Panascleroticoxylon crystallosa gen. et sp. nov.: a new Miocene malpighialean tree from Panama

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ABSTRACT

We report fossil wood specimens from two Miocene sites in Panama, Central America: Hodges Hill (Cucaracha Formation; Burdigalian, c.19 Ma) and Lago Alajuela (Alajuela Formation; Tortonian, c.10 Ma), where material is preserved as calcic and silicic permineralizations, respectively. The fossils show an unusual combination of features: diffuse porous vessel arrangement, simple perforation plates, alternate intervessel pitting, vessel–ray parenchyma pits either with much reduced borders or similar to the intervessel pits, abundant sclerotic tyloses, rays markedly heterocellular with long uniseriate tails, and rare to absent axial parenchyma. This combination of features allows assignment of the fossils to Malpighiales, and we note similarities with four predominantly tropical families: Salicaceae, Achariaceae, and especially, Phyllanthaceae, and Euphorbiaceae. These findings improve our knowledge of Miocene neotropical diversity and highlight the importance of Malpighiales in the forests of Panama prior to the collision of the Americas.

Keywords: Miocene, Panama, fossil wood, Malpighiales, Neotropics.

[In the online version of this paper Figure 1–12 & 13–18 are reproduced in colour.]

INTRODUCTION

Neotropical forests are among the richest in the world, and Panama (Central America) is a key area to study factors that promote high biodiversity in a small region. Paleobotanical studies contribute an important historical perspective that enhances our understanding of how the Neotropical forest structure and composition has changed through time. The recent expansion of the Panama Canal (2007–2016) provided a once-in-a-century opportunity to collect plant macrofossils from localities formerly

obscured by overburden and dense vegetation. This work also led to renewed interest in the palaeontology of other localities outside the canal zone. Ongoing fossil studies are contributing new information concerning the systematics and biogeographic history of a variety of plant families, including Humiriaceae (Herrera *et al*. 2010), Malvaceae (Rodriguez-Reyes *et al*. 2014), Chrysobalanaceae (Jud *et al*. 2016), Calophyllaceae (Nelson & Jud, in press), and Fabaceae (Rodriguez-Reyes *et al*., under review). In the present paper we describe a new fossil wood type from the Miocene of Panama, which further broadens our knowledge of ancient diversity of Central America.

MATERIALS AND METHODS

The specimens reported here were collected from two locations in Panama where fossil wood is abundant. The first specimen was collected from Hodges Hill on the Gaillard Cut of Panama Canal Zone, c. 25 km west of Panama City (latitude 09° 02' 51.75" N; longitude 79° 39' 14.02" W) and the second specimen was collected from the shore of Lago Alajuela (formerly Lake Madden) in Chagres National Park (latitude 09° 16' 37.1" N; longitude 79° 34' 40.8" W), c. 40 km northwest of Panama City. Both localities are Miocene in age.

Geological context

The Hodges Hill specimen was obtained from the lower Miocene Cucaracha Formation (MacFadden *et al*. 2014), a tidally-influenced fluvial succession that has yielded a rich assemblage of fossil plants, including diverse angiosperm woods, fruits, and leaves (Berry 1918; Herrera *et al*. 2010; Rodriguez-Reyes 2014; Rodriguez-Reyes *et al*. 2014; Jud *et al*. 2016). The specimen lies c. 30 metres below a silicic tuff with a radiometric age of $^{40}Ar/^{39}Ar$ age of 18.96 ± 0.90 Ma and a U-Pb zircon age of 18.81 ± 0.30 Ma (MacFadden *et al*. 2014), which places it in the Burdigalian Stage.

The Lago Alajuela specimen was obtained from the upper Miocene Alajuela Formation, a shallow marine unit (Stewart *et al*. 1980; Jones *et al*. 2015), which is a prolific source of invertebrate, vertebrate, and plant fossils (Macfadden *et al*. 2015; Macfadden *et al*. 2017). The wood was collected as float in the lower part of the formation along the shore of the lake. The lower part of the Alajuela Formation consists of interbedded matrix-supported conglomerates and litharenite sandstones, and transitions to predominantly calcareous sandstones and calcarenites in the upper portion (Woodring 1957; Henderek *et al*. 2014). Strontium-isotope ratio analyses of scallop shells from the lower part of the formation indicate an age of 9.77 ± 0.22 Ma, and place the fossils in the Tortonian Stage (MacFadden *et al*. 2017).

Accession data, specimen preparation, and imaging

Petrographic thin sections of fossil material were prepared in transverse (TS), radial longitudinal (RLS), and tangential longitudinal (TLS) sections. Sections were mounted on glass slides using EpoFix resin, ground to a thickness of ~30 μm, and coverslips were affixed with Canada balsam. Material was observed and imaged using an Olympus binocular BH-5 with a Nikon digital camera system and software.

The fossil woods were compared with the available images of modern and fossil woods in the InsideWood Database (IWD; insidewood.lib.ncsu.edu), Plant Resources of Tropical Africa (PROTA), key literature (Miller 1975; Mennega 1987; Hayden & Hayden 2000), and modern wood slides in the Jodrell Laboratory of the Royal Botanic Gardens, Kew, U.K. (RBGK). Modern woods used for comparative analysis were imaged using a Leica DM LB microscope with Zeiss Axiocam HRc camera attachment and Zeiss Axiovision software.

IAWA feature description and codification

Fossil wood specimens were described using the International Association of Wood Anatomists (IAWA) List of Features for Hardwood Identification (IAWA Committee 1989). For quantitative data of vessel frequency, ray density and vessel grouping, measurements were made in 10 different fields of 1 mm^2 area. For other quantitative features (mean vessel diameter, intervessel pit diameter, vessel–ray parenchyma pit diameter, vessel element length, ray height), a minimum of 30 measurements was obtained. At the start of descriptions, a list of IAWA code numbers is given modified by the following symbols: '?' indicates that there is uncertainty as to whether the feature is present and 'v' indicates that the feature is variable in occurrence.

SYSTEMATIC DESCRIPTION

Order: Malpighiales

Family: *incertae sedis*

Genus: *Panascleroticoxylon* Rodríguez-Reyes, Gasson, Thornton, Falcon-Lang *et* Jud, *gen. nov.* (Fig. 1–18).

Type species: *Panascleroticoxylon crystallosa gen. et sp.nov.*, Rodríguez-Reyes, Gasson, Thornton, Falcon-Lang *et* Jud (Fig. 1–18).

Diagnosis: Wood diffuse porous; perforation plates simple; intervessel pits alternate; vessel–ray parenchyma pits with much reduced borders or occasionally similar to the intervessel pits; sclerotic tyloses present; paratracheal and apotracheal parenchyma extremely rare or absent; rays 1–3(–4)-seriate, strongly heterocellular, with long uniseriate tails of upright cells, occasionally >1 mm; crystals of varying size are present in some upright ray cells and may be solitary or of two distinct sizes per cell.

Specific diagnosis: as for the genus.

Etymology of generic name: *Panascleroticoxylon* is a composite of *Pana*, from Panama, *sclerotic*, indicating the abundance of sclerotic tyloses, and *xylon*, Greek for wood. The specific epithet *crystallosa* comes from the Greek, krýstallo and refers to the abundant crystals.

Holotype: STRI 36272 from Miocene (Burdigalian) of Hodges Hill, Panama, designated here, consisting of one hand specimen, and three petrographic thin sections (TS, TLS, RLS). The hand sample retrieved from the field had dimensions of 0.31 m (incomplete length) and 0.25 m (incomplete diameter).

Additional material: UF 063124 from Miocene (Tortonian) of Lago Alajuela, Panama, consisting of one hand specimen and three thin sections (TS, TLS, RLS). This small sample is water-worn, with approximate dimensions of 70 mm (incomplete length) and 20 mm (incomplete diameter).
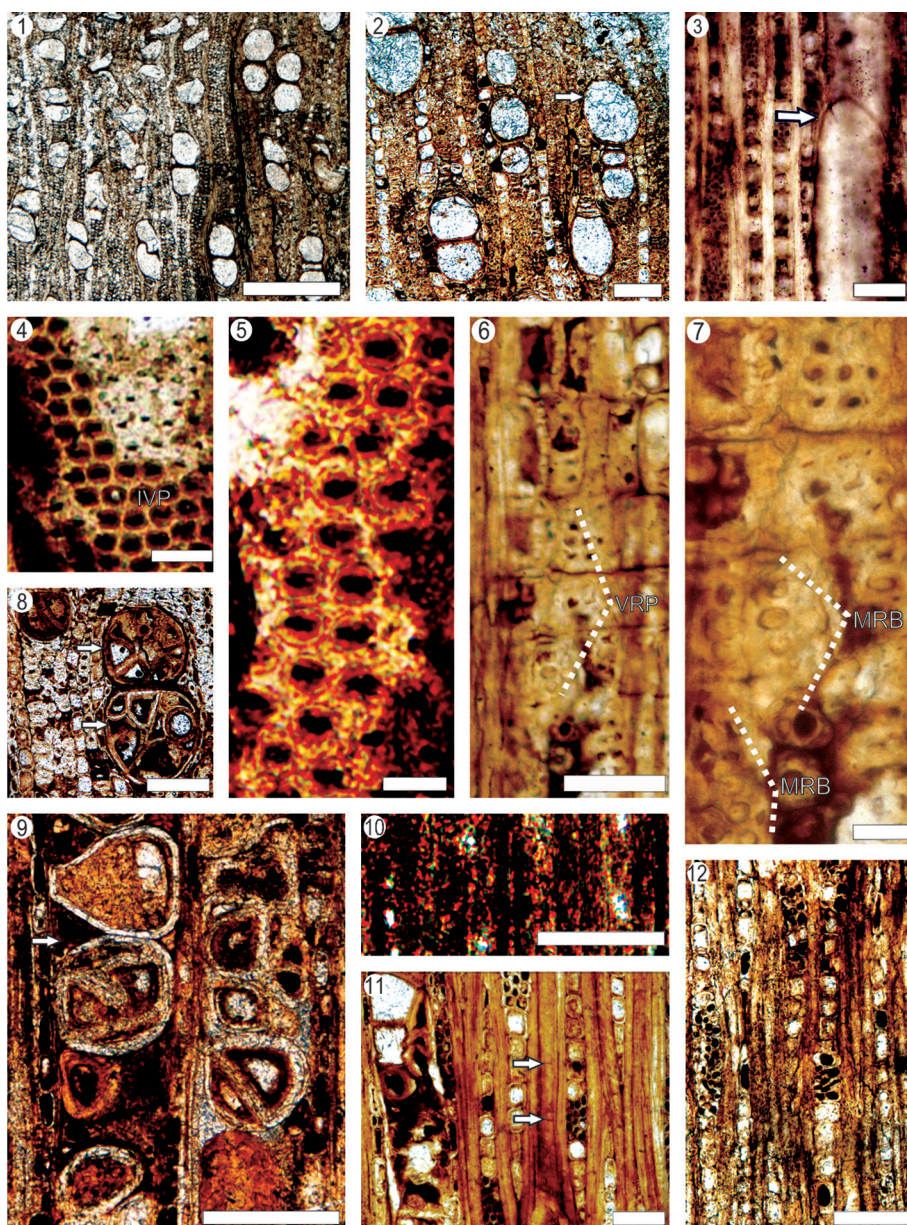
Figures 1–12. *Panascleroticoxylon crystallosa* Rodriguez-Reyes, Gasson, Thornton, Falcon-Lang *et* Jud, sp. nov. (1, 2, 4–12: STRI 36272; 3: UF 063124). – 1: Growth rings indistinct, wood diffuse porous and absent axial parenchyma. TS. – 2: Vessels in short radial multiples of 2–3(–4), vessel outline oval (arrow). TS. – 3: Simple perforation plate (arrow). TLS. – 4: Intervessel pitting alternate. TLS. – 5: Intervessel pitting medium to large. TLS. – 6: Vessel–ray pitting with much reduced borders to apparently simple (dotted bracket). RLS, TLS. – 7: Vessel–ray pitting showing much reduced borders to apparently simple (MRB) and occasionally

IAWA features present: 2, 5, 13, 22, 25v, 26, 31, 42, 47v, 48, 53, 56, 57, 61, 63v, 65v, 66, 69v, 70, 75, 78v, 97v, 98, 100v, 102v, 107v, 108, 110v, 115, 116v, 136, 137, 140, 155v.

Descriptive note: In the following description, the mean of each specimen is reported separately, followed by the total range of values for both specimens.

Description: Growth rings indistinct; wood diffuse porous (Fig. 1); vessels solitary (31 % and 39 %) or in short radial multiples of 2–3(–4) (Fig. 1, 2); solitary vessel outline oval (Fig. 1, 2, 13); perforation plates simple (Fig. 3); intervessel pits alternate (Fig. 4, 5) and small to medium (mean pit diameter 6 and 7 μm; total range, up to 12 μm for both specimens) (Fig. 5); vessel–ray pits with much reduced borders and occasionally similar to intervessel pitting (mean diameter 6 μm; total range 4–9 μm) (Fig. 6, 7); mean tangential vessel diameters of 110 μm and 112 μm (total range 60–182 μm); mean vessel density of 18.2 and 21.0 per mm^2 (total range 15–27 per mm^2); mean vessel element length of 435 and 579 μm (total range 324–850 μm); sclerotic tyloses present (Fig. 8, 9); vascular / vasicentric tracheids not observed.

Fibres with minutely bordered pits common in radial walls (Fig. 10) and occasionally in tangential walls; mostly non-septate (Fig. 11, 12) but occasionally septate (Fig. 11); thin-to-thick walls (Fig. 8, 13).

Paratracheal and apotracheal parenchyma extremely rare or absent (Fig. 1,2,13,18); axial parenchyma strands not observed.

Rays strongly heterocellular (Fig. 11, 12, 14–16), 1–3(–4)-seriate (mean 3–5) (1–5-seriate in UF 063124) (Fig. 15) and occasionally > 1 mm (means 0.7 and 0.8; total range 0.22–1.6 mm) (Fig. 11, 14); rays per mm 11 and 15 (total range 9–18 per mm), with long uniseriate tails (Fig. 11, 12, 14) composed of procumbent cells in the body of the ray and > 4 rows of marginal square cells (Fig. 16); sheath cells occasionally present in UF 063124 (Fig. 15).

Solitary rhomboidal crystals abundant in non-chambered (Fig. 17) and chambered square and upright ray cells (Fig. 18); crystals of varying size are present in some ray cells (Fig. 17).

Remarks: This combination of rare axial parenchyma, large alternate intervessel pits, heterocellular rays with procumbent body cells and long uniseriate tails composed of upright cells, sclerotic tyloses, and abundant crystals is unlike any other specimen known from the Miocene of Panama to date. This combination is also uncommon in the descriptions of modern and fossil wood available on the online InsideWood Database (IWD*)*, the micromorphology reference slide collection and database in the Jodrell Laboratory of the Royal Botanic Gardens, Kew, U.K. (RBGK), and other key literature (*e.g.*, Ilic 1991; Gasson 1996).

←

with distinct borders. RLS. – 8. Sclerotic tyloses present (arrows). TS. – 9: Sclerotic tyloses seen in longitudinal section (arrows). TLS. – 10: Fibres with minutely bordered pits. RLS. – 11: Fibres mostly non-septate alternating with a few septate fibres (arrows) and rays with long uniseriate tails. TLS. – 12: Fibres non-septate and rays with long uniseriate tails. TLS. – Scale bars: 1 = 500 μm; 2, 3, 4, 9, 10, 11 = 100 μm; 6, 8 = 50 μm; 5, 7 = 25 μm.
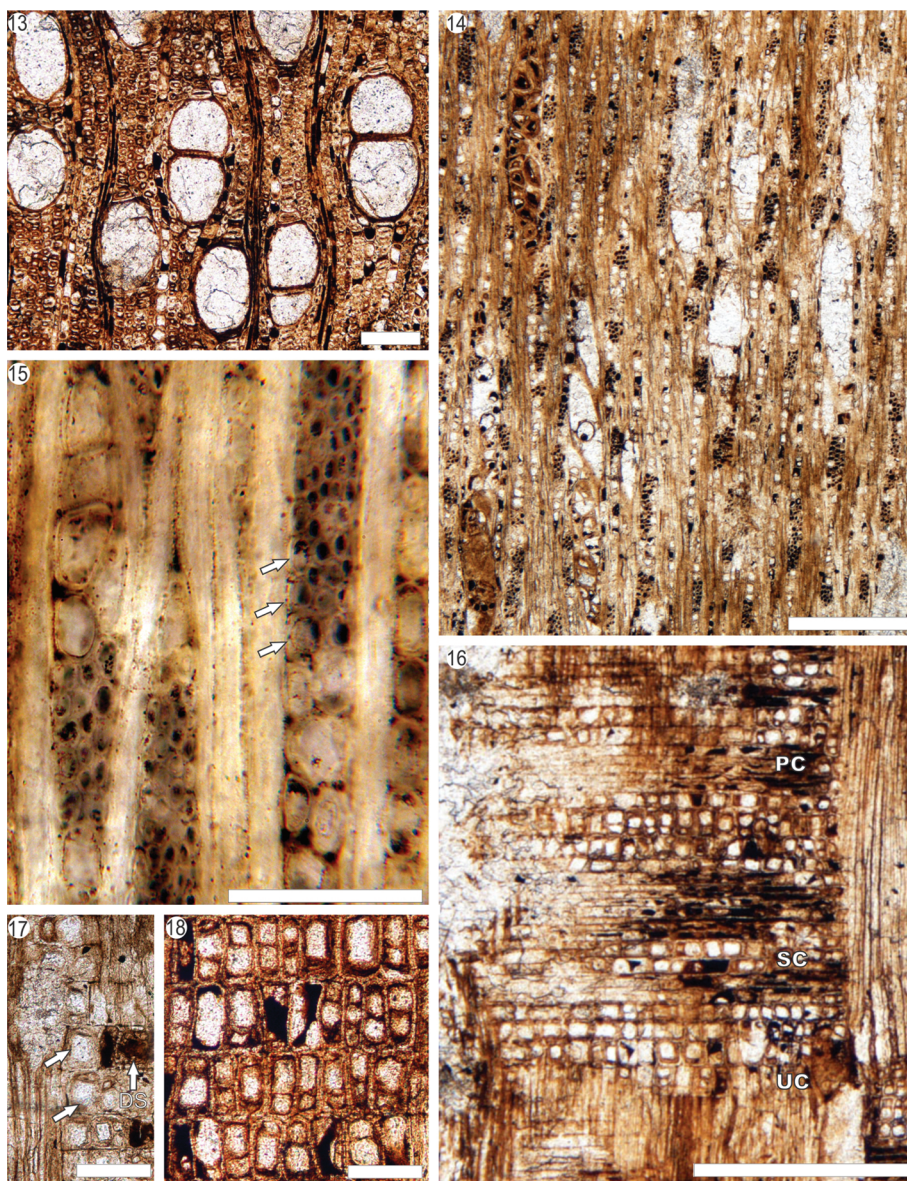
Figure 13–18. *Panascleroticoxylon crystallosa* Rodriguez-Reyes, Gasson, Thornton, Falcon-Lang *et* Jud, sp. nov. (13, 14, 16–18: STRI 36272; 15: UF 063124). – 13: Fibres, thin- to thick-walled. TS. – 14: Rays with long uniseriate tails. TLS. – 15: Rays 1–5-seriate and one portion with uniseriate portions as wide as multiseriate portions and occasional sheath cells present (arrows). TLS. – 16: Rays composed of procumbent cells (PC) and > 4 rows of marginal square and upright cells (SC, UC). RLS. – 17: Solitary rhomboidal crystals in ray cells (arrows) and more than one crystal per ray cell chamber (DS, arrows). RLS. – 18: Rhomboidal crystals in chambered square and upright ray cells. RLS. – Scale bars: 13 = 500 µm; 14–17 = 100 µm; 18 = 50 µm.

Table 1. Anatomical comparison of Achariaceae, Elaeocarpaceae and *Panascleroticoxylon crystallosa*.

Data are taken from Miller (1975), Gasson (1996) and IWD. Headings: GR = growth rings; VD = vessel distribution; IVP = intervessel pitting; VRP = vessel–ray pitting; PP = perforation plates; F = fibre type; ST = spiral thickenings; AP = apotracheal parenchyma; RW = ray width (number of cells); RTDS = rays of two distinct sizes; SC = sheath cells; CL = crystal location; T = tyloses. Coding: p = present; a = absent; rm = radial multiples; sol. = solitary vessels; A = alternate; O = opposite; S = scalariform pits; MRB = much reduced borders; R = rounded; H = horizontal; DB = distinct borders; simp. = simple perforation plates; scal. = scalariform perforation plates; s = septate fibres; ns = non-septate fibres; v = helical thickenings in vessel element tails; m = marginal parenchyma; * = variable occurrence; proc. = procumbent ray cells; upr = upright ray cells; ? = uncertain occurrence.

	GR	VD	IVP	VRP	PP	F	ST	AP	RW	RTDS	SC	CL	T
Achariaceae													
Erythrospermum	a	rm	O-A	MRB: R, H	scal.	s	a	a	2–6	a	a	proc, upr	a
Ahernia	a	rm	A	MRB: H	simp.	s	a	a	2–6	*p	a	upr	a
Buchnerodendron	a	rm	A	DB, MRB	simp., scal.	s	a	a	1–3	?p	a	proc, upr	a
Dasylepis	a	rm	A	MRB: R, H	scal.	s	a	a	4–6	a	a	proc	a
Scottellia	a	rm	A	MRB: R	scal.	s	v	a	3–7	a	*p	proc, upr	a
Camptostylus	a	rm	A	MRB: R–C	simp., scal.	s	v	a	4–10	*p	*p	proc, upr	a
Rawsonia	a	rm	A	MRB: R, H	scal.	s	a	a	2–12	*p	a	proc, upr	a
Carpotroche	a	rm	O-A	MRB: R	simp., scal.	s	a	a	2–5	a	a	proc, upr	a
Mayna	a	rm	O-A	MRB: R, H	simp., scal.	s	v	a	3–5	a	a	proc, upr	a
Caloncoba	a	rm	A	MRB: R	simp., scal.	s	a	a	2–7	a	a	proc	a
Lindackeria	a	rm	A	MRB: R	simp., scal.	s	v	a	2–7	*p	a	proc	a
Hydnocarpus	a	rm	O-A	MRB: R,H	scal.	s	v	a	2–3	a	a	proc, upr	a
Eleutherandra	a	rm	A	MRB: R, H	simp.	s	a	a	1–3	a	a	proc, upr	*p
Gynocardia	a	rm	A	MRB: R, H	simp., scal.	s	a	a	1–2	a	a	proc, upr	a
Pangium	a	rm	A	MRB: R, H	simp.	s	a	a	3–5	a	a	proc, upr	a
Trichadenia	a	rm	A	MRB: R, H	simp.	s	a	a	2–5	p	a	proc, upr	*p
Scaphocalyx	a	rm	A	MRB: R, H	simp.	s	a	a	2	a	a	proc, upr	a
Ryparosa	a	rm	A	MRB: R, H	simp., scal.	s	a	a	3–8	a	a	proc, upr	a
Kiggelaria	a	rm	A	MRB: R	simp.	s	v	a	3–4	*p	a	proc	*p
Prockia	a	rm	A	DB	simp.	s	a	a	2–3	a	a	proc, upr	a
Elaeocarpaceae													
Aceratium	p/a	rm	A	MRB: R-H	simp.	ns, *s	a	a, m	1–3; 4–10	a	*p	proc, upr	a
Aristotelia	p/a	rm	O-A	MRB: R-H	simp.	ns, s	a	a, sc, dif	1(–3)–7	a	p	abs	p
Crinodendron	p	rm	A	MRB: R-H	simp.	s, ns	a	sc	1–3	a	a	proc, upr	a
Dubouzetia	p	rm	A	MRB: R-H	simp.	ns, *s	a	a	1–3	*p	*p	proc, upr	a
Elaeocarpus	p/a	rm	A-O	MRB: R-H	simp., scal.	s, ns	v	a, sc, dif, *m	1–3; 4–10	a	p	proc, upr	p
Peripentadenia	p/a	rm	A	MRB: R; *TDS	simp.	ns	a	a	4–10; 1–3 v	a	p	proc, upr	p
Sericolea	p	rm	A	MRB: R	simp.	s, ns	a	a	1–3	a	p	proc, upr	a
Sloanea	p/a	rm	O-A ; S	MRB: R	simp., *scal.	s, ns	a	a, sc, *m	1–10	p	p	proc, upr	*p
Vallea	p	rm	O-S	MRB: H	simp., *scal.	s	a	a	1–4	a	p	abs	a
P. crystallosa	a	rm	A	MRB: R	simp.	ns, s	a	a	1–3(4); 1–7	a	*p	proc, upr	p

PRELIMINARY SEARCHES

We conducted searches for comparable modern material in the InsideWood Database (insidewood.lib.ncsu.edu*)*. Our most restrictive search included wood ring porous absent (3a), wood semi-ring porous absent (4a), wood diffuse porous (5p), vessels in tangential bands absent (6a), vessels in diagonal and/or radial pattern absent (7a), vessels in dendritic pattern absent (8a), vessels exclusively solitary absent (9a), vessel clusters common absent (11a), perforation plates simple (13p), perforation plates scalariform absent (14a), intervessel pitting alternate (22p), vessel–ray pitting with much reduced borders to apparently simple (31p); axial parenchyma diffuse-in-aggregates absent (77a), axial parenchyma vasicentric absent (79a), axial parenchyma aliform absent (80a), axial parenchyma confluent absent (83a), axial parenchyma unilateral paratracheal absent (84a), axial parenchyma bands with more than three cells wide absent (85a), axial parenchyma in narrow bands up to three cells wide absent (86a), rays 1–3-seriate (97p), rays 4–10-seriate (98p); body ray cells procumbent with >4 rows of upright and/or square marginal cells (108p); oil and mucilage cells associated with ray parenchyma absent (124a); radial canals absent (130a). This search yielded 31 descriptions for modern woods in three orders: Oxalidales (Elaeocarpaceae), Malpighiales (Achariaceae, Malpighiaceae, Phyllanthaceae), and Lamiales (Acanthaceae, the monotypic shrub *Trichanthera gigantea*).

Lamiales (Acanthaceae) excluded

Carlquist (1988) showed that Acanthaceae typically have relatively narrow vessels with simple perforation plates, septate libriform fibres, scanty vasicentric axial parenchyma, rays both multiseriate and uniseriate, erect ray cells abundant in rays, numerous small crystals or cystoliths in ray cells in a few genera, and non-storied structure – features that are similar to *Panascleroticoxylon*. Upon further examination, Lamiales and most Acanthaceae (including *Trichanthera*) we noted they have significantly more abundant vasicentric axial parenchyma than observed in the fossils. We therefore excluded Lamiales (Acanthaceae) from further consideration.

Oxalidales (Elaeocarpaceae) excluded

Two species of Elaeocarpaceae that bear some resemblance to the fossils are *Elaeocarpus reticulatus* (Kew 1951) (synonym *E. cyaneus*) from Queensland, Australia, and *E. rugosus* (Kew D6074) from Peninsular Malaysia and Singapore. These two species and the fossil type share the following characters: wood diffuse porous, simple perforation plates, intervessel pitting alternate and medium to large in size, vessel–ray pits with much reduced borders to apparently simple, rounded pits, tyloses common, albeit not as thick-walled as the tyloses in the fossils, fibres mostly septate but with a few non-septate ones, parenchyma absent or extremely rare, rays strongly heterocellular, 1–5-seriate with long uniseriate tails, crystals abundant in chambered ray cells and occasionally with more than one crystal of different sizes per chamber. We conducted a broader survey of the wood anatomy of Elaeocarpaceae, based on Gasson (1996) and the IWD (Table 1), and it shows that *Panascleroticoxylon* differs from most Elaeocarpaceae in

the absence of opposite intervessel pitting, horizontal and in palisade vessel–ray pits, scalariform perforation plates and diverse patterns of axial parenchyma. We therefore excluded Elaeocarpaceae from further consideration.

COMPARISON WITH MALPIGHIALES

We focused subsequent comparison on the order Malpighiales. This is a diverse order of angiosperms that is important in tropical forest canopies (Davis *et al.* 2005; Wurdack & Davis 2009; Xi *et al.* 2012). Since the work of Metcalfe and Chalk (1950) that summarised dicotyledonous anatomy, the circumscription of several constituent families has changed significantly with the advent of molecular phylogenetics (Chase *et al.* 2002). Based on our survey of the information available in InsideWood, the families

Table 2. Anatomical comparison of selected modern woods and *Panascleroticoxylon crystallosa*.

Data are taken from the IWD. Headings: FAM = family; GR = growth rings (+ = distinct growth rings, – = indistinct growth rings); P = porosity (+ = ring porous or semi-ring porous; – = diffuse porous); PP = perforation plates; IVP = intervessel pitting size category; V-R P = vessel–ray pits; T = tyloses; AP = apotracheal parenchyma; SF = septate fibres; RW = maximum ray width; C = crystals abundant. Coding: a = absent, p = present, v = variable; dp = diffuse porous wood; simp = simple perforation plates, scal = scalariform perforation plates; min = minute; s = small; m = medium; l = large; MRB = much reduced borders to apparently simple; DB = distinct borders and similar to intervessel pits; GL = gash like or in palisade.

Taxon	FAM	GR	P	PP	IVP	V-R P	T	AP	SF	RW	C
Panascleroticoxylon crystallosa	?	a	dp	simp	s-m	MRB; DB	p	p	v	1–3 (4)	p
Oncoba brachyanthera	Salicaceae	a	dp	scal/ simp	s-m	MRB; GL	a	p	v	1–3	p
Casearia arborea	Salicaceae	a	dp	simp	min-s	DB	p	p	v	4–10	a
Casearia corymbosa	Salicaceae	v	dp	simp	min	DB	a	p	p	1–3	p
Casearia gossypiospermum	Salicaceae	v	dp	simp	min	DB	a	p	v	4–10	a
Eleutherandra pes-cervi	Achariaceae	a	dp	simp	s-m	MRB; GL	p	p	p	1–3	p
Margaritaria anomala	Phyllanthaceae	a	dp	simp	s	MRB; GL	p	p	v	1–3; 4–10	p
Margaritaria discoidea	Phyllanthaceae	a	dp	simp	m	MRB; GL	p	a	v	1–3; 4–10	p
Margaritaria indica	Phyllanthaceae	a	dp	simp	m-l	MRB	p	p	p	1–3	p
Margaritaria nobilis	Phyllanthaceae	a	dp	simp	s-m	MRB; GL	p	p	v	1–3; 4–10	p
Phyllanthus salvifolius	Phyllanthaceae	a	dp	simp	m-l	MRB; GL	p	p	v	1–3; 4–10	a
Acalypha	Euphorbiaceae	a	dp	scal/ simp	?	MRB; GL	a	p	p	4–10	a

with genera most like *Panascleroticoxylon* are in the Achariaceae, Euphorbiaceae, Phyllanthaceae and Salicaceae; however, it is difficult to assign the new taxon to any one of those families because of the substantial overlap in wood anatomical features. Unfortunately, there are many species of Euphorbiaceae that are not represented in the collections we examined nor reported in the literature, which limits the total coverage of the family for this comparison.

In the IWD search result reported above, genera of Malpighiales represented by only one species include *Mahurea* sp. (Calophyllaceae), *Rinorea pugionifera* (Violaceae), and *Glandonia macrocarpa* (Malpighiaceae). The first two differ from the fossil type because they have reticulate perforation plates, diffuse axial parenchyma and the occasional rays of two distinct sizes, whereas the latter differs in its exclusively septate fibres and small vessels in long radial multiples. About half of the results of the IWD search were species that belong to four families of the Malpighiales: Achariaceae, Euphorbiaceae, Phyllanthaceae, and Salicaceae. We therefore conducted a detailed study of these families. In Table 2, we provide a comparative summary of *Panascleroticoxylon crystallosa* and selected modern woods including Phyllanthaceae, Salicaceae and Euphorbiaceae.

Comparison with Salicaceae

Salicaceae Mirbel comprises 54 genera and 1200 species (Stevens 2001-onwards). Diffuse porous wood, intervessel pitting alternate, axial parenchyma rare to absent, tyloses common and abundant crystals are traits present in most of the tropical Salicaceae and are traits shared with *P. crystallosa*. From the surveyed Salicaceae, several features not present in *Panascleroticoxylon* include scalariform perforation plates (*e.g.*, *Idesia polycarpa*, *Hasseltia* sp., *Oncoba brachyanthera*); helical thickenings in *Azara*, *Bennettiodendron leprosipes*, *Carrierea calycina*, *Macrohasseltia macroterantha*; very small vessels (*e.g.*, *Calantica cerasifolia*, *Trimeria tropica*); druses abundant (*e.g.*, *Carrierea calycina*, *Casearia battiscombei*); vessel-ray pits unilaterally compound (*e.g.*, *Itoa stapfii*); axial parenchyma present (*e.g.*, *Oncoba spinosa*); ray density >12/mm in *Trimeria tropica*; rays mostly biseriate (*e.g.*, *Xylosma japonicum*, *X. sumatrana*). Species of *Casearia*, a genus widely distributed in South America, has intervessel pitting minute (although not in all species) and exclusively septate fibres; whereas intervessel pits small to medium and abundant non-septate fibres combined with a few septate fibres occur in *Panasclaroticoxylon crystallosa*. There are scalariform perforation plates in *Dovyalis*, *Olmediella*, *Azara*, *Benettiodendron*, *Hasseltiopsis*, *Hecatostemon*, *Ludia*, *Tisonia*, *Lunania*, *Neoptychocarpus*, *Scolopia*, *Tetrathylacium*, *Zuelania* and *Homalium*. *Laetia* possesses minute intervessel pitting. Septate fibres are abundant in species of *Ahernia*. *Salix* and *Populus* can be distinguished because of the numerous narrow vessels, very commonly with angular outline and exclusively uniseriate rays. Almost all *Banara* species have helical thickenings. Species of *Bembicia*, *Flacourtia*, *Ophyobotris* possess vessel–ray pitting similar to intervessel pitting in shape and size. *Bivinia* and *Scolopia* have long radial multiples and numerous narrow vessels. Based on our review of Salicaceae, we conclude that among Malpighiales, it is probably the least likely match for *P. crystallosa*.

Comparison with Achariaceae

Achariaceae Harms is a pantropical family with 30 genera and 145 species. Further study of the Achariaceae was conducted using IWD, samples in the collection of the RBGK and key literature (Miller 1975) (Table 1). This review revealed key traits that are very common for the family and that are not observed in the fossils, such as the occurrence of scalariform perforation plates (*e.g.*, *Buchnerodendron*, *Carpotroche*, *Dasylepis*, *Erythrospermum*, *Gynocardia*, *Hydnocarpus*, *Lindackeria*, *Rawsonia* and *Scottellia*). Exclusively septate fibres occur in *Erythrospermum*, *Lindackeria*, *Rawsonia*, *Ryparosa*, *Trichadenia*. Other characters that differ from the fossil are the absence of crystalliferous chains (*e.g.*, *Gynocardia*, *Hydnocarpus*, *Mayna*, *Rawsonia*, *Scaphocalyx*) and the occurrence of opposite intervessel pitting as reported in Miller's (1975) work for species of *Carpotroche*. Among all of the surveyed Achariaceae, the taxon that best matches the anatomy of *Panascleroticoxylon crystallosa* is *Eleutherandra*, a monotypic genus from South-East Asia. It differs from the fossils in having exclusively septate fibres, and there are no crystals in parenchyma cells. Therefore, *Eleutherandra* is, also, considered an unlikely match. While we note that some Achariaceae combine many features that also occur in the fossils, members of the family typically have scalariform perforation plates making it an unlikely match for the fossils.

Affinities with Phyllanthaceae

Phyllanthaceae Martynov is a family of 59 genera and includes most of the former Phyllanthoideae (Euphorbiaceae) except for *Drypetes* and relatives (Stevens 2001-onward). Phyllanthaceae is a very diverse family in terms of wood anatomical features as we discovered through a review of the IWD, literature such as Mennega (1987), PROTA and studies of slides in the RBGK collection. Based on the work of Mennega (1987), where 12 tribes of Phyllanthoideae (under the old Euphorbiaceae) are described and photographed, it appears that diffuse apotracheal parenchyma is present in most of the taxa (although the author recognised a few exceptions) and scalariform and simple perforation plates commonly co-occur in individual specimens.

For the IWD-listed Phyllanthaceae, several species can be ruled out as potential matches because they have distinct growth rings and gums, rather than tyloses, in heartwood vessels (*e.g.*, *Bischofia javanica*, *Glochidion acuminatum*); minute inter-vessel pitting (*Glochidion lanceolatum*); crystals in enlarged ray cells (*Glochidion lanceolatum*, *G. marchionicum*, *G. zeylanicum*); exclusively septate fibres (*e.g.*, *Glochidion philippicum*, *G. rubrum*, *Hymenocardia acida*, *Phyllanthus emblica*); fibres with distinctly bordered pits (*Hymenocardia ulmoides*, *Phyllanthus polyanthus*); rays commonly >10 cells wide (*e.g.*, *Phyllanthus pervilleanus*). *Antidesma madagascariense* and *A. pulvinatum*, both with rays of two distinct sizes.

Margaritaria is the listed Phyllanthaceae that most resembles *Panascleroticoxylon*, with a few differences, *e.g.*, vessels are very narrow and numerous (40–100 mm^{-1}) in *M. anomala*, same as *M. indica* (Prakash-Jangid & Gupta 2016); diffuse axial parenchyma is present in *M. discoidea* and *M. nobilis* lacks the highly heterocellular rays and the abundant crystals of *P. crystallosa*. In general, diffuse axial parenchyma occurs in several species of *Margaritaria*, and it is not observed in the fossils. Furthermore, the

combination of vessel–ray pits with much reduced borders with a few ones similar to the intervsessel pitting that occurs in the fossils, was not observed in *Margaritaria*.

Comparison with Euphorbiaceae

To survey the wood anatomy of the 6745 species of Euphorbiaceae is beyond the scope of this publication. Some features that are very common in the family are: combination of vessels solitary and in radial multiples, simple perforation plates, large alternate intervessel pitting, septate fibres, rays markedly heterocellular, absence of parenchyma and crystals in chambered ray parenchyma (Wheeler & Manchester 2002).

We note some of the important and common characters for the family among the taxa we reviewed, based on IWD searches, PROTA and observations in the RBGK slide collection as follows: axial parenchyma is abundant and commonly diffuse-in-aggregates (*e.g.*, *Adelia*, *Alchornea*, *Aleurites*, *Brasiliocroton*, *Cleidion*, *Macaranga*, *Trewia*); axial parenchyma reticulate (*e.g.*, *Glycydendron*, *Hevea*); axial parenchyma in narrow bands up to 3 cells wide (*e.g.*, *Balakata*, *Colliguaja*, *Discoglypremna*, *Dodecastigma*, *Hancea*, *Homonoia*, *Klaineanthus*, *Omphalea*, *Pausandra*, *Plagiostyles*, *Wetria*). Another common characteristic in Euphorbiaceae woods is exclusively uniseriate rays (*e.g.*, *Adelia*, *Alchornea*, *Aparisthium*, *Cyrtogonone*, *Dodecastigma*, *Hancea*, *Mallotus*, *Plagiostyles*, *Sapium*). Following examination of the available Euphorbiaceae slides in the RBGK collection and images in the IWD, we did not find any genus with a combination of characters that matches the fossil, *Panascleroticoxylon crystallosa*.

Acalyphoideae is the largest and most complex of the five subfamilies of the Euphorbiaceae. Its diversity can be summarised via statistics from Webster's (1994) classification: 20 tribes, 116 genera, and c. 2,000 species that are found throughout the world, but are especially abundant in the tropics; approximately 86% of acalyphoid genera can be characterised as woody. Hayden and Hayden (2000) reviewed the Alcalyphoideae. Their survey indicates that similarity to the Panamanian fossil wood in features such as absence of growth rings, vessels solitary and in short radial multiples, perforation plates exclusively simple in most of the genera (except for *Microdesmis* and *Panda*), intervessel pitting alternate, vessel–ray pits circular to elongate, fibres mostly non-septate, sclerotic tyloses, heterocellular rays, and crystals. However, there are features that distinguish some genera, *e.g.*, simple and scalariform perforation plates combined in *Acalypha*, *Adenophaedra*, *Agrostistachys*, *Aparisthmium*, *Bernardia tamanduana*, *Botryophora*, *Caryodendron grandifolium*, *Claoxylon*, *Cleidion*, *Cnesmone*, *Coccoceras*, *Conceveiba krukoffii*, *C. guianensis*, *Dicoelia*, *Discoclaoxylon*, *Galearia*, *Macaranga zenkeri*, some species of *Mallotus*, *Mareya*, *Mercurialis* (Williams 1936; Metcalfe & Chalk 1950; Normand 1955), *Pogonophora* (Metcalfe & Chalk 1950), and *Tragia* (Metcalfe & Chalk 1950). The most obvious difference between the subfamily and the Panamanian fossil wood is the occurrence of diffuse axial parenchyma.

Mennega (1987) provided the most complete survey for the Euphorbiaceae wood anatomy available to date. Putranjavaceae (former Drypeteae) and Pandaceae (former Dicoelieae), have minute intervessel pitting and vessel–ray pitting similar to the intervessel pits, different from the fossils. As the author details, a circumscription of the anatomy of euphorbiaceous woods is difficult; however, a few generalised patterns are

Table 3. Anatomical comparison of fossil woods assigned to Euphorbiaceae, Phyllanthaceae and *Panascleroticoxylon crystallosa*.

Data are taken from the IWD. Headings: GR = growth rings; P = porosity; PP = perforation plates; IVP = intervessel pitting size category; V-R P = vessel–ray pits; T = tyloses; AP = apotracheal parenchyma; SF = septate fibres; RW = maximum ray width; C = crystals abundant; +1 CRY = crystals of different sizes in a single ray cell. Coding: K = Cretaceous, E = Eocene, M = Miocene, C = Cenozoic, N = Neogene, O = Oligocene; p = present, a = absent, v = variable; MRB = vessel–ray pits with much reduced borders to apparently simple; DB = vessel–ray pits with distinct borders and similar to intervessel pits, GL = vessel–ray pits gash-like (or in palisade); d-i-a = apotracheal parenchyma diffuse-in-aggregates; r = parenchyma rare or absent; sc = parenchyma scanty paratracheal; u = parenchyma unilateral; vas = apotracheal parenchyma vasicentric.

Taxon	Age	GR	P	PP	IVP	V-R P	T	AP	SF	RW	C	+1 CRY
Panasclericoxylon crystallosa		a	a		s-m	MRB; DB	p	r	v	1–3 (4)	p	p
Securinegeoxylon biseriatum	K	a	a	+/-	?	MRB	p	r	p	1–3	a	a
Securinegeoxylon bacense	K	a	a	+/-	?	MRB	p	d-i-a	p	1–3	p	a
Heveoxylon microporosum	E	a	a	a	min	MRB	p	r; sc	p	1–3	a	a
Piranheoxylon stockmansi	E	a	a	a	min	DB	a	d-i-a; b	p	1–3	a	a
Aleurites miocenica	M	a	p	a	l	MRB	a	d-i-a	p	1	a	a
Bischofia palaeojavanica	M	a	a	a	l	DB; MRB	p	r; sc	p	4–10	a	a
Bischofia javanoxyla	M	a	a	a	l	MRB	a	r; sc	p	4–10	p	a
Bischofia maomingensis	E	a	a	a	l	MRB	p	r; u	p	4–10	p	a
Bischofioxylon miocenicum	M	p	a	a	l	MRB	p	sc; vas	p	1–3; 4–10	p	a
Bischofinium deccani	K	a	a	a	?	MRB	p	sc; vas	p	4–10	a	a
Phyllanthus wuhanensis	C	a	a	a	?	GL	a	r	p	2–6	a	a
<u>*Bridelia*</u> *wuhanensis*	C	a	a	a	?	GL	p	r	p	3–4 (5)	p	a
Bridelioxylon arnouldii	O	a	a	a	?	?	a	sc	p	1–3	a	a
Bridelioxylon cuddalorense	N	a	a	a	?	MRB; DB	a	sc; vas	p	1–3	a	a
Bridelioxylon fibrosum	K	a	a	a	?	MRB	p	r; sc	p	1–3	a	a
Bridelioxylon keriense	M	a	a	a	l	MRB	p	d-i-a; sc	?	1–3	a	a
Mallotoxylon assamicum	M	a	a	a	l	?	p	d-i-a	a	1–3	a	a

as follows: simple perforation plates, medium to large intervessel pitting, apotracheal parenchyma, and numerous narrow heterocellular rays. From that premise, we could say that many Euphorbiaceae possess axial parenchyma, which is absent in *Panascleroticoxylon crystallosa*. Nonetheless, we cannot totally rule out the family, because there is a limited representation of Euphorbiaceae in reference collections. We only point out that from all the species reviewed, we have not found any reasonable match with *P. crystallosa*.

COMPARISON WITH FOSSIL WOODS

Many of the fossil taxa assigned to families of the order Malpighiales have not been critically re-evaluated in the light of its modern phylogeny, so it represents an issue when studying the fossil record. However, evaluating the accuracy of the identifications of fossils assigned to the Malpighiales is beyond the scope of this publication. We focus our discussion on fossil woods considered related to Euphorbiaceae and Phyllanthaceae, because those are the two families that appear to be a better match to the fossils described in this paper, and we show that *Panascleroticoxylon* differs from all of these in combining absent parenchyma, vessel–ray pits with much reduced borders to apparently simple and rays heterocellular with long uniseriate tails. (Table 3).

Cretaceous records

Cretaceous woods whose names suggest malpighialean affinities are: *Bridelioxylon bohemicum, Securinegeoxylon biseriatum,* and *S. bacense. Bridelioxylon bohemicum* was described based on fossils from the Cretaceous of Bohemia (Prakash & Brezinova 1970); it has abundant diffuse axial parenchyma. *Securinegeoxylon biseriatum* and *S. bacense* were described from Maastrichtian localities in South Africa and they both have scalariform perforation plates and scanty paratracheal parenchyma (Mädel 1962). All of these are readily distinguished from *Panascleroticoxylon crystallosa*. *Bridelioxylon krauselii*, retrieved from the Deccan Intertrappean Beds, has vessels in very long radial multiples and distinct growth rings, different from *P. crystallosa*.

Eocene records

A few woods from Eocene localities are assigned to Euphorbiaceae and Phyllanthaceae (Table 3), but none of these match *Panascleroticoxylon*. *Heveoxylon microporosum* from Eden Valley, Wyoming (Kruse 1954) has axial scanty paratracheal parenchyma, but lacks crystals, and has ray–vessel pitting unlike *Panascleroticoxylon*. *Paraphyllanthoxylon lignitum* from different Eocene deposits of Europe has rays of two distinct sizes, a trait that is absent in *Panascleroticoxylon crystallosa*. Numerous permineralised specimens related to Malpighiales are known from the Nut Beds flora (Wheeler & Manchester 2002). Several of those have not been assigned to any family, *e.g.* Clarno Malpighialean Wood Type 1 (?Euphorbiaceae) and *Hydnocarpoxylon*, both possess scalariform perforation plates, not observed in *P. crystallosa*. Also, crystals were not observed in the Clarno Nut Beds woods (Wheeler & Manchester 2002), a feature that is very abundant in the Panamanian fossil wood type. *Piranheoxylon stockmansi*

(Grambast 1961), retrieved from the Eocene of Belgium, has diffuse axial parenchyma, marginal bands of parenchyma and vessel–ray pitting similar to the intervessel pitting.

Oligocene and Miocene records

One of the few reported Malpighiales Oligocene woods is *Bridelioxylon arnouldi* (Koeniguer 1966). It has scanty paratracheal parenchyma and opposite intervessel pits, two traits absent in *Panascleroticoxylon crystallosa*. Reports of Malpighian fossil woods are abundant in the Miocene (see Table 3). *Aleurites miocenica* from Japan (Watari 1956) has abundant parenchyma. *Bischofia palaeojavanica* from the Dhemaji and Lakhimpur districts of Assam, considered to be of middle–upper Miocene, possesses scanty paratracheal parenchyma and fibres exclusively septate (Mehrotra *et al*. 2011). *Bischofia javanica* has scanty paratracheal parenchyma (Cheng *et al*. 2005). *Bischofia javanoxyla* has rays 1–6 cells wide (Li *et al*. 2003), possess wide vessels in radial multiples of 4–10, whereas *P. crystallosa* tends to have multiples of only up to 4 in the Alajuela specimen. Another species, *Bischofioxylon miocenicum* from South India, is also easily distinguished from *P. crystallosa* because it has vasicentric parenchyma (Ramanujan 1960). Qi *et al*. (1997) published three euphorbian woods from Wuhan: *Phyllanthus wuhanensis* has vessel–ray pits gash-like, tyloses sclerotic common, septate fibres dominant; *Bridelia wuhanensis,* with long radial multiples (up to 6), axial parenchyma apotracheal diffuse, sclerotic tyloses, and *Bischofia polycarpa* with vasicentric parenchyma. Species of *Bridelioxylon* are also distinct from the Panamanian fossil. *Bridelioxylon keriense* does not show rays with long uniseriate tails. *Bridelioxylon cuddalorense* (South Arcot district, India) has vasicentric parenchyma.

MALPIGHIALES IN NEOTROPICAL FORESTS

Malpighiales is strongly supported as a monophyletic group, based on broad and comprehensive studies of the extant diversity (*e.g*., Davis *et al*. 2005; Wurdack & Davis 2009; Xi *et al*. 2012); however, some relationships within the order remain problematic. The complicated determination of deep relationships within Malpighiales seems to be related to the rapid origin and diversification of the group in mid-Cretaceous times (Davis *et al*. 2005; Wurdack & Davis 2009). Our knowledge of relationships within Malpighiales has been in flux in recent years. This is especially the case for the former Flacourtiaceae, whose members were re-distributed into Salicaceae, Achariaceae and Samydaceae, following extensive analysis using *rbcL*DNA sequences (Chase *et al*. 2002), and the Euphorbiaceae, which remained largely unresolved until the 4-gene analysis of Davis *et al*. (2005).

Fossil record in Panama

Fossil Malpighiales have been reported from the Panama Canal and other basins in Panama. Most of the permineralised plant fossils described from the Lirio East plant locality so far belong to the Malpighiales, including fruits of Humiriaceae (Herrera *et al*. 2010). Humiriaceous wood was also reported from the Eocene-Miocene deposits of the Azuero Peninsula (Stern & Eyde 1963; Herrera *et al*. 2014). Jud *et al*. (2016)

reported Chrysobalanaceae retrieved from lower Miocene deposits along the Panama Canal. The identifications were based on fossil permineralised endocarps of *Parinari panamensis* and a fossil wood, *Parinarioxylon panamense*, both representing the oldest evidence of Chrysobalanaceae. Calophyllaceae is represented in the flora as well by a fossil *Mammea* (Calophyllaceae) identified from wood and bark anatomy (Nelson & Jud, in press).

Euphorbiaceae (*Alchornea*, *Sapium*) have been identified from pollen grains from the lower Miocene Culebra Formation and the Pliocene Gatun Formation (Graham 1988, 1991). Recently, 'euphorboid' fossil woods were reported from the late Miocene Alajuela Formation (McFadden *et al*. 2015). Also, endocarps from the Cucaracha Formation have been assigned to Euphorbiaceae (Herrera *et al*. 2014).

Biogeographic implications

Today Malpighiales have c. 16,000 species (c. 6% of all angiosperms), comprising many well-known tropical families and they are an important component of the understory in tropical rainforests worldwide (Davis *et al*. 2005). Early members of this order probably occupied closed-canopy tropical forests and rainforests during the mid-Cretaceous and dominated in the wettest environments by Late Cretaceous (Whitmore 1998; Davis *et al*. 2005). Therefore, Malpighiales are a key element in the origin of rainforests and persist today as one of their most important components. This study, together with other plant remains from the Panama Canal, support a rich fossil record of Malpighiales for the Miocene of Panama and Central America and adds to the evidence of a rich diversity of Malpighiales in the Neotropics during the Miocene.

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