



A new species of *Carlquistoxylon* from the Early Cretaceous of Patagonia (Chubut province, Argentina): the oldest record of angiosperm wood from South America

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ABSTRACT

An angiospermous wood from the Lower Cretaceous (upper Albian) of the Cerro Barcino Formation, Chubut Group, central Patagonia, Argentina, is described. Its estimated minimum diameter is 40 cm and it is significant as the oldest known angiosperm wood for South America.

It has indistinct growth ring boundaries, vessels solitary and in radial multiples, simple perforation plates, alternate intervessel pits, vessel-ray parenchyma pits oval to horizontally elongated, heterocellular rays, non-septate fibres, axial parenchyma absent, and abundant tyloses. Because this Albian wood has non-septate fibres we assign it to *Carlquistoxylon*, even though it has a general combination of characters similar to that of *Paraphyllanthoxylon*, which has septate fibres. The number of vessels per radial multiple, vessel tangential diameter and frequency, vessel-ray parenchyma pitting, and absence of axial parenchyma distinguish the fossil described here from the only previously known species of *Carlquistoxylon*: *Carlquistoxylon nacimientense*; therefore, a new species is erected. Because of the close similarities between this new specimen and *Paraphyllanthoxylon* species, comparisons with all the species included in both genera are provided. Systematic affinities for this wood are discussed considering previous discussions for both *Paraphyllanthoxylon* and *Carlquistoxylon* affinities. As the oldest described angiosperm wood in South America to date, this specimen provides critical information on the diversity and growth habit of Cretaceous angiosperms from the Southern Hemisphere.

Keywords: *Carlquistoxylon*, *Paraphyllanthoxylon*, Albian, fossil wood, South America, angiosperm.

INTRODUCTION

Flowering plants are the most diverse and abundant group of seed plants. Their fossil record provides direct evidence of their rapid diversification during the middle part of the Cretaceous in both Northern and Southern hemispheres, resulting in their extraordinary diversity today (see Simpson 2006; Taylor *et al.* 2009; Herendeen *et al.* 2017 and citations therein). However, understanding the events related to this radiation is still a difficult task in a global context, therefore, the finding of new mid-Cretaceous fossil localities is crucial for broadening our knowledge about the early evolution of the angiosperms and how they developed into the dominant group in most of the tropical and temperate forests worldwide (see Taylor & Hickey 1996; Doyle & Endress 2000; Archangelsky *et al.* 2009; Herendeen *et al.* 2017 and citations therein).

Although the record of Cretaceous angiosperms in the Southern Hemisphere is sparse compared to the Northern Hemisphere, what is known for the southernmost part of South America indicates that paleofloristic patterns associated with the radiation of flowering plants were similar to those reported for the Northern Hemisphere (see Archangelsky *et al.* 2009 and citations therein). This conclusion is based on fossil pollen, compressions, and impressions. Fossil angiosperm woods in South America are scarce until the Cenozoic (Archangelsky *et al.* 2009; InsideWood 2004-onwards; Wheeler 2011; Gregory *et al.* 2008); and only a few angiosperm fossil woods have been described from its Late Cretaceous (*i.e.*, Milanez 1935; Torres & Rallo 1981; Nishida & Nishida 1987; Mourier *et al.* 1988; Nishida *et al.* 1990; Franco *et al.* 2015; Egerton *et al.* 2016). In particular, the fossil record of angiosperm woods in central Patagonia is restricted to a few Cenozoic and Late Cretaceous occurrences (*i.e.*, Romero 1970; Petriella 1972; Ragonese 1980; Brea 1998; Brea & Zucol 2006; Raigemborn *et al.* 2009).

Recently, an abundant megafloora associated with sauropod remains has been discovered in Lower Cretaceous deposits of the Chubut Group (see Carballido *et al.* 2017). These sediments belong to the Cerro Castaño Member of the Cerro Barcino Formation and dating of associated tuffs indicates they are upper Albian (101.6 ± 0.11 Ma; Carballido *et al.* 2017). The flora consists of impressions and compressions of fern pinnules, conifer leaves, angiosperm leaves and flowers, and silicified woods (Nunes *et al.* 2015). Among the impressions and compressions, the angiosperm remains are the most abundant. In contrast, gymnospermous wood remains dominate the fossil wood assemblage, with only one specimen being an angiosperm.

MATERIALS AND METHODS

The specimen herein described was collected at the La Flecha ranch, from deposits of the Chubut Group, in a site referred as “La Flecha Plantas 1”, Chubut Province, central Patagonia (Fig. 1). The Chubut group comprises the lower Los Adobes and the upper Cerro Barcino formations, both composed mainly of fluvial and volcanoclastic sediments (Rauhut *et al.* 2003). The Cerro Barcino Formation is divided into four members, from bottom to top: La Paloma, Cerro Castaño, Las Plumas, and Puesto Manuel Arce. (Marveggio & Llorens 2013; Figari *et al.* 2015; Carballido *et al.* 2017). The sample

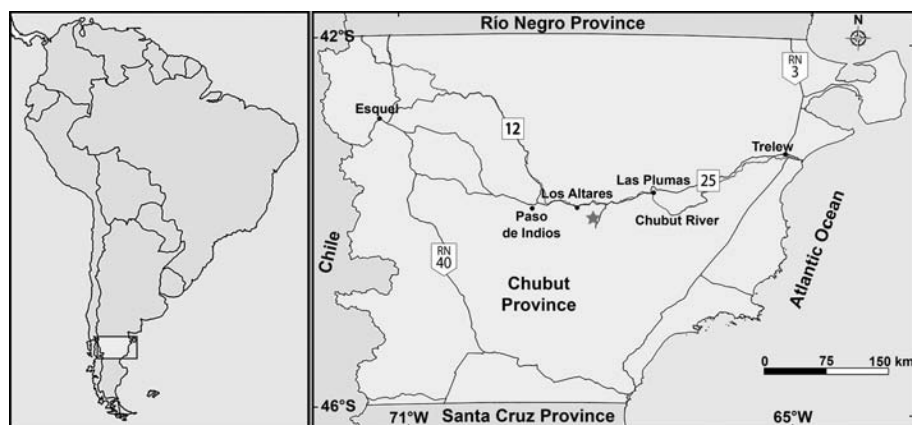


Figure 1. Location map of the La Flecha ranch (star), Chubut province, Argentina. References of previously described South America Cretaceous angiosperm woods localities: 1. Mourier *et al.* 1988. – 2. Torres & Rallo 1981. – 3. Nishida & Nishida 1987. – 4. Nishida *et al.* 1990. – 5. Egerton *et al.* 2016. – 6. Franco *et al.* 2015. – 7. Milanez 1935.

described herein was found at the Cerro Castaño member of the Cerro Barcino Formation. The Cerro Castaño Member was dated at 101.6 ± 0.11 Ma (upper Albian, Lower Cretaceous) at the sauropod excavation (Carballido *et al.* 2017) from an ash layer a few metres below the plant horizon. The fossiliferous deposits are siltstones and fine to medium-grained sandstones that represent sandy floodplains and meandering channels (Carmona *et al.* 2017), rich in plant and dinosaur remains, including a giant sauropod (Carballido *et al.* 2017). Plant impressions and compressions were collected from the La Flecha ranch, at two stratigraphically equivalent sites known as “La Flecha Pb 1” (FLPb 1) and “La Flecha Pb 2” (FLPb 2). Most of the permineralized logs, which are largely dominated by gymnosperms, are dispersed on a conglomerate that lies on top of the clay and sandstone layers. Angiosperm diversity at FLP 1 and FLP 2 comprises six leaf morphotypes, well preserved pentamerous flowers, and a small permineralized fragment of wood found among the gymnospermous woods (Nunes *et al.* 2015).

The permineralized angiosperm wood specimen is a decorticated fragment, of 4×5.5 cm approximately (Fig. 2–13). Transverse, tangential longitudinal, and radial longitudinal thin sections were prepared following standard methodology (Archangelsky 1962; Jones & Rowe 1999). Slides were observed using transmitted light and epifluorescence microscopy, and small fragments of the wood were observed with a scanning electron microscope as well. All images were taken with a Nikon DS-Fi1 camera attached to a Nikon Eclipse 80i microscope. In addition, general views of the transverse sections were taken using a Canon 7D camera with a Canon macro lens of 60 mm, magnified with 50 mm extension tubes, in a light box with fluorescent tubes. We used an image-stacking technique to obtain greater depth of focus for high magnification images (Bercovici *et al.* 2009). Helicon Focus software (<http://www.heliconsoft.com/heliconfocus.html>) was used, with the “Method B” (Depth Map) parameter, and the resulting image was carefully checked for the presence of artifacts. Several smaller, partially overlapping

images were merged to create high-quality images of critical features. This technique was applied both manually and using the Adobe Photoshop CS5 Photomerge macro. A minimum of 25 measurements or observations of each character were obtained. Measurements are expressed as the mean followed by the range between brackets. The terminology of IAWA Committee (1989) was followed for describing the wood anatomy.

The macro-specimen and its section are housed at the Paleobotanical Collection of the Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina, under accession number MPEF-Pb 7018.

SYSTEMATIC PALEONTOLOGY

Genus: *CARLQUISTOXYLON* Wheeler, McClammer & LaPasha

Type species: *Carlquistoxylon nacimientense* Wheeler, McClammer & LaPasha 1995

Remarks

The fossil here described shows most characters present in *Carlquistoxylon*. In the original diagnosis of the fossil-genus the value ranges of continuous features are highly restricted. Minor differences in continuous traits are not enough to justify the creation of a new fossil-genus; therefore, the diagnosis was expanded for those features. Bold letters indicate the amended characters.

Carlquistoxylon Wheeler, McClammer & LaPasha emend. Nunes, Pujana, Escapa, Gandolfo, Cúneo

Amended generic diagnosis

Wood diffuse-porous. Vessels solitary and in radial multiples **normally of 2–3, and up to 8**; mean tangential diameter 50–150 μm ; **generally, fewer than 40 vessels per mm^2 , sometimes up to 80 per mm^2** ; perforation plates exclusively simple, vessel element length between 500 and 800 μm ; intervessel pits crowded alternate; vessel-ray parenchyma pits with reduced borders; axial parenchyma absent or rare, if present, scanty paratracheal; non-septate fibres; pits not obvious; rays 4 or fewer cells wide; uniseriate rays rare.

CARLQUISTOXYLON AUSTRALE Nunes, Pujana, Escapa, Gandolfo & Cúneo, *sp. nov.* – Fig. 2–13.

Specific diagnosis

Growth rings boundaries indistinct. Vessels solitary and in radial multiples of 2–4, sometimes more; tangential diameter usually smaller than 100 μm ; normally 30–80 vessels per mm^2 . Vessel-ray parenchyma pits opposite to scalariform, when opposite oval to horizontally elongated. Axial parenchyma absent. Rays 1–4 cells wide (uniseriate rays very rare), heterocellular, with procumbent and square cells mixed through the ray, upright cells occasionally present at the ray margin and throughout the ray.

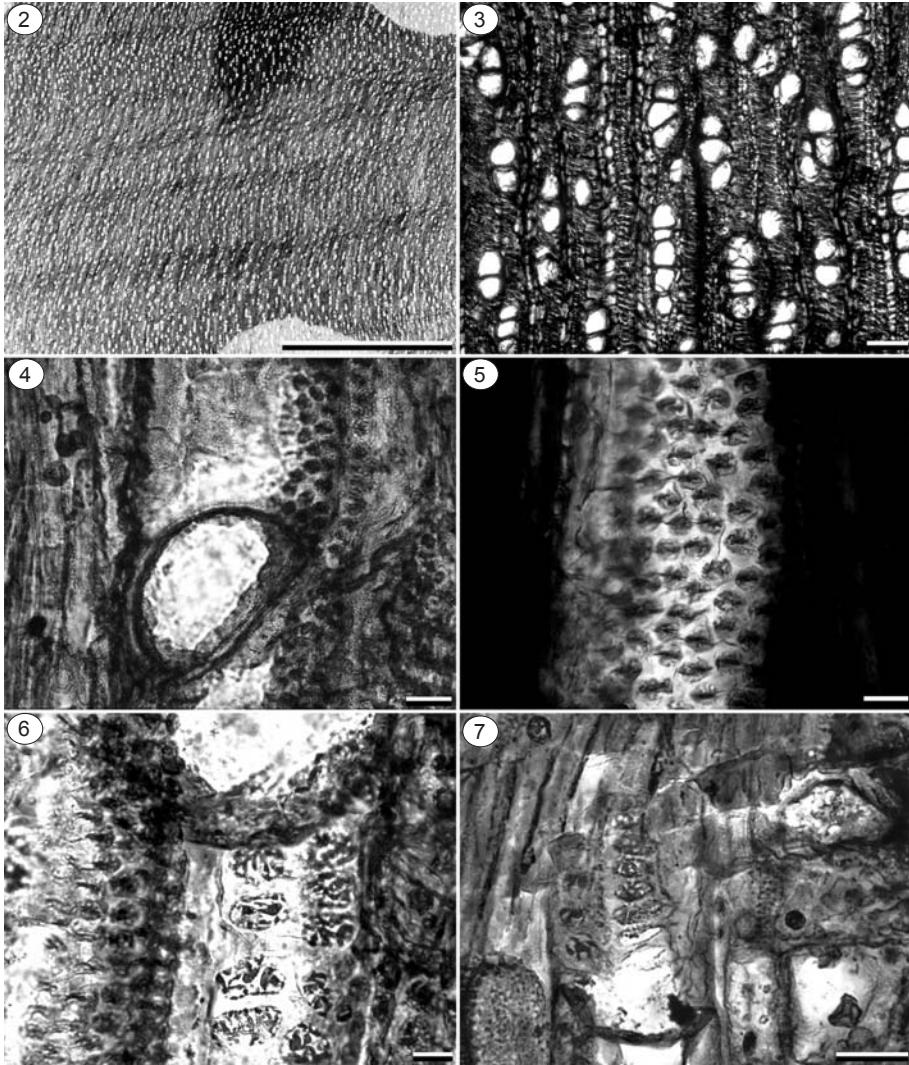


Figure 2–7. *Carlquistoxylon australe* sp. nov. Holotype: MPEF-Pb 7018. – 2: Macroscopic view of transverse section (TS) showing indistinct to absent growth ring boundaries and diffuse porosity. – 3: Vessel arrangement, TS. – 4: Radial longitudinal section (RLS) showing a simple perforation plate. – 5: Tangential longitudinal section (TLS) showing intervessel pits arrangement and morphology. – 6 & 7: Vessel-ray parenchyma pitting, scalariform to opposite, RLS — Scale bar for 3 = 50 μ m, for 4–6 = 10 μ m, for 7 = 25 μ m.

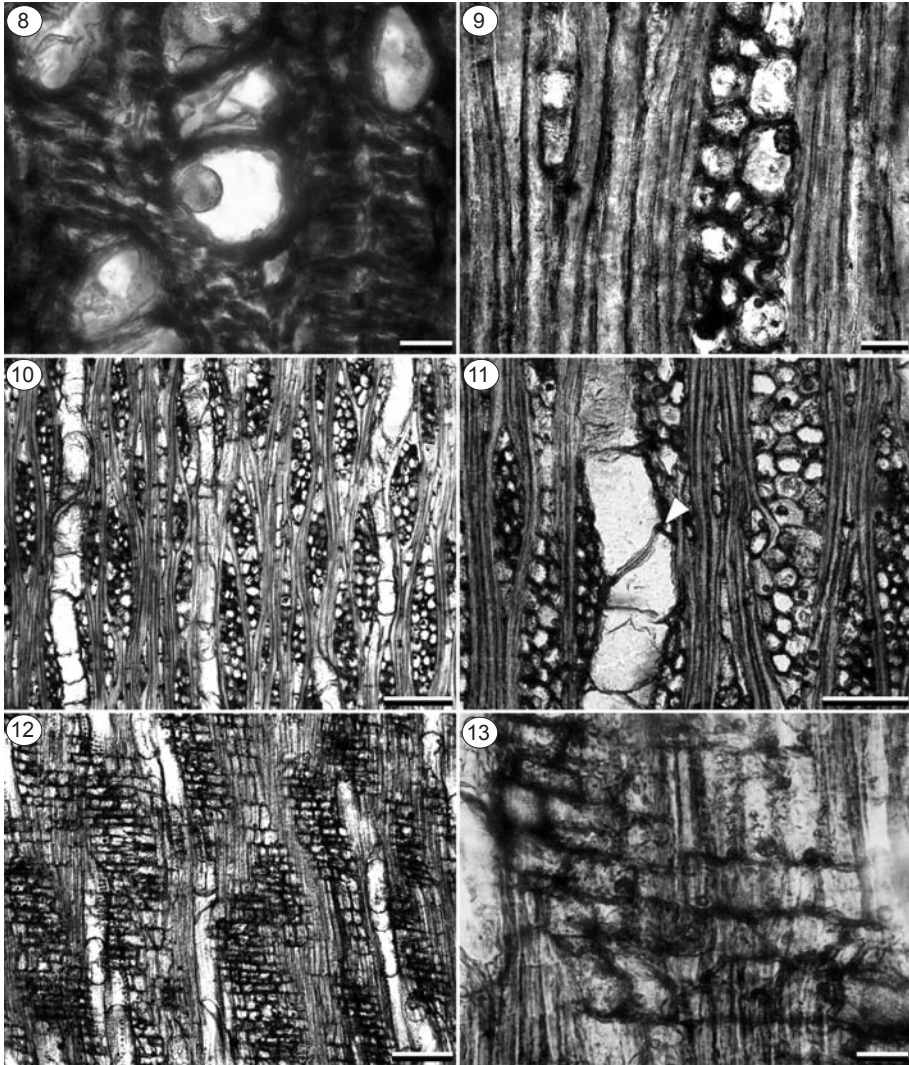


Figure 8–13. *Carlquistoxylon australe* sp. nov. Holotype: MPEF-Pb 7018. – 8: Developing tyloses, TS. – 9: Fibre details, TLS. – 10: Rays, TLS. – 11: Rays and a simple perforation plate (arrowhead), TLS. – 12 & 13: Heterocellular rays, RLS. — Scale bar for 8 & 13 = 30 μm , for 9 = 20 μm , for 10 & 12 = 150 μm , for 11 = 100 μm .

Stratigraphic horizon: Cerro Castaño Member, Cerro Barcino Formation, Chubut Group.

Age: late Albian (Early Cretaceous).

Type locality: “La Flecha Plantas 1”, La Flecha ranch, Chubut province, Argentina.

Holotype: MPEF-Pb 7018.

Etymology: the specific epithet *australe* refers to the Southern Hemisphere provenance of the fossil.

Description

The specimen is a fragment of 4 × 5.5 cm (minimum estimated diameter based on the curvature of the growth rings is 40 cm). Growth ring boundaries indistinct to absent, hardly observed macroscopically, slightly curved (Fig. 2).

Wood is diffuse-porous. Vessels are solitary (21%), and in radial multiples of 2 (36%), 3 (33%) or 4–8 (10%), average 49 (29–76) per mm². Vessels have a tangential diameter of 62 (31–100) µm and are circular to oval in outline in transverse section, sometimes radially flattened when in radial multiples (Fig. 3). Perforation plates are exclusively simple and oblique (Fig. 4, 11). Intervessel pits are crowded, oval, sometimes polygonal, alternate, medium, 7.95 (5.5–11.5) µm in horizontal diameter (Fig. 5). Vessel-ray parenchyma pitting is scalariform to opposite, with narrow borders to apparently simple, circular to horizontal (gash-like) (Fig. 6, 7). Tyloses are common (Fig. 8).

Fibres are non-septate and thin-walled, pits not observed on either tangential or radial walls (Fig. 9).

Axial parenchyma is absent.

Rays are up to 4 cells wide, mostly 2–3 cells wide, and 110–860 µm high (generally 350–380 µm), uniseriate rays very rarely observed (Fig. 10, 11). Rays are heterocellular, with procumbent, square and upright cells mixed through the ray, occasionally with one or two marginal rows of upright cells (Fig. 12, 13). Ray frequency is 14 (11–18) rays per mm.

Comparisons with fossil woods – Genera (Table 1)

Fossil woods assigned to *Paraphyllanthoxylon* Bailey 1924 are characterized by diffuse porosity, vessels solitary and in radial multiples, simple perforation plates, alternate intervessel pits, vessel-ray pits circular to horizontal, heterocellular rays, axial parenchyma rare or absent and, if present, scanty paratracheal, and abundant tyloses (e.g., Bailey 1924; Mädél 1962; Thayne & Tidwell 1984; Herendeen 1991). This fossil-genus was diagnosed by Bailey (1924) when he described the type species *Paraphyllanthoxylon arizonense* Bailey 1924, from the Upper Cretaceous (Cenomanian) of Arizona, USA. The presence of septate fibres was mentioned as a distinctive feature in the original description; however, this feature is absent in some species subsequently assigned to the genus (e.g., *P. yvardi* Koeniguer 1970; *P. obiraense* Takahashi & Suzuki 2003). Afterwards, Wheeler *et al.* (1995) proposed using the name *Carlquistoxylon* for fossil woods sharing the basic combination of features present in *Paraphyllanthoxylon*, but lacking septate fibres. The Patagonian specimen lacks septate fibres, therefore, it is assigned to *Carlquistoxylon*. Nevertheless, we consider it important to compare it with *Paraphyllanthoxylon*.

The general combination of characters mentioned above partially overlaps the diagnoses of additional Mesozoic and Cenozoic wood fossil-genera (see Thayne & Tidwell 1984; Wheeler *et al.* 1995; Gryc *et al.* 2009 and citations therein). Differences between *Paraphyllanthoxylon*, *Carlquistoxylon* and other genera are often subtle (Table 1). They are discussed below by the orders they were assigned.

(text continued on page 13)

Table 1. Comparison of *Carlquistoxylon* with similar wood fossil-genera.

Bold letters indicate characters shared with *Carlquistoxylon*. GR = growth rings, A = absent, I = indistinct, D = distinct — Po. = porosity, D = diffuse — VA = vessel arrangement, S = solitary, M = radial multiples, C = clusters — VTD = vessel diameter, S = small, M = medium, L = large — PP = perforation plates, Si. = simple, Sc. = scalariform — IP = intervessel pits, S = small, M = medium, L = large, VL = very large — VRP = vessel-ray parenchyma pits — RWC = ray width and composition — Ty. = tyloses, A = absent, C = common — Fi. = fibres, S = septate, N = non-septate — DS = distinctive structures — Age, K = Cretaceous, Cz = Cenozoic — Dis. = distribution — ? = missing information.

Genus	GR	Po.	VA	VS	PP	IP	VRP	RWC	Ty.	Fi.	AP	DS	Age	Dis.
<i>Carlquistoxylon</i> Wheeler, McClammer & LaPasha 1995	?	D	S, M 2-3	M	Si.	Crowded, alternate	Reduced borders	1-4-seriate, heterocellular	C	N	Rare, when present scanty paratracheal		K-Cz	North and South America
<i>Paraphyllanthoxylon</i> Bailey 1924	A or I	D	S, M 2 or more	S-L	Si.	Crowded, alternate, M-L	Enlarged, elongate, reduced borders to simple	1-7, heterocellular	C	S	Rare or ab- sent, when present scanty paratracheal		K-Cz	Worldwide
<i>Aplectotremas</i> Serlin 1982	?	D	M 2 or more	L	Si.	?	?	1-4-seriate, heterocellular	?	?	Vasentric paratracheal		K	North America
<i>Bridelioxylon</i> Ramanujam 1956	D	D	S, M 2-5 or more	S-M	Si.	Alternate-L	Small to medium, simple, rounded	1-4-seriate, heterocellular	A	S	Scanty, mostly paratracheal, often diffuse		K-Cz	Worldwide
<i>Patranjivoxylon</i> Ramanujam 1956	A	D	S, M 2-5	S (M)	Si., often sc.	Alternate, S	Large, rounded or elongate, simple or bordered	1-3-seriate, heterocellular	A	N	Abundant, apotracheal		Cz	Central South Asia

(continued on the next page)

(Table 1 continued)

Genus	GR	Po.	VA	VS	PP	IP	VRP	RWC	Ty.	Fi.	AP	DS	Age	Dis.
<i>Burseroxylon</i> Prakash & Tripathi 1975	D or I	D	S, M 2-5 or more	S-L	Si.	Alternate, L	?	1-5-seriate (or more) heterocellular	C	S	Paratracheal, scanty to vasicentric		K-Cz	Central South Asia
<i>Elaeocarpoxyton</i> Prakash & Dayal 1964	?	D	S, M 2-4 or more	S-M	Si.	Alternate and oppo- site, L	Enlarged	Uniseriate homocellular and multiseriate heterocellular	C	S	Scanty paratracheal terminal present or absent	Traumatic, vertical intercellu- lar canals	K-Cz	Central South Asia, Temperate South America
<i>Laurinoxylon</i> (syn. <i>Ultimum</i>) Felix emend. Dupéron, Dupéron-Laudoueneix, Sakala & De Franceschi 2008	D	?	S, M	M	Si.	Alternate, VL	Very large, elongate	1-5 seriate, heterocellular	C	?	Paratracheal	Idioblasts present	K-Cz	Worldwide
<i>Beilschmiedioxylon</i> Dupéron-Laudoueneix & Dupéron 2005	I or D	D	S, C	M	Si.	Alternate, L	Large	1-6-seriate, heterocellular	?	?	Paratracheal	Idioblasts present	Cz	Africa

Table 2. Comparisons among *Paraphyllanthoxylon* and *Carlquistoxylon* species.

Bold letters indicate characters shared with *Carlquistoxylon australe*. GR = growth rings, A = absent, I = indistinct — VF = vessels per mm² — VA = vessel arrangement, S = solitary, M = radial multiples, C = clusters, Rar. = rarely, Occ. = occasionally — **VTD = vessel ???** — RW = ray width — UR = uniseriate rays, A = absent, C = common, R = rare — RF = ray frequency — MURC = margin of up-right cells — IPS = intervessel pit size, S = small, M = medium, L = large — VRP = vessel-ray parenchyma pits — Fi. = Fibres, S = septate, N = non-septate, rar. = rarely — AP = axial parenchyma — AL = Age and Location — Obs./Ref. = Observations/References — ? = missing information.

Species	GR	VF	VA	VTD	RW	UR	RF	MURC	IPS	VRP	Fi.	AP	AL	Obs./Ref.
<i>P. abbotii</i> Wheeler 1991	I	2–16	S, M 2-4	141 (sd = 25) - 234 (sd = 41)	2–4	R	6–9	1–2	L	Rounded to horizontal or vertically elongate. Reduced borders	S	Absent to Rare	Paleocene, Texas, USA	
<i>P. alabamense</i> Cahoon 1972	A	12*	S, M 2 (7) Occ. C	150 (60–260)	2–5	R	?	1–2	L	Circular to oval. Simple	S	Scanty, paratracheal	Upper Cretaceous, Alabama, USA	*from Thynn & Tidwell 1984
<i>P. anazasi</i> Wheeler, McClammer & LaPasha 1995	I*	20–25	S, M 2 (3)	84 (sd = 16)*	2–3	R	7–10 (6–16)*	1–2	M	Enlarged. Reduced borders	S/ N to rar. S*	Scanty paratracheal/ Absent to rare*	Upper Cretaceous-Paleocene, New Mexico, USA	* <i>P. cf. anazasi</i> Wheeler & Lehman 2000
* <i>P. arizonense</i> Bailey 1924	I	8–14	S, M 2-4	175*1 (123–247)	2–7	R *2	?	1–5	L*2	Elongate. Reduced borders	S	Scanty, paratracheal	Upper Cretaceous Arizona, USA	*1 from Wheeler 1991 *2 from Wheeler <i>et al.</i> 1995
<i>P. boreense</i> Iamandei & Iamandei 2000	A	21–29	S Rar. M 2	(50) (80–130)	1–3	C	13–16 (21)	1–4	?	Rounded to elliptical. Simple	S	Scanty, apotracheal and paratracheal. Diffuse	Upper Cretaceous-Paleocene? Romania	
<i>P. capense</i> Mädel 1962	A	39 (24–60)	S, M 2-5 (6)	60 (35–100)	1–5	R	1–14	1–6	M-L	Enlarged. Oval to irregular. Reduced borders	S	Scanty, paratracheal	Upper Cretaceous, South Africa	
<i>P. cenomaniata</i> Takahashi & Suzuki 2003	A	11 (6–16)	S, M 2-5	174 (80–240)	2–5	R	?	?	L	Round to elliptical. Horizontal or vertically elongate. Simple	S	Scanty, paratracheal	Upper Cretaceous, Japan	

(continued on the next page)

(Table 2 continued)

Species	GR	VF	VA	VTD	RW	UR	RF	MURC	IPS	VRP	FI.	AP	AL	Ob./Ref.
<i>P. coloradensis</i> Martínez-Cábrera, Cevallos-Ferriz & Poole 2006	I	?	S, M 2-4	>100	1-3	C	5-11	1-8	L	Horizontally elongate to scalariform. Simple to reduced borders	S	Absent	Miocene, Mexico	
<i>P. idahoense</i> Spackman 1948	A	?	S, M 2-3, Occ. C	100 (60-160)	2-4	R	?	?	L	Elongate to oval	S	Scanty, paratracheal	Lower Cretaceous, Idaho, USA	
<i>P. illinoisense</i> Wheeler, Lee & Matten 1987	I	(12) 13-27 (32)	S, M 2-4 (8)	102-131	1-6	C	11-15	1-10	L	Enlarged, horizontally elongate. Small borders	S	Absent	Upper Cretaceous Illinois, USA	
<i>P. kobense</i> Suzuki 1984	I	50-82	S, M 2-3 (5)	120	1-4	C	8	1-4 (6)	M	Oval and horizontally long elliptical. Nearly scalariform	S	Scanty, paratracheal	Miocene, Japan	
<i>P. lewisii</i> Crawley 2001	A	9-12	S, M 2-5	125-168 (6)	(2) 3-5 (6)	A	5-7	1	L	Round and horizontally to vertically elongate. Simple to reduced borders	S	Absent	Paleocene, Berkshire, UK	
<i>P. lignitum</i> Daniou & Dupéron-Loudoueneix 1978	A	14-25	S, M 2-4 (12), Rar. C	34-108	1-6	C	8-16	1-16	S-L	Elongate, oval and rounded. Reduced borders	S	Rare, paratracheal	Eocene, France	
<i>P. marylandense</i> Herendeen 1991	A	35-60	S, M 2-3 (5)	55-114	1-4	R	?	1-3 (7)	S-M	Round to elongate. Reduced borders	S	Absent	Upper Cretaceous Maryland, USA	
<i>P. mamegate</i> Martínez-Cábrera, Cevallos-Ferriz & Poole 2006	I	?	S, M 2-4 (5)	<100	1-3	C	6-9	1-6	S	Oval to irregularly shaped, horizontally elongate to scalariform	S	Absent	Miocene, Mexico	
<i>P. obiraense</i> Takahashi & Suzuki 2003	A	22-36	S, M 2-5	93 (65-130)	1-3	R	?	?	L	Round to oval, horizontally or vertically elongate. Simple	N	Moderately abundant, vasicentric	Upper Cretaceous Japan	
<i>P. palaeoamblica</i> Prakash, Bande & Lalitha 1986	A	5-9	S, M 2-5 Occ. C	75-90	1-7 (9)	C	6	?	M-L	Horizontally elongate. Simple	S	Scanty, paratracheal	Early Cenozoic, India	

(continued on the next page)

(Table 2 continued)

Species	GR	VF	VA	VTD	RW	UR	RF	MURC	IPS	VRP	Fl.	AP	AL	Ob./Ref.
<i>P. pfefferi</i> Mädel 1962	A	16-44	M 2-10	86	1-5	?	?	?	M-L	?	S	Absent	Neogene, California, USA	
<i>P. pseudohobashiraii</i> (Ogura) Mädel 1962	I	23-40	S, M 2-4	100-200 80-120	1-4	R	5-7*	1-2	L	Horizontally elongate. Reduced borders to simple	S	Scanty, paratracheal	Paleogene, Asia	*from Watarai, 1943
<i>P. romanicum</i> Petrescu, Ianoflu & Dragos 1978	A	?	S, M 2-7 (9)	(40) 80-100 (150)	(2), 3-4 (7)	At	?	?	M-L	?	?	Rare	Upper Cretaceous, Romania	
<i>P. sahnii</i> (Prakash) Mädel 1962	I	24-50*	S, M 2-5	48-100	1-7	C	13-15*	1-4	M	Circular. Simple	S	Scanty	Cenozoic, India	*from Thayne & Tidwell 1984
<i>P. telense</i> Privé 1965*	A	8-16	S, M	38-110	1-6	?	6-7	?	M-L	Horizontally elongate	S	Scanty, paratracheal	Oligocene, France	*from Thayne & Tidwell 1984
<i>P. tertiarum</i> (Ramanujam) Mädel 1962	I	20-25	S, M 2-4	75-130	1-4	R	5-12	?	L	?	S	Scanty	Cenozoic, India	
<i>P. utahense</i> Thayne, Tidwell & Stokes 1983	A	12	S, M 2-3 (5)	93 (48-165)	1-5	R	12	2 (1-6)	M-L	Circular. Scleriform. Reduced borders	S	Rare, apotracheal. Scanty, paratracheal	Lower Cretaceous, Utah, USA	
<i>P. vanconverense</i> Jud, Wheeler, Rothwell & Stockey 2017	I	6-7-10	S, M 2-4	118 (82-167)	1-4	R	6-10	1-2	M	Oval to horizontally elongate. Reduced borders	S & N	Rare, scanty paratracheal	Upper Cretaceous Canada	
<i>P. yvardi</i> Koeniguer 1970	A	45-60	S, M 2-8	50-80	3-7	R	5-8	1-3	S	?	N	Scanty	Neogene, France	
<i>Carquistoxylon nacinianense</i> Wheeler, McClammer & LaPasha 1995	?	4-26	S, M 2-3	106	1-4	R	?	?	L	Enlarged. Reduced borders to simple	N	Scanty, paratracheal	Paleocene, New Mexico, USA	
<i>Carquistoxylon australe</i> sp. nov.	I	49 (29-76)	S, M 2-4 (8)	62 (31-99)	2 (1-4)	R	14 (11-18)	1-2	M	Opposite to scalariform. Horizontally elongate. Much reduced borders to simple	N	Absent	Lower Cretaceous, Patagonia, Argentina	

Bridelioxylon, *Putranjivoxylon* — *Bridelioxylon* Ramanujam 1956, widely distributed in Cretaceous and Tertiary sediments of Europe, Africa, Central South Asia, Oceania, and South America (Ramanujam 1956; Mädler 1962; Koeniguer 1967; Petriella 1972; Bamford & McLoughlin 2000) and *Putranjivoxylon* Ramanujam 1956, from the Tertiary of India (Ramanujam 1956), are similar to *Carlquistoxylon australe* in having vessels in radial multiples, presence of simple perforation plates, heterocellular rays, and alternate intervessel pits. However, *Bridelioxylon* differs from *Carlquistoxylon* in showing distinct growth rings, septate fibres, rays weakly heterocellular, parenchyma paratracheal scanty or diffuse, and absence of tyloses (Ramanujam 1956). *Putranjivoxylon* also lacks tyloses and has both simple and scalariform perforation plates, rays markedly heterocellular and abundant apotracheal parenchyma (Ramanujam 1956).

Burseroxylon — *Burseroxylon* Prakash & Tripathi 1975, from the Cretaceous and Tertiary of India and Africa (Prakash & Tripathi 1975; Bande & Prakash 1983; Bamford 2003), shares with the Patagonian specimen the presence of indistinct growth rings, diffuse porosity, small to medium vessel diameters, simple perforation plates, alternate intervessel pitting, heterocellular rays, and presence of tyloses. However, *Burseroxylon* has large intervessel pits and scanty to vasicentric axial parenchyma (Prakash & Tripathi 1975).

Elaeocarpoxyton — *Elaeocarpoxyton* Prakash & Dayal 1964 found in the Cretaceous and Tertiary of India (Prakash & Dayal 1964; Prakash & Tripathi 1975) and South America (Petriella 1972; Nishida et al. 1988) also shares a high number of features with the specimen described here. However, it has septate fibres, large intervessel pits, and differences in ray structure.

Aplectotremas — *Aplectotremas* Serlin 1982, from the Early Cretaceous of North America (Serlin 1982), has poor preservation and lacks a detailed description. It shares with our specimen a similar wood pattern (diffuse porosity, short radial multiples, simple perforation plates, heterocellular rays 1–4 cells wide). However, it differs from *Carlquistoxylon australe* in its large vessels and its vasicentric paratracheal axial parenchyma.

Lauraceae — The specimen described here is similar to the lauraceous genera *Laurinoxylon* Felix emend. Dupéron, Dupéron-Laudoueneix, Sakala & De Franceschi 2008, and *Beilschmiedioxylon* Dupéron-Laudoueneix & Dupéron 2005. The shared features include the arrangement and size of vessels, presence of simple perforation plates, alternate intervessel pitting, and ray width and composition. However, *Carlquistoxylon* lacks oil cells, a distinctive feature of the aforementioned genera.

Comparisons with fossil woods – Species (Table 2)

Until now, only one species of *Carlquistoxylon* has been described: *Carlquistoxylon nacimientense* Wheeler, McClammer & LaPasha, and it differs from *Carlquistoxylon australe* mostly in quantitative features. *Carlquistoxylon nacimientense* has wider vessels and fewer vessels per mm²; the radial multiples are shorter and the intervessel pits are larger than those observed in *Carlquistoxylon australe*. Another difference is the lack of axial parenchyma in *C. australe*, while *C. nacimientense* has scanty paratracheal parenchyma. On the base of these anatomical differences, the erection of a new species is justified.

Although this wood is assigned to *Carlquistoxylon*, it also resembles several species assigned to *Paraphyllanthoxylon* that, as mentioned earlier, differs from *Carlquistoxylon* mainly in the absence/presence of septa in the fibres. Given the similarities shared by *Paraphyllanthoxylon* and *Carlquistoxylon*, comparisons among the species of both genera are informative (Table 2). Species assigned to *Paraphyllanthoxylon* that lack septate fibres are *P. yvardi* Koeniguer 1967 and *P. obiraense* Takahashi & Suzuki 2003. *Paraphyllanthoxylon obiraense* differs from *C. australe* in vessel diameter and frequency, intervessel pits size, and presence of axial parenchyma. *Paraphyllanthoxylon yvardi* is more similar to *C. australe* in vessel arrangement, diameter and frequency, and intervessel pit size (Koeniguer 1970). According to the diagnoses of *Carlquistoxylon* and *Paraphyllanthoxylon*, these two fossil-species, *Paraphyllanthoxylon obiraense* and *Paraphyllanthoxylon yvardi*, should not be placed in *Paraphyllanthoxylon*, and could be transferred to *Carlquistoxylon*. However, *P. yvardi* has rays up to seven cells wide and *P. obiraense* has moderately abundant axial parenchyma and they do not conform with the generic diagnosis of *Carlquistoxylon*. Consequently, we suggest that these fossil-species should be revised and a transference to *Carlquistoxylon* should be considered.

We noticed that most similarities are shared especially with the species grouped in Herendeen's (1991) *Paraphyllanthoxylon* Anatomical Group A. This group is characterized by having a few marginal rows of upright cells on the multiseriate rays and few or rare uniseriate rays (Herendeen 1991; Martínez-Cabrera *et al.* 2006; Gryc *et al.* 2009). In *C. australe*, marginal rows of upright cells in the multiseriate rays are occasional, and the square to upright cells are mostly mixed with the procumbent cells through the ray body, which are consistent with all species from Anatomical Group A. Of the *Paraphyllanthoxylon* species included in Group A, the Patagonian specimen is similar to the Cretaceous North American species *P. anzasii* Wheeler, McClammer & LaPasha 1995 and *P. marylandense* Herendeen 1991 in vessel diameters and frequency, and lack of axial parenchyma, but these species have septate fibres; also axial parenchyma can be rarely observed in *P. anzasii* (Table 2).

DISCUSSION

The new Patagonian specimen is characterized by a combination of characters that occurs in some woods assigned to *Paraphyllanthoxylon*. However, given the absence of septate fibres, this wood is assigned to *Carlquistoxylon*. Due to the anatomical similarity of these genera, the specimen was compared with all *Paraphyllanthoxylon* and *Carlquistoxylon* species. Based on these comparisons we conclude that it represents a new species of *Carlquistoxylon*.

Systematic affinities

The combination of anatomical features present in *Paraphyllanthoxylon* and *Carlquistoxylon* has been referred to as the phyllanthoid xylotype, one of the earliest patterns known for angiosperm woods (Thayn & Tidwell 1984; Wheeler & Baas 1991; Wheeler *et al.* 1995; Oakley & Falcon-Lang 2009; Jud *et al.* 2017). The anatomical

pattern of *Paraphyllanthoxylon* occurs in more than one order and in multiple families: Laurales – Lauraceae; Malpighiales – Euphorbiaceae, Salicaceae; Rosales – Cannabaceae; Oxalidales – Elaeocarpaceae; Sapindales – Burseraceae, Anacardiaceae; and Lamiales – Verbenaceae (Mädel 1962; Thayne & Tidwell 1984; Wheeler et al. 1987; Herendeen 1991; Wheeler et al. 1995; Martínez-Cabrera et al. 2006; Gryc et al. 2009; APG IV 2016), indicating the genus does not represent a natural group. Similarly, due to the anatomical similarities with *Paraphyllanthoxylon*, *Carlquistoxylon nacimientense* was compared to some of those families. Wheeler et al. (1995) noticed that the general pattern of this fossil-genus occurs in families from two separate clades, equivalent to Cronquist (1981) subclasses, Magnoliidae and Rosidae. These authors also suggested that *Carlquistoxylon* could be related to the Lauraceae (Magnoliidae) or to the Anacardiaceae, Burseraceae, Melastomataceae, and Euphorbiaceae (Rosidae).

Most comparisons of the so-called phyllanthoid fossil woods including *Paraphyllanthoxylon* and *Carlquistoxylon*, have been with the Lauraceae and Euphorbiaceae (Thayne & Tidwell 1984; Prakash et al. 1986; Wheeler et al. 1987; Herendeen 1991; Wheeler 1991; Wheeler et al. 1995; Martínez-Cabrera et al. 2006; Gryc et al. 2009). *Carlquistoxylon nacimientense* was compared with Euphorbiaceae because of its similarity to *Euphorbioxylon* Felix emend. Mädel 1962 (Mädel 1962; Wheeler et al. 1995). However, Wheeler et al. (1995) pointed out that *Euphorbioxylon* needs to be revised because it has been used for woods with different combinations of features, which occur in the large family Euphorbiaceae. Thus, they hesitated about the relationship between their specimen and this genus.

They noted that among all the species of *Euphorbioxylon*, *Carlquistoxylon nacimientense* is most similar to *Euphorbioxylon saggarensis* Mahabale & Deshpande 1963, a species whose affinities with the Euphorbiaceae are questionable (Mahabale & Deshpande 1963). Wheeler et al. (1995) also compared *C. nacimientense* with *Laurinoxylon* (syn. *Uminium* Felix emend. Dupéron, Dupéron-Laudoueneix, Sakala & De Franceschi 2008), a fossil-genus for Lauraceae woods, but were not sure about this possible affinity because *C. nacimientense* lacks idioblasts so could not be assigned to this genus (Wheeler et al. 1995). Even though oil cells are an extremely common feature of Lauraceae wood, they are not always present in extant genera (Metcalf & Chalk 1950; Stern 1954). *Paraphyllanthoxylon marylandense*, a species that resembles *Carlquistoxylon australe* and is unambiguously related to Lauraceae due to its attachment to a lauraceous fruit, lacks idioblasts (Herendeen 1991). There is variation in the distinctiveness of oil cells in modern woods (Richter 1987). *Paraphyllanthoxylon vancouverense* from the Turonian of British Columbia, Canada, has some enlarged ray cells suggesting oil cells (Jud et al. 2017) and Campanian-Maastrichtian woods from Texas show a continuum from rays with well-defined oil cells to slightly enlarged cells (Jud et al. 2017). Jud et al. (2017) conclude that the idioblasts' distinctiveness in Lauraceae is variable enough to support considering their fossil wood a Lauraceae.

As explained before, the main feature that separates *Carlquistoxylon* species from *Paraphyllanthoxylon* is the presence/absence of septa in the fibres. Septate fibres seem to be a common character in the woods of the Euphorbiaceae *sensu lato*, at least in the morphological Group B or *Glochidion* type of Metcalfe and Chalk (Metcalf &

Chalk 1950), which *Paraphyllanthoxylon* has been related to (Prakash *et al.* 1986). In the other morphological group defined by Metcalfe and Chalk (1950), Group A or *Aporosa* type, fibres are mostly non-septate, but it is difficult to relate our wood to them due to the lack of axial parenchyma in *C. australe*. In Lauraceae, the presence of septa in the fibres is variable among the genera and species, but axial parenchyma is constantly present, ranging from scanty paratracheal to abundant (Metcalfe & Chalk 1950; Stern 1954; Herendeen 1991); *Paraphyllanthoxylon marylandense* also lacks axial parenchyma (Herendeen 1991).

Herendeen (1991) focused his attention on the variation of ray structure among the *Paraphyllanthoxylon* species and suggested there are two distinct *Paraphyllanthoxylon* anatomical groups probably with different affinities: Anatomical Group A and Anatomical Group B. Anatomical Group A, characterized by a few short marginal rows of vertical upright cells in the multiseriate rays and few or rare uniseriate rays, has features seen in the Lauraceae, Elaeocarpaceae, Anacardiaceae, Burseraceae, and Verbenaceae. The Anatomical Group B, characterized by abundant uniseriate rays and long marginal rows of upright cells in the multiseriate rays, has features seen in the Euphorbiaceae, Cannabaceae, Salicaceae, and Simaroubaceae. Herendeen (1991) pointed out that, given the variation in ray structure and oil cell occurrence, it is possible that *Paraphyllanthoxylon* Group A species were produced by extinct members of Lauraceae, perhaps one widespread genus. Nonetheless, he was circumspect in pointing that it is still necessary to have information from reproductive structures to validate such woods' familial relationships (Herendeen 1991).

Additional phenetic grouping analyses have included phyllanthoid woods; however, no definitive conclusions were reached in terms of internal relationships within the groups, and their results are similar to those of previous reports (*e.g.* Oakley & Falcon-Lang 2009; Méndez-Cárdenas *et al.* 2013).

Unfortunately, the systematic affinities of *Carlquistoxylon* and *Paraphyllanthoxylon* are unresolved. Future studies on the flowers preserved at the Cerro Barcino Formation and six (or more) angiosperm leaf morphotypes from the same strata where this wood was collected may help with suggesting affinities. However, given the absence of organic connections between flowers, leaves, and wood, it is difficult to establish an unambiguous reconstruction for this plant. As Jud *et al.* (2017) and Manchester and Tiffney (2001) have pointed out, for establishing affinities it is important to find repeated co-occurrences of different plant parts for whole plant reconstructions.

Biogeography implications

Carlquistoxylon australe represents the first mention of the genus in South America, but considering that this is a genus of relatively recent creation (Wheeler *et al.* 1995), it is not surprising that more species have not been described yet. However, *Carlquistoxylon australe* also represents the first mention in South America of a phyllanthoid xylotype wood. The other phyllanthoid wood reported for the Southern Hemisphere is *Paraphyllanthoxylon capense* Mädél 1962, from the Upper Cretaceous of South Africa. The anatomical pattern shared by *Carlquistoxylon* and *Paraphyllanthoxylon* is now also represented in another region of the Southern Hemisphere, indicating that these wood types were more widespread than previously known.

With a late Albian absolute age obtained for the La Flecha ranch, this fossil represents the oldest record of angiosperm wood for South America, and one of the oldest for the Southern Hemisphere. Previously described Cretaceous angiosperm woods from South America are of Upper Cretaceous age (Milanez 1935; Ragonese 1977; Torres & Rallo 1981; Nishida & Nishida 1987; Mourier *et al.* 1988; Nishida *et al.* 1990; Franco *et al.* 2015; Egerton *et al.* 2016). Thus, this finding increases our knowledge of the diversity of angiosperm organs in the Cretaceous of South America (see Archangelsky *et al.* 2009). In addition, the minimum estimated diameter for this specimen (at least 40 cm) suggests its habit was arboreal rather than shrubby. This adds useful information about the possible life habit that early flowering plants had in the Southern Hemisphere.

CONCLUSIONS

This is the first direct evidence of the presence of woody angiosperms in the Lower Cretaceous of South America and is important for documenting that by the middle part of the Cretaceous woody flowering plants were of global occurrence. Additionally, the estimated minimum diameter for this tree suggests an arboreal habit for this early flowering plant.

The generalized anatomical patterns found in *Carlquistoxylon* and *Paraphyllanthoxylon* will continue to generate debates about the lineages these woods represent. Their combination of characters is found in multiple unrelated families (*e.g.* Lauraceae, Euphorbiaceae, Anacardiaceae, and Burseraceae) and this suggests that their anatomical pattern may be homoplastic. However, it is also possible that some of these woods could represent basal nodes in angiosperm history.

The finding of new Cretaceous localities from different regions of the world, with repeated association of angiosperm woods and leaves is critical for determining the affinities of the so-called phyllanthoid fossil woods.

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