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Woods from the Miocene Bakate Formation, Ethiopia Anatomical characteristics, estimates of original specific gravity and ecological inferences

E.A. Wheeler [a,*], M.C. Wiemann [b], J.G. Fleagle [c]

[a] Department of Wood and Paper Science, North Carolina State University, Raleigh, N.C. 27605-8005, USA
[b] Center for Wood Anatomy Research, USDA Forest Products Laboratory, Madison, WI 53726, USA
[c] Department of Anatomical Sciences, Health Sciences Center, Stony Brook University, Stony Brook, NY 11794-8081, USA

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Abstract

An assemblage of permineralized woods from the Miocene Bakate Formation, Fejej Plain, Ethiopia, is described. This assemblage of twelve wood types differs from other Miocene wood assemblages known from Ethiopia. Cell wall percentages of the woods were determined to estimate the original specific gravities of the woods in order to better understand the Miocene vegetation and environment of Fejej. The relatively high specific gravities (0.63 to 0.82) and numerous and narrow vessels of these Miocene woods are characteristics of dry deciduous forests or woodlands. The affinities of some of the Fejej woods could not be determined because critical diagnostic features could not be determined, but others have characteristics seen in the Sapotaceae, Leguminosae, Combretaceae, and Bignoniaceae (a ring porous wood). None of the families represented by a fruit and seed assemblage from Fejej are represented in the wood assemblage.

Keywords: fossil wood; Ethiopia; specific gravity; Miocene; Bakate Formation

1. Introduction

Exposures of the Miocene Bakate Formation occur in the Fejej Plain of southern Ethiopia, near the Kenyan border north of Lake Turkana. The Bakate Formation has yielded significant mammalian remains (e.g., Tiffney et al., 1994; Richmond et al., 1998; Fleagle et al., 2000), as well as seven types of fruits and seeds (Tiffney et al., 1994). There also are extensive deposits of fossil woods (Fig. 1). This paper describes and discusses one collection of those woods, from a site referred to in this paper as Locality FJ-18. Selected characteristics of this Fejej wood assemblage have been used to infer MAT at 26.0 °C, an estimate that is within 1 °C of the present MAT (Wiemann et al., 1999). One objective of this paper is to document the wood types used for those inferences, and to discuss their likely affinities to extant plants. Other objectives of this paper are to address the questions (1) are the affinities of the woods similar to those of the fruits and seeds recovered from the Bakate Formation? (2) is the Fejej wood assemblage similar to other fossil wood assemblages from Ethiopia? (3) what are the specific gravities of the

* Corresponding author.
E-mail addresses: eisabeth_wheeler@ncsu.edu (E.A. Wheeler), mwiemann@fs.fed.us (M.C. Wiemann), john.fleagle@stonybrook.edu (J.G. Fleagle).

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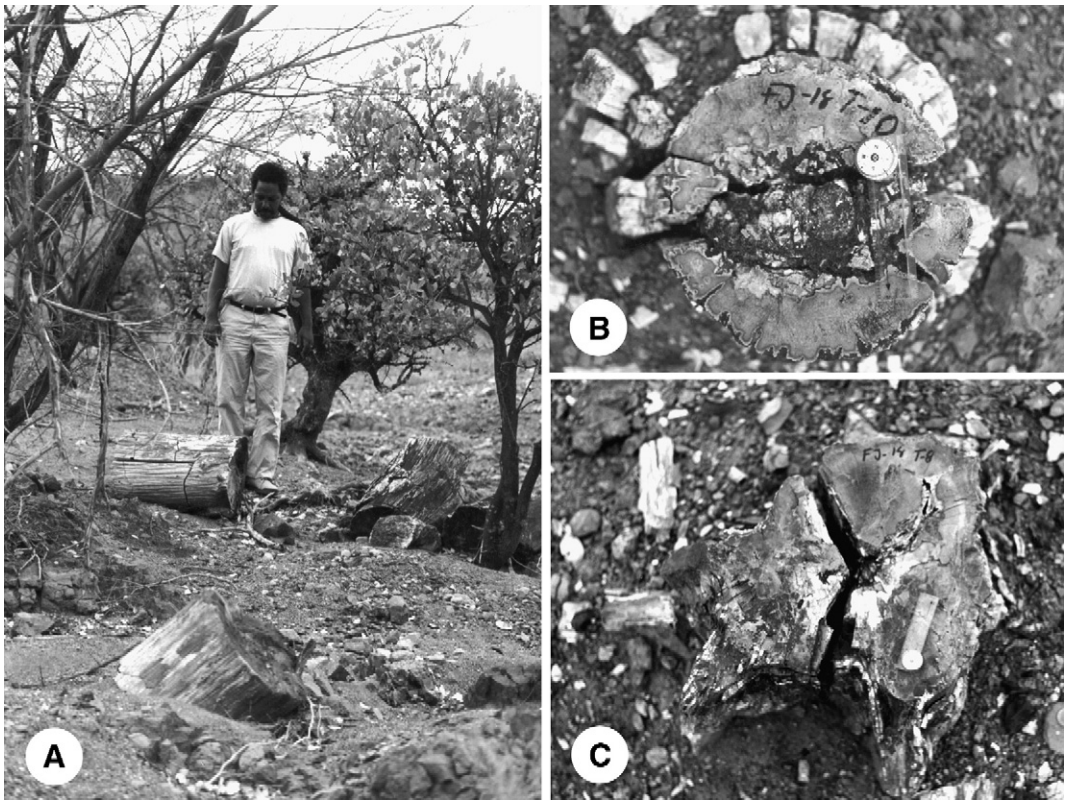

Fig. 1. Locality FJ-18, Fejej, Ethiopia. A. Permineralized logs and stumps exposed on the surface, small trees typical of modern vegetation. B. Tree 10. C. Tree 8.

Fejej woods, and what are the paleoenvironmental implications of those data? Well-dated paleofloras from tropical Africa are rare, so that paleoclimate and paleovegetation records for the region are sparse. The Fejej wood assemblage furthers our understanding of the Miocene of Tropical Africa, a region that is globally important with respect to climate and human evolution. Dechamps and others have made paleoenvironmental interpretations based on fossil woods' affinities with extant species, and the growing conditions of those extant species (e.g., Dechamps, 1983; Dechamps and Maes, 1985). However, the affinities of the majority of the Fejej woods cannot be established with certainty, so paleoenvironmental inferences based on the present-day environments of the nearest living species are not possible.

Different vegetation types have different averages and ranges of wood specific gravities (SG) (Chudnoff, 1976; Wiemann and Williamson, 2002). Humid tropical forests typically have wide SG ranges. It is possible there is a bias in the fossil record towards overrepresentation of higher SG woods as they typically are slower to decay than low SG woods and so have a longer opportunity for fossilization. Nonetheless, information about the SGs of fossil trees has potential for providing additional information about ancient forest types and tree growth. In this paper, we present data on the estimated specific gravities of the Fejej woods, and the implications of those data.

2. Materials and methods

2.1. Geographic and geologic occurrence

The fossil woods described in this paper come from the Miocene Bakate Formation of southernmost Ethiopia located on the Fejej Plain between the upper end of Lake Turkana to the west and Chew Bahir (Lake Stephanie) to the East. (Davidson, 1983). The fossil wood site is adjacent to and similar in age to a rich locality, FJ-18 that has yielded abundant fossil mammals and plant parts (Tiffney et al., 1994). Radiometric dating of capping basalts provides a minimum age of 16.18+ 0.05 MYA for Locality FJ-18 (see Richmond et al., 1998

for a description of the geology and dating of this locality). The fossil mammals from the FJ-18 Locality as well the radiometric dates are very similar to those of the Buluk locality from northernmost Kenya (Leakey and Walker, 1985; Watkins, 1989; Fleagle et al., 2000) and it seems likely that the two are roughly contemporaneous.

2.2. Collections, sample characteristics, and preparation

All samples were collected by J.G. Fleagle in 1992. All are permineralized (Fig. 1); in many samples much of the original cell wall has been lost, so that they represent only replicates of the cell wall structure, and preservation is such that fine anatomical detail is not always visible. One wood shows evidence of insect damage. Ground thin sections were prepared. Thick sections (wafers) of cross, radial, and tangential surfaces were cut with a diamond lapidary saw. These wafers were sent to a professional thin-sectioner, who smoothed saw marks from the wafers, affixed them to glass slides, and ground them until they were thin enough for viewing anatomical details with a light microscope. Cover slips were mounted using Canada Balsam. Wood descriptions are based on these slides.

2.3. Comments about identification

Evidence to date about Miocene floras indicates that plants of this age are similar to extant genera (and sometimes highly similar to extant species or species groups). It is highly probable that the woods described in this paper have affinities with extant genera, and certainly with extant families, but because of uncertainty about important diagnostic features, e.g. vestured pits, most are not identified. Woods of some genera of the Combretaceae, Leguminosae, Sapindaceae, Bignoniaceae, and Simarubaceae share similar patterns. The Combretaceae and Leguminosae have vestured pits, but the other aforementioned families do not. However, vestured pitting is a feature that can be difficult to verify in extant wood, especially when pits are minute to small, and cannot be determined with certainty in fossil woods unless they are extremely well preserved. The Fejej woods were not well enough preserved to determine whether vestured pits were present or not.

The collections of African woods at the Musée Royal de l'Afrique Centrale, Tervuren, Belgium are excellent, and there are atlases of African woods (e.g., Normand and Paquis, 1976), yet many species of African woods have never been sectioned and studied. Descriptions of some species are based on but one or two samples. Thus, the range of variability within genera and species of African woods is not well known, except for some commercially important woods. It is likely that the affinities of the Fejej woods could be better determined with additional comparative work and preparation of additional sections of extant woods, but for now the purpose of this paper is to (1) describe the woods, (2) indicate which families and genera they appear similar to, and (3) profile the woods in terms of the characteristics that are considered of ecological significance based on previous work on extant plants.

2.4. Sample descriptions and identification

The terminology for the wood descriptions generally conforms to the format of the IAWA List of Features Suitable for Hardwood Identification (IAWA Committee, 1989). Mean values for tangential vessel diameter and ray height are followed by the standard deviation in parentheses.

Affinities of the fossil woods initially were determined by consulting descriptions in "Anatomy of the Dicotyledons" (Metcalfe and Chalk, 1950), and searches of the computerized OPCN (Oxford/Princes Risborough/CTFT/NCSU) wood database, which contains more than 5000, coded descriptions of extant dicotyledonous wood (Wheeler et al., 1986; LaPasha and Wheeler, 1987; InsideWood, 2004). Subsequently, the fossils were compared with slides of extant woods from the collections of the Musée Royal de l'Afrique Centrale (Tervuren, Belgium), National Herbarium of the Netherlands (Leiden University branch), David A. Kribs collection at NCSU, and to descriptions in standard references (listed in Gregory, 1980, 1994). The Fejej woods were compared to other fossil woods of known provenance using a database prepared for a survey of changes in dicotyledonous wood structure through time (Wheeler and Baas, 1991).

2.5. Estimates of specific gravity

The specific gravity of cell wall substance (SG_{cw}) is considered to be similar in unrelated woods (conifers and dicotyledons). The SG_{cw} of swollen cell wall substance is close to 1.05 (computed from data in Stamm, 1964; C. A. Hart, N.C. State University, personal communication). We are assuming that the cell walls in silicified woods are preserved in a swollen state because what is known of the silicification process indicates that impregnating silica must be water-borne and infiltrate cell walls to produce well-preserved woods (e.g., Leo and Barghoorn, 1976). With an estimate of the

Table 1
Characteristics of the Fejej Woods. MEAN TD = mean tangential diameter of vessels (μm); sd = standard deviation; MIN = minimum; MAX = maximum; VPMM = vessels per square mm; VUL = mean tangential diameter / mean vessels per square mm; %Sol = percentage of solitary vessels; SGg = specific gravity, based on green volume; PAR = axial parenchyma distribution, alif. = aliform, confl. = confluent, vc = vasicentric; RW = ray width in cell number; RPMM = rays per linear mm; MRH = mean ray height (standard deviation) in μm; MRH.c = mean ray height in cell number

Sample	MEAN TD	sd	MIN TD	MAX TD	VPMM MIN	AVG	MAX	VUL	% Sol.	SGg	PAR	RW	RPMM	MRH	MRH.c
Group I: Narrow vessels, radial multiples, 1s rays, banded parenchyma															
T17	44	5	36	53	64	98	150	0.4	56	0.71	banded, straight	1	15–17	203 (43)	10.7 (2.6)
Group II: Narrow vessels, radial multiples, narrow rays, paratracheal parenchyma															
T5	45	4.2	35	55	113	201	360	0.2	40	0.72	paratracheal	1(2)	9–11–14	238 (45)	13.6 (3.8)
T10	48	6	33	57	88	105	142	0.5	53	0.72	paratracheal	1(2)	10–11–13	243 (28)	14.6 (2.8)
T11	62	8	42	73	35	58	91	1.5	67	0.79	paratracheal	1	10–11–13	227 (52)	14.4 (4.4)
Group III: Aliform-confluent parenchyma															
T4 (AW)	72	13	55	98	11	15	18	4.8	64	0.76	alif.–confl.	(1,2) 3	6–7–10	252(80)	16(5)
T12	77	11	50	93	21	32	59	2.4	41	0.79	alif.–confl.	1–2	11–14–17	119 (45)	14.2 (5.9)
T14	87	16	51	121	11	14	18	6	45	0.75	alif–confl.	1–3	5–7	333 (147)	22 (9.7)
Group IV Solitary and radial multiples, scanty paratracheal to vasicentric parenchyma															
T6	74	10	55	104	17	26	35	2.9	55	0.75	vc.– barely alif	1	7–10–14	143 (34)	7.7 (2.2)
T8	77	12	56	100	22	28	37	2.8	32	0.82	vc – lozenge alif.	1 (2)	12–15	177 (53)	16.9 (3.5)
T9	92	11	74	123	24	31	41	3	58	0.77	vc ?	2	7–9	193 (66)	17.6 (6.9)
T15	139	19	112	189	4	7	11	19.9	63	0.69	vc, zonate	3–4	4–7	304 (68)	19.8 (6.2)
Group V: Ring porous															
T1	155	26	112	209	14	19	26	8.1	70	0.63	vc, alif.	1–4		278 (87)	18.3 (6.1)
Group VI: Radial pattern, banded parenchyma															
T18	132	18	67	163	13	24	27	5.6	11	0.63	banded	1–2	7–9	295 (97)	11.7 (3.8)
T7	79	9	64	99	40	48	61	1.6	26		banded	1–2	12–14	86 (27)	5.8 (1.7)
T1	109	21	63	161	3	6	11	18.2	52	0.78			7–13–16	?	?

percentage of the fossil wood that is cell wall, it is possible to estimate the original SG_g (green specific gravity, based on oven-dry weight and green volume) of the fossil. For example, if 30% of a wood's cross-sectional area is cell wall, then the estimated SG_g would be $1.05 \times 0.30 = 0.315$. A dot grid method was used to determine cell wall percentage from well-preserved areas of cross sections, and was based on a 500-point count per sample. A compound light microscope was interfaced with a personal computer, the cross sectional image was viewed on the computer screen and a grid with 100 points overlain on the image. The number of dots that were on cell wall or lumen was counted to estimate the percentage of cell wall (Wheeler, 1991).

3. Descriptions

Table 1 presents information on selected features of the Fejej woods. Woods are grouped using features visible in transverse section, especially vessel size and

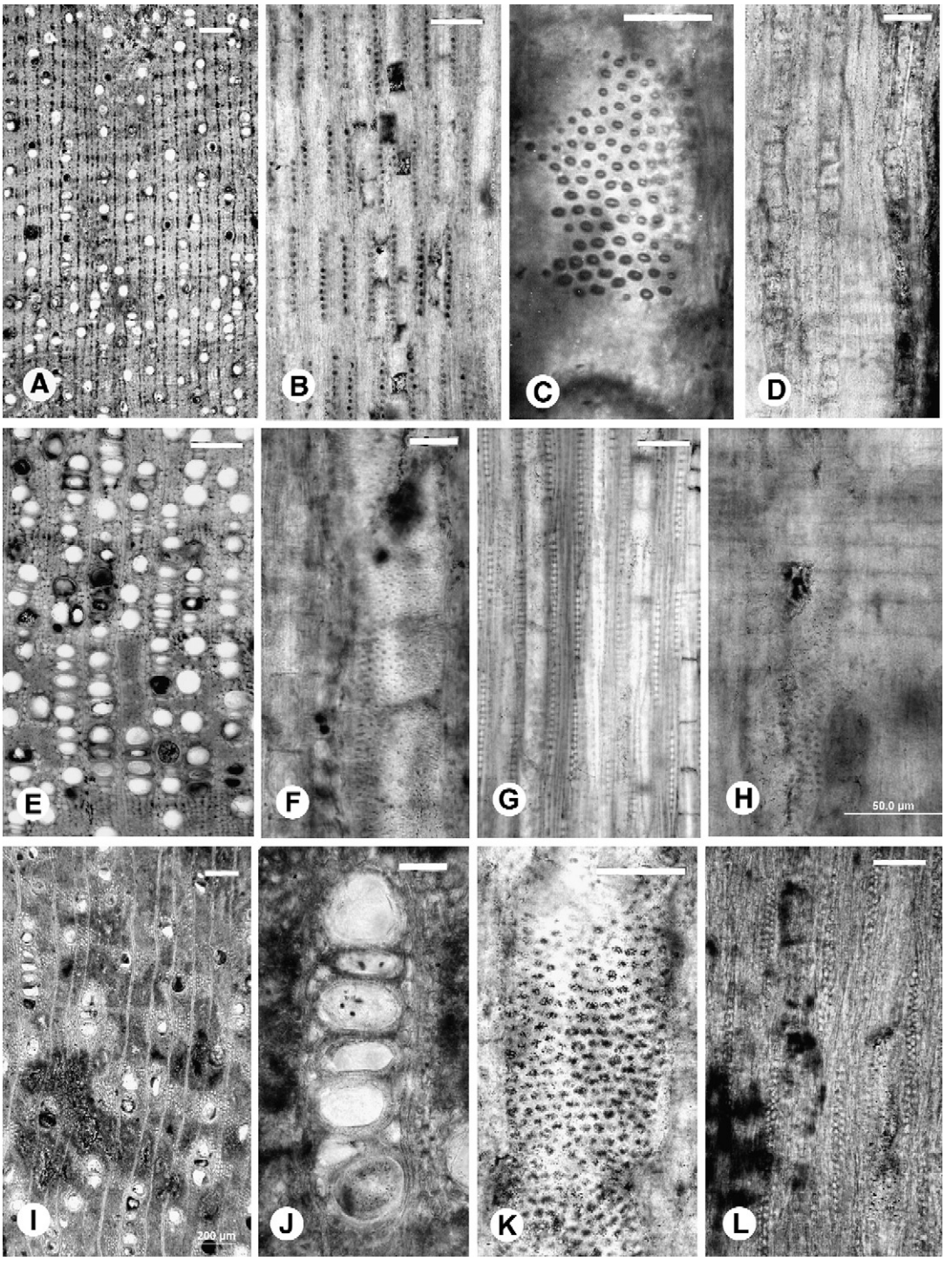

Fig. 2. A–D. Tree 17. A. Diffuse porous wood with indistinct growth rings; vessels solitary and in short radial multiples; axial parenchyma banded, TS. B. Storied uniseriate rays, TLS. C. Crowded alternate intervessel pits. D. Strand of chambered crystalliferous axial parenchyma, RLS. E–H. Tree 5. E. Diffuse porous wood, vessels rounded in outline and with thick walls, vessels solitary and in radial multiples. F. Crowded alternate intervessel pitting. G. Narrow rays, vessels with dark colored contents resembling gum deposits collected on perforation plate rims. H. Procumbent ray parenchyma cells; vessel-ray parenchyma pits crowded and alternate. I–L. Tree 4 I. Diffuse porous wood, vessels rounded in outline, paratracheal axial parenchyma, vasicentric, tending to lozenge aliform, and confluent, TS. J. Vessel multiple, TS. K. Crowded alternate intervessel pitting, TS. L. Rays 1–3 seriate, mostly 3-seriate, TLS. Scale = 200 µm for A, I; 100 µm for B, E, G, L; 50 µm for D, F, H, J, K; 25 µm for C.

arrangement, and axial parenchyma arrangement and abundance. Six groups are recognized.

GROUP I. Banded parenchyma, Uniseriate rays

Wood Type 1. Tree 17 *Cynometroxylon* sp. (Fig. 2 A–D)

Growth rings present, marked by marginal parenchyma.

Wood diffuse porous. Vessels solitary (56%) and in radial multiples of 2–4, solitary vessels rounded in outline. Mean tangential diameter of 44 (5) μm, range 36–53 μm; 98–150 per sq. mm; perforations exclusively simple; intervessel pits crowded alternate, minute to small, less than 5 μm; vessel-ray parenchyma pits similar to intervessel pits. Vessel wall thickness about 5 μm. Mean vessel element length 304 μm. Tyloses not observed.

Fibers: very thick-walled, pits not obvious.

Parenchyma: abundant, paratracheal banded, bands usually 2 (3) cells wide, and marginal, bands relatively straight to slightly wavy, in some regions bands appear regularly spaced; 4–8 cells per strand.

Rays: exclusively uniseriate. Composed of procumbent ray cells. Mean ray height 203 (43) μm, 11 cells (3); 15–17 per mm; storied to irregularly storied in some regions, non-storied in others.

Inclusions: solitary prismatic crystals in chambered axial parenchyma.

Affinities: In the InsideWood database, *Cynometra* is the only African species that has the combination of numerous narrow vessel elements, simple perforation plates, small alternate pits, narrow bands of parenchyma, exclusively uniseriate rays that are storied, and chambered crystalliferous axial parenchyma. Rays are narrow in extant *Cynometra*, but not all species have exclusively uniseriate rays; *Cynometra alexandri* does. The number of parenchyma cells per axial parenchyma strand is also similar.

Lemoigne (1978) reported *Cynometroxylon schlagintweitii* from the Miocene of the Omo Valley. The Omo Valley species has wider (to 180 μm) and fewer (3–6 per mm2) vessels than the Fejej wood. This is a considerable difference in vessel size and density, but there are comparable differences in quantitative features between modern species of *Cynometra* (OPCN database; InsideWood accessed 2006).

GROUP II. — Oleaceae / Rutaceae / Sapindaceae

There are three samples in Group II (Table 1); all have narrow vessels, minute-small intervessel pitting, and vessel-ray parenchyma similar to the intervessel pits, narrow rays composed predominantly of procumbent cells. Trees 5 and 10 have similar vessel diameters, but differ in number of vessels per sq. mm; Tree 11 has wider and fewer vessels and in some regions more axial parenchyma. Variation in quantitative vessel features can reflect either within or between species variation. We consider Trees 5 and 10 as a single wood type because of the similarity in qualitative features, and Tree 11 to be a separate wood type because of its more abundant axial parenchyma, as well as the differences in quantitative features (see Table 1).

Wood Type 2. Tree 5, Tree 10 (Fig. 2E–H)

Growth rings present, but indistinct, marked by radially flattened fibers, growth ring boundaries intermittent, as they are not continuous tangentially, also variation in vessel frequency.

Diffuse porous, vessels solitary (40%–67%) and in radial multiples of 2–10, solitary vessels rounded in outline, mean tangential diameters of 45 (4)–48 (6) μm , 88–300 per sq. mm; perforation plates exclusively simple; intervessel pits crowded alternate, minute to small 3–5 μm across; vessel-ray parenchyma pits similar to intervessel pits; vessel element lengths 294–355 μm, widely spaced tyloses.

Fibers: apparently very thick-walled.

Parenchyma: mostly scanty paratracheal to vasicentric, with 1 cell deep sheath around vessels; sometimes confluent when vessels especially closely spaced; most axial parenchyma strands chambered crystalliferous, with 12(–20) chambers.

Rays: 1–2 seriate, composed predominantly of procumbent cells; not storied; 9–14 per mm.

Inclusions: Chambered axial parenchyma with one crystal per chamber, 12–20 chambers per strand.

Affinities: The combination of narrow, numerous vessels in radial multiples, minute to small alternate intervessel pits, narrow non-storied rays composed primarily of procumbent cells, and predominantly paratracheal parenchyma occurs in the Oleaceae, Pteroxylaceae, Rutaceae, and Sapindaceae. These four families occur in present-day Ethiopia, and fossil woods attributable to the Rutaceae (three species of *Evodioxylon*) and Sapindaceae (two species of *Sapindoxylon*) have been reported. No fossil woods of the Oleaceae or Pteroxylaceae have been reported (Gros, 1992).

Tree 11 — The qualitative characteristics of this tree are as above, except for more abundant axial parenchyma. Differences in quantitative features are shown in Table 1.

GROUP III — Axial parenchyma aliform to confluent

There are three samples in this group, each of which we recognize as different wood types because of the variation in whether axial parenchyma is storied or not, and ray frequency and size.

Wood type 3. Tree 4 (Fig. 2I–L)

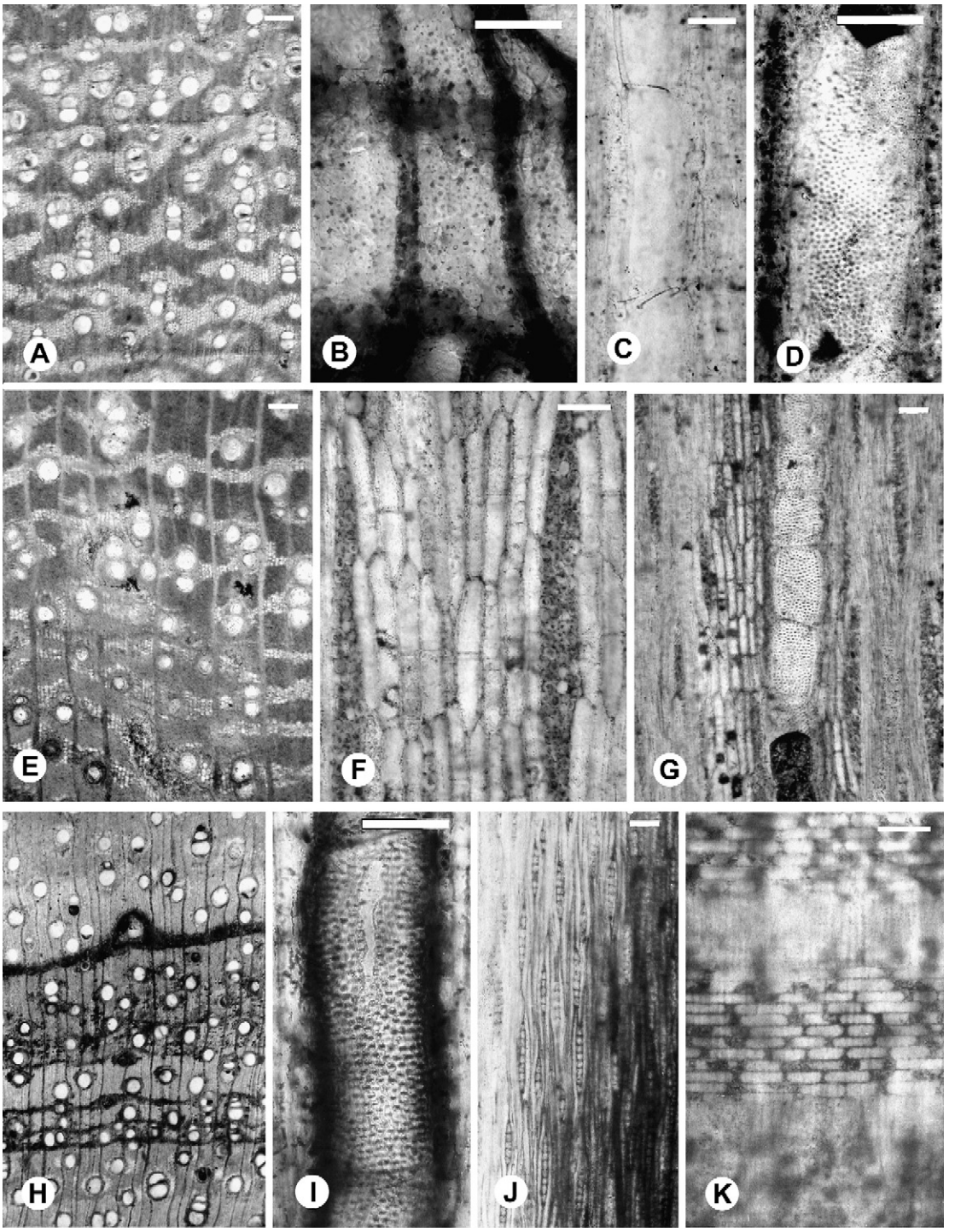

Fig. 3. A–D. Tree 12 A. Diffuse porous wood, aliform-confluent parenchyma, vessels solitary and in short radial multiple. B. Thick-walled fibers. C. Simple perforation plates. D. Crowded alternate intervessel pitting, E–G. Tree 14 E. Diffuse porous wood, confluent-banded parenchyma. F. Fusiform and 2-cell strands axial parenchyma. G. Storied axial parenchyma, crowded alternate intervessel pitting., H–K. Tree 6 H. Diffuse porous wood, vessels mostly solitary and occasional radial multiples of 2. Axial parenchyma vasicentric and lozenge-aliform, traumatic axial canals, TS I. Crowded alternate intervessel pitting, TLS,. J. Exclusively uniseriate rays , TLS. K. Homocellular ray composed of procumbent cells, RLS. Scale = 200 μm for A, E, H, J; 100 μm for G, K; 50 μm for B, C, D, F, I.

Growth rings indistinct, with a zone of solitary, widely spaced narrow vessels, or if radial multiples across that zone with narrow vessels at that zone.

Diffuse porous. Vessels solitary (64%) and in radial multiples of 2–3 (–5). Mean tangential diameter of 72 (13), 55–98 μm; 11–15–18 per sq. mm. Perforations exclusively simple; intervessel pits crowded alternate, minute.

Parenchyma: vasicentric, aliform lozenge to winged, and confluent, connecting 3–4 vessels or vessel multiples. Most of the axial parenchyma is chambered with solitary rhomboidal crystals, with more than 12 chambers per strand.

Rays: 2–3 seriate, uniseriate rays rare, mean height of multiseriate rays 252 μm (80); 6–10 per mm; non-storied.

Comments: Preservation of this sample is relatively poor. Vessel-ray parenchyma pits were not observed with certainty, but likely are similar to the intervessel pits. Rays appear to be homocellular composed exclusively of procumbent cells, but this could not be determined with certainty in radial sections. In tangential section, multiseriate rays have uniseriate margins of 1 to 4 cells, but these cells do not have an obviously different shape than the body cells.

There is evidence of insect damage in this sample.

Wood type 4. Tree 12 (Fig. 3A–D)

Growth rings present, marked by zonate / marginal parenchyma or radially narrower fibers, and variations in vessel frequency.

Diffuse porous, vessels solitary (41%) and in radial multiples of 2–3 (4). Mean tangential diameter of 77 (11) μm, range 50–93 μm; some regions with two distinct sizes of vessels; 21–32–59 per sq. mm. Perforations exclusively simple; intervessel pits crowded alternate, minute, 2–4 μm; pits to parenchyma slightly larger than intervessel pits, and more widely spaced; mean vessel element length (n=15) 211 (37), 150–265 μm.

Fibers: thick to mostly very thick walled. No pits or septae observed.

Parenchyma: abundant, aliform, mostly confluent, forming wavy discontinuous bands; marginal; strands of 4–8 cells. Non-storied.

Rays: 1–2-seriate, -homocellular, composed of procumbent cells. Not storied; 14–17 per mm.

Inclusions: Possible occasional strands of crystalliferous axial parenchyma, 1 rhomboidal crystal per chamber, 18 chambers per strand, and in unchambered axial parenchyma.

Affinities: The combination of vessels solitary and in radial multiples, simple perforation plates, narrow (<100 μm mean tangential diameter) vessels, vasicentric, aliform, and confluent parenchyma, narrow unstoried rays, and chambered crystalliferous parenchyma occurs in woods of Combretaceae, Leguminosae (especially Caesalpinoideae), Rutaceae, and Sapindaceae. Intervessel pits are usually larger in the Combretaceae, so the affinities of Tree 4 and Tree 12 are more likely with the Leguminosae, Rutaceae, or Sapindaceae. Unfortunately, the preservation of this wood is not good enough to determine whether or not the pits are vestured, a characteristic of the Leguminosae, but not of the Rutaceae or Sapindaceae.

Wood type 5. Tree 14 (Fig. 3E–G)

Growth rings indistinct to distinct, marked by radially flattened and slightly thicker walled fibers.

Diffuse porous. Vessel solitary (45%) and in radial multiples of 2–3. Mean tangential diameter of 87 (16), 51–121 μm, 10–18 per sq. mm. Perforations exclusively simple, intervessel pitting alternate, 7–9 μm; vessel elements 123–207 μm long, mean 183 (19) μm.

Fibers: thick walled, no pits or septa observed.

Parenchyma: confluent banded, wavy bands mostly 3–4 cells wide; aliform parenchyma rare and unilateral paratracheal; fusiform or in strands of two cells. Occasionally, some strands chambered (up to 8 chambers) and apparently crystalliferous.

Rays: multiseriate rays up to 3–4 cells wide, multiseriate rays non-storied; uniseriate rays storied. Composed exclusively of procumbent cells, or with 1–2 marginal rows of square cells. Multiseriate ray height 333 (147) μm; 22 (10), 6–46 cells high; 5–7 per mm.

Axial parenchyma and uniseriate rays storied, multiseriate rays 2 to 8 tiers high.

Comments: The radial sections did not reveal much information, and vessel-ray parenchyma pits were not observed with certainty. It is possible they are similar to the intervessel pitting. The rays are likely composed of procumbent cells, but it was difficult to be sure of whether the cells of the marginal rows of the rays were square or procumbent.

Affinities: Even though some diagnostic features are not visible, the combination of narrow vessels that are solitary and in radial multiples, simple perforations, alternate intervessel pits, thick-walled fibers, banded axial parenchyma which is storied and fusiform suggests affinities with Leguminosae, subfamilies Caesalpinoideae or Papilinoideae.

GROUP IV: Axial parenchyma scanty paratracheal to vasicentric

This group contains 4 woods, which represent 4 different wood types, distinguished by parenchyma abundance and distribution, and intervessel pit size.

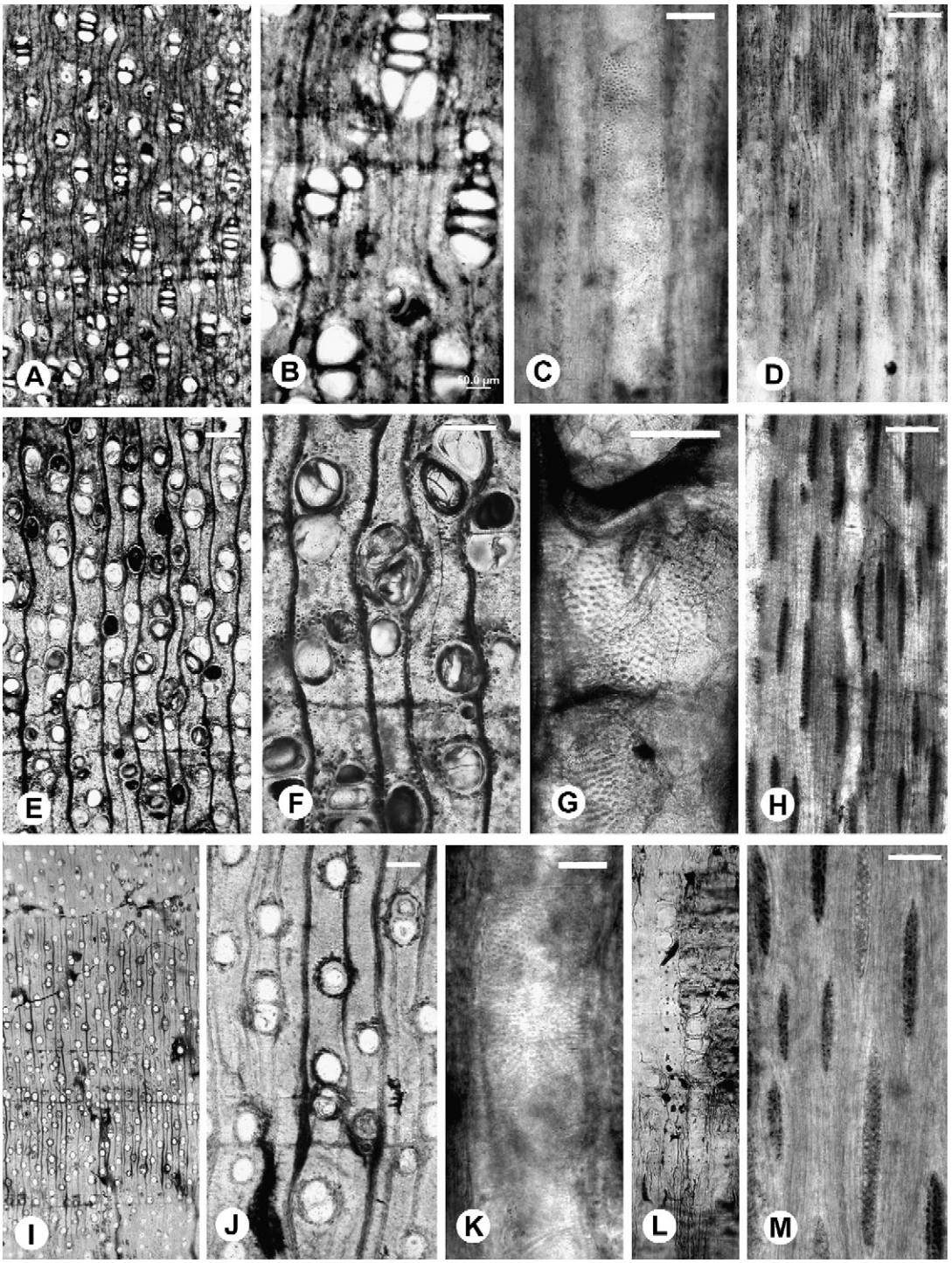

Fig. 4.

Wood type 6: Tree 6 (Fig. 3H–K)

Growth rings distinct, marked by marginal parenchyma. and radially narrowed fibers.

Wood diffuse porous. Vessels solitary (55%) and in radial multiples of 2–3(4); solitary vessels rounded in outline. Mean tangential diameter of 74 (10), 55–

104 μm; 17–35 per sq. mm. Perforations exclusively simple; intervessel pits crowded alternate, 5–6 μm, polygonal in outline; mean vessel element length 192 μm, range 123–297 μm.

Fibers: medium-thick-walled, no pits observed.

Parenchyma: vasicentric and lozenge-aliform and marginal/zonate and associated with traumatic canals; strands of 4 cells.

Rays: Exclusively uniseriate, non-storied, composed of all procumbent cells, not greatly elongated radially. Mean ray height 143 μm (34); 8 (2) cells; 7–14 per mm.

Inclusions: solitary rhomboidal crystals in chambered crystalliferous strands, 4 to more than 20 chambers.

Traumatic canals present and associated with zonate parenchyma.

Comments: It is possible that this wood has septate fibers, but it was difficult to tell whether some of the fine lines traversing the fibers were septae or fungal hyphae. The only pitting observed in radial sections appeared similar to the intervessel pitting viewed in tangential section, so it is likely that the vessel-ray parenchyma pitting is similar to the intervessel pitting.

Affinities: The combination of traumatic canals, vasicentric parenchyma, and uniseriate rays composed of procumbent cells does not occur in many families, and is seen in some members of the Combretaceae (*Terminalia*) and Caesalpinoideae of Leguminosae (*Microberlinia, Monopetalanthus, Tetraberlinia*). Both families occur in present day Ethiopia, and woods of the Combretaceae (19 species) and Caesalpinioideae (16 species) are the two most commonly represented groups in the fossil wood record of Ethiopia (Gros, 1992).

Terminalia is a large genus with some 150 species (Mabberley, 1997), and is variable in its anatomy. Van Vliet (1979) classified extant *Terminalia* wood into five groups based on moisture availability, and examined the variability in quantitative vessel element features (diameter, density, length). There is a broad range of the quantitative features within each of the five groups, but if the wood described above is a *Terminalia,* its characteristics are consistent with species that occur in the drier vegetation zones, e.g. dry deciduous forest, savanna or dry thicket.

Wood type 7. Tree 8 (Fig. 4A–D)

Growth rings distinct to indistinct, marked by marginal parenchyma and radially narrowed fibers.

Wood diffuse porous. Vessels solitary (32%) and in radial multiples of 2–3(4); solitary vessels rounded in outline. Mean tangential diameter of 77 (12) μm , range 56–104 μm; 22–37 per sq. mm. Perforations exclusively simple; intervessel pits crowded alternate, minute; vessel element lengths 235–410 μm.

Fibers: medium-thick to thick-walled, no pits or septae observed.

Parenchyma: vasicentric, lozenge-aliform, and marginal/zonate.

Rays: Uniseriate, rarely biseriate; non-storied, composed of all procumbent cells, not greatly elongated radially. Mean ray height 177 μm (53); 17 (7) cells; 12–15 per mm.

Inclusions: solitary rhomboidal crystals in chambered strands, crystalliferous cells inflated.

Affinities: The combination of diffuse porous woods, with randomly arranged vessels, minute-small intervessel pits, predominantly paratracheal parenchyma that is vasicentric to slightly aliform, predominantly uniseriate rays that are composed of procumbent cells, and chambered crystalliferous axial parenchyma occurs commonly in the Caesalpinoideae. Members of the Combretaceae, Meliaceae, Rutaceae, and Sapindaceae also have this combination of features.

Wood type 8. Tree 9 (Fig. 4E–H)

Growth rings present, marked by marginal parenchyma, but without obvious change in vessel diameter or density.

Wood diffuse porous. Vessels solitary (58%) and in radial multiples of 2 (–3), solitary vessels round to slightly oval in outline. Mean tangential diameter 92 (11), range 74–123 μm; 24–41 per sq. mm; intervessel pits crowded alternate, small, 4–5 μm; vessel-ray parenchyma pits similar; vessel element lengths of 210–300 μm.

Fibers thick-walled, no pits or septae observed.

Parenchyma: scanty paratracheal to vasicentric, confluent when vessels close to other vessels; zonate, most parenchyma cells chambered and crystalliferous, more than 16 chambers.

Rays: almost exclusively 2-seriate; composed of procumbent cells, cells thick-walled; mean ray height 193 (66) μm, 18 (7) cells; 7–9 per mm.

Inclusions: solitary rhomboidal crystals in chambered axial parenchyma.

Comments*:* The ray cells in this sample are filled with colored contents, making it easy to determine that the rays are composed of procumbent cells only.

Leguminosae

Wood type 9. cf. *Acacia* Tree 15 (Fig. 4I–M)

Growth rings distinct to indistinct. Marked by marginal parenchyma.

Wood diffuse porous. Vessels solitary (63%) and in radial multiples of 2, solitary vessels rounded in outline. Mean tangential diameter of 139 (19) μm, range 112–189 μm; 4–7–11 per sq. mm; intervessel pits with coalescent apertures, crowded alternate, angular in outline.

Fibers: No pits or septae observed.

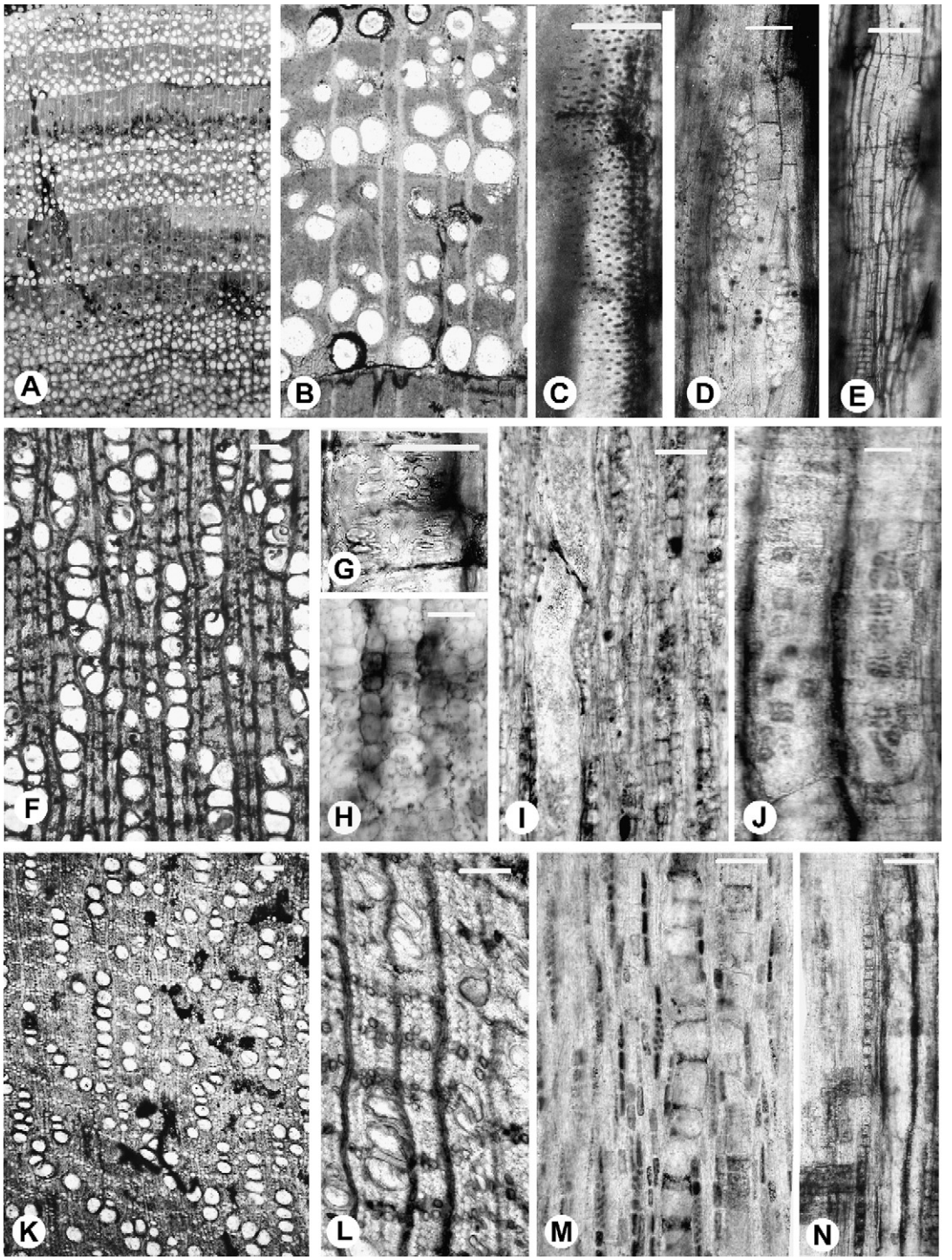

Fig. 5.

Parenchyma: marginal/zonate bands of 2 cells deep, narrow vasicentric 1–2 cells deep, sometimes sheath not completely encircling the vessels, rarely lozenge-aliform.

Rays: mostly 3–4 cells wide, occasionally 5-seriate, uniseriates rare. Composed exclusively of procumbent cells; 4–7 per mm.

Inclusions: Solitary prismatic crystals in chambered axial parenchyma strands, 15–+ chambers; often in strands adjacent to rays.

Affinities: The combination of medium-sized vessels, alternate intervessel pits, vasicentric parenchyma, 3–4 seriate rays composed of procumbent cells, and chambered crystalliferous axial parenchyma occurs in *Acacia*, as well as in other legumes.

There have been 5 reports of fossil woods of *Acacia* from Ethiopia (Gros, 1992). The genus *Acacia* has a long history in East Africa, with leaves referable to the genus known from the Eocene of Tanzania (Herendeen and Jacobs, 2000).

Comments: Vessel-ray parenchyma pitting was not observed.

GROUP V. Ring porous

Wood type 10. Bignoniaceae

cf. *Stereospermoxylon eoacuminatissumum* (Prakash et al., 1982) (Fig. 5A–E)

Growth rings distinct, marked by differences in vessel diameter of latewood and earlywood vessel and thick-walled and radially flattened latewood fibers. Ring porous. Earlywood vessels solitary and in occasional radial multiples of 2 (3) and oblique pairs, earlywood pore ring at least 3 vessels deep, solitary vessels circular in outline. Latewood vessels solitary and in radial multiples. Mean tangential diameter of the earlywood vessels 155 (26), range 112–209 μm. Perforations exclusively simple; intervessel pits crowded alternate, 5–6 μm; pits to axial parenchyma similar in size and shape to intervessel pits. Mean vessel element length 252 μm.

Fibers: no pits or septae observed, fibers thick-walled.

Parenchyma: vasicentric, aliform, and confluent, aliform and confluent more obvious in the latewood of wider rings. Strands of 4 cells, locally storied.

Rays: mostly 4 cells wide. Mean multiseriate ray height 278 μm (sd-87), 18 cells, Uniseriate rays rare, less than 5 cells high. Composed of procumbent cells only.

Comments: Growth ring width in this fossil is variable. In some places the rings are narrow, so that there are only 1–2 rows of earlywood vessels, and wood appears diffuse porous in these rings. In wider rings, there is a marked difference between earlywood and latewood vessel diameter.

Affinities: Semi-ring porous and ring porous woods are rare in the tropics (e.g., Wheeler and Baas, 1991). In the InsideWood database (http://insidewood.lib.ncsu.edu/search), *Markhamia*, and *Stereospermum* are the only woods from Tropical Africa that have semi-ring to ring porous wood, aliform to confluent (but not banded) axial parenchyma, and rays composed of procumbent cells (Normand and Paquis, 1976).

One of the Blue Nile Valley, Ethiopia, woods (Mio-Pliocene) that Prakash, Awasthi and Lemoigne described (1982) was diffuse porous to semi-ring porous. They used the combination of characteristics of wood diffuse to nearly semi-ring porous, vessels medium to large, aliform-confluent parenchyma, 1–4 seriate rays, composed of procumbent cells to infer relationships with Bignoniaceae, and so named the wood *Stereospermoxylon eoacuminatissimum*. In their discussion, they note that it is not possible to distinguish wood of *Markhamia* and *Stereospermum*. The differences between earlywood and latewood vessel diameters are more pronounced in the Fejej wood than in the Blue Nile Valley wood, but otherwise the two are similar. The illustrations of this species indicate that uniseriate rays are rare, as is true for the Fejej wood.

GROUP VI: Sapotaceae

There are two woods with the distinctive pattern of radially arranged vessels and banded parenchyma. They differ in vessel diameter and frequency, ray width, and number of rays per mm.

Wood type 11: *Sapotoxylon* sp. 1— Tree 18 (Fig. 5F–J)

Growth rings present, but indistinct, marked by change in spacing of parenchyma bands, vessel density, and occurrence of radial multiples with markedly narrower vessels in the midst of a radial multiple.

Vessels. Diffuse porous, with radial to oblique pattern, vessels commonly in radial multiples, multiples of 4 or more common, 11% solitary vessels. Mean tangential diameter of 132 (8), range 67–163 μm; 13–27 per sq. mm; perforations exclusively simple; intervessel pits crowded alternate, minute to small, 3–5 μm; mean vessel element length 589 μm, vessel-ray parenchyma pitting enlarged, scalariform.

Fibers: Walls thick to very thick. Possible vascular/vasicentric tracheids, narrow cells with abundant pitting adjacent to the vessels.

Axial parenchyma: Scanty paratracheal, diffuse-in-aggregates to 1–2 cell wide apotracheal parenchyma bands; 8 or more cells per strand, frequency with a portion of the strand chambered and crystalliferous.

Rays: Two to three seriate, body of ray of procumbent cells and with long uniseriate margins of upright cells, marked differences in sizes of body and marginal cells; uniseriate rays composed of all upright cells. In some rays, width of the 2–3 seriate portion similar to that of the uniseriate portion of the ray. Height of the multiseriate portion 295 μm (87); 7–9 per mm.

Inclusions: Common, as solitary prismatic crystals in chambered axial parenchyma, 4 to more than 12 chambers in a series.

Wood type 12: *Sapotoxylon* sp. 2 — Tree 7 (Fig. 5K–N).

Growth rings indistinct.

Vessels. Diffuse porous, with radial / oblique pattern, vessels commonly in radial multiples, multiples of 4 or more common, 26% solitary vessels. Solitary vessels rounded in outlined. Mean tangential diameter of 79 (9) range 64–99 μm; 40–48–61 per sq. mm; perforations exclusively simple; intervessel pits crowded alternate, 4–6 μm; vessel-ray parenchyma pitting enlarged, scalariform with much reduced borders. Widely spaced thin-walled tyloses present.

Fibers: Very thick-walled. Possibly some vasicentric tracheids.

Axial parenchyma: Scanty paratracheal, and abundant apotracheal 2–3 cell wide parenchyma bands; usually about 8–10 bands per radial mm; strands of more than 8 cells.

Rays: Uniseriate to biseriate; composed of procumbent cells and long uniseriate margins of upright cells, marked differences in sizes of body and marginal cells; uniseriate rays composed of all upright cells; upright cells often with prominent pits, sometimes the walls appearing nodular. In some rays width of the 2-seriate portion similar to that of the uniseriate portion of the ray, but not in all rays. Height of the multiseriate portion 86 (27) μm; 12–14 per mm.

Inclusions solitary prismatic crystals present in chambered axial parenchyma, mostly more than 20 chambers per strand.

Comments: Because of the tyloses it was not possible to reliably measure vessel element length.

Affinities: The combination of vessels in radial multiples and with a radial pattern, banded parenchyma, alternate intervessel pits, and vessel-ray parenchyma pits that are enlarged and with reduced borders, narrow heterocellular rays, and chambered crystalliferous parenchyma occurs in the Sapotaceae. As pointed out by Prakash et al. (1980), the wood of the Sapotaceae is quite uniform, with considerable overlap between the genera in their wood anatomy. While it is relatively easy to recognize a wood as belonging to the Sapotaceae, it is difficult to assign it to a single genus within that family.

Members of the Sapotaceae occur in present-day Ethiopia, including upland rain forest and riverine forests (Friis et al., 1982). Three types of *Sapotoxylon* wood have been reported from the Tertiary of Ethiopia; they differ from the Fejej woods. *Sapotoxylon aethiopicum* Lemoigne, Beauchamp and Samuel (1974) from the Miocene of Debre Sian, has shorter radial multiples (2–3, rarely 4); *S. lecomtedoxiodes* Lemoigne (1978) from the Miocene of Welkite has markedly wider vessels (150–250 μm) and shorter radial multiples; and *S. multiporosum* Prakash, Awasthi and Lemoigne (1982) from the Mio-Pliocene of the Blue Nile Valley has longer radial multiples (up to 18), a higher vessel density (60–120 per sq. mm), and more rays per mm (18–20).

4. Discussion

4.1. General characteristics of the woods

Table 1 shows that the majority of the woods have narrow vessel elements, and none have average tangential diameters of more than 200 μm. Only deciduous species form ring porous woods, so the ring porous Fejej wood indicates that at least one member of the assemblage was deciduous. Growth rings in ring porous woods almost always are annual, and the variability in the ring width of the Fejej ring porous woods indicates year to year variation in water availability. Growth rings in the other Fejej woods are mostly indistinct, but the absence of distinct growth rings does not indicate equable climates because indistinct rings are known to occur in some trees growing where there is seasonality in water availability and the trees are deciduous.

4.2. Specific gravity

The Fejej woods have thick-walled fibers, and this characteristic is reflected in the specific gravity estimates. There is a relatively narrow range in the SGg of the Miocene Fejej woods (0.63–0.82), with most being between 0.71 and 0.76. The range of variation in SGg is much lower than would be expected for a lowland tropical forest (Chudnoff, 1976; Fearnside, 1997; Wiemann and Williamson, 2002) and suggests the Fejej trees grew where humidity was not high. Baraja-Morales (1985, 1987) has suggested that there is a high correlation between humidity and wood specific gravity in tropical forests. She has compared the dry specific gravity (SG_d) distributions of two tropical forests in Mexico (Baraja-Morales, 1987**)** and found that woods of the dry deciduous forest had a higher average SG_d (0.78) than did woods of the more humid rain forest (0.58). Moreover, in the dry deciduous forest, 73% of the species had SG_d values of more than 0.7. Some relatively recent work (e.g., Hacke et al., 2001) has suggested that wood with relatively high density and thick-walled vessels may contribute to a plant's drought tolerance as this helps the water column to resist the effects of high negative pressure. If this is true, the thick-walled vessels of the Fejej woods are consistent with characteristics of trees able to withstand drought conditions.

We have not yet compiled comparable data for extant African wood assemblages, but comparison of images of woods from the Sahel and Sahara (Neumann et al., 2001) with those from more humid regions of the continent (e.g., Normand and Paquis, 1976) supports the generalization that in drier regions there is a higher proportion of very thick-walled fibers and narrower vessels with thick-walls. The findings of Fahn et al. (1986) and Baas and Schweingruber (1987) for Israel and adjacent regions and for Europe, respectively, are similar.

It is possible there might be a preservational bias towards relatively high density woods as they are slower to decay and so would have a longer resident time favoring silicification. Also, there is the possibility that woods of similar specific gravity would sort out together during transport to the depositional environment. However, the Fejej wood assemblage does not seem to have been transported far, with some of the stumps appearing to have been preserved *in situ*, and there is no rounding of the samples as would be expected if they had been transported.

4.3. Comparison with the fruits and seeds

None of the Fejej woods have a combination of characteristics that occurs in Annonaceae, Anacardiaceae, or Chrysobalanaceae, the families represented by fossil fruits and seeds. Tiffney, Fleagle, and Bown (1994: p 38) used the present-day climatic affinities of the fruits and seeds to "suggest a possible range from, at wettest, a moist forest (possibly a marginal rain forest) to, at driest, a semi-humid, semi-deciduous forest on the interface between wetter and dryer environments…The conservative interpretation of the early–middle Miocene Fejej vegetation would thus be of a seasonally-dry forest." As discussed above, the characteristics of the woods are not consistent with those of a moist forest, but with a seasonally dry woodland or forest.

4.4. Comparison with other Ethiopian wood assemblages

Gros (1992) lists 31 genera and 47 species (17 families) of fossil woods for the Miocene of Ethiopia. Lemoigne (1978) and Lemoigne and Beauchamp (1972) described wood assemblages from Welkite (9 wood types), Omo (18 wood types), and Bulbulla (6 wood types), believed to be Lower Miocene. These three assemblages differed in composition, with no shared species. Lemoigne suggested that differences in composition could be due to differences in environment or age. The Fejej wood assemblage is distinct from these three assemblages and further document differences in Ethiopian vegetation during the Miocene.

4.5. Vulnerability indices

The vulnerability index (VI), which is defined as vessel tangential diameter / number of vessels per square mm, was introduced by Carlquist (1975) as a means of assessing the relative vulnerability of wood. Woods with few wide vessels are considered to be more vulnerable than woods with many narrow vessels. If a single vessel embolizes in a wood with few wide vessels, this event constitutes a greater loss of water conductivity than in woods with many narrow vessels. For the Fejej wood assemblage, the VI range is 0.2–19.9, with an average of 4 for the assemblage. Tree 15 and Tree 1 are remarkable for the assemblage, as they have VIs greater than 15. Tree15 likely is *Acacia*, a genus that includes many species with deep roots. Deep-rooted species avoid the water stresses of shallower rooted species, thus explaining the higher VI of this wood type.

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