

1 *Psidium guajava* L.: Taxonomy, Relatives and Possible Origin

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1.1 Introduction

The guava (*Psidium guajava* L.) belongs to the genus *Psidium* L. of the family *Myrtaceae*. The family *Myrtaceae* has c.130 genera and nearly 6000 accepted species names (PoWO, 2020). Because many groups have not been studied in depth, we know that many species remain to be discovered and many names will eventually be recognized to be synonyms by future monographers. So, the numbers of species must remain approximate for now.

The family *Myrtaceae* is apparently of Gondwanan origin with centres of diversity in tropical America and Australasia and with fewer species in Africa, the Mediterranean and southern Asia (Raven and Axelrod, 1974; Thornhill *et al.*, 2015).

Several species have economic importance: *Syzygium aromaticum* (L.) Merrill & L.M. Perry (clove) and *Pimenta dioica* (L.) Merrill (allspice) are spices; *P. guajava* (guava) is the best-known tropical fruit, but other species of *Psidium* (e.g. *Psidium cattleianum* Sabine, *Psidium friedrichsthalianum* (O. Berg) Nied.), *Acca sellowiana* (O. Berg) Burret (= *Feijoa sellowiana* (O. Berg) O. Berg; pineapple guava), *Plinia cauliflora* (Mart.) Kausel (jaboticaba), *Syzygium jambos* (L.)

Alston (rose-apple) and *Syzygium malaccense* (L.) Merr. & Perry (Malay apple) are commonly cultivated; species of *Eucalyptus* L'Heritier are widely planted for timber and as ornamentals. *Myrtus communis* L., *Melaleuca* L. (including *Callistemon* R. Brown) and other genera are planted as ornamentals.

Psidium is a genus of at least 60 species and perhaps as many as 100 (McVaugh, 1968; Govaerts *et al.*, 2008), ranging from Mexico and the Caribbean to Argentina and Uruguay. The state of Bahia, Brazil is particularly rich in species of *Psidium* with 28 known so far (Landrum, 2017), about half the total for South America. A few species have been introduced as cultivated plants in the Old World and Pacific Island tropics and subtropics, and some are weedy invasives (Global Invasive Species Database, 2017). The distinguishing characters of *Psidium* are discussed in Landrum (2003) and Landrum and Sharp (1989) and are: flowers (4–)5(–6)-merous (occasionally flowers have more petals) with multiovulate locules; placenta often peltate; mature seedcoat rough or dull, covered with a pulpy layer when wet; hard portion of seedcoat (5–)8–30 cells thick at the narrowest point, with the cells thick-walled, elongate and overlapping; and a C-shaped embryo

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with cotyledons much shorter than the hypocotyl. Based on small samples of two to nine species, recent molecular studies of *Myrtaceae* (Lucas *et al.*, 2007; Murillo *et al.*, 2012; Rivero *et al.*, 2012; Vasconcelos *et al.*, 2017; Flickinger *et al.*, 2020) indicate that *Psidium* may be a monophyletic group and place it in clades with such genera as *Acca* O. Berg, *Amomyrtus* (Burret) Legrand & Kausel, *Campomanesia* Ruiz & Pavon, *Legrandia* Kausel, *Mosiera* Small and *Myrrhinium* Schott and Pimenta L. These are all members of the morphologically based subtribe *Myrtinae* (i.e. those genera with embryos with relatively small cotyledons and a large hypocotyl) that appears to be a basal, paraphyletic group in the tribe.

In a new subtribal classification of the *Myrteae*, a mainly American group of berry-fruited genera, Lucas *et al.* (2019) have divided traditional paraphyletic *Myrtinae* into five subtribes that they recognize as monophyletic based mainly on molecular data. *Psidium* belongs to *Pimentinae* O. Berg in their system. Larger samples will be needed to determine which genera are the closest relatives of *Psidium* and if it is truly monophyletic.

Two genera of *Myrtaceae* that are similar to *Psidium* and sometimes confused with it are *Campomanesia* Ruiz & Pav. and *Calycolpus* O. Berg because they have generally 5-merous flowers, and seeds and embryos similar to *Psidium*. The three genera are compared in the key below. For comparison with other genera of *Myrtaceae*, see Landrum and Kawasaki (1997).

1. Ovary with (3–)6–18 locules, the locules when fertile usually 1-seeded; locular wall in fruits glandular, functioning as a false seedcoat in the fruit so that the ‘seedcoat’ appears to be glandular, the locules arranged in a ring in the fruit, several often without a seed inside; leaves with broadly arching lateral veins and often no clear marginal vein; bark flaky or crusty; hypocotyl swollen, much wider than the cotyledons; anthers usually with 1 gland in the connective, or none ***Campomanesia***.

1'. Ovary with 2–5(–6) locules, the locules when fertile with 1 to many seeds; locular

wall in fruits usually not glandular, not functioning as a false seedcoat, the true seedcoat not glandular, the seeds distributed throughout the fruit, not oriented in a ring; leaves variable but often with a distinct marginal vein; bark variable, but often smooth; hypocotyl not swollen, about the same width as the cotyledons; anthers often with more than 1 gland in the connective.

2. Seedcoat dull or rough, several cells thick; cells of the hard seedcoat surface elongate, overlapping (Fig. 1.1A–E); calyx closed or nearly so in the bud, or the calyx lobes usually broader than long, more or less triangular, sometimes only evident as a sinuate margin ***Psidium***.

2'. Seedcoat shiny, 1 to a few cells thick; cells of hard seedcoat surface not elongate, abutting each other in a mosaic-like pattern (Fig. 1.1F and G); calyx open, the lobes often longer than broad ***Calycolpus***.

1.2 Geography

Psidium is naturally an American genus, although *P. guajava*, *Psidium guineense* Sw. and *P. cattleianum* are subtropical and tropical weedy species in many other parts of the world. The greatest number of species (c.50) is found in South America and those of Central America and Mexico are a subset of that group. Presumably then, the Central American species are geologically recent arrivals from South America because they have not diverged from their South American relatives. The Caribbean islands are home to an unknown number of species, perhaps 20 or more, most of which are endemic to the Caribbean, and may, because of their diversity and distinctness from mainland species, represent multiple, geologically old colonizations.

The Brazilian Atlantic Coastal Forest and the adjacent cerrado and caatinga can be considered a centre of diversity for *Psidium*. We can speculate, at least, because of that diversity and endemism, that *Psidium* has a long history in the Atlantic Coastal Forest and adjacent areas. It is notable that the genus is not found in temperate south-western

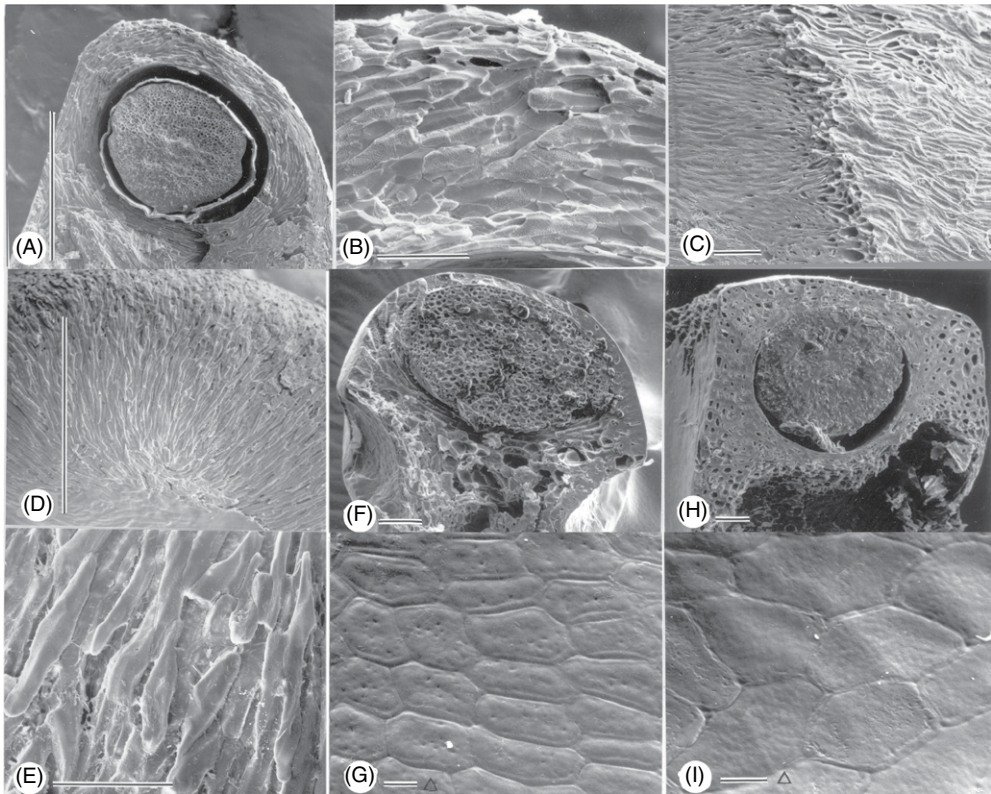


Fig. 1.1. Scanning electron micrographs of seedcoats of *Psidium*, *Calycolpus* and *Mosiera*. (A–C) *Psidium acidum*: section of seed showing cylindrical cavity and embryo (A), upper portion of seedcoat in section (B) and outer surface of seed on right and tangential section (C). (D, E) *Psidium australe*: outer seed surface from which outer pulpy covering has rotted away. (F, G) Seed of *Calycolpus moritzianus*. (H, I) Seed of *Mosiera elliptica*. Note dense overlapping, elongate cells of *Psidium* versus the mosaic pattern of non-overlapping cells in *Calycolpus* and *Mosiera*. (A–C, from Huashikat 1311, MO; D, E, from Montes 851, NY; F, G, from Davidse and Gonzalez 21134, MO; H, I, from Clemente 2831, NY.) Vertical lines = 1 mm; horizontal lines without triangle = 1/10 mm; horizontal lines with triangle = 1/100 mm. All photographs reproduced with permission from Landrum and Sharp (*Systematic Botany* 14(3), 370–376. 1989).

South America; in this respect it is similar to the large Neotropical *Myrtaceae* genera *Calyptranthes* Sw., *Eugenia* L. and *Myrcia* DC., all of which are quite diverse in the Atlantic Coastal Forest (Sobral *et al.*, 2009). *Psidium* is present but less locally diverse in the rest of Brazil, the Andean countries (excluding Chile) and the Guianas.

The Isthmus of Panama has been dated at c.2.8 million years old (O’Dea *et al.*, 2016). So, prior to that date, direct migration without dispersal over water barriers may have been impossible to Central America and beyond. *Psidium oligospermum*

DC., at least, is clearly able to cross significant water barriers, having become established on some oceanic islands (e.g. Galapagos). Colonization of islands, especially when they are new, relatively uninhabited and with reduced biological competition, would be more likely than colonization of a continent with many species already growing there. Because of their edible fruits some species of *Psidium* in Central America may have been carried there by humans. The author does not know of any fossil evidence of *Psidium* in Central America and Mexico other than archaeological finds of

P. guajava that are about 2000 years old in the Tehuacán Valley of Mexico (Smith, 1965).

1.3 Taxonomy

The taxonomically useful morphological characters have been discussed in Landrum (2017). A few of the more important characters are summarized here.

1.3.1 Leaf venation

In *Psidium* the most common type is brochidodromous with the lateral veins (i.e. secondary veins) looping towards the apex near the margin to connect with each other to form a marginal vein that follows the margin, either as a series of arches or as a scarcely arching vein that nearly parallels the margin (e.g. *P. cattleianum*, Fig. 1.2A). Less common is eucamptodromous venation, where the laterals diminish near the margin and no clear marginal connecting vein is evident. In some species leaves

may be eucamptodromous proximally and brochidodromous distally (e.g. *P. guineense*, Fig. 1.2B) and intermediate conditions are sometimes encountered.

The tertiary veins that connect the lateral, marginal and midveins may have a dendritic pattern (Fig. 1.2A) or a ladder-like pattern (the latter found in eucamptodromous leaves only; Fig. 1.2B). The dendritic pattern may seem to be without clear direction or may seem to arise from the marginal vein.

Species of the *P. guajava* complex have, to varying degrees, the eucamptodromous venation with ladder-like tertiary veins. This pattern is well developed in *P. guajava*, *Psidium rutidocarpum*, and usually in *P. guineense*. In *Psidium guyanense*, *Psidium nutans* and *Psidium rostratum*, this pattern may be less pronounced or lacking.

1.3.2 Twig shape

Young twigs vary from terete or compressed, to quadrangular, or 4-winged. *P. guajava* and other species of the complex often have quadrangular or 4-winged twigs.

1.3.3 Flower size

A good measure of flower size in *Psidium* that is a convenient way to compare species is the length of the style. In *Psidium* the style varies from 3 to 23 mm long. In the *P. guajava* complex lengths are usually between 10 and 15 mm. Other species complexes (*Psidium acidum* complex, *Psidium grandifolium* complex and *Psidium acutangulum* complex) have similarly large flowers but are distinct because of other characteristics. Other measures of flower size are stamen number, locule number or ovule/locule number, but these are less easily seen.

1.3.4 Calyx

The calyx structure is especially important in *Psidium*. For convenience, calyx

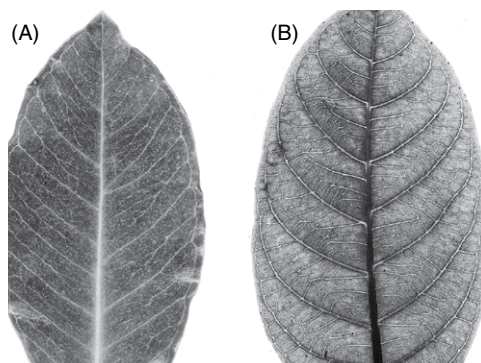


Fig. 1.2. Scanned leaves of (A) *Psidium cattleianum* and (B) *Psidium guineense*. *P. cattleianum* has brochidodromous venation with a marginal vein that connects the lateral (secondary) veins and parallels the margin; tertiary veins between the laterals are dendritic. *P. guineense* illustrates eucamptodromous venation without a clear marginal vein for most of the leaf; in this specimen the ladder-like connecting tertiary veins link between the laterals; this is the typical venation of the *P. guajava* complex. Photograph by L.R. Landrum.

morphology may be divided into two types: (i) bowl-like, with the globe of the corolla clearly visible in the closed flower bud (Fig. 1.3C); and (ii) closed, hiding the globe of the closed corolla completely or enclosing it except for a terminal pore (Fig. 1.3A and G). The amount of closure of the calyx is variable between and sometimes within species.

In *P. guajava* and its relatives the calyx is closed in the bud or has a terminal pore with no clear lobes before the flower bud opens.

1.3.5 Ovary and ovules

Psidium ovaries are 2–5(–6)-locular. In *Psidium* the number of ovules per locule

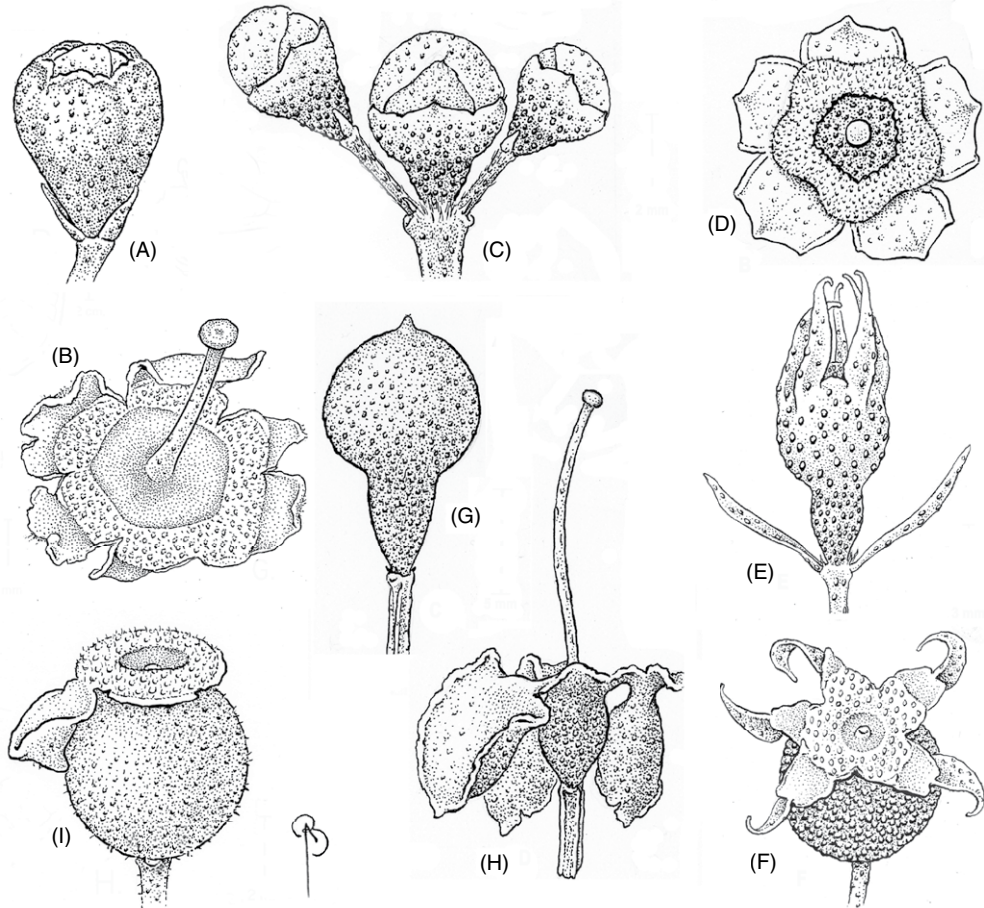


Fig. 1.3. *Psidium* flowers before and after anthesis. *Psidium cattleianum*: (A) closed bud before anthesis with apical pore; (B) apical view of flower after anthesis showing tears in staminal ring. *Psidium occidentale*: (C) 3-flowered dichasium with closed buds; (D) view from above after anthesis, tears forming between lobes but not penetrating the staminal ring. *Psidium appendiculatum*: (E) a nearly closed calyx before anthesis with a flange-like apical appendage on each lobe; (F) after anthesis, tears forming between lobes penetrating the staminal ring. *Psidium acidum*: (G) bud with completely closed calyx; (H) calyx tears irregularly at anthesis, the staminal ring, not visible in this drawing, is not penetrated by tears at anthesis. *Psidium brownianum*: (I) side view of immature fruit showing persistent calyptra and no tears in staminal ring. (A, from Rossato et al. 4855, ASU; B, from Folli 4925, ASU; C, D, from the isotype Rubio and Quelal 659, ASU; E, from Proença et al. 1445, ASU; F, from Filgeiras and Lopes 2406, ASU; G, H, from Perea et al. 2098, ASU; I, from Stannard et al. H515615, ASU.) All illustrations by Bobbi Angell.

varies from as few as 3 to over 250. Numbers below 10 and more than 100 are relatively rare. The placenta often protrudes as two lamellae that form a peltate structure (Figs 1.7G and 1.13E below). The number of rows of ovules on the edge of a lamella varies from 1 to about 4. In the *P. guajava* complex, the locules are 3–5(–6), the placenta is often peltate and the ovules number 50 to about 200, except in *P. rutidocarpum* with 25–40 ovules per locule.

1.3.6 Fruits and seeds

The seeds of *Psidium* are unique among the *Myrteae* because of their dense cell structure (Landrum and Sharp, 1989; Fig. 1.1A–E). The cells of the seedcoat are elongate, with little or no lumen, are closely packed together and in a few to several layers (Fig. 1B).

The seed surface is not a smooth, shiny mosaic of non-overlapping cells as in most other genera of subtribe *Myrtinae* with hard seeds (e.g. *Calycolpus*, Fig. 1.1F and G; *Mosiera*, Fig. 1.1H and I), but rather a rough or dull surface when dry and a pulpy layer when wet. The very hard, dense seedcoat is hard to break and this characteristic may be related to fruit predators. The germinating embryo emerges via a pore in the hard seedcoat covered by a plug-like operculum (Rotman, 1976; Fig. 1.4A). The operculum is found in several other genera with hard seedcoats of the subtribe *Myrtinae* in the broad traditional sense.

In *Psidium* the number of seeds in a fruit varies from 1 to 300, but the ranges for a particular species are much smaller. The size of seeds varies from c.2.5 to 12 mm long. Seed morphology is often important. Seeds may be approximately reniform with uniformly rounded surfaces (e.g. *Psidium*

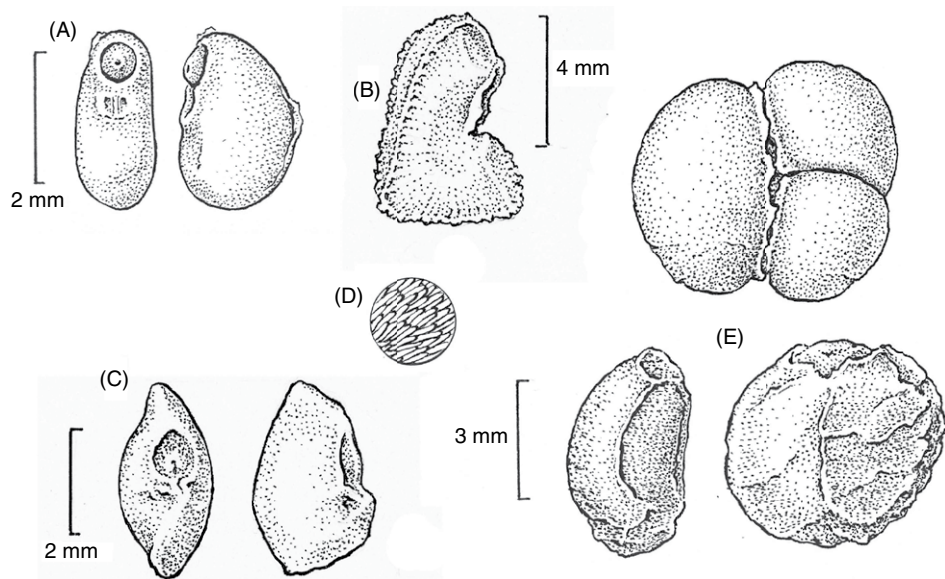


Fig. 1.4. Seeds of *Psidium*. (A) Two views of seed of *Psidium firmum* with rounded edges and generally smooth surface. (B) Angular seed of *Psidium riparium* with rough surface. (C) Two views of seed of *Psidium myrsinites* with compressed sides. (D) Close-up of cell structure of a general *Psidium* seed. (E) Top: three seeds of a fruit with rounded smooth surface towards fruit wall and flat rough surface where two seed abut. Bottom: two views of a seed showing internal rough surface. (A, from Irwin et al. 9189, MICH; B, from da Silva et al. 4200, ASU; C, from Azevedo et al. 1098, ASU; E, from Pereira s.n., ASU.) All illustrations by Bobbi Angell.

firmum, Fig. 1.4A). In this case the author believes the seeds mature in the fruit without abutting the fruit wall or other seeds. When seeds develop tightly packed within the fruit, they may have nearly flat sides where they abut other seeds and rounded sides that are adjacent to the fruit wall (e.g. *Psidium myrtoides*, Fig. 1.4E) or are isolated in the pulp of the fruit. In one mainly Amazon group (*P. acutangulum* complex) the seeds are tightly packed in the fruit and are often angular, C- or L-shaped, or irregularly shaped, with few rounded surfaces (e.g. *Psidium riparium*, Fig. 1.4B).

In *P. guajava* and its relatives, the seeds are relatively small (c.2–5 mm long) and numerous (often over 100). *P. rostratum* is an exception with seeds 8–11 mm long and few (4–12). Seeds of the complex are rounded (never angular) but sometimes have flattened sides.

1.4 Chromosome Number and Genome Size

Chromosome number and genome size are not subjects the author has worked on himself, but they have been researched by others and should be valuable in better understanding the evolution of *Psidium*. The common chromosome number in *Myrtaceae* is $2n = 22$, but polyploidy is found in *Eugenia* and *Psidium* (Rye, 1979). Chromosome numbers for *Psidium* have been reported by Atchison (1947), Costa and Forni-Martins (2006, 2007), Costa *et al.* (2008), Chakraborti *et al.* (2010), Machado (2016) and Marques *et al.* (2016). In *P. cattleianum* polyploidy seems especially common with levels up to $2n = 12x = 132$ (Machado, 2016). Genome size can be a measure of ploidy level in *Psidium* and may prove to be a valuable tool in assessing ploidy level in many species of *Psidium* (Costa *et al.*, 2008; Marques *et al.*, 2016). Based on the author's own studies, hybridization appears to be frequent in *Psidium*; hybridization coupled with polyploidy may explain some of the confusing variation in *Psidium* in such groups as the *P. grandifolium* complex (Landrum, 2005) and in *P. guineense*.

1.5 Phytochemistry and Medicinal Uses

P. guajava is known around the world for its medicinal properties and has been frequently studied for its chemical components and their effects. Pérez Gutiérrez *et al.* (2008) offer an excellent summary of these subjects complete with an illustrated appendix of the known chemical components of *P. guajava*. The lesser-known relatives of *P. guajava* have not been studied so frequently but a few recent contributions are cited here: *P. guineense* (Fernandes *et al.*, 2012); *P. acutangulum* (Wen *et al.*, 2011; Houël *et al.*, 2015); *P. friedrichsthalianum* (Flores *et al.*, 2013); and *P. cattleianum* (Medina *et al.*, 2011). Further studies of the medicinal potential of other *Psidium* species should prove rewarding. Essential oils are the most frequently studied compounds in *Psidium*. Commonly several essential oils are found in a single individual, but a few will be much more abundant than the others. Among the more common dominant essential oils in *Psidium* are α -pinene, α -selinene, γ -selinene, 1,8-cineole, β -pinene, β -caryophyllene, β -bisabolene and *p*-cymene (Tucker *et al.*, 1995; Silva *et al.*, 2003). There seems to be considerable variation within species as to which oils dominate and whether or not essential oils will be taxonomically important is still unclear.

Flavonoid chemistry has proved helpful in distinguishing between *P. guajava*, on the one hand (myricetin absent), and *P. guineense* (and its suspected hybrid with *P. guajava*), on the other (myricetin present) (Landrum *et al.*, 1995). Flavonoid chemistry may prove useful in other studies of hybridization.

1.6 What are the Closest Relatives of *Psidium guajava*?

Knowing which of the 60 or more species of *Psidium* are the closest relatives of *P. guajava* would be useful in deducing where *P. guajava* originated and what species might provide useful genetic materials for

the improvement of the species. As a working hypothesis, the present author proposes that six species belong to the *P. guajava* complex: *P. guajava*, *P. guineense*, *P. guyanense* Pers., *P. nutans* O. Berg, *P. rostratum* McVaugh and *Psidium rutidocarpum* Ruiz & Pav. This analysis will be based mainly on morphology, but it is worth noting that in a molecular phylogenetic study of *Mosiera*, including 12 species of *Psidium*, Salywon (2003) found that the closest relative of *P. guajava* to be *P. guineense*. He found *P. grandifolium* DC. to be sister to the *P. guajava*–*P. guineense* clade. Other species of what the present author considers to be members of the *P. guajava* complex were not included. Salywon (2003) used internal transcribed spacer (ITS) sequences only but his study has been the one to include the most species of *Psidium* so far.

1.7 Method for Development Key to Species Complexes

Taxonomic studies often proceed slowly and that has been the case with the study of *Psidium*. For each species, a description has been prepared in a standardized format that includes vegetative and reproductive features and examination of multiple specimens, usually 20 to 100 or more. In a few cases species are known from one or a few collections only. Unfortunately, these descriptions were sometimes written years apart from each other. After descriptions for the great majority of the mainland species (but not species restricted to Caribbean islands) had been completed, they were checked for consistency. Concurrently a database of characters was constructed using the descriptions. This allowed for the efficient comparison of all species or subgroups of species. Usually potential groups of species were perceived without using the character database, but with the database it was possible to find characters that supported these taxonomic concepts.

It is worth mentioning that the important values when comparing species are the ranges of characters rather than averages. This key is not meant to be useful in the

identification of species. It does not use some of the most easily observable characters (e.g. indumentum density, degree of calyx closure) because these vary across more than one complex. For identification it will be better to use regional keys.

1.8 Key to the Species Complexes of *Psidium*

1. Flowers large: style usually 10–15 mm long (shorter in *P. grandifolium* complex); stamens 200–800; ovary locules usually 3–5; ovules per locule usually 20–200; calyx closed in most species (open in some species of *P. grandifolium* and *P. acutangulum* complexes); young twigs frequently 4-winged to quadrangular.

2. Leaves brochidodromous, with a clear marginal vein from the base to the apex.

3. Seeds rounded or with some flat sides; southern Mexico to Peru including upper Amazon basin (some species cultivated); locules usually 3–5; anthers often with a few to several co-equal glands; twigs always 4-winged; peduncle sometimes 4-winged; calyx always closed ***P. acidum* complex:** *P. acidum*, *P. friedrichsthalianum*, *Psidium guayaquilense* and *Psidium montanum*.

3'. Seed angular; mainly Amazon basin (one species in Paraná river basin); locules usually 2–4; anthers with a terminal gland and often with smaller gland below; twigs 4-angled or terete; peduncle not winged; calyx open in some species ***P. acutangulum* complex:** *P. acutangulum*, *Psidium densicomum*, *Psidium kennedyanum*, *Psidium maribense*, *P. riparium* and *Psidium striatum*.

2'. Leaves eucamptodromous (entirely without a clear marginal vein), or eucamptodromous proximally and brochidodromous distally (with a clear marginal vein for part of the leaf).

4. Placenta barely protruding into locule; locule walls sometimes incomplete; calyx open or with a terminal pore in the

bud (rarely closed); anthers up to about 1 mm long; seeds mostly less than 85, 3–5(–6) mm long; tertiary veins connecting lateral veins in a dendritic pattern; shrubs and subshrubs of open areas (campo, cerrado, savannahs)

***P. grandifolium* complex:** *Psidium australe*, *P. grandifolium*, *Psidium missionum*, *Psidium ratterianum* and *Psidium suffruticosum*.

4'. Placenta protruding into locules as a peltate structure; locule walls complete; calyx closed or with a terminal pore in the bud; anthers often over 1 mm long; seeds sometimes few but often over 100, 2.5–5(–11) mm long; tertiary veins commonly connecting lateral veins in a ladder-like pattern, less often in a dendritic pattern; shrubs and trees of forested areas, sometimes in riparian or disturbed habitats ***P. guajava* complex:** *P. guajava*, *P. guineense*, *P. guyanense*, *P. nutans*, *P. rostratum* and *P. rutidocarpum*.

1'. Flowers small; style usually 3–8 mm long; stamens usually less than 200; ovary locules usually 2–3; ovules per locule usually 3–50; calyx closed or open and bowl-like; young twigs terete to compressed (not known to be 4-winged or quadrangular).

5. Flowers cauliflorous; eastern Bahia and Espirito Santo, Brazil ***Psidium cauliflorum* complex:** *P. cauliflorum* and *Psidium grazielae*.

5'. Flowers not cauliflorous; widespread.

6. Calyx with apical appendages (not always in *P. oligospermum*), appearing closed or nearly so in bud, tearing into nearly regular lobes at anthesis (or usually irregularly in *P. oligospermum*) ***P. oligospermum* complex:** *Psidium appendiculatum*, *Psidium glaziovianum*, *P. oligospermum* and *Psidium schenckianum*.

6'. Calyx without apical appendages, open or closed in bud.

7. Shrubs and subshrubs of open areas (campo, cerrado, savannahs); calyx open ***Psidium salutare* complex:** *Psidium laruotteanum* and *P. salutare*.

7'. Shrubs or trees of forests and open habitats; calyx open or closed.

8. Andean species with small flowers (styles 3–6 mm long); dichasial inflorescences common (these sometimes aggregate into panicles); calyx open

***Psidium pedicellatum* complex:** *Psidium fulvum*, *P. pedicellatum* and *Psidium occidentale*.

8'. Species of eastern South America (mainly Brazil) with small or large flowers; dichasial inflorescence occasional; calyx open or closed. Miscellaneous species without clear affinities.

1.9 Key to Species of *Psidium guajava* Complex

1. Lateral veins usually 12–20 pairs; tertiary veins clearly ladder-like; leaves frequently more than 2.6 times as long as wide.

2. Leaves usually 3–4 times as long as wide, narrowly lanceolate-elliptic, tapering from mid-leaf or below, with an acuminate apex; inner surface of calyx densely covered with reddish brown or whitish hairs; immature fruit with a few longitudinal ridges; ovules per locule up to about 40; endemic to eastern Peru; not cultivated ***P. rutidocarpum*.**

2'. Leaves usually less than 3 times as long as wide, mostly elliptic-oblong, not tapering from below mid-leaf, usually with an acute to obtuse apex; inner surface of calyx glabrous to pubescent, the hairs whitish; immature fruit smooth; ovules per locule usually more than 90; widespread in subtropical and tropical regions; frequently cultivated ***P. guajava*.**

1'. Lateral veins usually 4–10 pairs; tertiary veins ladder-like or dendritic; leaves usually less than 2.6 times as long as wide.

3. Seeds 4–12, 8–11 mm long; closed calyx often with a rostrate apex; ovules per locule up to c.26; stamens 500 or more; anthers 0.6–1 mm long, with 0 or 1 gland; endemic to north-western

Peru and western Ecuador

***P. rostratum*.**

3'. Seeds 27–300, 3–5 mm long; closed calyx without a rostrate apex; ovules per locule 50 or more; stamens up to c.400; anthers 1–3 mm long, usually with a few to several glands; widespread species.

4. Young growth hirtellous, the hairs mainly less than 0.1 mm long; closed bud often with an apical pore clearly exposing a portion of the corolla; leaves elliptic, the apex acute to acuminate; eastern Amazon basin ***P. guyanense*.**

4'. Young growth glabrous to pubescent, the hairs mainly over 0.5 mm long; closed bud normally without an open apical pore exposing the corolla; leaves elliptic-oblong, elliptic or obovate, the apex obtuse, rounded or acute; widespread.

5. Leaves, twigs and flowers usually abundantly pubescent; tertiary veins usually predominantly ladder-like; calyx closed completely or nearly closed and with 5 minute lobes at the apex; disturbed habitats or occasionally cultivated

***P. guineense*.**

5'. Leaves, twigs and flowers glabrous or very sparsely pubescent; tertiary veins often predominantly reticulate, but ladder-like veins common; calyx nearly closed and with 5 minute lobes at the apex; habitats frequently wet

***P. nutans*.**

1.10 *Psidium guajava* L., Sp. Pl. 470.

1753. TYPE: 'Habitat in India', Cultivated Plant from Hortus Cliffortianus (LECTOTYPE: BM-628598)

George Clifford was governor of the Dutch East India Company and hired Carl Linnaeus to describe plants growing in his garden in Bennebroek, Netherlands. Clifford and Linnaeus probably thought that *P. guajava* was native to the East Indies, rather than America.

P. guajava has been described as a 'new' species several times. Some of the more commonly found synonyms are listed below. A more complete list with citations can be found in Landrum (2017).

- *Psidium cujavus* L.
- *Psidium pomiferum* L.
- *Psidium pyrifera* L.
- *Psidium cujavillus* Burm.
- *Psidium angustifolium* Lamarck
- *Psidium sapidissimum* L.
- *Psidium pumilum* Vahl
- *Psidium aromaticum* Blanco
- *Psidium fragrans* Macfad.

SHRUB or TREE up to c.12 m high, subglabrous to densely appressed pubescent on young growth and lower leaf surfaces, the trunk smooth, light brown to light grey-green, with large flaky scales; *hairs* whitish, yellowish or silvery, up to c.0.7 mm long, erect or appressed; *young twigs* quadrangular, slightly to strongly winged, often sulcate (at least when dry), densely to moderately appressed pubescent, the older twigs at first scaly with longitudinal striations or fibres, eventually smooth with irregular scales falling as patches. LEAVES elliptic, oblong, elliptic-oblong, elliptic-obovate or lanceolate, 4.5–14 cm long, 2.4–7.5 cm wide, 1.6–4 times as long as wide, densely to sparsely appressed pubescent below, subglabrous except for puberulent midvein above; *apex* acute, acuminate, to rounded; *base* rounded to slightly cordate; *petiole* 2–5 mm long, 1–2 mm thick, channelled, densely pubescent to subglabrous; *venation* brochidodromous distally to eucamptodromous proximally, the midvein impressed above, prominent below, the lateral veins 9–22 prominent pairs, ascending at angle of c.45°, nearly straight, curving towards apex near the margin and connecting with the next lateral, the marginal vein not clearly present or arching between the laterals, the tertiary veins connecting the laterals in a ladder-like to reticulate pattern; *blades* coriaceous to submembranous, drying yellow-green, grey-green, to dark reddish brown. FLOWER BUDS subfusiform to pyriform, 9–14 mm long, sometimes strongly constricted near the midpoint, the hypanthium

narrowly campanulate, barrel-shaped or fusiform, 4–6 mm long, the distal portion of bud more or less ovoid, sometimes strongly so with a conical apex, 4.5–9.5 mm long; *indumentum pattern of buds* with peduncles, hypanthium and bracteoles sparsely to moderately appressed pubescent, the calyx without glabrous to sparsely pubescent (usually less densely covered than that hypanthium), the calyx within glabrous or densely pubescent, the petals, disk and style glabrous; *peduncles* 1–3-flowered, 1–3.5 cm long, 1–1.5 mm thick, terete; *bracteoles* linear to narrowly triangular, 2–5 mm long. CALYX closed, tearing irregularly as the bud opens, persisting or falling in c.3 parts; *petals* obovate to elliptic, 13–22 mm long; *disk* 4–6 mm across; *stamens* 280–720, 7–15 mm long;

anthers 0.7–1 mm long, with 1–7(–10) glands; *style* 10–15 mm long; *ovary* 3–6-locular; *ovules* 90–180 per locule, multiseriate. FRUIT globose to pyriform, 2–6(–8) cm long, green to yellow without, with pink, yellow or white flesh, aromatic; *seeds* numerous, subreniform, 3–4 mm long, more or less smooth, the seedcoat c.0.25 mm thick. $2n = 22, 44$ (Figs 1.5 and 1.6A).

PHENOLOGY. Flowering mainly in spring months; fruiting throughout year but mainly in summer months.

HABITAT AND DISTRIBUTION. Disturbed areas such as roadsides, pastures and frequently cultivated, from near sea level to 1000 m. Widely distributed as a cultivated and

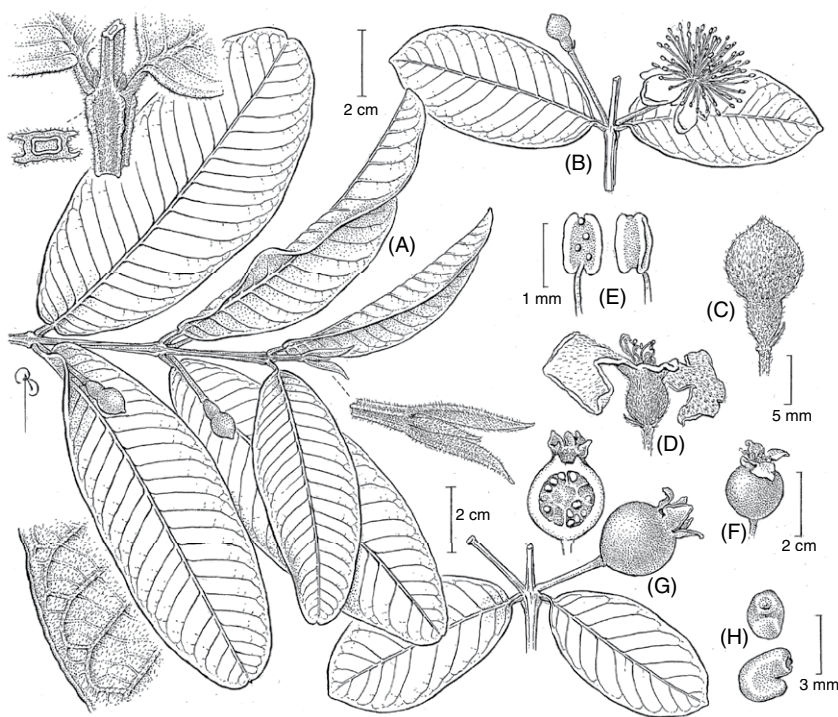


Fig. 1.5. *Psidium guajava*. (A) Branch with flower buds, including close-ups of node showing wings on twigs (upper left) and growing tip with two decussate pairs of immature leaves (right), and ladder-like tertiary veins (lower left). (B) Node with open flower and closed bud. (C) Closed bud with one persistent bracteole. (D) Flower after anthesis with irregularly torn calyx. (E) Two views of anther with multiple glands. (F) Fruit. (G) Node with fruit attached and longitudinal section of fruit showing seeds. (H) Two views of a seed. (A, from fresh material from Tempe, Arizona, USA, unknown origin; B, E, from *Sanders 8615*, ASU0004830; C, D, F, from *Landrum 6301*, ASU0004836; G, H, from *Landrum 6343*, ASU0004869.) All illustrations by Bobbi Angell.



Fig. 1.6. (A) *Psidium guajava* and (B) *Psidium rutidocarpum*. (A) Cultivated plant from Tempe, Arizona, USA (photograph by L.R. Landrum). (B) Wild-growing plant from Estación Biológica Huampal, Parque Nacional Yanachaga-Chemillen, Oxapampa, Peru (photograph by Rocío Rojas).

escaped-weedy species in tropical and subtropical regions around the world.

COMMON NAMES. Goiaba (Portuguese); guayaba (Spanish); guava (English); gobaya (French Guiana); bayabas (Philippines).

DISTINGUISHING FEATURES. Calyx closed in flower bud or open only as a terminal pore, tearing irregularly as the bud opens, usually in 2 or 3 parts; lateral veins usually more than 10 pairs; hairs on lower leaf surface appressed, whitish or silvery.

P. guajava is frequently confused with similar *P. guineense*; they have been hypothesized to hybridize (Landrum *et al.*, 1995). They are contrasted in the key below.

1. Lateral veins usually 9–22 pairs; young twigs quadrangular, more or less winged; indumentum of lower leaf surface appressed, whitish, yellowish or silvery; calyx usually tearing into 2 or 3 parts; anthers 0.7–1 mm long, usually with less than 10 glands *P. guajava*.

1'. Lateral veins 5–10 pairs; young twigs more or less terete or compressed (some vigorous shoots sometimes 4-winged); indumentum of lower leaf surface more or less erect, reddish brown, or less often appressed, whitish or greyish; calyx usually tearing into 5 parts; anthers 1–3 mm long, often with more than 10 glands *P. guineense*.

The origin of cultivated *P. guajava* is unknown, but various interesting clues exist. The original habitat may have been riparian areas with periodic drought because roadsides with occasional abundant water, and disturbed areas, such as pastures, are where the species thrives presently.

The earliest archaeological remains known to the author that are thought to be of *P. guajava* come from two South American sites. The oldest is from Teotônio, Rondônia, Brazil (5000–9000 cal. BP), a locality especially good for fishing along the Madeira River (a tributary of the Amazon River) with evidence of human habitation as early as 9000 years ago. Evidence of other edible plants includes remains of squash (*Cucurbita* L. sp.), beans (*Phaseolus vulgaris* L.), manioc (*Manihot esculenta* Cranz) and pequiá (*Caryocar* L. sp.) (Watling *et al.*, 2018). The second site is Caral, Supe River valley, Peru along a river valley of arid coastal Peru and may have been cultivated there as early as 4000 years ago along with plants such as squash, beans, camote (*Ipomoea batatas* (L.) Lam.) and cotton (*Gossypium barbadense* L.), but not maize (*Zea mays* L.) (Shady Solis *et al.*, 2001). These two South American sites are quite different in climate and separated by the Andes mountain range, but geographically separated by only 1500 km. So, for the present, this part of South America seems like a likely area of origin for cultivated *P. guajava*.

P. rutidocarpum, an endemic species of eastern central Peru, appears to be a close relative of *P. guajava*. It lives between these two archaeological sites, which lends support to the hypothesis that this region gave rise to cultivated *P. guajava*.

In Central America and Mexico, the earliest archaeological find of *P. guajava* is about 2000 years old in the Tehuacán Valley of Mexico (Smith, 1965). The earliest records of peanut (*Arachis hypogaea* L., another

South American cultivated plant) in Mexico are also from the Tehuacán Valley and of the same approximate age (Smith, 1965).

By the time of European contact, *P. guajava* was widely cultivated in the Caribbean region and various cultivars had been selected according to Fernández de Oviedo y Valdez (1851, vol. 1, p. 304) who wrote his account in the early 1500s.

It is interesting that ‘goiaba’ is the common name frequently used for this species in Brazil, a variant of ‘guayaba’ reported by Fernández de Oviedo y Valdez (1851) and the name frequently used in Spanish-speaking countries. Other species of *Psidium* in Brazil are usually called ‘araçá’ (Legrand and Klein, 1977), a name from Guarani language. So, it is possible that *P. guajava* is a relatively recent arrival in much of Brazil.

In conclusion, *P. guajava* likely originated in South America because the large majority of *Psidium* species live there.

Based on archaeological evidence and the related species *P. rutidocarpum*, Peru and the western Brazilian Amazon are hypothesized as being its area of domestication.

1.11 Gallery of *Psidium* Species

Several species of *Psidium* have been mentioned in this chapter as close relatives of *P. guajava* or as cultivated species of other complexes. Some are frequently cultivated and may be of interest to readers of this book. Drawings and/or photographic images are provided for the following species: *P. guajava* (Figs 1.5 and 1.6A), *P. rutidocarpum* (Fig. 1.6B), *P. guineense* (Figs 1.7 and 1.8) and *P. rostratum* (Fig. 1.9), all of the *P. guajava* complex. Cultivated species of other complexes are: *P. acidum* (Figs 1.10 and 1.11), *P. friedrichsthalianum* (Fig. 1.12) and *P. cattleianum* (Figs 1.13 and 1.14).

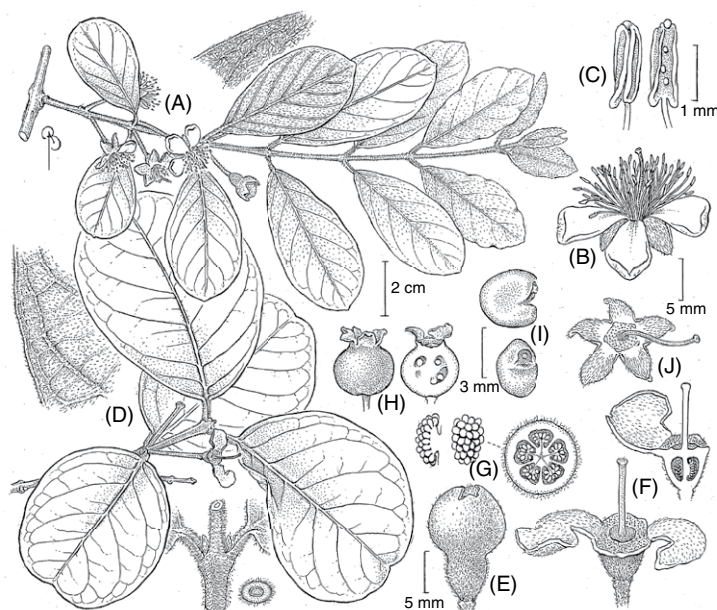


Fig. 1.7. *Psidium guineense*. (A) Branch with flowers and flower bud; detail of lower leaf surface (form with appressed hairs on lower leaf surface). (B) Open flower. (C) Anthers with glands. (D) Branch with old flower; detail of lower leaf surface and ladder-like tertiary veins (form with erect spreading hairs). (E) Closed bud just beginning to open. (F) Flowers after anthesis with irregularly opening calyx. (G) Cross section of ovary showing 5 locules; detail of placentation and ovules. (H) Fruit, whole and sectioned. (I) Two views of seed. (J) Flower after anthesis showing calyx tearing in 5 nearly equal lobes. (A, B, from Landrum 8804, ASU0008042; C, from Landrum 5676, ASU0004988; D–I, from fresh material grown from seeds from Chiapas, Mexico; J, from Nee 39697, ASU0007532.) All illustrations by Bobbi Angell.

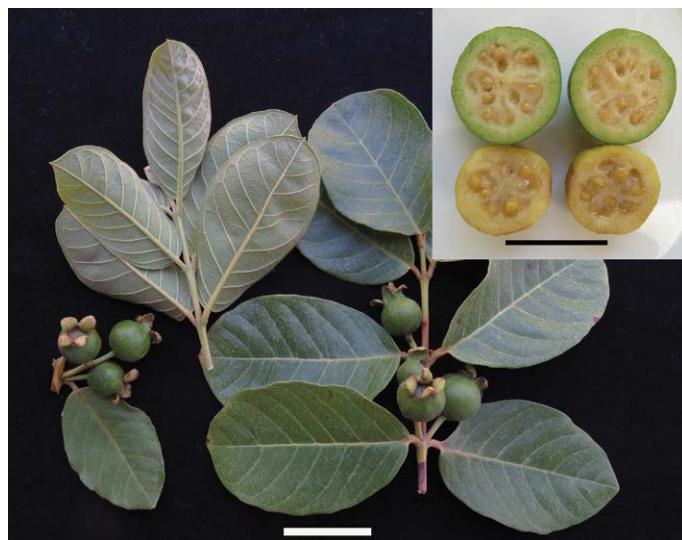


Fig. 1.8. *Psidium guineense*. Plant cultivated at Tempe, Arizona, USA; grown from seeds collected in Chiapas, Mexico. Bars = 3 cm. Photographs by L.R. Landrum.

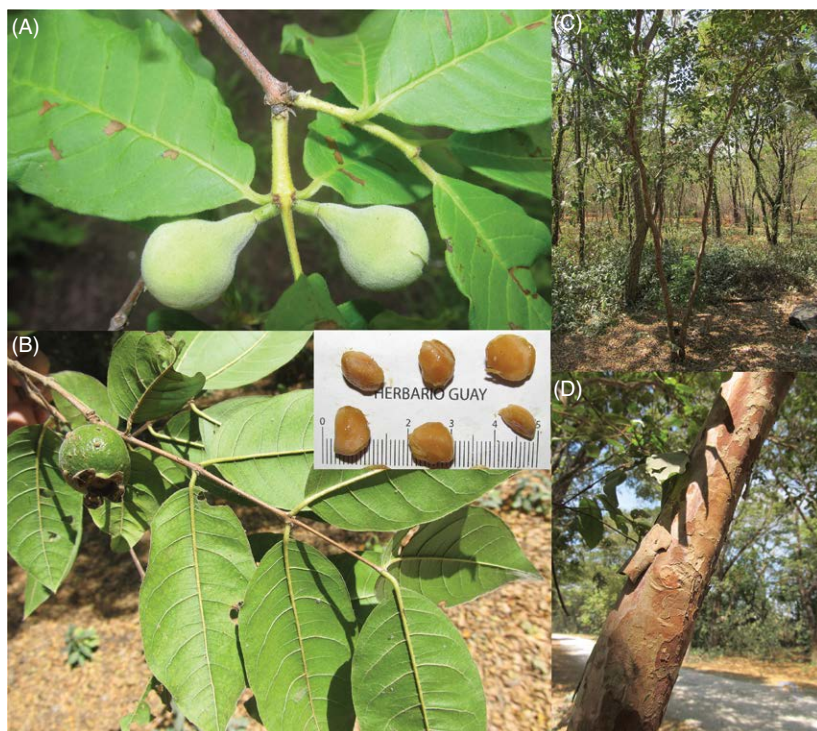


Fig. 1.9. *Psidium rostratum*. (A) Flower buds. (B) Twig with fruit and insert showing seeds. (C) Trees. (D) Bark of trunk. All photos of plants growing wild. (A, *Cornejo 8777*, Cerro Seco Biological Reserve, Manabi, Ecuador; B–D, *Cornejo 8829*, Bosque Protector Cerro Blanco, Guayas, Ecuador.) All photographs by X. Cornejo.

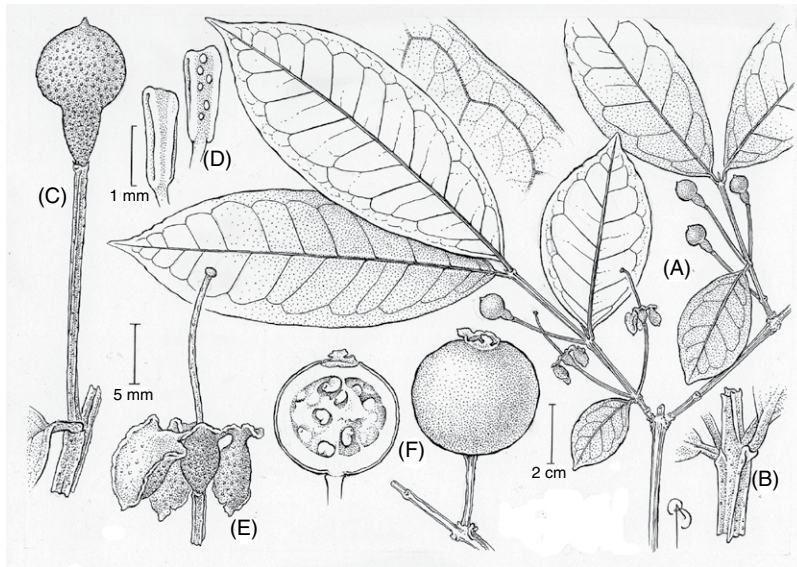


Fig. 1.10. *Psidium acidum*. (A) Flowering branch. (B) Detail of winged twig. (C) Closed flower bud. (D) Anthers with multiple glands. (E) Flower after anthesis. (F) Fruit, whole and sectioned. (A–E, from Perea *et al.* 2098, ASU0005139; F, from Ceron 3634, ASU0005129.) All illustrations by Bobbi Angell.



Fig. 1.11. *Psidium acidum*. (A) Habit. (B) Bark. (C) Fruits, with insert of fruit showing persistent calyx. (D) Leaves and winged twig. (All from Orejuela & E. Trujillo 3004, Centro Demostrativo Agroforestal Guacayaco, Piamonte, Cauca, Colombia.) All photographs by Edwin Trujillo.



Fig. 1.12. *Psidium friedrichsthalianum*. (A) Flower branches with fruits. (B) Open flower. (C) Fruits. (A, C, cultivated plant (L.R. Landrum 6555) from Heredia, Santo Domingo, Costa Rica; B, cultivated plant from Tempe, Arizona, USA.) All photographs by L.R. Landrum.

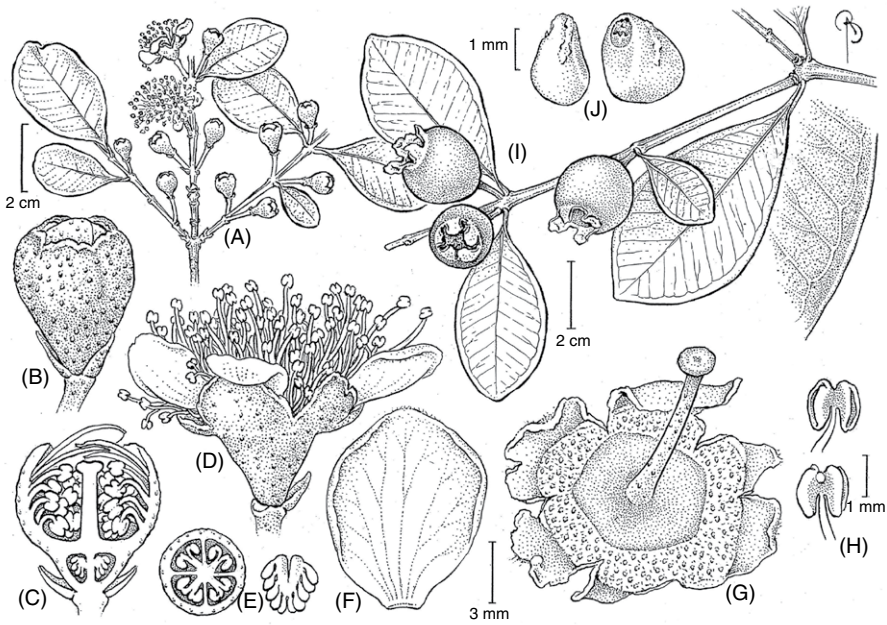


Fig. 1.13. *Psidium cattleianum*. (A) Twig at beginning of anthesis. (B) Flower bud. (C) Longitudinal section of flower bud. (D) Opening flower. (E) Cross-section of ovary and extracted placenta with ovules. (F) Petal. (G) Apical view of flower after anthesis showing tears in calyx cutting into staminal ring. (H) Two views of stamen and anther with single terminal gland. (I) Fruiting twig. (J) Seeds. (A–C, from Rossato et al. 4855, ASU0006118; D, from photograph of live specimen; E–H, from Folli 4925, ASU0006103; I, from Baitello 414, ASU0006091; J, from Carvalho et al. 6859, ASU0006121.) All illustrations by Bobbi Angell.



Fig. 1.14. *Psidium cattleianum*. (A) Branches with young fruits, from a cultivated plant at Universidade Federal de Santa Catarina, Florianópolis, Brazil (photograph by Marla Ibrahim). (B–E) Flower buds, open flower and young fruit at different stages of development, from a cultivated plant at Tempe, Arizona, USA (photographs by L.R. Landrum). (F) Plant in fruit growing wild at Kōke'e State Park, Kauai, Hawaii, USA (photograph by D. Wolkis).

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