

Wood anatomy of *Tabaroa*, a monotypic papilionoid legume genus narrowly endemic to the Brazilian Caatinga seasonally dry tropical forests

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Abstract

Wood anatomy can serve as a source of phylogenetically informative characteristics, as well as a model of how more plastic characters have evolved over time in plants, e.g., through ancestral reconstructions of wood anatomical traits across well-resolved phylogenies. However, the evolution of wood anatomy is largely unexplored within a phylogenetic context due to limited availability of anatomical data across taxa. When compared with other angiosperm families, Leguminosae is relatively well-documented, yet it still lacks comprehensive wood anatomical information, particularly in undersampled papilionoid clades. In order to contribute to the understanding of micromorphological diversity across papilionoid legumes, we newly characterize the wood anatomy of *Tabaroa caatingicola*, a papilionoid species narrowly endemic to the Brazilian Caatinga seasonally dry tropical forests, that has been molecularly placed in the poorly anatomically studied tribe Brongniartieae. Optical histology and scanning electron microscopy (SEM) were used to examine and describe the wood anatomy of *T. caatingicola* and compare it with six phylogenetically related Brongniartieae genera: *Amphiodon*, *Behaimia*, *Haplormosia*, *Harpalyce*, *Limadendron*, and *Poecilanthe*. Wood anatomy of *Tabaroa* suggests adaptations to the irregular rainfall of the harsh Caatinga environment, featuring distinct growth rings, prone to semi-ring-porous wood, multiple narrow vessels, simple perforation plates, and small and vestured pits. These traits increase water flow during abundance and ensure hydraulic safety during scarcity, minimizing embolism formation and spread. By focusing on the genus *Tabaroa*, an ecologically distinctive and evolutionarily isolated lineage, this study contributes to the understanding of the systematic and functional wood anatomy variation in the papilionoid legume tribe Brongniartieae.

1 Introduction

Wood anatomical features have consistently been recognized to provide valuable sources of phylogenetic information (Baas et al. 2000; Carlquist 2013; Herendeen and Miller 2000; Olson 2005), as well as a model of how characters more plastic have evolved over time in plants, through ancestral character reconstructions in well-resolved phylogenies (e.g. Pace et al. 2022; Silva et al. 2021). Wood anatomical features are able to shed light on obscure relationships at deeper nodes (Lens et al. 2007). However, the evolution of wood anatomy is still poorly unexplored within a phylogenetic context, perhaps due to the large knowledge gaps of microscopic wood structures across clades (Lens et al. 2007).

Wood anatomy has been instrumental for delimitating several flowering plant families including the Marcgraviaceae, Tetrameristaceae (Lens et al. 2005), and Sapotaceae (Kukachka 1980). Likewise, the wood anatomy of the ecologically and economically important family Leguminosae is relatively well documented, when compared with other angiosperm families. (Gasson 1996; Gasson et al. 2004; Stepanova et al. 2013). However, most tribes within the Papilionoideae are yet to be anatomically studied. Describing wood anatomical features of endemic, rare, monospecific or poorly diverse genera is therefore critical for understanding evolutionary patterns of the micromorphological diversity across legumes. This is particularly critical in understanding how tree species can behave in the face of climate change, especially in relation to temperature and precipitation variations that directly affect xylem transport and the survival capacity of plants (Anfodillo and Olson 2021; Breshears et al. 2018; Fontes et al. 2022; Hajek et al. 2016)

The papilionoid legume genus *Tabaroa* and its only known species *T. caatingicola* L.P. Queiroz, G.P. Lewis & M.F. Wojc. of the tribe Brongniartieae (Fig. 1) have been described more than ten years ago (Queiroz et al. 2010), yet wood anatomy in this phylogenetically important branch of the tribe remains fully unknown. *T. caatingicola* is narrowly endemic to a small area of seasonally dry tropical forest and woodland (SDTFW) on sandy soils of the Brazilian Caatinga domain, in southwestern Bahia (Fig. 2a), whereas its most closely related species *Amphiodon effusus* Huber is ecologically confined to the Amazon rainforest (Cardoso et al. 2013). This clade, in turn, is sister to the genus *Harpalyce*, resulting in the topology (*Harpalyce* (*Tabaroa*, *Amphiodon*)) that has been corroborated in several publications involving phylogenetic analyses of nuclear and plastid DNA sequence data (Cardoso et al. 2012, 2013, 2017; Meireles et al. 2014; Queiroz et al. 2010, 2017) (Fig. 1). Brongniartieae is a taxonomically intriguing tribe within the Papilionoideae subfamily of the Leguminosae, comprising 15 genera, mostly monospecific or with few species, totalling approximately 180 species (POWO 2024; WFO 2024). Despite the modest number of species, the Brongniartieae tribe displays significant morphological diversity, and a wide geographic distribution across continents and biomes, with marked variation in ecological preferences. For this reason, many of its morphologically disparate genera were previously placed in at least four distantly related tribes (Cardoso et al. 2017; Queiroz et al. 2017).

Caatinga is an indigenous *Tupi* word that means “white forest”, describing the grey and light aspect during the dry season, when the majority of trees and shrubs are devoid of leaves, allowing light to reach the ground, consists predominantly of xeric shrub, thorn and drought resistant species, dominated by legume trees (Giulietti et al. 2004; Queiroz 2009). The region is characterized by an extended dry season and erratic rainfall, resulting in sparse foliage and undergrowth (Leal et al. 2005) (Fig. 1). It harbours numerous endemic species, with 34% of the flora exclusive to the area, many featuring unique physiological adaptations to mitigate water loss during prolonged drought periods (Giulietti et al. 2004).

Although relatively common locally, *T. caatingicola* only occupies a restricted geographic area of about 12 Km² and has been classified as Critically Endangered (IUCN 2001). Here we newly present wood anatomical description for the ecologically distinctive, phylogenetically isolated, and highly threatened species *T. caatingicola* and compares it with six phylogenetically related genera within the Brongniartieae, for which any wood anatomical data are available: *Amphiodon*, *Behaimia*, *Haplormosia*, *Harpalyce*, *Limadendron*, and *Poecilanthe* (Fig. 2). Furthermore, we analyze the wood anatomy of *T. caatingicola* in light of the most modern theories and functional hypotheses of secondary xylem.

2 Material and methods

2.1 Wood sampling and anatomical characterization – Wood samples from three trees were collected from the trunk at diameter at breast height (DBH = 1.30 m), in trees with apparent health and straight stem in a population of *Tabaroa caatingicola* in the municipality of Dom Basílio, state of Bahia, northeastern Brazil (S 13°47'19"; W 41°30'04") (Fig. 3a). Non-destructive wood collection followed the procedure described by Silva et al. (2022b). Samples were vouchered, recorded, and deposited in the Herbarium and Xylotheque of the Instituto de Biologia of the Universidade Federal de Pelotas (Table 1). The climate from the

collection area is dry, semi-arid of the low latitude and altitude (BSH), according to Köppen-Geiger's classifications, with annual mean precipitation between 588–619 mm, and temperature 23.3–24.0 °C, with great thermal amplitude throughout the year, 14.7–31.8 °C (Fick and Hijmans 2017). The main biome in the Caatinga phytogeographical domain is the seasonally dry tropical forest and woodland (Queiroz et al. 2017), which can be characterized as a xerophytic vegetation across most of the semi-arid region of Northeastern Brazil, including mostly sparse vegetation that covers massifs and plateaus where rivers are usually seasonal. Leguminosae species are among the most dominating flowering plants of the Caatinga (Queiroz 2006; Queiroz et al. 2017). Despite comprising almost 10% of Brazil's territory, the Caatinga is inadequately explored, with only 1% designated as a Conservation Protection Area. The region faces threats from deforestation and unsustainable agricultural practices, such as agriculture and cattle ranching, leading to soil salinization (Leal et al. 2005; Silva et al. 2004).

Table 1
Diameter at breast height, height and quantitative data on the wood anatomy of *Tabaraea caatingicola* (Leguminosae) for the three tree samples analyzed, recorded, and deposited in the xylotheque of the Instituto de Biologia of the Universidade Federal de Pelotas (PELw). Additionally, vulnerability and mesomorphy indices (sensu Carlquist 1977) are provided. Herbarium voucher: PEL 27325.

Morphological and anatomical parameters / Samples	PELw 01	PELw 02	PELw 03
Diameter at breast height (1.30 m) (cm)	5.1	3.5	4.8
Height (m)	4.5	3.0	4.0
Vessels per square millimeter	119 ± 32	129 ± 11	147 ± 17
Vessel tangential diameter (µm)	44.0 ± 23.0	49.5 ± 16.2	63.1 ± 20.9
Vessel element length (µm)	163 ± 64	180 ± 31	197 ± 26
Intervessel/vessel-ray pit size (µm)	4.0 ± 1.5	4.4 ± 1.1	4.3 ± 1.2
Fibre length (µm)	727 ± 255	709 ± 140	799 ± 128
Fibre diameter (µm)	13.4 ± 3.7	13.1 ± 2.0	14.0 ± 2.1
Fibre wall thickness (µm)	4.7 ± 1.8	5.0 ± 0.8	5.4 ± 1.0
Fibre pit size (µm)	3.7 ± 1.3	2.8 ± 0.9	2.5 ± 0.5
Rays/mm	9.7 ± 2.3	11.4 ± 1.3	10.4 ± 1.1
Ray width (µm)	14.0 ± 4.3	18.2 ± 3.6	22.6 ± 4.1
Ray width (cell numbers)	2.0 ± 0.5	2.1 ± 0.4	2.5 ± 0.5
Ray height (µm)	126 ± 22	117 ± 15	129 ± 18
Ray height (cell numbers)	6.9 ± 1.3	6.1 ± 0.9	7.2 ± 1.0
Vulnerability index	0.4 ± 0.2	0.4 ± 0.1	0.4 ± 0.1
Mesomorphy index	68.2 ± 51.8	68.9 ± 25.5	83.1 ± 27.0

The preparation of histological slides followed the usual plant anatomical methods described by Johansen (1940) and Sass (1951). Histological sections between 18–30 µm in thickness were made using a Leica® sliding microtome. Sections of each sample were clarified with sodium hypochlorite (50%), coloured with 1% alcoholic safranin, dehydrated in a 50–100% alcoholic series and mounted in synthetic Canada Balsam® or Entellan®. The method proposed by Franklin (1945), modified by Kraus and Arduin (1997), was followed to analyze dissociated cell elements. For the Scanning Electron Microscopy (SEM) analyses, longitudinal wood sections, 18–30 µm thick were dehydrated in an alcoholic series, dried in a dry chamber (60°C ~ 12hs), placed on a stub with a double-faced carbon label and metallized with gold. The observation of the samples was carried out with a SEM JEOL 6390LV® in the Instituto Gonçalo Moniz (Fundação Oswaldo Cruz – FIOCRUZ).

The following quantitative wood anatomy characters were measured: vessels (vessels per square millimeter, tangential diameter, length, intervessel/vessel-ray pit outer aperture diameter); fibres (length, width, and wall thickness); and rays (rays/mm, width, and height). Indices of vulnerability (vessel diameter / vessels per square millimeter) and mesomorphy (indices of vulnerability × vessel element length) were calculated according to Carlquist (1977). The measurements of vessels per square millimeter were obtained with ANATI QUANTI® software (Aguiar et al. 2007). The other measurements were carried out with an Olympus CX40® microscope coupled with a micrometric lens and the factors obtained were converted to µm through a conversion factor. The terminology used in the anatomical descriptions is in accordance with the IAWA Committee (1989). The measurement of the anatomical parameters n = 30 was fixed.

2.2 Mapping distribution across geographic and climatic spaces – To assess the distribution range across geographic and climatic spaces, we used built a taxonomically verified specimen record data from the analyses of herbarium collections (ALCB, CEPEC, CEN, HUEFS, MO, MBM, NY, RB, RON, SP, SPF, US); acronyms according to Thiers 2022) as available in the online databases of speciesLink (<https://specieslink.net/>) and Reflora (<https://reflora.jbrj.gov.br/reflora/PrincipalUC/PrincipalUC.do>). Any erroneous georeferenced records were filtered with the R package coordinateCleaner (Zizka et al. 2019), but whenever possible these specimens and others without geographic coordinates were included based on the closest georeferenced locality accessed by comparing with localities of other plant specimens in the speciesLink database.

From the latitude and longitude of each herbarium collection (a total of 153 specimens recorded, Appendix S1), the variables BIO12 (Annual Precipitation) and BIO4 (Temperature Seasonality) were extracted from the WorldClim v.2.0 model layers (WGS84 projection; Fick and Hijmans 2017) using the R library *raster* (Hijmans 2024). Bioclimatic variables (O'Donnell and Ignizio 2012) were derived from these climate models using the *extract* function in the *raster* library. We mapped the range distribution of *Tabaroa* and its most phylogenetically closely related genus *Amphiodon* against the BIO12 bioclimatic variable, by using the R packages *raster*, *ggmap* (Kahle and Wickham 2013), *ggplot2* (Wickham et al. 2016), *ggspatial* (Dunnington 2023), and *maturalearth* (South 2017) as implemented in RStudio (2022). The built a scatterplot to show the bioclimatic space of *Tabaroa* and *Amphiodon* across the BIO12 and BIO4 axes.

3 Results

Here, we provide a full description of the wood anatomy of *Tabaroa caatingicola*. This species exhibits “bark light grey with darker wavy stripes that interlink and cross over to form a pattern suggestive of crocodile skin, inner bark dark green” (Fig. 3b), hence the vernacular name *pau-jacaré* (crocodile wood) because of the resemblance of the bark to crocodile skin, as described by Queiroz et al. (2010, p. 199).

- 3.1 General, organoleptic, and macroscopic wood anatomical characters** – Wood with a brown heartwood and yellowish sapwood (Fig. 3c-d), highly dense, and resistant to cutting. Odorless; straight grain; fine texture; gloss present. Distinct growth ring, macroscopically demarcated by fibrous zone (Fig. 3c-d). Diffuse porosity, tending towards semi-ring porosity. Vessels arranged in a radial pattern; solitary and multiple radial vessels of 2–5, less frequently 6–10; noticeable only under magnification; small in tangential diameter; very numerous; some vessels obstructed by deposits in the heartwood. Axial parenchyma indistinct even under magnification. Rays noticeable only under magnification, storied.
- 3.2 Microscopic anatomical description of wood** – **Growth rings** are well defined, marked by thick-walled and radially flattened fibres and distended rays, prone to semi-ring-porous wood (Fig. 4a-b). **Vessels** are wood diffuse-porous with a tendency to semi-porous (Fig. 4a-b). Vessel arrangement in radial pattern (Fig. 4a-b). Vessel groupings: solitary and radial multiples of 2–5 (solitary 20–29%, radial multiples of two 26–29%, of three 18–27%, of four 10–15%, of five 4–7%) occurring less frequently radial multiples of 6–10, 4–12% (Fig. 4a-b); simple perforation plates (Fig. 4f); intervessel pits alternate, small and vested (Fig. 4g); vessel-ray pits with distinct borders, similar to intervessel pits in size and shape throughout the ray cell (Fig. 4d). Deposits in heartwood vessels. **Fibres** with simple to minutely bordered pits, few, common in both radial and tangential walls. Nonseptate fibres present. Fibres very thick-walled (Fig. 4b). **Axial parenchyma** diffuse and paratracheal, both scanty (Fig. 4a-b). Fusiform and two cells per parenchyma strand (Fig. 4c), less often 3–4 cells per parenchyma strand. **Rays** width 1 to 3 cells (Fig. 4c). Cellular composition of rays: homocellular, all ray cells procumbent (Fig. 4d); and heterocellular, body ray cells procumbent with one or more row of procumbent cells more high, upright and/or square marginal cells (Fig. 4e). Perforated ray cells present, rare. **Storied structure** includes rays, axial parenchyma and vessel elements that are storied or irregularly storied (4c). **Mineral inclusions** include prismatic crystals in chambered axial parenchyma cells (Fig. 4c, e), and in procumbent, upright and square ray cells (Fig. 4e), less often in chambered upright and/or square ray cells.

The anatomical quantitative features of the wood are described in Table 1. Data on wood anatomy for the tribe Brongniartieae is largely scarce. Among the 15 genera and approximately 180 species constituting this tribe, only six genera and merely eight species, about 4%, have any data on wood anatomy. Yet, some species such as *A. effusus* and *Limadendron amazonicum* (Ducke) Meireles & A.M.G.Azevedo only have quite incomplete anatomical information (Table 2).

Table 2

Comparative wood anatomy of *Tabaroa caatingicola* with eight species from the Brongniartieae tribe for which some wood anatomy data is available. For qu data, the classes indicated by the IAWA Committee (1989) are presented, and when available, the range of variation (minimum – maximum), mean, and/or standard deviation. (-) Not applicable; (?) Information is missing. The list of anatomical character follows the IAWA Committee (1989).

Anatomical character / Species	<i>Tabaroa caatingicola</i> L.P. Queiroz, G.P. Lewis & M.F. Wojc.	<i>Amphiodon effusus</i> Huber	<i>Behaimia cubensis</i> Griseb.	<i>Harpalyce formosa</i> DC.	<i>Harpalyce arborescens</i> A. Gray	<i>Haplormosia monophylla</i> (Harms) Harms	<i>Limadendron amazonicum</i> (Ducke) Meireles & A.M.G. Azevedo	<i>Limadendron hostmannii</i> (Benth.) Meireles & A.M.G. Azevedo	<i>Poea parv</i> Bent
Growth rings	Present	Absent	Absent	Present	Present	Absent	?	Present	Pres
Growth rings: anatomical markers	Thick-walled and radially flattened fibres and distended rays, prone to semi-ring-porous wood	-	-	Marginal parenchyma	Marginal parenchyma, semi-ring-porous and thick-walled and/or radially flattened latewood fibres	-	?	Marginal parenchyma	Thick and/radially flattened latewood fibre margin
Porosity	Diffuse-porous with a tendency to semi-porous	Diffuse-porous	Diffuse-porous	Diffuse-porous	Diffuse-porous with tendency to semi-ring porosity	Diffuse-porous	?	Diffuse-porous	Diffuse-porous
Vessel arrangement	Vessels in radial pattern	No specific arrangement	No specific arrangement	No specific arrangement	No specific arrangement	No specific arrangement	?	No specific arrangement	No specific arrangement
Vessel groupings	Solitary and radial multiples of 2–5, less common radial multiples of 6–10	?	Vessels in radial multiples of 4 or more common	Vessels in radial multiples of 4 or more common	Vessels in radial multiples of 4 or more common	Solitary and radial multiples of 2–3	?	Solitary and radial multiples of 2–3, less common radial multiples of 4–5	Solitary and radial multiples of 2, radial multiples of 3–4
Perforation plate	Simple	?	Simple	Simple	Simple	Simple	Simple	Simple	Simple
Intervessel pits arrangement	Alternate	?	Alternate, polygonal	Alternate, polygonal	Alternate	Alternate, polygonal	Alternate	Alternate, polygonal	Alternate
Intervessel pits size	Small	?	Small	Small	?	Medium to large	?	Medium	Small to Medium
Vestured pit	Present	?	Present	Present	Present	Present	?	Present	Present
Vessel–ray pits	Similar to intervessel pits in size and shape throughout the ray cell	?	Similar to intervessel pits in size and shape throughout the ray cell	Similar to intervessel pits in size and shape throughout the ray cell	?	Similar to intervessel pits in size and shape throughout the ray cell	Similar to intervessel pits in size and shape throughout the ray cell	Similar to intervessel pits in size and shape throughout the ray cell	Similar to intervessel pits and throughout the ray cell
Mean tangential diameter of vessel (µm)	≤ 50 to 50–100 (44.0–63.1)	50–100 (50–60)	50–100	50–100 (61)	50–100 (61.16 ± 10.90)	100–200	?	50–200 (100)	50–100
Vessels per square millimeter	≥ 100 (119–147)	5–20 (8.3)	?	40–100 (68)	40–100 (45 ± 15; 29–66)	≤ 5 to 5–20	?	5–20 (10–15)	5–40 (38)
Mean vessel element length (µm)	≤ 350 (163–197)	?	?	≤ 350 (208; (173–270))	350–800 (187.06 ± 20.66)	?	?	?	?
Tyloses	Absent	?	Absent	Absent	Absent	Absent	Present	Absent	Present
Deposits in heartwood vessels	Present	?	Absent	Absent	Present	Present	?	Present	Present oleoresin
Ground tissue fibres	Fibres with simple to minutely bordered pits	?	Fibres with simple to minutely bordered pits	Fibres with simple to minutely bordered pits	Fibres with simple to minutely bordered pits	Fibres with simple to minutely bordered pits	?	Fibres with simple to minutely bordered pits	Fibres with simple to minutely bordered pits

Anatomical character / Species	<i>Tabaroa caatingicola</i> L.P.Queiroz, G.P.Lewis & M.F.Wojc.	<i>Amphiodon effusus</i> Huber	<i>Behaimia cubensis</i> Griseb.	<i>Harpalyce formosa</i> DC.	<i>Harpalyce arborescens</i> A.Gray	<i>Haplormosia monophylla</i> (Harms) Harms	<i>Limadendron amazonicum</i> (Ducke) Meireles & A.M.G.Azevedo	<i>Limadendron hostmannii</i> (Benth.) Meireles & A.M.G.Azevedo	<i>Poa parv</i> Bent
Septate and nonseptate fibres	Nonseptate fibres	?	Nonseptate fibres	Nonseptate fibres	Nonseptate fibres	Nonseptate fibres	?	Nonseptate fibres	?
Fibre wall thickness	Very thick-walled	?	Very thick-walled	Very thick-walled	Thin- to thick-walled and very thick-walled	Very thick-walled	?	Very thick-walled	Very wall
Fibre diameter (µm)	13.1–14.0	?	?	12	13.51 ± 1.77	?	?	?	?
Fibre wall thickness (µm)	4.7–5.4	?	?	4	3.13 ± 0.74	?	?	?	?
Fibre length (µm)	≤ 900 (709–799)	?	?	900–1600 (947; 799–1021))	≤ 900 (270.30 ± 43.14)	900–1600	?	?	?
Axial parenchyma	Diffuse and paratracheal, both scanty	Bands more than three cells wide	Diffuse and paratracheal, both scanty and marginal	Scanty paratracheal, vasicentric, confluent and marginal	Unilateral paratracheal, lozenge-aliform, confluent, bands more than three cells wide and marginal	Scanty paratracheal and bands with 2–6 cells wide	?	Scanty paratracheal, bands with 2–4 cells wide and marginal	Scar para and narrow bands three wide
Axial parenchyma cell type / Strand length	Fusiform and two cells, less often 3–4 cells	?	2–4 cells	1–2 cells	2 cells	3–4 cells	2–4 cells	2–4 cells	3–4
Ray width	1–3 cells	?	1–3 cells	2 cells	1–3 cells	1–3 cells	1–4 cells	1–3 cells	2–3
Rays with multiseriate portion(s) as wide as uniseriate portions	Absent	?	Absent	Absent	Absent	Absent	Present	Absent	Absent
Ray height	14.0–22.6 µm; 6.1–7.2 cells	?	7–10 cells	230 µm	178.68 ± 31.89 µm	?	?	?	120–
Rays: cellular composition	All ray cells procumbent and body ray cells procumbent with one or more row of procumbent cells more high, upright and/or square marginal cells	?	All ray cells procumbent and body ray cells procumbent with one row of upright and/or square marginal cells	Body ray cells procumbent with one row of upright and/or square marginal cells	All ray cells procumbent	All ray cells procumbent and body ray cells procumbent with one or more row of upright and/or square marginal cells	Body ray cells procumbent with one row of upright and/or square marginal cells	Body ray cells procumbent with one row of upright and/or square marginal cells	Hor
Sheath cells	Absent	?	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Perforated ray cells	Present, rare	?	Absent	Absent	Absent	Absent	?	Absent	Absent
Rays per millimeter	9.7–11.4	?	4–12	4–12 (12)	4–12 (4 ± 1; 2–6)	4–12 to ≥ 12	?	4–12 (6–7)	4–12 (8–1
Storied structure	Rays, axial parenchyma and vessel elements	?	Rays, axial parenchyma and vessel elements	Rays, axial parenchyma and vessel elements	Rays, axial parenchyma and vessel elements	Rays, axial parenchyma and vessel elements	Absent	Absent	Rays pare and elern

Anatomical character / Species	<i>Tabaroa caatingicola</i> L.P.Queiroz, G.P.Lewis & M.F.Wojc.	<i>Amphiodon effusus</i> Huber	<i>Behaimia cubensis</i> Griseb.	<i>Harpalyce formosa</i> DC.	<i>Harpalyce arborescens</i> A.Gray	<i>Haplormosia monophylla</i> (Harms) Harms	<i>Limadendron amazonicum</i> (Ducke) Meireles & A.M.G.Azevedo	<i>Limadendron hostmannii</i> (Benth.) Meireles & A.M.G.Azevedo	<i>Poe. parv</i> Bent
Mineral inclusions	Prismatic crystals in chambered axial parenchyma cells, and in procumbent, upright and square ray cells, less often in chambered upright and/or square ray cells.	?	Prismatic crystals in upright and/or square ray cells and in chambered axial parenchyma cells	Prismatic crystals in upright, square and procumbent ray cells and in chambered axial parenchyma cells	Absent	Prismatic crystals in chambered axial parenchyma cells	?	Prismatic crystals in procumbent ray cells	Absent
Reference	This paper	Tsuchiya et al. (2002)	Gasson et al. (2004)	Bonilla et al. (2004)	Ramírez-Martínez et al. (2017)	Loupe et al. (2008)	InsideWood (2004-onwards)	Detienne and Jacquet (1983)	Man Chin (198)

4 Discussion

External characteristics of the bark, as well as the general, organoleptic, and macroscopic anatomical features of wood, can assist regulatory bodies in wood identification and in combating illegal exploitation and trade. This information can thereby contribute to the conservation efforts for this species (Silva et al. 2022b).

4.1 Systematic wood anatomy – The wood anatomy of *Tabaroa caatingicola* differs from other Brongniartieae genera by having more than 100 vessels.mm⁻², the vessels arranged in a radial pattern and perforated ray cells. Although comparing *T. caatingicola* with its closest genus, *Amphiodon*, is impeded by limited anatomical data for the latter, distinctions arise in growth rings, porosity, and axial parenchyma type: *Tabaroa* exhibits growth rings, semi-porous wood, and diffuse and scanty paratracheal, while *Amphiodon* lacks growth rings, displays diffuse-porous wood, with paratracheal parenchyma bands more than three cells wide (Tsuchiya et al. 2002). With the current data, no anatomical feature of the wood is exclusive to these two sister genera. A comprehensive wood anatomical description is advised for *Amphiodon effusus*.

Most wood anatomical features observed in *Tabaroa* and all other Brongniartieae genera are also widely observed in woody angiosperms: wood diffuse-porous (some tend to semi-porosity), vessels multiples, simple perforation plates, intervessel pits alternate, vessel–ray pits with distinct borders similar to intervessel pits in size and shape, libriform fibres with very thick-walled and non-septate, 4–12 rays.mm⁻² and gums and other deposits in heartwood vessels (except *Behaimia*) (Carlquist 2001; Wheeler and Baas 1991; Wheeler et al. 2007); or in Leguminosae wood: vested pits, 1–4 cells per parenchyma strand, and all rays, axial parenchyma and vessel elements storied (except *Limadendron*) (Carlquist 2001; Gasson 1996; Gasson 1999; Höhn 1999; Pernía and Melandri 2006; Ramanantsialonina et al. 2022; Stepanova et al. 2013). Hence, considering the limited data available among species of the Brongniartieae tribe, no anatomical trait can be inferred as synapomorphic of this clade. However, the composition of ray cells, diffuse and/or paratracheal scanty axial parenchyma (except *Amphiodon effusus* and *Harpalyce arborescens*), and the presence of prismatic crystals (except *H. arborescens* and *Poecilanthus parviflora*) appear to be very characteristic of the tribe.

The anatomical markers semi-ring-porous wood and thick-walled and radially flattened fibres are reported for *Harpalyce arborescens* A.Gray (Loupe et al. 2008), the latter also being described for *Poecilanthus parviflora* Benth. (Manieri and Chimelo 1989). The other Brongniartieae species either lack growth rings or exhibit marginal parenchyma, a more common anatomical marker in Leguminosae, also associated with deciduous species (Carlquist, 2001; Höhn 1999; Pernía and Melandri 2006; Silva 2006; Stepanova et al. 2013; Worbes and Fichtler 2010), although it does not occur in *Tabaroa*. *Tabaroa caatingicola* shares with its phylogenetically related genus *Harpalyce* tendency to semi-ring-porous wood and short vessel element length ($\leq 350 \mu\text{m}$) (Bonilla et al. 2004; Ramírez-Martínez et al. 2017).

Other anatomical similarities can be noted among the other Brongniartieae genera. For example, marginal parenchyma is characteristic of *Harpalyce*, *Limadendron*, and *Poecilanthus* (Bonilla et al. 2004; Detienne and Jacquet 1983; Manieri and Chimelo 1989; Ramírez-Martínez et al. 2017), being a type of parenchyma widely distributed across Leguminosae species (Carlquist 2001; Gasson 1996; Gasson 1999; Höhn 1999; Pernía and Melandri 2006; Ramanantsialonina et al. 2022; Stepanova et al. 2013). The polygonal intervessel pits are characteristic of *Behaimia*, *Haplormosia*, *Harpalyce*, and *Limadendron* (Bonilla et al. 2004; Detienne and Jacquet 1983; Gasson et al. 2004; Loupe et al. 2008). Tyloses is present in *Limadendron* and *Poecilanthus* (InsideWood 2004-onwards; Manieri and Chimelo 1989), it goes against the data which indicate that species with vessel–ray pits similar to intervessel pits, normally with small diameter, have a low probability of having tyloses (Bonsen and Kučera 1990; De Micco et al. 2016). The absence of deposits in heartwood vessels is indicated for *Behaimia* and *Harpalyce* (Bonilla et al. 2004; Gasson et al. 2004). Rays with multiseriate portions as wide as uniseriate portions are limiting to *Limadendron amazonicum* (InsideWood 2004-onwards).

4.2 Functional and ecological wood anatomy – Growth rings are present in the wood of *T. caatingicola* and are identified by three distinct anatomical markers: thick-walled and radially flattened fibres and distended rays, prone to semi-ring-porous wood. Anatomical markers can be characterized as histological contrasts arising from traits that vary between cells produced throughout a growing season, giving rise to early- and latewood (Silva 2023). Each of these

variations, whether in isolation or combination, generates identifiable features in the secondary xylem, recurring across multiple growing seasons. Currently, growth rings are conceived not only as a result of the vascular cambium's ability to respond to environmental and physiological changes but also to effect changes in the secondary xylem with significant functional implications (Carlquist 2000; Silva et al. 2019, 2021; Silva 2023).

Fibers with a smaller lumen and thicker walls are hypothesized to enhance the security of transport in vessel elements, representing the most widespread anatomical marker among angiosperms, particularly in tropical regions (Jacobsen et al. 2005; Silva et al. 2021). Semi-ring-porous wood is more commonly found in species distributed in subtropical and temperate regions (Silva et al. 2021). However, it is also present in tropical species, particularly in more seasonal habitats, like the Caatinga dry woodlands, where gradations between diffuse and semi-ring porosity can be observed (Aragão and Lisi 2019; Gasson et al. 2017; Silva 2006). This anatomical marker shows varying degrees of specialization in balancing the trade-off between embolism protection and efficient conduction. Broad vessels in the earlywood facilitate conduction capacity with a lower risk of embolism during periods of ample water availability. In contrast, narrower vessels in conditions of water scarcity, although less efficient for transport, ensure continuous xylem flow while minimizing the risk of embolism formation and the subsequent disruption of conduction (Baas et al. 2004; Sperry et al. 2006; Tyree and Zimmermann 2013). Distended rays, on the other hand, adapt to adjacent cells, preventing the formation of large intercellular spaces and, consequently, cracks in the secondary xylem (Silva et al. 2021; Silva 2023).

The seasonality and irregularity of rainfall in the Caatinga explain the formation of growth rings with an annual periodicity (Mattos et al. 2015; Nogueira Jr et al. 2018; Silva 2006) and infra-annual, potentially forming multiple annual ring (*sensu* Silva et al. 2019; Pagotto et al. 2015). The latter periodicity is also recognized for dry forests in East Africa (Gourlay 1995a, b; Jacoby 1989). The growth rings of *T. caatingicola* should be studied to determine the periodicity.

Given that *T. caatingicola* is ecologically confined to a semi-arid region, the vessel characteristics outlined here – including a degree of semi-porosity, predominantly multiple vessels, small diameter, high number of vessels per square millimeter, short vessel element length, simple perforation plates, and vested pits – are consistent with the well-established trade-off between safety × efficiency in conduction. This trade-off is widely recognized as the primary factor influencing the evolution of secondary xylem in seed plants (Baas et al. 2004). While the mechanisms of freeze-induced embolism are better understood, drought-induced embolism is a theme that has gained strength in recent years (Hacke et al. 2023; Olson 2022). Failures in sap transport through the xylem are among the main causes of death or reduced productivity in plants subjected to drought (Anfodillo and Olson 2021; Breshears et al. 2005, 2018; Brodrick and Cochard 2009; McDowell et al. 2018). So, cavitation vulnerability is a relevant hydraulic trait that determines a species' competitiveness under water stress (Islam et al. 2018).

Wider vessels are at a higher risk of embolism than narrower vessels within a tissue and when we compare species. Typically, wider vessels tend to be more vulnerable to drought-induced embolism, whereas embolism-resistant vessels are generally narrow (Hacke et al. 2023). This explanation justifies the small mean vessel diameter, as well as the slightly semi-ring porosity observed in *T. caatingicola*. The vessel diameter influences the variation in vessels per square millimeter. The inverse correlation between diameter and vessel frequency has been previously reported and is widely supported in the literature (Chave et al. 2009; Sperry et al. 2008).

The high percentage of multiple vessels, ranging from 71–80%, stands out in the wood of *T. caatingicola*. The performance of different levels of vessel grouping in secondary xylem is a controversial subject in the literature since Carlquist (1984). Some authors argue that multiple vessels increase the chances of propagating cavitation of air-seeding (Jacobsen et al. 2007; Tyree and Zimmermann 2013), while others suggest that a higher connection between vessels improves hydraulic integration, providing alternative pathways when embolism blocks flow in one vessel, reducing the potential loss of water transport capacity associated with cavitation (Loepfe et al. 2007; Trifilò et al. 2014). Despite many gaps in understanding the functioning of different vessel grouping levels, the latter argument is gaining strength by providing data that cavitation can be more easily removed in grouped vessels than in solitary ones (Hölttä et al. 2009), and that multiple vessels are more resistant to cavitation (Lens et al. 2011). In any case, *T. caatingicola* is part of the species in dry forests that exhibit greater vessel connectivity (Apgaua et al. 2022; Scholz et al. 2014).

The considerably short vessel elements described for the wood of *T. caatingicola* also have a functional relationship with the water-limited, arid environment in which this species grows. Carlquist (1975) hypothesized that shorter vessel elements have adaptive value, resisting mechanical deformation under negative pressure. Recently, a comparative analysis of over 1000 species confirmed Carlquist's prediction, indicating that shorter vessel elements affect vessel resistance to deformation. Species with exceptionally short vessel elements tend to grow in arid lands, while those with exceptionally long vessel elements tend to thrive in humid climates (Echeverría et al. 2023). Simple perforation plates are widely found in angiosperms, prevailing in species distributed across the tropics. Simple perforation plates provide considerably less resistance to sap flow between vessel elements, being crucial, when compared to compound perforation plates, for high flow demands (Carlquist 2001; Wheeler and Baas 1991; Wheeler et al. 2007), notably for plants growing in environments with scarce and irregular precipitation such as the Caatinga.

The vested pits described for the vessel elements of *T. caatingicola* are an anatomical trait of wood with systematic and functional value. They are generally associated with simple perforation plates, bordered pits, and dry environments, characterizing taxa such as the orders Myrtales and Gentianales, and families such as Malpighiaceae and Leguminosae (Jansen et al. 2001, 2008). Although vested pits are related to safety in hydraulic conduction, reducing vulnerability to cavitation or assisting in embolism repair, the mechanisms associated with these functionalities remain poorly understood (Jansen et al. 2008; Rabaey et al. 2010). The presence of highly lignified structures within the pit chamber can influence hydraulic resistance. Vested pits appear to facilitate embolism reversal in xeric and warmer regions with high transpiration rates (Jansen et al. 2003), like the Caatinga seasonally dry vegetation. The small pit apertures recorded for the vessel elements of *T. caatingicola* are associated with the small diameters of the vessel elements, as this trait covaries with vessel element diameter (Silva et al. 2022a).

The xylem of *T. caatingicola* is considered to have a high degree of xeromorphism based on the vulnerability and mesomorphy index values. Carlquist (1977) considered vulnerability index values significantly below 1.0, as observed here, to indicate a high degree of xeromorphy. Meanwhile, mesomorphy index values above 200 indicate mesophytic species. For these indices, higher values are associated with greater efficiency, while lower values are linked to greater safety

(Carlquist 1977). The vulnerability and mesomorphy indices proposed by Carlquist (1977) help quantify the degree of mesomorphy or xeromorphy exhibited in the plant xylem, contributing to a quantitative approach to plant anatomy, particularly in the fields of functional and ecological anatomy (Ewers et al. 2023).

Despite of the few data available for comparison, the other species of the Brongniartieae tribe exhibit a series of wood anatomy traits common to *T. caatingicola*. However, most of these traits are widely found in angiosperms and/or in Leguminosae. *Tabaroa caatingicola* has a set of wood anatomy traits that distinguishes it from other Brongniartieae genera. The wood anatomy of *T. caatingicola* reveals a set of adaptations to the SDTFW biome of the Brazilian Caatinga domain, where the low precipitation with irregular rains, high temperatures, and high transpiration potential increases the likelihood of drought-induced embolism formation (Hacke et al. 2023; Olson et al. 2023). These adaptations include semi-ring-porous wood with distinct growth ring boundaries, multiple narrow vessels, simple perforation plates, small and vested pits. These traits increase flow during periods of higher water availability and ensure hydraulic safety during scarcity, while also providing mechanisms to minimize the formation and spread of embolisms.

Declarations

Author contributions

The research project was initiated, and the study designed by M.S.S. and D.C. M.S.S. and D.C. conducted fieldwork and prepared the figures. M.S., L.B.S. and D.B. did the laboratory work and anatomical analyses. C.S. performed the SEM analyses. All authors contributed to the writing of the manuscript as well as approving the final submitted version of the paper.

Statements and Declarations

Conflict of interests: The authors declare that the manuscript does not present any kind of conflict of interests. The purpose and content of the work are original and not previously published. The published data are of non-financial interest.

References

1. Aguiar TV, Sant'anna-Santos BF, Azevedo AA, Ferreira RS (2007) ANATI QUANTI: software de análises quantitativas para estudos em anatomia vegetal. *Planta Daninha* 25:649–659. <https://doi.org/10.1590/S0100-83582007000400001>
2. Anfodillo T, Olson ME (2021) Tree mortality: testing the link between drought, embolism vulnerability, and xylem conduit diameter remains a priority. *Front glob change* 4:704670. <https://doi.org/10.3389/ffgc.2021.704670>
3. Apgaua DMG, Tng DYP, Laurance SGW (2022) Tropical wet and dry forest tree species exhibit contrasting hydraulic architecture. *Flora* 291:152072. <https://doi.org/10.1016/J.FLORA.2022.152072>
4. Aragão JRV, Lisi CS (2019) Caatinga tree wood anatomy: perspectives on use and conservation. *Floresta e Ambiente* 26:e20170997. <https://doi.org/10.1590/2179-8087.099717>
5. Baas P, Ewers FW, Davis SD, Wheeler EA (2004) Evolution of xylem physiology. In: Hemsley A, Poole I (eds) *The evolution of plant physiology: from whole plants to ecosystems*. Academic, Amsterdam, pp 273–295
6. Baas P, Wheeler E, Chase M (2000) Dicotyledonous wood anatomy and the APG system of angiosperm classification. *Bot J Linn Soc* 134:3–17. <https://doi.org/10.1111/J.1095-8339.2000.TB02343.X>
7. Bonilla LAM, Barajas Morales J, Tenorio Lezama P (2004) Anatomía de maderas de México. árboles y arbustos del Matorral Xerófilo de Tehuacán. *Publicaciones especiales del Instituto de Biología UNAM* 1–97
8. Bonsen KJM, Kučera LJ (1990) Vessel occlusions in plants: morphological, functional and evolutionary aspects. *IAWA J* 11:393–399. <https://doi.org/10.1163/22941932-90000528>
9. Breshears DD, Carroll CJW, Redmond MD et al (2018) A dirty dozen ways to die: metrics and modifiers of mortality driven by drought and warming for a tree species. *Front glob change* 01:415118. <https://doi.org/10.3389/FFGC.2018.00004/BIBTEX>
10. Breshears DD, Cobb NS, Rich PM et al (2005) Regional vegetation die-off in response to global-change-type drought. *PNAS* 102:15144–15148. <https://doi.org/10.1073/PNAS.0505734102>
11. Brodribb TJ, Cochard H (2009) Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiol* 149:575–584. <https://doi.org/10.1104/PP.108.129783>
12. Cardoso D, Harris DJ, Wieringa JJ et al (2017) A molecular-dated phylogeny and biogeography of the monotypic legume genus *Haplormosia*, a missing African branch of the otherwise American-Australian Brongniartieae clade. *Mol Phylogenet Evol* 107:431–442. <https://doi.org/10.1016/J.YMPEV.2016.12.012>
13. Cardoso D, Pennington RT, de Queiroz LP et al (2013) Reconstructing the deep-branching relationships of the papilionoid legumes. *S Afr J Bot* 89:58–75. <https://doi.org/10.1016/j.sajb.2013.05.001>
14. Cardoso D, Queiroz LP, Toby Pennington R et al (2012) Revisiting the phylogeny of papilionoid legumes: New insights from comprehensively sampled early-branching lineages. *Am J Bot* 99:1991–2013. <https://doi.org/10.3732/ajb.1200380>
15. Carlquist S (1975) *Ecological strategies of xylem evolution*. University of California Press, Berkeley, CA. 10.1525/9780520320567
16. Carlquist S (1977) Ecological factors in wood evolution: a floristic approach. *Am J Bot* 64:887–896. <https://doi.org/10.1002/j.1537-2197.1977.tb11932.x>
17. Carlquist S (1984) Vessel grouping in Dicotyledon wood. *Aliso: J Syst Floristic Bot* 10:505–525

18. Carlquist S (2013) Comparative Wood Anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood, 1st edn. Springer, Berlin, Heidelberg, Berlin, Heidelberg
19. Carlquist S (2000) Wood and stem anatomy of *Sarcobatus* (Caryophyllales): systematic and ecological implications. *Taxon* 49(1):27–34. <https://doi.org/10.2307/1223929>
20. Carlquist S (2001) Wood anatomy of the endemic woody Asteraceae of St Helena I: phyletic and ecological aspects. *Bot J Linn Soc* 137:197–210. <https://doi.org/10.1111/J.1095-8339.2001.TB01116.X>
21. Chave J, Coomes D, Jansen S et al (2009) Towards a worldwide wood economics spectrum. *Ecol Lett* 12:351–366. <https://doi.org/10.1111/J.1461-0248.2009.01285.X>
22. De Micco V, Balzano A, Wheeler EA, Baas P (2016) Tyloses and gums: a review of structure, function and occurrence of vessel occlusions. *IAWA J* 37:186–205. <https://doi.org/10.1163/22941932-20160130>
23. Détienne P, Jacquet P (1983) Atlas d'identification des bois de l'Amazonie et des regions voisines. Centre Technique Forestier Tropical, Nogent-Sur-Marne
24. Dunnington D (2023) ggspatial: Spatial Data Framework for ggplot2. <https://paleolimbot.github.io/ggspatial>, <https://github.com/paleolimbot/ggspatial>
25. Echeverría A, Petrone-Mendoza E, Anfodillo T et al (2023) Testing carlquistian hypotheses on the functional significance of vessel element length. *IAWA J* 44:399–428. <https://doi.org/10.1163/22941932-BJA10126>
26. Ewers FW, Jacobsen AL, López-Portillo J (2023) Carlquist's indices for vulnerability and mesomorphy of wood: are they relevant today? *IAWA J*. <https://doi.org/10.1163/22941932-bja10113>
27. Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol* 37:4302–4315
28. Fontes CG, Pinto-Ledezma J, Jacobsen AL et al (2022) Adaptive variation among oaks in wood anatomical properties is shaped by climate of origin and shows limited plasticity across environments. *Funct Ecol* 36:326–340. <https://doi.org/10.1111/1365-2435.13964>
29. Franklin GL (1945) Preparation of thin sections of synthetic resins and wood-resin composites, and a new macerating method for wood. *Nature* 155:51
30. Gasson P (1996) Wood anatomy of the tribe Swartzieae with comments on related papilionoid and caesalpinoid Leguminosae. *IAWA J* 17:45–74. <https://doi.org/10.1163/22941932-90000624>
31. Gasson P (1999) Wood anatomy of the tribe Dipterygeae with comments on related papilionoid and caesalpinoid Leguminosae. *IAWA J* 20:441–455. <https://doi.org/10.1163/22941932-90001570>
32. Gasson P, Cartwright C, Leme CLD (2017) Anatomical changes to the wood of *Croton sonderianus* (Euphorbiaceae) when charred at different temperatures. *IAWA J* 38:117–123. <https://doi.org/10.1163/22941932-20170161>
33. Gasson P, Wray E, Schrire BD (2004) Wood anatomy of the tribe Millettieae with comments on related papilionoid Leguminosae. *IAWA J* 25:485–545. <https://doi.org/10.1163/22941932-90000380>
34. Giulietti AM, Luiza du Bocage Neta A, Alberto F, Castro AJ et al (2004) Diagnóstico da vegetação nativa do bioma Caatinga. Biodiversidade da Caatinga: áreas e ações prioritárias para a conservação 48–90
35. Gourlay ID (1995a) Growth ring characteristics of some African *Acacia* species. *J Trop Ecol* 11:121–140. <https://doi.org/10.1017/S0266467400008488>
36. Gourlay ID (1995b) The definition of seasonal growth zones in some African *Acacia* species - a review. *IAWA J* 16:353–359. <https://doi.org/10.1163/22941932-90001425>
37. Hacke UG, Jacobsen AL, Pratt RB (2023) Vessel diameter and vulnerability to drought-induced embolism: within-tissue and across-species patterns and the issue of survivorship bias. *IAWA J* 44:304–319. <https://doi.org/10.1163/22941932-BJA10107>
38. Hajek P, Kurjak D, von Wühlisch G et al (2016) Intraspecific variation in wood anatomical, hydraulic, and foliar traits in ten european beech provenances differing in growth yield. *Front Plant Sci* 7:14. <https://doi.org/10.3389/fpls.2016.00791>
39. Herendeen PS, Miller RB (2000) Utility of wood anatomical characters in cladistic analyses. *IAWA J* 21:247–276. <https://doi.org/10.1163/22941932-90000247>
40. Hijmans R (2024) raster: Geographic Data Analysis and Modeling. R package version 3.6–27
41. Höhn A (1999) Wood anatomy of selected West African species of Caesalpinioideae and Mimosoideae (Leguminosae): a comparative study. *IAWA J* 20:115–146. <https://doi.org/10.1163/22941932-90000672>
42. Hölltä T, Cochard H, Nikinmaa E, Mencuccini M (2009) Capacitive effect of cavitation in xylem conduits: results from a dynamic model. *Plant Cell Environ* 32:10–21. <https://doi.org/10.1111/J.1365-3040.2008.01894.X>
43. IAWA Committee (1989) IAWA list of microscopic features for hardwood identification with an Appendix on non-anatomical information IAWA Committee. *IAWA Bull n s* 10:219–332
44. InsideWood (2004) -onwards In: Published on the Internet. <http://insidewood.lib.ncsu.edu/search>. Accessed 26 June 2023
45. Islam M, Rahman M, Bräuning A (2018) Long-term hydraulic adjustment of three tropical moist forest tree species to changing climate. *Front Plant Sci* 9:1761. <https://doi.org/10.3389/FPLS.2018.01761/BIBTEX>
46. IUCN - International Union for Conservation of Nature and Natural Resources (2001) IUCN Red list categories and criteria. Versão 3.1 IUCN species survival Comission. Gland, Switzerland and Cambridge, UK
47. Jacobsen AL, Ewers FW, Pratt RB et al (2005) Do xylem fibers affect vessel cavitation resistance? *Plant Physiol* 139:546–556. <https://doi.org/10.1104/PP.104.058404>
48. Jacobsen AL, Pratt RB, Ewers FW, Davis SD (2007) Cavitation resistance among 26 chaparral species of southern California. *Ecol Monogr* 77:99–115. <https://doi.org/10.1890/05-1879>

49. Jacoby GC (1989) Overview of tree-ring analysis in tropical regions. *IAWA J* 10:99–108. <https://doi.org/10.1163/22941932-90000478>
50. Jansen S, Baas P, Gasson P, Smets E (2008) Vestured pits: a diagnostic character in the secondary xylem of Myrtales. *J Plant Sci* 20:328–339. <https://doi.org/10.1086/374369>
51. Jansen S, Baas P, Gasson P, Smets E (2003) Vestured pits: do they promote safer water transport? *Int J Plant Sci* 164:405–413. <https://doi.org/10.1086/374369>
52. Jansen S, Baas P, Smets E (2001) Vestured pits: their occurrence and systematic importance in eudicots. *Taxon* 50:135–167. <https://doi.org/10.2307/1224516>
53. Johansen DA (1940) *Plant microtechnique*. McGraw-Hill Book Company, Inc: London; 530p
54. Kahle D, Wickham H (2013) ggmap: spatial visualization with ggplot2. *R J* 5:144
55. Kraus JE, Arduin M (1997) *Manual básico de métodos em morfologia vegetal*. Universidade Rural. Seropedica, RJ
56. Kukachka BF (1980) Wood anatomy of the neotropical Sapotaceae: *Paralabatia*. XVI, 6th edn. Forest Products Laboratory, Forest Service, US Department of Agriculture, USA
57. Leal IR, Da Silva JMC, Tabarelli M, Lacher TE (2005) Changing the course of biodiversity conservation in the caatinga of northeastern Brazil. *Conserv Biol* 19:701–706. <https://doi.org/10.1111/j.1523-1739.2005.00703.x>
58. Lens F, Dressler S, Jansen S et al (2005) Relationships within balsaminoid Ericales: a wood anatomical approach. *Am J Bot* 92:941–953. <https://doi.org/10.3732/ajb.92.6.941>
59. Lens F, Schönenberger J, Baas P et al (2007) The role of wood anatomy in phylogeny reconstruction of Ericales. *Cladistics* 23:229–294
60. Lens F, Sperry JS, Christman MA et al (2011) Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus *Acer*. *New Phytol* 190:709–723. <https://doi.org/10.1111/J.1469-8137.2010.03518.X>
61. Loepfe L, Martínez-Vilalta J, Piñol J, Mencuccini M (2007) The relevance of xylem network structure for plant hydraulic efficiency and safety. *J Theor Biol* 247:788–803. <https://doi.org/10.1016/J.JTBI.2007.03.036>
62. Louppe D, Oteng-Amoako AA, Brink M (eds) (2008) *Plant resources of tropical Africa. Prota 7(1): 704p timbers 1*. Backhuys Publishers, Wageningen, Netherlands
63. Mainieri C, Chimelo JP (1989) *Fichas de características das madeiras brasileiras*, 2nd edn. ITP - Instituto de Pesquisas Tecnológicas, Divisão de Madeiras, São Paulo
64. Mattos PP, Muñoz Braz E, Dressano Domene V et al (2015) Climate-tree growth relationships of *Mimosa tenuiflora* in seasonally dry tropical forest. *Brasil CERNE* 21:141–149. <https://doi.org/10.1590/01047760201521011460>
65. McDowell N, Allen CD, Anderson-Teixeira K et al (2018) Drivers and mechanisms of tree mortality in moist tropical forests. *New Phytol* 219:851–869. <https://doi.org/10.1111/NPH.15027>
66. Meireles JE, Tozzi AMGA, Lavin M (2014) A phylogenetic analysis of molecular and morphological data reveals a paraphyletic *Poecilanthus* (Leguminosae, Papilionoideae). *Syst Bot* 39:1142–1149. <https://doi.org/10.1600/036364414X683912>
67. Nogueira FC, Pagotto MA, Roig FA et al (2018) Responses of tree-ring growth in *Schinopsis brasiliensis* to climate factors in the dry forests of northeastern Brazil. *Trees - Struct Function* 32:453–464. <https://doi.org/10.1007/S00468-017-1642-3/TABLES/5>
68. O'Donnell MS, Ignizio DA (2012) *Bioclimatic predictors for supporting ecological applications in the conterminous United States*. U.S. Geological Survey, Data Series 691, Virginia, U.S
69. Olson ME (2005) Commentary: typology, homology, and homoplasy in comparative wood anatomy. *IAWA J* 26:507–522. <https://doi.org/10.1163/22941932-90000131>
70. Olson ME (2022) Linking xylem structure and function: the comparative method in from the cold. *New Phytol* 235:815. <https://doi.org/10.1111/NPH.18179>
71. Olson ME, Pace MR, Anfodillo T (2023) The vulnerability to drought-induced embolism-conduit diameter link: breaching the anatomy-physiology divide. *IAWA J* 44:335–354. <https://doi.org/10.1163/22941932-BJA10123>
72. Pace MR, Gerolamo CS, Onyenedum JG et al (2022) The wood anatomy of Sapindales: diversity and evolution of wood characters. *Rev Bras Bot* 45:283–340. <https://doi.org/10.1007/S40415-021-00764-2>
73. Pagotto MA, Roig FA, de Souza Ribeiro A, Lisi CS (2015) Influence of regional rainfall and Atlantic Sea surface temperature on tree-ring growth of *Poincianella pyramidalis*, semiarid forest from Brazil. *Dendrochronologia (Verona)* 35:14–23. <https://doi.org/10.1016/J.DENDRO.2015.05.007>
74. Pernía NE, Melandri JL (2006) Wood anatomy of the tribe Caesalpinieae (Leguminosae, Caesalpinioideae) in Venezuela. *IAWA J* 27:99–114. <https://doi.org/10.1163/22941932-90000140>
75. POWO - Plants of the World Online (2024) *Plants of the World Online | Kew Science*. In: Facilitated by the Royal Botanic Gardens, Kew. <https://powo.science.kew.org/cite-us>. Accessed 27 Dec 2023
76. Queiroz LP (2006) The Brazilian Caatinga: Phytogeographical Patterns Inferred from Distribution Data of the Leguminosae. In: Pennington R, T, Lewis GP, Ratter J. A (eds) *Neotropical Savannas and Seasonally Dry Forests: Plant Diversity, Biogeography, and Conservation*. CRC, London, UK, pp 121–157
77. Queiroz LP (2009) *Leguminosas da caatinga*. Universidade Estadual de Feira de Santana, Feira de Santana
78. Queiroz LP, São-Mateus W, Delgado-Salinas A et al (2017) A molecular phylogeny reveals the Cuban enigmatic genus *Behaimia* as a new piece in the Brongniartieae puzzle of papilionoid legumes. *Mol Phylogenet Evol* 109:191–202. <https://doi.org/10.1016/j.ympev.2017.01.001>

79. Queiroz LP, Lewis GP, Wojciechowski MF (2010) *Tabaroa*, a new genus of Leguminosae tribe Brongniartieae from Brazil. *Kew Bull* 65:189–203. <https://doi.org/10.1007/S12225-010-9202-7/FIGURES/6>
80. Rabaey D, Lens F, Smets E, Jansen S (2010) The phylogenetic significance of vestured pits in Boraginaceae. *Taxon* 59:510–516. <https://doi.org/10.1002/TAX.592016>
81. Ramanantsialonina RN, Cramer S, Sandratrinaiaina NA et al (2022) Comparative wood anatomy of 16 Malagasy *Dalbergia* species (Fabaceae) using multivariate techniques. *IAWA J* 44:225–252. <https://doi.org/10.1163/22941932-BJA10105>
82. Ramírez-Martínez M, Terrazas T, Aguilar-Rodríguez S et al (2017) Madera y bosques 23:21–41. <https://doi.org/10.21829/MYB.2017.2321126>. Anatomía de la madera de especies de la selva baja caducifolia de Tamaulipas, México
83. Reflora - Herbario Virtual. Disponível em: <https://reflora.jbrj.gov.br/reflora/herbarioVirtual/> Acesso em 30/1/2024
84. RStudio Team, RStudio (2022) RStudio: integrated development for R. PBC, Boston, MA URL. <http://www.rstudio.com/>
85. Sass JE (1951) Botanical microtechnique 2. Iowa State College 97, ed. Ames
86. Scholz A, Stein A, Choat B, Jansen S (2014) How drought and deciduousness shape xylem plasticity in three Costa Rican woody plant species. *IAWA J* 35:337–355. <https://doi.org/10.1163/22941932-00000070>
87. Silva JMC (ed) (2004) Biodiversidade da caatinga: áreas e ações prioritárias para conservação. Ministério do Meio Ambiente, Brasília
88. Silva LB (2006) Variação na estrutura da madeira de quatro espécies da caatinga nordestina e seu potencial para o desenvolvimento sustentável. Dissertação, Universidade Estadual de Feira de Santana
89. Silva MS, Apgaua DMG, Silva CCS et al (2022a) Expanding the wood anatomy economics spectrum: the correlates of vessel element lengths and pit apertures sizes in tropical forest trees. *Plant Ecol Divers* 14:279–291. <https://doi.org/10.1080/17550874.2022.2053600>
90. Silva MS, Funch LS, Silva LB (2019) The growth ring concept: seeking a broader and unambiguous approach covering tropical species. *Biol Rev* 94:1161–1178. <https://doi.org/10.1111/BRV.12495>
91. Silva MS, Funch LS, Silva LB, Cardoso D (2021) A phylogenetic and functional perspective on the origin and evolutionary shifts of growth ring anatomical markers in seed plants. *Biol Rev* 96:842–876. <https://doi.org/10.1111/BRV.12681>
92. Silva MS (2023) Carlquist's growth ring classification: a functional approach that reinforces porous and annual rings. *IAWA J* 44:539–556. <https://doi.org/10.1163/22941932-BJA10128>
93. Silva MS, Silva LB, Santos NC et al (2022b) Timbers of Bahia: wood anatomy of native species of the Atlantic Forest, 1st edn. EDUFBA, Salvador - Bahia
94. South A (2017) `maturalearthdata`: world vector map data from natural earth used in `maturalearth` & #8217
95. SpeciesLink network (2024) <https://specieslink.net/search/>. Accessed 29
96. Sperry JS, Hacke UG, Pittermann J (2006) Size and function in conifer tracheids and angiosperm vessels. *Am J Bot* 93:1490–1500. <https://doi.org/10.3732/AJB.93.10.1490>
97. Sperry JS, Meinzer FC, McCulloh KA (2008) Safety and efficiency conflicts in hydraulic architecture: scaling from tissues to trees. *Plant Cell Environ* 31:632–645. <https://doi.org/10.1111/J.1365-3040.2007.01765.X>
98. Stepanova AV, Kotina EL, Tilney PM, Van Wyk BE (2013) Wood and bark anatomy of *Hypocalyptus* support its isolated taxonomic position in Leguminosae. *S Afr J Bot* 89:234–239. <https://doi.org/10.1016/J.SAJB.2013.07.004>
99. Thiers B, (continuously updated) (2022) Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/science/ih>. Accessed 27 Jan 2022
100. Trifilò P, Barbera PM, Raimondo F et al (2014) Coping with drought-induced xylem cavitation: coordination of embolism repair and ionic effects in three Mediterranean evergreens. *Tree Physiol* 34:109–122. <https://doi.org/10.1093/TREEPHYS/TPT119>
101. Tsuchiya A, Hirabuki Y, Nishizawa T et al (2002) The relationship between stem vessel parameters and the development of strata in the early stages of secondary forest succession in Amazonia. *Acta Amazon* 32:241–241. <https://doi.org/10.1590/1809-43922002322256>
102. Tyree MT, Zimmermann MH (2013) Xylem structure and the ascent of sap. Springer Science & Business Media, Berlin
103. WFO (2024) World Flora Online. Published on the Internet; <http://www.worldfloraonline.org>. Accessed on 30 Jan 2024'
104. Wheeler EA, Baas P (1991) A survey of the fossil record for dicotyledonous wood and its significance for evolutionary and ecological wood anatomy. *IAWA J* 12:275–318. <https://doi.org/10.1163/22941932-90001256>
105. Wheeler EA, Baas P, Rodgers S (2007) Variations in dicot wood anatomy: a global analysis based on the Insidewood database. *IAWA J* 28:229–258. <https://doi.org/10.1163/22941932-90001638>
106. Wickham H (2016) `ggplot2` - elegant graphics for data analysis. Springer, New York, USA
107. Worbes M, Fichtler E (2010) Wood anatomy and tree-ring structure and their importance for tropical dendrochronology. In: Junk WJ et al (eds) Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management. Springer, Berlin, pp 329–346
108. Zizka A, Silvestro D, Andermann T et al (2019) CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. *Methods Ecol Evol* 10:744–751. <https://doi.org/10.1111/2041-210X.13152>

Figures

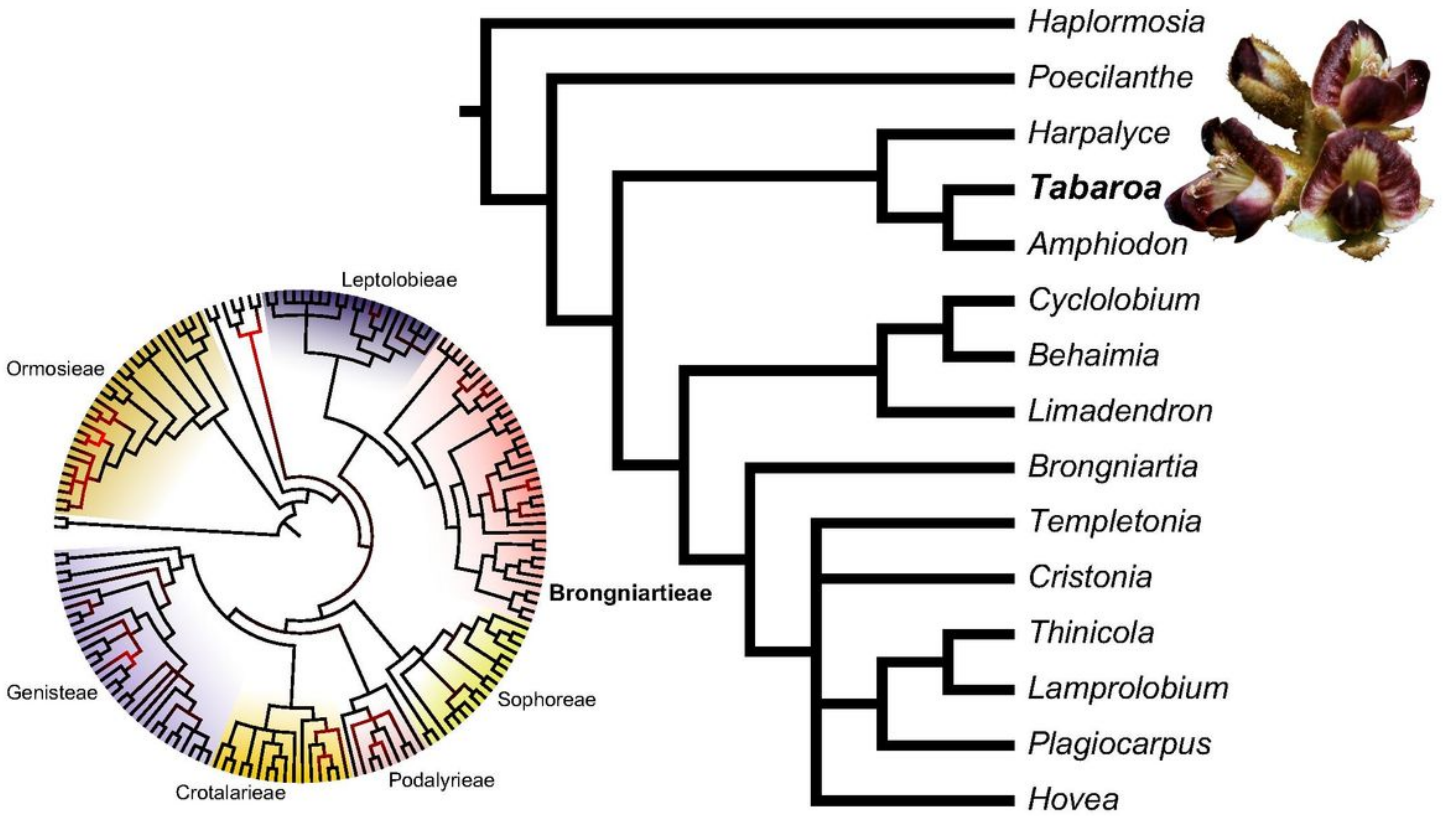


Figure 1
 Bayesian majority-rule consensus tree based on *matK* sequence data (from Cardoso et al. 2017) showing the relationship of the tribe Brongniartieae with respect to the main lineages of the early branching Genistoid clade of papilionoid legumes (circular cladogram on the lower left), and a summary of the genus-level Brongniartieae phylogeny showing the placement of *Tabaroa* (cladogram on the right). Photo of the *Tabaroa* flowers by Luciano Paganucci de Queiroz.

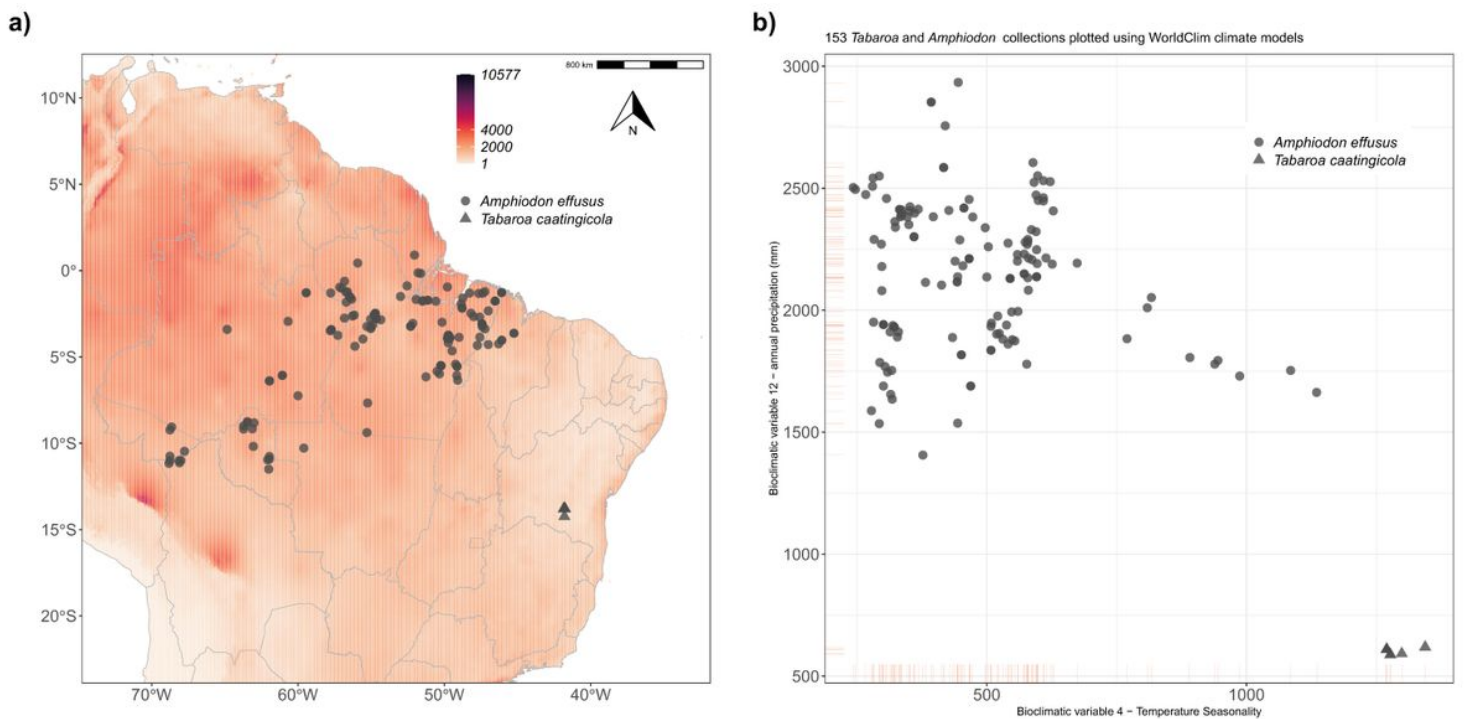


Figure 2
 153 *Tabaroa* and *Amphiodon* collections plotted using WorldClim climate models

Distribution of the phylogenetically closely related monotypic genera *Tabaroa* (focus of the current anatomical characterization) and *Amphiodon* across geographic and climatic spaces. a) The geographical distribution of *Tabaroa* is narrowly restricted to areas with low annual precipitation in the Caatinga of the Brazilian Northeast, whereas *Amphiodon* distribution spans a wide range across wetter areas of the Amazon. b) Climate space of *Tabaroa* and *Amphiodon* plotted using the WorldClim-derived bioclimatic variable BIO12 and BIO4 (Fick and Hijmans 2017).

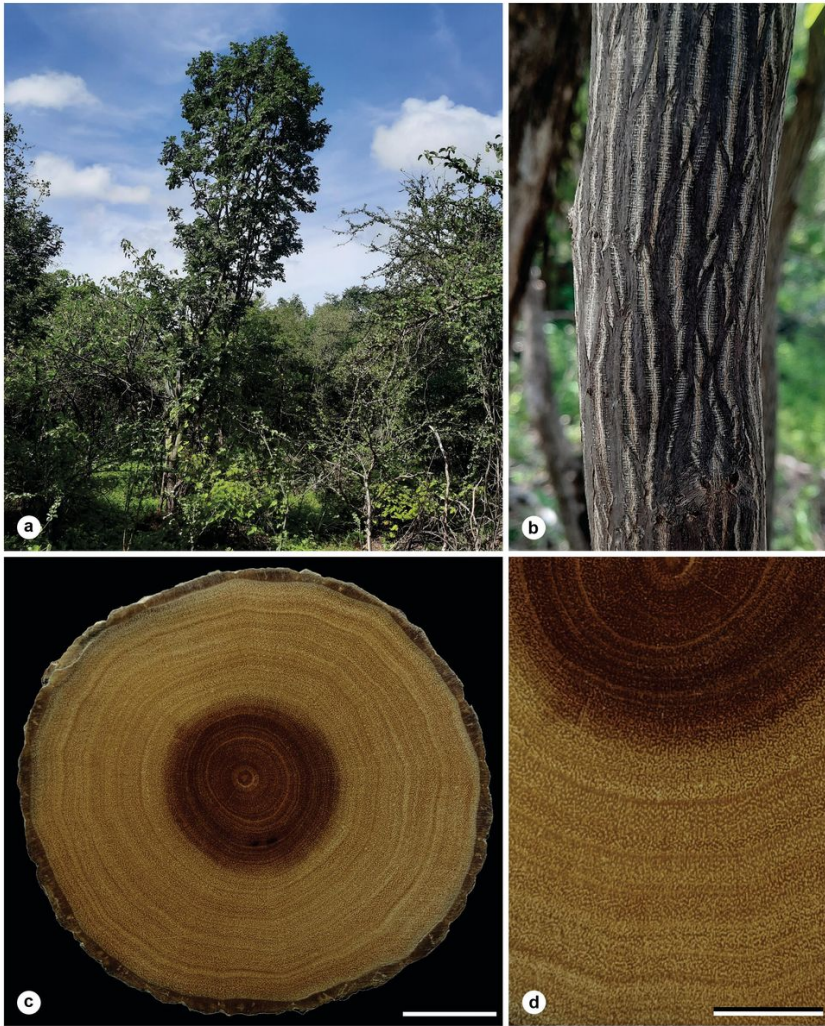


Figure 3
Tabaroa caatingicola (Leguminosae). **a:** *T. caatingicola*, most prominent tree in the center of the image, in its natural habitat during the rainy season. **b:** Trunk showing the characteristic 'crocodile skin' bark pattern. **c-d:** Transversely cut stem showing the brown heartwood and yellowish sapwood, in addition to the growth rings. Scale bar – c: 1.0 cm; d: 0.5 cm. Photos: Marcelo dos S. Silva.

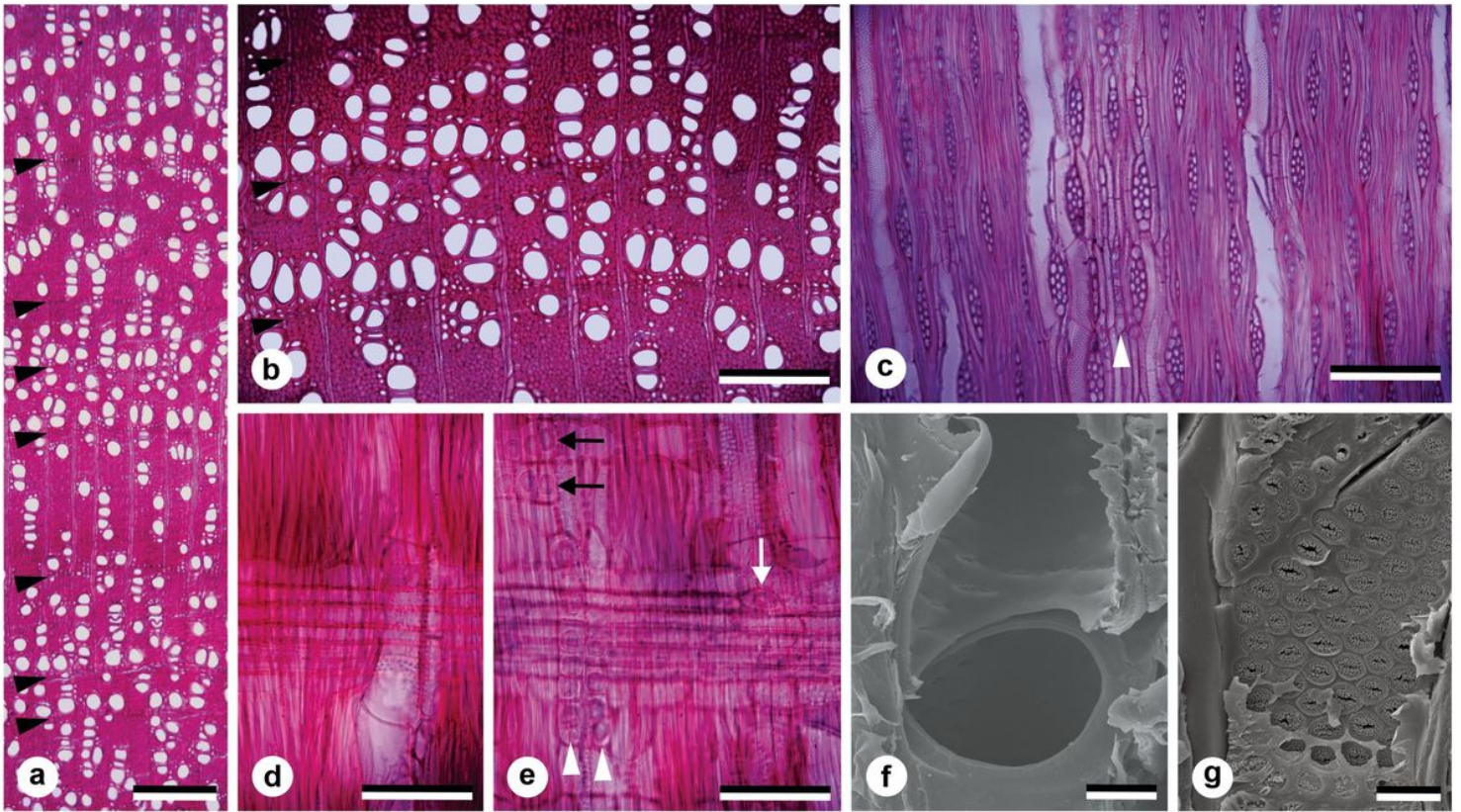


Figure 4

Wood anatomy of the papilionoid legume *Tabaroa caatingicola*. **a – e**: Light microscopy. **f – g**: Scanning electron microscope. **a – b**: Cross section, black arrowhead indicates the limit of the growth rings. **c**: Tangential section, white arrowhead indicates prismatic crystals in chambered axial parenchyma cells. **d – e**: Radial section, white arrowhead indicates prismatic crystals in chambered axial parenchyma cells; white arrow identifies prismatic crystals in procumbent ray cells and black arrow indicates prismatic crystals in upright ray cells. **f**: Radial section showing a detail of vessel elements with simple perforation plate. **g**: Detail of a vessel element in tangential view showing intervessel pits alternate and vestured. Scale bar – a: 300 mm; b – c: 200 mm; d – e: 100 mm; f – g: 10 mm.