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Palaeoxylotomical studies in the Cenozoic petrified forests of Greece. Part one – palms

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ABSTRACT. The paper reports a palaeoxylotomical study of petrified palm remains (stem, root, rachis) collected from some fossil sites of Greece (Evros, Lemnos, Lesbos and Kastoria) aged to the late Oligocene to early Miocene. Five species of *Palmoxylon* were identified: *P. daemonoropsoides* (Unger) Kirchheimer, corr., *P. chamaeropsoides* Iamandei et Iamandei, sp. nov., *P. coryphoides* Ambwani et Mehrotra, *P. sabaloides* Greguss, *P. trachycarpoides* Iamandei et Iamandei, sp. nov. and *P. phoenicoides* Hofmann. Also found were two species of *Rhizopalmoxylon* (*R. daemonoropsoides* Iamandei et Iamandei, sp. nov., *R. phoenicoides* Iamandei et Iamandei, sp. nov.) and *Palmocaulon* sp. aff. *Phoenix* L. These new identifications add new elements to the forest assemblages of the Oligocene–Miocene Greek flora, useful for understanding the evolution of the Cenozoic palaeoclimate in the Aegean area.

KEYWORDS: *Palmoxylon*, *Rhizopalmoxylon*, *Palmocaulon*, fibrovascular bundles, petrified forest, Evros, Lemnos, Lesbos

INTRODUCTION

Greece is a “Heaven of Cenozoic Petrified Forests”, with many fossiliferous localities in the insular as well as continental parts. The evolution of the Cenozoic flora in this large region is generally known from various palaeobotanical and palynological studies, but a systematic palaeoxylotomical study of those petrified forests is still needed.

From the vegetal associations already described (Velitzelos D. et al. 2014), we can infer the type of forests that lived under a subtropical to warm-temperate palaeoclimate in a quasi-continental area during the Hellenic orogeny. In recent years, numerous petrified wood remains of conifers and angiosperms (e.g. Laurales, Fagales, Myrtales) and monocots (e.g. Arecales) have also been found, some of them still being studied. The results should contribute to a better understanding of the evolution of the arboreal vegetation of Greece during the Oligocene to early–middle Miocene, and the evolution of the Tertiary palaeoclimate in the Aegean area.

GEOLOGICAL SETTING OF THE GREEK AREAS OF PALAEOBOTANICAL INTEREST

EVROS REGION

Almost the entire region of Evros (Eastern Macedonia and Thrace, see Fig. 1) is full of vegetal fossil remains, especially as petrified plants (see also Velitzelos D. et al. 2014). For the Cenozoic, the geological setting includes sedimentation initiated in the Eocene (probably in the Lutetian) with deposition of a basalclastic formation composed of conglomerates

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Fig. 1. Map of Greece, with the locations (*) where the studied palm fossil samples were collected (from d-maps.com, with modifications)

and sandstones, overlain by the Priabonian Formation including marls alternating with sandstones, conglomerates and intercalations of brown coal horizons at the upper levels.

Synthesizing previous views on the geological evolution of Evros, Voudouris et al. (2007) showed that the main phase of Cenozoic magmatism took place during the Oligocene until the earliest Miocene (Innocenti et al. 1984, Del Moro et al. 1988) and is represented by submarine/terrestrial volcanic and subvolcanic rocks. Christofides et al. (2004) give radiometric ages of 30–28 Ma for the area north of Tycheron, which suggests late Rupelian/early Chattian age. With them is associated a volcano-sedimentary series comprising marls, sandstones and clays, with intercalations of volcanic rock as lava, tuff and pyroclastics.

In the Evros region, the magmatic activity was closely related to the development of basin-controlled volcano-sedimentary formations which discordantly cover the basement rock of the Rhodope massif and of the Circum Rhodope Belt. Closer to the volcanic centers, in the Dadia area, the geology includes:

a) A lower series of Priabonian marine sediments associated with andesitic lavas.

b) Pyroclastics and lavas of dacitic to rhyolitic composition with intercalated sediments of lower to upper Oligocene age. The volcanics include pyroclastic flows, air-fall deposits, as well as lava flows and domes.

c) Upper Oligocene shallow marine sediments dominated by sandstones, marls and conglomerates (the Provatonas series), discordantly covering acidic volcanics. The area is also dominated by ignimbrites several meters thick (Papadopoulos 1982).

The Lykofi–Fylakto–Lefkymi area is characterized by numerous occurrences of silicified fossil plants hosted within the Oligocene volcano-sedimentary formation. According to Kopp (1965), Petrescu et al. (1980) and Velitzelos et al. (2002), the fossil plants are related mainly to the Rupelian–Chattian lignite-bearing volcano-sedimentary levels of the Provatonas series (around Fylakto village), which discordantly cover the volcanics. Coral reefs and abundant mollusks within the silt layers, indicating a shallow marine environment, have been observed (Kopp 1965, Voudouris et al. 2007). Around Lefkimi village, rocks of rhyolitic and andesitic composition appear in a submarine environment (as hyaloclastites) and are overlain by coral-bearing reefs and then by fine-grained volcano-sedimentary layers including silicified wood.

Very interesting is the occurrence of large vegetal remains preserved within the volcano-sedimentary deposits, showing signs of transport. It is most probably a lahar generated by unstable volcanic superstructures mobilized by, for example, catastrophic rainfall. The volcanic material was transported as flows of cold volcanic unsorted mud, or as pebbles from reworked volcanic rocks (lavas, volcanic bombs, lapili, coarse pyroclastics, volcanic ash) often mixed with terrigenous material and sedimented in the neighboring marine basin, sometimes also preserving nearby fossil wood and other vegetal remains (leaf or fruit impressions), bones of terrestrial animals and shallow-water mollusks or corals which have been found and documented (Voudouris et al. 2007).

Plant remains have been found in late Oligocene volcano-sedimentary formations in numerous localities, and a complex flora is suggested by palaeobotanical studies that revealed the presence of arboreal coniferous taxa as *Quasisequoia couttsiae* (Heer) L. Kunzmann, *Taxodium dubium* (Sternberg) Heer, *Calocedrus suleticensis* (Brabanec) Kvaček, *Pinus palaeostrobus* Ettingshausen (needle leaves in fascicles of five), cf. *Cunninghamia miocenica* Ettingshausen, *Pinus* cf. *rigios* Ettingshausen (needle leaves in fascicles of three), and angiospermous taxa as *Daphnogene cinnamomifolia* (Brongniart) Unger, *Laurophyllum* sp., *Eotrigonobalanus furcinervis* (Rossmässler) Walther et Kvaček, *Dicotylophyllum* sp. aff. *Quercus daphnes* Unger or cf. *Quercus rhenana* (Kräusel et Weyland) Erw. Knobloch et Kvaček, *Fagus castaneifolia* Unger [as *Fagus* aff. *antipofii* Heer], Fagaceae gen. et sp. indet., *Comptonia difformis* (Sternberg) Berry fm. *dryandroides* (Unger) E. Velitzelos, Kvaček et D. Velitzelos, *Dicotylophyllum* sp. cf. *Nyssa haidingeri* (Ettingshausen) Kvaček et Bůžek, cf. *Juglans acuminata* A. Braun, *Alnus* aff. *schmalhausenii* Grubov, *Alnus gaudinii* (Heer) Erw. Knobloch et Kvaček, *Populus* aff. *balsamoides* Göppert, *P. germanica* (Menzel) Walther, *Cedrela attica* (Unger) Palamarev et Petkova, *Ziziphus ziziphoides* (Unger) Weyland, *Myrica longifolia* Unger, *Sterculia labrusca* Unger, *Platanus neptuni* (Ettingshausen) Bůžek, Holy et Kvaček, and other taxa including *Rhodomyrtophyllum*, *Smilax*, *Salix*, *Castanea*, *Matudaea*, *Laria* and some Monocots such as *Phoenicites* aff. *salicifolius* (Presl, in Sternberg) Unger, *Sabal lamanonis* (Brongniart) Heer and *Sabal raphifolia* (Sternberg) Erw. Knobloch et Kvaček (see Velitzelos D. et al. 2014).

Petrified wood frequently appears in the Evros region, especially at Lagina, Lira, Lykofi, Fylakto, Provatonas, Tycheron, Trifili, Lefkymi, Sapes and Aëtohori. Visiting these fossiliferous sites, we have collected a lot of samples of petrified wood representing angiosperms and conifers, but only around Aëtohori, on the slopes of the Pefka volcano, within similar dominantly volcano-sedimentary rocks (hard fine-grained tuffite), have impressions of integer leaves of a fan-palm tree been found (see Kopp 1965, Velitzelos et al. 2002, Velitzelos D. et al. 2014). Some years ago we also collected petrified palm stem remains from the Aëtohori area. In this paper, two species of *Palmoxylon* Schenk from Aëtohori are described: *P. daemonoropsoides* (Unger) Kirchheimer, corr. and *P. coryphoides* Ambwani & Mehrotra.

LEMNOS (= LIMNOS)

Lemnos Island (Fig. 1) is another area full of fossil vegetal remains (Velitzelos D. et al. 2014). Its geology is characterized by a sedimentary basement including molassic deposits of Middle Eocene–Lower Miocene age, overlain by volcanic products (lava domes, flows and pyroclastics) of Lower Miocene age and by an Upper Quaternary sedimentary formation (Davis 1960, Innocenti et al. 1984, Roussos 1993). The volcanic rock units which cover the major part of the island are subdivided into the Katalako Unit, Romanou Unit and Myrina Unit.

Silicified and opalized plant fossils are found mainly in the Romanou Unit. The pyroclastic rocks of this unit have been radiometrically dated at 19.8 Ma, representing the Burdigalian (Innocenti et al. 1994, Voudouris et al. 2007, Velitzelos D. et al. 2014). A subvolcanic body of quartz monzonitic composition intrudes the volcanics and sediments in the southern part of the Fakos Peninsula. The intense hydrothermal alteration and quartz veining in the Fakos area are very similar to those described from Kassiteres in the Evros region (Voudouris & Skarpelis 1998, Voudouris et al. 2007).

Hence, the Romanou Unit is the main host for the petrified wood of Lemnos Island. It is constituted of up to 160 m thick pyroclastic deposits which extend over broad areas mainly around the Moudros Gulf. This unit is dominated at the base by white pyroclastic flows rich in lithic components and pumiceous fragments, followed by intercalations of ignimbrites, volcanic breccias and pyroclastic flows, related with K-rich dacites to latites. These rocks are radiometrically dated at 19.8 Ma (Innocenti et al. 1994), indicating the lowermost Miocene.

In this area, around the Moudros–Roussopouli–Varos–Portianou localities, pyroclastic beds bearing silicified wood are abundant. Here the stratigraphy consists of tuffitic layers at the base, overlain by volcaniclastic material locally penetrated by lava domes, which flows along the same orientation (NE–SW) as the fault zones. The entire area is characterized by hydrothermal activity, similar to that of the Evros region (more details in Voudouris et al. 2007). It is known that silicified woods occur in two distinct environments:

– in slightly altered pyroclastics (argillic alteration): typical for this type of occurrence are the localities of Varos, Portianou and Moudros villages, where large petrified trunks several meters long occur, hosted within the pyroclastics (see Fig. 5c in Voudouris et al. 2007);

– in several layers of opaline "silica sinter"; similar silicification appears extending from Moudros to Roussopouli. The fossiliferous zones (see also Papp 1953) are intercalated between the pyroclastic beds and are up to 3 m thick each. At least six silica sinter horizons have been recognized (see Fig. 5d in Voudouris et al. 2007).

Some plant macroremains collected from Lemnos were identified as *Pronephrium stiriacum* (Unger) Erw. Knobloch et Kvaček, *Glyptostrobus europaeus* (Brongniart) Unger, *Sequoia abietina* (Brongniart) Erw. Knobloch, as *Daphnogene polymorpha* (A. Braun) Ettingshausen [of *Cinnamomum* type], cf. *Quercus drymeja* Unger, diverse Dicotyledoneae indet. (aff. *Myrica*, Fagaceae, Lauraceae), *Acer tricuspidatum* Bronn, *Zelkova zelkovifolia* (Unger) Bůžek, Kotlaba and *Eriolaena* sp. (Velitzelos D. et al. 2014).

From Lemnos, numerous remnants of fossil woods have been collected, sometimes from excavations, from around the villages of Fergani, Romanou, Moudros, Varos, Rossopouli, Portianou, Thanos and Kontias, and on the hill of Paradisi, representing the specific "Petrified Forest of Limnos". However, a few lignotaxa have already been described from there: *Laurinoxylon ehrendorferi* and *Cornoxylon pappi*, described by Berger (1953), and later, a problematic conifer: *Pinoxylon parenchymatosum* Süss & Velitzelos (1993) later revised as *Lesbosoxylon* by Süss & Velitzelos (2010). A study of new samples collected from Lemnos is in progress, representing wood of angiosperms and conifers (Iamandei, unpublished data). Also some Monocots such as gen. et spec. indet. (aff. Cyperaceae) or *Phragmites* sp., but especially palm roots, palm seeds or palm leaves, possibly of *Sabal* type, have been found in the Kastron–Myrina and Antissa areas, and leaf imprints of *Phoenix* type within tuffitic layers from the Moudros area (Velitzelos D. et al. 2014).

From this area, two species of *Palmoxylon* Schenk have been described (*P. trachycarpoides* Iamandei et Iamandei, sp. nov., *P. phoenicoides* Iamandei et Iamandei, sp. nov.), and also a species of *Rhizopalmoxylon* (*R. phoenicoides* Iamandei et Iamandei, sp. nov.).

LESBOS (= LESVOS)

Numerous specimens of petrified tree trunks and other fossil vegetal remains found on Lesbos Island (Fig. 1) constitute the "Petrified Forest of Lesvos", organized as a geopark (see Velitzelos D. et al. 2014).

The geology of the island is characterized by a sedimentary basement including molassic deposits, found in the areas of the villages of Megalonisi, Bali Alonia, Eressos, Antissa and Sigri, and on Megalonisi Islet, places that expose large accumulations of silicified tree trunks. Other numerous dispersed samples of petrified wood have been found and collected in many other places on the island, including the village areas of Hidira, Gavathas, Molyvos, Polichnitos, Mesotopos, Plomari and Akrasi.

The petrifaction of the woody material was directly related to intense volcanic activity on Lesbos Island during the Early Miocene (Aquitanian–Burdigalian). The Eressos Formation (age ~21.5 Ma) is overlain by the Skoutaros Formation which includes the Sigri pyroclastics, resulting from the main stage of volcanic activity on Lesbos, which occurred between 18.5 and 17 Ma. (Zouros et al. 2007). The silicified lacustrine marls bearing plant remains and mammal fossils (*Prodeinotherium bavaricum* Meyer 1831) just below the volcanic rocks suggest an age of 18–19 Ma (Koufos et al. 2003). The remains of micromammals, lizard dentaries and crocodile teeth indicate MN3/MN4 (Vasileiadou & Zouros 2012).

At that time, the volcanic eruptions produced a high quantity of acidic rocks, mostly ignimbrites, with normal shoshonite REE patterns (Pe-Piper 1980a, b, Pe-Piper & Piper 1993) as lavas, pyroclastic materials and volcanic ash, which covered the entire vegetation of the area so rapidly that they preserved the tree trunks *in situ*, destroying or preserving fragmentary branches or other plant parts. Along with the volcanic activity, but also afterwards, hot or even cold solutions of silicon dioxide circulated within the volcanic material that covered the vegetal remains. Sometimes the pyroclastic flows transported the plant remains far from their growth sites. The major fossilization process started: ionic solutions penetrated the cellular membranes and precipitated inside the cells as amorphous silica, or opal, filling all the empty spaces. The organic matter remained as a carbon pellicule preserving the cell wall details. Some authors point out that the organic matter can be replaced later, molecule by molecule, by inorganic material. Thus the anatomical structure of the tree trunks, such as the annual rings, medullary rays, vessels, fibers and parenchyma are entirely well preserved. An extensive and documented analysis of the silicification processes is presented in Matysová et al. (2010) and Matysová (2016).

The "Petrified Forest of Lesvos", now an important European protected geopark (http://www.europeangeoparks.org/), with numerous petrified tree trunks in their growth positions, is a splendid geological monument of great scientific significance, spread over a wide area, which offers an opportunity to study the entire vegetation, often preserving all the plant parts as leaf imprints, fruit compressions, and silicified trunks, branches or roots and leaves or fruits.

The first reports of Cenozoic petrified wood from Lesbos were made by Unger (1845–1847), identifying forms such as *Peuce lesbia* Unger, *Taxoxylon priscum* Unger and *Thujoxylum peucinum* Unger. The first taxon was revised and renamed later by Goeppert (1848) as *Pinites lesbius* (Unger) Goeppert, then by Kraus (1870) as *Cedroxylon lesbium* (Unger) Kraus. Mantzouka et al. (2017) revised it again as a new combination: *Taxodioxylon lesbium* (Unger) Mantzouka & Sakala. *Thujoxylum peucinum* became *Thujoxylon antisum* Süss & Velitzelos (1998). Also, *Juglandinium mediteraneum* Unger and *Mirbelites lesbius* Unger were both revised by Mantzouka et al. (2013) as *Juglandoxylon mediteraneum* (Unger) Mantzouka et al. Probably this taxon is still a subject to be revised as a species of *Rhysocaryoxylon* Dupéron, a valid genus. Another taxon described by Unger, *Brongniartites graecus* Unger, remained unrevised, and has no an extant equivalent.

Flinche (in De Launay 1898) identified some petrified trees from Lesbos as "*Cedroxylon*" and "*Pityoxylon*" (?), taxa difficult to equate to some extant taxa, and also some charcoalfied forms of "*Cedroxylon*" type, "*Ebenoxylon*" type and *Palmoxylon* type. Later, Berger (1953) made some references to fossil tree trunks from the whole area of the Aegean Sea in his palaeobotanical studies of Greece.

After a brief visit to Lesbos (only around Eressos and Sigri), Kräusel noted the possible scientific value of the petrified wood from there, supposing the relative age to be "probably older than the Pliocene". He only suggested the relation of the fossil wood to Taxodiaceae, probably of *Sequoia* type, and to dicots of *Quercus* type (Kräusel R. 1965 – The Petrified Forest of Lesvos – Unpublished Report, quoted by Mantzouka et al. 2013 and by Velitzelos D. et al. 2014).

Since 1979, the Division of Historical Geology and Palaeontology of the Department of Geology at the University of Athens has been conducting important palaeobotanical research in Lesbos and elsewhere. This work has concentrated mainly on the petrified wood remains of Lesbos (Süss 1997, Süss & Velitzelos 1994a, b, 1997, 1998, 1999, 2000, 2001), and less on fossil leaves of the litter horizon of the petrified forest (Velitzelos & Symeonidis 1978, Velitzelos et al. 1981a, b, 2000, Velitzelos & Gregor 1990, Velitzelos & Zouros 2000, Zouros et al. 2007). The autochthonous nature of the petrified wood allows even the forest zonation to be reconstructed.

East of Sigri, some conifers of unclear affinity have been described by Süss & Velitzelos (1994b, 1999) as a new genera, *Chimairoidoxylon*, with two species (*Chimairoidoxylon lesboense* Süss & Velitzelos 1999, *C. conspicuum* Süss & Velitzelos 2001), and *Lesbosoxylon* Süss et Velitzelos 2010 (by revision of some previous species attributed to *Pinoxylon* Knowlton emend. Read), with some new species described (*Lesbosoxylon paradoxum*, *L. pseudoparadoxum*, *L. diversiradiatum*, *L. parenchymatosum*, *L. graciliradiatum*, *L. ventricosuradiatum*, described by Süss & Velitzelos 1994b, 2010). Besides these, *Taxodioxylon gypsaceum* Kräusel 1965, *T. albertense* (Penhallow) Shimakura, *T. pseudoalbertense* Nishida et. Nishida, *T. megalonissum* Süss & Velitzelos (in Süss & Velitzelos 2000), all of them usually compared with the extant *Sequoia* Endl. (or with the extinct genus *Quasisequoia* Kunzmann; see Teodoridis & Sakala 2008), and other conifers such as *Tetraclinoxylon velitzelosi* Süss 1997, *Thujoxylon antissum* Süss et Velitzelos 1998 and *Taxaceoxylon biseriatum* Süss et Velitzelos 1994a.

A fossil gymnosperm of *Ginkgo* type was also described from Lesbos, with two new species, by Süss (2003): *Ginkgoxylon lesboense* and *G. diversicellulatum*, as a rare element in the fossil wood records found at Sigri and Megalonissi, which may have been accessory elements in the lake shore vegetation of the lowlands.

Selmeier & Velitzelos (2000) reported for Lesbos, probably after an unfinished study, an Angiosperm assemblage of Betulaceae (*Alnus*?), Euphorbiaceae (?), Fagaceae (*Fagus*?, *Quercus*?), Lauraceae (*Laurus*?, *Cinnamomum*?), Leguminosae (*Robinia*?), Monimiaceae(?), Myrtaceae(?) and Platanaceae (*Platanus*?).

From the same area, other fossilized plant parts were described as *Tetraclinis salicornioides* (Unger) Kvaček, *Sequoia abietina* (Brongniart) Erw. Knobloch vel *Taxodium* sp., *Cunninghamia miocaenica* Ettingshausen and *Pinus* sp. (cone) (Velitzelos D. et al. 2014). Also, based on the fossil leaf record, were identified numerous lowland and/or riparian elements including *Daphnogene polymorpha* (A. Braun) Ettingshausen, Lauraceae vel Fagaceae gen. et spec. indet., *Pungiphyllum cruciatum* (A.Braun) Frankenhäuser et Wilde, *Quercus apocynophyllum* Ettingshausen, aff. *Castanopsis bavarica* Knobloch et Kvaček, *Carpinus pliofauriei* Ratiani, *Carpinus uniserrata* (Kolakovski) Ratiani, aff. *Cedrela attica* (Unger) Palamarev, *Engelhardia orsbergensis* (Weber) Jähnichen, Mai et Walter, *Engelhardia* sp., *Populus balsamoides* Göppert, *Populus* sp., *Rhus* sp., *Tilia* sp., partly *Alnus cycladum* Unger forma *parvifolia* n. f., *Phoenicites* sp. and *Sabal major* (Unger) Heer (Velitzelos D. et al. 2014). Interestingly, the enigmatic plant *Pungiphyllum* appears to have been part of the lowland/riparian vegetation. A reviewed list of all the fossil taxa described so far from Lebos appears in Mantzouka et al. (2013) and in Velitzelos D. et al. (2014).

Beside these, new ongoing studies of the Velitzelos Collection of fossil wood from Lesbos indicate angiosperm and conifer forms (Iamandei, unpublished data). In this paper, six species of *Palmoxylon* Schenk are described: *P. daemonoropsoides* (Unger) Kirchheimer, corr., *P. chamaeropsoides* Iamandei et Iamandei, sp. nov., *P. coryphoides* Ambwani & Mehrotra, *P. sabaloides* Greguss, *P. trachycarpoides* Iamandei et Iamandei, sp. nov., and *P. phenicoides* Hofmann, a form of *Palmocaulon* sp. aff. *Phoenix* L., and two forms of *Rhizopalmoxylon*: *R. daemonoropsoides* Iamandei et Iamandei, sp. nov. and *R. phoenicoides* Iamandei et Iamandei, sp. nov.

KASTORIA–KOZANI–GREVENA AREA (WEST MACEDONIA)

The Kastoria–Kozani–Grevena area (West Macedonia, see Figure 1) belongs to the Meso-Hellenic Basin, which is an elongated depression running NW–SE along the axis of the Hellenides, filled with molassic sediments of late Eocene to middle Miocene age (Brunn 1956, Ferrière et al. 2004, Velitzelos D. et al. 2014). The last deposits, of Miocene age, consist of thick conglomerates alternating with sandstones and sandy marls which, at Grevena, preserve an interesting mid-Miocene flora with riparian elements such as *Pronephrium stiriacum* (Unger) Erw. Knobloch et Kvaček, *Daphnogene polymorpha* (A. Braun) Ettingshausen of *'cinnamomifolia'* type, *Myrica lignitum* (Unger) Saporta (vel *Apocynophyllum*), *Populus populina* (Brongniart) Erw. Knobloch, *Pterocarya paradisiaca* (Unger) Iljinskaya and *Phoenicites sp.*, but also with elements of the surrounding forest vegetation including acorns of *Quercus* sp., *Quercus pseudocastanea* Göppert, *Populus* sp., *Ulmus braunii* Heer, *Zelkova zelkovifolia* (Unger) Bůžek et Kotlaba, *Cryptomeria* sp., *Acer tricuspidatum* Bronn and *Carpinus* sp. (see Velitzelos D. et al. 2014).

Sometimes petrified wood is also preserved. For example, in Kastoria, fossil plants, especially petrified wood, have been discovered recently in some Early Miocene deltaic alluvial deposits (15–20 Ma) at Nostimo and Anthiro. Many fragments of petrified tree trunks 40–80 cm in diameter and 5 m to 10 m or even 20 m long are exposed now in the schoolyard of the local primary school of Nostimo, which designated a room for a small museum of palaeontology to hold a collection of petrified tree trunks representing the “Nostimo Petrified Forest”.

Selmeier and Velitzelos (2000) described some petrified wood from that area as species of *Quercoxylon*. A study of a new collection of fossil wood from that area is in progress; it consists of angiosperms and conifers (Iamandei, unpublished data). In this paper, four species of *Palmoxylon* Schenk are described: *P. chamaeropsoides* Iamandei et Iamandei, sp. nov., *P. coryphoides* Ambwani & Mehrotra, *P. trachycarpoides* Iamandei et Iamandei, sp. nov. and *P. phenicoides* Hofmann.

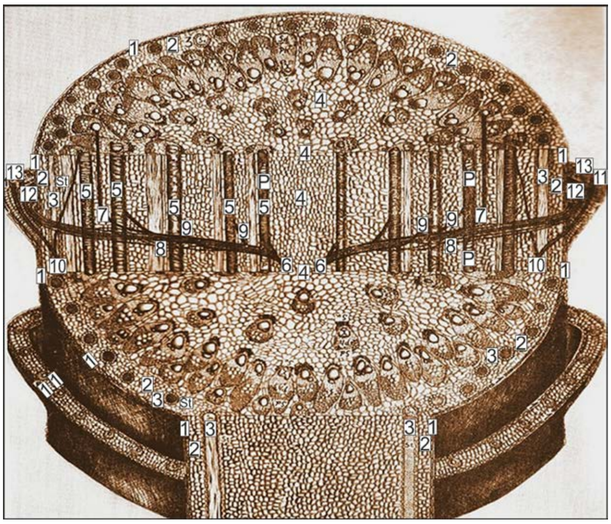

Fig. 2. Palm stem anatomy of Raphis (from Greguss 1968, slightly modified). Epidermis (1), parenchyma cells in bark (2), sclerenchyma fibers with stegmata (3), medullary parenchyma (4), metaxylem vessels with scalariform perforations, pitting and spiral thickenings (5), radially inclined bundle (6), vertical bundles (7), foliar traces (8), satellite bundles for links (9), foliar thin traces (10), bases (11, 12, 13), perforations (P), sclerenchyma fibers (Sc), stegmata (St)

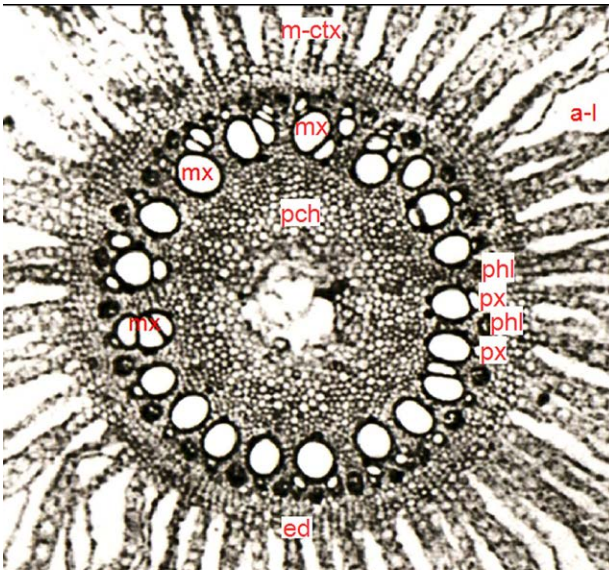

Fig. 3. Palm – root anatomy (from Tomlinson 1961, modified). Middle cortex (m-ctx), air lacunae (a-l), metaxylem vessel (mx), protoxylem (px), phloem (phl), parenchyma pith (pch), endodermis (ed)

MATERIAL AND METHODS

It is well known that palm stems have a very uniform fascicular structure and present few anatomical details of taxonomic value. Most of these anatomical features are related to the ecological conditions of the plant. Not all palms have an arboreal habit, and when you find a fragment of a fossil palm stem you should relate its anatomical structure to an extant type of palm (see Tomlinson 1961, 1990, Tomlinson et al. 2011, Thomas & De Franceschi 2013).

If possible, systematic sampling should be done, so that the classical zones of the cortex and central cylinder are well represented, in order to obtain standard oriented thin sections (transversal and longitudinal), using the petrographic methodology. After microscopy of these thin sections and description of all the anatomical details observed, good micrographs with taxonomical details must be made and the identification work can begin.

Generally, a palm stem in cross section shows the central cylinder to be composed of three distinct zones: dermal, subdermal and central (see Mahabalé 1958, and Kaul 1960 quoting Mohl 1845–1850), or external, intermediary and central in the Euro-American school (see Tomlinson 1961), or subcortical (as periferal sclerotic zone), transitional and central, as Thomas & De Franceschi (2013) established latterly. The shape, size and density of the fibrovascular bundles, the quantity of parenchyma, and the abundance and arrangement of parenchymatous cells must be considered.

When present, the cortical zone must be described. A general view of stem or root anatomy (Figs 2, 3) and good references on the anatomical structure of the extant palm stem or palm root can be found in Tomlinson (1961, 1990), Tomlinson et al. (2011), Greguss (1959, 1968) or Schweingrüber (1990). An important attempt to realize a program of computer-aided identification for palm stem anatomy has been made by Thomas (2011a, b, 2013) and Thomas & De Franceschi (2012, 2013), taking the Coryphoideae as a case study. Studies of fossil remains of palm tree stems are also very useful as references for their taxonomic identification (see CiteULike site, 2018 – Millevacs’s *Palmoxylon*), accessed May 5, 2018).

The references are always incomplete when it comes to fossil palms and even extant palms. Stokmans & Williere (1943) cautioned that the difficulty of fossil palm identification will continue, “since we haven’t a recent, complete study of the extant palms made for paleobotanical aims”, and Privé-Gill & Pelletier (1981) stated that “depending on the region of the stem studied, you can have a lot of groups of Stenzel and of Sahni”.

All our systematics respect APG (2009, 2016) and the *Shenzhen Code* (Turland et al. 2018).

SYSTEMATIC DESCRIPTION OF THE IDENTIFIED TAXA

ANGIOSPERMS – MONOCOTS (APG IV, 2016)

Order ARECALES Bromhead 1840 (APG III, 2009)

Family ARECACEAE Berchtold et Presl 1820 (nom. cons.)

Genus **Palmoxylon** Schenk 1882

Palmoxylon daemonoropsoides (Unger) Kirchheimer 1937 corr.

Pl. 1, figs 1–9; Pl. 2, figs 1–9

Synonymy:

1845 *Palmacites daemonorops* Unger.
1937 *Palmoxylon daemonorops* (Unger) Kirchheimer

Material. Two samples with similar anatomy were attributed to this species: one collected from the Evros region, Aëtohori area (sample AH-1133) and the second from Lesbos Island (sample 376), both representing palm-stem fragments. There, volcano-sedimentary deposits hosting petrified plant remains are of late Oligocene (Aëtohori area) and, respectively, early Miocene age (in Lesbos). Both these samples are now kept in the collection of Athens University (NKUA), Faculty of Geology and Geoenvironment, under the above-specified accession numbers.

Description. Only the subdermal and central zones were present in the studied samples.

The subdermal zone is well preserved in specimen 376. In cross section it is represented by a portion showing gradual transition to the central zone. The fibrovascular bundles, of open-collateral type, are surrounded by parenchyma. The bundles are usually oriented with the vascular part to the center and the fibrous part to the outside, and are slightly spaced distributed apart from each other. Their sclerenchyma caps (= fibrous sheaths, in cross section) are of “Cordata type” (*sensu* Stenzel 1904). The constituent fibers (sclerenchyma cells) are thick-walled and are slightly enlarged towards the marginal zone. Fibrovascular bundle size varies (all numeric values represent minimum and maximum), with radial/tangential diameter (r/tg.d.) of (300)600–1000/200–600 µm, phloematic (or anterior) sclerenchyma cap r/tg.d. of 200–800/200–600 µm, and f/v ratio of 1.2/1–3/1 (the f/v ratio is fibrous to vascular parts ratio, expressed as their radial diameters ratio). Bundle density within this zone is 195/cm^2. The phloem, often poorly preserved, appears in a single small island as non-divided phloem, gently protected under the cordate sclerenchyma cap. The metaxylem appears in cross section as (1)2–3 round to oval or slightly deformed and thick-walled vessels with r/tg.d. of 50–90/50–100 µm, but usually the entire vascular zone is crushed under the sclerenchyma cap. In longitudinal view the vessels have helical thickenings and tyloses. Scalariform pitting and scalariform perforations were also observed. The protoxylem appears as small, round, thick-walled cells 14–25 µm in diameter and can be seen just under the metaxylem. The intrafascicular parenchyma consists of small polygonal to oval thin-walled cells filling the space between vessels. The vascular zone is surrounded by rows of slightly sclerified parenchyma cells as a second sclerenchyma cap. The interfascicular parenchyma is of tabular type, as 1–2 rows of elongated cells compactly arranged directly around the fibrovascular bundles, and also as ground tissue from crushed or deformed parenchyma cells among the bundles. Large cells, round to oval, 25–46 µm in diameter, most probably mucilaginous, rarely appear among them. The fibrous bundles are frequent, varying in size (90–320 µm in diameter), built of thick-walled small-lumened fibrous cells. In longitudinal view, numerous spherical stegmata appear in long rows arranged among the fibrous bundles.

The central zone of the central cylinder presents fibrovascular bundles (*fvb*) of open-collateral type, having large rounded sclerenchyma caps of “Cordata type” (Stenzel 1904), with slightly rounded lateral wings (i.e. auricular lobes) and a relatively smaller median sinus. The sclerenchyma cap is usually oriented toward the exterior of the central cylinder, and is formed of thick-walled cells with oval to point-like lumina. In cross section the fibers increase gradually in size toward the exterior of the cap, where they are 30–70 µm in diameter, which may suggest centrifugal differentiation (see Thomas & De Franceschi 2013). The size of the *fvb* is also variable, with r/tg.d. of 600–1000/400–650 µm, phloematic sclerenchyma cap r/tg.d. of 350–700/400–650 µm,

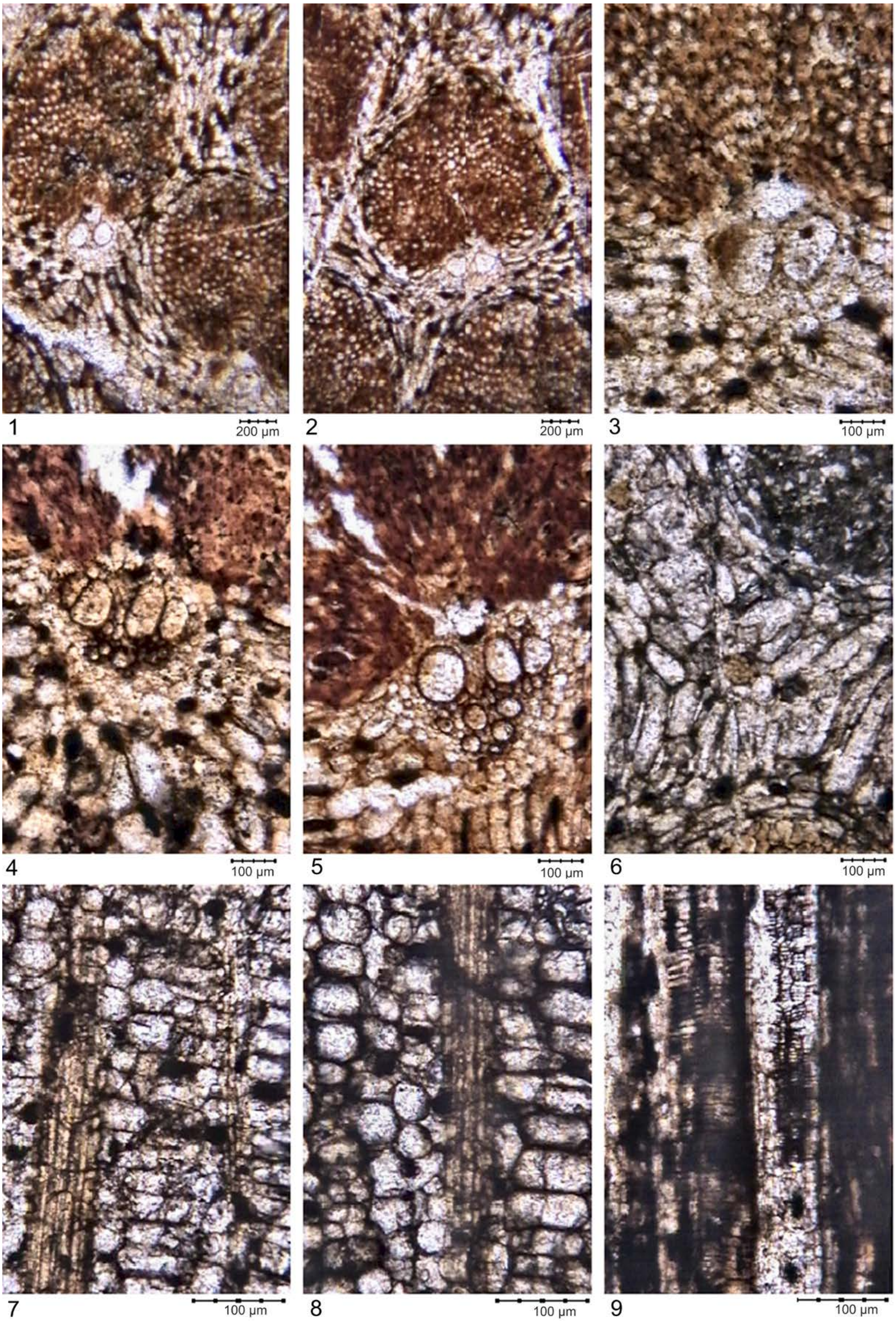

Plate 1. **1–9**. *Palmoxylon daemonoropsoides* (Unger) Kirchheimer 1937, corr. (specimen AH1133). **1–2**. Cross sections: fibrovascular bundles and interfascicular parenchyma, parenchyma of tabular type around sclerenchyma caps. **3–5**. Cross sections: fibrovascular bundles with 2–3 metaxylem vessels and with protoxylem radial parenchyma around vascular part of *fvb*. **6**. Cross section: intervascular parenchyma in false radial arrangement. **7–8**. Longitudinal sections: long rows of stegmata on fibrous bundles; interfascicular parenchyma. **9**. Longitudinal section: helical thickenings and scalariform pitting on metaxylem vessels

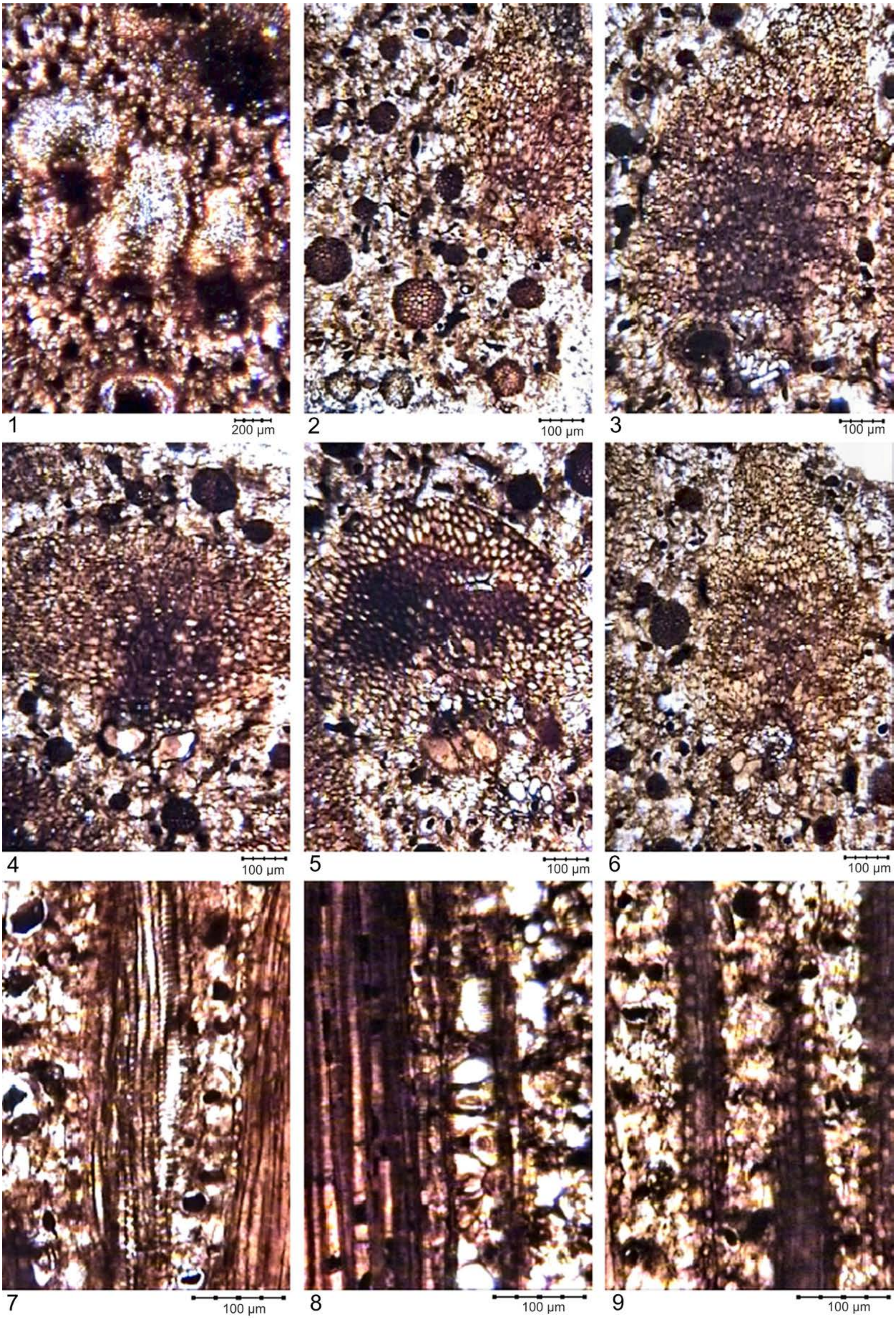

Plate 2. **1–9**. *Palmoxylon daemonoropsoides* (Unger) Kirchheimer 1937, corr. (specimen 376). **1**. Cross section: fibrovascular bundles within subdermal zone. **2**. Cross section: parenchyma, fibrous and fibrovascular bundles within subdermal zone. **3–6**. Cross sections: fibrovascular bundles with 1–4 metaxylem vessels (detail). **7–**8. Longitudinal sections: helical thickenings on vessels, long rows of stegmata on fibrous bundles

and f/v ratio of 2/1–3.6/1. Their density within this zone is 91bundles/cm^2. The phloem is situated just under the sclerenchyma cap and is crushed, attacked by fungi, or degraded by lysis, appearing as a nonspecific lacuna instead, which suggests a usually non-divided or rarely only apparently divided phloem. The metaxylem, occupying the greater portion of the vascular part, is represented by 2–3 large vessels with r/tg.d. of 70–100/50–100 µm, with thick-walled, circular to oval in cross section, or crushed and deformed. In longitudinal view the metaxylem vessels have close, thin helical thickenings, scalariform pitting and scalariform perforations, rarely seen as remains, and sometimes tyloses. The foliar bundles have more than 6 smaller metaxylem vessels. The protoxylem is represented by 3–5 small circular to oval vessels 35–50 µm in diameter, relatively thick-walled. The intrafascicular parenchyma appears as slightly lignified, polygonal, rounded cells, regularly arranged. The interfascicular parenchyma is abundant and is represented by mixed unequally-sized and variably shaped, circular to elliptic, thin-walled parenchymal cells. Usually the elongated cells, having r/tg.d. of 35–50/75–200 µm, are irregularly arranged in a compact structure among the bundles. Sometimes, enlarged cells, probably mucilaginous, can be seen there. Around the sclerenchyma caps of the fibrovascular bundles, a typical tabular parenchyma is present as 2–3 compact rows of cells, elongated, closely connected between them and with the cap. Around the vascular part, parenchyma of radial type is present. Often, the radial arrangement is not very clear, since variably shaped parenchymal cells are also implied in it.

Starch grains or dark tanninous content are often present inside the parenchyma cells, located around or between the bundles as ground tissue. The fibrous bundles vary in size in cross section (40–125 µm diameter) and are built of up to 80 thick-walled fibers. Phytoliths are present on the fibers of the fibrous bundles but also of the fibrous part of the fibrovascular bundles, visible as spherical stegmata partially sunken in the basal wall of the silica cell, and arranged in long vertical rows.

Affinities and discussion. Our studied material presents typical fascicular structure of palm-stem type (see Greguss 1968) and is assigned to the fossil genus *Palmoxylon* Schenk, being in conformity with the original diagnosis of this genus given by Schenk (1882).

A specific taxonomic identification is hampered by the relatively uniform anatomical structure of the palm stem in the whole family of Arecaceae, in which the systematics is based mainly on the morphological features of extant plants.

A palm, whether extant or fossil, is a member of the family Arecaceae Berchtold et Presl, 1820 (nom.cons); the family name also appears in the literature as Palmae Jussieu, 1789 (nom. cons. et nom. alt.) (see APG III 2009, APG IV 2016, Turland et al. 2018).

We compared the studied structures with those of extant palms, using the comprehensive syntheses of Tomlinson (1961, 1990), Tomlinson et al. (2011), Dransfield et al. (2005) and Thomas & De Franceschi (2012, 2013), and found many similar features suggesting that our studied material should be assigned to the Lepidocarioid group of palms, especially the genus *Daemonorops* Blume ex Schult.f., from Calamoideae Beilschm., which is also characterized by fibrous sheaths of "Cordata type" (*sensu* Stenzel 1904).

Unger (1845) described a type of fossil palm, studying two fragments of petrified stem, one from England and one from Transylvania (today Romania), and named it *Palmacites daemonorops* Unger, which was later revised by Kirchheimer (1937) as *Palmoxylon daemonorops*, a form with fibrous sheath of "Cordata type" (*sensu* Stenzel 1904), which is very similar to our studied material.

Other fossil species described by Schenk (in Zittel 1883) as *Palmoxylon zitteli* and *P. ascheroni* clearly differ from our specimens in the shape of the sclerenchyma cap, the round fibrovascular bundles, the distribution of fibrous bundles, and the parenchyma. Another form, *P. lacunosum* (Unger) Felix, described and figured by Berry (1924), also differs by its typical lacunose structure.

Chiarrugi (1933) described three different new palm species from the Cretaceous of Somalia: *Palmoxylon benadirense* with reniform sclerenchyma caps (of Reniformia type, *sensu* Stenzel 1904), *P. scebelianum* of Lunaria type (*sensu* Stenzel 1904) and *P. somalense* of Cordata type (*sensu* Stenzel 1904). The last would be interesting for comparison but it usually has a single giant metaxylem vessel in the vascular part, rarely two or more, so it differs from our material which usually has numerous metaxylem vessels.

Other species of *Palmoxylon* previously described must be excluded from this comparison as having other types of sclerenchyma caps. For example, *P. sabal* Greguss 1954 and *P. hungaricum* Greguss 1959, which are similar to *Livistona* and other two forms (*P. dorogense* Greguss 1969 and *P. sabaloides* Greguss 1969), are both of sabaloid type. *P. lacunosum* var. *axonense* Watelet (in Greguss 1969) and *P. eocenum* Prakash (1962) have sclerenchyma caps of Reniformia type (*sensu* Stenzel 1904). *P. parthasarathyi* of Rao & Menon (1964b) of Lunaria and Reniformia type (*sensu* Stenzel 1904). *P. maheshwari* of Rao & Menon (1964a) and *P. fibrosum* of Menon (1965) all have sclerenchyma caps of *Mauritia*-like type.

Grambast (1957) described *P. gignacense* Grambast with sclerenchyma of Reniformia type (*sensu* Stenzel 1904), and in 1962 noted *Palmoxylon* sp. with sclerenchyma caps of Complanata type (*sensu* Stenzel 1904) and in 1964 noted the affinities of *P. vestitum* (Saporta) Stenzel with *Phytelephas*, *Trachycarpus* and *Chamaerops*. *Palmoxylon keriense* of Trivedi & Verma (1971b) has sclerenchyma caps of Reniformia type (*sensu* Stenzel 1904) and was considered a *Cocos*-like palm. Kramer (1974) described forms of *Palmoxylon* sp. with sclerenchyma caps of Reniformia type, wrongly attributed to other types. Privé-Gill & Pelletier (1981) described a *Palmoxylon* sp. of Reniformia type (*sensu* Stenzel 1904) but raised doubts by saying "depending on the region of the stem studied, you can have a lot of groups of Stenzel and Sahni". Gottwald (1992) described *P. fasciculosum* Vater and *Palmoxylon* sp. (form 3 of Kramer 1974). *Palmoxylon* cf. *variabile* Vater and *P. hebbertii* of Nambudiri & Tidwell (1998) are of Reniformia type (*sensu* Stenzel 1904), with clear sabaloid affinities. *P. bautschii* Kahlert et al. (2005) is of Vaginata-Reniformia type (*sensu* Stenzel 1904), and *P. techerense* of Iamandei & Iamandei (2006) is of Reniformia type (*sensu* Stenzel 1904), also with Sabaloid affinities. Another species, *P. garridoi* of Martinez (2012), is of *Mauritia*-like type, of the group *Antiguensia*, so it is clearly different from our material. Recently, Iamandei et al. (2018) described some forms of *Palmoxylon* similar to the extant *Corypha* L., *Trachycarpus* H. Wendl. and *Borassus* L.

From this discussion we can conclude that the closest resemblance of our specimens with an already described form is with the original species of Unger (1845), revised by Kirchheimer (1937) as *Palmoxylon daemonorops*. Since our description corresponds with the species diagnosis, we assign our studied material to it, slightly correcting the original name of the species to "*daemonoropsoides*" (after the model of Hoffman 1944) to suggest, if possible, the relation with the extant corresponding genus, so the corrected name will be *Palmoxylon daemonoropsoides* (Unger) Kirchheimer, 1937, corr.

Palmoxylon chamaeropsoides
Iamandei et Iamandei. sp. nov.

Pl. 3, figs 1–9; Pl. 4, figs 1–9

Material. The studied material attributed to this species is represented by 10 samples: 5 samples (no. 120, 449, 450, L525, L526) collected at different locations of Lesbos Island from Larpsana, Sigri and Gavathas, and 5 samples (no. 367, 401, 497, 535, 536) from the Kastoria area in the continental part of Greece. They are from palm stems of various ages and from different levels of the palm stem, often found buried *in situ* or dispersed in volcano-sedimentary deposits of Early Miocene age. All these specimens are kept in the collection of Athens University (NKUA), Faculty of Geology and Geoenvironment.

Description. The cortical zone is not clearly present in any sample. Some samples show poorly preserved structures in various stages of bacterial rotting or compression of the tissue (samples 449, 450, 525, 526, 535, 536), but the central cylinder is well represented in all the selected samples by the three typical zones – dermal, subdermal and central.

The dermal zone appears at the outer part of the stem, well visible in specimens 120 and 367. Here the structure is formed of 4–5 rows of collateral fibrovascular bundles (*fvb*) having a sclerenchyma cap with reniform aspect (Reniformia type, *sensu* Stenzel 1904), with the lateral parts elongate (lobes) to protect the phloem island and all of the vascular part. The constituent sclerenchymatous cells are polygonal and have small circular or point-like lumina. The bundles vary in size, with r/tg.d. of (550)1100–1400/(250)400–450 µm, phloematic sclerenchyma cap r/tg.d. of (350)550–900/(250)400–450 µm, and f/v ratio of 1/1–1.7/1. Bundle density within this zone is 125–225/cm^2. The phloem, when it can be observed, appears as a single island (undivided phloem) of various sizes. Under it, the xylematic zone is represented by 1–2 large metaxylem vessels 80–270/50–100 µm in diameter (min./max.). The protoxylem is poorly preserved and the intrafascicular parenchyma is very compressed and thus difficult to observe. The interfascicular parenchyma appears as relatively thin-walled cells surrounding the fibrous part of the fibrovascular bundles as parenchyma of tabular type and of radial type around the vascular part. All the fibrovascular bundles are uniformly oriented with the vascular part to the center of the central cylinder, and appear slightly congested in this zone. The fibrous bundles are present as small fascicles of 4–6 brown fibers which appear in the ground tissue among the fibrovascular bundles. Around them, the parenchyma cells are in a radial arrangement.

The subdermal zone, which appears more clearly in specimens 367 and 497, is represented by some rows of fibrovascular bundles of collateral type, of various sizes and with a more rounded shape. They are congested in this zone, oriented with the vascular part to the center of the central cylinder, and have 1–2 islands of phloem beneath the sclerenchyma cap, which has a reniform aspect (Reniformia type *sensu* Stenzel 1904). Bundle size varies, with r/tg.d. of 500–800/250–650 µm, sclerenchyma cap r/tg.d. of 250–500/250–650 µm, and f/v ratio of 1/1–2.5/1. Bundle density within this zone is 78–95/cm^2. Beneath the sclerenchyma cap, the phloem occurs as an undivided island or apparently divided. Usually it is degraded by lysis and only a nonspecific lacuna is present. Phloem cells are rarely discernible. Beneath the phloem, 2–3 thick-walled metaxylem vessels appear, with r/tg.d. of 50–150/50–100 µm. Protoxylem rarely appears, occurring as numerous small, round and relatively thick-walled cells. The intrafascicular parenchyma is less visible. The interfascicular parenchyma is of tabular type, as a single row of cells around the sclerenchyma cap, and of radial type around the vascular part of the fibrovascular bundles. The ground tissue consists of polygonal and elongated parenchyma cells, mixed or, often, arranged star-like between the fascicles. These parenchyma cells sometimes have starch grains or tanninous content, and even a short mucilaginous duct has been observed between them. Fibrous bundles appear rarely among them.

The central zone of the central cylinder, better seen in specimens 497 and 401, presents, in cross section, a loose distribution of fibrovascular bundles in well-developed ground tissue. The fibrovascular bundles present voluminous sclerenchyma caps of reniform aspect (= Reniformia type *sensu* Stenzel 1904) and sometimes appear fused. Their sclerenchymatous cells are small and polygonal, and have thickened walls and round or elliptic lumina. Toward the marginal part they are larger, suggesting their centrifugal differentiation inside the fibrous sheath. Fibrovascular bundle size varies, with r/tg.d. of 500–800(1400)/(500)700–1000 µm, phloematic sclerenchyma cap r/tg.d. of 500–700(900)/(500)700–1000 µm, and f/v ratio of 1.3/1–7/1. Bundle density within this zone is 34–36/cm^2. Under the sclerenchyma cap, the phloem appears as two distinct but connected islands, so it can be described as apparently divided phloem. The sieve cells of the phloem rarely were observed; usually they were destroyed by lysis, leaving only an empty space (i.e. nonspecific lacuna). The xylematic zone is less developed, sometimes seeming to be degraded or even absent. However, the metaxylem, when it can be seen, is represented by 2–3 thick-walled vessels having r/tg.d. of 50–100/60–150 µm, sometimes larger, up to 200/200 µm. They are more numerous, up to 6, in the foliar bundles, which appear often. In longitudinal view the metaxylem vessels show numerous and close helical thickenings, adjacent or spaced slightly apart and connected by vertical bars, and scalariform pitting is present on the walls. Fragmentarily preserved scalariform perforations are also visible, so it is difficult to measure their height or the number of bars. Protoxylem is rarely observed, occurring as small round cells, relatively thick-walled and with annular thickenings in longitudinal view. The intrafascicular parenchyma, when it can be observed, consists of uniform, thin-walled, small rounded cells filling the space among the vessels. The entire vascular zone is surrounded by some rows of elongated, slightly sclerified parenchyma cells as a second sclerenchyma cap. The interfascicular parenchyma is of radial type around the vascular zone of the fibrovascular bundles, and of tabular type around the dorsal sclerenchyma cap. In the interfascicular ground tissue, the orientation of the parenchyma cells is disturbed by a special type of secondary growth of all the elements of the structure, which determined diverse orientations of the large, elongated parenchyma cells with r/tg.d.

of 40–50/125–150 µm and often having a star-like arrangement or diversely oriented. Sometimes such polygonal elongated parenchyma cells connect one bundle to another, visible even in cross section. Usually the parenchyma cells bear starch grains or dark tanninous content. The fibrous bundles are round, varying in size in cross section (60–100 µm diameter) and surrounded by radial parenchyma. Phytoliths are present on the vertical walls of the fibers of the fibrous bundles, and appear as spherical stegmata, slightly spinulose but with rounded spines, partially sunken in the basal wall of the silica cell and arranged in numerous long rows covering the entire surface of the bundle. It seems that these stegmata had assumed a definite size from the beginning. In other words, they did not grow more over time. In this way they seem to connect the fibers, enhancing the solidity of the structure.

Affinities and discussion. A petrified fragment of palm stem has a specific aspect, but is not easy to identify it more precisely, since all the palms have a very uniform fascicular structure. There are many papers describing fossil palms (see CiteULike site – Millevacs's *Palmoxylon*. Accessed: 05.05.2018) and some good published syntheses on the anatomy of the extant palms (see Tomlinson 1961, 1990, Tomlinson et al. 2011, Dransfield et al. 2005), and even a tentative means of computer-aided identification (see Thomas & De Franceschi 2012, 2013) where similarities of microscopic features observed in one's material can be searched in order to identify it, but Stenzel (1904) is still useful, as are the other previously published fossil form descriptions.

After our first observations, it seems that the studied specimens probably represent a smaller type of palm, so we can reduce the number of searches to this category. Taking into account the reniform aspect of the sclerenchyma cap of *fvb* (Reniformia type *sensu* Stenzel 1904) and the metaxylem vessels' distribution, the aspect of the interfascicular parenchyma and the type of stegmata observed on the fibrous bundles, with their shape and arrangement, we concluded that our specimens resemble a type of palm from the Coryphoideae subfamily (see Dransfield et al. 2005, Thomas & De Franceschi 2013), especially the extant genus *Chamaerops* L., a palm that still lives in the wild in Greece (*Chamaerops humilis* L.). We compared the structure of our studied material with that of that extant species, described and figured in Tomlinson (1961, 1990), Schweingruber (1990) and Thomas (2011a, b, 2013). We found many details that fit those of our specimens, supporting close similitude with the extant *Chamaerops* type.

In comparing these specimens with already described fossil forms, we found characters similar to those of our material: the sclerenchyma cap of *fvb*, voluminous and of Reniformia type (*sensu* Stenzel 1904), with 2–3 large and thick-walled metaxylem vessels (or up to 6 in the foliar bundles), which in longitudinal view show helical thickenings, scalariform pitting and scalariform perforations; interfascicular parenchyma of tabular and radial type around the *fvb*; and phytoliths as spherical and slightly spinulose stegmata arranged in numerous long rows on the fibrous bundles.

Analyzing the many forms of fossil Coryphoideae already described from the Late Cretaceous and Cenozoic deposits, we restrict ourselves to the *Palmoxylon* characterized by sclerenchyma caps of Reniformia type (*sensu* Stenzel 1904), but must first exclude some types: *Palmoxylon zitteli* and *P. ascheroni* (described by Schenk, in Zittel 1883) which have round *fvb*, different from our specimens; also *P. scebelianum* and *P. somalense*, described by Chiarrugi (1933) which are of Lunaria and Cordata type (*sensu* Stenzel 1904), respectively; and *Palmoxylon* sp. described by Grambast (1962), which is of Complanata type (*sensu* Stenzel 1904) and similar to *Corypha* L.

Some species of *Palmoxylon* described as *P. maheshwari* Rao et Menon (1964a), *P. fibrosum* Menon (1965) and *P. garridoi* Martinez (2012) were referred to the *Mauritia*-like palms, so they are clearly different, and *P. parthasarathyi* of Rao & Menon (1964b) has a sclerenchyma cap of Lunaria and/or Reniformia type (*sensu* Stenzel 1904) and was referred to the *Cocos*-like palms, so it is also different.

Some forms of *Palmoxylon* sp. were described by Kramer (1974) as of Cordata and Lunaria type (*sensu* Stenzel 1904) but we doubt the interpretation, since all of them seem to be of Reniformia type (*sensu* Stenzel 1904); also, *P. fasciculosum* Vater and *Palmoxylon* sp. (form 3 – Kramer 1974) described by Gottwald (1992) are stated as having Lepidocarioid affinities.

Some other described fossil palms with sclerenchyma caps of Reniformia type (*sensu* Stenzel

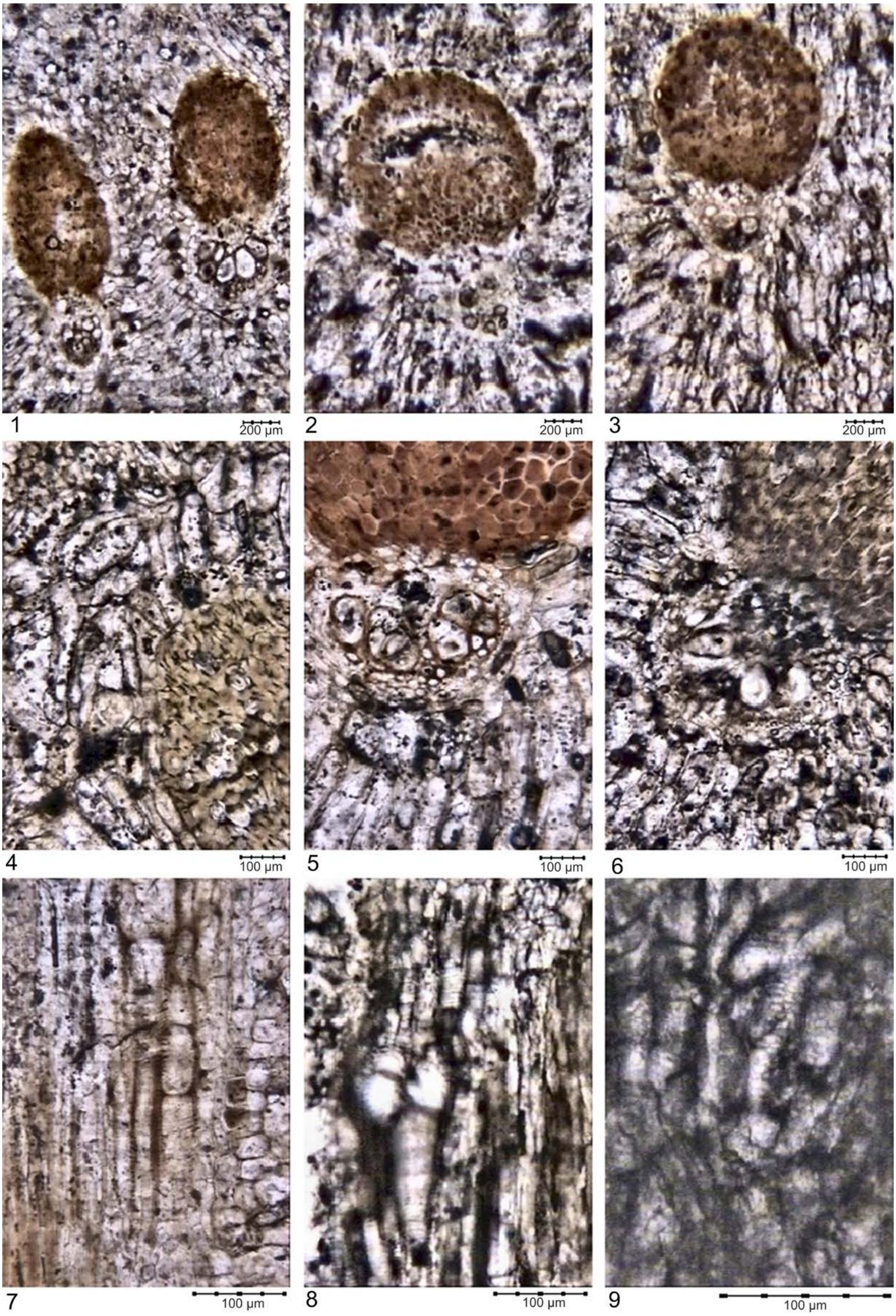

Plate 3. **1–9**. *Palmoxylon chamaeropsoides* sp. nov. (specimen 497, holotype). **1–4**. Cross sections: fibrovascular bundles with sclerenchyma caps of reniform acpect, ground tissue of radial and tabular type or with star-like disposition within central zone. **5–6**. Cross sections: within central zone, details of fibrovascular bundles with parenchyma of radial type around vascular part. **7–9**. Longitudinal sections: poorly preserved helical thickenings, poorly preserved scalariform perforations with few bars, and scalariform pitting on vessels

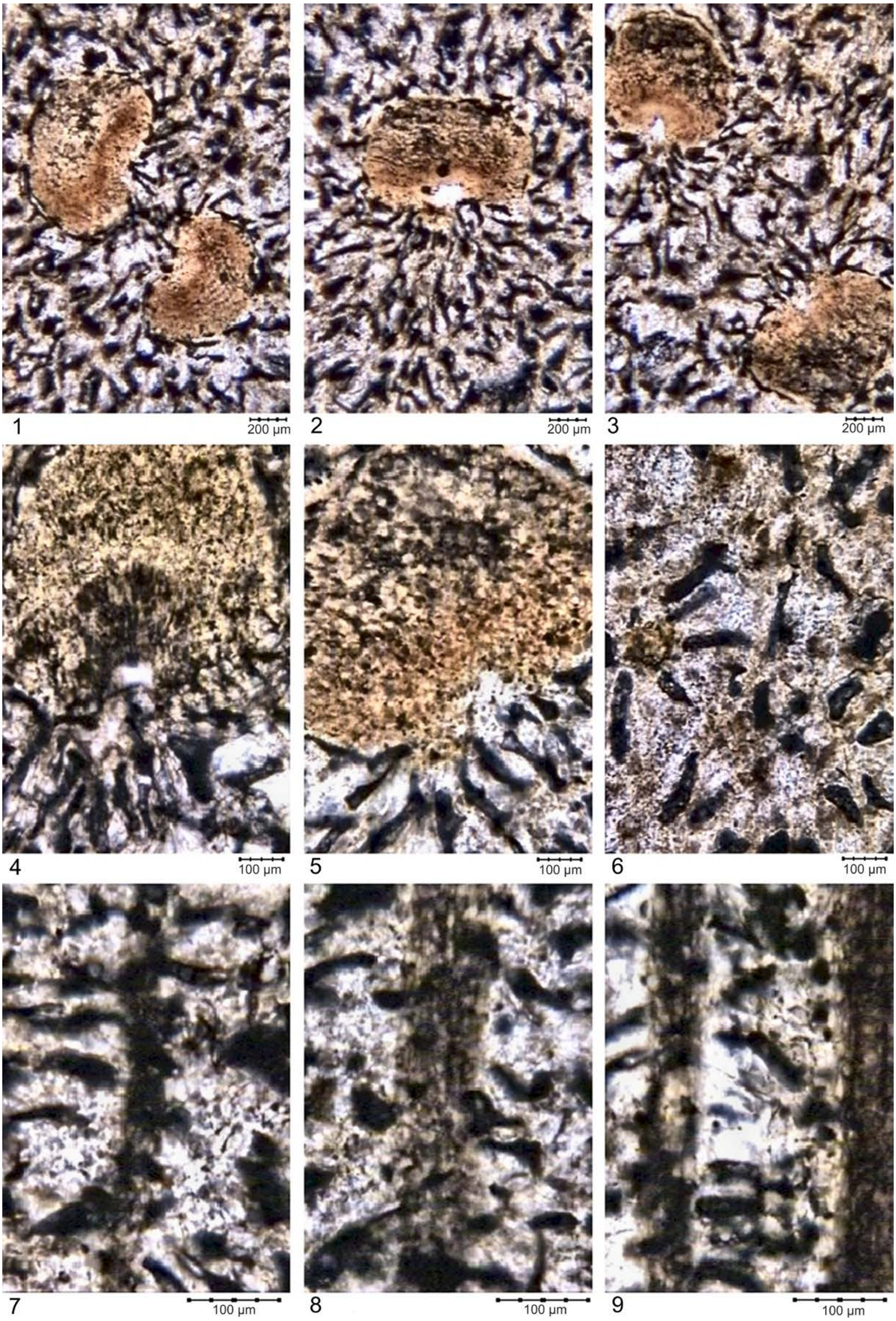

Plate 4. **1–9**. *Palmoxylon chamaeropsoides* sp. nov. – (specimen 401, paratype). **1–5**. Cross sections: fibrovascular bundles with sclerenchyma caps of reniform aspect and interfascicular parenchyma of radial and tabular type, and interfascicularly with star-like disposition within central zone; details of fibrovascular bundles with sclerenchyma caps of reniform acpect and parenchyma of radial type around vascular part within central zone. **6**. Cross section: ground tissue with radially disposed around fibrous bundles. **7–9**. Longitudinal sections: fibrous bundles with long rows of stegmata

1904) deserve to be taken into account in our comparative analysis even if other characters assign them to other palm types. For example, *P. lacunosum* (Unger) Felix described by Berry (1924) seems to differ from our studied material by its lacunose parenchymal ground tissue, and *P. benadirense* of Chiarrugi (1933) is different even though it has reniform sclerenchyma caps.

The forms *P. sabal* Greguss (1954) and *P. sabaloides* Greguss (1969) are similar to the extant *Sabal* Adans. *P. hungaricum* Greguss (1959) is similar to extant *Livistona* R.Br., as is *P. superbum* Trivedy & Verma 1971a. Also, the forms *P. dorogense* and *P. lacunosum* var. *axonense* Watelet described by Greguss (1969) are also different, as the author specified their phoenicoid affinities.

Trivedi and Verma (1971b) described *P. keriense*, considered a *Cocos*-like palm. Gottwald (1992) described *Palmoxylon* cf. *variabile* Vater, also with reniform fibrous caps but having affinities especially with *Trachycarpus* H.Wendl.

Another form, *P. hebbertii* Nambudiri & Tidwell (1998), with reniform fibrous caps, but is slightly different from our material, as is *P. techerense* Iamandei & Iamandei (2006), closer to extant *Sabal* Adans.

The species of *Palmoxylon* of Nour-El-Deen et al. (2017) seem to be closer to *Trachycarpus* H.Wendl. Also, Iamandei et al. (2018) described some forms of *Palmoxylon* similar to the extant *Corypha* L., *Trachycarpus* H.Wendl. and *Borassus* L.

The form *P. homeochamaerops* Biondi et Filigheddu (1990) was described from the Lower Miocene of Sardinia as equivalent to the extant *Chamaerops humilis* L., but in our analysis it is slightly different, mixing characters which define other plant parts (including characters of foliar bundles and roots).

Palmoxylon bautschii Kahlert et al. (2005), with fibrous caps of Vaginata-Reniformia type (*sensu* Stenzel 1904), bears some similarity to our material, since it has a similar type of interfascicular parenchyma, but it has very numerous metaxylem vessels in the *fvb*.

However, there are other fossil forms which present similarities and could be compared with our material, such as *P. gignacense* Grambast (1957) and *P. eocenum* Prakash (1962), which seem closer in structure to our material, at least in having quite similar reniform fibrous (or sclerenchymatous) caps. Grambast (1964) showed that *P. vestitum* (Saporta) Stenzel has many affinities with *Trachycarpus* H.Wendl. or with *Chamaerops* L. so it could be slightly similar to our studied material. Another form of *Palmoxylon* sp., of Reniform type, described by Privé-Gill & Pelletier (1981), is slightly similar to our studied material, though not identical.

Taking into account the above discussion, and the close resemblance of our specimen to the extant genus *Chamaerops* L. as described and figured by Tomlinson (1961), Schweigruber (1990) and Thomas & De Franceschi (2012, 2013), and the partial similarity of our studied specimens to some fossil forms suspected to be ancestors of the *Chamaerops* L., we propose to assign our studied material to a new species whose correct binomial name will be *Palmoxylon chamaeropsoides* Iamandei et Iamandei, sp. nov. We designate specimen 497 as the holotype for this new species, and specimen 401 as paratype.

Diagnosis. Fibrovascular bundles of collateral type, loosely distributed in central zone, more congested in subdermal and dermal zone, with large sclerechyma caps of Reniformia type, more voluminous in central zone, sometimes fusing; f/v ratio 1–1.3 or more; bundle density 125–225/cm^2 in dermal zone, 78–95/cm^2 in subdermal zone, 34–36/cm^2 in the central zone. Phloem undivided in dermal zone, to apparently divided in central zone. Metaxylem as 1–3 large vessels which in longitudinal view show helical thickenings with vertical connections, scalariform pitting and scalariform perforations. Protoxylem as small round vessels with annular thickenings. Interfascicular parenchyma as large elongated cells of tabular type around sclerenchyma and of radial type in vascular zone of fibrovascular bundles; also interfascicularly the parenchyma cells appear more or less oriented or in star-like arrangement, sometimes containing starch grains, tannin or mucilage. Round fibrous bundles present, small or of different sizes in cross section, 60–100 μm, longitudinally with numerous spherical spinulose stegmata in long rows.

Palmoxylon coryphoides
Ambwani & Mehrotra 1990

Pl. 5, figs 1–9; Pl. 6, figs 1–9; Pl. 7, figs 1–9

Material. From the studied material, eight specimens were attributed to this species. They were collected from Lesbos Island (field numbers: 61A, L503, L505, L509, L514, from Larpsana and Antissa), from Evros (from Aëtohori: 316, AH919) and from Kastoria (K515). They are palm stem fragments from different levels or parts, preserved within volcanosedimentary deposits of late Oligocene (those from Aëtohori) and early Miocene age (those from Lesbos and Kastoria). This material is now kept in the collection of Athens University (NKUA), Faculty of Geology and Geoenvironment, under the above-specified accession numbers.

Description. A small part of the cortical zone appears in a cross section of sample L503, where numerous spaced-apart fibrous bundles of 16–22 cells (30–50 µm diameter) are present, sparsely interspersed with small fibrovascular bundles of r/tg.d. 400–700/200–350 µm. The fibrovascular bundles have very elongated sclerenchyma caps of reniform aspect, protecting them beneath (in the median sinus) the phloem and the entire small xylematic zone. This vascular part looks like a small wedge. The metaxylem is represented by a single large circular vessel, rarely two, 40–60 µm in diameter. The intrafascicular parenchyma is very compressed. The interfascicular parenchyma (ground tissue) consists of small cells, usually crushed or destroyed by rotting and thus difficult to observe in detail.

The dermal zone is built of 3–4 rows of relatively small and congested fibrovascular bundles oriented with the vascular part to the center. Their radial elongated sclerenchyma caps are of reniform shape, slightly tending to cordate aspect. The thick-walled fibers constituting the sclerenchyma cap are circular to oval in cross section, possess point-like lumina, and are often attacked by fungi. Bundle size varies, with r/tg.d. of 600–1000/250–350 µm, phloematic (anterior) sclerenchyma cap r/tg.d. of 500–800/250–350 µm, and f/v ratio of 3.3/1–8/1. Fibrovascular bundle density in this zone is 212–258/cm^2. The phloem appears just under the sclerenchyma cap as a single island of undivided phloem. The xylematic zone is represented by 1–2(3) large circular or oval metaxylem vessels 50–60/50–75 µm in diameter. In longitudinal view, helical thickenings on the vessel walls can be seen, and rarely remains of scalariform pitting and scalariform perforations. The protoxylem vessels are usually hard to observe because the entire zone is crushed; sometimes 1–2 small round cells beneath the metaxylem vessels can be seen. The intrafascicular parenchyma is also difficult to describe because it is crushed and poorly preserved. The fibrous bundles are infrequent and are very similar to the cortical ones. In longitudinal view, long rows of spherical stegmata can be seen on them.

The subdermal zone is well developed (especially in sample 61A) and consists of rows of congested round to oval fibrovascular bundles with somewhat untypical (strange-shaped) sclerenchyma caps, but still of reniform aspect. These caps are formed of cells that are progressively larger towards the marginal zone, most probably representing “centrifugal differentiation of the fibrous part” (see Thomas & De Franceschi 2013). Fibrovascular bundle size varies, with r/tg.d. of 400–600/400–600 µm, phloematic (anterior) sclerenchyma caps r/tg.d. of 350–550/400–600 µm, and f/v ratio of 1/1–1.5/1. Bundle density within this zone is 127–154/cm^2. The phloem appears as a single island of nondivided phloem situated just beneath the sclerenchyma cap. The metaxylem is represented by 2–4 round or oval vessels 100–250/100–200 µm in diameter, and filled with tyloses in longitudinal view. The protoxylem is represented by 1–6 small round vessels located just under the metaxylem. The intrafascicular parenchyma is very organized and appears as polygonal to oval thin-walled cells regularly arranged around the metaxylematic vessels as continuous compact rows, similar to a tabular parenchyma. The interfascicular parenchyma is formed of polygonal, rounded to oval, thin-walled cells, sometimes poorly preserved. The fibrous bundles are small and not too frequent in this zone.

The central zone of the central cylinder seems to have an important role in the mechanical function of the palm stem, due to the special distribution of the fibrovascular bundles within it. In cross section, the studied specimens (especially AH919) show clear signs of centrifugal differentiation of the fibrous part (*sensu* Thomas & De Franceschi 2013), particulary in the fibrovascular bundles, where the external cells of the sclerenchyma caps are systematically larger. The fibers are polygonal in cross-section, with thickened walls and circular or elliptic lumina, and without intercellular spaces. The sclerenchyma caps are of Reniformia type, sometimes tending to Complanata type (*sensu* Stenzel 1904). In this zone the fibrovascular bundles have various orientations, sometimes divergent or face to face. Fibrovascular bundle size varies, with r/tg.d. of 700–1500/400–800 µm, anterior sclerenchyma cap r/tg.d. of 400–950/400–800 µm, and f/v ratio of 0.7/1–1.6/1. Bundle density within this zone is 67/cm^2. The phloem is arranged in 1–2 islands, clearly separated (divided phloem) or sometimes connected (apparently divided phloem). A single island (undivided phloem) appears rarely, situated just under the sclerenchyma cap. When preserved, the phloem appears in cross section as small (or slightly varying in size) and relatively thick-walled cells mixed with thin-walled ones in the same island. The metaxylem can be represented by 2–4(5) round vessels 60–400 µm in diameter. There can be more than 6 smaller metaxylem vessels in the foliar bundles. The metaxylem vessels are usually thick-walled, sometimes suggesting gelification; in longitudinal view the metaxylem vessels show closely arranged, thin helical thickenings, scalariform pitting, and scalariform, perforated, tilted plates with 6–13 thick bars. The protoxylem is sometimes absent or not visible, but when observed it is represented by 1–6 circular to oval small vessels 80–120 µm in diameter, more numerous in the foliar bundles (up to 13 smaller vessels). In longitudinal view these vessels have spaced annular or helical thickenings, scalariform pitting, and scalariform perforations with up to 10–12 thick bars spaced apart on tilted plates. The intrafascicular parenchyma appears as polygonal cells regularly arranged as 2–3 rows of elongate cells (as of tabular type) around metaxylem vessels, or as smaller, rounded, thin-walled cells among the vessels, sometimes bearing starch grains or dark tanninous content. Some marginal rows of larger polygonal cells that are slightly elongated and sclerified, and protect all of the vascular part as a second sclerenchyma cap (also known as a ventral fibrous cap). The interfascicular parenchyma is abundant and loosely distributed here in the central zone. It is represented by mixed, unequally sized and variously shaped (circular to elliptic or elongated) parenchyma cells. Sometimes some rows of tangentially elongated cells appear in the lateral part of the fibrovascular bundles (in cross section). In fact, around the entire fibrovascular bundle, parenchyma of tabular type is present as 2–3 compact rows of cells which are elongated, closely connected between them and with the bundle. Starch grains or dark tanninous content are often present inside the parenchyma cells. In longitudinal view, short rows of enlarged cells appear, most probably of mucilaginous type. The fibrous bundles are not too numerous; they are round and of various sizes in cross section, numbering 20–24 thick-walled fibers. In longitudinal view, phytoliths can be seen on the walls of the fibers of the fibrous bundles and of the fibrous part of the fibrovascular bundles. They appear as spherical stegmata, slightly rugose (i.e. having small knots), partially sunken in the basal wall of the silica cell, and are arranged in numerous short rows. Another type of stegmata also appears, arranged in long rows; they are only of spherical type, sometimes slightly ovoid, have a smooth surface and are lodged in a weakly sclerified silica cell.

Affinities and discussion. After anatomical study of our petrified material with fascicular structure of palm stem type that generally can be attributed to the fossil genus *Palmoxylon* Schenk, we separated eight specimens having very similar structure, with the following important features: fibrovascular bundles with reniform sclerenchyma cap (of Reniformia type), tending to Cordata type (*sensu* Stenzel 1904) in the dermal zone and to Complanata type in the central zone, and with 2–4(5) large round metaxylem vessels with scalariform perforations with thick bars, and scalariform pitting; usually undivided phloem but also apparently divided or definitely divided, in the central zone; and tabular type of interfascicular parenchyma surrounding all the fibrovascular bundle, in 2–3 compact rows.

We compared the anatomy of our material with the structure of the extant genera presented in works by Tomlinson (1961, 1990), Tomlinson et al. (2011), Thomas (2011a, b, 2013) and Thomas and De Franceschi (2012, 2013). In those papers we found quite interesting suggestions regarding the possible affinity of our specimens with the typical Coryphoideae and especially with *Corypha* L. Thus, the outer fibrovascular bundles are more congested in the dermal zone than those of the inner part (central zone), their frequency decreases inside the central cylinder, and the f/v ratio of the subcortical (or dermal) zone is higher than that of the central zone. According to the cited authors, such characters are typical for *Corypha*-type palms.

The most similar combination of anatomical features is presented by the genus

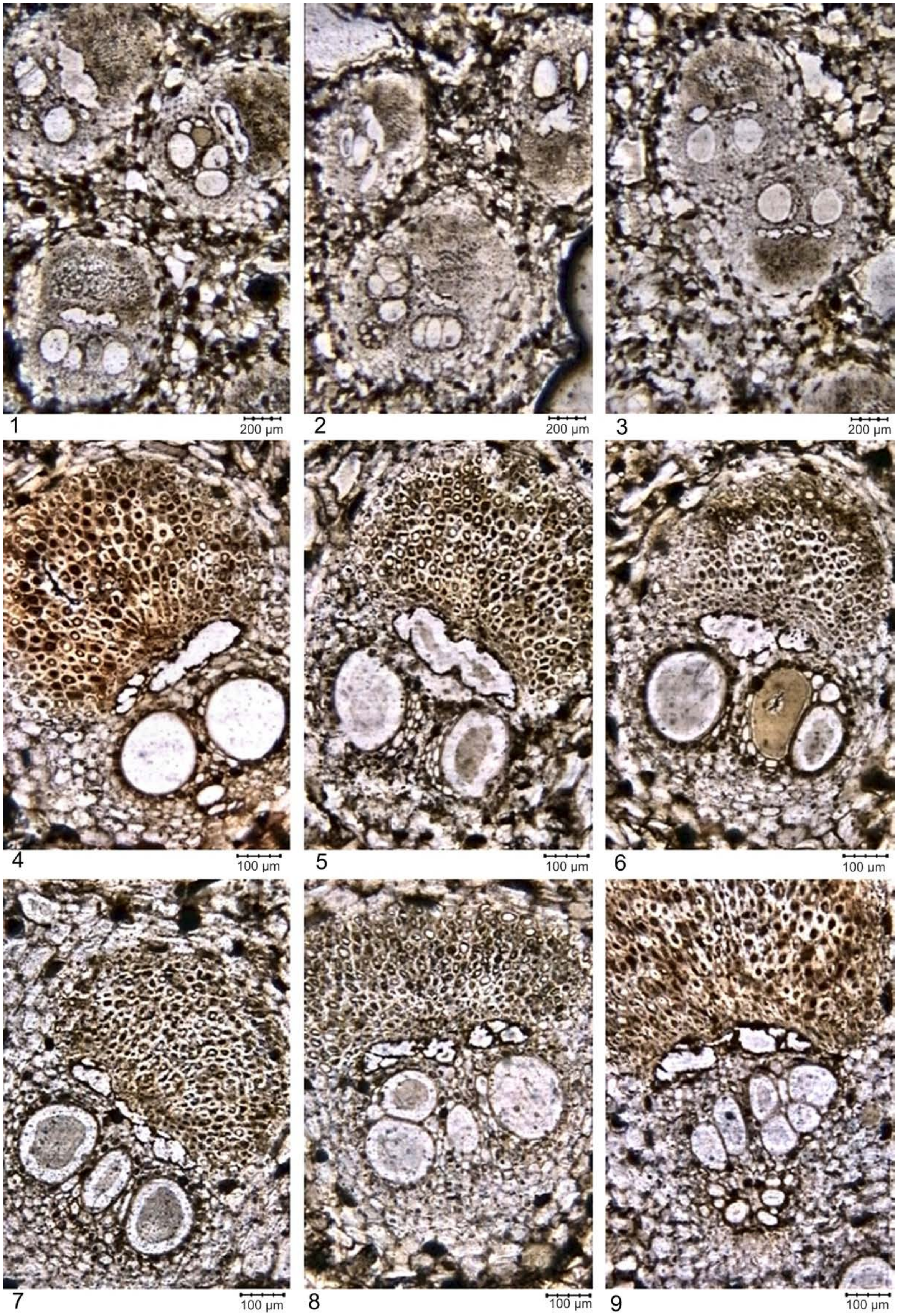

Plate 5. 1–9. *Palmoxylon coryphoides* Ambwani et Mehrotra 1990 (specimen AH919). **1–3**. Cross section: big fibrovascular bundles with 2–4(6) metaxylem vessels, with sclerenchyma caps of reniform type tending to Complanata type and interfascicular parenchyma of tabular type all around the bundle and non-oriented ground tissue within central zone. In 2 and 3, fused fibrovascular bundles can be seen. **4–9**. Cross section: fibrovascular bundles with 2–4(6) big metaxylem vessels, small protoxylem vessels and well organized intrafascicular parenchyma, with sclerenchyma caps of reniform type tending to complanata type and intrafascicular parenchyma only of tabular type all around the bundle, and, as non-oriented ground tissue within central zone

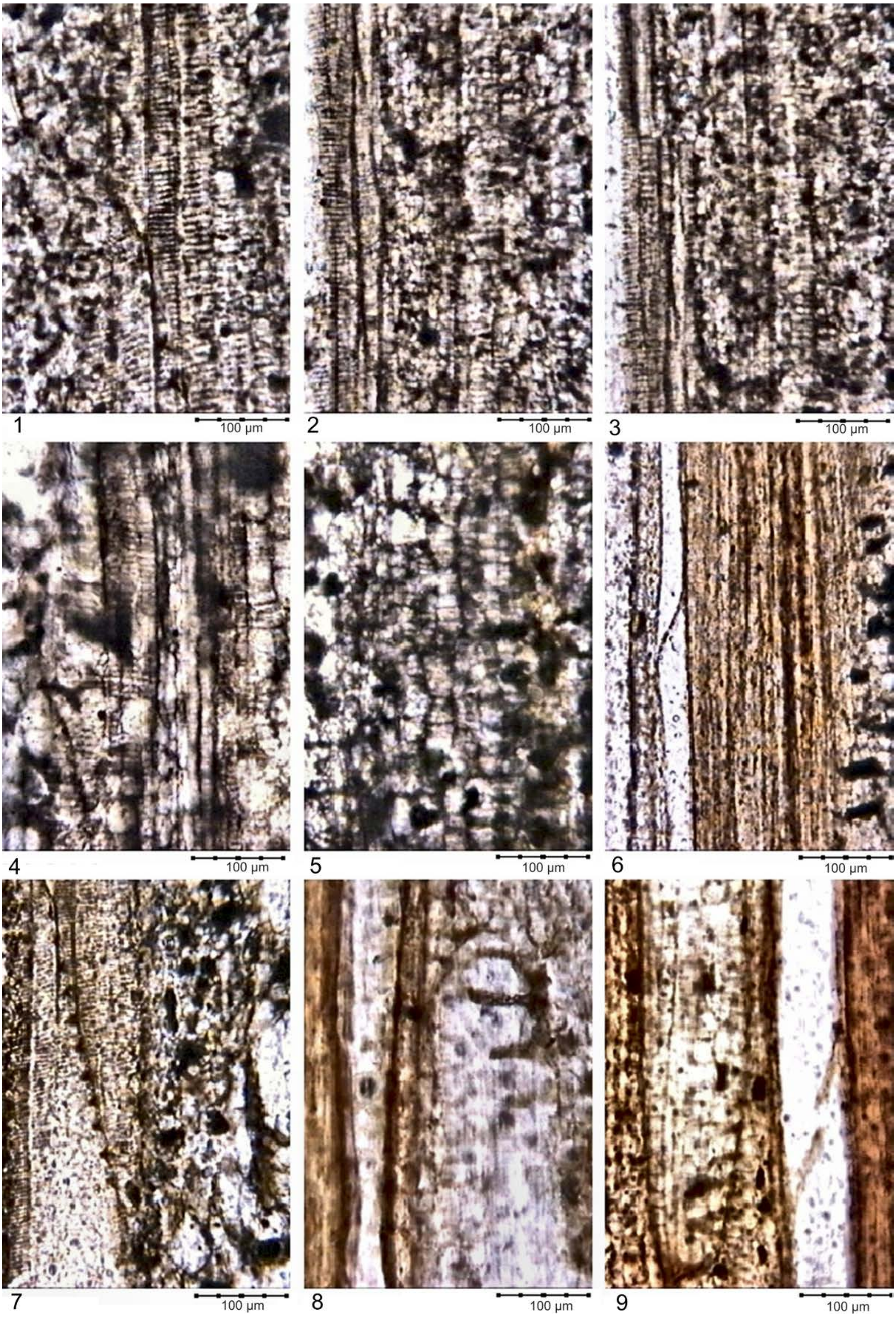

Plate 6. 1–9. *Palmoxylon coryphoides* Ambwani et Mehrotra 1990 (specimen AH919). **1–3**. Longitudinal sections: helical thickenings, badly preserved scalariform pitting on vessels (3). **4**, **5**, **7**. Longitudinal sections: badly preserved scalariform pitting on vessels. **6**, **8**, **9**. Longitudinal sections: badly preserved pitting on vessels and scalariform perforations with thick bars

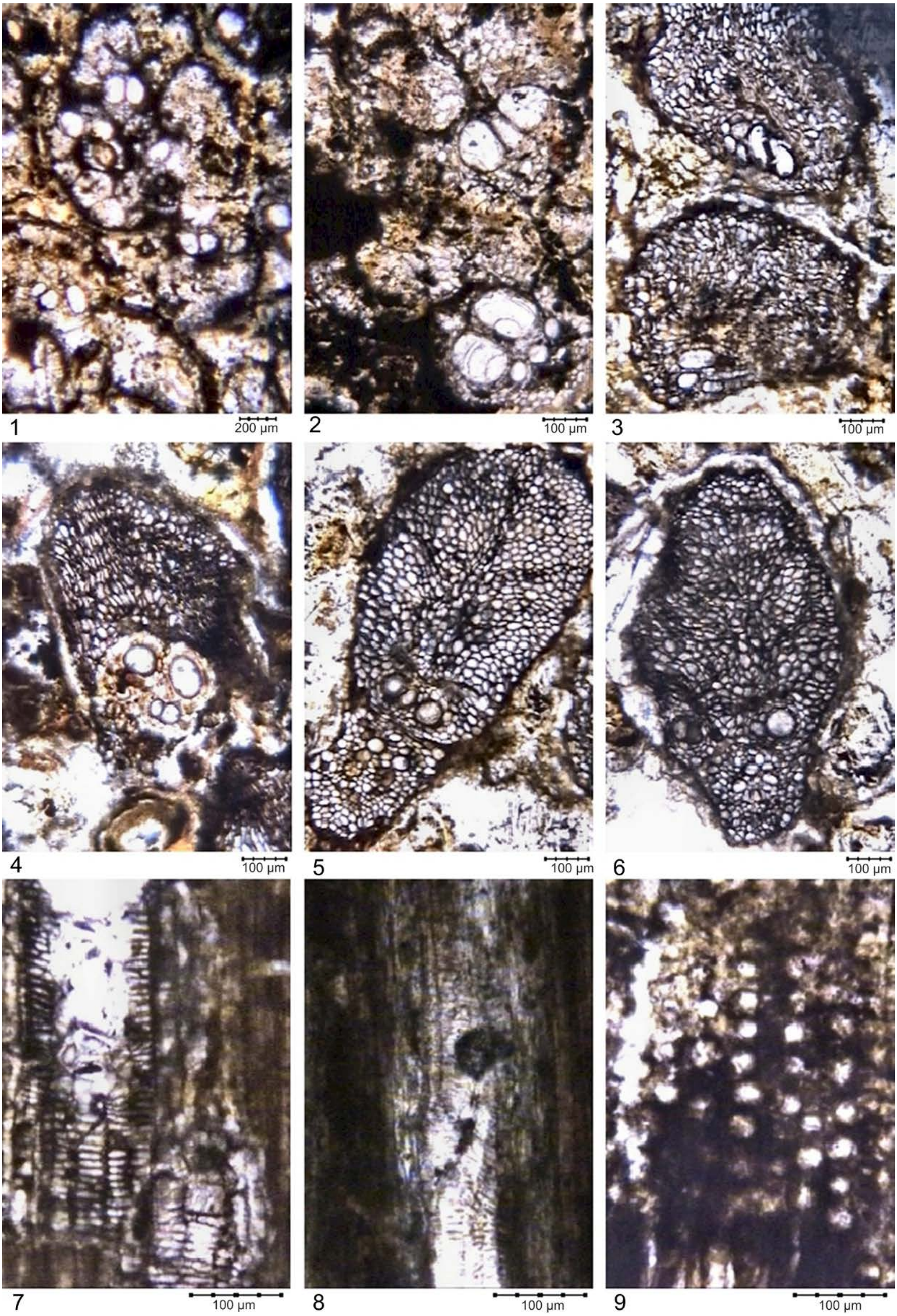

Plate 7. **1–9**. *Palmoxylon coryphoides* Ambwani et Mehrotra, 1990 (specimen L509). **1–6**. Cross sections: fibrovascular bundles with big sclerenchyma caps of reniform type, and badly preserved interfascicular parenchyma within cortical zone. Photos **7–8**. Longitudinal sections: badly preserved scalariform pitting on vessels and scalariform perforation. **9**. Longitudinal section: abundant stegmata in long rows on fibrous bundle

Corypha L., comprising extant palms native to India, Malaysia, Indonesia, New Guinea, the Philippines and northeastern Australia (Cape York Peninsula, Queensland). This is a type of fan palm 20–40 m high, with leaves having a long petiole (2–5 m) terminating in a rounded fan of numerous leaflets. (Thomas 2011a, b, 2013, Thomas & De Franceschi 2012, 2013, Wikipedia, accessed 20.07.2018).

In comparing our xylotomical structures with some fossil forms already published, we took into account all the available descriptions of so-called "sabaloid palms", in fact members of the Coryphoideaea subfamily, after the last phylogenetic classification of Arecaceae of Dransfield et al. (2005), usually having sclerenchyma caps of Reniformia type (*sensu* Stenzel 1904), as described by Schenk (1883), Berry (1924) Chiarrugi (1933), Rao & Menon (1964a), Menon (1965), Trivedi & Verma (1971a, b), Prakash (1962), Grambast (1957, 1964), Greguss (1954, 1959, 1969), Privé-Gill & Pelletier (1981), Gottwald (1992), Nambudiri & Tidwell (1998), Kahlert et al. (2005) and Iamandei & Iamandei (2006), in which a possible extant corresponding taxon is only sometimes given.

Other comparisons to fossil palms with reniform sclerenchyma caps (of Reniformia type, Stenzel 1904, as discussed above) show dissimilarity with our material, being related mainly to *Sabal*, *Trachycarpus* or *Chamaerops* but not to *Corypha*. Only Grambast (1962) saw in his *Palmoxylon* sp., of Complanata type, some similarities to the extant *Corypha* L.

More recently, Nour-El-Deen et al. (2017) described three *Palmoxylon* species from Egypt, with some possible affinities within Coryphoideae, but especially resembling *Trachycarpus* type.

Two fossil specimens described by Iamandei et al. (2018) from Miocene deposits of southwestern Turkey were described as *Palmoxylon* sp. cf. *Borassus* L. and *Palmoxylon* sp. cf. *Trachycarpus* H. Wendl., and another two specimens were identified as *Palmoxylon coryphoides* Ambwani et Mehrotra, being almost identical in xylotomy to the material we studied. Also all the microscopic details observed in our specimens are similar to those comprising the diagnosis of *P. coryphoides* as given by Ambwani & Mehrotra (1990), in terms of the fibrovascular bundles and the type of interfascicular parenchyma and stegmata; this allows us to attribute our material to this taxon under the name *Palmoxylon coryphoides* Ambwani & Mehrotra 1990.

Palmoxylon sabaloides Greguss 1969

Pl. 8, figs 1–9; Pl. 9, figs 1–9; Pl. 10, figs 1–9;
Pl. 11, figs 1–9; Pl. 12, figs 1–9

Material. The material attributed to this species is represented by ten samples (no. L15, L415, L424, L501, L507, L511, L520, L523, L524, L527), all of them collected from various points of Lesbos Island: on the western beach, the Museum area, Angali, Palomari, Eressos, Gavathas and Sigri and other unspecified sites. They are fragments of large stems, sometimes *in situ*, buried by volcano-sedimentary deposits of early Miocene age. They are housed under the above numbers in the collection of Athens University (NKUA), Faculty of Geology and Geoenvironment.

Description. The cortical zone, in cross section, is better preserved in samples L415 and L520. In the latter, which seems to come from a relatively thin stem 5–6 cm in diameter, the cortical zone is marked by the presence of fibrous bundles, mixed and of different sizes. They are relatively loosely arranged in the ground tissue, which is formed of elliptic or elongate parenchyma cells, some containing starch grains. In sample L415 the cortex is less apparent because the structure is invaded by fungi. Sometimes the cross sections show rootlets, which appear longitudinally sectioned. Most probably this sample comes from the basal part of the stem close to the rhizotil, where such rootlets appear.

The dermal zone is present, especially in samples L415 and L520, but is not very developed: it has 4–5 rows of open collateral fibrovascular bundles in a congested arrangement. They are smaller towards the outer part of the central cylinder and larger towards the inner part, where they have elongated sclerenchyma caps of reniform aspect and are slightly deformed (due to congestion). The constituent fibers are polygonal in cross section and have very thick walls and small circular to pointlike lumima. The fibrovascular bundles vary in size, with r/tg.d. of 450–700/200–300 µm, phloematic sclerenchyma cap r/tg.d. of 400–600/200-300 µm, and f/v ratio of 3.5/1–6/1. Bundle density within this zone is 308–612/cm^2. The phloem, when it can be observed, is arranged in a single island beneath the sclerenchyma cap in the median sinus (as undivided phloem). In these bundles the metaxylem is represented by a single large round vessel ~100 µm in diameter. The protoxylem consists of up to 6 small vessels, most often difficult to observe (and apparently absent in the foliar bundles). The intrafascicular parenchyma is very compressed and can barely be observed. The interfascicular parenchyma is of typical tabular type just around the fibrovascular bundles, and formed of elongated cells, compressed as ground tissue between the fibrovascular bundles, often bearing starch grains. Numerous small fibrous bundles can also be observed among the parenchymal cells of the ground tissue.

The subdermal zone was well visible in many of the studied specimens (L415, L424, L507, L520, L523, L524, L15). It is moderately developed as 4–5 rows of collateral fibrovascular bundles, slightly larger than in the dermal zone, varying in shape from rounded to elongated. They are congested and oriented with the vascular part toward the center of the stem. Beneath the sclerenchyma cap, which is of reniform aspect, 1–2 islands of divided or undivided phloem appear. Fibrovascular bundle size varies, with r/tg.d. of 450–500/250–300 µm, phloematic sclerenchyma cap r/tg.d. of 250–300/250–300 µm, and f/v ratio of 1.2/1–3.33/1. Bundle density within this zone is 275–300/cm^2. The protoxylem is represented by numerous small rounded vessels. There are also 1–2 metaxylem vessels with r/tg.d. of 100–250/80–250 µm. Sometimes within some younger stems (in samples L507, L524) the subdermal zone appears to be formed by very elongated fibrovascular bundles of uniform size and somewhat spaced apart, and has 1–3(4) slightly smaller metaxylematic vessels. The intrafascicular parenchyma consists of small, rounded, thin-walled polygonal cells. The interfascicular parenchyma is formed of rounded to slightly elongate polygonal cells which are relatively large (40–60 µm), and close to the bundles it is organized as tabular parenchyma all around the fibrovascular bundles. Scattered within the ground tissue of this zone are infrequent fibrous bundles.

The central zone of the central cylinder is well visible in almost all the specimens (L501, L507, L511, L520, L523, L524, 527) and represents palm stems of different ages and from different heights of the stem. In cross section, rounded or pyriform collateral fibrovascular bundles appear, very irregularly oriented. Their sclerenchyma caps are of reniform aspect (Reniformia type, Stenzel 1904), having constituent fibers polygonal in cross section, thickened walls and circular to point-like lumina. Fibrovascular bundle size varies, with r/tg.d. of 300–1000/600–150 µm, phloematic (anterior) sclerenchyma cap r/tg.d. of 200–625/600–150 µm, and f/v ratio of 0.7/1–1.7/1. Bundle density within this zone is 250–270/cm^2. The phloem appears as 1–2 islands (nondivided or apparently divided phloem) beneath the sclerenchyma cap, but usually is degraded and only an empty space appears instead (as a nonspecific lacuna). Some phloem sieve cells are rarely observed (13–15 µm or more in diameter), which in longitudinal view appear as thin-walled elongated cells. The metaxylem is represented by 2 large, round, thick-walled vessels having r/tg.d. of 60–150/70–150 µm in cross section. Between 3 and 6 smaller vessels can be seen in the foliar bundles. In longitudinal view the metaxylem vessels show spaced apart, thick or thin annular thickenings, or they are fine and helical and also have scalariform pitting. The perforated plates are highly inclined and scalariform, with 2–12 thick bars. The protoxylem is represented by 1–4 small round-lumened vessels, or they are absent. In the foliar bundles up to 9 similar protoxylem vessels appear. In longitudinal view the protoxylem vessels present annular or helical thickenings and scalariform perforations. The intrafascicular parenchyma consists of small, uniform, thin-walled polygonal cells adjacent to the metaxylem vessels in regular rows, arranged as in tabular type. The entire vascular zone is protected by some marginal rows of sclerified cells which function as a second sclerenchyma cap. The interfascicular parenchyma consists mainly of thin-walled cells of polygonal to rounded shape, or elongate, mixed in the mature structures and often bearing starch grains. Typical tabular parenchyma, compactly arranged in 1–2 rows, appears surrounding the fibrovascular bundles entirely. The fibrous bundles appear among the large elongated cells of the interfascicular parenchyma. They are numerous, uniform in size, and have 18–20 fibers which are polygonal in cross section. In longitudinal view, phytoliths are visible on the fiber walls as spherical stegmata, slightly spinulose (with rounded spines), partially sunken in the basal wall of the silica cell. They appear in numerous long rows,

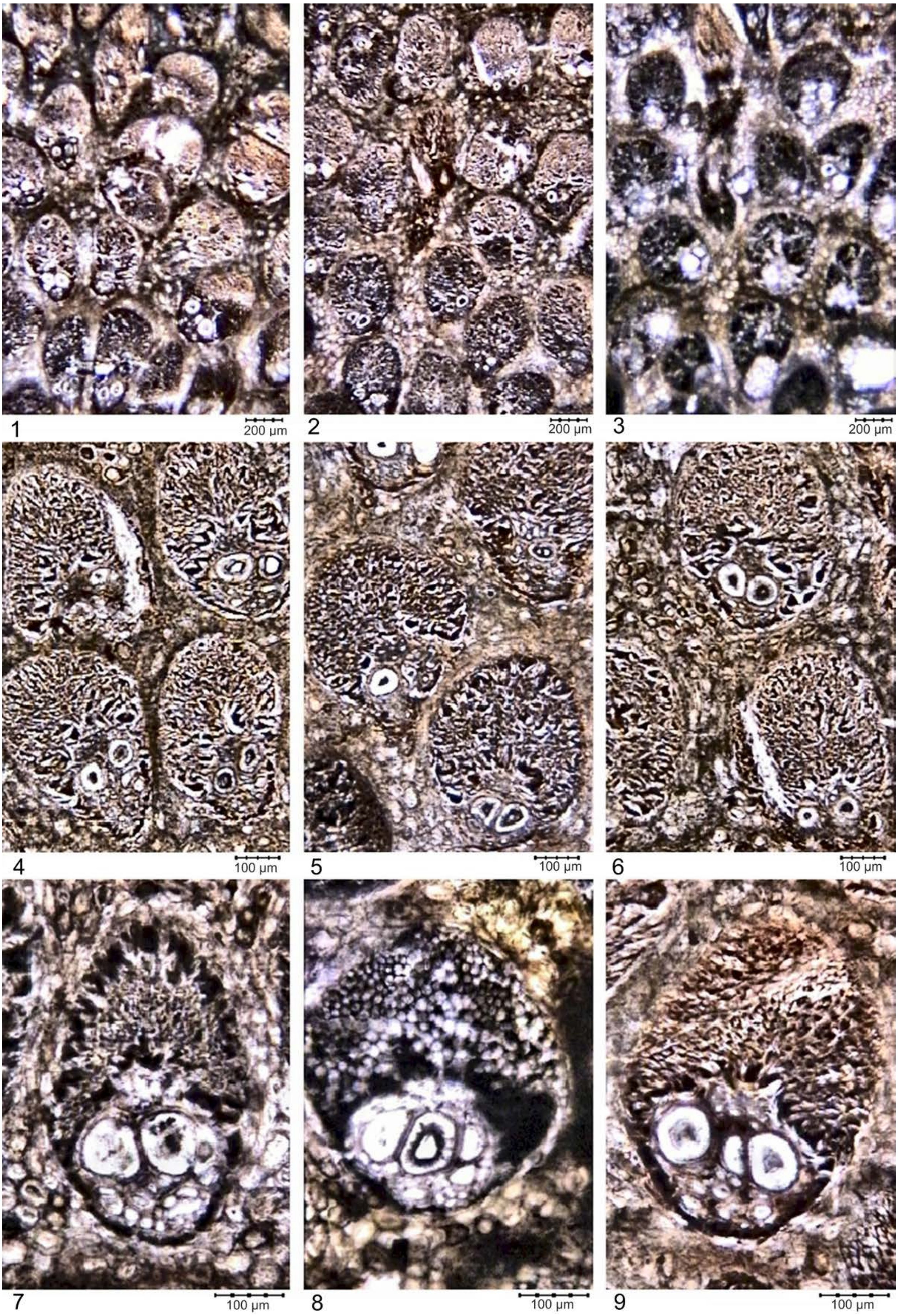

Plate 8. **1–9**. *Palmoxylon sabaloides* Greguss 1969 (specimen L15). **1–3**. Cross sections: fibrovascular bundles usually with 2 metaxylem vesels and elongated sclerenchyma caps of reniform aspect; ground tissue of tabular type and interfascicularly with non-oriented disposition within subdermal zone. **4–6**. Cross sections: fibrovascular bundles with 2 vessels and sclerenchyma caps of reniform aspect; thick-walled ground tissue only of tabular type and non-oriented interfascicular parenchyma within central zone zone. **7–9**. Cross sections: details of fibrovascular bundles with 2(3–4) metaxylem vessels, parenchyma of tabular type around the entire bundle and non-oriented interfascicular parenchyma, in central zone

Plate 9. **1–9**. *Palmoxylon sabaloides* Greguss 1969 (specimen L15). **1–7**. Longitudinal sections: scalariform pitting and scalariform perforations with thick bars, on vessels (in 1, 2, 6, 7). **8–9**. Longitudinal sections: long rows of stegmata on fibers

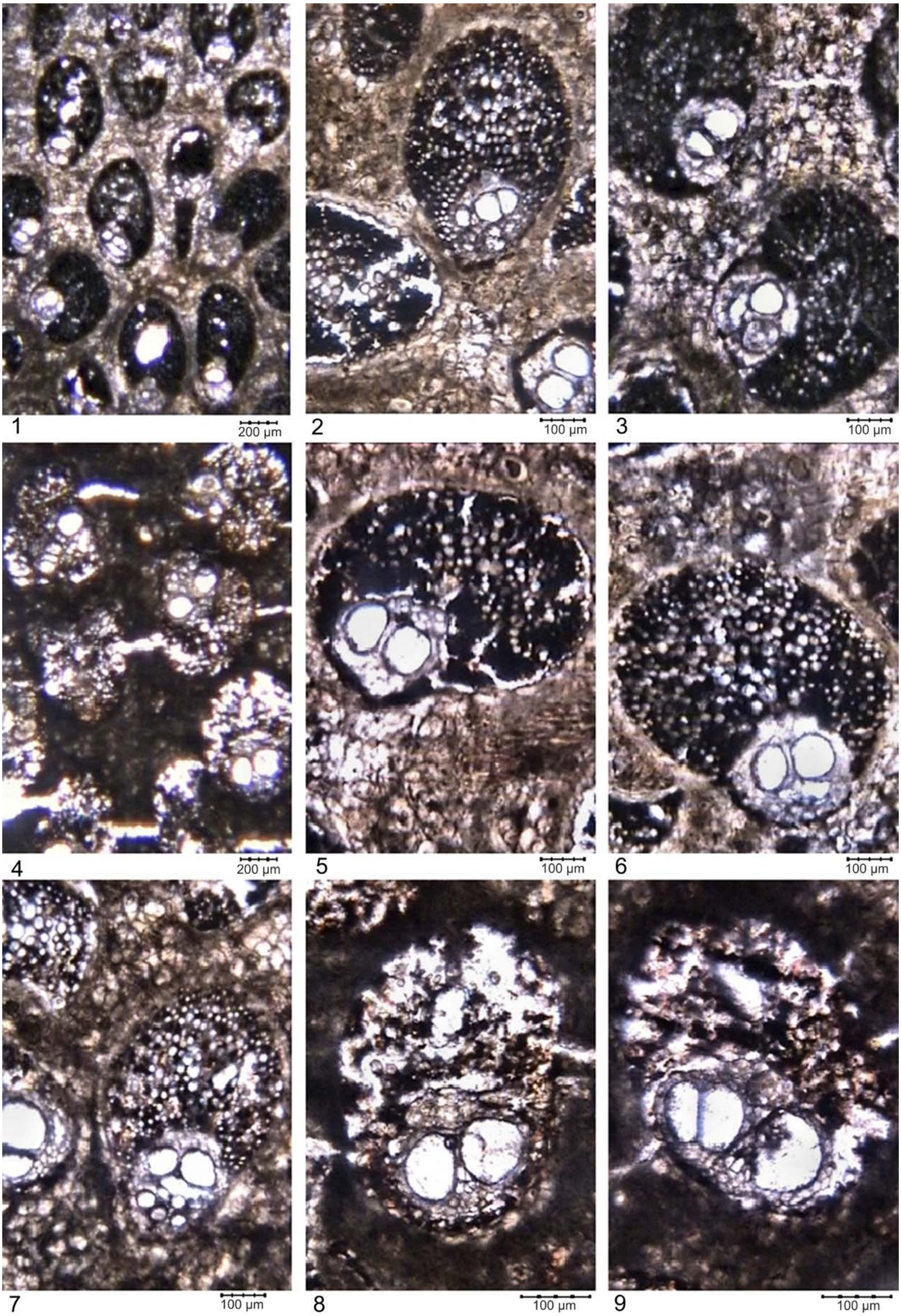

Plate 10. **1–9**. *Palmoxylon sabaloides* Greguss 1969 (specimen L507). **1–3**. Cross sections: fibrovascular bundles with sclerenchyma caps of reniform aspect and with tabular parenchyma within subdermal zone. **4–9**. Cross sections: fibrovascular bundles with 2 metaxylem vessels, protoxylem vessels, tabular parenchyma and interfascicular parenchyma, as large, round, thick-walled cells

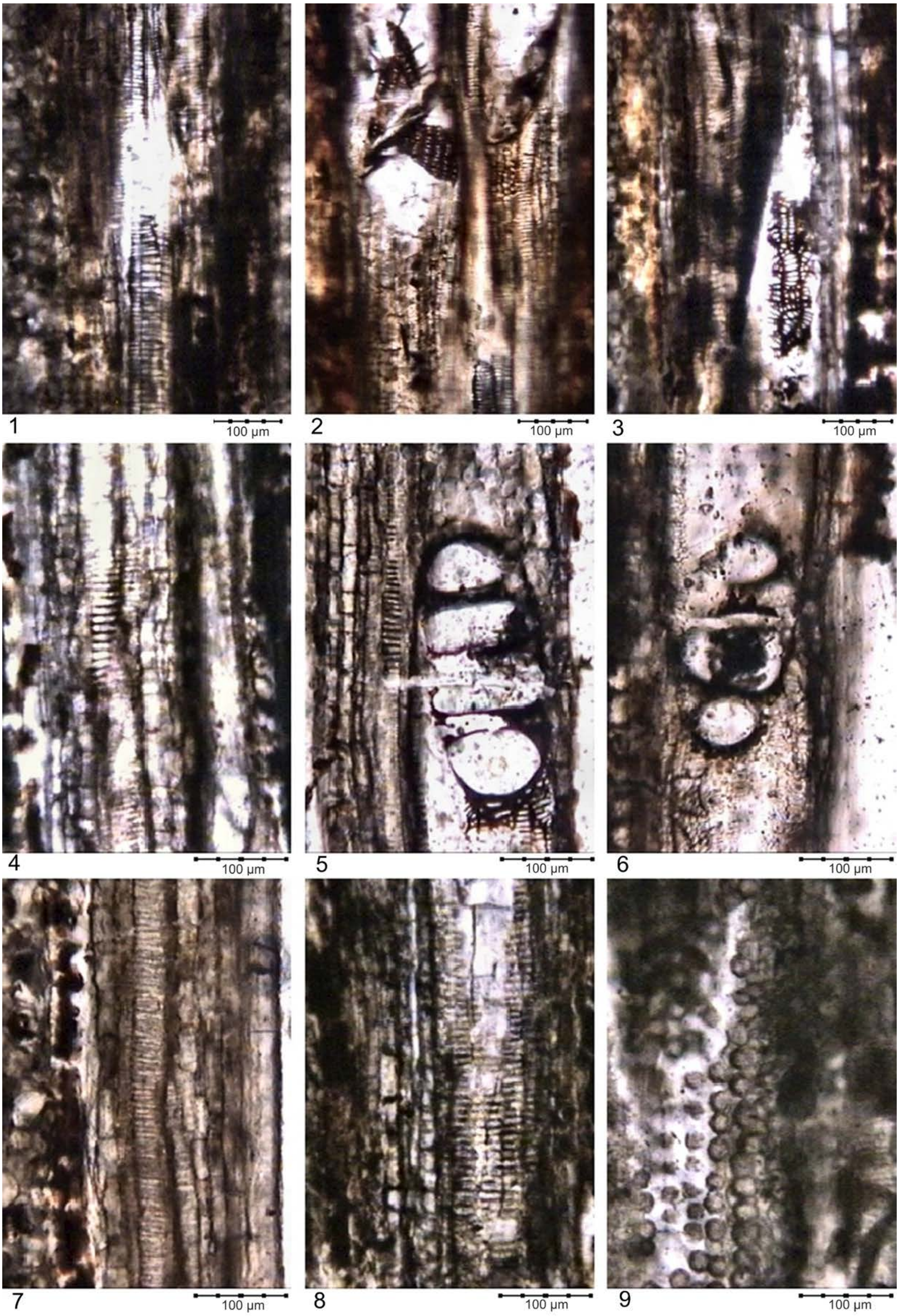

Plate 11. **1–9**. *Palmoxylon sabaloides* Greguss 1969 (specimen L507). **1–4**, **7**, **8**. Longitudinal sections: with helical thickenings and scalariform pitting on vessels. **5**, **6**. Longitudinal sections: vessels with perforations with thick bars and scalariform pitting, poorly preserved. **9**. Longitudinal section: with numerous long rows of stegmata on fibrous bundle

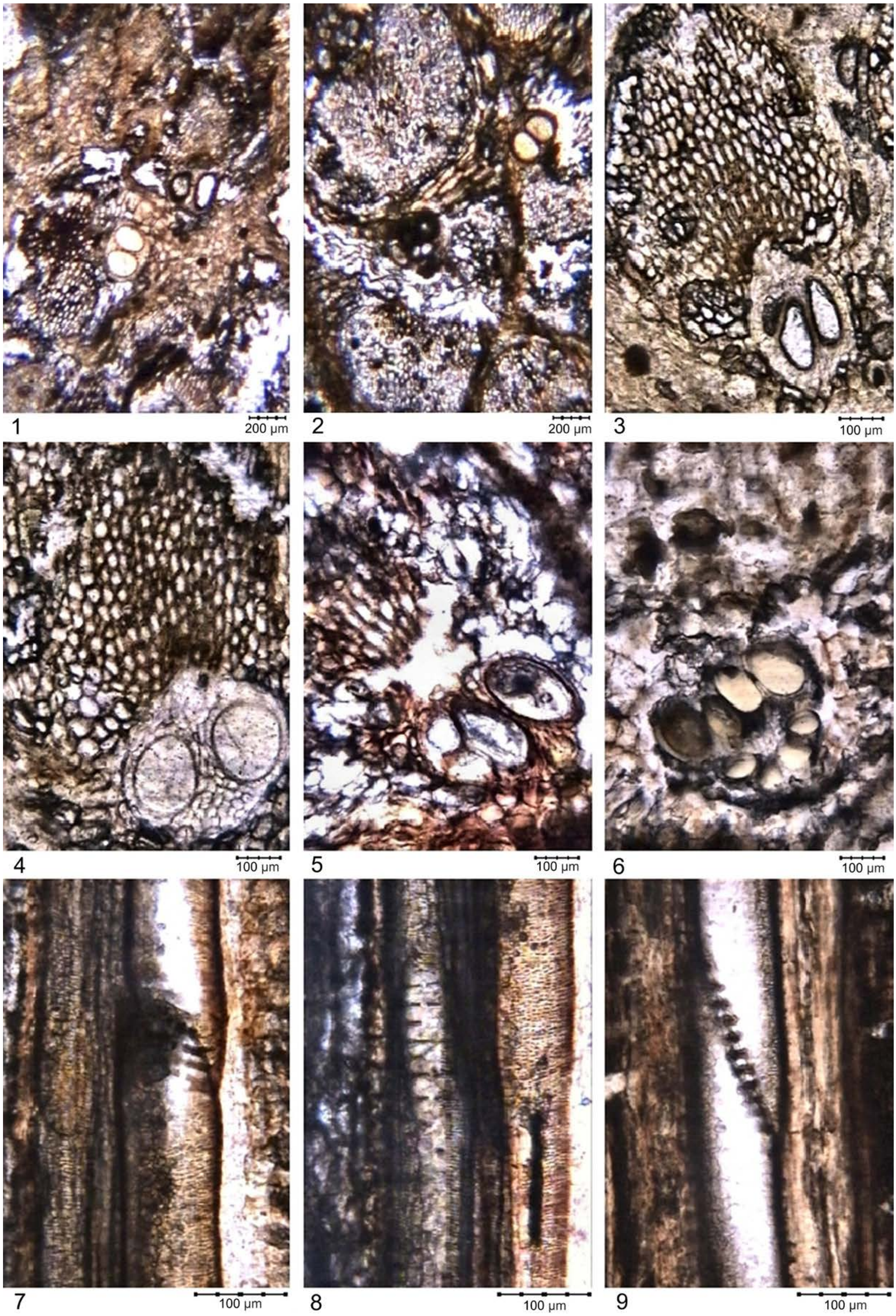

Plate 12. **1–9**. *Palmoxylon sabaloides* Greguss 1969 (specimen L501). **1–6**. Cross sections: fibrovascular bundles with 2–4 metaxylem vessels and protoxylem vessels, with sclerenchyma caps of reniform aspect and poorly preserved intrafascicular parenchyma within subdermal zone. **7–9**. Longitudinal sections: perforations with thick bars and scalariform pitting on vessels

covering large surfaces on the fibrous bundles as well as on the fibrous part of the fibrovascular bundles.

Affinities and discussion. From the studied material we selected 10 samples of fossil palm stems having very similar structural features.

To identify the original palm we made a comparison with the anatomical structure of extant types of palms and observed a great resemblance with the extant genus *Sabal* L. as presented in the works of Tomlinson (1961, 1990), Tomlinson et al. (2011) and Thomas & De Franceschi (2012, 2013).

Sabal L. is a fan palm that grows up to 20 m in height, with a stem up to 60 cm in diameter. It is native to the southeastern United States, Cuba and the Bahamas. It is extremely salt-tolerant and is often seen growing near the Atlantic coast, and also frost-tolerant, surviving short periods of temperatures as low as –14°C (Tomlinson 1961; Wikipedia, accessed 19.07.2017).

Fossil remains of this genus have been found frequently in Europe but it is does not now grow naturally there. For example, Rásky (1964: 67) described fossil leaves remains of *Sabal* L. from Hungary, also citing other fossil leaf remains described from the European Cenozoic by Unger, Ettinghausen, Heer, Staub, Saporta, Czeczot, Reid & Chandler, Depape, Weyland, Chandler and Palfalvy, and also various other types of palm remains described by Müller-Stoll, Kräusel, Kirchheimer, Stockmans & Williére, Grambast and Zimmermann (for citations see Rásky 1964).

We analyzed many published species of *Palmoxylon* Schenk and decided to compare only the species with fibrous sheaths of reniform type, attributed more or less explicitly to the sabaloid palms, keeping in mind that they in fact now represent the Coryphoideaea subfamily after the last phylogenetic classification of Arecaceae (see Dransfield et al. 2005). The species described by Schenk (1883), Berry (1924) Chiarrugi (1933), Rao & Menon (1964), Menon (1965), Trivedi & Verma (1971a, b), Prakash (1962), Grambast (1957, 1964), Greguss (1954, 1959, 1969), Prive-Gill & Pelletier (1981), Gottwald (1992), Nambudiri & Tidwell (1998), Kahlert et al. (2005), Iamandei & Iamandei (2006) and Iamandei et al. (2018) were compared with the synthetic description of our specimens, and from the above discussion it is clear that most of them are too different from the specimens we studied, or else they are clearly identified with other forms.

However, some Cenozoic fossil remains from Hungary were described as *Palmoxylon sabal* (Greguss 1954), and also as *P. sabaloides* and *P. dorogense* (Greguss 1969), as forms with many similarities to the extant *Sabal palmetto* Lodd., Eams & McDaniels (see Tomlinson 1961: 289, and Greguss 1968, 1969). Another form described as *P. hungaricum* (Greguss 1959) was considered to be similar to the extant *Livistona* R.Br. Another two forms described by Greguss (1969) as *Palmoxylon lacunosum* var. *axonense* Watelet definitely differ from our material, but the form described by Privé-Gill and Pelletier (1981) as *Palmoxylon* sp., of Reniformia type, may bear some resemblance to our material. A late Cretaceous sabaloid palm, *P. techerense* Iamandei & Iamandei (2006), resembles the extant *Sabal* L., having a similar shape, structure and arrangement of the fibrovascular bundles in the central cylinder, surrounded by parenchyma of tabular type, features also resembling our material.

Using the fundamental studies of palms by Tomlinson (1961, 1990), Tomlinson et al. (2011), Thomas (2011a,b, 2013) and Thomas & DeFranceschi (2012, 2013), we found good suggestions of the affinity of our specimens with the Coryphoideae, especialy those of *Sabal* L. type, regarding the distribution of the fibrovascular bundles in the central cylinder zones, and the variation of their density and f/v ratio from the subcortical to the central zone. Analyzing all the features of our specimens, which have many similarities with those of fossil or extant forms of *Sabal* type already described and quoted above, we believe that they are similar, to the point of identity, with the fossil species described by Greguss, and we attribute our studied material to *Palmoxylon sabaloides* Greguss 1969.

Palmoxylon trachycarpoides
Iamandei et Iamandei, sp. nov.

Pl. 13, figs 1–9; Pl. 14, figs 1–9; Pl. 15, figs 1–9; Pl. 16, figs 1–9

Material. From the studied material, 12 specimens showing similar anatomical structure are attributed to this species. Ten of these (samples 369, 375, 377, 491, L502, L510, L512, L516, L517, L518, 529, 533) were collected from Lesvos Island (Angali, Phaneromeni, Gavathas, Sigri and another unspecified site), one from Lemnos (sample 491) and one from Kastoria (sample 368), from volcano-sedimentary deposits of early Miocene age. They are fragments of palm stems of different ages and levels in the stem, not methodically sampled. Some of them were dispersed samples. They are now kept the collection of Athens University (NKUA), Faculty of Geology and Geoenvironment, under the above numbers.

Description. All the samples we had for study represent only the central zone of the central cylinder. The cortical, dermal and subdermal zones are missing, but for the analysis of typical palm stem structure the central zone is the most representative, and its anatomical structure has diagnostic value (see Thomas & DeFranceschi 2013).

In cross section the central zone has fibrovascular bundles of open collateral type, usually uniform in size, more or less uniform in orientation, sometimes grouped, or irregularly arranged. Their sclerenchyma caps are highly developed and have a rounded shape, of reniform type. Fibrovascular bundle size varies, with r/tg.d. of 570–1550/400–900 µm, sclerenchyma caps r/tg.d. of 320–1300/400–900 µm, and f/v ratio of 0.6/1 – 4.5/1. Bundle density within this zone is 46–177/cm^2, most frequently 70–75/cm^2. The constituent fibers of the sclerenchyma caps have are polygonal in cross section, or rounded to oval, without any intercellular spaces; all of them have thick walls and circular or elliptic lumina. They are smaller close to the vascular zone and 2–3 times larger toward the outer part, showing centrifugal differentiation of the fibrous part (see Thomas & De Franceschi 2013). The phloem usually appears as two islands just beneath the sclerenchyma cap, occupying the median sinus as divided phloem. It is sometimes lysed and appears only as two non-specific lacunae. In the xylematic zone the metaxylem is represented by 2–6(8) large vessels which are round to elliptic, thick-walled and sometimes of very different sizes, ranging in diameter from 50 to 200 µm. The foliar bundles, rarely observed, may have even more numerous metaxylem vessels. In longitudinal view these vessels show numerous and closely spaced helical thickenings, even merged, or spaced slightly apart and connected by vertical bars. Scalariform pitting is also present, as well as scalariform perforated tilted plates with up to 21 thin bars, sometimes branched and connected by vertical bars. The protoxylem is usually absent or degraded by lysis. When present it is represented by up to 7 small vessels 25–60(75) µm in diameter. In longitudinal view, annular thickenings were observed on them, and tapered endings. The pitting and perforations on the protoxylem vessels are scalariform. The intrafascicular parenchyma cells in cross section are polygonal or rounded, filling the space between the vessels; marginally, some rows of slightly sclerified cells protect the entire vascular part as a second schrenchyma cap (also called the ventral sclerenchyma cap). The intervascular parenchyma is of lacunar type or is partially absent in mature structures, and it appears either as a few restricted patches or as rounded or elongated cells covering large areas in younger structures. Starch grains are often present inside the cells. Around the vascular zone of the fibrovascular bundles, parenchyma of radial type is present. Around the sclerenchyma cap, parechyma of tabular type is present. Fibrous bundles are also present, varying in size in cross section, having 15–20 or more thick-walled fibers, with point-like lumina. Phytoliths seem to occur only on the fibrous bundles (in longitudinal view), presented as long rows of small slightly rugose spherical stegmata which are almost entirely sunken in the wall of the silica cell.

Affinities and discussion. We took into account the essential anatomical features of the studied samples selected for their similarity, and compared them with those of extant palms as described and figured in Tomlinson (1961, 1990), Tomlinson et al. (2011) and Thomas & De Franceschi (2012, 2013). We observed many similarities in the distribution of the fibrovascular bundles in the central zone, their frequency and f/v ratio in the central zone, and also the aspect of the interfascicular parenchyma, with extant palms from subfamily Coryphoideae, especially those of *Trachycarpus* type (see Dransfield et al. 2005).

Trachycarpus H.Wendl. is not present in the Mediterranean region today but it has been found frequently in Cenozoic deposits of Europe. It lives (with 8 species) in Southern and Eastern Asia (India, Nepal, eastern China, Burma), being relatively frost-resistant. It is

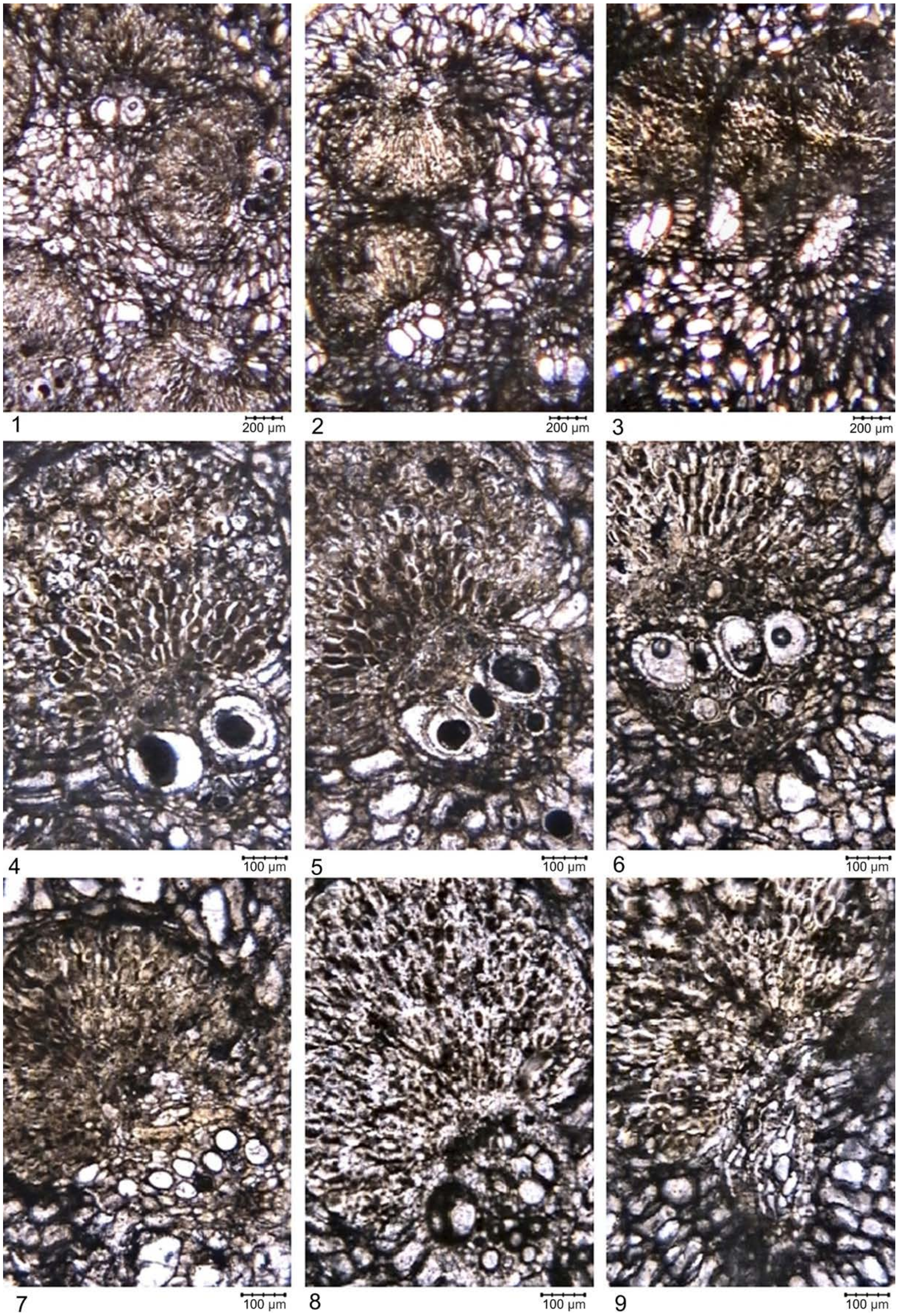

Plate 13. **1–9**. *Palmoxylon trachycarpoides* Iamandei et Iamandei, sp. nov. (specimen L512, holotype). **1–3**. Cross sections: fibrovascular bundles in central zone, with 2–4 or more metaxylem vessels, smaller protoxylem vessels beneath, and sclerenchyma caps of reniform aspect, surrounded by parenchyma of tabular type, the vascular part being surrounded by radial-type parenchyma, and, interfascicularly, parenchyma cells of various sizes. **4–9**. Cross sections: more detailed images of fibrovascular bundles in central zone, with 2–6 or more metaxylem vessels, thick-walled protoxylem vessels beneath, and sclerenchyma caps of reniform type with enlarged sclerenchyma cells, surrounded by tabular parenchyma; the vascular part is surrounded by radial parenchyma

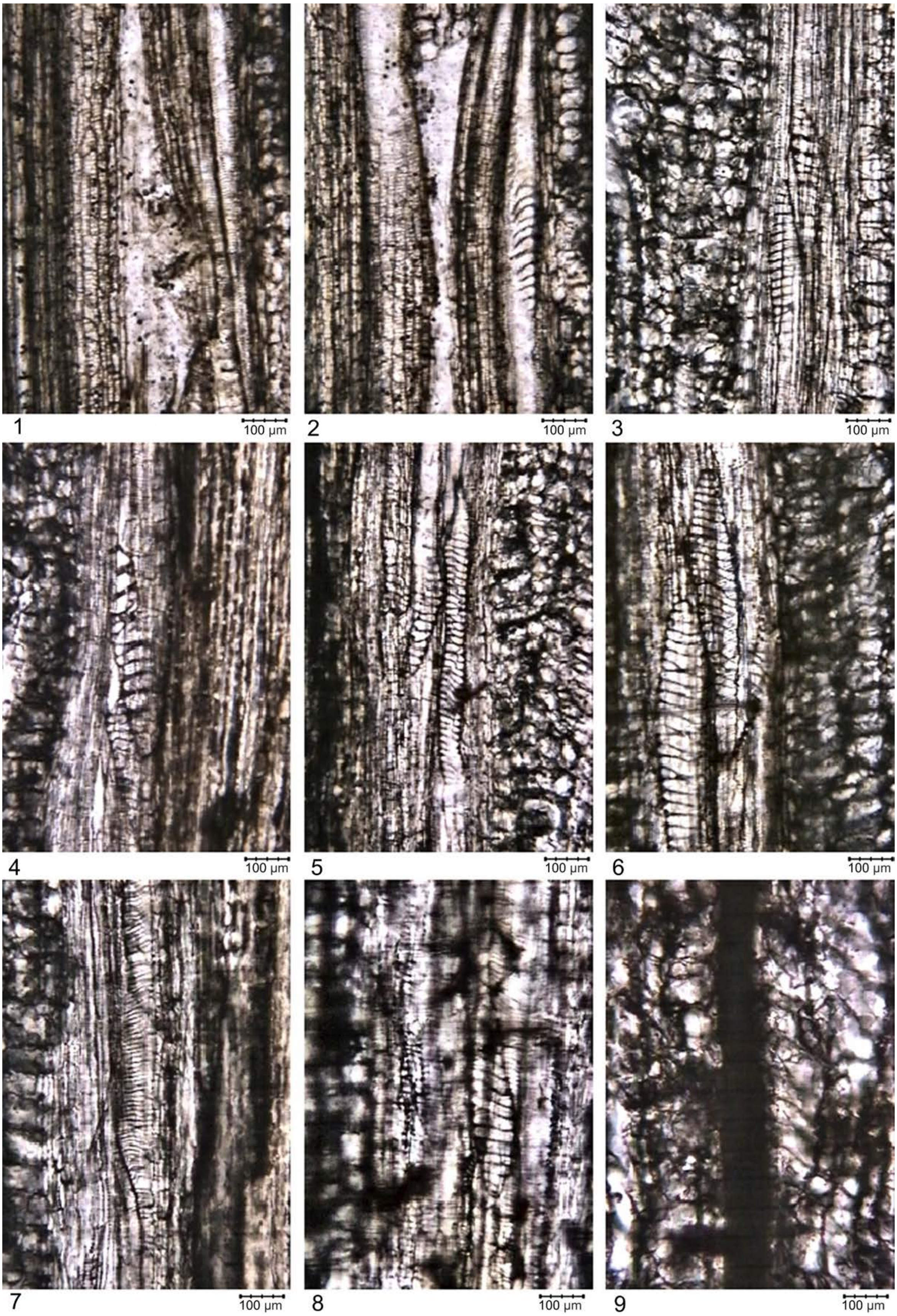

Plate 14. **1–9**. *Palmoxylon trachycarpoides* Iamandei et Iamandei, sp. nov. (specimen L512, holotype). **1–8**. Longitudinal sections: helical thickenings and scalariform pitting on vessels, high scalariform perforations with numerous thin bars, often branched, on metaxylem vessels. **9**. Longitudinal section: stegmata on fibrous bundle

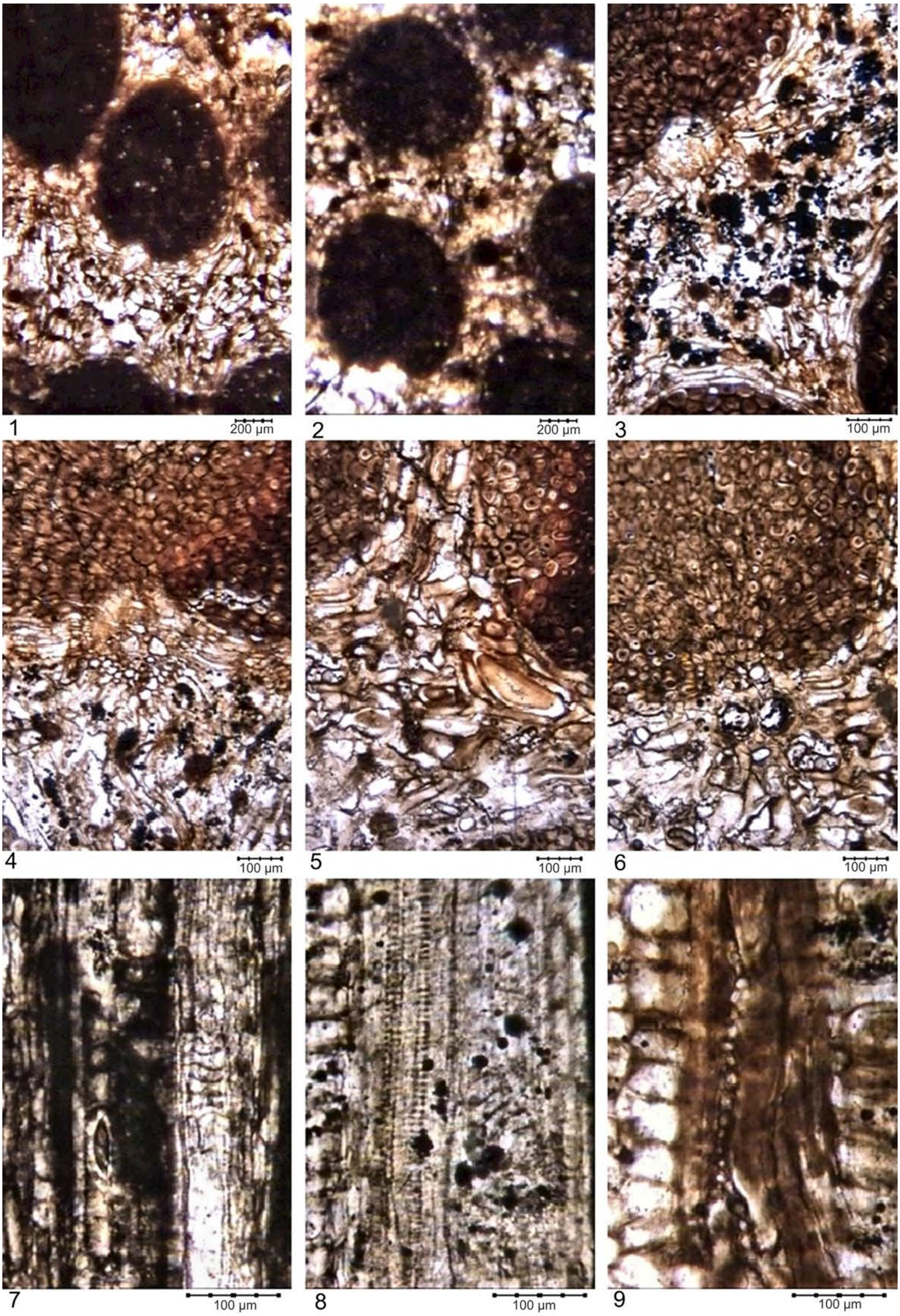

Plate 15. **1–9**. *Palmoxylon trachycarpoides* Iamandei et Iamandei, sp. nov. (specimen L529, paratype). **1**, **2**. Cross sections: fibrovascular bundles with large sclerenchyma caps of reniform aspect, tabular and radial parenchyma and interfascicular parenchyma with cells of various sizes, and also fibrous bundle within central zone. **3**, **5**. Cross sections: detail of interfascicular parenchyma with cells of various sizes, sometimes with granular content, and of tabular and radial parenchyma around the fibrovascular bundles within central zone. **4**, **6**. Cross sections: fibrovascular bundles with large sclerenchyma caps of reniform type, and tabular, radial and interfascicular parenchyma within central zone. **7**, **8**. Longitudinal sections: scalariform perforations with thin bars, helical thickenings and scalariform pitting on vessels. **9**. Longitudinal sections: with rows of stegmata on fibrous bundle

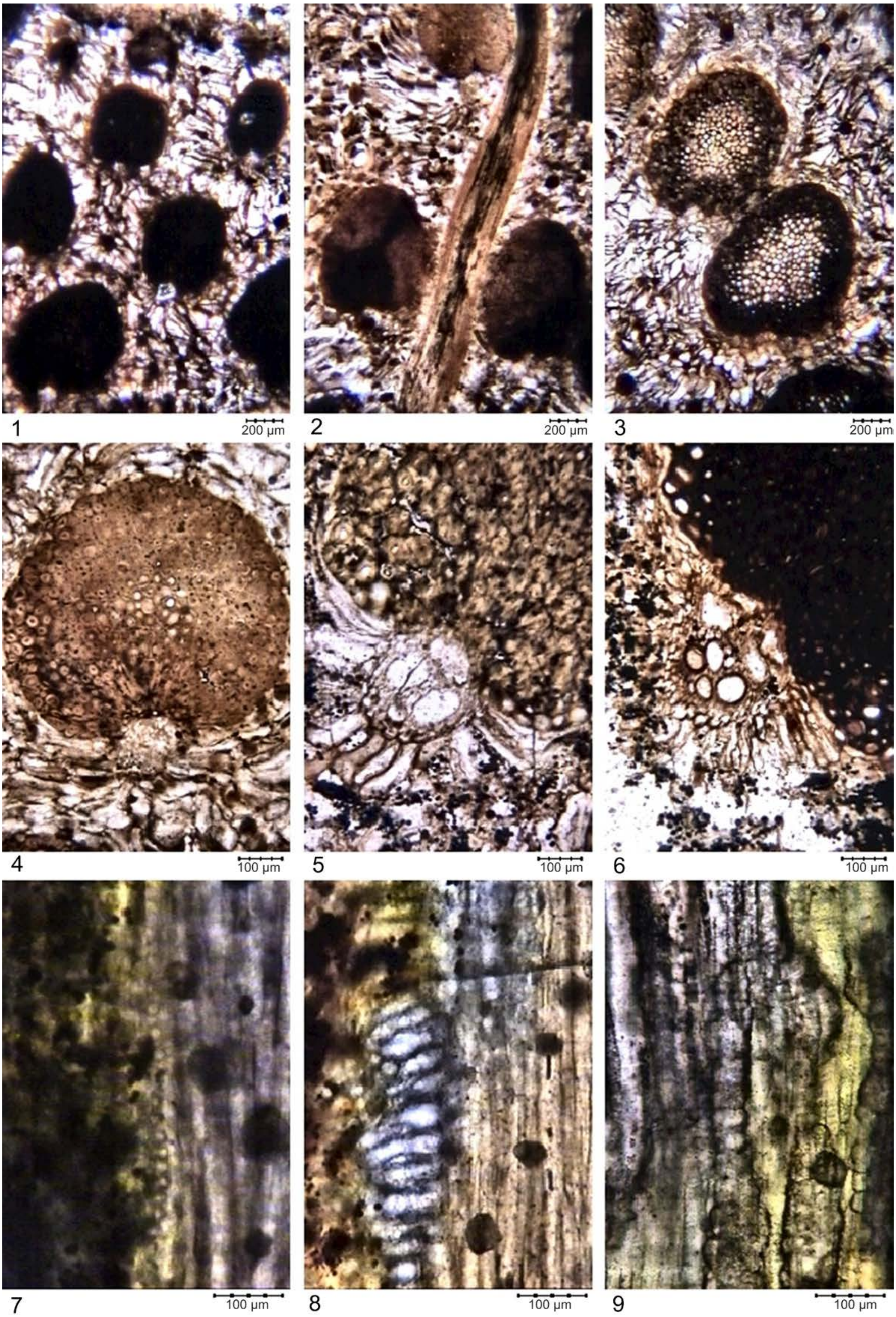

Plate 16. **1–9**. *Palmoxylon trachycarpoides* Iamandei et Iamandei, sp. nov. (specimen 533). **1**. Cross section: fibrovascular bundles with large sclerenchyma caps of reniform aspect, with tabular and radial parenchyma and intrerfascicular parenchyma with cells of various sizes, often elongate within subdermal zone. **2**. Cross section: adventitious rootlet longitudinally seen crossing the fascicular structure of the stem within subdermal zone. **3–6**. Cross sections: fibrovascular bundles with 2–4 metaxylem vessels, also protoxylem vessels, tabular parenchyma and large, round, thick-walled interfascicular parenchyma within central zone. **7**. Longitudinal section: with rows of stegmata on fibrous bundle. **8–9**. Longitudinal sections: poorly preserved helical thickenings and scalariform perforations on vessels

a fan palm 10–20 m tall and up to 20–30 cm in stem diameter. The trunk is very rough, with persistent leaf bases clasping the stem as layers of coarse fibrous material (Tomlinson 1961, Thomas & De Franceschi 2012, 2013, Wikipedia, accessed 19.07.2018).

After analyzing the features of some fossil forms of *Palmoxylon* with reniform sclenchyma caps (of Reniformia type, in Stenzel 1904), described by Schenk (in Zittel 1883), Berry (1924), Chiarrugi (1933), Prakash (1962), Grambast (1957, 1962), Rao & Menon (1964), Menon (1965), Kramer (1974), Privé-Gill and Pelletier (1981), Gottwald (1992), and Kahlert et al. (2005), we conclude that they refer to other palm types, sometimes with and sometimes without a specified extant corresponding taxon. Among these, *Palmoxylon eocenum* described by Berry (1924), *P. lacunosum* (Unger) Felix described by Chiarrugi (1933), *P. benadirense* described by Prakash (1962) and *P. bautschii* described by Kahlert et al. (2005) are of Reniform type (Reniformia type, Stenzel 1904) and have more or less lacunar ground tissue (interfascicular parenchyma), so they share some important anatomical similarities with our specimens. Some other Cretaceous or Cenozoic petrified palm stems described from Europe suggest close affinities with *Trachycarpus*-type structure. For example, Grambast (1964), in discussing the species *Palmoxylon vestitum* (Saporta) Stenzel, which was considered a fossil corresponding taxon of the extant *Phytelephas* Ruiz. et Pav., gave a new interpretation of the anatomical details originally described, and after a new study of the original material she concluded that *Palmoxylon vestitum* (Saporta) Stenzel shows similarities mostly with the extant *Trachycarpus* H.Wendl. and less with *Chamaerops* L. Similar features also appear in our specimens, regarding the fibrovascular bundles and ground tissue.

Some other “sabaloid” Cenozoic palm stem structures were described from Hungary as *Palmoxylon sabal?* of Greguss (1954), *P. sabaloides* (Greguss 1969) with affinity to extant *Sabal* L., and *P. hungaricum* with affinity to extant *Livinstona* R.Br. (Greguss 1959), and *P. dorogense* with phoenicoid affinities, but *P. lacunosum* var. *axonense* Watelet (Greguss 1969) has affinities mostly to *Trachycarpus* H.Wendl., presenting many anatomical similarities with our specimens. Another similar palm was described by Gottwald (1992) as *Palmoxylon* cf. *variabile* Vater and was considered almost identical to *Trachycarpus* H.Wendl.

Iamandei and Iamandei (2006) described another form of *Sabal* type, *Palmoxylon techerense*, but suspected some affinity with *Trachycarpus* type. More recently, Nour-El-Deen et al. (2017) described some Oligocene species of *Trachycarpus* type from Egypt, with anatomy very comparable to our specimens. Iamandei et al. (2018) described *Palmoxylon coryphoides* Ambwani et Mehrotra, *Palmoxylon* sp. cf. *Borassus* L. and *Palmoxylon* sp. cf. *Trachycarpus* H. Wendl. from Turkish Miocene deposits, also from the Aegean area. Our studied material shows many microscopic details mostly resembling *Trachycarpus* H. Wendl. as figured by Tomlinson (1961, 1990), Tomlinson et al. (2011) and Thomas & De Franceschi (2012, 2013). It also resembles fossil species described by Grambast (1964), Greguss (1969), Gottwald (1992), Nour-El-Deen et al. (2017) and Iamandei et al. (2018), and it obviously represents a new species of *Palmoxylon*, to which we assigned a new name after the model of Hofmann (1944), clearly reffering to the name of the extant corresponding genus. Our studied material belongs to a new species with the binomial name *Palmoxylon trachycarpoides* Iamandei et Iamandei, sp. nov., for which we have designated specimen 512 as holotype and specimen 529 as paratype, both housed in the collection of Athens University (NKUA), Faculty of Geology and Geoenvironment, in the Velitzelos Collection, together with all the studied material.

Diagnosis. Central zone of central cylinder built of uniform-sized, sometimes irregularly arranged fibrovascular bundles with large sclerenchyma caps of Reniformia type (*sensu* Stenzel 1904), r/tg.d. 320–1550/400–900 µm, f/v ratio 0.6–1.1 – 4.5, bundle density 46–177/cm^2, usually 70–75/cm^2. Phloem appears as divided phloem in two distinct islands. Xylematic zone presents 2–6(8) round to elliptic, thick-walled, different-sized metaxylem vessels 50–200 µm in diameter, in longitudinal view showing helical thickenings, scalariform pitting and high scalariform perforations with up to 21 thin branched bars. Protoxylem has up to 7 small vessels 25–60(75) µm in diameter, in longitudinal view showing annular thickenings. Intravascular parenchyma cells polygonal or rounded. Intervascular parenchyma of lacunar type, with enlarged mucilaginous parenchyma cells, of tabular type around sclerenchyma cap, of radial type around vascular zone of fibrovascular bundles. Fibrous bundles varying in size of 15–20 fibers (in cross section); in longitudinal view showing long rows of spherical stegmata, slightly rugose.

Palmoxylon phoenicoides Hofmann 1944

Pl. 17, figs 1–9; Pl. 18, figs 1–8; Pl. 19, figs 1–9;
Pl. 20, figs 1–9; Pl. 21, figs 1–9; Pl. 22, figs 1–9

Material. Rich material represented by 26 petrified palm stem fragments of very similar anatomical structure, attributed to this species.

Of these, 23 specimens (no. 364, 371, 372, 378, 459, 492, 494, 495, 496, 498, 500, L504, L506, L508, L513, 519, L521, L522, 528, 530, 531, 532, 534) were sampled from Lesbos Island (from Antissa, Larpsana, Park Zone, Sigri, Gavathas, Eressos and some from unspecified sites), two from Lemnos (L1, 528) and one from Kastoria (368). They are fragments of palm stems of different ages and from different levels, sometimes from the basal part, where rootlets already appear. The sampled stems are sometimes preserved *in situ* or as dispersed fragments buried by sedimentary or volcano-sedimentary deposits of early Miocene age. All these samples are now kept under the above numbers in the collection of Athens University (NKUA), Faculty of Geology and Geoenvironment.

Description. Standard sections of a young stem (sample 495) show all the tissues preserved, even the epidermis (in transversal section), but in a fossil it is difficult to compare very young with mature stem structure, and to find details of taxonomic value.

The cortical zone was well visible in cross section in samples 378, L1 and L531. In the first two specimens a region of adventitious rootlets is encountered, so the structure is not very representative. But in specimen L531, taken from a higher part of a thicker stem, 1.3 cm of cortical tissue is present, albeit incomplete. This tissue consists of mixed, various-sized and loosely arranged fibrous bundles, each comprising 15–25 fibrous cells in cross section; the cells are very thick-walled and point-like lumened. Small round fibrovascular bundles also occur, with a small triangular vascular part penetrating the large sclerenchyma cap, which represents 90% of the bundle cross section. The fibers forming the sclerenchyma cap are slightly larger than those in the fibrous bundles. Phloem was infrequently observed, usually as a single small island of undivided phloem or, much more rarely, apparently divided. The metaxylem appears as one single round or oval vessel 40–50 µm in diameter. In the foliar bundles up to 6 smaller metaxylem vessels appear. Also, up to 4 smaller round to oval vessels of protoxylem occur, sometimes poorly preserved. The intrafascicular parenchyma is very compressed and difficult to observe. The interfascicular parenchyma, as ground tissue, is clearly present and consists of polygonal or rounded to oval cells in a radial type of arrangement around the fibrous or fibrovascular bundles. Cell content is less present. Adventitious rootlets, when present in cross sections, disrupt the cortical tissue.

The central cylinder comprises the dermal, subdermal and central zones (or external, intermediary and central), and the features of the fibrovascular and fibrous bundles and the parenchyma in this zone may have some taxonomic value.

The dermal zone (external zone) is the zone conferring solidity to the stem via the close arrangement of 3–4 rows of small fibrovascular bundles of collateral type, which are oriented with the vascular part to the center of the stem, clearly seen especially in samples 371, 378, 459, 521, 530, 531 and 532. Their sclerenchyma caps, slightly larger in the inner part of this zone, are of reniform aspect. The thick-walled fibers of the sclerenchyma cap are circular to oval in cross section, with point-like lumina, and are often degraded by fungi. Bundle size varies, with r/tg.d. of 550–1050/400–750 µm, phloematic sclerenchyma cap r/tg.d. of 400–600/400–750 µm, and f/v ratio of 1.6/1–4.6/1. Fibrovascular bundle density within this zone is 177–354/cm^2. The phloem is located just under the sclerenchyma cap in the median sinus as a single island, sometimes two: that is, undivided and sometimes divided phloem. The xylematic zone is represented by 1–2 large round metaxylem vessels 60–125 µm in diameter. When an adventitious rootlet appears, there are also bundles with up to 10 relatively thin-walled smaller round vessels. The protoxylem is difficult to observe because the zone is often crushed; rarely, 6–10 thin-walled small vessels 25–35 µm in diameter can be seen. The intrafascicular parenchyma is formed of small polygonal thin-walled cells. The interfascicular

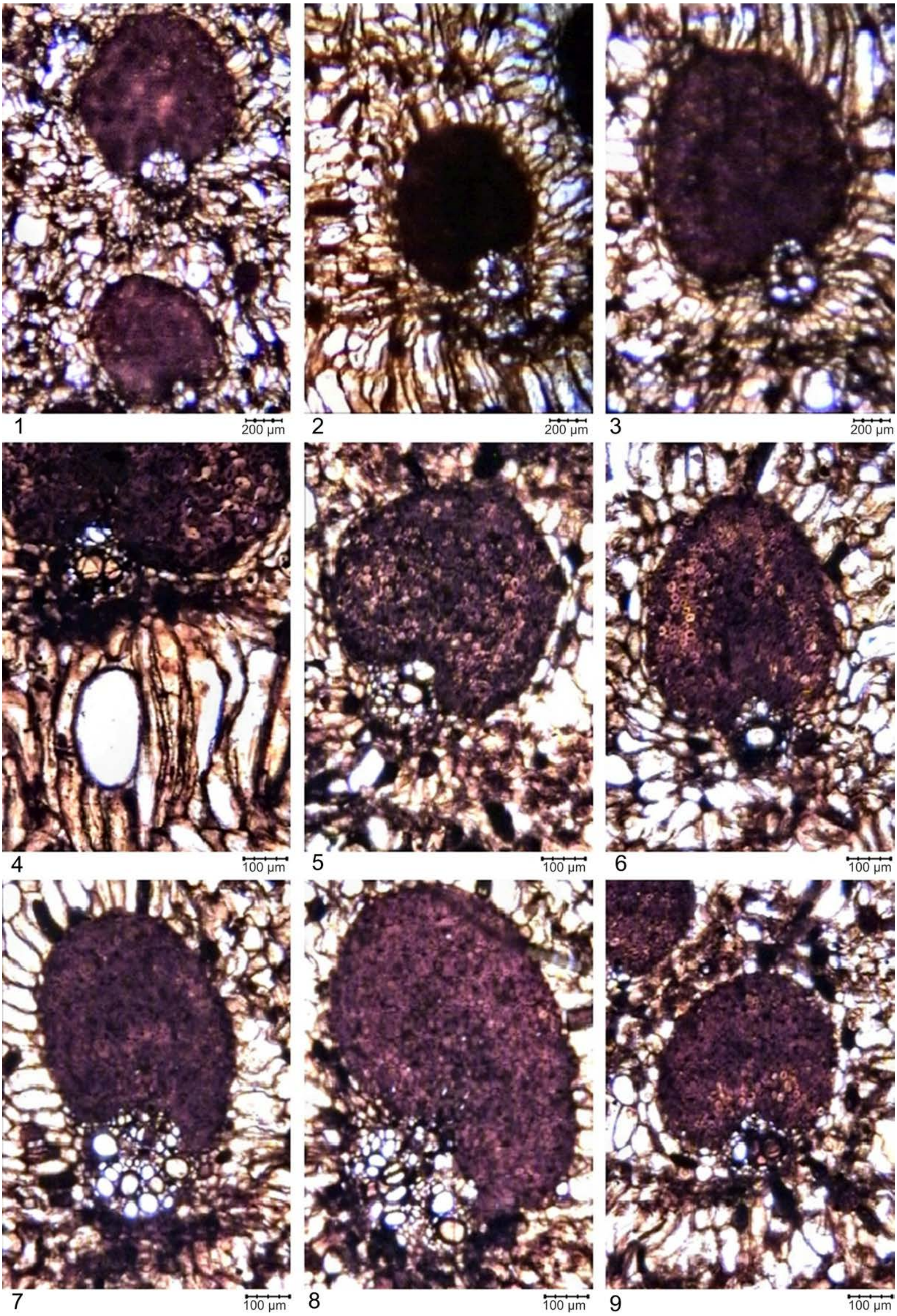

Plate 17. **1–9**. *Palmoxylon phoenicoides* Hofmann 1944 (specimen L508). **1–3**. Cross sections: fibrovascular bundles with sclerenchyma caps of reniform aspect surrounded by radial and tabular parenchyma; fibrous bundles surrounded by radial type of parenchyma; ground tissue of elongate cells with false radial disposition in central zone. **4–9**. Cross sections: fibrovascular bundles with 2–3 or more oval metaxylem vessels mixed with numerous round protoxylem vessels, interfascicular tabular and radial parenchyma, and ground tissue with false radial disposition in central zone

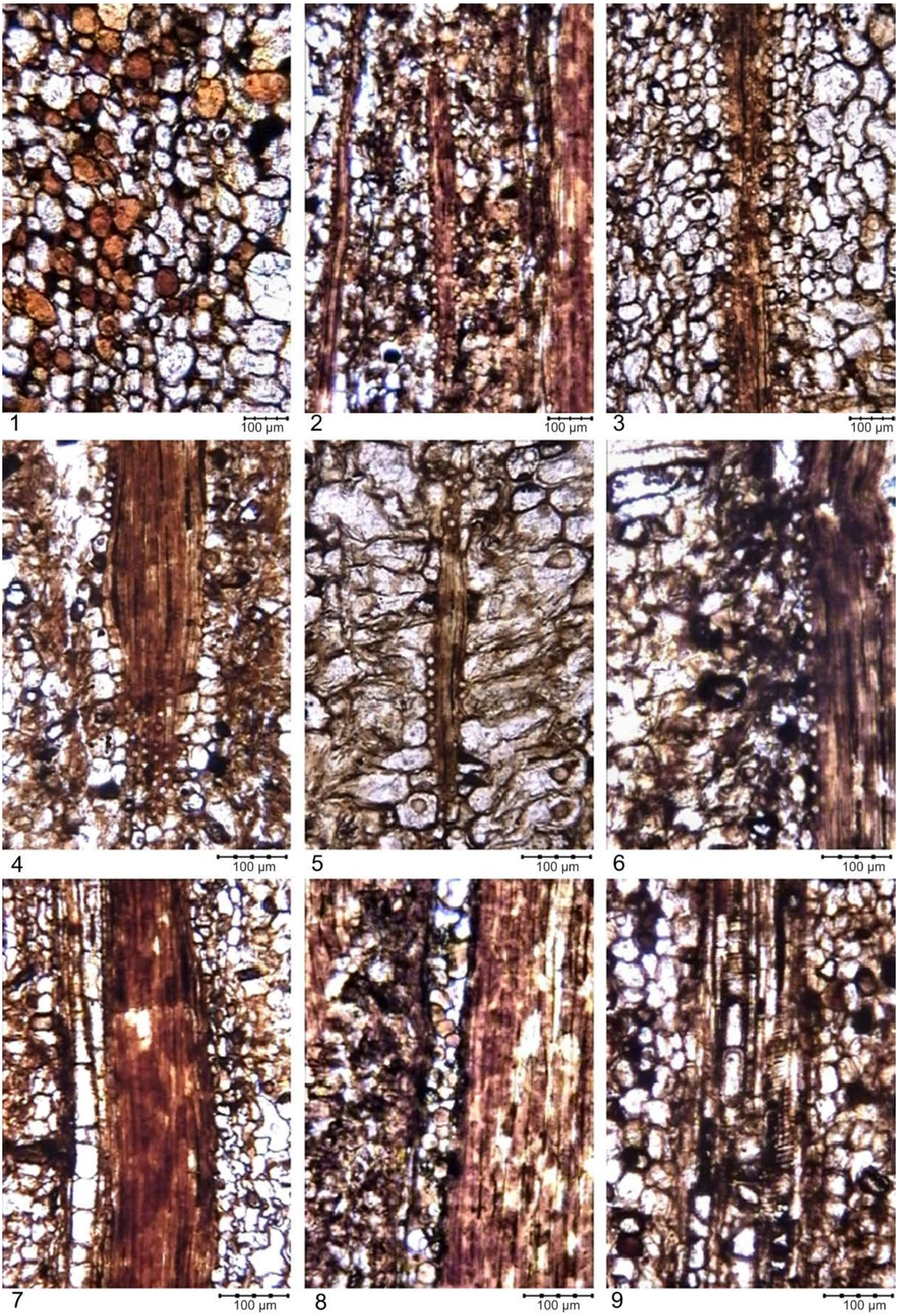

Plate 18. **1–9**. *Palmoxylon phoenicoides* Hofmann 1944 (specimen L508). **1**. Longitudinal section: parenchyma cells of ground tissue, detail, in central zone. **2–6**. Longitudinal sections: parenchyma cells, long rows of stegmata on fibrous bundles in central zone. **7–9**. Longitudinal sections: central zone with parenchyma cells, fibrous sheaths, helical thickenings and tyloses on vessels

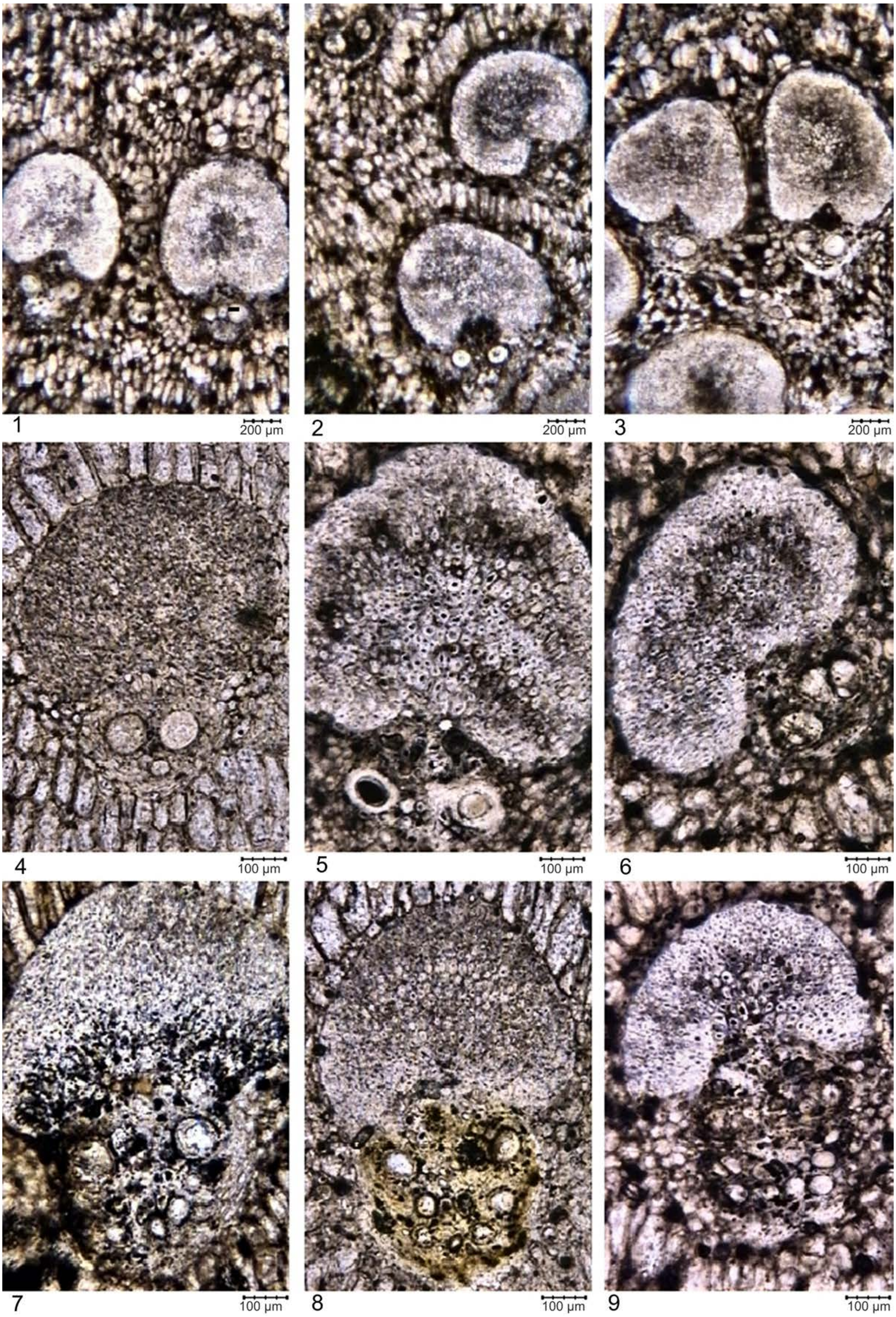

Plate 19. **1–9**. *Palmoxylon phoenicoides* Hofmann 1944 (specimen L1). **1–3**. Cross sections: fibrovascular bundles with sclerenchyma caps of reniform aspect with 2–3 large oval metaxylem vessels, numerous smaller round protoxylem vessels, fibrous bundles, interfascicular parenchyma of elongate cells. **4–9**. Cross sections: fibrovascular bundles with typical reniform sclerenchyma caps with 2–3(4) round metaxylem vessels and more numerous smaller round protoxylem vessels, the sclerenchyma caps being surrounded by a row of parenchyma of tabular type, and the vascular part being surrounded by parenchyma of radial type; the elongate cells of the interfascicular parenchyma often show a false radial arrangement

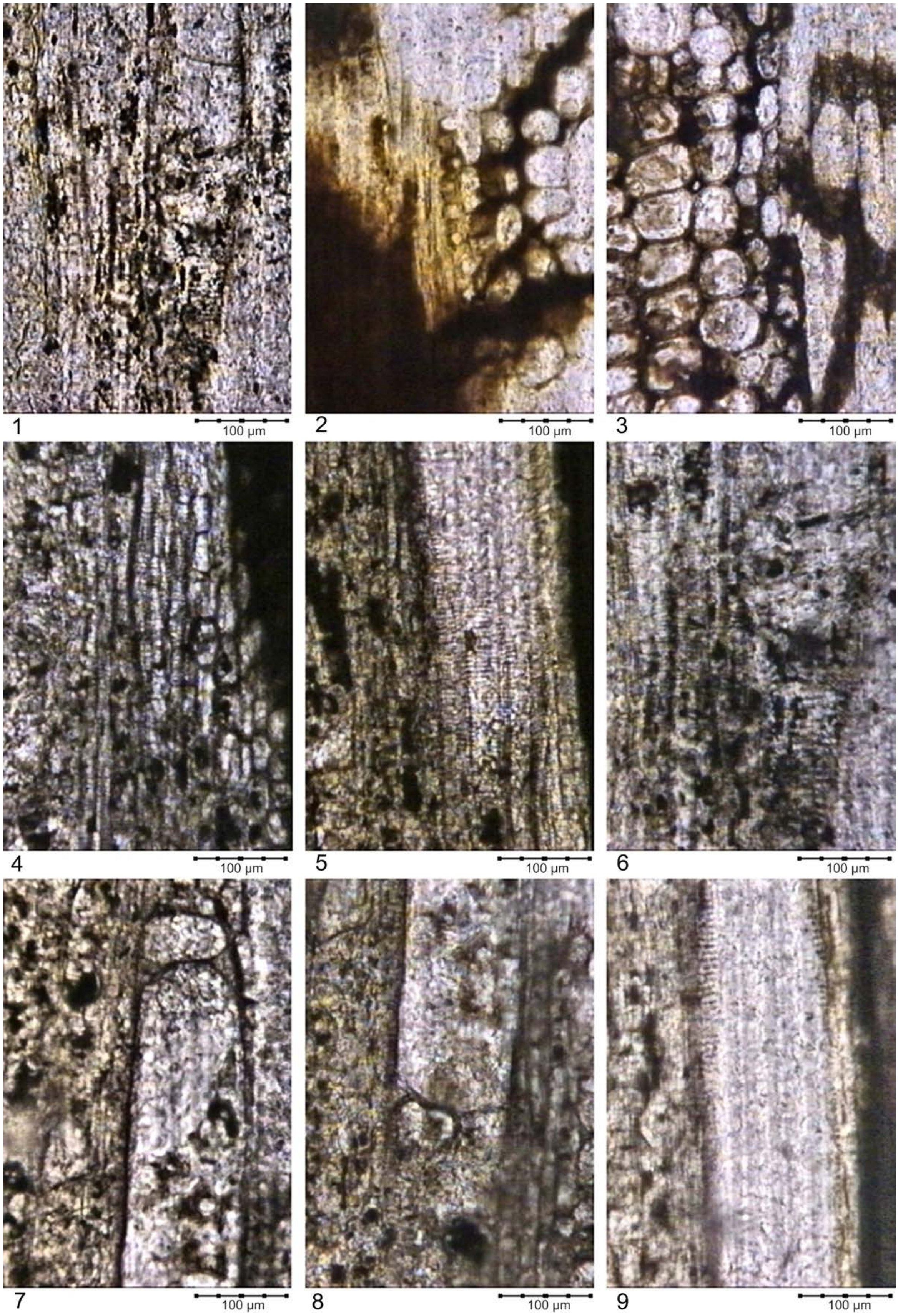

Plate 20. **1–9**. *Palmoxylon phoenicoides* Hofmann 1944 (specimen L1). **1–3**. Longitudinal sections: poorly preserved vessels with helical thickenings and tyloses, rows of stegmata on fibrous bundles (2), parenchyma as ground tissue (2, 3). **4–9**. Longitudinal sections: vessels with poorly preserved scalariform pitting and scalariform perforation with thick bars (7)

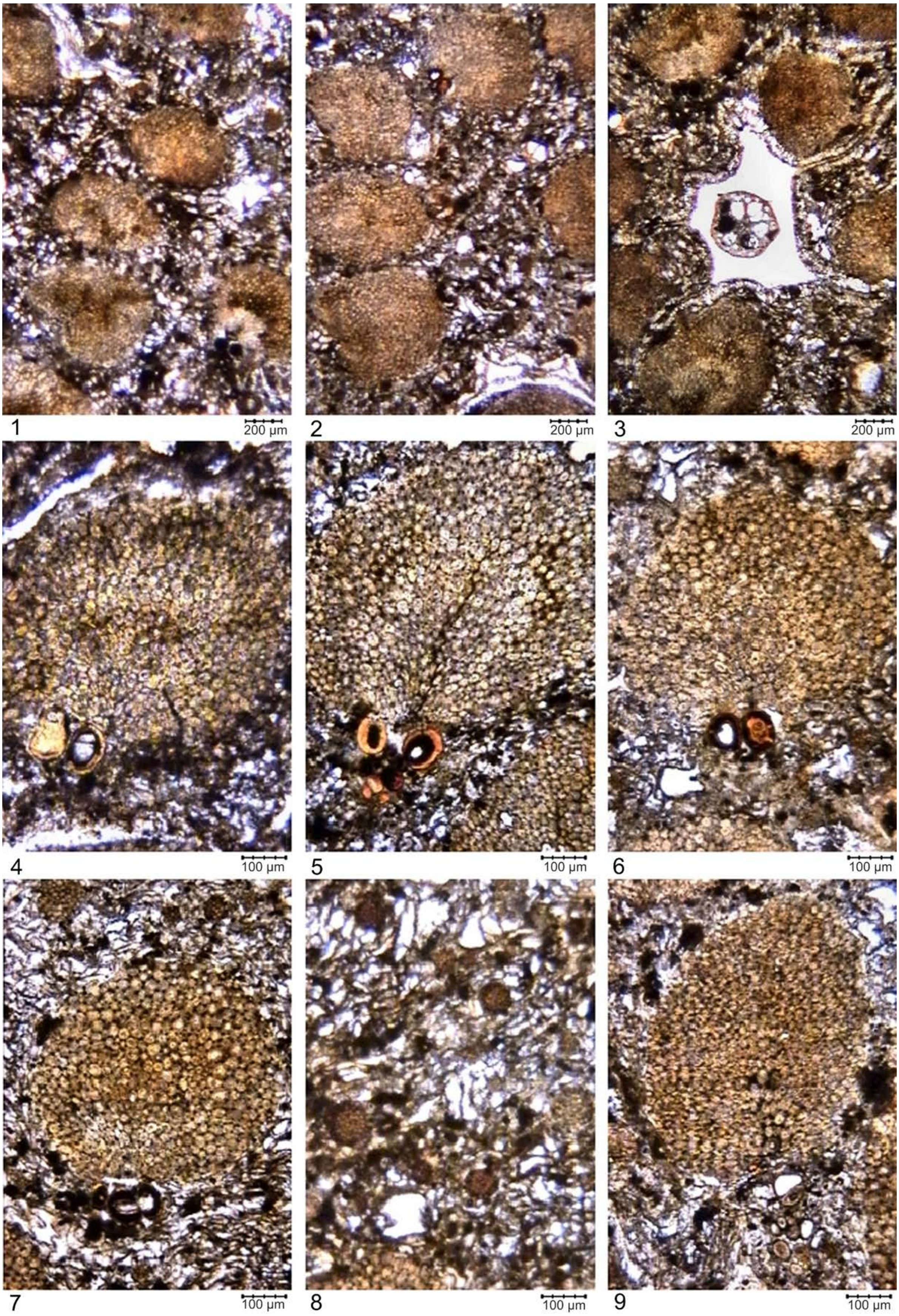

Plate 21. **1–9**. *Palmoxylon phoenicoides* Hofmann 1944 (specimen 368). **1–3**. Cross sections: outer part of central zone with fibrovascular bundles having sclerenchyma caps of reniform aspect, and ground tissue and small fibrous bundles; small cross-sectioned rootlet structure in (3). **4–7**, **9**. Cross sections: fibrovascular bundles with 2–4 large metaxylem vessels, small round protoxylem vessels, tabular and radial parenchyma within central zone. **8**. Cross section: interfascicular parenchyma within central zone, and fibrous bundles

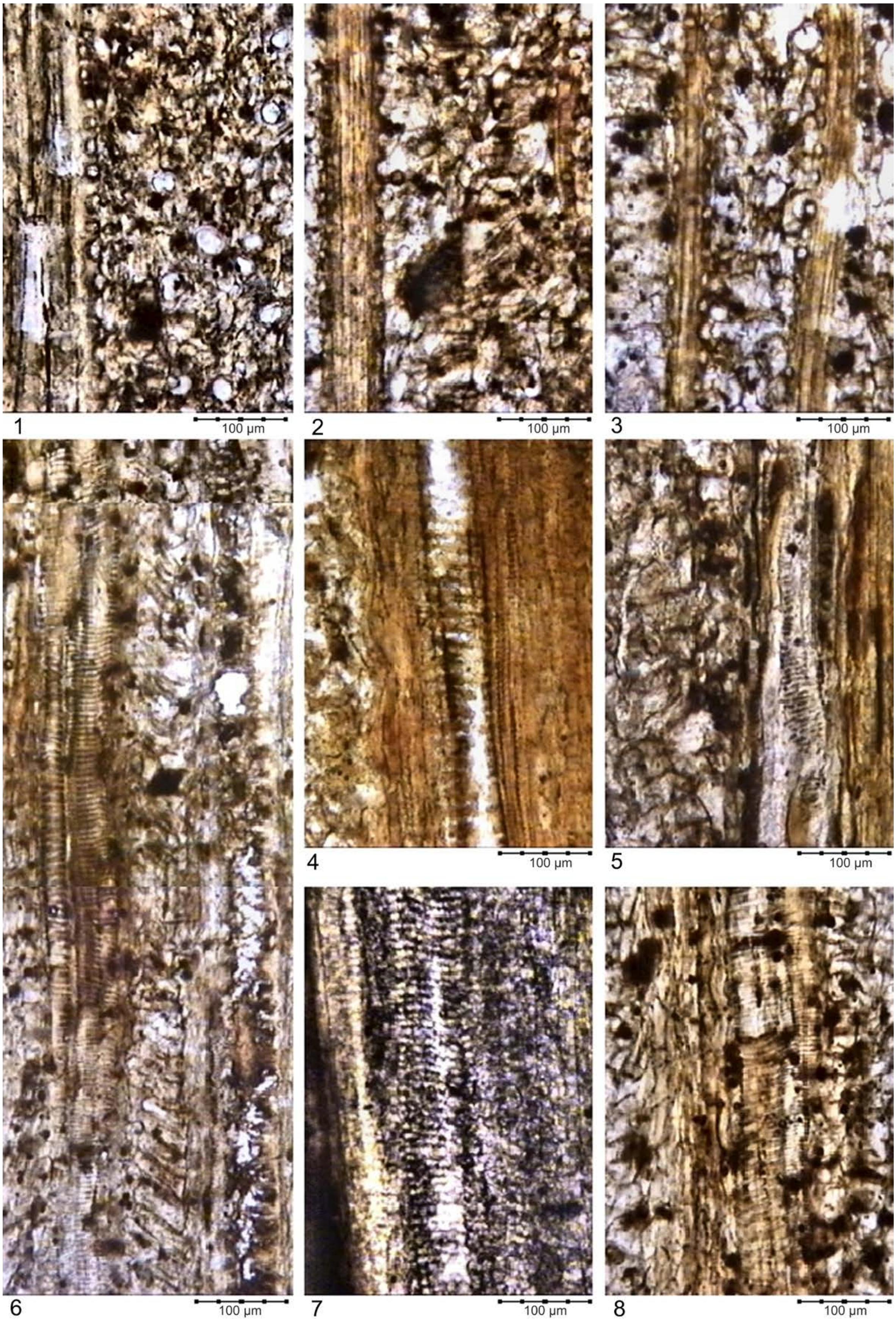

Plate 22. **1–8**. *Palmoxylon phoenicoides* Hofmann 1944 (specimen 368). **1–3**. Longitudinal sections: long rows of stegmata on fibrous bundles, ground tissue of parenchyma cells. **4–8**. Longitudinal sections: vessels with helical thickenings (4, 6, 8), with poorly preserved scalariform pitting (5, 7)

parenchyma consists of relatively thin-walled parenchyma cells, elongated in cross section, arranged between the fibrovascular bundles as false radial parenchyma, because 1–2 rows of tabular parenchyma can be seen close to the sclerenchyma caps. Around the vascular part, radial parenchyma is present. The intervascular parenchyma cells sometimes have dark brown content. Fibrous bundles are not frequent and are very similar to the cortical bundles.

The subdermal zone is better expressed in cross section in samples 368, 371, 459, 519, L504, L508, L521 and L528, and consists of 3–4 rows of round to oval fibrovascular bundles, relatively more closely arranged, with large sclerenchyma caps of reniform aspect oriented toward the exterior, and with the vascular zone usually crushed and oriented toward the axial part of the central cylinder. Bundle size varies, with r/tg.d. of 400–875/450–800 µm, phloematic (anterior) sclerenchyma cap r/tg.d. of 400–750/450–800 µm, and f/v ratio of 0.9/1–5/1. Bundle density in this zone is 134–175/cm^2. Just beneath the sclerenchyma cap, 1–2 islands of phloem occur as undivided and divided phloem. The metaxylem is represented by 2–3 oval vessels with r/tg.d. of 60–230/50–200 µm. The protoxylem and intrafascicular parenchyma are crushed and difficult to observe. The interfascicular parenchyma is formed of polygonal, rounded and usually elongated cells, quasi-radially arranged relative to the fascicles, but close to the sclerenchyma caps of the fibrovascular bundles are 1–2 rows of parenchyma cells of typical tabular type; around the vascular part only radial parenchyma is present. The fibrous bundles are 50–100 µm in diameter, are rather frequent, and are surrounded by radial parenchyma cells.

The central zone of the central cylinder was seen in most of the studied specimens (371, 372, 378, 459, 495, 496, 498, 500, L504, 519, L521, L522, L528, 530, 531, 532). In cross section, closer to the subdermal zone there are round to elongated fibrovascular bundles, and rounded or slightly deformed bundles appear in the axial zone, dispersed in the ground tissue. All the fibrovascular bundles are large and of reniform aspect. The constituent fibers of the sclerenchyma cap are small and polygonal in cross section, with thickened walls and small circular to elliptic or point-like lumina. Fibrovascular bundle size varies, with r/tg.d. of 600–950/550–800 µm, phloematic sclerenchyma cap r/tg.d. of 300–600/550–800 µm, and f/v ratio of 0.9/1–3.4/1. Bundle density within this zone is 34–71/cm^2, toward the margins slightly more. The phloem is arranged in 1–2 distinct islands hosted by the median sinus just under the sclerenchyma cap as divided and undivided phloem. In the vascular part, the metaxylem is represented by 2 large round vessels 50–100 µm in diameter. In young stems or foliar bundles, 1–3(5) smaller metaxylem vessels appear. In longitudinal view, the metaxylem vessels are spaced-apart, have thin or thick walls, helical or annular thickenings, sometimes in the same specimen. Also, scalariform pitting is present and the perforations are of scalariform type, on tilted plates, with spaced-apart, thick or thin bars, fragmentarily preserved and difficult to count. Sometimes numerous large tyloses appear inside the vessels (in specimens L508, 531), and often traces of fungal attack are seen. The protoxylem, when it can be observed, is represented by up to 10 small circular vessels 25–50 µm in diameter, which in longitudinal view show spaced apart and annular or helical thickenings. The intrafascicular parenchyma is represented by polygonal or rounded cells 10–20 µm in diameter, often having thickened walls and filling the space between the vessels. The marginal parenchyma cells are slightly sclerified. The interfascicular parenchyma is represented by large, thin-walled, elongate cells 20/150 µm in diameter, usually in a radial arrangement around the fibrous bundles; around the sclerenchyma caps of the fibrovascular bundles, however, the intervascular parenchyma is arranged as false radial parenchyma, since close to the sclerenchyma caps there are 1–2 rows of parenchyma cells of tabular type. Sometimes there is dark brown content inside the parenchyma cells. The fibrous bundles vary in size in cross section, with diameter between 50 and 150 µm and formed of 18–20 small fibers. In longitudinal view, on the fibers of the fibrous bundles but on the fibrous part the fibrovascular bundles also, spherical stegmata appear. They are slightly rugose (i.e. with small knots) and are partially sunken in the basal wall of the silica cell in long rows (see in Plate 18). Even in cross section they appear as crowns of stegmata around the fibrous bundles.

Affinities and discussion. We selected 26 samples of Cenozoic petrified palm stem remains showing rather uniform anatomical structure, which fit the description and illustration of the extant palm *Phoenix* L. as figured by Tomlinson (1961: pl. 1, fig. D, 1990), Schweingruber (1990) and Thomas & De Franceschi (2013).

Only two palms are known to be native to and extant in Greece: *Chamaerops humilis* L. and *Phoenix theophrasti* Greuter (see also Georgi et al. 2005). However, the Cenozoic history of palm evolution in Greece includes other palm types, some of them first described here as petrified wood remains. We compared the anatomical structure of our specimens with that of other already described fossil palm remains, some of them having more or less similar structure.

The forms described by Schenk (in Zittel 1883), Berry (1924), Chiarrugi (1933), Prakash (1962), Grambast (1962, 1964), Rao & Menon (1964), Menon (1965), Kramer (1974), Privé-Gill & Pelletier (1981), Gottwald (1992), Kahlert et al. (2005), Iamandei & Iamandei (2006) and Iamandei et al. (2018) must be excluded from the comparison because they either have another specified extant corresponding taxon or they show a very different type of structure. For example, *Palmoxylon lacunosum* (Unger) Felix of Berry (1924), *P. benadirense* of Chiarrugi (1933), *P. eocenum* of Prakash (1962) and *P. bautschii* of Kahlert et al. (2005) are of Reniformia type (*sensu* Stenzel 1904) or almost so, and have more or less lacunar ground tissue, but there is no clear affiliation to possible extant forms, so it is difficult to say whether they are similar to the studied material.

Greguss (1954, 1959, 1969) described some fossil "sabaloid" palms from Hungary as *Palmoxylon sabal*?, *P. sabaloides*, *P. hungaricum*, *P. lacunosum* var. *axonense* Watelet and *P. dorogense*, the last especially suspected to have phoenicoid affinities. The same can be said for *P. gignacense* of Grambast (1957) or the forms of *Palmoxylon* sp. described by Kramer (1974), which all seem to be of Reniformia type (*sensu* Stenzel 1904). More recently, a new species, *P. lametaei* described by Dutta et al. (2011) from Late Cretaceous deposits of India, has anatomical features very similar to modern species of *Phoenix* L. and is also similar to our described specimens. Prasad et al. (2013) described Early Eocene material from India as *P. vastanensis* (correctly: *vastanense*), also characterized by a reniform aspect of sclerenchyma cap and highly lacunar ground tissue, yet having affinities to the extant *Areca catechu* L.

Our specimens have rounded sclerenchyma caps of fibrovascular bundles of Reniformia type (*sensu* Stenzel 1904), ground parenchyma of radial and tabular types, scalariform perforations and long rows of spherical, slightly rugose stegmata partially sunken in the basal wall of the silica cell, details that match the species described by Hofmann (1944) from Prambachkirchen, Germany, as *P. phoenicoides*, perfectlly corresponding to the extant genus *Phoenix* L. Based on the almost complete identity of the anatomical features of our studied specimens with those of *P. phoenicoides* Hofmann and of extant *Phoenix* L., and on the above discussion, we assign all 26 specimens described and partially figured here to *Palmoxylon phoenicoides* Hofmann 1944.

Genus ***Rhizopalmoxylon***
(Felix)Gothan 1942

Rhizopalmoxylon daemonoropsoides
Iamandei et Iamandei, sp. nov.

Pl. 23, figs 1–8; Pl. 24, figs 1–9

Material. The studied material (sample 499) comes from Lesbos, from volcano-sedimentary deposits of late Early Miocene age. It represents the basal part of a palm stem. The rhizotil is present and rootlet structure can be studied. The sample is housed under the above field number in the collection of Athens University (NKUA), Faculty of Geology and Geoenvironment.

Description. It is very difficult to cut well-oriented sections in this special region of the stem, the rhizotil, which is full of rootlets in diverse positions and usually with soil remains. Mucilaginous material that includes fungi and bacteria is observed among the rootlets. Those microorganisms are interpreted as helping the plant to extract water from the soil and to retain moisture in the radicular region. We observed thin sections of some well cross-cut rootlets which present typical stelar structure.

The outer cortex is represented by a thick layer of up to 13 suberized cells (peridermis) in which it is difficult to separate the poorly preserved rhizodermis.

The middle cortex is well developed, and formed of thick-walled, polygonal, rounded to oval parenchyma cells of various sizes and mixed. Enlarged mucilaginous cells sometimes appear singly or in small groups. Air lacunae are absent. The inner part of the middle cortex has thickened-walled cells in a more regular arrangement around the central cylinder. The endodermis, that is, the inner layer of cells of the cortex (i.e. rootlet bark) is represented by a single row of elongated thickened-walled cells.

The central cylinder of a rootlet has, in cross section, 13–19 thick-walled metaxylem vessels which are round to oval, tylosed, and arranged in a circle at the marginal zone of the stele. At the top of the metaxylem vessels are islands of 1–8 small protoxylem vessels, alternating with small islands of phloem. In longitudinal view the vessels present spaced-apart annular and helical thickenings, scalariform pitting and scalariform perforated plates, slightly inclined and with thin bars and also frequent tyloses. All of them appear in ground tissue which in the axial part of the stele forms the parenchymatous pith. Toward the exterior this tissue has smaller and slightly thicker-walled cells. Toward the center they are larger, round or oval and thin-walled, and often delineating intercellular spaces. These cells sometimes have dark tanninous content.

Affinities and discussion. The root structure of monocotyledons is very specific to them. The palms have a radicular system grouped in a so-called "rhizotil" (Cook 1941, in Tomlinson 1961, 1990), that is, a special "pillow" of numerous adventitious rootlets. The structure of a rootlet (see Fig. 3) comprises the exodermis, cortex, the central cylinder which is marked by the endodermis, and inside it, the ground parenchyma, with the vascular elements (metaxylem vessels, sieve tubes) and cell inclusions (stegmata, tannin, mucilage or crystals) (Tomlinson 1961: pl. 1, fig. D), details which appear in our fossil material also. However, few anatomical features of taxonomical value are present in the studied fossil root structure. We attempted to find them and to compare our material with an extant corresponding taxon.

We compared the studied structure with corresponding images of palm rootlets from extant flora, in terms of the obvious presence of mucilaginous cells in the cortex and the distribution of vessels in the stele. On this basis we observed similarities in the structural details of our specimen, most probably corresponding to the genus *Daemonorops* Blume ex Schult.f., rattan palms from the Calamoideae subfamily (see Fig. 4, from Tomlinson 1961).

For this type of fossil structure a fossil organ-genus, *Rhizopalmoxylon*, was created by Felix (1883), but this taxon comprising a general radicular structure had neither a description nor a diagnosis, so it became an invalid name (*nomen nudum*). It was Gothan (1942) who gave a correct diagnosis for this taxon, naming a new type species (*Rhizopalmoxylon glaseli* Gothan) from Cenozoic coals of Böhlen, Sachsen, Germany.

For comparison with other fossil forms of *Rhizopalmoxylon* already described and published, we reviewed most of them: *R. indicum* of Sahni (1938), *R. glaseli* and *R. bohlenianum* of Gothan (1942), *Rhizopalmoxylon* sp. of Grambast (1962), *R. pilosum* of Van der Burgh & Meulenkamp (1966), *R. libycum* of Koeniguer (1970), *R. behuninii*, *R. blackii* and *R. scottii* described by Tidwell et al. (1972), *R. sundaram* of Mahabale & Rao (1973), *R. borassoides* of Awasthi et al. (1996), *R. macrorhizon* (related to *Palmoxylon macrorhizon* Stenzel 1904) described by Bonde et al. (2008), *Rhizopalmoxylon angiorhizon* (related to *Palmoxylon angiorhizon* Stenzel, 1904) and *Rhizopalmoxylon singulare* described also by Bonde et al. (2009), but our studied specimen has special anatomy; the comparison with these forms was inconclusive. We could add the forms *Rhizopalmoxylon huepaciense* and *R. teguachachiense* described by Cevallos Ferriz & Ricalde-Moreno (1995) and interpreted as palm rhizomes, but this is

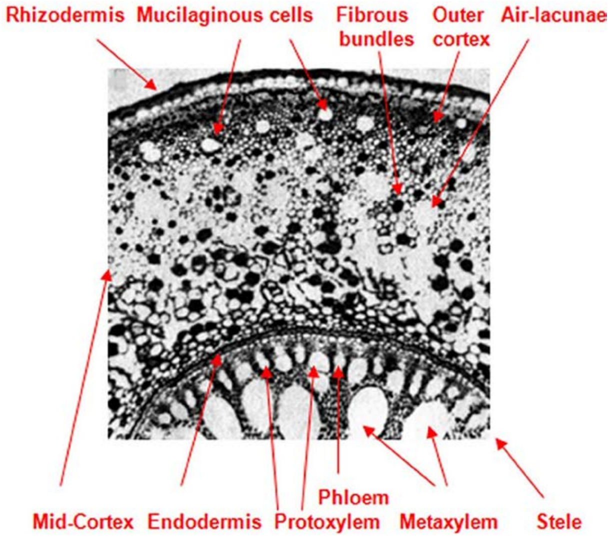

Fig. 4. A type of extant *Daemonorops* root structure (from Tomlinson 1961, slightly modified)

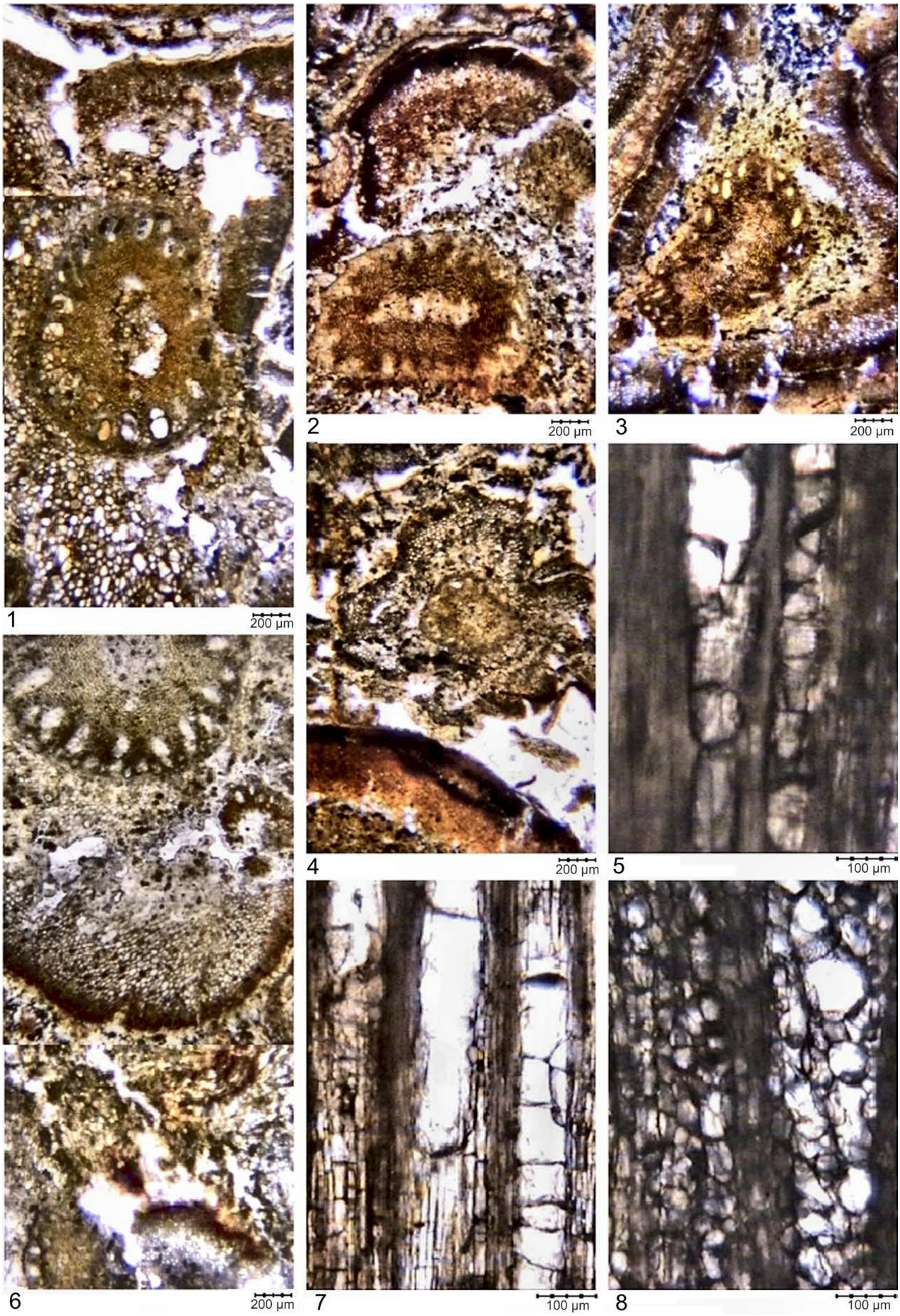

Plate 23. **1–8**. *Rhizopalmoxylon daemonoropsoides* Iamandei et Iamandei, sp. nov. (specimen 499). **1–4**, **6**. Cross sections: detailed rootlet structure, cortex, stele with crown of metaxylem vessels and pith. **5**, **7**, **8**. Longitudinal sections: vessels with scalariform pitting, poorly preserved annular thickenings and large tyloses (8)

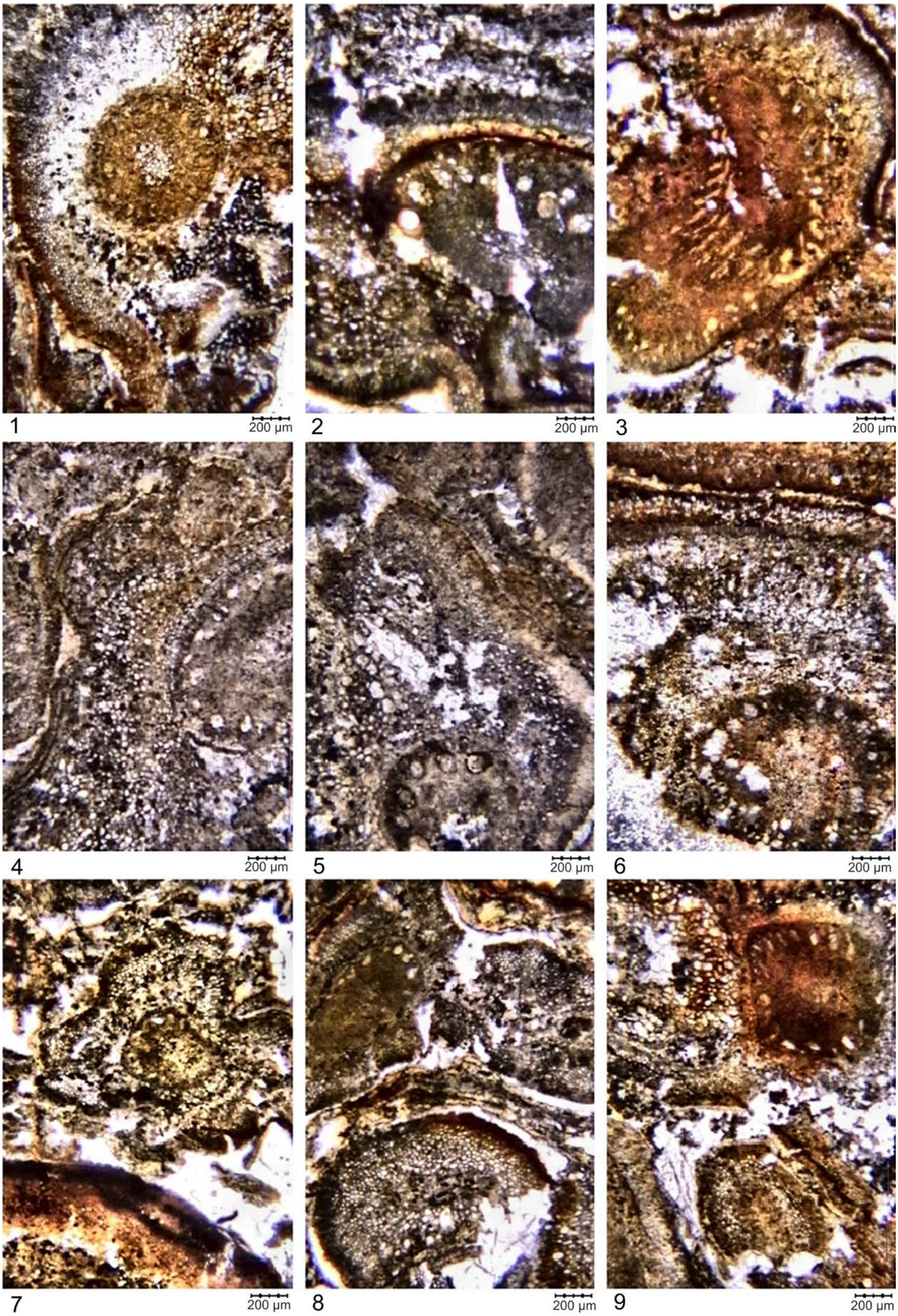

Plate 24. **1–9**. *Rhizopalmoxylon daemonoropsoides* Iamandei et Iamandei, sp. nov. (specimen 499). **1–9**. Cross sections: rootlets transversally sectioned or almost so, showing cortex with regular parenchymal cells and stele with metaxylem vessels arranged in a circle and with parenchymatous pith

another plant part. More recently, a new species from India was described by Kathal et al. (2017) as *R. nipoides*, which clearly corresponds to the extant *Nypa* Steck., a mangrove palm. Similarly, *Rhizopalmoxylon* sp. aff. *sabaloides* described by Iamandei & Iamandei (2017) corresponds to the extant *Sabal* L. Also, a form described below in this paper, identified as *R. phoenicoides* sp. nov., definitely differs from our specimen.

It is very difficult to find a corresponding taxon among the already described forms and also among the extant types, since almost all the palms have very similar root structure. Taking into account the great similarity of our specimen, found in the same region where a lot of fossil palm remains have been identified, it is possible that our root structure belongs to one of the already described palms there. We did note its great resemblance to *Daemonorops* type (Fig. 4), whose structure type is presented in Tomlinson (1961: pl. 1, fig. D).

From the above discussion of the possible affinities of our specimen with other types of root structures of extant palms and with other already described fossil forms, we conclude that the root structure is highly similar to that of extant *Daemonorops*, so we assign it to *Rhizopalmoxylon daemonoropsoides* Iamandei et Iamandei, sp. nov. and designate specimen 499 as holotype for this species.

Diagnosis. The rootlets present a stelar structure: outer cortex thick, consisting of ~13 suberized cells, including exodermis; middle cortex of thickened parenchyma cells, without air lacunae; inner cortex more compact, includes endodermis. In stele, circular arrangement of 13–19 round, thick-walled metaxylem vessels. In longitudinal view, metaxylem vessels have annular and helical thickenings, scalariform pitting and scalariform perforations with thin bars. In cross section, toward the exterior, alternating small islands of protoxylem and phloem are arranged in a circle. In the central part, parenchymatous pith is present.

Rhizopalmoxylon phoenicoides
Iamandei et Iamandei, sp. nov.

Pl. 25, figs 1–8; Pl. 26, figs 1–9

Material. In many of the samples studied here, structures of adventitious rootlets appear, with phoenicoid structure in the basal portion of the palm stem (e.g. in L1, 368, 459, 531), but typical root structures appear in some samples (especially 378 and 534 collected from Lesbos, and 492 and 494 collected from Lemnos) found in Early Miocene volcano-sedimentary deposits. They were selected for their similarity of anatomical features, and are housed in the collection of Athens University (NKUA), Faculty of Geology and Geoenvironment, under the above numbers.

Description. In thin sections of these specified samples there frequently appear rootlets showing the primary structure of the stele. We often observed adventitious rootlets inside the stem attempting to push outward, very much disturbing the cortical tissue of the palm stem, as in specimen 531. Here we describe microscopic observations of typical anatomical details of these palm root structures, focusing on cross sections. The exodermis, the protective external layer of the rootlets (also called the rhizodermis), is usually not preserved in the studied material.

The cortex is parenchymatous and has three relatively distinct parts. The outer cortex (i.e. bark) consists of up to 5–6 rows of suberized parenchyma cells. The middle cortex (bark) is usually well developed and consists of rounded–polygonal to oval parenchyma cells which are thick-walled, various in size and shape, and mixed. Often the cells are partially destroyed by lysis, creating polygonal air lacunae which are radially elongated and of a very specific shape (see Fig. 5). Enlarged mucilaginous cells, as pockets and small ducts,

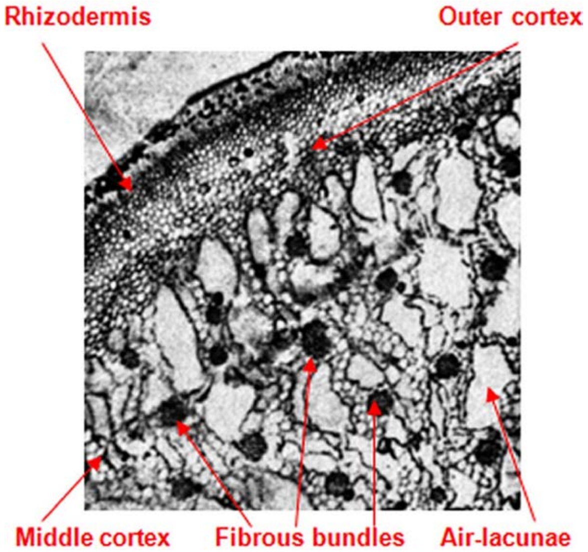

Fig. 5. A type of extant *Phoenix* cortical root structure (from Tomlinson 1961, slightly modified)

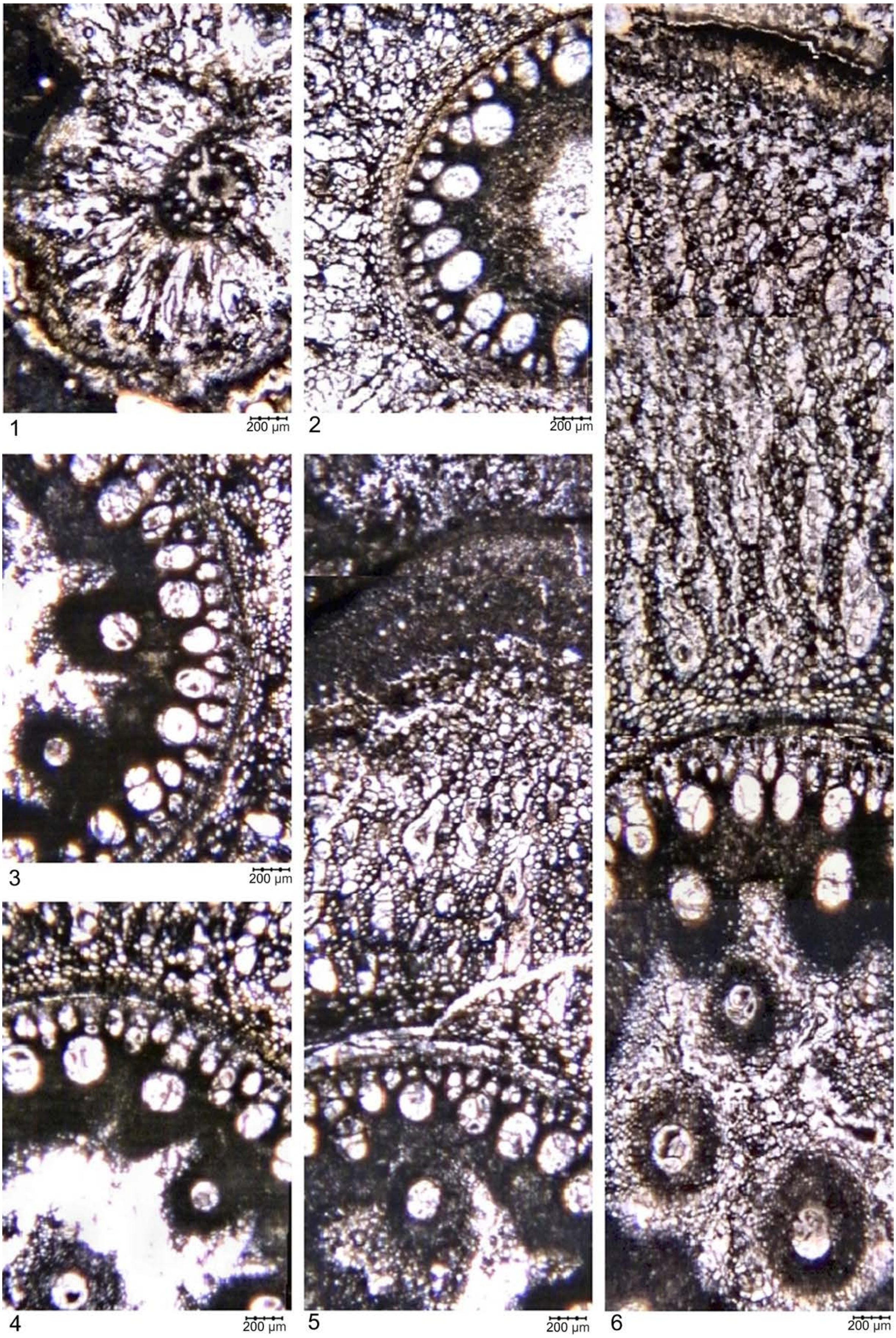

Plate 25. **1–6**. *Rhizopalmoxylon phoenicoides* Iamandei et Iamandei, sp. nov. (specimen 494, holotype). **1–6**. Cross sections: detailed rootlet structure, cortex with typical parechymatous structures in middle part, with polygonal, radially elongated air lacunae (5, 6), mucilaginous pockets or ducts, and stele with the xylematous crown having small alternate islands of protoxylem and phloem on top, and also with thick-walled metaxylem vessels inside parenchymatous pith (2–6)

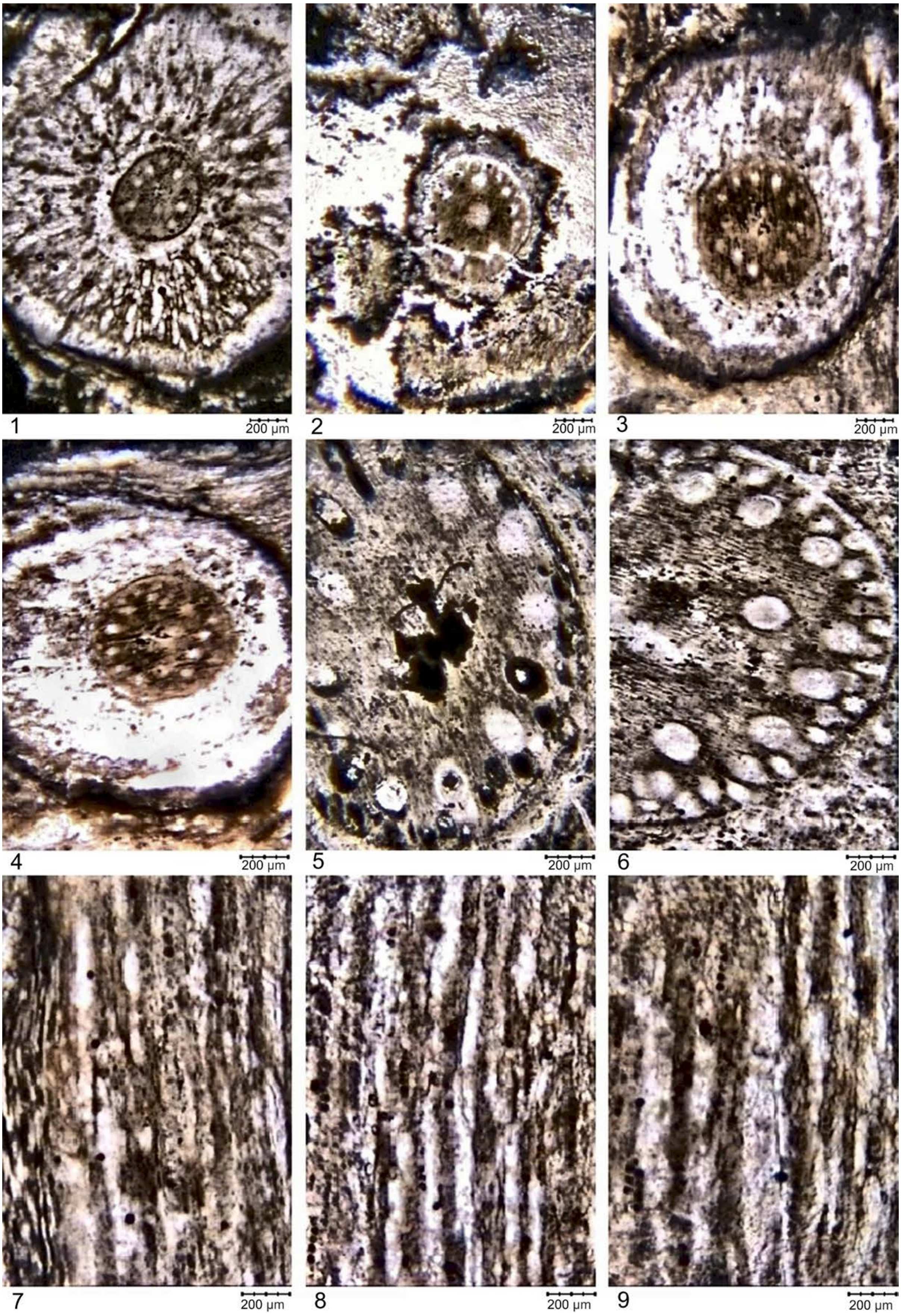

Plate 26. **1–9**. *Rhizopalmoxylon phoenicoides* Iamandei et Iamandei, sp. nov. (specimen 492). **1–6**. Cross sections: detailed rootlet structure, cortex with typical parechymatous structures with air lacunae (1), often poorly preserved (2–4), stele with xylematous crown, and thick-walled metaxylem vessels inside parenchymatous pith. **7–9**. Longitudinal sections: poorly preserved metaxylem vessels with simple perforations, sometimes with granular content

are sometimes present singly or in small groups, also observed in longitudinal sections. The inner part of the middle cortex and inner cortex are formed of more regularly arranged thick-walled cells around the central cylinder (sample 494). In younger rootlets (sample 368) the endodermis, the last layer of cells of the rootlet bark (cortex) which outlines the stele, horseshoe-shaped Caspary thickenings can be seen in the constituent cells. This row of endodermal cells seems to be interrupted by "passaging cells" located just in front of the vascular islands of the central cylinder.

The stele (i.e. central cylinder) has up to 7 or more thick-walled, round to oval, large metaxylem vessels arranged on a circle in its marginal zone. Toward the exterior, islands of small protoxylematic vessels alternating with phloem islands appear. Longitudinally, the xylem vessels in some thicker rootlets sometimes present tyloses (sample 492). In longitudinal view, poorly preserved annular and helical thickenings and poorly preserved simple perforations sometimes can be seen on the vessels. The ground parenchyma has two aspects: toward the exterior it surrounds the vessels as small thick-walled polygonal cells with point-like lumina; and toward the center, where it forms the pith, it shows large, thin-walled, round or oval cells and intercellular spaces. Thick-walled metaxylematic vessels often appear in the pith, irregularly arranged.

Affinities and discussion. Many specimens identified as *Palmoxylon phoenicoides* in this paper also contain this type of rootlet structure (e.g. L1), but samples 378, 492, 494 and 534 strictly represent the rhizotil (*sensu* Cook 1941, in Tomlinson 1961, 1990) formed only from rootlets, described here.

In transversal section, rootlets of the extant genus *Phoenix* L. show very specific features: polygonal, radially elongated air lacunae, mucilaginous pockets and ducts in the middle cortex (see Fig. 5). Also the disposition and aspect of the vascular part inside the stele are very specific (Tomlinson 1961, 1990). These few anatomical features have a great taxonomical value, and they were observed in our specimens, suggesting their identification with a phoenicoid rootlet type of structure.

We compared our specimens with previously described fossil forms. *Rhizopalmoxylon* described by Felix (1883), Sahni (1938), Gothan (1942), Grambast (1962), van der Burgh & Meulenkamp (1966), Koeniguer (1970), Tidwell et al. (1972), Cevallos Ferriz & Ricalde-Moreno (1995), Mahabale & Rao (1973), Awasthi et al. (1996), Bonde et al. (2008, 2009) Kathal et al. (2017) and Iamandei & Iamandei (2017) clearly differ anatomically from our material and are referred to other palm types.

After this comparison and a consideration of the affinities and even obvious similarities of the studied material with the transversal structure of rootlets of the extant genus *Phoenix* L. as presented by Tomlinson (1961, 1990), especially regarding the aspect of the cortex, in which very specific polygonal and radially elongated air lacunae appear, as well as frequent mucilaginous pockets and ducts, we assign these studied specimens to *Rhizopalmoxylon phoenicoides* Iamandei et Iamandei, sp. nov. We designate specimen 494 as holotype, and specimen 492 as paratype.

Diagnosis. Outer cortex consists of ~5–6 large suberized cells, including exodermis, which usually is destroyed. Middle cortex built of thickened parenchyma cells with a very specific polygonal, radially elongated air lacunae, and with frequent mucilaginous pockets and ducts. Inner cortex more compact, includes endodermis, where passage cells with visible Caspary thickenings appear. Stele has up to 7 (or more) round thick-walled metaxylem vessels and, toward the exterior at their top, small alternate islands of protoxylem and phloem appear. Metaxylem vessels have simple perforations and annular and helical thickenings. Ground tissue surrounds the vessels as smaller thick-walled polygonal parenchyma cells with point-like lumina. Central part occupied by parenchymatous pith, with larger, thin-walled, round to oval cells, with intercellular spaces. Thick-walled metaxylem vessels also appear in the pith, irregularly arranged.

Genus ***Palmocaulon***
(Desphande) Menon 1964

Palmocaulon sp. aff. *Phoenix* sp.

Pl. 27, figs 1–9

Material. A petrified sample (field number 493) collected from Early Miocene deposits of Lesvos presents interesting structure even under the magnifying glass: it combines small

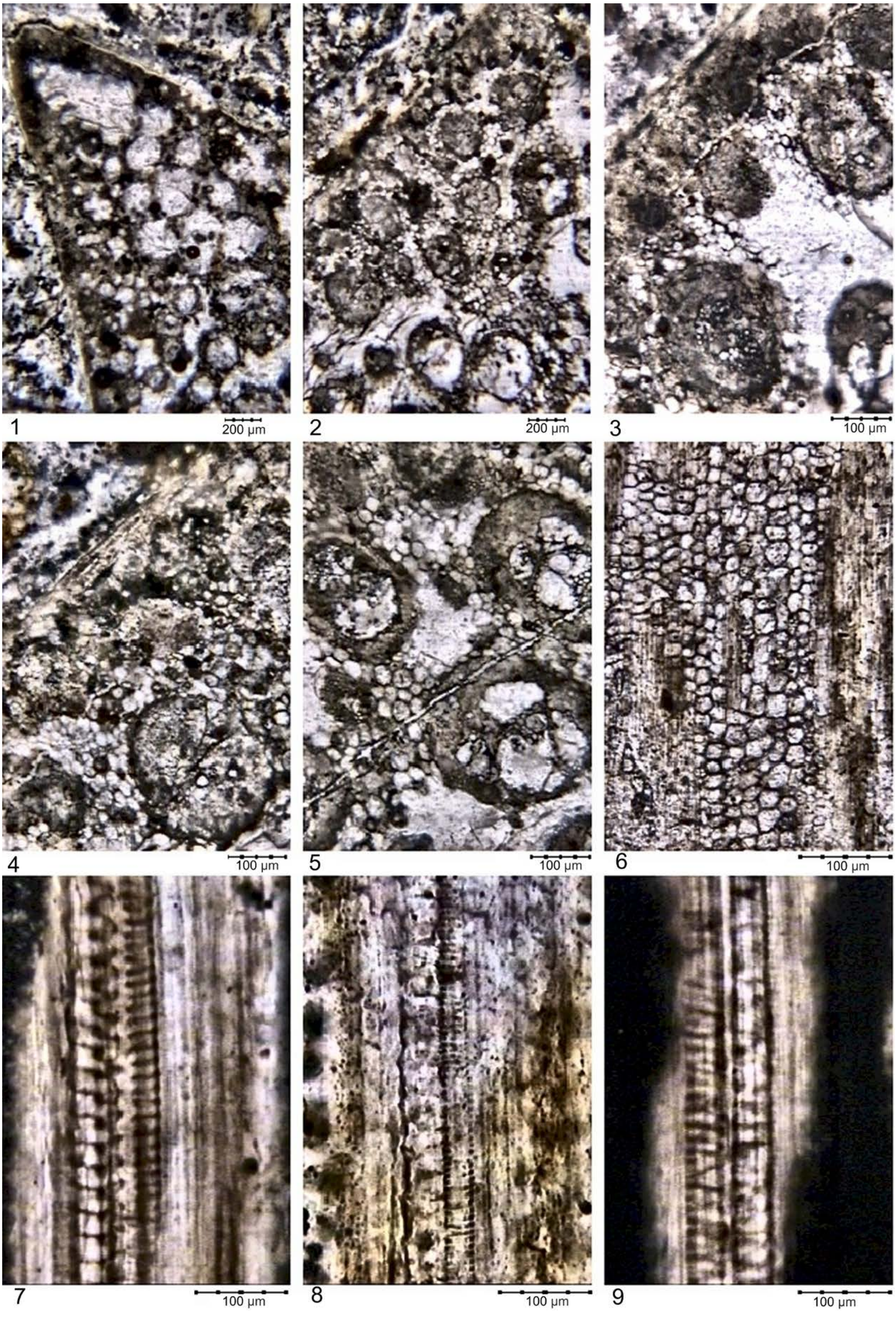

Plate 27. **1–9**. *Palmocaulon* sp. (aff. *Phoenix* sp.), (specimen 493). **1–5**. Cross sections: epidermis, hypodermis (1, 3, 4), fibrovascular and fibrous bundles, ground tissue. **6–9**. Longitudinal sections: ground tissue (6), metaxylem vessels with helical and annular thickenings (7–9)

wood fragments or leaves of dicots, soil particles, and a petrified fragment with a palm structure that is not from a thin young stem or rootlet but rather from a rachis of a pinnate palm leaf (feather-like leaf). The other plant remains are unidentifiable for the moment, so we studied only the palm remains. The sample is kept in the collection of Athens University (NKUA), Faculty of Geology and Geoenvironment, under the above number.

Description. The epidermis of the "ventral surface" apears in a small portion of the transversal section and consists of a single row of very thick-walled elongated cells, with scattered remains of papillae.

The hypodermis is represented by the next three rows of cells, which are slightly elongate, thick-walled, and have larger lumina. Small fibrous bundles arranged in a row and rare small fibrovascular bundles with a single round metaxylem vessel in the middle are present in this zone.

The central zone in cross section starts with a zone of larger, moderately thick-walled parenchyma cells, with fibrovascular bundles presenting large sclerenchyma caps, usually surrounding a single large round metaxylem vessel. No protoxylem or phloem vessels were observed; probably they were lost due to poor preservation. These fibrovascular bundles are congested, arranged in at least two circular rows toward the outer part of the central cylinder, becoming more enlarged toward the inner part; usually they are poorly preserved. Toward the central part of the rachis, fibrovascular bundles appear more spaced apart arranged, and have a sclerenchyma cap of Lunaria type, sometimes slightly varying in outline. Just beneath it, the phloem appears as two distinct islands (divided phloem). The metaxylem is represented by 1–4 large vessels with r/tg.d. of 40–75/50–100 μm, and the protoxylem is formed by 2–8 smaller circular vessels. In longitudinal view, spaced-apart annular thickenings or closely spaced helical thickenings can be seen on the vessels, and a few remains of scalariform pitting and scalariform perforations, with up to six spaced-apart thin bars, usually poorly preserved. The intravascular parenchyma is formed by rounded polygonal cells with slightly thickened walls. Sometimes a smaller ventral fibrous cap is present, formed by marginal, sclerified parenchyma cells. The interfascicular parenchyma consists of round to oval parenchyma cells sometimes containing starch grains.

Affinities and discussion. This studied fascicular structure no doubt represents a fragment of a petiole or rachis of a pinnate (feather-like) palm leaf, found in the studied sample among diverse wood remains and leaves from litter which had fallen on the ground and become petrified, together with soil particles. Such a fossil organ genus of palm was first created by Desphande (in his unpublished doctoral thesis at the University of Poona, India, in 1960) as a new genus with a single species, *Palmocaulon mohgaonse*, described by him from the Deccan Intertrappean beds of India.

Since there was a problem of validity, Menon (1964) validated this genus, describing a new species of *Palmocaulon*: *P. raoi* Menon, giving a more complete description for the new type species of this genus, considered later as a revision of the genus diagnosis even though the author gave no specification in this direction. Later, Boureau & Prakash (1969) described a petrified palm petiole from Senegal as *Palmocaulon monodii*, and Lakhanpal (1970) presented a synthesis of the Tertiary flora of India with many described species of the organ genera *Palmoxylon*, *Palmocarpon*, *Palmocaulon* and *Palmophyllum*. Also, Kulkarni & Patil (1977) described *Palmocaulon costapalmatum*, a petrified palm leaf axis,

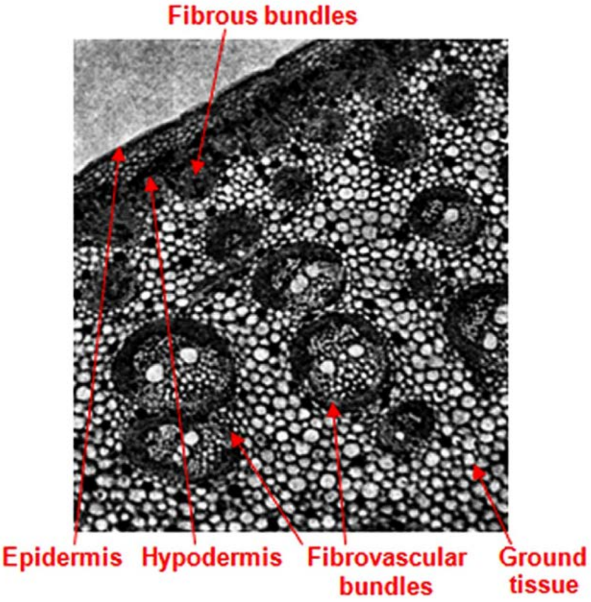

Fig. 6. A type of petiole structure in extant *Nannorrhops* H.Wendl. (from Tomlinson 1961, with modifications)

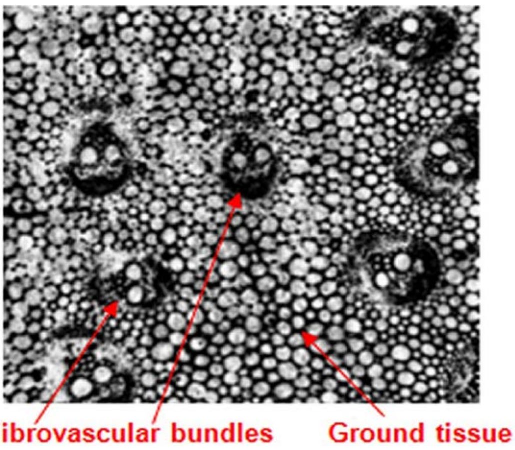

Fig. 7. A type of petiole structure in *Phoenix* L. (from Tomlinson 1961, with modifications)

and *P. hyphaeneoides*, a petrified palm petiole, from India (Shete & Kulkarni 1980).

Another petrified palm petiole was described by Filigheddu et al. (1996) from the early Miocene of Sardinia, Italy, as *Palmocaulon logudorense*, most probably of *Chamaerops* type. Other new genera for almost the same plant part have been described, including *Sabalocaulon* by Trivedi & Verma (1981) and *Parapalmocaulon* by Bonde (1987) as leaf petioles, and also *Phoenicicaulon* by Bonde et al. (2000) as a sheath leaf base. Harley (2006), however, ignored the genus *Palmocaulon* (Desphande) Menon in a summary of previously recorded fossil generic taxa of Arecaceae.

In our studied specimen we noted some details that allowed us to place it in the genus *Palmocaulon* (see Figs 6, 7 for comparison), specifying its possible affinities with the same plant part (petiole or rachis) of the extant genus *Phoenix* L. (Tomlinson 1961: pl. 6, figs D, E, 1990, Thomas 2013). However, taking into account the poor preservation of our specimen, we do not have sufficient structural details to describe a new species or to identify it with an already described one, so our studied specimen remains identified only as *Palmocaulon* sp. aff. *Phoenix* sp.

CONCLUSIONS

A more systematic approach to the study of petrified plant remains and fossil wood in Greece could lead to better knowledge of the evolution of the Cenozoic flora in the Aegean area, and a more accurate reconstruction of the synchronous regional palaeoclimate. Our present study was based on previously selected material consisting of 96 samples, from which more than 290 oriented thin sections were made, all of them showing palm structure. The largest share of specimens (83) came from Lesbos Island, seven from Lemnos, three from Kastoria (continental part) and three from Evros (Aëtohory area) (see Appendix 1). Anatomical study identified six species of *Palmoxylon* (two of them as new species), two species of *Rhizopalmoxylon* (both as new species) and a single form of *Palmocaulon*, as follows:

– *Palmoxylon daemonoropsoides* (Unger 1845) Kirchheimer, 1937, corr., as palm stem of extant *Daemonorops* type;

– *Palmoxylon chamaeropsoides* Iamandei et Iamandei, sp. nov., as palm stem of extant *Chamaerops* type;

– *Palmoxylon coryphoides* Ambwani et Mehrotra 1990, as palm stem of extant *Corypha* type;

– *Palmoxylon sabaloides* Greguss 1969, as palm stem of extant *Sabal* type;

– *Palmoxylon trachycarpoides* Iamandei et Iamandei, sp. nov., as palm stem of extant *Trachycarpus* type;

– *Palmoxylon phoenicoides* Hofmann 1944 – as palm stem of extant *Phoenix* type;

– *Rhizopalmoxylon daemonoropsoides* Iamandei et Iamandei, sp. nov., as palm root of extant *Daemonorops* type;

– *Rhizopalmoxylon phoenicoides* Iamandei et Iamandei, sp. nov., as palm root of extant *Phoenix* type;

– *Palmocaulon* sp. aff. *Phoenix* L., as rachis structure of palm of extant *Phoenix* type.

The number of fossil palm records is continuously increasing, and the names of fossil species are in the hundreds. Many species names have no taxonomic significance, referring to names of persons or regions honored. For our new species we used names derived from the name of the most probable corresponding extant genus, after an older, logical model.

The numerous palaeobotanical studies of material from all Aegean areas make it clear that during the Cenozoic these regions evolved as forested lands; their present floras most probably can be explained mainly by anthropogenic factors. Taking into account the fossil plant associations already described for this region, we can infer that mixed mesophytic forests occurred in a subtropical to warm temperate palaeoclimate, strongly influenced by the presence of the Tethys and Paratethys Seas from the south and north. As presented above, in this region there was, besides conifers, a rich association of arboreal dicotyledons (Laurales, Fabales, Myrtales) and monocotyledons (especially Arecales) described earlier.

Deep, comprehensive and systematic studies are still needed to give better support to reconstructions of palaeoclimate development during the entire Cenozoic in the Aegean area, and to give us a better understanding of its future course. The results of such studies, mainly based on palaeobotanical research, will complete the data on the forest associations of each fossil-bearing site and will help elucidate the evolution of the arboreal vegetation of Greece, at least from the Oligocene to the Miocene.

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Appendix 1. Appendix 1. Studied and identified fossil palm samples from Greece

(Key for observations, sampled parts: Co – cortical zone; D – dermal zone; SD – subdermal zone; C – central zone; R – root wood; Ra – rachis)

Crt. No.	Field No.	Location	Geological age	Identification	Observations
1	376	Lesbos	Lower Miocene	*Palmoxylon daemonoropsoides* (Ung.) Kirchh., corr.	D, C
2	AH1133	Aëtohori	Late Oligocene	Idem	C
3	120	Lesbos	Lower Miocene	*Palmoxylon chamaeropsoides* Iamandei et Iamandei, sp. nov.	D
4	367	Lesbos	Lower Miocene	Idem	D, SD, C
5	401	Lesbos	Lower Miocene	Idem	C
6	497	Lesbos	Lower Miocene	Idem	C
7	449	Lesbos	Lower Miocene	Idem, poorly preserved	C
8	450	Lesbos	Lower Miocene	Idem, poorly preserved	C
9	K525	Lesbos	Lower Miocene	Idem, poorly preserved	C
10	K526	Lesbos	Lower Miocene	Idem, poorly preserved	C
11	K535	Lesbos	Lower Miocene	Idem, poorly preserved	C
12	K536	Lesbos	Lower Miocene	Idem, poorly preserved	C
13	61A	Lesbos	Lower Miocene	*Palmoxylon coryphoides* Ambwani et Mehrotra	SD, C
14	316	Aëtohori	Late Oligocene	Idem	SD, C
15	L503	Lesbos	Lower Miocene	Idem	D, SD
16	L505	Lesbos	Lower Miocene	Idem	C
17	L509	Lesbos (Larpsana)	Lower Miocene	Idem	C
18	L514	Lesbos (Antissa)	Lower Miocene	Idem	C
19	K515	Kastoria	Lower Miocene	Idem	SD, C
20	AH919	Aëtohori	Late Oligocene	Idem	C
21	L15	Lesbos (Museum)	Lower Miocene	*Palmoxylon sabaloides* Greguss	SD, C
22	415	Lesbos	Lower Miocene	Idem	Co, D, SD
23	424	Lesbos (Meer)	Lower Miocene	Idem	SD
25	L501	Lesbos (Angali)	Lower Miocene	Idem	C
26	L507	Lesbos (Museum)	Lower Miocene	Idem	SD, C
27	L511	Lesbos (Palomari)	Lower Miocene	Idem	C
28	L520	Lesbos (Eressos)	Lower Miocene	Idem	Co, D, SD, C
29	L523	Lesbos (Sigri-Gavathas)	Lower Miocene	Idem	SD, C
30	L524	Lesbos (Sigri)	Lower Miocene	Idem	D, SD, C
31	527	Lesbos?	Lower Miocene	Idem	C
32	369	Kastoria	Lower Miocene	*Palmoxylon trachycarpoides* Iamandei et Iamandei, sp. nov.	C
33	375	Lesbos	Lower Miocene	Idem	C
34	377	Lesbos	Lower Miocene	Idem	C
35	491	Lemnos	Lower Miocene	Idem	C
36	L502	Lesbos (Gavathas)	Lower Miocene	Idem, young stem	C
37	L510	Lesbos (Phaneromeni)	Lower Miocene	Idem, young stem	C
38	L512	Lesbos (Phaneromeni)	Lower Miocene	Idem, young stem	C
39	L516	Lesbos (Sigri)	Lower Miocene	Idem, fibrous bundles absent	C
40	L517	Lesbos (Sigri)	Lower Miocene	Idem, young stem	C
41	L518	Lesbos (Sigri)	Lower Miocene	Idem, fibrous bundles absent	C
42	529	Lesbos (Gavathas)	Lower Miocene	Idem, young stem	C
43	533	Lesbos	Lower Miocene	Idem, young stem + rootlets	C
44	L1	Lemnos	Lower Miocene	*Palmoxylon phoenicoides* Hofmann	D, SD+R
45	364	Lesbos	Lower Miocene	Idem	C
46	368	Kastoria	Lower Miocene	Idem	D, SD
47	371	Lesbos	Lower Miocene	Idem	SD, C
48	372	Lesbos	Lower Miocene	Idem	C
49	378	Lesbos	Lower Miocene	Idem	Co, D, SD, C+R
50	459	Lesbos	Lower Miocene	Idem	Co, D, SD, C+R
51	495	Lesbos	Lower Miocene	Idem	D, SD
52	496	Lesbos	Lower Miocene	Idem	Co, D, SD, C

Appendix 1. Continued

Crt. No.	Field No.	Location	Geological age	Identification	Observations
53	498	Lesbos	Lower Miocene	Idem	SD, C
54	500	Lesbos (Park)	Lower Miocene	Idem	C
55	L504	Lesbos (Antissa)	Lower Miocene	Idem	SD, C
56	L506	Lesbos (Larpsana)	Lower Miocene	Idem	D, SD
57	L508	Lesbos (Gavathas)	Lower Miocene	Idem	D, SD
58	L513	Lesbos	Lower Miocene	Idem	D, SD
59	519	Lesbos (Sigri)	Lower Miocene	Idem	D, SD
60	L521	Lesbos (Eressos)	Lower Miocene	Idem	D, SD
61	L522	Lesbos (Larpsana)	Lower Miocene	Idem	D, SD
62	528	Lemnos	Lower Miocene	Idem	D, SD
63	530	Lesbos	Lower Miocene	Idem	D, SD
64	531	Lesbos	Lower Miocene	Idem	Co, D, SD, C
65	532	Lesbos	Lower Miocene	Idem	D, SD
66	499	Lesbos	Lower Miocene	*Rhizopalmoxylon daemonoropsoides* Iamandei et Iamandei, sp. nov.	R
67	378	Lesbos	Lower Miocene	*Rhizopalmoxylon phoenicoides* Iamandei et Iamandei, sp. nov.	R
68	492	Lemnos	Lower Miocene	Idem	R
93	494	Lemnos	Lower Miocene	Idem	R
94	534	Lesbos (Sigri)	Lower Miocene	Idem	R
95	L1	Lemnos	Lower Miocene	Idem	R
96	493	Lesbos	Lower Miocene	*Palmocaulon* sp. aff. *Phoenix* sp.	Ra