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## Passifloraceae

Passifloraceae Juss. ex Roussel, Fl. Calvados, ed. 2:334 (1806), 'Passifloreae', nom. cons.

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Tendrillate climbers, less often erect herbs, shrubs, or small trees without tendrils, commonly with cyanogenic compounds; stems woody, often with anomalous secondary growth, or herbaceous, sometimes forming annual shoots from perennial rootstocks or underground runners; nodes trilacunar; supra-axillary accessory buds usually present; tendrils simple, or bi- or trifid near apex. Leaves alternate, often with nectaries on petiole, blade, or stipules; blade variable, unlobed, lobed or seldom compound; venation pinnate, palmate or pedate; stipules usually present, often small and caducous, sometimes foliose. Inflorescences axillary, usually with cymose (seldom racemose) arrangements of triads, rarely on cauline axis; rarely flowers solitary. Flowers usually perfect, regular, perigynous, usually with a saucer-shaped to tubular floral cup, commonly with a gynophore or an androgynophore, rarely with a sessile ovary, or rarely hypogynous; sepals (3–)5(–8), imbricate, free or partially united; petals as many as and alternating with the sepals, imbricate, free or shortly united, or seldom 0; extrastaminal corona of threads, tubercles or scales, in 1–many rows; nectary extrastaminal, either a ring or five discrete antesepalous nectar glands or a nectariferous ring often concealed by an operculum and limen; stamens (4)5 or 8(–numerous), sometimes borne by an androgynophore; carpels (2)3(–5), forming a unilocular ovary; stylodia solid or grooved, mostly distinct or basally fused, rarely style simple; stigmas capitate to discoid and papillate, or lacinate; ovules  $\pm$  numerous or rarely (*Dilkea*) few, usually anatropous, rarely orthotropous, mostly on a long funiculus, bitegmic and crassinucellar. Fruit a capsule or often a berry, rarely fleshy with irregular, apical dehiscence; pericarp thick and rind-like to papery and very thin; seeds few to many, often compressed, with a bony testa, often pitted or ridged, rarely winged, surrounded by an apical, pulpy aril; embryo large, straight; endosperm fleshy. Germination

is almost always epigeal (*Adenia*, *Passiflora*).  $x = 6, 9, 12$ .

The family contains 17 genera and 700–750 species. Its distribution is essentially pantropical, with a few temperate species in North and South America, southern China, and New Zealand.

**VEGETATIVE MORPHOLOGY.** The family comprises erect, non-climbing woody plants and subligneous to herbaceous tendril-climbers. An accessory (serial) bud on top of the axillary bud is generally present (Figs. 96, 98B). In the tendrillate genera, the axillary bud grows into a cymose inflorescence with the tendril. If the accessory bud develops, it will grow into a vegetative or an inflorescence-bearing shoot. After or even during flowering, the apex of the inflorescence-bearing shoots can resume vegetative growth, as in *Passiflora balbis*, *P. macrophylla* (subg. *Astrophea*), *P. coriacea* (subg. *Decaloba*), *P. glandulosa* (subg. *Passiflora*), and others. In non-climbing genera, the axillary bud develops into a vegetative shoot that also bears axillary flowers or inflorescences. The accessory bud is mostly abortive, or rarely develops into a normal branch. Several species of the genus *Barteria* have hollow stems hosting ants.

The leaf blade varies greatly, from unlobed to trilobed or bilobed, and to palmately or pedately (but never pinnately) lobed or compound. The stipules are usually small (Fig. 98B), persistent or caducous, and sometimes lacking (*Androsiphonia*, *Barteria*), but in some *Passiflora* they are large, often asymmetric or pinnately veined; sometimes the apical portion mimics in form and color an egg or a larva of a heliconiine butterfly. Heterophylly is widespread, and juvenile leaves can be quite different from those of the adult stage. For tendrils and thorns, see under Inflorescences.

Most species have extrafloral nectar glands on the apices, margins, or bases of the leaf blades, on petioles, or on stipules. They are generally functional, producing a sweet secretion, but sometimes

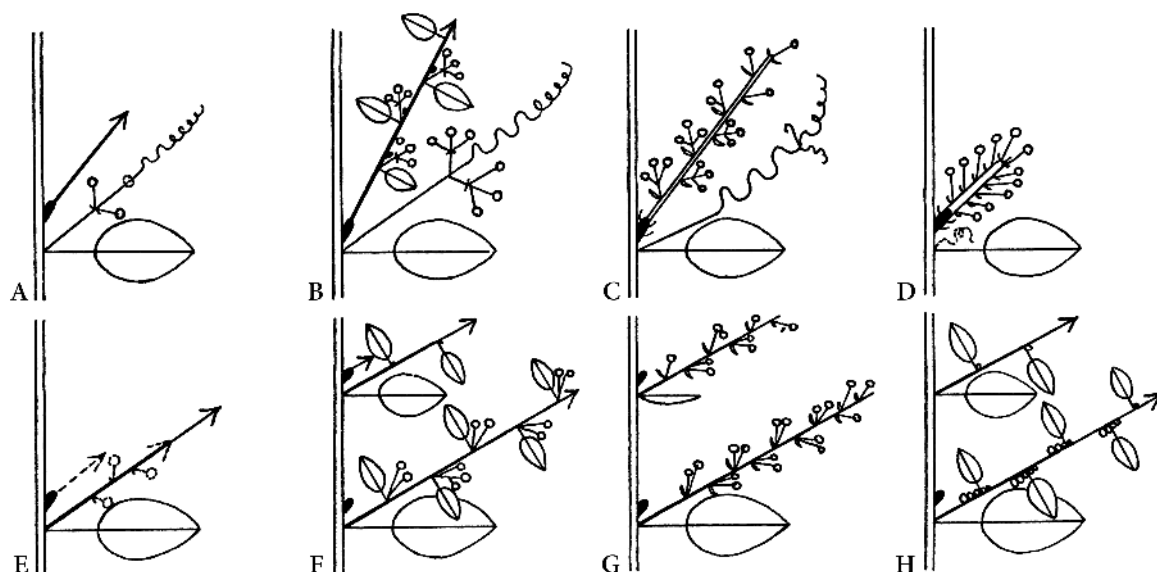


Fig. 96. Passifloraceae. Mode of ramification and position of inflorescences and tendrils; accessory bud in solid black. A Basic pattern in tendrillate Passifloraceae. B Most *Passiflora* and *Adenia*. C *Passiflora racemosa*, *P. ovalis*, *Adenia racemosa*, *A. venenata*. D *Passiflora*

*arbores*, *P. spicata*, *Dilkea*, *Adenia globosa*, *A. fasciculata*. E Basic pattern in non-tendrillate Passifloraceae. F *Paropsia*, *Paropsiopsis*, *Smeathmannia*. G *Paropsia guineensis*, *Androsiphonia*. H *Barteria*. (de Wilde 1971b)

are indurate and callous, and sometimes mimic eggs, being plump and yellow. The presence of these egg mimics has been an important element in the argument for the existence of co-evolution between *Passiflora* and the heliconiine butterflies (Gilbert 1971, 1975).

**ANATOMY.** Stomata are usually anomocytic. Calcium oxalate is present in the form of druses and simple crystals. Growth rings are only exceptionally developed. The vessel elements are almost exclusively simple, but both simple and some scalariform perforation plates occur in the free-standing arborescent genera. The imperforate tracheary elements consist of non-septate fiber-tracheids, occasionally tracheids, and libriform wood fibers, the latter commonly found in tree species of the family. Axial wood parenchyma is abundant, usually in apotracheal arrangement. In the lianaceous *Passiflora* species, besides the normal pattern of secondary thickening, three anomalous types have been observed: (1) the included phloem type, in which patches of phloem are embedded in the xylem cylinder; (2) the interrupted type, in which wedge-shaped sections of xylem alternate around the stem with similarly shaped portions of phloem; and (3) the dispersed type, in which irregularly

shaped strands of xylem and phloem are associated with fragments of vascular cambium spread throughout a parenchymatous matrix (Ayensu and Stern 1964). The interrupted type has also been observed in *Crossostemma*, and anomalous growth may be more widespread among lianaceous species; to date, only 44 species of 9 genera have been studied.

**INFLORESCENCES.** The typical inflorescence in the tendrillate genera is an axillary dichasium, and the tendril is the modified pedicel of the central flower (Figs. 96A, B, 98A; see Cusset 1968). The apexes of the tendrils are sometimes trifid, as in *Dilkea*, some *Adenia*, and rarely in *Passiflora*, and may be provided with adhesive tips (de Wilde 1971a). In most species of *Passiflora*, the peduncle is lacking and the bracts are displaced onto the pedicels they subtend. Therefore, the inflorescence is sessile, and the pedicels are provided with three bracts (one shifted subtending bract and two prophylls), which arise collateral with the tendril in the leaf axil. In several genera, the cymes are enriched and form dichasial complexes with one or more flowers replaced by tendrils or hooks. In some *Adenia* (*A. globosa*, *A. ballyi*, and *A. spinosa*), tendrils can be transformed into thorns. 'Sterile'