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Wood anatomy of two species of the genus *Chrysochlamys* (Clusiaceae: Clusioideae: Clusieae) from the northern Andes of Colombia

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ABSTRACT

Chrysochlamys is a genus of neotropical angiosperms distributed in wet and riparian forests from Bolivia to Mexico in altitudes from near sea-level to close to 3000 m. The wood anatomy of two species of the genus was investigated. Branches of mature stems were collected in a secondary wet forest in Colombian Northern Andes. Slides were obtained and visualized using light microscopy. Gelatinous fiber bands were found and described in *C. colombiana* and *C. dependens*. There was a higher amount of septate fibers in the latter. Average ray height and pigment deposit content in ray cells was greater in *C. colombiana* relative to *C. dependens*, but rays were commonly wider in the second one. The diversity of vessel-ray pit shapes in *C. dependens* is greater than in *C. colombiana*. In both cases rays are considered to be paedomorphic type I. Scanty to absent axial and apotracheal parenchyma was found for both species. We discuss the similarities and differences of the two species in order to establish diagnostic wood features. Also we include brief notes in comparative anatomy with other members of the Clusieaceae family, emphasizing in the incongruences found with previous reports for the genus. This is the first descriptive work in wood anatomy of *C. colombiana* and *C. dependens*.

1. Introduction

The Clusiaceae family has 24 accepted genera distributed among three tribes: Clusieae, Garcinieae, and Symphonieae. The genus *Chrysochlamys* has been classified in the Clusieae tribe and is distributed in wet to very wet primary and secondary forests from Mexico to Bolivia, Brazil, and St. Lucia in the Caribbean at altitudes up to 3000 m.a.s.l. *Chrysochlamys colombiana* (Cuatrec.) Cuatrec. is an endemic species of Colombia and Ecuador while *Chrysochlamys dependens* Planch & Triana has a range that covers only northern Andean forests [1, 2, 3]. *Chrysochlamys* shrubs and trees are characterized by coriaceous opposite leaves in decussate branching. Usually with white or yellow latex and a lack of stilt roots. Inflorescences generally axillary with imperfect flowers [2]. Fruits are reddish at maturity with dehiscent carpels with orange-like arillate seeds [4].

It has been observed that *C. colombiana* and *C. dependens* trees are abundant in middle elevation and lowland rainforests from central and western Colombia. Due to the durability of their wood, they represent a useful timber resource for adjacent human communities that employ them for the construction of pillars and ceilings of houses, the crafting of kitchen utensils, and as firewood [5, 6]. Additionally, the production of secondary metabolites from other *Chrysochlamys* species points out the potential of this group as a target for bioprospecting studies related to allelopathy, antiparasitic properties and inhibition of HIV replication [7, 8, 9, 10].

Despite the ethnobotanical and scientific importance of *Chrysochlamys* species, there are very few studies about the wood anatomy of the genus that could serve as references of diagnostic and ecological value. The goal of this study is to describe the wood anatomy of *C. colombiana* and *C. dependens* with brief notes on the physical properties of these woods and their anatomical relationships with other species of the Clusieae tribe.

2. Methods

2.1. Collection site

Mature branches of *C. colombiana* and *C. dependens* were collected using a pole pruner from trees with an average height of 16 m growing in an Andean forest ecosystem (~1900 masl). The sampling site was located in the slopes of small river terraces and is part of a private well-preserved forest patch located in Filandia, Quindío Department, Colombia (Fig. 1).

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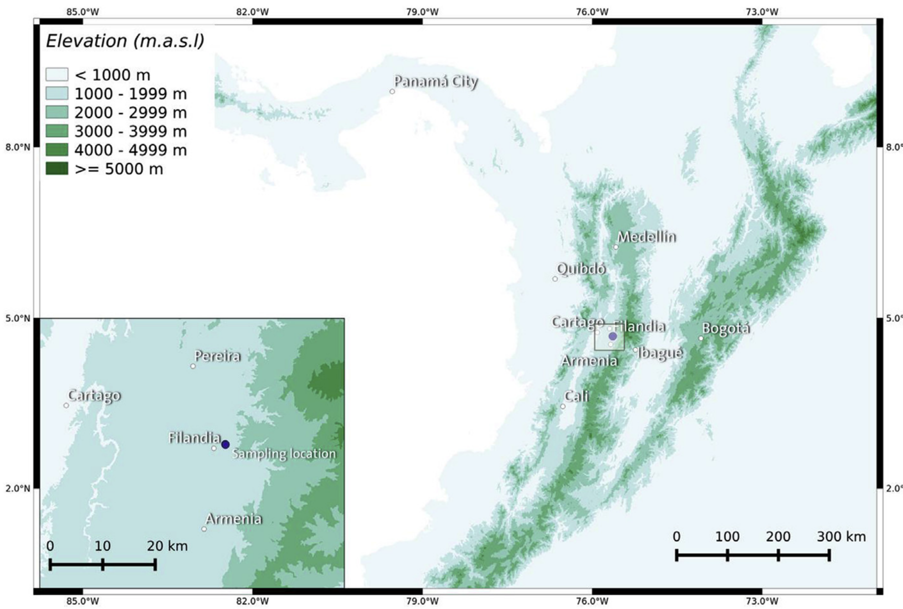

Fig. 1. Map of the sampling area of the study. The purple circle represents the location of the sampling transepts. The contour color scale corresponds to an elevation model of the terrain derived from CGIAR-CSI SRTM 90m Database [19]. White circles represent the main cities in the region.

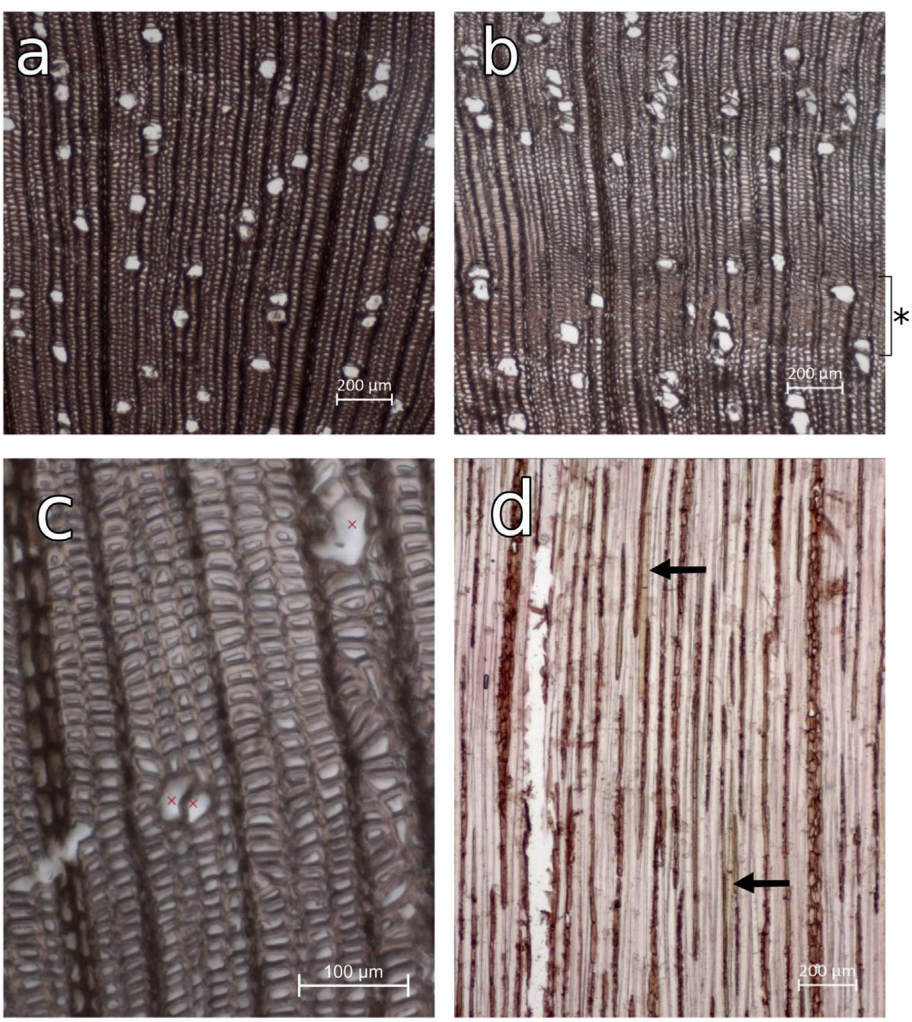

Fig. 2. Anatomical features of *Chrysochlamys colombiana*. Part I. a) Transverse section showing diffuse porosity of the wood and diffuse arrangement of the vessels (commonly in small clusters of 2–3 and without a specific pattern across the wood). b) Transverse section showing a tangential band of gelatinous fibers, delimited by a bracket and an asterisk, corresponding to a region of tension wood. Note the change in cell wall thickness and lumen diameter of the cells. c) Detail of gelatinous fibers in transverse section. Red crosses represent the lumen of vessels. d) Tangential section showing a high density of rays per mm. Black arrows indicate parenchyma cells.

Branches from four trees of *C. dependens* (n = 4) were collected in the transept from 4° 40′49.728″ N 75° 38′18.167″ W to 4° 40′50.412″ N 75° 38′18.347″ W. Branches from six trees of *C. colombiana* (n = 6) were collected in the transept from 4° 40′52.860″ N 75° 38′19.176″ W to 4° 40′50.484″ N 75° 38′17.627″ W. The diameter of the collected branches ranged from 20 to 45 cm. Wood samples were brought to the Laboratory of Palynology and Tropical Paleoecology at Universidad de los Andes for further analysis.

2.2. Sample sectioning and anatomical description

The branches were allowed to dry at ambient conditions for a week due to transportation constraints. Three small blocks, suitable for microtome sectioning, were cut out from each branch. The blocks were rehydrated and softened for sectioning by subjecting them to 4–5 cycles of autoclaving at 121 °C for 20 min in a variation of the method proposed by Yeung et al. [11]. Then, blocks were kept in Strasburger Solution (95% ethanol, 99% glycerol, and distilled water, 1:1:1) until sectioning in order to preserve the cell structure and avoiding biodegradation. Transversal, longitudinal tangential, and longitudinal radial sections (thickness: 20–30 μm) were obtained from the blocks using a Leica RM2125 RTS rotary microtome. Staining of the sections was carried out with 1% ethanolic solution of safranin (3 min) and washing with serial dilutions of ethanol: 95% (1 min), 70% (1 min), and 50% (1 min). The final sections were mounted with glycerol jelly and deposited in the archive of the Laboratory of Palynology and Tropical Paleoecology of the Universidad de los Andes, Colombia. These slides can be consulted upon request. The wood slides were microphotographed with an Axio Imager A2 microscope (Carl Zeiss, Jena). All the feature descriptions were made following the criteria of the International Association of Wood Anatomists [12] and Carlquist (2001) [13].

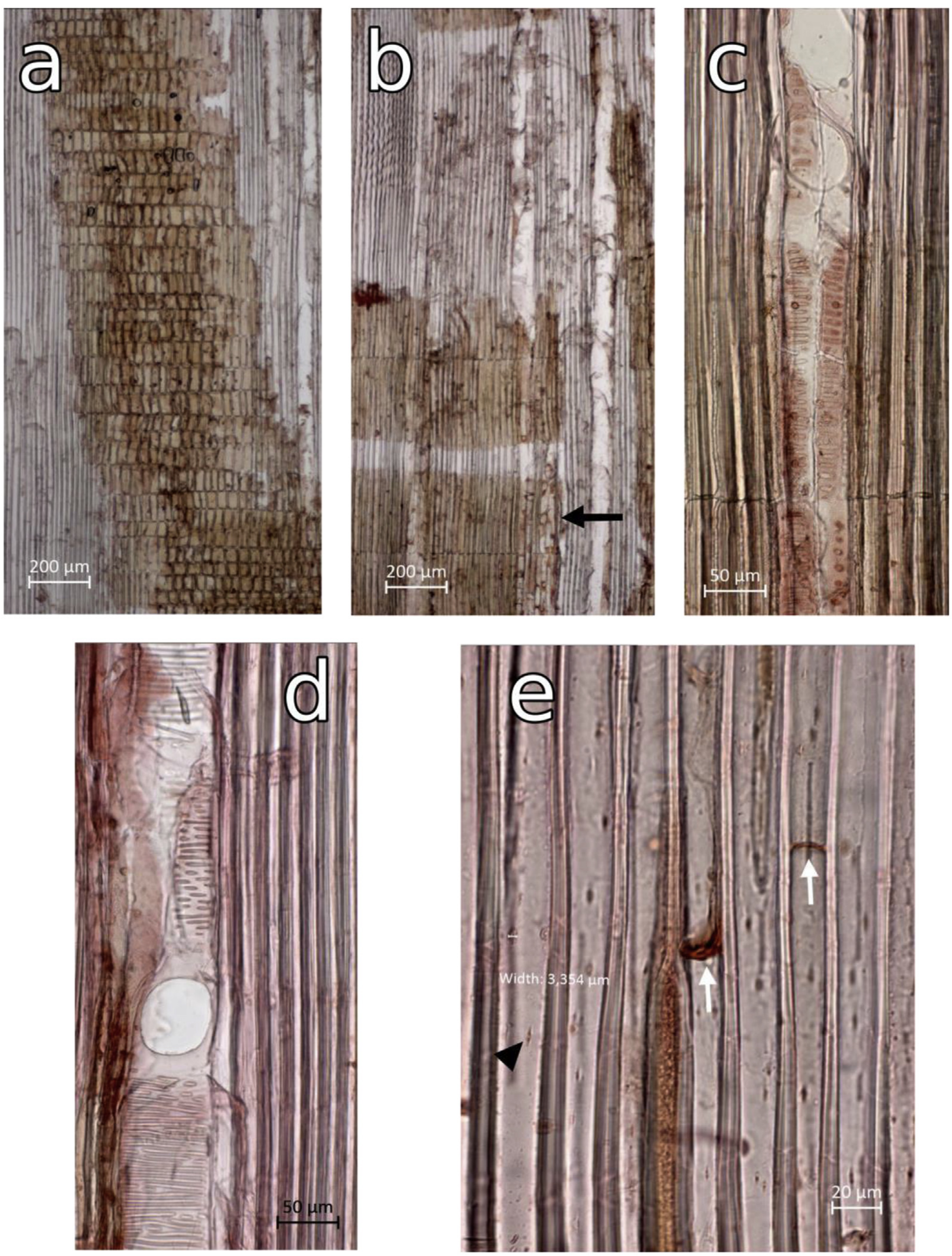

Fig. 3. Anatomical features of *Chrysochlamys colombiana*. Part II – Radial sections. a) Multiseriate rays are tall (>1 mm height) and composed mainly of upright and square cells with abundant pigment deposits. b) Uniseriate rays are composed exclusively by upright cells. The black arrow indicates a row of ray cells. c) Radial section overview of the scalariform vessel-ray pits that connect upright ray cells with vessel elements. d) Detail of a vessel element with a simple perforation plate in subterminal position and long scalariform intervessel pits. e) Radial view of the features of libriform fibers. Minutely bordered pits with a diameter of ~3 μm can be observed in low abundance. The black arrowhead indicates a simple pit, and white arrows indicate the septum in septate fibers.

3. Results

3.1. Chrysochlamys colombiana

Chrysochlamys colombiana is a diffuse porous wood that shows frequently visible discontinuous bands of thick-walled gelatinous fibers that macroscopically resemble tree rings (Fig. 2a-b). The average density of vessels per square millimeter was 15.4 (Standard Deviation (SD) = 4.6, Range = 11–23, n = 5 fields and 77 vessels) (Supplementary Table 1). The tangential diameter of vessels is very regular throughout the wood with an average value of 52.9 μm (SD = 12.4, Range = 32.5–73.4, n = 15 vessels) (Supplementary Table 1). There is no particular vessel arrangement as seen in cross section, where vessels occur solitary or grouped in pairs with an angular outline (Fig. 2a,c).

Rays of two different sizes exist in *C. colombiana* at an average density of 12.1 rays per millimeter (SD = 1.1, Range = 11–14, n = 8 fields) (Fig. 2d; Supplementary Table 1). Uniseriate rays are are composed of exclusively upright cells, whereas multiseriate rays are two to three cells wide and contain both upright and square cells (Fig. 3a-b). Brown-reddish colored pigment deposits are abundant in rays, particularly in multiseriate ones, and are also present in some vessels (Supplementary Table 1, Supplementary Figure 5). The vast majority of multiseriate rays in this wood exceeds 1 mm of height (Fig. 2d; Supplementary Table 1). Rays are not clustered and show a non-storied structure. Vessel-ray pits are scalariform in the contacts of vessels with both uniseriate and multiseriate ray cells (Fig. 3c), although they seem to be laterally shortened in an oval shape in multiseriate ray cells (Supplementary Table 1, Supplementary Figure 6). In tangential and radial section, simple perforation plates can be seen, as well as non-vestured scalariform intervessel pits (Fig. 3d). No tyloses, gum deposits, or specialized transport structures for other substances were observed.

In *C. colombiana* most of the ground tissue is comprised of thin-to-thick walled non-septate libriform fibers, although septate fibers might occur (Fig. 2a-b,d; Fig. 3e). Simple to minutely bordered pits and occasionally very small bordered pits (3–4 μm wide) appear in tangential and radial sections (Fig. 3e). No tracheids were observed.

Axial parenchyma is extremely rare in this wood, and very scanty apotracheal parenchyma strands can be observed in radial or tangential sections. These parenchyma strands had two to four cells of height and can be differentiated from ground tissue by their yellowish color (Fig. 2d). No arrangement of parenchyma was observed.

3.2. Chrysochlamys dependens

Chrysochlamys dependens is also a diffuse porous wood with visible discontinuous bands of gelatinous fibers that macroscopically resemble tree rings (Fig. 4a-b). The average density of vessels per square millimeter is 21.8 (SD = 7.8, Range = 13–32, n = 5 fields and 109 vessels) (Supplementary Table 1). The average tangential diameter of vessels is 52.9 μm (SD = 12.4, Range = 32.5–73.4, n = 15 vessels) (Supplementary Table 1) and it is very regular across the examined sections. Vessels occur solitary or grouped in pairs with an angular outline, and no particular vessel arrangement can be observed in cross section (Fig. 4a-b).

The wood has rays of two different sizes at an average density of 10.2 rays per millimeter (SD = 0.9, Range = 9–12, n = 8 fields) (Fig. 4c-d). Uniseriate rays contain exclusively upright cells, while multiseriate rays in *C. dependens* are two to four cells wide and are comprised by square and upright cells (Fig. 4c-d; Fig. 5a-b). The rays contain brown-reddish pigment deposits, although they are mainly observed in multiseriate ones (Fig. 4c; Fig. 5a-b). No tyloses, gum deposits, or specialized

Fig. 4. Anatomical features of *Chrysochlamys dependens*. Part I. a) Transverse section showing diffuse porosity of the wood and diffuse arrangement of the vessels (commonly in small clusters of 2–3 and without a specific pattern across the wood). b) Transverse section showing tangential band of gelatinous fibers delimited by a bracket and an asterisk. The band is related to a region of tension wood. c) Tangential section showing multiseriate rays (3-to-4 cells wide), uniseriate rays, and a high content of septate fibers. An overview of scalariform intervessel pits can be seen in a vessel element at the center of the picture. d) Detail of rays and septate fibers in tangential section. The white arrowhead indicates a septum in a fiber.

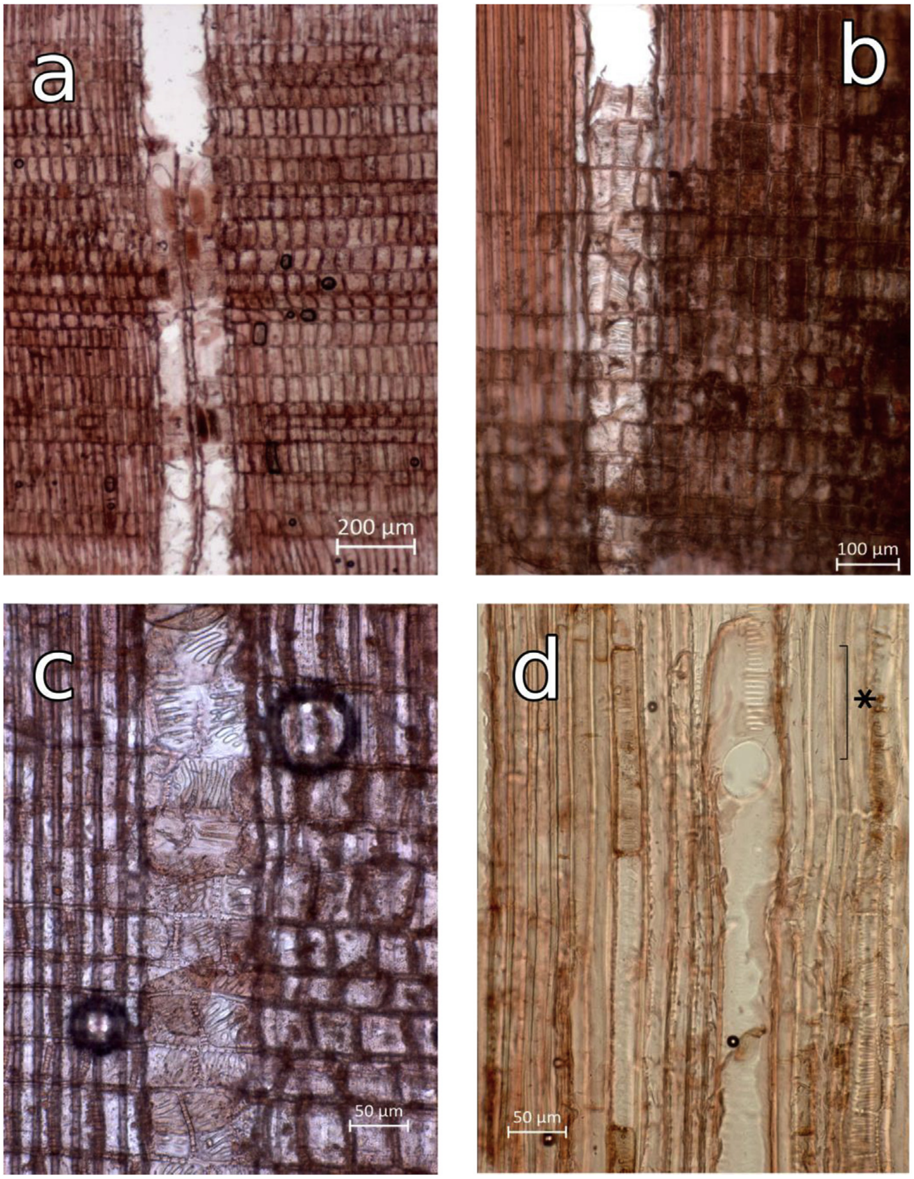

Fig. 5. Anatomical features of *Chrysochlamys dependens*. Part II – Radial sections. a) Tall multiseriate rays (commonly <1 mm of height) are composed of upright and square cells. b) Vessel-ray pits appear at the intersection of vessel elements and multiseriate rays. Pigment deposits are very common, but not ubiquitous in ray cells. c) Detail of the diverse morphology of vessel-ray pits, showing complex palisade and mesh-like shapes in addition to scalariform patterns. d) Detail of a simple perforation plate in subterminal position in a vessel element. A bracket and asterisk mark the location of several small simple pits in a libriform fiber.

transport structures for other substances were observed. The height of the rays is highly variable and seems to be correlated to the width. The widest rays in this wood commonly exceed 1 mm of height, whereas uniseriate and narrower multiseriate rays are usually shorter (Fig. 4c-d; Supplementary Table 1). Additionally, rays are not clustered and show a non-storied structure. Simple perforation plates can be observed, as well as non-vestured scalariform intervessel pits in both tangential and radial section (Fig. 4c-d, Fig. 5d). Vessel-ray pitting is scalariform in the contacts of vessels with uniseriate rays, but a broad diversity of pit shapes can be observed in the contacts between vessels and multiseriate rays. There scalariform, palisade, diagonal and mesh-like patterns appear (Fig. 5a-c).

The ground tissue of *C. dependens* is comprised of thin-to-thick walled, mostly septate libriform fibers with simple pits (Fig. 4c-d). No tracheids were observed in the specimens. Axial parenchyma is absent or extremely rare in this species, and no apotracheal parenchyma cells were found in the sections examined.

4. Discussion

In this study we described for the first time the wood anatomy of two species of *Chrysochlamys* from the Northern Andes of Colombia. According to Metcalfe and Chalk [14] *Chrysochlamys* belongs to the group of *Clusia*-type woods along with genera *Clusia*, *Tovomitopsis*, *Havetiopsis*, and *Tovomita*. Although *C. colombiana* and *C. dependens* wood features fit well in the description given in the literature for this group, there are several diverging traits that might be proposed as having diagnostic value for these species.

Ray features of *C. colombiana* and *C. dependens* show some differences relative to other species of the tribe. Rays of *Clusia*-type woods are described in Metcalfe & Chalk [14] as having two distinct widths: uniseriate and multiseriate; the largest being 4–6 cells wide and 1 mm high or taller. *Chrysochlamys dependens* resembles closely the description of ray height for the widest (4-seriate) rays, although it is interesting to notice that the 2- or 3-seriate rays present in this wood are shorter. In average, multiseriate rays of *C. colombiana* are narrower than those of *C. dependens*, and both uniseriate and multiseriate rays are tall in the former. A broad diversity of shapes in vessel-ray pits of *C. dependens* was observed: palisade, scalariform, and mesh-like pitting occurs where multiseriate ray cells, either square or upright, meet vessels. In contrast, *C. colombiana* only shows scalariform pitting and it mostly appears in the contacts between upright cells from uniseriate rays and vessel elements.

The exclusive presence of square or upright cells in the rays of both species classifies these trees as having paedomorphic type I rays as per the definitions of Carlquist [13]. This category also applies for all those woods in Metcalfe and Chalk [14] classified as Kribs's heterogeneous type I that lack procumbent cells in the ray body. Upon searching in InsideWood database [15], the registered *Chrysochlamys* species possess type I and type II heterogeneous rays as indicated by the presence of IAWA features 106, 107 or 108 [12] that imply the presence of varying amounts of procumbent cells in the ray body. Nonetheless, we did not observe procumbent cells in our samples. According to the same database, paedomorphic woods within the Clusiaceae family (feature 105, all cells upright and/or square) are exclusively found in trees of the Garcinieae tribe (genera *Allanbackia*, *Garcinia*, and *Pentadesma*) and *Symphonia*, however these species would be classified as paedomorphic type II since no uniseriate rays are reported. While the information above would make *C. colombiana* and *C. dependens* two unusual species within their genus, the scarcity of radial sections of Clusiaceae woods in public databases makes quite difficult to verify the existent anatomical descriptions and, thus, to draw further conclusions.

Ray parenchyma abundance may play a key role in the mechanical strength of woods. The thickness of the secondary cell wall of rays relative to that of ground tissue fibers is a key factor in mechanical resistance [13]. Ray cell walls were somewhat thinner compared to fiber walls in both species, implying that a large amount of ray cells relative to fibers would reduce wood strength. This can be proposed as having an adaptive role for *C. dependens*, as its reduced ray density and height, relative to *C. colombiana*, allows it to support its large size.

In both *C. colombiana* and *C. dependens,* libriform fibers comprise the ground tissue of the wood, and are qualitatively thin-to thick-walled following the nomenclature of IAWA list [12]. This is very different to other *Clusia*-type woods in which fibers are reported to be thick walled [14]. In *C. colombiana* a markedly lower proportion of septate fibers can be found compared to *C. dependens*, but the fibers of the latter tend to be somewhat thicker. In regards to apotracheal parenchyma, very few strands of cells could be observed in *C. colombiana* in line with previous literature [14]. The absence of parenchyma cells in *C. dependens* would need further confirmation with a broader sampling effort. Carlquist [13] associates fiber wall thickness and reduced parenchyma content with greater strength in woods. As *C. dependens* has larger and more robust leaves and stems than *C. colombiana* [2], it can be proposed that the ground tissue composition of the former makes this wood sturdier and also reflects an adaptation to its size.

The presence of tension wood bands was a common trait of the two species here described. Tension wood is characterized by the presence of gelatinous fibers with most of the lignin content of the cell wall substituted by cellulose [16]. Due to this chemical composition, it has been shown that their occurrence is related to an increase in wood flexibility in comparison to ordinary fibers [13]. However, although one might expect that such fibers will imply a less durable or resistant wood, it can be also considered that the flexibility gain might act as a buffer of mechanical stress in cases where stems are not straight [17]. The occurrence of tension wood thus depends heavily on the ecology of the individual tree; but also might give information about the natural growth rate of the species, since fast growth stimulates the occurrence of reaction wood [18]. The presence of tension wood might reflect the fact that our samples were collected from individuals growing in steep slopes, but sampling of individuals in locations with a different landscape could help to assess the contribution of the growth rate to this trait.

Another interesting feature to consider is the variation in the amount and distribution of pigmented deposits in the woods. *Chrysochlamys colombiana* showed a much higher abundance of pigmented deposits in ray parenchyma cells when compared to *C. dependens*. Deposits in vessel elements were observed only in *C. colombiana*. The biological significance of this finding beyond its diagnostic value remains to be explored.

Finally, we propose that ray morphology, vessel-ray pitting, libriform fiber morphology, and parenchyma presence are key diagnostic features for species of the *Chrysochlamys* genus. We expect this to be the starting point for a better understanding of the morphology and ecology of the species here described.

Declarations

Author contribution statement

David A. Ayala-Usma, Rafael E. Lozano-Gutiérrez: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Catalina González-Arango: Contributed reagents, materials, analysis tools or data.

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Competing interest statement

The authors declare no conflict of interest.

Additional information

Supplementary content related to this article has been published online at https://doi.org/10.1016/j.heliyon.2019.e02078.

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