



## A NEW FOSSIL FABACEAE WOOD FROM THE PLEISTOCENE TOURO PASSO FORMATION OF RIO GRANDE DO SUL, BRAZIL

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Benicio, J. R. W., Pires, E. F., Da Rosa, A. A. S., Spiekermann, R., Uhl, D., Jasper, A. (2016): A new fossil Fabaceae wood from the Pleistocene Touro Passo Formation of Rio Grande do Sul, Brazil. – Fossil Imprint, 72(3-4): 251–264, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

**Abstract:** A fossil angiosperm wood from the Touro Passo Formation (Pleistocene) in the northwestern part of Rio Grande do Sul State, Brazil, is described as the new fossil-taxon *Itaquixylon heterogenum* BENICIO, PIRES, DA ROSA, SPIEKERMANN, UHL et JASPER gen. nov. et sp. nov. The fossil wood is silicified, and is 9.9 cm in diameter and 16.6 cm in length, with small pith. The main anatomical features are diffuse porosity, vessels solitary and in radial multiples, simple perforation plates, alternate vested intervessel pits, vessel-ray and vessel-parenchyma pits bordered, axial parenchyma scanty paratracheal and vasicentric, heterocellular rays, non-septate fibers, extremely short and with simple pits, as well as distinct growth rings. The unique set of anatomical features allows the proposing of a new fossil-genus with an affinity to the subfamily Mimosoideae of the Fabaceae. This record extends the area from which fossil woods are known in the western portion of Rio Grande do Sul State. The systematic classification proposed here, adds a new fossil-taxon related to the currently diverse family Fabaceae, thus contributing to knowledge of past biodiversity on the basis of wood anatomy in this family during the Pleistocene of Southern Brazil.

**Key words:** Fossil wood, *Itaquixylon heterogenum* gen. nov. et sp. nov., Fabaceae, Mimosoideae, Touro Passo Formation, Rio Grande do Sul State, Brazil

Received: November 16, 2016 | Accepted: December 2, 2016 | Issued: December 30, 2016

### Introduction

The Touro Passo Formation (Pleistocene – Holocene) in the northwestern part of the Rio Grande do Sul State, is one of the most important sources of information about Late Pleistocene palaeobiodiversity in Southern Brazil. The recorded fossil content of the formation includes vertebrates (e.g. Scherer and Da Rosa 2003, Kerber and Oliveira 2007, 2008, Hsiou 2007, Ribeiro et al. 2009, Oliveira and Kerber 2009), invertebrates (Oliveira and Milder 1990, Kotzian and Simões 2006, Erthal et al. 2015) and wood (Bolzon et al. 1991, Bolzon 1997, 1999, Bolzon and Oliveira 2000, Pires and Da Rosa 2000, Bolzon and Marchiori 2002).

The taxonomic studies of fossil woods recorded from the Cenozoic of South America, together with information about geology, climate and plant geography, allows us to infer

patterns of taxonomic similarities and endemisms, which can be used to reconstruct palaeoenvironmental patterns as well as changes in plant diversity over time (e.g. Franco and Brea 2013, Moya and Brea 2015). The occurrence of Cenozoic fossil angiosperm wood is documented in several regions of South America, with published records from Argentina (e.g. Kräusel 1925, Brea 1995, Franco and Brea 2010, Moya and Brea 2015) Colombia (e.g. Schönfeld 1947, Mirioni 1965, Pons 1969), Chile (e.g. Gonzalez 1981, Torres and Rallo 1981, Nishida et al. 1990), Peru (Salard 1961, 1963), and Uruguay (e.g. Gros 1992). In Brazil 21 fossil-genera based on angiosperm wood have been so far recognized from Cenozoic deposits (e.g. Silva-Curvello 1935, Mussa 1958, 1959, Suguui 1971, Suguui and Mussa 1978, Bolzon 1999, Bolzon and Marchiori 2002). These fossils are distributed in 11 botanical families and several of them belong to the family Fabaceae.

The Fabaceae or Leguminosae includes approximately 730 genera and 19,400 species of trees, shrubs, herbs and vines with a worldwide geographical distribution (Lewis et al. 2005). The fossil record of Fabaceae is composed of permineralized wood, leaves, flowers, fruits and pollen, and the oldest (questionable) fossils of the family are permineralized stems from the Upper Cretaceous of Sudan (Giraud and Lejal-Nicol 1989). In the Rio Grande do Sul State, southernmost portion of Brazil, four fossil-species of wood related to Fabaceae (*Santanoxylon marchiorii*, *Santanoxylon guerrasommeri*, *Quaraoxylon gracillis*, *Ramboxylon sanpedrensis*) were described by Bolzon (1999).

The aim of the present study is the anatomical description and characterization of a large fragment of well-preserved fossil wood, collected in the Northwest of Rio Grande do Sul State, in order to improve and extend the existing information about Quaternary fossil wood occurring in sediments of the southern part of Brazil.

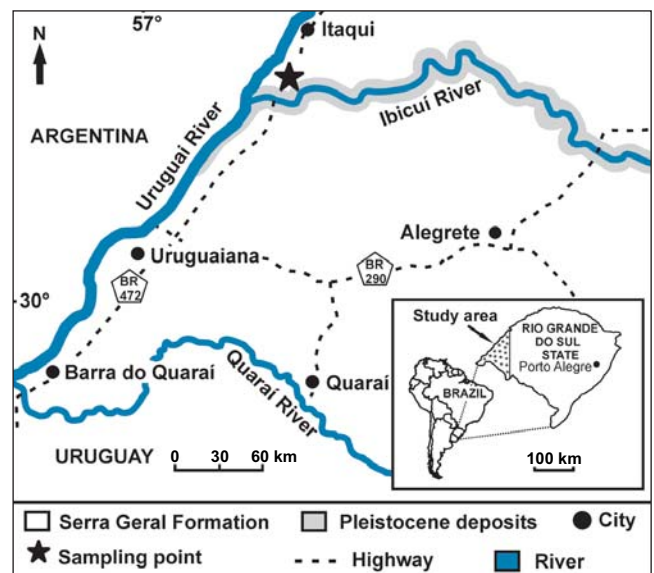
## Geological setting

According to Da Rosa (2009), the continental Pleistocene and Holocene sediments of Rio Grande do Sul State consist of alluvial deposits occurring in isolated and thus difficult to correlate terraces. These deposits are generally related to recent and sub-recent drainages, and they are usually considered in the context of two separate basins, i.e. the Uruguay and the South Atlantic Basin.

The post-Cretaceous geological history of Rio Grande do Sul consists of river deposits, on top of the magmatic rocks of the Serra Geral Formation (Lisboa and Schuck 1990). Over the past few thousand years, several alluvial cycles produced superimposed sediments, resulting in extensive plains in the western part of Rio Grande do Sul, usually covered by vegetation. These deposits are equivalent to the plaining surfaces described by Ab'Saber (1969), Lisboa and Schuck (1990) and Lisboa (1990).

The material studied here comes from an outcrop located in the Itaqui municipality, in the Northwest of Rio Grande do Sul State, at 29°23'55.9"S/56°42'05.9"W (Text-fig. 1). The geological profile of the outcrop demonstrates the occurrence of a palaeo-river cycle followed by a modern river and soil formation (Text-fig. 2). The outcropping levels in the study area can be correlated to the Touro Passo Formation, as described by Bombin (1976), which is recognized in several drainages in the Uruguai region, belonging to the Uruguay River Basin. Da Rosa (2009) characterizes the Touro Passo Formation as a sedimentary deposit over magmatic rocks on the top of the Serra Geral (Paraná Basin).

According to Bombin (1976), the Touro Passo Formation consists of conglomeratic deposits (Rudáceo Member) and mudstone (Lamítico Member), deposited by the so called Touro Passo river after the Last Glacial Maximum (LGM). The Rudáceo Member consists of a polymictic ortho-cluster with metaquartzitic phenocrysts, basalt, chalcedony and calcium carbonate concretions. The Lamítico Member consists of silt-clay sediments and silty sand lenses. The Rudáceo Member probably represents an accumulation of palaeosoils and soil removed by rain during a period of transition to more humid climates,



**Text-fig. 1.** Map of westernmost part of Rio Grande do Sul showing the position of the sampling locality (star). Adapted from Oliveira and Kerber (2009).

during which the deposition of the Lamítico Member took place.

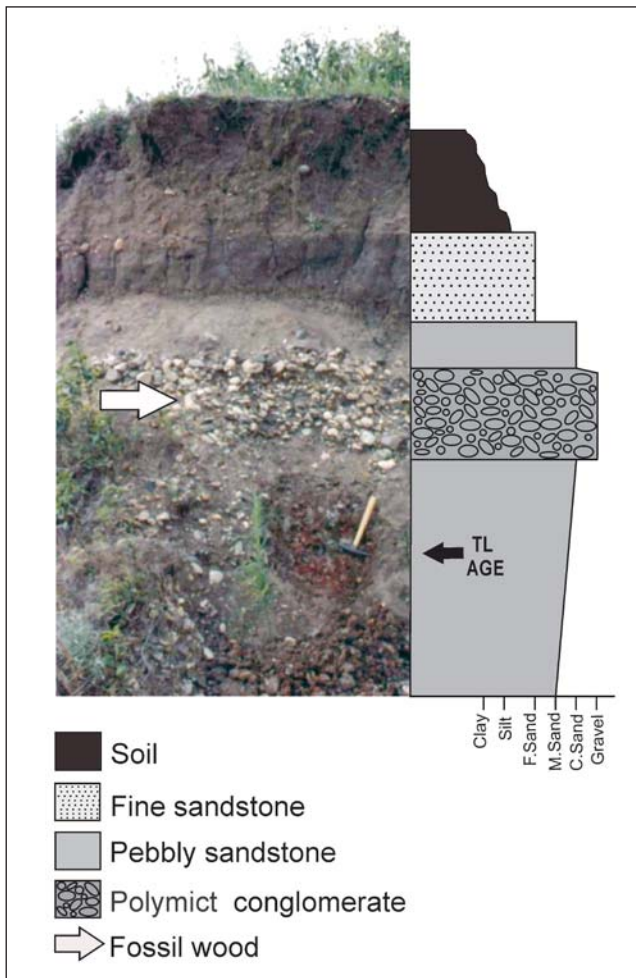
Further studies by Oliveira and Lavina (2000) considered that the members defined by Bombin (1976) characterize only a local sedimentation episode. Nevertheless, the formal name Touro Passo Formation has been widely used in the literature for comparable deposits (cf. Oliveira and Kerber 2009).

The Touro Passo Formation was proposed formally by Bombin (1975, 1976) as well as Bombin and Klamt (1976), and was assigned to the Late Pleistocene – Holocene. Deposits from a similar age are also known from northern Argentina (Tonni et al. 2003). Considering the age of the formation, data obtained by Milder (2000) suggested a multicyclic and diachronous sedimentary regime, as indicated by ages ranging up to 42,000 years BP.

Pires and Da Rosa (2000) used thermoluminescence to date sediments assigned to the Touro Passo Formation, and reported an age of 14,600 years (Pleistocene) for the fossil bearing conglomerate layer of the locality studied here and 8,200 years (Holocene) for the sandy-silty-clay layer ( $\pm 4.6\%$  SD). Da Rosa (2009) also used the same technique to date the sandstones and conglomerates from the Touro Passo Formation in the Itaqui municipality, suggesting ages between 6,400 and 42,900 years BP.

## Materials and methods

The material studied consists of a fragment of fossil wood, stored in the Palaeontological Collection of the Universidade Federal de Santa Maria (UFSM), under accession number UFSM 12032. The fossil wood was recovered from a conglomeratic matrix, with horizontal orientation (Text-fig. 2). This specimen was mentioned previously by Pires and Da Rosa (2000), while dealing with mineralogical aspects of the specimen and the age of the source sediments.

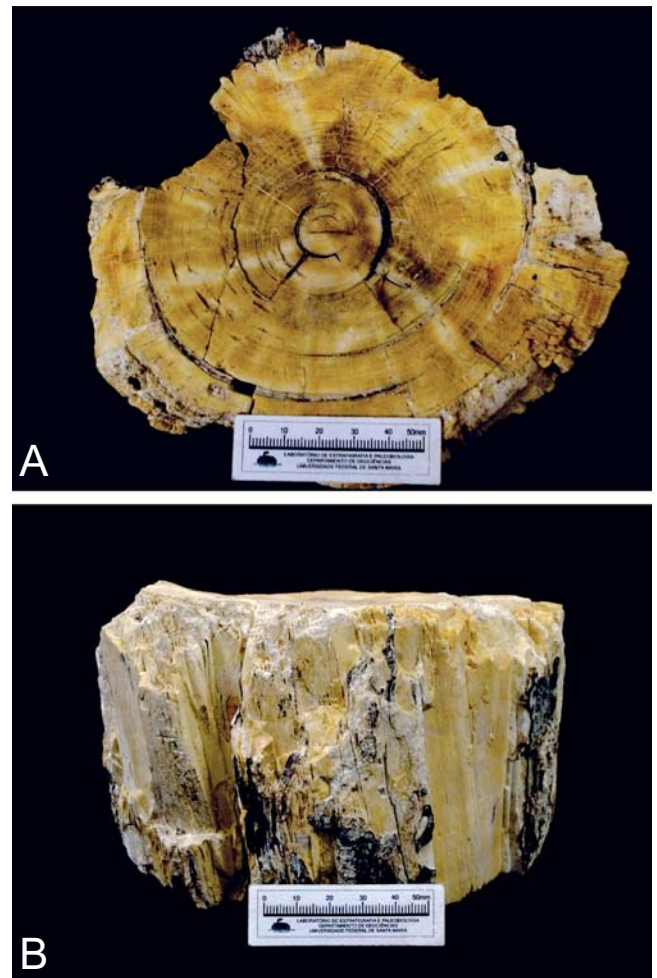


Text-fig. 2. Field photograph of the sampling locality, together with a schematic profile. Stratigraphic horizon from which the fossil wood fragment was extracted (white arrow) (Modified from Pires and Da Rosa 2000).

The fossil wood is silicified (*sensu* Schopf 1975), and has a diameter of 9.9 cm and a length of 16.6 cm. The primary xylem, external cortex and phloem are not preserved. The surface is irregular, yellowish to black, and the inner surface exhibits yellowish to beige colors (Text-fig. 3).

According to standard methodology for the analysis of fossil woods, a total of seven thin sections were prepared in transverse, tangential longitudinal and radial longitudinal orientation. These are deposited in the Paleontology Collection (CPALEOUFT) at the Universidade Federal do Tocantins (UFT) under accession numbers UFT 0456, 0457, 0458, 0459, 0460, 0461 and 0462. The anatomical details were observed and photographed using a light microscope coupled to a digital camera (Leica DM LB2).

The description of the anatomical features of the wood followed the procedures recommended by the International Association of Wood Anatomists, list of microscopic features for hardwood identification (IAWA Committee 1989). The identification and classification of the fossil wood was made following Metcalfe and Chalk (1950), Cozzo (1951), Tortorelli (1956), Baretta-Kuipers (1981), Wheeler and Bass (1992), Carlquist (2001), Evans et al. (2006) in addition to the InsideWood web site (<http://insidewood.lib.ncsu.edu/>



Text-fig. 3. Longitudinal (A) and lateral (B) views of the fossil wood (UFSM 12032), highlighting the preservation of growth rings.

search, accessed:15/10/2016). The systematic assignment followed the Angiosperm Phylogeny Group (APG III 2009).

Due to the varying states of tissue preservation in the different sections, it was not possible to perform the same number of measurements for all anatomical characters analyzed. Nevertheless, we made at least 25 measurements on each thin section analyzed, for all quantitative values utilized to produce the anatomical description.

### Systematic palaeobotany

Order **Fabales** BROMHEAD, 1938  
 Family **Fabaceae** LINDLEY, 1836  
 Subfamily **Mimosoideae** CANDOLLE, 1825  
 Genus ***Itaquixylon*** BENICIO, PIRES, DA ROSA,  
 SPIEKERMANN, UHL et JASPER *gen. nov.*

Type species. *Itaquixylon heterogenum* BENICIO, PIRES, DA ROSA, SPIEKERMANN, UHL et JASPER *sp. nov.*

Etymology. Generic name, *Itaquixylon*, refers to Itaqui city, where the type species was found.

Diagnosis. The same as for species.



***Itaquiylon heterogenum* BENICIO, PIRES, DA ROSA,  
SPIEKERMANN, UHL et JASPER sp. nov.**

**Holotype.** UFSM 12032 (Repository: Coleção Paleontológica da Universidade Federal de Santa Maria, Rio Grande do Sul, Brazil).

**Etymology.** The specific name, *heterogenum*, is due to the presence of heterocellular rays.

**Type horizon.** Touro Passo Formation.

**Age.** Late Pleistocene, 14,600 years (TL).

**Type locality.** (29°23'55.9"S/56°42'05.9"W), Itaqui city, Rio Grande do Sul State, Brazil.

**Diagnosis.** Angiosperm wood, diffuse porosity, numerous vessels in tangential bands; vessels generally solitary, sometimes in radial multiples of 3 to 5, circular to oval in outline, with narrow diameter and short length, helical thickenings absent, tyloses present; simple perforation plates; alternate intervessel pits, vestured, circular, small with lenticular irregular aperture slightly oblique; vessel-ray pits and vessel-parenchyma pits bordered; libriform fibres, non-septate, extremely short and narrow, with simple minute pits; paratracheal axial parenchyma, vasicentric and scanty and apotracheal axial parenchyma diffuse; rays are numerous, exclusively heterocellular, composed of procumbent and square marginal cells, short and extremely narrow, simple pits of minute size; mostly uniseriate, less frequently biseriata and triseriate, rarely tetraseriata; aggregate rays are absent.

**Description.** Distinctive growth rings, alternately separated by light and dark bands (Pl. 1, Fig. 1), marked by radially flattened thick-walled latewood fibres versus thin-walled earlywood fibers. Absence of stratification in secondary xylem elements. Wood diffuse-porous (Pl. 1, Figs 1–2). Vessels in tangential bands (Pl. 1, Figs 1–2), numerous (16–36/mm<sup>2</sup>), occupying 25.6% of the cross section (Pl. 1, Figs 1–2). Vessels generally solitary, sometimes in radial multiples of 3 to 5, circular to oval in outline (Pl. 1, Figs 2–3). Mean tangential diameter 65.5 (32–96) µm, mean length 186.5 (48–360) µm. Helical thickenings in vessel elements are absent. Simple perforation plates (Pl. 2, Fig. 4), intervessel pits alternate, small 4.1 (2–8) µm, vestured, with lenticular irregular slightly oblique apertures (Pl. 1, Figs 4–5). Vessel-ray pits with distinct borders, rounded and bordered (Pl. 1, Figs 4–5). Vessel-parenchyma pits are similar to vessel-ray pits. Tyloses (Pl. 1, Figs 2–6) and prismatic crystals are present in the marginal square ray cells (Pl. 2, Figs 4–6). Fibres libriform, non-septate, with simple and minutely bordered pits 2.3 (1–4) µm (Pl. 2, Figs 1–4), occupying 45% of the wood. The fibres are extremely short, mean length 162 (30–360) µm, narrow 3.2 (1–8) µm and thin-walled 1.9 (1–4) µm, with a narrow diameter of 3.9 (2–8) µm. The paratracheal axial parenchyma is vasicentric and scanty, occupying only 5.45% of total wood volume (Pl. 1, Figs 2–3). The apotracheal axial parenchyma is diffuse, with dispersed cells between the fibers (Pl. 1, Fig. 2–3). Axial parenchyma cells are rectangular (Pl. 2, Fig. 2), mean length 36.9 (16–80) µm and mean width 18.5 (8–32) µm, constituting a series with mean length 364.8 (176–896) µm, composed of 13 (3–6) cells. Rays are numerous, occupying

24% of the volume of the wood (Pl. 1, Figs 1–2). They are mostly uniseriate (44%), less frequent biseriata (27%), triseriate (21%) and tetraseriata (8%) (Pl. 2, Figs 1–3). Aggregate rays are absent. Rays are heterocellular, composed of procumbent cells and 1–4 rows of square marginal cells, most commonly 2 rows (Pl. 2, Figs 4–5). Uniseriate rays extremely short, mean length 204.9 (112–424) µm, and extremely narrow, mean width 12.4 (8–24) µm, 7 to 27 cells high (Pl. 2, Figs 1–3). The multiseriate rays are narrow, mean width 26.8 (16–40) µm, 1 to 4 cells wide, and very short, mean length 241.5 (120–556) µm, 8 to 27 cells high (Pl. 2, Figs 1–3). In tangential section, the ray cells are circular to oval (Pl. 2, Figs 1–3) with minute simple pits, ranging from 1 to 4 µm.

## Comparison

**Comparisons with extant taxa.** The synapomorphies that connect the fossil wood described here with the Fabales are the presence of vestured intervessel pits and vessel elements with simple perforation plates (Judd et al. 2007). Moreover, the combination of anatomical characteristics such as diffuse porous, short vessels solitary and in radial multiples, simple perforation plates, alternate and vestured intervessel pits, non-septate libriform fibres with simple small pits are synapomorphies which suggest that the fossil here investigated has an affinity with the Fabaceae (Metcalfe and Chalk 1950, Cozzo 1951, Tortorelli 1956, Baretta-Kuipers 1981, Wheeler and Baas 1992, Barros and Callado 1997, Evans et al. 2006).

The Fabaceae have been traditionally considered as a monophyletic family, composed of three subfamilies, Caesalpinioideae, Mimosoideae and Papilionoideae (Metcalfe and Chalk 1950, Polhill et al. 1981, Thorne 1992, Judd et al. 2007). Considering the combination of anatomical features, diffuse porosity, solitary to multiple vessels, simple perforation plates, alternate and vestured intervessel pits, vessel-ray and vessel-parenchymal bordered pits, parenchyma paratracheal vasicentric scanty, and extremely short fibres with simple pits, it is possible to assign this fossil wood to the Mimosoideae. This subfamily has a global geographical distribution and is composed of approximately 60 genera, with *Acacia*, *Mimosa* and *Inga* the most species-rich genera (Elias 1981).

The fossil wood analyzed here is most similar to taxa of the tribe Mimosae, especially to the *Piptadenia* group, which is considered as monophyletic and consists of eight genera (Luckow et al. 2003, Evans et al. 2006, Jobson and Luckow 2007) (Tab. 1). Despite such a grouping there is considerable variation in wood anatomy between species of the same genus, the main diagnostic features of the *Piptadenia* group are: vessels mostly small to medium in size, with high density, radial multiples and clusters ranging from rare to common, which can be large or small, variable intervessel pit size, septate and non-septate fibres, axial parenchyma ranging from scanty to banded, and in many cases confluent parenchyma linking many vessels leading to an almost banded appearance, rays are commonly 2–3 cells wide and uniseriate rays are always present (Evans et al. 2006).

**Table 1. Anatomical features of Piptadenia group (Tortorelli 1956, Evans et al 2006 and InsideWood – on-line database at insidewood.lib.ncsu.edu/search; available since 2004, accessed on 15/10/2016).**

Abbreviations: Growth rings: A – absent, D – distinct, I – indistinct, Radial multiples: R – rare (<10%), O – occasional (10–30%), F – frequent (30–60%), C – common (60–80%), VC – very common (>80%), Clusters: R – rare (<10%), O – occasional (10–30%), F – frequent (30–60%), C – common (60–80%), N – not observed, Septate fibers: P – present, N – not present, Axial parenchyma: A – aliform, V – vasicentric, S – scanty paratracheal, C – confluent, B – banded, Axial parenchyma confluent: N – not observed, R – rare, O – occasional, F – frequent, C – common, VC – very common, Number of vessels linked: number of vessels or groups of tangential vessels included in confluent parenchyma, Ray type: H – homocellular, He – heterocellular, Crystals: F – present in the fibers, A – present in axial parenchyma, R – present in rays cells.

Taxa	Growth Rings	Tangential vessel diameter (µm)	Vessels/mm	Radial Multiples	No. of Vessels	Clusters	No. of Vessels/ Cluster	Intervessel pit diameter(µm)	Fiber Wall Thickness	Septate Fibers	Axial Parenchyma	Axial Parenchyma Confluent	No. of vessels linked	Ray Height/N cells	Ray Height (µm)	Rays/ mm	Ray Width	Ray Type	Crystals
<i>Anadenanthera</i> SPEGAZZINI	D	86–98	50–57	F–C	2–7	O–F	2–7	6–9	Thick	N	V/A	F–VC	2–8+	11–17	246	8	1–40	H	F, A
<i>Microlobius</i> PRESL	A–I	42–110	7–30	F–C	1–4	R–C	2–4+	?	Thin–thick	N	V/A/C/B	F	2–(many)	?	800	8–12	1–2(3)	H	F, A
<i>Mimosa</i> LINNAEUS	A–I	79–112	15–50+	F/VC	2–10	R–C	2–5(10)	3–6	Thin–thick	P/N	V–C	C–VC	2–6+	8–130	20–250	6–15	1–3	H/He	F, A
<i>Parapiptadenia</i> BRENNAN	A–D	112–123	23–30+	O/VC	2–7	R/O–F	2–7	3–9	Med–thick	P/N	V/A	O–C	2–4+	11–24	30–450	8–10	1–3	H/He	F, A
<i>Parkia</i> BROWN	D–I	160–241	3–9	R–F	2–5(6)	N/R–F	2–8	4–9	Thin–med	N	A–C	R–VC	2–7+	14–19	20–380	4–7	1–4	H	F, A
<i>Piptadenia</i> BENTHAM	D–I	54–170	13–50+	R–C	2–9(15)	R–F	2–7+	4–12	Thin–thick	P	V–B	N–C	2–7+	12–24	20–620	5–13	1–2(4)	H/He	F, A
<i>Pseudopiptadenia</i> RAUSCHERT	D	142	20	O/F	2–4(7)	R/O	3–6(12)	3–6	Thin–med	N	V–A	R–O	2–3	ca. 15	20–260	ca. 7	1(2)	H	F, A
<i>Stryphnodendron</i> MARTIUS	D–I	95–133	14–33	F–C	2–7	R/O	2–4	6–12	Thin–med	N	S–A	N–O	N/2	ca. 8	20–170	9–11	1(2)	H	F, A
<i>Itaquiexylon</i> gen. nov.	D	40–96	20–30	R–O	1–6	R	2–5	2–8	Thin	P	V/S	N	N	7–27	112–424	2–8	1–4	He	R

Although the anatomy of wood is heterocellular in the subfamily Mimosoideae, the combination of anatomical features of the fossil wood described here suggest a strong affinity with the genus *Mimosa* (Tab. 1). The wood anatomy of this genus is poorly investigated, probably due the limited economic interest in these plants (Marchiori 1996a). However, it is well established that the genus *Mimosa* presents a wide variation in wood anatomy, being classified as “structurally heterocellular”, due to the absence of a common set of anatomical characters (Cozzo 1951).

The genus *Mimosa* currently comprises ca. 510 species. These plants are predominantly American, with a few representatives in Africa and Asia. In the Americas the genus is present in all warm regions, from the southern United States to Uruguay and central Argentina (Burkart 1952). For the extant Brazilian species, descriptive studies have so far been published for *Mimosa scabrella* (Richter and Charvet 1973, Marchiori 1980), *Mimosa bimucronata* (Marchiori 1980, 1993), *Mimosa daleoides* (Marchiori 1982), *Mimosa cruenta* (Marchiori 1985), *Mimosa eriocarpa* (Carnieletto and Marchiori 1993), *Mimosa sparsa* (Maccari and Marchiori 1994), *Mimosa artemisiana* (Paula 1995), *Mimosa incana* (Marchiori 1996a), *Mimosa berroi* (Marchiori 1996b), *Mimosa uruguayensis* (Marchiori 1996c), *Mimosa trachycarpa* (Marchiori and Muñiz 1997a), *Mimosa pilulifera* (Marchiori

and Muñiz 1997b), *Mimosa ophthalmocentra* (Dias-Leme et al. 2010, Silva et al. 2011), *Mimosa tenuiflora* (Dias-Leme et al. 2010, Silva et al. 2011), *Mimosa micropteris* (Pereira et al. 2013), *Mimosa flocculosa* (Pereira et al. 2014), *Mimosa ramulosa* (Tomasi et al. 2015, Machado and Marchiori 2016) and *Mimosa parvipinna* (Machado and Marchiori 2016). Of these species, this fossil wood has a close affinity to the southern Brazilian species *M. flocculosa*, *M. micropteris*, *M. ramulosa* and *M. parvipinna*, which share several secondary xylem anatomical features, such as diffuse porosity, numerous vessels which are solitary and in radial multiples, simple perforation plates, alternate vested intervessel pits, scanty paratracheal and vasicentric axial parenchyma, heterocellular rays, and extremely short libriform fibres with simple pits.

Comparisons with fossil woods. The fossil record of Mimosoideae wood is currently represented by 24 fossil-taxa (Tab. 2). The fossil-genera *Euacacioxylon*, *Metacacioxylon*, *Mimosaceoxylon* and *Dichrostachyoxylo* differ from the fossil here investigated by the presence of wide homocellular rays, medium-sized intervascular pitting as well as axial parenchyma pattern (Tab. 2). The fossil-genera *Ingoxylon*, *Albizzinium* and *Cathormion* differ from the fossil here investigated by the presence of slightly wider homocellular

**Tabela 2. Comparison of the characters of the Mimosoideae fossil genera. Adapted from Gros (1992).**

Fossil genus	Vassels	Intervascular pitting size	Ray type	Ray width	Axial parenchyma type	Fiber type
<i>Adenantheroxylon</i> PRAKASH et TRIPATHI, 1968	Mostly solitary	–	Homocellular	1–3 seriate	Diffuse, vasicentric to aliform, confluent	Nonseptate
<i>Albizzinium</i> PRAKASH, 1975	Mostly solitary	Medium	Homocellular	1–6 seriate	Diffuse, vasicentric to mostly aliform, occasionally terminal	Septate
<i>Cathormion</i> GROS, 1994	Predominantly solitary	–	Homocellular	1–6 seriate	Vasicentric aliform to confluent	Generally septate
<i>Albizzioxylon</i> NIKITIN, 1935	Solitary, some in radial groups	–	–	–	Paratracheal	–
<i>Dichrostachyoxyton</i> MÜLLER-STOLL et MÄDEL, 1967	Solitary; radial small groups	Medium	Homocellular, slightly heterocellular	1–10 seriate	Narrow vasicentric; frequently slightly aliform; rarely confluent; terminal or initial	Nonseptate
<i>Euacacioxyton</i> MÜLLER-STOLL et MÄDEL, 1967	Solitary and in radial small groups	Medium	Homocellular	1–10 seriate	Aliform, often confluent and small or long tangential bands	Nonseptate
<i>Ingoxyton</i> MÜLLER-STOLL et MÄDEL, 1967	Solitary or in radial groups	Medium	Homocellular	1–5 seriate	Vasicentric, wide aliform; rarely confluent, mostly diffuse	Septate
<i>Metacacioxyton</i> GROS, 1981 (apud Kloster et al. 2015)	Mostly solitary, and small groups	Medium	Homocellular	1–18 seriate	Vasicentric to aliform, and in oblique bands	Nonseptate
<i>Mimosaceoxyton</i> MÜLLER-STOLL et MÄDEL, 1967	Solitary, radial multiples and clusters	Medium	Homocellular	1–9 seriate	Usually paratracheal and diffuse strands	Septate?
<i>Prosopisinoxylon</i> MARTÍNEZ, 2010	Vassels of two distinct diameter classes; solitary, radial multiplex and clusters	Small to medium	Homocellular	1–9 seriate	Paratracheal vasicentric, aliform and confluent to banded; apotracheal diffuse	Nonseptate
<i>Anadenantheroxylon</i> BREA et al., 2001	Solitary, radial multiplex of 2–4 and clusters	–	Homocellular	1–2 seriate	Paratracheal vasicentric and confluent	Nonseptate
<i>Piptadenioxylon</i> SUGUIO et MUSSA, 1978	Solitary, rarely radial multiple	Small	Homocellular	2–3 seriate	Vasicentric	Nonseptate
<i>Paraalbizzioxylon</i> GROS, 1992	Solitary and radial multiple	Small to medium	Homocellular	1–6 seriate	Paratracheal, in some cases apotracheal, diffuse, terminal	Septate and nonseptate
<i>Paracacioxyton</i> MÜLLER-STOLL et MÄDEL, 1967	Solitary, radial multiplex of 2–4 and clusters	Small to medium	Homocellular	1–6 seriate	Paratracheal vasicentric, aliform, confluent; apotracheal diffuse	Septate and nonseptate
<i>Acacioxyton</i> SCHENK, 1883	Predominantly solitary	–	Homocellular	1–3 seriate	Paratracheal, uniseriate apotracheal in bands	Libriform
<i>Mimosoxyton</i> MÜLLER-STOLL et MÄDEL, 1967	Solitary, radial multiple	Small to medium	Homocellular, rarely weakly heterocellular	1–3 seriate	Narrow vasicentric, partly weakly aliform, rare confluent, terminal or initial	Nonseptate
<i>Tetrapleuroxyton</i> MÜLLER-STOLL et MÄDEL, 1967	Solitary and radial multiplex	Medium	Homocellular to weakly heterocellular	1–5 seriate	Vasicentric aliform, partly confluent, terminal or initial	Nonseptate
<i>Menodoxylon</i> LUTZ, 1979	Predominantly solitary, radial multiplex of 2–3	Small to medium	Homocellular to heterocellular	1–3 seriate	Vasicentric aliform, shorts bands	Nonseptate, sporadically septate
<i>Zygiaxyton</i> KLOSTER et al., 2015	Solitary and multiples	Small to medium	Homocellular	1–2 seriate	Paratracheal vasicentric, aliform to confluent forming irregularly wide bands of 4–10 cells height	Nonseptate
<i>Abaremaxylon</i> MOYA et BREA, 2015	Solitary, radial multiples of 2–4 and clusters	Small to Medium	Homocellular	1 seriate	Paratracheal vasicentric, aliform, unilateral aliform and confluent	Nonseptate
<i>Cylicodiscuxylon</i> MOYA et BREA, 2015	Solitary, radial multiples of 2–5 and clusters	Small to Medium	Homocellular	1–3 seriate	Paratracheal vasicentric, aliform, unilateral aliform and confluent	Nonseptate
“ <i>Quaraoxyton</i> ” (Bolzon 1999; nom. nud.)	Mostly solitary	Small to medium	Homocellular	1–3	Paratracheal in aliform bands, confluent, apotracheal diffuse	Libriform, nonseptate
“ <i>Ramboxyton</i> ” (Bolzon 1999; nom. nud.)	Mostly solitary	Small to medium	Homocellular	1–3	Paratracheal vasicentric to aliform confluent, apotracheal diffuse	Libriform, nonseptate
“ <i>Santanoxyton</i> ” (Bolzon 1999; nom. nud.)	Mostly solitary	Small to large	Homocellular	1–3	Paratracheal vasicentric, or aliform confluent	Libriform, nonseptate
<i>Itaquiexylon gen. nov.</i>	Solitary to multiple	Small	Homocellular	1–4	Paratracheal vasicentric scanty, apotracheal diffuse	Libriform, nonseptate

rays and septate fibres (Tab. 2). Moreover, *Adenantheroxylon* and *Acacioxyton* differ from the fossil here studied by the presence of homocellular rays, 1–3 seriate and by parenchyma

arrangement (Tab. 2). A comparison with the fossil-genus *Albizzioxylon* was impossible, due to incomplete anatomical information.



In South America, the fossil wood record of the subfamily Mimosoideae is represented by the fossil-genera *Mimosoxylon*, *Tetrapleuroxylon*, *Paracacioxylon*, *Piptadenioxylon*, *Menodoxylon*, *Anadenantheroxylon*, *Prosopisinoxylon*, *Microlobiusxylon*, *Paraalbizzioxylon*, *Zygiaxylon*, *Abaremaxylon* and *Cylicodiscuxylon*. Moreover, Bolzon (1999) described three new fossil-genera (*Santanoxylon*, *Quaraoxylon*, *Ramboxylon*) related to Mimosoideae. However, according to the International Code of Nomenclature (ICN) for algae, fungi, and plants (McNeill et al. 2012), these fossil-genera attributed to Mimosoideae have to be considered as *nomina nuda*, since the description of these fossil-taxa is part of an unpublished doctoral thesis (Tab. 2).

The fossil-genera *Paraalbizzioxylon* and *Paracacioxylon* differ from the fossil here investigated by the presence of homocellular rays, 1–6 seriate, small and medium size intervacular pitting and septate to non-septate fibres (Tab. 2). *Prosopisinoxylon* differs from the fossil here investigated by the presence of vessels of two distinct diameters, small to medium-sized intervacular pitting and homocellular rays 1–9 seriate (Tab. 2), while *Piptadenioxylon* differs from the fossil here studied by the presence of homocellular rays 2–3 seriate (Tab. 2). The fossil-genera *Mimosoxylon* and *Menodoxylon* differ from the fossil by the presence of small to medium-sized intervessel pitting, homocellular to heterocellular (heterocellular only rarely in *Mimosoxylon*) rays 1–3 seriate and by parenchyma pattern (Tab. 2), while *Cylicodiscuxylon* differs from the fossil studied by the presence of small to medium-sized intervessel pitting, exclusively homocellular rays 1–3 seriate and parenchyma arrangement (Tab. 2). *Anadenantheroxylon*, *Abaremaxylon*, *Zygiaxylon* differ from the fossil studied by the presence of small to medium-sized intervessel pitting, exclusively homocellular narrow rays and parenchyma arrangement (Tab. 2). Moreover, the fossil-genus *Tetrapleuroxylon* differs from the fossil studied by the presence of medium-sized intervessel pitting, homocellular, weakly heterocellular 1–5 seriate rays, and by parenchyma arrangement (Tab. 2).

The fossil woods described by Bolzon (1999) and the fossil wood described here are from the same region of the Rio Grande do Sul State, the southernmost part of Brazil. They were extracted from a similar depositional environment which might present similar or at least comparable age. The three fossil-genera proposed by Bolzon (1999), *Quaraoxylon*, *Ramboxylon* and *Santanoxylon* are similar to each other, with predominantly solitary vessels, alternate intervacular pitting, homocellular rays 1–3 seriate and libriform non-septate fibres, differing in intervacular pitting size and parenchyma type (Tab. 2). The fossil studied here differs from *Ramboxylon*, *Santanoxylon* and *Quaraoxylon* in particular by the presence of exclusively well-defined heterocellular rays 1–4 seriate, exclusively small intervacular pitting and by parenchyma arrangement (Tab. 2).

Although the fossil wood studied here shares anatomical elements with the fossil Mimosoideae fossil-genera that have already been described, the unique set of anatomical characters and the presence of exclusively heterocellular rays, allow the erection of the new fossil-genus and fossil-species *Itaquixylon heterogenum* from the Pleistocene of the Rio Grande do Sul State in Brazil.

## Final remarks

Silicified angiosperm fossils from the Cenozoic of South America are abundant, and several species related to Fabaceae have been described based on wood anatomical patterns, demonstrating that this family had a relatively high palaeobiodiversity (i.e. species richness) during this time (Pujana et al. 2011). The family is widely distributed in South America, ranging from the southernmost region of Patagonia to northern Colombia, and is mostly represented by fossil wood from the subfamily Mimosoideae (61%) rather than Caesalpinioideae and Papilionoideae (39%) (Pujana et al. 2011, Moya and Brea 2015). In Rio Grande do Sul Cenozoic fossil woods, assigned to the Touro Passo Formation, have been known for more than two decades (Bolzon et al. 1991, Bolzon 1997, 1999, Pires and Da Rosa 2000, Bolzon and Marchiori 2002). Until now only four fossil-species and three fossil-genera of Fabaceae (*Santanoxylon marchiorii*, *S. guerrasommeri*, *Quaraoxylon gracillis*, *Ramboxylon sanpedrensis*) are known from Rio Grande do Sul (Bolzon 1999). However, these fossil genera are invalid, since their formal and nomenclaturally valid descriptions have still not been published in the scientific literature.

The fossil wood investigated here shows anatomical characters which are related to the Fabaceae, especially to the subfamily Mimosoideae. Due the unique combination of anatomical characteristics, especially the well-defined heterocellular rays, the fossil studied here differs from all the Mimosoideae fossil woods described until now, and thus is interpreted as the new fossil-taxon *Itaquixylon heterogenum* gen. nov. et sp. nov. According to Baretta-Kuipers (1981), the presence of heterocellular rays is not a common characteristic of the subfamily Mimosoideae, since ray heterogeneity is considered as an anatomical character related to the low ray specialization, and probably assigned to a more primitive group. However, the frequent occurrence of heterocellular rays is well documented in the scientific literature in extant Brazilian Mimosoideae, such as *M. daleoides*, *M. eriocarpa*, *M. pilulifea*, *M. incana*, *M. sparsa*, *M. micropteris*, *M. flocculosa*, *M. ramulosa* and *M. parvipinna* (Marchiori 1982, Carneletto and Marchiori 1993, Maccari and Marchiori 1994, Marchiori 1996a, Marchiori and Muniz 1997a, Pereira et al. 2013, 2014, Tomasi et al. 2015, Machado and Marchiori 2016).

Pires and Da Rosa (2000) identified the permineralization agent of the wood described herein as opal-CT using X-ray-diffraction. This mineral corresponds to a form of silica, with crystallinity intermediate between opal, cristobalite and tridymite (Brindley and Brown 1980). The fossilization of the wood described here corroborates the observations made by Buurman (1972) and Mussa and Coimbra (1984), who concluded that the degree of preservation of cellular structures in opalized fossils is higher than in specimens with quartz microcrystalline structure. The horizontal position of the wood in the polycyclic conglomerate, which represents a high-energy depositional system, as well as the absence of phloem and external cortex, indicates transport prior to deposition and thus allochthonous deposition. Moreover, the presence of well-defined grow rings suggests that *Itaquixylon heterogenum* probably grew in an environment with marked seasonality (see Schweingruber 1996). However, considering that only a

single fossil was discovered and studied, and the allochthonous condition of the fossil, we cannot infer meaningful palaeoclimatic patterns.

This fossil wood adds another fossil-taxon to the Fabaceae subfamily Mimosoideae, and supports previous records which demonstrated the presence of the family in the Pliocene – Pleistocene of Rio Grande do Sul State based on fossil wood (e.g. Bolzon 1999) and pollen (Behling et al. 2005).

## Acknowledgements

The authors acknowledge Prof. Dr. Saul Milder (in memoriam) from the Universidade Federal de Santa Maria for support during field work, and Professor Dr. Robson Tadeu Bolzon, from the Universidade Federal do Paraná, for preliminary discussions regarding this study. The authors also acknowledge the suggestions given by Prof. Dr. Peter Gasson and anonymous Reviewer 2, which significantly improved the paper. J.R.W. Benicio acknowledges CAPES/PROSUP, for a doctor scholarship; E.F. Pires acknowledges CNPq (401845/2010-9); R. Spiekermann acknowledges CNPq (166622/2014-1); A. Jasper acknowledges CAPES (Brazil – 8107-14-9), CNPq (305436/2015-5; 444330/2014-3), Alexander von Humboldt Foundation (Germany BRA 1137359 STPCAPES) and FAPERGS. D. Uhl acknowledges financial support from CAPES (“Science without Borders Program” – A072/2013).

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## Explanations of the plates

### PLATE 1

Wood anatomical details of *Itaquiexylon heterogenum* gen. nov. et sp. nov.

Cross sections

1. Small core with fractures incrustated by quartz; distinct growth rings and diffuse porosity.
2. Solitary to multiple vessels, some of them with tyloses (arrow indicates twin vessel).
3. Detail of vessels with scanty paratracheal and vasicentric axial parenchyma (arrow).

Tangential section

4. Small alternate vested intervessel pits.
5. Detail of the alternate vested intervessel pits, with lenticular aperture (arrow).

Cross section

6. Presence of tyloses (arrow).

### PLATE 2

Wood anatomical details of *Itaquiexylon heterogenum* gen. nov. et sp. nov.

Tangential sections

1. Uniseriate (low and narrow rays) and biseriate rays (arrow).
2. Rectangular axial parenchyma cells directly adjacent to a vessel (arrow).
3. Detail of rays.

Radial sections

4. Heterocellular ray with one or two rows of square/upright marginal cells.
5. Detail of the heterocellular ray showing prismatic crystals (arrow).
6. Detail of prismatic crystal in the marginal square ray cells (arrow).

PLATE 1

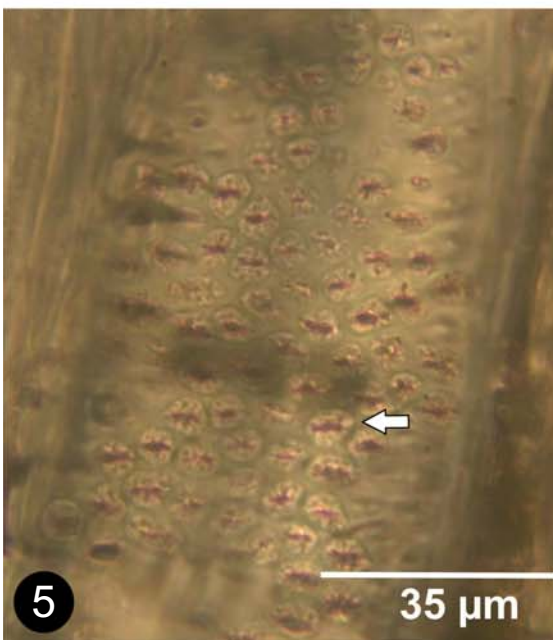
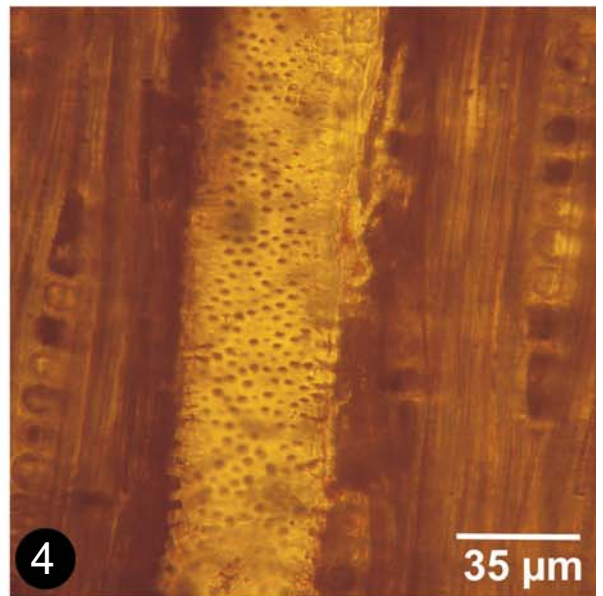
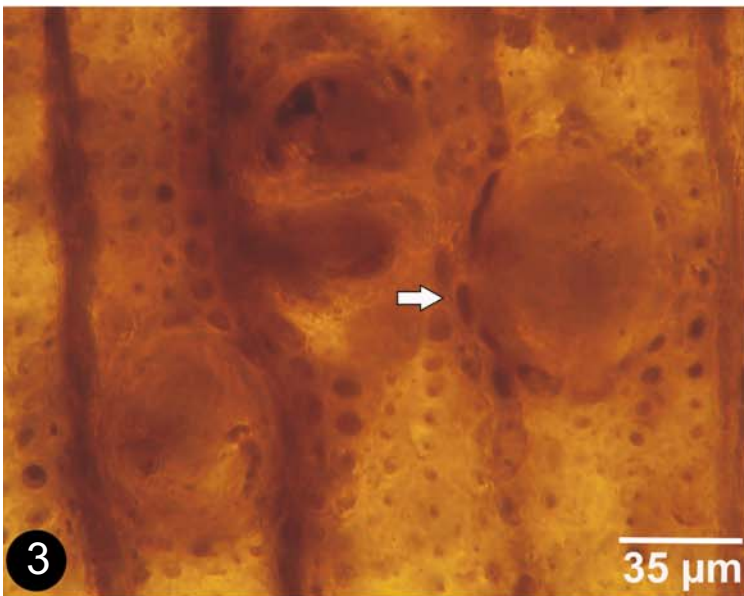
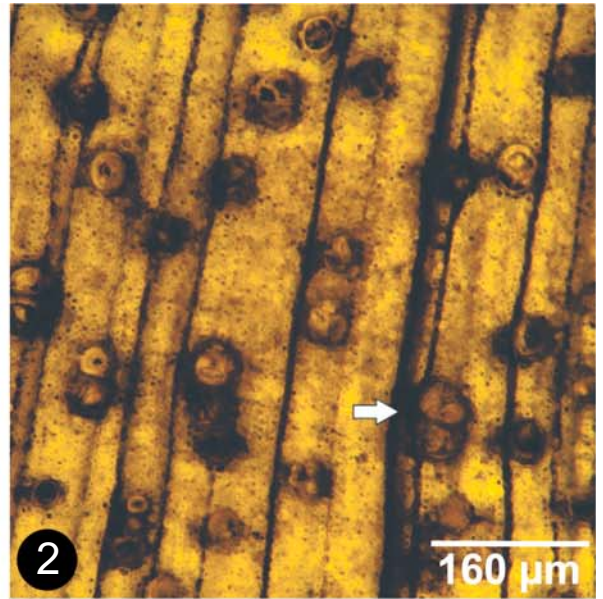
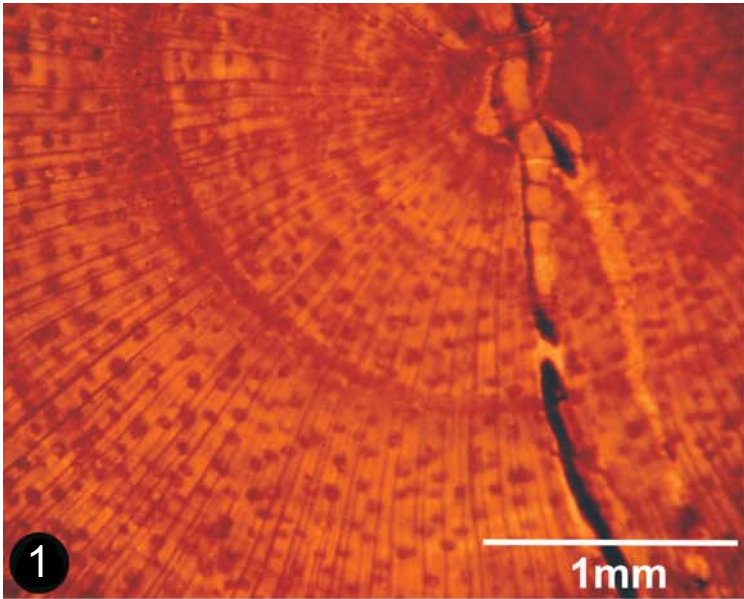




PLATE 2

