

THE SYSTEMATIC POSITION OF TRIBE PAROPSIEAE,  
IN PARTICULAR THE GENUS ANCISTROTHYSUS,  
AND A KEY TO THE GENERA OF PASSIFLORACEAE

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SUMMARY

The members of tribe *Passifloreae* of the *Passifloraceae* are assumed to be originally all tendril-climbers. They have essentially axillary cymose inflorescences, and the vegetative ramification occurs always through the accessory bud. In tribe *Paropsieae* and *Flacourtiaceae* (mostly shrubs or trees, no tendril-climbers) the inflorescences are axillary, most likely essentially racemose, and the vegetative ramification is mostly through the axillary bud.

The tendril-climbing neotropical genus *Ancistrothyrus* appeared to belong to *Passifloreae*.

Though the tribe *Paropsieae* remains to occupy an intermediate position between *Passifloraceae* and *Flacourtiaceae*, they can best be classified with the *Passifloraceae*.

A new key is proposed for the distinction of both families and the genera of *Passifloraceae*.

During the preparation of my revision of the genus *Adenia*, and the treatment of the *Passifloraceae* for the Flora Malesiana, I became of course interested in the systematics of the family, amongst others in the position of the tribe *Paropsieae* on which subject several papers were recently published. Almost all authors agree that this tribe occupies a more or less transitional place between *Flacourtiaceae* and *Passifloraceae*. These two families are certainly more closely allied mutually than to others and show consequently also phytochemical similarities (Hegnauer, 1969).

The tribe was first recognized by De Candolle (1828) in *Passifloraceae*; also e.g. Perrier de la Bâthie (1945) and Fernandes (1958) included it in that family. By most British authors, from Bentham & Hooker (1867) onwards to Hutchinson (1967), the genera it contains are accommodated in *Passifloraceae* but without the recognition of a supra-generic taxon.

For not very convincing anatomical reasons and the different habit, viz. arboreous versus climbing, the tribe was transferred to the *Flacourtiaceae* by Harms (1893), an opinion followed until modern time by various German authors, e.g. Engler (1921), Gilg (1925), Melchior in Engler's Syllabus (1964), and Sleumer (1954). Recent anatomical and palynological investigations, however, induced Sleumer (1970) to refer the genus *Paropsia* to *Passifloraceae*.

Since the treatment of *Paropsieae* by Gilg (1925) it has appeared that the genus *Soyauxia* should be excluded from the tribe, whereas *Hounea* proved synonymous with *Paropsia*. Two new Paropsiaceous genera have been added, viz. *Ancistrothyrus*, a liana from East Peru and West Brazil (Harms, 1931, 1932) and *Viridivia*, a shrubby tree closely related to *Paropsia*, from Rhodesia (Hemsley & Verdcourt, 1956).

At present the tribe *Paropsieae* is composed of the following genera: *Paropsia*, *Androsiphonia*, *Viridivia*, *Paropsiopsis*, *Smeathmannia*, and *Barteria*, all shrubs or small trees from the Old World, and *Ancistrothyrus*, a liana from South America.

When included in *Flacourtiaceae*, the tribe is distinguished mainly by the presence of a corona. Within *Passifloraceae* it is remarkable that the *Paropsieae*, with the exception of the climbing South American *Ancistrothyrsus*, are deviating by their arboreous habit; the genera constituting the tribe *Passifloreae* are all tendril-climbers with a few herbaceous, erect derivatives in *Adenia* and *Tryphostemma* and a few shrub-like outliers in the large genus *Passiflora* and the related genus *Dilkea*.

During my investigations in *Adenia* and Malesian *Passifloraceae* I have been impressed by the uniform mode of ramification in *Passifloraceae*, namely through the second, serial, accessory bud. Already Harms (1893, 1925) wrote (family diagnosis in Nat. Pfl. Fam., 1925, p. 471): 'oberhalb der Ranke oder des Blütenstandes eine serielle Beiknospe, die zu einem Laubspross oder durch Reduktion der Blätter zu einem Blütenstand auswachsen kann'.

Searching for characteristics for the distinction of the tribe *Paropsieae* within the *Passifloraceae* better than 'shrubs or trees without tendrils' versus 'climbers, mostly provided with tendrils' I checked the presence of the serial accessory buds and the corresponding mode of (vegetative) ramification in all the genera of the *Passifloreae*: *Passiflora* (incl. *Tetrastylus*), *Dilkea*, *Mitostemma*, *Hollrungia*, *Tetrapathaea*, *Adenia*, *Tryphostemma*, *Crossostemma* (incl. *Schlechterina*), and *Deidamia* (incl. *Efulensia*), the *Paropsieae*, and a large number of *Flacourtiaceae*. This revealed the following:

1) In all *Passifloraceae* (*Passifloreae* & *Paropsieae*) an axillary and an accessory bud are always present; in *Flacourtiaceae* an accessory bud is either present (e.g. in *Lindackeria*, *Ryparosa*, *Hydnocarpus*, many *Casearias*) or absent.

2) In all *Passifloreae* the axillary bud is either abortive, or developed into a cymose inflorescence (either tendril-bearing or not) or into a sterile tendril; the second, serial, accessory bud always provides for the vegetative ramification, whereas in certain species (e.g. *Passiflora racemosa*, *Tetrastylis ovalis*, *Adenia racemosa*, *A. globosa*, *Dilkea* sp.) this appears as an raceme-like inflorescence, i.e. an inflorescences-bearing shoot or short-shoot. The ultimate 'true' inflorescences, which are essentially cymose, never develop from the accessory bud. Fig. 1 a—d.

3) In the *Paropsieae* the axillary bud develops into a flower- or inflorescences-bearing shoot; it also provides for the vegetative ramification. The accessory bud is either abortive or rarely developed into a normal branch. In the flower- or inflorescences-bearing shoots the flowers or inflorescences apparently are situated axillary. Fig. 1 e—h

4) In the *Flacourtiaceae* the ramification generally resembles that in *Paropsieae*. The axillary bud usually provides for the vegetative ramification, or it may produce a racemose inflorescence (raceme-like or thyrsoid e.g. in *Homalium*, *Lindackeria*, *Casearia*, *Ryparosa*, *Hydnocarpus*, and others), or a flower-bearing short-shoot, sometimes reduced to fascicles or even to a single flower (e.g. the Australian *Streptothamnus*). In the South African genus *Kiggelaria* the vegetative ramification seems to occur always through the accessory bud, but the axillary inflorescences are racemose, i.e. flower-bearing short-shoots. Fig. 1 e, k—p.

The difference in mode of ramification between the *Passifloreae* on the one hand, and the *Paropsieae* and *Flacourtiaceae* on the other, leads me to the assumption that the inflorescences in the two latter groups are likely essentially racemose. Whether the simple uni- or few-flowered ultimate inflorescences, as found e.g. in *Paropsia* or various *Flacourtiaceae* (e.g. *Casearia*, *Hydnocarpus*, etc.), are essentially reduced racemes or cymes remains, of course is difficult to decide.

If my observations and considerations on the mode of ramification are correct (which needs additional checking on several genera of *Flacourtiaceae*), this would mean a rather fundamental difference between *Passifloreae* and *Paropsieae* (together with *Flacourtiaceae*),

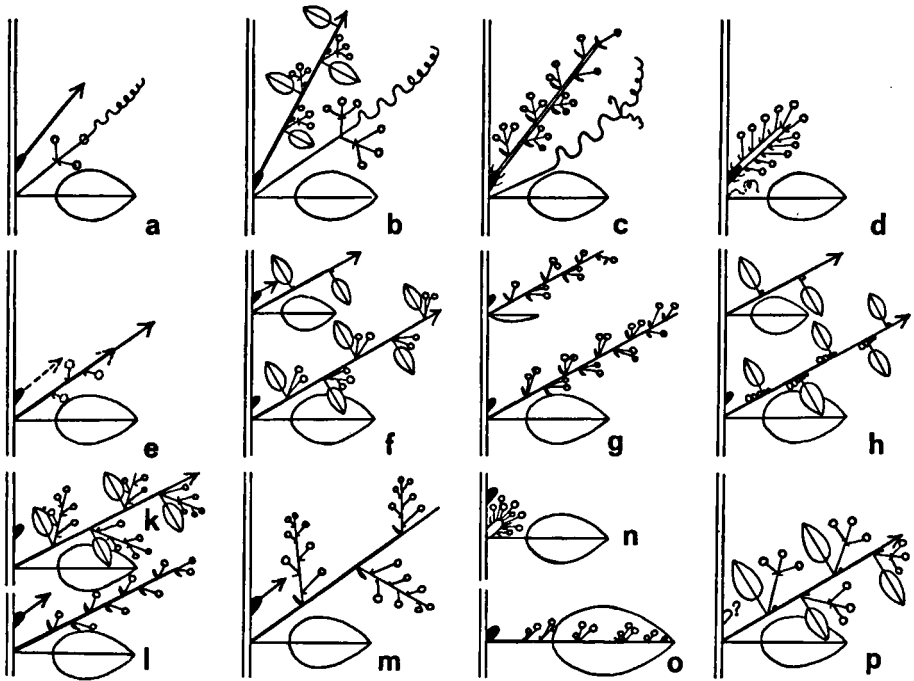


Fig. 1. Mode of vegetative ramification and various inflorescences in a—d. *Passifloreae*, e—h. *Paropsiaceae*, and e, k—p. some *Flacourtiaceae*; all diagrammatic. Accessory bud solid black. a. Essence of ramification in *Passifloreae*; b. Most *Passifloras* and *Adenias*; c. *Passiflora racemosa*, *Tetrazyllis ovalis*, *Adenia racemosa*, *A. venenata*; d. *Passiflora arborea*, *P. spicata*, *Dilkea*, *Adenia globosa*, *A. fasciculata*; e. Essence of ramification in *Paropsiaceae* and *Flacourtiaceae*; f. *Paropsia*, *Paropsiopsis*, *Smeathmannia*; g. *Paropsia guineensis*, *Androsiphonia*; h. *Barteria*; k—n. Various genera of *Flacourtiaceae*, e.g. *Homalium*, *Lindackeria*, *Ryparosa*, *Scolopia p.p.*, *Hydnocarpus*, etc.; o. *Phyllobotriaceae*; p. Axillary dichasial inflorescences in *Laetia* sect. *Laetia*.

in addition to the only rather arbitrary character used up till now of 'climbing' versus 'arborescent'. This would carry even more weight if a third differential character would be 'inflorescences essentially cymose' against 'inflorescences predominantly racemose'.

To test these assumptions it appeared interesting to investigate the few cases of exceptional habit in both groups.

In *Passifloreae* some species of the large genus *Passiflora* are arborescent, e.g. *P. arborea* and *P. spicata*; the genus *Dilkea* mainly consists of non-climbing shrubs of small trees; and in *Adenia* and *Tryphostemma* some erect non-climbing herbaceous species occur.

It appeared that the mode of ramification in all these species is essentially the same as in the 'normal' climbing *Passifloras*, as explained above. Checking of the genus *Dilkea* gave some difficulties because of the rather poor material at hand. Here the situation in the ramification is usually obscured by the fact that the true axillary bud is suppressed; in a few cases, however, an abortive tendril between leaf scar and inflorescence (i.e. a flower-bearing short-shoot) revealed that the situation is exactly as in other *Passifloreae*. Moreover, *Dilkea* is closely related to *Mitostemma*, in which the situation is quite the same as in *Passiflora*.

The few scandent *Flacourtiaceae*, i.e. the Australian *Streptothamnus* and *Berberidopsis*

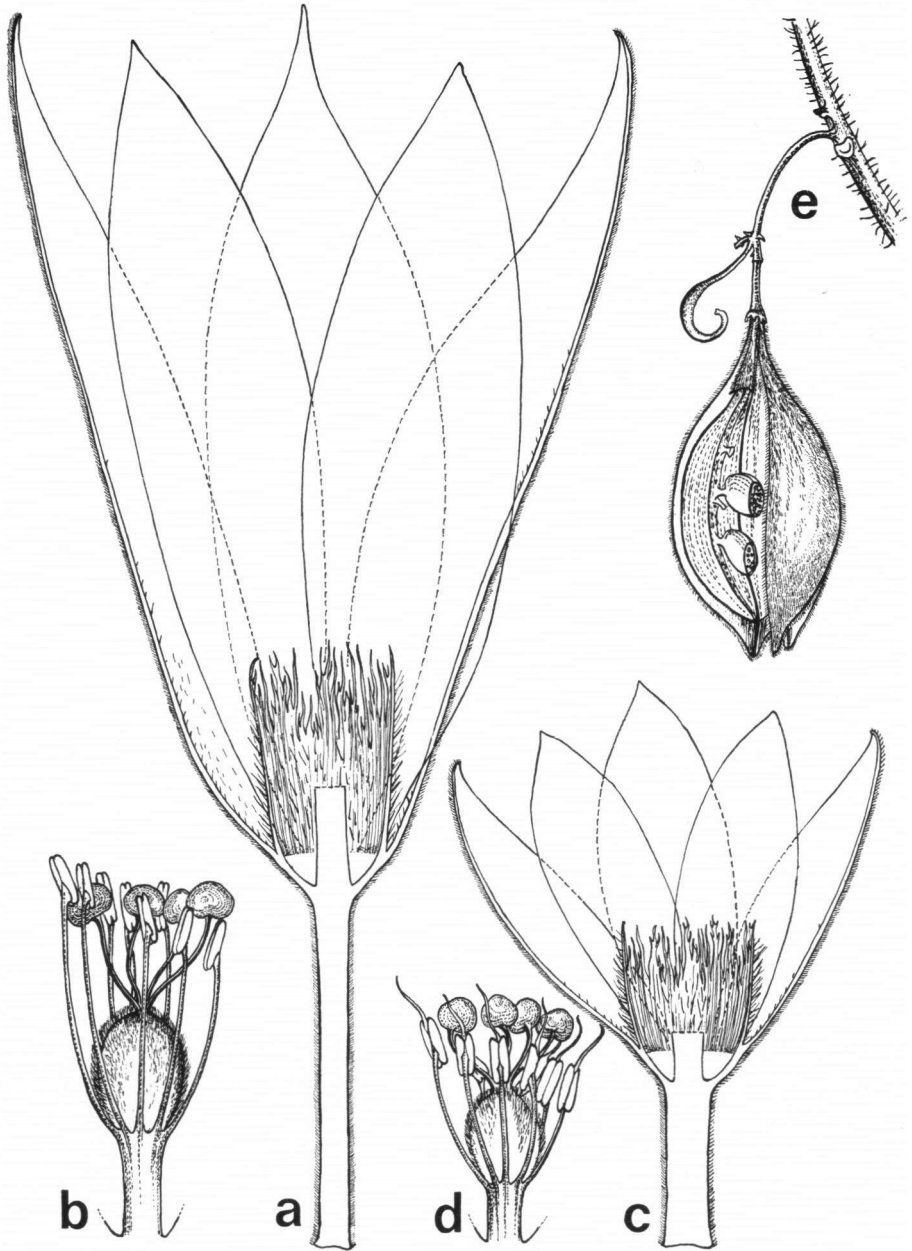


Fig. 2. Two remarkably different flowers of *Ancistrothyrsus tessmannii* Harms. a—b. Longitudinal section and separate androgynoecium of a mature flower from *Ducke* 24385, anthers non-apiculate,  $\times 3$ . c.—d. Ditto, from *Ducke* 35681, a small-flowered specimen; note the longly apiculate anthers,  $\times 3$ . e. Infructescence in the axil of a leaf-scar; note the accessory bud; from *Ducke* 24384,  $\times \frac{1}{2}$ .

from Chile, are no tendril-climbers and their ramification is similar to that of other *Flacourtiaceae*. In the erect, but rarely ramified *Phyllobotryeae* (*Phyllobotryum*, *Phylloclinium*, and *Moquersia*), the racemose inflorescence, from the axillary bud, is concaulescent with the midrib of the leaf, and the accessory bud here occupies the place of the axillary bud. The only examples in *Flacourtiaceae* in which the inflorescences are cymose and in which also an accessory bud is sometimes present, seem to be the few species of *Laetia* sect. *Laetia* (fig. 1 p). The seemingly cymose inflorescences of some species of *Hydnocarpus* are in fact of a basically racemose construction.

As to the *Paropsieae*, all are non-climbing except the genus *Ancistrothyrsus*. The deviating horseshoe-shaped inflorescences in *Barteria* can be explained by assuming that the racemose inflorescence [in which the flowers develop from the bottom to the top, and not the reverse as erroneously depicted by Warburg (1893, p. 8, f. 2) and again by Gilg (1925, p. 384)] is 'locked in' between the axis and the petiole which are concaulescent; the many bracts below each flower suggest originally a compound inflorescence in which each lateral raceme is reduced to a single flower.

The climbing habit in *Ancistrothyrsus*, unique in the *Paropsieae*, induced me to a closer examination of that genus. Harms (1931) described this genus in the *Paropsieae*, but in his discussion he pointed to the intermediate position of the tribe, between *Passifloraceae* and *Flacourtiaceae*. Furthermore he stated on *Ancistrothyrsus*: 'Oberhalb des Blütenstandes steht, wie bei *Passiflora*, eine winzige Beiknospe, die jedenfalls die Verzweigung besorgt'. He also pointed to the tendril-bearing inflorescences, resembling those of *Passiflora*. In a later article (1932, p. 599) Harms wrote: 'Wie bei den *Passifloraceae* ist die Ranke der primäre Axelspross, und über ihr sitzt eine winzige Beiknospe, die die Verzweigung fortsetzen soll'.

A re-examination of the flowers and the fruit of three collections from the Utrecht Herbarium (*Ducke 24384, 24385, 35681*) revealed that *Ancistrothyrsus* must be referred to *Passifloraceae*; only the pubescence of the corona is reminiscent of a *Paropsia* flower. It also appeared that in this genus specimens occur with highly differently shaped flowers, apparently hermaphroditic, but possibly functionally unisexual. Both types of flowers are depicted in fig. 2. The smaller type of flowers has not been described by Harms.

The findings on the mode of ramification in the *Paropsieae* strengthens affinity of this tribe with *Flacourtiaceae*. For other reasons, however, mainly the presence of a corona, and also anatomical and palynological evidence, the tribe — which remains to occupy an intermediate position — seems better be classified in *Passifloraceae*. Not unlikely, the fundamental divergence into a group of tendril-climbers — in which essentially the axillary buds, through the mediation of the cymose axillary inflorescences, provided for the necessary tendrils — and an arboreous group must have been an early event in evolution.

A tentative key to the genera of the *Passifloraceae*, also serving to distinguish *Flacourtiaceae* and *Passifloraceae*, may run as follows<sup>1</sup>):

- 1. (Extra-staminal) corona absent. Shrubs or trees, rarely scandent, without tendrils. Inflorescences axillary, racemose or rarely cymose. Vegetative ramification mostly through the axillary bud. Stamens 5 to many . . . . . FLACOURTIACEAE
- 1. (Extra-staminal) corona present . . . . . PASSIFLORACEAE
  - 2. Shrubs or trees, never with tendrils. Inflorescences axillary, racemose or cymose (?); these always produced on inflorescences-bearing shoots which develop from the axillary bud. Vegetative ramifi-

<sup>1</sup>) As compared with Hutchinsons key and list (1967) the genus *Carania* Chiov. (type examined in Florence) is a synonym of *Tryphostemma*; the ill-known genus *Trichostephanus*, and also the genera *Physena* and *Soyauxia* seem to be excluded from *Passifloraceae*; *Machadoa* and *Keramanthus* are synonymous with *Adenia*.

- cation through the axillary bud. Stamens 5 to many. . . . . Tribe *Paropsieae*
3. Style single, with one broad stigma. Corona double. Stamens numerous . . . . *Barteria*
3. Styles (2—)3—6.
4. Corona double . . . . . *Paropsiopsis*
4. Corona single.
5. Stamens 5.
6. Filaments connate at the base into a tube enveloping the ovary . *Androsiphonia*
6. Filaments free . . . . . *Paropsis*
5. Stamens 10 or more.
7. Stamens 10—16. Androgynophore present. . . . . *Viridivia*
7. Stamens 6 or more. Androgynophore absent. . . . . *Smeathmannia*
2. Mostly tendril-climbers. Inflorescences axillary, cymose; these along normal stems or often in special inflorescences-bearing shoots, or rarely in raceme-like short-shoots from the accessory bud. Vegetative ramification always through the accessory bud. Stamens 4—10 . . . . . Tribe *Passiflorae*
8. Androgynophore distinct, if not so than the gynophore distinct (much longer than the ovary).
9. Whole plant, incl. the tubiform lacinate corona hairy. Flowers 4-merous. Plant (leaves) with scale-like glands . . . . . *Ancistrothyrsus*
9. Corona various, but not hairy itself. No scale-like glands.
10. Androgynophore long. Hypanthium well-developed. Stigmas  $\pm$  globular. Flowers mostly 5-merous . . . . . *Passiflora*
10. Androgynophore short. Hypanthium small. Stigmas finely lobed.
11. Flowers 5-merous. Corona composed of two rows of filaments. Styles short  
*Hollrungia*
11. Flowers 4-merous. Corona a single row of filaments. Styles long. Flowers unisexual  
*Tetrapathaea*
8. Androgynophore absent or very short; gynophore shorter than the ovary.
12. Leaves simple, though sometimes deeply incised.
13. Corona well-developed. Disk ring-shaped, or absent. Anthers rather broad, dorsifixed. Flowers bisexual.
14. Style-arms 3 or 4, free or partly connate.
15. Filaments inserted on the hypanthium.
16. Hypanthium short, cup-shaped. Styles free. . . . . *Mitostemma*
16. Hypanthium tubiform. Styles partly united . . . . . *Dilkea*
15. Filaments inserted on the inner side of the inner corona. . *Tryphostemma*
14. Style single, with a simple stigma. . . . . (incl. *Schlechterina*) *Crossostemma*
13. Corona ill-developed. Disk mostly consisting of 5 strap-shaped segments. Anthers narrow, basifixed. Flowers mostly unisexual . . . . . *Adenia*
12. Leaves compound. . . . . (incl. *Efulensia*) *Deidamia*

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