ARISTOTLE UNIVERSITY OF THESSALONIKI
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# A CASE STUDY OF FOSSIL LEAVES FROM THE EARLY MIOCENE PETRIFIED FOREST AT AKROCHEIRAS SITE IN SIGRI AREA (LESVOS ISLAND)

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ΚΑΦΕΤΖΙΔΟΥ Λ. ΑΙΚΑΤΕΡΙΝΗ

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# ΜΕΛΕΤΗ ΤΩΝ ΑΠΟΛΙΘΩΜΕΝΩΝ ΦΥΛΛΩΝ ΑΠΟ ΤΟ ΚΑΤΩ ΜΕΙΟΚΑΙΝΟ ΤΟΥ ΑΠΟΛΙΘΩΜΕΝΟΥ ΔΑΣΟΥΣ ΤΗΣ ΘΕΣΗΣ ΑΚΡΟΧΕΙΡΑΣ ΤΗΣ ΠΕΡΙΟΧΗΣ ΤΟΥ ΣΙΓΡΙΟΥ (ΝΗΣΙ ΤΗΣ ΛΕΣΒΟΥ)

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Dr. Ioannis Zidianakis


A CASE STUDY OF FOSSIL LEAVES FROM THE EARLY MIOCENE PETRIFIED FOREST AT AKROCHEIRAS SITE IN SIGRI AREA (LESVOS ISLAND)- *Master Thesis*


ΜΕΛΕΤΗ ΤΩΝ ΑΠΟΛΙΘΩΜΕΝΩΝ ΦΥΛΛΩΝ ΤΟΥ ΚΑΤΩ ΜΕΙΟΚΑΙΝΟΥ ΑΠΟ ΤΟ ΑΠΟΛΙΘΩΜΕΝΟ ΔΑΣΟΣ ΛΕΣΒΟΥ- ΘΕΣΗ ΑΚΡΟΧΕΙΡΑΣ, ΣΙΓΡΙ (ΛΕΣΒΟΣ) – *Μεταπτυχιακή Διπλωματική Εργασία*

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## ABSTRACT

The Early Miocene macro- floral remains (leaf imprints) from the Akrocheiras site in Petrified Forest of Lesvos Island in Sigri area (North Aegean, Greece) are described. Sixteen different taxa were identified based on macroscopic morphological characteristics of about 235 leaf imprints. Dominant species are *Daphnogene polymorpha* (21%) *Pungiphyllum cruciatum* (15,0%), *Phoenicites* sp. (15,0%), and Lauraceae vel Fagaceae gen. et spec. indet., represented by numerous leaf remains. The rest taxa are rather rare with percentages between 1-3%, as cf. *Alnus*, *Myrica* sp., aff. *Engelhardia osbergensis,* Lauraceae gen. et. spec. indet, cf. *Populus balsamoides*. Half of the identified taxa, i.e., *Celtis japeti, Carya* sp., *Decodon* sp., cf. *Ilex* sp., *Juglans* sp., *Leguminosite*s sp. and *Smilax weberi* are reported for the first time from the Neogene deposits of the Lesvos Island.

Vegetation assessment is attempted both empirically-sociologically and by the Integrated Plant Record (IPR) vegetation analysis. Climate is estimated based on the Climate Leaf Analysis (CLAMP). According to the results of IPR analysis, the plant assemblage of Akrocheiras site is classified to the zonal subtropical, subhumid sclerophyllous or microphyllous forests (ShSF). The palaeoclimatic results for the flora of Akrocheiras site, revealed a warm temperate to subtropical climate (MAT 13.4- 16.5 $^{o}$C and MAP 566- 834 mm), with seasonal alternations from wetter to drier conditions. The type of climate shows affinities to Cfa (sensu KÖPPEN-GEIGER).

Finally, the studied flora of Akrocheiras is compared to the Early Miocene fossil record of the Greek Peninsula, the Early- Middle Miocene record of eighteen European sites, as well as to the modern flora of the area.

**ΠΕΡΙΛΗΨΗ**

Η παρούσα μελέτη βασίστηκε στα μακροφυτικά απολιθώματα της Κάτω- Μειοκαινικής θέσης Ακρόχειρας, που εντάσσεται στην ευρύτερη περιοχή του Απολιθωμένου Δάσους της Λέσβου στην περιοχή του Σιγρίου (Βόρειο Αιγαίο, Ελλάδα). Στη θέση Ακρόχειρας μελετήθηκαν 235 αποτυπώματα φύλλων, εκ των οποίων αναγνωρίστηκαν δεκαέξι διαφορετικά τάξα, των οποίων η αναγνώριση βασίστηκε στα μακροσκοπικά μορφολογικά χαρακτηριστικά. Μεταξύ αυτών, κυρίαρχοι αντιπρόσωποι είναι τα *Daphnogene polymorpha* (21%), ενώ ως πολυπληθή χαρακτηρίζονται τα είδη *Pungiphyllum cruciatum* (15%), *Phoenicites* sp. (15%), ενώ σημαντική είναι και η παρουσία των Lauraceae vel Fagaceae gen. et spec. indet. Τα ποσοστά των υπολοίπων αναγνωρισμένων taxa είναι υπολοιπόμενα, καθώς κυμαίνονται από 1-3%, όπως τα cf. *Alnus*, *Myrica* sp., aff. *Engelhardia osbergensis,* Lauraceae gen. et. spec. indet και cf. *Populus balsamoides.* Μεγάλο ποσοστό του ταξινομημένου απολιθωμένου υλικού, με αντιπροσωπους τα *Celtis japeti, Carya* sp., *Decodon* sp., cf. *Ilex* sp., *Juglans* sp., *Leguminosite*s sp. και *Smilax weberi* υποδεικνύει την πρώτη καταγραφή αυτών των taxa στο Νεογενές απολιθωματοφόρο αρχείο της Λέσβου.

Η παλαιοοικολογική εξέταση της θέσης Ακρόχειρας, υπέδειξε ίχνη αλληλεπίδρασης μεταξύ φυτών- αρθροπόδων, κυρίως με την ύπαρξη μορφών προσβολής του φυλλώματος. Η κατανάλωση μέρους του φυλλώματος που εντοπίστηκε σε ένα από τα υπό μελέτη δείγματα αποτελεί τον τρόπο της ζημίωσης του φυλλώματος στη θέση. Η μελέτη της αλληλεπίδρασης των φυτών- αρθροπόδων αποτελεί μία σημαντική μέθοδο για την εξαγωγή παλαιοοικολογικών αποτελεσμάτων.

Τα φυτικά λείψανα της θέσης Ακρόχειρας, διερευνήθηκαν με βάση την ταξινόμησή τους, των στοιχείων της βλάστησης και του κλίματος της περιοχής κατά το Κατώτερο Μειόκαινο. Η εφαρμογή της μεθόδου IPR (Integrated Plant Record), κατέταξε τις φυτικές συναθροίσεις της θέσης Ακρόχειρας στα υποτροπικά σκληρόφυλλα ή μικρόφυλλα δάση (ShSF). Η χρήση της μεθόδου CLAMP (Climatic Leaf Analysis Multivariate Program) για την ποσοτική εκτίμηση του παλαιοκλίματος της θέσης υπέδειξε ένα θερμό εύκρατο έως υποτροπικό κλίμα (μέση ετήσια θερμοκρασία 13.4- 16.5 $^oC$ και μέση ετήσια βροχόπτωση 566- 834 mm) με εποχιακές εναλλαγές μεταξύ υγρών και ξηρότερων περιόδων, πιθανόν τύπου Cfa με βάση το σύστημα των KÖPPEN-GEIGER. Τέλος, πραγματοποιήθηκε μια σύγκριση της υπό μελέτη χλωρίδας με τις υπόλοιπες Κάτω Μειοκαινικές Ελληνικές θέσεις με φυτικά απολιθώματα ιδίου τύπου, καθώς και με δεκαοχτώ απολιθωματοφόρες Ευρωπαϊκές θέσεις φυτικών λειψάνων ηλικίας Κατώτερου- Μέσου Μειοκαίνουκαι με τη σύγχρονη χλωρίδα της περιοχής.

*To*

*my parents,*

*Lena & Leonidas*

*and my grandfather,*

*Konstantino Tasioula*

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# 1.INTRODUCTION

## 1.1. The history of palaeobotany in Lesvos Island

Lesvos Island is a unique monument with an exceptional palaeobotanical heritage, focused on the occurrence of the Petrified Forest at the Western part of the Island. This geological monument has been providing information about the Early Miocene subtropical vegetation of the Aegean- Anatolian area since the 3rd century B. C. The finding of petrified trees, branches, leaf imprints and cones, which have been preserved inside layers of pyroclastic material, have attracted the interest of the scientific community. Studies on fossil plants from the Neogene sediments of Lesvos are diverse including the Early Miocene leaf imprints and wood remains of the region of the Petrified Forest and wood remains from Rougada and Vatera fossiliferous sites (Fig. 1).

The first traces of the palaeontology and palaeobotany of Greece were made by the ancient philosophers due to their interest to the fossiliferous localities and fossil plants. The first palaeobotanical research of the fossil flora of Lesvos took place at the 3rd century B. C by Theophrastus (372-287 B.C.) from Eressos, Lesvos Island, Greece. This work probably contained a systematic treatment of the fossil trees of Lesvos, in recognition of the different types of fossilization, for description petrification and carbonization Almost 2000 years after the first recording of Lesvos fossil plants by Theophrastus, the scientific interest returned on Lesvos. The Austrian botanist Franz Unger was the first scientist who described the fossil plants from Lesvos in several works. In 1898 Fliche, determinated lignitic and permineralized trees, not only from the region of Ordymnos Mountain, but also at the islet of Nissiopi. The significance of this unique monument was underlined first by Richard Krausel, following his visit at the area of the Petrified Forest of Lesvos, during 1956. Sixteen years later, Greek scientists initiated an extensive research of the palaeofloristic remains of Lesvos, based on the identification of the leaf imprints. These studies revealed an exceptionally rich flora and contributed significantly to the reconstructions of the climatic conditions (subtropical climate) and the fossil forest's relative age (Upper Oligocene-Middle Miocene: Velitzelos, Petrescu and Symeonidis, 1981a, 1981b). More recent anatomical studies in the fossil record of the Petrified Forest of Lesvos, along with the identification of leaf imprints (Velitzelos, 2014). In 2014, Velitzelos et al. published a comprehensive review of the Cenozoic floras of Greece, providing amended species lists for the already known Lesvos floras.

Finally, assemblages of fossil trunks from the southeastern part of Lesbos were reported and studied by Matzouka (2016).

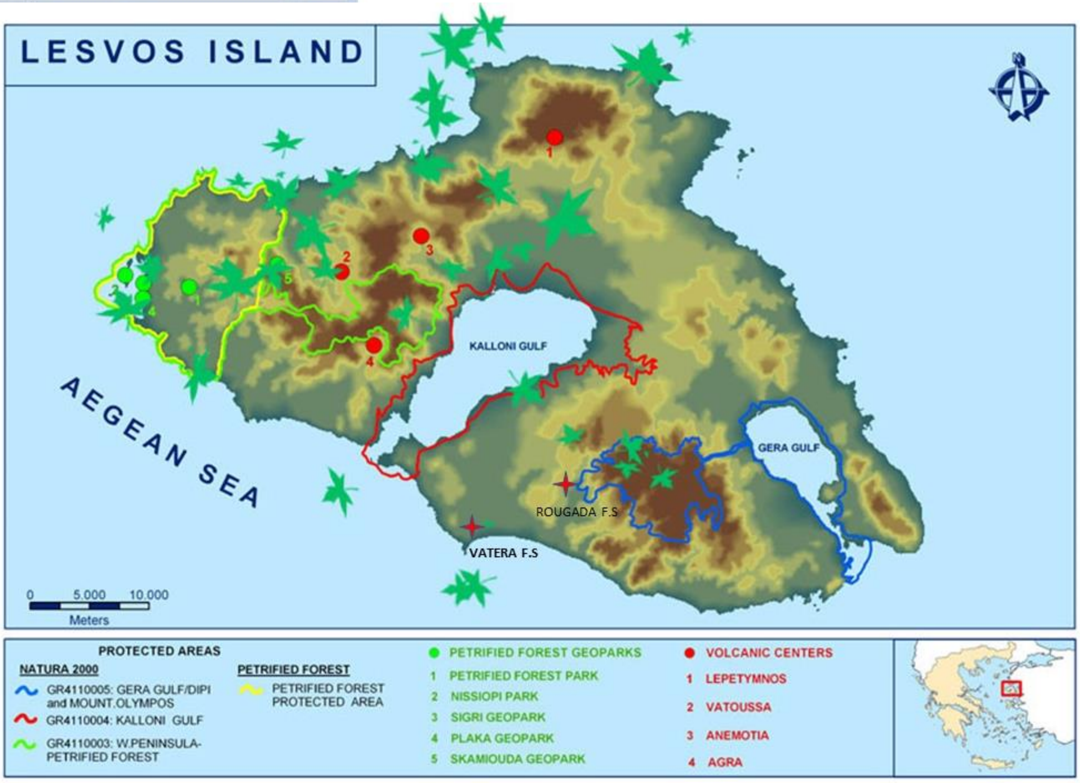



Figure 1. The fossiliferous sites of Lesvos Petrified Forest of Island during the Neogene period (Museum of Petrified Forest of Lesvos, modified)

### 1.2 Purpose and scope of the study

This study aims to enrich our knowledge on the structure of the past flora and environmental conditions of Lesvos Island, based on early Miocene plant macro-remains provided from the new site Akrocheiras of the Petrified Forest of Lesvos, in Sigri. From this site, several newly reported leaf taxa of the Early Miocene fossil record of Lesvos are identified. The detailed taxonomy based on macroscopic examination of the specimens of Akrocheiras aspires to analyse the floristic and ecological results, to provide evidence of the composition of the plant communities, to extract palaeoclimatic results and to compare the studied material with contemporary Greek and Early- Middle European floras, as well as with the modern flora of Lesvos, providing evidence about their biogeographical and floristic relationships.

# 2. GEOGRAPHICAL AND GEOLOGICAL SETTINGS-AGE

## 2.1 The island of Lesvos

Lesvos is the third largest island of Greece with an area of 1639 $km^2$ in the NE part of the Aegean Sea, very close to the coast of Asia Minor. It is located southwest of Adramytti Gulf, opposite Ayvali, in an important recess of the Asia Minor coastline, bound on its north by the Adramyttian rift. The Adramyttian rift delimits the northern part of the Adramytti Gulf and forms the major recess of the Asia Minor coastline (Fig. 2).


Figure 2. Lesvos Island (source: Google Earth)

The most significant feature of Lesvos geomorphology is the two large closed bays in its southern part, the Kalloni and the Gera Gulfs, which are apparently related to the tectonic evolution of the wider area of the North Aegean and particularly to the neotectonic action that resulted in the sinking of Aegeis. The geological structure and petrographic composition of Lesvos played a key role in the geomorphology of the island. The western and northern parts of Lesvos, where the major volcanic centers on the island are found, are mostly covered by volcanic rocks. This contributes a morphology with large calderas (Vatousa, Lepetymnos, Anemotia, Agra), as well as to the presence of significant domes, that typically elevate the morphology of the island, creating large topographic differences with dense clumps without vegetation. On the contrary, the south-eastern part of Lesvos, is characterized by a mountainous landscape with significant vegetation cover.

**2.1.1 Geo-tectonic setting**

Fault geometry and kinematics in the Northern Aegean have been studied by several authors (McKenzie, 1978, Pavlides et al., 1990, Tranos, 2009). The tectonic history of Lesvos has played a decisive role in shaping the morphology of the Island, as it is responsible for the large drafts and sharp transitions that occur. Lesvos is known for its strong neotectonic activity, as it is geotectonically in a position with high modern mobility (Mercier et al., 1989). The tectonic and volcanic activity of the island was controlled by its geodynamic position in the Aegean-Anatolian microplate (Fig. 3), between the convergent African and Eurasian plates (Pe-Piper and Piper, 2007). The closure of Neotethys between Africa-Arabia, the Anatolia subduction along the dextral north Anatolian fault and the southwest rollback of the Hellenic subduction zone have led to the expansion of the Aegean region (Jolivet et al., 2013). During the Early Miocene, the larger part of the NE Aegean Sea and NW Anatolia was occupied by shoshonitic volcanoes (Dilek and Altunkaynak, 2009; Pe-Piper and Piper, 2002), related to melting of subcontinental lithospheric mantle by upwelling asthenosphere (Fig. 4). The upwelling process was due to either the subduction-transform edge progator between the Cyprus and Hellenic arcs, along the western margin of Anatolia, or to the slab break-off from the former Pindos Ocean (Govers and Wortel, 2005). Yilmaz et al. (2000), based on tectonic and stratigraphic data, showed that during the Early Miocene a series of NE-trending grabens developed, bounded by strike-slip faults, representing splays of the North Anatolian fault. These faults were intruded by shear-zone granitoid plutons. These faults linked to the development of the basin and the volcanism in the Island of Lesvos (Pe-Piper and Piper, 2007). In the Late Miocene, sinistral strike-slip occurred on E-W or WSW-ENE faults. During the Pliocene, NNE-SWW strike-slip faults and NW-SE normal faults developed. In the Quaternary, N-S extension developed E-W normal faults and reactivated older geological structures (Velitzelos and Zouros, 1998).

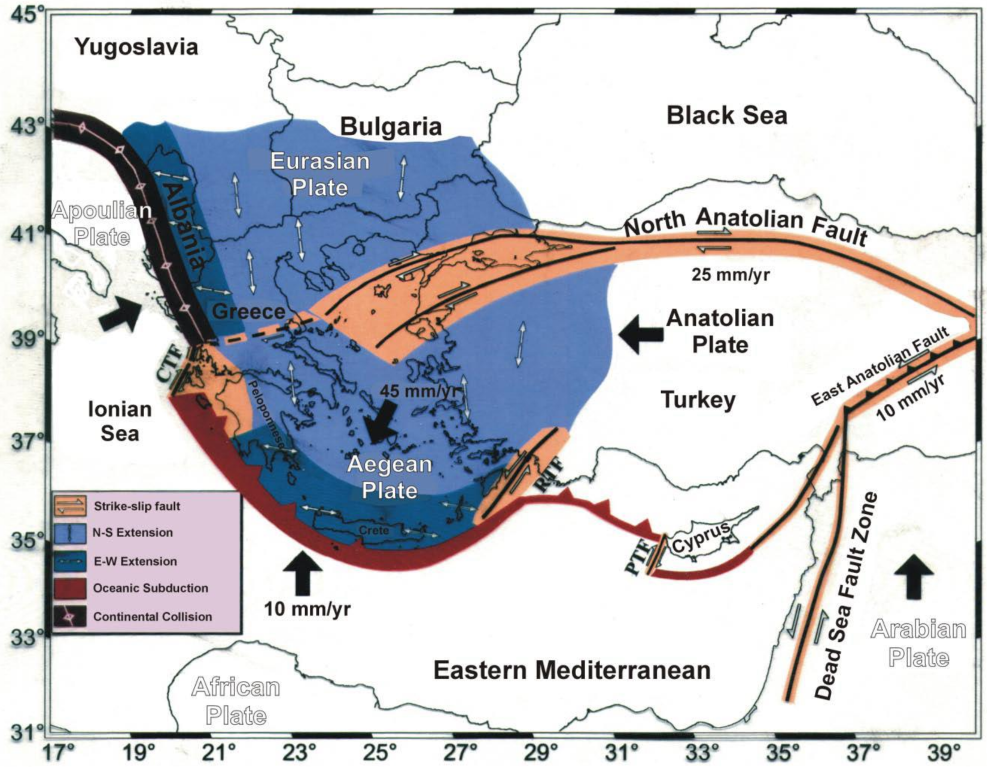



Figure 3. General map of the active geodynamics of East Mediterranean (Papazachos and Papazachou, 2003).

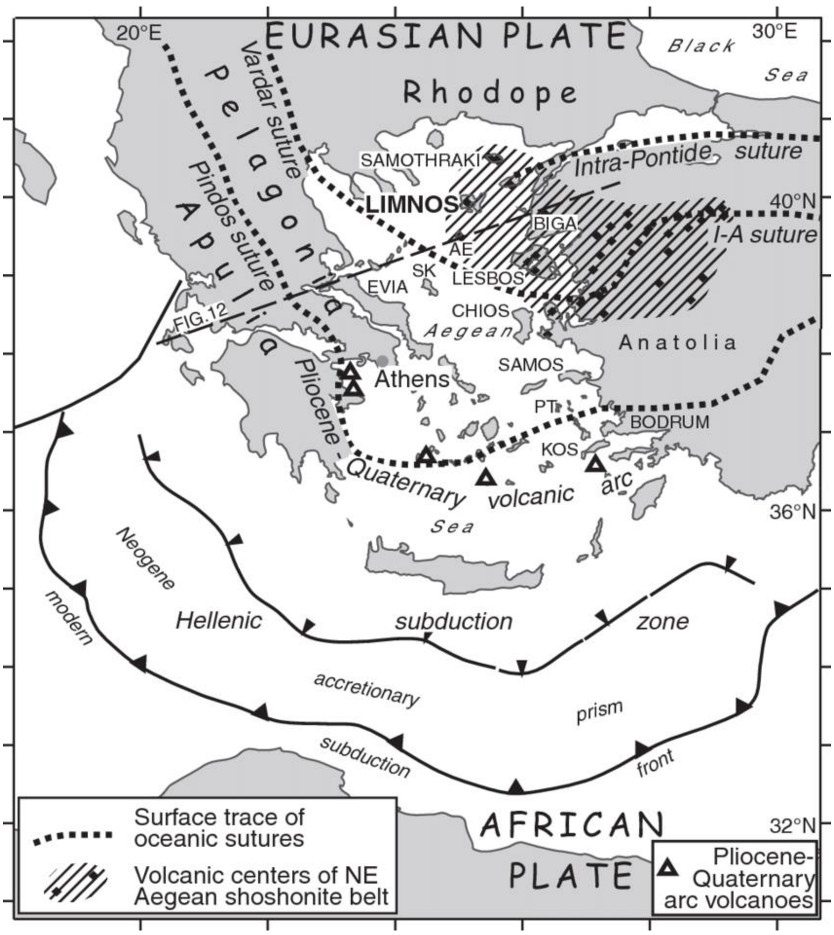



Figure 4. Map showing the location of Lesvos Island within the modern plate-tectonic setting, during the early Miocene (Pe-Piperand Piper, 2007). Early Miocene graben and granites in northwestern Anatolia from Yılmaz et al. (2000).

#### 2.1.1.1. The Geology of Lesvos Island

The geology of Lesvos Island has been studied by several scientist, as Hecht (1972, 1973, 1974a, b, 1975), Pe-Piper (1978), Katsikatsos et al. (1982, 1986) and Pe-Piper and Piper (1993). The local geology can be summarized as a basement of Alpidic and pre-Alpidic rocks, covered by Miocene post- Alpine formation, mainly volcanic rocks, and Neogene marine and lacustrine deposits. The geological structure of Lesvos Island consists of six main units:

- The autochthonous unit of Permo- Triassic age, including mica schists, quartzites, meta- sandstones and phyllites. The upper part of the unit consists of a carbonate sequence, often more than 400m thick (Fig. 5). These rocks appear mainly in the south- eastern part of the Island, while in the north-western part they have a smaller extension. The autochthonous unit is considered as a remnant of the Cimmerian continent (Katsikatsos et al., 1986, Mountrakis et al., 1983, Papanikolaou, 1999).
- Two allochthonous units representing the volcano- sedimentrary nappe and the ophiolitic nappe. The volcanic- sedimentary nappe is of Triassic age and consists of metabasites and metamorphic sedimentary rocks, such as crystalline limestones, amphibolitic schists, metapellites and metacherts. The ophiolite nappe consists mainly of serpentinized dunites and peridotites, as well as of amphibolites and amphibole schists, which are part of the metamorphic sole. The initial emplacement of both allochthonous units took place during Jurassic (Papanikolaou, 1999) and they are considered as remnants of an old Tethyan oceanic crust (Mountrakis et al., 2001), which was odbucted over the Eurasian continental margin.
- The Neogene volcanic rocks, which cover the central and western part of the Island. They exhibit a calcium- alkaline and shoshonitic composition originating from the volcanic activity which took place at the Central- Northern Aegean area and ended at the Western Anatolia during the L. Oligocene- Middle Miocene (Fytikas et al., 1984). These rocks are exposed in a series of eroded volcanic venters along a SW- NE direction (Lepetymnos, Vatousa, Agra calderas) (Novak et al., 2001).
  Several different volcanic rocks including ignimbrites, basalts, lavas and tuffs (Pe-Piper, 1978; Borsi et al., 1972) have been recognized in the volcanic units of Lesvos. Their age ranges from 21.5 to 16.2 Ma (Pe- Piper and Piper, 1993).
- Marls, marly limestones, silts and sandstones, which constitute the Neogene marine and lacustrine deposits, are dominants along the eastern coast of the Island, as well as on the northwestern coast, in Gavathas area.
- The Pleistocene and Holocene terrestrial deposits cover the small palins which were formed by the main river valleys.

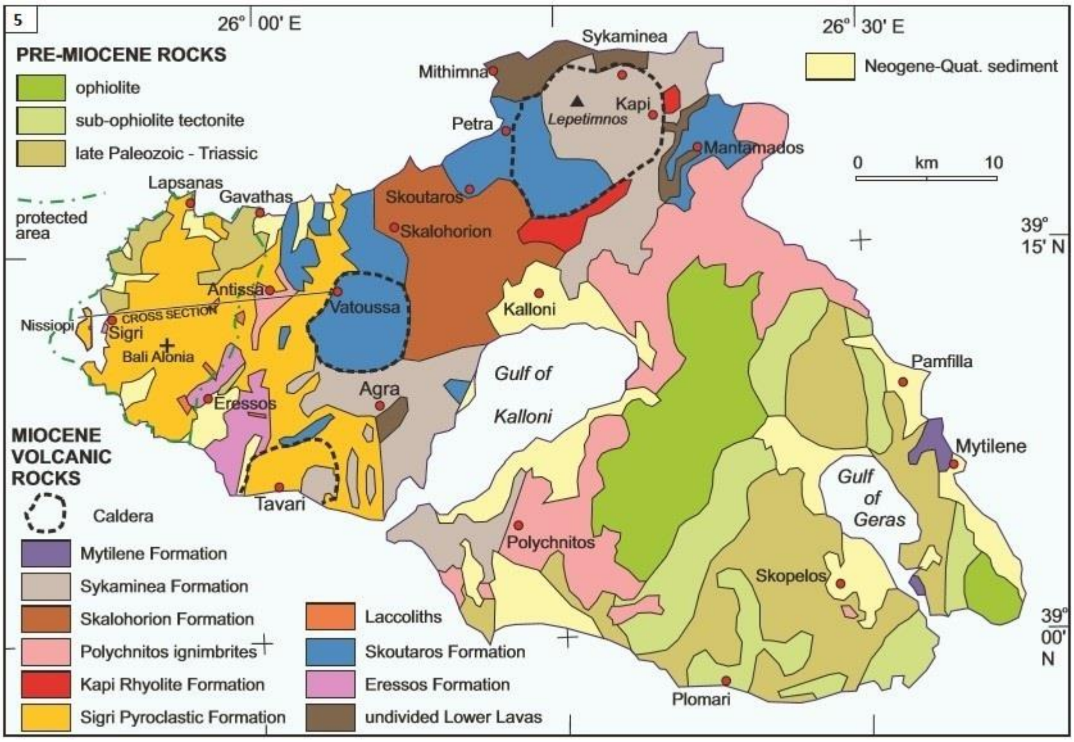



Figure 5. General map of the geology of Lesbos based on Hecht (1972–1976) as modified by Pe-Piper (1980b).

### 2.1.2. Stratigraphy- Volcanic activity

2.1.2.1. The Sigri Pyroclastic formation

The lithology of the Petrified Forest of Lesvos is connected to the Sigri pyroclastics, a part of Skoutaros Fm (Zouros et al., 2007), which overlies the lacustrine Gavathas Formation in the north and the volcanic Eressos Formation in the south. The Eressos Formation consists of calc-alkaline andesite-dacite domes, which overlie the metamorphic basement in the Eressos area of western Lesvos, and it is dated at 21.6± 0.5 Ma (K-Ar, hbl; Pe-Piper and Piper, 1993). Compared to the later K-rich shoshonites, the Eressos rocks are more calc-alkaline (Pe-Piper, 1980a). The Sigri Pyroclastic Formation is several hundred meters thick in the western part of Lesvos. It is mainly composed of tuffs. There are few intercalated fluvial conglomerates and volcanic clastic sandstone layers, as well as a minor appearance of mudstone and paleosols. The beds of tuff are mainly composed of andesite, some of which are rich in andesite clasts, are sharp, and are usually covered by fine-grained tuff, showing normal grading. Sigri Formation include thick volcanic conglomerates between Jithra and Vatoyssa, as well as mudstones and paleosols (Fig. 5). To the east, the formation intercalates with fluvial conglomerates, which get thinner towards both the north and south. Younger lavas overlie the Sigri Pyroclastic Formation, unconformably, with a paleosol visible in some places. In the areas of Skoutaros, Skalororion and Sykaminea, volcanic activity was active between 18.5 and 17 Ma, causing erosion of the shoshonitic lavas with minor appearences of the calcium-alkaline andesite interlayers. The Sigri Pyroclastic Formation stratigraphically underlies the Skoutaros Formation.

The detailed stratigraphy of the Sigri- Antissa road, east of the Bali Alonia park, from which the studied material comes, shows the typical pyroclastic succession. Tuff beds with thickness ranging from a few decimeters to several meters are present. The tuff beds in the lower part are sharp based and mainly overlain by thin fine- grained tuff beds (<2 cm) which show normal grading (Fig. 6). The presence of a paleosol, that shows patchy alternation to red or green color, indicates the presence of leaf litter and constitutes the site of the material of the present thesis (Fig. 6). In some cases, the leaf litter horizons comprise the later Fe- Mn hydrothermal veins that also occupy the faults and fractures (Pe-Piper et al., 2019). The dispersed pumice and lithic lapilli in the ash matrix are common, and only in exceptional cases they are clast- supported. The ash matrix mainly includes glass, small lithic clasts with feldspar crystals or blocky pumice, with generally little deformed vesicles. In some beds, the grain size of the lithic lapilli decreases upwards (Fig. 6, in the intermediate bed), but generally, there is no obvious system for the distribution of lapilli. Lahars (mudflow deposits) have a high proportion of muddy matrix with floating lithic and pumice clasts and poor shorting. These poorly shorted deposits have a high proportion of angular lithic clasts, which may represent a high concentration of river ot gravel flow. These facies are overlain by better sorted conglomerate, tuffs and in some cases by the Antissa- Jithra ignimbrite. Cobble and clast-supported pebble conglomerates, mainly with basal erosion surfaces, are well sorted, with outsize clasts (<2 m). These are locally interbedded with bedded or cross- bedded coarse to fine- grained sandstones. Generally, they interbed with and are subordinate to tuffs, in most of the study area. The conglomerates appear to be older than the ignimbrite, heading westward into the poorly exposed Sigri tuffs. The southern margin of the conglomerates is delimited by E- W faults that contrast the conglomerates with tuffs. Northwards, the conglomerates appear to enter the tuff laterally over a distance of a few km. Among the outcrops on the Sigri- Antissa road, the presence of conglomerates and sandstones is poor (Pe-Piper et al., 2019).

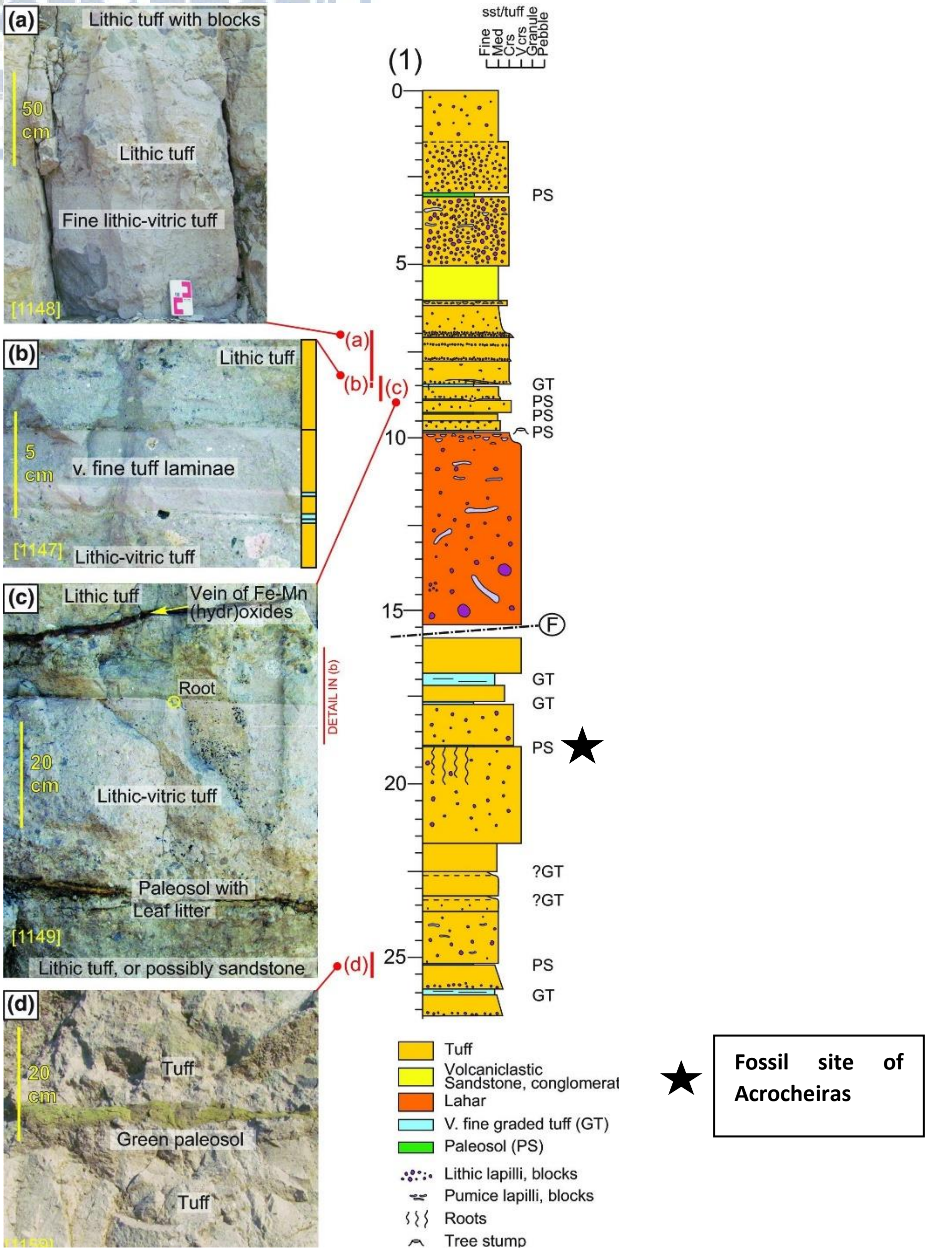



Figure 6. Detailed stratigraphic column showing the pyroclastic succession of Sigri- Antissa Road east of Bali Alonia park (from Pe- Piper et al., 2019)

### 2.1.3. The Petrified Forest of Lesvos

In the area of 15.000 ha enclosed by Eressos, Antissa and Sigri massive accumulations of fossilized tree trunks observed, comprising the Petrified Forest of Lesvos, declared as a Protected Natural Monument since 2012. During 2012, the whole Island of Lesbos (and not only the area of the Petrified Forest) recognized 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). On the western part of Lesvos, a great number of fossiliferous sites with standing and lying petrified tree trunks and leaves were found. The Petrified Forest of Lesvos represents an important stage of the earth's evolutionary processes and constitutes a unique natural monument. The Greek State recognized its exceptional and paleontological value and protected the Petrified Forest by declaring five terrestrial and marine areas with fossil accumulation, including the isolated fossils, as Protected Natural Monument with a special Presidential Decree (443/ 1985). The protection of the Petrified Forest was achieved though the establishment of the National History Museum of Lesvos Petrified Forest, in 1994. The protected area is a founder member of the European Geoparks Network (2000) and is included in the Global Geoparks Network in 2004. The protected area includes the already recognized Lesvos Petrified Forest Geopark and the remaining 148.000 ha of the total surface of the Island (Zouros, 2004).

2.1.3.1 The age of the Petrified Forest

The Petrified Forest was developed during Late Oligocene to Early- Middle Miocene, due to the extensive volcanic activity between approx. 18.5 to 17 Ma. Radiometric dating of the volcanic material and the presence of the lower jaw of *Prodeinotherium bavaricum* (v. Meyer, 1831) in silicified lacustrine marls below the volcanic rocks, suggested an age 19 to18 Ma for the plant assemblages of Lesvos (Koufos et al., 2003). Findings of micromammals along with lizard and crocodile remains in lacustrine deposits beneath the pyroclastic sequence, were classified in MN3/MN4 zone, about 16.9 to 20 Ma (Vasileiadou and Zouros, 2012), confirming the age of the formation of Sigri.

2.1.3.2. The fossilization of the Petrified Forest

The volcanic eruptions during that time, produced lava, pyroclastic materials and volcanic ash, which covered the vegetation of the area. The orientation of the trees indicates the possible direction of the pyroclastic flow units from E to W. The wood protection from decomposition, achieved through rapid burial and isolation from atmospheric conditions. Silicification may be the most important process in the preservation of plants in the fossil record, as involves the filling of pore spaces in the wood structure, known as perminelization. By this process, the organic cellular tissue replaced with $SiO_2$ so rapidly and delicately, that the structural details of the wood cells and morphology of leaf structure are retained (Ballhaus et al., 2012). The substrate that is able to bring elevated silica into solution is the volcanic tephra rich in glassy material (Murata, 1940; Karowe and Jefferson, 1987) or immature sediment with abundant detrital feldspar (Jefferson, 1987; Weibel, 1996; Matysova´ et al., 2010). The infiltration of silica to the wood achieved possibly by a combination of molecular diffusion via the interconnected solution in the lithic matrix and inside the tree, by fluid advections. The experiment techniques in the silicification of wood by Ballhaus et al. (2012) shown that the solution precipitation reactions are selective in bringing silica into solution and in reprecipitating it in the wood as opal. During the hydrolysis process of the obsidian with the water, silica and alkali- oxides readily enter the solution, when during the reaction of the solution with wood, silica is immobilized and precipitated in the cells with alkalis remain. By this process, silicified tree trunks may be composed almost totally of $SiO_2$ (Sigleo, 1979). The same experts, (Ballhaus et al., 2012), identified two forces that drive aqueous silica species into the wood and precipitate them as opal. The first driving force is the development gradient in pH between wood and the pyroclastic material. The infiltration of the acid environment of the wood by alkaline- silica waters drive in the opal precipitation. The second important force is the ability of wood to extract silica from an aqueous solution. These two forces confirm the hypothesis supported by Leo and Barghoorn (1976), that aquatic silica material can undergo chemical bonding with organic material.

2.1.3.3. The paleoflora of the Petrified Forest

Paleobotanical research has concentrated not only on the wood remains of Lesvos, but also on leaf fossils of the litter horizon of the Petrified Forest which gave useful data about the paleoflora, the climate and the age of the Petrified Forest (Velitzelos et al., 1981; Velitzelos and Zouros, 2000). The large number of the fossilized leaves and in situ tree trunks (autochthonous) allows the classification of the material and the reconstruction of the vegetation zones. The first scientific study of wood remains by the Austrian Botanist Franz Unger (Unger 1845, 1847, 1862) include: *Thujoxylum peucinum*, *Taxoxylum priscum* (= *Taxoxylon priseum* Ung.), *Peuce lesbian* (= *Cedroxylon lesbium* Kr.), *Juglandinium mediterraneum* (= *Juglandoxylon mediterraneum* Ung.), *Mirbellites lesbius* (= *Juglandoxylon mediterraneum* Ung.), *Brongniartites graecus*. Fliche (1898) described silicified trunks from Ordymos Mountain, with references to the fossil plants *Cedroxylon*, *Palmoxylon* and *Ebenoxylon*. The first results, based on the identification of leaf imprints, include: *Cinnamomum polymorpha* (= *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.), *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 and Kvacek), *Myrsinites* sp. [= *Dicotylophyllum* sp. 1- aff. *Cedrela attica*, *Rhus* sp., Sapotaceae (= *Dicotylophyllum sp*. 3)] (Velitzelos et al., 1981a; 1981b; revised by Velitzelos et al., 2014). Recent research in the area of the Petrified Forest of Lesvos indicated new species,

- amongwood remains: *Taxaceoxylon biseriatum*, the first occurrence of *T. albertense*, *T. pseudoalbertense* in the Tertiary of Europe and Greece, *Taxodioxylon megalonissum, Glyptostroboxylon lesboense*, *Podocarpoxylon articulatum*, *P. graciliradiatum*, *Chimairoidoxylon conspicum*, *Ginkoxylon lesboense*, *G. diversicellulatum*, *Lesbosoxylon (Pinoxylon*) *diversiradiatum*, *Lesboxylon* (*Pinoxylon*) *graciliradiatum*, *L. ventricosuradiatum;* and
- αmong leaf imprints: *Pronephrium stiriacum*, *Tetraclinis* sp., *Pungiphyllum cruciatum* (= *Quercus cruciata*), *Phoenix* sp. (= *Phoenicites* sp.), *Platanus* sp*., Acer* sp*., Laurus primigenia* (= Lauraceae vel Fagaceae gen. et al spec. indet.), *Daphnogene polymorpha*, *Quercus* sp*., Pinus sp., Sequoia abietina* (= *Sequoia abietina* vel *Taxodium* sp.), *Tetraclinis salicornioides*, *Rubus* sp*., Engelhardia orsbergensis*, *Rubus niacensis* ( partly = *Alnus cycladum*), *Sabal major*

The recent research on the classification of *Laurinoxylon* (Lauraceae) from new fossiliferous localities in Lesvos, indicated the first occurrence of several species, such as *Laurinoxylon* aff. *czechense* (*Laurinoxylon* Type 1), *Laurinoxylon* cf. *daberi* (*Laurinoxylon* Type 2a), *Laurinoxylon* aff. *diluviale* (*Laurinoxylon* Type 2b), *Cinnamomoxylon seemannianum* (*Laurinoxylon* Type 3), *Cryptocaryoxylon*, *Quercoxylon* and *Cedroxylon lesbium* (*Peuce lesbia*) (Mantzouka, 2016).

All the to date reported taxa (Table 1) belong to the higher plant groups of Angiospermae and Gymnospermae exept of the fern species *Pronephrium striatum*. From a phytogeographic point of view, the above-mentioned plant fossils can be distinguished in two main categories. The first group includes the subtropical plants like *Laurus* (laurel) and *Cinnamomum* (cinnamon), who's related modern species are found in south- eastern Asia forests. The second group comprises plants of mild temperature affinities such as *Alnus* (alder), *Carpinus* (hornbeam), *Populus* (poplar), *Quercus* (oak), *Pinus* (pine), Taxodioxylon gypsaceum (sequoia), etc. Related modern vegetation flourishes in the warm continental zones of south-eastern Asia and North America. The above data suggest a subtropical to warm temperate seasonal climate during Late Oligocene–Early Miocene (Velitzelos and Gregor, 1990; Suss and Velitzelos, 1994a,b).

Table 1. The early Miocene fossil record of Lesvos Island, including wood and leaf remain

| Taxa | Type of fossil | Author/ Reference |
|---|---|---|
| **Pteridophytes** | | |
| *Pronephrium stiriacum* | leaf | (Unger) Knobloch et Kvaček, 1976 |
| **Gymnosperms** | | |
| *Brongniartites graecus* | Wood | Unger 1845, 1847, 1862 |
| *Cedroxylon* | Wood | Fliche, 1898 |
| *Cedroxylon lesbium* | Wood | (Unger) Kraus Kräusel, 1919 |
| *Chimairoidoxylon conspicum* | Wood | Suss and Velitzelos, 2001 |
| *Chimairoidoxylon lesboense* | Wood | Suss and Velitzelos, 1999 |
| *Ginkoxylon diversicellulatum* | Wood | Suss and Velitzelos, 2003 |
| *Ginkoxylon lesboense* | Wood | Suss and Velitzelos, 2003 |
| *Glyptostroboxylon lesboense* | Wood | Suss and Velitzelos, 1997 |
| *Lesbosoxylon (Pinoxylon) diversiradiatum* | Wood | Suss and Velitzelos, 2010 |
| *Lesbosoxylon ventricosuradiatum* | Wood | Suss and Velitzelos, 2010 |
| *Lesboxylon* (*Pinoxylon*) *graciliradiatum* | Wood | Suss and Velitzelos, 2010 |
| *Peuce lesbian* | Wood | Unger 1845, 1847, 1862 |
| *Podocarpoxylon articulatum* | Wood | Suss and Velitzelos, 2000 |
| *Podocarpoxylon graciliradiatum* | Wood | Suss and Velitzelos, 2000 |
| *Taxaceoxylon biseriatum* | Wood | Suss and Velitzelos, 1994 |
| *Taxodioxylon albertense* | Wood | Suss and Velitzelos, 1997 |
| *Taxodioxylon megalonissum* | Wood | Suss & Velitzelos ,1997 |
| *Taxodioxylon pseudoalbertense* | Wood | Suss and Velitzelos, 1997 |
| *Taxoxylum priscum* | Wood | Unger 1845, 1847, 1862 |
| *Thujoxylum peucinum* | Wood | Unger 1845, 1847, 1862 |
| *Tetraclinis* sp. | Leaf | Velitzelos, 1993 |
| *Pinus* sp. | Leaf | Velitzelos and Zouros 2008 |
| *Sequoia abietina* | Leaf | Velitzelos and Zouros 2008 |
| *Taxodium* sp. | Leaf | Selmeier and Velitzelos 2000, |
| *Tetraclinis* sp. | Leaf | Velitzelos, 1993 |
| *Tetraclinis salicornioides* | Leaf | (Unger) Kvacek Velitzelos and Zouros 2008 |
| **Angiosperms** | | |
| *Brongniartites graecus* | Wood | Unger 1845, 1847, 1862 |
| *Cinnamomoxylon seemannianum* | Wood | (Mädel) Gottwald Gottwald, 1997 |
| *Cryptocaryoxylon* | Wood | Leisman, 1986 |
| *Ebenoxylon* | Wood | Fliche, 1898 |
| *Juglandinium mediterraneum* | Wood | Unger 1845, 1847, 1862 |
| *Laurinoxylon aff. Czechense (Laurinoxylon* Type *1)* | Wood | Prakash, Březinová and Bůžek Mantzouka, 2016 |
| *Laurinoxylon aff. diluviale (Laurinoxylon* Type 2) | Wood | (Unger) Felix emend. Dupéron et al. Mantzouka, 2016 |
| *Laurinoxylon cf. daberi (Laurinoxylon* Type 2) | Wood | Mantzouka, 2016 |
| *Mirbellites lesbius* | Wood | Unger 1845, 1847, 1862 |

| | | |
|---|---|---|
| *Palmoxylon* | Wood | Fliche, 1898 |
| *Quercoxylon* | Wood | Gros, 1983 |
| *Acer* sp. | Leaf | Velitzelos, 1993 |
| *Alnus cycladum* | Leaf | Unger<br>Velitzelos et al., 2014 |
| *Carpinus pliofaurei* | Leaf | Ratiani<br>Velitzelos et al., 2014 |
| *Carpinus uniserrata* | Leaf | (Kolakovski) Ratiani<br>Velitzelos et al., 2014 |
| *Daphnogene polymorpha* | Leaf | (A. Braun, 1845)<br>Velitzelos et al., 2014 |
| *Dicotylophyllum* sp. 1- aff. *Cedrela attica* | Leaf | Velitzelos et al., 2014 |
| *Dicotylophyllum sp*. 3 | Leaf | Velitzelos et al., 2014 |
| *Engelhardia orsbergensis* | Leaf | (Wessel & Weber) Jähnichen<br>Velitzelos and Zouros 2008 |
| Lauraceae vel Fagaceae | Leaf | Velitzelos et al., 2014 |
| Lauraceae vel Fagaceae aff. *Castanopsis bavarica* | Leaf | Velitzelos et al., 2014 |
| *Laurophyllum sp*. | Leaf | Velitzelos et al., 2014 |
| *Phoenicites* sp. | Leaf | Velitzelos, 1993 |
| *Populus balsamoides* | Leaf | Göppert<br>Velitzelos et al., 2014 |
| *Populus* sp. | Leaf | Velitzelos et al., 2014 |
| *Pungiphyllum cruciatum* | Leaf | (A. Braun) Frankenhäuser and Wilde (1995) Velitzelos, 1999 |
| *Quercus* sp. | Leaf | Velitzelos, 1999 |
| *Rhus* sp. | Leaf | Velitzelos et al., 2014 |
| *Rubus niacensis* | Leaf | Laurent<br>Velitzelos et al., 2014 |
| *Rubus* sp. | Leaf | Velitzelos and Zouros 2008 |
| *Sabal sp.* | Leaf | Velitzelos et al., 2014 |
| *Tilia* sp. | Leaf | Velitzelos et al., 2014 |

# 3. Material and Methods

## 3.1. Material

The present study deals with plant fossil material that was collected by the scientific team of the Natural History Museum of the Lesvos Petrified Forest, during the works took place in the context of opening the new road Sigri- Antissa. The fossil material was collected from a single outcrop, Akrocheiras (Sigri- Antissa road). The majority presents leaf imprints in blocks, without carbonized substance. The fossil material from Akrocheiras constitutes the majority of the examined leaf imprints in Sigri Pyroclastic Formation. Approximately 105 slabs with more than 235 macro-fossils were studied. All of them were collected from the thin-bedded lithic tuffs (main fossiliferous layer) and the related layers of paleosol.

Their surface is typically lightly grey-, black- or brownish-colored showing morphological features of the lamina and its venation. Due to severe oxidation, the cuticle on leaf imprints has not been preserved. All studied material is housed in in the Natural History Museum of the Lesvos Petrified Forest, under the collection numbers:

AKY 150 - AKY 447 for Akrocheiras site

## 3.2. Methods

### 3.2.1. Fossil collection

Akrocheiras Site

The bulk amount of the studied material was collected during the systematic excavation that was conducted from April to August in 2019. Initially, the loose, weathered material, which had been exposed to surface erosion, was removed. The main excavation work, during the opening of the new road, concentrated in the rich horizon of leaf imprints. For the main fossiliferous layer, due to its extensive thickness (about 2.8 m), hardness and compactness, the material was shred.

The fossiliferous sediments were already broken in blocks of various sizes by natural fracturing. The sediment blocks were removed by technical tools (compressor). The larger ones, were recorded, labeled, covered and put into wooden boxes stored at the laboratory of the Natural History Museum of the Petrified Forest of Lesvos. There, using hammers and knives the sediment blocks were split carefully seeking for fossils. The smaller blocks were split in the field and the recovered specimens were packed and transported to the laboratory for conservation and storage.

### 3.2.2 Taphonomic remarks on Akrocheiras assemblage

The Akrocheiras fossil assemblage comprises exclusively plant material, especially leaf imprints. Micro- mammal fossils or gastropod shells have not been found yet in this site. Nevertheless, the studied material presents direct evidence of other organisms related to the plants, such as feeding damage by invertebrate herbivores. Such co- occurrence of plants and arthropods in the fossil record is providing palaeoecological evidence concerning their interaction within the same habitat (Stork, 1987; Schoonhoven et al., 2005; Price, 2002). Moreover, the presence of arthropod feeding damages on leaf remains adds a new approach of past climatic estimations (Wilf and Labandeira, 1999; Wilf et al., 2001; Smith, 2008; Currano et al., 2010; Knor et al., 2012). In the fossil assemblage of Akrocheias, a single leaf remain of *Daphnogene polymorpha* bears evidence of arthropod feeding traces. This leaf with severely deformed lamina, probably represents external foliage feeding caused in an early stage of leaf growth (Zidianakis, 2018). The surrounding area of Akrocheiras, due to its geological and lithological composition, implies a transitional lake environment where estuarine paleoenvironments were interfacing with floodplain and riverbank that occurring close to the lake. The findings of micromammals along the adjacent area with lizard, gastropods, fish and crocodile remains in lacustrine deposits beneath the pyroclastic sequence supports the hypothesis of a fresh- water ecological environment (Zouros et al., 2012).

### 3.2.3. Methodology

Photographs were taken with a Canon digital camera, always in comparison with a scale. For image adjustments and drawings, the Photo Editor PIXLR X was used. The editing of the photos and the drawings of the Figs. achieved using Inkscape 0.92.4. Measurements of morphological characteristics of the leaf imprints, as well as the dimension and the size of angles of venation, were performed with the program ImageJ.

The identification of foliage was based on the macro- morphological features of the leaf imprints. The morphological characteristics used for the identification of the selected specimens are illustrated in Fig. 7. The used terminology for leaf architecture is based on Hickey (1973), Dilcher (1974), Ash et al. (1999) and Ellis et al. (2009) descriptions.

For the classification of the studied material in terms of zonal vegetation type, the integrated plant record (IPR) vegetation analysis, a semi- quantitative method based on taxonomic and ecological evidence, was applied (Kovar-Eder et al., 2008, Teodoridis et al. 2011).

For palaeoclimatic estimates the Climate Leaf Analysis Multivariate Program (CLAMP) (Kovach and Spicer, 1995; Wolfe and Spicer, 1999; Spicer, 2000; 2007; 2008; Spicer et al., 2004, Spicer et al., 2009, Yang et al., 2011; 2015) was applied. Finally, for palaeofloristic comparisons and statistical results, the Past3 software® (Hammer and Harper, 2009) was applied.

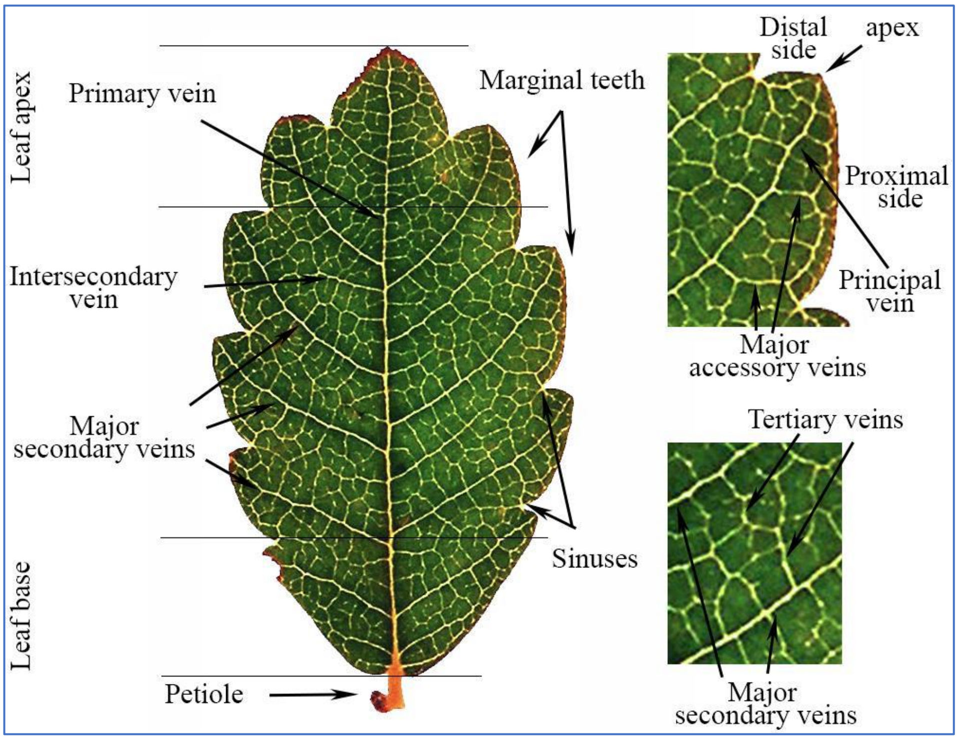



Figure 7. Leaf characters taken under consideration in the present study (Zidianakis, 2018).

# 4. RESULTS

## 4.1. Systematic paleontology

In the following chapter the identified plant taxa from Akrocheiras site are presented. All studied specimens are referred with the collection numbers of the Natural History Museum of the Petrified Forest of Lesvos.

### 4.1.1 The paleoflora of Akrocheiras

**Angiospermae**

**Monocotyledonae**

Family ARECACEAE

Genus *Phoenix L.*

*Phoenicites* sp.

Figs. 8–9

**Material**

Akrocheiras (AKY), thirty-five leaves; fragmentary: (Numbers AKY150a, AKY151, AKY161a, AKY161b, AKY165b, AKY168b, AKY170d, AKY173a, AKY173b, AKY176a, AKY178a, AKY188, AKY189, AKY217c, AKY217f, AKY220c, AKY227, AKY228, AKY231, AKY232, AKY233a, AKY234f, AKY235, AKY239, AKY244e, AKY245a, AKY258, AKY260, AKY269a, AKY269d, AKY311, AKY316a, AKY353, AKY430b, AKY441)

**Description:** Unarmed, -Fragments of compound pinnate leaves, 14–240 mm long and 9–87 mm wide, L/W ratio 2.6; rachis strong (preserved in specimens AKY353, AKY441); segments linear, V- shaped, at angles of 36-54˚, 14-186mm long and 14-101mm wide; base acute, apex not preserved; entire margin; venation parallelodromous, midrib delicate.

**Remarks:** *Phoenicites* sp. remains are dominant in the leaf assemblage of Akrocheiras. The genus was already known in North Aegean area, from the Early Miocene of Lesvos and the adjacent Island of Lemnos (Velitzelos et al., 2014). The Akrocheiras material shows strong affinities to the Early Miocene *Phoenicites* of Guvem area described by Denk et al. (2017: Plate 10, Figs 2, 4). The paleoecology of *Phoenicites sp.* indicates an element of riparian and swamp forests, defining the dominant environment of Akrocheiras site (Denk, 2017)

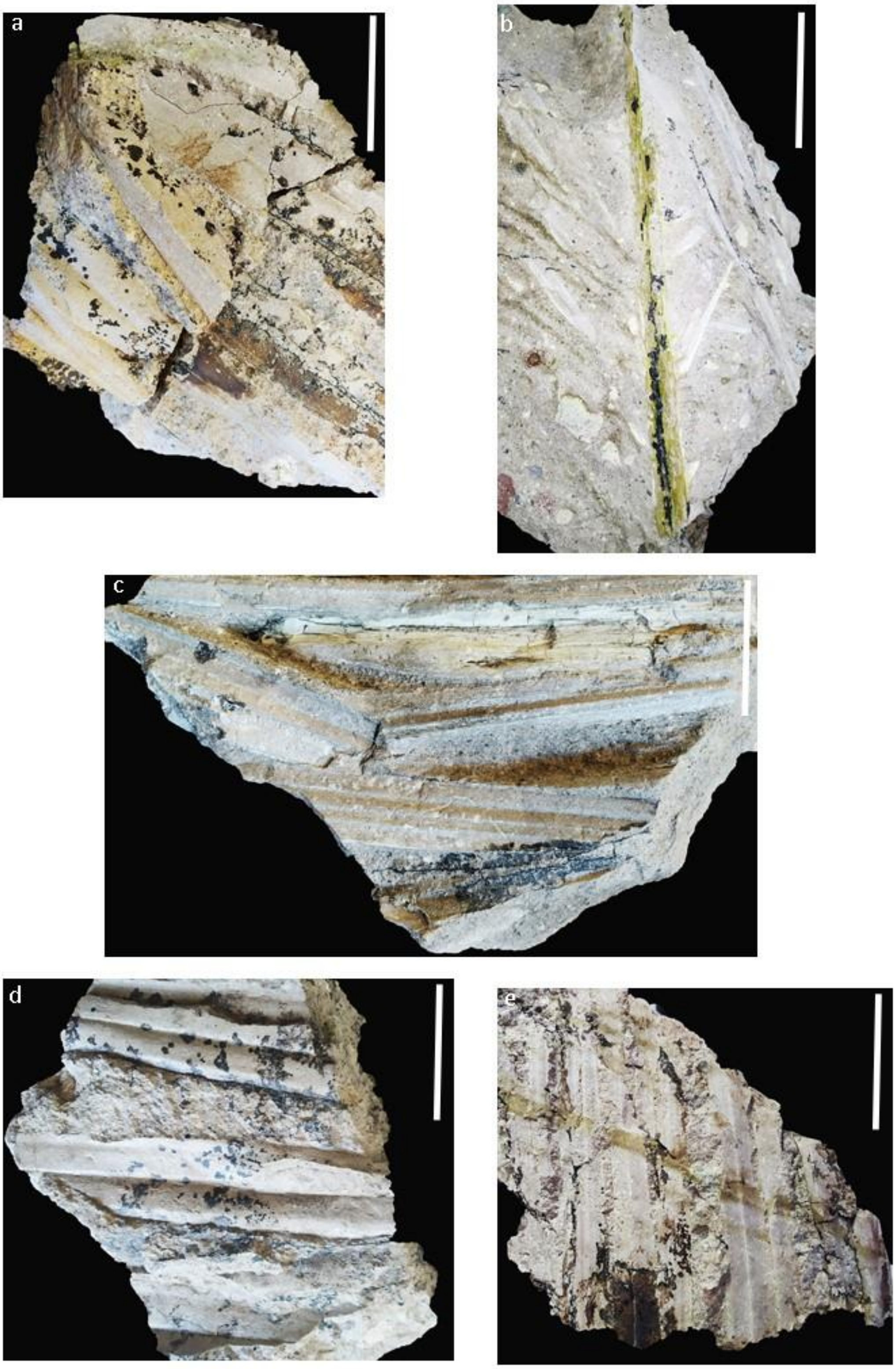



Figure 8. Aracaceae from Akrocheiras: Pictures a-e of *Phoenicites* sp. Scale bar 1cm (a: AKY165b, b: AKY353, c: AKY239, d: AKY 244e, e: AKY311


Figure 9. Aracaceae from Akroxeiras site. Pictures a-c of *Phoenicites* sp. Scale bar 1cm (a: AKY170d, b: AKY441, c: AKY316a

**Angiospermae**

**Dicotyledonae**

Family AQUIOFOLIACEAE DE CANDOLLE EX RICHARD

Genus *Ilex* L.

cf. *Ilex* sp.

Fig. 10a

**Material**

Akrocheiras (AKY): one complete leaf (Number AKY434a)

**Description:** Leaf simple, lamina shape elliptic, almost symmetrical, 78 mm long, 41 mm wide, L/W ratio 1.9, base angle acute, base shape cuneate, apex angle acute; margin serrate, regular spiny, teeth in the 1/3 upper part of the lamina, tooth shape apical side straight, basal side concave, sinus rounded, tooth apex spinose; venation semicraspedodromous, primary vein straight, slightly curved on the base, secondary veins strong, spacing irregular, arising from the midvein slightly convex, at angles of 35-55°, increasing angle towards the base, forming loops close to the margin from which small veinlets enter the spinose teeth; intersecondaries thinner, almost parallel to the secondary veins.

**Remarks:** The lamina shape and size, the spinose margin and especially the secondary venation pattern suggest affinities of genus *Ilex* for this specimen. This genus is refered from Lesvos for first time, as it was only known from the Late Miocene Cretan site (Makrilia) (Velitzelos et al., 2014), as well as from the Early Pliocene site of Ptolemaida, west Macedonia (Velitzelos et al., 2014) in the Greek Peninsula.

Family BETULACEAE GRAY
Genus *Alnus* Mill.
cf. *Alnus* sp.
Figure 10b

**Material**
Akrocheiras (AKY): one leaf, almost complete (Number AKY173b).

**Description:** Leaf petiolate, laminar size nanophyll, 20 mm long and 12 mm width, L/W ratio 1.66; lamina shape ovate, symmetrical; base angle acute and shape cuneate, apex angle acute and shape probably straight; margin serrate, tooth simple, tiny, distantly spaced, sinus shallow; venation distinct, midvein mediate in thickness, almost straight, secondaries thinner, craspedodromous, straight or slightly S-like, at angles of 40-55˚.

**Remarks:** The profound venation, the lamina size and the simply serate margin indicate that this single specimen could represents an extreme leaf form of *Alnus* and especially of *Alnus cycladum* Unger which is already known from the Early Miocene of Lesvos. Its poor preservation accounts for an ambiguous assignment. Velitzelos et al. (2014) reported from Lesvos a leaf fragment of possible *Alnus* affinity (cf. *Alnus* sp.: Pl. XII, fig. 4) which is close morphologically to that of Akrocheiras. The paleoecology of this genus indicates an element of riparian to well- drained lowland forests (Denk, 2017).

Family CANNABACEAE MARTYNOV
Genus *Celtis* L.
*Celtis japeti* UNGER
Figs. 10c–e

Original: 1852 *Celtis japeti* Unger – Unger: p. 44, pl. 20, figs 25, 26.
Synonym List in: Denk et al., 2017: p. 260, Pl. 10, fig.4

**Material**
Akrocheiras (AKY): two almost complete leaves and two fragmentary (Numbers AKY270c, AKY431a, AKY434b, AKY206b).

**Description:** Leaves simple, microphyll, asymmetric; lamina shape elliptical to ovate, 49–55 mm long (average 52 mm) and 27–32 mm width (average 29.5 mm), L/W ratio 1.5–2.0 (average 1.8); base distinctly asymmetrical, angle acute to obtuse, shape convex, apex not preserved; margin serrate, at the upper 2/3 part of the lamina, teeth closely, irregularlly spaced,variable in size rangings from tiny to large(mostly in the middle part of the lamina), tooth apex acute; primary venation acrodomous, one lateral primary vein almost straight, the other curved, at angles of approx. 25–50˚; secondary venation semicraspedodromous, originating from the primary vein at angles 40–65˚; intersecondaries thinner, almost parallel to the secondaries; tertiary veins opposite to alternate percurrent, sinuous, percurrent to forked percurrent, tertiary vein angle obtuse to almost perpendicular.

**Remarks:** We follow Knobloch (1998) and ascribe these leaves to *C. japeti* due to their venation, serrate margin and size. Similar leaves are also described from Guvem area in Turkey by Denk et al. (2017: Pl. 10, Fig. 5). In the Greek Neogene, this genus was already known from the early Miocene fossil record of Euboea, with the taxon *Celtis lacunosa* (Reuss) Kirchheimer, but this material indicates the first appearance of *Celtis* in Lesvos.

Figure 10. Aquiofoliaceae, Betulaceae and Cannabaceae from Akroxeiras site: a) cf. *Ilex* sp., b) cf. *Alnus* sp., c, d, e) *Celtis japeti*. Scale bar 1cm (a: AKY434a, b:173b, c: AKY270c, d: AKY431a, e: AKY206l)

Family FABACEAE

Genus *Leguminosites* BOWERBANK emend. SCHIMPER

*Leguminosites* sp.

Figs. 11 a–b

**Material**

Akrocheiras (AKY): two leaves almost complete (Numbers AKY159a, AKY206f).

**Description:** Leaflets petiolate, petiole partly preserved, about 1 mm long; texture coriaceous, lamina shape elliptic, 32-33 mm long, 10–16 mm wide, L/W ratio 2-3.2; base angle acute, asymmetric, apex angle obtuse, shape retuse, margin entire; venation brochidodromous, midrib prominent, almost straight, secondary veins much finer, hardly visible.

**Remarks:** These specimens show features common among Fabaceae, such assymmetrical base, retuse apex, brochidodromous venation and entire margin, introducing the first appearance of the genus in Lesvos. The presence of these fossil taxa indicates the first appearance of genus *Leguminosites* in the Early Miocene fossil record of Lesvos, as it was only known from the Late Miocene fossiliferous sites of Vegora (Velitzelos, 2014) , Metochia, Kassanoi and Pitsidia in Crete (Zidianakis, 2018) and Gavdos Island (Manzouka, 2016).

FAMILY JUGLANDACEAE

Genus *Carya* NUTTALL

*Carya* sp.

Figs. 11 c–d

**Material**

Akrocheiras (AKY): three leaves almost complete (Numbers AKY157, AKY159d, AKY262e).

**Description:** Lateral leaflets, subsessile; lamina shape elliptic to ovate, slightly asymmetrical, 45–75 (average 55) mm long and 24–30 (average 27) mm wide, L/W ratio 1.5–2.5 (average 2.0),; apex not preserved, base rounded to widely cuneate, asymmetric; margin simply serrate; teeth dense, irregular in shape, acute, basal side mostly convex; venation craspedodromous to semi- craspedodromous, primary vein moderate in thickness, bent, secondary veins thinner, almost opposite to alternate, interspacing in 4–6 mm, arising from the midrib at angles of 55–85˚, dixotomised close to the margin, sending veinlets into the marginal teeth; intersecondaries present, one per intercostal area, almost parallel to the secondaries; tertiary veins dense, percurrent.

**Remarks:** The leaf architecture of these samples, especially the margin, the course of secondaries, percurrent tertiaries, resembles leaflets of Juglandaceae and especially to the genera *Carya, Juglans and Pterocarya.* The ovate shape of the lamina, the irregular serration of the teeth in the margin and the occasionally craspedodromous venation of the secondary veins indicates an affinity to *Carya* sp., introducing the first appearance of the genus in Lesvos. *Carya* remains are rare in the Early Miocene fossil record of Greece, as the only representative, *Carya ventricosa* (Sternberg) Unger identified in the Burdigalian assemblage of Euboea. On the contrary the studied material shows great affinities to the Late Miocene paleoflora of Pitsidia, Crete (Zidianakis, 2018: PLATE XXXI, figure 3-13), In Upper Miocene assembalges this genus is rather common in several Greek localities (e.g. Lala in Peloponnesus, Makrilia and Pitsidia in Crete, Samos, Ptolemaida), in combination with the genus of *Pterocarya.*

Genus *Engelhardia* LESCHENAULT ex BLUME

aff. *Engelhardia osbergensis* (WEBER) JÄHNICHEN, MAI and WALTER

Figs. 11 e–f

**Original:** 1977 Engelhardia orsbergensis (WESSEL and WEBER) – JÄHNICHEN et al., p. 326, pls 38–49; text-figs 1–3

**Synonym List in**: Zidianakis, 2018: p.86, Pl. XLIX, figs ?13,14

### Material

Akrocheiras (AKY), three leaves almost complete: (Numbers AKY206, AKY435a, AKY436).

**Description:** Leaflet shortly petiolutate (in specimen AKY206e) lamina shape lanceolate, slightly asymmetrical, 52–117 mm long and 23–35 wide, L/W ratio approx. 3, base rounded to cuneate, slightly asymmetric, apex acute (in specimen AKY436), margin simply dentate, tooth spacing irregular, teeth small, acute; venation semicraspedodromous, primary vein strong, more or less curved, secondary veins thinner, originating at angles of 40–75˚, usually densely spaced, intersecondaries delicate, almost parallel to secondaries.

**Remarks**: The asymmetric lamina with the simply dentate margin and the venation pattern are characteristic of *Engelhardia osbergensis* (Weber) Jähnichen, Mai and Walter, a well-documented thermophilous taxon of the European Tertiary (Jähnichen et al., 1984). This taxon is common in the Early Miocene sediments of Lesvos. It commonly thrived in sub-tropical towarm-temperate mesophytic forests (Jähnichen et al., 1977).


Figure 11. Leguminosae and Juglandaceae from Achroxeiras site: a, b) Leguminosites sp., c, d) *Carya* sp., e, f) aff. *Engelhardia* sp. Scale bar 1cm (a: AKY206f, b: AKY159a, c: AKY157, d: AKY159d, e: AKY435a, f: AKY436

Genus *Juglans* L.

*Juglans* sp.

Figs. 12 a–d

**Material**

Akrocheiras (AKY), four leaves almost complete: (Numbers AKY214a, AKY207c, AKY431c, AKY445).

**Description**: Leaves possibly sessile, lamina shape ovate, slightly asymmetrical, 27–83 mm long (average 56 mm) and 9–20 mm wide (average 20 mm), L/W ratio approx. 3-4; base angle acute, base shape cuneate to convex, slightly asymmetrical, apex acute to acuminate; margin simply serrate, teeth small, irregular spacing, denser in the middle and the upper part of the lamina, tooth basal side mostly straight, apical side straight to concave, sinus shallow, rounded to anglar,; venation brochidodromous to semicraspedodromous, primary almost straight, secondary veins thin, originating at angles of 35–60˚, alternate, widely spaced, strongly bent from about half of their course to the leaf margin, forming wide loops close to the margin.

**Remarks:** The leaf architecture of these samples, especially the lamina shape and serrate margin and the pattern of venation, resembles leaflets of *Juglans.* In the Greek Early Miocene this genus is only known from the paleofloras of Euboea with the taxon of *Juglans acuminata* A. Braun. This material marks the first appearance of the genus in Lesvos, based on leaf imprints, through its presence is supported by the existence of wood remains of *Juglandoxylon mediterraneum* (Unger) Kraus (Mantzouka, 2016).


Figure 12. Juglandaceae from Akroxeiras site: Pictures a-d from *Juglans* sp. Scale bar 1cm (a: AKY445, b: AKY214a, c: AKY207c, d:AKY431c

Family LAURACEAE

Genus *Daphnogene* UNGER

*Daphnogene polymorha* (A. BRAUN) ETTINGSHAUSEN

Figs. 13 a–f

**Original**: 1992 *Daphnogene polymorpha* (A. Braun) Ettingshausen – Velitzelos et al., pl. 6, figs 6–7 (Aliveri, Euboea, Early Miocene)
**Synonym list in:** Zidianakis, 2018, p.50, Pl. XVII, figs 1-11; Pl. XLIII, figs. 3,6-17; Pl. XLIX, fig.5

## Material

Akrocheiras (AKY): thirty one complete or almost complete leaves and nineteen fragmentary (Numbers AKY154a, AKY154b, AKY154c, AKY155; AKY158a, AKY158b; AKY170a; AKY170b; AKY175b, AKY 175c; AKY198a; AKY202b; AKY206a,AKY206g,AKY206i; AKY207d; AKY209g; AKY217d, AKY217e; AKY220a, AKY220b; AKY229b, AKY229c, AKY229d; AKY233b; AKY234c,AKY234d, AKY234e; AKY241; AKY244a,AKY244b,AKY244d; AKY245b,AKY245d,AKY245e; AKY246; AKY257; AKY259; AKY262a,AKY262b, AKY262c, AKY262d; AKY270b, AKY270d; AKY284b; AKY329b; AKY348b; AKY431b, AKY432b, AKY432c).

**Description:** Leaves simple, petiole robust, mostly incompletely preserved; lamina coriaceous in texture, polymorphic in shape, mostly lanceolate, elliptic to ovate, rarely obovate or falcate; 22-107 mm long and 10-31 mm wide, L/W 2.2- 3.4 index; base angle acute, rarely obtuse, base shape variable, cuneate to convex, rarely rounded or decurrent, apex acute to acuminate, leaf margin entire; venation suprabasal acrodromous, central primary vein stout, commonly gently curved apically or throughout its length, lateral primary veins thinner, arranged almost parallel to the margin of leaf, arising from the central vein at angles of 20–30˚, distances of 4–7 mm from the leaf base, extending to the 1/3 upper part of the lamina; secondary veins quite thinner, originating at angles of 35–60˚, mainly straight in course, curved close to the margin forming wide loops with the adjacent ones.

**Remarks:** This species is a dominant element in the flora of Akrocheiras, with leaves similar in shape and size with those of Kymi (Velitzelos, 1993; Velitzelos et al., 2002b), but narrower and thinner than those of Evros (Velitzelos et al., 2002a) and Kassanoi (Crete), possibly suggesting different ecological growth conditions. In specimen AKY432b lamina distortion caused by arthropod action is documented.

In the Greek Neogene, *D. polymorpha* is common with the exception of the Messinian floras of W. Macedonia and of N. Thessaly. This taxon is considered as an evergreen element mostly in mixed mesophytic forests. A direct correlation to an extant genus of Lauraceae is not possible so far (Ferguson, 1971; Kvaček and Walther, 1974).

Figure 13. Lauraceae from Akroxeiras site: Pictures a-f from *Daphnogene polymorpha*. Scale bar 1cm.(a: AKY155, b:AKY198a, c:AKY170a, d:AKY175c, e:AKY246, f:AKY432b

Lauraceae gen. et spec. indet.

Figs. 14a–b

**Material**

Akrocheiras (AKY) two almost complete leaves and one fragmentary (Numbers AKY171, AKY172a, 270a)

**Description:** Leaves simple, petiolate, lamina shape elliptic, symmetrical, both ~58 mm long and 24 mm wide, L/W ratio 2.4 (Appendix A), base angle acute, base shape cuneate, apex not preserved, margin entire; venation weak brochidodromous, midrib moderate in thickness, slightly curved, secondary veins delicate, irregular, widely spaced, opposite arranged, arising at angles of 35–45˚, intersecondaries weak, hardly visible.

**Remarks:** The lamina shape, the entire margin, and the brochidodromous pattern of venation suggest a Lauraceae origin for these specimens. Lauraceae leaves are common in the European Tertiary fossil record and is already known from the fossil assemblages of Lesvos. These taxa are already known from Güvem area (Early Miocene), as described by Denk et al., (2017: Pl. 22, figs 9). Unfortunately, the complexity and the heterogeneity of this family makes it impossible for a further systematic position.

Lauraceae vel Fagaceae gen. et. spec. indet.

Figs. 14 c, ?d, e

**Material**

Akrocheiras (AKY)sixteen almost complete leaves and four fragmentary (Numbers AKY168a, AKY174b, AKY176b, AKY205, AKY206h, AKY206i, AKY209d, AKY209e, AKY225, AKY226, AKY234b, AKY284e, AKY285a, AKY218b, AKY437, AKY438, AKY440, AKY442)

**Description:** Leaves simple, petiolate (preserved in the specimens 168a, 206h, 284e), petiole approx. 8 mm long, often slightly twisted; lamina shape elliptic to ovate, 20– 113 mm long (average 66mm) and 8–45mm wide (average 26 mm), L/W ratio 2.6; base angle acute, shape cuneate to slightly convex, apex angle acute, shape mostly straight; margin entire; venation semi-craspedodromous (occasionally craspedodromous) to weak brochidodromous, midvein stout, more or less straight, secondary veins strong, originating from the midrib at angles of 40–70 ˚, alternate, , dense usually curved, and widely spaced, bent in course; intersecondaries thinner, almost parallel to the secondary veins, tertiary veins opposite to alternate percurrent.

**Remarks:** The lamina shape, the entire margin and the venation pattern of these specimens are common characteristics in both Lauraceae and Fagaceae, during the Early Miocene. Many genera from Lesvos, previously assigned to the family of Lauraceae, as *Laurus* sp. (Velitzelos et al., 1981), *Laurus primigenia* (Velitzelos et al., 1999), *Litsea primigenia* (Velitzelos eta l., 1981), where revised by Velitzelos et al. (2014) to Lauraceae vel Fagaceae. The specimens of Akrocheiras site resemble in gross morphology to the Lauraceae vel Fagaceae from Lesvos island that described by Velitzelos et al. (2014: Pl. XII, figs 5, 6, 9).


Figure 14. Lauraceae from Akroxeiras site: a, b) Lauraceae gen. et spec. indet., c, d, e) Lauraceae vel Fagaceae gen. et spec. indet. Scale bar 1cm (a: AKY171, b: AKY172a, c: AKY318b, d: AKY438, e: AKY437, f: AKY440)

FAMILY LYTHRACEAE

Genus *Decodon* J.F. GMELIN

*Decodon* sp.

Figs. 15 a–b

**Material**

Akrocheiras (AKY): five almost complete leaves (Numbers AKY444a, AKY444b, AKY444c, AKY444d, AKY444e)

**Description:** leaves simple, lamina shape linear to lanceolate, 200–230 mm long and 40–60 mm wide, L/W index 3.5, base angle acute, shape cuneate, apex not preserved, entire margined; venation brochidodromous, midvein prominent, straight, secondaries dense, interspacing at distances of 5–6 mm, almost perpendicular to the midvein, straight in course or slightly curved, joined into an intramarginal vein.

**Remarks:** This foliage is well distinguished from other lanceolate, entire leaves by the presence of the prominent intramarginal vein. Such leaves are common in Central Europe during the Early Miocene, such as Most Basin in northern Bohemia and Altmittweida in northwestern Saxony (Wójcicki and Kvaček, 2002). Initially, this foliage from the Most Basin assemblages, have been misinterpreted, assigned to *Sapindus* (Ettingshausen, 1869) or *Salix angusta* A. Braun (Engelhardt, 1891). The studied fossils from Akrocheiras present strong affinities to the L. Miocene material of Most Basin, Northern Bohemia (PLATE II, Figs. 8-12), while the laminar shape, the density of the tertiary veins and the angles of the secondary veins are the characteristics that match the variation of *Decodon gibbosus* (E. M Reid) E. M Reid*,* as reposted by Kvaček and Sakala (1999). Leaves of *Apocynophyllum helveticum* from the Early Miocene of Saxony, are probably identical to those from Most Basin and Akrocheiras. The examined material from Akrocheiras indicates the first occurence of *Decodon* in the fossil record of Lesvos. This genus is less frequent in the Early Miocene of Greece, as is known only from the fossil record of Euboea (Velitzelos, 2014), while it is well-documented in many Late Miocene localities, such as Vegora, Pikermi-Chomateri (Gregor and Velitzelos, 1985) and Kassanoi in Crete (Zidianakis, 2018). The paleoecology of many Lythraceae suggests shallow water to swampy paleoenvironments.

Family MYRICACEAE
Genus *Myrica* L.
*Myrica* sp. SAPORTA
Figs. 15 c–d

**Material**
Akrocheiras (AKY): four fragmentary leaves (Numbers AKY153a, AKY153b, AKY196, AKY209f)

**Description:** Leaves simple, petiolate, petiole incompletely preserved; lamina texture coriaceous; lamina shape lanceolate to linear, size microphyll or less frequently mesophyll, 44–90 mm long (average 67 mm) and 12–25mm wide (average 18 mm), L/W ratio 3.6, base decurrent, apex not preserved; margin entire; venation weak brochidodromous, primary vein prominent, more or less straight, secondary veins fine hardly visible.

**Remarks:** The lamina shape, the venation and the entire margin of these specimens match to the morphology of *Myrica.* In the Greek area, this genus is already known from the early Miocene sites of Lesvos, Grevena and Euboea. The entire margined leaves from Akrocheiras, shows affinities to *Myrica lignitum* of Euboea*,* as described by Velitzelos (2002: Pl. 10, figs 2, 20, 21, 24). On the contrary, the *M. lignitum* leaf material from Guvem (Denk et al., 2014) and Kymi (Velitzelos et al., 2014) shows a distintly serrate margin. *Myrica* is usually considered as component of swamp and riparian forests.

Family SALICAEAE
Genus *Populus* L.
cf. *Populus balsamoides* GÖPPERT
Figure 15 e

**Original:** 1855 Populus balsamoides Goeppert, p. 23, pl. 15, figs. 5–6.

**Material**
Akrocheiras (AKY): Two fragmented leaves (Numbers, AKY172b, AKY207b).

**Description:** Leaves simple, lamina broadly ovate, about 36 mm long and 30 mm wide (the preserved parts) in the best preserved specimen AKY172b, base and apex not preserved, margin poorly preserved, probably dentate to serrate; primary vein moderate in thickness, secondary veins semicraspedodromous, slightly thinner, arising at angles of 30–70˚ angle decreasing distaly, curved in course; the first pair arising to the base more prominent than the others, tertiary veins percurrent, opposite to alternate, perpendicular to the secondaries, slightly sinous.

**Remarks:** The lamina shape and margin as well asthe density of the tertiary veins match to *P. balsamoides.* This element is already known from the fossil record of Lesvos and constitutes a common species in the European Neogene.


Figure 15. Lythraceae, Myricaceae and Salicaceae from Akrocheiras site: a, b) *Decodon* sp., c, d) *Myrica* sp., e) cf. *Populus balsamoides.* Scale bar 1cm (a: AKY444a, b, b: AKY444c, d, c: AKY153a, b, d: AKY209f, e: AKY172b)

Family SMILACACEAE VENT.
Genus *Smilax L.*
*Smilax weberi* P. WESSEL
Figure 16 a

**Original**: 1856 Smilax weberi Wessel in Wessel & Weber – Wessel & Weber: p. 127, pl. 21, fig. 1.
**Synonym List in**: Denk et al., 2017, p. 304, Pl. 35, figs 3, 4

### Material

Akrocheiras (AKY): one fragmentary leaf (Number AKY159c)

**Description:** Leaf simple, lamina shape widely ovate- auriculate, preserved maximum length76 mm, 82 mm wide; base angle reflex, shape broad cordate , apex not preserved; margin entire; primary venationacrodromous, midvein relatively thick, lateral primaries 3 in each side, bent towards the apex outer lateral veins sending curved veinlets towards the margin; interior secondary veins thin, hardly visible.

**Remarks:** Based on gross morphology, the specimen from Akrocheiras matches well to *Smilax weberi*. According to Denk et al. (2015), all the records of *Smilax* from the Oligocene and Miocene sediments of Euraesia and North America can be attributed to four different morphotypes. The "Weberi morphotype" in which the studied specimen can be undoubtelly assigned corresponds to the most widespread leaf type in modern *Smilax*, found in all main clades of the genus. Although this genus was already known from the Early Miocene fossil record of Euboea (Velitzelos et al., 2014; Denk et al., 2015) the single specimen from Akrocheiras documented the occurrence of *Smilax* in Lesvos for first time. In Euboea and Guvem the genus of *Smilax* is represented by two different species, *S. weberi* and *S. miohavanensis* (Denk et al., 2017). *Smilax weberi* is considered as a liana thrived mostly in swampy or riparian environments.

Genus *Pungiphyllum* FRANKENHÄUSER and WILDE
*Pungiphyllum cruciatum* (A. BRAUN) FRANKENHÄUSER and WILDE
Figs. 16 b–g

**Original:** 1995 *Pungiphyllum cruciatum* (A. Braun) Frankenhäuser and Wilde, p. 101 (Öhningen).

**Synonym List in**: Kvaček, Z., Walther, H., 2004, p. 35, Pl. 16, fig. 8, text-fig. 12.1

### Material

Akrocheiras (AKY): twenty-seven complete or almost complete leaves and nine fragmentary (Numbers AKY162, AKY163, AKY169, AKY170c, AKY202a, AKY207a, AKY209b, AKY269c, AKY238, AKY284a, AKY284c, AKY284d, AKY289a, AKY289b, AKY293, AKY295b, AKY306, AKY318a, AKY329a, AKY349, AKY384a, AKY404, AKY408b, AKY408c, AKY410b, AKY410c, AKY432a, AKY434c, AKY434d, AKY434e, AKY446, ? AKY443, AKY447a, AKY447b, AKY447c, AKY446).

**Description:** leaves or leafletsmicrophyllum to mesophyllum in size, lamina chartaceous; 137 mm – 30 mm long (average 66 mm) and 132 mm –16 mm width (average 57 mm), L/W ratio 1.15; margin mostly deeply lobate (Kvaček, 2004) with varied number of thorny simple lobes, 0-3-5 i lobes on either leaf side, the larger lobes in the upper part of the lamina, margin lamella- like thickened; venation craspedodromous to camptodromous, midrib strong, secondary veins attached at an angle of 38–70˚, intersecondaries forked, tending to a comptodromous pattern, tertiary veins irregular, usually not visible.

**Remarks:** The systematic position of this species remains obscure (Frankenhäuser and Wilde, 1995). Previously, it has been assigned to *Ilex*, *Mahonia* or *Quercus*. However, the stomata of this species do not correspond to the type of *Quercus* or *Ilex* (Kvaček and Walther, 1981). The enigmatic leaves of *P. cruciatum* rarely occur in the Oligocene and Early to Middle Miocene floras of North Bohemia (Kvaček, 2002a). On the contrary, they are abundant in Akrocheiras and in other fossiliferous sites of Lesvos, representing possibly a thermophilous, xerophytic element (Krutzsch, 1992). Similar features also occur in leaf imprints from Kučlín and in Ipolytarnoc, Czech Republic, described as *Pungiphyllum cf. waltheri* (Frankenhäuser and Wilde) (Kvaček, 2002a).


Figure 26. Smilacaceae from Akroxeira site, a) *Smilax weberi*., b- g) *Pungiphyllum cruciatum*. Scale bar 1cm (a: AKY159c, b: AKY163, c: AKY384a, d: AKY202a, e: AKY208b, f: AKY443, g: AKY169)

# 5. DISCUSSION

## 5.1. The composition of the palaeoflora of Akrocheiras

The palaeoflora of Akrocheiras comprises thirty-five speciments of Monocots and at least one hundred forty-five of Dicots, documented by foliage and defoliated shoots leafy shoots. Among them, arboreal elements prevail. Floristically the assemblage is characterized by the predominance of Palaeotropic elements, while Arctotertiary elements are less common (Fig. 17).

*Daphnogene polymorpha* predominates, represented by more than 20% of the examined specimens, while *Phoenicites* sp. (20%), *Pungiphyllum cruciatum* (20.4%) and Lauraceae vel Fagaceae gen. et. spec. indet. (11%), are abundant (Figure 18). Among accessory elements, documented by a few specimens, are cf. *Alnus* sp., *Carya* sp., *Celtis japeti*, *Decodon* sp., aff. *Engelhardia orsbergensis*, cf. *Ilex* sp., *Juglans* sp., Lauraceae gen et spec. indet., *Leguminosites* sp., *Myrica* sp., cf. *Populus balsamoides* and *Smilax weberi*.

Gymnosperm elements are absent while Monocots are represented by a single genus, *Phoenicites.* Additionally, there are several leaf remains, mostly heavily fragmented or poorly preserved of problematic affinity.

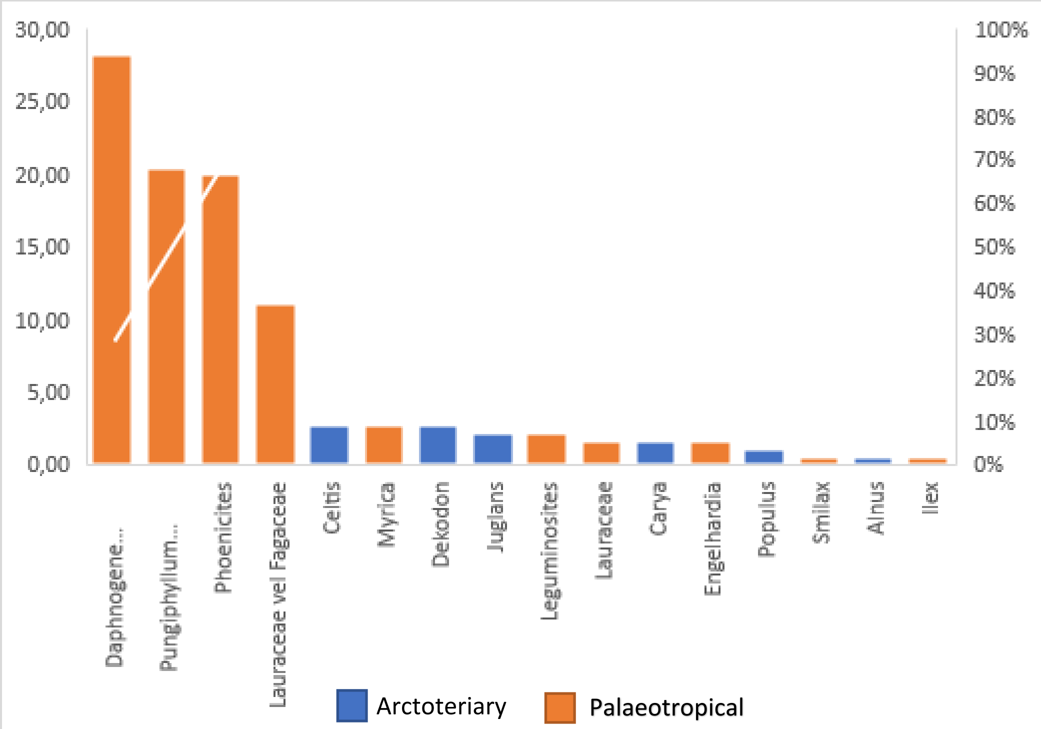



Figure 17. Frequencies (%) of the identified plant taxa of Akroxeiras site. Classification of the Arctotertiary and the dominant Palaeotropical taxa of the fossil material.

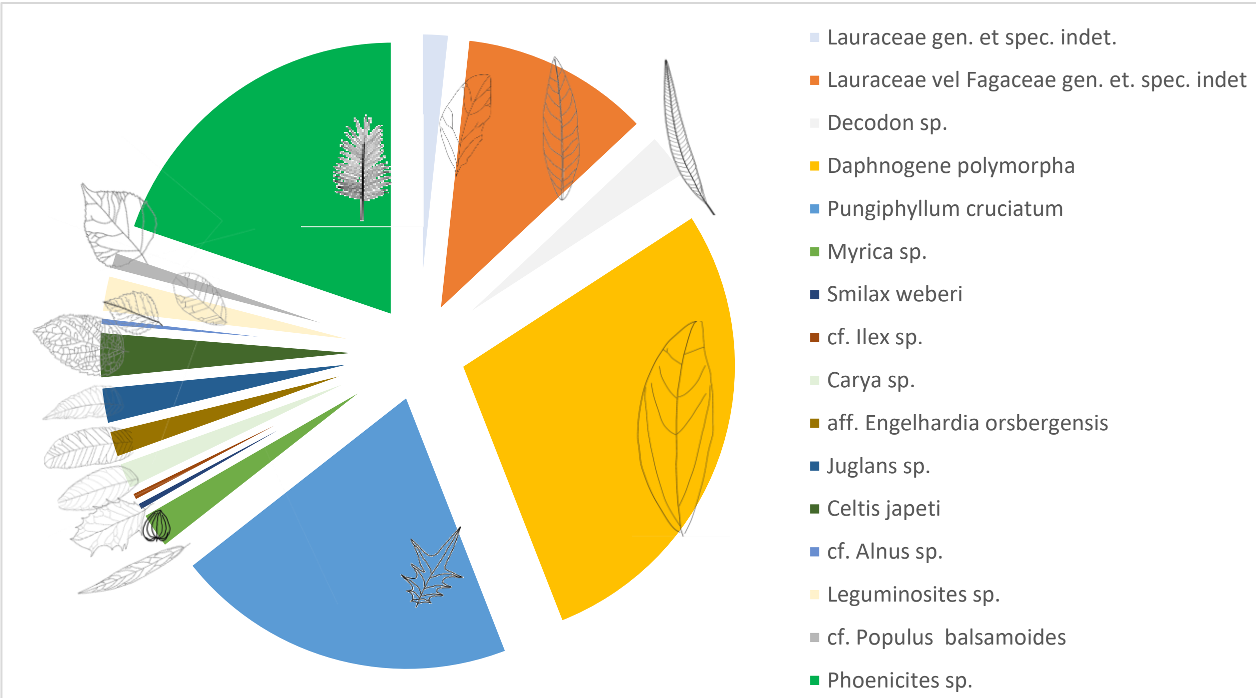



Figure 18. Frequencies of plant taxa in Akrocheiras site

## 5.2. Vegetation reconstruction

### 5.2.1 Intergrated plant record- vegetation analysis

According to the key components for defining vegetation types of the material, the plant assemblages of Akrocheiras belong to the zonal subtropical, subhumid sclerophyllous or microphyllous forest (ShSF). The percentages of the main components are as follows: broad-leaved deciduous component (BLD) 36.8%, broad- leaved evergreen component (BLE) 36.8%, sclerophyllous+ legume- like components (SCL+ LEG) 22.6 %, zonal- azonal palms 1%. The results are presented in the Table 2.

Table 2. Results and assigning zonal vegetation types of Akrocheiras site by using IPR vegetation analysis for the assemblages (sensu Kovar-Eder et al., 2008).

| Locality | % of BLD | % of BLE | % of SCL+LEG | Zonal Palm | % of DRY HERB | % of MESO HERB | Azonal Woody | Azonal non-woody | % 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., 2011 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Akrocheiras | 36.8 | 36.8 | 22.6 | 1 | 0.66 | 0.00 | 1.33% | 1.00% | 0.00 | 13.59 | 13.59 | 16.8 | 0 | ShSF |

### 5.2.2 Phytosociological approach

The area of Sigri comprised lowlands with freshwater lakes, as confirmed by the finding of lizard dentaries, crocodile remains, lacustrine gastropods and lacustrine fish (Vasileiadou et al., 2012), surrounded by highlands. The herein described assemblage dpresents a mixed environmental signal, pointing to a heterogenous landscape in Akrocheiras site (Table 3). The Akrocheiras fossil assemblage comprises of leaves that mostly underwent natural shedding. There is no evidence for extreme natural phenomena, as strong winds, severe infections or animal action which caused strong loss of plant parts. The high percentages of *D. polymorpha*, *Phoenicites* sp. and *Pungiphyllum cruciatum* indicate that these taxa were probably dominant in this part of the forest or close to the depositional area.Taxa with a few representatives in the fossil material, probably played a minor role in the composition of the vegetation of the area.

From a phytosociological approach, the taxa of the Akrocheiras assemblages, could be assigned to five different habitat types (vegetation units-VUs, Denk 2016), depending on the altitude and the distance of the coastline/ river and lakes (Fig. 19): open landscapes with shrubs and/ or small trees in subtropical/moist and/or dry forests (VU 0), swampy and lowland riparian forest on waterlogged substrates (VU 3, 4), and mesophytic forests on well drained soils (VU 5,6). The plant assemblages correlated to open landscape (VU0), are characterized by the presence of Fabaceae leaflets (*Leguminosites* sp.1) and the enigmatic evergreen *Pungiphyllum cruciatum*, as shrubs or lianas, indicative of a xerophytic environment. The vegetation surrounding lakes (VU 3 & 4) is characterized by swamp elements and representatives of the wetland, such as *Myrica* sp. and cf. *Alnus* sp., *Smilax* sp. *and Decodon* sp. Swamp forest communities and wet meadows also contained palms (*Phoenicites* sp.). A rich riparian forest, which was present along the active river channels and slightly- drained areas around the lake (VU4), indicated by cf. *Alnus* sp., *D. polymorpha*, *Populus* sp., *Carya* sp., *Celtis japeti,* and *Ilex* sp. *Juglans* sp. and cf. *Populus balsamoides* are also part of the riparian vegetation. The mesophytic elements, such as *Leguminosites, Engelhardia* sp., *Juglans* sp. and representatives of Lauraceae-Fagaceae, occurring further away from the deposition area, comprised the well- drained lowland forest (VU 5, 6).

Table 3. Origin, ecological preferences and the modern type of the Akrocheiras floristic elements

| Number | Fossil taxa | Origin | Ecological preference | VU (Denk 2016) | Modern type | Distribution of modern species |
|---|---|---|---|---|---|---|
| 1 | *Daphnogene polymorpha* | Palaeotropic | Mesophytic, Riparian | VU3,4,5 | Lauraceae | Cosmopolitan, present on warm temperatures |
| 2 | *Leguminosites sp.* | Palaeotropic | Mesophytic, xerophytic | VUO | Fabaceae | Cosmopolitan |
| 3 | *Smilax* weberi | Palaeotropic | Swamp, riparian | VU3,4 | *Smilax* spp. | Asia, North America |
| 4 | *Carya* sp. | Arctotertiary | Riparian | VU3,4 | *Carya* spp. | Asia, N. America |
| 5 | *Juglans* sp. | Arctotertiary | Mesophytic, Riparian | VU3,4 | *Juglans* spp. | Eurasia, America |
| 6 | *aff. Engelhardia orsbergensis* | Palaeotropic | Mesophytic | VU5,6 | *Engelhardia* spp. | E. Asia, Central America |
| 7 | *Myrica* sp. | Palaeotropic | Costal, Swampy, ?Riparian | VU3,4 | *Myrica* spp. | North, Central America |
| 8 | cf. *Populus balsamoides* | Arctotertiary | Riparian | VU3,4 | *Populus* spp. | N. Hemisphere |
| 10 | cf. *Ilex sp.* | Palaeotropic | Riparian, mesophytic | VU3,4 | *Ilex* spp. | Europe, N. America |

| | | | | | | |
|---|---|---|---|---|---|---|
| 9 | *cf. Alnus* sp. | Arctotertiary | Swamp, riparian | VU3,4 | *Alnus* spp. | N. temperate zone, C. America, Andes |
| 10 | Lauraceae | Palaeotropic | Mesophytic | VU5,6 | Lauraceae | SE Asia, S. America |
| 11 | *Phoenicites* sp. | Palaeotropic | Swamp, Riparian, costal | VU3,4 | *Phoenix* spp. | Cosmopolitan |
| 12 | *Pungiphyllum cruciatum* | Palaeotropic | Xerophytic | VUO | *Quercus* sp. | N. Hemisphere |
| 13 | *Decodon* sp. | ---- | Aquatic, Swampy | VU3,4 | *Decodon* spp. | North America |
| *14* | *Celtis japeti* | Palaeotropic | Riparian | VU3,4 | *Celtis* spp. | N. Hemisphere |
| *15* | Lauraceae vel Fagaceae | Palaeotropic | Mesophytic | | | |

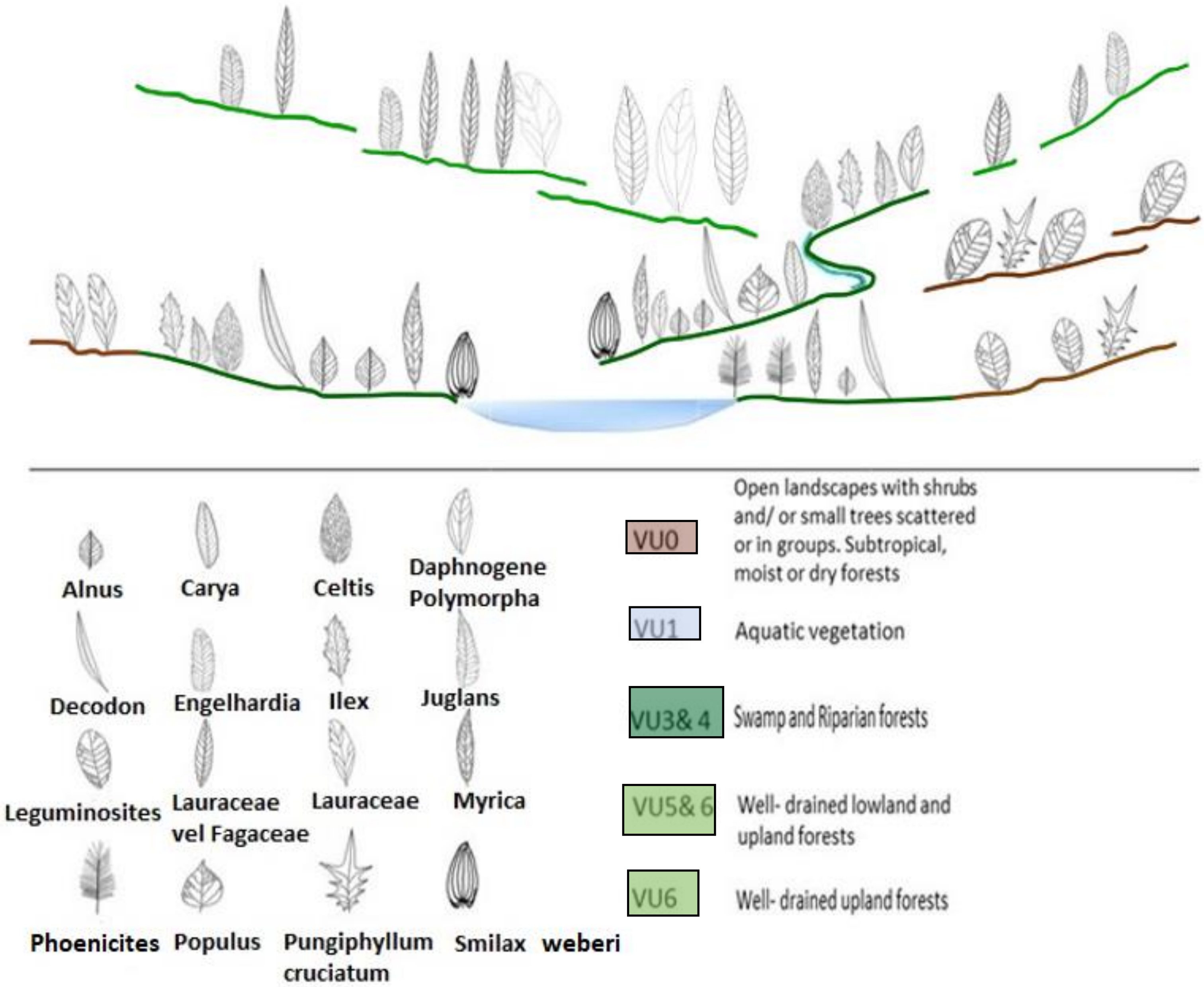



Figure 19. Landscape reconstruction for the Early Miocene of Acrocheiras site. The schematic vegetation transects from low land aquatic, swampy and riparian vegetation to middle altitude forests, as described in the text. Vegetation units correspond to these described in Table 3. The plant taxa referred to vegetation units (VUs), as described by Denk (2016).

### 5.3. Climate Proxies from the studied Palaeofloras

The floristic composition of the Akrocheiras taphocoenosis points warm- temperate to subtropical climate conditions. The presence of *Daphnogene polymorpha* in a great number and of other thermophillous elements, like Aracaceae, indicates warm climate conditions. The extremely laurophyllous flora is dominated by Lauraceae gen. et sp. indet., *Engelhardia* sp., *Daphnogene polymorpha*, *Pungiphyllum cruciatum* and *Phoenix* sp., Fagaceae *(Fagus*, *Quercus mediterranea*, *Q. kubinyii)* are absent, an indication of a warmer environmental origin (Mantzouka et al., 2019). The presence of the swamp and riparian vegetation elements recorded by both the thermophyllous taxa, as *Celtis* sp., *Smilax* sp. *and Phoenix* sp., which probably tolerate periodic drier climatic conditions, and the Arctotertiary elements, such as *Carya* sp., *Populus* cf. *balsamoides*, *Alnus* sp., and *Decodon* sp., which connected with the time of high rainfall at the end of Burdigalian (Böhme, 2003), supporting the interpretation of the numeric seasonal humidity. Temperate elements, like *Populus* cf. *balsamoides* had a subordinate role. These climatic conditions are also confirmed by Zachos et al. (2001) who indicates a period of warm global climate for the Early Miocene flora, not dramatically cooler than during the Late Oligocene Warming. For palaeoclimatic estimates, the Climate Leaf Analysis Multivariate Program (CLAMP) is applied in order to extract the quantitive results for the temperature and the precipitation in the Early Miocene Arocheiras site, based on the leaf morphology of the fossil plants.The Climate Leaf Analysis (CLAMP) is a multivariate statistical technique that decodes the climatic signal inherent in the physiognomy of leaves of woody dicotyledonous plants (Kovach and Spicer, 1995; Wolfe and Spicer, 1999; Spicer, 2000; 2007; 2008; Spicer et al., 2004, Spicer et al., 2009, Yang et al., 2011; 2015). The calibration of Akrocheiras paleoflora achieved by using the Physg3arcAZ Calibration, a set of 173 modern sites, predominantly from the Northern Hemisphere, characterized by cold winter.

The CLAMP results indicate a warm temperate to subtropical climate, probably Cfa- type sensu KÖPPEN-GEIGER system, with a mean annual temperature (MAT) between 13.4 to 16.5˚C, warm season mean month temperature (WMMT) between 22.7 to 23.7˚C and cold season mean month temperatures (CMMT) between 3.2 to 7.2˚C. Growing season period (GROWSEAS) is calculated to 8.45 months and during this interval growing season precipitation (GSP) is calculated to 1133-1523 mm. The values of the mean monthly growing season precipitation (MMGSP) are 159-209 mm (Table 4). The climatic analysis implies seasonal drought (mean precipitation of the three consecutive driest months (3-DRY) 189 239 mm, coinciding with the wettest period of the year as illustrated by the mean precipitation of the three consecutive wettest months (3- WET) 566-834 mm.

Table 4. Palaeoclimatic estimates using the climatic leaf analysis multivariate program (CLAMP); Mytilini Meteorological Station, Hellenic National Meteorological Inst.,

| Locality | MAT Min | MAT Max | WMMT min | WMMT max | CMMT Min | CMMT max | 3-WET Min | 3-WET max | 3-DRY min | 3-DRY max | GSP min | GSP Max | GROWSEAS (months) | MMSGP min | MMGSP max |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Akrocheiras | 13.4 | 16.5 | 22.7 | 27.3 | 3.2 | 7.2 | 566 | 834 | 189 | 239 | 1133 | 1523 | 8.45 | 159 | 209 |
| North Aegean (Mytilini) | 17.6 | | 21.6 (July) | 30.4 (July) | 6.7 (Jen) | 12.1 (Jen) | 117 | | 4 | | 540 | | | 22 (July) | 142 (Dec) |

http://www.hnms.gr/emy/el/climatology/climatology_city?perifereia=North%20Aegean&poli=Mytilini; MAT: mean annual temperature, WMMT: warm season mean month temperature, CMMT: cold season mean month temperature, 3- WET: mean precipitation of the three wettest months, 3- DRY: mean precipitation of the three driest months, GSP: growing season precipitation, MMGSP: Mean monthly growing season precipitation.

Today, the climate of Mytilini (Lesvos Island), in North Aegean, is slightly warmer and much drier, indicating a Csa type sensu KÖPPEN-GEIGER system. The climatic data obtained from CLAMP analysis, based on the temperatures, tended to be lower, not only than today (MAT 17.6 ˚C, WMMT 26 ˚C, CMMT 9.5 ˚C) but also than we expected due to the dominance of the thermophillous taxa in the fossil material of Akrocheiras site.

Comparisons with the climatic data calculated for the Early Miocene flora of Bulgaria and Serbia, obtained from CA analysis. The Coexistence Approach, a different method for palaeoclimatic estimates, was established by Mosbrugger and Utescher (1997) as a plant-based method to reconstruct palaeoclimate by considering recent climatic distribution ranges of the nearest living relatives of each fossil taxon. CA analysis display higher values for CMMT (5-12.6 ˚C), WMMT (25.7-28.1 ˚C) and MATs 15.6 to 21.1 ˚C for Bulgaria and lower for the Serbian record (MAT 15 ˚C, CMMT 4 ˚C) (Ivanov et al., 2011).

There are some differences between our climate reconstruction and the ones based on the Bulgarian flora. This could be attributed to that CLAMP data generally tend to produce cooler estimates than those obtained with the CA, especially for less diverse floras, and stay slightly out of the main tendency. This is probably due to the large number of predictor variables, most of which without correlation with the temperature parameters used in CLAMP analysis, and this can disturb the results (Ivanov et al., 2019) .Finally, the study of a larger number of samples could probably contribute to a more accurate statistical result, as the increasing number of samples would reduce the statistical error that led to these conflicting climatic results.

## 5.4. Paleoflora Comparisons

### 5.4.1. The studied floras in the Greek Early Miocene period

More than 40 types of floras have been reported from the Cenozoic of Greece ranging from Oligocene to Pleistocene (Velitzelos et al., 2014; Zidianakis, 2018). Early and Late Miocene floras are better represented than Middle Miocene ones (Fig. 20). Based on the floristic composition (Figure 20), the Early Miocene floras could be divided into two groups. The first one includes Euboea (Aliveri and Kymi), where deciduous woody taxa, especially *Fagus* and sclerophyllous species of the *Quercus* Group *Ilex* (*Quercus drymeja*, *Quercus mediterranea*) are dominant, while subtropical evergreens are limited in the area of the riparian forests. The second group includes the older localities of Grevena (Tsotyli- Ondrias Formation) from the Meso- Hellenic Trough and Lemnos and Lesvos Island (Velitzelos et al., 2914). The palaeoflora of Lesvos, Lemnos and Grevena lacks *Fagus* and members of *Quercus* Group *Ilex* (*Q. drymeja* and *Q. mediterranea*), while lobed oaks (white oaks) are dominant in Grevena, indicating its first Early Miocene appearance in western Eurasia. The thermophilous elements such as Lauraceae, *Myrica* sp. and swampy representatives (palms) are dominant (Velitzelos et al., 2014).

The Early Burdigalian floras of Lesvos (including Akrocheiras) appear to be connected floristically to Lemnos sharing not only physiognomic aspects but also several important taxa (e.g. *Daphnogene polymorpha, Myrica* sp*.,* palms), and reflecting the same paleoenvironmental conditions. The Akrocheiras floras shares with the floras of Grevena (Tsotyli/ Ondrias Formation), *Daphnogene polymorpha, Myrica, Populus* and *Phoenix* sp. but lack deciduous lobed oaks (*Quercus* group).

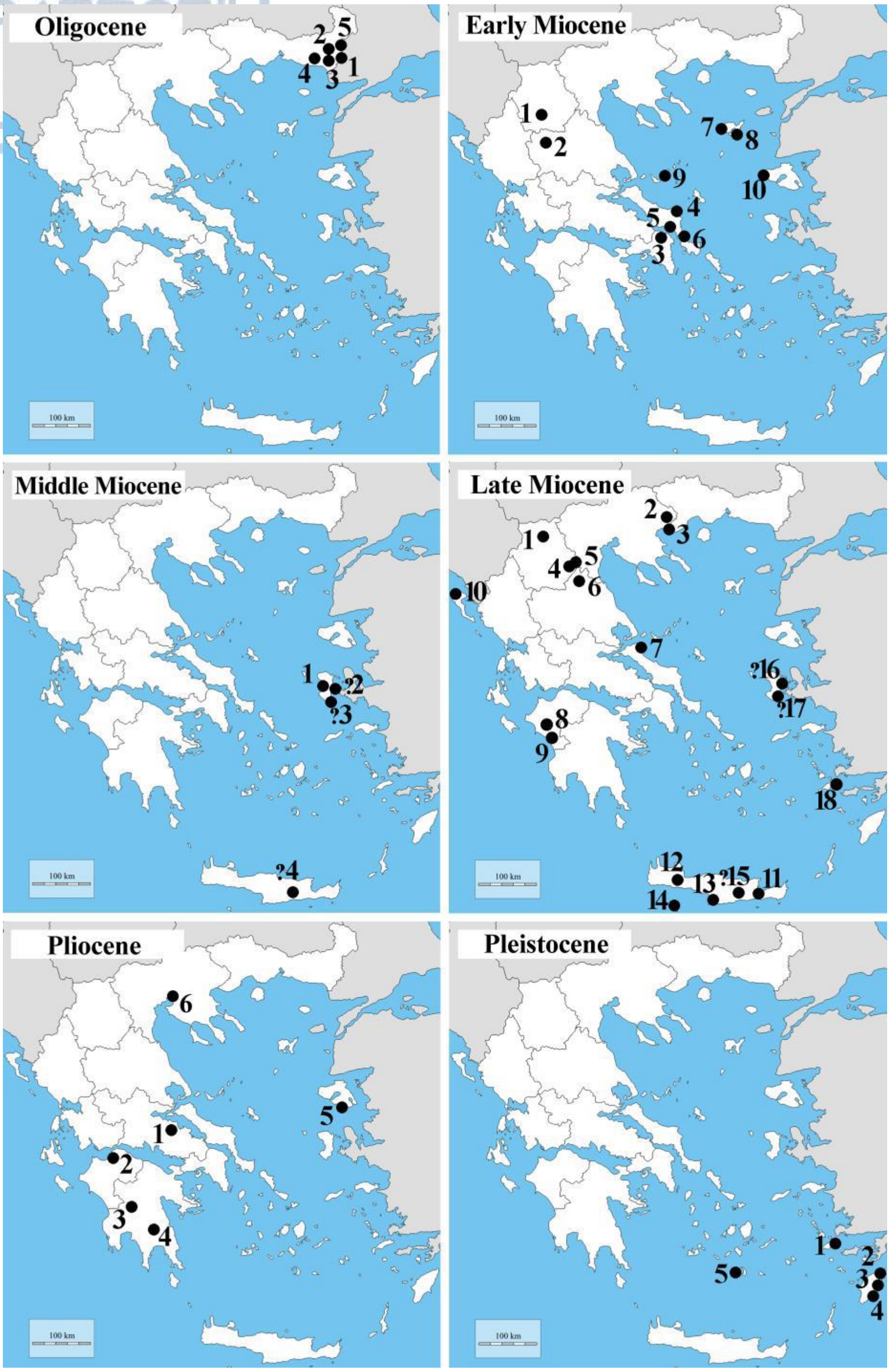



Figure 20. The Cenozoic localities with macro- floristic remains in Greece (**Oligocene**: 1)Lagina, 2)Lyra, 3)Fylakton, 4)Aetochori, 5)Lykovi, **Early Miocene**:1)Grevena (Tsotyli- Ondrias Formation), 2)Platanos/Paliopyrgos, 3)Oropos, 4)Kimi, 5)Aliveri, 6)Nea stira, 7)Kastron- Lemnos Island, 8)Moudros-Lemnos Island, 9) Allonisos (Iliodroma) Island, 10. Lesvos Island, **Middle Miocene**: 1) Zyfia-Chios Island, 2) ?Kap Nenita-Chios Island, 3) ?Kato Komi-Chios Island, 4) ?Kassanoi-Crete Island, **Late Miocene**: 1) Vegora, 2) Iliokomi/Kormitsa 3) Akropotamos-Kavala, 4) Prosilio, 5) Lava, 6) Elassona (Likoudi and Drymos), 7) Pappades, 8) Lala, 9) Pyrgos and Zacharo basins ("Platana Fm"), 10) Paghi-Corfu Island, 11) Makrilia-Crete Island, 12) Vrysses-Crete Island, 13) Pitsidia- Crete Island, 14) Metochia-Gavdos Island, 15) ?Kassanoi-Crete Island, 16) ?Kap Nenita-Chios Island, 17) ?Kato Komi-Chios Island, 18) Vasilio Fm-Kos Island, **Pliocene**: 1) Atalanti, 2) Rio, Patras and Corinth basins, 3) Makrision, 4) Skoura, 5) Vatera-Lesbos Island, 6) Allatini, **Pleistocene**: 1) Irakli Fm-Kos Island, 2) Kallithea-Rhodes, 3)Kolymbia-Rhodes, 4)Archangelos- Rhodes Island, 5)Santorini Island (Zidianakis, 2018)

### 5.4.2 The Early- Middle Miocene flora of Europe

The taxonomic composition (presence/absence matrix for 52 taxa) of early and middle Miocene assemblages from two sites of Germany, four sites of Austria, one site of Hungary, one site of Turkey, one site of Bulgaria, six sites of Greece (including Acrocheiras), one site of Czech Republic and three sites of Poland (Table 5) has been analyzed using Detrended Correspondence Analysis (Past3 software®, Hammer and Harper, 2009) and Hierarchical clustering analysis for present/absent taxa (Paired group, Raup-Crick similarity Index). Based on the taxonomy of the fossil material of nineteen European sites, the hierarchical clustering analysis divided the sites into two main clusters (Fig. 21). This separation seems to roughly reflect chronology, as the first main clade includes the Middle Miocene European sites, while the second one incorporrates Early Miocene floras. The first (Middle Miocene) subcluster (cluster A) includes the Middle Miocene site of Czech Republic (Horni Briza) which seems to show strong affinities to the sites of Poland (Wieliczka and Glow Bay) due to the presence of *Sequoia, Taxodium, Abies, Ziziphus, Platanus, Cornus* and *Q. gigas.* The second subcluster (cluster B), that includes all Early Miocene fossil sites (except Swoszowice) is further divided into the subcluster $B_1$ and $B_2$. This separation seems to reflect latitude, as the subcluster $B_1$ incorporates South- European, Mediterranean sites, while the subcluster $B_2$ includes the North- European localities. Sucluster $B_1$ includes all the Early Miocene sites of Greece, Turkey, Bulgaria, Austria and Poland, while the subluster $B_2$ shows the floristic similarities of the northern European sites. Subcluster $B_1$, is divided into two clades, based on latitudinal affinities. The first clade (Clade 1), which includes all the Early Miocene sites of the southern European countries, shows the affinities of the early Miocene fossil sites of Euboea, Bodovdol (Bulgaria) and Guvem area (Turkey) (Clade 1a) influenced by the presence of the taxa *Zekova*, *Q. pseudocastanea, Ulmus*, as well as, Grevena, Myrina and Akrocheiras (Clade 1b), controlled by the presence of taxa *Carya, Populus, Celtis, Smilax* and representatives of Lauraceae. Akrocheiras is separated from the rest floras of its clade likely because of the lack of *Quercus* group. The second clade includes (Clade 2) includes the Early Miocene fossil site of Moudros and the two northern sites of Poland (Swoszowice) and Austria (Engelswies); it is mainly influenced by the presence of *Phoenix* sp.*, Daphnogene polymorpha* and *Sequoia.* This clade presents some affinities with the Clade 1 but it differs in the type of vegetation from both the Clade 1 and the subclade $B_2$. Subclade $B_2$ includes sites of Germany, Austria and Hungary and it is controlled by the presence of the taxa *Trapa, Typha, Q. kubinyii, Ailanthus, Chaneya, Potamogemon.*

The Early and Middle Miocene sites are divided into three ecologically controlled groups (Fig. 22), based on the Integrated Plant Record (IPR) vegetation (Tab. 6), along the first ordination axis, which explains about 43% of total variation.The left group includes all Miocene fossil sites with vegetation type of subhumid sclerophyllous forests (ShSF) (Teodoridis et al., 2011: Tab. 3), indicating that their geographical and chronological exclusion is not strictly related to their floristic association. The right group includes the early (Moudros and Bodovdol Basin) and Middle (Glow Bay and Wieliczka) Miocene sites of Greece-Bulgaria and Poland respectivelly, which although geographically and chronologically far away, they exhibit a similar floristic association due of broad -leaved deciduous and evergreen forests (BLDF/BLEF), as described by Teodoridis et al. (2011). These results confirm the correlation of the Poland flora to the Early Miocene flora of Moudros, which presented in the Fig. 22. The third group includes the only Middle Miocene site of Poland (Swoszowice) with broad -leaved deciduous or mixed mesophytic forest (vegetation type BLDF/MMF), which differs from the other Polish localities.

Table 5. The age of the floristic fossil sites used in the Hierarchical clustering and Detrended Correspondance analysis (Rüffle 1963, Rasser et al. 2013; Schweigert 1992; Hantke 1954; Kovar-Eder et al. 2004; Berger and Zabusch 1953; Kováts 1856a, b; Velitzelos et al. 2002; Kvaček et al. 2002; Ivanov et al., 2011)

| **Fossil site** | **Country** | **Age of site** |
|---|---|---|
| Stenheim | Germany | Middle Miocene |
| Randecker Maar | | Early Middle Miocene |
| Engelswies | Austria | Early Middle Miocene |
| Parschlug | | Early Middle Miocene |
| Schrotzburg | | Late Middle Miocene |
| Erdöbenye | Hungary | Middle Miocene |
| Türkenschanze | | Late Middle Miocene |
| Bodovdol | Bulgaria | Early Miocene |
| **Akroxeiras** (Lesvos) | Greece | Early Miocene |
| Aliveri (Euboea) | Greece | Early Miocene |
| Kimi (Euboea) | Greece | Early Miocene |
| Grevena | Greece | Early Miocene |
| Moudros (Limnos) | Greece | Early Miocene |
| Myrina (Limnos) | Greece | Early Miocene |
| Horni Biza | Czech Republic | Middle Miocene |

| | | |
|---|---|---|
| Gdow Bay | Poland | Middle Miocene |
| Swoszowice | Poland | Middle Miocene |
| Wieliczka | Poland | Middle Miocene |
| Guvem area | Turkey | Early Miocene |

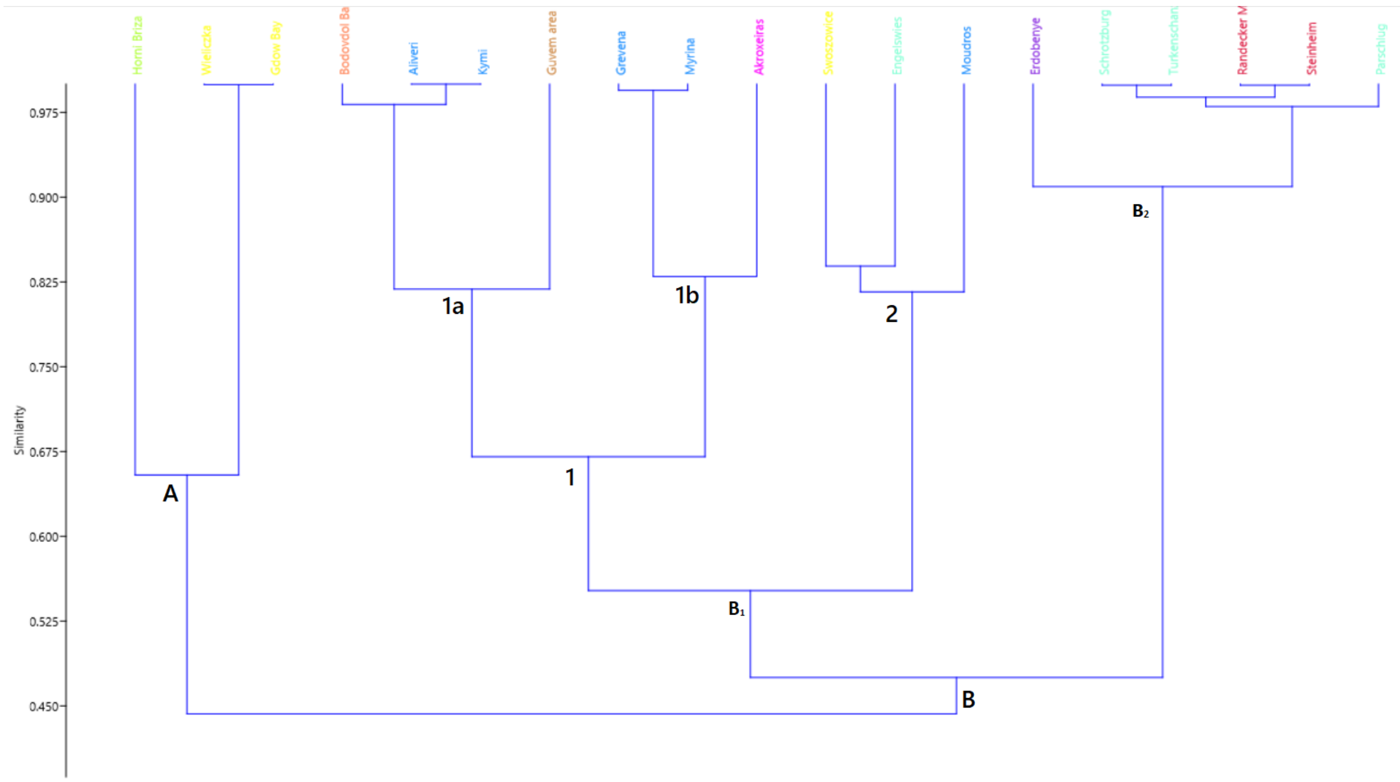



Figure 21. Hierarchical clustering analysis (Ward's method, Raup- Crick) for the presence/ absence of 52 floristic taxa of the nineteen Early and Middle Miocene European sites; Horni Briza (Czech Republic, Middle Miocene), Wielicza and Gdow Bay (Poland, Middle Miocene), Bodovdol Basin (Bulgaria, early Miocene), Aliveri and Kymi (Euboea/Greece, Early Miocene), Guvem area (Turkey, Early Miocene), Grevena (Greece, Early Miocene), Myrina (Lemnos/Greece, Early Miocene), Akrocheiras (Lesvos/Greece, Early Miocene), Moudros (Lemnos/Greece, early Miocene), Swoswowice(Poland, Middle Miocene), Engelswies (Austria, early Miocene), Erdobenye (Hungary, Middle Miocene), Schrotzburg (Germany, late Middle Miocene), Turkenschanze (Austria, Late Middle Miocene), Randecker Maar (Germany, early Middle Miocene), Steinheim (Germany, Middle Miocene), Parschlug (Austria, early Middle Miocene).

Table 6. The vegetation types as difined by the IPR vegetation analysis (Teodoridis et al., 2011) for the flora fossil sites used in the Detrended Correspondence Analysis (Kovar-Eder and Kvaček 2007, Kovar-Eder et al. 2008).

| | | |
|---|---|---|
| Stenheim | Germany | ShSF |
| Randecker Maar | | ShSF |
| Engelswies | Austria | ShSF |
| Parschlug | | ShSF |
| Schrotzburg | | ShSF |
| Erdöbenye | Hungary | ShSF |

| | | |
|---|---|---|
| Türkenschanze | | ShSF |
| Bodovdol | Bulgaria | - |
| **Akroxeiras** (Lesvos) | Greece | ShSF |
| Aliveri (Euboea) | Greece | ShSF |
| Kimi (Euboea) | Greece | ShSF |
| Grevena | Greece | ShSF |
| Moudros (Limnos) | Greece | ShSF |
| Myrina (Limnos) | Greece | ShSF |
| Horni Biza | Czech Republic | ShSF |
| Gdow Bay | Poland | BLDF |
| Swoszowice | Poland | BLDF |
| Wieliczka | Poland | BLEF |
| Guvem area | Turkey | ShSF |

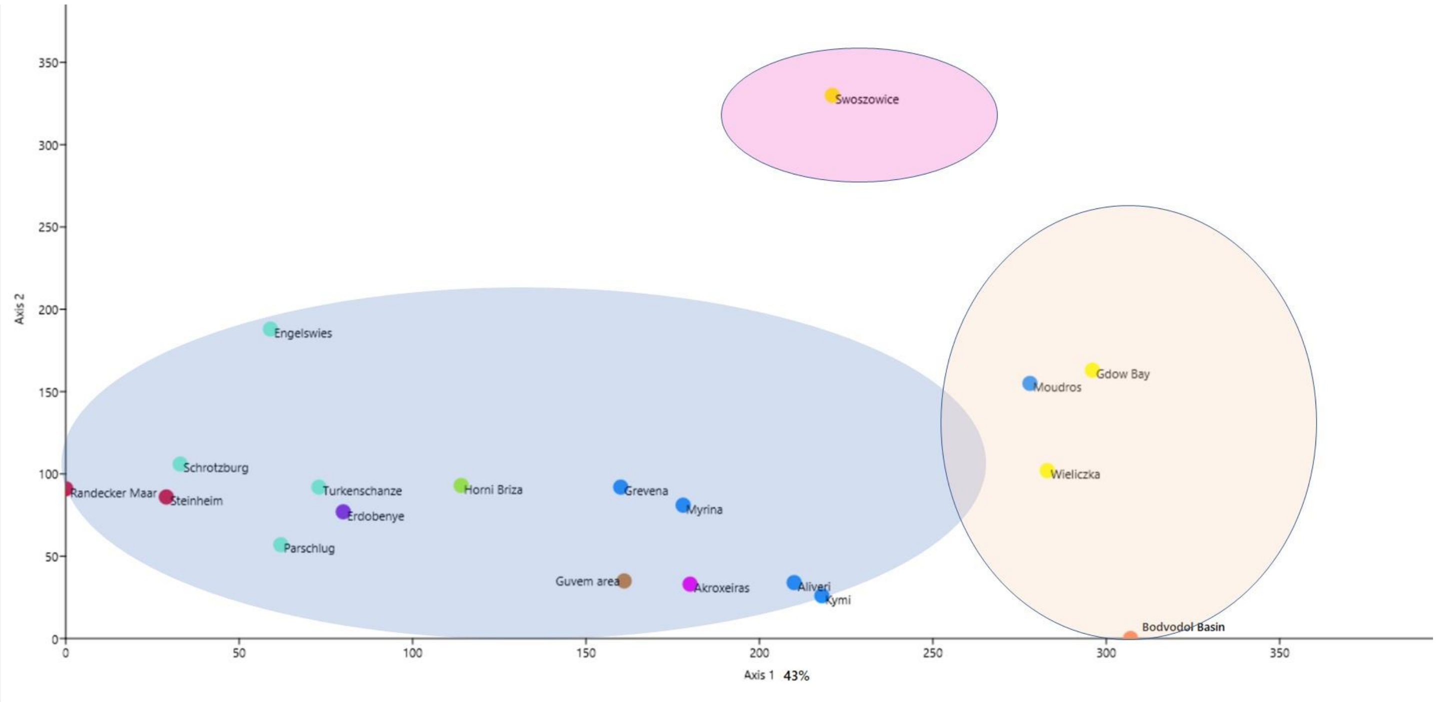
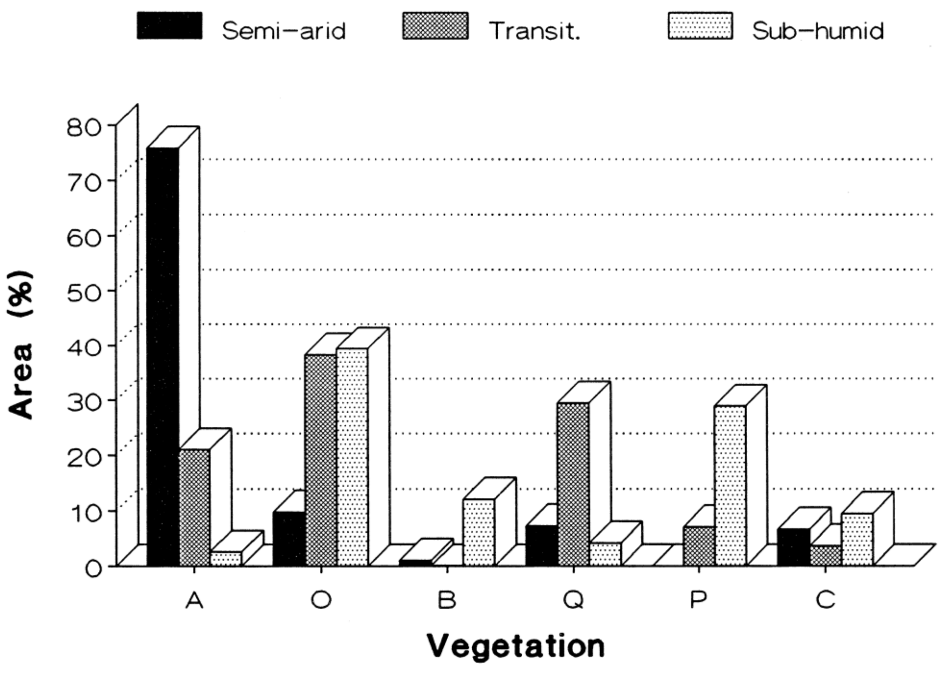



Figure 22. Detrended Correspondence Analysis of the Early and Middle Miocene sites of Europe based on their flora. The three groups reflect the different vegetation types (IPR vegetation) based on Teodoridis et al., 2011.

### 5.4.3. Comparison with the modern flora of the area

The modern vegetation of Lesvos indicates a transitional zone of the Mediterranean winter rain climate to the continental steppe of Asia Minor (Strid, 1991; Phitos et al., 1997). Degraded secondary shrub communities, phrygana and maquis are widely distributed (semi- arid), while the zonal vegetation (sub- humid part) includes a *Quercus* forest (*Quercus ithaburiensis* subsp. *macrolepis*, *Q. pubescens*), in the west and north and a *Pinus* forest (*P. brutia)* between the two gulfs of the island, indicating a Mediterranean evergreen sclerophyllous forest (Horvat et al., 1974). Olive groves prevail in the eastern half of the island in the western part of Kalloni. A *Castanea sativa* zone is restricted only to the higher altitudes of Mt. Olympos and Lepetymnos, representing the montane forest. The paleoflora and the modern flora of the island share four genera *(Pinus, Acer, Rubus, Quercus)* and some taxa of Rosaceae and Fabaceae. Modern gallery forest of Akrocheiras site (western part) is dominated by representatives of semi- arid condition such as maquis (*Sarcopoterium spinosum, S. verucosum*), up to 75.9% of this area, while olives and oak trees (*Quercus* sp.) cover only 17.1% of the area. The 6.7% is confined to the recent alluvial palins (Figure 23), which are cultivated with annual crops, as presented in Fig. 23 (Kosmas et al., 2000).




A= Sclerophyllous, O= Olives, B= evergreen oak, Q= deciduous oak, P= Pines, C= annual crop

Figure 23. Modern vegetation present in three climatic zones of Lesvos. The semi – arid conditions reflects the vegetation type in the west part of Lesvos Island (Kosmas et al., 2000)

Based on the above data and the floristic composition, there are obvious differences between the environment and the climatic conditions of the Early Miocene paleoflora and the modern flora of the western part of Lesvos. Genera as *Daphnogene polymorpha, Alnus, Myrica and Phoenicites* sp. and thermophilus taxa, which are common in the Early Miocene of the area, are no longer present. On the contrary, the modern flora of the area consists of the dominant sclerophyllous taxa, while the olives, deciduous oaks and annual crops are often. The floristic discrepancies are linked to the different climatic conditions prevailing during the Early Miocene, namelly warm- temperate to subtropical climate (Cfa- type sensu Köppen-Geiger system) in contrast to present the Mediterannean climate (Csa- type sensu Köppen-Geiger system).

## 6. CONCLUSION

The palaeoflora of Akrocheiras comprises one genus of Monocot (*Phoenicites* sp.) and at least fifteen different taxa of Dicots. One species, *Daphnogene polymorpha*, is clearly dominant represented by a great number of leaf imprints, while *Phoenicites* sp. and *Pungiphyllum cruciatum,* are common. The fossil leaves of Lauraceae vel Fagaceae, *Celtis japeti*, *Leguminosites*, *Juglans* sp., *Myrica* sp. and *Decodon* sp. are well-represented.
The material of Akrocheiras indicated the first appearance of several leaf taxa, such as *Celtis japeti*, *Decodon* sp., *Smilax weberi*., *Juglans* sp., *Carya* sp. and cf. *Ilex* sp., in the fossil record of Lesvos.The identification of these taxa is based on their morphological characteristics by macroscopic study. Moreover, the palaeocological study of the leaf imprints intercorporate interaction traces caused by arthropods, giving taphonomical and palaecological information. The IPR vegetation analysis, assigned the palaeoflora of Akrocheiras to subtropical subhumid sclerophyllous or microphyllous forest (ShSF). The Climate Leaf Analysis (CLAMP) delivered a warm temperate to subtropical climate (MAT: 13.4- 16.5$^{o}$C and MAP 566- 834 mm), with seasonal alternations from wetter to drier conditions. The type of climate shows affinities to Cfa (sensu KÖPPEN-GEIGER) for Akrochiras site. The cluster analysis indicated floristic similarities between Akrocheiras site and Grevena (Tsotyli Formation) and Moudros (Lemnos Island) in the Greek area, as well as with the Mediterranean sites. On the contrary, the site of study (Akrocheiras) present a floristic deviation with respect to the sites of Euboea (Aliveri, Kymi) and the north European sites.

**REFERENCES**

Ash, A. W., Ellis, B., Hickey, L. J., Johnson, K. R., Wilf, P., 1999. Manual of Leaf Architecture: morphological description and categorization af dicotyledons and net-veined monocotyledonous angiosperms. Smithsonian Institution, Washington D. C.

Ballhaus, C., Gee, C. T., Bockrath, C., Greef, K., Mansfeldt, T., Rhede, D., 2012. The silicification of trees in volcanic ash-An experimental study. Geochimica et Cosmochimica Acta 84, 62-74.

Berger, W., 1953. Jungtertiäre Pflanzenreste aus dem Gebiete der Ägäis (Lemnos, Thessaloniki). Ann. Géol. Pays Hellén. 5, 34–65.

Berger, W., ZaBusch, F., 1953. Die obermiozäne (sarmatische) Flora der Türkenschanze in Wien. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 98(2), 226–276.

Böhme, M., 2003.The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. Palaeogeogr. Palaeoclimatol. Palaeoecol 195, 389-401.

Borsi, S., G. Ferrara, F. Innocenti, and R., Mazzuoli, 1972. Geochronologyand petrology of recent volcanics in the Eastern Sea (West Anatolia and Lesvos Island), Bulletin of Volcanology 36, 473–496.

Braun, A., 1845. Die Tertiär-Flora Von Öhningen. N. Jb. Mineral. Geol. Pal. 1845, 164–173.

Braun, A., 1851. Verzeichnung der fossilen Pflanzen von Öhningen. Stizenberger, Übersicht über die Versteinerungen Badens, Freiburg.

Buzek, C., Dvorák, Z., Kvacek, Z., Proks, M., 1992. Tertiary vegetation and depositional environments of the Bílina delta in the North-Bohemian brown-coal basin. Časopis pro mineralogii a geologii 37(2), 117-133.

Bůžek, Č., Fejfar, O., Konzalová, M., Kvaček, Z., 1990. Floristic changes around Stehlin's Grande Coupure. – In: Knobloch, E., Kvaček, Z. (eds) Proc. Symp. Palaeoflor. Palaeoclim. Changes Cret. Tert., Prague 1989. Geol. Surv., Praha, 167–181.

Currano, E. D., Labandeira, C. C., Wilf, P., 2010. Fossil insect folivory tracks paleotemperature for six million years. Ecological Monographs 80, 547–567.

Denk, T., 2016. Palaeoecological interpretation of the late Miocene landscapes and vegetation of northern Greece: A comment to Merceron et al., 2016 (Geobios 49, 135–146). Geobios 49(6), 423-431.

Denk, T., Güner, T. H., Kvaček, Z., Bouchal, J. M., 2017. The early Miocene flora of Güvem (Central Anatolia, Turkey): a window into early Neogene vegetation and environments in the Eastern Mediterranean. Acta Palaeobot. 57, 237–338.

Denk, T., Velitzelos, D., Güner, H. T., Ferrufino-Acosta, L., 2015. *Smilax* (Smilacaceae) from the Miocene of western Eurasia with Caribbean biogeographic affinities. American Journal of Botany 102(3), 423-438.

Dilcher, D. L., 1974. Approaches to the identification of angiosperm leaf remains. Botanical Review 40(1), 1–157.

Dilek, Y., Altunkaynak, Ş., 2009. Geochemical and temporal evolution of Cenozoic magmatism in western Turkey: Mantle response to collision, slab break‐off, and lithospheric tearing in an orogenic belt. Geological Society, London, Special Publications, 311, 213–233.

Ellis, B., Daly, D. C., Hickey, L. J., Johnson, K. R., Mitchell, J. D., Wilf, P., Wing, S. L., 2009. Manual of leaf architecture. Cornell University Press, New York, 190.

Engelhardt, H., 1891. Uber die Flora der uber den Braunkohlen befindlichen Tertiarschichten von Dux. A. Acta Leop. Carol. Acad 57, 129–219.

Erdei, B., Kvaček, Z., 1997. A newly recorded collection of the Early Miocene flora of Kymi (Greece) previously misinterpreted as the Upper Miocene flora of Tallya (NE Hungary). Ann. Hist. Nat. Mus. Hung 89, 5–10.

Ettingshausen, C. V., 1851. Die tertiäre Flora der Umgebungen von Wien. Abhandlungen der Kaiserlich – Königlichen Geologischen Reichsanstalt, Wien 1, 1–36.

Ettingshausen, C. V., 1869. Die fossile Flora des Terti~irbeckens von Bilin III. Denkschr. Akad. Wiss 29, 1-110.

Ferguson, D. K., 1971. The Miocene flora of Kreuzau, Western Germany. The leaf remains. Verh. K. Ned. Akad. Wet. (afd. Natuurkunde, Tweede Reeks) 60, 1–297.

Ferguson, D. K., Knobloch, E., 1998. A fresh look at the rich assemblage from the Pliocene sink-hole of Willershausen, Germany. Review of Palaeobotany and Palynology 101(1-4), 271-286.

Fliche, P., 1898. Note sur les Bois Fossiles de Mételin. Annales des Mines (9) Mémoires 13, 293-303.

Frankenhäuser, H., Wilde, V.,1995. Stachelspitzige Blätter aus dem Mitteleozän von Eckfeld (Eifel). Abh. Staatl. Mus. Mineral. Geol. Dresden 41, 97–115.

Fyticas, M., Innocenti, F., Manetti, P., 1984. Tertiary to Quaternary Evolution of the Volcanism in the Aegean Region, in The Geological Evolution of the Eastern Mediterranean, Dixon, J.E. and Robertson, A.H.F., Eds. Geol. Soc. London, Spec. Publ., 17, 687–699.

Gottwald, H.P.J., 1997. Alttertiäre Kieselhölzer aus miozänen Schottern der ostbayerischen Molasse bei Ortenburg. Documenta Naturae 109, 1–83.

Govers, R., Wortel, M.J.R., 2005. Lithosphere tearing at STEP faults: Response to edges of subduction zones. Earth and Planetary Science Letters 236, 505–523.

Gregor, H. J., Velitzelos, E., 1985. Preliminary comparisons of Neogene floras in the Mediterranean (Spain, France, Italy, Turkey and especially Greece) with those of Paratethys-areas. Rapports et procès verbaux des réunions-Commission internationale pour l'exploration scientifique de la Mer Méditerranée 29(2), 223-227.

Gros, J.P., 1983. Nouveau bois fossile d'Eggenburgian d'Autriche: Quercoxylon furwaldense n.sp. Révue Générale de Botanique 90, 43-80.

Hammer, Ø., Harper, D. A. T., Ryan, P. D., 2009. Paleontological statistics. Ver 1, 92.

Hantke, R., 1954. Die fossile Flora der obermiozänen OehningerFundstelle Schrotzburg (Schienerberg, Süd-Baden). Denkschriften der Schweizerischen Naturforschenden Gesellschaft 80/2, 1–118.

Hatzfeld, D., 1999. The present ‐ day tectonics of the Aegean as deduced from seismicity. Geological Society of London Special Publication 156, 416–426.

Hecht, J., 1972. Geological Map of Lesvos Island (Plomari – Mytilene) Sheet, 1:50 000, Greek Institute of Geology and Mineral Exploration-IGME.

Hecht, J., 1973. Geological Map of Lesvos Island (Agia Paraskevi) Sheet, 1:50 000, Greek Institute of Geology and Mineral Exploration-IGME.

Hecht, J., 1974a. Geological Map of Lesvos Island (Polychnitos) Sheet, 1:50 000, Greek Institute of Geology and Mineral Exploration-IGME.

Hecht, J., 1974b. Geological Map of Lesvos Island (Mythimna) Sheet, 1:50 000, Greek Institute of Geology and Mineral Exploration- IGME.

Hecht, J., 1975. Geological Map of Lesvos Island (Eressos) Sheet, 1:50 000, Greek Institute of Geology and Mineral Exploration- IGME.

Heer, O., 1856. Flora Tertiaria Helvetiae, II. J. Wurster et comp, Winterthur, 110.

Hickey, L. J., 1973. Classification of the architecture of dicotyledonous leaves. Am. J. Bot. 60, 17–33.

Horvat, I., Glavac, V., Ellenberg, H., 1974. Die Vegetation Südosteuropas, Stuttgart and New York.

Ivanov, D., Tsenov, B., Utescher, T., Kováčová, M., Mosbrugger, V., Ashraf, A. R., 2019. Climate reconstructions based on Miocene leaf flora from NW Bulgaria: Comparing leaf physiognomy and nearest living relative approach. Phytol. Balc. 25, 137–144.

Ivanov, D., Utescher, T., Mosbrugger, V., Syabryaj, S., Djordjević-Milutinović, D., Molchanoff, S., 2011. Miocene vegetation and climate dynamics in Eastern and Central Paratethys (Southeastern Europe). Palaeogeography, Palaeoclimatology, Palaeoecology 304(3-4), 262-275.

Jähnichen, H., Friedrich, W. L., Takács, M., 1984. Engelhardioid leaves and fruits from the European Tertiary.

Jähnichen, H., Mai, D. H., Walther, H., 1977. Blätter und Früchte von Engelhardia LESCH. ex BL.(Juglandaceae) aus dem europäischen Tertiär. Feddes Repertorium 88(5-6), 323-363.

Jefferson, T. H., 1987. The preservation of conifer wood - examples from the Lower Cretaceous of Antarctica. Palaeontology 30, 233–249.

Jolivet, L., Faccenna, C., Huet, B., Labrousse, L., Le Pourhiet, L., Lacombe, O., Driussi, O. 2013. Aegean tectonics: Strain localisation, slab tearing and trench retreat. Tectonophysics 597, 1–33.

Karowe, A. L., Jefferson, T. H., 1987. Burial of trees by the eruption of Mount St. Helens, Washington: implications for the interpretation of fossil forests. Geol. Mag 124, 191–204.

Katsikatsos, G., Mataragas, D., Migiros, G., Triantaphyllis, E., 1982. Geological study of Lesvos Island I.G.M.E (internal report), Athens.

Katsikatsos, G., Migiros, G., Triantaphyllis, M., Mettos., A., 1986. Geological structure of the internal Hellinides (East Thessaly – southwest Macedonia, Euboea Attica Northern Cyclades Islands and Lesvos) I.G.M.E., Geology and Geophysical Research, Special issue, 191–212.

Kleinhölter, K., 1994a. Die neogenen Floren der Peloponnes. Ph.D. Thesis, Münster University, Münster.

Knobloch, E., Kvaček, Z., 1976. Miozane Blatterfloren vom Westrand der Bohmischen Masse. Rozpr. Ustr. Ust. Geol 42, 1-131

Knor, S., Prokop, J., Kvaček, Z., Janovský, Z., Wappler, T., 2012. Plant-arthropod associations from the Early Miocene of the Most Basin in North Bohemia – palaeoecological and palaeoclimatological implications. Palaeogeography, Palaeoclimatology, Palaeoecology, 321, 102–112.

Kosmas, C., Gerontidis, S., Marathianou, M., 2000. The effect of land use change on soils and vegetation over various lithological formations on Lesvos (Greece). Catena 40(1), 51-68.

Koufos, G.D., Zouros, N., Mourouzidou, O., 2003. Prodeinotherium bavaricum (Proboscidea, Mammalia) from Lesvos island, Greece; the appearance of deinotheres in the Eastern Mediterranean. Geobios 36, 305–315.

Kovach, W.L., Spicer, R.A., 1995. Canonical Correspondence Analysis of Leaf Physiognomy: A Contribution to the Development of a New palaeoclimatological Tool. Palaeoclimates 1, 125-138.

Kovar-Eder, J., Jechorek, H., Kvaček, Z., Parashiv, V., 2008. The integrated plant record: the ultimate tool to reconstruct Neogene zonal vegetation in Europe. Palaios 23, 97–111.

Kovar-Eder, J., Kvaček, Z., 2007. The integrated plant record (IPR) to reconstruct Neogene vegetation – the IPR vegetation analysis. Acta Palaeoboanica 47(2), 391– 418.

Kóvats, J., 1856a. Fossile Flora von Erdöbenye. – Arbeiten der geologischen Gesellschaft für Ungarn 1, 1–37.

Kóvats, J., 1856b. Fossile Flora von Tállya. Arbeiten der geologischen Gesellschaft für Ungarn 1, 39–52.

Kräusel, R., 1919. Die fossilen Koniferenhölzer (unter Ausschluß von Araucarioxylon Kraus). Palaeontographica, 185-275.

Krutzsch, W., 1992. Paläobotanische Klimagliederung des Alttertiärs (Mitteleozän bis Oberoligozän) in Mitteldeutschland und das Problem der Verknüpfung mariner und kontinentaler Gliederungen. Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen 186, 137–253.

Kvaček, Z., 2002a. Late Eocene landscape, ecosystems and climate in north Bohemia with particular reference to the locality Kučlín near Bílina. Bull. Czech Geol. Surv 77, 217–236.

Kvaček, Z., Sakala, J., 1999. Twig with attached leaves, fruits and seeds of Decodon (Lythraceae) from the Lower Miocene of northern Bohemia, and implications for the identification of detached leaves and seeds. Review of Palaeobotany and Palynology 107(3-4), 201-222.

Kvaček, Z., Walther, H., 1974. Bemerkenswerte und seltene cinnamomoide Blätter aus dem Grenzbereich des Oligo-Miozäns Mitteleuropas. Abh. Staatl. Mus. Mineral. Geol., Dresden 21, 197– 221.

Kvaček, Z., Walther, H., 1981. Studium über "*Quercus*" cruciata und analoge Blattformen aus dem Tertiär Europas. – Acta Palaeobot 2, 77–100.

Leisman, G.A., 1986. *Cryptocaryoxylon gippslandicum* gen. et sp. nov. from the Tertiary of eastern Victoria. Alcheringa 10, 225—234.

Mantzouka, D.V., 2016. Research of the Cenophytic Palaeoflora of the Eastern Mediterranean (Lesbos, Lemnos, Alonissos, Gavdos Islands). Ph. D Thesis, National and Kapodistrian University of Athens.

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 275(1), 47–81.

Mantzouka, D., Sakala, J., Kvacek, Z., Koskeridou, E., Karakitsios, V., 2019. Petrified Forest of Lesbos Island (Greece): A Palaeobotanical Puzzle of a Unique Geopark and the New Discoveries. In IOP Conference Series: Earth and Environmental Science. 221(1), p. 012146). IOP Publishing.

Matysová, P., Rössler, R., Götze, J., Leichmann J., Forbes G., Taylor E. L., Sakala J., Grygar T., 2010. Alluvial and volcanic pathways to silicified plant stems (Upper Carboniferous–Triassic) and their taphonomic and palaeo-environmental meaning. Palaeogeogr. Palaeoclimatol. Palaeoecol 292, 127– 143.

McClusky, S., Balassanian, S., Barka, A., Demir, C., Ergintav, S., Georgiev, I., Veis, G., 2000. Global positioning system constraints on plate kinematics and dynamics in the eastern Mediterranean and Caucasus. Journal of Geophysical Research 105, 5695–5719.

McKenzie, D., 1978. Active tectonics of the Alpine-Himalayan belt: the Aegean Sea and surrounding regions, Geophysical Journal of the Royal Astronomical Society 55, 217–254.

Mercier, J.L., Sorel, D., Vergely, P., Simeakis., K., 1989. Extensional tectonic regimes in the Aegean basins during the Cainozoic, Basin Research 2, 49–71.

Meyer, H. V., 1831. Das Genus Aptychus. – Verhandlungen der kaiserlich Leopoldinisch-Carolinischen Akademie der Naturforscher 15, 125-170.

Mosbrugger, V., Utescher, T., 1997. The coexistence approach—a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. Palaeogeography, Palaeoclimatology, Palaeoecology 134(1-4), 61-86.

Mountrakis, D., Sapountzis, E., Kilias, A., Elleftheriadis, G., Christofides, G., 1983. Paleogeographic conditions in the western Pelagonian margin in Greece during the initial rifting of the continental area, Canadian Journal Earth Science 20, 1673–1681.

Mountrakis, D., Thomaidou, E., Zouros, N., Kilias., A., 2001. Kinematic analysis and tertiary evolution of the Lesvos ophiolites and metamorphic sole (Aegean Sea, Greece), Bulletin of the Geological Society of Greece 34(1), 267–274.

Novak, I.D., Soulakellis, N., Zouros, N., 2001. Identifying former centers of volcanic activity on Lesvos Island, Greece, Geological Society of America, Abstracts with Programs 33(6), 398.

Paicheler, J. C., Blanc, C. P., 1981. La flore du bassin lacustre miocène de Bés-Konak (Anatolie spetentrionale, Turquie). Géologie méditerranéenne 8(1), 19-60.

Papanikolaou, D., 1999. The Triassic ophiolites of Lesvos Island within the Cimmeride orogene event, EUG 10, Symposium D06: Inter-relations Between Paleotethys and Neotethys in Europe and Asia, 315.

Papazachos, B., Papazachou, C., 2003. The Earthquakes of Greece. Ziti, Thessaloniki.

Pavlides, S., Tsapanos, Th., Zouros, N., Sboras, S., Koravos, G., Chatzipetros, A., 2009. Using active fault data for assessing seismic Hazard: a case study from NE Aegean Sea, Greece. Proceedings of the technical committee, TC4 Earthquake Geotechnical Engineering Conference 2-3 October 2009, Alexandria, Egypt.

Pe-Piper, G., 1978. Cainozoic Volcanic Rocks of Lesvos Island, Ph.D. Thesis, University of Patras, 365.

Pe-Piper, G., 1980a. Geochemistry of Miocene shoshonites, Lesbos, Greece. Contributions to Mineralogy and Petrology 72(4), 387– 396.

Pe-Piper, G., D.J.W. Piper., 1993. Revised stratigraphy of the Miocene volcanic rocks of Lesvos, Greece, Neues Jahrbuch Geologie und Palaeontologie Munchen 2, 97–110.

Pe-Piper, G., A., Piper, D. J. W., 2002. The igneous rocks of Greece: The anatomy of an orogen, p. 573. Stuttgart: Borntraeger.

Pe-Piper, G., A., Piper, D. J. W., 2007. Neogene backarc volcanism of the Aegean: New insights into the relationship between magmatism and tectonics. Geological Society of America Special Paper 418, 17–31.

Pe-Piper, G., Imperial, A., Piper, D.J.W., Zouros, N., Anastasakis, G., 2019. Nature of thehydrothermal alteration of the Miocene Sigri Petrified Forest and host pyroclasticrocks, western Lesbos, Greece. J. Volc. Geol. Res 369, 172–187.

Phitos, D., Strid, A., Snogerup, S., 1997. Flora hellenica 1, Koenigstein.

Pingen, M., Ferguson, D. K., Collinson, M. E., 1994. Homalanthus costatus MAI: a new Miocene fruit of Cinnamomum Schaeffer (Lauraceae). Palaeontogr. Abt. B 232, 155–174.

Price, P. W., 2002. Resource-driven terrestrial interaction webs. Ecological Research 17, 241–247.

Rasser, M. W., Bechly, G., Böttcher, R., Ebner, M., Heizmann, E. P. J., Höltke, O., Roth-Nebelsick, A., 2013. The Randeck Maar: palaeoenvironment and habitat differentiation of a Miocene lacustrine system. Palaeogeography, Palaeoclimatology, Palaeoecology 392, 426-453.

Rüffle, L., 1963. Die obermiozäne (sarmatische) Flora vom Randecker Maar (Doctoral dissertation, Akademie-Verlag).

Sachse, M., 1997. Die Makrilia-flora (Kreta, Griechenland) - Ein Beitrag zur Neogenen Klima- und Vegetationsgeschichte des östlichen Mittelmeergebietes. PhD Thesis, ETH, Eidgenössischen Technischen Hochschule Zürich, Switzerland, 312.

Saporta, G., 1873. Examen critique d'une collection de plants fossiles de Coumi (Eubée). Ann. Sci. Éc. Norm. Supér., Sér. 2, 2, 325–352. Selmeier A. & Velitzelos E. 2000 Neue Aufsammlungen von verkieselten Holzresten aus tertiären Schichten Griechenlands (Lesbos, Kastoria, Thrakien). Mitt. Bayer. Staatsslg. Palaeont. Hist. Geol 40, 213-227.

Schimani, V., Schneider, H., 1993–1995. Die Pflanzenfossilien des Burdigal der Mittel-Hellenischen Senke im Gebiet Nordöstlich von Trikala. Ann. Géol. Pays Hellén 36, 467–476.

Schoonhoven L. M., Jermy T., Van Loon J. J. A., 2005. Insect-Plant Biology. Second edition, Oxford University press, New York, 421.

Schweigert, G. 1992. Die untermiozäne Flora (Karpatium, MN 5) des Süßwasserkalks von Engelswies bei Messkirch (Baden-Württemberg). Stuttgarter Beiträge zur Naturkunde, Serie B 188, 1–55

Sigleo A. C., 1979. Geochemistry of silicified wood and associated sediments, Petrified Forest National Park, Arizona. Chem. Geol 26, 151–163.

Smith, D. M., 2008. A comparison of plant-insect associations in the middle Eocene Green River Formation and the Upper Eocene Florissant Formation and their climatic implications, In: MEYER, H. W. and SMITH, D. M. (eds), Paleontology of the Upper Eocene Florissant Formation. Colorado, 89–103.

Spicer, R.A., 2000. Leaf Physiognomy and Climate Change. In: S.J. Culver and P. Rawson (Editors), Biotic Response to Global change: The Last 145 Million Years. Cambridge University Press, Cambridge, 244-264.

Spicer, R.A., 2007. Recent and Future Developments of CLAMP: Building on the Lagacy of Jack A. Wolfe. Cour. Forsch. -Inst. Senckenberg 258, 109-118.

Spicer, R.A., 2008. CLAMP. In: V. Gornitz (Editor), Encyclopedia of Paleoclimatology and Ancient Environments. Springer, Dordrecht, 156-158.

Spicer, R.A., Herman, A.B., Kennedy, E.M., 2004. The Foliar Physiognomic Record of Climatic Conditions During Dormancy: CLAMP and the Cold Month Mean Temperature.Journal of Geology 112, 685-702.

Spicer, R.A., Valdes, P.J., Spicer, T.E.V., Craggs, H.J., Srivastava, G., Mehrotra, R.C., Yang, J., 2009. New Developments in CLAMP: Calibration using global gridded meteorological data. Palaeogeography, Palaeoclimatology, Palaeoecology 283, 91-98.

Stitzenberger, E., 1851. Übersicht der Versteinerungen des Grossherzogtums Baden. – Freiburg, 144.

Stork, N. E., 1987. Guild structure of arthropods from Bornean rain-forest trees. Ecological Entomology 12, 69–80.

Strid, A., 1991. The Flora Hellenica Project. Bot. Chron 10, 81-94.

Süss H., 1997. *Tetraclinoxylon velitzelosi sp. nova.* ein neues fossiles Holz aus tertiären Schichten des Versteinerten Waldes von Lesbos. Feddes Repertorium 108, 289-298.

Süss H., 2003. Zwei neue fossile Hölzer der Morphogattung *Ginkgoxylon* Saporta emend. Süss aus tertiären Schichten der Insel Lesbos, Griechenland, mit einer Übersicht über Fossilien mit ginkgoaler Holzstruktur. Feddes Repertorium 114(5–6), 301–319.

Süss H., Velitzelos E., 1994a. Ein neues fossiles Koniferenholz, *Taxaceoxylon biseriatum sp. nova*, aus tertiären Schichten der Insel Lesbos, Griechenland. Feddes Repertorium 105, 257-269.

Süss H., Velitzelos E., 1994b. Zwei neue tertiäre Hölzer der Gattung *Pinoxylon* Knowlton emend. Read aus dem Versteinerten Wald von Lesbos, Griechenland. Feddes Repertorium 105, 403–423.

Süss H., Velitzelos E., 1997. Fossile Hölzer der Familie Taxodiaceae aus tertiären Schichten des Versteinerten Waldes von Lesbos, Griechenland. Feddes Repertorium 108, 1-30.

Süss H., Velitzelos E., 1998. *Thujoxylon antissum* sp. nov.: ein fossiles Wurzelholz aus tertiären Schichten des Versteinerten Waldes von Lesbos, Griechenland. Feddes Repertorium 109, 341-350.

Süss H., Velitzelos E., 1999. *Chimairoidoxylon* gen. nov. sp. nova, ein endemisches Holzfossil aus dem Tertiar von Lesbos, Griechenland. Feddes Repertorium 110, 329-339.

Süss H., Velitzelos E., 2000. Zwei neue fossile Hölzer der Formgattung Podocarpoxylon GOTHAN aus tertiären Schichten der Insel Lesbos, Griechenland. Feddes Repertorium 111, 135-149.

Süss H., Velitzelos E., 2001. *Chimairoidoxylon conspicuum sp. nova*, ein neues fossiles Holz der Formgattung Chimairoidoxylon Süss & Velitzelos emend.

Süss, mit einer Übersicht über das Vorkommen fossiler Hölzer auf der Insel Lesbos, Griechenland. Feddes Repertortium 112, 149–157.

Süss H., Velitzelos E., 2009. Zwei neue fossile Hölzer der Morphogattung *Pinoxylon* Knowlton emend. Read aus dem Tertiär der Insel Lesbos, Griechenland. Feddes Repertorium 120, 3–14.

Süss H., Velitzelos E., 2010. *Lesboxylon* gen. nov., eine neue Morphogattung mit dem Typus Lesbosoxylon ventricosuradiatum sp. nova aus dem Tertiar der Insel Lesbos, Griechenland. Feddes Repertorium 121(1–2), 18–26.

Teodoridis, V., Kovar-Eder, J., Mazouch, P., 2011. Integrated plant record (IPR) vegetation analysis applied to modern vegetation in southeastern China and Japan. Palaios 26, 623–638. DOI 10.2110/palo. 2010. p10-149r.

Tranos, M., 2009. Faulting of Lemnos Island; a mirror of faulting of the North Aegean Trough (Northern Greece). Tectonophysics, 467, 72-88.

Unger, F., 1845. Synopsis plantarum fossilium. Leopold Voss, Leipzig.

Unger, F., 1847. Chloris protogaea. Beiträge zur Flora der Vorwelt. Wilhelm Engelmann, Leipzig.

Unger, F., 1862. Wissenschaftliche Ergebnisse einer Reise in Griechenland und in den ionischen Inseln. VIII. Die fossile Flora von Kumi auf Euboea. Wilhelm Braumüller, Wien 143–186.

Unger, F.,1867. Die fossile Flora von Kumi auf der Insel Euboea. Denkschr. Kaiserl. Akad. Wiss. Math. - Naturwiss. Kl. 27, 27–87.

Vasileiadou, K., Zouros, N., 2012. Early miocene micromammals from the lesvos petrified forest (Greece): preliminary results. Palaeobiodiversity and Palaeoenvironments 92(2), 249-264.

Velitzelos, D., 2002. Field guide to the Neogene of the Island of Evia—early Miocene flora of Kymi. In Field guide, 6th European palaeobotany-palynology conference, University of Athens, Greece.

Velitzelos D., Bouchal J.M., Denk T., 2014. Review of the Cenozoic floras and vegetation of Greece. Review of Palaeobotany and Palynology 204, 56-117.

Velitzelos, E., 1993. Neue paläofloristische Daten zu känophytischen Floren Griechenlands. Doc. Nat 78, 1–17.

Velitzelos, E., Bůžek, C., Kvaček, Z., 1992. Contribution to the Lower Miocene flora of Aliveri (Island of Evia, Greece). Doc. Nat 74, 10–25.

Velitzelos, E., Gregor, H.-J., 1990. Some aspects of the Neogene floral history in Greece. Rev. Palaeobot. Palynol. 62, 291–307.

Velitzelos, E., Kvaček, Z., 1999. Review of the Late Miocene flora of Vegora, Western Macedonia, Greece. Acta Palaeobot 2, 419–427.

Velitzelos, E., Kvaček, Z., Denk, T., Velitzelos, D., 2002a. Palaeontology and palaeobotany. In: VELITZELOS D. (ed.), Field Guide to the Neogene of the Island of Evia – Early Miocene flora of Kymi. Field Guide, 6th Europ. Palaeobotany-Palynology Conf., University of Athens.

Velitzelos, E., Petrescu, I., 1981. Seltene pflanzliche Fossilien aus dem Braunkohlenbecken von Vegora. Ann. Géol. Pays Hellén. 30, 767–777.

Velitzelos, E., Petrescu, I., Symeonidis, N., 1981. Tertiäre Pflanzenreste aus der Ägäis. Die Makroflora der Insel Lesvos (Griechenland). Ann. Géol. Pays Hellén. 30, 500–514.

Velitzelos E., Petrescu I., Symeonidis N., 1981a. Tertiary Plant Reminants from Aegiis. Macro - Palaeo - Flora of Lesbos Island (in Greek). Ann. Géol. Pays Hellén. Athens XXX/2, 500 514.

Velitzelos E., Petrescu I., Symeonidis N., 1981b. Tertiäre Pflanzenreste von der Ägäischen Insel Lesbos (Griechenland) [Tertiary Plant Fossils from Lesbos Island (Aegean, Greece)]. Cour. Forsch. Inst. Senckenberg Frankfurt 50, 49– 50.

Velitzelos, E., Zouros, N., 1998. New results on the petrified forest of Lesvos. Bulletin of the Geological Society of Greece 32(2), 133–142.

Velitzelos, E., Zouros, N., 2000. Petrified forest of Lesvos. Natural History Museum of Petrified Forest of Lesvos. Publ. TOPIO 1–141.

Velitzelos E., Zouros N., Velitzelos D., 1999. Contribution to the study of the palaeoflora of the Lesbos Petrified Forest. International Symposium "Protected natural areas and environmental education" Sigri, Lesbos Island.

Voutos, N., Papagiannis, I., 1994. Palaeobotanical and stratigraphic studies in the coal-bearing Basin of Kimi. Diploma Thesis, University of Athens, Athens, 87 (in Greek).

Weibel R., 1996. Petrified wood from an unconsolidated sediment, Voervadsbro. Denmark. Sed. Geol 101, 31–41.

Wilf, P., Labandeira, C. C., 1999. Response of plant–insect associations to Paleocene-Eocene warming. Science 284, 2153–2156.

Wilf, P., Labandeira, C. C., Johnson, K. R., Coley, P. D., Cutter, A. D., 2001. Insect herbivory, plant defense, and early Cenozoic climate change. Proceedings of the National Academy of Sciences USA 98, 6221–6226.

Wójcicki, J. J., Kvacek, Z., 2002. Schenkiella genus novum, thorny disseminules of unknown affinities from the Lower Miocene of Central Europe. Acta Palaeobotanica-Krakow 42(2), 109-116.

Wolfe, J.A., 1990. Palaeobotanical evidence for a marked temperature increase following the Cretaceous/Tertiary boundary. Nature 343, 153-156.

Wolfe, J.A., 1993. A method of obtaining climatic parameters from leaf assemblages. U.S. Geol. Surv. Bull 2040, 73.

Wolfe, J.A., Spicer, R.A., 1999. Fossil Leaf Character States: Multivariate Analysis. *In* Jones, T.P., and Rowe, N.P. (eds.) Fossil Plants and Spores: Modern Techniques. Geological Society, London, 233-239.

Wolfe, J.A., Uemura, K., 1999. Using fossil leaves as palaeoprecipitation indicators: an Eocene example - Comment. Geology 27, 91-92.

Yang, J., Spicer, R.A., Spicer, T.E.V., Li, C-S., 2011. 'CLAMP' Online: a new web-based palaeoclimate tool and its application to the terrestrial Paleogene and Neogene of North America. Palaeobiodiversity and Palaeoenvironments 91: 163-183.

Yang, J., Spicer, R.A., Spicer, T.E.V., Arens, N.C., Jacques, F.M.B., Su, T., Kennedy, E.M., Herman, A.B., Steart, D.C., Srivatsva, G., Mehrotra, R.C., Valdes, P.J., Mehrotra, N.C., Zhou, Z.-K., m Lai, J.-S., 2015. Leaf form-climate relationships on the global stage: an ensemble of characters. Global Ecology and Biogeography 24, 1113-1125.

Yılmaz, Y., Gen., Ş. C., Gürer, F., Bozcu, M., Yılmaz, K., Karacik, Z., Elmas, A., 2000. When did the western Anatolian grabens begin to develop? Geological Society, London, Special Publication 173, 353–384.

Zachos, J. C., Shackleton, N. J., Revenaugh, J. S., Pälike, H., & Flower, B. P.,2001. Climate response to orbital forcing across the Oligocene-Miocene boundary. Science 292(5515), 274-278.

Zidianakis, I., 2018. The floral study and the observed vegetational changes during Miocene regarding the palaeoenvironmental evolution of the Messara- Gavdos area in Crete. Ph. D Thesis, University of Patras.

Zidianakis, G., Mohr, B. A. R., Fassoulas, C., 2007. A Late Miocene leaf assemblage from Vrysses, western Crete, Greece, and its paleoenvironmental and paleoclimatic interpretation. Geodiversitas 29(3), 351–377

Zidianakis, G., Iliopoulos, G., Fassoulas, C., 2010. A new late Miocene plant assemblage from Messara Basin (Crete, Greece). Bull. Geol. Soc. Greece 63, 781–792.

Zouros, N., Velitzelos, E., Valiakos, I., Labaki, O., 2007. The Plaka Petrified Forest Park in Western Lesvos - Greece. Proceedings of the 11th International Congress. Bulletin of the Geological Society of Greece 40, 1880–1891.