PASSIFLORACEAE

Christian Feuillet and P. Acevedo-Rodríguez

A predominantly tropical family with few species reaching warm-temperate regions, of ~15–17 genera and 850 species of tendrilled lianas or vines, or sometimes shrubs, small trees, or annuals with a perennial rootstock or a fleshy caudex. Represented in the Neotropics by 4 genera and ~600 species, occupying diverse habitats, from savanna to flooded forests, but most abundant in tropical rainforests on terra firme. Most species occur at low to middle elevations, but some grow above the tree line on Andean slopes.

Diagnostics: Distinguished by the flowers with an extrastaminal corona and usually a gynophore, and by the common presence of petiolar nectaries. Sterile collections of Passifloraceae may be confused with members of Cucurbitaceae as both families may have simple, alternate leaves, axillary tendrils, and petiolar nectaries. However, Passifloraceae is differentiated by the presence of stipules, unbranched axillary tendrils (trifid in Dilkea) [vs. exstipulate and axillary-lateral tendrils (forming a 90º angle with the petiole) that are commonly branched in Cucurbitaceae]. Also, resembles Vitaceae but tendrils and inflorescence in this family are opposite to the leaves, not axillary.

General Characters

1. STEMS. Woody or herbaceous depending on the species. Woody, mature stems are usually 1–2 cm in diameter, although in cultivated Passiflora they may reach 8 cm or more in diameter, and up to 25 m in length. Stems are cylindrical, trigonous, trilobed, or pentagonal in cross section (Figure 191), and usually deeply furrowed but never flattened. In the Neotropics, stems of climbing Passifloraceae have abundant wide ray tissue within the xylem (Figure 191A, B, E), and most species have phloem wedges formed by the
Figure 191. Cross sections of stems of climbing *Passiflora*. A. *Passiflora* sp. with nearly cylindrical stems and wide rays and phloem wedges. B. *P. edulis* with cylindrical stems, shallow phloem wedges and wide rays. C. *Passiflora cf. coccinea* with trigonous stems, phloem wedges, and neoformations. D. *P. laurifolia* with angular stem, with regular anatomy and narrow rays. E. *P. actinia* with pentagonal stems, wide rays, and shallow phloem wedges. F. *P. multiflora* with obtusely pentagonal stems and dispersed xylem. Photos by P. Acevedo.
differential production of xylem and phloem in regions of the cambium. The cambium can remain a continuous ring (Figure 191B) or become discontinuous and lined by wide rays that demarcate the phloem from the surrounding xylem (Figure 191A, C). Fissured stems where the xylem becomes dispersed by parenchyma proliferation is known only for *Passiflora multiflora* (Figure 191F). Neoformation of vascular bundles in the bark, is here documented for a collection of *Passiflora cf. coccinea* Aubl. from Bolivia (Figure 191C). Included phloem was reported for the African *Adenia cissampeloides* Harms (Obaton 1960).

2. EXUDATES. Odorless and colorless, commonly not noticeable.

3. CLIMBING MECHANISMS. For the most part, climbing Passifloraceae have tendrils that are homologous to the pedicel of the distal flower in a dichasium. These are commonly simple and helicoidal (Figure 192A), but circinate or hook shaped in *Ancistrothyrsus*, trifid in *Dilkea*, and sometimes forming an adhesive pad in some *Passiflora*. *Mitostemma* commonly are scrambling shrubs although sometimes it may bear helicoidal tendrils.

4. LEAVES. Alternate, simple, lobed or seldom compound, quite variable in shape and size, entire or sometimes with serrate margins, venation pinnate, palmate or pedate, often with laminar nectaries; petioles commonly with extrafloral nectaries of variable shape or size (Figure 192B, C).

5. STIPULES. Commonly small and caducous, but sometimes large and foliose.
Figure 192. A. *P. rugosissima* with simple, helicoidal tendril. B. *Passiflora* sp. with one pair of petiolar glands. C. *Passiflora* sp. with two pairs of petiolar glands. Photos: A by J. Amith; B, C by P. Acevedo.
Figure 194. Fruits in Passiflora. A. *P. cincinnata* indehiscent baccate fruit. B. *P. rubra* with tardily dehiscent capsule. C. *P. cincinnata* longitudinal section showing parietal placentation and young seeds. Photos by P. Acevedo.
6. INFLORESCENCES. Simple or rarely compound cymes, seldom a racemose arrangement of triads (e.g., *Mitostemma*), axillary, rarely terminal or cauliflorous (some *Passiflora*). The typical inflorescence is a dichasial cyme that terminates in a tendril with flowers on the second order side branches. In most species of *Passiflora*, the peduncle is lacking, and the cyme is sessile, the prophylls are displaced onto the pedicels they normally subtend, giving rise to 3-bracteate pedicels that are collateral to the tendril.

7. FLOWERS. Bisexual in the New World taxa (mostly unisexual in the Old World), with a small to large hypanthium (Figure 193A–C), sepals (3–)5(–8), petals as many as and alternating with the sepals, or seldom lacking, an extrastaminal corona of filaments in one to many rows (Figure 193B, C, F), often an operculum (membrane) within the corona and the column limiting access to the nectar, a limen (inconspicuous membrane) between the operculum and the column (in most *Passiflora*) (Figure 193C), an androgynophore commonly present and conspicuous (Figure 193C, F), (4–)5 or 8(–10) stamens and 3(–5) carpels (Figure 193A, C, D, F).

8. FRUITS. Berries (Figure 194A) or seldom capsules (Figure 194B), variable in shape, size and color, ranging from pea-sized, <0.5 cm diameter to large, obovoid thick-walled berries ~15 cm diameter, with few to many arillate seeds. The pericarp can be thick (Figure 194C) and rind like to papery and very thin. Placentation is parietal (Figure 194C).

9. Seeds. The seed are bean-shaped to laterally compressed, consisting of a large, straight embryo, embedded in an oily, fleshy endosperm. Seed coat sclerified, usually pitted or furrowed, or papyraceous. Germination when known (*Adenia, Passiflora*) is almost always epigeal.
USES

Several species of *Passiflora* from the Neotropics are widely cultivated throughout the tropics for their fruits, known as maracuja (Portuguese) or maracuyá, parcha or chinola (Spanish), which are used in the production of juice or jelly, e.g., *P. edulis* Sims, or alcoholic drinks. A few other species are cultivated for their pharmacological properties. In Brazil, a tea of *Passiflora* is believed to help releasing stress. Several species of *Passiflora* are cultivated for their beautiful flowers in tropical gardens.

Key to the genera of climbing Passifloraceae

1. Androgynophore conspicuous, ≥ 3 mm long .................................................................2
1. Androgynophore inconspicuous, ≤ 2 mm long or lacking.............................................3
2. Flowers 4-merous, with 8 stamens; inflorescence a pedicellate compound cyme, with a distal
   circinate or hook-shaped, sometimes thickened tendril ......................1. *Ancistrothyrsus*
2. Flowers 5-merous, with 5 stamens; inflorescence mostly sessile, a simple or reduced cyme,
   with an helicoidal tendril .................................................................................4. *Passiflora*
3. Corona filaments in 2 rows, outer series white; flower with androgynophore 1–2 mm long;
   styles connate to halfway.............................................................................2. *Dilkea*
3. Corona filaments in 3 rows, outmost series orange; flower with a short gynophore instead of
   an androgynophore; styles free .................................................................3. *Mitostemma*

Woody climbers. Young stems terete. Tendrils apically swollen and sclerified (hook-shaped). Leaves alternate, simple and unlobed; petiole short, lacking nectaries; lamina margin entire, abaxially with lepidote glandular trichomes/peltate scales and/or pubescent. Inflorescences axillary, cymose; peduncles elongate, bearing two triads and a hook-like (circinate) tendril. Flowers 4-merous; hypanthium lacking; sepals 4, white; petals 4, white; corona tubular, laciniate or filamentous at margin; operculum and limen lacking; stamens 8; androgynophore very short; styles 4. Fruits capsular, ellipsoid; pericarp coriaceous; placentae 4. Seeds oblong somewhat laterally compresses, with a papyraceous coat.

**Distinctive features:** Robust, large lianas with simple, alternate leaves with lepidote or peltate scales, deciduous stipules, and circinate or hook-shaped tendrils.

**Distribution:** Two species distributed in lowlands of northern South America (Colombia to the Guianas, Brazil, Ecuador and Peru).

Shrubs, small trees, or lianas. Tendrils when present axillary and trifid at apex. Leaves simple and unlobed, margin entire; petiole with a basal pulvinus, lacking nectaries. Flowers 4-merous, lacking hypanthium, but the perianth parts separating late simulate one at first; sepals 4; petals 4; corona in 2–3 rows of filaments, the outmost longer, often sinuous, often hairy; lacking operculum and limen, androgynophore 1–2 mm long; stamens 8, inserted on the bottom of the floral cup or on a 1–2 mm long androgynophore; ovary sessile or usually on a short gynophore, styles 4, united at base. Fruits baccate, ovoid or globose, pericarp coriaceous, placentas 4, seeds few, bean-shaped, not flattened, and sarcotesta thin, neither sclerified, nor ornamented.

**Distinctive features:** Petiole with a basal pulvinus; tendrils trifid at the apex. Vegetatively, some *Dilkea* resemble *Moutabea* in the Polygalaceae which usually has spiny branches and stems with successive cambia that give rise to discontinuous concentric arcs of xylem and phloem, two characters not found in *Dilkea*.

**Distribution:** A neotropical genus of 12 species distributed in the lowlands of Panama, and Colombia to the Guianas and Amapá (Brazil) and south to Peru and Mato Grosso (Brazil). Six species are lianas with axillary tendrils or leaning shrubs with no tendrils.
*Dilkea johannensis*. A. Flowering branch. B. Portion of perianth showing petals, and corona segments. Bud with nectary, frontal, lateral, & dorsal views & longitudinal section of nectary. C. Androecium and gynoecium, with anther detail. D. Androecium and gynoecium, longitudinal section, showing placentation. Drawing courtesy of Bobbi Angell.
**MITOSTEMMA** Masters, J. Bot. 21: 33. 1883.

Lianas or scrambling shrubs. Sometimes bearing helicoidal tendrils. Leaves alternate; petiole short lacking nectaries; lamina oblong to oblong-ovate. Inflorescences terminal or axillary racemes, when axillary, sometimes reduced to 1 or 2 flowers. Flowers bisexual, 4-5-merous; floral tube reduced; sepals 4; petals 4, shorter than the sepals; corona in 3 rows, the filaments of the outmost series subterete, those of the middle series winged, and the innermost ones spatulate and distally fimbriate; operculum lacking; stamens 8 or 10, inserted on the floor of the tube, free or united at base; gynophore present; ovary 1-celled, 4 parietal placentae; styles 4, free to base. Fruits ovoid, baccate, indehiscent. Seeds not known to us.

**Distinctive features:** Inflorescences racemose; gynophore present.

**Distribution:** Three species distributed in the lowlands of French Guiana and Guyana south to Mato Grosso and Rio de Janeiro (Brazil).

**PASSIFLORA** Linnaeus, Sp. Pl. 955. 1753 (nom. cons.).
Herbaceous or woody climbers with tendrils, rarely shrubs or small trees, sometimes becoming fertile before climbing. Leaves alternate; petiole often bearing nectaries; lamina simple or compound, lobed sometimes bearing nectaries, entire to serrate at margins. Flowers axillary, sometimes cauliflorous, solitary, or in epedunculate simple cymes, with 1–2 lateral flowers and a terminal helicoidal tendril, rarely not accompanied by a tendril and in a short and dense or loose inflorescence-like hanging stem with reduced leaves. Bracts and bracteoles often verticillate on the pedicels, small to foliaceous, sometimes dissected. Flowers bisexual, 5-merous; floral cup flat to tubular; sepals 5; petals 5, sometimes wanting; corona in 1-several series of filaments, sometimes tubular; operculum present; nectar ring rarely lacking; limen sometimes lacking; stamens 5, on an androgynophore; ovary 1-celled, with 3 parietal placentae; styles 3, free or united at base. Fruits indehiscent berries in most species, rarely capsular; pericarp thin to thick, sometimes cardboard-like and breakable (subgenus Astrophea Mast.). Seeds numerous, often flat, sculptured, rarely winged, covered by a fleshy aril.

**Distinctive features:** Petioles often with large nectary glands; leaf lamina often with glandular ocellae. Flowers with showy coronas and conspicuous androgynophore.

**Distribution:** A genus of ~600 species, most of which (~550) are native in the Neotropics constituting the largest genus of climbers in this region; occurring in diverse habitats such as cerrado, savannas, forests, and along forest margins.