First Miocene record of Akaniaceae in Patagonia (Argentina): a fossil wood from the early Miocene Santa Cruz formation and its palaeobiogeographical implications

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Today, Akaniaceae are confined to south-eastern Queensland and north-eastern New South Wales (Australia), south-eastern China and northern Vietnam. *Akanioxylon santacrucensis* gen. and sp. nov. is described as the first fossil wood of Akaniaceae from the early Miocene Santa Cruz Formation (*c*. 18–16 Ma; Burdigalian) on the Atlantic coast of Santa Cruz Province, Argentina. The diagnostic features are growth rings inconspicuous, with most latewood vessels only slightly narrower than earlywood vessels; diffuse porous wood; mainly solitary vessels, occasionally radial or tangential multiples and clusters; mainly simple, occasionally reticulate and rarely scalariform with many interconnections between bars perforation plates; bordered, minute to small intervessel pits; axial parenchyma scanty paratracheal and apotracheal diffuse; vessel-ray parenchyma pits with much reduced borders to apparently simple; vessel-axial parenchyma pits scalariform or transitional; mainly multiseriate (four to six cells wide) and rare uniseriate rays, heterocellular, occasionally crystals in ray cells; septate and non-septate fibres with simple to minutely bordered pits. These features resemble the extant *Akania* and *Bretschneidera*. The eco-anatomical analysis suggests that this fossil wood grew under temperate to warm-temperate and semi-arid climatic conditions. This record of *Akania*/*Bretschneidera*-like wood in South America reinforces the existence of an old relationship with the Australasia flora. The discovery of Akaniaceae in the Santa Cruz Formation extends the record of the taxon in South America *c*. 30 Ma and 10°S in latitude and suggests that the family was widespread in Patagonia as a component of forests developed in a frost-free humid biome in South American at mid to high latitudes.

ADDITIONAL KEYWORDS: early Miocene fossil wood – high latitudes – Santa Cruz Formation – South America.

INTRODUCTION

Akaniaceae are a family of Brassicales composed of deciduous or evergreen trees. Traditionally, the monotypic genera *Akania* Hook.f. and *Bretschneidera* Hemsl. were

included in Sapindales (e.g. Dahlgren, 1980; Cronquist, 1981; Takhtajan, 1997; Thorne, 1992; Carlquist, 1996), but anato-morphological data and molecular studies have confirmed that these genera belong to Brassicales (Rodman *et al.*, 1994, 1996; Doweld, 1996; Ronse de Craene & Haston, 2006; APG IV, 2016; Beilstein *et al.*, 2010). Furthermore, similarity in embryology between

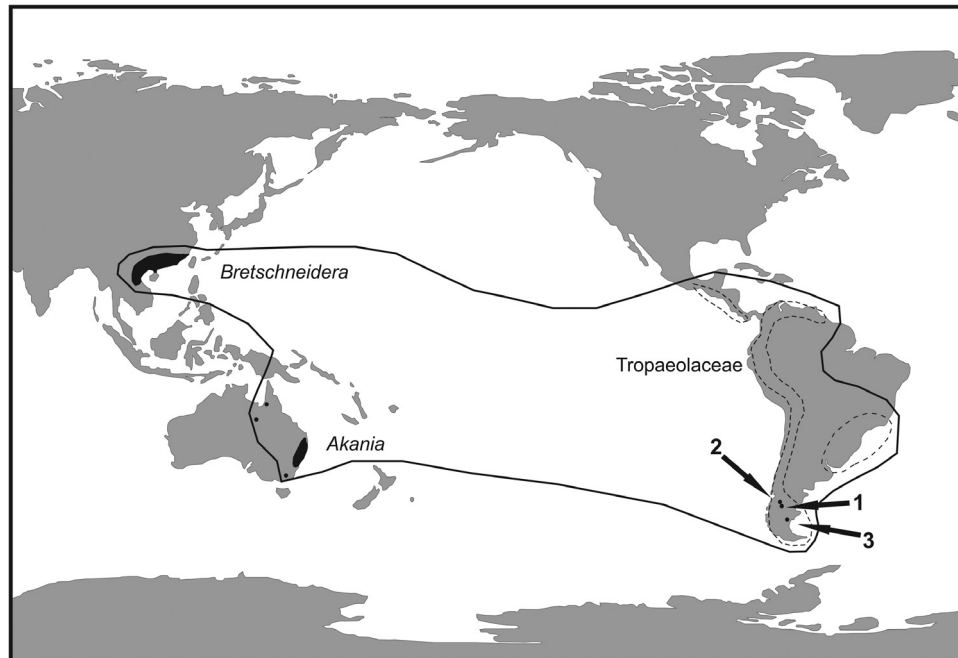*Corresponding author. E-mail: cidmbrea@gmail.com

Figure 1. Biogeography distribution of extant genera of Akaniaceae (dark grey shading) and Tropaeolaceae (dotted line). The black line shows the trans-Pacific distribution of the first-branching clade in Brassicales: Akaniaceae (including Bretschneideraceae) and Tropaeolaceae [Tropicos, Missouri Botanical Garden, 20 August 2015 (http://www.tropics.org) and Australia's Virtual Herbarium (AVH), 20 August 2015 (http://avh.chah.org.au/), Stevens (2001 onwards) and Heads (2013)]. The fossil records: (1). Fossil leaf of *Akania* sp. (Iglesias *et al.*, 2007) from Palacio de Los Loros flora (Salamanca Formation, 64.7–63.5 Ma, Palaeocene). (2). Fossil leaf of *Akania americana* (Romero & Hickey, 1976) and *Akania patagonica* (Berry, 1938; Gandolfo *et al.*, 1988) from the Laguna del Hunco flora and Pichileufú floras (La Huitrera and Ventana formations, 51.9–47.5 Ma, early Eocene), Chubut province, Argentina; (3). Fossil wood of *Akanioxylon santacrucensis* gen. & sp. nov. (this paper) from the late early Miocene (*c.* 16–18 Ma) Punta Sur locality (Santa Cruz Formation), Santa Cruz, Argentina (Modified from Heads, 2013).

Akania and *Bretschneidera* has been demonstrated (Tobe & Peng, 1990; Tobe & Raven, 1995).

Today, Akaniaceae extend from *c*. 24°N to 32°.55´S (Fig. 1). *Akania* is restricted to coastal and near-coastal rainforests of south-eastern Queensland and north-eastern New South Wales, Australia (Floyd, 1977; Cronquist, 1981; Hewson, 1985; Bayer & Appel, 2002; Heads, 2013), whereas *Bretschneidera* is widely distributed throughout south-eastern China from Yunnan and Sichuan to Taiwan and northern Vietnam, growing in broad-leaved evergreen and deciduous mixed forests at 100–1600 m (Lu, Hu & Fan, 1986; Santisuk, 1989; Ying, Zhang & Boufford, 1993; Bayer & Appel, 2002; Heads, 2013). Despite the marked geographical separation of *Akania* and *Bretschneidera* (Fig. 1), the genera agree in many wood anatomical features (Carlquist, 1996).

Akania and *Bretschneidera* form the Akaniaceae clade, with Tropaeolaceae as the sister group, in the clade of glucosinolate-producing Brassicalean families (Gadek *et al.*, 1992; Ronse de Craene & Haston, 2006) (Fig. 2). According to the most recent taxonomic revision (Anderson & Anderson, 2000), Tropaeolaceae comprise a single genus, *Tropaeolum* L., with *c*. 90 species, all annual and perennial herbaceous plants native of South and Central America.

Akaniaceae do not currently occur in South America, but fossil leaf impressions attributed to *Akania* are known from Chubut Province (Patagonia, Argentina) (Fig. 1), from the Palacio Los Loros (*c*. 46°S), Laguna del Hunco and Río Pichileufú (*c.* 42°S) floras (Salamanca Formation, Palaeocene; La Huitrera and Ventana formations, early Eocene, respectively) (Berry, 1925, 1938; Romero & Hickey, 1976, Gandolfo, Dibbern & Romero, 1988; Gandolfo *et al.*, 2011; Wilf et al., 2005, 2013; Iglesias *et al.*, 2007). These records are the only fossil worldwide for Akaniaceae.

The main goal of this paper is to describe a fossil wood with diagnostic features of Akaniaceae. This specimen was recovered in sediments of the Santa Cruz Formation (early Miocene), Santa Cruz Province, Argentina (Figs 3, 4). It represents the first record in the world of a fossil wood with affinities to Akaniaceae, adding new information for the historical biogeography of this family.
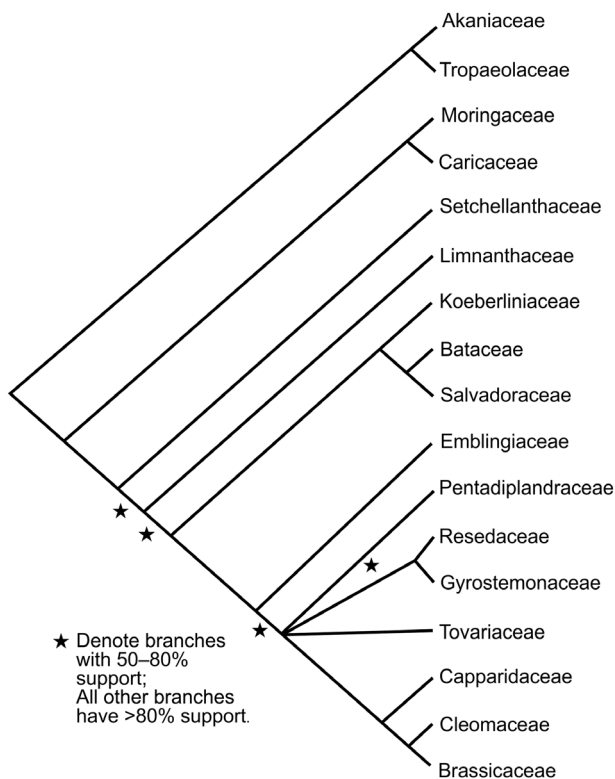
Figure 2. Relationships in Brassicales showing that Akaniaceae are sisters to Tropaeolaceae (Missouri Botanical Garden, http://www.mobot.org/mobot/research/apweb/orders/brassicalesweb.htm).

GEOLOGICAL AND PALAEOBOTANICAL SETTING

The Santa Cruz Formation in the coastal area of Santa Cruz Province (Patagonia, Argentina), known for an exceptional rich mammal fossil fauna of Santacrucian Age (early Miocene; *c.* 18–16 Ma; Burdigalian; Vizcaíno, Kay & Bargo, 2012a and references therein), is composed of two members: the lower Estancia La Costa member, with a predominance of pyroclastic deposits, and the upper Estancia La Angelina member, mainly composed of claystones, mudstones and sandstones (Tauber, 1997, 1999; Matheos & Raigemborn, 2012).

Recently, the compositional and palaeoenvironmental analyses of the lower member, Estancia La Costa Member, allowed the differentiation of three sections: lower, middle and upper (see Matheos & Raigemborn, 2012: fig. 4.4, p. 64). Plant fossils (phytoliths, carbonized wood and leaf compressions) were recovered from the lower section of the Estancia La Costa member, which comprises a basal part with bioclastic sandstones and bioturbated heterolithic facies of continental-marine transitional environment. These facies were replaced by tuffs and sandstone from volcanic source, associated with immature palaeosols deposited in a low-energy fluvial system with vegetated floodplains (Matheos & Raigemborn, 2012) (Fig. 4).

The palaeoflora of the Estancia La Costa member was characterized by the presence of herbaceous elements including chloridoid, panicoid, danthoniod, pooid and festucoid grasses, and arboreal components including Araucariaceae, Lauraceae, Nothofagaceae, Myrtaceae, Cunoniaceae, Proteaceae and Arecaceae (Brea, Zucol & Iglesias, 2012). This Miocene vegetation was a mixture of open temperate semi-arid forests and humid warm-temperate forests, and the integrated analysis of multiple sets of proxy data suggests that south-eastern Patagonia, during the early Miocene, was characterized by a temperate to warm-temperate and semi-arid to humid climate and seasonal low levels of precipitation served as a limiting factor for plant growth. The mean annual temperature estimates using eco-anatomical wood features were 19.31 ± 1.7 °C and values of the vulnerability index (V = mean vessel diameter/mean vessel frequency) and mesomorphy ratio (M = vulnerability index × mean vessel member length) suggest that the fossil woods had well-developed xeromorphic features (Brea *et al.*, 2012).

MATERIAL AND METHODS

The wood consists of only one carbonized specimen with well-preserved secondary xylem, recovered at 20 m below the tuff levels in the Estancia La Costa member (see Vizcaíno *et al.*, 2012a; Matheos & Raigemborn, 2012), from the Punta Sur locality (Fig. 3). Thin sections were made using petrographic techniques for the three characteristic sections (cross, tangential and radial section). The carbonized material breaks easily. For this reason, the specimen was embedded into epoxy resin at ambient temperature without vacuum or pressure so as not to alter it. Once consolidated, it was cut by hand or with a bench grinder using a diamond blade. Then, it was re-impregnated with epoxy resin, left to dry at 30–35 °C for 3 h and cut in cross, tangential and radial sections. Epoxy resin was applied over the glass slide and allowed to cool for 24 h before polishing the surfaces with silicon carbide with different grain sizes and aluminium oxide, to a thickness of 30–50 μm. Finally, it was covered with a coverslip using epoxy resin or photosensitive adhesive (Ricardo Ponti, personal communication). Anatomical terms used in this paper follow the recommendations of the *IAWA List of Microscopic Features for Hardwood Identification* (IAWA Committee, 1989) and Carlquist (2001). The bibliographic list of Gregory (1994) and Gregory, Poole & Wheeler (2009) was used. For comparison with
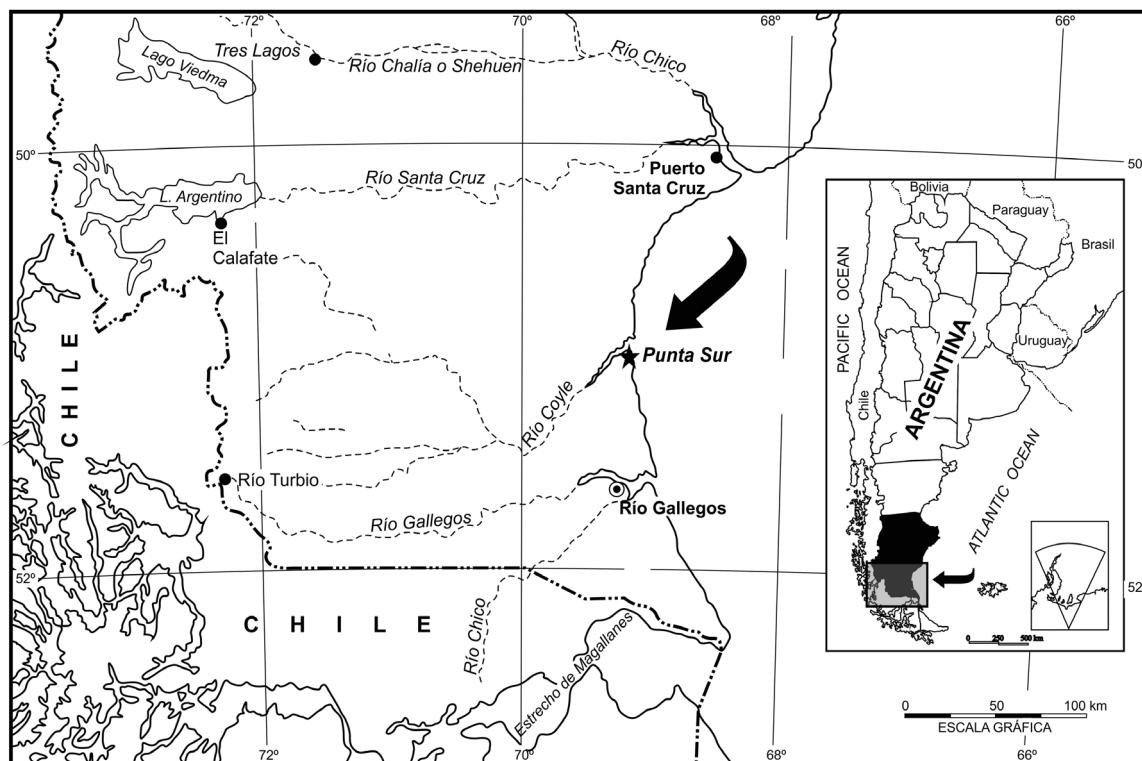
Figure 3. Map of Santa Cruz Province showing the Punta Sur locality.

extant species, we used the InsideWood website and its codings (InsideWood, 2004 onwards; Wheeler, 2011) and descriptions by Heimsch (1942), Metcalfe & Chalk (1950a, 1950b) and Carlquist (1996). The systematic assignment follows APG IV (2016). Names used are found in the *International Plant Names Index* (www.ipni.org).

The quantitative values provided in the anatomical description are averages of 25 measurements; in all cases the average is cited first, followed by the minimum and maximum values in parentheses. The material was studied with a Nikon Eclipse E200 light microscope and photomicrographs were taken with a Nikon Coolpix S4 digital camera. The material was prepared for SEM by cutting a 2-cm³ block of wood that was mounted on SEM stubs without coating and observed under low vacuum using a Phenom Pro Desktop SEM scanning electron microscopy at the Laboratorio de Microscopía Electrónica (EMLAB), CICYTTP-CONICET, Diamante, Entre Ríos, Argentina. The ImageJ program Version 1.46r was used to measure the elements through photomicrographs. The fossil specimen and microscope slides are deposited in the Colección Paleobotánica of the Museo Regional Provincial Padre Manuel Jesus Molina, Río Gallegos, Santa Cruz Province, Argentina, under the acronym MPM-PB.

SYSTEMATIC PALAEOBOTANY

AKANIACEAE

Genus *Akanioxylon* Brea, Zucol, Bargo, Fernicola & Vizcaíno **gen. nov.**

Type species. ***Akanioxylon santacrucensis*** Brea, Zucol, Bargo, Fernicola & Vizcaíno **sp. nov.** Figs 5–7.

2012 aff. *Xilotype* 3 Pujana in Brea, Zucol & Iglesias (2012): fig. 7.7a–l, p. 118.

GENUS AND SPECIES DIAGNOSIS

Diffuse porous wood; vessels mainly solitary, occasionally in radial and tangential series of two or three elements and clusters; tangential diameter vessels 50–100 μm, numerous (≥ 100 per mm²); perforation plates are mainly simple, occasionally reticulate and rarely scalariform with many aberrant interconnections between bars; intervessel pits bordered, alternate or opposite, minute to small; axial parenchyma scanty paratracheal and apotracheal diffuse; vessel-ray parenchyma pits with much reduced borders to apparently simple; vessel-axial parenchyma pits scalariform; rays heterocellular, mainly multiseriate (four to six cells wide) and rarely uni- or biseriate; rays numerous (4–12 per linear mm); sheath cells present; occasionally crystals in ray cells; fibres septate and
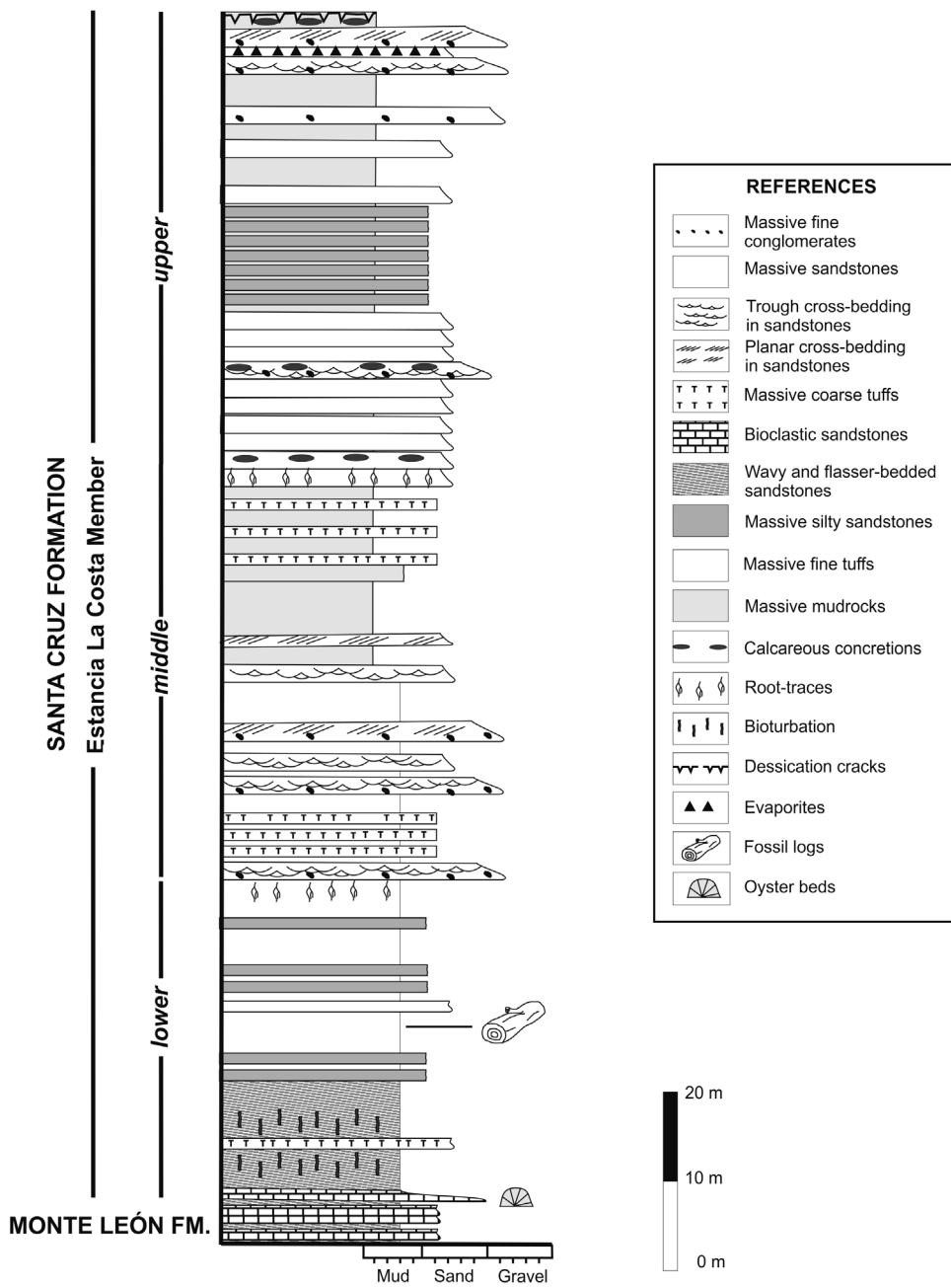
Figure 4. Sedimentary profile of the Estancia La Costa Member of the Santa Cruz Formation (modified from Matheos & Raigemborn, 2012).

non-septate, with simple to minutely bordered pits; not storied structure.

ETYMOLOGY

The generic name, *Akanioxylon*, refers to the affinity with Akaniaceae. The specific name, *santacrucensis*, refers to the geographical (Santa Cruz Province) and

stratigraphic (Santa Cruz Formation) provenance of the type specimens.

Age: early Miocene Burdigalian, (Santa Cruz Formation, Estancia La Costa member).

Type locality: Punta Sur, Santa Cruz Province, Argentina (*c*. 51°S) (Vizcaíno, Kay & Bargo, 2012b).

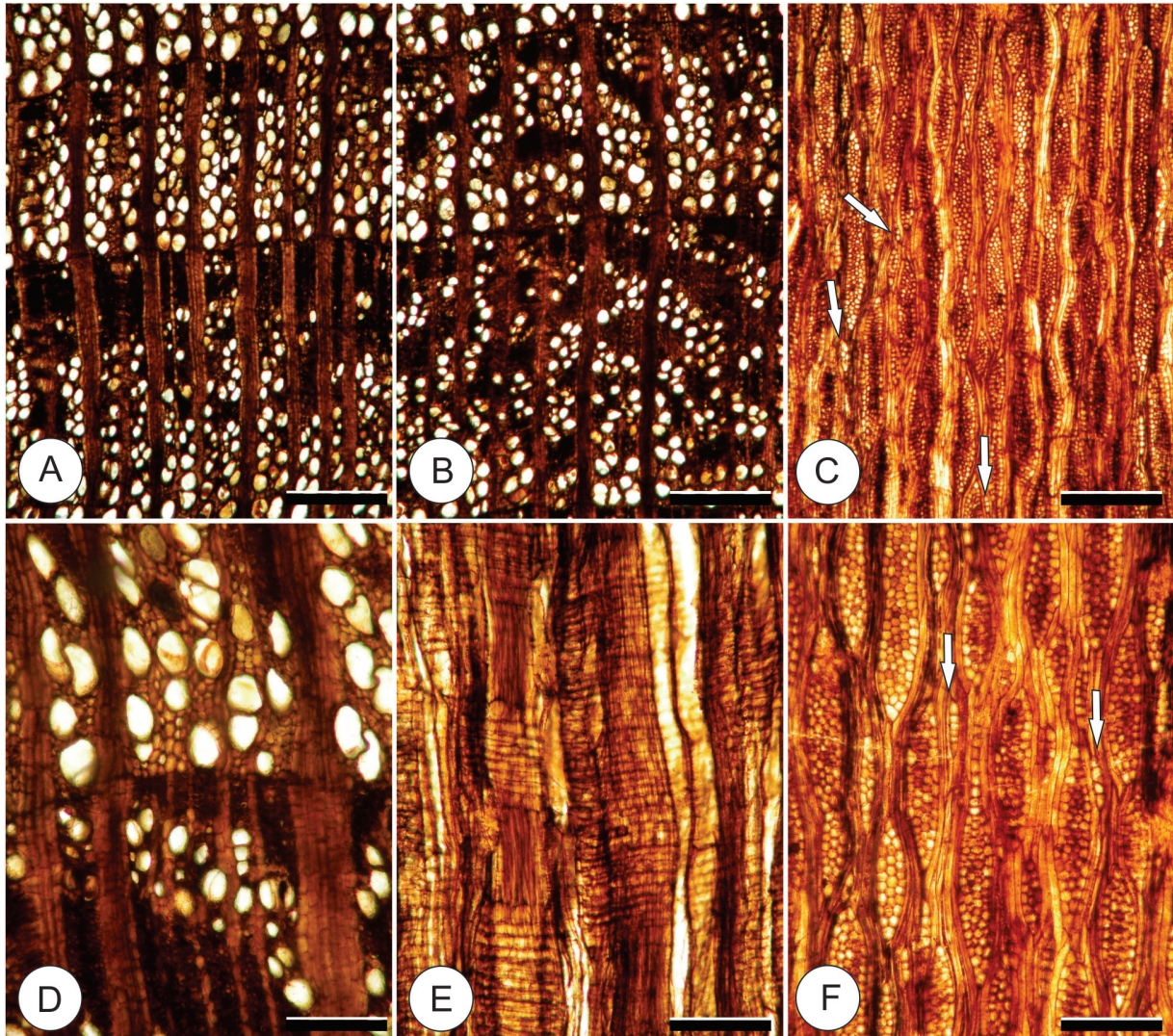*Holotype*. MPM-PB 4390 (one megafossil and three microscope slides).

Figure 5. Section of *Akanioxylon santacrucensis* gen. & sp. nov. (A–B). Cross-section, general view shows growth rings, vessels, axial parenchyma rays and fibres. (C). Tangential section, multi-, uni- and biseriate rays (arrows). (D). Cross-section, details show vessels, fibres, axial parenchyma and rays. (E). Radial section, shows heterocellular rays and vessels. (F). Tangential section, details show uniseriate (arrows) and multiseriate rays. Scale bar = 400 µm in A, B and C; Scale bar = 160 µm in D, E and F.

DESCRIPTION

The growth rings are indistinct, with most latewood vessels only slightly narrower than earlywood vessels, and it is diffuse porous wood (Fig. 5A, B). Vessels are mainly solitary (50%), in radial and tangential series of two to three elements (33%), or in clusters (17%) (Figs 5A, B, D, 8A). In some sectors of the specimen and in latewood, tangential bands of vessels and diagonal and irregular dendritic patterning of vessels are observed (Fig. 5A, B). Vessels are circular, oval to angular in cross-section (Figs 5D, 6A, B, 8A). Mean tangential vessel diameter is 70 (37–94) µm, and mean radial vessel diameter is 53 (40–70) µm. Mean vessel element length is 214 (160–285) µm with end walls oblique. Mean vessel density is 137 (114–181)/mm². Perforation plates are mainly simple (Fig. 6I), occasionally reticulate (Fig. 6K), and rarely scalariform with many aberrant interconnections between bars (Fig. 6J). Intervessel pits are bordered round to irregular in outline with alternate or opposite arrangement with a mean diameter of 6 (3–9) µm, minute to small (Figs 6M, 8D, E). Narrow vessel elements are present (Figs 6L, 8G). The mean narrow vessel length is 112 (89–141) µm and the bordered pits with a mean diameter of 7 (4–10) µm with alternate or opposite arrangement (Figs 6L, 8G). Axial parenchyma is scanty paratracheal and apotracheal diffuse
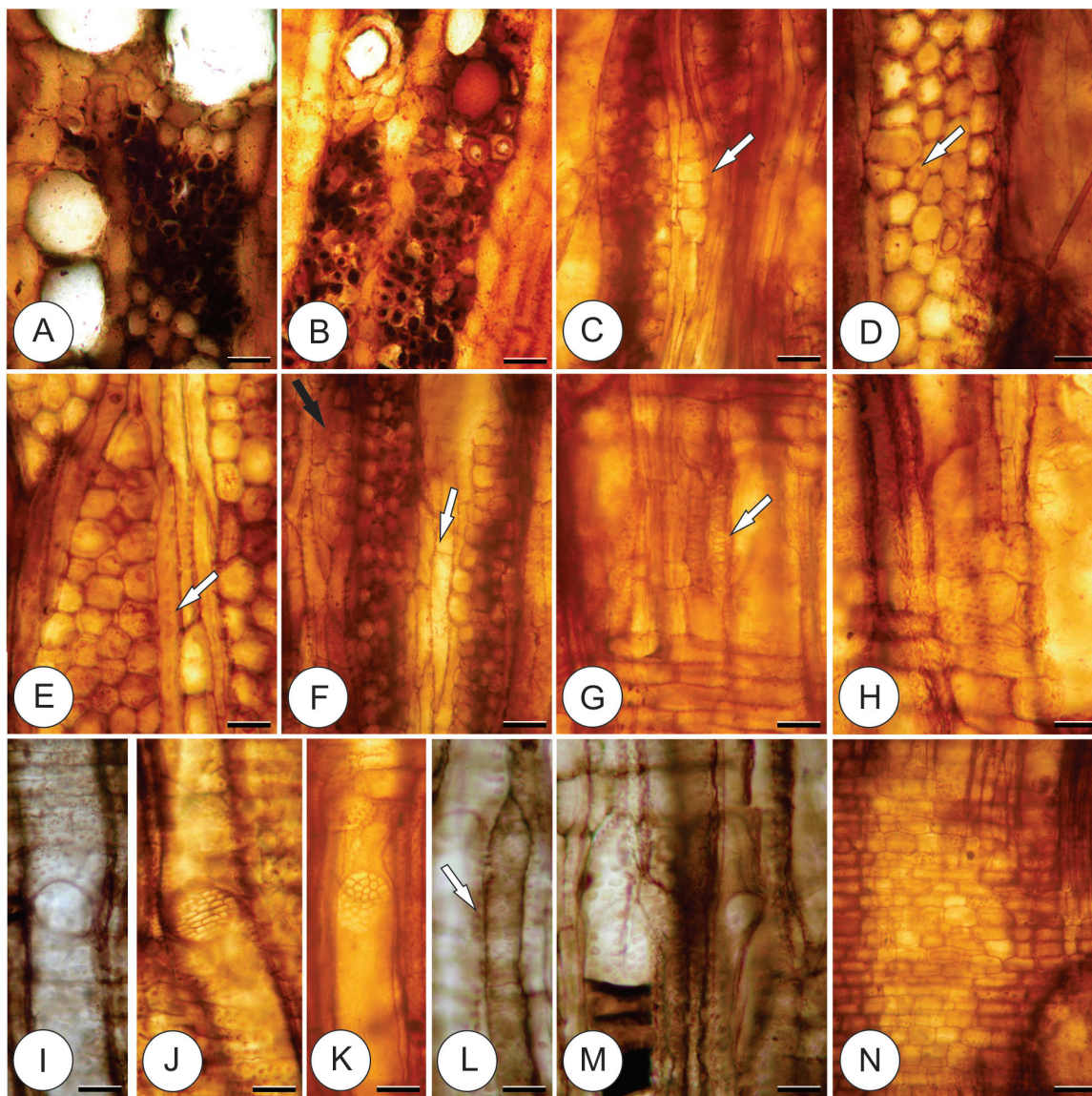
Figure 6. Section of *Akanioxylon santacrucensis* gen. & sp. nov. (A–B). Cross-section, details show vessels, axial parenchyma scanty paratracheal, fibres and rays. (C). Tangential rays, details of uniseriate (arrow) and multiseriate rays. (D). Tangential section, details of rhomboidal crystal (arrow) in multiseriate ray. (E). Tangential section, details show simple to minutely bordered pits (arrow). (F). Tangential section, detail of septate fibre (white arrow) and uniseriate ray (black arrow). (G). Radial section, shows vessel-axial parenchyma pits scalariform or transitional (arrow). (H). Radial section, details of simple pits in ray cells. (I). Radial section, details of simple perforation plate. (J). Radial section, details of aberrant scalariform perforation plate. (K). Radial section, details of reticulate perforation plate. (L). Tangential section, details of a narrow vessel element (arrow). (M). Radial section, shows bordered round to irregular in outline and alternate intervessel pits. (N). Radial section, heterocellular rays composed of procumbent and upright cells. Scale bar = 40 μm.

(Figs 5D, 8A). Axial parenchyma in strands of four to eight cells (Fig. 7I). Rays are heterocellular composed mostly of procumbent cells in the body with two to four upright cells in the margins (Figs 5E, 6N). The rays are uniseriate, biseriate and multiseriate, four to six cells wide (Figs 5C, F, 6C, D, E, F). Percentage of the multiseriate rays is 88% and uniseriate rays is 12%.

The mean height of uniseriate rays is 133 (55–165) μm and 5 (3–7) cells high, and the mean width of uniseriate rays is 22 (20–25) μm (Fig. 4C, F). The mean height of biseriate rays is 205 (160–260) μm and 8 (6–11) cells high and the mean width of biseriate rays is 39 (37–40) μm (Fig. 5C). The mean height of multiseriate rays is 680 (316–1417) mm and 18 (9–28) cells high and the
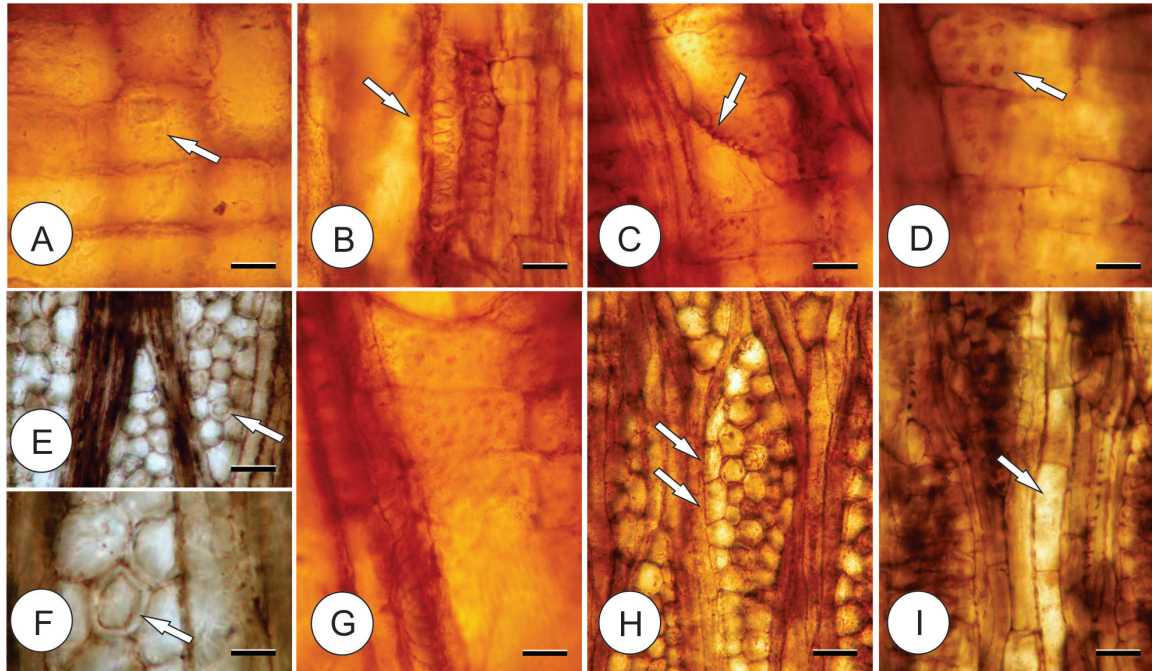
Figure 7. Section of *Akanioxylon santacrucensis* gen. & sp. nov. (A). Radial section, rhomboidal crystal (arrow) in ray cell. (B). Radial section, shows vessel-axial parenchyma pits scalariform or transitional (arrow). (C). Radial section, arrow shows pitting on tangential wall of the ray. (D). Radial section, details of simple and opposite pits in ray cells (arrow). (E–F). Tangential section, details of rhomboidal crystals in ray cells (arrows). (G). Radial section, details of vessel-ray pits with much reduced borders to apparently simple. (H). Tangential section, details of sheath cells (arrows). (I). Tangential section, details of axial parenchyma in strands of four cells. Scale bar = 10 µm in A, B, D, F and G; Scale bar = 40 µm in C, E, H and I.

mean width of multiseriate rays is 71 (55–90) µm and 5 (4–6) cells wide (Figs 5C, F, 6C, D, E, F). Mean number of rays per linear millimetre is 8 (6–11 per linear mm). Occasionally, rhomboidal crystals in ray cells are present (Figs 6D, 7A, E, F). Sheath cells are present (Fig.7H). Pits in ray cells are simple and opposite (Figs 6H, 7D). Pits are in tangential walls of ray cells (Fig. 7C). Vessel-ray pits are with much reduced borders to apparently simple and transitional to opposite (Figs 6N, 7G, 8F). Vessel-axial parenchyma pits are scalariform or transitional (Figs 6G, 7B). Fibres are septate (Fig. 6F) and non-septate, and hexagonal in cross-section (Fig. 6A, B) with simple to minutely bordered pits (Figs 6E, 8H). They are thin- to thick-walled, with a mean thickness of 3.0 (2.5–5.0) µm and a mean diameter of 13 (9–20) µm. Storied structure is not observed.

DISCUSSION

Current taxon similarities and affinities

The combination of the perforation plates simple and/or scalariform and reticulate (13p, 14p, 19p), intervessel pits alternate (22p), fibres septate (65p) and four- to ten-seriate rays (98p) are found in families including Adoxaceae,

Araliaceae, Elaeocarpaceae, Ericaceae, Phyllanthaceae and Akaniaceae. Adoxaceae are highly diverse in wood characters but commonly have solitary vessels with outline angular or in series of two elements, one- to five-seriate rays, vessel density varies from 200 to 250/mm², scalariform perforation plates have >20 bars and are simple, and vessel-ray pits have distinct borders or reduced borders (Schweingruber, Börner & Schulze, 2013; Lens *et al.*, 2016). Araliaceae commonly have vessels in short radial multiples and clusters, often ring-porous or semi-ring-porous, vessel-ray pits with large apertures, heterocellular rays with few square and upright marginal cells or homocellular with procumbent cells, and intercellular canals present in the rays of several genera (Metcalfe & Chalk, 1950b; Schweingruber *et al.*, 2013).

In members of Elaeocarpaceae, the perforation plates are exclusively simple, intervessel pits large and typically opposite, axial parenchyma in narrow terminal bands, and paratracheal usually limited to a few cells round the vessels and sometimes extremely sparse or absent (Metcalfe & Chalk, 1950a).

Ericaceae typically have very small (≤50 µm) and extremely small (≤25 µm) vessels, but in some species they are small to medium in size (50–200 µm). Intervessel pits are typically opposite, transitional and
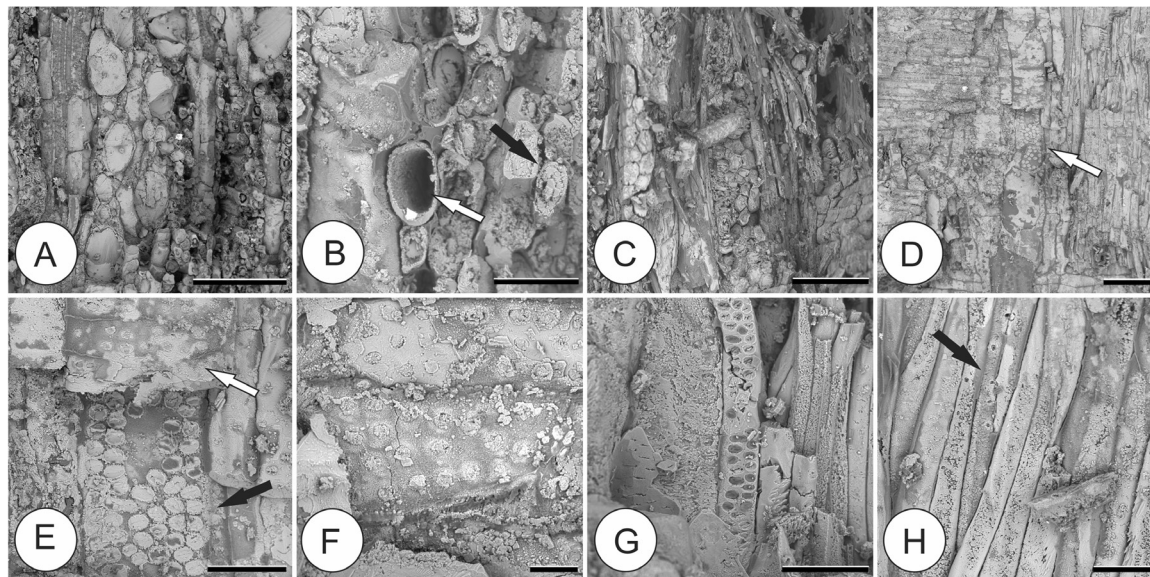
Figure 8. Section of *Akanioxylon santacrucensis* gen. & sp. nov. (A). Cross-section, details show vessels, axial parenchyma scanty paratracheal, fibres and rays. (B). Cross-section, details of axial parenchyma cell (white arrow) and fibre cell (black arrow). (C). Tangential section, multiseriate rays. (D). Radial section, shows vessel element. (E). Radial section, details of the alternate to opposite intervessel pits (black arrow) and vessel-ray pits (white arrow). (F). Radial section, details of vessel-ray pits with much reduced borders to apparently simple and transitional to opposite. (G). Tangential section, details of a narrow vessel element with alternate or opposite pits. (H). Tangential section, details show simple to minutely bordered pits (black arrow). Scale bar = 100 µm in A and D; Scale bar = 20 µm in B and H; Scale bar = 80 µm in C; Scale bar = 30 µm in E; Scale bar = 10 µm in F; Scale bar = 50 µm in G.

scalariform, rays commonly have gummy deposits and lack crystals; many species have rays of two distinct sizes (two- to five-seriate and uniseriate) and mostly homocellular with square and upright cells, but some species have two- to five-seriate heterocellular rays (Metcalfe & Chalk, 1950b; Schweingruber, Börner & Schulze, 2011).

Phyllanthaceae have two wood types. The *Aporosa*-type has vessels with scalariform perforation plates, intervessel pits small to minute, axial parenchyma abundant, diffuse, strands of 8–16 cells, rays with 4–17 cells wide, heterogeneous, with ≥10 marginal rows of upright cells. The *Glochidion*-type has vessels with simple perforation plates, intervessel pits minute to large, axial parenchyma absent or rare, rays with 3–11 cells wide, heterogeneous, with ≥10 marginal rows of upright cells (Metcalfe & Chalk, 1950b).

The anatomical characteristics of the fossil wood agree with the features described for extant Akaniaceae (Carlquist, 1996). Akaniaceae are characterized by the following combination of anatomical features: simple, scalariform and/or reticulate perforation plates, alternate intervessel pits, vessel-ray pits with reduced borders to apparently simple, axial parenchyma scanty paratracheal, septate fibres and four- to ten-seriate rays (Carlquist, 1996).

The presence of vessel elements with scalariform perforation plates and axial parenchyma scanty paratracheal

are potential synapomorphies in Akaniaceae and Tropaeolaceae (Stevens, 2001 onwards). The combination of inconspicuous growth rings, occasional perforation plates with numerous bars, but often in aberrant arrangements, intervessel pits predominantly alternate, vessel-axial parenchyma pitting scalariform, vessel-ray pitting scalariform to opposite, vessels relatively long, septate fibres with borders vestigial or absent, axial parenchyma scanty paratracheal and paratracheal (possibly with a few terminal cells in growth rings) in strands of four to five cells, multiseriate rays tall and composed predominantly of procumbent cells, wood nonstoried and with sparse dark deposits in cells occur in *Akania* and *Bretschneidera* (Carlquist, 1996).

Using the InsideWood database, the following combination of features are shared with the fossil wood: 5p 13p 19p 22p 24p 25p 32p 61p 65p 66p 78p 107p 110p with 0 mismatches allowed (see coding in IAWA Committee, 1989); this yields only one extant species, *Akania bidwillii* (Hogg) D.J.Mabberley, and six fossil woods: *Celastrinoxylon celastroides* (Schenk) Kräusel (Celastraceae), a species of *Fagus* L. (Fagaceae), *Dombeyoxylon oweni* (Carruthers) Kräusel (Malvaceae group), *Ternstroemioxylon dachelense* Kräusel (Pentaphylacaceae), a species of *Platanoxylon* Hofmann, and a species of *Platanus* L. (Platanaceae).

Table 1. Comparisons between *Akanioxylon santacrucensis* gen. & sp. nov. and extant genera of Akaniaceae

		Akania bidwillii[*,++]	*Bretschneidera sinensis*[*,++]	*Akanioxylon santacrucensis* gen. nov. & sp. nov.
Growth rings	Distinct	Inconspicuous[1]	Inconspicuous[1]	Inconspicuous[1]
	Indistinct or absent	Absent	Absent	Absent
	False rings	?	?	Present
Vessels	Porosity	Diffuse-porous	Diffuse-porous	Diffuse-porous
	Arrangement	Absent	Absent	Oblique vessel pattern in the latewood (in some sectors of piece)
	Perforation plates	Mostly scalariform, simple, reticulate	Mostly simple, occasionally scalariform or reticulate	Mostly simple, occasionally scalariform or reticulate
	Grouping	Mostly solitary or in small clusters or radial multiples	Mainly solitary or in clusters	Mostly solitary or in small clusters or radial multiples
	Tangential diameter	82 µm	81 µm	70 (37–94) µm
	Radial diameter	–	–	53 (40–70) µm
	Vessel element length	730 µm	624 µm	214 (160–285) µm
	Vessels/mm^2	63	87	137
	Intervessel pits	Alternate	Alternate or opposite	Alternate or opposite
	Diameter pits	5 µm	6 µm	6 µm
	Helical thickenings	Absent	Present	Absent
Axial paren-chyma	Apotracheal	Absent	Present	Present
	Paratracheal	Present[2]	Present[2]	Present[2]
	No. of cells/strand	4–8 (mostly 5)	4–5	4–8
	Vessel-axial parenchyma pits	Scalariform or transitional	Scalariform	Scalariform or transitional
Rays	Uniseriate	Absent	Present	Present
	Multiseriate	Present (3–10)	Present (4–7)	Present (4–6)
	Cellular composition	Heterocellular	Heterocellular	Heterocellular
	Height of uniseriate rays	–	173 µm	133 µm
	Height of multiseriate rays	2793 µm	1654 µm	680 (316–1417) µm
	Rays per mm	4–12	4–12	6–11
	Crystals	Rhomboidal	Absent	Rhomboidal
	Sheath cells	Present	Present	Present
	Ray pits	Simple	Bordered	Simple
	Vessel-ray pits	Scalariform or transitional	Scalariform, transitional or opposite	Transitional or opposite
Fibres	Septate	Present	Present	Present
	Non-septate	Present (v)	Present (v)	Present
	Fibre pits	Simple to minutely bordered	Simple to minutely bordered	Simple to minutely bordered
	Diameter	?	?	13 (9–20)
	Walled	Thin- to thick-walled	Thin- to thick-walled	Thin- to thick-walled

Note: 1. Most latewood vessels only slightly narrower than earlywood vessels. 2. Axial parenchyma scanty paratracheal. Data from *Carlquist (1996), ++InsideWood Database.

According to the result of this search and affinity with Akaniaceae, the fossil wood was compared with the following extant taxa: *Akania bidwillii* and *Bretschneidera sinensis* Hemsl. that show a resemblance to *A. santacrucensis* (Table 1). In addition, this fossil wood was compared with six fossil woods retrieved in the InsideWood search.

Key diagnostic features seen in *A. santacrucensis* are the presence of simple (13p), scalariform (14p) and reticulate (19p) perforation plates, intervessel pits alternate (22p), vessel-ray pits with much reduced borders to apparently simple (32p), septate fibres (65p), axial parenchyma is scanty paratracheal (78p), multiseriate rays (98p, 107p). A detailed study of *A. santacrucensis* reveals that this taxon has features in common with both species of Akaniaceae: *A. bidwillii* and *B. sinensis*. It differs from *B. sinensis* in having helical thickening in vessel elements, axial parenchyma in marginal or in seemingly marginal bands, and body ray cells procumbent with more than four rows of upright and/or square marginal cells. *Akania bidwillii* has larger rays that are commonly more than ten-seriate, absence of uniseriate rays and four rays or less per millimetre (Carlquist, 1996), three characters not observed in *A. santacrucensis*.

The fossil specimen has distinct growth rings, inconspicuous growth rings (most latewood vessels only slightly narrower than earlywood vessels) and false growth rings (unusual climatic extremes, traumatic events and/or insect attacked) in different sectors of the piece. As the differences between indistinct and distinct boundaries are somewhat arbitrary in the piece of the fossil specimen, we did not code 'growth rings" in the InsideWood search.

The diagonal and/or irregular dendritic arrangement of vessels in the fossil wood is not found in extant genera of Akaniaceae. The significance of diagonal/tangential/dendritic arrangement lies in being a form of vessel redundancy and, therefore, conductive safety in taxa that have either narrow vessels or vasicentric tracheids mixed with wider vessels. All of the vessels in a stem are potentially linked with each other in a single group with intermixed narrow vessels and/or vasicentric tracheids forming a safeguarding subsidiary conductive system for its entirety (Carlquist, 2001). The presence of diagonal and/or irregular dendritic arrangement of vessels in the fossil wood, in some sectors of the piece, is interpreted here as an ecological adaptation.

In summary, the combination of characters seen in *A. santacrucensis* is characteristic of Akaniaceae; it exclusively shares anatomical features with two species of this family (perforation plates with bars numerous but often in aberrant arrangements, intervessel pits alternate, vessel-axial parenchyma pitting scalariform, vessel-ray pitting scalariform to opposite, septate fibres, axial parenchyma scanty is paratracheal and multiseriate rays).

COMPARISONS WITH FOSSIL SPECIES

The InsideWood search using the above coding returned six fossil woods: *Celastrinoxylon celastroides*, *Fagus* sp., *Dombeyoxylon oweni*, *Ternstroemioxylon dachelense*, *Platanoxylon* sp. and *Platanus* sp. All of these can be immediately eliminated, using the following differences. *Celastrinoxylon celastroides* has vessels mainly arranged in tangential bands, simple perforation plates and scalariform with five to ten bars, axial parenchyma bands two- to four-cells wide and uniseriate rays (Kräusel, 1939; Kamal El-Din, 2003). *Dombeyoxylon oweni* has simple perforation plates, 5–20 vessels/mm² and ray width one to three cells (Kräusel, 1939; InsideWood, 2004 onwards). *Ternstroemioxylon dachelense* has exclusively solitary vessels, scalariform perforation plates with ≥40 bars, scalariform intervessel pits, one- to three-seriate rays and fibres with distinctly bordered pits (Kräusel, 1939; van der Burgh, 1973). *Platanoxylon* sp. has exclusively solitary vessels, commonly simple perforation plates and larger rays commonly more than ten-seriate (Andreanszky, 1951); *Platanus* sp. (Slijper, 1932, in InsideWood, 2004 onwards) has exclusively solitary vessels, intervessel pits opposite, helical thickenings in vessel elements and larger rays commonly more than ten-seriate. Finally, *Fagus* sp. has exclusively solitary vessels and scalariform perforation plates (Slijper, 1932, in InsideWood, 2004 onwards).

BIOGEOGRAPHY AND PHYLOGENETIC RELATIONSHIPS OF AKANIACEAE

Molecular data show *Akania* and *Bretschneidera* to form a well-supported clade with *Tropaeolum* in Brassicales (99% support, see fig. 1 in Rodman *et al.*, 1996; 100% support, see fig. 2 in Ronse de Craene & Haston, 2006). Wood anatomy of Akaniaceae strongly supports this clade (Carlquist, 1996). The age of this clade is estimated as 71.3 Ma (Beilstein *et al.*, 2010), 72–68 Ma (Wikström, Savolainen & Chase, 2001), (90.5–)72–(–47.9) Ma (Couvreur *et al.*, 2010), (90–)79, 65(–55) Ma (Bell, Soltis & Soltis, 2010), (68–)54(–38) Ma (Zhang *et al.*, 2012) and 39.0 or 36.3 Ma (Xue *et al.*, 2012).

Wood anatomical characters tend to be linked to climatic and environmental adaptations, but many characters also have major taxonomic, systematic and evolutionary significance. In this case, heterocellular rays are reconstructed as plesiomorphic with three independent derivations of homocellular rays, two in Sapindales and the other in the earliest branching clade of Brassicales with four reversals (Ronse de Craene & Haston, 2006).

Akaniaceae do not currently occur in South America, but fossil leaf impressions attributed to *Akania*

have been recorded in Patagonia (Chubut Province, Argentina): *Akania americana* Romero & Hickey and *Akania patagonica* Gandolfo, Dibber & Romero from the Laguna del Hunco (La Huitrera Formation, 52.2 ± 0.22 Ma, early Eocene) and *A. patagonica* from Río Pichileufú floras (Ventana Formation, 47.5 ± 0.05 Ma, early Eocene) (Berry, 1925, 1938; Romero & Hickey, 1976; Gandolfo *et al.,* 1988, 2011; Wilf *et al.,* 2005, 2013). Recently, *Akania* sp. was recorded from Palacio de Los Loros flora (Salamanca Formation, 64.7–63.5 Ma, Palaeocene) (Iglesias *et al.*, 2007).

Bell *et al.* (2010) suggested that *Akania* and *Bretschneidera* diverged between (12–)6(–2) Ma, whereas Wikström et al. (2001) estimated the divergence to be between 31 and 23 Ma. This age, based on molecular clock estimates of phylogenetic analyses, is younger than South American fossils belonging to Akaniaceae. The oldest known Akaniaceae records are from the Palaeocene (*c.* 64 Ma, Salamanca Formation) (Iglesias *et al.*, 2007) and the early Eocene (*c.* 52–47 Ma, La Huitrera and Ventana formations) of Patagonia (Romero & Hickey, 1976; Gandolfo *et al.,* 1988, 2011).

An important area of overlap and diversity in many plant groups is the McPherson-Macleay Overlap (MMO), located on the coast of Queensland/New South Wales (Australia), and several interesting MMO taxa have intercontinental affinities (Burbidge, 1960; Heads, 2013). *Akania* (Akaniaceae) is a small understorey tree endemic to the MMO and *Bretschneidera* (Akaniaceae) occurs in northern Vietnam, south-eastern China and Thailand. These are sister group to *Tropaeolum* (Tropaeolaceae), present in the Neotropics from Mexico to temperate South America, thus forming a transtropical Pacific disjunction (Heads, 2013). Heads proposed the hypothesis that the split between the genera occurred before the rifting in the Pacific basin. The connections between South America palaeoflora and extant subtropical and tropical Australasia are supported by the presence of fossils of *Papuacedrus* H. L. Li, (Wilf *et al.*, 2009), *Eucalyptus* L'Hér. (Gandolfo *et al.*, 2011), *Dacrycarpus* (Endl.) de Laub. (Wilf *et al.,* 2012), *Todea* Willd. ex Bernh. (Carvalho *et al.*, 2013), *Ripogonum* J.R.Forst. & G.Forst. (Raymond *et al.*, 2014) and *Agathis* Salisb. (Wilf *et al.*, 2014).

The mean tangential vessel diameters of <100 μm, high vessel density (≥40/mm²), vessel element lengths of <400 μm and simple perforation plate present in *A. santacrucensis* support the idea that this fossil wood probably lived under temperate to warm-temperate, semi-arid environmental conditions (Wheeler & Baas, 1991, 1993; Lindorf, 1994; Brea *et al.*, 2012). The radial and diagonal patterns of vessel arrangement are more common in temperate (Wheeler & Baas, 1991) and dry areas (Carlquist, 1987). The *V* and *M* values for *A. santacrucensis* are 0.43 and 92 (Brea *et al.*, 2012), respectively, indicating that this wood shows evidence of xeromorphic features. In extant woods, features and values such as these are more frequently adapted to temperate and xeric conditions.

CONCLUSIONS

A new genus and species of Akaniaceae is erected, *Akaniaxylon santacrucensis*, based on a fossil wood recovered from the Santa Cruz Formation (early Miocene). It constitutes the first record for the Miocene in Patagonia (Santa Cruz Province, Argentina).

Akaniaxylon santacrucensis extends the biochron of Akaniaceae in South America by *c*. 30 Ma, from the early Eocene to the early Miocene. It also extends the latitudinal range by 10°S. All these evidence suggest that the family was widespread in Patagonia as a component of forests developed in a frost-free humid biome in South American mid to high latitudes.

The fossil record of *A. americana* (Romero & Hickey, 1976), *A. patagonica* (Gandolfo *et al.*, 1988) and *A. santacrucensis* outside Australasia provides further evidence of the southern biogeographic connections between South America, Antarctica and Australia during the early Cenozoic.

REFERENCES

Anderson L, Anderson S. 2000. A molecular phylogeny of Tropaeolaceae and its systematic implications. *Taxon* **49:** 721–736.

Andreanszky G. 1951 **[1952].** Der versteinerte Wald von Mikofalva und einge andere verkieselte Baumstamme aus Ungarn. *Annals of Biology University Hungary* **1:** 15–24.

APG IV. 2016. An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* **181:** 1–20.

Bayer C, Appel O. 2002. Akaniaceae In: Kubitzki K, Bayer C, eds. *The families and genera of vascular plants. Vol. V. Malvales, Capparales and non-betalain Caryophyllales.* Berlin: Springer-Verlag, 21–24.

Beilstein MA, Nagalingum NS, Clements MD, Manchester SR, Mathews S. 2010. Dated molecular phylogenies indicate a Miocene origin for *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences* **107:** 18724–18728.

Bell CD, Soltis DE, Soltis PS. 2010. The age and diversification of the angiosperms re-revisited. *American Journal of Botany* **97:** 1296–1303.

Berry EW. 1925. A Miocene flora from Patagonia. *Johns Hopkins University Studies in Geology* **6:** 183–233.

Berry EW. 1938. Tertiary flora from the Río Pichileufú, Argentina. *Geological Society of America Special Papers* **12:** 1–149.

Brea M, Zucol AF, Iglesias A. 2012. Fossil plant studies from late early Miocene of the Santa Cruz Formation: paleoecology and paleoclimatology at the passive margin of Patagonia, Argentina. In: Vizcaíno SF, Kay RF, Bargo MS, eds. *Early Miocene paleobiology in Patagonia. Height-latitude paleocommunities of the Santa Cruz Formation*. Cambridge: Cambridge University Press, 104–128.

Burbidge NT. 1960. The phytogeography of the Australian region. *Australian Journal of Botany* **8:** 75–211.

Carlquist S. 1987. Diagonal and tangential vessel aggregations in wood: function and relationship to vasicentric tracheids. *Aliso* **11:** 451–462.

Carlquist S. 1996. Wood anatomy of Akaniaceae and Bretschneideraceae: a case of near-identity and its systematic implications. *Systematic Botany* **21:** 607–616.

Carlquist S. 2001. *Comparative wood anatomy*. Berlin: Springer-Verlag.

Carpenter RJ, Wilf P, Conran JG, Cúneo NR. 2014. A Paleogene trans-Antarctic distribution for *Ripogonum* (Ripogonaceae: Liliales)? *Palaeontologia Electronica* **17**, Issue 3;39A; 9p.

Carvalho MR, Wilf P, Hermsen EJ, Gandolfo MA, Cúneo NR, Johnson KR. 2013. First record of *Todea* (Osmundaceae) in South America, from the early Eocene paleorainforests of Laguna del Hunco (Patagonia, Argentina). *American Journal of Botany* **100:** 1831–1848.

Couvreur TLP, Franzke A, Al-Shehbaz IA, Bakker FT, Koch MA, Mummenhoff K. 2010. Molecular phylogenetics, temporal diversification, and principles of evolution in the mustard family (Brassicaceae). *Molecular Biology and Evolution* **27**: 55-71.

Cronquist A. 1981. *An integrated system of classification of flowering plants*. New York: Columbia University Press.

Dahlgren RMT. 1980. A revised system of classification of the angiosperms. *Botanical Journal of the Linnean Society* **80:** 90–124.

Doweld AB. 1996. The systematic relevance of fruit and seed anatomy and morphology of *Akania*. *Botanical Journal of the Linnean Society* **120:** 379–389.

Floyd AG. 1977. Family Akaniaceae. *Forestry Commission New South Wales* **32:** 80–83.

Gadek PA, Quinn CJ, Rodman JE, Karol KG, Conti E, Price RA, Fernado ES. 1992. Affinities of the Australian endemic Akaniaceae: new evidence from *rbcL* sequences. *Australian Systematic Botany* **5:** 717–724.

Gandolfo MA, Dibbern MC, Romero EJ. 1988. Akania patagonica n. sp. and additional material on *Akania americana* Romero & Hickey (Akaniaceae), from Paleocene sediments of Patagonia. *Bulletin of the Torrey Botanical Club* **115:** 83–88.

Gandolfo MA, Hermsen EJ, Zamaloa MC, Nixon KC, González CC, Wilf P, Cúneo NR, Johnson KR. 2011. Oldest known *Eucalyptus* macrofossils are from South America. *PLoS ONE* **6:** e21084.

Gregory M. 1994. Bibliography of systematic wood anatomy of dicotyledons. *IAWA Journal* **1**(Suppl.): 1–265.

Gregory M, Poole I, Wheeler E. 2009. Fossil dicot wood names, an annotated list with full bibliography. *IAWA Journal.* **6** (Suppl.): 1–220.

Heads M. 2013. *Biogeography of Australasia. A molecular analysis*. Cambridge: Cambridge University Press.

Hewson HJ. 1985. Akaniaceae. In: Bureau of Flora and Fauna, Canberra. Flora of Australia. Volume 25 Melianthaceae to Simaroubaceae: 2-4. Australian Government Publishing Service. Camberra.

Heimsch C. 1942. Comparative anatomy of the secondary xylem in the 'Gruinales' and 'Terebinthales', of Wettstein with reference to taxonomic grouping. *Lilloa* **18:** 83–198.

Iglesias A, Wilf P, Johnson KR, Zamuner AB, Cúneo NR, Matheos SD, Singer BS. 2007. A Paleocene lowland macroflora from Patagonia reveals significantly greater richness than North American analogs. *Geology* **35:** 947–950.

IAWA Committee. 1989. IAWA list of microscopic feature for hardwood identification. International Association of Wood Anatomists. *IAWA Bulletin* **10:** 219–332.

InsideWood. 2004 onwards. Published on the Internet. Available at: http://insidewood.lib.ncsu.edu/search.

Kamal El-Din MM. 2003. Petrified wood from the Farafra oasis, Egypt. *IAWA Journal* **24:** 163–172.

Kräusel R. 1939. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. IV. Die fossilen Floren Ägyptens. *Abhandlungen der Bayerischen Akademie der Wissenschaften Mathematisch-naturwissenschaftliche Abteilung* **47:** 1–140.

Lens F, Vosl RA, Charrier G, van der Niet1 T, Merckx V, Baas P, Aguirre Gutierrez J, Jacobs B, Chacon Dória L, Smets E, Delzon S, Janssens SB. 2016. Scalariform-to-simple transition in vessel perforation plates triggered by differences in climate during the evolution of Adoxaceae. *Annals of Botany* **118:** 1043–1056.

Lindorf H. 1994. Eco-anatomical wood features of species from a very dry tropical forest. *IAWA Journal* **15:** 361–376.

Lu SY, Hu KS, Fan FH. 1986. Bretschneideraceae, a new family record for the flora of Taiwan. *Quarterly Journal of Chinese Forestry* **19:** 115–119 (in Chinese with English summary).

Matheos SD, Raigemborn MS. 2012. Sedimentology and paleoenvironment of the Santa Cruz Formation. In: Vizcaíno SF, Kay RF, Bargo MS, eds. *Early Miocene paleobiology in Patagonia. High-latitude paleocommunities of the Santa Cruz Formation*. Cambridge: Cambridge University Press, 59–82.

Metcalfe CR, Chalk L. 1950a. *Anatomy of the dicotyledons Vol. 1*. Oxford: Clarendon Press.

Metcalfe CR, Chalk L. 1950b. *Anatomy of the dicotyledons Vol. 2*. Oxford: Clarendon Press.

Rodman JE, Karol KG, Price RA, Conti E, Sytsma KJ. 1994. Nucleotide sequences of *rbcL* confirm the capparalean affinity of the Australian endemic Gyrostemonaceae. *Australian Systematic Botany* **7:** 57–69.

Rodman JE, Karol KG, Price RA, Sytsma KJ. 1996. Molecular, morphology, and Dahlgren's expanded order Capparales. *Systematic Botany* **21:** 289–307.

Romero EJ, Hickey LJ. 1976. A fossil leaf of Akaniaceae from Paleocene beds in Argentina. *Bulletin of the Torrey Botanical Club* **103:** 126–131.

Ronse de Craene LP, Haston E. 2006. The systematic relationships of glucosinolate-producing plants and related families: a cladistic investigation based on morphological and molecular characters. *Botanical Journal of the Linnean Society* **151:** 453–494.

Santisuk T. 1989. The monotypic family Bretschneideraceae newly recorded for Thailand. *Natural History Bulletin of the Siam Society* **37:** 173–176.

Schweingruber FH, Börner A, Schulze ED. 2011. *Atlas of stem anatomy in herbs, shrubs and trees. Vol. 1.* Berlin, Heidelberg: Springer Verlag.

Schweingruber FH, Börner A, Schulze ED. 2013. *Atlas of stem anatomy in herbs, shrubs and trees. Vol. 2.* Berlin, Heidelberg: Springer Verlag.

Slijper EJ. 1932. Über pliozäner Hölzer aus dem Ton von Reuver (Limburg, Holland). *Recueil des Travaux Botaniques Néerlandais* **29:** 18–35.

Stapf O. 1912. LII. Akaniaceae: a new family of Sapindales. *Bulletin of Miscellaneous Information Kew* **1912:** 378–380.

Stevens PF. (2001 onwards). *Angiosperm Phylogeny Website. Version 12, July 2012* Available at: http://www.mobot.org/MOBOT/research/APweb/

Takhtajan A. 1997. *Diversity and classification of flowering plants.* New York: Columbia University Press.

Tauber AA. 1997. Bioestratigrafía de la Formación Santa Cruz (Mioceno inferior) en el extremo sudeste de la Patagonia. *Ameghiniana* **34:** 413–426.

Tauber AA. 1999. Los vertebrados de la Formación Santa Cruz (Mioceno inferior-medio) en el extremo sureste de la Patagonia y su significado paleoecológico. *Revista Española de Paleontología* **14:** 173–182.

Thorne RF. 1992. Classification and geography of the flowering plants. *The Botanical Review* **58:** 225–348.

Tobe H, Peng CL. 1990. The embryology and systematic relationships of *Bretschneidera* (Bretschneideraceae). *Botanical Journal of the Linnean Society* **103:** 139–152.

Tobe H, Raven PH. 1995. Embryology and relationships of *Akania* (Akaniaceae). *Botanical Journal of the Linnean Society* **118:** 261–274.

van der Burgh J. 1973. Hölzer der niederrheinischen Braunkohlenformation, 2. Holzer der Braukohlengruben "Maria Theresia" zu Herzogenrath, "Zukunft West" zu eschweiler und "Victor" (Aulpich Mitte) zu Zulpich, nebst einer systematisch-anatomischen bearbeitung der gattung Pinus L. *Review of Palaeobotany and Palynology* **15**: 73-275.

Vizcaíno SF, Kay RF, Bargo MS. 2012a. *Early Miocene paleobiology in Patagonia. High-latitude paleocommunities of the Santa Cruz Formation.* Cambridge: Cambridge University Press.

Vizcaíno SF, Kay RF, Bargo MS. 2012b. Background for a paleoecological study of the Santa Cruz Formation (late Early Miocene) on the Atlantic coast of Patagonia. In: Vizcaíno SF, Kay RF, Bargo MS, eds. *Early Miocene paleobiology in Patagonia. High-latitude paleocommunities of the Santa Cruz Formation.* Cambridge: Cambridge University Press, 1–22.

Wilf P. 2012. Rainforest conifers of Eocene Patagonia: attached cones and foliage of the extant Southeast Asian and Australasian genus *Dacrycarpus* (Podocarpaceae). *American Journal of Botany* **99:** 562–584.

Wilf P, Escapa IH, Cúneo NR, Kooyman RM, Johnson KR, Iglesias A. 2014. First South American *Agathis* (Araucariaceae), Eocene of Patagonia. *American Journal of Botany* **101:** 156–179.

Wilf P, Little SA, Iglesias A, Del Carmen Zamaloa M, Gandolfo MA, Cúneo NR, Johnson KR. 2009. *Papuacedrus* (Cupressaceae) in Eocene Patagonia: a new fossil link to Australasian rainforests. *American Journal of Botany* **96:** 2031–2047.

Wheeler EA, Baas P. 1991. A survey of the fossil record for dicotyledonous wood and its significance for evolutionary and ecological wood anatomy. *IAWA Bulletin* **12:** 275–332.

Wheeler EA, Baas P. 1993. The potentials and limitations of dicotyledonous wood anatomy for climatic reconstructions. *Paleobiology* **19:** 487–498.

Wheeler EA. 2011. InsideWood – a web resource for hardwood anatomy. *IAWA Journal* **32:** 199–211.

Wikström N, Savolainen V, Chase MW. 2001. Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society B: Biological Sciences* **268:** 2211–2220.

Wilf P, Johnson KR, Cúneo NR, Smith ME, Singer BS, Gandolfo MA. 2005. Eocene plant diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina. *The American Naturalist* **165:** 634–650.

Wilf P, Cúneo NR, Escapa IH, Pol D, Woodburne MO. 2013. Splendid and seldom isolated: the paleobiogeography of Patagonia. *Annual Review of Earth and Planetary Sciences* **41:** 561–603.

Xue B, Su YCF, Thomas DC, Saunders RM K. 2012. Pruning the polyphyletic genus *Polyalthia* (Annonaceae) and resurrecting the genus *Monoon*. *Taxon* **61**: 1021-1039.

Ying TS, Zhang YL, Boufford DE. 1993. *The endemic genera of seed plant of China.* Beijing: Science Press.

Zhang N, Zeng L, Shan H, Ma H. 2012. Highly conserved low-copy nuclear genes as effective markers for phylogenetic analyses in angiosperms. *New Phytologist* **95**: 923-937.