C. R. Palevol 9 (2010) 1–4

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

Systematic palaeontology (Palaeobotany)

Ficoxylon sp., a fossil wood of 4.4 Ma (Middle Awash, Ethiopia)

Ficoxylon SP., un bois fossile de 4,4 Ma (vallée moyenne de l'Awash, Éthiopie)

Marie-Claude Jolly-Saad[a,*], Monique Dupéron-Laudoueneix[b], Jean Dupéron[b], Raymonde Bonnefille[c]

[a] *Centre Henri-Elhaï, université Paris-Ouest–La-Défense, 200, avenue de la République, 92001 Nanterre, France*
[b] *UMR 5143 paléobiodiversité & paléoenvironnements, MNHN, 57, rue Buffon, 75231 Paris cedex 05, France*
[c] *CEREGE, europôle de l'Arbois, BP 80, 13545 Aix-en-Provence cedex 04, France*

ARTICLE INFO

Article history:
Received 17 February 2009
Accepted after revision 18 November 2009
Available online 15 January 2010

Presented by Philippe Taquet

Keywords:
Xylotomy
Dicotyledonous fossil wood
Ficoxylon sp.
Middle Awash
Pliocene
Ethiopia

ABSTRACT

In this article we describe the microscopic structures of a silicified piece of wood collected in the Middle Awash Valley (Ethiopia). The fossil wood was extracted from sediment precisely dated 4.4 Ma. Its attribution to the *Ficoxylon* species is based upon detailed comparison with published data and with comparisons of some modern species of the genus *Ficus* and similar characters encountered in fossil woods from West Africa, Egypt, Libya and Ethiopia previously described and attributed to this taxon.

Mots clés :
Xylotomie
Bois fossile de Dicotylédones
Ficoxylon sp.
Middle Awash
Pliocène
Éthiopie

RÉSUMÉ

Cet article décrit les structures microscopiques d'un fragment de bois fossile, silicifié, récolté dans la vallée moyenne de l'Awash (Éthiopie). Le bois fossilisé a été trouvé dans des dépôts datés avec précision de 4,4 Ma. Son attribution en tant que *Ficoxylon* sp. est basée sur la comparaison du bois de quelques espèces modernes du genre *Ficus*, connues en Afrique et la présence de caractères décrits pour les spécimens de bois fossiles d'Afrique de l'Ouest, de Libye, d'Égypte et d'Éthiopie, antérieurement attribués à *Ficoxylon*.

1. Methods

The Pliocene fossil wood sample (SIMA 98-39), was collected in 1998 from the Pliocene deposit in the Aramis area of the Middle Awash study area of Ethiopia. It was collected at Aramis Vertebrate Paleontology Locality 6, the holotype site for *Ardipithecus ramidus* (White et al., 1994). The analyzed fossil wood sample comes from the top 10 cm of a carbonate horizon about 30 cm thick, stratigraphically located in the interval of two $^{40}Ar/^{39}Ar$ dated tuffs (Renne et al., 1999). Therefore, a precise age of 4.4 Ma can be attributed to this fossil specimen (WoldeGabriel et al., 1994).

* Corresponding author.
E-mail address: mcsaad@u-paris10.fr (M.-C. Jolly-Saad).

1631-0683/$ – see front matter © 2009 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.
doi:10.1016/j.crpv.2009.12.001

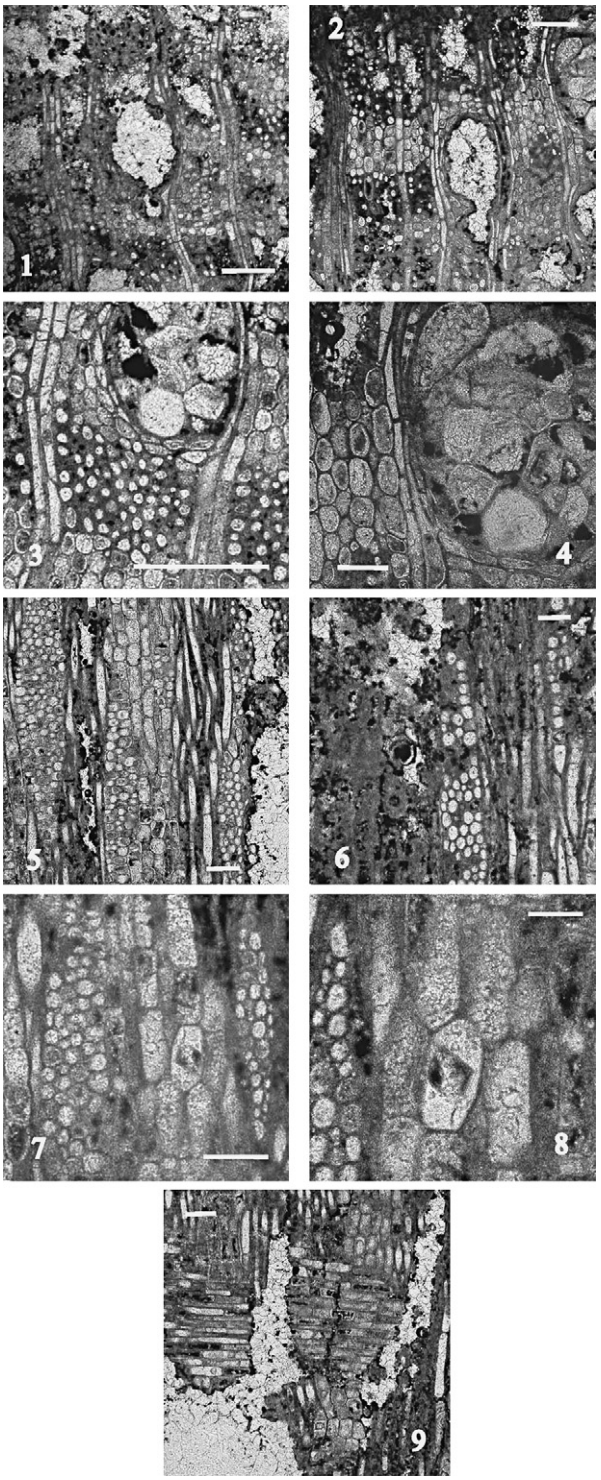

Plate 1. 1. Transverse section, general view, axial parenchyma in bands more than three cells (scale bar 160 μm). 2. Transverse section, general view, axial parenchyma in band more than three cells (scale bar 145 μm). 3. Transverse section, detail of vessel with tyloses and parenchyma band, (scale bar 190 μm). 4. Transverse section, detail of vessel with tyloses, (scale bar 35 μm). 5. Tangential section, disposition of rays, general view (scale bar 108 μm). 6. Tangential section, detail of ray, (scale bar 62 μm) 7. Tangential section, detail of rays and prismatic crystal in axial parenchyma (scale bar 45 μm). 8. Tangential section, detail of heterocellular ray structure and prismatic crystal in parenchyma cell (scale bar 84 μm). 9. Radial section, ray structure, ray composed mainly of procumbent cells with upright marginal cells (scale bar 53 μm).

The sample measures 10 cm in length, 6 × 7 cm in width. It is blackish grey in color and strongly silicified. Nine distinct thin sections along the transverse, tangential and radial planes were made from this sample at the Laboratory of Palaeobotany, MNHN Paris. They revealed only partially preserved structures. Analysis of structural characters and measurements along each plane could only be made on surfaces no greater than 5 mm^2, therefore too small to allow statistical comparisons of the measurements.

Descriptions of the microscopic structures and characteristics of the Middle Awash fossil specimen conform to the hardwood feature list of diagnostic characters as recommended by the International Association of Wood Anatomists (IAWA Committee, 1989). Identification of the fossil also refers to descriptions of wood structure by Metcalfe and Chalk, 1950; Normand and Paquis, 1976, illustrated in an atlas from Normand, 1950–1960; Lebacq, 1955–1957; Neumann et al, 2001, and was controlled through the online wood database called "Insidewood, 2008". *Ficus* fossil wood list was compared to the work of Gregory et al., 2009. Although these documents are critical tools for wood anatomy identification, the atlases mainly describe wood of commercial value geographically restricted to the Ivory Coast (Normand, 1950–1960) and to the Congo (Lebacq, 1955–1957). The database "Insidewood", containing excellent descriptions of more geographically widespread species, is still incomplete and does not include most tree species of Ethiopia. Greater precision in the identification of the Middle Awash fossil wood could be achieved in the future when a more detailed comparative reference collection of extant woods becomes available for this country.

FAMILY: MORACEAE
Genus: *FICOXYLON* Kaiser 1880
Species: *Ficoxylon* sp.

2. Anatomical description *(SIMA 98-39); MAW15 (ARA-VP-6)*

Growth rings are absent or indistinct.

- Vessels: diffuse, mostly solitary. There are five per square millimeter. Tangential diameter ranges from 138 μm to 299 μm, with a mean of 220 μm. Radial diameter ranges from 195.5 μm to 368 μm, the mean is 240 μm. Because of the poor preservation of the sample the mean was calculated only from 11 measurements.

Planche 1. 1. Section transversale, vue générale, vestige de vaisseaux et parenchyme en bandes (échelle 160 μm). 2. Section tranversale, vue générale, vestige de vaisseaux et parenchyme en bandes (échelle 145 μm). 3. Section transversale, détail d'un vaisseau et du parenchyme en bande (échelle 190 μm). 4. Section transversale, détail d'un vaisseau avec présence de thyllose (échelle 35 μm). 5. Section tangentielle, vue générale, disposition des rayons (échelle 108 μm). 6. Section tangentielle, détail d'un rayon (échelle 62 μm). 7. Section tangentielle, détail d'un rayon et parenchyme cristallifère (échelle 45 μm). 8. Section tangentielle, détail de la structure hétérocellulaire des rayons, et parenchyme cristallifère (échelle 84 μm). 9. Section radiale, structure des rayons composés de cellules couches, avec cellules dressées terminales (échelle 53 μm).

Tyloses are abundant (Plate 1 [fig. 3, 4]). Vessel members are not distinct in tangential section, their length cannot be measured and vascular pitting and the perforation plate are indistinct.

- Parenchyma: Two types of parenchyma can be distinguished. One vasicentric, surrounding the vessels, with one or two rows of elongated cells greater in length (30.8 μm) than in width (14 μm), (Plate 1, fig. 3). The second forms axial parenchyma bands more than three cells wide, three to six cells (Plate 1 [fig. 3, 4]); the cells tangential diameter range from 22.5 μm to 40 μm. The thickness of axial parenchyma bands is between 162 μm and 207 μm. Prismatic crystals occur in the parenchyma (Plate 1, fig. 7, 8).
- Rays: the tangential section shows rays one to six cells wide (27 μm to 115 μm) (Plate 1, fig. 5). Their heights range from 425.5 μm to 1127 μm (14 to 60 cells). The poor preservation of the fossil wood structures did not allow calculation of the ray density. Rays are heterocellular (Plate 1 [fig. 7, 8]), composed of procumbent cells with one or two rows of upright/square cells in the marginal cells. Prismatic crystals are present in the terminal cells. The dimensions of procumbent cells (width × height) range from 9 μm × 9 μm to 31.5 μm × 31.5 μm, and for upright cells we have 22.5 μm × 46 μm to 27 μm × 49.5 μm.
- Fibres: they are also not well preserved, and the thickness of their wall not appreciable, with no visible pits and septae. Fibres are generally circular, and the diameter measures between 13.5 μm and 18 μm in the tangential section (Plate 1 [fig. 3]).

3. Affinities

3.1. Comparisons with modern wood structure

The structural characteristics described for the Middle Awash fossil wood sample: medium size of the vessels (150 μm -300 μm), the pore density (5 pores/mm^2), large bands of abundant axial parenchyma, heterocellular, irregular and long rays, occurrences of crystals inside the parenchyma and terminal ray cells indicate a clear affinity with modern wood of trees from the Moraceae family, in particular with the genus *Ficus* (Metcalfe and Chalk, 1950; Insidewood, 2008). In Tropical Africa, the genus *Ficus* includes several hundred species. On the basis of comparison with existing descriptions or collection, it is possible to exclude a few species such as *F. mucuso* Fil., *F. sycomorus* L., et *F. vallis-choudae* Del. that have much larger rays than those shown in the Middle Awash fossil sample described in this paper (Insidewood, 2008). Strong resemblance exists between the Middle Awash fossil wood and the wood structure of *F. sur* Forssk, *F. salicifolia* Vahl. et *F. ingens* (Miq.) Miq (Insidewood, 2008), all species that cannot be distinguished from one another by their wood anatomy.

3.2. Comparisons with other fossil specimens identified as Ficoxylon

In Ethiopia, attribution to the genus *Ficus,* has been provided to six distinct specimens of fossil wood. *Ficoxylon* sp. from Upper Cretaceous/Eocene of Ethiopia (Beauchamp et al., 1973) does not include sufficient description to allow a valuable comparison with our Pliocene specimen. *Ficoxylon cretaceum* (Schenk et al., 1883) identified from the Lower Miocene site Molaie (Lemoigne et al., 1974) is clearly distinguished from the ARA VP6 fossil wood by its one to three seriate rays. *Ficoxylon blanckenhornii* (Kraüsel, 1939), from the Wondo Miocene site (Lemoigne et al., 1974) seems an erroneous attribution in regard to the original primary description of the type specimen (Kraüsel, 1939). However, as it showed small vessels (150 μm), large parenchyma bands of five to 10 cells, and three to six seriate rays, these characters exclude any attribution to *Ficoxylon blanckenhornii* for the Middle Awash fossil wood. From the Plio-Pleistocene site of the Lower Omo Valley (Dechamps and Bande, 1994) have attributed fossil wood to modern species: *Ficus* sp. with large vessels (140 μm to 450 μm), rays 25 seriate, large band of parenchyma (up to 14 cells each); *Ficus capensis* Thunb. (syn.: *F. sur* Forssk) having middle size vessels, large parenchyma bands of more than 15 cells and large rays not described more precisely by the author; *F. vallis-choudae* also having middle to large vessels, but with parenchyma bands made of three to 12 cells and one to nine seriate rays therefore larger than those in the fossil wood specimen from Middle Awash.

Attribution of the fossil wood to *Ficus*, extends elsewhere in Africa. *Ficoxylon blanckenhornii* was described from the Upper Oligocene-Lower Miocene in Egypt (Kraüsel, 1939). *Ficoxylon cretaceum* (Schenk et al., 1883) was identified in sediments dating from the Cretaceous (Kamal-El-Din, 2003) to Lower Oligocene-Lower Miocene in Egypt (Kraüsel, 1939), the Danian of Asselar, Mali (Boureau and Monod, 1949) was recorded as well in the Oligocene of Tunisia (Fessler-Vrolant, 1979), the Oligocene-Miocene of Sudanese Sahara (Boureau, 1949). Both *Ficoxylon cretaceum* and *F. blanckenhornii* appear to be present up to the Miocene. Another *Ficoxylon* sp. (Kraüsel, 1939), was noted in Upper Senonian of Egypt (Dupéron-Laudoueneix and Dupéron, 1995). Oligocene *Ficoxylon guettarense* from Libya has rays of 1 or 3 cells but intravascular pittings less than 4 μm in size (Fessler-Vrolant, 1977). Oligocene *Ficoxylon melahense* also from Libya and related to Asiatic species of *Ficus* (Louvet, 1971) is clearly distinguished from the Ethiopian Middle Awash specimen by the occurrence of storied parenchyma.

4. Discussion

Many fossil wood structures close to *Ficus* are known at least since the Cretaceous and are widespread from West Africa to Egypt, Libya and Ethiopia since the Oligocene. Among these available descriptions of fossil wood specimens, the closest resemblance of the 4.4 Ma old Pliocene specimen from Middle Awash, Ethiopia, is with *F. capensis* from the lower Omo Valley (P588-65 sect. 9, Lower Member C dated 2.7 Ma (Dechamps and Bande, 1994). However the two specimens differ in the thickness of the parenchyma. The Middle Awash fossil wood studied has thinner axial parenchyma bands than *F. capensis* (Plate 1 [fig. 2, 3, 4]).

Some authors have discussed the relationships between climate variables and wood anatomical char-

acters. (Woodcock and Ignas, 1994) indicate, "marginal parenchyma may serve as a precipitation indicator". More particularly some findings on *Ficus* have shown a seasonal variation in the size of fusiform initials; the initials are shortest and broadest in summer, especially during the rainy season. Likewise short and narrow rays increase during this period (Ajmaland and Iqbal, 1987).

However, before going further in this investigation we need a more precise calibration between extant wood anatomy and climatic variability, notably for Ethiopian species. For interpreting environmental variables, other wood anatomical characters (wood ring porous, vessels mean tangential diameter less than 100 μm, vessels with multiple perforations, spiral thickenings present in the vessels, fibre septae, rays more than 10 cells wide, rays heterocellular with 4 or more upright cells, rays storied, presence or not of axial parenchyma) have been used to estimate mean annual temperature (MAT), cold monthly mean temperature (CMMT), mean annual precipitation (MAP) and length of dry season (DRY) (Wiemann et al., 1998) and (Wiemann et al., 1999). These studies point to new opportunity for estimating paleoclimatic conditions at Middle Awash 4.4 Ma ago based upon analysis of fossil wood assemblages, providing the fact that at least ten distinct species are identified from the same beds. Until further and better preserved fossil wood specimens from the Pliocene Middle Awash study will be analyzed, the parsimonious attribution of the Middle Awash sample should remain *Ficoxylon sp*. Other descriptions of modern wood from most common trees in Ethiopia are required to relate the fossil to a modern botanical species that could also provide relevant and more precise paleoecological information. At last, this wood with additional precision from phytoliths and endocarps studies which include some species like Celtis, Myrica, palms and grasses suggests that the surroundings of the hominid site were probably open woodlands (WoldeGabriel et al., 2009).

Acknowledgements

This study was supported by grants from Berkeley University, we thank Pr. T. White. We thank the Middle Awash research project and its primary sponsors, the National Science Foundation (BCS 99-10344) and IGPP Los Alamos, and to the Revealing Hominid Origins Initiative (NSF-HOMINID-RHOI BCS-0321893). We are grateful to Mr Lemoine (CNRS, MNHN-Paléontologie. Paris) for preparing the thin sections. Mr Nicaise (UMR 5143 Paléodiversité & Paléoenvironnements, MNHN Paris) for helpful photographs. We thank the reviewers for their corrections.

References

Ajmaland, S., Iqbal, M., 1987. Seasonal rhythms of structure and behaviour of vascular cambium in Ficus rumphii. Ann. Bot. 60, 649–656.).

Beauchamp, J., Lemoigne, Y., Petrescu, I., 1973. Les paléoflores tertiaires de Debré-Libanos (Éthiopie). Ann. Soc. géol. Nord 93, 17–32.

Boureau, E., 1949. Étude paléoxylologique du Sahara. III. Présence du *Ficoxylon cretaceum* Schenk dans la flore fossile d'El Mraiti (Sahara soudanais). Bull. Mus. Natl. Hist. Nat. 21 (2), 316–320, Paris, 2e sér., t.

Boureau, E., Monod, Th., 1949. Sur l'âge des couches à *Ficoxylon cretaceum* Schenk en Afrique. C. R. Somm Soc. geol. France 13, 294–295.

Dechamps, R., Bande, M., 1994. Anatomic description of fossil woods from Lybia, Aethiopia and Zaïre. (Report not published, Royal Museum for Central Africa, Tervuren).

Dupéron-Laudoueneix, M., Dupéron, J., 1995. Inventory of Mesozoic and Cenozoic woods from Equatorial and North Equatorial Africa. Rev. Palaeobot. Palynol. 84, 439–480.

Fessler-Vrolant, C., 1977. Étude paléoxylologique du Tertiaire de la Tunisie septentrionanle (I) : présence d'un bois de la famille des Moraceae. C.R. 97e Congr. Nat. Soc. Savantes, Nantes 1972. Science 4, 19–30.

Fessler-Vrolant, C., 1979. Étude paléoxylologique de l'Afrique du Nord : sur un échantillon de *Ficoxylon cretaceum* Schenk du Djebel Cherichira (Tunisie). C.R. 104e Congr. Nat. Soc. Sav. Bordeaux 1979. Science. 1, 301–311.

Gregory, M., Poole, I., Wheeler, E., 2009. Fossil dicot wood names: an annotated list with full bibliography. IAWA J. (Suppl. 6), 220.

IAWA Committee, 1989. IAWA list of microscopic features for hardwood identification, in: Wheeler, E.A., Baas, P., Gasson, P. (Eds), IAWA Bulletin n.s. 10, pp. 219–332.

Insidewood, 2008. onwards. Published on the Internet. http://insidewood/lib.ncsu.edu/search. (Wheeler, E., Baas, P., Beeckman, H., Gasson, P., Ilic, J., Noshiro, S. et al.).

Kamal-El-Din, M.M., 2003. Petrified wood from the Farfara oasis, Egypt. IAWA J. 24 (2), 163–172.

Kraüsel, R., 1939. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Aegyptens. IV: Die Fossilen Floren Agyptens. Abhand. Bayer. Ak. Wiss., nov. ser., t. 17, 1–140.

Lebacq, L., 1955–1957. Atlas anatomique des bois du Congo. Musée royal Afrique Centrale, Tomes I, II, III, IV, V. Tervuren.

Lemoigne, Y., Beauchamp, J., Samuel, E., 1974. Étude paléobotanique des dépôts volcaniques d'âge Tertiaire des bordures est et ouest du système des rifts éthiopiens. Géobios 7 (3), 267–288.

Louvet, P., 1971. Sur l'évolution des flores tertiaires de l'Afrique Nord Equatoriale. Thèse de Doctorat d'État. Univ. Paris VI, Paris, pp. 497, 2 vols.

Metcalfe, C.R., Chalk, L., 1950. Anatomy of the Dicotyledons. Clarendon Press, Oxford, 1500 p.

Neumann, K., Schoch, W., Detienne, P., Schweingruber, F.H., Richter, H.G., 2001. Woods of the Sahara & Sahel. Verlag Paul Haupt, Bern, Stuttgart, Wien, 465 p.

Normand, D., 1950–1960. Atlas anatomique des bois de la Côte d'Ivoire. C.T.F.T., Tomes, I, II, III, IV. Nogent-sur-Marne.

Normand, D., Paquis, J., 1976. Manuel d'identification des Bois Commerciaux. 2. Afrique Guinéo-congolaise. Centre technique forestier tropical, Nogent-sur-Marne, pp. 336.

Renne, P.R., WoldeGabriel, G., Hart, W.K., Heiken, G., White, T.D., 1999. Chronostratigraphy of the Miocene-Pliocene Sagantole Formation, Middle Awash Valley, Afar Rift, Ethiopia. Geological Society of American Bulletin 111, 869–885.

Schenk, A., Fossile, Hölzer, D., Zittel, K.A., 1883. Beiträge zur Geologie und Paläontologie der libyschen Wüste und den agrenzeden Gebieten von Aegypten. Palaeontographica. Abt. I 30 (1), 1–19.

White, T.D., Suwa, G., Asfaw, B., 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. Nature 371, 306–312.

Wiemann, M.C., Wheeler, E.A., Manchester, S.R., Portier, K.M., 1998. Dicotyledonous wood anatomical characters as predictors of climate. Palaeogeogr. Palaeoclimat. Palaeoecol. 139, 83–100.

Wiemann, M.C., Manchester, S.R., Wheeler, E.A., 1999. Palaeotemperature estimations from dicotyledonous wood anatomical characters. Palaios 14, 459–474.

WoldeGabriel, G., White, T.D., Suwa, G., Renne, P.R., de Heinzelin, J., Hart, W.K., et al., 1994. Ecological and temporal placement of Early Pliocene hominids. Nature 371, 558–559.

WoldeGabriel, G., Ambrose, S.H., Barboni, D., Bonnefille, R., Bremond, L., Currie, B., et al., 2009. The Geological, Isotopic, Botanical, Invertebrate, and Lower Vertebrate Surroundings of *Ardipithecus ramidus* Sediments containing *Ardipithecus ramidus* were deposited 4.4 million years ago. Sciences (accepted).

Woodcock, D.W., Ignas, C.M., 1994. Prevalence of wood characters in eastern North America: what characters are more promising for interpreting climates from fossil woods? Am. J. bot. 81, 1243–1251.