

***Terminalioxylon edwardsii* from the Oligocene of Egypt, with a review of the genus in Africa**

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W. E. El-Saadawi, M. M. Kamal El-Din, M. W. El-Faramawi and N. A. Ziada 2013. *Terminalioxylon edwardsii* from the Oligocene of Egypt, with a review of the genus in Africa. *Taeckholmia* **33**: 47-63.

Petrified wood resembling modern wood of *Terminalia* (Combretaceae) is described from the Oligocene of the Cairo Petrified Forest, Egypt. On the bases of xylotomical homologies, the fossil wood is attributed to *Terminalioxylon edwardsii*. A summary is given on *Terminalioxylon* and Combretaceae, with inferences on palaeoclimate.

Key words: Oligocene, Egypt, fossil wood, Combretaceae, Africa, palaeoclimate.

Introduction

The Oligocene epoch (34-23 million years ago) was the last major geologic subdivision of the Paleogene period (65-23 million years ago), following the Paleocene (65-56 million years ago) and Eocene (56-34 million years ago) epochs. It represents a transitional period within plant evolution stages where climate conditions changed and new environments began to form (www.stratigraphy.org).

Received 6 Feb. 2014, accepted 26 Feb. 2014

The majority of African plant fossils consists of pollen assemblages and petrified wood (Pan, 2007). To date, about 400 dicot fossil woods have been recorded from Africa (Gros, 1992; Dupéron-Laudoueneix & Dupéron, 1995; Gregory *et al.*, 2009; El-Saadawi *et al.*, 2011; Cantrill *et al.*, 2013); represented in the fossil record from the Cretaceous to the Quaternary. Fossil wood is mostly scattered across North Africa, but in some cases the age and taxonomic affinity may not be well known or are questionable (Pan, 2007).

The Oligocene dicot wood flora of Africa is represented by 43 taxa, with affinities to fourteen families: Fabaceae (14 species), Combretaceae (six species), Moraceae (five species), Meliaceae (four species), Clusiaceae, Ebenaceae, Euphorbiaceae, Malvaceae (two species each), Fagaceae, Juglandaceae, Monimiaceae, Sapindaceae, Tamaricaceae and Opiliaceae (one species each) (Dupéron-Laudoueneix & Dupéron, 1995; Gregory *et al.*, 2009; El-Saadawi *et al.*, 2011).

Oligocene dicot woods recorded from Egypt reach a total of 22 taxa (Table 1); which contributes just over 50% of the total Oligocene woods recorded from Africa. These fossil woods are known from 17 Egyptian sites, with 19 taxa being reported from the Cairo Petrified Forest (CPF) at Qattamiya (Fig. 1).

As shown in Table (1), the 22 Egyptian Oligocene dicot wood taxa are assigned to nine families namely Fabaceae (ten species), Combretaceae (three species), Malvaceae and Moraceae (two species each), Ebenaceae, Fagaceae, Monimiaceae, Sapindaceae and Tamaricaceae (one species each).

The aim of this paper is to report on the occurrence of a fossil wood species attributed to family Combretaceae, for the first time, in the Oligocene CPF at Qattamiya, to give a summary of fossil *Terminalioxylon* and Combretaceae and finally, to try to reconstruct palaeoclimate of the original growth site of the discussed species; taking into account the ecological and distributional characteristics of its nearest living relative.

Collection and sample preparation

The specimens used in this study were collected during a field excursion on 21st of June 2012. All the specimens were collected from inside the protected area borders. They vary in size from 5 to 20 cm in length. Some of them were collected from large logs (ranging in length from 1 to 25 m and in diameter from 0.2 to 1.6 m) after chopping them off in the field. The rest of the samples were already loose fragments.

Cross, tangential and radial longitudinal sections were obtained using a standard thin-section technique following the procedure described by Andrews (1961) and Kamal El-Din (1996). The sections were studied using a light microscope and photographed with an attached Canon PowerShot G12 digital camera. All images were then post-processed using Adobe Photoshop CS.

All the fossil specimens and the prepared slides are numbered¹ and deposited in the palaeobotanical collection of the Palaeobotany Unit, Botany Department, Faculty of Science, Ain Shams University, Cairo, Egypt.

Sample description and identification

The descriptions have mostly been made according to the International Association of Wood Anatomists Committee recommendations (IAWA Committee, 1989). Affinities were determined by consulting the literature (e.g. Metcalfe & Chalk, 1950) and searches in the online wood database Insidewood (2004-onwards). Relevant fossil wood genera were discussed in light of the comprehensive survey of fossil woods (Gregory et al., 2009). Systematic assignment follows the APG III (2009).

Results and Description

Microscopic examination revealed that the preservation of the collected specimens is satisfactory to good. However, only sample 8NZ was identified as *Terminalioxylon edwardsii* (Kräusel) Mädél-Angeliewa & Müller-Stoll, whilst the remaining ones need further investigation.

Systematic palaeobotany

Family: *Combretaceae* Robert Brown

Genus: *Terminalioxylon* Schönfeld, 1947 emend Mädél-Angeliewa & Müller-Stoll, 1973

¹ The number is followed by the initials of the collector, where NZ refers to Nermeen Ziada.

Generic diagnosis- Growth rings distinct or indistinct, marginal parenchyma sometimes present, vessels solitary or in short to long radial multiples (up to 14 vessels), perforation plates simple, intervessel pits alternate, fibres septate or non-septate, axial parenchyma paratracheal, vasicentric narrow to broad, often more or less aliform, seldom also confluent, chambered crystalliferous strands present or absent, rays 1(-2) cells wide, homocellular or weakly heterocellular, solitary crystals frequently present, mostly in enlarged square to upright cells in rows in between procumbent ray cells (Mädel-Angeliewa & Müller-Stoll, 1973; El-Saadawi *et al.*, 2014).

Species: *Terminalioxylon edwardsii* (Kräusel) Mädel-Angeliewa & Müller-Stoll, 1973 (*Leguminoxylon edwardsi* Kräusel, 1939)

Specimen No. 8NZ; Plate I, 1-5

Description- **Growth rings** indistinct or absent. **Wood** diffuse-porous. **Vessels** mainly solitary (73%) and in radial multiples of 2-4 (27%); mean tangential diameter of 95 μm (range 65-130 μm), mean radial diameter of 210 μm (range 150-280 μm); average vessel frequencies of 5/mm² (range 3-8/mm²). Perforation plates simple with horizontal end-walls. Intervessel pits alternate. Mean vessel element length 250 μm (range 190-320 μm), medium-sized. **Fibres** non-septate and thin- to thick-walled. **Axial parenchyma** vasicentric, weakly aliform, sometimes confluent connecting two vessels together.

Diffuse parenchyma cells also present. **Rays** homocellular, composed of procumbent cells; exclusively uniseriate; non-storied, mean height is 180 μm (range 90-390 μm).

Comparisons, Affinities and Discussion

The diagnostic anatomical characteristics of the fossil wood are: absence of growth rings, diffuse porous wood, mostly solitary vessels, simple perforation plates, alternate intervessel pits, vasicentric, weakly aliform, sometimes confluent, including diffuse axial parenchyma and exclusively uniseriate rays.

The combination of these features may occur in woods of families Anacardiaceae, Combretaceae, Fabaceae and Sapindaceae. However, the absence of large vessels of ring porous type and gum canals excludes Anacardiaceae; of abundant paratracheal parenchyma and generally multiseriate rays excludes Fabaceae and of mostly scanty parenchyma excludes members of Sapindaceae. The above affinities therefore point to family Combretaceae (Ahmed *et al.*, 2007).

All the above described characters indicate close affinity with the extant species of *Terminalia* Linnaeus. All fossil woods resembling *Terminalia* are assigned to the genus *Terminalioxylon* which was established by Schönfeld (1947) [emended by Mädler-Angeliewa & Müller-Stoll (1973)]. Since then, a number of fossils have been described under this genus to reach a total of 51 species worldwide (De Franceschi et al., 2008; Castañeda-Posadas et al., 2009; Gregory et al., 2009). Comparison between the 51 species is difficult as many of them are based on poorly preserved samples, and figures frequently do not clearly show important distinguishing features.

Species of *Terminalioxylon* were spread in four continents² (35 species in Asia, 11 species in Africa (Table 2), 6 species in South America and one species in North America). Each continent had its own distinct species, i.e. not found in other continents except for only two species, namely *T. chowdhurii* and *T. intermedium*, which were found to be common between Asia and Africa.

Considering the African *Terminalioxylon* species (Table 2), it is clearly evident from the data presented that:

1. *Terminalioxylon* was reported from nine countries and had a long vertical time span from the Cretaceous to Pliocene/Quaternary.
2. *T. geinitzii* and *T. intermedium* were the oldest species; both are from the Cretaceous of Somalia, in addition *T. intermedium* exists as well in the Cretaceous of Egypt.
3. *T. intermedium* is the most widespread species as it had been noted from six countries. Table (1) showed that this species is also widespread in Egypt, but second to *T. primigenium*.
4. Only three species, namely *T. geinitzii*, *T. intermedium* and *T. primigenium* are reported from more than one country.
5. Egypt, Ethiopia and Libya have the greatest number of *Terminalioxylon* species (four species each), followed by Somalia (three species) (Fig. 2).
6. It is noticeable that the *Terminalioxylon* floras of Egypt, Libya and Somalia were similar to one another.

²De Franceschi et al. (2008) stated that *Terminalioxylon* was reported from the Tertiary deposits of Europe but neither the reference nor the species recorded are documented.

Table (2). Age and distribution of *Terminalioxylon* species in Africa. Based on 1- Schenk, 1883; 2- Schuster, 1910; 3- Chiarugi, 1933; 4- Kräusel, 1939; 5- Boureau, 1955; 6- Boureau, 1958; 7- Louvet, 1973; 8- Lemoigne *et al.*, 1974; 9- Lemoigne, 1978; 10- Fessler Vrolant, 1980; 11- Boureau *et al.*, 1983; 12- Youssef, 1993; 13- Bamford, 1999; 14- El-Saadawi & Kamal El-Din, 2004; 15- present work. K = Cretaceous, T = Tertiary, E = Eocene, O = Oligocene, M = Miocene, P = Pliocene, Q = Quaternary; S = South.

Taxa	Country									Frequency of sp.
	Egypt	Libya	Tunisia	Algeria	Sudan	Mali	Ethiopia	Somalia	S. Africa	
<i>Terminalioxylon cheidense</i> Fessler Vrolant			O10							1
<i>T. chowdhurii</i> Prakash & Navale									M13	1
<i>T. doubingeri</i> Lemoigne							M9			1
<i>T. edengense</i> Boureau						T5				1
<i>T. edwardsii</i> (Kräusel) Mädel-Angeliewa & Müller- Stoll	O15; O/M4									1
<i>T. fezzanense</i> Boureau		O6								1
<i>T. geinitzi</i> (Schenk) Mädel- Angeliewa & Müller-Stoll	O11, 14; O/M4; M12	O7						K3; O/M7		3
<i>T. intermedium</i> (Kräusel) Mädel-Angeliewa & Müller- Stoll	K4; K/E11; O7, 11, 14; M12	K/E11; M11		K/E11	K/E11		K/E11	K11; M11		6
<i>T. primigenium</i> (Schenk) Mädel-Angeliewa & Müller- Stoll	O1, 4, 14; O/M7; M2	O/M7						O/M3		3
<i>T. sp.</i> of Lemoigne, Beauchamp & Samuel							M8			1
<i>T. sp.</i> of Lemoigne							P/Q9			1
No. of taxa/ country	4	4	1	1	1	1	4	3	1	



Fig. 2. Map showing the geographic distribution of *Terminalioxylon* and the number of species in African countries. sp. = species.

As shown in Table (2), four *Terminalioxylon* species are reported from Egypt, namely *T. edwardsii*, *T. geinitzii*, *T. intermedium* and *T. primigenium*. Table (1) shows that *T. primigenium* is the most widespread species of this genus in Egypt (12 sites), followed by *T. intermedium* (six sites) then *T. geinitzii* (two sites). The present work and Table (2) show that *T. edwardsii* occurs also in two sites, from the Oligocene of the CPF (present work) and from the Oligocene/Miocene of Giza Pyramids (Kräusel, 1939). Tables (1) and (2) show also that *T. primigenium* occurs in all the sites in which the other three species of the genus exist and that the CPF at Qattamiya is, hitherto, the only site in which the four species are known to exist together. Table (3) includes a comparison between *T. edwardsii* reported from the Giza Pyramids and the present specimen, where it is clearly evident that both specimens are anatomically similar, although slight differences in the quantitative features are noticed.

Table (3). Comparison between *T. edwardsii* described by Kräusel (1939) and the studied specimen 8NZ.

Features	<i>T. edwardsii</i>	8NZ
	Giza Pyramids (Oligocene/Miocene) Kräusel, 1939	Cairo Petrified Forest (Oligocene) Present Work
Vessels	Solitary & in radial multiples of 2-3 (rarely 4)	Solitary (73%) & in radial multiples of 2-4 (27%)
Vessel tangential diameter	65-100 μm	65-130 μm (av. 95)
Vessel frequency	4-16/ mm^2	3-8/ mm^2
Vessel element length	150-450 μm	190-320 μm (av. 250)
Axial Parenchyma	Aliform, sometimes confluent between two vessels, diffuse parenchyma cells present	Vasicentric, weakly aliform, sometimes confluent between two vessels, diffuse parenchyma cells present
Ray width	Mostly uniseriate, rarely 2-(3) seriate	Exclusively uniseriate

This is the first report of this species from the study area which sums up the dicot species revised previously by Gregory *et al.* (2009) and El-Saadawi *et al.* (2011) from the CPF to reach a total of 20 species belonging to the following seven families: Fabaceae (nine species), Combretaceae (four species), Malvaceae and Moraceae (two species each), Ebenaceae, Fagaceae and Monimiaceae (one species each). Family Combretaceae is therefore the second largest dicot family (following Fabaceae) not only in the CPF or even Egypt but also in the African continent at large (Dupéron-Laudoueneix & Dupéron, 1995; El-Saadawi *et al.*, 2011). Seven combretaceous genera are reported from Africa (asterisked below) in addition to three unnamed fossil woods, from a total of twelve represented in the world at large, namely *Angeissoxylon*, *Angeissus*, *Angeissuoxylon**, cf. *Buchenavia*, *Combretoxylon**, *Combretum**, *Lumnitzeroxylon*, *Terminalia**, cf. *Terminalia*, cf. *Terminalioxylon**, *Terminalioxylon** and *Pteleopsis** (Dupéron-Laudoueneix & Dupéron, 1995; Gregory *et al.*, 2009; El-Saadawi *et al.*, 2014). The largest of these genera is *Terminalioxylon* (51 spp.). Three combretaceous genera are known from Egypt, namely *Terminalioxylon*, cf. *Terminalioxylon* and *Combretoxylon*. *Combretoxylon*

sp. of Beauchamp, Lemoigne & Petrescu was reported to occur in the Miocene of Egypt by Boureau et al. (1983) without mentioning a locality (Dupéron-Laudoueneix & Dupéron, 1995; El-Saadawi & Kamal El-Din, 2004) whereas cf. *Terminalioxylon edwardsii* was described from the Miocene of Cairo-Bahariya Oasis Desert Road (El-Saadawi et al., 2014). In addition to the woods, a combretaceous leaf species *Terminaliophyllum africanum* Lejal-Nicol, was recorded from the Eocene of Suez by Lejal-Nicol (1987).

Palaeoclimatic reconstruction

Members of present day Combretaceae are noted to occur throughout the tropical and subtropical regions with a limited spread into warm temperate zones. The family is particularly more diverse along tropical seacoasts, in African savannas and in Asian monsoon forests (Singh et al., 2011).

The study of fossil plants to shed light and reconstruct past climates has long been practiced. One of the most favoured methods to infer past conditions is to apply the environmental envelope of the Nearest Living Relative (NLR), which assumes that the fossil taxon has a similar climatic tolerance and habitat to its NLR. The modern counterpart of the identified fossil is *Terminalia* (as mentioned earlier). This genus consists of about 150 species of large trees widely distributed in the tropical regions of both hemispheres (Tiwari et al., 2012) in dry deciduous forests and savannas. Considering the modern distribution, the fossil wood indicates a tropical climate unless the species has been adopted to a different climate by the lapse of millions of years.

Xylotomical characters are also reliable indicators for palaeoclimatic interpretation as plants have a direct relationship with their environment and climatic change is encoded in physiognomic change. The main physiognomic features of the described wood (absence of growth rings, diffuse-porous wood, simple perforation plates, low vessel densities, non-storied homocellular uniseriate rays and abundance of axial parenchyma) indicate a subtropical to tropical non-seasonal climate. In contrast, woods growing in temperate regions show narrow vessel diameters (< 100 µm), high vessel densities, storied heterocellular thick rays and absence of axial parenchyma (Wiemann et al., 2001; Shukla et al., 2013).

Palaeoclimatic inferences derived from the fossil woods in the absence of other plant remains such as roots, twigs, leaves, seeds and fruits may not be very reliable because woods are usually transported before preservation (Shukla et al., 2013). Consequently, the wood physiognomic features of the

fossil cannot be taken as an indication of the climate at the locality, but of the site of growth.

Wolfe and Upchurch (1987) used Carlquist's vulnerability index (1975) for measuring the susceptibility or vulnerability of wood to water shortage or drought conditions. The high 'V' (vulnerability) value (= mean vessel tangential diameter/ mean number of vessels per mm²) of 19 (95/5, see description) reported for the specimen under study suggests that the tree grew in an area of low water stress and that the tree was large because large trees have higher 'V' values than small trees and shrubs (Carlquist, 1988). A high 'M' (mesomorphy) index (= V x mean vessel element length) of 4750 (19 x 250, see description) further indicates a mesomorphic nature (Carlquist, 1975).

Evidence from the present fossil wood features is in accord with the observations on the present day distribution of genus *Terminalia* and is further justified by the V value and the M index. Accordingly, a wet subtropical to tropical non-seasonal palaeoclimate for the site of growth of this species is deduced. It must not be forgotten, however that palaeoclimate inferences based on features of only one wood species are not as informative and hence as reliable as inferences based on the study of woods of the plant assemblage, which is therefore highly needed in case of the CPF.

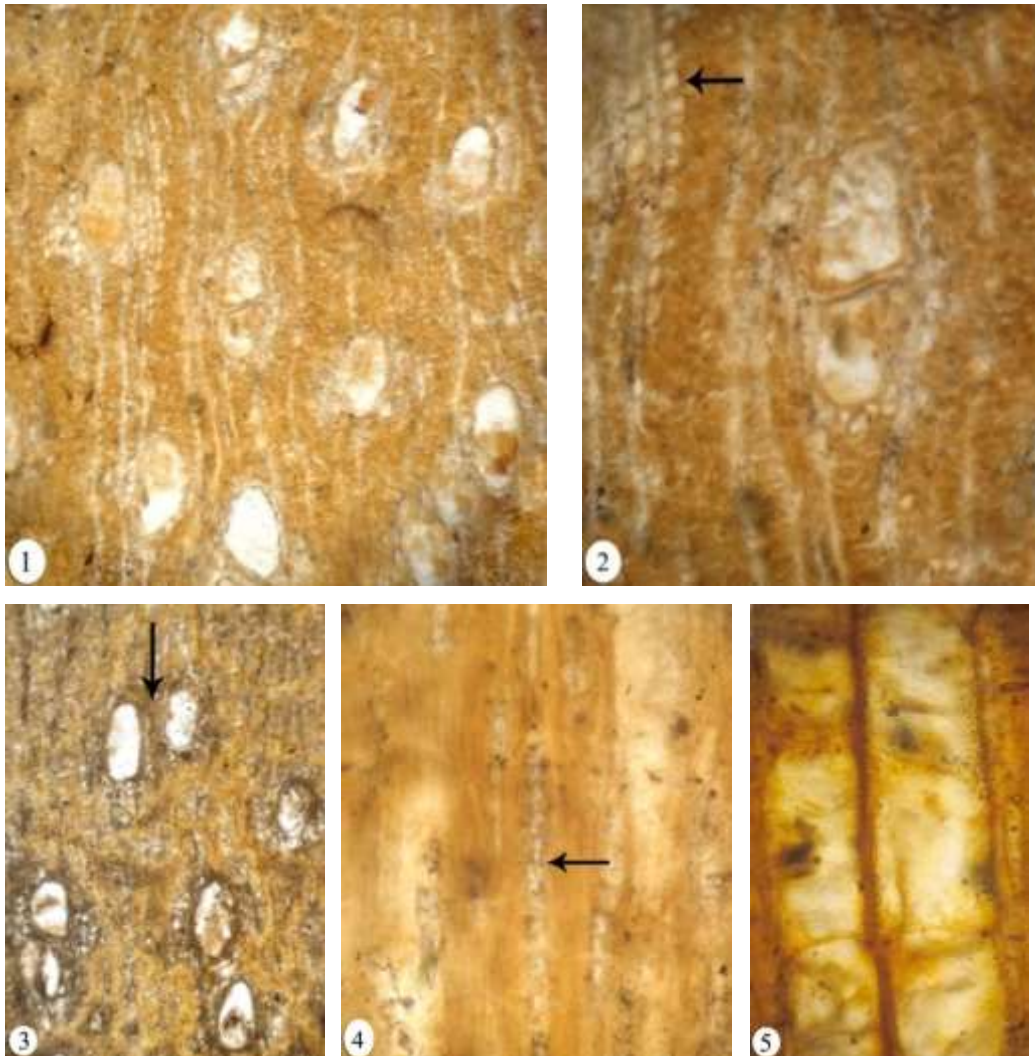


Plate I. *T. edwardsii*. 1: Cross-section showing diffuse-porous wood, vessels mostly solitary, vascentric and diffuse parenchyma, x 20; 2: Cross-section showing diffuse parenchyma (arrow), x 25; 3: Cross-section showing confluent parenchyma connecting two vessels together (arrow), x 20; 4: Tangential longitudinal section showing uniseriate rays (arrow), x 50; 5: Longitudinal section showing medium-sized vessel elements, with horizontal end-walls, x 50.

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