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Foreground: Omo Beds, Shungura Formation, 1968; photo: R. Bonnefille/background created from the Figures of the article.

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Plio-Pleistocene wood from the Lower Omo Valley, Ethiopia: paleoenvironmental implications for paleoanthropological and paleontological sites

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ABSTRACT

Plio-Pleistocene sediments of the Shungura Formation in the Lower Omo Valley in Ethiopia, have been intensively prospected for their abundant African fossil fauna, including early hominin remains. In this paper, we present descriptions of 65 wood samples collected in these sediments and dated from 3.6 to 1.7 Ma. Geological studies performed during half a century all over the Turkana Lake Basins now provide precise absolute dates for each of the fossil wood samples we have studied. A total of 17 botanical families, 26 genera and four species are identified, all belonging to tropical taxa. Most of them bring new information that increases present knowledge of the late Cenozoic flora from the tropical lowlands of Ethiopia. Our interpretation of the past environment of the studied area shows the occurrence of a permanent and dense riverine forest, with tall trees and diversified taxa that varied through time. Taxa of humid tropical forests occurred during the Late Pliocene. Deciduous trees indicating seasonal climate attested to variations in the amount of rainfall and the length of dry seasons that persisted throughout the Pleistocene. These changes are discussed in parallel with other indicators such as pollen and fauna. Reconstruction of the past environment at the selected time intervals of fossil wood deposition emphasizes the great diversity of past ecosystems available to early hominins mainly *Australopithecus*, *Paranthropus* and *Homo* found in the Lower Omo valley during this time interval.

KEY WORDS

Ethiopia,
Lower Omo Valley,
Shungura Formation,
Plio-Pleistocene,
fossil wood,
hominins.

RÉSUMÉ

Bois fossiles dans la basse vallée de l'Omo (3,6-1,7 Ma), Éthiopie. Implications paléoenvironnementales pour les sites paléanthropologiques et paléontologiques.

En Éthiopie, dans la basse vallée de l'Omo, les sédiments plio-pléistocènes de la Formation de Shungura ont été intensivement prospectés pour leur abondante faune fossile africaine comprenant des restes d'homininés. Dans cet article, nous présentons les descriptions anatomiques de 65 échantillons de bois fossiles prélevés dans les sédiments datés de 3,6 à 1,7 Ma. Les nombreuses études géologiques réalisées durant un demi-siècle nous permettent d'attribuer une datation précise pour chaque échantillon. Au total, 17 familles botaniques, 26 genres et quatre espèces sont identifiés, tous appartenant à des taxons tropicaux. Ils apportent de nouvelles informations qui complètent notre connaissance de la flore des régions tropicales de basse altitude en Éthiopie, à la fin du Cénozoïque. L'interprétation des environnements passés, basée sur l'étude des bois fossiles, souligne l'existence d'une forêt riveraine permanente, et riche en taxons divers de grands arbres qui varient au cours de la période considérée. Des taxons de forêt dense humide sont présents au cours du Pliocène supérieur. Des d'arbres à feuilles caduques indiquant un climat saisonnier soumis aux variations du montant des précipitations et à celles de la durée de la saison sèche persistent pendant le Pléistocène. Les changements floristiques sont discutés en parallèle avec d'autres indicateurs tels que le pollen et la faune qui permettent de reconstruire les environnements passés durant la période de dépôt des sédiments, qui contiennent bois fossiles et restes d'homininés. Les résultats obtenus illustrent la diversité des environnements disponibles pour les hominins, *Australopithecus*, *Paranthropus* et *Homo*, trouvés dans la basse vallée de l'Omo durant la période étudiée.

MOTS CLÉS

Éthiopie,
basse vallée de l'Omo,
Formation de Shungura,
Plio-Pléistocène,
bois fossile,
homininés.

INTRODUCTION

In Ethiopia, the Plio-Pleistocene deposits of the Lower Omo Valley from south-western Ethiopia contain abundant fossil wood fragments associated with mammalian fauna including hominins. Meticulous geological work has established the stratigraphy of fluvio-lacustrine sediments (Heinzelin 1983). Numerous tuff horizons provided the first radiometric dates (Brown *et al.* 1978; Brown & McDougall 1983), and later were improved following significant progress (Brown *et al.* 1992; Brown *et al.* 2013; McDougall & Brown 2008) with regard to the great interest in these sediments for palaeoanthropological research. Geological studies have continued in the studied area until recently (Boisserie *et al.* 2008; Nutz *et al.* 2018). The age of the Lower Omo fossil macroflora is exceptionally well constrained, spanning a 2 Ma period from 3.6 to 1.7 Ma. Since the discovery of partial fossil remains of hominins from the genera *Paranthropus* Broom, 1938, *Australopithecus* Dart, 1925 and *Homo* Linnaeus, 1758 (Boaz & Howell 1977; Suwa *et al.* 1996; Daver *et al.* 2018), reconstructing the palaeoenvironmental context of the area reveals a crucial issue for understanding human evolution through time (Bonnefille 1983, 1995, 2010; Bobe *et al.* 2002; Alemseged 2003; 2023).

From 1967 to 1974, fossil woods have been intensively collected (n= 660 fragments) by the members of both the French and American Omo Research Expeditions (Coppens *et al.* 1976) from surface sediments of the Mursi, Usno and Shungura geological formations (Heinzelin 1983). Some Pliocene woods from Usno have already been described (Jolly-Saad & Bonnefille 2023), but the study presented in this paper con-

stitutes the richest collection of Plio-Pleistocene fossil woods from Ethiopia. It provides critical information to complete fossil wood and palaeobotanical data from the Mid-Miocene sediment nearby (Wheeler *et al.* 2007), and the Pleistocene exposures at the East Turkana region (Bamford 2011; Bamford 2017).

Most of the collected wood samples were assembled and curated at the Royal Museum of Central Africa in Tervuren. Many of them, sectioned for observations by the late Roger Dechamps led to cursory identifications, although not supported by formal anatomical descriptions (Dechamps 1983; Dechamps & Maes 1985). In this study, we provide new detailed descriptions and botanical identifications based upon observations of some original slides of specimens preserved in the Tervuren collection, to which we added observations of 80 new thin slides made from some other original fossil wood samples. The detailed anatomical characters are achieved through comparison with wood descriptions from modern tropical trees as available in wood databases (InsideWood 2004-onwards) and concerned literature (Wheeler 2011; Wheeler & Baas 1998). Allowing the fact that most tree species of the highly diverse forests from Ethiopia and East Africa have not yet been described, our botanical identifications of trees can only be performed at the rank of botanical family or genus and rarely at the specific level.

We address three questions: 1) was the Shungura fossil wood assemblage similar to extant subdesertic vegetation in the area? 2) what are the implications of the palaeoenvironmental results with regards to palaeoanthropological research related to the occurrence of our ancestors? and 3) how our study contributes to increase our knowledge in the history of the past vegetation in the lowlands of Ethiopia?

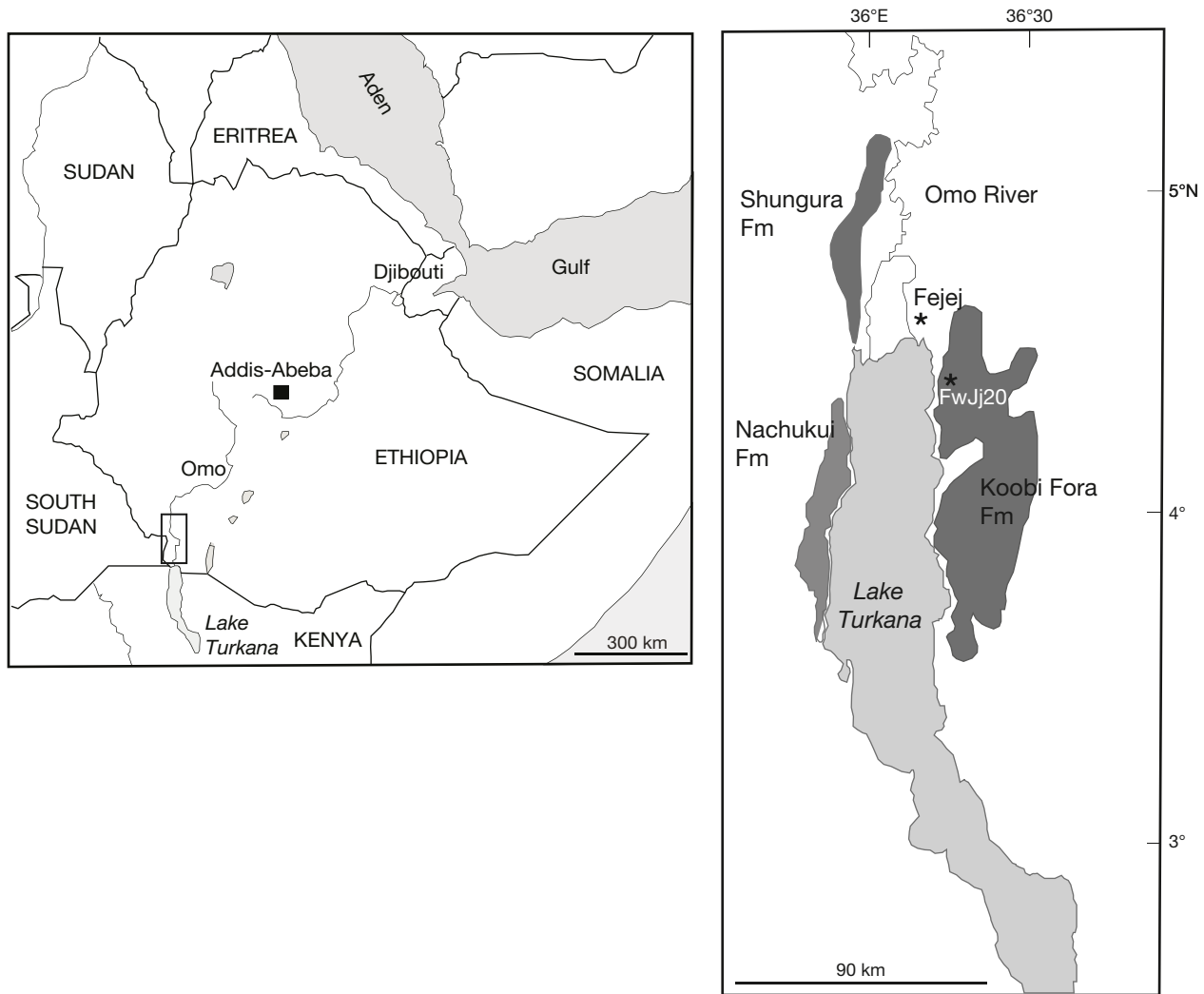


FIG. 1. — Location map of the upper Pliocene-Pleistocene Shungura Formation in the Lower Omo valley, Ethiopia.

PAST VEGETATION HISTORY IN ETHIOPIA

In Ethiopia, many sites yield abundant fossil wood fragments. The oldest concerns Cretaceous-Eocene strata from eastern Ethiopia (Beauchamp & Lemoigne 1973) whereas some others are from Tertiary deposits elsewhere, unfortunately not precisely dated (Beauchamp *et al.* 1973; Lemoigne *et al.* 1974). Fossil wood collected from the Upper Omo Valley (Lemoigne 1978) document the highlands where various forests and woodlands exist at present (Friis *et al.* 2022). These palaeobotanical studies attest to the occurrence of taxa belonging to various tropical families of angiosperms established since a very long time. For the Oligocene, abundant macrobotanical remains associated with a vertebrate fauna have been studied at Chilga, a site located in the north-western Ethiopian highlands, near Lake Tana, and dated 28-27 million years (Ma) based upon $^{40}\text{Ar}/^{39}\text{Ar}$ ages and palaeomagnetic stratigraphy (Kappelman *et al.* 2003; Jacobs *et al.* 2005). Contemporaneous with pollen (Yemane *et al.* 1985), leaf, flowers and fruit compressions with preserved cuticle, fossil wood and seeds have been intensively studied (Pan *et al.* 2006; 2010). Leaves and fruit remains from Caesalpiniaceae, *Afzelia* Sm. and *Cynometra* L. were described

(Pan *et al.* 2010) together with material of Cola Schott & Endl. (Sterculiaceae) and the palm *Sclerosperma* G. Mann & H. Wendl., now restricted to West and Central Africa (Grímsson *et al.* 2018; Pan & Jacobs 2009). Leaves and flowers indicate occurrence of *Hyphaene* Gaertn. and *Eremospatha* (G. Mann & H. Wendl.) Schaedtler, among Arecaceae (Pan *et al.* 2006) and the fern *Acrostichum* L. (García Massini *et al.* 2006). Altogether pollen and plant macrofossils from the Oligocene site at Chilga document rich and diversified forests having floristic affinities with modern West and Central African flora.

For the early Miocene, the Mush Valley site dated at 21 Ma is also located at high elevation (2480 m) on the northern Ethiopian Plateau (Pan *et al.* 2012; Currano *et al.* 2020). Abundant preserved fossil leaves indicate another type of closed canopy forest with limited palm diversity. It is dominated by a new fossil legume taxon *Englerodendron mulugetanum* Pan, Jacobs, Bush, Estrella, Grímsson, Herendeen, Burgt & Currano (Detarioideae) and includes the occurrence of *Anthonotha shimaglae* Pan, Jacobs, Currano, Estrella, Herendeen & Burgt, another extinct new fossil species of a legume Detarioideae from the *Berlinia* clade of the Miombo (Pan *et al.* 2023a). Together

with the swamp lowland palm *Sclerosperma*, the hygrophilous evergreen forest included *Hagenia* (Bruce) J.F. Gmel. (Rosaceae pollen), *Astropanax* Seem. (Schefflera, Araliaceae) and *Zanthoxylum* L. seeds (Rutaceae, syn. *Fagara* L.) (Pan *et al.* 2025). Leaf analysis yield palaeo-rainfall estimates *c.* 1600 mm/yr (Bush *et al.* 2017). The early Miocene Mush Forest has no modern analogue with regard to its floristic composition.

Mid-Miocene fossil woods recovered at Fejej, east of the Turkana Lake in lowlands of south-western Ethiopia, are dated at 16 Ma (Wheeler *et al.* 2007). At this locality, characteristic features of the fossil woods have affinities with Fabaceae, Combretaceae, Sapotaceae and Bignoniaceae. Other families, such as Annonaceae, Anacardiaceae or Chrysobalanaceae are represented by fossil fruits and seeds (Tiffney *et al.* 1994). According to the authors, characteristics of the Fejej woods are not consistent with those of a moist forest. A seasonally dry woodland or forest that include trees able to withstand drought conditions or seasonally dry conditions is more likely inferred at Fejej, located in lowlands, at a few ten kilometers distance to northeast of the Turkana depression (Fig. 1). In conclusion, former palaeobotanical studies point to a great diversity in forests types existing during the Miocene, both in the lowlands and the highlands of Ethiopia. Moreover, a significant change from rainforest to deciduous woodlands has occurred in the lowlands since the middle Miocene (Jacobs 2004).

Our paper describes fossil wood samples collected within the Plio-Pleistocene strata of the Shungura Formation located in the southwestern Ethiopian lowlands (at *c.* 400 m elevation), north of Lake Turkana, roughly between 4 and 5° North, but on the western side of the Omo River, north of its delta at Lake Turkana (Fig. 1).

GEOLOGICAL SETTING

The Shungura Formation consists mainly of sands, silts, clays, and ash layers transported by the Omo River. These deposits represent a perennial channel system and an extensive drainage basin from the Ethiopian highlands located north of Lake Turkana (Butzer 1971). The sedimentary succession of the Shungura Formation is subdivided into twelve members starting with the Basal Member, and then numbered A to L (omitting I). Numerical labeling starts from the base of the succession (Heinzelin 1983). A silicic volcanic tuff lies at the base of each member except the Basal Member (Bonnefille *et al.* 1973). For example, Member A starts at the base of Tuff A and ends at the base of Tuff B (Fig. 2). Each member is then divided into sub-members, also called units (e.g. A-1) on the basis of fining upward sequences or occurrence of an erosional surface. Some sub-members are also internally subdivided following the same procedure from the base upward (A-1-1) arranged in fining upward cycles, often ending with a palaeosol at the top (Brown *et al.* 2013). Therefore, each fossil wood sample is precisely located in the stratigraphy according to the same nomenclature (Tables 1; 2). After the first exploration of the Lower Omo Valley (Arambourg 1943), the region was intensively prospected, subsequently from 1967 to 1973, by two

distinct teams of the “International Omo Research Expedition” respectively led by the paleontologist Yves Coppens and the paleoanthropologist F. Clark Howell (Coppens & Howell 1985). The collection of most of the fossil wood was made at the same time that the whole stratigraphy of the 766 m thick deposits of the Shungura Formation was achieved (Heinzelin 1983). Dating the sediments used palaeomagnetic polarity stratigraphy (Brown *et al.* 1978; Shuey *et al.* 1974; Kidane *et al.* 2014). $\text{Ar}^{40}/\text{Ar}^{39}$ single crystal dating of anorthoclase phenocrysts followed the conventional K/Ar method (Feibel *et al.* 1989). New paleomagnetic and tephrostratigraphic correlations with dated volcanic ashes from other geological formations of the Turkana Lake added further precision to the available dates (Brown *et al.* 1992; McDougall & Brown 2006, 2008; McDougall *et al.* 2012). Most of the main dated volcanic ashes of the Turkana Basins have been identified in northern Ethiopia (Walter & Aronson 1993), and recognized in deep-sea sediments of the Indian Ocean (Sarna-Wojcickie *et al.* 1985; Feakins *et al.* 2013). The link between terrestrial and marine chronologies allows an interpretation of past vegetation changes in the Turkana Basin in light of past global climate changes. Indeed, the period included from 3.60 to 1.7 Ma experienced crucial world-wide climatic changes (Bonnefille 2010; DeMenocal 1995).

The studied samples come from specific stratigraphic units and geographical localities from almost all Members A to J (Table 1; 2). For example, G-29 corresponds to unit 29 within Member G that crops out at a geological locality P 743 (P for point) that refers to the location of a geological section described in the monograph and maps (Heinzelin 1983). In the 1970s when the fossil woods were collected, GPS technology was not available. Exact location of fossil wood samples has been made possible due to the continuity of research in the area (Boisserie *et al.* 2008; 2010, Nutz *et al.* 2020; Schuster & Nutz 2018). Geographical coordinates mentioned in Tables 1 and 2 have been recalculated with the help of C. Guillemot and J.R. Boisserie. They returned to the mentioned spots and faunal collecting localities indicated by symbols L for the USA faunal catalog and O for OMO the French catalog (Table 1; 2). In the Lower Omo Valley deposition continued from 3.75 Ma to 1.09 Ma, but appears to have ceased around 1.09 Ma without any observed major unconformity. The boundary between the Pliocene and the Pleistocene era relies upon palaeomagnetic studies and is indicated by Tuff D, equivalent to the Lokalelei Tuff exposed at West Turkana and well dated at 2.53 ± 0.01 Ma (McDougall & Brown 2008; McDougall *et al.* 2012).

In this study, we present anatomical descriptions and identifications of fossil woods according to their respective attribution to the Pliocene and Pleistocene epochs, following the stratigraphic order of the units in which they had been collected (Table 1; 2). Such presentation has been preferred since it offers the possibility of new revision of taxonomy when xylotomic descriptions of modern trees from Ethiopia may become available in the future. For palaeobotanical purposes, we include a new table illustrating the succession of botanical families according to the time scale (Table 6).

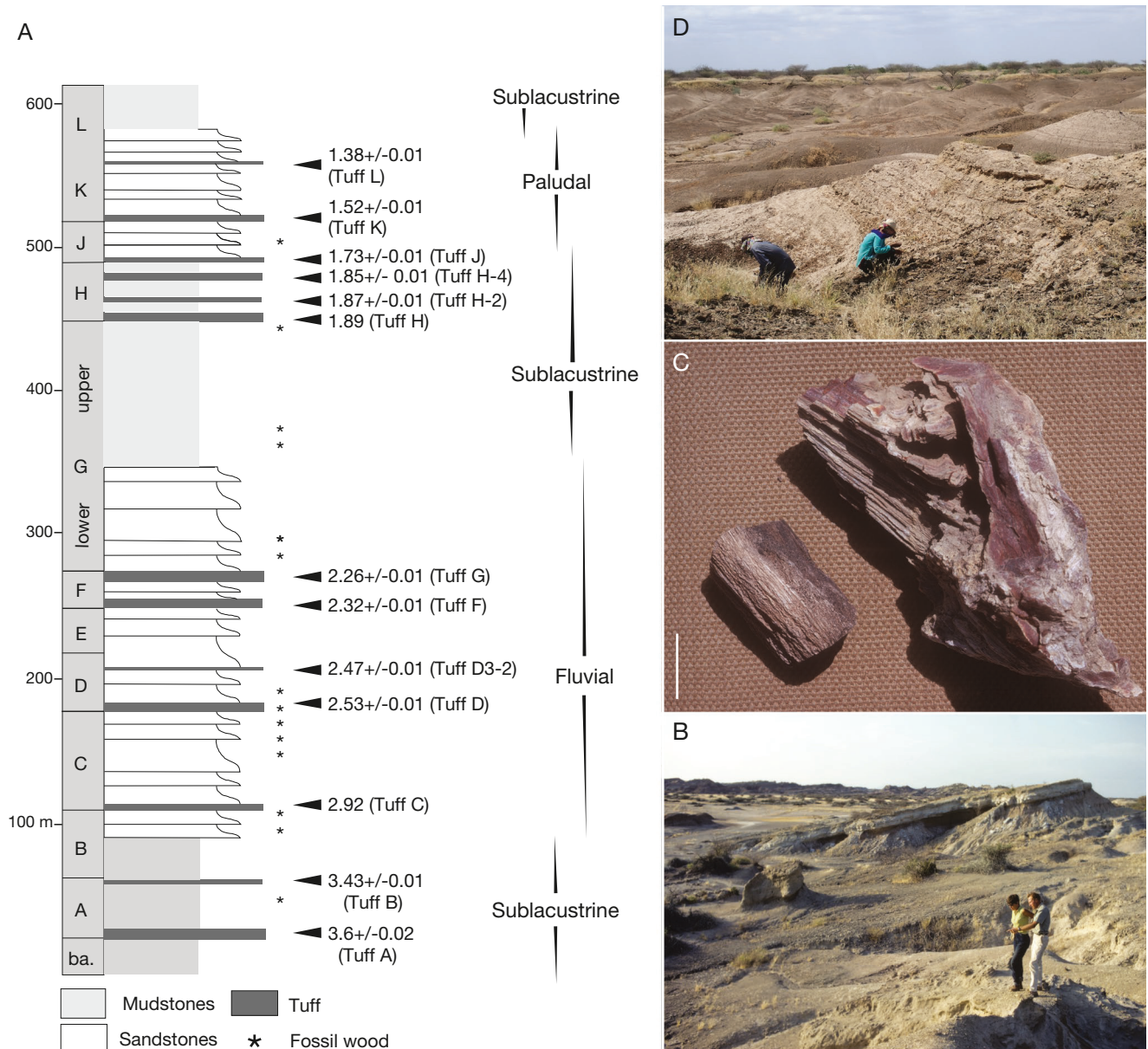


FIG. 2. — **A**, Stratigraphic succession of deposits of the Shungura Formation, Lower Omo Valley, Ethiopia (simplified from Nutz *et al.* pers. comm.), with indication of K/Ar dating of successive tuffs and levels of studied fossil wood samples; **B**, general view of the Shungura Formation with R. Bonnefille and J. Chavaillon; volcanic ash (tuff) on the top of the hill; photo: N. Zuber; **C**, fossil wood sample; **D**, sublacustrine deposit of Member G-29. Photo: J.-R. Boisserie. Scale bar: C, 2 cm.

MATERIAL AND METHODS

The collection of the studied wood from the Lower Omo Valley (Ethiopia) includes silicified twigs of various sizes, fragments of branches, and rare trunks, all preserved in the department of geology “Musée Royal d’Afrique Centrale” (MRAC) at Tervuren (Belgium). Associated slides, previously made and examined by Roger Dechamps are, for the time being, deposited and curated in the xylotheque of the department of Biology. A total of 286 slides were loaned to us, many of them remain unidentifiable due to the poor state of preservation of the wood structures. For some of them, we have made new thin sections in order to achieve proper diagnoses (Tables 1; 2).

The Shungura fossil woods are fairly well preserved, having some secondary xylem and piths suggesting rapid infiltration of the wood by a mineral, such as here silica. Mineralization process in which organic matter is gradually replaced cell by cell occurs by the infiltration of the wood in an oxygen free environment. Some of the Omo woods have fungal hyphae and spores in parenchyma and vessels. This implies that many of the wood were sapwood. The abundance of hyphae indicates that the wood fragments were in moist conditions, but not in waterlogged aerobic background. It is likely that they were wood debris on the forest floor for some time, and not water transported before being fossilized.

Standard techniques were employed to prepare thin sections of the transverse (Tr), tangential (Tg) and radial (Rd) surfaces,

TABLE 1. — List of studied and described fossil wood from the Pliocene, Shungura Formation, Lower Omo Valley, Ethiopia. *, O 127 and P 64 are the same locations, one being faunal and the other geological site. Abbreviations: **Tr**, Transversal section; **Tg**, Tangential section; **Ra**, Radial section.

Sample Number	Thin sections	Locality	Geographic coordinates	Stratigraphy	Age (Ma)	Identification	Figures
Twf 17730	Tr-Tg-Ra	P 424, sect. 15	5°04'04"N, 36°01'22"E	C-9	2.56	Combretaceae/Fabaceae gen. and sp. indet. 2	Fig. 20
Twf 17638	Tr-Tg-Ra	P 755, sect 24	5°00'09"N, 36°01'03"E	C-8	2.57	<i>Albizia</i> sp. 1	Fig. 19
Twf 17788	Tr	L 447, sect. 11	5°05'26"N, 36°01'29"E	C-8	2.57	<i>Raphia</i> sp.	Fig. 11
Twf 17805	Tr-Tg-Ra	L 448, sect. 11	5°05'26"N, 36°01'30"E	C-8	2.57	<i>Maytenus</i> sp. 1	Fig. 18
Twf 17808	Tr-Tg-Ra	L 448, sect. 11	5°05'26"N, 36°01'30"E	C-8	2.57	<i>Maytenus</i> sp. 1	
Twf 17713	Tr-Tg-Ra	L 642, sect.3	5°08'58"N, 36°01'50"E	C-6	2.61	<i>Trichilia</i> sp.	Fig. 17
Twf 17683	Tr-Tg-Ra	P 106, sect. 4	5°08'39"N, 36°01'34"E	C-5	2.62	<i>Diospyros</i> cf. <i>mespiliformis</i>	Fig. 16
Twf 17611	Tr-Tg-Ra	P 508, sect. 2	5°09'23"N, 36°02'01"E	Middle C	2.62	<i>Terminalia</i> cf. <i>macroptera</i>	Fig. 15
Twf 17812	Tr-Tg-Ra	L 46, sect. 4	5°08'39"N, 36°01'35"E	C-5	2.62	<i>Celtis</i> cf. <i>integrifolia</i>	Fig. 14
Twf 17748	Tr-Tg-Ra	P 811, sect. 4	5°08'24"N, 36°01'30"E	C-5	2.62	<i>Cordia</i> sp. 1	Fig. 12
Twf 17610	Tr-Tg-Ra	P 59, sect. 4	5°08'45"N, 36°01'32"E	C-5	2.62	<i>Cordia</i> sp. 2	Fig. 13
Twf 17839	Tr	P 180, sect. 10	5°06'10"N, 36°01'30"E	C-5	2.62	<i>Borassus</i> sp.	Fig. 11
Twf 17609	Tr-Tg-Ra	P 782 sect. 18	5°02'47"N, 36°01'27"E	B-12	2.95	<i>Maytenus</i> sp. 1	Fig. 10
Nfw 001	Tr-Tg-Ra	Locality1-North	5°03'53"N, 36°01'34"E	B-10	2.97	<i>Terminalia</i> sp. 2	Fig. 9
Twf 17679	Tr-Tg-Ra	P 788 sect. 18	5°02'38"N, 36°01'35"E	B-10	2.97	Unidentifiable	–
Twf 17872	Tr-Tg-Ra	P 64, sect. 18	5°02'58"N, 36°01'52"E	A-1-1	3.60	<i>Entandophragma</i> sp. 3	Fig. 8
Twf 17854	Tr-Tg-Ra	P 64, sect. 18	5°02'58"N, 36°01'52"E	A-1-1	3.60	<i>Entandophragma</i> sp. 2	Fig. 7
Twf 17914	Tr-Tg-Ra	O 127 = P 64*	5°02'58"N, 36°01'52"E	A-1-1	3.60	<i>Entandophragma</i> sp. 2	Fig. 7
Twf 17913	Tr-Tg-Ra	O 127 = P 64*	5°02'58"N, 36°01'52"E	A-1-1	3.60	<i>Entandophragma</i> sp. 1	Fig. 6
Twf 18054	Tr-Tg-Ra	P 64, sect. 18	5°02'58"N, 36°01'52"E	A-1-2	3.60	Fabaceae gen. and sp. indet.	Fig. 5
Twf 17873	Tr-Tg-Ra	P 64, sect. 18	5°02'58"N, 36°01'52"E	A-1-1	3.60	Combretaceae/Fabaceae gen. and sp. indet. 1	Fig. 4
Twf 17918	Tr- Tg- Ra	O 127 = P 64*	5°02'58"N, 36°01'52"E	A-1-1	3.60	<i>Terminalia</i> sp. 1	Fig. 3
Twf 18047	Tr-Tg-Ra	O 127 = P 64*	5°02'58"N, 36°01'52"E	A-1-1	3.60	Unidentifiable	–

using a diamond lapidary saw. Subsequently, the sections were ground until they reached 30 µm thickness, allowing the observation of anatomical details using a transmitted light microscope. For the anatomical descriptions, estimated values are average of 35 measurements. We photographed the petrographic thin sections using a Nikon Eclipse E 600POL microscope with a Zeiss Axiocam 305 color camera attachment and Zeiss Axiovision software. Our studied samples (n=67) are designated under their catalog number of the Tervuren Wood Fossil collection (Twf). 22 of them correspond to the Pliocene (Table 1), and 45 are from the Pleistocene (Table 2). After publications, all thin sections will be returned to the Tervuren Museum.

Wood descriptions of the thin sections of each sample follow the standardized characters defined by the International Association of Wood Anatomists (IAWA) (IAWA Committee 1989; Wheeler & Baas 1998; Wheeler *et al.* 2020). Most features are descriptive with additional quantitative measurements. Anatomical characters of the Shungura fossil woods are compared with former published descriptions of palaeobotanical species identified in Ethiopia and Africa. However, our priority is to achieve botanical affinities with the modern tropical flora of Ethiopia. We use reference material found in the InsideWood database (InsideWood 2004-onwards; Wheeler 2011) and descriptions available in published atlases (Lebacqz 1955-1963; Normand 1950; Normand & Paquis 1976; Metcalfe & Chalk 1950). Similar anatomical features being found in distinct botanical families or between families, genera or species make the botanical attribution difficult to achieve and sometimes questionable, whereas the species level is rarely reached.

The presentation of our descriptions follows the chronology and the geological ages of the wood samples, starting from the oldest one (Member A), indicated at the bottom of table 1. When many samples were found in the same stratigraphic unit and therefore having the same age, either coming from a single (for example A-1-1) or several localities (C-5), the order of the descriptions follows the alphabetic order of the taxon family (Table 1).

ABBREVIATIONS

fvb	fibrovascular bundle;
H	fungal hyphae;
Rd	radial section;
Tg	tangential section;
Tr(s)	transverse section(s);
V	vessel.

FOSSIL WOOD FROM THE PLIOCENE
(3.6 TO 2.5 MA)

MEMBER A (3.60-3.44 MA)

Member A, 35 meters thick, lies at the bottom of the Shungura Formation above Tuff A dated to 3.60 ± 0.05 Ma (McDougall & Brown 2008; Brown & McDougall 2011). This tuff corresponds to the base of the Gilbert/Gauss boundary of the palaeomagnetic timescale (Brown *et al.* 1978). Overlying Tuff B-γ has an age of 3.44 ± 0.02 Ma (Brown & McDougall 2011). Therefore, an interpolated age slightly younger than 3.6 Ma is attributed to Unit A-1-1 just above Tuff A. During earliest field prospections, abundant fossil woods were

found and collected (n = 200) from unit A-1 at the geological locality P 64, sector 18 (Heinzelin 1983). They are associated with fossil stones of the fruits of *Antrocaryon*, a genus that belongs to the Anacardiaceae (Bonnefille & Letouzey 1976). Abundant fossil bones from mammals, birds and reptiles were also collected at the same spot (paleontological locality OMO 127). Among the 39 samples sectioned by R. Dechamps, this study concerns the description and revision of 23 fossil specimens (Table 1), many of them previously attributed to *Garcinia huilensis*. They constitute the oldest wood record of the Shungura Formation dated 3.60 Ma.

Family COMBRETACEAE R.Br.
Genus *Terminalia* L.

Terminalia sp. 1
(Fig. 3)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, locality P 64; 3.6 Ma; R. Bonnefille leg.; XI.1973; Twf 17918; Tervuren collection.

DESCRIPTION

The fossil is moderately well-preserved in longitudinal sections and exhibits numerous fungal hyphae and spores within the vessel lumina, suggesting the wood was likely degraded prior to mineralization. The wood exhibits diffuse porosity with indistinct growth rings (Fig. 3A, B). Vessels are solitary (51%) or arranged in radial multiples of 2 (26.4%), 3 (18%), 4 (4%), and 5 (1%). The mean tangential diameter of the vessels is 90 µm (ranging from 34 to 145 µm), with thick walls measuring 9 µm. There are 7-15 vessels per square millimeter, featuring simple, horizontal or oblique perforation plates. Vessel element lengths measure 180-270 µm; gum deposits are visible within the vessel lumina. Intervessel-pits are alternate, small (4-5 µm), and they appear to be probably vested (Fig. 3G), vessel-ray pits are similar to intervessel-pits. The parenchyma is vasicentric, confluent, and seemingly banded, with strands likely composed of 2-4 cells. The rays are 1-3 seriate, irregular in shape, and heterocellular (Fig. 3D, H), with a frequency of 12-14 per mm (Fig. 3C, D); ray height varies (90-450 µm) and ray width range is 10-58 µm, uni-seriate rays are exclusively composed of upright cells, and pluri-seriate rays containing one or two rows of marginal upright cells. The preservation of the fossil does not allow for precise characterization of the fibres. Crystals are distinct in enlarged cells and druses are found in ray cells, and in the parenchyma cells (Fig. 3E, F).

AFFINITIES AND COMPARISONS

Twf 17918 was initially attributed to *Garcinia huilensis* (Dechamps & Maes 1985). However, several anatomical features differentiate the specimen from *Garcinia* (Clusiaceae), including the presence of crystals in ray cells, druses in parenchyma cells, and small, vested intervessel pits. The combination of vasicentric, confluent, and seemingly

banded parenchyma, heterocellular rays with variable and abundant crystals (in enlarged cells, druses in parenchyma), are more consistent with members of the subfamily Combretaceae and the subtribe Terminaliinae (InsideWood 2004-onwards; Van Vliet 1979). *Terminalia* includes ten species from Ethiopia (Vollensen 1995a). Two of them, *Terminalia brevipes* Pamp. and *T. prunoides* M.A. Lawson, have uniseriate rays. We note some similarities of our fossil with *Terminalia albida* Scott. Elliot, but due to the lack of description for other species, we identify Twf 17918 as *Terminalia* sp.

Twelve fossil wood specimens attributed to *Terminalioxylon*, the morphotype close to modern *Terminalia*, are known in Africa since the Eocene (Bamford 2003; Boureau 1955, 1958; Dupéron-Laudoueneix 1973; El-Saadawi *et al.* 2014; Fessler-Vrolant 1978, 1980; Lemoigne 1978; Lemoigne & Beauchamp 1972; Mädel-Angeliewa & Müller-Stoll 1973; Wheeler *et al.* 2007). None of them match with the Shungura fossil wood. Another fossil specimen (Twf 17919) from the Usno Formation, Omo valley, north of the Shungura Formation and extracted from Unit-19 dated 3.21 Ma) was attributed to *Terminalia* (Jolly-Saad & Bonnefille 2023). But the Usno specimen differs from the Shungura one by having less axial parenchyma and septate fibres. Twf 17918 from the Shungura Formation may represents a different and an older species than that recorded at Usno, although designated *Terminalia* sp.

Family COMBRETACEAE R.Br./FABACEAE Lindl.

Combretaceae/Fabaceae gen. and sp. indet. 1
(Fig. 4)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, locality P 64 sect. 19a; Unit A-1-1, 3.6 Ma; Twf 17873; Jean de Heinzelin leg.; Tervuren collection.

DESCRIPTION

The cross section is very poorly preserved, with fungi visible in vessels. Growth rings are absent. Wood is diffuse-porous. Vessels are solitary (37 %) or in radial multiples of 2 (37 %), 3 (18 %), 4 (5 %), 5 (1%) (Fig. 4A). Vessels are rounded in outline or slightly oval. Mean tangential diameter of 90 µm, range 76-103 µm, 11-16 per mm². Perforation plates are exclusively simple; intervessel-pits are alternate, minute, less than 4 µm and densely distributed (Fig. 4E); vessel-ray pits are indistinct. Vessel wall thickness is about 9 µm. Vessel element length is not distinct.

Rays are 2-3 seriate with short uniseriate ends, uniseriate rays are rare, 6-8 per mm, heterocellular, composed of procumbent body cells with 1-4 or more than 4 rows of square and upright cells. Ray height range is between 157-421 µm (11-37 cells); width is between 17-21 µm. Gum or other deposits are present in vessels (Fig. 4C, D). Axial parenchyma is confluent, anastomosed in irregular and wavy bands. Parenchyma strands are composed of 3-4 or 5-8 cells. Fibres are septate

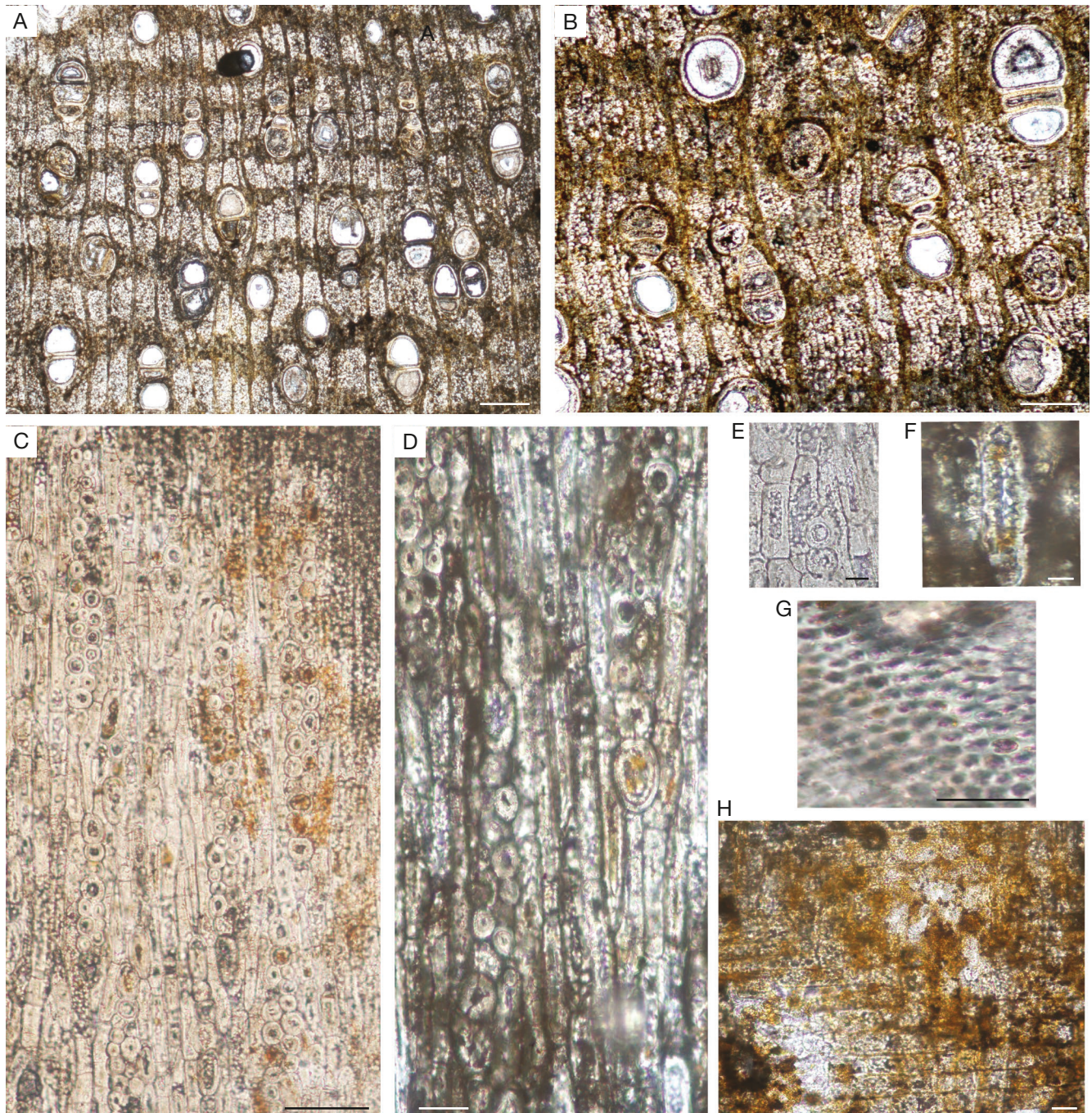


FIG. 3. — *Terminalia* sp. 1 (Combretaceae), Twf 17918: **A**, Transverse section (**Tr**), solitary vessels or in radial multiple and banded or seemingly banded parenchyma; **B**, **Tr**, detail of axial parenchyma **C**, Tangential section (**Tg**), 1-3 seriate heterocellular rays; **D**, **Tgs**, detail of rays with crystal in enlarged cells; **E**, **Tg**, vestured intervessel-pits; **F**, **Tg**, druses in parenchyma cell; **H**, Radial section (**Rd**), heterocellular rays. Scale bars: A, 200 µm; B, 100 µm; D, 50 µm; E, F, 10 µm; G, H, 20 µm. Photographs: M.-C. Jolly-Saad.

or not septate, with diameter range of 9-18 µm, medium to thick-walled; pits are not observed. Mineral inclusions are visible in all ray cells and in parenchyma (Fig. 4D).

AFFINITIES AND COMPARISONS

The combination of diffuse-porous wood, with randomly arranged vessels, minute-small vessel-pits, predominantly

paratracheal parenchyma that is vasicentric to slightly aliform, predominantly triseriate rays composed of heterocellular cells, and chambered crystalliferous axial parenchyma occur commonly in the Combretaceae or Fabaceae. Due to its poor preservation, the fossil cannot be identified more precisely than Combretaceae/Fabaceae gen. and sp. indet. 1.

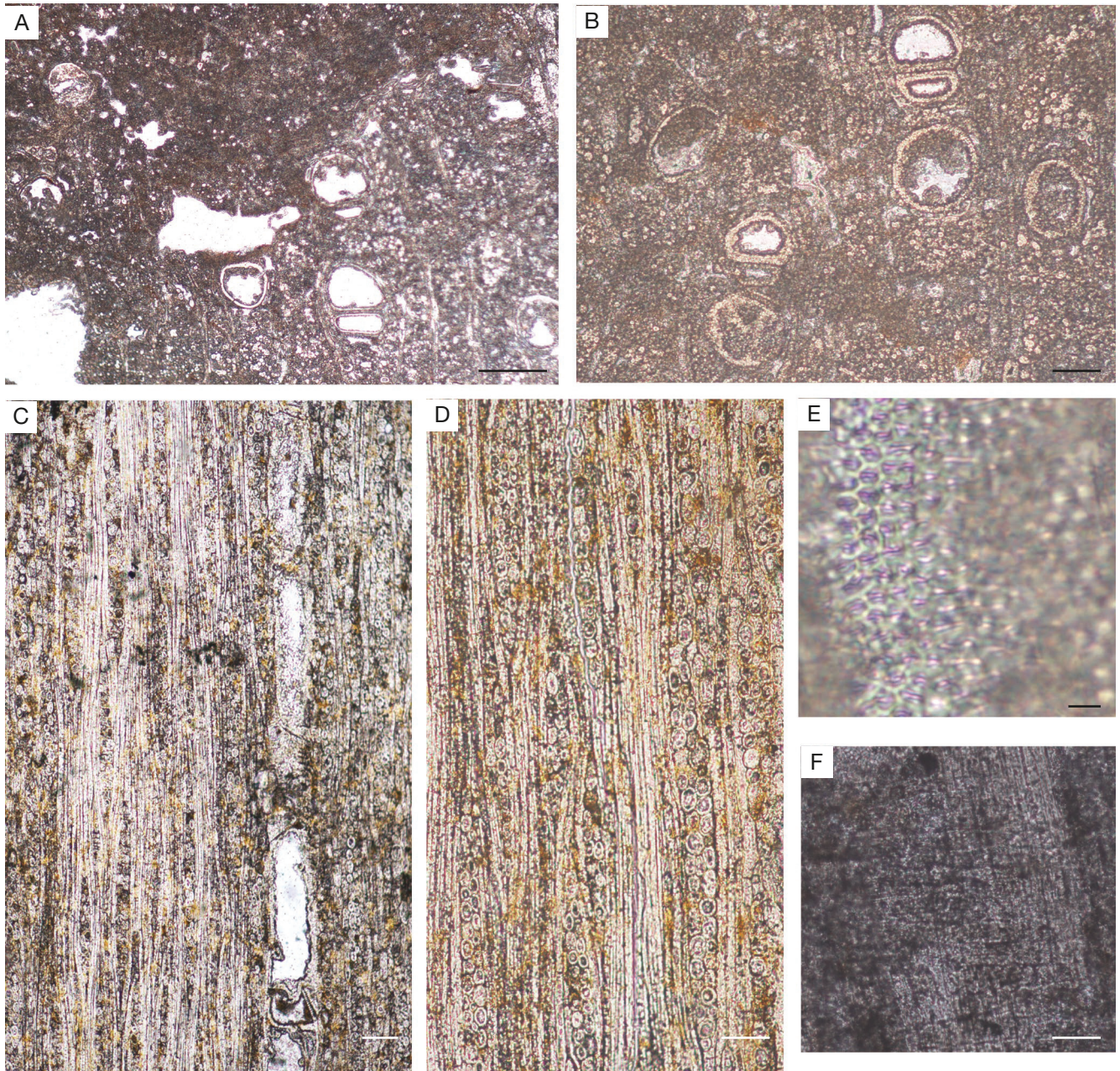


FIG. 4. — Combretaceae/Fabaceae gen. and sp. indet. 1, Twf 17873: **A, B**, Trs, diffuse vessels and seemingly and wavy banded parenchyma arrangement; **C, D**, Tg, rays 1-2 (3) seriate; **E**, Tg, vestured intervessel-pits; **F**, Rd, heterocellular rays. Scale bars: A, 200 μ m; B, C, 100 μ m; D-F, 50 μ m; E, 10 μ m. Photographs: M.-C. Jolly-Saad.

Family FABACEAE Lindl.
Subfamily MIMOSOIDEAE DC.

Fabaceae gen. and sp. indet.
(Fig. 5)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 64; Unit A-1-1, 3.6 Ma; R. Bonnefille leg.; R. Bonnefille 73-11; Twf 18054; Tervuren collection.

DESCRIPTION

Twf 18054 structure is well preserved in transverse section, but longitudinal sections appear roughly per-mineralized

and are badly preserved. Wood is diffuse-porous, growth rings marked by radially flattened latewood fibers. Vessels are mostly solitary (90%) or in radial multiple of 2-4, rounded in outline (Fig. 5A, B), with small to medium, mean tangential diameter of 108 μ m (range 54-162 μ m), 2-8 per mm²; vessel wall is thick (9 μ m). Perforation plates are exclusively simple, horizontal to slightly oblique; intervessel-pits and vessel-ray pits are indistinct, mean vessel element length 200 μ m, range 180-202 μ m, tylose is not observed.

Axial parenchyma vasicentric, aliform, strands of 1-2 cells. Rays are exclusively 1-3 seriate, not storied, consisting of procumbent cells with one row of upright cells, not greatly elongated

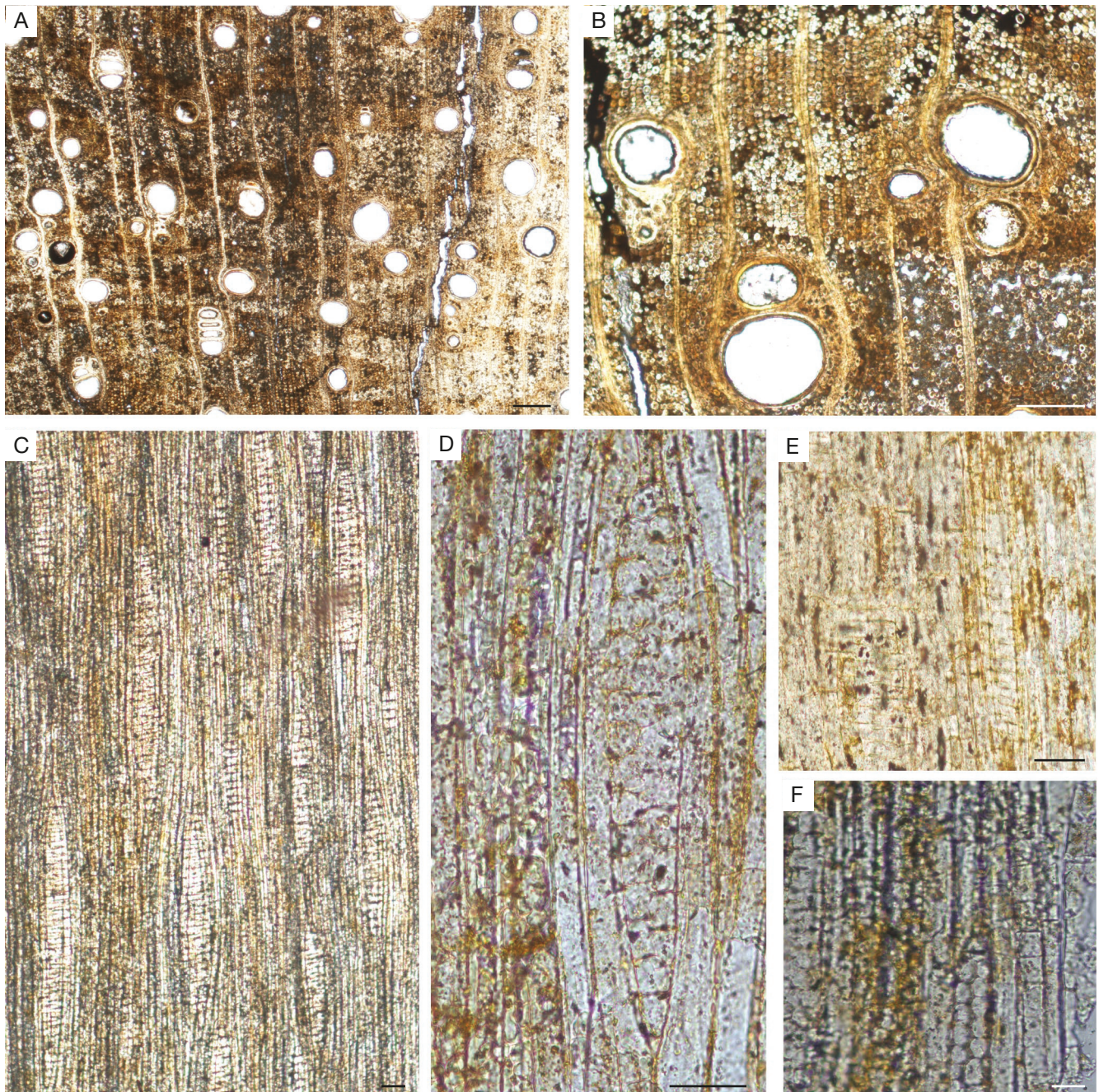


FIG. 5. — Fabaceae gen. and sp. indet. (Mimosoideae), Twf 18054: **A, B**, wood diffuse porous with axial parenchyma vasicentric aliform confluent; **C, D**, Tg, rays 1-3 seriate and homocellular; **E**, Rd, homocellular rays; **F**, uniseriate rays and parenchyma cells with crystal. Scale bars: A, 200 μ m; B, 100 μ m; C-E, 50 μ m; F, 20 μ m. Photographs: M.-C. Jolly-Saad.

radially, 8-10 rays per mm (Fig. 5C, D). Ray height range is between 190 μ m (11 cells) and 544 μ m (27 cells), ray width range is 9-15 μ m. Fibres are (likely) septate, walls medium to thick, no pits are observed. Crystals are distinct in ray cells and in chambered parenchyma in short chains (Fig. 5F).

AFFINITIES AND COMPARISONS

The combination of diffuse-porous wood, vessels solitary and in radial multiples, mean vessel diameter greater than 100 μ m, simple perforation plates, slightly heterocellular rays that can

be up to 4 or more cells wide and fewer than 12 per mm, septate fibres, crystals in parenchyma, all together suggest affinity with modern Fabaceae characterized by vested pits (Wheeler & Baas 1992). They also fit with the anatomical structure of the Mimosoideae subfamily (Evans *et al.* 2006) now re circumscribed into Caesalpinioideae subfamily by the Legume Phylogeny Working Group (LPWG 2017). However, these characters also occur in the Bignoniaceae, Sapindaceae, Moraceae and Meliaceae, but the presence of vested pits is diagnostic of Fabaceae (Wheeler & Baas 1992).

Twf 18054 specimen resembles the fossil genus *Mimosoxylon* (Müller-Stoll & Mädél 1967), but it is distinct from the five species of the genus *Mimosoxylon* described in Ethiopia and Africa. *Mimosoxylon krameri* Lemoigne from the Tertiary of the Ghibe River has uniseriate rays. *M. calpocalycoides* Lemoigne shows paratracheal vasicentric, confluent in marginal or in seemingly marginal bands axial parenchyma. *Mimosoxylon mbakaouense* Dupéron-Laudoueneix from the Tertiary of Cameroon has 1-2 seriate rays, and rare triseriate rays. *M. ducis-aprutii* (Chiarugi) has 2-3 seriate rays (Müller-Stoll & Mädél 1967). From the Pliocene in Middle Awash (Ethiopia), MA 94-73A, reported as *Mimosoxylon* sp., has less axial parenchyma and non-septate fibres (Jolly-Saad *et al.* 2012). It differs from the Shungura specimen. Other Legums fossil wood such as *Leguminosylon ouniangaense* Koeniguer from the Miocene of Chad is semi-ring porous and has biseriate rays (Koeniguer 1968). *L. lefrancii* Koeniguer from the Tertiary of eastern Fezzan in the Sahara has biseriate rays (Bonnet *et al.* 1970). In conclusion, Twf 18054 from the Shungura Formation related to the Mimosoideae subfamily does not fit any *Mimosoxylon* described in the literature. We attribute this sample to Fabaceae with a special reference to Mimosoideae.

Family MELIACEAE Juss.
Genus *Entandrophragma* DC.

Entandrophragma sp. 1
(Fig. 6)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality O 127; Unit A-1-1, 3.6 Ma; R. Bonnefille leg.; Twf 17913; Tervuren collection.

DESCRIPTION

Twf 17913 has moderate preservation and is highly mineralized with abundant fungal hyphae and spores in vessel lumina. Its structure has been partly disturbed by damage and amorphization processes. Wood is diffuse-porous with indistinct, growth rings (Fig. 6A). Vessels are solitary (40%) and in radial multiples of 2 (34%), 3 (18%), 4 (6%), 7 (1%), and clusters (1%), mean tangential diameter is 92 µm, (range 34-126 µm), vessel element range is 115 to 670 µm high, round or slightly oval in shape, 3 to 9 per mm². Tyloses are absent, gum is observed in vessels. Vessel element length varies from 135 to 368 µm. Perforation plates are exclusively simple and oblique. Minute inter-vessel pits (< 4 µm) are alternate, mostly polygonal in shape and not vested (Fig. 6E). Vessel-ray pits are not distinct. Axial parenchyma is vasicentric with 1 or 2 rows of flattened cells, bands with 3 to 6 cells height including vessels and arranged in a reticulate pattern. Bands are irregular, wavy often anastomosing. Parenchyma strands are composed of 3-8 cells.

Rays are 1 to 5 seriate, exceptionally uni or biseriate, heterocellular (Fig. 6C, D, G), 8 to 10 per mm, irregularly storied, composed of procumbent cells with one row of upright cells

(Fig. 6D). Ray height range is between 115-667 (4-31 cells), ray width range is 14-41 µm.

Fibres 5 to 18 µm in diameter have thick walls, pits are not observed, and septae clearly distinct (Fig. 6F). There are crystal inclusions in ray cells (Fig. 6G).

AFFINITIES AND COMPARISONS

Twf 17913 was initially assigned to *Garcinia huilensis* Welw. ex Oliv., among the Clusiaceae (Dechamps 1983). However, a comparison with the Insidewood database, anatomical atlas and Tervuren xylarium material references of *Garcinia huilensis* (Tw 24240) do not justify such attribution. Medium vessels, winged aliform or seemingly banded or reticulate parenchyma, simple perforation plate, heterocellular rays 1-5 wide, minute non-vestured intervessel pits, septate fibres; parenchyma in numerous, wavy or nearly straight, continuous or broken lines are all characters showing greater similarities with wood of modern Meliaceae DC., particularly with *Entandrophragma* DC. Detailed anatomical descriptions exist for seven modern species of *Entandrophragma* from Africa (Jackson 1956; Kasongo Yakusu *et al.* 2018). *E. angolense* DC., *E. congoense* (Pierre ex De Wild.) A. Chev., *E. delevoiyi* De Wild. and *E. excelsum* (Dawe et Sprague) Sprague are characterized by continuous, regularly spaced bands of parenchyma and circum vascular aliform parenchyma, rays are 3-5 seriate with oxalate crystals in the terminal cells. *E. utile* (Dawe & Sprague) Sprague has parenchyma in continuous bands and discontinuous, sinuous in growth ring, rays are 2-3 seriate, and crystal in ray cells. *E. cylindricum* (Sprague) Sprague has continuous bands and wide bands, 10-15 pore per mm², and crystal in ray cells (Panshin 1933). *E. candollei* Harms and *E. palustre* Staner are the two species having abundant parenchyma, and silica bodies in ray cells (Lebacqz 1955-1963; InsideWood 2004-onwards). But we have no information about the three modern species, *Entandrophragma bussei* Harms ex Engl., *E. caudatum* Sprague and *E. spicatum* that have a Zambezian and Afromontane geographical distribution (Kasongo Yakusu *et al.* 2018).

Among the palaeobotanical species, *Entandrophragmoxylon boureaui* Louvet (Oligocene of Algeria and Miocene of Libya) is characterized by the presence of axial canals and relatively wide rays (Louvet 1963; Koeniguer & Louvet 1968). *E. mkrataense* Louvet and *E. normandii* Louvet (Mio-Pliocene of Algeria), as well as another Meliaceae from the Miocene in Congo (Lakhanpal & Prakash 1970) differ from the Omo sample by the absence of septate fibers (Louvet 1968).

In conclusion, the Shungura fossil shares more common characters with extant species, notably *E. candollei* and *E. palustre* than with most Tertiary paleobotanical species. We assign sample Twf 17913 to *Entandrophragma* sp. 1.

Entandrophragma sp. 2
(Fig. 7)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 64 sect. 18; Member A, Unit A-1-1, 3.6 Ma; J. de Heinzelin leg.; Twf 17854, Twf 17914; Tervuren collection.

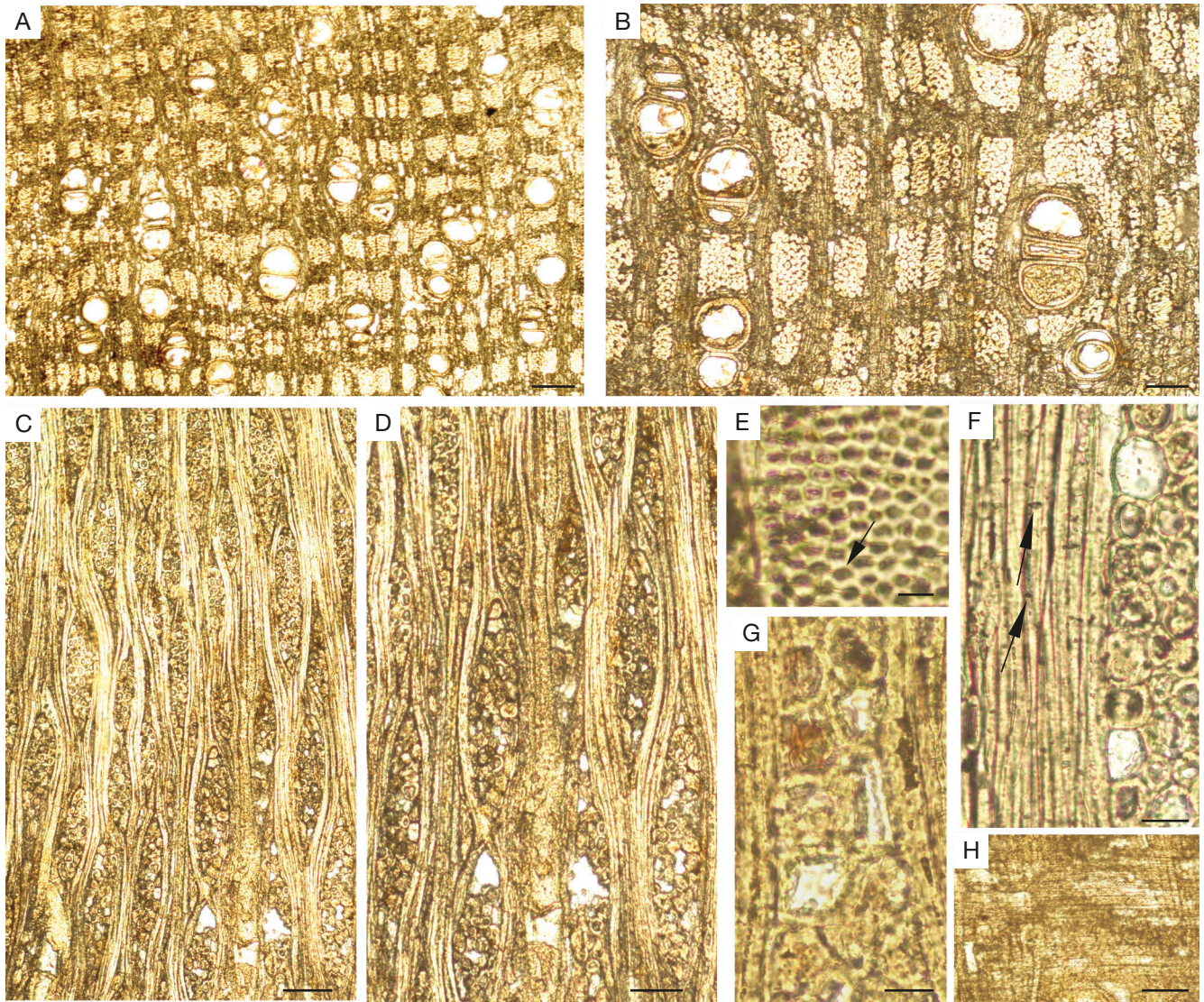


FIG. 6. — *Entandrophragma* sp. 1 (Meliaceae Juss.), Twf 17913: **A, B**, Tr, vessels solitary or in radial multiple, axial parenchyma with wavy band arrangement; **C**, Tg, 1-5 seriate rays; **D**, Tg, detail of rays with rays marginal square and upright cells; **E**, Tg, fibres with septae; **F**, Tg, minute and not vested minute intervessel-pits; **G**, Rd, heterocellular rays; **H**, Rd, crystal in ray cell (arrow). Scale bars: A, 200 μ m; B, C, 100 μ m; D, F, H, 50 μ m; E, 25 μ m; G, 5 μ m. Photographs: M.-C. Jolly-Saad.

DESCRIPTION

Twf 17854 is highly mineralized with abundant fungal spores present in vessels. The wood is diffuse-porous. Growth rings are fairly distinct (Fig. 7A) and delineated by a line of 1-2 cells of initial/terminal parenchyma (Fig. 7A, B). Vessels are solitary (59%) and in radial multiples of 2 (16%), 4 (5%) and 5 (1%), small to medium, circular to oval in shape and evenly distributed 4 to 16 vessels per mm², average thickness of vessel wall is 8-9 μ m (Fig. 7A). Tangential diameter range is 29-92 μ m (average 72 μ m), Perforation plates are simple and more or less horizontal, range of vessel element length varies from 200 to 500 μ m, inter-vessel pits are alternate, round to polygonal, small (< 4 μ m), probably not vested but the quality of the conservation makes it very difficult to make a decision (Fig. 7F). Vessel-ray pits are similar to intervessel-pits. Brown and dark deposits occur in vessels. Axial parenchyma is vasicentric, winged-aliform, banded or seemingly banded

with 1 to 6 rows of cells, densely organized (6 to 12 bands/mm), either regular or irregular, short or incomplete (Fig. 7B). Rays are (1)-2- 3 seriate, with variable height between 91 to 540 μ m, narrow width from 9 to 40 μ m (Fig. 7C, D), not storied, numerous with 12 per mm²; uniseriate rays are rare and heterocellular composed of mixed square and upright cells (Fig. 7F). Pluriseriate rays are composed of procumbent cells and have uniseriate margins of 1 to 4 cells not strongly different in shape from the body cells, 1-2 rows of distinct upright cells. Prismatic crystals occur in the ray and in non-chambered parenchyma cells. Fibres are septate with 8-14 μ m diameter width.

AFFINITIES AND COMPARISONS

The earlier identification of Twf 17854 as *Cryptosepalum exfoliatum* De Wild (Fabaceae) in Dechamps (1983) does not seem appropriate to the presently observed anatomical

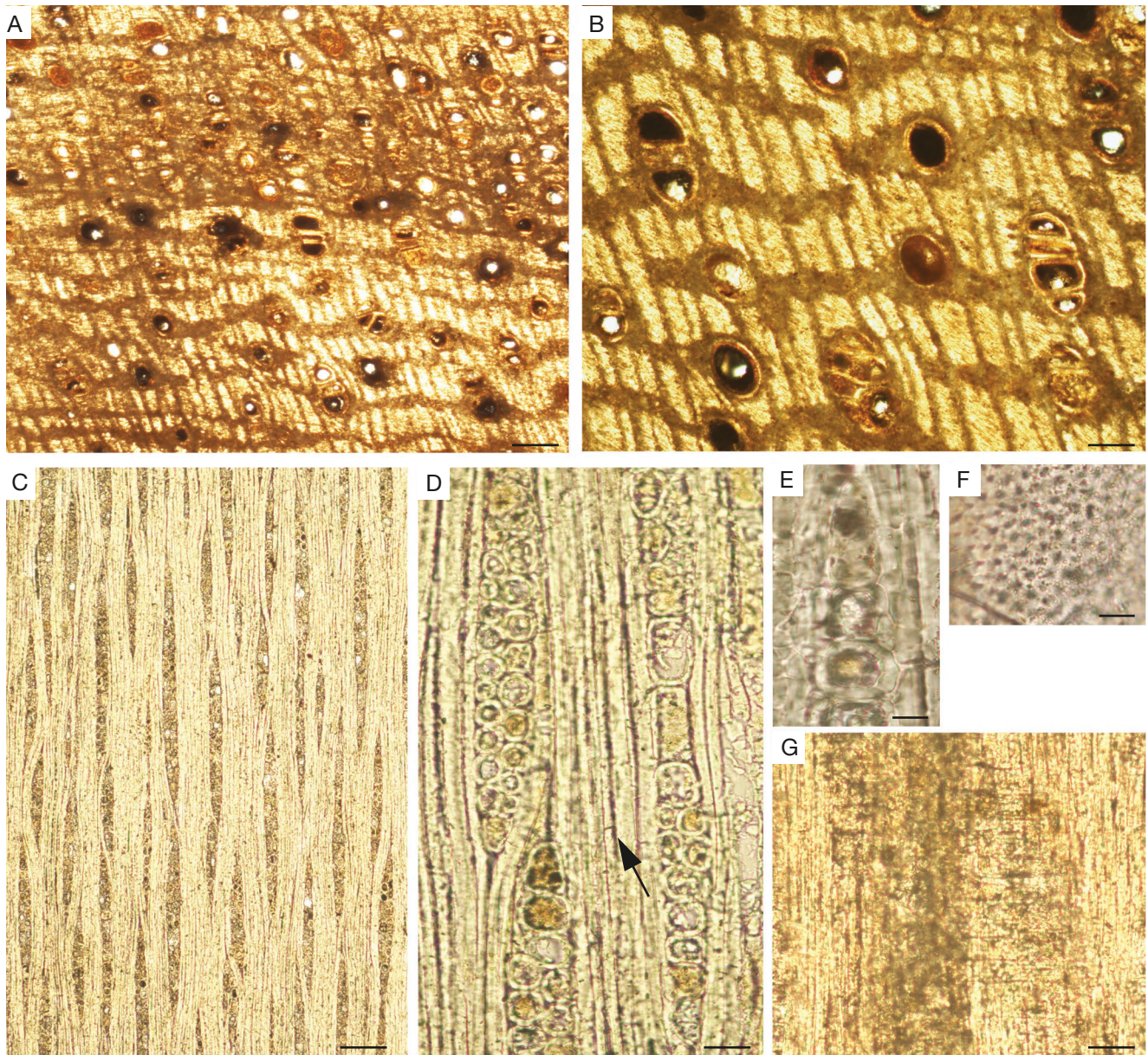


FIG. 7. — *Entandrophragma* sp. 2 (Meliaceae Juss.), Twf 17854: **A, B**, Tr, diffuse vessels and seemingly and wavy banded parenchyma arrangement; **C, D**, Tg, rays 1-2 (3) seriate and fibres with septae (**arrow**); **E**, Tg, detail of procumbent ray cells with crystals; **F**, Tg, minute intervessel-pits; **G**, Rd, heterocellular rays. Scale bars: A, 200 μ m; B, C, 100 μ m; E, F, 10 μ m; G, 50 μ m. Photographs: M.-C. Jolly-Saad.

features of the wood. In the Fabaceae, *Cynometra* shows great similarities with Twf 17854. However, the absence of septate fibres excludes it from the diagnosis. Comparison with the InsideWood database, reveals that the combination of traits, such as wood diffuse-porous with small vessels, winged aliform or seemingly banded parenchyma, simple perforation plate; 1-2-(3) seriate heterocellular rays, minute vessels-pits, septate fibres are also found in the Sapindaceae, Meliaceae and Fabaceae, but not in *Cryptosepalum*. The Sapindaceae have seemingly or banded parenchyma. However, many species of this family mentioned in the Ethiopian flora (Puff 2003) can be excluded. This is the case for *Filicium decipiens* (Wight & Am.) and *Zanha gongungensis* Hiern that differ from sample Twf 17854 by having

procumbent cells in rays, wider intervessel pits (4-7 μ m) and prismatic crystals present in ray cells. *Cardiospermum corindum* L. has prismatic crystals in fibres and in ray cells, rays 4-10 seriate with two different sizes. *Allophyllus africanus* P. Beauv. and *A. macrobotrys* Gilg have exclusively uniseriate rays. *Deinbollia kilimandscharica* Taub and *Lepisanthes senegalensis* (Fuss. ex Poir.) Leenh have prismatic crystals in the ray cells. *Haplocoelum foliolosum* (Hiem) Bullock has procumbent cells (InsideWood 2004-onwards; Klaassen 1999). Among the Meliaceae, the closest match of the Omo fossil wood fragment appears to be with *Entandrophragma*. However, sample Twf 17854 is different from Twf 17913 that has wider rays. It may belong to a different species than *Entandrophragma* sp. 2.

Entandrophragma sp. 3
(Fig. 8)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 64 sect. 19 a; Unit A-1-1, 3.6 Ma; J. Heinzelin leg.; Twf 17872; Tervuren collection

DESCRIPTION

Structures are better preserved in transversal section than in longitudinal section. Wood diffuse-porous. Growth rings absent. Vessels are solitary (45%) and in radial multiples of 2 (29 %), 3 (16 %), 4 (7 %), 5 (1%), 6 (1 %), clusters (2 %) (Fig. 8A, B). Vessels are rounded in outline or slightly oval, vessel wall thickness about 8-9 µm. Mean tangential diameter of 90 µm, range 76-103 µm, 3-18 per mm²; perforation plates are exclusively simple, intervessel pits are alternate, polygonal, less than 4 µm. The poor quality of the conservation of the material does not allow us to conclude if intervessel-pits are vested or not vested (Fig. 8E). Vessel-ray-pits are not clearly distinct. Length of vessel cannot be evaluated. Tylose and gum deposits are not observed in vessels. Axial parenchyma is vasicentric with 1 or 2 rows of flattened cells, banded (3 to 10 cells with height 22 µm to 112 µm, wavy and sometimes confluent (anastomosed). Parenchyma strands 3-5 cells.

Rays are 1-2 (3) seriate, uniseriate and triseriate rays are rare, 16-18 per mm, heterocellular (Fig. 8D, F), composed of procumbent cells with 1-2 rows of square and upright cells (Fig. 8C, D). Ray height ranges from 81 µm to 690 µm (9-34 cells), ray width ranges 20-23 µm. Short rays are storied and high rays are sometimes irregularly storied. Sheath cells are visible on some rays. Uniseriate rays are composed of square and upright cells. Fibre diameter is 13-27 µm, very thick-walled and pits are not observed, septate and non-septate fibres are observed. Crystals are distinct in ray cells that are procumbent and square and upright (Fig. 8D) and possibly present in unchambered parenchyma and fibres.

Twf 17854 and Twf 17872 differ only in the distribution of the axial parenchyma. In the case of Twf 17854, the parenchyma is irregular, or appears to be banded with patches of parenchyma that are wavy aliform and visually oblique. These two wood samples may represent two different species of *Entandrophragma*, respectively called *Entandrophragma* sp. 2 and *Entandrophragma* sp. 3 (Table 1).

Fam., gen. and sp. indet. 1

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 64; Unit A-1, 3.6 Ma ; R. Bonnefille (73-11) leg.; Twf 18047; Tervuren collection.

REMARK

The poor preserved structure of Twf 18047 in transversal section does not justify the previous attribution to *Garcinia* (Dechamps 1983). Twf 18047 remains unidentifiable.

MEMBER B (3.44-2.94 MA)

Member B has a combined thickness of 93 m and has been subdivided into twelve sedimentary units. Tuff B is a composite set of three separate ash layers (tuffs B- α , B- β , B- γ , and B- δ). After the first Potassium/Argon calculated age considered too old (Brown & Nash 1976; Heinzelin 1983), it was then established that chemical composition of Tuff B- γ was the same as the Tulu Bor Tuff from the Koobi Fora Formation (Brown & Cerling 1982) and the Sidi Hakoma Tuff (SHT) from the Hadar Formation in Northern Ethiopia (Brown 1982; Brown *et al.* 1992). The source volcano of this extensive widespread Sidi Hakoma (SHT) /Tulu Bor Tuff has been recently established as a caldera near Munesa in the Main Ethiopian Rift (WoldeGabriel *et al.* 2013). Recalculation of all published SHT ages following recent recalibration of the ⁴⁰Ar/³⁹Ar system leads to a mean age of 3.446 ± 0.041 Ma, in good agreement with the orbitally tuned age of 3.41 ± 0.01 Ma (DeMenocal & Brown 1999). This age appears in agreement with the maximum age of 3.438 ± 0.023 Ma for the Tulu Bor Tuff (McDougall & Brown 2008), and the latest age of Tuff B from the Shungura Formation (McDougall *et al.* 2012). Accordingly, a good 3.44 Ma age is attributed to the base of Member B. At the top of member B, two fossil wood samples, respectively collected from Units B-10 have a calculated age of 2.97 ± 0.01 Ma (Brown & McDougall 2011; Brown *et al.* 2013), and 2.94 Ma for unit B-12, the last unit of Member B lying just below Tuff C (Table 1).

Family COMBRETACEAE R.Br.
Genus *Terminalia* L.

Terminalia sp. 2
(Fig. 9)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality 1 North; Unit B-10-2, 2.97 Ma; R. Bonnefille leg.; Nfw 001.

DESCRIPTION

Nfw 001 is better preserved in transverse section than in longitudinal sections. The wood is diffuse-porous with growth rings only slightly marked by a reduction in fibres diameter (Fig. 9A). Vessels are solitary or in radial multiples of 2, 3 and exceptionally up to 5, there have rounded or oval outlines, and there are 5-10 per square millimeter. The mean vessel diameter is 90 µm (47-117 µm); vessels have medium thick walls. Length of vessel element is short; intervessel-pits are vested and 6-7 µm wide (Fig. 9E), vessel-ray pits are indistinct. The axial parenchyma is vasicentric, confluent or winged aliform (Fig. 9A, B). The rays are 1-4 (5) seriate but occasionally 3 cells wide (Fig. 9C, D), consisting of procumbent, square, and upright cells that are evenly dispersed throughout the rays (Fig. 9F), range height is 102-291 µm (8-47 cells). There are approximately 10-12 rays per millimeter. Prismatic crystals are visible in the ray cells (Fig. 9E).

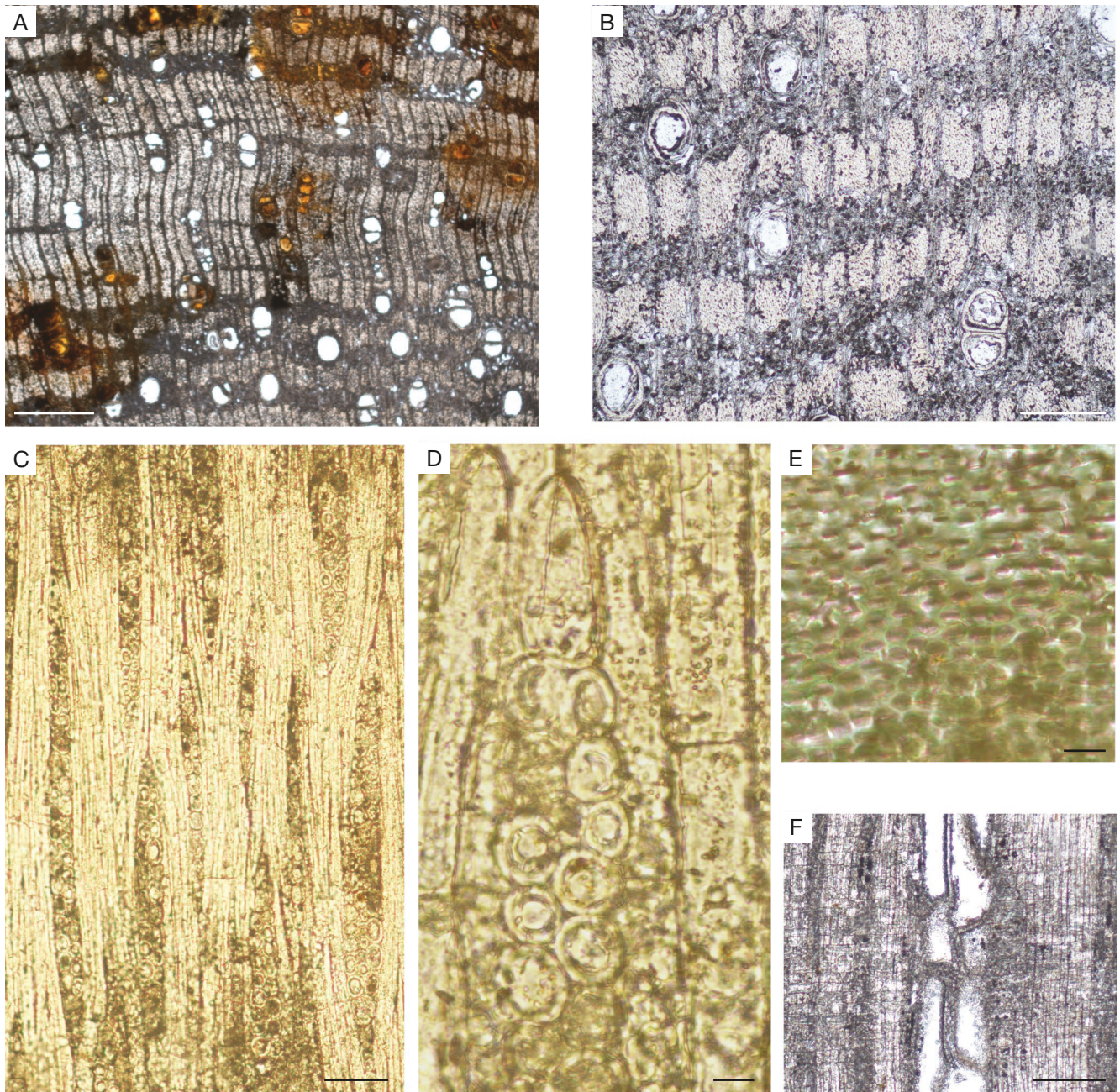


FIG. 8. — *Entandrophragma* sp. 3 (Meliaceae Juss.), Twf 17872: **A, B**, (Tr), diffuse vessels and seemingly and wavy banded parenchyma arrangement; **C, D**, Tg, 1-2 (3) seriate rays; **E**, Tg, minute intervessel pits; **F**, Ra, heterocellular rays. Scale bars: A: 200 μ m; B, C, 100 μ m; D, E, 10 μ m; F, 50 μ m. Photographs: M.-C. Jolly-Saad.

AFFINITIES AND COMPARISONS

The features that characterize Nfw 001 are: vessels solitary or in radial multiples, simple perforation plates, minute and vested vessel-pits, axial parenchyma vasicentric confluent and winged aliform; 1-4 (5) seriate rays with mixed procumbent, square and upright cells, prismatic crystals distinct in ray cells and druses in parenchyma. They are common in Combretaceae. In this family, ray cells with crystalliferous idioblasts occur in *Combretum*, *Guiera*, *Finetia* (van Vliet 1979) and *Terminalia*. The first two genera have two sizes of vessels and the third has only uniseriate rays (InsideWood 2004-onwards). *Terminalia* with vessels of one size class,

solitary or in low radial multiple, simple perforation plates, crowded and alternate vested vessel pits, confluent parenchyma, rays heterocellular with idioblasts is the most probable attribution to the Shungura fossil wood sample illustrated in Fig. 9. We do not have information on the wood structure of all the 9 species recorded in Ethiopia (Vollensen 1995a). Information is missing for *Terminalia orbicularis*, *T. spinosa* Engl., *T. prunioides* M.A.Lawson, *T. polycarpa* Engl. & Diels., *T. basilei* Chiov., *T. laxiflora* Engl. & Diels. and *T. schimperi* Hochst. ex Engl. & Diels. However, we can exclude *T. macroptera* Guill. & Perr. and *T. brownii* Fresen having 1-3 seriate rays (InsideWood 2004-onwards). *Terminalia brevipes*

Pamp., a common component of riparian forests in southern Ethiopia differs from the fossil wood sample. We have observed uniseriate rays in the tangential section of a modern specimen of *T. brevipes* (P00950891) from of the Herbarium of the Paris Museum of Natural History.

Nfw 001 also shares some diagnostic features (rays with procumbent cells and square cells mixed in the rays with one row of upright cells, intervessels pits vested, druses in chambered parenchyma and crystals in rays) described in *Terminalioxylon* G.Schönfeld (InsideWood 2004-onwards). More than 60 fossil species have been described for this palaeobotanical taxon of worldwide distribution from the Eocene to the Miocene (Gregory *et al.* 2009). Among the species identified in Africa, we can exclude those that have thinner rays such as *Terminalioxylon tunesense* Dupéron-Laudoueneix (Dupéron-Laudoueneix 1973; Delteil-Desneux 1981), *T. crystallinum* Bamford (Bamford 2003), *T. mozambicense* and *T. edwardsii* (Kräusel) Mädel-Angeliowa & Müller-Stoll, *T. primigenium* (Schenk) Mädel-Angeliowa & Müller-Stoll (El-Noamani 2020). *T. edwardsii* (Kräusel) Mädel-Angeliowa & Müller-Stoll has uniseriate rays (El-Saadawi *et al.* 2014). *T. orangensis* Bamford (Bamford 2003). Other species from Ethiopia or Sudan, such as *T. edengense* Boureau (Bureau 1955), *T. cheidense* Fessler-Vrolant (Fessler-Vrolant 1980), *T. doubingeri* (Lemoigne 1978), *T. welkitii* (Lemoigne & Beauchamp 1972), *T. fezzanense* Bureau have uniseriate rays (Bureau 1958). *T. tunesense* Dupéron-Laudoueneix has 1-3 seriate rays (Fessler-Vrolant 1980).

The late Pliocene fossil wood from the Shungura Formation is better referred to the extant genus *Terminalia* than to any *Terminalioxylon* paleobotanical species. Taking into account the state of preservation of the material, the identification involves some uncertainty; the material is designated *Terminalia* sp. 2. It differs from *Terminalia* sp. 1 (Twf 17918), collected from Member A, by its noticeably wider rays and a different distribution of axial parenchyma.

Fam., gen. and sp. indet. 1

EXAMINED MATERIAL. — Ethiopia • Lower Omo Valley, Shungura Formation, Member B; Unit B-10, 2. Ma; Twf 17679; Tervuren collection.

DESCRIPTION

Twf 17679 is poorly preserved, particularly in the tangential section and poor quality thin sections. Growth ring boundaries are not visible. The wood is diffuse-porous, vessels occurring exclusively as solitary or in radial multiple of 2 or (3), oval in shape, 5-8 per mm², gum deposits distinct in vessels. Axial parenchyma is vasicentric and banded. Vessel elements, vessel pits and rays are not visible on longitudinal sections, and no prismatic crystals observed in wood tissue.

AFFINITIES AND COMMENTS

Twf 17679 was originally identified as *Ficus* sp. (Dechamps 1983). However, due to the lack of diagnostic characters

about vessel elements, vessel pits, and rays, prismatic crystals not observed in the longitudinal planes, the identification to *Ficus* does not seem to be well founded. Twf 17679 remained unidentified (Table 1).

Family CELASTRACEAE R.Br.

Genus *Maytenus* Molina

Maytenus sp. 1

(Fig. 10)

EXAMINED MATERIAL. — Ethiopia • Lower Omo Valley, Shungura Formation, locality P 782 sect. 18; Member B, Unit B-12, 2.95 Ma; J. Heinzelin leg.; Twf 17609; Tervuren collection.

DESCRIPTION

Twf 17609 exhibits good preservation. The wood is diffuse-porous, without distinct growth ring boundaries. Vessels are exclusively solitary (Fig. 10A), round in shape with an angular outline, 35-40 per mm², mean vessel diameter is 40 µm (range between 14-58 µm); vessels are thick walled 4-5 µm. Gum deposits are distinct in vessels (Fig. 10B). Vessel elements measure 350-650 µm in length, intervessel-pits measure 3-4 µm wide and are alternate (Fig. 10F), vessel-ray pits are not visible. Axial parenchyma is extremely rare (Fig. 10B). Rays are 1-2 seriate (occasionally 3) cells wide and 20-25 per mm, composed of procumbent, square and upright cells mixed throughout the rays (Fig. 10C-E), mean height is 1500 µm, range 50-2000 µm (53-70 cells), ray width range is 12-15 µm. Alternating bands of medium to thick-walled septate fibres and thinner-walled non-septate fibres have diameters between 9-22 µm (Fig. 10A, B). Prismatic crystals are present in ray cells (Fig. 10C-E).

AFFINITIES AND COMPARISONS

The anatomical features described, such as diffuse-porous wood, solitary vessels, simple perforation plates, bands of fibres resembling parenchyma that alternate with ordinary fibres, both non-septate and septate ones, absent or scanty axial parenchyma, heterocellular rays 1-(3) seriate, axial parenchyma absent or scanty paratracheal are typical of the Celastraceae. These diagnostic characters are not found in the Ebenaceae and do not support the previous identification to *Diospyros* (Dechamps 1983).

In Ethiopia, the family Celastraceae is represented by four genera (*Catha*, *Elaeodendron*, *Maytenus* and *Mystroxydon*) comprising a total of seven species. *Catha edulis* (Vahl) End Forssk. ex Endl. has no crystal inclusions in ray cells (InsideWood 2004-onwards). *Elaeodendron buchananii* (Loes) Loes has scalariform perforations plates (InsideWood 2004-onwards). We exclude *Mystroxydon aethiopicum* (Thunb.) Loes (syn.: *Cassine aethiopica* Thunb.) which exhibits banded parenchyma, composed rays of procumbent cells with 2-4 rows of upright cells (InsideWood 2004-onwards), anatomical features not observed in the

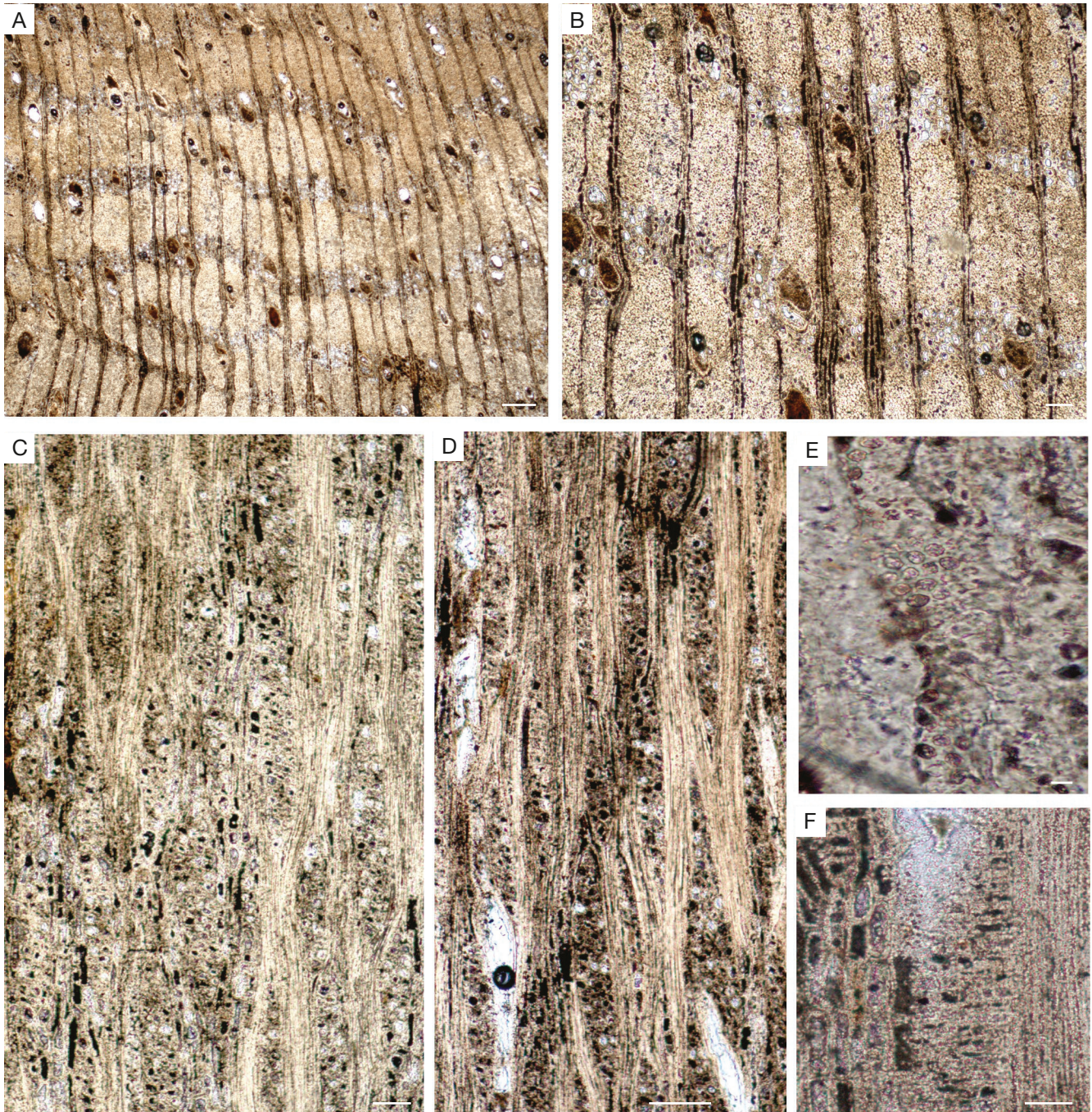


FIG. 9. — *Terminalia* sp. 2, Nfw001: **A, B**, Trs, vessels located in short wavy bands of parenchyma; **C, D**, Tgs, heterocellular rays; **E**, Tg, vestured intervessel-pits; **F**, Rds, heterocellular rays. Scale bars: A, 200 μ m; B, C, 100 μ m; D, F, 50 μ m; E, 5 μ m. Photographs: M.-C. Jolly-Saad.

fossil sample. Twf 17609 shows close affinity to *Maytenus* Molina and is attributed to *Maytenus* sp. 1.

In Ethiopia there are 12 species of *Maytenus* (Demissew 1985, 1989; Robson & Demissew 1989). Among them *M. senegalensis* (Lam.) Exell is the only species common in deciduous woodland, open dry scrub or river margins that shows similarities with Twf 17609 but exhibits a higher proportion of 3 seriate rays (InsideWood 2004-onwards).

Few paleobotanical fossil wood have been attributed to the Celastraceae. *Celastrinoxylon celastroides* (Schenk) Kräusel was recorded in Cretaceous deposits of Egypt (Kräusel 1939) and in Eocene-Paleocene strata from Harar in Ethiopia (Beauchamp & Lemoigne 1973). These paleobotanical species differ from the Shungura specimen in having wider vessel pits and banded parenchyma. Therefore, Twf 17609 is attributed to *Maytenus* sp. 1.

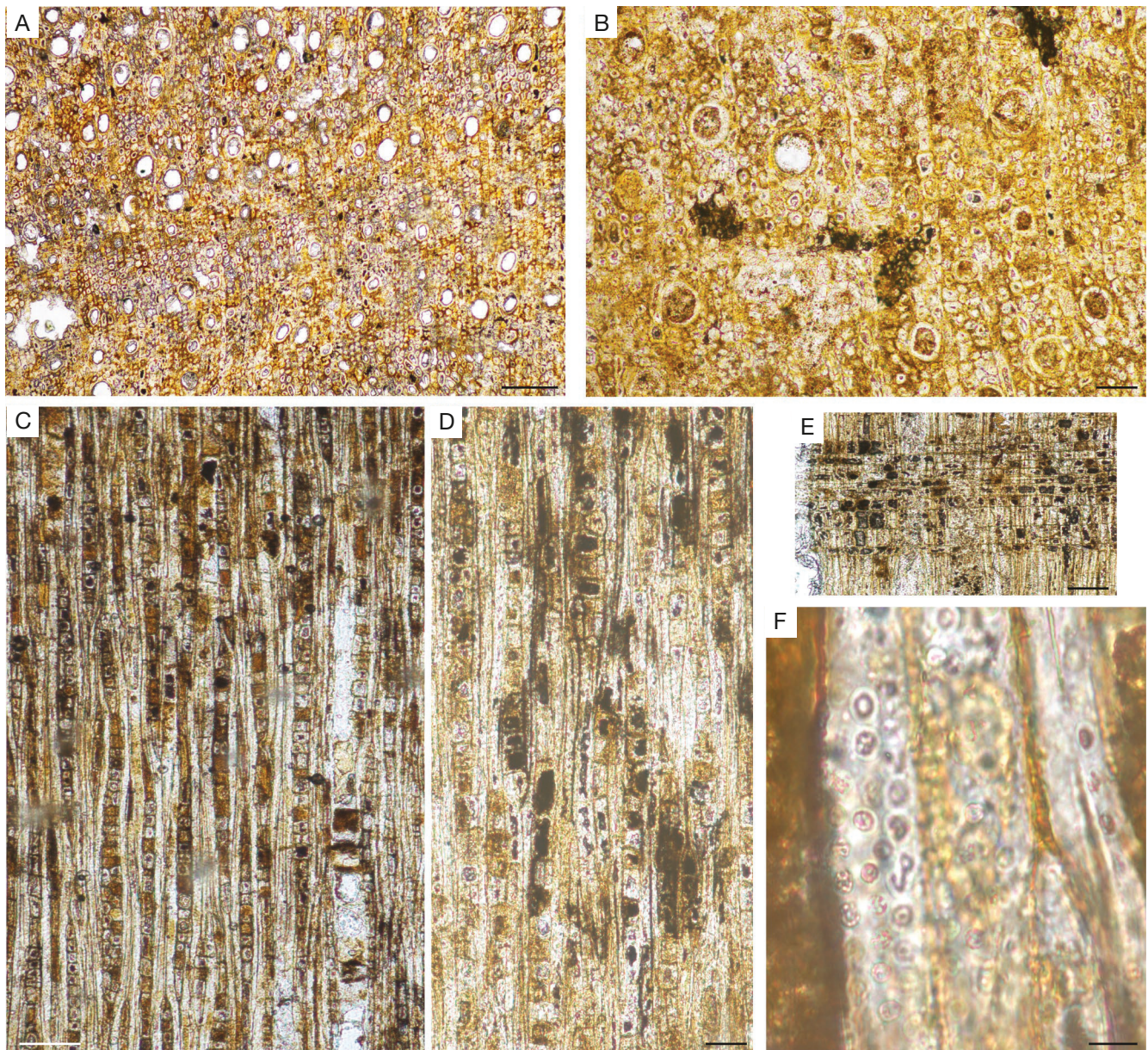


FIG. 10. — *Maytenus* sp. 1 (Celastraceae R.Br.), Twf 17609: **A, B**, Tr, diffuse porosity with small and solitary vessels, alternating bands of fibres septae and not septate; **C, D**, Tg, 1-2 seriate heterocellular rays; **E**, Rd, heterocellular rays; **F**, Tgs, small intervessel-pits. Scale bars: A, C, 100 μ m; B, D, E, 50 μ m; F, 20 μ m. Photographs: M.-C. Jolly-Saad.

MEMBER C (2.92-2.53 MA)

Member C is less than 80 m thick and represents about half a million years from 2.92 to 2.53 Ma (Kidane *et al.* 2014). It has been subdivided into nine units. The Gauss/Matuyama normal to reverse geomagnetic polarity transition occurs within unit C-7 (Kidane *et al.* 2014) and corresponds to an age of 2.59 Ma (Cande & Kent 1995; Cohen & Gibbard 2019), or 2.603 Ma using the most recent palaeomagnetic time scale (Gradstein *et al.* 2020). Tuff C-4 of the Shungura Formation correlates with the Ingumwai Tuff that lies below the Burgi Tuff dated 2.64 ± 0.04 Ma in the Koobi Fora Formation on the eastern side of Lake Turkana (Brown & McDougall

2011). Fossil wood samples collected from Units C-5 and C-6 have been attributed a minimum age of 2.62 Ma. Overlying Member C, Tuff D of the Shungura Formation, a vitric Tuff divided into two parts and containing pumices is the same as the Lokalelei Tuff dated 2.53 ± 0.03 Ma (Brown & McDougall 2011; Brown *et al.* 2013). Just below Tuff D, fossil woods from units C-8 and C-9 are slightly older with an estimated age of 2.57 Ma, well constrained between the end of the Gauss/Matuyama geomagnetic transition at 2.59 Ma (or 2.603) and the age of 2.53 Ma attributed to Tuff D. Altogether, the eleven fossil wood samples collected from Member C come from sediments deposited within a 60 ka time interval.

ANGIOSPERM MONOCOTYLEDONS

Family ARECACEAE Bercht & Presl.

Genus *Borassus* L.*Borassus* sp.

(Fig. 11)

EXAMINED MATERIAL. — Ethiopia • Lower Omo Valley, Shungura Formation, locality P 180 sect. 10; Unit C-5; 2.62 Ma; J. Heinzelin leg.; Twf 17839; Tervuren collection.

DESCRIPTION

Twf 17839 keeps the central zone of the central cylinder, but it is poorly preserved with abundant fungal hyphae (Fig. 11A). Fibrovascular bundles (fvb) are more or less crowded and mainly regular in distribution (average size 900–950 µm, average frequency 16 fvb per cm²). Sclerenchyma cap is reniform with auricular lobes rounded, median sinus deep rounded (Fig. 11B, C). Fibrous bundles are absent. The sclerenchyma cap has the r/tg mean diameters (919/463 µm). The sclerenchyma cap is made by fibrous cells having a round cross-section of 31 µm (range 13–48 µm) mean diameter; they are thick-walled (Fig. 11B). The metaxylem is badly preserved, most often compressed with a single large metaxylem vessel (90–225 µm). The phloem, usually protected under the median sinus, is not distinct. Ground tissue is compact, composed of small round thin-walled cells, tabular parenchyma and radiate parenchyma are absent or indistinct. Longitudinal thin section is missing.

AFFINITIES AND COMPARISONS

In cross section, the diagnostic xylotomical features of Twf 17839 are fibrovascular bundles with reniform sclerenchyma caps with rounded auricular lobes, badly preserved vascular part with few details on the compressed or destroyed phloem and one large metaxylem vessel. The ground tissue consists of rounded, densely packed cells.

Twf 17839 mostly resembles *Borassus* L. from the *Arecaceae* family (Tomlinson 1961; Dransfield *et al.* 2005; Tomlinson *et al.* 2011; Thomas & de Franceschi 2013). Others Ethiopian *Arecaceae* such as *Phoenix* and *Hyphaene* have been described with two metaxylem vessels (Tomlinson 1961). We exclude also *Draceana* Mand. among the Dracenoid, clade of *Asparagaceae* (APG 2016). Indeed, this genus has scattered vascular bundles in parenchyma. In transverse section, around the primary tissue at the center of the stem, the stem anatomy shows a secondary tissue that contained crowded amphivasal vascular bundles. In addition, the parenchymal cells in secondary tissue were radially and orderly arranged around amphivasal bundles in a strip shape.

Twf 17839 presents the typical structure of the stem of a palm tree, a member of the *Arecaceae* Berchtold & Presl. This structure was well defined in the original diagnosis of the paleobotanical *Palmoxylon* Schenk. Fossil remains of *Arecaceae* in Africa are documented from the Aptian to the Pleistocene including fruits, leaves, petioles, pollen, stems and phytoliths

(Pan *et al.* 2006; El-Saadawi *et al.* 2002, 2004; Kamal El-Din *et al.* 2013). The paleobotanical genus *Palmoxylon* Schenk includes 28 species described from Africa (Chiarugi 1929a, b; Louvet 1971; Delteil-Desneux & Koeniguer 1974; Dechamps 1983; El-Saadawi *et al.* 2002, 2004, 2014; Nour-El-Deen *et al.* 2018). In Ethiopia, two specimens from the Upper Omo valley have been identified as *Palmoxylon ethiopicum* (Lemoigne 1978). These specimens differ from Twf 17839 by having two large vessels and tabular parenchyma. Our specimen bears some resemblance with *P. aschersonii* Schenk notably, regarding the shape of sclerenchyma cap of fvb, and the parenchymal ground-tissue aspect. *P. aschersonii* Schenk described again from Paleogene/Neogene deposits in Algeria and Miocene of Libya was compared with the extant species *Borassus aethiopicum* Mart. (Boureau 1947). In conclusion, Twf 17839 is attributed to *Borassus* sp.

ANGIOSPERM DICOTYLEDONS

Family BORAGINACEAE Juss.

Genus *Cordia* L.*Cordia* sp. 1

(Fig. 12)

EXAMINED MATERIAL. — Ethiopia • Shungura Formation, Lower Omo Valley, locality P 811 sect. 4, Unit C-5; 2.62 Ma; Jean de Heinzelin leg.; Twf 17748; Tervuren collection.

DESCRIPTION

Twf 17748 is poorly preserved, with no fungal structures observed in any thin sections. It exhibits a diffuse, porous feature and lacks discernible growth rings. Vessels are arranged in radial lines of 2–3 pores, clusters are present (Fig. 12A). The vessel mean tangential diameter is 120 µm (range 115–138 µm), there are 2–5 vessels per mm². The mean vessel element length is 220 µm (range 100–250 µm). Intervessel-pits and vessel-ray-pits are indistinct. Distinct tyloses are visible within the vessel lumens (Fig. 12B, C). Axial parenchyma is vasicentric with one or two rows of cells and banded, usually consisting of 5–6 cells wide (Fig. 12C). Parenchyma strands have fusiform cells that are storied (Fig. 12E). Rays are 1–6 seriate, 5–6 per mm, and can reach a height of 1 mm (Fig. 12E–G), mean ray width is 80 µm (range is 75–100 µm). They are composed of procumbent cells that are accompanied by a row of square or upright cells (Fig. 12D). Sheath cells are noticeable (Fig. 12E). Fibers are medium to thick walled, storied and probably non-septate. Crystal inclusions are distinct in ray cells.

AFFINITIES AND COMPARISONS

Wide vessels solitary or in radial groups, high heterocellular pluriseriate rays, paratracheal parenchyma reticulate and in wide bands and partly storied cells, short vessel elements and sheath cells shows similarities with *Boraginaceae* and more specifically in *Cordia* (Dechamps 1983). Of the six Ethiopian

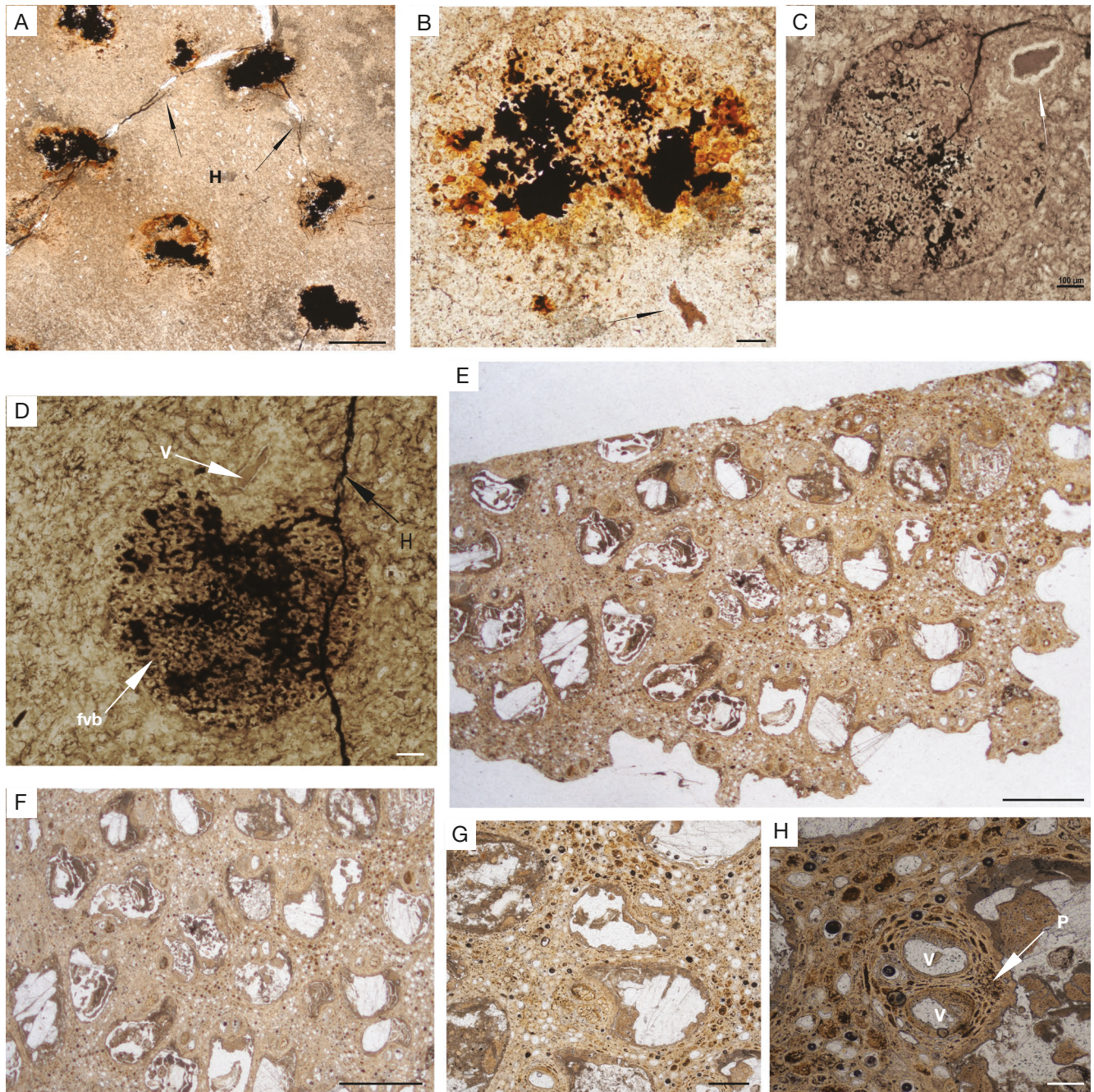


FIG. 11. — **A-D**, *Borassus* sp. 1 (Arecaceae Bercht & Presl.), Twf 17839, Tr, Poorly preserved fibrovascular bundle (**fvb**); **A**, hyphae (**arrow**) **B-D**, detail of fibrovascular bundle (**fvb**) with one vessel; **E-H**, *Raphia* sp., Twf 17788, Tr, Fibrovascular bundles (**fvb**); **G**, **H**, detail of reniforma fibrovascular bundles with two vessels and round parenchyma cells; **H**, fvb with two vessels and phloem. Abbreviations: **fvb**, fibrovascular bundle; **V**, vessel; **H**, fungal hyphae. Scale bars: A, 500 µm; B, 50 µm; C, H, 100 µm; E, 1000 µm; F, 400 µm; G, 200 µm. Photographs: M.-C. Jolly-Saad.

species (Hedberg *et al.* 2006), *Cordia africana* Lam. shows similar characters, although we have no anatomical description for the other five species *C. sinensis* Lam., *C. quercifolia* Klotzsch, *C. monoica* Roxb., *C. ellenbeckii* Gurke, *C. crenata* Del. (Riedl & Edwards 2006). Therefore Twf 17748 is attributed to *Cordia* sp. 1 with a special reference to *C. africana*.

A palaeobotanical species *Cordioxylon barthelii* Süss has been described from the southwestern Sahara in Egypt (Paleogene), but it differs from the Omo specimen by its vasicentric axial parenchyma (Süss 1987). In conclusion, due to the limited number of comparative references to extant species, Twf 17748 is attributed to *Cordia* sp. 1

Cordia sp. 2
(Fig. 13)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 59 sect. 4, Member C-5; 2.62 Ma; Jean de Heinzelin leg.; Twf 17610; Tervuren collection.

DESCRIPTION

The preservation of Twf 17610 is poor, and certain micro-anatomical features are indistinct. No fungi are visible in thin sections, the wood underwent alteration prior to its fossilisation. The wood is diffuse-porous, growth rings are absent; vessels are arranged in low radial lines of 1-3 pores, primarily singular, and few clusters are present (Fig. 13A, B). Vessel frequency is 1-4 per mm². The mean vessel element is 245 µm, and the tangential diameter of vessels ranges from 140 µm to 345 µm. Intervessels and vessel-ray pits are indistinct in thin sections. Tylosis is observed in vessels' lumina (Fig. 13B). Axial parenchyma is predominantly vasicentric, with a banding pattern, mostly 8-10 cells high or seemingly banded (Fig. 13A, B). Parenchyma strands are irregularly storied and consist of fusiform or 5-8 cells. Rays are 1-6 seriate composed of procumbent cells with 1-2 rows of square and upright cells, more than 1 mm high (range 595-1299 µm), mean ray width 80 µm (range 43-130 µm) (Fig. 37C), they are 4 per mm. Sheath cells are present. The fibres are medium to thick walled, storied (Fig. 37D) and most likely not septate. Ray cells contain clear crystal inclusions, idioblast (Fig. 37E, F).

AFFINITIES AND COMPARISON

Twf 17610 shows wide solitary vessels or radial groupings, high heterocellular pluriseriate rays, paratracheal parenchyma that is reticulate in wide bands and partly composed of storied cells, short vessel elements, sheath cells, indicating similarities with Boraginaceae and more specifically with *Cordia* in accordance with Dechamps' diagnosis.

Twf 17610 is related to Twf 17748, described above as *Cordia* sp. 1 (Table 1; Fig. 12). However, it differs by having larger vessels and therefore is designated as *Cordia* sp. 2. (Fig. 13; Table 1).

Family CANNABACEAE Martinov
Genus *Celtis* L.

Celtis cf. *integrifolia*
(Fig. 14)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality L 46-36 sect. 4; Unit C-5, 2.62 Ma; Jean de Heinzelin leg.; Twf 17812; Tervuren collection.

DESCRIPTION

Twf 17812 shows moderate preservation, devoid of any fungal presence. It belongs to the diffuse-porous type, with either indistinct or entirely absent growth rings. The vessels

are mostly solitary (61%), with some in radial multiples of 2 (28%) and 3 (11%) (Fig. 14A). Their mean tangential diameter is 185 µm, ranging from 138-230 µm, and there are 1-4 per square millimeter. Intervessel-pits are 7-8 µm wide, sometimes coalescent, crowded alternate, and have an angular outline (Fig. 14A). Vessel-ray-pits are similar to intervessels-pits. The axial parenchyma is vasicentric, around 1-5 cells wide, aliform, and sometimes confluent around 3 to 4 vessels (Fig. 14A). Parenchyma strands are made of 3-4 to 5-8 cells. The rays range from 1-10 cells wide (Fig. 14C, D), mean ray height is 400 µm (range is 268-618 µm) and mean rays width is 90 µm (range 70-100 µm) they are composed of procumbent cells containing one or two rows of square and upright cells (Fig. 14D, E). Uniseriate rays are entirely formed of upright cells, totaling 7-8 per mm. Sheath cells are clearly distinguishable. Fibres have thin walls and are not partitioned. Prismatic crystals are present in both the ray cells and chambered parenchyma cells (Fig. 14F-G).

AFFINITIES AND COMPARISONS

The observed anatomical features: diffuse-porous wood, vasicentric to confluent axial parenchyma, prismatic crystal in square or upright cells, wide multiseriate rays and sheath cells, resemble more closely *Celtis* cf. *C. integrifolia* than *Kigelia africana* to which it was erroneously attributed (Dechamps 1983), prismatic crystals are absent in *Kigelia* and intervessel pits are bigger than those of Twf 17812.

To the best of our knowledge, no fossil *Celtis* wood are known from Africa. Three generic names – *Celtisoxylon* Triverdi, *Celtixylon* Greguss and *Celtoxylon* Wurzinger – created for fossil woods resembling *Celtis* were not properly diagnosed (Gregory *et al.* 2009). *Celtisoxylon* was applied to a wood from Deccan inter-trappean beds of India, but only mentioned in an abstract without diagnosis or designation of holotype, *Celtixylon* was never formally diagnosed and *Celtoxylon*, mentioned in a Ph'D thesis, was never formally published. Woods thought to have affinities with *Celtis* have been reported from the Miocene Europe, and Asia (Selmeier 1989, 2015), and North America (Wheeler & Manchester 2021). Twf 17812 attributed to *Celtis* thus represents the first documented occurrence of this genus in Africa.

Family COMBRETACEAE R.Br.
Genus *Terminalia* L.

Terminalia cf. *macroptera*
(Fig. 15)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 508; Middle Member C, 2.62 Ma; Jean de Heinzelin leg.; Twf 17611; Tervuren collection.

DESCRIPTION

The specimen displays moderate preservation in both transverse and tangential sections, and better preservation in the

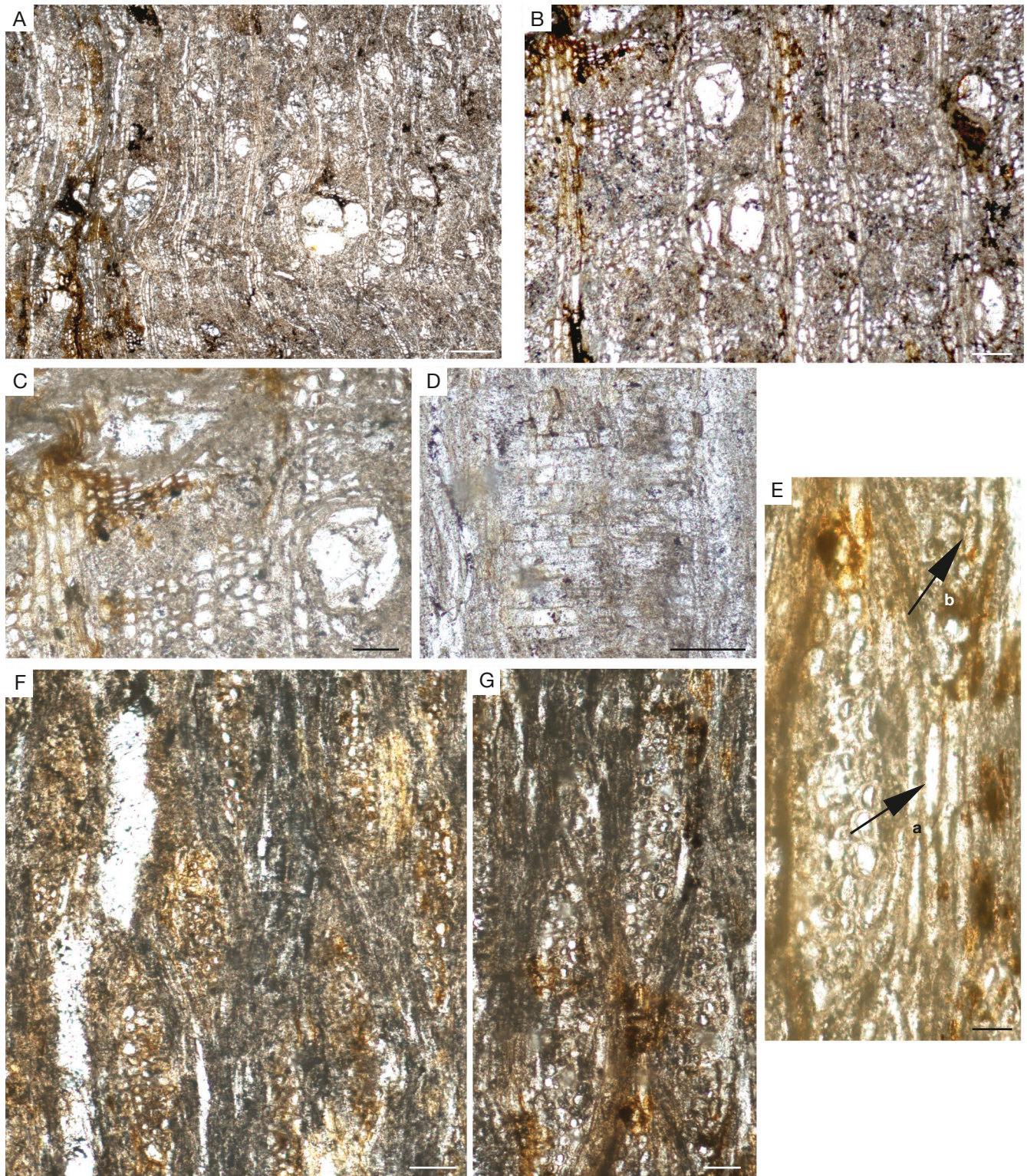


FIG. 12. — *Cordia* sp. 1 (Boraginaceae Juss.), Twf 17748: **A-C**, Tr, vessels solitary or in short radial multiple and banded axial parenchyma; **D**, Rd, heterocellular rays; **E**, Tg, (a) storied parenchyma (arrow) and (b) sheath cells (arrow); **F, G**, Tg, rays organization. Scale bars: A, 200 μ m; B, D, F, 100 μ m; C, E, G, 50 μ m. Photographs: M.-C. Jolly-Saad.

radial section. Fungi are not present. Wood diffuse-porous is without growth rings. Vessels are solitary (63%) and in radial multiples of 2 (29%), 3 (7%), 4 (0.5%) and 5 (0.5%). Mean tangential diameter of 86 μ m (range 34-103 μ m), 6-20 vessels

per mm^2 (Fig. 15A, B). Perforation plates are exclusively simple; intervessel-pits are crowded alternate with areoles, 5-6 μ m wide and vested (Fig. 15E); vessel-ray pits are similar to vessel-pits; mean vessel element length short 126-137 μ m, gum-like

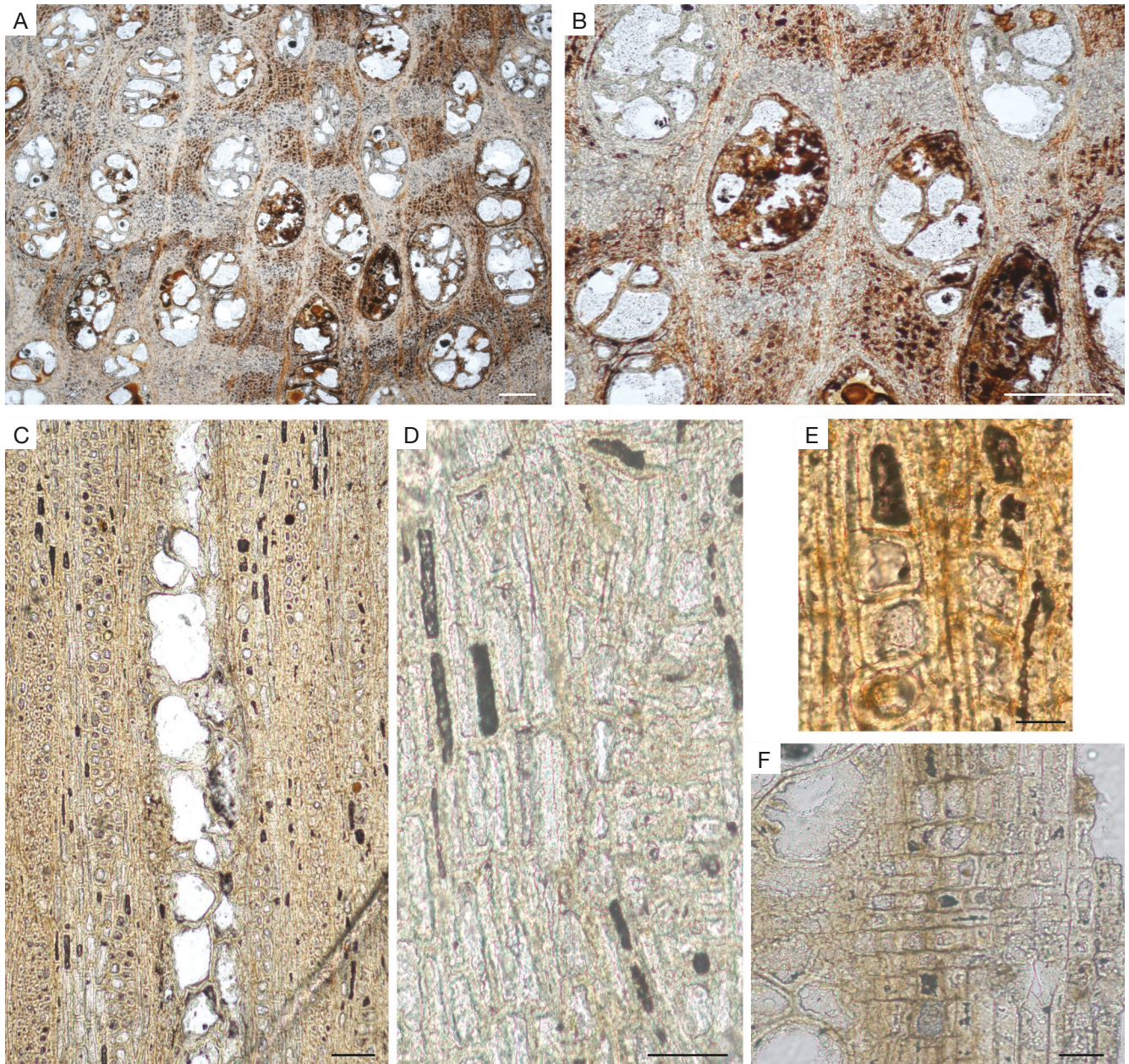


FIG. 13. — *Cordia* sp. 2 (Boraginaceae), Twf 17610: **A**, Tr, wide vessel solitary or in radial multiple; **B**, Tr, detail of vessels with tylose, reticulate or seemingly banded parenchyma; **C**, Tg, 1-6 seriate rays; **D**, Tg, storied parenchyma; **E**, Tg, crystal inclusions in ray cells (arrow); **F**, Ra, heterocellular rays with crystals. Scale bars: A, 200 µm; B, C, 100 µm; D, F, 50 µm; E, 20 µm. Photographs: M.-C. Jolly-Saad.

deposits are present in vessels. Axial parenchyma paratracheal, confluent to irregularly, seemingly sinuous banded (2-4 cells), sometimes up to 8 cells wide, in strands of cells 2-3 (2-4 cells). Rays are (1)-2-3-seriate (Fig. 14C, D), heterocellular composed of procumbent cells with square and upright cells or exclusively composed of square and upright cells (Fig. 15F), 6-9 per mm, mean height of the rays is 290 µm (range 172-483 µm), and width 22-80 µm. Fibers are thick to mostly very thick walled with distinct septae. Possible occasional strands of crystalliferous axial parenchyma, one rhomboidal crystal per chamber, 8 chambers per strand, crystal are distinct in ray cells too and sometimes in enlarged cells (Fig. 15D).

AFFINITIES AND COMPARISONS

The combination of vessels solitary and in radial multiple, simple perforation plates, narrow (100 µm mean tangential diameter) vessels, vasicentric, aliform, and banded or seemingly banded, narrow rays, chambered crystalliferous parenchyma occurs in woods of Combretaceae and Fabaceae. Vessel-pits are usually smaller in some Combretaceae. The affinities of Twf 17611 fossil wood are more likely with the genus *Terminalia*. Among the African *Terminalia* with sinuous, seemingly banded parenchyma, broad bands in long tangential lines are found in *T. macroptera* (Neumann *et al.* 2001). Among african species *T. avicennioides* Guill. & Perr. and *T. glauces-*

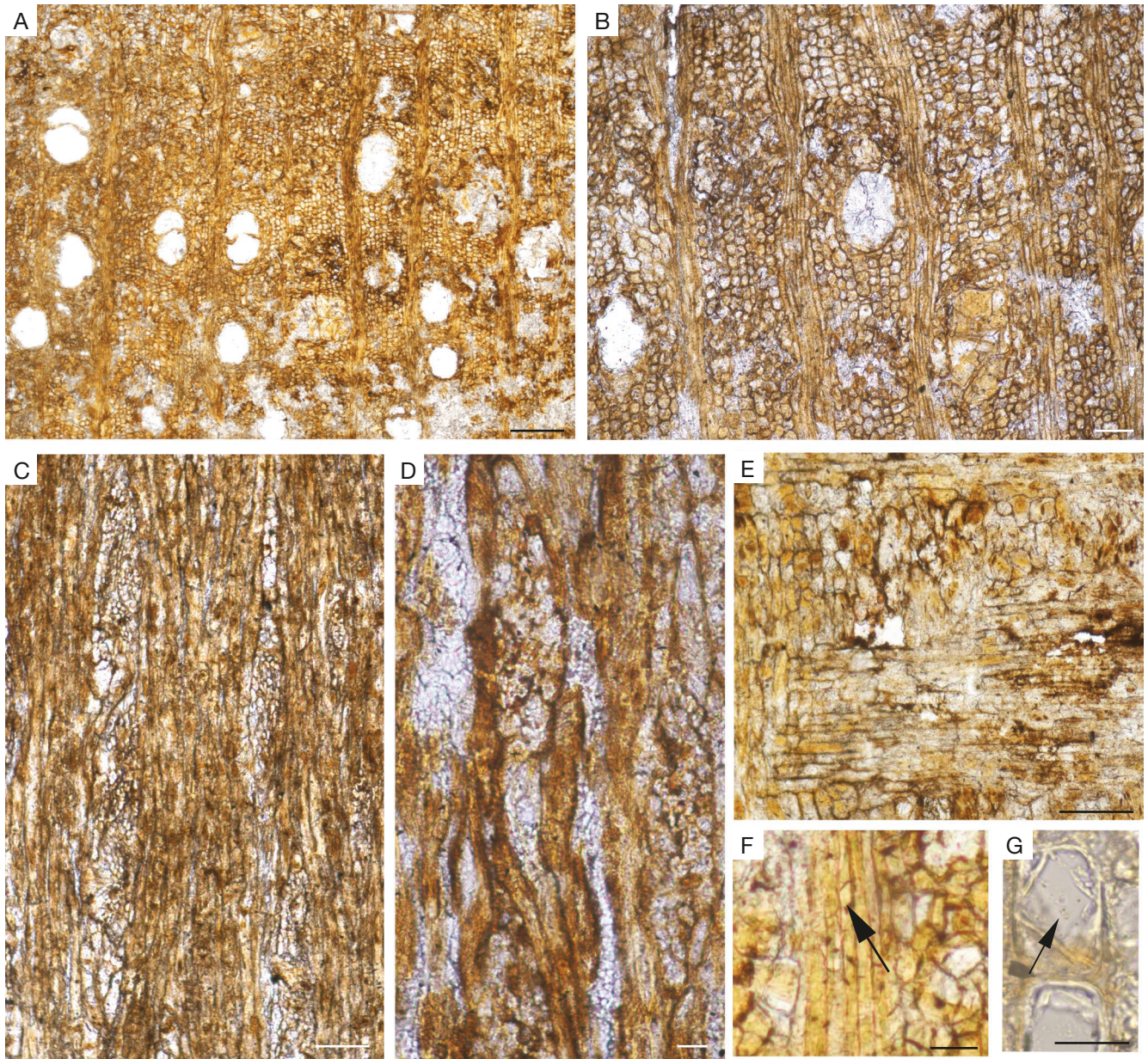


FIG. 14. — *Celtis* cf. *integrifolia*, Twf 17812: **A, B**, Tr, mostly solitary vessels with confluent or seemingly banded axial parenchyma; **C, D**, Tg, wide heterocellular rays; **E**, Rd, heterocellular rays; **F**, Tr., Prismatic crystal in ray-cell (**arrow**); **G**, Tg, detail of crystal in ray cells. Scale bars: A, 200 μ m; B, C, E, 100 μ m; F, 50 μ m; D, G, 20 μ m. Photographs: M.-C. Jolly-Saad.

cens Planch. ex Benth have 1-3 seriate rays but no crystals in ray cells. *T. boivinii* Tul and *T. macroptera* are described with axial parenchyma seemingly banded mostly 1-3 cells wide, often discontinuous. *T. macroptera* showing rather confluent to banded pattern (Neumann *et al.* 2001) is the most similar species to our Pliocene Shungura sample Twf 17611.

Among the twelve palaeobotanical *Terminalioxylon* species of Africa that we have already mentioned in Member A, *Terminalioxylon welkitii* Lemoigne (Lemoigne & Beauchamp 1972) and *Terminalioxylon* sp. Lemoigne, Beauchamp & Samuel (Lemoigne *et al.* 1974) have been identified from the Cenozoic in Ethiopia. These species exhibit uniseriate rays with procumbent cells. *T. doubingeri* Lemoigne (Miocene, Upper Omo Valley)

displays 1-3 seriate homocellular rays, terminal parenchyma and septate fibres (Lemoigne 1978). *T. endengense* Boureau (Eocene, northern Sahara) displays abundant parenchyma, fibres are not septate and rays are uniseriate (Boureau 1955). *T. primigenium* Madel Angeliewa & Muller-Stoll, 1972 *T. qeinitzii*, and *T. intermedium* Madel-Angeliewa & Muller-Stoll, 1973 (late Cretaceous-Eocene, Sudan) display mostly small vessels, usually in multiples, and vasicentric parenchyma. *T. edwardsii*, described by Madel Angeliewa & Muller-Stoll in 1973 from the Oligocene to Miocene in Egypt, exhibits a high abundance of parenchyma and longer rays. Among other *Terminalioxylon* described with 1-3 seriate rays, *T. orangensis* Bamford has scanty axial parenchyma, *T. crystallinum* Bamford has vasicentric paren-

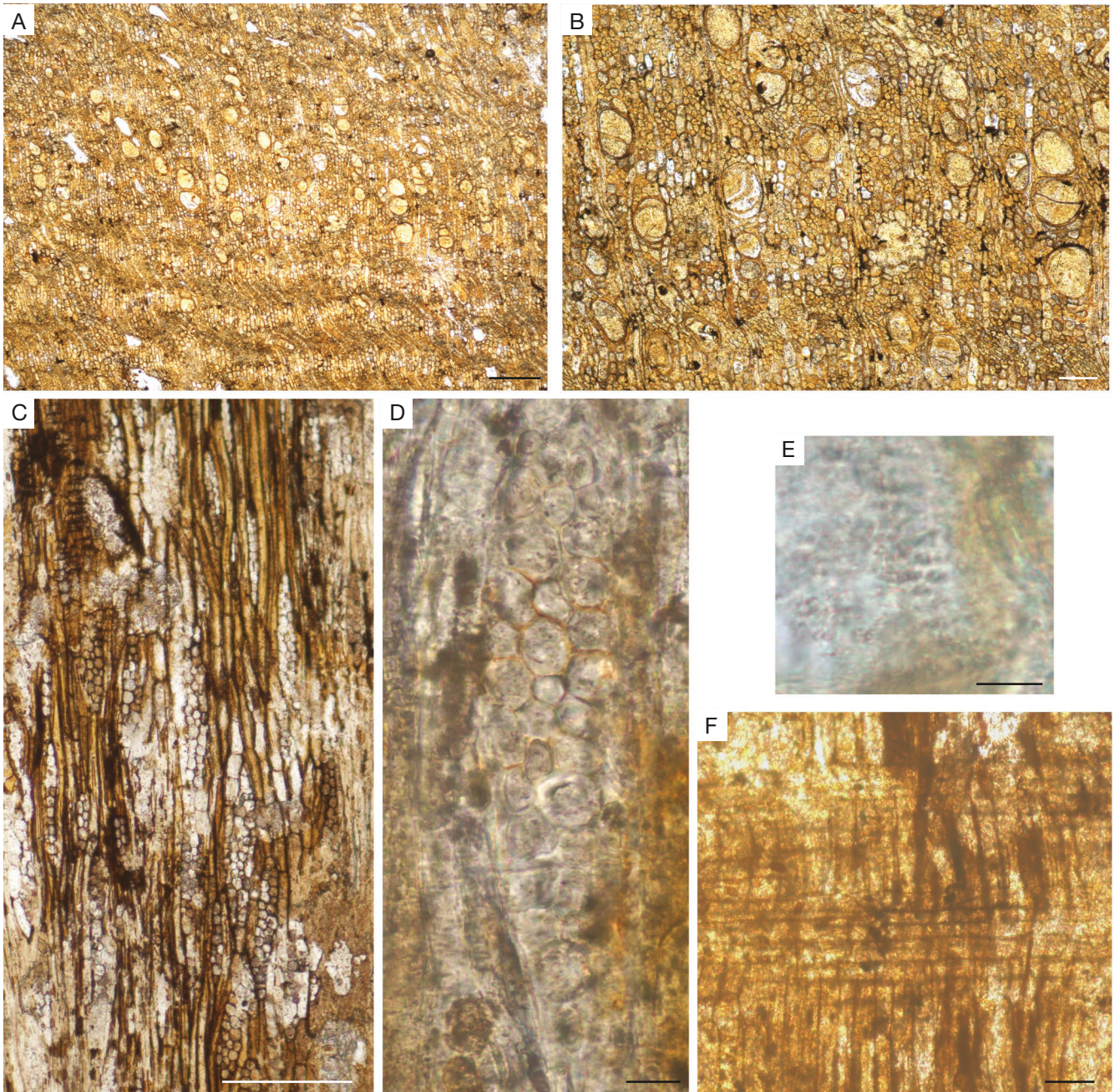


FIG. 15. — *Terminalia* cf. *macroptera*, Twf 17611: **A, B**, Tr, wood diffuse porous, vessels solitary or in radial multiple; **C, D**, Tg, rays (1)-2-3-seriate, heterocellular composed of procumbent cells with square and upright cells or exclusively composed of square and upright cells; **D**, detail of ray-cells with mineral inclusions; **E**, Tg, vestured intervessel-pits; **F**, Rd, detail ray cells. Scale bars: A, 200 µm; B, C, 100 µm; D, F, 50 µm; E, 10 µm. Photographs: M.-C. Jolly-Saad.

chyma (Bamford 2003), *T. doubingeri* Lemoigne has vasicentric, confluent or seemingly banded parenchyma (Lemoigne 1978), *T. tunesense* Dupéron-Laudoueneix has vasicentric parenchyma (Fessler-Vrolant 1978). The Omo fossil specimen does not correspond to any of these paleobotanical species. Unlike Twf 17918, described before from Member A, dated 3.6 Ma and that was attributed to *Terminalia* sp., the wood sample Twf 17611 from Member C, dated 2.62 Ma, is more precisely attributed to the species *T. cf. macrocarpa*.

Family EBENACEAE Gürke
Genus *Diospyros* L.

Diospyros cf. *mespiliformis*
(Fig. 16)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 106 sect. 4; Unit C-5, 2.62 Ma; Jean de Heinzelin leg.; Twf 17683; Tervuren collection.

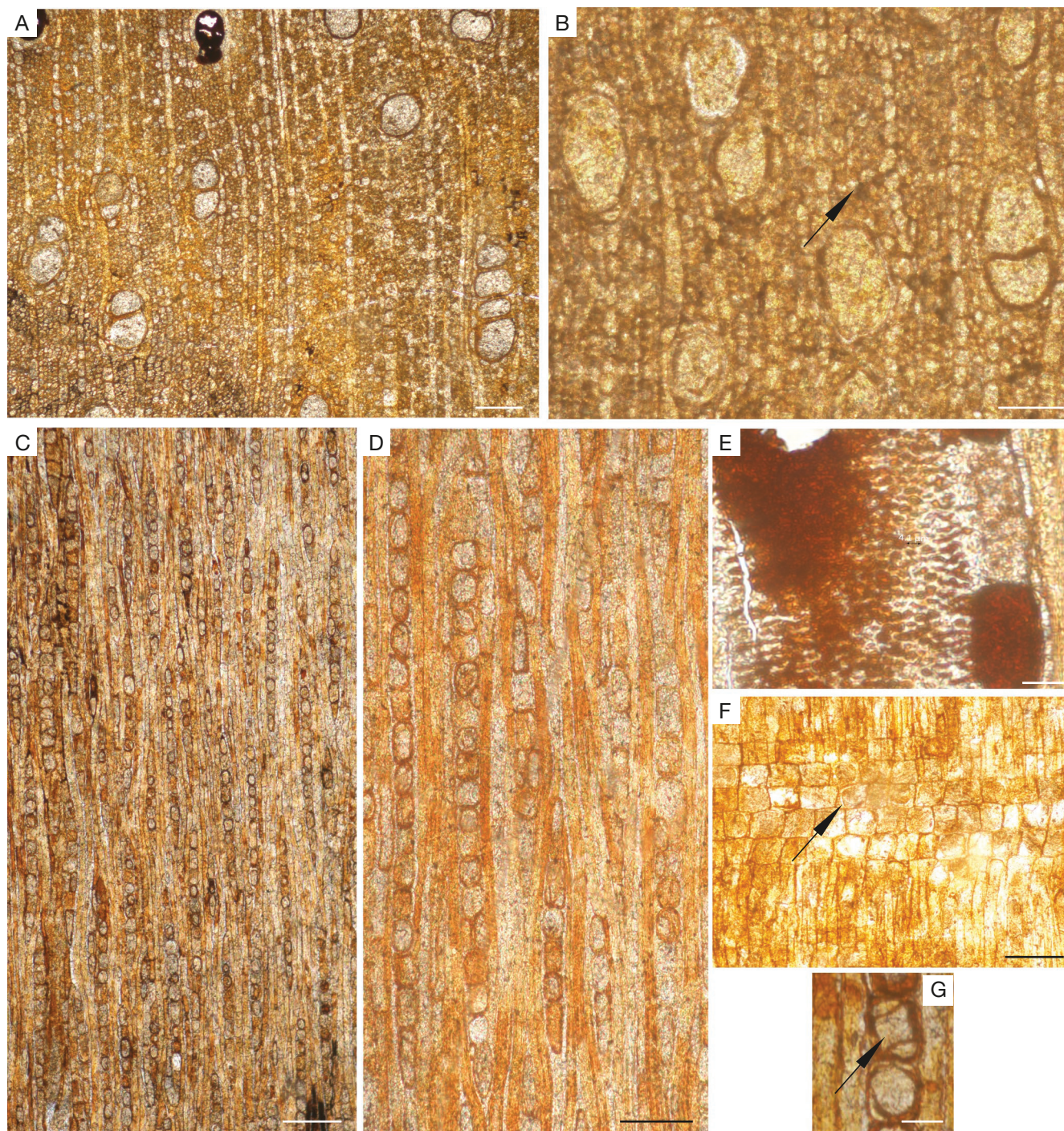


FIG. 16. — *Diospyros* cf. *mespiliformis*, Twf 17683: **A, B**, Tr, wood diffuse porous, vessels solitary or in radial multiple, parenchyma diffuse-in-aggregates; **B**, Trs, detail of diffuse-in-aggregate parenchyma (arrow); **C, D**, Tg, heterocellular uniseriate rays; **E**, Tg, minute intervessel-pits; **F**, Rd, heterocellular rays with square and upright cells, crystals in ray cells (arrow); **G**, Tg., prismatic crystal in ray cells (arrow). Scale bars: A, D, 100 µm; B, F, 50 µm; C, 20 µm; G, 10 µm. Photographs: M.-C. Jolly-Saad.

DESCRIPTION

Twf 17683 exhibits well-preserved micro-anatomical structures, without any visible presence of fungi. The wood is diffuse-porous; growth rings are absent (Fig. 16A, B). Vessels are solitary (38%) or in radial lines of 2 (42%), 3 (12%) and 4-5 (8%). The frequency is 10-20 vessels per mm². Mean tangential diameter is 80 µm (range 57-90 µm). Vessel

element length is 184-621 µm; perforation plates are simple. Intervessel-pits, poorly preserved are alternate, 3-4 µm wide and not vested (Fig. 16E); gum is distinct in vessels. Axial parenchyma is scanty to vasicentric with 1-2 rows of cells, and diffuse-in-aggregates (Fig. 16B).

Rays are uniseriate and reach heights ranging from 161 to 520 µm. They are numerous (26-28 per mm) and are

composed of square and upright cells mixed throughout the body of the rays (Fig. 16C, D). Fibres are medium to thick walled and septate. Prismatic crystals are distinct in ray cells (Fig. D, F-G).

AFFINITIES AND COMPARISONS

Vessels solitary or in radial multiple, rare parenchyma with irregular narrow bands, and uniseriate heterocellular rays with enlarged crystalliferous cells occur in woods of some members of the Annonaceae, Apocynaceae, Balanaceae, Ebenaceae, Euphorbiaceae, Clusiaceae, Malvaceae *sensu lato* (including Tiliaceae), and Sapotaceae (InsideWood database 2004-onwards). Among the Ebenaceae, we exclude *Euclea* for which two montane species, *Euclea racemosa* Murr. (1774) subsp. *schimperii* (A.D.C.) F. White and *E. divinorum* Hiern have uniseriate rays (InsideWood database 2004-onwards). Twf 17683 shows characters found in *Diospyros*. Among the three *Diospyros* species known in the Ethiopian flora (Friis & White 2005), *D. scabra* (Chiov.) Cufod. is not described in databases. *D. abyssinica* (Hiern) F. White possesses uniseriate rays and has both diffuse and diffuse-in-aggregates parenchyma, as well as reticulate axial parenchyma (InsideWood database 2004-onwards; Metcalfe & Chalk 1950). But its vessels are generally smaller than those of Twf 17683. In conclusion, this sample shows similarities with *D. mespiliformis* that has diffuse-in-aggregates parenchyma.

Among the palaeobotanical species from Libya (Cretaceous) and related to the Ebenaceae, *Ebenoxylon ebenoides* Kräusel (Schenk) Edwards (synonym of *Jordania ebenoides* Schenk) shows solitary vessels and scalariform perforation plates but its attribution to the Ebenaceae is probably an erroneous identification (A. Pan in *lettris*). Nevertheless, it differs from Twf 17683. *E. aegyptiacum* Kräusel from the Oligocene of Egypt and *E. tunetanum* (Fliche) Edwards (synonym of *Jordania tunetana* Fliche) from the Oligocene of Tunisia show some similarities to the Omo fossil. In contrast, *E. saharicum* Süss from the Paleogene of Egypt displays larger vessel diameters (150–215 µm) and rays are 1–3 seriate (Süss 1987).

Diospyros sp. has been identified in Pleistocene (1.95 Ma) deposits of the Koobi Fora Formation, Lake Turkana Basin in Kenya (Bamford 2011). This specimen is characterized by wider vessels (164 µm) and short radial multiple, all features that distinguish it from Twf 17683, identified as *Diospyros* cf. *mespiliformis*.

Family MELIACEAE Juss.
Genus *Trichilia* L.

Trichilia sp.
(Fig. 17)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality L 642-8 sect. 8; Unit C-6, 2.61 Ma; American Staff leg.; Twf 17713; Tervuren collection.

DESCRIPTION

Twf 17713 displays moderate preservation, with no visible presence of fungi (Fig. 17A). It exhibits characteristics of diffuse-porous wood, with either absent or indistinct growth rings. Vessels are solitary (31%) and in radial multiples of two (36%), 3 (21%), 4 (11%) and 5 (1%). They are 20–35 per mm², round to oval in outline (Fig. A, B). Mean tangential diameter is 45 µm (range 21.5–66 µm). Perforation plates are simple (Fig. 17C); intervessel-pits are alternate, 3–4 µm wide and not vested (Fig. 17E). Vessel-ray pits are indistinct. Mean vessel element height is short (range 185–350 µm). Fibres are irregular thin-medium walled (4 µm), non-septate observed. Gum is distinct in vessel lumina (Fig. A).

Not well preserved on the transverse section, it is particularly difficult to differentiate parenchyma from fibres. Axial parenchyma seems vasicentric, with one or two rows of flattened cells, diffuse and probably diffuse in-aggregates. Parenchyma strands are 3–4 cells. Rays are uniseriate, locally biseriate, they are 12–14 per mm (Fig. 17C, D), square and upright cells are mixed in the rays (Fig. 17F), mean ray height is 320 µm (range 165–520 µm (7–28 cells) mean ray width is 30 µm (range 15–34 µm), Crystals are visible in ray cells and in parenchyma.

AFFINITIES AND COMPARISONS

The wood shows the anatomical features of Meliaceae characterized by minute and not vested intervessel-pits, rare axial parenchyma, septate fibres and heterocellular rays. Among the Meliaceae, the combinations of crystals in marginal cells or parenchyma, homocellular or heterocellular rays and septate or non-septate fibres are used to distinguish subfamilies (Kribs 1930). Twf 17713 can be attributed to the Melioideae subfamily (Muellner *et al.* 2003) with characters found in *Trichilia*. The wood anatomy of *Trichilia* and *Pseudobersama* differs very little, except in regard with the vessels frequencies and grouping (Gasson & Cheek 1992; Inside Wood database 2004-onwards). The secondary xylem of *Pseudobersama* can be distinguished from the African species of *Trichilia* by the very large numbers (80–100 per mm²) of small, vessels (20–40 µm) arranged in radial rows of 2–5 and the rather sparse aliform and confluent parenchyma. African species of *Trichilia* have up to 30 vessels per mm² with a tangential diameter from 40–220 µm. In *Pseudobersama* the number of solitary vessels is greater, rays are exclusively uniseriate, inclusions are absent in ray cells. *Trichilia dregeana* and *T. emetica* have larger vessels (100–200 µm) than Twf 17713. *T. prieureana* have exclusively uniseriate ray composed of procumbent cells with 1–2 rows of square and upright cells.

Of the two palaeobotanical species linked to *Trichilia*, *Paratrachiloxylon grambastii* Lemoigne (Lemoigne 1978), from the Upper Omo Valley possesses three seriate rays, *P. russelli* Koeniguer from the Paleocene in Niger (Koeniguer *et al.* 1971) has axial parenchyma in narrow bands or lines up to three cells wide. They strongly differ from Twf 17713, which is likely attributable to *Trichilia* sp.

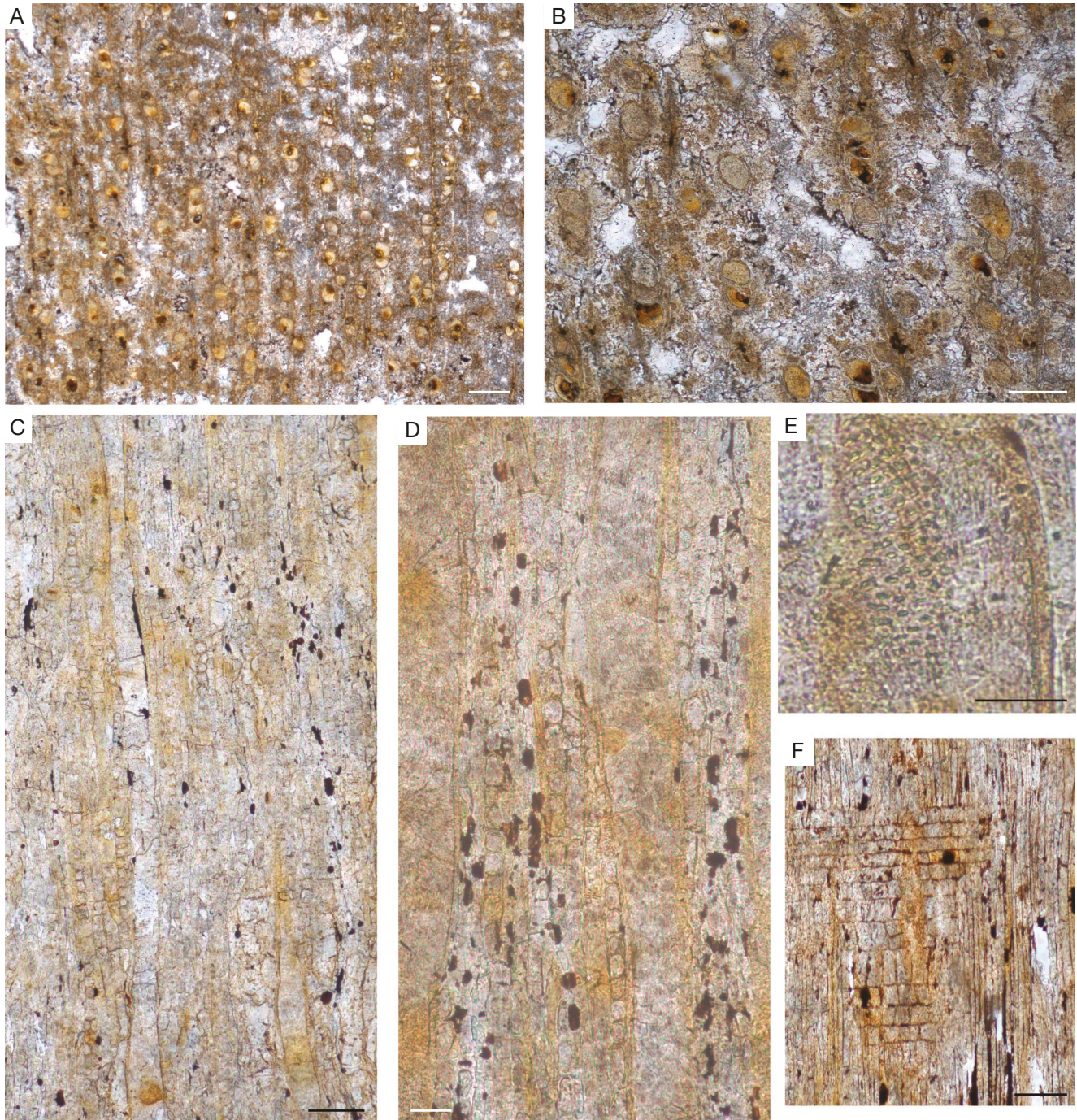


FIG. 17. — *Trichilia* sp. (Meliaceae Juss.), Twf 17713: **A, B**, Tr, vessel in solitary or in radial multiple of poorly preserved wood; **C, D**, Tg, rays uniseriate; **E**, Tg, minute inter-vessel pits; **F**, Rd, heterocellular rays. Scale bars: A, C, 100 µm; B, E, F, 50 µm; D, 20 µm. Photographs: M.-C. Jolly-Saad.

Family CELASTRACEAE R.Br.
Genus *Maytenus* Molina

Maytenus sp. 1
(Fig. 18)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality L 448 sect. 11; Unit C-8, 2.57 Ma; American Staff leg.; Twf 17805, Twf 17808; Tervuren. collection.

DESCRIPTION

Twf 17805 and Twf 17808 closely resemble Twf 17609 already described in Member B-12. Sharing the same characteristics, we attribute all of these samples to *Maytenus* sp. 1

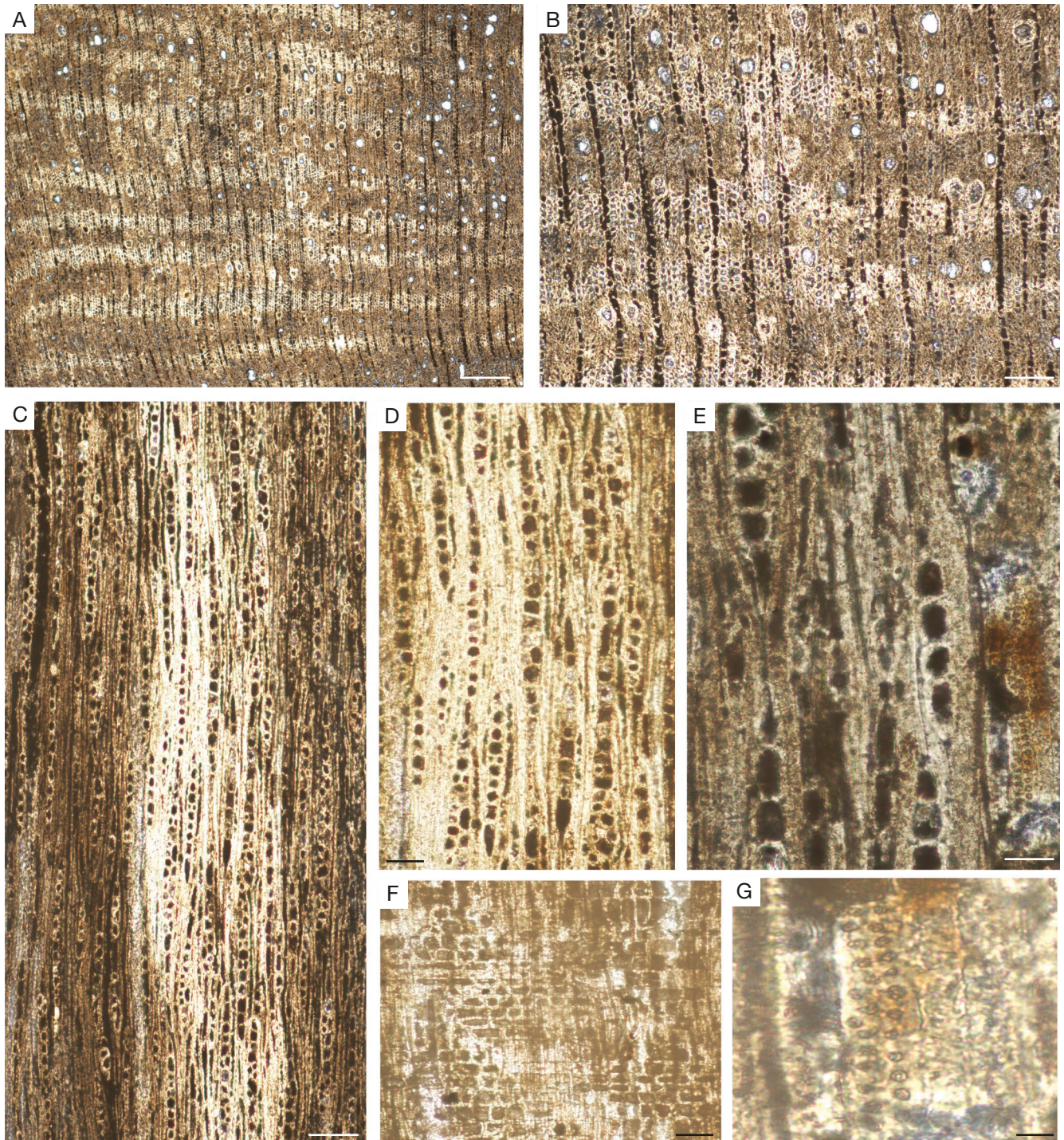


FIG. 18. — *Maytenus* sp. 1 (Celastraceae R.Br.), Twf 17805: **A, B**, Tr, small and solitary vessels, alternating bands of septate and non-septate fibres; **C-E**, Tg, numerous 1-2 seriate heterocellular rays; **D, E**, detail of rays cells; **F**, Rd, heterocellular rays; **G**, minute intervessel-pits. Scale bars: A, 200 µm; B, C, 100 µm; D, F, 50 µm; E, 20 µm; G, 10 µm. Photographs: M.-C. Jolly-Saad.

ANGIOSPERM MONOCOTYLEDONS

Family ARECACEAE Bercht. & Presl.

Genus *Raphia* P.Beauv.

Raphia sp.
(Fig. 11)

EXAMINED MATERIAL. — Ethiopia • Lower Omo Valley, Shungura Formation, locality L 447-1 sect. 11; Member C-8, 2.57 Ma; American Staff leg.; Twf 17788; Tervuren collection.

DESCRIPTION

Twf 17788 is well preserved showing fibro-vascular bundles irregular in distribution, having developed reniform scleren-

chyma caps, with a small median sinus, with rounded auricular lobes, frequency 30-35 per mm². Xylem with two round vessels and compact parenchymal ground tissue (Fig. 11E F). The fibrous bundles are missing. The sclerenchyma cap is 400-470 µm in height and 500-600 µm wide (Fig. 11G). The phloem is indistinct (Fig. 11H). The xylem appears in cross-section with 2 round large vessels of 100-150 µm diameters in cross section. The ground parenchyma is composed of round cells, tabular parenchyma is present and radiating parenchyma is absent. Longitudinal section being absent, the vertical walls of the metaxylem vessels could not be observed.

AFFINITIES AND COMPARISONS

In cross section, Twf 17788 presents a monocotyledonous fascicular structure typical for the stem of palm tree of the Arecaceae Bercht. & Presl. The general organisation of the central cylinder stem pattern (ex-von Mohl's classification) of *Corypha*-type and *Mauritia*-type shows reniforma fibrovascular bundles with an excluded vascular part and two large vessels elements with little paravascular parenchyma in Twf 17788 the phloem is not partitioned. The ground parenchyma is compact, made of spheroid cells. Tabular parenchyma is present (Fig. 11H). No fibrous bundles were observed in the ground parenchyma. These features are similar to the Calamoideae - Lepidocaryeae and more specifically to the genus *Raphia*.

The fossil corresponds to *Palmoxylon* that generally defines "wood of Palm" (Schenk 1883). Twf 17788 is similar to *Palmoxylon rewahense* Sahni, and *Palmoxylon libycum* described in the early Miocene of Qaret El-Raml, from Egypt (Lemoigne 1978).

Family FABACEAE Lindl.
Subfamily CAESALPINIOIDEAE DC.
Genus *Albizia* Durraz

Albizia sp. 1
(Fig. 19)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 755 sect. 24; Unit C-8, 2.57 Ma; Jean de Heinzelin leg.; Twf 17638; Tervuren collection.

DESCRIPTION

Twf 17638 is poorly preserved diffuse-porous, with indistinct growth rings Vessels are frequently solitary (87%), and in radial multiple of 2 (%), 3 (%), 8-11 vessels per mm² (Fig. 19A, B). Very few vessel clusters were seen (0.5%). Mean vessel tangential diameter is 150 µm (range 58 µm - 254 µm). Perforation plates are simple horizontal to slightly oblique. Intervessel pits are polygonal, relatively dense, alternate, and 7-8 µm in size, They appear vested (Fig. 19E). Mean vessel length is 350 µm (range 166 µm to 676 µm). Vessel-ray pits are indistinct. Gum is visible in the vessels (Fig. 19A).

Axial parenchyma is paratracheal, vasicentric, aliform and sometimes confluent (Fig. 19A, B).

Rays are 1-4 (5) seriate, 5-6 per mm, uniseriate are rare, homocellular composed of procumbent cells, (Fig. 18C, D, F). Mean ray length is 234 µm (range 169-676 µm), mean ray width is 25 µm (range 13-30 µm). Fibers are septate. Strands of crystalliferous axial parenchyma, single one rhomboidal crystals are distinct in fibers and in parenchyma strands, there are 10-24 chambers per strand (Fig. 19G).

AFFINITIES AND COMPARISONS

The combination of the characters: vessels solitary (87%), vested intervessel-pits, axial parenchyma paratracheal vasicentric, aliform and confluent, 1-5 seriate rays with only procumbent cells, prismatic crystals in chambered parenchyma and septate fibres are features found in the Fabaceae, especially the Mimosoideae (now included in the Caesalpinoideae subfamily by the Legume Phylogenetic Working Group) (LPWG 2017). Storied rays, which would have placed Twf 17638 closer to the Faboideae or some Caesalpiniaceae are absent (Metcalf & Chalk 1950; Müller-Stoll & Mädler 1967). In Ethiopia, trees of the Mimosoideae include six distinct genera: *Dichrostachys*, *Albizia*, *Entada*, *Prosopis*, *Mimosa* and *Acacia* (Thulin 2003). With septate fibres, Twf 17638 is similar to *Albizia*. It was previously attributed to *A. antunesiana* (Deschamps 1983). However, it differs from *A. antunesiana* as described in the literature (InsideWood 2004-onwards), notably in its higher vessel density per mm², larger vessels and pits, and more abundant parenchyma. Twf 17638 also differs from other Ethiopian species for which anatomical data are currently available. Given the absence of anatomical data for many other Ethiopian and East African species, a confident species-level identification is not possible; Twf 17638 is therefore conservatively assigned to *Albizia* sp. 1, excluding *A. antunesiana* (Dechamps 1983).

Among fossil wood reported to *Albizia* in Africa, few specimens have been related to *Albizia*, one from Cameroon, *Ingoxylon albizzoides* (Dupéron-Laudoueneix 1991) has bigger vessels and shorter rays than the Omo fossil specimen. *A. cf. gummifera*.

Family COMBRETACEAE R.Br./FABACEAE Lindl.

Combretaceae/Fabaceae gen. and sp. indet. 2
(Fig. 20)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 424 sect. 15; Unit C-9, 2.56 Ma; Jean de Heinzelin leg.; Twf 17730; Tervuren collection.

DESCRIPTION

Twf 17730 is poorly preserved. Wood diffuse-porous, growth rings are absent. Vessels are round or oval in shape, soli-

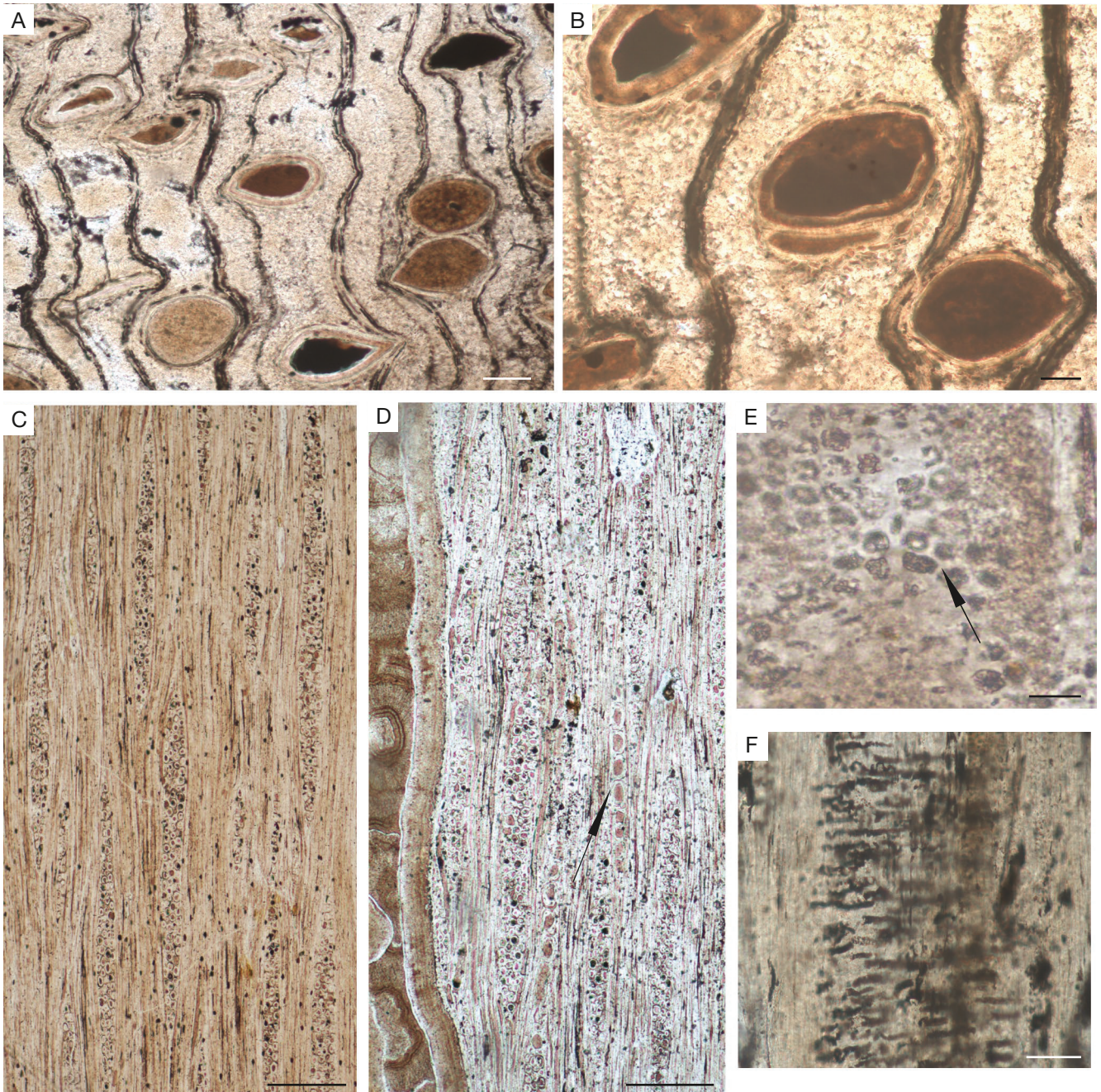


FIG. 19. — *Albizia* sp. 1 (Fabaceae Lindl.), Twf 17638: **A, B**, Tr, diffuse porous wood with vasicentric or confluent parenchyma; **C, D**, Tg, 1-5 seriate rays homocellular; **D**, Tg., ray arrangement and chambered parenchyma cells (arrow); **E**, Tg, vestured intervessel-pits (arrow); **F**, Rd, homocellular rays. Scale bars: A, C, 100 μ m; B, D, F, 50 μ m; E, 10 μ m. Photographs: M.-C. Jolly-Saad.

tary or in short radial multiple 2-3 with mean tangential diameter of 90 μ m (range 95-81 μ m), 2-4 vessels per sq. mm, vessels are thin-walled. (Fig. 20A, B). Gum deposits are distinct in vessel lumina, tylosis is not observed. Vessel element length is 200 μ m (range 80-270 μ m), perforation plates are simple and horizontal. Intervessel pits are opposite and vestured 7-8 μ m wide (Fig. 20F), vessel-ray pits are indistinct. Axial parenchyma is vasicentric to confluent (Fig. 20B). Parenchyma strands are 2-4 cells.

Rays are 1-3 (4) seriate, heterocellular, 11-12 or > 12 per mm. Mean ray height is 235 μ m range 72-460 μ m 39 μ m (range 26-48) (Fig. 20C, D-F). Fibres are wide and they are septate. Inclusions are distinct in chambered parenchyma and in ray cells.

AFFINITIES AND COMPARISONS

Twf 17730 was initially identified as *Kigelia africana* from the Bignoniaceae (Dechamps 1983). However, upon closer

TABLE 2. — List of studied and described fossil wood from the Pleistocene Shungura Formation, Lower Omo Valley, Ethiopia. Fossil wood specimens from Ter-vuren collection are assigned the code Twf, in which T refers to Ter-vuren, W to wood, and f to fossil. Modern wood specimens are designated Tw. Abbreviations: **Tr**, Transversal section; **Tg**, Tangential section; **Ra**, Radial section.

Sample Number	Thin sections	Locality	Geographic coordinates	Strati-graphy	Age (Ma)	Identification	Figures
Twf 17601	Tr, Tg, Ra	Kalam road, sect. 19	5°02'35"N, 36°59'35"E	J-2	1.70	<i>Salvadora persica</i> L.	Fig. 52
Twf 17985	Tr, Tg	Kalam road, sect. 19	5°02'35"N, 36°59'35"E	J-2	1.70	<i>Salvadora persica</i> L.	—
Twf 17986	Tr, Tg, Ra	Kalam road, sect. 20	5°02'35"N, 36°59'35"E	J-2	1.70	<i>Diospyros</i> sp. 1	Fig. 51
Twf 17780	Tr-Tg-Ra	P 742b sect. 22	5°01'16"N, 36°01'19"E	G-29	1.92	<i>Lecaniodiscus</i> sp.	Fig. 50
Twf 17987	Tr-Tg-Ra	P 742b sect. 22	5°01'16"N, 36°01'19"E	G-29	1.92	<i>Lecaniodiscus</i> sp.	—
Twf 17966	Tr-Tg-Ra	Loc NA sect. 22	—	G-29	1.92	Sapindaceae gen. and sp. indet.	Fig. 49
Twf 17636	Tr-Tg-Ra	P 743 sect. 22	5°01'20"N, 36°01'29"E	G-29	1.92	Sapotaceae gen. and sp. indet.	Fig. 48
Twf 17629	Tr-Tg-Ra	P 743c sect. 22	5°01'20"N, 36°01'29"E	G-29	1.92	<i>Ochna</i> sp. 2	Fig. 47
Twf 17630	Tr -NA	P 743c sect. 22	5°01'20"N, 36°01'29"E	G-29	1.92	<i>Ochna</i> sp. 3	—
Twf 17725	Tr-Tg-Ra	P 769 sect. 22	5°00'55"N, 36°01'19"E	G-29	1.92	<i>Ficus</i> sp. 2	Fig. 46
Twf 17625	Tr-Tg-Ra	P 743 sect. 22	5°01'20"N, 36°01'29"E	G-29	1.92	<i>Sterculia</i> sp.	Fig. 45
Twf 17825	Tr-Tg-Ra	P 742 sect. 22	5°01'16"N, 36°01'19"E	G-29	1.92	Fabaceae/Apocynaceae gen. and sp. indet.	Fig. 44
Twf 17968	Tr-Tg-Ra	P 743 sect. 22	5°01'20"N, 36°01'29"E	G-29	1.92	<i>Peltophorum</i> sp.	Fig. 43
Twf 17826	Tr-Tg-Ra	P 742 sect. 22	5°01'16"N, 36°01'19"E	G-29	1.92	<i>Bussea</i> sp.	Fig. 42
Twf 17907	Tr-Tg-Ra	P 726 sect.19	5°02'31"N, 35°59'56"E	G-29	1.92	<i>Diospyros</i> sp. 2	Fig. 41
Twf 17965	Tr-Tg-Ra	P 743 sect. 22	5°01'20"N, 36°01'29"E	G-29	1.92	<i>Combretum</i> sp.	—
Twf 17973	Tr-Tg-Ra	P 743 sect. 22	5°01'20"N, 36°01'29"E	G-29	1.92	<i>Combretum</i> sp.	Fig. 40
Twf 17906	Tr-Tg-Ra	P 726 sect. 19	5°02'31"N, 35°59'56"E	G-29	1.92	<i>Maytenus</i> sp. 1	Fig. 39
Twf 17912	Tr-Tg-Ra	P 726 sect. 19	5°02'31"N, 35°59'56"E	G-29	1.92	<i>Commiphora</i> sp.	Fig. 38
Twf 17770	Tr-Tg-Ra	P 726 sect. 19	5°02'31"N, 35°59'56"E	G-29	1.92	<i>Brachylaena</i> sp. 2	Fig. 37
Twf 17823	Tr	P 742 sect. 22	5°01'16"N, 36°01'19"E	G-29	1.92	<i>Borassus</i> sp. 1	—
Twf 17830	Tr-Tg-Ra	P 742 sect. 22	5°01'16"N, 36°01'19"E	G-29	1.92	<i>Borassus</i> sp. 1	Fig. 36
Twf 17928	Tr-Tg-Ra	O 27-2	5°02'52"N, 36°00'02"E	G-19	2.01	<i>Ficus</i> sp. 1	Fig. 35
Twf 17929	Tr-Tg-Ra	O 27-2	5°02'52"N, 36°00'02"E	G-18	2.02	<i>Albizia</i> sp. 2	Fig. 34
Twf 18069	Tr-Tg-Ra	P 729 sect. 19	5°2'40"N, 36°0'5"E	G-19	1.92	<i>Terminalia</i> sp. 3	Fig. 33
Twf 17707	Tr-Tg-Ra	P 553 sect. 6	5°07'33"N, 36°01'34"E	G-18	2.02	<i>Brachylaena</i> sp. 1	Fig. 32
Twf 17754	Tr-Tg-Ra	P 719 sect. 18	5°02'32"N, 36°00'19"E	G-13	2.06	<i>Erythrophleum</i> sp.	Fig. 31
Twf 17714	Tr-Tg-Ra	L 560-1	5°06'42"N, 36°01'34"E	G-3	2.19	<i>Canthium</i> sp. 2	Fig. 30
Twf 17640	Tr-Tg-Ra	P 794 sect. 5	5°08'23"N, 36°02'27"E	G-5	2.13	<i>Canthium</i> sp. 1	Fig. 29
Twf 17665	Tr-Tg-Ra	P 388 sect.19	5°06'41"N, 36°01'31"E	G-5	2.13	<i>Celtis</i> cf. <i>integrifolia</i>	Fig. 28
Twf 17712	Tr-Tg-Ra	L 560-1	5°06'42"N, 36°01'34"E	G-3	2.19	<i>Celtis</i> cf. <i>integrifolia</i>	Fig. 27
Twf 18028	Tr-Tg-Ra	L 28 sect. 13	5°04'54"N, 36°01'41"E	F-3-2	2.30	<i>Rothmannia</i> sp.	Fig. 26
Twf 17950A	Tr-Tg-Ra	L 28 sect. 13	5°04'54"N, 36°01'41"E	F-3-2	2.30	<i>Psychotria</i> sp. 1	Fig. 25
Twf 17949A	Tr-Tg-Ra	L 28 sect. 13	5°04'54"N, 36°01'41"E	F-3-2	2.30	<i>Ochna</i> sp. 1	Fig. 24
Twf 17995	Tr-Tg-Ra	L 28 sect. 13	5°04'54"N, 36°01'41"E	F-3-2	2.30	<i>Grewia</i> sp.	Fig. 23
Twf 17804	Tr-Tg-Ra	L 553-1 sect. 9	5°06'42"N, 36°01'14"E	D-1	2.53	<i>Syzygium</i> cf. <i>guineense</i>	Fig. 22
Twf 17613	Tr-Tg-Ra	L 553-2 sect. 9	5°06'42"N, 36°01'14"E	D-1	2.53	<i>Baphia</i> sp.	Fig. 21
Twf 17624	Tr-Tg-Ra	P 743 a sect.22	5°01'20"N, 36°01'29"E	G-29	1.92	Unidentifiable	—
Twf 17612	Tr-Tg/Ra	L 618 sect.4	5°07'23"N, 36°01'34"E	G-15	2.04	Unidentifiable	—
Twf 17615	Tr-Tg-Ra	L 35-58 sect. 4	5°08'36"N, 36°01'57"E	G-5	2.12	Unidentifiable	—

examination, its characteristics strongly differ from those of the Bignoniaceae, notably its vested vessel-pits, crystals in ray cells, in parenchyma cells and septate fibers. Other traits such as medium-sized vessels, alternate and vested vessel-pits, vasicentric to confluent axial parenchyma, 1-4 seriate rays comprising procumbent cells, and chambered crystalliferous axial parenchyma suggest affinities with Combretaceae or Fabaceae with no more precision because of poor preservation of this sample.

FOSSIL WOODS FROM THE PLEISTOCENE

According to many previous geological and paleontological studies performed on sediment and environmental interpretation of the deposits of the Shungura Formation in the famous site of the Lower Omo Valley, our presentation of the anatomical descriptions of Pleistocene fossil

woods follows the stratigraphic succession of each Member, starting from D (2.53 Ma) to J (1.7 Ma). Descriptions of the fossil wood samples from each stratigraphic unit of the corresponding Member are presented according to the alphabetic order of the botanical family. Table 2 summarizes the list of studied samples hereby designed by their reference number in the Ter-vuren collection, together with indication of their respective collecting localities and stratigraphic position (as in the Heinzelin's monograph [Heinzelin 1983]). We have added our new estimated geographical coordinates, and corresponding ages updated from most recent geological publications.

MEMBER D (2.53-2.33 MA)

Tuff D of the Shungura Formation is chemically the same as the Lokalelei tuff of the Nachukui Formation,

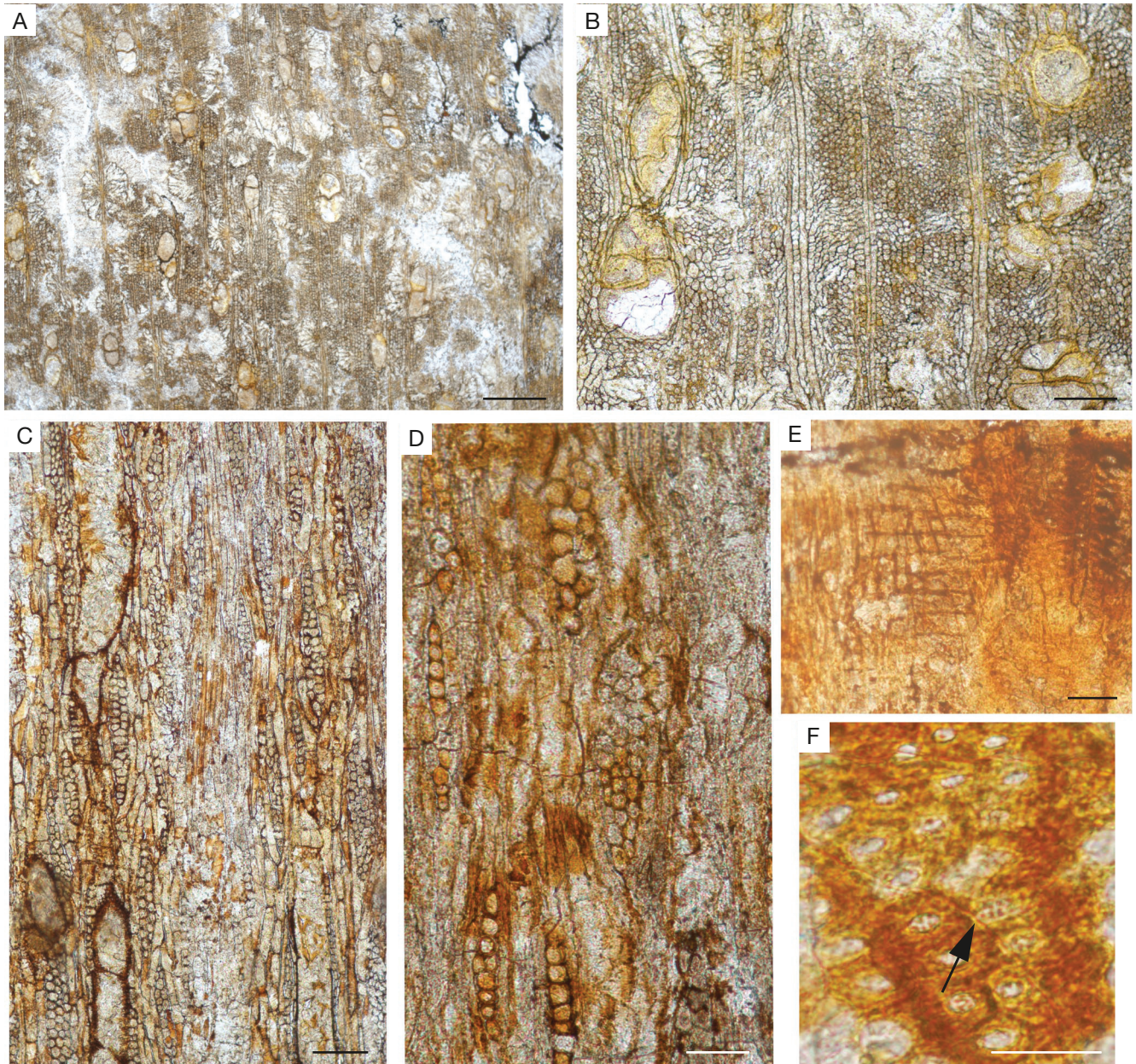


FIG. 20. — Combretaceae/Fabaceae gen. and sp. indet. 2, Twf 17730: **A, B**, Tr, diffuse porous wood, axial parenchyma vasicentric and confluent parenchyma; **C, D**, Tg, 1-3 seriate rays; **D**, Tg, detail of rays; **E**, heterocellular rays; **F**, Tg, vestured intervessels-pits (arrow). Scale bars: A, 200 µm; B, C, 100 µm; D, E, 50 µm; F, 10 µm. Photographs: M.-C. Jolly-Saad.

West Turkana (Kenya), a widespread tuff in the Turkana Depression dated at 2.53 ± 0.02 Ma (Brown & McDougall 2011; McDougall & Brown 2006). Member D has an integrated thickness of 37 m but slightly variable, and is subdivided into five units. D-1, a 4 m layer of silty clay with abundant root casts, lies on top of Tuff D. Therefore, 2.53 ± 0.01 Ma is a maximum age for the two fossil wood samples from D-1 (Table 2). A minimum age is provided by the weighted mean $^{40}\text{Ar}/^{39}\text{Ar}$ age of 2.44 ± 0.04 Ma of Tuff D-3-2, above D-1 (McDougall & Brown 2008).

Family FABACEAE Lindl.
Genus *Baphia* Afzel. ex. G. Lodd.

Baphia sp. (Fig. 21)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality L 553-2 sect. 9; Member D-1, 2.53 Ma; J. de Heinzelin leg; Twf 17613; Tervuren collection.

DESCRIPTION

Twf 17613 is poorly preserved, abundant fungal spores are visible in vessel lumina. Wood is diffuse-porous and growth

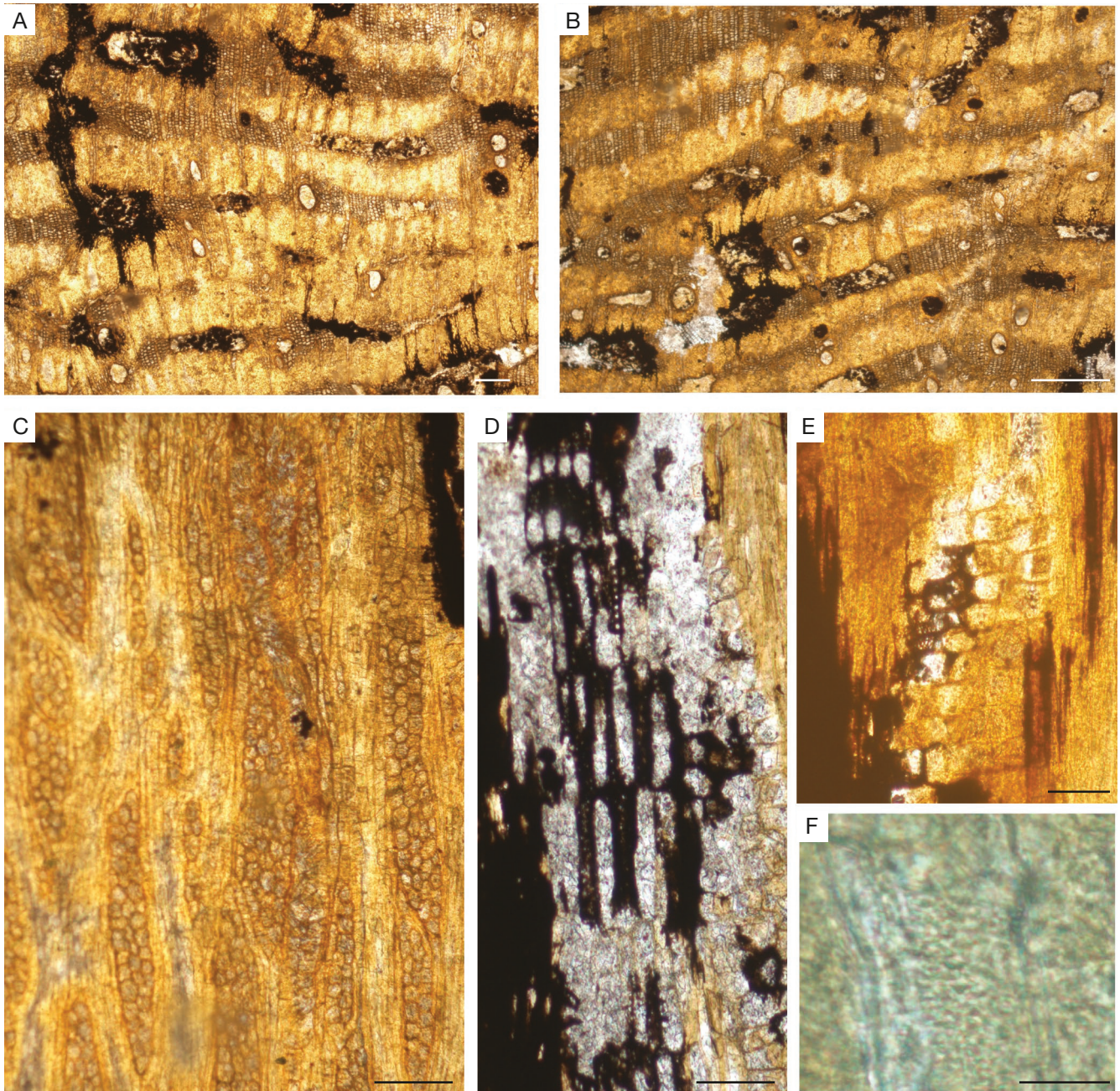


FIG. 21. — *Baphia* sp. (Fabaceae Lindl.), Twf 17613: **A, B**, Tr, diffuse porous wood, banded or seemingly banded; **C, D**, Tg, 1-3 seriate rays; **E**, vestured inter-vessel pits; **F**, Rd, heterocellular rays. Scale bars: A : 200 μ m; B-D, 100 μ m; E, 50 μ m; F, 10 μ m. Photographs: M.-C. Jolly-Saad.

boundaries are indistinct. Vessels are solitary (71%) and in radial groups of 2-3 (5), few clusters are present (Fig. 21A). Mean vessel diameter is 85 μ m (range 34-138 μ m), vessel wall is thick (11 μ m thickness), there are 1-8 vessels per mm². Perforation plates are exclusively simple; intervessel-pits are crowded alternate, 5-6 μ m and seem vestured (Fig. 21F), vessel-ray pits are indistinct. Gum is not visible in vessels. Parenchyma is abundant, vasicentric and banded; bands are wavy, 2 cells wide (34 μ m) up to 20 cells (345 μ m) (Fig. 21A, B); parenchyma strands are fusiform and storied. Rays are 1-4-(5) seriate with short uniseriate marginal parts, heterocellular and composed

of procumbent cells and upright cells (Fig. 21B, C). Uniseriate rays are short (2-5 cells high) and seem partially storied (Fig. 21), 6-7 per mm, mean height range is 600 μ m (70-977) (4-43 cells), mean width range is 11 to 90 μ m. Strands of crystalliferous axial parenchyma show one rhomboidal crystal per chamber and crystals are visible in upright cells of rays.

AFFINITIES AND COMPARISONS

The combination of solitary vessels and in radial multiples, simple perforation plates, axial parenchyma vasicentric, confluent and aliform, crystalliferous parenchyma with cham-

bers, heterocellular rays 1–4 seriate occurs in the woods of Fabaceae. Crystals in Caesalpinioideae are primarily found in axial parenchyma with chambers, often in ray cells and occasionally in fibers with chambers (Gasson *et al.* 2004). Twf 17613 was initially attributed to *Platysepalum chevalieri* Harms (Dechamps 1983). A detailed description of two species, namely *P. chevalieri* Harms and *P. violaceum* Baker (Lebacqz 1955–1963), shows that these two species, in contrast to other Millettieae, exhibit less pronounced banding, axial parenchyma, diffuse and scanty paratracheal, aliform, confluent, and that parenchyma strands are fusiform, 2 or 2–4 cells per strand. The rays typically include 5–6 cells in width and up to 50 cells in height, with only the shortest being storied. The intervessel-pits are wide, 8–13 μm . The specimen Twf 17613 displays distinct differences from *P. chevalieri*. Specifically, the rays are heterocellular and thinner (1–4 seriate), while the parenchyma strands are composed of 3–4 cells. Unfortunately, no xylem anatomical data are available for *P. inopinatum*, a species found in East Africa (Gillett *et al.* 1971). Among the Fabaceae family, the species that possess heterocellular rays and prismatic crystals in both procumbent and upright cells are *Mundulea*, *Chadsia*, *Craiba* (Millettieae) and *Bauhinia*. However, it should be noted that these species have only 1 to 3 seriate rays (Gasson *et al.* 2004). Among the taxa of the Detarioideae (Fabaceae), *Cynometra* is characterized by heterocellular rays and prismatic crystals found in the ray cells. While these characteristics are also present in the Shungura specimen, most members of the *Cynometra* species described in data bases have thin rays that are either uniseriate or triseriate. Extant trees or shrubs displaying traits similar to our fossil belong to *Baphia* (subfamily Faboideae, tribe Baphieae). Similarities exist with the western African species *Baphia bequaertii* De Wild. However, *B. bequaertii* differs with narrower axial banded parenchyma and 2–4 cells per parenchyma strands. *Baphia leptobotrys* Harms is 1–3 seriate; *Baphia nitida* Lodd. is the most similar species. Unfortunately, we do not have anatomical data for *B. abyssinica* Brummitt, the only species recorded in Ethiopia (Thulin 2003).

Among morphotypes, *Baphioxylon abyssinica* Lemoigne from the Miocene of Upper Omo Valley differs from the Shungura fossil specimen with no crystal inclusions and distinct tylose in vessels (Lemoigne 1978), *Baphioxylon dechampsii* Lakhanpal & Prakash from early Miocene of Lake Albert has thinner rays (Lakhanpal & Prakash 1970). In conclusion, we attribute Twf 17613 to the extant genus *Baphia* without any specific attribution.

Family MYRTACEAE Juss.
Genus *Syzygium* Gaertn.

Syzygium cf. *guineense* (Willd.) DC.
(Fig. 22)

EXAMINED MATERIAL. — Ethiopia • Lower Omo Valley, Shungura Formation, locality L 553-1 sect. 9 Member D-1, 2.53 Ma; Jean de Heinzelin leg.; Twf 17804; Tervuren collection.

DESCRIPTION

Twf 17804 is diffuse-porous and growth rings are indistinct. Vessels are frequently solitary (87%), and in radial multiple of 2 (2%) or 3 (1%) with very few clusters, 10–15 vessels per mm^2 (Fig. 22A, B), round to elliptic in cross section, very often deformed. Mean tangential diameter 80 μm (range 40–90 μm) (Fig. 22A, B). Vessel elements are short 104 μm (60–192 μm), perforation plate simple horizontal to slightly oblique, intervessel-pits, alternate, possibly vestured and 4–7 μm wide. Vessel-ray pits are horizontal (scalariform, gash-like) to vertical and wider than intervessel-pits. Gum is visible in vessels. Axial parenchyma is vasicentric or in narrow bands up to four cells, 3–4 or 5–8 cells per parenchyma strands (Fig. 22A, B). Rays 1–4 seriate, abundant (15–20 per mm), uniseriate rays are heterocellular composed of square and upright cells, pluriseriate rays are composed of procumbent cells with over 4 rows of upright and / or square marginal cells (Fig. 22C, D). Ray height range is 131–524 μm (4–26 cells), wide range is 20–32 μm (1–3 cells). Fibers are not septate (Fig. 22D). No crystals were observed in parenchyma cells.

AFFINITIES AND COMPARISONS

The combination of diffuse-porous wood, simple perforation plates, vessels solitary or in radial multiple, axial parenchyma vasicentric or in narrow bands diffuse-in-aggregates, heterocellular 1–4 seriate rays with 2–4 or more marginal cells, cannot be related to *Psorospermum* (Dechamps 1983). Indeed, *Psorospermum* (Guttiferae) has vessels arranged in diagonal and/or radial pattern, tracheid fibers and rays that are wider than those observed in the Shungura fossil. Twf 17804 is close to woods of the Myrtaceae (Metcalf & Chalk 1950; InsideWood 2004-onwards) and notably to *Syzygium* showing more vessels in radial than *Eugenia*. In Ethiopia, there is only one variable indigenous species *S. guineense* Willd. DC. (Friis 1995). Twf 17804 differs from others African species: *S. parkeri* Labat & Schatz, *S. cuneifolium* Boj., *S. danguyanum* Labat & Schatz, *S. micropodium* Labat & Schatz and *S. bernieri* that have fewer rays per mm and no vestured pit. So, Twf 17804 seems more similar to the Ethiopian *S. guineense* than to any other African species.

A fossil specimen identified as *Syzygium* was described from the Middle Awash Valley of Ethiopia where it is dated 4.4 Ma (Jolly-Saad *et al.* 2012). However, it differs from the Shungura specimen Twf 17804 in having bigger vessels and more vessels per mm^2 . Twf 17804 differs from other paleobotanical species, such as (*Barringtonioxylon allamblackiodes* Lemoigne from the Upper Omo Valley (Lemoigne 1978) or *Myrtioxylon secretans* Bureau (Bureau 1953) and *Myrtioxylon kirdimiense* Koeniguer (Koeniguer *et al.* 1971) also attributed to Myrtaceae.

In conclusion, Twf 17804 is identified as *Syzygium* cf. *guineense*.

MEMBER F (2.32–2.26 MA)

Member F is 35 m thick and divided into five units bracketed between two well-dated tuffs, it lasted around 50 ka. At

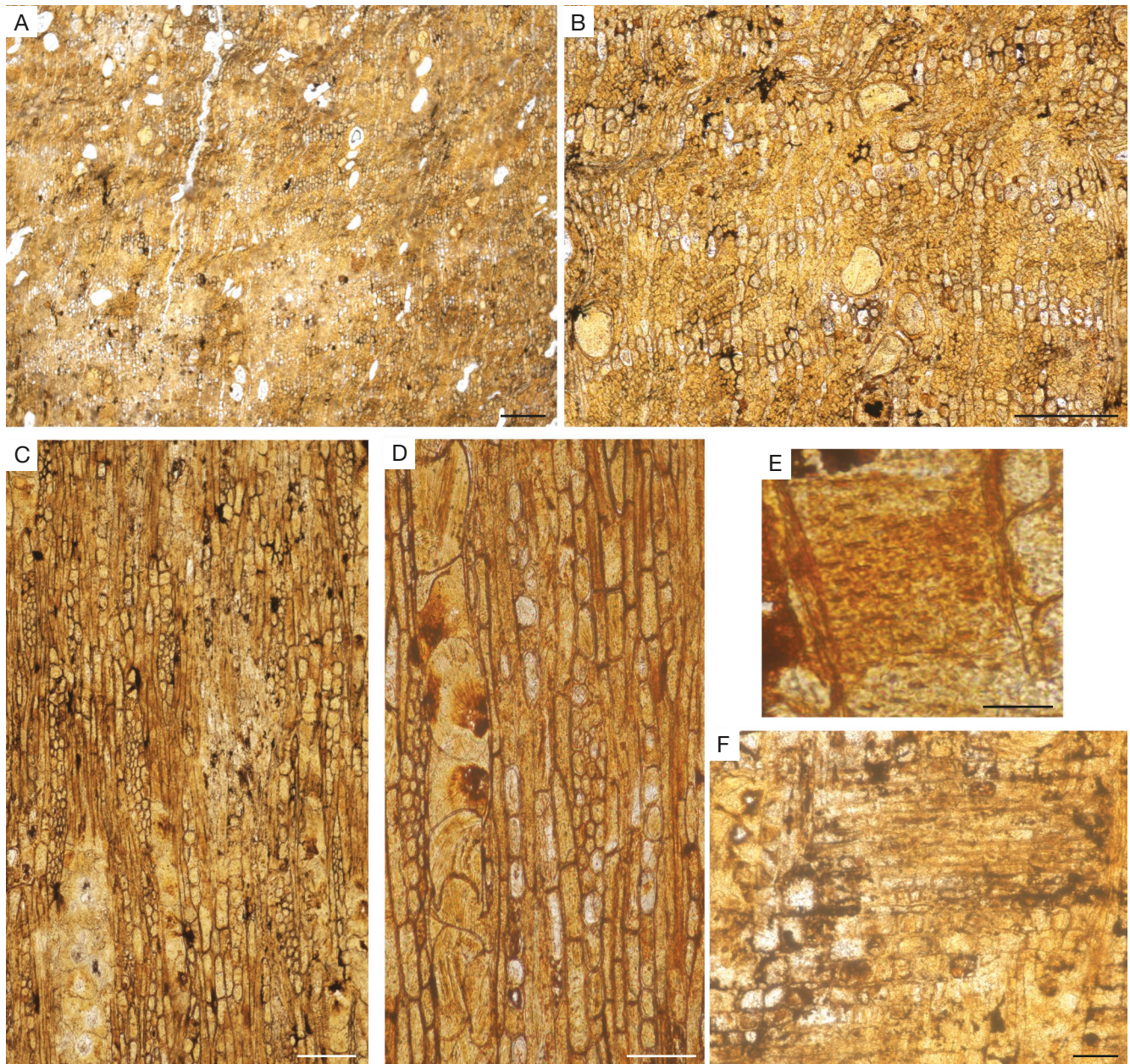


FIG. 22. — *Syzygium cf. guinense* (Myrtaceae Juss.), Twf 17804: **A, B**, Trs, wood diffuse porous, vessels mostly solitary or in radial multiple and axial parenchyma is paratracheal, vasicentric, aliform and sometimes confluent; **C, D**, Tg, rays 1-4 seriate; **E**, Ra, heterocellular rays; **F**, Tg, Inter-vessel pits. Scale bars: A-C, 200 μ m; B, 100 μ m; E, 10 μ m; D-F, 50 μ m. Photographs: M.-C. Jolly-Saad.

the bottom, Tuff F is the same as the Kalochoro Tuff from the Nachukui Formation at West Turkana (Kenya) that is dated 2.32 ± 0.02 Ma (McDougall & Brown 2008). The first units F-1 and F-2 have produced quartz flakes extracted at various localities (Chavaillon 1976; Merrick *et al.* 1973) and units F-2 and F-3 (Delagnes *et al.* 2011, Maurin *et al.* 2017). The four fossil wood samples collected from a single sub unit F-3-2 are estimated 2.30 Ma in age (Table 2) and

therefore contemporaneous to the archeological industry. R. Bonnefille collected 46 fossil wood samples from locality 28 (Loc 28) in Member F, with an additional six samples found by the American team. Dechamps identified 37 of these samples, while the remaining 16 had not been previously studied. Most of the slides prepared by R. Dechamps have been lost. This study reexamines four samples: Twf 17949A, Twf 17950A, Twf 17995, and Twf 18028.

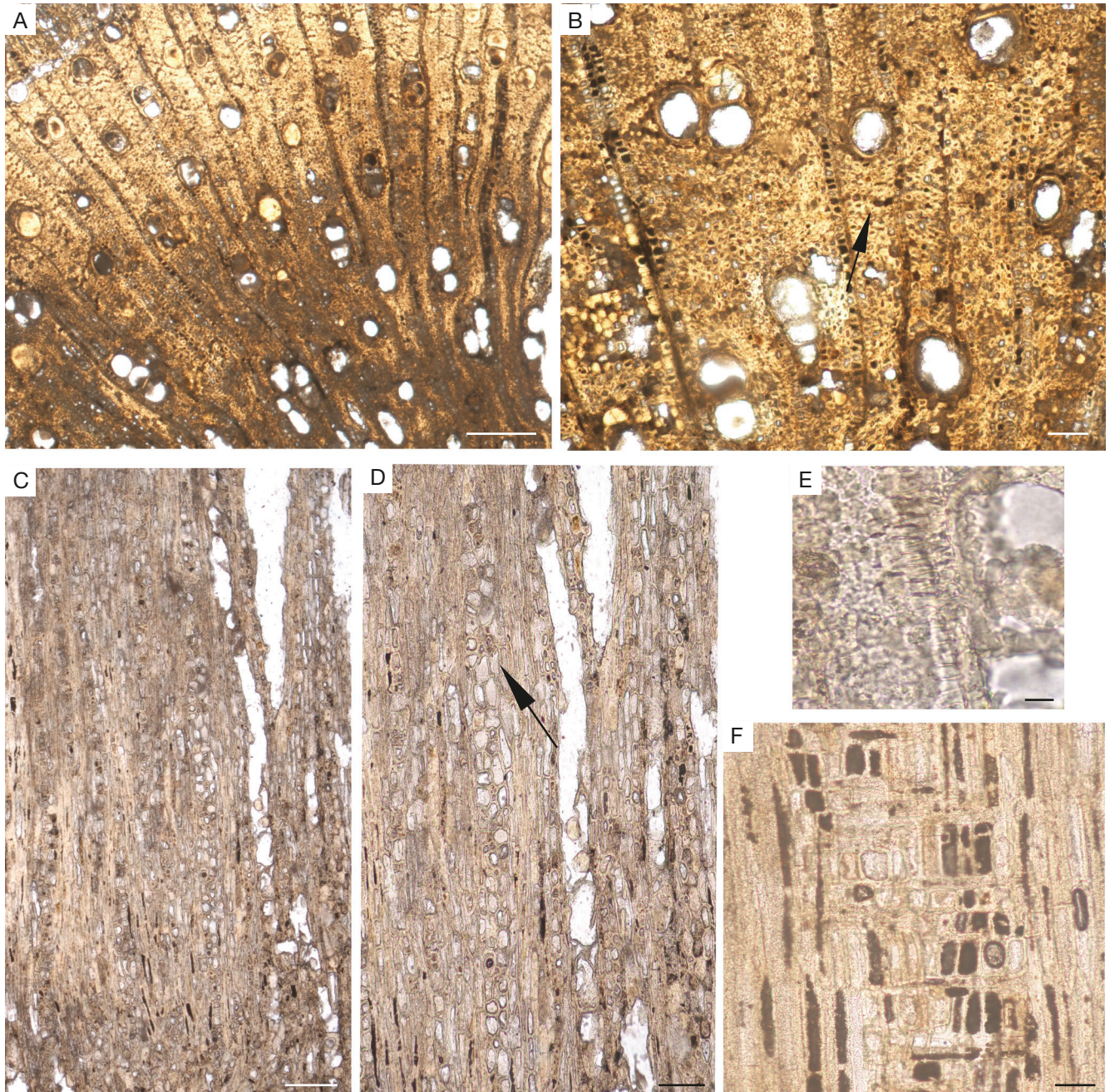


FIG. 23. — *Grewia* sp. (Malvaceae Juss.), Twf 17995: **A**, Tr, wood diffuse porous, axial parenchyma vasicentric with one or two rows of flattened cells and apotracheal diffuse aggregate (arrow); **C, D**, Tg, rays 1-4 seriate heterocellular rays, sheath cell (arrow); **E**, Tg, non-vestured intervessel-pits; **F**, Rd, heterocellular rays. Scale bars: A, 200 μ m; B, C, 100 μ m; D, F, 50 μ m; E, 10 μ m. Photographs: M.-C. Jolly-Saad.

Family MALVACEAE Juss.
Subfamily GREWIOIDEAE Dippel
Genus *Grewia* L.

Grewia sp.
(Fig. 23)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality L 28 sect. 3; Member F-3-2, 2.3 Ma; R. Bonnifille leg.; Twf 17995; Tervuren collection.

DESCRIPTION

Twf 17995 is well preserved and wood diffuse-porous. Vessels are 9-14 per mm², solitary (48%) and also in radial multiples of 2-5 (Fig. 23A, B); mean tangential diameter of vessel is 200 μ m (range 115-322 μ m), mostly round to oval in outline; vessel walls thin; perforation plates exclusively simple with oblique end walls; intervessel-pits are alternate about 5-6 μ m across (Fig. 23E), vessel-ray pits are indistinct. Gum deposits are visible in vessels. Rays are 1-3 (4) seriate, heterocellular composed of procumbent, square upright and procumbent

cells mixed throughout the rays, mean rays height is 600 μm (range 538–1981 μm), uniseriate rays with only upright cells of multiseriate rays composed of procumbent and upright cells (Fig. 23F); marginal rows 1–4 of upright cells (Fig. 23C, D), mean ray width 100 μm (range 86–120 μm); no crystalliferous elements observed; radiovascular pits are not observed. Axial parenchyma is vasicentric with one or two rows of flattened cells and apotracheal diffuse in-aggregates (Fig. 23B). Fibers have medium-thick walls, predominantly non-septate, but are occasionally septate (Fig. 23D).

AFFINITIES AND COMPARISONS

Micro-anatomical features of Twf 17995 such as solitary (or in short radial group) vessels, 1–3 seriate heterocellular rays, apotracheal parenchyma in narrow tangential bands (Fig. 23B) are structures found in the wood of Malvaceae subfamily Grewioideae. Twf 17995 was previously identified as *Crotalaria* L. (Dechamps 1983). However, in *Crotalaria* vessels are narrow (average tangential diameter ca. 34 μm), and numerous (129 per mm^2), mostly in radial to diagonal pattern; axial parenchyma scanty paratracheal or in incomplete uniseriate sheaths (*C. capensis*, *C. pallida*), or vasicentric, in 1–3 seriate sheaths near vessels and vessel groups, strands of 2–4 cells (also fusiform in *C. pallida*); rays are 1–3 (4)-seriate, composed of procumbent and square cells with upright cells in 1–3 marginal rows and in incomplete sheaths or mostly of procumbent cells, sometimes with few square and upright cells in 1–5 marginal rows and as solitary sheath cells (Oskolski *et al.* 2014). In *C. capensis* silica bodies are common in ray and axial parenchyma cells (Oskolski *et al.* 2014). Therefore, we exclude the attribution to *Crotalaria*.

Among the Grewioideae, *Grewia* is easily recognized by its characteristic ray structures with tile cells. There are many species of *Grewia* in tropical Africa and 21 species in Ethiopia (Vollesen & Demissew 1995), some of which are excluded because they have storied lower rays, non-storied high rays and parenchyma vasicentric or seemingly banded (InsideWood 2004-onwards). Other species have storied rays and fibers (cf. *G. eriocarpa* Juss). *G. coriacea* Mast. and *G. oligoneura* Sprague rays are composed of procumbent cells with one or two rows of square and upright cells. *G. trifloral* Walp., *G. bicolor*, and *G. flavescens* from Ethiopia are similar to the fossil and can be separated from other African species by their axial apotracheal parenchyma diffuse-in-aggregate (Inside wood 2004). In the modern riverine forest of the Lower Omo Valley, Carr (1998) identified five species of *Grewia*, *G. fallax* K. Schum (syn. *G. arborea* (Forssk.) Lam.), *G. ferruginea* A. Rich. (syn. *G. bequintii* Lanza), *G. parvifolia* Hochst. ex A. Rich., *G. reticulata* Hochst. ex Mast., and *G. tembensis* Fresen. (syn.: *Grewia membranacea* A. Rich) for which we have no microanatomical descriptions. Without more detailed information on the wood anatomy of the different Ethiopian species, Twf 17995 remains identified as *Grewia* sp.

Grewioideae fossil record is sparse (Manchester 1992; Gregory *et al.* 2009). Many fossil woods close to *Grewia* are described under the morphotype *Grewioxylon* from Asia and Europe, but not from Africa.

Family OCHNACEAE DC.

Genus *Ochna* L.

Ochna sp. 1

(Fig. 24)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality L 28 sect. 3; Member F-3-2, 2.30 Ma; American Staff leg.; Twf 17949A; Tervuren collection.

DESCRIPTION

The three thin sections of the specimen are very poorly preserved; several features are indistinct. The wood is diffuse-porous, growth rings are absent or indistinct (Fig. 24A). Vessels are mostly solitary or in radial multiple of 2 or 3, they are 3–7 per mm^2 , mean tangential diameter 80 μm (range 46–115 μm) (Fig. 24A, B). Vessel element length is indistinct, perforation plates are simple, intervessel-pits are minute ($< 4 \mu\text{m}$). Although not well preserved they appear probably vested. Axial parenchyma is diffuse-aggregate (Fig. 24B). Pluriseriate rays are composed of wide procumbent cells with 1–5 rows of square cells and upright cells. Pluriseriate rays (1–4 seriate) are high (1 mm and more) with distinct sheath cells (Fig. 22D). Uniseriate rays are exclusively composed of high upright cells and are shorter than pluriseriate rays (Fig. 23D), ray range height is 108–575 μm , ray width is 13–50 μm . Prismatic crystals and silica are distinct in ray cells, at times in enlarged cells. Fibers are septate. The radial section shows perforated cells (Fig. 24F).

AFFINITIES AND COMPARISONS

Micro-anatomical features of the fossil wood include mostly solitary vessels with a few in radial multiple, mean vessel diameter is less than 100 μm , diffuse-in-aggregate parenchyma, heterocellular rays of two sizes and large prismatic crystals in ray cells. The presence of perforated cells and these combined characters do not fit the attribution to *Garcinia* (Dechamps 1983). More likely, the specimen shows greater affinity with some Rubiaceae or Ochnaceae. The presence of perforated cells and large rays is particularly indicative of the Ochnaceae family. Within the Ochnaceae, the wood of *Ouratea* differs from Twf 17949A by having longer and thinner rays. The Omo fossil wood shows greatest resemblance with the wood of *Ochna*. From the Ethiopian flora, two species restricted to montane forest (Friis 1992) *O. holstii* Engl. have no perforated cells and *O. insculpta* Sleumer is not documented. Among other species *O. afzelii* R. Brown ex Oliv. and *O. membranacea* Oliv. have vascular/vasicentric tracheids and perforated cells. *O. polycarpa* Baker has no perforated cells (InsideWood 2004-onwards). *O. arborea* Burch. ex DC., *O. calodendron* Gilg & Mildbr., and *O. multiflora* DC are species similar to our studied fossil species, but they are not found in Ethiopia today.

We do not know any fossil wood reported to the Ochnaceae or to *Ochna* in Africa. *Ochnaceoxylon tertia* described from the Tertiary in Deccan (India) has vasicentric parenchyma and wide rays (Ramteke & Kapgate 2016).

Twf 17949A is attributed to *Ochna* sp. 1

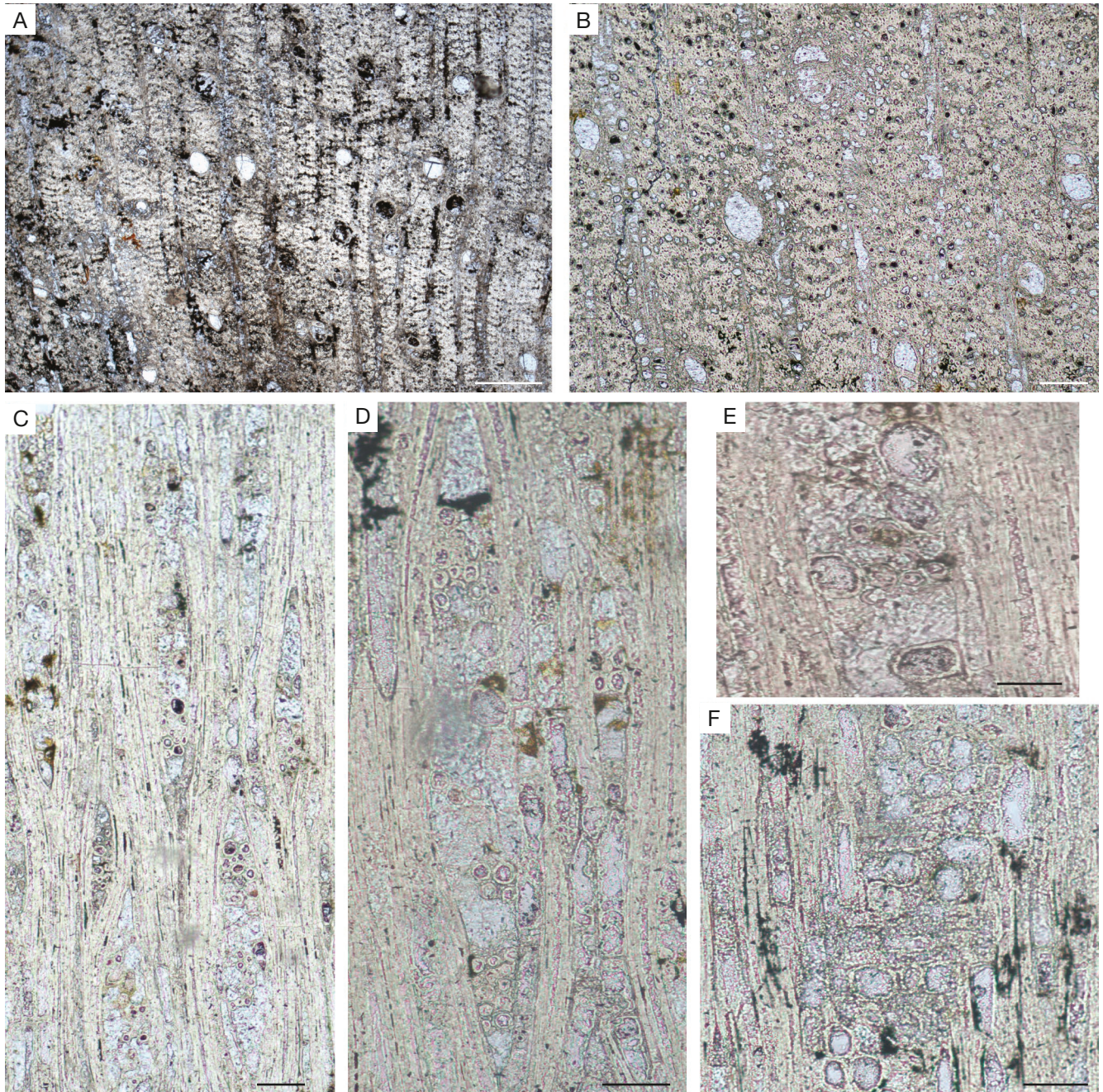


FIG. 24. — *Ochna* sp. 1 (Ochnaceae DC.), Twf 17949A: **A, B**, Tr, wood diffuse porous, axial parenchyma; **C, D**, Tg, rays 1-6 seriate, heterocellular with sheath cells (arrow); **E**, Tg, detail of ray cells; **F**, Rd, heterocellular rays, perforated ray-cells. Scale bars: A, 200 µm; B, C, 100 µm; D, F, 50 µm; E, 20 µm. Photographs: M.-C. Jolly-Saad.

Family RUBIACEAE Juss.
Genus *Psychotria* L.

Psychotria sp. 1
(Fig. 25)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality L 28 sect. 3, Member F-3-2, 2.30 Ma; American staff; Twf 17950A; Tervuren collection.

DESCRIPTION

Twf 17950A displays heterogeneously preservation, with notable alterations observed in tangential section. The wood is diffuse-porous and growth rings are not present. Vessels are rounded in outline, mostly solitary (58 %) and in radial multiples of 2 (21 %), 3 (9 %), 4 (4 %), 5 (4 %), 6 (0.8%), 7 (1.6%) (Fig. 25A), there are 40-65 per mm². Mean tangential diameter of 40 µm (range 25-53 µm); perforation plates are exclusively simple, vessel elements are short (range 81-100 µm);

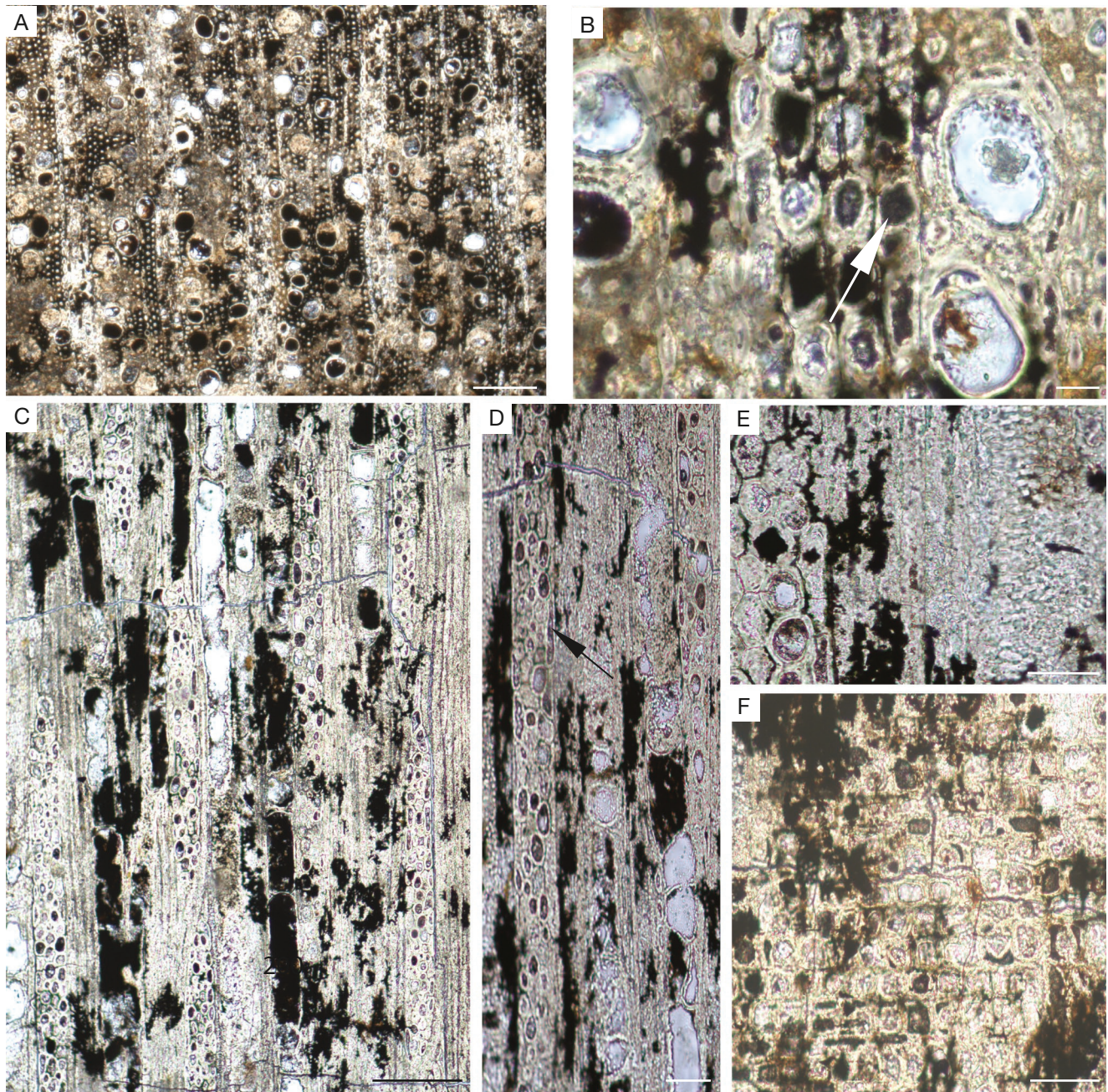


FIG. 25. — *Psychotria* sp. 1 (Rubiaceae Juss.), Twf 17950A: **A**, Tr, wood diffuse porous, small and solitary vessels; **B**, Tr, Crystal in ray cell (arrow); **C**, **D**, heterocellular rays with sheath cells (arrow); **E**, Tg, intervessel-pits; **F**, Rd, heterocellular rays. Scale bars: A, 100 μ m; B, 20 μ m; C, 200 μ m; D-F, 50 μ m. Photographs: M.-C. Jolly-Saad.

intervessel-pits are alternate, 5-6 μ m wide and they may be vested (Fig. 25E), vessel-ray pits are indistinct; vessel wall thickness is about 5 μ m. Black and yellow deposits are distinct in vessels. Rays are (1)-4 seriate, 5-7 per mm, heterocellular, composed of procumbent with 1-4 row of square and upright cells, mean rays height is 1500 μ m (range 780-2200 μ m), mean ray width varies between 75 μ m to 80 μ m, uniseriate rays are exclusively composed of square and upright cells. Some rays are interconnected. Sheath cells are distinct (Fig. 24D). Prismatic crystals are distinct in ray cells (Fig. 25B). This specimen clearly exhibits distinct perforated cells (Fig. 25F).

AFFINITIES AND COMPARISON

Apocynaceae and Rubiaceae have members exhibiting radial multiples of four or more vessels, simple perforation plates, alternate, minute intervessel-pits, and septate fibers are found. Rubiaceae can be identified by several unique characteristics: vested intervessel-pits, vessel density of 20-40 vessels per square millimeter, very long vessel elements, diffuse and diffuse-in-aggregates axial parenchyma, scanty axial parenchyma, and narrow heterocellular rays that are 1-3 (rarely 4) cells wide with 1 to over 4 uniseriate marginal rows (Metcalf & Chalk 1950; Jansen *et al.* 2001). Among this family, *Canthium*,

TABLE 3. — Comparisons of anatomical features of Pliocene and Pleistocene *Celtis* L. fossil woods from the Shungura Formation with extant *Celtis integrifolia* Lam. (InsideWood 2004-onwards). Abbreviations: **v**, vasicentric; **a**, aliform; **la**, lozenge-aliform; **wa**, winged-aliform; **c**, confluent; **b**, banded; **sb**, seemingly banded; **(NA)**, not available.

	Extant	Fossil specimens		
Anatomical characters	<i>Celtis integrifolia</i> Lam.	Twf 17812, Fig. 14, 2.62 Ma	Twf 17665, Fig. 27b, 2.13 Ma	Twf 17712, Fig. 27, 2.19 Ma
Preservation	Very good	Moderate, Fungi absent	Moderate, Fungi absent	Poor, Fungi absent
Wood porosity	–	Diffuse-porous	Diffuse-porous	Diffuse-porous
Growth ring	NA	Absent or indistinct	Absent or indistinct	Absent or indistinct
Vessels diameter mean (range) (µm)	100-200	183 (138-230)	115 (60-160)	143 (67-153)
Vessels density/ sq.mm	5-20	1-4	4-11	3-10
Vessel grouping	Solitary and in radial multiples of 1, 2, 3	Solitary and in radial multiples of 1 (61%), 2 (28%), 3 (11%)	Solitary and in radial multiples of 1 (61%), 2 (29%), 3 (9%), 4-5 (1%)	Solitary and in radial multiples of 1 (73%), 2 (18%), 3 (7%), 4 (2%)
Vessel element length (µm)	<= 350 and 350-800	indistinct	190-230	230-253
Intervascular pit size (µm) and type	4-7/7-10, not vested	7-8, not vested, angular outline	5-8, not vested	5-6, not vested
Tyloses/Gums	None	None	None	None
Axial parenchyma	v-a-la-wa-c-b-sb	v-a-c-sb	v-a-c-b-sb	v-a-c-b-sb (difficult to distinguish from fibres)
Parenchyma strands	3-4/5-8	3-4/5-8	2-4	indistinct
Rays	4-10 seriate	1-5 seriate	1-6 seriate	1-5 seriate
Ray width mean (range) (µm)	Non available	90 (70-100)	40 (35-45)	40 (23-45)
Ray height mean (range) (µm)	Non available	400 (268-618)	200 (92-328) (3-21 cells)	450 (103-965) (1-16 cells)
Rays/mm	4-12	7-8	6-9	12
Rays cells	Procumbent-square and upright cells (1-2/2-4 rows)	Procumbent-square and upright cells (1-2/2-4 rows)	Procumbent -square and upright cells (1-2/2-4 rows)	Procumbent -square and upright cells (1-2/2-4 rows)
Sheath cells	Possible	Distinct	None	None
Fibres	Non-septate fibres	Non-septate fibres	Non-septate fibres	Non-septate fibres
Crystals in rays	Prismatic cells in rays cells	Prismatic cells in rays cells	Prismatic cells in rays cells	Prismatic cells in rays cells
Crystal in parenchyma	In non-chambered parenchyma cells	In non-chambered parenchyma cells	In parenchyma cells	In non-chambered parenchyma cells

Crossopterix febrifuga, *Gardenia ternifolia*, *Nauclea latifolia* and *Rothmannia* have axial parenchyma diffuse and diffuse-in-aggregates (InsideWood 2004-onwards), a character that we have not observed in the Omo fossil wood. *Rothmannia* has shorter rays. Twf 17950A has particular similarities to Psychotriaceae, including *Psychotria*. In Ethiopia, *Psychotria capensis* grows in riverine forest, between 1150-1300 m. For *Psychotria kirkii*, *P. pedicularis*, *P. orophila*, the three taxa from montane evergreen forest, no xylomorphic data exist.

Fossil wood specimens identified as Rubiaceae in Africa are known since the Oligo-Miocene with *Mitragynaxylon gevinii* Gevin from the Tindouf of Algeria differing from the Omo fossil specimen with solitary vessels and 1-3 seriate rays (Gevin *et al.* 1971). A specimen belonging to the Rubiaceae was described from the Early Miocene Gebel El-Khashab Formation, located west of the Giza Pyramid in Egypt. This specimen differs from the Omo fossil wood by having both simple and scalariform perforation plates (El-Saadawi *et al.* 2016). *Rubioxylon vincenti* Boureau & Koeniguer from the Miocene of the Upper Omo Valley is described with scalariform perforation plates (Lemoigne 1978). *Rubioxylon vincenti* Koeniguer from the Plio-Pleistocene of Angamma in Chad has uniseriate rays (Koeniguer 1975). All these fossil specimens differ from Twf 17950A that is attributed to an extant species of *Psychotria* sp. (Table 4).

Family RUBIACEAE Juss.
Genus *Rothmannia* Thunb.

Rothmannia sp.
(Fig. 26)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality L 28 sect. 3; Member F-3-2, 2.3Ma; R. Bonnifille leg.; Twf 18028; Tervuren collection.

DESCRIPTION

Twf 18028 comprises a well-preserved cylinder displaying mineralized heteroxylous wood structure, representative of a stem fragment. The wood is diffuse-porous or noticeably semi-porous, with areas of higher concentrations of vessels (Fig. 26A). Vessels mostly solitary (90 %) other in short radial multiple of 2 and 3, clusters are absent (Fig. 26B). Vessels are rounded in outline with mean tangential diameter of 30 µm, (18 µm up to 45 µm); 40-70 per mm²; wall thickness about 5 µm. Perforation plates are exclusively simple and horizontal and vessels are short (range 81-100 µm); intervessel-pits are alternate, oval and 5-6 µm wide. Black and yellow deposits are distinct in vessels. Axial parenchyma is scanty paratracheal (Fig. 26B). Rays are 1-6 seriate, uniseriate rays are composed of upright cells, pluriseriate rays composed of procumbent

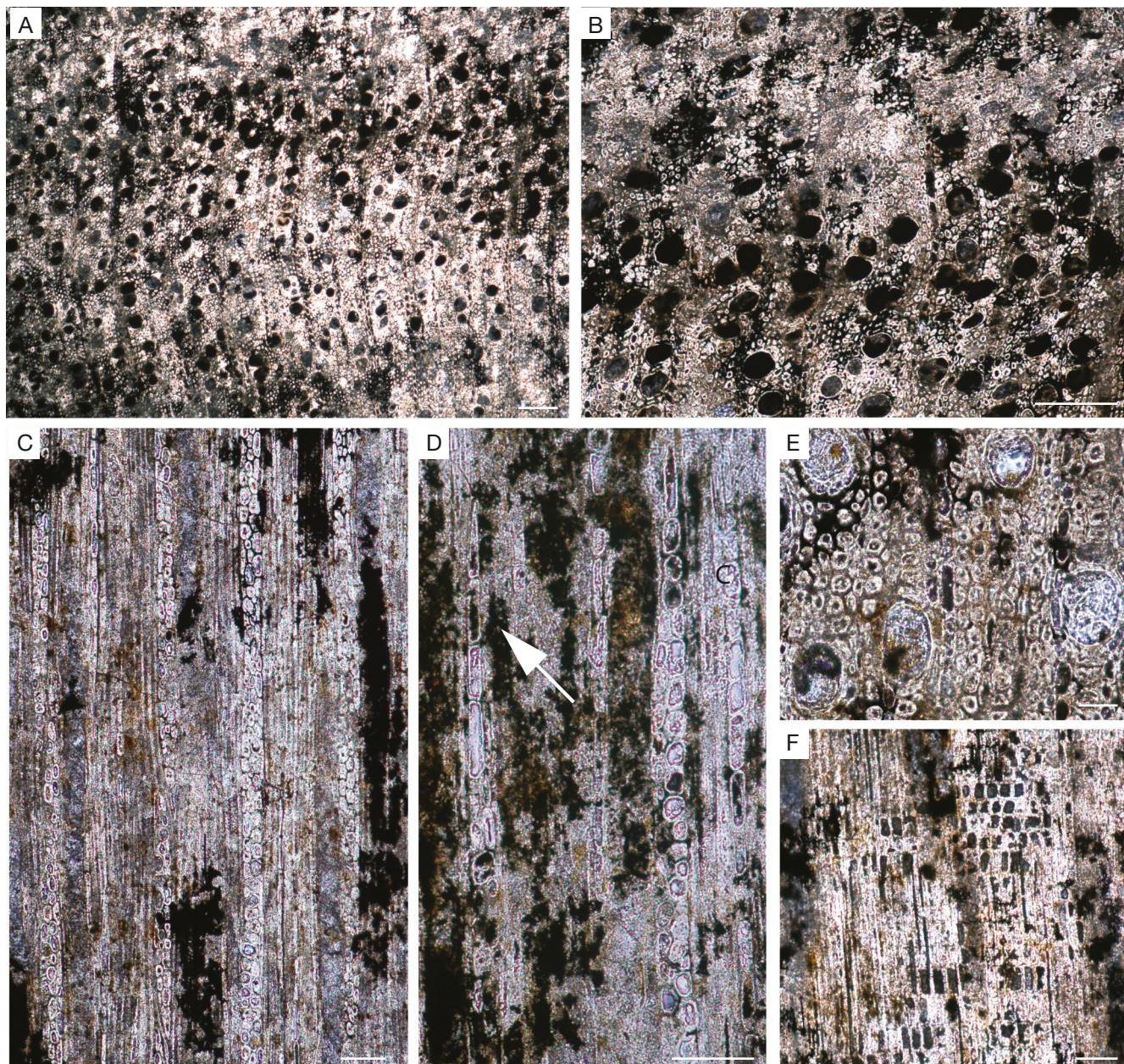


FIG. 26. — *Rothmannia* sp. (Rubiaceae Juss.), Twf 18028: **A, B**, Tr, wood with small and solitary vessels; **C, D**, Tg, thin and long rays; **E**, Tr, detail of transversal section with paratracheal parenchyma (arrow); **F**, Rd, heterocellular rays. Scale bars: A, C, 100 μ m; B, D, 50 μ m; E, F, 20 μ m. Photographs: M.-C. Jolly-Saad.

cells with long ends of 4 or more than 4 rows of upright cells (Fig. 26C, D), 11–12 per mm, mean ray height is 850 μ m (range 495 to 1848 μ m), mean ray width range 34–36 μ m, sheath cells distinct (Fig. 26C). Fibers are medium to thick walled; pits or septae are not observed in tangential section.

AFFINITIES AND COMPARISONS

Twf 18028 was first identified as *Diospyros* (Dechamps 1983; Dechamps & Bande 1994). However, anatomical features such as mostly solitary vessels, heterocellular multiseriate rays, scanty paratracheal parenchyma, and long heterocellular rays with sheath cells, rather indicate affinities with the Rubiaceae. According to the comparison with some genera of

the Rubiaceae family in the Ethiopian flora, some similarities exist between Twf 18028 and *Rothmannia*.

Few Rubiaceae fossil woods have been described from Africa. *Rothmannia* was identified from the early Pliocene of the Middle Awash Valley, Ethiopia, and dated 4.3 Ma (Jolly-Saad *et al.* 2012). However, Twf 18028 differs with the Middle Awash sample by the presence of disjunctive ray cell, 1–3 seriate ray cell and the absence of tracheid fibers. Twf 18028 may represent a distinct younger species. Among other fossil species from Ethiopia, we can exclude *Rothmannia aethiopica* (Gros 1990, later invalidated by Gregory *et al.* 2009), and *Rothmannia omoensis* (Gros 1990) characterized by numerous small to medium-sized vessels, uni to pluriseriate rays,

TABLE 4. — Comparison of the anatomical characters of four wood specimens attributed to the Rubiaceae, from the Pleistocene of Shungura Formation, Lower Omo Valley, with one from Middle Awash, Ethiopia. Symbol: *, after Jolly-Saad & Bonnefille 2012: pl. 6.

Wood samples	Twf 18028, 2.30 Ma, Fig. 26	Twf 17950A, 2.30 Ma, Fig. 25	Twf 17714, 2. 19 Ma, Fig. 30	Twf 17640, 2.13 Ma, Fig. 29	MA 94-89c *, 4.3 Ma
Identification	<i>Rothmannia</i> sp.	<i>Psychotria</i> sp. 1	<i>Canthium</i> sp. 2	<i>Canthium</i> sp. 1	<i>Rothmannia</i> cf. <i>whitfieldii</i>
Preservation	Good	Not so good	Moderate	Good	Good
Porosity and Growth ring	Diffuse porous semi ring	Diffuse porous	Diffuse porous	Diffuse porous	Diffuse porous
Vessels diameter, mean range (µm)	30 (18-45)	40 (25-53)	102 (54-130)	76 (24-118)	31 (18-45)
Vessels density/ sq.mm	40-70	40-65	12-14	12-25	100-150
Vessels grouping	Solitary (90%), 2 (9%), 3 (1%)	Solitary (58%), 2 (21%), 3 (9%), 4 (4%), 5 (3%), 6-7 (2.4%)	Solitary (28%), 2 (47%), 3 (19%), 4 (6%)	solitary (23%), 2 (59%), 3 (15%), 4 (3%)	Solitary (100%), round to slightly polygonal
Vessel element length, mean and range (µm)	100 (81-100)	95 (81-100)	200 (90-300)	indistinct	223 (185-261)
Perforation plate	Simple	Simple	Simple	Simple	Simple
Intervascular pit size (µm) and type	5-6, Vestured	5-6, Vestured	3-4, Vestured	3-4, Indistinct	3-4, Vestured, alternate and spaced
Tyloses/Gums	Black and yellow deposits	Black and yellow deposits	Tylose	Gum	Yellow deposits
Axial parenchyma arrangement	Rare or scanty paratracheal	Rare or scanty paratracheal	Scanty paratracheal apotracheal diffuse and diffuse-in-aggregates (1 row)	Scanty paratracheal, diffuse-in-aggregate	Rare or scanty paratracheal
Parenchyma strands	Indistinct	NA	Indistinct	Indistinct	Indistinct
Rays	1-6 seriate	1-4 seriate	1-4 seriate	1-4 seriate	1-3 seriate
Ray width, mean (range) µm	31 (34-36)	50 (26-66)	35 (13-62)	60 (31-92)	14-28
Ray height, mean (range) µm	1000 (850-1848)	1500 (780-2500)	400 (195-740)	800 (414-1092)	715 (225-1150)
Rays/mm	11-12	5-7	12-13	4-5	8-11
Rays cells	Uniseriate composed of upright cells; pluriseriate composed of procumbent cells with long ends of 4 rows or more of upright cells	Pluriseriate composed of procumbent with 1-4 row of square and upright cells; uniseriate, exclusively composed of square and upright cells	Multiseriate composed of procumbent and 1-4 or more rows of square and upright cells; rare uniseriate portion; few interconnected rays	Uniseriate composed of upright cells, multiseriate composed of procumbent cells with 1-4 rows of square and upright cells	Uniseriate composed of upright cells, pluriseriate composed of procumbent cells with long ends of 4 or more rows of upright cells
Disjunctive ray cells	Indistinct	Indistinct	Indistinct	Absent or indistinct	Distinct
Sheath cells	Absent	Present	Absent	NA	Absent
Fibres	Non-septate	NA	Non-septate	Septate and non septate	Tracheid
Perforated cells	Indistinct	Distinct	Indistinct	Indistinct	Indistinct
Crystals in rays	Absent	Distinct	Distinct	Absent	Absent
Crystals in parenchyma	Indistinct	Indistinct	Indistinct	Distinct	Absent

diffuse axial parenchyma, and the presence of tracheids. In conclusion, Twf 18028 remains identified as *Rothmannia* sp. with no mention of a specific attribution.

MEMBER G (2.19-1.92 MA)

Member G is the thickest unit of the whole Shungura Formation, exceeding 110 m and being divided into 29 units (Heinzelin 1983). It lies above Tuff G dated 2.27 ± 0.04 Ma (McDougall *et al.* 2012), and below Tuff H. An approximated age of between 1.91-1.89 Ma is attributed to Tuff H on the

basis that, within Member H, tuffs H-2 and H-4 correlate, respectively with the KBS (Kay Behrenmeyer Site) Tuff and the Malbe Tuff of the Koobi Fora Formation in the eastern Turkana region. H-2 and H-4 are respectively dated 1.86 ± 0.02 Ma (McDougall & Brown 2006) and 1.84 ± 0.02 Ma (Brown & McDougall 2011; Brown *et al.* 2013).

Fossil wood samples are highly abundant in this Member and have been collected from numerous localities, indicating that deposits from Member G are widespread across the Shungura sediment exposures (Heinzelin 1983) (Table 2). Sediments from the lower part of Member G, below G-14 (*c.* 2.27-2.06 Ma) mainly consist of fluvial channels interspersed by floodplain

deposits. Sediments from the upper part of Member G (G-14 to G-27; *c.* 2.06-1.92 Ma) derived from pro-deltaic to offshore lacustrine sediments (Heinzelin *et al.* 1976; Heinzelin 1983; Howell *et al.* 1987). The two oldest wood samples of this Member coming from Unit G-3 dated to 2.19 ± 0.04 Ma (Brown & MacDougall 2011) are close in stratigraphy with Unit G-4 from which two hominin mandibles most probably derive (Heinzelin 1983). The above units, G-4 to G-7, correspond to the Reunion Event estimated between 2.15 to 2.11 Ma (Kidane *et al.* 2014; Cohen & Gibbard 2019), leading to an estimated age of 2.13 Ma attributed to the three fossil wood samples from G-5. At the hominin locality OMO 323 located in unit G-8, hominin fossil remains (cranium and limb bones), found in 1976, are attributed to *Paranthropus boisei* and estimated 2.12 Ma in age (Alemseged *et al.* 2002; Daver *et al.* 2018). Unit G-13 poorly records a normal paleomagnetic zone (Kidane *et al.* 2014), and is rather dated at 2.08-2.06 Ma (Gardin *et al.* 2024). Inside the reversed Matuyama paleomagnetic Epoch, lacustrine units G-14 to G-28 correspond to the deposits above the Kangaki Tuff dated at 2.063 ± 0.032 Ma in the Nachukui Formation of West Turkana (Brown & McDougall 2011). This tuff lies near the base of the lacustrine succession at West Turkana, perhaps corresponding to the lacustrine deposits in the Lower Omo Valley. These bounds set good dating constraints to fossil woods collected between units G-18 to G-19, with ages of *c.* 2.02 Ma (Brown comm. pers. 2016). Above these layers, G-28 is located just below the lower boundary of the normal paleomagnetic polarity of the Olduvai subchron, now estimated to be 1.930 Ma (Kidane *et al.* 2014; Cohen & Gibbard 2019).

Member G yields the richest collection of fossil wood samples, with 32 included in this study leading to the identification of 21 wood taxa for the same unit G-29 of an estimated age of 1.92 Ma. Sands from this unit mark the end of the major lacustrine incursion inside the Shungura Formation and were likely spread on emerging shorelines and/or paludal deltaic mouth bars, deposited slightly before the thick covering spread of Tuff H. We now describe fossil woods from Units G-3-G-5 dated 2.19 to 2.13 Ma, following alphabetic order of their corresponding botanical families.

UNIT G-5 TO G-13 (2.13-2.06 MA)

Family CANNABACEAE Martinov
Genus *Celtis* L.

Celtis cf. *integrifolia* Lam.
(Figs 27; 28)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 560-2 sect. 9; Member G-3, 2.19 Ma; American Staff leg.; Twf 17712; Tervuren collection (Fig. 27) • same data; locality P 388 sect 19, Member G-5, 2.13 Ma; Twf 17665; Tervuren collection (Fig. 28).

DESCRIPTION

Twf 17712 is poorly preserved. But Twf 17665 shows anatomical features (axial parenchyma vasicentric, confluent,

seemingly banded, ray heterocellular 1-6 seriate, prismatic crystals in ray cells and intervessel-pits not vested) and quantitative values comparable to those previously described for Twf 17812 (Fig. 28) that was identified as *Celtis* cf. *integrifolia*. All these characters are summarized in Table 3.

Twf 17712 and Twf 17665 were initially attributed to *Lannea* or *Ozoroa* among Anacardiaceae (Dechamps 1983). However, the presence of abundant parenchyma contradicts this diagnosis, as both genera exhibit sparse parenchyma. Furthermore, *Ozoroa* is characterized by larger vessel pits, septate fibers and does not have prismatic crystals in ray. Therefore, we exclude such previous identification.

From Africa, three generic names, *Celtisoxylon* Trivedi, *Celtixylon* Greguss, and *Celtoxylon* Wurzingen have been attributed to fossil woods resembling *Celtis*, although not properly diagnosed (Gregory *et al.* 2009). *Celtisoxylon* applied to a wood from Deccan Intertrappean beds of India was only mentioned in an abstract without description and designation of holotype. *Celtixylon* was never formally diagnosed, and *Celtoxylon* was used in a thesis, not formally published. Woods thought to have affinities with *Celtis* have been reported from the Miocene of temperate Europe and Asia (Selmeier 1989) and North America (Wheeler & Manchester 2021).

Family RUBIACEAE Juss.

Genus *Canthium* Lam.

Canthium sp. 1
(Fig. 29)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 794 sect. 5, Member G-5, 2.13 Ma; Jean de Heinzelin leg; Twf 17640; Tervuren collection.

DESCRIPTION

The preservation is quite good in the transverse section, but moderate in the tangential section where all the cellular details are not very clear. Wood is diffuse-porous, growth rings boundaries are absent, vessel are solitary (23 %) and in radial multiples of 2 (59%), 3 (15%) and 4 (3%) (Fig. 29A, B), 12-25 per mm². Mean tangential diameter of 76.4 µm, range 24-118 µm. Perforation plates are exclusively simple, vessel elements are not distinct, intervessel-pits are 3-4 µm wide, probably vested but the details are hard to distinguish (Fig. 29E), vessel-ray pits are not visible. Gum deposits are observed in vessel lumina. Parenchyma is scanty paratracheal, diffuse-in-aggregates (Fig. 29B), parenchyma strands are not clearly distinct, probably 5-8 cells per strands. Rays are 1-4-seriate and heterocellular; uniseriate rays are composed of upright cells, multiseriate rays composed of procumbent cells with one row of upright cells. 4-5 per mm, mean ray height is 800 µm (range 414-1092 µm) (3-23 cells), mean ray width is 60 µm (range 31-92 µm). Fibers are thin to medium walled of various size and shape. Septate and not septate

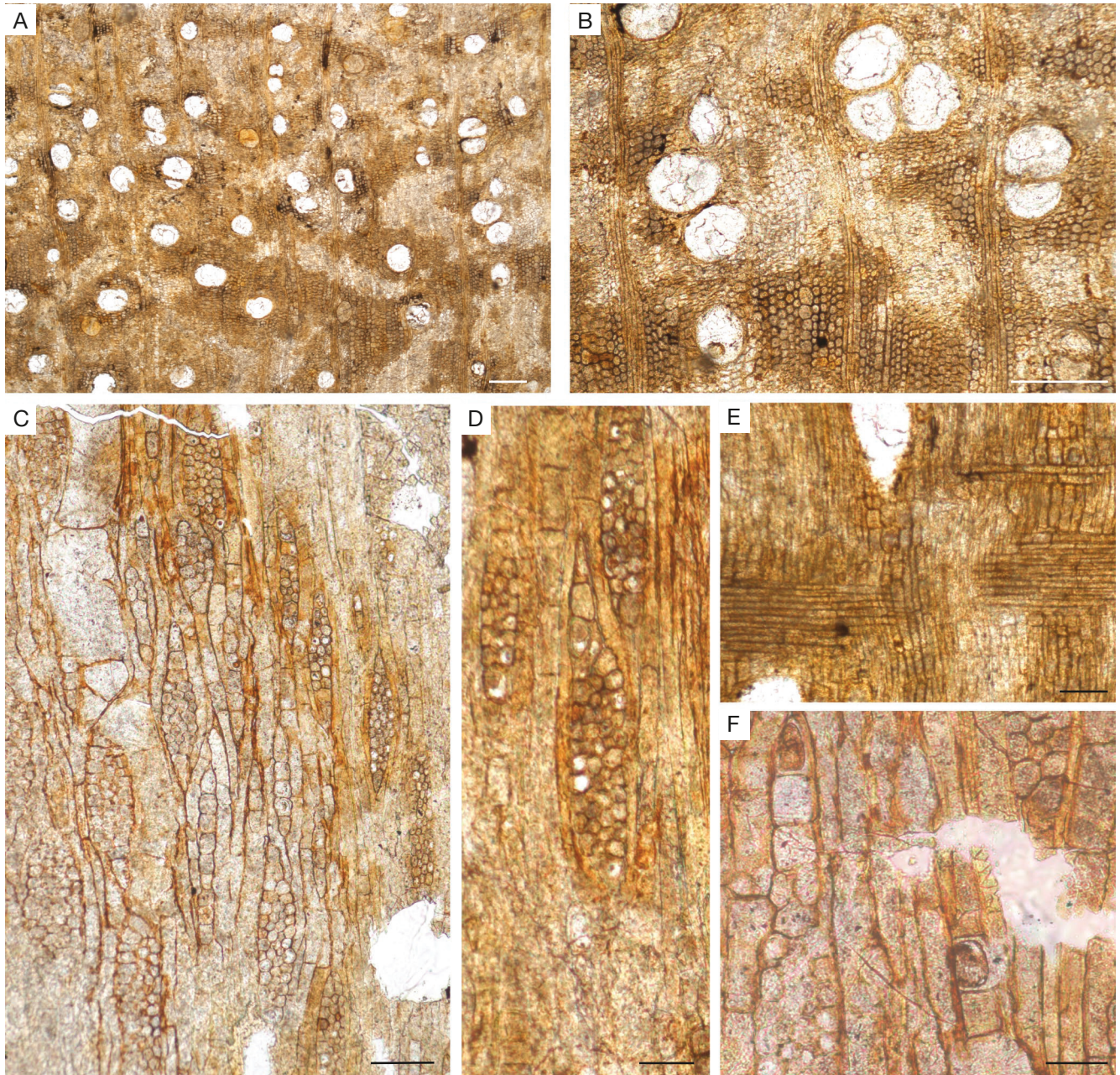


FIG. 27. — *Celtis* cf. *integrifolia* (Cannabaceae Martinov), Twf 17712: **A, B**, Tr, wood diffuse porous, axial parenchyma vasicentric, confluent seemingly banded; **C, D**, Tg, rays 1-5 seriate; **D**, Tg, detail of rays, crystal in upright cell (**arrow**); **E**, Rd, heterocellular rays with prismatic crystals (**arrow**); **F**, Tg, Prismatic crystal in square rays cells (**arrow**). Scale bars: A, B, 200 μ m; C, D, 100 μ m; E, 50 μ m; F, 10 μ m. Photographs: M.-C. Jolly-Saad.

fibers are observed, strands of crystalliferous axial parenchyma with one rhomboidal crystal per chamber (Table 4).

AFFINITIES AND COMPARISONS

Anatomical features of Twf 17640 such as vessels in radial multiple, perforation simple, small vested intervessel pits, axial parenchyma scanty paratracheal and diffuse-in-aggregates, 1-4 seriate heterocellular rays are wood characteristics similar to those of the Rubiaceae (Jansen *et al.* 2002; Inside-wood). In Ethiopia, this botanical family includes 31 genera as trees or shrubs (Puff 2003) (Friis

et al. 2011). For the comparison with the fossil Twf 7640, we exclude all the species having exclusively solitary vessels such as *Catunaregam* Wolf, *Coffea* L. (*C. arabica* L., *C. richardii* Leroy, *Gardenia* Colden, *Mitragyna* (Wild.), *Paederia* L., *Sarcocephalus latifolius* (Smith) Bruce, *Tricalysia* DC., *Feretia* Del., *Pavetta* L., *Psilanthus* Hook f., *Keetia* E.P. Philips, *Tarenna* Gaertn., *Rytigynia* Blume, *Uncaria* Schreb. *Paederia* and *Vangueria* Juss.). In the group of taxa comprising vessels in small radial multiple up to 3 rarely, vessels in small radial multiple up to 3 rarely 4, *Anthospermum* L., *Breonadia salicina* and *Hymenodictyon floribundum*

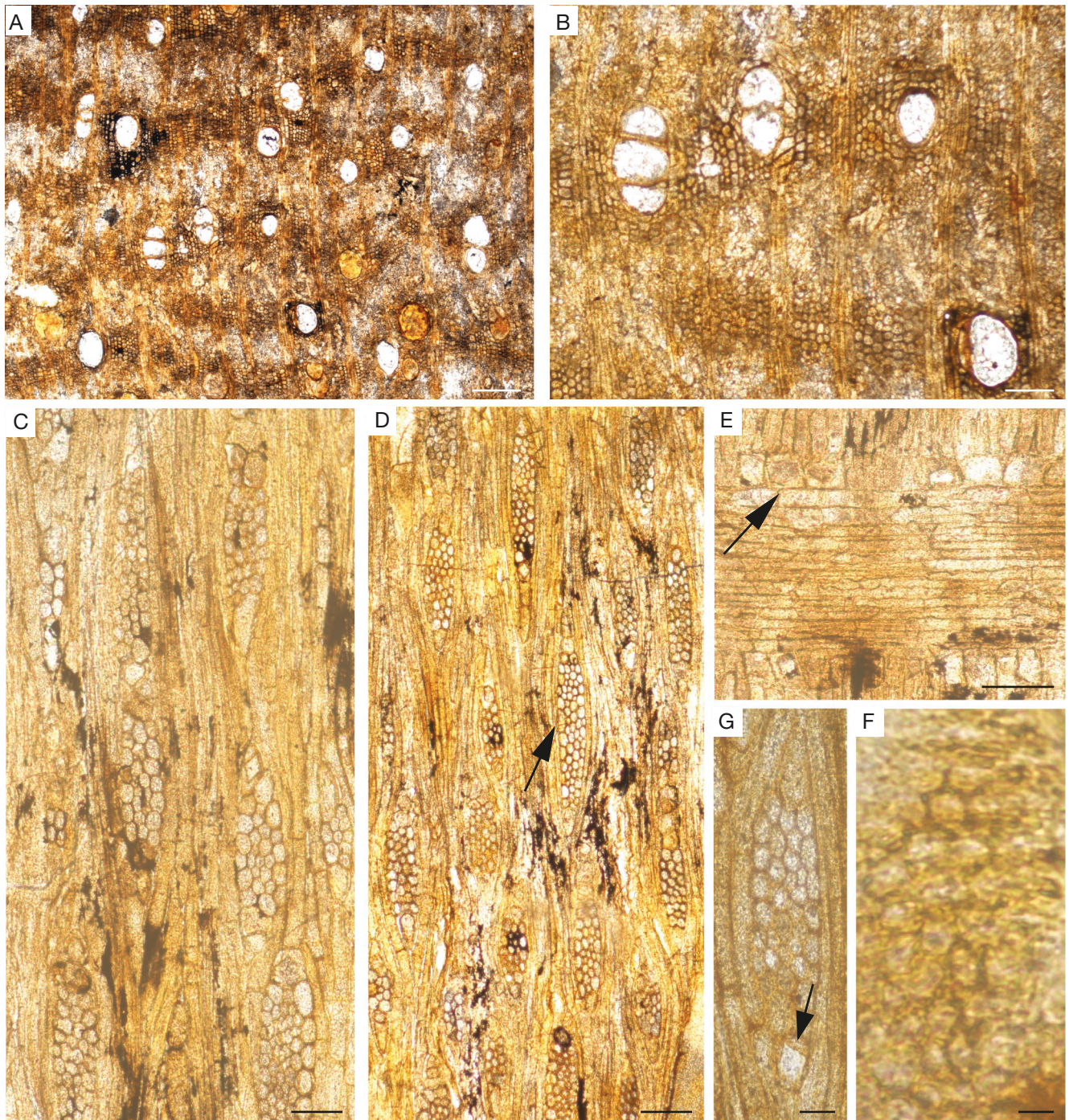


FIG. 28. — *Celtis* cf. *integrifolia* (Cannabaceae Martinov), Twf 17665: **A, B**, Tr, wood diffuse porous, axial parenchyma vasicentric, confluent seemingly banded; **C, D**, Tg, rays 1-5 seriate; **D**, detail of rays, crystal in upright cell, sheath cells (arrow); **E**, Rd, heterocellular rays, crystal in ray cells (arrow); **F**, Tg, non-vestured, alternate, intervessel-pits; **G**, Tg, Prismatic crystal in upright cell (arrow). Scale bars: A, 200 μ m; B, C, 100 μ m; D, E, 50 μ m; F-G, 10 μ m. Photographs: M.-C. Jolly-Saad.

(Hochst. & Steud.) Robinson have scarce axial parenchyma and thinner rays. *Galiniera* Del., *Hymenodictyon*, *Mussaenda* L. have thinner rays. *Craterispermum* Benth., has banded parenchyma. *Carphalea* Juss. has wider rays and crystals in enlarged cells. *Psydrax schimperianus* (A. Rich) Bridson has no crystal in ray cells. *Psydrax parvifolia* has larger rays. We have no available microanatomical data for *Chazaliella* E.M.A. Petit & Verdc., *Meyna* Roxb. ex. Link,

or for *Polysphaeria* Hook f., to compare with Twf 17640 and sample Twf 17714.

Anatomical characteristics, including diffuse porous wood, scanty paratracheal and diffuse-in-aggregate axial parenchyma, rays heterocellular composed of procumbent cells and 1-4 rows of square and upright marginal cells, as well as small and probably vestured intervessel-pits, are found in modern Rubiaceae such as *Canthium* sp. 1.

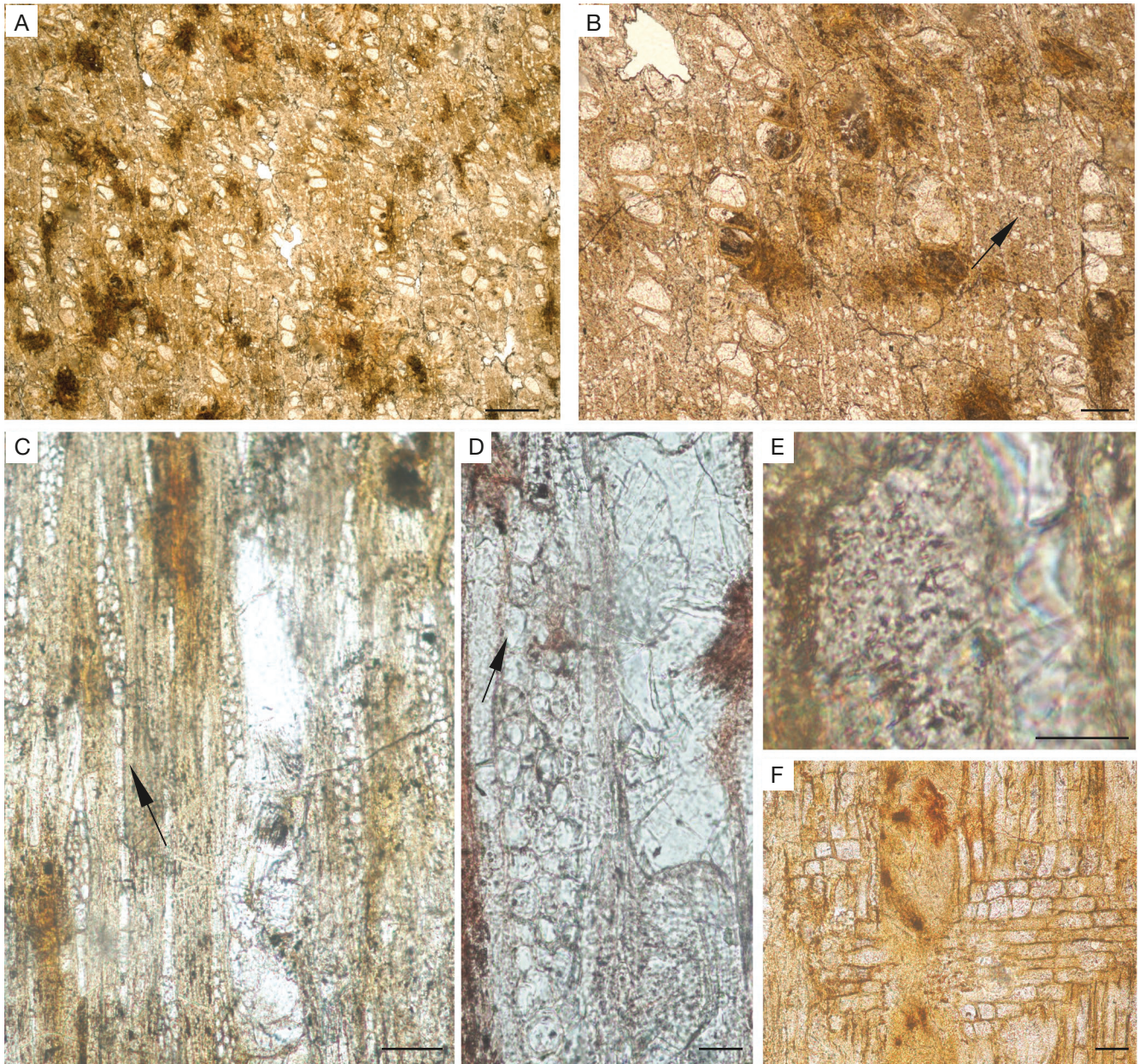


FIG. 29. — *Canthium* sp. 1 (Rubiaceae Juss.), Twf 17640: **A, B**, Tr, wood diffuse porous, vessels in radial multiple, axial parenchyma diffuse-in-aggregates (**arrow**); **C, D**, Tg, rays 1-3 seriate with four or more marginal upright cells (**arrow**); **E**, Tg, vestured intervessel-pits; **F**, Rd, heterocellular rays. Scale bars: A, 200 μ m; B, 100 μ m; C, F, 50 μ m; D, E, 20 μ m. Photographs: M.-C. Jolly-Saad.

Canthium sp. 2 (Fig. 30)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality L 560-1; Member G-3, 2.13 Ma; American Staff leg; Twf 17714; Tervuren collection.

DESCRIPTION

Twf 17714 exhibits very similar characteristics to Twf 17640, but with some differences (Table 5) justifying an attribution to a distinct species *Canthium* sp. 2, illustrated in Figure 30.

A small number of Rubiaceae fossil wood morphotypes are known from Africa; the oldest dating from the Oligocene-Miocene (Gevin *et al.* 1971). In Ethiopia, *Rubioxylon vincenti*

Boureau & Koeniguer, briefly described from the Miocene of the Upper Omo Valley (Lemoigne 1978), has thinner rays and scalariform perforation plates. *Rubioxylon vincenti* Koeniguer from Pliocene deposits in Chad has uniseriate rays, medium-sized vessels, and paratracheal vasicentric parenchyma (Koeniguer 1975). *Rothmannia* cf. *R. whitfieldii* from the Sagantole Formation at Aramis locality, Middle Awash (Ethiopia) and dated 4.3 Ma shows solitary vessels, thinner rays and disjunctive ray cells, and does not resemble the Omo fossil specimen Twf 17640. Another fossil from the Lower Omo Valley (Pa 8036A), collected by Coppens *et al.* was assigned to *Canthium omoense* (Gros 1990) in Member G28–29 (Argile du Château), differs from the two specimens

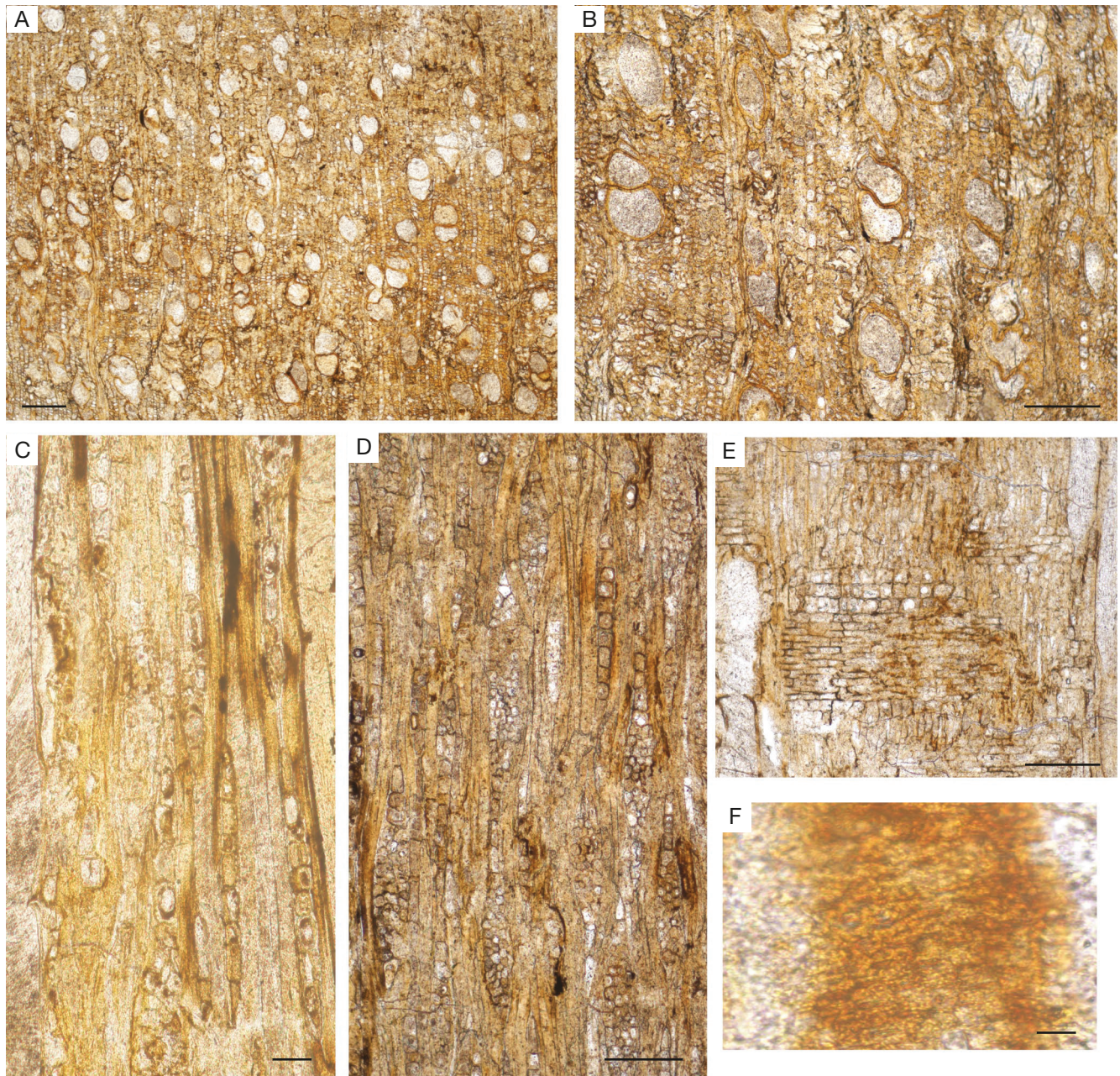


FIG. 30. — *Canthium* sp. 2 (Rubiaceae Juss.), Twf 17714: **A, B**, Tr, wood diffuse porous, vessels in radial multiple, axial parenchyma; **C, D**, Tg, rays 1-3 seriate with four or more marginal upright cells (**arrow**); **E**, Rd, Heterocellular rays; **F**, Tg, intervessel pits. Scale bars: A, 200 µm; B, E, 100 µm; C, 50 µm; D, 50 µm; F, 10 µm. Photographs: M.-C. Jolly-Saad.

studied here (Twf 17640 and Twf 17714). This fossil specimen differs from the Shungura specimens by the absence of diffuse-in-aggregates parenchyma.

In conclusion, the closest affinities of the fossil specimen Twf 17640 are with the extant genus *Canthium* in the Vanguerieae A. Rich. (Gros 1990; Lens *et al.* 2000; Mouly *et al.* 2021). It is considered as *Canthium* sp. 1, a distinct species from *Canthium* sp. 2 showing non-septate fibers (Table 4), attributed to Twf 17714 (Fig. 30) a wood sample moderately preserved, collected from a slightly younger stratigraphic Unit G-3 (Table 2).

UNIDENTIFIED ANGIOSPERMS

Fam., gen. and sp. indet. 3

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality L 35-58 sect. 4, Member G-5, 2.13 Ma; American Staff leg; Twf 17615; Tervuren collection.

DESCRIPTION

Due to poor preservation, several anatomical features of the specimen are unclear or indistinct. The wood is diffuse-

porous and growth rings boundaries indistinct. Vessels are solitary (77%) and in radial multiples of 2-3, 1-2 per mm². Mean tangential diameter of 213 µm, range 81-345 µm. Perforation plates exclusively simple; vessel elements are not clearly distinct (n=1: 189 µm), vessel pits are indistinct. Sclerotic tyloses are visible in vessel lumina. Axial parenchyma abundant, banded; bands are 4 cells wide (46 µm) up to 14 cells (230 µm); strands of parenchyma 5-8 cells. Rays are 2-6-seriate, heterocellular, composed of procumbent with one row of upright cells. 4-5 per mm. Length is between 414 µm to 1092 µm and 31 to 92 µm wide. They are 4-5 per mm. Fibres are not septate.

AFFINITIES AND COMPARISONS

Twf 17615 characteristics are: vessels that are solitary and in radial multiples, simple perforation plates, alternate intervessel-pits, thick-walled fibers, banded axial parenchyma, which is storied and fusiform. As some diagnostic features are not visible due to the poor preservation of the wood, it is not possible to provide a diagnosis for Twf 17615.

Family FABACEAE Lindl.
Subfamily CAESALPINIOIDEAE DC.
Genus *Erythrophleum* Afzel. ex. R.Br.

Erythrophleum sp.
(Fig. 31)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 719 sect. 18 Member G-13, 2.06 Ma; Jean de Heinzelin leg.; Twf 17754; Tervuren collection.

DESCRIPTION

The preservation of Twf 17754 is relatively good, with distinct fungal hyphae visible within the vessel elements. The wood is diffuse-porous, growth rings boundaries indistinct (Fig. 31A, B). Vessels are round or oval in shape mostly solitary (90%), few of them in short radial multiples of 2 or 3, clusters distinct. There are 10-15 vessels per mm². Vessel wall is thin (2-3 µm). Gum deposits are distinct in vessel lumina. Mean tangential diameter is 172 µm (range 92-253 µm). Mean vessel element height is 340 µm (range 364-405 µm). Perforation plates are exclusively simple and horizontal. Intervessel pits are vested, alternate, 4-5 µm wide (Fig. 31E), some are coalescent, vessel-ray pits are similar to intervessel pits. Axial parenchyma has various distributions, vasicentric unilateral (1 to 3 rows of cells), vasicentric and often confluent up to 3 vessels. Parenchyma strands have 2-4 cells. Rays are 1-3 (4) seriate wide (Fig. 31C), 9-10 per mm. Mean ray height is 500 (range 104-1380 µm; 8-12-91 cells), mean ray width is 30 µm (range 21-54 µm). They are composed of procumbent cells and 1-2 rows of square and upright cells. Prismatic crystals are distinct in chambered parenchyma up to ten strands. Fibers are irregular thin to medium thick walled, range in diameter is between 8-14 µm; no pits or septae have been observed.

AFFINITIES AND COMPARISONS

This fossil exhibits several distinctive anatomical features including diffuse-porous wood, simple perforation plate, large vessels, parenchyma vasicentric unilateral, vested pits, long homocellular rays 1-5 seriate. These features clearly indicate affinities with the Fabaceae family, but not with *Bridelia* (Phyllanthaceae) as previously suggested (Dechamps 1983). Comparison of Twf 17754 with various Fabaceae shows that few species combine axial unilateral parenchyma and vested pits. Among them, *Erythrophleum* is the most similar. Within the genus, *E. suaveolens* most closely resembles the wood anatomy of the Twf 17754 specimen.

Erythrophloeoxylon was identified as a fossil morphotype close to *Erythrophloeum* (Müller-Stoll & Mädler 1967). In Africa, one fossil species, *Erythrophleum africanum*, was mentioned from the Pliocene of the Lower Omo valley (Dechamps 1976). However, no description, illustration, or thin section of this material was provided. A fossil taxon most closely related to Twf 17754 appears to be *Peltophoroxylon embergeri* Lemoigne from the Upper Omo valley (Lemoigne 1978). This wood exhibits diffuse porosity and less vessels (8-10 vessels per mm²), vasicentric or vasicentric unilateral parenchyma and wider (2-6 seriate) rays than our sample. In conclusion, based on the observed anatomical features and comparative analysis, we attribute Twf 17754 to *Erythrophleum* sp.

UNITS G-18 TO G-19; 2.02-2.01 MA

Family ASTERACEAE Bercht. & J. Presl.
Genus *Brachylaena* R.Br.

Brachylaena sp. 1
(Fig. 32)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 553 sect. 6, Member G-18, 2.12 Ma; Jean de Heinzelin leg.; Twf 17707; Tervuren collection.

DESCRIPTION

The fossil exhibits poor preservation, and the longitudinal section has not the appropriate thickness for detailed analysis. The wood displays diffuse porosity. The presence of a growth ring is discernible (Fig. 32A), exhibiting the reduction of fiber diameter in three or four rows and variation in vessel density. Vessels are solitary (47%) or in radial multiple of 2 (21%), 3 (14%), 4 (7%), 5 (8%), 6 (2%) and 7 (1%); 100 and more per mm² (Fig. 32A, B). Mean vessel diameter is 22 µm (range 13-42 µm), perforation plates are simple, horizontal to slightly oblique. Vessel elements are short 108-112 µm. Intervessel pits are crowded alternate, minute to small (3-4 µm), bordered, and not vested (Fig. 32E). In radial section, vessel-ray pits are similar to vessel pits. Rays are uniseriate, exceptionally biseriate with sometime uniseriate ends (Fig. 32C, D). They are composed of procumbent cells with one row of square and upright cells. Mean ray height is 135 µm (range 50-227 µm; 4-19 cells), mean ray width is 15 µm (range 8-20 µm). Fiber diameter is between 9 to 22.4 µm, apparently not very thick-walled. Parenchyma is rare, scanty paratracheal and apotracheal.



FIG. 31. — *Erythrophleum* sp. (Fabaceae Lindl.), Twf 17754: **A, B**, Tr, wood diffuse porous with axial parenchyma vasicentric mostly unilaminar; **C**, Tg, rays 1-5 seriate and homocellular; **D**, Tgs, vessels with minute intervessel-pits; **E**, Tg, vessel-pits vestured; **F**, Rd, homocellular rays. Scale bars: A, 200 µm; B-D, 100 µm; E, 10 µm; F, 50 µm. Photographs: M.-C. Jolly-Saad.

AFFINITIES AND COMPARISONS

The combination of anatomical features observed in Twf 17707 including: narrow vessels occurring solitary or in long radial multiples, minute to small alternate intervessel pits, and narrow rays primarily composed of procumbent cells does not support initial identification as *Populus euphratica* (Dechamps 1983). Species of *Populus* typically exhibit larger vessel pits and exclusively uniseriate rays. Instead, the wood anatomy of Twf 17707 shows

close affinities with families such as Asteraceae and Rutaceae (including Ptaerodactylaceae (APG II, 2003)). Among the Asteraceae, *Brachylaena* exhibits both thin and storied rays, a feature consistent with the anatomy of Twf 17707 that represents the first fossil wood specimen described for this family in Africa (Gregory *et al.* 2009). Indeed, among the Rutaceae, we can exclude the morphotype *Ptaerodactylon* for its occurrence of prismatic crystal, a character not seen in our fossil.

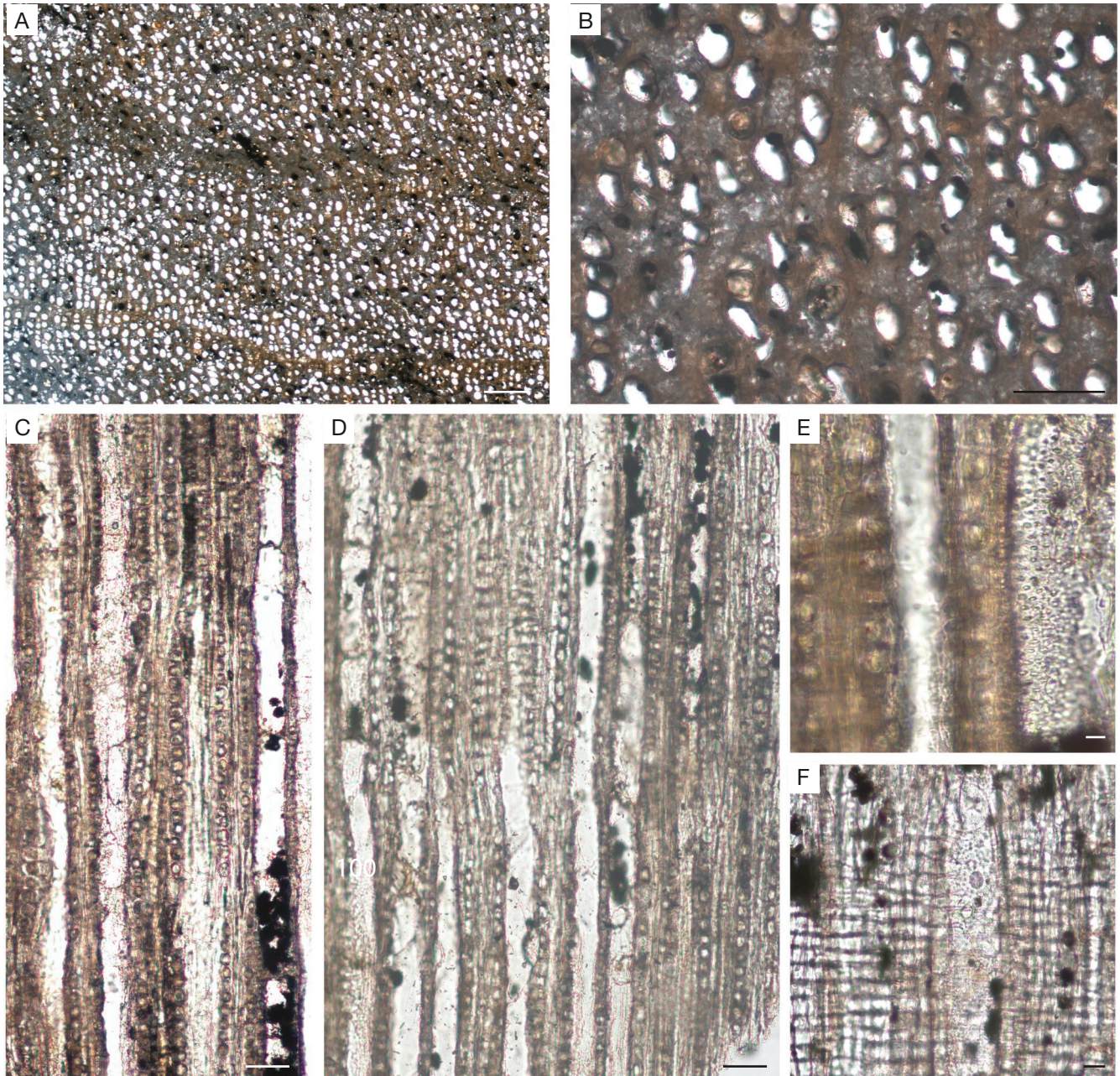


FIG. 32. — *Brachylaena* sp. 1 (Asteraceae Bercht. & J.Presl.), Twf 17707: **A, B**, Tr, growth ring discernible with variation in vascular density, small vessels mostly solitary; **C, D**, Tg, rays uniseriate irregularly storied; **E**, Tg, minute intervessel-pits; **F**, Rd, rays slightly heterocellular. Scale bars: A-C, 100 μ m; D, 50 μ m; E, F, 20 μ m. Photographs: M.-C. Jolly-Saad.

Family COMBRETACEAE R.Br.
Genus *Terminalia* L.

Terminalia sp. 3 (Fig. 33)

EXAMINED MATERIAL. — Ethiopia • Lower Omo Valley, Shungura Formation, locality P 729 sect. 19, Member G-19, 2.01Ma; R. Bonnefille leg.; Twf 18069; Tervuren collection.

DESCRIPTION

Twf 18069 is a small branch that retains evidence of central pith. The wood is diffuse-porous, growth rings absent.

Vessels are solitary (73%) and in radial multiples of 2 (22%), 3 (2%). Mean tangential diameter of 70 μ m, range 21-115 μ m, 15-20 vessels per mm² (Fig. 33A). Perforation plates are exclusively simple; intervessel-pits crowded alternate, bordered, minute and vested (fig. 33E); vessel-ray pits are similar to intervessel-pits (Fig. 41E); Gum is visible in vessels. Axial parenchyma is vasicentric, aliform to confluent, strands of cells 2-3. Rays are 1-3 (4) seriate, heterocellular, composed of procumbent and square cells mixed throughout the rays and showing uniseriate ends (Fig. 33C, D). Rays are not storied, 10-12 per mm, mean ray height is 300 μ m (range 172-483 μ m), mean ray width

is 40 µm (range 22-80 µm). Fibers are thick with mostly very thick wall, septae present. Crystals are distinct in parenchyma and in ray cells.

AFFINITIES AND COMPARISONS

Twf 18069 is characterized by diffuse-porous wood, small to medium-sized vessels, solitary or in radial multiple, predominantly paratracheal parenchyma that is vasicentric to slightly aliform, confluent, 1-3 seriate heterocellular rays, septate fibres, and crystal inclusions in rays and parenchyma. Twf 18069 was initially identified as *Acacia mellifera* (Dechamps 1983). But the presence of heterocellular rays, with mixed procumbent square cells throughout the ray structure, along with the occurrence of mineral inclusions in the ray cells, challenge the original identification.

These features are not characteristic of *Acacia*, which typically exhibit homocellular rays with procumbent cells. Instead, the anatomical characteristics of the specimen, particularly the ray cells composition and mineral inclusions, more closely resemble those observed in *Terminalia* L. (Inside Wood online-2004-onwards (Van Vliet 1979). Consequently, Twf 18069 is attributed to *Terminalia* sp.

Twf 18069 also shares some diagnostic features (mostly, rays with procumbent cells and square cells mixed in the rays with one row of upright cells, intervessel pits vested, druses in chambered parenchyma and crystals in rays) with *Terminalioxylon* G.Schönfeld, a palaeobotanical taxon of worldwide distribution recorded with more than 60 fossil species described from the Eocene to the Miocene in Africa (Gregory *et al.* 2009). All these fossil species differ from Twf 18069 with their exclusively uniseriate rays, bigger vessels, and in ray composition for some of them.

We rather refer Twf 18069 to the extant genus *Terminalia*. However, with regards to the great number (150) of modern African species (Mabberley 1997), including nine from Ethiopia (Vollensen 1995a), a specific attribution remains impossible in the current state of knowledge. We can exclude *Terminalia brevipes* Pamp., common from riparian forests in Southern Ethiopia and previously described (Jolly-Saad & Bonnefille 2023). In conclusion, we report Twf 18069 (Fig. 33) to *Terminalia* sp.

Family MIMOSOIDEAE DC.

Genus *Albizia* Durazz.

Albizia sp. 2
(Fig. 34)

EXAMINED MATERIAL. — Ethiopia • Lower Omo Valley, Shungura Formation, locality Omo 27-2, Member G-18, 2.02 Ma; R. Bonnefille (73-5) leg.; Twf 17929; Tervuren collection.

DESCRIPTION

Twf 17929 is not well preserved. Wood diffuse-porous, growth ring boundaries are indistinct. Vessels are mostly solitary (86 %) or grouped by 2 (12 %), 3 (1%) and

rarely cluster (1%), 4 to 12 per mm² (mean 8) (Fig. 34A). Mean tangential diameter is 126 µm, range 57-195 µm, vessel wall thin (2-3 µm wide). Tyloses are absent. Vessel element length is not visible. Perforation plates are exclusively simple, intervessel pits alternate (4-5 µm) are vested and not crowded (Fig. 34E). Vessel-ray pits are similar to intervascular pits. Axial parenchyma is mostly vasicentric, slightly aliform, sometimes confluent. Prismatic crystals are distinct in chambered parenchyma cells (14 µm wide). Rays are 1-6 (8) seriate wide, uniseriate rays are rare, 6-9 per mm. Mean ray height is height is 400 µm (range 90-805 µm), mean ray width is 60 µm (range 9-72 µm). They are composed of procumbent cells (Fig. 34C, D-F). Fibers show poorly distinct walls, diameter of fibers range is 5-11 µm, pits are not observed and septae visible (Fig. 34D).

AFFINITIES AND COMPARISONS

The most characteristic features of Twf 17929 are diffuse-porous wood, vessels solitary or in radial of 2-3, axial parenchyma paratracheal vasicentric, aliform, sometimes confluent, vessel pits vested, 1-6 (8) seriate rays with only procumbent cells, prismatic crystals in chambered parenchyma, fibers are septate. These features are found in modern Fabaceae and particularly in the Mimosoideae subfamily (now in the recircumscribed Caesalpinioideae subfamily) (LPWG 2017). In modern wood of Mimosoideae, the parenchyma aliform, confluent, rays with procumbent cells combined with the presence of septate fibers are mainly found in two African genera: *Albizia* Inga Mill. and *Pithecellobium* Mart (InsideWood 2004-onwards). Our fossil wood is more likely attributed to *Albizia*.

A previously described Pliocene sample Twf 17638, also attributed to *Albizia* showed affinities with the Ethiopian species *A. autunensis* (Jolly-Saad & Bonnefille 2012). In this study, because of the lack of data on other species, the most reasonable attribution of Twf 17638 is *Albizia* sp. 1. Sample Twf 17929 is slightly different and, therefore considered *Albizia* sp. 2.

From the Ethiopian flora we exclude some forest species such as *A. coriaria* Welw. Ex Oliv., *A. isenbergiana* and *A. petersiana* having 1-3 seriate rays whereas they are 1-4 seriate in *A. grandibractea* and 2-5 seriate in *A. schimperi* (Jolly-Saad *et al.* 2012; Table 5). Based on these comparisons, Twf 17929 is definitely assigned to *Albizia*. Its anatomical characters do not match those of *Albizia* sp. 1 (Twf 17638) from the late Pliocene characterized by 1-8 seriate rays (Table 2), It is also distinct from *Albizia* type *gummifera*, a Miocene wood (MA 94-73C) of the Middle Awash valley (Ethiopia), dated 5.8 Ma. This older specimen displays fewer vessels per square millimeter (2-5/mm²) and 1-6 seriate rays (Jolly-Saad *et al.* 2012; Table 4).

Among morphotypes, *Mimosoxylon mbakkaouense* Dupéron-Laudoueneix from Cameroon exhibits 1-3 seriate thinner rays (Dupéron-Laudoueneix 1991; Gros 1992). In conclusion, this fossil is attributed to a new species *Albizia* sp. 2 (Fig. 33).

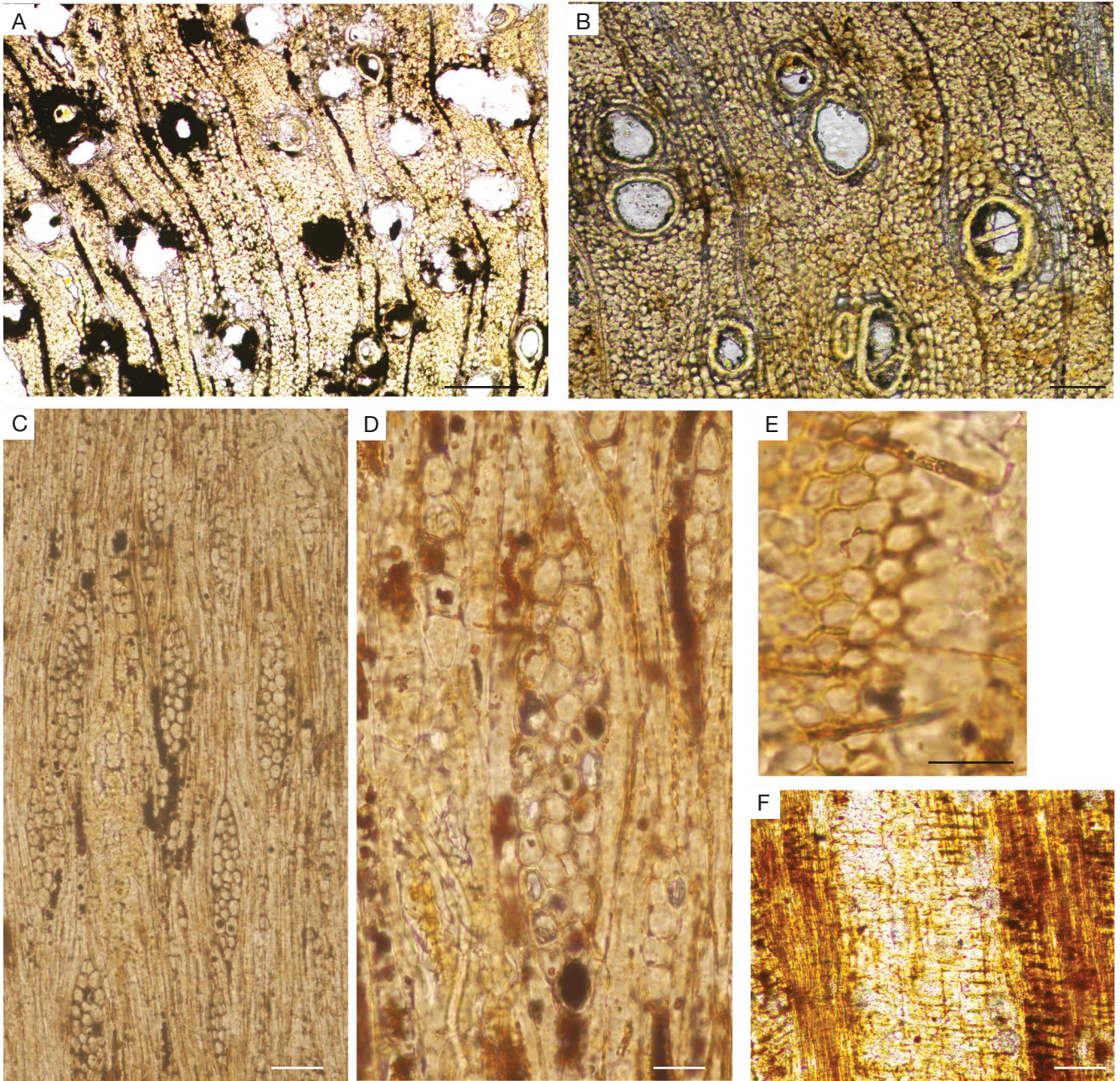


FIG. 33. — *Terminalia* sp. 3 (Combretaceae R.Br.), Twf 18069: **A, B**, Tr, wood diffuse porous; **B**, parenchyma is vasicentric, aliform to confluent; **C, D**, Tg, short and thin heterocellular rays; **E**, Tg, vested intervessel pits; **F**, Rd, heterocellular rays. Scale bars: A, 250 μ m; B, C, 100 μ m; D, E, 10 μ m; F, 50 μ m. Photographs: M.-C. Jolly-Saad.

Family MORACEAE Gaudich.

Genus *Ficus* L.

Ficus sp. 1 (Fig. 35)

EXAMINED MATERIAL. — Ethiopia • Lower Omo Valley, Shungura Formation, locality O 27-2, Member G-19, 2.01 Ma; R. Bonnefille 73-6 leg; Twf 17928; Tervuren collection.

DESCRIPTION

Fossil wood very poorly preserved with diffuse-porous wood and indistinct growth rings. Vessels are solitary

(56%) or in radial multiple of 2 (31%), 3 (7%), 4 (4%) up to 5 (2%), clusters are absent; vessels are 2-11 per square, circular (Fig. 35A, B). Mean tangential diameter of 145 μ m, range (67-160 μ m). Perforation plates are not distinct because of important tyloses in vessels; vessel elements, intervessel pits and vessel-ray pits are not clearly visible. Axial parenchyma banded or irregularly banded forming seriate tangential row, marginal bands composed of three up to 5 or 6 cells, number difficult to evaluate due to the poor preservation of this sample. Parenchyma strands of 5-8 cells are locally storied. Rays are commonly 1-8 seriate and some are more than 10

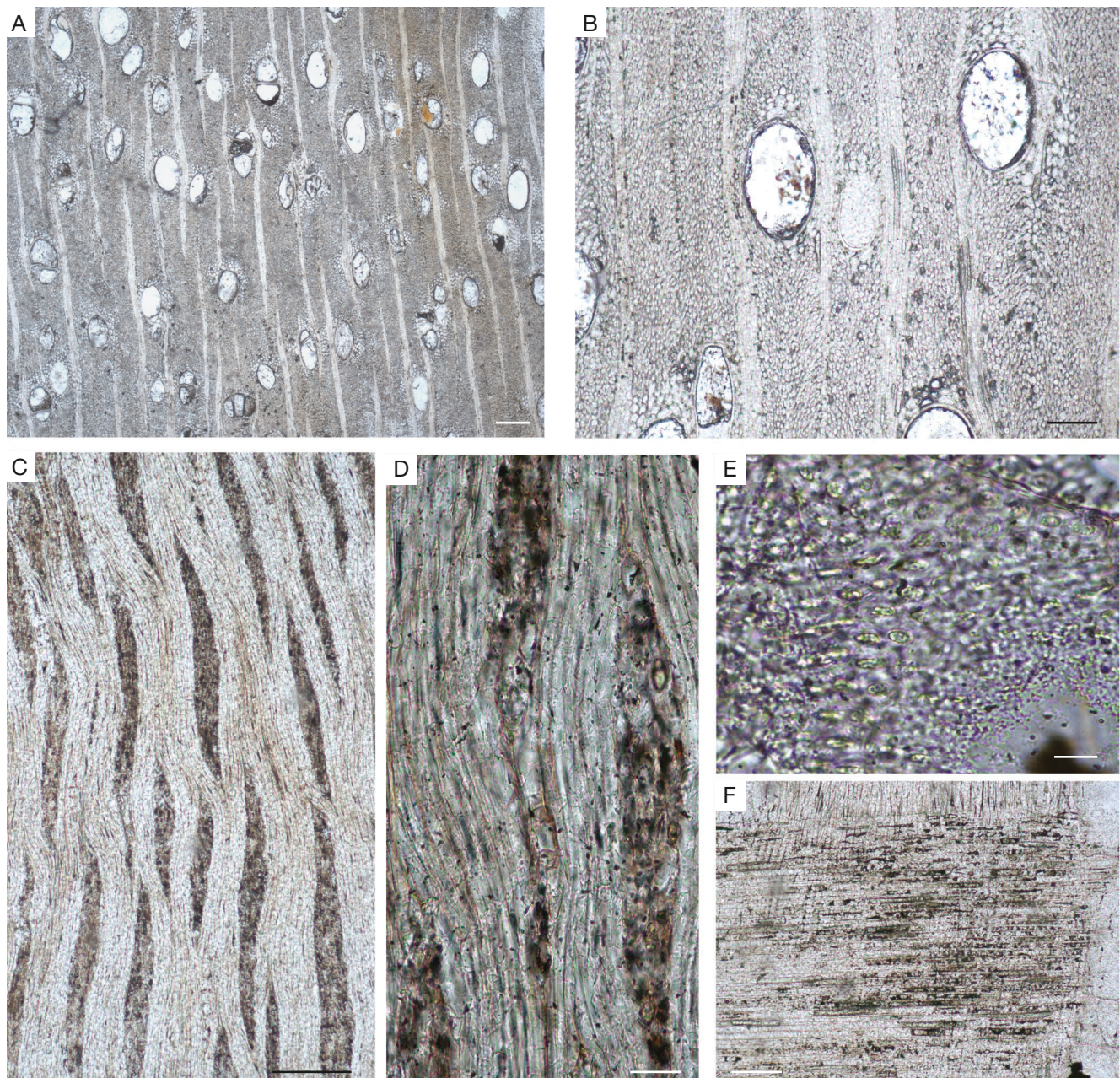


FIG. 34. — *Albizia* sp. 2 (Fabaceae DC.), Twf 17929: **A, B**, Tr, diffuse porous wood with vasicentric or confluent parenchyma; **C, D**, Tg, 1-5 seriate rays homocellular; **D**, Tg, ray arrangement and chambered parenchyma cells (arrow); **E**, Tg, vestured intervessel-pits (arrow); **F**, Rd, homocellular rays. Scale bars: A, C, 100 μ m; B, D, F, 50 μ m; E, 10 μ m. Photographs: M.-C. Jolly-Saad.

cells wide, uniseriate are rare, exclusively composed of square and upright cells, pluriseriate rays are composed of procumbent cells with 1-3 rows of marginal square and upright cells (Fig. 35C, D). Rays are 6-10 rays per mm, mean ray height is 60 μ m (range 23-79 μ m) and width ranges from 107 to 670 μ m. Fibers are thick walled and not septate. Rhomboidal crystals are distinct in ray cells and prismatic crystal in parenchyma.

AFFINITIES AND COMPARISONS

Initially identified as *Myrianthoxylum coppensii*, the misidentification of Twf 17928 is due to its poor preservation. Twf 17928 differs from *Myrianthus* due to the presence of challenging regular parenchyma bands. Additionally, features such as irregular rays and locally storied parenchyma strands in a tangential section suggest closer affinities with *Ficus*, without any more precision upon the species attribution than *Ficus* sp. 1 (Table 5).

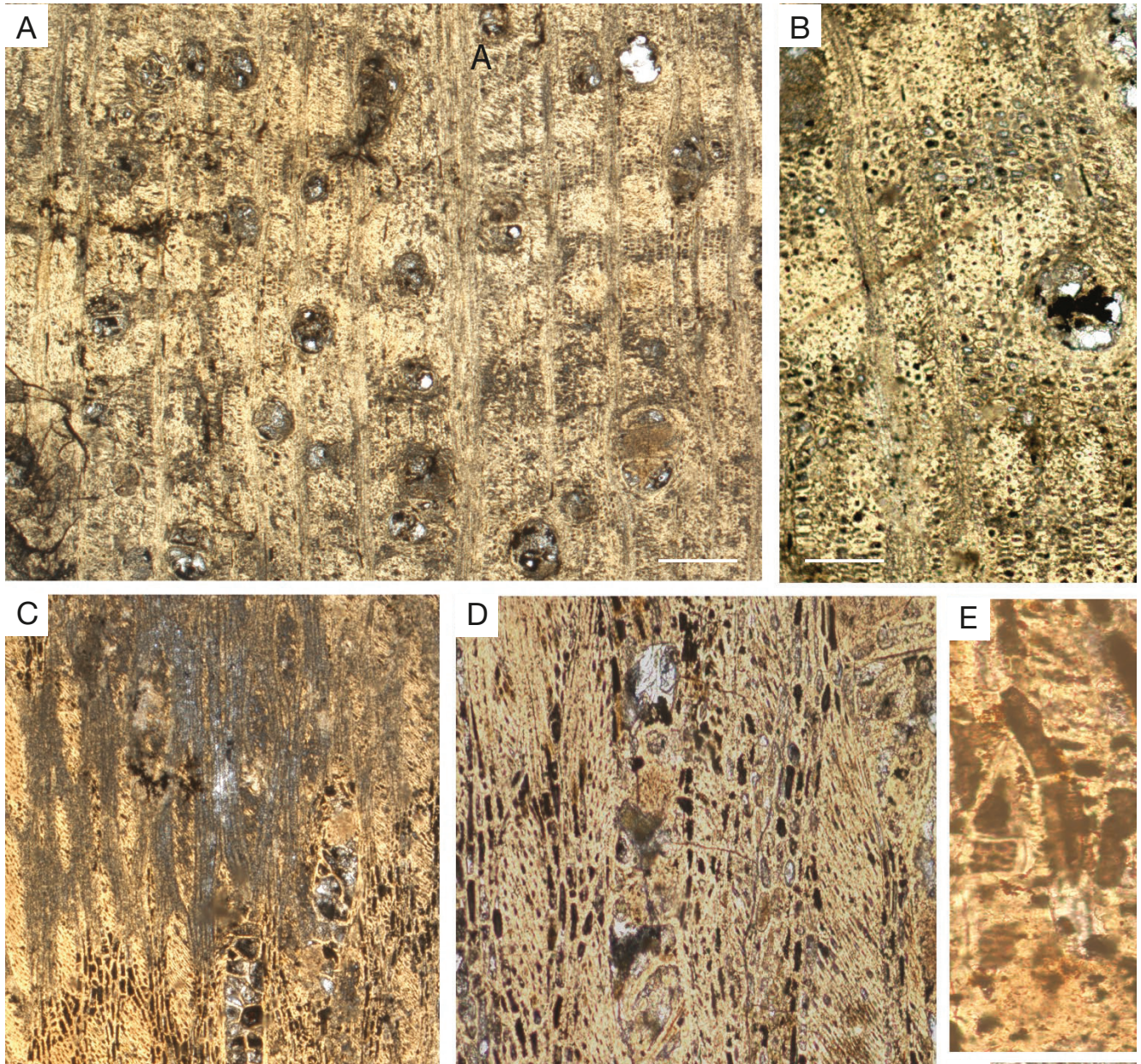


FIG. 35. — *Ficus* sp. 1 (Moraceae Gaudich.), Twf 17928: **A, B**, Tr, wood diffuse porous, banded parenchyma; **C, D**, Tg, rays 1-8 seriate heterocellular rays; **E**, Tg, wide intervessel-pits; **F**, Rd, heterocellular rays. Scale bars: A, C, 200 µm; B, C, 100 µm; D, E, 50 µm. Photographs: M.-C. Jolly-Saad.

UNIT G-29 (1.92 MA)

ANGIOSPERM MONOCOTYLEDONS

Family ARECACEAE Bercht. & J. Presl.
Genus *Borassus* L.

Borassus sp. 1
(Fig. 36)

EXAMINED MATERIAL. — Ethiopia • Lower Omo Valley, Shungura

Formation, locality P 742 sect. 22, Member G-29, 1.92 Ma; Jean de Heinzelin leg.; Twf 17823, Twf 17830; Tervuren collection.

DESCRIPTION

Twf 17823 and Twf 17830 closely resemble a fossil wood fragment from Member C-5 in the Pliocene, Twf 17839, fully described and attributed to *Borassus* sp. 1 (Arecaceae; Fig. 11). The two samples from G-29 in the Pleistocene are also similar as illustrated in Fig. 36, and therefore attributed to the same species *Borassus* sp. 1 (Table 2), in agreement with former identifications (Dechamps 1983).

TABLE 5. — Comparisons of anatomical characters of Pleistocene *Ficus* sp. 1 and *Ficus* sp. 2 fossil wood from the Shungura Formation and Pliocene *Ficus* sp. (*) (from Jolly-Saad & Bonnefille 2012: pl. 5) and *Ficoxylon* (**) (from Jolly-Saad *et al.* 2010) from Middle Awash.

Fossil samples	Twf 17725, 1.92 Ma, Fig. 46	Twf 17928, 2.01 Ma, Fig. 35	MA94-89b, 4.3 Ma	MA W15 ARA VP 6, 4.4 Ma
Identification	<i>Ficus</i> sp. 2	<i>Ficus</i> sp. 1	<i>Ficus</i> sp.*	<i>Ficoxylon</i> sp.**
Preservation	Poor	Poor	Good	Poor
Fungi	Absent	Absent	Absent	Absent
Wood porosity	Diffuse-porous	Diffuse-porous	Diffuse-porous	Diffuse-porous
Growth ring	Absent	Indistinct	Indistinct	Indistinct
Vessels diameter mean (range) (µm)	230 (92-400)	145 (67-160)	133 (90-175.5)	220 (138-299)
Vessels density/Nb per sq.mm	4-6	2-11	4-7	Indistinct
Vessels grouping	Mostly solitary and in radial multiples of 1 to 4	Solitary and in radial multiples of 1 (56%), 2 (31%), 3 (7%), 4 (4%), 5 (2%)	Solitary and in radial multiples of 1 (76%), 2 (19%), 3 (4%), more 1%	Mostly solitary
Vessel element length (µm)	100-360	NA	148-360	NA
Intervascular pit size (µm), type	9-10 wide, alternate, not vested	NA	7-9 wide, alternate, not vested	NA
Tyloses/Gums	Present	Abundant	Distinct	Abundant
Perforation plates	Simple	Simple	Simple	Simple
Axial parenchyma	Vasicentric around vessels, axial large bands of 3 to 7 cells high	Banded or forming tangential row marginal bands 5-6 cells	Abundant, banded 2-9 cells	Vasicentric around vessels, banded of 3 to 7 cells high
Parenchyma strands	5-8	5-8	2-9	Indistinct
Rays	1-8 seriate	1-8 seriate (10)	1-5 (6) seriate	1-6 seriate
Ray width mean (range) (µm)	45 (34-52)	107-670	NA	70 (27-115)
Ray height mean (range) (µm)	800 (400-1000)	60 (23-79)	247-724	800 (425-1127)
Rays/mm ²	12-16	6-10	11-15	NA
Rays cells	Procumbent-square and upright cells (1-2 rows)	Procumbent-1-3 square and upright cells	Procumbent-2 to 4 rows square and upright cells	Procumbent-1 to 2 rows square and upright cells
Sheath cells	Not mentionned	None	Not mentionned	None
Lactifer canal	Distinct	Indistinct	Distinct	Indistinct
Fibres	Non-septate	Non-septate, thick wall	Septate, thick wall	Non-septate, thick wall
Crystals in rays cells	Prismatic crystals in upright cells	Rhomboidal	Prismatic crystal in upright cells	Prismatic crystal in upright cells
Crystal in parenchyma	Distinct	Distinct	Distinct	Distinct

Family ASTERACEAE Bercht. & J. Presl.
Genus *Brachylaena* R.Br.

Brachylaena sp. 2
(Fig. 37)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, Member G-29, locality P 726 sect. 19; Jean de Heinzelin leg.; Twf 17770; Tervuren collection.

DESCRIPTION

Twf 17770 is not well preserved. Wood is diffuse-porous. Growth rings are slightly marked by the reduction of fiber diameters on two up four rows. Vessels are solitary (67.5 %) or in radial multiple of 2 (17.5 %), 3 (10 %), 4 (2.5 %) and 5 (2.5 %), they are more than 100 per mm² (Fig. 37A, B). Mean vessel tangential diameter of 30 µm, range (20-37 µm). Perforation plates are exclusively simple; vessel-pits crowded alternate, minute (< 4 µm). Vessel wall is thick 6-7 µm. Vessel elements length and parenchyma strands are not distinct because of the poor preservation of the longitudinal section and high permineralization in vessels

lumina. Axial parenchyma is rare, scanty paratracheal, it is difficult to distinguish it from fibres in longitudinal section. Rays are uniseriate, rarely bi-seriate composed of procumbent cells with one row of upright cells, more than 12 per mm. Rays are short, mean height 250 µm (225-301 µm), mean width 15 µm, they are storied, or irregularly storied (Fig. 37C). Other structures of parenchyma are not visible due to the poor preservation of the fossil wood. Fibers have very thick walled with diameter between 11-20 µm. Inclusions are absent or indistinct.

AFFINITIES AND COMPARISONS

The fossil exhibits diffuse porosity, scanty paratracheal parenchyma, and uniseriate, storied rays. These anatomical features are consistent with *Androstachys johnsonii* (Picrodendraceae, Euphorbiaceae) and *Brachylaena* (Asteraceae). However, *Androstachys* shows a higher proportion of solitary vessels (90%) and consistently storied rays. Our specimen shows the closest affinity with *Brachylaena*. It may represent a different species than *Brachylaena* sp. 1 inferred to the oldest Twf 17707 (2.02 Ma from G-18; Fig. 32). Twf 17770 from unit G-29 and dated 1.92 Ma is attributed to *Brachylaena* sp. 2. (Fig. 37).

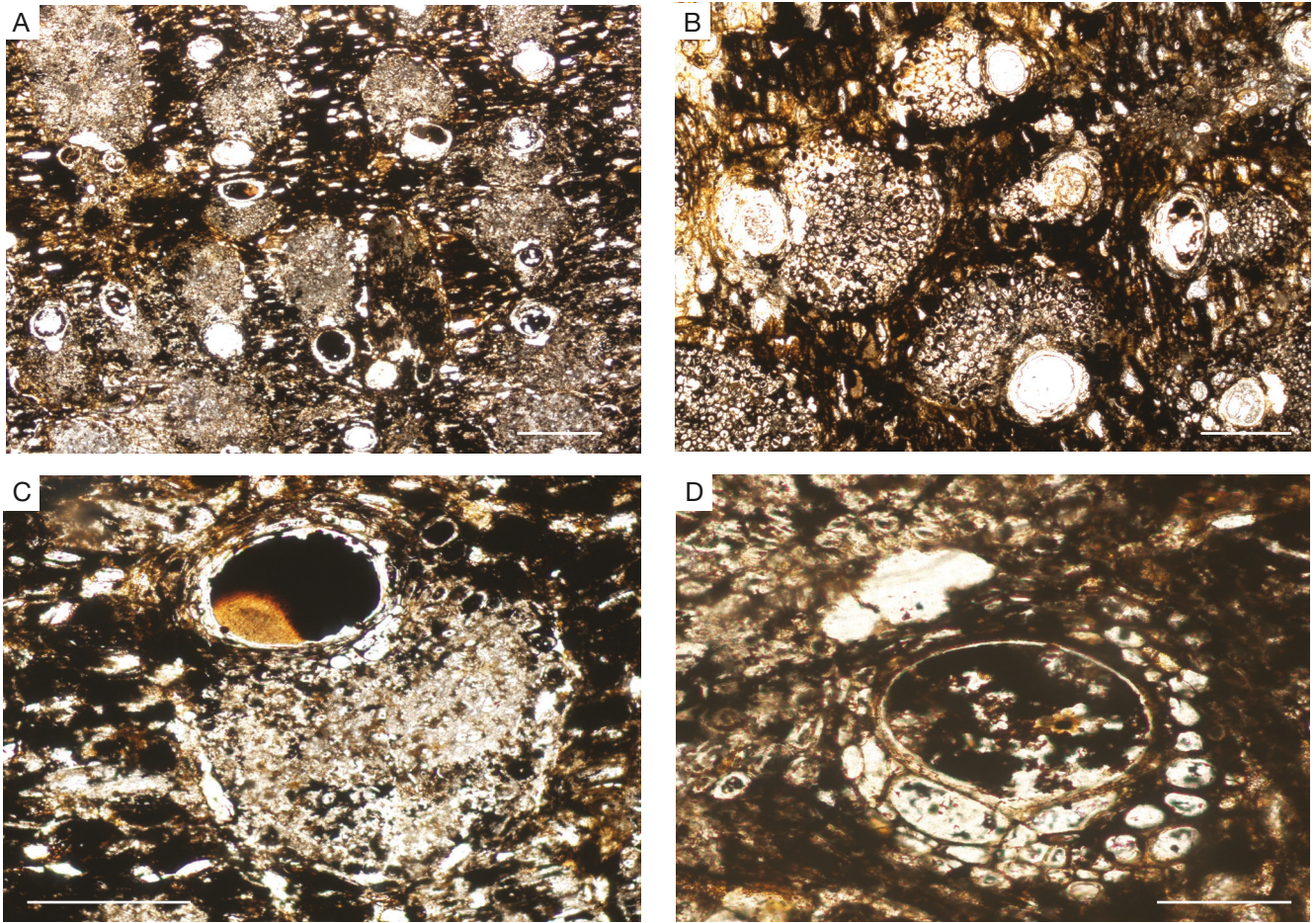


FIG. 36. — *Borassus* sp. 1 (Arecaceae Bercht. & J.Presl.), Twf 17830: **A-D**, Tr, fibrovascular bundles with one vessel. Scale bars: A, D, 200 μ m; B, 100 μ m; C, 90 μ m. Photographs: M.-C. Jolly-Saad.

Family BURSERACEAE Kunth.
Genus *Commiphora* Jacq.

Commiphora sp.
(Fig. 38)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, Member G-29, locality P 726 sect. 19; Jean de Heinzelin leg.; Twf 17912; Tervuren collection.

DESCRIPTION

Twf 17912 is moderately preserved as can be seen in the longitudinal section where a large number of fungal hyphae are observed. The preservation in the cross section is good. Twf 17912 is diffuse-porous, growth ring are clearly defined by the large bands of dense and bigger vessels. Vessels are solitary (62 %) or in radial multiple of 2 (28%), 3 (8 %) and 4 (1 %) and with also tangential arrangement (Fig. 38A, B), density. 20-25/mm², mean tangential diameter of 80 μ m (range 56-120 μ m), vessels are thin walled. Perforation plates are exclusively simple; vessel elements are not distinct because of abundant tyloses; intervessel-pits are large (8-10 μ m), crowded alternate and not vestured (Fig. 38F).

Tyloses are abundant in vessel lumina. Axial parenchyma is extremely rare or scanty paratracheal. Parenchyma strands are not distinct. Rays are 2-4 (5) cells wide, with radial canals, heterocellular composed of procumbent cells with one or 4 rows of square and upright cells (Fig. 38C, D). Some rays are interconnected at their ends. Rays are short, mean ray height is 350 μ m (range 180-600 μ m), mean ray width is 50 μ m (range is 25-80 μ m), 7-10 per mm. Radial canals with epithelium cells are present (Fig. 38E). Vessel-ray pits have thin borders. Fibres have very thick wall and are septate. Another feature is the radial alignment of fibers in the transverse section. Crystals or silica are visible in ray cells and in tyloses.

AFFINITIES AND COMPARISONS

Twf 17912 is characterized by small to medium vessels, solitary or in radial multiple of 2-4, 20-25 per square millimeter, perforation plates simple, vessel-rays pits with much reduced borders, tyloses observed, septate fibres, axial parenchyma absent extremely rare or scanty paratracheal, 2-4 (5) seriate heterocellular rays consisting of a body of procumbent cells with 2-4 rows of upright and/or square marginal ray cells, rays non-storied, radial canals, prismatic crystals present in upright and/or square ray cells, radial canal are the most

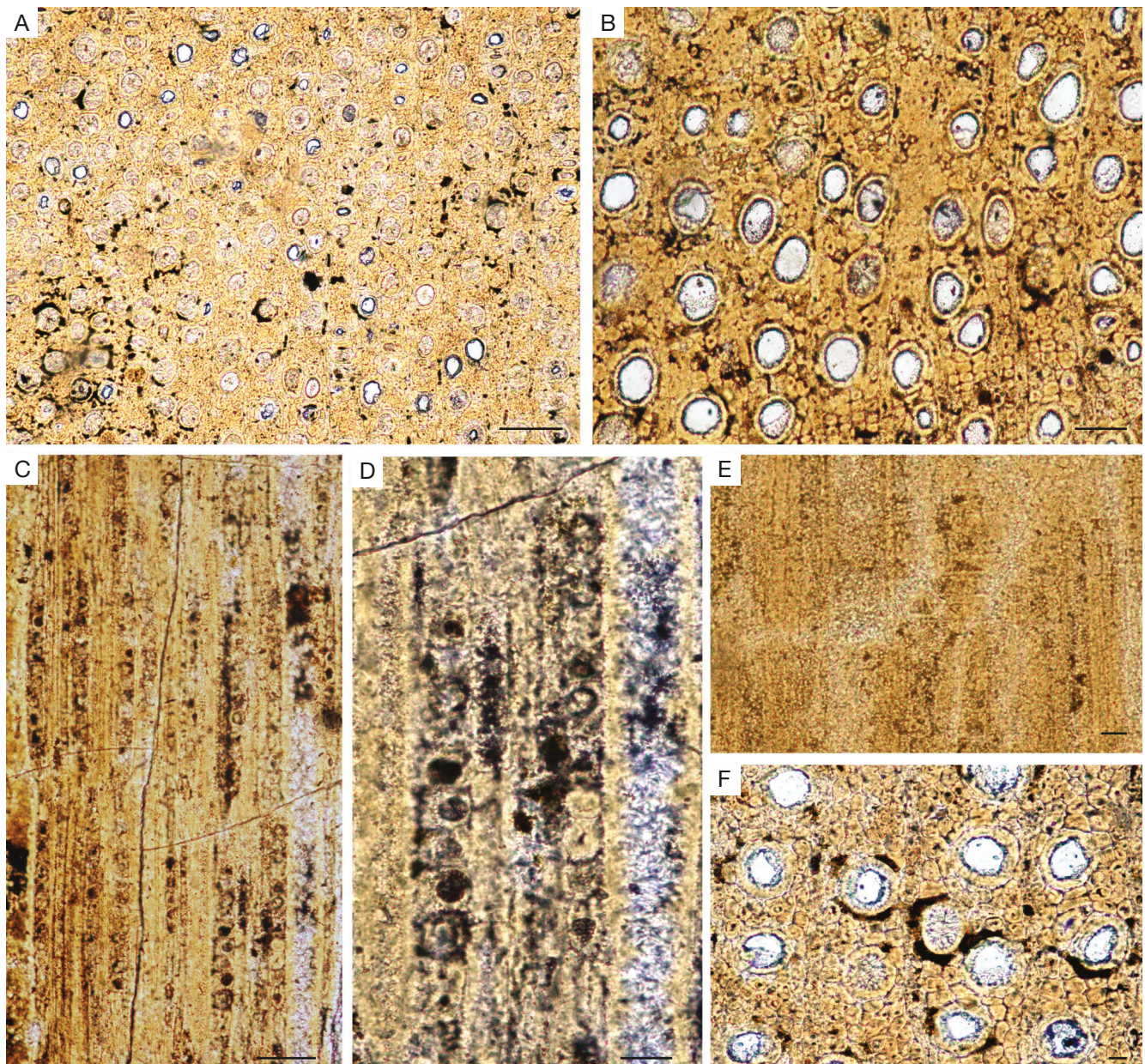


FIG. 37. — *Brachylaena* sp. 2 (Asteraceae Bercht. & J. Presl.), Twf 17770: **A, B, F**, Tr, wood diffuse with small and solitary vessel, few are in radial multiple of 2. **C, D**, Tg, rays uniseriate irregularly storied; **E**, Rd, heterocellular rays. Scale bars: A, 200 µm; B, C, 50 µm; D, 100 µm; E, F, 20 µm. Photographs: M.-C. Jolly-Saad.

important characteristics linking Twf 17912 with extant members of the Anacardiaceae and Burseraceae (Metcalf & Chalk 1950; Inside Wood 2004-onwards). Both families have very similar anatomical features. However, the presence of septate fibres, crystals and silica in rays and the radial alignment of fibers in the transverse section are found in the Burseraceae (Normand 1950). Among the homogenous characters of the Burseraceae wood, *Canarium* has rare axial parenchyma (Gregory *et al.* 2009), *Boswellia* has no crystal in ray cells. The Omo fossil wood is most similar to *Commiphora*, a genus known in Ethiopia through over 50 species.

Fossil woods of the Burseraceae family are not abundant in Africa (Gregory *et al.* 2009). They are grouped into two genera: *Burseroxylon* including fossils related to *Bursera* Jacq. ex L. and *Canarioxylon* Prakash, Březinová & Awasthi including fossils related to *Canarium*. A fossil wood known as *Burseroxylon africanum* Bamford and related to Burseraceae was documented from the early Miocene Orange River gravels in Namibia (Bamford 2003). Unlike the Omo fossil wood, this species lacks crystals in the ray cells and radial canals are absent. In conclusion, the identification of Twf 17912 is confirmed as *Commiphora* sp. (Fig. 38).

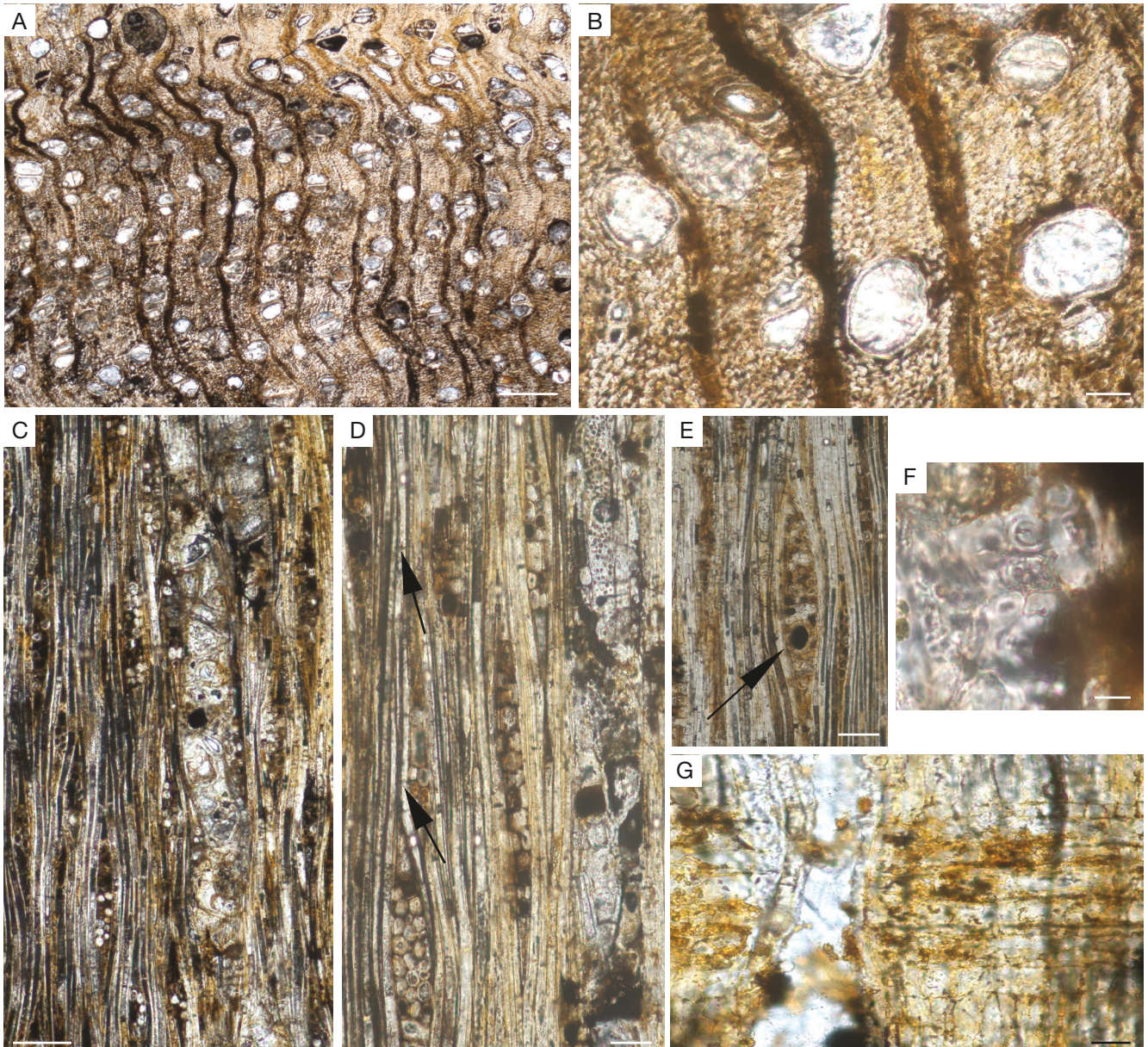


FIG. 38. — *Commiphora* sp. (Burseraceae Kunth.), Twf 17912: **A, B**, Tr, vessels mostly solitary or in radial multiple; **C**, Tg, 2-5 seriate rays; **D**, Tg, detail of rays and fibres with septae (arrow); **E**, Tg, radial canal with a row of epithelium cells (arrow); **G**, Rd, heterocellular rays. Scale bars: A, 200 μ m; B, C, 100 μ m; D, E, 50 μ m; F, 10 μ m; G, 20 μ m. Photographs: M.-C. Jolly-Saad.

Family CELASTRACEAE R.Br.
Genus *Maytenus* Molina

Maytenus sp. 1
(Fig. 39)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 726 sect. 19; Member G-29, 1.92 Ma; Jean de Heinzelin leg.; Twf 17906; Tervuren collection.

DESCRIPTION

Twf 17906 is well preserved in all three Member sections. It is a small fossil stem with a central cylinder and an estimated diameter of approximately 2 cm. Its anatomical features

closely resemble Twf 17609 from B-12 (Fig. 39), as well as Twf 17805 and Twf 17808, from Member C-8 (Fig. 17). Given the shared characteristics, the specimen is attributed to *Maytenus*, as previously described, and most probably belongs to the same species *Maytenus* sp. 1.

Family COMBRETACEAE R.Br.
Genus *Combretum* Loeff.

Combretum sp. (Fig. 40)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 743 sect. 22, Member G-29, 1.92 Ma; Franck

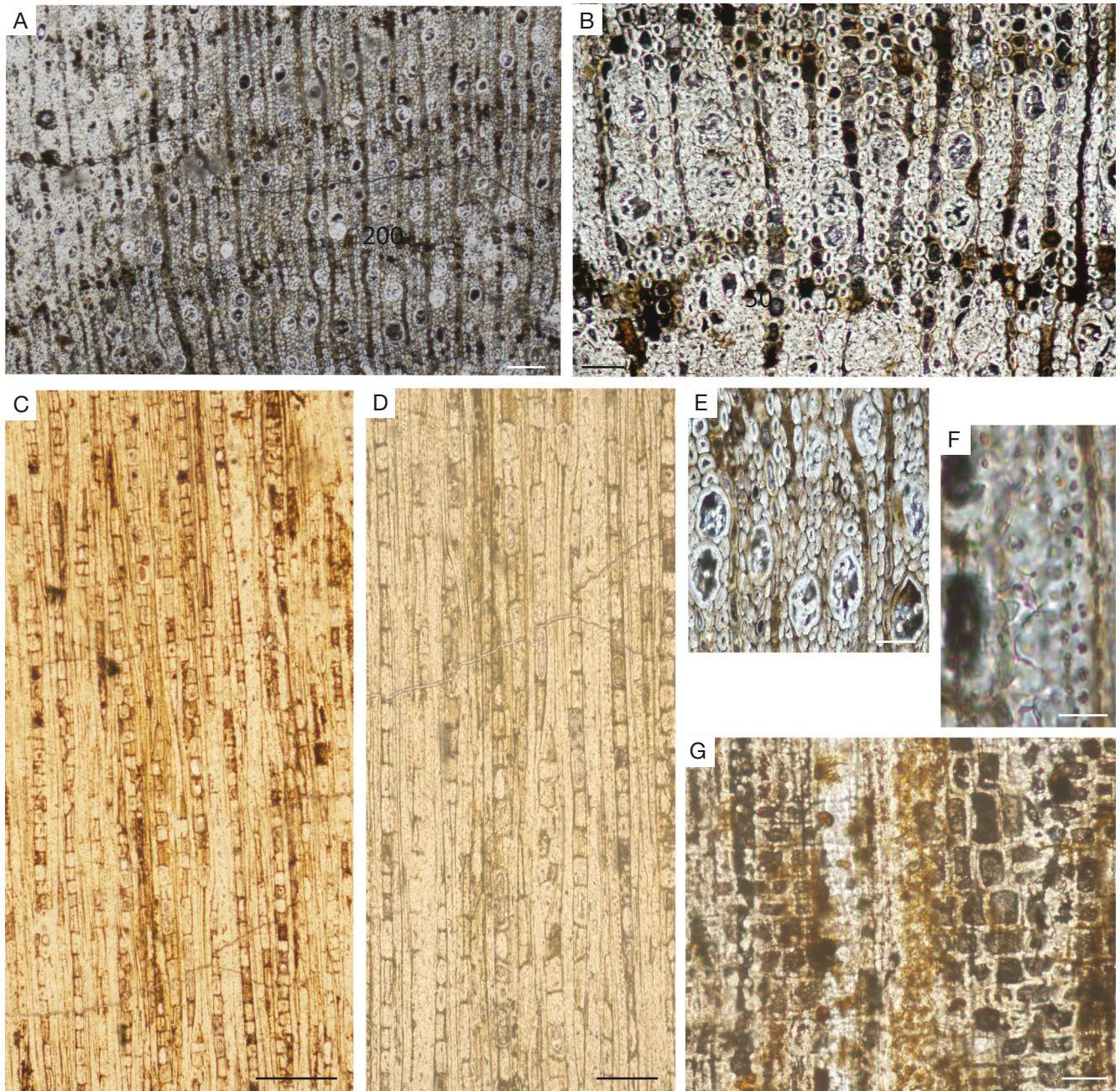


FIG. 39. — *Maytenus* sp. 1 (Celastraceae R.Br.), Twf 17906: **A, B**, Tr, wood diffuse porous with alternating rows of septate and non septate fibres; **C, D**, Tg, heterocellular rays; **E**, Tr, parenchyma rare or scanty paratracheal; **F**, Tg, minute, alternate intervessel-pits; **G**, Rd, heterocellular rays. Scale bars: A, 200 µm; B, D, E, G, 50 µm; C, 100 µm; F, 20 µm. Photographs: M.-C. Jolly-Saad.

Brown & Jean de Heinzelin leg.; Twf 17965; Tervuren collection • same data; R. Bonnefille & Jean de Heinzelin leg.; Twf 17973; Tervuren collection.

DESCRIPTION

Twf 17965 is a small twig fairly well preserved. Wood is diffuse-porous. Growth rings are marked by different density of vessels repartition. Vessels are mostly solitary (91 %), 4-6 per mm² (Fig. 40A, B). Vessels of two distinct size. Mean tangential diameter of 100 µm, range 80-150 µm, thin wall. Vessel elements length are 200-250 µm; perforation plates are

simple and horizontal; intervessel pits are crowded alternate, 4-5 µm wide and vested (Fig. 40E).

Axial parenchyma is diffuse, vasicentric, aliform, confluent or seemingly banded. Parenchyma strands with 2-4 cells. Rays are 1-2 (3), they are short, mean ray height is 320 µm (range 282-424 µm (4-37 cells), mean ray width is 60 µm (range 58-78 µm), heterocellular composed of procumbent with one row of square cells, 12-14 per mm (Fig. 40C, D) Disjunctive ray cells occasionally visible. Crystals in ray cells and in chambered parenchyma in chains of 7-15 cells, 18 µm wide.

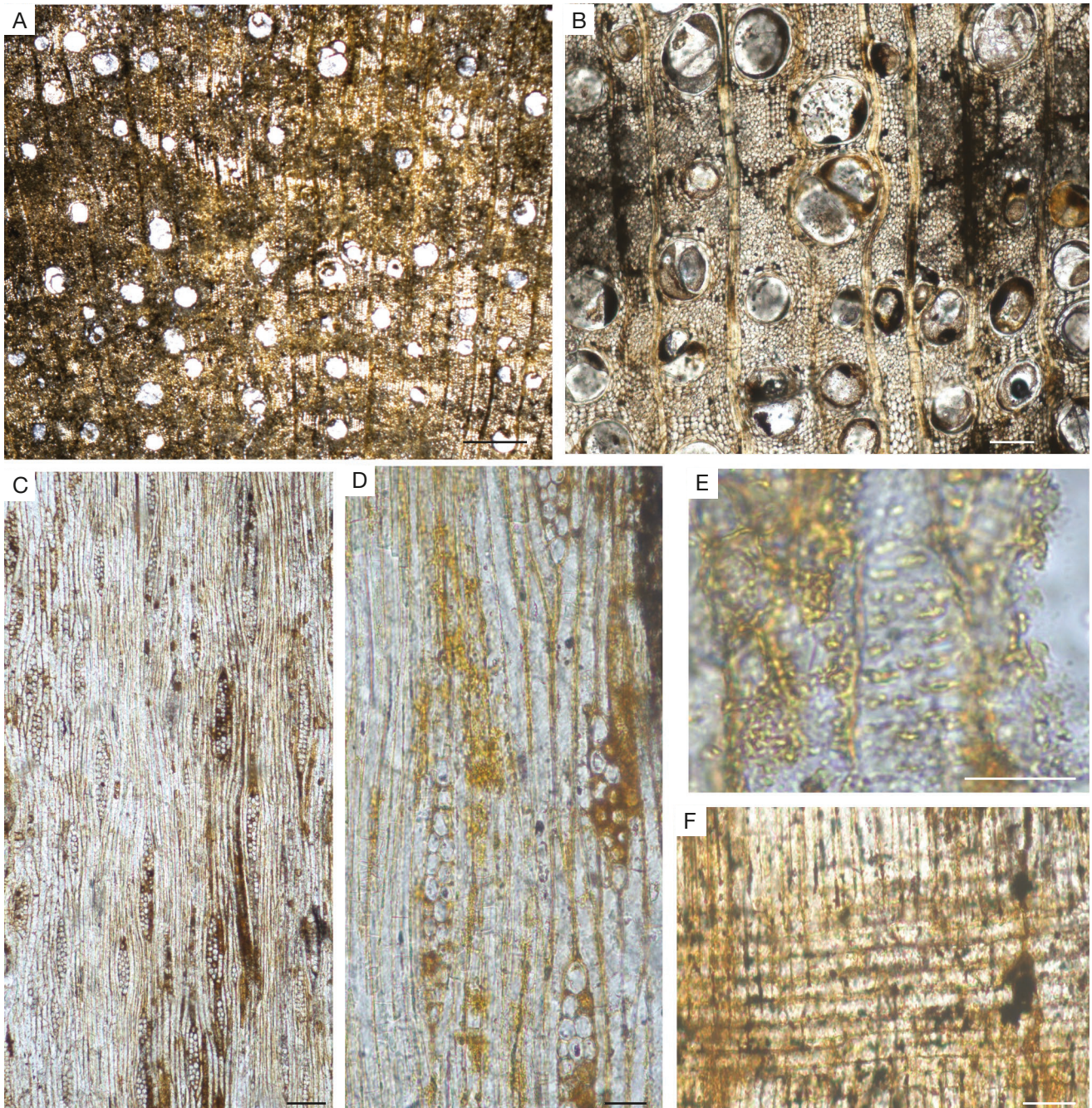


FIG. 40. — *Combretum* sp. (Combretaceae R.Br.), Twf 17965: **A, B**, Tr, wood diffuse porous, axial parenchyma is diffuse, aliform, vasicentric, aliform, confluent, or seemingly banded; **C, D**, Tg, short rays 1-3 seriate with crystal in cells; **E**, Tg, vestured intervessel-pits; **F**, Rd, heterocellular rays. Scale bars: A, 200 μ m; B, C, 100 μ m; D, E, 20 μ m; F, 50 μ m. Photographs: M.-C. Jolly-Saad.

AFFINITIES AND COMPARISONS

Twf 17965 and Twf 17973 exhibit identical anatomical characteristics: vessels mostly solitary, axial parenchyma vasicentric and confluent, rays 1-3 seriate, vestured pits. These features differ notably with those of *Myrianthus* Dechamps (1983). Instead, Twf 17965 and Twf 17973 show greater anatomical affinity with extant species of *Combretum*. From the Ethiopian flora, *Combretum aculeatum* is characterized by the presence of perforated cells, *C. adenogonium* present uniseriate rays, *C. rochetanum* and *C. molle* have uniseriate and included

phloem a feature also observed in *C. adenogonium*, *C. paniculatum* and *C. nigriscans*. *C. aculeatum* are present uniseriate or 1-3 seriate rays, axial parenchyma is scanty paratracheal or vasicentric. No xyloanatomical data are currently available for the Ethiopian species: *C. contractum*, *C. hartmanninum*, *C. hereroroense*, *C. capitiliflorum* (Friis *et al.* 2011) No species attribution can be given to Twf 17965 or to Twf 17973 so, they are simply attributed to *Combretum* sp.

In Ethiopia, *Combretoxylon* Lemoigne has been described under several species including *C. desrotoris* and *C. sp. 3* from

the Miocene (Lemoigne 1978). They differ from the Shungura Pleistocene wood by having vessels in long radial multiples. From the same deposits *Combretoxylon* sp. 1 is characterized by 1-2 seriate rays, whereas *C.* sp. has wider vessels. *Combretoxylon* sp. from Debre-Libanos (Beauchamp *et al.* 1973) and *C. namaensis* Bamford from South Africa exhibit wider vessels (Bamford 2003). In contrast, *C.* cf. *C. collinum* from the Yellow Sands deposits differs from the Shungura fossil wood in lacking included phloem (Koeninger pers. comm.). Therefore, we consider that Twf 17965 and Twf 17973 both belong to *Combretum* without more specific precision than *Combretum* sp.

Family EBENACEAE Gürke
Genus *Diospyros* L.

Diospyros sp. 2
(Fig. 41)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, Member G-29, locality P 726 sect. 19; R. Bonnefille & Jean de Heinzelin leg.; Twf 17907; Tervuren collection.

DESCRIPTION

Twf 17907 is a small and poorly preserved twig measuring 1.5-2 cm in diameter with pith located at the center. It is diffuse-porous (Fig. 41A, B), growth rings indistinct. The vessels are solitary (40%) or arranged in radial multiple of two (37%), three (11%) up to six, with clusters being noticeable (Fig. 41). Their density ranges from 40-100 per mm². Mean tangential diameter of 50 µm (range 30-100 µm), vessels are thin walled. Perforation plates are simple, vessel elements are indistinct, intervessel pits crowded alternate, minute (5-6 µm) and not vested (Fig. 41E), vessel ray pits are indistinct, tyloses are observed in vessels. Axial parenchyma is diffuse-in-aggregate (Fig. 41A, B), parenchyma strands not distinct in longitudinal section. Rays are 1-(2) seriate, they are high, heterocellular composed of procumbent and square cells mixed in the rays, they are 20-22 per mm (Fig. 43C, F); mean ray height is 150 µm. Fibres are not septate (Fig. 41D). Crystals are visible in ray cells and parenchyma.

AFFINITIES AND COMPARISONS

The diagnostic features of Twf 17907, including vessel solitary and in radial multiple of 2-3, 40-100 per mm², simple perforation plate, axial parenchyma apotracheal diffuse or diffuse-in-aggregate and forming very narrow bands, rays uniseriate or 2 seriate, heterocellular with mixed procumbent, square and upright cells, prismatic crystal in ray cell and parenchyma indicate affinities with extant members of the families Apocynaceae, Ebenaceae, Rubiaceae and Sapotaceae (Metcalf & Chalk 1950; InsideWood 2004-onwards). However, the occurrence of broader rays and vasicentric tracheids in wood of Apocynaceae, Rubiaceae and Sapotaceae excludes any attribution of Twf 17907 to these families. Instead, the presence of small to medium-sized vessels occluded with tyloses,

scanty paratracheal to diffuse-in-aggregate axial parenchyma, 1-3 seriate heterocellular rays, bordered intervessel pits and simple perforation plates together suggest a closer affinity with the Ebenaceae in particular *Diospyros* or *Euclea*. In Ethiopia, *Euclea racemosa* Murray subsp. *schimperi* (A.DC.) F. White, and *E. divinorum* Hiern are montane species with uniseriate rays. *Diospyros* is represented in the Ethiopian vegetation by three species. *D. scabra* is not described in available databases, *D. abyssinica* (Hiern) F. White is characterized by exclusively uniseriate rays. We conclude that Twf 17907 belongs to *Diospyros*. Since its characteristics resemble that of the Omo sample Twf 17683 from the Pliocene (*Diospyros* cf. *mespiliformis*; Table 1). However, the Pliocene sample has only uniseriate rays. Therefore, we attribute Twf 17907 to a different species, *Diospyros* sp. 2 (Table 2; Fig. 42).

Fossil wood close to *Diospyros* are documented since the late Cretaceous period under the morphotype *Ebenoxylon* Felix with *Ebenoxylon ebenoides* (Schenk) Kräusel Kaiser from the Libyan desert (Kräusel 1939). A second species, *Ebenoxylon aegypticum* Krausel is known from in the Oligo-Miocene deposits of Egypt (Kräusel 1939).

Family FABACEAE Lindl.
Subfamily CAESALPINIOIDEAE DC.
Genus *Bussea* Harms

Bussea sp.
(Fig. 42)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 742 sect. 22, Member G-29, 1.9 Ma; Jean de Heinzelin leg.; Twf 17826; Tervuren collection.

DESCRIPTION

Twf 17826 is not well preserved; fungal hyphae are noticed in vessel lumina. The wood displays a diffuse-porous structure (Fig. 42A, B), growth ring boundaries are indistinct. The majority of vessels are solitary (80%), with a few in radial multiples of 2 (14%) or 3 (5%); only a small proportion of clusters are visible (1%). The mean tangential diameter measures 167 µm (range 69-253 µm), 20-26 vessels per square millimeter, and the vessel wall thickness measures between 12-13 µm, perforation plates are exclusively simple, vessel elements length are short, mean 110 µm (range 90-113 µm). Intervessel-pits are crowded, alternate and vested, measuring 8-11 µm (Fig. 42E), gum-like deposits can be observed in the vessels. Axial parenchyma is abundant, vasicentric, with up to 6 rows of aliform cells that are confluent up to 6-7 vessels, or wavy and discontinuous banded. These bands are 1-3 cells wide (27 µm) but can be up to 8 cells wide (115 µm). Strands of 1-2 and 3-4 cells can also be observed. The parenchyma lacks storied or irregular structure. The fibers diameter presents medium to mostly thick walls, without any septae or pits observed. Rays are (1)-8 seriate, composed of procumbent cells (Fig. 42D, F), and occur at a density of 5-6 per mm² (Fig. 42C, D).

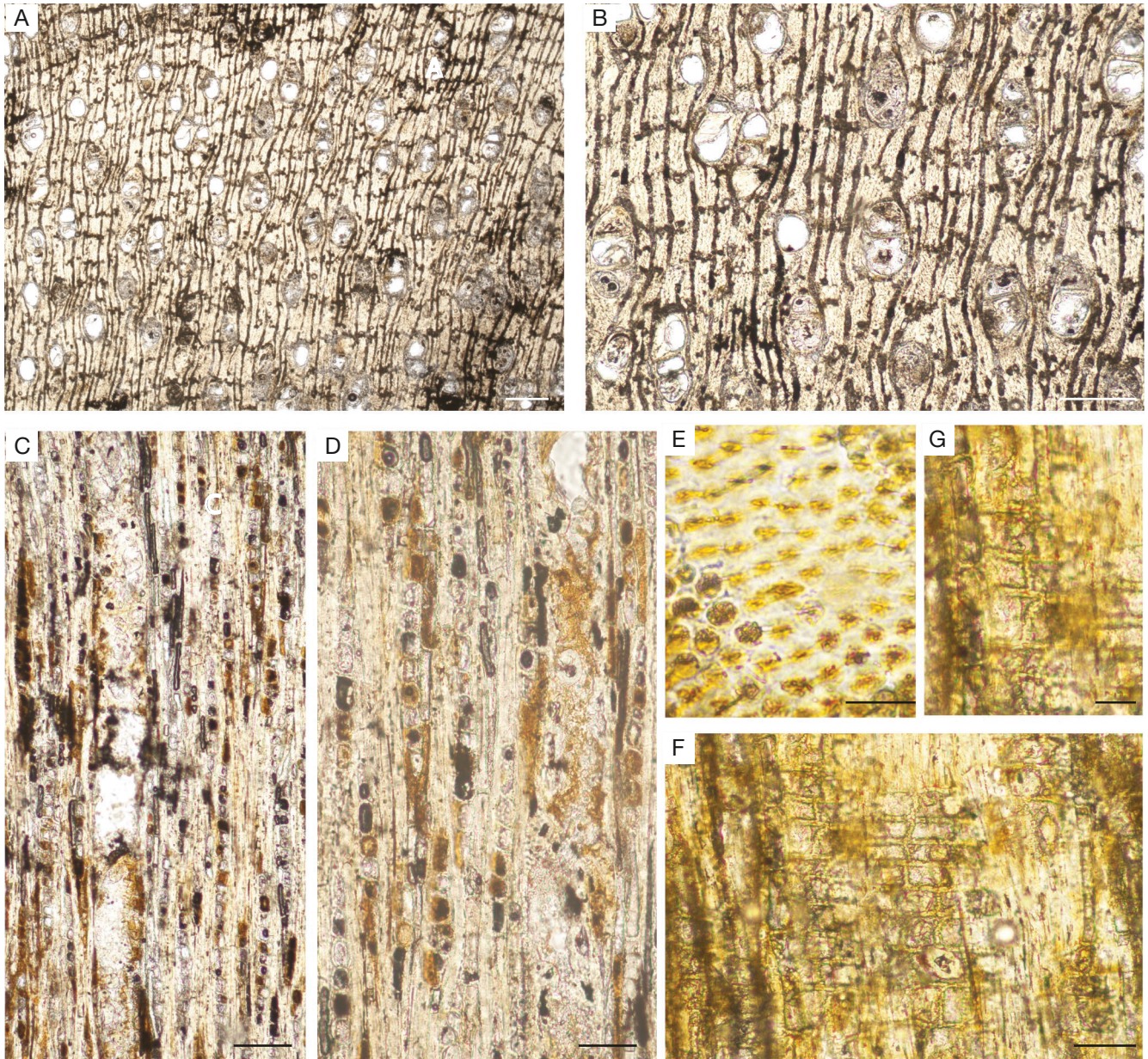


FIG. 41. — *Diospyros* sp. 2 (Ebenaceae Gürke), Twf 17907: **A, B**, Tr, wood diffuse porous, axial parenchyma diffuse-in-aggregate; **C, D**, Tg, heterocellular rays; **E**, Tg, intervessel pits; **F, G**, Rd, heterocellular rays. Scale bars: A, 200 μ m; B, 100 μ m; C, F, G, 50 μ m; D, 10 μ m. Photographs: M.-C. Jolly-Saad.

Mean ray height is 430 μ m (range 85–790 μ m), mean ray width 50 μ m (18–85 μ m). Strands of crystalliferous axial parenchyma exhibit one rhomboidal crystal that distinguishes the fibers and parenchyma. Each strand consists of 10–24 chambers.

AFFINITIES AND COMPARISONS

Although some diagnostic features are not clearly visible, the associated diffuse-porous wood, banded parenchyma, alternate and vested pits, homocellular rays 1–8 seriate and prismatic crystals in fibers, clearly distinguish the fossil from *Millettia* (Dechamps 1983) and from other members of the tribe Millettieae (Gasson *et al.* 2004; InsideWood 2004-onwards). Species of Millettieae consistently exhibit

storied parenchyma, whereas the Omo fossil specimen Twf 17826 does not. Furthermore, Twf 17826 differs from *Millettia* with its wider rays (1–8 seriate) and the presence of crystals in the fibers. The closest affinities are with the genera *Bussea* and *Burkea*. However, *Burkea africana* differs from the Twf 17826 by the absence of irregularly arranged parenchyma strands. Therefore, *Bussea* is considered a better match, although it does not exist in Ethiopia (Friis *et al.* 2011). The species of *Bussea occidentalis*, commonly found in West Africa, exhibits only 1–3 seriate, whereas *B. perrieri* and *B. sakalava* are endemic to Madagascar. *B. massaiensis* (Taub.) Harms, found in East Africa, could be a possibility. But in the lack of description for that species, Twf 17826 remains identified as *Bussea* sp. (Fig. 42)

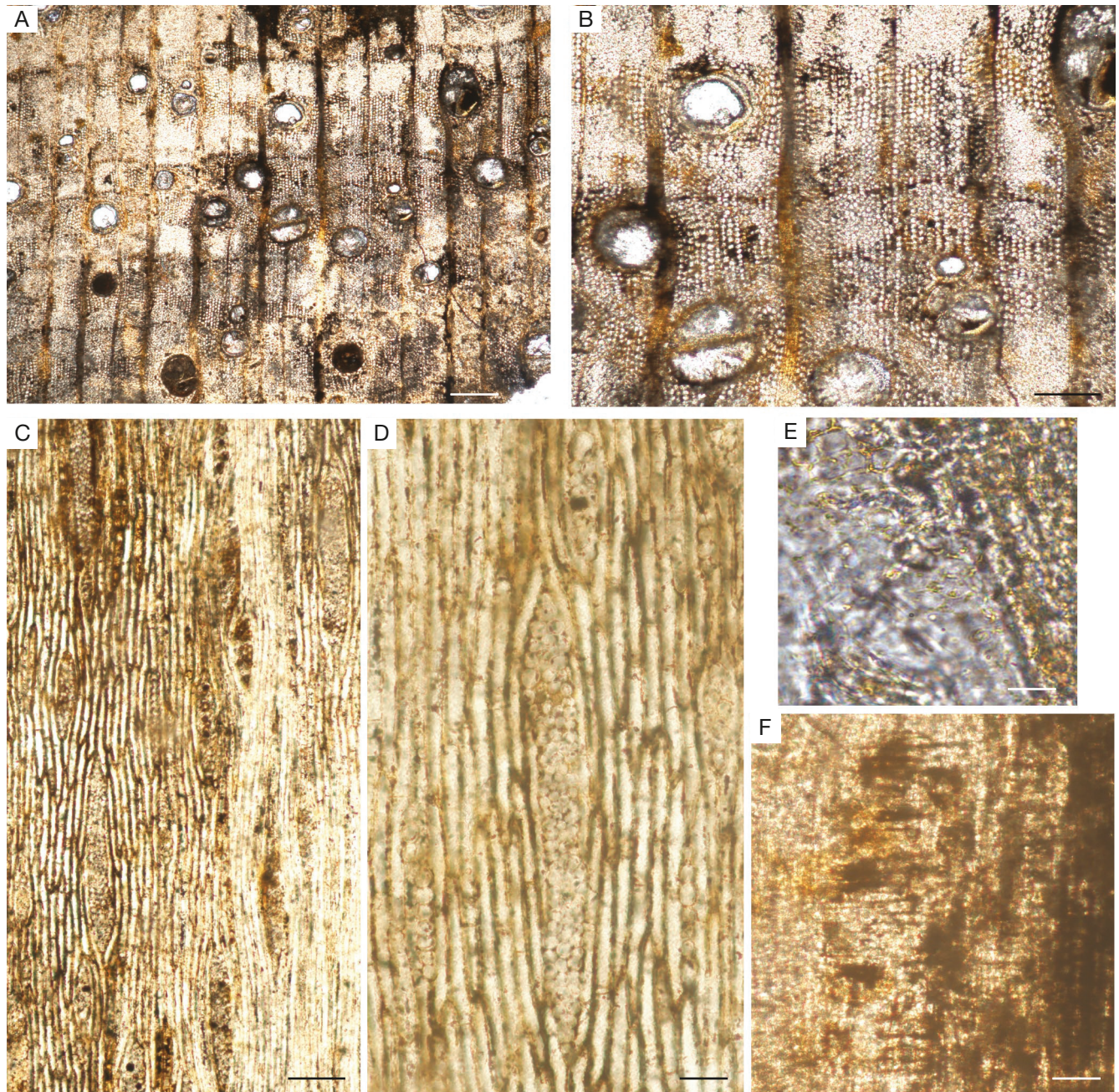


FIG. 42. — *Bussea* sp. (Fabaceae Lindl.), Twf 17826: **A, B**, Tr, wood diffuse porous, axial parenchyma is abundant and vasicentric, with up to six rows of aliform cells that are confluent or wavy and discontinuous banded; **C, D**, rays pluriserial with procumbent cells; **E**, interessel-pits; **F**, Rds, Rays heterocellular. Scale bars: A, 200 μ m; B, C, 100 μ m; D, F, 50 μ m; E, 10 μ m. Photographs: M.-C. Jolly-Saad.

In Africa, several palaeontological specimens assigned to *Caesalpinioxylon* Schenk have been described from the Pliocene. *C. faurei* Koeniguer from North Africa (Koeniguer 1973b) is characterized by uniseriate rays and septate fibers, while *C. tchadense* Koeniguer from Chad exhibits storied rays and septate fibers. *C. mogadaense* Boureau has banded parenchyma (Boureau 1950). In Northern Kenya, another Fabaceae fossil wood from the archaeological site of FwJj20, dated to 1.95 Ma, has been attrib-

uted to *Schotia* Jacq., among the Detarioideae (Bamford 2011). This specimen is distinguished by smaller vessels, septate fibers and abundant prismatic crystals in chambered parenchyma and fibers. From the Pliocene Usno Formation in the Omo Valley, the specimen Twf 17923d related to *Caesalpinia* sp. shows banded parenchyma and small vessels (Jolly-Saad & Bonnefille 2023). It is clearly distinguished from the Omo sample Twf 17826 that we attribute to *Bussea* sp.

Genus *Peltophorum* (Vogel) Benth.*Peltophorum* sp.
(Fig. 43)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 743 sect. 22, Member G-29, 1.92 Ma; Raymond Bonnefille & Jean de Heinzelin leg.; Twf 17968; Tervuren collection.

DESCRIPTION

Twf 17968 exhibits moderate preservation. The wood is diffuse-porous (Fig. 43A), with distinct growth ring boundaries characterized by a reduction in fiber diameter and marginal parenchyma bands, typically 1-2 cells wide, often accompanied by small vessels or vessel groups. Vessels are solitary (83%) or in radial multiple of 2 (17%), clusters are present, circular. Mean tangential diameter of 121 µm (range 3- 207 µm), 3-10 per mm per mm², gums and tyloses are distinct. Vessel element range is 98-231 µm, perforation plates are exclusively simple, intervessel pits alternate, 5-6 µm and vested, vessel-ray pits are not discernible (Fig. 43E). Axial parenchyma is vasicentric enclosing vessels or group of vessels forming aliform, winged aliform to confluent 1-3 seriate tangential row, marginal bands composed of two or three cells. The marginal parenchyma is continuous with the paratracheal parenchyma; parenchyma strands of 2-4 cells are distinct (Fig. 43B). Rays are 1-3 seriate, homocellular to slightly heterocellular (Fig. 43C, D), 1-2 rows of marginal upright cells or square or upright cells, 6-10 rays per mm, mean ray height is 230 µm (range 112-632 µm) (3-44 cells), mean ray width 21 µm (range 5-18 µm). Chambered parenchyma cells with crystals up to 14 chambers and crystals in ray cells. Fibers are septate with thin wall and a diameter size between 6-11 µm.

AFFINITIES AND COMPARISONS

The predominant anatomical characteristics of Twf 17968 are: mostly solitary vessels (83%) and vested intervessel pits; axial parenchyma is paratracheal vasicentric, featuring aliform, winged aliform, and confluent patterns, with marginal bands up to 2 cells wide; rays typically 1-3 seriate and homocellular to slightly heterocellular. Prismatic crystals are present in chambered parenchyma and ray cells, and the fibers are septate. Twf 17968 was initially identified as *Cathormion altissimum* (Hook. f.) Hutch. & Dandy a morphogenus later invalidated (Gregory *et al.* 2009). In the Omo fossil Twf 17968, the presence of marginal bands excludes affinity with the Mimosoideae and more specifically with *Cathormion*, a genus of West African and not listed in the Atlas of potential vegetation of Ethiopia (Friis *et al.* 2011). The combination of lozenge shaped parenchyma, low radial multiples of large vessels, and prismatic crystals in the ray and parenchyma cells indicate that our described specimen (Fig. 44) rather belongs to the Fabaceae, with homocellular 1-3 seriate rays, initial/terminal axial parenchyma suggesting closer affinities to the Caesalpinoideae, Detarioideae or Papilionoideae. Vessels solitary and in multiples, simple perforation plates, vested intervessel pits, axial parenchyma abundant, vasicentric ali-

form to confluent and or bands, simple fibers, homogeneous rays (mostly 1-3 seriate) are diagnostic of the Caesalpinoideae (Metcalf & Chalk 1950; Wheeler & Baas 1992), and more specifically with genera such as *Afzelia*, *Berlinia/isoberlinia*, *Cryptosepalum*, *Peltophorum* (DC.) Backer ex K. Heyne, *Tessmannia*, and *Tamarindus*. According to Müller-Stoll & Mädler (1967), parenchyma distribution is crucial for distinguishing these weakly delimited types. *Afzelia* and *Peltophorum* look similar. Septate fibers do not exist in *Afzelia* and *Tamarindus* but only in *Peltophorum* making it the most likely match for Twf 17968.

Among comparable fossil wood described in the literature, *Caesalpinioxylon* Schenk, *Caesalpinioxylon* aff. *quirogae* Schenk from the Miocene of Western Sahara (Koeniguer 1967) lacks septate fibers; *C. faurei* Koeniguer has banded parenchyma and storied rays. *C. morajonesiae* Crawley from the Paleocene of Mali (Crawley 1988) and *C. tchadense* Koeniguer from the Pliocene of Chad (Koeniguer 1975) both exhibit storied rays. *C. mogadaense* Boureau from the Miocene of Algeria has uniseriate rays and no septate fibers (Boureau 1950). *Pahudioxylon welkiti* Lemoigne & Beauchamp, from the Miocene at Welkite (Ethiopia), is characterized by large rays (Lemoigne & Beauchamp 1972). *Afzelioxylon* species generally have septate fibers, and rays, axial parenchyma and vessel elements that are commonly storied (Louvét 1965). *A. kiliani* Louvét 1965 (Oligocene from Algeria), *A. aethiopicum* Lemoigne, Beauchamp & Samuel from the Miocene of the upper Omo valley (Lemoigne *et al.* 1974) and *A. furoni* Koeniguer from the Paleocene from Sessao (Niger) lack septate fibers. *Caesalpinioxylon* typically has short to medium vessel element lengths, mainly solitary vessels, axial parenchyma confluent and banded, uniseriate rays that are heterocellular and usually storied (Müller-Stoll & Mädler 1967). *Copaiferoxylon* has regular axial canals. *Pterogynoxylon* (Müller-Stoll & Mädler 1967) has prismatic crystals in rays and storied rays and axial parenchyma. *Cassinium* has rays 1-4 (mostly 3-4) seriate, which are homocellular to weakly heterocellular and occasionally storied (Prakash 1973). These comparisons highlight that, although the Shungura fossil wood shares some features with these taxa, it also exhibits key differences, particularly regarding the presence/absence of storied structures, septate fibers, and ray composition. Twf 17968 remains attributed to *Peltophorum* sp. (Fig. 43; Table 2).

Family FABACEAE Lindl. or APOCYNACEAE Juss.

Fabaceae/Apocynaceae gen. and sp. indet.
(Fig. 44)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 742 sect. 22, Member G-29, 1.92 Ma; Jean de Heinzelin leg.; Twf 17825; Tervuren collection.

DESCRIPTION

Twf 17825 has a diameter ranging from 1.8 to 2.4 cm and shows minor compression. Preservation quality is good or fairly

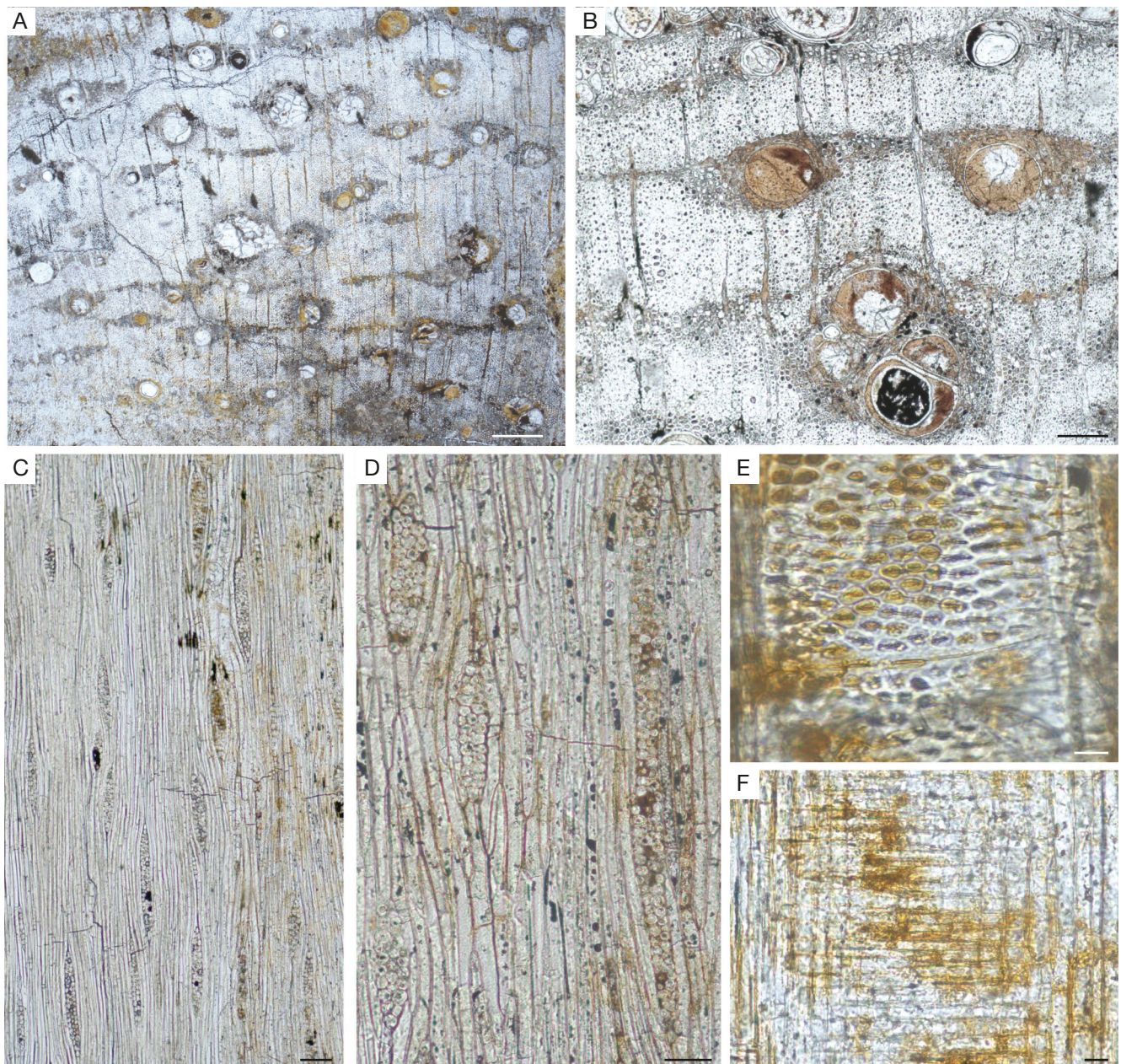


FIG. 43. — *Peltophorum* sp. (Fabaceae Lindl.), Twf 17968: **A, B**, Tr, wood diffuse porous, Parenchyma is vasicentric enclosing vessels or group of vessels to form aliform, winged aliform to confluent and marginal bands composed of 2-3 cells; **C, D**, Tg, rays 1-3 seriate; **E**, intervessel-pits vestured; **F**, Rd, heterocellular rays. Scale bars: A, 200 µm; B, C, 100 µm; D, 50 µm; E, 10 µm; F, 20 µm. Photographs: M.-C. Jolly-Saad.

good in transverse sections, but poor in the longitudinal plane. The thin sections of this specimen are too thick for precise identification of cells and tissues. Abundant fungal hyphae are distinct in the vessel lumina (Fig. 44C), while the peripheral region displays an amorphous structure. Possibly, Twf 17825 may have been degraded before mineralization took place.

The wood is diffuse-porous, no apparent growth rings. Vessels are primarily solitary, with a round or oval shape, although some are in radial multiples of 3-4, with 8-12 vessels per square millimetre. The mean tangential diameter is 250 µm (with a range of 57-350 µm), the perforation is simple. In addition, dark deposits and abundant fungi hyphae can be found in the

vessels, with small intervessel pits (<4 µm) that are possibly vestured and alternate-scalariform in shape. Axial parenchyma is scanty paratracheal. Rays are 1-3 seriate, predominantly 2 seriate composed of procumbent cells with a single row of upright cell (Fig. 44D), 8-10 per mm, ray range height is 350 µm (range 153-552 µm) (8-33 cells), mean ray width is 35 µm (18-51 µm). Fibres show thin walls and likely are non septate. Crystals are present in non-chambered parenchyma.

AFFINITIES AND COMPARISONS

Twf 17825 is characterized by predominant solitary large vessels, vestured intervessel pits, rays composed of

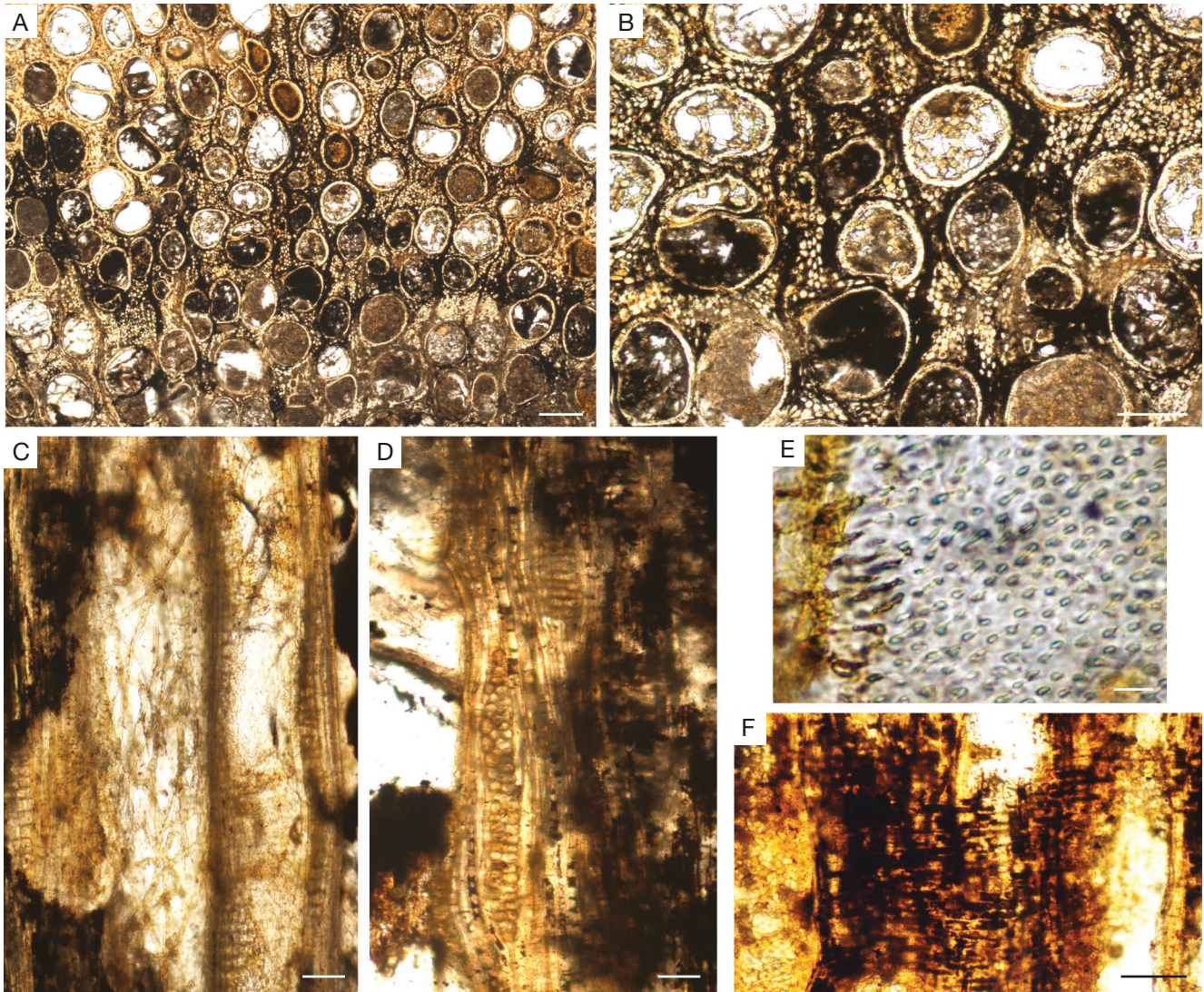


FIG. 44. — Fabaceae/Apocynaceae gen. and sp. indet., Twf 17825: **A, B**, wood diffuse porous with wide vessels; **C**, Tg, hyphae in vessels; **D**, rays with procumbent cells; **E**, minute intervessel-pits; **F**, Rd, homocellular ray. Scale bars: A, C, 100 μ m; B, 200 μ m; D, F, 50 μ m; E, 10 μ m. Photographs: M.-C. Jolly-Saad.

procumbent cells. Diagnosis of Twf 17825 is challenging due to the poor preservation of the longitudinal sections. It shares similarities with some taxa of the Fabaceae or Apocynaceae.

Family MALVACEAE Juss.
Subfamily STERCULIOIDEAE Burn.
Genus *Sterculia* L.

Sterculia sp.
(Fig. 45)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, Member G-29, locality P 743 sect. 22 coupe A; Jean de Heinzelin leg.; Twf 17625; Tervuren collection.

DESCRIPTION

Twf 17625 is poorly preserved with marks of compression. The wood is diffuse-porous, growth rings indistinct. Vessels are round to oval in shape, solitary (49%) or in radial lines of 2 (30%), 3 (11%), 4 (8%), 5 (1%), 4-9 vessels per mm² (Fig. 46A, B), mean tangential diameter is 102 μ m (range 60-150 μ m). Vessel elements are short, mean 280 μ m (range 250-300 μ m), perforation simple, horizontal, intervessel pits are 5-6 μ m wide, sometimes coalescent to slightly scalariform (Fig. 45), vessel-ray pits are not discernible. Gum and black deposits are distinct in vessels; axial parenchyma vasicentric, banded with 3 or 4 rows of cells, strands of 2-4 and 5-8 cells; sheath cells are visible. Rays are 1-7 seriate heterocellular, composed of procumbent cells with one or 2-4 rows of square upright cells (Fig. 45C-E). Mean ray height is 1000 μ m (range

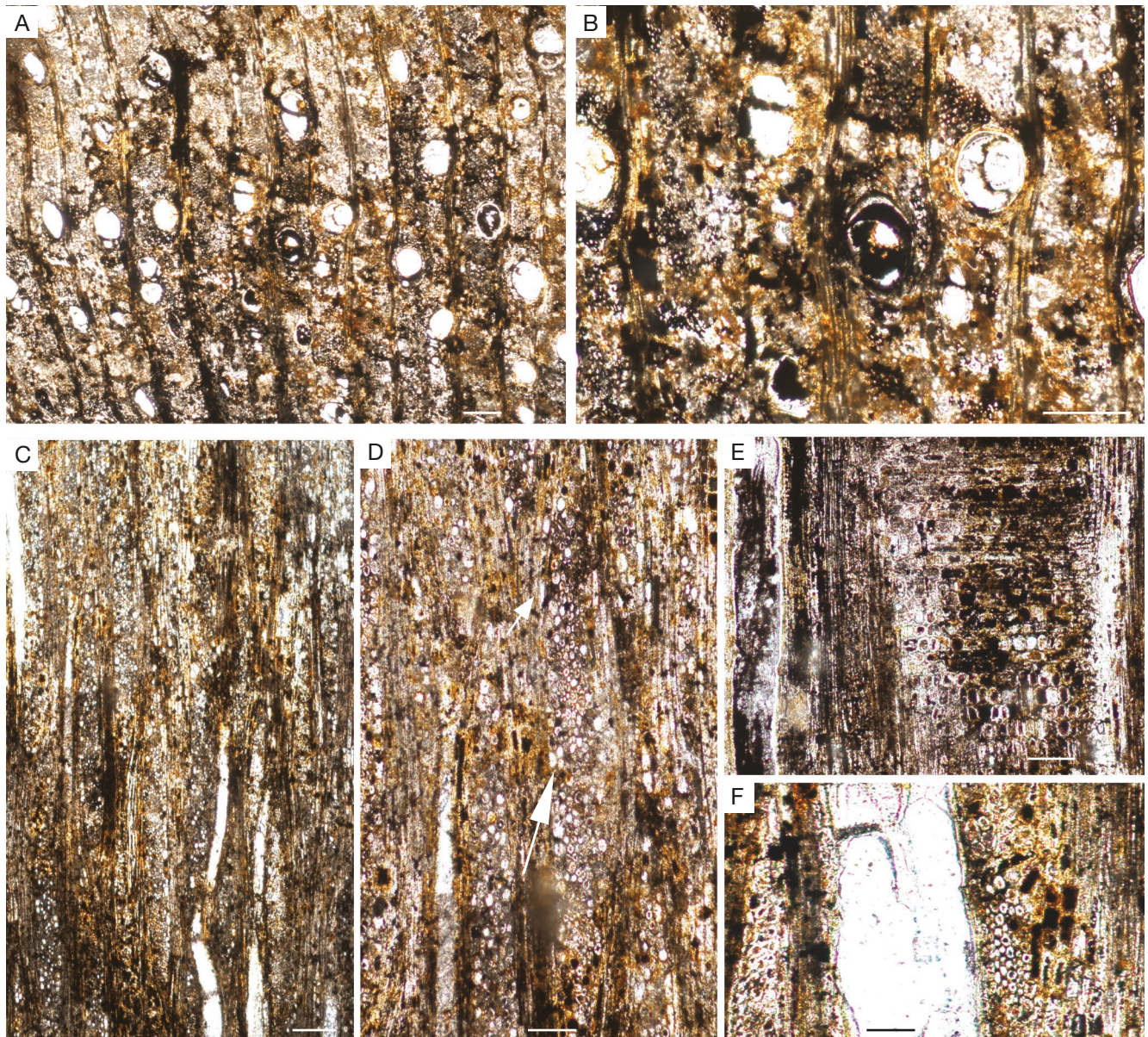


FIG. 45. — *Sterculia* sp. (Malvaceae Juss., Sterculioideae), Twf 17625: **A, B**, Tr, wood diffuse porous, vessel solitary and in radial multiple, axial parenchyma reticulate; **C, D**, Tg, rays heterocellular with sheath cells (**D**, arrow); **E**, Rd, rays heterocellular composed of procumbent, square and upright cells; **F**, stored parenchyma (arrow). Scale bars: A-C, 200 μ m; D-F, 100 μ m. Photographs: M.-C. Jolly-Saad.

600-1552 μ m), ray width is 130 μ m (range 99-137 μ m). Uniseriate rays are rare and exclusively composed of square and upright cells. Fibers are not septate. Prismatic crystals are visible in ray cells.

AFFINITIES AND COMPARISONS

This wood shows characteristics such as solitary or radial grouped vessels, heterocellular pluriseriate rays, narrow bands of 1-3 cells wide, forming an axial parenchyma arranged in a reticulate pattern, the rays as storied cells, sheath cells, intervessel pits medium, coalescent or scalariform. These traits indicate that this wood has the closest affinities with some extant Malvaceae-Sterculioideae genera. Interestingly, *Eriobroma*

and *Tarrietia* have fewer vessels per mm^2 compared to the Shungura fossil specimen, *Pterigota* has larger parenchyma bands, whereas *Cola* species possess silica bodies in their ray cells. Some similarities exist between Twf 17625 and *Sterculia*, the only genus from Ethiopia, known under five species (Vollensen 1995c). *S. setigera* differs from Twf 17625, with less vessels per mm^2 (< 5) and coalescent or scalariform pits. Since we have no description of other species, Twf 17625 is designed as *Sterculia* sp. (Table 2; Fig. 45).

In North Africa, *Sterculinium freulonii* Boureau from post-Eocene deposits (Boureau 1957), *Sterculioxylon aegyptiacum* (Unger) Kräusel (Louvet 1969) from Eocene-Oligocene have no storied structures.

Family MORACEAE Gaudich.
Genus *Ficus* L.

Ficus sp. 2
(Fig. 46)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 769 sect. 22, Member G-29, 1.92 Ma; Jean de Heinzelin leg.; Twf 17725; Tervuren collection.

DESCRIPTION

Twf 17725 exhibits a black color and very poor preservation. It is diffuse-porous, with the absence of growth rings (Fig. 46A). Vessels are mostly solitary or in radial multiple up to 4, mean tangential diameter is 230 μm (range 92–400 μm), with a density of 4–6 per square millimeter, tyloses are present. Vessel member length range is 100–360 μm with simple perforation plates. Vessel pits are alternate, 9–10 μm wide (Fig. 46E). Two types of axial parenchyma can be distinguished, one vasicentric, surrounding the vessels, the second forming axial parenchyma large bands with 3 up to 7 cells high (Fig. 46A). Parenchyma strands are composed of 5–8 cells; Rays are 1–8 seriate (Fig. 46C, D), mean ray height is 800 μm (range 400 μm –1000) and width varies from 34 to 52 μm . Rays are heterocellular, composed of procumbent cells, with one or two rows of upright/square cells in the marginal Twf 17707 cells. Prismatic crystals are present in the terminal cells; fibers non-septate. Laticifer canals are present (Fig. 46A–F). Prismatic crystals occur in the parenchyma and in ray cells.

AFFINITIES AND COMPARISONS

The fossil is characterized by diffuse-porous wood composed of small to medium-sized vessels, occurring singly or in short radial multiples, exclusively simple perforation plates and tyloses in vessels. It also exhibits banded axial parenchyma, typically 3- to 7-seriate, that form undulating, anastomosed lines, along with heterocellular 1 to 8-seriate rays. These characteristics closely resemble those of *Ficus* (Dechamps 1983), notably wider rays (more than four cells wide) and regular parenchyma bands. In Ethiopia there are over 12 species of *Ficus* (Friis *et al.* 2011). We can exclude two of them. *F. capensis* Thunb. (syn.: *F. sur* Forssk) has middle size vessels, large parenchyma bands of more than 15 cells and large rays. *F. vallis-choudae* has middle to large vessels, parenchyma bands made of 3 to 12 cells and 1 to 9 seriate rays, therefore larger than those of Twf 17725.

In Africa, several fossil wood samples have been related to *Ficus*. In Ethiopia, the Late Cretaceous/Eocene *Ficoxylon* sp. has no sufficient description (Beauchamp *et al.* 1973) to enable a meaningful comparison with our Pleistocene specimen. *Ficoxylon cretaceum* (Schenk 1883) from a lower Miocene site (Lemoigne *et al.* 1974) is clearly distinguished from our studied sample Twf 17725 by its 1–3 seriate rays. *Ficoxylon blanckenhornii* Kräusel, from the Wondo Miocene site (Lemoigne *et al.* 1974) is 3–6 seriate. *Ficoxylon* sp. from the Pliocene (4.4 Ma) at Middle Awash differs from the Shungura fossil wood with 1–6 seriate rays (Jolly-Saad *et al.* 2010). *Ficus* sp. also from

Middle Awash is 1–5 seriate (Jolly-Saad & Bonnefille 2012: pl. 5). *Ficus* sp. from the Lower Omo Valley (Dechamps & Bande 1994) has large vessels (140 à 450 μm), rays 2–5 seriate, large band of parenchyma (up to 14 cells each). Elsewhere, in Africa, many fossil woods have been attributed to several species of *Ficoxylon*. *F. cretaceum* come from the Cretaceous (Boureau 1949a, b; Dupéron-Laudoueneix & Dupéron 1995; Kräusel 1939), *F. blanckenhornii* from the Oligocene and early Miocene of Egypt (Kräusel 1939) Sudanese Sahara (Boureau 1949b) and the Oligocene of Tunisia (Fessler-Vrolant 1979). From the Oligocene in Libya, *Ficoxylon guettarensense* has rays of 1 or 3 cells but intravascular pittings less than 4 μm in size (Fessler-Vrolant 1972). *Ficoxylon melahense*, related to Asian species of *Ficus* (Louvet 1971) is clearly distinguished from the studied fossil specimen Twf 17725 by the occurrence of storied parenchyma. The Omo fossil sample species with narrow rays exhibits a similar undulating pattern as *Ficoxylon guettarensense* (Fessler-Vrolant 1972). However, Twf 17725 differs in having less dense vessels (4–6/mm²) and denser rays (12–16/mm²). It is related to *Ficus*. Differences in anatomical characteristics of Twf 17725 (Fig. 47) and Twf 17928 (Fig. 38), mean it is likely that they represent two distinct species, respectively *Ficus* sp. 2 and *Ficus* sp. 1. (Table 2). The anatomical characters and measurements of the two Pleistocene *Ficus* are clearly distinct from those of the two species previously described in the Pliocene at Middle Awash, in Ethiopia (Jolly-Saad *et al.* 2010; Jolly-Saad & Bonnefille 2012) as reported in Table 5.

Family OCHNACEAE DC.
Genus *Ochna* L.

Ochna sp. 2
(Fig. 47)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, Member G-29, locality P 743 C sect. 22; Jean de Heinzelin leg.; Twf 17629; Tervuren collection.

DESCRIPTION

Twf 17629 is not very well preserved. Wood is diffuse-porous, growth ring boundaries absent. Vessels are exclusively solitary, 20–22 vessels per mm² (Fig. 47A). Mean tangential diameter of vessels is 43 μm (range 10–81 μm), vessel walls thick, mean vessel elements 170 μm (range 160–195 μm), perforation plates simple. Intervessels pits alternate, 3–4 μm wide and vested. Vessels-ray pits are similar to vascular pits. Axial parenchyma diffuse-aggregates (Fig. 47B), one row of cells. Perforate ray cells are visible. Rays are 1–4 (5) seriate (Fig. 47C, D), mean ray height is 350 μm (range 80–621 μm), a few up to 1.2 mm, mean ray width is 90 μm (range 58–103 μm). Uniseriate rays are exclusively composed of upright cells. There are 4–5 per sq mm, they are composed of square and upright cells mixed throughout the rays (Fig. 47F). Sheath cells are distinct (Fig. 47D, E). Fibre tracheids are visible. Fibres are medium to thick walled. Inclusions are visible in square and upright cells.

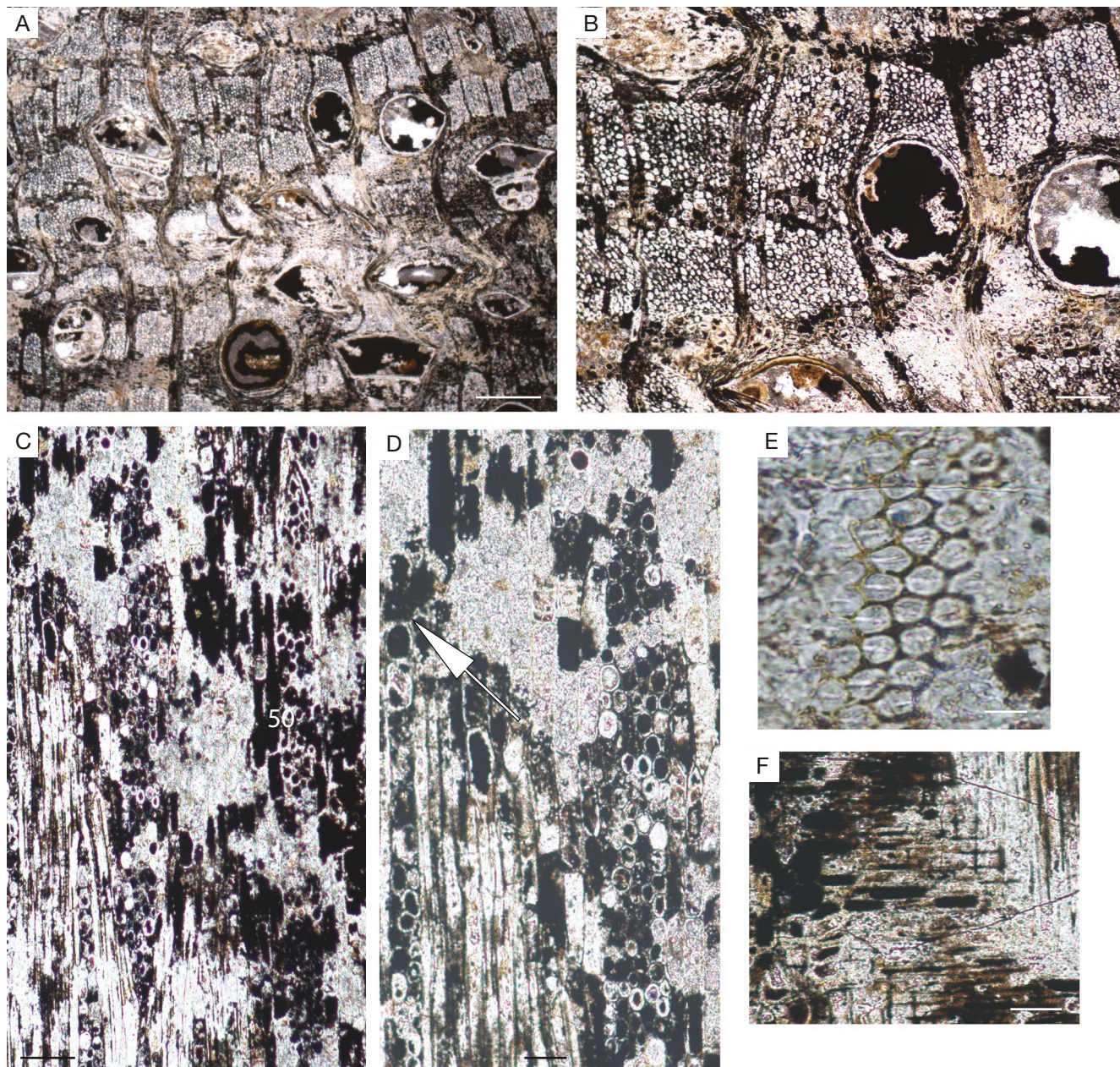


FIG. 46. — *Ficus* sp. 2 (Moraceae Gaudich.), Twf 17725: **A, B**, Tr, wood diffuse porous with banded parenchyma; **C**, Tg, heterocellular rays; **D**, large rays, prismatic crystal in square cells (**arrow**); **E**, Tg, large vessel pits not vested; **F**, Rds, heterocellular rays. Scale bars: A, 200 μ m; B, C, 100 μ m; D, F, 50 μ m; E, 10 μ m. Photographs: M.-C. Jolly-Saad.

Ochna sp. 3

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 743 C sect. 22, Member G-29, 1.92 Ma; Jean de Heinzelin leg; Twf 17630; Tervuren collection.

DESCRIPTION

Longitudinal section is not correctly preserved. Wood diffuse-porous, growth rings absent. Vessels are solitary, round or oval in shape, few clusters are present (1%). Mean tangential diameter of 50 μ m, range (20-75 μ m). Vessel wall

is 8 μ m thick. 20-35 vessels per mm². Perforation plates exclusively simple; vessel elements are short, vessel-pits crowded alternate and vested, 3-4 μ m. Fibers diameter is medium to mostly thick walled. Fibres are septae. No pits observed. Parenchyma diffuse-in-aggregates, one row, parenchyma is not storied. Strands of parenchyma cells are indistinct. Rays are 1-5-seriate, heterocellular composed of procumbent cells. 5-6 per mm, mean ray height is 450 μ m (range 80-921 μ m), few up to 1.2 mm, mean ray width is 90 μ m (range 60-110 μ m). Uniseriate rays are composed of upright cells.

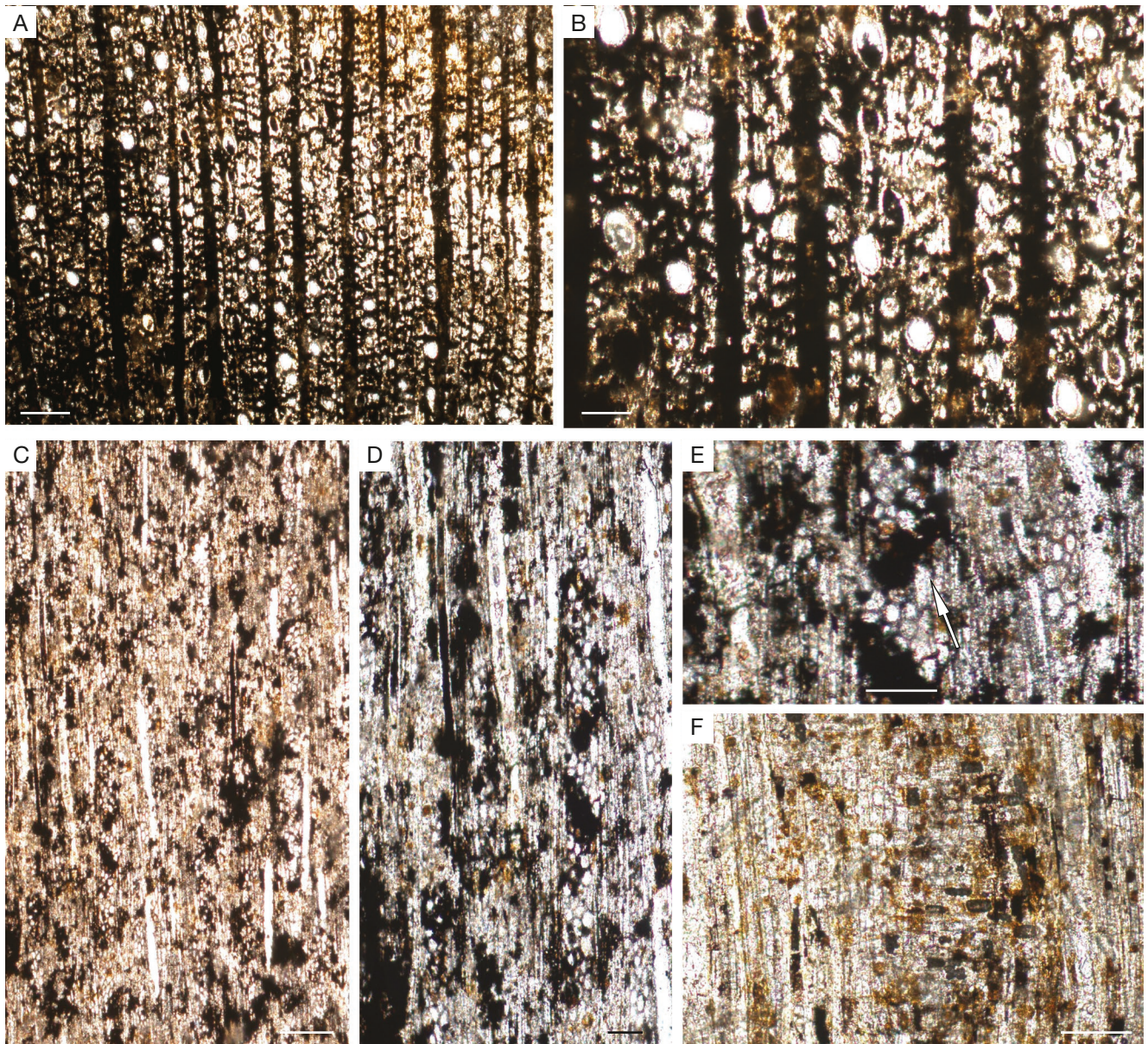


FIG. 47. — *Ochna* sp. 2 (Ochnaceae DC.), Twf 17629: **A, B**, Tr, wood diffuse porous, small vessels, axial parenchyma diffuse-in-aggregates; **C, D**, Tg, rays 1-5 seriate; **E**, Tg, detail of ray with sheath cells (**arrow**); **F**, Rd, heterocellular rays. Scale bars: A, C, 200 μ m; B, D, E, F, 100 μ m. Photographs: M.-C. Jolly-Saad.

AFFINITIES AND COMPARISONS

The most diagnostic features of Twf 17629 and Twf 17630 are: small vessels, intervessels pits vested, axial parenchyma diffuse-aggregates, wide and long heterocellular rays, perforated ray cells which resemble to those of extant Ochnaceae and more specifically to *Ochna* as proposed by Dechamps.

Twf 17629 and Twf 17630 attributed to *Ochna* and dated 1.92 Ma (Fig. 48). They represent the only fossil record of the Ochnaceae from Ethiopia or elsewhere in Africa. Distinct anatomical structures from that of sample Twf 17949A in F3-2, dated 2.3 Ma, and attributed to

Ochna sp. 1 (Fig. 23; Table 2) indicate that three distinct species of *Ochna* may have existed in the Lower Omo valley between 2.3 to 1.9 Ma. Four species are described in the Flora of Ethiopia (Friis *et al.* 2011; Vollensen 1995c). *Ochna bracteosa* is from the transitional rainforest; *O. inermis* Forssk. Schweinf ex. Penzig from the *Acacia-Commiphora* woodland and bushland (500 to 1900 m). *O. leucophlocos* Hochst. ex. A. Rich. 1847, and *O. schweinfurthiana* F. Hoffm are both from the *Combretum-Terminalia* woodland. Unfortunately, no xyloanatomical data are available for any of these species.

Family SAPOTACEAE Juss.

Sapotaceae gen. and sp. indet.
(Fig. 48)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 743 C sect. 22; Member G-29, 1.92 Ma; Jean de Heinzelin leg; Twf 17636; Tervuren collection.

DESCRIPTION

Twf 17636 exhibit relatively good preservation. The wood is diffuse-porous and lacks growth rings. The majority of vessel distribution is solitary (88%) with a minority occurrence in radial multiples of 2 (11%) and 3 (1%), organized in an oblique and dendritic pattern (Fig. 48A, B). The vessels are oval in shape and outline, the mean tangential diameter is 31 μm with a range of 14 μm to 57 μm , and a density of 25-40 per mm^2 . Perforations are solely horizontal and uncomplicated; vessel elements and intervessel pits are not visible. Axial parenchyma is diffuse-in-aggregates in row of 2 or 3 cells, lacking a clear distinction (Fig. 48B, E). The parenchyma strands are not distinct in longitudinal section. The rays are predominantly uniseriate, biseriate rays rarely occurring (Fig. 48C, D). They consist of mixed square and upright cells observed at a frequency of 10-12 per mm^2 , mean ray height is 500 μm (range 330-598 μm) (14-27 cells), a few exceed 1mm. Mean ray width is 14 μm (range 13-15 μm) with fibers possessing thick walls (5 μm) and a diameter ranging from 11 to 20 μm . No pits or septae have been observed, while prismatic crystals are distinct in ray cells.

AFFINITIES AND COMPARISONS

The combination of vessels in an oblique dendritic pattern, narrow heterocellular rays, uniseriate sometimes biseriate and chambered crystalliferous parenchyma, are not found in the genera *Manniophyton* or *Macaranga* (Euphorbiaceae) as suggested by Dechamps (1983). In the Ebenaceae family, only *Diospyros abyssinica* displays vessels in a diagonal pattern, but axial parenchyma shows diffuse-in-aggregates cells in one, 2 or 3 rows. Fossil wood sample Twf 17636 displays resemblances to the Sapotaceae family. Today, Sapotaceae are found in Ethiopia, especially in the highland rainforest and riverine forests (Friis 2003; Friis *et al.* 1982). The family consists of five genera, namely *Mimusops* L., *Vitellaria* Gaertn. f., *Manilkara* Adans, *Sideroxylon* L., *Pouteria* Aublet. As pointed out by Prakash *et al.* (1982), the wood anatomy of the Sapotaceae is quite uniform, with considerable overlap between the genera (Wheeler *et al.* 2007). Our Shungura sample can only be attributed to the Sapotaceae family without further generic attribution (Table 2; Fig. 48).

Five fossil “*Sapotoxylon*” morphotypes have been described from the Tertiary in Ethiopia, “*Sapotoxylon aethiopicum*” (Lemoigne *et al.* 1974), from the Miocene at Debre Sina, has 1-3 seriate rays with sheath cells. *S. lecomtedoxiodes* (Lemoigne, 1978), from the Miocene of Welkite, has considerably wider vessels (150-250 μm). *S. multiporosum* from the Mio-Pliocene of the Blue Nile Valley has heterocellular and 1-3 seriate rays,

a higher vessel density (60-120 per mm^2), and more rays per mm^2 (18-20) (Prakash *et al.* 1982). At Fejej (tree 18) features of the species *Sapotoxylon* sp. 1, has large vessels (132 μm) with a radial to oblique pattern, 2-3 seriate rays, a body of procumbent cells with long uniseriate margins of upright cells, and inclusions. Solitary prismatic crystals are commonly found within chambered axial parenchyma in a series of 4 to more than 12 chambers (Ref). Twf 17636 differs from all these fossil specimens.

Family SAPINDACEAE Juss.

Sapindaceae gen. and sp. indet.
(Fig. 49)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality non available, sect. 22, Member G-29, 1.92 Ma; Frank Brown & Jean de Heinzelin leg; Twf 17966; Tervuren collection.

DESCRIPTION

The transverse and radial sections are fairly well preserved, while the longitudinal and tangential sections are poorly preserved. Diagnostic features are only distinct in limited areas of each section. The studied sample is a small stem with a central cylinder of parenchyma. The wood is diffuse-porous with distinct growth rings (Fig. 49A). Vessels are mostly solitary (84%) and few in radial multiples of 2 (11%), 3 (5%) (Fig. 49B). Mean tangential diameter of 80 μm , range 65-100 μm , 16-30 vessels per mm^2 . Perforation plates are exclusively simple, inter-vessel pits not distinct, vessel-rays pits large and bordered (Fig. 49G). Axial parenchyma is scanty paratracheal and in marginal bands, initial/final parenchyma (one row), strands of parenchyma not seen in longitudinal section. Rays are uniseriate, few of them are biseriate on one row, composed of procumbent cells with one row of upright cells, 10-12 per mm^2 , mean ray height range is 240 μm (range 73-312 μm) (5-28 cells), mean ray width is 11 μm (range 10-12 μm) (Fig. 49C, D). Fibers are thick-walled and septate. Crystals are distinct in ray cells. Fibers are thick to mostly very thick walled, not clearly distinct in tangential view.

AFFINITIES AND COMPARISONS

The fossil is characterized by diffuse-porous wood with distinct growth rings. Vessels occur singly or in radial multiples of 2 or 3, featuring exclusively simple perforation plates. Axial parenchyma is scanty paratracheal, forming marginal bands and initial/final parenchyma. The general wood anatomy of the Shungura sample closely resembles that of the fossil genus *Terminalioxylon* (Mädel-Angeliwewa & Müller-Stoll 1973), but it has small vessels with well-defined pits rather than vested pits. This observation excludes affinities with *Terminalia*, as the presence of vested pits is one of the diagnostic features of this genus (Van Vliet 1979). The Twf 17966 fossil specimen more likely corresponds to the structure of the family Sapindaceae (Klaassen 1999).

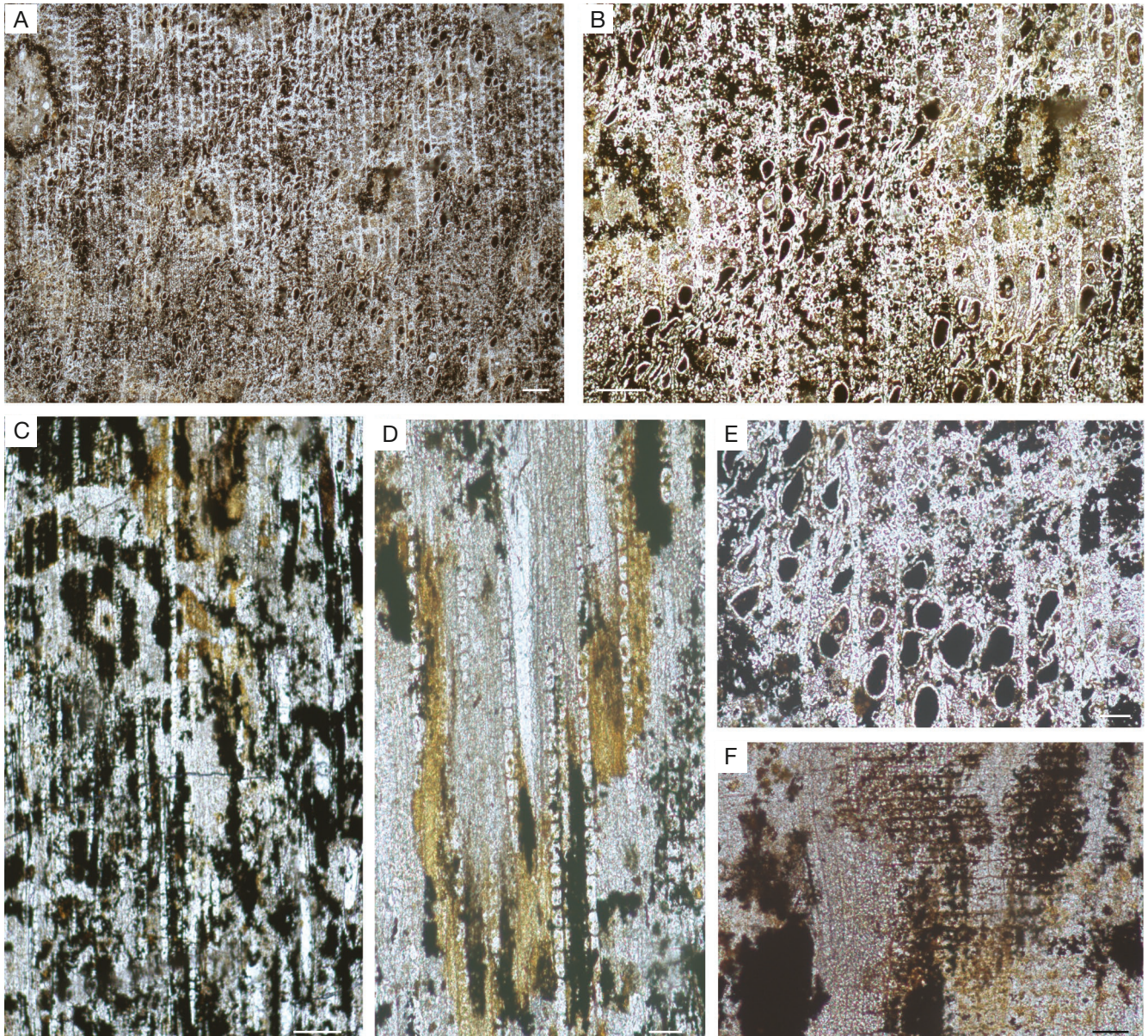


FIG. 48. — Sapotaceae gen. and sp. indet., Twf 17636: **A, B**, Tr, wood diffuse porous with a dendritic arrangement; axial parenchyma diffuse-in-aggregate; **E**, Tr, detail transversal section with vessel repartition and parenchyma cells; **C, D**, Tg, rays 1-2 seriate with square and upright cells; **F**, Rd, heterocellular rays. Scale bars: A-C, 100 μ m; D-F, 50 μ m. Photographs: M.-C. Jolly-Saad.

Micro-anatomical structure of Twf 17966 is near that of the morphotype *Sapindoxylon* Kräusel, described from the Cretaceous to the Plio-Pleistocene, in Africa as well as in Ethiopia. *Sapindoxylon* sp. Beauchamp (Cretaceous-Eocene) has large rays (Beauchamp *et al.* 1973). *S. almelai* Koeniguer (Mio-Pliocene Sahara) has more bigger vessels than Twf 17966 (Koeniguer 1967). *S. haileselassiei* Lemoigne (Oligo-Miocene from Ethiopia) has 1-3 seriate rays, vasicentric parenchyma and wider vessels in radial multiple up 15 vessels (Lemoigne 1970). *S. (Blighioxylon) koholense* Koeniguer (Algeria) and *S. sp.* Koeniguer (Libya) have 1-3 seriate rays, large vessels and less vessels density than the Omo fossil and scanty paratracheal parenchyma (Koeniguer 1967, 1972). *S. mbaense* Koeniguer (Eocene,

Senegal) has uniseriate rays and scanty paratracheal parenchyma (Koeniguer 1973a). *S. stromeri* Kräusel (Oligo-Miocene from Egypt) has vasicentric parenchyma, wider vessels in radial multiple up 15 vessels, septate fibers and prismatic crystals in rays and parenchyma, two features indistinct in Twf 17966. A fossil wood placed in *Sapindoxylon*, related to the type specimen *S. stromeri* has been described from the site Fwjj 14, dated 1.56 to 1.36 Ma at Illeret, East Turkana, Kenya. It differs from Twf 17966 by having bigger vessels, smaller radial multiples, exclusively uniseriate rays and parenchyma that is either rare or sparse paratracheal (Bamford 2017). In conclusion, Twf 17666 is attributed to the Sapindaceae without any generic precision (Table 2; Fig. 50).

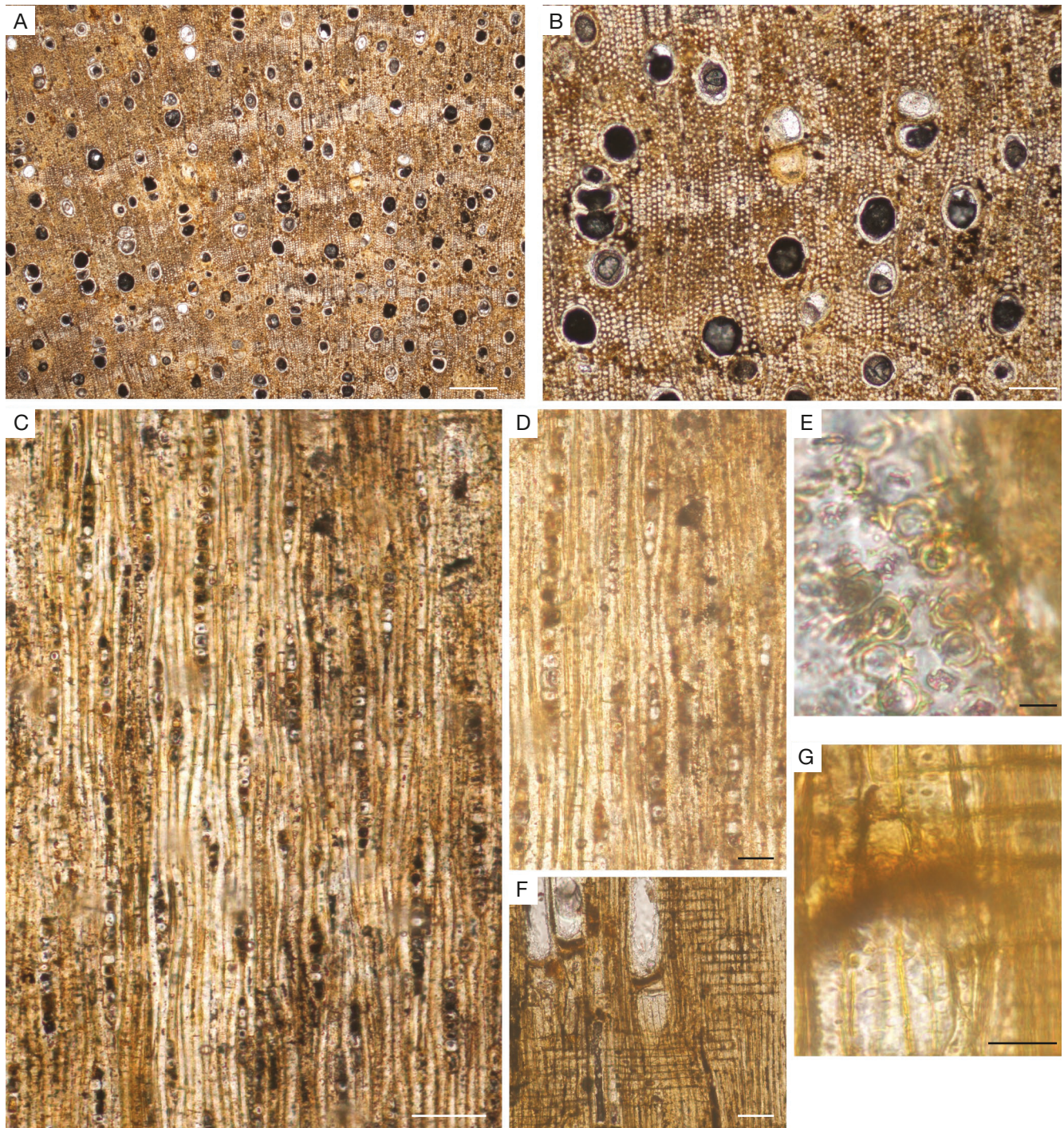


FIG. 49. — Sapindaceae gen. and sp. indet., Twf 17966: **A, B**, Tr, vessels diffuse, axial parenchyma scanty paratracheal and in marginal bands; **C, D**, Tg, rays uniseriate or locally biseriate; **E**, Tg, intervessel pits; **F, G**, Rd, heterocellular rays; **G**, detail of radiovascular pits. Scale bars: A, 200 µm; B, C, 100 µm; D, F, 50 µm; E, 10 µm; G, 20 µm. Photographs: M.-C. Jolly-Saad.

Genus *Lecaniodiscus* Planch. ex. Benth.

Lecaniodiscus sp.
(Fig. 50)

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 742b sect. 22, Member G-29, 1.92 Ma; Jean de Heinzelin leg; Twf 17780 (Fig. 50), Twf 17987; Tervuren collection.

DESCRIPTION

Both specimens consist of small twigs that contain a central cylinder of parenchyma. Their three thin sections are well preserved with similar anatomical structures. The description and illustrations (Fig. 50) are from Twf 17780. The wood is diffuse-porous with clear growth ring boundaries, marked by the presence of initial or terminal parenchyma. Vessels exist either in solitary formation (67%) or arranged in radial mul-

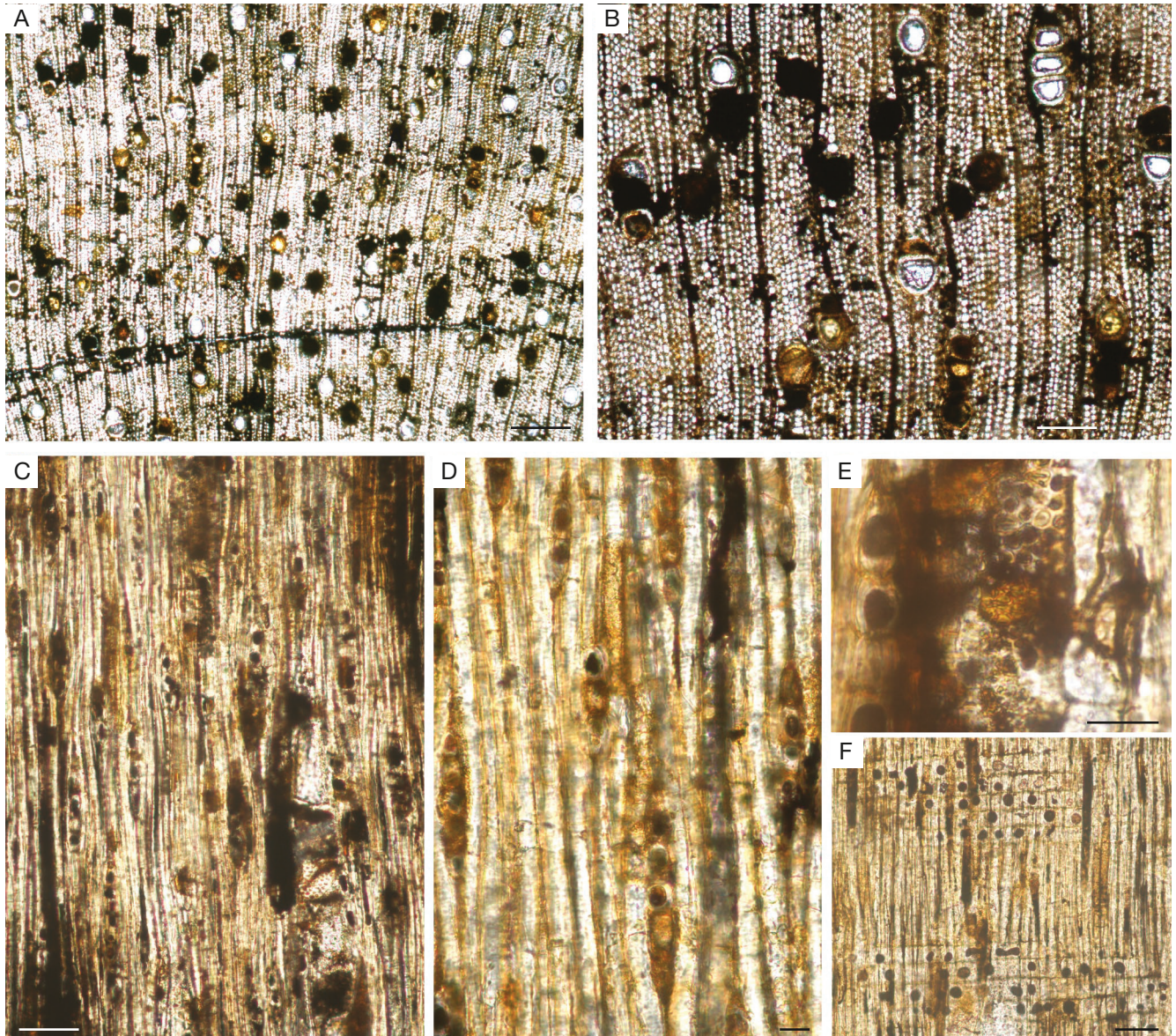


FIG. 50. — *Lecaniodiscus* sp. (Sapindaceae Juss.), Twf 17780: **A, B**, Tr, diffuse porous and small vessels, parenchyma cells (arrow); **C, D**, Tg, short uniseriate rays; **E**, Tg, intervessel pits; **F**, Rd, heterocellular rays with procumbent and square cells. Scale bars: A, 100 μ m; B, C, G, 50 μ m; D-F, 20 μ m. Photographs: M.-C. Jolly-Saad.

tuple of 2 (20%), 3 (8%), 4 (3%), or 6 (2%) (Fig. 50A). The tangential vessel diameter mean is 76 μ m (range 27-90 μ m), 14-20 vessels per mm^2 . The vessel wall is thick measuring 8-9 μ m (Fig. 49F). Vessel element length range is 176 μ m (200-350 μ m). Helical thickenings are present on few vessel walls. Intervessel pits are round to polygonal, and 3-4 μ m wide, while perforation plates are simple and horizontal. Gum deposits are noticeable in vessels, but vessel-ray pits were not observed. Axial parenchyma is scanty paratracheal to vasicentric with 1-2 row of terminal/initial parenchyma, occasionally diffuse (Fig. 50B). Prismatic crystals are distinct in chambered parenchyma. Rays are mostly uniseriate but some are locally biseriate on one or two rows, mean ray height is 100 μ m (range 45-195 μ m), up to 12 cells, mean ray width is 15 μ m (range 11 to 16 μ m) (Fig. 50C, D). They are 12 or

more rays per mm^2 . Composed of mixed procumbent, square and upright cells and one row of marginal upright cells, the rays are heterocellular and have dark deposits. Fibers seem aligned, their diameter is between 8-18 μ m, they have also thick walls and are not septate. Crystals are distinct in ray cells and in chambered parenchyma.

AFFINITIES AND COMPARISONS

The combination of solitary vessels and in radial multiple, simple perforation plates, narrow tangential diameter of vessels, scanty paratracheal and seemingly banded parenchyma, narrow non-storied rays, and chambered crystalliferous parenchyma occurs in woods of Combretaceae, Fabaceae, Rutaceae, and Sapindaceae. Vessel pits are usually larger in the Combretaceae, Fabaceae have vestured pits. The affinity

of Twf 17780 and Twf 17987 is more likely with the Sapindaceae (Klaassen 1999).

In Ethiopia, the Sapindaceae comprise several genera (Friis *et al.* 2011; Vollensen 1989). *Allophylus africanus* P. Beauv., *A. abyssinicus* (Hochst.) Radlk. and *Haplocoelum* Radlk. exhibit an absence or scarcity of axial parenchyma. No xyloanatomical data are available for *Bottegoa insignis* Chiov. *Cardiospermum corindum* L. and *C. halicacabum* L. have larger rays *Deinbollia kilimandscharica* Taub. and *Zanha golungensis* Hiern. possess a greater amount of axial parenchyma than Twf 17780. *Pappea capensis* displays a higher density of vessels per mm² and a greater quantity of parenchyma as well. *Dodonaea* and *Lecaniodiscus* are the most closely related modern relatives. Septate fibers are not distinctive of *Dodonaea*. Twf 17780 shows similarities with *Lecaniodiscus* (Metcalf & Chalk 1950). With uniseriate rays, parenchyma initial/terminal and septate fibers, both samples Twf 17780 and Twf 17987 correspond to *Lecaniodiscus* sp. (Klaassen 1999) (Table 2; Fig. 50). They do not fit description of any *Sapindoxylon* morphotypes as discussed during description of Twf 17966 attributed to Sapindaceae.

UNIDENTIFIED ANGIOSPERMS

Fam., gen. and sp. indet. 4

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 743 A sect. 29, Member G-29, 1.92 Ma; Jean de Heinzelin leg; Twf 17624; Tervuren collection.

COMMENTS

The description of Twf 17624 cannot be achieved due to insufficient preservation. The transverse section is not preserved. In longitudinal tangential section, rays are 1-2 seriate, featuring distinct crystals. The fossil wood was mentioned as *Diospyros* (Dechamps 1983), but not seem acceptable with regard to poorly preserved transverse section.

Fam., gen. and sp. indet. 5

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality P 742 sect. 22, Member G-29, 1.92 Ma; Jean de Heinzelin leg; Twf 17824; Tervuren collection.

DESCRIPTION

Twf 17824 has undergone severe degradation in all three sections, likely before mineralization, leading to an amorphous structure. Some vessels display evident fungal hyphae. The wood is diffuse-porous and growth rings are absent. Vessels are solitary round or oval in shape. Mean tangential diameter of 45 µm (range 35-55 µm). Vessel walls are thick, 20-35 vessels per mm². Perforation plates are exclusively simple; vessel elements are short, vessel pits are 4-5 µm wide. It is not possible to see whether they are vested or not. Rays-pits are not distinct. Parenchyma is indistinct. Rays are 1-5 seriate and heterocellular. Characteristics of the fiber not visible.

AFFINITIES AND COMPARISONS

Twf 17824 was initially attributed to *Ochna* (Dechamps 1983). However, it lacks the diffuse-in-aggregate parenchyma characteristic of *Ochna* species that would be necessary for a conclusive identification of this specimen.

Fam., gen. and sp. indet. 6

EXAMINED MATERIAL. — **Ethiopia** • Lower Omo Valley, Shungura Formation, locality L 618 sect. 4, Member G-15, 2.04 Ma; American Staff leg; Twf 17612; Tervuren collection.

DESCRIPTION

Twf 17612 displays very poor preservation, lacking several tangential features. Its black color suggests similarity to charred material. Degradation most probably occurred before fossilization. Notably, no evidence of fungi is observed. The wood is diffuse porous, growth rings are distinctly marked by the reduction of fibers diameters. Vessels are mostly solitary or in radial multiple of 2 or 3 up to 6. Mean vessels diameters vary little from 180-to 200 µm. Vessels are 10 per mm². Abundant gum and black deposits are visible in vessel lumina; vessels element high not distinct, vessel pits and ray pits are indistinct. Axial parenchyma in narrow apotracheal bands combined with scanty paratracheal parenchyma. The tangential section is very poorly preserved, few features are visible: rays are wide, composed of large cells, pluriseriate and heterocellular, sheath cells are distinct and are heterocellular, thick-walled fibers.

AFFINITIES AND COMPARISONS

Twf 17612 was previously assigned to *Landolphia* (Apocynaceae) (Dechamps 1983), yet micro-anatomical structures are severely degraded. Nevertheless, the observed characteristics do not support an attribution to *Landolphia*, that typically exhibits mostly solitary vessels (90%), lacks deposits in vessels, and possesses 1-3 seriate rays. Twf 17612 remains an unidentified dicotyledonous wood.

MEMBER J (1.70 MA)

Chronology of Member J relies on cross correlation with volcanic ashes of identical composition deposited in other basins of the Turkana Depression. At the bottom of Member, Tuff J of the Shungura Formation correlates with the Orange Tuff found at West Turkana (Nachukui Formation) and at East Turkana (Koobi Fora Formation) where it was dated to 1.76 ± 0.03 Ma (McDougall & Brown 2008). At the top of Member J, Tuff K is dated 1.53 ± 0.02 Ma (Brown & McDougall 2011). Unit J-4 was estimated 1.60 ± 0.01 Ma (McDougall & Brown 2006). Therefore, fossil woods collected in Unit J-2 can be safely estimated at c. 1.70 Ma (1.73-1.68 Ma) (Table 2).

Family EBENACEAE Gürke
Genus *Diospyros* L.

Diospyros sp. 1
(Fig. 51)

EXAMINED MATERIAL. — Ethiopia • Lower Omo Valley, Shungura Formation, locality Kalam road, sect. 19, Member J-2, 1.70 Ma; Jean de Heinzelin leg; Twf 17986; Tervuren collection.

DESCRIPTION

Twf 17986 is a small twig measuring 1 × 2 cm in diameter with pith located at the centre. It is diffuse-porous, growth rings indistinct. The vessels are solitary (40%) or arranged in radial multiple of two (37%), three (11%) up to six (Fig. 51A, B). Their density ranges from 40 to 60 per mm². Mean tangential diameter is 70 µm (range 30-95 µm). Vessels are thin walled, perforation plates simple, vessel elements indistinct, vessel-pits crowded alternate, minute (5-6 µm) and not vested (Fig. 51A-E), vessel ray pits indistinct, axial parenchyma is diffuse-in-aggregate very narrow bands (Fig. 51B). Parenchyma strands is not seen in longitudinal section. (Fig. 51G), Rays mostly uniseriate, becoming locally biseriate and high (more 1mm height), heterocellular composed of procumbent and square cells mixed in the rays. Rays width averages 30 µm (range 20-35 µm), and density of 20-22 rays per mm (Fig. 52C). Crystals are visible in ray cells and in parenchyma; fibers are not septate.

AFFINITIES AND COMPARISONS

The diagnostic features of Twf 17986, including that of vessels, 1-(2) rays, perforation plate, axial parenchyma and prismatic crystals in ray cells and in parenchyma, altogether indicate affinity with extant members of Ebenaceae such as *Diospyros*. However, it differs from Twf 17683 from Member C, dated 2.62 Ma (Fig. 15), which has only uniseriate rays and was attributed to *Diospyros mespiliformis* (Table 1). Twf 17986 from Member J looks more similar to Twf 17907, dated 1.92 Ma, from Member G. (Fig. 42), and indicated *Diospyros* sp. 2 (Table 2).

Family SALVADORACEAE Lindl.
Genus *Salvadora* L.

Salvadora persica L.
(Fig. 52)

EXAMINED MATERIAL. — Ethiopia • Lower Omo Valley, Shungura Formation, locality Kalam road, sect. 19, Member J-2, 1.7 Ma; Jean de Heinzelin leg; Twf 17601-Twf 17604, Twf 17985, Tervuren collection.

COMMENT

Five samples, Twf 17601 to Twf 17604 and Twf 17985, were re-examined in this study among the seven fossil samples collected at the same locality and previously reported as a

single taxon, *Staeganotaenoxylon araliacea* (Dechamps 1977). In this study, we provide description of Twf 17601 illustrated in Fig. 52 and identified as *Salvadora persica*. All other examined samples show the same anatomical characteristics and are therefore attributed to the same taxon.

DESCRIPTION

The preservation of Twf 17601, both in transversal and tangential sections is quite good with the exception of the radial section which is not perfectly preserved. Fungi are present. The wood is diffuse-porous, growth rings boundaries present. Vessels are solitary or in groups, few in radial multiple of 2-4, or group in irregular clusters. Vessels show two distinct diameter classes; mean tangential diameter of the larger and smaller size 140 µm (range 31-240 µm). There are few vessels per mm² (3-5) (Fig. 52A, B). Perforation plates exclusively simple, vessel pits are simple, average diameter is 4-5 µm and not vested (Fig. 52F). Vessel wall is thick, brownish gum-like deposits present. Vessel elements length is short, less than 350 µm. Vessel-ray pits with distinct borders similar to vessels pits. Included phloem is visible. Fibers have thick-wall. Axial parenchyma is paratracheal varying from few cells to vasicentric and rarely confluent. Fusiform or two cells per parenchyma strands and storied. Rays up to 1-3 (4) seriate, uniseriate are few, they are heterocellular composed of mixed procumbent square and upright cells or exclusively composed of square and upright cells (Fig. 52G). They are not storied; 5-10 per mm. height range 86-456 µm and 14-51 µm wide. Prismatic crystals are abundant and located in ray cells and in chambered parenchyma (Fig. 52).

Large and short vessels elements, included phloem in concentric rows (interxylary phloem sensus Carlquist 2002), prismatic crystals and no radial canals, differ from the Apiaceae family and exclude an attribution to *Staeganotaenia* (InsideWood 2004-onwards; Oskolski *et al.* 2010), notably *Staeganotaenoxylon araliacea* inferred by Dechamps (1977). Fossil samples have affinity with Asclepiadaceae, Menispermaceae and Salvadoraceae. *Cocculus* in the Menispermaceae has higher and wider rays and exclusively solitary vessels. *Lepadenia*, a desert shrub in the Asclepiadaceae, has larger rays up 20 cells wide and diffuse phloem. The Twf 17601 wood is similar to the Salvadoraceae including three genera in East Africa *Salvadora*, *Dobera* and *Azima* (Verdcourt 1989). *Azima tetracantha* has smaller vessel diameter, larger rays and axial parenchyma in bands, and does not exist in Ethiopia. There is currently a lack of information regarding the microanatomical characteristics of *Dobera*. In the Lower Omo Valley, fossil wood samples similar with *Salvadora* (Metcalf & Chalk 1950; Carlquist 2002), represented the earliest fossil wood record from Ethiopia. However, the pollen has been found since 2.8-2.5 Ma (Bonnefille 1976b). The new identification of this genus known through a unique species *Salvadora persica* agrees with modern habitat of the corresponding trees in the borders of seasonally dry rivers and streams in the subdesertic region of Ethiopia today.

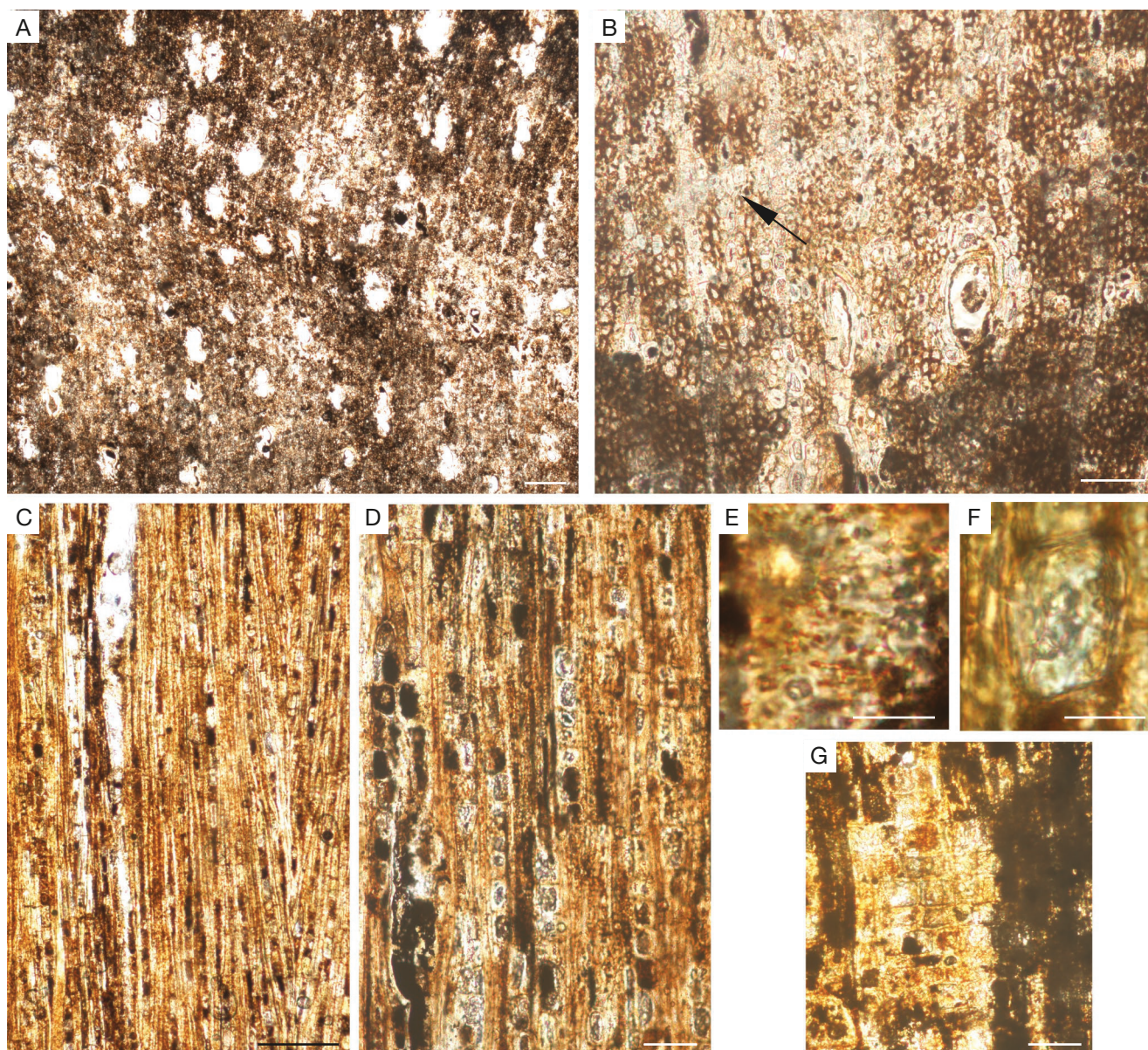


FIG. 51. — *Diospyros* sp. 1 (Ebenaceae Gürke), Twf 17986: **A, B**, Tr, wood diffuse porous, axial parenchyma diffuse-in-aggregate; **C, D**, Tg, uniseriate rays; **E**, Tg, minute intervessel pits not vested; **F**, crystal in ray cell; **G**, Rd, heterocellular rays. Scale bars: A, 200 µm; B, D, G, 50 µm; C, 100 µm; E, F, 10 µm. Photographs: M.-C. Jolly-Saad.

DISCUSSION

Our study of fossil wood from the Lower Omo Valley fills a gap of information in the past vegetation history of Ethiopia between what is known for the Oligo-Miocene and the Pleistocene. Many tree taxa described in this work for the Lower Omo Valley are new and differ significantly from those of older and younger fossil flora.

COMPARISON OF THE SHUNGURA PLIO-PLEISTOCENE FLORA WITH KNOWN CENOZOIC FLORAS IN ETHIOPIA

Information on past vegetation has been recently obtained from sites located today at high elevation on the Ethiopian Plateau. For the Oligo-Miocene (27-23 Ma), plant remains

(mainly leaves, seeds, fruits) of the Chilga site, north of Lake Tana in the northwestern Ethiopian Plateau, include taxa with related species known in the lowlands or submontane forests of tropical Africa: *Afzelia* (Fabaceae; Pan 2007), *Cola* (Malvaceae/Sterculioideae; Pan & Jacobs 2009), leaves and flowers referable to *Hyphaene* and *Eremospatha* belonging to the palms (Arecaceae/Calamoideae; Pan *et al.* 2006), *Vepris* (Rutaceae; Pan 2010), *Ocotea* (Lauraceae) and *Dioscorea* (Dioscoreaceae). Another palm *Sclerosperma* (Arecaceae) now restricted to West and Central Africa (Pan & Jacobs 2009; Grímsson *et al.* 2018) has also been identified. Several ferns (García Massini *et al.* 2006) and silicified forest of trunks over 25 m height (Jacobs *et al.* 2005) are added to this long list. The recovery of *Cynometra* and *Afzelia* attests of the sig-

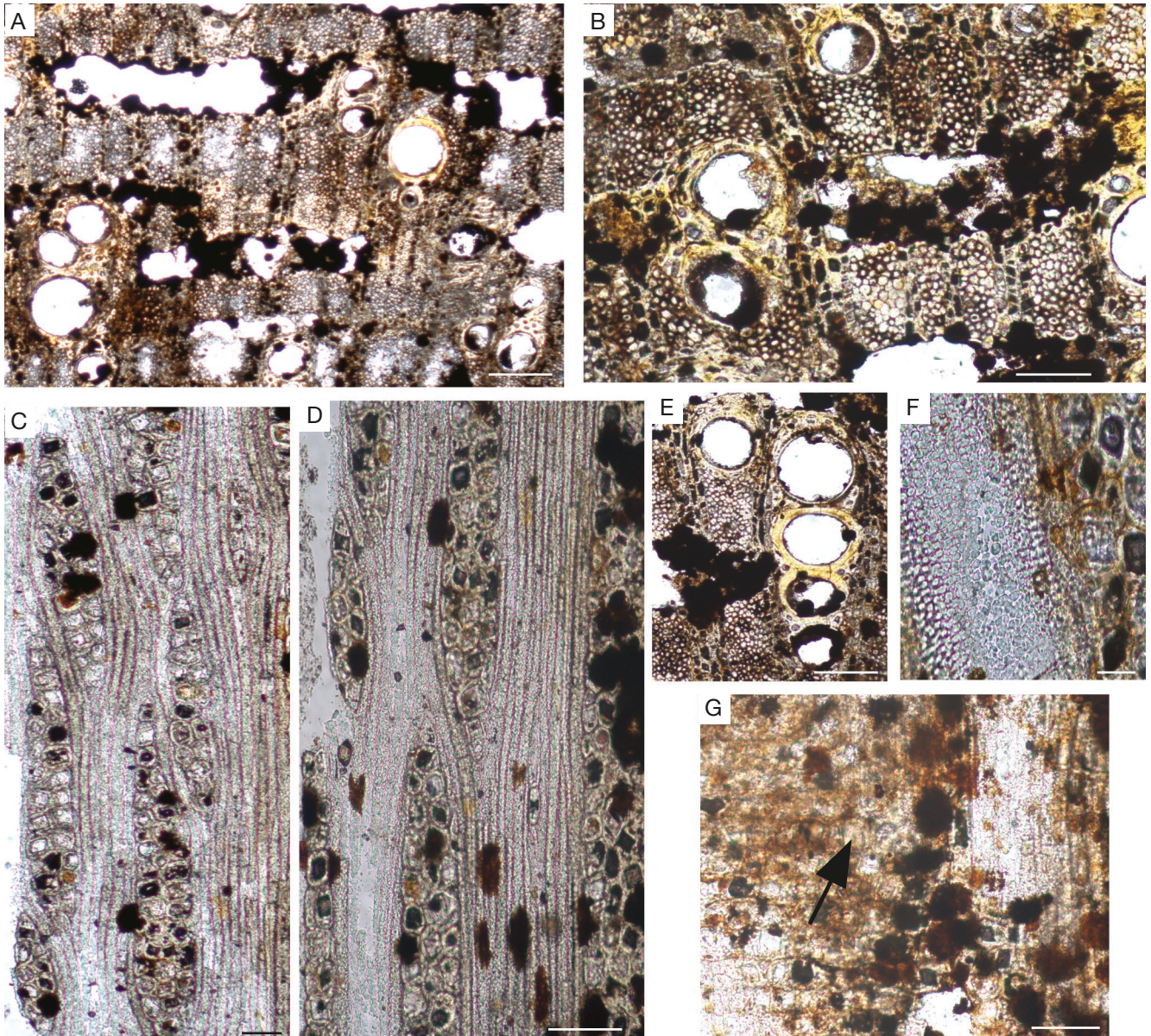


FIG. 52. — *Salvadora persica* (Salvadoraceae Lindl.), Twf 17601: **A, B**, Tr, wood diffuse porous, parenchyma vasicentric, confluent and included phloem (arrow); **C, D**, Tg, heterocellular rays with crystals; **E**, vessels in radial multiple; **F**, Tg, intervessel-pits; **G**, Rd, heterocellular rays with crystal (arrow). Scale bars: A, 200 μ m; B, C, 100 μ m; D, E, G, 50 μ m; F, 20 μ m. Photographs: M.-C. Jolly-Saad.

nificant contribution of the legume subfamily Detarioideae in the Oligo-Miocene forests (Pan *et al.* 2010). It is remarkable that floristic composition of the Oligo-Miocene plant communities changed through a short time interval, such changes were attributed to the dynamic of past vegetation under palaeogeographical changes (Jacobs 2004). During the Oligo-Miocene, rich and diversified forests, including rain forests, were present on the northwestern Ethiopian Plateau. At that time, palaeoprecipitation based upon leaf assemblages was estimated between 1200 to 1500 mm/yr (Pan 2007).

From the early Miocene, information on past vegetation is documented in lacustrine sediments from the Mush Valley, a site located on the northeastern Ethiopian plateau, at 2700 m elevation and dated at *c.* 21.7 Ma. Abundant fossil

leaves, dominated by the legume family (Fabaceae) attest to a closed canopy forest (Currano *et al.* 2020), with limited palm diversity (Pan *et al.* 2023a, b) documented by seeds of *Newtonia* (Pan *et al.* 2012)

After a long gap without any information upon past vegetation, fossil fruits and seeds such as *Antrocaryon* (Anacardiaceae), *Parinari* (Chrysobalanaceae) and Annonaceae have been studied in the early-middle Miocene deposits, north of Lake Turkana, at Fejej dated 16 Ma (Tiffney *et al.* 1994). From their occurrence and present distribution of extant species, it seems that a continuous forest was widespread beyond the immediate river margin on the northeastern part of the Turkana Lake, located in the lowlands plain of southern Ethiopia. For the same site, large size of associated

fossil trunks provided the description of over fifteen taxa that belong to the families Combretaceae, Fabaceae, Sapotaceae and Bignoniaceae (Wheeler *et al.* 2007), therefore distinct from those represented in the seed assemblage extracted from the same strata (Tiffney *et al.* 1994). A measure of the wood specific gravity is added to the wood structure description. The vulnerability index (Carlquist 1975), defined as vessel tangential diameter divided by vessel density per mm², reflects wood hydraulic vulnerability. Woods with few wide vessels are more susceptible to embolism than those with many narrow vessels. In the Fejej assemblage, VI ranges from 0.2 to 19.9 (mean = 4), with Trees 1 and 15 showing notably high values (>15). narrow vessels and values of the specific gravity are interpreted as indicating dry deciduous forests or woodlands (Wheeler *et al.* 2007). Characteristics of the Fejej fossil woods are consistent with trees able to withstand drought conditions in a seasonally-dry forest under a seasonal climate (Wheeler *et al.* 2007). It is remarkable that the Fejej wood assemblages differed in composition from other Miocene woods collected elsewhere in Ethiopia but not precisely dated (Beauchamp & Lemoigne 1972). In conclusion, during the Miocene, lowland forests were strongly distinct from moist forests that have been evidenced by fossil leaf studies in the highlands. A great diversity of forest types, varying from rainforest to deciduous woodlands, existed during the Miocene. Studies of the Fejej fossil woods clearly establish that climatic conditions in the Turkana region experienced a dry season, 16 Ma ago, a long time before the Pliocene, and the establishment of any glaciation in the north pole. Nowadays, moist forest with Guineo-Congolian affinity and deciduous woodlands with Sudanian affinity coexist in the south-eastern part of South Sudan and southwestern Ethiopia, showing the great floristic diversity of modern vegetation (Friis 1992; Friis & Vollensen 2005; Friis *et al.* 2011, 2022). Diversity of forest types may have existed throughout the Miocene, in different geographical regions and perhaps at various elevations.

For the Mio-Pliocene, we have information provided by fossil wood studies from the Middle Awash paleontological site in northern Ethiopia. *Albizia* cf. *gummifera*, among the Mimosoideae was found in the Adu-Asa Formation dated 5.8 Ma. (Jolly-Saad *et al.* 2012). Within a site now located in the sub-desertic *Acacia/Commiphora* steppe, under arid conditions, the occurrence of *Albizia*, known through many species from humid forests, indicates significantly more humid conditions at c. 1500 mm/yr. In the nearby Aramis paleontological site that yielded the hominin *Ardipithecus ramidus* White, Suwa & Asfaw, 1994, eleven fossil wood fragments dated from 4.8 to 4.3 Ma include *Anogeissus* cf. *A. leiocarpus* (Combretaceae), *Vitex* cf. *simplicifolia* (Verbenaceae), *Syzygium* cf. *guineense* (Myrtaceae), *Ficus* sp., (Moraceae), and *Rothmannia* cf. *whitfieldii* (Rubiaceae) (Jolly-Saad *et al.* 2010; Jolly-Saad & Bonnefille 2012). *Ficus* and *Rothmannia* have modern species in the riverine forest along the Awash River. But *Anogeissus*, *Vitex* and *Syzygium* have extant representatives in dense woodlands or forests of southwestern Ethiopia growing under wetter and cooler climatic conditions than those prevailing today in the studied area. It is likely that regional

climatic conditions were significantly more humid than today also in the North Ethiopian Rift, during the Early Pliocene, 4.8 to 4.3 Ma ago (Jolly-Saad & Bonnefille 2012).

Later on, during the middle Pliocene, in southern Ethiopia of the Lower Omo Valley, at Usno, upstream of the Shungura Formation, fossil woods document tropical forests and Combretaceae-rich woodlands existing 3.3 to 3.2 Ma ago (Jolly-Saad & Bonnefille 2023). The identified wood samples include *Caesalpinia* (Mimosoideae), *Terminalia* sp., *Combretum* cf. *C. molle* (Combretaceae), *Albizia* sp. (Mimosoideae), *Entada* sp. (Mimosoideae), *Erythrina* sp., cf. *abyssinica*, (Fabaceae). The occurrence of *Albizia* and Combretaceae offers a floristic continuity with the early Pliocene flora at Middle Awash.

From the Pleistocene, fossil woods have been studied from two archaeological sites located in East Turkana. Those from the archaeological site FwJj20 located in the Dura region of Koobi Fora and dated 1.95 Ma (Bamford 2011) will be discussed in a next chapter. Nearby, at the paleontological site FwJj14 E, alongside one tributary of the Ileret River, close to the Ileret village, fossil woods represent a time-averaged assemblage included between two tuffs, respectively dated 1.56 and 1.36 Ma in the Okote Member where hominin (hand and arm) and bovid footprints have been described. Taxonomically, the identified trees *Didelotia idae* (Caesalpinaceae), *Anogeissus* sp. (Combretaceae), *Drypetes* (Euphorbiaceae), *Premna* sp., (Lamiaceae), *Heritiera* sp., (Malvaceae), *Sapindoxylon* sp. (Sapindaceae) have not much in common with those recovered four hundred thousand years earlier. But, interestingly the anatomical descriptions show that these woods have large vessels with an averaged vulnerability index of 40, which implies a mesic megathermal environment with no water stress. The interpretation of a tall dense riverine forest with evergreen and semi deciduous trees of the Miombo (Zambezian region), and even mangroves margins has been proposed (Bamford 2017). Therefore important rainfall fluctuations are to be inferred in order to explain such strong changes in floristic tree diversity that have occurred between 1.95 to 1.5 Ma, during the Mid-Pleistocene.

INTERPRETATION OF THE SHUNGURA PLIO-PLEISTOCENE FOSSIL WOODS

The Shungura fossil woods from the Lower Omo Valley of South Ethiopia span a time range of c. two million years during the Plio-Pleistocene (3.6-1.7 Ma). Within this time interval, our study documents past vegetation of the Late Pliocene and Early Pleistocene (Table 6). Moreover, we provide very precise dates for all the wood samples that provide a unique knowledge of the successive temporal evolution in taxonomic composition of the flora inside the same area. We assume, as admitted for associated fossil bones, that fossil woods were fossilised in situ, along the bank of the ancestral Omo River or its lacustrine delta into Lake Turkana, rather than transported over long distance. This hypothesis is also accepted by paleobotanical studies from East Turkana (Bamford 2017). On the other hand, pollen data from the same sediments yield *Olea*, *Podocarpus* and *Juniperus*, all regular tree components of the montane forests, therefore attributed to water or wind transport from upstream highlands forests (Bonnefille 1976a). These Afromontane taxa have not

TABLE 6. — List of taxa and botanical families identified in the studied fossil wood of the Shungura Formation, Lower Omo Valley, presented according to their respective occurrence from –3.6 to –1.7 Ma.

Age (Ma)	Represented Families	Identified Fossil Wood
1.70	Ebenaceae, Salvadoraceae	<i>Salvadora persica</i> L. (Salvadoraceae), <i>Diospyros</i> sp. 1 (Ebenaceae)
1.92	Arecaceae, Asteraceae, Burseraceae, Celastraceae, Combretaceae, Ebenaceae, Fabaceae, Malvaceae, Moraceae, Sapotaceae, Sapindaceae, Fabaceae-Apocynaceae	<i>Borassus</i> sp. (Arecaceae), <i>Brachylaena</i> sp. 2 (Asteraceae), <i>Commiphora</i> sp. (Burseraceae), <i>Maytenus</i> sp. 1 (Celastraceae), <i>Combretum</i> sp. (Combretaceae), <i>Diospyros</i> sp. 2 (Ebenaceae), <i>Bussea</i> sp., <i>Peltophorum</i> sp. (Fabaceae), <i>Sterculia</i> sp. (Malvaceae), <i>Ficus</i> sp. 2 (Moraceae), <i>Ochna</i> sp. 1 (Ochnaceae), <i>Lecaniodiscus</i> sp., Sapindaceae gen. and sp. indet., Sapotaceae gen. and sp. indet. (Fabaceae/Apocynaceae)
2.01	Asteraceae, Combretaceae, Mimosoideae, Moraceae	<i>Albizia</i> sp. 1 (Fabaceae), <i>Brachylaena</i> sp. 1 (Asteraceae), <i>Ficus</i> sp. (Moraceae)
2.08-2.06	Fabaceae Caesalpinioidae	<i>Erythrophleum</i> sp. (Fabaceae, Caesalpinioidae)
2.13-2.12	Cannabaceae, Rubiaceae	<i>Celtis</i> cf. <i>integrifolia</i> (Cannabaceae), <i>Canthium</i> sp. 1 (Rubiaceae)
2.19	Cannabaceae	<i>Celtis</i> cf. <i>integrifolia</i> (Cannabaceae), <i>Canthium</i> sp. 2 (Rubiaceae)
2.30	Ochnaceae, Rubiaceae, Tiliaceae	<i>Grewia</i> sp. (Tiliaceae), <i>Ochna</i> sp. 1 (Ochnaceae), <i>Psychotria</i> sp. 1 (Rubiaceae), <i>Rothmannia</i> sp. (Rubiaceae)
2.53	Fabaceae	<i>Baphia</i> sp. (Fabaceae)
Limite Pliocene-Pleistocene		
2.57-2.56	Combretaceae, Arecaceae, Celastraceae, Fabaceae	<i>Albizia</i> sp. 1 (Fabaceae), <i>Maytenus</i> sp. 1 (Celastraceae), <i>Raphia</i> sp. (Arecaceae), Combretaceae/Fabaceae gen. and sp. indet. 2
2.62-2.61	Combretaceae, Arecaceae, Boraginaceae, Cannabaceae, Ebenaceae, Meliaceae	<i>Celtis</i> cf. <i>integrifolia</i> (Cannabaceae), <i>Borassus</i> sp. (Arecaceae), <i>Cordia</i> sp. 1, <i>Cordia</i> sp. 2 (Boraginaceae), <i>Diospyros</i> cf. <i>mespiliformis</i> (Ebenaceae), <i>Terminalia</i> cf. <i>macroptera</i> (Combretaceae), <i>Trichilia</i> sp. (Meliaceae)
2.96	Combretaceae, Celastraceae	<i>Maytenus</i> sp. 1 (Celastraceae), <i>Terminalia</i> sp. 2 (Combretaceae)
3.60-3.56	Meliaceae, Combretaceae, Fabaceae	<i>Entandrophragma</i> sp. 1, <i>E.</i> sp. 2, <i>E.</i> sp. 3 (Meliaceae), <i>Terminalia</i> sp. 1 (Combretaceae), Combretaceae/Fabaceae gen. and sp. indet. 1 (Combretaceae/Fabaceae)

been identified in the fossil wood data. Their absence in the fossil wood record may indicate that fossil woods are preferably sampling the local arboreal vegetation and riverine forest through overbank flooding rather than trees long distance transported by the river. Pollen and fossil wood provide complementary information for reconstructing different plant ecosystems at the regional scale around the studied site.

Our study describes several fossil wood taxa, identified from different wood samples, collected in different stratigraphic layers, sometimes in the same stratigraphic layer, either at the same site, such as at faunal locality Omo 127 (dated 3.6 Ma ago), or at different localities (P 726, 742, 769 etc) following the geographical extension of the same strata, such as for Unit G-29 dated at 1.92 Ma (Tables 1, 2). For a palaeobotanical study site concerning temperate regions characterized by homogenous forests, the occurrence of a single (or few) tree taxa would be very informative of the type of forest. But the interpretation of paleobotanical data in a tropical context showing a much greater diversity of several tree taxa is more complex. In this study, we are far from recording the whole tree diversity of past vegetation although we provide evidence of about 20 distinct taxa occurring together at 1.92 Ma (G-29) within an area of a few ten kilometres apart. This is crucial for documenting the high tree diversity encountered in tropical forests.

Within the time deposition of the Shungura Formation, informative wood assemblages of various trees are documented significantly for three distinct critical periods. The oldest one is dated 3.6 Ma (A-1-1), a second one dated 2.57 Ma (C-8), and the youngest one dated 1.92 Ma (G-29), each providing the most reliable reconstruction of past ecosystems. Between these periods, we note several changes in the tree taxa and floristic

composition at the path interval of the order of hundreds or a few thousand years (Tables 1; 2). Changes in tree diversity illustrate a long-term dynamic of tropical vegetation within the lowlands of Ethiopia. During next explorations of the studied geological deposits, many fossil woods remained not collected and could be available for additional detailed studies.

Regarding the general composition of described and identified taxa of the Plio-Pleistocene fossil wood from the Shungura Formation in the Lower Omo Valley (Ethiopia) (Table 6), 16 angiosperm families have been recognized: Anacardiaceae/Burseraceae, Arecaceae, Asteraceae, Burseraceae, Boraginaceae, Celastraceae, Combretaceae, Ebenaceae, Fabaceae, Meliaceae, Moraceae, Ochnaceae, Rubiaceae, Salvadoraceae, Tiliaceae and Sterculiaceae. This list clearly establishes the tropical character (mean temperature of the coldest month over 15°C) of the past vegetation. This is not surprising according to the geographical position of the site at 5° north latitude. The fossil wood taxa from lowlands in the Omo Valley are related to the extant flora of tropical East Africa (Friis 1992), with Fabaceae and Combretaceae being the two most important botanical families. They are recorded several times in different fossil wood assemblages and at various time periods. In tropical East Africa, these families are known through a great number of distinct tree genera and species. Among the fossil woods from the Shungura Formation we also found evidence of two palm trees, *Borassus* at 2.6 Ma and *Raphia* at 2.57 Ma (Table 1). This is in agreement with the low diversity of current African palms, although *Hyphaene* and *Eremospatha* would have been dominant at earlier periods on the Ethiopian plateau (Pan *et al.* 2006).

From the Pliocene Shungura deposits, a total of 11 genera have been identified (*Albizia*, *Borassus*, *Canthium*, *Celtis*,

Cordia, *Cynometra*, *Diospyros*, *Entandophragma*, *Maytenus*, *Terminalia* and *Trichilia*) including three species with affinities to *Terminalia macroptera*, *Entandophragma cylindricum* and *Celtis integrifolia*. Regarding the former occurrence of Guineo-Congolian taxa, *Platysepalum chevalieri* (Dechamps 1977), re-examination of the slides of this wood sample indicates that material should now be attributed to *Baphia* sp., a tree found in East Africa. Formerly identified *Cathormium altissimum* is now attributed to *Peltophorum*. We also consider erroneous the identification of *Monotes* (Dipterocarpaceae) (Dechamps 1977) and attribute the described specimen to *Diospyros* (Ebenaceae), a common genus with many species encountered in Ethiopia. Among our described taxa, only two of them *Entandophragma* (Meliaceae), and *Trichilia* (Meliaceae) are exclusive of the Pliocene. In the oldest strata dated 3.6 Ma, *Entandophragma* carries affinities with the Guineo-Congolian flora. It is registered through several collected samples, possibly indicating a monospecific tall forest. Such humid forest also included *Antrocaryon* (Anacardiaceae), a genus nowadays distributed in West African forests and recorded by the stones of its fruits in the Pliocene deposits of the Lower Omo Valley (Bonnefille & Letouzey 1976).

From the Pleistocene, 21 distinct tree genera (*Albizia*, *Baphia*, *Borassus*, *Brachylaena*, *Bussea*, *Canthium*, *Celtis*, *Combretum*, *Commiphora*, *Cordia*, *Diospyros*, *Erythrophleum*, *Ficus*, *Grewia*, *Lecaniodiscus*, *Maytenus*, *Ochna*, *Peltophorum*, *Rothmannia*, *Salvadora*, *Sterculia*) have been identified. Among them *Albizia*, *Borassus*, *Canthium*, *Celtis*, *Cordia*, *Diospyros* and *Maytenus*, are found in common within the Pliocene and the Pleistocene flora. Three samples have been identified to the species level (*Celtis integrifolia*, *Diospyros mespiliformis* and *Salvadora persica*) and four identifications were made at the family level (Table 2). Detailed observations of the former slides do not confirm the evidence of the temperate taxon, *Populus euphratica* (Dechamps 1977). We now attribute this sample to *Brachylaena* a genus having many species represented in the East African vegetation. *Steganotaenia* is now identified as *Salvadora persica*, a widespread tree in the region today.

Previous information about past vegetation and floristic composition of the arboreal components had been provided by pollen data from the same deposits, sometimes from the same dated layers containing fossil woods (Bonnefille 1976a, b; Bonnefille & Vincens 1985; Bonnefille & Bourel 2021). A comparison with palynological results led to the addition of 45 arboreal pollen taxa (trees and shrubs) to the 25 distinct wood taxa from the Plio-Pleistocene. Consequently, a total number of 70 tree taxa, recorded by both pollen and wood, documents the tropical diversity of the past vegetation during c. two million years in the region. Five genera *Celtis*, *Combretum*, *Commiphora*, *Cordia* and *Salvadora persica* found in common in the fossil wood and pollen records still have representative species in the extant vegetation. Their occurrence establishes the modern character of the Plio-Pleistocene fossil flora.

Both in deposits of the Lower Omo Valley and at many other paleontological sites investigated in Ethiopia there

are many unstudied preserved or not collected fossil wood specimens. There is hope to undertake possible palaeobotanical studies in order to complete our knowledge of past vegetation diversity and to achieve better interpretation of ecological conditions of past ecosystems in which evolved abundant fauna and early hominin ancestors during the Plio-Pleistocene.

EVIDENCE FOR HUMID FORESTS DURING THE MID-PLIOCENE

In the oldest layer (3.6–3.5 Ma), the joint occurrence of *Entandophragma* (Meliaceae), *Terminalia* (Combretaceae) and Fabaceae (Table 1) is completed by that of *Antrocaryon micraster* (Anacardiaceae), found as fossil stones, at the same site in the A-1-1 strata (Bonnefille & Letouzey 1976), now redated at 3.6 Ma (Kidane *et al.* 2014). *Entandophragma* (Meliaceae) is a genus with common trees from the tropical humid forest in the Republic of the Congo and Cameroun where also *Antrocaryon* does exist. *Entandophragma* occurs today in the Imatong Mountains from Sudan (Friis & Vollesen 2005) and in East Africa in lowlands and mid-altitude rainforest, moist semi-deciduous forests under precipitation of 1800 mm/yr or in gallery forest. *Entandophragma angolense* prefers well-drained localities with good holding capacity (Tchinda 2008). Therefore, the assemblage of trees in Member A indicates heavily forested humid past vegetation quite different in composition from the extant humid forests of southern Ethiopia (Friis *et al.* 2011) or from the present riverine forest where *Entandophragma* is absent (Carr 1998). The wood assemblage described in Member A would resemble the semi-deciduous forest described in South Sudan (Friis & Vollensen 2005). The climatic conditions of these forests are poorly documented; the annual rainfall is between 1500 and 1600 mm/yr, with a seasonal rainfall (Jackson 1956). Indeed, fossil wood samples from this level are mineralized with a high degree of silica impregnation attesting high humidity during their fossilisation. Humid deciduous forests and woodlands have been documented at Usno, a few hundred thousand years later on from 3.3 to 3.2 Ma ago (Jolly-Saad & Bonnefille 2023). They stand for a 1000–1500 mm annual rainfall such as registered today in the eastern part of the Nile Valley and the lower slopes of the western Ethiopian escarpment (Friis 1992; Friis *et al.* 2011). Wood records from Shungura/Omo and Usno imply that humid climatic conditions were widespread over the Lower Omo valley during the period between 3.6 to 3.2 Ma. Such a favourable regional climate maintaining humid forests cannot be explained only through the occurrence of groundwater forest and connectivity between freshwater and lake systems (Boës *et al.* 2024). The forest's presence indicates a wetter regional climate with higher precipitation and shorter dry season during the Mid-Pliocene. Several changes registered by phytoliths, plant wax and pedogenic carbonates in the nearby East Turkana basin within the 3.6 to 3.4 Ma period show that significant fluctuations at a shorter time resolution could occur in past vegetation during this time interval (Villaseñor *et al.* 2023).

FLUCTUATING RIVERINE FOREST

Most of the tree taxa identified in fossil wood from the Plio-Pleistocene deposits of the Lower Omo Valley (Tables 1; 2) have forest species recorded in riparian habitats, notably riverine forests. A few exist in the riverine forest observed today along the Omo River (Carr 1998). However, *Acacia*, Capparidaceae, *Ziziphus*, *Balanites*, all common trees from the sub-desertic steppe, widespread today in the lowlands under arid climatic conditions (Bonnefille 1971) and also components of the riverine forest, are not found in the fossil wood record. It is likely that Shungura fossil woods are sampling a past vegetation existing during climatic conditions significantly more humid than now. During some periods of higher and more regular rainfall pattern in the whole region, deciduous forest or woodlands may have expanded further, outside the proximity of fresh water bodies. We can postulate that a diversified well-developed tall riverine forest persisted along the Omo River, throughout the 2 million years of the studied time interval (3.6 to 1.7 Ma). However, such riverine forest varied in its floristic composition, fluctuated in its extension or disappeared, notably at 2.4 Ma while no fossil woods were found, and at 1.7 Ma when impoverished tree riparian vegetation was limited to the single occurrence of *Salvadora persica* (Salvadoraceae).

Our studied fossil woods have been collected in a region, located 5° North latitude, nowadays under an arid climate of 350 mm/yr mean annual rainfall, distributed between two irregular rainy seasons following migration of the Intertropical Convergence Zone. Growth rings have not been observed in the fossil wood structures, but this does not indicate uniform climate. Most tropical trees growing in areas with seasonal rainfall exhibit indistinct rings.

Many of the identified tree taxa are semi-deciduous, losing leaves during the dry season, suggesting that rainfall would have always been seasonal during the Plio-Pleistocene, in continuity with seasonality in climate evidenced in the region nearby since the Mid-Miocene (Wheeler *et al.* 2007). Plants provide clear indication of ecological and climatic conditions when identified at the species level. However, such precision is rarely available in identified fossil wood because incomplete preservation of anatomical structures or mainly lack of appropriate knowledge of modern trees from East Africa and Ethiopia. Attributing fossil wood taxa to extant botanical ecosystems (Friis *et al.* 2011) is challenging to achieve.

COMPARISON WITH OTHER

PALEOENVIRONMENT INDICATORS

Fortunately, the fossil wood study from the Shungura Formation was part of multidisciplinary studies involving other paleoenvironmental indicators (or proxies), such as pollen, fauna and isotopes. A comparison of all these markers provide a unique opportunity to visualize habitat and landscape at selected time slices. However, during such comparison one should remember that whereas fossil wood samples have been collected in single stratigraphic units, such as for pollen and micromammals, this is not the case for surface collected faunal assemblages that often concerned mixed remains found within several stratigraphic units, therefore integrating a few hundred

thousand years, a time range during which we know that climatic variations could have modified the past vegetation.

Pollen data provide information about herbaceous plants associated to the trees and help reconstructing past ecosystems at the regional scale. In the pollen record, despite the fact that grasses may be overrepresented because their high pollen productivity, the abundance of grass pollen definitely excludes dense tropical rainforest. Palynological studies already highlighted the occurrence of three main plant ecosystems (riverine forest, open woodland, montane forest) in the large basin of the Omo Valley (Bonnefille 1976a; Bonnefille 1995). Grass abundance fits well with the abundance of herbivore remains and species diversity within this mammalian bovid fauna (Bobe & Eck 2001). When associated with aquatic freshwater plants, such as sedges and *Typha* (cattail), grasses indicate humid herbaceous cover in which the abundance of reduncine bovids (waterbuck) characterizes the fossil fauna. This is the case during the Pliocene (Bobe 2011). At 2.97 Ma, within Unit B-10, the fossil wood *Terminalia* (Table 1) is associated with a diverse pollen assemblage including *Celtis* trees and *Acalypha* shrubs (Bonnefille & Vincens 1985). In the same layer, among more than a hundred specimens of micromammals, 38% of them come from a lowland forest block (Wesselman 1984). The pollen data also contain a noticeable proportion of trees such as *Cordia*, *Commiphora*, *Boscia* and *Salvadora*. These taxa, known to disperse their pollen locally, attest to the local presence of drier woodland. On the other hand, associated *Podocarpus*, *Juniperus*, *Olea* and *Dodonaea viscosa*, all components of montane forests, indicate that an Afromontane conifer forest in which *Syzygium* provides a humid indicator occupied areas at a few kilometres distance. Fossil wood, micromammal remains and fossil pollen from the same layer (at the same spot) provide similar conclusions leading to infer c. 1000-1200 mm/yr precipitation over the Lower Omo Valley, 2.97 Ma ago. Mammalian fossil fauna of Members A and B (3.6 to 2.97 Ma), characterized by many reduncine bovids (Bobe & Eck 2001), preponderance of arboreal and frugivorous taxa (Reed 1997), abundance of primates, cercopithecine and colobine monkeys (Eck 1976), agree with humid conditions during the late Pliocene confirmed by analysis of well-developed palaeosol resulting from high illuviation (Haesaerts *et al.* 1983).

The upper layer of member B (2.95 Ma) registers the first appearance of *Maytenus* (Celastraceae), close to *M. senegalensis*, a widespread species from West Africa to Ethiopia in open forests, woodland and evergreen scrub (Friis 1992) and present today in the Omo riverine forest (Carr 1998). The occurrence of *M. senegalensis* persists until member C where it is associated to Combretaceae also found as pollen. *Canthium* fossil wood found in Unit C-9 would be the first indicator of an Afromontane component (Friis 1992), whereas the pollen assemblage of the same age shows five markers (*Macaranga*, *Buddleia*, *Myrsine africana*, *Hagenia abyssinica* and *Hypericum*) of the upper belt of the Afromontane forests of Ethiopian highlands (Friis 1992). These taxa would mark the impact of a significant cooling of regional climatic conditions in a good timing correspondence with the increase of the Northern Hemisphere Glaciation (Haug *et al.* 2005).

At the limit between the Pliocene and the Pleistocene at 2.57 Ma, a significant increase (60%) in grass pollen (Bonnefille 1976a, b; Bonnefille & Vincens 1985) most probably indicating an expansion of grasslands in the lowlands region was accompanied by dietary changes shown by isotopic studies performed on teeth of the bovid *Tragelaphus nakuae* (Kudu) and *Kolpochoerus limnetes* (Bibi *et al.* 2013). Taxonomic turnover in the whole fossil fauna (Vrba 1995) reflects increased aridity occurring in the lowlands synchronously to cooling in highlands. Onset of more arid conditions (Bobe & Behrensmeyer 2004; Bobe 2006; Bobe 2011) coincides with the first appearance datum of the hominid *Paranthropus aethiopicus* in the Shungura Formation (Arambourg & Coppens 1968).

Just above Tuff D dated at 2.53 Ma, two fossil woods from Unit D-1 correspond to Combretaceae and *Baphia* (Table 2). Among the Fabaceae (Faboideae), *Baphia* is a small tree of the dry semi-evergreen transitional rain forest and riverine forest common in southwestern Ethiopia and nearby South Sudan, most probably endemic, but having some affinities with Guineo-Congolian vegetation (Friis 1992). Changes in vegetation cover are involved to explain new isotopic analysis (Negash *et al.* 2015) changes in dietary habits of bovids (Blondel *et al.* 2018; 2022), and faunal analysis (Reed 1997).

There is no fossil wood from Member E. The pollen assemblage E-4 (2.4 Ma), is dominated by 72% grass pollen associated with 15% Amaranthaceae (mainly herbs and shrubs from hot arid countries) and the occurrence of *Commiphora* and *Acacia*, both common trees of the arid steppe, as well as *Tribulus* a widespread herb of dry plains (Bonnefille 1972; 1976; Bonnefille & Vincens 1985; Fig. 5). These pollen taxa reveal a striking change towards more aridity in the lowlands, also attested by the occurrence of *Lepus* (hares) at the hominin skull site in E-3 (Wesselman 1984). Two rich assemblages of micromammals from Tuff F, at locality Omo 33, and from Unit F-1 (locality 28), corroborate the large development of arid scrub and dry savanna woodlands (Wesselman 1984). At the same time an increase in the horn cores of impala (*Aepyceros*) (Gentry 1976), accompanies an increase in the grass-eating suid *Kolpochoerus* (Cooke 2007), and a majority of taxa indicating dry open environment at locality Omo 33 (Alemseged 1996).

Unit F-3-2 (2.31 Ma) yielded *Grewia*, *Ochna*, *Rothmannia* wood taxa distinct from those recorded in older strata. Many species of *Grewia* are unique in the *Acacia-Commiphora* woodland and bushland covering large areas of dry lowlands, including the Rift Valley (Friis *et al.* 2011). *Grewia trichocarpa* occurs together with *Baphia* in the riverine forest of the Baro River near Gambela, in southwestern Ethiopia (Friis 1992). Among the Ochnaceae, a few species of *Ochna* have an Afromontane distribution while more species occur in the currently drier zone. *Ochna holstii* is a large tree dominant in the Imatong Range of South Sudan and is also found in southwestern Ethiopia (Friis 1992). *Rothmannia* (Rubiaceae), a small tree from scrub forest or semi-evergreen bushland and thicket occurs in region under 500 mm/yr rainfall (Friis 1992). *Rothmannia urcelliformis* is a species of the Afromontane forest that persists in riverine forest (Friis 1992). The association

of *Rothmannia*, *Grewia*, *Ochna* may come from a less dense type of riparian vegetation such as encountered today in arid countries. At 2.4–2.3 Ma, climatic conditions were drier in the lowlands and perhaps cooler. A major faunal change correlates in time with the appearance of *Australopithecus boisei* at 2.3 Ma (Alemseged 2003).

An abundant and diversified pollen assemblage was extracted from a thin layer of clay interstratified within the 2.27 Ma dated Tuff G. Its interpretation confirms the existence of two distinct ecosystems. First a dry savannah/woodland including *Commiphora*, *Acacia*, *Salvadora*, various Cappariaceae (*Boscia*, *Capparis*), ligneous herbs of *Suaeda*, *Aerva*, *Digera* (Amaranthaceae) and *Tribulus* agree with “dry *Acacia* scrub and woodlands” habitats inferred from the layer G-3 micromammals (Wesselman 1984). Grass pollen grains are abundant (over 50%) and fit with many Bovidae in the fossil macrofauna (Alemseged 2023). The second ecosystem is a riverine forest shown by pollen of riparian trees such as *Celtis* (Cannabaceae) and *Cissampelos* (Menispermaceae) associated with *Acalypha* (Euphorbiaceae) and *Ricinus* (Euphorbiaceae) shrubs, and *Achyranthes* (Amaranthaceae) herbs frequent under the shade of tree cover such as along the banks of the Omo River today. Fossil woods from Fabaceae and *Celtis integrifolia* confirm the occurrence of a riverine forest.

From Middle Member G (G-13 to 19), 2.07 to 2.02 Ma, the fossil wood taxa include *Erythrophleum* (Fabaceae: Caesalpinoideae), a component of the Imatong forest (Friis & Vollensen 1998) also found in the coastal evergreen forest and bushland at the border between Kenya and Somalia. In the latter, *Erythrophleum* is associated with *Ficus* (Moraceae) in regions receiving under 700 mm/yr of precipitation (Friis 1992). The *Albizia* fossil wood of unit G-18 (*Albizia* sp. 2 at 2.02 Ma) is different from the Pliocene wood samples found in C-8 (*Albizia* sp. 1, at 2.57 Ma) and distinct of that recorded at 4.4 Ma at Middle Awash (Jolly-Saad *et al.* 2012). This is not surprising since many species of *Albizia* are forest trees in Ethiopia. Within the fossil wood record, *Albizia* is associated with *Brachylaena* (Asteraceae) and *Ficus*. *Brachylaena* is a small tree not known in Ethiopia, but recorded in Kenya where it occurs in thicker “forêt broussailleuse” or transitional Afromontane forest under 800 mm/yr precipitation (White & Bamps 1986). Among the 22 species included in *Ficus* sp. most are known as forest components of northeastern Africa and some occurring in riverine forest, such as in the Lower Omo today (Carr 1998). The fossil wood material supports the likelihood of a dense and humid riverine forest with tall trees of *Celtis*, *Albizia*, *Ficus* re-established in the Lower Omo Valley, 2 million years ago.

A total of 22 wood samples from the unit G-29 have been described providing the richest fossil wood assemblage dated 1.92 Ma. This association includes 14 taxa identified at the genus level, and 4 at family level distributed within 7 localities geographically dispersed but corresponding to the same stratigraphic unit.

At the geological site P 743 (“Château”) *Sterculia*, *Ochna*, Sapotaceae, *Combretum*, *Peltophorum*, Sapindaceae have been recognized. From site P 742 at a few hundred meters distance

from P743 come *Lecaniodiscus*, *Borassus*, *Bussea*. *Sterculia* (Sterculiaceae) and *Lecaniodiscus* (Sapindaceae) of lowland and riverine forest are related to the Sudano-Zambezian flora, a characteristic confirmed by the occurrence of *Bussea*, a Caesalpiniaceae not present in Ethiopia today, but found in deciduous thicket of the dry region in the Zambezian zone (White 1983). *Ochna* (Ochnaceae) is known from six species in Ethiopia, two of which are associated with forest vegetation, one endemic to the highlands under high rainfall and the other restricted to the transition zone between Afromontane region and the Somali-Masai region, under rainfall range about 700 mm/yr (Friis 1992). One species is associated with dry Afromontane forest, two species with *Combretum-Terminalia* woodlands on the western slopes of the highlands, and one with *Acacia-Commiphora* woodland and bushland (Vollensen 1995a). Together *Canthium* (Rubiaceae) and *Ochna* (Ochnaceae) may provide a link with the Afromontane forest.

From locality P 726, 4 kilometres to the North west, *Maytenus* and *Commiphora*, *Brachylaena* are found associated with *Diospyros* (Ebenaceae). All these trees attest to a rich and diversified lowland forest with tall trees and shrubs. *Diospyros mespiliformis* are shrubs or small trees found in riverine forest while *Commiphora* occurs in deciduous woodlands and bushlands and a wide range of habitats under variable precipitation of 500 to 1000 mm/yr (Friis *et al.* 2011). *Ficus* is from locality P 769 and *Canthium* (Rubiaceae) from locality 392 are found 13 kilometres to the North.

To summarize, the rich assemblage of various trees from G-29 can be interpreted as a mosaic of diversified forests and woodlands ecosystems. At that time (1.92 Ma), forests may have occupied new large spaces left over after the regression of the Lorenyang Lake to the south (Feibel *et al.* 1991). Such forest seems characterized by a mixed association of Afromontane and Sudano-Zambezian taxa which characterizes habitats marked by an increased length in the dry season. Today, in the Sudano-Zambezian region, total amount of rainfall is significantly higher than in the arid Turkana Basin. In conclusion, the well-documented wood assemblage dated 1.92 Ma indicates a marked climatic change towards a significant increase in length of the dry season, while total annual precipitation remained significant at 700/1000 mm per year. Cooler temperature favoured the descent of a few Afromontane trees becoming closer to the lowlands while C_4 grass vegetation prevailed in the flood plains outside the edge of the delta of the Omo River (Levin *et al.* 2011).

Fossil wood assemblage from Unit G-29 is dated 1.92 Ma, a few thousand years younger in time than silicified wood described from an archaeological site (FwJ20), located in the Koobi Fora area of the northeastern side of the Turkana Lake and dated 1.95 Ma (Bamford 2011). Combretaceae Apocynaceae and *Diospyros* (Ebenaceae), are represented in the two distant fossil wood records. But *Funtumia* (Apocynaceae), *Schotia* (Fabaceae/Detarioideae), *Drypetes* (Putranjivaceae), *Khaya* (Meliaceae), *Acacia* (Fabaceae/mimosoid clade) and *Ziziphus* (Rhamnaceae) identified at East Turkana (Bamford 2011) are not found in our record of the Lower Omo Valley. The high diversity of tropical woodlands and forests may explain such

disparities. However, *Schotia*, *Funtumia*, and *Khaya* are not mentioned in the Ethiopian vegetation today (Friis 1992). Some species of these genera characterize the Zambezian or Sudanian regions and occur in evergreen, dry seasonal forests and woodlands. Disparities between wood flora from the Lower Omo Valley and that from Ileret (East Turkana), c. 100 km to the South East, could be explained by local variations in climatic conditions. The fluvial system of the paleo-Omo River and Lorenyang palaeo-Lake are considerably larger than the Ileret river close to the archaeological site at East Turkana. It is also possible that the time interval of the a few ten thousand years between the two records explains such floristic disparity that could be attributed to precipitation changes related to climatic fluctuations, such as the twenty thousand years monsoon cycle that prevailed in tropical regions.

CONCLUSION

The detailed description of anatomical structures of 65 fossil wood samples presented in this paper provides critical new data upon the floristic composition of the tree cover in the lowlands of Ethiopia from 3.6 to 1.7 Ma ago. Four of them are identified at the species level, 26 as genera and 17 as botanical families. Combretaceae and Fabaceae are the dominant botanical families throughout the time range of 2 million years. The studied fossil woods are precisely dated. They document tree components of the terrestrial vegetation along a time range much longer than any previous publications. Such long record for the same region points to several and continuous vegetation changes. The paleogeographical context remaining the same under fluvial or lacustrine geological background, such changes are not explained by any differential deposition mode. They attest to climatic fluctuations also indicated by other contemporaneous indicators such as pollen, isotopes and composition of mammalian fauna.

Many fossil wood tree taxa indicate a riverine habitat that fits with a permanent river system. The past riverine forest was most often more diverse than the extant one in the studied area. Its floristic composition changes through time, some at intervals of the order of hundred or a few thousand years. The most significant characteristics of the regional past tree cover composition are the occurrence of components of 1). A tropical rainforest between 3.6 to 3.2 Ma, 2) An Afromontane forest at 2.6 Ma, 3) Some deciduous Sudano-Zambezian woodland at 1.9 Ma. These facts attest to an increased aridity through time, a reduction of mean annual rainfall followed by an increased seasonality in the precipitation. The attenuated signal of a temperature cooling that modified composition of the highlands forests appears in good synchronisation with past global climatic changes during the Plio-Pleistocene (DeMenocal 1995, 2014; Bonnefille 2010).

This region was the habitat of many different animals and hominins. Diverse and fluctuating plant ecosystems offered many opportunities for them to survive despite significant vegetation changes far from any old concept of permanent stability of a tropical savanna vegetation. Changes in rainfall

(amount and seasonal distribution) are likely to have had the greatest impact in plant geographical distribution because low elevation, changes in temperature were expectedly too small for plant response (Ritchie 2008). Forest under humid conditions (1500 mm/yr rainfall) and a short dry season occurred at 3.6 Ma ago, followed by the occurrence of mixed deciduous forest or woodland with more Sudano-Zambezian affinities under *c.* 700 mm/yr rainfall and a longer dry season (5 to 7 months ?) at 1.92 Ma. Precipitation values inferred from wood species are in astonishing agreement with an aridity index calculated from isotopic measurements on tooth enamel (Blumenthal *et al.* 2017). However, the driest conditions shown in our study at 2.3 Ma were less arid than conditions prevailing in the region today (300 mm/yr rainfall).

In the Lower Omo Valley, during the Late Pliocene and Early Pleistocene, various types of hominins could have occupied different habitats in the lowlands. At about 2.9 Ma two clades existed, a gracile hominin (Suwa *et al.* 1996) and, *Paranthropus aethiopicus* Arambourg & Coppens, 1968. A transitional hominin between *Australopithecus* and early *Homo* existed 2.5 Ma ago (Boisserie *et al.* 2008). *Paranthropus boisei* (Leakey, 1959) occurred at 2.0 Ma and their occurrences increased from 2.27 to 1.9 Ma when that of the genus *Homo* became the most frequent. In the same landscape, under changing climatic conditions following the vegetation dynamic, these hominins may have shifted from dense forests to more open woodlands and wooded grasslands. Distinct possible habitats (niches), permanent occurrence of tall trees with large leaves and canopy cover for building nests and abundant attractive food resources may have always been available to them.

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