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Comparative wood anatomy of 15 Malagasy *Diospyros* species (Ebenaceae)

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ABSTRACT

Diospyros L. (Ebenaceae) is an important source of ebony, a precious wood used for several economically important timber products. Species are overexploited in many regions, including Madagascar, for both the national and international trade, but little is known about their wood anatomy, despite its importance for forensic identification. Wood anatomy has a major role to play in ensuring the sustainable and equitable utilization of *Diospyros* species that are not threatened by extinction, and in law enforcement to protect threatened species from illegal logging. This study aims to identify, describe, and test the usefulness of anatomical features to support a taxonomic revision of the genus in Madagascar and to enrich databases for wood identification. Ninety-nine wood specimens were collected from the various bio-geographical regions of Madagascar, representing 15 endemic species (twelve previously described and three new) of large trees (reaching DBH ⩾ 20 cm and/or height ⩾ 20 m) were investigated. Standard methods for wood anatomical studies were used. Statistical analysis of the data using Factorial Analysis on Mixed Data was performed for 14 wood anatomical characters. Detailed descriptions and comparisons of the wood anatomy of the 15 species are provided, along with a wood identification key. Analyses showed that all the characters are highly significant ($P < 0.005$) in the separation of the species studies.

Keywords: *Diospyros*; precious wood; Madagascar; wood anatomy; Ebenaceae.

INTRODUCTION

Ebenaceae (*sensu* APG IV 2016) is a medium-sized pantropical family with the majority of its species in Asia and the Indo-Pacific region, while the greatest morphological diversity of Ebenaceae is found in Africa and Madagascar (White 1983; Wallnöfer 2001; Duangjai *et al.* 2006). *Diospyros* is the largest genus of Ebenaceae, comprising 761 currently recognized species of shrubs and trees, primarily distributed in tropical areas (Schatz & Lowry 2020; Schatz *et al.* 2020; Govaerts 2021; Linan *et al.* 2021), and is among the ten genera with the greatest number of tree species in the world (Beech *et al.* 2017). A total of 114 species are currently recognized in Madagascar, all but three of which are endemic, and ca. 135 additional new species remain to be described, bringing the estimated total to about 250 species (Madagascar Catalogue 2021; Schatz *et al.* 2021b).

Species of *Diospyros* provide essential ecosystem services (Wallnöfer 2001; Mason *et al.* 2016) and are a source of several economically important products (Duangjai *et al.* 2006). The fruits of several species are widely appreciated, and ebony timber is among the exotic materials that have been highly valued since classical times (Wallnöfer 2001). Precious woods obtained from *Diospyros* species are traded internationally and are often used for carvings, musical instruments, and furniture (Mason *et al.* 2016). Illegal timber trade is a complex global issue (Lowe *et al.* 2016; Waeber *et al.* 2019) and over the last

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20 years, the illegal exploitation and export of *Diospyros* have become a recurrent problem in Madagascar, threatening the island's ecosystems and its exceptional biodiversity (Ballet *et al.* 2010; Mason *et al.* 2016).

Two main types of Malagasy precious woods, rosewood (*Dalbergia*) and ebony, were listed under Appendix II at the 16th CITES Conference of the Parties in 2013 (Convention on International Trade in Endangered Species of Wild Fauna and Flora 2013a) to ensure sustainability and prevent over-exploitation of species. However, the enforcement of CITES trade restrictions is problematic due to difficulties in species identification. Current knowledge of the taxonomy of *Dalbergia* and *Diospyros* is insufficient, making it impossible to identify the species, and often even the genus, to which standing trees belong. The problem is even more serious with cut logs and timber products that no longer possess leaves, flowers and fruits, which contain most of the diagnostic features required for plant identification (Waeber *et al.* 2019). Because CITES and most environmental protection laws are applied to species (Lowe *et al.* 2016), control of the logging trade requires wood identification skills that are accurate to the species level (Baas 1994). To date, no reliable wood identification tools are, however, available in Madagascar.

In addition to the listing of both *Dalbergia* and *Diospyros* from Madagascar in CITES Appendix II (Convention on International Trade in Endangered Species of Wild Fauna and Flora 2013a), a decision was also made by CITES to establish an action plan to support the implementation of the listing (Convention on International Trade in Endangered Species of Wild Fauna and Flora 2013b). This plan calls for the determination of a precautionary, science-based export quota for listed taxa, the main species to be exported, and the preparation of identification material and tests for use in CITES enforcement to determine the main taxa as they are traded (Mason *et al.* 2016).

The study of Malagasy Ebenaceae was initiated by Perrier de la Bâthie (1952) in the Flora of Madagascar and Comoros, and a taxonomic re-evaluation of *Diospyros* has been carried out over the last decade (Schatz & Lowry 2011, 2018, 2020; Schatz *et al.* 2013, 2020, 2021a, 2021b; Linan *et al.* 2021; Madagascar Catalogue 2021). All of this work was based on field observations and herbarium studies on morphological features of flowers, fruits, and leaves. However, scientific identification of cut trees, sawn timber, and finished products must be based solely on the inherent characteristics of the wood itself (Lowe *et al.* 2016).

A consortium working on Madagascar's precious woods is finalizing a taxonomic review of all Malagasy *Diospyros* species and is developing wood identification tools to assist the country in the implementation of the CITES action plan. This consortium is focusing its work on five components: taxonomy, anatomy, near-infrared spectrometry, molecular identification, and conservation. The study presented here is a part of a multidisciplinary approach to a taxonomic revision of Malagasy *Diospyros* and the development of practical identification tools. It is focused specifically on wood anatomy, a significant source of information for fields such as systematics, ecology, adaptive evolution, and wood identification (Olson 2005; Lens *et al.* 2007; Boura & De Franceschi 2008; Maiti *et al.* 2016).

Little is known about the wood anatomy of Malagasy *Diospyros*. Some species were described and illustrated in the InsideWoodweb-database, mainly based on unpublished work by Pierre Détienne (InsideWood 2004-onwards; http://insidewood.lib.ncsu.edu/search). The wood anatomy of 31 species of Malagasy *Diospyros* was described by Ravaomanalina *et al.* (2017) using only a single sample per species and Jahanbanifard *et al.* (2020) described the wood of nearly 250 species of *Diospyros*, including 27 from Madagascar (two of which, however, are now regarded as synonyms and two are not valid names).

The objectives of this study are to describe anatomical features to support taxonomic revision of the genus using broad sampling with a representative set of species of Malagasy *Diospyros*, to enrich databases for wood identification and to provide an initial wood identification key.

MATERIALS AND METHODS

Sampling

Wood specimens were collected in a variety of bio-geographical regions of Madagascar. Ninety-nine specimens of wood (most of them were sapwood) representing 15 endemic species of *Diospyros* were investigated. The specimens were taken from stems at breast height (1.3 m). Herbarium voucher material was also collected; initial identifications were made by taxonomists of the Missouri Botanical Garden's Madagascar Program, and were confirmed by specialists working on the genus (P. Lowry, G. Schatz and H. Rakouth). Voucher specimens are deposited in the herbaria of the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar (TAN), the Museum National d'Histoire Naturelle, Paris, France (P) and the Missouri Botanical Garden, Saint Louis, Missouri, USA (MO). Collection data are available online in TROPICOS (www.tropicos.org) and the Catalogue of Vascular Plants of Madagascar (Madagascar Catalogue 2021), but because the species studied here can form large enough trees to be potential sources of commercially valuable ebony wood, public access to geo-coordinates and detailed locality data are restricted. Wood specimens of *Diospyros* species examined here are listed in Table A1 in the Appendix, which includes associated bioclimate information.

Table 1.
Codes for wood anatomical characters used in statistical analysis.

Character code	Description
Quantitative characters	
VL	Vessel length (μm)
TVD	Tangential vessel diameter (μm)
VD	Vessel density (vessels/mm²)
RH	Ray height (μm)
NR	Number of rays/mm
FL	Fibre length (μm)
IPD	Intervessel pit diameter (μm)
CS	Prismatic crystals size (μm)
Qualitative characters	
GR	Growth rings present (+) or absent (–)
VG	Vessel groupings
AP	Axial parenchyma type
FWT	Fibre wall thickness
RW	Ray width (number of cells)
SS	Storied structure present (+) or absent (–)

Anatomical procedures

Wood sections were prepared according to techniques described by Johansen (1940) and Sass (1951). Transverse (TS), tangential longitudinal (TLS), and radial longitudinal (RLS) sections 15–20 μm in thickness were prepared using a sledge microtome. They were then double-stained with aqueous 1% safranin and aqueous 1% Astra blue (Bukatsch 1972) and permanently mounted in Euparal. Slides of macerated tissue were made according to Jeffrey's Method (Johansen 1940).

The terminology used to describe the wood anatomy of the species studied followed the IAWA list of microscopic features for hardwood identification (IAWA 1989) except the diameter of intervessel pits, we measured vertical diameter but not the horizontal diameter. For quantitative data, at least 25 measurements or counts were taken for each character, and the mean, maximum, and minimum values were given. We also included the size of observed crystals in enlarged cells, a character that is not found in the IAWA list but which inclusion is essential for a complete description of *Diospyros* species.

Statistical analysis

Statistical analysis of the data was performed using Factorial Analysis on Mixed Data (Chavent *et al.* 2015) to classify the 99 specimens of wood by a mixture of quantitative and qualitative variables. This analysis aimed to determine the wood anatomical characters that distinguish each species. In total, 14 wood anatomical characters were analyzed, including both qualitative and quantitative features (Table 1). All statistical analyses were made using the R software (R x 64 4.0.3).

RESULTS

Microscopic wood descriptions

Numerical characters are presented as follows: (minimum) — mean — (maximum).

Growth rings

Growth ring boundaries, marked by thick latewood fibres, are distinct in *Diospyros analamerensis*, *D. bardotiae*, *D. cupulifera*, *D. gracilipes*, *D. lewisiae*, *D. littoralis*, *D. randrianasoloi*, *D. rubripetiolata*, and *D. tropophylla* (Fig. 1A) and absent in the other species.

Vessels

All species are diffuse-porous with radially arranged vessels, which are usually solitary and in radial multiples of 2 to 12 or more, and sometimes in clusters. Solitary vessels are rounded and oval to circular in cross-section. Intervessel pits are alternate and polygonal (Fig. 2 A, B), minute (1.5) — 3 — (4) μm in *Diospyros bardotiae*, *D. baronii*, *D. gracilipes*, *D. lewisiae*, *D. littoralis*, *D. malandy*, *D. randrianasoloi*, *D. rubripetiolata*, *D. squamosa*, and *D. toxicaria*, small (4) — 6 — (7) μm in *D. analamerensis*, *D. chitoniophora*, *D. cupulifera*, and *D. tropophylla*, and small to medium-sized (4) — 6 — (10) μm in *D. humbertiana*. Vessel perforations are always simple (Fig. 3A). Vessel-ray pits have distinct borders and are similar to intervessel pits in size and

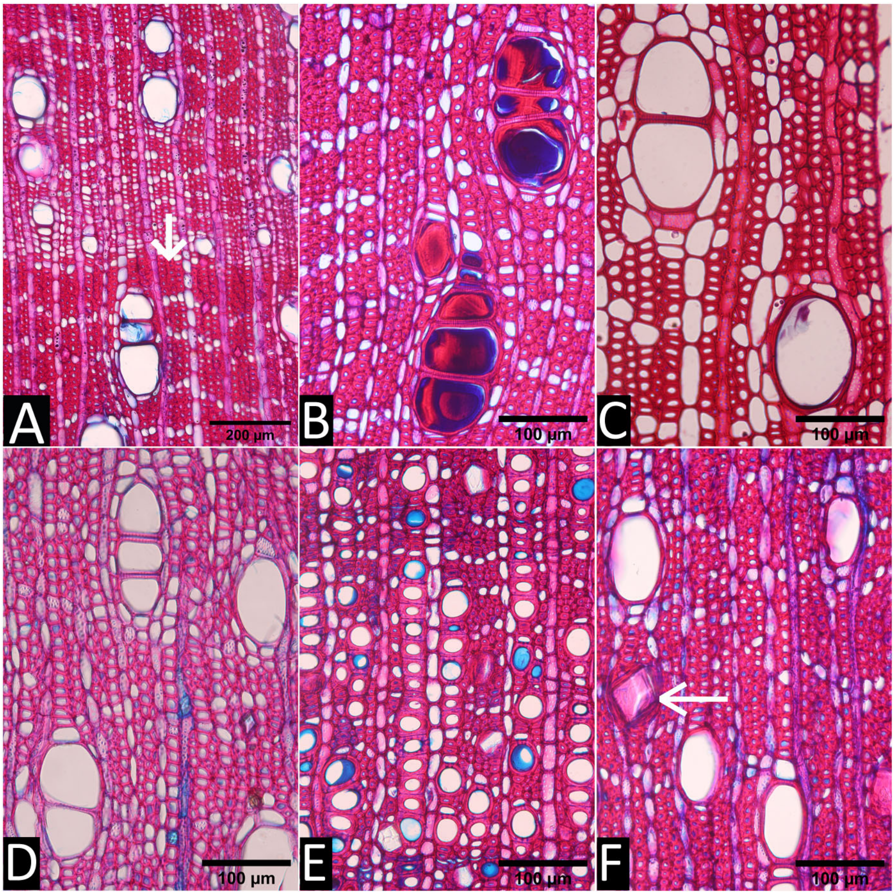

Figure 1. Transverse sections. (A) *Diospyros lewisiae*, growth rings distinct due to thick-walled latewood fibres (arrows). (B) *Diospyros squamosa*, vessels solitary or in short radially multiples, paratracheal parenchyma scanty and vasicentric, apotracheal parenchyma reticulate, fibres thin to thick- and very thick-walled, vessels filled with gums. (C) *Diospyros rubripetiolata*, vessels solitary or in short radial multiples, paratracheal parenchyma scanty and vasicentric, apotracheal parenchyma diffuse-in-aggregates and in narrow bands, fibres thin- to thick-walled. (D) *Diospyros baronii*, vessels solitary or in short radial multiples, paratracheal parenchyma scanty and vasicentric, apotracheal parenchyma diffuse or diffuse-in-aggregates, fibres very thin-walled. (E) *Diospyros humbertiana*, vessels solitary or in radial multiples of 2 or more than 12 cells, paratracheal parenchyma scanty, apotracheal parenchyma diffuse, fibres very thick-walled. (F) *Diospyros bardotiae*, large prismatic crystals (arrows).

shape throughout the ray cells (Fig. 3B). Vessel diameters are in two classes: (10) — 37 — (70) µm in *D. analamerensis*, *D. chitoniophora*, *D. cupulifera*, *D. humbertiana*, *D. malandy*, and *D. tropophylla*, and (20) — 73 — (150) µm in *D. bardotiae*, *D. baronii*, *D. gracilipes*, *D. lewisiae*, *D. littoralis*, *D. randrianasoloi*, *D. rubripetiolata*, *D. squamosa*, and *D. toxicaria*. The vessel frequency is divided into three classes: (2) — 14 — (46) vessels/mm^2 in *D. lewisiae*, *D. rubipetiolata*, and *D. toxicaria*, (4) — 28 — (109) in *D. bardotiae*, *D. baronii*, *D. littoralis*, *D. randrianasoloi*, and *D. squamosa*, and (20) — 245 — (615) vessels/µm^2 in *D. analamerensis*, *D. chitiniophora*, *D. cupulifera*, *D. humbertiana*, *D. malandy*, and *D. tropophylla*. There are two classes of vessel element length: (50) — 311 — (560) µm in *D. humbertiana*, *D. littoralis*, and *D. tropophylla*, and (51) — 412 — (1110) µm in the other species. Gum was commonly observed in all studied species (Fig. 1B); it is abundant in *D. squamosa*.

Fibres

Fibres are non-septate with simple to minutely bordered pits. They are usually thin to thick-walled (Fig. 1C) but are thin- to thick- and very thick-walled (Fig. 1B) in *Diospyros cupulifera*, *D. gracilipes*, *D. squamosa*, and *D. tropophylla*, very thin-walled in *D. baronii* (Fig. 1D), and very thick-walled in *D. humbertiana* and *D. chitoniophora* (Fig. 1E). Fibres are usually between 900–1600 µm long, except in *D. humbertiana*, *D. malandy*, and *D. tropophylla*, where they are (100) — 822 — (1340) µm.

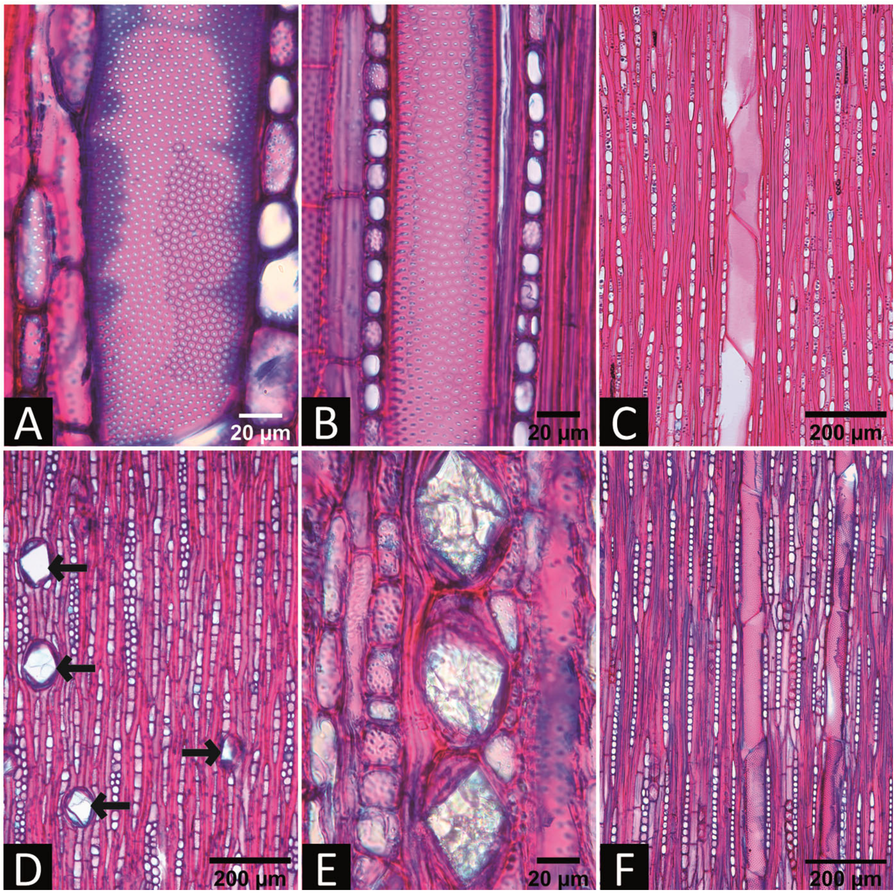

Figure 2. Longitudinal tangential section. (A) *Diospyros bardotiae*, minute alternate and polygonal intervessel pits, minute. (B) *Diospyros tropophylla*, small alternate and polygonal intervessel pits. (C) *Diospyros lewisiae*, exclusively uniseriate rays. (D) *Diospyros bardotiae*, rays 1–2 cells wide, solitary prismatic crystals (arrows). (E) *Diospyros humbertiana*, prismatic crystals grouped in chambered axial parenchyma. (F) *Diospyros tropophylla*, storied ray structure.

Axial parenchyma

Paratracheal parenchyma is scanty (Fig. 1E) or scanty and vasicentric (Fig. 1B, C). Apotracheal parenchyma is diffuse (Fig. 1E), diffuse-in-aggregates (Fig. 1D), in narrow interrupted or continuous bands up to three cells wide (Fig. 1C), and reticulate (Fig. 1B). There are usually 3–4 cells per parenchyma strand.

Rays

Uniseriate rays are always present. Rays are exclusively uniseriate in *Diospyros gracilipes*, *D. lewisiae*, *D. littoralis*, and *D. malandy* (Fig. 2C), but are usually uni- or biseriate (Fig. 2D) or one to three seriate in *D. analamerensis*, *D. baronii*, *D. rubripetiolata*, *D. squamosa*, and *D. tropophylla*. They are (80) — 356 — (1160) µm in height. The rays are heterogeneous throughout the species studied (Fig. 3C, D). They are generally composed of all ray cells upright and or square and body ray cells procumbent with two or over four rows of upright and or square marginal cells but mostly composed by body ray cells procumbent with two to four rows of upright and or square marginal cells in *D. tropophylla* and all ray cells upright and or square and ray with mixed procumbent, square and upright cells in *D. gracilipes*, *D. lewisiae* and *D. malandy*.

Storied structure

Storied structure is present only in *Diospyros humbertiana* and *D. tropophylla*. Low rays are storied and high rays are non-storied (Fig. 2F), with three ray tiers per mm for both species.

Prismatic crystals

Prismatic crystals are commonly present in chambered axial parenchyma cells (Fig. 3E), in radial alignment in procumbent ray cells (Fig. 3F) in some species, and sometimes in chambered upright or square ray cells. The size varies from 18 to 88 µm. They are either solitary (Fig. 2D) or grouped (Fig. 2E).

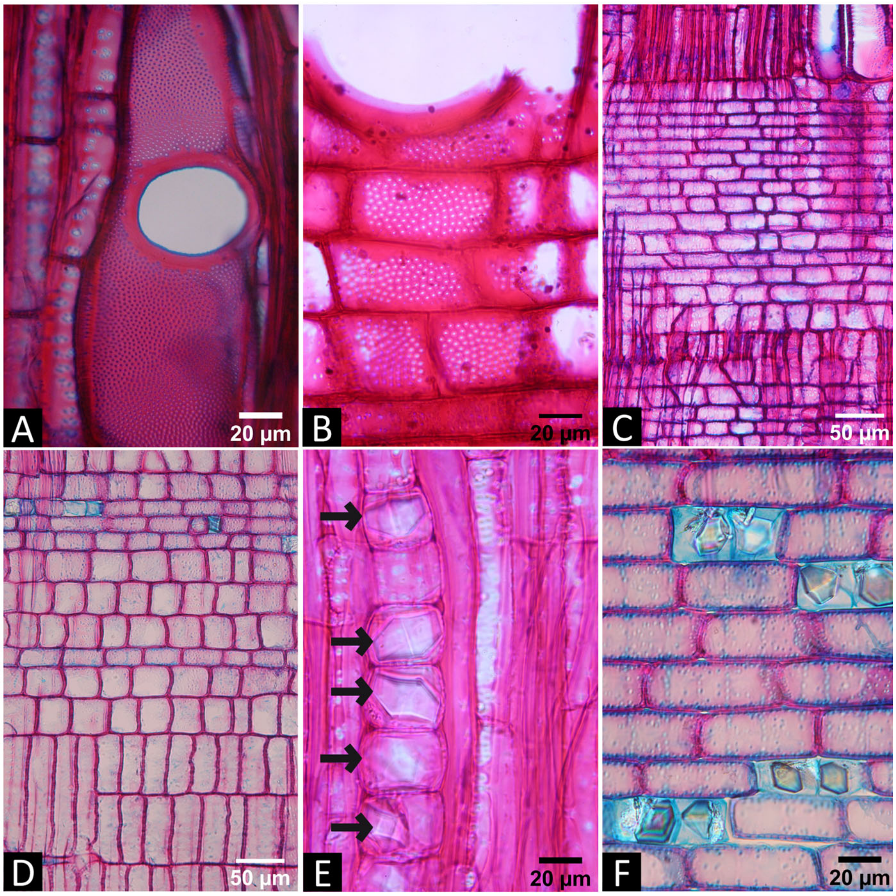

Figure 3. Longitudinal radial section. (A) *Diospyros squamosa*, simple perforation. (B) *Diospyros randrianasoloi*, ray-vessel pits similar to intervessel pits in size and shape. (C) *Diospyros tropophylla*, heterogeneous rays with body ray cells procumbent with one row of upright and/or square marginal cells. (D) *Diospyros gracilipes*, heterogeneous rays with procumbent, square and upright cells mixed throughout the ray. (E) *Diospyros baronii*, prismatic crystals (arrows) grouped in chambered axial parenchyma. (F) *Diospyros lewisiae*, prismatic crystals in radial alignment in procumbent ray cells.

A summary of the results presented above is provided in Table 2.

Results of the statistical analysis

Results of the Multiple Factor Analysis for Mixed Data showed that all of the quantitative and qualitative characters are highly significant ($P < 0.005$) in the separation of the species (Table 3). The dendrogram (Fig. 4) showed that classification carried out on the individual specimens revealed two major groups and six subgroups, with all species well separated from one another excepted *Diospyros lewisiae* and *D. gracilipes*. These two species have very similar anatomical characteristics of wood.

The first group comprises individuals belonging to *Diospyros bardotiae*, *D. baronii*, *D. gracilipes*, *D. lewisiae*, *D. randrianasoloi*, *D. rubripetiolata*, *D. squamosa*, and *D. toxicaria*. This group is characterized by the presence of both scanty and vasicentric parenchyma, a high TVD mean value of 50–100 µm, a low mean value of VD < 50 vessels/mm², and an IPD usually ⩽ 4 µm. This first group is subdivided into two subgroups (Fig. 4).

The second group includes individuals belonging to the following species: *Diospyros analamerensis*, *D. chitoniophora*, *D. cupulifera*, *D. humbertiana*, *D. littoralis*, *D. malandy*, and *D. tropophylla*. Unlike the first group, the individuals of this second group share only the presence of scanty axial parenchyma, a high value of the mean of VD (50–100 or more vessels/mm²), and a low value of the mean of TVD (< 50 µm), except for those belonging to *D. littoralis*, which have TVD of 50–100 µm and VD < 50 vessels/mm² and the IPD usually ⩾ 4 µm, and except *D. littoralis* and *D. malandy*, which both have an IPD consistently < 4 µm. This second group is subdivided into four subgroups (Fig. 4). The fourth subgroup includes individuals belonging to *D.* section *Forbesia*.

Table 2.
Wood anatomical characteristics of 15 Malagasy *Diospyros* species.

Scientific name	GR	VG	TVD	VD	VL	FWT	FL	APP	APA	RW	RH	NR	IPD	SS
D. analamerensis H. Perrier	+	S, RM (2–8)	(15) 37 ± 7 (50)	(60) 195 ± 95 (386)	(170) 403 ± 82 (600)	Tn–Tk	(550) 969 ± 179 (1500)	S	A	1–3	(120) 294 ± 109 (720)	(9) 15 ± 2 (20)	(5) 6 ± 0.65 (8)	–
D. bardotiae H.N. Rakouth. G.E. Schatz & Lowry	+	S, RM (2–6)	(20) 65 ± 18 (140)	(17) 40 ± 14 (10)	(160) 439 ± 96 (660)	Tn–Tk	(110) 917 ± 237 (1960)	S, V	D, A	1–2	(100) 361 ± 137 (840)	(11) 19 ± 3 (24)	(1.5) 2 ± 0.29 (4)	–
D. baronii (H. Perrier) Lowry *et al.* ined.	–	S, RM (2–6)	(25) 64 ± 16 (100)	(6) 22 ± 8 (42)	(120) 376 ± 136 (750)	VTn	(370) 972 ± 192 (1550)	S, V	D, A	1–3	(110) 262 ± 89 (550)	(8) 13 ± 2 (22)	(2) 3 ± 0.64 (5)	–
D. chitoniophora Capuron ex G.E. Schatz & Lowry	–	S, RM (2–12)	(20) 33 ± 6 (50)	(98) 297 ± 98 (521)	(230) 438 ± 88 (740)	Vt	(97) 837 ± 208 (1230)	S	D, A	1–2	(100) 296 ± 104 (650)	(9) 14 ± 2 (20)	(5) 6 ± 0.64 (8)	–
D. cupulifera H. Perrier	+	S, RM (2–8)	(20) 40 ± 7 (60)	(73) 194 ± 61 (312)	(70) 394 ± 83 (650)	Tn–Tk, VTk	(500) 969 ± 162 (1450)	S	D, A	1–2	(100) 302 ± 110 (630)	(9) 14 ± 2 (19)	(4) 6 ± 0.79 (7)	–
D. humbertiana H. Perrier	–	S, RM (⩾12)	(10) 26 ± 6 (50)	(255) 443 ± 69 (594)	(110) 295 ± 48 (420)	VTk	(590) 812 ± 111 (1230)	S	D	1–2	(100) 291 ± 112 (570)	(14) 19 ± 2 (25)	(6) 7 ± 0.81 (10)	+
D. gracilipes Hiern	+	S, RM (2–12)	(40) 66 ± 10 (95)	(9) 27 ± 6 (61)	(51) 488 ± 156 (810)	Tn–Tk, VTk	(320) 1083 ± 196 (1650)	S, V	NB, R	1	(160) 515 ± 181 (900)	(11) 17 ± 2 (25)	(1.5) 2 ± 0.37 (3)	–
D. lewisiae Mas. G.E. Schatz & Lowry. ined.	+	S, RM (2–10)	(40) 73 ± 14 (100)	(7) 18 ± 6 (34)	(70) 360 ± 144 (690)	Tn–Tk	(630) 1093 ± 184 (1600)	S, V	INB	1–2	(130) 523 ± 203 (970)	(9) 14 ± 2 (19)	(1.5) 3 ± 0.51 (4)	–
D. littoralis Capuron ex G.E. Schatz & Lowry	+	S, RM (2–8)	(40) 62 ± 8.80 (100)	(10) 27 ± 10 (61)	(50) 280 ± 115 (500)	Tn–Tk	(500) 861 ± 137 (1320)	S	A	1	(100) 286 ± 119 (780)	(10) 16 ± 2 (23)	(1.5) 2 ± 0.44 (3)	–
D. malandy H.N. Rakouth *et al.*	–	S, RM (⩾12)	(20) 43 ± 8 (70)	(82) 172 ± 55 (419)	(180) 372 ± 84 (610)	Tn–Tk	(340) 740 ± 175 (1310)	S	D, A	1	(110) 280 ± 106 (650)	(10) 17 ± 3 (25)	(2) 2 ± 0.27 (3.5)	–
D. randrianasoloi G.E. Schatz. Lowry & Mas. ined.	+	S, RM (2–6)	(90) 79 ± 17 (120)	(3) 25 ± 10 (45)	(70) 376 ± 175 (740)	Tn–Tk	(550) 1079 ± 224 (1630)	S, V	NB or NB, R	1–2	(120) 513 ± 241 (1160)	(11) 16 ± 2 (19)	(1.5) 3 ± 0.58 (4)	–
D. rubripetiolata G.E. Schatz & Lowry	+	S, RM (2–4)	(40) 85 ± 20 (150)	(2) 14 ± 7 (37)	(110) 435 ± 112 (680)	Tn–Tk, VTk	(660) 1125 ± 169 (1780)	S, V	A, NB	1–3	(130) 428 ± 172 (850)	(8) 14 ± 2 (20)	(3) 3 ± 0.36 (4)	–
D. squamosa Bojer ex A. DC.	–	S, RM (2–8)	(30) 77 ± 20 (120)	(4) 29 ± 13 (76)	(100) 421 ± 150 (1110)	Tn–Tk, VTk	(220) 914 ± 261 (1580)	S, V	NB, R	1–3	(100) 308 ± 120 (810)	(6) 14 ± 3 (25)	(1.5) 2 ± 0.21 (3)	–
D. toxicaria Hiern	–	S, RM (2–6)	(45) 82 ± 17 (130)	(2) 13 ± 6 (46)	(100) 442 ± 123 (800)	Tn–Tk	(600) 1122 ± 206 (1950)	S, V	NB	1–2	(100) 402 ± 148 (770)	(9) 15 ± 2 (21)	(2.5) 4 ± 0.57 (6)	–
D. tropophylla (H. Perrier) G.E. Schatz & Lowry	+	S, RM (2–12)	(20) 45 ± 8 (70)	(20) 216 ± 157 (615)	(110) 331 ± 68 (560)	Tn–Tk, VTk	(100) 859 ± 149 (1340)	S	D, A	1–3	(80) 284 ± 100 (600)	(11) 17 ± 2 (24)	(4) 5 ± 0.49 (6)	+

GR, growth rings present (+) or absent (–); VG, vessel groupings (S, solitary; RM, in radial multiple); VD, vessel density; VL, vessel element length (μm); FWT, fibre wall thickness (Tn, thin; Tk, thick; VTn, very thin; VTk, very thick); FL, fibre length (μm); APP, axial paratracheal parenchyma (S, scanty; V, vasicentric); APA, axial parenchyma apotracheal (D, diffuse; A, diffuse-in-aggregates; NB, in narrow bands; INB, in interrupted narrow bands; R, reticulate); RW, ray width; RT, ray type; RH, ray height; NR, number of rays per mm; IPD, intervascular pit diameter; SS, storied structure present (+) present or absent (–); (min) mean ± standard deviation (max).

Table 3.
Characteristics of each subgroup and the species of *Diospyros* they include.

Subgroup	Characteristics	Species
1	High value of TVD Low value of IPD, VD and NR Storied structure absent Growth rings absent Ray width 1 to 3 cells	*D. baronii* *D. squamosa* *D. toxicaria*
2	High value of TVD Low value of IPD, VD and NR Storied structure absent Growth rings present	*D. bardotiae* *D. gracilipes* *D. lewisiae* *D. randrianasoloi* *D. rubripetiolata*
3	Low value of IPD Fibre wall thickness thin to thick Storied structure absent Rays exclusively uniseriate	*D. littoralis* *D. malandy*
4	High value of IPD, VD and NR Low value of TVD, FL, VL, CS and RH Storied structure present	*D. tropophylla*
5	High value of IPD, VD, NR and CS Low value of TVD, FL, VL, and RH Storied structure present	*D. humbertiana*
6	High value of IPD and VD Low value of TVD, FL, VL, NR, CS and RH Storied structure absent	*D. chitoniophora* *D. analamerensis* *D. cupulifera*

Tangential diameter of vessel, vessel density and intervessel pits diameter can thus be regarded as important features for the separation of species within the genus.

Interspecific and infraspecific variations

Diospyros toxicaria is the only species having a fiber length lower than 900 μm among the 8 species of the first group, *Diospyros baronii* is the only species that has very thin fibre wall and *D. bardotiae* is distinguished from others by the size of the crystals prismatic more than 65 μm in the parenchyma cells.

Among the species that have tangential diameter less than 50 μm and vessel density more than 100 cells/mm^2, *Diospyros malandy* is the only species that has intervessel pits less than 4 μm and exclusively uniseriate rays. *Diospyros humbertiana* and *Diospyros tropophylla* distinguished from others species by the presence of storied structure.

The Infraspecific variations are significant only in three species. They are mainly observed on the number of groupings of vessels in *Diospyros gracilipes* and both on the number of groupings of vessels and the density of the vessels in *D. squamosa* and *D. tropophylla*.

Wood identification key of the 15* Diospyros *species examined

Using the results obtained through the statistical analysis of wood anatomical data (Multiple Factor Analysis for Mixed Data), the following identification key was established.

1. Paratracheal parenchyma scanty and vasicentric 2
– Paratracheal parenchyma exclusively scanty 9
2. Growth rings absent 3
– Growth rings present 5
3. Mean fibre length < 900 μm, mean vessel density < 20 cells/mm^2 .... *D. toxicaria*
– Mean fibre length $\geqslant$ 900, mean vessel density > 20 cells/mm^2 4

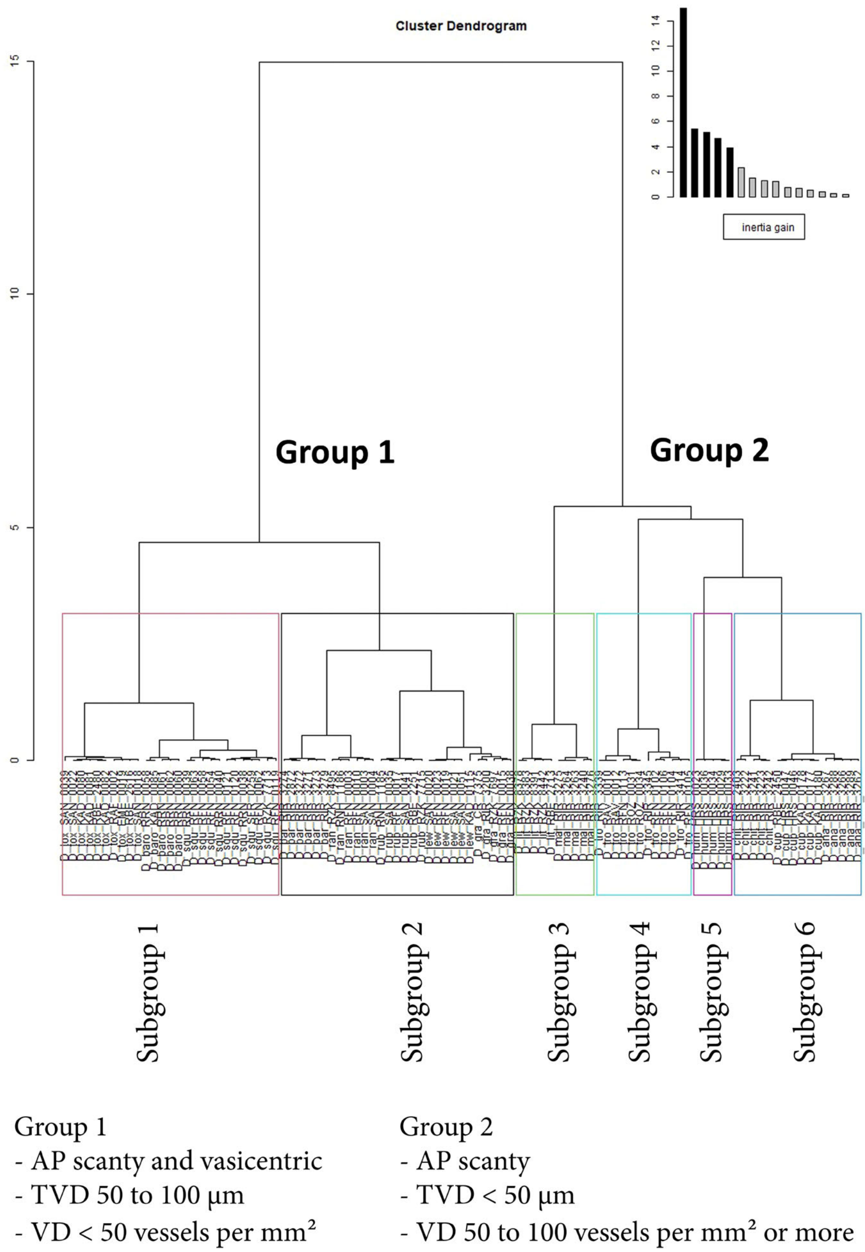

Figure 4. Dendrogram based on 14 wood anatomical characters of 100 *Diospyros* L. specimens (D_ana, *D. analamerensis*; D_bar, *D. bardotiae*; D._baro, *D. baronii*; D_chit, *D. chitoniophora*; D_cup, *D. cupulifera*; D_gra, *D. gracilipes*; D_hum, *D. humbertiana*; D_lew, *D. lewisiae*; D_lit, *D. littoralis*; D_mal, *D. malandy*; D_ran, *D. randrianasoloi*; D_rub, *D. rubripetiolata*; D_squ, *D. squamosa*; D_tox, *D. toxicaria*; D_tro, *D. tropophylla*). The characteristics of each subgroup are summarized in Table A1 in the Appendix.

4. Fibre walls very thin .... *D. baronii*

– Fibre walls very thin to thick and very thick .... *D. squamosa*

5. Ray exclusively uniseriate 6

– Ray width biseriate or triseriate 7

6. Fibres thin- to thick-walled .... *D. lewisiae*

– Fibres thin- to thick and very thick-walled .... *D. gracilipes*

7. Rays triseriate . . . . . *D. rubripetiolata*

– Rays biseriate 8

8. Prismatic crystal size > 65 μm . . . . . *D. bardotiae*

– Prismatic crystal size < 35 μm . . . . . *D. randrianasoloi*

9. Intervessel pit diameter < 4 μm and ray exclusively uniseriate 10

– Intervessel pit diameter ⩾ 4 μm and ray uniseriate to biseriate and uniseriate to triseriate 11

10. Mean vessel density < 40 cells/mm², mean tangential diameter of vessels 50–100 μm, growth rings present and vessel groupings solitary and in radial multiple of 2 to 8 cells . . . . . *D. littoralis*

– Mean vessel density > 100 cells/mm², mean tangential diameter of vessels < 50 μm, growth rings absent and vessel groupings solitary and in radial multiple of 2 to more than 12 cells . . . . . *D. malandy*

11. Intervessel pit diameter ⩽ 5 μm . . . . . *D. tropophylla*

– Intervessel pit diameter ⩾ 6 μm 12

12. Storied structure present, crystal size > 45 μm, vessel groupings solitary and in radial multiple of 2 to more than 12 cells, intervessel pit diameter ⩾ 7 μm, mean tangential diameter < 30 μm . . . . . *D. humbertiana*

– Storied structure absent, crystal size < 35 μm, vessel groupings solitary and in radial multiples of 2 to 12 cells and mean vessel tangential diameter ⩾ 30 μm 13

13. Growth rings absent and fibre walls very thick . . . . . *D. chitoniophora*

– Growth rings present, fibres thin- to thick- and very thick-walled 14

14. Rays uniseriate to biseriate . . . . . *D. cupulifera*

– Rays uniseriate to triseriate . . . . . *D. analamerensis*

DISCUSSION

Wood anatomical characteristics

The 15 *Diospyros* species studied share a common set of wood anatomical features: simple perforations, intervessel and ray-vessel pits alternate and small to minute (up to 8 μm in diameter), parenchyma predominantly apotracheal, and rays heterogeneous, less than 1 mm in height. The present study confirms the results of previous work on *Diopsyros* species from throughout the world (InsideWood 2004 onwards; Wickremasinghe & Herat 2006; Jahanbanifard *et al.* 2020). Wood structure within Ebenaceae is reported to be very uniform (Metcalfe & Chalk 1957; Detienne & Jacquet 1983; Wallnöfer 2001), and our results confirm this. However, by combining several wood characteristics, we can distinguish among the 15 Malagasy species studied here. According to the Factorial Analysis on Mixed Data analysis (AFDM), all the considered parameters contribute to the separation of the species.

The results of AFDM showed that the number of vessels, the arrangement of the parenchyma, ray width, and fibre wall thickness are all statistically significant ($P < 0.05$), indicating that these characters are very important in separating the 15 species studied. According to Wallnöfer (2001), these characters are the main sources of variation in Ebenaceae wood.

Intervessel pit diameter, vessel grouping, tangential diameter, and density of vessels are the characters with the lowest P values, indicating that they are the most important in separating species. According to Detienne (1988), the size of the intervessel pitting is a very stable character, and the diameter and frequency of vessels are good characters for taxonomy in wood anatomy.

The results of the classification by statistical analysis showed that the specimens studied were separated into two large groups (Fig. 4). The first group comprises individuals that were collected at sites in the eastern part of Madagascar, in the humid and subhumid bioclimatic regions, except for *Diospyros bardotiae*, which is found at Ankarana in the dry bioclimate region, although it always grows at locally humid, lowland sites. The second group includes individuals collected in the western part of the island, in the dry and subarid bioclimate regions, except for *D. littoralis*, which occurs at Point à Larrée in the humid region, although it grows on well-drained white sand substrate and is therefore probably subjected to locally dry edaphic conditions. This species presents all the characteristics of the eastern species except for the exclusive presence of scanty axial parenchyma.

In general, these wet zone species possess smaller numbers of vessel groups per unit area (< 100 cells/mm²) and larger vessels (50–100 µm tangential diameter) than those occurring in the dry zone, which have more than 100 cells/mm² and ⩽ 50 µm tangential diameter. Numerous studies have previously shown these ecological trends in wood structure: vessel diameter decreases from wet to dry regions, whereas the reverse is true for vessel density (van der Graaff & Baas 1974; van den Oever *et al.* 1981; Carlquist & Hoekman 1985; Baas 1986; Dickison 2000; Noshiro & Baas 2000; Carlquist 2001). Wickremasinghe & Herat (2006) found the same results in their studies of *Diospyros* species from Sri Lanka. According to Zimmermann (1982, 1983), vessel width has a significant effect on conductivity; the wider the vessels, the higher their hydraulic conductivity. The results of the present study agree with the findings of Wright (1904) in that dry zone species showing high frequencies of vessels per area compared to wet zone taxa. Previous studies suggest that the increased number of groups of vessels indicates a xeric tendency of the habitat preferences of a species. According to Metcalfe and Chalk (1957), the most valuable taxonomic vessel character is the distribution and pattern of the pores as seen in transverse section, but the number and size of the vessels may be markedly influenced by the environment, so they are of limited value in the delimitation of taxa that occur in the same habitats. However, in the present study, parameters such as the tangential diameter and the density of vessels can be used to distinguish the species from western parts of Madagascar, which present numerous and small vessels, as opposed to those from eastern part, with fewer and larger vessels.

The results of our analyses on the 15 species of Malagasy *Diospyros* showed that there was no correlation between tree height and bioclimate and tree diameter and bioclimate, the same for tree height and vessel density and tree height and vessel diameter. Olson and Rossel (2013), Anfodillo *et al.* (2013) and Lazzarin *et al.* (2016), however, proved the opposite. According to these authors, vessels are expected to be narrower in drier forests and woodlands because trees are on average much smaller. According to our results, Malagasy *Diospyros* in dry bioclimate are not necessarily small and Malagasy *Diospyros* in wet bioclimate are not always large.

Among the 15 species of *Diospyros* studied here, nine show distinct growth rings. However, many studies have demonstrated that growth rings are often inconspicuous or absent in Ebenaceae and especially in *Diospyros*. Wickremasingjhe and Herat (2006) found the same result with the 25 species of *Diospyros* they examined from Sri Lanka.

Visible growth rings are a response to seasonal environmental conditions (Carlquist 1980). According to Worbes (1995), growth rings are generally induced by seasonal changes from favorable to unfavorable growing conditions, which for tropical trees primarily involve periods of drought or annual flooding. Among the nine species that show distinct growth rings, four of them (*Diospyros analamerensis*, *D. bardotiae*, *D. cupulifera*, and *D. tropophylla*) grow in the dry zone, and five (*D. gracilipes*, *D. lewisiae*, *D. littoralis*, *D. randrianasoloi*, and *D. rubripetiolata*) occur in the wet zone.

The production of tree rings is not only environmentally but also genetically determined (Schweingruber *et al.* 2006). However, Pierre Detienne did not think these features were generally useful for species identification (Wheeler *et al.* 2020).

Among the 15 studied species, *Diospyros humbertiana* and *D. tropophylla* possess storied structure, which can be an important distinguishing feature. According to Metcalfe and Chalk (1957), storied structure is one of the most taxonomically useful anatomical characters and according to Wheeler *et al.* (2020) this feature is uncommon and is highly diagnostic

Exclusively uniseriate rays occur in *Diospyros gracilipes*, *D. lewisiae*, *D. littoralis*, and *D. malandy*. The presence of exclusively uniseriate rays is of great value for identification according to Metcalfe & Chalk (1957) and Wheeler *et al.* (2020).

The woods of *Diospyros bardotiae* and *D. humbertiana* are easily recognized by the size of the crystals in the axial parenchyma cells. *Diospyros bardotiae* is a western species that occurs in the dry part of the island and that has all the anatomical characteristics of species found in the humid eastern part of the island, but it can be distinguished from it by the size of its crystals.

Interspecific and infraspecific variations

The dendrogram showed that classification carried out on the individual specimens revealed that all species well separated from one another excepted *Diospyros lewisiae* and *D. gracilipes*. These two species have very similar anatomical characteristics of wood. However, they can be distinguished from other species by exclusively uniseriate rays. According to Wheeler *et al.* (2020), it is not possible to distinguish species based on their microscopic anatomy. In this research, we can distinguish 13 species among the 15 species studied.

Infraspecific variation is not significant. The variations are only observed in three species. This is due to the fact that most of the specimens per species were collected at the same location and in the same bioclimate, with the exception of some species such as *Diospyros gracilipes*, *D. squamosa* and *D. tropophylla*. For *Diospyros gracilipes*, 3 specimens were collected in Tsitongambarika (in the southern part of Madagascar) and 2 specimens were collected in Lokobe (in the northern of

Madagascar), for *Diospyros squamosa*, 9 specimens were collected in humid bioclimate and 3 in subhumid bioclimate and for *Diospyros tropophylla*, 6 specimens were collected in dry bioclimate and 6 in sub arid bioclimate.

Comparison with previous research on Malagasy Diospyros species

Six of the 15 species studied here were reported to be examined by Jahabanifard *et al.* (2020), viz. *Diospyros analamerensis*, *D. cupulifera*, *D. humbertiana*, *D. squamosa*, *D. toxicaria* and *D. tropophylla* and four by Pierre Détienne (InsideWood 2004-onwards; http://insidewood.lib.ncsu.edu/search), *Diospyros cupulifera*, *D. gracilipes*, *D. squamosa* and *D. tropophylla* were described, we found similar results: simple vessel perforations, vessels usually solitary or in radial multiples, paratracheal parenchyma scanty or vasicentric, fibre pits simple to minutely bordered on radial walls, rays heterogeneous, and presence of prismatic crystals in ray cells and in chambered axial parenchyma cells. The main differences between their results and ours were as follows: Jahabanifard *et al.* (2020) observed distinct growth rings in *D. squamosa* and *D. toxicaria* whereas rings were absent in our material of these species; rays exclusively uniseriate in *D. analamerensis*, *D. squamosa*, and *D. tropophylla*, as opposed to comprising 1- to 3-seriate rays in the material we examined. We observed distinct growth rings in *Diospyros cupulifera* and *D. tropophylla* but Pierre Détienne and Jahabanifard *et al.* (2020) did not observe the same case for *Diospyros gracilipes* and the storied structure in *D. tropophylla*. These differences may be due to errors of identification of the material used by Jahabanifard *et al.* (2020) and Pierre Detienne, which was obtained from wood collections and the botanical identification of the vouchers was not updated. According to Wheeler *et al.* (2021), it is difficult to make decisions about the presence or absence of growth rings in tropical woods so the qualification of a distinct or indistinct growth ring boundary is different.

Strengths and limitations of the study

Various scientific methodologies have the potential for use as forensic timber identification tools (Dormontt *et al.* 2015; Ugochukwua *et al.* 2018; Vlam *et al.* 2018). Wood anatomy is routinely employed in the daily regulation and control of cut wood and wood products because wood structure is currently the most effective means for the identification of CITES-protected timbers (Dormontt *et al.* 2015; Koch *et al.* 2015; Helmling *et al.* 2018).

A large number of carefully collected and accurately identified specimens were available for our study of the wood anatomy of Malagasy *Diospyros*. Since the implementation of the taxonomic revision of the genus in Madagascar, our understanding, characterization, and delimitation of the species has greatly improved thanks to the collaboration of multidisciplinary specialists. For this first study, we only examined species for which at least five replicas were available in order to ensure that any infra-specific variation was adequately identified and measured. There are, however, nearly 70 additional *Diospyros* species in Madagascar that can produce large enough trees to be potential sources of commercially valuable ebony wood. In order to establish a practical and reliable wood anatomical identification key, at least the most exploited species must be included, and ultimately, they all should be. This initial study thus serves to establish a reliable basis for the identification of commercially important species, and the number of species analyzed will be increased as further work progresses.

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APPENDIX

Table A1.
Information on *Diospyros* samples analysed.

Scientific name	Collector	Collection No.	DBH (cm)	Height (m)	Bioclimate
Diospyros analamerensis H. Perrier	RIR	3262	14	21	Dry
Diospyros analamerensis H. Perrier	RIR	3266	15	23	Dry
Diospyros analamerensis H. Perrier	RIR	3267	10	18	Dry
Diospyros analamerensis H. Perrier	RIR	3288	12	12	Dry
Diospyros analamerensis H. Perrier	RIR	3289	17	22	Dry
Diospyros bardotiae H.N. Rakouth, G.E. Schatz & Lowry	RIR	2872	22	19	Dry
Diospyros bardotiae H.N. Rakouth, G.E. Schatz & Lowry	RIR	3271	16	12	Dry
Diospyros bardotiae H.N. Rakouth, G.E. Schatz & Lowry	RIR	3272	15	15	Dry
Diospyros bardotiae H.N. Rakouth, G.E. Schatz & Lowry	RIR	3273	15	13	Dry
Diospyros bardotiae H.N. Rakouth, G.E. Schatz & Lowry	RIR	3274	16	17	Dry
Diospyros bardotiae H.N. Rakouth, G.E. Schatz & Lowry	RIR	3279	13	21	Dry
Diospyros baronii (H. Perrier) Lowry *et al.*, ined.	KAD	0085	5	8	Humid
Diospyros baronii (H. Perrier) Lowry *et al.*, ined.	RRN	0058	5	11	Humid
Diospyros baronii (H. Perrier) Lowry *et al.*, ined.	RRN	0060	6	10	Humid
Diospyros baronii (H. Perrier) Lowry *et al.*, ined.	RRN	0061	5	15	Humid
Diospyros baronii (H. Perrier) Lowry *et al.*, ined.	RRN	0062	5	9	Humid
Diospyros chitoniophora Capuron ex G.E. Schatz & Lowry	RIR	2403	8	15	Dry
Diospyros chitoniophora Capuron ex G.E. Schatz & Lowry	RIR	3222	8	12	Dry
Diospyros chitoniophora Capuron ex G.E. Schatz & Lowry	RIR	3223	11	13	Dry
Diospyros chitoniophora Capuron ex G.E. Schatz & Lowry	RIR	3241	15	16	Dry
Diospyros chitoniophora Capuron ex G.E. Schatz & Lowry	RIR	3242	8	12	Dry
Diospyros cupulifera H. Perrier	HRS	0046	8	13	Subarid
Diospyros cupulifera H. Perrier	HRS	0047	8	11	Subarid
Diospyros cupulifera H. Perrier	KAD	0177	11	14	Subarid
Diospyros cupulifera H. Perrier	KAD	0178	9	18	Subarid
Diospyros cupulifera H. Perrier	KAD	0180	10	13	Subarid
Diospyros cupulifera H. Perrier	RBE	2450	13	14	Subarid
Diospyros gracilipes Hiern	CR_	7375	6	13	Humid
Diospyros gracilipes Hiern	RFN	0015	10	9	Humid
Diospyros gracilipes Hiern	RFN	0038	6	7	Humid
Diospyros gracilipes Hiern	RIR	3200	8	10	Humid
Diospyros gracilipes Hiern	RZK	7697	13	10	Humid
Diospyros humbertiana H. Perrier	HRS	0023	8	12	Subarid
Diospyros humbertiana H. Perrier	HRS	0029	5	13	Subarid
Diospyros humbertiana H. Perrier	HRS	0033	11	11	Subarid
Diospyros humbertiana H. Perrier	HRS	0034	6	15	Subarid
Diospyros humbertiana H. Perrier	HRS	0036	8	14	Subarid
Diospyros lewisiae Mas, G.E. Schatz & Lowry, ined.	KAD	0115	8	16	Humid
Diospyros lewisiae Mas, G.E. Schatz & Lowry, ined.	RFN	0019	9	11	Humid
Diospyros lewisiae Mas, G.E. Schatz & Lowry, ined.	RFN	0023	7	10	Humid
Diospyros lewisiae Mas, G.E. Schatz & Lowry, ined.	SAN	0020	12	10	Humid
Diospyros lewisiae Mas, G.E. Schatz & Lowry, ined.	SAN	0021	12	10	Humid
Diospyros lewisiae Mas, G.E. Schatz & Lowry, ined.	SAN	0051	NA	NA	Humid
Diospyros littoralis Capuron ex G.E. Schatz & Lowry	RBE	2713	12	18	Humid
Diospyros littoralis Capuron ex G.E. Schatz & Lowry	RZK	8378	9	10	Humid
Diospyros littoralis Capuron ex G.E. Schatz & Lowry	RZK	8383	10	13	Humid
Diospyros littoralis Capuron ex G.E. Schatz & Lowry	RZK	8391	8	11	Humid
Diospyros littoralis Capuron ex G.E. Schatz & Lowry	RZK	8442	8	9	Humid
Diospyros malandy H.N. Rakouth *et al.*	RIR	3240	15	14	Dry
Diospyros malandy H.N. Rakouth *et al.*	RIR	3263	8	8	Dry
Diospyros malandy H.N. Rakouth *et al.*	RIR	3264	12	18	Dry
Diospyros malandy H.N. Rakouth *et al.*	RIR	3275	12	23	Dry

Table A1.
(Continued.)

Scientific name	Collector	Collection No.	DBH (cm)	Height (m)	Bioclimate
Diospyros malandy H.N. Rakouth *et al.*	RIR	3276	25	25	Dry
Diospyros randrianasoloi G.E. Schatz, Lowry & Mas, ined.	RFN	0003	8	11	Humid
Diospyros randrianasoloi G.E. Schatz, Lowry & Mas, ined.	RFN	0010	10	11	Humid
Diospyros randrianasoloi G.E. Schatz, Lowry & Mas, ined.	RNH	1186	12	13	Humid
Diospyros randrianasoloi G.E. Schatz, Lowry & Mas, ined.	RZK	8495	8	9	Humid
Diospyros randrianasoloi G.E. Schatz, Lowry & Mas, ined.	SAN	0003	10	24	Humid
Diospyros randrianasoloi G.E. Schatz, Lowry & Mas, ined.	SAN	0004	8	11	Humid
Diospyros rubripetiolata G.E. Schatz & Lowry	RBE	2251	11	13	Humid
Diospyros rubripetiolata G.E. Schatz & Lowry	RFN	0017	11	13	Humid
Diospyros rubripetiolata G.E. Schatz & Lowry	RNH	1185	16	25	Humid
Diospyros rubripetiolata G.E. Schatz & Lowry	RZK	7715	NA	NA	Humid
Diospyros rubripetiolata G.E. Schatz & Lowry	SAN	0035	15	18	Humid
Diospyros rubripetiolata G.E. Schatz & Lowry	SAN	0041	18	20	Humid
Diospyros squamosa Bojer ex A. DC.	RFN	0054	8	9	Humid
Diospyros squamosa Bojer ex A. DC.	RFN	0058	9	10	Humid
Diospyros squamosa Bojer ex A. DC.	RFN	0062	7	10	Humid
Diospyros squamosa Bojer ex A. DC.	RFN	0063	8	10	Humid
Diospyros squamosa Bojer ex A. DC.	RFN	0119	16	25	Humid
Diospyros squamosa Bojer ex A. DC.	RFN	0120	14	17	Humid
Diospyros squamosa Bojer ex A. DC.	RFN	0121	10	13	Humid
Diospyros squamosa Bojer ex A. DC.	RRN	0038	8	15	Subhumid
Diospyros squamosa Bojer ex A. DC.	RRN	0039	11	30	Subhumid
Diospyros squamosa Bojer ex A. DC.	RRN	0040	7	17	Subhumid
Diospyros squamosa Bojer ex A. DC.	RZK	7713	13	25	Humid
Diospyros squamosa Bojer ex A. DC.	SFR	0259	10	8	Humid
Diospyros toxicaria Hiern	EME	0019	10	21	Humid
Diospyros toxicaria Hiern	KAD	0080	8	24	Humid
Diospyros toxicaria Hiern	KAD	0081	9	26	Humid
Diospyros toxicaria Hiern	KAD	0082	16	15	Humid
Diospyros toxicaria Hiern	RAF	0002	NA	NA	Humid
Diospyros toxicaria Hiern	RBE	2480	6	24	Humid
Diospyros toxicaria Hiern	RBE	2616	19	22	Humid
Diospyros toxicaria Hiern	SAN	0018	16	15	Humid
Diospyros toxicaria Hiern	SAN	0022	6	10	Humid
Diospyros toxicaria Hiern	SAN	0039	7	13	Humid
Diospyros tropophylla (H. Perrier) G.E. Schatz & Lowry	RAV	0010	12	35	Dry
Diospyros tropophylla (H. Perrier) G.E. Schatz & Lowry	RAV	0012	7	17	Dry
Diospyros tropophylla (H. Perrier) G.E. Schatz & Lowry	RIR	3339	17	20	Dry
Diospyros tropophylla (H. Perrier) G.E. Schatz & Lowry	RIR	3345	8	15	Dry
Diospyros tropophylla (H. Perrier) G.E. Schatz & Lowry	ROZ	0031	12	17	Dry
Diospyros tropophylla (H. Perrier) G.E. Schatz & Lowry	ROZ	0034	11	40	Dry
Diospyros tropophylla (H. Perrier) G.E. Schatz & Lowry	RFN	0102	7	11	Subarid
Diospyros tropophylla (H. Perrier) G.E. Schatz & Lowry	RFN	0104	8	14	Subarid
Diospyros tropophylla (H. Perrier) G.E. Schatz & Lowry	RFN	0105	9	14	Subarid
Diospyros tropophylla (H. Perrier) G.E. Schatz & Lowry	RFN	0106	7	11	Subarid
Diospyros tropophylla (H. Perrier) G.E. Schatz & Lowry	RFN	0113	6	11	Subarid
Diospyros tropophylla (H. Perrier) G.E. Schatz & Lowry	RIR	3414	10	12	Subarid

Collector: CR, Charles Rakotovao; KAD, Dochard Karatra; EME, Emeline; RAF, Fenonirina Rakotoarison; RAV, Rota Ravaoherinavalona; RBE, Roger Bernard; RIR, Richard Randrianaivo; RFN, Fanilo Malala Ramanitrinizaka; RNH, Nivo Rakotonirina; RRN, Ravo Ramanantsialonina; RZK, Richardson Razakamalala; SAN, Ninah Sandratriniaina.