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Couverture / *Cover* :
Red colored elements: *Pinuxylon alonissianum* Mantzouka & Sakala, sp. nov.; grey color elements: *Taxodium europaeum* holotype.

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Two fossil conifer species from the Neogene of Alonissos Island (Iliodroma, Greece)

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ABSTRACT

Alonissos (Iliodroma) Island is really famous to palaeobotanists because of the type locality of *Glyptostrobus europaeus* (Brongniart) Unger only. Since the first report of the latter holotype no palaeobotanical work has taken place in Alonissos. This is the first research of the fossiliferous locality, along with new palaeobotanical, palynological and gastropod findings, revealed after 200 years. Among the collected material, a xylitic specimen was studied and identified as *Pinuxylon alonissianum* Mantzouka & Sakala, sp. nov. The presence of this species points to botanical affinities with sections of Diploxylon Pines (*Pinus leiophylla* var. *chihuahuana* (Engelm.) Shaw, *P. arizonica* Engelm., *P. arizonica* var. *cooperi* (C.E.Blanco) Farjon, *P. engelmannii* Carrière and *P. jeffreyi* Balf.) especially from Central America (Sierra Madre Occidental and Oriental of Mexico, Arizona, California, Oregon and Sierra Nevada). This is the first research of this kind revealing as the Nearest Relative bioprovince of the studied Greek fossil pine wood Central America and not Himalayas or Asia. Moreover, a palynological study and an analysis of fossil molluscs were carried out for the first time, giving more data regarding the palaeovegetation and palaeoclimate of the area. Finally, the holotype of *Glyptostrobus europaeus* (Brongniart) Unger, housed in the collections of the Muséum national d'Histoire naturelle, Paris (MNHN), is found, photographed and presented for the first time.

KEY WORDS
Alonissos (Iliodroma) Island,
Glyptostrobus europaeus,
fossil wood anatomy,
conifer,
Diploxylon Pines,
new species.

RÉSUMÉ

Deux espèces de conifères fossiles du Néogène de l'île d'Alonissos (Liadrómia, Grèce).

L'île d'Alonissos (Liadrómia) est connue par les paléobotanistes comme le gisement type de *Glyptostrobus europaeus* (Brongnart) Unger. Cette recherche est la première présentant de nouvelles découvertes en paléobotanique, en palynologie et sur les gastropodes de ce site fossilifère depuis 200 ans. Parmi les restes fossiles, un spécimen xylitique est étudié et identifié comme *Pinuxylon alonissianum* Mantzouka & Sakala, sp. nov. Ce taxon présente des affinités avec les pins de type Diploxylon (*Pinus leiophylla* var. *chihuahuana* (Engelm.) Shaw, *P. arizonica* Engelm., *P. arizonica* var. *cooperi* (C.E.Blanco) Farjon, *P. engelmannii* Carrière and *P. jeffreyi* Balf.) de l'Amérique centrale en particulier (Mexique : Sierra Madre occidentale et orientale, Arizona, Californie, Oregon, Sierra Nevada). C'est la première affiliation de ce genre à des pinacées fossiles en Grèce. Ce travail sur la pinède grecque révèle qu'elle est plus proche de la bioprovince d'Amérique centrale que de celle de l'Himalaya ou de l'Asie. De plus l'analyse palynologique et des mollusques associés apporte de nouvelles informations sur la couverture végétale et l'environnement de la région. Finalement, l'holotype de *Glyptostrobus europaeus* (Brongniart) Unger a été redécouvert dans les collections du Muséum national d'Histoire naturelle, Paris, photographié et présenté en détail pour la première fois.

MOTS CLÉS
Île d'Alonissos (Liadrómia),
Glyptostrobus europaeus,
anatomie du bois fossile,
conifère,
pins de type Diploxylon,
espèce nouvelle.

INTRODUCTION

Alonissos Island has been a geological attraction from the 3rd century B.C. with the findings of giant skeletons accompanied by myths. During the 19th century the explorations for mineral resources had lead the famous geologists of the time to visit the Island. The discovery of lignite had also generated the interest of the palaeobotanists for the palaeoflora of the island. Among the palaeofloristic findings was the first occurrence (the holotype) of *Taxodium europaeum* Brongniart. This species was later revised by Unger and classified as *Glyptostrobus europaeus* (Brongniart) Unger. During this study there was an effort of revealing the exact locality where this species had been found almost 200 years ago and presenting new information concerning the palaeobotany of Alonissos Island.

GEOLOGY AND LOCALITY

Alonissos (or Iliodroma or Chilidromia or Chelidromi) is a long, narrow, mountainous island belonging to the North Sporades, situated close to the Magnesian peninsula (Thessaly – Volos) at the South-eastern of Euboea Island (Fig. 1).

The geology of the island is studied by several scientists (e.g. Virlet 1833; Schneider 1972; Kelepertsis 1973, 1975; Pe-Piper *et al.* 1996; Poulimenos & Karkanas 1998; Papanikolaou *et al.* 2002; Evelpidou *et al.* 2013) and extensively discussed in Jacobshagen & Matarangas (2004), from the bottom to the top consists of (Fig. 2):

PELAGONIAN UNIT

Composed of meta-carbonates of up to 500 m thickness (light grayish color, thin- to medium-bedded dolomitic in the bottom of Triasso-Jurassic age and calcitic marbles nearly unbedded at the top). According to Kelepertsis (1973, 1975) the age of the upper part of the succession is Kimmeridgian (Upper Jurassic) as proved by the following fossils: *Cladocoropsis* sp., *Clypeina* sp., *Ellipsactinia*, *Pseudocyclammina* sp., *Trocholina* sp., *Nerinea* Defrance, 1824.

EOHELLENIC NAPPE RELICS

Composed of grayish phyllites and calcschists, with intercalations of thin-bedded black marbles and quartzites (metaturbidites).

MESOAUTOCHTHONOUS COMPLEX

With an 8-meters unit of Basal Conglomerates of Albian or Cenomanian age resting upon a karstic relief (which contains relics of metabauxite filling in places) and the overlying Rudist Limestones with thick bedded to massive, roughly recrystallised grayish marbles of several hundred meters thickness of Cenomanian-Turonian age.

PALOUKI FORMATION

Overlies the Pelagonian marbles or the Eohellenic metabasites, respectively, with tectonical contacts and includes an alternation of marbles, metasandstones, and schists.

NEOGENE DEPOSITS

Consisting of conglomerates, limestones and marls, lignitic formation and reddish clastics.

Concerning the Neogene, in Kelepertsis study (1975) for the Institute of Geology & Mineral Exploration (I.G.M.E.), the Neogene formations of Alonissos Island include Pontian red clays and continental conglomerates overlying the formation of the marls, clays and limestones interbedded by thin layers of lignite. Pontian some decades ago was treated as a part of Pliocene but today this concept has been revised and Pontian stage belongs to the late Miocene period (upper Tortonian-Messinian, see in Popov *et al.* 2006: fig.1). Inside these red clays mammal remains have

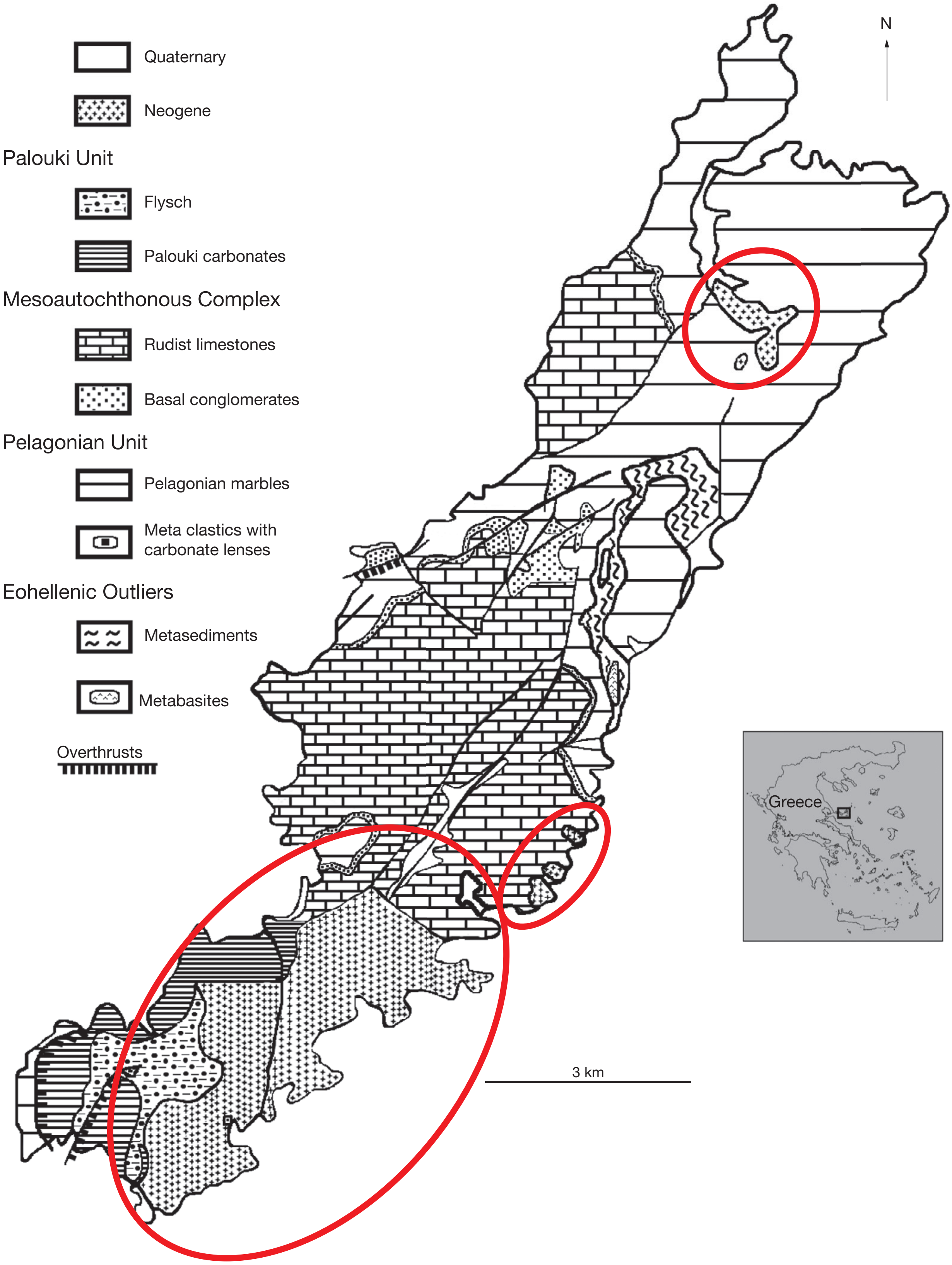


Fig. 1. — Geological sketch – map of Alonissos Island, by Jacobshagen & Matarangas (2004) (based on the work of Kelepertsis [1975] for the Institute of Geology and Mineral Exploration [I.G.M.E.]), modified. The Neogene formations are included by the **red circles**.

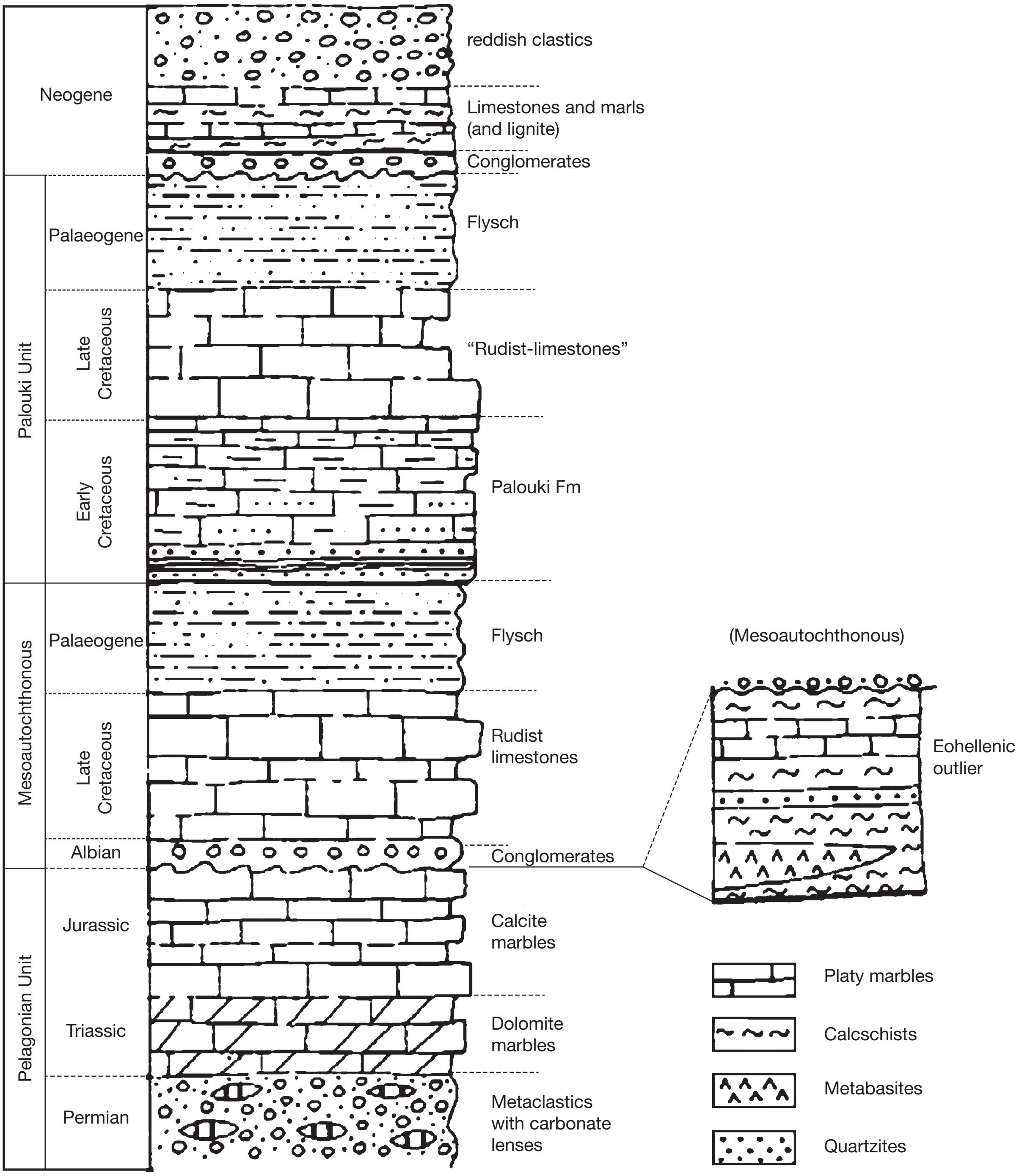


FIG. 2. — Tectonostratigraphic column of Alonissos island (according to Jacobshagen & Matarangas 2004, modified).

been found (e.g., Schneider [1972] had found the upper jaw of *Hipparion* Christol, 1832). Consequently the plant fossiliferous layer is early-middle Miocene in age, although the age of the plant fossiliferous layer as proposed by Mai (1995) and LePage (2007) is Burdigalian, early Miocene. This latter layer includes also *Planorbis* sp., *Massylaea cf. vermiculata* (O.F. Müller, 1774), *Melanopsis buccinoidea* (Olivier, 1801) and fresh water ostracodes (Kelepertsis 1975).

Virlet (1835) had described the geological formations of Alonissos Island (from the bottom to the top) with a detailed description of the Neogene as follows: 1) mica-slate, clay-slate and limestone; 2) blue and grey limestone; and 3) a fresh water tertiary formation containing lignites which occupies half of the surface of the island, and was mistaken for coal. The lower part of the last formation is situated 200 or 300 meters above the sea, and is constituted of blue or green marls with a great deposit of fresh water and

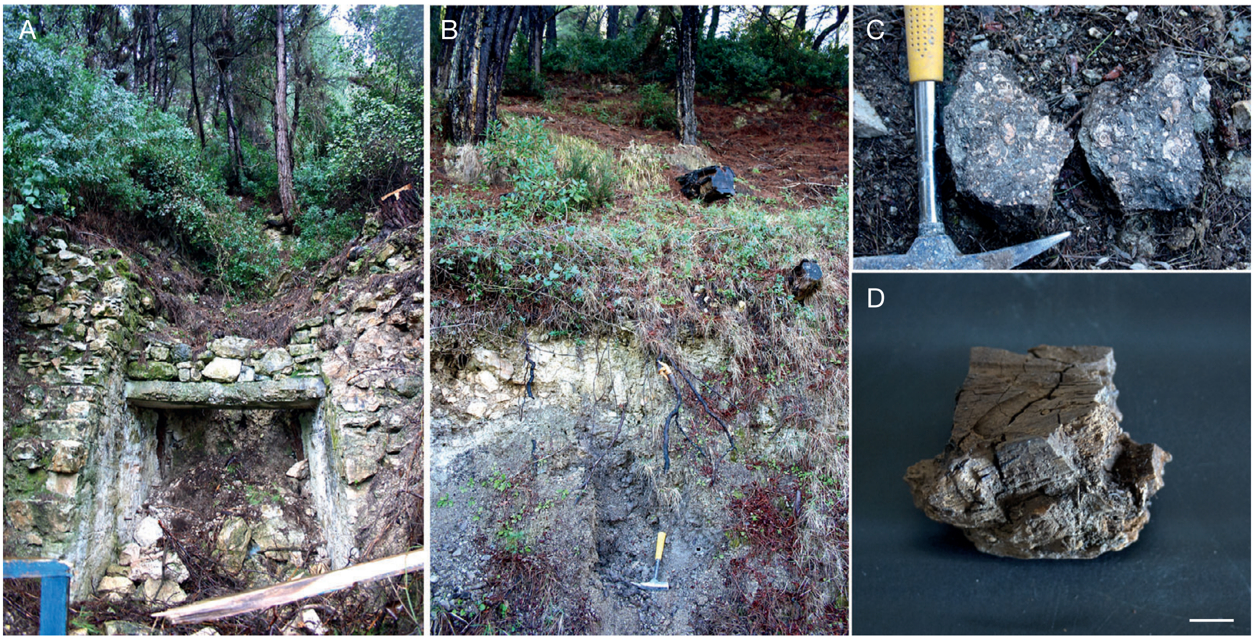


FIG. 3. — **A**, Abandoned quarry where the lignite was exported from; **B**, section with the fossil gastropods layer (**bottom**), the lignite and the plant fossiliferous marls (**top**); **C**, gastropod fossiliferous samples; **D**, lignite sample (DMALNS6) studied microscopically and found that belonged to *Pinuxylon* Gothan, identified as *Pinuxylon alonissianum* Mantzouka & Sakala, sp. nov. Scale bar: D, 1 cm.

land shells belonging chiefly to the genera *Planorbis* O.F. Müller, 1774*, Viviparus* Montfort, 1810*, Helix* Linnaeus, 1758. Over these marls lie thin strata of marly limestone without fossils, containing a lignite layer of about 0.6 meters, intermixed with clay and shells. Above the lignite grey marls occur, filled with the debris of fossil plants. The whole succession is about 58 meters in thickness. Among the fossils obtained from this formation, the most numerous belonged to a species examined by Adolphe Théodore Brongniart and named by him as *Taxodium europaeum*.

Almost 200 years after the first reference about the lignitic horizon and *Taxodium europaeum* finding and taking into account the publication of the 19th century (e.g., Brongniart 1833, 1861; Virlet 1833, 1835; Gaudry 1860) we found the locality where the lignite and the plant fossils were hosted, in a close distance of Votsi village (Fig. 3A, B).

MATERIAL AND METHODS

More than 80 specimens with gastropods, plant remnants and lignites have been collected from the latter locality (Votsi village, Fig. 3A, B). The specimens we collected from the field have mainly fossil gastropods (intact and fragments, Fig. 3C) and fossil plant remnants which unfortunately cannot be determined (bad preserved and mainly belongings to mixed horizons). The material collected is hosted at the Faculty of Geology and Geoenvironment, National and Kapodistrian University of Athens, Greece.

Among the lignite elements we collected there was a part of a xylite (Fig. 3D). This fossil sample has been boiled in water to become softer, then cut with razor blades and mounted in glycerin jelly (e.g. Gryc & Sakala 2010). This procedure was followed for its preparation for thin sections in order to be photographed. This process took place at the Faculty of Forestry and Wood Technology, Department of Wood Science, Mendel University in Brno in order to be studied microscopically. The anatomical description has followed the observations by Phillips (1941) and is in accordance with IAWA Softwood List (IAWA Committee 2004).

Unfortunately we were not able to find again *Taxodium europaeum* or leaves' imprints because the area was an active mine until some decades ago and the plant fossiliferous material situated on the top of the lignite has been disappeared (removed).

After a research we found that the holotype of *Taxodium europaeum* from Alonissos Island is hosted at the Muséum national d'Histoire naturelle, Paris (MNHN). Therefore we asked for photos of the sample in order to include them at this study (Fig. 4).

The sandy marl sediments from Alonissos Island were sampled for palynological analysis. The technique of pollen extraction (prepared) were wet sieved through 125 μm and ultrasonic10 μm sieves and palynomorphs were extracted using HCl 30% and HF 40% to remove carbonate and dissolve silicates. Then treatment with KOH that dissolve soluble the organic matter of the sediments was applied. The residues were mounted in glycerin gel on microscope slides for analysis under a binocular NIKON transmission microscope and one or two slides of each processed sample were analyzed at ×500 and ×1000 magnification (oil immersion). Pollen grains, terrestrial spore and algae cysts were identified and counted following the methods and taxonomy of Iversen (Faegri & Iversen 1989). Percentage of pollen and cysts taxa have been calculated on the basis of minimum sums of 400 specimens (most samples). Four hundred palynomorphs were included in the quantitative analysis.

For the molluscs analysis, the bulk samples were dried and then soaked for 24h in diluted hydrogen peroxide. They were subsequently wet sieved through a series of strainers with three different mesh sizes (2000, 1000, 500 µm). The molluscs (fragments mostly) were picked and identified. The studied gastropod taxonomy follows the FreshGEN database (Neubauer *et al.* 2014) and ecological information was based on the assumed preferred ecological requirements outlined by Fechter & Falkner (1990) and Glöer (2002).

HISTORY OF THE RECOGNITION AND IDENTIFICATION OF THE PLANT AND ANIMAL FOSSILS IN ALONISSOS ISLAND

Philostratus (3rd century B.C.), the ancient Greek philosopher from Lemnos Island, has given two descriptions about a giant skeleton of a mammal in Alonissos island, Greece (of about 5.5 m long) declared as one of the giants of the Gigantomachy, and in Imbros island (Imroz), Turkey (the last one has been found and identified as a Miocene mastodon) (Philostratus: On Heroes in Mayor 2000 and Higgins & Higgins 1996). In 1971 the archaeological research has revealed the skeletons of Miocene hipparion and rhinoceros close to the ancient village Ikos (Aupert 1976). Schneider (1972) refers to a Pontian mammal fauna of the Island including *Hipparion* indicative of a late Messinian age.

During the 19th century the research for the discovery of energy sources (e.g. coal) in Greece was widespread. Virlet had visited Greece soon after was said to have been observed coal. He visited the Sporades Septentrionales or Devil's Archipelago, situated at the mouth of the Gulfs of Volo and Salonica, near the coasts of Thessaly and Macedonia, where it was incorrectly said coal existed (Virlet 1833).

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

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

Unger (1862) in his work 'Reise in Griechenland' has a reference on the fossil plants from Chelidhromi (as was the name of Alonissos) Island found inside the same 'freshwater formation' with the one of Kymi, Euboea. Unger had studied the work by Virlet (1833) and Gaudry (1860) who believed that the age of the fossiliferous formation is the same with the one of Kymi, Kalamos, Markopoulo and Oropos and not older than Miocene (as also reported in Sauvage 1861 and Brongniart 1861).

SYSTEMATICS/RESULTS

Alonissos (Iliodroma) Island is really famous to the palaeobotanists because of the first report of *Glyptostrobus europaeus* (Brongniart) Unger. The holotype of the fossil today is preserved on a marly limestone slab of the following dimensions (in cm): 15 × 10, from Alonissos Island, Greece and is hosted in the palaeontological collections of the MNHN with the code MNHN.F.1744 (Fig. 4). The fossil was recognized, described and named as *Taxodium europaeum* (basionym) by Brongniart (1833).

Brongniart (1833) in his famous description of the fossil is talking about complete fossils of the species and about numerous findings. The holotype MNHN.F.1744 is represented by one complete sample which we believe that fits identically to Brongniart's description.

Family CUPRESSACEAE *sensu lato*
Genus *Glyptostrobus* Endlicher

Glyptostrobus europaeus (Brongniart) Unger
(Fig. 4A-F)

Taxodium europaeum Brongniart, 1833: 168 (Iliodroma = Alonissos).

Taxodites europaeus – Endlicher 1847: 278 (Iliodroma = Alonissos).

Glyptostrobus europaeus – Unger 1850: 434 (Iliodroma and others). — Schneider & Velitzelos 1973: 246, pl. 35, fig. 1 (Vegora). — Velitzelos & Schneider 1977: 173, figs 1-3 (Vegora). — Mai & Velitzelos 1997: 510, pl. 4, figs 1-4 (Vegora).

ORIGINAL DIAGNOSIS. — "*Ramis fastigiatis, elongatis, gracilibus: Foliis subtristichis, alternis, brevissimis, basi decurrentibus, apice acutiusculis: Strabilis subglobosis vel ovoideis: Squamis sub octofariis, disco terminali, margine superne armato, crenato, medio crista transversali prominente partito, saliis radiantibus in parte superiore notato*" (Brongniart 1833: 168-176).

DESCRIPTION

According to the new study of the holotype the following characteristics have been observed: Branched twigs with cupressoid foliage (Fig. 4A). No taxodioid foliage was observed. Ripe cone (male) 1.6 cm long and it consists of about 16 elongated imbricated scales (Fig. 4B). Branches/shoots with leaves scale-like, cupressoid type (or even linear-subulate as discussed in Ma *et al.* 2013) or if one follows the terminology by Vickulin *et al.* (2003) the leaves are squamate with cupressoid appearance, helically/spirally arranged or even slightly decussate. The leaves are short (leaf length: 1-2 cm and width: 0.5-1 cm) and their apex is not mucronate as in the modern *G. pensilis* but globose to broadly ovoid/concave (Fig. 4D, F). Cones (Fig. 4C, D) and perennial branchlets/shoots with cupressoid foliage (Fig. 4E) are observed.

DISCUSSION

According to Kvaček *et al.* (2002), *Glyptostrobus* in Euboea develops relatively smaller cones and heteromorphic foli-

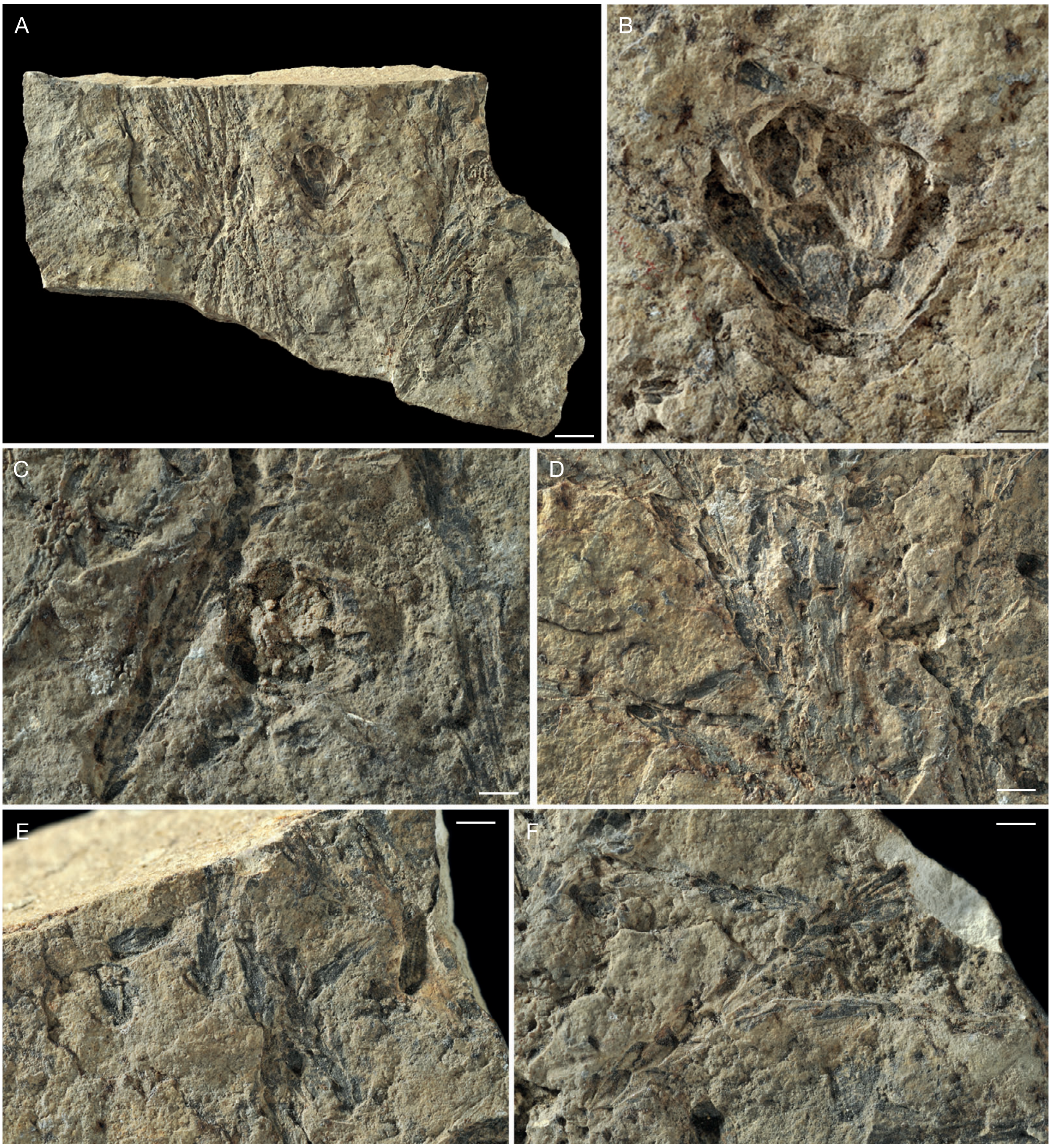


Fig. 4. — *Glyptostrobus europaeus* (Brongniart) Unger: **A**-**F**, *Taxodium europaeum* holotype, hosted in the collections of the MNHN (Paris) with the code MNHN.F.1744; **A**, branched twigs with cupressoid foliage; **B**, ripe cone (male) 1.6 cm long consisting of about 16 elongated imbricated scales; **C**, **D**, cones; **D**, **F**, short leaves (length: 1-2 cm; width: 0.5-1 cm) with globose to broadly ovoid/concave apex; **E**, perennial branchlets / shoots with cupressoid foliage. Scale bars: A, 1 cm; B, C, E, F, 0.2 cm; D, 0.25 cm.

age, which is in contrast to Early Miocene specimens from Central Europe.

Glyptostrobus europaeus represents a species found in several localities in Greece during the Cainozoic. Apart from the findings of this species from Kymi (Euboea Island) and Alonissos Island of Burdigalian age (Early Miocene) and from Vegora (Macedonia) of Messinian age (Upper Miocene) given in LePage (2007: 393), the geographical distribution of this species in Greece includes additional localities (Velitzelos *et al.* 2014), such as Aliveri and Nea Styra (Euboea Island) and Moudros (Lemnos Island) of Burdigalian age, Komnina (Macedonia), Platana (Western Peloponnese), Prosilio and Lava (Kozani, eastern West Macedonia), Likoudi and Drymos (Elassona, Northern Thessaly) and Iliokomi-Kormitsa (Strymon Basin-Thrace) of Upper Miocene (Messinian) age, Crete (Makrilia) of Middle Tortonian age, Pikermi-Chomateri (Attica) of

Tortonian-Messinian age, Ptolemaida (West Macedonia) of Lower Pliocene age, Skoura (Sparti, Laconia) of Pliocene age, Kolymbia (Rhodes) of Pleistocene age.

According to Manchester (1999), *Glyptostrobus* has a continuous presentation at the fossil floras of Europe from the Palaeocene until the Pliocene/Pleistocene, of North America during Palaeocene, Eocene and Miocene and a constant one from Palaeocene to present in Asia.

Glyptostrobus europaeus taxonomic and biogeographic history started in Canada (Aptian) and is given in detail in LePage (2007). Unfortunately, the assignment of the fossil conifer described in Li *et al.* (2018) to *Glyptostrobus europaeus* is considered ambiguous because the sample has seed cones falling into scales, a characteristic not in accordance with any known fossil representative of *Glyptostrobus europaeus* until now. Recent studies (Dolezych & van der Burgh 2004) had correlated for the first time *Glyptostrobus europaeus* with *Glyptostroboxylon rudolphii* Dolezych & van der Burgh. Numerous information for the "whole-plant" reconstruction of the species providing by the connection between fossil stumps, trunks and twigs of the taxon are also given in Vassio *et al.* (2008) or by an indirect association of different organs within the same site (Teodoridis & Sakala 2008).

Glyptostrobus pensilis Koch is the only extant species in its genus inhabited today in SE China, Viet Nam and Lao PDR (Henry & McIntyre 1926; Farjon & Filer 2013).

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

CONIFERS

Family Pinaceae L.
Genus *Pinuxylon* Gothan

Pinuxylon alonissianum Mantzouka & Sakala, sp. nov.
(Figs 3D; 5A-O)

Plant Fossil Names Registry Number: PFN000281

Holotype. — Designated here. Specimen DMALNS6 (Repository: Museum of Geology and Palaeontology in the National and Kapodistrian University of Athens).

Etymology. — The epithet, *alonissianum*, is due to the origin of the described material (Alonissos Island, Greece).

Type horizon. — Lignite horizon.

Age. — Early Miocene.

Type locality. — Votsi, Central Alonissos Island, Greece.

Diagnose. — Coniferous wood with distinct growth ring boundaries, gradual transition from early to latewood, thin walled latewood tracheids, axial and radial resin canals (mainly at the latewood), thin-walled epithelial cells, bordered pits in radial walls with well-defined disc-shaped torus, no axial parenchyma observed, rays: exclusively uniseriate, fusiform rays with average height of rays 4-12 (-20) cells, tracheid pits uniseriate, ray tracheids present with up to four rows of cells, cell walls of ray tracheids smooth and occasionally slightly dentate, ray tracheid pit borders with dentate thickenings, horizontal and end walls of ray parenchyma cells smooth, no indentures observed, cross-field pitting pinoid in1-2 rows of 1-2 (-6) pits per cross-field.

Description

Macroscopic description

The sample belongs to a xylitic remnant of dark brown colour with the following dimensions: 6 × 5 × 4 cm (Fig. 3D).

Microscopic description

Transverse section. Growth ring boundaries distinct, transition from early- to latewood gradual (Fig. 5A), latewood tracheids thin walled (Fig. 5A-D), large resin canals (axial and radial distributed but mainly at the latewood) with thin-walled epithelial cells (Fig. 5-C), bordered pits in radial walls with well-defined disc-shaped torus (Fig. 5D), no axial parenchyma observed.

Tangential section. Exclusively uniseriate rays (fusiform because they contain radial intercellular canals and have a specific shape), average height of rays 4-12 cells (mostly "medium" sized but they can be up to 20 cells). Resin canals in rays with thin-walled epithelial cells (Fig. 5L-O).

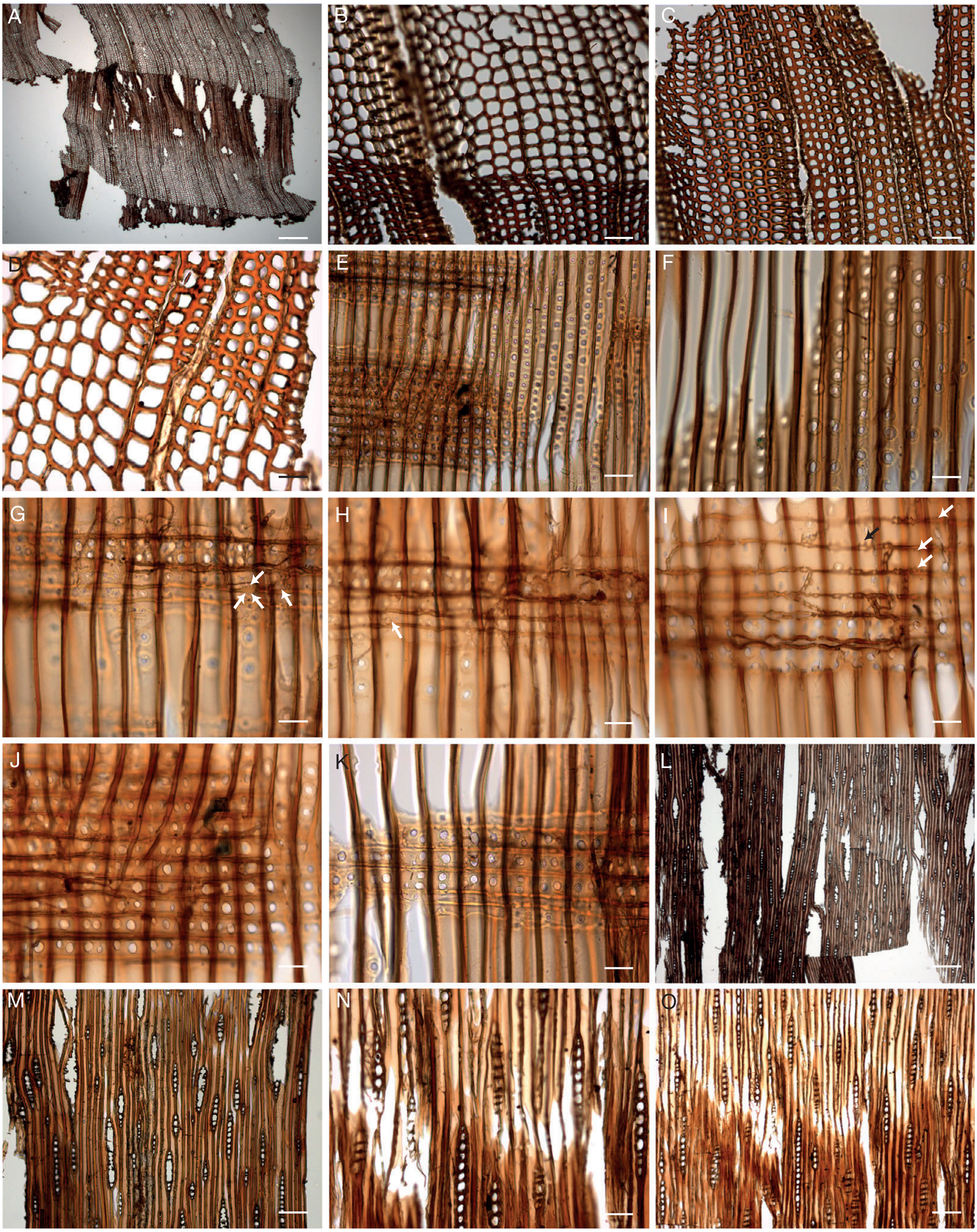
Radial section. Tracheid pits uniseriate (Fig. 5E, F). Ray tracheids present with up to four rows of cells (Fig. 5G, H, K), cell walls of ray tracheids smooth (Fig. 5G, K) and occasionally slightly dentate (Fig. 5G-I), ray tracheid pit borders with dentate thickenings (Fig. 5I). End walls of ray parenchyma cells smooth (Fig. 5J, K). Horizontal walls of ray parenchyma cells smooth (Fig. 5J, K), no indentures were observed, cross-field pitting pinoid in 1-2 rows of usually 1-2 pits per cross-field but up to 6 (Fig. 5E, G, H, J, K).

Discussion on the wood anatomical characteristics

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

The cell walls of ray tracheids of our sample have been described as "smooth and occasionally slightly dentate" following the terminology by Ickert-Bond (2001: 361) and in

Fig. 5. — *Pinuxylon alonissianum* Mantzouka & Sakala, sp. nov.: **A**, growth ring boundaries distinct, transition from early- to latewood gradual, latewood tracheids thin walled, large resin canals with thin-walled epithelial cells; **B**, growth ring boundaries distinct, latewood tracheids thin walled, large resin canals (axial and radial) with thin-walled epithelial cells; **C**, latewood tracheids thin walled, large resin canals with thin-walled epithelial cells; **D**, growth ring boundaries distinct, latewood tracheids thin walled, bordered pits in radial walls with well-defined disc-shaped torus; **E**, cross-field pitting pinoid in horizontal 2 rows of usually 1-2 pits per cross-field but up to 6; **F**, bordered pits in radial tracheid walls uniseriate; **G**, tracheid pits uniseriate. ray tracheids with up to four rows of cells, cell walls of ray tracheids smooth and slightly dentate (**white arrows**), cross-field pitting pinoid in 2 rows of usually 1-2 pits per cross-field but up to 6; **H**, tracheid pits uniseriate.



Ray tracheids with up to four rows of cells, cell walls of ray tracheids slightly dentate (**white arrow**), cross-field pitting pinoid in 2 horizontal rows of usually 1-2 pits per cross-field but up to 6; **I**, cell walls of ray tracheids slightly dentate (**white arrows**), ray tracheid pit borders with dentate thickenings (**black arrow**); **J**, end walls of ray parenchyma cells smooth, horizontal walls of ray parenchyma cells smooth, cross-field pitting pinoid in 1-2 rows of usually 1-2 pits per cross-field but up to 6; **K**, tracheid pits uniseriate. Ray tracheids with up to four rows of cells, cell walls of ray tracheids smooth, end walls of ray parenchyma cells smooth, horizontal walls of ray parenchyma cells smooth, cross-field pitting pinoid in 1-2 rows of usually 1-2 pits per cross-field but up to 6; **L**-**O**, exclusively uniseriate rays (fusiform because they contain radial intercellular canals and have a specific shape), average height of rays 4-12 cells (mostly “medium”sized but they can be up to 20 cells). Resin canals in rays with thin-walled epithelial cells. **A**-**D**, transversal section; **E**-**K**, radial longitudinal sections; **L**-**O**, tangential longitudinal sections. Scale bars: A, 400 μm; B, C, E, N, 50 μm; D, F-K, 25 μm; L, 200 μm; M, O, 100 μm.

accordance with the "smooth as well as slightly dentate ray tracheids" as discussed in van der Burgh (1964: 254-259; 1973: 104-106) and in Dolezych *et al.* (2011: 53). The same kind of identification of the cell walls of ray tracheids has been pointed out as "inconspicuously dentate" in Phillips (1941: 265, feature 17, pl. 15, fig. 30, judging from the "thickest parts") and as "less prominent (and with outer tracheid walls typically sinuous) dentate" (cause the term "smooth" is used only for generally thin walls with no ornamentation at all) discussed in IAWA Committee (2004: 43, feature 82).

In Greece a lot of fossil pine remnants have been found (e.g. Velitzelos *et al.* 2014; Zidianakis *et al.* 2016) but only a few pine fossils in the form of wood have been identified until now. Moreover, the fossil pine cones and seeds from Greece have been related to *Pinus roxburghii* Sarg. and *P. canariensis* C.Sm. (Mai & Velitzelos 2002, 2007; Boyd 2009; Kvaček *et al.* 2014).

Our specimen has been compared with the fossil pine woods from Greece and has been found to have a lot of differences with them: *Pinoxylon parenchymatosum* Süss & Velitzelos (Süss & Velitzelos 1993) from Lemnos Island is characterized by the occurrence of axial parenchyma, a feature not in accordance with our fossil. *Pinoxylon paradoxum* Süss & Velitzelos (Süss & Velitzelos 1994) from Lesbos Island is characterized by the existence of spirals and *P. pseudoparadoxum* (Süss & Velitzelos 1994, Lesbos Island) has high rays – up to 50 – cells. Our specimen differs also from two more species from Lesbos Island identified by Süss & Velitzelos (2009): from *Lesbosoxylon* (= *Pinoxylon*) *diversiradiatum* Süss & Velitzelos because the latter one has bi-seriate rays and from *L.* (= *Pinoxylon*) *graciliradiatum* Süss & Velitzelos which has large rays with "idioblast-like" cells. There are also differences with *Lesbosoxylon* (= *Pinoxylon*) *ventricosuradiatum* Süss & Velitzelos (e.g. rays with "idioblast-like" cells and pits in the cross-field and ray tracheids not ascertainable) (Süss & Velitzelos 2010). Our specimen has also been compared with *Pinuxylon* sp. cf. *Pinus sylvestris* L. (Iamandei *et al.* 2011, 2016) and found different because the fossil from the Romanian Carpathians has axial parenchyma and 2-3-seriate rays. It has been also compared with *Pinoxylon yabei* Shimakura (Shimakura 1936) which is completely different from our fossil having axial parenchyma, bordered pits arranged in three rows, thick-walled epithelial cells of resin canals, occurrence of traumatic canals and 1-3 seriate rays with up to 70 cells height.

Our fossil has dentate horizontal walls of ray tracheids, therefore it is assigned to Diploxylon pines. So, we immediately reject from comparison the fossil pine woods belonging to Haploxylon type. Wang *et al.* (2017) have made a list including the majority of the fossil pine woods described in literature and their characteristics. This study has divided their list in two categories: a) Haploxylon; and b) Diploxylon pines.

Haploxylon

The fossil Haploxylon pines (with smooth horizontal walls of ray tracheids as also seen in Wang *et al.* 2017: table 1) which are rejected from being correlated with our fossil are the following: *Pinus uniseriata* H.B.Wang, A.A.Oskolski & Z.K.Zhou (Wang *et al.* 2017), *P. albicauloides* S.K.Choi & K.Kim (Choi *et al.* 2010), *Pinuxylon chemrylensis* Blokhina (Blokhina 1995), *Pinoxylon dakotense* Knowlton emend. Read (Nishida & Nishida 1995), *Pinuxylon cembraeforme* Rössler (Rössler 1937), *P. microporosum* Ogura (Nishida & Nishida 1995) or *P. microporum* Ogura (Ogura 1944), which has no ray tracheids (and as also discussed in Blokhina & Bondarenko [2016] shouldn't be assigned to *Pinuxylon*), *P. similkameenensis* Miller (Miller 1973), *Pinuxylon* sp. (Tao *et al.* 1994; Zhang *et al.* 2008 as discussed in Wang *et al.* 2017), *P. woolardii* Tidwell, Parker & Folkman (Tidwell *et al.* 1986), *P. zobelianum* (Göppert) Kräusel (van der Burgh 1964).

Our research has also revealed some more Haploxylon fossil pine woods not in accordance with our fossil described by: 1) Greguss (1967), Petrescu & Bican-Brişan (2004) & Iamandei *et al.* (2016): *Pinuxylon haploxyloides* Greguss (only with a single pinoid cross field pit; holotype still available in Budapest, see in Sakala *et al.* 2018), *P. albicauloides* Greguss (has only fenestroid cross field pits), *P. tarnocziense* (Tuzśon) Greguss and *Pinuxylon* sp.; 2) Dolezych *et al.* (2011): *Pinuxylon succiniferum* (Göppert) Kräusel emend. Dolezych; 3) Vozenin-Serra (1971): *Pinuxylon nightigalense* Vozenin-Serra (as discussed in Iamandei *et al.* 2016); 4) van der Burgh (1964): *Pinuxylon parryoides* (Gothan) Kräusel emend. van der Burgh; and 5) Iamandei & Iamandei (2000): *Pinuxylon marinasii* Iamandei & Iamandei.

Diploxylon

The selected Diploxylon fossil pines of the literature for the purposes of the work by Wang *et al.* (2017) which have similarities with our fossil wood are: *Pinus nanfengensis* Wang, Oskolski & Zhou (Wang *et al.* 2017), *Pinus* cf. *armandii* Franchet (Yi *et al.* 2005), *Pinus hatamuraenase* Jeong & Kim (Jeong *et al.* 2012), *Pinus henanensis* J.J.Yang (Yang *et al.* 1990, 1996; Qi *et al.* 2005, as discussed in Wang *et al.* 2017), *Pinuxylon arjuzanxianum* Huard (Huard 1966; van der Burgh 1973), *Pinuxylon eschweilerence* van der Burgh (van der Burgh 1973), *Pinuxylon halepensoides* van der Burgh (van der Burgh 1973), *Pinuxylon parryoides* (Kräusel) van der Burgh (van der Burgh 1964, 1973; Iamandei 2000), *Pinuxylon paxii* Kräusel (Rössler 1937; van der Burgh 1973), *Pinuxylon pinastroides* (Kraus) Stockmans & Willière (van der Burgh 1973), *Pinuxylon ponderosoides* van der Burgh (van der Burgh 1973), *Pinuxylon taedioides* Kräusel (van der Burgh 1964, 1973; former *Pinuxylon landensis* Huard, 1966), *Pinuxylon tarnocziense* (Tuzśon) Greguss (van der Burgh 1973), *Pinuxylon vateri* (Platen) Rössler (Rössler 1937).

P. nanfengensis (Wang *et al.* 2017) from the late Miocene of the Xianfeng Basin (central Yunnan, southwestern China) is different from our sample in terms of having partially biseriate rays (and not only uniseriate), smooth to slightly pitted ray tracheids and different cross-field pitting (pinoid and taxodioid).

Other similarities

There are also similarities with the fossil pines from China, i.e., *Pinus armandii* Franchet (Yi *et al.* 2002) and *P.* cf. *armandii*

(Yi *et al.* 2005) which belong to Diploxylon pines of *Cembra* section but they have different cross-field pitting (fenestroid in 1-2 rows with 1-4 pits instead of pinoid in 1-2 rows and 1-6 pits in our sample).

Our fossil has similarities with *Pinus hatamuraense* Jeong & Kim (Jeong *et al.* 2012) from the Akita Prefecture but it differs at the height of rays (*P. hatamuraense* has very long rays up to 32 cells), the fact that our fossil does not have parenchyma but *P. hatamuraense* does and the cross field pitting which, in the case of *P. hatamuraense*, includes also taxodioid pits.

Pinus henanensis J.J.Yang (as described in Wang *et al.* 2017 because the original sources are published in Chinese only) is also different from our sample having very high rays consisting of up to 33 cells and pinoid and taxodioid cross-field pitting.

Pinuxylon arjuzanxianum Huard (Huard 1966; van der Burgh 1973; Dupéron & Dupéron-Laudoueneix 1985) is close to our wood but it has 8-9 pits in tangential tracheid walls and up to four pits per cross-field.

Pinuxylon eschweilerence van der Burgh (van der Burgh 1973) has up to two pits per cross-field of pinoid and fenestroid type.

Pinuxylon halepensoides van der Burgh (van der Burgh 1973) differs from our wood in having 7-8 pits in tangential tracheid walls, pits of piceoid, cupressoid and pinoid type and up to two pits per cross-field.

Pinuxylon parryoides (Kräusel) van der Burgh (van der Burgh 1964, 1973; Privé 1972), differs from our wood in having 10-12 pits in tangential tracheid walls, biseriate pits in radial wall of tracheids, pits of pinoid and piceoid type and up to five pits per cross-field.

Pinuxylon paxii Kräusel (Rössler 1937; van der Burgh 1973) has up to two fenestroid pits per cross-field.

Pinuxylon pinastroides (Kraus) Stockmans & Willière (van der Burgh 1973) differs from our wood in having 10-12 pits in tangential tracheid walls, biseriate pits in radial wall of tracheids, pits of cupressoid, taxodioid and pinoid type and up to four pits per cross-field.

Pinuxylon taedioides Kräusel (van der Burgh 1964, 1973; former *Pinuxylon landensis* Huard, 1966; Dupéron & Dupéron-Laudoueneix 1985), differs from our wood in having distinctly dentate horizontal walls of ray tracheids, biseriate pits in radial wall of tracheids, and 1-3 pinoid pits per cross-field.

Pinuxylon tarnocziense (Tuzśon) Greguss (van der Burgh 1973), differs from our wood in having weakly dentate horizontal walls of ray tracheids, biseriate pits in radial wall of tracheids, and 2-3 pinoid pits per cross-field.

Pinuxylon vateri (Platen) Rössler (Rössler 1937) differs from our wood in having taxodioid and pinoid pits per cross-field.

Pinuxylon ponderosoides van der Burgh (van der Burgh 1973) is very close to our sample but it has only up to four pinoid pits per cross field.

As resumed from the aforementioned comparison none of the above-mentioned species was identical to the new finding from Alonissos. Consequently the fossil pine wood from Alonissos Island is declared as a new species, named according the ICBN rules (McNeill *et al.* 2006: art. 23; art. 60, ICBN – Vienna Code) after the place where it was found: *Pinuxylon alonissianum* Mantzouka & Sakala, sp. nov.

BOTANICAL AFFINITIES

The distinction between the sections *Pinus* (Diploxylon or hard pines) and *Strobus* (Haploxylon or soft pines) has been discussed more than a hundred years ago (Shaw 1914) and along with the history of the fossil findings of the genus is well documented in Xu *et al.* (2015). This divergence took place probably during the mid-Cretaceous (Keeley 2012).

Following the identification key by van der Burgh (1973) we come to the conclusion that our fossil modern relative belongs to one of the following: section *Pinaster*, or section *Sula* (*P. leucodermis*), or section *Leiophylla* or section *Lumholtzii*.

Following the classification by Price *et al.* (1998) and the detailed work of the wood anatomical characteristics of the conifers by Esteban *et al.* (2004) we examined the modern species belonging to Diploxylon pines (and especially the species of the sections that van der Burgh's identification key had revealed) in order to find the botanical affinities of ours:

1) Section *Pinus* (Subsection *Pinus* – because some of the species revealed following van der Burgh's identification key are now belonging to this subsection). *Pinus densiflora* Siebold & Zuccarini, *P. mugo* Turra, *P. mugo* subsp. *uncinata* (Ramond) Domin, *P. nigra* J.F. Arnold, *P. resinosa* Aiton, *P. sylvestris* L. and *P. tabuliformis* Carrière are excluded because they have 1-2- fenestroid pits per cross-field.

Pinus heldreichii H. Christ has rays very high of up to 30 cells, ray parenchyma with pitted horizontal walls and 1-2 pinoid pits per cross-field.

Pinus kesiya Royle ex Gordon has axial parenchyma.

Pinus massoniana Lambert, *P. lumholtzii* B.L. Robinson & Fernald and *P. pinaster* Aiton have biseriate bordered pits on the radial walls of the axial tracheids.

Pinus merkusii Junghuhn & de Vriese ex de Vriese and *P. thunbergii* Parlatore have biseriate bordered pits on the radial walls of the axial tracheids and fenestroid cross-field pits.

2) Section *Pinus* (Subsection *Canarienses* – Canary Islands, Himalayas). *Pinus canariensis* C. Smith ex Buch has axial parenchyma and biseriate bordered pits on the radial walls of the axial tracheids.

Pinus roxburghii Sargent (former named as *P. longifolia*) has biseriate bordered pits on the radial walls of the axial tracheids (Groom & Rushton 1913).

3) Section *Pinus* (Subsection *Halepenses* – S. Europe, W. Asia, N. Africa). *Pinus brutia* Tenore, is excluded because it has ray parenchyma with nodular end walls and with pitted horizontal walls.

Pinus halepensis Miller is excluded because it has biseriate bordered pits on the radial walls of the axial tracheids and ray parenchyma with nodular end walls and with pitted horizontal walls.

4) Section *Pinus* (Subsection *Pineae* – S. Europe). *Pinus pinea* L. is excluded because it has biseriate bordered pits on the radial walls of the axial tracheids and ray parenchyma with nodular end walls and with pitted horizontal walls.

5) Section *Pinus* (Subsection *Leiophyllae* – Mexico and adjacent SW USA). *Pinus leiophylla* Schiede ex Schlechtendal & Chamisso has up to two pinoid pits per cross-field.

P. leiophylla var. *chihuahuana* (Engelm.) Shaw has up to four pits per cross-field. Therefore we believe that this species could be the modern analogue of our fossil.

6) Section *Pinaster*. *Pinus banksiana* Lambert, *P. caribaea* Morelet, *P. clausa* (Chapman ex Engelmann) Vasey ex Sargent, *P. coulteri* D. Don, *P. echinata* Miller, *P. glabra* Walter, *P. hartwegii* Lindley , *P. lawsonii* Roezl ex Gordon & Glendinning, *P. montezumae* Lambert, *P. occidentalis* Swartz, *P. palustris* Miller, *P. patula* Schiede ex Schlectendahl & Chamisso, *P. pseudostrobus* Lindley, *P. pungens* Lambert, *P. radiata* D. Don, *P. rigida* Miller, *P. sabiniana* Douglas ex D.Don, *P. serotina* Michaux, *P. taeda* L. are excluded because they have biseriate bordered pits on the radial walls of the axial tracheids.

Pinus attenuata Lemmon, *P. elliottii* Engelmann, *P. muricata* D. Don, *P. ponderosa* Douglas ex Lawson, *P. teocote* Schiede ex Schlechtendal & Chamisso, *P. torreyana* Parry ex Carrière, *P. virginiana* Miller are excluded for having ray parenchyma with nodular end walls and/or with pitted horizontal walls.

Pinus contorta Douglas ex Loudon is excluded for having ray parenchyma with nodular end walls and fenestroid cross-field pits.

From this section it seems that *Pinus arizonica* Engelmann ex Rothrock, *P. arizonica* var. *cooperi* (C.E.Blanco) Farjon, *P. engelmannii* Carrière, *P. jeffreyi* Greville & Balfour could also resemble the modern representatives of our fossil.

PALAEOENVIRONMENTAL DISCUSSION

About *Glyptostrobus*

LePage (LePage *et al.* 2005; LePage 2007) points out that the extinction of *Glyptostrobus* from North America and Europe along with its increased tolerance in cold and arid environments should most probably be related to increased aridity, decreased global temperature or increased competition for resources from the Pinaceae.

Concerning *Glyptostrobus pensilis*, Farjon & Filer (2013) have reported that it occurs in river banks and low lying marshland between 500 and 700 m a.s.l. in SE China, Viet Nam and Lao PDR and is the only extant species of this genus. The size of the ovulate cones from Kymi (Early Miocene) is smaller and more rounded than the Late Miocene material from the Pannonian area and there are more differences with the only extant species *G. pensilis* (Stauton ex D. Don) K. Koch.

The modern *G. pensilis* seems to be more demanding than its ancestor judging from the temperature and precipitation requirements for its occurrence as reported in Fang *et al.* (2011) (MAT: 18.8 [10.6-23.0°C]; MTCM: 9.0 [-0.2-15.2°C]; MTWM: 27.6 [21.1-29.7°C]; ABT: 18.8 [10.6-23.0°C]; WI: 166.2 [79.4-216.2°C]; CI: 0.3 [0.0-12.1°C]; PET: 996 [643-1247 mm]; AP: 1526 [950-2148 mm]; PWQ: 629 [411-1234 mm]; PCQ: 141 [27-259 mm]; Im: 54.6 [8.0-137.5]; AET: 993 [643-1247 mm]; NPP: 208.2 [95.3-551.6]. The abbreviations are explained as follows: mean annual temperature [MAT, °C], mean temperature of the coldest month [MTCM, °C], mean temperature of the warmest month [MTWM, °C], annual biotemperature [ABT, °C], warmth index [WI, °C], coldness index [CI, °C], potential evapotranspiration [PET, mm], annual precipitation [AP, mm], precipitation of warmest quarter [PWQ, mm], precipitation of coldest quarter [PCQ, mm], moisture index [Im], annual actual evaportranspiration [AET, mm], vegetation net primary productivity [NPP, g · a^{-1} · m^{-2}]).

On the other hand *Glyptostrobus europaeus* of the Mediterranean region had as the minimum thermic requirements MATmin a temperature of 16.2°C (Martinetto *et al.* 2017) in the warmer and drier south Mediterranean region of the past but had to face climatic, sea level and topogeny changes (e.g. first and third phase of Zanclean flood in Fauquette *et al.* 1998, 2007; Biltekin *et al.* 2015). LePage (2007) gives also the preferred habitats of *Glyptostrobus*, among of which is the lowland swamp to riparian area. This palaeohabitat corresponds perfectly to our case (under the spectrum, of course, of and orogenetic changes).

The characterization of this palaeoenvironment of ours is also supported by Farjon (2005) because *Glyptostrobus* is known to be tolerant of competition only in environments characterized by wet conditions.

The spectacular morphological stasis of this taxon over a long period of geological time has been stated in several works the last decade, for instance in LePage (2007), in Martinetto *et al.* (2007, 2015); Martinetto & Macaluso (2018); Macaluso *et al.* (2018) concerning the deposits of late Piacenzian age (2.8 Ma) and even Gellasian from Italy, in Teodoridis *et al.* (2017) where the latter localities where correlated with the ones of the same age from Czech Republic, in Biltekin *et al.* (2015) concerning the recent *Glyptostrobus* swamp ecosystems' disappearance from the southern Black Sea shoreline. Concerning the Greek findings similar theories had been already discussed (e.g. Velitzelos & Gregor 1990) pointing out that *Glyptostrobus* must have had a dominant role in extant swamps (in basins like Aliveri or Prosilion) mostly representing biotopes of long-time evolvement.

About *Pinuxylon*

As stated above, the xylitic remnant we studied is closer to *Pinuxylon arjuzanxianum* Huard (Huard 1966; van der Burgh 1973; Dupéron & Dupéron-Laudoueneix 1985) but not identical, therefore is has been named as *P. alonissianum* Mantzouka & Sakala, sp. nov. The botanical affinities of this fossil were really interesting including the species *Pinus leiophylla* var. *chihuahuana*, *P. arizonica*, *P. arizonica* var. *cooperi*, *P. engelmannii* and *P. jeffreyi*.

According to Farjon & Filer (2013) *P. leiophylla* var. *chihuahuana*, is widespread in the Sierra Madre Occidental of Mexico and extends into the southernmost parts of Arizona and New Mexico in the USA being the more northern variety and preferring lower altitudes with drier forest.

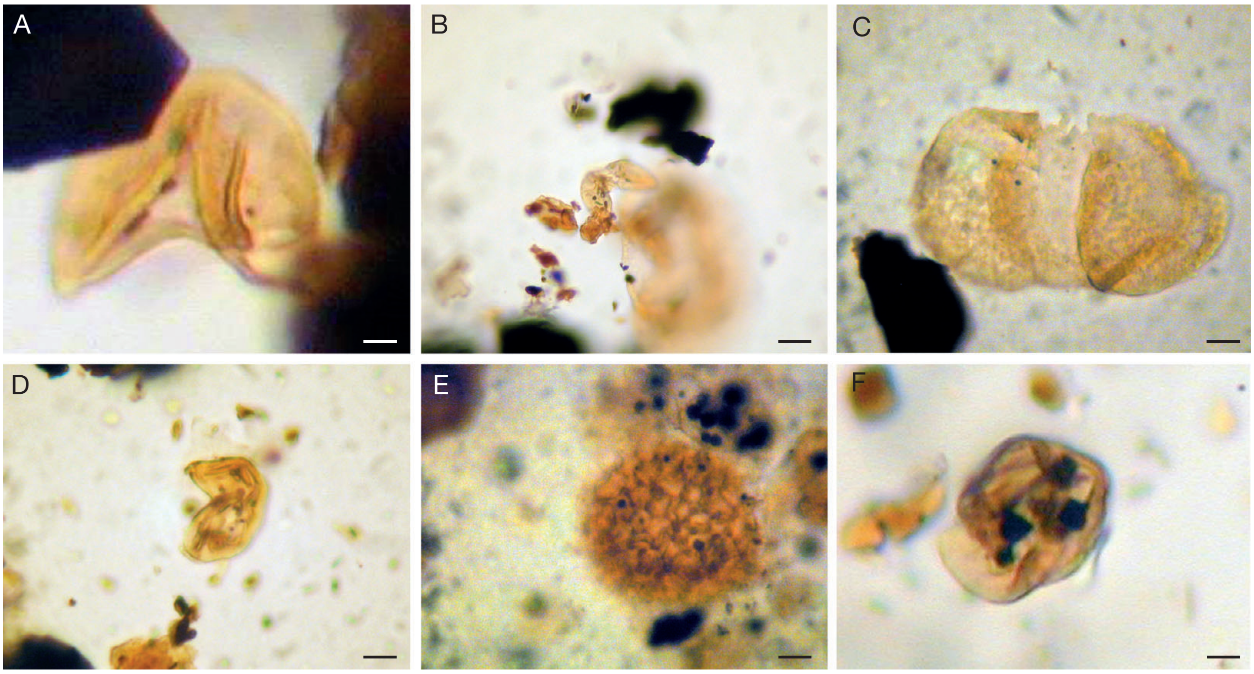


Fig. 6. — Palynology: **A**, **B**, **D**, Taxodiaceae (today part of the Cupressaceae s.l.); **C**, Pinaceae (*Pinus*-Diploxylon pollen type sensu Hesse *et al.* 2006: 22, 23); **E**, Pteridophyta (Osmundaceae); **F**, Fagaceae (*Quercus*). Scale bars: **A**, **F**, 2 µm; **B-E,** 10 µm.

According to Farjon & Filer (2013): *Pinus arizonica* is a species of the Sierra Madre Oriental and the northern parts of the Sierra Madre Occidental (with var. *cooperi*), extending into Arizona and New Mexico and possibly in Trans-Pecos Texas living in an environment of moderate rainfalls (700-900 mm) and high altitude (above 2000 m with the only exception of an isolated population of var. *cooperi* in the Serranias del Burro in N Coahuila; at only 1300 m a.s.l). *Pinus engelmannii* occurs also in the Sierra Madre Occidental, and in the Sierra Madre Oriental as well, in an altitude ranging from 1200 to 3000 m and is tolerant to cold. *Pinus jeffreyi* is distributed in California, Oregon, Sierra Nevada, Mexico occurring in mixed coniferous dry and hot environment of middle elevation.

The remarkable specialization of *Pinus* was the corner stone which lead this genus to survive through great geologic and climatic changes by making adaptations correlated to the environmental conditions (Farjon 1996). The origin and evolution of the genus has been the subject of several works based mostly on the classification of fossil organ findings (e.g. cones, needles and rarely based on fossil wood anatomy) and molecular phylogenetic studies (e.g. Eckert & Hall 2006; Miller 1976; Price *et al.* 1998). Moreover the biogeography of this genus has been also the main focus for the establishment of scientific hypotheses, such as the "Gnepine" which indicates that the center of diversity is not necessarily the place of origin (Wang & Ran 2014) or the interpretation of pine evolution based on fire-prone traits and abiotically stressful habitats (Keeley 2012). This theory could be supported also with the work by Kvaček & Rember (2000) where the Miocene populations of *Glyptostrobus* found in North America and in Europe show a close relationship but also independence. Concerning *Pinus*, although the genus is well diversified in Europe and North America during the Miocene (Kvaček & Rember 2000) a reliable comparison remains open.

According to Eckert & Hall (2006) the molecular clocks date the divergence between *P. jeffreyi*-*P. arizonica* and *P. engelmannii*-*P. devoniana* at about 17.5 Ma, while the separation between *P. jeffreyi* and *P. arizonica* occurred at 10 Ma, the separation between *P. engelmannii* and *P. devoniana* occurred before 12.5 Ma as also the separation between *P. leiophylla* and *P. herrerae*.

The co-occurrence of fossil *Glyptostrobus* (as *Glyptostroboxylon*) and *Pinuxylon* has been reported in several works as well, as for instance in the work of Rössler (1937) on the Pliocene coniferous woods around Gleichenberg in Styria (Austria).

What is also interesting is that the plant fossiliferous locality of Alonissos is strongly related to the one of Kymi (Euboea). In Kymi there are a lot of *Glyptostrobus europaeus* findings as well as pine remnants and a cycadalean foliage described by Saporta (1874). This specimen has been revised by Kvaček & Velitzelos (2000) as "*Encephalartos*" *gorceixianus* Saporta closer to the genus *Dioon* Lindley growing in Central America and Mexico rather than to Africa (as Saporta [1874] stated). According to Erdei *et al.* (2010) fossil Encephalartoideae from the Oligo-Miocene of Europe could represent an extinct group of conspecific species of cycads inhabited southern Europe following the trait: Turkey (*Pseudodioon akyoli* Erdei, Akgün & Lumaga, 2010) – Greece ("*Encephalartos*" *gorceixianus* Saporta) – France ("*Zamites*" *epibius* Saporta) – Switzerland ("*Zamites*" *tertiarius* Heer). The extratropical area of Sierra Madre Orientale (NE Mexico) is referred in the palaeobotanical literature by Kvaček (2014) as the inhabitant of the modern *Ceratozamia* Brongniart, suggesting subtropical to warm-temperate, almost frostless climate and a high amount of precipitation also to its fossil ancestor.

About palaeontological studies

The preliminary results of an ongoing study on fossil gastropods from the area supports the palaeoenvironmental conditions of our plant findings as a wet and warm "swamp-*Glyptostrobus*" biotope.

The composition of the aquatic gastropod assemblage which is almost monospecific, dominated in species and individual numbers by *Planorbarius mantelli* (Dunker, 1848) with rare *Gyraulus* sp. and very rare *Pseudamnicola* sp., indicate a shallow ephemeral lake.

Extant *Planorbarius corneus* (Linnaeus, 1758) prefers vegetated, stagnant to slowly running waters, feeding on detritus (Fechter & Falkner 1990; Glöer 2002) and most *Gyraulus* species live in stagnant or slowly running waters also.

The freshwater molluscs of the samples, with the very high number of pulmonate gastropods, suggest a shallow and stagnant water body with densely vegetated watersides. The scarceness of fluvial taxa, such as *Pseudamnicola* sp., indicates a very limited riverine influx.

The composition of the microflora which is enclosed at the studied sediments is characterized by the presence of pollen of trees, shrubs, Poaceae, spores of Pteridophytes and algae of Zygnemataceae (Fig. 6).

The main characteristics of this microflora are the following:

1) a remarkable presence of the pollen of Pinaceae (especially of *Pinus* type) followed by the taxa of *Abies* Miller and *Tsuga* (Endlicher) Carrière in lower percentages. Fossil pollen of Taxodiaceae – Cupressaceae (*Inaperturopollenites hiatus* Thomson & Pflug – *Glyptostrobus europaeus*) was also identified in even lower percentages;

2) angiosperms pollen of trees and shrubs were identified in notable percentages and in great diversity with taxa of *Quercus*, mainly *Q. pubescens* Willd. and *Q. coccifera*-type, *Carya* Nuttall, cf. *Castanea*, *Nyssa* Gronov. ex Linnaeus, *Alnus* Miller, *Pterocarya* Nuttall ex Moquin-Tandon, *Carpinus* L., *Corylus* L., etc.;

and 3) notable participation of pollen of Poaceae, such as: Gramineae, Compositae, Cruciferae, Polygonaceae, Amaranthaceae-Chenopodiaceae. Spores of Pteridophytes of Lycopodiaceae and Osmundaceae are associated in good percentages.

Moreover, taxa-indicators of aquatic environments along with species of Zygnemataceae algae were identified.

The palynofloristic analysis indicates local vegetation composed of a canopy of conifers dominated by Pinaceae and a minor sub-canopy of *Taxodium – Glyptostrobus europaeus*, as well as an understory of hydrophilous ferns, mosses and herbaceous angiosperms, indicative of a warm and humid climate in a swampy area.

Finally, the new evidence in combination with the bibliographic data on the palaeobotany of Greece and the Eastern Mediterranean lead to the conclusion that the sediments studied here, were deposited during the Lower Miocene (MN3/MN4 biozone).

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