

**Fossil woods from the lower Miocene of Myanmar (Natma Formation):  
paleoenvironmental and biogeographic implications**

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

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**ABSTRACT -**

The paleobotanical record of Myanmar is poorly documented despite its importance for understanding the evolution of Asian monsoonal ecosystems through time. Here, we describe seventeen species of fossil wood from silicified specimens collected in the upper lower to lowermost middle Miocene Natma Formation, central Myanmar. These species share affinities with modern Fabaceae, Dipterocarpaceae, Burseraceae,

Moraceae and Cupressaceae. Five new species are described, belonging to genera *Koompassioxylon* Kramer (*K. kalewensis* n. sp.), *Pahudioxylon* Chowdhury, Ghosh & Kazmi (*P. adenantheroides* n. sp.), *Dipterocarpoxyton* (Holden) Den Berger (*D. fugax* n. sp.), *Shoreoxylon* Den Berger (*S. glomeratum* n. sp.), *Artocarpoxyton* Prakash & Lalitha (*A. informe* n. sp.). They include the first record of genus *Dryobalanoxylon* Den Berger in Myanmar, as well as a great variety of fossil dipterocarps (7 species) as found in today's Southeast Asian rainforests. The nearest living relatives of this assemblage 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 -

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 dix-sept espèces de bois fossile de la Formation de Natma (Myanmar central) datant du Miocène inférieur tardif au début du Miocène moyen. Ces espèces sont affiliées aux familles modernes des Fabaceae, Dipterocarpaceae, Burseraceae, Moraceae et Cupressaceae. Cinq nouvelles espèces sont décrites, appartenant aux genres *Koompassioxylon* Kramer (*K. kalewensis* n. sp.), *Pahudioxylon* Chowdhury, Ghosh & Kazmi (*P. adenantheroides* n. sp.), *Dipterocarpoxyton* (Holden) Den Berger (*D. fugax* n. sp.), *Shoreoxylon* Den Berger (*S. glomeratum* n. sp.), *Artocarpoxyton* Prakash & Lalitha (*A. informe* n. sp.). Nos spécimens incluent le premier enregistrement du genre *Dryobalanoxylon* Den Berger en Birmanie, ainsi qu'une grande variété de diptéropacées fossiles (7 espèces) comme trouvée 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 en Birmanie durant le Miocène inférieur tardif. La présence d'espèces fossiles de diptéropacées typiques de forêts humides sempervirentes contraste avec les assemblages forestiers birmans de l'Eocène, dominés par des forêts sèches à diptéropacées, et indiquent des conditions plus humides. Ces reconstructions suggèrent un

changement à long-terme des diptérocarpacées d'environnements saisonniers à des environnements plus humides.

#### KEYWORDS -

Fossil wood, Miocene, Myanmar, dipterocarp, wet dipterocarp forest, monsoon, paleoenvironment

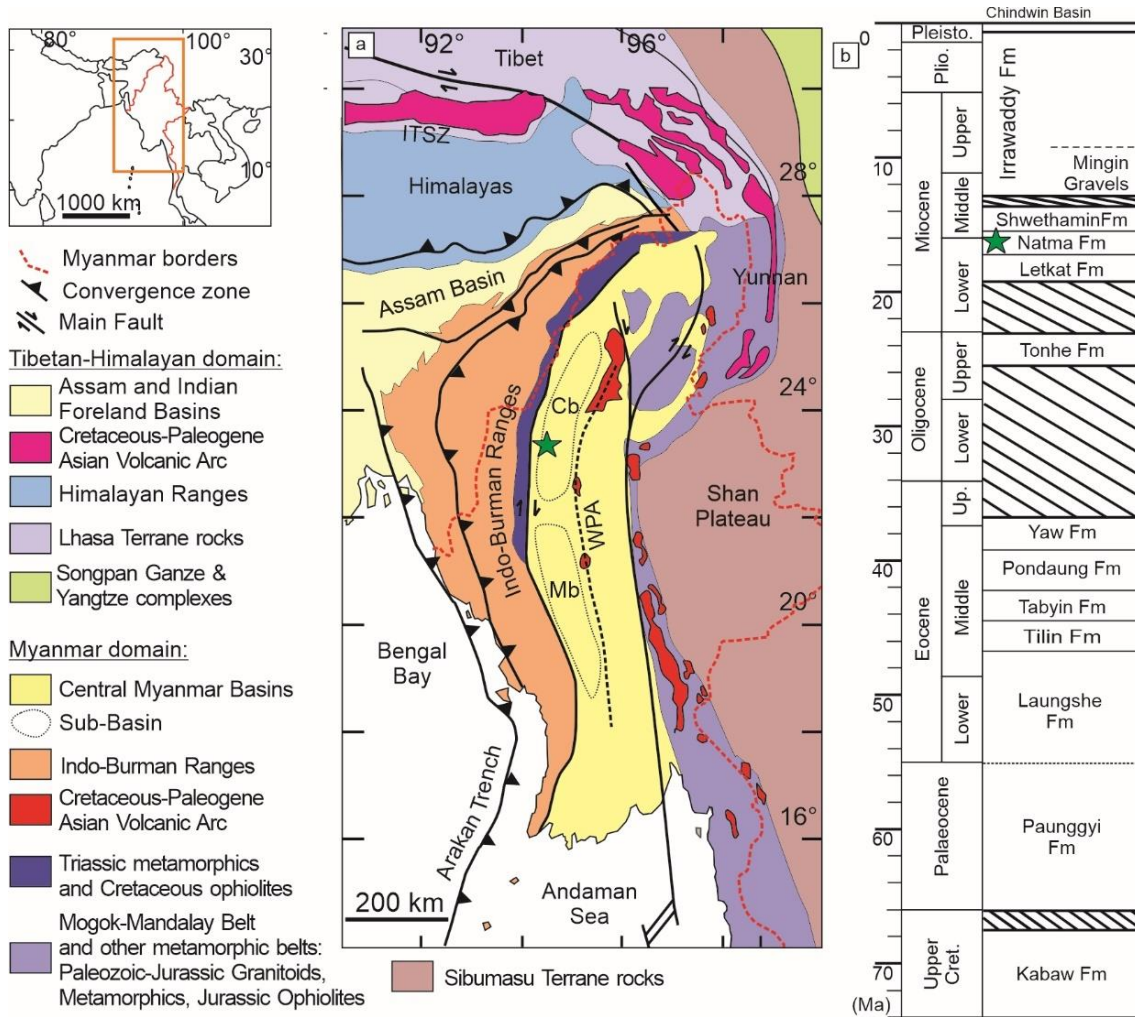
#### MOTS CLÉS :

Bois fossile, Miocène, Myanmar, diptérocarpacée, forêt humide de diptérocarpacées, mousson, paléoenvironnement

#### 1. INTRODUCTION -

Myanmar is located at the eastern edge of the Bengal Bay and today lies in the Asian monsoonal domain (Fig. 1a); its paleobotanical 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-Xylia-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) and studies on fossil wood specimens (Prakash 1965a, 1965b, 1965d, 1973; Prakash & Bande 1980; Du 1988a; Gottwald 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.



**Figure 1.** (a) Simplified map of Myanmar showing the location of the field sites. Location of the fossil site is indicated with a green star; 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.

Studies of the Burmese paleobotanical 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). 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 a toposequence from the coast to the inland foothills as it is seen in the actual Bay of Bengal (Licht *et al.* 2015). In addition, pollen from the Yaw Formation highlights a high abundance of palms that remain absent from the fossil wood record (Huang *et al.* 2020). Most of the species identified in the Pondaung Formation grow today in climates with a well-marked seasonality. Their ecological requirements were used as pieces of evidence for monsoonal rainfall and support paleontological 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-Angeliwewa & Müller-Stoll 1973), palms (Sahni 1964), *Swintonia* Griff., *Albizia* Durazz., *Careya* Roxb., *Cynometra*, *Araucaria-Agathis* (Prakash & Bande 1980), *Diospyros* L., *Saraca* L., *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 thus is 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 and identify seventeen fossil wood taxa 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.

## 2. GEOLOGICAL AND PALEOENVIRONMENTAL 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 ~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 paleosol horizons rich in root traces and pedogenic carbonates, which indicate the occurrence of a well-marked dry season at the time of deposition (Driese & Mora 1993; Pustovoytov 2002; Pustovoytov *et al.* 2007; Gocke *et al.* 2012; Zamanian *et al.* 2016).

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 (*Tetralophodon cf. falconeri*, *Bunolophodon cf. pandionis*, *Bunolophodon angust. palaeoindicus*, *Listriodon pentapotamiae*) 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 ~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 paleo-drainage flowing southward into the Minbu Basin and the Andaman Sea

further South, by 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.

### 3. MATERIAL AND METHODS:

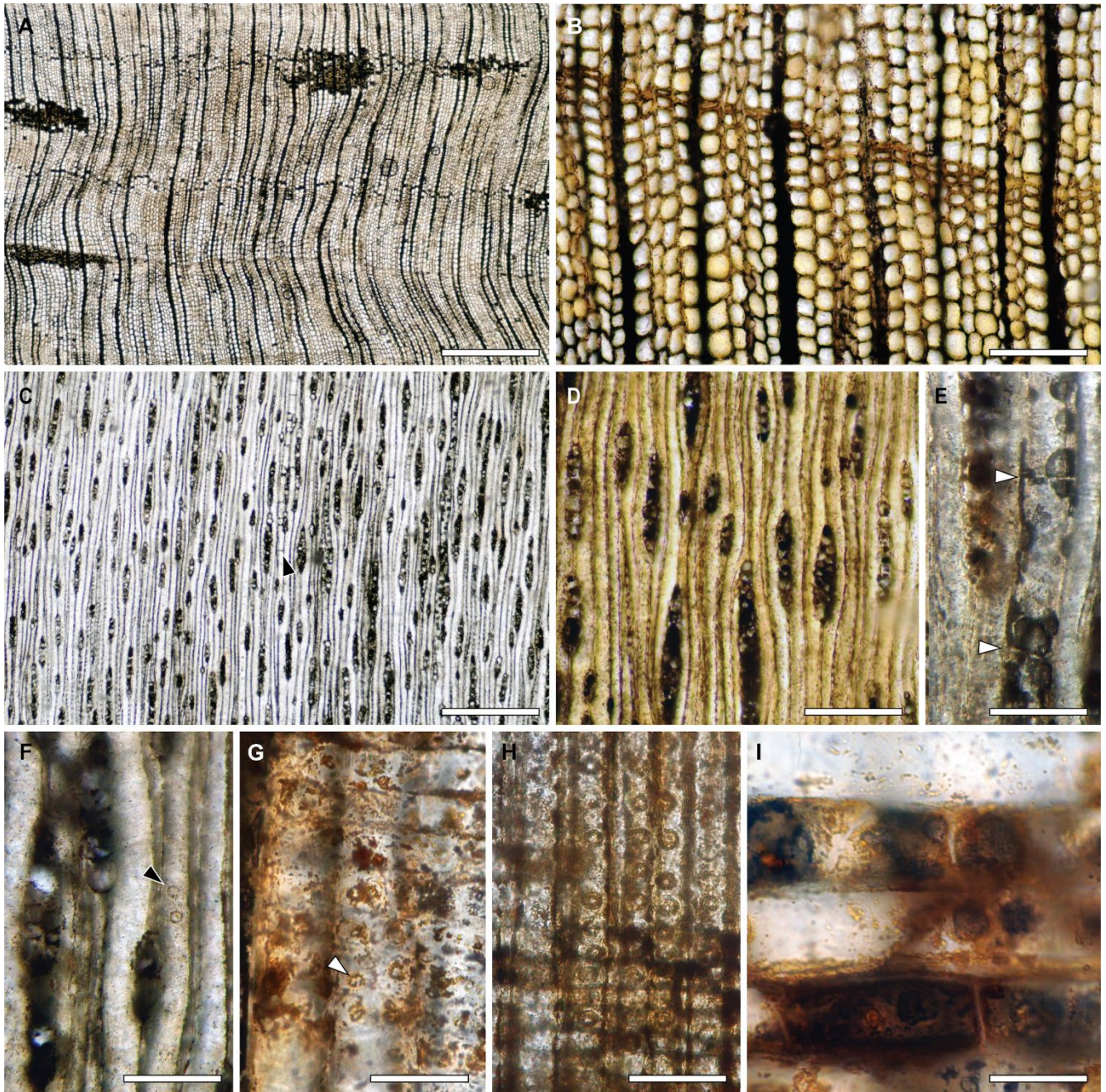
Thirty specimens of fossil wood from the Natma Formation were collected in the Kalewa Township, Sagaing Region, Myanmar, exposed in a wide badland system along the Kalewa-Mawlaik road (23°16'23.1"N, 94°18'25.3"E; see Fig. 1a for location). Fossil wood specimens are completely silicified and were found in-situ in basal lags of sandy channel bodies or on the ground next to these bodies. Sections of transverse, radial and tangential surfaces of the fossil woods were prepared following the standard techniques (Hass & Rowe 1999) at the Muséum national d'Histoire naturelle (MNHN), Paris, France, and described following the IAWA list of microscopic features for hardwood and softwood identification (Wheeler *et al.* 1989; Richter *et al.* 2004). Botanical affinities were determined using the Inside Wood database (InsideWood 2004-onwards; Wheeler 2011) and literature on fossil and extant Asian woods (e.g. Gamble 1902; Metcalfe & Chalk 1950; Gregory *et al.* 2009 and references therein). Nearest Living Relatives (NLR) ecology was determined using tropical plant databases (including World Agroforestry databases: Orwa *et al.* 2009; Kindt *et al.* 2019; World Agroforestry 2020), floras and forestry guides. All microscopic slides, including one transverse, one longitudinal radial and one longitudinal tangential section per specimen and remains of the original specimens are deposited in the collection of the MNHN.

### 4. RESULTS / TAXONOMY:

Seventeen species out of the thirty fossil wood samples were identified, belonging to eleven fossil genera and four families. Three specimens are still undetermined at the family and genus level.



## CONIFERS



**Figure 2.** *Cupressinoxylon* sp.: **A**, transverse section (Ts), growth rings and zonate parenchyma (large black areas are cells filled with sediments); **B**, Ts, growth ring with gradual transition from earlywood to latewood; **C**, tangential longitudinal section (Tls), 1- sometimes 2- seriate rays and parenchyma lines (arrow); **D**, Tls, 1- sometimes 2- seriate rays; **E**, Tls, smooth longitudinal parenchyma walls (arrows); **F**, Tls, 1-2-seriate rays and tangential pits (arrow); **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  $\mu$ m; E-F, H, 100  $\mu$ m; G, 50  $\mu$ m; I, 20  $\mu$ m.

Family CUPRESSACEAE Rich. ex Bartl.

Genus *Cupressinoxylon* (Göppert) Gothan 1905

*Cupressinoxylon* sp.

(Fig. 2; A-I)

MATERIAL - MNHN.[under registration]; field number: 17FN15.

LOCALITY - Kalewa Township, Sagaing Region, Myanmar

AGE - upper lower to lowermost middle Miocene

DESCRIPTION -

*Growth rings 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  $\mu\text{m}$  long (average 2730  $\mu\text{m}$ ), tangential diameter 20-50  $\mu\text{m}$  (average 30  $\mu\text{m}$ ), thin walled with polygonal cross-section. *Radial pits* 1-seriate, rounded, spaced, 15-24  $\mu\text{m}$  in diameter (average: 21  $\mu\text{m}$ ) (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  $\mu\text{m}$  tangential diameter (average: 25  $\mu\text{m}$ ). *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  $\mu\text{m}$  in tangential diameter (average: 30  $\mu\text{m}$ ), both vertical and horizontal walls smooth (Fig. 2I), indentures absent. *Cross-field* pits possibly cupressoid or podocarpoid, maybe both, seemingly 2-4 pits per cross-field (Fig. 2G); 6-15  $\mu\text{m}$  in diameter (mean 11). Crystals not found. Resin ducts absent.

DISCUSSION -

This specimen 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, (6) smooth axial parenchyma and ray cell walls. The clear absence of vessels as well as the presence of thin rays indicate that the specimen is a conifer wood. Presence of axial parenchyma is reported in Podocarpaceae and Cupressaceae (including Taxodiaceae). According to Greguss (1955, 1972), Trivedi & Srivastava (1989) and Richter *et al.* (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. 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, abundant parenchyma, resin ducts absent), which are wide enough to include most of Cupressaceae species (Vaudois & Privé 1971) and is thus attributed to this genus. The bad preservation of cell walls and the relatively small size of our specimen makes it difficult to determine the affinity of this specimen at the species level.

According to Phillips (1948), wood species of the cupressoid group are poorly distinguishable from each other based on wood anatomy. Moreover, extant Cupressaceae are sometimes distinguished only on qualitative features such as color or odor of the wood (Wheeler & Dillhoff 2009). These authors also note that “there are more species of *Cupressinoxylon* than there are distinctive wood anatomical types within extant Cupressaceae” (Wheeler & Dillhoff 2009, p.84). Kress *et al.* (2003) record 23 species of Cupressaceae in Myanmar, including *Cryptomeria* D. Don which shares common traits with our specimen, especially uni- to biseriate rays and *Libocedrus* Endl. (Greguss 1972). 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 loving trees such as *Metasequoia glyptostroboides* Hu & W.C.Cheng from China living in mesic forests or along rivers (Pittermann *et al.* 2012; Farjon 2013a) or *Taxodium distichum* (L.) Rich., known to grow in seasonally inundated or waterlogged Louisiana swamps (Pittermann *et al.* 2012; Farjon 2013b) to very drought-tolerant *Juniperus californica* Carr. (Pittermann *et al.* 2012). Our fossil specimen shares common traits with *Cryptomeria japonica* (L. f.) D. Don or the genus *Libocedrus*. The former is a wet and montane temperate tree from Japan growing in mixed evergreen forests up to 2500 m (Wu & Raven 1999; Pittermann *et al.* 2012; Thomas *et al.* 2013), the later are tropical moist climate rainforest to montane trees from Borneo, Papua and New-Zealand often found in altitude from 600 m (De Laubenfels 1984; Wilf *et al.* 2009; Pittermann *et al.* 2012; Lemmens *et al.* 1995). But these analogies are not robust enough to consider them as proper NLR, and no clear modern relative among modern Cupressaceae could be found for our fossil while using InsideWood (2004-onward).



## ANGIOSPERMS

Family FABACEAE Lindl.

Genus *Albizinium* Prakash 1975

Can be found in literature as “*Albizzinium*”

***Albizinium eolebbekianum* Prakash 1975**

(Fig. 3; A-D)

*Albizinium eolebbekianum* - Prakash 1975: 199 (Himachal Pradesh)

ORIGINAL HOLOTYPE - Birbal Sahni Institute of Paleobotany Museum no. 150/1014

MATERIAL - MNHN.[under registration]; field number: 17FN04.

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. *Vessels* mostly solitary (80%) or grouped by 2, rarely 3, oval, 0-5 per mm<sup>2</sup> (average: 2) (Fig. 3A); tangential diameter 140-260 µm (average: 210 µm). Tylose absent. Vessel elements 180-460 µm long (average: 290 µm). Perforation plates simple. Vessel pits alternate. Axial *parenchyma* apotracheal and paratracheal, apotracheal parenchyma arranged in marginal bands enclosing little vessels (Fig. 3A), also probably some diffuse parenchyma, paratracheal parenchyma aliform, sometimes confluent when vessels are close (Fig. 3A); 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. 3B). *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. 3B), homocellular made of procumbent cells (Fig. 3C). *Fibres* with poorly preserved walls, apparently septate (Fig. 3D), 15-22 µm wide (average: 18 µm).

DISCUSSION -

This taxon is characterized by (1) diffuse-porous wood, (2) exclusively simple perforation plates, (3) aliform parenchyma, (4) presence of septate fibres, (5) homocellular and mostly 2- to 3-seriate rays. These characters suggest affinities with modern Fabaceae and particularly with the group of Mimosaceae for which 35% of specimens described in InsideWood (2004-onward) have septate fibres. Among fossil wood specimens with aliform parenchyma and septate fibres, our fossil is close to genera *Albizinium* and

*Acrocarpoxylon* Gottwald, but the latter has more often heterocellular rays. The characteristics of this fossil wood specimen are compatible with the *Albizinium* genus diagnosis; among *Albizinium* fossil species available for comparison (Appendix 1), *A. arunachalensis* Mehrotra, Awasthi & Dutta has non-septate fibres, larger vessels and lacks marginal parenchyma; Jolly-Saad *et al.* (2012) have argued against the attribution of *A. arunachalensis* Mehrotra, Awasthi & Dutta (as well as *A. borjanensis* Prakash, Lalitha & Tripathi) to the genus *Albizinium*. *A. eolebbekianum* has shorter rays and *A. pondicherriensis* Awasthi has a higher ray density and more grouped vessels; the diagnoses of *A. eolebbekianum* and *A. pondicherriensis* are remarkably similar which raises the question of the relevance of separating these fossils into two species. 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 attributed to *A. eolebbekianum* given the propensity to *A. pondicherriensis* to form vessel clusters.

In modern Fabaceae, the parenchyma arrangement found in *A. eolebbekianum* combined with the presence of septate fibres is found in genera *Albizia*, *Afzelia*, *Cassia*, *Pithecellobium* Mart. and *Cylicodiscus* Harms. Unlike our specimen, *Cassia* shows confluent parenchyma sometimes forming bands, *Pithecellobium* and *Cylicodiscus* have respectively higher and larger rays (Awasthi 1979). Our specimen shows clearer similarities with *Albizia lebbek* (L.) Benth. though it has often larger, longer, and less homogeneous rays; and with *A. ferruginea* (Guill. & Perr.) Benth. which has rays of similar length, marginal parenchyma, and little confluent parenchyma. *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 of altitude (Nielsen 1992; Sosef *et al.* 1998). *A. lebbek* is a deciduous tree, probably native to tropical mainland Asia of 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 altitude (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 riverbeds, coral loam or limestone (Prakash 1975; Nielsen 1992; Jensen 1999; Orwa *et al.* 2009; Wu & Raven 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; Twum-Ampofo 2007; Orwa *et al.* 2009).



**Figure 3.** *Albizinium eolebbekianum* Prakash (**A-D**): **A**, Ts, vessels and parenchyma arrangement; **B**, Tls, 1-3-seriate rays and crystalliferous parenchyma (arrow); **C**, Rls, homocellular rays; **D**, Tls, possible septate fibre. *Cynometroxylon holdenii* (Gupta) Prakash & Bande (**E-H**): **E**, Tr, banded parenchyma and vessels pattern; **F**, Tls, heterocellular and mostly 2-seriate rays; **G**, Rls, heterocellular rays with 1-2 uprights marginal rays cells; **H**, Ts, included phloem present in 17FN17. Scale bars: A, E, H, 1 mm; C, G, 500 µm; B, F, 200 µm, D, 25 µm.

Genus *Cynometroxylon* Chowdhury & Ghosh 1946

*Cynometroxylon holdeni* (Gupta) Prakash & Bande 1980

Also written “*Cynometroxylon holdenii*”

(Fig. 3; E-H)

*Dipterocarpoxyylon holdeni* - Gupta, 1935

*Cynometroxylon indicum* - Chowdhury & Ghosh, 1946

*Cynometroxylon cf. Cynometroxylon indicum* - Prakash, 1967

*Cynometroxylon schlagintweitii* - Müller-Stoll & Mädler, 1967

*Cynometroxylon siwalicus* - Trivedi & Ahuja, 1978

*Cynometroxylon sp. cf. C. indicum* - Prakash, 1978

*Cynometroxylon holdeni* - Prakash & Bande, 1980: 266 (Burma)

HOLOTYPE - Birbal Sahni Institute of Paleobotany Museum no. 29785

MATERIAL - MNHN.[under registration], MNHN.[under registration], MNHN.[under registration]; field number: 17FN17, 17FN19, NAT17-3.

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 fibre band thickness and the presence of tiny 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. 3E); tangential diameter 50-200 µm (average: 115 µm). Tylose absent. Vessel elements 130-510 µm (average: 300 µm) long. Perforation plates simple. Vessel pits alternate, seemingly polygonal, 2-5 µm wide (average: 3 µm). *Parenchyma* paratracheal, vasicentric with 1-3 cells thick sheath around vessel and in continuous, waved and sometimes anastomosed tangential bands (Fig. 3A), 2- to 11- (average: 7-) seriate, as large as fibre bands or thinner, including most of the vessels, 2-6 bands per tangential mm; 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. 3F), 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. 3G), occasionally with a faint storied tendency. *Fibres* libriform, non-septate, 8-22 µm in tangential diameter (average 14 µm), thick-walled, without any particular arrangement. *Included phloem*, nonconducting,

present as liber alternating broad fibre bands and broad parenchyma bands but less continuous than in the wood (Fig. 3H), 1-5 cells high; rays with the same size and pattern as wood.

#### DISCUSSION –

These fossils are characterized by (1) diffuse-porous wood, (2) exclusively simple perforation plates, (3) banded parenchyma as thick as fibre bands, (4) heterocellular and mainly 2-seriate rays, (5) a slight tendency to storied rays, (6) non-septate fibres. The presence of included phloem is likely due to a wound; 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 fibre bands (less than 30 cells thick). This feature can be found in 16 families and 40 genera, mostly in Meliaceae, Malvaceae, Clusiaceae, Fabaceae, the genera *Terminalia* (Combretaceae) and *Ficus* (Moraceae). All the other features of our fossil specimens are also found in Fabaceae.

The combination of features cited above is shared by the fossil genus *Cynometroxylon* (Chowdhury & Ghosh 1946). 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. We compare our fossils to some *Cynometroxylon* already described and available in literature in Appendix 2. The specimens 17FN17 and 17FN19 display a closer resemblance with *C. holdeni*, especially with the Burmese specimens described by Prakash & Bande (1980) from the Miocene and by Licht *et al.* (2014) from the middle Eocene. They show a slightly higher density of vessels (7-24 per square millimeters for our fossils against 3-4 per square millimeters for *C. holdeni*), which might be related to environmental factors and is not enough to exclude their attribution to this species.

The specimen NAT17-3 shows some variations of character such as irregular size of bands, both for parenchyma and fibres, which can be interpreted as growth zones. These irregular bands are seen in extant *Cynometra* (e.g. *Cynometra ananta* Hutch. & Dalziel, *Maniltoa polyandra* (Roxb.) Harms : InsideWood, 2004-onward) but rarely in *Cynometroxylon*. In some places, a storied tendency is seen and can remind of *Bauhinium* (Prakash & Prasad 1984) or *Crudioxylon* (Pons 1980). But *Bauhinium* commonly has a large proportion of uniseriate rays, which is not the case for our fossil. The main difference between *Cynometroxylon* and *Crudioxylon* is that *Crudioxylon* has rarely joining parenchyma bands, more straight

bands and also homocellular rays with some storied tendency, which are not particularly diagnostic in our specimens.

Among *Cynometroxylon* specimens (Appendix 2), only *C. schlangintweitti* Müller-Stoll & Mädél and *C. tunesense* Delteil-Desneux are described with a storied ray tendency, but both have homocellular rays. Only *C. holdeni* (Nareerat 2008), *C. indicum* Chowdhury & Ghosh and *C. schlangintweitti* have crystalliferous parenchyma; the two latter fossil species are now included in *C. holdenii*. Thus, except for the irregular bands, all these features have been described in *Cynometroxylon*, but not all in the same specimen. Even if rare in *Cynometroxylon*, irregular bands are found in modern *Cynometra*. Considering the variability seen among *Cynometroxylon* and the examination of the synonyms of *C. holdeni*, all our specimens are attributed to *Cynometroxylon holdeni*.

Our fossil specimens display similar features to genera *Baphia* Afzel. ex Lodd., *Clitoria* L., *Calliandra* Benth., *Crudia* Schreb., *Cynometra* and *Maniltoa* Scheff. (closely related to *Cynometra*) within extant Fabaceae with banded parenchyma as thick as fibre bands (Chowdhury & Ghosh 1946; Calquist 2001). Nevertheless, *Baphia* has homocellular rays; *Clitoria* has two distinct sizes of vessels; *Calliandra* has vessels not included in parenchyma bands; *Crudia*, *Maniltoa* and *Cynometra* are the most similar to our fossils. Even though they are hardly distinguishable from each other based on wood anatomy (Vozenin-Serra & Privé-Gill 1989; Soerianegara & Lemmens 1993), *Crudia* is presumed to have larger and thicker parenchyma bands than *Cynometra* (Vozenin-Serra & Privé-Gill 1989). *Maniltoa* has chambered crystals confined to upright ray cells, is more heterocellular and has radial vessel multiples up to 6 (Soerianegara & Lemmens 1993). *Cynometra ramiflora* L. and *Maniltoa polyandra* (synonym of *Cynometra polyandra* Robx.) are the most anatomically similar species to our fossils. The relationships between *Cynometra* and *Maniltoa* are often discussed on morphological and genetic levels (Soerianegara & Lemmens 1993; Hou *et al.* 1996; Radosavljevic *et al.* 2017; De la Estrella *et al.* 2018), but if we consider the identification key of Knaap Van Meeuwen (1970), our fossils are closer to *Maniltoa*.

*Cynometra* species are mainly tropical shrubs or trees present in South and East Asia, Philippines, Australia, pacific islands, Mexico, Brazil and Africa. They are found in forests up to 1300 m of altitude, or along rivers, on swampy soils, in dense wet lowland forests or mixed with mangrove species (Soerianegara & Lemmens 1993; Hou *et al.* 1996). *C. 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 of altitude (Soerianegara & Lemmens 1993; Hou *et al.* 1996). The genus *Maniltoa*, exclusive to Asia, is present in primary lowland forests at low altitude, mostly in swampy areas, sometimes in mangroves (Soerianegara & Lemmens 1993; Hou *et al.* 1996). *M. polyandra* is a wet evergreen or semi-evergreen forest tree (Knaap Van Meeuwen 1970; Soerianegara & Lemmens 1993), up to 1300m of altitude (Soerianegara & Lemmens 1993; Hou *et al.* 1996).



**Figure 4.** *Cynometroxylon parinaequifolium* Prakash (A-G). Specimen 17FN10 (A-C): **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 upright marginal cells. Specimen 19NAT07-1 (**D**, **F**): **D**, Ts, vessel size and pattern, banded parenchyma with some aliform parts (arrow); **F**, Tls, 1-2

seriate heterocellular rays with upright marginal cells. Specimen NAT17-7 (**E, G**): **E**, Ts, vessel size and pattern, banded parenchyma with some aliform parts (arrow); **G**, Tls, 1-3 seriate heterocellular rays with upright marginal cells. Scale bars: A, D-E, 1 mm; B, F-G, 200  $\mu\text{m}$ ; C, 85  $\mu\text{m}$ .

Genus *Cynometroxylon* Chowdhury & Ghosh 1946

***Cynometroxylon parinaequifolium* Prakash 1979**

(Fig. 4; A-G)

*Cynometroxylon parinaequifolium* - Prakash, 1979: 51 (Thailand)

HOLOTYPE - Birbal Sahni Institute of Paleobotany Museum no. 35263

MATERIAL - MNHN.[under registration], MNHN.[under registration], MNHN.[under registration]; field number: 17FN10, NAT17-7, 19NAT07-1.

LOCALITY - Kalewa Township, Sagaing Region, Myanmar

AGE - upper lower to lowermost middle Miocene

DESCRIPTION -

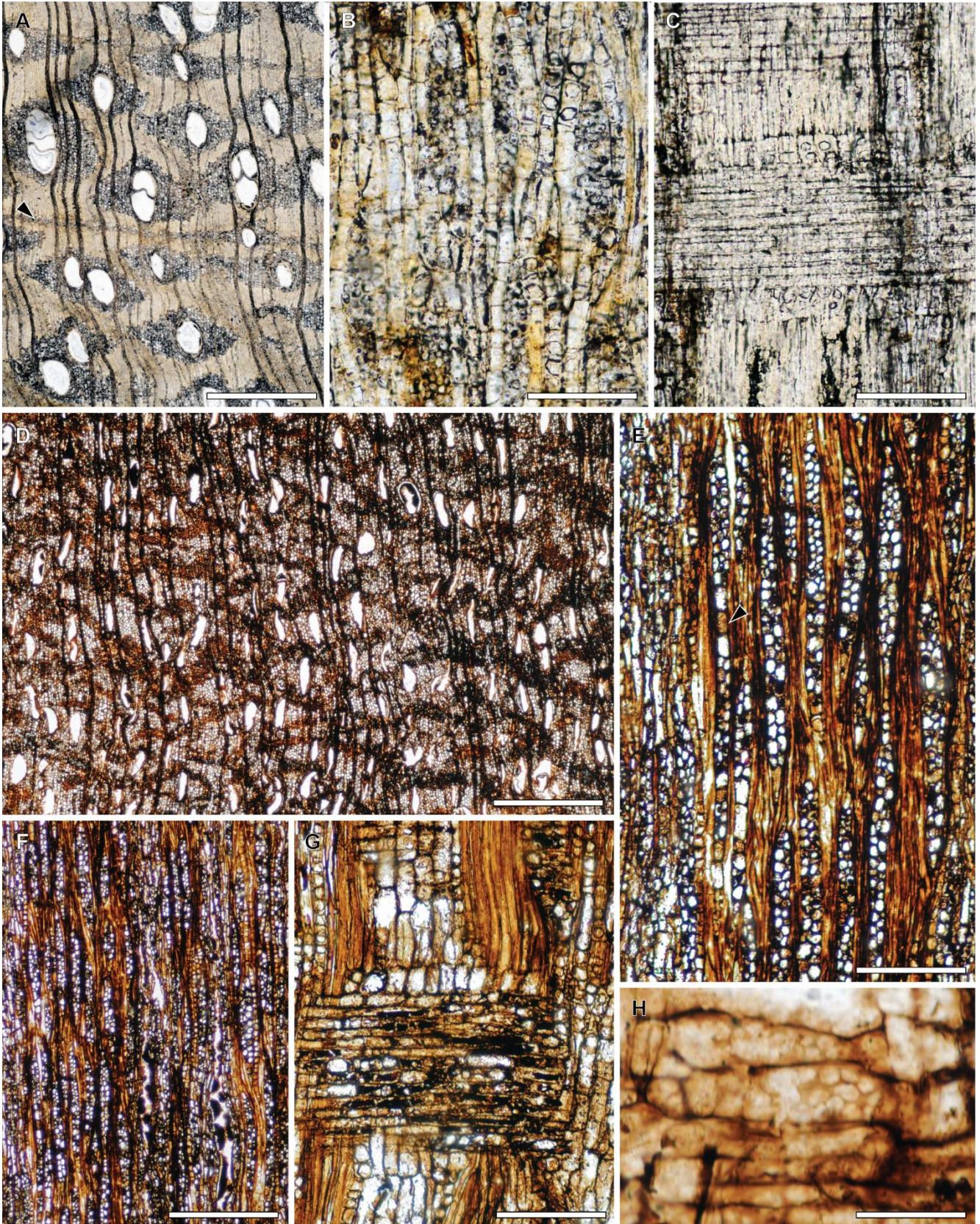
*Wood* diffuse-porous. Growth rings hardly distinguishable marked by small marginal parenchyma bands, a change in vessels or fibre bands size or growth line (Fig 4A). *Vessels* solitary (40-75%) or in radial groups of 2-5, round to oval, 3-16 per  $\text{mm}^2$  (average 8 per  $\text{mm}^2$ ); tangential diameter 50-170  $\mu\text{m}$  (average: 120  $\mu\text{m}$ ). Tylose absent. Vessel elements 150-600  $\mu\text{m}$  (average: 330  $\mu\text{m}$ ) long. Perforation plates simple. Vessel pits alternate, 2-4  $\mu\text{m}$  wide (average: 3  $\mu\text{m}$ ). *Parenchyma* mostly banded but also aliform or vasicentric close to growth rings, bands wavy and sometimes anastomosed, enclosing most of vessels (Fig. 4A, D, E), 3- to 8- (average: 5-) seriate, as large as fibre bands or thinner, 3-5 bands per mm; parenchyma cells 35-160  $\mu\text{m}$  (average: 100  $\mu\text{m}$ ) long, 10-36  $\mu\text{m}$  (average: 22  $\mu\text{m}$ ) wide in tangential section; 5 to 8 cells per parenchyma strands. *Rays* 1- to 3- seriate (mostly 2) (Fig. 4B, F, G), 6-13 rays per mm (average: 9 per mm), 140-1080  $\mu\text{m}$  (average: 470  $\mu\text{m}$ ) or up to 35 (sometimes 55) cells long, heterocellular made of procumbent cells with 1-3 square or upright marginal cells (Fig. 4C), frequent end-to-end fusions resulting in very high rays. *Fibres* non-septate, 5-20  $\mu\text{m}$  in tangential diameter (average 13  $\mu\text{m}$ ), thick-walled, without any particular arrangement.

DISCUSSION -

These specimens share all the diagnostic features of the genus *Cynometroxylon* including (1) diffuse-porous wood, (2) banded parenchyma about as thick as fibre bands, (3) 1-3 seriate heterocellular rays, (4) non-septate fibres, (5) non-storied elements. Rays are rarely uniseriate and always heterocellular, parenchyma bands are mostly wavy, which make it compatible with the diagnosis of genus *Crudioxylon* as well. Our fossils are remarkable in having small parenchyma bands (around 5 cells high), high rays and ray fusion frequent. When compared with other *Cynometroxylon* (Appendix 2), our specimens resemble closely to *C. parainaequifolium*, which also has small vessels (< 200 µm of diameter), small parenchyma bands, 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 for *C. parainaequifolium*). 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. parainaequifolium*. 17FN10 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* fossils. Discontinuous bands and aliform parenchyma are also observed in the *Cynometroxylon holdeni* of Nareerat (2008) and the fossil *Cynometra grandis* of Woodcock *et al.* (2017). It is also visible in extant *Cynometra ananta* and *Maniltoa polyandra* of InsideWood (2004-onward) and Nareerat (2008, p. 111, fig. 4.41; p. 112, fig. 4.42). We thus consider that discontinuous bands in *Cynometra*, *Cynometroxylon* and *Maniltoa* are a variable character and not a diagnostic feature of our fossils. All these observations lead us to attribute these three specimens to *Cynometroxylon parainaequifolium*.

Similar to our previous *Cynometroxylon* specimens, these three specimens are comparable to extant *Cynometra* and *Maniltoa*. They display a close resemblance to *Maniltoa polyandra* because of its variability of parenchyma pattern and ray width, and to *Cynometra inaequifolia* A. Gray because of ray width and the occasional presence of long rays (up to 1 mm long). *Cynometra inaequifolia* is a small lowland tree of Malaysia, Philippines, and Thailand resembling *C. ramiflora* (Knaap Van Meeuwen 1970; Hou *et al.* 1996; World Conservation Monitoring Centre 1998). *M. polyandra* is a wet evergreen or semi-evergreen forest tree (Knaap Van Meeuwen 1970; Soerianegara & Lemmens 1993), found up to at 1300 m of altitude (Knaap Van Meeuwen 1970; Hou *et al.* 1996; World Conservation Monitoring Centre 1998).





**Figure 5.** *Koompassioxylon elegans* Kramer (A-C): **A**, Ts, Vessel size and groups, aliform parenchyma with pointed wings and marginal parenchyma (arrow); **B**, Tls, 2-3 seriate rays with crystalliferous



parenchyma; **C**, Rls, heterocellular rays with crystals in upright marginal cells. *Koompassioxylon kalewensis* n. sp. (**D-H**): **D**, Ts, mostly solitary vessels with aliform and aliform-confluent parenchyma, sometimes forming short bands; **E**, Tls, 1-3 seriate heterocellular rays with end-to-end fusions (arrow); **F**, Tls, storied tendency of rays; **G**, Rls, heterocellular rays, sometimes with mixed character, with upright marginal cells and crystalliferous parenchyma; **H**, Rls, vessel-ray pits. Scale bars: A, D, 1mm; B-C, E, G, 200 µm; F, 500 µm; H, 50 µm.

Genus *Koompassioxylon* Kramer 1974

***Koompassioxylon elegans* Kramer 1974**

(Fig. 5; A-C)

*Koompassioxylon elegans* - Kramer, 1974: 117 (Darvel Bay)

HOLOTYPE - Senckenberg Museum, Frankfurt. No. SM.B 12 509/1 - 12 509/3

MATERIAL - MNHN.[under registration], MNHN.[under registration], MNHN.[under registration]; field number: 17FN13, 17FN14, 19NAT03-2.

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. 5A), 1-7 cells thick. *Vessels* mostly solitary (70-90%) or grouped by 2 or 3 (Fig. 5A), oval, 0-6 per mm<sup>2</sup> (average: 3); tangential diameter 120-370 µm (average: 230). Tylose absent. Vessel elements 160-570 µm long (average: 340). Perforation plates simple. Vessel pits alternate, 6-11 µm (average: 8) in diameter. *Parenchyma* apotracheal and paratracheal; apotracheal arranged in marginal bands enclosing some little vessels (Fig. 5A), paratracheal widely aliform and confluent laterally or in diagonal, forming anastomosed shapes and bands, joining up to 10 vessels (Fig. 5A); 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. 5B), especially in border ones. *Rays* 2- to 3-seriate (mainly 3, rarely 4) (Fig. 5B), tendency to storied arrangement, 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. 5C); crystals in upright ray cells (Fig. 5C). *Fibres* thin to thick-walled, non-septate, 8-22 µm (average: 14 µm) wide.

## DISCUSSION -

These specimens are characterized by (1) diffuse-porous wood, (2) exclusively simple perforation plates, (3) crystalliferous aliform-confluent parenchyma, (4) marginal parenchyma bands, (5) 2- to 3-seriate rays with a storied tendency, (6) low vessel density, (7) heterocellular rays, (8) crystalliferous rays. Aliform-confluent parenchyma and 2-3 seriate rays are common features in fossil Fabaceae as in fossil genera *Pahudioxylon*, *Albizinium*, *Cassinium* Prakash, and *Adenantheroxylon* Prakash & Tripathi, but heterocellular rays with crystals in upright cells are uncommon. Among fossil genera with marginal and aliform-confluent parenchyma, *Pericopsoxylon* Awasthi shares the vessel arrangement of our specimens but all its elements are storied, and its rays are homocellular; *Saracoxylon* Du has mostly 1-2 seriate rays, no crystals in parenchyma or ray cells, and no storied ray tendency; *Cassinium* has homocellular to weakly heterocellular rays; *Ormosioxylon* Bande & Prakash has storied rays but they are mostly homocellular to weakly heterocellular and lack crystals. *Koompassioxylon* shares most of the features of our fossil specimens: mostly solitary vessels, marginal parenchyma, crystalliferous aliform-confluent parenchyma with often pointed wings, heterocellular rays with at least 1 upright and crystalliferous marginal cell and a ray tendency. Only two species of *Koompassioxylon* have been described (Appendix 3): *K. keralaensis* Srivastava & Awasthi has less confluent parenchyma, mostly homocellular rays, storied parenchyma and rays and no crystals. By contrast, *K. elegans* Kramer has marginal parenchyma as well as pointed aliform-confluent with crystals, heterocellular rays with crystalliferous upright marginal cells and storied ray tendency but it has smaller vessels and sometimes homocellular rays. Nevertheless, our specimens are compatible with the diagnosis of *Koompassioxylon elegans* and are attributed to this fossil species.

Some of the characteristic features cited above are common in extant genera *Afzelia* and *Intsia*; however, the strong confluence of the aliform parenchyma is uncommon in these two genera, as well as heterocellular rays with 1-2 rows of upright crystalliferous cells. Other extant species resembling our specimens include: (1) *Desmodium oojeinense* (Roxb.) Ohashi which has similar axial parenchyma pattern and ray width but all elements storied (parenchyma cells, rays and vessel elements); (2) several species of *Ormosia* Jacks., such as *O. panamensis* Benth. which has a strong confluent parenchyma, a storied and heterocellular rays but no marginal parenchyma nor crystals in upright parenchyma cells, and *O. robusta* Baker which has a similar parenchyma pattern but wider rays; and (3) three species of *Koompassia* Maingay ex Benth.: *K. excelsa* (Becc.) Taub. and *K. grandiflora* Kosterm. which have both banded parenchyma, and *K.*

*malaccensis* Benth. which resembles the most to our specimens and has crystalliferous aliform-confluent parenchyma, pointed at the extremities, storied but bigger rays (Soerianegara & Lemmens 1993; InsideWood 2004-onward).

*Desmodium oojeinense* is common in mixed deciduous and sal (*Shorea robusta* C.F.Gaertn.) forests in hot climates. It is also associated with pine trees (Gamble 1902). *Ormosia* are south American, Asian and Australian tropical trees, leaving mainly in lowland rain forests but also along riverbanks or in seasonal swampy, littoral, and monsoon forests (Sosef *et al.* 1998). *Koompassia* are southeast Asian giant tropical trees growing in primary rainforests below 650 m of altitude (Soerianegara & Lemmens 1993). *Koompassia malaccensis* lives in lowland forests and in freshwater peat and freshwater swamp forest, also in dry lands mostly up to 150 m of altitude (rarely up to 800 m; Soerianegara & Lemmens 1993; Hou *et al.* 1996).

Genus *Koompassioxylon* Kramer 1974

***Koompassioxylon kalewensis* n. sp.**

(Fig. 5; D-H)

DESIGNATED HOLOTYPE - MNHN.[under registration]

REPOSITORY – Muséum national d'Histoire naturelle, Paris, France

ETYMOLOGY – After Kalewa locality where the fossil was found.

MATERIEL - MNHN.[under registration]; field number: NAT17-06.

LOCALITY - Kalewa Township, Sagaing Region, Myanmar

AGE - upper lower to lowermost middle Miocene

DIAGNOSIS - Wood diffuse-porous. Vessels mostly solitary as well as in small radial groups, medium sized, without tylose. Perforation plate simple. Parenchyma abundant, aliform mostly confluent joining several vessels together, abundantly crystalliferous, 1-3-seriate, heterocellular with 1-4 upright marginal cells, fusions common, upright cells mixed throughout some rays, storied tendency. Fibre non-septate.

DESCRIPTION -

Wood diffuse-porous. *Growth rings* present but hardly visible. *Vessels* mostly solitary (80 %) or grouped by 2 or 3, oval, 4-9 per mm<sup>2</sup> (average: 7); tangential diameter 140-250 µm (average: 180 µm). Tylose absent. Vessel elements 220-460 µm long (average: 300 µm). Perforation plates simple. Vessel pits alternate, 6-13 µm (average: 10 µm) in diameter. Vessel-ray pits apparently simple, rounded or angular

(Fig. 5H), 5-21  $\mu\text{m}$  in diameter. *Parenchyma* widely aliform and confluent laterally or in diagonal, forming anastomosed shapes and bands (Fig. 5D); parenchyma cells 50-130  $\mu\text{m}$  long (average: 85  $\mu\text{m}$ ), 10-30  $\mu\text{m}$  wide (average: 20  $\mu\text{m}$ ); 4-8 or more cells per parenchyma strands; abundant crystals in chambered parenchyma cells (Fig. 5E, G), especially in border ones. *Rays* 1- to 3-seriate (few uniseriate) (Fig. 5E), tendency to storied arrangement (Fig. 5F), 8-16 rays per mm (average: 11), 150-870  $\mu\text{m}$  (average: 400  $\mu\text{m}$ ) or up to 30 cells high, end-to-end fusion frequent (Fig. 5E), heterocellular with one to multiple rows of upright or square cells at both ends (Fig. 5G), as well as upright and bigger cells in the middle, sometimes alternating giving the appearance of mixed rays (procumbent and upright cells mixed throughout) in radial section, probably resulting from fusions. *Fibres* mostly thick-walled, non-septate, 12-24  $\mu\text{m}$  (average: 17  $\mu\text{m}$ ) wide.

#### DISCUSSION -

The specimen is characterized by (1) diffuse-porous wood, (2) exclusively simple perforation plates, (3) crystalliferous aliform-confluent parenchyma, (4) 1- to 3-seriate heterocellular rays, (5) mostly solitary vessels (Fig. 5, D-H). As for *Koompassioxylon elegans*, these features are similar to those of the Fabaceae family.

The distinction between fossil genera *Koompassioxylon* and *Ormosioxylon* is delicate. The first genus to be described is *Koompassioxylon* by Kramer (1974), who made a precise diagnosis; this genus gather fossil wood specimens with growth rings, eye-shaped parenchyma with pointed wings, sometimes confluent connecting 1-3 vessels, rays 1-3 seriate and mainly 15 cells high, heterocellular rays with at least 1 upright marginal cells (sometimes 2-3) and with a storied arrangement, crystals are found in both chambered parenchyma cells and chambered upright marginal ray cells. By contrast, *Ormosioxylon* described by Bande & Prakash (1980) include fossil wood specimens with aliform-confluent parenchyma sometimes forming bands including vessels, 1-4 seriate rays mostly homocellular to weakly heterocellular, a storied tendency. Both genera share similarities about parenchyma configuration, though some differences can be pointed out: (1) less confluent tendency for *Koompassioxylon* with marked wing-shapes, (2) always heterocellular rays for *Koompassioxylon*, (3) an absence of crystals in *Ormosioxylon*, both in parenchyma and ray cells. Our fossil specimen displays well-marked confluent parenchyma as seen in *Ormosioxylon* but its compression might exaggerate this tendency; by contrast, it doesn't display strictly heterocellular rays and

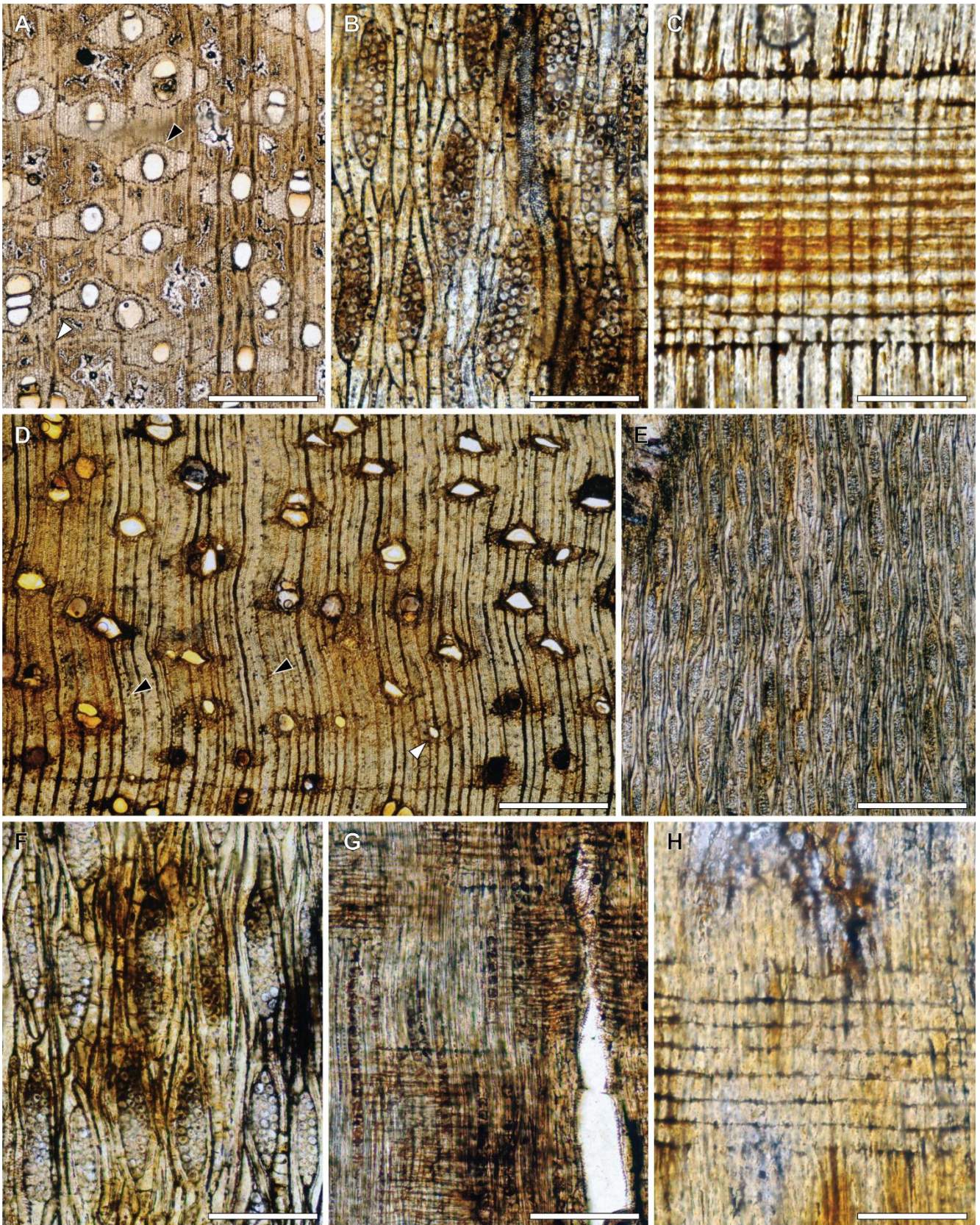
crystalliferous parenchyma. Thus, our specimen is closer to the diagnosis of *Koompassioxylon* though it does not have any crystals in ray cells.

Two features clearly distinguish this specimen from *K. elegans*: our fossil has (1) no crystalliferous rays, (2) less uniform rays and sometimes with procumbent and upright cells mixed throughout.

No species in the *Koompassioxylon* genus displays this type of rays (Appendix 3). *K. keralaensis* (Srivastava & Awasthi 1996) has no crystals in rays but its rays are mostly homocellular. Therefore, a new species is created: *Koompassioxylon kalewensis* n. sp.

A comparison of our specimen with modern *Ormosia* and *Koompassia* highlight resemblances with *Ormosia panamensis* which has a high confluence of parenchyma, and with *Ormosia coccinea* which has aliform-confluent parenchyma, sometimes crystalliferous, faint growth rings marked by smaller vessels at some places, and 1-3-seriate rays with marginal upright cells and some mixed rays with end-to-end fusion. However, the rays of *O. coccinea* do not show any storied tendency. *Ormosia* are South American, Asian, and Australian tropical trees living in lowland rain forests and also found along riverbanks, seasonal swamps, in monsoon and coastal forests (Sosef *et al.* 1998). As the wood anatomy of many modern species is not documented nor reported in databases, we can assume that a closest relative possibly exists within Asian species. *Ormosia coccinea* is an American tropical rainforest tree of well drained, sandy soils. It is also found at the edges of savannas and in coastal forests (Rudd 1965).





**Figure 6.** *Pahudioxylon bankurensis* Chowdhury, Ghosh & Kazmi (A-C): **A**, Vessels, aliform parenchyma with marginal crystals (black arrow) and marginal parenchyma (white arrow); **B**, 2-3 seriate rays with



crystalliferous parenchyma; **C**: homocellular rays. *Pahudioxylon adenanthroides* n. sp. (**D-H**): **D**, mostly solitary vessels, aliform parenchyma with marginal crystals (white arrow), marginal parenchyma and diffuse parenchyma (black arrows); **E**, storied rays; **F**, 1-3 seriate homocellular rays and parenchyma cells; **G**, crystals in parenchyma strands; **H**, homocellular ray. **A, D**, transversal sections; **B, E, F**, tangential longitudinal sections; **C, G, H**: radial longitudinal section. Scale bars: A, D, 1 mm; B, F-G, 200 µm; C, H, 100 µm; E, 500 µm.

Genus *Pahudioxylon* Chowdhury, Ghosh & Kazmi 1960

***Pahudioxylon bankurensis* Chowdhury, Ghosh & Kazmi 1960**

(Fig. 6; A-C)

*Pahudioxylon bankurensis* - Chowdhury *et al.*, 1960: 23 (Bankura)

*Albizzioxylon sahnii* - Ramanujam, 1960

*Pahudioxylon sahnii* - Ghosh & Kazmi, 1961

*Pahudioxylon deomaliense* - Prakash, 1965c

*Ingoxylon sahnii* - Müller-Stoll & Madel, 1967

*Pahudioxylon welkitii* - Lemoigne & Beauchamp 1973

*Pahudioxylon assamicum* - Prakash & Tripathi, 1975

*Pahudioxylon indicum* - Prakash 1979

*Pahudioxylon bengalensis* - Ghosh & Roy, 1982

MATERIAL - MNHN.[under registration]; field number: 17FN03.

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, 4-5 cells thick (Fig. 6A). *Vessels* solitary (55%) as well as in radial groups of 2-4 (45%) (Fig. 6A), round to oval, 1-5 per mm<sup>2</sup> (average: 3); tangential diameter 120-275 µm (average: 185 µm). Tylose absent. Vessel elements 120-370 µm (average: 225 µm) long. Perforation plates simple. Vessel pits alternate, polygonal shaped, 4-7 µm (average: 6 µm) wide. Axial *parenchyma* paratracheal and apotracheal, paratracheal lozenge-aliform up to 13 cells wide for each wing and 5 cells around vessels, often confluent joining 2-4 vessels or groups

of vessels (Fig. 6A), apotracheal parenchyma in marginal bands including smaller vessels; parenchyma cells 35-160  $\mu\text{m}$  (average: 90  $\mu\text{m}$ ) long, 15-40  $\mu\text{m}$  (average: 26  $\mu\text{m}$ ) wide; around 5 cells per parenchyma strand, abundant crystals in chambered parenchyma cells at the margin of the aliform parenchyma (Fig. 6A, B), crystals are visible as black dots in the transversal section. Rays 2- to 3- seriate (almost exclusively 3) (Fig. 6B), storied tendency, 5-7 rays per mm (average: 6), 140-370  $\mu\text{m}$  (average: 245  $\mu\text{m}$ ) or 8-21 cells high, mostly homocellular made of procumbent cells (Fig. 6C), rarely 1 row of marginal upright and sometime crystalliferous cells. *Fibres* non-septate, 7-30  $\mu\text{m}$  (average: 19  $\mu\text{m}$ ) wide.

#### DISCUSSION -

This specimen is characterized by (1) diffuse-porous wood, (2) exclusively simple perforation plates, (3) storied, homocellular and 2- to 3- seriate rays (4) aliform to aliform-confluent parenchyma, (5) marginal parenchyma and (6) storied rays. These combined features are shared by some Fabaceae, including modern Caesalpinieae, and by fossil genera *Adenanthoxylon* and *Pahudioxylon* (Appendix 4; Chowdhury *et al.* 1960). When compared with fossil species of these two genera (Appendix 4), all features of our fossil are compatible with the diagnosis of *P. bankurensis*; our specimen is thus attributed to this species. It is noteworthy that the black outlines of crystals in the aliform parenchyma found in our specimen are also observed in previous specimens by Chowdhury *et al.* (1960). Six species are synonymized with *P. bankurensis* (*P. assamicum*, *P. bangalensis*, *P. deomaliense*, *P. indicum*, *P. sahnii* and *P. welkitii*) by Awasthi (1992) and Feng *et al.* (2015) because of the minor differences observed between these species reflect intraspecific variability in their closest living relatives, *Afzelia* and *Intsia*.

Our specimen is anatomically close to the genera *Afzelia* and *Intsia* which are indistinguishable based on xylological characters (Prakash 1966; Müller-Stoll & Mädel 1967) but have different geographical distribution. *Afzelia* is mainly present in Africa and *Intsia* in Asia. Based on a comparison with some species of *Afzelia* and *Intsia* from the InsideWood (2004-onward) database and the xylotheque of the MNHN (Paris), our specimen shows the closest affinity with *Intsia bijuga* (Colebr.) Kuntze, which is often given as an extant relative for *Pahudioxylon bankurensis* specimens. All *Intsia* are Asian tropical trees that live in wet evergreen forests, with rainfall higher than 2000 mm per year, and associated with *Anisoptera* Korth. and *Hopea* Roxb. (Soerianegara & Lemmens 1993). They are mostly found in coastal habitat, near beaches or mangroves (Loo & Tan 1997) and are absent from peat swamps. *Intsia bijuga* are found along seacoasts, river edges, tidal or temporarily inundated places (sometimes salty water), in back-mangroves, primary and



secondary forests, up to 600 m of altitude (Soerianegara & Lemmens 1993; Hou *et al.* 1996; Orwa *et al.* 2009)

Genus *Pahudioxylon* Chowdhury, Ghosh & Kazmi 1960

***Pahudioxylon adenantheroides* n. sp.**

(Fig. 6; D-H)

DESIGNATED HOLOTYPE - MNHN.[under registration]; field number: 17FN16.

PARATYPE - MNHN.[under registration], MNHN.[under registration]; field number: 17FN06, 17FN18.

REPOSITORY – Muséum national d'Histoire naturelle, Paris

ETYMOLOGY – After a resemblance with *Adenantheroxylon* species.

MATERIAL - MNHN.[under registration], MNHN.[under registration] , MNHN.[under registration]; field number: 17FN06, 17FN16, 17FN18.

AGE - upper lower to lowermost middle Miocene

LOCALITY - Kalewa Township, Sagaing Region, Myanmar

DIAGNOSIS - Wood diffuse-porous. Growth rings delimited by marginal parenchyma bands. Vessels mostly solitary, rarely in small radial groups, medium to large (100-300 µm diameter), quite sparse. Tylose absent. Perforation plates simple. Vessels pits alternate. Parenchyma marginal, apotracheal diffuse and paratracheal mostly aliform not very extended laterally; weakly confluent when vessels are close. Parenchyma crystalliferous. Rays 1-3-seriate, mostly storied, homocellular, quite short (up to around 20 cells). Fibres non septate.

DESCRIPTION -

Wood diffuse-porous. *Growth rings* present, marked by marginal parenchyma bands 1-7 cells thick high (Fig. 6D). *Vessels* mostly solitary (70-90%) or grouped by 2-4 (Fig. 6D), round to oval, 1-7 per mm<sup>2</sup> (average 3); tangential diameter 100-300 µm (average 200 µm). Tylose absent. Vessel elements 160-570 µm (average 310 µm) long. Perforation plates simple. Vessel pits alternate, 4-12 µm (average 8) in diameter. Axial *parenchyma* apotracheal and paratracheal, apotracheal diffuse and arranged in marginal bands enclosing some little vessels, paratracheal aliform but not very extended, diamond shaped and sometimes confluent when vessels are close (Fig.6D); parenchyma cells 40-145 µm (average 80 µm) long, 10-49 µm (average 25 µm) wide; 4 or more cells per parenchyma strands; crystals in chambered

parenchyma cells (Fig. 6D, F, G), mostly in borders of aliform parenchyma and diffuse parenchyma (up to 16 crystals per parenchyma strands) (Fig. 6G). Rays 1- to 3-seriate (Fig. 6F), storied at some places (Fig. 6E), a storied tendency at others and sometimes no storied rays at all depending on specimens and zones, 5-12 rays per mm (average 8), 130-400  $\mu\text{m}$  (average 240  $\mu\text{m}$ ) or 6-20 cells high, homocellular made of procumbent cells (Fig. 6H). Fibres thin to thick-walled, non-septate, 8-26  $\mu\text{m}$  (average 16  $\mu\text{m}$ ) wide.

#### DISCUSSION -

Two of our three specimens (17FN06 and 17FN16) are very similar in color and mineralization, and display the same compressed aspect, suggesting that they might represent different parts of the same broken piece, even though we cannot confirm it. The third specimen (17FN18) has a different preservation and deformation, bigger and less dense vessels, but share all the key characters of the first two. They are characterized by (1) diffuse-porous wood, (2) exclusively simple perforation plates, (3) aliform parenchyma, (4) marginal bands of parenchyma, (5) 1-3-seriate and storied rays. Like for *Pahudioxylon bankurensis*, these features are shared by some Fabaceae, including modern Caesalpiniaceae, and by fossils genera *Adenantheroxylon* and *Pahudioxylon* (Appendix 4; Chowdhury *et al.* 1960). These features are similar to those of *Pahudioxylon bankurensis* and *P. kiliani* (Louvet) Prakash (Appendix 4). However, the presence of diffuse parenchyma is unique to our specimens, and has never been documented in any species of *Pahudioxylon*. Their aliform parenchyma is also less developed and less confluent than in most *Pahudioxylon*. Only *Adenantheroxylon pavoninium* Prakash & Tripathi is described with diffuse parenchyma; however, it also has thinner rays and no marginal parenchyma. The fossil genus *Cassinium* is described with both diffuse and aliform parenchyma, but its parenchyma is very confluent, sometime banded and its rays are never storied. We thus attribute our specimen to a new species of *Pahudioxylon*: *P. adenantheroides* n. sp.

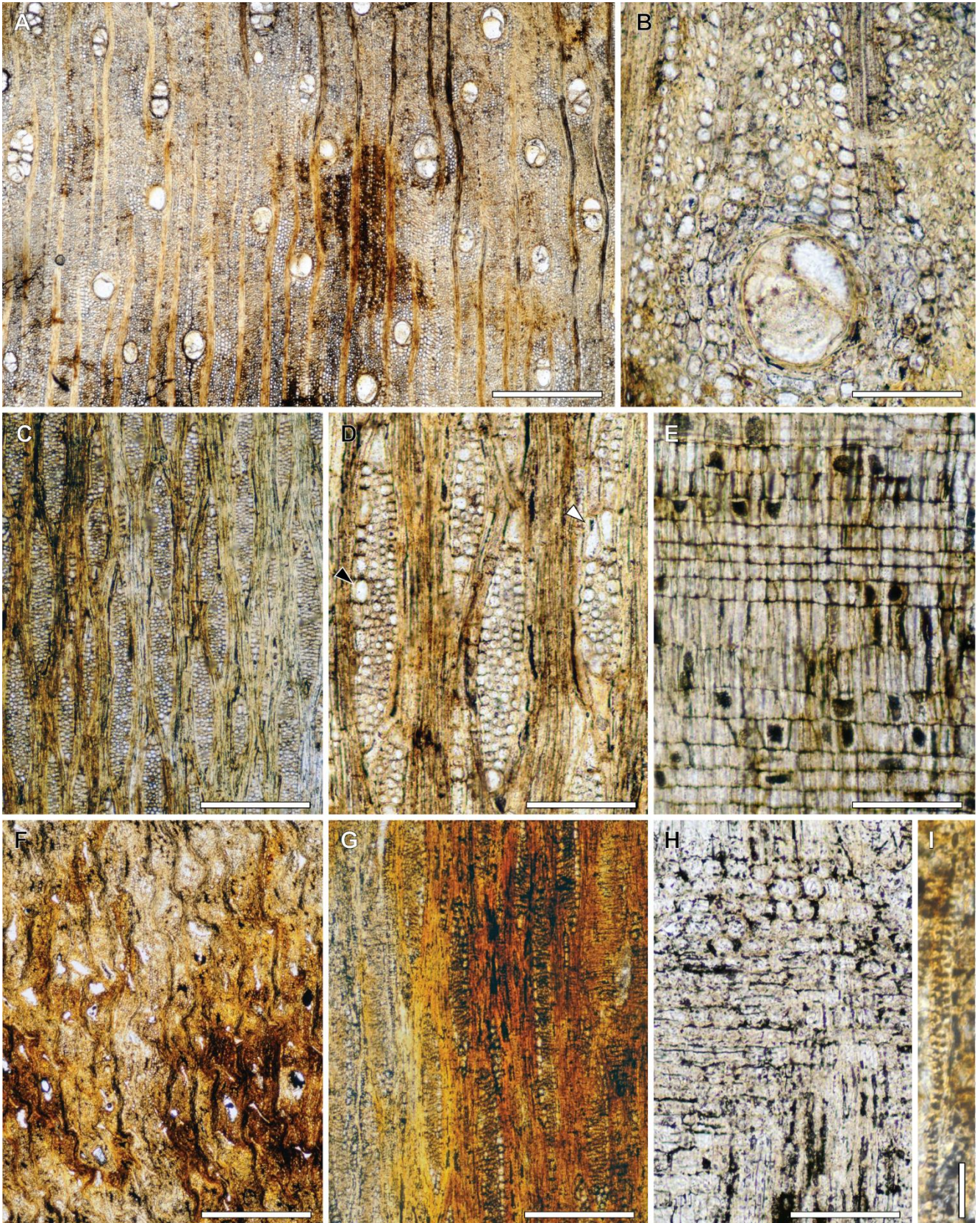
The two most determinant features to find a modern relative to our specimens are the presence of diffuse parenchyma and storied rays. No perfect match comes out on InsideWood (2004-onward) with the storiation of rays taken into consideration, which is unfortunate regarding the importance it can have in our specimens. This character apart, our fossils share most features with *Afzelia* and *Intsia* species as for most *Pahudioxylon*; these two genera rarely display diffuse parenchyma or storied rays. Soerianegara & Lemmens (1993) mention diffuse parenchyma in only a few *Afzelia* and *Adenanthera* L. species. The closest living relatives we could identify in these genera are *Afzelia africana* Pers. and *Adenanthera*

*intermedia* Merr. *Afzelia africana* is described with diffuse parenchyma but it has no storied rays, or with just a faint tendency. *Adenanthera intermedia* has crystalliferous parenchyma, sometimes diffuse, marginal parenchyma, 1-3-seriate homocellular rays, but also no storied ray structure.

*Cassia* are pantropical and subtropical trees growing at low altitude (Ali 1973; Hou *et al.* 1996). *Cassia fistula* is a tropical drought-resistant tree probably native from the Indian region. It grows in dry to mixed deciduous forests at lower altitudes, sometimes up to 1200 m of altitude (Sam *et al.* 2004), with an average annual temperature of 25 °C and annual rainfall 500-2700 mm (Ali 1973; Hou *et al.* 1996; Orwa *et al.* 2009). *Afzelia* are tropical trees mostly present in Africa at low altitude up to 400 m of altitude (Ali 1973; Hou *et al.* 1996; Orwa *et al.* 2009), growing in mixed deciduous and dry evergreen forests, on well-drained soils and in periodically inundated lowlands (Soerianegara & Lemmens 1993). *Afzelia africana* is tolerant to a wide range of climate from humid to dry forests, but is essentially found in the wooded savanna / dense dry forests borders and in semi-deciduous forests up to 1400 m of altitude. It can also occur in lowland rainforests, dry forests, gallery forests, periodically inundated areas and savannas but mostly needs annual rainfall of more than 900 mm (African Regional Workshop 1998; Orwa *et al.* 2009; Gérard & Louppe 2011)

*Adenanthera* are tropical Asian and Australian trees growing in evergreen to dry deciduous rainforests, and also in open savanna up to 700 m of altitude (Sosef *et al.* 1998). *Adenanthera intermedia* grows commonly in understory of evergreen to dry deciduous rainforests. It can also be found in open savanna-like vegetation (Nielsen 1992; Tropical Plants Database 2020).





**Figure 7.** *Artocarpoxylon informe* n. sp. (A-E): **A**, Ts, Sparse vessels, vascentric parenchyma sometimes aliform, mostly without any particular arrangement; **B**: Ts, vascentric parenchyma; **C**, Tls, 1-6 seriate rays



with upright marginal cells; **D**, Tls, 1-6 seriate rays with sheath cells (black arrow) and end-to-end fusions (white arrow); **E**, Rls, heterocellular sometimes appearing with upright and procumbent cells mixed due to sheath cells and fusions. *Anisopteroxylon cf. garoense* (Chowdhury) Prakash & Tripathi (**F-I**): **F**, Ts, strongly compressed wood, poorly distinguishable vessels, seemingly mainly solitary; **G**, Tls, 1-7 seriate rays with continuous sheath cells all around multiseriate rays; **H**, Rls, heterocellular rays sometimes appearing mixed due to sheath cells; **I**, Tls, tracheid. Scale bars: A, F, 1 mm; B, D-E, H, 200  $\mu$ m; C, G, 500  $\mu$ m; I, 50  $\mu$ m.

Family MORACEAE Gaudich.I

Genus *Artocarpoxylon* Prakash & Lalitha 1978

***Artocarpoxylon informe* n. sp.**

(Fig.7; A-E)

DESIGNATED HOLOTYPE - MNHN.[under registration]

REPOSITORY – Muséum national d'Histoire naturelle, Paris

ETYMOLOGY - “*Informe*” in Latin means “shapeless” and refers to the parenchyma of this specimen which is without clear layout around vessels

MATERIAL - MNHN.[under registration]; field number: NAT17-2.

AGE - upper lower to lowermost middle Miocene

LOCALITY - Kalewa Township, Sagaing Region, Myanmar

DIAGNOSIS - Wood diffuse-porous. Growth ring absent. Vessel solitary as well as in radial multiple, evenly distributed, oval, scattered, 80-300  $\mu$ m diameter (small to large). Tylose present. Simple perforation plates. Vessel pits alternate, small. Parenchyma diffuse and vasicentric, poorly delimited, seemingly aliform in places. Rays 1-6 seriate, uniseriate homocellular, multiseriate heterocellular. Sheath cells present. Fibres non-septate, thin-to-thick walled.

DESCRIPTION -

Wood diffuse-porous. *Growth rings* absent. *Vessels* solitary (70%) as well as in groups of 2 to 6, evenly distributed (Fig. 7A), oval, 0-8 per mm<sup>2</sup> (average: 3); tangential diameter 85-300  $\mu$ m (average: 180  $\mu$ m). Tyloses present (Fig. 7A, C). Vessel elements 130-430  $\mu$ m (average: 260  $\mu$ m) long. Perforation plates simple. Vessel pits alternate, 3-9  $\mu$ m diameter (mean 6  $\mu$ m). *Parenchyma* apotracheal and paratracheal;

apotracheal parenchyma diffuse and abundant (Fig. 7A, B); paratracheal vasicentric or aliform on several sheath of cells with no distinct limit between parenchyma and fibres (Fig. 7A, B); parenchyma cells 45-160  $\mu\text{m}$  high (average: 90  $\mu\text{m}$ ), 10-45  $\mu\text{m}$  wide (average: 25  $\mu\text{m}$ ) in tangential section; 4-8 cells per parenchyma strands. Rays 1- to 6- seriate, mostly 5-seriate (Fig. 7C, D), non-storied, 4-7 rays per mm (average: 5), 190-950  $\mu\text{m}$  (average: 480  $\mu\text{m}$ ) or up to 50 cells high with end-to-end fusion possible (Fig. 7D), 1-seriate and some 2-seriate rays made of upright cells, other multiseriate rays heterocellular made of procumbent cells with 1-4 upright marginal cells (Fig. 7E). Some sheath cells present, sometimes much bigger and longer than other ray cells (Fig. 7D). Fibres non-septate, 6-30  $\mu\text{m}$  (average: 15  $\mu\text{m}$ ) wide, thin-to-thick walled with visible lumen sometimes quite wide. *Secretory canals* absent.

#### DISCUSSION -

This specimen is characterized by (1) diffuse-porous wood, (2) scattered vessels, (3) up to 6 seriate and heterocellular rays, (4) diffuse and vasicentric parenchyma, (5) no growth rings, (6) abundant tylose. These features are not frequently combined all together and are only found in Tetramelaceae and Moraceae. Tetramelaceae are only represented by two extant monospecific genus (*Tetrameles* with *T. nudiflora* R.Br. and *Octomeles* with *O. sumatrana* Miq.) and one fossil species, *Tetrameleoxylon prenudiflora* (Lakhanpal & Verma 1966). They display mostly solitary vessels, evenly distributed, paratracheal and aliform parenchyma, 1-6 seriate heterocellular rays with some sheath cells; by contrast to our specimen, they display growth rings, no tylose, parenchyma strands and storied fibres. Fossil Moraceae are mainly represented by the genus *Ficoxylon* Kaiser which shows mostly banded parenchyma. The fossil genus *Artocarpoxylon*, also a Moraceae, displays a close affinity to our specimen as it shows no growth rings, mostly solitary vessels, tylose, vasicentric to aliform parenchyma, 1-6 seriate heterocellular rays and some sheath cells. But it sometimes displays horizontal latex tubes, which are absent in our specimen (Prakash & Lalitha 1978). 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 (Appendix 5): *A. kartikcherraensis* Prakash & Lalitha and *A. deccanensis* Mehrotra, Prakash & Bande. They strongly resemble our fossil with some differences: both have no diffuse parenchyma and have radial latex tubes in some rays; the first has more scattered rays and the latter has smaller and more numerous vessels (Prakash & Lalitha 1978; Mehrotra *et al.* 1984). Due to these differences, we assign our specimen to a new species: *Artocarpoxylon informe* n. sp.

We found no clear resemblance between our specimen and extant Tetramelaceae. Most Moraceae display banded parenchyma, including *Ficus*; few have no crystals (less than 25% on InsideWood 2004-onward). *Artocarpus* J.R.Forst. & G.Forst. is the only Moraceae genus without crystals nor parenchyma bands. Three *Artocarpus* species have sometimes no canals: *Artocarpus chama* Buch.-Ham.; *A. hirsutus* Lam. and *A. nitidus* Trecul. These three species are very similar but *A. hirsutus* is described without sheath cells; the presence of sheath cells and canals in *A. chama* is also unclear and varies among publications (Pearson & Brown 1932; Purkayastha *et al.* 1976; Singh *et al.* 2017). *Artocarpus* are Asian tropical trees growing in everwet climates or with short dry seasons. In evergreen forests and in areas with mild monsoon climate, usually scattered in lowland dipterocarp forests below 1000 m of altitude (Lemmens *et al.* 1995; Berg *et al.* 2006). *Artocarpus nitidus* lives in evergreen forests, rarely in semi-deciduous forests or savanna woodlands. It is commonly found in mixed dipterocarp and sub-montane forests up to 1500 m of altitude, on hillsides and ridges (Lemmens *et al.* 1995; Berg *et al.* 2006; Tropical Plants Database 2020).

**Table 1.** A simplified identification key for fossil Dipterocarpaceae (based on Schweitzer 1958; Prakash & Awasthi 1970, 1971; Prakash 1973).

1 - Diffuse canals or in short lines	
2 - Small vessels.....	<i>Vaterioxylon / Vaticoxylon</i>
2' - Big vessels	
3 - Diffuse and small canals, sheath cells abundant.....	<i>Anisopteroxylon</i>
3' - Canals in short lines, solitary vessels.....	<i>Dipterocarpoxyton</i>
1' - Canals in long lines	
2 - Solitary vessels, tracheid fibers.....	<i>Dryobalanoxyton</i>
2' - None of these combined.....	<i>Shoreoxylon / Hopenium</i>

#### Family DIPTEROCARPACEAE Blume

Genus *Anisopteroxylon* (Ghosh & Kazmi) Poole 1993

#### ***Anisopteroxylon cf. garoense* (Chowdhury) Prakash & Tripathi 1970**

(Fig. 7; F-I)

*Dipterocarpoxyton garoense* - Chowdhury, 1938

*Anisopteroxylon garoense* - Prakash & Tripathi, 1970: 186 (Assam)

HOLOTYPE - Repository not mentioned - specimen No. G. S. I. 16502

MATERIAL - MNHN.[under registration]; field number: 17FN07.

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> (average: 6) (Fig. 7F); tangential diameter 80-230 µm (average: 150 µm). Tyloses present. Vessel elements 130-290 µm long (average: 220 µm). Perforation plates simple. Vasicentric tracheids present (Fig. 7I). *Parenchyma cells* probably paratracheal and/or diffuse; without mineral inclusions. *Rays* 1 to 7- seriate, mostly 6- to 7- seriate (Fig. 7G), 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 sheath cells (Fig. 7G) which may appear as a mix of procumbent and upright cells in radial section (Fig. 7H), 2 to 3- seriate rays with over 4 rows of upright or square marginal cells, otherwise, only one row. *Fibres* non-septate, tangential diameter 9-25 µm (average: 16 µm). *Secretory canals* cannot be identified but we observed some scattered, very small pores, without 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) isolated vessels, (4) heterocellular rays, widely multiseriate, (5) continuous sheath cells, (6) vasicentric tracheids. These features suggest an affinity with modern Malvaceae and Dipterocarpaceae. 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 genera *Monotes* De Candolle and *Marquesia* Gilg (Chowdhury & Ghosh 1958). Seven fossil genera of Dipterocarpaceae have been described and their classification is mostly based on the features of extant genera (see Table 1, based on Schweitzer 1958; Prakash & Awasthi 1970, 1971; Prakash 1973). Even though our fossil has no visible canals which could be due to bad preservation and extreme compression, its big and isolated vessels, vasicentric tracheids and abundant sheath cells make it compatible with the diagnosis of the genus *Anisopteroxylon*, originally described by Ghosh & Kazmi (1958) and emended by Poole (1993). The genus *Anisopteroxylon* has only rare and scattered, often small canals (Schweitzer 1958), which is compatible with the apparent absence of canals in our specimen.



Appendix 6 presents all fossil species described as *Anisopteroxylon*. Following Den Berger (1927), the genus also includes the species *Dipterocarpoxydon goepperti* Kräusel. Indeed, all features given by Kräusel (1926) are those shared by most *Anisopteroxylon* species, including abundant sheath cells, solitary vessels and diffuse secretory canals; these features were already observed by Den Berger (1927), at a time the genus *Anisopteroxylon* did not exist. *Anisopteroxylon* was later created by Ghosh & Kazmi (1958). Schweitzer (1958) also described a specimen of *D. goepperti* and highlighted the fact it was very likely related to a modern *Anisoptera*. As a consequence, we transfer *D. goepperti* into the genus *Anisopteroxylon*, and a new combination is made:

*Anisopteroxylon goeppertii* (Kräusel) n. comb.

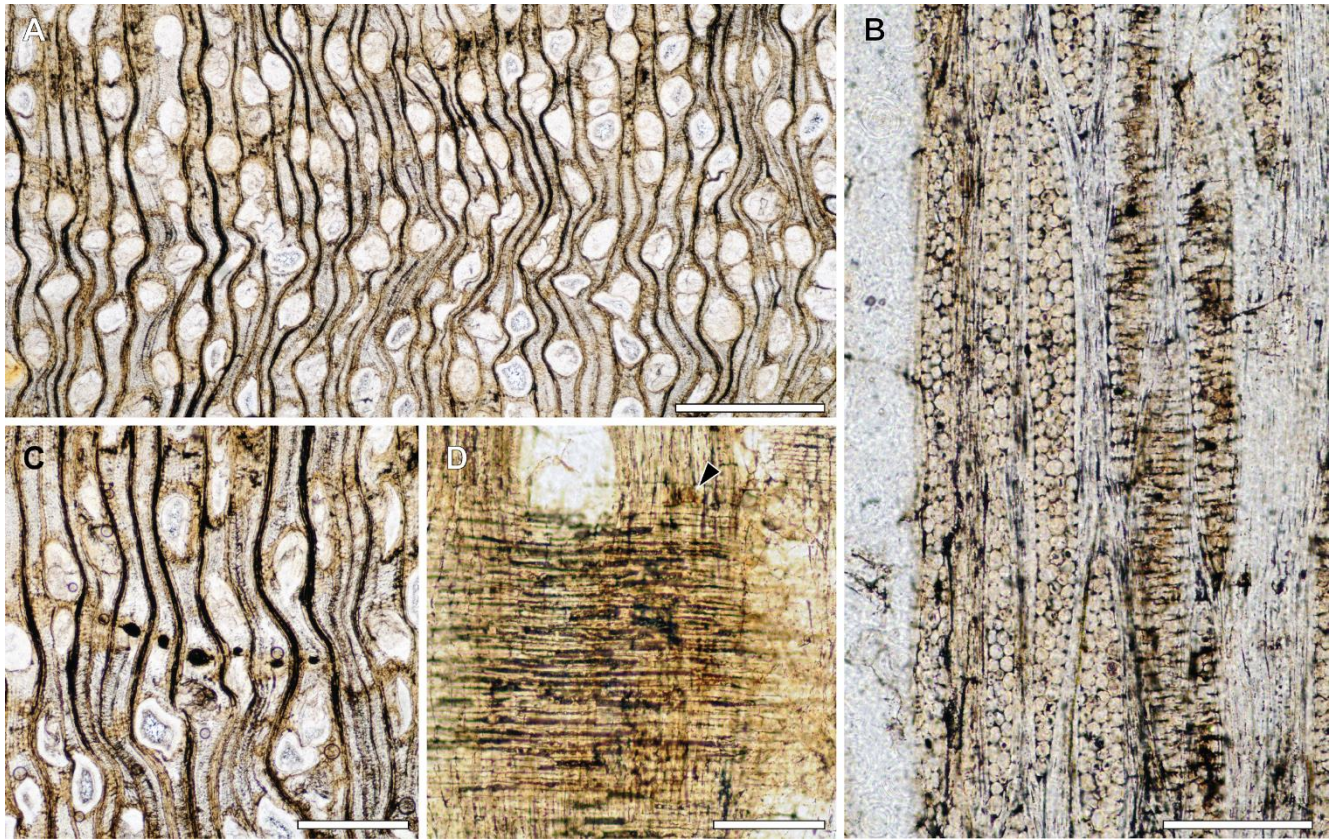
*Dipterocarpoxydon goepperti* Kräusel, 1926; pp. 4-6; pl. 1, fig. 3-4; pl. 2, fig. 5-6

*Dipterocarpoxydon goepperti* Schweitzer, 1958; pp. 16-17; ill. 3; pl. 2, fig. 2-3

Our specimen displays many features of *A. garoense* from the upper Miocene of India, including similar ray size, vessel diameter and density, and the presence of identical continuous sheath cells. *A. oblongoides* Yadav and *A. surmaensis* Prasad, Agarwal & Mandaokar also share some of these features but the former has long tangential lines of canals of the same size as vessels and the latter has narrower rays. *Anisopteroxylon jawalamukhi* Ghosh & Ghosh can also be a candidate but seems to have longer rays (up to 1950 µm). Due to the relatively poor state of preservation of our specimen, we name it *Anisopteroxylon* cf. *garoense*.

Among extant Dipterocarpaceae with continuous sheath cells, *Anisoptera costata* Korth. (synonym: *A. oblonga* Dyer) and *Anisoptera scaphula* (Roxb.) Kurz are the most anatomically close to our specimen, and display the same wide rays as well as uniform and rare uniseriate rays and isolated vessels. These two species are hardly distinguishable from each other based on xylotomy (Chowdhury & Ghosh 1958). *Anisoptera* is a genus of south-east Asian trees, but absent in India, living in evergreen or semi-evergreen forests; in mixed dipterocarp, mixed swamp and heath forests; on well-drained soil or in peat swamps. Rarely above 1000 m of 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 forest but grows well along rivers and streams, at up to 700 m of altitude. (Ashton 1982; Smitinand *et al.* 1990; Soerianegara

& Lemmens 1993; Sam *et al.* 2004; Nguyen *et al.* 2017). *A. scaphula* grows in semi-evergreen and evergreen dipterocarp forests on foothills (Ashton 1982; Soerianegara & Lemmens 1993; Ly *et al.* 2017c).



**Figure 8.** *Dipterocarpoxyton fugax* n. sp.: **A**, Ts, mostly solitary vessels and vasicentric parenchyma; **B**, Tls, 2-4 seriate homo- to heterocellular rays; **C**, Ts, short tangential line of secretory canals, smaller than vessels, embed in parenchyma band; **D**, Rls, an example of heterocellular ray with one line of upright marginal cells (arrow). Scale bars: A, 1 mm; B, D, 200 µm; C, 500 µm.

Genus *Dipterocarpoxyton* (Holden) Den Berger 1927

***Dipterocarpoxyton fugax* n. sp.**

(Fig. 8; A-D)

DESIGNATED HOLOTYPE - MNHN.[under registration]

REPOSITORY – Muséum national d’Histoire naturelle, Paris

ETYMOLOGY – *Fugax* means “shy” in latin and relates to the small canals of the specimen, which are hard to find.

MATERIAL - MNHN.[under registration]; field number: 17FN09

LOCALITY - Kalewa Township, Sagaing Region, Myanmar

AGE - upper lower to lowermost middle Miocene

DIAGNOSIS - Wood diffuse-porous. Growth rings indistinct. Vessels mostly solitary, numerous, average diameter between 170-230  $\mu\text{m}$ , filled with tylose. Perforation plate simple. Vasicentric tracheids present. Parenchyma visible, vasicentric, sometimes aliform or in thin tangential bands crossing vessels and rays. Rays 1-4 seriate, up to 1200  $\mu\text{m}$ , end-to-end fusion possible. Homocellular or heterocellular with one upright marginal cell, rare sheath cells. Fibres non septate. Secretory canals diffuse or in short tangential lines of 2-7, small.

DESCRIPTION -

*Wood* diffuse-porous. *Growth rings* indistinct or absent. *Vessels* mostly solitary (>90 %) (Fig. 8A), round to oval, 5-13 per  $\text{mm}^2$  (average: 8); tangential diameter 140-260  $\mu\text{m}$  (average: 200  $\mu\text{m}$ ). Tyloses present (Fig. 8A, C). Vessel elements 140-290  $\mu\text{m}$  (average: 210  $\mu\text{m}$ ) long. Perforation plates simple. Vessel pits alternate, 3-6  $\mu\text{m}$  of diameter (average: 5  $\mu\text{m}$ ). *Vasicentric tracheids* present. *Parenchyma* paratracheal vasicentric, sometimes aliform or confluent; apotracheal as thin tangential bands crossing several rays that can contain secretory canals (Fig. 8A, C); parenchyma cells 75-130  $\mu\text{m}$  long (average: 110  $\mu\text{m}$ ) 10-30  $\mu\text{m}$  wide (average: 20  $\mu\text{m}$ ) in tangential section; without crystals. *Rays* 1- to 4-seriate (mainly 3) (Fig. 8B), slight tendency to storied structure, 6-9 rays per mm (average: 8), 320-1140  $\mu\text{m}$  (average: 540  $\mu\text{m}$ ) or 15-50 cells high, homocellular or weakly heterocellular with 1 upright or square cell at the ends (Fig. 8D); made of mainly procumbent cells and very few sheath cells, end-to-end fusion possible but not frequent (Fig. 8B). *Fibres* non-septate, 9-21  $\mu\text{m}$  (average: 15  $\mu\text{m}$ ) wide. *Secretory canals* appear diffuse and quite sparse or in bands seemingly short (7 canals or less) surrounded by parenchyma (Fig. 8C), 40-90  $\mu\text{m}$  of diameter (average: 60  $\mu\text{m}$ ).

DISCUSSION -

Our fossil has (1) vertical secretory canals in short tangential lines or diffuse, (2) mostly solitary and numerous vessels, (3) vasicentric tracheids, (4) long and narrow rays (Fig. 8); these combined features are only found in the Dipterocarpaceae family. According to the identification key of fossil Dipterocarpaceae (Table 1), and despite the poor preservation of the sample (high compression, and poorly preserved cell

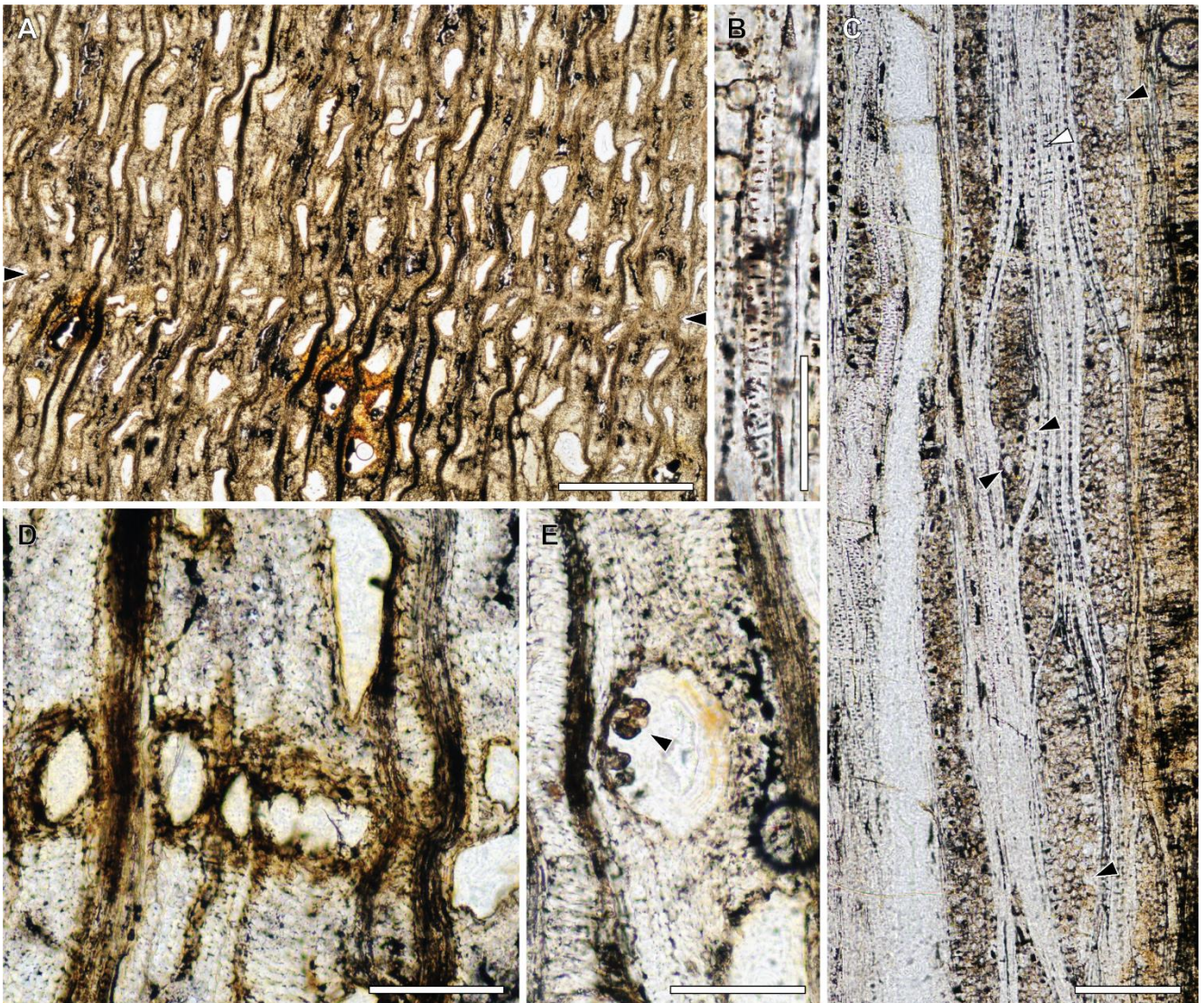
walls), some of its features are diagnostic of the genus *Dipterocarpoxydon* (mostly solitary vessels), isolated or small lines of secretory canals).

Homocellular to weakly heterocellular rays are found in several *Dipterocarpoxydon* species even though most of them are heterocellular (Appendix 7). Four of them share most characteristics with our fossil specimen but do not perfectly match its diagnostic features: *Dipterocarpoxydon pondicherriense* Awasthi has more frequent canals, more tailed rays and less abundant parenchyma; *Dipterocarpoxydon kalaicharporensis* Eyde has longer, more tailed rays, less vessels and its canals are not described; *Dipterocarpoxydon perforatum* Schweitzer has less parenchyma and crystalliferous rays; *Dipterocarpoxydon bolpurensis* Ghosh & Roy has bigger canals and longer rays. No *Dipterocarpoxydon* seem to display homocellular rays with numerous big vessels and very small canals. Therefore, our specimen is attributed to a new species: *Dipterocarpoxydon fugax* n. sp.

Among extant Dipterocarpaceae, our specimen shares all the diagnostic features of the genus *Dipterocarpus* (Den Berger 1927; Metcalfe & Chalk 1950; Chowdhury & Ghosh 1958; Schweitzer 1958; Prakash 1973; Awasthi 1980; Soerianegara & Lemmens 1993). *Dipterocarpus zeylanicus* Thwaites has a similar vessel density, short rays with end-to-end fusion time to time, and some thin banded apotracheal; *Dipterocarpus gracilis* Blume has a similar vessel density very small canals as well as thin rays; *Dipterocarpus confertus* Slooten has a similar density of vessels, few parenchyma, discrete canals but larger and higher rays; *Dipterocarpus alatus* Roxb. shares less common features but has short rays and numerous small canals. Thin rays, as observed in our specimen, are rare in extant *Dipterocarpus* and generally absent in these four species. According to Soerianegara & Lemmens (1993), *Dipterocarpus* often hybrids naturally which could make it even more complicated to attribute one specimen to a precise species if mixed characters appear. This, added to strong resemblances within *Dipterocarpus* wood species, makes it impossible to attribute a specific NRL to our fossil specimen. *Dipterocarpus* are common in evergreen, semi-evergreen forests or savannah up to 1400 m of altitude. (Ashton 1982; Soerianegara & Lemmens 1993). *D. zeylanicus* grows in lowland wet evergreen forests or semi-evergreen moist forests up to 900 m of altitude (Gamble 1902; Ashton 1998); *D. gracilis* is mainly found in lowland seasonal semi-evergreen, mixed dipterocarp or evergreen dipterocarp forests on well-drained soils, but also in valleys and foothills up to 800 m of altitude; it occurs rarely in everwet areas (Ashton 1982; Soerianegara & Lemmens 1993; Ly *et al.* 2017d; Tropical Plants Database 2020). *D. confertus* grows in mixed dipterocarp forests, on low hills and undulated land



below 800 m (Ashton 1982; Soerianegara & Lemmens 1993; Kusumadewi *et al.* 2019). *D. alatus* is common along rivers, in evergreen and semi-evergreen dipterocarp forests in foothills and valleys up to 500 m of altitude. It is also found in dipterocarp monsoonal forests and dry deciduous forests; it favors humid soils and tolerates flooding or heavy rainfall. It grows within annual rainfall of 110-2200 mm and annual temperature of 20-30 °C (Smitinand *et al.* 1990; Soerianegara & Lemmens 1993; Jøker & Luu 2002; Sam *et al.* 2004; Orwa *et al.* 2009; Ly *et al.* 2017b).



**Figure 9.** *Dryobalanoxylon indicum* (Ramanujam) Awasthi: **A**, Ts, Vessel arrangement, mostly solitary, and long tangential line of secretory canals embed in parenchyma band (between arrows); **B**, Tls, tracheid fibre; **C**, Tls, 1-6 seriate rays with some sheath cells (black arrows), vasicentric tracheids and tracheid fibres

(white arrow); **D**, Ts, detail of secretory canals; **E**, Ts, budding of tyloses (arrow). Scale bars: A, 1 mm; B, 100 µm; C-E, 200 µm.

Genus *Dryobalanoxyton* Den Berger 1923

***Dryobalanoxyton indicum* (Ramanujam) Awasthi 1971**

(Fig. 9; A-E)

*Dipterocarpoxyton indicum* - Ramanujam, 1956

*Dryobalanoxyton indicum* – Awasthi, 1971: 225

HOLOTYPE - Birbal Sahni Institute of Paleobotany - specimen No. 6964

MATERIAL - MNHN.[under registration]; field number: 17FN20

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 due to compression (Fig. 9A), 3-8 per mm<sup>2</sup> (average: 5); tangential diameter 130-260 µm (average: 180). Tylose present (Fig. 9E). Vessel elements 230-610 µm long (average: 450). Perforation plates simple. Vessel pits alternate. *Tracheids fibres* and *vasicentric tracheids* present (Fig. 9B, C). *Parenchyma cells* apotracheal and paratracheal; apotracheal diffuse, around axial canals forming more or less continuous bands, paratracheal vasicentric; parenchyma cells 80-100 µm long (average: 90), 15-30 µm wide (average: 20) wide; crystals absent. *Rays* 1- to 6- seriate, mainly 4- to 5-seriate, rare uniseriate (Fig. 9C), 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), sheath cells present (Fig. 9C). *Fibres* thick-walled, non-septate, 10-22 µm wide (average: 16). *Canals* in clear long tangential lines sometimes interrupted by vessels (Fig. 9A, D), but also in shorter lines or even rarely diffuse, numerous and surrounded by parenchyma, tangential diameter 40-120 µm (average: 80).

DISCUSSION -

The strong compression of this specimen makes it difficult to precisely assess vessel and canal diameters. This specimen is characterized by (1) diffuse-porous wood, (2) exclusively simple perforation plates, (3) large and solitary vessels, (4) normal vertical secretory canals in short lines, (5) vasicentric tracheids and



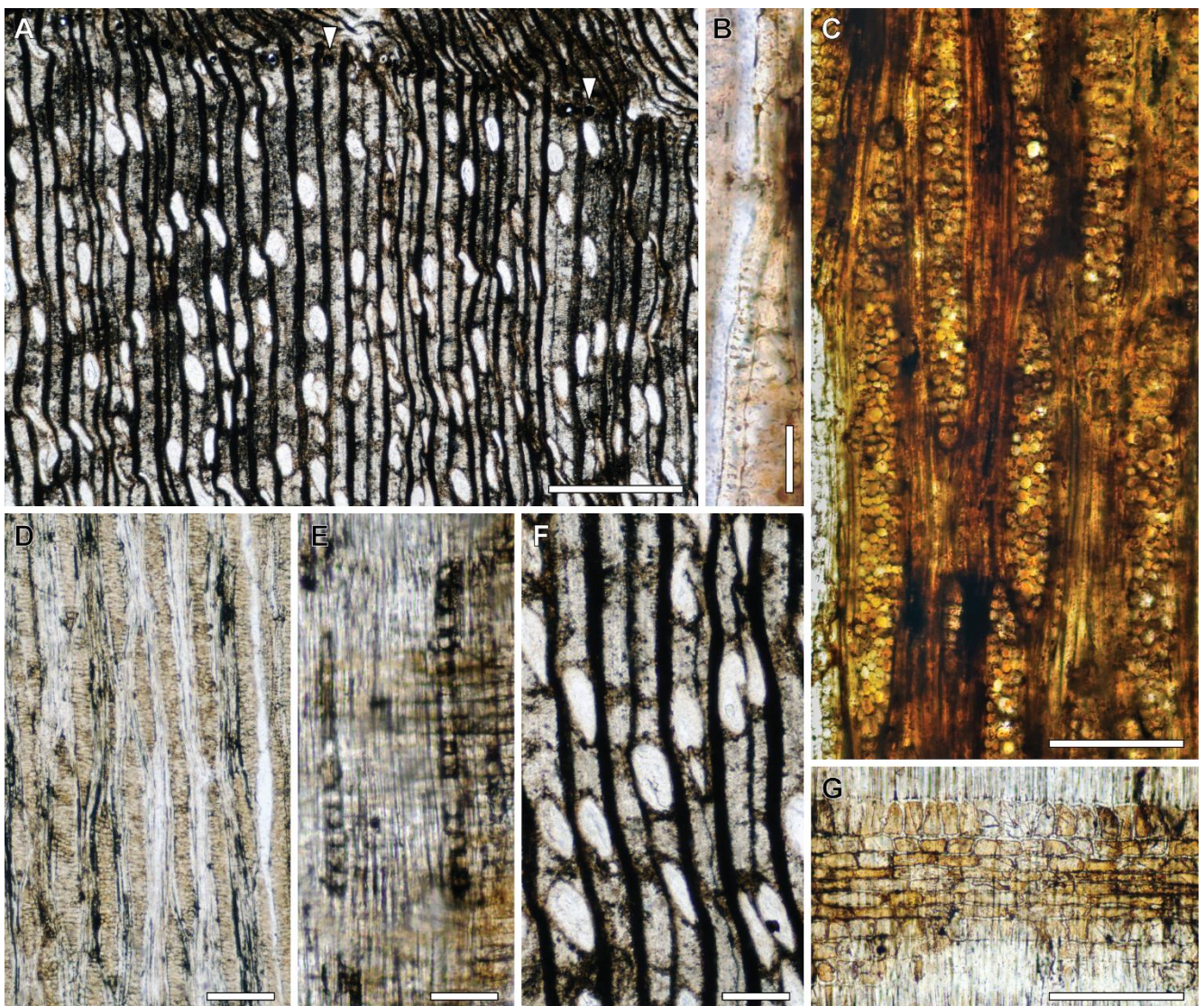
tracheid fibres, (6) heterocellular rays, often higher than 1 millimeter, (7) abundant parenchyma. These combined features indicate an affinity with modern Dipterocarpaceae, which are often characterized by secretory canals and vasicentric tracheids.

Solitary vessels and vascular tracheid fibres are diagnostic features of the fossil genus *Dryobalanoxylon*. A comparison with *Dryobalanoxylon* species (Appendix 8) shows that most of them have thin rays (up to 4-seriate maximum). Two species have wider rays and are comparable to our fossil with only few differences: *D. bogorense* Srivastava & Kageromi, has shorter rays (up to 1200 µm against 1530 µm), no sheath cells and possibly silica in parenchyma. *D. indicum* from the Tertiary of India has sheath cells, but it has higher (up to 1900 µm) and thinner rays (mainly 3-4-seriate) and tails of upright ray cells up to 15 cells (against 9). Considering the state of preservation of our specimen, we do not consider that these differences are enough to describe a new species. We thus attribute this fossil to *Dryobalanoxylon indicum* as it can have very long rays and clear sheath cells. The main differences between our fossil specimen and the holotype of *D. indicum* is the smaller density of vessels, sometimes slightly broader rays and shorter maximum rays length.

Most *Dryobalanoxylon* specimens are recorded in Indonesia, but some are also found in Vietnam, Cambodia, as well as three species found in India (Srivastava & Kageromi 2001). Our fossil is the first record of *Dryobalanoxylon* in Myanmar. Comparison with some species of both genera of *Dipterocarpus* and *Dryobalanops* C.F.Gaertn. (which is exclusively present in south-east Asia and absent in India and Myanmar; Maury-Lechon & Curtet 1998; Ghazoul 2016) show that our specimen resembles closely to *Dryobalanops keithii* Sym. and *Dryobalanops oblongifolia* Dyer for its ray width (up to 6- or 7-seriate), shape of rays, and canals distribution (long bands sometimes interrupted by vessels). As species of *Dipterocarpus* and *Dryobalanops* easily produce hybrids and mixed characters can be found (Chowdhury & Ghosh 1958; Soerianegara & Lemmens 1993), some resemblance with *Dipterocarpus turbinatus* C.F.Gaertn. is noticeable, tracheid fibres apart, as it displays heterocellular rays of two sizes with more than 30% of uniseriate rays, sheath cells, large and solitary vessels. Its axial canals are also usually gathered in long, almost- continuous bands, as found in our fossil.

*Dryobalanops* are south-east Asian tropical canopy trees growing on hillsides or along streams, at up to 800 m of altitude; they are also present in lowland dipterocarp forests, mixed peat-swamp forests, and sometimes also found in heath forests (Ashton 1982; Soerianegara & Lemmens 1993). *Dryobalanops keithii*

always occurs near water on lowlands and foothills up to 250 m of altitude (Ashton 1982; Soerianegara & Lemmens 1993; Randi *et al.* 2019). *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). *Dipterocarpus turbinatus* lives in moist tropical evergreen, semi-evergreen or deciduous forests as well as in savannas up to 1000-1100 m of altitude; it is also found in gallery forests and prefers high humidity soils. *D. turbinatus* is often associated with *D. costatus*, *D. retusus* and *D. gracilis* (Smitinand *et al.* 1990; Soerianegara & Lemmens 1993; Ly *et al.* 2017a).



**Figure 10.** *Shoreoxylon cf. deomaliense* Prakash & Awasthi: **A**, Ts, vessels and long tangential line of secretory canals embed in parenchyma bands (arrows); **B**, Tls, vasicentric tracheid; **C-D**, Tls, long 1-6 seriate rays with end-to-end fusion; **E**, Rls, crystals in parenchyma; **F**, Ts, detail of vasicentric to aliform

parenchyma, possibly also diffuse parenchyma; **G**, Rls, heterocellular ray with upright marginal cells. **A**, **F**, transversal sections; **B-D**, Tls, tangential longitudinal sections; **E**, **G**, Rls, radial longitudinal section. Scale bars: A, 1 mm; B, 50 µm; C, G, 200 µm; D, F, 250 µm; E, 100 µm.

Genus *Shoreoxylon* Den Berger, 1923

***Shoreoxylon cf. deomaliense* Prakash & Awasthi 1971**

(Fig. 10; A-G)

TAXONOMIC HISTORY -

*Shoreoxylon deomaliense* - Prakash & Awasthi, 1971: 219 (Deomali)

HOLOTYPE - Birbal Sahni Institute of Paleobotany Museum, India, specimen No. 34050

MATERIAL - MNHN.[under registration]; field number: NAT17-4

LOCALITY - Kalewa Township, Sagaing Region, Myanmar

AGE - upper lower to lowermost middle Miocene

DESCRIPTION -

Wood diffuse-porous, showing lateral compression. *Growth rings* marked by tangential canal lines. *Vessels* about 90% solitary (Fig. 10A), 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). Tylose present. Vessel elements 140-460 µm (average: 330 µm) long. Perforation plates simple. Vessel pits alternate. *Vasicentric tracheids* present (Fig. 10B). *Parenchyma* apotracheal diffuse; paratracheal vasicentric to aliform, sometimes confluent (Fig. 10F); parenchyma cells 50-90 µm long (average: 70 µm), 15-35 µm wide (average: 25 µm) in tangential section; sometimes crystalliferous (Fig. 10E). *Xylem rays* 1- to 6- seriate (mainly 4) (Fig. 10C), uniseriate rare, non-storied, 5-10 rays per mm (average: 8), 270-1600 µm (average: 650 µm) or up to 40 (even 70) cells high, heterocellular made of procumbent cells with 1-4 or more upright cells at the ends (Fig. 10G), fusion end-to-end possible resulting in very high rays (Fig. 10D). *Fibres* non-septate, 5-19 µm (average: 12 µm) wide, thick walled. *Secretory canals* in long tangential bands surrounded by parenchyma (Fig. 10A), 30-100 µm in tangential diameter (average 60 µm).

DISCUSSION -

This specimen is characterized by (1) diffuse-porous wood, (2) almost exclusively solitary vessels, (3) crystalliferous and mostly aliform parenchyma, (4) 1-6 seriate heterocellular rays, (5) long tangential lines of horizontal secretory canals, (6) vasicentric tracheids. As for our previous specimens, these features are diagnostic of the Dipterocarpaceae family. The specimen has long tangential lines of secretory canals which is only found in fossil genera *Dryobalanoxylon*, *Shoreoxylon* and *Hopenium* Awasthi. Solitary vessels are found in all of these genera, but they are exclusively solitary in *Dryobalanoxylon*; however, as no tracheid fibre has been clearly and undoubtedly identified in this specimen, an attribution to this fossil genus is inadequate. *Hopenium* species display upright ray cells in the middle of rays, which is not the case in our fossil. Therefore, our specimen appears at first sight closer to the genus *Shoreoxylon*.

Among *Shoreoxylon* with mostly solitary vessels, aliform parenchyma, and crystalliferous parenchyma (Appendix 9), *Shoreoxylon tipamense* Prakash & Awasthi differs from our specimen with longer ray tailed and less abundant vessels; *Shoreoxylon indicum* Awasthi has much more parenchyma, sometimes in bands; our specimen is closer to *Shoreoxylon deomaliense* though it has bigger canals and wider rays.

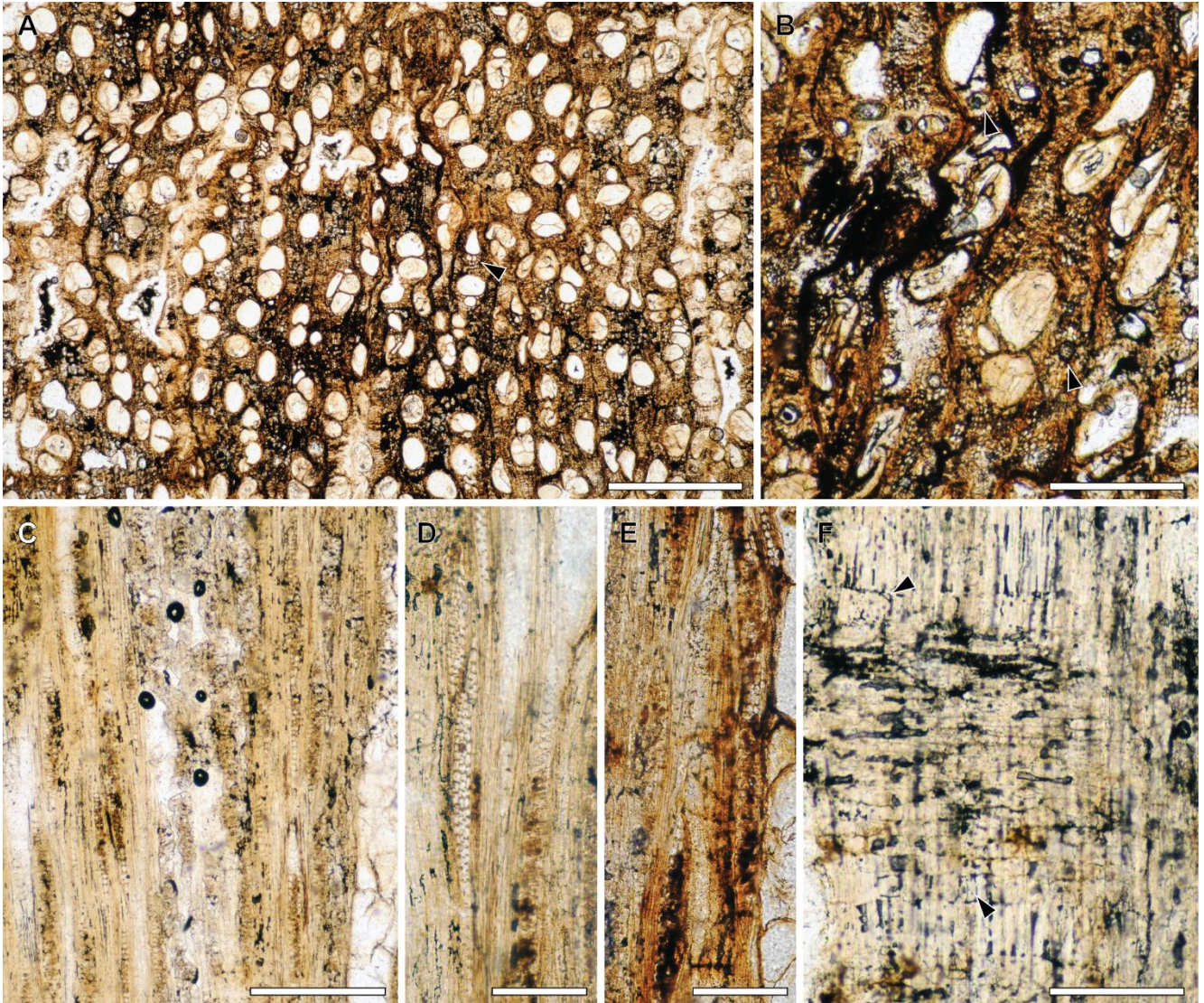
We also compared our specimen to *Dryobalanoxylon* species (Appendix 8), arguing that the presence of tracheid fibres is not a very adequate diagnostic feature considering the poor preservation of our specimen. Our specimen shares similarities with *Dryobalanoxylon indicum* but has no sheath cells and crystalliferous parenchyma. Its closest affinity is with *Dryobalanoxylon bogorensis* from the Pliocene of Java; main differences include the size and number of vessels, but our observations likely underestimate vessel diameter and overestimate their density due to the compression of our specimen. Rays are also slightly longer in our specimen (270-1600 µm long against 500-1200 µm for *D. bogorensis*). Srivastava & Kageromi (2001) mention possible silica bodies in the parenchyma of *D. bogorensis*; our specimen seems to have crystals in parenchyma, but it is impossible to detail their nature. Due to the uncertainty related to the preservation of the specimen, we however consider that it is not possible to state about the presence or absence of tracheid fibres and decide to put this fossil under the genus *Shoreoxylon* with the name: *Shoreoxylon cf. deomaliense*.

Among extant Dipterocarpaceae, some *Shorea* display big vessels, crystalliferous parenchyma, no storied elements, abundant parenchyma and tylose, as observed in our specimen, but only few have solitary vessels. Our specimen also shares features with genus *Dryobalanops* (such as solitary and numerous vessels, small canals, presence of crystals) but it has no observed tracheid fibres, sheath cells or storied tendency to

elements. Extant *Hopea* are unlikely analogues as they have upright ray cells in the middle of rays. Some extant species share similarities with our specimen *Dryobalanops keithii* displays aliform parenchyma, long tangential lines and rays sometimes up to 6-seriate; *Dryobalanops oblongifolia* and *Shorea acuminata* Dyer are also valid analogue for their long tangential bands, aliform parenchyma and ray width. The closest resemblance is with *Shorea laevis* Ridl. for the aliform parenchyma, the vessel size and density, the similar rays with small tails and few uniseriate ones.

As many other *Dryobalanops*, *Dryobalanops keithii* is a common tree in Southeast Asian mixed-dipterocarp forests, in undulating lands and hills, near water (banks or streams) and below 250 m of altitude (Ashton 1982; Soerianegara & Lemmens 1993; Randi *et al.* 2019). *Dryobalanops oblongifolia* lives in lowland mixed dipterocarp forests and in periodically inundated forests as well as in hillsides and near rivers below 600 m (Soerianegara & Lemmens 1993; Barstow 2018a). *Shorea* are tropical Asian trees growing in humid lowland areas, podzols and peat swamps, mostly below 1000 m of altitude (Ashton 1982; Soerianegara & Lemmens 1993). *Shorea acuminata* lives in well-drained undulating lands in mixed dipterocarp forests below 1000 m of altitude (Ashton 1982; Soerianegara & Lemmens 1993; Wu & Raven 2007; Barstow 2019). *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).





**Figure 11.** *Shoreoxylon cf. sumatraense* Du: **A**, Ts, vessel in groups, sometime in clusters of small vessels (arrow); **B**, Ts, long tangential lines of secretory canals (arrows) close to each other; **C-E**, Tls, 1-4 seriate rays; **F**, Rls, heterocellular ray with upright marginal cells (arrows). Scale bars: A, 1 mm; B, 330  $\mu$ m; C, 500  $\mu$ m; D-F, 200  $\mu$ m.

Genus *Shoreoxylon* Den Berger, 1923

***Shoreoxylon cf. sumatraense* Du 1988**

(Fig. 11; A-G)

TAXONOMIC HISTORY -

*Shoreoxylon sumatraense* - Du 1988b: 342

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



MATERIAL - MNHN.[under registration]; field number: 17FN12

LOCALITY - Kalewa Township, Sagaing Region, Myanmar

AGE - upper lower to lowermost middle Miocene

DESCRIPTION -

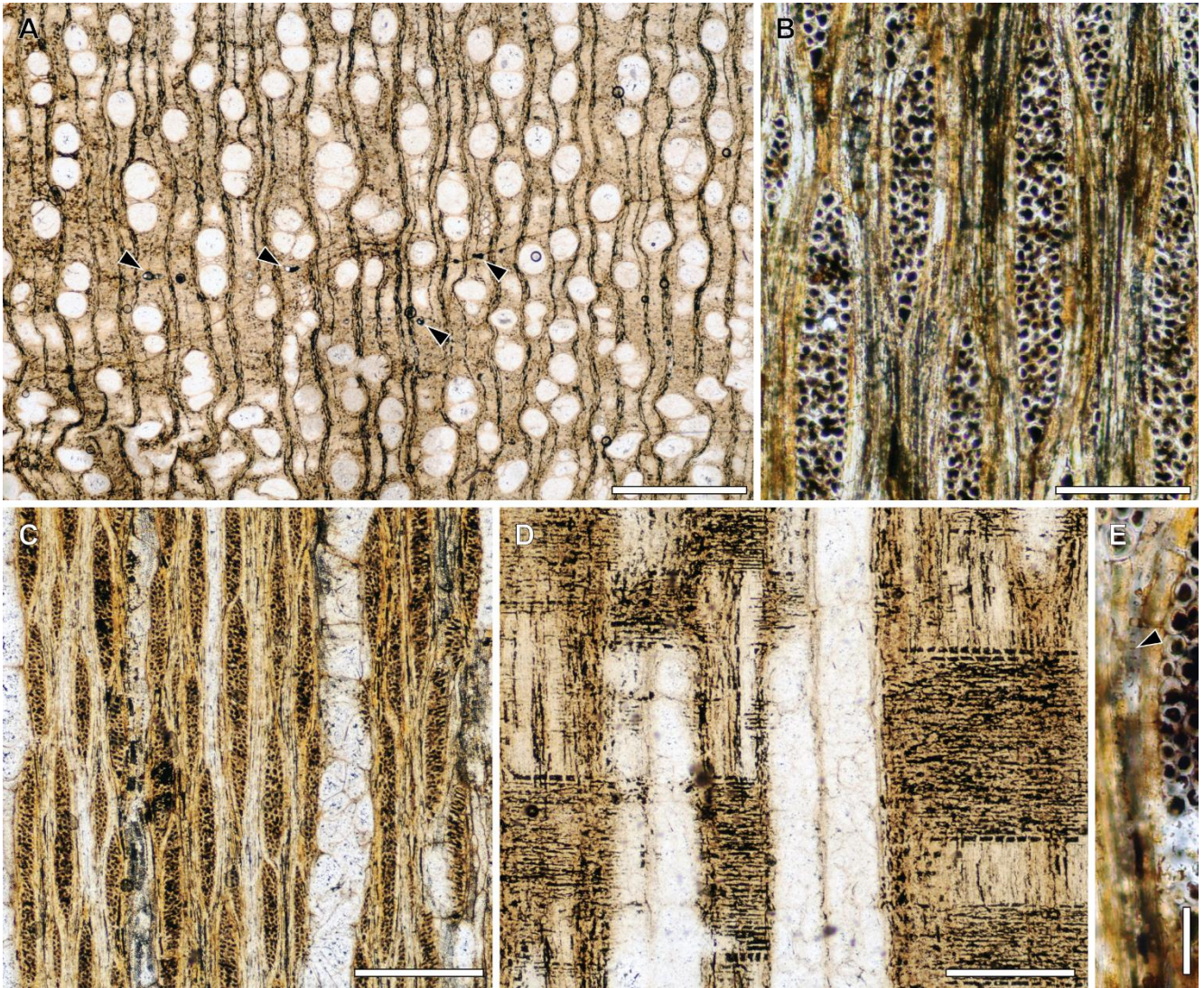
Wood diffuse-porous. *Growth rings* marked by tangential canal lines. *Vessels* 70% solitary, 30% in groups and clusters with small vessels surrounding bigger vessels (Fig. 11A), round to oval, 8-20 per mm<sup>2</sup> (average: 15); tangential diameter 80-240 µm (average: 160 µm). Tylose present (Fig. 11A, B). Vessel elements 150-570 µm (average: 350 µm) long. Perforation plates simple. Vessel pits alternate, 3-6 µm of diameter (average: 4 µm). *Vasicentric tracheids* present. *Parenchyma* at least vasicentric, maybe aliform, around canals; parenchyma cells 40-120 µm long (average: 90 µm) 10-30 µm wide (average: 20 µm) in tangential section; no crystals. *Xylem rays* usually 1- to 4- seriate (mainly 3-, rare 5-) (Fig. 11C, D, E), uniseriate quite common, non-storied, 4-8 rays per mm (average: 6), 340-1040 µm (average 620 µm) or 10-45 cells high, uniseriate mainly made of upright cells, multiseriate heterocellular made of procumbent cells with 1-4 and more (9) upright cells at the ends (Fig. 11F). Rare sheath cells occasionally present on broader rays. *Fibres* non-septate, 8-20 µm (average: 13 µm) wide, apparently thin walled. *Secretory canals* in long tangential bands surrounded par parenchyma, regularly and closely spaced (about 2 lines per mm) (Fig. 11B), 40-75 µm in tangential diameter (average: 60 µm).

DISCUSSION -

This specimen is characterized by (1) diffuse-porous wood, (2) exclusively simple perforation plates, (3) small secretory canals in long tangential bands, (4) vasicentric tracheids, (5) presence of sheath cells, (6) vessels forming groups or clusters, (7) absence of tracheid fibres other than vasicentric. The poor quality of preservation of the fossil makes our observations in tangential and transversal sections uncertain, especially regarding rays and parenchyma arrangement. Nonetheless, these features indicate an affinity with modern and fossil Dipterocarpaceae; long tangential bands of canals and grouped vessels are only compatible with extant *Shorea* and fossil genus *Shoreoxylon*. Among *Shoreoxylon*, our specimen is among the few to have a high density of vessels, closely spaced canal lines and thin rays with many uniseriate (Appendix 9). Three species share many similarities with our fossil : *S. arcotense* Awasthi has a high density of vessels and small canals but exclusively solitary and smaller vessels; *S. pachitanensis* Sukiman has close bands of canals but bigger rays and canals; *S. sumatraense* from the Quaternary of Sumatra shares most of

the main features of our specimen although it displays slightly higher rays, bigger vessels, and a storied tendency in the parenchyma which cannot be observed in our specimen; moreover, vessel clusters are described for this species, which is an important and visible trait in our specimen. The higher density and smaller vessels in our specimen could be explained by compression or environmental constraints. Thus, the only differences between our fossil and *S. sumatraense* are vessel density and size, and the presence of 5-seriate rays in our fossil. Thereby, and regarding to the state of preservation of our fossil we attribute our specimen to *Shoreoxylon cf. sumatraense*.

Du (1988b) indicates that *S. sumatraense* shares most features with extant *Shorea negrosensis* Foxw. We compared our specimen with slides and pictures (InsideWood 2004-onward) of extant *Shorea* and confirmed this close affinity. *Shorea negrosensis* grows today in the Philippines in evergreen, semi-evergreen and seasonal dipterocarp forests at low altitude (Ashton 1982; Soerianegara & Lemmens 1993; Energy Development Corporation 2020).



**Figure 12.** *Shoreoxylon glomeratum* n. sp.: **A**, Ts, Vessels sometimes in clusters, abundant parenchyma, short lines and diffuse secretory canals (arrows); **B-C**, Tls, 1-5 seriate rays; **D**, Rls, heterocellular rays with one line of upright cells; **E**, Tls, tracheid (arrow). Scale bars: A, 1 mm; B, 200 µm; C-D, 500 µm; E, 50 µm.

Genus *Shoreoxylon* Den Berger, 1923

***Shoreoxylon glomeratum* n. sp.**

(Fig. 12; A-E)

DESIGNATED HOLOTYPE - MNHN.[under registration]

REPOSITORY – Muséum National d'Histoire Naturelle, Paris

ETYMOLOGY – Named after the propensity of vessels to form groups and clusters.

MATERIAL - MNHN.[under registration]; field number: 19NAT03-1

LOCALITY - Kalewa Township, Sagaing Region, Myanmar

AGE - upper lower to lowermost middle Miocene

DIAGNOSIS - Wood diffuse-porous. Growth rings indistinct. Vessels equally grouped and solitary, often forming clusters, average diameter of 180  $\mu\text{m}$ , filled with tylose. Perforation plate simple. Vasicentric tracheids present. Parenchyma abundant, apotracheal diffuse-in-aggregate and around canals, paratracheal aliform to aliform-confluent forming thin bands. Rays 1-5 seriate, up to 800  $\mu\text{m}$  (50 cells high), fusiform. Heterocellular with one upright marginal cell. Fibres non septate. Secretory canals irregularly spaced in short tangential bands, small.

DESCRIPTION -

*Wood* diffuse-porous. *Growth rings* indistinct. *Vessels* 55% solitary or in groups of 2-4 and often clusters (Fig. 12A), round to oval due to radial compression, 4-16 per  $\text{mm}^2$  (average: 9) counting vessels independently; tangential diameter 70-270  $\mu\text{m}$  (average: 180  $\mu\text{m}$ ). Tyloses present. Vessel elements 150-400  $\mu\text{m}$  (average: 300  $\mu\text{m}$ ) long. Perforation plates simple. Vessel pits alternate. *Vasicentric tracheids* present (Fig. 12E). *Parenchyma* apotracheal and paratracheal abundant; apotracheal diffuse-in-aggregate joining rays, 4-cells sheath around canals, paratracheal mostly aliform and aliform-confluent forming thin bands crossing rays and joining vessels together (Fig. 12A); parenchyma cells 40-110  $\mu\text{m}$  long (average: 80  $\mu\text{m}$ ), 13-26  $\mu\text{m}$  wide (average: 20  $\mu\text{m}$ ) in tangential section, 4-5 or more cells per parenchyma strands. *Xylem rays* 1- to 5- seriate (mainly 4) (Fig. 12B, C), 4-8 rays per mm (average: 6), 130-800  $\mu\text{m}$  (average: 460  $\mu\text{m}$ ) or 6-50 cells high, heterocellular made of procumbent cells with 1-2 upright cells at the ends (Fig. 12 D), rays quite uniform and fusiform in shape (Fig. 12C), all rays cells filled with dark content, very rare sheath cells. *Fibres* non-septate, 12-20  $\mu\text{m}$  in diameter (average: 17  $\mu\text{m}$ ). *Secretory canals* in irregularly spaced short tangential bands up to 5-6, sometimes just on top of each other, always embed in parenchyma bands but not easily visible (Fig. 12A), maybe crushed and also diffuse, 30-50  $\mu\text{m}$  in tangential diameter (average: 40  $\mu\text{m}$ ).

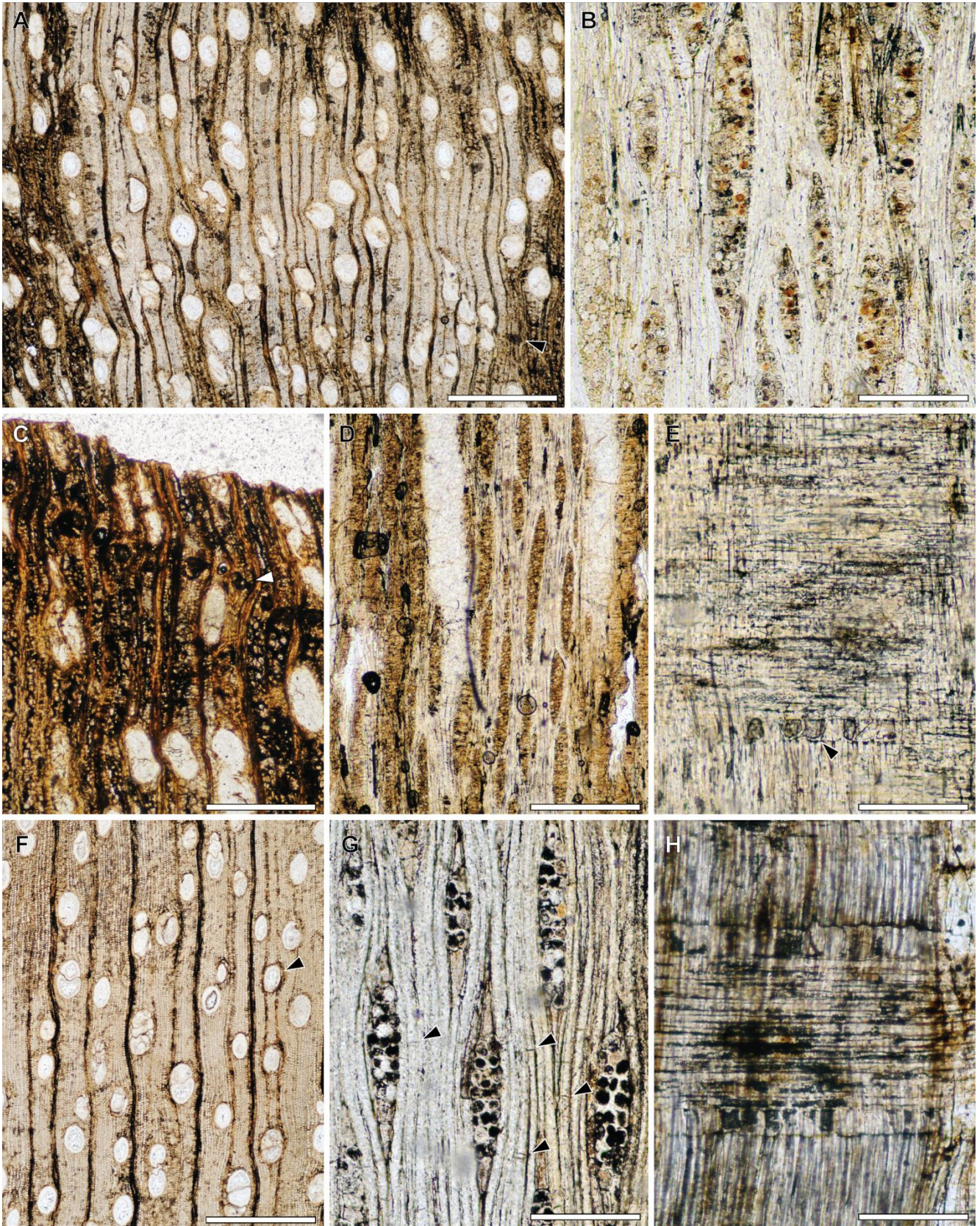
DISCUSSION –

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

Like for previous specimens, secretory canals and vasicentric tracheids are diagnostic of the Dipterocarpaceae family. Very few canals are distinguishable, and it is hard to determine if they are arranged in short or long lines, but the unequivocal presence of many clusters of vessels indicate an affinity with *Shoreoxylon* (Soerianegara & Lemmens 1993). Indeed, such a proportion of grouped vessels is not found in any other genus of Dipterocarpaceae. The presence of clusters is an important feature in our fossil, but it is only described in two fossil species: *Shoreoxylon sumatraense* and *Shoreoxylon holleisii* Selmeier, but almost none of their characters match to our fossil. Among *Shoreoxylon* (Appendix 9) without clusters, five species share similar characters to our fossil. *S. burmense* Prakash, from the Tertiary of Myanmar; *S. indicum* from the Tertiary of India; *S. posthumi* Schweitzer from the Quaternary of Sumatra; *S. pachitanensis* from the Miocene of Java and *S. irrawaddiensis* from the Mio-Pliocene of Myanmar but the diagnoses of these species never perfectly fit the features of our specimen, especially regarding their vessel density and presence of clusters (with additional differences such as canal size, ray size and composition, or presence of crystals). Therefore, a new species is created: *Shoreoxylon glomeratum* n. sp.

Among extant species, our specimen recalls modern *Shorea*, including: *Shorea robusta* for its abundant parenchyma, large, short and fusiform ray and vessels often in group and clusters; *Shorea obtusa* Wall. (ex Blume) for abundant parenchyma, short rays with only one upright marginal ray cells, vessels often in group and in radially aligned clusters, and *Shorea parvifolia* Dyer for aliform parenchyma forming very thin lateral lines, up to 5-seriate rays with short tails and grouped and big vessels. The species *S. parviflora* Dyer mentioned by InsideWood (2004-onward) and GBIF Secretariat (2019) seems to be a mistake according to other databases (The Plant List 2013; IPNI 2020). *Shorea parvifolia* lives in well-drained clay soils on alluvial or dry sites. It is common in dipterocarp forests up to 1100 m of altitude (Soerianegara & Lemmens 1993; Barstow 2018b; Tropical Plants Database 2020); *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 of altitude (Soerianegara & Lemmens 1993; Ghazoul 2016); *Shorea robusta* is a common semi-deciduous tree in South Asia in area 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 moist forest and evergreen moist forests on well-drained soil and riverbanks. It is sensitive to frost and usually found below 800 m of altitude (Wu & Raven 2007; Timilsina *et al.* 2007; Orwa *et al.* 2009).





**Figure 13.** *Shoreoxylon* sp. (A-E): A, Ts, vessel arrangement, often solitary, sometime in groups and clusters, with one line of presumed parenchyma (arrow) possibly marking a line of secretory canals of



growth limit; **B, D**, Tls, 1-5 seriate rays; **C**, Ts, long tangential line of secretory canals embed in parenchyma band (arrow); **E**, Rls, heterocellular ray with one line of upright marginal cells (arrow). *Burseroxylon preserratum* Prakash & Tripathi (**F-H**): **F**, Ts, vessels with tylose and vasicentric parenchyma (arrow); **G**, Tls, (1)-4 seriate rays, septate fibres (arrow); **H**, Rls, heterocellular rays with upright marginal cells. Scale bars: A, F, 1 mm; B, E, G-H, 200  $\mu$ m; C, D, 500  $\mu$ m.

Genus *Shoreoxylon* Den Berger, 1923

***Shoreoxylon* sp.**

(Fig. 13 ; A-E)

MATERIAL - MNHN.[under registration]; field number: 19NAT07-2

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. 13A). *Vessels* 80% solitary or in groups of 2-3 and small clusters (Fig. 13A), with oblique tendency, round to oval, 3-9 per mm<sup>2</sup> (average: 6); tangential diameter 100-270  $\mu$ m (average: 190  $\mu$ m). Tylose present. Vessel elements 180-400  $\mu$ m (average: 280  $\mu$ m) long. Perforation plates simple. Vessel pits alternate. *Vasicentric tracheids* present. *Parenchyma* apotracheal and paratracheal; apotracheal diffuse, paratracheal vasicentric to aliform; parenchyma cells 50-130  $\mu$ m long (average: 100  $\mu$ m), 12-19  $\mu$ m wide (average: 16  $\mu$ m) in tangential section. *Xylem rays* 1- to 5- seriate (mainly 4) (Fig. 13B, D), 7-9 rays per mm (average: 8), 100-850  $\mu$ m (average: 430  $\mu$ m) or 6-40 cells high, heterocellular made of procumbent cells with 1 upright cell at the ends (Fig. 13E). *Fibres* non-septate, thick walled. *Secretory canals* in long tangential bands (more than 30 canals) surrounded by parenchyma (Fig. 13C), 40-85  $\mu$ m in tangential diameter (average 60  $\mu$ m).

DISCUSSION -

This wood is characterized by (1) diffuse-porous wood, (2) mostly solitary vessels with oblique tendency, (3) heterocellular 1-5-seriate rays that are quite short (< 1000  $\mu$ m), (4) small canals (<100  $\mu$ m) in long tangential lines, (5) vasicentric tracheids. These features indicate an affinity with Dipterocarpaceae. Long tangential lines of canals, groups or clusters of vessels and no vascular tracheids are features only shared with the fossil genus *Shoreoxylon*. This specimen shares some features of *Shoreoxylon glomeratum* and

*Shoreoxylon cf. deomaliense* especially regarding its rays. But this specimen has far more solitary and less numerous vessels than *Shoreoxylon glomeratum* as well as less confluent parenchyma and clear long lines of canals; and it has also more grouped vessels than *Shoreoxylon cf. deomaliense*.

Among *Shoreoxylon* (Appendix 9), only four have very small canals together with short rays; these four species are yet clearly different from our specimen: larger and longer rays, sometimes homocellular and wider canals for *Shoreoxylon irrawaddiensis* Prakash & Bande; thinner rays, more numerous and solitary vessels for *S. arcotense*; banded and crystalliferous parenchyma and solitary vessels for *S. indicum*; homocellular rays for *S. kraeuselii* Ramanujam & Rao. Thus, our specimen always displays at least one important diverging characteristic that makes any species attribution difficult. As the state of preservation of this specimen precludes the creation of a new species, it is considered as *Shoreoxylon sp.*

Our specimen shows close affinities with several extant species of *Shorea*, including *Shorea laevis* for their aliform parenchyma, short rays, and small canals and *Shorea balangeran* Dyer for its big vessels 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. These *Shorea* species are found in Southeast Asian dipterocarp forests; *Shorea laevis* mostly grows on well drained to dry, sandy or clay soils, on 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 of altitude (Soerianegara & Lemmens 1993; Robiansyah 2020).

#### Family BURSERACEAE Kunth

Genus *Burseroxylon* (Prakash & Tripathi) Lakhanpal *et al.* 1981

#### ***Burseroxylon preserratum* Prakash & Tripathi, 1975**

(Fig. 13; F-H)

#### TAXONOMIC HISTORY -

*Burseroxylon preserratum* - Prakash & Tripathi, 1975: 60 (Sultanicherra)

HOLOTYPE - Birbal Sahni Institute of Paleobotany Museum, specimen No. 33914

MATERIAL - MNHN.[under registration], MNHN.[under registration], MNHN.[under registration]; field number: 17FN05, 17FN11, NAT17-01

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. 13F), oval to round, 2-13 per mm<sup>2</sup> (average: 7); tangential diameter 90-280 µm (average: 190 µm). Tylose abundant (Fig. 13F). Vessel elements 130-540 µm long (average: 310 µm). Perforation plates simple. Vessel pits alternate, polygonal shaped, 7-15 µm wide (average: 9 µm). Axial *parenchyma* paratracheal vasicentric forming a thin but quite distinct sheath of cells around vessels (Fig. 13F); parenchyma cells 45-90 µm long (average: 60 µm), 25-45 µm wide (average: 35 µm) in tangential section. *Rays* 1- to 4- seriate (Fig. 13G), 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. 13H; rare crystals in upright ray cells. *Fibres* thin walled, septate (Fig. 13G), tangential diameter 10-30 µm (average: 18 µm).

DISCUSSION -

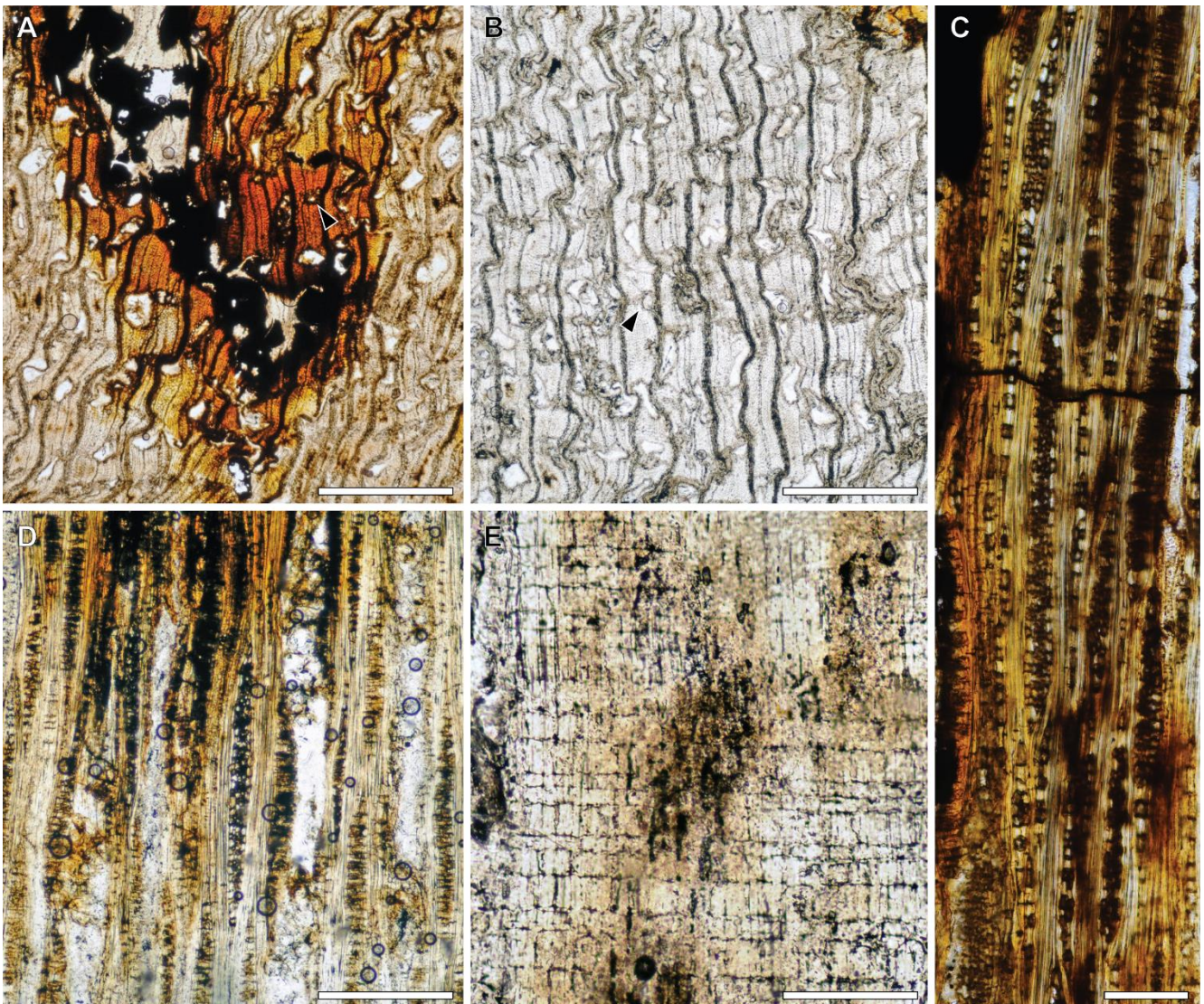
These specimens are characterized by (1) diffuse-porous wood with isolated and tylosed vessels, (2) exclusively simple perforation plates, (3) septate fibres which although are not always very well preserved are clearly present throughout the whole sample, (4) rare or scanty paratracheal parenchyma, (5) growth rings indistinct or absent and (6) 2- to 4- seriate heterocellular rays. These features suggest affinities with Burseraceae (Metcalf & Chalk 1950). Our three specimens show slight differences in vessels and ray density, ray height and width, but the range of these variations is within the intraspecific diversity of Burseraceae (Metcalf & Chalk 1950). The wood anatomy of Burseraceae is very homogenous, both among extant and fossil species (Awasthi & Srivastava 1989; Prasad 1993). Burseraceae are not very numerous in the fossil record (Gregory *et al.* 2009) and include two dominant fossil genera: *Burseroxylon* and *Canarioxylon* Prakash, Březinová & Awasthi (Appendix 10). The descriptions of *Bursera* Jacq. ex L. and *Canarium* L. wood anatomy are very similar, as well as for the diagnosis of *Burseroxylon* and *Canarioxylon*; *Burseroxylon* is different in having (only sometimes) visible growth rings, crystalliferous rays, vasicentric parenchyma, radial canals, and being more than 5-seriate. Our specimens share all the diagnostic features of *Burseroxylon preserratum*, despite a slightly higher vessel and ray density which

could be explained by tangential compression. All other fossil species display features incompatible with our specimens (Appendix 10).

Our specimens display many similar features with extant Burseraceae species *Protium serratum* (Wall. ex Colebr.) Engl. and *Canarium bengalense* Roxb. including their vessel arrangement, ray height and composition, crystals potentially present in ray cells, tylose and scanty paratracheal parenchyma. *P. serratum* appears close to our specimens as it displays common 3-seriate rays, but it has smaller vessels and sometimes radial canals which are absent in our specimens. *C. bengalense* is particularly close to our specimens as it displays a similar vessel diameter and no radial canals, but its rays are mostly 2-seriate. There are 85 species of *Protium* Burm. growing in America, Madagascar and Asia in evergreen to semi-deciduous forests up to 800 m altitude (Sosef *et al.* 1998). *P. serratum* lives in humid areas of India and tropical forests of Myanmar (Prasad 1993), also in moist evergreen and deciduous forests of Thailand (Tropical Plants Database 2020), usually along sides of streams (Gamble 1902). Up to 600-1000 m of altitude (Wu & Raven 2008). About 80 species of *Canarium* live in Africa, Asia and Australia in wet evergreen rain forests, mainly in lowlands, but also in monsoonal climate and open forests (Lemmens *et al.* 1995). *C. bengalense* is a tree living in evergreen, moist and mixed dipterocarp forests below 1300 m of altitude (Leenhouts 1959; Wu & Raven 2008; Ayyappan & Kokilavani 2020). *C. strictum* Roxb. is also considered very close to *C. bengalense* (Leenhouts 1959); it lives in evergreen forest and moist hill forests up to 1600 m of altitude (Leenhouts 1959); but its wood anatomy has never been properly described and is thus not considered here as a NLR.



# UNDETERMINED



**Figure 14.** *Indet. sp.1*: **A**, Ts, vessel arrangement, few parenchyma, some small pores surrounded par parenchyma that could be isolated canals (arrow); **B**, Ts, the parenchyma seems to be vasicentric or aliform (arrow), maybe also diffuse; **C-D**, Tls, 1-5 seriate rays, with sometimes long uniseriate tails and sheath cells; **E**, Rls, heterocellular rays with upright and procumbent cells mixed throughout the rays. Scale bars: A-B, 1 mm; C-E, 200  $\mu$ m; D, 500  $\mu$ m.

## *Indet. sp.1*

(Fig. 14; A-E)

MATERIAL - MNHN.[under registration]; field number: 17FN01

LOCALITY - Kalewa Township, Sagaing Region, Myanmar

AGE - upper lower to lowermost middle Miocene

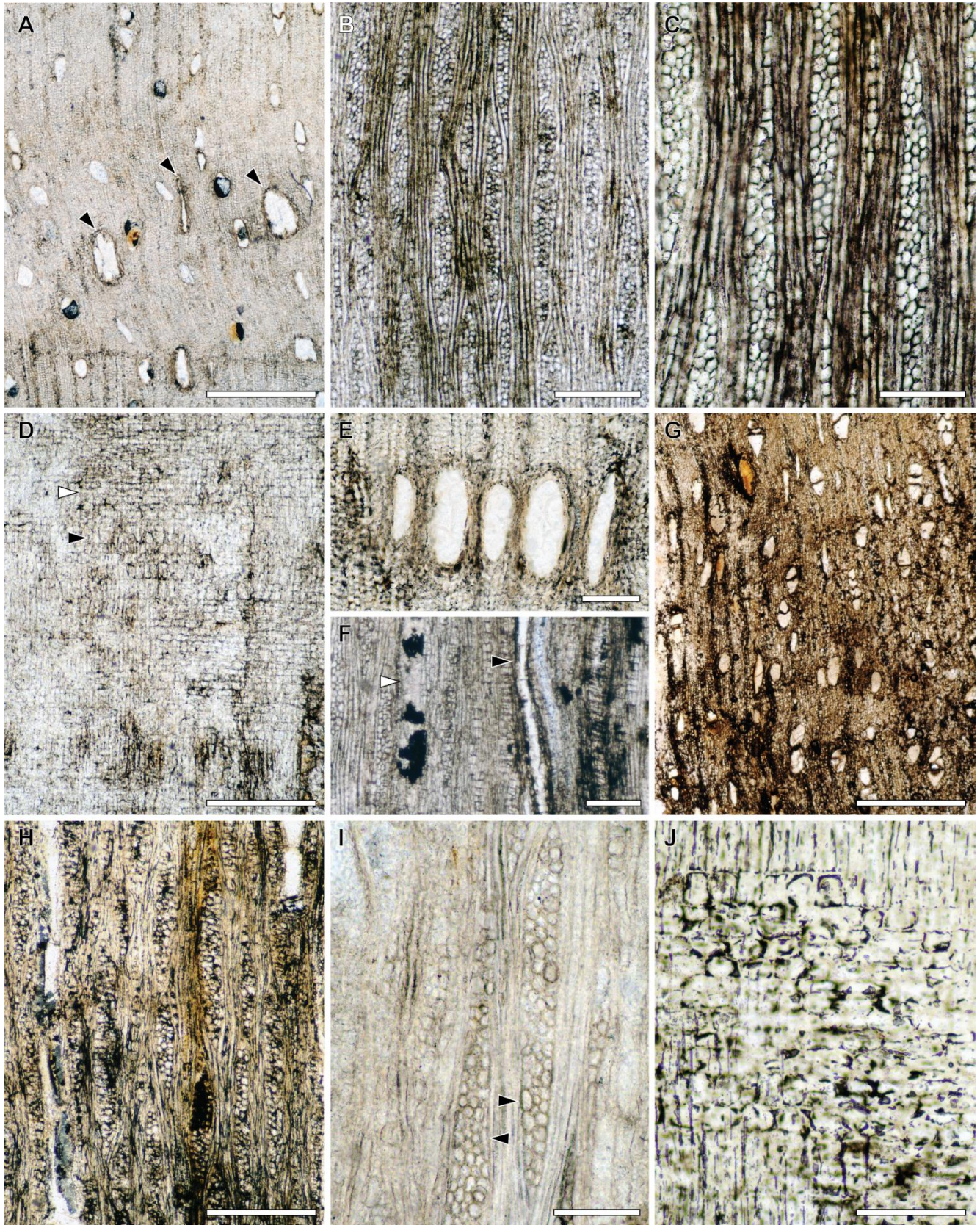
DESCRIPTION -

*Wood* diffuse-porous. *Growth rings* indistinct. *Vessels* mostly solitary (Fig. 14A, B), round to oval, 4-9 per mm<sup>2</sup> (average: 7); tangential diameter 115-230 µm (average: 170 µm). Tylose possibly present. Vessel elements 90-300 µm (average: 170 µm) long. Perforation plates simple. Vessel pits not preserved. *Vasicentric tracheids* not preserved. *Parenchyma* paratracheal vasicentric to mostly aliform (Fig. 14B); parenchyma cells estimated 75 µm average long, 21-31 µm wide (average: 26 µm) in tangential section. *Xylem rays* 1- to 4- seriate (rarely 5) (Fig. 14D, C), uniseriate frequent, 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 1-10 upright cells at the ends, abundant sheath cells (Fig. 14C); rays appear with both upright and procumbent cells throughout the ray in radial section (Fig. 14E). *Fibres* non-septate, 13-32 µm in diameter (average: 20 µm), thick-walled. *Secretory canals* not identifiable although small isolated pores are visible (Fig. 14A).

DISCUSSION –

The preservation state of this specimen does not allow us to relate it to a specific fossil genus with confidence. However, some features are distinguishable from our other specimens, especially in tangential section. It displays rays that are heterocellular to mixed and often uniseriate, with common sheath cells and upright marginal cells, which is typical of Dipterocarpaceae and Malvaceae (Metcalfe & Chalk 1950). However, Malvaceae often have apotracheal and paratracheal parenchyma vasicentric to confluent, and often storied rays with two distinct sizes (Metcalfe & Chalk 1950). An affinity with Dipterocarpaceae is thus more likely. The fossil specimen displays small, isolated pores which could be secretory canals, small vessels, or preservation artefacts. If these were canals, their presence, together with the frequent sheath cells would suggest an affinity with fossil genus *Anisopteroxylon* (Metcalfe & Chalk 1950; Schweitzer 1958; Prakash 1973; Awasthi 1974, 1980).





**Figure 15.** *Indet. sp.2* (A-F): **A**, Ts, Vessels and few parenchyma cells, vasicentric, some remarkably big pores (arrows); **B-C**, Tls, 1-4 seriate rays with sometimes long uniseriate tails and maybe sheath cells; **D**,



Rls, heterocellular rays with procumbent (white arrow) and upright (black arrow) cells mixed throughout; **E**, Tls, detail of big pores often gathered and tangentially aligned; **F**, Tls, comparison of a well identified vessel (white arrow) and a possible secretory canal (black arrow) as perforations are not seen and parenchyma is found all along. *Indet. sp.3* (**G-J**): **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 upright cells. Scale bars: A, G, 1 mm; B, D, F, H, 500 µm; C, E, I-J, 200 µm.

### *Indet. sp.2*

(Fig. 15; A-F)

MATERIAL - MNHN.[under registration]; field number: 17FN08

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. 15A). *Vessels* mostly solitary (80%) or in groups of 2, rarely 3, oval in shape, 1-7 per mm<sup>2</sup> (average: 3); tangential diameter 120-200 µm (average 160 µm). Tylose absent. Vessel elements 190-430 µm (average: 310 µm) long. Perforation plates simple. Vessel pits not alternate, 3-6 µm in diameter (average: 5 µm). *Parenchyma* scanty paratracheal or vasicentric; parenchyma cells 60-130 µm long (mean 90 µm), 20-50 µm wide (average: 35 µm) in tangential section, 5 cells per parenchyma strand. *Xylem rays* 1- to 4- seriate (mostly 1-3) (Fig. 15B, C), uniseriate rays quite abundant, 4-7 rays per mm (average: 6), 310-1260 µm (average: 720 µm), heterocellular made of procumbent cells with 1-8 upright cells at the ends, some rays appear with mixed procumbent and upright cells in radial section (Fig. 15D). Rays irregularly storied (Fig. 15B). *Fibres* non-septate, 11-26 µm in diameter (average: 20 µm). *Canals* diffuse or in short tangential lines, tangentially as big as vessels (Fig. 15A, E), radially longer up to 500 µm (average: 350 µm); possibly secretory or traumatic canals (Fig. 15F).

DISCUSSION -

The specimen displays the same ray arrangement as modern Dipterocarpaceae; it also has marginal or seemingly marginal parenchyma bands without tylose, as found within the Fabaceae family. 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 and arrangement of these canals would indicate an affinity with Dipterocarpaceae and the fossil genus *Dipterocarpoxyton*. Only *D. arcotense* Awasthi has canals at least as big as vessels. Unfortunately, the poor preservation of the cell walls does not allow us to determine with certainty if these pores are secretory canals, traumatic canals, or preservation artefacts.

***Indet. sp.3***

(Fig. 15; G-J)

MATERIAL - MNHN.[under registration]; field number: NAT17-5

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. 15G), round to oval, 4-12 per mm<sup>2</sup> (average: 7); tangential diameter 90-200 µm (average: 150 µm). Tylose absent. Vessel elements 210-420 µm (average: 330 µm) long. Perforation plates simple. Vessel pits alternate, 3-6 µm in diameter (average: 5 µm). *Parenchyma* paratracheal vasicentric possibly aliform; parenchyma cells 60-100 µm long (average: 80 µm), 12-30 µm wide (average: 20 µm) in tangential section. *Xylem rays* 1- to 5- seriate (mostly 3) (Fig. 15H, 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. 15J); some sheath cells present (Fig. 15I). *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. 15G), also coloring the surrounding cells. This could be a result of resin.

DISCUSSION -

This fossil recalls Dipterocarpaceae because of: (1) long rays, strongly heterocellular, (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 transversal section, nor any vasicentric tracheids. This specimen resembles *Shoreoxylon glomeratum* n. sp. or *Shoreoxylon cf. deomaliense* for ray size and arrangement, as well as vessels size. The state of preservation of this specimen is yet not good

enough for a conclusive determination; it is impossible to clearly distinguish parenchyma, fibres and pores outlines, suggesting that the specimen has been degraded by a long exposition to water.

## 5. DISCUSSION:

### 5.1 On the preservation of fossils

The poor state of preservation of some specimens, as well as the presence of hyphae and spores might indicate that some fossils have already experienced bacterial and fungal degradation 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 to wetter ecosystems are poorly preserved and heavily compressed, with highly degraded cell walls and inflated cells in many samples indicating a long residence time spent in water (e.g. *Shoreoxylon cf. sumatraense*, *Dryobalanoxylon indicum*); our specimens of Dipterocarpaceae, mostly associated with the wet evergreen forests, are rarely well enough preserved to identify them without any doubt. This poor preservation could be interpreted as a result of transportation in river waters. However, the poor preservation of specimens associated with a given type of forest is not systematic: *Koompassioxylon kalewensis*, associated with evergreen forests, has perfectly preserved cell walls, while *Albizinium eolebbekianum*, associated with seasonal to dry deciduous forests, is poorly preserved. No clear mark of transportation was observed on our specimens, but this absence is likely due to the moderate size of our specimens: less than 1 dm<sup>3</sup>.

### 5.2 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 2):

(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.

(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; transport of the specimens is corroborated by the fact that they are found in channel lags. Specimens attributed to *tropical evergreen* forests likely represent wetter areas in the upstream highlands of the drainage basins; 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 holdenii*, *Pahudioxylon bankurensis*. Mangroves are present since the end of 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 ~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.

**Table 2:** Distribution of fossil taxa for the Natma Formation among extant tropical forests of the Indo-Burman region, according to their Nearest Living Relatives (after Soerianegara & Lemmens 1993; Lemmens *et al.* 1995; Sosef *et al.* 1998; IUCN 2020; Tropical Plants Database 2020; and other publications cited above). Only the one or two most convincing NLR have been taken into consideration. ● : 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 savannas. The specimen of *Cupressoxylon* is not used here, as not diagnostic of any particular environment.

Fossil species	NLR	Modern ecosystems	1	2	3	4	Forest type
<i>Cynometroxylon holdeni</i>	<i>Cynometra ramiflora</i> / <i>Maniltoa polyandra</i>	Tidal, back-mangrove, wet evergreen and semi-evergreen forests. In lowlands up to 400-1300m	●	○			Coastal forests
<i>Cynometroxylon parinaequifolium</i>	<i>Cynometra inaequifolia</i> / <i>Maniltoa polyandra</i>	Tidal, back-mangrove, wet evergreen and semi-evergreen forests. In lowlands up to 400-1300m	●	○			
<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 <i>Anisoptera</i> . Up to 600m.	●	●		○	
<i>Koompassioxylon kalewensis</i>	<i>Ormosia coccinea</i>	Mostly rainforest. Also at the edge of savannas and coastal forests. In lowlands.	○	●		○	Wet evergreen forests
<i>Koompassioxylon elegans</i>	<i>Koompassia malaccensis</i>	Mostly freshwater peat-swamps. Also dry lands. Up to 150m (800m in elevated areas)		●		○	
<i>Burseroxylon preserratum</i>	<i>Canarium bengalense</i> / <i>Protium serratum</i>	Mixed evergreen and moist dipterocarp forests, also along rivers or deciduous forests. Up to 1300m.		●	○		
<i>Anisopteroxylon cf. garoense</i>	<i>Anisoptera costata</i> / <i>Anisoptera scaphula</i>	Moist (not everwet) evergreen and semi-evergreen dipterocarp forests, along rivers, in seasonal forest and foothills. Up to 700m.		●	○		
<i>Dipterocarpoxyton fugax</i>	<i>Dipterocarpus confertus</i> / <i>D. gracilis</i>	Mixed evergreen or semi-evergreen dipterocarp forests, low hills and undulated lands. Also in seasonal forests. Up to 900m.		●	○		
<i>Dryobalanoxylon indicum</i>	<i>Dryobalanops keithii</i> / <i>D. oblongifolia</i>	Near water (periodically inundated, streams, poorly-drained soils...), in mixed dipterocarps forests. Up to 600 (-1100)m.		●	○		
<i>Shoreoxylon cf. sumatraense</i>	<i>Shorea negrosensis</i>	Evergreen, semi-evergreen and seasonal dipterocarp forests. In lowlands.		●	○		
<i>Artocarpoxylon informe</i>	<i>Artocarpus nitidus</i>	Mixed dipterocarp evergreen forests, but also in semi-deciduous forests or savanna. Up to 1500m.		●	○	○	
<i>Shoreoxylon cf. deomaliense</i>	<i>Shorea leavis</i> / <i>Shorea acuminata</i>	On undulated lands and well-drained soils, in mixed dipterocarp forests. Up to 1000m.		●	○		
<i>Shoreoxylon sp.</i>	<i>Shorea leavis</i> / <i>Shorea balangeran</i>	On well-drained soils or peat-swamp forests. Also in lowland mixed dipterocarp forests and hillsides. Up to 100(-1000)m.		●	●		
<i>Albizinium eolebbekianum</i>	<i>Albizia lebbeck</i> / <i>Albizia ferruginea</i>	Semi-deciduous monsoonal forests, but also in evergreen rainforests, dry-deciduous forests and savannas. Up to 1200m.		○	●	○	Seasonal and dry forests
<i>Pahudioxylon adenanthroides</i>	<i>Azelia africana</i> / <i>Adenanthra intermedia</i>	Both present in humid evergreen and dry deciduous forests. Frequent in savannas. Up to 1400m.		○	●	○	
<i>Shoreoxylon glomeratum</i>	<i>Shorea parvifolia</i> / <i>Shorea obtusa</i>	Deciduous dry dipterocarp forests and under seasonal monsoonal climates. Sometimes in moister forests or savannas. Up to 1000m.		○	●	●	

None of the specimens indicate significant altitude in the Miocene drainage basin; many of the NLR of our specimens are not found above 1000 m of altitude (9 over 17, including *Shorea*, *Dryobalanops*, *Anisoptera*), or even above 600 m (*Intsia*, *Koompassia*). Some NLR associated with wet evergreen forests appreciate undulated lands and hills (*Shorea*, *Dipterocarpus*) but others are more common in lowlands



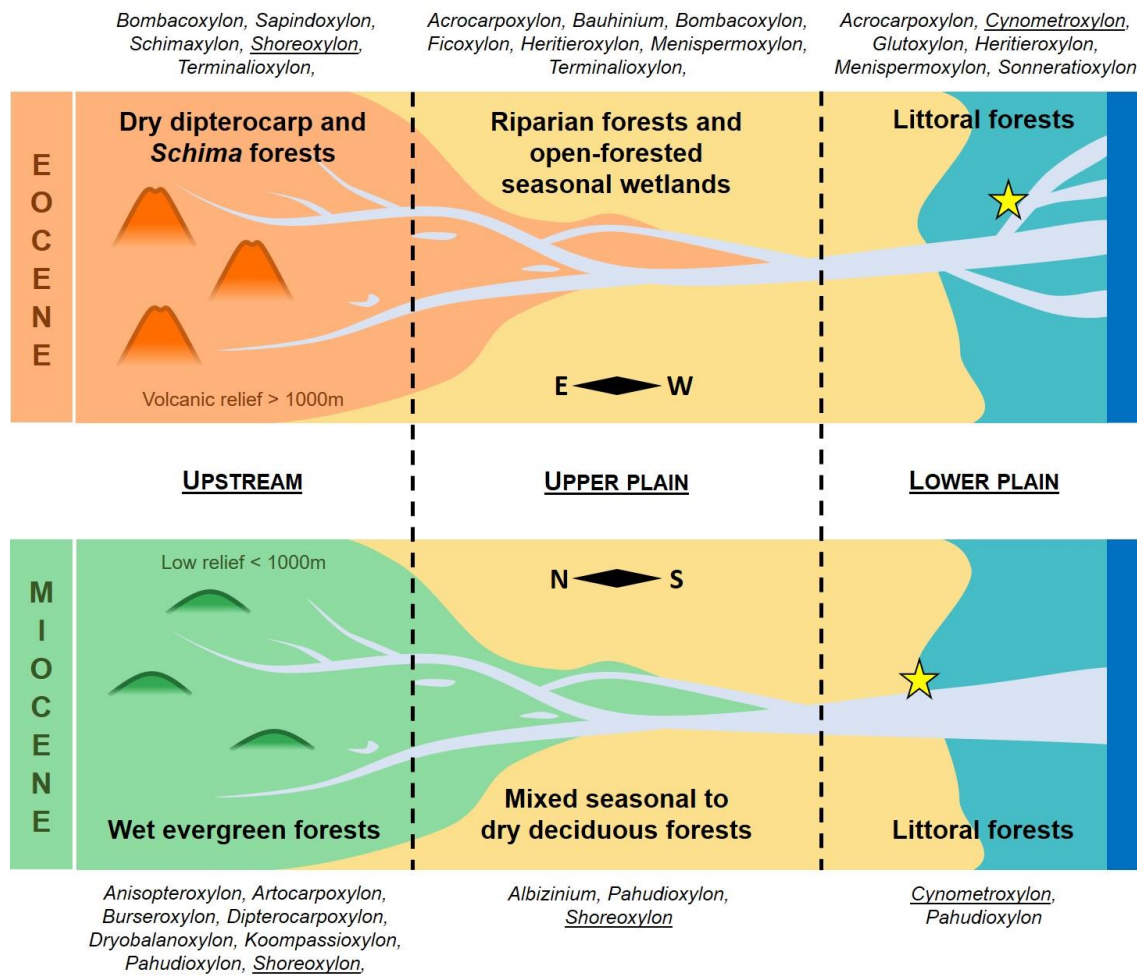
(*Cynometra*, *Ormosia*). Some NLR can occasionally be found above 1000 m (*Canarium*, *Artocarpus*, *Albizia*, *Cynometra*) but are mostly common in plains. This contrasts with the modern elevation in the surrounding highlands of the Chindwin Basin, that reaches up to 3000 m in the Indo-Burman Ranges, and with the presence of taxa indicating moderate elevations in the middle Eocene flora of the Pondaung Formation (*Schimoxydon benderi* Licht, Bours & De Franceschi, NLR of which, *Schima wallichii* Choisy, usually occurs in mid-altitude forests above 1000 m; Licht *et al.* 2015). We could explain our low-altitude assemblage and the shift of 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 Natogyi deposits remain unclear.

### **5.3 The wet dipterocarp forests of the upper lower Miocene: implications for the origin of dipterocarps**

The wet evergreen forest taxa identified in the Natogyi Formation are dominated by dipterocarps, both in the number of species and in 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 *Dryobalanoxylon* is interesting as it is the first record of this genus in Myanmar. Nowadays, *Dryobalanops* are absent from India and Myanmar but previous *Dryobalanoxylon* of poorly constrained Tertiary age have been described in India, attesting that the geographic distribution of the genus has reduced through time (Maury-Lechon & Curtet 1998). This study also provides the first occurrence of *Anisopteroxylon* in Myanmar, which had already 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 Natogyi Formations of Myanmar (Fig. 16) indicates a major ecological shift for dipterocarps. Wet evergreen forests are completely absent in the middle Eocene. In contrast with the dipterocarps of the Natogyi Formation, *Shoreoxylon* 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 glomeratum* n. sp.) relate to these seasonal and dry forests.



**Figure 16.** Comparison between Eocene (Licht *et al.* 2014, 2015) and Miocene (this study) forest assemblage and diversity of Myanmar with the list of related fossil genus and supposed forest type they belong to. Underlined names are genus found in both formations. Yellow stars mark the schematic position of sampling sites.

Burmese fossil dipterocarps seem thus to have undergone a diversification through the Cenozoic which has allowed some of them to occupy new ecosystems, from dry seasonal ecosystems in the Eocene (Licht *et al.* 2014, 2015) to mostly wet evergreen forests in the Miocene (this study). 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). It has been proposed that

Dipterocarpaceae originated from Gondwana during the late Cretaceous and latter spread to eastern regions (Madagascar, India, South-East Asia; Appanah & Turnbull 1998; Maury-Lechon & Curtet 1998; Morley 2000; Gunasekara 2004; Dutta *et al.* 2011), 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).

### 5.3 Paleoenvironmental 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  $\mu$ m). Only 4 out of 17 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) taphonomic bias in our Miocene sampling that would favor higher-altitude and wetter taxa, (2) changes of drainage that would favor wetter areas, (3) increased summer monsoonal rainfall. 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 actually 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, but 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 suggests a wetter climate in central Myanmar during the Miocene compared to the Eocene, with some taxa suggesting more than 2000 mm of annual rainfall. This interpretation would be in agreement with data from other areas in South Asia indicating strong monsoons during the late early to early middle Miocene (Clift *et al.* 2008)

## 6. 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 17 species) and Dipterocarpaceae (7 out of 17 species), similar to the diversity found nowadays in Southeast Asian forests. The assemblage also provides the first record of *Dryobalanoxylon* and *Anisopteroxylon* in Myanmar. 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 very wet season, with some 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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## APPENDICES

**Appendix 1.** Synthetic table describing a selection of fossil wood specimens of *Albizinium* and *Acrocarpoxylon*. ( ) : occur rarely. Authors in parentheses: data about the species found in this publication whereas in the original one.

<i>Species</i>	<b>Growth rings</b>	<b>Vessels t.diam.(µm); frequency (/mm<sup>2</sup>)</b>	<b>Intervessel pits ; diam. (µm)</b>	<b>Fibers</b>	<b>Axial parenchyma</b>	<b>Rays</b>	<b>Ray height (µm ; cells)</b>	<b>Crystals</b>	<b>Geologic age / country</b>	<b>Authors</b>
<i>Albizinium eolebbekianum</i>	Distinct (terminal parenchyma)	150-300 3-5	Alternate, vestured 6-10	Septate, thin- walled	Diffuse, vasicentric, aliform, (confluent)	1-4 seriate 7-10/mm homocellular	35-280 3-14	(Axial parenchyma)	Miocene / India	Prakash 1975
<i>Albizinium pondicherriensis</i>	Distinct (terminal parenchyma)	40-285 3-5	Alternate, vestured 8-10	Septate, thin- walled	Diffuse, vasicentric, aliform, confluent	1-3 seriate 10-15/mm homocellular	80-300 4-15	Axial parenchyma	Mio-Plio / India	Awasthi 1979
<i>Albizinium arunachalensis</i>	Indistinct	100-360 2-7	Alternate, vestured 8-12	Nonseptate, thick-walled	(Diffuse), vasicentric, confluent	1-4 seriate 6-9/mm homocellular	- 12-24	-	Moi-Plio / India	Mehrotra, Awasthi & Dutta 1999
<i>Albizinium borjanensis</i>	Indistinct	150-225 4-5	Alternate, vestured 4-6	Nonseptate	Diffuse, vasicentric, (aliform, confluent)	1-4 seriate 6-11/mm homocellular	108-450 6-28	Axial parenchyma	Miocene / India	Prakash, Lalitha & Tropathi 1994
<i>Albizioxylon chinjiensis</i>	Distinct (terminal parenchyma)	115-280 3-6	Alternate, vestured 4-6	Septate, thin- walled	Vasicentric, aliform, confluent	1-4 seriate 7-10/mm homocellular	60-343 3-25	-	Miocene / Pakistan	Soomro <i>et al.</i> 2016
<i>Acrocarpoxylon siwalicus</i>	Distinct	100-250 12-14	Alternate 5-7	Septate, thick- walled	Aliform, confluent	1-5 seriate, 6-8/mm homocellular / heterocellular	90-560 5-35	Axial parenchyma, upright ray cells	Miocene / India	Gottwald 1994 (Yadav 1989)
<i>Albizinium eolebbekianum</i>	Distinct	140-460 (mean 210) 0-5	Alternate 5-9	Septate ?	Diffuse ?, aliform, (confluent)	1-3 seriate 5-8/mm homocellular	150-340 5-20	Axial parenchyma	Miocene / Myanmar	This study

**Appendix 2.** Synthetic table describing a selection of fossil wood specimens of *Cynometroxylon*, *Bauhinium* and fossil *Bauhinia* and *Cynometra*. () : occur rarely.

Authors in parentheses: data about the species found in this publication whereas in the original one.

<i>Species</i>	<b>Growth rings</b>	<b>Vessels t.diam.(μm); frequency (/mm<sup>2</sup>)</b>	<b>Intervessel pits ; diam. (μm)</b>	<b>Fibers</b>	<b>Axial parenchyma</b>	<b>Rays</b>	<b>Ray height (μm ; cells)</b>	<b>Crystals</b>	<b>Geologic age / country</b>	<b>Authors</b>
<i>Cynometroxylon holdenii</i>	Indistinct	105-225 3-4	Alternate, polygonal, vestured, 4-6	Nonseptate, thick-walled	Vasicentric, concentric bands, 2-9 cells high	(1-4)2-3 seriate, heterocellular	- up to 85	-	Mio-Plio / Myanmar	Prakash & Bande 1980
<i>Cynometroxylon parinaequifolium</i>	Indistinct	75-180 6-7	Alternate, vestured, 4-6	Nonseptate	Concentric bands, 4- 5/mm, 2-5(7) cells high	1-2 seriate, heterocellular 1-2 cells tailed, end-to-end fusion	- 13-60	-	Tertiary / Thailand	Prakash 1979
<i>Cynometroxylon darkshinense</i>	Indistinct	108 -	- <4	Nonseptate	Concentric bands, 3-6 cells high	1-2 seriate, homocellular	- 20-22	-	Mio-Plio / India	Navale 1959
<i>Cynometroxylon tunense</i>	Indistinct	36-204 5	Alternate, polygonal, vestured, 3-7	Nonseptate, thin to thick- walled	Vasicentric, banded, 3-4/mm, 2-7 cells high, storied tendency	1-3 seriate, 10-12/mm, homo/heterocellular, storied tendency	70-500 2-28	-	Miocene / Tunisia	Delteil- Desneux 1981
<i>Cynometroxylon ranikotense</i>	Indistinct	(47)104-243 -	-	-	Aliform-confluent, banded, concentric, 8-17 cells high	1-(2) seriate, homocellular	227 5-20	-	Tertiary / Pakistan	Rajput & Khan 1982
<i>Cynometroxylon tanganyensis</i>	Absent	100-190 4 (spiral thickening ?)	Alternate 5-7,5	Nonseptate, thick-walled	Banded of same size/bigger than fiber bands, 3-5/mm, 3-5 cells high	2-3(5) seriate, 9/mm, homocellular	480-725 5-25	Parenchyma, ray cells	Paleocene / Tanzania	Cantrill <i>et al.</i> 2013
<i>Cynometra grandis</i>	Distinct	50-100 ? / 147-209 ? 15-25	Alternate, polygonal 5	Nonseptate, (septate), thin to thick- walled, storied tendency	Scanty paratracheal, vasicentric, aliform, confluent, banded, 3-4 cells high, storied tendency	2(1-3) seriate, 9/mm, homo/heterocellular, storied	214-312 -	Parenchyma, fibers	Eocene / Peru	Woodcock, Meyer & Prado 2017
<i>Bauhinium palaeomalabaricum</i>	Indistinct	80-220 6-10 storied tendency	Atlernate, vestured 6-8	Nonseptate, thin to thick walled	Banded, bigger than fiber bands, storied tendency, 3-4/mm, 3-9 cells high	1-(2) seriate homo/heterocellular 1- 2-cells tailed or mixed, storied	130-720 4-32	-	Miocene / India	Prakash & Prasad 1984



<i>Bauhinium miocenicum</i>	-	132-176 -	-	-	Banded, 2-6 cells high	1-3 seriate, heterocellular	-	-	Mio-Plio / India	Trivedi & Panjwani 1986 (Prakash & Prasad 1984)
<i>Bauhinia deomalica</i>	Indistinct	60-160 storied	Alternate, vestured, 8	Nonseptate, thick-walled	Aliform-confluent, banded, smaller than fiber bands, 4-5/mm, 3-5 cells high, storied	1 seriate, 20-25/mm, homo/heterocellular, storied	160-2809-20	Chambered parenchyma	Mio-Plio / India	Awasthi & Prakash 1987
<i>Bauhinia tertiaria</i>	Absent	72-180 3-11, tylose, storied	Alternate 4-8	Nonseptate, thick-walled	Vasicentric, aliform, confluent, banded, storied	1-(2) seriate, 9-12/mm, weakly heterocellular, storied	160-960 8-60	-	Miocene / India	Awasthi & Mehrotra 1990
<i>Bauhinia miocenica</i>	Absent	66-165 4-8, storied	Alternate, vestured, 4-7	Non-septate, thick walled, storied tendency	Banded, bigger than fiber bands, 3-8 cells high, storied	1-(2) seriate, weakly heterocellular, irregularly storied	192-550 5-15	Ray cells	Miocene / India	Mehrotra <i>et al.</i> 2011
<i>Cynometroxylon holdenii</i>	Indistinct	50-200 3-24	Alternate 2-5	Nonseptate, thick-walled, (included phloem)	Vasicentric, banded, same or smaller than fiber bands, 2-6/mm, 2-11 cells high	(1)-3 seriate, 8-13/mm, heterocellular 1-2 cells tailed, (storied tendency)	160-740 7-35	(Parenchyma)	Miocene / Myanmar	This study
<i>Cynometroxylon parinaequifolium</i>	Indistinct	50-170 1-16	Alternate 3-4	Nonseptate, thick-walled	Vasicentric, aliform, confluent, banded 2-8 cells high	1-3 seriate, 6-13/mm, heterocellular 1-3 cells tailed, end-to-end fusion	140-1080 9-55	Absent	Miocene / Myanmar	This study

**Appendix 3.** Synthetic table describing a selection of fossil wood specimens of *Ormosioxylon*, *Koompassioxylon* and *Saracoxylon*. () : occur rarely.

<i>Species</i>	Growth rings	Vessels		Fibers	Axial parenchyma	Rays	Ray height (µm ; cells)	Crystals	Geologic age / country	Authors
		t.diam.(µm); frequency (/mm <sup>2</sup> )	Intervessel pits ; diam. (µm)							
<i>Ormosioxylon bengalensis</i>	Indistinct	75-225 4-7	Alternate-opposite 6-8	Nonseptate, thick-walled	Aliform-confluent, (banded)	(1-4)2-3 seriate, 7-9/mm, homocellular to weakly heterocellular 1-cell tailed, storied tendency	100-500 5-25	-	Tertiary / India	Bande & Prakash 1980
<i>Ormosioxylon chinjiensis</i>	Indistinct	110-214 5-8	Alternate 4-6	Nonseptate, thick-walled	Aliform, confluent	1-5 seriate, 4-8/mm, homocellular to weakly heterocellular 1-2 cells tailed	30-420 9-19	-	Miocene / Pakistan	Soomro <i>et al.</i> 2016
<i>Koompassioxylon elegans</i>	Distinct	210-230 2-3	Alternate 7-8	Nonseptate, thick-walled	Pointed aliform, confluent	1-3 seriate, 6-7/mm, heterocellular, sometimes homocellular, storied tendency	330-400 14-16	Rays, parenchyma	Miocene / India	Kramer 1974
<i>Koompassioxylon keralaensis</i>	Indistinct	110-225 4-6	Alternate, vestured 6-8	Nonseptate	Pointed aliform, (confluent), storied tendency	1-3 seriate, homocellular to weakly heterocellular, storied	140-525 5-33	-	Miocene / India	Srivastava & Awasthi 1996
<i>Saracoxylon irrawaddiense</i>	Distinct (marginal parenchyma)	90-270 3-4	Alternate, polygonal, 5	Nonseptate, thick-walled	Vascentric, aliform, (confluent), marginal lines of 1-6 cells	1-2(3) seriate, 7-10/mm, heterocellular 1-2 cells tailed	100-700 3-22	-	Pliocene / Myanmar	Du 1988
<i>Koompassioxylon elegans</i>	Distinct	120-370 (mean 230) 0-6	Alternate, polygonal, 6-12	Nonseptate, thin to thick-walled	Aliform, confluent, marginal	2-3(4) seriate, 3-10/mm, heterocellular 1-2 cells tailed, storied tendency	220-500 8-18	Rays, parenchyma	Miocene / Myanmar	This study
<i>Koompassioxylon kalewensis</i> sp. nov.	Indistinct ?	140-250 (mean 180) 4-9	Alternate, 6-13	Nonseptate, thick-walled	Aliform, confluent	1-3 seriate, 8-16/mm, heterocellular 1-n cells tailed, (mixed), end-to-end fusion, (storied tendency)	150-870 <30	Parenchyma	Miocene / Myanmar	This study

**Appendix 4.** Synthetic table describing a selection of fossil wood specimens of *Pahudioxylon* and *Adenantheroxylon*. ( ) : occur rarely. Authors in parentheses: data about the species found in this publication whereas in the original one.

<i>Species</i>	Growth rings	Vessels t.diameter (µm); frequency (vessels/mm <sup>2</sup> )	Intervessel pits ; vertical diameter (µm)	Fibers	Axial parenchyma	Rays	Crystals	Geologic age / country	Authors
<i>Pahudioxylon afzeloides</i>	Indistinct	140-278 4-8	Alternate / opposite 5	Nonseptate, thin-walled	Aliform, (confluent), marginal bands	1-3(4) seriate, 8/mm, homocellular, <380 µm or 27 cells high, (storied)	Absent	Neogene / Vietnam	Prakash, Boureau & Louvet 1967, Boureau 1952
<i>Pahudioxylon arcotense</i>	Indistinct	135-225 -	Alternate, vested	Nonseptate, thin-walled	Vasicentric, aliform, confluent, marginal bands	(1)2-3 seriate, homocellular, 5-35 cells high	Absent	Tertiary / India	Navale 1963
<i>Pahudioxylon garbetaense</i>	Indistinct	73-102 4-7	Alternate, vested 4-6	Nonseptate	Vasicentric, aliform, confluent, marginal terminal	1-3 seriate, 5-8/mm, homocellular, 165-248 µm or 15-20 cells high	Absent	Neogene / India	Bera & Banerjee 2001
<i>Pahudioxylon gehanemense</i>	Indistinct	-5	Alternate, vested 5-8	Nonseptate, thin-walled	Aliform, confluent, marginal bands	1-3(4) seriate, 7-10/mm, homocellular, 65-350 µm high, storied tendency	Absent	Miocene / Lybia	Louvet 1974
<i>Pahudioxylon irregulare</i>	Indistinct	50-125 8-20	Alternate, 3-4	Nonseptate	Vasicentric, aliform, confluent, narrow bands	1-3(4) seriate, 8-10/mm, homocellular / weakly heterocellular, 70-550 µm or 2-35 cells high, (end to end fusion)	Parenchyma	Miocene / Caribbean	Müller-Stoll & Mädel 1967
<i>Pahudioxylon kiliani</i>	Distinct	100-250 4-5	Alternate 5-6	Nonseptate, thin-walled	Aliform, confluent, marginal bands	1-4 seriate, homocellular	Absent	Eocene-Oligocene / Egypt	Prakash, Boureau & Louvet 1967, Louvet 1965 (Feng <i>et al.</i> 2012)
<i>Pahudioxylon menchikoffii</i>	Indistinct	100-300 2-5	Alternate	Nonseptate	Vasicentric, aliform, confluent, nonmarginal	1-2(3) seriate, homocellular	Absent	Eocene / France-Algeria	Müller-Stoll & Mädel 1967, Boureau 1951 (Feng <i>et al.</i> 2012)
<i>Pahudioxylon panonicum</i>	Distinct	30-140 16-40	Alternate 3-6	Nonseptate	Vasicentric, aliform, confluent, marginal ?	1-4 seriate, 11-14/mm, homocellular	Parenchyma	Tertiary / Hungary	Müller-Stoll & Mädel 1967

<i>Pahudioxylon paracochinchinense</i>	Indistinct	65-215 2-9	Alternate, vestured 6-8,5	Nonseptate, thin-walled	Aliform, confluent, marginal bands	2-3 seriate, 6-11/mm, homocellular, 153-540 µm or 7- 28 cells high, storied tendency	Absent	Pliocene / Vietnam	Vozenin-Serra 1981
<i>Pahudioxylon zoharyanum</i>	Indistinct	<110 6-9	Alternate 4-5	Nonseptate	Vasicentric, aliform / confluent, nonmarginal	1-2(3) seriate homocellular	Absent	Miocene- Pliocene / Israel	Müller-Stoll & Mädel 1967, Lorch & Fahn 1959 (Feng <i>et al.</i> 2012)
<i>Pahudioxylon furoni</i>	Distinct	150-200 5-7	Vestured 4-6	Nonseptate	Vasicentric, aliform, marginal	(1)2-4 seriate, homocellular	Absent	Cret-Tert / Tchad	Koeniguer 1973
<i>Pahudioxylon bankurensis</i>	Distinct	50-180 2-3	Alternate, vestured	Nonseptate, thin to thick- walled	Aliform-confluent, marginal bands	(1)2-3 seriate, homocellular, <365 µm or 15-25 cells high, storied tendency	Parenchyma	Miocene / India	Chowdhury, Ghosh & Kazmi 1960
<i>Pahudioxylon tchadense</i>	Distinct	115-155 3-8	Alternate, vestured 6-7	Nonseptate	Vasicentric, aliform, confluent, marginal bands	(1)2-4 seriate homocellular	Absent	Mio-Plio / Tchad	Laudoueneix 1973
<i>Adenantheroxylon pavoninium</i>	Indistinct	144-204 -	Vestured 6-8	Nonseptate, thin-walled	Diffuse, vasicentric, (aliform, confluent)	1-3 seriate, homocellular	(Parenchyma)	Tertiary / India	Prakash & Tripathi 1969
<i>Pahudioxylon bankurensis</i>	Distinct	120-280, 1-5	Alternate 4-7	Nonseptate	Aliform, confluent, marginal bands	1-3 seriate, 5-7/mm, homocellular / rare heterocellular, 140-370 µm or 8- 21 cells high, storied tendency	Parenchyma, (Rays)	Miocene / Myanmar	This study
<i>Pahudioxylon adenantheroides n. sp.</i>	Distinct	100-300, 1-7	Alternate 4-12	Nonseptate, thin to thick- walled	Diffuse, aliform, (confluent), marginal bands	1-3 seriate, 5-12/mm, homocellular, 130-400 µm or 6- 20 cells high, storied tendency	Parenchyma	Miocene / Myanmar	This study



**Appendix 5.** Synthetic table describing a selection of fossil wood specimens of *Artocarpoxylon* and *Tetrameloxylon*. ( ) : occur rarely.

<i>Species</i>	Growth rings	Vessels t.diam.(µm); frequency (/mm <sup>2</sup> )	Intervessel pits diam.(µm)	Fibers	Axial parenchyma	Rays	Ray height (µm ; cells)	Canals diameter (µm)	Geologic age / country	Authors
<i>Artocarpoxylon kartikherraensis</i>	Absent	105-315 2-3, tylose	Alternate 10-12	Nonseptate, thin to thick- walled	Vasicentric, aliform, (confluent)	(1-6)3-5 seriate, 3-4/mm, heterocellular 1-3 cells tailed, (sheath cells)	-	(Radial latex canals)	Tertiary / India	Prakash & Lalitha 1978
<i>Artocarpoxylon deccanensis</i>	Absent	80-180 9-20, (tylose)	Alternate 8-12	Nonseptate	Vasicentric, (aliform, confluent)	(1)4-6 seriate, 7-9/mm, heterocellular 1-3 cells tailed, (sheath cells)	200-800 9-48	(Radial latex canals) 13-36	Tertiary / India	Mehrotra <i>et al.</i> 1984
<i>Tetrameloxylon prenudiflora</i>	Distinct (vessel density)	90-240 3-5	Alternate 6-8	Nonseptate, thin-walled, storied	Vasicentric, aliform, (confluent), storied	(1-6)3-5 seriate, 4-5/mm, homocellular to heterocellular 1- 6 cells tailed, (sheath cells)	195-1995 6-87	-	Tertiary / India	Lakhanpal & Verma 1966
<i>Artocarpoxylon informe n. sp.</i>	Absent	80-300 (mean 180) 0-8, tylose	Alternate, 3-9	Nonseptate	Diffuse, vasicentric, (aliform)	1-6 seriate, 4-7/mm, heterocellular 1-4 cells tailed, (sheath cells)	192-950 up to 50+ (end to end fusion)	-	Miocene / Myanmar	This study

**Appendix 6.** Synthetic table describing a selection of fossil wood specimens of *Anisopteroxylon*. () : occur rarely. Authors in parentheses: data about the species found in this publication whereas in the original one.

<i>Species</i>	Growth rings	Vessels t.diam. (µm); frequency (/mm <sup>2</sup> )	Fibers	Axial parenchyma	Rays	Ray height (µm ; cells)	Canals	Canals t.diam.(µm)	Geologic age / country	Authors
<i>Anisopteroxylon oblongoides</i>	Indistinct	120-230 4-5 solitary, tylose	Nonseptate, thick-walled, vasicentric tracheids	Diffuse, diffuse-in- aggregate, vasicentric	(1-11)7-9 seriate, 4-8/mm heterocellular 1-2+ cells tailed, continuous sheath cells	150-1080 5-56	(Diffuse), long tangential lines	120-150	Miocene / India	Yadav 1989
<i>Anisopteroxylon garoensis</i>	Indistinct	110-255 8-12 solitary, (tylose)	Nonseptate, thick-walled, vasicentric tracheids	Diffuse, diffuse-in- aggregate, scanty paratracheal, vasicentric	(1-8)5-6 seriate, 5-12/mm, heterocellular 1-8 cells tailed, sheath cells	180-1350 6-30	Diffuse, short tangential lines of 2-3	40-55	Miocene / India	Prakash & Tripathi 1970
<i>Anisopteroxylon surmaensis</i>	Indistinct	130-230 6-10 solitary, tylose	Nonseptate, thick-walled, vasicentric tracheids	Diffuse, diffuse-in- aggregate, scanty paratracheal	(1-6)4-5 seriate, 5-6/mm, heterocellular, continuous sheath cells	210-1200 5-55	Diffuse	100-130	Miocene / India	Prasad, Agarwal & Mandaokar 2009
<i>Anisopteroxylon bengalensis</i>	Indistinct	95-210 - solitary, tylose	Nonseptate, vasicentric tracheids	Diffuse, diffuse-in- aggregate, scanty paratracheal, vasicentric	1-6 seriate heterocellular, sheath cells	546-1386 20-60	Diffuse	60-77	Mio-Plio / India	Ghosh & Kazmi 1958 (Prakash & Tripathi 1970)
<i>Anisopteroxylon kalagharensis</i>	Indistinct	105-255 7-9 solitary, tylose	Nonseptate, vasicentric tracheids	Diffuse, diffuse-in- aggregate, scanty paratracheal	(1)4-5 seriate heterocellular, continuous sheath cells	150-1725 3-55	Diffuse	75-105	Tertiary / India	Prakash 1978
<i>Anisopteroxylon varkalaensis</i>	Indistinct	80-160 25-30 solitary, tylose	Nonseptate, vasicentric tracheids	Diffuse, diffuse-in- aggregate, scanty paratracheal	(1-7)4-5 seriate heterocellular 2-10 cells tailed, continuous sheath cells	350-2000 16-120	Diffuse, (short tangential lines of 2)	40-96	Mio-Plio / India	Awasthi & Srivastava 1990
<i>Anisopteroxylon jawalamukhi</i>	Indistinct	154-300 - solitary, tylose	Nonseptate, vasicentric tracheids	Diffuse, diffuse-in- aggregate, vasicentric	1-7 seriate heterocellular, sheath cells	460-1950 15-67	Diffuse, (short tangential lines of 2-3)	98-168	Mio-Plio / India	Ghosh & Ghosh 1958 (Prakash & Tripathi 1970)

<i>Anisopteroxylon geopperti</i> n. comb.	Indistinct	120-250 6-10, solitary, tylose	Nonseptate, thick-walled	(Diffuse), vasicentric, around canals	(1-6)2-5 seriate, heterocellular 1-4 cells tailed, sheath cells	- 6-50	Diffuse	30-50	Tertiary / Java	Kraüsel 1926 This study
<i>Anisopteroxylon aduriensis</i>	Indistinct	52-325 6-12 solitary, tylose	Septate, nonseptate, thick-walled, vasicentric tracheids	Diffuse-in-aggregate, vasicentric, (aliform)	1-5 seriate, many 1s, 7/mm, heterocellular 1-5 cells tailed, sheath cells	520-1430 -	Diffuse, short tangential lines of 2-3	130-195	Mio-Plio / India	Acharya & Roy 1989
<i>Anisopteroxylon ramunculiformis</i>	Indistinct	30-105 60 (solitary)	Nonseptate, thin-walled, helical thickening	Banded, paratracheal	1-2(3) seriate heterocellular	- <30	Diffuse ?	36	Eocene / England	Poole 1993
<i>Anisopteroxylon santiketanense</i>	Indistinct	166-266 6-12 solitary, tylose	Nonseptate, thick-walled, vasicentric tracheids	Diffuse, scanty paratracheal, vasicentric	(1)4-5 seriate, 6-12/mm, heterocellular 1-6 cells tailed, sheath cells	166-999 12-52	Diffuse	66-133	Miocene / India	Ghosh & Roy 1980
<i>Anisopteroxylon coromandelense</i>	Indistinct	180-215 3-4 solitary, tylose	Nonseptate, thick-walled, vasicentric tracheids	Diffuse, diffuse-in-aggregate, scanty paratracheal, vasicentric	(1)3-6 seriate continuous sheath cells	- 12-35	Diffuse, (short tangential lines of 2)	36-48	Tertiary / India	Navale 1963
<i>Anisopteroxylon cf. garoense</i>	Indistinct	80-230 2-13 solitary, tylose	Nonseptate, vasicentric tracheids	Diffuse, scanty paratracheal	(1)6-7 seriate, 4-7/mm, heterocellular 1-4+ cells tailed, continuous sheath cells	510-1500 up to 60	Diffuse ?	-	Miocene / Myanmar	This study

**Appendix 7.** Synthetic table describing a selection of fossil wood specimens of *Dipterocarpoxyton*. () : occur rarely.

<i>Species</i>	Growth rings	Vessels				Ray height (µm ; cells)	Canals	t.diam.(µm)	Geologic age / country	Authors
		t.diam.(µm); frequency (/mm <sup>2</sup> )	Fibers	Axial parenchyma	Rays					
<i>Dipterocarpoxyton tertiarum</i>	Indistinct	130-315 4-6, solitary, tylose	Nonseptate, thin to thick-walled, vasicentric tracheids	Diffuse, diffuse-in-aggregate, scanty paratracheal, around canals	(1-9)5-7 seriate, 4-6/mm, heterocellular, sheath cells ?	-	Diffuse, short tangential lines of 2-7	70-120	Tertiary / Myanmar	Prakash 1965
<i>Dipterocarpoxyton chowdhurri</i>	Indistinct	165-225 6-8, solitary, tylose	Nonseptate, vasicentric tracheids	Diffuse, diffuse-in-aggregate, scanty paratracheal, around canals	1-4-6 seriate, 6-9/mm, (mixed ?), sheath cells	90-2240 2-74	Diffuse, short tangential lines of 2-4	80-160	Miocene ? / India	Ghosh 1956, Prakash 1973
<i>Dipterocarpoxyton sivalicus</i>	Indistinct	160-240 5-7, solitary, 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 -	(Diffuse), short tangential lines of 2-6	40-68	Miocene / India	Prakash 1975
<i>Dipterocarpoxyton nalagarhense</i>	Indistinct	105-255 4-6, solitary, tylose	Nonseptate, thick-walled, vasicentric tracheids	Diffuse, diffuse-in-aggregate, scanty paratracheal, around canals	(1-10)8-9 seriate, 4-7/mm, heterocellular, sheath cells	225-1425 -	Diffuse, short tangential lines of 3-4	90-200	Miocene / India	Prakash 1975
<i>Dipterocarpoxyton premacrocarpus</i>	Indistinct	150-270 4-6, solitary, tylose	Nonseptate, thick-walled, vasicentric tracheids	Diffuse, diffuse-in-aggregate, scanty paratracheal, around canals	1-5 seriate, 6-10/mm, heterocellular, sheath cells	225-1575 -	Diffuse, short tangential lines of 2-3	135-225	Miocene / India	Prakash 1975
<i>Dipterocarpoxyton arcotense</i>	Indistinct	100-320 6-15, solitary, tylose	Nonseptate, thick-walled, vasicentric tracheids	Diffuse, diffuse-in-aggregate, vasicentric, (aliform), around canals	(1-7)4-5 seriate, 5-8/mm, heterocellular, sheath cells	180-840 5-55	Diffuse, short tangential lines of 2-6(8)	100-280 bigger than vessels	Mio-Plio / India	Awasthi 1980
<i>Dipterocarpoxyton nungarhense</i>	Indistinct	110-176 8-15, solitary, tylose	Nonseptate, thick-walled, vasicentric tracheids	Diffuse, vasicentric, (aliform, confluent), around canals	(1-6)3-5 seriate, rare uniseriate, 6-11/mm, heterocellular 1-3 cells tailed, sheath cells	492-792 13-22	Diffuse, short tangential lines of 2-3	57-88	Mio-Plio / India	Trivedi & Ahuja 1980
<i>Dipterocarpoxyton pondicherriense</i>	Indistinct	120-370 3-8, solitary, tylose	Nonseptate, thick-walled, vasicentric tracheids	(Diffuse), vasicentric, (aliform), around canals	(1-5)3-4 seriate, heterocellular 1-5 cells tailed, sheath cells	- 10-50	Diffuse, short tangential lines of 2-8(10)	80-120	Tertiary / India	Awasthi 1974
<i>Dipterocarpoxyton kalaicharporensis</i>	Indistinct	68-285 5-7, solitary, oblique tendency	Nonseptate, thick-walled	Scanty paratracheal / vasicentric, around canals	1-5 seriate, 4-5/mm, heterocellular 1-2+ cells tailed, sheath cells	375-1500 7-43	Diffuse, short tangential lines	- smaller than vessels	Tertiary / India	Eyde 1963

<i>Dipterocarpoxydon malavii</i>	Indistinct	80-240, 5-7, solitary, tylose	Nonseptate, thick-walled, vasicentric tracheids	Diffuse, diffuse-in-aggregate, scanty paratracheal, (aliform)	(1-7)3-5 seriate, 6-8/mm, heterocellular, sheath cells	120-1600 10-60	Diffuse, short tangential lines of 4-5	40-120	Pliocene / India	Ghosh & Ghosh 1959, Guleria 1983
<i>Dipterocarpoxydon kalagarhensis</i>	Indistinct	116-224 4-6, solitary, tylose	Thin to thick-walled, vasicentric tracheids	Diffuse, diffuse-in-aggregate, scanty paratracheal, around canals	(1-6)4-5 seriate, 5-8/mm, heterocellular, sheath cells	120-1540 5-40	Diffuse, short tangential lines of 2-4, (long tangential lines)	88-180	Miocene / India	Yadav 1989
<i>Dipterocarpoxydon surangei</i>	Indistinct	128-290 4-6, solitary	Nonseptate, thick-walled, vasicentric tracheids	Diffuse, diffuse-in-aggregate, scanty paratracheal, around canals	(1-8)5-7 seriate, 3-5/mm, heterocellular, sheath cells	160-1620 -	Diffuse, short tangential lines of 2-5	240-440 bigger than vessels	Miocene / India	Prakash 1981
<i>Dipterocarpoxydon africanum</i>	Indistinct	- solitary	-	Vasicentric, around canals	(1-5)3 seriate, heterocellular 1-6 cells tailed, (end-to-end fusion)	- 8-30	Diffuse, short tangential lines of 2-6	- same size as vessels	Tertiary / Uganda	Bancroft 1933
<i>Dipterocarpoxydon schenkii</i>	Indistinct	125-325, 4-7, solitary	Nonseptate, thin-walled, vasicentric tracheids	Diffuse, diffuse-in-aggregate, scanty paratracheal, around canals, cristalliferous	1-6 seriate, heterocellular, sheath cells, (end-to-end fusion, cristalliferous)	- 30-50	Diffuse, short tangential lines of 2	80-110	Tertiary / Java	Schweitzer 1958
<i>Dipterocarpoxydon sarapeense</i>	-	160-320 4-7, solitary	Nonseptate, thin to thick walled, vasicentric tracheids	Diffuse to diffuse-in-aggregate, vasicentric, around canals	1-5 seriate, 6-8/mm heterocellular 2-7+ cells tailed, sheath cells, (end-to-end fusion)	<2400 <80	Short tangential lines of 2-7	80-118	Plio-Pleisto / Thailand	Vozenin-Serra & Privé-Gill 2001
<i>Dipterocarpoxydon resiniferum</i>	Indistinct	150-300 5-6, solitary	Nonseptate, thick-walled, vasicentric tracheids	(Diffuse), around canals	1-4 seriate, homo/heterocellular 1-3 cells tailed, sheath cells	- 40-50	Diffuse, short tangential lines of 2-7	100-125 numerous	Pliocene / Java	Schweitzer 1958
<i>Dipterocarpoxydon perforatum</i>	Indistinct	100-200 13-20	Nonseptate, thin to thick walled, vasicentric tracheids	(Diffuse, diffuse-in-aggregate), around canals	1-4 seriate, homocellular, cristalliferous, end-to-end fusion	- 5-50	Diffuse, short tangential lines of 4	50-110	Quaternary / Sumatra	Schweitzer 1958
<i>Dipterocarpoxydon anisopteroides</i>	Indistinct	150-250 5-10, solitary, tylose	Nonseptate, thick-walled, vasicentric tracheids	Diffuse, (diffuse-in-aggregate, scanty paratracheal), around canals	1-6 seriate, homocellular, (cristalliferous ?)	- 4-65	Diffuse	60 rare	Pliocene / Java	Schweitzer 1958
<i>Dipterocarpoxydon bolpureense</i>	Indistinct	86-230, solitary, tylose	Nonseptate, thick-walled, vasicentric tracheids	Vasicentric, around canals	3-4 seriate, heterocellular 1-3 cells tailed, sheath cells	499-1498 15-52	Diffuse, short tangential bands of 2-4	99-132	Tertiary / India	Ghosh & Roy 1979



<i>Dipterocarpoxydon gracile</i>	Indistinct	100-175 5-14, solitary	Nonseptate, thick- walled, vasicentric tracheids	Diffuse, scanty paratracheal, around canals, crystalliferous	1(2-5) seriate, homocellular	- <40	Diffuse, short tangential lines of 2	60-75	Pliocene / Java	Schweitzer 1958
<i>Dipterocarpoxydon jammuense</i>	Indistinct	80-260 3-9, solitary, tylose	Nonseptate, vasicentric tracheids	(Diffuse), vasicentric, around canals	(1-6)3-5 seriate, 5-9/mm, heterocellular 2-12 cells tailed, sheath cells	200- 1260 5-45	Diffuse, short tangential lines of 2-5	65-80	Miocene / India	Guleria, Gupta & Srivastava 2001
<i>Dipterocarpoxydon javanicum</i>	Indistinct	150-250, 3- 8, solitary, tylose	Nonseptate, thick- walled, vasicentric tracheids	Diffuse, diffuse-in- aggregate, scanty paratracheal, around canals	(1-8)6-7 seriate,± homocellular, (sheath cells), crystalliferous	- 10-50	Diffuse, short tangential lines of 4	60-100	Tertiary / Java	Schweitzer 1958
<i>Dipterocarpoxydon parabaudii</i>	Indistinct	165-330 4-7, solitary, tylose	Nonseptate, vasicentric tracheids	Diffuse, diffuse-in- aggregate, scanty paratracheal, around vessels	(1-5)3-4 seriate, 7-9/mm, heterocellular 1-4+ cells tailed, sheath cells	375- 1425 8-35	Diffuse, short tangential lines of 2-5	75-165	Tertiary / India	Prakash 1978
<i>Dipterocarpoxydon monotoides</i>	Distinct	100-175 10-12	Nonseptate	Diffuse-in-aggregate, vasicentric, marginal	1-2(3) seriate, 10-12/mm, heterocellular 1- cell tailed	- <15	-	-	Miocene / Ethiopia	Lemoigne 1978
<i>Dipterocarpoxydon fugax n. sp.</i>	Indistinct	140-260 (mean 200) 5-13, solitary, tylose	Nonseptate, vasicentric tracheids	Vasicentric, (aliform, confluent), around canals	1-4 seriate, rare uniseriate, 6- 9/mm, homocellular/ heterocellular 1 cell tailed, (sheath cells, end-to-end fusion)	320- 1140 15-50	Diffuse, short tangential lines of 2-7	40-90	Miocene / Myanmar	This study

**Appendix 8.** Synthetic table describing a selection of fossil wood specimens of *Dryobalanoxylon*. () : occur rarely. Authors in parentheses: data about the species found in this publication whereas in the original one.

<i>Species</i>	<b>Growth rings</b>	<b>Vessels t.diam.(µm); frequency (/mm<sup>2</sup>)</b>	<b>Fibers</b>	<b>Axial parenchyma</b>	<b>Rays</b>	<b>Ray height (µm ; cells)</b>	<b>Canals</b>	<b>Canals t.diam. (µm)</b>	<b>Geologic age / country</b>	<b>Authors</b>
<i>Dryobalanoxylon holdeni</i>	Indistinct	60-280 9-15, solitary, tylose	Vascular / vasicentric tracheids, nonseptate, thick-walled	Vasicentric, aliform, around canals	1-4 seriate, heterocellular 1- 5 cells tailed, sheath cells	<900 up to 30	Long tangential lines	40-60	Tertiary / India	Awasthi 1971
<i>Dryobalanoxylon indicum</i>	Indistinct	< 250 8-16, solitary, tylose ?	Vascular / vasicentric tracheids, nonseptate, thick-walled	Vasicentric, (aliform, confluent), around canals, crystalliferous	(1-5)3-4 seriate, 7-8/mm, heterocellular 1-15 cells tailed, sheath cells	<1900 up to 90	Long tangential lines	80-100	Tertiary / India	Awasthi 1971
<i>Dryobalanoxylon bangkoense</i>	Indistinct	75-250 7-13	Vascular / vasicentric tracheids, nonseptate, thick-walled	Diffuse, diffuse-in- aggregate, scanty paratracheal	(1-5)3-4 seriate, heterocellular 2-5 cells tailed, crystalliferous	- 4-70	Long tangential lines	25-125	Quaternary / Sumatra	Schweitzer 1958
<i>Dryobalanoxylon bogoreense</i>	Indistinct	120-286 3-4, solitary, tylose	Vascular / vasicentric tracheids, nonseptate	Vasicentric, aliform, around canals	1-6 seriate, uniseriate rare, heterocellular 1-4 cells tailed	500-1200 11-36	Long tangential lines	33-100	Pliocene / Java	Srivastava & Kagemori 2001
<i>Dryobalanoxylon borneense</i>	Indistinct	60-125 10-16, solitary	Vascular / vasicentric tracheids, nonseptate, thick-walled	Around canals	1-3 seriate, heterocellular, (big cells in the middle), sheath cells, end-to-end fusion	- up to 55	Long tangential lines	40-70	Miocene / Borneo	Schweitzer 1958
<i>Dryobalanoxylon mirabile</i>	Distinct	100-175 9-22, (solitary), tylose	Vascular / vasicentric tracheids, nonseptate, thick-walled	Diffuse, diffuse-in- aggregate, scanty paratracheal, around canals, crystalliferous	(1-5)3-4 seriate, rare uniseriate, homocellular, crystalliferous	- 3-40	Long tangential lines	60-120	Quaternary / Sumatra	Schweitzer 1958
<i>Dryobalanoxylon musperi</i>	Distinct	(60)100-200 10-22, solitary, tylose	Vascular / vasicentric tracheids, nonseptate, thick-walled	Diffuse, scanty paratracheal, around canals	1-4 seriate, homo/heterocellular 20 cells tailed, crystalliferous ?	- 20-30	Long tangential lines	40-75	Mio-Plio / Java	Schweitzer 1958
<i>Dryobalanoxylon neglectum</i>	Indistinct	150-225 7-13, solitary, tylose	Vascular / vasicentric tracheids, nonseptate, thin-walled	Diffuse-in-aggregate, scanty paratracheal	1-3 seriate, homo/heterocellular, crystalliferous	- up to 56	Long tangential lines	40-150	Quaternary / Sumatra	Schweitzer 1958

<i>Dryobalanoxylon rotundatum</i>	Distinct ?	50-300 10-16, solitary	Vascular / vasicentric tracheids, nonseptate, thick-walled	Diffuse-in-aggregate, around canals	1-3(4) seriate, homo/heterocellular 1-4 cells tailed, storied	- 2-30	Short / long tangential lines	50-100(300)	Quaternary / Sumatra	Schweitzer 1958
<i>Dryobalanoxylon sumatrense</i>	Indistinct	75-200 4-8, solitary	Vascular / vasicentric tracheids, nonseptate, thin to thick-walled	Diffuse, vasicentric, (aliform)	1-5 seriate heterocellular 1-15 cells tailed, crystalliferous	- 4-90	Short tangential bands of 5 or more	75-110	Pliocene / Sumatra	Schweitzer 1958
<i>Dryobalanoxylon tambouense</i>	-	125-234 2-10, (solitary, tylose)	Vascular / vasicentric tracheids, nonseptate, thin to thick-walled	Vasicentric, aliform, around canals, narrow bands up to 9 vessels	(1)2-5 seriate, 6-8/mm, heterocellular 1-6 cells tailed, sheath cells, storied tendency	192-1194 5-38	Long tangential lines	30-80	Neogene / Vietnam	Vozenin-Serra 1981
<i>Dryobalanoxylon khmerinum</i>	Indistinct	100-260 7-8, solitary, tylose	Vascular / vasicentric tracheids, nonseptate, thin-walled	Scanty paratracheal, vasicentric, around canals	1-3 seriate, 7-8/mm, heterocellular, (big cells in the middle), sheath cells	420-700 12-29	Long tangential lines	55-215	Tert-Quat / Cambodia	Boureau 1952 Schweitzer 1958
<i>Dryobalanoxylon lunaris</i>	Indistinct	195-257 5-8, solitary, tylose	Vascular / vasicentric tracheids, thick-walled	Diffuse-in-aggregate, vasicentric, aliform, around canals	1-4 seriate, 5-7/mm, heterocellular 1-4 cells tailed, cristalliferous, storied tendency, (end-to-end fusion)	<2980 5-90	(Diffuse), long tangential lines	90-242	Pliocene / Java	Mandang & Kagemori 2003
<i>Dryobalanoxylon keralaensis</i>	-	100-240 15-20	-	-	1-5 seriate, 6-8/mm, heterocellular, sheath cells	- up to 45	-	100-120	Miocene / India	Awasthi & Ahuja 1982 (Biswas et al. 2019)
<i>Dryobalanoxylon spectabile</i>	Indistinct	95-200 10-16, tylose	Vasicentric tracheids	(Diffuse), vasicentric, banded around canals	1-6 seriate, heterocellular 1-3 cells tailed, 4-12/mm, crystalliferous, sheath cells	- 3-35	Long tangential lines	30-120	Pliocene / Indonesia	Berger 1927, Krausel 1926 (Biswas et al. 2019)
<i>Dryobalanoxylon javanense</i>	-	70-120 8-16	-	-	1-6 seriate, 2-19/mm, (crystalliferous ?), sheath cells	- 3-45	-	30-100	Pliocene / Java	Berger 1927 (Biswas et al. 2019)
<i>Dryobalanoxylon tobleri</i>		80-230 8-16	-	-	1-6 seriate, 6-8/mm, (crystalliferous ?), sheath cells	- 35-50	-	50-250	Pliocene / Indonesia	Berger 1923 (Biswas et al. 2019)
<i>Dryobalanoxylon neosumatrense</i>	Indistinct	288-336 4-6, solitary	Vascular / vasicentric tracheids, nonseptate, thick-walled	Vasicentric, aliform, around canals	1-4 seriate, 10-12/mm, heterocellular, sheath cells	736-960 up to 40	Tangential lines	80-112	Miocene / India	Biswas et al. 2019

<i>Dryobalanoxylon neyveliensis</i>	Indistinct	60-170 7-9, solitary	Vascular / vasicentric tracheids, nonseptate, thick-walled	Diffuse, vasicentric, around canals	(2)-3 seriate, 10-12/mm, heterocellular	- 21-66	Tangential lines	60-110	Miocene / India	Kumarasamy & Elayaraja 2016
<i>Dryobalanoxylon indicum</i>	Indistinct	130-260 3-8, solitary, tylose	Vascular / vasicentric tracheids, nonseptate, thick-walled	Diffuse, scanty paratracheal, vasicentric, around canals	(1-6)4-5 seriate, rare uniseriate, 3-7/mm, heterocellular 1-9 cells tailed, sheath cells	330-1530 up to 50+	(Diffuse, short)-long tangential lines	40-120	Miocene / Myanmar	This study

**Appendix 9.** Synthetic table describing a selection of fossil wood specimens of *Shoreoxylon* and *Hopenium*. () : occur rarely. Authors in parentheses: data about the species found in this publication whereas in the original one.

<i>Species</i>	<b>Growth rings</b>	<b>Vessels t.diam.(<math>\mu</math>m); frequency (/mm<sup>2</sup>)</b>	<b>Fibers</b>	<b>Axial parenchyma</b>	<b>Rays</b>	<b>Ray height (<math>\mu</math>m ; cells)</b>	<b>Canals</b>	<b>Canals t.diam. (<math>\mu</math>m)</b>	<b>Geologic age / country</b>	<b>Authors</b>
<i>Shoreoxylon panganense</i>	Distinct	50-250 8-9	(Vasicentric tracheids), nonseptate, thin to thick walled	Diffuse-in-aggregate, vasicentric, crystalliferous , around canals	5-8 seriate, 3-5/mm, heterocellular 1-3 cells tailed	400-1000 -	Long tangential lines	80-200	Eocene / Myanmar	Licht <i>et al.</i> 2014
<i>Shoreoxylon deomaliense</i>	Indistinct	65-256 8-16, tylose	Vasicentric tracheids, nonseptate, thin to thick walled	(Diffuse), vasicentric, aliform, (confluent), around canals, crystalliferous	1-7 seriate, 6-9/mm, heterocellular 1-8 cells tailed	- 4-65	Long tangential lines	35-240	Mio-Plio / India	Prakash & Awasthi 1971
<i>Shoreoxylon burmense</i>	Indistinct	135-240 5-6, tylose	Vasicentric tracheids, nonseptate, thick-walled	Diffuse, diffuse-in-aggregate, vasicentric, (confluent), around canals	(1)4-5 seriate, 7-10/mm, homocellular to weakly heterocellular	<1275 -	Long tangential lines, 1 to 4	45-150	Tertiary / Myanmar	Prakash 1965
<i>Shoreoxylon thailandense</i>	-	120-180 1-6	Nonseptate, thin-walled	Diffuse, diffuse-in-aggregate, vasicentric, around canals	1-5 seriate, 4-7/mm, heterocellular 2-3 cells tailed, (storied tendency)	68-1230 3-58	Long tangential lines	45-150	Plio-Pleisto / Thailand	Vozenin-Serra & Privé-Gill 1989
<i>Shoreoxylon tipamense</i>	Distinct	112-332 3-9, tylose	Vasicentric tracheids, nonseptate, thin-walled	(Diffuse, diffuse-in-aggregate), vasicentric, aliform, (confluent), around canals, crystalliferous	1-5 seriate, heterocellular 1-12 cells tailed, sheath cells	- 6-66	Long tangential lines	80-160	Tertiary / India	Prakash & Awasthi 1970
<i>Shoreoxylon ranikotense</i>	Indistinct	135-240 5-6, tylose	Vasicentric tracheids, nonseptate, thick-walled	Diffuse, diffuse-in-aggregate, vasicentric, (aliform), around canals	1-5 seriate, 7-10/mm, homocellular	100-1275 3-75	Long tangential lines, 1 to 4	45-150	Pleistocene / Pakistan	Shar et al. 2007
<i>Shoreoxylon indicum</i>	Indistinct	45-240 5-10, tylose	Vasicentric tracheids, nonseptate, thick-walled	Diffuse, vasicentric, aliform, confluent, crystalliferous	1-6 seriate, 5-9/mm, (homocellular) / heterocellular 1-2 cells tailed	- up to 60	Long tangential lines	40-120	Tertiary / India	Awasthi 1974
<i>Shoreoxylon parvum</i>	Indistinct	125-200 10-19	Vasicentric tracheids, nonseptate	-	1-3 seriate, 6-8/mm, heterocellular, crystalliferous	- up to 94	Long tangential lines	50-125	Pliocene / Java	Schweitzer 1958



<i>Shoreoxylon evidens</i>	Indistinct	135-345 <3, (tylose)	Nonseptate, libriform, thin-walled	Aliform, canals	(1)3-5 seriate, rare uniseriate, 5-7/mm, homocellular to heterocellular 1 tailed	450-690 13-25	Long tangential lines	120-195	Tertiary / India	Eyde 1963
<i>Shoreoxylon arcotense</i>	Indistinct	45-165 15-20, solitary, tylose	Vasicentric tracheids, nonseptate, thin- walled	Scanty paratracheal, vasicentric, around canals	1-4 seriate, heterocellular 1-5 cells tailed	- 4-40	Long tangential lines	40-60	Tertiary / India	Awasthi 1974
<i>Shoreoxylon pentacmeoides</i>	Indistinct	121-197 4-10	Vasicentric tracheids, nonseptate	Diffuse, (diffuse-in- aggregate), scanty paratracheal	1-2(3) seriate, 8-12/mm, heterocellular 1-9 cells tailed, sheath cells, crystalliferous	- 6-26	Diffuse, short tangential lines of 2	30-110	Plio-Pleisto / India	Bera & Banerjee 2001
<i>Shoreoxylon swedenborgii</i>	Distinct	180-207 solitary ?	Thick-walled	Vasicentric, around canals	2-6 seriate, heterocellular, sheath cells	1680- 2240 50-80	Long/short ? tangential lines	90	Tertiary / Indonesia	Schweitzer 1958 Schuster 1910 Du 1988
<i>Shoreoxylon sumatraense</i>	Indistinct	200-360 9-14, cluster, tylose	Thin-walled	Diffuse, diffuse-in- aggregate, vasicentric, aliform, (confluent), irregularly storied	1-4 seriate, 4-5/mm, heterocellular 1-n cells tailed, (crystalliferous)	80-1400 4-50	Long tangential lines	40-90	Quaternary / Sumatra	
<i>Shoreoxylon posthumi</i>	Indistinct	200-300 5-10, tylose	Vasicentric tracheids, nonseptate, thin- walled	Diffuse, diffuse-in- aggregate, vasicentric, around canals, crystalliferous	1-5 seriate, homocellular, end-to-end fusion	- 3-45	Long/short tangential lines, diffuse, (double lines)	60-150	Quaternary / Sumatra	Schweitzer 1958
<i>Shoreoxylon rengatense</i>	Indistinct	50-150 8-14, tylose	Thin walled	Vasicentric, around canals	1-4 seriate, 8-10/mm, heterocellular 1-n cell tailed, sheath cells	150-1200 5-63	Long tangential lines, radial	40-80 (radial : 19-22)	Tertiary / Sumatra	Vozenin- Serra 1980
<i>Shoreoxylon pulchrum</i>	Indistinct	250-320 2-5, storied elements	Vasicentric tracheids, nonseptate, thin- walled	Vasicentric, aliform, around canals	1-4 seriate, homocellular, (crystalliferous)	- up to 100	Short-long ? tangential lines	75-125	Quaternary / Sumatra	Schweitzer 1958
<i>Shoreoxylon penzesi</i>	Indistinct	70-300 ? -	Vasicentric tracheids	Aliform, marginal	1-(2) seriate, heterocellular, (crystalliferous ?)	- 20-25	-	-	Miocene / Hungary	Greguss 1969
<i>Shoreoxylon pachitanensis</i>	Indistinct	200-240 6-10, tylose	Nonseptate, thin to thick-walled	Vasicentric, banded, around canals	1-4 seriate, 6-10/mm, heterocellular	750-1450 -	Short/long ? tangential lines	70-190	Miocene / Java	Sukiman 1977

<i>Shoreoxylon ornatum</i>	Indistinct	155-230 5-9, solitary, tylose	Nonseptate, vasicentric tracheids	Diffuse, diffuse-in- aggregate, vasicentric, around canals	(1-5)3-4 seriate, 5-8/mm, heterocellular 2-12 cells tailed, sheath cells	484-1870 -	Diffuse, long/short tangential lines of 2-3, close, (double or triple rows)	-	Tertiary / India	Bande & Prakash 1980, Trivedi & Ahuja 1979
<i>Shoreoxylon multiporosum</i>	Indistinct	200-325 9-12	Vasicentric tracheids, nonseptate, thick- walled	Vasicentric, (diffuse, diffuse-in-aggregate, aliform), around canals	1-5 seriate, sheath cells, crystalliferous	- 30-60	Short tangential lines of 5-8, long tangential lines (Diffuse), Long/Short tangential lines	80-200	Quaternary / Sumatra	Schweitzer 1958
<i>Shoreoxylon moroides</i>	Indistinct	150-350 5-8	Nonseptate	Diffuse, vasicentric, aliform, around canals	1-5 seriate	- 40	(Diffuse), Long/Short tangential lines	35-200	Tertiary / Java	Berger 1927, Krausel 1926
<i>Shoreoxylon holleisii</i>	Indistinct, (but bigger vessels)	50-217 8-13, cluster, tylose	(Vasicentric tracheids ?), nonseptate, thick- walled	Vasicentric, around canals	1-6 seriate, 5-8/mm, heterocellular 1-9 cells tailed, sheath cells, crystalliferous	260-1200 2-43	Long tangential lines, (diffuse ?, traumatic ?)	98-238 (455 ? traumatic)	Tertiary / Germany	Selmeier 1998
<i>Shoreoxylon maximum</i>	Indistinct	200-350 1-4	Vasicentric tracheids, nonseptate, thin- walled	Diffuse-in-aggregate, vasicentric, around canals	1-3 seriate, homocellular	- 40-80	Long tangential lines	50	Tertiary / Sumatra	Schweitzer 1958
<i>Shoreoxylon cuddalorensis</i>	Indistinct	115-283 6-8	Nonseptate, thin- walled	Vasicentric, around canals	4-5 seriate, 8-10/mm, homocellular	- 7-18	Long tangential lines	30-50	Mio-Plio / India	Gurusamy & Kumarasamy 2007
<i>Shoreoxylon krauselii</i>	Indistinct	150-200 2-8	Vasicentric tracheids, nonseptate	Diffuse, diffuse-in- aggregate, scanty paratracheal, vasicentric, around canals	(1-5)3-4 seriate, rare uniseriate, 6-9/mm, homocellular	- 5-60	Long tangential lines	75-95	Mio-Plio / India	Ramanujam & Rao 1967
<i>Shoreoxylon asiaticum</i>	Indistinct	200-350 3-6	Vasicentric tracheids, nonseptate, thin to thick-walled	(Diffuse, scanty paratracheal), around canals	1-9 seriate, homocellular	- 3-50	Long tangential lines, radial 1-3/ray	75	Tertiary / Sumatra	Schweitzer 1958
<i>Shoreoxylon irrawaddiensis</i>	Indistinct	90-300 6-8, tylose	Vasicentric tracheids, nonseptate	Diffuse-in-aggregate, vasicentric, banded around canals	(1-7)3-5 seriate, 5-8/mm, homocellular to weakly heterocellular 1 cell tailed	< 1200 up to 50	Long tangential lines	< 140	Mio-Plio / Myanmar	Prakash & Bande 1980
<i>Shoreoxylon robustoides</i>	-	147-186 6-9	Nonseptate	Vasicentric, around canals	3-4 seriate, heterocellular	-	Long tangential lines	-	Tertiary / India	Roy & Ghosh 1981 (Biswas <i>et al.</i> 2019)

<i>Hopenium pondicherriense</i>	Distinct	30-150 25-75, tylose, (oblique)	Vasicentric tracheids, nonseptate, thick- walled	Diffuse, diffuse-in- aggregate, (thin bands), vasicentric, aliform, confluent, around canals	1-4(5) seriate, 7-10/mm, heterocellular 1-5 cells tailed, square/upright cells in the middle, crystalliferous	- 6-80	Long tangential lines	40-100	Mio-Plio / India	Awasthi 1980
<i>Hopenium payangadiensis</i>	Distinct	48-240 23-28, tylose	Vasicentric tracheids, nonseptate	Diffuse, diffuse-in- aggregate, vasicentric	1-4 seriate, heterocellular 1-4 cells tailed, square/upright cells in the middle, crystalliferous	200-600 8-38	Long tangential lines	48-144	Mio-Plio / India	Awasthi & Srivastava 1990
<i>Shoreoxylon cf. sumatraense</i>	Indistinct	80-240, (mean 160), 8-20, cluster, tylose	Vasicentric tracheids, nonseptate, thin- walled	Scanty paratracheal, vasicentric ?, banded around vessels	1-5 seriate, 4-8/mm, heterocellular 1-9 cells tailed, (sheath cells)	340-1040 10-45	Long tangential lines, close	38-75	Miocene / Myanmar	This study
<i>Shoreoxylon sp.</i>	Indistinct	110-270 3-9, tylose	Vasicentric tracheids, nonseptate, thick- walled	Diffuse, vasicentric, aliform, marginal ?, around canals	1-5 seriate, 7-9/mm, heterocellular 1 cell tailed	100-850 6-40	Long tangential lines	40-85	Miocene / Myanmar	This study

**Appendix 10.** Synthetic table describing a selection of fossil wood specimens of Burseraceae available during this study. ( ) : occur rarely. Authors in parentheses: data about the species found in this publication whereas in the original one.

<i>Species</i>	<b>Growth rings</b>	<b>Vessels t.diam.(µm); frequency (/mm<sup>2</sup>)</b>	<b>Fibers</b>	<b>Axial parenchyma</b>	<b>Rays</b>	<b>Ray height (µm ; cells)</b>	<b>Crystals</b>	<b>Canals diameter (µm)</b>	<b>Geologic age / country</b>	<b>Authors</b>
<i>Burseroxylon preserratum</i>	Absent	80-200 12-18, tylose	Septate, thin-walled	Scanty paratracheal, vasicentric	1-4 seriate, 8-10/mm, heterocellular	160-480 4-17	Ray cells	Absent	Mio-Plio / India	Prakash & Tripathi 1975
<i>Burseroxylon garugoides</i>	Absent	105-345 5-10, tylose	Septate, thin to thick walled	Scanty paratracheal, vasicentric	1-5 seriate, 10-15/mm, heterocellular	- 6-18	Ray cells	Absent	Mio-Plio / India	Lakhanpal <i>et al.</i> 1981
<i>Canarioxylon ceskobudejovicense</i>	Absent	< 225 8-24, tylose	Septate, thin to thick walled	Scanty paratracheal	1-4 seriate, 6-9/mm, heterocellular 1-2 cells tailed, (end-to-end fusion)	-	(Ray cells)	Absent	Oligocene ? / Czech Rep.	Prakash <i>et al.</i> 1974
<i>Canarioxylon chieveleyense</i>	Absent	101-121 15-22, tylose	Septate, thin-walled	Vasicentric	1-4 seriate, 9-17/mm, heterocellular 1 cell tailed	295-366 15-18	Absent	Absent	Paleocene / England	Crawley 2001
<i>Canarioxylon indicum</i>	Absent	133-266 -, tylose	Septate, thick-walled	Scanty paratracheal, vasicentric	1-3 seriate, heterocellular	199-732 8-35	Absent	Absent	Tertiary / India	Ghosh & Roy 1978
<i>Canarioxylon noduliforme</i>	Distinct	85-140 15-20, tylose	Septate, thin to thick-walled	Scanty paratracheal, (vasicentric)	1-5 seriate, 5-7/mm, heterocellular 3-5 cells tailed, end-to-end fusion	- 20-35	Rays cells, axial parenchyma	Radial / diffuse 25-40	Tertiary / China	Yang <i>et al.</i> 1995
<i>Canarioxylon shapurensis</i>	Absent	75-250 12-25	Septate	Scanty paratracheal, vasicentric	1-4 seriate, heterocellular	-	Absent	Absent	Tertiary / India	Trivedi & Srivastava 1985
<i>Canarium palaeolazonicum</i>	Absent	50-170 11-18, tylose	Septate, thick-walled	Scanty paratracheal, (vasicentric)	1-4(7) seriate, heterocellular 1-2+ cells tailed	- up to 40	Ray cells	Radial 48-96	Moi-Plio / India	Awasthi & Srivastava 1989
<i>Garugoxylon pinnatoides</i>	Distinct	44-200 12-27, tylose	Septate, thin to thick-walled	Scanty paratracheal	1-4 seriate, 7-8/mm, heterocellular, 1-5 cells tailed	80-560 2-20	Rays cells	Radial 31-43	Pleistocene / Cambodia	Vozenin-Serra & Privé Gill 1991

<i>Boswellioxylon indicum</i>	Absent	60-180 -	Thick-walled	Scanty paratracheal	(1-6)2-4, heterocellular	-	Absent	Present	Tertiary (Eocene ?) / India	Dayal 1966 (Awasthi & Srivastava 1989)
<i>Tetragastroxylon magniporus</i>	Indistinct	140-327 (5)7-16, tylose	Septate	Absent	1 seriate, heterocellular, (multiseriate 1-4 cells tailed), 5-11/mm,	- 6-14	Druse (and oil drops ?) in procumbent parenchymal rays	Radial in multiseriate 50-95	Miocene / Mexico	Martinez- Cabrera, Cevallos-Ferriz & Poole 2006
<i>Burseroxylon preserratum</i>	Absent	90-280 (mean 190) 2-13, tylose	Septate, thin- walled	Scanty paratracheal, vasicentric	1-4 seriate, 3-12/mm, heterocellular 1-3 cells tailed	150-640 4-23	(Ray cells)	Absent	Miocene / Myanmar	This study



#### TABLE CAPTIONS:

**Table 1.** A simplified identification key for fossil Dipterocarpaceae (based on Schweitzer 1958; Prakash & Awasthi 1970, 1971; Prakash 1973).

**Table 2:** Distribution of fossil taxa for the Natma Formation among extant tropical forests of the Indo-Burman region, according to their Nearest Living Relatives (after Soerianegara & Lemmens 1993; Lemmens *et al.* 1995; Sosef *et al.* 1998; IUCN 2020; Tropical Plants Database 2020; and other publications cited above). Only the one or two most convincing NLR have been taken into consideration. ● : 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 savannas. The specimen of *Cupressoxylon* is not used here, as not diagnostic of any particular environment.

#### FIGURE CAPTIONS:

**Figure 1.** (a) Simplified map of Myanmar showing the location of the field sites. Location of the fossil site is indicated with a green star; 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.

**Figure 2.** *Cupressinoxylon sp.*: **A**, transverse section (Ts), growth rings and zonate parenchyma (large black areas are cells filled with sediments); **B**, Ts, growth ring with gradual transition from earlywood to latewood; **C**, tangential longitudinal section (Tls), 1- sometimes 2- seriate rays and parenchyma lines (arrow); **D**, Tls, 1- sometimes 2- seriate rays; **E**, Tls, smooth longitudinal parenchyma walls (arrows); **F**, Tls, 1-2-seriate rays and tangential pits (arrow); **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.

**Figure 3.** *Albizinium eolebbekianum* Prakash (**A-D**): **A**, Ts, vessels and parenchyma arrangement; **B**, Tls, 1-3-seriate rays and crystalliferous parenchyma (arrow); **C**, Rls, homocellular rays; **D**, Tls, possible septate fibre. *Cynometroxylon holdenii* (Gupta) Prakash & Bande (**E-H**): **E**, Tr, banded parenchyma and vessels pattern; **F**, Tls, heterocellular and mostly 2-seriate rays; **G**, Rls, heterocellular rays with 1-2 uprights marginal rays cells; **H**, Ts, included phloem present in 17FN17. Scale bars: A, E, H, 1 mm; C, G, 500 µm; B, F, 200 µm, D, 25 µm.

**Figure 4.** *Cynometroxylon parinaequifolium* Prakash (A-G). Specimen 17FN10 (A-C): **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 upright marginal cells. Specimen 19NAT07-1 (D, F): **D**, Ts, vessel size and pattern, banded parenchyma with some aliform parts (arrow); **F**, Tls, 1-2 seriate heterocellular rays with upright marginal cells. Specimen NAT17-7 (E, G): **E**, Ts, vessel size and pattern, banded parenchyma with some aliform parts (arrow); **G**, Tls, 1-3 seriate heterocellular rays with upright marginal cells. Scale bars: A, D-E, 1 mm; B, F-G, 200  $\mu$ m; C, 85  $\mu$ m.

**Figure 5.** *Koompassioxylon elegans* Kramer (A-C): **A**, Ts, Vessel size and groups, aliform parenchyma with pointed wings and marginal parenchyma (arrow); **B**, Tls, 2-3 seriate rays with crystalliferous parenchyma; **C**, Rls, heterocellular rays with crystals in upright marginal cells. *Koompassioxylon kalewensis* n. sp. (D-H): **D**, Ts, mostly solitary vessels with aliform and aliform-confluent parenchyma, sometimes forming short bands; **E**, Tls, 1-3 seriate heterocellular rays with end-to-end fusions (arrow); **F**, Tls, storied tendency of rays; **G**, Rls, heterocellular rays, sometimes with mixed character, with upright marginal cells and crystalliferous parenchyma; **H**, Rls, vessel-ray pits. Scale bars: A, D, 1mm; B-C, E, G, 200  $\mu$ m; F, 500  $\mu$ m; H, 50  $\mu$ m.

**Figure 6.** *Pahudioxylon bankurensis* Chowdhury, Ghosh & Kazmi (A-C): **A**, Vessels, aliform parenchyma with marginal crystals (black arrow) and marginal parenchyma (white arrow); **B**, 2-3 seriate rays with crystalliferous parenchyma; **C**, homocellular rays. *Pahudioxylon adenanthroides* n. sp. (D-H): **D**, mostly solitary vessels, aliform parenchyma with marginal crystals (white arrow), marginal parenchyma and diffuse parenchyma (black arrows); **E**, storied rays; **F**, 1-3 seriate homocellular rays and parenchyma cells; **G**, crystals in parenchyma strands; **H**, homocellular ray. **A, D**, transversal sections; **B, E, F**, tangential longitudinal sections; **C, G, H**, radial longitudinal section. Scale bars: A, D, 1 mm; B, F-G, 200  $\mu$ m; C, H, 100  $\mu$ m; E, 500  $\mu$ m.

**Figure 7.** *Artocarpoxylon informe* n. sp. (A-E): **A**, Ts, Sparse vessels, vasicentric parenchyma sometimes aliform, mostly without any particular arrangement; **B**, Ts, vasicentric parenchyma; **C**, Tls, 1-6 seriate rays with upright marginal cells; **D**, Tls, 1-6 seriate rays with sheath cells (black arrow) and end-to-end fusions (white arrow); **E**, Rls, heterocellular sometimes appearing with upright and procumbent cells mixed due to sheath cells and fusions. *Anisopteroxylon cf. garoense* (Chowdhury) Prakash & Tripathi (F-I): **F**, Ts, strongly compressed wood, poorly distinguishable vessels, seemingly mainly solitary; **G**, Tls, 1-7 seriate

rays with continuous sheath cells all around multiseriate rays; **H**, Rls, heterocellular rays sometimes appearing mixed due to sheath cells; **I**, Tls, tracheid. Scale bars: A, F, 1mm; B, D-E, H, 200  $\mu$ m; C, G, 500  $\mu$ m; I, 50  $\mu$ m.

**Figure 8.** *Dipterocarpoxyton fugax* n. sp.: **A**, Ts, mostly solitary vessels and vasicentric parenchyma; **B**, Tls, 2-4 seriate homo- to heterocellular rays; **C**, Ts, short tangential line of secretory canals, smaller than vessels, embed in parenchyma band; **D**, Rls, an example of heterocellular ray with one line of upright marginal cells (arrow). Scale bars: A, 1 mm; B, D, 200  $\mu$ m; C, 500  $\mu$ m.

**Figure 9.** *Dryobalanoxylon indicum* (Ramanujam) Awasthi: **A**, Ts, Vessel arrangement, mostly solitary, and long tangential line of secretory canals embed in parenchyma band (between arrows); **B**, Tls, tracheid fibre; **C**, Tls, 1-6 seriate rays with some sheath cells (black arrows), vasicentric tracheids and tracheid fibres (white arrow); **D**, Ts, detail of secretory canals; **E**, Ts, budding of tyloses (arrow). Scale bars: A, 1 mm; B, 100  $\mu$ m; C-E, 200  $\mu$ m.

**Figure 10.** *Shoreoxylon cf. deomaliense* Prakash & Awasthi: **A**, Ts, vessels and long tangential line of secretory canals embed in parenchyma bands (arrows); **B**, Tls, vasicentric tracheid; **C-D**, Tls, long 1-6 seriate rays with end-to-end fusion; **E**, Rls, crystals in parenchyma; **F**, Ts, detail of vasicentric to aliform parenchyma, possibly also diffuse parenchyma; **G**, Rls, heterocellular ray with upright marginal cells. **A**, **F**, transversal sections; **B-D**, Tls, tangential longitudinal sections; **E**, **G**, Rls, radial longitudinal section. Scale bars: A, 1 mm; B, 50  $\mu$ m; C, G, 200  $\mu$ m; D, F, 250  $\mu$ m; E, 100  $\mu$ m.

**Figure 11.** *Shoreoxylon cf. sumatraense* Du: **A**, Ts, vessel in groups, sometime in clusters of small vessels (arrow); **B**, Ts, long tangential lines of secretory canals (arrows) close to each other; **C-E**, Tls, 1-4 seriate rays; **F**, Rls, heterocellular ray with upright marginal cells (arrows). Scale bars: A, 1 mm; B, 330  $\mu$ m; C, 500  $\mu$ m; D-F, 200  $\mu$ m.

**Figure 12.** *Shoreoxylon glomeratum* n. sp.: **A**, Ts, Vessels sometimes in clusters, abundant parenchyma, short lines and diffuse secretory canals (arrows); **B-C**, Tls, 1-5 seriate rays; **D**, Rls, heterocellular rays with one line of upright cells; **E**, Tls, tracheid (arrow). Scale bars: A, 1 mm; B, 200  $\mu$ m; C-D, 500  $\mu$ m; E, 50  $\mu$ m.

**Figure 13.** *Shoreoxylon* sp. (**A-E**): **A**, Ts, vessel arrangement, often solitary, sometime in groups and clusters, with one line of presumed parenchyma (arrow) possibly marking a line of secretory canals of growth limit; **B, D**, Tls, 1-5 seriate rays; **C**, Ts, long tangential line of secretory canals embed in parenchyma band (arrow); **E**, Rls, heterocellular ray with one line of upright marginal cells (arrow). *Burseroxylon*

*preserratum* Prakash & Tripathi (**F-H**): **F**, Ts, vessels with tylose and vasicentric parenchyma (arrow); **G**, Tls, (1)-4 seriate rays, septate fibres (arrow); **H**, Rls, heterocellular rays with upright marginal cells. Scale bars: A, F, 1 mm; B, E, G-H, 200 µm; C, D, 500 µm.

**Figure 14.** *Indet. sp.1*: **A**, Ts, vessel arrangement, few parenchyma, some small pores surrounded par parenchyma that could be isolated canals (arrow); **B**, Ts, the parenchyma seems to be vasicentric or aliform (arrow), maybe also diffuse; **C-D**, Tls, 1-5 seriate rays, with sometimes long uniseriate tails and sheath cells; **E**, Rls, heterocellular rays with upright and procumbent cells mixed throughout the rays. Scale bars: A-B, 1 mm; C-E, 200 µm; D, 500 µm.

**Figure 15.** *Indet. sp.2* (**A-F**): **A**, Ts, Vessels and few parenchyma cells, vasicentric, some remarkably big pores (arrows); **B-C**, Tls, 1-4 seriate rays with sometimes long uniseriate tails and maybe sheath cells; **D**, Rls, heterocellular rays with procumbent (white arrow) and upright (black arrow) cells mixed throughout; **E**, Ts, detail of big pores often gathered and tangentially aligned; **F**, Tls, comparison of a well identified vessel (white arrow) and a possible secretory canal (black arrow) as perforations are not seen and parenchyma is found all along. *Indet. sp.3* (**G-J**): **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 upright cells. Scale bars: A, G, 1 mm; B, D, F, H, 500 µm; C, E, I-J, 200 µm.

**Figure 16.** Comparison between Eocene (Licht *et al.* 2014, 2015) and Miocene (this study) forest assemblage and diversity of Myanmar with the list of related fossil genus and supposed forest type they belong to. Underlined names are genus found in both formations. Yellow stars mark the schematic position of sampling sites

#### APPENDICES CAPTIONS:

**Appendix 1.** Synthetic table describing a selection of fossil wood specimens of *Albizinium* and *Acrocarpoxylon*. () : occur rarely.

**Appendix 2.** Synthetic table describing a selection of fossil wood specimens of *Cynometroxylon*, *Bauhinium* and fossil *Bauhinia* and *Cynometra*. () : occur rarely. Authors in parentheses: data about the species found in this publication whereas in the original one.

**Appendix 3.** Synthetic table describing a selection of fossil wood specimens of *Ormosioxylon*, *Koompassioxylon* and *Saracoxylon*. () : occur rarely.

**Appendix 4.** Synthetic table describing a selection of fossil wood specimens of *Pahudioxylon* and *Adenantheroxylon*. () : occur rarely. Authors in parentheses: informations about the species found in this publication whereas in the original one.

**Appendix 5.** Synthetic table describing a selection of fossil wood specimens of *Artocarpoxylon* and *Tetrameloxylon*. () : occur rarely.

**Appendix 6.** Synthetic table describing a selection of fossil wood specimens of *Anisopteroxylon*. () : occur rarely. Authors in parentheses: data about the species found in this publication whereas in the original one.

**Appendix 7.** Synthetic table describing a selection of fossil wood specimens of *Dipterocarpoxyton*. () : occur rarely.

**Appendix 8.** Synthetic table describing a selection of fossil wood specimens of *Dryobalanoxyton*. () : occur rarely. Authors in parentheses: informations about the species found in this publication whereas in the original one.

**Appendix 9.** Synthetic table describing a selection of fossil wood specimens of *Shoreoxylon* and *Hopenium*. () : occur rarely. Authors in parentheses: data about the species found in this publication whereas in the original one.

**Appendix 10.** Synthetic table describing a selection of fossil wood specimens of Burseraceae available during this study. () : occur rarely. Authors in parentheses: data about the species found in this publication whereas in the original one.