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IAWA Journal 44 (2), 2023: 225-252

iawa

Comparative wood anatomy of 16 Malagasy *Dalbergia* species (Fabaceae) using multivariate techniques

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Accepted for publication: 19 October 2022; published online: 8 November 2022

Summary – Rosewood and palisander (*Dalbergia* L.f., Fabaceae) are sources of highly valuable tropical timber and include species threatened by habitat degradation and selective logging for national and international trade. Law enforcement depends on reliable and cost-effective species-level identification of timber along the supply chain. The potential of wood anatomy to distinguish between species has not yet been systematically investigated for *Dalbergia* species from Madagascar. We assessed 36 qualitative and eight quantitative wood anatomical features in 16 Malagasy *Dalbergia* species that form medium-sized to large trees, representing each species by at least five individuals. We integrated and contrasted the newly collected data with existing data from InsideWood and two previous studies. Principal component analysis of 93 individuals and 29 variables resulted in non-overlapping hulls for eight species with respect to the first two dimensions. Four quantitative features (number of ray tiers per millimetre, number of rays per millimetre, vessel density, and vessel element length) and two qualitative features (scanty paratracheal axial parenchyma and irregular to absent storied structure) were found to be potentially diagnostic to distinguish three single species and three pairs of closely related species. Following our analyses, we provide a provisional microscopic wood anatomical identification key for the 16 *Dalbergia* species, which can be applied to both logs and sawn wood.

Keywords – *Dalbergia*, Fabaceae, rosewood, wood anatomy, Madagascar, identification.

Introduction

Dalbergia L.f. (Fabaceae) is a pantropical plant genus containing about 270 currently accepted species (WCVP 2021), which grow as trees, shrubs, or lianas. Madagascar represents a unique center of *Dalbergia* diversity, where the genus is represented by 55 currently accepted species, of which 54 are endemic to the island (Bosser & Rabevohitra 1996, 2002, 2005; Wilding *et al.* 2021a,b; Crameri *et al.* 2022; Madagascar Catalogue 2022). The species occur in various vegetation types across the island's five major terrestrial ecoregions (Dinerstein *et al.* 2017; Madagascar Catalogue 2022). The arborescent species include sources of high-quality precious woods, which are referred to as *Madagascar rosewood* in English, *bois de rose* or *palissandre* in French, and various vernacular names such as *andramena*, *manary*, or *voamboana* (Normand 1988, Bosser & Rabevohitra 2002). Recent sampling efforts and integrative analyses revealed

Published by Koninklijke Brill NV, Leiden

DOI 10.1163/22941932-bja10105

that the taxonomy of the genus may require substantial revision (Crameri 2020; Wilding *et al.* 2021a,b; Crameri *et al.* 2022), and multiple existing species delimitations remain problematic and are the subject of ongoing taxonomic work.

The major threats to Malagasy *Dalbergia* species are habitat loss through deforestation, land clearing and fire for subsistence agriculture (Brown *et al.* 2015; Vieilledent *et al.* 2018; Morelli *et al.* 2020; Global Forest Watch 2021; Wilding *et al.* 2021b), as well as over-exploitation through selective logging (Schuurman & Lowry 2009; Waeber *et al.* 2019). At least 43 currently accepted species reach 20 m total height or 20 cm in diameter at breast height (Madagascar Catalogue 2022) and therefore represent likely targets of logging for timber. Selective logging of rosewood has a long history in Madagascar, but its overall impact has drastically increased over the last two decades and is largely driven by foreign demand (Patel 2007; Randriamalala & Liu 2010; Mason *et al.* 2016; Waeber *et al.* 2019). In the period between 2000 and 2014, China's imports of rosewood logs and sawn wood grew by an estimated 1250%, of which an increasing proportion was sourced from African countries (Treanor 2015). In 2009, Madagascar was hit by a political crisis, which led to massive illegal rosewood logging, especially in the northeastern part of the island (Schuurman & Lowry 2009). In an attempt to prevent further unsustainable exploitation, the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) placed all Malagasy populations of *Dalbergia* spp. and *Diospyros* spp. (ebony) on its Appendix II in 2013, and a zero-export quota has since been in place (CITES 2013, 2015). In the following years, there were several seizures of Madagascar rosewood along global trade routes, culminating in the Singapore interception of approx. 29 000 logs of Madagascar rosewood, one of the largest CITES-related rosewood seizures ever made (Butler 2014, UNODC 2016). This shows that existing national laws and international regulations are being circumvented on a large scale.

The ability to identify and distinguish among species listed in CITES Appendix II is essential for both the convention's application via so-called Non-Detriment Findings, demonstrating that "export will not be detrimental to the survival of that species" (CITES Article IV), and for its enforcement via forensic timber identification. Therefore, a CITES Action Plan for *Dalbergia* spp. (and *Diospyros* spp.) from Madagascar was adopted at the Conference of the Parties (CoP) in 2013 (Decision 16.152; CITES 2013) and reaffirmed at later meetings in CITES 2017 (Decision 17.204) and CITES 2018 (Decision 18.96). The Action Plan specifies, inter alia, that Madagascar shall "d) continue the production of identification materials for timber and timber products of species of the genera *Dalbergia* and *Diospyros* from Madagascar" (CITES 2018, 2019). Collaborative efforts towards conservation and sustainable management of Malagasy precious woods (*Dalbergia* spp. and *Diospyros* spp.) have been undertaken since 2014, and resulted in collection of new plant material in the field using a standardized sampling protocol that includes sampling of heartwood and herbarium voucher specimens, taxonomic investigations, and conservation assessments. In parallel, these resources have also been used to develop reference collections and databases for various forensic timber identification methods (reviewed in Dormontt *et al.* 2015 and Schmitz *et al.* 2020).

In this study, we focus on timber identification using wood anatomy. This method has been the traditional means for timber identification and can be applied to logs, sawn wood, and finished products (Gasson *et al.* 2011; Dormontt *et al.* 2015). Wood features are known to contain phylogenetic signals at the level of plant orders, families, genera and below (Baas *et al.* 2000; Carlquist 2001; Dormontt *et al.* 2015), although species of the same genus can only occasionally be distinguished with certainty (Dormontt *et al.* 2015). For example, four quantitative wood anatomical features provided sufficient resolution to distinguish *Dalbergia nigra* (Vell.) Allemão ex Benth. from six other Latin American species with a true positive rate of 100%, although with a high false positive rate of 36% (Gasson *et al.* 2010).

Didier Normand (1988) initiated systematic wood anatomical studies on Malagasy *Dalbergia*, providing an anatomical characterization and identification key for three economically significant species from the easter of Madagascar. After the taxonomic revision of the genus by Bosser & Rabevohitra (1996), Détienne, Gasson and Lemmens (see https://prota4u.org/database/) substantially expanded on Normand's work by preparing wood anatomical characterizations of approx. 25 Malagasy *Dalbergia* species, following the IAWA list of microscopic features for hardwood identification (IAWA Committee 1989). These characterizations were published in the

InsideWood online database (InsideWood 2004–onwards; Wheeler 2011). They were based on wood collections from one to nine individuals per taxon, many of which have associated herbarium vouchers deposited in the herbaria of Paris (P), Kew (K) and Antananarivo (TAN and TEF, acronyms following Thiers 2021), which can be investigated to review or revise the species identity in face of further taxonomic changes. In addition, an Atlas on the stem anatomy of 19 Malagasy *Dalbergia* taxa was prepared by Ravaomanalina *et al.* (2017). The Atlas includes many suspected targets of international trade, but analyses were limited to a single individual per taxon. Fifteen of these individuals are fully documented with herbarium vouchers and precisely georeferenced, and fourteen fully documented individuals were also genotyped by Crameri (2020).

These previous wood anatomical investigations already represent important resources for forensic timber identification. However, many knowledge gaps still exist, especially with regard to systematic study of intraspecific versus interspecific differences in wood anatomical features based on a larger number of individuals per taxon, the relationship of wood anatomical variation and eco-geography including climatic conditions, and the association of wood anatomical features and known phylogenetic relationships. Moreover, it is currently unclear to what extent the documented wood anatomical variation in certain species resulted from a false aggregation of individuals belonging to different evolutionary lineages. The present study expands on previous work and represents a first step towards filling these knowledge gaps based on fully vouchered and authoritatively identified collections, considering recent taxonomic developments, and including at least five individuals per species. Specifically, we (1) performed a microscopic wood anatomical characterization of 93 individuals belonging to 16 species of Malagasy *Dalbergia* that grow to an exploitable diameter, six of which have not been investigated in earlier wood anatomical studies, (2) investigated the variation of 44 wood anatomical features within and between species using multivariate methods, (3) integrated and compared our results with previous findings to identify patterns that are consistent across datasets and potentially diagnostic, and (4) developed an initial dichotomous wood anatomical identification key.

Materials and methods

SAMPLING

Heartwood specimens of 93 *Dalbergia* trees were collected between 2014 and 2019 across three bioclimatic regions of Madagascar as defined by Dinerstein *et al.* (2017): 52 in dry deciduous forests of west and north Madagascar, 33 in humid forests in east Madagascar, and 8 in arid (succulent) woodlands in southwest Madagascar (Fig. A1 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159). The wood specimens were taken at breast height (approx. 1.3 m above ground) from trees with total heights ranging approx. (3–)8–14(–30) m and stem diameters at breast height (DBH) ranging approx. (4–)11–22(–85) cm. Wood specimens were deposited in the xylotheque of the Plant Biology and Ecology Department at the University of Antananarivo, and herbarium voucher specimens were deposited in the DBEV, MO, P, TAN and ZT herbaria, acronyms following Thiers (2021). The 93 wood specimens belonged to 16 *Dalbergia* species endemic to Madagascar, which were each represented by five to eight individuals. The 16 species all form medium to large trees (reaching at least 20 cm DBH and/or a total height of 20 m) and included thirteen species accepted by Bosser & Rabevohitra (1996, 2002, 2005). One additional species was recently resurrected from synonymy (*D. obtusa* Lecomte; Madagascar Catalogue 2022), one species was described recently (*D. razakamalalae* Crameri, Phillipson & N. Wilding; Crameri *et al.* 2022), and one suspected new species has recently been submitted for review (*D. oronjiae* ined.; N. Wilding, pers. commun.). Initial identifications were made by taxonomists of the Missouri Botanical Garden Madagascar Program and were confirmed or revised by specialists working on the taxonomy of *Dalbergia* species from Madagascar (S. Crameri, N. Wilding, and P. B. Phillipson). Collection details are given in Table A1 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159.

WOOD ANATOMICAL PROCEDURES

We prepared wood sections following the techniques of Gärtner & Schweingruber (2013). We used a GLS1 microtome to produce transverse (TS), longitudinal tangential (TLS), and longitudinal radial (RLS) sections (15–25 μm), and double stained all sections with aqueous 1% safranin (stains lignified cell structures red) and aqueous 1% Astra Blue (stains unlignified structures blue) for 5 minutes following Bukatsch (1972) and Gärtner & Schweingruber (2013). We then dehydrated the stained sections in an alcohol dilution series (5 minutes each in 50, 70, 95 and 100% ethanol) and permanently mounted them in Euparal following Chaffey (2002) and Gärtner & Schweingruber (2013). Slides of macerated tissue were prepared using Jeffrey's solution (Johansen 1940).

We took photomicrographs of all slides using an Olympus BX 43 light microscope coupled to a Canon 800D digital camera and EOS software. We described xylem anatomical features following the IAWA list of microscopic features for hardwood identification (IAWA Committee 1989) as a guide, but with modifications that allowed for more subtle differences to be measured. Specifically, we assessed 36 qualitative features from 17 feature groups, and 8 quantitative features in each photomicrograph (Table 1).

FEATURE CODING

Qualitative features of the same feature group (Table 1) were not mutually exclusive but often found to co-occur in slides of the same individual, leading to various combinations of qualitative features in different individuals. We therefore coded dummy variables for each occurring qualitative feature (e.g., WP_a, WP_b, and WP_c) rather than for each occurring combination of qualitative features (e.g., WP_a, WP_ab, WP_b and WP_c). This reduced the total number of dummy variables, and preserved information on multiple individuals sharing a single feature, regardless of whether that feature occurred in combination with other features or not. We scored qualitative features independently of each other, except that we always scored individuals with differences in vessel diameter between earlywood and latewood (TGR_b) as having distinct growth rings (GR_a) and either ring-porous (WP_a) or semi-ring-porous (WP_b) wood, whereas individuals with indistinct or absent growth rings (GR_b) were always scored as having diffuse-porous wood (WP_c). Furthermore, we treated growth rings boundaries (GR_a and GR_b), ray width (RW_a and RW_b), and storied structure (SS_a and SS_b) as binary but preserved two redundant dummy variables to allow the new data to be integrated with and contrasted against existing data aggregated by species (see next paragraph).

We assessed quantitative features based on approx. 30 (16–65) separate measurements per individual. We then calculated the median value for each individual, which is unaffected by rare extremes (outliers) and therefore a more robust descriptive measure of central tendency compared to the mean. Finally, we calculated the expected value and variability of each quantitative feature for each species as the mean and standard deviation of a population of median values.

DATASET INTEGRATION AND SPECIMEN DETERMINATION

We integrated and contrasted the wood anatomical dataset collected in this study (hereafter referred to as "the new dataset") with three wood anatomical datasets of the same species available from previous studies. This served to increase the number of individuals per species and geographic region where possible, while updating and valorizing existing resources that have potentially become outdated due to the ongoing taxonomic revision of the genus in Madagascar. The previous studies consisted of (1) the stem wood anatomy Atlas by Ravaomanalina *et al.* (2017), which we hereafter refer to as "the Atlas dataset", (2) previously unpublished data collected by P. Détienne, which we hereafter refer to as "the Détienne dataset", and (3) data published in the InsideWood online database, which consisted of the Détienne dataset with additional observations from other wood anatomists (notably Gasson and Lemmens), and which we hereafter refer to as "the InsideWood dataset".

Table 1. List of 44 wood anatomical features for characterization of *Dalbergia* heartwood.

	Code	IAWA
Qualitative features		
Growth rings boundaries (GR)		
Distinct	GR_a	1
Indistinct to absent	GR_b	2
Growth ring boundary types (TGR)		
Thick-walled and radially flattened fibers	TGR_a	–
Differences in vessel diameter between latewood and earlywood	TGR_b	–
Marginal parenchyma	TGR_c	–
Wood porosity (WP)		
Ring-porous	WP_a	3
Semi-ring-porous	WP_b	4
Diffuse-porous	WP_c	5
Vessel groupings (VG)		
Predominantly (⩾90%) solitary	*VG_a*	*9*
Perforation plates (PP)		
Simple	*PP_a*	*13*
Intervessel pit arrangement (IPA)		
Opposite	IPA_a	21
Alternate	*IPA_b*	*22*
Vestured pits (VP)		
Present	*VP_a*	*29*
Vessel-ray pitting (VRP)		
With distinct borders; similar to intervessel pits in size and shape throughout the ray cell	*VRP_a*	*30*
Ground tissue fibres (GTF)		
With simple to minutely bordered pits	*GTF_a*	*61*
Apotracheal axial parenchyma (APA)		
Diffuse	APA_a	76
Diffuse-in-aggregates	APA_b	77
Paratracheal axial parenchyma (APP)		
Scanty paratracheal	APP_a	78
Vasicentric	APP_b	79
Aliform	APP_c	80/82
Confluent	APP_d	83
Banded	APP_e	–
Banded parenchyma (BP)		
In narrow bands or lines up to three cells wide	BP_a	86
Bands more than three cells wide	BP_b	85
Marginal	BP_c	89
Reticulate	BP_d	87
Axial parenchyma cell type/strand length (APCT)		
Fusiform	*APCT_a*	*90*
Two cells per parenchyma strand	*APCT_b*	*91*

Table 1. (Continued.)

	Code	IAWA
Ray width (RW)		
Predominantly (⩾80%) uniseriate	RW_a	~96
Predominantly (⩾80%) biseriate	RW_b	~97
Ray cellular composition (RCC)		
All ray cells procumbent	RCC_a	104
Body ray cells procumbent with one row of upright and / or square marginal cells	RCC_b	106
Storied structure (SS)		
Distinct	SS_a	120
Irregular to absent	SS_b	~119
Prismatic crystals (PC)		
Present	*PC_a*	*136*
In chambered axial parenchyma cells	*PC_b*	*142*
Quantitative characters		
Intervessel pit diameter (µm)	IPD	24–27
Vessel density (cells/mm^2)	VD	46–50
Vessel element length (µm)	*VL*	*52–54*
Fibre length (µm)	FL	71–73
Ray height (µm)	RH	approx. 102
Rays per mm	RMM	114–116
Number of cells per ray	NCR	–
Number of ray tiers per mm	NSS	–

Feature abbreviations used in this study (Code) and corresponding IAWA feature numbers (IAWA Committee 1989) are given. A tilde (~) indicates partial correspondence, and a hyphen (–) indicates no correspondence to any IAWA feature number. Ten qualitative features present in all individuals of the new dataset and the Atlas dataset, and one quantitative feature spanning a single IAWA category in all datasets are shown in italics.

We first reviewed the species identification of the individuals forming the basis of the Atlas and Détienne datasets, respectively, and provided updated determinations on the Tropicos database where necessary (Madagascar Catalogue 2022; also see Supplementary Table A3 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159). While it was possible to review the species identification of all 19 individuals of the Atlas dataset, we could only review 58 out of 74 individuals forming the basis of the Détienne and InsideWood datasets. The remaining 16 cited individuals either possessed ambiguous collection numbers (s.n.), or the herbarium vouchers could not be located.

We then selected 8 out of the 19 individuals of the Atlas dataset that corresponded to 7 of the 16 species of the new dataset, and we selected 4 out of 24 taxa from the Détienne and InsideWood datasets. These four taxa were characterized by Détienne on the basis of one or several individuals, which were revealed to be correctly identified, and which corresponded to species of the new dataset. The other 20 taxa from the Détienne and Insidewood datasets consisted of 8 taxa corresponding to an aggregate of different species, 7 taxa for which the species identity could not be assessed for all cited individuals, and 5 taxa corresponding to correctly identified species or species complexes, but without overlap to the new dataset (Table A3 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159).

We translated strings of IAWA feature numbers for each individual of the Atlas dataset to the corresponding qualitative features listed in Table 1 using a specifically developed R function (https://github.com/scrameri/

DalbergiaWoodAnatomy/wiki/recode.IAWA), extracted the individual mean of quantitative variables provided in the Atlas for VD, VL, RH, and RMM, and we assigned the mean of ranges for IPD and NSS provided in the Atlas (the FL and NCR features were not assessed by Ravaomanalina *et al.* (2017), and the TGR, APA, APP, and BP features were not assessed for all species). We applied an analogous procedure to the Détienne and InsideWood datasets, which consisted of strings of IAWA feature numbers. In contrast to the Atlas dataset, we only considered feature numbers that corresponded to any of the 36 qualitative features listed in Table 1, because quantitative data can only be approximately estimated from IAWA feature numbers. Finally, we recoded the qualitative features of all four datasets as dummy variables (1, feature present; 0, feature absent), except that we assigned a value of 0.5 and NA (not available) to IAWA feature numbers annotated with “v” (variable) or “?” (unsure) in the Détienne or InsideWood datasets, respectively.

In addition, we supplemented the new dataset and the Atlas dataset, which consisted of relatively recent and accurately georeferenced collections, with bioclimatic data from the CHELSA version 1 Bioclim database (https://chelsa-climate.org/bioclim; Karger *et al.* 2017). We selected eight bioclimatic variables: mean annual air temperature (Bio01), isothermality (i.e., the ratio of diurnal variation to annual variation in temperatures; Bio03), temperature seasonality (Bio04), annual range of air temperature (Bio07), annual precipitation amount (Bio12), precipitation amount of the wettest month (Bio13), precipitation amount of the driest month (Bio14), and precipitation seasonality (Bio15). We extracted the bioclimatic values from the raster files (resolution of 30 arc seconds or approx. 900 m) at the geo-coordinates of individuals of the new dataset and the Atlas dataset using the R package terra (Hijmans 2021) version 1.4-22. The bioclimatic data are provided in Table A4 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159.

MULTIVARIATE ANALYSES

We first identified and removed variables with zero variation from all datasets. We then visualized the recoded qualitative wood anatomical variables as a heatmap comprising all datasets using the ComplexHeatmap package (Gu *et al.* 2016) version 2.6.2, and we visualized the quantitative wood anatomical variables of the new dataset and the Atlas dataset as parallel coordinates plots (Inselberg 2009) for each species using the ggplot2 package (Wickham 2016) version 3.3.5, highlighting the different datasets.

We also applied principal component analysis (PCA) to the wood anatomical variables of the new dataset only, because the quantitative variables were partially or completely missing in the other datasets. Specifically, we first imputed 13 missing FL values, 5 missing RMM values, and 2 missing NSS values using the species mean, then removed constant variables and completely redundant dummy variables (e.g., GR_b = −GR_a). We then divided the dummy variable values of 1 such that the row sums within feature groups all added up to 1 if a feature was present (zero otherwise). Finally, we centred and scaled the weighted dummy variables and the quantitative variables to unit variance, and subjected the data to PCA using the *prcomp* function in R. We visualized the PCA scores and loadings of the first four components as scatterplots and variable plots using the ggplot2 package and added species hulls using the ggforce package (Pedersen 2021) version 0.3.3.

We also investigated correlations between wood anatomical features and bioclimatic variables based on the new dataset and the Atlas dataset. Specifically, we computed a Spearman’s rank correlation matrix of all pairs of variables and visualized highly correlated variables (Spearman’s $\rho \geqslant 0.7$) as a correlation heatmap using the GGally package version 2.1.2 (Schloerke *et al.* 2021) and as spider graphs or scatterplots as before. For a subset of quantitative wood anatomical features, we also tested for significant differences between specimens from the humid eastern part of Madagascar and the remaining specimens, using non-parametric two-sample Wilcoxon rank sum tests (a.k.a. Mann–Whitney *U*-tests).

FEATURES OF POTENTIALLY DIAGNOSTIC SIGNIFICANCE

We identified wood anatomical features with either low or a high frequency in a single or a few species or other groups of individuals, based on the 36 qualitative features and the 8 quantitative features of all four datasets. We wrote the R function *get.diag* (https://github.com/scrameri/DalbergiaWoodAnatomy/wiki/get.diag) to evaluate the diagnostic value of each feature. The function can evaluate both dummy variables (recoded from qualitative features) and quantitative variables, and searches for character states (qualitative features) or numerical thresholds (quantitative features) with a user-specified minimum true positive rate (TPR, a.k.a. sensitivity, or the probability that an individual possesses a group's characteristic feature given that it actually belongs to that group) and a low false positive rate (FPR, a.k.a. fall-out, 1 — specificity, or the probability that an individual possesses a group's characteristic feature given that it actually belongs to another group) given any grouping. One grouping factor can be processed at a time, but several grouping factors can be analysed one after the other, and the results finally combined. Our groupings consisted of (1) the botanical species, (2) the subgeneric section (see Groups 1 and 2 in Bosser & Rabevohitra 2002), which have strongly contrasted morphological divergence in flower and fruit characters, and (3) the broad geographic region, namely the North (<14° south latitude), humid East, or seasonally dry to arid West/Southwest (⩾14° south latitude) of the island (species occur in one or two of these geographic regions). We identified features of potentially diagnostic significance in a single or a pair of two groups from the remaining groups, using a filtering threshold of 100% for TPR and ⩽5% for FPR.

Dataset integration, processing, Wilcoxon tests, multivariate and diagnostic feature analyses were performed using R software version 4.0.2 (R Core Team 2021). All used R code and functions are provided in supplementary file and on Github (https://github.com/scrameri/DalbergiaWoodAnatomy).

Feature abbreviations used in this study (Code) and corresponding IAWA feature numbers (IAWA Committee 1989) are given. A tilde (~) indicates partial correspondence, and a dash (–) indicates no correspondence to any IAWA feature number. Ten qualitative features present in all individuals of the new dataset and the Atlas dataset, and one quantitative feature spanning a single IAWA category in all datasets are shown in italics.

Results

MICROSCOPIC WOOD DESCRIPTION

Representative photomicrographs of transverse (Fig. 1), tangential (Fig. 2), and radial (Fig. 3) sections are given for a selection of species. The following descriptions highlight which features were found to be present in all or a subset of 16 assessed Malagasy *Dalbergia* species, and they provide the observed ranges of quantitative features based on median values per individual. They also highlight potentially diagnostic features to identify single species, or to distinguish between groups of related species. The variation in quantitative features across the new dataset and the Atlas dataset is presented as parallel coordinates plots (Fig. 4A) and in Table 2, and qualitative features across all four datasets are presented as a heatmap (Fig. 4B). Qualitative features and individual medians of the new dataset are provided in Table A2 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159, and repeated raw measurements of quantitative features are provided in Table A6 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159.

GROWTH RINGS AND WOOD POROSITY

Distinct growth rings and ring-porous and/or semi-ring-porous wood were observed in all assessed species considering all datasets, except for two species (*Dalbergia normandii* and *D. razakamalalae*). Eight species always

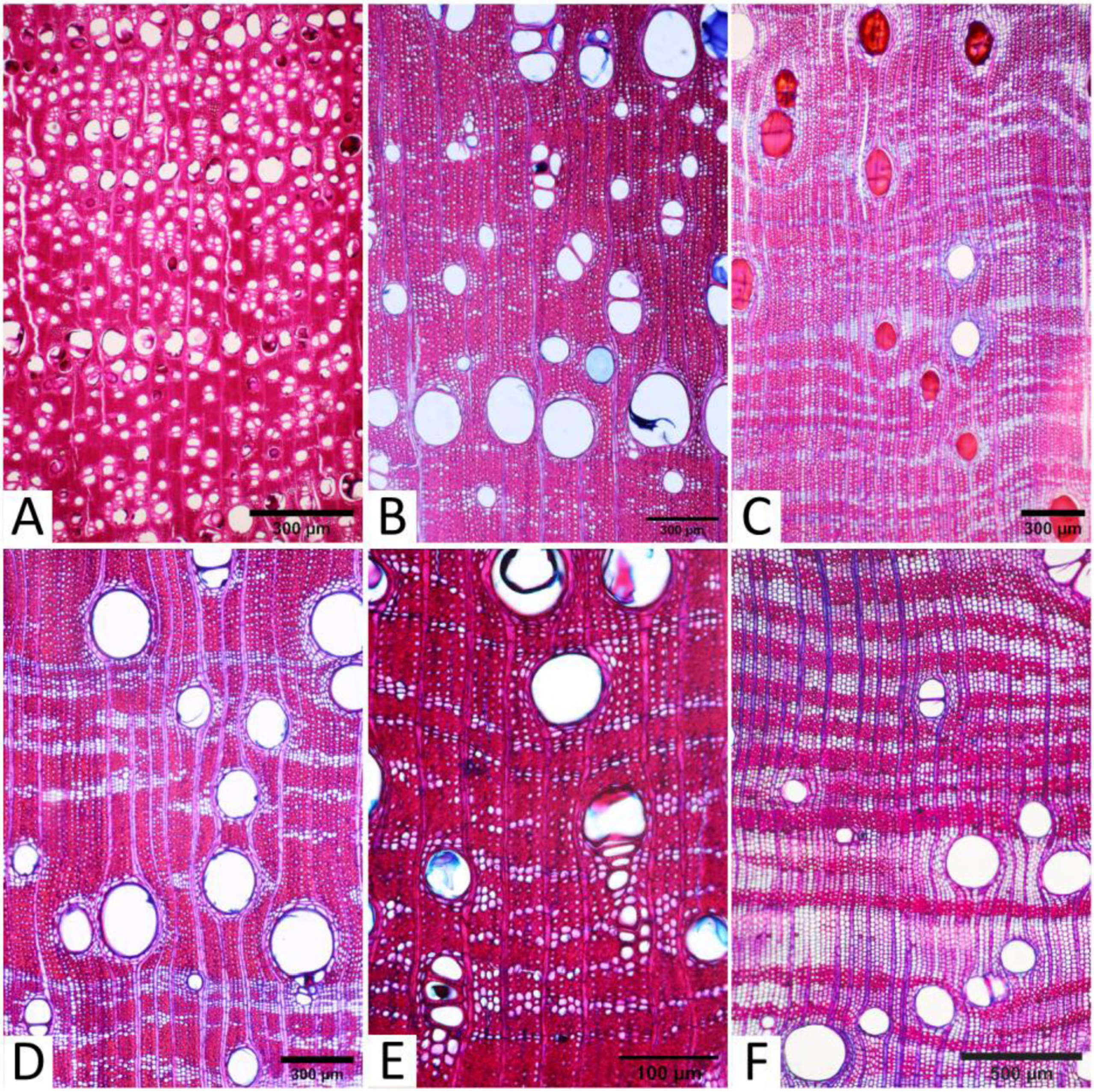


Fig. 1. Transverse sections of *Dalbergia* species. (A) *D. lemurica* (*Rakotovao 6514*), Growth ring distinct marked by differences in vessel diameter earlywood and latewood, wood ring-porous. (B) *D. purpurascens* (*Randrianaivo 3335*), growth rings distinct, marked by differences in vessel diameter between earlywood and latewood and marginal parenchyma, wood semi-ring porous with solitary vessels and in short radial multiples of up to four. (C) *D. normandii* (*Razakamalala 8223*), growth rings indistinct, wood diffuse-porous, paratracheal axial parenchyma confluent and wing-aliform, deposit in vessel. (D) *D. urschii* (*Ramanantsialonina 44*), axial parenchyma vasicentric and aliform. (E) *D. abrahamii* (*Bernard 2765*), parenchyma in bands up to three cells wide. (F) *D. baronii* (*Bernard 2254*), diffuse-porous wood narrow and broad (up to 20, arrow) bands of axial parenchyma.

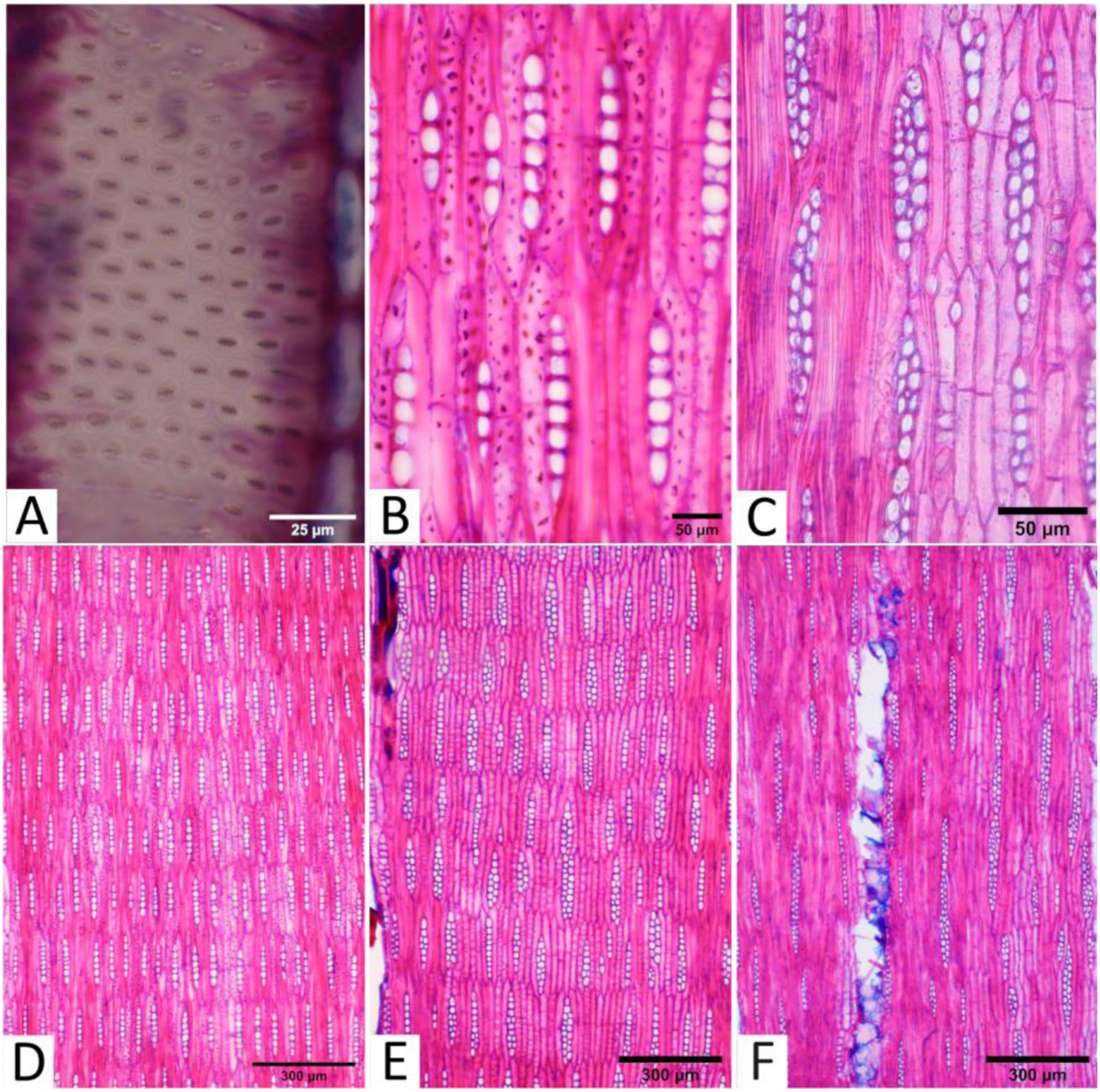


Fig. 2. Tangential sections of *Dalbergia* species. (A) *D. davidii* (*Randrianaivo 3352*), small alternate and opposite intervessel pits. (B) *D. razakamalalae* (S. N. *Andrianarivelo 255*), *ray uniseriate*libriform fibre. (C) *D. abrahamii* (*Karatra 59*), axial parenchyma fusiform and in strands of two cells, prismatic crystals. (D) *D. razakamalalae* (*Ramanitrinizaka 1*), rays uniseriate, axial parenchyma, libriform fibers and rays storied. (E) *D. pseudobaronii* (*Ramanantsialonina 26*), storied axial parenchyma and rays (predominatly biseriate). (F) *D. davidii* (*Randrianaivo 3352*), predominantly biseriate, not storied.

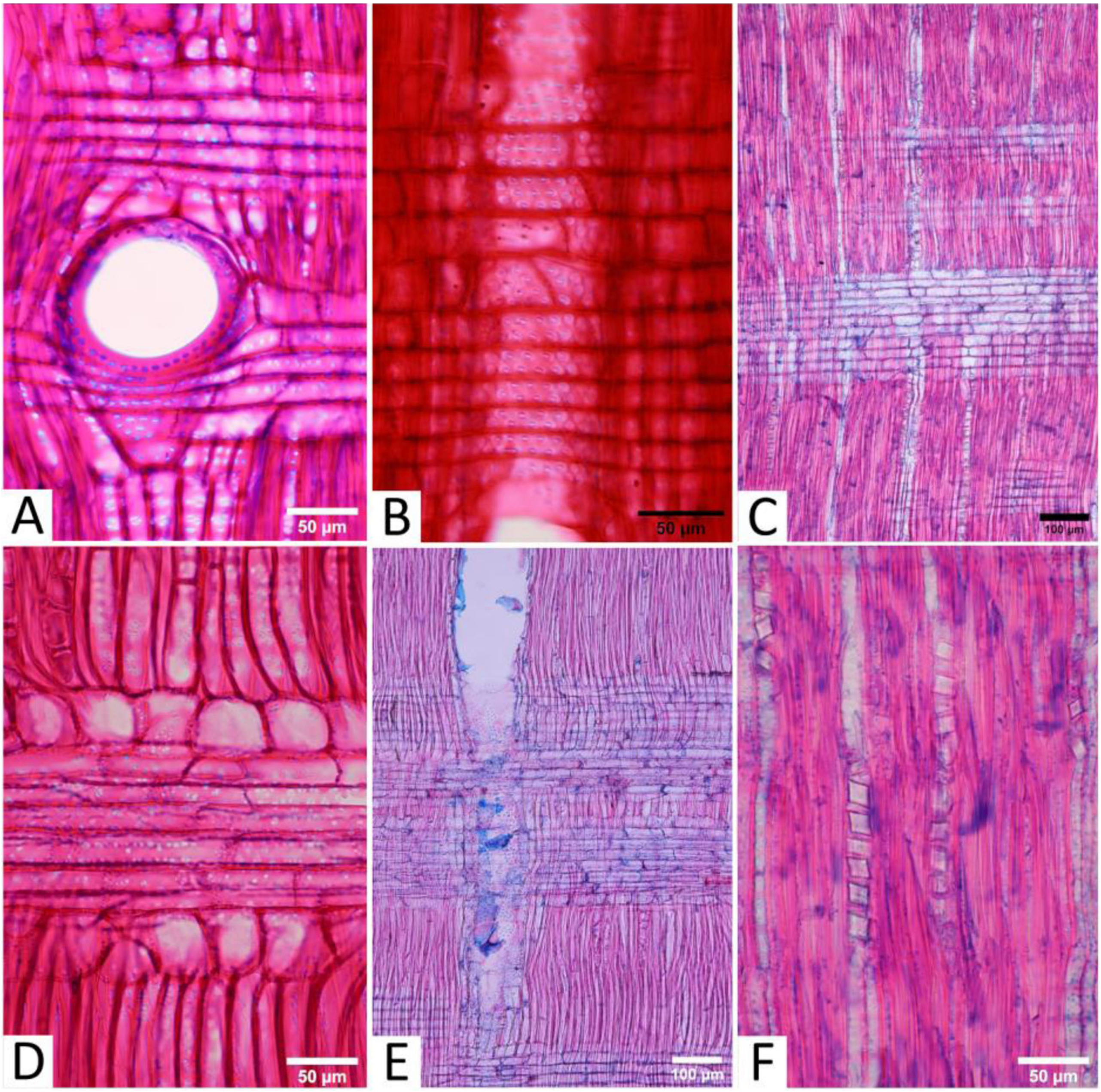
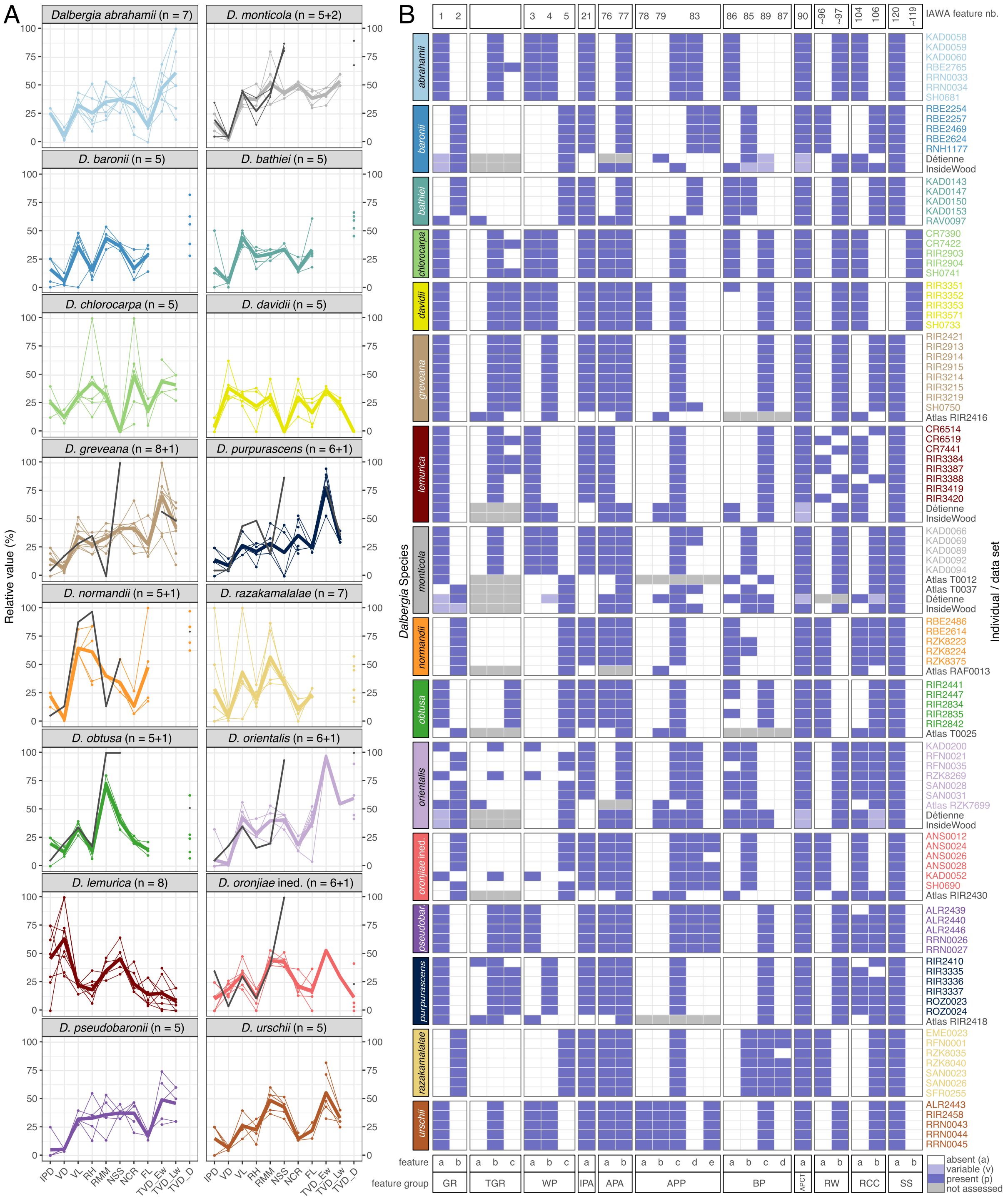


Fig. 3. Radial sections of *Dalbergia* species. (A) *D. abrahamii* (*Ramanantsialonina 34*), simple perforation plate (arrow). (B) *D. lemurica* (*Rakotovao 6675*), ray-vessel pits similar to intervessel pits in size and shape. (C) *D. abrahamii* (*Ramanantsialonina 33*) homogeneous ray with procumbent cells. (D) *D. monticola* (*Karatra 94*), heterogeneous rays with procumbent body cells procumbent and with square cells in one marginal row. (E) *D. purpurascens* (*Randimbison 23*), homogeneous (a) and heterogenous (b) rays. (F) *D. abrahamii* (*Ramanantsialonina 33*), prismatic crystals in chambered axial parenchyma cells.


A
Dalbergia abrahamii (n = 7)
D. monticola (n = 5+2)
D. baronii (n = 5)
D. bathiei (n = 5)
D. chlorocarpa (n = 5)
D. davidii (n = 5)
D. greveana (n = 8+1)
D. purpurascens (n = 6+1)
D. normandii (n = 5+1)
D. razakamalalae (n = 7)
D. obtusa (n = 5+1)
D. orientalis (n = 6+1)
D. lemurica (n = 8)
D. oronjiae ined. (n = 6+1)
D. pseudobaronii (n = 5)
D. urschii (n = 5)
Relative value (%)
0
25
50
75
100
IPD
VD
VL
RH
RMM
NSS
NCR
FL
TVD_Ew
TVD_Lw
TVD_D
B
IAWA feature nb.
1
2
3
4
5
21
76
77
78
79
83
86
85
89
87
90
~96
~97
104
106
120
~119
Dalbergia Species
abrahamii
baronii
bathiei
chlorocarpa
davidii
greveana
lemurica
monticola
normandii
obtusa
orientalis
oronjiae ined.
pseudobar.
purpurascens
razakamalalae
urschii
Individual / data set
KAD0058
KAD0059
KAD0060
RBE2765
RRN0033
RRN0034
SH0681
RBE2254
RBE2257
RBE2469
RBE2624
RNH1177
Détienne
InsideWood
KAD0143
KAD0147
KAD0150
KAD0153
RAV0097
CR7390
CR7422
RIR2903
RIR2904
SH0741
RIR3351
RIR3352
RIR3353
RIR3571
SH0733
RIR2421
RIR2913
RIR2914
RIR2915
RIR3214
RIR3215
RIR3219
SH0750
Atlas RIR2416
CR6514
CR6519
CR7441
RIR3384
RIR3387
RIR3388
RIR3419
RIR3420
Détienne
InsideWood
KAD0066
KAD0069
KAD0089
KAD0092
KAD0094
Atlas T0012
Atlas T0037
Détienne
InsideWood
RBE2486
RBE2614
RZK8223
RZK8224
RZK8375
Atlas RAF0013
RIR2441
RIR2447
RIR2834
RIR2835
RIR2842
Atlas T0025
KAD0200
RFN0021
RFN0035
RZK8269
SAN0028
SAN0031
Atlas RZK7699
Détienne
InsideWood
ANS0012
ANS0024
ANS0026
ANS0028
KAD0052
SH0690
Atlas RIR2430
ALR2439
ALR2440
ALR2446
RRN0026
RRN0027
RIR2410
RIR3335
RIR3336
RIR3337
ROZ0023
ROZ0024
Atlas RIR2418
EME0023
RFN0001
RZK8035
RZK8040
SAN0023
SAN0026
SFR0255
ALR2443
RIR2458
RRN0043
RRN0044
RRN0045
feature
a
b
a
b
c
a
b
c
a
a
b
a
b
c
d
e
a
b
c
d
a
a
b
a
b
a
b
feature group
GR
TGR
WP
IPA
APA
APP
BP
APCT
RW
RCC
SS
absent (a)
variable (v)
present (p)
not assessed

showed distinct growth rings and ring-porous or semi-ring-porous wood (*D. abrahamii*, *D. chlorocarpa*, *D. davidii*, *D. greveana*, *D. lemurica* (Fig. 1A), *D. pseudobaronii*, *D. purpurascens* (Fig. 1B), and *D. urschii*). Six species showed either distinct or indistinct to absent growth rings (*D. baronii*, *D. bathiei*, *D. monticola*, *D. obtusa*, *D. oronjiae* ined., and *D. orientalis*). Three species (*D. davidii*, *D. obtusa*, and *D. pseudobaronii*) always showed growth ring boundaries with marginal parenchyma.

Vessels

Vessels in all assessed species were circular in cross section, and at least 90% solitary, with up to 10% in radial multiples of two, three, four (Fig. 1B) or more, and rarely clustered. The median tangential vessel diameters ranged from 60–204 µm in individuals with diffuse-porous wood, and from 67.5–260 µm (earlywood) or 40–140 µm (latewood) in individuals with ring-porous wood. Perforation plates were always found to be simple (Fig. 3A), and vestured pits were always present in all assessed species. Intervessel pits were alternate to opposite (Fig. 2A), and similar in size and shape to vessel-ray pits (Fig. 3B). The Intervessel pit diameter (IPD) ranged from 5–15 µm, spanning the upper three out of four IAWA categories. The variation in IPD was found to be large within species, with substantial overlaps between species. Vessel density ranged from 2–90 cells/mm^2, spanning the first four out of five IAWA categories. A potentially diagnostic pattern was found for *Dalbergia davidii* and *D. lemurica*, two species with consistently higher vessel density ($\geqslant$27 cells/mm^2) compared to all other assessed species. All assessed species had short vessel elements (VL $\leqslant$350 µm), ranging from 85–350 µm and spanning a single IAWA category (52). One species (*D. normandii*) showed consistently higher vessel element lengths compared to other species ($\geqslant$230 µm), except that the maximum value was found for an individual of *D. razakamalalae*. Brown to yellowish-brown deposits were commonly seen in vessels, most abundantly in *D. bathiei*, *D. normandii* (Fig. 1C), *D. purpurascens*, and *D. greveana*.

Libriform fibres

Libriform fibres in all assessed species were thin- to thick-walled and appeared as elongated cells with simple or minutely bordered pits. Libriform fibres length ranged from 630–1900 µm, spanning all three IAWA categories. The variation in libriform fibres length was found to be large within some species, notably within *Dalbergia normandii*, and overlapped considerably among species.

Fig. 4. Comparative wood anatomy of 16 Malagasy *Dalbergia* species. (A) Parallel coordinates plot of 11 quantitative wood anatomical features measured in 101 individuals (93 new dataset, 8 Atlas dataset). Each panel represents one species. Similar species are shown in adjacent panels and then sorted in alphabetical order. Strong lines represent species means of the new dataset (colour-coded) or the Atlas dataset (dark grey). Points and thin lines represent medians of repeated measures per individual. Lines are interrupted if a value could not be measured. Percentages on the *y*-axis represent values presented in Table 2 but rescaled to the minimum (0) and maximum (100) observed value for each feature. The order of features shown along the *x*-axis was intended to promote readability but is otherwise arbitrary. TVD: tangential vessel diameter (Ew, earlywood vessels; Lw, latewood vessels; D, diffuse-porous); see Table 1 for remaining codes of wood anatomical features. (B) Heatmap of qualitative wood anatomical features. Each row represents a single individual (new dataset and Atlas dataset) or an aggregation of multiple individuals (Détienne and InsideWood datasets). Rows are organized into colour-coded species blocks, and alphabetically sorted by species, dataset, and individual. Columns represent wood anatomical features, sorted by IAWA feature numbers (top legend) and organized into feature blocks (bottom legend). Nine qualitative features with no observed variation in any dataset (VG_a; PP_a; IPA_b; VP_a; VRP_a; GTF_a; APCT_b; PC_a; PC_b) are not shown. See bottom-right legend for meaning of heatmap colours. See Table 1 for codes of wood anatomical features, and Tables A1–A4 for collection details.

Table 2. Quantitative wood anatomical features of 16 Malagasy *Dalbergia* species.

Species	IPD	VD	VL	TVD_Ew	TVD_Lw	TVD_D	FL	RH	RMM	NCR	NSS
Dalbergia abrahamii	7.57 ± 0.19	7.93 ± 3.68	164 ± 14	159 ± 27	101 ± 32		813 ± 135	130 ± 23	11.36 ± 2.06	9 ± 2.78	5.86 ± 0.9
(*n* = 7)	(7.5–8)	(4–14)	(150–190)	(120–200)	(60–140)		(630–1000)	(105–170)	(9–14)	(5–12.5)	(4–7)
D. baronii	6.6 ± 1.24	7.1 ± 3.75	171 ± 49			136 ± 30	993 ± 113	113 ± 10	12.5 ± 1.29	6.5 ± 1.73	5.6 ± 0.55
(*n* = 5)	(5–7.5)	(4–13.5)	(85–200)			(100–178)	(805–1100)	(100–120)	(11–14)	(5–9)	(5–6)
D. bathiei	6.75 ± 1.9	6.3 ± 2.66	190 ± 16			142 ± 12	1053 ± 205	132 ± 12	10.4 ± 0.65	6.4 ± 0.89	5.2 ± 0.45
(*n* = 5)	(5–10)	(2.5–10)	(170–205)			(125–155)	(855–1400)	(115–145)	(9.5–11)	(6–8)	(5–6)
D. chlorocarpa	7.6 ± 0.98	13.8 ± 3.75	160 ± 8	153 ± 23	81 ± 11		866 ± 127	157 ± 53	10.8 ± 0.84	11.4 ± 5.32	
(*n* = 5)	(6.25–9)	(9–19.5)	(148–170)	(135–190)	(67.5–90)		(700–1000)	(110–245)	(10–12)	(5–19)	
D. davidii	5.38 ± 0.56	36.3 ± 12.36	159 ± 13	138 ± 6	64 ± 5		845 ± 139	125 ± 24	10.7 ± 1.4	8.6 ± 1.85	
(*n* = 5)	(5–6.25)	(27.5–57)	(140–170)	(130–145)	(60–70)		(685–1000)	(90–150)	(9.5–13)	(6–11)	
D. greveana	6.5 ± 0.85	8.62 ± 2.94	169 ± 24	204 ± 47	83 ± 20		988 ± 147	133 ± 10	11.06 ± 1.32	10.38 ± 2.13	6.5 ± 0.53
(*n* = 8)	(5–7.5)	(5–13.5)	(145–210)	(135–260)	(50–105)		(850–1310)	(120–150)	(9–13)	(7–14)	(6–7)
D. lemurica	9.59 ± 2.62	57.69 ± 23.58	139 ± 9	97 ± 26	49 ± 8		814 ± 136	119 ± 14	11.31 ± 0.96	7.56 ± 1.43	7.12 ± 1.46
(*n* = 8)	(5–12.5)	(29–89.5)	(120–150)	(68–140)	(40–60)		(685–1000)	(100–145)	(10–13)	(6.5–10.5)	(5–10)
D. monticola	6.8 ± 0.97	5.2 ± 1.1	178 ± 15	149 ± 12	94 ± 6		1123 ± 91	148 ± 13	13.8 ± 2.95	11.6 ± 0.55	6.7 ± 0.45
(*n* = 5)	(5.5–7.5)	(4–7)	(160–195)	(130–160)	(90–100)		(1015–1220)	(135–170)	(11–18)	(11–12)	(6–7)
D. normandii	7.25 ± 0.56	4.3 ± 1.48	240 ± 22			174 ± 19	1238 ± 485	185 ± 40	12 ± NA	6 ± 1.22	5.3 ± 1.86
(*n* = 5)	(6.25–7.5)	(3–6.5)	(230–280)			(150–200)	(855–1900)	(140–220)	(12–12)	(5–8)	(4–8.5)
D. obtusa	7 ± 1.12	13.2 ± 2.89	166 ± 12			99 ± 31	815 ± 55	110 ± 8	16.8 ± 0.84	7.3 ± 0.45	6.2 ± 0.84
(*n* = 5)	(5–7.5)	(10–17.5)	(150–180)			(70–150)	(750–900)	(100–120)	(16–18)	(7–8)	(5–7)
D. orientalis	5.54 ± 1.33	4.42 ± 1.11	188 ± 20	252 ± 4	87 ± 14	146 ± 32	1116 ± 226	135 ± 10	12 ± 1.67	6.83 ± 0.75	6.33 ± 0.82
(*n* = 6)	(5–8.25)	(3–6)	(165–220)	(250–255)	(70–95)	(120–190)	(680–1300)	(130–155)	(9–14)	(6–8)	(5–7)
D. oronjiae ined.	6.04 ± 1.23	19.08 ± 5.51	161 ± 25	170 ± 0	70 ± 0	77 ± 24	854 ± 154	108 ± 12	12.67 ± 0.82	7.25 ± 1.21	6.67 ± 0.82
(*n* = 6)	(5–7.5)	(13–25.5)	(130–200)	(170–170)	(70–70)	(60–120)	(630–1100)	(90–120)	(12–14)	(6–9.5)	(6–8)
D. pseudobaronii	5.5 ± 1.12	7.3 ± 1.04	162 ± 11	162 ± 38	86 ± 15		848 ± 48	141 ± 24	11.4 ± 2.3	9.6 ± 1.78	5.8 ± 0.84
(*n* = 5)	(5–7.5)	(5.5–8)	(150–180)	(120–210)	(70–80)		(800–895)	(110–175)	(8–14)	(7–11)	(5–7)
D. purpurascens s.l.	6.46 ± 0.94	10.58 ± 3.28	150 ± 16	218 ± 29	72 ± 4		950 ± 53	124 ± 12	10.33 ± 1.51	9.42 ± 2.18	3.25 ± 3.77
(*n* = 6)	(5–7.5)	(6.5–16)	(130–180)	(170–250)	(70–80)		(895–1000)	(102–135)	(9–13)	(7–12)	(0–7)
D. razakamalalae	7.86 ± 3.59	6.5 ± 2.69	189 ± 70			110 ± 22	933 ± 46	121 ± 11	14.5 ± 3.03	5.57 ± 1.13	5.29 ± 0.49
(*n* = 7)	(5–15)	(3–10.5)	(90–325)			(85–142)	(900–1000)	(110–140)	(11–19)	(4–7)	(5–6)
D. urschii	6.5 ± 1.37	8.2 ± 1.79	148 ± 22	174 ± 40	73 ± 7		910 ± 127	125 ± 13	13.3 ± 1.48	6.2 ± 0.45	6.6 ± 1.14
(*n* = 5)	(5–7.5)	(6–10)	(120–180)	(130–225)	(65–80)		(820–1000)	(105–140)	(11.5–15)	(6–7)	(5–8)

IPD, intervessel pit diameter (μm); VD, vessel density (cells/mm^2); VL, vessel element length (μm); TVD, tangential vessel diameter (μm); Ew, early wood vessels; Lw, late wood vessels; D, diffuse-porous (if a species included ring and diffuse porous, values are included for Ew, Lw and D); FL, fibre length (μm); RH, ray height (μm); RMM, rays per mm; NCR, number of cells per ray; NSS, number of ray tiers per mm. Numbers represent median values per individual and summarized as the species mean ± standard deviation, with ranges given in parentheses.

Axial parenchyma

Axial parenchyma cells were present in all assessed species, appearing predominantly fusiform and storied. There were two cells per parenchyma strand in all assessed species (Fig. 2C). Axial parenchyma appeared diffuse-in-aggregates in all assessed species except *Dalbergia lemurica*, where most individuals had diffuse parenchyma. Paratracheal axial parenchyma was found to be aliform (frequently observed in all assessed species except *D. baronii* and *D. bathiei*), confluent (frequently observed in *D. abrahamii*, *D. baronii*, *D. bathiei*, *D. monticola*, *D. orientalis*, *D. oronjiae* ined., and *D. pseudobaronii*), vasicentric (frequently observed in *D. urschii*), or scanty (always and exclusively observed in *D. davidii* and *D. urschii*, Fig. 1D). Parenchyma bands were observed in all assessed species except *D. greveana*, *D. pseudobaronii*, *D. purpurascens*, and *D. urschii*. Two species (*D. abrahamii* [Fig. 1E] and *D. chlorocarpa*) always showed narrow bands up to three cells wide, and one species (*D. razakamalalae*) always showed broad bands more than three cells wide. Parenchyma band width was found to be highly variable in some species, notably *D. baronii* with up to 20 cells (Fig. 1F). Prismatic crystals in chambered axial parenchyma cells were observed in all assessed species (Fig. 3F).

Rays

Rays were found to be predominantly (⩾80%) uniseriate in all assessed individuals of three species (*Dalbergia normandii*, *D. obtusa*, and *D. razakamalalae*, (Fig. 2B and Fig. 2D), almost all individuals of *D. oronjiae* ined., and the majority of *D. baronii* individuals. Rays appeared predominantly biseriate in all individuals of the other assessed species (Fig. 2E), except *D. lemurica*, where rays of four individuals were scored as predominantly uniseriate and six individuals were scored as predominantly biseriate. All assessed species showed small ray heights (RH ⩽1 mm), ranging from 90–245 μm. The number of rays per millimeter ranged from 8 to 21 rays/mm, spanning all three IAWA categories. Two types of ray cellular composition were observed in the assessed species. Ray cells were always homogeneous (Fig. 3C) in three species (*D. abrahamii*, *D. chlorocarpa*, and *D. davidii*), and always heterogeneous (body ray cells procumbent with one row of square cells, Fig. 3D) in three other species (*D. bathiei*, *D. razakamalalae*, and *D. urschii*). Both these types of ray cellular composition were observed in the other assessed species, and the combination of both types was frequently observed in four species (*D. normandii*, *D. orientalis*, *D. pseudobaronii*, and *D. purpurascens*, Fig. 3E). The number of cells per rays ranged from 4 to 19, with substantial overlap between species.

Storied structure

A distinct storied structure (storied rays, axial parenchyma and/or libriform fibres) was observed in all assessed individuals of fourteen species because vessel elements and axial parenchyma cells were of similar length (Fig. 2D–E). The number of ray tiers per millimeter ranged from 4 to 15 in these species, with substantial overlap among species. Two species (*Dalbergia chlorocarpa* and *D. davidii*) consistently showed rays, vessel elements and axial parenchyma cells of different lengths, rendering the ray and axial elements irregularly storied to non-storied (Fig. 2).

Multivariate analyses

Correlation analysis

Qualitative features of feature groups GR, RW, and SS were found to be binary (RW and SS; $\rho = -1$) or nearly so (GR; $\rho = -0.98$; Fig. A2 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159). The majority of individuals with distinct growth rings (GR_a) showed differences in vessel diameter between latewood and earlywood (TGR_b; $\rho = 0.85$), and also often ring-porous (WP_a) or semi-ring-porous (WP_b) rather than diffuse-porous wood (WP_c; $\rho = -0.84$; Fig. A2 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159). Conversely, the majority of individuals lacking distinct growth rings (GR_b) also showed no differences in vessel diameter between latewood and earlywood (TGR_b; $\rho = -0.87$), a diffuse-porous wood (WP_c; $\rho = 0.86$), and a banded parenchyma with broad bands more than three cells wide (BP_b, $\rho = 0.72$, Fig. A2 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159). Growth ring boundaries with thick-walled and radially flattened fibers (TGR_a) were inversely related to opposite intervessel pit arrangement (IPA_a; $\rho = -0.77$).

Several correlated wood anatomical features also showed high positive Spearman's rank correlations with isothermality, which is the ratio of diurnal variation to annual variation in temperature (Bio03), namely the presence of distinct growth rings (GR_a; $\rho = 0.75$), differences in vessel diameter between latewood and earlywood (TGR_b; $\rho = 0.82$), and semi-ring-porous wood (WP_b; $\rho = 0.76$). High negative correlations with isothermality were found for the absence of distinct growth rings (GR_b; $\rho = -0.77$), diffuse-porous wood (WP_c; $\rho = -0.83$), and broad banded parenchyma bands (BP_b; $\rho = -0.7$).

Principal component analysis

The first four principal components (Fig. 5) explained 57% of the total assessed variation in wood anatomical variables (24, 13, 10, and 10%, respectively). Eight species appeared as non-overlapping or adjacent hulls in the PCA subspace defined by the first two components (Fig. 5A), namely *Dalbergia abrahamii*, *D. baronii*, *D. chlorocarpa*, *D. davidii*, *D. lemurica*, *D. obtusa*, *D. razakamalalae*, and *D. urschii*. The wood anatomical variation within species, as indicated by the variation along the first two principal components, was revealed to be relatively large compared to the variation between pairs of species with overall similar wood anatomy, especially in *D. bathiei*, *D. orientalis*, and *D. oronjiae* ined. (Fig. 5A).

The first principal component primarily separated individuals with a diffuse-porous wood and lacking distinct growth rings (square symbols in Fig. 5A; *Dalbergia baronii*, most *D. bathiei*, *D. normandii*, most *D. orientalis* and *D. oronjiae* ined., and *D. razakamalalae*) from the remaining individuals (round symbols in Fig. 5A; Fig. 5C). The second principal component primarily separated individuals lacking an apotracheal axial parenchyma that is diffuse-in-aggregates (large symbols in Fig. 5A; *D. lemurica*) from the remaining individuals (small symbols in Fig. 5A; Fig. 5C). The third principal component primarily separated individuals lacking an aliform paratracheal axial parenchyma (square symbols in Fig. B; *D. baronii*, most *D. bathiei*) from the remaining individuals (round symbols in Fig. 5B; Fig. 5D). Finally, the fourth principal component primarily separated individuals with an all-procumbent ray cellular composition (large symbols in Fig. 5B; *D. abrahamii*, *D. chlorocarpa*, *D. davidii*, most *D. lemurica*, *D. normandii*, *D. orientalis*, *D. oronjiae* ined., and most *D. pseudobaronii* and *D. purpurascens*) from the remaining individuals (small symbols in Fig. 5B; Fig. 5D).

Features of potentially diagnostic significance

We identified two qualitative features (APP_a and SS_b) and four quantitative features (VD, VL, RMM, and NSS) that met the strict threshold of 100% for TPR and $\leqslant$5% for FPR in distinguishing a single or a pair of two species from the remaining species (Table 3). Three single species (*Dalbergia lemurica*, *D. normandii*, and *D. obtusa*) were found to be distinguishable from all other assessed species based on a single feature. No features meeting these thresholds were found for subgeneric sections or broad geographic regions, respectively. A full list including features below strict thresholds is given in Table A5 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159.

Provisional wood identification key for 16 Malagasy *Dalbergia* species

The following provisional identification key for 16 Malagasy *Dalbergia* species is based on five quantitative features (VD, VL, RH, NCR, and NSS, see Table 1) and nine groups of qualitative features, of which some are more readily assessed and therefore used with higher priority (SS, WP, APP, TGR), while others are considered more difficult to assess and therefore only appear where needed (APA, BP, RCC, RWW, and GR). Some species appear more than once in this key. Broad geographic regions are indicated where species distribution ranges clearly differ.

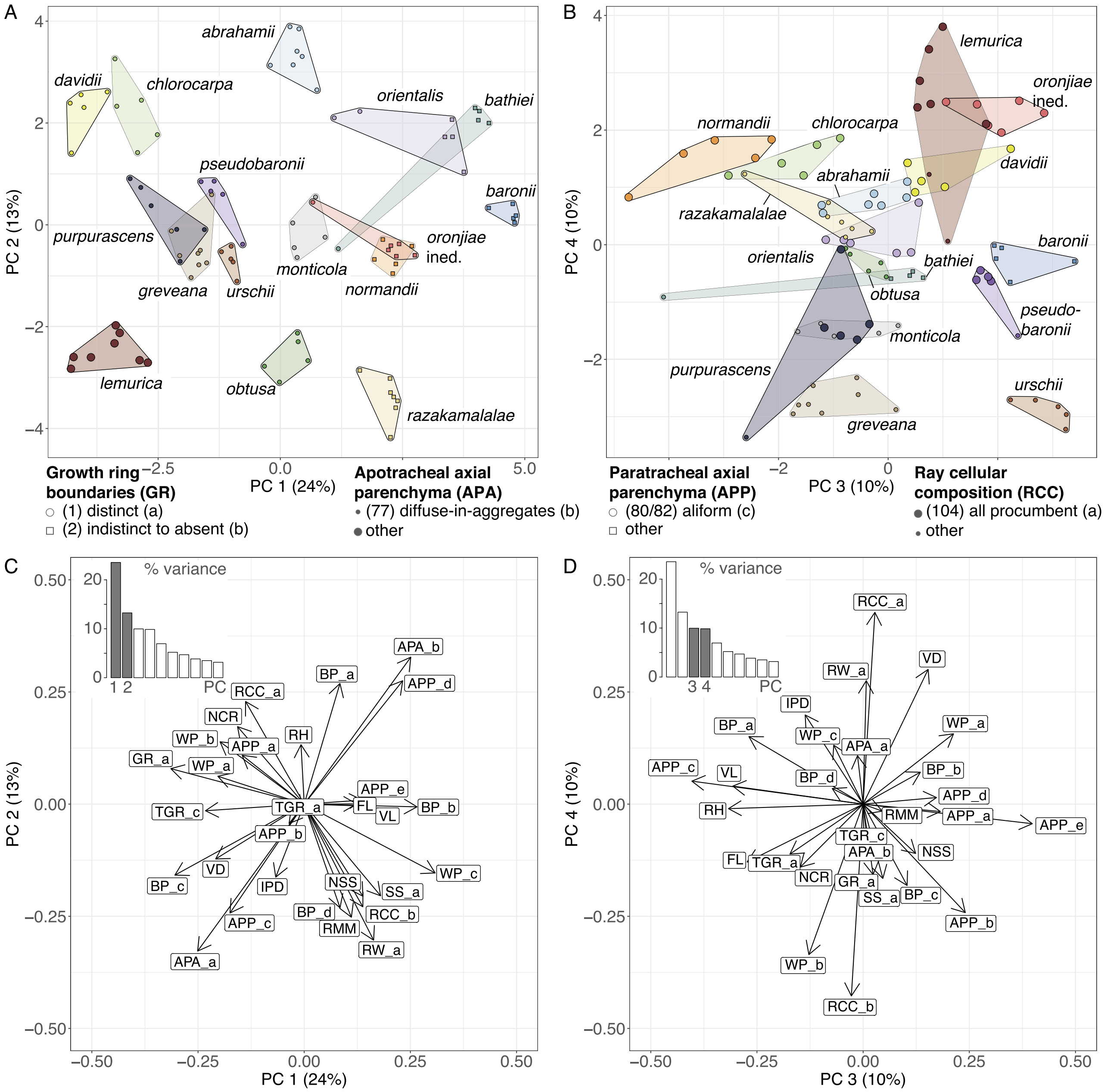


Fig. 5. Principal component (PC) analysis of 29 wood anatomical features measured in 93 individuals of Malagasy *Dalbergia* species (new dataset). Features with no observed variation and four redundant dummy variables (GR_b = −GR_a; TGR_b = −WP_c; RW_b = −RW_a; SS_b = −SS_a) were excluded from analysis. (A) Scatterplot of first two PCs. Filled colour-coded symbols represent individuals and labelled colour-coded hulls denote taxa. See legend for symbol size and shape. (B) Scatterplot of third and fourth PCs. (C) PCA loadings of wood anatomical features to first two principal components. The inset bar plot shows the percentage of variance explained by the first ten PCs, the displayed components are shaded. (D) PCA loadings of wood anatomical features to third and fourth PCs. Inset bar plot as in panel approx. See Table 1 for codes of wood anatomical features.

Table 3. Wood anatomical features of potentially diagnostic significance for identification of single or pairs of closely related species.

Species (group)	Character	Threshold	IAWA	FPR
Dalbergia lemurica	Vessel density (cells/mm^2)	$\geqslant$29		3%
D. normandii	Vessel element length (µm)	$\geqslant$230		2%
D. obtusa	Rays per mm	$\geqslant$16		3%
D. chlorocarpa + *D. davidii*	Storied structure irregular to absent		119	0%
	Number of ray tiers per mm	<4		2%
D. davidii + *D. lemurica*	Vessel density (cells/mm^2)	$\geqslant$27		0%
D. davidii + *D. urschii*	Paratracheal axial parenchyma scanty		78	0%

All these characters showed a true positive rate (TPR) of 100%. FPR: false positive rate.

1 Storied structure irregular to absent; wood ring-porous and semi-ring-porous, growth rings distinct, axial parenchyma in marginal or seemingly marginal bands; west Madagascar 2
– Storied structure present (rays, axial parenchyma and/or vessel elements storied), wood (semi-)ring-porous or diffuse-porous, growth rings distinct or indistinct 3

2 Vessel density $\geqslant$23 cells/mm^2; paratracheal axial parenchyma scanty and aliform . . . . *D. davidii*
– Vessel density <23 cells/mm^2; paratracheal axial parenchyma aliform, not scanty . . . . *D. chlorocarpa*

3 Vessel density $\geqslant$29 cells/mm^2; apotracheal axial parenchyma diffuse, rarely also diffuse-in-aggregates; arid southwest Madagascar . . . . *D. lemurica*
– Vessel density <29 cells/mm^2; apotracheal axial parenchyma diffuse-in-aggregates, often also diffuse 4

4 Paratracheal axial parenchyma scanty, vasicentric, aliform, and banded, not confluent; north and northeast Madagascar . . . . *D. urschii*
– Paratracheal axial parenchyma not scanty, often aliform and/or confluent, sometimes banded or vasicentric 5

5 Vessel element length $\geqslant$220 µm; east Madagascar 6
– Vessel element length <220 µm 8

6 Paratracheal axial parenchyma confluent; rays predominantly ($\geqslant$80%) biseriate; growth rings distinct or indistinct . . . . *D. orientalis*
– Paratracheal axial parenchyma not confluent; rays predominantly ($\geqslant$80%) uniseriate; growth rings indistinct to absent 7

7 Ray height >140 µm; parenchyma in narrow bands or lines up to or sometimes exceeding three cells wide, not marginal or reticulate; ray cellular composition homogeneous and heterogeneous; northeast Madagascar . . . . *D. normandii*
– Ray height <140 µm; parenchyma bands more than three cells wide, marginal and often reticulate; ray cellular composition heterogeneous (one row of upright and/or square marginal cells); southeast Madagascar . . . . *D. razakamalalae*

8 Wood ring-porous or semi-ring-porous, differences in vessel diameter between earlywood and latewood; rays predominantly ($\geqslant$80%) biseriate; throughout Madagascar 9
– Wood without the above combination of characters; east and north Madagascar 14

9 Axial parenchyma in marginal or seemingly marginal bands, aliform or rarely vasicentric; rays 7–14 cells high; wood ring-porous or semi-ring-porous; growth rings distinct 10
– Wood without the above combination of characters 12

10 Paratracheal axial parenchyma aliform, confluent and banded; libriform fibres length ⩽895 μm; ray 7–11 cells high; north Madagascar, south of the Ankarana/Analamerana plateaux . . . . *D. pseudobaronii*
– Wood without the above combination of characters; north and west Madagascar 11

11 Number of ray tiers mostly ⩾6 per millimeter; ray cellular composition mostly heterogeneous (one row of upright and/or square marginal cells); libriform fibres length ⩾850 μm . . . . *D. greveana*
– Number of ray tiers mostly <6 per millimeter; ray cellular composition mostly homogeneous; libriform fibres length ⩽1000 μm . . . . *D. purpurascens*

12 Vessel density ⩽14 cells/mm^2; libriform fibres length ⩽1000 μm; ray cellular composition homogeneous; north Madagascar . . . . *D. abrahamii*
– Vessel density ⩽7 cells/mm^2; libriform fibres length ⩽1300 μm; ray cellular composition homogeneous or heterogeneous; east Madagascar 13

13 Rays 11–12 cells high; ray cellular composition rarely homogeneous; east Madagascar, at (160–)900(–1500) m elevation . . . . *D. monticola*
– Rays 6–8 cells high; ray cellular composition often homogeneous; east Madagascar; at (0–)350(–920) m elevation . . . . *D. orientalis*

14 Rays predominantly (⩾80%) uniseriate; axial parenchyma in marginal or seemingly marginal bands; paratracheal axial parenchyma never confluent; ray ⩽19 per millimeter 15
– Wood without the above combination of characters 16

15 Vessel density mostly ⩾10 cells/mm^2; libriform fibres length ⩽900 μm; north Madagascar . . . . *D. obtusa*
– Vessel density mostly <10 cells/mm^2; libriform fibres length ⩽1000 μm; southeast Madagascar . . . . *D. razakamalalae*

16 Rays predominantly (⩾80%) uniseriate; paratracheal axial parenchyma often banded; east and north Madagascar 17
– Rays predominantly (⩾80%) biseriate; paratracheal axial parenchyma never banded; east Madagascar 18

17 Vessel density mostly <14 cells/mm^2; ray cellular composition mostly heterogeneous (one row of upright and/or square marginal cells); east Madagascar . . . . *D. baronii*
– Vessel density mostly ⩾14 cells/mm^2; ray cellular composition homogeneous; north Madagascar . . . . *D. oronjiae* ined.

18 Rays 11–12 cells high; ray cellular composition rarely homogeneous; east Madagascar, at (160–)900(–1500) m elevation . . . . *D. monticola*
– Wood without the above combination of characters 19

19 Paratracheal axial parenchyma not vasicentric; growth rings rarely distinct; rays mostly <11 per millimeter; ray cellular composition heterogeneous (one row of upright and/or square marginal cells); central-east Madagascar . . . . *D. bathiei*
– Paratracheal axial parenchyma often vasicentric; growth rings often distinct; rays mostly ⩾11 per millimeter ⩽14; ray cellular composition homogeneous and heterogeneous; east Madagascar . . . . *D. orientalis*

Discussion

COMMON WOOD ANATOMICAL FEATURES OF MALAGASY *DALBERGIA*

All individuals of sixteen *Dalbergia* species characterized in the new dataset and the Atlas dataset showed the following ten features (IAWA feature numbers in parentheses): (9) predominantly (⩾90%) solitary vessels, (13) simple perforation plates, (22) alternate intervessel pits, (29) presence of vestured pits, (30) vessel-ray pits with distinct borders and of similar size and shape as intervessel pits, (61) libriform fibres with simple to minutely bordered pits, (90) presence of fusiform axial parenchyma with (91) two cells per parenchyma strand, and (136) presence of prismatic crystals in (142) chambered axial parenchyma cells. Eight of these features (13, 22, 29, 30, 61, 91, 136, and 142) were also found to be consistently present in the 24 Malagasy *Dalbergia* taxa analyzed by Détienne (unpublished). In contrast to the new dataset and the Atlas dataset, Détienne found fusiform parenchyma cells (90) to be a variable feature in all assessed taxa, while he scored features 26, 79, 104, 115, and 120 as consistently present in all assessed taxa. A full comparison to our study is not possible because to our knowledge, Détienne did not score vessel grouping (9).

Some features that we identified as common and consistently present in Malagasy *Dalbergia* were also identified as such in studies on non-Malagasy *Dalbergia*. For example, Gasson (2010) found six of these features (13, 22, 29, 30, 61, and 136) to be consistently present in all of seven assessed *Dalbergia* species from Latin America, Richter *et al.* (1996) found nine of these features (9,13, 29, 30, 61, 90, 91, 136 and 142) in *D. congestiflora* Standl. from central America, and Neumann *et al.* 2001 found seven of these features (13, 22, 29, 30, 61, 136 and 142) in *D. melanoxylon* Guill. et Perr. from continental Africa. Furthermore, a small ray height (Table 2) may be a common feature of *Dalbergia*, and we are not aware of any study where ray height was reported to exceed 1 mm.

Growth ring formation

The formation of growth rings is influenced by both the genotype and the environment (Metcalfe & Chalk 1957; Schweingruber *et al.* 2006) and is known to be induced in tropical trees in response to prolonged annual dry periods (Worbes 1995). Among the 16 species studied, eight species (*Dalbergia abrahamii*, *D. chlorocarpa*, *D. davidii*, *D. greveana*, *D. lemurica*, *D. pseudobaronii*, *D. purpurascens*, and *D. urschii*) showed ring-porous or semi-ring-porous wood with distinct growth rings in all assessed collections. All these species are mainly distributed in dry deciduous forests and/or arid woodlands in west and north Madagascar (Dinerstein *et al.* 2017; Madagascar Catalogue 2022; Fig. A3 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159), which are characterized by a higher precipitation seasonality compared to the humid east Madagascar (Moat & Smith 2007; Karger *et al.* 2017). Two further species, which are restricted to north Madagascar, lacked distinct growth rings in a subset of collections (square symbols in Fig. A3A in the Appendix that can be accessed at 10.6084/m9.figshare.21378159). The single collection of *D. oronjiae* ined. (*Karatra 52*) with distinct growth rings originated from a different area than the others, which was located inland rather than near the coast and may therefore be exposed to higher annual temperature differences (Table A4 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159). The single collection of *D. obtusa* lacking distinct growth rings (*DBEV 25*) originated from the same broader area as conspecific collections with distinct growth rings, and neither precipitation nor temperature seasonality could therefore be attributed to this difference.

Two species (*Dalbergia normandii* and *D. razakamalalae*) showed diffuse-porous wood with consistently indistinct or absent growth rings in all assessed collections. Both these species are restricted to the humid ecoregion in east Madagascar, which is characterized by abundant rainfall and comparatively low precipitation seasonality (Moat & Smith 2007; Karger *et al.* 2017; Fig. A3B in the Appendix that can be accessed at 10.6084/m9.figshare.21378159). Four species restricted to the humid ecoregion of east Madagascar (*D. baronii*, *D. bathiei*, and *D. orientalis*) or extending to higher elevations in the subhumid ecoregion (*D. monticola*) showed distinct growth rings in a subset of collections (round symbols in Fig. A3B). One of the *D. baronii* collections with growth rings inspected by P. Détienne (*Service Forestier 15306*) originated from the upper elevational range of that species (approx. 500 m a.s.l.), and *D. orientalis*, which is distributed at low and mid elevation across the eastern escarpment, only showed distinct growth rings in collections from above approx. 220 m elevation (*Karatra 200*, *Razakamalala 7699* & *8269*), although two collections (*Decaryi 5567* and *Razakamalala 7699*) showed both distinct and indistinct growth rings in different wood sections of the same individual.

Growth ring differences in *Dalbergia bathiei*, *D. monticola*, and *D. obtusa* could not be attributed to pronounced differences in precipitation or temperature seasonality. Growth ring distinctiveness of *D. bathiei* collections from the same broader area was scored differently by the same person (distinct in *Ravaoherinavalona 97*). A further complication is that growth rings and wood porosity may be interpreted and described differently by different wood anatomists. According to Wheeler *et al.* (2020), it is often difficult to score the presence or absence of growth rings in tropical woods.

Our observations and comparisons between the data sets support this view, as growth rings of *D. baronii*, *D. monticola* and *D. obtusa* were found to be consistently distinct or indistinct in the new dataset but of opposite or variable distinctiveness in the Atlas and/or Détienne and InsideWood datasets. Notably, two authors of this study interpreted growth ring types differently for at least two collections (*Randrianaivo 2418* and *Razakamalala 7699*) scored by both. Together, this suggests that the presence or absence of growth rings has a limited value for species identification, a finding already noted by Gasson *et al.* (2010).

Vessel formation

Wood of species occurring in dry deciduous forests or arid woodlands in north and west Madagascar tended to form higher vessel density (19 ± 19 vessels/mm^2) compared to wood of species occurring in humid forests in east Madagascar (6 ± 3 vessels/mm^2, $W = 2035.5$, $p < 0.001$), although this difference was very small (11 ± 5 vs. 6 ± 3 vessels/mm^2) when *Dalbergia davidii* and *D. lemurica* were excluded from the comparison ($W = 1554.5$, $p < 0.001$). The difference in vessel density among ecoregions was too small for reliable determination of eco-geographic origin, except that vessel densities above 27 vessels/mm^2 were only found in species from seasonally dry or arid forests in west Madagascar (Fig. A3C). This result agrees with a theory proposed by Carlquist (1975), who stated that the density of vessels increases with increasing forest aridity. Moreover, the single assessed species from arid woodlands (*D. lemurica*) showed the smallest earlywood vessels (97 ± 26 µm) and latewood vessels (49 ± 8 µm) of all assessed species. Patterns of tangential vessel diameter were not consistent across species from the dry ecoregion. Differences between the seasonally dry or arid north and west (earlywood: 165 ± 48 µm; latewood: 77 ± 22 µm; diffuse: 90 ± 29 µm) and the humid east (earlywood: 179 ± 52 µm; latewood: 94 ± 4 µm; diffuse: 145 ± 33 µm) were found to be too small and the variation within ecoregions too large for a reliable determination of eco-geographic origin (Fig. A3D), although the difference was statistically significant for latewood vessel diameter ($W = 61$ µm, $p = 0.06$) and diffuse-porous wood vessel diameter ($W = 42$ µm, $p < 0.001$). This finding could be related to a lower water transport capacity in drier climate, where a combination of numerous but small vessels may provide resistance to water stress (Ohashi *et al.* 2013). Similar patterns were observed by Détienne & Jacquet (1983), who found lower vessel densities ($\leqslant 3$ vessels/mm^2) and larger vessels ($\leqslant 200$ µm in diameter) in *D. nigra*, *D. spruceana* Benth., and *D. frutescens* (Vell.) Britton (= *D. variabilis* Vogel), which occur in the humid and warm Amazonian climate, whereas they observed higher vessel densities ($\leqslant 40$ vessels/mm^2) and smaller vessels ($\leqslant 80$ µm) in *D. cearensis* Ducke and *D. decipularis* Rizzini & A. Mattos, two species that occur in or extend to non-Amazonian climate with higher precipitation seasonality.

Axial parenchyma and rays

Patterns of axial parenchyma are known to be highly informative for wood identification, especially for tropical woods (Wheeler *et al.* 2020). However, features of apotracheal, paratracheal, and banded axial parenchyma often co-occur or integrate (Wheeler *et al.* 2020), and may therefore be especially prone to being interpreted and described differently by different wood anatomists. Vasicentric parenchyma (IAWA feature 79) was reported for the majority of *Dalbergia* species assessed by Ravaomanalina *et al.* (2017) and found to be present in all *Dalbergia* collections assessed by Détienne (unpublished). Conversely, vasicentric parenchyma (APP_b) was found and interpreted to occur exclusively in *D. urschii* in this study. Similarly, paratracheal axial parenchyma was scored as aliform for *D. greveana* in this study, but as vasicentric by Ravaomanalina *et al.* (2017). Features of banded parenchyma were also scored differently between studies, notably in *D. monticola*. Parenchyma bands were scored as broad (more than three cells wide, BP_b) in this study, while Ravaomanalina *et al.* (2017) and Détienne (unpublished) observed a variable width and often marginal or seemingly marginal bands.

There were further cases where collections of the same species were described differently between studies. These include the description of rays of *D. baronii*, which could admittedly have resulted from our modified definition of uniseriate vs. biseriate (see Table 1), which does not fully coincide with the IAWA feature list (IAWA Committee 1989). A blinded experiment where different wood anatomists describe the same photomicrographs would be informative to determine whether such differences result from varying interpretations of the same wood anatomical structures.

Multivariate analyses

The multivariate analyses presented in this study could be expanded to use statistical modelling and supervised classification techniques, such as discriminant analysis or random forest classification, or naïve Bayes classification (Gasson *et al.* 2010). We decided against the use of such models in this study because the analysed individuals are unlikely to adequately represent the total wood anatomical variation present within these species, as indicated by the covariance of several wood anatomical and ecological variables (Figs. A2–A3 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159). Multiple investigated species have large distribution ranges, notably *D. baronii*, *D. chlorocarpa*, *D. greveana*, *D. monticola*, *D. orientalis*, and *D. purpurascens*, and these ranges span large eco-geographic variation, which was sampled inadequately in this study.

Features of potentially diagnostic significance

We identified six out of 44 assessed wood anatomical features as potentially diagnostic to distinguish a single or a pair of closely related *Dalbergia* species from all other assessed species (Table 3). Each of these six features is briefly discussed below.

Features of paratracheal axial parenchyma are known to co-occur and integrate, especially in legumes (Wheeler *et al.* 2020). Our results indicate that paratracheal axial parenchyma in Malagasy *Dalbergia* is most often aliform, sometimes confluent or banded (often in combination). However, scanty paratracheal parenchyma was consistently and exclusively found in *D. davidii* and *D. urschii* (Fig. 4B), two related species restricted to west and north Madagascar, respectively (Bosser & Rabevohitra 2002).

Storied structure has been proposed as a feature of systematic significance (Metcalfe & Chalk 1957), and it is often found in papilionoid legumes (Wheeler *et al.* 2020). Our results suggest that a reversal in this feature (leading to irregular to absent storied structure) appears to be of high diagnostic value to distinguish *D. davidii* and *D. chlorocarpa* from the other assessed species (Table 3), which all showed a storied structure across all data sets. An irregular to absent storied structure always co-occurred with zero ray tiers per millimetre, although the reverse was not always the case (Table A2 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159).

Vessel density is known to vary with rainfall regime and can also be influenced by specimen age (Wheeler *et al.* 2020). The wood of *Dalbergia lemurica*, a species from arid woodlands in southwest Madagascar, was one of the most easily identifiable of all species assessed in this study. It is characterized by the presence of numerous $\geqslant$29 vessels/mm^2) and small vessels $\geqslant$120 μm element length, in combination with a storied structure. While a positive relationship between vessel density and cambium age (estimated via tree height and trunk diameter at breast height (DBH)) was evident in *D. lemurica*, young trees of 10 cm DBH and 8 m total height already showed $\geqslant$29 vessels/mm^2 (Tables 2–3; see also Tables A1–A2 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159). Moreover, Détienne (unpublished) also found a high vessel density ($\geqslant$20 and/or $\geqslant$40 vessels/mm^2) for this species. Although these findings suggest that vessel density may be of diagnostic significance (Table 2; Fig. A3C in the Appendix that can be accessed at 10.6084/m9.figshare.21378159), *D. lemurica* represented the only investigated collections from arid woodlands in southwest Madagascar. Even though this region is comparably species poor as far as *Dalbergia* is concerned, other species do occur there (Bosser & Rabevohitra 2002; Wilding et al. 2021b; Madagascar Catalogue 2022), some of which may also form similarly numerous and small vessels.

Vessel element length has not been assessed by Détienne (unpublished), and less than half of the descriptions in InsideWood contain information on this feature (Wheeler *et al.* 2020). Similar to vessel density, this feature is known to vary with rainfall regime, showing a positive relationship (Carlquist & Hoekman 1985). Our results indicate that such a trend is present in Malagasy *Dalbergia* (Fig. A3B in the Appendix that can be accessed at 10.6084/m9.figshare.21378159), but variation within species appears to be larger than variation among species or ecoregions, which reduces the feature's diagnostic value. Nevertheless, the mean vessel element length was exceptionally large in *D. normandii*, a species from northeast Madagascar, where annual precipitation amounts is exceptionally high (Moat & Smith 2007; Dinerstein *et al.* 2017), and significantly larger than in *D. baronii*, with which it co-occurs (Bosser & Rabevohitra 2002).

The number of rays per millimeter was found to be higher in *D. obtusa* compared to other species, although there was an overlap with both *D. monticola* and *D. razakamalalae*, which increased the false positive rate. By contrast, the presence of exclusively uniseriate rays is known to be of great value for wood identification (Metcalfe & Chalk 1957; Wheeler *et al.* 2020). Our results support this view on the basis of a slightly modified feature definition, for discrimination among closely related *Dalbergia* species. All except three assessed species were consistently scored as having predominantly (⩾80%) uniseriate or predominantly (⩾80%) biseriate rays, although rays three or more cells wide were observed very rarely. This trait appears especially useful because it does not leave much room for interpretation, and we therefore used it several times in the identification key.

Wood anatomy supporting ongoing taxonomic revision

Some wood anatomical features have been attributed taxonomic significance at the level of species or species groups (Détienne 1988). Two assessed taxa (*Dalbergia lemurica* and *D. oronjiae* ined.) are part of a species complex that is currently investigated taxonomically (N. Wilding, pers. commun.). The type specimen of *D. lemurica* (*Service Forestier 15555*) originates from the Antanambao forest near Morondava in southwest Madagascar. In their original description, Bosser & Rabevohitra (1996) included material from the extreme north of the island (e.g., *Service Forestier*, *Capuron 24684* & *24695*) and three collections from scattered localities in west Madagascar in what they regarded as a widely distributed species. However, they expressed doubts regarding the identity of the collections from the extreme north and suggested that flowering material from areas outside of Morondava was needed to confirm their identity. In recent years, additional collections of the populations from the extreme north were made, including flowering (e.g., *Ramanitrinizaka 154*) and fruiting material (e.g., *Randrianaivo 1474* & *2505*). Collections from the same northern populations were included in a phylogenomic study (Crameri 2020), which found them to be closely related to typical *D. lemurica*, but more closely associated to *D. abrahamii* and *D. urschii*, two further and morphologically similar species restricted to north Madagascar. Morphological comparisons suggested that the northern material differs from typical *D. lemurica* in characters of their leaves (more numerous in the northern populations), fruits (different shape), and flowers (indument present on flowers of northern populations). For these reasons, the northern material is currently regarded as separately evolving from *D. lemurica* and is given full consideration as a new species *D. oronjiae* ined. (N. Wilding, pers. comm.).

In this wood anatomical study, typical *Dalbergia lemurica* and *D. oronjiae* ined. showed great similarity in some wood characteristics such as the number of ray tiers per millimeter (10–13 in *D. lemurica* vs. 12–14 in *D. oronjiae* ined.), the number of cells per ray (6.5–10.5 vs. 6–9.5), the libriform fibres length (685–1000 µm vs. 630–1100 µm), or the vessel element length (120–150 µm vs. 130–200 µm). However, specimens of *D. oronjiae* ined. could be readily distinguished from typical *D. lemurica* by the combination of the following features: mostly diffuse-porous wood with indistinct growth rings (vs. consistently distinct growth rings), mostly aliform and confluent axial parenchyma with bands more than three cells wide (vs. aliform but not confluent, with marginal bands), and most importantly, a smaller vessel density in *D. oronjiae* ined. (13–26 cells/mm^2 vs. 29–90 cells/mm^2). These differences in multiple features were also indicated by PCA (Fig. 5A–B) and provide further support for recognizing *D. oronjiae* ined. as a distinct species.

Implications for the stem wood anatomy Atlas by Ravaomanalina et al. (2017)

The Atlas of Stem Anatomy of *Dalbergia* species from Madagascar (Ravaomanalina *et al.* 2017, Atlas hereafter) was prepared based on wood anatomical characterization of 19 individuals collected in 2013 and 2014. None of these were flowering collections, and only two were collected with fruits. This lack of important morphological characters, coupled with the unawareness about frequent identification errors and taxonomic problems with multiple species concepts by Bosser & Rabevohitra (1996, 2002, 2005) led to multiple wrong associations between wood anatomical characterizations and species names and evolutionary lineages inferred by Crameri (2020), who collected and analyzed genome-wide sequencing data for 14 out of the 19 Atlas specimens together with topotypic material or type specimens of all Malagasy *Dalbergia* species known at the time, and subsequent taxonomic papers (Wilding *et al.* 2021a,b; Crameri *et al.*, 2022). Specifically, ten out of 19 Atlas specimens are still placed in the same species today. One Atlas specimen (*Randrianaivo 2478*) belongs to a species that has recently undergone nomenclatural change (Wilding *et al.* 2021b). The remaining eight Atlas specimens were wrongly identified with respect to recent advances in the taxonomy and understanding of the genus (Table A3 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159). Four of these identifications were clearly wrong and can be explained by the absence of diagnostic characters on voucher specimens, and four identifications involve taxonomic conundrums around the species *D. neoperrieri*, *D. louvelii*, *D. lemurica*, and *D. pervillei*, which were thought to be widely distributed and polymorphic species that are now delimited more narrowly. We are therefore currently preparing a second edition of the Stem Wood Anatomy Atlas (Ravaomanalina *et al.* 2017), which will reflect recent taxonomic developments. The new edition is intended as a reference work for both microscopic and macroscopic wood identification, as macroscopic features visible with the naked eye or a 5× or 10× magnifying lens will be added.

Recommendations for future wood anatomical work

Our results demonstrate that wood anatomical studies in taxonomically challenging genera can greatly profit from collaborative work between researchers with competence in wood anatomy, taxonomy, and data science. Most of the interpretations in such studies relate to the variance of wood anatomical features within and between particular taxa (Wheeler *et al.* 2020). It is therefore important that the investigated specimens be fully documented (including high-quality herbarium vouchers deposited in one or several herbaria, with precise indication of the locality of origin) and confidently identified to species level by expert taxonomists (Schmitz *et al.* 2020). Even though the set of analyzed features was highly overlapping, we could only compare our results to four out of nine overlapping species documented in the InsideWood database, because the collections on which InsideWood is based were revealed to constitute a mixture of different species in two cases, an entirely different species in one case, while the species identity could not be fully verified in two further cases. This strongly suggests that wood anatomical datasets in taxonomically challenging groups such as *Dalbergia* should not be collected in an aggregated form (such as a string of IAWA feature numbers representing multiple collections) but should instead list all investigated characters for every analysed collection separately. In the case where taxonomic changes have become necessary after wood anatomical data was collected for a particular set of taxa, individual-based data can simply be regrouped and aggregated according to the revised taxonomy, while aggregated data becomes virtually useless.

Sampling design is another important factor to consider, owing to the covariance and potential confounding effect of species-level differences and ecological differences (Figs. A2–A3 in the Appendix that can be accessed at 10.6084/m9.figshare.21378159). While we included at least five collections per species in this study, these did often not adequately represent the full eco-geographic distribution range of a species. Great care should be taken when selecting wood collections for wood anatomical characterizations, to ensure that they represent both different species growing in similar climatic conditions, and the same species growing in different climatic conditions, depending on their eco-geographic distribution.

This study includes a wood anatomical characterization of sixteen species of Malagasy *Dalbergia*, with five or more analysed collections per species. While this represents a major effort, it only represents a subset of medium-sized to large Malagasy *Dalbergia* species of potential economic interest. The currently available collections indicate that at least 43 described and accepted species reach tree heights of 20 m or more and/or a DBH of 20 cm or more (Madagascar Catalogue 2022). Seventeen species that reach the same dimensions are currently being considered as potentially new species (N. Wilding & P. B. Phillipson, pers. commun.). It is therefore vital to continue the ongoing efforts to make and document wood collections. Work towards a more complete assessment of wood anatomical features of Malagasy *Dalbergia* is currently in progress, and we plan to integrate novel wood anatomical characterizations and analyses with the existing data sets.

Acknowledgements

The first two authors contributed equally to this work. The authors would like to thank the "Ministry of Environment and Sustainable Development-Madagascar" for permission to work in the forests and for general assistance. We are grateful to Nicholas Wilding, the team of Missouri Botanical Garden in Madagascar and in Missouri for their taxonomic and technical assistance. We wish to acknowledge all members of the Plant Anatomy Laboratory in Madagascar for their support during the completion of this study. This work was funded by grants from the European Union ("Gestion durable des bois précieux *Dalbergia* et *Diospyros* de Madagascar, appui scientifique à la mise en œuvre du plan d'action de la CITES" — G3D project n° FED/2018/396-916) and USAID ("Building a reference collection for Malagasy rosewood, palisander and ebony identification" — Partnerships for Enhanced Engagement in Research (PEER) Cycle 7, Grant #: 477 Madagascar), in support of the conservation and sustainable management of Madagascar's precious woods. SC's contribution to this manuscript was supported by the Swiss Federal Food Safety and Veterinary Office (ARAMIS No. 3.20.01) and a grant from the Rübel Foundation. We further thank the editor and two anonymous reviewers for their valuable suggestions on this manuscript.

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Edited by Alexei Oskolski