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Comparative anatomy of young stems and leaves of 16 *Dalbergia* species (Fabaceae) from Madagascar and their taxonomic significance

RAVO NANTENAINA RAMANANTSIALONINA[1,3*], NINAH ANDRIANASOLO SANDRATRINIAINA[1,4], BAKOLIMALALA RAKOUTH[1,5], MICHAEL C. WIEMANN[2,6] & BAKO HARISOA RAVAOMANALINA[1,7]

[1]*Département de Biologie et Écologie Végétales, Université d'Antananarivo, B.P. 906, Antananarivo 101, Madagascar*
[2]*Forest Products Laboratory, University of Wisconsin Madison*
[3] *r.ramanantsialonina@gmail.com; https://orcid.org/0000-0001-6700-7774*
[4] *asandratriniaina@gmail.com; https://orcid.org/0000-0001-9525-4879*
[5] *ba.rakouth@gmail.com; https://orcid.org/0000-0001-5710-2006*
[6] *michael.wiemann@usda.gov; https://orcid.org/0009-0001-6754-2029*
[7] *harisoa.ravaomanalina@univ-antananarivo.mg; https://orcid.org/0009-0007-9547-4725*
[*]*Author for correspondence*

Abstract

Rosewood and palisander belonging to *Dalbergia* (Fabaceae) are some of the most studied tree species in Madagascar. *Dalbergia* species can be identified based on morphological differences, mainly of flower and fruit, but are practically impossible to tell apart when these structures are missing. To support their sustainable management reliable identification of living *Dalbergia* is necessary prior to any exploitation. Studies of the vegetative anatomy of *Dalbergia* are lacking. This is the first report on young stems and leaves in endemic *Dalbergia* species. We studied 16 *Dalbergia* species from Madagascar using standard methods of anatomical investigation. Tissues and cells were examined, photographed, and comparisons were made among the taxa. Combinations of some characters can distinguish the species from one another, and six species (*Dalbergia baronii*, *D. greveana*, *D. lemurica*, *D. purpurascens*, *D. razakamalalae*, and *D. urschii*) can be distinguished by a single character. A microscopic leaf anatomical identification key for the 16 *Dalbergia* species is provided, which can help with the conservation and sustainable management of *Dalbergia*.

Key words: palisander, plant anatomy, rosewood, taxonomy

Introduction

Fabaceae is considered to be the third largest angiosperm family (Lewis *et al*. 2005, Vatanparast *et al.* 2013) and the third most-represented family in Madagascar (Lowry II *et al.* 2018). *Dalbergia* (Fabaceae) contains about 282 currently accepted species with pantropical distribution (WCVP 2024). Most *Dalbergia* species from Madagascar, also known as rosewood or palisander, are especially sought-after due to their high-quality wood used for furniture and musical instruments (Barrett *et al*. 2010).

A current revision of *Dalbergia* from Madagascar has increased the number of recognized species from 48 to 64, and only one species is shared with mainland Africa (Bosser & Rabevohitra 1996, 2002, 2005; Wilding *et al.* 2021a,b, Crameri *et al.* 2022, Rakotonirina *et al.* 2023, Wilding *et al.* 2023). Fifty-two of the 64 species are considered to grow large enough—20 m tall and/or 20 cm in diameter at breast height (DBH)—to be a source of timber (Madagascar Catalogue 2022). They grow in various vegetation types across the island's five major terrestrial ecoregions (Dinerstein *et al.* 2017, Madagascar Catalogue 2022).

Recent analyses incorporating morphological and phylogenomic data on more than 600 accessions of Malagasy *Dalbergia*, including nomenclatural type specimens, revealed that the taxonomy of the genus may require substantial revision (Crameri 2020). Although some taxonomic issues have been resolved in recent publications (Wilding *et al.* 2021a, Wilding *et al.* 2021b, Crameri *et al.* 2022), many existing species delimitations remain problematic and are subject to ongoing taxonomic work. The consortium "Gestion durable des bois précieux *Dalbergia* et *Diospyros* de Madagascar" with five disciplines: taxonomy, anatomy, near-infrared spectrometry, molecular identification,

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and conservation, working on Madagascar's precious woods, is finalizing a taxonomic review of *Dalbergia* species and is trying to clarify the ambiguity of species with similar characters. This consortium assists the country in the implementation of the CITES action plan.

The genus *Dalbergia* is threatened by habitat degradation and selective logging for national and international trade (Brown *et al.* 2015, Morelli *et al.* 2020). Overexploitation of rosewood has been important since 2009 due to the international market (Patel 2007, Randriamalala & Liu 2010, Mason *et al.* 2016, Waeber *et al.* 2019). In an effort to reduce and ultimately halt illegal logging and trade of Malagasy rosewoods, 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. In addition, a ban on the exportation of *Dalbergia* timber established by the Malagasy government currently prohibits any trade of these species (decree 2010-141). Most Malagasy species are currently threatened with extinction (IUCN 2021). Also, reliable identification of each standing tree is necessary before any exploitation (Waeber *et al.* 2019). Because *Dalbergia* species have been described based on morphological traits such as leaflet shape and form, inflorescence, flowers and fruits, their identification is difficult without reproductive organs. Flowers are rare, and the flowering times of the different species are dissimilar.

In recent years, wood anatomical features have been employed in taxonomic separations (Jahanbanifard et *al*. 2020, Sandratriniaina *et al.* 2021, Ramanantsialonina *et al.* 2022), and leaf anatomical features have been used to delimit species level (Kharazian 2007, Migacz *et al.* 2018, Sandratriniaina *et al.* 2023).

Systematic leaf anatomical studies of *Dalbergia* were initiated by Metcalfe and Chalk (1957) and were followed by Moreira *et al.* (2013), Marques Das Neves *et al.* (2016) for Latin American species and Bijauliya *et al*. (2016) with Indian species. No anatomical study of the leaves of Malagasy *Dalbergia* has been undertaken so far. Thus, the aim of this study is to identify distinctive traits that may constitute parameters to support the taxonomic revision of the genus. The present research shows a detailed description of young stem and leaf anatomy.

Materials and methods

Samples: Young stems and leaves of sixteen *Dalbergia* species: *Dalbergia abrahamii* Bosser & R. Rabev., *D. baronii* Baker, *D. bathiei* R. Vig., *D. chlorocarpa* R. Vig., *D. davidii* Bosser & R. Rabev., *D. greveana* Baill., *D. lemurica* Bosser & R. Rabev., *D. monicola* Bosser & R. Rabev., *D. normandii* Bosser & R. Rabev., *D. obtusa* Lecomte, *D. orientalis* Bosser & R. Rabev., *D. oronjiae* N. Wilding, Phillipson & Crameri, *D. purpurascens* Baill., *D. pseudobaronii* R. Vig., *D. razakamalalae* Crameri, Phillipson & N. Wilding, *D. urschii* Bosser & R. Rabev were studied. These samples were collected from four ecoregions of Madagascar (Dinerstein *et al.* 2017). Each ecoregion is represented by five to eight individuals. As the species studied are classified as threatened by the IUCN and listed in Appendix II of CITES, we propose strict measures regarding the non-disclosure of accurate locality information on specimens, in any publication. Specimens were deposited at the DBEV, MO, P, TAN, and ZT herbaria (Thiers, 2022). 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). The data on the collection are available online in TROPICOS (www.tropicos.org) and the Catalogue des Plantes Vasculaires de Madagascar (Madagascar Catalogue 2022). Young stems and leaves of the *Dalbergia* specimens examined are listed in table 1.

Anatomy: Young stems and leaves from fresh or herbarium specimens were used. Dry materials were boiled in water for a few minutes until they were completely saturated. All materials were preserved in 50% alcohol. Cross-sections were made on the young stem, at the middle part of the lamina, and at the proximal, median and distal regions of the petiole using a GLS1 microtome. The sections were double stained with carmine (stains cellulosic cell structures pink) and brilliant green (stains lignified structures green) and mounted in glycerin (N'Guessan e*t al*. 2012). Photomicrographs were taken of all slides using an Olympus CX33 or BX43 light microscope coupled with a Canon 800D digital camera and EOS software.

TABLE 1. Information on specimens of *Dalbergia* species examined.
N: number of specimens per species, Collectors (ALR: Andriamiarisoa Roger Lala; ANS: Andriamiadana Stephano; CR: Rakotovao Charles; KAD: Karatra Dochard; SH: Hassold Sonja; RAV: Ravaoherinavalona Rota, RBE: Roger Bernard; RIR: Randrianaivo Richard; RFN: Fanilo Ramanitrinizaka; RNH: Rakotonirina Nivo; ROZ: Randimbison Maherizo; RRN Ramanantsialonina Ravo Nantenaina; RZK: Razakamalala Richardson; SAF: Andrianarivelo Sandratra; SAN: Sandratriniaina Ninah; SFR: Andrianarivelo Soafara Niaina)

Species	N	Collection number
Dalbergia abrahamii	5	KAD58–60; RBE2765; RRN33–34
D. baronii	5	RBE2254; RBE2257; RBE2624; RNH1177
D. bathiei	5	KAD143; KAD147; KAD150; KAD153; RAV97
D. chlorocarpa	5	CR7421 ; CR7390 ; RIR3359-RIR3415 ; SH741
D. davidii	5	RIR3350–3353 ; SH733
D. greveana	5	RIR2913–2915 ; RIR3214 ; RIR3219
D. lemurica	5	CR7441–7442 ; RIR3369 ; RIR3379 ; RIR3384
D. monticola.	5	KAD66; KAD69; KAD89; KAD92; KAD94
D. normandii	5	RBE2614; RBE2627; RZK8375; RZK8384; RZK8388
D. obtusa	5	RIR2441 ; RIR2447 ; RIR2834–2835 ; RIR2842
D. orientalis	6	KAD200; RFN21; RFN35; RZK8409; SAF35; SAN28
D. oronjiae	6	ANS2 ; ANS12 ; ANS24 ; ANS26 ; KAD52 ; SH0690
D. pseudobaronii	5	ALR2439–2440; RRN26–27; RRN42
D. purpurascens	7	RAV22; RIR3335–3336; RIR3370; RIR3373; ROZ23–24
D. razakamalalae	7	ALR2424; RFN1; RFN13; RFN25; RZK8032; RZK8035; SFR255
D. urschii	5	ALR2443; RIR2458; RRN0043–0045

Results

Young stem: The epidermis is comprised of a single layer of tangentially elongated cells (Fig. 1A). Epidermal cells, with evenly thin walls, are covered with a prominent cuticle and are sometimes topped with multicellular trichomes (Fig. 1B).

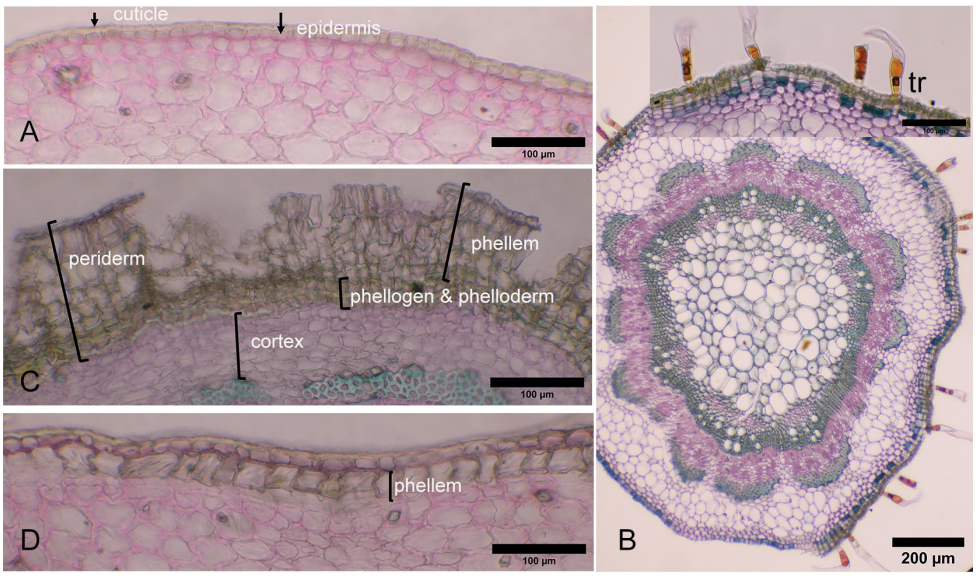

FIGURE 1. Cross-sections of young stem**. A.** Young stem of *D. normandii* epidermis covered with a prominent cuticle. **B.** *D. pseudobaronii,* general view of young stem with pericycle sclerenchyma always forming a discontinuous ring, inset shows epidermis with trichomes multicellular under higher magnification. **C.** *D. razakamalalae***,** periderm composed of phellem, phelloderm and phellogen. **D.** *D. normandii***,** the first periderm in the process of formation composed by phellem and poorly differentiated phellogen and phelloderm. **tr**: trichome multicellular.

The cortex consists of angular-laminar collenchyma in 2–3 layers and parenchyma in 5–11 (8) layers of isodiametric thin-walled cells. Prismatic crystals usually occur in the cells of cortical parenchyma. Dilatation of the cortex has not been observed in any of the species.

Pericycle sclerenchyma always forms a discontinuous ring of thick-walled cells, sometimes with prismatic crystals (Fig. 1B). A mature periderm of phellem, phelloderm and phellogen was observed only in *D. razakamalalae, D. baronii, D. bathei* (Fig. 1C). The initiation of the first-formed periderm was observed in the subepidermal cell layer in *D. normandii* (Fig. 1D).

Leaf

Petiole epidermis and cortex: The epidermis is single-layered and cutinized in all species. The cells are small, rounded, or slightly elongated and thin-walled. The epidermis is underlain by the cortex of 3–5 cells. The cortex consists of 1–2 cell layers of the angular collenchyma, followed by 2 to 3 cell layers of cortical parenchyma.

Vascular Bundles: Figures 2–3 show different patterns of vascular bundles.

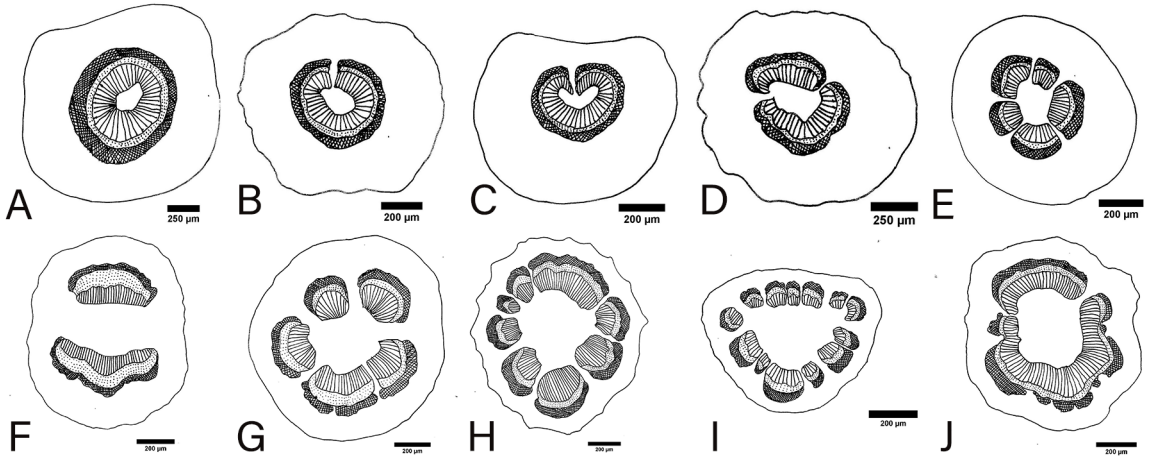

FIGURE 2. Cross-sections of the petiole at the proximal region. **A.** *D. razakamalalae,* a closed arc vascular bundle. **B.** *D. orientalis* an open arc. **C.** *D. occidentalis,* an open arc with slightly incurved ends. **D.** *D. urschii,* an open arc with one adaxial vascular bundles. **E.** *D. bathiei,* five vascular bundles. Cross-sections at the distal part of the petiole. **F.** *Dalbergia pseudobaronii*, 2 vascular bundles (1 adaxial and 1 abaxial). **G.** *D. orientalis,* 5 vascular bundles (2 adaxial and 3 abaxial). **H.** *D. greveana,* 9 vascular bundles (3 adaxial and 6 abaxial). **I.** *D. urschii,* 13 vascular bundles (5 adaxial and 8 abaxial). **J.** *D. normandii,* an open arc with one adaxial vascular bundle. Dot-filled areas= phloem, striped areas =xylem, tile areas sclerenchyma.

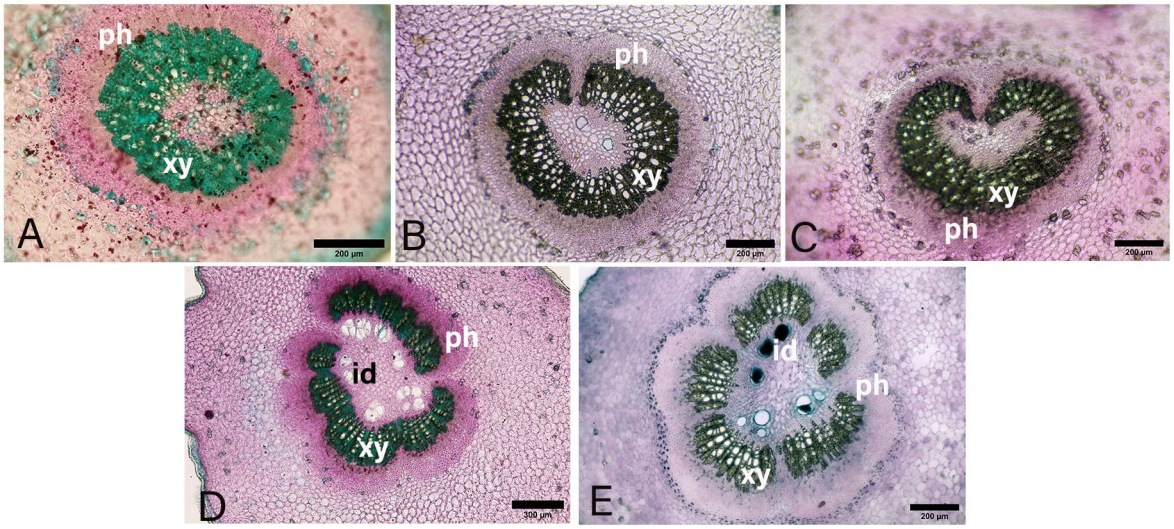

FIGURE 3. Patterns of vascular bundles at proximal part of petiole. **A.** *D. razakamalalae,* a closed arc vascular cylinder. **B.** *D. orientalis* an open arc. **C.** *D. occidentalis,* an open arc with slightly incurved ends. **D.** *D. urschii,* an open arc with one adaxial vascular bundle. **E.** *D. bathiei,* five vascular bundles. **id:** idioblast, **ph:** phloem, **xy:** xylem.

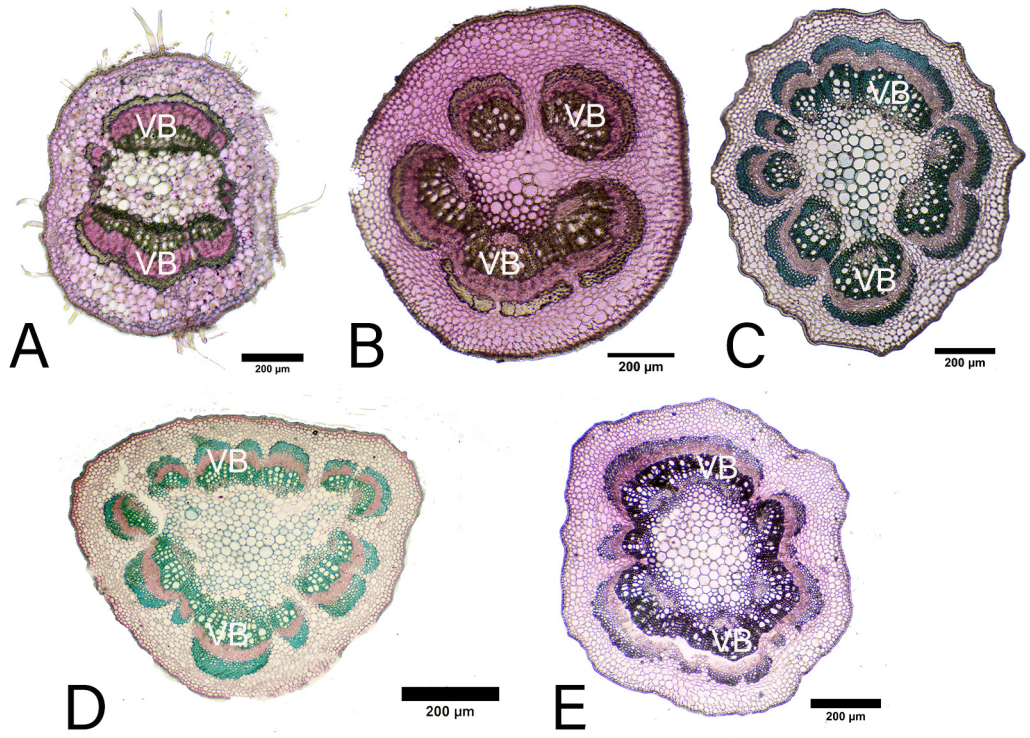

FIGURE 4. Patterns of vascular bundles at distal part of the petiole **A.** *Dalbergia pseudobaronii*, 2 vascular bundles (1 adaxial and 1 abaxial). **B.** *D. orientalis,* 5 vascular bundles (2 adaxial and 3 abaxial). **C.** *D. greveana,* 9 vascular bundles (3 adaxial and 6 abaxial. **D.** *D. urschii,* 13 vascular bundles (5 adaxial and 8 abaxial). **E.** *D. normandii,* open arc with one adaxial vascular bundle. VB: vascular bundles.

Five types of vascular bundles at the proximal part of the petioles are observed:

- closed arc vascular bundle (Fig. 2A, 3A)
- open arc (Fig. 2B, 3B)
- open arc with slightly curved ends towards the centre or heart-shaped (Fig. 2C, 3C)
- open arc with one adaxial vascular bundle (Fig. 2D, 3D)
- open arc clearly separated into five vascular bundles (Fig. 2E, 3E).

Patterns of vascularization were observed at the distal part of each petiole, clearly separated into:

- 2 vascular bundles (1 adaxial and 1 abaxial) (Fig. 2F, 4A),
- 5 vascular bundles (2 adaxial and 3 abaxial) (Fig. 2G, 4B),
- 6 to 9 vascular bundles (3 adaxial and 3–6 abaxial) (Fig. 2H, 4C)
- 9 to 12 vascular bundles (3–4 adaxial and 8–9 abaxial, in *D urschii* (Fig. 2I, 4D)
- open arc with one adaxial vascular bundles (Fig. 2J, 4E).

The patterns of vascular bundles differ among species at the proximal to distal part (table 2). In *D. urschii* and *D. bathiei* the medullar parenchyma with idioblasts underlies xylem (Fig. 4E–F).

TABLE 2. Vascularization in the petiole of 16 *Malagasy Dalbergia* species.

Species	Proximal	Distal Vascular Bundles
Dalbergia abrahamii	Open arc with ends slightly curved ends	2 adaxial and 3 abaxial
D. baronii	Open arc with ends slightly curved	Open arc with one adaxial
D. bathiei	5 vascular bundles	Open arc with one adaxial
D. chlorocarpa	Open arc with ends slightly curved	Open arc with one adaxial
D. davidii	Open arc with ends slightly curved	3 adaxial and 3–6 abaxial
D. greveana	Closed arc vascular cylinder	3 adaxial and 3–6 abaxial

...continued on the next page

TABLE 2. (Continued)

Species	Proximal	Distal Vascular Bundles
D. lemurica	Closed arc vascular cylinder	2 adaxial and 3 abaxial
D. monticola	Closed arc vascular cylinder	Open arc with one adaxial
D. normandii	Open arc with slightly curved ends towards the centre	Open arc with one adaxial
D. obusta	Open arc with ends slightly curved	3 adaxial and 3–6 abaxial
D. orientalis	Open arc	Open arc with one adaxial
D. oronjiae	Open arc	2 adaxial and 3 abaxial
D. pseudobaronii	Open arc	1 adaxial and 1 abaxial
D. purpurascens	Open arc with ends slightly curved	2 adaxial and 3 abaxial
D. razakamalalae	Closed arc vascular cylinder	3 adaxial and 3–6 abaxial
D. urschii	Open arc with one adaxial vascular bundle	3–4 adaxial and 8–9 abaxial

Lamina

The cross sections of the leaves have three layers: adaxial epidermis, mesophyll and abaxial epidermis. Some leaf measurements are given in the supplementary data.

Cuticle, epidermis, hypodermis:—Leaves have dorsiventral symmetry. Epidermal cells are square to rectangular, covered by cuticle in all species. The epidermal cells are larger on the adaxial than on the abaxial side in *D. abrahamii, D. monticola, D. lemurica, D. normandii, D. bathiei and D. orientalis,* but they are similar in size in the rest of species. Two layers of hypodermis cells occur adjacent to the adaxial side, comprised of large rectangular parenchyma cells in *D. greveana* (Fig. 5A). They are twice or three times larger than the epidermal cells. The lower epidermis is papillose only in *D. baronii* (Fig. 5B).

Mesophyll.—Mesophyll is dorsiventral, with two regions visibly differentiated as palisade and spongy tissues. The palisade parenchyma is stratified, and cells are tall and rather elongated. The number of palisade layers varies between one to three in all studied species. Mesophyll was exclusively uniseriate in *D. chlorocarpa* (Fig. 5C). It was comprised of one to two palisade layers in *D. baronii D. bathiei, D. daviii, D. normandii, D. obusta, D. occidentalis* and *D. oronjiae* (Fig. 5D) and 2–3 palisade layers in *D. abrahamii, D. greveana, D monticola, D. lemurica, D. pseudobaronii and D. urschii* (Fig. 5E). In *D. razakamalalae* 5–6 layers, with starch grains present in the mesophyll in *D. abrahamii, D. lemurica*, and *D. davidii* (Fig. 5F). Irregularly shaped spongy mesophyll cells with intercellular spaces are present in all studied *Dalbergia* except *D. razakamalalae*. The spongy mesophyll is composed of 3–5 layers. Styloids are present in mesophyll tissue, particularly in palisade parenchyma and around the veins (Fig. 5H). The small vascular bundles are collateral and surrounded by a sheath of parenchymatous cells.

Midrib.—Six shapes of the midrib are found:

Flat-flat: adaxial surface flat and abaxial surface flat in *D. lemurica* (Fig. 6A);

Flat-slightly convex: Adaxial surface and abaxial surface flat to slightly convex in *D. abarhamii, D. davidii* and *D. oronjiae* (Fig. 6B);

Slightly-flat convex: Adaxial surface slightly flat and abaxial surface convex in *D. obusta* (Fig. 6C);

Flat-convex: Adaxial surface flat to slightly concave and abaxial convex in *D. greveana, D. razakamalala* and *D. chlorocarpa* (Fig. 6D);

Flat-strongly convex: adaxial surface flat and abaxial surface convex in *D. baronii* and *D. urschii* (Fig. 6E);

Slightly convex-convex: adaxial surface slightly convex and abaxial surface convex *D. purpurascens* (Fig. 6F);

Concave-convex: Adaxial surface flat to strongly concave and abaxial surface in convex *D. bathiei, D. baronii. D. monticola* and *D. normandii* (Fig. 6G);

Strongly concave-convex: adaxial surface strongly concave and abaxial surface convex in *D. pseudobaronii* (Fig. 6H)

The vascular bundle in the midrib has three different shapes: flat arc (Fig 6A) in *D. abrahamii, D. chlorocarpa, D. davidii, D. lemurica, D. oronjiae, D. pseudobaronii, D. purpurascens, D. normandii*, U-shaped (Fig. 6C) in *D. obusta, D. greveana, D. orientalis, D. razakamalalae. D. urschii.* and V-shaped (Fig. 6E) in *D. monticola, D. bathiei, D. baronii.* According to table 3, the size of the vascular bundles (their width and the length) is similar. However, in *D. bathiei* and *D. normandii* the size of the vascular bundle is larger than in other species, and *D. davidii* has the smallest vascular bundles.

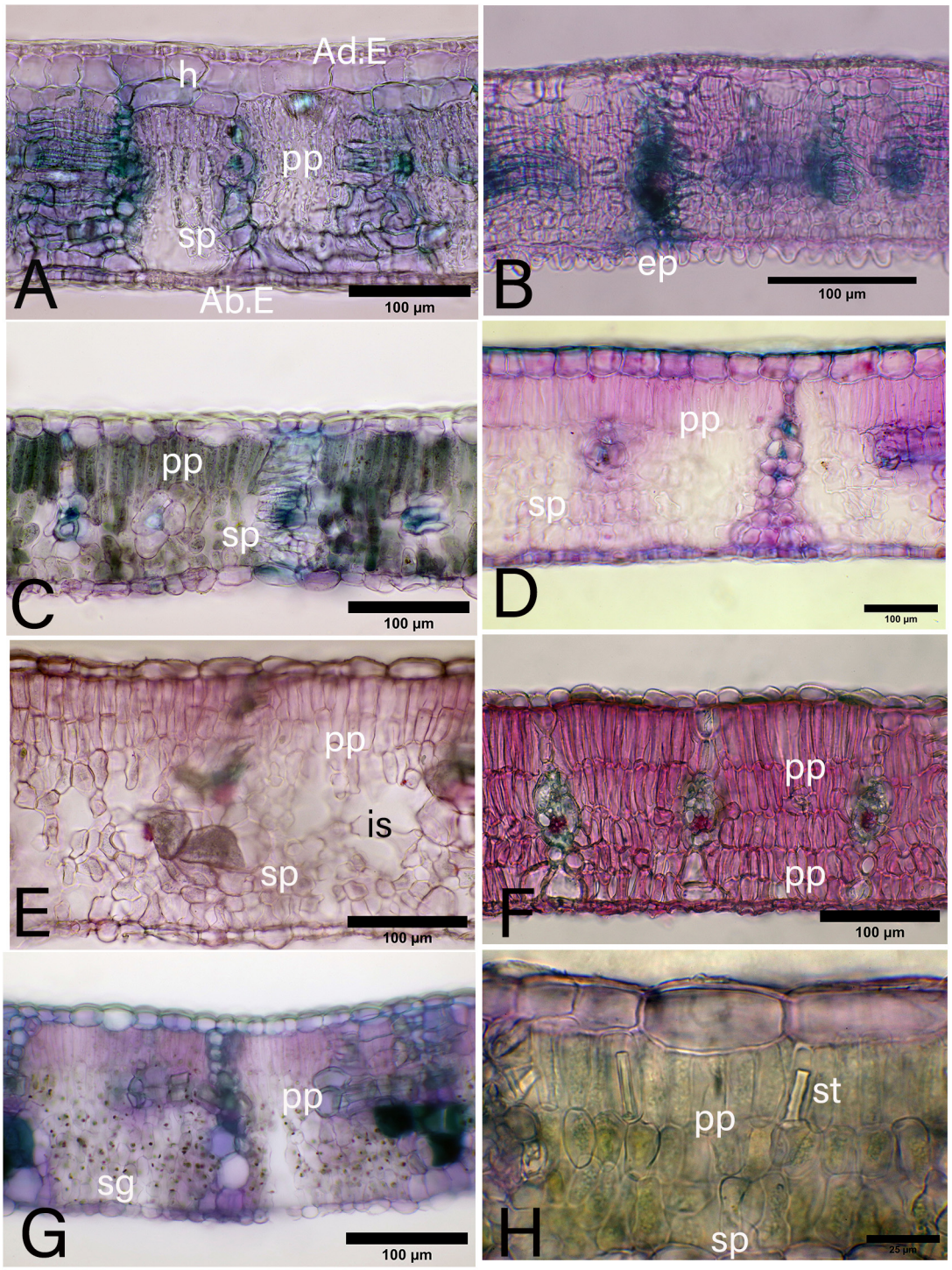

FIGURE 5. Cross-sections of the lamina. **A.** *D. greveana,* three layers of palisade parenchyma, two layers of hypoderm. **B.** *D. baronii*, hypodermis, abaxial epidermis papillose **C.** *Dalbergia chlorocarpa,* one layer of palisade parenchyma. **D.** *D. normandii,* one to two layers of palisade parenchyma. **E.** *D. urschii,* two layers of palisade parenchyma, intercellular spaces in spongy parenchyma. **F.** *D. razakamalalae,* mesophyll entirely occupied by 5 layers of palisade parenchyma. **G.** *D. lemurica,* starch grains in spongy parenchyma. **H.** *D. purpurascens,* styloid in palisade parenchyma. **Ab. E:** abaxial epidermis, **Ad. E:** adaxial epidermis, **is:** intercellular space, **h:** hypodermis, **sg:** starch grain, **ep**: epidermis papillose, **st:** styloid, **pp:** palisade parenchyma, **sp:** spongy parenchyma.

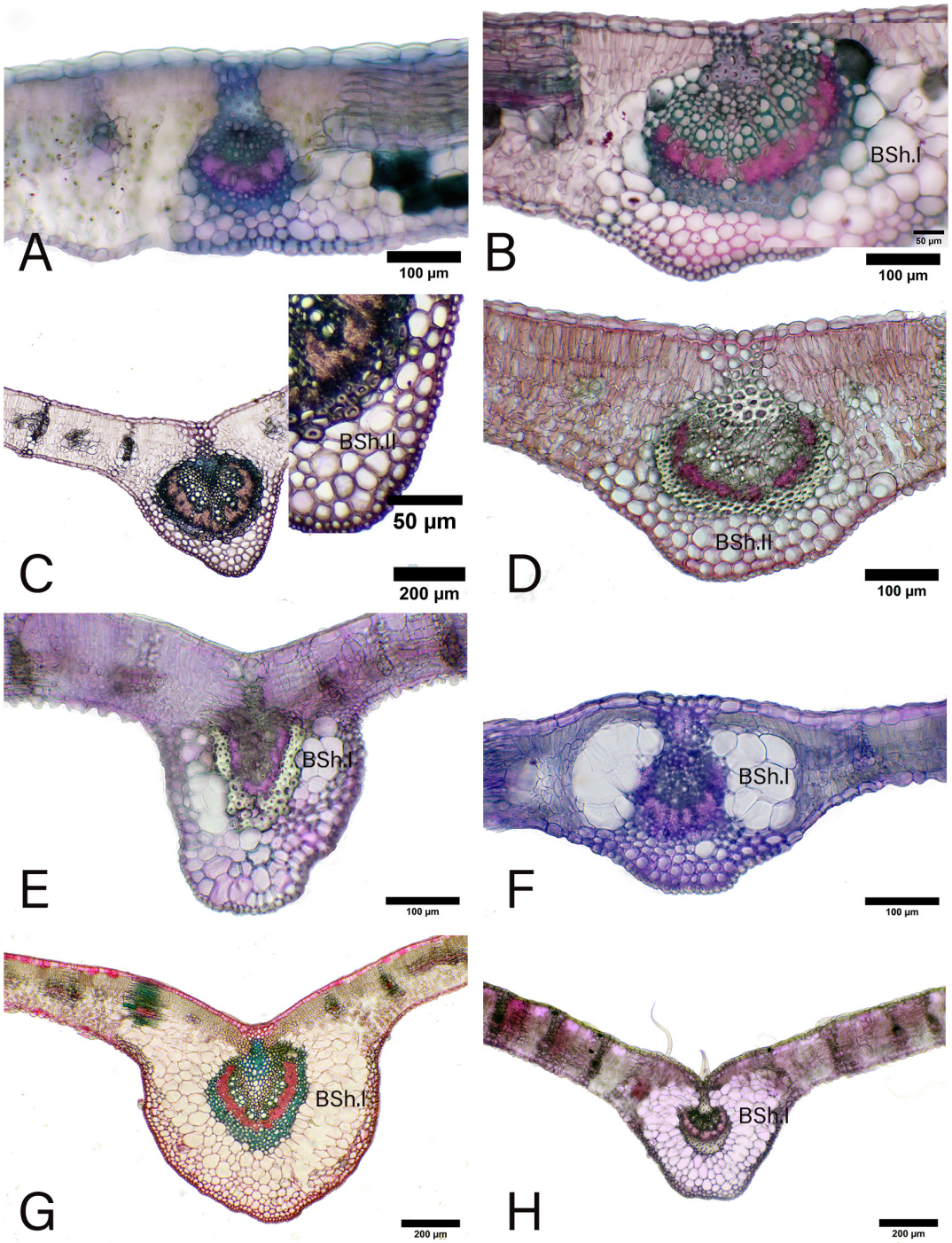

FIGURE 6. Cross-sections in the midrib, shape, vascularization and type of bundle sheath. **A.** *Dalbergia lemurica,* flat-flat, flat arc and bundle sheath type I on abaxial side of vascular bundle. **B.** *D. abrahamii,* flat-slightly convex, flat arc and bundle sheath type I partially surrounds the vascular bundle, inset show the large parenchyma cells, thin-walled, irregularly shaped. **C.** *D. obtusa,* slightly-fat convex, U-shaped vascular bundle and bundle sheath type II completely surrounds the vascular bundle. Inset shows the parenchyma cells, thick-walled, round shaped. **D.** *D. razakamalalae,* flat-convex, U-shaped and bundle sheath type II partially surrounds the vascular bundle. **E.** *D. baronii,* flat-strongly convex, V-shaped, bundle sheath type I partially surrounds the vascular bundle. **F.** *D. purpurascens,* slightly convex-convex, flat arc, bundle sheath type I at left and right sides of vascular bundle. **G.** *D. bathiei*, concave-convex, V-shaped, bundle sheath type I almost completely surrounds the vascular bundle. **H.** *D. pseudobaronii,* strongly concave-convex, flat arc and bundle sheath type I completely surrounds the vascular bundle. **BSh.I**: Bundle sheath type I, **BSh.II:** Bundle sheath type II.

The midrib vascular bundle is surrounded by sclerenchyma. All the species studied have 1–2 layers of angular collenchyma on the abaxial side of the vascular bundle. Sometimes collenchyma cells are present between the adaxial epidermis and at the adaxial side of the sclerenchyma in *D. razakamalalae.*

Two types of bundle sheaths are observed. Type I is composed of large parenchyma cells, thin-walled and irregularly shaped. Type II is composed of parenchyma with a thick-wall and round shape.

Bundle sheath arrangement varies and could be used to distinguish among the species. Type I completely surrounds the vascular bundle (in *D. bathiei, D monticola, D. pseudobaronii)* (Fig. 6G–H)*,* partially surrounds the vascular bundle (in *D. abrahamii, D. baronii, D. chlorocarpa, D. davidii, D. lemurica, D. oronjiae and D. urschii*) (Fig. 6A–B) or is at both sides of the vascular bundles in *D. purpurascens* (Fig. 6F)*.* Type II completely surrounds completely the vascular bundles in *D normandii, D. obtusa* (Fig. 6C)*,* or partially surrounds the abaxial part of the vascular bundles in *D. greveana, D.purpurascens, D. orientalis D. razakamalalae* (Fig. 6D)*.*

Discussion

Among the 16 species assessed, some of the common characters in *Dalbergia* initially observed by Metcalfe & Chalk (1957); followed by Moreira *et al.* (2016); Marques Das Neves *et al.* (2016), and Bijauliya *et al.* (2016) were found in this study;these are, the cross-section of the leaf is usually dorsiventral, several small collateral vascular bundles are distributed throughout the mesophyll, the vascular bundle is surrounded by sclerenchyma, and there are multicellular trichomes. However, in general, there is a single vascular bundle in the midrib, and prismatic crystals are common in *Dalbergia.*

Arrangements and number of vascular bundles in the petiole can be used as diagnostic characteristics. For instance, *D. bathiei* has five vascular bundles at the proximal part, *D. pseudobaronii* has two vascular bundles and *D. urschii* has at least nine vascular bundles for at the distal part, separating it from the rest of the assessed species.

Vascular bundle arrangement in the petiole has been used in the taxonomy of some plant families, for instance, number of vascular patterns in a petiole in Dipterocarpaceae from Sri Lanka (Noraini *et al.* 2016, Talip *et al.* 2017). In addition, anatomical structures of the petiole are useful for identifying *Cinnamomum* (Lauraceae) found in Sri Lanka (Abeysinghe & Scharaschkin 2019). Park *et al*. (2021) reported that the number of vascular bundles in the petiole was useful for species discrimination in *Clematis* (Ranunculaceae) from South Korea. Recently, petiole and midrib vascular patterns have been useful in distinguishing species groups of *Diospyros* (Ebenaceae) in Madagascar (Sandratriniaina *et al.*, 2023).

Idioblasts are observed in medullar parenchyma in the petiole of *D. urschii* and *D. bathiei,* and Marques Das Neves *et al.* (2016) also reported this character in the internal region of the vascular tissue of the leaf and stem in *D. ecastaphyllum* (L.) Taub.

Metcalfe and Chalk (1957) reported that hypodermis is present in some species of *Dalbergia.* The number of layers of palisade parenchyma varied from 1 to 3 among assessed species. In our assessed species two layers of hypodermis were observed only in *D. greveana* (Figs 3D and 3E). A single layer of palisade parenchyma occurs only in *D. chlorocarpa* and *D. normandii*.

The size, shape, and arrangement of parenchymatous cells and the shape of vascular bundles in the midrib vary among the assessed species and could be used to distinguish them. Large, thin-walled parenchymatous cells located at the two sides of the vascular bundle occur in *D. purpurascens*. Ekeke, C. & Mensah, S. (2015) found that the shape and arrangement of vascular bundles in the midrib were useful in classifying the Asteraceae from Nigeria and Ekeke *et al.* (2016) also found these characters to be useful to distinguish species of *Emilia*. Three types of midrib vascular patterns were used to distinguish groups of this species.

The presence of papillose lower epidermis was only observed in *D. baronii*; this character could distinguish assessed species from each other. Farooqui *et al.* (1989) reported that two closely related *Dalbergia* species can be separated by the presence of epidermal papillae; *D. latifolia* Roxb. is prominently papillate while *D. sissoides* J. Graham ex Wight & Arn. is non-papillate. Metcalfe and Chalk (1957) reported that this character is also present in some species of *Dalbergia* and it is also reported by Marques Das Neves *et al.* (2016) for *D. ecastaphyllum.*

The shape of the midrib varies in assessed *Dalbergia*, and it could be used to distinguish two species: *D. lemurica*, which has flat-flat, and *D. purpurascens,* which shows slightly convex-convex. This character was also reported as a useful feature in an identification key of 18 species of *Banisteriopsis* (Malpighiaceae) (Araújo *et al.* 2020) and in a group in the Myrtaceae (Cardoso *et al.* 2009). The midrib shape also showed distinctive differences which are used as anatomical markers for species identification and differentiation for six *Eucalyptus* (Migacz *et al*. 2018).

This study reveals for the first time the presence of palisade parenchyma throughout the mesophyll in *D. razakamalalae*. However, palisade parenchyma occurs only in the abaxial side for the other 15 *Dalbergia* species from Madagascar and in three *Dalbergia* from America (*D. ecastaphyllum, D. miscolobium. D. nigra)* and in *D. sissoo* from Asia (Moreira *et al*. 2013, Marques Das Neves *et al.* 2016, Bijauliya *et al.* 2017). This presence of palisade parenchyma in adaxial and abaxial mesophyll is observed in other eudicots, e.g. *Eucalyptus baxteri* (Edwards *et al.* 2000).

Identification key for the 16 studied Malagasy *Dalbergia*

The following identification key for the 16 Malagasy *Dalbergia* species is based on qualitative features that are easy to observe: the shape of the lamina, the pattern of vascularization in the petiole, presence or absence of papillae, hypodermis and its type, arrangement and disposition of bundle sheath.

1a Shape of lamina: Flat-flat ..... *D. lemurica*
1b Shape of lamina: other 2
2a Presence of papillae in lower epidermis ..... *D. baronii*
2b Lower epidermis lacking papillae 3
3a Hypodermis present at mesophyll ..... *D. greveana*
3b Hypodermis absent at mesophyll 4
4a Palisade parenchyma in all mesophyll ..... *D. razakamalalae*
4b Palisade parenchyma only on the adaxial side of mesophyll 5
5a Bundle sheath Type I (parenchyma thin-walled irregularly shaped) 6
5b Bundle sheath Type II (parenchyma thick-walled and rounded) 14
6a Bundle sheath Type I on the left and right-sides of the vascular bundles ..... *D. purpurascens*
6b Bundle sheath Type I surrounding the vascular bundle 7
7a Bundle sheath Type I partially surrounding the vascular bundle 8
7b Bundle sheath Type I completely surrounding the vascular bundle 12
8a Open arc vascular bundles with one adaxial vascular bundle at proximal part of petiole ..... *D. urschiii*
8b Open arc vascular bundles at proximal part of petiole 9
9a Simple open arc vascular bundles at proximal part of petiole ..... *D. oronjiae*
9b Open arc vascular bundles with slightly incurved ends at proximal part of petiole 10
10a Open arc vascular bundle at distal part of petiole ..... *D. davidii*
10b Vascular bundle clearly separated at distal part of petiole 11
11a Vascular bundle clearly separated into 5 at distal part of petiole ..... *D. abrahamii*
11b Vascular bundle clearly separated into 6 to 9 at distal part of petiole ..... *D. chlorocarpa*
12a Closed arc vascular cylinder at distal part of petiole ..... *D. monticola*
12b Open arc vascular bundles at distal part of petiole 13
13a Simple open arc vascular bundle at proximal part of petiole ..... *D. pseudobaronii*
13b Open arc clearly separated into five vascular bundles at proximal part of petiole ..... *D. bathiei*
14a Bundle sheath Type II completely surrounding the vascular bundles ..... *D. orientalis*
14b Bundle sheath Type II on abaxial side 15
15a Open arc with one adaxial vascular bundles at distal part of petiole ..... *D. normandii*
15b Vascular bundle clearly separated into 6 to 9 at distal part of petiole ..... *D. obtusa*

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SUPPLEMENTARY TABLE. Quantitative leaf anatomical characters of the 16 Malagasy *Dalbergia* species. Numbers represent the species mean ± standard deviation. Value in µm.

Species	Length of Adaxial Epidermal Cells **(µm)**	Width of Adaxial Epidermal Cells **(µm)**	Length of Abaxial Epidermal Cells **(µm)**	Width of Abaxial Epidermal Cells **(µm)**	Length of Vascular Bundle **(µm)**	Width of Vascular Bundle **(µm)**
Dalbergia abrahamii	15.13 ± 3.39	22.93 ± 8.12	10.34 ± 2.60	17.26 ± 4.72	118.68 ± 13.99	174.65 ± 21.18
D. baronii	16.23 ± 3.23	18.31 ± 5.13	13.29 ± 3.76	16.79 ± 4.10	107.1 ± 25.30	134.16 ± 26.18
D. bathiei	21.47 ± 5.76	21.7 ± 4.31	13.2 ± 4.72	16.77 ± 5.04	239 ± 37.47	315.87 ± 59.78
D. chlorocarpa	19.96 ± 5.02	25.39 ± 6.58	13.93 ± 3.52	18.89 ± 6.23	78.8 ± 17.39	124 ± 36.62
D. davidii	15.35 ± 3.06	17.03 ± 4.15	10.99 ± 2.36	15.33 ± 4.15	52.5 ± 5.90	70.50 ± 29.75
D. greveana	17.04 ± 3.08	19.28 ± 4.08	15.58 ± 3.25	17.71 ± 3.68	112.76 ± 18.81	204.51 ± 51.28
D. lemurica	29.23 ± 4.54	31.92 ± 8.41	14.79 ± 3.31	22.65 ± 5.76	91.9 ± 8.16	137.1 ± 24.61
D. monticola	21.8 ± 4.29	17.73 ± 5.21	11.41 ± 2.80	15.02 ± 2.91	84.89 ± 16.19	154.47 ± 22.86
D. normandii	36.95 ± 6.51	35.53 ± 9.53	19.56 ± 3.31	22.9 ± 6.22	188.08 ± 56.84	306.63 ± 65.19
D. obutsa	19.85 ± 6.94	16.52 ± 3.72	17.23 ± 5.63	13.01 ± 3.99	147.83 ± 46	209.54 ± 36.47
D. orientalis	21.73 ± 2.80	18.35 ± 5.17	13.04 ± 2.52	17.37 ± 4.54	147.11 ± 21.22	236.45 ± 32.01
D. oronjiae	19.03 ± 3.82	22.26 ± 5.09	15.98 ± 3.63	17.45 ± 3.85	74.01 ± 13.21	116.98 ± 31.10
D. pseudobaronii	17.67 ± 3.78	20.14 ± 5.64	14.75 ± 3.06	19.54 ± 4.17	74.9 ± 8.88	124.1 ± 20.21
D. purpurascens	18.42 ± 3.84	21.76 ± 8.78	16.57 ± 3.62	17.78 ± 4.38	136.33 ± 20.78	196.33 ± 30.39
D. razakamalalae	13.3 ± 3.13	19.48 ± 4.26	10.02 ± 3.13	13.52 ± 3.07	84.13 ± 15.56	158.36 ± 36.93
D. urschii	16.38 ± 3.79	22.91 ± 7.84	14.51 ± 2.60	18.81 ± 6.97	128.68 ± 29.15	196.76 ± 44.43