

THE GENERA OF TRIBE PASSIFLOREAE (PASSIFLORACEAE), WITH SPECIAL REFERENCE TO FLOWER MORPHOLOGY

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SUMMARY

A comparison of the structure of the flowers of various genera of the tribe *Passifloraceae*—*Passifloreae* supported the view of staminodial origin of the disk.
The East African genus *Schlechterina* is kept separate from the West African genus *Crossostemma*. The genus *Efulensia* from Equatorial Africa is recognized beside the Madagascan genus *Deidamia*. Revised key to the genera of the *Passifloreae*, together with short descriptions.

INTRODUCTORY CONSIDERATIONS

I. The genus concept

For the delimitation of the genera of *Passifloraceae* flower characters as the shape of the corona and the disk, the number and position of stamens, etc. are of major importance (Harms, 1925; Killip, 1938; Hutchinson, 1967; De Wilde, 1971).

In my publication of a key to the genera of *Passifloraceae* (De Wilde, 1971) the status of two genera in the tribe *Passifloreae*, viz. *Schlechterina* and *Efulensia*, remained dubious. The genus *Schlechterina* was tentatively included in *Crossostemma*, partly on the authority of Hutchinson (1967). *Efulensia*, which was kept separate by Hutchinson, was tentatively included in *Deidamia*.

In the present study I have reached the conclusion that both *Schlechterina* and *Efulensia* deserve the status of genus, though their relationship to *Crossostemma* and *Deidamia*, resp., is closer than to the other genera.

The main differentiating characters for *Efulensia* are the 5 stamens, which are connate at base, and the absence of an extra-staminal disk; in *Deidamia* there are 5—8 free stamens and a distinct extra-staminal disk. One of the main characters of *Crossostemma* is the strongly developed intra-staminal disk which is lacking in *Schlechterina*. Harms, in his treatment of the *Passifloraceae* (1925), had approximately the same circumscription of the family as presently my tribe *Passifloreae* (De Wilde, 1971), hence tribe *Paropsieae* excluded. *Crossostemma* and *Schlechterina* were considered as separate genera, whereas *Efulensia* was treated as a section of *Deidamia*.

Hutchinson (1967) accepted a large family *Passifloraceae*, with 23 genera. Some of these, however, should be excluded from the family (*Soyauxia*, *Physena*), whereas others are clearly synonyms. Hutchinson included *Schlechterina* in *Crossostemma*, apparently only on the basis of the great resemblance in the vegetative parts, i.e. juvenile forms of both show a striking similarity in the mode of incision of the leaves. The differences in flower structure are not mentioned in his key and genus descriptions.

As to the characters advanced by Hutchinson to separate *Deidamia* and *Efulensia* in his key as well as in the descriptions of the genera, it should be observed that these are contradictory, irrelevant, and partly erroneous, as can be seen in the present article from figures, key and descriptions. Indeed, both genera are similar in leaf shape and position of glands, but still they should be kept apart on sensible characters of the flower apparently not observed by Hutchinson.

To demonstrate the facts, the flower diagram and a longitudinal section of the flower of one or two representative species of all Old World genera is depicted in figures 1—4. These figures may serve further as a help with the identification, in addition to the key.

Regarding the weight of the characters used for generic delimitation everybody can judge for himself.

It should be observed that the longitudinal sections of the flowers, and the accompanying diagrams are drawn from single specimens, regarded as illustrative for the genera concerned. The drawings of the longitudinal sections are semi-schematic, showing the optical section through the flower (except the gynoecium, which is shown in front view) and some insight in the hinder lying part of the flower; irrelevant details in this latter are omitted. In some cases only a part of the flower stipe is drawn. The flower diagrams need little explanation; they are in accordance with current use, as introduced by Eichler (1875). In the diagrams, from outside to inside, the following elements are present: one bract and 2 bracteoles (solid black); 4 or 5 imbricate sepals (hatched); (3) 4 or 5 imbricate petals (solid black); outer and, if present, inner corona (various; the small open circles represent corona threads); disk (solid black); 4—8 stamens (free or connate); gynoecium (bold black, with stigmas free or connate indicated).

2. On the origin of the disk

Little is known of the morphological origin of the corona in its broad sense in *Passifloraceae*, where in many cases it has a conspicuous complicated structure, being composed of rings of threads, annular folds, etc. Corona structures are most extensively developed in the genus *Passiflora*, with nearly four hundred species. The structure of the corona in this genus, and in some other genera of *Passifloraceae*, is discussed by Harms (1925), Killip (1938), and Puri (1948).

For *Passiflora* a subdivision of the various corona constituents, partly based on the flower biology, is proposed by various authors; see Harms (1925) and Puri (1948). According to Harms (1925) in this genus the outer corona (radii, pali), with its often showy whorls of threads, is regarded as a show apparatus to attract pollinators. The more inward situated annular parts of the corona (operculum, annulus, disk or nectary, limen, trochlea) are partly supposed to serve for the protection of the nectary.

In the other genera of *Passifloreae* the corona is usually less complicated in structure as compared to *Passiflora*, but terms as 'outer corona' or 'filamental column', 'disk' or 'annulus', 'inner corona', or 'cup', etc. are frequently used in descriptions. In these cases usually the hard-fleshy structure(s), mostly in the shape of a ring or annulus is (are) indicated as disk. A disk is found in most species. It has presumably predominantly an excretory function.

Formerly the corona was generally regarded as of staminodial origin, but already Masters (1871) and Eichler (1875) advocated the corona as being composed of emergences from the receptacle or torus, without any relation to stamens.

In two more recent publications Puri (1947, 1948) treats the floral structure and anatomy of *Passiflora*, on the basis of a number of species. Regarding the outer corona (radii, pali) and the operculum he argues convincingly (by the anatomy of the vascular supply) (Puri, 1948) that these are outgrowths from the inner side of the sepals and petals. The upper part of the receptacle (or hypanthium), from which the corona threads emerge, is shown to be of tepaloid origin. The annulus is considered as merely a folding of the receptacle, whereas the limen is interpreted to be staminodial in nature. This latter agrees with my present considerations based on the comparison of the flowers of various other Old World genera of *Passifloraceae*, with which the disk is regarded as of staminodial origin.

For *Adenia* Harms (1925, p. 477) mentions the ill-developed outer corona as being only an incised menbrane or a simple ring of threads, and the disk as composed of (4 or) 5 lingulate glands opposite the sepals; see also De Wilde (1971-bis, p. 20—23, fig. 3). Harms continues (o.c., p. 479, 480): 'Bei einigen Gattungen (*Dilkea*, *Mitostemma*, *Deidamia*, *Schlechterina*, *Passiflora octandra*) übertreffen die Stam. die Pet. an Zahl oder sind in doppelter Anzahl vorhanden; sonst sind meistens nur 5 Stam. vorhanden. Da aber bei *Machadoa**) und *Crossostemma* zwischen den 5 Stam. Spitzchen vorkommen, die sich als Staminodien deuten lassen und da diese Deutung auch für die 5 schuppenförmigen Effigurationen von *Adenia* gelten könnte, so ist das Andrözeum der *Passifloraceae* vielleicht ursprünglich diplostemon'.

From the diagrams in the present article, in fig. 3b and 4b it appears that in two genera, viz. *Efulensia* and *Crossostemma p.p.*, the disk is situated inside the whorl of stamens (intra-staminal disk); in the other genera the disk, and of course all other corona constituents, are situated outside the stamens (extra-staminal disk).

In *Crossostemma* the disk consists of two alternating whorls of 5 fleshy teeth, together forming a fleshy plate with the five alternating stamens inserted at the margin. This plate screens off the underlying chamber formed by the hypanthium; the wall of this chamber possibly has an excretory function.

In *Efulensia* only in a part of the specimens of *E. clematoides* there merely are 5 fleshy teeth inside of and alternating with the 5 stamens.

From the relative position of the stamens and the disk in the two genera mentioned above and from the position of the 5 disk-glands in *Adenia* (fig. 2a, b) it seems conclusive to accept a staminodial origin of the disk in these genera and to assume for tribe *Passifloreae* as a whole an androecium originally composed of three whorls of 5, instead of diplostemony as suggested by Harms.

Although it remains likely that in some of the genera the disk is partly derived from the torus, it may be assumed that the stamens, and in several cases the disk, in both of which the basic number (4 or) 5 is retained, are derived from the inner three whorls of stamens (or the predecessors of these) in the flowers of the ancestors. This in contradistinction to the outer corona with its infinite number of laciniae or threads in which this basic number 5 is not recognizable and of which a possible relation to stamens is obscure. The reasoning is in full agreement with the findings of Puri (1948) as mentioned above, in which the limen of *Passiflora* (which is homologous with the disk in other genera) is found to be

*) presently sunk into *Adenia*.

of staminodial nature, also because in certain species it was found to be distinctly 5-merous in its anatomy.

In respect to the above the following commentary on the situation in the various genera of the tribe *Passifloreae* can be given:

In *Crossostemma* and *Efulensia* (*p.p.*) (fig. 4b and fig. 3b) the two inner whorls resp. the inner whorl of stamens are (is) transformed into the parts of the disk, whereas the outer whorl is retained as stamens.

In *Deidamia* (fig. 3a) the inner one or two whorls are supposed to be retained as stamens, the outer presumably having formed the annular disk. The precise position of the 5 styles in respect to the stamens is not known.

Schlechterina (fig. 4a), where no disk is present, fits in beside *Crossostemma*.

In *Adenia* (fig. 2b) the 5 disk-glands present in most species are homologous with the outer whorl of the supposedly originally three whorls of stamens, and possibly the 'septa' (which in this genus divide the hypanthium into 5 parts) are homologous with the middle whorl. The appendages on the septa alternating with the filaments, as found in *Machadoa* (now a synonym of *Adenia*), are, in addition, suggestive of this. The inner whorl is retained as stamens in *Adenia*.

In sect. *Ophiocaulon* of *Adenia* (fig. 2a) the disk-glands are adnate to the hypanthium and form the fleshy, more or less 5-lobed annular disk replacing the corona threads as found in other *Adenias*.

In *Basananthe* (formerly *Tryphostemma*; fig. 2c), with (4 or) 5—9 stamens there is an annular disk, probably (in part) derived from the outer whorl of stamens. The membranous cup-shaped inner corona, at the inner side of which the filaments are inserted, is possibly a derivative of these filaments itself.

In *Passiflora* (fig. 1a) species with 5 stamens the inner whorl, and in species with 6—8 stamens possibly the inner two whorls, are retained as functioning stamens.

The situation in *Hollrungia* (fig. 1c) and *Tetrapathea* (fig. 1b) (the former genus with partly functionally unisexual, the latter with completely unisexual flowers), in the South American genera *Mitostemma* and *Dilkea* (stamens 8—10), and to a less extent in *Ancistrothyrsus* (stamens 8), can be derived from *Passiflora* by partial or complete suppression of the disk.

Ontogenetic studies on the question whether basically one or two staminal whorls are involved have unfortunately not been carried out on the few Asian species of *Passiflora* with 6—8 stamens (fig. 1a), nor in the other genera with usually more than 5 stamens.

In passing it is worth mentioning that in the genus *Paropsia* (tribe *Paropsieae*) the extra-staminal corona is often split up into 5 epipetalous bundles.

REVISED KEY TO AND ACCOUNT OF THE GENERA OF THE PASSIFLOREAE

As a matter of fact, the distinction of genera in *Passifloraceae* remains rather difficult. In a number of notes, added to the key, several weak points in the key are noted or explained. Additional characters and further explanation can be found in the short descriptions of the genera, and in the figures of the longitudinal sections of the flowers (fig. 1—4).

KEY TO THE GENERA

1. Androgynophore mostly distinct, *c.* 2 mm or longer. Gynophore absent or shorter than the ovary.
2. Flowers 4-merous. Corona tubiform, laciniate above; dispersed hairy all over

- (note 1). Leaves with scale-like glands. Styles 4 (note 7) . . . **I. Ancistrothyrus**
2. Flowers 5-merous. Corona various, not hairy all over, nor on the outer side. No scale-like glands on leaves. Styles 3—5 . . . **2.** (incl. *Tetrastylis*, note 4) **Passiflora**
1. Androgynophore absent or short, up to 2 mm. Gynophore absent to much longer than the ovary.
3. Stamens mutually free or nearly so, inserted close to the gynophore (note 3).
4. Flowers unisexual (dioecious), 4-merous. Stamens 4. Styles 3 . . . **5. Tetrathalpa**
4. Flowers hermaphroditic, 4- or 5-merous. Stamens 5—10. Styles 3—5.
5. Disk absent. Leaves simple, not lobed.
6. Styles free **3. Mitostemma**
6. Styles up to half-way connate (note 5) **4. Dilkea**
5. Disk present, extra-staminal. Leaves 5- or 7-foliolate. **9. Deidamia**
3. Stamens either connate (note 2), or adnate to (or inserted on) the hypanthium or inner corona (note 3), or on an androgynophore.
7. Styles 3 or 4 (or 5), free or partially connate.
8. Corona well-developed. Disk, if present, either extrastaminal and annular, or intra-staminal and consisting of lobules. Flowers hermaphroditic or functionally unisexual.
9. Stamens inserted on the hypanthium, or on a short androgynophore.
10. Outer corona single. Gynophore shorter than ovary. Flowers partly functionally unisexual (♂). Leaves 3- or 5-foliolate . . . **10. Efulensia**
10. Outer corona double. Gynophore longer than ovary. Flowers mostly functionally unisexual. Leaves simple, not lobed. . . . **6. Hollrungia**
9. Stamens inserted on the inner side of the cup-shaped inner corona
- 7. Basanthe**
8. Corona ill-developed or absent (note 1, 6). Disk extra-staminal, mostly consisting of 5 strap-shaped segments (note 6). Flowers mostly unisexual (dioecious) **8. Adenia**
7. Style single.
11. Gynophore about as long as ovary. Stigma 3- or 4-lobed. Disk absent. Stamens 6—8. **11. Schlechterina**
11. Gynophore absent. Stigma (sub)globose. Disk intra-staminal, distinct, forming a fleshy plate at the end of androgynophore, screening off the hypanthium. Stamens 5 **12. Crossostemma**

Notes to the key to the genera

1. In *Ancistrothyrus* the corona is tubiform, 5—10 mm long, deeply lacinate, hairy all over. In most other genera the corona is usually more complicated, consisting of one to several series of threads and (or) fleshy glabrous annules, etc. In these cases the outer threads are usually longest, and often partially united into a tube. This tube is not hairy all over itself, but there is mostly a zone of short additional threads or appendages inside in the upper half (in *Passiflora p.p.*; *Crossostemma*, *Schlechterina*, *Deidamia*, *Efulensia*). In *Adenia* the corona is absent or ill-developed, usually consisting of but a single fringe of short hairs. (See also under note 6).
2. In *Adenia* and *Hollrungia* the staminal filaments are sometimes almost free, or apparently so; see further under note 3.
3. In *Adenia* the staminal filaments are often adnate to the hypanthium; their insertion is then at some distance from the ovary or the gynophore.

4. According to Killip (J. Wash. Acad. Sci. 16, 1926: 365, 566) *Tetrastylis* is a genus separate from *Passiflora*, mainly because of the stamens being united beyond the androgynophore and by the 4 styles. These features, however, are also present in some Asian *Passifloras* (see De Wilde, *Blumea* 20, 1972: 227). *Tetrastylis* is included in *Passiflora* by Harms, 1925.
5. *Mitostemma* and *Dilkea* are closely related (see Killip, o.c., 570).
6. In species of sect. *Ophiocaulon* of *Adenia* the corona is replaced by a ring-shaped, sometimes more or less 5-lobed disk. In *Adenia* the disk-glands are rarely absent.
7. As a rule the number of placentas and fruit valves is equal to the number of styles, style-arms, or stigma-lobes.

ACCOUNT OF THE GENERA

1. *Ancistrothyrsus* Harms

Ancistrothyrsus Harms, Notizbl. Bot. Gart. Berl.-Dahl. 11 (1931) 146, fig. 4; Hutch., Gen. Fl. Pl. 2 (1967) 369; De Wilde, *Blumea* 19 (1971) 99—104, fig. 2. — Type: *A. tessmannii* Harms.

Liana to c. 30 m, pubescent or glabrescent in addition to golden scale-like gland-hairs especially on the leaves. *Leaves* simple, not lobed; glands (except gland-hairs) none. *Flowers* hermaphroditic, pubescent. *Hypanthium* narrow, shallow cup-shaped. *Sepals* 4, free, 10—40 mm. *Petals* 4, free. *Corona* single, hairy at both sides (see also note 1 to the key). *Androgynophore* 2—5 mm. *Stamens* 8, free; anthers dorsifixed, not versatile. *Gynophore* absent. *Styles* 4, free; stigmas subglobose, glabrous. *Disk* absent.

1 (or 2?) sp. in W. Brazil and E. Peru.

2. *Passiflora* L. — Fig. 1a.

Passiflora L., Sp. Pl. 1 (1753) 955; Harms in E. & P., Nat. Pfl. Fam. ed. 2, 21 (1925) 495; Killip, Field Mus. Nat. Hist. Chicago, Bot. 19, 1 (1938) 1—613; Hutch., Gen. Fl. Pl. 2 (1967) 370; De Wilde, *Blumea* 20 (1972) 227. — Type: *P. incarnata* L.

Tetrastylis Barb. Rodr., Rev. Engenharia 4 (1882) 260; Killip, op. cit., 566; Hutch., Gen. Fl. Pl. 2 (1967) 371. — *Passiflora* sect. *Tetrastylis* Harms in E. & P., Nat. Pfl. Fam., Nachtr. 1 (1897) 256; ed. 2, 21 (1925) 498. — Type: *T. montana* Barb. Rodr.

For other synonyms and subdivision see Harms and Killip, ops cit. sub. *Passiflora*.

Climbing herbs to large lianas, rarely shrubs or trees, glabrous or hairy. *Leaves* simple, entire to deeply incised; glands various, on blade and petiole. *Flowers* hermaphroditic, glabrous or hairy. *Hypanthium* various, flattish to long tubiform. *Sepals* 5, free, c. 5—50 mm. *Petals* 0 or 5, free. *Corona* various, simple or mostly double or composed of several series of threads, annules, etc. *Androgynophore* distinct, 3 mm or more, rarely nearly absent. *Stamens* 5—8 (5 in the New World), free or up to 5 mm connate; anthers dorsifixed, versatile. *Gynophore* absent or sometimes up to 7 mm. *Styles* 3—5 (3 in the New World), free or rarely united at base; stigmas subglobose, glabrous. *Disk* extra-staminal, various, annular etc., or absent.

C. 375 spp. in (mainly tropical) America, SE. Asia, Malesia, W. Pacific, and Australia.

3. *Mitostemma* Mast.

Mitostemma Mast., J. Bot. 21 (1883) 33; Harms in E. & P., Nat. Pfl. Fam. ed. 2, 21 (1925) 484; Killip, Field Mus. Nat. Hist. Chicago 19, 1 (1938) 569; Hutch., Gen. Fl. Pl. 2 (1967) 370. — Type: *M. glaziovii* Mast.

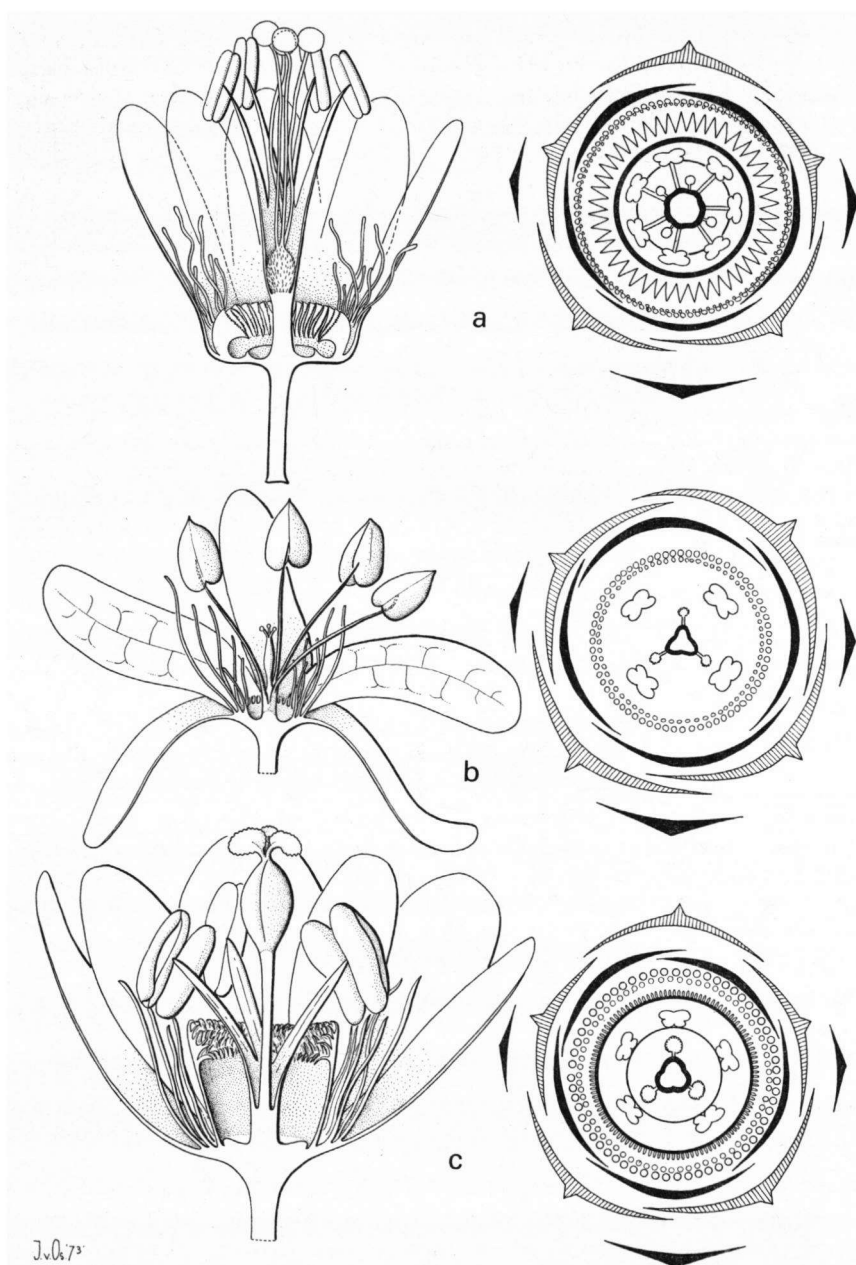


Fig. 1. Longitudinal sections of flowers, and flower diagrams of species of various genera of *Passifloraceae*. — a. *Passiflora tonkinensis* De Wilde, $\times 2\frac{1}{2}$ (Pételot 2203, P); flower hermaphroditic; note distinct androgynophore, 7 stamens which are connate at base, and 4 styles. Most *Passifloras* have 5 stamens and 3 styles. — b. *Tetrapathaea tetrandra* Cheeseman, $\times 5$ (Hb. Kirk 117, CAM); flower unisexual, 4-merous; note stamens free or almost free. — c. *Hollrungia aurantioides* K. Schum., $\times 5$ (Kairo NGF 27973, L); flower hermaphroditic, 5-merous; note double corona, stamens connate at base.

Scandent or erect shrubs, glabrous. *Leaves* simple, not lobed; glands on blade none to several, on petiole none. *Flowers* hermaphroditic, glabrous. *Hypanthium* rather narrow, short cup-shaped. *Sepals* 4 (or 5), free, 15—20 mm. *Petals* 4 (or 5), free. *Corona* single, consisting of 3 series of threads. *Androgynophore* absent. *Stamens* 8 or 10, free or nearly so; anthers sub-dorsifixed, versatile. *Gynophore* c. 4—7 mm. *Styles* 4, free; stigmas subglobose, glabrous. *Disk* absent.

3 spp. in Brazil and Guyana.

4. *Dilkea* Mast.

Dilkea Mast., Trans. Linn. Soc. Bot. 27 (1871) 627; Fl. Bras. 13, 1 (1872) 533, t. 56; Harms in E. & P., Nat. Pfl. Fam. ed. 2, 21 (1925) 485; Killip, Field Mus. Nat. Hist. Chicago 19, 1 (1938) 572; Hutch., Gen. Fl. Pl. 2 (1967) 370. — T y p e: *D. retusa* Mast.

Lianas, shrubs, or trees, glabrous. *Leaves* simple, not lobed; glands on blade 0, on petiole none or 1 pair. *Flowers* hermaphroditic, glabrous. *Hypanthium* narrow, flattish. *Sepals* 4 or 5, when young united below the middle into a tube, later on free, 12—30 mm. *Petals* 4 or 5, free. *Corona* double. *Androgynophore* absent. *Stamens* 8, free or connate at the very base; anthers sub-dorsifixed, versatile. *Gynophore* 0—4 mm. *Styles* 4, up to half-way connate; stigmas subglobose or reniform, glabrous. *Disk* absent.

2(—5) spp. in Brazil, Peru, and Colombia.

5. *Tetrapathaea* Reichb. — Fig. 1b.

Tetrapathaea Reichb., Consp. (1828) 132; Raoul, Ann. Sc. Nat. 3, 2 (1844) 122; Harms in E. & P., Nat. Pfl. Fam. ed. 2, 21 (1925) 507. — *Passiflora* sect. *Tetrapathaea* DC., Mém. Soc. Phys. Genève 1 (1822) 435; Prodr. 3 (1828) 323. — T y p e: *Passiflora tetrandra* Banks & Sol. [= *T. tetrandra* (Banks & Sol.) Cheeseman; syn. *T. australis* Raoul].

Liana to c. 20 m, glabrous. *Leaves* simple, not lobed; glands 0 or 1 pair, minute, at very base of blade. *Flowers* unisexual (dioecious) (with remnants of stamens or ovary), glabrous. *Hypanthium* narrow, flattish. *Sepals* 4, free, 5—7 mm. *Petals* 4, free. *Corona* single, consisting of 2 or 3 series of threads. *Androgynophore* 0—0.5 mm. *Stamens* 4, free; anthers basifixed-subdorsifixed, ± versatile. *Gynophore* 0.5—2.5 mm. *Styles* 3, free or partially connate; stigmas subglobose, woolly-papillose. *Disk* absent.

1 sp. in New Zealand (N. of Banks Peninsula).

6. *Hollrungia* K. Schum. — Fig. 1c.

Hollrungia K. Schum., Bot. Jahrb. 9 (1888) 212; Harms in E. & P., Nat. Pfl. Fam. ed. 2, 21 (1925) 494; van Steenis, Acta Bot. Neerl. 15 (1966) 40—44, fig. 1—7; Hutch., Gen. Fl. Pl. 2 (1967) 370; De Wilde, Fl. Males. I, 7 (1972) 431. — T y p e: *H. aurantioides* K. Schum.

Liana to c. 30 m, glabrous. *Leaves* simple, not lobed; glands on blade 0, or 1 or 2(—6), flat, mostly paired, on petiole 0, or 1 (or 2) pair(s). *Flowers* hermaphroditic or functionally unisexual, glabrous. *Hypanthium* narrow, flattish. *Sepals* 5, free, 5.5—10 mm. *Petals* 5, free. *Corona* double. *Androgynophore* 0.5—2 mm. *Stamens* 5, connate at base for up to 4 mm, sometimes free; anthers sub-dorsifixed, versatile. *Gynophore* (1—)1.5—6 mm. *Styles* 3, free; stigmas flattish, lobed-papillate. *Disk* extrastaminal, obscure, being the thickened bottom of the hypanthium.

1 sp. in E. Malesia.

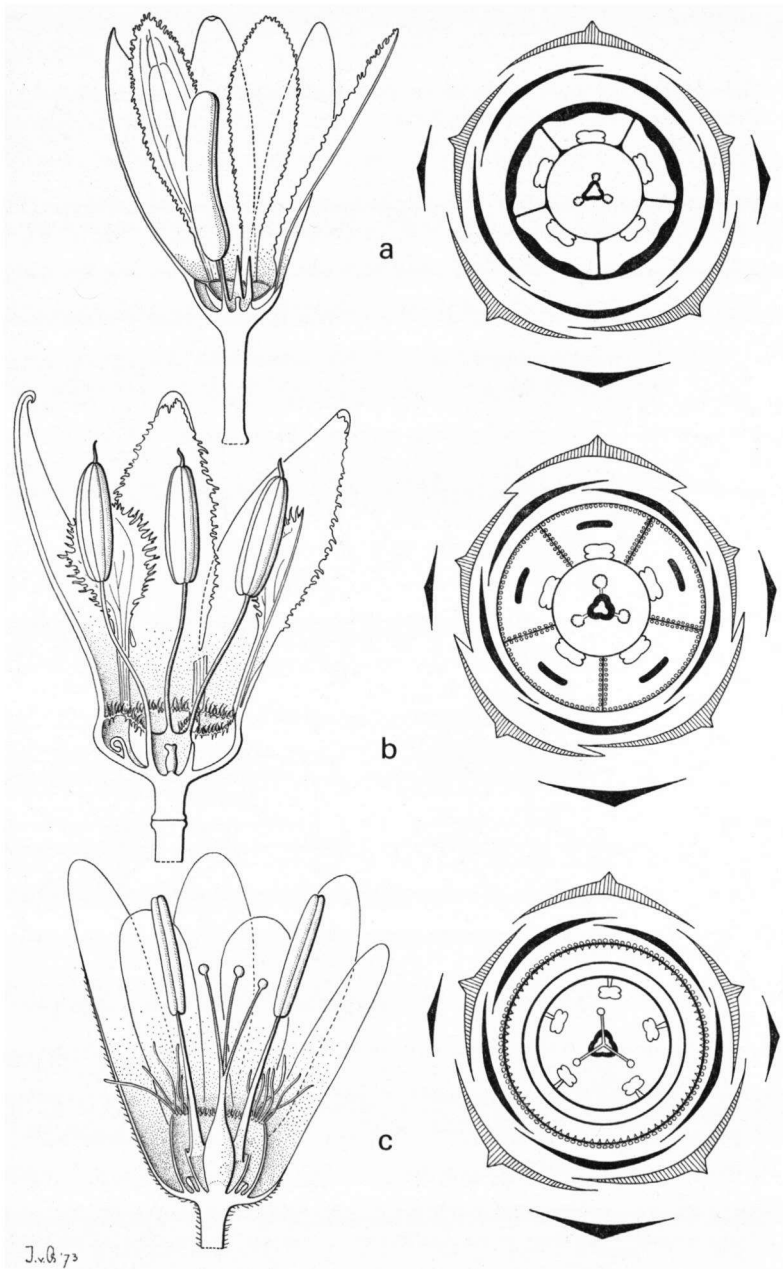


Fig. 2. Longitudinal sections of flowers, and flower diagrams of species of various genera of Passifloraceae; all $\times 5$. — a. *Adenia cissampeloides* Harms (Oldeman 76, WAG); flower unisexual, 5-merous; note disk-glands replacing corona as compared with b. — b. *Adenia schweinfurthii* Engl. (Schweinfurth 3485, K); flower unisexual, 5-merous; note shape of petals different from sepals, the 5 septa of the corona, and the 5 separate disk glands. — c. *Basananthe pubiflora* De Wilde (Richards 11646, K); flower hermaphroditic, 5-merous; note stamens inserted inside inner corona.

7. *Basananthe* Peyr. — Fig. 2c.

- Basananthe* Peyr., Bot. Zeitg. 17 (1859) 101; (in Wawra & Peyritsch, Sertum Benguelense in) Sitzungsber. Acad. Wien 38 (1860) 569; Hook. f. in Benth. & Hook. f., Gen. Pl. 1 (1867) 812; De Wilde, Blumea 21 (1973) 327, fig. 1—4. — T y p e: *B. littoralis* Peyr.
- Trypostemma* Harvey, Thes. Cap. 1 (1859) 32, t. 51; Hook. f. in Benth. & Hook. f., Gen. Pl. 1 (1867) 811; Engl., Bot. Jahrb. 14 (1891) 387—388; Hutch. & Pearce, Kew Bull. (1921) 257—266; Harms, Notizbl. Berl.-Dahl. 8 (1923) 291—293; in E. & P., Nat. Pfl. Fam. ed. 2, 21 (1925) 487, fig. 218A, 222; Hutch., Gen. Fl. Pl. 2 (1967) 371 (incl. *Carania*). — T y p e: *T. sandersonii* Harvey.
- Carania* Chiov., Fl. Somalia (1929) 175, t. 19 fig. 3; Hutch., Gen. Fl. Pl. 2 (1967) 372; De Wilde, Blumea 19 (1971) 103. — T y p e: *C. berberoides* Chiov.

Herbs or climbers to c. 3 m, rarely low shrubs, glabrous or hairy or scabrous. *Leaves* simple, entire or deeply lobed; glands small on teeth at blade-edge, sometimes on petiole. *Flowers* hermaphroditic, glabrous or hairy. *Hypanthium* flattish to cup-shaped, mostly narrow. *Sepals* 5 (or 6), free, 1.5—1.5 mm. *Petals* absent, or (4 or) 5, free. *Corona* double; inner corona cup-shaped, membranous. *Androgynophore* absent. *Stamens* 5 (—9), free*, inserted inside in the upper part of the inner corona; in *B. berberoides* this inner corona forms small additional cups around the bases of the filaments; anthers basifixed. *Gynophore* absent or up to 1 mm. *Styles* 3 (or 4), free or partially connate; stigmas globose, subglabrous. *Disk* extra-staminal, annular, or rarely absent.

25 spp. in Africa.

8. *Adenia* Forssk. — Fig. 2a, b.

- Adenia* Forssk., Fl. Aegypt.-Arab. (1775) 77; Engl., Bot. Jahrb. 14 (1891) 374; Harms in E. & P., Nat. Pfl. Fam. ed. 2, 21 (1925) 488 (incl. *Machadoa*); Hutch., Gen. Fl. Pl. 2 (1967) 373 (incl. *Machadoa* and *Keramanthus*); De Wilde, Meded. Landbouwhogeschool Wageningen 71—18 (1971) 1—281. — T y p e: *A. venenata* Forssk.
- Modecca* Lamk., Encycl. Méth. Bot. 4 (1797) 208. — *Blepharanthus* J. E. Smith, Gram. Bot. (1821) 188, nom. illeg. (as a substitute for *Modecca*). — T y p e: *M. palmata* Lamk. = *A. hondala* (Gaertn.) De Wilde.
- Kolbia* P. Beauv., Fl. d'Oware 2 (1807) 91, t. 120. — T y p e: *K. elegans* P. Beauv. = *A. lobata* (Jacq.) Engl.
- Paschanthus* Burch., Trav. Afr. 1 (1822) 543. — T y p e: *P. repandus* Burch. = *A. repanda* (Burch.) Engl.
- Microblepharis* (W. & A.) Roem., Syn. Mon., 2 Pepon. (1846) 133, 200. — T y p e: *Modecca wightiana* Wall. ex Wight & Arnott = *A. wightiana* (W. & A.) Engl.
- Erythrocarpus* Roem., Syn. Mon., 2 Pepon. (1846) 133, 204. — T y p e: *Modecca populifolia* Bl. = *A. heterophylla* (Bl.) Koord.
- Clemanthus* Klotzsch in Peters, Reise Mossamb. Bot. (1861) 143. — T y p e: *C. senensis* Klotzsch = *A. digitata* (Harv.) Engl.
- Ophiocaulon* Hook. f. in Benth. & Hook. f., Gen. Pl. 1 (1867) 813. — L e c t o t y p e: *Modecca cissampeloides* Planch. ex Hook. = *A. cissampeloides* (Planch. ex Hook.) Harms.
- Machadoa* Welw. ex Benth. & Hook. f., Gen. Pl. 1 (1867) 814. — T y p e: *M. huillensis* Welw. ex Benth. & Hook. f. = *A. huillensis* (Welw.) A. & R. Fernandes.
- Keramanthus* Hook. f., Bot. Mag. (1876) t. 6271. — T y p e: *K. kirkii* Hook. f. = *A. keramanthus* Harms.
- Jaggia* Schinz, Verh. Bot. Verein Brand. 30 (1888) 253. — T y p e: *J. repanda* Schinz = *A. repanda* (Burch.) Engl.
- Echinothamnus* Engl., Bot. Jahrb. 14 (1891) 383. — T y p e: *E. pachuëlii* Engl. = *A. pachuëlii* (Engl.) Harms.

Perennial herbs, climbers, or lianas to c. 40 m, sometimes pachypodous; glabrous or rarely hairy. *Leaves* simple, entire or lobed to deeply incised**); glands on blade (0—) 2 to many, on petiole 1 or 2 at the top. *Flowers* mostly unisexual, dioecious, glabrous. *Hypanthium* various, mostly narrow to broad cup-shaped, sometimes 5-saccate, or saucer-

*) If the inner corona is regarded as a derivative of the existing stamens, then the filaments are actually connate at base.

***) In a few spp. sometimes reminiscent of truly compound leaves, e.g. in *A. fruticosa*.

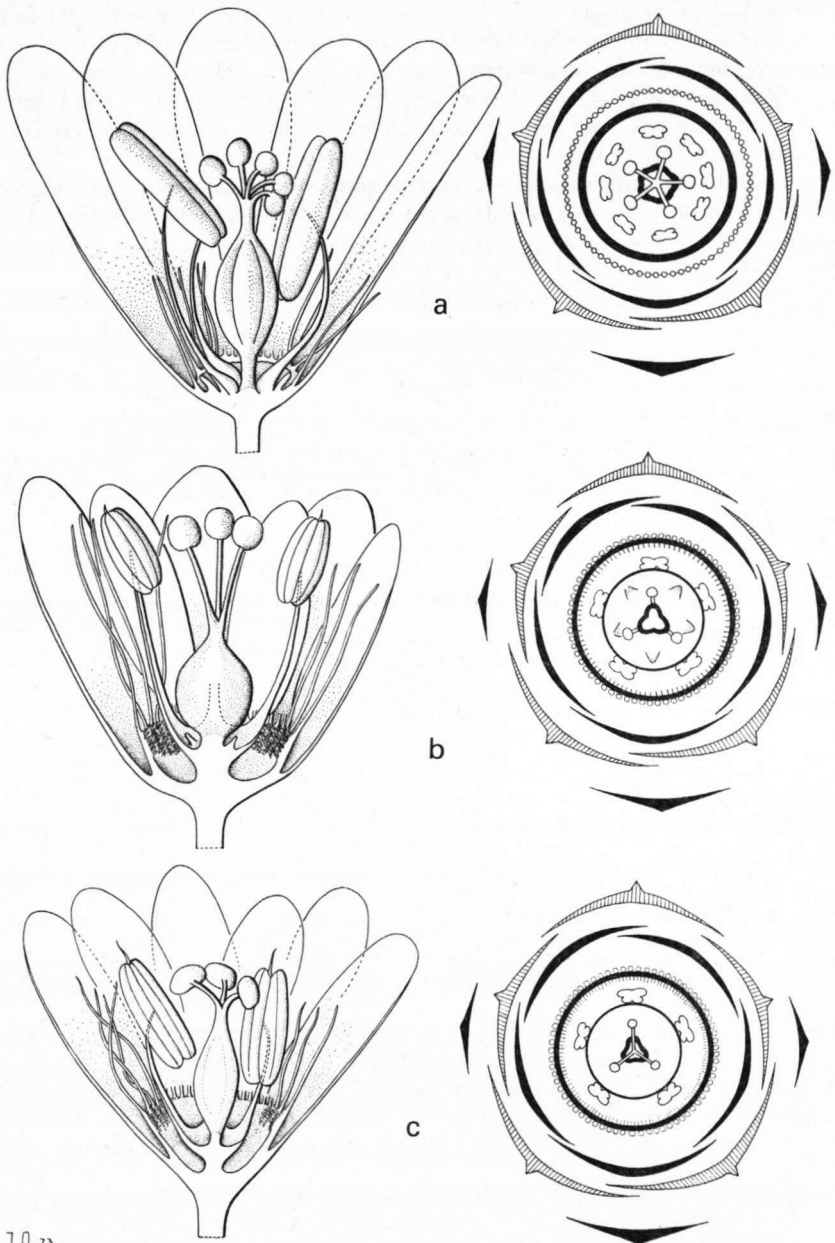


Fig. 3. Longitudinal sections of flowers, and flower diagrams of species of various genera of *Passifloraceae*; all $\times 5$. — a. *Deidamia alata* Thouars (Decary 10812, K); flower hermaphroditic; note 8 free stamens, 5 styles. — b. *Efulensia clematoides* C. H. Wright (De Wilde & De Wilde-Duyfjes 1308, WAG); flower hermaphroditic, 5-merous; note 5 stamens connate at base and 5 small tooth-like intra-staminal appendages or staminodes. — c. *Efulensia montana* De Wilde (Lebrun 5574, BR); flower hermaphroditic, 5-merous; note 5 stamens connate at base.

shaped or tubiform. *Sepals* (4 or) 5 (or 6), free or partially connate, 1—65 mm. *Petals* (4 or) 5 (or 6), free or sometimes adnate with calyx tube. *Corona* ill-developed, various, mostly consisting of fine threads, sometimes replaced by cup-shaped or annular disk-glands (sect. *Ophiocaulon*), rarely absent. *Androgynophore* absent. *Stamens* (4 or) 5 (or 6), free and then inserted at some distance from the gynophore or ovary, or mostly partially connate into a tube; anthers basifixed. *Gynophore* absent or up to 14 mm. *Styles* 3(—5), free or partially connate, sometimes nearly absent; stigmas lacinate, or branched, or reniform to subglobose, papillate or woolly. *Disk* extra-staminal, consisting of 5 strap-shaped parts, or absent, in sect. *Ophiocaulon* replacing the corona (see above); in addition often septa originating from the filamental tube, separating the disk-glands.

92 spp. in Africa, Madagascar, SE. Asia, Malesia, and N. Australia.

9. *Deidamia* Noronha ex Thouars. — Fig. 3a.

Deidamia Noronha ex Thouars, Hist. Vég. Iles Austr. Afr. (1806) 61, t. 20; Harms in E. & P., Nat. Pfl. Fam. ed. 2, 21 (1925) 486 (excl. sect. *Efulensia*); Perrier de la Bâthie, Fl. Madag. Fam. 143 (1945) 38—45, fig. 8; Hutch., Gen. Fl. Pl. 2 (1967) 372. — T y p e: *D. alata* Noronha ex Thouars. *Thompsonia* R. Br., Trans. Linn. Soc. Bot. 13 (1821) 221. — T y p e: *Deidamia thompsoniana* DC. = *T. browniana* J. Roem.

Lianas to c. 25 m, glabrous. *Leaves* compound, leaflets 5 or 7; glands 1 or 2 pairs on petiole, sometimes also on petiolules. *Flowers* hermaphroditic, glabrous. *Hypanthium* narrow, flattish. *Sepals* 4 or 5, free, 8—13 mm. *Petals* 4 or 5, free. *Corona* single, consisting of 1 or 2 series of threads. *Androgynophore* absent. *Stamens* 5—8, free; anthers dorsifixed, versatile. *Gynophore* 1—3 mm. *Styles* 3—5, partially connate; stigmas subglobose, papillate. *Disk* extrastaminal, distinct, annular, 0.5—1 mm high, sometimes shallowly lobed.

5 spp. in Madagascar.

10. *Efulensia* Wright. — Fig. 3b, c.

Efulensia C. H. Wright, Hook. f. Ic. Pl. 6 (1897) tab. 2518; Hutch., Gen. Fl. Pl. 2 (1967) 373; de Wilde, Blumea 22 (1974) 31. — *Deidamia* sect. *Efulensia* Harms in E. & P., Nat. Pfl. Fam. ed. 2, 21 (1925) 487. — T y p e: *E. clematoides* C. H. Wright. *Giorgiella* de Wildeman, Feddes Rep. 13 (1914) 384. — T y p e: *G. congolana* de Wildeman. *Sematanthera* Pierre ex Harms, Notizbl. Bot. Gart. Berl.-Dahl. 8 (1923) 291 (nom., in syn. of *Deidamia*). — T y p e: *S. klainei* Pierre (in sched.).

Liana to c. 30 m, glabrous. *Leaves* 3- or 5-foliolate; glands 1 pair on petiole. *Flowers* hermaphroditic or partly functionally unisexual, glabrous. *Hypanthium* narrow, shallowly cup-shaped or flattish. *Sepals* 5, free, 6—10 mm. *Petals* 5, free. *Corona* single. *Androgynophore* absent or up to 1 mm. *Stamens* 5, connate at base for c. 1—1.5 mm; anthers dorsifixed, versatile. *Gynophore* up to 1 mm. *Styles* 3, almost free to over half-way connate; stigmas subglobose, (sub) glabrous; placentas 3, rarely 4. *Disk* absent, or intra-staminal, composed of 5 tooth-like appendages up to 1 mm, alternating with the stamens.

2 spp. in Equatorial Africa.

11. *Schlechterina* Harms — Fig. 4a.

Schlechterina Harms, Bot. Jahrb. 33 (1902) 148; Ber. Deutsch. Bot. Ges. 24 (1906) 177—184, text fig., t. 12; in E. & P., Nat. Pfl. Fam. ed. 2, 21 (1925) 485. — T y p e: *S. mitostemmatoides* Harms.

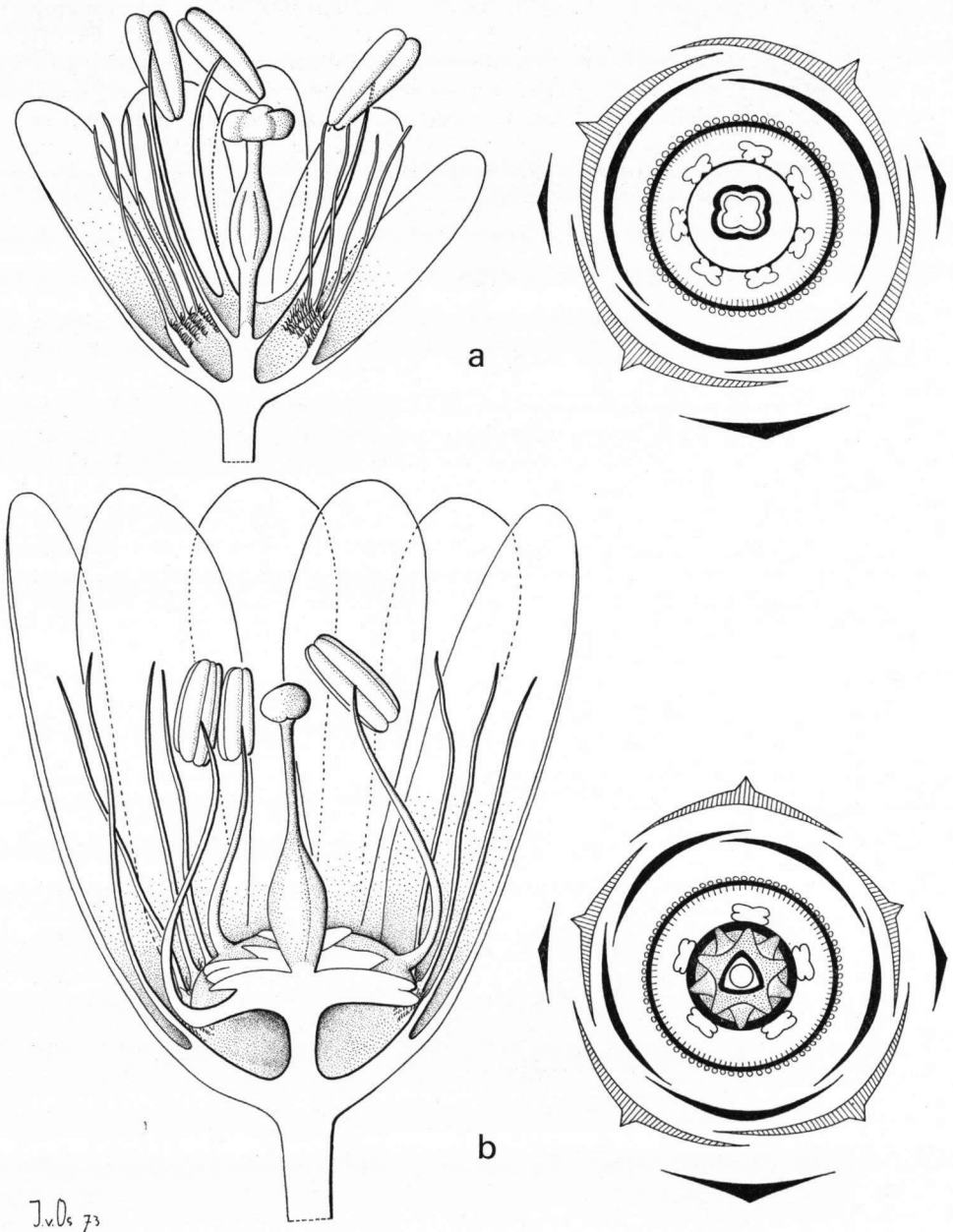


Fig. 4. Longitudinal sections of flowers, and flower diagrams of species of various genera of Passifloraceae; all $\times 5$. — a. *Schlechterina mitostemmatoides* Harms (Faulkner 3764, K); flower hermaphroditic; note variable number of sepals and petals, stamens (6—)8, connate at base, stigma lobes (placentas) 4. — b. *Crossostemma laurifolium* Planch. ex Benth. (De Wilde 302, WAG); flower hermaphroditic, 5-merous; note conspicuous intra-staminal disk, single style, and ovary with 3 placentas.

Climber 0.5—5 m, glabrous. *Leaves* simple, (sub)entire, in juvenile specimens deeply pinnately lobed; glands small, 1 pair at blade-base (at transition to petiole). *Flowers* hermaphroditic, glabrous. *Hypanthium* rather narrow, shallow cup-shaped. *Sepals* 3 or 4, free, 7—11 mm. *Petals* 2—4, free. *Corona* single. *Androgynophore* c. 1 mm. *Stamens* 6—8, connate at base into a broad cup, sometimes with small tooth-like appendages at edge of cup in between the filaments; anthers dorsifixed, versatile. *Gynophore* 2—2.5 mm. *Style* 1; stigma simple, 3 or 4-lobed, subglabrous. *Disk* absent.

1 sp. in E. Africa (Kenya, Tanzania, Mozambique).

12. *Crossostemma* Planch. ex Benth. — Fig. 4b.

Crossostemma Planch. ex Benth. in Hook., Niger Fl. (1849) 364; Harms in E. & P., Nat. Pfl. Fam. ed. 2, 21 (1925) 485; Hutch., Gen. Fl. Pl. 2 (1967) 370 (excl. *Schlechterina*). — Type: *C. laurifolium* Planch. ex Benth.

Lianas to c. 25 m, glabrous. *Leaves* simple, entire, (deeply) pinnately lobed in juvenile specimens; glands on blade absent, on petiole minute, 1 pair near the top, or absent. *Flowers* hermaphroditic, glabrous. *Hypanthium* rather narrow, cup-shaped. *Sepals* 5, free, 9—14 mm. *Petals* 5, free. *Corona* single. *Androgynophore* 1—1.5 mm. *Stamens* 5, mutually connate and adnate to disk at base; anthers dorsifixed, versatile. *Gynophore* 0—0.5 mm. *Style* 1; stigma simple, (sub)globose, sometimes faintly 3—(or 4—) lobed, glabrous; placentas 3 (or 4). *Disk* intra-staminal, consisting of two alternating whorls of fleshy subtriangular excrescences, adnate to the bases of the filaments, and forming a fleshy plate screening off the hypanthium.

1. sp. in W. Africa (Guinea to Ghana).

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