Charcoal anatomy of Brazilian species. II. 15 native species occurring in Atlantic or Amazon rainforest

NATACHA R. DE SOUZA-PINTO & RITA SCHEL-YBERT

Abstract: Anthracology is the identification of charcoal remains through wood anatomy. Paleoecological and paleoethnobotanical evidence from anthracological studies provides information on past environments as well as the fuel economy and use of plants by those living in ancient societies. Historical ecology and forest conservation can also accrue from findings in anthracological studies. Charcoal identification must rely on adequate reference material, in particular reference collections and descriptions of charcoal anatomy. This paper presents charcoal anatomy descriptions of fifteen Brazilian native species that occur in the Atlantic Forest and the Amazon Rainforest. The charcoal anatomy of six of these species is here described for the first time. Samples were analyzed under a reflected light microscope; the descriptions followed the procedures and terminology recommended by the International Association of Wood Anatomists. Increased knowledge of the charcoal and wood anatomy of native tropical species may improve taxonomic identification, thereby increasing accordingly the amount and quality of data for sociocultural inferences about past societies. In addition, it contributes to a better knowledge of the native flora, which helps to prevent deforestation and to drive more sustainable charcoal production chains.

Key words: anthracology, archeobotany, paleoecology, wood anatomy, nature conservation.

INTRODUCTION

Archeology, the study of past human societies, has many fields of specialization. In one of them, archeobotany (paleoethnobotany), the botanical remnants from archeological sites are studied to investigate the interrelations between humans and plants in ancient societies (Ford 1989). Archeobotanists recover (from fieldwork) and analyze (in the laboratory) micro- and macro-botanical remains. Phytoliths, starch grains, and pollen are the main types of plant micro-remains. Seeds, nuts, underground organs, and charcoal are the principal macro-remains. Botanical analysis, description, and identification of these remains are followed by social and cultural interpretations of the uses that the plants from which they originated might have had within each particular society in the past (Ford 1989, Scheel-Ybert 2016a).

Charcoal remains are the object of study of anthracology. Charcoal identification, based on wood anatomy, provides information on the environment, fuel economy, and the use of plants of ancient societies (Scheel-Ybert 2020). The identification of plant species based on the analysis of charred remains has been done since the 19th century, but anthracology developed as a scientific field from the 1970s in Europe. Brazilian anthracology began in the late 20th century, with the establishment of the first charcoal collection of tropical species in 1994.
European anthracology focuses mainly on paleoecological data. In Brazil, both paleoecological and paleoethnobotanical inferences are based as much as possible on the same samples. Different studies have shown that these two interpretative lines are not incompatible and can be deduced from the same material (Scheel-Ybert 2004, 2020). These interpretations, however, depend on accurate charcoal identifications, which must rely on adequate reference material – especially comparative collections and studies of charcoal anatomy (Scheel-Ybert 2020).

To contribute to the effort of providing adequate reference material to such studies, and therefore improving the quality of charcoal determination, this paper presents descriptions of charcoal anatomy for 15 Brazilian native species that occur in the Atlantic Forest or the Amazon Rainforest. Besides its importance for archeological research, it may be useful for many other scientific areas that are also interested in charcoal anatomy and identification, such as botany, ecology, paleoecology, paleobotany, forest science, and geology (Scheel-Ybert 2016b).

**MATERIALS AND METHODS**

For this study, 28 wood samples of 15 species from 12 families native to Brazil were described: *Anemopaegma prostratum* DC. (Bignoniaceae), *Cordia ecalyculata* Vell. (Boraginaceae), *Kielmeyera coriacea* Mart. & Zucc., *Kielmeyera excelsa* Cambess. (Calophyllaceae), *Terminalia glabrescens* Mart. (Combretaceae), *Bauhinia forficata* Link, *Copainera langsдорfii* Desf., *Copainera trapezifolia* Hayne, *Peltophorum dubium* (Spreng.) Taub. (Fabaceae Caesalpinioideae), *Anadenanthera colubrina* var. *cebil* (Griseb.) Altschul (Fabaceae Mimosoideae), *Bowdichia viriloides* Kunth., *Dalbergia nigra* (Vell.) Allemão ex Benth. (Fabaceae Papilionoideae), *Mouriri chamussoana* Cogn. (Melastomataceae), *Myrcia minutiflora* Sagot. (Myrtaceae), and *Qualea grandiflora* Mart. (Vochysiaceae). These species were selected because they are representative of forest formations in areas of important precolonial occupation.

Wood samples were obtained through field sampling (by R Scheel-Ybert [RS] and ME Solari [ME]) and donations from institutional wood collections: *Instituto de Pesquisas Tecnológicas do Estado de São Paulo* (BCTw), *Instituto de Botânica de São Paulo* (SPw), *Jardim Botânico do Rio de Janeiro* (RBw), *Instituto Florestal de São Paulo* (SPSFw). For carbonization, samples were wrapped in aluminum foil and charred in a muffle furnace at 400 °C for 40 minutes. All samples are deposited in the charcoal collection of the National Museum in Rio de Janeiro (*Antracoteca do Museu Nacional, UFRJ – Laboratório de Arqueobotânica e Paisagem, Universidade Federal do Rio de Janeiro*) (cf. Scheel-Ybert 2016b). Collection information is provided according to the herbaria or wood collections label data, including voucher number when available (a wood sample’s voucher consisting of the herbarium specimen of vegetative and reproductive structures that allowed the individual taxonomic identification).

For the microscopic analysis, the charcoal samples were manually split along the three wood structural sections: transversal, longitudinal tangential, and longitudinal radial. Samples were analyzed under a reflected light brightfield/darkfield microscope at 50x to 1000x magnification. The descriptions followed the procedures and terminology recommended by the International Association of Wood Anatomist (IAWA Committee 1989), except for intervessel pits size, for which the internal horizontal diameter of pits apertures was
measured (Scheel-Ybert & Gonçalves 2017). Arithmetic means and amplitude (minimum and maximum values) are given for quantitative measurements. Micrographs were obtained using a JEOL 6300F SEM from University Montpellier (France); specimens were sputter-coated with platinum. Numbers between parentheses in the anatomical descriptions correspond to codes for the definitions of wood anatomical characters described by the IAWA Committee (1989).

Data regarding vernacular names, geographical distribution, ecological features and uses for each one of the analyzed species, provided in Table I, were retrieved from the specialized literature, from the internet, and from the List of Species of the Brazilian Flora (JBRJ 2012).

RESULTS

The anatomical descriptions for each one of the analyzed species are presented below. A synthesis of the quantitative and some qualitative data is provided in Table II.

**BIGNONIACEAE – Anemopaegma prostratum DC.** (Figure 1 a-b-c)

**Material studied:** BRASIL: São Paulo, Araraçá, SP, junto à Caixa d’água. F.C. Hoehne. voucher SP1826 (SPw731).

**Growth rings:** distinct (1); boundaries marked by thick-walled and radially flattened fibers in latewood.

**Vessels:** wood diffuse-porous (5), in random arrangement; solitary (85,8%) and in multiples; solitary vessel outline circular to oval; vessels of two distinct diameter classes, wood not ring-porous (45); larger vessels tangential diameter 162 (80-300) µm (42); 18 (11-6-23,3) vessels/mm² (47); perforation plates simple (13); intervessel pits alternate (22); non-vestured, aperture diameter 4,8 (2-6) µm; vessel-ray pits similar to intervessel pits in size and shape throughout the ray cell (30).

**Axial parenchyma:** scanty paratracheal (78); 1-3 cells per parenchyma strand (91).

**Rays:** 5-6-(8) seriate (98); 4,7 (4-6) rays/mm (115); ray height 1-2 mm (102); rays of two distinct sizes (uni and multiseriate) (103); multiseriate rays with procumbent, square, and upright cells mixed throughout the ray (109), uniseriate rays with all ray cells upright and/or square (105).

**Fibers:** septate (65), thin- to thick-walled (69), with simple to minutely bordered pits (61).

**Mineral inclusions:** Prismatic crystals present (136).

**BORAGINACEAE – Cordia ecalyculata Vell.** (Figure 1 d-e-f)


**Growth rings:** absent or indistinct (2).

**Vessels:** wood diffuse-porous (5), in random arrangement; solitary (61,4%) and in multiples of 2 (29,8%), 3 (7%), and 4 (1,7%); solitary vessel outline angular (12); tangential diameter 81,2 (50-110) µm (41); 9,1 (6,7-13,5) vessels/mm² (47); perforation plates simple (13); intervessel pits alternate (22), with coalescent chambers probably due to carbonization, non-vestured, aperture diameter 12,8 (8-20) µm; vessel-ray pits similar to intervessel pits in size and shape throughout the ray cell (30).

**Axial parenchyma:** aliform (80), lozenge-aliform (81), and confluent (83); 2-3 cells per parenchyma strand (91-92).

**Rays:** 5-7 seriate (98); 6,5 (5-8) rays/mm (115); ray height 1-2 mm (102); sheath cells (110); body ray cells procumbent with mostly 2-4 rows of upright and/or square marginal cells (107), sometimes procumbent cells of variable width.

**Fibers:** septate (65), thin- to thick-walled (69), with simple to minutely bordered pits (61).
Table I. Supplementary data for the studied species (common names, geographical distribution, ecological data, phytogeographical domains, uses).

<table>
<thead>
<tr>
<th>Species</th>
<th>Common names</th>
<th>Geographical distribution</th>
<th>Ecological data / Phyto-geographical domains</th>
<th>Uses</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anemopaegma prostratum DC. (Bignoniaceae)</td>
<td>catuaba</td>
<td>Brazilian Northeast (Bahia), Southeast (Espírito Santo, Minas Gerais, São Paulo, Rio de Janeiro), South (Paraná, Rio Grande do Sul, Santa Catarina)</td>
<td>Native to Brazil, not endemic. Liana / Atlantic Forest</td>
<td>medicine: bark decoction (for treating impotence, agitation, nervousness, pain, weakness, memory loss)</td>
</tr>
<tr>
<td>Cordia ecalyculata Vell. (Boraginaceae)</td>
<td>chá-de-bugre</td>
<td>Brazilian Northeast (Bahia), Center-West (Mato Grosso do Sul), Southeast (Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo), South (Paraná, Rio Grande do Sul, Santa Catarina)</td>
<td>Native to Brazil, not endemic. Tree / Atlantic Forest</td>
<td>medicine: tannins are reported to have thermogenic and healing properties and to reduce appetite</td>
</tr>
<tr>
<td>Kielmeyera coriacea Mart. &amp; Zucc. (Calophyllaceae)</td>
<td>pau-santo</td>
<td>Brazilian North (Amazonia, Pará, Rondônia, Tocantins), Northeast (Bahia, Maranhão, Piauí), Center-West (Distrito Federal, Goiás, Mato Grosso do Sul, Mato Grosso), Southeast (Minas Gerais, São Paulo), South (Paraná)</td>
<td>Native to Brazil, not endemic. Tree, Shrub, Liana / Amazon Rainforest, Cerrado</td>
<td>medicine: essence (for treating skin and muscle diseases); wood ashes (for treating external wounds); bark decoction (for treating stomach disorders)</td>
</tr>
<tr>
<td>Kielmeyera excelsa Cambess. (Calophyllaceae)</td>
<td>pau-santo</td>
<td>Brazilian Southeast (Rio de Janeiro)</td>
<td>Native to Brazil, endemic. Tree / Atlantic Forest</td>
<td>not known</td>
</tr>
<tr>
<td>Terminalia glabrescens Mart. (Combretaceae)</td>
<td>capitão, cerne-amarelo, garrote, maria-preta, pau-sangue</td>
<td>Brazilian North (Tocantins), Northeast (Alagoas, Bahia, Ceará, Maranhão, Piauí, Rio Grande do Norte), Center-West (Distrito Federal, Goiás, Mato Grosso do Sul, Mato Grosso), Southeast (Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo), South (Paraná)</td>
<td>Native to Brazil, not endemic. Shrub, Tree / Amazon Rainforest, Caatinga, Cerrado, Atlantic Forest</td>
<td>medicine: for treating infections of the female genito-urinary system, diarrhea, wounds, stomach pain, indigestion, gingivitis, intestinal infections, stomach ulcer, intestinal colic, constipation other uses: wood products (decorative coating and carpentry); non-wood products (beekeeping, handicrafts, ecological, ornamental)</td>
</tr>
<tr>
<td>Bouhinia forficata Link. (Fabaceae Caesalpinoideae)</td>
<td>pata-de-vaca</td>
<td>Brazilian Northeast (Alagoas, Bahia, Pernambuco), Southeast (Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo), South (Paraná, Rio Grande do Sul, Santa Catarina)</td>
<td>Native to Brazil, not endemic. Tree / Amazon Rainforest, Cerrado</td>
<td>medicine: leaf infusion (for treating bladder or kidney stones, diabetes, hypertension, hemophilia, anemia, obesity, heart diseases, urinary disorders)</td>
</tr>
</tbody>
</table>
Table I. Continuation

| Copaifera langsdorffii Desf. (Fabaceae Caesalpinioideae) | copaíba, bálsamo, caobi, copaúba, cupauá, pau-óleo | Brazilian North (Acre, Amazonas, Rondônia, Tocantins), Center-West (Distrito Federal, Goiás, Mato Grosso do Sul, Mato Grosso), Southeast (Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo), South ( Paraná, Rio Grande do Sul) | Native to Brazil, not endemic. Tree / Amazon Rainforest, Caatinga, Cerrado, Atlantic Forest | medicine: oleoresin (as antiseptic, healing, expectorant, diuretic, laxative, stimulant, emollient and tonic) other uses: wood is commonly used in carpentry; the tree trunk’s oleoresin is used for fuel |
| Copaifera trapezifolia Hayne (Fabaceae Caesalpinioideae) | copaíba, copuva, óleo, pau-óleo | Brazilian Northeast (Bahia, Pernambuco), Southeast (Minas Gerais, Rio de Janeiro, São Paulo), South ( Paraná, Santa Catarina) | Native to Brazil, not endemic. Tree / Atlantic Forest | medicine other uses: construction, charcoal, resin, honey production |
| Peltophorum dubium (Spreng.) Taub. (Fabaceae Caesalpinioideae) | angico-amarelo, cambuí, canafistula, farinha-seca, faveira, sobral, tamboril-bravo, guarucaia, ibirapuitá | Brazilian Northeast (Bahia, Paraíba, Pernambuco), Southeast (Minas Gerais, Rio de Janeiro, São Paulo), South ( Paraná, Santa Catarina) | Native to Brazil, not endemic. Tree / Cerrado, Atlantic Forest, Pantanal, Riparian Forests | medicine other uses: wood in carpentry, construction and shipbuilding; plant used for beekeeping, saponin and tanning substances |
| Bowdichia virgilioides Kunth. (Fabaceae Faboideae) | sucupira | Brazilian North (Amazonas, Amapá, Pará, Rondônia, Roraima, Tocantins), Northeast (Alagoas, Bahia, Ceará, Maranhão, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, Sergipe), Center-West (Distrito Federal, Goiás, Mato Grosso do Sul, Mato Grosso), Southeast (Espírito Santo, Minas Gerais, São Paulo), South ( Paraná) | Native to Brazil, not endemic. Tree / Amazon Rainforest, Caatinga, Cerrado, Pantanal | medicine: seeds infusion (for controlling body uric acid, tonsilitis, arthritis, asthma, gonorrhea, ovarian and uterus cysts, organic weakness, skin diseases, diabetes, sore throat, spasmodic pain, wounds, bleeding, inflammations, rheumatism, syphilis, worms); bark and seeds oil (in the treatment of arthritis and joint pains; reported to be tonic and to have anticancer action; root tubers (for diabetes)) |
| Dalbergia nigra (Vell.) Allemão ex Benth. (Fabaceae Faboideae) | jacarandá-da-baía, caviúna, graúna, jacarandá-cabiu, jacarandá-prego, jacarandá-uma, pau-preto | Brazilian Northeast (Alagoas, Bahia, Paraíba, Pernambuco, Sergipe), Southeast (Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo), South ( Paraná) | Native to Brazil, endemic. Tree / Atlantic Forest | other uses: wood commonly used in the manufacture of string instruments, pianos and luxury carpentry |
Anadenanthera colubrina var. cebil (Griseb.) Altschul (Fabaceae Mimosoideae)

**angico**

Brazilian Northeast (Bahia, Ceará, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, Sergipe), Center-West (Distrito Federal, Goiás, Mato Grosso do Sul, Mato Grosso), Southeast (Minas Gerais)

Native to Brazil, not endemic. Tree / Caatinga, Cerrado, Atlantic Forest

**medicine:** bark (as antiseptic, expectorant, stimulant, emollient, tonic) seeds (roasted and powdered, are snuffed for headaches and colds)

**other uses:** wood is commonly used in carpentry

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Mouriri chamissoana Cogn. (Melastomataceae)

**mandapuçá, guaramiririm-ripa**

Brazilian Northeast (Bahia), Southeast (Espírito Santo, Rio de Janeiro, São Paulo), South (Paraná, Santa Catarina)

Native to Brazil, endemic. Tree / Atlantic Forest

not known

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Myrcia minutiflora Sagot. (Myrtaceae)

**guamirim, camboi, cambium, camboi-bravo, pedra-ume, caá, uva**

Brazilian North (Pará, Amazonas, Acre, Amapá), Northeast (Maranhão), Center-West (Mato Grosso)

Native to Brazil, not endemic. Tree / Amazon Rainforest

not known

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Qualea grandiflora Mart. (Vochysiaceae)

**pau-terra, pau-terra-da-folha-grande, pau-terra-do-cerrado, cinheiro, pau-tucano**

Brazilian North (Pará, Amazonas, Acre, Northeast (Maranhão, Piauí, Ceará, Bahia), Center-West (Mato Grosso, Goiás)), Southeast (Minas Gerais, São Paulo), South (Paraná)

Native to Brazil, not endemic. Tree / Amazon Rainforest, Caatinga, Cerrado, Atlantic Forest

**medicine:** bark infusion (for diarrhea, inflammations, cramps)

**other uses:** dry fruits used in crafts; green fruits and roots used as yellow dye

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**Mineral inclusions:** Prismatic crystals present (136), in axial parenchyma cells (141/142), crystal sand frequent (153).

**CALOPHYLLACEAE – Kielmeyera coriacea** Mart. & Zucc. (Figure 1 g-h-i)

**Material studied:** BRASIL: prox. Luminárias, Minas Gerais. Carmen Regina Marcati (BCTw15140).

**Growth rings:** distinct (1); boundaries marked by thick-walled and radially flattened fibers in late wood, but the difference between late and early wood is tenuous and hardly observable.

**Vessels:** wood diffuse-porous (5), in random arrangement; solitary (76,8%) and in multiples of 2 (15,7%), 3 (3,1%), 4 (3,1%), and 5 (1%); solitary vessel outline circular to oval; tangential diameter 125,2 (90-180) μm (42); 12,2 (8,7-16,5) vessels/mm² (47); perforation plates simple (13); intervessel pits alternate (22), non-vestured, aperture diameter 7,4 (6-10) μm; vessel-ray pits larger than intervessel pits, borders much reduced to apparently simple, rounded (31) or horizontally elongate (32). Vascular or vasicentric tracheids present (60).

**Axial parenchyma:** in narrow bands up to three cells wide (86).

**Rays:** exclusively uniseriate (96); 4,1 (3-8) rays/mm (115); all ray cells upright and/or square (105), rays with procumbent, square, and upright cells mixed throughout the ray (109).

**Fibers:** non-septate (66), thin- to thick-walled (69), with simple to minutely bordered pits (61).
Table II. Synthesis of main qualitative and quantitative data for wood anatomical features of the studied species and number of individuals analyzed. (+)= present; (-)= absent

<table>
<thead>
<tr>
<th>Feature</th>
<th>Species</th>
<th>Vessels tangential diameter (µm)</th>
<th>Vessel frequency (vessels/mm²)</th>
<th>Tyloses</th>
<th>Intervessel pits (µm)</th>
<th>Rays width (number of cells)</th>
<th>Rays frequency (rays/mm)</th>
<th>Secretory elements</th>
<th>Crystals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Anemopaegma prostratum DC.</td>
<td>162 (80-300)</td>
<td>18 (11,6-23,314)</td>
<td>-</td>
<td>4,8 (2-6)</td>
<td>5-6 (8)</td>
<td>4,7 (4-6)</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Cordia ecalyculata Vell.</td>
<td>81,2 (50-110)</td>
<td>9,1 (6,7-13,5)</td>
<td>-</td>
<td>12,8 (8-20)</td>
<td>5-7</td>
<td>6,5 (5-8)</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Kielmeyera coriacea Mart. &amp; Zucc.</td>
<td>125,2 (90-180)</td>
<td>12,2 (8,7-16,5)</td>
<td>-</td>
<td>7,4 (6-10)</td>
<td>1</td>
<td>4,1 (3-8)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Kielmeyera excelsa Cambess.</td>
<td>107,6 (70-150)</td>
<td>5,5 (1,6-13,1)</td>
<td>+</td>
<td>8,6 (6-10)</td>
<td>1</td>
<td>9 (6-11)</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Terminalia glabrescens Mart.</td>
<td>107,4 (70-150)</td>
<td>14,6 (8,2-25,4)</td>
<td>+</td>
<td>5,5 (4-6)</td>
<td>1</td>
<td>9,1 (7-11)</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Bauhinia forficata Link.</td>
<td>87,0 (70-115)</td>
<td>15,0 (7,3-21,3)</td>
<td>+</td>
<td>4,1 (3-5)</td>
<td>3-5</td>
<td>8,2 (5,5-10)</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Copaifera langsdorffii Desf.</td>
<td>111,0 (70-170)</td>
<td>7,5 (5-11)</td>
<td>-</td>
<td>4,3 (3-6)</td>
<td>1-2</td>
<td>9,2 (6-14)</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Copaifera trapezifolia Hayne</td>
<td>78,0 (60-90)</td>
<td>11,5 (9-17)</td>
<td>+</td>
<td>4,8 (4-6)</td>
<td>(1)-2</td>
<td>8,3 (6-11)</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Peltophorum dubium (Spreng.) Taub.</td>
<td>119,9 (70-180)</td>
<td>3,4 (0-8)</td>
<td>-</td>
<td>4,6 (4-6)</td>
<td>1-2</td>
<td>10,3 (7-15)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Anadenanthera colubrina var. cebil (Griseb.) Altschul</td>
<td>87,6 (70-110)</td>
<td>13,4 (8,9-18,8)</td>
<td>+</td>
<td>5 (4-6)</td>
<td>1-3</td>
<td>7,6 (6-9)</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Bowdichia virgilioides Kunth.</td>
<td>110 (70-160)</td>
<td>7,2 (4-13,9)</td>
<td>-</td>
<td>8,4 (6-10)</td>
<td>1-2 (3)</td>
<td>8,4 (5-10)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Dalbergia nigra (Vell.) Allemão ex Benth.</td>
<td>131,9 (80-190)</td>
<td>3,4 (1-7,4)</td>
<td>+</td>
<td>6,2 (4-8)</td>
<td>1-2</td>
<td>14 (9-18)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Mouriri chamissoana Cogn.</td>
<td>77,6 (52-118)</td>
<td>14,0 (10,1-19,3)</td>
<td>-</td>
<td>6,1 (4,5-8)</td>
<td>1</td>
<td>5 (4-10,5)</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Myrcia minutiflora Sagot.</td>
<td>64,8 (50-90)</td>
<td>23,5 (18-27)</td>
<td>-</td>
<td>4,4 (3-6)</td>
<td>(3)-4 (5)</td>
<td>6,5 (5-9)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Qualea grandiflora Mart.</td>
<td>55,8 (30-80)</td>
<td>31,8 (22,9-37,7)</td>
<td>-</td>
<td>6,3 (4,5-7,5)</td>
<td>2-3</td>
<td>8,2 (6-10,5)</td>
<td>-</td>
<td>+</td>
</tr>
</tbody>
</table>
Mineral inclusions: absent.

**CALOPHYLLACEAE – Kielmeyera excelsa**

Cambess.


**Growth rings:** absent or indistinct (2).

**Vessels:** wood diffuse-porous (5), in random arrangement; solitary (66,6%) and in multiples of 2 (22,2%), 3 (5,5%), and 4 (5,5%); solitary vessel outline circular to oval; tangential diameter 107,6 (70-150) µm (42); 5,5 (1,6-13,1) vessels/mm² (47); tyloses common (56); perforation plates simple (13); intervessel pits alternate (22), vestured (29), aperture diameter 5,5 (4-6) µm; vessel-ray pits similar to intervessel pits in size and shape throughout the ray cell (30).

**Axial parenchyma:** vasicentric (79) (BCTw3820), aliform (80), lozenge-aliform (81), and confluent (83).

**Rays:** exclusively uniseriate (96); all ray cells upright and/or square (105) (SPw018) or body ray cells procumbent with one row of upright and/or square marginal cells (106) (BCTw3820); 9,1 (7-11) rays/mm (115).

**Fibers:** septate (65); thin- to thick-walled (69); simple to minutely bordered pits (61).

**Mineral inclusions:** styloids (151) and prismatic crystals present in axial parenchyma (141/142).

**FABACEAE CAESALPINOIDEAE – Bauhinia forficata** Link. (Figure 3 a-b-c)


**Growth rings:** absent or indistinct (2).

**Vessels:** wood diffuse-porous (5), in random arrangement; solitary (74%) and in multiples of 2 (20,5%), 3 (3,5%), 4 (1%), and 6 (1%); solitary vessel outline circular to oval; tangential diameter 87,0 (70-115) µm (41); vessels frequency 15,0 (7,3-21,3) (47) (RBw236) to 34,6 (31,9-40,1) (48) (BCTw8774) vessels/mm²; tyloses common (56) (RBw236) or absent (BCTw8774); perforation plates simple (13); intervessel pits alternate (22), non-vestured, aperture diameter 4,1 (3-5) µm; vessel-ray pits larger than intervessel pits, borders much reduced to apparently simple, rounded (31). Vascular or vasicentric tracheids present (60).

**Axial parenchyma:** aliform (80), lozenge-aliform (81), and confluent (83).
Figure 1. a-b-c. Anemopaegma prostratum DC. (Bignoniaceae / SPw731) [Arrows: a- vessels of two distinct diameter classes, wood not ring-porous; b- rays of two distinct sizes (uni and multiseriate); c- vessel-ray pits similar to intervessel pits (up left) and procumbent and square cells mixed in a multiseriate ray]. d-e-f. Cordia ecalyculata Vell. (Boraginaceae / BCTw3799) [Arrows: d- axial parenchyma; e- sheath cells; f- crystal sand]. g-hi Kielmeyera coriacea Mart. & Zucc. (Calophyllaceae / BCTw 15140) [Arrows: g- growth rings (inclined lower arrows) and axial parenchyma (horizontal arrows); h- uniseriate rays; i procumbent and square cells mixed in the ray (left arrow); axial parenchyma cells (middle arrow); vessel-ray pits larger than intervessel pits (right arrow)]. a-d-g: Transverse section. – b-e-h: Tangential section. – c-f-i Radial section. Bars = 100 µm.
Rays: 3-5 seriate (98); 8,2 (5,5-10) rays/mm (115); body ray cells procumbent with one row of upright and/or square marginal cells (106).

Fibers: non-septate (66), thin- to thick-walled (69), with simple to minutely bordered pits (61).

Mineral inclusions: Prismatic crystals present (136) in RBw236, frequently in axial alignments in chambered cells (142), also in fibers (143).

Storied structure: absent.

FABACEAE CAESALPINOIDEAE – Copaifera langsdorffii Desf. (Figure 3 d-e-f)


Growth rings: distinct, boundaries marked by thick-walled and radially flattened fibers in late wood, marginal parenchyma, and axial canals in tangential lines.

Vessels: wood diffuse-porous (5), in random arrangement, solitary (89,3%) and in multiples of 2 (6,9 %) and 3 (3,8%); solitary vessel outline circular to oval; tangential diameter 111,0 (70-170) µm (42); vessels frequency 7,5 (5-11) vessels/mm² (47); perforation plates simple (13); intervessel pits alternate (22), vestured (29), aperture diameter 4,3 (3-6) µm; vessel-ray pits similar to intervessel pits in size and shape throughout the ray cell (30).

Axial parenchyma: vasicentric (79), aliform (80), and lozenge-aliform (81).

Rays: 1-2 seriate (97); 9,2 (6-14) rays/mm (115); body ray cells procumbent with one row of upright and/or square marginal cells (106).

Fibers: non-septate (66); very thin-walled (68); with simple to minutely bordered pits (61).

Secretory elements: axial canals in tangential lines (127, 128).

Mineral inclusions: absent.

Storied structure: absent.

FABACEAE CAESALPINOIDEAE – Copaifera trapezifolia Hayne


Growth rings: distinct (1), boundaries marked by marginal parenchyma and axial canals in tangential lines.
**Vessels**: wood diffuse-porous (5), in random arrangement, solitary (71,1%) and in multiples of 2 (15,7%), 3 (10,6%), 4 (1,5%), and 5 (1,1%); solitary vessel outline circular to oval; tangential diameter 78,0 (60-90) µm (41) (BCTw4115) to 129,2 (110-150) µm (42) (RBw3682); vessels frequency 11,5 (9-17) (47) (BCTw4115) to 24,6 (19-29) (48) (RBw3682) vessels/mm²; tyloses common (56); perforation plates simple (13); intervessel pits alternate (22), vestured (29); aperture diameter 4,8 (4-6) µm; vessel-ray pits similar to intervessel pits in size and shape throughout the ray cell (30).

**Axial parenchyma**: vasicentric (79), lozenge-aliform (81).

**Rays**: (1)-2 seriate (97); 8,3 (6-11) rays/mm (115); body ray cells procumbent with one row of upright and/or square marginal cells (106).

**Fibers**: non-septate (66); very thin-walled (68) (BCTw10950, RBw2234) or thin- to thick-walled (69) (BCTw10936, BCTw s/nº, BCTw8390); with simple to minutely bordered pits (61).

**Mineral inclusions**: absent.

**Storied structure**: absent.

**FABACEAE CAESALPINIOIDEAE – Peltophorum dubium** (Spreng.) Taub. (Figure 3 g-h-i)


**Vessels**: wood diffuse-porous (5), in random arrangement, solitary (71,8%) and in multiples of 2 (26,1%) and 3 (2,0%); solitary vessel outline circular to oval; tangential diameter 119,9 (70-180) µm (42); vessels frequency 3,4 (0-8) vessels/mm² (46); tyloses absent (BCTw10936, RBw2234, BCTw10950) or common (56) (BCTw s/nº, BCTw8390); perforation plates simple (13); intervessel pits alternate (22), vestured (29), aperture diameter 4,6 (4-6) µm; vessel-ray pits similar to intervessel pits in size and shape throughout the ray cell (30).

**Axial parenchyma**: vasicentric (79), lozenge-aliform (81), confluent (83).

**Rays**: 1-2 seriate (97); 10,3 (7-15) rays/mm (115); all ray cells procumbent (104).

**Fibers**: septate (65); very thin-walled (68) (BCTw10950, RBw2234) or thin- to thick-walled (69) (BCTw10936, BCTw s/nº, BCTw8390); with simple to minutely bordered pits (61).

**Mineral inclusions**: absent.

**Storied structure**: absent.

**FABACEAE FABOIDEAE – Bowdichia virgilioides** Kunth. (Figure 4 a-b-c)

**Material studied**: BRASIL: Espírito Santo (SPSfw1148).

**Growth rings**: distinct (1), boundaries marked by parenchyma marginal bands (89).

**Vessels**: wood diffuse-porous (5), in random arrangement; solitary (51%) and in multiples of 2 (18,5%), 3 (24,5%), and 4 (6%); solitary vessel outline circular to oval; tangential diameter 110 (70-160) µm (42); vessels frequency 7,2 (4-13,9) vessels/mm² (47); perforation plates simple (13); intervessel pits alternate (22), vestured (29), aperture diameter 8,4 (6-10) µm; vessel-ray pits similar to intervessel pits in size and shape throughout the ray cell (30).

**Axial parenchyma**: in marginal or seemingly marginal bands (89) and aliform (81), lozenge-aliform (81), and confluent (83); 5-10 cells per parenchyma strand (93-94).
Figure 3. a-b-c. *Bauhinia forficata* Link. (Fabaceae Caesalpinoideae / BCTw8774) [Arrows: a- axial parenchyma; b- rays; c- row of square marginal cells siding procumbent ray cells; vessel-ray pits larger than intervessel pits (right arrows)]. d-e-f. *Copaifera langsdorffii* Desf. (Fabaceae Caesalpinoideae / SPSFW139) [Arrows: d- axial canals; axial parenchyma; growth ring (horizontal arrow); e- rays; f- ray cells]. g-h-i *Peltophorum dubium* (Spreng.) Taub. (Fabaceae Caesalpinoideae / BCT w s/nº) [Arrows: g- axial parenchyma; h- rays; i ray cells]. a-d-g: Transverse section. – b-e-h: Tangential section. – c-f-i Radial section. Bars = 100 µm.
Rays: 1-2-(3) seriate (97); 8,4 (5-10) rays/mm (115); body ray cells procumbent with one row of upright and/or square marginal cells (106), sometimes procumbent cells of variable width.

Fibers: non-septate (66); very thick-walled (70), with simple to minutely bordered pits (61).

Mineral inclusions: absent.

Storied structure: all rays storied (118); axial parenchyma storied (120).

FABACEAE FABOIDEAE – Dalbergia nigra (Vell.) Allemão ex Benth. (Figure 4 d-e-f)


Growth rings: absent or indistinct (2) (BCTw1473, BCTw1479) or distinct (1), boundaries marked by marginal parenchyma bands (RBw2222).

Vessels: wood diffuse-porous (5), in random arrangement, solitary (81,7%) and in multiples of 2 (12%), 3 (5,8%) and 5 (0,2%); solitary vessel outline circular to oval; tangential diameter 87,6 (70-110) µm (41); vessels frequency 13,4 (8,9-16,8) vessels/mm² (47); tyloses common (56); perforation plates simple (13); intervessel pits alternate (22), vestured (29); aperture diameter 5 (4-6) µm; vessel-ray pits similar to intervessel pits in size and shape throughout the ray cell (30).

Axial parenchyma: vasicentric (79)

Rays: 1-3 seriate (97), but larger rays commonly 4-5 seriate (98); 7,6 (6-9) rays/mm (115); all ray cells procumbent (104).

Fibers: non-septate (66); thin to thick-walled (69); with simple to minutely bordered pits (61).

Mineral inclusions: axial alignments of prismatic crystals in chambered cells.

Storied structure: absent.

MELASTOMATACEAE – Mouriri chamissoana Cogn. (Figure 5 a-b-c)


Growth rings: absent or indistinct (2).

Vessels: wood diffuse-porous (5), in random arrangement; solitary (88,8%) and in multiples of 2 (10,1%) and 3 (1,2%); solitary vessel outline
Figure 4. a-b-c. *Bowdichia virgilioides* Kunth. (Fabaceae Faboideae / SPSFw1148) [Arrows: a- axial parenchyma; b- storied rays; storied parenchyma cells (right arrows); c- procumbent ray cells]. d-e-f. *Dalbergia nigra* (Vell.) Allemão ex Benth. (Fabaceae Faboideae / BCTw s/nº) [Arrows: d- aliform axial parenchyma; e- storied rays; f- ray cells]. g-hi *Anadenanthera colubrina* var. *cebil* (Griseb.) Altschul (Fabaceae Mimosoideae / SPSFw1121) [Arrows: g- vasicentric axial parenchyma; h- rays; axial alignment of prismatic crystals (vertical arrow); i axial alignments of prismatic crystals]. a-d-g: Transverse section. – b-e-h: Tangential section. – c-f-i Radial section. Bars = 100 µm.
circular to oval; tangential diameter 77.6 (52-118) µm (41); vessels frequency 14.0 (10.1-19.3) vessels/mm² (47); tyloses usually absent, but common (56) in BCTw645; perforation plates simple (13); intervessel pits alternate (22), vestured (29), aperture diameter 6.1 (4.5-8) µm; vessel-ray pits similar to intervessel pits in size and shape throughout the ray cell (30).

Axial parenchyma: scanty paratracheal (78), vasicentric (79), and apotracheal diffuse (76); 2-4 cells per parenchyma strand (91-92).

Rays: exclusively uniseriate (96); 5 (4 -10.5) rays/mm (115); all ray cells upright and/or square (105).

Fibers: non-septate (66), thin- to thick-walled (69), with simple to minutely bordered pits (61).

Mineral inclusions: crystal sand (153).

Cambial variants: Included phloem diffuse (134).

MYRTACEAE – Myrcia minutiflora Sagot. (Figure 5 d-e-f)


Growth rings: distinct (1) boundaries marked by thick-walled and radially flattened fibers in late wood.

Vessels: wood diffuse-porous (5), in diagonal arrangement; solitary (53.3%) and in multiples of 2 (39.4%), 3 (9%), 4 (1.5%), 5 (0.4%), and 6 (1.5%); Solitary vessel outline circular to oval; tangential diameter 55.8 (30-80) µm (41); vessels frequency 31.8 (22.9-37.7) (48) (BCTw11246) to 58.9 (41.8-78.6) (49) (ME187) vessels/mm²; perforation plates simple (13); intervessel pits alternate (22), vestured (29), aperture diameter 6.3 (4.5-7.5) µm; vessel-ray pits similar to intervessel pits in size and shape throughout the ray cell (30). Vascular or vasicentric tracheids present (60).

Axial parenchyma: diffuse-in-aggregates (77); 1-2 cells per parenchyma strand (90-91).

Rays: (3)4-5(6) seriate (98); 6.5 (5-9) rays/mm (115); body ray cells procumbent with one row of upright and/or square marginal cells (108).

Fibers: non-septate (66), thin- to thick-walled (69), with distinctly bordered pits (62).

Mineral inclusions: prismatic crystals in rays and in non-chambered parenchyma cells (141).

VOCHYSIACEAE – Qualea grandiflora Mart. (Figure 5 g-h-i)


Growth rings: hardly distinct (1); boundaries marked by thick-walled and radially flattened fibers in late wood.

Vessels: wood diffuse-porous (5), in random arrangement; solitary (53.3%) and in multiples of 2 (39.4%), 3 (9%), 4 (1.5%), 5 (0.4%), and 6 (1.5%); Solitary vessel outline circular to oval; tangential diameter 55.8 (30-80) µm (41); vessels frequency 31.8 (22.9-37.7) (48) (BCTw11246) to 58.9 (41.8-78.6) (49) (ME187) vessels/mm²; perforation plates simple (13); intervessel pits alternate (22), vestured (29), aperture diameter 6.3 (4.5-7.5) µm; vessel-ray pits similar to intervessel pits in size and shape throughout the ray cell (30).

Axial parenchyma: aliform (80), lozenge-aliform (81), and confluent (83); 4 cells per parenchyma strand (92).

Rays: mostly 2-3 seriate (97), but 1 to 4-seriate present; 8.2 (6-10.5) rays/mm (115); body ray cells procumbent with one row of upright and/or square marginal cells (106).

Fibers: septate (65), very thick-walled (70), with simple to minutely bordered pits (61); pits common in both radial and tangential walls (63).

Mineral inclusions: prismatic crystals (136), both in procumbent ray cells (138) and in axial parenchyma cells (141).

Storied structure: rays and/or axial elements irregularly storied (122).
Figure 5. a-b-c. *Mouriri chamissoana* Cogn. (Melastomataceae / SPw1138) [Arrows: a- included phloem; b-uniseriate rays; c- all ray cells upright or square]. d-e-f. *Myrcia minutiflora* Sagot. (Myrtaceae / SPSFw2576) [Arrows: d- axial parenchyma diffuse-in-aggregates; e-f- uniseriate portion of multiseriate rays, composed of many rows of square and upright cells]. g-hi *Qualea grandiflora* Mart. (Vochysiaceae / BCTw11246) [Arrows: g- axial parenchyma; hi rays]. a-d-g: Transverse section. – b-e-h: Tangential section. – c-f-i Radial section. Bars = 100 µm.
DISCUSSION

The anatomical description of charcoal aims to improve taxonomical identification and to provide better means to anthracological studies in the tropics.


However, some quantitative features differed from these previous descriptions. Differences, of small amplitude, were observed concerning tangential diameter and frequency of vessels, ray frequencies, and pit diameters. The discrepancies may be explained by the carbonization process, ecological factors, or intraspecific variability. Mass loss and wood shrinkage may cause changes in diameter and frequency of vessels and rays, while the fusion of secondary cell walls frequently obliterates pit chambers. These changes, however, do not prevent taxonomic identification, since they lie within the range of individual variation in wood anatomy (Gonçalves et al. 2012, Gonçalves & Scheel-Ybert 2016).

A few qualitative features also differed from previous descriptions. We identified growth rings in Bowdichia virgilioides and Kielmeyera coriacea, conversely of what was previously described (Détienne & Jacquet 1983, Richter & Dallwitz 2000, Mattos et al. 2003, Sonsin et al. 2014, Sonsin-Oliveira 2006 for B. virgilioides; Paula 1974 for K. coriacea). The specimens of Qualea grandiflora that we analyzed presented simple perforation plates and tyloses absent, while Sonsin et al. (2014) described the perforation plates as scalariform and the tyloses as common. These discrepancies, especially regarding growth rings and tyloses, are easily explained by ecological factors, intraspecific variability, and timber age.

These results reiterate the similarity between charcoal and wood anatomy, already enunciated by Gonçalves & Scheel-Ybert (2016), as, despite morphometrical changes due to the carbonization process, wood anatomical features seem directly comparable between carbonized and non-carbonized samples. Yet, we restate the advantage of studying charcoal anatomy to assist anthracological research. Charcoal identification is much more effective when unknown samples are compared to charred extant equivalents, instead of to wood slides (Scheel-Ybert & Gonçalves 2017).

Some charcoal anatomy studies for the Brazilian flora already exist, but much work is still needed on the subject. Up to the present time, there are studies comparing wood and charcoal anatomy to investigate anatomical changes (Dias Leme et al. 2010, Gonçalves et al. 2012, Albuquerque 2012), charcoal anatomy descriptions aiming to assist anthracological studies (Pinto et al. 2017, Gonçalves & Scheel-Ybert 2016, Scheel-Ybert & Gonçalves 2017), and charcoal anatomy investigations aiming to contribute to control the use of illegal logged native wood as charcoal (Nisgoski et al. 2012, 2015, Carvalho et al. 2017, Muñiz et al. 2016, Gonçalves...

By these means, this contribution discloses its importance not only to charcoal-related disciplines, such as anthracology, archeobotany, paleobotany, paleoecology, forest science, and environmental conservation, but also to wood anatomy.

CONCLUSION

This work successfully described the charcoal anatomy of 15 species from 12 families native to different Brazilian phytogeographical domains. This is the first time that charcoal anatomy is described for six of these species (Anemopaegma prostratum DC., Bauhinia forficata Link., Cordia ecalyculata Vell., Copaifera trapezifolia Hayne, Kielmeyera excelsa Cambess., and Myrcia minutiflora Sagot.).

Increasing the knowledge of charcoal and wood anatomy of native tropical species improves taxonomic identification. In consequence, it helps to achieve better paleoenvironmental and paleoethnobotanical interpretations and, ultimately, a better comprehension of sociocultural aspects of past societies. Concurrently, it contributes to a better knowledge of the native flora, to preventing deforestation, and to driving more sustainable charcoal production chains.

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