

Leaf morphology and anatomy of *Manilkara* Adans. (Sapotaceae) from northeastern Brazil

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Abstract Aiming to complement the group's taxonomy, the objective of this work is to describe and characterise, searching for morpho-anatomical patterns, the leaf anatomy of the *Manilkara* species occurring in the northeast region of Brazil. The leaves of all *Manilkara* species were analysed, using herbaria specimens and collections made in the field by the authors. The characterisation of the leaf blades was performed according to the usual protocols in vegetal anatomy. As diagnosed by anatomical characters, the *Manilkara* Adans. genus presents petioles with a thick cuticle, a uniseriate epidermis, a sclerenchymatous sheath involving the vascular bundle, and laticifers on the cortical and medullar regions. The anatomical data increase the *M. elata* and *M. huberi* synonymisation and show the importance of the anatomy as a complementary tool to the taxonomy based on external morphology.

Keywords Laticifer · Leaves · Sapotaceae · Taxonomic anatomy

Introduction

The pantropical Sapotaceae family is composed of approximately 800 species in 53 genera (Pennington 1991). In Brazil, the family has nearly 14 genera, comprising 200 species, especially in the Amazon Rainforest (Barroso 1991; Souza and Lorenzi 2008). The family is characterised by trees and shrubs with the following: a milky sap, with or without stipules; simple, alternate leaves, grouped on the top of the branches; non-showy flowers, small, solitary or grouped; sepals in numbers from 4 to 12 in 1–2 series, usually free or united on the base; corolla united 4–12; stamens 6–10; upper, 6–12 locular ovary; and berry fruit (Pennington 1990).

Manilkara Adans. is the fourth largest genus in the family and has approximately 30 species in the neotropics; they are popularly known as maçaranduba and are economically important due to their wood and latex quality (Ricardi 1992). In Brazil, 19 species are registered of which 11 are distributed in areas of Atlantic Forest and coastal vegetation (restinga) and eight in the Amazon Forest (Pennington 1990; Almeida-Jr. et al. 2009). In the northeast region, *Manilkara* comprises 12 species distributed in coastal areas, with records also in areas of the Atlantic Forest, Caatinga, Cerrado and in areas with influences of the Amazon biome. Currently, the *Manilkara* genus is considered monophyletic (Anderberg and Swenson 2003; Bartish et al. 2005; Swenson and Anderberg 2005; Swenson et al. 2007, 2008). Armstrong (2010) also suggested a monophyletic *Manilkara*, considering it however to be within the Manilkarinae subtribe. It is worth highlighting that in his study Armstrong (2010) reported on the biogeography of *Manilkara* species and pointed out that the delimitation of some species of African *Manilkara* are problematic due to the lack of clear diagnostic characters,

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which was not observed for the South American species, despite the low number of specimens observed by the author.

Recent taxonomic approaches have been presented by Almeida-Jr. (2010), who conducted a study of the genus by re-evaluating the main taxonomic characters and updating the biogeographical distribution and conservation status of the species. The *Manilkara elata* and *Manilkara huberi* species have characters that make it difficult to separate them. Monachino (1952) considered *M. elata* a co-species of *M. huberi*; however, Pennington (1990) highlights the size of the petiole and sepals, the quantity of fascicle flowers, and the quantity of locules in the ovary as characters to distinguish these species. However, Almeida-Jr. (2010) commented on the overlap of morphological characters indicated by Pennington (1990) and, studying the morphology and using an analysis of the geographical distribution, proposed the synonymisation of these species.

The morpho-anatomical studies can be used as another characterisation tool of the group, and the leaf is the most analysed organ in anatomical studies. Even though the leaf is anatomically variable, considering the several hierarchical levels (species, genus or even family) and the influence of the environmental factors, the numerous anatomical characters are valuable for systematics, especially the leaf epidermis, which is particularly useful for this purpose (Metcalf and Chalk 1979; Dickison 2000). Therefore, since the 19th century, taxonomists have sought anatomical characters that can help in identifying these species (Solereider 1908; Metcalf and Chalk 1950, 1979).

Gomes et al. (2005), Rio et al. (2005), Fonseca et al. (2007) and Araújo et al. (2010) are highlighted among the most recent works in anatomy, as applied to taxonomy, conducted in species of the Brazilian flora. For Sapotaceae, few references with regard to anatomy applied to taxonomy were found (Kukachka 1981; Monteiro et al. 2007a), showing the scarcity of this kind of study for these taxa.

Metcalf and Chalk (1979) mentioned that Sapotaceae has many taxonomic problems, especially regarding intergeneric distinctions. Experts in Sapotaceae, Baehni (1942) and Lam (1939), in antagonistic positions, disagreed and evaluated the morphology of the family in more detail. Whereas Baehni (1942) aimed at simplifying the group's taxonomy and considered the use of anatomy in taxa definitions irrelevant, Lam (1939), performing the fusion of several taxa, considered a more detailed characterisation that placed less importance on exomorphic characters in association with anatomical data. Considering such contrary ideas, and aiming to complement the group's taxonomy, the objective of this work is to describe and characterise the leaf anatomy, seeking morpho-anatomical patterns, of *Manilkara* species in the northeast region of Brazil.

Materials and methods

The criteria used for selecting the leaves were as follows: (1) herborised material quality, (2) fully expanded leaves, and (3) identification by experts in Sapotaceae (Table 1).

Leaves were boiled in distilled water until their submersion, treated with 2 % potassium hydroxide for 2 h at room temperature (Smith and Smith 1942), dehydrated in ethanolic series, and then stored in 70 % ethanol.

The leaf blade (including basal, middle, and distal parts) and petiole were hand sectioned. Cross and longitudinal sections were cleared using a 50 % sodium hypochlorite and stained with basic fuchsin-Astra blue. The slides were mounted in glycerogelatin and sealed with transparent nail polish (Kraus and Arduin 1997).

To analyse the venation pattern, samplings of 20 mm² were subjected to diaphanisation and staining with alcoholic safranin (Shobe and Lersten 1967). The slides were then mounted in glycerogelatin and sealed with transparent nail polish (Kraus and Arduin 1997). The vascular bundle arrangement in the petiole was classified according to Howard (1979). The venation pattern of the leaf blade was classified according to Metcalf and Chalk (1979). Trichomes were analysed according to the classification proposed by Theobald et al. (1979).

All 13 of the *Manilkara* species were compared according to their analysed structural characteristics using a presence/absence matrix (Table 2). This matrix used Sorensen's index and an average group linkage technique (also known as unweighted pair-group method using arithmetic averages, UPGMA) with the MVSP 3.13 m program (Mueller-Dombois and Ellenberg 1974). The definition of the maximum similarity values was made using the software RANDMAT 1.0. A total of two thousand replications were used ($\alpha = 1 \%$).

Results

As diagnosed by anatomical characters, *Manilkara* has petioles with a thick cuticle, a uniseriate epidermis, a sclerenchymatic sheath involving the vascular bundle and articulated laticifers present on the cortical and medullary regions.

The shape of the petiole presented variations among the studied species: a circular shape in *M. decrescens*, *M. elata*, *M. huberi*, *M. longifolia*, *M. maxima*, *M. multifida* and *M. triflora* (Fig. 1-1,2); a concave-convex shape in *M. cavalcantei*, *M. paraensis*, *M. rufula*, *M. dardanoi*, and *M. salzmännii* (Fig. 1-3-5); and a flat-convex shape in *M. bidentata* (Fig. 1-7).

The petiole vascular bundle conformation was another character that varied among the analysed species: a flat

Table 1 List of *Manilkara* Adans. species occurring in the northeast region of Brazil, analyzed in relation to the anatomy of the petiole and the leaf blade

Species	Voucher (Herbarium and registration)
<i>Manilkara bidentata</i> (A. DC.) A. Chev.	RBR 23783; ALCB 06862; INPA 188372
<i>Manilkara cavalcantei</i> Pires & W.A. Rodrigues ex T.D. Penn.	HAF 153; UEC 28641; HAF955
<i>Manilkara dardanoi</i> Ducke	PEUFR 32275; HB 33886; PEUFR 52356
<i>Manilkara decrescens</i> T.D. Penn.	CEPEC 31088; CEPEC 60106; PEUFR 21011
<i>Manilkara elata</i> (Allemão ex Miq.) Monach.	ALCB 73835; HUEFS 113529
<i>Manilkara huberi</i> (Ducke) Chevalier ^a	UEC 33168; INPA 149910
<i>Manilkara longifolia</i> (A. DC.) Dubard	CVRD 611; CVRD 2539
<i>Manilkara maxima</i> T.D. Penn.	HUEFS 127452; PEUFR 9274
<i>Manilkara multifida</i> T.D. Penn.	CEPEC 35580; CEPEC 54134
<i>Manilkara paraensis</i> (Huber) Standl.	UEC 23234; HUEFS 68195
<i>Manilkara rufula</i> (Miq.) H.J. Lam	PEUFR 33215; PEUFR 9274
<i>Manilkara salzmannii</i> (A. DC.) H.J. Lam	PEUFR 43787; PEUFR 41275; IPA 66744
<i>Manilkara triflora</i> (Allemão) Monach.	EAC 15149; ALCB 22839; HAF 645

^a Samples that were also analyzed to confirm the synonymisation proposal of this species suggested by Almeida-Jr. (2010)

convex made by two bundles, one flat and one convex, in *M. cavalcantei*, *M. dardanoi*, *M. rufula* and *M. salzmannii* (Fig. 1-4,5); a flat-convex in *M. decrescens* and *M. multifida* (Fig. 1-6); a concave convex in *M. bidentata*, *M. elata*, *M. huberi*, *M. longifolia* and *M. maxima* (Fig. 1-2,7); and an open arc shape with convolute edges in *M. paraensis* and *M. triflora* (Fig. 1-3).

Accessory bundles were present only in *M. dardanoi* (Fig. 1-4) and *M. salzmannii* (Fig. 1-5), showing differences as to the number of bundles, varying from one to two, respectively. Malpighiaceae trichomes were observed in most of the species, except in *M. bidentata*, *M. dardanoi*, *M. decrescens*, *M. salzmannii* and *M. triflora*, which presented glabrous petioles.

It is worth highlighting that some species, such as *M. elata*, *M. decrescens*, *M. longifolia*, *M. huberi*, *M. paraensis*, *M. multifida*, *M. maxima* and *M. rufula*, presented long petioles and no variation regarding the analysed characters for this region of the leaf was observed, with the exceptions of *M. huberi*, which presented two accessory bundles on the apical and basal regions, and *M. elata*, which presented four accessory bundles only on the apical region.

A thick cuticle, with epidermal cells varying from quadrangular to rectangular, stomata present only on the abaxial surface and dorsiventral mesophyll (Fig. 1-8,9), with sclereids crossing the abaxial and adaxial surfaces (Fig. 1-8), were observed on the leaf blade. All of the analysed species presented a thick cuticle and uniseriate epidermis of the abaxial surface. Regarding the adaxial surface of the leaf, *M. salzmannii*, *M. dardanoi* and *M. rufula* presented a biseriata epidermis (Fig. 1-8), and the others presented a uniseriate epidermis (Fig. 1-9). The

presence of prismatic crystals was detected only in *M. elata*, *M. bidentata*, *M. dardanoi* and *M. salzmannii*, in the region of the petiole and the leaf blade (Fig. 1-10).

The observed vascular bundles were collateral and involved a sclerenchymatic sheath (Fig. 1-10). Concentric and laticifer bundles were also found on the medullary region of the midrib (Fig. 1-10,11). The laticifers are articulated, distributed in longitudinal rows, and observed in the cortical and medullary regions.

With respect to the venation pattern, all of the species analysed showed secondary venation, with a uniformly curved direction. In *M. bidentata* and *M. rufula*, the ramification forms an upper adjacent loop to the secondary veins in an acute angle (Fig. 2-5). In *M. dardanoi*, *M. decrescens*, *M. elata*, *M. maxima*, *M. multifida*, *M. paraensis*, *M. salzmannii* and *M. triflora*, the ramifications form closed loops with secondary, tertiary or quaternary arches (Fig. 2-2-4,6). *M. cavalcantei* and *M. longifolia* ramifications form an upper adjacent loop to the secondary veins in obtuse angles. Most of the species analysed showed simple intersecondary ribs. *M. decrescens*, *M. elata*, *M. longifolia*, *M. multifida*, *M. salzmannii* and *M. triflora* presented composed intersecondary veins (Fig. 2-2-4,6). Random reticulate tertiary veins were observed in 11 of the 13 analysed species (Fig. 2-2-5), except for *M. cavalcantei* and *M. rufula*, which showed tertiary orthogonal reticulate veins (Fig. 2-1,6). The vein formed reticula of higher orders, which have been observed in *M. decrescens*, *M. elata*, *M. longifolia*, *M. maxima* and *M. triflora*. Most of the species analysed showed the last marginal venation as incomplete, whereas *M. decrescens*, *M. maxima*, *M. multifida* and *M. paraensis* showed submarginal loops.

Table 2 Presence (1) and absence (0) matrix of 13 *Manilkara* Adans. species occurring in the northeast region of Brazil

Analyzed characteristics	Mb	Mc	Mda	Mde	Me	Mh	MI	Mma	Mmu	Mp	Mr	Ms	Mt
Petiole on cross-section circular	0	0	0	1	1	1	1	1	1	0	0	0	1
Petiole on cross-section with plan-convex	1	0	0	0	0	0	0	0	0	0	0	0	0
Petiole on cross-section with concave-convex	0	1	1	0	0	0	0	0	0	1	1	1	0
Single-layered epidermis on both sides of the leaf blade	1	1	0	1	1	1	1	1	1	1	0	0	1
Bilayered epidermis on some regions of the adaxial leaf	0	0	1	0	0	0	0	0	0	0	1	1	0
Trichomes type malpighiaceous	0	1	0	0	1	1	1	1	1	1	1	0	0
Petiolar vascular system arranged as a open arc and ends convolute	0	0	0	0	0	0	0	0	0	1	0	0	1
Petiolar vascular system arranged as a plan-convex	0	1	1	1	0	0	0	0	1	0	1	1	0
Petiolar vascular system arranged as a concave-convex	1	0	0	0	1	1	1	1	0	0	0	0	0
One conspicuous accessory bundle in the petiole	0	0	1	0	0	0	0	0	0	0	0	0	0
Two conspicuous accessory bundles in the petiole	0	0	0	0	0	0	0	0	0	0	0	1	0
Lack of accessory bundles	1	0	0	0	0	0	0	0	0	0	0	1	0
Sclereids sheath around bundles	1	1	1	1	0	0	1	1	1	1	1	1	1
Laticifer occurrence	1	1	1	1	1	1	1	1	1	1	1	1	1
Mesophyll dorsiventral	1	1	1	1	1	1	1	1	1	1	1	1	1
Medullary phloem	1	1	1	1	1	1	1	1	1	1	1	1	1
Thickness of secondary veins moderate	1	1	1	1	1	1	1	1	1	1	1	1	1
Secondary vein orientation uniformly curved	1	1	1	1	1	1	1	1	1	1	1	1	1
Branches that form loops superadjacent secondary acute angle	1	0	0	0	0	0	0	0	0	0	1	0	0
Branches that form loops closed by arches secondary, tertiary or quaternary	1	0	1	1	1	0	0	1	1	1	0	1	1
Branches that form loops superadjacent secondary obtuse angle	0	1	1	0	0	0	1	0	0	0	0	0	0
Vein intersecondaries simple	1	1	1	0	0	1	0	1	0	1	1	0	0
Vein intersecondaries composed	1	0	1	1	1	0	1	0	1	0	0	1	1
Randomly reticulate tertiary veins	1	0	1	1	1	1	1	1	1	1	0	1	1
Orthogonal reticulate tertiary veins	0	1	0	0	0	0	0	0	0	0	1	0	0
Veined superior orders forming a reticle whose orders can not be differentiated	1	1	1	0	0	1	0	0	1	1	1	1	0
Veined higher order differential	1	0	1	1	1	0	1	1	0	0	0	1	1
Incomplete last marginal venation	1	1	1	0	1	1	1	0	0	0	1	1	1
Loop last marginal venation	1	0	1	1	0	0	0	1	1	1	0	1	0
Areoles arranged in an oriented pattern	1	0	0	0	0	0	0	0	0	0	0	0	0
Randomly arranged areoles	1	1	1	1	1	1	1	1	1	1	1	1	1
Well-developed areoles	1	1	1	0	0	0	0	0	0	0	0	0	0
Incompletely closed anastomose areoles	0	0	1	0	0	0	0	1	0	0	1	0	0
Imperfectly developed areoles	1	0	1	1	1	1	1	0	1	1	0	1	1
Pedicele pubescent to glabrous	0	1	0	1	1	1	0	0	0	1	0	1	0
Pedicele puberulent	1	0	0	0	0	0	0	1	0	0	0	0	0
Pedicele tomentose	0	0	0	0	0	0	1	0	0	0	1	0	1
Pedicele with indumentum adpress	0	0	0	0	0	0	0	0	1	0	0	0	0
Pedicele with indumentum crisped	0	0	1	0	0	0	0	0	0	0	0	0	0
Leaves along the branch	0	0	0	0	0	0	0	0	0	0	1	0	0
Leaves at the apex of the branches	1	1	1	1	1	1	1	1	1	1	0	1	1
Leaf glabrous	0	1	1	1	1	1	0	1	0	0	0	1	1
Leaves glabrous on the upper surface and tomentose lower	0	0	0	0	0	0	1	0	0	0	1	0	0
Leaves glabrous on the upper surface and puberulent lower	1	0	0	0	0	0	0	0	1	1	0	0	0
Flower solitary axillary	0	0	1	0	0	0	0	1	0	0	0	0	0
Inflorescence a fascicle	1	1	0	1	1	1	1	0	1	1	1	1	1

Table 2 continued

Analyzed characteristics	Mb	Mc	Mda	Mde	Me	Mh	MI	Mma	Mmu	Mp	Mr	Ms	Mt
Ovary pubescent	0	0	0	0	1	1	0	0	1	0	0	0	0
Ovary glabrous	1	1	1	1	0	0	1	1	0	1	1	1	1

Mb *Manilkara bidentata*, Mc *M. cavalcantei*, Mda *M. dardanoi*, Mde *M. decrescens*, Me *M. elata*, Mh *M. huberi*, MI *M. longifolia*, Mma *M. maxima*, Mmu *M. multifida*, Mp *M. paraensis*, Mr *M. rufula*, Ms *M. salzmannii*, Mt *M. triflora*

The arrangement of areoles also varied among the species, and the analysed *M. bidentata* individuals presented three different arrangements: oriented, random and well-developed; the other analysed species exhibited a random arrangement. Areoles with imperfect development were observed in all of the species, except *M. dardanoi*, *M. longifolia* and *M. rufula*. The anatomical character comparison indicated that *M. huberi* and *M. elata* presented similarities, with an index equivalent to 90 % (Fig. 3). *M. decrescens* and *M. triflora* also presented similarities for the analysed characters (>84 %). The other associations were below the minimum similarity level (<80 %).

Discussion

The analysis of the Sapotaceae species allowed the observation of important taxonomic characters for the *Manilkara* genus. It is worth highlighting that researchers have long sought other areas of botany to aid in species identification (Metcalf and Chalk 1950, 1979).

The petiole outline was an important character in distinguishing some species: the circular shape was the most common among the individuals (occurring in seven species), followed by the concave–convex shape (six species), and the flat–convex shape, which was observed in only one individual. The petiole analysis of the *Manilkara bidentata* individuals showed a thick cuticle, which is usually related to environmental factors, especially in avoiding water loss. The presence of druse and prismatic crystals was found in the mesophyll, which also occurs in *Pouteria* species (Monteiro et al. 2007a).

The anatomical data-grouping analysis showed similarities between *M. elata* and *M. huberi* with regard to the petiole shape and the vascular bundle conformation. These characteristics, together with the external morphological characters (pedicel pubescent to glabrous, size of the leaf blade, ovary puberulous, and variation of quantity of ovary locules) (Almieda-Jr. 2010), reinforce the synonymisation proposed in this study. Despite the fact that the species present five different characters relating to the format of the venation pattern (indicated in Table 1), misunderstandings about the definition of these characters can arise. According to a review of *Pleurothyrium*, Lauraceae by van der

Werff (1993), although the type of venation has a pattern for each species, the possible patterns have peculiarities that complicate their precise description.

Armstrong (2010) reported that the South American clade species was divided into two subclades, with a clade composed of Atlantic Forest species (*M. salzmannii*, *M. elata*, *M. maxima*, *M. rufula*, *M. decrescens*, and *M. longifolia*) and a clade of the Amazon Forest species (*M. huberi*, *M. bidentata*, *M. paraensis*, and *M. inundata*). The author does not question the taxonomy of the group and only made inferences about their biogeography. However, in the studies developed by Ducke (1950) and Monachino (1952), the authors agreed with the addition of these species by considering the similarity between the floristic areas in southern Bahia State to species in the Amazon region. Based on the questioning of Ducke (1950) and Monachino (1952), analysing a larger amount of material, plus the geographical distribution of *M. elata* and *M. huberi*, Almeida-Jr. (2010) observed that the differences between these species were not sufficient to warrant them being treated as separate species. Moreover, regarding the potential geographical distribution modelling analysis, the *M. elata* species presented a disjunct distribution, with records in the Amazon Province and Hiléia Baiana (Almeida-Jr. 2010), strengthening the inclusion of *M. huberi* as a synonym of *M. elata*.

Studying the anatomy of *Manilkara decrescens*, *M. multifida*, *M. rufula*, *M. salzmannii* and *M. triflora*, Araújo and Carneiro (unpublished) observed the configuration of the vascular bundle in the flat-convex shape, confirming the data found in this study for the aforementioned species. In addition to the conformation type mentioned above, the concave-convex shape and the open arc shape with convoluted edges were also observed. Several studies on taxonomic anatomy consider the vascular system conformation a relevant character to distinguish species (Reis et al. 2004; Gomes et al. 2005; Dunthorn 2009; Araújo et al. 2010).

The presence and the quantity of accessory bundles are also characters considered relevant for species differentiation, but only two species (*M. dardanoi* and *M. salzmannii*) presented accessory bundles (varying from one to two bundles). In a study conducted with Erythroxylaceae, Bieras and Sajo (2004) highlighted that some species are

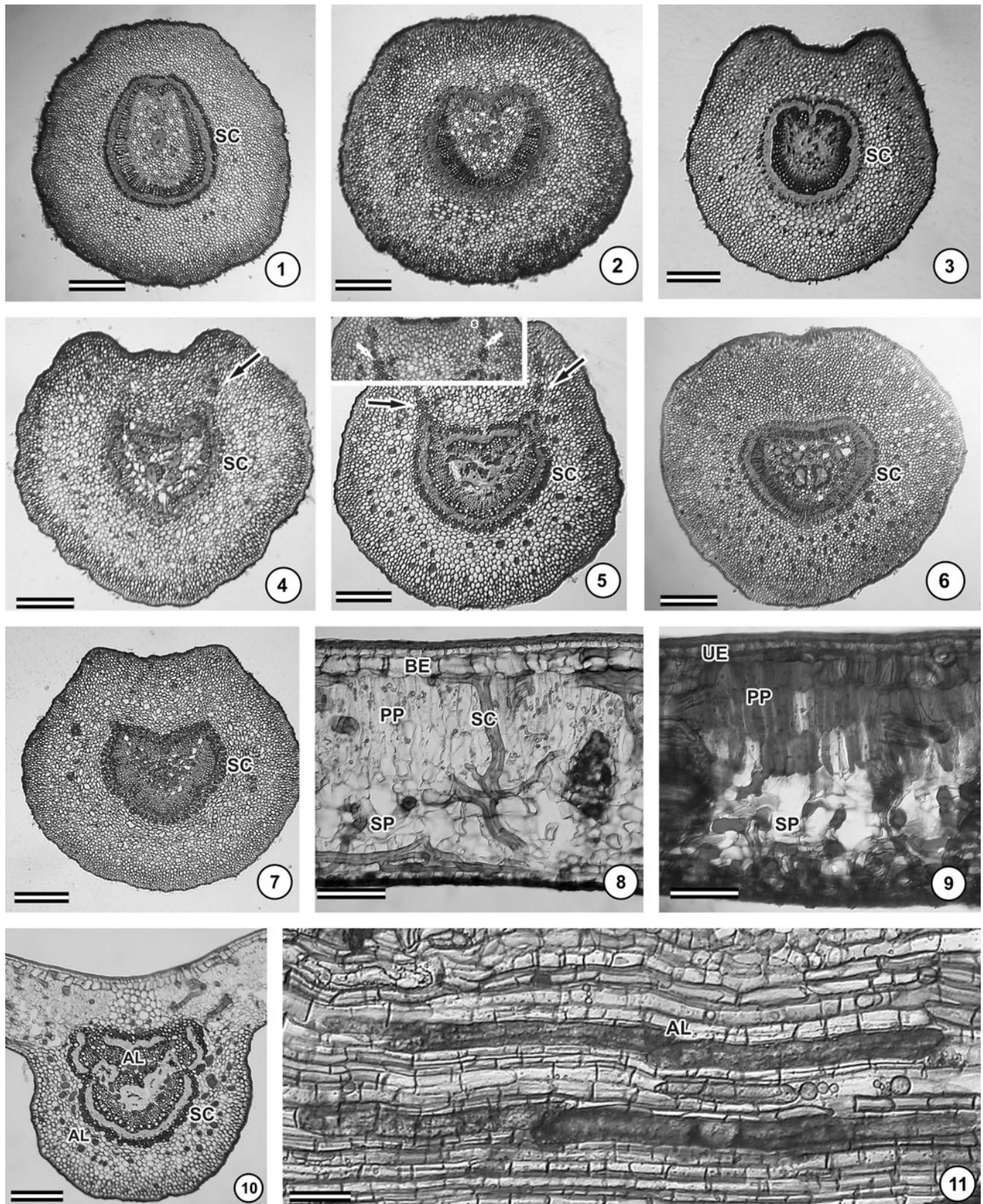


Fig. 1 Cross-sections of the petiole (1–7), leaf (8–10), and longitudinal sections (11) species of *Manilkara*. **1** *M. multifida*; **2** *M. elata*; **3** *M. paraensis*; **4** *M. dardanoi*; **5** and **8** *M. salzmännii*; **6** *M. decrescens*; **7** and **10** *M. bidentata*; **9** and **11** *M. triflora*. (BE, biseriate epidermis;

SC, sclereids; UE, uniseriate epidermis; AL, articulated laticifers; PP, palisade parenchyma; SP, spongy parenchyma); Arrow accessory bundles. Scale 1–7 and 10 400 μm ; 8 and 9 200 μm ; 11 and 12 100 μm

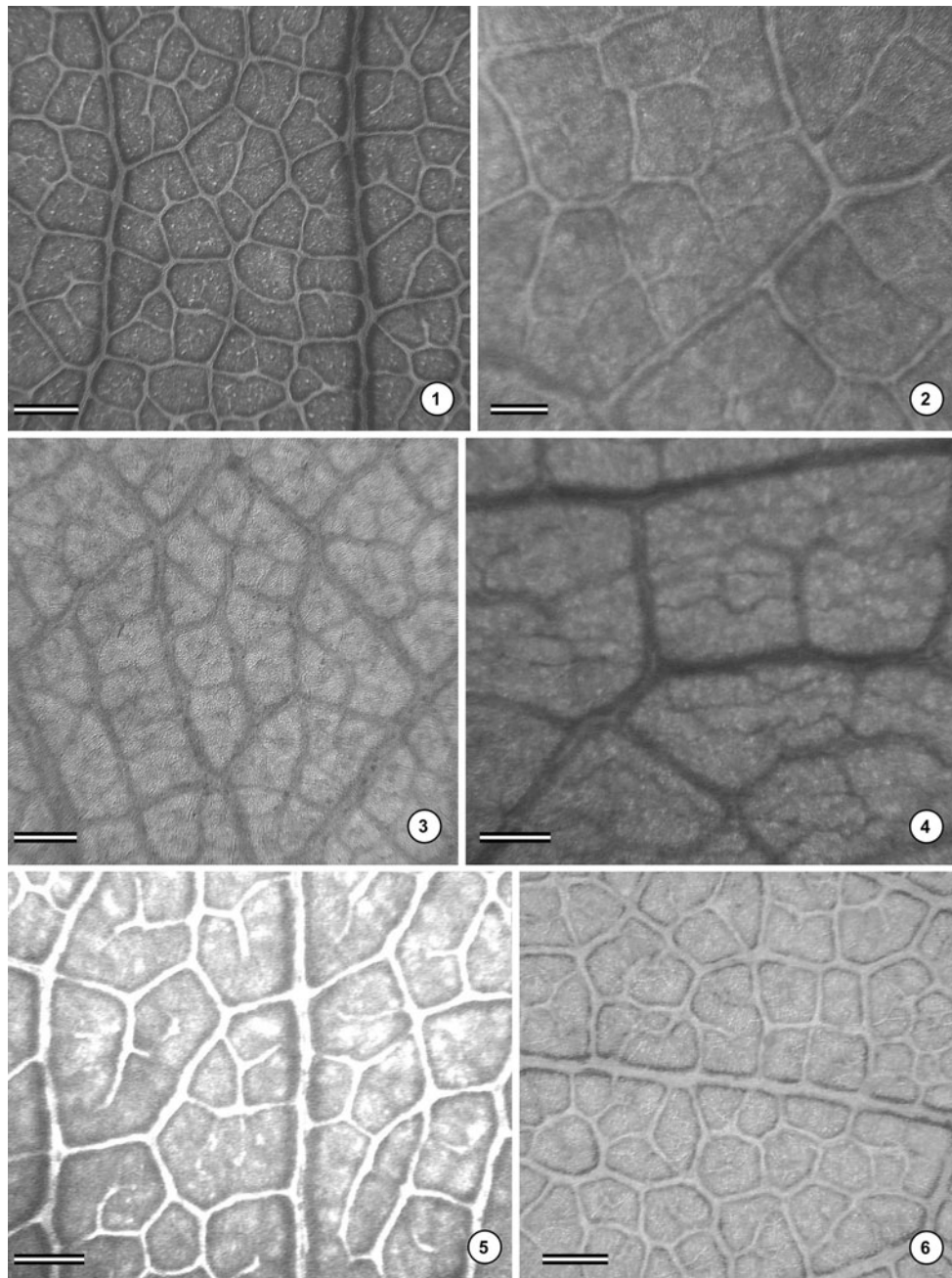


Fig. 2 Venation patterns on cleared leaf blades from *Manilkara* species. **1** *M. cavalcantei*: ramifications with loops over adjacent to the secondary ramification in obtuse angle, simple intersecondary vein and orthogonal reticulate secondary veins. **2** *M. decrescens*: ramifications with loops closed by secondary, tertiary or quaternary arcs, composed intersecondary vein and random reticulate tertiary vein. **3** *M. elata*: ramifications with loops closed by secondary, tertiary or quaternary arcs, composed intersecondary vein and random reticulate

tertiary vein. **4** *M. maxima*: ramifications with loops closed by secondary, tertiary or quaternary arcs, simple intersecondary vein, random reticulate secondary vein. **5** *M. rufula*: ramifications with loops over adjacent to the secondary ramification in acute angle, composed intersecondary vein and random reticulate tertiary vein. **6** *M. multifida*: ramifications with loops closed by secondary, tertiary and quaternary arcs, composed intersecondary vein and orthogonal reticulate secondary veins. *Scale* 400 μ m

characterised precisely by the presence or absence of accessory bundles.

Regarding the trichomes, Metcalfe and Chalk (1950) suggested the presence of several types of trichomes for the

family; however, only the malpighiaceous type, i.e., the long bifida conformation and short stem, was observed in the present study. Among the species that presented glabrous leaves, only *M. dardanoi* had variations in this

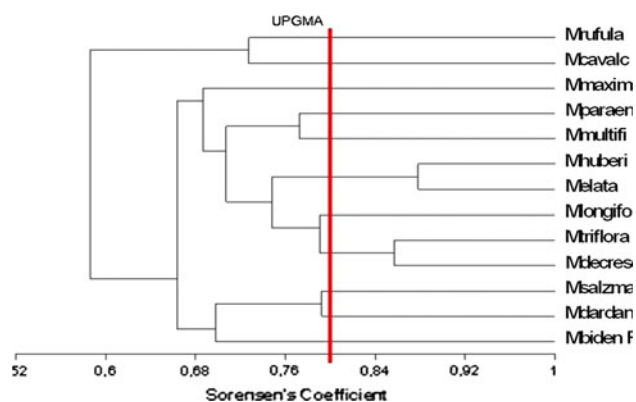


Fig. 3 Grouping analysis of the *Manilkara* species. Similarity index: Sorensen -0.80 . $\alpha = 1\%$. 2,000 replications. Mbinden, *Manilkara bidentata*; Mcavalc, *M. cavalcantei*; Mdardan, *M. dardanoi*; Mdecres, *M. decrescens*; Melata, *M. elata*; Mhuberi, *M. huberi*; Mlongifo, *M. longifolia*; Mmaxima, *M. maxima*; Mmultifi, *M. multifida*; Mparaens, *M. paraensis*; Mrufula, *M. rufula*; Msalzman, *M. salzmanni*; Mtriflora, *M. triflora*. Red perpendicularly line indicates minimum similarity value

character; this species can present glabrescent leaves with a crisped indumentums, according to Almeida-Jr. (2010), a characteristic that may have occurred due to the quality of the used sample.

Metcalf and Chalk (1950) also mentioned the presence of a biseriate epidermis. This characteristic, found only in *M. salzmanni*, *M. dardanoi*, and *M. rufula*, also contributes in the separation of the species. Characters, such as the presence of sclerenchyma sheaths, stomata located only on the abaxial surface and laticifers, are typical in Sapotaceae, according to Solereder (1908) and Metcalfe and Chalk (1979). The presence of laticifers is a dominant characteristic for the different genera of the family, being found in almost all Sapotaceae organs (Monteiro et al. 2007b). Solereder (1908) and Metcalfe and Chalk (1979) observed laticifers in the cortex, medullary region, leaf mesophyll, and vascular tissues. Solereder (1908) also described the presence of resinous substances, calcium oxalate crystals, and starch in the laticifers. All of the analysed species presented dorsiventral mesophyll, different from some species of *Pouteria*, which can present isobilateral mesophyll (Monteiro et al. 2007a) and is a relevant character in the separation of these genera.

Finally, it can be considered that *Manilkara* presented variations in the internal structure of the petiole, strengthening Lam's idea (1939) that these differences would help settle doubts on the separation of the species for this group. The 12 species analysed showed differences that indicate the importance of anatomy for taxonomic evaluation. It was possible to indicate promising characters for future taxonomic and phylogenetic studies on Sapotaceae, in addition to confirming the synonymisation between *M. elata* and *M. huberi*.

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