



Original article

Targeted DNA sequencing and morphology show that *Psidium decussatum* and *P. salutare* are distinct species

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Abstract: The *Psidium salutare* complex comprises a widely distributed group of two species, *P. laruotteanum* and *P. salutare*, the latter with five varieties. One of these varieties, *Psidium salutare* var. *decussatum* (basonym, *P. decussatum*) was used for a subgroup of *P. salutare*, here called “narrow-leaved salutare”. With better knowledge of the type of *P. decussatum* and modern collections, together with high-throughput sequencing and target enrichment with the Angiosperm 353 probe set, we compare *Psidium decussatum* to *P. salutare* (specifically the “narrow-leaved salutare” form) and other species of *Psidium*. Herbarium specimen analysis demonstrates that the names *P. decussatum* and *P. salutare* var. *decussatum* have often been erroneously applied to specimens of taxa other than *P. decussatum* or “narrow-leaved salutare”. Comparison of DNA of specimens of “narrow-leaved salutare” and the true *P. decussatum* confirm that these taxa are indeed distinct and for now, “narrow-leaved salutare” is considered an extreme morphotype of *P. salutare*. Here we re-circumscribe *Psidium decussatum* and present an identification key, along with images of relevant specimens.

Keywords: Angiosperms353, Myrtaceae, phylogenomics.

Resumo: (Sequenciamento direcionado de DNA e morfologia evidenciam que *Psidium decussatum* e *P. salutare* são espécies distintas) O complexo *Psidium salutare* compreende um grupo amplamente distribuído de duas espécies, *P. laruotteanum* e *P. salutare*, esta última com cinco variedades. Uma dessas variedades, *Psidium salutare* var. *decussatum* (basiônimo, *P. decussatum*) foi usada para um subgrupo de *P. salutare*, aqui chamado de “salutare de folhas estreitas”. Com um melhor conhecimento do tipo de *P. decussatum* e coleções modernas, juntamente com sequenciamento de alto rendimento e enriquecimento de sequências alvo com o conjunto de sondas Angiosperm 353, comparamos *P. decussatum* com *P. salutare* (especificamente o morfotipo “salutare de folhas estreitas”) e espécies relacionadas. A análise de espécimes de herbário demonstrou que os nomes *P. decussatum* e *P. salutare* var. *decussatum* têm sido frequentemente aplicados erroneamente a espécimes de táxons diferentes de *P. decussatum* ou “salutare de folhas estreitas”. A comparação do DNA de espécimes de “salutare de folhas estreitas” e o verdadeiro *P. decussatum* confirma que esses táxons são de fato distintos e, por enquanto, “salutare de folhas estreitas” é considerado um morfotipo extremo de *P. salutare*. Aqui, re-circunscrevemos *Psidium decussatum* e apresentamos uma chave de identificação, juntamente com imagens de espécimes relevantes.

Palavras-chave: Angiosperms353, Myrtaceae, filogenômica.

Introduction

The *Psidium salutare* complex was circumscribed and discussed by Landrum (2003) as a group with two species, *P. salutare* (Kunth) O.Berg (Kunth 1823:105; Berg

1856:356) and *P. laruotteanum* Cambess. (1829:282), ranging from Argentina to Mexico and the Caribbean. The complex is distinguished from other species of the genus by 1) a usual habit of subshrub or shrub, but reaching tree size in *P. salutare* var. *pohliianum* (O.Berg) Landrum

(Berg 1857:390; Landrum 2003:1466); 2) a habitat mainly of grasslands or low shrubby growth (cerrado s.s.) that is frequently burned; 3) an ability to sprout back from underground stems even after fires; 4) leaves with brochidodromous venation with a well-marked marginal vein that closely follows the margin and tertiary veins that form a reticulate-dendritic pattern; 5) relatively small flower buds (5–9 mm) with the calyx open; and 6) a peltate placenta with 1–2(–3) rows of ovules on the edge of each lamina.

Currently (Plants of the World Online, 2024), *Psidium salutare* is recognized as a widely distributed species with five varieties: 1) *P. salutare* var. *salutare*, a variable entity ranging from Mexico and the Caribbean to Paraguay and Paraná, Brazil; 2) *P. salutare* var. *mucronatum* (Cambess.) Landrum (Cambess. 1829: 294; Landrum 2003: 1463) and 3) *P. salutare* var. *sericeum* (Cambess.) Landrum (Cambess. 1829: 295; Landrum 2003: 1467) from Uruguay, northern Argentina, Paraguay, and southern Brazil; 4) *P. salutare* var. *pohlium* from Bolivia to Bahia, Brazil; and 5) *P. salutare* var. *decussatum* (DC.) Landrum (DC. 1828: 235; Landrum 2003: 1463), the subject of this paper. This last entity, here called “narrow-leaved *P. salutare*,” is found from south-central Brazil from Goiás to Paraná and has narrowly elliptic to elliptic leaves, (1–)2–5.3 cm long, 0.7–1.7 cm wide, (1.5–)2.5–4.5 times as long as wide, the apex usually rounded, and pedicels 0.5–1.5 cm long. Typical of the complex, it is a low subshrub that resprouts after disturbance.

With a better knowledge of the type specimen of *P. decussatum* and with additional, modern collections of that species, it is evident that *P. decussatum* is distinct from “narrow-leaved *P. salutare* and all the varieties of that species. Therefore, the name *P. salutare* var. *decussatum* was erroneously applied to “narrow-leaved *salutare*” by Landrum (2003). The work presented here aims to compare *Psidium decussatum* to *P. salutare* and other species using comparative analysis of morphological data from herbarium specimens and molecular data from complementary collections. A key to these species is provided and *Psidium decussatum* is newly circumscribed.

Material and Methods

Herbarium specimens were examined in the ASU, HB, K, RB, MBM, NY, P, and UB herbaria (acronyms according to Thiers, 2024), as well as specimen images available through SpeciesLink (2024) and the Reflora Virtual Herbarium (2024). Measurements were made using dried herbarium specimens or photographs of these. Terminology follows Lawrence (1951) and Stearn (1983). To examine relationships based on molecular data, DNA was extracted from six never previously sequenced species of *Psidium*, as well as the outgroup species *Mosiera gracilipes* (Liogier 1973: 269) Salywon (2007: 899) (Table 1).

DNA extractions were performed using a modified CTAB protocol (Doyle & Doyle, 1987). DNA extracts were sent to Neogen Corporation (NE, USA) where li-

brary preparation, bait hybridization and Sequencing was performed. The amount of DNA required per sample was of an optimum amount of 700ng eluted in 36µl of TE buffer, however with some plant material being from herbarium origin only a lower amount could be retrieved. DNA extracts were evaluated on a 1.5× agarose gel to assess average fragment size and quantified using a Qubit 3.0 fluorometer (Thermo Fisher Scientific, Waltham, MA, USA). Neogen prepared libraries using the KAPA HyperPrep Kits (Roche, Basel, Switzerland) or Paired-end sequencing libraries were constructed according to the manufacturer’s instructions (Illumina Inc., San Diego, CA, USA). Libraries were analysed for size distribution using the TapeStation System using High Sensitivity D1000 ScreenTape (Agilent Technologies, Santa Clara, CA, USA) and a Qubit fluorometer to evaluate the quality and concentration of the libraries produced, respectively. Batches of 24 libraries were hybridized using the myBaits Expert Predesigned Panel (Arbor Biosciences, Ann Arbor, MI, USA) Angiosperms353 v1 (Catalog #308196; Johnson et al., 2019) following the manufacturer’s protocol with v4 chemistry (<http://www.arborbiosci.com/mybaits-manual>) and sequencing was performed on the Illumina NovaSeq 6000 platform (Illumina, San Diego, CA, USA) at PE150. The resulting sequence data was combined with existing sequence data of *Psidium appendiculatum* Kiaersk. (1893: 32) (published as *Psidium* sp.) and *Feijoa sellowiana* (O.Berg) O.Berg (Berg 1856: 440; Berg 1857: 615) (an additional outgroup), generated within the context of the Plant and Fungal Trees of Life (PAFTOL) Project and made publicly available via European Nucleotide Archive and the Kew Tree of Life Explorer (Maurin et al., 2021; Baker et al., 2022).

Sequence assembly and phylogenetic analysis followed the workflow described by Maurin et al. (2021) except for using HybPiper version 2.2.0 (Johnson et al. 2016). The bioinformatics and computational analyses were performed on Crop Diversity HPC, described by Percival-Alwyn et al. (2025). We applied a multispecies-coalescent approach, in which gene trees were generated for each trimmed locus alignment using IQ-TREE v2.0 (Minh et al., 2020), selecting the ultrafast bootstrap (1000 replicates, UFBoot2; Chernomor et al., 2016) and the model selection option (-m MFP). Branches with support values 10% (Mirarab, 2019), then collapsed in each gene tree using Newick Utilities v1.6 (Junier & Zdobnov, 2010). We performed an initial coalescent analysis using ASTRAL-III (Mirarab & Warnow, 2015) with extensive branch annotations (-t 2 flag). These annotations allowed recovery of both normalised quartet score (QS) values and local posterior probabilities (LPP). The first set of gene trees were evaluated using TreeShrink (Mai & Mirarab, 2018) to remove outlier taxa and then realigned, trimmed, and analysed using IQ-TREE as described above. The final coalescent analysis was conducted on the second set of gene trees. We finally conducted a quartet-based polytomy test using ASTRAL-III as described by Sayyari & Mirarab (2018) to evaluate gene tree discordance in the data set. Quartet values are expressed as pie charts that show genes support for all possible topologies at a given

node; if one pie wedge is dominant it shows high gene support for a node, if no pie is dominant, it suggests low gene support and that the node may be a polytomy.

The relationships among the species identified in this study were also compared with the classification proposed by Proença et al. (2022) in their first phylogeny of *Psidium*, based on molecular markers and morphology, in which they recognized four sections within *Psidium*: *Psidium* sect. *Psidium*, *Psidium* sect. *Obversifolia* O.Berg, *Psidium* sect. *Apertiflora* O.Berg, and *Psidium* sect. *Mitranthes* (O.Berg) Tuler & Proença.

Results and discussion

Herbarium specimen analysis revealed only a few specimens of true *Psidium decussatum* (Fig. 1), two from the early 19th century and two collected in the last 27 years. From examination of images available on Species-Link (accessed in 2024) we determined that the name *Psidium salutare* var. *decussatum* has most commonly been applied to specimens of *P. schenckianum* Kiaersk. (1893: 34). One specimen of *Psidium decussatum* has now been identified as *P. ovale* (Spreng.) Burret (Spreng. 1825: 479; Burret 1941: 485). Most specimens of narrow-leaved *P. salutare* have been identified as *Psidium luridum* (Spreng.) Burret (Spreng 1825: 480; Burret 1941: 484), a synonym of *P. salutare* var. *mucronatum* (Landrum 2003).

Phylogenetic results presented follow the phylogenomic reconstructions shown in Fig. 2. Comparison of DNA of specimens of narrow-leaved *P. salutare* and *Psidium decussatum* (Tab. 1) confirm that these taxa are indeed distinct and for now, narrow-leaved *P. salutare* can be considered an extreme morphotype of *P. salutare*. The study sample used to achieve the objectives of this report includes three of the four sections of *Psidium* proposed by Proença et al. (2022) and shows strong posterior probability support for all nodes (LPP 1.00 and Quartet scores suggesting in general that are dominance of one topology),

except for the *Psidium* crown node, which exhibits a lower value (LPP 0.75, and a quartet score suggesting no one topology dominates this node).

Species sequenced for the first time are arranged as follows: *Psidium parvifolium* (Cuba), *P. appendiculatum* (disjunct between Isla Margarita, Venezuela and eastern Brazil) and *P. decussatum* (Brazil, Minas Gerais), that belong to *P.* sect. *Mitranthes*; *P. friedrichsthalianum* (Mexico, Central America and northwestern South America), *P. huanucoense* (Peru), *P. guajava* (South American widespread) and *P. rutidocarpum* (Peru), that belong to *P.* sect. *Psidium*; *P. salutare*, that belongs to *P.* sect. *Apertiflora*. These new sequences that we generate also bring new insights into the relationship between the *P. rutidocarpum* and *P. guajava*, which will be discussed in a future paper by the authors.

Psidium decussatum can be distinguished from *P. salutare* by its small leaves rarely over 15 mm long (versus 20–90 mm long in *P. salutare*) with obscure venation (versus usually clearly visible); small flower buds, ca. 4 mm long (versus up to 7 mm long); calyx surrounding the lower half of closed corolla in bud, with a margin that is sinuate to shallowly lobed (versus usually lobed, usually not surrounding the closed corolla); petals 2–3 mm long (versus 5 or more mm long). In addition, as far as is known, *Psidium decussatum* is a small tree or shrub (not a subshrub adapted to disturbance).

Psidium decussatum has a restricted distribution currently known to be endemic to the state of Minas Gerais (Fig. 3). In contrast, “narrow-leaved *P. salutare*” central region (Federal District and Goiás) and the southern region (Paraná) of Brazil. More collections are needed to better understand the range of *P. decussatum* and to accurately assess its conservation status.

We here distinguish, in the following key, *Psidium salutare* (including narrow-leaved *salutare* and *P. luridum*), from *P. decussatum*, *P. ovale*, and *P. schenckianum*.

Table 1. List of voucher specimens included in the phylogenomic analysis, with collector numbers, herbarium barcodes and country of collection. The DNA sequences generated in this study are not currently available in public databases as they are part of the ongoing PhD thesis of the first author. They will be deposited upon completion of the thesis.

Species name	Collector name	Collector number	Barcode	Country
<i>Feijoa sellowiana</i>	Chase, M.W.	10349	K	Cultivated at Kew
<i>Mosiera gracilipes</i>	Salywon, A.	1300	ASU029696	Dominican Republic
<i>Psidium appendiculatum</i>	Lucas, E.	1173	SORO002890	Brazil
<i>Psidium decussatum</i>	Pirani, J.R.	3851	ASU000671	Brazil
<i>Psidium friedrichsthalianum</i>	Landrum, L.R.	12307	ASU0306935	Cultivated (Origin: Ecuador)
<i>Psidium guajava</i>	Landrum, L.R.	10044	ASU0060198	Cultivated (Origin: Mexico)
<i>Psidium huanucoense</i>	Monteagudo	3934	ASU0008057	Peru
<i>Psidium parvifolium</i>	Urquiola	9180	ASU006945	Cuba
<i>Psidium rutidocarpum</i>	Rojas, R.	7939	ASU0300549	Peru
<i>Psidium salutare</i> var. <i>decussatum sensu</i> Landrum (2003)	Proença C.E.	1458	ASU001556	Brazil

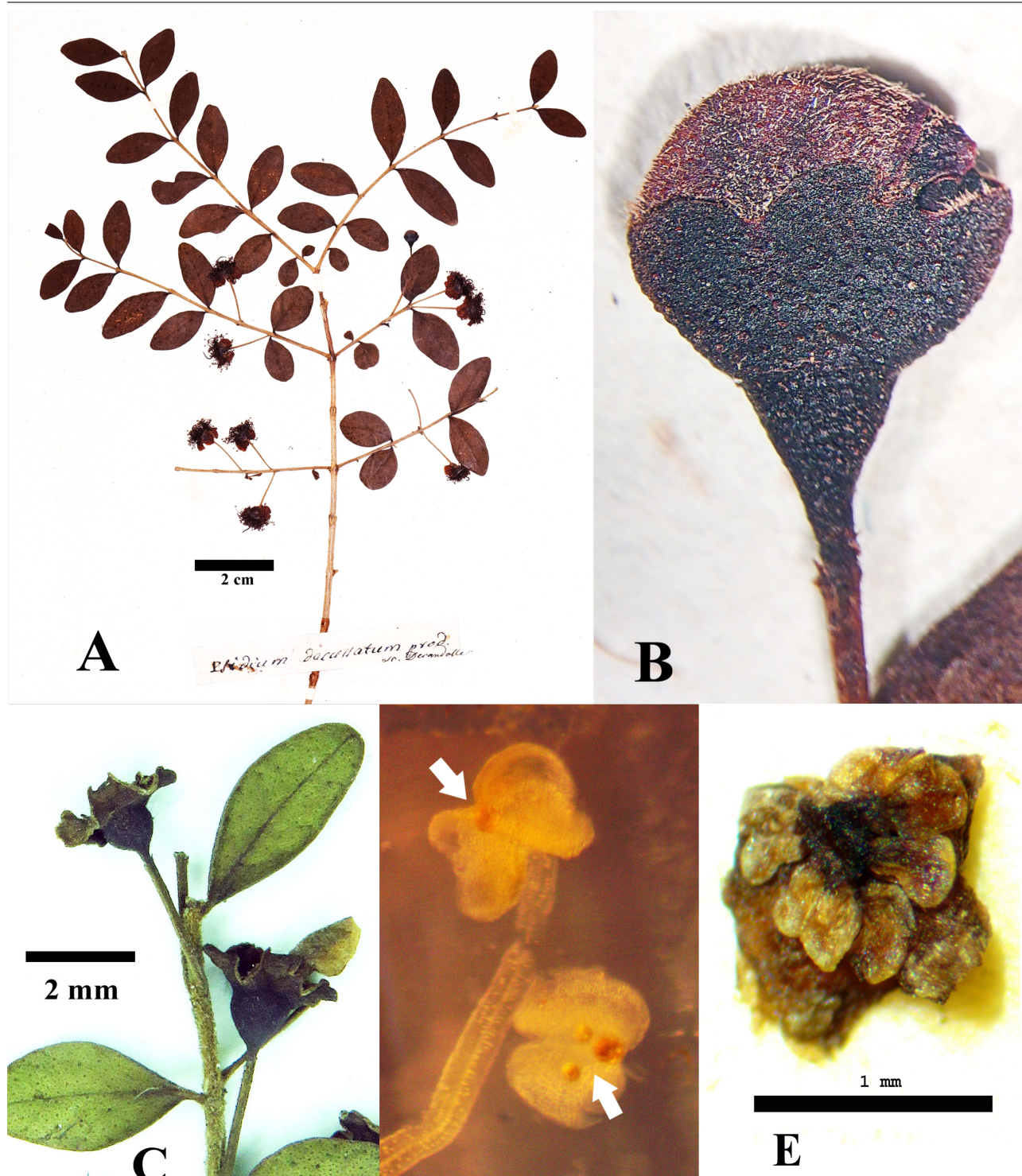


Figure 1. *Psidium decussatum*. A, portion of holotype at M; B, flower bud from holotype, showing cup-like calyx enclosing lower portion of closed corolla; C, twig with flowers shortly after anthesis showing tears in calyx; D, cleared anthers, the upper having a single terminal gland and the lower having terminal gland and two additional glands below; E, placenta with ca. 8 ovules attached. (A & B from holotype, courtesy of the Botanische Staatssammlung München [M] and photographer Suvrat Kotagal at M; C, D & E, photos by L. R. Landrum, from Pirani et al. 3851 at ASU).

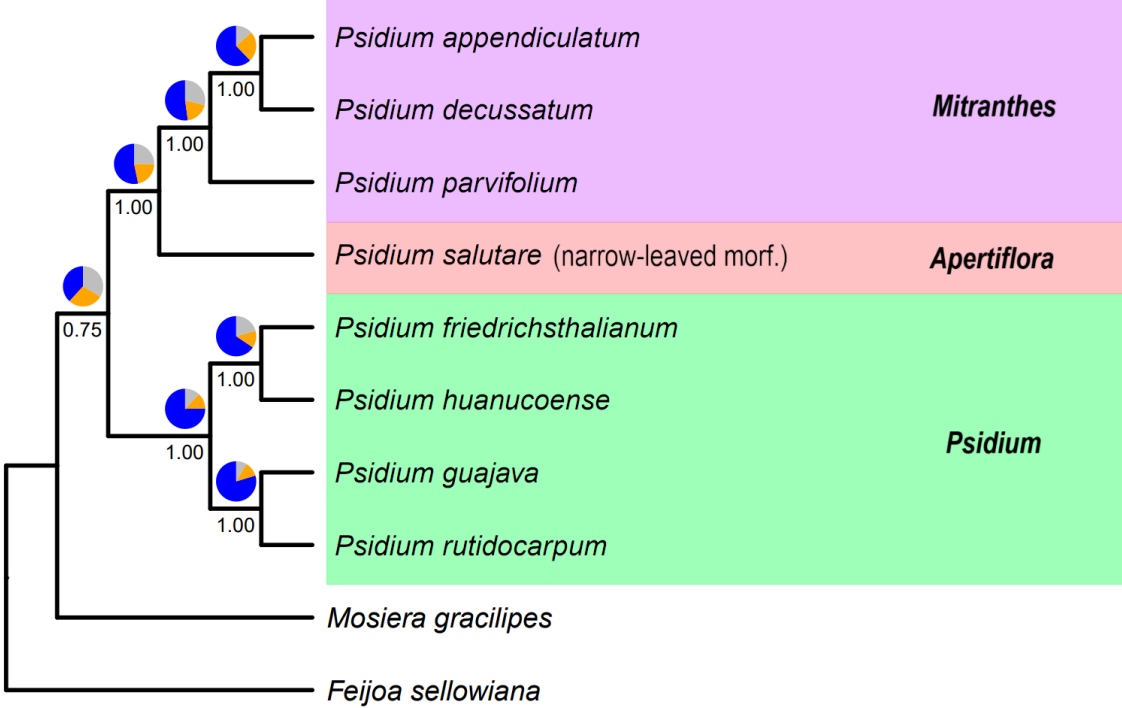


Figure 2. Coalescent tree using Supercontings showing the relationships between the selected *Psidium* species. The pies charts near the nodes display quartet score (QS) values for each node (blue = species tree topology QS; orange = first alternative topology QS; gray = second alternative topology QS). Local posterior probability values are presented below the pies chart. The colors indicate the assignment of species to sections, following the classification proposed by Proença et al. (2022), as follows: purple corresponds to *Psidium* sect. *Mitranthes*; red to *Psidium* sect. *Apertiflora*; and green to *Psidium* sect. *Psidium*.

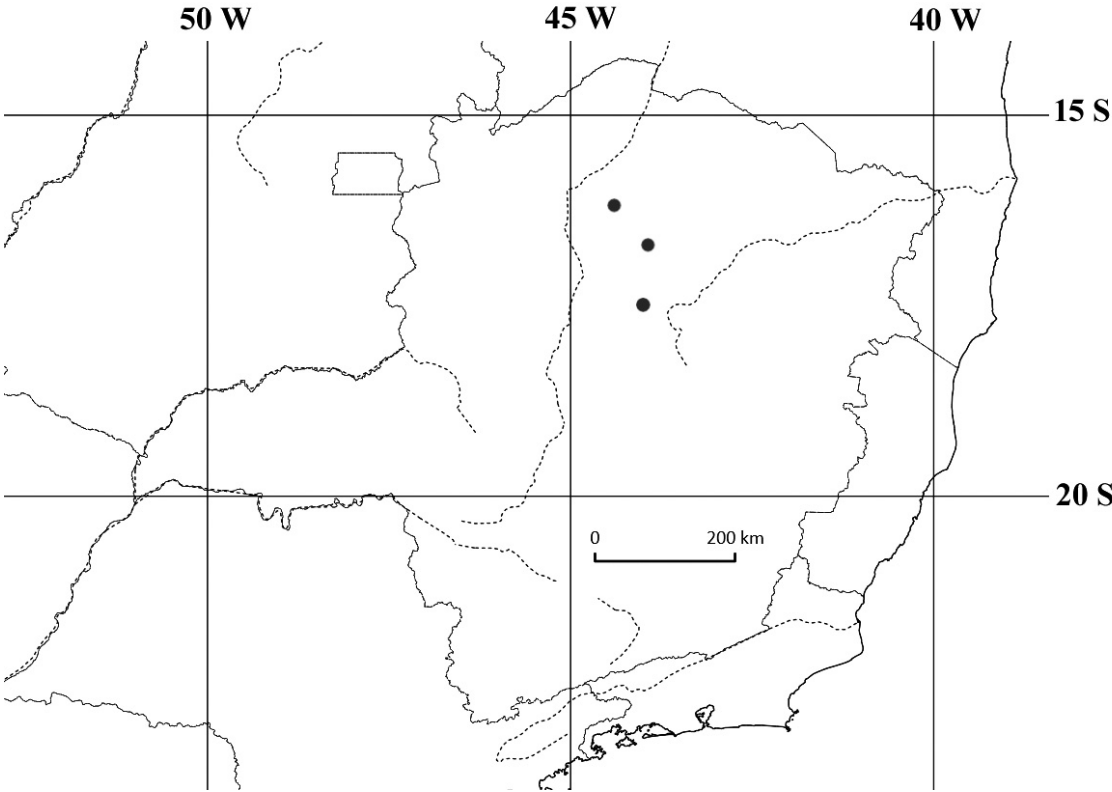


Figure 3. *Psidium decussatum* – Map. of distribution. Black dots indicate known occurrences of the species.

Key to *Psidium decussatum* and morphologically similar species

1. Calyx with 5 flange-like subapical appendages (Fig. 6A), tearing between the appendages into subrectangular pieces, these 1–2 mm long and wide *P. schenckianum* (Fig. 6)
1. Calyx without flange-like appendages, tearing irregularly, tearing between lobes, or with little or no tearing
 2. Leaves 0.5–1.5(–2) cm long; flower buds ca. 4 mm long; stamens 75–100; style ca. 3 mm long; calyx without notable lobes, mainly a fused tube extending ca. 2 mm beyond the ovary summit (Fig. 1B), hiding about half or more of the closed corolla *P. decussatum* (Fig. 1)
 2. Leaves usually over 2 cm long; flower buds usually over 4 mm long; stamens 60–200; style 4–8 mm long; calyx with or without notable lobes, the fused portion extending 0–1 mm beyond the ovary summit, if present hiding only the base of the closed corolla
 3. Subshrubs generally less than 1 m tall (except for *P. salutare* var. *pohlianum* that reaches small tree size), resprouting from an underground or ground level stem after fires or disturbance; leaves often over 4 cm long and 2 cm wide, often more than 2.5 times as long as wide; petiole 0–2 mm long; flower bud 5–7 mm long; calyx with distinct lobes as long as or longer than wide, or less often with indistinct lobes wider than long; plants monoclinal as far as known (with bisexual flowers only) *P. salutare* (all varieties; Fig. 5 of narrow-leaved entity)
 3. Shrubs or trees, generally over 1 m high at maturity; leaves rarely over 4 cm long and 2 cm wide, generally less than 2.5 times as long as wide; petiole 1–4 mm long; flower bud 2–6 mm long; calyx lobes indistinct, wider than long or calyx with a sinuate margin; some plants andromonoecious (with bisexual and male flowers on the same individual) *P. ovale* (Fig. 4)

Recircumscription of *Psidium decussatum*

Psidium decussatum DC., Prodr. 3: 235. 1828. TYPE:—BRAZIL: “prov. Minarum” “*Habitat in Campis ad Contendas*” ex label, currently Brasília de Minas [ca.

16.2°S, 44.4°W] Martius s.n. (HOLOTYPE: M-0032373! (seen as image).

Guajava decussata (DC.) Kuntze, Revis. Gen. Pl. 1: 239. 1891.

Psidium salutare var. *decussatum* (DC.) Landrum, Sida 20(4): 1463. 2003.

Shrub or small tree ca. 2 m high, densely branched, sparsely to densely pubescent on young growth; hairs yellowish brown to whitish, up to ca. 0.3 mm long, somewhat curled to straight and erect; young twigs densely pubescent, with hairs persisting in part until first bark falls, the bark light reddish brown, becoming gray and somewhat scaly with age. **Leaves** elliptic to oblanceolate or obovate (3–)5–15(–20) mm long, 2–5 mm wide, 1.5–2.8 times as long as wide; apex obtuse to rounded; base acute; petiole 0.5–1 mm long, 0.2–0.5 mm wide; venation brochidodromous (in a cleared leaf), obscure, with up to ca. 5 lateral veins each side, leaving the midvein at angles of ca. 45 degrees; blades subcoriaceous, densely glandular abaxially, the margin ciliate, slightly revolute. **Flower buds** pyriform, ca. 4 mm long; hypanthium plus calyx tube ca. 3 mm long, widening at summit of ovary, attenuate at base; indumentum pattern of buds with petals moderately to densely pubescent without, glabrous within, with hypanthium sparsely pubescent, with calyx tube sparsely pubescent without and densely pubescent within, with peduncles moderately pubescent; peduncles 1-flowered, 5–10 mm long, ca. 0.5 mm wide borne in the axils of leaves, at leafless nodes, or in the axils of small bracts ca. 0.3 mm long; bracteoles usually falling before anthesis, linear, up to 1 mm long. **Calyx** bowl-like, surrounding lower half of closed corolla in bud, with margin sinuate to shallowly lobed, tearing irregularly at anthesis, the tears mainly not penetrating the staminal ring; petals 2–3 mm long; disk within staminal ring ca. 1–1.5 mm across, glabrous, the staminal ring pubescent, ca. 1–1.5 mm wide after anthesis; stamens 75–100 based on scars, 2–3 mm long, anthers globose, 0.25–0.5 mm long, with a terminal gland and often with 2 glands below; style ca. 3 mm long, glabrous, the stigma punctiform; ovary 2-locular; ovules ca. 8–14 per locule. **Fruit** (1 seen in photo) globose, ca. 6 mm wide; seeds ca. 3 mm wide.

BRAZIL. Minas Gerais: Montes Claros, P. E. de Lapa Grande, without date (fr), Durães 51 (UB227671); Montes Claros, P. E. de Lapa Grande, Mata Ciliar do Córrego dos Bois, próximo a gruta Boqueirão da Nascente, (–16.71°, –43.94°), 760 m, 1 Feb 2009 (st) Durães & Miranda-Melo s.n. (MCCA04527, MCCA04528, MCCA04529, seen as images on SpeciesLink); Bocaiuva, Engenheiro Dolabela, BR 135, a 51 km N do trevo para Buenópolis, afloramento calcário a leste da Rodovia, 600 m na estrada para Eng. Dolabela, (–17.50°, –44.00°), 10 Jan 1998 (fl), Pirani et al. 3851 (ASU0006713, ASU0030918); without locality, 1816–1821 (fl), Saint-Hilaire 26 (P00258331).

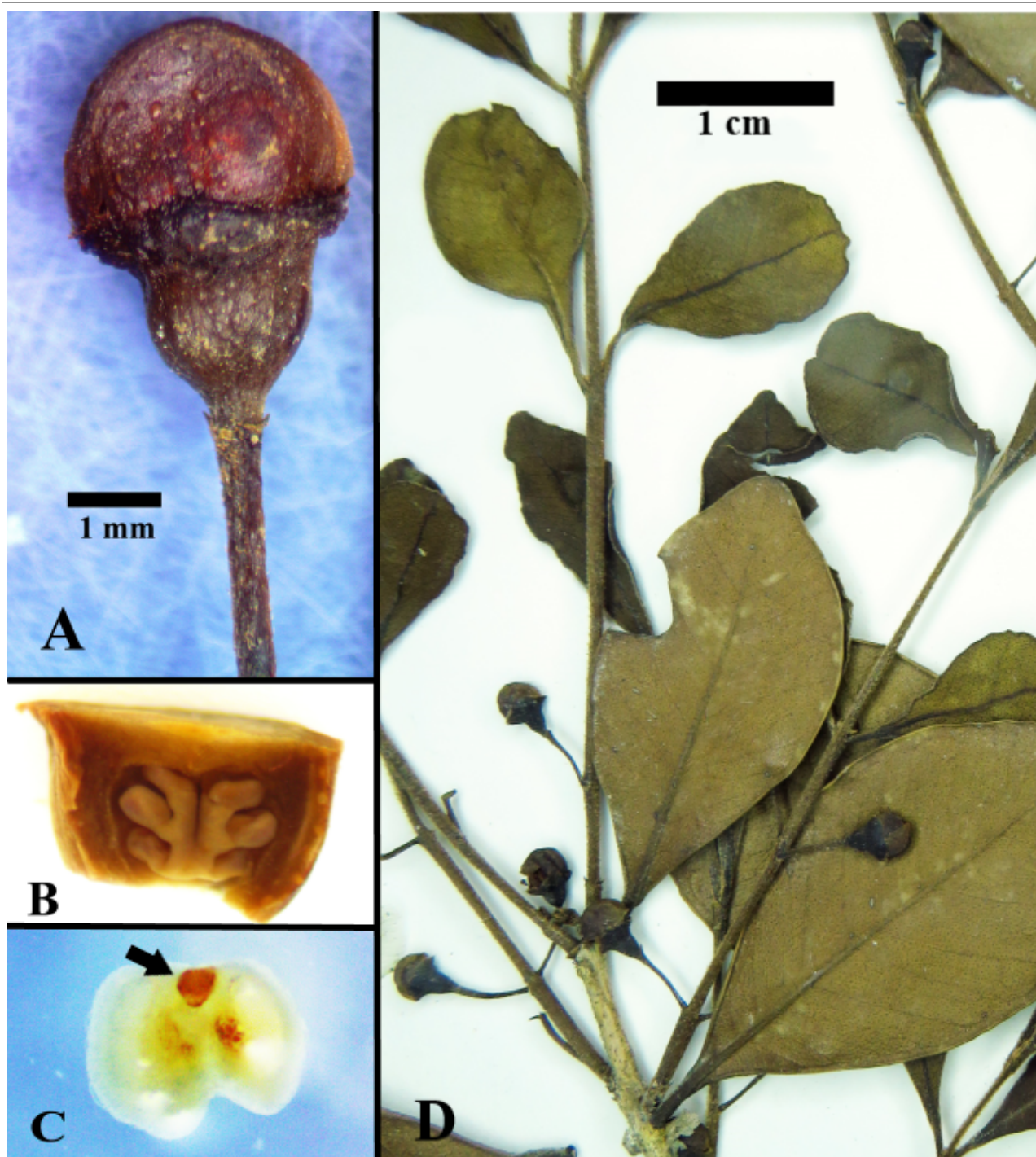


Figure 4. *Psidium ovale*. A, closed flower bud, showing calyx as an expanded rim around the base of the closed corolla; B, longitudinal section of ovary showing placenta with 6 ovules; C, anther with terminal gland only, the brown areas below are uncleared portions of anther; D, portion of herbarium sheet, showing leaves and flower buds arising from basal nodes on young twigs. (All photos from L. R. Landrum 2371 at ASU).



Figure 5. *Psidium salutare*. This specimen belongs to the morphological entity here called “narrow-leaved *P. salutare*” for which the name *P. salutare* var. *decussatum* was used by Landrum (2003). A plant with a woody base, remnants of previous shoots, some charred, and two new leafy shoots with leaves and flower buds; B, close up of lower flower bud, showing prominent calyx lobes. (All from Proença 1458 at ASU).

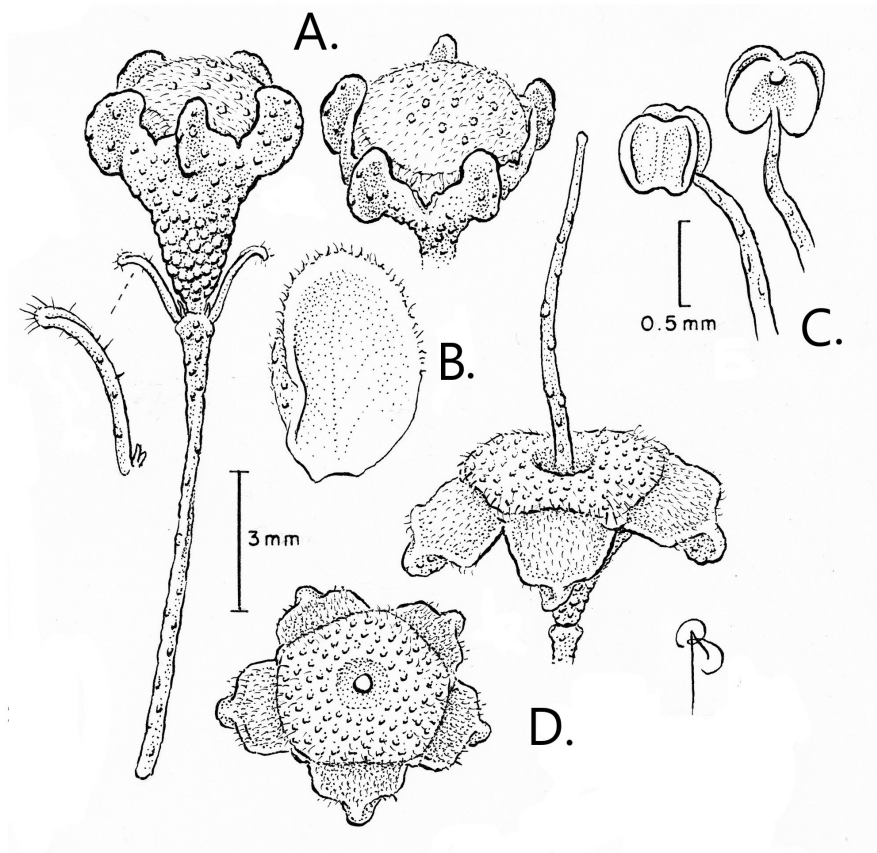


Figure 6. *Psidium schenckianum*. A. Flower buds, the beginning of tears between the calyx lobes evident on right bud. B. Petal with ciliate margin. C. Two views of an anther with a terminal gland. D. Flowers after anthesis showing tears between calyx lobes not penetrating the staminal ring. Portion of Figure 28 from Landrum (2017). Illustration by Bobbi Angell.

Conclusion

Comparative morphological study of herbarium specimens and new molecular data show that *Psidium decussatum* should not be treated as a synonym of *P. salutare* and is here recircumscribed as a species accepted in its own right. Species assignments to sections and the relationships between tips of the phylogenomic tree (species) are corroborated both by a taxonomically broader, unpublished study relating to the PhD thesis of the first author (Conceição, unpublished data). The new collections also show the distribution of *P. decussatum* (Fig. 3).

Based on morphology, the placement of *Psidium decussatum* in *P.* sect. *Mitranthes* makes sense, as species of this section often have a closed or incompletely closed calyx (Proença et al., 2022), as found in *P. decussatum*. The general morphology of *Psidium decussatum* suggests it may be related to similar, small-leaved members of the *P. amplexicaule* Pers. complex (also placed in *P.* sect. *Mitranthes*), from the Caribbean region, but *P. decussatum* differs from the Caribbean species, only by having the calyx more open and fewer glands on the anthers (Landrum et al., 2024).

Acknowledgements

A modern, fertile collection of *Psidium decussatum* was key to understanding the true identity of this species. We thank J. R. Pirani and his collaborators for making available his collection 3851 and M. L. Kawasaki for sending duplicates to LRL with the suggestion that the collection might be of *P. decussatum*. The authors acknowledge funding for DNA sequencing available through the Royal Botanic Gardens, Kew Creative Challenge project, ‘Accelerating the pace of species description using a DNA first approach 2023/24’. The first author would also like to acknowledge the support of the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Coordination for the Improvement of Higher Education Personnel) - Brazil (CAPES) - Finance Code 001, for granting scholarships for international doctoral internships that allowed the first author to develop part of his doctorate at the Royal Botanic Gardens, Kew. The authors acknowledge Research Computing at the James Hutton Institute for providing computational resources and technical support for the “UK’s Crop Diversity Bioinformatics HPC” (BBSRC grants BB/S019669/1 and BB/X019683/1), use of which has contributed to the results reported within this paper.

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