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# Fossil wood from the lower Miocene of Myanmar (Natma Formation): palaeoenvironmental and biogeographic implications

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## ABSTRACT

### KEY WORDS

Petrified wood,  
Fabaceae,  
Cenozoic,  
Southeast Asia,  
dipterocarp,  
monsoon.

The palaeobotanical record of Myanmar (Burma) is poorly documented despite its importance for understanding the evolution of Asian monsoonal ecosystems through time. Here, we describe 20 taxa of fossil wood from 30 silicified specimens collected in the upper lower to lowermost middle Miocene Natma Formation, central Myanmar. These fossils share affinities with modern Fabaceae, Dipterocarpaceae, Burseraceae, Moraceae and Cupressaceae. They include a great variety of fossil dipterocarps (eight species) as found in today's Southeast Asian rainforests. The nearest living relatives of this as-

semblage reflect different ecotones of seasonal forests with coastal, mixed to dry deciduous, and wet evergreen species. This reconstruction implies a wet, warm, and monsoonal climate in Myanmar during the late early Miocene. The presence of fossil dipterocarp species typical of wet evergreen forests contrasts with Burmese Eocene dry dipterocarp assemblages and indicates wetter conditions during the Miocene. Our reconstructions support a long-term change from seasonal to everwet ecosystems for dipterocarp trees.

## RÉSUMÉ

*Bois fossiles du Miocène inférieur du Myanmar (formation de Natma) : implications paléoenvironnementales et biogéographiques.*

Le registre botanique fossile du Myanmar (Birmanie) est faiblement documenté malgré son importance pour comprendre l'évolution des écosystèmes de mousson au cours des temps géologiques. Nous décrivons ici 20 taxa de bois fossile issus de 30 spécimens silicifiés de la Formation de Natma (Myanmar central) datant du Miocène inférieur tardif au début du Miocène moyen. Ces fossiles sont affiliés aux familles modernes des Fabaceae, Dipterocarpaceae, Burseraceae, Moraceae et Cupressaceae. Nos spécimens incluent une grande diversité de diptérocarpées fossiles (huit espèces) retrouvée aujourd'hui dans les forêts tropicales d'Asie du Sud-Est. Les analogues modernes de ces espèces fossiles révèlent différents écotones de forêts saisonnières avec des espèces côtières, de forêts mixtes ou décidues sèches, et de forêts humides sempervirentes. Cette reconstruction implique un climat chaud et humide de mousson au Myanmar durant le Miocène inférieur tardif. La présence d'espèces fossiles de diptérocarpées typiques de forêts humides sempervirentes contraste avec les assemblages forestiers birmanes de l'Eocène, dominés par des forêts sèches à diptérocarpées, et indiquent des conditions plus humides. Ces reconstructions suggèrent un changement à long-terme des diptérocarpées d'environnements saisonniers vers des environnements plus humides.

## MOTS CLÉS

Bois fossile,  
Fabaceae,  
Cénozoïque,  
Asie du Sud-Est,  
diptérocarpée,  
mousson.

## INTRODUCTION

Myanmar is located at the eastern edge of the Bengal Bay and today lies in the Asian monsoonal domain (Fig. 1A); its Palaeobotanical record has been shown to be critical to reconstruct the evolution of monsoons in deep time and the biogeographic connections between South and Southeast Asia (Licht *et al.* 2015; Huang *et al.* 2020). Most of Myanmar is today characterized by intense seasonal rainfall (> 2 m) over its coasts and highlands, whereas the central part of the country, lying in the rain-shadow of the Indo-Burman Ranges (IBR), receives less than 600 mm of annual precipitation (Aung *et al.* 2017). Burmese ecosystems are dominantly considered as tropical to subtropical and are all strongly influenced by the seasonal monsoonal rainfall (Kress *et al.* 2003; Ashton 2014; Beck *et al.* 2018). While tidal and swampy forests are present with some mangroves along the coasts (*Rhizophora-Sonneratia* associations), and temperate forests occur at high altitude (Kress *et al.* 2003; ASFN 2016), the majority of forested areas of Myanmar are covered by mixed deciduous forests and temperate (semi-)evergreen forests of moderate altitude typical of Asian monsoonal climates (FAO 2007). Seasonally dry lowlands are composed of acacia woodlands, mixed deciduous forests (*Tectona-Xylocarpus-Terminalia* associations), and dry subtropical forests dominated by few species of dipterocarps (Sal-type forests) or *Tectona-Acacia* associations, which are common in the driest part of monsoonal South Asia; subtropical evergreen and semi-evergreen forests dominated by a wider variety of dipterocarps are present in wetter areas. Fossil flora studies investigating the persistence of these seasonally dry ecosystems have consisted

so far in few pollen studies (Morley 2000, 2018; Huang *et al.* 2020, 2021) and studies on fossil wood specimens (Prakash 1965a, b, d, 1973; Prakash & Bande 1980; Du 1988a; Gortwald 1994; Privé-Gill *et al.* 2004; Licht *et al.* 2014, 2015). The age of most previously studied sites is commonly poorly constrained, and it remains unclear when the modern seasonally dry ecosystems of central Myanmar, typical of the regional monsoonal climate, were set up.

Studies of the Burmese palaeobotanical record with a clear stratigraphic context exclusively come from the late middle Eocene of central Myanmar, namely from the Pondaung Formation (Privé-Gill *et al.* 2004; Licht *et al.* 2014, 2015) and the overlying Yaw Formation (Huang *et al.* 2020, 2021). The Pondaung Formation has yielded numerous fossil wood specimens associated with three types of forest ecotones: dry dipterocarp forests (with fossil specimens related to modern *Shorea* Roxb. ex C.F. Gaertn., *Pentacme* A. DC., *Amesiodendron* Hu, *Schima* Reinw. ex Blume, *Terminalia* L., *Bombax* L.); riparian and open seasonal wetlands typical of the Terai ecosystem of South Asia (with fossil specimens related to modern *Terminalia*, *Bombax*, *Bauhinia* L., *Acrocarpus* Wight ex Arn., *Ficus* L., *Pycnarrhena* Miers ex Hook.f. & Thomson, *Saraca* L., *Heritiera* Aiton), and tidal / littoral forests (with fossil *Pycnarrhena*, *Saraca*, *Heritiera*, *Sonneratia* L.f., *Gluta* L., *Cynometra* L.). These assemblages follow as it is seen in the actual Bay of Bengal (Licht *et al.* 2015). Most of the species identified in the Pondaung Formation grow today in climates with a well-marked seasonality. In addition, pollen from the Yaw Formation highlights a high abundance of palms that remain absent from the fossil wood record (Huang *et al.*



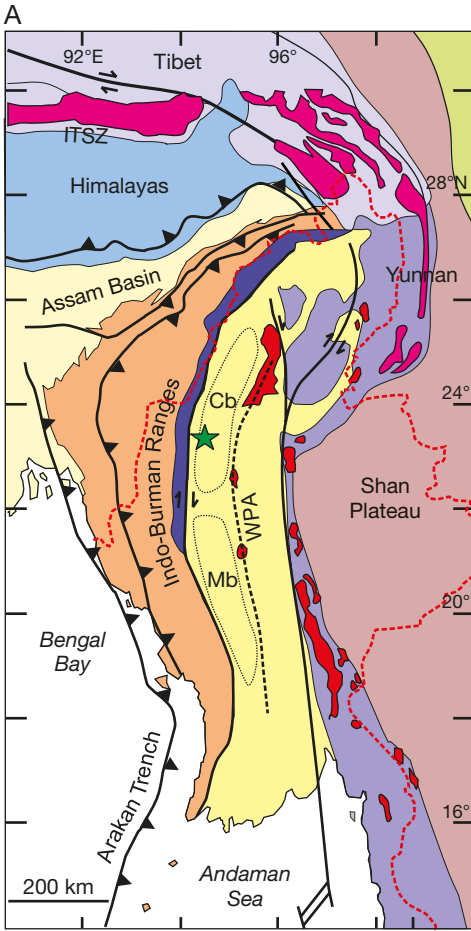


Fig. 1. — **A**, Simplified map of Myanmar showing the location of the field sites. Location of the fossil site is indicated with a green star (★). Abbreviations: **Cb**, Chindwin Basin; **Mb**, Minbu Basin; **WPA**, Wuntho-Popa Arc (volcanic arc of central Myanmar); **B**, stratigraphy of the Chindwin Basin, after Westerweel *et al.* (2020). The Natma Formation is indicated with a green star (★).

2020). The late Eocene palynoflora of the same formation reveals a sequence of three ecosystems similar to the one of the Pondaung Formation with seasonally dry forests; swamp, gallery and evergreen forests; and tidal / littoral forests (Huang *et al.* 2021). All the ecological requirements of the species were used as pieces of evidence for monsoonal rainfall and support palaeontological and isotopic findings highlighting intense Eocene seasonality (Jaeger *et al.* 2004; Licht *et al.* 2014).

The Burmese floral diversity during the Neogene is less well-known; published fossils with only cryptic age and location data but attributed to this period have been related to modern *Dipterocarpus* C.F. Gaertn., *Shorea*, *Sterculia* L., *Gluta*, *Acacia* Mill., *Azelia* Sm., *Intsia* Thouars, *Cynometra*, *Cassia* L., *Lagerstroemia* L. (Prakash 1973), *Terminalia* (Chowdhury & Tandon 1964; Mädel-Angeliewa & Müller-Stoll 1973), palms (Sahni 1964), *Swintonia* Griff., *Albizia* Durazz., *Careya* Roxb., *Cynometra*, *Araucaria-Agathis* (Prakash & Bande 1980), *Diospyros* L., *Saraca*, *Grewia* L., *Acrocarpus* (Gottwald 1994). It remains unclear if these specimens were found at the same sites or in the same geological units and it is thus impossible to reconstruct Neogene floral assemblages based on these incomplete data.

Documenting the development and expansion of seasonally dry ecosystems in central Myanmar during the Miocene provides direct insights into the long-term evolution of monsoonal activity and of the rainshadow effect of the Indo-Burman Ranges. It has been proposed that monsoonal intensity significantly increased during the early middle Miocene and decreased in the late Miocene (Clift *et al.* 2008); the uplift chronology of the Indo-Burman Ranges is less documented. Sedimentological and low-temperature thermochronology data indicate that uplift began between the late middle Eocene and the late Oligocene (Licht *et al.* 2019; Najman *et al.* 2020), but it remains unclear when high topography (> 2000 m) was acquired, and rain-shadow effects became significant.

This paper is the first to examine fossil wood specimens from the upper lower to lowermost middle Miocene Natma Formation, central Myanmar. We describe twenty fossil wood taxa, we identify eighteen of them from a new collection and reconstruct Miocene forested ecotones based on their nearest living relatives. We then compare the Natma Formation ecosystems with late middle Eocene and modern ecosystems of central Myanmar to document the regional landscape evolution.

## GEOLOGICAL AND PALAEOENVIRONMENTAL CONTEXT

East of the Indo-Burman Ranges in central Myanmar, the Chindwin Basin (Fig. 1A) constitutes the northern basin of the Burmese forearc and is filled up with Cenozoic clastic sedimentary rocks. Neogene deposits consist in the fluvial Lektat, Natma, Shwethamin, and Irrawaddy Formations, in stratigraphic order (Fig. 1B; Bender 1983; Licht *et al.* 2019). The *c.* 1 km thick Natma Formation consists of afossiliferous sandstones and pedogenised finer-grained sands and mudstones. The sedimentology of the Natma Formation recalls the one of the earlier Pondaung Formation in the same basin (Licht *et al.* 2013). Sandstones occur in 10 to 50 m wide channel bodies; finer-grained layers display well-marked palaeosol horizons rich in root traces and pedogenic carbonates, which indicate the occurrence of a well-marked dry season at the time of deposition (Retallack 2005; Zamanian *et al.* 2016). Growth temperatures from Natma pedogenic carbonates, derived from clumped isotope data, fall in the range of modern winter-to-spring temperatures and indicate a dry season during the coldest part of the year, similar to the modern monsoonal regime (Licht *et al.* 2022).

The age of the Natma Formation is constrained by the age of geological units higher and lower in the Chindwin Basin stratigraphy. The Letkat Formation has yielded detrital zircons and apatite ages as young as 20–17 Ma, indicating a lower Miocene age or younger (Wang *et al.* 2014; Licht *et al.* 2019; Westerweel *et al.* 2020). The base of the Irrawaddy Formation, also named Mingin Gravels in the Chindwin Basin, has yielded fossil mammals indicating a late middle Miocene (14–11 Ma) age, coeval to the Chinji fauna of Pakistan (Bender 1983); a similar age for the base of the Irrawaddy Formation has also been found in the nearby Shwebo Basin (Chavasseau *et al.* 2006). There is *c.* 1.5 km of sediment thickness (Shwethamin Formation) between the top of the Natma Formation and the base of the Mingin Gravels, implying some significant time lag between both units. Based on these constraints, the Natma Formation is attributed to the upper lower Miocene to lowermost middle Miocene (Westerweel *et al.* 2020).

At the time of deposition of the Natma Formation, the Indo-Burman Ranges were already forming a topographic barrier, of yet unknown elevation (Licht *et al.* 2019; Najman *et al.* 2020). The Natma Formation reflects deposition from a palaeo-drainage flowing southward into the Minbu Basin and the Andaman Sea further south, in contrast to the Pondaung Formation, which was opened to the Bengal Bay (Licht *et al.* 2019). Though no specific study has focused on the provenance of the Natma Formation, Westerweel *et al.* (2020) propose the Indo-Burman Ranges, the Wuntho Popa Arc in central Myanmar, and the eastern Himalayan Syntaxis further north as potential sources for the underlying unit, the Letkat Formation.

## MATERIAL AND METHODS:

Thirty specimens of fossil wood from the Natma Formation were collected in the Kalewa Township, Sagaing Region, Myanmar,

exposed in a wide badland system along the Kalewa-Mawlaik road (23°16'23.1"N, 94°18'25.3"E; see Fig. 1A for location). They are composed exclusively of small fragments from 3 to 10 cm across, cut from bigger ones. They are completely silicified and were found in-situ in basal lags of sandy channel bodies or on the ground next to these bodies, in a badland where only the Natma Formation is exposed. Sections of transverse, radial and tangential surfaces of the fossil wood specimens were prepared following the standard techniques (Hass & Rowe 1999) at the Muséum national d'Histoire naturelle (MNHN), Paris, France. Fossils were glued with Araldite AY 103 and covered with Araldite 2020. They are described following the IAWA lists of microscopic features for hardwood and softwood identification (IAWA Committee 1989, 2004). A rough estimate of the minimum stem diameter was carried out using the average geometrical intersection of the rays to locate a virtual center, as already done by De Franceschi *et al.* (2008) and following Dufraisse *et al.* (2020), rather than using the radius of curvature of the growth limits. Botanical affinities were determined using the InsideWood database (InsideWood 2004-onwards; Wheeler 2011; Wheeler *et al.* 2020), literature on fossil (Gregory *et al.* 2009 and references therein), including fossil wood slides from the palaeobotanical collection of Sorbonne Université (specimen no. 5790) described by Vozenin-Serra & Privé-Gill (1989), extant asian and non-asian wood samples and slides from the xylarium of the MNHN Herbarium (P) (specimen number starting by MNHN-P) or from the Cirad Xylarium (specimen number starting by CTFT). Nearest Living Relatives (NLR) ecology was determined using tropical plant databases, floras and forestry guides (referencies are given in concerned paragraphs). All microscopic slides, including at least one transverse, one longitudinal radial and one longitudinal tangential section per specimen are deposited in the collection of the MNHN (Table 2). The remains of the original specimens are dedicated to be sent back to the collections of the Department of Geology at the University of Yangon (Myanmar).

## RESULTS/TAXONOMY

Of the 30 fossil wood samples, we identified 18 species in 11 fossil genera representing five families. Two specimens are still undetermined at the family and genus level.

## CONIFERS

Family CUPRESSACEAE Rich. ex Bartl.  
Genus *Cupressinoxylon* (Göppert) Gothan

*Cupressinoxylon* sp.  
(Fig. 2)

MATERIAL. — MNHN.F50171 (field number: 17FN15). Estimated minimal diameter: 15–25 cm.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar

AGE. — Upper lower to lowermost middle Miocene



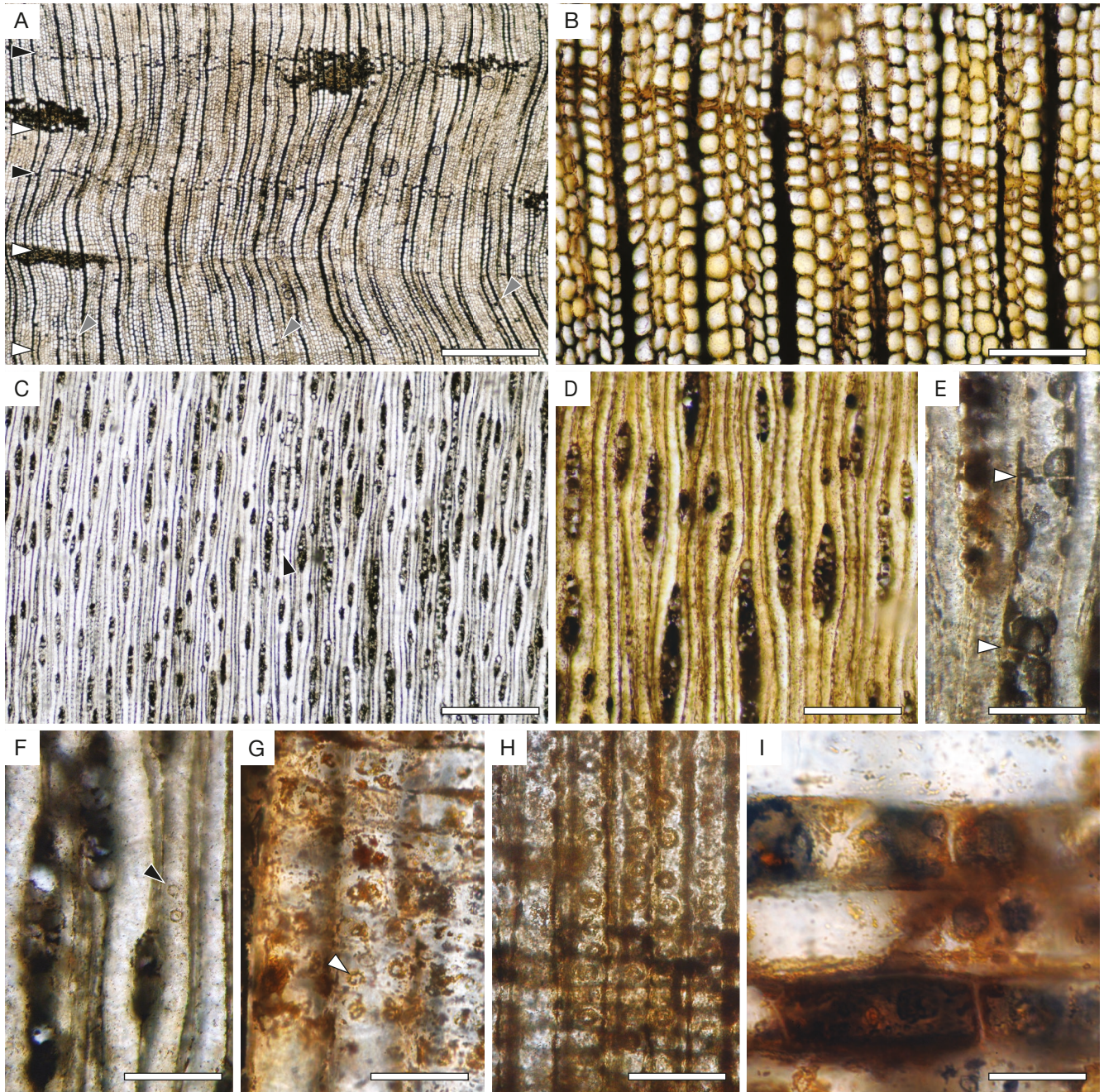


FIG. 2. — *Cupressinoxylon* sp. MNHN.F.50171: **A**, transverse section (Ts), growth limits (white arrows), diffuse parenchyma (grey arrows) and zonate parenchyma (black arrows), large black areas are cells filled with deposit material; **B**, Ts, growth limit with gradual transition from earlywood to latewood; **C**, tangential longitudinal section (Tls), 1- sometimes 2-seriate rays and parenchyma lines (arrow); **D**, Tls, detail of 1- sometimes 2-seriate rays; **E**, Tls, smooth longitudinal parenchyma walls (arrows); **F**, Tls, 1-2-seriate rays and tangential pits (arrows); **G**, radial longitudinal section (Rls), possibly cupressoid and/or podocarpoid crossfield pits (arrow); **H**, Rls, uniseriate radial pits; **I**, Rls, smooth parenchyma cell walls. Scale bars: A, C, 1 mm; B, 200 µm; E-F, H, 100 µm; G, 50 µm; I, 20 µm.

#### DESCRIPTION

Growth ring boundaries distinct (Fig. 2A), marked by 1-5 lines of flattened tracheids (Fig. 2B). Transition from earlywood to latewood gradual or indistinguishable due to flattening. Tracheids 2100-3200 µm long (average 2730 µm,  $n=20$ ), tangential diameter 20-50 µm (average 30 µm), thin walled with polygonal cross-section. Radial pits 1-seriate, rounded, spaced, 15-24 µm in diameter (average: 21 µm) (Fig. 2H). Tangential pits present, minute to small (Fig. 2F). Axial parenchyma diffuse and zonate in the vicinity of growth ring

boundaries (Fig. 2A, C), both horizontal and vertical walls smooth (Fig. 2E), 17-33 µm tangential diameter (average: 25 µm). Rays 1- to 2-seriate, biseriate parts are present here and there ( $\leq 10\%$ ), only composed of parenchyma cells, 3-22 cells high (average: 8) (Fig. 2C, D); ray cells 13-30 µm in tangential diameter (average: 30 µm), both vertical and horizontal walls smooth (Fig. 2I), indentures not visible. Cross-field pits possibly cupressoid or podocarpoid, maybe both, seemingly 2-4 pits per cross-field (Fig. 2G); 6-15 µm in diameter (average: 11 µm). Crystals not found. Resin canals absent.



## DISCUSSION

This specimen of homoxylate wood is characterized by: 1) tracheids with a polygonal transverse section; 2) uniseriate and spaced tracheid pits; 3) 1- to 2-seriate and rather short rays; 4) presence of tangential pits; and 5) smooth axial parenchyma and ray cell walls. It is thus attributed to conifers. The presence of axial parenchyma is reported in Podocarpaceae and Cupressaceae (including Taxodiaceae). According to Greguss (1955, 1972), Trivedi & Srivastava (1989) and the IAWA Committee (2004), zonate axial parenchyma is more frequent in Cupressaceae but is not completely diagnostic. It is yet a diagnostic feature of Cupressaceae when it includes dark content in the transverse section and in the transverse end walls of parenchyma cells in longitudinal sections, which is the case for our specimen.

Wood species of the cupressoid group are poorly distinguishable from each other based on wood anatomy alone (Phillips 1948; Wheeler & Dillhoff 2009). Kress *et al.* (2003) record 23 species of Cupressaceae (most of them are non-native) in Myanmar, including *Cryptomeria* D. Don which shares common traits with our specimen, especially uni- to biseriate rays and *Libocedrus* Endl. (Greguss 1972).

Within the InsideWood (2004-onward) database, *Chamaecyparis formosensis* Matsumura and *Taxodium distichum* (L.) Rich. match partially with our sample (InsideWood input code: 44p 61a 72p 73p 74p 80p 98p 99p 103p 108p). With less restrictive searches (e.g., excluding criteria such as smooth cell wall, cross-field pits cupressoid or podocarpoid and / or ray width from 1- to 2-seriate) most taxa still belong to Cupressaceae (*Chamaecyparis* Spach., *Cupressus* L., *Juniperus* L.). However, no clear modern relative among modern Cupressaceae can be found for this fossil. Nonetheless, our specimen shares all the diagnostic features of the fossil genus *Cupressinoxylon* (cross-field pits oblique and more or less narrow, ray walls mostly smooth, parenchyma often present, resin ducts absent), which are wide enough to include most of Cupressaceae species (Vaudois & Privé 1971). The poorly preserved cell walls and the relatively small size of our specimen makes it difficult to determine the affinity at the species level. Wheeler & Dillhoff (2009) also note that “there are more species of *Cupressinoxylon* than there are distinctive wood anatomical types within extant Cupressaceae” (Wheeler & Dillhoff 2009: 84).

Cupressaceae are mainly mesic-hydric (from balanced hydric conditions to wet conditions) trees in temperate or seasonal climates (Wilf *et al.* 2009; Pittermann *et al.* 2012) and all kinds of climate adaptation can be found in this pangeographic family, from moist tolerant trees to very drought-tolerant (Pittermann *et al.* 2012). Today, few species of Asian and Western-Pacific Cupressaceae grow in tropical areas from lowlands (600 m) to tree line: *Papuacedrus* H.L.Li, some *Calocedrus* Kurz and *Libocedrus* (De Laubenfels 1988; Earle 2004-onward). They are found in the tropics above 600 m of elevation, but few species occur in lowland tropical areas (< 600m): *Libocedrus yateensis* Guillaumin and *Callitris pancheri* (Carrière) Byng from New-Caledonia, *Callitris macleayana* (F.Muell.) F.Muell. from Australia or *Glyptostrobus pensilis* (Staunton ex D.Don) K.Koch in China and Southeast Asia (Farjon 2005).

## ANGIOSPERMS

Family FABACEAE Lindl.  
Genus *Albizinium* Prakash

*Albizinium eolebbekianum* Prakash  
(Fig. 3)

*Albizinium eolebbekianum* Prakash, 1975: 197, pl. 3, figs 9, 11, 12.

ORIGINAL HOLOTYPE. — Birbal Sahni Institute of Palaeosciences Museum no. 150/1014.

MATERIAL. — MNHN.F50172 (field number: 17FN04). Estimated minimal diameter: 30 cm.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar

AGE. — Upper lower to lowermost middle Miocene

## DESCRIPTION

Wood diffuse-porous. Growth ring boundaries indistinct. Vessels mostly solitary (80%) or grouped by 2, rarely 3, oval, 0-5 per mm<sup>2</sup> (average: 2) (Fig. 2A, B); tangential diameter 140-260 µm (average: 210 µm). Tyloses absent. Vessel elements 180-460 µm long (average: 290 µm). Perforation plates simple, mostly horizontal to slightly oblique (Fig. 3C). Intervessel pits alternate, polygonal in shape and crowded, 6-10 µm in size (Fig. 3C). Vessel-ray pits not preserved. Axial parenchyma lozenge-aliform, sometimes confluent, and seemingly marginal bands (Fig. 3A, B); also, maybe some diffuse parenchyma; parenchyma cells 100-150 µm (average: 120 µm) long in tangential plan, 20-50 µm (average: 30 µm) wide; crystals present in chambered cells (Fig. 3D). Rays 1- to 3-seriate (mainly 2), non-storied, 5-8 rays per tangential mm (average: 6), 150-340 µm (average: 220 µm) or 5-20 cells high (Fig. 3D), homocellular made of procumbent cells (Fig. 3F). Fibres with poorly preserved walls, septa present in some fibres (Fig. 3D, E), 15-22 µm wide (average: 18 µm).

## DISCUSSION

This specimen is characterized by: 1) diffuse-porous wood; 2) exclusively simple perforation plates; 3) aliform parenchyma; 4) the presence of septate fibres; and 5) homocellular and mostly 2- to 3-seriate rays.

These characters suggest affinities with modern Fabaceae and particularly with the traditional Mimosoideae subfamily (now in the recircumscribed Caesalpinoideae subfamily) (LPWG 2017). In InsideWood (2004-onward), 35% of described specimens of the traditional Mimosoideae have septate fibres. Ogata *et al.* (2008) also indicate that homocellular rays are mostly found in Mimosoideae. In modern wood of Mimosoideae, the lozenge-aliform parenchyma combined with the presence of septate fibres and homocellular rays is mainly found in genera *Albizia*, *Inga* Mill. and *Pithecellobium* Mart. (InsideWood 2004-onward). *Pithecellobium*, however, has higher and wider rays (Awasthi 1979). *Albizia* and *Inga* share a close anatomy. According to Evans *et al.* (2006), *Inga* has slightly more frequent radial multiples of vessels, as well as confluent parenchyma. A comparison with



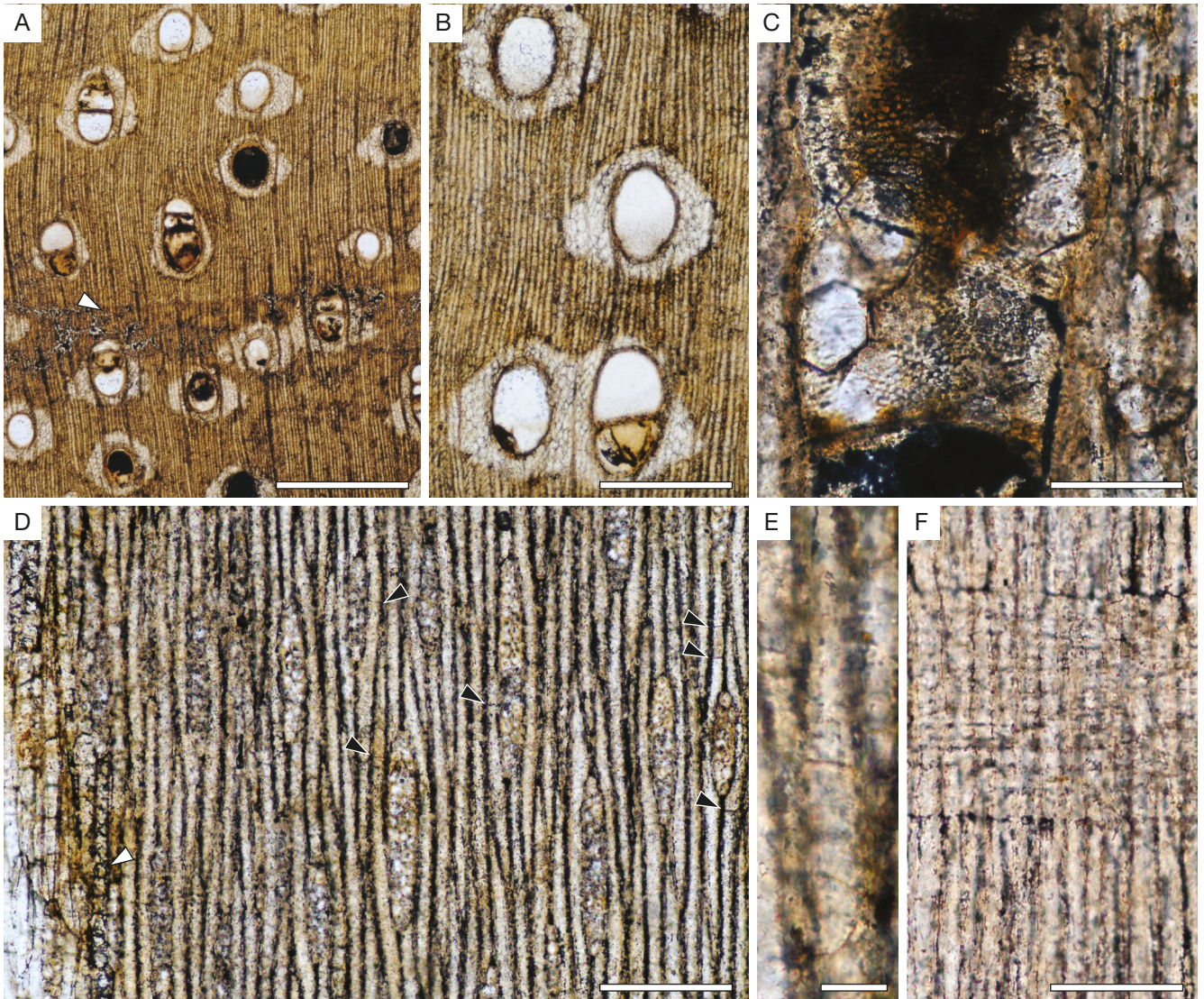


FIG. 3. — *Albizinium eolebbekianum* Prakash, MNHN.F.50172: **A**, Ts, vessels and parenchyma arrangement, marginal parenchyma band (arrow); **B**, Ts, lozenge-aliform parenchyma, sometimes confluent, fibres radially aligned; **C**, Ts, alternate intervessel pits, simple perforation plates; **D**, Ts, 1-3-seriate rays, septa (black arrows) and crystalliferous parenchyma (white arrow); **E**, Ts, detail of a septate fibre; **F**, Rls, homocellular ray. Scale bars: A, 1 mm; B, 500 µm; D, 200 µm; C, F, 100 µm; E, 25 µm. Abbreviations: see Fig. 2.

specimens and plates available on InsideWood (2004-onward) also reveal higher and thinner rays for *Inga* (frequently with uniseriate portion, and 2-seriate), with more often uniseriate rays, whereas most of *Albizia* species have fusiform and shorter rays. Thus, our specimen shows closer similarities to the genus *Albizia*, including three specific species: *Albizia lebbeck* (L.) Benth., regarding its parenchyma arrangement, the presence of septate fibres and non-septate fibres. However, it often has wider rays (up to 5-seriate); *A. ferruginea* (Guill. & Perr.) Benth. for its lozenge-aliform parenchyma and vessel density, resulting in a few confluences, similar ray size; and *A. procera* (Roxb.) Benth. for its aliform parenchyma rarely confluent and similar ray size (1-3 seriate, fusiform).

Fossil wood specimens resembling *Albizia* species are designated under the genus *Albizinium* (Prakash 1975) or described as *Albizia* (Gregory *et al.* 2009). The features of the present

specimen are compatible with the diagnosis of *Albizinium*. Although the anatomically close genus *Acrocarpoxylon* Gottwald has aliform parenchyma and septate fibres, it has more often heterocellular rays (Gottwald 1994). Among *Albizinium* fossil species close to our fossil (Awasthi 1979; Prakash *et al.* 1994; Mehrotra *et al.* 1999), *A. eolebbekianum* has shorter rays (up to 280 µm compared to 340 µm in our fossil) and *A. pondicherriensis* Awasthi has a higher ray density (10-15 / mm as opposed to 5-8 / mm) and more frequent vessels in groups than our fossil. The diagnoses of *A. eolebbekianum* and *A. pondicherriensis* are remarkably similar. Our fossil resembles *A. eolebbekianum* from the Miocene of India for the proportion of solitary vessels and the parenchyma arrangement, whereas it resembles more *A. pondicherriensis* for ray and vessel size. Our specimen is *in fine* attributed to *A. eolebbekianum* given the propensity of *A. pondicherriensis* to form vessel groups.



*Albizia* species are tropical or subtropical trees occurring in open secondary vegetation, in primary deciduous to monsoonal forests, and in savannas and shrublands of Asia, Africa, and America, up to 1700 m altitude (Nielsen 1992; Sosef *et al.* 1998). *Albizia lebbbeck* is a deciduous tree, probably native to tropical mainland Asia or East-Africa, mostly cultivated or naturalized. It grows in monsoonal semi-evergreen forests and monsoonal dry-deciduous forests with mean annual rainfall of 1300–1500 mm and very dry winter, at low elevation (0–750 m, sometimes up to 1700 m). It is also found along rivers and sand beaches. It is resistant to long hot and dry periods as well as cold winters and tolerates a wide range of soils including sandy river beds, coral loam or limestone (Prakash 1975; Nielsen 1992; Jensen 1999; Orwa *et al.* 2009; Wu *et al.* 2010); *A. ferruginea* is only found in Africa, mainly in lowlands, semi-deciduous forests, but also in evergreen forests, rainforests, and savannas (Sosef *et al.* 1998; Orwa *et al.* 2009). *Albizia procera* is found across all Southeast Asia and is tolerant to a wide range of climates; it is mostly found in open secondary forests and in areas with a pronounced dry season, as well as in grasslands, savannas, monsoon forests or swamp forests and rainforests up to 1500 m altitude (Nielsen 1981, 1992) in areas with more than 2500 mm of annual rainfall and mean annual temperature of 21–32°C (Orwa *et al.* 2009).

## Genus *Cynometroxylon* Chowdhury & Ghosh

### *Cynometroxylon holdeniae*

(Gupta) Prakash & Bande  
(Fig. 4)

*Dipterocarpoxyton holdenii* [sic] Gupta, 1935: 633, pl. 64.

*Cynometroxylon indicum* Chowdhury & Ghosh, 1946: 435, pl. 10-11, text-fig. 5-9

*Cynometroxylon schlagintweitii* Müller-Stoll & Mädler, 1967: 130, pl. 33, fig. 57, pl. 34, figs 59–62, ill. 8

*Cynometroxylon* cf. *indicum* – Prakash 1967: 93.

*Cynometroxylon* sp. cf. *indicum* – Prakash 1978: 383, pl. 3, figs 12–14.

*Cynometroxylon holdeniae* Prakash & Bande, 1980: 266, pl. 3, figs 11–14 (*holdenii*).

*Cynometroxylon siwalicus* Trivedi & Ahuja, 1978: 638, figs 1–3.

NOTE ON NOMENCLATURE. — According to the article no. 60.8 of the *International Code of Nomenclature for algae, fungi, and plants* (Turland *et al.* 2018), the specific epithet “*holdenii*” (or “*holdeni*”), derived from the personal name of Miss Ruth Holden, has to be treated as an error and corrected to “*holdeniae*”, a feminine name.

ORIGINAL HOLOTYPE. — Birbal Sahni Institute of Palaeosciences Museum no. 29785.

MATERIAL. — MNHN.F.50173 (field number: 17FN17), MNHN.F.50174 (field number: 17FN19), MNHN.F.50175 (field number: NAT17-3). Estimated minimal diameter: 8–38 cm. The specimen MNHN.F.50175 shows a differential growth as seen in modern *Cynometra polyandra* Robx. (MNHN-P-P00395888).

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.

AGE. — Upper lower to lowermost middle Miocene.

## DESCRIPTION

Wood diffuse-porous. Growth rings indistinct or weakly distinguishable by a change of parenchyma and fibres band thickness and the presence of narrow marginal parenchyma bands. Vessels mostly solitary (60–80%) or in radial groups of 2–4, round to oval, 3–24 per mm<sup>2</sup> (average: 10 per mm<sup>2</sup>) (Fig. 4A); tangential diameter 50–200 µm (average: 115 µm). Tyloses absent. Vessel elements 130–510 µm (average: 300 µm) long. Perforation plates simple, oblique to horizontal. Intervessel pits alternate, seemingly polygonal, 2–5 µm wide (average: 3 µm) (Fig. 4F). Parenchyma paratracheal, vasicentric with 1–3 cells thick sheath around vessel and in continuous, wavy and sometimes anastomosed tangential bands, 2–11 cells wide (average: 7 cells), as large as fibres bands or thinner, including most of the vessels, 2–6 bands per tangential mm (Fig. 4A, D); parenchyma cells 40–100 µm (average: 72 µm) long, 9–40 µm (average: 19 µm) wide in tangential section; 4–6 (average: 5) cells per parenchyma strand, sometimes crystals in chambered parenchyma cells. Rays 2- to 3-seriate (mostly 2) (Fig. 4E), 8–13 rays per tangential mm (average: 10 per mm), 150–740 µm (average: 310 µm) or 7–35 cells long, heterocellular made of procumbent cells with 1 (or 2) square or upright cells at both ends (Fig. 4G), occasionally with a faint storied tendency. Fibres libriform, non-septate, 8–22 µm in tangential diameter (average 14 µm), thin- to thick-walled (lumina about 0.42 times the double wall thickness), without any particular arrangement (Fig. 4D). Wound healing zone marked by alternating bands of fibres and parenchyma but less continuous and regular than in the normal wood (Fig. 4C), parenchyma bands 1–5 cells wide; no vessel present; rays are mostly continuous throughout the wounded area. This pattern recalls debarking events (Fig. 4C).

## DISCUSSION

These fossils are characterized by: 1) diffuse-porous wood; 2) exclusively simple perforation plates; 3) banded parenchyma as thick as fibres bands; 4) heterocellular and mainly 2-seriate rays; 5) a slight tendency to storied rays; and 6) non-septate fibres. The presence of a debarking healing zone is not considered for wood identification because it is a life event, independent of the wood traits. Thus, the most discriminant feature is the presence of banded parenchyma. According to the classification of Chowdhury & Ghosh (1946), our specimens belong to the group of angiosperms with parenchyma bands of the same (or almost) size as fibres bands (less than 30 cells wide). Following the identification of these authors leads to the Fabaceae.

Within extant Fabaceae, the present fossil specimens display similar features to the ones of genera *Cynometra*, *Crudia* Schreb. and *Maniltoa* Scheff. (synonym of *Cynometra*) including heterocellular rays, only one size of vessels, and vessels included in parenchyma bands (Chowdhury & Ghosh 1946; Carlquist 2001). Even



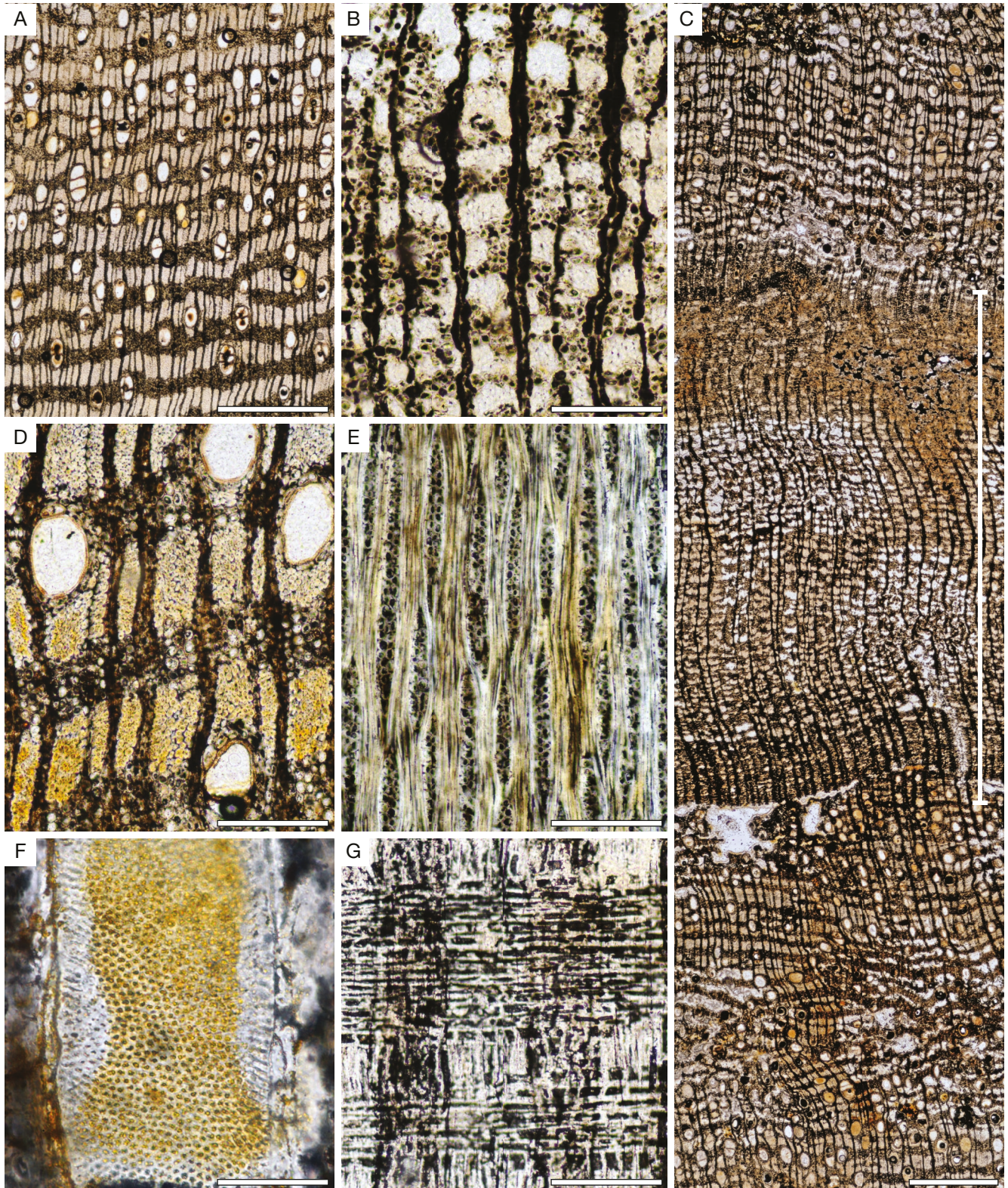


FIG. 4. — *Cynometroxylon holdeniae* (Gupta) Prakash & Bande, MNHN.F.50174 (A, D–G), MNHN.F.50173 (B, C): A, Ts, banded parenchyma and vessel arrangement; B, Ts, detail of the wounded part of the wood with irregular pattern of parenchyma, vessels are absent; C, Ts, wounded part (white segment) in between the normal wood; D, Ts, detail of banded parenchyma 2–11 cells wide bands; E, Tls, heterocellular and mostly 2-seriate rays; F, Tls, minute alternate intervessel pits; G, Rls, heterocellular rays with 1–2 rows of marginal ray cells. Scale bars: A, C, 1 mm; B, D, E, G 200  $\mu$ m, F, 50  $\mu$ m. Abbreviations: see Fig. 2.

though these species are hardly distinguishable from each other based on wood anatomy (Vozenin-Serra & Privé-Gill 1989; Soerianegara & Lemmens 1993; Ogata *et al.*

2008), *Crudia* is presumed to have larger and thicker parenchyma bands than *Cynometra* (Vozenin-Serra & Privé-Gill 1989).



*Cynometra* and *Maniltoa* are extremely close genera, and Radosavljevic (2019) recently put the genus *Maniltoa* as a synonym of *Cynometra*. *Cynometra ramiflora* L. and *Cynometra polyandra* (synonym: *Maniltoa polyandra* (Roxb.) Harms) are the most anatomically similar species to our fossils, especially concerning ray arrangement and composition, vessel size, and parenchyma band arrangement.

Fossil wood specimens resembling *Cynometra* are described under the fossil genus *Cynometroxylon* (Chowdhury & Ghosh 1946). All characters cited above fit with its diagnosis. Superficial resemblance with the genus *Millettioxylon* Awasthi can be pointed out, but the obvious storied character of rays, parenchyma and vessel elements, in addition to frequently homocellular rays dismiss this analogy (Awasthi 1967). We compare our fossils to some *Cynometroxylon* already described in the literature. The specimens MNHN.F.50173 and MNHN.F.50174 display a closer resemblance with *C. holdeniae*, especially with the Burmese specimens described by Prakash & Bande (1980) from the Mio-Pliocene and by Licht *et al.* (2014) from the middle Eocene. They show a slightly higher density of vessels (7–24 per mm<sup>2</sup> for our fossils as opposed to 3–4 per mm<sup>2</sup> for *C. holdeniae*), which might be related to environmental factors and is not enough to exclude their attribution to this species. The specimen MNHN.F.50175 shows some variations of character such as irregular size of bands, both for parenchyma and fibres, which could be interpreted as growth zones. These irregular bands are seen in extant *Cynometra* (e.g. *Cynometra ananta* Hutch. & Dalziel, *Cynometra polyandra*: InsideWood 2004-onward). In some places, a storied tendency is observed.

Among *Cynometroxylon* specimens, only *C. schlangintweitti* and *C. tunesense* Delteil-Desneux are described with a storied ray tendency, but both have homocellular rays (Müller-Stoll & Mädler 1967; Delteil-Desneux 1980). Only some specimens of *C. holdeniae* have crystalliferous parenchyma (Chowdhury & Ghosh 1946; Müller-Stoll & Mädler 1967; Awasthi 1992; Boonchai 2008). Thus, except for the irregular bands, all these features have been described in *Cynometroxylon*, but not all in the same specimen. Considering the variability seen among *Cynometroxylon*, all our specimens are attributed to *Cynometroxylon holdeniae*.

*Cynometra* species are pantropical shrubs or trees (Lewis *et al.* 2005), though Radosavljevic (2019) recently excluded African species from the genus (except species from Madagascar). They are found in forests up to 1300 m altitude, often along rivers, on swampy soils, in dense wet lowland forests, or mixed with mangrove species (Soerianegara & Lemmens 1993; Hou *et al.* 1996), and also in seasonally dry forests (Lewis *et al.* 2005). *Cynometra ramiflora* is present in tidal forests of Myanmar, South India, Sri-Lanka, Andaman Islands and Malay Peninsula (Privé-Gill *et al.* 2004), in the back-mangrove forests and inland up to 400 m altitude (Soerianegara & Lemmens 1993; Hou *et al.* 1996). *Cynometra polyandra* is a wet evergreen or semi-evergreen forest tree (Knaap-van Meeuwen 1970; Soerianegara & Lemmens 1993), found up to 1300 m altitude (Soerianegara & Lemmens 1993; Hou *et al.* 1996).

## *Cynometroxylon parinaequifolium* Prakash (Fig. 5A–G)

*Cynometroxylon parinaequifolium* Prakash, 1979: 51, pl. 2, figs 5, 7.

ORIGINAL HOLOTYPE. — Birbal Sahni Institute of Palaeosciences Museum no. 35263

MATERIAL. — MNHN.F.50176 (field number: 17FN10), MNHN.F.50177 (field number: 19NAT07-1), MNHN.F.50178 (fieldnumber: NAT17-7). Estimated minimal diameter: 9–20 cm (> 50 cm for specimen MNHN.F.50178, which has almost parallel rays).

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.

AGE. — Upper lower to lowermost middle Miocene.

### DESCRIPTION

Wood diffuse-porous. Growth rings hardly distinguishable marked by small marginal parenchyma bands, a change in vessel or fibres band size or growth line (Fig. 5A). Vessels solitary (40–75%) or in radial groups of 2–5, round to oval, 3–16 per mm<sup>2</sup> (average 8 per mm<sup>2</sup>); tangential diameter 50–170 µm (average: 120 µm) (Fig. 5A, F, G). Tyloses absent. Vessel elements 150–600 µm (average: 330 µm) long. Perforation plates simple, sometime slightly oblique. Intervessel pits alternate, 2–4 µm wide (average: 3 µm) (Fig. 5E). Parenchyma mostly banded but also aliform or vasicentric close to growth rings, bands wavy and sometimes anastomosed, enclosing most of vessels (Fig. 5A, F, G), 3–8 cells wide (average: 5 cells), as large as fibres bands or thinner, 3–5 bands per mm; parenchyma cells 35–160 µm (average: 100 µm) long, 10–36 µm (average: 22 µm) wide in tangential section; 5 to 8 cells per parenchyma strands, crystals sometimes present in chambered parenchyma cells (Fig. 5D). Rays 1- to 3-seriate (mostly 2-seriate) (Fig. 5B, C), 6–13 rays per mm (average: 9 per mm), 140–1080 µm (average: 470 µm) or up to 35 (sometimes 55) cells long, heterocellular made of procumbent cells with 1–3 square or upright marginal cells (Fig. 5C), sometimes end-to-end fusions resulting in very high rays. Fibres non-septate, 5–20 µm in tangential diameter (average 13 µm), thin- to thick-walled (lumina about 0.42 times the double wall thickness).

### DISCUSSION

This specimen has: 1) diffuse-porous wood; 2) banded parenchyma about as thick as fibres bands; 3) 1–3 seriate heterocellular rays; 4) non-septate fibres; and 5) non-storied elements. Similar to our previous *Cynometroxylon* specimens, these three specimens are comparable to extant *Cynometra*. They also are remarkable in having thinner parenchyma bands (around 5 cells high), higher rays and frequent ray fusions.

They display a close resemblance to *Cynometra polyandra* because of its variability of parenchyma pattern and ray width, and to *Cynometra inaequifolia* A. Gray because of its ray width and the occasional presence of long rays (up to 1 mm long) (InsideWood 2004-onward).

These specimens also share all the diagnostic features of the genus *Cynometroxylon*. Rays are rarely uniseriate and always





FIG. 5. — *Cynometroxylon parinaequifolium* Prakash, MNHN.F.50176 (A–C, E), MNHN.F.50177 (D, F), MNHN.F.50178 (G): A, Ts, vessels, parenchyma alternately banded, aliform and vasicentric, growth limits between arrows; B, Tls, 1–3 seriate rays, non-septate fibres; C, Rls, heterocellular rays with 1–2 rows of marginal cells (arrows); D, Tls, mostly 2-seriate rays with parenchyma sometimes crystalliferous (arrow); E, Tls, alternate intervessel pits; F, Ts, banded and aliform parenchyma; G: Ts, banded and aliform parenchyma. Scale bars: A, 1 mm; F–G, 500  $\mu$ m; B, D, 200  $\mu$ m; C, 100  $\mu$ m; E, 50  $\mu$ m. Abbreviations: see Fig. 2.

heterocellular, parenchyma bands are mostly wavy, which make them somehow compatible with the diagnosis of *Crudioxylon* Pons (1980) as well. When compared with other *Cynometroxylon*, our specimens resemble closely to *C. parinaequifolium*, which also has small vessels (< 200  $\mu$ m of diameter), parenchyma bands 2–7 cells wide, and sometimes long rays (up to 60 cells high) with frequent fusions. Our specimens have a slightly higher density of vessels and display sometimes 3-seriate rays (only 1–2-seriate reported in *C. parinaequifolium*). Two out of three of our fossil specimens display parenchyma bands that are sometimes discontinuous (Fig. 4A, D) which is not in the diagnosis of *C. parinaequifolium*. MNHN.F.50176 is the specimen where this morphology is the most visible (Fig. 4A–C).

These differences could yet be explained by intra-individual variations, as proposed by Pons (1980) for *Crudioxylon*. Discontinuous bands and aliform parenchyma are also observed in the *Cynometroxylon holdeniae* specimen of Boonchai (2008) and the fossil *Cynometra grandis* Woodcock, Meyer & Prado specimen of Woodcock *et al.* (2017). It is also visible in extant *Cynometra ananta* and *Cynometra polyandra* of InsideWood (2004–onward) and Boonchai (2008: 111–112, fig. 4.41, fig. 4.42). An examination of the specimen MNHN-P-P00395888 of *C. polyandra* reveals that parenchyma arrangement and band width can change throughout the life of the tree. We thus consider that discontinuous bands in *Cynometra* and *Cynometroxylon* are a variable character and not a diagnostic feature of our



fossils. All these observations lead us to attribute these three specimens to *Cynometroxylon parinaequifolium*.

*Cynometra inaequifolia* is a small lowland tree (up to 20 m tall) of Malaysia, Philippines, and Thailand resembling *C. rami-flora* (Knaap-van Meeuwen 1970; Soerianegara & Lemmens 1993; Hou *et al.* 1996; World Conservation Monitoring Centre 1998). *Cynometra polyandra* is a wet evergreen or semi-evergreen forest tree species (Knaap-van Meeuwen 1970; Soerianegara & Lemmens 1993), found up to at 1300 m altitude (Knaap-van Meeuwen 1970; Hou *et al.* 1996; World Conservation Monitoring Centre 1998).

## Genus *Koompassioxylon* Kramer

### *Koompassioxylon elegans* Kramer (Fig. 6)

*Koompassioxylon elegans* Kramer, 1974: 117, pl. 27, figs 94, 95, 97-101, 103, pl. 28, fig. 105, ill. 12a-c, 13.

ORIGINAL HOLOTYPE. — Senckenberg Museum, Frankfurt. no. SM.B 12 509/1-12 509/3

MATERIAL. — MNHN.F.50179 (field number: 17FN13), MNHN.F.50180 (field number: 17FN14), MNHN.F.50181 (field number: 19NAT03-2). Estimated minimal diameter: 17-51 (-81) cm; 130-230 cm for specimen MNHN.50179.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.

AGE. — Upper lower to lowermost middle Miocene.

## DESCRIPTION

Wood diffuse-porous. Growth rings present, marked by marginal parenchyma bands (Fig. 6A). Vessels mostly solitary (70-90%) or grouped by 2 or 3 (Fig. 6A), oval, 0-6 per mm<sup>2</sup> (average: 3); tangential diameter 120-370 µm (average: 230). Tyloses absent. Vessel elements 160-570 µm long (average: 340). Perforation plates simple horizontal to slightly oblique. Vessel pits alternate, 6-11 µm (average: 8) in diameter, likely non-vestured (for specimen MNHN.F.50180, see Fig. 6C). Vessel-ray pits not preserved. Parenchyma widely winged-aliform (Fig. 6A, B), also confluent laterally or in diagonal, forming anastomosed and/or band-like shapes, joining up to 10 vessels depending on the specimen and the position in the wood (Fig. 6A), also in 1-7 cells wide marginal bands enclosing some small vessels (Fig. 5A), maybe rare diffuse parenchyma; parenchyma cells 30-145 µm long (average: 85), 10-50 µm wide (average: 30); 4-8 or more cells per parenchyma strand; crystals in chambered parenchyma cells (Fig. 6D, E), especially in border ones. Rays 2- to 3-seriate (mainly 3, rarely 4) (Fig. 6D, E), tendency to storied arrangement resulting in discreet ripple marks visible in some parts with the naked eye (Fig. 6F), 3-10 rays per mm (average: 7), 160-490 µm (average: 340 µm) or up to 18 cells high, heterocellular with 1-2 rows of upright or square cells at both ends (Fig. 6G); 1-2 crystals in upright ray cells, sometimes subdivided (Fig. 6G). Fibres thin-to-thick walled (lumina about 0.84 times the double wall thickness), non-septate, 8-22 µm (average: 14 µm) wide.

## DISCUSSION

These specimens are characterized by: 1) diffuse-porous wood; 2) large vessels (> 200 µm); 3) exclusively simple perforation plates; 4) crystalliferous winged-aliform and confluent parenchyma; 5) marginal parenchyma bands; 6) 2- to 3-seriate rays with a storied tendency; 7) low vessel density; 8) heterocellular rays; and 9) crystalliferous rays. Aliform parenchyma, marginal parenchyma and 2-3 seriate rays are common features in Fabaceae. Modern analogs with all characteristics cited above have not been found on InsideWood (2004-onward), but a less restrictive code (5p 13p 22p 40a 48a 49a 50a 65a 80p 82p 83p 89p 96a 97p 99a 105a 108a 109a 116a 136p 137p 142p with 0 mismatches) shows similarities with: *Dalbergia assamica* Benth.; *Distemonanthus benthamianus* Baill.; *Angylocalyx* Taub.; *Desmodium oojeinense* (Roxb.) Ohashi; and several species of *Ormosia* Jacks. which either lack storied features, crystals, have all elements storied or diffuse parenchyma (InsideWood 2004-onward, Ogata *et al.* 2008). When considering the possible non-vestured pits of one of our specimens, *Kalappia celebica* Kosterm. and *Koompassia* Maingay ex Benth. are the closest genera, but the former has well-marked storied rays with no crystals in marginal cells (Ogata *et al.* 2008). *Koompassia* is thus the best living relative as it has irregularly storied rays, non-vestured pits, crystals in rays and parenchyma, aliform-confluent, sometimes winged-aliform parenchyma and marginal parenchyma bands. The preservation state of our specimens is yet not good enough to determine whether the pits are vestured or not for all the specimens. In this genus, *K. excelsa* (Becc.) Taub. has more often banded parenchyma, often crystals in upright ray cells; *K. malaccensis* Benth. bears the closest resemblance with our specimens, and has aliform-confluent parenchyma, sometimes pointed at the extremities, but less often crystals in upright ray cells than *K. excelsa* (Soerianegara & Lemmens 1993; InsideWood 2004-onward; Ogata *et al.* 2008).

Kramer (1974) defined the fossil genus *Koompassioxylon* for fossils resembling *Koompassia* (*K. malaccensis* more specifically). The genus *Koompassioxylon* is thus described with marginal parenchyma, vessel-ray pits similar to intervessel pits, crystalliferous aliform-confluent to winged aliform parenchyma, 2-4 seriate rays with irregularly storied pattern, heterocellular rays with at least one row of upright marginal cells, sometimes subdivided with crystal included. In opposition to the modern relative *Koompassia*, which has non-vestured intervessel pits, *Koompassioxylon* has vestured intervessel pits. The genus *Ormosioxylon* Bande & Prakash was described by Bande & Prakash (1980) for wood specimens resembling *Ormosia*. Although the two diagnoses significantly overlap, *Ormosioxylon* is described without any mineral inclusion, which is not compatible with our specimens.

Vestured/non-vestured intervessel pits are very delicate to observe in fossils and should be considered with great caution according to Wheeler *et al.* (2020). With this limitation in mind, our fossils share most of the features of *Koompassioxylon*. Among the two species of *Koompassioxylon*, *K. keralaensis* Srivastava & Awasthi (1996) has less frequent confluent parenchyma, mostly homocellular rays, irregularly storied parenchyma and rays, and no crystals; by contrast, *K. elegans* is more similar to



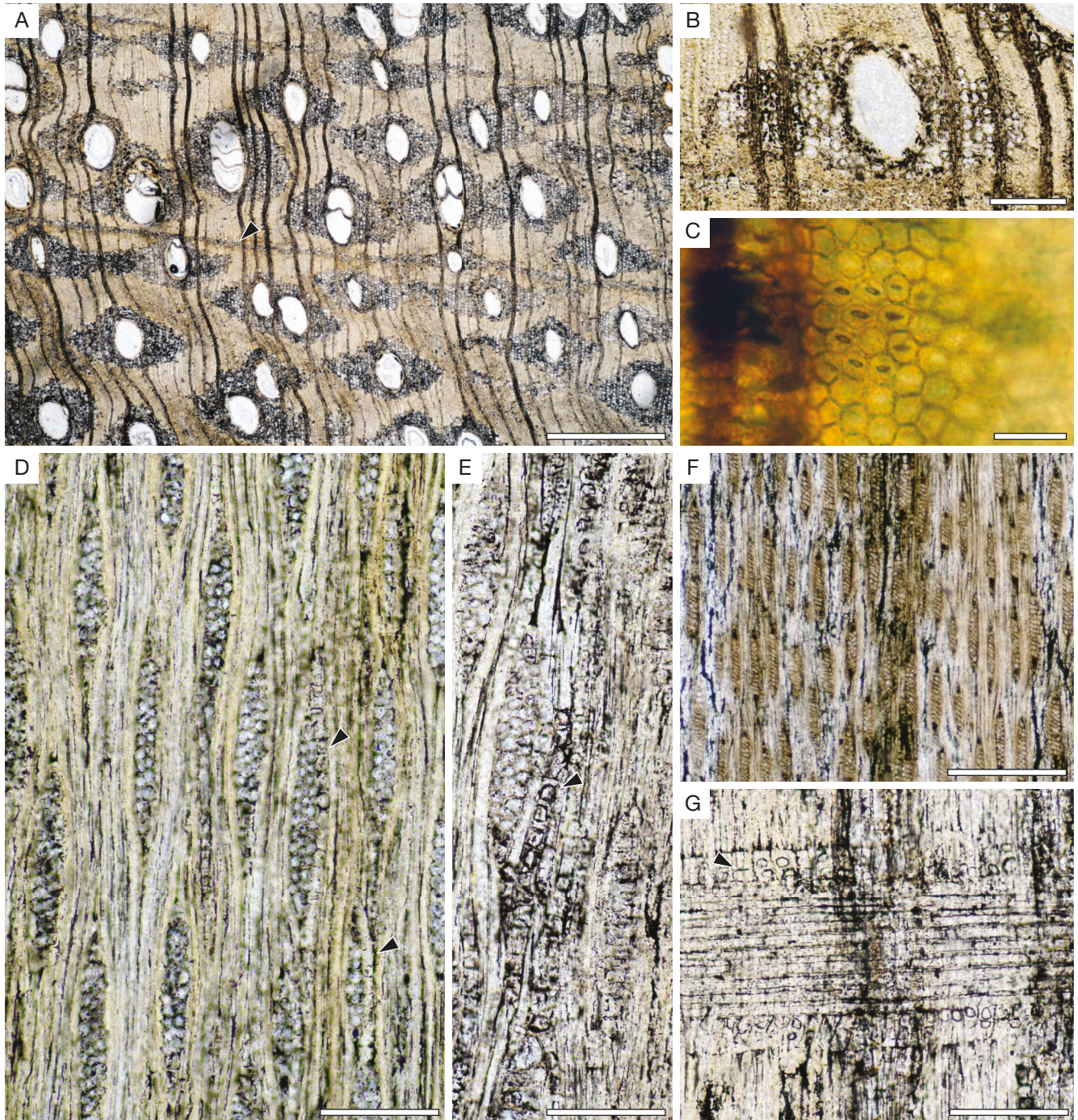


FIG. 6. — *Koompassioxylon elegans* Kramer, MNHN.F.50180 (A-E, G), MNHN.F.50181 (F): A, Ts, vessel size and groups, aliform parenchyma with pointed wings and marginal parenchyma sometimes merged with small vessels (arrow); B, Ts, detail of winged-aliform parenchyma; C, Tls, non-vestured, alternate and polygonal intervessel pits; D, Tls, 2-3-seriate rays with crystalliferous parenchyma (arrow); E, Tls, detail of the chambered crystalliferous parenchyma (arrow); F: storied ray tendency, mostly 2-3-seriate rays; G, Rls, heterocellular rays with crystals in upright (sometimes subdivided) marginal cells (arrow). Scale bars: A, 1 mm; F, 500 µm; B, D-E, G, 200 µm; C, 20 µm. Abbreviations: see Fig. 2.

our fossil specimens as it has marginal parenchyma, as well as pointed aliform-confluent with crystals, weakly heterocellular rays with crystalliferous upright marginal cells, a storied ray tendency, but it has mainly 2-seriate rays (compared to mainly 3-seriate in our specimens). This minor difference aside, and with the exception of possibly non-vestured pits, our specimens are compatible with the diagnosis of *K. elegans*.

*Koompassia* is a genus of Southeast Asian tropical trees growing in primary rainforests, coastal plain, foothills, ridge slopes and river valleys, and occasionally in peat and freshwater swamps, below 650 m altitude (Soerianegara & Lemmens 1993; Lewis *et al.* 2005). *Koompassia* are large trees, often dominating the canopy; the large estimated diameter of our specimens is in adequacy with this genus of ‘giant’ trees. Indeed, they can



grow up to 85 m tall, with a diameter up to 290 cm (Soerianegara & Lemmens 1993). *Koompassia malaccensis* lives in lowland forests and in freshwater peat and swamp forests, as well as in dry lands up to 150 m altitude (rarely up to 800 m; Soerianegara & Lemmens 1993; Hou *et al.* 1996).

cf. *Koompassioxylon*  
(Fig. 7)

MATERIEL. — MNHN.F.50182; field number: NAT17-06. Estimated minimal diameter: 11 cm.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.

AGE. — Upper lower to lowermost middle Miocene.

DESCRIPTION

Wood diffuse-porous. Growth rings indistinct, but possible marginal bands. Vessels mostly solitary (80 %) or grouped by 2 or 3 (Fig. 7A, C), oval, 4–9 per mm<sup>2</sup> (average: 7); tangential diameter 140–250 µm (average: 180 µm; measured on less compressed vessels but still underestimated). The radial diameter (71–350 µm, average: 225 µm) assumes a large tangential diameter. Tylose absent or rarely present (Fig. 7C). Vessel elements 220–460 µm long (average: 300 µm). Perforation plates simple. Intervessel pits alternate, bordered, 6–13 µm (average: 10 µm) in diameter, non-vestured (Fig. 7G). Vessel-ray pits rather similar in shape and size to intervessel pits (Fig. 7I), 4–11 µm in diameter (average: 7.3 µm). Parenchyma widely aliform and mostly confluent laterally or in diagonal, forming anastomosed shapes, no proper tangential bands (Fig. 7A–C); also, maybe in marginal or seemingly marginal thin bands merging with the paratracheal parenchyma; parenchyma cells 50–130 µm long (average: 85 µm), 10–30 µm wide (average: 20 µm); 3–8 (or more ?) cells per parenchyma strands (Fig. 7F); abundant crystals in chambered parenchyma cells (Fig. 7H, J), especially in the margin ones. Rays 1- to 3-seriate (mostly 2-seriate, very few uniseriate) (Fig. 7E, F), irregularly storied (Fig. 7D) resulting in ripple marks visible with the naked eye, 8–16 rays per mm (average: 11), 150–870 µm (average: 400 µm) or 6–27 cells high (average: 16–17 cells), occasional interconnections of rays (Fig. 7E) with alternating uniseriate and 2–3-seriate portions probably resulting from end-to-end fusions, thereby some rays are up to 30 cells high, weakly heterocellular to heterocellular to with mostly one to sometimes 2–3 rows of upright or square cells at both ends (Fig. 7H) or at least larger procumbent cells, possibly very rarely with 1–2 crystals in marginal cells; a tendency to have biseriate portions as wide as multiseriate ones, but not to be considered as a distinctive feature. Fibres commonly thin-to-thick walled (lumina 0.66 times the double wall thickness) to occasionally very thick-walled, non-septate, 12–24 µm (average: 17 µm) wide.

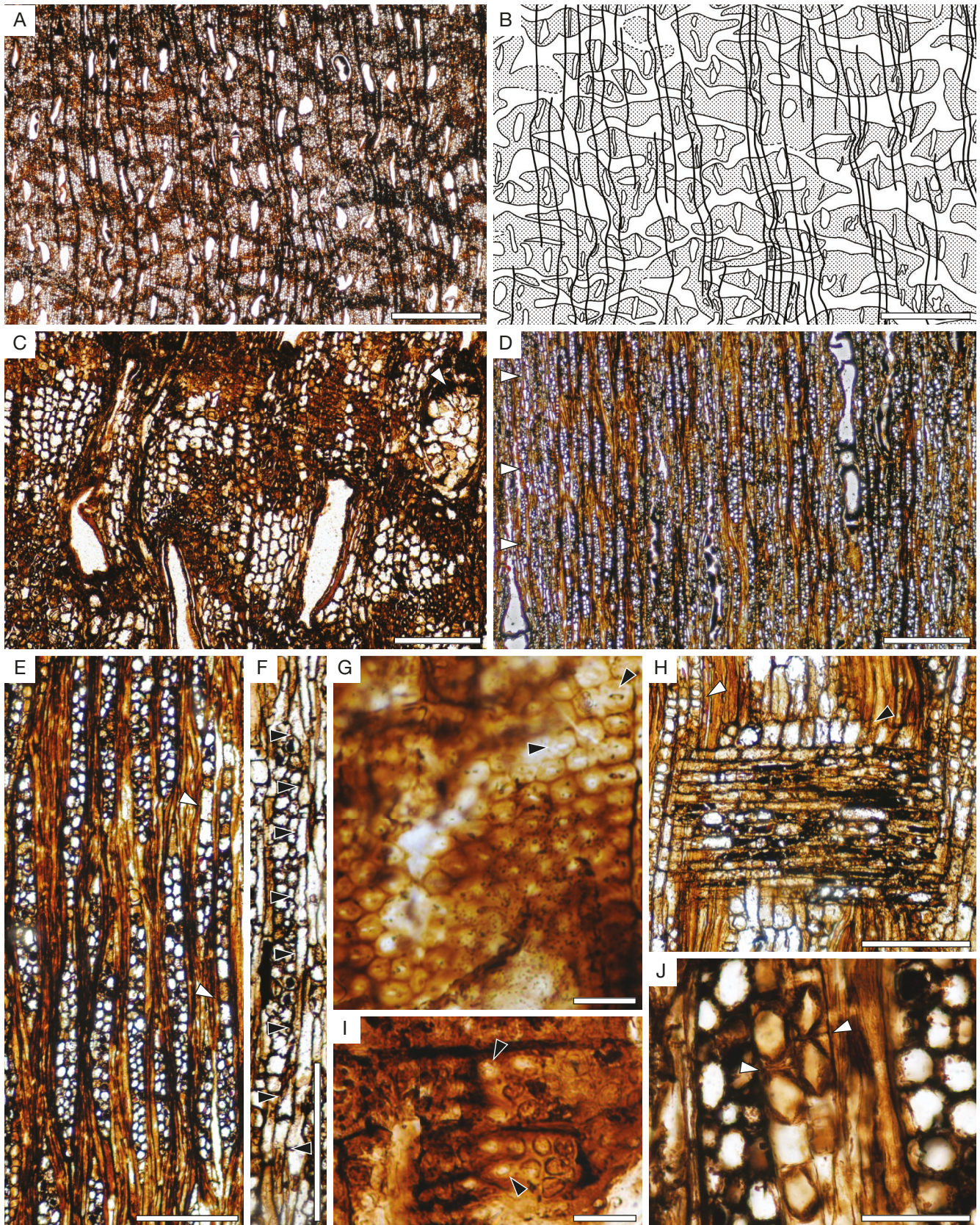
DISCUSSION

This wood is characterized by: 1) diffuse-porous; 2) aliform parenchyma; 3) crystals in parenchyma cells; 3) mostly 2-seriate rays; 4) non-septate fibres; 5) vessel-ray pits similar to intervessel pits; and 6) simple perforation plates; these features are typical of modern Fabaceae (Metcalf & Chalk 1950; Baretta-Huipers 1981; InsideWood 2004–onward). A search on the InsideWood (2004–onward) database shows affinities with species from the traditional Caesalpinioideae subfamily because of the number of cells per parenchyma strand that goes up to four cells, compared to hardly exceeding two cells for the traditional Papilionoideae subfamily. Concerning the traditional Mimosoideae, most species have homocellular rays, often septate fibres and rarely storied structures. Non-vestured pits are uncommon in Fabaceae and are restricted to three recircumscribed basal subfamilies: Cercidoideae, Duparquetioideae and Dialioideae (Herendeen 2000; Gasson *et al.* 2003; LPWG 2017; Zimmerman *et al.* 2017), all previously in the traditional Caesalpinioideae subfamily. An investigation of wood anatomy of these subfamilies was made with available literature (Gasson *et al.* 2003; InsideWood 2004–onward; Ogata *et al.* 2008; Pérez-Lara *et al.* 2019). *Duparquetia* Baill., the only genus of Duparquetioideae, is ruled out as it is a vine with no mineral inclusion and very thin-walled fibres. In Cercidoideae, only *Bauhinia* (which has a wide range of morphology) can be related to this fossil, but it shows more frequent uniseriate rays, sometimes septate fibres, homocellular rays or regular bands of parenchyma. Moreover, the number of cells per parenchyma strand is restricted to 4 in average in *Bauhinia* (compared to more than 4 in our fossil). Among Dialioideae, only *Kalappia* Kosterm., *Koompassia* and *Martiodendron* Gleason share features with our fossil: storied or irregularly storied rays, aliform-confluent parenchyma, 1–3 seriate rays, crystals in parenchyma, at least medium size intervessel pits and heterocellular rays. *Kalappia* and *Martiodendron* yet differ in having a strongly storied parenchyma, vessel elements and rays, fewer or more wavy confluent parenchyma, as well as smaller rays for *Kalappia* (up to 350 µm compared to 400 µm in average in our fossil). *Koompassia* wood is thus closer to our fossil than the other identified modern analogues, but has more frequent crystals in marginal cells; however, no specific NLR really stands out in regards of the state of preservation of the present fossil.

The fossil genus *Tzotziloxylon* Pérez-Lara & Estrada-Ruiz (Pérez-Lara *et al.* 2019) covers fossils sharing features of the Cercidoideae/Dialioideae which includes non-vestured intervessel pits, aliform to occasionally confluent parenchyma as well as diffuse and sometimes banded, 1–4-seriate rays, crystalliferous parenchyma and non-storied structure. Our fossil is thus incompatible with this genus. Among Cercidoideae, woods resembling *Bauhinia* are described under the name *Bauhinia* and *Bauhinium* Trivedi & Panjwani with regularly storied and mostly uniseriate rays as well as regular parenchyma bands

Fig. 7. — cf. *Koompassioxylon*, MNHN.F.50182: **A**, Ts, mostly solitary vessels with aliform and aliform-confluent parenchyma, sometimes forming anastomosed shapes; **B**, Ts, interpretation of **A** of the parenchyma pattern (dotted) showing mostly confluent parenchyma, aliform parenchyma, but no regular bands; **C**, Ts, detail of aliform parenchyma and one vessel with tyloses (although rare, arrow); **D**, Tls, storied tendency of rays (arrows); **E**, Tls, 1–3 seriate heterocellular rays, sometimes with some rays with alternating uniseriate and multiseriate portions (arrows); **F**, Tls, detail of a 2-seriate ray bordered by a strand of parenchyma





made of at least eight cells (each marked by **arrow**); **G**, RIs, non-vestured (**arrows**), alternate, polygonal intervessel pits; **H**, RIs, heterocellular rays, sometimes with upright marginal cells (**black arrow**) and crystalliferous parenchyma, with more than 11 crystals per strand (**white arrow**); **I**, RIs, vessel-ray pits with distinct border (**arrows**) of the same size and shape as intervessel-pits; **J**, TIs, detail of crystals in chambered (**arrows**) parenchyma cells. Scale bars: A, B, 1 mm; D, 500 µm; C, E, F, H, 200 µm; G, I, J, 20 µm. Abbreviations: see Fig. 2.



(Ramanujam & Rao 1966; Prakash & Prasad 1984; Trivedi & Panjwani 1986; Awasthi & Prakash 1987; Awasthi & Mehrotra 1990). The diagnosis of these genera is yet incompatible with our specimen. Among Dialioideae, woods resembling *Koompassia* are described under the name *Koompassioxylon* (Kramer 1974; Srivastava & Awasthi 1996). Although most of the features of the genus diagnosis are compatible with our fossil, some differences have to be pointed out: the aliform to confluent parenchyma with only a few vessels, marginal ray cells can be subdivided and contain crystals (presence of which is ambiguous in the present fossil as it is hard to determine if crystals belong to ray cells or the underneath axial parenchyma cells). Moreover, intervessel pits are vested in previously described specimens of *Koompassioxylon*. This specimen is different from the *K. elegans* described above (p. 864) because of the absence of numerous crystals in marginal ray cells, mainly confluent parenchyma and mainly 2-seriate rays. Pending more comprehensive studies about fossil Cercidoideae/Dialioideae and other related Fabaceae, we name it cf. *Koompassioxylon* to emphasize its close affinity to this genus.

*Koompassia* ecology has been previously described (p. 864). *Kalappia* trees reach up to 40 m tall, 90 cm in diameter, and are restricted to wet lowland forests of Sulawesi, up to 300 m (rarely 500 m) altitude (Hou *et al.* 1996; Sosef *et al.* 1998). *Martiodendron* are South American canopy trees, often riparian, growing in rainforests, periodically inundated forests, but also in tropical savanna woodlands, deciduous or seasonally dry forests, below 600 m altitude (Koeppen & Iltis 1962; Lewis *et al.* 2005). These genera have relatively hard and durable wood (Scheffer & Morrell 1998).

#### Genus *Pahudioxylon* Chowdhury, Ghosh & Kazmi

##### *Pahudioxylon bankurensis* Chowdhury, Ghosh & Kazmi (Fig. 8)

*Pahudioxylon bankurensis* Chowdhury, Ghosh & Kazmi, 1960: 22, pl. 2, figs 1-6, ill. 1.

*Albizzioxylon sahnii* Ramanujam, 1960: 118, pl. 21, ill. 25.

*Pahudioxylon sahnii* Ghosh & Kazmi, 1961: 96, figs 1, 2.

*Pahudioxylon deomaliense* Prakash, 1965c: 433, figs. 1, 2.

*Ingoxylon sahnii* – Müller-Stoll & Mädler 1967: 112.

*Pahudioxylon welkitii* Lemoigne & Beauchamp, 1972: 336, pl. 12.

*Pahudioxylon assamicum* Prakash & Tripathi, 1975: 63, pl. 2, figs 7, 9, 11, 12.

*Pahudioxylon indicum* Prakash, 1979: 66, pl. 2, figs 1-5.

*Pahudioxylon bengalensis* Ghosh & Roy, 1982: 52, figs 1, 2.

ORIGINAL HOLOTYPE. — Geological Survey of India (G.S.I.) no. P2/126.

MATERIAL. — MNHN.F.50183 (field number: 17FN03). Estimated minimal diameter: 14-34 cm.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.

AGE. — Upper lower to lowermost middle Miocene.

#### DESCRIPTION

Wood diffuse-porous. Growth ring boundaries distinct, marked by marginal parenchyma bands (Fig. 8). Vessels solitary (55%) as well as in radial groups of 2-4 (45%) (Fig. 8A), round to oval, 1-5 per mm<sup>2</sup> (average: 3); tangential diameter 120-275 µm (average: 185 µm). Tyloses absent. Vessel elements 120-370 µm (average: 225 µm) long. Perforation plates simple. Intervessel pits alternate, polygonal shaped, 4-7 µm (average: 6 µm) wide (Fig. 8C). Parenchyma paratracheal lozenge-aliform up to 13 cells wide for each wing and 5 cells around vessels, also confluent joining 2-4 vessels or groups of vessels (Fig. 8A, B), marginal bands 4-5 cells wide, sometimes surrounding narrower vessels; parenchyma cells 35-160 µm (average: 90 µm) long, 15-40 µm (average: 26 µm) wide; around 3-5 cells per parenchyma strand (Fig. 8E), crystals in chambered parenchyma cells at the margin of the aliform parenchyma (Fig. 8E), crystals are visible as black dots on the transversal section (Fig. 8A, B); possibly some rare diffuse parenchyma cells. Rays 1- to 3- seriate (mostly 3) (Fig. 8E), a very faint storied tendency in some parts of the section (Fig. 8D), 5-7 rays per mm (average: 6), 140-370 µm (average: 245 µm) or 8-21 cells high, mostly homocellular made of procumbent cells (Fig. 8F), rarely 1 row of marginal square (or larger procumbent) cells with sometimes crystals in them (Fig. 8G). Fibres non-septate, 7-30 µm (average: 19 µm) wide, thin-to-thick walled (lumina 1.6 times the double wall thickness in average).

#### DISCUSSION

This specimen is characterized by: 1) diffuse-porous wood, 2) exclusively simple perforation plates; 3) homocellular and 2- to 3-seriate rays; 4) aliform to aliform-confluent parenchyma; 5) marginal parenchyma; and 6) storied ray tendency in places. These combined features are shared with some Fabaceae (Baretta-Kuipers 1981; Gasson *et al.* 2003; Evans *et al.* 2006; InsideWood 2004-onward), and in particular with many traditional Caesalpinioideae because most of the genera have heterocellular rays as well as rays more than 500 µm high and the number of cells per parenchyma strand often goes up to 4 and even more (compared to hardly exceeding 2 for the traditional Papilionoideae subfamily). Traditional Mimosoideae are ruled out as many genera have septate fibres (about 30 %), exclusively homocellular rays with small ray cells, rare storied structures and no crystals in ray cells. A comparison with Caesalpinioideae genera reveals that our specimen looks similar to the genera *Afzelia* and *Intsia* (Gasson *et al.* 2003; InsideWood 2004-onward), especially for their well-defined aliform parenchyma, sometimes confluent, their marginal parenchyma bands, the distinct crystals present in the margin of the aliform parenchyma (even in transverse section), and the strands commonly from 2 to 5 cells long. Both genera are hardly distinguishable based on xylological characters (Prakash 1966; Müller-Stoll & Mädler 1967; Gasson *et al.* 2003; Ogata *et al.* 2008) although they have a different geographical distribution (Léonard 1950). *Afzelia* is a genus of Africa and South-East Asia (mostly in Africa) (Léonard 1950; POWO 2019). *Intsia* is a South and South-East Asian



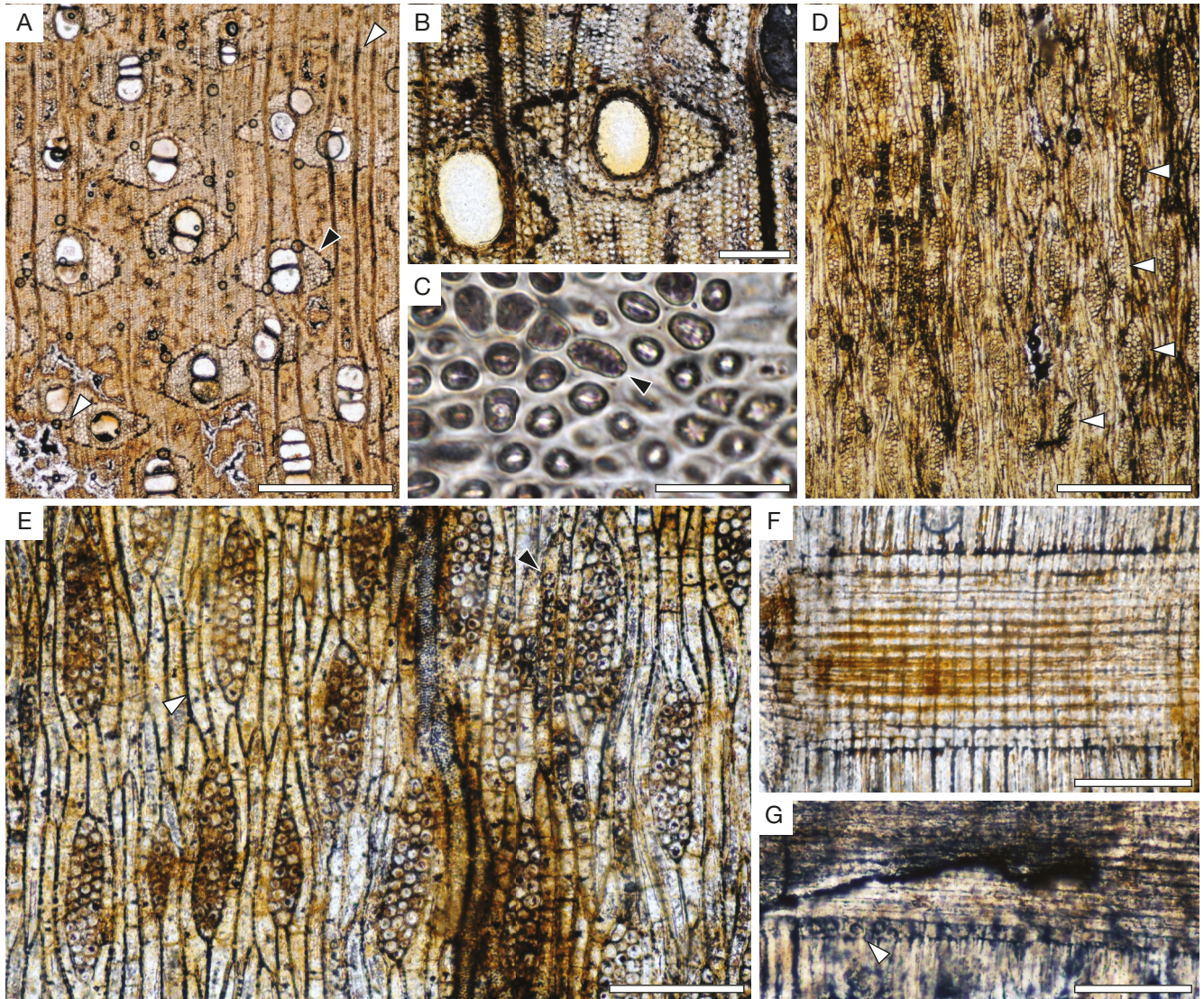


FIG. 8. — *Pahunioxylon bankurensis* Chowdhury, Ghosh & Kazmi, MNHN.F.50183: **A**, Ts, solitary vessels or in radial multiples of 2-4, aliform parenchyma with marginal crystals (**black arrow**) and marginal parenchyma (**white arrow**); **B**, Ts, detail of aliform parenchyma with crystals in marginal cells; **C**, Tls, alternate intervessel pits, probably vestured (**arrow**); **D**, Tls, rays with storied tendency (**arrows**); **E**, Tls, 2-3 seriate, not storied rays with crystalliferous parenchyma (**black arrow**), strand of parenchyma made of 4 cells (**white arrow**); **F**, Rls, homocellular ray; **G**, Rls, sometimes but rarely crystals in marginal ray cells (**arrow**). Scale bars: A, 1 mm; D, 500 µm; B, E, 200 µm; F-G, 150 µm; C, 20 µm. Abbreviations: see Fig. 2.

genus, with species also present in Australia, Madagascar or Tanzania (POWO 2019). Based on a comparison with some species of *Afzelia* and *Intsia* from the InsideWood (2004-onward) database and the Xylarium of the MNHN (specimen MNHN-P-P00396553), our specimen shows the closest affinity with *Intsia bijuga* (Colebr.) Kuntze because of the clear margin of crystalliferous aliform parenchyma cells, a tendency to irregular storied rays, clear marginal bands of parenchyma often in contact with small vessels and the frequency of vessels. Although, this species does not display any marginal square ray cells with crystals, this feature is only sporadically observed in our fossil and should not be used as a distinctive feature.

Based on their similar wood anatomy, fossil wood resembling both *Afzelia* and *Intsia* are described under the genus *Pahunioxylon* (Chowdhury *et al.* 1960). When compared

with fossil species of this genus (a synthetic table is provided by Feng *et al.* 2015), all features of our fossil are compatible with the wide diagnosis of *P. bankurensis*. Our specimen is thus attributed to *P. bankurensis*.

*Intsia* trees are tropical and live in wet evergreen forests, with rainfall higher than 2000 mm per year, and is associated with *Anisoptera* Korth. and *Hopea* Roxb. (Soerianegara & Lemmens 1993). *Intsia* are mostly found in coastal habitat, near beaches, mangroves (Loo & Tan 1997) and sometimes in peatlands (Tanjung *et al.* 2020). *Intsia bijuga* is found along coasts, river edges, tidal or temporarily inundated places (sometimes salty water), in mangroves and back-mangroves, primary and secondary forests, up to 600 m altitude (Soerianegara & Lemmens 1993; Hou *et al.* 1996; Orwa *et al.* 2009). Its seeds are sea-dispersed (Lewis *et al.* 2005).



*Pahudioxylon* cf. *bankurensis*  
(Fig. 9)

Same synonymy list as *Pahudioxylon bankurensis*.

ORIGINAL HOLOTYPE. — Geological Survey of India (G.S.I.) no. P2/126.

MATERIAL. — MNHN.F.50184 (field number: 17FN06), MNHN.F.50185 (field number: 17FN16), MNHN.F.50186 (field number: 17FN18). Estimated minimal diameter: 10–28 cm, 38–60 cm for specimen 17FN18.

AGE. — Upper lower to lowermost middle Miocene.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.

DESCRIPTION

Wood diffuse-porous. Growth rings present, marked by marginal parenchyma bands (Fig. 9A). Vessels mostly solitary (70–90%) or grouped by 2–4 (Fig. 9A), round to oval, 1–7 per mm<sup>2</sup> (average 3); tangential diameter 100–300 µm (average 200 µm). Tyloses absent. Vessel elements 160–570 µm (average 310 µm) long. Perforation plates simple (Fig. 9E). Intervessel pits alternate, 4–12 µm (average 8 µm) in diameter, apparently vested (Fig. 9G). Axial parenchyma lozenge-aliform to weakly confluent when vessels are close to each-other, and in marginal bands 1–7 cells wide, sometimes merging with the aliform parenchyma of smaller vessels (Fig. 9A); diffuse sometimes present, larger than fibres cells, often in the vicinity of the rays but also scattered among fibres (Fig. 9A, B); parenchyma cells 40–145 µm (average 80 µm) long, 10–49 µm (average 25 µm) wide; 2–4 or more cells per parenchyma strands; crystals in chambered parenchyma cells (Fig. 9E) (up to 16 crystals per parenchyma strands), mostly in the margin of aliform parenchyma and diffuse parenchyma. Rays 1- to 3-seriate (Fig. 9D), storied in some places (Fig. 9C), sometimes not storied, varying within the same specimen and among individuals, ripple marks visible with the naked eye to a greater or lesser extent for all specimens, 5–12 rays per mm (average 8), 130–400 µm (average 240 µm) or 6–20 cells high, homocellular made of procumbent cells (Fig. 9F). Fibres thin to thick-walled (lumina 1.2 times the double wall thickness in average, for best preserved fibres), non-septate, 8–26 µm (average 16 µm) wide, a storied tendency when it is the case for the rays.

DISCUSSION

Two out of three specimens (MNHN.F.50184 and MNHN.F.50185) are very similar in color and mineralization, and display the same compression, suggesting that they might represent different parts of the same broken piece. The third specimen (MNHN.F.50186) has a different preservation and deformation, bigger and less dense vessels, but shares all the key characters of the first two. They are characterized by: 1) diffuse-porous wood; 2) exclusively simple perforation plates; 3) lozenge-aliform parenchyma; 4) marginal bands of parenchyma; and 5) 1–3-seriate and storied rays. These specimens are

very close to our *Pahudioxylon bankurensis* but display distinctive features that allow us to put them apart: the lozenge-aliform parenchyma is less extended, vessels (or vessel groups) are more separated from each other which leads to a lesser degree of confluence; clear diffuse parenchyma is present; the degree of storied structures is greater, as ripple marks are visible. No perfect match comes out on InsideWood (2004-onward) with the storiation of rays taken into consideration as well as diffuse-parenchyma. These characters apart, our fossils share most features of *Afzelia* and *Intsia* species as well as of *Pahudioxylon bankurensis*. The two living genera are yet rarely described with diffuse parenchyma or storied rays. Soerianegara & Lemmens (1993) mention diffuse parenchyma in only a few *Afzelia* and *Adenanthera* L. species. The latter having no storied structures nor more than four cells per parenchyma strands (InsideWood 2004-onward). Diffuse parenchyma is mentioned in *Afzelia africana* Sm. ex Pers. and *A. javanica* (Miq.) J. Léonard (Soerianegara & Lemmens 1993, InsideWood 2004-onward, Feng *et al.* 2015), but they have no or faint storied rays (as seen in figures of Gérard & Louppe 2011). Storied tendency of the rays is mentioned for *Intsia* (Ogata *et al.* 2008, Feng *et al.* 2015), *A. rhomboideae* (Blanco) Fern.-Vill. and can be seen in *A. xylocarpa* (Kurz) Craib. It is noteworthy that *A. xylocarpa* and *A. martabanica* (Prain) J. Léonard grow today in Myanmar (Léonard 1950; POWO 2019; Haw 2019). The latter is restricted to this area, but no information on its wood anatomy or ecology is available. We consider that no single species can be assigned as NLR, but the genera *Afzelia*–*Intsia* as a whole regarding diffuse parenchyma.

Similarities are found between our specimens and *Adenantheroxylon pavoninium* Prakash & Tripathi (1968, 1969), but *A. pavoninium* has commonly 2-seriate rays, vasicentric parenchyma (rarely aliform) and no marginal parenchyma. Among species of *Pahudioxylon*, our specimens are very close to *Pahudioxylon bankurensis* as well as *P. kiliani* (Louvet) Prakash (Prakash *et al.* 1967). Storied rays (or a storied tendency) and diffuse parenchyma are only (and variably) found in *P. bankurensis* (Feng *et al.* 2015). The specimen no. 5790 of Vozenin-Serra & Privé-Gill (1989), attributed to the species *P. sahnii* (synonym of *P. bankurensis*) displays the same diffuse parenchyma and portions of the wood with storied rays; in addition, Feng *et al.* (2015) also described some specimens of *P. bankurensis* for which the parenchyma is not in contact with vessels and could be interpreted as diffuse parenchyma (Feng *et al.* 2015: 489, fig. 2K). These features seem to be variable among individuals of the same species and among the species of the same genus, and we do not consider them as diagnostic to establish a new species or to exclusively attribute the specimens to *Pahudioxylon bankurensis*. Consequently, we assign these specimens to *Pahudioxylon* cf. *bankurensis*.

*Afzelia* are tropical trees present in Africa and Asia at low elevation up to 400 m altitude (Ali 1973; Hou *et al.* 1996; Orwa *et al.* 2009). *Afzelia* trees grow in mixed deciduous



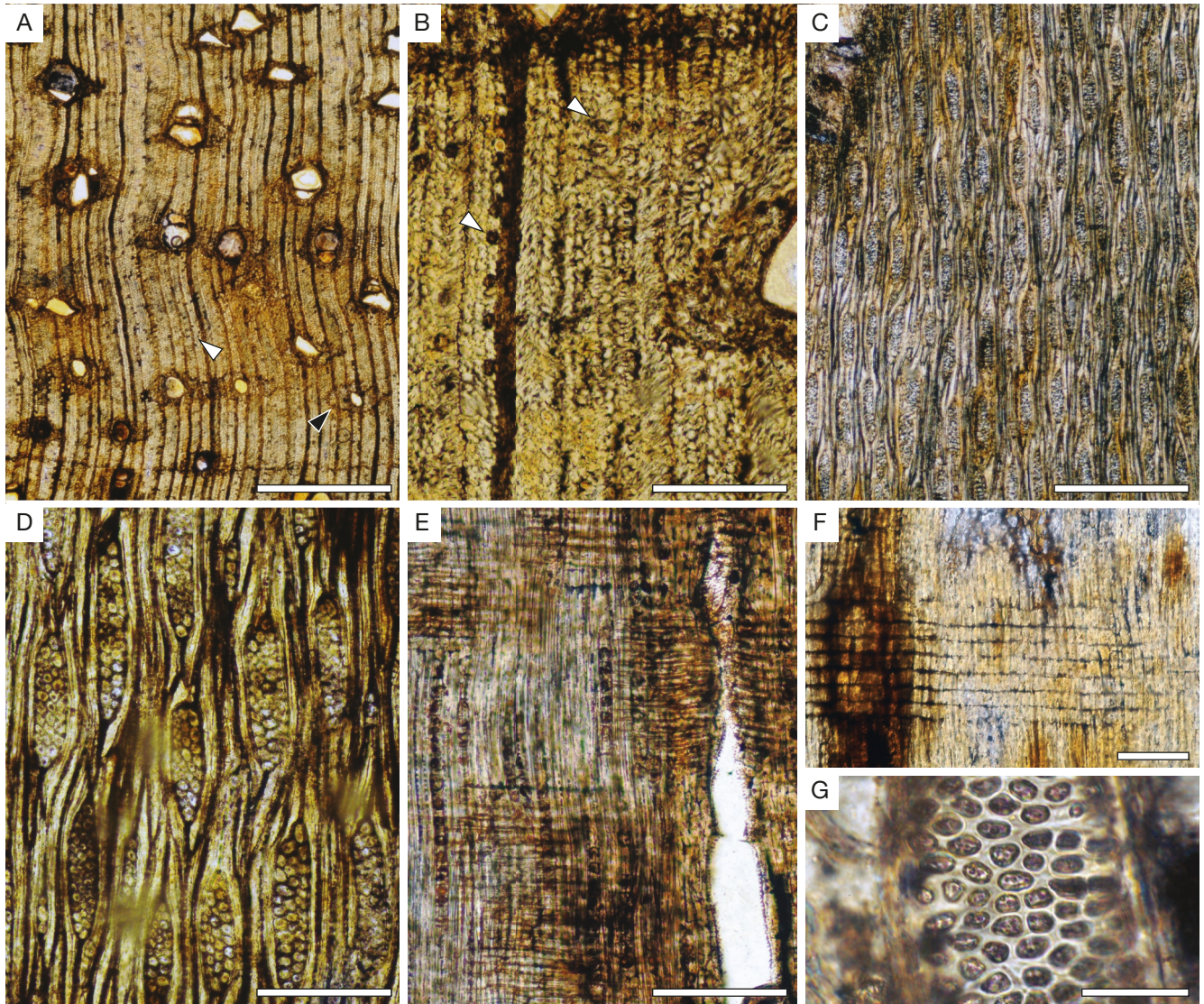


FIG. 9. — *Pahudioxylon* cf. *bankurensis* Chowdhury, Ghosh & Kazmi, MNHN.F.50184: **A**, Ts, mostly solitary vessels, aliform parenchyma with crystals in marginal cells (**black arrow**), marginal parenchyma (bottom) and diffuse parenchyma (**white arrow**); **B**, Ts, detail of diffuse parenchyma (**white arrow**), often in contact with rays; **C**, Ts, storied rays in some parts of the section; **D**, Ts, 1-3-seriate homocellular rays in a non-storied part of the section; **E**, Rls, crystals in parenchyma strands, the strand on the left being diffuse parenchyma; **F**, Rls, homocellular ray; **G**, Ts, alternate intervessel pits, apparently vested. Scale bars: A, 1 mm; C, 500  $\mu$ m; B, D-E, 200  $\mu$ m; F, 100  $\mu$ m; G, 50  $\mu$ m. Abbreviations: see Fig. 2.

and dry evergreen forests, on well-drained soils and in periodically inundated lowlands (Soerianegara & Lemmens 1993). The habitat of *Intsia* is given p. 868. Among the available species with sometimes diffuse parenchyma, *Afzelia africana* is tolerant to a wide range of climate from humid to dry forests, but is essentially found in the savanna woodland/dense dry forests borders and in semi-deciduous forests up to 1400 m altitude; it can also occur in lowland rainforests, dry forests, gallery forests, periodically inundated areas and savannas, but commonly requires annual rainfall above 900 mm (Orwa *et al.* 2009; Gérard & Louppe 2011; Hills 2020); *Afzelia javanica* grows in primary and secondary forests, in dry places, mostly in lowlands up to 800 m altitude (Hou *et al.* 1996). These two species, pending more comprehensive anatomical data on the genus, are considered as the most adequate NLR.

Family MORACEAE Gaudich.  
Genus *Artocarpoxylon* Prakash & Lalitha

*Artocarpoxylon kartikcherraensis* Prakash & Lalitha  
(Fig. 10)

*Artocarpoxylon kartikcherraensis* Prakash & Lalitha, 1978: 132, fig. 1.

ORIGINAL HOLOTYPE. — Birbal Sahni Institute of Palaeosciences Museum no. 35317.

MATERIAL. — MNHN.F.50187 (field number: NAT17-2). Estimated minimal diameter: 25-37 cm.

AGE. — Upper lower to lowermost middle Miocene.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.



## DESCRIPTION

Wood diffuse-porous. Growth rings absent. Vessels solitary (70%) as well as in groups of 2 to 6, evenly distributed (Fig. 10A), oval, 0–8 per mm<sup>2</sup> (average: 3); tangential diameter 85–300 µm (average: 180 µm). Tyloses present (Fig. 10B). Vessel elements 130–430 µm (average: 260 µm) long. Perforation plates simple. Intervessel pits alternate, 3–9 µm diameter (mean 6 µm) (Fig. 10C). Vessel-ray pits not preserved. Parenchyma paratracheal in vasicentric sheath, broad to aliform with no distinct limit between parenchyma and fibres (Fig. 10A, B), maybe diffuse and rarely confluent; parenchyma cells 45–160 µm high (average: 90 µm), 10–45 µm wide (average: 25 µm) in tangential section; 4–8 cells per parenchyma strands. Rays 1–to 6-seriate, mostly 5-seriate (Fig. 10D, E), non-storied, 4–7 rays per mm (average: 5), 190–950 µm (average: 480 µm) or up to 50 cells high with end-to-end fusion possible (Fig. 10E), 1-seriate and some 2-seriate rays made of upright cells only or mixed with procumbent cells, other multiseriate rays heterocellular made of procumbent cells with 1–4 upright marginal cells (Fig. 10H). Some sheath cells present (Fig. 10E). Fibres non-septate, 6–30 µm (average: 15 µm) wide, thin-to-thick walled (lumina 1.46 times the double wall thickness) with visible lumen sometimes wide. Radial laticifer tubes present in rays, of the same size as ray cells, visible when filled with black content (Fig. 10F, G). In tangential section, much larger or longer cells are visible, with a non-circular shape in the flank of vessels, sometimes even modifying the shape of the rays or between two ray ends (Fig. 10E).

## DISCUSSION

This specimen is characterized by: 1) diffuse-porous wood; 2) scattered vessels; 3) up to 6-seriate and heterocellular rays, occasionally with sheath cells; 4) diffuse and broad sheath vasicentric to aliform parenchyma; 5) no growth rings; 6) abundant tylose; and 7) radial laticifer tubes of the same size as ray cells. These features are characteristic of the Moraceae family (InsideWood 2004-onward). Tetramelaceae are also anatomically close but can have growth rings, parenchyma strands or fibres storied, no laticifer tubes and no tyloses (InsideWood 2004-onward). Most of the Moraceae genera can be ruled out based upon some diagnostic characters: the presence of septate fibres, banded parenchyma (58% of the specimens described on InsideWood [2004-onward]), frequent homocellular rays, no diffuse-porous wood, often unilateral parenchyma or almost never sheath cells. One genus is clearly apart from other Moraceae genera because of the absence of any crystal in any type of cells: *Artocarpus* J.R.Forst. & G.Forst. This feature is also observed in our specimen. Among *Artocarpus*, 5 species have at least sometimes laticifers according to InsideWood (2004-onward), and three with sheath cells in addition: *A. chama* Buch.-Ham. (although it is unclear and varies among publications Pearson & Brown 1932; Purkayastha *et al.* 1976; Singh *et al.* 2017), *A. dadah* Miq., and *A. integer* (Thunb.) Merr. (which has no tylosis). According to Ter Welle *et al.* (1986), *Artocarpus* has common tyloses, non-septate fibres, heterocellular mostly 3–5-seriate rays with 1–2 (5) upright or square

marginal cells, sometimes few sheath cells. Parenchyma is mostly aliform, sometimes confluent. Radial latex tube are common, and axial latex tubes can sometimes be present. Singh *et al.* (2017) described four species of *Artocarpus* and mention laticifers in *A. chama*, *A. heterophyllus* Lam., *A. lamellosus* Blanco and *A. lacucha* Roxb. Ex Buch.-Ham. Unfortunately, the figure does not provide clear illustrations (Singh *et al.* 2017: 76, fig. 1). Latex tubes usually appear in radial section as long lines inside rays (which is the case in our fossil) or among fibres, sometimes irregularly crossing both of them; their walls are irregular and the lumina bigger than that of parenchyma cells (Fariás *et al.* 2009). All of these species are quite similar, and their characters (i.e. non-septate fibres, sheath cells, tyloses, confluent parenchyma and laticifers) seem to vary from authors to others. However, given the descriptions provided in references cited above and figures in InsideWood (2004-onward), *A. chama* appears the most anatomically close species to our fossil, as well as *A. lacucha* and *A. lamellosus*.

Fossil Moraceae are mainly represented by the genus *Ficoxylon* Kaiser (Gregory *et al.* 2009) which shows mostly banded parenchyma. The fossil genus *Artocarpoxyton*, also in Moraceae, groups fossils resembling modern *Artocarpus* (Prakash & Lalitha 1978). It displays close similarities with our specimen as it shows no growth rings, mostly solitary vessels, tyloses, vasicentric to aliform parenchyma, 1–6 seriate heterocellular rays and some sheath cells. It also sometimes displays horizontal latex tubes, as in our specimen. Fossil remains related to modern *Artocarpus* are known as far as the Cretaceous from Asia to North America, Europe and even Greenland (Ball 1930; Mehrotra *et al.* 1984; Williams *et al.* 2017). Two species of this genus are described: *A. kartikcherraensis* and *A. deccanensis* Mehrotra, Prakash & Bande (Mehrotra *et al.* 1984). They both have laticifers in rays and strongly resemble our fossil. *Artocarpus deccanensis* has smaller and more numerous vessels (80–180 µm and 9–20/mm<sup>2</sup>) and narrower sheath of vasicentric parenchyma than our fossil. *Artocarpus kartikcherraensis* has vessel diameter and density closer to our fossil (105–315 µm and 2–3/mm<sup>2</sup>). The present fossil is thus attributed to *Artocarpus kartikcherraensis*.

*Artocarpus* is a genus of Asian (also in Pacific and Australia) tropical trees growing in everwet climate or with a short dry season, in evergreen forests or in areas with mild monsoon climate, usually scattered in lowland dipterocarp forests below 1000 m altitude (Lemmens *et al.* 1995; Berg *et al.* 2006). *Artocarpus lamellosus* lives in evergreen forests, rarely in semi-deciduous forests or savanna woodlands, commonly found in mixed dipterocarp and sub-montane forests up to 1500 m altitude, on hillsides and ridges (Lemmens *et al.* 1995; Berg *et al.* 2006; Tropical Plants Database 2014-onward). *Artocarpus chama* lives in evergreen, semi-evergreen and moist deciduous forests up to 1500 m attitude, in areas with a monsoon climate and rainfall of at least 2000 mm a year (Gamble 1902; Jarrett 1959). *Artocarpus lacucha* lives up to 1200–1800m of attitude (Gamble 1902; Jarrett 1960) in evergreen, semi-evergreen and moist deciduous forests, with a distinct dry season (Jarrett 1960).



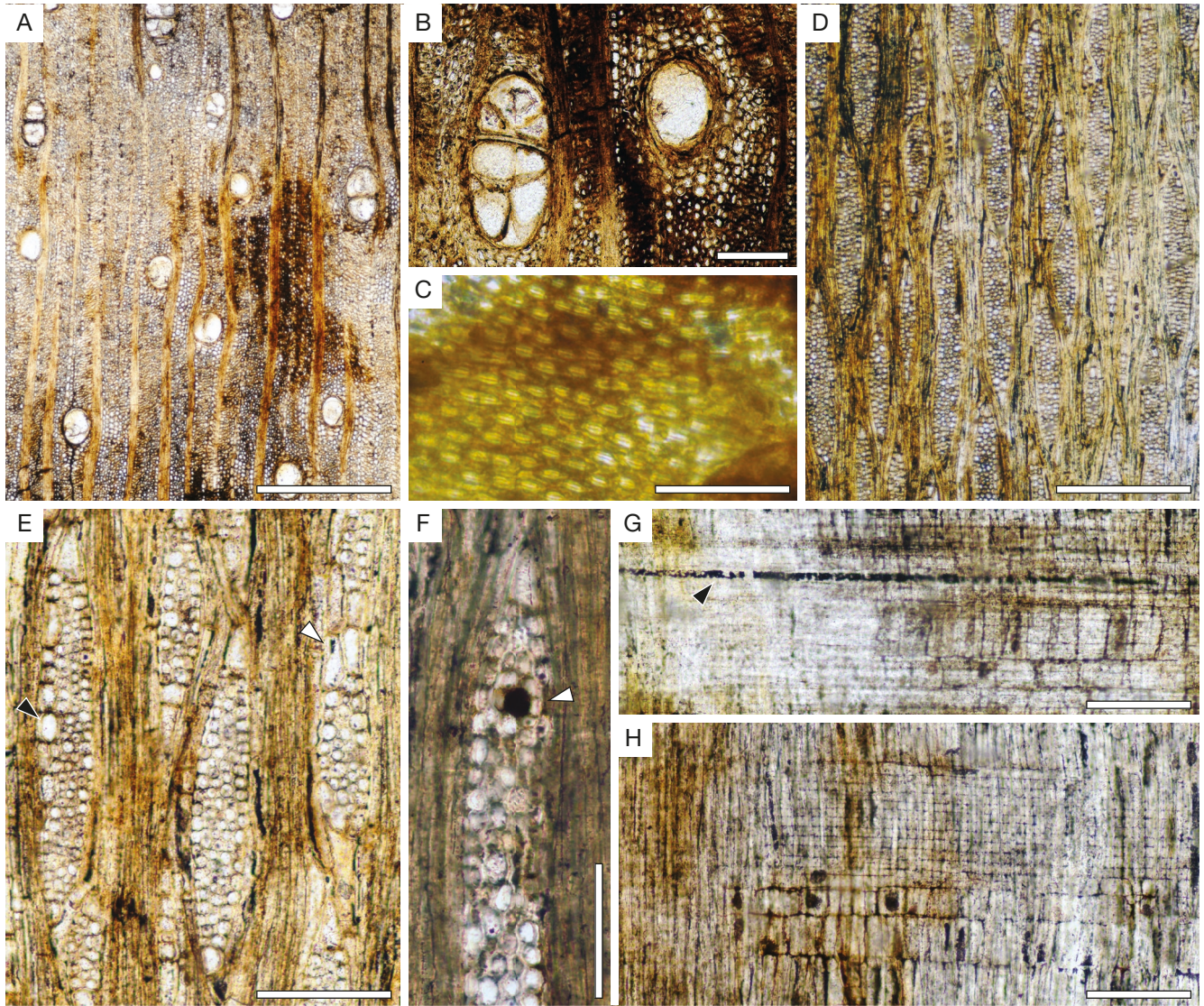


FIG. 10. — *Artocarpoxyylon kartikcherraensis* Prakash & Lalitha, MNHN.F.50187: **A**, Ts, sparse vessels, vasicentric parenchyma sometimes slightly aliform; **B**: Ts, detail of vasicentric parenchyma and vessels plugged with tyloses; **C**, Tls, alternate intervessel pits with lenticular apertures; **D**, Tls, 1-6 seriate rays with upright marginal cells; **E**, Tls, 1-6 seriate rays with sheath cells (**black arrow**) and end-to-end fusions (**white arrow**); **F**, Tls, latex tube in ray, mostly of the same size as ray cells (**arrow**); **G**, Rls, view of a latex tube in ray, recognizable as a continuous black line in radial section; **H**, Rls, heterocellular ray with 1-4 rows of marginal cells, sometimes appearing with upright and procumbent cells mixed due to sheath cells or end-to-end fusions. Scale bars: A, 1 mm; D, 500 µm; B, E, G-H, 200 µm; F, 100 µm; C, 50 µm. Abbreviations: see Fig. 2.

Family DIPTEROCARPACEAE Blume  
Genus *Anisopteroxylon* (Ghosh & Kazmi) Poole

*Anisopteroxylon* sp.  
(Fig. 11)

MATERIAL. — MNHN.F.50188 (field number: 17FN07). Estimated minimal diameter: non-assessable due to compression.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.

AGE. — Upper lower to lowermost middle Miocene.

DESCRIPTION

Wood diffuse-porous. Growth rings indistinct or absent. Vessels mostly solitary (>90%) oval, 2-13 per mm<sup>2</sup> (aver-

age: 6) (Fig. 11A); tangential diameter 80-230 µm (average: 150 µm; measured on less compressed vessels, n=30). Tyloses present. Vessel elements 130-290 µm long (average: 220 µm). Intervessel and vessel-ray pits not found due to compression and rare occurrence of vessel multiples. Perforation plates simple (Fig. 11B). Vasicentric tracheids present (Fig. 11B). Axial parenchyma not well defined due to compression, probably vasicentric and/or diffuse; without mineral inclusions. Rays 1- to 7-seriate, mostly 6- to 7-seriate (Fig. 11C, D), rare uni- or biseriate made of upright or square cells, non-storied, 4-7 rays per mm (average: 5), 510-1500 µm (average: 1050 µm) or up to 60 cells high, heterocellular made of procumbent cells and continuous 1-seriate margin of sheath cells (Fig. 11C, D) which may appear as a mix of procumbent and upright cells in radial section, 2- to 3-seri-



## SIMPLIFIED IDENTIFICATION KEY FOR FOSSIL DIPTEROCARPACEAE BLUME

This identification key is based on Schweitzer (1958); with additional informations of *Anisopteroxylon* Ghosh & Kazmi and *Hopenium* Awasthi from Poole (1993) and Awasthi (1980) respectively.

1. Secretory canals diffuse or in short tangential lines up to 8. Rarely long lines ..... 2  
 — Secretory canals almost always in long tangential lines. Rarely isolated ..... 4
2. Narrow vessels (mean diameter < 150 µm) .....  
     ..... *Vaterioxylon* Trivedi & Misra/ *Vaticoxylon* Schweitzer  
 — Wide vessels (mean diameter > 150 µm) ..... 3
3. Diffuse and small canals, sheath cells abundant ..... *Anisopteroxylon* Ghosh & Kazmi  
 — Canals in short lines, solitary vessels ..... *Dipterocarpoxydon* Holden
4. Exclusively solitary vessels, fibre-tracheids ..... *Dryobalanoxylon* Den Berger  
 — None of these combined ..... 5
5. Upright or square cells interspaced with procumbent cells ..... *Hopenium* Awasthi  
 — Only procumbent cells in median portion (or sheath cells) ..... *Shoreoxylon* Den Berger

ate rays with over 4 rows of upright or square marginal cells (Fig. 11E), otherwise, only one row; silica bodies (?) present in some ray cells (Fig. 11F). Fibres non-septate, tangential diameter 9–25 µm (average: 16 µm). Secretory canals cannot be identified but we observed some scattered, very small pores (Fig. 11A); no signs of tangential bands of any kind that could indicate a presence of canal lines.

## DISCUSSION

This specimen is characterized by: 1) diffuse-porous wood; 2) exclusively simple perforation plates; 3) solitary vessels; 4) heterocellular with mostly 5–6-seriate rays; 5) continuous sheath cells; and 6) vasicentric tracheids. These features suggest an affinity with modern Malvaceae and Dipterocarpaceae (Metcalf & Chalk 1950). Most Malvaceae have vasicentric to confluent parenchyma, apotracheal parenchyma, rays of two distinct sizes (1- and 4- to 9-seriate; Metcalfe & Chalk 1950), and no vasicentric tracheid, which contrast with our specimens. Dipterocarpaceae share all these features, but are additionally characterized by vertical canals, except for non-Asian genera *Monotes* De Candolle, *Marquesia* Gilg and *Pakaraimaea* Maguire & P.S. Ashton (Chowdhury & Ghosh 1958; Ogata *et al.* 2008). The character of secretory canals apart, and searching for diffuse-porous woods with vasicentric tracheids, exclusively solitary vessels, rays more than 4-seriate, heterocellular and with sheath cells on InsideWood (2004-onward) (code: 5p 9p 60p 96a 98p 104a 105a 110p 118a) gives us back multiple results. But adding the features 159 and 160 (silica bodies present in ray cells), only the Dipterocarpaceae family matches with our specimen. Even without silica bodies in ray cells, the affinity with Dipterocarpaceae is the most likely. Among them, *Cotylelobium* Pierre and *Dryobalanops* C.F. Gaertn. genera are ruled out because of smaller vessels (< 150 µm) and secretory canals in long lines respectively (Schweitzer 1958; Ogata *et al.* 2008). Although the preservation state of our fossil is not good enough to see individual secretory canals or parenchyma surrounding them, their long lines or

seemingly bands should have been observable if they were present, as mentioned by Schweitzer (1958).

Following the identification key of the main genera of Dipterocarpaceae provided by Schweitzer (1958), we narrow down the identification to two genera: *Anisoptera* or *Dipterocarpus*. They are not always distinguishable from each other when the information about the secretory canals is not available. However, *Anisoptera* has solitary secretory canals or in short tangential lines (rarely more than 2–3 canals), and sheath cells are frequent in rays; *Dipterocarpus* has comparatively longer tangential lines (2–8 canals), more frequent uniseriate rays and uniseriate portions in rays and less sheath cells, although they can sometimes be present in the whole ray (Chowdhury & Ghosh 1958; Gottwald & Parameswaran 1966; Prakash & Tripathi 1970; Ogata *et al.* 2008). We also observed these trends on *Anisoptera* and *Dipterocarpus* specimens available at the MNHN (CTFT19039, CTFT18446, CTFT11366, MNHN-P-P00402617, P00400540, P00415879, P00406060) and on InsideWood (2004-onward). Our specimen displays features closer to those of genus *Anisoptera*, and in particular with species *Anisoptera costata* Korth. and *Anisoptera scaphula* (Roxb.) Kurz. Both display the same wide rays (up to 7–8-seriate) as well as uniform and unfrequent uniseriate rays and solitary vessels. These two species are hardly distinguishable from each other based on xylotomy (Chowdhury & Ghosh 1958).

Seven fossil genera of Dipterocarpaceae are described (Gregory *et al.* 2009). The genus *Anisopteroxylon* has been instituted by Ghosh & Kazmi (1958) and emended by Poole (1993) for fossil resembling *Anisoptera*, leaving the genus *Dipterocarpoxydon* (Holden) Den Berger for fossil resembling *Dipterocarpus* only (see Prasad & Gautam 2016, p. 263). The differences between *Anisopteroxylon* and *Dipterocarpoxydon* are mostly based on secretory canals (solitary for *Anisopteroxylon* and in short tangential bands for *Dipterocarpoxydon*). The quantity of sheath cells is not mentioned in the diagnosis, although Ghosh & Kazmi (1958) describe them as “rather common”, and uniseriate rays as “not very



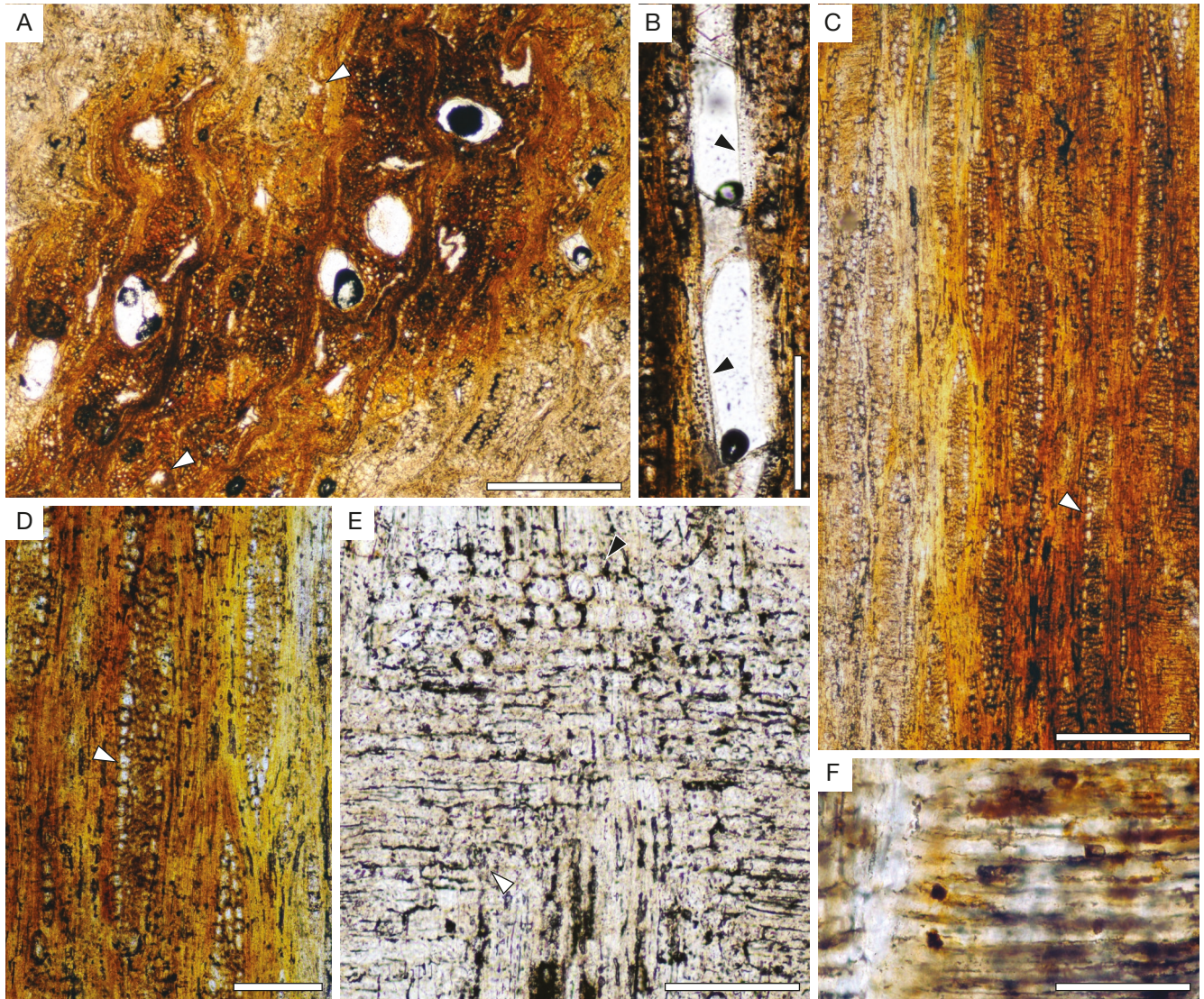


FIG. 11. — *Anisopteroxylon* sp., MNHN.F.50188: **A**, Ts, strongly compressed wood, poorly distinguishable vessels, seemingly exclusively solitary, small pores that could be solitary secretory canals (arrows); **B**, Tls, simple perforation plates, vasicentric tracheids (arrows); **C**, **D**, Tls, 1-7-seriate rays with continuous sheath cells all around multiseriate rays (arrows); **E**, Rls, heterocellular rays with procumbent cells in median portion (white arrow) and square or upright marginal cells (black arrow), sometimes appearing with both types mixed due to sheath cells; **F**, Rls, silica bodies (?) in ray cells. Scale bars: A, C, 500  $\mu$ m; B, D-E, 200  $\mu$ m; F, 100  $\mu$ m. Abbreviations: see Fig. 2.

common” (Ghosh & Kazmi 1958: 486). Even though our fossil has no visible canals, which is possibly due to poor preservation and compression, its solitary vessels, vasicentric tracheids, abundant sheath cells, broad rays with silica bodies in some cells, make it compatible with the genus *Anisopteroxylon*. Some specimens of this genus are close to our fossil (Appendix 1): *A. garoense* (Chowdhury) Prakash & Tripathi (Prakash & Tripathi 1970) from the upper Miocene of India, for its 7-9-seriate rays, 4-5 vessels/mm<sup>2</sup>, and the presence of identical continuous sheath cells; *A. oblongoides* Yadav (Yadav 1989) and *A. surmaensis* Prasad, Agarwal & Mandaokar (Prasad *et al.* 2009) but the former has long tangential lines of canals of equal size as vessels and the latter has narrower rays (mostly 4-5-seriate); *Anisopteroxylon jawalamukhi* Ghosh & Ghosh (Ghosh & Ghosh 1958) has longer rays (up to 1950  $\mu$ m). Considering the lack of several

diagnostic characters at the species level in our specimen, we only assign it to *Anisopteroxylon* sp.

*Anisoptera* is a genus of south-east Asian trees, absent in India, living in evergreen or semi-evergreen forests; in mixed dipterocarp, mixed swamp or heath forests; on well-drained soils or in peat swamps, rarely above 1000 m altitude (Ashton 1982; Soerianegara & Lemmens 1993). *Anisoptera costata* is a tropical tree that can be found in Myanmar, living in semi-evergreen dipterocarps forests and evergreen forests of seasonal areas. Mostly in moist or slightly dry areas. It rarely occurs in everwet forests but grows well along rivers and streams, at up to 700 m altitude (Ashton 1982; Smitinand *et al.* 1990; Soerianegara & Lemmens 1993; Sam *et al.* 2004; Nguyen *et al.* 2017). *Anisoptera scaphula* grows in semi-evergreen and evergreen dipterocarp forests on foothills (Ashton 1982; Soerianegara & Lemmens 1993; Ly *et al.* 2020).



Genus *Dipterocarpoxydon*  
(Holden) Den Berger

*Dipterocarpoxydon* cf. *jammuense*  
Guleria, Gupta & Srivastava  
(Fig. 12)

*Dipterocarpoxydon jammuense* Guleria, Gupta & Srivastava, 2002: 230, pl. 1, figs 1-5.

MATERIAL. — MNHN.F.50189 (field number: 17FN01). Estimated minimal diameter: non-assessable due to compression, but seemingly very parallel rays.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.

AGE. — Upper lower to lowermost middle Miocene.

# DESCRIPTION

Wood diffuse-porous. Growth rings indistinct. Vessels exclusively solitary (Fig. 12A), rounded to oval, 4-9 per mm<sup>2</sup> (average: 7); tangential diameter 115-230 µm (average: 170 µm). Tyloses sometimes present (Fig. 12E). Vessel elements 90-300 µm (average: 170 µm) long. Perforation plates simple, horizontal. Intervessel pits not visible. Vasicentric tracheids present and abundant (Fig. 12G). Parenchyma mostly vasicentric and surrounding secretory canals in aliform-shaped short bands (Fig. 12A, B, D, E); parenchyma cells estimated 75 µm long in average, 21-31 µm wide (average: 26 µm) in tangential section. Rays 1- to 6-(7)-seriate, numerous uniseriate rays (25-50%) made of procumbent, upright and square cells, multiseriate rays being mainly 4-6-seriate (Fig. 12C), leading to a tendency of 2 distinct sizes, 5-9 rays per mm (average: 6), 440-1230 µm (average: 780 µm) or up to 50 cells high or more, heterocellular made of procumbent cells with 1-19 upright or square cells at one or both ends (Fig. 12F); rays can appear with both upright and procumbent cells throughout the ray in radial section due to frequent uniseriate rays or sheath cells (Fig. 12C). Fibres non-septate, 13-32 µm in diameter (average: 20 µm), very thick-walled with sometimes almost no lumina (Fig. 12E). Secretory canals isolated or in short or seemingly short lines, often crushed, but the parenchyma band is still visible (Fig. 12A, B, D, E); also recognizable in tangential and radial section as tubes surrounded by dislocated parenchyma cells, 40-80 µm of tangential diameter, 60-100 µm in radial diameter (Fig. 12D).

# DISCUSSION

Despite its poor state of preservation, this wood specimen displays several diagnostic features. It is characterized by: 1) solitary secretory canals or in short lines; 2) vasicentric tracheids; 3) vasicentric parenchyma; 4) mostly 1-6-seriate rays; 5) heterocellular rays with a row of up to 19 uniseriate cells; and 6) sheath cells. The first two features are diagnostic of most Dipterocarpaceae (Metcalf & Chalk 1950, Schweitzer 1958). Solitary secretory canals in short lines, as well as almost exclusively solitary vessels indicate an affinity with the genus *Dipterocarpus* (Schweitzer 1958). However, the compression and the preservation state of the wood make it complicated to precisely describe the pattern of the canals.

Solitary or paired vessels and canals are also found in the genus *Anisoptera* and *Upuna* Symington, in addition to sheath cells (Schweitzer 1958; Gottwald & Parameswaran 1966; InsideWood 2004-onward; Ogata *et al.* 2008). The genus *Anisoptera* has frequently larger rays (up to 8-seriate or more) and more or less continuous sheath cells in rays with shorter row of marginal ray cells. *Upuna* has less pronounced sheath cell, more tylose and canals less distinguishable in size from vessels than *Dipterocarpus* (Richter & Dallwitz 2000-onward). In addition, *Upuna* can have diffuse and diffuse-in-aggregate parenchyma (Soerianegara & Lemmens 1993) and is usually described with short lines of canals up to two canals maximum. However, the pictures on InsideWood (2004-onward) show lines up to 4 canals and Soerianegara & Lemmens (1993) mention also short and long tangential lines. *Dipterocarpus* (and *Anisoptera*) have silica bodies in ray cells in opposition to *Upuna*. Unfortunately, the preservation state of our fossil does not allow us to distinguish any mineral inclusion. Genus *Dipterocarpus* is the best modern analogue to our specimen because of the frequent short bands of parenchyma in transverse section, the great frequency of uniseriate rays, the length of the marginal part of the rays (InsideWood 2004-onward; wood specimens of extant species MNHN-P-P00400540, P00415879, P00402617 and CTFT19039), and numerous sheath cells (Gottwald & Parameswaran 1966). Among *Dipterocarpus*, our specimen resembles modern species *D. retusus* Blume, *D. alatus* Roxb. ex G. Don, *D. dyeri* Pierre ex Laness., *D. cornutus* Dyer, *D. grandiflorus* (Blanco) Blanco and *D. kunstleri* King because of their rays with long uniseriate row of marginal cells and sheath cells as well as few paratracheal parenchyma other than scanty / vasicentric.

Fossil wood related to *Dipterocarpus* are grouped under the genus *Dipterocarpoxydon* (Ghosh & Kazmi 1958; Prasad & Gautam 2016). To our knowledge, no fossil wood resembling *Upuna* has been described. It is yet difficult to attribute our specimen to an individual *Dipterocarpoxydon* species due to its poor preservation. Among the closets described *Dipterocarpoxydon* (Appendix 1), *D. jammuense* shows the closest anatomy, with parenchyma restricted to vasicentric and very rarely diffuse, 1-6-seriate rays, uniseriate ones 2-11 cells high, marginal row of ray cells up to 12 cells, common sheath cells and small canals (up to 80 µm in diameter); *D. jammuense* differs in having mostly 3-5-seriate rays (compared to mostly 1- and then 5-seriate) and longer vessel elements (up to 600 µm, compared to up to 300 µm); other species display a similar ray composition, such as *D. gracile* Schweitzer, *D. siwalicus* Prakash (1975), *D. malavii* Ghosh & Ghosh (1959), *D. sarapeense* Vozenin-Serra & Privé-Gill (2001), but they often differ by either higher rays, shorter lines of canals, bigger canals, mostly diffuse or diffuse-in-aggregate parenchyma or less sheath cells. Our specimen is thus attributed to *Dipterocarpoxydon* cf. *jammuense*.

*Dipterocarpus* is common in evergreen, sometimes present in semi-evergreen forests or dry deciduous dipterocarp forests, mostly in lowlands and occasionally up to 1400 m altitude. (Ashton 1982; Soerianegara & Lemmens 1993; Ghazoul 2016). All extant *Dipterocarpus* species mentioned





FIG. 12. — *Dipterocarpoxydon* cf. *jammuense* Guleria, Gupta & Srivastava, MNHN.F.50189: **A**, Ts, seemingly exclusively solitary vessels, vasicentric parenchyma, small pores interpreted as solitary secretory canals or in short lines (arrows); **B**, **D**, Ts, short lines of secretory canals (arrows); **C**, Tls, 1-6-seriate rays, with rows of uniseriate marginal cells up to 19 cells, frequent uniseriate rays and sheath cells present (arrow); **E**, Ts, vessel pugged with tyloses, surrounded par vasicentric parenchyma (black arrow), secretory canals solitary or in short lines, surrounded by parenchyma (white arrow); **F**, Rls, heterocellular rays with square or upright cells (black arrow) and procumbent cells (white arrow) mixed throughout the rays because of the presence of sheath cells, uniseriate rays and long row of marginal cells; **G**, Tls, vasicentric tracheids (arrow). Scale bars: A, B, 1 mm; C-F, 200  $\mu$ m; G, 100  $\mu$ m. Abbreviations: see Fig. 2.

above grow in evergreen or semi-evergreen lowland tropical forests, in mixed dipterocarp forests and sometimes seasonal forests (Ashton 1982; IUCN 2021). *Dipterocarpus retusus* is also found in montane forests (Ashton 1982;

Ly *et al.* 2017). *Upuna* is a genus endemic to Borneo that grows in lowland mixed dipterocarp forests and on coastal hills up to 350 m altitude (Ashton 1982; Soerianegara & Lemmens 1993).



Genus *Dryobalanoxylon* Den Berger

*Dryobalanoxylon* cf. *javanense*

(Kräusel) Den Berger

(Fig. 13)

*Dipterocarpoxydon javanense* Kräusel, 1922: 9-15, figs 1-5, ill. 1-2.

*Dryobalanoxylon javanense* – Den Berger 1927: 497, 498.

ORIGINAL HOLOTYPE. — Mineralogical-Geological Institute of the University of Groningen, no. unknown.

MATERIAL. — MNHN.F.50190 (field number: 17FN20). Estimated minimal diameter: 30 cm.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.

AGE. — Upper lower to lowermost middle Miocene.

DESCRIPTION

Wood diffuse-porous. Growth rings indistinct or absent. Vessels almost exclusively solitary (90-95%), oval due to compression (Fig. 13A), 3-8 per mm<sup>2</sup> (average: 5); tangential diameter 130-260 µm (average: 180 µm). Tyloses present (Fig. 13C). Vessel elements 230-610 µm long (average: 450 µm). Perforation plates simple. Intervessel pits alternate. Vessel-ray pits apparently simple, up to 5 per cell; 8-20 µm long, 3-9 µm large (Fig. 13F). Fibre-tracheids and vasicentric tracheids present (Fig. 13D). Axial parenchyma scanty paratracheal to mostly vasicentric and diffuse, occasionally slightly aliform, also forming more or less continuous bands of 3-10 cells thick that may contain secretory canals (Fig. 13B). Bands of parenchyma are closely spaced but their relative arrangement is difficult to determine due to compression and bad preservation. Parenchyma cells 80-100 µm long (average: 90), 15-30 µm wide (average: 20) wide, more than 8 cells per parenchyma strand; crystals absent. Parenchyma abundant visible in tangential section. Rays with a two-size tendency; 1- to 6-(7)-seriate, mainly 4- to 6-seriate with 5-seriate being the most frequent, uniseriate regularly present made of (up to 15) procumbent and square or upright cells (Fig. 13D), 3-7 rays per mm (average: 5), 330-1530 µm (average: 830 µm) or up to 50 cells high or more, heterocellular made of procumbent cells with 1-4 square or upright cells at one or both ends (once seen with 9 cells) (Fig. 13H), sheath cells present and easily distinguishable (Fig. 13D). Fibres thin-to-thick walled (lumina 0.7 times the double wall thickness in average) to very-thick walled, non-septate, 10-22 µm wide (average: 16 µm). Numerous canal lines, embedded in parenchyma bands (Fig. 13B). They can be from 1 to 5 canals long (Fig. 13E), possibly longer as vessel walls are not always preserved and can be confused with canals. At least one long tangential line of canals crossing the section from edge to edge (Fig. 13A, B); vessels often interrupting the line. We thus considered only unmistakable canals. Tangential diameter 40-120 µm (average: 80). Silica bodies (?) present in ray cells (Fig. 13G).

DISCUSSION

This specimen is characterized by: 1) diffuse-porous wood; 2) exclusively simple perforation plates; 3) large and mostly

solitary vessels; 4) axial canals in long and short lines; 5) vasicentric tracheids and fibre-tracheids; 6) heterocellular rays, often higher than 1 mm; and 7) vasicentric and diffuse parenchyma. These combined features indicate an affinity with extant Dipterocarpaceae, which are often characterized by secretory canals and vasicentric tracheids. Mostly solitary vessels, fibre-tracheids and long tangential lines of secretory canals are diagnostic of the genus *Dryobalanops* (Schweitzer 1958). However, due to the poor preservation of this fossil, many cell walls (especially for vessels) are not preserved; it is thus difficult to distinguish small vessels from canals and precisely assess vessel and canal diameter. Parenchyma is also not always identifiable everywhere. Although we identified a clear long line of canals, apparently embedded in a tangential band of parenchyma, many other short lines of canals are found throughout the section (Fig. 13B). Because of the compression, we cannot always determine if a band of parenchyma is tangentially connecting these canals. Some species of *Dipterocarpus* have canals grouped in long lines (as mentioned in InsideWood 2004-onward for *D. indicus* Bedd., *D. baudii* Korth. and *D. turbinatus* C.F.Gaertn.; also seen in the specimen MNHN-P-P00402617 of *D. turbinatus*). A compressed and decayed fossil wood could easily display closely spaced short tangential lines that appear as a single long line. But the presence of fibre-tracheids, tyloses and silica bodies (?) in ray cells suggest a closer affinity with *Dryobalanops* (Metcalf & Chalk 1950; Schweitzer 1958; Gottwald & Parameswaran 1966; Soerianegara & Lemmens 1993; Ogata *et al.* 2008). Our specimen resembles closely to *Dryobalanops keithii* Sym. and *D. lanceolata* Burck for ray width mostly 4-5 seriate, parenchyma vasicentric to aliform, few diffuse and interruption of long tangential lines of canals; and to *D. oblongifolia* Dyer for its ray width (up to 6- or 7-seriate), shape of rays, quite abundant diffuse parenchyma, and canal distribution (also interrupted by vessels). The latter being the most resembling all things considered.

This fossil is attributed to the genus *Dryobalanoxylon* because of the presence of a long tangential line of canals, solitary vessels and visible fibre-tracheids. A comparison with the most resembling *Dryobalanoxylon* species shows that most of them have rays up to 4-5-seriate. Among species with wider rays (Appendix 1; Den Berger 1923; Boureau 1952; Schweitzer 1958; Awasthi 1971; Srivastava & Kagemori 2001; Mandang & Kagemori 2004), *D. bogorensis* Srivastava & Kagemori has rays up to 6-seriate, but more abundant parenchyma with aliform being present, as well as no sheath cells; *D. khmerinum* Boureau has up to 7-seriate rays but shorter rays, bigger canals and smaller vessels; *D. javanense* of Schweitzer (1958) has rays up to 6-seriate rays, as well as long lines and few short lines of 2-4 canals; *D. cf. bangkoense* of Schweitzer (1958) has rays up to 7-seriate. The last two are very similar to each other and share most features of our fossil, with some minor differences: *D. javanense* has slightly thinner and shorter rays, mostly scanty paratracheal parenchyma (compared to mostly vasicentric) and very pronounced sheath cells. *Dryobalanoxylon* cf. *bangkoense* has a lesser proportion of solitary vessels, a greater amount of apotracheal parenchyma (diffuse-in-aggregate is



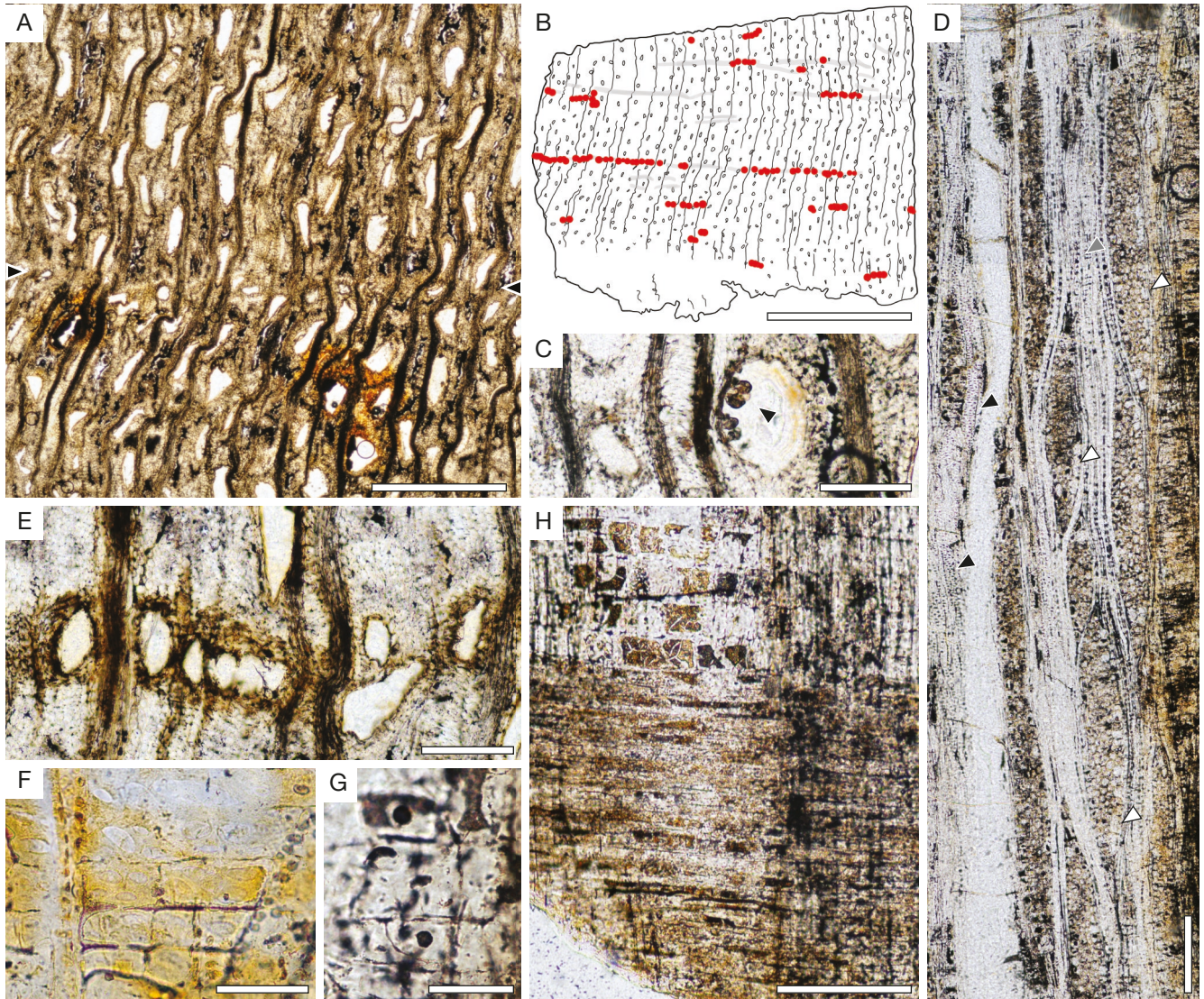


FIG. 13. — *Dryobalanoxylon* cf. *javanense* (Kräusel) Den Berger, MNHN.F.50190: **A**, Ts, Vessels seemingly exclusively solitary and long tangential line of secretory canals embedded in parenchyma bands (between arrows); **B**, Ts, synthetic drawing of the transversal section (with only some vessels and rays displayed); visible bands of parenchyma as grey lines and secretory canals as red dots, arranged mostly in long tangential lines; **C**, Ts, tyloses in vessels (arrow); **D**, Tls 1-6 seriate rays with some sheath cells (white arrows), vascentric tracheids (black arrows) and fibre-tracheids (grey arrow); **E**, Ts, detail of secretory canals embedded in tangential bands of parenchyma; **F**, Rls, simple vessel-ray pits with reduced borders in irregular shapes; **G**, Rls, silica bodies (?) in ray cells; **H**, Rls, heterocellular ray with mostly 1-4 rows of square or upright marginal cells. Scale bars: B, 1 cm; A, 1 mm; C-E, H, 200 µm; F-G, 50 µm.

mentioned) and has no sheath cells described. We do not consider that these differences are enough to describe a new species; neither too few to attribute this fossil to any species. We thus attribute this fossil to *Dryobalanoxylon* cf. *javanense* as it is the only specimen described with both long and short lines of secretory canals.

Most *Dryobalanoxylon* specimens are recorded in Indonesia (Appendix 1; Schweitzer 1958; Srivastava & Kagemori 2001) but they are also found in Vietnam, Cambodia, India (Appendix 1; Srivastava & Kagemori 2001) and Myanmar (Gottwald 1994). Our fossil is the second record of *Dryobalanoxylon* in Myanmar.

*Dryobalanops* is today exclusively present in southeast Asia and absent in India and Myanmar (Maury-Lechon & Curtet 1998; Ghazoul 2016). It is a genus of tropical

canopy trees growing on hillsides or along streams, at up to 800 m altitude; they are also present in lowland dipterocarp forests, mixed peat-swamp forests, sometimes also in heath forests (Ashton 1982; Soerianegara & Lemmens 1993). *Dryobalanops oblongifolia* lives in lowland mixed dipterocarp forests, also in periodically inundated, freshwater swamps, near streams, in poorly drained forests or on hillsides below 600 m (Ashton 1982; Soerianegara & Lemmens 1993; Barstow 2018a). *Dryobalanops keithii* always occurs near water on lowlands and foothills up to 250 m altitude (Ashton 1982; Soerianegara & Lemmens 1993; Randi *et al.* 2019). *Dryobalanops lanceolata* lives in mixed dipterocarp forests and can occur in logged (open) forests, on clay soils and rolling hills up to 700 m altitude (Ashton 1982; Bodos *et al.* 2019).



*Dryobalanoxylon* sp.  
(Fig. 14)

MATERIAL. — MNHN.F.50191 (field number: 17FN09). Estimated minimal diameter: 10–22 cm.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.

AGE. — Upper lower to lowermost middle Miocene.

DESCRIPTION

Wood diffuse-porous. Growth rings indistinct or absent. Vessels mostly solitary (81–90%) (Fig. 14A) or in radial groups of 2(–3), round to oval, 5–13 per mm<sup>2</sup> (average: 8); tangential diameter 140–260 µm (average: 200 µm). Tyloses present (Fig. 14G). Vessel elements 140–290 µm (average: 210 µm) long. Perforation plates simple (Fig. 14D). Intervessel pits alternate, 3–6 µm of diameter (average: 5 µm). Vessel-ray pits not preserved. Vasicentric tracheids present (Fig. 14C). Parenchyma aliform with small wings, or at least vasicentric forming a sheath of 1–3 cells around vessels (Fig. 14A, G); occasionally confluent; diffuse parenchyma may occur but not as an obvious feature. The parenchyma also seems to be in tangential bands, 1–6 seriate, possibly crossing the whole section or at least some portion; they can contain secretory canals (Fig. 14A, B); these bands are separated by 1.5–4 mm. Parenchyma cells 75–130 µm long (average: 110 µm) 10–30 µm wide (average: 20 µm) in tangential section; without crystals. Rays 1- to 4-seriate, mostly 3–4-seriate (Fig. 14D, E), with a possible storied tendency, but faint and limited to zones with shorter rays (Fig. 14D), 6–9 rays per mm (average: 8), 320–1140 µm (average: 540 µm) or 15–50 cells high, heterocellular with 1-(maybe more?) upright or square cell at the ends to possibly homocellular (Fig. 14F); sheath cells absent or very rare, end-to-end fusion present but not frequent. Fibres non-septate, 9–21 µm (average: 15 µm) wide, walls commonly not preserved. Secretory canals in short (to long) lines of 2–5 (–7) canals surrounded by parenchyma (Fig. 14A), 40–90 µm of diameter (average: 60 µm). These lines seem to be parts of longer bands of parenchyma, but the compression of the wood may have crushed canals, which do not allow us to determine if lines are longer. Some scattered canals found.

DISCUSSION

This specimen has: 1) vertical secretory canals in short to long tangential lines or diffuse; 2) mostly solitary vessels; 3) vasicentric tracheids; 4) up to more than 1 mm long and mainly 3-(4-)seriate rays (Fig. 8D, E); and 5) tyloses. Vasicentric tracheids and axial secretory canals indicate an affinity with the Dipterocarpaceae family. Features of the specimen could fit the diagnosis of both *Dipterocarpus* and *Dryobalanops* genera. This greatly depends on author's definitions of "short tangential lines" (Metcalf & Chalk 1950; Schweitzer 1958; IAWA Committee 1989). Schweitzer (1958) highlighted the fact that the inter- and intraspecific variation are sometimes too wide to define precise limits between these genera. Solitary secretory canals together with lines up to 7 canals, the parenchyma pattern (vasicentric and aliform), the size of the

vessels, the relatively thin rays (up to 4-seriate) recall *Dipterocarpus* (Metcalf & Chalk 1950; Gottwald & Parameswaran 1966; Soerianegara & Lemmens 1993; Ogata *et al.* 2008). The presence of tylose, of weakly heterocellular rays (mostly one row of upright marginal cells), quite thin and short rays, the quasi-absence of sheath cells, and very few uniseriate recall *Dryobalanops* even though the unilateral arrangement of the parenchyma is not obvious (Metcalf & Chalk 1950; Gottwald & Parameswaran 1966; Soerianegara & Lemmens 1993; Ogata *et al.* 2008). The canals we identified are relatively small (<100 µm) and they seem to occur in tangential bands of parenchyma. These bands cross at least a part of the section and it is possible that they contain two of these lines of secretory canals. As they are relatively regularly spaced, they could be interpreted as long tangential band of secretory canals, if we consider that most of them are crushed by the compression of the wood (Fig. 14B). After a comparison with modern species of both genera, we note a close affinity with *Dryobalanops aromatica* C.F. Gaertn. (specimens CTFT19577 and MNHN-P-P00402611) that displays frequent vessels, slightly aliform parenchyma as well as diffuse, no silica bodies in ray cells, rays 2–4-seriate with numerous 3-seriate, fusiform rays with short rows of marginal cells (1 or 2 cells) that are sometimes storied, and similar thin tangential bands of parenchyma that can contain diffuse to long lines of canals interrupted by vessels. *Dryobalanops aromatica* differs from our fossil in the absence of tylose and the presence of diffuse-in-aggregate parenchyma. *Dryobalanops oblongifolia* from InsideWood (2004-onward) displays regular tangential lines of secretory canals embedded in parenchyma bands as well as a pattern of parenchyma that matches the one of our fossil, but its rays are broader (up to 7-seriate in the pictures provided). Due to the strong resemblance and variation among *Dryobalanops* species, we only attribute as NLR of this fossil the genus *Dryobalanops*, with a noted affinity for *D. aromatica*.

The fossil genus *Dryobalanoxylon* was instituted for fossil woods resembling *Dryobalanops* (Den Berger 1923; Schweitzer 1958). The only difference within the diagnosis of *Dryobalanoxylon* and *Dipterocarpoxydon* (extracted from Schweitzer 1958) is that *Dryobalanoxylon* can have storied structures, somehow smaller vessels, secretory canals mostly in long tangential bands, rarely short, and common fibre-tracheids. No distinction is made based on rays; however, it can be seen within the described species, more or less the same differences as between modern species. Although we do not observe any fibre-tracheids, probably because of the poorly preserved cell walls, an examination of the resembling species shows a closer affinity for *Dryobalanoxylon* (Den Berger 1927; Schweitzer 1958; Awasthi 1971; Vozenin-Serra 1981; Awasthi & Ahuja 1982; Mandang & Kagemori 2004; Biswas *et al.* 2019) especially: *D. sumatrense* Schweitzer, *D. tobleri* Den Berger, *D. lunaris* Mandang & Kagemori, *D. holdeniae* ('*holdenii*') Awasthi and *D. tambouense* Vozenin-Serra (Appendix 1). Few differences distinguish these *Dryobalanoxylon* species from each other as the descriptions display a great degree of overlapping. We note a closer resemblance with *D. tambouense*, which has vasicentric to aliform parenchyma, a similar size of rays (2–5-seriate, up to 1194 µm)



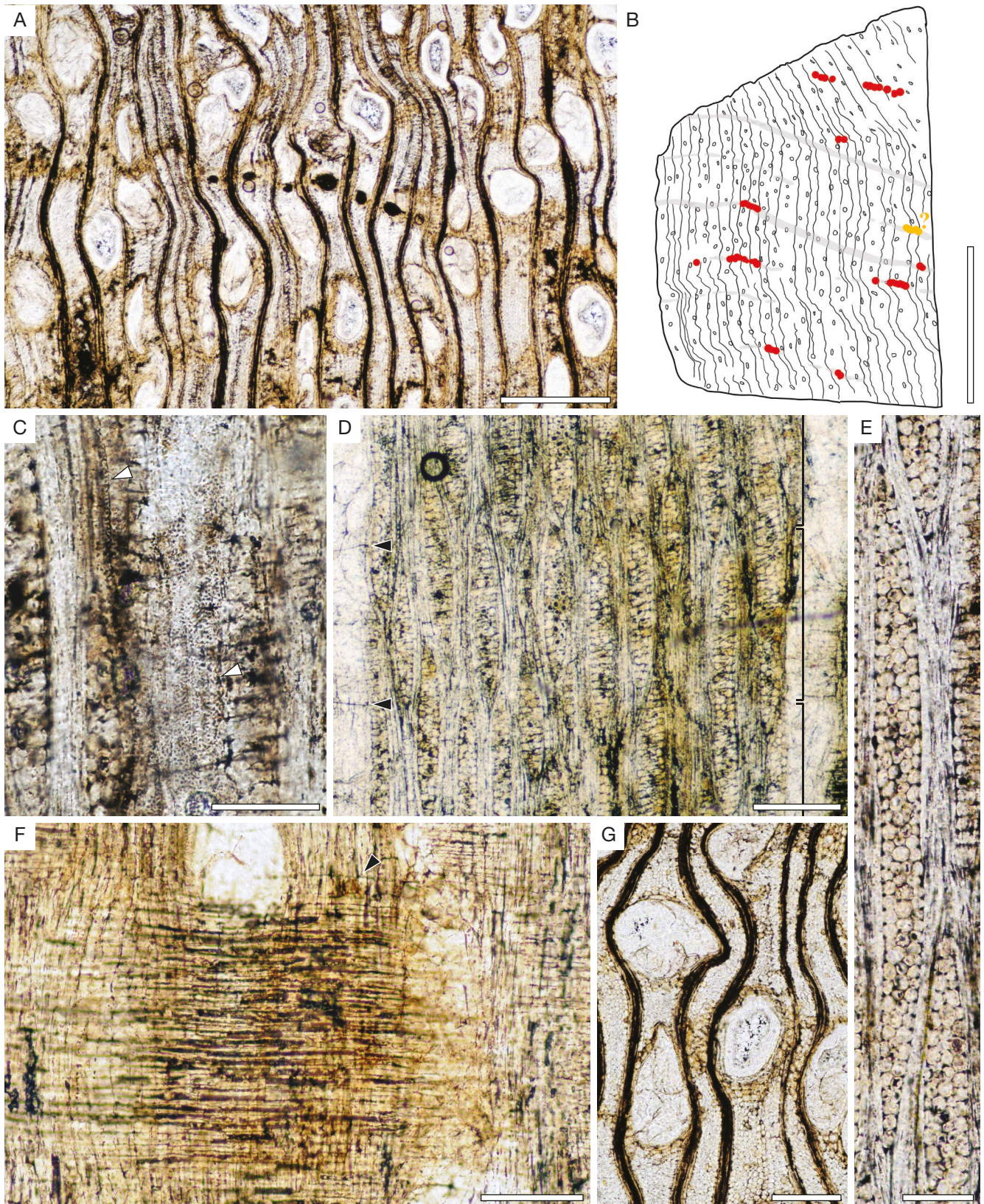


FIG. 14. — *Dryobalanoxylon* sp., MNHN.F.50191: **A**, Ts, mostly solitary vessels and vasicentric to slightly aliform parenchyma, short line of secretory canals embedded in long tangential bands of parenchyma; **B**, Ts, synthetic drawing of the transversal section (with only some vessels and rays displayed), visible bands of parenchyma as grey lines and recognized secretory canals as red dots; **C**, Tls, vasicentric tracheids (arrows); **D**, Tls, simple perforation plates (arrows), 2–4 seriate homocellular to weakly heterocellular rays with a storied tendency at some places (segments); **E**, Tls, detail of a 4-seriate ray; **F**, Rls, heterocellular ray with one row of square marginal cells (arrow); **G**, Ts, solitary vessels with tyloses and surrounded by vasicentric to slightly aliform parenchyma. Scale bars: B, 1 cm; A, 500 µm; D, 250 µm; F–G, 200 µm; C, E, 100 µm. Abbreviations: see Fig. 2.



with a storied tendency, and a similar size and frequency of vessels. The state of preservation of our fossil and its unclear canal distribution pattern does not allow us to attribute the specimen to an individual species with certainty nor to create a new species. Thus, we name this fossil *Dryobalanoxylon* sp.

*Dryobalanops* general ecology and distribution is given p. 878; *Dryobalanops aromatica* lives in lowland mixed dipterocarp forests, on dry sandy or gravelly soils near the coast up to 400 m (Ashton 1982; Tropical Plant Database 2014-onward; Barstow & Randi 2018). *Dryobalanops oblongifolia* lives in lowland mixed dipterocarp forests, also in periodically inundated, freshwater swamps, near streams, in poorly drained forests or on hillsides below 600 m (Ashton 1982; Soerianegara & Lemmens 1993; Barstow 2018a).

### Genus *Shoreoxylon* Den Berger

#### *Shoreoxylon* cf. *deomaliense* Prakash & Awasthi (Fig. 15)

*Shoreoxylon deomaliense* Prakash & Awasthi, 1971: 219, pl. 1, figs 3-4.

HOLOTYPE. — Birbal Sahni Institute of Palaeosciences Museum, India, specimen no. 34050.

MATERIAL. — MNHN.F.50192 (field number: NAT17-4). Estimated minimal diameter: 25-37 cm.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.

AGE. — Upper lower to lowermost middle Miocene.

#### DESCRIPTION

Wood diffuse-porous, showing lateral compression. Growth limits marked by tangential canal lines. Vessels about 77-90% solitary (Fig. 15A) and in radial groups of 2-4, oval due to lateral compression, 4-13 per mm<sup>2</sup> (average: 8; likely overestimated due to compression); tangential diameter 120-200 µm (average: 150 µm; likely underestimated due to compression). Tyloses present (Fig. 15F). Vessel elements 140-460 µm (average: 330 µm) long. Perforation plates simple. Intervessel pits alternate. Vessel-ray pits not preserved. Vasicentric tracheids present (Fig. 15F). Parenchyma mostly vasicentric and aliform with short wings, sometimes confluent (Fig. 15B) or rarely forming thin bands from several rays to rays; diffuse parenchyma with cells larger than fibres ones (Fig. 15K), sometimes gathered in small groups; thin bands of parenchyma are tangentially crossing the section at regular intervals (5-7 mm). They can contain secretory canals but these ones are not always visible (Fig. 15H). When no canal is present, the bands are only 1-4 cells wide. Parenchyma cells 50-90 µm long (average: 70 µm), 15-35 µm wide (average: 25 µm) in tangential section; sometimes crystals in chambered cells (up to 8 crystals per strand seen) (Fig. 15E). Parenchyma cells

can be more or less enlarged in the form of idioblasts. Rays 1- to 5-(6-)seriate (mainly 4) (Fig. 15C), uniseriate about 15% of the rays, non-storied, 5-10 rays per mm (average: 8), 270-1600 µm (average: 650 µm) or up to 30-40 (even 70) cells high, heterocellular made of procumbent cells with 1-4 or more upright cells at the ends (Fig. 15G), end-to-end fusion possible resulting in very high rays (Fig. 15D). Fibres non-septate, 5-19 µm (average: 12 µm) wide, thin-to-thick walled (lumina 1 time the double wall thickness in average) (Fig. 15J). Secretory canals in long tangential lines surrounded by parenchyma (Fig. 15A, H, I), but also in seemingly short lines probably due to compression in concentric parenchyma bands, or very rarely scattered by 2 in the section, 30-100 µm in tangential diameter (average 60 µm).

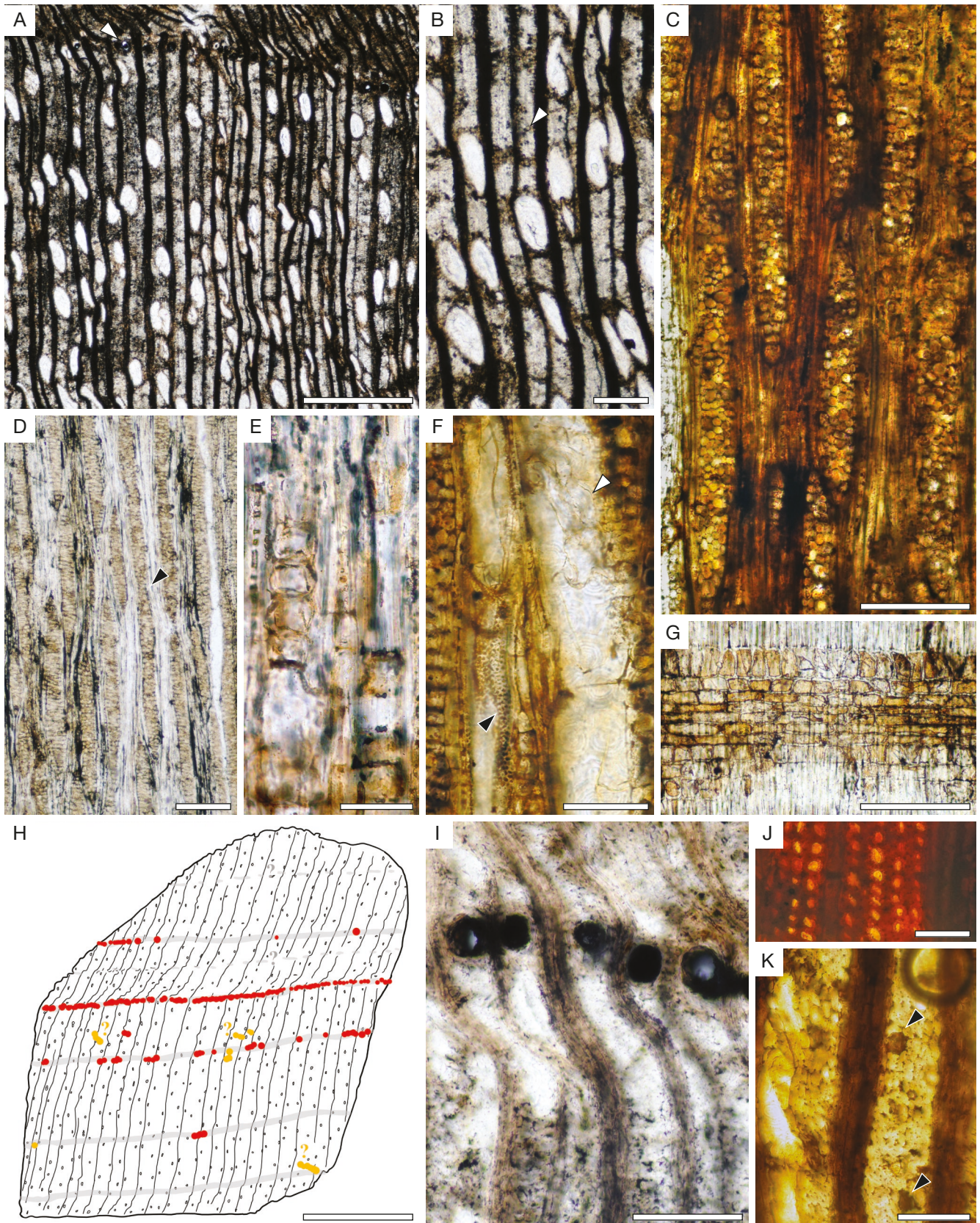
#### DISCUSSION

This specimen is characterized by: 1) diffuse-porous wood; 2) mostly solitary vessels as well as in radial groups; 3) crystalliferous and mostly aliform parenchyma, as well as diffuse; 4) 1-6-seriate heterocellular rays; 5) long tangential lines of secretory canals; and 6) vasicentric tracheids. As for our previous specimens (start p. 878), these features are diagnostic of the Dipterocarpaceae family. According to the identification key of Schweitzer (1958), long tangential lines of canals are found in the genera *Shorea*, *Dryobalanops*, *Hopea*, and *Parashorea* Kurz but the latter three can be dismissed: the genus *Dryobalanops* has exclusively solitary vessels and visible fibre-tracheids, *Hopea* has smaller and more frequent vessels (less than 200 µm in average diameter for 10-20 or more vessels per mm<sup>2</sup>), while *Parashorea* has less vessels and larger rays (up to 7-seriate) (Metcalf & Chalk 1950; Gottwald & Parameswaran 1966; Soerianegara & Lemmens 1993; Richter & Dallwitz 2000-onward; Ogata *et al.* 2008). The genus *Shorea* is divided into several sections that are more or less phylogenetically supported and roughly characterized by few features: section 'Pentacme' by big vessels, section 'Richetioides' (or 'Richetia') by the presence of radial canals, section 'Anthoshorea' by the presence of silica bodies in ray cells as well as short rays, thin-walled fibres and rare crystals in parenchyma, sections 'Rubroshorea' by solitary crystals or in short chain of non-chambered (or chambered) parenchyma cells and idioblasts, section 'Shorea' by short rays, few marginal ray cells and crystals in long chains of chambered parenchyma cells and idioblasts. The present wood would thus be close to the section 'Shorea'.

Among *Shorea* extant species, *Shorea laevis* Ridl. shares many features of our fossil including the aliform parenchyma (but without crystals), the vessel size and density, the similar rays (mostly 3-5-seriate) with few marginal cells and few uniseriate rays. The same arrangement of crystalliferous parenchyma and ray size is found in *S. parvifolia* Dyer, *S. pauciflora* King, *S. atrinervosa* Symington., and with a lesser extent in *S. maxwelliana* King and *S. almon* Foxw.

FIG. 15. — *Shoreoxylon* cf. *deomaliense* Prakash & Awasthi, MNHN.F.50192: **A**, Ts, mostly solitary vessels and long tangential line of secretory canals embedded in parenchyma bands (arrow); **B**, Ts, zoom in on solitary vessels, mostly aliform parenchyma as well as some diffuse parenchyma (arrow); **C**, **D**, Tls, long 1-6-seriate rays with end-to-end fusion (arrow); **E**, Rls, crystals in chambered parenchyma cells; **F**, Tls, vasicentric tracheids (black arrow) and tylose in vessel





(white arrow); **G**, Rls, heterocellular ray with upright marginal cells; **H**, Ts, synthetic drawing of the transversal section (with only some vessels and rays displayed); visible bands of parenchyma are shown as grey lines and secretory canals as red dots (orange when their identification is less clear), arranged mostly in long tangential lines; **I**, Ts, zoom in on secretory canals embedded in parenchyma; **J**, Ts, thin-to-thick walled fibres; **K**, Ts, diffuse parenchyma (arrows). Scale bars: H, 1 cm; A, 1 mm; B, D, I, 250  $\mu$ m; C, G, 200  $\mu$ m; F, K, 100  $\mu$ m; E, J, 50  $\mu$ m. Abbreviations: see Fig. 2.



*Shoreoxylon* groups the fossil specimens close to all *Shorea* and *Parashorea*. The genus *Hopenium* was instituted (Awasthi 1980) for woods resembling *Hopea*, with upright ray cells in the middle of the rays. Species descriptions in *Shoreoxylon* are often overlapping and rarely consider inter- and intraspecific variations. In addition, they sometimes lack diagnostic characters or qualitative illustrations. Consequently, it is difficult to identify a unique species that could be attributed to our specimen. Some species display features that are close to our fossil (Appendix 1): *Shoreoxylon burmense* Prakash (Prakash 1965a, 1973; Licht *et al.* 2014) share the same type of rays, the parenchyma is also quite similar, but the secretory canals are grouped in very close lines, from 2 to 4, which is not the case in our fossil, and it has no crystal in parenchyma. *Shoreoxylon indicum* Awasthi (1974) has the same vessel and ray distribution, crystals in parenchyma cells, but its apotracheal and confluent parenchyma are more developed with only 5 crystals per parenchyma strands (up to 8 in our fossil). *Shoreoxylon posthumi* Schweitzer (1958) has crystals in parenchyma as well as enlarged parenchyma cells, but it has much developed apotracheal parenchyma and its canal lines are irregularly distributed or superimposed. *Shoreoxylon tipamense* Prakash & Awasthi (1970) has similar vessel, parenchyma and ray arrangement, but it also has bigger vessels, larger canals, thinner fibres cell walls and sheath cells. *Shoreoxylon deomaliense* is the closest fossil species to our specimen (Prakash & Awasthi 1971; Licht *et al.* 2014), though the present fossil has a lesser frequency of vessels, more aliform parenchyma and slightly thinner rays (up to 6-seriate, compared to 7-seriate for *S. deomaliense*) with shorter rows of marginal ray cells. Considering its preservation, we attribute our fossil to *Shoreoxylon* cf. *deomaliense*.

*Shorea* is a genus of tropical Asian trees growing in humid lowland areas, on podzols and peat swamps, mostly below 1000 m altitude (Ashton 1982; Soerianegara & Lemmens 1993). *Shorea laevis* mostly grows on well-drained to dry soils, on ridges or hillsides up to 1000 m. It is also found in lowland mixed dipterocarp forests and on alluvial sites (Ashton 1982; Soerianegara & Lemmens 1993; Pooma *et al.* 2017). All the other species cited above are found in mixed dipterocarp forests in lowlands or on rolling hills, on well-drained soils at up to 1000 m altitude (Ashton 1982, 2004).

*Shoreoxylon* cf. *sumatraense* Du  
(Fig. 16)

*Shoreoxylon sumatraense* Du, 1988b: 342, pl. 1, figs 1-4, pl. 2, figs 1-4, pl. 5, fig. 4.

HOLOTYPE. — National Museum of Geology and Mineralogy, Leiden, specimen no. RGM B (RGM 383446).

MATERIAL. — MNHN.F.50193 (field number: 17FN12). Estimated minimal diameter: 10-14 cm.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.

AGE. — Upper lower to lowermost middle Miocene.

## DESCRIPTION

Wood diffuse-porous. Growth rings marked by tangential canal lines. Vessels 45-70% solitary, otherwise in radial multiple of 2-4 and clusters of different size with sometimes many small vessels surrounding bigger ones (Fig. 16A), round to oval, 8-20 per mm<sup>2</sup> (average: 15); tangential diameter 80-240 µm (average: 160 µm); walls of the vessel cells are thick compared to other cells (about 6-11 µm). Tyloses present, common and visible (Fig. 16A-C). Vessel elements 150-570 µm (average: 350 µm) long. Perforation plates simple. Intervessel pits alternate, 3-6 µm of diameter (average: 4 µm). Vessel-ray pits apparently irregular in size and shape, simple, 4-10 µm (Fig. 16F). Vasicentric tracheids present (Fig. 16H). In cross section, parenchyma indistinguishable from fibres due to poorly preserved cell walls and no obvious difference of size. At least vasicentric and around canals appearing as little flattened cells; parenchyma easily recognizable in tangential section and abundant in places, 4-8 cells per strand (Fig. 16E), it seems as abundant as fibres; parenchyma cells 40-120 µm long (average: 90 µm) 10-30 µm wide (average: 20 µm) in tangential section; no crystal. Rays usually 1- to 4-seriate (mainly 3-, very rarely 5-seriate) (Fig. 16C, D), uniseriate for about 20% of the rays, non-storied, 4-8 rays per mm (average: 6), 340-1040 µm (average 620 µm) or 10-45 cells high; multiseriate rays are heterocellular, made of procumbent cells mostly with 1-4 but sometimes more (9) square or upright cells at the ends (Fig. 16E, I); no mineral inclusion seen. Fibres non-septate, 8-20 µm (average: 13 µm) wide, apparently thin-walled (lumina 1.9 times the double wall thickness in average where the walls are best preserved; or individual cell wall 3-4.4 µm thick), fibres cell walls are poorly preserved; clearly aligned in radial rows. Secretory canals in long tangential bands surrounded by parenchyma, frequent and closely spaced (every 0.4-3 mm) (Fig. 16B, G), 40-75 µm of diameter (average: 60 µm). Black spots and long lines crossing tangentially the section (well visible in low magnification) are interpreted as potential lines of canals, even though their origin remains to be confirmed (Fig. 16G).

## DISCUSSION

This specimen is characterized by: 1) diffuse-porous wood; 2) exclusively simple perforation plates; 3) closely and frequently spaced long tangential lines of secretory canals; 4) vasicentric tracheids; 5) presence of sheath cells; 6) vessels mostly in groups and sometime forming clusters; and 7) 1-4-seriate rays, mostly less than 1mm high. The poor preservation of the specimen makes our observations on ray and parenchyma arrangement uncertain. Nonetheless, its features indicate an affinity with modern and fossil Dipterocarpaceae. As discussed p. 882, long tangential bands of canals, grouped vessels and no fibre-tracheids are features compatible with extant *Shorea*. Among this genus, the sections 'Shorea' and 'Rubroshorea' are the more compatible with our fossil: 'Shorea' for the frequency of vessels (4-10[16] per mm<sup>2</sup>), the frequency of solitary vessels (55-85%), common tylose, mostly 3-4-seriate rays; 'Rubroshorea' for the thickness of fibres, the composition of the rays (with 1-4 row of marginal cells and sometimes



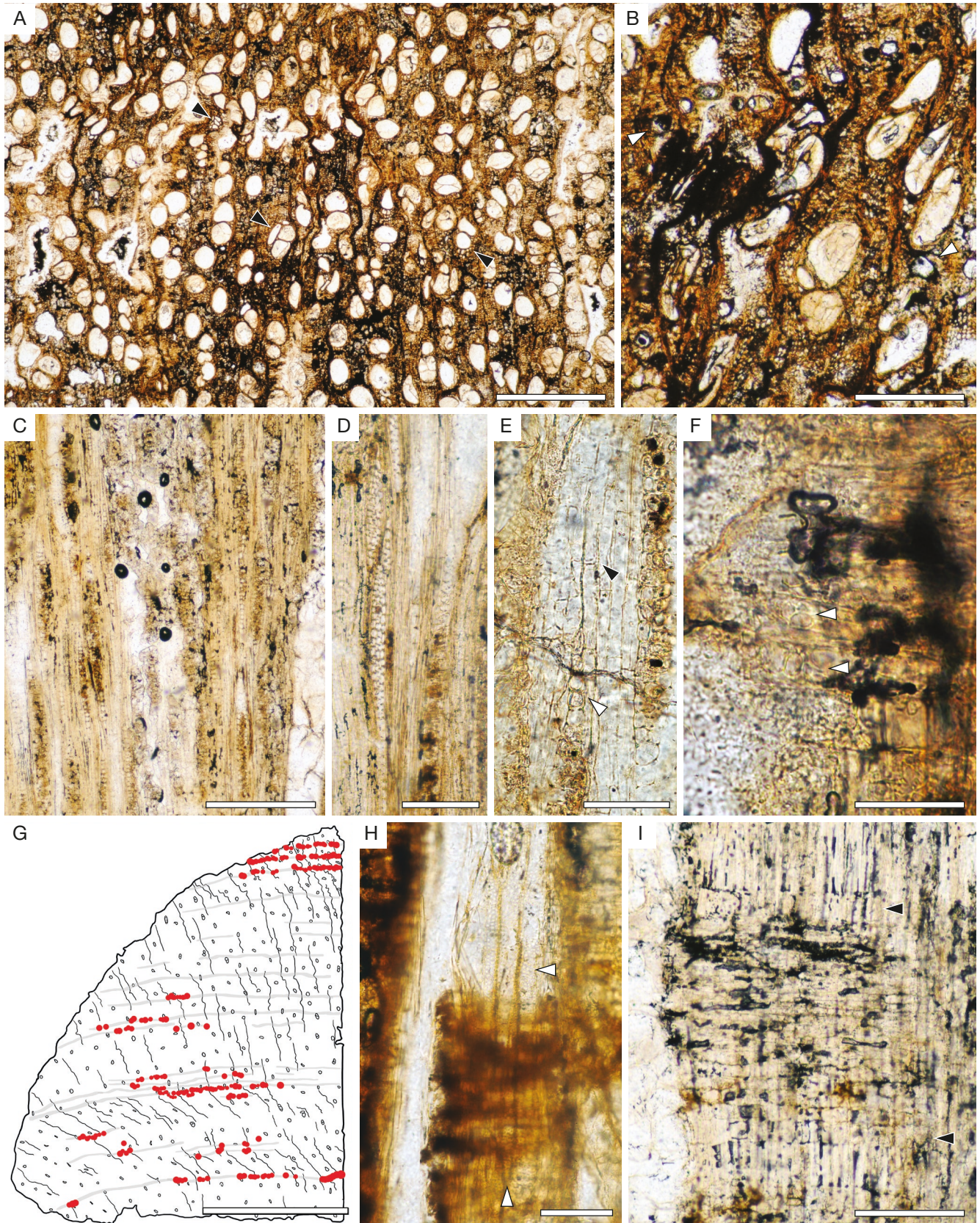


FIG. 16. — *Shoreoxylon* cf. *sumatraense* Du, MNHN.F.50193: **A**, Ts, vessel often in groups, sometimes in clusters (arrows); **B**, Ts, long tangential lines of secretory canals (arrows) close to each other; **C**, **D**, Tls, 1-4-seriate rays; **E**, Tls, 3-seriate rays with a uniseriate row of six marginal cells (white arrow), abundant parenchyma (black arrow), 4-8 cells per strand; **F**, Rls, vessel-ray pits irregular in shape, simple with reduced borders (arrows); **G**, Ts, synthetic drawing of the transversal section (with only some vessels and rays displayed), visible bands of parenchyma as grey lines and recognized secretory canals as red dots, arranged mostly in long and closely spaced tangential lines; **H**, Rls, vasicentric tracheids (arrows); **I**, Rls, heterocellular ray with square or upright marginal cells (arrows). Scale bars: G, 1 cm; A, 1 mm; C, 500 µm; B, 330 µm; D, 200 µm; E, H, 100 µm; F, 50 µm. Abbreviations: see Fig. 2.



more), the propensity to have lines of canals spaced by less than 1 mm and small canals (40–80 µm). An examination of different species of *Shorea* shows that this fossil is similar to *Shorea negrosensis* Foxw. ('Rubroshorea' section). This species has closely spaced canals that are sometimes small (surrounded by only four parenchyma cells), thin-to-thick fibres walls, parenchyma cells mostly of the same diameter as fibres and flattened around canals, frequent groups of vessels, as well as similar vessel groups and clusters, and aliform to aliform-confluent parenchyma. The modern specimen in our possession (no. CTFT25647) has mostly 3–4-seriate rays with 1–4 marginal rows of cells, sometimes more for thinner rays.

As for the previous *Shorea*-like fossil, we compared this one with the genus *Shoreoxylon*. Our specimen is among the few to have a high frequency of vessels, closely spaced canal lines and thin rays with not so rare uniseriate ones. Four species of *Shoreoxylon* share many similarities with our fossil (Appendix 1; Awasthi 1974; Sukiman 1977; Trivedi & Ahuja 1979; Bande & Prakash 1980; Du 1988b): *S. arcotense* Awasthi has a high density of vessels and small canals, but exclusively solitary and smaller vessels; *S. pachitanensis* Sukiman has similar bands of canals, but higher rays and wider canals; *S. ornatum* (Trivedi & Ahuja) Bande & Prakash also has similar bands of canals, but less frequent and more solitary vessels, rays up to 5-seriate and higher (up to 1870 µm) and sheath cells are present; *S. sumatraense* from the Quaternary of Sumatra shares most of the main features of our specimen. It has frequent vessels (9–14 per mm<sup>2</sup>), multiples up to 5 vessels, sometimes clusters, thick walls (15 µm, 6–11 µm in our fossil), parenchyma abundant, rays 1–4-seriate with similar composition and height, radially aligned and thin-walled fibres (3 µm, compared to 3–4.4 µm in our fossil), small canals (40–90 µm compared to 40–75 µm in our fossil). However, it displays wider vessels (200–360 µm), a storied tendency in the parenchyma that cannot be observed in our specimen, and no visible vasicentric tracheids (but they seem present in the figures provided) and sometimes crystals in ray cells. The higher density and smaller vessels in our specimen could be explained by compression or environmental constraints. These differences are minor and can be related to intraspecific variations and the poor preservation of our specimen; we thus attribute our specimen to *Shoreoxylon* cf. *sumatraense*. Du (1988b) indicates that *S. sumatraense* shares most features with extant *Shorea negrosensis*, which is in adequacy with our own observations.

*Shorea negrosensis* grows today in the Philippines in evergreen, semi-evergreen and seasonal dipterocarp forests at low elevation (Ashton 1982; Soerianegara & Lemmens 1993; EDC 2020).

*Shoreoxylon* sp. 1  
(Fig. 17)

MATERIAL. — MNHN.F50194 (field number: 19NAT03-1). Estimated minimal diameter: 13–17 cm.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.

AGE. — Upper lower to lowermost middle Miocene.

# DESCRIPTION

Wood diffuse-porous. Growth rings indistinct. Vessels solitary (55–60%) or in groups of 2–4, sometimes in clusters made of a mix of small vessels and vasicentric tracheids (Fig. 17A, D), round to oval due to radial compression, 4–16 per mm<sup>2</sup> (average: 9); tangential diameter 70–270 µm (average: 180 µm). Tyloses present and common, especially in tangential section (Fig. 17C). Vessel elements 150–400 µm (average: 300 µm) long. Perforation plates simple (Fig. 17E). Intervessel pits alternate, 4–7 µm. Vasicentric tracheids present, interspaced with parenchyma (Fig. 17F). Parenchyma frequent, mostly aliform or aliform-confluent, crossing rays and joining vessels together but without any particular arrangement (Fig. 17A), diffuse-in-aggregate or drawing a network between rays in the form of small bands or groups; 4 cells sheath around canals (Fig. 17D); parenchyma cells 40–110 µm long (average: 80 µm), 13–26 µm wide (average: 20 µm) in tangential section, 4–5 cells (possibly more) per parenchyma strand, possibly subdivided (Fig. 17F). Rays 1- to 5-seriate (dominantly 4-seriate) (Fig. 17B, C), uniseriate few (< 10%) and short (mainly less than 10 cells high), 4–8 rays per mm (average: 6), 130–800 µm (average: 460 µm) or 6–50 cells high. Heterocellular made of procumbent cells with 1–2 upright cells at the ends (Fig. 17E), rarely more (up to 7). Sometimes rays appear weakly heterocellular as the marginal rows are composed of enlarged procumbent cells (Fig. 17E); rays homogeneous in shape (fusiform) and size (Fig. 17C), all ray cells filled with dark content. Fibres non-septate, 12–20 µm in diameter (average: 17 µm), (lumina 1 times the double wall thickness on average). Secretory canals few and small (Fig. 17A, D), in irregularly spaced short (to long) tangential bands up to 4–6 canals, embedded in parenchyma bands (Fig. 17G), canals possibly crushed, 30–50 µm in tangential diameter (average: 40 µm).

# DISCUSSION

This specimen is characterized by: 1) diffuse-porous wood; 2) high density of vessels, often in groups and sometimes in clusters; 3) short fusiform rays; 4) short lines of very small secretory canals; 5) abundant parenchyma, mostly aliform-confluent and diffuse-in-aggregate; and 6) vasicentric tracheids.

Like for previous specimens (from p. 873), secretory canals and vasicentric tracheids are diagnostic of the Dipterocarpaceae family. Few canals are distinguishable, and it is hard to determine if they are arranged in short or long lines. Our specimen is only compatible with genera *Hopea*, *Parashorea* and *Shorea* as they have vessels smaller than 150 µm of average diameter, not exclusively solitary vessels, no fibre-tracheids, and canals in short or long lines. A closer affinity to *Shorea* genus is indicated because of its homogeneous rays, common tyloses, vessel density sometimes more than 10/mm<sup>2</sup>. Following the discussion of the page 882, the sections 'Pentacme' and 'Shorea' are the closest to this fossil although 'Shorea' is the best option with short rays sometimes weakly heterocellular, with frequent tyloses, a variable frequency of groups of vessels, sometimes short lines of canals and frequent apotracheal parenchyma. This specimen recalls: *Shorea robusta* C.F.Gaertn.



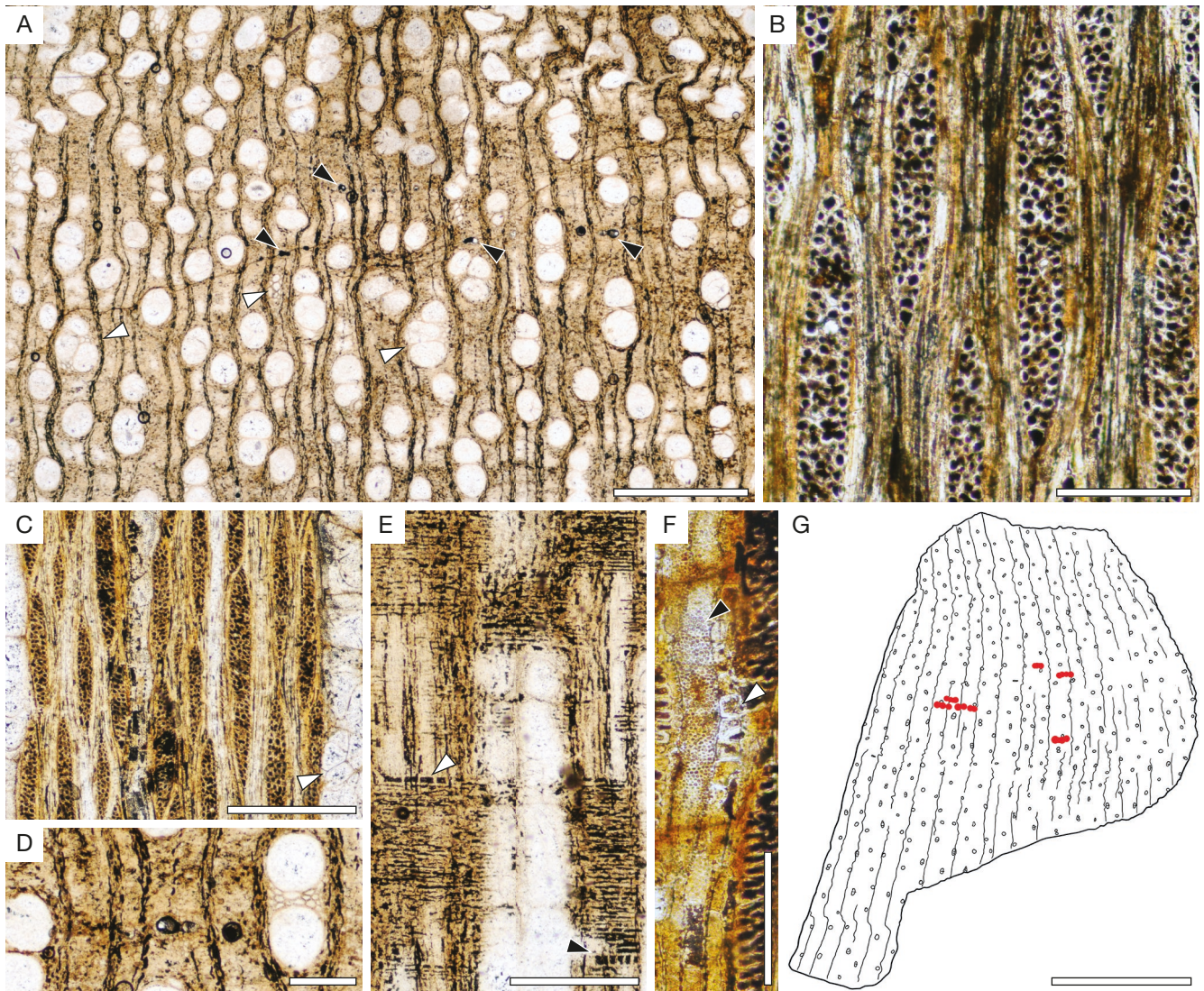


FIG. 17. — *Shoreoxylon* sp. 1, MNHN.F.50194: **A**, Ts, vessels often grouped, sometimes in clusters (**white arrows**), abundant parenchyma, aliform to aliform-confluent, short lines and diffuse secretory canals (**black arrows**); **B, C**, Tls, 1-5-seriate rays, tyloses (**arrow**); **D**, Ts, zoom in on secretory canals in short lines and vessels in clusters with vasicentric tracheids or small vessels; **E**, Rls, weakly heterocellular rays with one row of larger procumbent cells (**white arrow**) or square to upright cells (**black arrow**); **F**, Tls, vasicentric tracheid (**black arrow**) and vasicentric parenchyma (**white arrow**); **G**, Ts synthetic drawing of the transverse section (only a few vessels and rays are displayed); secretory canals are displayed as red dots, very few are preserved. Scale bars: A, 1 mm; B, F, 200  $\mu$ m; C, E, 500  $\mu$ m; D, 250  $\mu$ m; G, 1 cm. Abbreviations: see Fig. 2.

for its abundant parenchyma, 4-5-seriate and short fusiform rays, and vessels often in groups and clusters; *Shorea obtusa* Wall. (ex Blume) for abundant parenchyma, rays with only one upright marginal ray cell, vessels often in group and in radially aligned clusters; *Shorea siamensis* Miq. for the mostly aliform parenchyma, yet without a defined arrangement, abundant diffuse to diffuse-in-aggregate parenchyma, short (yet shorter than 50 cells high) and fusiform rays. All of them have few and short uniseriate rays (often less than 10 cells high). In a lesser extend, we can find some similarities with *Shorea parvifolia* for aliform parenchyma forming very thin lateral lines, rays up to 5-seriate, quite short and fusiform with few marginal cells.

The specimen shares all diagnostic features of fossil genus *Shoreoxylon*. Three fossil species with 1-5-seriate rays display

similar features to the ones of our fossil (Appendix 1; Schweitzer 1958; Prakash 1965a; Ramanujam & Rao 1967; Sukiman 1977; Prakash & Bande 1980; Gurusamy & Kumarasamy 2007): *S. indicum* for parenchyma, rays and crystals but with bigger canals, less frequent but more commonly solitary vessels; *S. posthumi* has short and fusiform rays but broader (mainly 5-seriate), enlarged parenchyma cells are frequent (idioblasts) and clearly visible in figures and secretory canals are wider; *S. burmense* has similar rays although slightly broader but its vessels are more solitary and canal lines are often grouped by 2-5. In a lesser extent: *S. irrawaddiensis* Prakash & Bande is described with larger vessels (up to 6-(7)-seriate) although mostly 3-5-seriate and solitary vessels, however the rays in the figures seem to be mainly 4-5-seriate. Even though it is probable that our fossil might belong to one of these spe-



cies, their descriptions are overlapping, often incomplete or lack clear figures; they do not allow us to attribute a clear identification to our specimen with confidence, nor to create a new species. As a consequence, we attribute this fossil to *Shoreoxylon* sp. with a noted resemblance with *S. indicum*, *S. posthumi* or *S. burmense*.

*Shorea parvifolia* is common in dipterocarp forests up to 1100 m altitude (Soerianegara & Lemmens 1993; Tropical Plants Database 2014-onward; Barstow 2018b); *Shorea obtusa* lives in dry lowland deciduous dipterocarp forests, in savannas and in monsoonal forests with a marked dry season and waterlogged periods, up to 1000 m altitude (Soerianegara & Lemmens 1993; Ghazoul 2016); *Shorea robusta* is a common semi-deciduous tree in South Asia in areas with a dry season lasting 4 to 8 months (a monsoon climate). Thus, it is mainly found in dry deciduous forests and savannas, but also in evergreen moist forests on well-drained soil and riverbanks. It is usually found below 800 m altitude (Wu *et al.* 2007; Timilsina *et al.* 2007; Orwa *et al.* 2009).

*Shoreoxylon* sp. 2  
(Fig. 18)

MATERIAL. — MNHN.F.50195 (field number: 19NAT07-2). Estimated minimal diameter: 73–105 cm.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.

AGE. — Upper lower to lowermost middle Miocene.

DESCRIPTION

Wood diffuse-porous. Growth rings indistinct or delimited by marginal parenchyma (Fig. 18A). Vessels 80% solitary or in groups of 2–3, occasionally small clusters (Fig. 18A); they display an oblique tendency, round to oval, 3–9 per mm<sup>2</sup> (average: 6); tangential diameter 100–270 µm (average: 190 µm). Tylose present (Fig. 18I). Vessel elements 180–400 µm (average: 280 µm) long. Perforation plates simple. Intervessel pits alternate, vested, 5–8 µm (Fig. 18J). Vessel-ray pits simple or minutely bordered, ovoid in shape, 8–12 µm in diameter (only 5 were observed) (Fig. 18K). Vasicentric tracheids present (Fig. 18I). Parenchyma vasicentric (sheath of 2–7 cells) and frequently aliform, also diffuse, and sometimes diffuse-in-aggregate in short lines mostly starting from the edge of paratracheal parenchyma (Fig. 18A, B); seemingly marginal lines that could contain secretory canals (Fig. 18A, G); sometimes crystals in chambered cells (up to 12 per strands) (Fig. 18H), mostly observed in the diffuse parenchyma; parenchyma cells 50–130 µm long (average: 100 µm), 12–19 µm wide (average: 16 µm) in tangential section; 4–5 parenchyma cells per strand. Xylem rays 1- to 5-seriate (mainly 4) (Fig. 18C, E), uniseriate short (< 10 cells) and about 19% of the rays; 7–9 rays per mm (average: 8), 100–850 µm (average: 430 µm) or

6–40 cells high, heterocellular made of procumbent cells with mostly 1 upright cell at the ends, sometimes more (Fig. 18F). Fibres non-septate, thick to very thick-walled (lumina from 0.5 to almost 0 times the double wall thickness in average). Secretory canals in long tangential bands (more than 30 canals) surrounded by parenchyma (Fig. 18D, G), 40–85 µm in tangential diameter (average 60 µm).

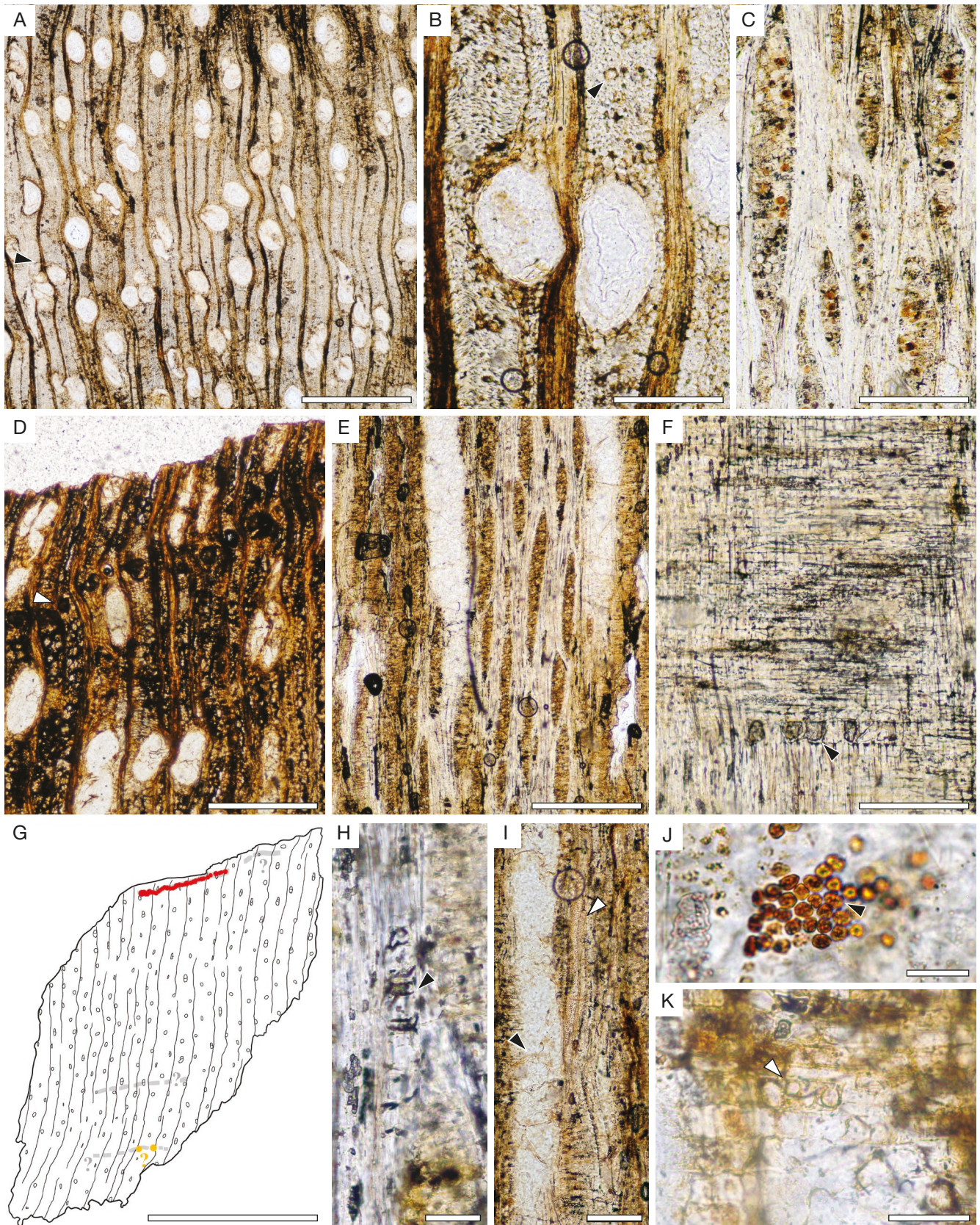
DISCUSSION

This wood is characterized by: 1) diffuse-porous wood; 2) mostly solitary vessels with an oblique tendency; 3) heterocellular 1–5-seriate rays that are short (< 1000 µm); 4) small canals (< 100 µm) in long tangential lines; 5) vasicentric tracheids; and 6) aliform and diffuse parenchyma. As for previous specimens (from p. 873), secretory canals and vasicentric tracheids are diagnostic of the Dipterocarpaceae family. Following the discussion p. 882, these features recall the genus *Shorea*, together with the presence of groups of vessels and clusters, the absence of vascular tracheids, and crystals in ray cells. More specifically with the sections ‘Rubroshorea’ and ‘Shorea’ for having frequent tyloses, crystals in parenchyma, rays with few marginal cells and small canals. Regarding rays, the section ‘Shorea’ has shorter ones (under 1000 µm) and less marginal cells, even though this observation is not a general fact. Our specimen recalls extant species *S. laevis* for its aliform parenchyma, similar ray width and length (mostly 3–5-seriate and up to 45 cells high), and small canals and *S. balangeran* Dyer for its wide vessels (sometimes > 200 µm) often solitary or in very small groups, its long and distinctive lines of canals, its rays of varying length and its aliform parenchyma sometimes forming a discrete network without particular arrangement between vessels.

The specimen shares all diagnostic features of fossil genus *Shoreoxylon* and shares most features of *Shoreoxylon* sp. 1 (p. 886) and *Shoreoxylon* cf. *deomaliense* (p. 882); it is yet clearly distinguishable from our two previous specimens. It has more solitary and less numerous vessels than *Shoreoxylon* sp. 1 as well as less confluent parenchyma and clear long lines of canals; it has more grouped vessels and shorter, less seriated rays than *Shoreoxylon* cf. *deomaliense*. Among *Shoreoxylon* species that are close to our fossil (Appendix 1; Den Berger 1923; Schweitzer 1958; Prakash 1965a; Prakash & Awasthi 1970; Awasthi 1974; Sukiman 1977; Trivedi & Ahuja 1979; Prakash & Bande 1980), two species share similar features: *S. burmense* has slightly larger rays and multiple bands of canals, mostly vasicentric parenchyma, but it has very thick walls; *S. tipamense* shares similar vessel and crystalliferous parenchyma arrangement in addition to 1–5-seriate rays up to 66 cells high, but has longer rows of marginal ray cells (1 to 12), some sheath cells, larger intervessel pits (8–10 µm compared to 5–8 µm) and thinner walls. Considering the poor preservation of the specimen, it is attributed to *Shoreoxylon* sp. 2, with noted resemblance with *S. tipamense* or *S. burmense*.

Fig. 18. — *Shoreoxylon* sp. 2, MNHN.F.50195: **A**, Ts, vessel arrangement, often solitary, sometimes in groups and clusters, with one parenchyma band (arrow); **B**, Ts, mostly vasicentric to slightly aliform parenchyma as well as some diffuse parenchyma (arrow); **C**, **E**, Tls, 1–5-seriate rays; **D**, Ts, long tangential line of secretory canals embedded in parenchyma band (arrow); **F**, Rls, heterocellular ray with one line of upright marginal cells (arrow); **G**, Ts, synthetic drawing of





the transversal section (only some vessels and rays are displayed) with bands of parenchyma as grey lines and secretory canals as red dots, arranged in long tangential lines; doubtful canals are displayed as orange dots; **H**, RIs, crystals in possibly chambered parenchyma cells (**arrow**); **I**, tyloses in vessels (**black arrow**) and vasicentric tracheids (**white arrow**); **J**, TIs, alternate, vestured (**arrow**) intervessel pits; **K**, simple vessel-ray pits with reduced borders and ovoid shape (**arrow**). Scale bars: G, 1 cm; A, D-E, 500 µm; B-C, F, 200 µm; H-I, 100 µm; J, 20 µm; K, 50 µm. Abbreviations: see Fig. 2.



*Shorea laevis* mostly grows on tropical ridges or hillsides up to 1000 m altitude; it is also found in lowland mixed dipterocarp forests and on alluvial sites (Ashton 1982; Soerianegara & Lemmens 1993; Pooma *et al.* 2017). *Shorea balangeran* is common in peat-swamp forests up to 100 m altitude (Soerianegara & Lemmens 1993; Robiansyah 2020).

Family BURSERACEAE Kunth

Genus *Burseroxylon*

(Prakash & Tripathi) Lakhanpal, Prakash & Awasthi

*Burseroxylon* sp.

(Fig. 19A-J)

**MATERIAL.** — MNHN.F.50196 (field number: 17FN05), MNHN.F.50197 (field number: 17FN11), MNHN.F.50198 (field number: NAT17-01). Estimated minimal diameter: > 30 cm, as rays are almost parallel.

**LOCALITY.** — Kalewa Township, Sagaing Region, Myanmar.

**AGE.** — Upper lower to lowermost middle Miocene.

#### DESCRIPTION

Wood diffuse-porous. Growth rings indistinct or absent. Vessels mostly solitary (75%) or in radial groups of 1-4 (25%) (Fig. 19A), oval to round, 2-13 per mm<sup>2</sup> (average: 7); tangential diameter 90-280 µm (average: 190 µm). Tyloses present in most vessels (Fig. 19A, D), budding from ray parenchyma cells. Vessel elements 130-540 µm long (average: 310 µm). Perforation plates simple. Intervessel pits alternate, polygonal shaped, 7-10 µm wide (average 8.5 µm). Vessel-ray pits apparently simple with different shapes and sizes, mostly horizontal (5-20 µm, 13 µm in average) (Fig. 19E). Parenchyma exclusively paratracheal, scanty and vasicentric forming a 1-cell sheath around vessels (Fig. 19A, D); parenchyma cells 45-90 µm long (average: 60 µm), 25-45 µm wide (average: 35 µm) in tangential section; some crystals are present in chambered parenchyma cells in the specimen MNHN.F.50197 Rays 1- to 4-seriate, mostly 3- or 2-seriate, always more than 50% of the rays are 3-seriate, rarely uniseriate, (Fig. 19B), non-storied, 3-12 rays per mm (average: 7), 150-640 µm (average: 380 µm) or 4-23 cells high, heterocellular made of procumbent cells with 1(-3) square or upright cells at both ends (Fig. 19C, F, G); crystals sometimes present in upright or enlarged marginal cells (Fig. 19F), maybe in procumbent cells as well (Fig. 19G). Fibres thin-to-thick to thin-walled (lumina 2.5 times the double wall thickness in average), almost all fibres are septate (Fig. 19B), tangential diameter 10-30 µm (average: 18 µm). Traumatic canals present (specimens MNHN.F.50197 and MNHN.F.50198) as holes of different size and shape surrounded by clusters of undifferentiated cells full of black content (Fig. 19H-J). The specimen MNHN.F.50198 displays an enlarged radial line of undifferentiated tissue embedding some rays that recalls a healed crack filled with tissue during the growth of the wood (Fig. 19J) that ends with a line of traumatic canals (Fig. 19I). Radial canals absent.

#### DISCUSSION

These specimens are characterized by: 1) diffuse-porous wood with isolated and tylosed vessels; 2) exclusively simple perforation plates; 3) septate fibres which although are not always very well preserved are clearly present throughout the whole sample; 4) exclusively vasicentric parenchyma; 5) growth rings indistinct or absent; and (6) 2- to 4-seriate heterocellular rays. These features suggest affinities with Burseraceae as well as some Anacardiaceae (Metcalf & Chalk 1950; InsideWood 2004-onward; Ogata *et al.* 2008). Both families share several similar anatomical features. However, the presence of septate fibres is more consistent in Burseraceae, as well as a greater homogeneity in rays and parenchyma patterns, and the presence of crystals in enlarged ray cells. Moreover, traumatic canals are not reported in Anacardiaceae, whereas they are reported in Burseraceae (Metcalf & Chalk 1950). One species of Anacardiaceae resembles our specimens: *Lannea coromandelica* (Houtt.) Merr., which has similar vessel, ray and parenchyma patterns, crystals in normal and enlarged marginal cells, in parenchyma and in procumbent cells; however, silica bodies are present in its ray cells and it is always described with radial canals (InsideWood 2004-onward; Gupta & Agarwal 2008), which are absent in our fossils. The three present specimens show slight differences in vessel and ray density, ray height and width, and crystal presence (the specimens MNHN.F.50197 has slightly shorter rays, more frequent 2-seriate rays, crystals in non-enlarged marginal cells, in parenchyma cells and possibly in procumbent ray cells) but the range of these variations is within the inter- and intraspecific diversity of Burseraceae (Metcalf & Chalk 1950; InsideWood 2004-onward; Ogata *et al.* 2008). The wood anatomy of Burseraceae is very homogenous, both among extant and fossil species (Awasthi & Srivastava 1989; Prasad 1993; Ogata *et al.* 2008). Among Burseraceae, our fossils resemble the genera *Canarium* L. and *Protium* Burm.f. which display homogeneous 1-3-(up to 4)-seriate rays and sometimes traumatic canals (Metcalf & Chalk 1950). The examination of Burseraceae from the Xylarium of the MNHN highlighted a resemblance between the fossil specimens MNHN.F.50196 and MNHN.F.50198 with *Canarium bengalense* Roxb. (specimen MNHN-P-P00395579), because of crystals only present in enlarged marginal ray cells, similar vessel size and frequency (sometimes < 5 / mm<sup>2</sup> and over 100 µm of diameter) and ray pattern (1-3-seriate, 3-16 cells high). Ogata *et al.* (2008) mention that the genus *Canarium* can have rays up to 4-seriate. The fossil specimen MNHN.F.50197 is closer to *Protium serratum* (Wall. ex Colebr.) Engl. (specimens MNHN-P-P00396706 and MNHN-P-P00396663) as it displays crystals in normal marginal cells as well as sometimes in procumbent cells and in parenchyma cells, smaller and more frequent rays than *Canarium* (sometimes > 10/mm<sup>2</sup> and under 100 µm of diameter). *Protium serratum* is described with and without radial canals (InsideWood 2004-onward).

Burseraceae are not numerous in the fossil record (Gregory *et al.* 2009) and include two dominant fossil genera: 1) *Burseroxylon* which includes fossils related to *Bursera* Jacq. ex L. (and by extension *Protium*) and some *Garuga* Roxb. (Lakhanpal *et*



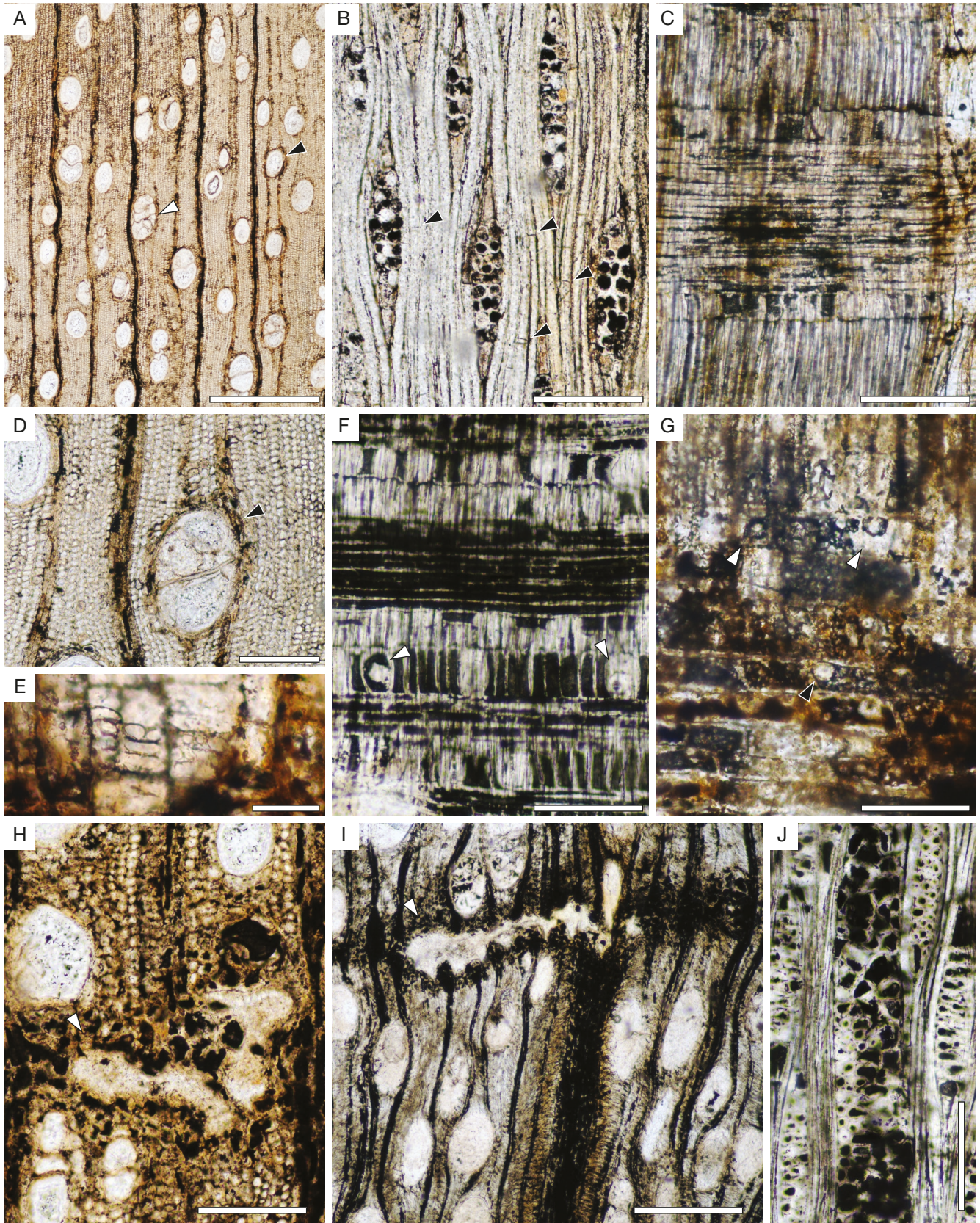


FIG. 19. — *Burseroxylon* sp., MNHN.F.50196 (C), MNHN.F.50197 (A, B, D-E, G, H), MNHN.F.50198 (F, I, J): A, D, Ts, vessels with tyloses (**white arrow**) and thin sheath of vasicentric parenchyma (**black arrow**); B, Tls, (1)-4-seriate rays, septate fibres (**arrow**); C, Rls, heterocellular rays with upright marginal cells; E, Rls, simple vessel-ray pits, oval in shape; F, Rls, heterocellular rays with upright marginal cells, some of them are enlarged and contain a single crystal (**arrow**); G, Rls, crystals in upright marginal cells (**white arrow**), maybe also in procumbent cells sometimes (**black arrow**); H, I, Ts, traumatic canals (**arrows**); J, Tls, tangential view of undifferentiated tissue surrounding a traumatic canal. Scale bars: A, 1 mm; B-D, F-H, J, 200  $\mu$ m; E, 50  $\mu$ m; I, 500  $\mu$ m. Abbreviations: see Fig. 2.



*al.* 1981); and 2) *Canarioxylon* Prakash, Březinová & Awasthi which includes fossils related to *Canarium*. Some fossils are also described under the name *Canarium*. The diagnoses of *Burseroxylon* and *Canarioxylon* are very similar; *Burseroxylon* is different in having (only sometimes) visible growth rings, crystalliferous rays, vasicentric parenchyma in addition to scanty paratracheal, sometimes radial canals, and rays 5-seriate or more (instead of 1–4 seriate in *Canarioxylon*). The genus *Garugoxylon* Vozenin-Serra & Privé-Gill (1991) is not taken into consideration as the diagnosis can be included in the one of *Burseroxylon* (Lakhanpal *et al.* 1981). Only one fossil is described with crystals in parenchyma cells: *Canarioxylon noduliforme* Yang, Guo & Wei, 1995, but it displays radial canals and larger rays among other incompatible features. If we strictly follow the diagnoses of the genera, our fossils are attributed to *Burseroxylon* and not *Canarioxylon*, because of the presence of vasicentric parenchyma and crystals in ray cells. Awasthi & Srivastava (1989) underline that Burseraceae species share overlapping descriptions and diagnoses; because of this overlap, we do not attribute our specimens to any *Burseroxylon* species and attribute our fossils to *Burseroxylon* sp. while awaiting a taxonomic clarification of the genus and the family.

*Protium* is a genus of trees growing in America, Madagascar and Asia in evergreen to semi-deciduous forests up to 800 m altitude (Sosef *et al.* 1998). *Protium serratum* lives in humid areas of India and tropical forests of Myanmar (Prasad 1993), and in moist evergreen and deciduous forests of Thailand (Tropical Plants Database 2014-onward), in riparian areas (Gamble 1902). Up to 600–1000 m altitude (Wu *et al.* 2008). *Canarium* species live in Africa, Asia and Australia in wet evergreen rainforests, mainly in lowlands, but also in monsoonal climate and open forests (Lemmens *et al.* 1995). *Canarium bengalense* is a tree living in evergreen, moist and mixed dipterocarp forests below 1300 m altitude (Leenhouts 1959; Wu *et al.* 2008; Ayyappan & Kokilavani 2020).

## UNDETERMINED TAXA

indet. sp. 1  
(Fig. 20A–F)

MATERIAL. — MNHN.F.50199 (field number: 17FN08). Estimated minimal diameter: 33 cm.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.

AGE. — Upper lower to lowermost middle Miocene.

## DESCRIPTION

Wood diffuse-porous. Growth rings distinct, marked by marginal parenchyma (Fig. 20A). Vessels mostly solitary (80%) or in groups of 2, rarely 3 (Fig. 20A), oval in shape, 1–7 per mm<sup>2</sup> (average: 3); tangential diameter 120–200 µm (average 160 µm). Tyloses absent. Vessel elements 190–430 µm (average: 310 µm) long. Perforation plates simple. Intervessel pits alternate, 3–6 µm in diameter (average: 5 µm). Vessel-ray pits

maybe of the same nature as intervessel pits. Parenchyma scanty paratracheal or vasicentric (Fig. 20A), in (2–6 cells wide?) marginal bands, also around canals; parenchyma cells 60–130 µm long (mean 90 µm), 20–50 µm wide (average: 35 µm) in tangential section (Fig. 20D), 2–5 cells per parenchyma strand; the epithelial parenchyma around the canals possibly contains crystals in chambered cells. Rays 1–to 4-seriate (mostly 3-seriate) (Fig. 20B, C), uniseriate rays about 10–20% of the rays, 2–12 cells high, 4–7 rays per mm (average: 6), multiseriate rays 310–1260 µm (average: 720 µm) high or 11–44 cells (average: 24 cells), heterocellular made of procumbent cells with 1–8 (or more) upright cells at the ends (Fig. 20B, C), sheath cells sometimes present, some rays appear with mixed procumbent and upright cells in radial section (Fig. 20F), ray cells possibly containing prismatic crystals. Fibres non-septate, 11–26 µm in diameter (average: 20 µm). Canals diffuse or in short tangential lines, tangentially as big as vessels, radially longer up to 500 µm (average: 350 µm) (Fig. 20A, E).

## DISCUSSION

The most diagnostic character of the fossil is the presence of wide pores (tangentially the same size as vessels but radially longer) that are often 2–6 tangentially grouped. In tangential section, these pores do not show any perforation plate and are surrounded by parenchyma, as expected for secretory canals. The presence of solitary secretory canals or in short tangential lines in diffuse-porous wood are only found in Dipterocarpaceae and Fabaceae (in the Detarioideae subfamily, more specifically in the Prioria, Detarieae and some of the Daniellia clades) (InsideWood 2004-onward; De la Estrella *et al.* 2018; Choo *et al.* 2020). The specimen displays the same ray arrangement as modern Dipterocarpaceae; it also has marginal or seemingly marginal parenchyma bands without tyloses, as found within the Fabaceae family. We note a close affinity with extant *Dipterocarpus*, as the presence of short tangential lines is very characteristic of this genus (Schweitzer 1958), but the attribution to Dipterocarpaceae is uncertain because we can not observe vasicentric tracheids or simple vessel-ray pits. In addition, vessels are not exclusively solitary as expected for *Dipterocarpus*. For the second family, short tangential lines of canals are mostly found in the genera: *Prioria* Griseb., *Daniellia* Benn., *Copaifera* L., *Detarium* Juss., *Eperua* Aubl. and *Sindora* Miq. (Gasson 1994). Canals at least as big as vessels are only reported in *Prioria* (synonyms: *Kingiodendron* Harms, *Gossweilerodendron* Harms, *Oxystigma* Harms, *Pterogopodium* Harms and *Eriander* H.J.P. Winkl.) and especially in *Prioria copaifera* Griseb., which is described with parenchyma scanty to aliform and in 3–4(6) cells wide bands; 2–4 cells per parenchyma strands, rays mostly 1–3-seriate up to 37 cells high with many uniseriate rays and upright marginal cells. Parenchyma can also contain crystals especially in the epithelial cells of canals (Banks & Gasson 2000; Gasson *et al.* 2003). The former genus *Kingiodendron* share similar characteristics (Banks & Gasson 2000; Gasson *et al.* 2003). However, *Prioria* is not reported with sheath cells and have vessel-ray pits similar to intervessel pits, as well as mostly diffuse canals.



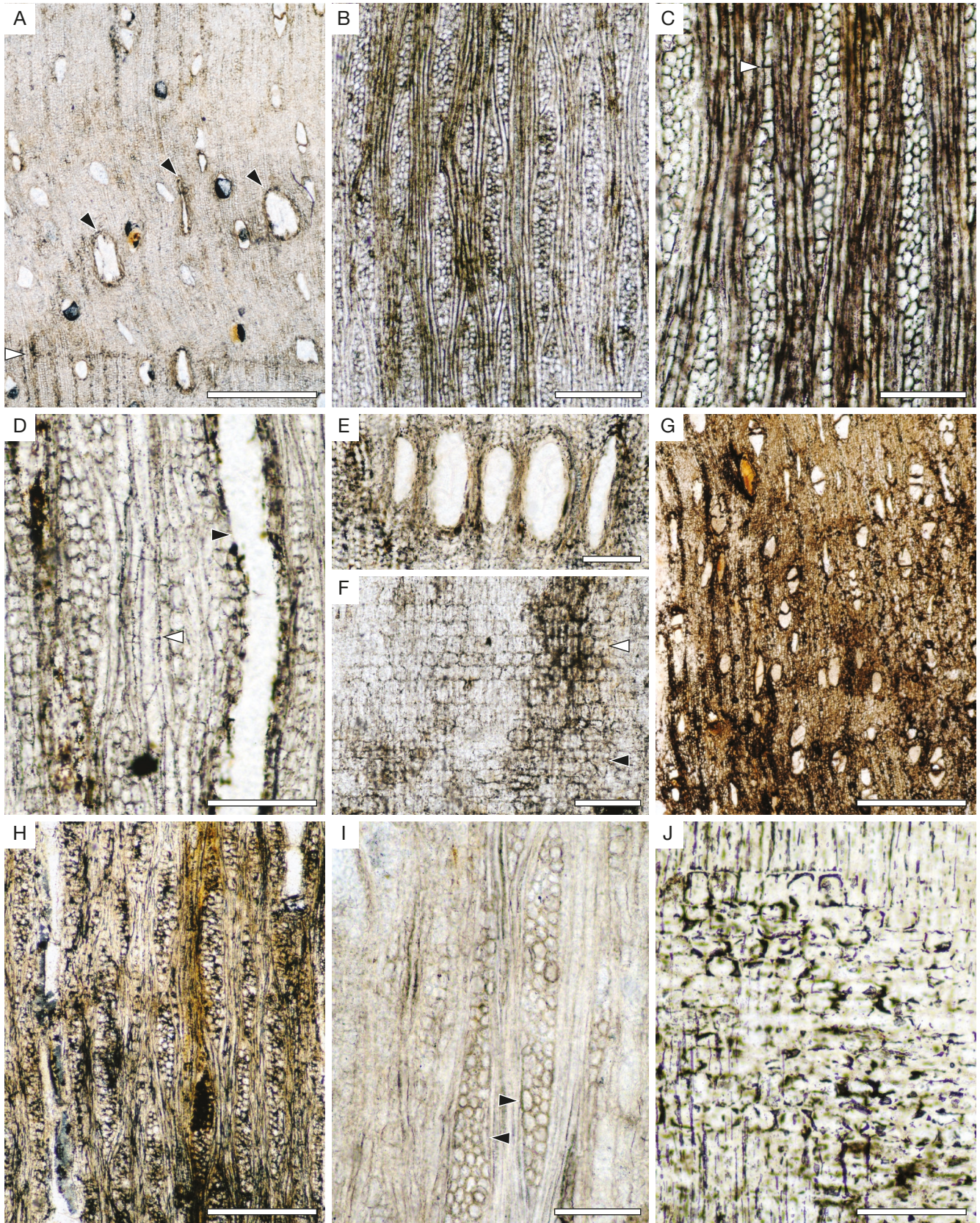


FIG. 20. — Indet. sp. 1, MNHN.F.50199 (A-F): **A**, Ts, vessels and few vasicentric parenchyma, solitary secretory canals (**arrows**) or in short tangential lines, surrounded by parenchyma, remarkably bigger than vessels; **B**, **C**, Tls, 1-4-seriate rays with sometimes long uniseriate row of marginal cells (**arrow**); **D**, Tls, parenchyma cells (**white arrow**) and secretory canal (**black arrow**); **E**, Tls, detail of secretory canals in short tangential line; **F**, Rls, heterocellular rays with procumbent cells (**black arrow**) and square or upright cells (**white arrow**). **G-J**, Indet. sp. 2, MNHN.F.50200: **G**, Ts, poorly preserved wood, vessel arrangement often in groups; **H-I**, Tls, 1-5-seriate rays, with maybe sheath cells (**arrows**); **J**, Rls, heterocellular rays with procumbent and square or upright cells. Scale bars: A, G, 1 mm; B, H, 500  $\mu$ m; C-F, I-J, 200  $\mu$ m. Abbreviations: see Fig. 2.



Fossils described with diffuse and short lines of secretory canals belonging to Dipterocarpaceae or Fabaceae, with the particularity of bigger canals than vessels are relatively few. They are reported bigger or of the same size as vessels in *Dipterocarpoxydon surangei* Prakash (1981), *D. premacarpum* Prakash (1975) and *D. arcotense* Awasthi (1980), but their vessels are almost exclusively solitary, and their rays are broader (up to 5- or 7-seriate). Bancroft described fossil specimens from Africa twice (Bancroft 1933, 1935) under the name *D. africanum* Bancroft. They share many features of our fossil, including 1-4-seriate rays (mostly 3-seriate) with many upright cells in rays with up to 6-cells in marginal rows (mostly for biseriate rays) and up to 30 cells high. Bancroft (1935) mentioned structures that looked like vasicentric tracheids which suggests an affinity to Dipterocarpaceae, though the author still mentions a possible affinity with Detarioideae, as vessel-ray pits are still not visible. Many fossil species related to Detarioideae have no canals. Among those with canals, *Hopeoxylon* Awasthi (1977) has often banded parenchyma and canals in short to often long lines, smaller than vessels. Several specimens of *Kingiodendron* (Awasthi & Prakash 1987; Awasthi 1992; Guleria *et al.* 2002; Pérez-Lara *et al.* 2021) have the same size and arrangement of canals than the present fossil, but rays are much shorter and less heterocellular or canals are smaller than vessels. Ramos *et al.* (2017) described two fossil genera: *Paraoxystigma* Ramos *et al.* which has only diffuse canals and only one row of marginal ray cells; and *Gossweilerodendroxylon* Ramos *et al.* which has no uniseriate rays, only weakly heterocellular rays and canals much smaller than vessels. Two fossil wood specimens of *Prioria* are described by Rodríguez-Reyes *et al.* (2017): *P. hodgesii* Rodríguez-Reyes *et al.* which has smaller canals than vessels and *P. canalensis* Rodríguez-Reyes, Gasson, Falcon-Lang & Collinson, which shares most of the features of our fossil except that it displays long lines of canals, parenchyma is sometimes aliform and strands of parenchyma are composed of 3-8 cells (down to 2 cells for our fossil). As it is not possible to determine precisely the nature of vessel-ray pits nor if there are any vasicentric tracheids or common crystals in our specimen, the attribution to a given family is difficult. As a consequence, we consider this specimen as undetermined.

Modern *Dipterocarpus* are mainly tropical trees growing in evergreen, sometimes present in semi-evergreen forests or dry deciduous dipterocarp forests, mostly in lowlands and occasionally up to 1400 m. (Ashton 1982; Soerianegara & Lemmens 1993; Ghazoul 2016). *Prioria s.l.* is a genus of large trees adapted to seasonally-flooded riparian environments (Rodríguez-Reyes *et al.* 2017). *Prioria s.s.* is an American tropical tree growing in lowlands often in coastal forests, sometimes swamps and along estuaries (Rodríguez-Reyes *et al.* 2017), whereas *Kingiodendron* is found in Asia in evergreen rainforests at low elevation, and flood-plains up to 800 m altitude (Hou *et al.* 1996; Pascal *et al.* 2004).

indet. sp. 2  
(Fig. 20G-J)

MATERIAL. — MNHN.F.50200 (field number: NAT17-5). Estimated minimal diameter: 11 cm.

LOCALITY. — Kalewa Township, Sagaing Region, Myanmar.

AGE. — Upper lower to lowermost middle Miocene.

#### DESCRIPTION

Wood diffuse-porous. Growth rings indistinct. Vessels solitary (55%), often grouped by 2 but also up to 4 (Fig. 20G), round to oval, 4-12 per mm<sup>2</sup> (average: 7); tangential diameter 90-200 µm (average: 150 µm). Tyloses absent. Vessel elements 210-420 µm (average: 330 µm) long. Perforation plates simple. Intervessel pits alternate, 3-6 µm in diameter (average: 5 µm). Parenchyma vasicentric possibly aliform; parenchyma cells 60-100 µm long (average: 80 µm), 12-30 µm wide (average: 20 µm) in tangential section. Rays 1- to 5-seriate (mostly 3-seriate) (Fig. 20H, I), 5-8 rays per mm (average: 6), 270-1130 µm (average: 650 µm) or 6-36 cells high, heterocellular made of procumbent cells with 1-2 upright cells at the ends (Fig. 20J); some sheath cells present (Fig. 20I). Fibres non-septate, 8-20 µm in diameter (mean 15 µm). Secretory canals possibly present as some ducts without perforation plates seem to be filled with an orange content (Fig. 20G), also coloring the surrounding cells, recalling a resin.

#### DISCUSSION

This fossil recalls Dipterocarpaceae because of: 1) ray height, strongly heterocellular; and 2) ducts filled with orange content and without any trace of perforation plates, which could be secretory canals, in tangential sections. Unfortunately, these potential canals are not observable in transverse section, nor any vasicentric tracheids. This specimen resembles *Shoreoxylon* sp. 1 or *Shoreoxylon* cf. *deomaliense* for ray size and arrangement, as well as vessel size. The state of preservation of this specimen is not good enough for a conclusive determination; it is impossible to clearly distinguish parenchyma, fibres and pore outlines, suggesting that the specimen has been degraded (see part 5.1).

#### DISCUSSION

##### ON THE PRESERVATION OF THE WOOD SPECIMENS

The poor state of preservation of some specimens, especially with degraded cell walls as well as the presence of hyphae and spores, suggests that some fossils have already experienced bacterial and fungal decay before their burial.

Several fossils associated today with seasonal / coastal ecosystems are well preserved and not compressed (e.g. *Pahudioxylon bankurensis*), while many fossils associated today with wetter ecosystems are poorly preserved and heavily compressed, with highly degraded cell walls and inflated cells in some samples indicating a long residence time spent in water (e.g. *Dipterocarpoxydon* cf. *jammuense*); our specimens of Dipterocarpaceae,



mostly associated with the wet evergreen forests, are rarely well enough preserved to identify them without any doubt. However, the poor preservation of specimens associated with a given forest type is not systematic: cf. *Koompassioxylon*, associated with evergreen forests, has quite well-preserved cell walls, while *Albizinium eolebbekianum*, associated with seasonal to dry deciduous forests, is poorly preserved.

The poor preservation could thus reflect a long immersion time. Indeed, cell walls of silicified wood are often considered preserved in a swollen state as the silicification process is water-borne (Leo & Barghoorn 1976; Wheeler *et al.* 2007; Mustoe 2017). Long-term water exposure results in changing physical and mechanical properties of the wood, such as swelling of the secondary walls, promoting hydrolyzation and biological degradation starting from the lumen toward the middle lamella (Fengel 1991). Our wood specimens have been found in channel log deposits, indicating transport in rivers and supporting some exposure to water. Most of the specimens are estimated with a diameter around or less than 30 cm, suggesting they come from branches or small individuals which facilitate transportation.

Different “durability” of the wood specimens (their susceptibility to decay) could also partly explain why the preservation of specimens varies. However, the term of “preservation” is ambiguous as degradation of the cell walls, the quality or the type of mineralization and the compression of the wood are all responsible for the loss of visible characters. Although this varies between species, individuals and within individuals, some genera and species are more durable than others (Scheffer & Morrell 1998). Dipterocarps are known to be sensible to decay (Scheffer & Morrell 1998), but there are great disparities in durability within dipterocarp genera. Some of our most preserved fossils have NLR with durable wood (i.e. *Intsia*, *Afzelia*, *Koompassia*, *Artocarpus* and some Cupressaceae) (Scheffer & Morrell 1998; FRDB 2016), but this is not systematic (i.e. *Protium*, *Canarium* are not durable but the fossils are relatively preserved). *Cynometra* and *Maniltoa* are not durable trees, but our specimens of *Cynometroxylon* display distinct features and sometimes quite well-preserved cell walls.

The polished aspect of the samples could be explained by weather erosion when they get exposed, or by stream erosion due to transportation after their fossilization. This would imply that they could belong to older or younger stages. However, the uniformity of the preservation state, the compression and the fossilization, as well as the thickness of the Natma Formation at the sampling site support that the fossils belong to the Natma Formation.

#### IMPLICATIONS FOR THE ECOSYSTEMS OF THE NATMA FORMATION

The fossil specimens identified in this study can be divided into three main forest ecosystems according to their NLR (Table 1):

1) “tropical littoral forests (or coastal)”, which include forests adapted to brackish water and/or soil water saturation year-round (Appanah & Turnbull 1998; Kress *et al.* 2003).

2) “tropical wet evergreen forests”, which are today, in Southeast Asia, dominated by dipterocarps (Gunasekara 2004), especially in lowlands and hills, and occur in areas with abundant annual rainfall (often >2000 mm) and limited water stress; the majority of our fossil specimens can be attributed to this ecosystem.

and 3) “tropical seasonal to dry and deciduous forests”, which include savanna-woodlands, monsoonal, dry forests and all type of forests with a marked alternance of dry and wet season;

We interpret the presence of specimens from different ecosystems as reflecting inputs from various areas in the drainage basin at the time of the Natma Formation. Specimens attributed to *tropical evergreen* forests likely represent wetter areas in the upstream highlands of the drainage basin; specimens from *seasonal to dry and deciduous forests* and *littoral* forests represent the most proximal ecosystems. The seasonal to dry and deciduous forests are likely associated with the depositional environments yielding pedogenic carbonates in the Natma Formation, as pedogenic carbonates imply a well-marked dry season and relatively low rainfall amount (commonly <1m of annual precipitation; Retallack 2005). The presence of pedogenic carbonates, rarely found in coastal forests, together with fossil wood specimens quite common in littoral forests, indicate that the fossil beds likely represent the transitional zone between a seasonally dry floodplain and littoral zone. The succession of wet forests upstream, drier forests in floodplains and littoral forests downstream is common in the Bay of Bengal (Gamble 1902), and also recognized in the fossil wood specimens of the middle Eocene Pondaung Formation of central Myanmar (Licht *et al.* 2015).

The three fossil specimens associated with littoral forests are today also associated with modern tidal or back-mangrove species: *Cynometroxylon parinaequifolium*, *Cynometroxylon holdeniae*, *Pahudioxylon bankurensis*. Mangroves have been present since the end of the Cretaceous (Srivastava & Prasad 2019), and *Cynometroxylon* is already present in the Eocene of Myanmar (Privé-Gill *et al.* 2004; Licht *et al.* 2014). The Chindwin Basin is nowadays c. 500 km North of the Andaman Sea and is separated from the coast by the Minbu Basin (Fig. 1); the presence of littoral elements likely marks a major episode of sea transgression across central Myanmar, which remains to be correlated with Miocene marine deposits further south in the Minbu Basin.

None of the specimens indicates significant altitude in the Miocene drainage basin; many of the NLR of our specimens are not found above 1000 m altitude (9 over 18, including *Shorea*, *Anisoptera*), or even above 600 m (*Intsia*, *Koompassia*, *Dryobalanops*). Some are found in undulated lands and hills (*Shorea*, *Dipterocarpus*); others can occasionally be found above 1000 m (*Canarium*, *Artocarpus*, *Albizia*, *Afzelia*, *Shorea*, *Cynometra*) but are still mostly common in lowlands. This contrasts with the modern elevation in the surrounding highlands of the Chindwin Basin, which reaches up to 3000 m in the Indo-Burman Ranges, and with the presence of taxa indicating moderate elevations in the middle Eocene flora of the Pondaung Formation (e.g. *Schimoxydon benderi*



TABLE 1. — Distribution of fossil taxa for the Natma Formation among extant tropical forests of the Indo-Burman region, according to their Nearest Living Relatives. Only the most convincing NLR have been taken into consideration. Symbols and abbreviations: ●, main environment; ○, alternative environment; 1, Tidal and coastal forests; 2, Moist evergreen and semi-evergreen forests; 3, Deciduous and seasonal forests; 4, Dry forests and savanna woodlands. The specimen of *Cupressinoxylon* is not used here, as not diagnostic of any particular environment. The specimen indet sp. 1 is shown as an indication of possible relative modern ecosystem because the possible related taxa are mostly found in ecosystems in adequacy with our other specimens.

| Fossil species                                | NLR                                                           | Modern ecosystems                                                                                                                     | 1 | 2 | 3 | 4 | Forest type              |
|-----------------------------------------------|---------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------|---|---|---|---|--------------------------|
| <i>Cynometroxylon holdeniae</i>               | <i>Cynometra ramiflora</i> /<br><i>Cynometra polyandra</i>    | Tidal, back-mangrove, wet evergreen and semi-evergreen forests. In lowlands up to 400-1300 m                                          | ● | ○ | — | — |                          |
| <i>Cynometroxylon parinaequifolium</i>        | <i>Cynometra inaequifolia</i> /<br><i>Cynometra polyandra</i> | Tidal, back-mangrove, wet evergreen and semi-evergreen forests. In lowlands up to 400-1300 m                                          | ● | ○ | — | — | Coastal forests          |
| <i>Pahudioxylon bankurensis</i>               | <i>Intsia bijuga</i>                                          | Coastal areas, along tidal rivers or at the dry back of mangroves. Also wet evergreen forest associated with Anisoptera. Up to 600 m. | ● | ● | — | ○ |                          |
| indet sp. 1                                   | <i>Dipterocarpus/Prioria</i>                                  | Wet evergreen forests, coastal forests, flooded and riparian forests, also in semi-evergreen forest or savannas. In lowlands.         | ● | ● | ○ | ○ | ?                        |
| <i>Dryobalanoxylon</i> sp.                    | <i>Dryobalanops aromatica</i> /<br><i>D. oblongifolia</i>     | Lowland mixed dipterocarp forests, in coastal areas in sandy or gravelly soils. Also in wetter soils. Up to 600 m.                    | ● | ● | ○ | — |                          |
| cf. <i>Koompassioxylon</i>                    | <i>Koompassia/Kalappia</i> /<br><i>Martiodendron</i>          | Mostly rainforest. Also in coastal forest, riparian forests or swamps. Rarely in savannas or dry forests. Up to 600 m.                | ○ | ● | — | ○ |                          |
| <i>Koompassioxylon elegans</i>                | <i>Koompassia malaccensis</i>                                 | Mostly freshwater peat-swamps. Also dry lands. Up to 150 m (800 m in elevated areas)                                                  | — | ● | — | ○ |                          |
| <i>Burseroxylon</i> sp.                       | <i>Canarium bengalense</i> /<br><i>Protium serratum</i>       | Wet evergreen and moist dipterocarp forests, mostly along rivers. Also in deciduous forests or monsoonal area. Up to 1300 m.          | — | ● | ○ | — |                          |
| <i>Anisopteroxylon</i> sp.                    | <i>Anisoptera costata</i> /<br><i>Anisoptera scaphula</i>     | Moist (not everwet) evergreen and semi-evergreen dipterocarp forests, along rivers, in seasonal forest and foothills. Up to 700 m.    | — | ● | ○ | — |                          |
| <i>Dipterocarpoxyton</i> cf. <i>jammuense</i> | <i>Dipterocarpus</i>                                          | Evergreen, semi-evergreen tropical forest, mixed dipterocarps forests. Also in seasonal forests. In lowland (rarely up to 1400 m).    | — | ● | ○ | — | Wet evergreen forests    |
| <i>Dryobalanoxylon</i> cf. <i>javanense</i>   | <i>Dryobalanops keithii</i> /<br><i>D. oblongifolia</i>       | Near water (periodically inundated, streams, poorly-drained soils...), in mixed dipterocarps forests. Up to 600 m.                    | — | ● | ○ | — |                          |
| <i>Shoreoxylon</i> cf. <i>sumatraense</i>     | <i>Shorea negrosensis</i>                                     | Evergreen, semi-evergreen and seasonal dipterocarp forests. In lowlands.                                                              | — | ● | ○ | — |                          |
| <i>Shoreoxylon</i> cf. <i>deomaliense</i>     | <i>Shorea laevis</i>                                          | Mixed dipterocarp forests. On undulated lands and well-drained soils. Up to 700-1000 m.                                               | — | ● | ○ | — |                          |
| <i>Artocarpoxylon kartikcherraensis</i>       | <i>Artocarpus lamellosus</i> /<br><i>Artocarpus chama</i>     | Mixed dipterocarp evergreen forests, but also in semi-deciduous forests, moist deciduous or monsoonal area. Up to 1500-1800 m.        | — | ● | ○ | ○ |                          |
| <i>Shoreoxylon</i> sp. 2                      | <i>Shorea balangeran</i> /<br><i>Shorea laevis</i>            | From well-drained soils to peat-swamp forests. Also in lowland mixed dipterocarp forests and hillsides. Up to 100(-1000)m.            | — | ● | ● | — |                          |
| <i>Albizinium eolebbekianum</i>               | <i>Albizia lebbeck</i> /<br><i>Albizia ferruginea</i>         | Wooded savannas, dry forests borders, semi-deciduous. Also rainforests, riparian or periodically inundated ofrests. Up to 1400 m.     | ○ | ○ | ● | ○ |                          |
| <i>Pahudioxylon</i> cf. <i>bankurensis</i>    | <i>Afzelia africana</i> /<br><i>A. javanica</i>               | Both present in humid evergreen and dry deciduous forests. Frequent in savannas. Up to 1400 m.                                        | — | ○ | ● | ○ | Seasonal and dry forests |
| <i>Shoreoxylon</i> sp. 1                      | <i>Shorea parvifolia</i> /<br><i>Shorea obtusa</i>            | Deciduous dry dipterocarp forests and under marked seasonal monsoon climates. Sometimes in moister forests or savannas. Up to 1000 m. | — | ○ | ● | ● |                          |

Licht, Boura & De Franceschi, NLR of which, *Schima wallichii* Choisy, usually occurs in mid-altitude forests above 1000 m; Licht *et al.* 2015). We could explain this low-altitude assemblage and the shift of the main altitude by the degradation of high-altitude taxa before reaching our fossil sites; alternatively, changes of drainage between the Eocene and the Miocene from east to west, to mainly north to south (Licht *et*

*al.* 2019; Zhang *et al.* 2019), might also explain these changes. Eocene Pondaung deposits were drained from the volcanic arc of central Myanmar (Licht *et al.* 2013); the provenance of the Miocene Natma deposits remains unclear.

The presence of a Cupressaceae specimen in the assemblage raises several questions about its origin, as this family is not very common in tropical climates (see p. 856). Differ-



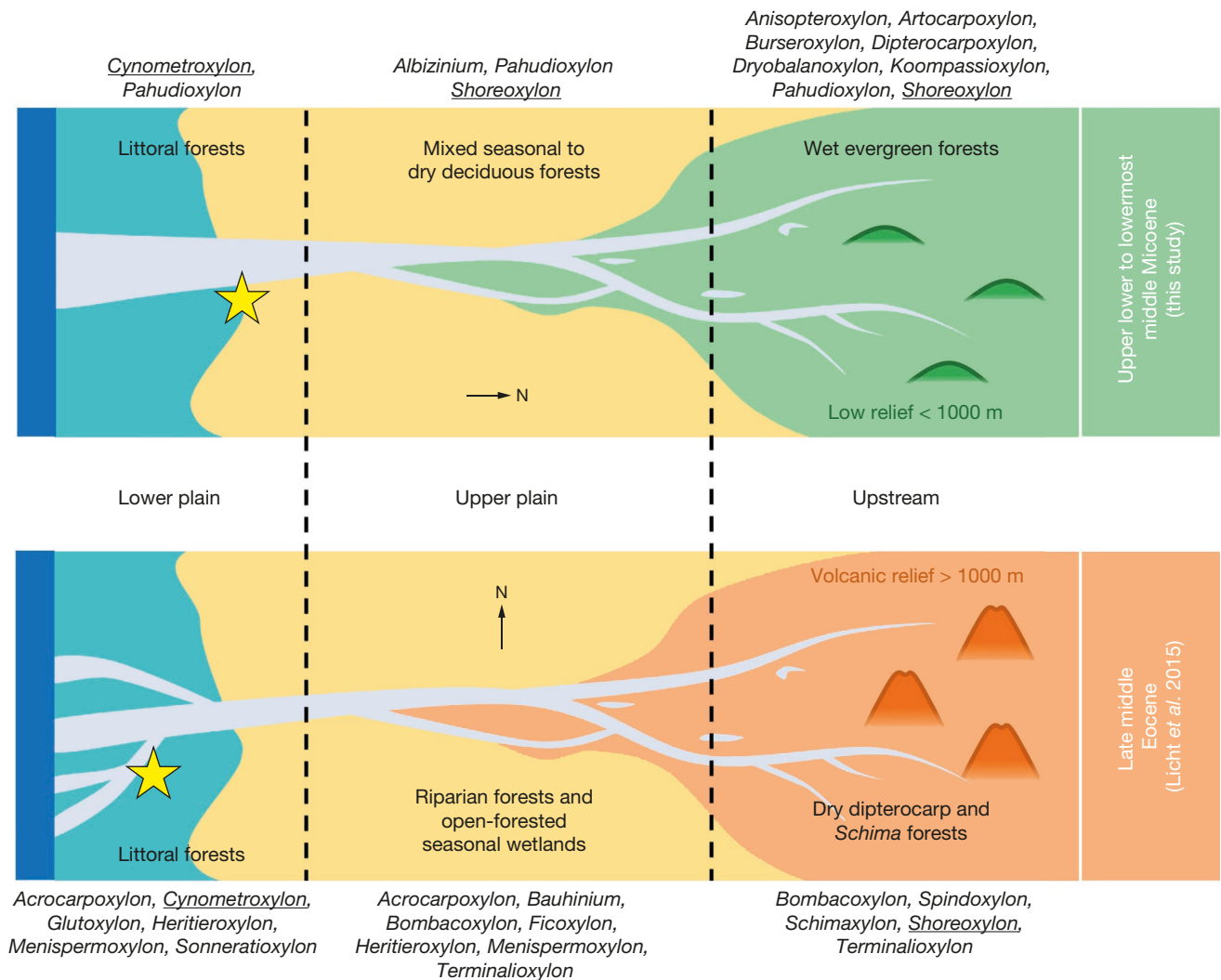


FIG. 21. — Comparison between Eocene (Licht et al. 2014, 2015) and Miocene (this study) forest assemblage and diversity of Myanmar with the list of related fossil genera and supposed forest types they belong to. Underlined names are genera found in both formations. Yellow stars mark the schematic position of sampling sites.

ent hypotheses could explain this: 1) an exogenous origin, resulting from a transportation from a higher elevation *via* streams; 2) a different geological origin as mentioned on p. 895; and 3) a misidentification due to bad preservation and ambiguous characters. Indeed, some Podocarpaceae and Casuarinaceae are more common in tropical areas.

#### THE WET DIPTEROCARP FORESTS OF THE UPPER LOWER MIOCENE: IMPLICATIONS FOR THE ORIGIN OF DIPTEROCARPS

The wet evergreen forest taxa identified in the Natma Formation are dominated by dipterocarps, both in the number of species and the number of specimens collected in the field. Some of the NLR are present in a broader range of ecosystems, while others are intolerant to strictly everwet conditions, likely indicating the presence of some seasonal hydric stress. The presence of *Dryobalanoxyton* is interesting as it is only the second record of this genus in Myanmar. Nowadays, *Dryobalanops* are absent from India and Myan-

mar. Still, previous *Dryobalanoxyton* of poorly constrained Tertiary age has been described in India, attesting that the geographic distribution of the genus has reduced through time (Maury-Lechon & Curtet 1998). This is the same trend for the genus *Anisopteroxylon*, which has also been described in the Miocene of India; the modern genus *Anisoptera* is today absent in India but present in Myanmar. Both findings support a long-term reduction of the distribution of dipterocarps to Southeast Asia, likely achieved later in the Neogene (Maury-Lechon & Curtet 1998).

A comparison between species of the middle Eocene Pondaung and the Miocene Natma Formations of Myanmar (Fig. 21) indicates a major ecological shift for dipterocarps. Wet evergreen forests are completely absent in the middle Eocene. In contrast with the dipterocarps of the Natma Formation, *Shoreoxylon* specimens of the Pondaung Formation have NLR that are today only found in seasonally dry monsoonal forests (*Shorea robusta*, *S. obtusa*, and *Pentacme siamensis* (Miq.) Kurz). Only one fossil from the Natma



Formation (*Shoreoxylon* sp. 1) relates to these seasonal and dry forests.

Burmese fossil dipterocarps seem thus to have undergone a change of diversity and distribution area through the Cenozoic. These results support the hypothesis that Dipterocarpaceae appeared first in seasonal and open ecosystems and later specialized to tropical wet conditions, based on flower and fruits studies as well as phylogenetic studies (Ashton *et al.* 1988; Maury-Lechon & Curtet 1998; Gunasekara 2004; Kurten *et al.* 2018; Bansal *et al.* 2022). It has been proposed that Dipterocarpaceae originated from Gondwana (tropical Africa) during the mid- or late-Cretaceous and later spread to eastern regions, reaching India during the Late Maastrichtian and Palaeocene (Madagascar, India, South-East Asia; Appanah & Turnbull 1998; Maury-Lechon & Curtet 1998; Morley 2000; Gunasekara 2004; Dutta *et al.* 2011; Bansal *et al.* 2022), potentially up to eastern Europe in the Eocene (Poole 1993; Morley & Ashton *in* Ashton 2014), although the attribution of European fossils has been disputed (Morley 2018). Regardless of the actual geographical origin of the dipterocarps, our results show that dipterocarp-dominated evergreen forests have been present in Southeast Asia since at least the late early Miocene, corroborating the long-standing feature of regional evergreen forests (Morley 2000).

#### PALAEOENVIRONMENTAL IMPLICATIONS

The presence of wet evergreen forest taxa in the Miocene fossil wood assemblage indicates that the ecosystem in the central Myanmar drainage basin was likely wetter than in the Eocene. Further evidence for wetter environments is supported by the fossil wood morphological characteristics. According to Wheeler & Dillhoff (2009), trees occurring in modern lowland tropical rainforests often show few (< 10 vessels per sq mm) and wide vessels (>200 µm). Only 4 out of 18 fossil species described here have wide vessels, but almost all of them have few vessels, unlike Pondaung fossil wood specimens, supporting higher humidity than in the Eocene.

Three mechanisms could explain this wetter assemblage: 1) changes of drainage that would favor wetter areas; 2) increased summer monsoonal rainfall; and 3) taphonomic bias in our Miocene sampling that would favor higher-altitude or wetter taxa. As explained in the previous subsection, there is no evidence for a bias toward higher altitudes in the Natma Formation assemblage; some fossil specimens in the Pondaung Formation suggest higher elevations in the Eocene than in the Miocene. Several studies have shown that central Myanmar river drainages experienced significant restructuring during the Oligocene based on changes of sedimentary provenance in nearby basins (Licht *et al.* 2016; Zhang *et al.* 2019; Westerweel *et al.* 2020). None of these studies specifically addressed the provenance history of the Natma Formation. Still, they showed no evidence for long-distance sediment transport into Myanmar, far outside the modern drainage basin of central Myanmar. Central Myanmar river drainages must

thus have been local and restricted to the modern Burmese low plains, the surrounding highlands of intermediate elevation, and the higher highlands of the Eastern Himalayan Syntaxis (Fig. 1; Zhang *et al.* 2019; Westerweel *et al.* 2020). The wetter ecosystems with no evidence for high elevation nor long-distance transport thus suggest a wetter climate in central Myanmar during the Miocene compared to the Eocene, with the majority of the taxa suggesting more than 2000 mm of annual rainfall. This interpretation is supported by stable isotopic data from Natma pedogenic carbonates, which suggest a wetter-than-today monsoonal regime (Licht *et al.* 2022). More broadly, this interpretation agrees with data from other areas in South Asia indicating strong monsoons during the late early to early middle Miocene (Clift *et al.* 2008).

#### CONCLUSION

This study details the first fossil wood assemblage from the upper lower to lowermost middle Miocene of Myanmar. This assemblage is dominated by Fabaceae (7 out of 18 species) and Dipterocarpaceae (8 out of 18 species), similar to the diversity found nowadays in Southeast Asian forests. We show that fossil taxa can be divided into three different types of low altitude (mostly < 1000 m) forests: tropical wet evergreen, tropical dry and deciduous, and tropical littoral ecosystems. The presence of taxa from these various ecosystems indicates some degree of mixing and transportation, though Miocene river drainages were likely local. The assemblage related to tropical wet evergreen forests is the most diverse and includes most of the fossil dipterocarps. The presence of these combined ecosystems indicates a monsoonal climate during the upper lower to lowermost middle Miocene with an alternance of a dry season and a wet season, with many taxa suggesting more than 2000 mm of annual rainfall. These ecosystems appear wetter than Eocene Burmese ecosystems that yet yielded fossil dipterocarps. These results support an evolution of the distribution of Dipterocarpaceae from seasonal to everwet ecosystems and an increase of summer monsoon rainfall in an overall Miocene climate change toward warmer and wetter conditions.

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TABLE 2. — Correspondences between the MNHN.F specimen numbers cited in the article and the corresponding pages on <https://science.mnhn.fr>.

| Specimen numbers | Corresponding slides and URLs                                        |
|------------------|----------------------------------------------------------------------|
| MNHN.F.50171     | MNHN.F.50171.1, 50171.2, 50171.3, 50171.4, 50171.5, 50171.6, 50171.7 |
| MNHN.F.50172     | MNHN.F.50172.1, 50172.2, 50172.3                                     |
| MNHN.F.50173     | MNHN.F.50173.1, 50173.2, 50173.3                                     |
| MNHN.F.50174     | MNHN.F.50174.1, 50174.2, 50174.3                                     |
| MNHN.F.50175     | MNHN.F.50175.1, 50175.2, 50175.3, 50175.4, 50175.5                   |
| MNHN.F.50176     | MNHN.F.50176.1, 50176.2, 50176.3                                     |
| MNHN.F.50177     | MNHN.F.50177.1, 50177.2, 50177.3                                     |
| MNHN.F.50178     | MNHN.F.50178.1, 50178.2, 50178.3                                     |
| MNHN.F.50179     | MNHN.F.50179.1, 50179.2, 50179.3                                     |
| MNHN.F.50180     | MNHN.F.50180.1, 50180.2, 50180.3, 50180.4                            |
| MNHN.F.50181     | MNHN.F.50181.1, 50181.2, 50181.3                                     |
| MNHN.F.50182     | MNHN.F.50182.1, 50182.2, 50182.3                                     |
| MNHN.F.50183     | MNHN.F.50183.1, 50183.2, 50183.3                                     |
| MNHN.F.50184     | MNHN.F.50184.1, 50184.2, 50184.3, 50184.4, 50184.5, 50184.6          |
| MNHN.F.50185     | MNHN.F.50185.1, 50185.2, 50185.3                                     |
| MNHN.F.50186     | MNHN.F.50186.1, 50186.2, 50186.3, 50186.4                            |
| MNHN.F.50187     | MNHN.F.50187.1, 50187.2, 50187.3                                     |
| MNHN.F.50188     | MNHN.F.50188.1, 50188.2, 50188.3, 50188.4, 50188.5, 50188.6          |
| MNHN.F.50189     | MNHN.F.50189.1, 50189.2, 50189.3, 50189.4, 50189.5, 50189.6          |
| MNHN.F.50190     | MNHN.F.50190.1, 50190.2, 50190.3                                     |
| MNHN.F.50191     | MNHN.F.50191.1, 50191.2, 50191.3, 50191.4, 50191.5, 50191.6          |
| MNHN.F.50192     | MNHN.F.50192.1, 50192.2, 50192.3                                     |
| MNHN.F.50193     | MNHN.F.50193.1, 50193.2, 50193.3, 50193.4, 50193.5, 50193.6          |
| MNHN.F.50194     | MNHN.F.50194.1, 50194.2, 50194.3                                     |
| MNHN.F.50195     | MNHN.F.50195.1, 50195.2, 50195.3                                     |
| MNHN.F.50196     | MNHN.F.50196.1, 50196.2, 50196.3                                     |
| MNHN.F.50197     | MNHN.F.50197.1, 50197.2, 50197.3                                     |
| MNHN.F.50198     | MNHN.F.50198.1, 50198.2, 50198.3                                     |
| MNHN.F.50199     | MNHN.F.50199.1, 50199.2, 50199.3, 50199.4                            |
| MNHN.F.50200     | MNHN.F.50200.1, 50200.2, 50200.3, 50200.4, 50200.5                   |



APPENDIX 1. — Synthetic summary of main characters of the Dipterocarpaceae fossil woods mentioned in the article, as described by the original authors (**first name**), the authors who redescribed a specimen of the same species or emended the original diagnosis (**second name**), or as extracted from another publication (**in parenthesis**). Features in parenthesis are less common.

| Species                                | Vessels      |                                                  |                                                         | Axial parenchyma                                                                  | Rays                                                                                               | Multiseriate ray height (µm; cells) | Canals t.diam. (µm)                                              | Geologic age/country      | Authors                                      |
|----------------------------------------|--------------|--------------------------------------------------|---------------------------------------------------------|-----------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------|-------------------------------------|------------------------------------------------------------------|---------------------------|----------------------------------------------|
|                                        | Growth rings | t.diam. (µm); frequency (/mm <sup>2</sup> )      | Fibres                                                  |                                                                                   |                                                                                                    |                                     |                                                                  |                           |                                              |
| <i>Anisopteroxylon oblongoides</i>     | Ind.         | 120-230<br>4-5<br>solitary,<br>tylose            | Nonseptate, thick-walled, vasicentric tracheids         | Vasicentric, diffuse, in-aggregate in irregular lines, around canals              | (1-11) 7-9 seriate, 4-8/mm, heterocellular 1-2+ marginal cells, continuous sheath cells            | 150-1080<br>5-56                    | 120-150<br>lines, (diffuse)                                      | Miocene/<br>India         | Yadav 1989                                   |
| <i>Anisopteroxylon garioensis</i>      | Ind.         | 110-255<br>8-12<br>solitary,<br>(tylose)         | Nonseptate, thick-walled, vasicentric tracheids         | Scanty to vasicentric, diffuse, in short lines, around canals                     | (1-8) 5-6 seriate, 5-12/mm, heterocellular 1-8 marginal cells, sheath cells                        | 180-1350<br>6-30                    | 40-55<br>Diffuse, (short tangential lines of 2-3)                | Miocene/<br>India         | Prakash & Tripathi 1970                      |
| <i>Anisopteroxylon surmaensis</i>      | Ind.         | 130-230<br>6-10<br>solitary,<br>tylose           | Nonseptate, thin-to-thick walled, vasicentric tracheids | Diffuse, diffuse-in-aggregate in thin lines, scanty to vasicentric, around canals | (1-6) 4-5 seriate, 5-6/mm, heterocellular 1-3 marginal cells, continuous sheath cells              | 212-1190<br>5-55                    | 102-130<br>Diffuse                                               | Miocene/<br>India         | Prasad, Agarwal & Mandaokar 2009             |
| <i>Anisopteroxylon jawalamukhi</i>     | Ind.         | 154-300<br>-<br>solitary,<br>tylose              | Nonseptate, vasicentric tracheids                       | Vasicentric, diffuse, diffuse-in-aggregate, around canals                         | 1-7 seriate, heterocellular, sheath cells                                                          | 458-1946<br>15-67                   | 98-168<br>Diffuse, (short tangential lines of 2-3)               | Mio-Plio/<br>India        | Ghosh & Ghosh 1958 (Prakash & Tripathi 1970) |
| <i>Dipterocarpaceoxylon sivalicus</i>  | Ind.         | 160-240<br>5-7,<br>solitary,<br>tylose           | Nonseptate, thick-walled, vasicentric tracheids         | Diffuse, diffuse-in-aggregate, (scanty paratracheal), around canals               | 1-5(6) seriate, often uniseriate, 7-14/mm, heterocellular, sheath cells                            | 250-1125<br>-                       | 40-68<br>Short tangential lines of 2-6, diffuse                  | Miocene/<br>India         | Prakash 1975                                 |
| <i>Dipterocarpaceoxylon malavi</i>     | Ind.         | 80-240,<br>mean 190,<br>5-7, solitary,<br>tylose | Nonseptate, thick-walled, vasicentric tracheids         | Diffuse, diffuse-in-aggregate, scanty to vasicentric, (aliform), around canals    | (1-7) 3-5 seriate, 6-8/mm, heterocellular 1-n marginal cells, (sheath cells)                       | 120-1600,<br>mean <1000<br>10-60    | 40-120<br>Diffuse/ paired, short tangential lines of 4-5         | Pliocene/<br>India        | Ghosh & Ghosh 1959, Guleria 1983             |
| <i>Dipterocarpaceoxylon africanum</i>  | Ind.         | -<br>(solitary),<br>tylose ?                     | Thin-to thick walled?, vasicentric tracheids?           | Vasicentric, (marginal, diffuse?) around canals                                   | (1-5) 1-3 seriate, heterocellular 1-6 marginal cells, (end-to-end fusion)                          | -<br>8-30                           | -<br>Diffuse, short tangential lines of 2-6 same size as vessels | Tertiary/<br>Uganda       | Bancroft 1933                                |
| <i>Dipterocarpaceoxylon sarapeense</i> | -            | 160-322<br>4-7,<br>solitary,<br>(tylose)         | Nonseptate, thin to thick walled, vasicentric tracheids | Vasicentric, diffuse to diffuse-in-aggregate, around canals                       | 1-5(4-5) seriate, 6-8/mm, heterocellular 2-7(23) marginal cells, sheath cells, (end-to-end fusion) | <2400<br>up to 80                   | 80-120<br>Short tangential lines of 2-7                          | Plio-Pleisto/<br>Thailand | Vozenin-Serra & Privé-Gill 2001              |
| <i>Dipterocarpaceoxylon gracile</i>    | Ind.         | 100-175<br>5-14,<br>solitary                     | Nonseptate, (very) thick-walled, vasicentric tracheids  | Around canals, scanty paratracheal, (diffuse)                                     | (1-5) 1 seriate, "homogeneous", (crystalliferous)                                                  | -<br>up to 40                       | 60-75<br>Diffuse, short tangential lines of 2                    | Pliocene/<br>Java         | Schweitzer 1958                              |
| <i>Dipterocarpaceoxylon jammuense</i>  | Ind.         | 80-260<br>3-9,<br>solitary,<br>tylose            | Nonseptate, vasicentric tracheids                       | Vasicentric, (diffuse), around canals                                             | (1-6) 3-5 seriate, 5-9/mm, heterocellular 2-12 marginal cells, sheath cells                        | 200-1260<br>5-45                    | 65-80<br>Diffuse, short tangential lines of 2-5                  | Miocene/<br>India         | Guleria <i>et al.</i> 2002                   |
| <i>Dryobalanoxylon holdeniae</i>       | Ind.         | 60-280<br>9-15,<br>solitary,<br>tyloses          | Fibre/vasicentric tracheids, nonseptate, thick-walled   | Vasicentric to aliform (aliform-confluent), banded around canals                  | 1-4 seriate, heterocellular 1-5 marginal cells, (sheath cells)                                     | <900<br>up to 30                    | 40-60<br>Long tangential lines                                   | Tertiary/<br>India        | Awasthi 1971                                 |



APPENDIX 1. — Continuation.

| Species                               | Vessels      |                                               | Fibres                                                        | Axial parenchyma                                                                              | Rays                                                                                                               | Multiseriate ray height (µm; cells) | Canals t.diam. (µm)                              | Geologic age/country       | Authors                                               |
|---------------------------------------|--------------|-----------------------------------------------|---------------------------------------------------------------|-----------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------|-------------------------------------|--------------------------------------------------|----------------------------|-------------------------------------------------------|
|                                       | Growth rings | t.diam. (µm); frequency (/mm <sup>2</sup> )   |                                                               |                                                                                               |                                                                                                                    |                                     |                                                  |                            |                                                       |
| <i>Dryobalanoxylon cf. bangkoense</i> | Ind.         | 75-250<br>7-13, (solitary)                    | Fibre/vasicentric tracheids, nonseptate, thick-walled         | Diffuse-in-aggregate, diffuse, vasicentric paratracheal                                       | (1-7)4-6 seriate, frequent uniseriate, heterocellular 2-5 marginal cells, crystalliferous                          | -<br>4-80                           | 25-125<br>lines                                  | Quaternary<br>?/Maluku Is. | Schweitzer 1958                                       |
| <i>Dryobalanoxylon bogorens</i>       | Ind.         | 120-286<br>mean 203<br>3-4, solitary, tyloses | Fibre/vasicentric tracheids, nonseptate, thin-to-thick walled | Vasicentric to aliform, (aliform-confluent), banded around canals                             | 1-6 seriate, uniseriate rare, heterocellular 1-4 marginal cells                                                    | 500-1200<br>11-36                   | 33-100<br>lines                                  | Pliocene/<br>Java          | Srivastava & Kagemori 2001                            |
| <i>Dryobalanoxylon sumatrense</i>     | Ind.         | 75-200<br>4-8, solitary                       | Fibre/vasicentric tracheids, nonseptate, thin to thick-walled | Vasicentric, (aliform), diffuse                                                               | 1-5 seriate heterocellular 1-15 marginal cells, crystalliferous, silica ?                                          | -<br>4-90                           | 75-110<br>line of 5 (or more ?)                  | Pliocene/<br>Sumatra       | Schweitzer 1958                                       |
| <i>Dryobalanoxylon tambouense</i>     | -            | 125-234<br>2-10, (solitary, tyloses)          | Fibre/vasicentric tracheids, nonseptate, thin to thick-walled | Vasicentric to aliform-confluent, banded around canals                                        | (1)2-5 seriate, 6-8/mm, heterocellular 1-6 cells tailed, (sheath cells, storied tendency)                          | 192-1194<br>5-38                    | 30-80<br>lines                                   | Pliocene/<br>Vietnam       | Vozenin-Serra 1981                                    |
| <i>Dryobalanoxylon khmerinum</i>      | Ind.         | 35-122<br>7-8, solitary, tyloses              | Fibre/vasicentric tracheids, nonseptate, thin-walled          | Vasicentric, banded around canals                                                             | (1?)3-7 seriate, 7-8/mm, heterocellular, (big cells in the middle, sheath cells)                                   | 417-700<br>12-29                    | 55-215<br>lines                                  | Tert-Quat/<br>Cambodia     | Boureau 1952<br>Schweitzer 1958                       |
| <i>Dryobalanoxylon lunaris</i>        | Ind.         | 195-257<br>5-8, solitary, tyloses             | Fibre/vasicentric tracheids, very thick-walled                | Vasicentric to aliform, banded around canals, (diffuse-in-aggregate in short lines)           | (1-4)3-4 seriate, 5-7/mm, heterocellular 1-4 marginal cells, crystalliferous, end-to-end fusion                    | <2980<br>mean 1405<br>5-90          | 90-242<br>mean<br>129<br>(diffuse)               | Pliocene/<br>Java          | Mandang & Kagemori 2004                               |
| <i>Dryobalanoxylon javanense</i>      | Ind.         | 70-120/125-225<br>(5)8-16, solitary, tyloses  | Fibre/vasicentric tracheids, very thick-walled                | Diffuse, diffuse-in-aggregate in short lines, scanty paratracheal                             | (1-6)3-5 seriate, 2-19/mm, heterocellular 2-4 marginal cells, (crystaliferous ?), sheath cells, end-to-end fusions | -<br>3-45                           | 30-100<br>lines, (short tangential lines of 2-4) | Pliocene/<br>Java          | Den Berger 1927 (Biswas et al. 2019; Schweitzer 1958) |
| <i>Dryobalanoxylon toberi</i>         | Ind.         | 80-230<br>(5)8-16, solitary, tyloses          | Fibre ?/vasicentric tracheids                                 | Diffuse ?                                                                                     | (1-6)3-4 seriate, 6-8/mm, crystalliferous ?, sheath cells                                                          | -<br>(8)35-50(60)                   | 50-250<br>lines                                  | Pliocene/<br>Indonesia     | Den Berger 1927 (Biswas et al. 2019; Schweitzer 1958) |
| <i>Shoreoxylon deomalense</i>         | Ind.         | 64-256<br>8-16, tyloses                       | Vasicentric tracheids, nonseptate, thin to thick walled       | Vasicentric, (aliform to aliform-confluent), banded around canals, (diffuse), crystalliferous | 1-7 seriate, 6-9/mm, heterocellular 1-8 marginal cells                                                             | -<br>4-65                           | 35-240<br>lines                                  | Mio-Plio/<br>India         | Prakash & Awasthi 1971                                |
| <i>Shoreoxylon burmense</i>           | Ind.         | 135-240<br>5-6, tyloses                       | Vasicentric tracheids, nonseptate, very thick-walled          | Vasicentric to aliform, (aliform-confluent), diffuse, in short lines, banded around canals    | (1-5)4-5 seriate, 7-10/mm, homocellular to weakly heterocellular                                                   | <1275<br>up to 75                   | 45-150<br>lines, 1 to 4 rows                     | Tertiary/<br>Myanmar       | Prakash 1965a, Prakash 1973                           |



APPENDIX 1. — Continuation.

| Species                          | Vessels            |                                             | Axial parenchyma                                                                                                                   | Rays                                                                                            | Multiseriate ray height (µm; cells) | Canals t.diam. (µm)                                                  | Geologic age/country | Authors                                    |
|----------------------------------|--------------------|---------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------|-------------------------------------|----------------------------------------------------------------------|----------------------|--------------------------------------------|
|                                  | Growth rings       | t.diam. (µm); frequency (/mm <sup>2</sup> ) |                                                                                                                                    |                                                                                                 |                                     |                                                                      |                      |                                            |
| <i>Shoreoxylon tipamense</i>     | Distinct (vessels) | 112-332<br>3-9, tyloses                     | Vascentric to aliform, (aliform-confluent, diffuse, diffuse-in-aggregate), banded around canals, crystalliferous                   | 1-5 seriate, 5-8/mm, heterocellular 1-12 marginal cells, (sheath cells)                         | -<br>3-66                           | Long tangential lines                                                | Tertiary / India     | Prakash & Awasthi 1970                     |
| <i>Shoreoxylon indicum</i>       | Ind.               | 45-240<br>5-10, tyloses                     | Vascentric, aliform confluent in thin bands, diffuse, in thin bands, banded around canals, crystalliferous                         | 1-6 seriate, 5-9/mm, heterocellular 1-2 marginal cells                                          | -<br>up to 60                       | Long tangential lines                                                | Tertiary / India     | Awasthi 1974                               |
| <i>Shoreoxylon arcotense</i>     | Ind.               | 45-165<br>15-20, solitary, tyloses          | Scanty paratracheal or vascentric, banded around canals                                                                            | (1-4)2-3 seriate, heterocellular 1-6 marginal cells                                             | -<br>12-40                          | Long tangential lines                                                | Tertiary / India     | Awasthi 1974                               |
| <i>Shoreoxylon sumatraense</i>   | Ind.               | 200-360<br>9-14, (clusters), tyloses        | Vascentric, aliform, (confluent in tangential bands), diffuse, diffuse-in-aggregate in short tangential lines, irregularly storied | (1-4)1-3 seriate, 4-5/mm, heterocellular 1-n marginal cells, (crystalliferous)                  | 80-1400<br>4-50                     | Long tangential lines                                                | Quaternary/ Sumatra  | Du 1988b                                   |
| <i>Shoreoxylon posthumi</i>      | Ind.               | 200-300<br>mean 250<br>5-10, tyloses        | Vascentric, diffuse-in-aggregate in tangential bands, diffuse, around canals, crystals in enlarged cells                           | (1-5)5 seriate, "homogeneous", end-to-end fusion                                                | -<br>3-45                           | Long/short tangential lines, diffuse, (double lines)                 | Quaternary/ Sumatra  | Schweitzer 1958                            |
| <i>Shoreoxylon pachitanensis</i> | Ind.               | 200-240<br>6-10, tyloses                    | Vascentric, irregularly banded, around canals                                                                                      | 1-4 seriate, 6-10/mm, heterocellular 1-n marginal cells                                         | 750-1450<br>-                       | Short/long ? tangential lines                                        | Miocene / Java       | Sukiman 1977                               |
| <i>Shoreoxylon ornatum</i>       | Ind.               | 155-230<br>5-9, solitary, tyloses           | Diffuse, diffuse-in-aggregate, vascentric, banded around canals                                                                    | (1-5)3-4 seriate, 5-8/mm, heterocellular 2-12 marginal cells, sheath cells                      | 484-1870<br>-                       | Diffuse, long/short tangential lines of 2-3, (double or triple rows) | Tertiary / India     | Bande & Prakash 1980, Trivedi & Ahuja 1979 |
| <i>Shoreoxylon irawaddiensis</i> | Ind.               | 90-300<br>6-8, tyloses                      | Banded in thin lines, vascentric, banded around canals                                                                             | (1-7)3-5 seriate, few uniseriate, 5-8/mm, homocellular to weakly heterocellular 1 marginal cell | < 1200<br>up to 50                  | Long tangential lines                                                | Mio-Plio/ Myanmar    | Prakash & Bande 1980                       |



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