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Anatomical and Palaeoecological Considerations of Neogene *Terminalioxylon* (Combretaceae, Dicots) from Egypt

Zainab M. El-Noamani

El-Saadawi Lab., Botany Department, Faculty of Science, Ain Shams University, Cairo, Egypt
Email: zainabelnoamani@yahoo.com

Abstract

Anatomical features of three species of the genus *Terminalioxylon* Schönfeld emend. Mädel-Angeliewa & Müller-Stoll *viz.*, *T. edwardsii*, *T. geinitzii* and *T. primigenium* were fully described and illustrated based on fossil wood specimens collected from three lower Miocene sites in the northern part of the Western Desert of Egypt *viz.*, Gebel El-Khashab, Wadi Natrun and Cairo-Bahariya desert road. Wood functional traits such as vessel porosity, vessel grouping, perforation plates, vessel diameters, vessel frequency and vessel element length; along with the probable nearest living relatives are used to reconstruct the palaeoclimatic and palaeoecological assumptions for the three described species. These data indicate that the three species were supposed to have inhabited lowland tropical dry forests where *T. edwardsii* and *T. primigenium* were medium-large trees with deep roots, thus not subjected to water stress in dry periods; while *T. geinitzii* was a shrub or small tree with shallow roots exposed to drought in seasonal dry periods.

Keywords: Combretaceae, Ecological wood anatomy, Egypt, Neogene, *Terminalioxylon*

Introduction

Combretaceae is a pantropical family of 20 genera and approximately 600 species of trees, shrubs, subshrubs and lianes (including some mangroves) (Stace 2007; Onefeli & Stanys 2019). The fossil records of this family are dated back to the Late Cretaceous (~ 110 mya) and extended to the Quaternary with most occurrence in Neogene Period, involving wood, leaves and reproductive organs (flowers, fruits and pollen) (Friis et al. 1992; Gere et al. 2015).

Fossil wood assigned to Combretaceae is very common worldwide and referred to an organ genus *Terminalioxylon*. *Terminalioxylon* was first introduced by Schönfeld (1947) to include fossil wood resembling the modern genus *Terminalia* L. from Palaeogene of Colombia, South America. Later, Mädel-Angeliewa & Müller-Stoll (1973) emended the generic diagnosis of *Terminalioxylon* and treated the genus *Terminalioxylon sensu lato* to generally encompass wood with features of *Terminalia*, *Anogeissus* Wallich and *Combretum* Löfling. In the same paper, Mädel-Angeliewa & Müller-Stoll transferred the three *Evodioxylon* species *viz.*, *E. geinitzii*, *E. intermedium*, *E. primigenium* and the *Leguminoxylon edwardsii* reported by Kräusel (1939) from Egyptian strata, to their emended genus *Terminalioxylon*. So far, approximately 50 species, excluding repetitions, have been assigned to this genus worldwide (Gregory et al. 2009; El-Saadawi et al. 2013, 2014). The earliest record of these is *Terminalioxylon intermedium* reported by Kräusel (1939) from the late Senonian (Late Cretaceous) of Egypt. All other species are reported from tertiary strata, especially Neogene Period (Gregory et al. 2009).

The aim of the present paper is to give full wood anatomical descriptions and illustrations of the three Egyptian Neogene *Terminalioxylon* species *viz.*, *T. edwardsii*, *T. geinitzii* and *T. primigenium* with a brief note on their previous records in the Egyptian strata and discuss their palaeoclimatic and palaeoecological inferences based on qualitative and quantitative data obtained from their wood anatomy and the habitat of their modern analogies.

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Material and Methods

The twelve specimens described here are part of the fossil wood collections kept in Prof. El-Saadawi's Lab, Botany Department, Faculty of Science, Ain Shams University collected earlier by the Lab members, guided by Dr. Rifaat Osman, Prof. of Geology, Benha University during several excursions to the many sites including: Gebel El-Khashab, Wadi Natrun and Cairo-Bahariya desert road (Fig. 1) in the period from 1995 to 2018. The two sites Gebel El-Khashab and Cairo-Bahariya desert road belong to Gebel El-Khashab Formation whereas Wadi Natrun to Moghra Formation, and both formations are of an early Miocene age (Said 1962).

For the study of xylotomical characters, thin sections (transverse, TS; tangential, TLS; and radial, RLS) of the present fossil wood specimens were prepared according to the method described by Jones & Rowe (1999) at the Rock Cutting Unit, Geology Department, Faculty of Science, Cairo University. The quantitative data and the descriptive terminology generally follow the format of the IAWA Hardwood list (IAWA Committee 1989). The identification process was performed by using the dichotomous key of the Egyptian dicotyledonous fossil wood species constructed by El-Noamani (2020), together with searching the online Insidewood database (Insidewood 2004-onwards). Systematic assignment follows the APG III (2009) classification system, and species names and their synonyms follow Gregory et al. (2009). The three ecological indices/ratios: vulnerability index (V), mesomorphy ratio (M) and conductive capability (C) were calculated using Carlquist (1977) equations: V= mean vessel tangential diameter/ mean number of vessels/mm^2 and M= V× mean vessel element length and Wolfe & Upchurch (1987) equation: C= radius of the vessel^4/10^6× mean number of vessels/mm^2.

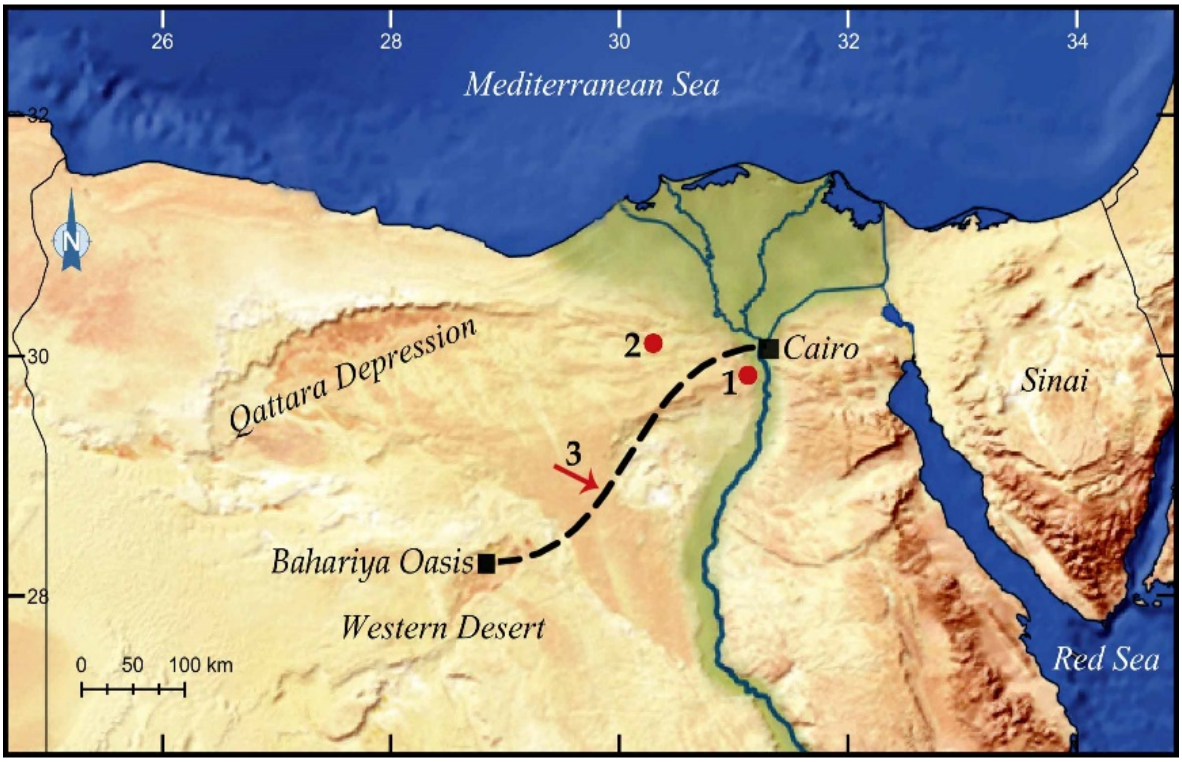

Figure 1. Map of Egypt showing the three sites from which the present fossil woods were collected: 1. Gebel El-Khashab, 2. Wadi Natrun, 3. Cairo-Bahariya desert road.

Results

Following the key steps provided by El-Noamani (2020) for Egyptian dicotyledonous fossil woods lead to the genus *Terminalioxylon*. The key steps followed were 1b) rays of one size or with intermediate ray sizes, 5a) ray exclusively uniseriate, rarely with biseriate portions as wide as uniseriate portion or completely biseriate, 6b) axial parenchyma abundant, 10b) diffuse and diffuse in aggregate apotracheal parenchyma absent or sparsely present, 12b) axial parenchyma bands absent or present only as discontinuous bands surrounding small secretory canals. At this step in the key the only choices left are three species of *Terminalioxylon: T. edwardsii, T. geinitzii* and *T. primigenium.*

Order: Myrtales Juss. ex Bercht. & J.Presl 1820
Family: Combretaceae R.Br. 1810, nom. cons.
Genus: *Terminalioxylon* Schönfeld 1947 emend. Mädel-Angeliewa & Müller-Stoll 1973
Species: *Terminalioxylon edwardsii* (Kräusel) Mädel-Angeliewa & Müller-Stoll 1973
Synonym: *Leguminoxylon edwardsii* Kräusel
Specimens: CBR-ZN.P112 & CBR-ZN.P114; Plate I
Locality: Cairo-Bahariya desert road

Description: Growth ring boundaries indistinct or absent. Wood diffuse-porous. Vessels solitary (76%) and in short radial multiples of 2–3. Solitary vessels oval in outline, medium to large, tangential diameter 115 (71–171) µm, radial diameter 153 (86–236) µm; vessel frequencies 13 (8–16) per mm^2. Perforation plates simple with horizontal end-walls. Intervessel pits crowded, alternate, polygonal, small to medium 6 (3.5–9) µm, vestures seen only in some vessel elements. Vessel ray pits with much reduced borders to apparently simple with rounded or angular pits. Vessel element length short 206 (107–321) µm; thin-walled tyloses present. Fibers libriform, septate, with thin- to thick-walls. Axial parenchyma paratracheal narrow vasicentric of 1–2 cells thick partially or completely surrounding the vessels, aliform and sometimes confluent when vessels are closely spaced; apotracheal diffuse and sometimes in narrow bands or lines of 1–3 cells wide. Rays exclusively uniseriate, rarely biseriate or triseriate locally; heterocellular, body ray cells procumbent with 2–4 rows of square marginal cells or intermixed; ray height 2–15 cells, 276 (93–464) µm; 15 (14–18) per mm; non-storied. Prismatic crystals solitary, large, located in large non-chambered square ray cells completely fill the cell, often in non-chambered parenchyma cells.

Previous stratigraphic records in Egypt: Oligocene of Cairo Petrified Forest (CPF) at Qattamiya (El-Saadawi et al. 2013); Oligocene/Miocene of west Giza Pyramids (Kräusel, 1939); as cf. *Terminalioxylon edwardsii* from Miocene of Cairo-Bahariya desert road (El-Saadawi et al. 2014).

Species: *Terminalioxylon geinitzii* (Schenk) Mädel-Angeliewa & Müller-Stoll 1973
Synonyms: *Capparidoxylon geinitzii* Schenk; part of *Evodioxylon oweni* (Carruthers) Chiarugi; *Evodioxylon geinitzii* (Schenk) Kräusel; *Combretoxylon geinitzii* (Schenk) Louvet

Specimens: GKH-MK. P031, WN-WE. P034, WN-WE. P035; Plate II
Localities: Gebel El-Khashab & Wadi Natrun
Description: Growth rings absent. Wood diffuse-porous; vessels solitary (34.5%) and in long radial multiples of 2–11. Solitary vessels with circular to oval outline, small to medium, tangential diameter 84 (43–128) µm; radial diameter 121 (71–150) µm; vessel frequencies 36 (33–49) per mm^2. Perforation plates simple with horizontal end walls. Intervessel pits vestured, alternate, polygonal, small 5.5 (5–7) µm; vessel ray pits not observed; vessel element length short 212 (78.5–286) µm; tyloses absent. Fibers libriform, septate, with very-thick walls. Axial parenchyma paratracheal narrow vasicentric of 1–2 cells thick and often forming an incomplete sheath around solitary vessels or vessel multiples, occasionally aliform or confluent; apotracheal marginal parenchyma bands of 1–3 cells wide

are observed in some places. Rays exclusively uniseriate; heterocellular with intermixed square and procumbent cells in nearby alternating pattern along the ray; ray height 3–27 cells, 439 (143–1107) µm; 10 (8–12) per mm; non-storied. Prismatic crystals solitary, large, located in non-chambered square ray cells completely fill the cell, often in chambered parenchyma cells.

Remark: The marginal parenchyma bands in specimen no. WN-WE. P034 (Plate II, fig. 2), were not recorded before in the descriptions/ illustrations of *Terminalioxylon geinitzii* (=*Evodioxylon geinitzii*) given by Kräusel (1939) or Mädel-Angeliewa & Müller-Stoll (1973) and can be attributed to an environmental condition such as abrupt, perhaps seasonal, interruptions of the stable conditions, as mentioned by Sakala (2000) in a similar wood case.

Previous stratigraphic records in Egypt: Oligocene of Qattamiya and Gebel Mokattam (Schenk 1883); Miocene of Der Abu Makar, Gebel Ruzza, Wadi Faregh and Wadi Natrun (Kräusel 1939; Kamal El-Din & El-Saadawi 2004).

Species: *Terminalioxylon primigenium* (Schenk) Mädel-Angeliewa & Müller-Stoll 1973

Synonyms: *Laurinoxylon primigenium* Schenk; part of *Nicolia oweni* (Carruthers) Schenk; *Caesalpinium oweni* (Carruthers) Schuster; part of *Evodioxylon primigenium* (Schenk) Kräusel; *Combretoxylon primigenium* (Schenk) Louvet

Specimens: GKH-MK. P011, GKH-MK. P019, GKH-MK. P035, GKH-MK. P036, GKH-MK. P037, WN-WE. P039, CBR-ZN. P105; Plate III

Localities: Gebel El-Khashab, Wadi Natrun & Cairo-Bahariya desert road

Description: Growth rings distinct to indistinct determined in some specimens by change in size and frequency of vessels. Wood semi-ring-porous or diffuse-porous. Vessels solitary (50–78.5%) and in short radial multiples of 2–3. Solitary vessels oval in outline, medium to large, tangential diameter 123(79–150) µm, radial diameter 184 (100–228) µm; vessel frequencies 11 (9–15) per mm^2. Perforation plates simple with oblique end-walls. Intervessel pits vestured, alternate, circular to oval, small to medium 7.5 (5.5–10.5) µm. Vessel ray pits not observed. Vessel element length short 179 (71–378) µm; tyloses absent. Vascular/vasicentric tracheids present. Fibers libriform, septate, with very thick-walls. Axial parenchyma abundant paratracheal broad vasicentric (2–4) cells thick partially or completely surrounding the vessels, aliform and confluent in association with closely adjacent vessels. Rays exclusively uniseriate, rarely biseriate or triseriate locally; almost straight but sometimes appear wavy around the large vessels in transverse section; heterocellular, body ray cells procumbent with 1–2 rows of square cells contain residues of large single crystals, these cells distinguished in tangential section by their larger width and brighter color due to crystal fragments; ray height 2–24 cells, 393(71–714) µm; 13 (10–15) per mm; non-storied. Prismatic crystals solitary, large, located in square ray cells completely fill the cell, often in chambered parenchyma cells.

Previous stratigraphic records in Egypt: Oligocene of Birket Qarun, Fayum (Widan-el-Faras, Gebel Qatrani Formation), Qattamiya, Gebel Mokattam, Gebel Amuna, Wadi Dugla and Wadi Ankebieh (Schenk 1883; Kräusel 1939; El-Saadawi & Kamal El-Din 2004); Oligocene/Miocene of Gebel El-Khashab and west Giza Pyramids (Kräusel 1939); Miocene of Der Baramus, Gebel Ruzza and Wadi Faregh (Schuster 1910; Kräusel 1939; Kamal El-Din & El-Saadawi 2004).

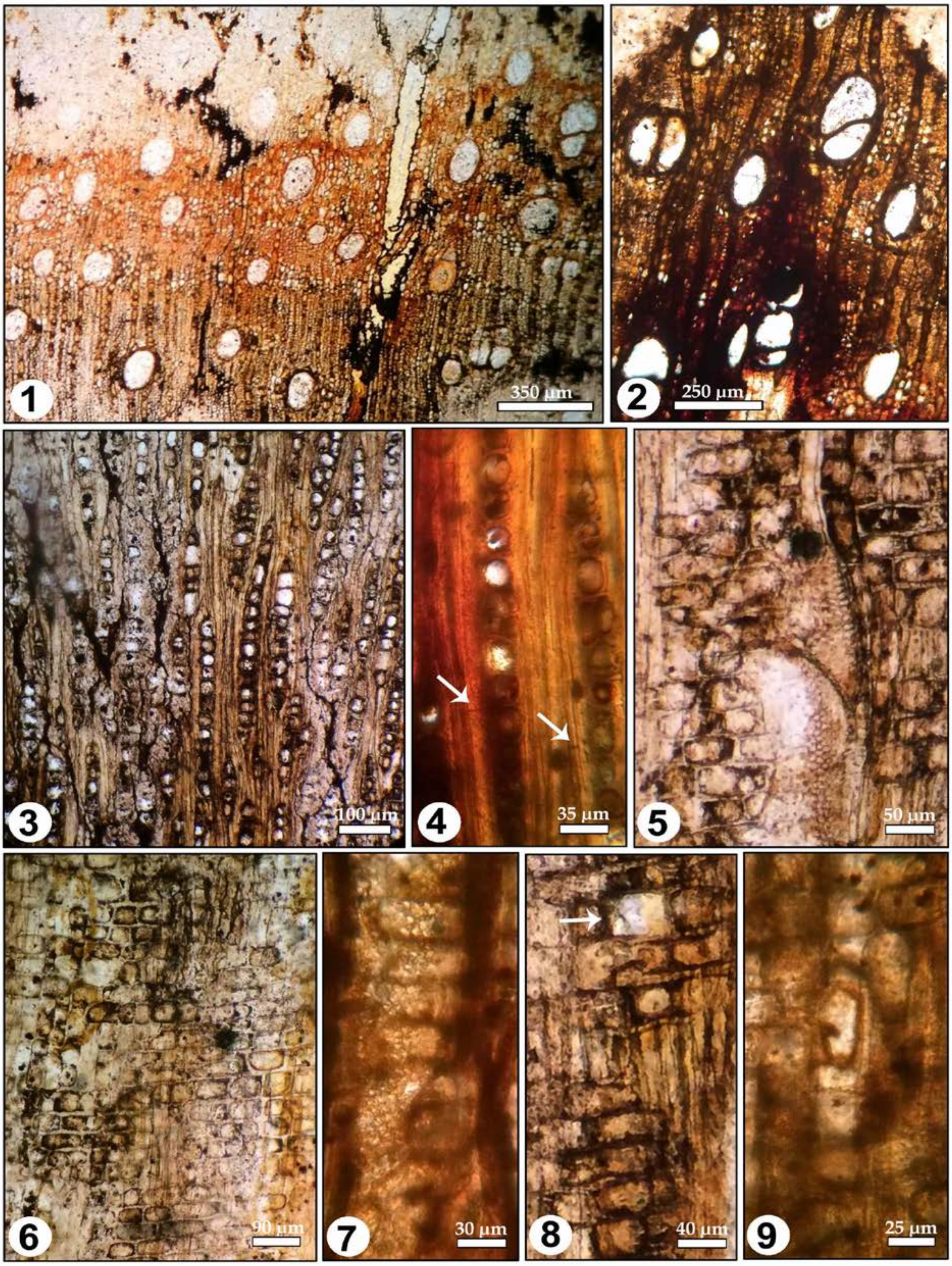

Plate I. *Terminalioxylon edwardsii* 1: Diffuse-porous wood, mostly solitary vessels, abundant axial parenchyma, TS, 2: Sparsely diffuse apotracheal parenchyma, TS, 3: Exclusively uniseriate rays, TLS, 4: Details of uniseriate, heterocellular rays and libriform, septate fibers (arrows), TLS, 5: Crowded alternate intervessel pits, RLS, 6: Heterocellular rays composed of intermixed procumbent and square/ upright cells, RLS, 7: Vessel-ray pits with distinct borders, similar to intervessel pits, RLS, 8: Prismatic crystal in a non-chambered square ray cell (arrow) RLS, 9: Prismatic crystal in an enlarged axial parenchyma cell, RLS.

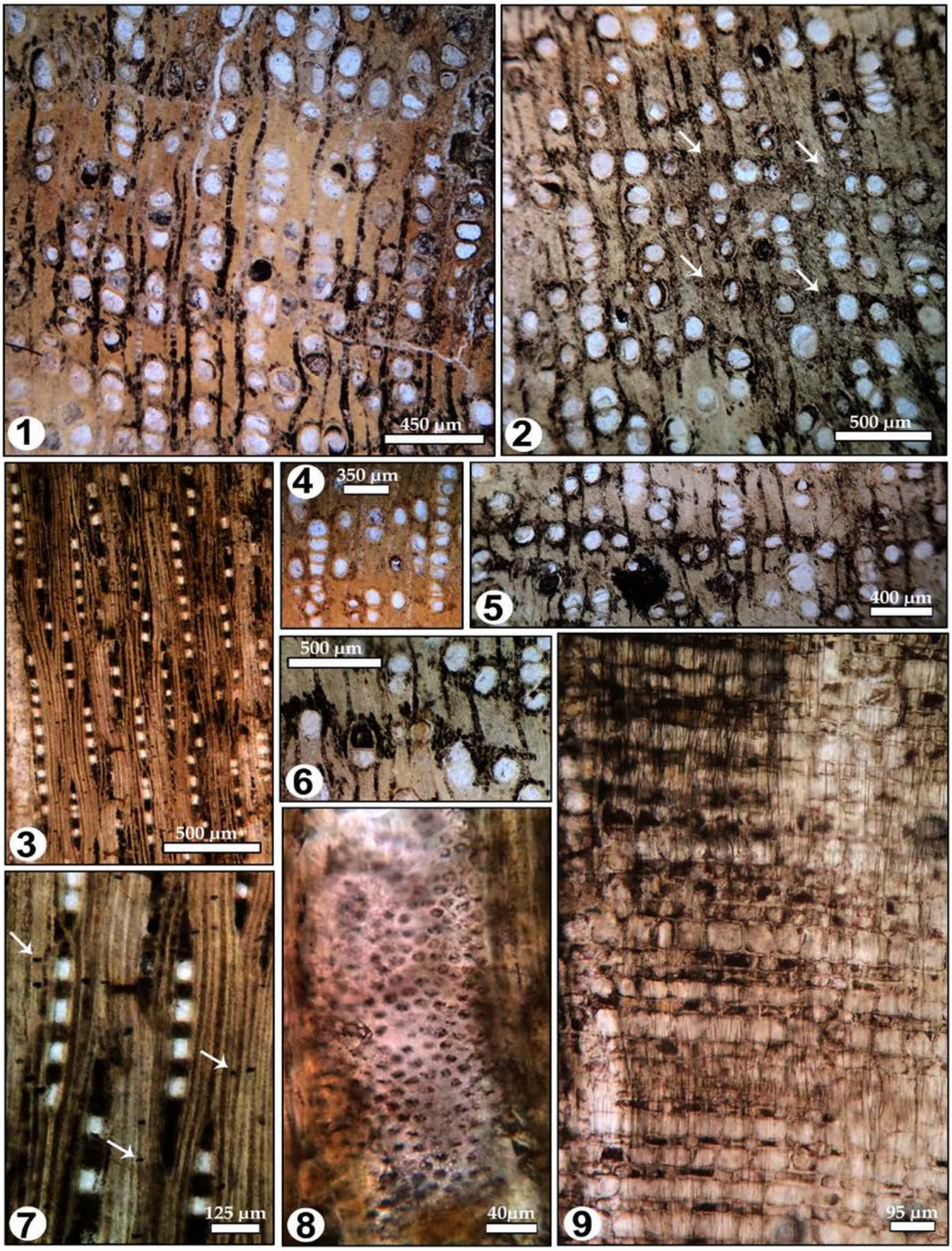

Plate II. *Terminalioxylon geinitzii* 1: Diffuse- porous wood, vessels numerous and commonly arranged in short and long radial multiples, TS, 2: Abrupt marginal parenchyma bands delimited by arrows, TS, 3: Exclusively uniseriate rays, TLS, 4: Long radial multiples of vessels (up to 11), TS, 5 & 6: Details of vessels and parenchyma, axial parenchyma vasicentric as an incomplete sheath around vessel multiple, confluent forming short and long irregular bands, TS, 7: Details of uniseriate, heterocellular rays and libriform, septate fibers (arrows), TLS, 8: Vestured alternate intervessel pits with polygonal outline, RLS, 9: Vestured alternate intervessel pits with polygonal outline, RLS.

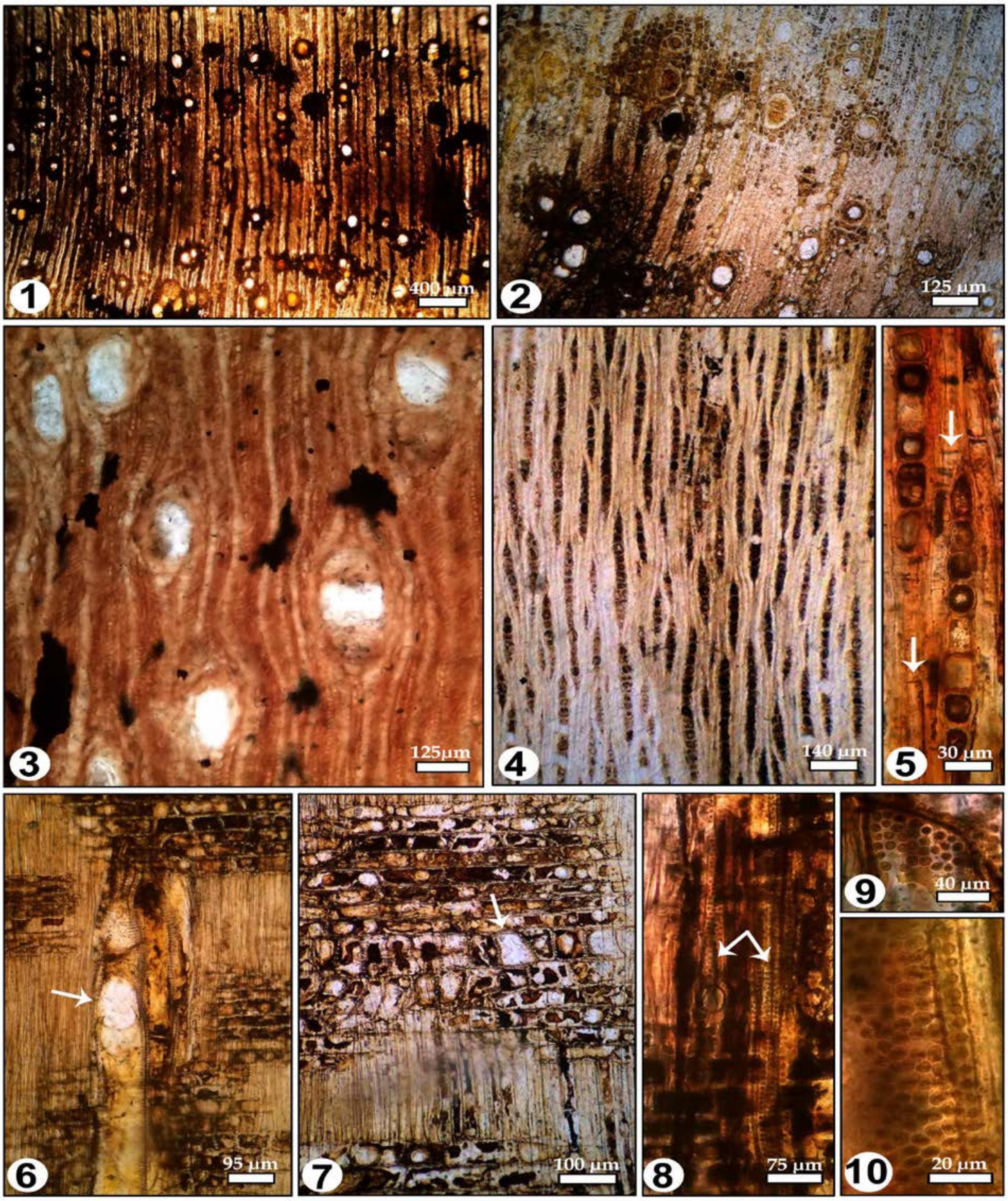

Plate III. *Terminalioxylon primigenium* 1: Semi-ring to diffuse- porous wood, vessels solitary and in short radial multiples of 2–3, abundant paratracheal parenchyma, TS, 2: Details of vessels and parenchyma, axial parenchyma vasicentric as a complete multi-layered sheath around vessels or vessel groups and irregular short band of confluent parenchyma surrounding adjacent vessels, TS, 3: The wavy ray pattern around the large vessels, TS, 4: Exclusively uniseriate rays, some of which with biseriate portions as wide as uniseriate portion, a cell contain crystal appears with light color in the middle of some rays, TLS, 5: Details of uniseriate, heterocellular rays and libriform, septate fibers (arrows), TLS, 6: A vessel element with simple perforation plate (arrow) and oblique end wall, TLS, 7: Heterocellular rays composed of procumbent cells and a row of square cells contain residues of large crystals (arrow), RLS, 8: Vascular/vasicentric tracheids (forked arrow), RLS, 9: Vestured alternate intervessel pits with circular outline, RLS, 10: Close-up view of vestured alternate intervessel pits and vascular/vasicentric tracheids, RLS.

Discussion

1. Comparison between the three described *Terminalioxylon* species

As can be gathered from the description, the three taxa share the following characters: Diffuse-porous wood; simple perforation plates; vestured intervessel pits; vasicentric, aliform or confluent paratracheal parenchyma; exclusively uniseriate heterocellular rays with crystalliferous cells; and libriform, septate fibers. These characters show the closest resemblance with the amended diagnosis of *Terminalioxylon* (Schönfeld) Mädel-Angeliewa & Müller-Stoll 1973.

Terminalioxylon geinitzii is unique in that it possesses small to medium-sized vessels with high frequency which are usually arranged in long radial multiples of 2–11. These characters set it apart from *T. edwardsii*, *T. primigenium* and also from other known *Terminalioxylon* species. Separation of *Terminalioxylon edwardsii* from *T. primigenium* is quite difficult as both of them are similar in the vessel's diameter, frequency and grouping. Nevertheless, the main difference between them is in the type and amount of axial parenchyma. *T. edwardsii* is characterized by having diffuse apotracheal parenchyma and less developed paratracheal parenchyma, while *T. primigenium* lacks diffuse apotracheal parenchyma and has only well-developed paratracheal parenchyma. Table (1) points out the anatomical similarities and differences between the three described taxa.

In addition to the three described Neogene species, there is another species, *T. intermedium*, which is reported from the Egyptian Upper Cretaceous strata and is considered the oldest species of the genus worldwide (Gregory et al. 2009). This species shows some similarities with *T. primigenium*, but it differs in having scanty paratracheal parenchyma and non-septate fibers against well-developed paratracheal parenchyma and septate fibers in *T. primigenium.*

2. Palaeoclimatic and palaeoecological implications

The palaeoclimatic and palaeoecological inferences (such as climate types, temperature, humidity, altitude and vegetation type) for the three Egyptian *Terminalioxylon* were drawn here based on two approaches: 1) the nearest living relatives (NLRs) to the fossil taxa, which suppose that the fossil taxon had similar climatic tolerance and habitat to its living analogue; 2) the wood physiognomy in terms of using qualitative and quantitative parameters of vessels and other wood components then analyzing the anatomical expression of these features in response to different ecological regimes.

2.1. Comparison of the fossil woods with their nearest living relatives

According to Mädel-Angeliewa & Müller-Stoll (1973) the modern equivalents of all fossil wood assigned to *Terminalioxylon* are the three living genera *Anogeissus*, *Combretum* and *Terminalia*. *Anogeissus* is a genus of only seven species of small to large trees found in savannas and open forests in western tropical Africa and Southeast Asia (Van Vliet 1979; Stace 2007). *Combretum* has about 255 species of mostly deciduous or semi-deciduous small trees, shrubs, scandent shrubs, subshrubs or woody climbers (lianas) distributed in tropical and subtropical regions with the greatest species diversity in Africa (Stace 2007; Jordaan et al. 2011). *Terminalia* consists of about 190 species of large trees widely distributed in rain forests, swamp forests, wet or dry deciduous forests and savannas in the tropical regions of the world (Van Vliet 1979; Stace 2007).

Although there is an overlap in the wood anatomical characters of the above three genera but according to the generic diagnosis presented in Van Vliet (1979) for each one it could be concluded that *Terminalioxylon geinitzii* seems in particular very close to the recent *Anogeissus* species in terms of vessel size and arrangement and parenchyma pattern; whereas both *T. edwardsii and T. primigenium* are particularly more related to *Terminalia* species in respect to the relatively large vessels and the abundant axial parenchyma.

Van Vliet (1979) categorized extant *Terminalia* wood into five groups based on the moisture availability and the quantitative features of vessel element (diameter, frequency and length) of 38 species worldwide. Although there is a broad range of the quantitative features within each of the five groups, but characteristics of both *T. edwardsii* and *T. primigenium* are consistent with some species that occur in the drier vegetation zones, e.g. dry deciduous forest, savanna or dry thicket.

2.2. Wood physiognomy as climate indicator

The main xylotomical features of both *T. edwardii* and *T. primigenium* are: indistinct growth rings, diffuse-porous wood, mostly solitary relatively wide vessels (> 100µ) with low frequency, simple perforation plates, short vessel element length and septate fibers. According to Wheeler & Bass (1991, 1993), absence of distinct growth rings and ring porosity in wood indicate a tropical environment. Few wide vessels are indicative of tropical lowland taxa of large trees. Simple perforation plates on the side walls of the vessel elements are typical of hot, lowland tropical forests as an adaptive mechanism to the high transpiration rates imposed by high temperature, which needs high conduction rates. Reduction in vessel element length is correlated with seasonality in temperature or in rainfall. Septate fibers are more common in tropical floras than in temperate ones. For *T. edwardii*, the vulnerability index (V), mesomorphy ratio (M) and conductive capability (C) are 8.8, 1822 and 142 respectively, while they are 11.2, 2005 and 157 respectively for *T. primigenium*. These values indicate that the two species would be large trees with well-developed mesomorphic features, as high C values are found only in large trees as mentioned by Wolfe & Upchurch (1987) and they lived in arid lowland tropical regions. The aridity is confirmed by the reduction in vessel element length. Although the high V value is generally an indicator of humid tropical climate, but it can also occur in trees of tropical arid regions as these trees probably have roots that penetrate to a permanent ground-water supply and by this way these trees are not subjected to the effect of seasonal drought (Baas et al. 1983).

Regarding *Terminalioxylon geinitzii*, there is an agreement between this species and the two previous species in some of mesomorphic features such as: absence of distinct growth rings and ring porosity; presence of simple perforation plates and septate fibers. The differences are in the reduction of vessel tangential diameter (<100µ), increase in vessel multiples and vessel frequency; and consequently, in V, M and C values which are 2.3, 494.5 and 112 respectively. Wolfe & Upchurch (1987) noticed that the size of woody plants (i.e., large tree, small trees or shrubs) has a positive correlation with vessel diameter and vessel frequency as shrubs and small trees have narrower vessels and higher vessel frequencies compared to large trees with wider vessels and low vessel frequencies. Zimmermann (1983) & Carlquist (1988) have suggested that tree species are more likely to show vessels in multiples in more arid climates as an alternative path for the xylem sap to bypass embolisms to improve safety for hydraulic conduction during periods of physical or physiological drought. Also, shallow-rooted shrubs and small trees in tropical, arid environments are probably subjected to seasonal drought and consequently they have low V values (Wolfe & Upchurch 1987).

Summing up from the data of the two approaches discussed above, the three *Terminalioxylon* species are deduced to be a part of an open-canopy lowland tropical vegetation either dry deciduous forests or savannas where *T. edwardsii* and *T. primigenium* were medium-sized or large trees, but not necessarily to be high, with deep roots which make ground-water available to the plant, so not subjected to seasonal drought; while *T. geinitizii* was a small trees or shrubs with shallow roots, so it was exposed to drought in seasonal dry periods.

Conclusion

Terminalioxylon is a wood morphogenus, which corresponds to a part of present-day *Terminalia* and to the modern species of *Anogeissus* and *Combretum*. In the present work three species of *Terminalioxylon*, *T. edwardsii* (Kräusel) Mädel-Angeliewa & Müller-Stoll, *T. geinitzii* (Schenk) Mädel-Angeliewa & Müller-Stoll and *T. primigenium* (Schenk) Mädel-Angeliewa & Müller-Stoll, were described and illustrated in more details based on well-preserved fossil wood specimens collected from three Miocene sites in the northern part of Western Desert *viz.*, Gebel El-Khashab, Wadi Natrun and Cairo-Bahariya desert road. Comparison between the three described Neogene species is made and also with the fourth species, *T. intermedium* which was described previously from the Cretaceous of Egypt. Based on the generic diagnosis of wood anatomy of the three living genera present in Van Vliet (1979), it was shown that *Terminalia* is the most congruent genus with the two fossil species *T. edwardsii* and *T. primigenium* which are of large trees distributed in the tropical regions of the world; while *T. genitzii* shows more similarities with the living genus *Anogeissus* which contains seven species of small to large trees found in savannas and open forests in western tropical Africa and Southeast Asia. Anatomical features common in the three taxa include indistinct growth rings, diffuse-porous wood, simple perforation plates, short vessel element length and septate fibers indicative of a lowland tropical dry vegetation. The narrow vessels and high vessel frequency along with increase vessel grouping in *T. geinitzii* indicate that it more likely to be a small tree or shrub with shallow roots; whereas wide vessels and low vessel frequencies in *T. edwardsii* and *T. primigenium* suggest that they would be medium-sized or large trees with deep roots.

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Table 1. Anatomical comparison of three *Terminalioxylon* species reported in this study.

Characters	***Terminalioxylon edwardsii***	***Terminalioxylon geinitzii***	***Terminalioxylon primigenium***
Vessels			
Vessel grouping	Solitary (76%) and in short radial multiples of 2–3	Solitary (34.5%) and in long radial multiples of 2–11	Solitary (50–78.5%) and in short radial multiples of 2–3
Tangential diameter	115 (71–171) µm	84 (43–128) µm	123(79–150) µm
Radial diameter	153 (86–236) µm	121 (71–150) µm	184 (100–228) µm
Number of vessels/mm^2	13 (8–16)	36 (33–49)	11 (9–15)
Vessel element length	206 (107–321) µm	212 (78.5–286) µm	179 (71–378) µm
Intervessel pit	Crowded, alternate, polygonal, small to medium 6 (3.5–9) µm	Alternate, polygonal, small 5.5 (5–7) µm	Alternate, circular to oval, small to medium 7.5 (5.5–10.5) µm
Vestured pits	Observed only in some vessel elements	Present	Present
Tyloses	Present	Absent	Absent
Tracheids and fibers			
Vascular/vasicentric tracheids	Absent	Absent	Present
Fiber nature	Libriform, septate	Libriform, septate	Libriform, septate
Fiber wall thickness	Thin-to thick-walled	Very thick-walled	Very thick-walled
Axial Parenchyma			
Paratracheal	Narrow vasicentric (1–2) cells thick, partially or completely surrounded the vessels; aliform and sometimes confluent	Narrow vasicentric (1–2) cells thick, partially surrounded the vessels; occasionally aliform or confluent	Broad vasicentric (2–4) cells thick, partially or completely surrounded the vessels; aliform and confluent
Apotracheal	Diffuse and sometimes in narrow bands or lines of 1–3 cells wide	Marginal parenchyma bands of 1–3 cells wide observed in some places	Absent
Prismatic crystals	Solitary, large crystal often in non-chambered parenchyma cells.	Solitary, large crystal often in chambered parenchyma cells.	Solitary, large crystal often in chambered parenchyma cells.
Rays			
Width	Exclusively uniseriate, rarely 2 (-3) seriate locally	Exclusively uniseriate	Exclusively uniseriate, rarely 2 (-3) seriate
Height	2–15 cells, 276 (93–464) µm	3–27 cells, 439 (143–1107) µm	2–24 cells, 393(71–714) µm
Number of rays/mm	15 (14–18)	10 (8–12)	13 (10–15)
Cellular composition	Heterocellular, body ray cells procumbent with 2–4 rows of square marginal cells or intermixed	Heterocellular with intermixed square and procumbent cells in nearby alternating pattern	Heterocellular, body ray cells procumbent with 1-2 rows of square cells
Prismatic crystals	Solitary, large, in non-chambered square ray cells	Solitary, large, in non-chambered square ray cells	Solitary, large, in square ray cells
Ecological indices/ratios			
Vulnerability index (V)	8.8	2.3	11.2
Mesomorphy ratio (M)	1822	494.5	2005
Conductive capability (C)	142	112	157

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