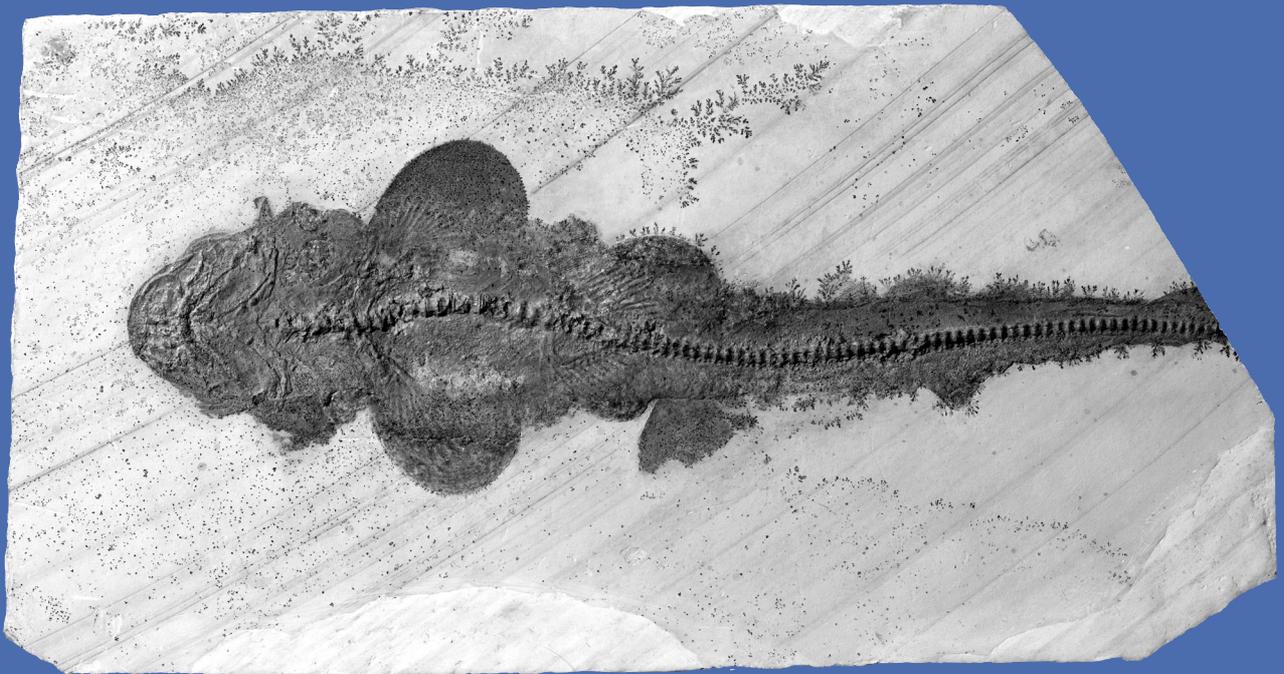


# Zitteliana

An International Journal  
of Palaeontology and Geobiology

Series A/Reihe A  
Mitteilungen der Bayerischen Staatssammlung  
für Paläontologie und Geologie

44



München 2004

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## CONTENTS/INHALT

REINHOLD R. LEINFELDER & MICHAEL KRINGS Editorial	3
DIETRICH HERM Herbert HAGN †	5
KAMIL ZÁGORŠEK & ROBERT DARGA Eocene Bryozoa from the Eisenrichterstein beds, Hallthurm, Bavaria	17
THORSTEN KOWALKE Evolution of the Pachychilidae TROSCHEL, 1857 (Chaenogastropoda, Cerithioidea) – from the Tethys to modern tropical rivers	41
HERBERT W. SCHICK The stratigraphical significance of <i>Cymaceras guembeli</i> for the boundary between Platynota Zone and Hypselocyclum Zone, and the correlation of the Swabian and Franconian Alb	51
GÜNTER SCHWEIGERT, RODNEY M. FELDMANN & MATTHIAS WULF <i>Macroacaena franconica</i> n. sp. (Crustaceae: Brachyura: Raninidae) from the Turonian of S Germany	61
JÜRGEN KRIWET & STEFANIE KLUG Late Jurassic selachians (Chondrichthyes, Elasmobranchii) from southern Germany: Re-evaluation on taxonomy and diversity	67
FELIX SCHLAGINTWEIT Calcareous green algae from the Santonian Hochmoos Formation of Gosau (Northern Calcareous Alps, Austria, Lower Gosau Group)	97
MICHAEL KRINGS & HELMUT MAYR <i>Bassonia hakeleensis</i> (BASSON) nov. comb., a rare non-calcareous marine alga from the Cenomanian (Upper Cretaceous) of Lebanon	105
ALFRED SELMEIER First record of <i>Matisia</i> (Bombacaceae) and <i>Crudia</i> (Caesalpinaceae) wood from the Tertiary of Rio Paranaibo, Brazil	113
ULRICH STRUCK, TOBIAS HEYN, ALEXANDER ALTENBACH, JÜRGEN ALHEIT & KAY-CHRISTIAN EMEIS Distribution and nitrogen isotope ratios of fish scales in surface sediments from the upwelling area off Namibia	125
Hinweise für Autoren/Instructions for authors	133

## EDITORIAL NOTE

As of in 2003, the journal *Zitteliana* is published in two series.

*Series A: Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Geologie* (ISSN 1612-412X) replaces the former „Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0077-2070). The numbering of issues is continued (last published: Heft 43, 2003).

*Series B: Abhandlungen der Bayerischen Staatssammlung für Paläontologie und Geologie* (ISSN 1612-4138) continues the previous „Zitteliana – Abhandlungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0373-9627).

Instructions for authors are included at the end of this volume.

## HINWEIS DES HERAUSGEBERS

Vom Jahr 2003 an erscheint die Zeitschrift *Zitteliana* in zwei Reihen.

Die *Reihe A: Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Geologie* (ISSN 1612-412X) ersetzt die bisherigen „Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0077-2070). Die Bandzählung (zuletzt erschienen: Heft 43, 2003) wird fortgesetzt.

Die *Reihe B: Abhandlungen der Bayerischen Staatssammlung für Paläontologie und Geologie* (ISSN 1612-4138) führt die bisherige „Zitteliana – Abhandlungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0373-9627) fort.

Hinweise für Autoren beider Reihen sind am Ende dieses Bandes enthalten.

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Für den Inhalt der Arbeiten sind die Autoren allein verantwortlich.

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**Cover illustration:** *Phorcynis catulina* THIOLLIÈRE, 1854 (BSP 1990 XVIII 51) from the lower Tithonian of Zandt / Denkendorf (Bavaria), ventral view, 25 cm. Photograph: G. JANßEN (LMU München, Department für Geo- und Umweltwissenschaften, Sektion Paläontologie)

**Umschlagbild:** *Phorcynis catulina* THIOLLIÈRE, 1854 (BSP 1990 XVIII 51) aus dem unteren Tithon von Zandt / Denkendorf (Bayern), Ventralansicht, 25 cm. Foto: G. JANßEN (LMU München, Department für Geo- und Umweltwissenschaften, Sektion Paläontologie)

# First record of *Matisia* (Bombacaceae) and *Crudia* (Caesalpiniaceae) wood from the Tertiary of Rio Paranaíba, Brazil

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## Abstract

The anatomy of *Matisianoxylon brasiliense* nov. gen. et sp. (Bombacaceae, i.e. Malvaceae s. l.) and *Crudioxylon brasiliense* nov. sp. (Caesalpiniaceae) is described and illustrated based on material collected in the 19<sup>th</sup> century from Tertiary deposits of Brazil. The anatomy of these fossil woods closely corresponds to that seen in the extant *Matisia* and *Crudia*. Especially noteworthy are tile cells that occur in the rays of *M. brasiliense*. This feature, which is found in only 1% of the extant woody plants, is significant with regard to phylogenetic considerations. The nearest living relatives of the fossils, *Matisia* and *Crudia*, are commercially unimportant trees that grow in neotropical rainforests.

**Key words:** Brazil, Deciduous trees, Bombacaceae KUNTH, Caesalpiniaceae R. BROWN, Malvales DUMORTIER, Tertiary, wood anatomy.

## Kurzfassung

Die anatomische Struktur von *Matisianoxylon brasiliense* nov. gen. et sp. (Bombacaceae, Malvaceae s. l.) und *Crudioxylon brasiliense* nov. sp. (Caesalpiniaceae) wird beschrieben und durch Mikrofotos dokumentiert. Die beiden Holzfossilien wurden im 19. Jahrhundert in tertären Schichten Brasiliens gesammelt. Die Feinstruktur ist weitgehend ähnlich und vergleichbar mit der der rezent verbreiteten Gattungen *Matisia* und *Crudia*. Erwähnenswert ist der Nachweis von Ziegelzellen in den Holzstrahlen von *M. brasiliense*. Diese phylogenetisch interessante Zellstruktur ist unter den heutigen Gehölzarten nur bei 1% der Taxa nachweisbar. Hölzer der Gattungen *Matisia* und *Crudia* zeigen die größte Übereinstimmung mit den beiden Fossilresten. Diese Bäume wachsen in neotropischen Regenwäldern und sind wirtschaftlich von geringer Bedeutung.

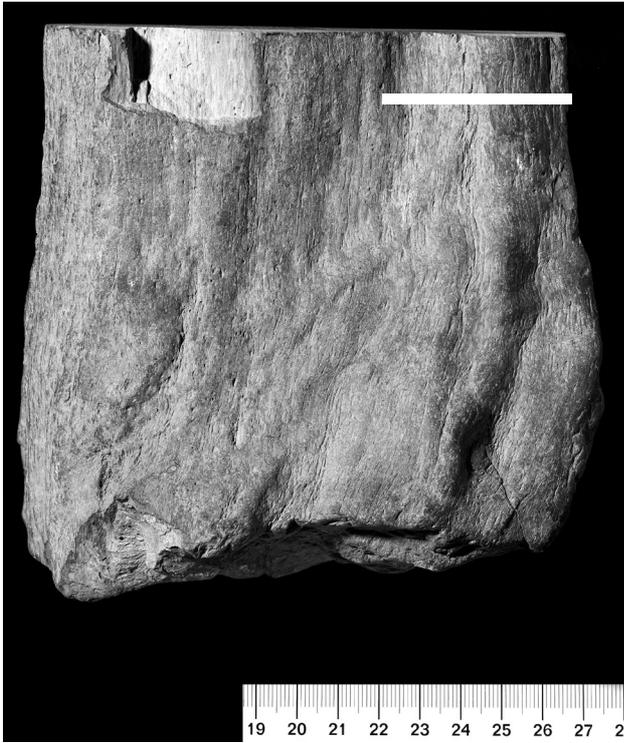
**Schlüsselwörter:** Brasilien, Bombacaceae KUNTH, Caesalpiniaceae R. BROWN, Malvales DUMORTIER, Holzanatomie, Laubbäume, Tertiär, Anatomie.

## 1. Introduction

Wood anatomical analysis has long since proven to represent an important tool in the reconstruction of ancient forest vegetation. In addition to providing a wealth of features significant in fossil plant taxonomy, wood anatomical data may also be useful with regard to paleoecological considerations. Silicified dicotyledonous wood, including stems up to 2 m long, are known to occur in various Tertiary localities in South America, e.g., Brazil, Columbia, and northern Peru. The fossil record of dicotyledonous wood includes *Carinianoxylon* SELMEIER from Brazil, *Anacardioxylon* FELIX, *Goupioxylon* G. SCHÖNFELD, *Guttiferoxylon* MIRIONI, *Leguminoxylon* K. M. GUPTA, and *Terminalioxylon* G. SCHÖNFELD from Columbia, and *Crudioxylon* PONS from Peru, among other taxa. A second type of dicot wood from Peru may represent a member of the Bombacaceae; PONS (1988) states that this fossil is "...clearly related to the South American Malvales, which are known with certainty since Palaeocene time". Although a fairly large number of studies on silicified wood from South America has been published to date (e.g., MILANEZ 1935; SCHÖNFELD 1947; PONS 1980, 1988; SELMEIER 2003), our knowledge about the species inventory, diversity, and paleoecology of the Tertiary forests of South America remains incomplete. Thus, every new silicified wood specimen represents a significant piece of information with regard to the characterization of these forests that deserves thoughtful consideration.

In this paper, the anatomy of two additional species of silicified wood from Tertiary deposits of South America is described. The Bavarian State Collection of Palaeontology and Geology houses an old collection of more than 20 specimens of permineralized wood from northeastern Brazil (region Rio Paranaíba) that was assembled by VON LUEDERS, Germany, during the second part of the 19<sup>th</sup> century. The collector eventually donated the specimens to the palaeobotanist Prof. MÄGDEFRAU during the mid 1950s. The old label that is attached to one of the original boxes provides only vague information about the locality where the fossils had been discovered. (cf. SELMEIER 2003). Unfortunately, no detailed information could be obtained to date that permits the exact determination of

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**Textfigure 1:** *Matisianoxylon brasiliense* nov. gen. et sp., silicified stem portion from Rio Paranaíba, BSP 1964 XXV 40; stem height 14 cm, tangential 13 cm, radial 4,5 cm, weight 2 kg.

the locality, stratigraphic occurrence or geological age of VON LUEDERS' collection.

One specimen described in this paper, *Matisianoxylon brasiliense* (family Malvaceae JUSS. *s. l.*), possesses distinct tile cells, and represents only the second record of a wood attributable to the order Malvales DUMORTIER from South America. The other specimen represents a new species of *Crudioxylon* PONS (family Caesalpinaceae R. BROWN). ALVES & ANGYALOSSY-ALFONSO (2000) have analyzed and compared the anatomical wood structure of trees from the 22 most representative families (133 genera) in extant Brazilian forests. However, these authors did not include *Matisia* and *Crudia* in their study.

## 2. Material and Methods

The two specimens examined are preserved as silicified cellular permineralisations. A diamond saw was used to cut thick sections (wafers) of transverse, longitudinal tangential and radial surfaces. The sections were then ground with a Logitech Lapp & Polish LP 50 (Edinburgh, Scotland) grinding machine until they were thin enough to permit analysis of the anatomical details by transmitted light microscopy (cf. HASS & ROWE 1999). The description of the fossils generally follows the list of microscopic features for hardwood identification as recommended by the IAWA Committee (1989). Photo documentation was accomplished with Zeiss Ultraphot analog camera. Images were processed, and plates and textfigures were constructed using Adobe Photoshop 5.5.



**Textfigure 2:** *Matisianoxylon brasiliense* nov. gen. et sp., cross section. Unpolished cut surface with conspicuous wood structure with multiseriate rays; tangential length 13 cm, radial 4,5 cm; BSP 1964 XXV 40.

## 3. Systematic Paleontology

### 3.1 *Matisianoxylon brasiliense* nov. gen. et sp.

Order Malvales DUMORTIER, 1829

Family Malvaceae JUSS., 1789 *sensu lato* (cf. BEYER et al. 1999; JUDD & MANCHESTER 1998)

**Aforehand comment:** According to BEYER et al. (1999) and JUDD & MANCHESTER (1998), an expanded concept of the Malvaceae *s. l.* includes the former families Bombacaceae KUNTH, Malvaceae *s. str.* JUSS., Sterculiaceae VENT., and Tiliaceae JUSS. All extant and fossil genera that have previously been attributed to these families are now accommodated in one broadly circumscribed family, the Malvaceae *sensu lato*.

Genus *Matisianoxylon* nov. gen.

**Generic diagnosis:** Growth rings indistinct. Vessel arrangement diffuse-porous, vessels exclusively solitary, evenly distributed without distinct pattern, mean tangential diameter 200 µm, simple perforation, intervessel pits alternate, 2-5 pores per square mm. Fibres non-septate, fibre-tracheids with bordered pits. Axial parenchyma banded, finely reticulated. Ray of two different sizes, uniseriate and multiseriate up to 25 cells wide, large rays up to 10 mm high, heterocellular composition with tile cells of the intermediate type (MANCHESTER & MILLER, 1978).

Type species: *Matisianoxylon brasiliense* SELMEIER

Species *Matisianoxylon brasiliense* nov. sp.

Pl. 1, Figs 1-4; Pl. 2, Figs 1-4; Textfigs 1-5

**Holotype:** BSP 1964 XXV 40. The holotype, including six thin sections, is deposited in the Bavarian State Collection of Palaeontology and Geology, Munich (Germany).

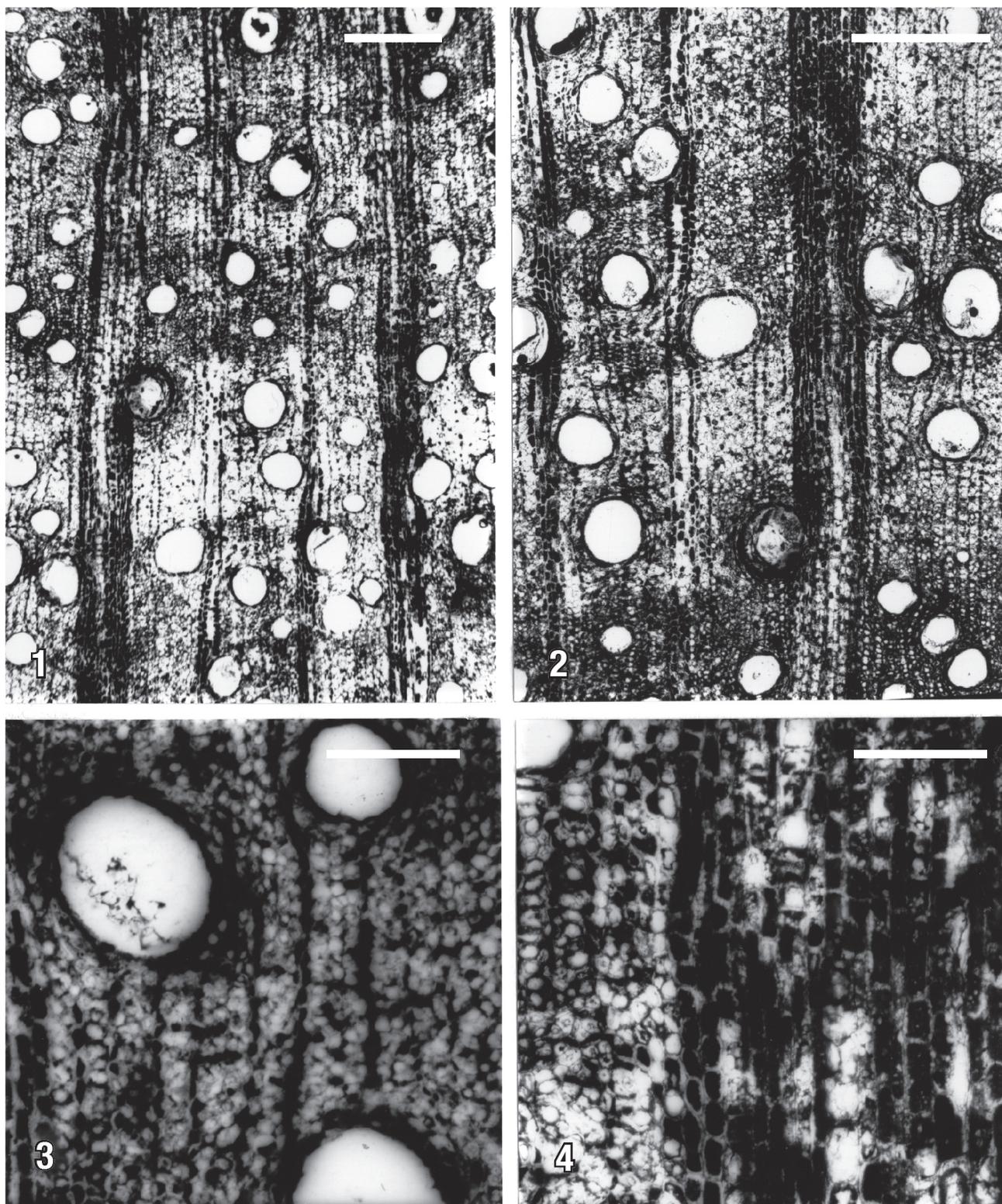


Plate 1: *Matisianoxylon brasiliense* nov. gen. et sp. from the Tertiary of Brazil; BSP 1964 XXV 40.

Fig. 1: Cross section. Rays and evenly distributed exclusively solitary vessels, shape rounded to oval; scale bar = 500  $\mu$ m, x 35.

Fig. 2: Cross section. Indistinctly growth ring boundary (middle), solitary vessels, rays and closely banded axial parenchyma (right below); scale bar = 500  $\mu$ m, x 50.

Fig. 3: Cross section. Uniseriate rays with banded axial parenchyma and ground tissue; scale bar = 200  $\mu$ m; x 120.

Fig. 4: Cross section. Cellular composition of a large ray; scale bar = 200  $\mu$ m, x 120.



**Textfigure 3:** *Matisianoxylon brasiliense* nov. gen. et sp., tangential section. Fibre-tracheids with distinctly bordered pits and crossed apertures; scale bar = 100  $\mu$ m, x 250.

**Material:** Two silicified wood samples; length 22 cm, perimeter 32 cm (Textfigs 1, 2), the second wood 8 cm long. The colour of the cut surfaces is yellowish-brown; area of transverse section 3 x 5 cm.

**Diagnosis:** Growth rings indistinct; vessels diffuse-porous, evenly distributed, exclusively solitary (100%), small and large vessels next to each other, range of tangential diameter 68-390 (mean 208)  $\mu$ m, simple perforation, intervacular pits alternate, 2-5 solitary vessels per square mm; fibres non-septate, fibre-tracheids with bordered pits; axial parenchyma banded and finely reticulate forming short discontinuous tangential lines; rays of two sizes, uniseriate rays with upright cells, large rays up to 25 cells wide, height up to 10 mm, partly with elongated margins and tile cells of the intermediate type.

**Locality:** Upper to middle reaches of Rio Paranaíba, southeastern part of the state of Maranhão, Brazil.

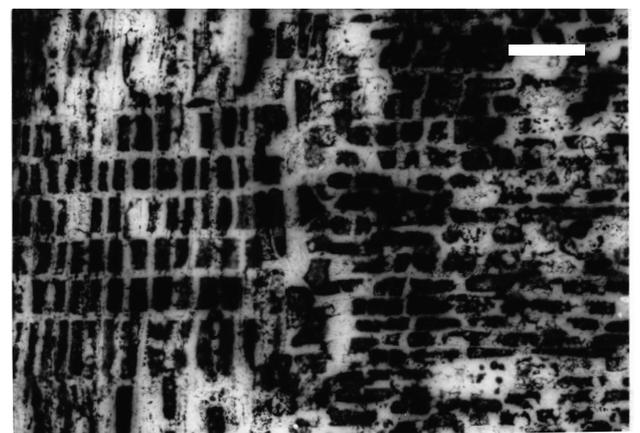
**Age:** Tertiary sediments. No further information available.

**Description:** Secondary xylem of dicotyledonous wood without bark or pith. Growth rings indistinct, more or less marked by 3-(4) radially flattened fibres that are recognizable by swollen, *Platanus*-like, multiseriate rays, presumably positioned at growth ring boundaries. Vessel arrangement diffuse-



**Textfigure 4:** *Matisianoxylon brasiliense* nov. gen. et sp., radial section. Multiseriate ray with heterocellular composition, procumbent (right below) and so-called tile cells; BSP 1964 XXV 40; scale bar = 1 mm, x 25.

porous, exclusively solitary, evenly distributed, but lacking a distinct pattern (Pl. 1, Figs 1-2), vessels round to oval in outline; mean tangential diameter 208  $\mu$ m (range: 68-390  $\mu$ m), oval vessels radial up to 435  $\mu$ m, small and large vessels next to each other, e.g., pores with tangential diameter of 68, 135, and 243  $\mu$ m side by side in 1 mm tangential; mean vessel element length 540  $\mu$ m (range: 472-675  $\mu$ m); simple perforation plates; intervacular pits crowded, alternate, about 6  $\mu$ m; 2-5 (mean 3,8) vessels per square mm. Fibres non-septate, polygonal in



**Textfigure 5:** *Matisianoxylon brasiliense* nov. gen. et sp., radial section. Multiseriate ray with so-called tile cells (left) and procumbent cells (right); BSP 1964 XXV 40; scale bar = 200  $\mu$ m, x 75.

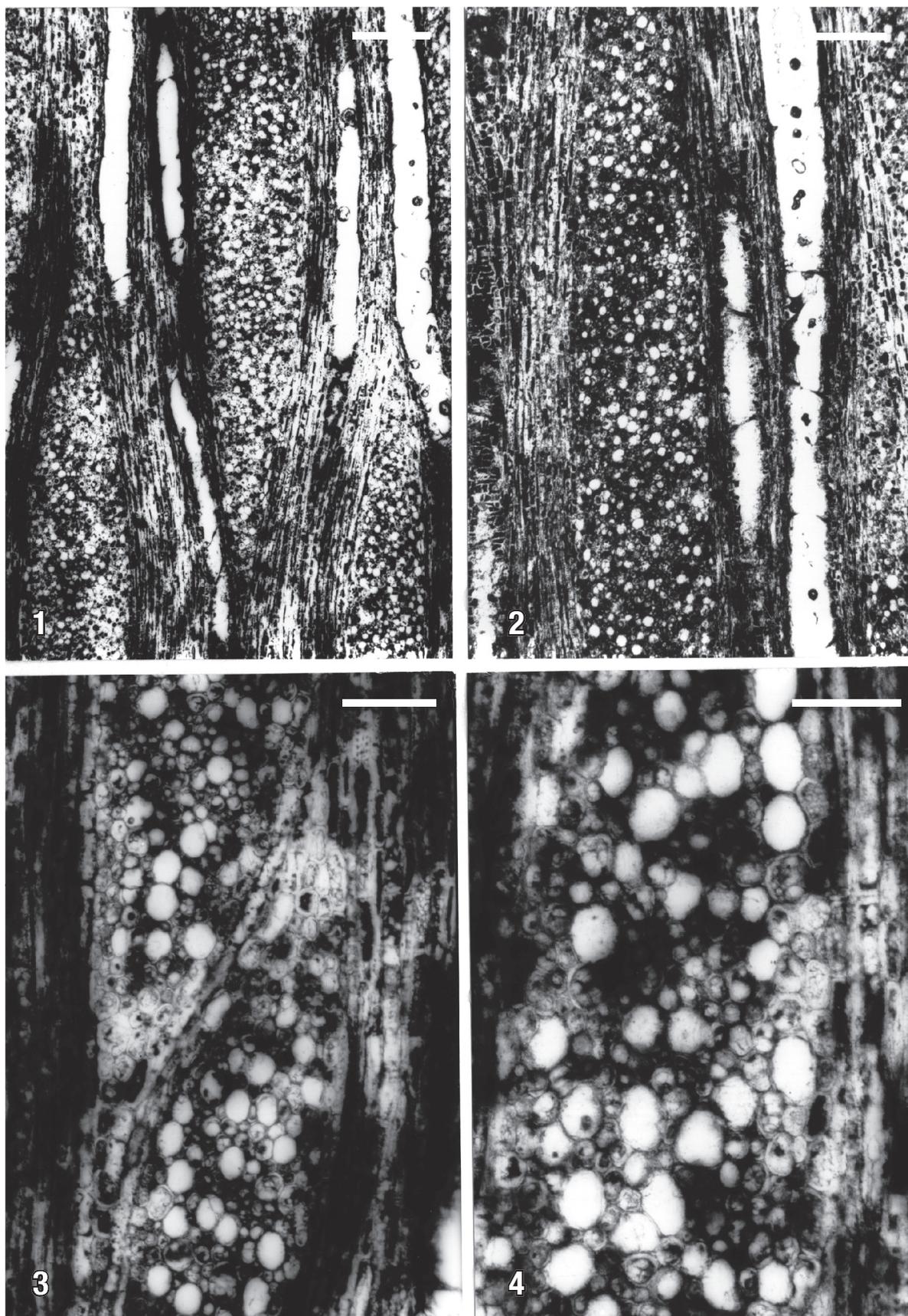


Plate 2: *Matisianoxylon brasiliense* nov. gen. et sp. from the Tertiary of Brazil; BSP 1964 XXV 40.

Fig. 1: Tangential section. Large *Platanus*-like rays; scale bar = 1 mm, x 15.

Fig. 2: Tangential section. Multiserial ray separated by vessel elements from three smaller rays (right); scale bar = 500  $\mu$ m, x 30.

Fig. 3: Tangential section. Marginal ends of two large rays with distinct heterocellular composition; scale bar = 300  $\mu$ m, x 60.

Fig. 4: Tangential section. Heterocellular composition with so-called tile cells in the middle part of a multiserial ray; scale bar = 200  $\mu$ m, x 105.

Microscopic features	<i>Matisia</i> spp.	<i>Matisianoxydon brasiliense</i>
<b>Growth rings</b>	indistinct	indistinct
<b>Vessels</b>	diffuse-porous	diffuse-porous
arrangement	solitary and multiples	exclusively solitary
tangential diameter	100-200 µm	68-390 µm, mean 208 µm
perforation plates	simple	simple
intervessel pits	alternate	alternate
<b>Fibres</b>	non-septate	non-septate
	thin- to thick-walled	rather thick-walled
	pits present	pits present
<b>Axial parenchyma</b>	abundant	abundant
	banded, finely reticulate	banded, finely reticulate
	some cells vasicentric	faintly vasicentric
<b>Rays</b>	uni- and multiseriate	uni- and multiseriate
width, large rays	commonly >10-seriate	up to 25 cells wide
composition	procumbent and tile cells	procumbent and tile cells
height	up to 10 mm	up to 10 mm
storied structure	absent	absent

**Table 1:** Comparison of anatomical features of *Matisia cordata*, *M. dolichosiphon*, *M. obliquifolia*, and *M. ochrocalyx* (RECORD 1939; METCALFE & CHALK 1950 with *Matisianoxydon brasiliense* from the Tertiary of Brazil.

cross section, diameter (21)-35-40 µm, partly thick-walled, 8-9 µm; fibre-tracheids with bordered pits (Textfig. 3), and crossed apertures, diameter 9-11 µm. Axial parenchyma abundant, banded and finely reticulate (Pl. 1, Fig. 3), bands 1-(2) cells wide, apotracheal banded parenchyma forming short discontinuous tangential or oblique lines; radial distance of bands 65-90 µm; axial parenchyma scantely, paratracheal with some cells. Rays of two distinct sizes (Pl. 1, Fig. 4; Pl. 2, Figs 1, 2): (a) uniseriate and homocellular, and (b) rays >10-seriate and heterocellular; multiseriate rays vary greatly in width and height, up to 25 cells wide, height up to 10 mm with more than 200 cells, often with uniseriate margins, large rays heterocellular with tile cells of the intermediate type (MANCHESTER & MILLER 1978). Cellular composition in tangential section: procumbent and oval-rounded to upright tile cells are scattered throughout the ray (Pl. 2, Figs 3, 4), procumbent cells in tangential section 21-34 µm, tile cells vertically in radial section up to 116 µm high, radial 37-58 µm (Textfigs 4, 5); uniseriate rays with upright cells (e.g., 8-11 cells); in some areas the height of uniseriate rays cannot be determined with certainty due to incomplete preservation of the longitudinal sections; 10-14 uniseriate rays per mm tangential. Storied structure is absent.

#### Synopsis of microscopic features:

- a) IAWA COMMITTEE (1989): 2, 5, 9, 13, 22, 25, 43, 46, 53, 66, 68, 69, 70, 76, 78, 86, 87, 99, 102, 103, 111.  
b) Fossil Wood Datasheet for Species (WHEELER 1991a, 1991b): 42, 45, 55, 56, 63, 65, 71, 84, 92, 94, 98, 101, 102, 106, 111.

Comparison with extant taxa: A single anatomical feature does not normally suffice to identify a group of taxa, e.g., the Malvales. Four families within the Malvales (Malvaceae *s. l.*, cf. WHEELER & MANCHESTER 2002: p. 92) possess an

unusual, special type of ray cellular composition that includes so-called tile cells (IAWA COMMITTEE 1989: feature 111). Tile cells occur in only 1% of the 342 families of woody plants that exist on Earth today. Wood samples that show unusual microscopic features in combination with characters of widespread occurrence can easily be identified (WHEELER & BAAS 1998). The ray cell dimorphism involving tile cells is clearly recognizable in the fossil described here, especially in radial and tangential sections. Wood with dimorphic ray structure occurs in many vines and lianas, but has also been reported for non-climbing plants (e.g., CARLQUIST 2001). Many woody representatives in the Malvales are upright, self-supporting shrubs or trees (METCALFE & CHALK 1950). The co-occurrence of (a) tile cells, (b) extremely large rays (i.e. up to 10 mm high and 25 cells wide), and (c) solitary vessels with simple perforation plates indicates that the affinities of this fossil lay within the genus *Matisia*, a member of the Bombacaceae (now included in the Malvaceae *s. l.*).

The Bombacaceae is a pantropic angiosperm family that includes approximately 31 genera with 250 species; among these are well-known trees such as *Adansonia* L. (baobab), *Ceiba* MILL. (kapok), *Durio* ADANS. (durian), and *Ochroma* SW. (balsa). Most members of this family, however, are not commercially used, and thus remain poorly investigated, despite the fact that they may represent important elements of primary lowland tropical forests of the New World. The genera *Matisia* HUMB. et BOUPL. and the anatomically very similar *Quararibea* AUBL. comprise a total of at least 60 species of large trees (ALVERSON 1989). *Matisia* is most common in the Amazon basin, but also found in Panama and Costa Rica.

The wood anatomy of *Matisia* and Bombacaceae has been described by RECORD & HESS (1937), RECORD (1939), METCALFE & CHALK (1950), MAINIERI (1958), DÉTIENNE et al. (1983), MILLER (1991), and SOLERA STEELER et al. (1998). Since RECORD's

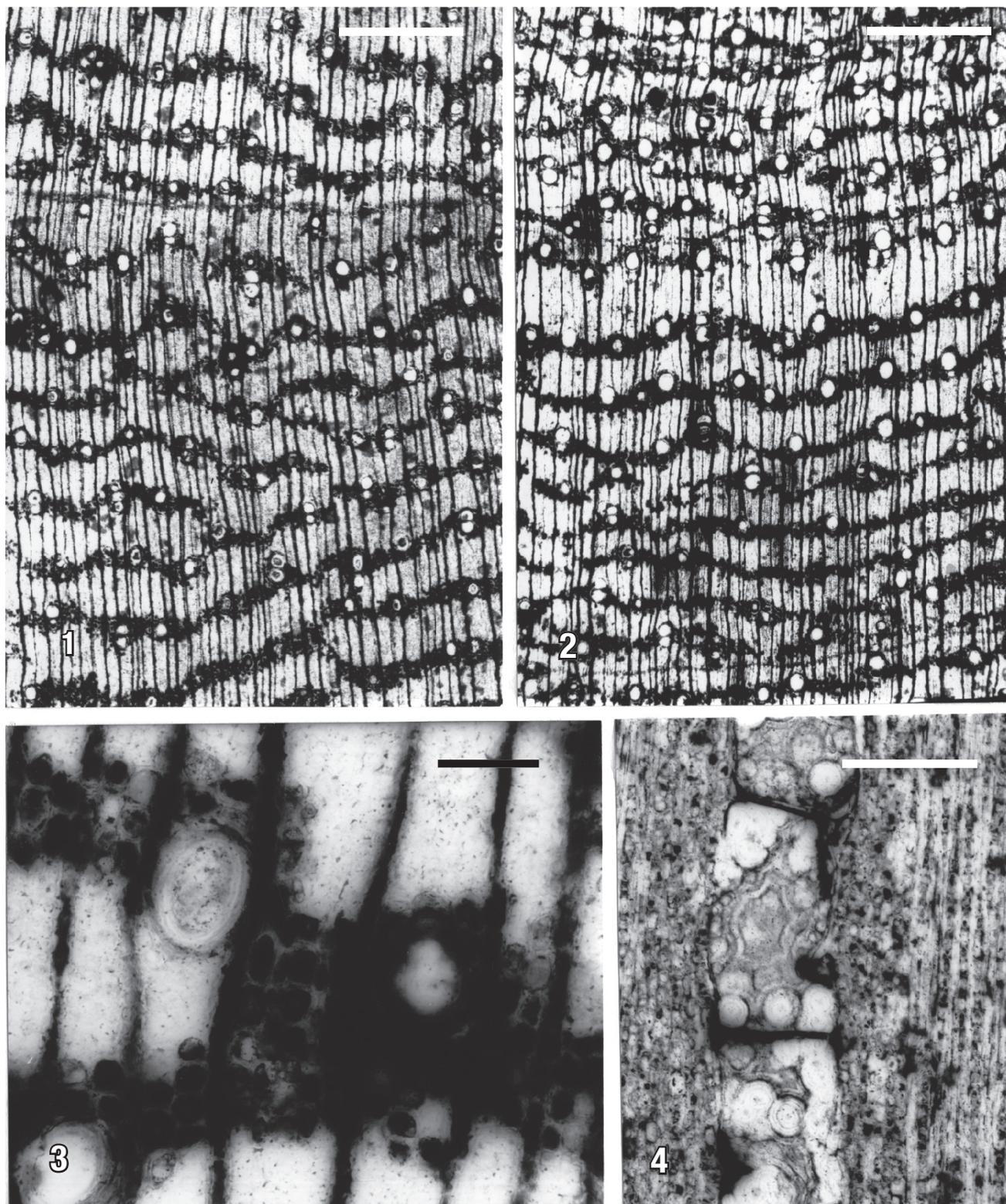


Plate 3: *Crudioxylon brasiliense* nov. sp. from the Tertiary of Brazil; BSP 1964 XXV 37.

Fig. 1: Cross section. Wavy axial parenchyma pattern, numerous small rays, indistinctly growth ring boundary; scale bar = 500  $\mu$ m, x 45.

Fig. 2: Cross section. Tangential axial parenchyma pattern with more or less included vessels and many small rays; scale bar = 500  $\mu$ m, x 45.

Fig. 3: Cross section. Dark axial parenchyma cells with included vessels, small rays, ground tissue decayed; scale bar = 100  $\mu$ m, x 180.

Fig. 4: Tangential section. Vessels elements with simple perforation, numerous uniseriate rays; scale bar 200  $\mu$ m, x 120.

work had been published in 1939, subsequent authors generally stated that no reliable basis exists for the discrimination of *Matisia* and *Quararibea* wood, i.e. the wood anatomical features of *Quararibea* are almost identical with those seen in *M. dolibosiphon* SCHUM., *M. obliquifolia* STANDL. and *M. ochrocalyx* SCHUM. The fossil from Brazil displays the closest similarity with *Matisia cordata* HUMB. et BOUPL., in particular with regard to the unusual ray structure: heterocellular composition with tile cells, >20 cells wide, up to 10 mm high (Tab. 1). Moreover, the fossil is characterized by exclusively possessing solitary vessels (counted and observed on a transverse section of an area 3 x 5 cm). Although there are currently 23 species (ALVERSON 1989) recognized within the genus *Matisia*, the wood anatomy has been detailed for only 4 or 5 of these species (Tab. 1). In addition to solitary vessels, however, these four species possess vessels in pairs and multiples. Thus, no extant taxon displays exactly the same complement of wood anatomical features as that recorded for the fossil.

Comparison with fossil taxa: In the last century, the Morerilla locality in South America (Bagua basin, northern Peru) has yielded a silicified Late Cretaceous wood; according to PONS (1988), this fossil is related to the Malvales. The multiseriate rays contain both procumbent and upright cells that are intermixed with vertically elongate cells similar to the tile cells of several members of the Bombacaceae (e.g., *Hampea* SCHLTDT., *Montezuma* DC., *Ochroma* Sw.) and Sterculiaceae (e.g., *Pterospermum* SCHREB.). However, the anatomy of the fossil from Morerilla is only briefly outlined, and a generic diagnosis or illustrations are not provided.

The here described *Matisia* wood from Brazil and the fossil from the Morerilla locality can be assigned to the South American Malvales with confidence. Since the fossil record of this group dates back into the Palaeocene (PONS 1988), tile cells, which have also been reported for fossil woods from the Tertiary of Oregon, USA (MANCHESTER & MILLER 1978; WHEELER & MANCHESTER 2002), and Germany (SELMEIER 1985), have obviously existed for a long time.

A comparison with *Matisia*-like fossil woods would be highly desirable; however, I am not aware of any reference to a fossil that displays a similar wood anatomy. Since the fossil described here clearly shows the wood structure of *Matisia*, it is assigned to a new form genus, for which the name *Matisianoxylon* nov. gen. is introduced.

### 3.2 *Crudioxylon brasiliense* nov. sp.

Order Fabales BROMHEAD, 1838

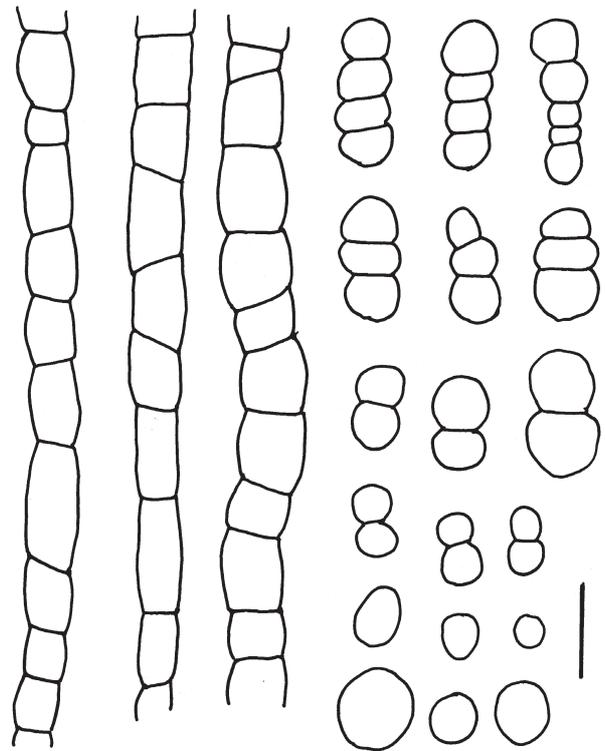
Family Caesalpiniaceae R. BROWN, 1814

Organ genus *Crudioxylon* PONS, 1980

Species *Crudioxylon brasiliense* n. sp.

Pl. 3, Figs 1-4; Pl. 4, Figs 1-4; Textfig. 6

Holotype: BSP 1964 XXV 37. The holotype, including 8 thin sections, is deposited in the Bavarian State Collection of Palaeontology and Geology, Munich (Germany).



Textfigure 6: *Crudioxylon brasiliense* n. sp., tangential section (left), vessel elements, and simple perforation plates. Cross section (right), solitary vessels and radial multiples of two or more common; BSP 1964 XXV 37; scale bar = 150  $\mu$ m.

Material: A single silicified wood sample; length 21 cm, perimeter 37.5 cm. The cut surface is brown; area of transverse section 4.5 x 2.8 cm.

Diagnosis: Growth rings indistinct; vessels diffuse porous, solitary or in short radial rows, tangential diameter range from 42 to 122, mean element length 168  $\mu$ m, perforation plates simple, intervessel pits small and alternate; fibres non-septate; axial parenchyma banded, wavy and conspicuous, up to 4 cells wide; rays uniseriate, homocellular, sometime heterocellular (KRIBS-type III), mean ray height 348  $\mu$ m, 16-21 rays per mm; storied structure absent.

Locality: Upper to middle reaches of Rio Paranaiba, southeastern part of the state of Maranhao, Brazil.

Age: Tertiary sediments. No further information available.

Description: Secondary xylem of dicotyledonous wood without bark or pith. Growth rings absent or indistinct, locally a decrease in vessel diameter can be observed, 2-3 radially flattened fibres recognizable as faintly dark lines, terminal parenchyma presumably present. Vessel arrangement diffuse-porous (Pl. 3, Figs 1, 2), unevenly or evenly distributed, vessels solitary, paired, or in radial groups of three, sporadically four or five; vessel outline in cross section more or less circular to radially elliptical with straight contact faces (Textfig. 6); vessels predominantly surrounded by, or in contact with, dark bands of axial parenchyma; mean tangential diameter

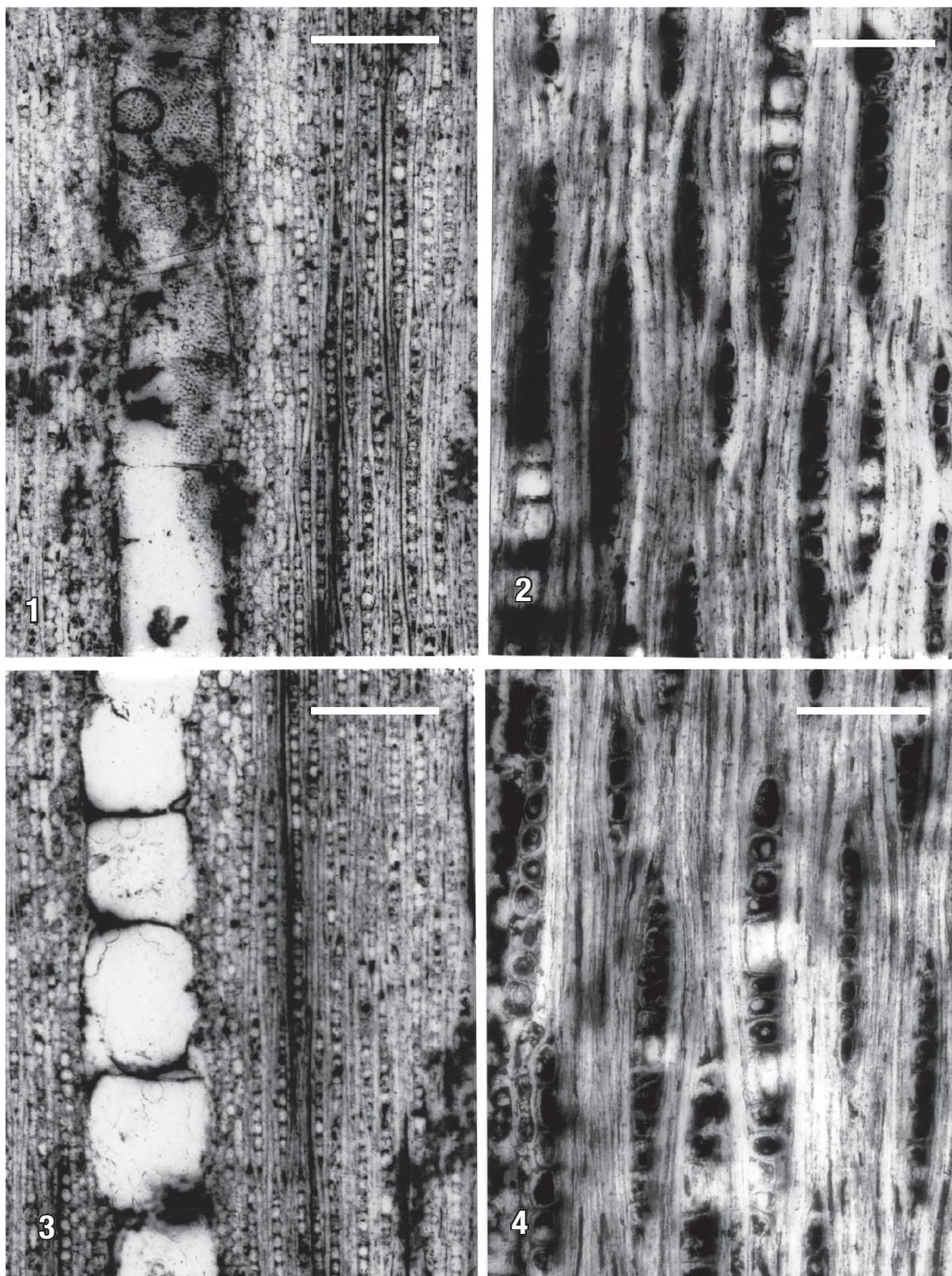


Plate 4: *Crudioxylon brasiliense* nov. sp. from the Tertiary of Brazil; BSP 1964 XXV 37.

Fig. 1: Tangential section. Vessel elements with alternate minute pits and numerous uniseriate rays; scale bar = 200  $\mu$ m, x 120.

Fig. 2: Tangential section. Heterocellular composition of rays with large upright and quadratic cells; scale bar = 100  $\mu$ m, x 230.

Fig. 3: Tangential section. Short vessel elements with horizontal simple perforation plates and numerous uniseriate rays; scale bar = 200  $\mu$ m, x 120.

Fig. 4: Tangential section. Uni- and twoseriate rays with translucent upright cells, pits on fibres not observed; scale bar = 100  $\mu$ m, x 230.

Microscopic features	<i>Crudioxylon pinalense</i> PONS	<i>Crudioxylon brasiliense</i>
<b>Growth rings</b>	indistinct	indistinct
<b>Vessels</b>	diffuse-porous	diffuse-porous
arrangement	solitary, radial multiples of 2-3-(8)	solitary, radial multiples of 2-3-(5)
tangential diameter	40-200 $\mu\text{m}$	42-122 $\mu\text{m}$ , mean 73 $\mu\text{m}$
perforation plates	simple	simple
intervessel pits	alternate	alternate
vessel elements	230-620 $\mu\text{m}$	74-286 $\mu\text{m}$ , mean 169 $\mu\text{m}$
vessels per $\text{mm}^2$	2-5-(7)	9-19, mean 14
<b>Fibres</b>	non-septate	non-septate
<b>Axial parenchyma</b>	abundant	abundant
	banded, wavy	banded, wavy
	vessels included or isolated	vessel included or isolated
	terminal parenchym	terminal parenchym
<b>Rays</b>		
width	1-2-(3)-seriate	1-2-seriate
composition	homo- or heterocellular	homo- or heterocellular
height	3-40 cells 80-800 $\mu\text{m}$	2-70 cells 208-1780 $\mu\text{m}$ , mean 552 $\mu\text{m}$
number per mm	10-13	16-21
storied structure	absent	absent

**Table 2:** Comparison of anatomical features of *Crudioxylon pinalense* (PONS 1980) with *Crudioxylon brasiliense* from the Tertiary of Brazil.

of vessels 73  $\mu\text{m}$  (range: 42-122  $\mu\text{m}$ ), radial diameter of pairs 42-202  $\mu\text{m}$ , of multiples with three (125-196  $\mu\text{m}$ ), with four (191-235  $\mu\text{m}$ ), with five (240-265  $\mu\text{m}$ ); vessel frequency 9-19 (mean 14), when each vessel is counted separately (as suggested by WHEELER 1986); wall thickness approximately 7  $\mu\text{m}$ ; perforation plates simple (Pl. 3, Fig. 4; Pl. 4, Figs 1, 3; Textfig. 6), mean vessel element length 169  $\mu\text{m}$  (range: 74-286  $\mu\text{m}$ ); intervessel pits crowded and alternate, polygonal in outline, slit-like apertures 4-5  $\mu\text{m}$ , vessel-ray pits not preserved; some pores in cross section with yellow or dark deposits. Fibres non-septate, forming the ground tissue of the wood, 2-9 rows between two rays, diameter of fibres in transverse section 12-25  $\mu\text{m}$ , approximately 3.5  $\mu\text{m}$  thick. Axial parenchyma abundant and conspicuous, paratracheal, confluent, wavy, more or less concentrically banded (Pl. 3, Figs 1-3), possesses tendency to form a reticulate pattern, locally diffuse, bands up to 4 cells wide, mean width of bands 84  $\mu\text{m}$  (range: 27-135  $\mu\text{m}$ ), diameter of individual cells in cross section 17-26  $\mu\text{m}$ , vertical length difficult to determine due to insufficient preservation of longitudinal sections, mean radial distance between two parenchyma bands, interrupted by ground tissue of fibres, 264  $\mu\text{m}$  (range: 63-445  $\mu\text{m}$ ). Rays predominantly uniseriate, homocellular to heterocellular (KRIBS-type III) with upright and quadratic cells, rare 2-seriate (Plate 4, Figs 2, 4); ray height 208-1780 (mean 552)  $\mu\text{m}$ , e.g., 34 (2 cells)  $\mu\text{m}$ , 207 (10 cells)  $\mu\text{m}$ , 345 (19 cells)  $\mu\text{m}$ , 896 (52 cells)  $\mu\text{m}$ , 1694 (72 cells)  $\mu\text{m}$ ; heterocellular rays composed of procumbent (vertical 17-22  $\mu\text{m}$ ) and 1-2 translucent large upright (vertical 40-55  $\mu\text{m}$ ) or square cells; crystals not observed, many procumbent ray cells contain dark deposits; 16-21 rays per mm tangential. Storied

structure is absent.

Synopsis of microscopic features:

a) IAWA COMMITTEE (1989): 2, 5, 10, 13, 25, (29), 41, 42, 53, 62, 66, (70), (76), 79, 83, 86, 96, 104, 109, 116.

b) Fossil Wood Datasheet for Species (WHEELER 1991a, 1991b): 42, 45, 54, 62, 65, 71, 80, 84, 87, 92, 95, 103, 104, 106, 107, 114.

Comparison with extant taxa: The most important feature of this fossil is the wavy and distinctly banded axial parenchyma, visible already with the naked eye. According to METCALFE & CHALK (1950), various types of banded parenchyma occur in different variations in 84 families of extant woody plants. PONS (1980: p. 172) lists 54 angiosperm families that display parenchyma patterns similar to that seen in the fossil wood from Brazil. However, only in certain members of the Leguminosae (Caesalpinaceae), this parenchyma pattern co-occurs with other characteristic microscopic features of the fossil, including vessels that are solitary or in radial multiples of 2-4, short vessel elements, simple perforation plates, minute intervessel pits, vessels that are more or less surrounded by axial parenchyma, numerous rays that are uniseriate, homocellular, or heterocellular.

The following descriptions and/or microphotographs of the wood of extant Caesalpinaceae have been used to compare with the fossil: BOUREAU (1957), BRAZIER & FRANKLIN (1961), CARLQUIST (2001), GOTTWALD (1958), GREGORY (1994), HESS (1948), ILIC (1991), MÜLLER-STOLL & MÄDEL (1967), (NEUMANN & SCHOCH et al. 2001), WAGENFÜHR & SCHEIBER (1985), and



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