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Research paper

Fossil woods (Malvaceae) from the lower Miocene (early to mid-Burdigalian) part of the Cucaracha Formation of Panama (Central America) and their biogeographic implications

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ABSTRACT

Nine fossil wood specimens are described from the Miocene (early to mid-Burdigalian) part of the Cucaracha Formation of Panama, Central America. The calcareous permineralised fossils, which contain *Teredolites* borings, occur in erosive-based pebbly conglomerate lenses, interpreted as tidally influenced fluvial channels. All specimens show tile cells characteristic of many clades of the diverse and widespread family Malvaceae sensu APG III. Fossils were identified, more precisely, through searches of the Insidewood Database, and detailed study of comparative extant material. Two novel types of fossil wood occur: (1) *Guazumaoxylon miocenica* gen. et sp. nov shows paratracheal axial parenchyma with a broad-sheath to winged-aliform distribution combined with intermediate-type tile cells, similar to tropical South American species of *Guazuma* (subfamily Byttnerioideae) and (2) *Periplanetoxylon panamense* gen. et sp. nov shows apotracheal axial parenchyma in irregular to regular bands >3 cells wide combined with *Pterospermum*-type tile cells, similar to tropical South American species of *Pentaplaris* (subfamily Malvoideae). The occurrence of fossils showing similarities to extant South American taxa in the Miocene of Panama is of palaeogeographic significance, suggesting intercontinental exchange of tree species at least ten million years before the traditional date for the final closure of the Panama Isthmus.

1. Introduction

The collision of the Americas and the formation of the Panama Isthmus was one of the most important events in the recent history of the planet. It altered global patterns of ocean circulation (Schneider and Schmittner, 2006), possibly contributing to the onset of the thermohaline circulation (Nisancioglu et al., 2003; Von der Heydt and Dijkstra, 2006) and also triggered what has been called the Great American Interchange — the migration of animals and plants between North and South America (Marshall et al., 1982; Burnham and Graham, 1999). Traditionally, the collision of the Americas was thought to have occurred around 3–4 million years ago (middle to late Pliocene), coinciding with the sharp rise in the proportion of North American ungulate genera in South America (Webb, 1991). However, more recent work (reviewed below) suggests that the event may have commenced earlier and was more complex than previously thought (Montes et al., 2012).

Although still incompletely understood, there is a growing consensus that the Panama Isthmus formed through the uplift of a jumble of small allochthonous terranes caught between the Farallon, Cocos and Nazca plates to the south and the Caribbean Plate to the north, in response to the northward convergence of South America (Case et al., 1984). There are two hypotheses about the nature and evolution of the Panama Isthmus in early Miocene times: (1) the isthmus region comprised a continuous southernmost peninsula of North America or (2) the isthmus region comprised a disconnected archipelago of volcanic islands (an island arc) extending south from North America. The Peninsula Hypothesis is supported by the close similarity between Panamanian and North American mammals (Whitmore and Stewart, 1965; Kirby and MacFadden, 2005) and also by inferences about body size, which are inconsistent with concepts of island biogeography (Kirby and MacFadden, 2005). The Archipelago Hypothesis is supported by geological studies of isolated outcrops, biostratigraphic and radiometric dating, and paleobathymetric data from benthic foraminifera (Coates and Obando, 1996; Coates et al., 2004). Whichever hypothesis is correct, marine units in Panama show that a moderately deep, but narrow, marine seaway, represented by sediments of the Punta Alegre Formation, connected northwestern Panama to the Pacific along a portion of the Central American Seaway in early Miocene times (c. 18.5–21.5 Ma; Coates et al., 2003). The seaway had shallowed significantly by the middle Miocene, and by latest middle Miocene times, the pre-isthmian Bocas del Toro region shallowed even further, so that by ~12 Ma there existed a substantial subaerial volcanic backarc parallel to the main Central Cordilleran arc (Montes et al., 2012). However, the

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degree to which this feature facilitated intercontinental biotic exchange is currently uncertain.

The recent widening of the Panama Canal, which commenced in 2007, has provided once-in-a-century access to Miocene successions deposited immediately before, and during, the complex convergence of the Americas. In these new sections, well-preserved assemblages of fossil wood have been exposed in the lower Miocene Cucaracha Formation. Determining the identity of these trees as precisely as possible, and assessing whether their affinities are with present-day North or South American taxa, is important because it could shed light on the timing and magnitude of intercontinental exchange of tree species prior to the final closure of the Panama Isthmus — a key biogeographic question. In this paper, we describe the anatomy of nine well-preserved specimens of Malvaceae fossil wood, identify them through qualitative and quantitative comparison with extant taxa, and consider their biogeographic implications.

2. Geological context

The nine fossil wood specimens studied here were collected at Hodges Hill (Latitude 09°02′51.75″N; Longitude 79°39′14.02″W), located in the Gaillard Cut, the narrowest section of the Panama Canal, Panama (Fig. 1). This locality exposes a succession through the lower Miocene Cucaracha Formation in weathered slopes on the western banks of the Panama Canal. The Cucaracha Formation is ~60 m thick and accumulated in terrestrial settings (Fig. 2).

2.1. Sedimentary facies and fossil wood assemblages

The lowermost part of the Cucaracha Formation, from which the fossil woods were obtained, contains two main facies: mottled claystones and pebbly sandstone lenses (Fig. 2). The claystone successions are typically purple-green and up to 10 m thick, and show red mottling and/or prominent carbonate rhizoconcretions at local horizons. The pebbly sandstone units are typically lenses, tens of metres wide and 1–3 m thick; they show a shallowly erosive base and may fine upwards. Ostreid bivalve fragments are rarely observed as clasts within the sandstone. Pebbles are sub-rounded and locally show invertebrate borings while others show a haematitic varnish. Where rare trough cross-beds are seen, they show herringbone beds with bimodal palaeocurrent azimuths of ~100° and ~280°.

The fossil woods described herein are found ~20 m above the base of the Cucaracha Formation, and occur as an allochthonous assemblage within the pebbly sandstone beds (Figs. 2, 3A). In some parts of the Hodges Hill locality, these woods are abundant and comprise trunks,

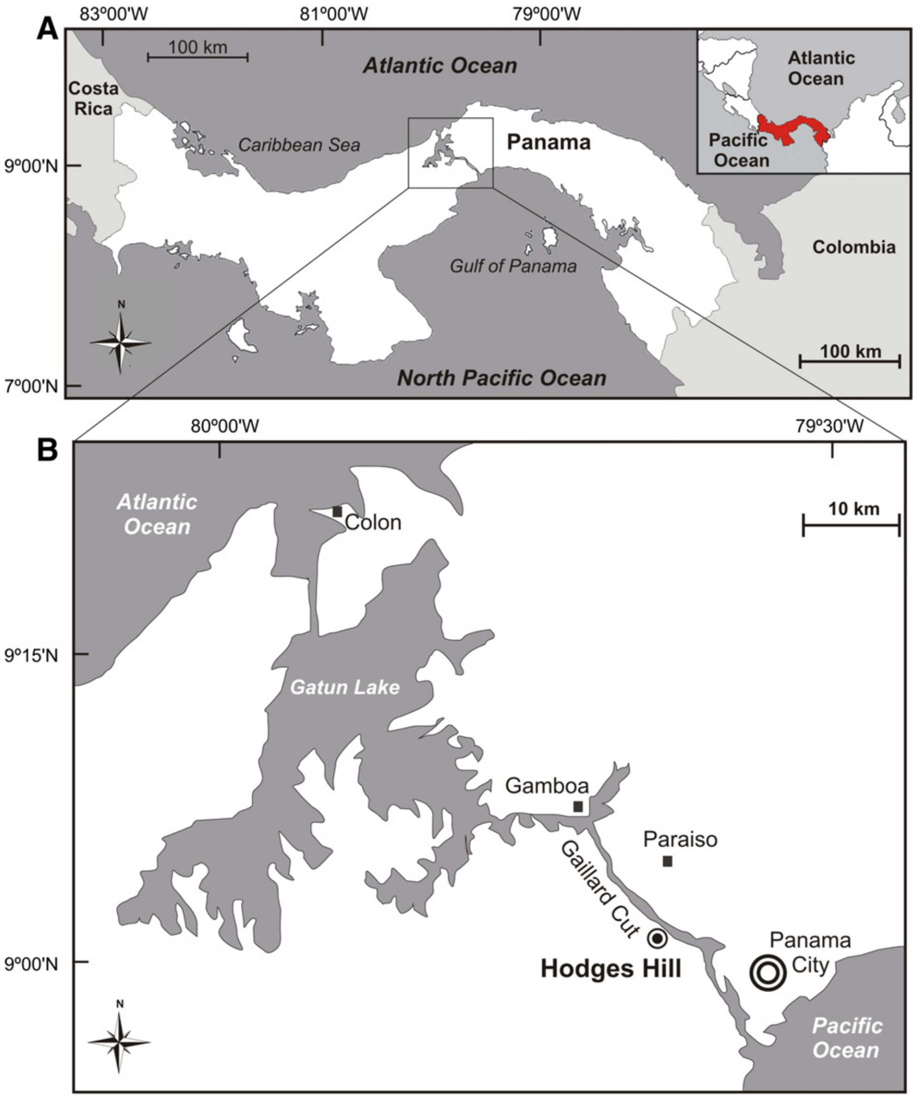

Fig. 1. Locality maps. A, shows the position of Panama in Central America. B, Panama Canal Zone, showing the location of the Hodges Hill fossil site within the Gaillard Cut.

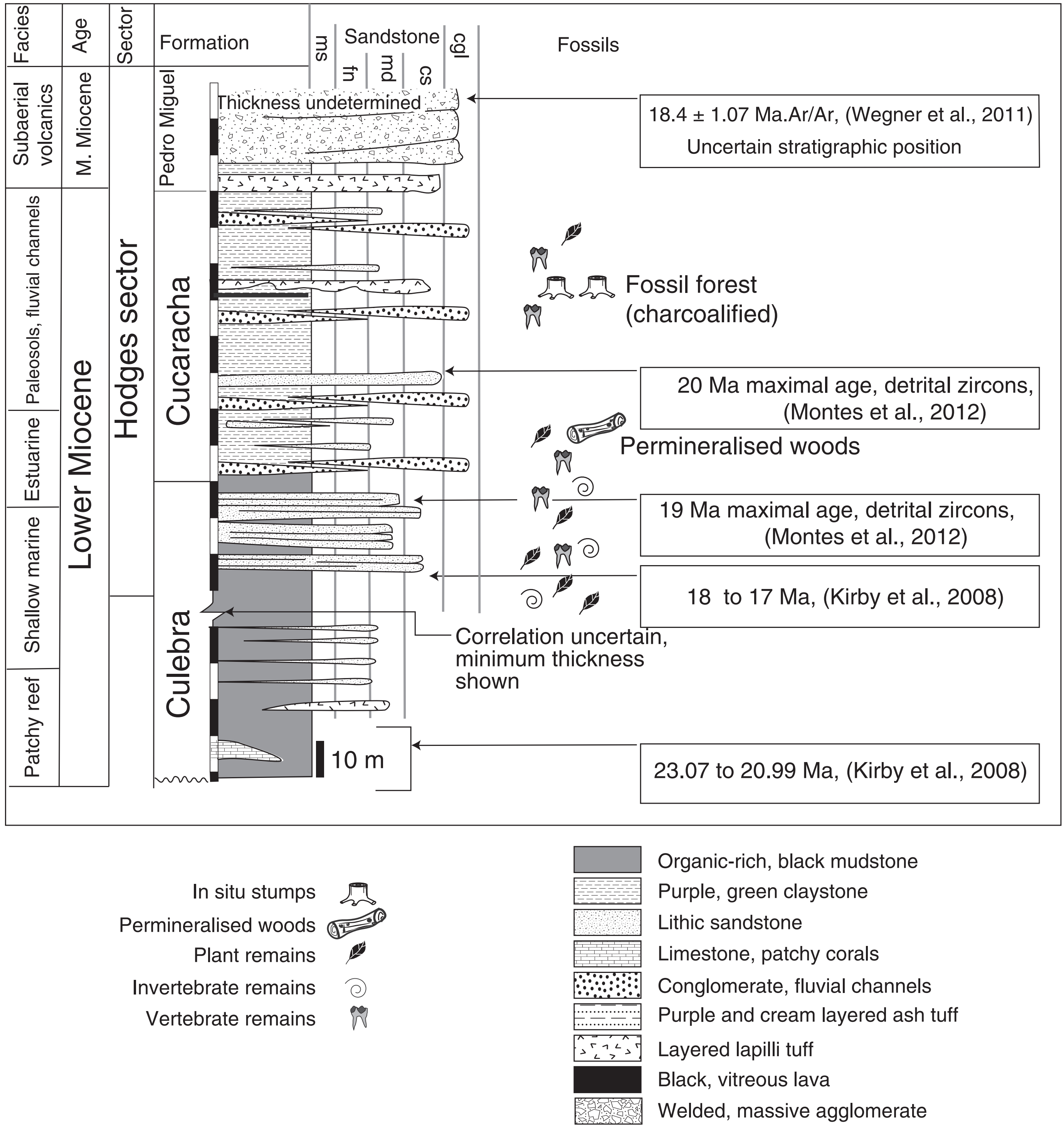

Fig. 2. Composite graphic log of the Miocene strata in the Panama Canal Zone showing key dated marker beds and the horizon with the permineralised wood studied here in the lowermost Cucaracha Formation.
After Montes et al. (2012).

0.4–3 m long and typically 0.2–0.6 m diameter. The fossil wood commonly contains *Teredolites* borings (Fig. 3B–C).

2.2. Palaeoenvironmental interpretation

The claystones that dominate the lower part of the formation are interpreted as a succession of cumulative paleosols. The pebbly sandstone units are interpreted as fluvial deposits (Miall, 1977, 1992). Based on (1) the presence of pebbles with invertebrate borings, (2) the occurrence of rare ostreid bivalve clasts, (3) the weak indications of bimodal palaeoflow, (4) the stratigraphic proximity to the shallow marine facies of the underlying Culebra Formation (Hendy, 2011), and (5) the abundant terrestrial vertebrate fossil fauna (MacFadden, 2006; MacFadden et al., 2010), these fluvial channels are interpreted as existing close to the marine coast, and could represent tidally-influenced estuaries (there is no indication of upward coarsening that might suggest a deltaic setting). This interpretation is supported by widespread *Teredolites* borings in the fossil wood, produced by

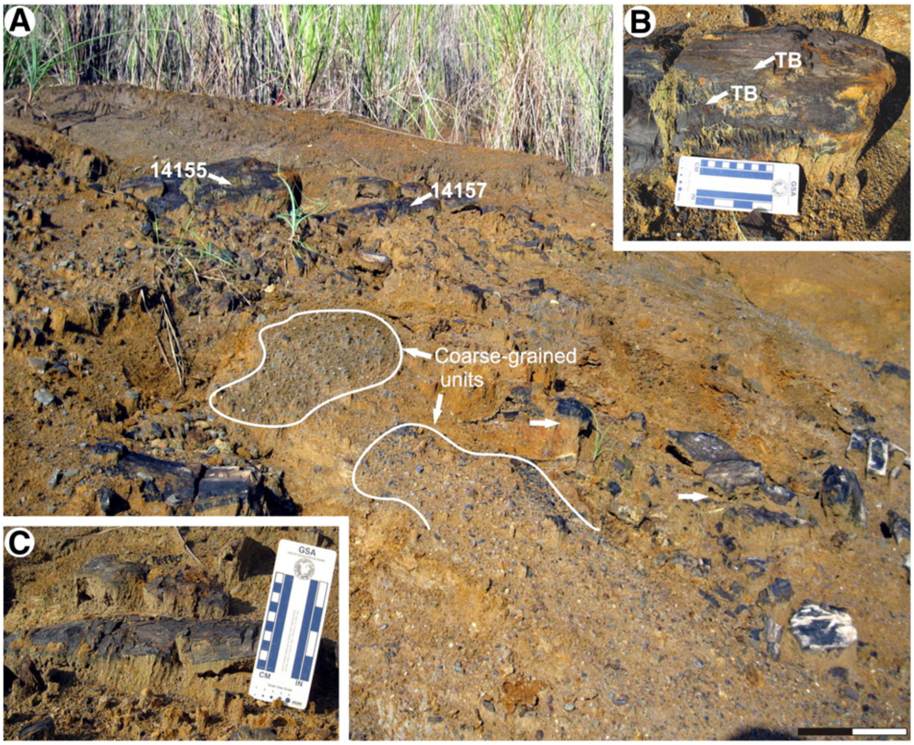

Fig. 3. Field context of the fossils preserved in weathered slopes at Hodges Hill, Panama Canal Zone. A., permineralised tree-trunks in coarse-grained sandstone facies; B–C., close-up of some of the fossil specimens (STRI 14155, STRI 14157), showing *Teredolites* borings (TB).

xylophagous bivalves (Lane, 1959; Carlton and Ruckelshaus, 1997; Rowley, 2005) found in a broad range of marine habitats including estuaries (Cohen and Carlton, 1995; Didziulis, 2007), and reported from the Pacific Coast of Panama and Colombia (Cantera, 2010).

2.3. Age of fossil woods

The Cucaracha Formation conformably overlies the Culebra Formation, which contains a rich marine fauna in its lower part (Retallack and Kirby, 2007; Hendy, 2011) of early Miocene (Aquitanian) age, and has yielded lower Miocene (early Burdigalian) strontium dates of 19.38–19.12 Ma in its upper part (Kirby et al., 2008). The Cucaracha Formation conformably underlies basalts and agglomerates in the lower part of Pedro Miguel Formation. A radiometric date of 18.4 ± 1.07 Ma was obtained from these volcanic strata in a different area, indicative of early Miocene (mid- to late Burdigalian age; Wegner et al., 2011); however, its exact stratigraphic position in relation to our studied section is uncertain (Montes et al., 2012). Detrital zircon populations with maximal ages of 19–20 Ma (early Burdigalian) were recovered from the upper part of the Culebra Formation and the lower part of the Cucaracha Formation (Montes et al., 2012). These absolute dates are in generally good agreement with relative ages for the Cucaracha Formation based on its mammalian assemblage, found in its upper part, which includes seven North American species typical of the Hemingfordian–lower Bastovian regional stages (early Miocene, Burdigalian–early Langhian; MacFadden and Higgins, 2004; MacFadden, 2006). The fossil woods described here, which come from ~20 m above the base of the Cucaracha Formation, are therefore, probably, of early to middle Burdigalian age (Fig. 2).

3. Material and methods

Nine fossil wood specimens were studied (accessioned as STRI 14151, 14155, 14157, 14159, 14160, 14161, 14164, 36269, and 36270) in the collections of the Center for Tropical Paleoecology and Archaeology, Smithsonian Tropical Research Institute, Panama.

3.1. Fossil wood preparation and imaging

Standard petrographic thin sections were prepared in the Department of Earth Sciences, Royal Holloway, University of London, orientated in Transverse Section (TS), Radial Longitudinal Section (RLS) and Tangential Longitudinal Section (TLS); material was not studied with the acetate peel technique because sub-cellular anatomy is generally poorly visible in angiosperm fossil wood peels. Petrographic thin sections were imaged using an Olympus binocular BH-5 microscope with a Nikon digital camera system and software. Anatomical preservation of these calcareously permineralised woods is generally good, allowing for detailed description and comparison with microscope slides of extant woods in reference collections. Images of modern woods were obtained, for comparative analysis, using a Leica DM LB microscope with Zeiss Axiocam HRc camera attachment and Zeiss Axiovision software.

3.2. IAWA feature description

Specimens were described using the International Association of Wood Anatomists (IAWA) List of Features for Hardwood Identification (IAWA (International Association of Wood Anatomists) Hardwood Committee, 1989). In this standard descriptive system, anatomical characters (termed features) are given a numerical code. Most features are qualitative (requiring determination of presence or absence) but others are quantitative (requiring measurement of a population). To obtain quantitative data for vessel and ray density, and the degree of vessel grouping, measurements were made in 10 different fields of 1 mm^2 area. For other quantitative features (e.g., mean vessel diameter, intervessel pit diameter, vessel-ray pit diameter, vessel element length, ray height), a minimum of 25 measurements was obtained, but where preservation allowed, 50 measurements were obtained. At the start of each of our fossil descriptions, anatomical features are listed as a string of numerical IAWA codes. In this list, features may be qualified by one of two signs as follows: "?" indicates that there is uncertainty as to whether the feature is present and "v" indicates that the feature is variable in occurrence.

3.3. Insidewood Database searches

Following description, we searched the modern wood section of the Insidewood Database (IWD, insidewood.lib.ncsu.edu) – an online database containing >8500 modern and fossil wood descriptions (last accessed 21 April 2014) – using different combinations of features that we considered especially diagnostic. In these searches the strategies recommended by Wheeler (2011) and Falcon-Lang et al. (2012) were followed, and we also avoided putting too much emphasis on variable quantitative features. Searches were repeated with different combinations, and an exhaustive study of micrographs in the IWD was undertaken, to create a short-list of potentially comparable taxa.

3.4. Comparison with wood collections of extant taxa

Fossils were compared with slides of modern taxa on the IWD short-list, and other taxa considered relevant, accessioned in the Utrecht University and Leiden University wood collections (both now housed in the National Herbarium, Leiden, Netherlands) and the Jodrell Laboratory collection (housed at the Royal Botanic Gardens, Kew, UK). These repositories are hereafter referred to collectively as the 'wood reference collections'. Some of the major monographs on wood identification (Chattaway, 1937; Metcalfe and Chalk, 1950; Manchester and Miller, 1978; Wheeler and Manchester, 2002) were also consulted.

4. Fossil wood descriptions

The nine specimens studied here comprise two distinct fossil wood types (Table 1). Although only limited fossil material is available for study, new fossil taxa are erected for this material because the combination of characters observed is very unusual, not only amongst previously described fossil woods but also in extant trees.

Fossil Wood Type 1

GUAZUMAOXYLON Rodríguez-Reyes, Falcon-Lang, Gasson, Collinson, Jaramillo, gen. nov., Plates (I–II).

Order: Malvales Jussieu ex Berchtold et J. Presl

Family: Malvaceae Jussieu

Type species: Guazumaoxylon miocenica Rodríguez-Reyes, Falcon-Lang, Gasson, Collinson, Jaramillo, sp. nov.

Combined generic and specific diagnosis: Wood diffuse-porous; vessels solitary or in radial multiples of 2–5 (–6); perforation plates simple; intervessel pitting alternate and minute; vessel-ray pits similar in diameter and shape to intervessel pits; rays are mostly 1–2 (–4)-seriate and >1 mm high; apotracheal axial parenchyma diffuse and paratracheal broad sheath to winged-aliform; fibres non-septate alternating with a few septate fibres; sheath cells and *Guazuma* intermediate-type tile cells present. Solitary crystals in square or upright cells.

Etymology: in reference to its similarity with extant *Guazuma*.

Discussion: This material shows intermediate-type tile cells, and other features, characteristic of the extant genus *Guazuma*. However, we are reluctant to place this specimen directly into the extant genus because of its antiquity and because fossil wood generally has a rather conservative preservation of anatomical characters. Therefore, we erect a new genus for the fossil to reflect its close inferred similarities to the extant plant. In doing so, we are aware of a number of fossil wood genera (e.g., *Grewioxylon*) with similar, though not completely overlapping features, and recommend a general revision of such malvacean fossil woods, which is well beyond the scope of this present paper.

Guazumaoxylon miocenica Rodríguez-Reyes, Falcon-Lang, Gasson, Collinson, Jaramillo, sp. nov. (Plates I–II).

Holotype: STRI 14151 (Plates I, 1–7; II, 1–7), designated here, comprising hand specimen, in two pieces, and three thin sections in TS, RLS, and TLS orientation. Axis has a preserved diameter of 0.12 m.

Other material: STRI 36270, comprising one hand specimen with a preserved diameter of 0.18 m and a preserved length of 0.5 m.

Repository: Center for Tropical Paleoecology and Archaeology, Smithsonian Tropical Research Institute, Panama.

Type locality: Hodges Hill (Gaillard Cut of Panama Canal) near Paraiso, Panama City, Panama (Latitude 09°02′51.75″N; Longitude 79°39′14.02″W).

Stratigraphic horizon: ~20 m above the base of the Cucaracha Formation (Gaillard Group); lower Miocene.

Etymology: specific epithet *miocenica* refers to the age of the wood.

IAWA feature numbers present: 2, 5, 13, 22, 23, 24, 30, 41v, 42, 47, 53,? 61, 65v, 66, 69, 77v, 80, 82, ?92, ?93, 97, ?102, 109, 110, 111, 115, 136, and 137.

Description: Growth rings indistinct; wood diffuse-porous (Plate I, 1); vessels commonly solitary (65 and 67% in the two specimens) or in radial multiples of 2–5 (–6) (Plate I, 1, 2); vessel outline oval (Plate I, 2); perforation plates simple (Plate I, 3); intervessel pits alternate and minute (mean pit diameter 3; total range 2–5 μm) (Plate I, 4); vessel-ray pits with distinct borders, similar in diameter (mean pit diameters 2–3; total range 1–5 μm) and shape to intervessel pits (Plate I, 5); mean tangential vessel diameter for the two specimens 105 and 139 μm (total range 70–180 μm for both specimens); mean vessel density for the two specimens, both 16 per mm^2 (total range 6–23 per mm^2 for both specimens); mean vessel element length for the two specimens 376 and 468 μm (total range 250–710 μm for both specimens); tyloses absent; vascular tracheids not observed.

Fibres mostly non-septate, interspersed with a few septate fibres (Plate I, 6), and mostly thin- to thick-walled (Plate I, 7). Fibre pits not clearly observed due to preservation, but probably minutely bordered and on radial walls only.

Axial parenchyma paratracheal with a broad vasicentric sheath to winged-aliform distribution (Plate II, 1, 2); apotracheal axial parenchyma scarce, and diffuse-in-aggregates (Plate II, 1, 2); axial parenchyma strands poorly preserved, but probably c. 4–>8 cells high (Plate II, 3).

Rays heterocellular, 1–3 (–4)-seriate (mean ray width 2.2–3.0-seriate) (Plate II, 4, 5) and c. 1 mm high, or commonly higher, with means for the two specimens of 0.9 and 1.0 mm (total range 0.3–3.0 mm for both specimens) (Plate II, 4); rays composed of procumbent, square and upright cells mixed throughout the body (Plate II, 6); sheath cells (Plate II, 4, 5) and *Guazuma* intermediate-type tile cells present (Plate II, 6); mean ray spacing for the two specimens 8 and 12.8 per mm (total range 6–15 per mm for both specimens).

Solitary rhomboidal crystals present in square or upright ray cells (Plate II, 7).

Fossil Wood Type 2

PERIPLANETOXYLON Rodríguez-Reyes, Falcon-Lang, Gasson, Collinson, Jaramillo, gen. nov., Plates (III–V).

Order: Malvales Jussieu ex Berchtold et J. Presl

Family: Malvaceae Jussieu

Type species: Periplanetoxylon panamense Rodríguez-Reyes, Falcon-Lang, Gasson, Collinson, Jaramillo, sp. nov.

Combined generic and specific diagnosis: Wood diffuse-porous; vessels solitary or in radial multiples of 2–4; perforation plates simple; intervessel pitting alternate, polygonal and minute to small; vessel-ray pits similar in diameter and shape to intervessel pits; axial parenchyma in regular to irregular bands, 3–10 (–12) cells wide; rays 1–7 cells wide and with mean heights of <1 mm; sheath cells and *Pterospermum*-type tile cells prominent; solitary crystals in square or upright ray cells and, rarely, in axial parenchyma cells. Inferred juvenile specimens show bands of axial parenchyma up to 20 cells wide and aggregate rays up to 13-seriate.

Table 1
Summary of IAWA (International Association of Wood Anatomists) features of the nine fossil wood specimens reported here, and of the extant comparative taxa. Abbreviations: sol, solitary; alt, alternate; poly, polygonal; d-i-a, diffuse in aggregates; upr/sq, upright/square; n/a, feature not present; ?, no data; *few data.

Taxon	Fossil Wood Type 1 *Guazumaoxylon miocenica*		*Guazuma ulmifolia*	Fossil Wood Type 2 *Periplanetoxylon panamense*							*Pentaplaris doroteae*
Ontogeny	Mature		Mature	Mature					Juvenile		Mature
Specimen number	STRI 14151	STRI 36270	Kew	STRI 14155	STRI 14159	STRI 14160	STRI 14164	STRI 36269	STRI 14157	STRI 14161	Kew
Growth rings	Indistinct	Indistinct	Distinct	Indistinct	Indistinct	Indistinct	Indistinct	Indistinct	Indistinct	Indistinct	Indistinct
Porosity	Diffuse-porous	Diffuse-porous	Diffuse-porous	Diffuse-porous	Diffuse-porous	Diffuse-porous	Diffuse-porous	Diffuse-porous	Diffuse-porous	Diffuse-porous	Diffuse-porous
Vessel multiples	2–5 (–6); 67% sol	2–4; 65% sol	2–3 (–6); 34% sol	2–4; 72% sol	2–3 (–6); 70% sol	2–3 (–4); 54% sol	2–3; 78% sol	2–3; 83% sol	2–5; 50% sol	2–4; 53% sol	2–3 (–4); 41% sol
Perforation plates	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple
Intervessel pitting	Alt	Alt	Alt	Alt, poly	Alt	Alt, poly	Alt, poly	Alt, poly	Alt	Alt	Alt, poly
IVP diameter (μm); mean (range); type	3 ± 1 (2–5); minute	3 ± 1 (2–5); minute	5 ± 1 (3–7); small	6 ± 2 (3–9); small	3 ± 1 (1–6); minute	3 ± 1 (2–5); minute	4 ± 1 (2–6); minute	4 ± 2 (2–8); minute	5 ± 1 (3–8); small	3 ± 1 (2–7); minute	2 ± 0.4 (2–4); minute
Vessel-ray pit diameter (μm); mean (range); type	2 ± 0.8 (1–4); similar to IVP	3 ± 1 (2–5); similar to IVP	4 ± 1 (2–8); similar to IVP	4 ± 1 (2–7); similar to IVP	3 ± 1 (2–5); similar to IVP	3 ± 1 (2–4); similar to IVP	3 ± 1 (1–5); similar to IVP	5 ± 1 (3–8); similar to IVP	4 ± 1 (2–4); similar to IVP	3 ± 1 (2–5); similar to IVP	3 ± 0.4 (2–4); similar to IVP
Mean tangential vessel diameter (μm); mean (range)	105 ± 14 (70–140)	139 ± 23 (100–180)	115 ± 24 (60–150)	99 ± 16 (57–130)	112 ± 30 (75–200)	113 ± 22 (80–150)	86 ± 16 (70–120)	89 ± 22 (50–130)	127 ± 21 (94–172)	83 ± 15 (50–110)	104 ± 30 (65–160)
Vessels/mm^2; mean (range)	16 ± 4.6 (9–23)	16 ± 4.4 (6–22)	16 ± 5 (8–25)	15 ± 4.6 (4–18)	18 ± 6.8 (10–28)	14 ± 4.3 (8–20)	14 ± 5.3 (6–22)	7 ± 2.0 (5–12)	14 ± 2.6 (10–18)	14 ± 2.8 (10–17)	8 ± 2.5 (5–12)
Mean vessel element length (μm); mean (range)	468 ± 135 (340–710)	376 ± 133 (250–680)	317 ± 69 (220–480)	350 ± 11 (157–680)	332 ± 105 (160–600)	374 ± 106 (230–710)	335 ± 60 (230–460)	413 ± 158 (210–790)	412 ± 131 (260–730)	299 ± 74 (200–420)	308 ± 58 (250–400)
Fibre pits	Minutely bordered?	Minutely bordered?	Minutely bordered	?	Minutely bordered	Minutely bordered	Minutely bordered	Minutely bordered	?	?	Minutely bordered
Septate fibres	Few	Few	Few	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Fibre wall thickness	Thin to thick	Thin to thick	Thin to thick	Thin to thick	Thin to thick	Very thin or thin to thick	Very thin or thin to thick	Very thin or thin to thick	Thin to thick	Thin to thick	Very thick
Apotracheal axial parenchyma	Locally d-i-a	Locally d-i-a	D-i-a	Absent	Absent	Absent	Absent	Absent	D-i-a	Absent	Absent
Paratracheal axial parenchyma	Broad sheath to winged-aliform	Broad sheath to winged-aliform	Broad sheath to small winged-aliform	Scarce vasicentric	Scarce vasicentric; broad-sheathed	Absent	Winged-aliform occasional	Winged-aliform	Vasicentric	Absent	Vasicentric
Banded axial parenchyma (ap)	Absent	Absent	?Few	Regular bands, 3–8 cells wide	Regular bands, 3–10 cells wide	Regular bands, 3–>5? Cells wide	Regular bands, 4–9 cells wide	Regular bands, 3–7 (–12) cells wide	Regular bands, 3–15 cells wide	Regular bands, 3–16 (20) cells wide	Regular bands, 3–5 cells wide
Band (ap) spacing (μm)	n/a	n/a	n/a	210 ± 50; 150–310	217 ± 94; 70–400	170 ± 30; 130–200	172 ± 30; 100–450	294 ± 124; 85–500	160 ± 30; 120–200	210 ± 70; 100–400	249 ± 53.3; 195–475
Axial parenchyma strand length (cells high)	6–>8*	4*	4–5 (locally 6)	>8 (locally 5–8)	>8 (locally 5–12)	6–8 (locally 9–12)	4–6 (locally 4–12)	3–5 (locally 3–9)	3–6 (locally 7–12)	3–8 (locally 9–12)	5–8 (locally 9)
Ray width (cells); mean (range)	2.2 ± 0.8 (1–4)	3 ± 0.7 (1–4)	3.8 ± 1.5 (1–8)	3.9 ± 1.6 (1–7)	4.0 ± 0.9 (2–5)	3.7 ± 0.8 (2–5)	4 ± 1.1 (1–6)	5 ± 1.0 (3–6)	3.1 ± 1.3 (1–8)	4.4 ± 2.1 (2–10)	4.06 ± 1.3 (2–7)
Ray height (mm); mean (range)	1.0 ± 0.4 (0.6–2.0)	0.9 ± 0.4 (0.3–3.0)	0.4 ± 0.1 (0.2–1.3)	0.5 ± 0.3 (0.2–1.4)	0.5 ± 0.4 (0.2–1.2)	0.7 ± 0.3 (0.3–1.5)	0.6 ± 0.2 (0.2–1.2)	0.8 ± 0.2 (0.2–2.6)	0.7 ± 0.4 (0.3–2.2)	0.6 ± 0.2 (0.2–1.2)	0.3 ± 0.2 (0.1–0.6)
Abnormal ray width (cells high); mean (range)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	8.3 ± 2.7 (4–13)	7.2 ± 1.7 (5–11)	n/a
Abnormal ray height (mm); mean (range)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	1.5 ± 0.7 (0.6–3.1)	0.7 ± 0.3 (0.3–1.4)	n/a
Ray cellular composition	Mixed	Mixed	1–2 rows of marginal up/sq cells	Mixed	Mixed	Mixed	Mixed	Mixed	Mixed	Mixed	Mixed
Sheath cells	Present	Present	Present	Present	Present	Weakly developed	Present	Present	Present	Present	Present
Tile cells	Present	Present	Present	Present	Present	Present	Present	Present	Present	Present	Present
Perforated ray cells	Absent	Absent	Absent	Present	Absent	Present	Absent	Absent	Absent	Absent	Absent

Rays per linear mm; mean (range)	12.8 ± 1.2 (11–15)	8.0 ± 1.3 (6–10)	9 ± 1.4 (7–12)	11.3 ± 1.4 (9–12)	9.0 ± 0.9 (7–10)	9.6 ± 1.8 (7–12)	8.0 ± 1.3 (6–10)	9.0 ± 1.6 (7–13)	7.8 ± 1.3 (7–10)	11.4 ± 1.7 (9–14)	6.9 ± 2.9 (4–13)
Storied parenchyma/fibres	Absent	Absent	Few	Absent	Absent	Absent	Absent	Absent	Few	Absent	Absent
Crystals in non chambered upr/sq ray cells	Present	Present	Few	Present	Present	Present	Present	Absent	Present	Present	Present
Crystals in chambered axial parenchyma cells	Absent	Absent	Present	Absent	Absent	Absent	Absent	Absent	Few	Absent	Absent
Crystals in non chambered axial parenchyma cells	Absent	Absent	Present	Absent	Absent	Absent	Absent	Present	Present	Present	Present

Etymology: From the Latin *Periplaneta*, the generic epithet of common "cockroaches", to refer to the Spanish name of the formation containing these woods.

Discussion: Erection of a new genus is warranted because the occurrence of axial parenchyma in bands of >3 cells wide (85p) and tile cells (111p) is a highly unusual character combination in extant woods (based on searches of the IWD and the wood reference collections) and has never before been described in fossil woods.

Periplanetoxylon panamense Rodríguez-Reyes, Falcon-Lang, Gasson, Collinson, Jaramillo, sp. nov. (Plates III–V).

Holotype: STRI 14155 (Plates III, 1–7; IV, 2, 4–9), designated here, comprising hand specimen, in two pieces, and three thin sections in TS, RLS, and TLS orientation. Axis has a preserved diameter of 0.23 m.

Other material: STRI 14157, 14159, 14160, 14161, 14164, and 36269, comprising six hand specimens with preserved diameters ranging from 0.11 to 0.30 m (mean 0.17 m) and preserved lengths exceeding 2 m. STRI 14157 and 14161 contain lateral branches embedded in a trunk, and may include some juvenile material; they are described separately. We also note that STRI 14155 and 14157 occur closely adjacent to one another at Hodges Hill (about 1 m apart) and are disposed at a similar angle; although organic connection cannot be proven in outcrop, it is probable they represent separate parts of the same trunk (Fig. 3A).

Repository: Center for Tropical Paleoecology and Archaeology, Smithsonian Tropical Research Institute, Panama. Note that part of the hand specimen of STRI 14161 is also accessioned in the Museum of Biodiversity, Panama.

Type locality: Hodges Hill (Gaillard Cut of Panama Canal) near Paraiso, Panama City, Panama (Latitude 09°02′51.75″N; Longitude 79°39′14.02″W).

Stratigraphic horizon: ~20 m above the base of the Cucaracha Formation (Gaillard Group); lower Miocene.

Etymology: *panamense*, to reflect the origin of the fossil from Panama.

IAWA feature numbers present: 2, 5, 13, 22, 23v, 24v, 25v, 30, 41v, 42, 47, 53, 61, 66, 68v, 69, 77v, 85, 93, 94, 97, 98v, 102v, 109, 110, 111, 112, 115, 120v, 137, and 141v, 142v (juvenile material additionally shows: ? 92, 99v, 101v).

Description of five specimens inferred to be mature (Plates III–IV): Growth rings indistinct; wood diffuse-porous (Plate III, 1); vessels commonly solitary (mean values in range of 54–83% for all specimens) or in radial multiples of 2–4 (–6) (Plate III, 2); vessel outline oval to circular (Plate III, 2); perforation plates simple (Plate III, 3); intervessel pits alternate, minute to small (mean diameters, variable, 3–6 μm; total range 1–8 μm for all specimens) and polygonal (Plate III, 4); vessel – ray pitting distinctly bordered, similar in diameter (mean pit diameters 3–5 μm; ranges 1–8 μm for all specimens) and shape to intervessel pits (Plate III, 5); mean tangential vessel diameter with means for individual specimens in the range of 86–113 μm (total range 50–200 μm for all specimens); vessel density with means for individual specimens in the range of 14–15 per mm^2 (total range 7–18 per mm^2 for all specimens); vessel element length with means for individual specimens in the range of 332–413 μm (total range 157–790 μm for all specimens); tyloses and vascular tracheids not observed.

Fibres non-septate (Plate III, 6), and mostly thin- to thick-walled (Plate III, 7), although one specimen (STRI 14160) has thinner walled fibres (Plate III, 8). The differences are probably due to taphonomic factors; fibre pitting minutely bordered on radial walls only, but preservation only sufficient for observation in STRI 14160 (Plate IV, 1).

Axial parenchyma prominent in regular to irregular bands, typically 3–10 (–12) cells wide (Plate IV, 2); mean band spacing for individual specimens in the range of 170–294 μm (total range 70–500 μm for all specimens); axial parenchyma strands 3–12 cells high, with strands 8 or >8 cells high most common (Plate IV, 3, 4, 5).

Rays heterocellular, (1–) 2–5 (–7)-seriate (mean ray widths for individual specimens in the range of 3.7–5.0-seriate) (Plate IV, 6);

mean ray height <1 mm, with values for individual specimens in the range of 0.5–0.8 mm (total range 0.2–2.6 mm for all specimens); rays composed of procumbent, square and upright cells (Plate IV, 7); sheath cells generally conspicuous (Plate IV, 6), but weakly developed in STRI 14160 (Plate IV, 3); *Pterospermum*-type tile cells prominent (Plate IV, 7); ray spacing with means for individual specimens in the range of 8.0–11.3 per mm (total range 6–13 per mm for all specimens); perforated ray cells present (Plate IV, 8).

Solitary rhomboidal crystals typically present in square or upright ray cells (Plate IV, 9, 10).

Description of inferred juvenile specimens (Plate V): The two specimens containing branches (STRI 14157 and 14161) differ from the mature Wood Type 2 specimens in a few significant features: they may show regular bands of axial parenchyma that are exceptionally broad (up to 20 cells wide) (Plate V, 1) and zones of exceptionally wide rays, which locally comprise aggregate rays (Plate V, 2, 3). In addition, STRI 14157 shows localized storied parenchyma strands and fibres (Plate V, 4) and a particular abundance of rhomboidal crystals, not only in ray cells (Plate V, 5), but also in non-chambered (Plate V, 7) and chambered (Plate V, 6, 8) parenchyma cells.

5. Justification for attribution to Malvaceae

A key diagnostic feature seen in all nine specimens (Fossil Wood Types 1 and 2) is the presence of tile cells (111p). The formal definition of this feature is as follows: “a special type of apparently empty upright (rarely square) ray cells occurring in intermediate horizontal series usually interspersed amongst the procumbent cells of multiseriate rays” (IAWA, 1989). Two end-member types of tile cells are generally recognised: (1) the *Pterospermum*-type, which is the most common, comprises tile cells that are substantially higher than the procumbent cells, while (2) the *Durio*-type, which is somewhat rare, comprises tile cells that are approximately the same height as the procumbent cells (IAWA, 1964, 1989). However, Chattaway (1933) proposed a broader

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Plate I. Wood Type 1. *Guazumaoxylon miocenica* gen. et sp. nov., Rodríguez-Reyes, Falcon-Lang, Gasson, Collinson, Jaramillo, STRI 14151 (holotype).

1. Growth rings indistinct; wood diffuse-porous. STRI 14151, TS, scale: 1 mm.
2. Vessels solitary with oval outline and in radial multiples of 2–5. STRI 14151, TS, scale: 250 μm.
3. Perforation plate simple (arrow). STRI 14151, RLS, scale: 100 μm.
4. Intervessel pitting (IVP, arrow) alternate and minute. STRI 14151, TLS, scale: 50 μm.
5. Vessel-ray pits (VRP, arrow) with distinct borders, similar in size and shape to the intervessel pits. STRI 14151, RLS, scale: 50 μm.
6. A few septate fibres (arrows) interspersed with non-septate fibres. STRI 14151, TLS, scale: 100 μm.
7. Thin- to thick-walled fibres. STRI 14151, TS, scale: 100 μm.

Plate II. Wood Type 1. *Guazumaoxylon miocenica* gen. et sp. nov., Rodríguez-Reyes, Falcon-Lang, Gasson, Collinson, Jaramillo, STRI 14151 (holotype). (see on page 20)

1. Paratracheal parenchyma in broad vasicentric sheath to winged-aliform (arrows mark the wing tips) and scarce diffuse parenchyma (DP, arrows). STRI 14151, TS, scale: 250 μm.
2. Paratracheal parenchyma in broad vasicentric sheath to winged-aliform parenchyma (arrows) and scarce diffuse parenchyma (DP, arrows). STRI 14151, TS, scale: 100 μm.
3. Parenchyma strands incomplete due to poor preservation (arrows mark some of the cells). STRI 14151, TLS, scale: 50 μm.
4. Rays 1–3-seriate and >1 mm high with sheath cells. STRI 14151, TLS, scale: 250 μm.
5. Rays 1–3-seriate with sheath cells (arrows). STRI 14151, TLS, scale: 100 μm.
6. Rays composed of procumbent, square and upright cells throughout the body and showing prominent tile cells (TC, arrows). STRI 14151, RLS, scale: 100 μm.
7. Rhomboidal crystals in square ray cells (arrows). STRI 14151, RLS, scale: 100 μm.

Plate III. Wood Type 2 (inferred mature material). *Periplanetoxylon panamense* Rodríguez-Reyes, Falcon-Lang, Gasson, Collinson, Jaramillo, sp. nov., STRI 14155 (holotype) and STRI 14160. (see on page 21)

1. Growth rings indistinct; wood diffuse-porous; prominent, regular to irregular bands of axial parenchyma. STRI 14155, TS, scale: 1 mm.
2. Vessels in radial multiples of 2-4. STRI 14155. TS, scale: 50 μm.
3. Perforation plates simple (arrow). STRI 14155, TLS, scale: 100 μm.
4. Intervessel pits alternate. STRI 14155, TLS, scale: 50 μm.
5. Vessel–ray pits (VRP) bordered, similar in size and shape to the intervessel pits. STRI 14155, RLS, scale: 50 μm.
6. Non-septate fibres (NSF). STRI 14155, TLS, scale: 100 μm.
7. Thin- to thick-walled fibres (F) and diffuse parenchyma (P). STRI 14155, TS, scale: 100 μm.
8. Very thin-walled fibres. STRI 14160, TS, scale: 100 μm.

Plate IV. Wood Type 2 (inferred mature material). *Periplanetoxylon panamense* Rodríguez-Reyes, Falcon-Lang, Gasson, Collinson, Jaramillo, sp. nov., STRI 14155 (holotype) and STRI 14160. (see on page 22)

1. Fibres with minutely bordered pits on radial walls only (arrows). STRI 14160, RLS, scale: 50 μm.
2. Axial parenchyma in regular to irregular bands, 3–8 cells wide. STRI 14155, TS, scale: 100 μm.
3. Axial parenchyma strands >8 cells high (arrows) and sheath cells weakly developed (SC). STRI 14160, TLS, scale: 100 μm.
4. Axial parenchyma strands 5 cells high. STRI 14155, TLS, scale: 25 μm.
5. Axial parenchyma strands 7–8 cells high. STRI 14155, TLS, scale: 25 μm.
6. Rays 2–5-seriate with sheath cells (arrows) STRI 14155, TLS, scale: 100 μm.
7. Rays composed of procumbent, square and upright cells throughout the body. Prominent *Pterospermum*-type tile cells (TC, arrows). STRI 14155, RLS, scale: 100 μm.
8. Perforated ray cell. STRI 14155, RLS, scale: 100 μm.
9. Rhomboidal crystals in square ray cells (arrows). STRI 14155, RLS, scale: 100 μm.
10. Rhomboidal crystal in square ray cell (arrow). STRI 14160, RLS, scale: 50 μm.

Plate V. Wood Type 2 (inferred juvenile material). *Periplanetoxylon panamense* Rodríguez-Reyes, Falcon-Lang, Gasson, Collinson, Jaramillo, sp. nov., STRI 14157. (see on page 23)

1. Axial parenchyma bands (PB) exceptionally broad (up to 20 cells wide) alternating with zones of fibres (F). STRI 14157, TS, scale: 100 μm.
2. Zones of exceptionally wide rays, locally comprising aggregate rays (AR, arrows). STRI 14157, TLS, scale: 500 μm.
3. Aggregate rays. STRI 14157, TLS, scale: 100 μm.
4. Localized storied parenchyma strands and fibres (arrows). STRI 14157, TLS, scale: 100 μm.
5. Abundant rhomboidal crystals in ray cells (arrows). STRI 14157, RLS, scale: 100 μm.
6. Abundant rhomboidal crystals in chambered parenchyma cells (arrows). STRI 14157, RLS, scale: 100 μm.
7. Rhomboidal crystal in non-chambered parenchyma cells (arrow). STRI 14157, RLS, scale: 50 μm.
8. Rhomboidal crystals in chambered parenchyma cells (arrow). STRI 14157, RLS, scale: 50 μm.

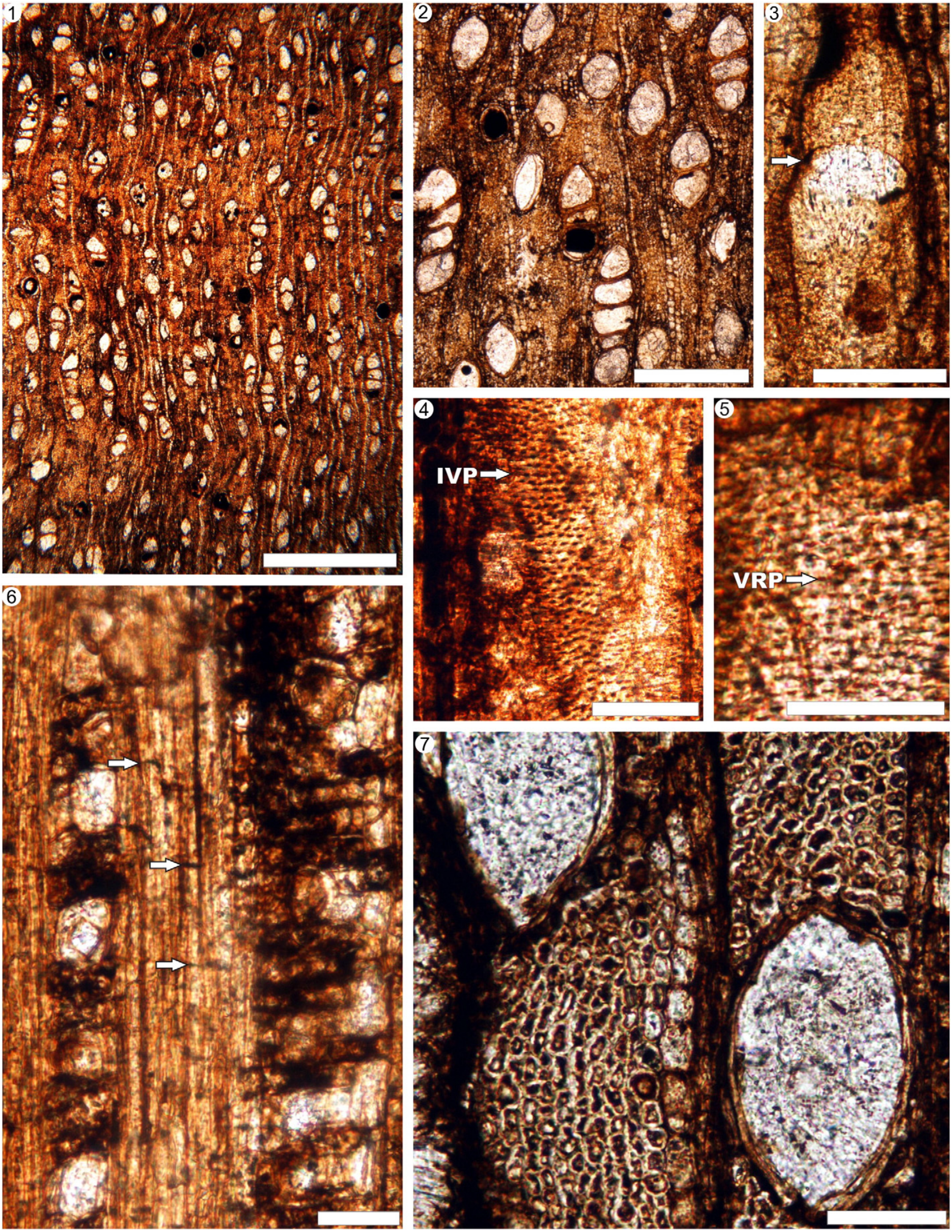

Plate I.

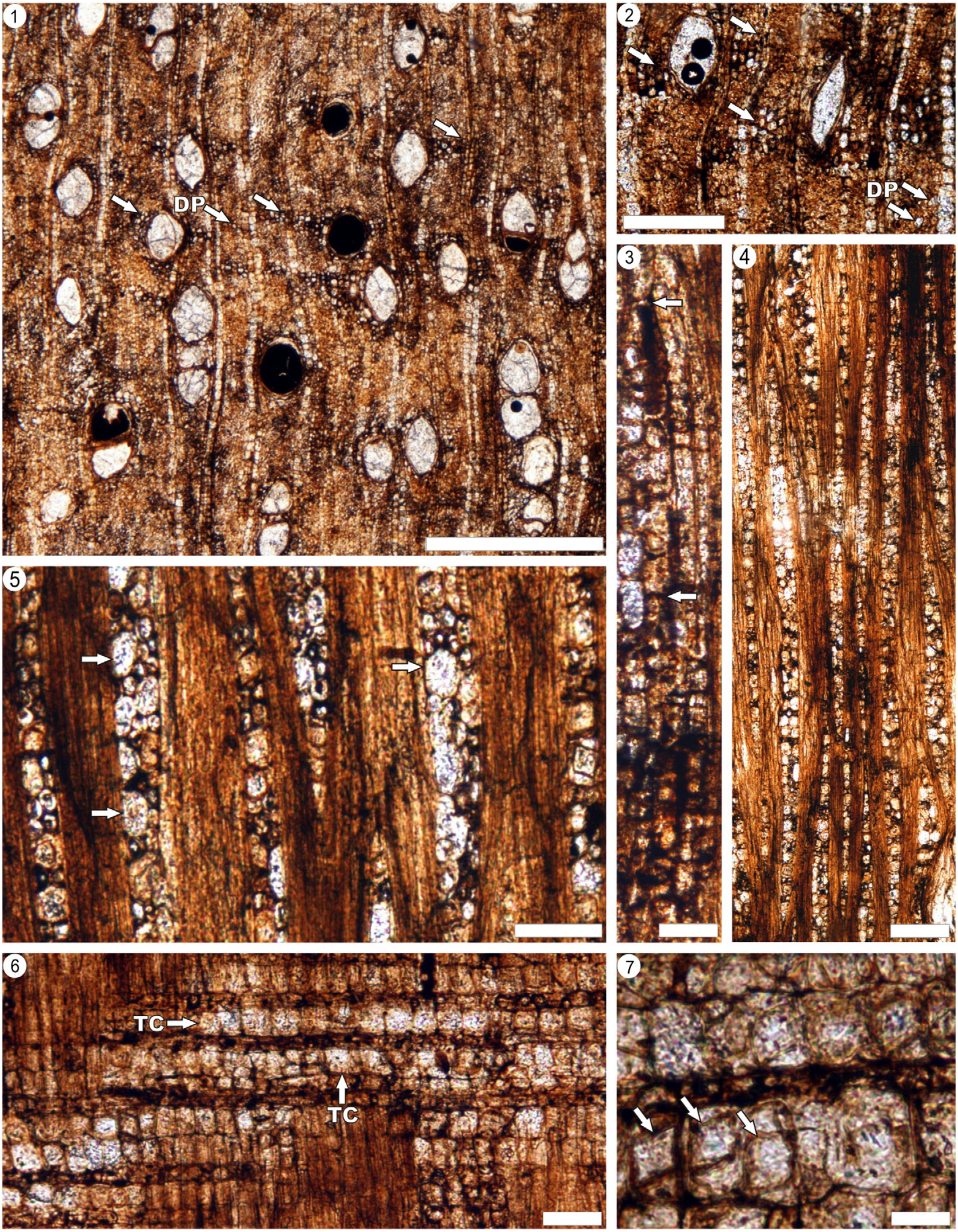

Plate II (*caption on page 18*).

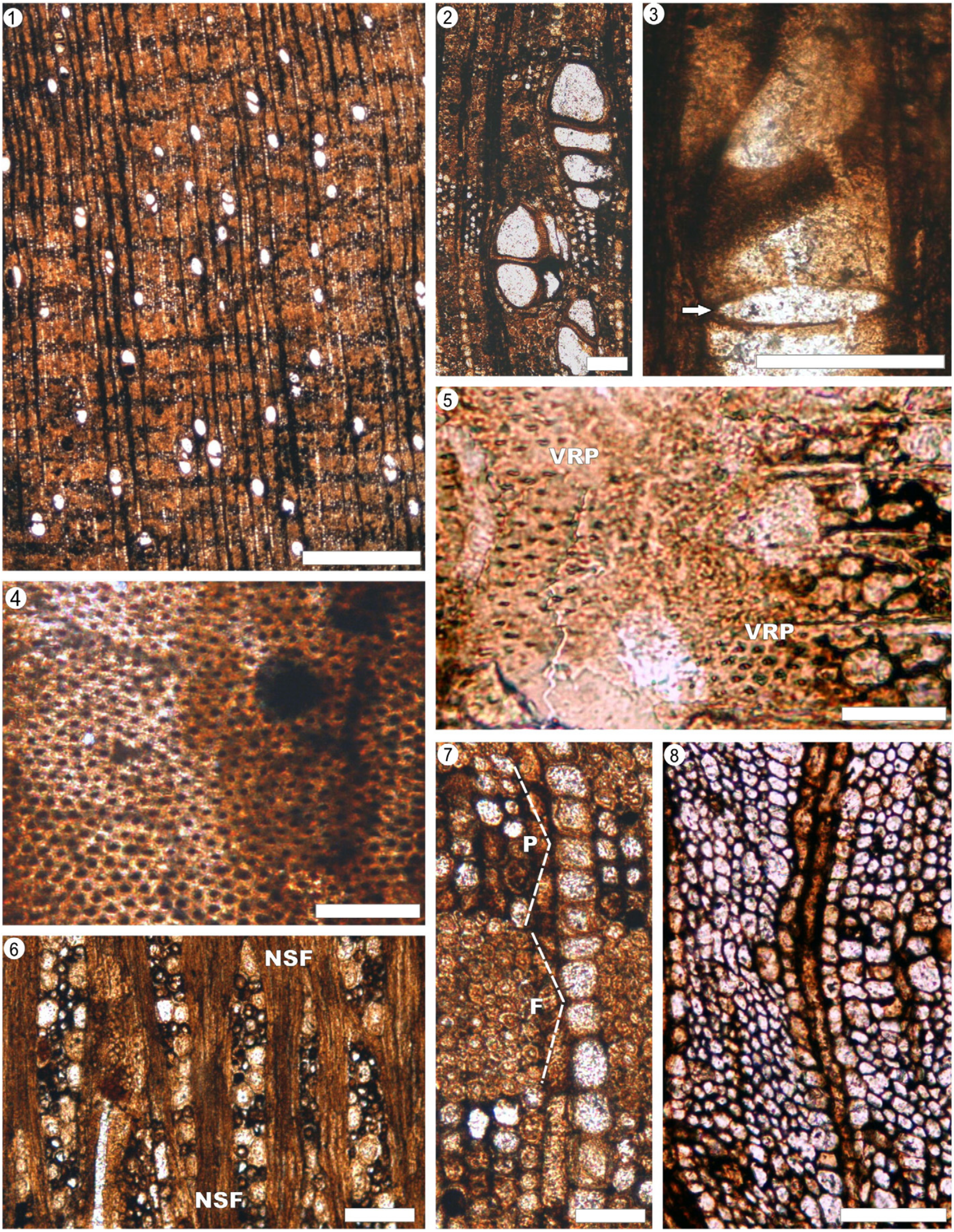

Plate III (*caption on page 18*).

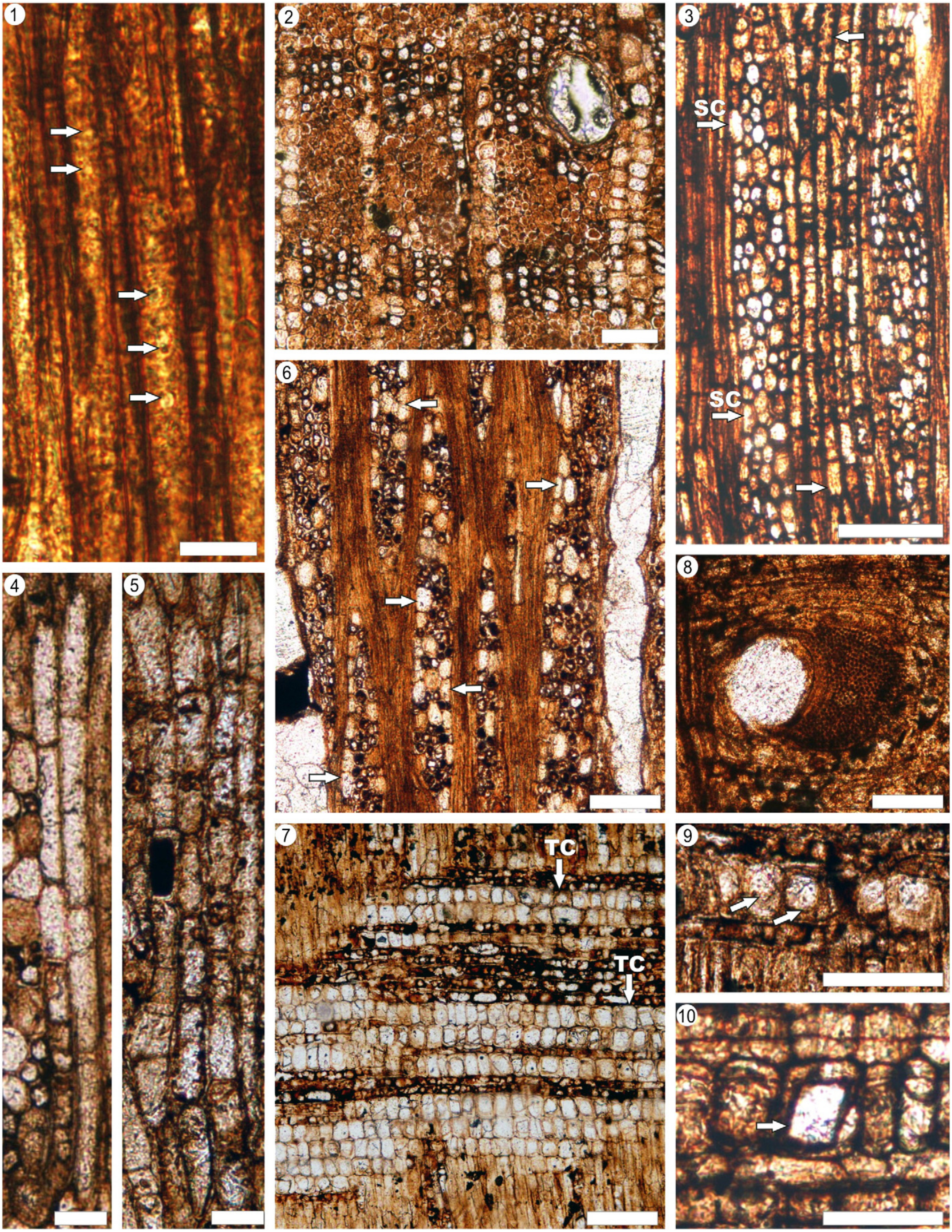

Plate IV (*caption on page 18*).

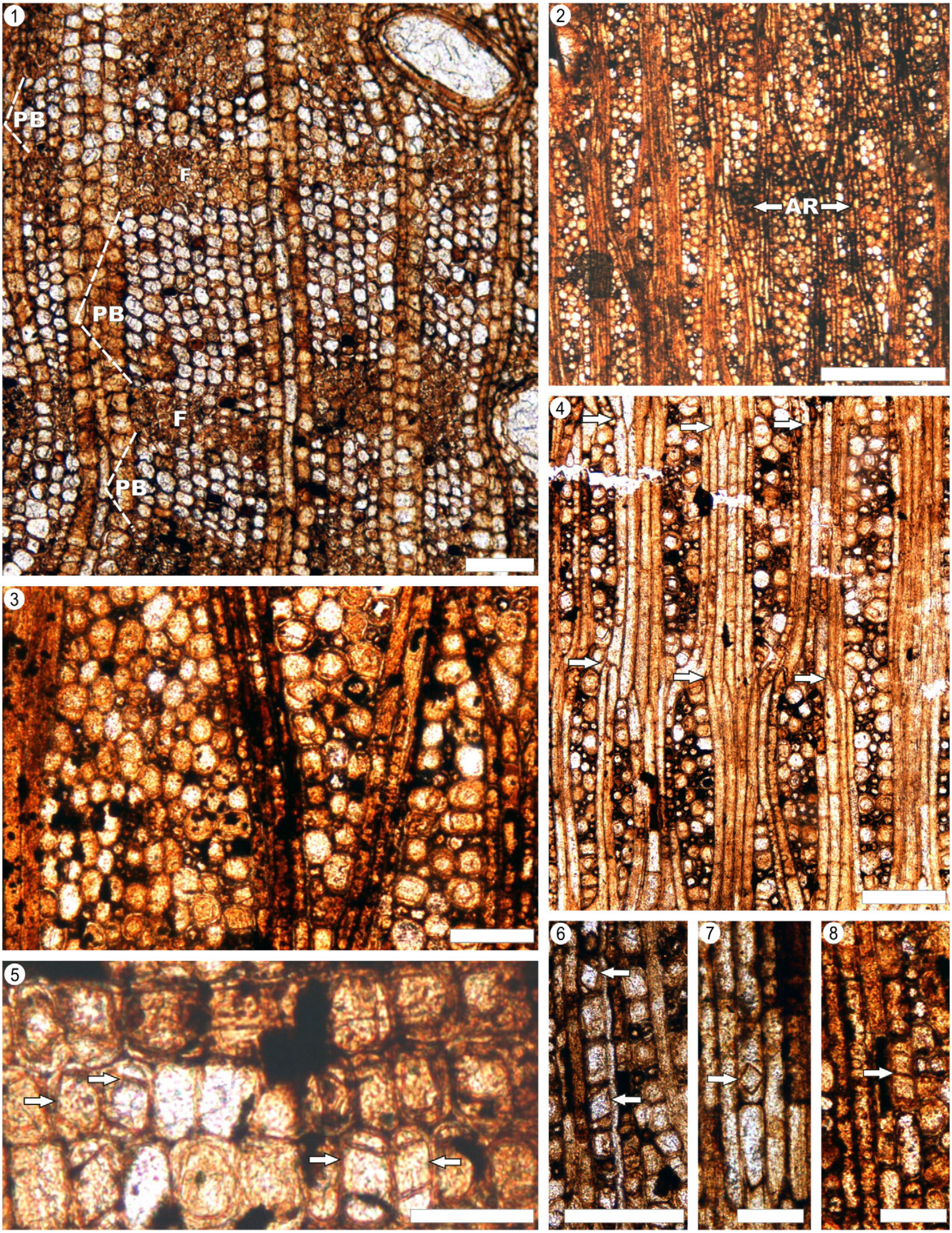

Plate V (*caption on page 18*).

definition, recognising intermediate types, comprising tile cells that are slightly bigger than the procumbent ray cells, as typified by *Guazuma* P. Miller and *Reevesia* Lindley (Fig. 4; Manchester and Miller, 1978). As Manchester et al. (2006) point out, there is a somewhat artificial distinction between tile cells and sheath cells (similar features viewed in RLS and TLS, respectively); however because the definition of the former feature precludes its occurrence in 1–2-seriate rays, tile cells have a much narrower distribution than sheath cells, and therefore it is very useful to make this distinction.

5.1. Occurrence of tile cells within the Malvales

Tile cells are restricted to the Order Malvales (IAWA, 1989). Based on searches of the Insidewood Database (IWD), wood anatomical monographs (e.g., Chattaway, 1937; Metcalfe and Chalk, 1950; Manchester and Miller, 1978; Carlquist, 2001; Wheeler and Manchester, 2002; Manchester et al., 2006) and observations in the wood reference collections, tile cells are found in at least six families of the Malvales as follows: Bixaceae, Dipterocarpaceae, Neuradaceae, Sphaerosepalaceae, Thymelaeaceae, and especially in the Malvaceae sensu APG III (comprising the former Bombacaceae, Malvaceae sensu stricto, Sterculiaceae, and Tiliaceae).

Several of these families can be immediately excluded from consideration. The Bixaceae shows regularly storied rays and fibres, features absent in our fossil specimens (IWD accessed 17 June 2013). The Dipterocarpaceae shows common tile cells only in the sub-family Dipterocarpoideae, especially in *Hopea* Roxburgh (Chattaway, 1933; Manchester and Miller, 1978; Cronquist, 1981; IAWA, 1989; IWD accessed 17 June 2013); however, an affinity with the Dipterocarpoideae is unlikely because the fossil and extant record of this group is restricted to Indo-China, and the fossils lack axial canals, a character found in most dipterocarps (Stevens, 2001). The Neuradaceae, a Saharo-Indian family, is another unlikely match because it exclusively comprises herbs and sub-shrubs (Schweingruber et al., 2013), whereas our fossils come from large trees based on preserved diameter. Also excluded from consideration is the wood of the Thymelaeaceae, which commonly has exclusively uniseriate rays, and some species additionally show included phloem (e.g., *Aquilaria* Lamarck, *Gyrinops* J. Gaertner; Van Vliet and Baas, 1984; Gasson et al., 2011), whereas our fossil wood specimens lack exclusively uniseriate rays (generally in the range of 1–6-seriate) and included phloem. In the Sphaerosepalaceae, rays are mostly >10-seriate and >1 mm high (Carlquist, 2001), much larger than in either of our fossil types. However, there are very good matches between our fossil specimens and several representatives of the Malvaceae sensu APG III. Therefore, through this process of elimination, subsequent comparative studies are confined to the Malvaceae sensu APG III as described more fully below.

5.2. Occurrence of tile cells within the Malvaceae sensu APG III

We studied the distribution of *Guazuma* intermediate-type tile cells (seen in the Fossil Wood Type 1 specimens) and *Pterospermum*-type tile cells (seen in the Fossil Wood Type 2 specimens) in two major data repositories: the Insidewood Database (IWD) and the wood reference collections. Through examination of these online resources and slide collections, we were able to directly or indirectly observe 128 of the c. 243 genera of Malvaceae sensu APG III.

Unfortunately, the IWD does not distinguish between the various types of tile cells, so it is not possible to maximize the use of this character for search purposes. Nonetheless, many IWD records do have micrographs associated with them, allowing searches to be refined. We searched the IWD for Malvaceae species showing tile cells (111p), and manually discarded records with *Durio*-type tile cells based on micrograph images. Excluding synonyms, we identified 35 genera distributed across the nine subfamilies that show *Pterospermum* and *Guazuma*/*Reevesia* intermediate-type tile cells as follows: Bombacoideae (*Adansonia* L., *Bombax* L., *Cavanillesia* Ruiz et Pavon, *Ceiba* P. Miller, *Ochroma* Swartz, *Commersonia* J. R. Forster et G. Forster, *Pachira* Aublet, *Quararibea* Aublet), Brownlowioideae (*Berrya* de Candolle), Byttnerioideae (*Abroma* Jacquin, *Guazuma* P. Miller, *Melochia* L., *Scaphopetalum* Mast, *Theobroma* L.), Dombeyoideae (*Dombeya* Cavanilles, *Pterospermum* Schrebius), Grewioideae (*Duboscia* Bocquet, *Grewia* L., *Triumfetta* L., *Trichospermum* Blume, *Vasivaea* Baillon), Helicteroideae (*Reevesia* Lindley, *Triplochiton* K. Schumann), Malvoideae (*Abutilon* P. Miller, *Hibiscus* L., *Lagunaria* (de Candolle) Reichenbach, *Lavatera* L., *Thespesia* Solander ex Correa), Sterculioideae (*Cola* Schott et Endlicher, *Firmiana* Marsili, *Heritiera* Aiton, *Pterygota* Schott et Endlicher, *Sterculia* L.) and Tilioideae (*Apeiba* Aublet, *Craigia* W.W. Smith).

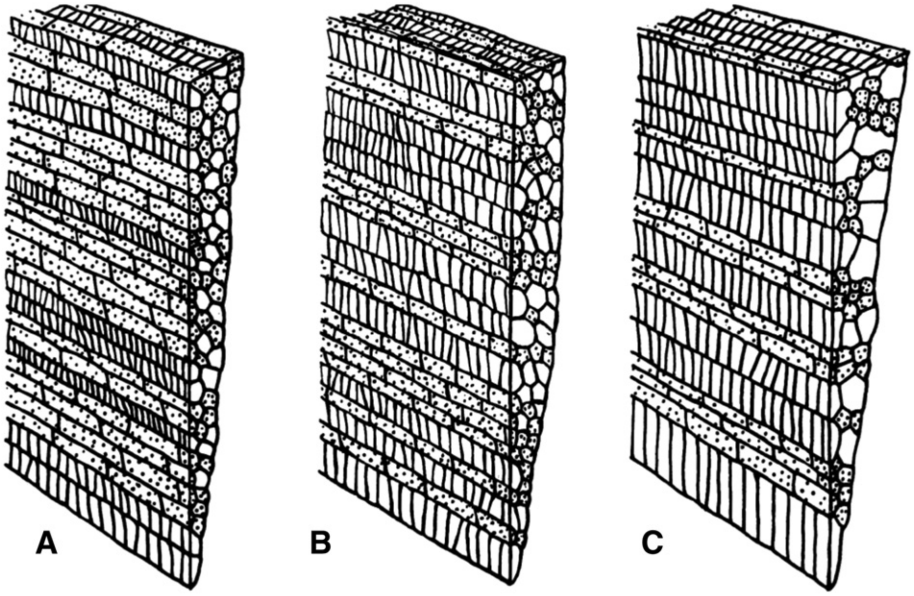

Fig. 4. Diagram illustrating the different types of tile cells seen especially in Malvaceae sensu APG III. A, *Pterospermum*-type tile cells; B, *Guazuma* intermediate-type tile cells; C, *Durio*-type tile cells. Tile cells are shown from both tangential and radial views and drawn without stipples, while the stippled cells are procumbent ray cells.
Reproduced from Manchester and Miller (1978).

Our study of the distribution of *Pterospermum* and *Guazuma*/*Reevesia* intermediate-type tile cells in Malvaceae sensu APG III in the wood reference collections reveals that a further nine genera in five of the nine subfamilies show these types of tile cells as follows: Bombacoideae (*Pseudobombax* Dugand), Dombeyoideae (*Melhania* Forsskål), Helicteroideae (*Helicteres* L.), Malvoideae (*Azanza* Alefeld, *Gossypium* L., *Malvaviscus* Fabricius, *Pavonia* Cavanilles, *Pentaplaris* L.O. Williams et Standley) and Sterculioideae (*Octolobus* Welwitsch).

In total, we identified 44 genera (out of 128 genera observed) distributed across the nine subfamilies that show *Pterospermum*-type tile cells and intermediate-type tile cells (Table 2). We used this short-list as a basis for identification of the two fossil wood types.

6. Identification of Fossil Wood Type 1 specimens

An initial IWD search, with no mismatches allowed, was made using the following suite of very general features seen in the Fossil Wood Type 1 specimen: Wood diffuse-porous (5p); simple perforation plates (13p); alternate intervessel pitting (22p); axial parenchyma winged-aliform (82p); and tile cells present (111p). This search gave the following limited results: *Hopea* (Dipterocarpaceae), *Grewia* L. (Malvaceae) and *Mollia* C.F.P. Martius (Malvaceae); however, as noted above, *Hopea* can be excluded from further consideration. Subsequent analysis revealed that it is, specifically, the combination of axial parenchyma winged-aliform (82p) and tile cells present (111p), which is especially rare in the IWD. Although a broader search for this combination of features in the wood reference collections revealed that this combination has a somewhat wider occurrence (present in certain species of the following ten genera: *Abutilon*, *Cola*, *Dombeya*, *Firmiana*, *Grewia*, *Heliocarpus*, *Hibiscus*, *Hopea*, *Mollia* and *Sterculia*), all these taxa typically also show wide banded parenchyma (85p), with coalescent bands in some cases (e.g., *Cola*, *Abutilon*) and very abundant diffuse in aggregates parenchyma (77p) (e.g., *Grewia*, *Dombeya*), which is not seen in our fossils. The only exceptions we found are *Grewia orientalis* L. and *Mollia lepidota* Spruce ex Bentham (both in the subfamily Grewioideae). We therefore made a detailed comparison with these two genera.

Grewia L. (subfamily Grewioideae) is a very large genus, mostly distributed in tropical and sub-tropical parts of Africa, Asia, and Australia. However, after studying all micrographs in the IWD, slides in the wood reference collections, and some published literature (Bancroft, 1935; Agarwal, 1991; Selmeier, 2000; Chung and Lim, 2005) for this genus (*Grewia asiatica* L., *Grewia bicolor* Jussieu, *Grewia barombiensis* K. Schumann, *Grewia crenata* Schinz et Guillaumin, *Grewia eriocarpa* Jussieu, *Grewia excelsa* Vahl, *Grewia flavescens* Jussieu, *Grewia globulifera* Masters, *Grewia glyphaeiodes* Baillon, *Grewia latifolia* F. Mueller ex Bentham, *Grewia microcos* L., *Grewia miqueliana* Kurz, *Grewia oppositifolia* Roxburgh, *Grewia orientalis* L., *Grewia paniculata* de Candolle, *Grewia populnifolia* Vahl, *Grewia polygama* Roxburgh, *Grewia rolfei* Merrill, *Grewia tenax* Fiori, *Grewia tiliifolia* Vahl, *Grewia umbellata* Roxburgh, *Grewia villosa* Willdenow) we excluded it as a probable match for the fossils. In general terms, the genus typically shows distinct growth rings (1p), rays of two distinct sizes (103p), and dominantly diffuse parenchyma, features absent in the fossils. Although *G. orientalis* is somewhat more similar to the fossils when viewed in TS, there are also some important differences such as vessel-ray pits showing much reduced and rounded borders (31p), rays of two very distinct sizes (103p), and an absence of crystals (136a).

Mollia (subfamily Grewioideae) is a medium-sized genus distributed especially in tropical Central and South America. Unfortunately, only one species, *Mollia lepidota*, is reported in IWD, the genus is not represented in the wood reference collections at all, and there are few published micrographs (Kukachka and Rees, 1943; Welle and Détienne, 1995). Acknowledging these very limited data, we suggest that this genus is also an unlikely match because it shows distinctly *Durio*-type tile cells and laticifers, features that are both absent in the fossils. In making this assessment, we note that tile cells in the fossil specimens, which are of the rare intermediate-type (Chattaway, 1933), are rather closer to *Pterospermum*-type than to the *Durio*-type (though we recognise that this is a qualitative assessment). Obviously, we cannot be as confident as we would like in excluding *Mollia* from consideration due to lack of comparative material available for study.

With no further taxa on the IWD short-list to investigate, we then reflected on the taxonomic significance of the intermediate-type tile cells, which is restricted to two extant genera, *Guazuma* and *Reevesia*. After the study of the available images of *Reevesia* in the IWD and the microscopic slides in Royal Botanic Gardens, Kew, we rule it out, because it shows vessels in clusters of six or more (11p), helical thickenings (36p), parenchyma diffuse in aggregates (77p) and scalariform apotracheal parenchyma, all of which are absent in the fossils. However, an initial assessment of species of *Guazuma* from the Royal Botanic Gardens, Kew revealed many promising similarities with the fossils. In this regard, we also noted that the intermediate-type tile cells seen in the fossils are more similar to the ones in *Guazuma* than those in *Reevesia*.

A detailed study of *Guazuma* (subfamily Byttnerioideae), a genus that is widely distributed in the tropics of Central and South America, was undertaken. We note that this taxon is relatively closely related to other taxa, *Grewia* and *Mollia*, similar to the fossil, within the Byttneriina-clade. Of the four extant species of *Guazuma*, two were available for study in the wood reference collections: *Guazuma crinita* C.F.P. Martius and *Guazuma ulmifolia* Lamarck, both present at Royal Botanic Gardens, Kew. These species share the following features with the Fossil Wood Type 1 specimen: wood diffuse porous (Plate VI, 1); vessels generally in radial multiples of 2–3 (and localized clusters of up to 6) (Plate VI, 1, 2); perforation plates simple (Plate VI, 3); intervessel pitting alternate (Plate VI, 4); vessel-ray pitting similar to intervessel pitting in size and shape (Plate VI, 5); some septate fibres interspersed with non-septate fibres (Plate VI, 6); thin- to thick-walled fibres (Plate VI, 8); apotracheal axial parenchyma scarce and diffuse (the frequency of this feature is variable in different observed specimens: Plate VI, 7, 8; Plate VII, 1, 2, 3, 4); axial parenchyma strands mostly 4–5 (–6) cells high (Plate VII, 5); sheath cells present (Plate VII, 6); and intermediate-type tile cells present (Plate VII, 7, 8).

Initially we thought that a significant difference between the fossils and *Guazuma* would be seen in its axial parenchyma because the IWD does not code this taxon for axial parenchyma of winged-aliform type. However, our fossil material is not classically winged-aliform showing a mixture of broad-sheaths and small wings. While most species of *Guazuma* do, indeed, differ from our fossil specimen in showing some examples of scalariform axial parenchyma (Plate VII, 2), one of the Royal Botanic Gardens, Kew samples (Dominica 166) of *Guazuma ulmifolia* closely resembles the fossils in showing axial parenchyma with broad vasicentric sheath to small winged-aliform (Plate VI, 7, 8) with scarcer diffuse axial parenchyma (Plate VII, 1), compared to other specimens of *G. ulmifolia* (Plate VII, 2, 4). Additionally, this species shows solitary rhomboidal crystals present in ray (Plate VII, 7, 8) and axial parenchyma cells, as in the fossil. The main differences from the fossil wood include distinct rings, shorter and wider rays on average and diffuse, scalariform parenchyma. However, we do not consider these features of great taxonomic significance and consider *G. ulmifolia* the most credible match for the Fossil Wood Type 1.

7. Identification of Fossil Wood Type 2 specimens

An initial IWD search, with no mismatches allowed, was undertaken using the following general suite of characters common to all four specimens of Fossil Wood Type 2 specimens: wood diffuse-porous (5p); intervessel pitting alternate (22p); vessel-ray pitting similar to intervessel pitting (30p); non-septate fibres present (66p); axial parenchyma in bands >3 cells wide (85p); and sheath and tile cells present (110p, 111p). This search produced no matches, and further investigation revealed that the combination of axial parenchyma in bands >3 cells wide *and* tile cells (85p, 111p) is unknown, not only in the Malvaceae sensu APG III, but also in the entire IWD.

A further study of the wood reference collections confirmed that this combination is generally uncharacteristic of the Malvaceae sensu APG III. Nonetheless, sixteen genera with tile cells, some of them not coded in IWD at all, show this combination as follows: *Abutilon*, *Berrya*, *Cola*, *Firmiana*, *Grewia*, *Heritiera*, *Hibiscus*, *Lavatera*, *Ochroma*, *Octolobus*, *Pavonia*, *Pentaplaris*, *Pseudobombax*, *Pterygota*, *Scaphopetalum*, and *Sterculia*. Therefore, we restrict subsequent comparison of the fossil specimens to these genera. In restricting our search, we are aware that we have observed only about half of the genera of Malvaceae sensu APG III, and note that it is possible that there may be additional genera showing both of the key features of Fossil Wood Type 2.

Table 2
List of genera of Malvaceae sensu APG III showing tile cells in the collections of Royal Botanic Gardens, Kew, Utrecht University, and Leiden University and those listed in the Inside Wood Database (IWD). Abbreviations: AP, axial parenchyma; P, *Pterospermum*-type; D, *Durio*-type; I, intermediate-type; 0, absent; 1, present.

Genus	Subfamily	Data source	AP aliform	AP bands	Tile cell type
Abutilon	Malvoideae	IWD/Kew	1	1	P
Adansonia	Bombacoideae	Kew/IWD	0	0	P
Abroma	Byttnerioideae	Leiden/IWD	0	0	P
Apeiba	Tilioideae	Kew/IWD	0	0	P
Ayenia	Byttnerioideae	Kew	0	1	D
Azanza	Malvoideae	Kew	0	1	P
Berrya	Brownlowioideae	Utrecht/Kew/IWD	0	1	P
Bombax	Bombacoideae	Kew/IWD	0	1	P
Boschia	Helicteroideae	Kew/IWD	0	1	D
Cavanillesia	Bombacoideae	Utrecht/Kew/IWD	0	0	P
Ceiba	Bombacoideae	Kew/IWD	0	1	P
Coelostegia	Helicteroideae	IWD	0	1	D
Colona	Grewioideae	IWD	0	1	D
Cola	Sterculioideae	Kew/IWD	1	1	P
Cullenia	Helicteroideae	Kew/IWD	0	1	D
Commersonia	Bombacoideae	Kew/IWD	0	0	P
Craigia	Tilioideae	IWD	0	1	P
Desplatzia	Brownlowioideae	IWD	0	1	D
Dombeya	Dombeyoideae	Kew/IWD	1	1	P
Duboscia	Grewioideae	IWD/Kew	0	1	P
Durio	Helicteroideae	IWD/Kew	0	1	D
Firmiana	Sterculioideae	Kew/Leiden/IWD	1	1	P
Fremontodendron	Bombacoideae	IWD	0	1	D
Gossypium	Malvoideae	Kew	0	0	P
Grewia	Grewioideae	Kew/Utrecht/IWD	1	1	P
Guazuma	Byttnerioidea	IWD/Kew	0	1	I
Hampea	Malvoideae	IWD	0	0	D
Helicteres	Helicteroideae	Kew	0	0	P
Heliocarpus	Grewioideae	Kew/IWD	1	1	D
Heritiera	Sterculioideae	Leiden/Kew/IWD	0	1	P
Hibiscus	Malvoideae	Kew/Utrecht/IWD	1	1	P
Kleinhovia	Byttnerioideae	IWD	0	1	D
Kostermansia	Helicteroideae	Kew/IWD	0	1	D
Kydia	Malvoideae	Kew/IWD	0	1	D
Lagunaria	Malvoideae	Kew/IWD	0	1	P
Lavatera	Malvoideae	Kew/IWD	0	1	P
Leptonychia	Byttnerioideae	IWD	0	0	D
Luehea	Bombacoideae	Kew/IWD	0	1	D
Lueheopsis	Grewioideae	IWD/Kew	0	1	D
Malvaviscus	Malvoideae	Kew	0	0	P
Melhania	Dombeyoideae	Kew	0	0	P
Melochia	Byttnerioideae	Kew/IWD	0	0	P
Microcos	Grewioideae	IWD/Kew	0	1	D
Mollia	Grewioideae	IWD	1	0	D
Mortoniodendron	Tilioideae	Literature	0	0	D
Neesia	Helicteroideae	IWD	0	0	D
Ochroma	Bombacoideae	Kew/IWD	0	1	P
Octolobus	Sterculioideae	Kew	0	1	P
Pachira	Bombacoideae	Kew/IWD	0	1	P
Pavonia	Malvoideae	Kew	0	1	P
Pentaplaris	Malvoideae	Kew	0	1	P
Pseudobombax	Bombacoideae	Kew	0	1	P
Pterospermum	Dombeyoideae	Leiden/IWD	0	1	P
Pterygota	Sterculioideae	Leiden/IWD	0	1	P
Quararibea	Bombacoidae	Kew/IWD	0	1	P
Reevesia	Helicteroideae	Kew/IWD	0	1	I
Scaphopetalum	Byttnerioideae	IWD	0	1	P
Sterculia	Sterculioideae	Kew/Leiden/IWD	1	1	P
Theobroma	Byttnerioideae	Kew/IWD	0	1	P
Thespesia	Malvoideae	Leiden/IWD	0	1	P
Trichospermum	Grewioideae	IWD/Kew	0	0	P
Triplochiton	Helicteroideae	Kew/IWD	0	1	P
Triumfetta	Grewioideae	IWD/Kew	0	0	P
Vasivaea	Grewioideae	IWD	0	1	P

Of these comparative taxa, several can be immediately eliminated because they show features not seen in the fossils. *Grewia*, *Hibiscus*, *Ochroma*, *Pseudobombax* and *Sterculia* show parenchyma that is dominantly diffuse or diffuse-in-aggregates. Additionally *Grewia* and *Firmiana* have two distinct sizes of rays. *Abutilon*, *Cola* and one species of *Berrya* (*B. cordifolia* Reg (Fernandez-Villar)) have very regular festooned bands of parenchyma, although the other two *Berrya* species show very scarce or absent parenchyma. The parenchyma is scalariform in *Heritiera* and some species of *Sterculia*. In *Lavatera*, vessels are grouped in clusters of mainly five. *Pterygota* has very broad bands of parenchyma, >8 cells wide, and also contains helical thickenings of vessels.

Close matches with the Fossil Wood Type 2 specimens are only found in *Pentaplaris*, a small genus of the subfamily Malvoideae (Baum et al., 2004), which is found in tropical South America and comprises three species: *Pentaplaris doroteae* L.O. Williams et Standley is endemic to Costa Rica, *Pentaplaris davidsmithii* L.J. Dorr et C. Bayer is found in Bolivia and Peru, and *Pentaplaris huaoranica* L.J. Dorr et C. Bayer is restricted to Ecuador. Only one specimen (Kw 20291) of one species, *P. doroteae*, was available in the wood reference collections at Royal Botanic Gardens, Kew, so our observations may not have captured the full range of variability of the genus. Nonetheless, this specimen shows remarkable similarity with the fossil woods insofar that it shows regular to irregular bands of parenchyma, 3–5 cells wide, in combination with *Pterospermum*-type tile cells.

Specimen Kw 20291 (*Pentaplaris doroteae*) has the following features: growth rings indistinct (Plates VIII, I); wood diffuse porous (Plate VIII, 1); vessels in radial multiples of 2–4 (Plate VIII, 2); vessels with an oval outline (Plate VIII, 3); perforation plates simple (Plate VIII, 4); intervessel pitting alternate, polygonal and minute (Plate VIII, 5); vessel-ray pitting similar in shape and size to the intervessel pitting (Plate VIII, 6); parenchyma strands mainly 8 cells high (Plate VIII, 7); fibre pits common on both radial and tangential walls; axial parenchyma in regular to irregular broad bands, 3–5 cells wide (Plate VIII, 1, 2); conspicuous sheath cells present (Plate VIII, 8); *Pterospermum*-type tile cells present (Plate VIII, 9); rays heterocellular, commonly 2–4-seriate (Plate VIII, 8); ray density 4–13 rays per mm (Plate VIII, 8); and rhomboidal crystals present in square ray cells and tile cells (Plate VIII, 9, 10) and in the axial parenchyma cells.

The Fossil Wood Type 2 specimens share all of the previously listed features of *Pentaplaris*, except that pits on the tangential fibre walls were not seen in the fossil; however, this may be a taphonomic feature as fibre pits are very difficult to observe in these fossil specimens. Furthermore, some of the juvenile fossil specimens show aggregate rays and locally storied fibres and parenchyma strands, features absent in *Pentaplaris doroteae*; however, we do not have juvenile material of *Pentaplaris* for comparison. In addition, we know of no fossil woods with features closely similar to those seen in *Periplanetoxylon panamense*. Therefore our survey of malvacean fossil woods supports our view that this fossil type is a novel taxon.

8. Comparison with fossil woods previously assigned to Malvaceae

In this section, we summarise the previously reported malvacean woods in the fossil record from the Cretaceous to Miocene. We focus on the main aspects, and for each fossil, list how it differs from the two wood types described in this paper.

8.1. Cretaceous woods

The oldest known malvalean woods date from the latest Cretaceous (Campanian–Maastrichtian) and include *Javelinoxylon* (Wheeler et al., 1994; Estrada-Ruiz et al., 2007; Estrada-Ruiz and Martinez-Cabrera, 2011), *Bombacoxylon langstonii* (Wheeler and Lehman, 2000) and *Wheeleroxylon atascoense* (Estrada-Ruiz et al., 2010). *Javelinoxylon* woods contain common tyloses, scarce paratracheal and apotracheal parenchyma and storied rays; *B. langstonii* shows diffuse-in-aggregates parenchyma, rays typically composed of only procumbent cells and no tile cells, whereas *W. atascoense* has tyloses, diffuse axial parenchyma, and rays that are homocellular and storied. Other Cretaceous woods that have been reported as Malvaceae include *Parabombacaceoxylon magniporosum*, from the Upper Cretaceous (Maastrichtian) of Illinois, U.S.A. (Wheeler et al., 1987), with >10 bar scalariform perforation plates and axial parenchyma diffuse-in-aggregates; *Hibiscoxylon niloticum* Kräusel from Lebanon (Beauchamp and Lemoigne, 1973), with tyloses common, axial parenchyma diffuse and occasionally, confluent and banded, rays of two distinct sizes; and woods of uncertain Late Cretaceous or Eocene age from Ethiopia described as *Dombeyoxylon owenii* (Carr) Kräusel showing parenchyma diffuse and all storied rays, and *Hibiscoxylon niloticum*, which resembles *Hibiscus*, having tyloses, axial parenchyma diffuse but combined with bands of 1–3 and >3 cells wide, rays of two distinct sizes, and crystals abundant in ray and axial parenchyma cells (Beauchamp et al., 1973).

8.2. Paleocene–Eocene woods

Paleocene–Eocene records of putative Malvaceae woods are more common (Gregory et al., 2009). In Paleocene sediments, they include *Camptostemomonoxylon mahurzarii*, *Dryoxylon mahurzarii*, *Dryoxylon intertrappea*, *Grewioxylon intertrappeaeum*, *Hibiscoxylon intertrappeum*, *Sterculioxylon shahpuraensis* (Trivedi, 1971; Prakash, 1974; Trivedi and Ambwani, 1976; Bande and Prakash, 1980, 1982), *Parabombacaceoxylon* (Wheeler and Michalski, 2003), *Sessaoxylon paleocenicum* (Koeniguer, 1971), *Tarrietioxylon hazzeldinewarrenii* (Crawley, 1989) and *Tilioxylon lueheaformis* (Crawley, 2001). All of these woods lack either dominantly banded or aliform parenchyma, but instead show parenchyma that is diffuse and diffuse-in-aggregates. Additionally, it is common to find two distinct sizes of rays in these taxa.

For the Eocene, the number of reports increases even further (especially in Europe and North America) and some of the woods show more diverse parenchyma types: *Bombacoxylon monodii* Boureau (Gottwald, 1969) has vessels arranged radially or diagonally, tyloses common and parenchyma that is diffuse-in-aggregates; *Chattawaya paliforme* (Wheeler and Manchester, 2002) has distinct growth rings, parenchyma that is diffuse-in-aggregates and rays in two distinct size classes; *Helictoxylon wilcoxianum* (Berry, 1923), as originally described in the Wilcox palaeoflora, resembles a liana with very closely spaced wide rays and abundant diffuse parenchyma; *Sterculioxylon freulonii* of southwest Germany (Guleria, 1982), shows axial parenchyma in concentric confluent bands, with some not confluent aliform parenchyma, axial parenchyma and fibres storied; *Sterculioxylon deccanensis* (Lakhanpal et al., 1976) has narrow paratracheal sheaths and apotracheal parenchyma diffuse to diffuse in aggregates; *Triplochitioxylon oregonensis* (Manchester, 1979; Wheeler and Manchester, 2002) has distinct growth rings, axial parenchyma diffuse-in-aggregates with occasional 1–3 cells wide parenchyma bands and axial parenchyma storied.

8.3. Oligocene–Miocene woods

Several more Malvaceae woods are known in the Oligocene–Miocene (Gregory et al., 2009). These include diverse *Sterculioxylon* specimens from Oligocene localities in India and Egypt described as *Sterculioxylon giarabubensis* (Kräusel, 1939), *Sterculioxylon foetidense* (Guleria, 1982), and *Sterculioxylon dattai* (Prakash and Tripathi, 1972; Guleria, 1982). In these specimens, parenchyma is dominantly diffuse-in-aggregates except for *S. giarabubensis*, where it is aliform and confluent forming concentric bands. *Pterospermoxylon*, found in the Kachchh Flora (Guleria, 1982) has distinct growth rings, common tyloses and parenchyma scanty paratracheal.

Other reports from the Miocene include *Dryoxylon siamensis* (Prakash, 1977) with distinct growth rings, semi-ring porous wood, common tyloses, axial parenchyma in narrow bands up to 3 cells wide, but without tile or sheath cells. Still other Miocene examples include *Reevesia japonoxyla* (Terada and Suzuki, 1998) with wood distinctly ring-porous, scanty paratracheal and diffuse apotracheal parenchyma with storied and fusiform strands; *Sterculioxylon kalagarhense* (Guleria, 1982), with paratracheal axial parenchyma in narrow to thick sheath around the vessels and some regular to irregular bands, rays 1–16 seriate and axial canals present; *Sterculioxylon pondicherriense* (Guleria, 1982) shows banded parenchyma 3–12 cells wide and rays up to 25-seriate; *Tarrietioxylon sumatrense* (Kräusel, 1922) shows common tyloses, axial parenchyma diffuse in aggregates combined with vasicentric and aliform parenchyma and all rays storied. Terada and Suzuki (1998) erected a new genus from Japan, *Wataria*, and reported two species: *Wataria miocenica* (Terada and Suzuki, 1998) with ring-porous wood, axial parenchyma diffuse in aggregates and rays of two distinct sizes and *Wataria parvipora* (Terada and Suzuki, 1998) with apotracheal parenchyma 1–2 cells wide, rays in two distinct sizes and no crystals.

8.4. Miocene specimens of Grewioxylon

Most similar to the Fossil Wood Type 1 specimen are specimens of *Grewioxylon*, a genus containing woods with similarities to extant *Grewia*, which are rather numerous in Miocene deposits. However, these woods differ from the fossils in having axial parenchyma that is dominantly diffuse and diffuse-in-aggregates (e.g., *Grewioxylon fontanesii* Vozenin-Serra, 1981; *Grewioxylon neumaieri* Selmeier, 1985; *Grewioxylon ortenburgense* Selmeier, 1985; *Grewioxylon microcoides* Agarwal, 1991; *Grewioxylon intertrappea* Shallom, 1963). Additionally, it is common to see bimodal and storied rays (*Grewioxylon indicum* Prakash and Dayal, 1964; *Grewioxylon burmense* Gottwald, 1994; *Grewioxylon canalisum* Bande and Srivastava, 1994; *Grewioxylon macroporosum* Gottwald, 1994; *Grewioxylon intertrappea*) in these specimens. Although some of these *Grewioxylon* with bimodal and storied rays show aliform parenchyma as in *Guazumaoxylon miocenica* (Fossil Wood Type 1) it is conspicuously confluent and combined with narrow or broad apotracheal bands as in *G. fontanesii*, *G. burmense*, and *G. canalisum*.

In contrast, we know of no fossil woods with features closely similar to those seen in *Periplanetoxylon panamense* (Fossil Wood Type 2). Therefore our survey of malvacean fossil woods supports our view that the two fossil types described in this paper are novel.

9. Discussion

Malvaceae sensu APG III comprises c. 243 genera containing c. 4225 species, ranging from shrubs to trees, with a few herbaceous members. The family is characterized by leaves that show, typically, palmate secondary venation, inflorescences consisting of cymose units, and fruits comprising a capsule, berry or schizocarp (Stevens, 2001 onwards). Malvaceae sensu APG III is not only mostly tropical in distribution but also contains numerous representatives in the temperate zones (Judd and Manchester, 1997; Bayer and Kubitzki, 2003; Carvalho et al., 2011), with a few examples, such as *Malva pusilla* Smith, reaching up to 65°N in Europe (Hinsley, 2004 onwards). In the tropics, the family can be found in a diverse range of habitats including humid, semi-arid and arid zones (Hinsley, 2004 onwards).

9.1. Phylogeny and evolution

Delimitation of groups inside Malvaceae sensu APG III, especially within the traditional Malvaceae, has been inconsistent for a long time, and there have been many attempts to establish a degree of order (Rendle, 1925; Edlin, 1935; Brizicky, 1965; Hutchinson, 1967; Cronquist, 1981; Chang and Miau, 1989; Dorr, 1990; Manchester, 1992; Judd et al., 1994; Zomlefer, 1994; Judd and Manchester, 1997). Based primarily on molecular data and morphology, with limited support from the anatomy, nine monophyletic subfamilies are now recognised as follows: Grewiodeae, Byttnerioideae, Sterculioideae, Tilioideae, Dombeyoideae, Brownlowioideae, Helicteroideae, Helicteroideae, Malvoideae and Bombacoideae (APG III, 2009). The fossils are inferred to include representatives of the subfamilies Byttnerioideae (Fossil Wood Type 1) and Malvoideae (Fossil Wood Type 2).

Plate VI. *Guazuma ulmifolia* Lamarck, Jodrell Laboratory, Royal Botanic Gardens, Kew, Specimen number: Dominica 166.

1. Wood diffuse-porous; vessels solitary and in radial multiples of 2–3. Dominica 166, TS, scale: 100 μm.
2. Close-up of vessels in radial multiples of mostly 2–3 and a cluster of 6. Dominica 166, TS scale: 100 μm.
3. Perforation plates simple (arrows). Dominica 166, TS, scale: 100 μm.
4. Intervessel pitting alternate. Dominica 166, TLS, scale: 50 μm.
5. Vessel-ray pitting similar to intervessel pits (arrows). Dominica 166, RLS, scale: 20 μm.
6. Some septate fibres (SF, arrows) combined with non-septate fibres. Dominica 166, TLS, scale: 50 μm.
7. Vessels with paratracheal axial parenchyma as broad vasicentric sheaths to small winged-aliform (arrows) and scarce, diffuse parenchyma. Dominica 166, TS scale: 100 μm.
8. Close-up of paratracheal axial parenchyma as broad vasicentric sheaths (arrows); thin to thick walled fibres. Dominica 166, TS, scale: 100 μm.

Plate VII. *Guazuma ulmifolia* Lamarck, Jodrell Laboratory, Royal Botanic Gardens, Kew, Specimen numbers: Dominica 166, W-16271. (see on page 30)

1. Scarce, diffuse axial apotracheal parenchyma (arrows). Dominica 166, TS, scale: 100 μm.
2. Abundant scalariform apotracheal parenchyma, i.e., forming transverse bars in the groundmass between the rays (arrows). W-16271, TS scale: 100 μm.
3. Rays 3–5-seriate with sheath cells and scarce apotracheal parenchyma strands (arrows). Dominica 166, TLS, scale: 100 μm.
4. Rays 1–6-seriate with sheath cells and abundant apotracheal parenchyma strands (arrows). W-16271, TLS, scale: 100 μm.
5. Parenchyma strands 4–5-cells high. Dominica 166, TLS, scale: 25 μm.
6. Sheath cells (arrows). Dominica 166, TLS, scale: 50 μm.
7. *Guazuma* intermediate-type tile cells with abundant rhomboidal crystals (arrows). Dominica 166, RLS, scale: 100 μm.
8. Close-up of tile cells (TC, arrows) with crystals. Dominica 166, RLS, scale: 50 μm.

Plate VIII. *Pentaplaris doroteae* L.O. Williams et Standley, Jodrell Laboratory, Royal Botanic Gardens, Kew, specimen number: Kw 20291. (see on page 31)

1. Growth rings indistinct; wood diffuse-porous; regular to irregular bands of apotracheal parenchyma 3–5 cells wide (arrows). Kw 20291, TS, scale: 200 μm.
2. Vessels in radial multiples of 2–4 and apotracheal banded parenchyma 3–5 cells wide. Kw 20291, TS, scale: 100 μm.
3. Close up of solitary vessel with oval outline. Kw 20291, TS, scale: 50 μm.
4. Perforation plate simple (SPP, arrow). Kw 20291, RLS, scale: 100 μm.
5. Intervessel pitting alternate, polygonal and minute. Kw 20291, TLS, scale: 50 μm.
6. Detail of bordered vessel-ray pits, similar in size and shape to the intervessel pits. Kw 20291, RLS, scale: 15 μm.
7. Parenchyma strands up to 8 cells high. Kw 20291, TLS, scale: 25 μm.
8. Rays 2–4 (–5) cells wide, showing conspicuous sheath cells (arrows); ray density 4–13 per mm. Kw 20291, TLS, scale: 100 μm.
9. *Pterospermum*-type tile cells (TC), some containing rhomboidal crystals (C, arrows), interspersed with procumbent ray cells. Kw 20291, TLS, scale: 100 μm.
10. Rhomboidal crystals in square ray cells. Kw 20291, RLS scale: 50 μm.

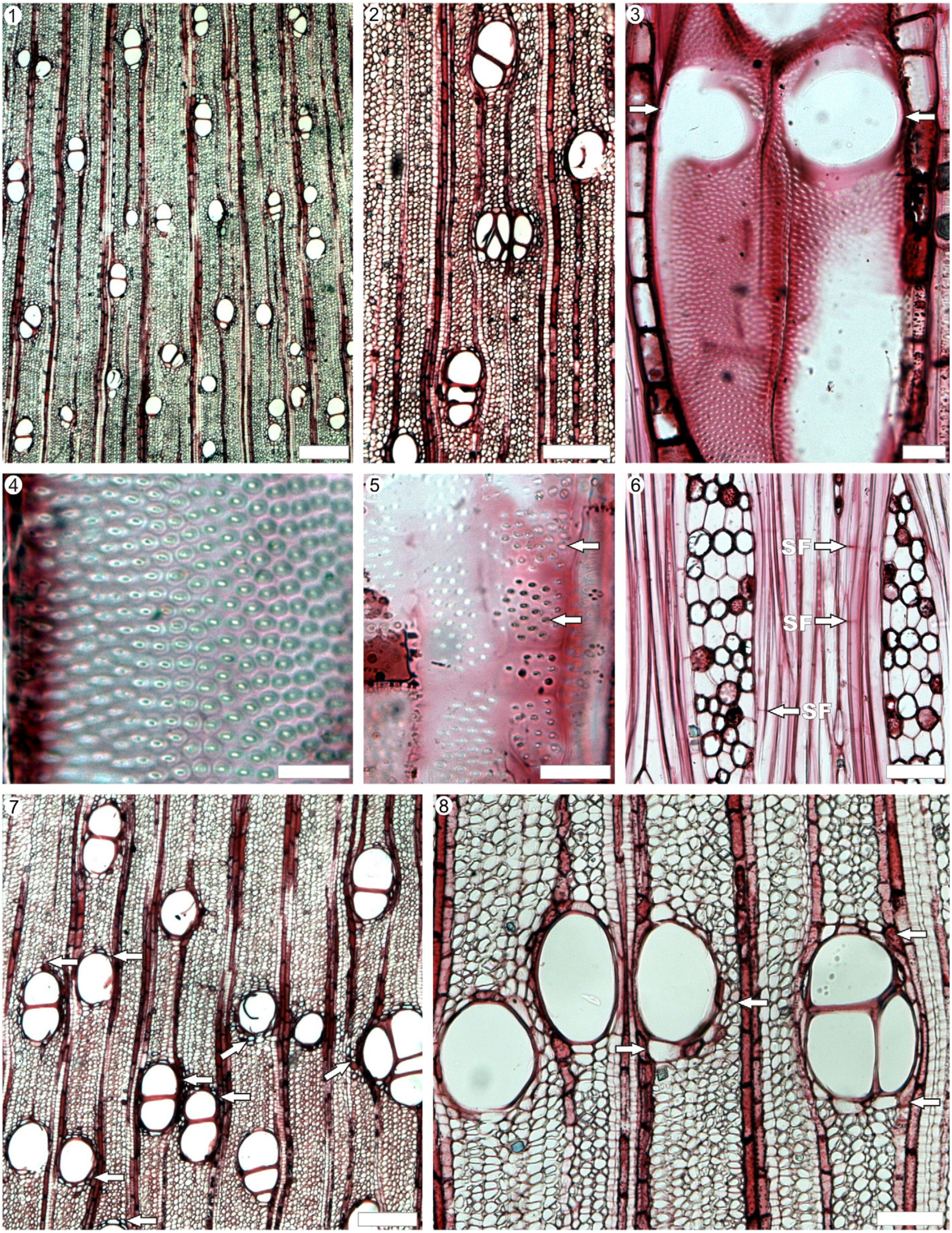

Plate VI.

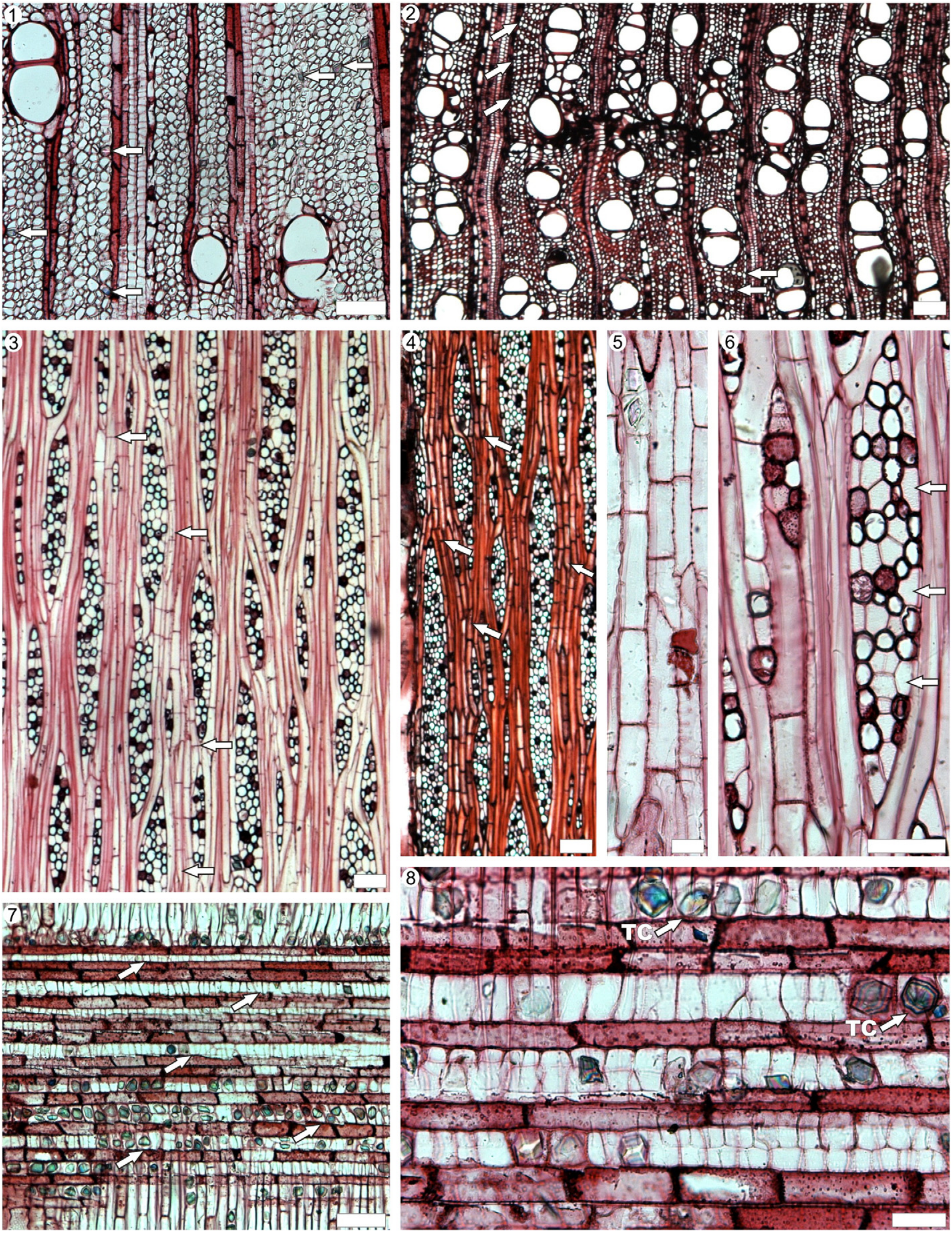

Plate VII (*caption on page 28*).

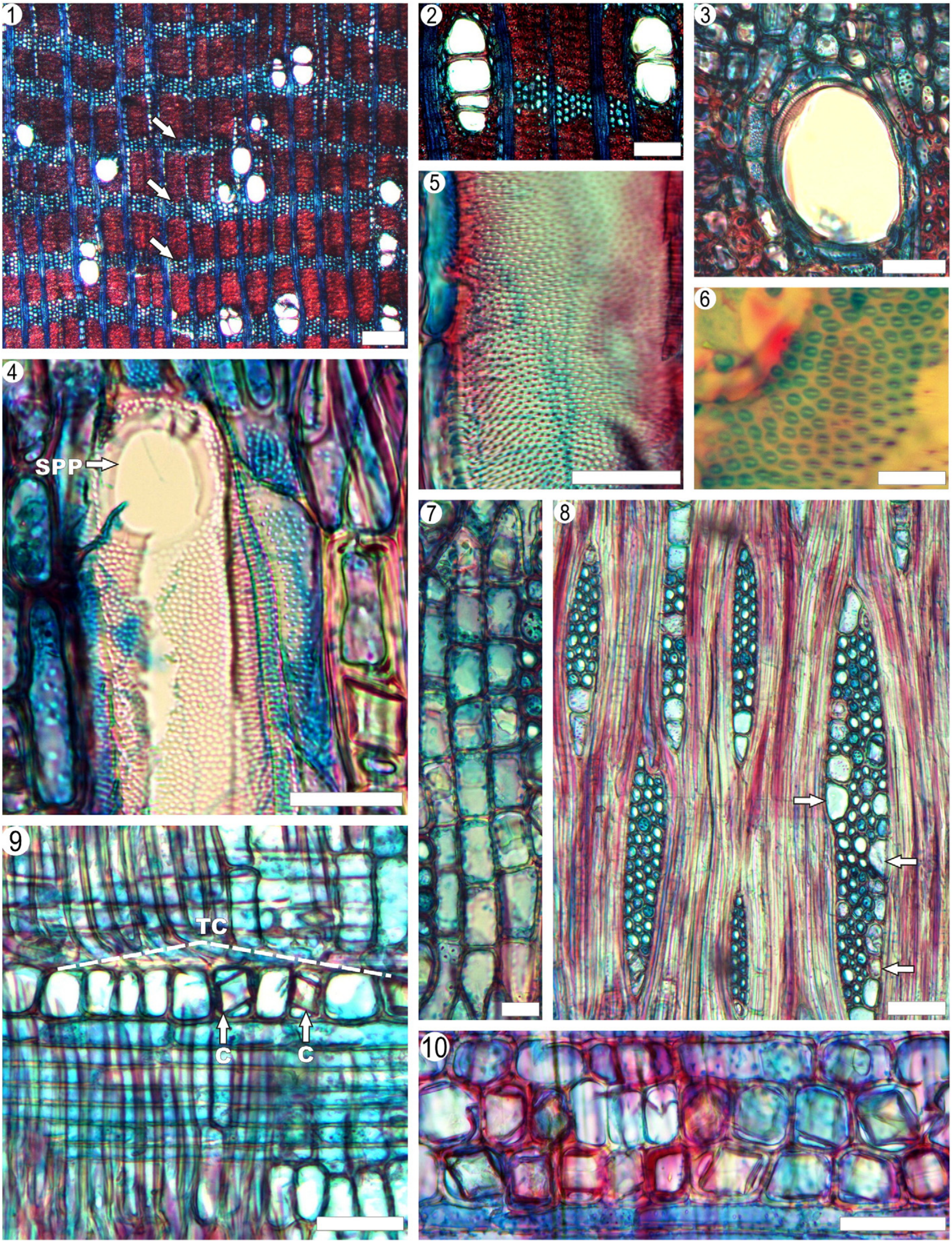

Plate VIII (*caption on page 28*).

Most of the genera of Byttnerioideae are endemic to Central and South America suggesting an origin in this region, consistent with the fossil discoveries reported here. In contrast, the subfamily Malvoideae, which is one of the most basal and diverse clades in the Malvaceae (Baum et al., 2004; Hinsley, 2004; APG III, 2009), has traditionally been considered to be of Australasian origin with multiple long-distance migrations invoked to explain the occurrence of the group in the Neotropics (Pfeil et al., 2002; Duarte et al., 2011). However, megafossils found in the Paleocene of Colombia (Carvalho et al., 2011) offer an alternative explanation suggesting a broader distribution in the past, favoured by warmer conditions, and more likely with a South American origin. Again, this is consistent with our new Miocene data.

9.2. Biogeographic significance of fossils

The two fossil woods described herein from the lower Miocene of Panama comprise material similar to extant *Guazuma* (Byttnerioideae), especially *Guazuma ulmifolia* (Fossil Wood Type 1) and *Pentaplaris* (Malvoideae), especially *Pentaplaris doroteae* (Fossil Wood Type 2). *Guazuma ulmifolia* is a shrub or tree 3–25 m tall and with trunk diameters up to 0. 8 m, found in lowland deciduous forest and pastures of Central America (Garguillo et al., 2008; USDA and NRCS, 2013). *Pentaplaris* is a genus of large rainforest trees restricted to the present-day Neotropics of Costa Rica, Bolivia, and Peru. The presence of South American taxa in the lower Miocene strata of Panama suggests floral interchange of large tree species through the Isthmus of Panama as early as c. 18–20 Ma. This is consistent with the recently proposed emergence of the Isthmus in the Miocene (Montes et al., 2012) evidenced by studies of plutonic zircons and inferences from mammal biostratigraphy.

10. Conclusions

1. Nine calcareous permineralised woods are described from tidally-influenced fluvial channel facies near the base of the Miocene (early to mid-Burdigalian) Cucaracha Formation at Hodges Hill, Panama.
2. The fossil specimens show a combination of tile cells, sheath cells, and other features that are generally diagnostic of the Malvaceae sensu APG III, and comprise two types, each representing a new taxon.
3. *Guazumaoxylon miocenica* gen. et sp. nov. (Fossil Wood Type 1) is characterized by axial parenchyma with a winged-aliform distribution. This taxon is probably related to species of extant *Guazuma*, especially those endemic to central South America.
4. *Periplanetoxylon panamense* gen. et sp. nov. (Fossil Wood Type 2) is characterized by axial parenchyma in regular to irregular bands >3 cells wide. This taxon is probably related to the extant genus, *Pentaplaris*, endemic to central South America.
5. The occurrence of trees of South American affinity in the lower Miocene of Panama is of palaeogeographic significance, suggesting the existence of plant migrations between South America and the Panama Isthmus as early as the Miocene.

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