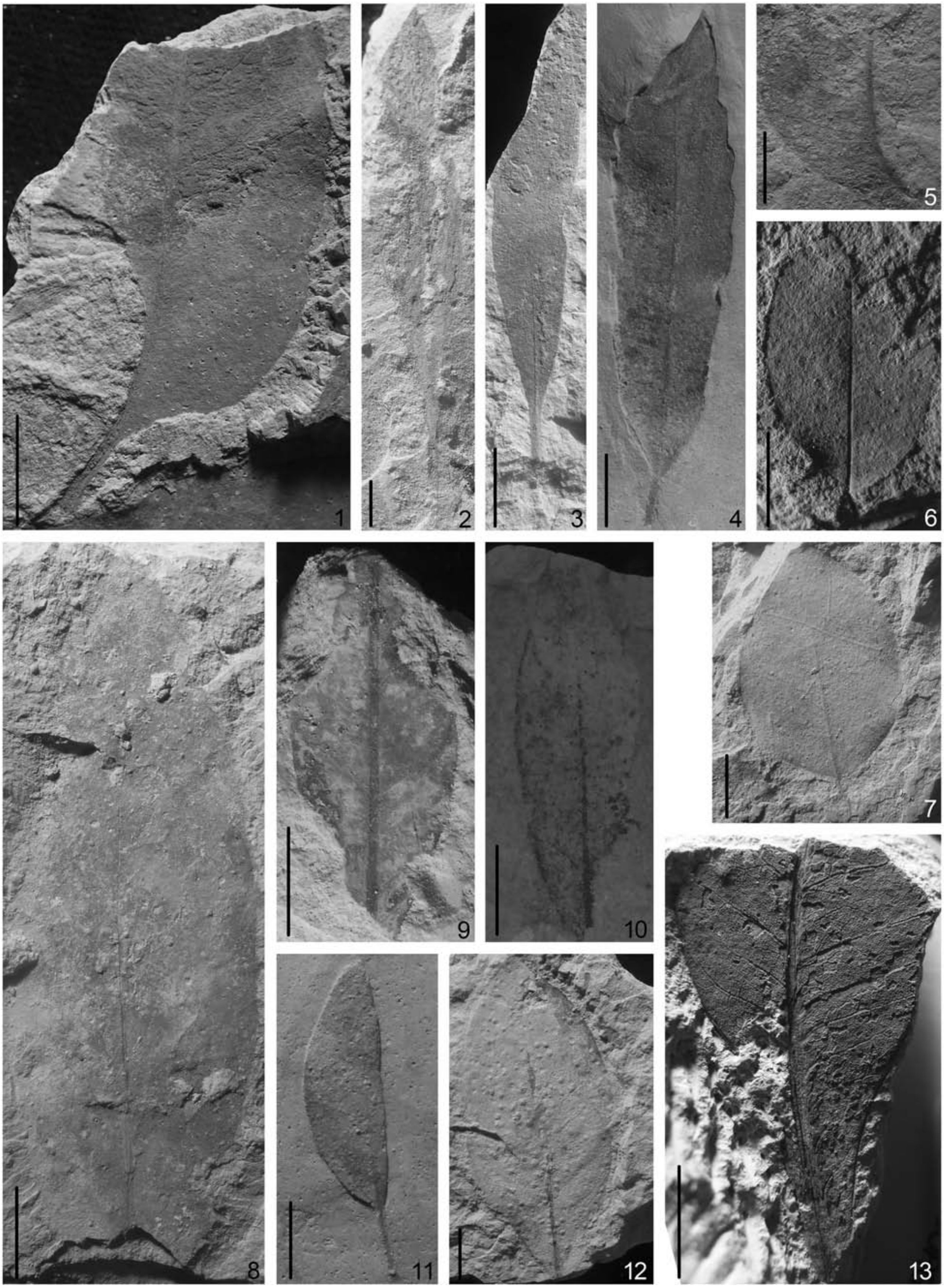

Fig. 6.

Discussion: According to Kovar-Eder et al. (2004), at least in the plant assemblage of Parschlug, *Myrica lignitum*, together with *Populus populina*, belongs either to azonal elements or, along with *Zelkova zelkovifolia*, may also represent an element of mesic forests. Zidianakis et al. (2010) commented widespread occurrence of *Myrica lignitum* stressing optimal conditions on acidic bogs for the Pitsidia locality. In these habitats, with low nutrient supply and ground water level lying near or above the earth surface, a dense population of *Myrica lignitum* apparently prevailed. Representatives of this fossil species have been published as ?*Salix varians* Göppert (Kolakovsky 1964, pl. 52, figs. 5-9) or *Quercus neriifolia* A. Braun (Kolakovsky 1964, pl. 30, figs. 2, 8-10) from the upper Miocene of Abchasia. Among the findings from the Makrilia outcrop are also leaves of *Myrica* type *lignitum* (Sachse & Mohr 1996; Sachse et al. 1999; Sachse 2004). *M. cerifera* is likely the nearest living relative species distributed on the eastern coast of E and SE North America.

Angiospermae incertae sedis

Dicotylophyllum sp. 1
Fig. 6.5

Material: Leaf fragment (GAVMT 584).

Description: Fragment of simple asymmetrical leaflet or leaf, probably elliptic to ovate, 20 mm long and 16 mm wide, base rounded, apex not preserved, margin simply serrate, venation semicraspedodromous, midrib strong, curved, secondary veins distinctly thinner, straight, alternate, originating at 50° to 80°, intersecondaries thin, parallel, tertiary veins percurrent straight to sinuous, venation of the higher orders regular polygonal reticulate, areolation well developed, 3 to 4 sided, veinlets lacking.

Discussion: This specimen is similar to the material assigned to *Pterocarya* from Vegora (Kvaček et al. 2002: 60, pl. 19, figs. 6-9) but is too incomplete to be reliably assigned to this genus. Foliage of this kind is unknown from the Makrilia outcrop (Sachse & Mohr 1996) or elsewhere in the Crete Island.

Dicotylophyllum sp. 2
Figs. 6.6-6.7

Material: Complete leaves/leaflets (GAVMT 353, GAVMT 648).

Description: Leaves or leaflets, elliptic to ovate, 38 and 45 mm long, 19 to 29 mm wide, base asymmetrical, widely cunate with petiolate/petiolulate, up to 2 mm long, apex rounded, margin entire, venation brochidodromous, midrib strong, straight, secondary veins thinner, looping, alternate, at angles of 70 to 85°, intersecondaries indistinct, thinner, parallel, venation of the higher orders are poorly preserved.

Discussion: The relationship of this type of foliage is fully uncertain.

Dicotylophyllum sp. 3
Fig. 6.8

Material: Incomplete leaf (GAVMT 452).

Description: Leaf simple, elliptic, 105 mm long and 40 mm wide, base incomplete, probably cuneate to rounded, apex acute, margin simply serrate, teeth regular, acute, venation semicraspedodromous, midrib strong, straight, secondary veins, thinner, alternate to subopposite, irregularly spaced, originating at angles of 30 to 45°, venation of the higher orders poorly preserved.

Discussion: The single specimen of this morphotype available is similar in venation and gross morphology to the material from Kodor assigned by Kolakovsky (1964) to several fossil taxa. Those assigned to *Ilex simile* Kolakovsky seems to match best our material (Kolakovsky 1964: 50, pl. 9, fig. 17, pl. 10, fig. 1), but some more come into question, such as *Ilex raridentata* Kolakovsky (Kolakovsky 1964, pl. 9, figs. 12-13). *Arbutus elegans* Kolakovsky (1964, pl. 22, figs. 9-10, pl. 13, figs. 1-5) or *Carya serraefolia* (Göpp.) Kräusel (Kolakovsky 1964, pl. 37, figs. 4-5) may also come into question. None of these generic affinities can be considered unequivocal without evidence of leaf epidermal anatomy.

Dicotylophyllum sp. 4
Figs. 6.9-6.10

Material: Incomplete simple leaf/leaflet and fragment (GAVMT 336, GAVMT 404 and counter-part GAVMT 463).

Description: Simple leaf (? or leaflet), elliptic, 43 and 58 mm long, 18 and 23 mm wide, base angle symmetrical, cuneate, apex round, margin entire, venation brochidodromous, midrib strong, straight, secondary veins, very thin, irregularly spaced, looping along margin, subopposite to alternate, at angles of 45 to 60°, intersecondaries parallel, thin, venation of the higher orders poorly preserved.

Discussion: In our opinion the generic affinity of this morphotype is equivocal and requires leaf anatomical evidence. Similar material was described from Kodor as *Cotoneaster palaeobacillaris* Kolakovsky (see Kolakovsky 1964, pl. 50, fig. 8), from Kymi as *Copaifera kymeana* Unger (D. Velitzelos in Kottis et al. 2002, pl. 15, fig. 41, as *Leguminosae* leaflets), and from the Miocene of Bulgaria (Palamarev et al. 2005) assigned to *Cotoneaster palaeobacillaris* Kolak. (Kolakovsky 1964, pl. 50, fig. 8), or ?*Persea* (Kolakovsky 1964, pl. 42, figs. 3, 5), ?*Nectandra euxina* Kolak. (Kolakovsky 1964, pl. 41, figs. 4-5) and *Quercus sosnowskyi* Kolak. forma *macrophylla* Kolak. (Kolakovsky 1964, pl. 34, fig. 4).

Dicotylophyllum sp. 5
Figs. 6.11-6.12

Material: Incomplete simple leaves (GAVMT 483, GAVMT 582).

Table 1. Results and predicted zonal vegetation types defined by IPR-vegetation analysis for the studied fossil sites from Greece (sensu Teodoridis et al. 2011a, table 8).

Localities	IPR-vegetation results											
	% of BLD	% of BLE	% of SCL + LEG	ZONPALM	% DRY HERB	% MESO HERB	% of zonal herbs of zonal taxa	Number of zonal taxa	Number of zonal woody angiosperms	Total number of taxa	Problematic taxa	Vegetation type sensu Teodoridis et al. (2011a)
Gavdos	75.51	22.45	2.04	0	0	0	0	26.5	24.5	30	0	BLDF/MMF
Makrilia	47.98	28.54	23.48	0	0	1.1	1.1	45	41	54	0	ShSF
Pitsidia	53.33	20	26.67	0	0	2.94	2.94	17	15	22	0	ShSF
Vrysses	40.14	25.85	34.01	0	0	0	0	26	24	31	0	ShSF

Description: Leaves simple, elliptic, 90 to 94 mm long, 24 to 45 mm wide, base cuneate with petiole up to 20 mm long, apex acute, margin entire, venation basal actinodromous, tri-veined, midrib strong, moderate, straight, lateral veins thinner, originating at 25° to 40°, higher secondaries brochidodromous, numerous, opposite originating also at 45 to 60°, intersecondaries thinner, parallel, tertiary veins opposite to alternate, percurrent, sinuous, venation of the higher orders poorly preserved.

Discussion: These two specimens are similar to entire-margined forms of *Populus mutabilis* Heer (1856: 19, pls. 60-62, pl. 63, figs. 1-4) from Öhningen in South Germany, particularly in the long petiole and slightly developed basal veins. The material from Kodor assigned to *Hedera* sp. cf. *H. colchica* C. Koch by Kolakovsky (1964: 54, pl. 12, figs. 3-4) is also quite similar but we doubt that it represents leaves of real *Hedera*. Contrary to our material, the Kodor morphotypes differ in much steeper secondaries. Regularly disposed dense secondaries seen in our material match, besides *Populus mutabilis*, also the venation of some Rhamnaceae, namely *Berchemia* (e.g., *B. multinervis* as illustrated in Bůžek 1971, pl. 32, figs.12-15, pl. 33, figs. 22-23), which differs in almost sessile leaves.

Dicotylophyllum sp. 6
Fig. 6.13

Material: Leaf fragment (GAVMT 396).

Description: Leaf base 40 mm long, 23 mm wide, decurrent, texture coriaceous as shown by thick lamina, margin entire, venation eucamptodromous, midrib strong, curved, secondary veins regularly spaced, at angles of 50 to 60°, single intersecondaries thin, parallel with secondaries, venation of the higher orders reticulate.

Discussion: This incomplete leaf base is not determinable without epidermal characters. A similar morphotype was described from the Makrilia flora as cf. Myrtaceae gen. sp. (Sachse et al. 1999, text-fig. 2.32; Sachse 2004, pl. 13, fig. 13). Such leaf fossils have also been compared with foliage of *Periploca* (e.g., Kolakovsky 1964: 124).

5. Comparison with related fossil floras in Europe

The Gavdos flora belongs, within the European Cenozoic system of floras composed by Mai (1995) to the Mediterranean – Tethys Bioprovince and is best included in the late Miocene floristic assemblages of Likudi – Vegora or Senigallia. This type of floras is characterized by a number of deciduous arboreal plants, particularly by *Fagus gussonii*, intermixed with still persisting subtropical evergreen elements. In Greece, most diversified assemblages of this type are those of Likudi and Vegora, Macedonia. Unlike the flora of Likudi composed of mostly deciduous mesic elements and lacking sclerophyllous Fagaceae (Knobloch & Velitzelos 1986), the Vegora flora (Kvaček et al. 2002) shows several features in common with Gavdos in the spectrum of deciduous taxa, in particular *Fagus gussonii*, the scarcity of laurophyllous evergreen component (only rare foliage of *Daphnogene* and *Laurophyllum*) but differs in much more common sclerophyllous angiosperms (*Quercus sosnowskyii*, *Q. mediterranea – drymeja* complex) and in absence of *Engelhardia*. It is more diversified and, partly due to long-lasting collections, richer in representation of various families, e.g. Fagaceae (in particular *Quercus*). Similarly analogous floras of this kind occur in the Caucasus area of the Paratethys Bioprovince, namely the late Miocene flora of Kodor (Kolakovsky 1964). The most similar flora, also close in the geographical position and age, is that of Makrilia, Crete (Meulenkamp et al. 1979; Mohr et al. 1991; Sachse & Mohr 1996; Sachse 1997, 2004; Sachse et al. 1999; Kovar-Eder et al. 2006) of late Tortonian age (8.6-7.7 Ma) sharing not only physiognomic aspects but also several important elements. A noteworthy combination of common occurrence of *Taxodium, Pinus* with double needled fascicles, *Tetraclinis salicornioides*, *Fagus gussonii*, *Engelhardia orsbergensis* and several further, partly enigmatic morphotypes stresses close floristic affinity of both assemblages. Less straightforward similarities are found also in the newly described localities of fossil plants from Crete, such as Vrysses (Zidianakis 2002; Zidianakis et al. 2004, 2007) of latest Tortonian – early Messinian age (ca. 7.5-6.0 Ma), and Pitsidia, Messara Basin (Zidianakis et al. 2010) of early Tortonian age (10.5 Ma). The comparison with the Vrysses flora may suggest a closer floristic relationship, although some noteworthy plants, e.g. *Buxus* and *Acer pseudomonspessulanum*, have not been recovered at Gavdos. Due to environmental bias the recently reported Pitsidia flora shows the least common features, being dominated mainly by azonal, partly mesic deciduous elements (*Pinus* with fascicles of three, *Myrica lignitum*, *Quercus roburoides*, *Liquidambar europaea,* etc).

6. Palaeoenvironmental analysis

6.1. Phytosociological approach

The fossil plant site of Gavdos has yielded 30 taxa of higher plants: 3 conifers, 27 angiosperms and one taxon of uncertain systematic affinity. Generally, the vegetation of Gavdos is characterized by a relatively frequent occurrence of zonal elements. It is possible to distinguish three relatively specific plant assemblages based on the phytosociological approach. The plant assemblages differ in their composition (depending on specific ecological conditions of biotopes). The first plant assemblage is a mixed-swamp forest, which is typical of elements preferring an environment with relatively low dynamic (stagnant water table or periodical, relatively long-lasting floods). This vegetation type is usually typical of the marginal zone of basins or oxbow lakes in the fluvial system. These plant elements do not occur frequently in Gavdos. This vegetation type contains mainly *Taxodium dubium* (E4), *Myrica lignitum* (E2), and possibly Monocotyledonae fam. et gen. indet. (E1). The next assemblage includes plants, which permanently occupy waterlogged (wet soil) substrate. It represents a riparian assemblage containing *Ulmus plurinervia* (E2-3), *Populus populina* (E3), ?*Sassafras* sp. (E2), *Salix* cf. *angusta* (E2) and Monocotyledonae fam. et gen. indet. (E1). The most diversified plant assemblage that occupied upland areas is a zonal mesophytic to sclerophyllous vegetation characterized by the co- occurrence of the following elements: *Pinus* sp. (E3), *Tetraclinis salicornoides* (E2), *Acer angustilobum* (E2-E3), *Ailanthus pythii* (E4), *Betula* sp. (E2-3), ?*Carpinus* sp. (E2-3), ?*Lindera ovata* (E3), *Laurophyllum* sp. (E3), *Daphnogene* sp. (E3), *Fagus gussonii* (E3), *Paliurus tiliifolius* (E2), *Leguminocarpon* spp./*Leguminosites* spp. (E2-E3), *Sapindus graecus* (E2-3), and *Engelhardia orsbergensis* (E3-4). Some of the elements are difficult to interpret because of dubious taxonomic affinities (*Dicotylophyllum* spp.).

6.2. IPR-vegetation analysis

The fossil plant assemblage of Gavdos was studied using the IPR-vegetation analysis (Kovar-Eder et al. 2008; Teodoridis et al. 2011a) including the following characteristic key components: broad-leaved deciduous (BLD) – 75.5%, broad-leaved evergreen (BLE) – 22.5%, sclerophyllous + legume-like (SCL+LEG) – 2.04%, dry herbaceous + mesophytic herbaceous / zonal herbaceous/ (D-HERB + M-HERB /ZONAL HERB/) – 0% (for a detailed taxa scoring see Table 1). According to the thresholds for the key components for defining vegetation types as detailed above (modified by Teodoridis et al. 2011a, table 8); the plant assemblage of Gavdos belongs to transitional vegetation (ecotone) between broad-leaved deciduous forest (BLDF) and mixed mesophytic forest (MMF). The results obtained for Gavdos can be negatively influenced by very poor preservation of the plant material, which in some cases does not permit a clear scoring into the categories of components. The IPR results obtained for the other studied Tortonian floras from Greece, namely Makrilia (Sachse & Mohr 1996; Sachse et al. 1999; Sachse 2004), Pitsidia (Zidianakis et al. 2010) and Vrysses (Zidianakis et al. 2007) are presented in Table 1. There are largely dependent on the quality of taxa determination bearing some uncertainties. Generally, the plant assemblages show values of the BLD component between 40 to 53%, the BLE component less than 30% and relatively high values of SCL+LEG components, exceeding 20% (Table 1). This combination of the components allows for assigning these plant assemblages to the zonal subtropical, subhumid sclerophyllous or microphyllous forest (ShSF) vegetation type sensu Kovar-Eder et al. (2008). Kovar-Eder et al. (2006, 2008) published results of IPR-vegetation analysis based on the plant material described by Sachse et al. (1999) as follows: BLD (23%), BLE (15%), SCL+LEG (63%) suggesting the same vegetation type of ShSF. The marked difference between the values of

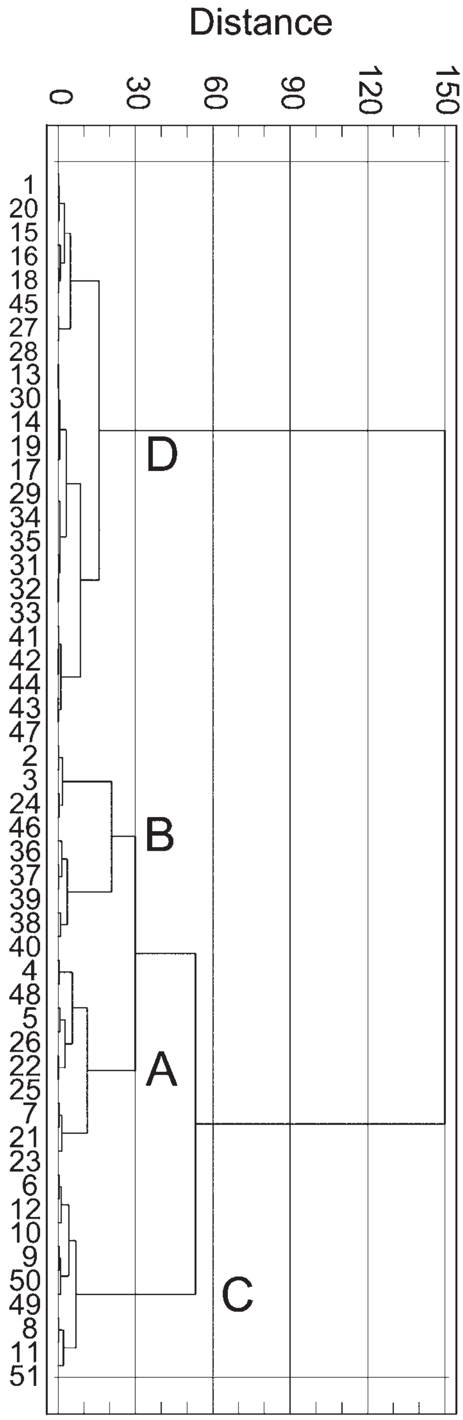

Fig. 7. Dendrogram (Ward's method, squared Euclidean distance) showing relation of the studied fossil floras from Greece to the modern tropical, subtropical and temperate vegetation types from China and Japan (sensu Teodoridis et al. 2011a, 2012) grouped into one cluster. Four subclusters (A to D) are distinguished. Numbers 1 to 47 represented the modern vegetation sensu Teodoridis et al. (2012), 48. Gavdos, 49. Makrilia, 50. Pitsidia, and 51. Vrysses.

the SCL+LEG components (see Table 1) is probably due to the poor preservation of the plant material there (Kovar-Eder et al. 2006). Kovar-Eder et al. (2008) evaluated another Greek flora of Vegora, which also corresponds to the ShSF vegetation type (BLD 56%, BLE 15%, SCL+LEG 26%). According to Sami & Teodoridis (2013), this assignment of Vegora to ShSF is very tentative, due to the lack of herbaceous elements in general (see above), which are very frequent in the modern Mediterranean floras or their equivalents in China and California (Ou et al. 2006; Tang 2006; Teodoridis et al. 2011a). To obtain an estimate of the diversity of herbaceous elements of the Vegora flora coeval pollen spectra would be needed.

Results of the cluster analysis (Ward's method, Euclidean square) comparing the studied Tortonian floras of Greece with 47 modern vegetation units from subtropical and tropical zones of China and Japan sensu Teodoridis et al. (2011a, 2012) are shown in Fig. 7. Focusing on a subcluster "A" in the dendrogram (Fig. 7), the flora of Gavdos (48) shows the closest affinity to broad-leaved deciduous vegetation of Mt. Emei in Sichuan, China (4) sensu Tang & Ohsawa (1997), moreover close relations to broad-leaved deciduous forests from the Meili Snow Mt. in Yunnan (5, 7), Mt. Fuji (25, 26) and Shirakami Sanchi area (21-23) in Japan. The vegetation units of the subcluster "A" show affinity to a subcluster "B", which group vegetation units of mixed mesophytic forests (MMF) from the Emei Mt. (2, 3), the Yakushima Island in Japan (*Eurya-Cryptomeria japonica* assoc. marked 36-40), a specific broad-leaved evergreen forest (BLEF – *Camellia japonica* region) from Mt. Fuji in Japan (24) and the monsoon forest in Xishuangbanna from the tropical zone of China (46). This close affinity of the subclusters A and B and plant assemblage of Gavdos corresponds to the transitional (ecotone) character of vegetation type determined by IPR vegetation analysis in Gavdos. The studied fossil plant assemblages of Makrilia, Pitsidia and Vrysses characterized with relatively high values of the SCL+LEG components are presented in a subcluster "C". The subcluster shows the closest affinity of Makrilia (49) and Pitsidia (50) and living ShSF vegetation (9) characterized by *Quercus aquifolioides* comm., *Q. aquifolioides* and *Pinus armandii* subcom. from the Meili Snow Mt. (Yunnan, China) sensu Ou et al. (2006). This group is closely associated with another ShSF vegetation unit (10) and summarized vegetation data of ShSF (12) from the Meili Snow Mt. and BLDF vegetation unit from the Meili Snow Mt. (6). Similarly, the studied plant assemblage of Vrysses (51) is clustered with other plant communities of ShSF from the Meili Snow Mt. i.e., 11 (*Quercus aquifolioides* comm., *Q. aquifolioides* and *Populus davidiana* subcomm.) and 8 (*Quercus guyavifolia* comm.). Other living plant assemblages of broad-leaved evergreen forests (BLEF) from China and Japan and tropical vegetation from China create an isolated subcluster D, which has no close relation to the studied fossil plant assemblage of Gavdos, Makrilia, Pitsidia and Vrysses. We have to stress that the living analogues derived from the cluster analysis may correspond to the fossil assemblages physiognomically (similar composition of the BLD, BLE, SCL+LEG components), but may not correspond to the climate conditions (e.g., areas of the Mt. Emei belonging to Cwa, and the Meili Snow Mt. to Cwb and/or Cwb>Dw climate conditions of the Köppen-Geiger system (e.g., Peel et al. 2007).

The studied floras from Greece belong to the High Resolution Interval 2 (HRI 2: 8.5-12 Ma) sensu Kovar-Eder et al. (2008), which includes about 60 sites evaluated by IPR vegetation analysis (Kovar-Eder et al. 2008, Supplementary Data) and the European vegetation scheme are characterized during this time as follows: Broad-leaved evergreen (BLEF) and Mixed Mesophytic forests (MMF) are mostly confined to the more southern European regions and the northern parts of the Balkan Peninsula. Records from the southern parts of Europe bear higher proportions of the SCL + LEG component than those recorded from more northerly regions, such as the Lower Rhine Embayment and the Polish Lowland. Broad-leaved deciduous forests (BLDF) were widely distributed in the Molasse basin north of the Alps and the Pannonian basin, while subhumid sclerophyllous forests (ShSF) were rather scarce and largely restricted to the southern parts of Europe. The first record of xeric grasslands is available from the northern margin of the Black Sea (Kovar-Eder et al. 2008: 108). The presented high values of SCL+LEG components at the studied sites from Greece correspond and prove the mentioned high abundance of SCL+LEG elements as well as ShSF vegetation in the southeast Mediterranean, Balkan Peninsula and the Black Sea regions.

Moreover, a study on early Tortonian vegetation in Western Eurasia based on quantitative interpretation of the diversity of arboreal functional types (PFTs), carried out earlier, revealed an overall comparable pattern. There, mixed mesophytic forests of the “M3 type” (high diversity of broadleaved evergreen trees, partly sclerophyllous, with broadleaved deciduous

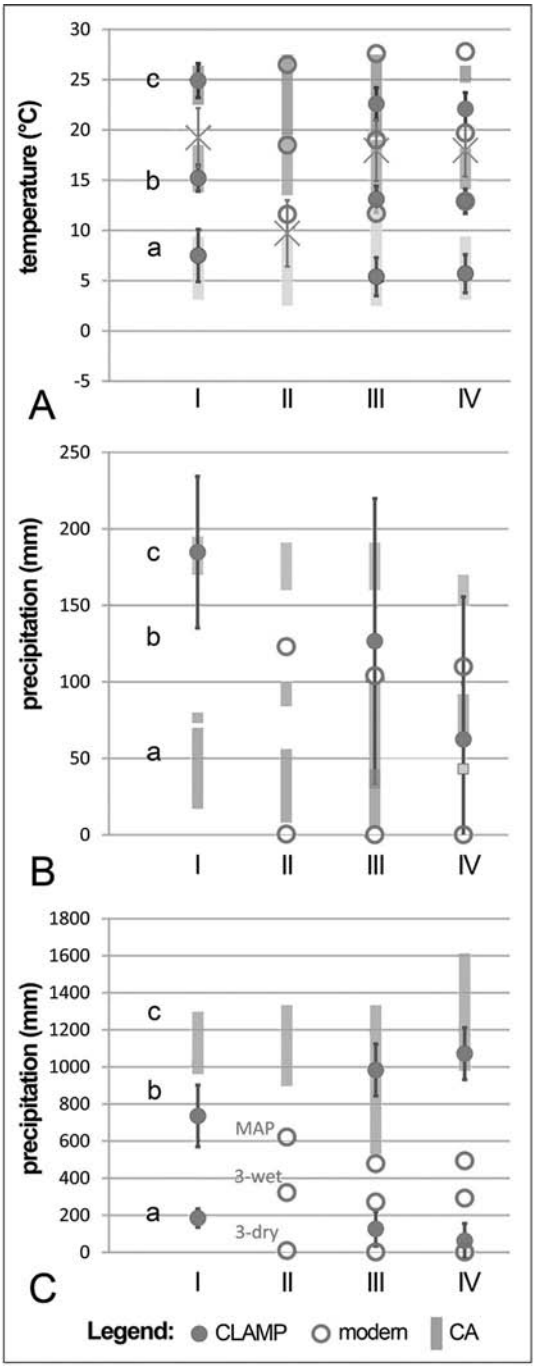

Fig. 8. Palaeoclimatic estimates for the studied floras from Greece and comparable meteorological datasets from the Crete Island. A. Temperatures with data for CMMT (a), MAT (b), and WMMT (c), LMA_3 data (X) sensu Traiser et al. (2005); B. Precipitation with data for MPdry (a), MPwarm (b) and MPwet (c). Modern MPwarm and MPdry are all close to 0 mm. CLAMP data refer to 3-DRY parameter; C. CLAMP data for 3-DRY (a) and 3-WET (b), CA data refer to MAP (c); Floras/sites: I. Gavdos, II. Pitsidia, III. Vrysses, IV. Makrilia (DATA source in Table 2).

Table 2. Palaeoclimate estimates from Leaf Margin Analysis (LMA), Climate Leaf Analysis Multivariate Program (CLAMP) and Coexistence Approach (CA) for the studied floras from Greece and comparable meteorological datasets from the Crete Island (Peel et al. 2007). Symbols: SE (sampling error), *n* (total species number), P (proportion of *n* species with entire margin, 0 < P < 1), MAT (mean annual temperature), WMMT (warmest month mean temperature), CMMT (coldest month mean temperature), 3-WET (precipitation during 3 consecutive wettest months), 3-DRY (precipitation during 3 consecutive driest months), MAP (mean annual precipitation), MPwet (wettest month precipitation), MPdry (driest month precipitation), MPwarm (warmest month precipitation) and STDEV Residuals (standard deviations). The source of climatic parameters from the meteorological stations from the Crete Island is derived from the websites of Emerica (http://emeric.ims.forth.gr)* and the Hellenic National Meteorological Institute (http://www.hnms.gr)**. For more details on the CA data see Appendix 2.

	Sites/floras	Palaeoclimatic method		Gavdos	Pitsidia	Vrysses	Makrilia		Chania Souda, close Vrysses (24°7'0" E, 35°29'0" N, 150 m alt.) – based on datasets from 1958 to 1997**	Tympaki, close Pitsidia (24°46'0" E, 35°4'0" N; 6 m alt.) – based on datasets from 1959 to 1997**	Ierapetra, close Makrilia (25°44'0" E; 35°0'0" N, 10 m alt.) – based on datasets from 1956 to 1997**
							Macroplant record	Bruch et al. (2006)			
Paleoclimatic estimates	MAT [°C]	LMA 1 (SE) sensu Wolfe (1979)		19.65	10.41	18.41	18.41	-	18.5	19	19.7
		LMA 2 (SE) sensu Su et al. (2010)		17.79	9.16	16.37	16.37	-			
		LMA 3 (SE) sensu Traiser et al. (2005)		19.23	9.75	17.96	17.96	-			
		SE sensu Miller et al. (2006)		2.94	3.3	3.04	2.61	-			
		n; P		26; 0.59615	17; 0.29411	27; 0.55556	43; 0.51163	-			
		CLAMP (STDEV Residuals)		15.2 (1.3)	-	13.1 (1.2)	12.9 (1.2)	-			
		CA	min. value	13.8	13.5	13.5	14.1	15.6			
			max. value	18.5	19.7	19	18.2	18			
	WMMT [°C]	CLAMP (STDEV Residuals)		24.9 (1.7)	-	22.6 (1.6)	22.1 (1.6)	-	26.5 (July)	27.6 (July)	27.8 (July)
		CA	min. value	22.5	19.6	19.3	24.7	25.6			
			max. value	26.4	27.5	27.5	26.4	27.5			
	CMMT [°C]	CLAMP (STDEV Residuals)		7.5 (2.6)	-	5.4 (1.9)	5.7 (1.9)	-	11.6 (January)	11.7 (January)	12.9 (January)
		CA	min. value	3.1	2.5	2.5	3.1	7.1			
			max. value	9.4	9.4	12.2	9.4	10.2			
	3-WET [mm]	CLAMP (STDEV Residuals)		735.8 (166.2)	-	983.9 (140.3)	1072.0 (140.3)	-	-	-	-
	3-DRY [mm]	CLAMP (STDEV Residuals)		184.8 (49.6)	-	126.6 (93.2)	62.4 (93.2)	-	-	-	-
	MAP [mm]	CA	min. value	843	897	828	961	979	622	479	494
			max. value	1741	1333	1333	1298	998			
	MPwet [mm]	CA	min. value	170	160	160	150	-	123 (January, February)	104 (December)	110 (December, January)
			max. value	195	191	191	170	-			
	MPdry [mm]	CA	min. value	17	8	4	43	-	0.5 (July)	0.1 (July)	0.1 (July)
			max. value	70	56	43	43	-			
	MPwarm [mm]	CA	min. value	73	84	30	60	-	0.5 (July)	0.1 (July)	0.1 (July)
			max. value	80	100	100	92	-			

trees being the most dominant PFT, and needle-leaved PFTs present) have been described as characteristic vegetation type of the mid- and lower latitudes of the Eastern Paratethys, Black Sea coastal area, and the Eastern Mediterranean realm (Utescher et al. 2007). The characterization given there for the M3 type coincides well with the characterization of the zonal vegetation of Gavdos obtained when applying the phytosociological approach (see above).

6.3. Palaeoclimate signals

The plant assemblages from Gavdos, Vrysses, Pitsidia and Makrilia were evaluated using a combination of physiognomic (LMA, CLAMP) and taxonomic techniques (CA), based on Nearest Living Relatives. The palaeoclimate data derived from the Gavdos flora, using LMA, CLAMP and CA techniques (Table 2, Fig. 8A-C), are summarized as follows: MAT 13.8-~20 °C, WMMT 22.5-26.4 °C, CMMT 3.1-9. °C, MAP 843-1741 mm, MPwet 170-195 mm, MPdry 17-70 mm. MPwarm 73-80 mm, 3-WET 735.8 mm (only CLAMP) and 3-DRY 184.8 mm (only CLAMP). The MAP and MPwarm parameters of Gavdos show relatively high values, which is in accordance with the overall mesophytic character of the vegetation (the BLDF/MMF vegetation type from IPR-vegetation analysis – see Table 1), with the lowest abundance of the SCL+LEG component (only 2%) among the studied sites of Crete. The climatic analysis of the Gavdos flora reveals a reasonable degree in overlapping of the results obtained by different approaches when considering the standard errors (Table 2). Regarding the temperature reconstructions, the LMA data (1-3) for MAT all plot in the warmer half of the related coexistence interval while the CLAMP values are all closer to the lower temperature limits the CA suggests, or even below (MAT and WMT reconstructions for the Makrilia flora) (Fig. 8A). Regarding precipitation CLAMP and CA reconstruct different variables and consequently a direct comparison of the data is not possible. However, both methods suggest the absence of a dry summer (MPwarm > 30 mm) but indicate the presence of a well expressed seasonality of precipitation (3-DRY ~180 mm; 3-WET ~740 mm; MPdry < 70 mm; MPwet > 150 mm). While CLAMP and CA provide similar estimates for rainfall in the dry season, the CLAMP estimate for 3-WET suggests a considerably higher MAP compared to the CA (MAP>828 mm) when extrapolating the data.

The comparison of climate data obtained for the Greek sites considered here reveals no significant differences in temperature based on the CA data while the results for the diverse Makrilia flora provide narrower climatic intervals and suggest a WMMT of ca. 25 °C as probable value. LMA data for MAT are again near the warmer ends of the CA intervals except for Pitsidia where only 10 °C are estimated (LMA 1-3). These values are considered less accurate, due to a relatively low number of woody dicots in the palaeoflora (17). CLAMP derived temperatures all tend to be lower but overlap or touch the CA range, except for WMMT of the Makrilia flora where the CLAMP estimate is cooler by at least 1 °C. According to CLAMP, Gavdos tends to be slightly warmer compared to Vrysses and Makrilia. Slightly different temperature values published by Bruch et al. (2006) refer to a differing, unrevised flora list (Sachse 1997; Sachse & Mohr 1996), the exclusion of *Tetraclinis* in the present study (cf. Appendix 4; excluded as relict), and updates in the climate database PALAEOFLORA.

Monthly precipitation rates obtained for the sites based on the CA show no significant difference, except for MPwet of Makrilia tending to be slightly lower compared to Gavdos. For Pitsidia and Vrysses, the CA derived MPdry is compatible with the existence of seasonal drought, but not in the warm season (MPwarm >~150 mm). This coincides with the aforementioned higher diversity of the SCL+LEG components and predicted ShSF vegetation type based on the IPR vegetation analysis (Table 1). According to the CA, MAP was generally high (>~800 mm), while CLAMP data point to even wetter conditions (3-WET >~600 mm). According to CLAMP, Gavdos had a significantly lower seasonality in precipitation compared to the floras on the mainland. Regarding the CA analysis of the Makrilia flora, the most diverse among the floras considered, no 100 %-overlapping of taxa ranges is obtained for some of the reconstructed climate variables. *Pistacia lentiscus* points to lower MPwarm compared to the majority of taxa. A possible explanation of this blurring would be mixture of floristic components from different stratigraphic levels and thus differing position in a climate cycle.

In the context of Tortonian climate patterns of western Eurasia, the sites considered here are of specific importance because they provide insight into the conditions of the lower latitudes from which only few data are currently available. In the context of published Tortonian temperature data (Bruch et al. 2006; data compiled in Table 3) our results confirm the shallow latitudinal gradient, also expressed in the Tortonian

Table 3. Palaeoclimate data for selected floras from the European late Miocene (Tortonian ~ Pannonian) calculated by Coexistence Approach (CA). Symbols: MAT (mean annual temperature), WMMT (mean temperature of the warmest month), CMMT (mean temperature of the coldest month), and MAP (mean annual precipitation).

Country	Site	MAT min [°C]	MAT max [°C]	WMMT min [°C]	WMMT max [°C]	CMMT min [°C]	CMMT max [°C]	MAP min [mm]	MAP max [mm]	References
Germany	Aubenham	14.1	14.5	23.8	24.3	0.1	4.1	1231	1237	Bruch et al. (2006)
	Frechen	14	15.5	25.7	26.8	0.6	4.5	1231	1337	
	Hambach	14.4	15.8	25.6	25.9	4.7	7.9	1231	1250	
	Klettwitz 12	15.7	16.3	25.7	25.7	4.7	6.2	979	1355	Mosbrugger et al. (2005)
	Leonberg	14.4	17.6	23	24.9	2.9	7.6	735	1475	Bruch et al. (2006)
	Massenhausen	13.3	13.8	25.6	26.4	0	4,1	-	-	Bruch et al. (2004)
Austria	Grossenreith	13.6	15.8	25.7	27,00	0.6	4.1	867	971	Bruch et al. (2006)
	Laaerberg	13.3	15.7	25.6	26.4	-0.5	5.1	897	1187	
	Lohnsburg	13.3	15.8	25.7	26.4	0.6	4.1	897	971	
	Neuhaus	15.6	15.8	25.3	26.4	0.6	5.8	1231	1355	
	Wien E-F	15.7	16.5	23.8	27.4	2.9	6.4	1231	1355	
	Wörth	13.3	17.3	25.7	26.7	-0.7	7	-	-	Bruch et al. (2004)
Hungary	Bukkabrany	14.4	16.6	25.6	28.2	2.9	5.8	897	1355	Bruch et al. (2006)
	Hidas	11.6	18.4	25.6	26.8	6.2	7	1187	1298	
	Sé	12.5	15.7	21.6	26.7	-0.1	5.1	-	-	Bruch et al. (2004)
	Visonta	13.4	15.7	25.6	25.6	0	5.1	897	1206	Bruch et al. (2006)
Serbia	Dubona	14.4	15.4	26.5	26.7	3.7	4.8	1122	1237	
	Durinci	15.6	16.5	25.7	26.4	1.8	4.8	1003	1237	
Greece	Triopetra	15.6	18.4	24.7	27.8	5	9.4	735	759	
	Vegora	13.3	14.6	23.8	24.6	0.4	4.5	897	1018	
Romania	Delureni	15.6	18.1	26.5	27.9	5		1122	1356	
	Oas Basin	14.1	15.5	25.7	26.4	0.1	7	867	1356	
Turkey	Elazig Area	15.6	21.3	24.7	28.1	5	13.3	823	1574	Akgün et al. (2007)
	Sivas Basin	16.5	20.8	27.3	28.1	-0.1	13.3	887	1520	

temperature anomalies with respect to present (Utescher et al. 2011) where data based on sites from the higher latitudes show a temperature anomaly while values of the lower latitude sites of western Eurasia plot at the present-day level. The overall high rates of annual precipitation and rainfall in the warm season resulting for the floras support reconstructions by Bruch et al. (2011) and Quan et al. (2014) reporting humid summers for most sites of the Eastern Mediterranean realm, findings that clearly stand against the existence of a Mediterranean type climate at that time. Moreover, our data reveal overall consistency of data based on CA and leaf physiognomy. A similarly good agreement between CLAMP and CA in climate reconstructions for the Neogene has previously been reported from lower latitude sites in SE China (e.g., Sun et al. 2011) while estimates for sites of the middle to higher latitudes from both methods may deviate (cf. Uhl et al. 2003, 2006, 2007a, b). Especially in warmer time-spans of the Neogene both approaches reveal the same trends but partly have differing absolute levels (Mosbrugger & Utescher 1997).

The aforementioned European vegetation scheme for HRI 2 (8.5-12 Ma) sensu Kovar-Eder et al. (2006, 2008) broadly coincides with the reconstructed palaeoclimatic pattern of this time period (Table 3). The western realm of the Paratethys, i.e., the Molasse Basin north of the Alps, and the Pannonian Basin was occupied by broad-leaved deciduous forests (BLDF). This vegetation type is indicative for temperate and humid climate conditions (Table 3). Towards the southern region of Europe (e.g., Serbia, Romania, Greece and Turkey) (Akgün et al. 2007) vegetation changed to more evergreen and sclerophyllous types, which were linked to warmer climates expressed by higher values of MAT, WMMT and CMMT parameters (and well comparable to our studied sites – see Tables 2 and 3, Bruch et al. 2006, figs. 2-6). On the other hand, the values of MAP are more or less balanced during the HRI 2 interval in Europe, which rules out a significant climate aridization in this area (Bruch et al. 2006, fig. 6; Table 3; Bruch et al. 2011). Therefore, the slightly lower values in the precipitation of the studied Greek plant assemblages and their sclerophyllous characters as well (Tables 1-2) probably reflect specific microclimatic condition rather than a regional climatic pattern.

The leaves of beech belong to dominant and reliably established elements of the Gavdos assemblage. The stenoecious nature of *Fagus* (Denk & Grimm 2009; Velitzelos et al. 2014), requiring fully humid, Cf to Df Koeppen type climate, would suggest that this taxon thrived at higher elevations in Gavdos and not in Crete and therefore might indicate a higher elevation of the site in Gads and/or remarkably humid climatic conditions.

Present-day climate data for the studied sites are given in Table 2 and are plotted together with the reconstructed palaeoclimate data (Fig. 8A-C). It is shown that modern temperature (data are available from stations nearby Pitsidia, Vrysses and Makrilia) all are at the warm end of the CA coexistence intervals and thus close to the results obtained from LMA, or even slightly above, and significantly warmer (in the order of 7 °C) than the values obtained using CLAMP. Thus it can be concluded that the elsewhere very pointed late Neogene cooling (e.g., Mosbrugger et al. 2005) hardly affected the SE Mediterranean realm. A comparable situation is reported from the lower latitudes of SE China where late Neogene Cooling was also minor but there, the interpretation is not straight forward because of tectonic uplift (Yao et al. 2011; Xing et al. 2012).

The modern precipitation parameters measured at stations on Crete islands (Table 2; Fig. 8B, C) correspond to the Dry-Summer Subtropical or Mediterranean climates (Csa/Csb) of the Köppen-Geiger system, with annual precipitation rates from ca. 500-600 mm (e.g., Peel et al. 2007, see Table 2). However, the Tortonian paleoclimatic datasets from Gavdos and Crete represent a humid subtropical climate without dry season during the warmest period (Cfa). This is evident from MPwarm data (CA) accounting for more than 50 mm for all sites studied (modern MPwarm at all stations: ~0 mm). Apart from the interpretation of MPwarm, key variable to identify Cs climates, MAP estimates from all applied methods suggest higher than modern annual rainfall (~800-1,200 mm). At present, the Cfa climate type is restricted to relatively small regions of Europe, e.g., the NE interior of the Iberian Peninsula, the Toulouse region in France, the Adriatic realm (coastal areas of Italy, Slovenia, and Croatia, Macedonia, Central Serbia) and the Black Sea coastal area (Bulgaria, Romania, Sochi-Russia) (Peel et al. 2007).

7. Conclusions

The newly recovered late Miocene flora of Gavdos in the southernmost Europe is closely related to the adjacent sites in Crete of approximately the same age. Gavdos has more floristic affinities with coeval floras of the eastern part of the Mediterranean compared to sites in the Southwest of the European continent. It can be assumed that palaeogeographical settings (Popov et al. 2004, Map 8. Mid-late Miocene) rather than climatic oscillations affected the floristic differentiation in the area of SE Europe at about 8 Ma.

The present climate reconstruction reveals agreement of CLAMP and CA to a large extent. Climate data reconstructed for the Gavdos flora and the other Greek localities show no signs of distinct aridization of climate and changes towards a summer-dry (“etesian”) regime. However, the possibility should be considered that the plant records in each case may represent the humid part of the Tortonian climate cycles. Tortonian temperatures estimated from a total of four megafloras of Southern Greece were about at the present-day level or even slightly below. This indicates that the global temperature decline during the late Neogene affected the study area much less, compared to the middle to higher latitudinal regions of Western Eurasia. In the context of the European data array our results show that the south-north climatic gradient across Europe was obviously much reduced compared to today.

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Addresses of the authors:

Dimitra Mantzouka, Nicolaos Tsaparas, Vasileios Karakitsios, National and Kapodistrian University of Athens, Faculty of Geology and Geoenvironment, Department of Historical Geology and Palaeontology, Greece;
e-mails: dmantzouka@geol.uoa.gr, ntsapar@geol.uoa.gr, vkarak@geol.uoa.gr,

Zlatko Kvaček, Charles University in Prague, Faculty of Science, Institute of Geology and Palaeontology, Albertov 6, 12843, Prague 2, Czech Republic,
e-mail: kvacek@natur.cuni.cz,

Vasilis Teodoridis, Charles University in Prague, Department of Biology and Environmental Studies, Faculty of Education, Magdalény Rettigové 4, 116 39 Prague 1, Czech Republic,
e-mail: vasilis.teodoridis@pedf.cuni.cz

Torsten Utescher, Senckenberg Research Institute, Frankfurt am Main; Steinmann Institute, University of Bonn, Nussallee 8, 53115 Bonn, Germany,
e-mail: utescher@geo.uni-bonn.de

Appendices

Appendix 1. Percentages of foliar physiognomic characters of the studied floras.

Foliar physiognomic characters [%]		Gavdos	Vrysses	Makrilia
Margin character states	Lobed	7.69	11.11	8.57
	No teeth	59.62	55.56	61.43
	Teeth regular	21.15	33.33	27.14
	Teeth close	18.27	22.22	6.43
	Teeth round	20.19	12.96	7.14
	Teeth acute	23.08	31.48	29.29
	Teeth compound	7.69	0.00	5.71
Size character states	Nanophyll	0.00	0.00	0.00
	Leptophyll I	0.00	0.00	1.43
	Leptophyll II	0.00	0.00	5.71
	Microphyll I	0.00	20.37	44.29
	Microphyll II	41.62	50.00	28.57
	Microphyll III	29.42	25.93	17.14
	Mesophyll I	27.50	3.70	2.86
	Mesophyll II	1.27	0.00	0.00
	Mesophyll III	0.00	0.00	0.00
Apex character states	Apex emarginate	0.00	0.00	1.43
	Apex round	34.23	49.37	27.14
	Apex acute	55.96	45.67	62.86
	Apex attenuate	9.81	4.93	8.57
Base character states	Base cordate	1.92	18.52	10.00
	Base round	40.38	35.19	47.14
	Base acute	57.69	46.30	42.86
Length to width character states	L:W < 1:1	0.00	9.26	4.29
	L:W 1-2:1	18.58	11.11	8.57
	L:W 2-3:1	26.27	20.37	28.57
	L:W 3-4:1	44.54	46.30	44.29
	L:W > 4:1	10.58	12.96	14.29
Shape character states	Obovate	4.62	16.67	15.23
	Elliptic	39.23	55.56	40.94
	Ovate	56.15	27.78	43.80

Appendix 2. Fossil taxa, nearest living relatives and climate date used in the Coexistence Approach (CA).

CA results Pitsidia

fossil taxon	reference taxa	MATmin	MATmax	CMTmin	CMTmax	WMTmin	WMTmax	MAPmin	MAPmax	MPwet min	MPwet max	MPdry min	MPdry max	MPwarm min	MPwarm max
Acer pseudomonspessulanum	Acer monspessulanum.	9.6	20.5	0.2	13.6	18.4	27.5	399	1333	77	191	0	85	0	100
Buxus pliocaenica	Buxus sp............	9.7	25.3	-1.2	20	17.3	29.4	399	2540	80	566	0	56	0	252
Carya minor	Carya sp............	4.4	26.6	-11.5	22.2	19.3	30.6	373	1724	68	434	8	93	45	258
Comptonia difformis	Comptonia peregrina.	relict													
Cupressaceae	Cupressaceae........	-15.6	26.5	-48.9	26.1	11.2	32.9	184	4486	22	409	0	326	0	378
Daphnogene polymorpha	Cinnamomum camphora	13.5	27.2	2.5	26.1	18.6	31.7	828	10798	160	2446	3	135	30	1100
Equisetum sp.	Equisetum sp........	unspecific													
Fagus gussonii	Fagus sylvatica ssp. orientalis **	5.9	19.7	-5	9.4	17.1	31.7	376	2115	46	195	5	94	5	195
Leguminosae	Leguminosae.........	-7.7	27.7	-22.7	25.9	10.5	28.1	224	3905	46	610	0	196	1	221
Liquidambar europaea	Liquidambar styr.or	12.5	21.3	-0.1	16.3	19.6	28.6	897	1613	106	265	2	93	84	195
Myrica lignitum	Myrica sp...........	-8.9	28.1	-29	27	8.9	33.9	233	3151	34	508	0	165	0	221
Pinus sp.	Pinus sp............	-9.2	25.5	-36.8	21.4	7.1	32.9	180	10798	28	2446	0	94	0	1100
Poaceae vel Cyperaceae	Poaceae.............	unspecific													
Podocarpium podocarpum	Leguminosae.........	-7.7	27.7	-22.7	25.9	10.5	28.1	224	3905	46	610	0	196	1	221
Populus crenata	Populus sp..........	-16	26	-49	13.6	9.8	35.6	25	2559	8	358	0	93	0	224
Quercus drymeja	Quercus sect. Cerris	4.7	22.2	-8.7	15.6	11.7	28.6	470	3000	48	2695	0	85	0	1781
Quercus ? kubinyi	Quercus sect. Cerris	4.7	22.2	-8.7	15.6	11.7	28.6	470	3000	48	2695	0	85	0	1781
Quercus mediterranea	Quercus sect. Cerris	4.7	22.2	-8.7	15.6	11.7	28.6	470	3000	48	2695	0	85	0	1781
Quercus roburoides	Quercus sp..........	-1.4	27	-25.1	25.9	8.4	28.3	201	10798	33	2446	0	180	5	1100
Salix sp.	Salix sp............	-17	27.7	-50.1	26.5	7.6	32.9	122	2399	22	448	0	108	0	252
Taxodium sp.	Taxodium sp.........	13.3	25	-0.1	19.8	18.9	31.2	290	2615	60	265	0	93	19	227
Zelkova zelkovaefolia	Zelkova sp..........	6.2	21.9	-12.8	13.6	19.4	29.7	246	2648	46	370	3	67	3	344
	taxa with climate data	19													
	coexistence intervals	13.5	19.7	2.5	9.4	19.6	27.5	897	1333	160	191	8	56	84	100
	coexisting taxa (%)		100		100		100		100		100		100		100

CA results Makrilia

fossil taxon	reference taxa	MATmin	MATmax	CMTmin	CMTmax	WMTmin	WMTmax	MAPmin	MAPmax	MPwet min	MPwet max	MPdry min	MPdry max	MPwarm min	MPwarm max
Acer angustilobum	Acer sect. Acer	2.7	24	-15.6	20.6	16.2	28.6	115	2559	19	370	1	135	1	366
Acer pseudomonspessulanum	Acer monspessulanum.	9.6	20.5	0.2	13.6	18.4	27.5	399	1333	77	191	0	85	0	100
Ailanthus sp.	Ailanthus sp........	6.9	26.7	-8.1	25.3	18.3	28.9	376	3459	92	638	1	119	73	304
Alnus sp. (cf.)	Alnus sp............	-13.3	27.4	-40.9	25.6	4.9	38.6	41	2559	8	353	0	135	8	207
Aquilaria sp.	Aquilaria sp........	13.8	27.7	-0.5	27	24.7	28.1	578	3151	116	389	5	165	89	221
Berberis, Mahonia	Berberis, Mahonia	-4.9	27.7	-32.4	27	15	28.1	304	3151	45	454	0	165	1	224
Buxus pliocaenica	Buxus sp............	9.7	25.3	-1.2	20	17.3	29.4	399	2540	80	566	0	56	0	252
Carpinus orientalis foss.	Carpinus orientalis.	7.7	18.3	-5.3	10.9	18.6	27.6	402	1548	71	191	3	82	3	122
Carya sp.	Carya sp............	4.4	26.6	-11.5	22.2	19.3	30.6	373	1724	68	434	8	93	45	258
Cladrastis sp.	Cladrastis lutea....	8.7	21.3	-3.9	13.3	21.6	29.4	776	1613	74	196	41	93	49	196
Cymodocea sp. vel Posidonia sp.	Cymodocea sp. vel Posidonia sp.	no data													
Cyperaceae gen.	Cyperaceae..........	unspecific													
Dalbergia sp.	Dalbergia sp........	12	28.1	-1.2	27	21.4	35.3	631	3151	111	554	1	165	20	462
Daphnogene sp.	Lauraceae...........	4.4	28.1	-16.8	27	19.3	30.1	191	10798	56	2446	0	165	0	1100
Elaeagnus sp.	Elaeagnus sp........	-0.4	27.7	-24.2	27	18.2	28.5	84	3151	28	389	2	165	13	221
Engelhardia sp.	Engelhardtia sp.....	13.8	27	3.1	25	20.6	33.6	800	10798	150	2446	5	152	79	1100
Equisetum sp.	Equisetum sp........	unspecific													
Ericaceae vel Myrtaceae		unspecific													
Fagus gussonii	Fagus sylvatica ssp. orientalis **	5.9	19.7	-5	9.4	17.1	31.7	376	2115	46	195	5	94	5	195
Fraxinus sp.	Fraxinus sp.........	0	24	-25.8	16.7	14.9	33.9	148	10798	28	2446	2	95	0	1100
Ilex aquifolium foss.	Ilex aquifolium L...	7.2	18.2	-0.4	12.2	14.1	27.6	563	1451	67	178	2	72	4	116
Laurophyllum sp.	Lauraceae...........	4.4	28.1	-16.8	27	19.3	30.1	191	10798	56	2446	0	165	0	1100
Leguminosae	Leguminosae.........	-7.7	27.7	-22.7	25.9	10.5	28.1	224	3905	46	610	0	196	1	221
Leguminosites sp.	Leguminosae.........	-7.7	27.7	-22.7	25.9	10.5	28.1	224	3905	46	610	0	196	1	221
Lonicera Typ etrusca	Lonicera etrusca....	10.4	21.4	-1.7	13.9	19.8	28.3	461	1298	70	198	1	56	2	60
Magnolia sp.	Magnolia sp.........	4.1	27	-10.2	25.9	17.1	28.6	578	3500	102	610	1	180	70	462
Myrica lignitum	Myrica sp...........	-8.9	28.1	-29	27	8.9	33.9	233	3151	34	508	0	165	0	221
Myrtaceae	Myrtaceae...........	11.3	27.7	0.1	27	18.8	28.1	250	3151	30	389	0	165	0	221
Phillyrea sp.	Phillyrea sp........	9.3	20.5	1	17.8	17.9	29.7	160	1356	20	170	2	71	2	92
Pinus cf. hampeana	Pinus thunbergiana..	9.4	19.2	-1.6	11.4	20.9	26.9	631	1724	177	258	6	43	118	258
Pinus cf. hepios	Pinus sp............	-9.2	25.5	-36.8	21.4	7.1	32.9	180	10798	28	2446	0	94	0	1100
Pinus sp.	Pinus sp............	-9.2	25.5	-36.8	21.4	7.1	32.9	180	10798	28	2446	0	94	0	1100
Pistacia lentiscus foss.	Pistacia lentiscus..	12	19.9	-0.4	12.6	22.3	28.8	187	1298	40	198	0	43	0	49
Podocarpium podocarpum	Leguminosae.........	-7.7	27.7	-22.7	25.9	10.5	28.1	224	3905	46	610	0	196	1	221
Populus sp	Populus sp..........	-16	26	-49	13.6	9.8	35.6	25	2559	8	358	0	93	0	224
Potamogeton sp.	Potamogeton sp......	-15	23.5	-41.4	23	10.2	28.2	114	2648	15	448	0	157	0	431
Quercus drymeja	Quercus sect. Cerris	4.7	22.2	-8.7	15.6	11.7	28.6	470	3000	48	2695	0	85	0	1781
Quercus kubinyi	Quercus sect. Cerris	4.7	22.2	-8.7	15.6	11.7	28.6	470	3000	48	2695	0	85	0	1781
Quercus cf. mediterranea	Quercus sect. Cerris	4.7	22.2	-8.7	15.6	11.7	28.6	470	3000	48	2695	0	85	0	1781
Quercus cf. rhenana	Quercus imbric.,laur	3.3	25	-11.3	17.9	14.9	31.2	180	1613	30	195	0	93	7	195
Ruppia sp. (cf.)	Ruppia sp...........	unspecific													
Salix purpurea foss.	Salix purpurea......	4.8	18.3	-6.1	12.3	13.1	26.4	528	1632	73	202	0	55	1	93
Salix sp.	Salix sp............	-17	27.7	-50.1	26.5	7.6	32.9	122	2399	22	448	0	108	0	252
Smilax sp. (cf.)	Smilax sp...........	-1.1	27.7	-25.8	27	15.1	33.1	37	10798	8	2446	0	165	0	1100
Symplocos minutula	Symplocos tinctoria.	13.6	21.1	2.7	13.3	23.6	28.9	961	1355	109	195	43	63	85	195
Taxodium dubium	Taxodium sp.........	13.3	25	-0.1	19.8	18.9	31.2	290	2615	60	265	0	93	19	227
Tetraclinis salicornoides	Tetraclinis (articul	relict													
Tilia sp.	Tilia sp............	1.3	22.2	-17.7	15.1	15	29.4	373	2336	68	454	3	95	15	258
Toddalia sp.	Toddalia sp. (monoty	14.1	27.3	-1.4	25	20.6	31.7	693	10798	135	2446	1	70	20	1100
Ulmus sp.	Ulmus sp............	-4.9	26.6	-25.8	26.1	16	29.4	201	3285	33	569	0	100	0	239
Zelkova zelkovaefolia	Zelkova sp..........	6.2	21.9	-12.8	13.6	19.4	29.7	246	2648	46	370	3	67	3	344
	taxa with climate data	45													
	coexistence intervals	14.1	18.2	3.1	9.4	24.7	26.4	961	1298	150	170	43	43	60	92
	coexisting taxa (%)		100		100		100		100		97.8		100		97.8

CA results Vrysses

fossil taxon	reference taxa	MATmin	MATmax	CMTmin	CMTmax	WMTmin	WMTmax	MAPmin	MAPmax	MPwet min	MPwet max	MPdry min	MPdry max	MPwarm min	MPwarm max
Acer pseudomonspessulanum	Acer monspessulanum.	9.6	20.5	0.2	13.6	18.4	27.5	399	1333	77	191	0	85	0	100
Acer sp.	Acer sp.............	-1.1	24	-25.8	20.6	9.5	29.3	115	10798	19	2446	0	135	0	1100
Buxus pliocaenica	Buxus sp............	9.7	25.3	-1.2	20	17.3	29.4	399	2540	80	566	0	56	0	252
Poaceae vel Cyperaceae	Poaceae vel Cyperaceae	unspecific													
Daphnogene polymorpha	Cinnamomum camphora	13.5	27.2	2.5	26.1	18.6	31.7	828	10798	160	2446	3	135	30	1100
Fabaceae	Fabaceae............	unspecific													
cf. "Juglans" acuminata	unknown.............														
cf. "Parrotia" pristina	Parrotia s.l. *	11.6	27.7	-4	23	25.1	29.5	235	3905	48	610	0	180	0	344
Pinus sp.	Pinus sp.	-9.2	25.5	-36.8	21.4	7.1	32.9	180	10798	28	2446	0	94	0	1100
Populus tremula foss.	Populus tremula.....	-16	19	-49	12.2	9.8	28.3	155	1958	33	236	2	83	2	141
Quercus sp.	Quercus sp.	-1.4	27	-25.1	25.9	8.4	28.3	201	10798	33	2446	0	180	5	1100
Quercus mediterranea	Quercus sect. Cerris	4.7	22.2	-8.7	15.6	11.7	28.6	470	3000	48	2695	0	85	0	1781
Rosaceae sp.	Rubus, Rosa.........	-12	21.7	-38.8	15.2	15.3	28.2	254	2100	34	322	4	71	5	269
cf. Salix sp.	Salix sp............	-17	27.7	-50.1	26.5	7.6	32.9	122	2399	22	448	0	108	0	252
Tetraclinis sp.	Tetraclinis (articul	relict													
Ulmaceae sp.	Ulmaceae............	-1.2	28.5	-25.8	26.7	16	33.4	201	3285	33	454	0	100	0	344
cf. Ziziphus ziziphoides	Ziziphus sp.........	7.3	27.6	-12.8	26.4	14.3	35.3	304	2328	45	371	1	43	1	366
	taxa with climate data	12													
	coexistence intervals	13.5	19	2.5	12.2	19.3	27.5	828	1333	160	191	4	43	30	100
	coexisting taxa (%)		100		100		100		100		100		100		100

CA results Gavdos

fossil taxon	reference taxa	MATmin	MATmax	CMTmin	CMTmax	WMTmin	WMTmax	MAPmin	MAPmax	MPwet min	MPwet max	MPdry min	MPdry max	MPwarm min	MPwarm max
Acer angustilobum	Acer sect. Acer	2.7	24	-15.6	20.6	16.2	28.6	115	2559	19	370	1	135	1	366
Ailanthus pythii	Ailanthus sp........	6.9	26.7	-8.1	25.3	18.3	28.9	376	3459	92	638	1	119	73	304
Betula sp.	Betula sp...........	-15	25.8	-41	21.1	1.3	28.7	110	10798	23	2446	0	135	2	1100
Carpinus sp.	Carpinus sp.........	0	25.8	-22.7	21.1	16.8	28.7	164	10798	20	2446	0	130	2	1100
Daphnogene sp.	Lauraceae...........	4.4	28.1	-16.8	27	19.3	30.1	191	10798	56	2446	0	165	0	1100
Engelhardtia orsbergensis	Engelh.,Oreom.,Alfar	13.8	27.4	3.1	26.1	18.9	33.6	748	10798	170	2446	0	152	48	1100
Fagus gussonii	Fagus sylvatica ssp. orientalis **	5.9	19.7	-5	9.4	17.1	31.7	376	2115	46	195	5	94	5	195
Laurophyllum sp.	Lauraceae...........	4.4	28.1	-16.8	27	19.3	30.1	191	10798	56	2446	0	165	0	1100
Leguminosites sp.	Leguminosae.........	-7.7	27.7	-22.7	25.9	10.5	28.1	224	3905	46	610	0	196	1	221
? Lindera ovata Kolak.	Lauraceae...........	4.4	28.1	-16.8	27	19.3	30.1	191	10798	56	2446	0	165	0	1100
Monocotyledonae	monocots............	unspecific													
Myrica lignitum	Myrica sp...........	-8.9	28.1	-29	27	8.9	33.9	233	3151	34	508	0	165	0	221
Paliurus tiliifolius	Paliurus sp.........	10	23.1	-7.3	17	22.5	28.8	396	1958	68	448	2	70	2	431
Pinus sp.	Pinus sp............	-9.2	25.5	-36.8	21.4	7.1	32.9	180	10798	28	2446	0	94	0	1100
Populus populina	Populus alba........	2.5	18.5	-14.6	12.5	17.9	26.4	419	1741	57	254	1	109	3	80
Salix angusta		-17	27.7	-50.1	26.5	7.6	32.9	122	2399	22	448	0	108	0	252
Sapindus graecus	Sapindus sp.........	10	27.7	-7.3	27	20.2	32.9	184	3151	22	389	2	165	20	304
Sassafras sp.	Sassafras sp........	9.3	22.8	-3.3	14.7	21.6	30.1	843	1864	71	295	17	93	64	195
Taxodium dubium	Taxodium sp.........	13.3	25	-0.1	19.8	18.9	31.2	290	2615	60	265	0	93	19	227
Tetraclinis salicornoides	Tetraclinis (articul	relict													
Ulmus (?) plurinervia	Ulmus sp..........	-4.9	26.6	-25.8	26.1	16	29.4	201	3285	33	569	0	100	0	239
	taxa with climate data	19													
	coexistence intervals	13.8	18.5	3.1	9.4	22.5	26.4	843	1741	170	195	17	70	73	80
	coexisting taxa (%)		100		100		100		100		100		100		100

* data set for Fothergilleae
** data set for European *Fagus*

within the range from Lebedyan RS to Turgenevo Beds (inclusive) of Plavsk RS of the Russian Plate.
Author is grateful to Pavel Beznosov for samples and co-operation.

A new methodological approach on *Laurinoxylon* and the importance of the oil &/or mucilage cells

TALK IN SESSION S5

Mantzouka, Dimitra[1] [dmantzouka@yahoo.gr]; Sakala, Jakub[2]; Karakitsios, Vasileios[1]

[1]Department of Historical Geology – Paleontology, National and Kapodistrian University of Athens, Athens (Greece)
[2]Institute of Geology and Palaeontology, Charles University of Prague, Prague (Czech Republic)

Wood anatomy of several specimens of *Laurinoxylon* from the Tertiary of southern part of Lesbos Island (Greece) Kadaň - Zadní Vrch Hill and Jáchymov (Czech Republic) and Ipolytarnóc (Hungary) was observed, mainly with respect to the type and distribution of idioblasts. These observations together with the published descriptions and data from the InsideWood Database, both modern and fossil, gave birth to a new methodology focused on the identification and classification of *Laurinoxylon*. Our observations on the exact occurrence of the oil &/or mucilage cells (in connection with the ray parenchyma, or with the vertical strand parenchyma or isolated from parenchymal tissues and embedded between the fibers or several combinations) allowed us to make four main groups of *Laurinoxylon*. On the other hand, presence of marginal bands of axial parenchyma, aliform to aliform-confluent paratracheal parenchyma, rays higher than 1 mm, exclusively homocellular rays, ring-porous wood or absence of idioblasts (oil &/or mucilage cells) can exclude a fossil lauraceous wood from being attributed to *Laurinoxylon*. In this context, the existence of crystals and SiO_2 along with the occurrence of crystalline masses inside the fibers of some species was also highly evaluated, as also the observation of septate fibers. The newly proposed methodology on *Laurinoxylon* shows that taxonomical information, palaeobotanical data, and exact botanical affinities can help to classify it, but also to exclude many fossil woods from that fossil genus which used to be treated as a 'waste bin', which surely overestimates its importance in the Cenozoic fossil wood record.

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Gavdos Island palaeoflora: A newly recovered late Neogene flora of the Eastern Mediterranean (Greece)

POSTER IN SESSION S22

Mantzouka, Dimitra[1] [dmantzouka@yahoo.gr]; Kvaček, Zlatko[2]; Teodoridis, Vasilis[3]; Utescher, Torsten[4]; Tsaparas, Nicolaos[1]; Karakitsios, Vasileios[1]

[1]Department of Historical Geology–Paleontology, National and Kapodistrian University of Athens, Athens (Greece)
[2]Institute of Geology and Palaeontology, Charles University of Prague, Prague (Czech Republic)
[3]Department of Biology and Environmental Studies, Charles University of Prague, Prague (Czech Republic)
[4]Rheinische Friedrich-Wilhelms-Universität Bonn and University of Bonn, Bonn and Senckenberg Research Institute, Frankfurt /M (Germany)

The study of more than 100 leaf impressions from the Metochia section, Gavdos Island, Greece, revealed a recently recovered late Miocene palaeoflora from the southernmost part of Europe. Fossiliferous strata – sapropels – of early to middle Tortonian age (9.6–9.1 million years b. p.) yielded a plant assemblage consisting of 3 conifers and ca 30 fossil species of angiosperms belonging to subtropical to warm temperate evergreen or deciduous shrubs and trees including legumes. The number of the identified specimens was sufficient to allow an application of several palaeoenvironmental techniques (phytosociological approach and Integrated Plant Record analysis, Leaf Margin Analysis technique, CLAMP analysis and Coexistence Approach). The results obtained from the Gavdos palaeoflora expand our knowledge about the late Neogene floras of the Mediterranean and complement previous studies recently accomplished in southernmost Greece, namely in Crete (Makrilia, Vrysses and Pitsidia).

This research has been co-financed by the European Union (European Social Fund–ESF) and Greek national funds through the Operational Program ''Education and Lifelong Learning'' of the National Strategic Reference Framework (NSRF) – Research Funding Program: THALIS–UOA– ''Messinian Salinity Crisis: the greatest Mediterranean environmental perturbation and its repercussions to the biota'' and supported by the grants J 13/98113100006, MSM 002162085 and PRVOUK P44.

PLANT FOSSILS AND TAPHONOMICAL PROCESSES FROM LESBOS ISLAND, GREECE

Dimitra Mamtzouka[1], Jakub Sakala[2], Vladislav Rapprich[3] & Vasileios Karakitsios[1]

[1] *National and Kapodistrian University of Athens, Faculty of Geology and Geoenvironment, Department of Hist. Geology - Paleontology, dmantzouka@geol.uoa.gr , vkarak@geol.uoa.gr*
[2] *Charles University of Prague, Czech Republic, Institute of Geology and Palaeontology, Albertov 6, 12843, Prague 2, rade@natur.cuni.cz*
[3] *Czech Geological Survey, Klarov 3, 11821 Prague, vladislav.rapprich@geology.cz*

Since the 3rd century BC the plant fossils of Lesbos Island have been objects of curiosity and subjects of observation and research. Theophrastus, a famous Greek philosopher and botanist from Eressos (372-287 B.C.) described them in his book 'On Petrifactions' ('Περί Λιθουμένων'), which, unfortunately is not saved, and made also some references about them in his book 'On Stones' ('Περί Λίθων'). In the 19th century AC the plant fossils of the western area of the Lesbos Petrified Forest started to reveal their secrets as they studied by some of the pioneers of palaeobotany as Unger or Fliche. From 1980's there was an intensive effort in studying the palaeoflora of the Lesbos Petrified Forest (e.g. Velitzelos et al. 1981, Süss & Velitzelos 2010; Velitzelos et al. 1999; Selmeier & Velitzelos 2000; Mantzouka et al. 2013) and also the palaeofauna findings (Koufos et al. 2003; Mantzouka 2009; Vasileiadou & Zouros 2012) as well as the geology of the area (Katsikatsos et al. 1993)

The importance of the plant fossils of the western peninsula of Lesbos Island has been recognized also by the Greek state and since 1985 has been declared as a Protected Natural Monument with a special Presidential Decree (No 443/1985) (Velitzelos et al., 1999). Until 2011 the plant fossils of the area of the Petrified Forest included:

1. permineralized and silicified (petrification) trunks – mainly "gymnosperms" - in the western, central, southern and northern part of the island,
2. lignified trunks in the western part of the island,
3. leaf impressions of "pterydophytes", "gymnosperms" and angiosperms in the western part of the island,
4. molds and casts of pine cones in the western part of the island.

New fossiliferous localities have been found since 2011, which add new data considering not only the extent of the Petrified Forest of Lesbos, but also the variety in plant genera, their fossilisation and so the different types of preservation (leaf impressions, molds and casts, permineralized, silicified and lignified trunks, fossiliferous block assemblages, lignitic horizons), while they have given birth to new questions about the taphonomical processes which have been followed.

According to Greenwood (1991) the plant taphonomy incorporates the processes of the initial abscission of plant parts, their transport (by air and/or water) to a place of eventual deposition, entrapment and eventual burial, and subsequent lithification. The 'Petrified Forest of Lesbos' comprise a lot of different types of fossilisation, generally related to the volcanic activity but with a wide variety of phenomena (direct influence of volcanism or fluvial or lacustrine facies associated with volcanic activity or pyroclastic fall, or pyroclastic flow or epiclastic flow-lahar?). The re-examination from a volcanological point of view for understanding the taphonomy processes conditions which took place on Lesbos Island during the Neogene and the succession of the right interpretation for each locality (e.g., Sakala et al., 2010; Matysová et al., 2010), seem to be necessary. The research is supported by the grant MSM0021620855.

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