

# Apocynaceae

## The Milkweed and Oleander Family

411 genera

4,650 species



### Distribution:

Widespread in pantropical and subtropical regions, though some occur in temperate zones.

### Economic Uses:

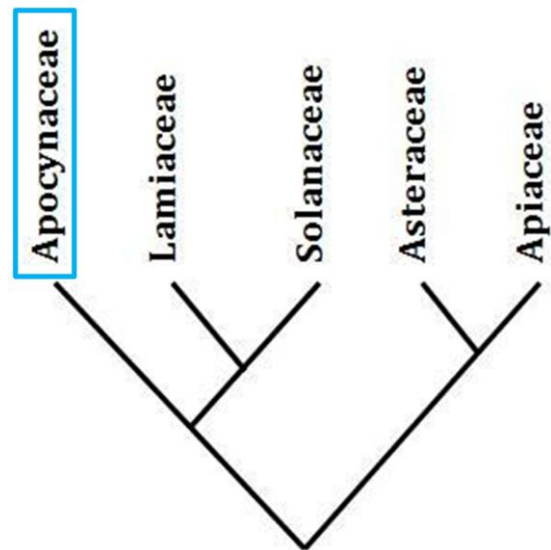
- Many genera of this family produce cardiac glycosides that are used for many medical treatments. These have traditionally been used in folk medicines but are also now important in treating mental illness and cancer.
- India rubber is valuable and extracted from *Hancornia speciosa*, *Funtumia elastic*, and species of *Landolphia*.
- Many members of this family are also cultivated as ornamentals, such as *Vinca* (periwinkles).
- In some regions, some taxa have large ecological importance, such as *Asclepias* (milkweed).

### Characteristic features:

- Trees, shrubs, herbs, lianas, and vines.
- Laticifers and usually milky sap.
- Usually opposite leaves.

- Flowers: usually 5 sepals, usually 5 petals, connate and forming bell- funnel- or tubular-shaped corolla; usually 5 stamens, filaments always adnate to the corolla, anthers distinct or connate and forming a ring fused to the stylar head; staminal outgrowths (corona) often present and petal-like; usually 2 carpels, connate by styles/stigmas only & ovaries distinct to fully connate, superior ovary; apex of style expanded and highly modified, forming a 5-sided stylar head, secreting viscin.
- Pollen in sticky masses (w/viscin) or in pollinia.
- Fruits: often paired, each ovary developing into a dry follicle, drupe or berry.
- Sees flattened, often with a tuft of hairs.

**Asterids:** Reduced Phylogeny of Required Families



References for further inquiry:

- Endress, M.E. & Bruyns, P.V. A revised classification of the Apocynaceae. *s.l. Bot. Rev.* 66:1-56 (2000).
- Heywood, V.H., Brummitt, R.K., Culham, A., & Seberg, O. Apocynaceae. Pp. 38-40. In: *Flowering Plant Families of the World*. New York, Firefly Books (2007).

## APOCYNACEAE

夹竹桃科 jia zhu tao ke

Li Ping-tao<sup>1</sup>; Antony J. M. Leeuwenberg<sup>2</sup>, David J. Middleton<sup>3</sup>

Trees, shrubs, or vines, rarely subshrubs or herbs, with latex or rarely watery juice. Leaves simple, opposite, rarely whorled or alternate, pinnately veined; stipules absent or rarely present. Inflorescences cymose, terminal or axillary, with bracteoles. Flowers bisexual, 5- [or 4]-merous, actinomorphic. Calyx 5- or rarely 4-partite, quincuncial, basal glands usually present. Corolla 5- or rarely 4-lobed, salverform, funnelform, urceolate, or rarely rotate, lobes overlapping to right or left, rarely valvate. Stamens 5 or rarely 4; filaments short; anthers mostly sagittate, free or connivent into a cone adherent to pistil head, dehiscing longitudinally, base rounded, cordate, sagittate, or prolonged into an empty spur; pollen granular; disc ringlike or cup-shaped, 2–5-lobed, or absent. Ovaries superior, rarely half-inferior, connate or distinct, 1- or 2-locular; ovules (1 or) 2–numerous per locule. Style 1; pistil head capitate, conical, or lampshade-shaped, base stigmatic, apex 2-cleft and not stigmatic. Fruit a berry, drupe, capsule, or follicle. Seeds with or without coma; endosperm thick and often horny, scanty, sometimes absent; embryo straight or nearly so, cotyledons often large, radicle terete.

About 155 genera and 2000 species distributed primarily in the tropics and subtropics, poorly represented in the temperate regions. Of the 44 genera and 145 species present in China, one genus and 38 species are endemic, and nearly 95% of the taxa grow in the southern and southwestern portions of the country.

Fruit type is highly diversified in the family, and it is diagnostic of many genera. Genera 1–4 produce 1, 2-celled berries from a flower; genus 5 produces 2, 1-celled berries from a flower; 6 and 7 produce mostly fleshy follicles containing deeply indented seeds with ruminant endosperm; 8 has follicles and winged seeds; 9 produces follicles and seeds with 2 comas; 10–12 have follicles with globose seeds; 13–18 have drupes mostly with fleshy mesocarp; 19 has samaroid fruit; 20 has spiny capsules with seeds winged all around; and 21–44 have free or fused follicles and comose seeds. Double flowers are known only from cultivated forms of *Nerium oleander*, *Tabernaemontana divaricata*, and *Wrightia religiosa*.

Plants of the Apocynaceae are often poisonous and are rich in alkaloids or glycosides, especially in the seeds and latex. Some species are valuable sources of medicine, insecticides, fibers, and rubber.

Tsiang Ying & Li Ping-tao. 1977. Apocynaceae. Fl. Reipubl. Popularis Sin. 63: 1–249.

- 1a. Herbs, sometimes with a woody base.
  - 2a. Plants with stolons; corolla violet ..... 12. *Vinca*
  - 2b. Plants without stolons; corolla mostly pink or white, sometimes bluish.
    - 3a. Leaf blade with pale venation; corolla tube narrow, 2–3 cm ..... 11. *Catharanthus*
    - 3b. Leaf blade without pale venation; corolla tube narrow or broad, up to 1 cm.
      - 4a. Corolla salverform, lobes overlapping to left; all leaves alternate ..... 10. *Amsonia*
      - 4b. Corolla campanulate or basin-shaped, lobes overlapping to right; usually some leaves opposite .... 36. *Apocynum*
- 1b. Trees, shrubs, or woody climbers.
  - 5a. Shrubs or climbers with straight spines ..... 1. *Carissa*
  - 5b. Plants without spines.
    - 6a. Leaves alternate.
      - 7a. Branchlets mostly 2–3 cm in diam.; flowers waxy; fruit a follicle; seeds winged ..... 8. *Plumeria*
      - 7b. Branchlets less than 1 cm in diam.; flowers not waxy; fruit a drupe; seeds wingless.
        - 8a. Corolla white, often with a deep pink-red or yellow throat, tube cylindrical or nearly so; fruit subglobose ..... 18. *Cerbera*
        - 8b. Corolla yellow, tube funnelform; fruit rhomboid or nearly so ..... 17. *Thevetia*
    - 6b. Leaves opposite or whorled.
      - 9a. Leaves whorled, at least toward tips of branches.
        - 10a. Corolla yellow, tube at least 4 cm; fruit globose, prickly ..... 20. *Allamanda*
        - 10b. Corolla variously colored, usually not yellow, tube up to 2.2 cm; fruit globose or not, smooth.
          - 11a. Corolla tube funnelform, 1.2–2.2 cm, with corona; leaves thick, lanceolate, with dark reticulate venation abaxially; fruit a united pair of follicles ..... 28. *Nerium*
          - 11b. Corolla tube almost cylindrical, mostly up to 1 cm, if longer than without a corona; leaves often not very thick, variously shaped; fruit a pair of drupes or free follicle.
            - 12a. Climbers, if erect shrubs then fruit moniliform with 1–4 drupelike articles.
              - 13a. Leaves with hairy domatia; fruit follicular, constricted; seeds comose ..... 39. *Parameria*
              - 13b. Leaves without hairy domatia; fruit moniliform, sometimes globose,

<sup>1</sup> Department of Forestry, South China Agricultural University, Wushan, Tianhe, Guangzhou, Guangdong 51064, People's Republic of China.

<sup>2</sup> Department of Plant Taxonomy, Wageningen Agricultural University, P. O. Box 8010, 6700 ED Wageningen, The Netherlands.

<sup>3</sup> Department of Botany, Trinity College, University of Dublin, Dublin 2, Ireland.

- transversely constricted into 2–5 drupelike articles ..... 14. *Alyxia*
- 12b. Erect trees or shrubs, fruit not moniliform.
- 14a. Fruit slender follicles; seeds hairy; disc of 2 separate glands alternating with carpels, small annular, or absent; often big trees ..... 9. *Alstonia*
- 14b. Fruit drupes; seeds not hairy; disc ringlike, cup-shaped, or absent; small trees or shrubs.
- 15a. Corolla lobes overlapping to right, often suberect; disc absent; drupes mostly more than 3 cm; mesocarp fibrous ..... 16. *Ochrosia*
- 15b. Corolla lobes overlapping to left, spreading; disc ringlike or cup-shaped; drupes up to 2 cm; mesocarp fleshy ..... 13. *Rauvolfia*
- 9b. All leaves opposite.
- 16a. Corolla lobes overlapping to left.
- 17a. Climbers.
- 18a. Corolla tube cylindrical or narrowed at throat; fruit berrylike.
- 19a. Disc absent; calyx without colleters inside; corolla with faucal corona scales, tube almost cylindrical ..... 3. *Melodinus*
- 19b. Disc cylindrical, thick, fleshy; calyx with basal colleters inside; corolla without faucal corona scales, tube inflated at base, contracted at mouth ..... 4. *Bousigonia*
- 18b. Corolla tube funnelliform or nearly so, not narrowed at throat; fruit follicular.
- 20a. Corolla tube 2–2.5 mm; follicles moniliform ..... 39. *Parameria*
- 20b. Corolla tube ca. 12 mm; follicles narrowly fusiform ..... 42. *Parepigynum*
- 17b. Trees or shrubs.
- 21a. Leaf blades with numerous parallel secondary veins; fruit samaroid follicles ..... 19. *Cameraria*
- 21b. Leaf blades with secondary veins clearly separate from each other and usually with tertiary veins; fruit berries or wingless follicles.
- 22a. Stamens well exerted; corona usually present; fruit long dry follicles; seeds comose ..... 29. *Wrightia*
- 22b. Stamens included or barely exerted; corona absent; fruit mostly berrylike; seeds not comose.
- 23a. Inflorescences fascicled, axillary; fruit of united carpels ..... 2. *Acokanthera*
- 23b. Inflorescences corymbose, terminal, at branch forks, or sometimes axillary; fruit of at least partly separated carpels.
- 24a. Branching not dichotomous; submarginal leaf veins present; corolla tube ca. 7 × as long as calyx ..... 5. *Hunteria*
- 24b. Branching dichotomous; submarginal leaf veins absent or obscure; corolla tube long or short.
- 25a. Corolla tube slightly shorter or longer than calyx; calyx shed before fruit develops, lobes recurved ..... 6. *Voacanga*
- 25b. Corolla tube at least 4 × as long as calyx; calyx persistent at fruit base, lobes erect in fresh flowers ..... 7. *Tabernaemontana*
- 16b. Corolla lobes overlapping to right.
- 26a. Trees or shrubs; corolla lobes not caudate.
- 27a. Corolla tube 2.3–5 cm, very narrow; fruit drupaceous; seeds not comose ..... 15. *Kopsia*
- 27b. Corolla tube up to 1.9 cm; fruit follicular; seeds comose.
- 28a. Peduncle 0.9–1.7 cm; sepals mostly pubescent outside; corolla tube 0.9–1.9 cm; seeds not beaked ..... 35. *Holarrhena*
- 28b. Peduncle absent or to 0.8 cm; sepals glabrous or sparsely puberulent outside; corolla tube up to 1.3 cm; seeds beaked.
- 29a. Stamens exerted; pedicel 1.5–3 cm; corolla lobes 1.2–1.8 × as long as tube; domatia mostly absent ..... 33. *Kibatalia*
- 29b. Stamens included; pedicel 2–8 mm; corolla lobes 0.4–0.9 × as long as tube; domatia consisting of pits ..... 34. *Funtumia*
- 26b. Climbers, if plants erect, corolla lobes caudate (*Strophanthus*).
- 30a. Corolla funnelliform to subcampanulate and/or tube more than 2 cm, nearly urceolate (*Urceola*) or subrotate (*Vallaris*).
- 31a. Corolla with corona, lobes caudate or sometimes (*S. gratus*) not; seeds beaked ..... 32. *Strophanthus*
- 31b. Corolla without corona, lobes not caudate; seeds mostly not beaked.

- 32a. Stamens exerted.
- 33a. Filaments long, without a dorsal gland; corolla broadly funnelform ..... 30. *Beaumontia*
- 33b. Filaments short, with a dorsal gland; corolla subtrotate ..... 31. *Vallaris*
- 32b. Stamens included.
- 34a. Corolla tube 1–4 mm, nearly urceolate; inflorescences many flowered, lax ..... 38. *Urceola*
- 34b. Corolla tube at least 20 mm; inflorescences usually few flowered, not lax.
- 35a. Plants glabrous or nearly so ..... 21. *Mandevilla*
- 35b. Plants conspicuously hairy.
- 36a. Corolla tube cylindric, limb spreading horizontally, often very wide; follicles more than 5 × as long as wide ..... 24. *Chonemorpha*
- 36b. Corolla tube clearly widened toward throat, limb probably not horizontal; follicles ca. 3 × as long as wide ..... 25. *Amalocalyx*
- 30b. Corolla salverform, tube up to 1.4 cm (1.5–2.5 cm in *Aganosma benthamiana*).
- 37a. Stamens exerted.
- 38a. Corolla tube 7–13 mm; filaments straight; follicles very slender, of separate carpels ..... 27. *Pottsia*
- 38b. Corolla tube to 5 mm; filaments strongly twisted; follicles rather thick, of united carpels ..... 26. *Parsonsia*
- 37b. Stamens included.
- 39a. Anther apex with long soft hairs.
- 40a. Corolla tube 5–15 mm, 3–8.7 × as long as sepals ..... 44. *Sindechites*
- 40b. Corolla tube 1.6–2.5 mm, 1.3–2.3 × as long as sepals ..... 43. *Cleghornia*
- 39b. Anther apex glabrous.
- 41a. Disc divided into 5 erect segments or 5 free scales.
- 42a. Corolla tube ca. 5 × as long as sepals, 1.5–1.7 cm; inflorescences terminal ..... 41. *Epigynum*
- 42b. Corolla tube mostly to 3 × as long as sepals, to 1.4 cm; inflorescences axillary and/or terminal.
- 43a. Corolla tube 4.5–14 mm, lobes 5–14 mm, forming in bud a large, rather narrowly ovoid, subacuminate head much wider than tube which is clearly widened around or above middle of stamens ..... 22. *Trachelospermum*
- 43b. Corolla tube 2.5–3 mm, lobes 3–5 mm, forming in bud a small subglobose or ovoid, rounded or blunt head not or slightly wider than tube which is ± barrel-shaped ..... 40. *Ichnocarpus*
- 41b. Disc entire or shortly 5-lobed.
- 44a. Sepals more than twice as long as wide, acuminate or acute, often spreading and longer than corolla tube, if about half as long, then leaf blade with a submarginal vein (*A. marginata*) ..... 23. *Aganosma*
- 44b. Sepals less than twice as long as wide, acute to rounded, erect or apically slightly spreading, up to half as long as corolla tube.
- 45a. Corolla lobes neither twisted nor forming a head in bud; bud rounded, almost cylindric ..... 40. *Ichnocarpus*
- 45b. Corolla lobes twisted in bud, forming a large ovoid head; bud subacute.
- 46a. Corolla tube bottle-shaped, clearly narrowed at apex; follicles cylindric ..... 24. *Chonemorpha*
- 46b. Corolla tube cylindric or nearly so; follicles very narrowly ovoid ..... 37. *Anodendron*

**1. CARISSA** Linnaeus, Mant. Pl. 1: 52. 1767, nom. cons.

假虎刺属 jia hu ci shu

Shrubs, climbers, or small trees, mostly spiny. Branches dichotomous. Leaves opposite; petiole 2–3 mm. Cymes terminal or axillary, dichotomous, pedunculate, usually many flowered. Flowers 5- [or 4]-merous. Calyx without glands or rarely with many basal glands inside. Corolla salverform, tube cylindric, dilated at staminal insertion, lobes overlapping to left or to right. Stamens included in throat; anthers lanceolate, obtuse or apiculate, base not appendaged; disc absent. Ovary 2-loculed; ovules 1–4 in each locule, rarely numerous, biseriate. Style filiform; pistil head narrowly oblong or fusiform, apex shortly 2-cleft. Berries 1- or 2-loculed. Seeds 2 or more, peltate; endosperm fleshy; cotyledons ovate, radicle inferior.

About 30 species: tropics and subtropics of Africa, Asia, and Australia; four species in China.

- 1a. Corolla lobes overlapping to left, as long as or longer than tube ..... 1. *C. macrocarpa*  
1b. Corolla lobes overlapping to right, shorter than tube.  
2a. Lateral veins of leaf blade ca. 8 pairs; corolla puberulent inside; fruit ellipsoid, 1.5–2.5 × 1–2 cm ..... 4. *C. carandas*  
2b. Lateral veins of leaf blade 3–5 pairs; corolla glabrous or pubescent inside; fruit globose, 0.5–1.2 cm in diam.  
3a. Secondary veins conspicuous on adaxial leaf surface; branches and abaxial leaf surface puberulent ..... 3. *C. spinarum*  
3b. Secondary veins of leaf blade inconspicuous; branchlets and leaves glabrous in plants introduced into China ..... 2. *C. edulis*

**1. *Carissa macrocarpa*** (Ecklon) A. de Candolle, Prodr. 8: 336. 1844.

大花假虎刺 da hua jia hu ci

*Arduina macrocarpa* Ecklon, S. African J. 1: 372. 1830; *A. grandiflora* E. Meyer; *Carissa grandiflora* (E. Meyer) A. de Candolle.

Shrubs or small trees to 5 m tall. Spines 1- or 2-forked, 2–4 cm, strong. Leaf blade broadly ovate, 2.5–7.5 × 2–5 cm, thick leathery, glabrous, base rounded to obtuse, apex mucronate, lateral veins obscure. Cymes terminal, (1–)3-flowered. Pedicel 2–3 mm. Flowers fragrant. Sepals very narrowly ovate, 3–6 mm. Corolla white or pink, tube 1.1–1.8 cm, pubescent inside; lobes oblong, 0.9–2.4 cm, overlapping to left. Ovules numerous. Berries bright red to violet, ovoid, 2–5 cm, ca. 16-seeded. Fl. Aug.  $2n = 66$ .

S Fujian and S Guangdong [introduced from S Africa].

Cultivated for its edible fruit.

**2. *Carissa edulis*** (Forsskål) Vahl, Symb. Bot. 1: 22. 1790.

甜假虎刺 tian jia hu ci

*Antura edulis* Forsskål, Fl. Aegypt.-Arab. 63. 1775; *Arduina edulis* (Forsskål) Spreng; *Carandas edulis* (Forsskål) Hiern; *Jasminonerium edule* (Forsskål) Kuntze.

Plants small trees or climbing in the wild, much branched shrubs to 5 m in cultivation; spines usually simple, straight or recurved, 2.5–5 cm. Leaf blade ovate to obovate or suborbicular, 2–5 × 2–4 cm, leathery, glabrous; lateral veins 3–5 pairs, inconspicuous. Sepals very narrowly oblong, 2–4.5 mm, ciliolate, glabrous outside. Corolla white or tinged with pink, glabrous outside, slightly hairy at mouth and on inner lobe surface, tube 0.9–2 cm; lobes ovate or oblong, 3–9 mm, convergent, anastomosing near margin. Cymes terminal, usually 3-flowered; peduncle 1.5–2.5 cm; bracteoles minute. Flowers fragrant. Pedicel about as long as calyx or slightly longer. Sepals 2.5–7 mm, with many basal glands inside.

acute at apex, overlapping to right. Berries purple to red, globose, 7–10 mm in diam. Seeds 2–4.  $2n = 22$ .

S Yunnan [native of tropical Africa and S Arabia].

Cultivated for its edible fruit.

**3. *Carissa spinarum*** Linnaeus, Mant. Pl. 2: 559. 1771.

假虎刺 jia hu ci

*Carissa diffusa* Roxburgh; *C. yunnanensis* Tsiang & P. T. Li.

Shrubs or small trees to 5 m tall; spines simple or forked, 1.2–6 cm. Leaf blade ovate to elliptic, 0.5–5.5 × 0.3–2.5 cm, leathery, finely puberulent abaxially, base rounded or acute, apex acute or short acuminate; lateral veins 3–5 pairs, conspicuous. Cymes terminal or axillary, 3–7-flowered, finely puberulent. Sepals ca. 2.5 × 1 mm, without glands. Corolla white, tube ca. 1 cm, lobes 5–7 mm, overlapping to right; ovules 1 in each locule. Berries shining black, subglobose, 5–12 mm. Seeds 3–5 mm. Fl. Mar–May, fr. Sep–Dec.  $2n = 22$ .

Bushes, roadsides, forest edges. Guizhou, Sichuan, Yunnan [India, Myanmar, Sri Lanka, Thailand].

The roots are used to treat hepatitis and rheumatoid arthritis.

**4. *Carissa carandas*** Linnaeus, Mant. Pl. 1: 52. 1767.

刺黄果 ci huang guo

*Arduina carandas* (Linnaeus) K. Schumann; *Damna-canthus esquirolii* H. Léveillé.

Shrubs, small trees, or climbers to 5 m tall. Spines simple or forked, to 5 cm. Leaf blade broadly ovate to oblong, 3–7 × 1.5–4 cm, base broadly cuneate to rounded, apex short apiculate; lateral veins ca. 8 pairs, ascending,

Corolla white or pale rose; tube to 2 cm, puberulent inside; lobes lanceolate, ca. 1 cm, acute, overlapping to right, puberulent, ciliate. Ovules numerous in each locule. Berries reddish purple, ellipsoid, 1.5–2.5 × 1–2 cm. Fl. Mar–Jun, fr.

Jul-Dec.  $2n = 22$ .

Fujian, Guangdong, Guizhou, Hainan, Taiwan [India, Indonesia, Malaysia, Myanmar, Sri Lanka, Thailand]. Cultivated for its edible fruit, which can be eaten raw, made into jelly, or used for pies.

## 2. ACOKANTHERA G. Don, Gen. Hist. 4: 485. 1838.

长药花属 chang yao hua shu

Shrubs or small trees, latex white. Leaves opposite. Corymbs short pedunculate or sessile, axillary, often fascicled. Flowers subsessile, usually sweet scented. Calyx small, without glands inside. Corolla white or pink tinged, salverform, tube slightly widened near mouth; lobes short, overlapping to left; corona absent. Stamens inserted in widened part of corolla tube; anthers ovate to oblong, connective produced into a short, minutely pilose point, shortly 2-lobed at base; disc absent. Ovary 1, 2-loculed; ovules 1 per locule. Style filiform; pistil head cylindrical or short conical, base with a ring of papillae, apex minutely 2-lobed. Berry globose or elliptic. Seeds 1 or 2, not comose; endosperm bony; cotyledons broadly ovate or subcordate, radicle superior.

Five species: S and tropical E Africa, Arabia; one species in China.

**1. *Acokanthera oppositifolia*** (Lamarck) Codd, *Bothalia* 7: 448. 1961.

长药花 chang yao hua

*Cestrum oppositifolium* Lamarck, *Tabl. Encycl.* 2: 5, t. 112, fig. 2. 1794.

Shrubs to 5 m tall. Branchlets compressed when young, terete with age. Petiole 2–6 mm; leaf blade mostly obovate, occasionally elliptic, 4–10 × 2–7 cm, lateral veins 6–10 pairs.

Inflorescences sessile or subsessile, clustered, glabrous or puberulent, usually many flowered; bracts brown or distal ones pinkish, ovate. Sepals ovate to very narrowly ovate. Corolla white to pink, tube 0.8–1.3 cm, glabrous or puberulent outside, hairy inside; lobes broadly ovate, 2–4.5 mm. Berry purplish black, globose, 2.5–3 cm in diam. Seeds semiglobose or semi-ellipsoid, 0.8–1.2 cm.  $2n = 22$ .

Beijing [native of S Africa].

Cultivated for medicine.

## 3. MELODINUS J. R. & G. Forster, *Char. Gen. Pl.* 37, t. 19. 1776.

山橙属 shan chen shu

Plants woody lianas or sometimes low shrubs, latex present. Leaves opposite. Cymes terminal or axillary. Flowers white. Calyx without glands. Corolla salverform; tube cylindrical, dilated at staminal insertion; lobes usually oblique-falcate, overlapping to left; corona scales 5 or 10, erect. Stamens inserted at or below middle of corolla tube, included; filaments very short; anthers free from pistil head, base rounded; disc absent. Ovary 2-loculed; ovules numerous. Style short; pistil head apex dilated, 2-cleft. Berry large, pulpy. Seeds numerous; coma absent.

About 50 species: tropical or subtropical Asia and Australia; 12 species in China.

- 1a. Flowers always axillary; apex of flower bud acuminate ..... 1. *M. axillaris*
- 1b. Flowers at least partly terminal; apex of flower bud rounded to subacute.
  - 2a. Leaves pubescent, at least abaxially.
    - 3a. Branchlets and leaf blade puberulent to glabrescent abaxially; lateral leaf veins ca. 15 pairs ..... 11. *M. fusiformis*
    - 3b. Branchlets and leaf blade densely pubescent abaxially; lateral leaf veins 8–10 pairs.
      - 4a. Leaf blade elliptic or oblong; sepals ca. 7 mm; corolla lobes narrowly elliptic, ca. 8 mm; berries ellipsoid; seeds narrowly elliptic, ca. 9 mm ..... 10. *M. hemsleyanus*
      - 4b. Leaf blade broadly ovate to orbicular; sepals 3–4 mm; corolla lobes oblong, falcate, ca. 13 mm; berries fusiform; seeds orbicular, ca. 6 mm ..... 12. *M. morsei*
  - 2b. Leaves glabrous or sparsely hairy along midvein only.
    - 5a. Leaf blade with lateral veins arcuate-ascending.
      - 6a. Fruit ca. 1.8 × 0.7 cm; shrubs to 0.6 m ..... 8. *M. chinensis*
      - 6b. Fruit 5.5–10.5 × 2–10.5 cm; woody lianas to 10 m.
        - 7a. Young branches and leaves scaly; sepals acute; fruit ca. 10.5 cm in diam. .... 2. *M. yunnanensis*
        - 7b. Plant glabrous except for inflorescences; sepals rounded; fruit to 9 cm.
          - 8a. Corolla lobes falcate with a distinct subterminal notch; fruit ± globose, to 8 cm in diam. .... 3. *M. suaveolens*
          - 8b. Corolla lobes ovate; fruit cylindrical-ellipsoid, ca. 5 cm wide ..... 9. *M. cochinchinensis*
      - 5b. Leaf blade with lateral veins closely parallel at 70–80° to midvein.
        - 9a. Material with flowers.

- 10a. Corolla lobes orbicular.  
 11a. Leaf blade very narrowly elliptic, up to 2.1 cm wide; (100–1000 m; Taiwan) ..... 4. *M. angustifolius*  
 11b. Leaf blade elliptic, 3(–4) cm wide; (1600–2900 m; Guizhou, Yunnan) ..... 5. *M. khasianus*  
 10b. Corolla lobes ovate, oblong, or obliquely obovate.  
 12a. Leaf blade thinly membranous; corolla exterior and corona scales glabrous ..... 6. *M. tenuicaudatus*  
 12b. Leaf blade somewhat leathery; corolla exterior and corona scales puberulent ..... 7. *M. magnificus*  
 9b. Material with fruit.  
 13a. Fruit ± fusiform, 2–3 cm wide, apex acuminate.  
 14a. Leaf blade very narrowly elliptic, ± leathery (100–1000 m; Taiwan) ..... 4. *M. angustifolius*  
 14b. Leaf blade oblong to narrowly oblong, membranous  
 (800–1800 m; Guangxi, Guizhou, Yunnan) ..... 6. *M. tenuicaudatus*  
 13b. Fruit ovoid or ellipsoid, 3–4 cm wide, apex rounded to subacute.  
 15a. Fruit ca. 5.5 cm; petiole glabrous; leaf blade 0.5–4 cm wide ..... 5. *M. khasianus*  
 15b. Fruit 6–8 cm; petiole pubescent; leaf blade 4–6.5 cm wide ..... 7. *M. magnificus*

**1. *Melodinus axillaris*** W. T. Wang ex Tsiang & P. T. Li, Acta Phytotax. Sin. 11: 349. 1973.

腋花山橙 ye hua shan chen

Lianas to 3 m. Branchlets angular, slightly pubescent. Petiole 5–9 mm; leaf blade oblong, 10–18 × 3.5–6 cm, papery, glabrous, base obtuse, apex acute; lateral veins 17–20 pairs, slightly prominent on both surfaces. Inflorescences axillary, 2–5-branched, 3.5–8 cm, pubescent; peduncle 2–3 cm; bracts and bracteoles narrowly elliptic, 2–3 mm, puberulent outside. Pedicel 2–3 cm. Flower buds narrowly oblong, short pubescent outside, acuminate. Sepals ovate, 3–3.5 × ca. 2 mm, glabrous outside, ciliate, apex obtuse. Corolla white, ca. 1.2 cm, tube pubescent inside; lobes oblong; corona scales villous. Filaments pubescent. Ovary glabrous. Style filiform; pistil head conical. Fl. May.

- Humid forests; 1000 m. S Yunnan.

The generic placement of this species is uncertain because no fruits have been seen.

**2. *Melodinus yunnanensis*** Tsiang & P. T. Li, Acta Phy-totax. Sin. 11: 355. 1973.

雷打果 lei da guo

Lianas to 10 m. Branches dark gray, glabrous; young branchlets and leaves scaly. Petiole 5–10 mm; leaf blade oblong or narrowly elliptic, 7–18 × 2.5–5.2 cm, papery, base rounded, apex acuminate; lateral veins 10–15 pairs, nearly flat on both surfaces. Cymes umbellate, terminal and axillary, 5–6.5 cm; peduncle 1.5–2 cm, glabrous; bracts and bracteoles 3–7 mm. Pedicel 5–7 mm, pubescent. Flower buds cylindrical, ca. 2 cm, glabrous outside. Sepals broadly ovate, ca. 7 × 5 mm, ciliate, apex acute. Corolla white, tube ca. 1.2 cm, pubescent inside; lobes oblong, ca. 1.1 cm; corona scales linear, decurrent to lower part of corolla tube, included. Ovary glabrous. Style very short. Berries globose, ca. 10.5 cm in diam. Fl. May.

- Dense montane forests; 1500–2000 m. W Guangxi, S Yunnan. ciliate, pubescent outside. Corolla white, 6–10 mm in diam., tube 5–8 mm; lobes orbicular, ca. 6 × 6 mm; corona scales 5, apex 2-cleft, slightly exerted from throat. Berries fusiform, 5–9 × 2–3 cm. Seeds black, triangular, smooth. Fl. summer-autumn.

**3. *Melodinus suaveolens*** (Hance) Champion ex Bentham, Hooker's J. Bot. Kew Gard. Misc. 4: 333. 1852.

山橙 shan chen

*Lycimnia suaveolens* Hance in Walpers, Ann. Bot. Syst. 3: 31. 1852; *Melodinus laetus* Champion ex Bentham.

Lianas to 10 m, glabrous except for inflorescences. Petiole to 1.2 cm; leaf blade elliptic or ovate, 5–10 × 1.8–5 cm, leathery, base attenuate to rounded, apex short acuminate. Cymes terminal and axillary. Flower buds rounded or obtuse at apex, minutely pubescent outside. Flowers fragrant. Sepals ovate, ca. 3 mm, minutely pubescent outside, apex rounded or obtuse. Corolla white, tube 1–1.4 cm; lobes 0.5–1 × as long as tube, suborbicular, falcate, with a distinct notch near apex; corona campanulate or tubular, apex 5-cleft, exerted from throat. Berries globose, 5–8 cm in diam. Fl. May–Nov, fr. Aug–Dec.

Open forests, humid brushwood; 100–800 m. Guangdong, Guangxi, Hainan [Vietnam].

A fine, strong bast fiber, obtained from the inner bark, is used in making ropes and sacks. The fruit is used to treat abdominal pain, infantile malnutrition due to intestinal parasites, indigestion, and hernia.

**4. *Melodinus angustifolius*** Hayata, J. Coll. Sci. Imp. Univ. Tokyo 30: 193. 1911.

台湾山橙 tai wan shan chen

Lianas to 5 m. Petiole 2–5 mm; leaf blade narrowly elliptic, 5–10 × 1–2.1 cm, somewhat leathery, base rounded to cuneate, apex acuminate; lateral veins subparallel, prominent on both surfaces. Cymes terminal and axillary, 1.5–2.5 cm, 3–12-flowered; bracts and bracteoles ovate, ca. 2 mm. Pedicel 2–4 mm. Sepals triangular, 1–2 mm,

- Thickets, coral rocks; 100–1000 m. Taiwan.

**5. *Melodinus khasianus*** J. D. Hooker, Fl. Brit. India 3: 629. 1882.

景东山橙 jing dong shan chen

Lianas to 10 m, glabrous except for flowers. Petiole 6–7 mm; leaf blade narrowly elliptic, 6–12 × 0.5–4 cm, base cuneate, apex short acuminate; lateral veins subparallel. Cymes or fascicles axillary near branch apex, 2.5–6.5 cm, few flowered; bracts ca. 3 mm. Sepals orbicular, ca. 3 mm, ciliate. Corolla white, tube ca. 6 mm; lobes orbicular, ca. 5.5 mm in diam., obliquely 2-lobed or 2-cleft at apex; corona scales 5, oblong. Berries ovoid, ca. 5.5 × 4 cm. Fl. Oct.

Humid forests, valleys; 1600–2900 m. Guizhou, Yunnan [India].

**6. *Melodinus tenuicaudatus*** Tsiang & P. T. Li, Acta Phytotax. Sin. 11: 353. 1973.

薄叶山橙 bao ye shan chen

Lianas to 4 m. Branches gray; branchlets gray yellowish. Petiole ca. 5 mm; leaf blade oblong to narrowly so, 6–15 × 1.5–4 cm, membranous, glabrous, base cuneate or broadly so, apex caudate-acuminate, acumen 1–1.5 cm; lateral veins numerous, subparallel at 70–80° to midvein, flat on both surfaces. Cymes umbellate, terminal, 4–6 cm, 3–5-flowered; peduncle ca. 1.2 cm, puberulent; bracts and bracteoles narrowly elliptic, 2.5–4 mm. Pedicel ca. 5 mm. Sepals ovate. Corolla white, tube ca. 1.8 cm, glabrous outside, pubescent inside; lobes oblong, as long as tube; corona scales 10, narrowly elliptic. Filaments puberulent. Berries sub-fusiform, 6.5–7 × 1.8–2.5 cm, acuminate at both ends or base obtuse. Fl. May-Sep, fr. Sep-Dec.

• Dense montane forests, brushwoods; 800–1800 m. Guangxi, Guizhou, Yunnan.

**7. *Melodinus magnificus*** Tsiang, Sunyatsenia 3: 128. 1936.

茶藤 cha teng

Lianas to 6 m. Branchlets dark brown, rust-colored pubescent. Petiole 6–8 mm, pubescent; leaf blade narrowly oblong, 12–21 × 4–6.5 cm, somewhat leathery, glabrous, base cuneate, apex acuminate or rarely obtuse; lateral veins 15–20 pairs, subparallel, pubescent. Cymes terminal, shorter than leaves; bracteoles sublinear, 3–5 mm, short pubescent. Sepals oblong, pubescent outside. Corolla white, puberulent outside; tube 1.5–1.7 cm, pubescent inside; lobes obliquely obovate, 1.5–1.8 cm; corona scales thick, indistinct, minutely pilose, adnate to corolla throat, apex shortly 2-cleft. Berries ellipsoid, 6–8 × 3–4 cm. Fl. Jun-Aug, fr. Oct-Dec.

• Sparse woods; 500–800 m. S Guangxi.

**8. *Melodinus chinensis*** P. T. Li & Z. R. Xu, Bull. Bot. Res., Harbin 5(2): 129. 1985.

贵州山橙 gui zhou shan chen

• Sparse montane woods; 500–1500 m. Guizhou, Sichuan, Yunnan.

**11. *Melodinus fusiformis*** Champion ex Benth, Hooker's J. Bot. Kew Gard. Misc. 4: 332. 1852.

尖山橙 jian shan chen

*Melodinus edulis* H. Léveillé; *M. esquirolii* H. Léveillé;

Shrubs to 60 cm tall. Branchlets yellowish gray, glabrous. Petiole ca. 5 mm; leaf blade narrowly elliptic, 5–9 × 1.5–3 cm, base cuneate, apex acuminate, midvein elevated abaxially; lateral veins numerous, nearly flat on both surfaces, glabrous. Cymes dichotomous, ca. 3-flowered; peduncle ca. 1 cm, glabrous; bracteoles 2, triangular, ca. 1.5 × 1.5 mm, pubescent. Pedicel 7–outside 10 mm, pubescent. Sepals ovate to triangular, ca. 3 mm, pubescent, glabrous inside, apex subacute to rounded. Berries ellipsoid, ca. 1.8 cm × 7 mm. Fl. May.

• Montane limestone brushwoods; 800 m. SE Guizhou (Lipo).

**9. *Melodinus cochinchinensis*** (Loureiro) Merrill, Trans. Amer. Philos. Soc. 24(2): 310. 1935.

思茅山橙 si mao shan chen

*Oncinus cochinchinensis* Loureiro, Fl. Cochinch. 1: 123. 1790; *Melodinus henryi* Craib.

Lianas stout, to 10 m, glabrous except for inflorescences. Branches dark brown. Petiole 6–10 mm; leaf blade elliptic or narrowly so, 6–19 × 2.2–6.5 cm, papery, base cuneate, apex acute or acuminate; lateral veins numerous, convergent, conspicuous. Cymes paniculate, terminal, 3-branched, 4–5.5 cm, minutely pilose; bracts and bracteoles minute. Pedicel short. Sepals orbicular or broadly elliptic, ca. 2 mm, ciliate, apex subacute to rounded. Corolla white; tube ca. 6 mm, pilose except at base; lobes ovate, ca. 3.5 mm; corona large, lobes 2-cleft, villous. Ovary glabrous. Style ca. 3 mm. Berries narrowly ellipsoid, ca. 9 × 5 cm. Seeds oblong or ovate, ca. 1.3 cm. Fl. Apr-May, fr. Sep-Nov.

Montane forests; 800–2800 m. S Yunnan [Myanmar, Thailand, Vietnam].

The fruit are used to treat infantile meningitis and fractures.

**10. *Melodinus hemsleyanus*** Diels, Bot. Jahrb. Syst. 29: 539. 1900.

川山橙 chuan shan chen

*Trachelospermum esquirolii* H. Léveillé.

Lianas stout, to 8 m, juvenile parts densely minutely tomentose. Petiole ca. 5 mm; leaf blade elliptic, oblong, or narrowly so, 7–15 × 4–5 cm, somewhat leathery, lustrous and glabrous adaxially, pubescent near veins abaxially, base cuneate or obtuse, apex acuminate; lateral veins ca. 10 pairs, conspicuous on both surfaces. Cymes terminal. Sepals ovate-oblong, ca. 7 mm, densely pubescent outside, apex acuminate. Corolla white, tube ca. 1 cm, puberulent on both surfaces; lobes narrowly elliptic, ca. 8 mm; corona scales minute, unequal. Berries ellipsoid, to 7.5 × 3 cm. Seeds narrowly elliptic, ca. 9 mm. Fl. May-Aug, fr. Jul-Dec.

*M. flavus* H. Léveillé; *M. seguinii* H. Léveillé; *M. wrightioides* Handel-Mazzetti.

Lianas stout, to 10 m, juvenile parts pubescent, later glabrescent. Bark gray-brown. Petiole 4–6 mm; leaf blade elliptic or oblong, rarely narrowly elliptic, 4.5–12 × 1–5.3 cm, somewhat leathery, base cuneate or rounded, apex acuminate; lateral veins ca. 15 pairs, obliquely spreading and reticulate



toward margin. Cymes terminal, 3–5 cm, 6–12-flowered. Pedicel 5–10 mm. Sepals ovate, 4–5 mm, acute. Corolla white, tube 1.2–2 cm; lobes obliquely narrow ovate or obovate, (0.8–)1.1–2 cm × 3.5–9 mm; corona scales 5, indistinct, exserted, villous, apex 2- or 3-cleft. Stamens inserted near base of corolla tube. Berries fusiform, 3.5–5.3 × 2.2–4 cm. Fl. Apr-Sep, fr. Jun-Dec.

• Sparse montane woods, valleys; 300–1500 m. Guangdong, Guangxi, Guizhou.

The plant is used for the treatment of rheumatism and injury. The fruit is poisonous.

**12. *Melodinus morsei*** Tsiang, Sunyatsenia 6: 110. 1941.

龙州山橙 long zhou shan chen

Lianas to 3 m. Branchlets tomentose. Petiole ca. 5 mm; leaf blade broadly ovate or orbicular, 4.5–9 × 2–7 cm, leathery, glabrescent and shiny adaxially, tomentose abaxially, base rounded or truncate, apex short acuminate; lateral veins 8–10 pairs, flat adaxially, slightly prominent abaxially. Cymes terminal, 6–8-flowered; peduncle 1–2 cm, tomentose. Pedicel ca. 3 mm. Sepals ovate, 3–4 × 2–2.5 mm, ciliate, villous outside, acute. Corolla white, tube ca. 1.5 cm, minutely tomentose; lobes oblong, falcate, ca. 13 × 4 mm; corona scales 5, oblong, pilose, apex 2-cleft. Filaments pilose. Ovary glabrous. Berries fusiform, ca. 8.5 × 2 cm, acuminate at both ends. Seeds orbicular, ca. 6 mm in diam. Fl. Aug-Oct, fr. Sep-Dec.

• Montane forests. N Guangdong, SW Guangxi.

**4. BOUSIGONIA** Pierre in Planchon, Prodr. Apoc. 324. 1894.

奶子藤属 nai zi teng shu

Lianas woody, latex white. Leaves opposite, veins parallel. Cymes axillary or terminal, long pedunculate. Flowers 5-merous. Calyx deeply divided, with basal glands inside. Corolla salverform, tube cylindrical, swollen at base, throat without corona scales; lobes overlapping to left. Stamens inserted at middle of corolla tube; filaments stout; anthers included, narrowly oblong, free from pistil head, lobes rounded at base; disc shorter than ovary, short cylindrical, fleshy, thick, apex entire or emarginate. Ovary entire, 1-loculed, placentas 2; ovules 2 on each placenta. Style short; pistil head dilated, apex 2-cleft. Fruit berrylike, pulpy. Seeds 3 or 4, not comose; embryo large, radicle short.

Two species: China, Laos, Vietnam; both in China.

- 1a. Lateral veins of leaf blade 8–12 pairs; disc puberulent ..... 1. *B. mekongensis*  
1b. Lateral veins of leaf blade 20–25 pairs; disc glabrous ..... 2. *B. angustifolia*

**1. *Bousigonia mekongensis*** Pierre in Planchon, Prodr. Apoc. 324. 1894.

奶子藤 nai zi teng

Lianas to 10 m. Young branches puberulent. Petiole 1.5–1.8 cm; leaf blade oblong, 6–15 × 2–4.8 cm, somewhat leathery, apex short acuminate, acumen less than 5 mm; lateral veins 8–12 pairs, subparallel, subhorizontally spreading. Cymes terminal and axillary, shorter than leaves; peduncle 5–11 cm; bracts and bracteoles triangular, ca. 1 mm. Pedicel 2–10 mm, puberulent. Sepals ovate, ca. 1.5 mm, ciliate. Corolla white, tube ca. 7 mm; lobes ovate, ca. 2 mm. Disc shorter than ovary, apex puberulent. Fruit globose or subglobose, 3–5 × 3–4 cm. Fl. Apr-Jun, fr. Aug-Dec.

Mixed forests or brushwoods; 500–1000 m. S Yunnan [Vietnam].

**2. *Bousigonia angustifolia*** Pierre in Spire & A. Spire, Contr. Apocyn. 129. 1905.

闷奶果 men nai guo

Lianas to 8 m, glabrous. Petiole 1–1.5 cm; leaf blade oblong or narrowly so, 7–15 × 2–4 cm, apex caudate-acuminate, acumen 5–10 mm; lateral veins 20–25 pairs, subparallel, subhorizontally spreading. Cymes 4–5.5 cm; peduncle 3–4 cm; bracts and bracteoles triangular, ca. 2 mm. Pedicel 2–3 mm. Sepals ovate, ca. 3 mm, subacute. Corolla white, tube ca. 7 mm; lobes broadly ovate, ca. 3 × 3 mm. Anthers oblong-lanceolate, ca. 2 mm; disc glabrous. Fruit ovoid, 2–3 × 1.5–3 cm. Fl. spring-summer.

Mixed forests, forest edges; 800–1400 m. S Yunnan [Laos, Thailand, Vietnam].

**5. HUNTERIA** Roxburgh, Fl. Ind. ed. 1832 1: 695. 1832.

仔榄树属 zi lan shu shu

Trees or shrubs, latex present. Branches slender, terete. Leaves decussate, leathery, glabrous, with a conspicuous marginal vein and numerous, straight lateral veins. Cymes corymbose or subpaniculate, terminal or axillary. Flowers 5-merous. Calyx small, without glands. Corolla salverform, tube cylindrical, inflated in distal half; lobes shorter than tube, overlapping to left; corona absent. Stamens inserted in inflated portion of corolla tube, included; anthers narrowly ovate; disc absent. Ovaries distinct or connate at base; ovules 2–4 per locule. Style filiform; pistil head thickened, apex minute, 2-cleft. Berry 1- or 2-seeded. Seeds ovate or oblong,

without coma; cotyledons leaflike, radicle erect.

Ten species: tropical Africa, one extending into tropical Asia, including China.

**1. *Hunteria zeylanica*** (Retzius) Gardner ex Thwaites, Enum. Pl. Zeyl. 191. 1860.

仔榄树 *zi lan shu*

*Cameraria zeylanica* Retzius, Observ. Bot. 4: 24. 1786;  
*Hunteria corymbosa* Roxburgh.

Trees to 15 m tall. Trunk often fluted; branches slender, glabrous. Petiole 1–1.5 cm; leaf blade oblong, elliptic, or narrowly ovate, 5–18 × 1–9 cm, base broadly cuneate to rounded, apex acuminate; lateral veins more than 30 pairs, subparallel, joining marginal veins. Flowers strongly fragrant,

white. Pedicel usually longer than calyx. Sepals ovate, 1.5–1.7 mm, acute. Corolla tube 7–10 mm, pubescent inside. Berries yellow, globose, usually paired, 1–2 cm in diam. Seeds brownish, ovoid, ca. 1.2 cm × 8 mm. Fl. Apr–Sep, fr. May–Dec.  $2n = 22$ .

Dense montane forests; low to middle altitudes. Hainan [India, Indonesia, Laos, Malaysia, Myanmar, Sri Lanka, Thailand, Vietnam; E Africa].

The leaves are used externally for the treatment of wounds and cuts, the fruit are edible, and the wood is used for making chopsticks in Hainan.

## 6. VOACANGA Du Petit-Thouars, Gen. Nov. Madagasc. 10. 1806.

马铃薯属 *ma ling guo shu*

Trees or robust erect shrubs, latex present, branches dichotomous. Leaves opposite; petioles or leaf bases of a node often connate into a short ocrea, with a single row of colleters in axils. Cymes terminal, pedunculate. Flowers often fragrant. Calyx campanulate to cylindrical, with many basal glands inside. Corolla white or yellow, salverform, large, tube widened at base and at or above middle, shorter or only slightly longer than calyx, throat with a fleshy ring, not scaly, lobes spreading or recurved, overlapping to left. Stamens inserted in distal widening of corolla tube, exerted or included; anthers sessile, sagittate, coherent to pistil head; disc ringlike or of five lobes adnate to ovaries. Ovaries 2, free or fused basally; ovules numerous. Pistil head lampshade-shaped, apex shortly 2-cleft. Follicles 2, pendulous. Seeds numerous, embedded in pulp, not comose.

Twelve species: seven in Africa, five in SE Asia; two species cultivated in China.

- 1a. Calyx (when lobes erect) 5–7 mm, lobes 1.5–2.5 × as long as tube, 2.5–3.5 × as long as wide; follicles partly united, transversely broad ellipsoid, green or yellow; leaf blade with fishbone-like venation ..... 2. *V. chalotiana*  
1b. Calyx (when lobes erect) 7–19 mm, lobes 0.8–1.3 × as long as tube, 0.7–1.3(–1.7) × as long as wide; follicles free, obliquely subglobose, with pale green spots; leaf blade with less regular venation ..... 1. *V. africana*

**1. *Voacanga africana*** Stapf, J. Linn. Soc., Bot. 30: 87. 1894.

非洲马铃薯 *fei zhou ma ling guo*

Trees to 10(–25) m tall. Bark pale gray-brown; branches lenticellate. Petiole short or absent; leaf blade obovate-oblong or obovate-elliptic, 7–41 × 3–20 cm, base cuneate or decurrent, apex obtuse or acute, glabrous on both surfaces or pubescent abaxially; lateral veins 8–22 pairs. Cymes 6–25 cm, usually many flowered. Calyx 0.7–1.9 cm, lobes broadly ovate to oblong. Corolla yellow or white, tube 0.7–1.5 cm, twisted; lobes obovate or elliptic, recurved, twisted in bud. Follicles obliquely subglobose, with pale green spots. Seeds dark brown, obliquely ellipsoid, 7–10 × 3.5–5 mm.  $2n = 22$ . S Yunnan [introduced from W Africa].

Cultivated for its latex which is used as rubber adulterant.

**2. *Voacanga chalotiana*** Pierre ex Stapf in Dyer, Fl. Trop. Afr.

4(1): 158. 1902.

马铃薯 *ma ling guo*

Trees to 35 m tall, glabrous throughout except for corolla. Trunk to 80 cm in diam.; bark pale gray-brown; branches with some large lenticels. Petiole 1–3 mm; leaf blade elliptic to narrowly elliptic, 5.5–21 × 1.5–6.5 cm, base obtuse, apex acuminate; lateral veins 10–25 pairs. Pedicel 0.6–1.5 cm. Calyx lobes narrowly triangular, recurved. Corolla white, throat pale ochre; tube 5–7 mm, appressed pubescent inside, not twisted; lobes obliquely oblong, spreading, recurved later, not twisted in bud. Fruit green or yellow and yellow spotted, transversely broadly ellipsoid, 2.5–3 × 4.5–6.5 cm, 2–3 cm in diam., follicles fused at base. Seeds dark brown.

S Guangdong [native of Africa].

Cultivated for wood.

## 7. TABERNAEMONTANA Linnaeus, Sp. Pl. 1: 210. 1753.

狗牙花属 *gou ya hua shu*

*Ervatamia* (A. de Candolle) Stapf; *Pagiantha* Markgraf; *Rejoua* Gaudichaud-Beaupré.

Shrubs or small trees, latex white. Stems repeatedly dichotomously branched. Leaves opposite; adaxial surface of petiole often with a basal semicircular or semiamplexicaul ocrea. Cymes corymbose or umbellate, at branch forks, many or rarely 1-flowered. Calyx divided halfway down or deeper, with few to many basal glands inside. Corolla salverform, widened at or near middle, lobes sharply overlapping to left [or right]. Stamens inserted in widened part of corolla tube; filaments short or almost none; anthers oblong or narrowly triangular, free from pistil head, base sagittate or deeply cordate and not spurred; disc absent. Ovaries 2, free; ovules numerous. Style filiform; pistil head with a subglobose or lampshade-shaped basal part and stigmoid, 2-cleft apical part. Follicles 2, divaricate. Seeds with a red or orange fleshy aril; coma absent.

Ninety-nine species: Africa, Asia, North America, Pacific Islands, South America; five species in China.

- 1a. Corolla double; plants cultivated ..... 4. *T. divaricata*  
 1b. Corolla single.  
 2a. Corolla lobes pubescent inside all over or only in basal half, ciliate, often pubescent outside ..... 3. *T. corymbosa*  
 2b. Corolla lobes glabrous inside or pubescent only at extreme base, mostly not ciliate.  
 3a. Corolla tube not twisted; stamens inserted at lower 1/4–1/3 of corolla tube ..... 4. *T. divaricata*  
 3b. Corolla tube mostly twisted; stamens inserted at middle or upper half of corolla tube.  
 4a. Sepals rounded, obtuse or sometimes acute; corolla tube 8–23 × as long as calyx  
 (see also *T. bufalina*).  
 5a. Corolla tube glabrous inside, twisted 0.25–0.5 turn just below anthers, up to 11 × as long  
 as calyx; fruit 1.2–7.1 cm, 2–40-seeded, if smaller and few seeded then with a lateral ridge  
 along each side ..... 5. *T. pandacaqui*  
 5b. Corolla tube pubescent or pilose inside around anthers, if twisted, 10–23 × as long as calyx;  
 fruit 1–1.6 cm, 1–3-seeded, not ridged when mature (see also *T. corymbosa*) ..... 1. *T. bovina*  
 4b. Sepals acuminate, awl-shaped or not; corolla tube 4–7 × as long as calyx.  
 6a. Corolla of mature bud with a subglobose or broadly ovoid, rounded or obtuse head, glabrous  
 inside; midvein and secondary veins mostly paler than blade on both leaf surfaces ..... 5. *T. pandacaqui*  
 6b. Corolla of mature bud with an ovoid, acuminate or acute head, hairy or glabrous inside;  
 veins not paler than blade.  
 7a. Peduncle rather robust; bracts scalelike; corolla head of mature bud 6–12 mm ..... 4. *T. divaricata*  
 7b. Peduncle slender; bracts not scaly; corolla head of mature bud mostly up to 5 mm ..... 2. *T. bufalina*

**1. *Tabernaemontana bovina*** Loureiro, Fl. Cochinch. 1: 118. 1790.

药用狗牙花 yao yong gou ya hua

*Ervatamia bovina* (Loureiro) Markgraf; *E. officinalis* Tsiang; *E. tonkinensis* (Pierre ex Pitard) Markgraf; *Tabernaemontana officinalis* (Tsiang) P. T. Li; *T. tonkinensis* Pierre ex Pitard.

Shrubs or small trees 0.5–5 m tall, glabrous except for flowers. Petiole 2–8 mm; leaf blade deep green adaxially, pale green abaxially, elliptic or narrowly so, 3–21 × 1–6 cm, papery, apex caudate or acuminate; lateral veins 4–12 pairs. Cymes shorter than leaves. Flower buds with a globose head, rounded at apex. Corolla white, tube 1.2–2.8 cm; lobes obliquely elliptic, 0.5–1.5 cm, puberulent on both surfaces. Stamens inserted above middle of corolla tube. Ovary glabrous. Follicles oblong, 1.5–2.4 × 0.6–1 cm, apex mostly acuminate. Fl. May–Jun, fr. Aug–Dec.

Sparse montane forests; 200–1000 m. W Guangxi, Hainan, Yunnan [Thailand, Vietnam].

**2. *Tabernaemontana bufalina*** Loureiro, Fl. Cochinch. 1: 117. 1790.

尖蕾狗牙花 jian lei gou ya hua

*Ervatamia bufalina* (Loureiro) Pichon; *E. ceratocarpa* Kerr; *E. chengkangensis* Tsiang; *E. hainanensis* Tsiang; *Tabernaemontana ceratocarpa* (Kerr) P. T. Li; *T.*

*cheng-kiangensis* (Tsiang) P. T. Li; *T. hainanensis* (Tsiang) P. T. Li; *T. jasminoides* Tsiang.

Shrubs or small trees 0.5–4 m tall, glabrous throughout. Petiole 1–8 mm; leaf blade elliptic or narrowly so, 4–17 × 1–6 cm, papery, apex acuminate; lateral veins 5–12 pairs. Cymes di- or trichotomous; bracts not scaly. Flower buds with an ovoid head, apex acute. Corolla white or yellow-white, tube 0.8–1.7 cm; lobes obliquely elliptic, mostly falcate, 5–15 × 3–10 mm. Stamens inserted at or above middle of corolla tube. Ovary glabrous. Follicles obliquely and narrowly ellipsoid, oblong, or very narrowly oblong, 2–12 × 0.5–1.5 cm, beak 1–2 cm. Fl. May–Aug, fr. Jul–Nov.

Mixed forests; 100–1000 m. Guangdong, Guangxi, Hainan, S Yunnan [Cambodia, Myanmar, Thailand, Vietnam].

The roots are used in Hainan to treat hypertension, snake poisoning, and rheumatism.

**3. *Tabernaemontana corymbosa*** Roxburgh ex Wallich, Bot. Reg. 15: t. 1273. 1829.

伞房狗牙花 san fang gou ya hua

*Ervatamia chinensis* (Merrill) Tsiang, *E. continentalis* Tsiang; *E. continentalis* var. *pubiflora* Tsiang; *E. corymbosa* (Roxburgh ex Wallich) King & Gamble; *E. kwangsiensis* Tsiang; *E. kweichowensis* Tsiang; *E. tenuiflora* Tsiang; *E. yunnanensis* Tsiang; *E. yunnanensis* var. *heterosepala* Tsiang; *Pagiantha corymbosa* (Roxburgh ex Wallich) Markgraf; *Tabernaemontana chinensis* Merrill; *T. continentalis* (Tsiang) P. T. Li; *T. continentalis* var. *pubiflora* (Tsiang) P. T.

Li; *T. kwangsiensis* (Tsiang) P. T. Li; *T. kweichowensis* (Tsiang) P. T. Li; *T. tsiangiana* P. T. Li; *T. yunnanensis* (Tsiang) P. T. Li; *T. yunnanensis* var. *heterosepala* (Tsiang) P. T. Li.

Shrubs or small trees 0.8–8 m tall, glabrous except for flowers. Petiole 0.3–2 cm; leaf blade ovate to obovate, 7–30 × 2–14 cm, papery, apex acuminate; lateral veins 6–16 pairs. Cymes shorter or longer than leaves; di- or trichotomous. Flower buds with a globose head, rounded at apex. Calyx lobes ovate, ciliate. Corolla white, puberulent to glabrous, tube 1.8–3.1 cm; lobes obliquely elliptic, mostly falcate, 9–16 × 4–10 mm. Stamens inserted above middle of corolla tube. Follicles obliquely ellipsoid, 2–4.5 × 0.6–3 cm, beaked or rounded, sometimes stipitate. Fl. May-Sep, fr. Jul-Dec.

Mixed woods, brushwoods; 500–1700 m. W Guangxi, S Guizhou, S Yunnan [Indonesia, Laos, Malaysia, Myanmar, Thailand, Vietnam].

The bark and leaves are used in Guangxi for the treatment of fractures.

**4. *Tabernaemontana divaricata*** (Linnaeus) R. Brown ex Roemer & Schultes, Syst. 4: 427. 1819.

狗牙花 *gou ya hua*

*Nerium divaricatum* Linnaeus, Sp. Pl. 1: 209. 1753; *Ervatamia coronaria* (Jacquin) Stapf; *E. divaricata* (Linnaeus) Burkill; *E. flabelliformis* Tsiang; *N. coronarium* Jacquin; *Tabernaemontana coronaria* (Jacquin) Willdenow; *T. flabelliformis* (Tsiang) P. T. Li.

Shrubs or small trees 0.5–5 m tall, glabrous. Petiole 3–10 mm; leaf blade elliptic or narrowly so, 3–18 × 1–6 cm, apex acuminate; lateral veins 5–17 pairs. Cymes dichotomous, 1–8-flowered; bracts scalelike. Flower buds with an ovoid head, apex acute or obtuse. Calyx lobes often ciliate. Corolla white, tube 1.5–2.7 cm; lobes simple or double, obovate or broadly so, 1.5–2.7 × 0.8–2 cm. Stamens inserted at basal third

of corolla tube. Follicles obliquely and narrowly ellipsoid, 2–7 × 0.6–1.5 cm. Fl. Apr-Sep, fr. Jul-Nov.  $2n = 22^*$ .

Montane brushwoods, sparse forests; 100–1600 m. S Yunnan (cultivated in Fujian, Guangdong, Guangxi, Hainan, Taiwan, Yunnan) [Bangladesh, Bhutan, India, Myanmar, Nepal, Thailand; cultivated in tropical and subtropical Asia].

All parts of the plant are poisonous. The roots, leaves, and flowers are used in Guangdong and Guangxi against snake and scorpion poisoning. In modern medicine, the roots are used to treat hypertension, headache, and scabies.

**5. *Tabernaemontana pandacaqui*** Lamarck, Tabl. Encycl. 1(2): 299. 1792.

平脉狗牙花 *ping mai gou ya hua*

*Ervatamia mucronata* (Merrill) Markgraf; *E. pandacaqui* (Lamarck) Pichon; *E. puberula* Tsiang & P. T. Li; *Pagiantha pandacaqui* (Lamarck) Markgraf; *Tabernaemontana guangdongensis* P. T. Li; *T. mollis* Hooker & Arnott; *T. mucronata* Merrill; *T. subglobosa* Merrill; *T. thailandensis* P. T. Li.

Shrubs or small trees 1–14 m tall. Branchlets pubescent to glabrous. Petiole 0.3–2 cm; leaf blade elliptic or narrowly so, 3–25 × 1–10 cm, sometimes pubescent abaxially, apex acuminate, caudate, or obtuse; lateral veins 4–16 pairs. Cymes 3–16 cm. Flower buds with a broadly ovate head, apex rounded or obtuse. Corolla white, tube 0.8–2.2 cm; lobes obliquely oblong, falcate, 0.6–1.9 cm. Stamens inserted at or above middle of corolla tube. Ovary glabrous. Follicles obliquely ellipsoid, 1.2–7 × 0.5–3 cm, apex beaked or rounded. Fl. May-Jul, fr. Jul-Nov.

Open forests, brushwoods; low to middle altitudes. S Guangdong, Taiwan, S Yunnan [Indonesia, Malaysia, Philippines, Thailand; Australia, Pacific Islands].

## 8. **PLUMERIA** Linnaeus, Sp. Pl. 1: 209. 1753.

鸡蛋花属 *ji dan hua shu*

Trees with copious latex. Branchlets 2–3 cm thick, nearly fleshy. Leaves alternate, long petiolate. Cymes terminal, 2- or 3-branched, pedunculate; bracts usually large, deciduous before anthesis. Flowers fragrant, waxy. Calyx small, without glands. Corolla white, yellowish, pink-red, or rose-purple, funnelform; tube narrow, hairy inside, faucal scales absent; lobes overlapping to left. Stamens inserted at or near base of corolla tube; anthers free from pistil head, oblong, rounded at base; disc absent. Ovaries 2, distinct; ovules numerous, multiseriate on each placenta. Style short; pistil head with obtusely 2-cleft apex. Follicles 2. Seeds many, flat proximally, with a membranous wing; endosperm fleshy; cotyledons oblong, radicle short.

Seven species: tropical America, two cultivated in China.

- 1a. Leaf blade acute or acuminate at apex, matte adaxially, glaucous ..... 1. *P. rubra*  
1b. Leaf blade rounded at apex, shiny adaxially, dark green ..... 2. *P. obtusa*

**1. *Plumeria rubra*** Linnaeus, Sp. Pl. 1: 209. 1753.

鸡蛋花 *ji dan hua*

*Plumeria acuminata* Aiton; *P. acutifolia* Poiret; *P. rubra* var. *acutifolia* (Poiret) L. H. Bailey.

Trees to 8 m tall. Bark pale green, smooth, thin. Petiole to 7 cm; leaf blade elliptic to very narrowly so, 14–30 × 6–8 cm, glaucous adaxially, apex acute or acuminate; lateral veins 30–40 pairs, slightly elevated abaxially. Corolla tinged with pink or purple at least outside, 4–6 cm in diam.; lobes pink, yellow, or white, with a yellow base, 3–4.5 × 1.5–2.5 cm,

obliquely spreading. Follicles oblong, 11–25 × 2–3 cm. Fl. Mar-Sep, fr. Jun-Dec.  $2n = 36$ .

Fujian, Guangdong, Guangxi, Hainan, Yunnan [native to Mexico and Central America].

Widely cultivated for medicine and as ornamental. The flowers are used for the treatment of dysentery. The small, white-flowered form is more valued medicinally in China than other forms of the species.

**2. *Plumeria obtusa*** Linnaeus, Sp. Pl. 1: 210. 1753.

钝叶鸡蛋花 *dun ye ji dan hua*

Trees to 5 m tall. Branchlets pale green, thick, fleshy. Petiole puberulent; leaf blade obovate to narrowly so, dark green and shiny adaxially, tertiary venation strongly prominent abaxially, apex rounded. Corolla white, ca. 4 cm in diam., throat yellow; lobes spreading, slightly recurved. Follicles to 15 × 1.5 cm.  $2n = 36$ .

Guangdong, Guangxi, Hainan, S Yunnan [native of the Caribbean Islands].

Cultivated for medicine and as an ornamental.

**9. ALSTONIA** R. Brown, Mem. Wern. Nat. Hist. Soc. 1: 75. 1811, nom. cons.

鸡骨常山属 *ji gu chang shan shu*

*Blaberopus* A. de Candolle; *Winchia* A. de Candolle.

Trees or shrubs, latex present. Branches whorled, mostly 4 or 5 together. Leaves whorled, rarely opposite; lateral veins numerous, ending in a marginal vein. Cymes terminal, usually 1–5 in thyrses or compound umbels, terminal. Flowers white, yellow, or pink. Calyx without glands inside, lobes connate at base. Corolla salverform, tube cylindric, dilated in distal half, pubescent inside, lobes overlapping to right or left. Stamens included, inserted near or above middle of corolla tube; anthers ovate, free from pistil head, not caudate; disc absent or of scales. Ovaries 2, distinct or connate, ovules numerous. Follicles 2, free or connate. Seeds oblong or linear, long bearded at both ends; endosperm thin; cotyledons up to twice as long as radicle.

About 60 species: tropical Asia, Africa, C America, N Australia, Pacific Islands; eight species in China.

1a. Trees; disc absent or small annular.

- 2a. Lateral leaf veins widely spaced, (3–)5–12 mm apart, ascending; corolla lobes in bud overlapping to right; seeds acuminate at 1 end ..... 2. *A. macrophylla*  
2b. Lateral leaf veins close together, 1–6 mm apart, horizontal or almost so; corolla lobes in bud overlapping to left; seeds obtuse or rounded at both ends.  
3a. Leaf apex long acuminate; ovary syncarpous; follicles solitary ..... 1. *A. rostrata*  
3b. Leaf apex rounded to short acuminate; ovary of 2 separate carpels; follicles paired ..... 3. *A. scholaris*

1b. Shrubs; disc of 2 scales alternating with ovaries.

- 4a. Leaves sessile, blade thick, papery to ± leathery, lateral veins at almost 90° to midvein.  
5a. Leaves pubescent abaxially; corolla to 3 cm ..... 5. *A. neriifolia*  
5b. Leaves glabrous abaxially; corolla ca. 1.1 cm ..... 6. *A. rupestris*  
4b. Leaves petiolate, blade thin, membranous, lateral veins at 45° to midvein.  
6a. Leaves pubescent on both surfaces; corolla pink to red ..... 4. *A. yunnanensis*  
6b. Leaves glabrous; corolla white or yellow.  
7a. Colleters few and inconspicuous; corolla white, to 3 cm, tube 1–2 cm; disc lower than ovary ..... 7. *A. mairei*  
7b. Colleters numerous, becoming ± indurated at base and persisting; corolla yellow, ca. 1 cm; tube ca. 0.8 cm; disc as long as ovary ..... 8. *A. henryi*

**1. *Alstonia rostrata*** C. E. C. Fischer, Bull. Misc. Inform. Kew 1929: 315. 1929.

盆架树 *pen jia shu*

*Alstonia glaucescens* (Wallich ex G. Don) Monachino; *Alstonia pachycarpa* Merrill & Chun; *Alyxia glaucescens* Wallich ex G. Don, not Wallich; *Winchia calophylla* A. de Candolle, not *Alstonia calophylla* Miquel; *W. glaucescens* (Wallich ex G. Don) K. Schumann.

Trees evergreen, glabrous, to 30 m tall. Branches greenish, angled when young. Leaves in whorls of 3 or 4, rarely opposite; petiole 1–2 cm; leaf blade narrowly elliptic, 7–20 × 2.5–4.5 cm, thick papery, lustrous adaxially, paler abaxially, apex caudate or acuminate; lateral veins 20–50 pairs, at 80–90° to midvein.

Cymes glabrous, ca. 4 cm; peduncle 1.5–3 cm. Pedicel to 3 mm. Corolla white, pubescent, tube 5–6 mm; lobes broadly ovate, 3–4 mm, overlapping to left. Disc absent. Ovaries connate. Follicles connate, 18–35 × 1–1.2 cm. Seeds narrowly elliptic; cilia brown-yellow, to 2 cm. Fl. Apr-Jul, fr. Aug-Dec.

Monsoon or montane rain forests; 300–1100 m. Hainan, S Yunnan [India, Indonesia, Malaysia, Myanmar, Thailand].

The wood is used for making furniture and stationery, and the leaves and bark are used to treat acute bronchitis.

**2. *Alstonia macrophylla*** Wallich ex G. Don, Gen. Hist. 4: 87. 1837.

大叶糖胶树 *da ye tang jiao shu*

Trees to 20 m tall. Bark smooth; branches nearly 4-angled. Leaves in whorls of 3 or 4; petiole 1–4 cm; leaf blade narrowly obovate or narrowly elliptic, 10–53 × 4–19 cm, leathery, pubescent abaxially, apex usually acuminate; lateral veins 16–33 pairs, at 60–70° to midvein. Cymes terminal, 3-branched, 5–9 together, pubescent; peduncle 4–6 cm. Pedicel 4–5 mm. Corolla tube slightly longer than lobes, 4.5–6 mm; lobes overlapping to right, ciliate; disc absent. Ovaries distinct, glabrous. Follicles linear, to 61 cm × 2–5 mm. Seeds pubescent, ends with deltoid wings, with long stiff hairs all around. Fl. Oct–Nov.  $2n = 22$ .

S Guangdong, S Yunnan [Indonesia, Malaysia, Philippines, Thailand, Vietnam].

Cultivated for medicine.

**3. *Alstonia scholaris*** (Linnaeus) R. Brown, Mem. Wern. Nat. Hist. Soc. 1: 76. 1811.

糖胶树 tang jiao shu

*Echites scholaris* Linnaeus, Mant. Pl. 1: 53. 1767; *Pala scholaris* (Linnaeus) Roberty.

Trees to 40 m tall, glabrous. Bark gray; branchlets copiously lenticellate. Leaves in whorls of 3–10; petiole 1–3 cm; leaf blade narrowly obovate to very narrowly spatulate, 7–28 × 2–11 cm, leathery, base cuneate, apex usually rounded; lateral veins 25–50 pairs, at 80–90° to midvein. Cymes dense, pubescent; peduncle 4–7 cm. Pedicel usually as long as or shorter than calyx. Corolla white, tube 6–10 mm; lobes broadly ovate or broadly obovate, 2–4.5 mm, overlapping to left. Ovaries distinct, pubescent. Follicles distinct, linear, to 57 cm × 2–5 mm. Seeds oblong, margin ciliate, ends with tufts of hairs 1.5–2 cm. Fl. Jun–Nov, fr. Oct–Dec.  $2n = 22, 44^*$ .

Mixed forests, village groves; 200–1000 m. SW Guangxi, S Yunnan; cultivated in Fujian, Guangdong, Hainan, Hunan, Taiwan [Cambodia, India, Malaysia, Myanmar, Nepal, New Guinea, Philippines, Sri Lanka, Thailand, Vietnam; Australia].

The bark and leaves are used to treat headache, influenza, bronchitis, and pneumonia. The wood is used for making coffins.

**4. *Alstonia yunnanensis*** Diels, Notes Roy. Bot. Gard. Edinburgh. 5: 165. 1912.

鸡骨常山 ji gu chang shan

*Alstonia esquirolii* H. Léveillé; *Acronychia esquirolii* H. Léveillé.

Shrubs erect, to 3 m tall. Branches conspicuously lenticellate, puberulent when young. Leaves in whorls of 3–5, petiolate; blade very narrowly obovate or oblong, 6–19 × 1.3–5 cm, thin papery, pubescent on both surfaces, apex acuminate; lateral veins 15–35 pairs, at 45° to midvein. Cymes puberulent; peduncle 0.5–2 cm. Pedicel to 8 mm. Corolla pink to red, tube 1–1.3 cm; lobes oblong, 2–6 mm, overlapping to left. Disc lobes 2, ligulate, as long as or longer than ovaries. Follicles distinct, linear, 3–5 cm × ca. 4 mm. Seeds oblong, ends with

very short cilia. Fl. Mar–Jun, fr. Jun–Nov.  $2n = 44^*$ .

• Montane brush fields, 800–2400 m. Guangxi, Guizhou, Yunnan.

The roots are used to cure hypertension and the leaves to treat hemostasis and fracture. The seeds yield up to 18% industrial oil.

**5. *Alstonia neriifolia*** D. Don, Prodr. Fl. Nepal. 131. 1825.

竹叶羊角棉 zhu ye yang jiao mian

*Alstonia guangxiensis* D. Fang & X. X. Chen.

Shrubs erect, to 2 m tall, glabrous except for leaves. Branches gray-brown, lenticellate. Leaves in whorls of 3 or 4, sessile; blade very narrowly elliptic or sublinear, 6–22 × 1–2.5 cm, thick papery, abaxially pubescent, apex acuminate; lateral veins 100–170 pairs, nearly at a right angle to midvein. Cymes to 10 cm. Calyx lobes ciliate. Corolla white, tube ca. 2 cm; lobes ca. 1 cm, overlapping to left. Stamens inserted at apex of corolla tube; disc shorter than ovaries. Follicles 6–13 × 2–4 cm. Seeds ciliate at ends, 5–10 mm.

Montane brush fields. SW Guangxi [India, Indonesia, Malaysia, Sri Lanka].

The leaves and roots are used to cure abscesses.

**6. *Alstonia rupestris*** Kerr, Bull. Misc. Inform. Kew. 1937: 43. 1937.

岩生羊角棉 yan sheng yang jiao mian

*Blaberopus rupestre* (Kerr) Pichon

Shrubs erect, to 4 m tall, glabrous. Bark gray-brown; branches lenticellate. Leaves in whorls of 3–5, sessile; blade very narrowly elliptic or sublinear, 4.5–10 × 0.5–1.5 cm, thick papery, glabrous, apex acuminate; lateral veins 45–80 pairs, nearly at a right angle to midvein. Cymes crowded. Pedicel ca. 3 mm. Corolla white, tube 7–8 mm; lobes oblong, 2.5–3 mm, overlapping to left. Disc lobes as long as ovary. Ovaries distinct. Follicles red-brown, linear, 7–10 cm. Seeds with brown cilia. Fl. May–Oct.

Limestone rocks in brushwoods or forests; 500–1800 m. W Guangxi [Thailand].

**7. *Alstonia mairei*** H. Léveillé, Cat. Pl. Yun-Nan 9. 1915.

羊角棉 yang jiao mian

*Alstonia paupera* Handel-Mazzetti; *Wikstroemia hems-leyana* H. Léveillé.

Shrubs erect, to 2 m tall, glabrous. Branchlets lenticellate. Leaves in whorls of 3–5; petiole 0.5–1.5 cm; leaf blade very narrowly obovate or elliptic, 4–14 × 0.8–3 cm, thin papery, glabrous, apex acuminate or caudate; lateral veins 27–70 pairs, at 45–60° to midvein. Cymes longer than leaves; peduncle 1.5–3.5 cm. Pedicel to 2–15 mm. Corolla white, tube 1–2 cm; lobes oblong, 6–10 mm. Disc lobes shorter than ovary. Ovaries distinct, ca. 1.5 mm. Follicles distinct, linear, 5–10 cm × 3–5 mm. Seeds oblong, ca. 7 mm; cilia at seed apex cream, to 5 mm. Fl. May–Oct.

• Rocky places in open evergreen forests; 700–1500 m. Guizhou, Sichuan, Yunnan.

The roots and leaves are used to stop external bleeding.

**8. *Alstonia henryi*** Tsiang, Sunyatsenia 6: 112. 1941.

黄花羊角棉 huang hua yang jiao mian

*Alstonia sebusii* (Van Heurck & Mueller-Argoviensis) Monachino var. *szemaoensis* Monachino.

Shrubs erect, to 3 m tall, glabrous except for flowers.

Branchlets lenticellate. Leaves in whorls of 3 or 4; petiole to 1.2 cm; leaf blade very narrowly elliptic, 5–11 × 1–2.5 cm, papery, apex acuminate; lateral veins to 70 pairs, at 45–60° to midvein. Cymes 3-branched; peduncle 2–3 cm. Pedicel 0.8–1.2 cm. Calyx lobes ciliate. Corolla yellow; tube ca. 8 mm, dilated above middle, densely villous inside; lobes broadly ovate, ca. 2 mm. Disc lobes as long as ovary. Ovaries distinct. Fl. Jun.

• Montane forests, 1500 m. S Yunnan (Simao).

**10. AMSONIA** Walter, Fl. Carol. 98. 1788.

水甘草属 shui gan cao shu

Herbs annual or perennial, erect, with latex, without stolons. Leaves alternate, membranous. Cymes thyrsoid or corymbose, terminal. Flowers blue or bluish. Sepals narrowly acuminate, usually without glands. Corolla blue or bluish, salverform; tube cylindrical, dilated above middle, villous inside; lobes overlapping to left. Stamens inserted inside dilated portion of corolla tube; anthers ovate or oblong, free from pistil head, base rounded. Carpels united by a filiform style; ovules numerous, biseriate on each placenta. Pistil head with a basal membranous appendage. Follicles 2, cylindrical-fusiform, erect. Seeds cylindrical, end obliquely truncate; coma absent.

About 20 species: North America, SE Asia; one species in China.

**1. *Amsonia elliptica*** (Thunberg ex Murray) Roemer & Schultes, Syst. Veg. 4: 432. 1819.

水甘草 shui gan cao

*Tabernaemontana elliptica* Thunberg ex Murray, Syst. Veg. ed. 14, 255. 1784; *Amsonia sinensis* Tsiang & P. T. Li.

Herbs perennial, to 40 cm tall, glabrous. Stems terete. Petiole 3–5 mm; leaf blade elliptic or narrowly so, 2.2–5 cm ×

5–8 mm, base and apex acuminate, lateral veins almost flat on both surfaces. Inflorescences terminal, short thyrses. Pedicel ca. 4 mm. Sepals ca. 2 mm. Corolla bluish, tube ca. 1 cm, villous inside and densely so at throat; lobes oblong, ca. 6 mm. Anther apex included. Ovary glabrous. Style ca. 5 mm. Fl. Jun.  $2n = 22$ .

Grasslands. Anhui, Jiangsu [Japan].

Decoction of all parts is used to cure chills and to induce sweat.

**11. CATHARANTHUS** G. Don, Gen. Hist. 4: 95. 1837.

长春花属 chang chun hua shu

Herbs erect, perennial and often woody at base, juice watery. Leaves opposite; petiole short, intra- and interpetiolar glands present; leaf blade herbaceous to somewhat leathery, entire. Flowers terminal and axillary, solitary or rarely in 2- or 3-flowered cymes. Sepals small, narrowly oblong, awl-shaped, without glands. Corolla purple, red, pink, or white, salverform; tube glabrous or sparsely puberulent, throat constricted, woolly to velvety; lobes spreading, obliquely obovate, overlapping to left, apex apiculate. Stamens inserted in widened portion of corolla tube; anthers free, oblong, base obtuse; disc of 2 glands. Ovaries 2; ovules numerous. Style filiform; pistil head with a cylindrical base and reflexed hyaline frill. Follicles 2, cylindrical, apex acute. Seeds black, oblong, testa rugose.

Eight species: seven endemic to Madagascar, one restricted to India and Sri Lanka; one species cultivated in China.

**1. *Catharanthus roseus*** (Linnaeus) G. Don, Gen. Hist. 4: 95. 1837.

长春花 chang chun hua

*Vinca rosea* Linnaeus, Syst. Nat. ed. 10. 944. 1759; *Ammocallis rosea* (Linnaeus) Small; *Catharanthus roseus* var. *albus* G. Don; *Lochnera rosea* (Linnaeus) Reichenbach ex Endlicher; *L. rosea* var. *alba* (G. Don) Hubbard; *L. rosea* var. *flava* Tsiang; *Pervinca rosea* (Linnaeus) Moench; *V. rosea* var. *alba* (G. Don) Sweet.

Subshrubs or perennial herbs to 1 m tall, erect

or decumbent. Young stems puberulent. Leaves obovate or elliptic, 2.5–9 × 1–3.5 cm, herbaceous, apex minutely apiculate; lateral veins 7–11 pairs. Corolla red to pink or white and then mostly with a pink or less often yellow eye; tube 2.5–3 cm, pilose inside, throat villous; lobes broadly obovate, 1.2–2 cm. Follicles 2–3.8 cm × ca. 3 mm. Fl. spring-autumn.  $2n = 16$ .

Fujian, Guizhou, Hunan, Jiangsu, Jiangxi, Sichuan, Yunnan, Zhejiang [native to Madagascar, cultivated or naturalized in all tropical countries].

Cultivated for medicine. Decoction of all parts is used in the

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treatment of malaria, skin diseases, Hodgkin's disease, diarrhea, hypertension, and diabetes.

**12. VINCA** Linnaeus, Sp. Pl. 1: 209. 1753.

蔓长春花属 man chang chun hua shu

Herbs with stolons and watery juice. Leaves opposite, entire, short petiolate, intra- and interpetiolar glands present. Flowers solitary or rarely in 2-flowered cymes, axillary. Calyx small, without glands. Corolla violet, funnelform, tube cylindric, hairy or with scales at throat; lobes obliquely obovate, spreading, shorter than tube, overlapping to left. Stamens inserted just below middle of corolla tube. Disc glands 2, ligulate, alternating with ovaries. Ovules 6—many. Style filiform; pistil head ringlike, apex densely hairy. Follicles 2, erect or spreading, cylindric, striate. Seeds glabrous.

About five species: W Asia, Europe; two species cultivated in China.

- 1a. Leaf blade truncate or subcordate at base, margin and calyx lobes ciliate; pedicel 3–5 cm ..... 1. *V. major*
- 1b. Leaf blade narrow at base, margin and calyx lobes glabrous; pedicel 1–1.5 cm ..... 2. *V. minor*

**1. Vinca major** Linnaeus, Sp. Pl. 1: 209. 1753.

Cultivated for medicine.

蔓长春花 man chang chun hua

*Vinca major* var. *variegata* Loudon.

Herbs to 1 m tall, flowering stems to 30 cm. Leaf blade elliptic, ovate, or broadly ovate, 2–9 × 2–6 cm, base truncate or subcordate, margin ciliate with hairs 0.1–1 mm; lateral veins to 5 pairs. Pedicel 3–5 cm. Sepals narrowly triangular, ca. 9 mm, densely ciliate. Corolla bluish purple, tube 1.2–1.5 cm, limb 3–5 cm in diam., lobes obliquely truncate. Anthers short, applanate, apex puberulent. Follicles spreading, ca. 5 cm. Fl. Mar-May.  $2n = 92$ .

Jiangsu, Taiwan, Yunnan, Zhejiang [native to Europe].

**2. Vinca minor** Linnaeus, Sp. Pl. 1: 209. 1753.

花叶蔓长春花 hua ye man chang chun hua

Herbs perennial. Flowering stems to 20 cm. Leaf blade oblong, ovate, or elliptic, 1–4.5 × 0.5–2.5 cm, base rounded or cuneate, margin not ciliate. Pedicel 1–1.5 cm. Sepals narrowly elliptic, 3–5 mm. Corolla lilac-blue, tube 0.9–1.1 cm, limb 2.5–3 cm in diam., lobes obliquely truncate. Filaments longer than anthers; anthers puberulent at apex. Follicles erect. Fl. May.  $2n = 46$ .

Jiangsu [introduced from Europe].

Cultivated for medicine.

**13. RAUVOLFIA** Linnaeus, Sp. Pl. 1: 208. 1753.

萝芙木属 luo fu mu shu

Trees or shrubs with latex. Leaves whorled, rarely opposite, with glands axillary and sometimes on petiole. Cymes pedunculate, terminal or axillary, each branch ends in as many inflorescences and/or branches as leaves in a whorl. Calyx deeply divided, without glands. Corolla white, yellow, green, or pink, rarely with a red tube, salverform or campanulate; tube cylindric, swollen on 1 side at or above middle, villous inside distal half, throat not scaly, often with long hairs inside; lobes overlapping to left. Stamens inserted in widening of corolla tube; filaments very short; anthers ovate, free from pistil head, base rounded; disc ringlike or cup-shaped, entire or lobed at apex. Ovaries 2, free or connate. Style filiform; pistil head drum-shaped, with a pendulous ring, apex shortly 2-cleft. Drupes 2, distinct or connate. Seed 1, without coma.

About 60 species: Africa, Asia, America; seven species in China.

- 1a. Trees; lateral veins 30–45 pairs, subparallel, nearly at right angles to midvein ..... 1. *R. sumatrana*
- 1b. Shrubs; lateral veins 5–20 pairs, arcuate ascending.
  - 2a. Ovaries and fruit of connate carpels, often only at base.
    - 3a. Leaves ovate or elliptic, tomentose when young; corolla tube 2–3 mm; fruit entire at apex ..... 2. *R. tetraphylla*
    - 3b. Leaves narrowly elliptic or obovate, glabrous; corolla tube 10–20 mm; fruit forked at apex.
      - 4a. Leaves usually narrowly elliptic, 7–20 cm, membranous; petiole 10–15 mm; inflorescences solitary; peduncle, pedicel, calyx, and corolla red or reddish; corolla lobes 1.5–3.5 mm; stamens inserted at middle of corolla tube ..... 3. *R. serpentina*
      - 4b. Leaves obovate, 1–6 cm, leathery; petiole 2–4 mm; peduncle, pedicel, and calyx green; corolla tube white, lobes 10–14 mm; stamens inserted at corolla throat ..... 4. *R. cubana*
  - 2b. Ovaries and fruit of free carpels.
    - 5a. Corolla white, tube widened at middle; stamens inserted at middle of corolla tube ..... 7. *R. verticillata*
    - 5b. Corolla reddish, green, or yellow, tube widened at top; stamens inserted at corolla throat.
      - 6a. Lateral veins of leaf blade prominent; inflorescences long, at least some branches puberulent;



- corolla greenish or green ..... 5. *R. vomitoria*  
 6b. Lateral veins of leaf blade inconspicuous; inflorescences short, glabrous; corolla yellow .... 6. *R. tiaolushanensis*

**1. *Rauvolfia sumatrana*** Jack, Malayan Misc. 1(5): 22. 1820.

苏门答腊萝芙木 *su men da la luo fu mu*

Trees to 20 m tall. Leaves in whorls of 3–5; petiole 2–3 cm; leaf blade oblong or narrowly obovate, 12–20 × 4–8 cm, leathery, glabrous, apex apiculate or nearly so; lateral veins 30–45 pairs, subparallel, nearly at a right angle to midvein. Inflorescences dense, 8–12 × 12–15 cm; peduncle 5–8 cm. Corolla white, tube cylindric, 4–6 mm; lobes broadly ovate, 1.2–1.7 mm; throat villous. Disc less than 0.5 mm. Ovaries distinct, ca. 1 mm. Drupes subglobose, 1.5–1.8 × 1.8–2.4 cm. Seeds 1 or 2.

S Guangdong [Indonesia, Malaysia, Philippines, Thailand].

Cultivated for medicine. The wood is used to make rapier scabbards in Java.

**2. *Rauvolfia tetraphylla*** Linnaeus, Sp. Pl. 1: 208. 1753.

四叶萝芙木 *si ye luo fu mu*

Shrubs to 2 m tall, pubescent or tomentose when young, glabrescent with age. Leaves in whorls of 3–5; petiole 2–5 mm; leaf blade ovate, narrowly ovate, or oblong, 1–15 × 0.8–4 cm, membranous, base broadly cuneate to rounded, apex acute or obtuse; lateral veins 5–12 pairs. Peduncle 1–4 cm. Corolla white, tube urceolate, 2–3 mm, long hairy inside distal half; lobes ovate or suborbicular. Stamens inserted at corolla throat. Ovaries connate. Drupes subglobose, 5–10 mm in diam., glabrous, connate. Seeds 2. Fl. May, fr. Jun-Aug.  $2n = 66$ .

S Guangdong, SW Guangxi, Hainan, S Yunnan [native to tropical America].

Cultivated for medicine.

The latex has been reported to be emetic, cathartic, and expectorant and is used for treating dropsy. The fruit juice is used as a substitute for ink.

**3. *Rauvolfia serpentina*** (Linnaeus) Bentham ex Kurz, Forest Fl. Burma 2: 171. 1877.

蛇根木 *she gen mu*

*Ophioxylon serpentinum* Linnaeus, Sp. Pl. 2: 1043. 1753; *O. majus* Hasskarl.

Shrubs to 1 m tall, erect, glabrous. Stems usually unbranched, slender, straw colored. Leaves grouped near stem apex, in whorls of 3–5; petiole 1–1.5 cm; leaf blade narrowly elliptic or obovate, membranous, 7–17 × 2–9 cm, base cuneate, apex acuminate or rarely obtuse; lateral veins 7–15 pairs. Cymes congested; peduncle 5–13 cm, red or reddish. Pedicel and calyx red or reddish. Corolla white, tube cylindric, 1–1.8 cm, inflated at middle and pilose inside distal half; lobes obliquely suborbicular, 1.5–3.5 mm. Stamens inserted at middle of corolla tube. Ovaries connate in basal half. Drupes

ellipsoid, ca. 8 mm, connate for half their length. Fl. Feb-Oct, fr. May-Dec.  $2n = 22$ .

Montane forests; 800–1500 m. S Yunnan (Gengma, Jing-hong), cultivated in S Guangdong, S Guangxi, Hainan [India, Indonesia, Malaysia, Myanmar, Sri Lanka, Thailand].

The roots are used as a sedative and in the treatment of hypertension. The bark, leaves, and roots are used against snake and scorpion poisoning.

**4. *Rauvolfia cubana*** A. de Candolle, Prodr. 8: 339. 1844.

古巴萝芙木 *gu ba luo fu mu*

Shrubs to 5 m tall, glabrous. Leaves usually in whorls of 3; petiole 2–4 mm; leaf blade obovate, 1–6 × 1–2 cm, leathery; lateral veins inconspicuous. Peduncle 2–4 cm. Pedicel 6–11 mm. Corolla white, tube cylindric, ca. 2 cm; lobes obovate-elliptic, 1–1.4 cm. Stamens inserted at corolla throat. Ovaries connate in basal half. Drupes obovoid, 1–1.2 cm × 5–7 mm, connate along lower half, apex 2-forked. Seeds rugose. Fl. Jul.

S Yunnan [introduced from Cuba].

Cultivated for medicine.

**5. *Rauvolfia vomitoria*** Afzelius, Stirp. Guinea Med. 1. 1817.

催吐萝芙木 *cui tu luo fu mu*

Shrubs to 5 m tall, glabrous. Stems erect, stiff. Leaves whorled; leaf blade broadly ovate or ovate-elliptic, 5–12 × 3–6 cm; lateral veins 8–17 pairs. Cymes usually 4 together. Corolla greenish or pale green, tube subcylindric, 6–12 mm, inflated at throat, pubescent inside; lobes dolabriform, 1–2 mm. Stamens inserted at corolla throat; disc ringlike, shorter than ovaries. Ovaries distinct. Style filiform, pubescent at base; pistil head fleshy, base membranous. Drupes 2, distinct, ovoid or ellipsoid, 0.8–1.4 cm × 6–9 mm. Fl. Aug-Oct, fr. Oct-Dec.  $2n = 22, 66$ .

S Guangdong, S Guangxi, S Yunnan [native to tropical Africa].

Cultivated for medicine. All parts are poisonous. The roots and leaves are reported to have emetic and cathartic properties, and the bark is used as a remedy for fever and indigestion.

**6. *Rauvolfia tiaolushanensis*** Tsiang, Sci. Rep. Kwantung Coll. Forest. 1: 10. 1962.

吊罗山萝芙木 *diao luo shan luo fu mu*

Shrubs to 1 m tall. Stems dark brown. Leaves opposite or in whorls of 3 or 4; petiole ca. 8 mm; leaf blade elliptic to oblong, 8–17 × 1.6–4 cm, lateral veins inconspicuous. Cymes ca. 2 cm; peduncle ca. 6 mm. Calyx lobes ca. 2.5 mm. Corolla yellow, tube cylindric, ca. 8 × 2 mm, dilated at throat, pubescent inside; lobes oblong or ovate, ca. 3.5 × 2.5 mm. Stamens inserted at corolla throat; filaments short; anthers broadly ovate, base rounded, apex short acuminate; disc cup-shaped, shorter than ovary. Ovaries distinct. Style filiform; pistil head club-shaped to capitate, base with a ringlike

membrane. Drupes distinct, ellipsoid, 1–1.7 cm × 5–8 mm. Fl. Mar, fr. May.

- Montane forests; 300–600 m. Hainan (Baoting, Waning).

**7. Rauvolfia verticillata** (Loureiro) Baillon, Hist. Pl. 10: 170. 1889.

萝芙木 *luo fu mu*

*Dissolena verticillata* Loureiro, Fl. Cochinch. 1: 137. 1790; *Cerbera chinensis* Sprengel; *Ophioxylon chinense* Hance; *Rauvolfia altodiscifera* Miau, *R. brevistyla* Tsiang; *R. cambodiana* Pierre ex Pitard; *R. chinensis* (Sprengel) Hemsley; *R. latifrons* Tsiang; *R. perakensis* King & Gamble; *R. superaxillaris* P. T. Li & S. Z. Huang; *R. taiwanensis* Tsiang; *R. verticillata* var. *hainanensis* Tsiang; *R. verticillata* var. *oblanceolata* Tsiang; *R. verticillata* var. *officinalis* Tsiang; *R. yunnanensis* Tsiang.

Shrubs to 3 m tall, erect, glabrous. Branchlets pale gray, lenticellate. Lower leaves opposite, terminal leaves in whorls of 3 or 4; petiole 0.5–1.5 cm; leaf blade narrowly to broadly ovate or oblong, 3.5–25 × 5–13 cm, nearly papery to membranous; lateral veins 6 or 7 pairs. Cymes rather lax, 3–9 together; peduncle 2–15 cm. Pedicel 3–6 mm. Corolla white, tube cylindric, 1–1.8 cm, inflated and villous from middle to throat; lobes broadly elliptic or ovate, 1–4.5 mm. Stamens inserted at middle of corolla tube. Ovaries distinct. Drupes ellipsoid or ovoid, distinct, ca. 10 × 5 mm. Seed 1. Fl. Feb–Oct, fr. Apr–Dec.  $2n = 22^*$ .

Lowland, montane rain forests, monsoon forests, brush fields, river banks, rice fields, seashores; 0–1700 m. Guangdong, Guangxi, Guizhou, Hainan, Taiwan, Yunnan [Cambodia, India, Indonesia, Malaysia, Myanmar, Philippines, Sri Lanka, Thailand, Vietnam].

Used in China to treat snake poisoning, malaria, and typhus. The roots are used to treat hypertension and as a sedative.

**14. ALYXIA** Banks ex R. Brown, Prodr. 469. 1810, nom. cons.

链珠藤属 *lian zhu teng shu*

Plants woody lianas or erect to trailing shrubs, with latex. Leaves in whorls of 3 or 4, rarely opposite. Cymes terminal and/or axillary, sometimes in clusters or short thyrses. Flowers small, 5-merous. Calyx deeply divided, without basal glands. Corolla white or rarely yellow, salverform, tube cylindric, widened at stamens insertion, lobes overlapping to left; corona scales absent. Stamens included, inserted at or above middle of corolla tube; filaments very short; anthers free from pistil head; disc absent. Ovaries 2, distinct; ovules biseriate, 4–6 in each ovary. Style filiform; pistil head capitate, apex shortly 2-cleft. Fruit usually paired, moniliform, transversely constricted into 1–5 drupelike articles, or not jointed. Seeds ovate or oblong; endosperm horny, ruminate; cotyledons leaflike, erect or curved.

About 70 species: tropical Asia, Australia, Pacific Islands; 12 species in China.

- 1a. Leaves densely pubescent abaxially; cymes spicate ..... 3. *A. villilimba*
- 1b. Leaves glabrous abaxially; cymes fascicled.
  - 2a. Inflorescences 2–10.5 cm.
    - 3a. Corolla pubescent ..... 1. *A. menglungensis*
    - 3b. Corolla glabrous.
      - 4a. Inflorescences 8–10.5 cm ..... 2. *A. siamensis*
      - 4b. Inflorescences 3–5 cm ..... 4. *A. reinwardtii*
  - 2b. Inflorescences 0.5–2 cm.
    - 5a. Leaf apex rounded, obtuse, or rarely retuse.
      - 6a. Leaves usually in whorls of 4; leaf blade 5.5–10 × 2.5–3.5 cm; petiole 10–15 mm; corolla tube 7–10 mm ..... 5. *A. insularis*
      - 6b. Leaves opposite or in whorls of 3; leaf blade 1.5–3.5 × 0.8–2 cm; petiole ca. 2 mm; corolla tube 2–3 mm ..... 6. *A. sinensis*
    - 5b. Leaf apex caudate, acuminate, or acute.
      - 7a. Leaf apex caudate or acuminate, acumen ca. 1.5 cm ..... 7. *A. fascicularis*
      - 7b. Leaf apex acute or short acuminate.
        - 8a. Leaf blade with marginal veins ..... 8. *A. marginata*
        - 8b. Leaf blade without marginal veins.
          - 9a. Ovary glabrous; articles of fruit ca. 6 × 4 mm ..... 9. *A. taiwanensis*
          - 9b. Ovary hairy; articles of fruit 7–22 × 5–10 mm.
            - 10a. Articles of fruit ca. 7 mm; corolla yellow ..... 11. *A. schlechteri*
            - 10b. Articles of fruit 10–22 mm; corolla greenish white or greenish yellow.
              - 11a. Sepals acuminate, 1.5–3 mm; corolla greenish white, tube ca. 3 mm; articles of fruit 10–13 × 8–10 ..... 10. *A. levinei*
              - 11b. Sepals obtuse or acute, 1.7–8 mm; corolla greenish yellow, tube 3–15 mm; articles of fruit 10–22 × 5–8 mm ..... 12. *A. odorata*

**1. *Alyxia menglungensis*** Tsiang & P. T. Li, Acta Phyto-tax. Sin. 11: 364. 1973.

勐龙链珠藤 meng long lian zhu teng

Lianas woody, to 4 m. Branchlets gray-green. Leaves opposite or in whorls of 3; petiole ca. 1 cm; leaf blade elliptic to narrowly so, 9–12 × 3–4.2 cm, papery, abaxially glabrous; lateral veins numerous, inconspicuous abaxially. Cymes terminal or axillary, solitary or umbellate in groups of 3 or 4, 2–6.7 cm, pubescent; peduncle 1–4 cm. Sepals ovate, ca. 2 mm, obtuse, densely pubescent. Corolla white, pubescent on both surfaces, tube ca. 6 mm; lobes ovate, ca. 2 mm. Stamens inserted at corolla throat. Ovary glabrous. Style filiform. Fl. Sep.

• Dense montane forests; 2000 m. S Yunnan.

**2. *Alyxia siamensis*** Craib, Bull. Misc. Inform. Kew 1911: 412. 1911.

长序链珠藤 chang xu lian zhu teng

*Alyxia balansae* Pitard; *A. yunkuniana* Tsiang.

Lianas stout, woody, to 8 m. Bark dull gray, glabrous, warty. Leaves opposite or in whorls of 3 or 4; petiole 1–1.5 cm; leaf blade elliptic to narrowly so, 7–19 × 3–4.4 cm, abaxially glabrous, base cuneate, margin revolute, apex short acuminate; lateral veins numerous, subparallel, slender, elevated on abaxial surface, obscure adaxially. Cymes fascicled, terminal or axillary, thyrsoid, 8–10.5 cm, puberulent. Sepals ovate, ca. 1 mm, acute or short acuminate, puberulent outside. Corolla yellow, glabrous, tube ca. 2 mm; lobes obliquely ovate, ca. 1 mm. Stamens inserted above middle of corolla tube. Ovary pubescent. Style filiform, ca. 1.5 mm; pistil head subcapitate. Fruit moniliform, paired or solitary, ellipsoid or ovoid-oblong, 3–4.5 × 1.2–1.5 cm. Fl. May-Jul.

Humid forests, valleys, brushwoods; 250–1000 m. Guang-dong, Guangxi, Yunnan [Thailand, Vietnam].

**3. *Alyxia villilimba*** C. Y. Wu ex Tsiang & P. T. Li, Acta Phytotax. Sin. 11: 366. 1973.

毛叶链珠藤 mao ye lian zhu teng

*Alyxia villilimba* var. *macrophylla* P. T. Li.

Shrubs to 3 m tall, densely pubescent. Leaves usually in whorls of 3; petiole 1–2 cm; leaf blade elliptic or narrowly so, 7–20 × 1.5–4.5 cm, papery, glabrous adaxially, pubescent abaxially; lateral veins 30–40 pairs, subparallel. Cymes spikelike, axillary; peduncle 2–4 cm; bracts and bracteoles ovate. Sepals narrowly elliptic, acuminate, pubescent. Corolla white, ca. 1.5 mm. Stamens inserted at middle of corolla tube. Ovary glabrous. Fruit moniliform, articles ellipsoid, ca. 2.5 × 1 cm.

• Limestone in humid forests; 500–1000 m. W Guangxi, SE Yunnan.

**4. *Alyxia reinwardtii*** Blume, Catalogus 43. 1823.

长花链珠藤 chang hua lian zhu teng

*Alyxia flavescens* Pierre; *A. forbesii* King & Gamble; *A. lucida* Wallich var. *meiantha* Stapf; *A. reinwardtii* var. *meiantha* (Stapf) Markgraf.

Lianas woody, to 3 m, glabrous except for inflorescences. Juvenile branchlets triangular, later terete. Leaves opposite or in whorls of 3 or 4; petiole to 5 mm; leaf blade narrowly elliptic or oblong, 8–11 × 1.5–2.5 cm, sub-leathery to leathery, abaxially glabrous, apex narrowly long acuminate, lateral veins obscure abaxially. Cymes fascicled, axillary, pubescent, 3–5 cm; peduncle 1–1.3 cm; bracteoles very narrowly ovate. Sepals ovate or narrowly so, ca. 2 × 1 mm, obtuse or acute, pubescent to subglabrous. Corolla yellowish white, glabrous, tube ca. 8.5 mm; lobes ovate, ca. 4 mm. Ovary villous. Fruit oblong-ellipsoid, ca. 1.5 cm × 5 mm. Fl. May-Oct, fr. Aug-Dec.

Forests, brushwoods; 800–1700 m. S Yunnan [Indonesia, Malaysia, Philippines, Thailand, Vietnam].

**5. *Alyxia insularis*** Kanehira & Sasaki, Trans. Nat. Hist. Soc. Taiwan 24: 402. 1934.

兰屿链珠藤 lan yu lian zhu teng

Shrubs to 3 m tall, trailing, glabrous. Branchlets 4-angled. Leaves usually in whorls of 4; petiole 1–1.5 cm; leaf blade ovate or narrowly so, 5.5–10 × 2.5–3.5 cm, thick leathery, abaxially glabrous, apex obtuse or rounded; midvein elevated abaxially, lateral veins inconspicuous. Cymes fascicled, axillary; peduncle short. Sepals ovate to triangular, 3–4 mm, apex obtuse. Corolla tube 7–10 mm, densely pubescent inside at middle; lobes ovate, ca. 5 mm. Stamens inserted above middle of corolla tube. Ovary pubescent. Fruit ellipsoid, 1–2 × 0.6–1.5 cm. Seeds 1 or 2. Fl. May.

• Brushwoods. Taiwan (Lanyu and Lutaou).

**6. *Alyxia sinensis*** Champion ex Bentham, Hooker's J. Bot. Kew Gard. Misc. 4: 334. 1852.

链珠藤 lian zhu teng

Lianas woody, to 3 m, glabrous except for inflorescences. Leaves opposite or in whorls of 3; petiole ca. 2 mm; leaf blade orbicular, elliptic, ovate, or obovate, 1.5–3.5 × 0.8–2 cm, leathery, abaxially glabrous, margin revolute, apex rounded or retuse; lateral veins inconspicuous. Cymes fascicled, axillary or subterminal, less than 2 cm. Flowers densely crowded, 5–6 cm. Sepals ovate, ca. 1.5 mm, obtuse, pubescent. Corolla reddish to white, constricted at apex, tube 2–3 mm; lobes ovate, ca. 1.5 mm. Ovary villous. Fruit moniliform, stipitate, with 2 or 3 ellipsoid articles ca. 10 × 5 mm. Fl. Jul.  $2n = 36^*$ .

• Brushwoods, forest margins; 200–500 m. Fujian, Guang-dong, Guangxi, Guizhou, Hainan, Hunan, Jiangxi, Taiwan, Zhejiang.

The roots are used for the treatment of injury, toothache, and rheumatoid arthritis.

**7. *Alyxia fascicularis*** Bentham in Bentham & J. D. Hooker, Gen. Pl. 2: 698. 1876.

尾尖链珠藤 wei jian lian zhu teng

Lianas woody, to 2 m. Bark pale, warty; branchlets gray, glabrous. Leaves opposite or in whorls of 3; petiole 3–5 mm; leaf blade oblong-elliptic, oblong, or oblanceolate, 6–10 × 1.7–3 cm, glabrous, base broadly cuneate, apex caudate-acuminate, acumen ca. 1.5 cm; veins numerous, parallel, slender, raised. Cymes fascicled, short pedunculate, densely flowered, glabrous or puberulent. Sepals ovate. Corolla tube ca. 3 mm; lobes small, rounded. Fruit moniliform, stipitate, with 2–4 cylindrical-ellipsoid articles ca. 2 × 1 cm. Fl. Sep-Nov.

Mixed forests; 1800 m. SE Xizang (Motuo) [India (Khasia Mountain), Thailand].

**8. *Alyxia marginata*** Pitard in Lecomte & Humbert, Fl. Indo-Chine 3: 1123. 1933.

陷边链珠藤 xian bian lian zhu teng

*Alyxia funingensis* Tsiang & P. T. Li.

Lianas woody, to 3 m, glabrous except for inflorescences. Branchlets dark gray, warty. Leaves opposite or in whorls of 3; petiole 3–10 mm; leaf blade elliptic, narrowly elliptic, or obovate, 7–17 × 1.4–5 cm, papery, abaxially glabrous; lateral veins numerous, inconspicuous abaxially, marginal veins present. Cymes axillary, 1–2 cm, puberulent. Sepals ovate, 3–3.5 mm, acute, pubescent outside. Corolla white or creamy white, tube 5–10 mm, densely pubescent inside, lobes ovate, ca. 3 mm. Ovary puberulent. Fruit moniliform, articles subglobose, 1–1.6 × 0.8–1.1 cm. Fl. Sep-Nov, fr. Oct-Dec.

Dense forests, brushwood, forest borders; 200–1800 m. SW Guangxi, Yunnan [Cambodia, Laos, Vietnam].

**9. *Alyxia taiwanensis*** Lu & Yang, Bot. Bull. Acad. Sin. 19: 195. 1978.

台湾链珠藤 tai wan lian zhu teng

Shrubs scandent. Branches pubescent. Leaves opposite or in whorls of 3 or 4; petiole 1–2.5 mm; leaf blade narrowly elliptic, 2–2.5 × 1–1.5 cm, leathery, abaxially glabrous, base acute, apex acuminate; lateral veins inconspicuous. Cymes fascicled, terminal, less than 2 cm. Sepals ovate to triangular, 2–3 mm, pubescent. Corolla tube 4–5 mm, pubescent; lobes obliquely ovate, ca. 2 mm. Stamens inserted above middle of corolla tube. Ovary glabrous. Fruit with 1–4 articles; drupes ovoid, ca. 6 × 4 mm. Seeds ovoid, hairy.

• Edges of open forests; 1200–1300 m. Taiwan (Taichung).

**10. *Alyxia levinei*** Merrill, Philipp. J. Sci. 15: 254. 1920.

筋藤 jin teng

*Alyxia acutifolia* Tsiang; *A. kweichowensis* Tsiang & P. T. Li.

Shrubs scandent, to 3 m. Branches and branchlets slender, somewhat angled or striate, later terete. Leaves opposite or in whorls of 3; petiole 4–7 mm; leaf blade elliptic, narrowly

elliptic, or oblong, 3.5–8 × 1.2–3 cm, papery to somewhat leathery, abaxially glabrous, apex acuminate or acute; lateral veins obsolete. Cymes fascicled, axillary, solitary to trichasial; peduncle 0.5–2 cm, puberulent; bracteoles 2 or more, elliptic-ovate. Sepals 1.5–3 mm, villous, ciliate, apex acuminate. Corolla greenish white; tube ca. 3 mm, glabrous; lobes broadly elliptic, ca. 1.5 mm. Ovary villous. Fruits with 1–3, drupelike, ellipsoid or globose articles 1–1.3 cm × 0.8–1 cm. Fl. Mar-Aug, fr. Sep-Dec.

• Montane sparse woods, brushwoods; 300–500 m. Guang-dong, Guangxi, Guizhou.

All parts of the plant are used to cure infantile malnutrition due to intestinal parasites, rheumatism, and furunculosis.

**11. *Alyxia schlechteri*** H. Léveillé, Repert. Spec. Nov. Regni Veg. 9: 453. 1911.

狭叶链珠藤 xia ye lian zhu teng

*Alyxia schlechteri* var. *salicifolia* P. T. Li.

Lianas woody, to 3 m. Branches gray, with many lenticels; branchlets puberulent, later glabrous. Leaves opposite or in whorls of 3 or 4, usually crowded on upper branchlets; petiole 2–4 mm, glabrous or pubescent; leaf blade narrowly to very narrowly elliptic, 2–12 × 0.5–1.5 cm, leathery, usually glabrous, base broadly cuneate, margin recurved, apex acuminate or acute; lateral veins inconspicuous abaxially. Cymes fascicled, axillary, 0.5–1 cm. Sepals narrowly elliptic, ca. 2.5 mm, keeled, minutely puberulent, apex long acute. Corolla yellow. Fruit with 2 or 3 ellipsoid articles ca. 7 × 5 mm.

Sparse woods, brushwoods; 500–1500 m. Guangxi, Guizhou, Yunnan [Thailand].

**12. *Alyxia odorata*** Wallich ex G. Don, Gen. Hist. 4: 97. 1837.

海南链珠藤 hai nan lian zhu teng

*Alyxia euonymifolia* Tsiang; *A. hainanensis* Merrill & Chun; *A. jasminea* Tsiang & P. T. Li; *A. leitungensis* Tsiang; *A. nitens* Kerr; *A. vulgaris* Tsiang.

Lianas woody, to 4 m. Branches slightly angled when young, later terete, puberulent or glabrous. Leaves opposite or in whorls of 3; petiole 3–10 mm; leaf blade elliptic, oblong, narrowly elliptic, or obovate, 2–12 × 1–4.5 cm, papery, glabrous, apex acute or short acuminate; lateral veins numerous, usually inconspicuous. Cymes fascicled, terminal and axillary, 1–2 cm, pubescent. Pedicel and calyx pubescent. Sepals ovate to narrowly elliptic, 1.7–8 mm, obtuse or acute, long pubescent, ciliate. Corolla yellowish green, glabrous or sometimes puberulent inside, tube 3–15 mm; lobes ovate, 1.5–4 mm. Stamens inserted at or above middle of corolla tube. Ovary pubescent. Fruit with 1–3 ellipsoid-globose articles 1–2.2 cm × 5–8 mm. Fl. Mar-Oct, fr. Jun-Dec.

Sparse woods, brushwoods; 200–2000 m. Guangdong, Guangxi, Guizhou, Hainan, Sichuan, Yunnan [Myanmar, Thailand].

**15. KOPSIA** Blume, Catalogus 12. 1823, nom. cons.

蕊木属 rui mu shu

Trees or shrubs with white latex. Leaves opposite. Cymes terminal, 3- to many flowered, bracteate; peduncle long or short; bracteoles small or large. Flowers white or rose, 5-merous. Calyx small, deeply divided, without glands. Corolla salverform, tube 2.3-5 cm, narrow, dilated at or below apex; throat without scales, pilose inside; lobes overlapping to right. Stamens inserted above middle of corolla tube; filaments very short; anthers narrowly oblong or ovate, included, free from pistil head, base rounded; disc scales alternate with ovaries. Ovaries 2, distinct; ovules 2 per locule. Style filiform; pistil head thickened, with a short basal collar and apiculate apex. Drupes 1 or 2, ellipsoid, 1- or 2-seeded. Seeds oblong, testa membranous, not comose.

About 20 species: SE Asia, three in China.

- 1a. Flowers many, ± crowded into corymbose, several-branched cymes; peduncle to 14 cm; disc longer than ovary; mature drupes blue-black ..... 1. *K. arborea*
- 1b. Flowers few, in little-branched, ± monochasial cymes; peduncle up to 1 cm; disc up to as long as ovary; mature drupe orange or red (color not known in *K. fruticosa*).
  - 2a. Lateral veins of leaf blade more than 20 pairs; corolla white; calyx and ovary glabrous ..... 2. *K. hainanensis*
  - 2b. Lateral veins of leaf blade 10-15 pairs; corolla pink; calyx and ovary pubescent ..... 3. *K. fruticosa*

1. **Kopsia arborea** Blume, Catalogus 13. 1823.

蕊木 rui mu

*Kopsia lancibracteolata* Merrill; *K. officinalis* Tsiang & P. T. Li.

Trees to 15 m tall. Branches greenish, terete, slightly compressed, puberulent when young. Petiole 5-15 cm; leaf blade elliptic, narrowly elliptic, or narrowly ovate, 8-24 × 3.5-8.5 cm, glabrous, apex acute or short acuminate; lateral veins 10-20 pairs. Cymes corymbose, many flowered; peduncle to 14 cm, puberulent or glabrous; bracteoles narrowly oblong, puberulent or glabrous. Pedicel 3-4 mm. Sepals narrowly oblong, 4-6 mm, puberulent or glabrous. Corolla white, tube ca. 2.5 cm; lobes narrowly oblong, 1.5-2 cm. Disc scales narrowly oblong, longer than ovary, fleshy. Ovary ovoid, puberulent. Drupes black or blue-black, ellipsoid, 2.5-3.5 × 1.5-2 cm. Fl. Apr-Sep, fr. Jul-Dec.  $2n = 72$ .

Montane forests, often along moist ravines; 400-1000 m. S Guangdong, SE Guangxi, Hainan, S Yunnan [Indonesia, Malaysia, Philippines, Thailand, Vietnam; N Australia].

A decoction of bark is used as an enema. The leaves and fruit are used to treat sore throat and tonsillitis.

2. **Kopsia hainanensis** Tsiang, Sunyatsenia 2: 111. 1934.

海南蕊木 hai nan rui mu

Shrubs or trees to 7 m tall, glabrous except for flowers. Branchlets gray-white, terete. Petiole 0.5-1.9 cm; leaf blade lustrous green adaxially, pale green abaxially, narrowly elliptic, 5-13.5 × 1-4.5 cm, apex obtuse or with a short acumen; lateral

veins more than 20 pairs. Cymes 6- or 7-flowered; peduncle 2-10 mm. Pedicel 1-2 mm. Sepals ovate, ca. 1.5 mm, obtuse, glabrous. Corolla white, glabrous outside, pilose inside to anthers; tube ca. 2.3 cm, ca. 1 mm in diam.; lobes oblong, ca. 1.5 cm. Disc scales sublinear, shorter than or as long as ovary. Ovary glabrous, 2-loculed; ovules 1 per locule. Drupes red or orange, subellipsoid, ca. 2.5 × 1 cm. Fl. Apr-Dec.

• Densely wooded ravines at lower and middle altitudes. Hainan.

3. **Kopsia fruticosa** (Ker Gawler) A. de Candolle, Prodr. 8: 352. 1844.

红花蕊木 hong hua rui mu

*Cerbera fruticosa* Ker Gawler, Bot. Reg. 5: t. 391. 1819; *Kopsia vinciflora* Blume.

Shrubs evergreen, to 4 m tall, glabrous except for inflorescences. Petiole ca. 1 cm; leaf blade narrowly elliptic or narrowly oblong, 10-23 × 2.5-9 cm, apex acute or obtusely caudate; lateral veins 10-15 pairs. Inflorescences few flowered, puberulent; peduncle to 1 cm; bracteoles to 1.5 mm, pubescent. Pedicel 5-7 mm. Sepals ovoid, 1.5-2.5 mm, pubescent, apex obtuse. Corolla pink, tube 3-5 cm, throat pubescent; lobes oblong, 1.5-2.5 cm. Disc scales sublinear, as long as or shorter than ovary. Ovary tomentose. Style 3-4 cm. Drupe ellipsoid, usually solitary, 1-seeded, to 2.5 × 2 cm, pubescent.  $2n = 36$ .

S Guangdong [India, Indonesia, Malaysia, Philippines, Thai-land].

Cultivated for medicine.

16. **OCHROSIA** Jussieu, Gen. Pl. 144. 1789.

玫瑰树属 mei gui shu shu

Trees with latex. Branches stout. Leaves in whorls of 3-5, rarely opposite; lateral veins numerous, subparallel, almost at a right angle to midvein. Cymes subterminal, pedunculate. Calyx deeply divided, usually without glands. Corolla salverform; tube slightly dilated above middle, to 1 cm, throat without scales; lobes overlapping to right. Stamens inserted in widening of corolla tube; anthers free from pistil head, narrowly oblong, rounded at base; disc absent. Ovaries 2, free or basally connate; ovules 2-6, biseriolate on each side of a prominent placenta. Style filiform; pistil head shortly 2-cleft at apex. Drupes 1 or 2, smooth;

endocarp thick, hard. Seeds 2–4 per locule, flat, not comose; endosperm none; cotyledons large, flat.

About 25 species: Malaysia, W Pacific Islands; three species cultivated in China.

- 1a. Sepals minutely ciliate; leaf apex usually rounded ..... 1. *O. borbonica*  
 1b. Sepals mostly not ciliate; leaf apex abruptly acuminate or obtuse.  
 2a. Corolla tube longer than lobes; leaves narrowly obovate to broadly elliptic ..... 2. *O. elliptica*  
 2b. Corolla tube as long as lobes; leaves elliptic ..... 3. *O. coccinea*

**1. *Ochrosia borbonica*** J. F. Gmelin, Syst. Nat. 2: 439. 1796.

玫瑰树 mei gui shu

Trees to 15 m tall. Trunk to 40 cm in diam. Terminal leaves in whorls of 3 or 4, others opposite; petiole 0.5–3.5 cm; leaf blade obovate or elliptic, 8–25 × 3–5 cm, apex usually rounded. Cymes many flowered; peduncle 2–12 cm. Flowers fragrant, short pedicellate or sessile. Sepals ovate, 2.5–3 mm, rounded, minutely ciliate. Corolla throat white, pink, or red, tube 7.5–10 mm; lobes oblong, 4–9 mm. Drupes 2, red, ca. 4.5 × 3.5 cm. Fl. throughout the year but mainly Jan–Jun.

S Guangdong [Indonesia, Malaysia, Singapore, Sri Lanka, Vietnam; Africa (Mascarenes)].

Cultivated for medicine.

**2. *Ochrosia elliptica*** Labillardière, Sert. Austro-Caledon. 25, t. 30. 1824.

古城玫瑰树 gu cheng mei gui shu

Trees to 6 m tall, glabrous. Petiole 1.5–2 cm; leaf blade obovate to broadly elliptic, 8–15 × 3–5 cm, apex obtuse or short acuminate. Cymes corymbose. Flowers sessile. Sepals ovate, ca. 2 mm, not ciliate, apex obtuse. Corolla white, cylindric, tube ca. 1 cm; lobes linear, ca. 6 mm. Anthers narrowly oblong. Drupes ellipsoid, 2–4 × ca. 1 cm. Seeds

suborbicular, narrow margined. Fl. Jun.

S Guangdong, Taiwan [introduced from Australia].

Cultivated for medicine.

**3. *Ochrosia coccinea*** (Teijsmann & Binnendijk) Miquel, Ann. Mus. Bot. Lugduno-Batavum 4: 138. 1869.

光萼玫瑰树 guang e mei gui shu

*Lactaria coccinea* Teijsmann & Binnendijk, Natuurk. Tijdschr. Ned. Indië. 29: 249. 1867; *Bleekeria coccinea* (Teijsmann & Binnendijk) Koidzumi; *Excavatia coccinea* (Teijsmann & Binnendijk) Markgraf.

Trees to 6 m, glabrous. Branchlets subangular, smooth. Leaves opposite or whorled; blade elliptic, 7–20 × 3–5 cm, apex abruptly acuminate. Cymes repeatedly dichasial, ending monochasial, many flowered; peduncle to 3 cm. Pedicel 2–4 mm. Sepals ovate, ca. 2 mm, glabrous, apex rounded. Corolla white, tube ca. 4 mm, as long as lobes. Stamens inserted near mouth of corolla tube. Ovaries distinct, oblong. Drupes 2, bright red, ellipsoid, 2.5–5 × 2–2.5 cm, spreading hori-zontally. Seeds 2 on each placenta.  $2n = 22$ .

S Guangdong [Malaysia, New Guinea, Singapore].

Cultivated for medicine.

**17. THEVETIA** Linnaeus, Opera Var. 212. 1758, nom. cons.

黄花夹竹桃属 huang hua jia zhu tao shu

*Cascabela* Rafinesque; *Plumeriopsis* Rusby & Woodson.

Trees or much-branched shrubs, evergreen, erect, latex white. Leaves alternate, rather densely together on slender branchlets. Cymes terminal and leaf opposed. Calyx deeply divided, with many basal glands inside. Corolla yellow, funnellform, lobes overlapping to left, throat with 5, narrow, long-hairy scales. Stamens inserted in distal narrow part of corolla tube; filaments very short; anthers narrowly oblong, small, free from pistil head, cells not appendaged proximally; disc absent. Ovary 2-loculed, placenta prominent. Style filiform; pistil head disclike, thick, dilated, apex shortly 2-cleft. Drupes depressed globose; endocarp hard, woody or fleshy. Seeds 2 per locule, wingless, not comose, without endosperm; cotyledons suborbicular, fleshy, radicle short.

Eight species: tropical America, two species cultivated in China.

- 1a. Leaves narrowly obovate; corolla tube longer than lobes ..... 1. *T. ahouai*  
 1b. Leaves very narrowly oblong; corolla tube shorter than lobes ..... 2. *T. peruviana*

**1. *Thevetia ahouai*** (Linnaeus) A. de Candolle, Prodr. 8: 345. 1844.

阔叶竹桃 kuo ye zhu tao

*Cerbera ahouai* Linnaeus, Sp. Pl. 1: 208. 1753.

Shrubs to 3 m tall. Wood with an offensive smell. Leaf blade narrowly obovate, glabrous adaxially, pubescent abaxially, apex obtuse. Sepals ovate, reflexed, glabrous, apex

acute. Corolla tube dilated distally, longer than lobes, closed at mouth, marked with 5 deep grooves; lobes oval, oblique or overlapping, with undulate margin; corona scales absent. Stamens inserted at apex of corolla tube, included. Style filiform; pistil head turbinate, apex 2-cleft. Fl. almost throughout the year.

S Guangdong [introduced from Brazil].

Cultivated for medicine. The sap and seeds are deadly poisonous to domestic animals.

**2. *Thevetia peruviana*** (Persoon) K. Schumann in Engler & Prantl, Nat. Pflanzenfam. 4(2): 159. 1895.

黄花夹竹桃 huang hua jia zhu tao

*Cerbera peruviana* Persoon, Syn. Pl. 1: 267. 1805; *Cascabela thevetia* (Linnaeus) Lippold; *Cerbera thevetia* Linnaeus; *Thevetia linearis* A. de Candolle; *T. neriifolia* Jussieu ex Steudel; *T. neriifolia* Jussieu ex A. de Candolle; *T. thevetia* (Linnaeus) Millspaugh.

Trees to 6 m tall. Bark chocolate-brown, lenticellate; lower branches pendulous, young branches greenish gray. Petiole ca. 3 mm; leaf blades lustrous green adaxially, light green abaxially, very narrowly oblong, 10–15 × 0.5–1.2 cm, somewhat leathery, glabrous, apex acuminate, lateral veins obscure. Pedicel 2.5–5 cm. Flowers fragrant. Sepals green, narrowly triangular, apex acuminate. Corolla 6–7 × 4.5–5.5 cm; tube 4–5 cm, shorter than lobes; corona scales present, connected by a transverse row of long white hairs, lobes obliquely obovate. Drupes compressed triangular-globose, 2.5–4 cm in diam. Seeds light gray, lenticular, ca. 2 × 3.5 cm. Fl. May-Dec.  $2n = 20$ .

Fujian, Guangdong, Guangxi, Hainan, Taiwan, Yunnan [native to Central and South America].

Cultivated for medicine. The sap and seeds are deadly poisonous to domestic animals. The seeds yield oil for industry and soap making. The bark is a powerful antiperiodic and febrifuge. A handsome ornamental.

## 18. *CERBERA* Linnaeus, Sp. Pl. 1: 208. 1753.

海芒果属 hai mang guo shu

Trees with latex. Branches stout. Leaves alternate, lateral veins 20–30 pairs, diverging almost at right angles to midvein. Cymes terminal, long pedunculate. Calyx deeply divided, without glands inside. Corolla white, funnelform, throat slightly dilated, ribbed, or with 5 pubescent scales; lobes broad, overlapping to left. Stamens inserted at corolla throat; anthers narrowly oblong, apiculate, free from pistil head, lobes rounded at base; disc absent. Ovaries 2, free, ovules 4 in each locule. Style filiform, dilated distally; pistil head shortly 2-cleft. Drupes 1 or 2, large, ellipsoid or globose, 1- or 2-loculed, with a thick, woody-fibrous endocarp. Seeds 1 or 2 per locule, wingless, not comose, without endosperm; cotyledons thin, radicle very short.

Three species: Africa, tropical Asia, Australia, Pacific Islands; one species in China.

**1. *Cerbera manghas*** Linnaeus, Sp. Pl. 1: 208. 1753.

海芒果 hai mang guo

Trees to 8 m tall. Bark gray-brown; branches whorled, marked with leaf scars. Petiole 2.5–6 cm; leaf blade narrowly ovate, 6–37 × 2.3–7.8 cm, base cuneate, apex acuminate. Peduncle stout, 5–21 cm. Pedicel terete, 1–2 cm. Flowers 4–7 cm wide. Corolla white, pinkish in center; tube 2.5–4 cm, villous inside; lobes ovate, falcate, 1.5–2.5 cm. Drupes 5–8 ×

4–6 cm, smooth. Seeds usually single. Fl. Mar-Oct, fr. Jul-Dec.  $2n = 40$ .

Seashore, tidal river banks. S Guangdong, S Guangxi, Hainan, S Taiwan [Cambodia, Indonesia, Japan (Ryukyu Islands), Laos, Malaysia, Myanmar, Thailand, Vietnam; Australia, Pacific Islands].

The fruit, and especially the seed, are very poisonous and contain hydrocyanic acid and the cardiac glycosides thevetin and cerberin. The wood is used for fine charcoal, and the seeds are used in Hainan to stupefy fish. The bark, latex, and leaves are sometimes used as an emetic and a purgative.

## 19. *CAMERARIA* Linnaeus, Sp. Pl. 1: 210. 1753.

鸭蛋花属 ya dan hua shu

Trees or shrubs. Leaves opposite, with numerous, parallel secondary veins. Cymes corymbose, axillary, terminal, or at branch forks, 1- to many flowered. Calyx small, without glands; lobes ovate, apex acute. Corolla yellow or white, funnelform or salverform; tube long, cylindrical, swollen on 1 side at base or apex, throat not scaly; lobes unequal sided, overlapping to left. Stamens inserted above middle of corolla tube; anthers subsessile, acuminate, free from pistil head, exerted or included, connective extending into a long, bristly appendage. Ovaries 2, distinct; ovules numerous on each placenta. Style short or long, filiform; pistil head conical, 2-partite. Follicles 2, samaroid, reflexed or horizontal, obtuse. Seeds numerous, ovate.

Four species: Caribbean, one species cultivated in China.

**1. *Cameraria latifolia*** Linnaeus, Sp. Pl. 1: 210. 1753.

鸭蛋花 ya dan hua

Trees to 10 m tall. Branches forked. Leaves elliptic or ovate, ca. 4 cm, membranous, lateral veins numerous, densely parallel. Cymes corymbose, terminal, few flowered. Sepals 1–1.5 mm. Corolla white, yellow at base, salverform; tube cylindrical, 5–8 mm; lobes obovate, 0.6–1.5 cm. Anthers oblong, as long as appendages. Style filiform. Follicles 1 or 2,

4–5 cm. Seeds ovate, with a membranous wing at proximal end.

Guangdong [introduced from Cuba].

Cultivated for medicine and frequently used in the preparation of poultice.

## 20. ALLAMANDA Linnaeus, Mant. Pl. 2: 146. 1771.

黄蝉属 huang chan shu

Shrubs erect or trailing. Leaves whorled, with axillary glands. Flowers large, in terminal or seemingly axillary corymbs. Calyx deeply divided, without basal glands. Corolla yellow, funnelform, narrow part with fringed scales, limb campanulate, lobes overlapping to left. Stamens inserted at narrow part of corolla; filaments very short; anthers narrowly oblong, base rounded, coherent with pistil head; disc cup-shaped, obscurely 5-lobed or entire, fleshy, thick. Ovary 1-loculed, with two parietal placentae; ovules numerous. Style filiform; pistil head thick, with a membranous, reflexed rim, apex conical, shortly 2-lobed. Capsules globose, glabrous, sharply spiny, 2-valved. Seeds numerous, imbricate, compressed, winged or with a membranous margin; radicle short.

Fourteen species: tropical America, two cultivated in China.

- 1a. Erect shrubs with clear sap; lateral veins elevated on abaxial leaf surface; corolla tube ca. 3 cm, distinctly swollen at base ..... 1. *A. schottii*  
1b. Climbing shrubs with white latex; lateral veins flattened on abaxial leaf surface; corolla tube 4–8 cm, not swollen at base ..... 2. *A. cathartica*

**1. Allamanda schottii** Pohl, Pl. Bras. Icon. Descr. 1: 73. 1827.

黄蝉 huang chan  
*Allamanda neriifolia* Hooker.

Shrubs erect, to 2 m tall, with clear sap. Leaves in whorls of 3–5, subsessile; leaf blade elliptic or narrowly obovate, 5–14 × 2–4 cm, minutely hispid along veins; lateral veins elevated on abaxial surface. Flowers 4–6 cm. Corolla tube rather narrowly funnelform, ca. 3 cm, distinctly swollen at base, limb ca. 4 cm in diam.; lobes pale yellow, ovate or orbicular, ca. 2 cm, obtuse. Capsules globose, ca. 3 cm in diam., long spiny. Seeds ca. 2 × 1.5 cm. Fl. May–Aug, fr. Oct–Dec.  $2n = 18$ .

Fujian, Guangdong, Guangxi, Hainan, Taiwan [introduced from Brazil].

Cultivated for medicine and as an ornamental.

**2. Allamanda cathartica** Linnaeus, Mant. Pl. 2: 214. 1771.

软枝黄蝉 ruan zhi huang chan

*Allamanda hendersonii* Bulliard ex Dombrain; *A. cathartica* var. *hendersonii* (Bulliard ex Dombrain) L. H. Bailey & Raffill.

Shrubs trailing, to 4 m, with white latex. Stems glabrous. Leaves opposite or in whorls of 3–5; petiole ca. 5 mm; leaf blade obovate, narrowly obovate, or oblong, 6–15 × 4–5 cm, glabrous or villous along veins on abaxial surface, lateral veins flattened. Peduncle short. Flowers 7–14 cm. Corolla yellow; tube 4–8 cm, funnelform, cylindrical in proximal half, campanulate in distal half, limb 9–14 cm in diam.; lobes obovate-truncate to orbicular. Capsules subglobose, 3–7 × 3–5 cm, with spines to 1 cm. Seeds compressed, winged or with a membranous margin. Fl. spring–summer.  $2n = 18$ .

Fujian, Guangdong, Guangxi, Hainan, Taiwan [native to South America].

Cultivated for medicine.

## 21. MANDEVILLA Lindley, Bot. Reg. 26: t. 7. 1840.

文藤属 wen teng shu

Lianas usually glabrous, with latex. Leaves opposite; stipules interpetiolar, reduced to many linear segments. Racemes axillary, few flowered. Flowers large. Calyx deeply divided, with many basal glands inside. Corolla funnelform; tube narrow, more than 2 cm, limb campanulate; faucal scales absent; lobes overlapping to right. Stamens inserted and included in widened part of corolla tube; filaments short; anthers oblong, adherent at middle to pistil head, cells obtusely caudate; disc 5-cleft. Ovaries free, glabrous; ovules numerous. Style glabrous; pistil head with a 2-cleft mucro. Follicles long, slender. Seeds narrowly oblong, not beaked, comose.

About 120 species: Central and South America, one species cultivated in China.

**1. Mandevilla laxa** (Ruiz & Pavon) Woodson, Ann. Missouri Bot. Gard. 19: 68. 1932.

文藤 wen teng

*Echites laxa* Ruiz & Pavon, Fl. Peruv. 2: 19, pl. 134.



1799; *Mandevilla suaveolens* Lindley.

Branchlets glabrous. Petiole long; leaf blade narrowly cordate, herbaceous, glabrous adaxially, glaucous and bearded at vein axils abaxially, apex acuminate. Racemes long pedunculate, nodding, simple, many flowered. Flowers fragrant. Sepals narrow, 0.7–1.3 cm, acute. Corolla white or pale

pink, limb 10-folded inside; lobes oblong, undulate at margin, apiculate. Filaments broad, pubescent, much shorter than glabrous anthers; disc apex obtuse or truncate, glabrous.

S Guangdong [native of Argentina].

Cultivated for medicine.

## 22. TRACHELOSPERMUM Lemaire, Jard. Fleur. 1: 61. 1851.

络石属 *luo shi shu*

Lianas woody, latex white. Leaves opposite. Cymes lax, terminal, pseudoaxillary, or axillary. Flowers white or purplish, 5-merous. Calyx small, deeply divided, basal glands 5–10, apex usually denticulate. Corolla salverform; tube cylindrical, 5-angled, dilated at staminal insertion, throat constricted; lobes sharply overlapping to right. Stamens inserted at lower third of corolla tube; anthers sagittate, connivent, adherent to pistil head, anther tips included or exerted, cells spurred at base; disc scales 5, free. Ovaries 2, free, usually longer than disc; ovules numerous in each ovary. Style short; pistil head conical. Follicles 2, linear or fusiform, divergent or parallel. Seeds linear-oblong, not beaked, coma silky white; endosperm copious; cotyledons linear, flat, radicle short.

About 15 species: one in North America, the others in Asia; six species in China.

- 1a. Anther apex exerted or slightly so ..... 1. *T. asiaticum*
- 1b. Anther apex included or reaching corolla mouth.
  - 2a. Corolla tube dilated at throat or middle.
    - 3a. Stamens inserted at corolla throat ..... 2. *T. bodinieri*
    - 3b. Stamens inserted at middle of corolla tube ..... 3. *T. jasminoides*
  - 2b. Corolla tube dilated at base.
    - 4a. Follicles divergent, linear, 3–5 mm in diam. .... 4. *T. brevistylum*
    - 4b. Follicles parallel, cylindrical to fusiform, 10–15 mm in diam.
      - 5a. Leaves usually obovate or narrowly so; flowers purplish; ovaries and fruit glabrous ..... 5. *T. axillare*
      - 5b. Leaves oblong, narrowly ovate, or elliptic; flowers white; ovaries and fruit pubescent ..... 6. *T. dunnii*

**1. *Trachelospermum asiaticum*** (Siebold & Zuccarini) Nakai in T. Mori, Enum. Pl. Corea 293. 1922.

亚洲络石 *ya zhou luo shi*

*Malouetia asiatica* Siebold & Zuccarini, Abh. Math. Phys. Cl. Königl. Bayer. Akad. Wiss. 4: 163. 1846; *Melodinus cavaleriei* H. Léveillé; *Trachelospermum asiaticum* var. *brevisepalum* (C. K. Schneider) Tsiang; *T. divaricatum* var. *brevisepalum* C. K. Schneider; *T. foetidum* (Matsumura & Nakai) Nakai; *T. gracilipes* J. D. Hooker; *T. gracilipes* var. *cavaleriei* (H. Léveillé) Tsiang; *T. gracilipes* var. *hupehense* Tsiang & P. T. Li; *T. jasminoides* (Lindley) Lemaire subsp. *foetidum* Matsumura & Nakai; *T. lanyuense* C. E. Chang; *T. siamense* Craib.

Lianas woody, to 10 m, glabrous or pubescent when young. Petiole 2–10 mm; leaf blade elliptic, narrowly ovate, or subobovate, 2–10 × 1–5 cm, membranous to papery, base acute or broadly cuneate, apex obtuse to acute, rarely caudate; lateral veins 6–10 pairs. Cymes terminal and axillary. Sepals appressed to corolla tube, 1.5–3 mm, puberulent to glabrous outside, apex obtuse to subacute; basal glands 10. Corolla white, tube 6–10 mm, dilated at throat, glabrous or puberulent inside facing stamens; lobes obovate, as long as tube. Stamens inserted at or near corolla throat; anther apex exerted or slightly so; disc scales shorter than to as long as ovary. Ovary glabrous. Follicles linear, 10–30 cm × 3–5 mm. Seeds oblong, 2–2.5 cm, coma to 3.5 cm. Fl. Apr-Jul, fr. Aug-Nov.  $2n = 20$ .

Dense or open montane forests, brushwoods, often clinging to trees; 100–1000 m. Fujian, Gansu, Guangdong, Guangxi, Guizhou, Hainan, Hubei, Hunan, Jiangxi, Sichuan, Taiwan, Xizang, Yunnan [India, Japan, Korea, Thailand].

**2. *Trachelospermum bodinieri*** (H. Léveillé) Woodson in Rehder, J. Arnold Arbor. 15: 312. 1934.

贵州络石 *gui zhou luo shi*

*Melodinus bodinieri* H. Léveillé, Repert. Spec. Nov. Regni Veg. 2: 113. 1906; *Trachelospermum cathayanum* C. K. Schneider; *T. cathayanum* var. *longipedicellatum* Lingelsheim; *T. cathayanum* var. *tetanocarpum* (C. K. Schneider) Tsiang & P. T. Li; *T. formosanum* Y. C. Liu & C. H. Ou; *T. longipedicellatum* (Lingelsheim) Woodson; *T. tetanocarpum* C. K. Schneider; *T. wenchowense* Tsiang; *T. yunnanense* Tsiang & P. T. Li.

Lianas woody, to 15 m, minutely tomentose to glabrous or glabrescent. Petiole 3–10 mm long; leaf blade elliptic, narrowly elliptic, or narrowly obovate, 3–10 × 1–4 cm, thick papery; lateral veins 8–13 pairs. Cymes paniculate, terminal or axillary, to 10 cm. Sepals narrowly elliptic, 2–3 mm, glabrous, ciliate, apex appressed to corolla or slightly spreading, acute or obtuse. Corolla white, tube 5–14 mm; throat dilated, pilose, glabrous outside; lobes obliquely obovate or narrowly obovate, as long as tube. Anthers apex reaching corolla throat; disc

5-lobed, shorter than ovary. Ovary glabrous. Follicles linear, 12–41 cm × 2–5 mm. Seeds oblong, ca. 1.5 cm, coma 2–3.5 cm. Fl. May-Aug, fr. Aug-Dec.

• Mixed woods, brushwoods; 500–2600 m. Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Sichuan, Taiwan, Xizang, Yunnan, Zhejiang.

**3. *Trachelospermum jasminoides*** (Lindley) Lemaire, Jard. Fleur. 1: t. 61. 1851.

络石 luo shi

*Rhynchospermum jasminoides* Lindley, J. Hort. Soc. London 1: 74. 1846; *Trachelospermum adnascens* Hance; *T. jasminoides* var. *heterophyllum* Tsiang; *T. jasminoides* var. *variogatum* W. T. Miller.

Lianas woody, to 10 m. Stem brownish, lenticellate; young branchlets pubescent, glabrous when older. Petiole 3–12 mm long; leaf blade ovate to obovate or narrowly elliptic, 2–10 × 1–4.5 cm, papery, glabrous or sometimes sparsely pubescent abaxially. Cymes paniculate, terminal and axillary; peduncle 2–6 cm, puberulent to glabrous. Sepals narrowly oblong, 2–5 mm, spreading or reflexed, pubescent outside, ciliate, apex obtuse or acute. Corolla white, tube dilated at middle, 5–10 mm, throat glabrous or pilose facing stamens; lobes obovate, as long as tube. Stamens included, inserted at middle of corolla tube; ovary glabrous. Follicles linear, 10–25 cm × 3–10 mm. Seeds oblong, 1.5–2 cm, coma 1.5–4 cm. Fl. Mar-Aug, fr. Jun-Dec.  $2n = 20$ .

Sunny edges of forests, brushwoods; 200–1300 m. Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hainan, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Shandong, Shanxi, Sichuan, Taiwan, Xizang, Yunnan, Zhejiang [Japan, Korea, Vietnam].

A strong bast fiber obtained from the inner bark is used in making rope, sacks, and paper. The stem is used for the treatment of rheumatism and injury. The flowers yield perfumed oil. The whole plant is poisonous.

**4. *Trachelospermum brevistylum*** Handel-Mazzetti, Akad. Wiss. Wien. Sitzungsber., Math.-Naturwiss., Kl., Abt. 1, 58: 228. 1921.

短株络石 duan zhu luo shi

*Trachelospermum cuneatum* Tsiang; *T. suaveolens* Chun.

Lianas woody, to 5 m, glabrous. Branches lenticellate. Petiole 5–8 mm; leaf blade narrowly elliptic, 5–10 × 1.2–3 cm, base obtuse, apex acuminate or caudate-acuminate; lateral veins 10–14 pairs. Cymes terminal and axillary; peduncle 1–2 cm. Pedicel 5–7 mm. Sepals narrowly elliptic, 1–2 mm, glabrous, apex acute, slightly spreading. Corolla white, tube ca. 4.5 mm, strigose-pilose inside; lobes obliquely obovate, 6–7 mm. Stamens included, inserted near base of corolla tube; disc rectangular, 5-lobed, free. Ovary glabrous. Follicles linear, divergent, 11–24 cm × 3–5 mm. Seeds oblong, 1–3 cm, coma

ca. 3 cm. Fl. Apr-Jul, fr. Aug-Dec.

• Open forests, often climbing on trees; 600–1100 m. Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hunan, Sichuan, Xizang.

**5. *Trachelospermum axillare*** J. D. Hooker, Fl. Brit. India 3: 668. 1882.

紫花络石 zi hua luo shi

*Maesa scandens* H. Léveillé; *Melodinus chaffanjonii* H. Léveillé; *Periploca astacus* H. Léveillé.

Lianas woody, to 10 m, glabrous except for young shoots and inflorescences. Stems densely lenticellate. Petiole 3–5 mm; leaf blade obovate, narrowly obovate, or narrowly elliptic, 8–15 × 3–4.5 cm, leathery, base cuneate or rounded, apex acute, abruptly caudate, or acuminate; lateral veins to 15 pairs. Cymes axillary or sometimes subterminal, to 3 cm. Pedicel 3–8 mm. Sepals appressed to corolla tube, ovate, obtuse, basal glands ca. 10. Corolla purplish, tube ca. 5 mm; lobes narrowly obovate, 5–7 mm. Stamens inserted at base of corolla tube, included. Follicles connate, cylindrical to fusiform, 10–15 × 1–1.5 cm, glabrous. Seeds broadly ovate, ca. 1.5 cm, coma ca. 5 cm. Fl. May-Jul, fr. Aug-Oct.

• Brushwoods, sunny open forests; 500–1500 m. Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangxi, Sichuan, Xizang, Yunnan, Zhejiang.

A fine, strong fiber is obtained from the inner bark and used in making paper. The whole plant is used in Guangxi as medicine for the treatment of injury, pulmonary tuberculosis, bronchitis, and rheumatism.

**6. *Trachelospermum dunnii*** (H. Léveillé) H. Léveillé, Fl. Kouy-Tchéou 31. 1914.

绣毛络石 xiu mao luo shi

*Melodinus dunnii* H. Léveillé, Repert. Spec. Nov. Regni Veg. 9: 453. 1911. *Trachelospermum eglanulatum* D. Fang; *T. rubrinerve* H. Léveillé; *T. tenax* Tsiang.

Lianas woody, to 20 m, rust colored tomentose. Petiole 3–5 mm; leaf blade oblong, elliptic, or narrowly so, 6–10 × 2–3 cm, base obtuse or subcordate to subauriculate-cordate, apex short acuminate or acute, lateral veins 10–14 pairs. Cymes terminal or axillary; peduncle 1.2–1.5 cm. Pedicel 1–2.5 cm. Sepals slightly spreading, narrowly elliptic, 3–4 mm, tomentose, apex acute, recurved. Corolla white, tube 5–6 mm, pilose; lobes obliquely obovate or elliptic, falcate, 8–9 mm. Stamens inserted near base of corolla tube; disc 5-lobed, as long as ovary. Follicles connate, cylindrical to fusiform, 8–9 × 1.2 cm, pubescent. Seeds ca. 1 cm, coma 3–4 cm. Fl. Mar-Aug, fr. Jun-Dec.

Open forests, brushwoods; 300–1600 m. Guangxi, Guizhou, Hunan, Yunnan, Zhejiang [Vietnam].

The young leaves are used in Guangxi as medicine for injury.

**23. AGANOSMA (Blume) G. Don, Gen. Hist. 4: 77. 1837.**

香花藤属 xiang hua teng shu

*Echites* sect. *Aganosma* Blume, Bijdr. 1040. 1826; *Amphineurion* (A. de Candolle) Pichon.

Lianas woody, with white latex. Leaves opposite, interpetiolar line evident. Cymes terminal or axillary, corymblike; bracts and bracteoles sepal-like. Flowers large. Calyx divided halfway or deeper, with 5 or more basal glands inside, sepals usually longer than corolla tube. Corolla white, salverform; tube long cylindrical, widened at base; lobes overlapping to right. Stamens inserted at lower third of tube; anthers included, sagittate, adherent to pistil head, cells with a rigid, empty basal tail; disc ringlike or tubular, lobed or dentate, surrounding ovary. Ovaries 2, distinct; ovules numerous. Style short; pistil head conical, apex 2-cleft. Follicles linear, terete. Seeds flat, not beaked, coma early deciduous.

About 12 species: tropical and subtropical Asia, five species in China.

- 1a. Corolla tube longer than sepals; calyx with a continuous row of basal glands inside; leaves with a strong intramarginal vein ..... 1. *A. marginata*  
 1b. Corolla tube shorter than sepals; calyx with basal glands only inside sepal edges; leaves without a strong intramarginal vein.  
 2a. Corolla glabrous at throat; all parts densely tomentose ..... 2. *A. cymosa*  
 2b. Corolla pubescent at throat; all parts glabrous or minutely pubescent, rarely tomentose.  
 3a. Corolla lobes 2.4–3.5 cm ..... 3. *A. siamensis*  
 3b. Corolla lobes 0.4–1.6 cm.  
 4a. Corolla lobes obovate, apex rounded ..... 4. *A. schlechteriana*  
 4b. Corolla lobes elliptic, apex acuminate ..... 5. *A. breviloaba*

**1. *Aganosma marginata*** (Roxburgh) G. Don, Gen. Hist. 4: 77. 1837.

香花藤 xiang hua teng

*Echites marginata* Roxburgh, Fl. Ind. ed. 1832 2: 15. 1832; *Aganosma acuminata* (Roxburgh) G. Don; *Amphi-neurion acuminatum* (Roxburgh) Pichon; *E. acuminata* Roxburgh.

Lianas to 8 m. Stems and branches lenticellate. Petiole ca. 1 cm; leaf blade oblong, 4.5–12 × 2–4 cm, abaxially pubescent especially along veins, base acute to rounded, apex acuminate or caudate; lateral veins 12–15 pairs, elevated abaxially. Cymes axillary, 3-branched; peduncle puberulent; bracts and bracteoles sublinear. Pedicel puberulent. Calyx with a continuous row of numerous basal glands inside; sepals sublinear, 5–7 mm, puberulent outside. Corolla white or yellowish, tube 8–10 mm, densely villous inside; lobes very narrowly elliptic, 1.5–2 cm × 2–3.5 mm. Stamens inserted below middle of corolla tube; disc ringlike, shorter than ovary. Ovary glabrous. Follicles 2, cylindrical, 15–40 × ca. 1 cm. Seeds oblong, flat, ca. 1 cm, coma ca. 2.7 cm. Fl. Mar-Sep, fr. Jun-Dec.

Montane forests, seashore brushwoods. Guangdong, Hainan [Cambodia, India, Indonesia, Laos, Malaysia, Philippines, Thailand, Vietnam].

**2. *Aganosma cymosa*** (Roxburgh) G. Don, Gen. Hist. 4: 77. 1837.

云南香花藤 yun nan xiang hua teng

*Echites cymosa* Roxburgh, Fl. Ind. ed. 1832 2: 16. 1832; *Aganosma cymosa* var. *fulva* Craib; *A. cymosa* var. *glabra* A. de Candolle; *A. cymosa* var. *lanceolata* J. D. Hooker; *A. harmandiana* Pierre in Spire & A. Spire.

Lianas to 10 m, pale brownish tomentose. Petiole 1–2 cm; leaf blade broadly ovate or orbicular, 5–16 × 4–12 cm, base rounded or obtuse, apex acuminate or obtuse, rarely retuse;

lateral veins 8–10 pairs. Cymes terminal, many flowered; peduncle to 6 cm; bracts and bracteoles very narrowly elliptic, 0.9–1.1 cm. Pedicel ca. 5 mm. Calyx with several glands inside margin of sepals; sepals very narrowly elliptic, 0.9–1.1 cm, pubescent on both surfaces. Corolla white, minutely tomentose outside, glabrous at throat; tube shorter than sepals, 6–7 mm; lobes oblong, as long as tube. Disc longer than ovary. Ovary pubescent at apex. Follicles 2, cylindrical, to 30 × 0.8–1.2 cm, yellow hirsute. Seeds oblong, 1–2 cm × ca. 5 mm, coma 2–4.5 cm. Fl. May-Aug, fr. Sep-Dec.

Open woods in humid valleys. SW Guangxi, S Yunnan [Bangladesh, Cambodia, India, Laos, Myanmar, Thailand, Vietnam].

The species is represented in China by var. *cymosa*. *Aganosma cymosa* var. *elegans* (G. Don) J. D. Hooker, which is readily distinguished by its densely pubescent corolla throat and smaller leaves, is restricted to southern India and Sri Lanka.

**3. *Aganosma siamensis*** Craib, Bull. Misc. Inform. Kew 1915: 433. 1915.

广西香花藤 guang xi xiang hua teng

*Aganosma kwangsiensis* Tsiang.

Lianas to 10 m. Juvenile branchlets and inflorescences pubescent. Petiole 1–1.5 cm; leaf blade dark green adaxially, greenish abaxially, elliptic or narrowly so, 5–10(–15) × 1.7–5(–6.7) cm, papery, glabrescent, base obtuse, apex acute or acuminate; lateral veins (6 or) 7–10 pairs, obliquely ascending, flattened abaxially. Cymes terminal, ca. 10 cm, 9–15-flowered. Pedicel 0.5–1.6 cm. Calyx with several basal glands inside margin of sepals; sepals unequal, sublinear, 1.5–2(–2.8) cm, longer than corolla tube. Corolla white, tube 7–12 mm, dilated at base, pubescent on both surfaces; lobes oblong, falcate, 2.4–3.5 cm. Stamens inserted at base of corolla tube. Ovary pubescent. Style short; pistil head conical. Follicles ca. 14 cm × 7 mm, appressed strigillose. Fl. May-Jun.

Dense montane forests, moist sparse woods; 300–1500 m.

Guangxi, Guizhou, Yunnan [Thailand].

**4. *Aganosma schlechteriana*** H. Léveillé, Repert. Spec. Nov. Regni Veg. 9: 325. 1911.

海南香花藤 hai nan xiang hua teng

*Aganosma montana* Kerr; *A. navaillei* (H. Léveillé) Tsiang; *A. odora* Tsiang; *A. radiata* Merrill; *A. schlechteriana* var. *breviloba* Tsiang; *A. schlechteriana* var. *leptantha* Tsiang; *Trachelospermum navaillei* H. Léveillé.

Lianas to 9 m. Young branchlets puberulent, soon glabrous. Petiole 1–1.5 cm; leaf blade elliptic, narrowly elliptic, or ovate, 6–14 × 2.5–5.5 cm, leathery, glabrous or puberulent when young, base cuneate or broadly so, apex acute to acuminate; lateral veins ca. 10 pairs. Cymes terminal, 3-branched, 4–9 × 6.5–15 cm, pubescent. Calyx pubescent, with several basal glands inside margin of sepals; sepals 1–1.2 cm, longer than corolla tube. Corolla white, tube 5–9 mm, slightly dilated at base, glabrous at throat; lobes obovate, 4–16 mm, apex rounded to obtuse. Stamens inserted at base of corolla tube; disc cup-shaped or 5-lobed. Ovary pubescent, shorter than disc. Follicles 2, cylindrical, to 30 cm × 5–10 mm, pubescent when young, glabrous when older. Seeds oblong,

flat, ca. 2 cm, coma 3.5–5 cm. Fl. Mar-Jul, fr. Aug-Dec.

Sparse woods, montane forests, brushwoods; 200–1800 m. Guangxi, Guizhou, Hainan, Sichuan, Yunnan [India, Myanmar, Thailand, Vietnam].

**5. *Aganosma breviloba*** Kerr, Bull. Misc. Inform. Kew 1937: 92. 1937.

贵州香花藤 gui zhou xiang hua teng

Stems sparsely strigose when young, glabrescent. Leaf blade elliptic, 5.5–10.6 × 2.2–4.9 cm, glabrous or sparsely strigose along petiole and midvein abaxially, base cuneate to obtuse, apex acuminate; lateral veins 5–10 pairs. Inflorescences terminal panicles 5.3–8 cm. Pedicel 3–10 mm. Calyx with several basal glands inside margin of sepals; sepals linear, 1–1.5 cm, pubescent, with narrow colleters at corners. Corolla white, glabrous at throat, tube 6.7–12 mm; lobes narrowly elliptic, acuminate, 5–11 × 1.8–2.6 mm. Stamens inserted in corolla tube 2–2.8 mm from base; disc narrow at top, 5-dentate. Ovary pubescent. Follicles un-known.

Forests. Guizhou [Myanmar, Thailand].

## 24. *CHONEMORPHA* G. Don, Gen. Hist. 4: 76. 1837, nom. cons.

鹿角藤属 lu jiao teng shu

*Rhynchodia* Bentham.

Lianas stout, woody, with latex. Leaves large, opposite; interpetiolar lines and colleters present. Cymes lax, paniculate or racemose, terminal or subaxillary. Flowers large. Calyx tubular, shortly 5-toothed or 5-partite, basal glands large, denticulate. Corolla white or reddish, funnelliform, tube cylindrical, throat not scaly; lobes overlapping to right. Stamens inserted near base or middle of corolla tube; anthers sagittate, connivent, adherent to pistil head, cells spurred at base; disc ringlike, fleshy, shorter than ovary, apex 5-cleft. Ovaries 2, free; ovules numerous in each ovary. Style filiform; pistil head club-shaped, slightly thickened, apex 2-cleft. Follicles 2, elongated, cylindrical. Seeds ovate-oblong, flat, short beaked, beak with a long coma.

About 15 species: tropical and subtropical Asia, eight species in China.

- 1a. Calyx less than 7 mm; corolla tube less than 1 cm ..... 8. *C. verrucosa*
- 1b. Calyx more than 7 mm; corolla tube more than 2 cm.
  - 2a. Calyx divided to middle or near base ..... 7. *C. griffithii*
  - 2b. Calyx shortly 5-toothed.
    - 3a. Corolla pink or reddish; style glabrous.
      - 4a. Calyx 1.5–1.8 cm; cymes to 35 cm; follicles to 25 cm ..... 2. *C. splendens*
      - 4b. Calyx 1.8–3 cm; cymes to 17 cm; follicles to 34 cm ..... 3. *C. megacalyx*
    - 3b. Corolla white; style often hairy.
      - 5a. Base of leaf blade cordate; calyx glabrescent outside; corolla limb up to 8 cm in diam. .... 1. *C. fragrans*
      - 5b. Base of leaf blade rounded or cuneate; calyx pubescent to tomentose outside; corolla limb up to 5 cm in diam.
        - 6a. Corolla pubescent throughout; disc longer than ovary; seed coma ca. 7 cm ..... 4. *C. eriostylis*
        - 6b. Corolla glabrous throughout; disc shorter than ovary; seed coma 4–5 cm.
          - 7a. Leaves thick leathery, obovate, densely floccose; calyx ca. 1 cm; corolla tube ca. 2 cm, lobes ca. 1.7 cm ..... 5. *C. floccosa*
          - 7b. Leaves membranous, elliptic, densely hirsute; calyx ca. 1.5 cm; corolla tube ca. 2.8 cm, lobes ca. 2.5 cm ..... 6. *C. parviflora*

**1. *Chonemorpha fragrans*** (Moon) Alston, Ann. Roy. Bot. Gard. (Peradeniya) 11: 203. 1929.

大叶鹿角藤 da ye lu jiao teng

*Echites fragrans* Moon, Cat. Pl. Ceylon 20. 1824; *Chonemorpha grandiflora* G. Don; *C. macrophylla* G. Don; *C. mollis* Miquel; *C. rheedei* Ridley; *E. macrophylla*

Roxburgh, not Kunth.

Lianas to 30 m, hirsute except for flowers. Petiole to 2 cm; leaf blade suborbicular to broadly ovate, 15–45 × 13–45 cm, papery, base cordate, apex acute or rounded, cuspidate; lateral veins 10–12 pairs. Calyx tubular, ca. 1 cm, apex toothed, glabrescent outside. Corolla white, limb to 8 cm wide; tube 3.5–4.5 cm, dilated at base, glabrous outside, throat villous; lobes obliquely obovate, ca. 3.5 cm. Filaments short pubescent. Follicles cylindrical to fusiform, to 30 × 2 cm. Seeds oblong, coma ca. 5 cm. Fl. May-Jul.  $2n = 20$ .

Dense montane forests, often clinging to trees. Guangxi, Yunnan; cultivated in Fujian and Guangdong [India, Indonesia, Malaysia, Myanmar, Sri Lanka, Thailand].

**2. *Chonemorpha splendens*** Chun & Tsiang in Tsiang, *Sunyatsenia* 2: 157. 1934.

海南鹿角藤 hai nan lu jiao teng

Lianas to 20 m, yellow tomentose. Petiole 1.5–2 cm; leaf blade usually broadly ovate or obovate, 18–20 × 12–14 cm, base rounded to shallowly cordate, apex acute; lateral veins 11 or 12 pairs. Cymes racemelike, to 35 cm, 9–13-flowered. Calyx tubular, 1.5–1.8 cm, apex toothed, erose-denticulate. Corolla pink or reddish, limb ca. 4 cm in diam., tube ca. 2.5 cm. Stamens inserted ca. 1 cm from base of corolla tube. Ovary and style glabrous. Follicles fusiform, ca. 25 × 2 cm, tomentose, eventually glabrescent. Seeds with silky coma to 5 cm. Fl. May-Jul, fr. Aug-Dec.

• Sparse woods, often clinging to trees; 300–800 m. Hainan, Yunnan.

The separation of this species from *Chonemorpha megacalyx* is not that clear.

**3. *Chonemorpha megacalyx*** Pierre in Spire, *Contr. Apocyn.* 76. 1905.

长萼鹿角藤 chang e lu jiao teng

Lianas to 20 m, yellowish brown tomentose. Petiole 1.5–3.5 cm; leaf blade obovate to narrowly ovate, 17–29 × 11–22 cm, base rounded, apex acute; lateral veins 8–12 pairs. Cymes terminal, to 17 cm; peduncle 3.5–9 cm. Calyx tubular, 1.8–3 cm, apex toothed. Corolla pink or reddish, limb ca. 4 cm in diam., tube ca. 4 cm, glabrous outside, hispid inside; lobes obovate, ca. 3.5 × 2 cm wide. Ovary and style glabrous. Follicles cylindrical, to 34 × 2 cm. Seeds with silky coma to 5.5 cm. Fl. spring-summer.

Borders of montane forests; 900–1500 m. S Yunnan [Laos, Thailand].

The stem is used in Yunnan as a medicine to treat backache and leg pain caused by rheumatism, fractures, and injury. The seed coma is used externally to treat hemostasis.

**4. *Chonemorpha eriostylis*** Pitard in Lecomte & Humbert, *Fl. Indo-Chine* 3: 1247. 1933.

鹿角藤 lu jiao teng

Lianas to 30 m, hirsute. Petiole 1.2–1.5 cm; leaf blade obovate or broadly oblong, 12–34 × 7–23 cm, papery, base

rounded, apex abruptly acute, adaxial surface pubescent; lateral veins 9–11 pairs. Cymes terminal, ca. 12 cm, 7–15-flowered. Calyx tubular, ca. 1.4 cm, tomentose outside, apex toothed. Corolla white, limb ca. 4 cm in diam., tube ca. 2 cm, pubescent on both surfaces; lobes obovate, ca. 2 cm. Stamens inserted near base of corolla tube; filaments puberulent; disc cup-shaped, longer than ovary, apex undate. Ovary glabrous. Style densely hirsute. Follicles linear, 25–40 × 1.5–2 cm, yellowish brown downy. Seeds ovate-lanceolate, flat, ca. 2.6 cm, coma ca. 7 cm. Fl. May-Jul, fr. Aug-Dec.

Sparse woods, humid valleys; 300–1000 m. Guangdong, Guangxi, S Yunnan [Vietnam].

The stem is used in Guangxi as medicine for rheumatgia.

**5. *Chonemorpha floccosa*** Tsiang & P. T. Li, *Acta Phyto-tax. Sin.* 11: 387. 1973.

丛毛鹿角藤 cong mao lu jiao teng

Lianas to 25 m. Branches, branchlets, and leaves densely yellowish brown floccose. Petiole 1.2–1.5 cm; leaf blade obovate, 10–14 × 6–10 cm, thick leathery, floccose, base broadly cuneate; lateral veins ca. 10 pairs. Calyx tubular, ca. 1 cm; apex toothed, pubescent outside. Corolla white, glabrous, tube ca. 2 cm; lobes obdeltoid, ca. 1.7 cm. Stamens inserted at base of corolla tube; disc ringlike, shorter than ovary, apex retuse. Ovary and style bearing bristles. Follicles linear, to 35 × 1 cm, densely yellowish brown pubescent. Seeds ovate-lanceolate, flat, ca. 2.5 cm, coma ca. 4 cm. Fl. May-Aug, fr. Aug-Dec.

• Mixed woods; 500–800. S Guangxi.

**6. *Chonemorpha parviflora*** Tsiang & P. T. Li, *Acta Phyto-tax. Sin.* 11: 389. 1973.

小花鹿角藤 xiao hua lu jiao teng

Lianas to 20 m. Branches, branchlets, and leaves densely yellow hirsute. Petiole 1.4–2 cm; leaf blade elliptic, 13–22 × 6–12 cm, membranous, hirsute, base broadly cuneate, apex acute; lateral veins 10–12 pairs. Cymes terminal. Pedicel ca. 1 cm, pubescent. Calyx tubular, ca. 1.5 cm, pubescent outside, apex 5-toothed. Corolla white, glabrous, tube ca. 2.8 cm; lobes narrowly obovate, ca. 2.5 cm. Stamens inserted near base of corolla tube; disc cup-shaped, shorter than ovary. Ovary and style villous. Follicles linear, 24–26 × ca. 1 cm, pubescent. Seeds narrowly ovate, flat, ca. 2.2 cm, coma ca. 5 cm. Fl. May-Aug, fr. Aug-Dec.

• Mixed woods; 500–1000 m. S Guangxi, S Yunnan.

**7. *Chonemorpha griffithii*** J. D. Hooker, *Fl. Brit. India* 3: 662. 1882.

漾濞鹿角藤 yang bi lu jiao teng

*Chonemorpha valvata* Chatterjee.

Lianas woody, to 20 m. Branchlets obscurely len-ticellate, tawny pubescent. Petiole 1.5–5 cm; leaf blade broadly ovate or suborbicular, 12–33 × 7–20 cm, abaxially pubescent, base broadly cuneate to rounded, apex rounded or acute; lateral

veins 9–12 pairs, subparallel, ascending. Cymes paniculate, terminal, to 15-flowered; bracteoles lanceolate, apex acute, ca. 1 mm. Calyx ca. 1.1 cm, eventually divided to base; lobes valvate, narrowly ovate, 8–12 × 3–4.5 mm, puberulent outside. Corolla reddish; tube cylindrical, ca. 7 cm, dilated at middle, distal half densely pubescent inside; lobes obovate to obtriangular, 3.5–4 × 3.5–4.3 cm. Stamens inserted at middle of corolla tube; filaments densely pubescent; disc ringlike, shallowly divided at apex, shorter than ovary. Ovary glabrous; style puberulent at apex. Follicles cylindrical, glabrous, ca. 34 × 1.2 cm. Fl. spring-summer.

Dense montane forests, moist valleys; 900–1600 m. E Xizang, S Yunnan [India, Myanmar, Nepal, Thailand].

The stem is used in Yunnan as medicine for the treatment of fractures and rheumatism.

**8. *Chonemorpha verrucosa*** (Blume) D. J. Middleton, *Novon* 3: 455. 1993.

尖子藤 jian zi teng

**25. AMALOCALYX** Pierre, *Bull. Mens. Soc. Linn. Paris*, ser. 2, 1: 28. 1898.

毛车藤属 mao che teng shu

Lianas woody, latex white. Leaves opposite. Cymes axillary, long pendunculate, with 2 or 3 monochasial branches. Calyx deeply divided, with basal glands inside. Corolla subcampanulate, tube cylindrical, slightly inflated distally, throat without scales, lobes overlapping to right. Stamens inserted at middle of corolla tube; filaments short; anthers sagittate, included, adherent to pistil head at middle, cells with an empty tail; disc ringlike, as long as ovary, apex entire or 5-lobed. Ovaries 2, free. Style filiform; pistil head cylindrical, apex long pubescent. Follicles 2, ellipsoid to narrowly so, connate. Seeds ovate, apex comose.

One species: China, Laos, Myanmar, Thailand, Vietnam.

**1. *Amalocalyx microlobus*** Pierre in Spire, *Contr. Apocyn.* 93. 1905.

毛车藤 mao che teng

*Amalocalyx burmanicus* Chatterjee; *A. yunnanensis* Tsiang.

Lianas to 10 m, densely rust colored villous when young, glabrous when older. Stems sometimes with corky wings. Petiole 1–3 cm; leaf blade broadly obovate or elliptic, 5–15 ×

*Tabernaemontana verrucosa* Blume, *Bijdr.* 1029. 1826; *Echites rhynchosperma* Wallich; *Rhynchodia rhynchosperma* (Wallich) K. Schumann; *R. verrucosa* (Blume) Woodson; *Trachelospermum verrucosum* (Blume) Boerlage.

Lianas to 10 m. Branches dark purple; branchlets glabrous, lenticellate. Petiole 1–3 cm; leaf blade broadly to narrowly ovate, 12–22 × 5–12 cm, abaxially pubescent, base obtuse to rounded, apex acute to caudate; lateral veins 7–15 pairs. Cymes 7–13 × 5–11 cm, puberulent. Calyx less than 7 mm. Corolla white, tinged pink; tube 5-angled, ca. 6 mm, densely pubescent inside; lobes obovate or obdeltoide, ca. 8 × 6 mm, apex rounded or truncate. Stamens inserted at middle of corolla tube. Follicles elongated, compressed, 19–40 cm × 7–10 mm. Seeds oblong, ca. 15 × 5 mm, coma 4.5–6 cm. Fl. Apr–Jun, fr. Aug–Dec.

Dense montane forests, ravines; 300–1000 m. Guangdong, Hainan, S Yunnan [Bhutan, India, Indonesia, Laos, Malaysia, Myanmar, Thailand, Vietnam].

2–10.5 cm, base truncate or subauriculate to cordate; lateral veins 8 or 9 pairs. Cymes longer than leaves, 15–30-flowered; peduncle 7–14 cm; bracts and bracteoles narrowly elliptic, ca. 1 cm. Pedicel 0.5–1.5 cm. Corolla whitish outside, pink to purple inside, glabrous, tube ca. 2.2 cm; lobes ovate, shorter than tube. Disc apex 5-lobed. Ovary glabrous. Follicles 8–10 × 1.2–1.5 cm. Seeds ovate, ca. 10 × 3 mm, coma ca. 4 cm. Fl. Apr–Oct, fr. Sep–Dec.

Sparse woods, often clinging to trees; 800–1000 m. S Yunnan (Simo, Jinghong) [Laos, Myanmar, Thailand, Vietnam].

**26. PARSONSIA** R. Brown, *Mem. Wern. Nat. Hist. Soc.* 1: 64. 1811, nom. cons.

同心结属 tong xin jie shu

Lianas woody, latex white. Leaves opposite. Cymes corymbose or paniculate, dichotomous, terminal or axillary, pedunculate. Flowers small. Calyx with basal glands inside or 5-scaled. Corolla salverform, tube short, hairy inside distally, faucal scales absent, lobes overlapping to right. Stamens inserted at middle of corolla tube or at throat; filaments long, strongly intertwisted or geniculate; anthers narrowly sagittate, exerted, glutinous, connivent into a subcylindrical cone, adherent to middle of pistil head, cells with an empty tail; disc 5-lobed or 5-scaled. Ovaries 2; ovules numerous in each carpel. Style filiform; pistil head thickened, apex entire or 2-cleft. Follicles 2, terete, parallel or divergent. Seeds linear or oblong, apex crowned with coma; endosperm scanty; cotyledons very narrowly oblong, flat, radicle superior.

About 50 species: SE Asia, Pacific Islands; two species in China.

- 1a. Leaf blade ovate to subelliptic; petiole 2–4 cm; stamens inserted at middle of corolla tube ..... 1. *P. alboflavescens*  
1b. Leaf blade narrowly or very narrowly elliptic; petiole 0.5–1 cm; stamens inserted at corolla throat ..... 2. *P. goniostemon*

**1. *Parsonsia alboflavescens*** (Dennstedt) Mabberley, Taxon 26: 532. 1977.

海南同心结 hai nan tong xin jie

*Periploca alboflavescens* Dennstedt, Schlüssel Hortus Malab. 12, 23, 35. 1818; *Echites laevigata* Moon; *Heligme spiralis* (Wallich ex G. Don) Thwaites; *Parsonsia helicandra* Hooker & Arnott; *P. howii* Tsiang; *P. laevigata* (Moon) Alston; *P. spiralis* Wallich ex G. Don.

Lianas woody, to 10 m, glabrous except for inflorescences. Branches pale gray. Petiole 2–4 cm; leaf blade ovate or subelliptic, 4–12 × 3–7.5 cm, base cuneate to shallowly cordate; lateral veins 5–7 pairs. Cymes 8–15 × 8–11 cm; peduncle 3–9 cm. Sepals ca. 2 mm, glands broadly triangular, membranous. Corolla white or greenish, tube ca. 5 mm, limb 1–2 cm wide, lobes ca. 6 mm. Anthers ca. 3.5 × 0.6 mm, inserted at middle of corolla tube. Ovary as long as or slightly shorter than disc, glabrous. Follicles 2, linear-cylindric, parallel, 7–16 × 1–2 cm. Seeds oblong 1.5–1.8 cm × ca. 2 mm, coma 2–4.5 cm. Fl. Apr–Oct, fr. Sep–Dec.

**27. POTTSIA** Hooker & Arnott, Bot. Beechey Voy. 198. 1837.

帘子藤属 lian zi teng shu

Lianas woody, latex white. Leaves opposite. Cymes racemose or paniculate, 3–5-branched, terminal or axillary. Flowers usually small, 5-merous. Calyx deeply divided, with many basal glands inside. Corolla salverform, tube cylindric, throat narrowed, without scales, lobes overlapping to right. Stamens inserted at apex of corolla tube; filaments short; anthers exerted, sagittate, connivent at middle, adherent to pistil head, cells spurred at base; disc 5-parted. Ovaries 2, free, shorter than disc; ovules numerous in each ovary. Style thickened at middle or near base; pistil head ovoid or fusiform, apex short conical. Follicles 2, elongated, linear. Seeds linear, elongated, not beaked, apex comose; endosperm copious; cotyledons linear, flat, radicle superior.

About four species: SE Asia, two species in China.

- 1a. Corolla ca. 7 mm, lobes spreading; style thickened at middle; ovary pilose ..... 1. *P. laxiflora*  
1b. Corolla ca. 13 mm, lobes reflexed; style thickened near base; ovary glabrous ..... 2. *P. grandiflora*

**1. *Pottisia laxiflora*** (Blume) Kuntze, Revis. Gen. Pl. 2: 416. 1891.

帘子藤 lian zi teng

*Vallis laxiflora* Blume, Bijdr. 1043. 1826; *Pottisia cantonensis* Hooker & Arnott; *P. hookeriana* Wight; *P. laxiflora* var. *pubescens* (Tsiang) P. T. Li; *P. ovata* A. de Candolle; *P. pubescens* Tsiang.

Lianas to 10 m. Branches and branchlets slender, pubescent or glabrous. Petiole 1.5–4 cm; leaf blade ovate, narrowly ovate, or elliptic, 6–12 × 3–7 cm, base obtuse to rounded or subcordate, pubescent or glabrous on both surfaces; lateral veins 4–6 pairs. Cymes to 25 cm, long pedunculate, many flowered. Corolla purple or rose, ca. 7 mm; tube glabrous, longer than lobes; lobes narrowly ovate, ca. 2 mm, spreading. Ovary pilose. Style thickened at middle. Follicles linear, to 55 cm × 3–5 mm, pubescent to glabrous. Seeds linear, ca. 2 cm, coma 2.5–3 cm. Fl. Apr–Aug, fr. Aug–Oct.

Open forests, forest borders, brushwoods; 200–1000 m. Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hunan, Yunnan, Zhejiang [Cambodia, India, Indonesia, Laos, Malaysia, Thailand,

Mixed montane woods; 200–500 m. Fujian, Guangdong, Hainan, Taiwan [Cambodia, India, Indonesia, Japan (Ryukyu Islands), Laos, Malaysia, Myanmar, Philippines, Sri Lanka, Thailand, Vietnam].

**2. *Parsonsia goniostemon*** Handel-Mazzetti in Tsiang, Sunyatsenia 2: 165. 1934.

广西同心结 guang xi tong xin jie

Lianas woody, to 13 m, glabrous except for inflorescences. Branches slender, lenticellate. Petiole 5–10 mm; leaf blade narrowly elliptic, 6–10 × 2–3 cm, base cuneate to narrowly rounded; lateral veins 5–7 pairs. Cymes to 7 × 7 cm; peduncle 2–3.5 cm. Pedicel 4–10 mm. Calyx ca. 1.5 mm, broader at base. Corolla greenish, ca. 5 mm. Stamens inserted at corolla throat; disc cupular. Ovary obscurely 2-lobed. Style long; pistil head ovoid. Follicles ca. 12 cm, connate, narrowly fusiform, glabrous. Seed coma ca. 4 cm. Fl. May–Aug, fr. Aug–Dec.

- Rocky areas; 500–800 m. Guangxi (Longjin, Lingyun).

Vietnam].

The stem and leaves are used to treat fractures and injury and the latex and roots for anemia and rheumatism.

**2. *Pottisia grandiflora*** Markgraf in Diels, Notizbl. Bot. Gart. Berlin-Dahlem 9: 1029. 1926.

大花帘子藤 da hua lian zi teng

Lianas to 5 m. Branches and branchlets greenish, terete. Petiole 1–2.2 cm; leaf blade ovate to subovate, 6.5–12 × 3–7 cm, somewhat leathery, base rounded, sometimes decurrent into petiole, glabrous; lateral veins ca. 6 pairs. Cymes up to 20 cm, glabrous, long pedunculate, many flowered. Corolla ca. 1.3 cm, purple or rose, glabrous, tube ca. 6 mm; lobes obovate, slightly longer than tube, reflexed. Ovary glabrous. Style ca. 6 mm, thickened near base; pistil head conical. Follicles 2, linear, to 42 cm × 6 mm. Seeds linear, coma yellowish, to 4.5 cm. Fl. Apr–Aug, fr. Aug–Dec.

- Montane forests, brushwoods; 400–1100 m. Fujian, Guangdong, Guangxi, Hunan, Yunnan, Zhejiang.

**28. NERIUM** Linnaeus, Sp. Pl. 1: 209. 1753.夹竹桃属 *jia zhu tao shu*

Trees or shrubs, evergreen, juice watery. Leaves in whorls of 3, midvein prominent abaxially, lateral veins numerous, parallel. Inflorescences corymbose, terminal. Corolla funnelform, cylindric near base, throat open, wide, lobes overlapping to right; corona segments 5, petal-like, large, fringed. Stamens inserted at apex of corolla tube; anthers sagittate, with a bristly, filiform apical appendage, pilose, connivent, adherent to pistil head; disc absent. Ovaries 2, distinct; ovules numerous in each locule. Follicles united until just before dehiscence. Seeds numerous, densely pilose, coma at truncate apex.

One species: Asia, Europe, North Africa.

**1. Nerium oleander** Linnaeus, Sp. Pl. 1: 209. 1753.夹竹桃 *jia zhu tao*

*Nerium indicum* Miller; *N. odorum* Solander.

Stem to 6 m tall. Leaves very narrowly elliptic, 5–21 × 1–3.5 cm, leathery, base cuneate or decurrent on petiole, apex acuminate or acute. Flowers showy, fragrant. Sepals narrowly triangular to narrowly ovate, 3–10 mm. Corolla purplish red,

pink, white, salmon, or yellow, tube 1.2–2.2 cm; lobes 1.3–3 cm, single or double. Follicles cylindric, 12–23 cm. Seeds oblong, coma 0.9–1.2 cm. Fl. spring-autumn.  $2n = 22$ .

Yunnan, widely cultivated and naturalized in tropical, sub-tropical, and temperate parts [Asia, Europe, North America].

All parts of the plant are extremely toxic. The seed-oil content is up to 58.5%.

**29. WRIGHTIA** R. Brown, Mem. Wern. Nat. Hist. Soc. 1: 73. 1811.倒吊笔属 *dao diao bi shu*

Trees or shrubs with latex. Leaves opposite, petiolate; glands axillary. Cymes terminal or subterminal, dichasial, few to many flowered. Sepals quincuncial, with 5–10, basal, scalelike glands inside. Corolla salverform, funnelform, subrotate, or rotate, tube cylindric to campanulate; lobes overlapping to left; corona ligulate, fringed, or cup-shaped, entire or subentire at apex, shallowly or deeply divided, sometimes absent. Stamens inserted at middle, apex, or rarely base of corolla tube; anthers sagittate, connivent and adherent to pistil head, exerted, spurred at base; disc absent. Ovaries 2, distinct or connate; ovules numerous in each locule. Style filiform; pistil head ovoid, usually dilated at base. Follicles 2, connate or divaricate. Seeds narrowly fusiform, with an apical coma directed toward fruit base, beakless.

About 23 species: tropical Africa, Asia, Australia; six species in China.

- 1a. Shrubs; corona obsolete; seeds (excluding coma) ca. 0.8 cm ..... 6. *W. religiosa*  
 1b. Trees; corona scales present; seeds (excluding coma) 1–2 cm.  
 2a. Leaves densely pubescent or tomentose abaxially.  
 3a. Corona lobes much shorter than stamens, glabrous inside; fruit lenticellate, usually glabrous ..... 1. *W. arborea*  
 3b. Corona lobes about as long as stamens, puberulent inside; fruit not lenticellate, usually minutely puberulent ..... 2. *W. pubescens*  
 2b. Leaves glabrous or minutely pubescent abaxially along veins.  
 4a. Ovaries and fruit connate.  
 5a. Apex of leaf blade short acuminate; corona with 10 scales, longer than anthers ..... 2. *W. pubescens*  
 5b. Apex of leaf blade caudate-acuminate; corona cup-shaped, shorter than anthers ..... 3. *W. coccinea*  
 4b. Ovaries and fruit distinct.  
 6a. Corolla funnelform, white; corona with 25–35 scales ..... 4. *W. laevis*  
 6b. Corolla rotate or subrotate, yellowish; corona with 10 scales ..... 5. *W. sikkimensis*

**1. Wrightia arborea** (Dennstedt) Mabberley, Taxon 26: 533. 1977.烟木 *yan mu*

*Periploca arborea* Dennstedt, Schlüssel Hortus Malab. 13, 23, 25. 1818; *Nerium tomentosum* Roxburgh; *Wrightia tomentosa* (Roxburgh) Roemer & Schultes.

Trees to 20 m tall. Branches gray or brown, pubescent, lenticellate. Petiole 2–10 mm; leaf blade elliptic to broadly so or obovate, 6–18 × 3–8.5 cm, pubescent to glabrescent adaxially, tomentose abaxially; lateral veins 10–15 pairs. Cymes pubescent; peduncle to 2 cm. Pedicel 1–1.5 cm. Sepals ovate or broadly so, ca. 3 mm. Corolla yellowish, pinkish, or

salmon, rotate or subrotate; tube 3–7 mm, glabrous; lobes narrowly elliptic to ovate, 0.8–1.6 cm, papillate; corona scales 10, shorter than anthers, glabrous inside, apex dentate. Ovaries connate. Follicles connate, cylindric, 14–21 × 3–4 cm, lenticellate. Seeds linear-fusiform, ca. 2 cm, coma ca. 3.5 cm. Fl. May-Oct, fr. Aug-Dec.  $2n = 22$ .

Deciduous or mixed forests; stream banks; 200–1500 m. Guangxi, Guizhou, Yunnan [India, Laos, Malaysia, Myanmar, Sri Lanka, Thailand, Vietnam].

**2. Wrightia pubescens** R. Brown, Mem. Wern. Nat. Hist. Soc. 1: 73. 1811.倒吊笔 *dao diao bi*



*Anasser laniti* Blanco; *Wrightia annamensis* Eberhardt & Dubard; *W. kwangtungensis* Tsiang; *W. laniti* (Blanco) Merrill; *W. pubescens* subsp. *laniti* (Blanco) Ngan.

Trees to 35 m tall. Trunk to 60 cm in diam.; bark yellowish brown; young branchlets yellowish pubescent, glabrate with age, densely lenticellate. Petiole ca. 1 cm; leaf blade narrowly oblong, ovate, or narrowly ovate, 5–10 × 3–6 cm, papery, puberulent to glabrous adaxially, densely pubescent to puberulent or glabrescent except along veins abaxially, veins 8–15 pairs. Cymes ca. 5 cm, pubescent. Sepals ovate to broadly so, 2–5 mm. Corolla white or pinkish white, funnellform, tube 5–6.5 mm; lobes oblong, 1–2 cm; corona fringed, scales 10, as long as or longer than anthers, puberulent inside. Stamens pubescent, inserted at mouth of corolla; anthers exerted. Ovaries connate, glabrous. Follicles connate, sublinear, 15–30 × 1–2 cm, not lenticellate. Seeds narrowly fusiform, coma to 3.5 cm. Fl. Apr-Aug, fr. Aug-Dec.

Secondary rain forests, dry woods; 400 m. Guangxi, Guangxi, Guizhou, Hainan, Yunnan [Cambodia, India, Indonesia, Malaysia, Philippines, Thailand, Vietnam; Australia].

The wood is used for making furniture, poles, seals, and musical instruments. Bark fibers are used for making paper and artificial cotton. Extracts from the roots and bark are used to treat scrofula and rheumatic arthralgia.

**3. *Wrightia coccinea*** (Loddiges) Sims, Bot. Mag. 53: t. 2696. 1826.

云南倒吊笔 yun nan dao diao bi

*Nerium coccineum* Loddiges, Bot. Cab. 9: t. 894. 1824.

Trees to 20 m tall. Bark pale gray to brownish; branchlets lenticellate, glabrous. Petiole ca. 5 mm; leaf blade elliptic to ovate, 5–17 × 3–8 cm, glabrous or puberulent along veins abaxially, base obtuse to acute, apex caudate-acuminate; lateral veins 8–14 pairs. Flowers solitary or in cymes, 2–3.5 cm. Sepals broadly ovate, 5–9 mm. Corolla reddish, funnellform; tube campanulate, shorter than calyx; lobes broadly obovate, papillate; corona crimson, cup-shaped, apex incised. Anthers exerted. Ovaries connate. Follicles linear, connate, 14–20 cm, conspicuously lenticellate. Seeds linear, ca. 2 cm, coma to 4 cm. Fl. Jan-May, fr. Jun-Dec.  $2n = 22$ .

Dense montane forests; 300–1800 m. SE Guangxi, S Yunnan [India, Myanmar, Pakistan, Thailand].

**4. *Wrightia laevis*** J. D. Hooker, Fl. Brit. India 3: 654. 1882.

蓝树 lan shu

*Wrightia hainanensis* Merrill; *W. hainanensis* var. *variabilis* Tsiang; *W. tinctoria* R. Brown var. *laevis* (J. D. Hooker) Pichon.

Trees to 40 m tall, glabrous except for flowers. Bark dark gray, branchlets brownish, lenticellate. Petiole 5–7 mm; leaf blade oblong or narrowly elliptic, rarely ovate, 7–18 × 2.5–8 cm, apex acuminate to caudate-acuminate; lateral veins 5–11 pairs. Cymes ca. 6 cm; peduncle ca. 1 cm, puberulent to glabrous. Pedicel 1–1.5 cm. Sepals broadly ovate, ca. 1 mm, pubescent outside, apex rounded or obtuse. Corolla white or

yellowish, funnellform, tube 1.5–3 mm; lobes narrowly elliptic, 5.5–13.5 mm, papillate; corona fringed, scales 25–35, linear, puberulent. Anthers as long as corona, puberulent. Ovaries 2, distinct. Follicles cylindrical, distinct, 20–35 cm × ca. 7 mm, lenticellate. Seeds sublinear, 1.5–2 cm, coma to 4 cm. Fl. Apr-Aug, fr. Jul-Dec.  $2n = 22$ .

Montane forests, valley thickets; 200–1000 m. Guangdong, Guangxi, Guizhou, Hainan, Yunnan [India, Indonesia, Laos, Malaysia, Myanmar, Philippines, Thailand, Vietnam; N Australia].

The roots and leaves are used to treat injury and cuts, and the fruits are used to cure pulmonary tuberculosis. A blue dye is extracted from the leaves.

**5. *Wrightia sikkimensis*** Gamble, Bull. Misc. Inform. Kew 1908: 447. 1908.

个溲 ge pu

*Wrightia hainanensis* Merrill var. *chingii* Tsiang; *W. schlechteri* H. Léveillé.

Trees to 12 m tall. Branchlets dark brown, puberulent to glabrous. Petiole ca. 5 mm; leaf blade ovate to obovate, 6–17 × 3–6 cm, glaucescent, glabrous except along veins on abaxial surface, apex caudate-acuminate; lateral veins 9–15 pairs. Cymes puberulent; peduncle to 3 cm. Pedicel ca. 1 cm. Sepals ovate, ca. 2.5 mm. Corolla yellowish, rotate or subrotate, tube 2–2.5 mm; lobes oblong or narrowly obovate, 1.2–1.4 cm, papillate; corona scales 10, the 5 inserted at base of corolla lobes ca. 6 mm, entire at apex, the 5 at corolla throat ca. 2.5 mm, 2-cleft at apex. Anthers puberulent, exerted. Ovaries distinct. Follicles cylindrical, distinct, to 35 cm × 4–7 mm, lenticellate. Seeds narrowly fusiform, 1.5–2 cm, coma to 4 cm. Fl. Apr-Jun, fr. Jun-Dec.

Montane forests, valleys, limestone brushwoods; 500–1500 m. Guangxi, Guizhou, Hainan, Yunnan [NE India, Sikkim, Vietnam].

**6. *Wrightia religiosa*** (Teijsmann & Binnendijk) Bentham in Bentham & J. D. Hooker, Gen. Pl. 2: 713. 1876.

无冠倒吊笔 wu guan dao diao bi

*Echites religiosa* Teijsmann & Binnendijk, Natuurk. Tijdschr. Ned. Indië 27: 34. 1864.

Shrubs to 3 m tall. Branchlets thin, terete, often with many lateral short branchlets, minutely puberulent. Petiole 2–4 mm; leaf blade elliptic, ovate, or narrowly oblong, 2.5–7.5 × 1.5–3 cm, pubescent along midvein; lateral veins 5–7 pairs. Cymes often on short, few-leaved branches, short pedunculate, 1–13-flowered. Pedicel 1.5–2 cm, thin, finely hairy. Sepals ovate, ca. 1.5 mm. Corolla white, subrotate; tube 3–4 mm, glabrous; lobes ovate, ca. 7 mm, densely pubescent on both surfaces; corona obsolete. Stamens inserted at mouth of corolla tube. Ovaries free. Follicles linear, free, 12–17 cm. Seeds narrowly fusiform, ca. 8 mm, coma to 3.5 cm. Fl. all year.  $2n = 22$ .

S Guangdong [Cambodia, Laos, Malaysia, Thailand, Vietnam].

Cultivated for medicine.

**30. BEAUMONTIA** Wallich, Tent. Fl. Nepal. 14. 1824.

清明花属 *qing ming hua shu*

Lianas woody, robust, with latex. Leaves opposite, usually with petiolar glands. Inflorescences terminal or axillary cymes; bracteoles leafy, large. Flowers large, fragrant. Sepals free, bearing many basal glands inside; lobes leafy, large. Corolla white, funnellform, tube short or long, limb widely campanulate, throat not scaly, lobes overlapping to right. Stamens inserted at distal narrow portion of corolla tube; filaments arcuate, long, thickened distally; anthers sagittate, usually exerted, connivent, adherent to pistil head, cells spurred at base; disc ringlike, shallowly 5-lobed. Ovaries 2, connate, surrounded by disc; ovules numerous in each locule. Style long; pistil head fusiform. Follicles elongated, thick, hard. Seeds compressed, apex attenuate, coma silky; cotyledons leaflike or thick, radicle short.

Nine species: E and SE Asia, five species in China.

- 1a. Leaves densely pubescent abaxially; corolla tube 1–2.7 cm, lobes rounded at apex ..... 1. *B. khasiana*  
 1b. Leaves pubescent abaxially when young, glabrous or glabrescent when older; corolla tube 4–13 cm, lobes acute or short acuminate at apex.  
 2a. Corolla tube puberulent inside.  
 3a. Sepals broadly elliptic or obovate, 3.5–5.3 × 2–3.3 cm; corolla ca. 12 cm in diam. .... 2. *B. brevitiba*  
 3b. Sepals narrowly elliptic, 1.5–2.5 × 0.3–0.6 cm; corolla ca. 5 cm in diam. .... 3. *B. pitardii*  
 2b. Corolla tube glabrous inside.  
 4a. Corolla funnellform, limb attenuate at base; stamens white, filaments 3.2–6 cm ..... 4. *B. grandiflora*  
 4b. Corolla broadly campanulate, limb abruptly constricted at base; stamens yellow or orange, filaments 1.5–2.5 cm ..... 5. *B. murtonii*

**1. *Beaumontia khasiana*** J. D. Hooker, Fl. Brit. India 3: 661. 1882.

云南清明花 *yun nan qing ming hua*

*Beaumontia yunnanensis* Tsiang & W. C. Chen.

Lianas to 15 m. Trunk stout; branches lenticellate, branchlets densely dark brown pubescent. Petiole 1–4 cm; leaf blade elliptic or obovate, 8–25 × 5–13.5 cm, sparsely puberulent or glabrescent adaxially, densely tomentose or velvety abaxially; midvein and lateral veins densely hairy. Cymes 13–20 cm, 9–13-flowered, densely pubescent; peduncle 6.5–12 cm. Pedicel 3.5–6 cm. Sepals narrowly ovate, 1–1.6 cm. Corolla white, tube 1–2.7 cm, cylindric proximally, broadly campanulate distally; lobes broadly ovate, 2.5–4 cm, rounded at apex. Stamens exerted; filaments 2–3 cm. Ovary pubescent. Style 2–3 cm, pubescent. Fl. spring-summer.

Dense montane forests; 1500–1800 m. SW Yunnan (Longling, Cangyuan) [India, Myanmar].

**2. *Beaumontia brevitiba*** Oliver, Hooker's Icon. Pl. 16: t. 1582. 1887.

断肠花 *duan chang hua*

Lianas to 12 m. Branchlets pale yellow or gray, pubescent when young, glabrescent, lenticellate. Petiole 1–3 cm; leaf blade narrowly obovate, 7–25 × 3–11 cm, base cuneate, apex acuminate to cuspidate, glabrous or sometimes pubescent along veins or when young. Cymes 13.5–21.5 cm, 3–6-flowered, puberulent; peduncle to 4 cm. Pedicel to 6 cm. Sepals pale yellow, broadly elliptic or obovate, 3.5–5.5 × 2–3.2 cm, puberulent on both surfaces. Corolla white, ca. 12 cm in diam.; tube 6–8.5 cm, puberulent, cylindric proximally, broadly obconical distally; lobes 4–5.5 × 3.5–5 cm, acute. Stamens exerted; filaments 5.5–6 cm; disc cup-shaped, apex sparsely puberulent. Ovary tomentose. Style 5.5–7 cm, glabrous. Follicles oblong, to 16 × 4 cm. Seeds brown, oblong, ca. 1.5 cm, coma to 4 cm. Fl. spring-summer.

• Montane forests, thickets, river banks; 300–1000 m. Guangxi, Hainan.

The leaves and latex are poisonous.

**3. *Beaumontia pitardii*** Tsiang, Sunyatsenia 2: 160. 1934.

广西清明花 *guang xi qing ming hua*

*Beaumontia campanulata* Pitard, not K. Schumann.

Lianas to 10 m. Branchlets dark brown, densely to sparsely pubescent. Petiole 1.5–3 cm; leaf blade obovate or oblong, 10–21 × 5.5–12 cm, glabrous or densely hairy along veins adaxially, puberulent abaxially; lateral veins 11–14 pairs. Cymes 14–17 cm, 5–9-flowered, minutely tomentose; peduncle 1–2.5 cm. Flowers fragrant; pedicel 2–3 cm. Sepals narrowly elliptic, 1.5–2.5 cm × 3–6 mm, minutely tomentose on both sides. Corolla white, ca. 5 cm in diam.; tube 7–10 cm, cylindric proximally, narrowly campanulate distally, puberulent on both surfaces; lobes broadly ovate, 2–3 cm, apex acute or acuminate. Stamens included; filaments 4.5–5 cm; disc cup-shaped. Ovary and style puberulent. Style 6–7 mm. Follicles oblong, ca. 29 × 3.5 cm. Seeds narrowly ellipsoid, 1.6–2.3 cm, coma ca. 5.5 cm. Fl. Mar-May.

Montane forests, valley brushwoods; 800–1500 m. SW Guangxi, S Yunnan [Vietnam].

**4. *Beaumontia grandiflora*** Wallich, Tent. Fl. Nepal. 15, t. 7. 1824.

清明花 *qing ming hua*

*Echites grandiflora* Roxburgh.

Lianas to 20 m. Bark corky; young branches rusty pubescent; branchlets dark brown, pubescent to glabrous. Petiole to 3 cm; leaf blade narrowly obovate or narrowly elliptic, 6–30 × 3.5–15 cm, sparsely to densely pubescent when young, glabrous when older; lateral veins 8–20 pairs. Cymes 12–25 cm, 3–19-flowered, sparsely

to densely pubescent; peduncle 2.5–9 cm; bracts leafy, pale green. Pedicel 2.5–4.5 cm. Sepals pale green, 3–6 mm. Corolla white, creamy, or pale yellow, base pale green; tube funnellform, 6.5–13 cm, glabrous inside; limb ca. 10 cm in diam., attenuate at base, sparsely to densely pubescent outside, glabrous inside; lobes suborbicular to broadly ovate, 1.7–4 cm, apex acuminate. Stamens white; filaments 3.2–6 cm; anthers 1.5–1.7 cm, included; disc ringlike, apex sparsely puberulent. Ovary tomentose. Style 7–9 cm. Follicles usually narrowly ellipsoid, 22–31 × 5–6 cm. Seeds 1.5–2.5 cm, coma 4–7 cm. Fl. spring-summer.  $2n = 24$ .

Humid montane forests, valleys, river banks; 300–1500 m. SW Guangxi, S Yunnan; cultivated in Fujian, Guangdong [Bangladesh, Bhutan, India, Laos, Myanmar, Nepal, Thailand, Vietnam].

Cultivated as an ornamental. The young branches are used for making coarse ropes. The roots and leaves are used in the treatment of fractures, injury, and backache and leg pain caused by rheumatism.

**5. *Beaumontia murtonii*** Craib, Bull. Misc. Inform. Kew 1914: 282. 1914.

思茅清明花 *si mao qing ming hua*

*Beaumontia fragrans* Pierre ex Pitard.

Lianas evergreen, woody, to 20 cm. Branchlets pale gray or dark brown, sparsely to densely rusty pubescent when young, glabrous when older. Petiole 1–3 cm; leaf blade obovate, narrowly obovate, or broadly elliptic, 10–30 × 3.5–15 cm, glabrous to pubescent abaxially; lateral veins 11–18 pairs. Cymes 12–20 cm, 6–12-flowered, pubescent; peduncle 3–9 cm. Pedicel 3–5 cm. Sepals pale green, elliptic, 2.7–4.5 cm, sparsely pubescent on both surfaces. Corolla white, broadly campanulate; tube 4–6.5 cm, cylindrical proximally, glabrous inside; limb ca. 5 × 5 cm, abruptly constricted at base; lobes ovate or tongue-shaped, 1.9–3 cm, apex acute. Stamens yellow or orange; filaments 1.5–2.5 cm. Ovary pubescent. Style to 4 cm, pubescent. Follicles oblong, 14–18 × 3–5 cm. Seeds narrowly ellipsoid, ca. 2 cm, coma 3–8 cm. Fl. spring-summer.

Mixed forests, montane thickets, river banks; 1000–1500 m. S Yunnan (Menghai) [Cambodia, Laos, Malaysia, Thailand, Vietnam].

The latex is used as an arrow poison.

### 31. VALLARIS N. Burman, Fl. Indica 51. 1768.

纽子花属 *niu zi hua shu*

*Parabeaumontia* (Baillon) Pichon.

Shrubs trailing or scandent, latex white. Leaves opposite, dotted. Cymes umbellate or compound corymbose, axillary or terminal. Sepals free, with or without basal glands inside. Corolla subtrotate, limb spreading, throat without scales; lobes broad, overlapping to right. Stamens inserted at apex or middle of corolla tube; filaments short, with a large subapical dorsal gland; anthers sagittate, partially or completely exerted, connivent, adherent to pistil head, cells with rigid basal spurs; disc ringlike or cup-shaped, 5-lobed, lobes sometimes free, ciliate. Ovaries 2, distinct. Follicles 2, free. Seeds numerous, biseriolate, apex crowned with coma; endosperm starchy; embryo straight; cotyledons elliptic, base subcordate, apex rounded.

Three species: India, Indonesia, Sri Lanka; two species in China.

- 1a. Sepals 9–15 mm; corolla limb 3–4 cm in diam., tube 1.3–1.5 cm, lobes mucronate at apex ..... 1. *V. indecora*  
1b. Sepals 2–7 mm; corolla limb 1.4–2.5 cm in diam., tube 0.5–1 cm, lobes rounded at apex ..... 2. *V. solanacea*

**1. *Vallaris indecora*** (Baillon) Tsiang & P. T. Li, Acta Phytotax. Sin. 11: 375. 1973.

大纽子花 *da niu zi hua*

*Beaumontia indecora* Baillon, Bull. Mens. Soc. Linn. Paris 1: 759. 1888; *Parabeaumontia indecora* (Baillon) Pichon; *Vallaris grandiflora* Hemsley & E. H. Wilson.

Shrubs trailing or scandent, to 6 m tall. Bark pale gray. Petiole 1–6 mm; leaf blade elliptic or obovate, 7–14 × 3–9 cm, base cuneate or rounded, pubescent, glabrescent, or glabrous on both surfaces; lateral veins 6–8 pairs. Cymes 3- or 4-flowered; peduncle 0.7–1.5 cm. Flowers fetid; pedicel 0.7–2 cm. Sepals oblong, 0.9–1.5 cm. Corolla pale yellow, tube 1.3–1.5 cm; limb 3–4 cm in diam., pubescent inside including throat; lobes mucronate at apex. Anthers and dorsal glands exerted from throat. Ovary and style pilose. Follicles narrowly ovoid, 6.5–14 × 1.5–3.5 cm. Seeds rhomboid or ellipsoid, ca. 2 cm, coma ca. 2.2 cm. Fl. Mar–Jun.

• Dense montane forests; 700–3000 m. Guangxi, Guizhou,

Sichuan, Yunnan.

All parts are used to treat worm diseases.

**2. *Vallaris solanacea*** (Roth) Kuntze, Revis. Gen. Pl. 2: 417. 1891.

纽子花 *niu zi hua*

*Peltanthera solanacea* Roth, Nov. Pl. Sp. 132. 1821; *Vallaris heynei* Sprengel; *V. solanacea* (Roth) K. Schumann.

Shrubs climbing, often twining, to 10 m. Bark dirty whitish gray; flowering branchlets, slender, grayish pubescent. Petiole 0.2–2 cm; leaf blade elliptic to narrowly so, 2–15 × 0.8–6 cm, densely pubescent on both surfaces, base cuneate or rounded; lateral veins 5–12 pairs. Cymes di- or trichasial; peduncle 0.5–3 cm. Flowers fragrant; pedicel 0.5–2.5 cm. Sepals ovate or narrowly elliptic, 2–7 mm. Corolla white or pale yellow, limb 1.4–2.5 cm in diam., tube 5–10 mm, lobes rounded at apex. Staminal glands yellow, globose; disc shorter than ovary, apex pilose. Follicles oblong, 8–14 × 1.5–3.5 cm. Seeds ellipsoid, 9–10 mm, coma 3–4 cm. Fl. Mar–Jul.  $2n =$

22.

India, Indonesia, Laos, Myanmar, Pakistan, Sri Lanka, Thailand, Vietnam].

Forests, thickets, stream banks; 0–2700 m. Hainan [Cambodia,

**32. STROPHANTHUS** de Candolle, Bull. Soc. Philom. Paris 3: 122. 1802.

羊角拗属 yang jiao niu shu

Lianas or erect or stolon-bearing shrubs, rarely trees, with latex. Leaves opposite or in whorls of 3. Cymes mostly dichasial, terminal, pedunculate or sessile. Flowers large. Sepals free or connate at base, imbricate or quincuncial, basal glands 5 to many. Corolla funnellform, usually turning darker and dark streaked at anthesis; tube short, throat wide; lobes overlapping and mostly twisted to right, distal portions mostly forming filiform, involute long tails; corona 10-lobed, inserted at base of corolla lobes. Stamens inserted at apex of corolla tube; filaments short; anthers sagittate, connivent, adherent to pistil head, spurred at base; disc absent. Ovaries 2, ± connate at base; ovules numerous in each locule. Style filiform. Follicles 2, divaricate. Seeds numerous, with beaked apical coma.

Thirty-eight species: tropical Africa, Asia; six species in China.

- 1a. Apex of corolla lobes rounded ..... 1. *S. gratus*  
 1b. Apex of corolla lobes long tailed.  
 2a. Plant densely hispid throughout ..... 2. *S. hispidus*  
 2b. Plant glabrous except for flowers.  
 3a. Anther connectives included.  
 4a. Corolla tube puberulent outside; ovary glabrous; latex clear or yellowish ..... 3. *S. divaricatus*  
 4b. Corolla tube glabrous outside; ovary puberulent; latex clear or white ..... 4. *S. sarmentosus*  
 3b. Anther connectives exerted.  
 5a. Sepals linear, recurved, densely puberulent; bracts 2 or 3 pairs, puberulent; corolla lobes including tails 1.8–5.5 cm; style 6–8.5 mm ..... 5. *S. wallichii*  
 5b. Sepals ovate or narrowly triangular, erect or suberect, glabrous; bracts 1 pair, glabrous or puberulent; corolla lobes including tails 4.3–25.5 cm; style 9–15 mm ..... 6. *S. caudatus*

**1. *Strophanthus gratus*** (Wallich & Hooker) Baillon, Hist. Pl. 10: 171. 1889.

旋花羊角拗 xuan hau yang jiao niu

*Roupellia grata* Wallich & Hooker, Bot. Mag. 75: t. 4466. 1849; *Strophanthus gratus* (Wallich & Hooker) Franchet.

Lianas woody, to 25 m, latex white. Trunk to 10 cm in diam.; branches dark or purplish brown, densely lenticellate, branchlets glabrous. Petiole 0.5–3.2 mm; leaf blade ovate, elliptic, or obovate, 5–18 × 2–9 cm, leathery, glabrous; lateral veins 5–11 pairs. Cymes 3–32-flowered, glabrous. Flowers fragrant. Sepals obovate or broadly so, 0.7–1.8 cm. Corolla white, turning yellow at base, reddish or purple above, throat reddish; tube 2.5–4.5 cm, inflated in distal half; lobes orbicular or nearly so, 1.5–3.5 × 1.5–3.2 cm, apex rounded; corona lobes pink, awl-shaped, 0.5–1.5 cm, exerted. Filaments pubescent adaxially, connective glabrous, extending into a tail 6–12 mm. Follicles divergent at 180°, cylindric, 23–41 × 3–4.3 cm. Seeds to 2 cm, beak 1.6–6.2 cm, coma to 5 cm. Fl. Feb.  $2n = 18$ .

Taiwan [native to W and WC Africa].

Cultivated for medicine. The juice is used as an arrow poison.

**2. *Strophanthus hispidus*** de Candolle, Bull. Soc. Philom. Paris 3: 123. 1802.

箭毒羊角拗 jian du yang jiao niu

Lianas or stolon-bearing shrubs when cut, to 5 m tall, densely hispid; latex clear, reddish or white. Petiole 1–5 mm; leaf blade ovate to obovate, 3–22 × 1.5–12 cm, base rounded or subcordate; lateral veins 6–11 pairs. Cymes 3–72-flowered. Sepals ovate, inner ones often linear, 1.3–3.5 cm. Corolla yellow, tube 1–2.2 cm; lobes including tails 15–22.5 cm, proximal part ovate, tail pendulous, puberulent on both sides, to 1 mm wide; corona lobes yellow spotted with red, purple, or brown, tongue-shaped. Anthers included, glabrous. Ovary hispid. Style to 1.2 cm. Follicles very narrowly oblong, to 54 × 3 cm, densely lenticellate. Seeds narrowly ellipsoid, beak 2.3–7.7 cm, coma to 5 cm. Fl. Feb–Apr, fr. Jun–Dec.  $2n = 18$ .

S Guangdong, S Guangxi, Hainan, S Yunnan [native to WC Africa].

Cultivated for medicine. All parts of the plant are deadly poisonous. The juice is used as an arrow poison and the seeds as heart stimulant and diuretic.

**3. *Strophanthus divaricatus*** (Loureiro) Hooker & Arnott, Bot. Beechey Voy. 199. 1837.

羊角拗 yang jiao niu

*Pergularia divaricata* Loureiro, Fl. Cochinch. 1: 169. 1790; *Emericia divaricata* (Loureiro) Roemer & Schultes; *Nerium chinense* Hunter ex Roxburgh; *Periploca divaricata* (Loureiro) Sprengel; *Strophanthus chinensis* (Hunter ex Roxburgh) G. Don; *S. dichotomus* de Candolle var. *chinensis* Ker Gawler; *S. divergens* Graham; *Vallaris divaricata*

(Loureiro) G. Don.

Lianas or sarmentose shrubs, stolon bearing when pruned, to 4.5 m tall, glabrous except for corolla, latex clear or yellowish. Trunk to 4 cm in diam.; branches dark gray, densely lenticellate, branchlets reddish brown. Petiole 5–10 mm; leaf blade elliptic or slightly obovate, 3–10 × 1.5–5 cm; lateral veins 4–9 pairs. Cymes 3–15-flowered; peduncle to 1.5 cm; bracts linear or narrowly ovate, deciduous. Pedicel to 1 cm. Sepals narrowly triangular, 4–11 mm. Corolla yellow, tube 0.9–1.6 cm, puberulent on both sides or glabrous inside; lobes with a red basal spot inside, ovate, to 10 cm, abruptly narrowed into pendulous tails to 1 mm wide; corona lobes 10, greenish yellow, triangular or awl-shaped, 0.9–3 mm. Anthers included, connective tail to 0.6 mm. Ovary glabrous. Follicles ellipsoid-oblong, 9–15 × 2–3.5 cm, hard, woody, divergent at 180–250°. Seeds fusiform, 1.3–2 cm, beak 1.2–3.4 cm, coma 3.5–5.5 cm. Fl. Mar-Jul.  $2n = 18$ .

Forests, thickets; 100–1000 m. Fujian, Guangdong, Guangxi, Guizhou, Hainan, Yunnan [Laos, Vietnam].

Various parts of the plant are used as heart stimulant and to treat injury and snake bites.

**4. *Strophanthus sarmentosus*** de Candolle, Bull. Soc. Philom. Paris 3: 123. 1802.

西非羊角拗 xi fei yang jiao niu

Shrubs stolon bearing, to 4 m tall, deciduous, latex clear or white. Branches densely lenticellate, branchlets dark or reddish brown. Petiole 0.2–2.1 cm; leaf blade elliptic or ovate, 2–15 × 1.5–7 cm, papery or thinly leathery, apex acuminate, acumen 0.2–2 cm; lateral veins 3–6 pairs, glabrous. Pedicel to 1.2 cm, puberulent. Sepals ovate or elliptic, 0.5–2 cm, puberulent. Corolla yellow-white outside, purple-yellow inside; tube 1.7–4 cm, glabrous outside; lobes including tail to 13.5 cm, pendulous. Anthers included. Ovary puberulent. Follicles 10–28 × 2.2–4.4 cm, apex obtuse. Seeds 0.8–2 cm, beak to 8 cm, coma 2.5–10.5 cm. Fl. Dec-May.  $2n = 18$ .

S Yunnan [native to WC Africa].

Cultivated for medicine.

**5. *Strophanthus wallichii*** A. de Candolle, Prodr. 8: 418. 1844.

云南羊角拗 yun nan yang jiao niu

Lianas woody, to 8 m, glabrous except for inflorescences, latex white. Trunk to 8 cm in diam.; branches sparsely to densely lenticellate. Petiole 5–10 mm; leaf blade elliptic or obovate, 4–13 × 2.5–6 cm, papery; lateral veins 5–9 pairs, base cuneate or rarely rounded. Cymes 5–25-flowered, puberulent to glabrous; peduncle to 7.5 cm; bracts 2 or 3 pairs, linear, 4–15 mm, spreading or recurved, puberulent. Pedicel 4–10 mm. Sepals linear or nearly so, 0.6–1.8 cm, puberulent on both sides. Corolla pinkish; tube 1–1.5 cm, puberulent inside, glabrous outside; lobes ovate, abruptly narrowed to tail, 1.8–5.5 cm, tail ca. 1 mm wide, glabrous to sparsely puberulent inside; corona lobes triangular, 2.8–6.5 mm. Stamens puberulent; filaments 6–8.5 mm, connective linear, exerted, 8.5–12.5 mm. Ovary minutely puberulent. Style 6–8.5 mm. Follicles oblong, 11–25 × 2.5–3 cm, woody, densely lenticellate, divergent at 180°. Seeds 1–1.8 cm, beak 2.2–4.4 cm, coma 5.5–9 cm. Fl. Mar-Jun, fr. Jul-Dec.  $2n = 22$ .

Mixed woods, brushwoods; 500–1500 m. S Yunnan [Bangladesh, India, Laos, Malaysia, Thailand, Vietnam].

**6. *Strophanthus caudatus*** (Linnaeus) Kurz, J. Asiat. Soc. Beng., Pt. 2, Nat. Hist. 46: 257. 1877.

卵萼羊角拗 luan e yang jiao niu

*Echites caudata* Linnaeus, Mant. Pl. 52. 1767; *Nerium caudatum* (Linnaeus) Lamarck.

Lianas woody, to 12 m, glabrous except for flowers, latex clear or white. Trunk to 1.5 cm in diam.; branches dark brown, lenticellate. Petiole 3–13 mm; leaf blade elliptic, obovate, or ovate, 5–24 × 2.5–11 cm, leathery or papery; lateral veins 5–13 pairs. Cymes 5–15 cm, 5–25-flowered; bracts 2, linear, 2–12 mm, deciduous. Pedicel 7–11 mm. Sepals ovate or narrowly triangular, 0.3–1.9 cm, glabrous. Corolla white, turning yellow then red, red or purple streaked inside, glabrous or only distal part puberulent, tube 1.2–2.6 cm; lobes broadly ovate, abruptly narrowed to tail, 4.3–25.5 cm, tail pendulous, 1.5–3.2 mm wide; corona lobes tongue- or awl-shaped, 3–10 mm. Stamens puberulent, connective exerted. Ovary glabrous or puberulent. Style 0.9–1.5 cm. Follicles oblong, 10–30 × 3–4.8 cm, divergent at 150–200°. Seeds 1–2.5 cm, beak 2.3–4.6 cm, coma 5–9 cm. Fl. Apr-Jun.  $2n = 20$ .

500–900 m. S Guangxi, cultivated in Taiwan [Cambodia, India, Indonesia, Laos, Malaysia, Myanmar, Philippines, Singapore, Thailand, Vietnam].

### 33. KIBATALIA G. Don, Gen. Hist. 4: 86. 1837.

倒纓木属 dao ying mu shu

*Paravallaris* Pierre ex Hua.

Trees or shrubs, with latex. Leaves opposite. Cymes axillary, almost umbel-like; peduncle short. Pedicel long. Calyx with many basal glands inside. Corolla ± funnellform or salverform; tube terete, constricted below throat, throat without scales; lobes overlapping to right. Filaments short, broad; anthers exerted [or included], sagittate, connivent, adherent to pistil head, lobes spurred at base; disc ringlike or cup-shaped, fleshy, margin 5-lobed, membranous. Ovaries 2, free; ovules numerous in each locule. Style linear. Follicles 2, reflexed, long, thick, hard, leathery. Seeds narrowly oblong, apex naked, base with a very fragile, long beak bearing reflexed coma.

Fifteen species: Asia, one species in China.

**1. *Kibatalia macrophylla*** (Pierre ex Hua) Woodson, Philipp. J. Sci. 60: 214. 1936.

倒纓木 *dao ying mu*

*Paravallaris macrophylla* Pierre ex Hua, Bull. Soc. Bot. France 51: 272. 1904; *Kibatalia anceps* (Dunn & R. Williams) Woodson; *P. yunnanensis* Tsiang & P. T. Li; *Trachelospermum anceps* Dunn & R. Williams; *Vallaris anceps* (Dunn & R. Williams) C. E. C. Fischer; *V. arborea* C. E. C. Fischer.

Trees to 15 m tall. Branchlets slightly compressed when young, terete when older, glabrous. Petiole 1–1.5 cm; leaf blade oblong or elliptic, 11–38 × 4–13 cm, base rounded to cuneate, abaxial surface glabrous or glabrescent; lateral veins 13–21 pairs, at a right angle to midvein. Cymes 4–7 cm,

3–12-flowered; peduncle 0.3–1.5 cm. Pedicel 1.5–3 cm, straight and slender at anthesis, curved and thick in fruit. Corolla white, salverform; tube 1.1–1.3 cm, cylindrical, throat villous; limb campanulate; lobes oblong, 1.2–1.4 cm, puberulent on both surfaces. Filaments with a pair of dorsal swellings; anthers exerted; disc cup-shaped, fleshy, apex 5-lobed. Ovary ovoid, puberulent. Style cylindrical, 0.9–1.2 cm. Follicle very narrowly ellipsoid, 8–24 cm × 7–9 mm. Seeds narrowly ellipsoid, flat, 1.5–2 cm × 2.5–3 mm, beak ca. 4 cm, coma 1.5–4.5 cm. Fl. Apr-Sep, fr. Sep-Dec.

Montane forests, stream banks, valleys, roadsides; 200–700 m. S Yunnan (Xishuangbanna, Hekou, Zhenkang, Chengjiang) [Cambodia, Laos, Myanmar, Thailand, Vietnam].

### 34. FUNTUMIA Stapf, Hooker's Icon. Pl. 27: t. 2694. 1901.

丝胶树属 *si jiao shu shu*

Trees or shrubs, evergreen, bark and pith with white latex, domatia present. Leaves opposite, margin undulate or revolute. Cymes axillary or terminal, many flowered. Calyx deeply divided, with basal glands inside. Corolla salverform, tube swollen on 1 side at middle; throat much constricted, without scales; lobes overlapping to right. Stamens inserted near middle of corolla tube; anthers sagittate, included, adherent to pistil head, lobe with an empty tail; disc cup-shaped, deeply 5-cleft. Ovaries 2, free; ovules numerous, pendulous. Style glabrous; pistil head club-shaped. Follicles 2, divaricate. Seeds with a slender comose beak directed toward base of fruit.

Two species: tropical Africa, one cultivated in China.

**1. *Funtumia elastica*** (Preuss) Stapf, Hooker's Icon. Pl. 27: t. 2694. 1901.

丝胶树 *si jiao shu*

*Kickxia elastica* Preuss, Notizbl. Königl. Bot. Gart. Berlin 2: 353. 1899.

Trees to 35 m tall. Trunk to 50 cm in diam.; bark greenish brown to gray. Petiole 0.5–1.5 cm; leaf blade oblong or narrowly so, 6–27 × 1.5–10 cm, leathery, margin undulate; lateral veins 7–11 pairs, with axillary domatia abaxially,

glabrous. Cymes short, glabrous; peduncle ca. 1 cm. Pedicel 2–8 mm. Sepals 4–5 mm, elliptic to broadly ovate, glabrous, glandular adaxially. Corolla tube pale green to white, 7–9 mm, glabrous; lobes 5–6 mm, apex obtuse. Anthers appressed pilose abaxially. Follicles narrowly spatulate, 8–19 cm, woody. Seeds fusiform, 4.5–7 cm, beak 3–5 cm, coma 4.5–7 cm. *2n* = 22.

Cultivated in S Yunnan [native to tropical Africa from Senegal to Tanzania].

A valuable source of rubber.

### 35. HOLARRHENA R. Brown, Mem. Wern. Nat. Hist. Soc. 1: 62. 1811.

止泻木属 *zhi xie mu shu*

Trees or shrubs with milky latex. Leaves opposite. Cymes terminal or axillary, many flowered. Calyx small, glandular inside at base, glands alternating with lobes. Corolla salverform, tube cylindrical, slightly inflated near base, lobes overlapping to right. Stamens inserted near base of corolla tube; filaments short; anthers narrowly ovate, free from pistil head, lobes rounded at base; disc absent. Ovaries 2, distinct; ovules numerous on each placenta. Style short. Follicles 2, distinct, cylindrical, dehiscent. Seeds numerous, linear, with coma at 1 end; endosperm scanty.

Four species: tropical Africa, SE Asia; one species in China.

**1. *Holarrhena pubescens*** Wallich ex G. Don, Gen. Hist. 4: 78. 1837.

止泻木 *zhi xie mu*

*Chonemorpha antidysenterica* (Roth) G. Don; *Echites antidysenterica* Roth, not (Linnaeus) Roxburgh ex Fleming; *E. pubescens* Buchanan-Hamilton, not Willdenow ex Roemer

& Schultes; *Holarrhena antidysenterica* Roth; *H. codaga* G. Don; *H. malaccensis* Wight; *H. villosa* Aiton ex Loudon.

Shrubs or trees to 10 m tall. Trunk to 20 cm in diam.; branchlets with whitish, dotlike lenticels. Petiole 1–5 mm, grooved, glandular inside groove; leaf blade ovate or elliptic, 10–24 × 4–11.5 cm, membranous, pubescent, sometimes densely so abaxially, base rounded, apex acute or obtuse;

lateral veins 10–15 pairs. Cymes 5–8 cm; peduncle 1–2 cm. Pedicel 0.3–3 cm. Sepals elliptic to linear, 2–12 mm. Corolla white, pubescent, tube 0.9–1.9 cm; lobes oblong, 1–3 cm. Anthers included, narrowly ovate, base rounded. Follicles linear, 20–43 × 0.5–1.5 cm, with whitish, dotlike lenticels. Seeds 0.9–1.6 cm, coma 2.5–4.5 cm. Fl. Apr-Jul, fr. Jun-Dec.

$2n = 22$ .

Montane forests; 500–1000 m. S Yunnan; cultivated in S Guangdong, Guangxi, Hainan, Taiwan [Bangladesh, Cambodia, India, Laos, Myanmar, Nepal, Thailand, Vietnam; Africa].

The bark and roots are used as a remedy for fever and dysentery.

### 36. APOCYNUM Linnaeus, Sp. Pl. 1: 213. 1753.

罗布麻属 *luo bu ma shu*

*Poacynum* Baillon; *Trachomitum* Woodson.

Herbs perennial, sometimes shrubs, latex white. Rhizomes fibrous. Leaves opposite, rarely alternate, margin denticulate. Inflorescences thyrselike, terminal. Corolla campanulate or basin-shaped; throat wide, open; lobes overlapping to right. Stamens inserted at base of corolla tube, alternate with corona lobes; anthers adherent to pistil head; disc scales fleshy. Ovary half-inferior; carpels 2, free; ovules numerous in each locule. Follicles 2, slender, divaricate. Seeds numerous, apically comose; embryo straight, cotyledons as long as radicle.

Nine species: temperate regions of North America, Europe, and Asia; two species in China.

- 1a. Corolla campanulate, deeper than wide; leaves usually opposite ..... 1. *A. venetum*  
 1b. Corolla basin-shaped, wider than deep; leaves usually alternate ..... 2. *A. pictum*

#### 1. *Apocynum venetum* Linnaeus, Sp. Pl. 1: 213. 1753.

罗布麻 *luo bu ma*

*Apocynum lancifolium* Russanov; *A. venetum* var. *ellipticifolium* Beguinot & Belanger; *A. venetum* var. *microphyllum* Beguinot & Belanger; *Trachomitum lancifolium* (Russanov) Pobedimova; *T. venetum* (Linnaeus) Woodson; *T. venetum* var. *ellipticifolium* (Beguinot & Belanger) Woodson; *T. venetum* var. *microphyllum* (Beguinot & Belanger) Woodson.

Stems to 4 m tall, glabrous except for inflorescences; branches and branchlets whitish gray, terete, finely striate. Leaves usually opposite; petiole 3–6 mm; leaf blade narrowly elliptic to narrowly ovate, 1–8 × 0.5–2.2 cm, base rounded or cuneate, margin denticulate, apex acute or obtuse, mucronate. Sepals narrowly elliptic or narrowly ovate, ca. 1.5 mm. Corolla purplish red or pink; tube campanulate, 6–8 mm, granulose; lobes 3–4 mm. Disc fleshy, 5-lobed; lobes rounded, base adnate to ovary. Follicles slender, 8–20 cm × 2–3 mm. Seeds ovoid or ellipsoid, 2–3 mm, coma 1.5–2.5 cm. Fl. Apr-Sep, fr. Jul-Dec.  $2n = 22$ .

Salt-barren zone, desert margins, alluvial flats, riversides. Gansu, Hebei, Henan, Jiangsu, Liaoning, Nei Mongol, Qinghai, Shaanxi, Shandong, Shanxi, Xinjiang, Xizang [India, Japan, Mongolia, Pakistan, Russia; SW Asia, Europe].

The strong bast fibers obtained from the inner bark are used

in making cloth, strings, sails, fishing nests, and high-quality paper. The leaves yield up to 5% gum, which is used for making rubber, and a medicine used as a sedative and to treat hypertension. The species has fragrant flowers and is grown as a honey plant.

#### 2. *Apocynum pictum* Schrenk, Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Petersbourg 2: 115. 1844.

白麻 *bai ma*

*Apocynum hendersonii* J. D. Hooker; *Poacynum hender-sonii* (J. D. Hooker) Woodson; *P. pictum* (Schrenk) Baillon.

Stems to 2 m tall. Branchlets pubescent when young, soon glabrous. Leaves usually alternate; petiole 2–5 mm, rarely shorter; leaf blade oblong to ovate, 1.5–4 × 0.2–2.3 cm, closely denticulate, granulose. Sepals ovate or triangular, 1.5–4 mm. Corolla pink or purplish red, often with distinct darker markings; tube basin-shaped, 2.5–7 mm; lobes broadly triangular, 2.5–4 mm; corona inserted at base of corolla tube, lobes broadly triangular, apex long acuminate. Follicles slender, pendulous, 10–30 cm × 3–4 mm. Seeds narrowly ovoid, 2.5–3 mm; coma 1.5–2.5 cm. Fl. Apr-Sep, fr. Jul-Dec.

Salt-barren areas, desert margins, riversides. Gansu, Qinghai, Xinjiang [Kazakhstan, Mongolia].

Same uses as the preceding species.

### 37. ANODENDRON A. de Candolle, Prodr. 8: 443. 1844.

鳝藤属 *shan teng shu*

*Formosia* Pichon.

Lianas with white latex. Leaves opposite, lateral veins usually wrinkled above. Cymes paniculate, terminal or axillary. Flowers small. Calyx deeply divided, with basal glands inside. Corolla salverform; tube cylindrical, slightly dilated at staminal insertion, throat constricted, faucal scales absent; lobes overlapping and twisted to right. Stamens included, inserted just below

middle of corolla tube; filaments short; anthers sagittate, connivent, adherent to pistil head, cells spurred at base; disc ringlike or cup-shaped, apex truncate or shortly 5-lobed. Ovaries 2, distinct, slightly higher than disc; ovules numerous in each ovary. Style short; pistil head thick, base with a ringlike membrane. Follicles divaricate, thick, narrowly ovoid, apex acuminate. Seeds compressed, ovate or oblong; beak with a long apical coma.

About 16 species: India, Malaysia, Sri Lanka, Vietnam; five species in China.

- 1a. Lateral leaf blade veins ca. 30 pairs ..... 5. *A. formicinum*  
 1b. Lateral leaf blade veins 6–16 pairs.  
 2a. Corolla tube 15–25 mm, lobes 15–25 mm; coma ca. 2 cm ..... 1. *A. benthamianum*  
 2b. Corolla tube 1.5–4.5 mm, lobes 3–5.5 mm; coma 4–6 cm.  
 3a. Branchlets, midvein, and petiole pubescent when young; fruit pilose ..... 2. *A. howii*  
 3b. Branchlets, midvein, and petiole glabrous; fruit glabrous.  
 4a. Leaves abaxially punctate with minute, sessile, brownish peltate glands; corolla tube shorter than lobes; follicles ca. 1 cm thick ..... 3. *A. punctatum*  
 4b. Leaves not punctate; corolla tube as long as or longer than lobes; follicles 1.6–3 cm thick ..... 4. *A. affine*

**1. *Anodendron benthamianum*** Hemsley in F. B. Forbes & Hemsley, J. Linn. Soc., Bot. 26: 98. 1889.

台湾鱗藤 tai wan shan teng

*Formosia benthamiana* (Hemsley) Pichon.

Lianas glabrous except for flowers. Branches dark brown, branchlets pale gray. Petiole 0.5–1.5 cm; leaf blade narrowly oblong or narrowly ovate, 5–14 × 1–5 cm, leathery, apex obtuse or acute; lateral veins 5–7 pairs. Cymes terminal, 5–15 × 8–9 cm, ca. 20-flowered. Sepals ovate, 3–4 × ca. 3 mm. Corolla tube 1.5–2.5 cm, pubescent inside; lobes oblong, 1.5–2.5 cm. Stamens inserted at base of corolla tube; disc cup-shaped, apex undulate. Ovary glabrous. Follicles narrowly oblong or ovoid-cylindric, 6–12 × ca. 1.5 cm. Seeds ca. 2 cm × 5 mm; beak ca. 2.5 mm; coma ca. 2 cm, recurved. Fl. Mar-Jun.

- Thickets, forests; 400 m. N Taiwan.

**2. *Anodendron howii*** Tsiang, Sunyatsenia 3: 141. 1936.

保亭鱗藤 bao ting shan ten

Lianas to 30 m. Young branchlets terete, rust colored pubescent, glabrescent when older, minutely lenticellate. Petiole 0.8–1.3 cm, pubescent when young; leaf blade elliptic to oblong, 10–15 × 4–6 cm, papery, base rounded or broadly cuneate, decurrent on petiole, apex acute, densely pubescent along veins abaxially; lateral veins 14–16 pairs. Cymes paniculate, axillary, 14–20-flowered, ca. 3.5 × 4 cm; peduncles paired or solitary, 2–2.5 cm, puberulent. Sepals ovate, ca. 1 mm. Corolla greenish white, tube ca. 1.5 mm; lobes falcate, oblong, ca. 5.5 mm, pilose inside, glabrous outside. Disc ringlike, apex obscurely 5-lobed. Follicles linear or nearly so, 11–12 × ca. 1 cm, shortly crisp pilose. Seeds ovate, ca. 2 cm, coma ca. 5 cm. Fl. May-Jun, fr. Jun-Aug.

- Sparse woods or brushwoods, usually in valleys. Guangxi, Hainan.

**3. *Anodendron punctatum*** Tsiang, Sunyatsenia 2: 129. 1934.

腺叶鱗藤 xian ye shan teng

Lianas to 20 m, glabrous except for corolla tube. Branches dark brown. Petiole 6–10 mm; leaf blade oblong or subovate,

5–9 × 2–3 cm, base obtuse or cuneate, apex acute, adaxially lustrous, abaxially with minute, scattered, peltate, brownish sessile glands; lateral veins ca. 13 pairs, wrinkled. Cymes thyrselike, axillary; peduncle ca. 6 cm. Pedicel ca. 0.5 mm. Sepals ovate to elliptic, ca. 2 mm. Corolla tube ca. 3 mm; lobes narrowly oblong, ca. 4 mm, apex slightly falcate; disc ringlike, 5-lobed. Ovary as long as disc. Style very short; pistil head thick, conical, 5-angled. Follicles paired, linear, 11–12 × ca. 1 cm, base sometimes slightly dilated. Seeds brown, ovate, ca. 2 cm × 5 mm, coma ca. 4 cm. Fl. Apr-May, fr. Jun-Dec.

- Dense montane forests; 300–800 m. Guangxi, Hainan, Sichuan.

**4. *Anodendron affine*** (Hooker & Arnott) Druce, Bot. Soc. Exch. Club Brit. Isles 4: 605. 1917.

鱗藤 shan teng

*Holarrhena affinis* Hooker & Arnott, Bot. Beechey Voy. 198. 1837; *Aganosma laevis* Champion ex Benth; *Anodendron affine* var. *effusum* Tsiang; *A. affine* var. *pingpienense* Tsiang & P. T. Li; *A. fangchengense* Tsiang & P. T. Li; *A. laeve* (Champion ex Benth) Maximowicz ex Franchet & Savatier; *A. salicifolium* Tsiang & P. T. Li; *A. suishaense* Hayata.

Lianas to 10 m, glabrous except for corolla. Branches pale gray. Petiole 0.5–2 cm; leaf blade deep green adaxially, lighter abaxially, narrowly oblong to narrowly ovate, 3–14 × 1.2–5 cm, papery or somewhat leathery; lateral veins 6–12 pairs, usually wrinkled in dry state. Cymes paniculate, terminal or axillary, 3–26 × 3–13 cm, long pedunculate. Sepals ovate, 2–3 mm. Corolla white or yellowish green, pilose inside, tube 3–4.5 mm; lobes falcate, narrowly oblong, as long as or shorter than tube. Stamens inserted at base of corolla tube; disc cup-shaped, shallowly 5-lobed or entire, attached to ovaries. Follicles narrowly ellipsoid, dilated at base, 8–13 × 1.6–3 cm. Seeds tawny, beaked, ca. 2 cm × 6 mm, coma ca. 6 cm. Fl. Apr-Nov.

- Sparse woods, brushwoods; 200–1000 m. Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hubei, Hunan, Sichuan, Taiwan, Yunnan, Zhejiang [India, Japan, Vietnam].

**5. *Anodendron formicinum*** (Tsiang & P. T. Li) D. J. Middleton, Novon 4: 152. 1994.



平脉藤 ping mai teng

*Micrechites formicina* Tsiang & P. T. Li, Acta Phyto-tax. Sin. 11: 385. 1973.

Lianas to 15 m, glabrous except for sepals. Petiole 5–13 mm; leaf blade oblong or narrowly so, 6–17 × 1.5–4 cm, base rounded, apex acute; lateral veins ca. 30 pairs, nearly at a right angle to midvein, flattened on both surfaces. Cymes

paniculate, terminal and axillary, 5-branched, ca. 14.5 × 19 cm, many flowered. Flowers small. Sepals ovate, puberulent outside. Corolla yellowish green, lobes longer than tube. Stamens inserted at base of corolla tube; disc ringlike, apex obscurely 5-cleft. Ovary glabrous, half sunken in disc. Style short; pistil head beaklike. Fl. May–July.

- Dense montane forests; 1800 m. S Yunnan.

### 38. URCEOLA Roxburgh, Asiat. Res. 5: 169. 1799, nom. cons.

水壶藤属 shui hu teng shu

*Chunechites* Tsiang; *Ecdysanthera* Hooker & Arnott; *Parabarium* Pierre in Spire; *Xylinabariopsis* Lý.

Lianas woody, latex white. Leaves opposite. Cymes paniculate, terminal or axillary, 3-branched. Flowers small. Calyx deeply divided, with basal glands inside. Corolla suburceolate, throat without scales; lobes short, overlapping to right. Stamens included, inserted at base of corolla tube; filaments short; anthers narrowly oblong, sagittate, connivent, adherent to pistil head, cells spurred at base; disc ringlike, entire or 5-lobed. Ovaries 2, longer than disc, villous at apex; ovules numerous in each locule. Style short; pistil head ovoid, conical or oblong, apex 2-cleft. Follicles cylindrical or narrowly ellipsoid, spreading, thick, acuminate. Seeds numerous, oblong or linear, compressed, pubescent, coma long; endosperm scanty; cotyledons oblong or ovate, leaflike, radicle short.

Fifteen species: SE Asia, eight species in China.

- 1a. Leaf blade pubescent abaxially, denser along veins.
  - 2a. Leaf blade very narrowly elliptic, lateral veins 5–7 pairs; corolla glabrous outside, lobe margin 1-toothed; fruit linear or nearly so, ca. 0.5 cm in diam. .... 1. *U. xylinabariopsoides*
  - 2b. Leaf blade ovate or narrowly elliptic, lateral veins ca. 10 pairs; corolla pubescent outside, lobe margin entire; fruit narrowly ovoid, 1.5–2 cm in diam. .... 2. *U. huaitingii*
- 1b. Leaf blade glabrous, sometime with hairy domatia in axils of lateral veins.
  - 3a. Petiole puberulent; corolla lobes 1-toothed near base; fruit ovoid ..... 3. *U. micrantha*
  - 3b. Petiole glabrous; corolla lobes entire; fruit sublinear or oblong, if ovoid then long beaked.
    - 4a. Leaf blade papillate abaxially, petiole 3–5 mm ..... 4. *U. quintaretii*
    - 4b. Leaf blade not papillate abaxially, petiole 6–25 mm.
      - 5a. Leaf blade narrowly oblong, 11–18 cm; fruit ca. 2 cm in diam. .... 5. *U. tournieri*
      - 5b. Leaf blade broadly elliptic, elliptic, or narrowly ovate, 3–10 cm; fruit 0.4–1 cm in diam.
        - 6a. Inflorescences glabrous ..... 8. *U. linearicarpa*
        - 6b. Inflorescences pubescent or puberulent.
          - 7a. Sepals ca. 4 mm; corolla lobes ± symmetrical, slightly longer than tube; follicles to 15 cm, terete, not stipitate ..... 6. *U. rosea*
          - 7b. Sepals ca. 0.8 mm; corolla lobes strongly asymmetrical, ca. 2 × longer than tube; follicles 5–7 cm, strongly stipitate ..... 7. *U. napeensis*

**1. *Urceola xylinabariopsoides*** (Tsiang) D. J. Middleton, Novon 4: 151. 1994.

乐东藤 le dong teng

*Chunechites xylinabariopsoides* Tsiang, Sunyatsenia 3: 306. 1937; *Ecdysanthera xylinabariopsoides* (Tsiang) P. T. Li; *Xylinabariopsis ventii* Lý; *X. xylinabariopsoides* (Tsiang) Lý.

Liana to 1.5 m, densely pubescent. Bark dark brown. Petiole 2–3 mm; leaf blade narrowly elliptic, 3–6 × ca. 1.7 cm, somewhat leathery, base broadly cuneate, apex short acuminate, glabrous adaxially except along veins, pubescent abaxially, denser along veins; lateral veins 5–7 pairs. Cymes paniculate, axillary and terminal, 3-branched, 5–8 cm. Sepals narrowly elliptic, ca. 1 mm, acute. Corolla reddish yellow, tube

ca. 1 mm; lobes sublinear, unequally falcate, 1.5–2 mm, 1-toothed at middle of margin, apex rounded or obtuse. Disc ringlike, obscurely 5-lobed. Ovary apex pilose. Follicles sublinear, 5–7 cm × ca. 5 mm, puberulent to glabrous. Seeds narrowly oblong, ca. 1 cm, pubescent, coma ca. 3 cm. Fl. Jun–Sep, fr. Sep–Dec.

Open montane forests. Hainan [Vietnam].

**2. *Urceola huaitingii*** (Chun & Tsiang) D. J. Middleton, Novon 4: 151. 1994.

毛杜仲藤 mao du zhong teng

*Parabarium huaitingii* Chun & Tsiang, J. Arnold Arbor. 28: 245. 1947.

Lianas to 15 m, minutely tomentose or densely pubescent. Petiole ca. 5 mm; leaf blade ovate or elliptic, 2.5–7.5 × 1.5–3.5

cm, papery; lateral veins ca. 10 pairs. Cymes corymbose, axillary or terminal, 4–6 cm; bracts leaflike, 1–3 × 0.5–1 mm. Sepals narrowly oblong, ca. 2 mm. Corolla yellow, tube ca. 2 mm; lobes obliquely oblong, falcate, longer than or as long as tube, entire. Disc 5-partite. Ovary pilose; ovules ca. 10 in each carpel. Follicles narrowly ovoid, 6–7 × 1.5–2 cm, dilated at base. Seeds very narrowly oblong, 1–1.5 cm × 2–3 mm, coma ca. 3 cm. Fl. Apr-Jun, fr. Jun-Dec.

• Open forests, moist valleys; 200–1000 m. Guangdong, Guangxi, Guizhou, Hainan.

The bark and roots are used to treat rheumatism and injury. The leaves are used externally to stop bleeding.

**3. *Urceola micrantha*** (Wallich ex G. Don) D. J. Middleton, *Novon* 4: 151. 1994.

杜仲藤 du zhong teng

*Echites micrantha* Wallich ex G. Don, *Gen. Hist.* 4: 75. 1837; *Ecdysanthera brachiata* A. de Candolle; *E. micrantha* (Wallich ex G. Don) A. de Candolle; *E. multiflora* King & Gamble; *E. utilis* Hayata & Kawakami; *Parabarium micranthum* (Wallich ex G. Don) Pierre; *P. multiflorum* (King & Gamble) Lý; *P. spireanum* Pierre; *P. utile* (Hayata & Kawakami) Lý; *P. utile* var. *kerrii* Lý.

Lianas to 50 m. Stems 10–30 cm in diam.; branches often lenticellate. Petiole puberulent, 1.5–3 cm; leaf blade elliptic or narrowly ovate, 5–15 × 1.5–6 cm, base obtuse, apex narrowly acuminate, glabrous; lateral veins 3–7 pairs. Cymes paniculate, compact, to 9 cm; peduncle pubescent. Sepals ovate, ca. 0.8–1 mm, apex subacute. Corolla pink, lobes oblong, as long as to longer than tube, to 2 mm, 1-toothed near base. Filaments ca. 0.5 mm; disc ringlike. Ovary pilose. Pistil head conical. Follicles narrowly ovoid, 9–23 × (0.4–)1–1.2 cm, base dilated. Seeds oblong, 2–4 cm, coma ca. 4 cm. Fl. Mar-Jun, fr. Jun-Dec.

Mixed forests, brushwoods; 300–1000 m. Fujian, Guangdong, Guangxi, Hainan, Sichuan, Taiwan, Xizang, Yunnan [India, Indonesia, Japan (Ryukyu Islands), Laos, Malaysia, Nepal, Thailand, Vietnam].

The bark and roots are used for the treatment of infantile paralysis, rheumatism, injury, and fractures.

**4. *Urceola quintaretii*** (Pierre) D. J. Middleton, *Novon* 4: 151. 1994.

华南杜仲藤 hua nan du zhong teng

*Ecdysanthera quintaretii* Pierre, *Rev. Cultures Col.* 11: 228. 1902; *E. micrantha* Quintaret, not (Wallich ex G. Don) A. de Candolle; *E. parameroides* Tsiang; *Parabarium chunianum* Tsiang; *P. hainanense* Tsiang; *P. handelianum* Tsiang; *P. quintaretii* (Pierre) Pierre.

Lianas to 10 m, glabrous except for inflorescences. Branches dark brown when young, dark gray when older. Petiole ca. 5 mm; leaf blade glaucous at first, deep lustrous green adaxially, pale green and with scattered black papillae abaxially, elliptic, narrowly elliptic, ovate, or obovate, 4.5–11 × 1.6–3 cm, apex short acuminate; lateral veins 5–7 pairs. Cymes paniculate, compact, terminal and axillary, 2- or

3-branched, as long as or longer than leaves. Sepals narrowly ovate, ca. 2 mm, pilose, apex obtuse. Corolla pilose, tube ca. 1 mm, lobes ca. 1 mm. Disc short, fleshy, ringlike or obscurely 5-lobed. Ovary pilose. Follicles very narrowly oblong, 4.5–6 cm × 7–10 mm. Seeds oblong, 1.3–1.6 cm, tomentose, coma 1.5–2.5 cm. Fl. Jan-Jun, fr. Aug-Dec.

Dense montane forests; 300–500 m. Guangdong, Guangxi, Hainan [Laos, Vietnam].

**5. *Urceola tournieri*** (Pierre) D. J. Middleton, *Novon* 4: 151. 1994.

云南水壶藤 yun nan shui hu teng

*Ecdysanthera tournieri* Pierre, *Rev. Cultures Colon.* 11: 228. 1902; *Parabarium burmanicum* Lý; *P. tournieri* (Pierre) Pierre.

Lianas stout, to 20 m, glabrous except for branches and inflorescences. Bark brown, prominently lenticellate; branches puberulent. Petiole 6–8 mm; leaf blade oblong, narrowly so, 11–18 × 2.5–6 cm, apex cuspidate; lateral veins 7–9 pairs. Cymes corymbose, axillary, 8–16 cm, puberulent. Pedicel 2–2.5 mm, puberulent. Sepals ovate, 0.5–0.7 mm. Corolla white, 1.6–2.2 mm, tube 1–1.5 mm; lobes 0.5–0.7 mm, asymmetric. Ovary villous. Follicles narrowly ovoid, to 10 × 2 cm, stout, nearly woody, with many lenticels. Seeds oblong, ca. 1.5 cm × 3 mm, coma yellowish, ca. 3 cm. Fl. summer-autumn.

Forests; 800–1800 m. S Yunnan [Laos, Myanmar].

**6. *Urceola rosea*** (Hooker & Arnott) D. J. Middleton, *Novon* 4: 151. 1994.

酸叶胶藤 suan ye jiao teng

*Ecdysanthera rosea* Hooker & Arnott, *Bot. Beechey Voy.* 198. 1837; *Antirrhoea esquirolii* H. Léveillé.

Lianas to 20 m. Stem dark brown, lenticels absent; branches tawny gray, young ones brownish. Petiole 0.8–1.2 cm; leaf blade broadly elliptic, rarely subovate, 3–7 × 1–4 cm, apex acute, glabrous, ± lustrous adaxially, glaucous abaxially, lateral veins 4–6 pairs. Sepals ovate, ca. 3 mm, obtuse. Corolla pink, tube ca. 4 mm; lobes ± symmetrical, slightly longer than tube, acute. Disc ringlike, entire. Ovary pubescent. Follicles to 15 cm, terete, densely spotted. Seeds oblong, ca. 1 cm, coma ca. 3 cm. Fl. Apr-Dec, fr. Jun-Dec.  $2n = 20^*$ .

Ravines at low and middle altitudes, scattered in montane forests. Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hunan, Sichuan, Taiwan, Yunnan [Indonesia, Thailand, Vietnam].

All parts are used to treat endosteum, injury, and rheumatism.

**7. *Urceola napeensis*** (Quintaret) D. J. Middleton, *Blumea* 39: 89. 1994.

华南水壶藤 hua nan shui hu teng

*Micrechites napeensis* Quintaret, *Compt. Rend. Hebd. Séances Acad. Sci.* 134: 438. 1902; *Ecdysanthera napeensis* (Quintaret) Pierre; *Parabarium napeense* (Quintaret) Pierre; *Xylinabaria reynaudii* Jumelle; *Xylinabariopsis napeensis*

(Quintaret) F. P. Metcalf; *X. reynaudii* (Jumelle) Pitard.

Lianas 5–20 m. Petiole 1–1.5 cm; leaf blade ovate, elliptic, or lanceolate, 5–9 cm, base rounded or obtuse, apex acuminate or obtuse; lateral veins 6–8 pairs. Inflorescences axillary, corymbose cymes 5–7 cm, pubescent; bracteoles linear. Pedicel 2–4 mm. Sepals ovate, ca. 0.8 mm, ciliate, obtuse. Corolla rose or white; lobes strongly asymmetrical, ca. 2 × longer than tube. Disc ringlike, with 5 rounded lobes. Follicles ovoid, long beaked, 5–7 cm × 6–7 mm, strongly stipitate. Seeds ca. 1.5 cm. Fl. Oct–May, fr. Dec–Aug.

Forests. Guangdong, Guangxi, Hainan [Laos, Thailand, Vietnam].

**8. *Urceola linearicarpa*** (Pierre) D. J. Middleton, Novon 4: 151. 1994.

线果水壶藤 *xian guo shui hu teng*

*Ecdysanthera linearicarpa* Pierre, Rev. Cultures Colon. 11: 228. 1902; *Parabarium linearicarpum* (Pierre) Pichon.

Lianas to 8 m, glabrous. Branches lenticellate. Petiole 6–10 mm; leaf blade green adaxially, greenish abaxially, elliptic or narrowly ovate, 6–8 × 3–3.5 cm, base broadly cuneate or nearly rounded, apex acute to caudate; lateral veins 5 or 6 pairs. Cymes axillary. Flowers small. Sepals ovate, ca. 0.5 × 0.5 mm, apex subacute. Corolla campanulate, yellowish, tube ca. 1.5 × 1.5 mm; lobes erect or incurved, ca. 1 × 0.7 mm. Disc ringlike, shorter than ovary. Ovary pilose. Pistil head ovoid. Follicles linear, 13–14 cm × 5–10 mm. Seeds brownish, oblong, ca. 1.5 cm, coma ca. 3 cm. Fl. Aug–Nov, fr. Oct–Dec.

Tropical rain forests, humid sparse woods; 500–1500 m. SE Xizang, S Yunnan [Laos].

### 39. PARAMERIA Bentham in Bentham & J. D. Hooker, Gen. Pl. 2: 715. 1876.

长节珠属 *chang jie zhu shu*

Lianas woody, latex white. Leaves opposite. Cymes broadly paniculate, terminal or axillary, pedunculate. Flowers small. Calyx deeply divided, with many nectar glands inside. Corolla salverform or subcampanulate, tube short; throat broad, not scaly; lobes overlapping to left, spreading or reflexed. Stamens inserted at base of corolla tube; filaments short; anthers included, sagittate, connivent, adherent at middle to pistil head, cells with an empty tail; disc scales 5. Ovaries 2, free, longer than disc; ovules numerous in each locule. Style short; pistil head conical, apex obscurely 2-cleft. Follicles moniliform, with widely separated swellings, pendulous, elongated. Seeds fusiform, coma apical, early deciduous; endosperm scanty; cotyledons oblong, radicle short.

About four species: SE Asia, one species in China.

**1. *Parameria laevigata*** (Jussieu) Moldenke, Revista Sudameric. Bot. 6: 76. 1940.

长节珠 *chang jie zhu*

*Aegiphila laevigata* Jussieu, Ann. Mus. Natl. Hist. Nat. 7: 76. 1806; *Parameria barbata* (Blume) K. Schumann; *Parsonsia barbata* Blume.

Lianas evergreen, to 10 m. Stems pale gray; branchlets shortly hairy when young, soon glabrescent. Petiole 2–4 cm; leaf blade narrowly oblong or subovate, rarely elliptic or ovate, 5–13 × 2–5 cm, glabrous; lateral veins 5 or 6 pairs, with domatia. Cymes 5–16 × 5–16 cm, puberulent distally. Sepals

broadly ovate, 0.5–1 mm, glabrous or pubescent, apex obtuse or acute. Corolla reddish to white, ca. 7 mm in diam., tube 2–2.5 mm; lobes broadly ovate or nearly orbicular, ca. 3 × 3 mm; disc shorter than ovary. Ovary pubescent. Follicles to 45 cm. Seeds ca. 1 cm, pubescent, coma ca. 3 cm. Fl. Jun–Oct, fr. Oct–Dec.

Montane forests, ravines; 800–1500 m. S Guangxi, S Yunnan [Cambodia, India, Indonesia, Laos, Malaysia, Myanmar, Philippines, Thailand, Vietnam].

All parts of plant are used to treat rheumatism, nephritis, and injury.

### 40. ICHNOCARPUS R. Brown, Mem. Wern. Nat. Hist. Soc. 1: 61. 1811, nom. cons.

腰骨藤属 *yao gu teng shu*

*Lamechites* Markgraf; *Micrechites* Miquel; *Otopetalum* Miquel; *Springia* Heurck & Müller Argoviensis.

Plants scramblers or woody lianas, with latex. Leaves opposite. Inflorescences cymose, terminal and/or axillary. Flowers small. Calyx with basal glands inside, lobes free. Corolla white, yellowish, or red, salverform; tube widened near base, throat hairy; lobes oblong, falcate, overlapping to right, in bud with inflexed distal halves. Stamens included, inserted at or below middle of corolla tube; filaments very short; anthers sagittate, adherent to pistil head, cells spurred at base; disc entire, 5-crenate or 5-dentate, or deeply divided into 5 erect segments. Ovaries adnate basally to disc, pubescent; ovules numerous. Pistil head ovoid or cup-shaped. Follicles 2, spreading or divaricate. Seeds numerous, linear, compressed, not or hardly beaked, comose; endosperm copious; cotyledons long, flat, radicle superior.

Twelve species: SE Asia, N Australia, Pacific Islands; four species in China.

1a. Disc lobes free and narrow, longer than ovary; anthers appearing elliptic ..... 1. *I. frutescens*

- 1b. Disc entire, 5-lobed or dentate, shorter than ovary or, rarely, of 5 wide separate lobes shorter than ovary; anthers narrow triangular.
- 2a. Ovary ± glabrous; corolla red; stems, underside of leaves, and inflorescences densely rufous tomentose ... 2. *I. jacquetii*
- 2b. Ovary densely pubescent; corolla white, cream, or yellow; indumentum variable.
- 3a. Lateral leaf veins ca. 25 pairs; corolla yellow, tube 7–8 mm ..... 3. *I. malipoensis*
- 3b. Lateral leaf veins 10–15 pairs; corolla white, tube ca. 3 mm ..... 4. *I. polyanthus*

**1. *Ichnocarpus frutescens*** (Linnaeus) W. T. Aiton, Hortus Kew. ed. 2, 2: 69. 1811.

腰骨藤 yao gu teng

*Apocynum frutescens* Linnaeus, Sp. Pl. 1: 213. 1753; *Echites frutescens* Wallich ex Roxburgh; *Gardenia volubilis* Loureiro; *Ichnocarpus ovatifolius* A. de Candolle; *I. volubilis* (Loureiro) Merrill; *Micrechites sinensis* Markgraf.

Lianas to 10 m. Branchlets pubescent when young, soon glabrous. Petiole 0.5–1.5 cm; leaf blade 5–11 × 2.5–4.5 cm, pubescent or glabrous abaxially; lateral veins 5–7 pairs. Inflorescences many flowered, 3–8 cm, most flowers in pedunculate heads. Calyx densely pubescent. Corolla tube ca. 2.5 mm; lobes narrowly oblong, ca. 5 mm. Anthers elliptic; disc lobes free, linear, longer than ovary. Ovaries pubescent. Follicles cylindric, 8–15 cm × 4–5 mm, slightly torulose, pubescent. Seeds linear, coma ca. 2.5 cm. Fl. May–Aug, fr. Aug–Dec.  $2n = 20$ .

Sparse woods, brushwoods; 200–900 m. Fujian, Guangdong, Guangxi, Guizhou, Hainan, Yunnan [Bangladesh, Bhutan, Cambodia, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, New Guinea, Pakistan, Philippines, Sri Lanka, Thailand, Vietnam; Australia].

A fine, strong fiber obtained from the inner bark is used in making ropes and sacks. The seeds are used for the treatment of rheumatism and the stem and leaves for acute urticaria.

**2. *Ichnocarpus jacquetii*** (Pierre) D. J. Middleton, Novon 4: 152. 1994.

少花腰骨藤 shao hua yao gu teng

*Micrechites jacquetii* Pierre in Spire, Contr. Apocyn. 48. 1905; *Ichnocarpus oliganthus* Tsiang.

Lianas to 20 m, rust colored tomentose. Petiole ca. 1 cm; leaf blade narrowly elliptic, 4–8 × 1.5–4 cm, thinly leathery; lateral veins 5–9 pairs. Cymes 2-forked, ca. 2 cm, 3–9-flowered, lower part bracteate; bracts many, ovate, ca. 2 mm, persistent. Calyx glands 20. Corolla red, ca. 4 × 6.5 mm, villous inside at throat and facing stamens; tube ca. 3 mm, dilated at middle; lobes long falcate, ca. 3 × 1.2 mm. Stamens inserted near base of corolla tube; anthers triangular; disc 5-lobed, slightly united at base, shorter than ovary. Ovary glabrous. Follicles linear-cylindric, 12–18 cm × ca. 5 mm, densely brown tomentose. Seeds dark brown, linear, 1–2 cm × ca. 1 mm, coma creamy white, to 3 cm. Fl. Aug, fr. Aug–Oct.

Montane sparse woods, brushwoods; 300–500 m. S Guangdong, Guangxi, Hainan [Laos, Vietnam]. The bark is used to treat rheumatism.

**3. *Ichnocarpus malipoensis*** (Tsiang & P. T. Li) D. J. Middleton, Novon 4: 152. 1994.

麻栗坡少花藤 ma li po xiao hua teng

*Micrechites malipoensis* Tsiang & P. T. Li, Acta Phytotax. Sin. 11: 381. 1973.

Lianas to 6 m. Branches and branchlets pubescent. Petiole stout, densely pubescent; leaf blade narrowly elliptic, 8–32 × 2.5–8.5 cm, base cuneate, apex caudate-acuminate, pubescent abaxially; lateral veins ca. 25 pairs. Cymes axillary, paniculate, to 5 cm, densely rust colored pubescent; peduncle to 4.5 cm. Corolla yellow, hirsute inside, tube 7–8 mm; lobes oblong, falcate, as long as tube, glabrous, margin 1-toothed at base. Stamens inserted near base of corolla tube; anthers triangular; disc ringlike, shorter than ovary, apex 5-cleft. Ovary densely hirsute. Fl. May–Nov.

- Dense montane forests; 1000–1200 m. SE Yunnan.

**4. *Ichnocarpus polyanthus*** (Blume) P. I. Forster, Austral. Syst. Bot. 5: 544. 1992.

小花藤 xiao hua teng

*Tabernaemontana polyantha* Blume, Bijdr. 1029. 1826; *Ichnocarpus baillonii* (Pierre) L'Y; *I. himalaicus* T. Yamazaki; *I. pubiflorus* J. D. Hooker; *Micrechites baillonii* Pierre; *M. elliptica* J. D. Hooker; *M. elliptica* var. *scortechinii* King & Gamble; *M. ferruginea* Pitard; *M. lachnocarpa* Tsiang; *M. malipoensis* Tsiang & P. T. Li var. *parvifolia* Tsiang & P. T. Li; *M. polyantha* (Blume) Miquel; *M. radicans* Markgraf; *M. rehderiana* Tsiang; *M. scortechinii* (King & Gamble) Ridley.

Lianas to 30 m, glabrous except for inflorescences. Petiole 1–2 cm; leaf blade narrowly ovate or narrowly elliptic, 6–13 × 2.5–5 cm, base broadly cuneate, apex short acuminate; lateral veins 10–15 pairs. Cymes paniculate, terminal and axillary; peduncle to 9 cm, pubescent. Pedicels 2–4 mm long. Sepals ovate, ca. 2.5 mm, pubescent outside. Corolla white; tube ca. 3 mm, pubescent inside; lobes narrowly oblong, ca. 2 mm. Stamens inserted near base of corolla tube; disc ringlike, apex shortly 5-cleft, shorter than ovary. Ovary densely pubescent. Follicles linear, 25–40 cm × ca. 5 mm, glabrous. Fl. Apr–Jun, fr. Sep–Dec.

Dense moist forests, often along valleys; montane brushwoods; 200–1800 m. Guangdong, Guangxi, Hainan, Yunnan [Bhutan, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Thailand, Vietnam].

#### 41. EPIGYNUM Wight, Icon. Pl. Ind. Orient. 4(2): 4. 1848.

思茅藤属 si mao teng shu

Lianas woody, latex white. Leaves opposite. Cymes terminal, corymbose or paniculate. Calyx deeply divided, basal glands inside present or absent. Corolla salverform; tube cylindrical, ca. 5 × as long as sepals, inflated at base; throat villous, not scaly; lobes overlapping to right. Stamens inserted below middle of corolla tube; filaments short; anthers sagittate, included, adherent at middle to pistil head, cells with an empty tail; disc deeply 5-lobed, longer than ovary. Carpels 2, distinct. Ovaries half-inferior or nearly inferior; ovules numerous in each carpel. Style filiform; pistil head long conical. Follicles 2, terete, free. Seeds oblong or narrowly so, flat, comose.

About 14 species: SE Asia, one species in China.

**1. Epigynum auritum** (C. K. Schneider) Tsiang & P. T. Li, *Acta Phytotax. Sin.* 11: 397. 1973.

思茅藤 si mao teng

*Trachelospermum auritum* C. K. Schneider in Sargent, *Pl. Wilson.* 3: 341. 1916; *Epigynum lachnocarpum* Pichon.

Liana to 8 m. Branchlets slightly reddish brown, densely minutely hirsute-villous when young. Petiole 5–10 mm; leaf blade broadly elliptic or slightly obovate, 8–15 × 4.5–11.5 cm,

base acuminate-cordate, villous on both surfaces; lateral veins ca. 10. Cymes as long as or longer than leaves, densely tawny pubescent; peduncle up to 8 cm. Pedicel ca. 1 cm. Corolla white, tube 1.5–1.7 cm; lobes obliquely obovate or narrowly spatulate, 1.2–1.3 cm. Disc 5-lobed. Ovaries pubescent at apex. Follicles 2, oblong, to 16 × 1–1.5 cm, densely tawny, apex distinctly recurved. Seeds oblong, to 2 cm, coma to 3.5 cm. Fl. Apr-Jul, fr. Aug-Dec.

Dense montane forests, clinging to trees. S Yunnan [Malaysia, Thailand].

## 42. PAREPIGYNUM Tsiang & P. T. Li, *Acta Phytotax. Sin.* 11: 394. 1973.

富宁藤属 fu ning teng shu

Lianas woody, large, latex white. Leaves opposite. Cymes corymbose, terminal and axillary, long pedunculate. Calyx glandular between sepals. Corolla salverform; tube terete, constricted below middle, with densely antrorse setae; lobes narrowly elliptic, overlapping to left. Stamens inserted near base of corolla tube; filaments short; anthers sagittate, included, adherent at middle to pistil head, cells spurred at base; disc fleshy, 5-partite, lobes nearly 4-angled, as long as ovary. Carpels 2, connate. Ovaries semi-inferior or nearly inferior; ovules numerous in each carpel. Style cylindrical, dilated at apex; pistil head conical. Follicles 2, narrowly fusiform, connate, parted distally when mature. Seeds narrowly elliptic, short beaked, coma silky.

One species: endemic to China.

**1. Parepigynum funingense** Tsiang & P. T. Li, *Acta Phytotax. Sin.* 11: 395. 1973.

富宁藤 fu ning teng

Lianas to 10 m, juvenile parts and inflorescences pubescent. Petiole 1.5–2 cm; leaf blade narrowly elliptic to oblong; 8–15 × 2.5–4.5 mm; lateral veins 10–13 pairs.

Inflorescences 6–13-flowered. Sepals narrowly elliptic, ca. 7 × 2 mm, pubescent on both sides. Corolla yellow, tube ca. 1.2 cm; lobes ca. 11 × 8 mm. Ovary hirsute at apex. Style ca. 3.5 mm. Follicles very narrowly fusiform, 14–18 × ca. 1.5 cm, stipe 2–3 cm. Seeds dark brown, narrowly ellipsoid, 2–3 cm × 2–6 mm; coma white, silky, ca. 2 cm. Fl. Apr-Sep, fr. Aug-Dec.

• Dense montane forests; 1000–1800 m. Guizhou, SW Yunnan.

## 43. CLEGHORNIA Wight, *Icon. Pl. Ind. Orient.* 4(2): 5. 1848.

金平藤属 jin ping teng shu

Lianas woody, with milky latex. Leaves opposite, lateral veins parallel. Inflorescences paniculate-corymbose, axillary or terminal, few to many flowered. Flowers small. Calyx glands present. Corolla yellow or white, salverform, tube cylindrical; lobes spreading, as long as or shorter than tube, overlapping to right. Stamens included, inserted at base of corolla tube; filaments very short; anthers sagittate, adnate to pistil head, connective narrowly oblong, densely pilose at apex; disc large, fleshy, obscurely 5-lobed, as long as or shorter than ovary. Ovaries 2, distinct; ovules numerous. Style short; pistil head club-shaped, apex 2-cleft. Follicles 2, slender. Seeds numerous, apically comose.

Four species: Laos, Malaysia, Myanmar, Sri Lanka, Thailand, Vietnam; one species in China.

**1. Cleghornia malaccensis** (J. D. Hooker) King & Gamble in Ridley, *Mat. Fl. Malay. Penins.* 491. 1907.

金平藤 jin ping teng

*Baissea malaccensis* J. D. Hooker, *Fl. Brit. India* 3: 663. 1882; *Giadotrum malaccense* (J. D. Hooker) Pichon.

Lianas to 35 m, glabrous throughout except for corolla throat. Stems to 5 cm in diam., dark brown; branchlets pale

brown. Petiole 0.7–2 cm; leaf blade elliptic, oblong, or subobovate, rarely narrowly ovate, 7–16 × 2–6.5 cm, base cuneate or rounded, apex caudate-acuminate; lateral veins 10–14 pairs, at ca. 90° to midvein. Cymes 4–7 cm, usually 3-branched. Corolla yellow or yellowish; tube short cylindrical, 1.6–2.5 mm, throat pubescent; lobes oblong, 1–3.2 × 0.1–1 mm. Stamens inserted near base or below middle of corolla tube; filaments minutely pubescent adaxially; anthers sagittate, ca.

2.5 mm; disc shorter than ovary. Follicles 2, linear, 7–22 × (0.5–)1–1.5 cm. Seeds narrowly fusiform, 2–3 cm, coma to 4 cm. Fl. Apr-Jul, fr. Jul-Oct.

Montane forests, brushes along river banks or streamsides; 500–1600 m. Guizhou, S Yunnan [Laos, Malaysia, Thailand,

Vietnam].

The species was treated in FRPS as *Bai-sea acuminata* (Wight) Bentham ex J. D. Hooker (*C. acuminata* Wight), which is a very different species not found in China.

#### 44. SINDECHITES Oliver, Hooker's Icon. Pl. 18: t. 1772. 1888.

毛药藤属 mao yao teng shu

Lianas woody, with milky latex. Leaves opposite, veins parallel or nearly so. Cymes paniculate or corymbose, terminal and axillary, few to many flowered. Flowers small. Calyx glandular inside. Corolla white, salverform, dilated at throat or middle of tube; lobes shorter than tube, overlapping to right. Stamens inserted above middle of corolla tube, included; filaments short; anthers sagittate, connivent, adherent to pistil head, connective usually pilose at apex, cells spurred at base; disc large, fleshy, entire or 5-lobed, shorter than or as long as ovary. Ovaries 2, distinct, usually dense pubescent on distal part; ovules numerous. Style long; pistil head club-shaped, apex 2-cleft. Follicles 2, narrowly cylindrical, slightly torulose, slender. Seeds comose apically.

Two species: Laos, Thailand; both in China.

- 1a. Lateral leaf veins 15–25 pairs; stamens inserted near corolla throat; corolla tube 5–8 mm; ovary densely pubescent; disc shorter than ovary ..... 1. *S. henryi*  
1b. Lateral leaf veins 4–6 pairs; stamens inserted at middle of corolla tube; corolla tube 9–15 mm; ovary glabrous; disc as long as ovary ..... 2. *S. chinensis*

**1. *Sindechites henryi*** Oliver, Hooker's Icon. Pl. 18: t. 1772. 1888.

毛药藤 mao yao teng

*Antirhea martinii* H. Léveillé; *Cleghornia henryi* (Oliver) P. T. Li; *Parameria esquirolii* H. Léveillé; *Sindechites esquirolii* (H. Léveillé) Woodson; *S. henryi* var. *parvifolia* Tsiang.

Lianas to 8 m, glabrous except for flowers. Petiole 4–10 mm; leaf blade narrowly oblong or narrowly ovate, 5.5–12.5 × 1.5–3.7 cm, membranous, base cuneate or rounded, apex long acuminate; lateral veins 15–25 pairs, subparallel, anastomosing near blade margin. Cymes 3–7 cm, di- or trichasial. Mature flower buds 7.5–9 mm, apex conical. Corolla white; tube 5–8 mm, throat dilated, pubescent inside; lobes ovate or broadly ovate. Stamens inserted near corolla throat; disc shorter than ovary. Ovary densely pubescent. Style long. Follicles 3–14 cm × 2–3 mm. Seeds narrowly oblong, ca. 1.3 cm, coma ca. 2.5 cm. Fl. May-Jul, fr. Jul-Oct.

• Forests, bushes, mountains, roadsides, near streams; 500–1500 m. Guangxi, Guizhou, Hubei, Hunan, Jiangxi, Sichuan, Yunnan, Zhejiang.

**2. *Sindechites chinensis*** (Merrill) Markgraf & Tsiang in Tsiang, Sunyatsenia 3: 152. 1936.

坭藤 ni teng

*Epigynum chinense* Merrill, Philipp. J. Sci. 23: 262. 1923; *Cleghornia chinensis* (Merrill) P. T. Li.

Lianas to 6 m. Branches brown or pale brown. Petiole 2–4 mm; leaf blade ovate or narrowly ovate, 4–9 × 2–4.5 cm, membranous, base rounded, apex acute or obtuse; lateral veins 4–6 pairs, minutely pubescent along veins abaxially when young, otherwise glabrous on both surfaces. Cymes 4–5 cm. Mature flower buds 1.2–1.7 cm, apex globose. Corolla white, tube 0.9–1.5 cm, slightly dilated at middle, densely pubescent at throat, sparsely so proximally; lobes broadly ovate, minutely pubescent outside. Stamens inserted at middle of corolla tube; disc as long as ovary. Ovary glabrous. Style long. Follicles 7–16 cm × 3–5 mm. Seeds dark brown, very narrowly oblong, flat, 1–1.5 cm; coma 2.5–3 cm. Fl. Mar-Jul, fr. Jun-Dec.

Dense montane forests, brushes along river banks; 100–700 m. Hainan [Laos, Thailand].



## A Contribution of the Palynological Criteria in Evaluating The Relationships among Some Species of Apocynaceae *Sensu Lato*

Hanan A. Dabbub<sup>(1)</sup>, Mohamed A. Salim<sup>(2)</sup>, Usama K. Abdelhameed<sup>(2,3)</sup>, Mohamed E. Tantawy<sup>(2)</sup>, Alsafa H. Mohamed<sup>(2)#</sup>

<sup>(1)</sup>Department of Biology, Faculty of Education, Alzawia University, Alzawia, Libya;

<sup>(2)</sup>Department of Botany, Faculty of Science, Ain Shams University, Cairo, Egypt;

<sup>(3)</sup>Department of Biology, College of Science, Taibah University, Madinah, Kingdom of Saudi Arabia.



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**A**POCYNACEAE *sensu lato* is an interesting family with respect to pollen diversification. The pollen grains of 19 species (representing four out of five subfamilies and 18 genera) of Apocynaceae were collected and investigated using LM & SEM. The specific objective of the present study is to shed light on the different pollen morphological characters of the species under investigation and to discuss whether pollen morphology is considered an additional fundamental tool that helps in explanation of the evolutionary trend within the family. The obtained pollen data are considered diagnostic at the specific level *viz.* pollen association, class, polarity, sculpture, orientation and attachment of the translator. *Carissa macrocarpa* (Rauvolfioideae) gathered with the studied species of Apocynoideae based on the presence of porate pollen. In *Cryptostegia grandiflora*, the pseudo-pollinarium is considered a link between monads (as in Rauvolfioideae and Apocynoideae) and the true pollinia (as in Asclepiadoideae). Pollen criteria facilitate the construction of dendrogram, a tentative presentation of phylogenetic relationship and an artificial key to achieve further delimitation between the species under investigation and discussing the interrelationships in the view of dicta of advancement. The palynological criteria in the present study reinforced the treatment of Apocynaceae *s.l.* as two distinct taxonomic families (Apocynaceae and Asclepiadaceae).

**Keywords:** Apocynaceae, Asclepiadaceae, Eurypalynous, Pollen morphology, Pollinarium.

### Introduction

Apocynaceae *s.l.* is a family of flowering plants that contains about 424 genus and 5100 species of evergreen trees, shrubs and herbs (Watson & Dallwitz, 1992; Li Ping-tao et al., 1995, Nazar, 2012; A.P.G., 2016). Tropical, subtropical rain forests or tropical arid environments are the suitable climatic conditions of these species; however, few species grow in temperate areas (Endress, 2000).

A controversy over the taxonomic relationship between the Apocynaceae and Asclepiadaceae persisted ever since. Cronquist (1981, 1988), Dahlgren (1983), Takhtajan (1987) and Rosatti (1989a, 1989b) treated Apocynaceae and Asclepiadaceae as two distinct families, while Judd et al. (1994), Sennblad & Bremer (1996), Struwe et al. (2004) and A.P.G. (2016) considered

them as one large family (Apocynaceae).

The phylogenetic studies supported the reunion of the Apocynaceae *s.s.* and Asclepiadaceae *s.s.* in one family; the Apocynaceae; with five subfamilies *viz.* Rauvolfioideae, Apocynoideae, Periplocoideae, Secamonoideae and Asclepiadoideae (Sennblad & Bremer, 1996; Endress & Bruyns, 2000; Potgieter & Albert, 2001; Endress, 2004; Endress et al., 2007; Livshultz, 2010; A.P.G., 2003, 2009, 2016; Simoes et al., 2010; Nazar, 2012). Rauvolfioideae and Apocynoideae, were previously allocated in Apocynaceae *s.s.*, while Periplocoideae, Secamonoideae and Asclepiadoideae in Asclepiadiaceae *s.s.* based on androecium morphological features and system of pollen transfer (Brown, 1811; Cronquist, 1981, 1988; Takhtajan, 1987).

#Corresponding author emails: alsafa98@hotmail.com; alsafa.alsherif@sci.asu.edu.eg Mobile: +20100-2404084

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In Apocynaceae there are great variation in pollen morphological features (Eurypalynous) *viz.* monad as in Rauvolfioideae and Apocynoideae, tetrad pollinarium (Pseudo- pollinarium) as in Periplocoideae or true pollinarium as in Secamonoideae and Asclepiadoideae (Van der Weide & Van der Ham, 2012; Chatterjee et al., 2014; El-Gazzar et al., 2018a, b). Monads, colporate as in Rauvolfioideae, porate as in Apocynoideae (Endress & Bruyns, 2000) or with psilate-perforate sculpture as in Apocynaceae *s.s.* (Middleton, 2007).

Pseudo-pollinarium is the arrangement of pollen cells in sticky masses of multiporate tetrads forming free pollinia without an outer wall or translator, while the true pollinia are the arrangement of pollen cells in compact sticky masses surrounded by an outer wall (Schill & Jakel, 1978; Kunze, 1993; Swarupandan et al., 1996; Verhoeven & Venter, 2001; Wyatt & Lipow, 2007). Fishbein (2001) mentioned that Periplocoideae (pseudo-pollinarium) is more advanced than Rauvolfioideae and Apocynoideae (monad pollen), and Asclepiadoideae (true pollinia) is more advanced than Rauvolfioideae, Apocynoideae (monad) and Periplocoideae, (tetrad and pseudo-pollinarium). Pollinium characters *viz.* size, shape, colour, breadth and length of pollinium sac, breadth and length of corpusculum, pollinium orientation and attachment of translator (caudicle) are diagnostic features in Asclepiadaceae *s.s.* (Yaseen & Anjum, 2014).

Walker & Doyle (1975) and El-Atroush et al. (2015) have recognized the importance of pollen morphology in the identification and classification of flowering plants. Kuijt & Van der Ham (1997) and Erik & Raymond (2006) recognized some specific pollen characters within 42 *Alstonia* species and 19 species of Apocynaceae respectively. Several authors checked the classification for genera and species of angiosperm by analyzed their results using different numerical programs, e.g. Moawad et al. (2015). El-Gazzar et al. (2018a, b) used the numerical analysis to reveal the relationships between Apocynaceae and Asclepiadaceae according to morphological and pollen grain characters.

The specific objective of the present study is to throw light on the different pollen

morphological characters of the species under investigation, to discuss whether pollen morphology is considered additional fundamental tool that can be of help in explanation of the evolutionary trend within the family.

## **Materials and Methods**

In the present study 19 wild and ornamental species representing four out of five subfamilies of Apocynaceae *s.l.* were collected from different localities and botanical gardens from Egypt and Libya (Table.1, according to Endress et al., 2014; A.P.G., 2016).

The wild species were identified by the aid of Täckholm (1974) and Boulos (2000), while the ornamental species by Bailey (1949). Synonyms were derived from the plant list (working list of all known plant species (<http://www.theplantlist.org/>), GRIN (Germplasm Resource Information Network, <http://www.ars-grin.gov/cgi-bin/npgs/html/index.pl>), and IPNI (The International Plant Names Index, <http://www.ipni.org/ipni/plantnamesearchpage.do>). For LM investigation (BEL: B103 T-PL light microscope), un-acetolyzed pollen grains were taken from the flowers of the species under investigation, fixed in 70% alcohol, the anthers were crushed or opened carefully by needle, mounted on glass slide with few drops drop of glycerin and stained with 4% safranin solution. The microphotographs were taken using digital camera (Canon power-shot A720, 8.0 mega pixels). About seven to ten pollen grains per species were subjected to the measurements. For Scanning Electron Microscope (SEM) investigation, pollen grains were dried, mounted onto stubs then coated with gold by sputter coater (SPI-Module) and tested with (JEOL-JSM 5500 LV) scanning electron microscope at the Regional Center of Mycology and Biotechnology, Al-Zhar University, Cairo, Egypt. The used pollen sculpture patterns were according to Stearn (1992). the pollen terminology in the present study were according to Erdtman (1952) and Punt et al. (2007). For numerical analysis, the recorded palynological characters were coded as binary codes (0, 1) and a dendrogram was constructed using the NTSYS-PC version 2.02 software program (Rohlf, 2002).



TABLE 1. Collection data according to Endress et al. (2014) and A.P.G. (2016).

Sub-family	Species	Source/locality
Rauvolfioideae	<i>Acokanthera oblongifolia</i> (Hochst.) Benth. & Hook.f. ex B.D.Jacks. -- Gen. Pl. [Bentham & Hooker f.] 2(2): 696. 1876 [May 1876]; nom. inval. (IK) = <i>A. spectabilis</i> (Sond.) Hook.f	D
	<i>Alstonia scholaris</i> (L.) R. Br. -- Mem. Wern. Nat. Hist. Soc. 1: 75. 1811 [dt. 1809; issued in 1811] (IK) = <i>Echites scholaris</i> L.	A
	<i>Carissa carandas</i> L. -- Mant. Pl. 52. 1767 [15-31 Oct 1767] (IK) = <i>C. carandas</i> var. <i>congesta</i> (Wight) Bedd.	D
	<i>Carissa macrocarpa</i> (Eckl.) A. DC. -- Prodr. [A. P. de Candolle] 8: 336. 1844 [mid Mar 1844] (IK) = <i>C. praetermissa</i> Kupicha	F
	<i>Cascabela thevetia</i> (L.) Lippold. -- Feddes Repert. 91: 52. 1980 (IK) = <i>Thevetia peruviana</i> (Pers.) K.Schum.	E
	<i>Catharanthus roseus</i> (L.) G.Don. -- Gen. Hist. 4(1): 95. 1837 (IK) = <i>Vinca rosea</i> L.	E
	<i>Cerbera odollam</i> Gaertn. -- Fruct. Sem. Pl. 2: 193. 1791 (IK) = <i>Odollamia malabarica</i> Raf.	C
	<i>Plumeria obtusa</i> L. -- Sp. Pl. 1: 210. 1753(IK) = <i>P. apiculata</i> Urb.	E
	<i>Tabernaemontana divaricata</i> (L.) R. Br. ex Roem. & Schult. -- Syst. Veg., ed. 15 bis [Roemer & Schultes] 4: 427. 1819 (IK) = <i>T. citrifolia</i> Lunan	D
	Apocynoideae	<i>Adenium obesum</i> Roem. & Schult. -- Syst. Veg., ed. 15 bis [Roemer & Schultes] 4: 411. 1819 (IK) = <i>A. arabicum</i> Balf. F
<i>Nerium oleander</i> L. -- Sp. Pl. 1: 209. 1753 [1 May 1753] (IK) = <i>N. carneum</i> Dum.Cours.		E
<i>Wrightia coccinea</i> (Roxb. ex Hornem.) Sims. -- Bot. Mag. 53: t. 2696. 1826 (IK) = <i>Nerium coccineum</i> Roxb. ex Hornem.		C
Asclepiadoideae	<i>Asclepias curassavica</i> L. -- Sp. Pl. 1: 215. 1753 [1 May 1753] (IK) = <i>A. margaritacea</i> Hoffmanns. ex Schult.	F
	<i>Calotropis procera</i> W.T. Aiton. -- Hort. Kew., ed. 2 [W.T. Aiton] 2: 78. 1811 (IK) = <i>C. persica</i> Gand.	H
	<i>Cynanchum acutum</i> L. -- Sp. Pl. 1: 212. 1753 [1 May 1753] (IK) = <i>C. acutum</i> var. <i>longifolium</i> (G.Martens) Ledeb.	B
	<i>Gomphocarpus sinaicus</i> Boiss. -- Diagn. Pl. Orient. ser. 1, 11 : 80. 1849 [Mar-Apr 1849] (IK) = <i>Asclepias sinaica</i> (Boiss.) Muschl	G
	<i>Huernia andreaeana</i> (Rauh) L.C.Leach. -- J. S. African Bot. 40 (1): 21. 1974 (IK) = <i>H. appendiculata</i> Berger.	H
	<i>Solenostemma argel</i> (Delile) Hayne. -- Getreue Darstell. Gew. ix. t. 38.1825. (IK) = <i>S. acutum</i> (L.) Wehmer.	A
Periplocoideae	<i>Cryptostegia grandiflora</i> Roxb. ex R. Br. -- Bot. Reg. 5 : t. 435. 1820 [1819 publ. 1820] (IK) = <i>C. grandiflora</i> Roxb. ex R.Br.	A

A, Agriculture Museum Garden; B, Al-Azhar University; C, Al-Zohriya Garden, Gizzira; Cairo; D, Botanical Garden, Botany Department, Faculty of Science, Ain Shams University, Alabbassia, Cairo; E, Botanical Garden, Botany Department, Al-Zawia University in Libya; F, Orman Botanical Garden, Giza; G, Saint Katherine, South Sinai; H, Western Mountain in Libya.

## Results

In the present study the pollen data of 19 studied species are summarized in Table 2 and the specific structures in Plate I; text Fig. a-p. Pollen grains monad as in 12 studied species (belonging to Rauvolfioideae and Apocynoideae) or pollinarium as in seven studied species (belonging to Asclepiadoideae and Periplocoideae).

For monad pollen grain; shape class; oblate spheroidal & sub-oblate as in *Carissa carandas*, prolate as in *Plumeria obtusa*, prolate spheroidal as in as in four studied species, oblate spheroidal as in the rest six studied species. Pollen size; small in *Alstonia scholaris*, *Nerium oleander* & *Tabernaemontana divaricata*, small-medium as in *Carissa carandas*, medium as five studied species or large as in *Carissa macrocarpa*, *Cerbera odollam* & *Cascabela thevetia*. Pollen class, colpate as in *Catharanthus roseus* & *Plumeria obtusa*, colpate and colporate as in *Carissa carandas*, colporate as in five studied species or porate as in four studied species. Shape of pollen in polar view; circumaperture as in *Nerium oleander* & *Wrightia coccinea* or angulaperture as in the rest ten studied taxa. Shape of pollen in equatorial view; spheroidal & sub-spheroidal as in *Carissa carandas*, elliptic as in *Catharanthus roseus*, subspheroidal in *Cascabela thevetia*, *Wrightia coccinea* or spheroidal in the rest eight studied species. Polarity; apolar as in *Adenium obesum*, *Carissa macrocarpa*, *Nerium oleander* & *Wrightia coccinea* or isopolar as in the rest eight studied species. Aperture; simple as in six studied species, simple and composite as in *Carissa carandas* or composite as in five studied species. Sculptur; glebulate as in *Alstonia scholaris*, scabrate-foveate as in *Cerbera odollam*, foveolate as in four studied species or psilate as in the rest six studied species. Columellae, distinct in all studied species.

For pollinarium; Pollinium shape; spoon-like (pseudo-pollinarium) as in *Cryptostegia grandiflora*, obovate as in *Calotropis procera*, long ovate as in *Solenostemma argel*, ovate as in *Huernia andreaeana* & *Cynanchum acutum* or oblong-ovate as in *Asclepias curassavica* & *Gomphocarpus sinaicus*. Pollinium colour; creamy as in *Calotropis procera*, brown as in *Solenostemma argel*, yellow as in *Asclepias curassavica* & *Gomphocarpus sinaicus* or brownish yellow as in *Cynanchum acutum*,

*Cryptostegia grandiflora* & *Huernia andreaeana*. Pollinium orientation; erect as in *Cynanchum acutum* or pendulous as in *Asclepias curassavica*, *Gomphocarpus sinaicus*, *Calotropis procera*, *Huernia andreaeana* & *Solenostemma argel*. Pollinium – translator attachment; apical as in *Huernia andreaeana*, basal in *Cynanchum acutum*, *Asclepias curassavica*, *Gomphocarpus sinaicus*, *Calotropis procera* & *Solenostemma argel* or wanting as in *Cryptostegia grandiflora*. Pollinium surface sculpture; tuberculate as in *Cryptostegia grandiflora*, reticulate as in *Cynanchum acutum* & *Huernia andreaeana*, colliculate as in *Calotropis procera*, reticulate-foveate as in *Gomphocarpus sinaicus* or psilate in *Asclepias curassavica* & *Solenostemma argel*. Wing; present as in *Huernia andreaeana* or not detected in the rest six studied species.

## Discussion

In the present study the palynological data were coded as binary codes (0, 1) then subjected for computation using the NTSYS-PC version 2.02 software program (Rohlf, 2002). From the obtained dendrogram (Fig. 1), the species under investigation separated under two series; series I and II. Series I comprises 12 out of the studied species (belonging to Rauvolfioideae and Apocynoideae) at a taxonomic distance 0.81 based on the presence of monad pollen grains. Series II comprises the remaining seven studied species (belonging to Asclepiadoideae and Periplocoideae) at taxonomic distance 0.72 based on the presence of pollinarium. The separation of the studied species into series I & II is in accord with Brown (1811), Cronquist (1981, 1988), Dahlgren (1983), Takhtajan (1987) and Rosatti (1989a, b).

Series I divided into two subseries; subseries A and B. Subseries A divided into two clusters; Cluster 1 and 2. The former cluster includes *Carissa carandas* due to the presence of two pollen class; colpate and colporate with simple and composite apertures. Cluster 2 includes five studied species due to sharing in colporate pollen grain with composite apertures. Subseries B divided into two clusters, 3 and 4. The former cluster includes *Catharanthus roseus* and *Plumeria obtusa* due to sharing in colpate pollen and isopolar. Cluster 4 includes four studied species due to sharing in porate pollen and apolar pollen grain.

TABLE 2. Palynological characters of the studied species of Apocynaceae s.l.

A. Monads										
Sp.	C.	Dimension (µm)	Shape class P/E x100	Pollen size 100P+E\	Pollen class	Shape in polar view	Shape in equatorial view	Polarity	Aperture	Sculpture
<i>Acokanthera oblongifolia</i>		P= 31.5 E= 32	Oblate Spheroidal	Medium	Trizono colporate	Angulaperture	Spheroidal	Isopolar	Composite ectoapertures: colpus slit-like with rounded end	Foveolate
<i>Adenium obesum</i>		P= 31.7 E = 34.7	//	//	Pantoporat 4-6	//	//	Apolar	Simple, ectoapertures: circular leveled.	Psilate
<i>Alstonia scholaris</i>		P= 22 E = 23	//	Small	Trizono colporate	//	//	Isopolar	Composite ectoapertures: colpus fusiform with rounded end	Glebulate
<i>Carissa carandas</i>		P =25 E = 26.5	Oblate spheroidal	Medium	Trizono colporate	//	Spheroidal	//	Composite ectoapertures: colpus -fusiform with tapered end	Foveolate
		P =17.5 E = 22	Sub-oblate	Small	Trizono colpate	//	Sub spheroidal	//	Simple ectoapertures: colpus slit-like with rounded end	Foveolate
<i>Carissa macrocarpa</i>		P=47.2 E = 45.4	Prolate Spheroidal	Large	Pantoporat 6-10	//,	spheroidal	Apolar	Simple ectoapertures: circular and leveled	Psilate
<i>Cascabela thevetia</i>		P= 64 E = 64.6	Oblate Spheroidal	//	Trizono colporate	//	Sub spheroidal	Isopolar	Composite ectoapertures: colpus slit-like with rounded end	Foveolate
<i>Catharanthus roseus</i>		P=41 E = 43.3	//	Medium	Trizono colpate	//	Elliptic	//	Simple ectoapertures: colpus slit-like with tapered end,	//
<i>Cerbera odollam</i>		P=73 E = 69	Prolate Spheroidal	Large	Trizono colporate	//	Spheroidal	//	Composite ectoapertures: colpus slit-like with tapered end	Scabrate-foveate
<i>Nerium oleander</i>		P= 24 E = 24	Oblate Spheroidal	Small	Pantoporat 4-6	Circumaperture	//	Apolar	Simple ectoapertures: circular, sunken	Psilate
<i>Plumeria obtusa</i>		P= 37 E = 20	Prolate	Medium	Trizono colpate	Angulaperture	//	Isopolar	Simple ectoapertures: colpus slit-like with rounded end	//
<i>Tabernaemontana divaricata</i>		P= 25.6 E = 23	Prolate spheroidal	Small	Trizono colporate	//	//	//	Composite ectoapertures: colpus short	//
<i>Wrightia coccinea</i>		P= 32.5 E = 30	//	Medium	Pantoporat 4-6	Circumaperture	Sub spheroidal	Apolar	Simple ectoapertures: circular, sunken	//

(//): As previous

TABLE 2 Cont.

Sp.	B. Pollinarium											
	C Length of pollinium sac (µm)	Breadth of pollinium sac (µm)	Length of translator sac (µm)	Breadth of translator sac (µm)	Length of Corpusculum sac (µm)	Breadth of Corpusculum sac (µm)	Shape of pollinium sac	Colors of pollinium	Orientation of pollinium	Translator attachment to the pollinium	Surface sculpture	Wing
<i>Asclepias curassavica</i>	933	346.6	493	133	440	266.6	Oblong-ovate	Yellow	Pendulous	Basal	Psilate	-
<i>Calotropis procera</i>	1035	517.6	411	58.8	470	200	Obovate	Creamy	//	//	Colliculate	//
<i>Cryptostegia grandiflora</i>	1666.6	1145.8	833.3	416.6	-	-	Spoon	Brownish yellow	-	-	Tuberculate	//
<i>Cynanchum acutum</i>	311	194.4	100	55.5	255.5	166.6	Ovate	Brownish yellow	Erect	Basal	Reticulate	//
<i>Gomphocarpus sinaiticus</i>	847	235.2	294	70.5	258.8	82.3	Oblong-ovate	Yellow	Pendulous	//	Reticulate- foveate	//
<i>Huernia andreaeana</i>	323.5	258.8	100	41	176.4	117.6	Ovate	Brownish yellow	//	Apical	Reticulate	+
<i>Solenostemma argel</i>	909	200	300	90.9	345.4	181.8	Long-ovate	Brown	//	Basal	Psilate	-

Small (10-24µm); Medium (25-49µm); Large (50-99µm); Very short (50-199µm); Short (200-399µm); Long (400-599µm); Very long up 600µm; C: Character; Sp.: Species; +: Present; -: Absent.

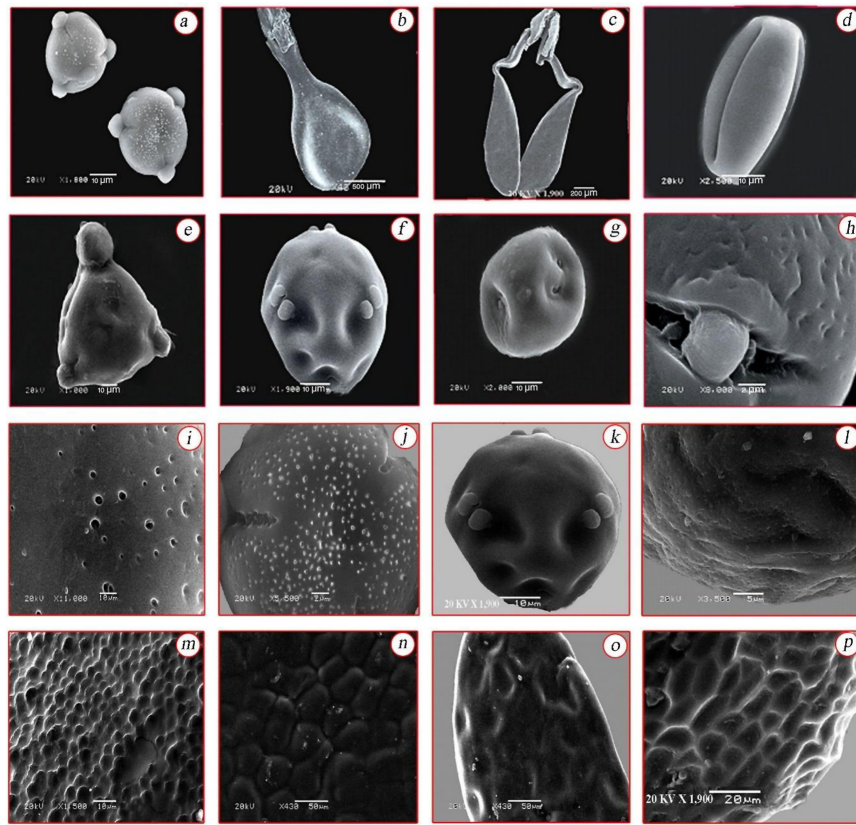


Plate I. (a-p) SEM photomicrograph of pollen morphology [a. Monad pollen in *Alstoniascholaris*; b. Pseudo-pollinium in *Cryptostegia grandiflora*; c. True pollinarium in *Asclepiascurassavica*; d. Colpate pollen in *Plumeriaobtusa*; e. Composite aperture in *Cascabelathevetia*. Porate pollen in *Carissa macrocarpa*; g. Simple aperture in *Adeniumobesum*; h. Composite aperture & isopolar in *Acokantheraoblongifolia*; i. Foveolate sculpture in *Catharanthusroseus*; j. Glebulate in *Alstoniascholaris*; k. Psilate in *Carissa macrocarpa*; l. Scabrate-foveate in *Cerberaodollam*; m. Tuberculate in *Cryptostegia grandiflora*; n. Colliculate in *Calotropisprocera*; o. Reticulate-foveate in *Gomphocarpussinaicus*; p. Reticulate in *Huerniaandreaeana*].

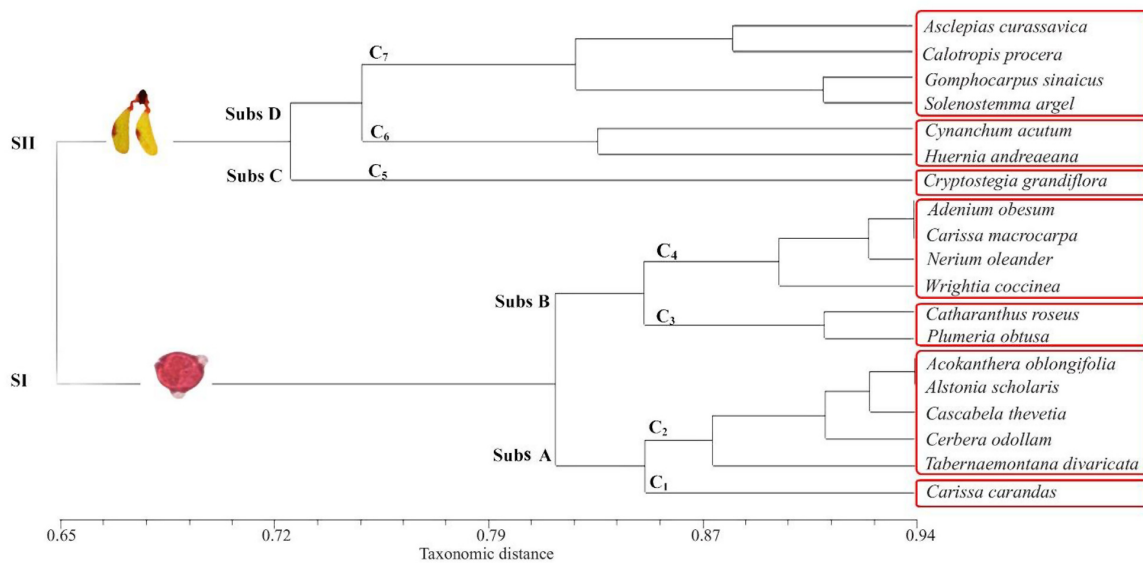


Fig. 1. Dendrogram showing the relationship between the studied species based on pollen criteria [S: Series; Subs: Subseries; C: Cluster].

The separation of series I into two subseries, A & B based on aspect of pollen class indicated that, the pollen class in studied species belonging to Rauvolfioideae show colpate and colpate manner except in *Carissa macrocarpa* (porate pollen class) which gathered with the studied species of Apocynoideae (porate pollen class). This is in accord with Endress & Bruyns (2000), Enderson et al. (2002) and Middleton (2007). Fishbein (2001) stated that Rauvolfioideae is considered the most basal subfamily of Apocynoideae based on pollen class from colpate and colpate vs porate.

Series II divided into two subseries C and D. Subseries C (cluster 5) includes *Cryptostegia grandiflora* (Periplocoideae), due to the presence of pseudo-pollinarium. Subseries D divided into two clusters: 6 & 7 (species with true pollinia). The former cluster includes *Cynanchum acutum* and *Huernia andreaeana* based on small sized pollinia with ovate shape pollinial sac, erect pollinium with basally attached translator (*Cynanchum acutum*) or apical attachment winged pollinarium (*Huernia andreaeana*). Cluster 7 gathered *Asclepias curassavica*, *Calotropis procera*, *Gomphocarpus sinaicus* and *Solenostemma argel*, all are sharing the features of pollinarium with pendulous orientation and basal attachment of translator. Pollinial sac shapes varied from ovate as in *Cynanchum acutum*, oblong ovate as in *Asclepias curassavica*, obovate as in *Calotropis procera* or spoon like as in *Cryptostegia grandiflora*. This is in accord with Mo et al. (2010), and Sinha & Mondal (2011), who stated that, the Asclepiadoideae showed great variation in shape of pollinial sac.

The separation of subseries D into cluster 6 & 7 (on the bases of pollinium orientation and translator attachment) is in agreement with Swarupanandan et al. (1996) and Sinha & Mondal (2011). The position of translators whether basal or apical and orientation of pollinia (erect, horizontal or pendulous) are considered diagnostic features for classification of Asclepiadiaceae s.s. (Brown, 1811; Swarupanandan et al., 1996; Endress & Bruyns, 2000).

The separation of the studied species of series II into two subseries are in accordance with El-Gazzar et al. (1974), Schill & Jäckel (1978),

Arekal & Ramakrishna (1978, 1979, 1980).

From the foregoing pollen criteria in the present study, *Cryptostegia grandiflora* is considered a transition state between the studied species of Rauvolfioideae, Apocynoideae and Asclepiadoideae and this is in accordance with Verhoeven & Venter (2001) and Wyatt & Lipow, (2007). Comparison of the evolutionary trends of the most specific pollen parameters encourage the construction of an evolutionary proposed tentative presentation (Fig. 2) and an artificial key to render identification and separation between the studied species more easily and accurate.

Among taxonomists a great argument has always been arising with respect to the taxonomic character as regard its weight and consistency. For instance, in the present work, the pollen criteria lead to the following diagnostic and evolutionary trends, which can be summarized in the following points through the line of advancement (primitive vs. advanced) based on the dicta of evolution (Bessey, 1915).

1. Monads (Rauvolfioideae and Apocynoideae) vs. true pollinia (Asclepiadoideae) through pseudo-pollinarium as in *Cryptostegia grandiflora* (Periplocoideae) (Verhoeven & Venter, 2001; Wyatt & Lipow, 2007).
2. Colpate pollen vs. colpate vs. porate. *Carissa carandas* (colpate and colpate pollen) is considered as intermediate stage between colpate and porate (new observation and record). In *Carissa macrocarpa* (Rauvolfioideae), the porate pollen encourage the gathering of it with the studied species of Apocynoideae (Walker & Doyle, 1975; Moore et al., 1991).
3. Aperturate pollen is from simple vs. composite (Walker & Doyle, 1975; Moore et al., 1991).
4. Isopolar vs. apolar (Walker & Doyle, 1975).
5. Large vs. small sized pollen (Ezcurra, 1993; Ueckermann & Rooyen, 2000).
6. Sculpture of monad pollen is from psilate vs. scarbate-foveate, vs. foveolate vs. glebulate (weak diagnostic character) (Walker, 1974; Walker & Doyle, 1975; Walker & Skvarla, 1975).

An artificial key of the studied species of Apocynaceae *s.l.* based on pollen characters.

1. Monad	2
+ Pollinarium	13
2. Apolar, porate pollen	3
+ Isopolar, colpate or colporate pollen	6
3. Pollen large sized	<i>Carissa macrocarpa</i>
+ Pollen medium or small sized	4
4. Spheroidal pollen	<i>Nerium oleander</i>
+ Otherwise	5
5. Oblate spheroidal pollen	<i>Adenium obesum</i>
+ Prolate spheroidal pollen	<i>Wrightia coccinea</i>
6. Pollen of two types (colpate&colporate)	<i>Carissa carandas</i>
+ Pollen one type (colpate or colporate)	7
7. Colpate pollen	8
+ Colporate pollen	10
8. Elliptic shape	<i>Catharanthus roseus</i>
+ Spheroidal shape	9
9. Scabrate-foveolate sculpture	<i>Cerbera odollam</i>
+ Psilate sculpture	<i>Plumeria obtusa</i>
10. Small pollen sized	11
+ Medium or large sized pollen	12
11. Glebulate sculpture	<i>Alstonia scholaris</i>
+ silate sculpture	<i>Tabernaemontana divaricata</i>
12. Pollen large sized	<i>Cascabela thevetia</i>
+ Medium sized	<i>Acokanthera oblongifolia</i>
13. Pollinarium winged	<i>Huernia andreaeana</i>
+ Pollinarium wingless	14
14. Pollinarium spoon shape & corpusculum absent	<i>Cryptostegia grandiflora</i>
+ Pollinarium otherwise & corpusculum present	15
15. Pollinium erect	<i>Cynanchum acutum</i>
+ Pollinium pendulous	16
16. Pollinium sculpture tuberculate	<i>Calotropis procera</i>
+ Pollinium sculpture otherwise	17
17. Pollinium sac, brown	<i>Solenostemma argel</i>
+ Pollinium sac, yellow	18
18. Psilate sculpture	<i>Asclepias curassavica</i>
+ Reticulate-foveate sculpture	<i>Gomphocarpus sinaiicus</i>

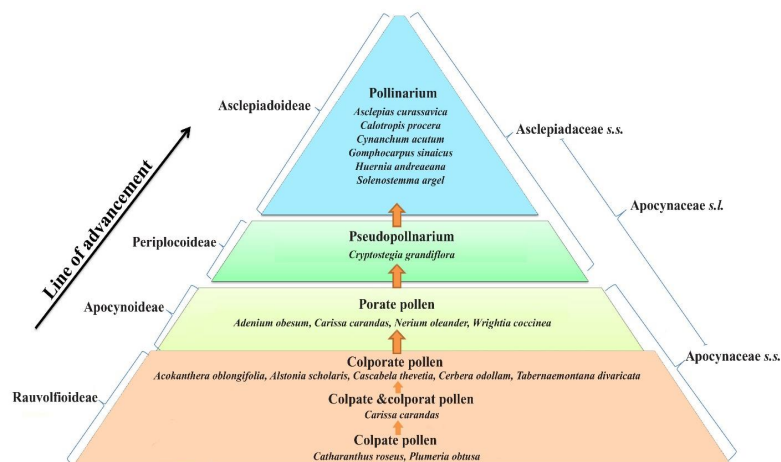


Fig. 2. Proposed schematic presentation illustrating the line of advancement within the studied species based on the pollen class based on the dicta of evolution of Bessey (1915).

## Conclusion

In the present study the most specific pollen characters of the studied species reinforced the treatment of Apocynaceae *s.l.* as two distinct families (Apocynaceae and Asclepiadaceae).

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## مساهمة دلالات حبوب اللقاح في تقييم العلاقات بين بعض الأنواع من الفصيلة السوسيبية بمفهومها الواسع

حنان أبو القاسم سالم دبوب<sup>(1)</sup>، محمد عبد الفتاح سالم<sup>(1)</sup>، أسامة كمال عبد الحميد<sup>(1,3)</sup>، محمد السيد طنطاوي<sup>(1)</sup>، الصفا حسن محمد<sup>(1)</sup>

<sup>(1)</sup> قسم النبات - كلية العلوم - جامعة عين شمس - القاهرة - مصر، <sup>(2)</sup> قسم الاحياء - كلية التربية - جامعة الزاوية - ليبيا، <sup>(3)</sup> قسم الاحياء - كلية العلوم - جامعه طيبة - المملكة العربية السعودية.

تعتبر الفصيلة الدفلية بمفهومها الواسع من الفصائل الجاذبة للإهتمام إستنادا لتنوع اشكال حبوب اللقاح. وقد شملت هذه الدراسة حبوب لقاح لتسعة عشر نوعا (تنتمي لأربعة تحت فصائل وثمانية عشر جنسا). تم تجميع وفحص صفات حبوب اللقاح باستخدام الميكروسكوب الضوئي والالكترونى الماسح. تهدف الدراسة إلى إلقاء الضوء على التباين في صفات حبوب اللقاح ومدى مساهمتها في الفصل بين الانواع قيد الدراسة و تقييم الوضع التصنيفى للفصيلة الدفلية بمفهومها الواسع. وقد خلصت الدراسة إلى مجموعة من الصفات التشخيصية على سبيل المثال: أشكال، تراكيب وتجمعات حبوب اللقاح، الزركشة، التباين في الفتحات والثقوب على السطح الخارجى وكذلك إتجاه وطريقة ربط الناقل في البولينيوات. وقد أظهرت صفات حبوب اللقاح في نوع *Carissa macrocrpa* التابعة لمجموعة (Rauvolfioideae) ضمها مع الأصناف المدروسة في مجموعة (Apocynoideae) بناءا على طريقة التثقيب على سطح الخارجى. كما أظهر شكل البولينيا في نوع *Cryptostegia grandiflora* حالة ربط بين الأنواع منفردة حبوب اللقاح (Monads) التابعة لتحت الفصيلة (Apocynoideae & Rauvolfioideae) و متجمعة حبوب اللقاح فى شكل بولينيا (Pollinia) التابعة لـ (Asclepiadoideae). تم إخضاع الصفات المستخلصة لبرنامج (NTSY, 2.02) والتحصل على شجرة تصنيفية بالإضافة إلى عمل رسم توضيحي تطورى وتصميم مفتاح اصطناعى لمناقشة العلاقات بين الأنواع المدروسة. وقد خلصت الدراسة إلى إعتبار الفصيلة الدفلية بمفهومها الواسع وحدتين تصنيفيتين منفصلتين (الفصيلة الدفلية والعشارية).

# **POLLEN ATAU SERBUK SARI : ASPEK MORFOLOGI, SISTEMATIKA DAN APLIKASINYA PADA TUMBUHAN KELUARGA MENTOL**

Sudarmono dan Sahromi  
Pusat Konservasi Tumbuhan – Kebun Raya Bogor, LIPI  
Jl. Ir. H. Juanda No. 13 Bogor 16003  
Phone/Fax. 0251-8322187  
e-mail : [s\\_darmono@yahoo.com](mailto:s_darmono@yahoo.com)

## **ABSTRACT**

### ***Pollen Powder or Sari : Aspects of Morphology, Systematics and Application on Menthol Family Plant***

*Pollen is the important component of plant to develop through reproductive. Pollen is the male organ of plants that plays an important role in the process of the evolution of plants. Menthol family plants (the Family Lamiaceae) is one of biggest families after Asteraceae. The process of the cross breeding often dominates the process of the evolution to the ment al Family. The research on the menthol Family's pollen aimed to know the affinity and the process of his pollination. The form of pollen of the Family Lamiaceae, was round and hexacolpate, the form was the same as the species member with their relatives. In the process of pollination often helped by the bee where pollen that clung to the abdomen part and the chest of the bee and moved to the other flower where the cross-pollination happen. The process of the cross-pollination happened also because of the same of maturity time between pollen of male and the stigma surface of female. The seed was still being the dominant factor in the reproductive in the Family Lamiaceae.*

*Key words : Pollen, Pollination, Lamiaceae, the Mint family, the bee, the seed*

## **ABSTRAK**

Serbuk sari atau dikenal dengan pollen merupakan komponen penting tanaman untuk berkembang melalui reproduktif. Serbuk sari merupakan organ jantan pada tumbuhan yang berperan penting dalam proses evolusi tumbuhan. Tumbuhan Keluarga Mentol (Famili Lamiaceae) merupakan salah satu Famili yang terbesar setelah Asteraceae. Proses perkawinan silang banyak mendominasi proses evolusi pada Keluarga Mentol. Penelitian terhadap serbuk sari Keluarga Mentol bertujuan untuk mengetahui kekerabatan dan proses penyerbukannya. Bentuk morfologi serbuk sari pada Famili Lamiaceae, yaitu bulat dan heksakolpat (hexacolpate), bentuk yang sama dengan jenis – jenis anggota Famili Lamiaceae. Pada proses penyerbukan banyak dibantu oleh lebah dimana pollen yang menempel pada bagian perut dan dada lebah penyerbuk dan berpindah pada bunga yang lain sehingga terjadi penyerbukan silang. Proses penyerbukan silang terjadi juga karena adanya waktu pemasakan yang sama antara serbuk sari sebagai organ jantan dan kepala putik sebagai organ betina. Biji masih merupakan faktor yang dominan pada perbanyakannya Famili Lamiaceae.

Kata kunci : Serbuk sari, Pollen, Lamiaceae, Keluarga Mentol, Lebah, biji.

## **PENDAHULUAN**

Pollen adalah serbuk kasar yang mengandung benih tanaman microgametophytes, yang menghasilkan gamet jantan (sel sperma). Serbuk sari memiliki mantel keras yang melindungi sel-sel sperma selama proses gerakan mereka antara benang sari ke putik tanaman berbunga atau dari kerucut jantan (cone) untuk betina pada organ reproduksi

tanaman konifer. Ketika serbuk sari di putik kompatibel pada tanaman berbunga, maka berkecambah dan menghasilkan tabung polen yang mentransfer sperma ke ovula dari ovarium reseptif. Transfer serbuk sari terhadap struktur reproduksi wanita (putik dalam angiosperma) disebut penyerbukan. Transfer ini bisa dimediasi oleh angin (anemophilous) pada serbuk sari yang sangat ringan. Tanaman berbunga Anemophilous umumnya

memiliki bunga mencolok. Tanaman entomophilous menghasilkan serbuk sari yang relatif berat, lengket dan kaya protein dan untuk penyebarannya oleh serangga penyerbuk. Banyak serangga dan beberapa tungau yang khusus untuk memakan serbuk sari, dan disebut palynivores.

Butir tepung sari ketika ditempatkan pada stigma, di bawah keadaan yang menguntungkan, akan membentuk suatu tabung polen (pollen tube) yang tumbuh menuju ke ovarium, dan membuat jalan sepanjang plasenta ke mulut ovula. Inti sel tabung akan membentuk sel – sel sperma.

Penelitian ini bertujuan untuk mengetahui secara jelas morfologi serbuk sari atau pollen sebagai organ reproduksi jantan dan proses penyerbukannya khususnya pada tanaman Keluarga Mentol.

## BAHAN DAN METODE

Sampel serbuk sari atau pollen dari anggota Keluarga Mentol (Famili Mint atau Lamiaceae / Labiatae), yaitu *Orthosiphon aristatus* dan *O. sp* yang berasal dari Papua Barat dipasang pada slide mikroskop dan diperiksa menggunakan mikroskop cahaya di Laboratorium kultur jaringan Kebun Raya Bogor dan mikroskop elektron scanning (SEM) di Laboratorium Zoologi, Cibinong Science Centre. Setelah serbuk sari diidentifikasi, kemudian diplot pada diagram serbuk sari, yang kemudian digunakan untuk interpretasi. Metode yang digunakan dalam pembuatan preparat ini adalah acetolisis yang merupakan pelisisan dengan menggunakan asam. Bagian yang dilisis adalah kotoran pada dinding – dinding serbuk sari agar bersih sehingga mudah diamati. Pelisisan terjadi pada waktu merendam serbuk sari pada Asam Acetat Glisial (AAG). Fungsi sentrifus (pengocokan) dengan Asam Acetat dan Sulfat adalah untuk mengendapkan serbuk sari, sehingga mudah untuk memisahkannya dari kotoran pada waktu pergantian cairan. Proses ini dapat dilakukan beberapa kali sampai serbuk sari dapat benar – benar bersih dari kotoran. Setelah itu diwarnai dengan safranin dan

ditutup dengan gelas penutup yang sebelumnya serbuk sari ditetesi dengan gliserin jeli sebagai perekat dan setiap sudut gelas penutup diberi sedikit potongan kecil parafin. Penutupan dilakukan dengan hati – hati untuk memperkecil kemungkinan timbul gelembung.

Perbandingan morfologi digunakan pada marga lain sesama anggota Famili Lamiaceae, yaitu marga *Scutellaria* dan marga *Leonotus* dari referensi Jurnal Internasional. Serbuk sari diperiksa dengan mikroskop elektron pemindai (SEM), dan perwakilan terbaik difoto secara umum dan rinci. Pada setiap sampel, 50 serbuk sari diukur dalam rangka untuk mendapatkan nilai – nilai ukuran maksimum, minimum dan rata – rata. Pengamatan juga dilakukan pada terjadinya tabung pollen atau pollen tube.

Ukuran serbuk sari dibedakan dalam enam kelas, berdasarkan aksis terpanjang (kecuali pada serbuk sari yang ekinat, maka durinya tidak dimasukkan dalam ukuran). Pembagian kelas ukuran tersebut adalah :

< 10 $\mu\text{m}$	=	sangat kecil
10 - 25 $\mu\text{m}$	=	kecil
25 - 50 $\mu\text{m}$	=	sedang
50 – 100 $\mu\text{m}$	=	besar
100 - 200 $\mu\text{m}$	=	sangat besar
> 200 $\mu\text{m}$	=	raksasa.

Terminologi pollen mengikuti Faegri dan Iversen (1989) dan Punt et al. (1994).

## HASIL DAN PEMBAHASAN

### Morfologi, anatomi dan kandungan isi pollen

Serbuk sari atau pollen merupakan komponen seksual jantan pada tumbuh – tumbuhan. Serbuk sari mempunyai kandungan protein yang tinggi. Bentuk morfologi serbuk sari biasanya simetris, isopolar, oblate-spheroidal sampai prolate-spheroidal atau sub-prolate sampai sub-oblate (Perveen & Qaiser, 2003). Dinding serbuk sari Angiospermae terdiri dari dua

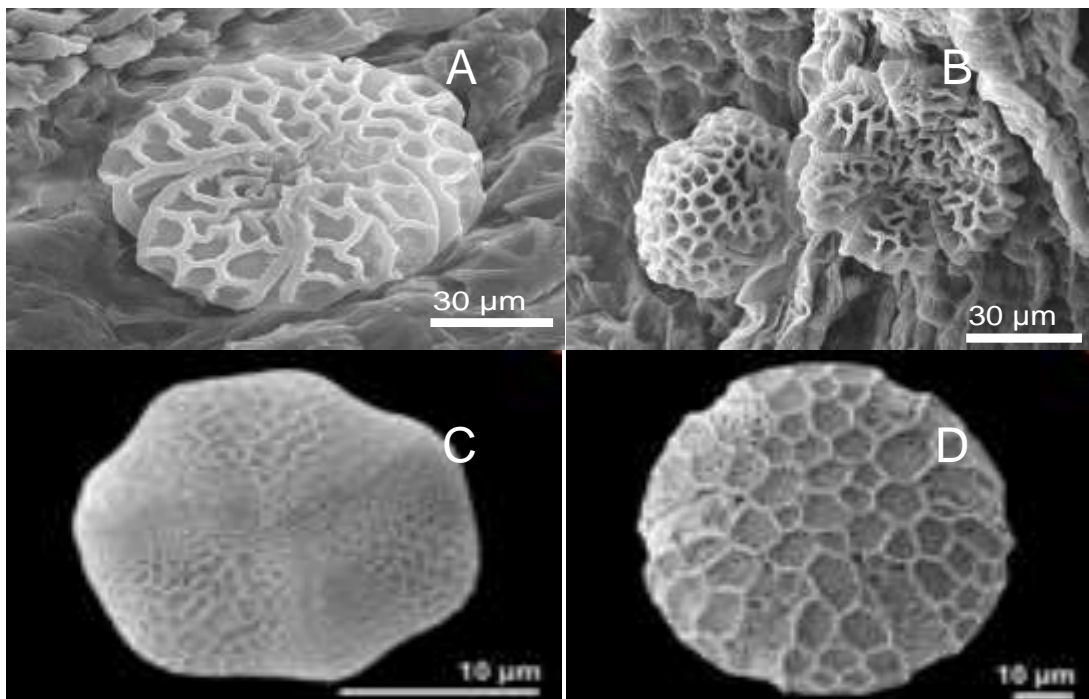
lapisan : eksin (lapisan luar) dan intin (lapisan dalam). Eksin tersusun atas sporopolenin, sedangkan intin tersusun atas selulosa. Lebih lanjut eksin terbagi atas dua lapisan, yaitu seksin dan neksin. Seksin merupakan lapisan yang memiliki ornamentasi, sedangkan neksin tidak.

Struktur dinding serbuk sari, khususnya bagian eksin, merupakan salah satu karakter yang digunakan dalam identifikasi. Struktur halus eksin dapat dibedakan menjadi tiga tipe, yaitu: tektat, semitektat, dan intektat. Serbuk sari umumnya 3 – 8 kolpat (*colpate*), jarang kolporat (*colporate*). Serbuk sari pada *Orthosiphon aristatus* dan *O. sp.* mempunyai ukuran berturut turut 90 $\mu$ m dan 60 $\mu$ m, sedangkan pada *Scutellaria baicalensis* dan *Ocimum basilicum* berturut turut 20  $\mu$ m dan 60  $\mu$ m (Gambar 1). Pada marga *Orthosiphon* dan *Ocimum basilicum* dapat dikategorikan termasuk serbuk sari yang berukuran besar, sedangkan *Scutellaria baicalensis*

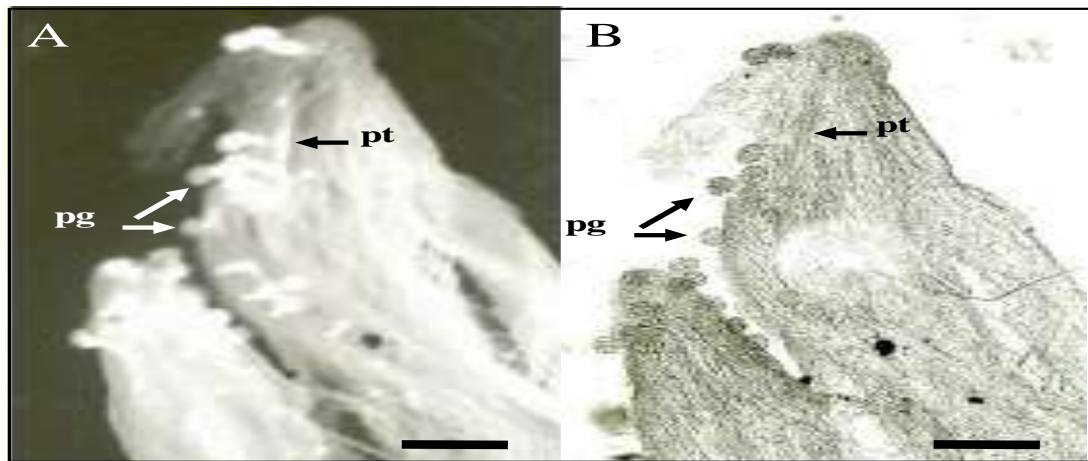
termasuk kecil. Akan tetapi pada keempat taksa tersebut mempunyai bentuk yang sama, yaitu heksacolpat dan bentuk ini umum pada famili Lamiaceae (Gençay, *et al.* 2008).

Ornamentasi dari eksin secara sistematika memberikan informasi sistematika kekerabatan yang jelas.

Berdasarkan data palinologi maka nilai sistematika ciri – ciri morfologi serbuk sari pada famili Lamiaceae dapat untuk mengevaluasi kekerabatan pada anggota famili Lamiaceae. Karena penelitian ini dilakukan pada semua anggota famili Lamiaceae, maka famili ini tergolong euripalineous (famili yang anggota jenisnya memiliki variasi morfologi serbuk sari) (Moon, *et al.* 2008). Meskipun setiap jenis menunjukkan variasi morfologi, tetapi juga terdapat persamaan – persamaan yang dapat dijadikan dasar untuk pemisahan atau pengelompokan setiap jenis tumbuhan tersebut.



Gambar 1. Serbuk sari Kumis kucing (*Orthosiphon aristatus*) (A); *Orthosiphon* sp. dari Papua Barat (B); *Scutellaria baicalensis* (C) dan *Ocimum basilicum* (D).



Gambar 2. Serbuk sari *Scutellaria slametensis* yang berkecambah membentuk tabung pollen pada permukaan kepala putik terlihat pada mikroskop Florescensis (A) dan gambar kontras (B). Pg = butir serbuk sari; pt = tabung pollen. Skala berukuran 100 mikrometer.

### Proses persilangan dan implementasinya pada pemuliaan tanaman

Pada kondisi receptive (matang dan siap dibuahi) maka permukaan kepala putik (stigma) akan mengeluarkan lendir atau bahan perekat sehingga bila ada serbuk sari maka akan menempel (Rodriguez-Rian and Dafni, 2006). Pada masa ini maka serbuk sari akan mudah menempel erat selain itu meskipun terdapat ratusan serbuk sari namun hanya beberapa yang tumbuh tabung pollennya atau *pollen tube*-nya (Gambar 2). Tabung pollen ini akan memanjang mengikuti saluran organ betina atau tangkai putik dan menuju ovula atau kandung telur. Selanjutnya proses pembuahan terjadi membentuk endosperma yang selanjutnya akan membentuk biji. Biji sebagai alat reproduksi dari suatu tumbuhan yang akan tumbuh sebagai keturunan dari proses penyerbukan jenis jantan atau serbuk sari dengan jenis betina atau kepala putik yang satu jenis. Varietas yang mempunyai morfologi baik warna daun atau warna bunga yang berbeda dapat menghasilkan

hibrid atau keturunan yang merupakan kombinasi dari kedua varietas tersebut.

### KESIMPULAN

Serbuk sari atau pollen mengandung bahan protein dan bentuk morfologi serbuk sari mirip satu sama lain pada Keluarga yang sama, yaitu berbentuk heksacolpat seperti pada serbuk sari Famili Lamiaceae atau Keluarga Mentol. Serbuk sari yang kompatibel akan membentuk tabung pollen (*pollen tube*) pada kepala putik atau *stigma* (organ betina) dan menuju ovula sehingga terbentuk biji. Pada Keluarga Mentol yang berpotensi tanaman hias bisa dilakukan penyerbukan buatan untuk membentuk hibrid hasil persilangan.

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## KARAKTERISASI DAN KEKERABATAN TUMBUHAN MANGROVE *RHIZOPHORACEAE* BERDASARKAN MORFOLOGI, ANATOMI DAN STRUKTUR LUAR SERBUK SARI

Budi Irawan<sup>1</sup>, Sahal Muadz<sup>1</sup> dan Adrian Rosadi<sup>1</sup>

<sup>1</sup>Jurusan Biologi FMIPA UNPAD  
Jl Raya Bandung Sumedang KM 21 Jatinangor, Sumedang, 45353  
Email: [budi\\_irawan@unpad.ac.id](mailto:budi_irawan@unpad.ac.id)

### ABSTRAK

**KARAKTERISASI DAN KEKERABATAN TUMBUHAN MANGROVE *RHIZOPHORACEAE* BERDASARKAN MORFOLOGI, ANATOMI DAN STRUKTUR LUAR SERBUK SARI.** Penelitian ini bertujuan untuk mengetahui karakterisasi dan kekerabatan jenis-jenis tumbuhan mangrove *Rhizophoraceae* berdasarkan ciri morfologi, anatomi dan struktur luar serbuk sari. Bahan penelitian berasal dari koleksi specimen Herbarium Jatinangor (BUNP) sebanyak 34 nomor koleksi, terdiri dari 7 jenis yaitu *Bruguiera gymnorrhiza* (L.) Lamk, *B. parviflora* (Roxb.) Wight & Arnold ex. Griffith, *B. sexangula* (Lour.) Poir, *Ceriops decandra* (Griff.) Ding Hou, *C. tagal* C. B Robinson, *Rhizophora mucronata* Lamk. dan *R. apiculata* Bl. Metode yang dilakukan dalam penelitian ini adalah metode kualitatif bersifat deskriptif analisis, meliputi pengumpulan dan pengelompokan spesimen herbarium, pengamatan morfologi, pengamatan anatomi melalui pembuatan preparat semi permanen, preparasi polen, penyusunan pertelaan dan kunci identifikasi serta melakukan analisis kekerabatan. Hasil penelitian menunjukkan bahwa karakter morfologi yang dapat digunakan untuk membedakan jenis-jenis tumbuhan mangrove *Rhizophoraceae* adalah bentuk tepi daun, bentuk ujung daun, tata susun letak daun, posisi kelopak bunga saat muncul hipokotil, jumlah kelopak bunga, tipe bunga, tipe mahkota bunga, dan warna kelopak bunga, sedangkan karakter anatomi adalah kerapatan stomata, bentuk dan ukuran sel epidermis, serta karakter struktur luar polen adalah bentuk dan ukuran polen. Berdasarkan karakter morfologi dan struktur luar polen dapat disusun kunci indentifikasi 7 jenis *Rhizophoraceae*, sementara karakter anatomi tidak dapat digunakan untuk menyusun kunci identifikasi. Kekerabatan dengan menggunakan software NTSys PC version 2.0 membagi 7 jenis *Rhizophoraceae* menjadi 2 cabang. Cabang 1 terdiri dari jenis-jenis *Bruguiera* dan cabang 2 terdiri dari jenis-jenis *Ceriops* dan *Bruguiera*.

**Kata kunci:** karakterisasi, kekerabatan, Mangrove, *Rhizophoraceae*

### ABSTRACT

**Characterization and Relationship of *Rhizophoraceae* Mangrove Plant Based on Morphological, Anatomical and Outer Pollen Structure Characters.** The research aims to determine the characterization and relationship of mangrove species *Rhizophoraceae* based on morphological, anatomical, and structure of pollen has been carried out. Collection of research material from Herbarium specimens Jatinangor (BUNP) collection number as many as 34, consists of seven species, namely as *Bruguiera gymnorrhiza* (L.) Lamk, *B. parviflora* (Roxb.) Wight & Arnold ex. Griffith, *B. sexangula* (Lour.) Poir, *Ceriops decandra* (Griff.) Ding Hou, *C. tagal* C. B Robinson, *Rhizophora mucronata* Lamk. and *R. apiculata* Bl. The method is performed in this study is a qualitative method and descriptive analysis, covering the collection and grouping of herbarium specimens, observation of morphological, anatomical observations through making semi-permanent preparations, pollen preparation, preparation of plant description, key identification and relationship analysis. The results showed that the morphological characters that can be used to distinguish the species of mangrove

*Rhizophoraceae are leaf-margin, leaf-tip, phyllotaxis, petal position now appears hypocotil, the number of flower petals, flower type, type petals, and color of petals, while the character of the anatomy are the density of stomata, shape and size of epidermal cells, as well as the character of the outer pollen structure are pollen-shape and pollen-size. Based on morphological characters and outer pollen structure can be arranged key identification, while anatomical characters cannot be used to develop identification keys. Relationship with the PC version 2.01 software NTSys divided Seven species of Rhizophoraceae into 2 branches. The first branch consists of the species of Bruguiera and the second branch consists of the species of Ceriops and Bruguiera.*

**Key words:** *Characterization, Relationship, Mangrove, Rhizophoraceae*

## 1. PENDAHULUAN

Mangrove didefinisikan sebagai tumbuhan atau komunitas yang terdapat di daerah pasang surut, juga didefinisikan sebagai formasi tumbuhan daerah litoral yang khas di pantai daerah tropis dan subtropis yang terlindung [1]. Vegetasi mangrove secara khas memperlihatkan adanya pola zonasi [1]. Hal ini berkaitan erat dengan tipe tanah, keterbukaan, dan salinitas serta pengaruh pasang surut. Kondisi salinitas sangat berpengaruh terhadap komposisi mangrove. Beberapa jenis mangrove mengatasi kadar salinitas dengan cara menghindari penyerapan garam dari media tumbuhnya secara selektif, sementara beberapa jenis lainnya mampu mengeluarkan garam dari kelenjar khusus pada daunnya. Mangrove memiliki fungsi sebagai penangkap sedimen di daerah estuaria, penahan gelombang aberasi, tempat asuhan dan meanvari makan berbagai jenis biota laut, sebagai sumber bahan obat, racun ikan dan penyamak.

Tumbuhan mangrove yang terdapat di Indonesia berjumlah 43 jenis mangrove sejati. Di seluruh dunia tercatat 60 jenis tumbuhan mangrove sejati dan dengan demikian Indonesia memiliki keanekaragaman jenis tumbuhan mangrove yang cukup tinggi. Salah satu suku tumbuhan mangrove adalah kelompok *Rhizophoraceae* yang memiliki karakteristik berupa akar tunjang akar papan ataupun akar lutut. Selain itu memiliki hipokotil yang sudah berkecambah ketika masih berada di pohon, sehingga suku ini relatif lebih mudah dikembangbiakkan untuk revegetasi wilayah pesisir.

Perkembangan taksonomi untuk kepentingan klasifikasi dan filogeni dapat diperoleh dari berbagai sumber. Karena seluruh bagian dari tumbuhan pada berbagai tahap perkembangannya dapat menyediakan karakter taksonomi, data harus berasal dari berbagai bidang. Penggunaan informasi dari

perbandingan anatomi, embriologi, palinologi, sitogenetika, kimia, dan yang lainnya telah memberikan kontribusi yang besar bagi klasifikasi tumbuhan modern [2]. Walaupun demikian penggunaan karakter morfologi dan anatomi memberikan kontribusi yang besar dalam menunjukkan tingkat keragaman dan kemudahan dalam identifikasi.

Struktur polen yang bervariasi menunjukkan karakter yang dapat digunakan untuk identifikasi, konstruksi klasifikasi, atau interpretasi filogenetik. Secara ringkas, identifikasi tumbuhan adalah menentukan persamaan dan perbedaan antara dua unsur tumbuhan. Tumbuhan yang belum diketahui jenisnya biasanya diidentifikasi dengan kunci identifikasi, atau dibandingkan dengan spesimen herbarium yang telah diketahui [2].

Herbarium Jatiningor merupakan salah satu sarana untuk menyimpan spesimen tumbuhan dari berbagai daerah, serta mendapatkan informasi mengenai berbagai jenis tumbuhan dan vegetasi. Herbarium ini menyimpan spesimen mangrove yang berasal dari wilayah pesisir di beberapa daerah di Indonesia, yaitu Pulau Jawa, Kepulauan Riau, Sulawesi, Sumbawa dan Papua. Berdasarkan jumlah koleksi yang ada di Herbarium Jatiningor, suku *Rhizophoraceae* memiliki nomor koleksi spesimen yang paling banyak. Untuk itu pada penelitian ini akan dilakukan karakterisasi dan kekerabatan dari suku *Rhizophoraceae*.

Penelitian dilakukan dengan tujuan untuk memberikan karakterisasi jenis-jenis mangrove *Rhizophoraceae*, sehingga dari karakter yang diperoleh dapat dijadikan dasar dalam mengidentifikasi tumbuhan dan mengelompokkan jenis-jenis mangrove *Rhizophoraceae*. Hasil penelitian ini diharapkan dapat menjadi dasar dalam mengenal dan memanfaatkan mangrove *Rhizophoraceae* khususnya dalam revegetasi wilayah pesisir di Indonesia. Selain itu dari koleksi spesimen yang ada dapat dijadikan dasar

referensi dan identifikasi tumbuhan mangrove.

## 2. TATA KERJA (BAHAN DAN METODE)

Metode yang dilakukan dalam penelitian ini adalah metode kualitatif bersifat deskriptif analisis, meliputi pengumpulan dan pengelompokan spesimen herbarium, pengamatan morfologi [3]; pengamatan anatomi melalui pembuatan preparat semi-permanen [4,5]; preparasi polen [6]. Penyusunan pertelaan [7,8]. Berdasarkan ciri tersebut disusun kunci identifikasi [3]. Hubungan kekerabatannya dapat diketahui dengan pengkodean ciri, yang selanjutnya diolah dengan menggunakan program NTSYSp version 2.0 [9,10].

## 3. HASIL DAN PEMBAHASAN

### 3.1. Koleksi Jenis-jenis suku Rhizophoraceae di Herbarium Jatinangor

Koleksi jenis-jenis dari suku Rhizophoraceae yang diamati di Herbarium Jatinangor sebanyak 34 nomor koleksi, terdiri dari 7 jenis yaitu *Bruguiera gymnorrhiza* (L.) Lamk, *B. parviflora* (Roxb.) Wight & Arnold ex. Griffith, *B. sexangula* (Lour.) Poir, *Ceriops decandra*(Griff.) Ding Hou, *C. tagal* C. B Robinson, *Rhizophora mucronata* Lamk. dan *R. apiculata* Bl. Umumnya jenis-jenis Rhizophoraceae yang dikoleksi berasal dari wilayah Indonesia Timur (Sulawesi dan Papua), namun beberapa diantaranya berasal dari wilayah Indonesia Barat (Kepulauan Riau) (Tabel 1).

Tumbuhan mangrove Rhizophoraceae terdiri dari dari 4 marga yaitu *Bruguiera*, *Ceriops*, *Kandelia* dan *Rhizophora* [11]. Namun, tumbuhan mangrove Rhizophoraceae yang dikoleksi oleh Herbarium Jatinangor baru tiga marga. Untuk pengamatan morfologi, anatomi dan struktur luar polen hanya dilakukan terhadap tiga marga yaitu, *Bruguiera*, *Ceriops* dan *Rhizophora*.

*Bruguiera* dan *Ceriops* ditemukan tersebar di India, Madagaskar, bagian utara Australia, dan seluruh wilayah Indonesia [12].

Sedangkan *Rhizophora* memiliki wilayah penyebaran yang lebih luas, yaitu Sampai ke benua Afrika dan Amerika [12]. Tomlinson berpendapat bahwa spesies mangrove awalnya berasal dari kawasan Indo-Malaysia. Spesies Mangrove dapat terdispersal ke wilayah lain karena propagul dan bijinya memiliki kekhasan

dapat mengapung dan terbawa arus laut ke area yang luas dan jauh dari asalnya.

**Tabel 1. Koleksi Jenis-jenis dari suku Rhizophoraceae di Herbarium Jatinangor**

No.	Nama Jenis	No. Koleksi	Lokasi
1.	<i>Bruguiera gymnorrhiza</i> (L.) Lamk.	BI 035, BI 014, BI 918, BI 1106, BI 1007, BI 1006	Papua, Sulawesi, Kepulauan Riau
2.	<i>B. parviflora</i> (Roxb.) Wight & Arnold ex. Griffith	BI 1145, BI 1146	Papua, Sulawesi
3.	<i>B. sexangula</i> (Lour.) Poir	BI 1127, BI 1131	Papua
4.	<i>Ceriops decandra</i> (Griff.) Ding Hou	BI 50, BI 1103, BI 1113, BI 981, BI 1005, BI 1010	Papua, Sulawesi
5.	<i>C. tagal</i> C. B Robinson	BI 1152, BI 1153	Papua
6.	<i>Rhizophora mucronata</i> Lamk.	BI & SS 35, BI 871, BI 886, BI 907, BI 996, BI 1112, BI 853, BI 938, BI 983, BI 941, BI 1103, BI & SS 011, BI 1008	Papua, Sulawesi, Kepulauan Riau
7.	<i>R. apiculata</i> Bl.	BI 1108, BI 1111, BI 1088	Papua, Sulawesi

### 3.2. Karakter Morfologi

Karakter morfologi yang dapat membedakan jenis-jenis Rhizophoraceae adalah bentuk ujung daun, tata susun letak daun, posisi kelopak bunga saat muncul hipokotil, jumlah kelopak bunga, tipe bunga, warna kelopak bunga, dan tipe mahkota bunga.

### 3.3. Karakter Anatomi

Karakter anatomi yang diamati adalah bentuk stomata, ukuran panjang stomata,

kerapatan stomata, serta bentuk dan ukuran sel epidermis. Stomata pada jenis-jenis dalam suku Rhizophoraceae bertipe anomositik [13]. Ciri khas dari tipe anomositik adalah sel penutup dikelilingi sel tetangga yang jumlahnya tidak tentu dan bentuk sel tetangga sama dengan bentuk sel epidermis. Hasil perhitungan rata-rata kerapatan stomata pada ketujuh jenis suku Rhizophoraceae, didapatkan hasil yang beragam [14]. Rata-rata kerapatan stomata *B. gymnorrhiza* adalah  $124,83/\text{mm}^2$ ; *B. parviflora*  $112,10/\text{mm}^2$ ; *B. sexangula*  $76,43/\text{mm}^2$ ; *C. decandra*  $70,32/\text{mm}^2$ ; *C. tagal*  $40,76/\text{mm}^2$ ; *R. apiculata*  $78,98/\text{mm}^2$ ; *R. mucronata*  $97,49/\text{mm}^2$ . Ciri kerapatan stomata seringkali digunakan untuk membedakan jenis-jenis tanaman dalam satu marga [15].

Rata-rata kerapatan stomata tertinggi terdapat pada *B. gymnorrhiza* ( $124,83/\text{mm}^2$ ), sedangkan rata-rata kerapatan stomata terendah terdapat pada *C. tagal* ( $40,76/\text{mm}^2$ ). Nilai rata-rata kerapatan stomata dapat disederhanakan untuk memudahkan pengelompokkan dalam analisis data. Rata-rata kerapatan stomata dibagi menjadi tiga sifat ciri, yaitu kerapatan stomata lebih kecil dari  $50/\text{mm}^2$ , diantara  $50/\text{mm}^2$  dan  $100/\text{mm}^2$  serta lebih besar dari  $100/\text{mm}^2$ . Kerapatan stomata  $<50/\text{mm}^2$  terdapat pada *C. tagal*, kerapatan stomata diantara  $50/\text{mm}^2$  dan  $100/\text{mm}^2$  terdapat pada *B. sexangula*, *C. decandra*, *R. apiculata* dan *R. mucronata* sedangkan kerapatan stomata  $>100/\text{mm}^2$  terdapat pada *B. gymnorrhiza* dan *B. parviflora*. Bentuk sel epidermis dapat dikelompokkan menjadi empat bentuk sel yaitu menyegi empat, menyegi lima, menyegi enam dan menyegi tujuh. Bentuk sel pada permukaan atas menyegi lima, menyegi enam dan menyegi tujuh terdapat pada jenis *B. gymnorrhiza*, *B. parviflora*, *C. tagal* dan *R. mucronata*; bentuk epidermis menyegi empat, menyegi lima dan menyegi enam terdapat pada *C. decandra*; sedangkan bentuk epidermis menyegi lima dan menyegi enam terdapat pada *B. sexangula* dan *R. apiculata*.

Bentuk sel epidermis pada permukaan bawah menyegi lima, menyegi enam, dan menyegi tujuh terdapat pada *B. gymnorrhiza*, *B. sexangula*, *C. tagal*, *R. mucronata*; bentuk epidermis menyegi empat, menyegi lima dan menyegi enam terdapat pada *C. decandra*; bentuk epidermis menyegi empat dan menyegi lima terdapat pada *B. parviflora*; bentuk epidermis menyegi lima dan menyegi

enam terdapat pada *R. apiculata*.

### 3.4. Karakter Struktur Luar Polen

Karakter struktur luar polen yang dapat digunakan untuk membedakan jenis dan marga mangrove Rhizophoraceae adalah bentuk dan ukuran butir polen. 7 jenis mangrove Rhizophoraceae yang dipreparasi polennya memiliki tipe apertur dan ornamentasi eksin yang sama. Tipe apertur yang dimiliki oleh mangrove Rhizophoraceae adalah trikolporus, sedangkan ornamentasi eksin bertipe reticulate (memata jala). Tipe apertur mangrove Rhizophoraceae sesuai dengan yang dideskripsikan oleh Tomlinson [12]. Tipe apertur merupakan pembeda tingkatan takson [6,16]. Walaupun untuk suku Rhizophoraceae memiliki tipe apertur yang sama.

Tumbuhan mangrove Rhizophoraceae memiliki bentuk butir polen membulat (*oblate spheroidal*) pada marga *Rhizophora* dan menyegi tiga sampai menyegi tiga-membulat pada marga *Bruguiera* dan *Ceriops*. Walaupun Erdtman mendeskripsikan karakter bentuk polen pada tingkat suku Rhizophoraceae berbentuk *oblate-spheroidal* hingga suprolet, pengamatan pada marga *Bruguiera* dan *Ceriops* menunjukkan bentuk yang berbeda [17].

Berdasarkan ukuran polen, tumbuhan mangrove Rhizophoraceae memiliki ukuran  $10 \times 10 - 25 \times 18 \mu\text{m}$  dan digolongkan menjadi polen berukuran kecil (*small spores*,  $10 - 25 \mu\text{m}$ ) dan polen berukuran sedang (*medium size spores*,  $25 - 100 \mu\text{m}$ ). Polen berukuran kecil terdapat pada *Bruguiera cylindrical*, *B. gymnorrhiza*, *B. parviflora*, *Ceriops decandra*, *C. tagal*, *Rhizophora apiculata* dan *R. mucronata*. Sedangkan *B. sexangula* memiliki ukuran butir polen kecil sampai sedang. Ukuran polen ini sesuai dengan deskripsi Erdtman yang menyebutkan bahwa ukuran butir polen *B. gymnorrhiza*, *R. mucronata* dan *Ceriops* berukuran kecil.

### 3.5. Taksonomi Treatment

Berdasarkan ciri morfologi, anatomi dan struktur luar polen dapat disusun kunci identifikasi dan pertelaan jenis. Namun untuk kunci identifikasi berdasarkan karakter anatomi, tidak dapat disusun karena hanya sedikit karakter pembeda jenis yang diperoleh

**Tabel 2. Kunci Identifikasi Jenis Rhizoporaceae Berdasarkan Karakter Morfologi**

1	a.	Tata susun letak daun berhadapan bersilangan, tipe bunga majemuk	.....	2
	b.	Tata susun letak daun sejajar, tipe bunga tunggal	.....	5
2	a.	Derajat kemiringan cabang tulang daun $\geq 60^\circ$ , tipe mahkota bunga entire	.....	3
	b.	Derajat kemiringan cabang tulang daun $< 60^\circ$ , tipe mahkota bunga berlobus	.....	4
3	a.	Bentuk ujung daun meruncing	.....	<i>Rhizophora apiculata</i>
	b.	Bentuk ujung daun bertugi	.....	<i>R. mucronata</i>
4	a.	Posisi kelopak bunga melengkung ke depan	.....	<i>Cerriops decandra</i>
	b.	Posisi kelopak bunga melengkung ke belakang	.....	<i>C. tagal</i>
5	a.	Warna kelopak bunga merah	.....	<i>Bruguiera gymnorrhiza</i>
	b.	Warna kelopak bunga hijau kekuningan	.....	6
6	a.	Jumlah kelopak bunga $< 9$ , derajat kemiringan cabang tulang daun $< 60^\circ$	.....	<i>B. parviflora</i>
	b.	Jumlah kelopak bunga $\geq 9$ cm, derajat kemiringan cabang tulang daun $\geq 60^\circ$	.....	<i>B. sexangula</i>

**Tabel 3. Kunci Identifikasi Jenis Rhizoporaceae Berdasarkan Karakter Struktur Luar Polen**

1	a.	Bentuk butir polen membulat	.....	2
	b.	Bentuk butir polen menyegitiga sampai menyegitiga-membulat	.....	3
2	a.	Ukuran butir polen $13 \times 13 - 15 \times 15 \mu\text{m}$	.....	7. <i>R. apiculata</i>
	b.	Ukuran butir polen $17 \times 17 - 20 \times 20 \mu\text{m}$ , kolpus lebih dalam	.....	8. <i>R. mucronata</i>
3	a.	Intin pada bagian apertur tipis, seksin tebal	.....	4
	b.	Intin pada bagian aperture sangat tebal, neksin lebih tebal dari seksin	.....	5
4	a.	Butir polen menyegitiga-membulat ukuran $15 \times 15 - 22 \times 20 \mu\text{m}$	.....	5. <i>C. decandra</i>
	b.	Butir polen menyegitiga ukuran $10 \times 15 \mu\text{m}$	.....	6. <i>C. tagal</i>
5	a.	Butir polen menyegitiga-membulat ukuran sangat kecil ( $< 15 \mu\text{m}$ )	.....	3. <i>B. parviflora</i>
	b.	Butir polen menyegitiga, ukuran kecil sampai sedang ( $> 15 \mu\text{m}$ )	.....	6
6	a.	Ujung apertur meruncing	.....	1. <i>B. cylindrica</i>
	b.	Ujung apertur membulat	.....	7
7	a.	Vestibulum pada apertur jelas, penipisan eksin pada interkolpium	.....	2. <i>B. gymnorrhiza</i>
	b.	Vestibulum pada apertur tidak jelas, eksin pada bagian apertur sangat tebal	.....	4. <i>B. sexangula</i>

### 3.6. Pertelaan Jenis

#### 3.6.1. *Bruguiera gymnorrhiza* (L.) Lamk.

*Bruguiera gymnorrhiza* (L.) Lamk., [12,17,18,19].

Pertelaan Morfologi: Diameter ranting 0,3-1,5 cm. Daun: panjang tangkai daun 0,7-4,5 cm, jarak antar tangkai daun 0,2-3 cm, tata susun letak daun tersebar, bentuk daun menjorong, panjang 0,5-18 cm, lebar 3-7 cm, ujung melancip, pangkal menirus, permukaan atas halus, permukaan bawah kasar, tepi mengutuh, pertulangan daun menyirip, jumlah cabang tulang daun 38-54, derajat kemiringan cabang tulang daun  $45^\circ-62^\circ$ . Bunga : tipe bunga tunggal, jumlah kelopak bunga 7-12, warna

kelopak bungamerah menyala. Hipokotil: Permukaan bergerigi, diameter 0,3-1,5 cm, panjang 2,5-17,5 cm.

Pertelaan anatomi: Bentuk stomata Anomositik, ukuran :  $8,50-11,6 \mu\text{m}$ , kerapatan stomata :  $107,00/\text{mm}^2-142,67/\text{mm}^2$ . Epidermis : bentuk permukaan atas : isodiametrik menyegi lima, menyegi enam, menyegi tujuh (p :  $7,8-11,0 \mu\text{m}$ ), bentuk permukaan bawah : isodiametrik menyegi lima, menyegi enam, menyegi tujuh(p:  $5,0-7,5 \mu\text{m}$ ).

Pertelaan struktur luar Polen: Butir polen menyegi tiga. Ukuran butir  $22 \times 22- 23 \times 23 \mu\text{m}$ . Apertur trikolporus, termodifikasi berupa vestibulum, ujung apertur membulat. Eksin tebal, terutama pada bagian apertur. Pada bagian interkolpium terjadi penipisan eksin.

Ornamentasi eksin reticulate. Bentuk menyegi tiga pada badan polen terlihat lebih jelas.

### 3.6.2. *Bruguiera parviflora* (Roxb.) W.& A. ex Griff.

*Bruguiera gymnorhiza* (L.) Lamk., [12,17,18,19].

Pertelaan Morfologi: Diameter ranting 0,3-1,5 cm. Daun: panjang tangkai daun 0,7-4,5 cm, jarak antar tangkai daun 0,2-3 cm, tata susun letak daun tersebar, bentuk daun menjorong, panjang 0,5-18 cm, lebar 3-7 cm, ujung melancip, pangkal menirus, permukaan atas halus, permukaan bawah kasar, tepi mengutuh, pertulangan daun menyirip, jumlah cabang tulang daun 38-54, derajat kemiringan cabang tulang daun 45°-62°. Bunga : tipe bunga tunggal, jumlah kelopak bunga 7-12, warna kelopak bungamerah menyala. Hipokotil: Permukaan bergerigi, diameter 0,3-1,5 cm, panjang 2,5-17,5 cm.

Pertelaan anatomi: Bentuk stomata Anomositik, ukuran : 8,50-11,6  $\mu\text{m}$ , kerapatan stomata : 107,00/ $\text{mm}^2$ -142,67/ $\text{mm}^2$ . Epidermis : bentuk permukaan atas : isodiametrik menyegi lima, menyegi enam, menyegi tujuh (p : 7,8-11,0  $\mu\text{m}$ ), bentuk permukaan bawah : isodiametrik menyegi lima, menyegi enam, menyegi tujuh (p: 5,0-7,5  $\mu\text{m}$ ). Pertelaan struktur luar Polen: Butir polen menyegi tiga. Ukuran butir 22X22- 23X23  $\mu\text{m}$ . Apertur trikolporus, termodifikasi berupa vestibulum, ujung apertur membulat. Eksin tebal, terutama pada bagian apertur. Pada bagian interkolpium terjadi penipisan eksin. Ornamentasi eksin reticulate. Bentuk menyegi tiga pada badan polen terlihat lebih jelas.

### 3.6.3. *Bruguiera sexangula* (Lour.) Poir.

*Bruguiera sexangula* (Lour.) Poir., [12,17,18,19].

Pertelaan Morfologi: Diameter ranting 0,4-1,1 cm. Daun: panjang tangkai daun 3-4 cm, jarak antar tangkai daun 0,2-0,3 cm, tata susun letak daun tersebar, bentuk daun menjorong, panjang 0,5-13 cm, lebar 4-6 cm, ujung melancip, pangkal menirus, permukaan atas halus, permukaan bawah kasar, tepi mengutuh, pertulangan daun menyirip, jumlah cabang tulang daun 34-40, derajat kemiringan cabang tulang daun 60°. Bunga : tipe bunga tunggal, jumlah kelopak bunga 11, warna kelopak bunga

hijau kekuningan. Hipokotil: Permukaan bergerigi, diameter 0,6 cm, panjang 5,2 cm.

Pertelaan Anatomi : Bentuk Stomata Anomositik, ukuran : 10,75  $\mu\text{m}$ , kerapatan stomata : 76,43/ $\text{mm}^2$ . Epidermis : bentuk permukaan atas : isodiametrik menyegi lima dan menyegi enam (p : 9,5  $\mu\text{m}$ ), bentuk permukaan bawah : isodiametrik menyegi lima, menyegi enam, menyegi tujuh (p: 8,0  $\mu\text{m}$ )

Pertelaan struktur luar polen: Butir polen menyegi tiga. Ukuran butir 19X18 – 25 X 18  $\mu\text{m}$ . Apertur trikolporus, lebih lebar daripada *B.gymnorhiza* dan *B.cylindrica*, ujung apertur membulat. Eksin pada bagian apertur sangat tebal. Ornamentasi eksin reticulate.

### 3.6.4. *Ceriops decandra* (Griff.) Ding Hou

*Ceriops decandra* (Griff.) Ding Hou., [12,17,18,19].

Pertelaan Morfologi: Diameter ranting 0,2-0,5 cm. Daun: panjang tangkai daun 0,5-3 cm, jarak antar tangkai daun 0,2-6 cm, tata susun letak daun berhadapan bersilangan, bentuk daun menjorong, panjang 1,7-10 cm, lebar 0,7-4,7 cm, ujung membulat, pangkal menirus, permukaan atas halus, permukaan bawah kasar, tepi mengutuh, pertulangan daun menyirip, jumlah cabang tulang daun 20-42, derajat kemiringan cabang tulang daun 40°-55°. Bunga : tipe bunga majemuk, jumlah kelopak bunga 4, warna kelopak bunga hijau. Hipokotil: Permukaan bulat atau bergerigi, diameter 0,2-0,4 cm, panjang 2-20 cm.

Pertelaan Anatomi : Bentuk Stomata Anomositik, ukuran : 16,0-20,6  $\mu\text{m}$ , kerapatan stomata : 61,15/ $\text{mm}^2$ -91,72/ $\text{mm}^2$ . Epidermis : bentuk permukaan atas : isodiametrik menyegi empat, menyegi lima dan menyegi enam (p : 4,5-11,0  $\mu\text{m}$ ), bentuk permukaan bawah : isodiametrik menyegi empat, menyegi lima dan menyegi enam (p: 5,3-9,0  $\mu\text{m}$ )

Pertelaan Struktur Luar Polen: Butir polen menyegi tiga- membulat. Ukuran butir 15X15 – 22X20  $\mu\text{m}$ . Apertur trikolporus menonjol, lebih jelas dibandingkan *C.tagal*. Eksin tebal. Ornamentasi eksin reticulate.

### 3.6.5. *Ceriops tagal* (Perr.) C.B.Rob.

*Ceriops tagal* (Perr.) C.B.Rob., [12,17,18,19].

Pertelaan Morfologi: Diameter ranting 0,2-0,4 cm. Daun: panjang tangkai daun 1-2 cm, jarak antar tangkai daun 2-7 cm, tata susun letak

daun berhadapan bersilangan, bentuk daun menjorong, panjang 4,5-9,5 cm, lebar 2-5 cm, ujung membundar, pangkal menirus, permukaan atas halus, permukaan bawah kasar, tepi mengutuh, pertulangan daun menyirip, jumlah cabang tulang daun 38-42, derajat kemiringan cabang tulang daun 50°-55°. Bunga : tipe bunga majemuk, jumlah kelopak bunga 4, warna kelopak bunga hijau. Hipokotil: Permukaan bergerigi, diameter 0,3-0,5 cm, panjang 13-15,5 cm.

Pertelaan Anatomi: Bentuk Stomata Anomositik, ukuran : 18,2  $\mu\text{m}$ , kerapatan stomata : 40,76/ $\text{mm}^2$ . Epidermis : bentuk permukaan atas : isodiametrik menyegi lima dan menyegi enam, menyegi tujuh (p : 12,8  $\mu\text{m}$ ), bentuk permukaan bawah : isodiametrik menyegi lima, menyegi enam, menyegi tujuh (p: 11,0  $\mu\text{m}$ )

Pertelaan Struktur Luar Polen: Butir polen menyegi tiga. Ukuran butir 10X15  $\mu\text{m}$ . Apertur trikolporus. Ornamentasi eksin reticulate.

### 3.6.6. *Rhizophora apiculata* Bl

*Rhizophora apiculata* Bl., Backer & Bakh., 1965, Fl. Jav, 2: 379-380; Giesen *et al.*, 1995, Fiel.Guid. Ind.Mangr.:182; Tomlinson, 1986, Bot.of mangr.: 333; Ertzman, 1986, Pol. Morph.: 378-379.

Pertelaan Morfologi: Diameter ranting 0,3-0,9 cm. Daun: panjang tangkai daun 1-2,5 cm, jarak antar tangkai daun 0,1-5 cm, tata susun letak daun berhadapan bersilangan, bentuk daun menjorong, panjang 8,5-11,5 cm, lebar 3,3-5 cm, ujung meruncing, pangkal menirus, permukaan atas halus, permukaan bawah kasar, tepi bergigi, pertulangan daun menyirip, jumlah cabang tulang daun 43-60, derajat kemiringan cabang tulang daun 60°-70°. Bunga : tipe bunga majemuk, jumlah kelopak bunga 4, warna kelopak bunga hijau kekuningan. Hipokotil: Permukaan bulat, diameter 3,5-5 cm, panjang 3,5-5 cm.

Pertelaan Anatomi: Bentuk Stomata Anomositik, ukuran : 16,4-18,0  $\mu\text{m}$ , kerapatan stomata : 76,43/ $\text{mm}^2$ -81,53/ $\text{mm}^2$ . Epidermis : bentuk permukaan atas : isodiametrik menyegi lima dan menyegi enam (p : 6,4-8,3  $\mu\text{m}$ ), bentuk permukaan bawah : isodiametrik menyegi lima dan menyegi enam (p: 6,5-11,0  $\mu\text{m}$ )

Pertelaan Struktur Luar Polen : Butir polen *oblate-spheroidal* (membulat). Ukuran butir 13X13 -15X15  $\mu\text{m}$ . Apertur trikolporus. Eksin tebal. Ornamentasi eksin reticulate.

### 3.6.7. *Rhizophora mucronata* Lmk

*Rhizophora mucronata* Lmk., [12,17,18,19]

Pertelaan Morfologi: Diameter ranting 0,3-0,9 cm. Daun: panjang tangkai daun 1-4 cm, jarak antar tangkai daun 0,1-3 cm, tata susun letak daun berhadapan bersilangan, bentuk daun menjorong, panjang 4,5-17 cm, lebar 1,5-7 cm, ujung bertugi, pangkal menirus, permukaan atas halus, permukaan bawah kasar, tepi mengutuh, pertulangan daun menyirip, jumlah cabang tulang daun 28-51, derajat kemiringan cabang tulang daun 40°-70°. Bunga : tipe bunga majemuk, jumlah kelopak bunga 4, warna kelopak bunga hijau kekuningan. Hipokotil: Permukaan bulat atau bergerigi, diameter 0,5-1 cm, panjang 3,5-48 cm.

Pertelaan Anatomi: Bentuk Stomata Anomositik, ukuran : 16,0-18,3  $\mu\text{m}$ , kerapatan stomata : 76,43 / $\text{mm}^2$ -132,48/ $\text{mm}^2$ . Epidermis : bentuk permukaan atas : isodiametrik menyegi lima, menyegi enam, menyegi tujuh (p: 7,45  $\mu\text{m}$ ), bentuk permukaan bawah : isodiametrik menyegi lima, menyegi enam , menyegi tujuh (p: 5,98  $\mu\text{m}$ ).

Pertelaan Struktur Luar Polen: Butir polen *oblate-spheroidal* (membulat). Ukuran butir 17X18 - 20X20  $\mu\text{m}$ . Apertur trikolporus, kolpus lebih dalam jika dibandingkan dengan *R.apiculata*. Eksin tebal. Pada bagian apertur terdapat penebalan neksin ke arah dalam. Ornamentasi eksin reticulate.

### 3.7. Analisis Kekekabatan

Analisis kekekabatan dilakukan dengan memilih ciri dan sifat ciri berdasarkan karakter morfologi, anatomi dan struktur luar polen. Sebanyak 14 ciri yang terdiri dari 7 ciri morfologi, 3 ciri anatomi dan 4 ciri struktur luar polen digunakan untuk menganalisis kekekabatan.

Berdasarkan ciri dan sifat ciri yang didapatkan, data tersebut diubah dalam bentuk angka) yang kemudian dimasukkan ke dalam matriks data untuk dianalisis. Berdasarkan analisis kekekabatan dengan menggunakan software NTSys PC version 2.0 diperoleh dendrogram yang membagi 7 jenis Rhizophoraceae menjadi 2 cabang (Gambar 1). Cabang 1 terdiri dari jenis-jenis *Bruguiera* dan cabang 2 terdiri dari jenis-jenis *Ceriops* dan *Bruguiera*. Cabang 1 dan cabang 2 terpisah

karena ciri 0 (bentuk ujung daun), ciri 1 (tata letak daun) dan ciri 3 (tipe bunga) dengan nilai kesamaan 0,3. Cabang 1 memisahkan jenis *B. sexangula* dengan jenis *Bruguiera* lainnya karena ciri 2 (jumlah kelopak bunga) dan ciri 11 (ukuran butir polen) dengan nilai kesamaan 0,52. Cabang 2 memisahkan marga *Ceriops* dan *Rhizophora* karena ciri 0 (bentuk ujung daun), ciri 6 (tipe mahkota bunga), ciri 12 (ujung aperture) dan ciri 13 (ketebalan eksin) dengan nilai kesamaan 0,52. Jenis-jenis yang memiliki kekerabatan terdekat adalah *B. parviflora* dan *B. gymnorrhiza* serta *R. apiculata* dan *R. mucronata* dengan nilai kesamaan 0,86 (Gambar 1)

#### 4. KESIMPULAN

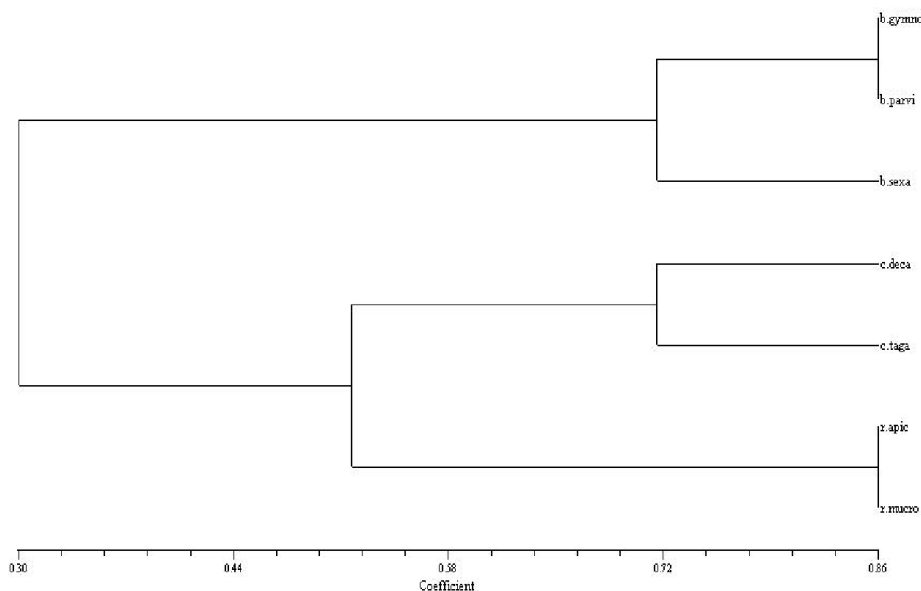
1. Karakter atau ciri morfologi yang dapat digunakan untuk membedakan jenis-jenis Rhizophoraceae adalah morfologi daun dan bunga, yaitu bentuk tepi daun, bentuk ujung daun, tata susun letak daun, posisi kelopak bunga saat muncul hipokotil, jumlah kelopak bunga, tipe bunga, tipe mahkota bunga, dan warna kelopak bunga.
2. Karakter anatomi kerapatan stomata, bentuk

dan ukuran sel epidermis dapat membedakan jenis-jenis suku Rhizophoraceae.

3. Struktur luar polen yaitu bentuk dan ukuran polen dapat digunakan untuk membedakan tingkatan marga dan jenis pada tumbuhan mangrove Rhizophoraceae.
4. Berdasarkan karakter morfologi dan struktur luar polen dapat disusun kunci indentifikasi 7 jenis Rhizophoraceae, sementara karakter anatomi tidak dapat digunakan untuk menyusun kunci indentifikasi
5. Kekerabatan dengan menggunakan software NTSys PC version 2.0 membagi 7 jenis Rhizophoraceae menjadi 2 cabang. Cabang 1 terdiri dari jenis-jenis *Bruguiera* dan cabang 2 terdiri dari jenis-jenis *Ceriops* dan *Bruguiera*.

#### 5. UCAPAN TERIMAKASIH

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Gambar 1. Dendrogram Kekerabatan Rhizophoraceae berdasarkan ciri Morfologi, Anatomi dan Struktur Luar Polen



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2. Kenapa karakteristik melalui morfologi?

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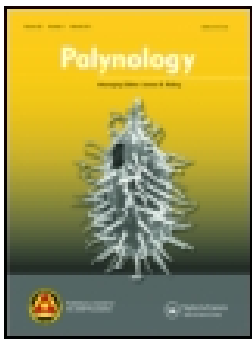
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## Pollen morphology of 25 species in the family Apocynaceae from the Adolpho Ducke Forest Reserve, Amazonas, Brazil

Isabella Dessaune Rodrigues<sup>a</sup>, Maria Lúcia Absy<sup>b\*</sup>, Silane Aparecida F. da Silva-Caminha<sup>b,c</sup>, Vania Gonçalves-Esteves<sup>d</sup>, Claudia Barbieri Ferreira Mendonça<sup>d</sup>, Marcos Gonçalves Ferreira<sup>b</sup> and Cleonice de Oliveira Moura<sup>b</sup>

<sup>a</sup>Instituto de Ciências Biológicas, Laboratório de Botânica, Universidade Federal do Amazonas, Av. General Rodrigo Octávio J. Ramos, 6200, Japiim, 69077000, Manaus, Amazonas, Brasil; <sup>b</sup>Instituto Nacional de Pesquisas da Amazônia (INPA), Coordenação de Pesquisas em Biodiversidade, Laboratório de Palinologia, Av. André Araújo, 2936, Bairro Petrópolis, 69067-375 Manaus, Amazonas, Brasil; <sup>c</sup>Departamento de Geologia Geral, Laboratório de Paleontologia e Palinologia, Universidade Federal de Mato Grosso (UFMT), Av. Fernando Corrêa da Costa, 2367, Boa Esperança, CEP:78060-900, Cuiabá-MT, Brasil; <sup>d</sup>Departamento de Botânica, Laboratório de Palinologia, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brasil

### ABSTRACT

The Apocynaceae family consists of approximately 4555 species worldwide, distributed among 415 genera. In Brazil, this family is represented by 90 genera and 850 species. The Adolpho Ducke Forest Reserve, part of the Instituto Nacional de Pesquisas da Amazônia (INPA) since 1963, comprises 100 km<sup>2</sup> of non-isolated continuous primary forest, and 40 species and 16 genera of Apocynaceae have been recorded in this area. Pollen grains, collected from flower buds and/or flowers of voucher specimens deposited at the INPA Herbarium collection, were processed using the acetolysis method, and measured, described and photographed by light microscopy and scanning electron microscopy. The study included 25 Apocynaceae species distributed among 14 genera. The pollen grains were porate to colpiate, with exine ornamentation varying from psilate or scabrate to microreticulate. Other morphological characteristics were pores with granules at the base of the annulus in *Odontadenia*, a distinct margo forming arches around the colpus in *Geissospermum*, and the presence of a thick endocingulum in the equatorial region in species of *Tabernaemontana*.

### KEYWORDS

pollen morphology;  
Apocynaceae; Amazon;  
Ducke Reserve; Brazil

### 1. Introduction

Apocynaceae Juss. belongs to the Order Gentianales, which includes four other families, namely Gelsemiaceae, Gentianaceae, Loganiaceae and Rubiaceae (APG III 2009). The Apocynaceae family can be divided into five subfamilies: Rauvolfioideae (cosmopolitan; 10 tribes/83 genera; 915 species), Apocynoideae (cosmopolitan; eight tribes/80 genera; 822 species), Periplocoideae (Old World; 33 genera), Secamonoideae (Old World; eight genera) and Asclepiadoideae (cosmopolitan; four tribes/172 genera) (Endress & Bruyns 2000; Endress et al. 2007; Middleton 2007).

Apocynaceae has been the subject of several taxonomic, evolutionary and phylogenetic analyses (Endress & Stevens 2001; Endress et al. 2007; Ionta & Judd 2007; Simões et al. 2007; Wyatt & Lipow 2007; Rapini 2012), many of which have described pollen grain morphological characteristics (Nilsson 1990; Nilsson et al. 1993; Verhoeven & Venter 1998; Furness 2007; Van Der Ham et al. 2010; Van der Weide & Van der Ham 2012). The earliest pollen record for Apocynaceae appears in the Paleocene of Borneo (Muller 1981). In Amazonia, Apocynaceae pollen fossil was also found in the Miocene as *Psilastephanoporites herngreenii* (Hoorn 1993) and *Ctenolophonidites suigeneris* (Silva-Caminha et al. 2010).

Approximately 100 genera and 1500 species of this family can be found in the American tropics (Rapini 2004), of which 90 genera and 850 species are present in Brazil (Souza & Lorenzi 2005).

The Adolpho Ducke Forest Reserve (RFAD) is located in Brazilian Amazonia and it contains 16 genera and 40 species, including trees, treelets, lianas and some shrubs such as *Tabernaemontana*, many of which have great economic and medicinal value. These species have white or brownish latex; opposite, verticillate or alternate leaves; bisexual flowers; simple fruits, berries, drupes, capsules or follicles; and single or multiple seeds. The flowers are pollinated by butterflies and bees and fruits dispersed by monkeys and birds (Ribeiro et al. 1999).

The objective of this study was to assess pollen morphology in 25 Apocynaceae species and compare them with others described in the literature. Plant taxonomy of RFAD was previously performed by Ribeiro et al. (1999) in the *Identification guide of the vascular plants of a terra-firme forest in the Central Amazon – Ducke Flora Reserve*. This study will contribute to the Amazon Palynologic Database of the National Institute of Amazonian Research (Instituto Nacional de Pesquisas da Amazônia – INPA) and will be used to expand the INPA Pollen Collection, as well as to provide information for future taxonomic analyses.

## 2. Materials and methods

The taxonomy of the species described in this study was determined by collaborators from the Ducke Flora Reserve Project, who are specialists in the Apocynaceae family (Hopkins 2005). It was not possible to describe all (40) of the species studied in this project due to the absence of voucher specimens with flower buds for pollen collection.

### 2.1. The Adolpho Ducke Forest Reserve (RFAD)

The RFAD was classified as a Biological Reserve in 1963. It is located to the north of Manaus city, at kilometre 26 along the AM-010 highway (Manaus-Itacoatiara) at, according to the mean geographic coordinate, 02°57'50.63"S, 59°57'18.21"W (Figure 1) and covers an area of 10,073 ha. The climate is classified as the Af group (humid equatorial) of Köppen, and the average yearly precipitation is 2000 mm, with two distinct seasons: rainy (November to May) and dry (June to October) (Köppen 1948). With a total area of approximately 100 km<sup>2</sup>, the reserve consists of terra-firme forests divided into plateau, slope, lowland and campinarana types, distributed according to soil type and topography. The species described in this study can be found in each of these vegetation types (Ribeiro et al. 1999).

### 2.2. Sample preparation and morphological descriptions

Pollen grains were collected from the flower buds of voucher specimens deposited in the INPA herbarium collection. The grains were treated using the acetolysis method (Erdtman

1960) and mounted on slides with glycerinated gelatine, and cover slips were affixed to the slides with paraffin. The slides were deposited in the INPA Pollen Collection, in Manaus (Amazonas). The pollen grains were measured, described and photomicrographed (Canon A620 digital camera) using a light microscope (Zeiss) at 1000× magnification. Measurements were taken of 25 pollen grains, randomly, in polar and equatorial views in the isopolar grains and diameter 1 (D1) and diameter 2 (D2) in the apolar grains. For the other measurements, 10 grains were measured (exine thickness, equatorial diameter in polar view, apocolpium side and apertures pollen grains). For the equatorial views, the polar and equatorial diameters were measured, and the shape of the grain was established based on the relationship between the polar and equatorial mean diameters (P/E). Pollen size was characterised according to the method of Erdtman (1952) and using the terminology of Punt et al. (2007). Statistical analyses were based on calculations of the arithmetic mean ( $\bar{x}$ ), standard deviation ( $s_x$ ), sample standard deviation ( $s$ ), coefficient of variation (CV%), 95% confidence interval (95% CI;  $n = 25$ ) and range of variation (RV).

Regarding the variation in the pore, the following sizes should be considered: very small: 1.0–2.0  $\mu\text{m}$ ; small: 3.0–5.6  $\mu\text{m}$ ; large: 6.2–11.7  $\mu\text{m}$ ; very large: up to 20  $\mu\text{m}$ .

To obtain electron micrographs using scanning electron microscopy (SEM), non-acetolysed pollen grains were spread on the surface of double-sided carbon tape covering numbered aluminium stands. The samples were transferred to a vacuum pump, metalised with a fine palladium-gold layer (ca. 150 Å thick), and then analysed using a ZEISS DS M960 device in the

**Table 1.** Measurements ( $\mu\text{m}$ ) of Apocynaceae pollen grains found in the Adolpho Ducke Forest Reserve. P: polar diameter; E: equatorial diameter;  $\bar{x}$ : arithmetic mean;  $S\bar{x}$ : mean standard deviation;  $s$ : standard deviation of sample; CV: coefficient of variation; VR: variation range; CI: 95% confidence interval ( $n = 25$ ).

Species	P					E					P/E
	VR	$\bar{x} \pm s\bar{x}$	$s$	CV (%)	CI	VR	$\bar{x} \pm s\bar{x}$	$s$	CV (%)	CI	
<i>Ambelania acida</i>	(30–39)	34.6 $\pm$ 0.48	2.4	6.9	(33.7–35.6)	(38–45)	40.7 $\pm$ 0.29	1.5	3.6	(40.1–41.3)	0.85
<i>Couma guianensis</i>	(23–30)	27.1 $\pm$ 0.35	1.7	6.4	(26.4–27.8)	(29–38)	33.7 $\pm$ 0.46	2.3	6.8	(32.7–34.6)	0.81
<i>Couma utilis</i>	(29–37)	34.0 $\pm$ 0.44	2.2	6.4	(33.1–34.9)	(35–40)	37.1 $\pm$ 0.28	1.4	3.7	(36.6–37.7)	0.91
<i>Forsteronia acouci</i>	(17–30)	24.7 $\pm$ 0.74	3.7	15.0	(23.2–26.3)	(19–33)	27.8 $\pm$ 0.74	3.7	13.4	(26.2–29.3)	0.89
<i>Forsteronia gracilis</i>	(17–22)	19.5 $\pm$ 0.29	1.4	7.4	(18.9–20.1)	(20–27)	23.3 $\pm$ 0.34	1.7	7.3	(22.6–24.0)	0.84
<i>Geissospermum argenteum</i>	(44–56)	49.3 $\pm$ 0.70	3.5	7.1	(47.9–50.8)	(40–48)	43.0 $\pm$ 0.43	2.2	5.0	(42.1–43.9)	1.15
<i>Himatanthus bracteatus</i>	(35–45)	39.6 $\pm$ 0.52	2.6	6.5	(38.5–40.7)	(41–53)	46.6 $\pm$ 0.59	2.9	6.3	(45.4–47.9)	0.85
<i>Himatanthus stenophyllus</i>	(33–42)	37.2 $\pm$ 0.58	2.9	7.8	(36.1–38.4)	(40–46)	43.2 $\pm$ 0.36	1.8	4.2	(42.5–44.0)	0.86
<i>Himatanthus sucuuba</i>	(33–43)	38.0 $\pm$ 0.53	2.7	7.0	(36.9–39.1)	(38–48)	42.7 $\pm$ 0.43	2.2	5.1	(41.8–43.6)	0.89
<i>Lacmellea arborescens</i>	(35–55)	42.3 $\pm$ 0.85	4.3	10.1	(40.5–44.0)	(35–48)	41.0 $\pm$ 0.70	3.5	8.5	(39.6–42.5)	1.03
<i>Lacmellea gracilis</i>	(25–39)	32.3 $\pm$ 0.69	3.5	10.7	(31.6–33.0)	(13–23)	17.2 $\pm$ 0.55	2.8	16.0	(16.1–18.4)	1.87
<i>Macoubea sprucei</i>	(36–48)	40.9 $\pm$ 0.59	2.9	7.2	(39.5–42.4)	(31–44)	37.2 $\pm$ 0.68	3.4	9.2	(35.7–38.6)	1.10
<i>Odontadenia perrotettii</i>	(36–65)	40.7 $\pm$ 1.47	7.4	18.1	(37.7–43.8)	(43–74)	55.8 $\pm$ 1.59	8.0	14.3	(52.5–59.1)	0.73
<i>Parahancornia fasciculata</i>	(30–51)	38.6 $\pm$ 0.85	4.3	11.0	(36.8–40.4)	(24–48)	36.7 $\pm$ 0.94	4.6	12.5	(34.8–38.6)	1.05
<i>Rauvolfia sprucei</i>	(87–118)	98.9 $\pm$ 1.43	7.1	7.2	(95.9–101.8)	(100–112)	106.8 $\pm$ 0.81	4.1	3.8	(105.1–108.5)	0.93
<i>Rhigospira quadrangulares</i>	(30–40)	37.0 $\pm$ 0.60	3.0	8.2	(35.8–38.3)	(28–41)	36.5 $\pm$ 0.68	3.4	9.3	(35.1–38.0)	1.01
<i>Secondatia duckei</i>	(19–29)	24.8 $\pm$ 0.57	2.9	11.5	(23.6–26.0)	(16–27)	20.6 $\pm$ 0.48	2.4	11.7	(19.6–21.6)	1.20
<i>Tabernaemontana angulata</i>	(45–75)	57.7 $\pm$ 1.65	8.3	14.3	(54.3–61.1)	(31–44)	37.2 $\pm$ 0.70	3.5	9.3	(35.8–38.7)	1.55
<i>Tabernaemontana flavicans</i>	(50–100)	83.4 $\pm$ 2.46	12.3	14.8	(78.3–88.4)	(38–78)	64.0 $\pm$ 1.76	8.8	13.8	(60.4–67.7)	1.30
<i>Tabernaemontana macrocalyx</i>	(75–105)	91.0 $\pm$ 1.64	8.2	9.0	(87.6–94.3)	(38–55)	46.0 $\pm$ 0.88	4.4	9.6	(44.1–47.8)	1.98
<i>Tabernaemontana muricata</i>	(46–68)	57.6 $\pm$ 1.08	5.4	9.4	(55.4–59.9)	(36–53)	44.4 $\pm$ 0.91	4.6	10.3	(42.5–46.3)	1.30
<i>Tabernaemontana undulata</i>	(52–75)	61.5 $\pm$ 1.10	5.5	8.9	(59.2–63.8)	(36–48)	41.6 $\pm$ 0.62	3.1	7.4	(40.4–42.9)	1.48

Species	D1					D2					
	VR	$\bar{x} \pm s\bar{x}$	$s$	CV%	CI	VR	$\bar{x} \pm s\bar{x}$	$s$	CV%	CI	
<i>Mandevilla scabra</i> *	(110–165)	139.0 $\pm$ 3.10	15.5	11.2	(132.6–145.4)	(107–170)	138.7 $\pm$ 4.17	20.9	15.0	(130.1–147.3)	–
<i>Odontadenia puncticulosa</i> *	(55–72)	62.9 $\pm$ 1.09	5.5	8.7	(60.6–65.1)	(45–63)	54.8 $\pm$ 1.04	5.2	9.5	(52.6–56.9)	–
<i>Odontadenia verrucosa</i> *	(37–65)	52.3 $\pm$ 1.26	6.3	12.0	(49.7–54.9)	(32–56)	45.2 $\pm$ 1.08	5.4	12.0	(43.0–47.4)	–

\*Pollen grains pantoporate.

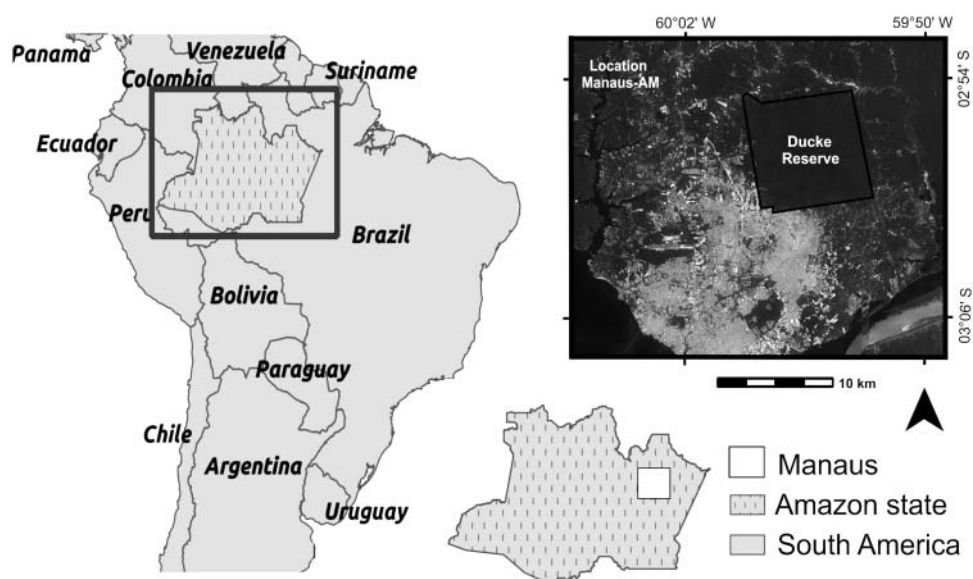


Figure 1. Adolpho Ducke Forest Reserve, located north of the city of Manaus, in the state of Amazon (Google Earth Satellite Image).

Hertha Meyer Laboratory of Cellular Ultrastructure, Institute of Biophysics, Federal University of Rio de Janeiro (Universidade Federal do Rio de Janeiro – UFRJ), or a Jeol 6390 LV device in the Scanning Electron Microscopy Centre of the Department of Invertebrates of the National Museum, UFRJ.

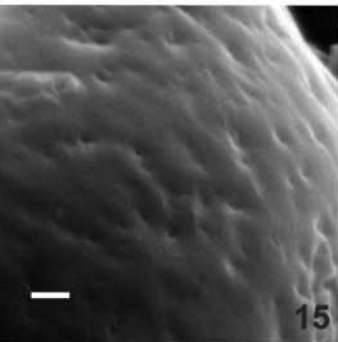
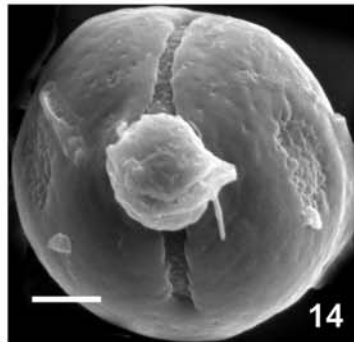
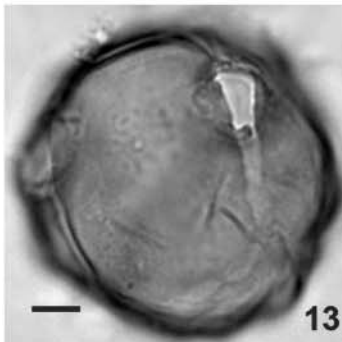
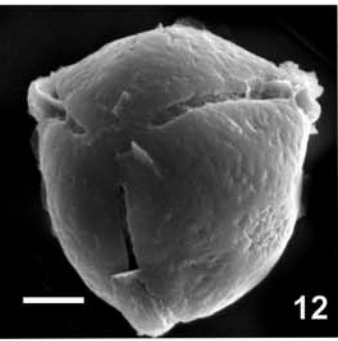
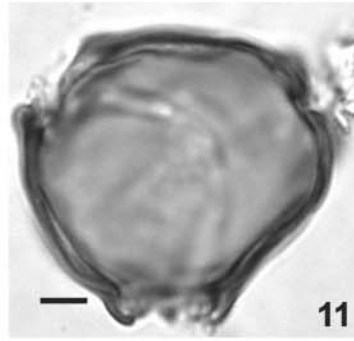
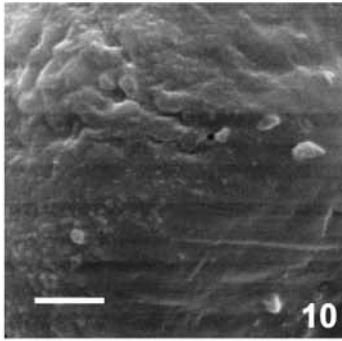
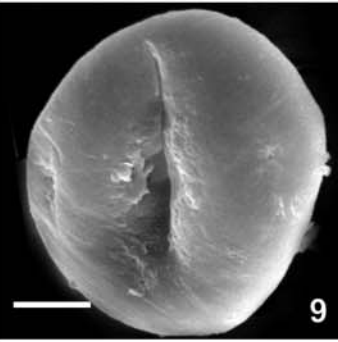
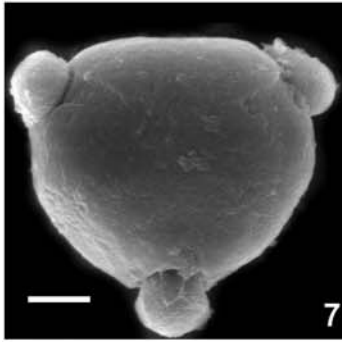
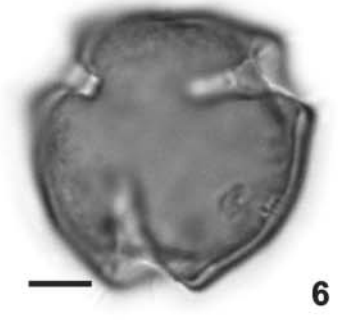
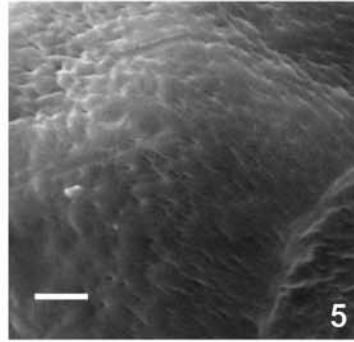
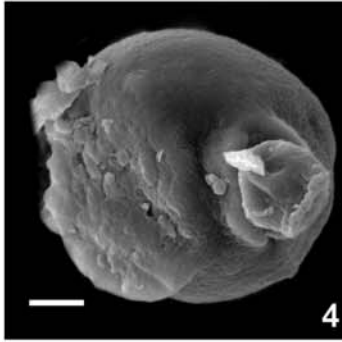
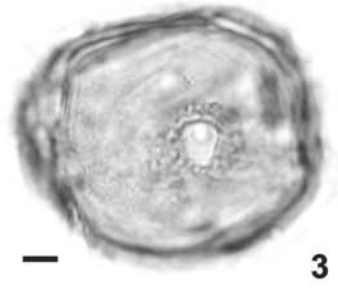
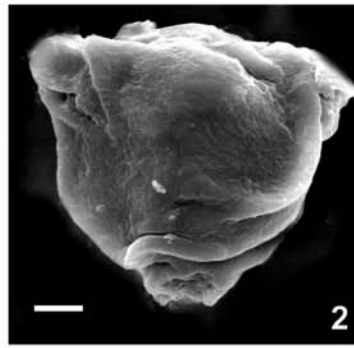
### 2.3. Analysed material

*Ambelania acida* Aublet: Brazil. Amazonas: Manaus, Reserva Florestal Ducke, 19 July 1963, fl., Rodrigues, W. 5380. 14049

(INPA). *Couma guianensis* Aublet: Brazil. Amazonas: Manaus, Reserva Florestal Ducke, fl., Assunção, P.A.C.L. 221 (INPA). *Couma utilis* (Mart.) Müll. Arg.: Brazil. Amazonas: Manaus, Reserva Florestal Ducke, 07 August 1957, fl., Rodrigues, W. 468. 228015 (INPA). *Forsteronia acouci* (Aublet) A. DC.: Brazil. Amazonas: Manaus-Itacoatiara, km 26 Reserva Florestal Ducke. 30 July 1997, fl., Assunção, P.A.C.L. & Silva, C.F. da 578. 191271 (INPA). *Forsteronia gracilis* (Benth.) Müll. Arg.: Brazil. Amazonas: Manaus-Itacoatiara km 26, Reserva Florestal Ducke. 27 November 1997, fl., Assunção, P.A.C.L. & Sothers, C.A. 723. 191674 (INPA).

Table 2. Arithmetic average ( $\mu\text{m}$ ) of the measures of EDPV (equatorial diameter in polar view), AS (apocolpium side) of the wall structures and apertures of Apocynaceae pollen grains species found in the Adolpho Ducke Forest Reserve. D: diameter ( $n = 10$ ).

	Layers			EDPV	AS	Endocingulo	Colpus		Endoaperture		Pore	
	Nexine	Sexine	Exine				Length	Width	D1	D2	D1	D2
<i>Ambelania acida</i>	–	–	1.4	–	–	–	–	–	–	–	7.3	7.1
<i>Couma guianensis</i>	–	–	1.2	31.4	9.4	–	21.7	7.6	11.2	6.2	–	–
<i>Couma utilis</i>	–	–	1.3	37.2	9.3	–	26.2	2.6	8.0	7.1	–	–
<i>Forsteronia acouci</i>	0.5	0.5	1.0	–	–	–	–	–	–	–	2.9	3.2
<i>Forsteronia gracilis</i>	–	–	1.0	–	–	–	–	–	–	–	1.9	2.0
<i>Geissospermum argenteum</i>	0.8	0.8	1.5	47.5	14.2	–	24.0	5.9	–	–	–	–
<i>Himatanthus bracteatus</i>	–	–	2.8	47.3	14.9	–	27.5	1.9	7.2	7.7	–	–
<i>Himatanthus stenophyllus</i>	1.1	2.1	3.2	44.2	12.8	–	22.7	2.1	4.9	2.1	–	–
<i>Himatanthus sucuba</i>	0.9	1.9	2.8	43.4	14.9	–	25.8	1.5	7.6	7.5	–	–
<i>Lacmellea arborescens</i>	–	–	1.6	40.2	28.8	–	8.2	1.9	2.4	2.4	–	–
<i>Lacmellea gracilis</i>	–	–	1.4	–	–	–	–	–	–	–	–	3.6
<i>Macoubea sprucei</i>	–	–	1.0	–	–	–	–	–	–	–	11.7	5.9
<i>Mandevilla scabra</i>	–	–	1.5	–	–	–	–	–	–	–	20.5	21
<i>Odontadenia perrotettii</i>	–	–	0.5	–	–	–	–	–	–	–	4.4	4.4
<i>Odontadenia puncticulosa</i>	–	–	1.4	–	–	–	–	–	–	–	6.2	6.2
<i>Odontadenia verrucosa</i>	–	–	2.0	–	–	–	–	–	–	–	9.0	9.0
<i>Parahancornia fasciculata</i>	–	–	1.7	–	–	–	–	–	–	–	7.6	7.6
<i>Rauvolfia sprucei</i>	–	–	1.1	83.8	63.2	–	17.8	6.6	8.7	8.7	–	–
<i>Rhigospira quadrangulares</i>	–	–	1.4	–	–	–	–	–	–	–	5.6	5.6
<i>Secondatia duckei</i>	–	–	1.2	–	–	–	–	–	–	–	2.0	2.0
<i>Tabernaemontana angulata</i>	–	–	1.5	–	–	7.7	20.4	0.8	–	–	–	–
<i>Tabernaemontana flavicans</i>	–	–	1.0	–	–	13.4	34.3	4.5	–	–	–	–
<i>Tabernaemontana macrocalyx</i>	–	–	3.2	–	–	9.4	30.3	1.8	–	–	–	–
<i>Tabernaemontana muricata</i>	–	–	2.3	–	–	10.3	23.4	2.8	–	–	–	–
<i>Tabernaemontana undulata</i>	–	–	3.3	–	–	4.6	26.4	0.7	–	–	–	–



*Geissospermum argenteum* Woodson: Brazil. Amazonas: Manaus-Itacoatiara km 26, Reserva Florestal Ducke. 19 August 1994, fl., Nascimento, J.R. & Silva, C.F. da 578. 180470 (INPA). *Himatanthus bracteatus* (A. DC.) Woodson var. *bracteatus*: Brazil. Amazonas: Manaus, Reserva Florestal Ducke, 05 October 1965, fl., Loureiro, A. 16151 (INPA). *Himatanthus stenophyllus* Plumel: Brazil. Amazonas: Manaus-Itacoatiara km 26, Reserva Florestal Ducke. 28 November 1994, fl., Nascimento, J.R. & Silva, C.F. da 667. 180471 (INPA). *Himatanthus sucubus* (Spruce ex Müll. Arg.) Woodson: Brazil. Amazonas: Manaus-Itacoatiara km 26, Reserva Florestal Ducke. 01 December 1994, fl., Assunção, P.A.C.L. 102. 180453 (INPA). *Lacmellea arborescens* (Müll. Arg.) Markgr.: Brazil. Amazonas: Manaus-Itacoatiara km 26, Reserva Florestal Ducke. 01 August 1995, fl., Oliveira, A.A. & Assunção, P.A.C.L. 2804. 180475 (INPA). *Lacmellea gracilis* (Müll. Arg.) Markgr.: Brazil. Amazonas: Manaus-Itacoatiara km 26, Reserva Florestal Ducke. 12 December 1995, fl., Souza, M.A.D. de & Silva, C.F. da 180. 189617 (INPA). *Macoubea sprucei* (Mull. Arg.) Markgr.: Brazil. Amazonas: Manaus-Itacoatiara km 26, Reserva Florestal Ducke. 09 August 1995, fl., Sothers, C.A. & Nee, M., Silva, C.F. da, Assunção, P.A.C.L., Pereira, E. da C. 547. 181862 (INPA). *Mandevilla scabra* (Roem. & Schult.) K. Schum.: Brazil. Amazonas: Manaus-Itacoatiara km 26, Reserva Florestal Ducke. 21 April 1998, fl., Souza, M.A.D., Pereira, E. da C., Martins, L.H.P. 675 192611 (INPA). *Odontadenia perrottetii* (A. DC.) Woodson: Brazil. Amazonas: Manaus-Itacoatiara km 26, Reserva Florestal Ducke, 14 September 1994, fl., Ribeiro, J.E.L.S., Vicentini, A., Silva, C.F. da, Pereira, E. da C., Athaide, S. 1413 (INPA). *Odontadenia punctulosa* (L. C. Rich.) Pulle: Brazil. Amazonas: Manaus-Itacoatiara km 50, Reserva Florestal Ducke, 05 October 1995, fl., Vicentini, A., Bonatto, F., Pereira, E. da C. 1069 (INPA). *Odontadenia verrucosa* (Willd. ex Roem. & Schult.) K. Schum. ex Markgr.: Brazil. Amazonas: Manaus-Itacoatiara km 50, Reserva Florestal Ducke, 14 September 1994, fl., Ribeiro, J.E.L.S. & Vicentini, A., Silva, C.F. da, Pereira, E. da C., Athaide, S. 1410 (INPA). *Parahancornia fasciculata* (Poir.) Benoist: Brazil. Amazonas: Manaus-Itacoatiara km 50, Reserva Florestal Ducke, fl., Sothers, C.A. 613 (INPA). *Rauvolfia sprucei* Mull. Arg.: Brazil. Amazonas: Manaus-Itacoatiara km 26, Reserva Florestal Ducke (02°53'S, 59°58'W). 21 July 1994, fl., Vicentini, A. & Assunção, P.A.C.L., Nascimento, J.R. 637. 180511 (INPA). *Rhigospira quadrangularis* (Müll. Arg.) Miers: Brazil. Amazonas: Manaus-Itacoatiara km 26, Reserva Florestal Ducke (02°53'S, 59°58'W). 16 September 1994, fl., Vicentini, A. & Ribeiro, J.E.L.S., Athayde, S.F. de, Silva, C.F. da, Pereira, E. da C. 697. 180513 (INPA). *Secondatia duckei* Markgr.: Brazil. Amazonas: Manaus-Itacoatiara km 26, Reserva Florestal Ducke (02°53'S, 59°58'W). 15 September 1994, fl., Vicentini, A. & Ribeiro, J.E.L.S., Athayde, S.F. de, Silva, C.F. da, Pereira, E. da C. 692. 180512 (INPA). *Tabernaemontana angulata* Mart. ex Müll. Arg.: Brazil. Amazonas: Manaus-Itacoatiara km 26, Reserva Florestal Ducke (02°53'S, 59°58'W). 25 April 1996, fl., Sothers, C.A. & Assunção, P.A.C.L., Pereira, E. da C. 854. 189613 (INPA). *Tabernaemontana flavicans* Willd. ex Roem. & Schult.: Brazil. Amazonas: Manaus, Reserva Ducke, 13 November 2007, fl., Koch, I.M. & Simões, A.O., Paula-Souza, J., Obando, S.,

Mesquita, J.R. 19. 228020 (INPA). *Tabernaemontana macrocalyx* Mull. Arg.: Brazil. Amazonas: Manaus-Itacoatiara km 26, Reserva Florestal Ducke (02°53'S, 59°58'W). 25 August 1994, fl., Sothers, C. A. & Pereira, E. da C., Silva, C.F. da, Assunção, P.A.C.L. 135 180499 (INPA). *Tabernaemontana muricata* Spruce ex Müll. Arg.: Brazil. Amazonas: Manaus-Itacoatiara km 26, Reserva Florestal Ducke (02°53'S, 59°5'W). 01 August 1995, fl., Oliveira, A. A. & Assunção, P. A.C.L. 2809. 180477 (INPA). *Tabernaemontana undulata* Vahl: Brazil. Amazonas: Manaus-Itacoatiara km 26, Reserva Florestal Ducke (02°53'S, 59°58'W). 31 October 1995, fl., Souza, M.A.D. & Pereira, E. da C. 134. 182009 (INPA).

### 3. Results

Information on the habit, habitat, geographic distribution, reproductive characteristics (Ribeiro et al. 1999) and detailed palynological descriptions of 25 Apocynaceae species from 14 genera are given below. Measurement of the grains are given in Tables 1 and 2.

#### *Ambelania* Aublet

##### *Ambelania acida* Aublet (Plate 1, figures 1–5)

Characteristics: tree, 15 m tall, 15 cm in diameter, cream flowers, rare, distributed in the Central and Eastern Amazon and in the Guianas; collected in clay soil, terra-firme forest.

Palynological description: monad, isopolar, average size ( $P = 34.6 \pm 0.48 \mu\text{m}$ ;  $E = 40.7 \pm 0.29 \mu\text{m}$ ),  $P/E = 0.85$ , suboblate, amb circular, tricolporate. The colpi are relatively short (ca.  $20 \mu\text{m}$  in length), thick margin (ca.  $2 \mu\text{m}$ ), acute extremities (Plate 1, figures 1, 2, 4), endoaperture lalongate (ca.  $3\text{--}6 \mu\text{m}$ ), with granulated surroundings (Plate 1, figure 3); exine thin ( $1.4 \mu\text{m}$ ), sexine scabrate with perforations (Plate 1, figure 5), best observed under SEM.

Species variations: stephanocolporate grains (tetracolporate) were also found.

Comparisons: Nilsson (1990) described the same species with densely perforated ornamentation.

#### *Couma* Aublet

##### *Couma guianensis* Aublet (Plate 1, figures 6–10)

Characteristics: canopy tree, diameter at breast height (DBH) = 29.0 cm, pink flower, common, distributed in Central America and northern South America.

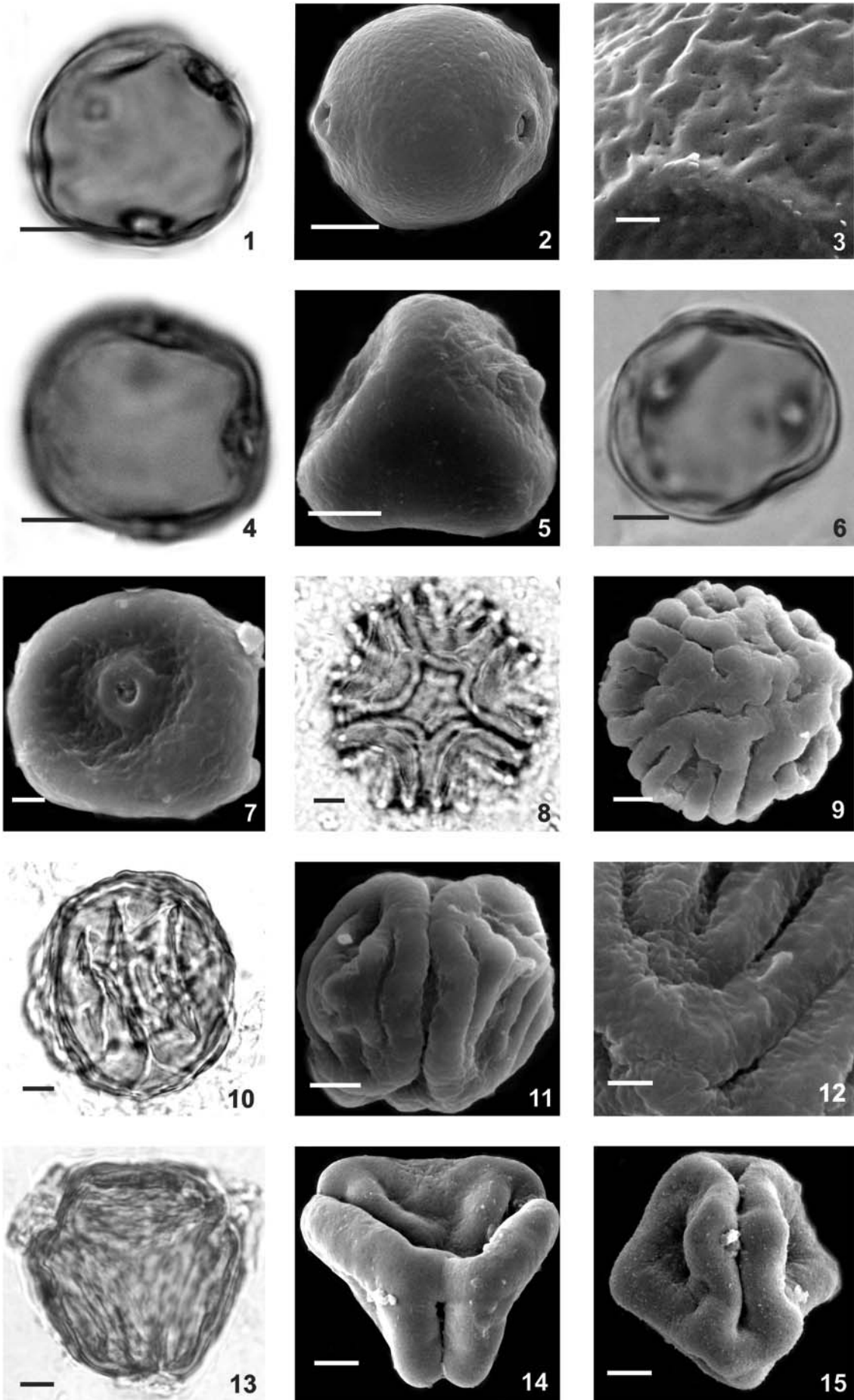
Palynological description: monad, isopolar, average size ( $P = 27.1 \pm 0.35 \mu\text{m}$ ;  $E = 33.7 \pm 0.46 \mu\text{m}$ ),  $P/E = 0.81$ , suboblate, amb subcircular (Plate 1, figures 6, 7), tectate, tricolporate. The colpi ( $21.7 \times 7.6 \mu\text{m}$ ) are long, margin undifferentiated, truncated extremities (Plate 1, figures 8, 9), endoaperture lalongate ( $11.2 \times 6.2 \mu\text{m}$ ); exine thin ( $1.2 \mu\text{m}$ ), sexine scabrate (Plate 1, figure 10), best observed under SEM.

Species variations: number of colpi, tetracolporate grains were also observed.

##### *Couma utilis* (Mart.) Müll. Arg. (Plate 1, figures 11–15)

**Plate 1.** Light micrographs (LM) and scanning electron micrographs (SEM) of Apocynaceae. *Ambelania acida*: figure 1, polar view, general view (LM); figure 2, general view (SEM); figure 3, equatorial view, aperture (LM); figure 4, aperture (SEM); figure 5, surface detail (SEM). *Couma guianensis*: figure 6, polar view, general view (LM); figure 7, general view (SEM); figure 8, equatorial view, aperture (LM); figure 9, general view (SEM); figure 10, surface detail (SEM). *Couma utilis*: figure 11, polar view, optical cross section (LM); figure 12, general view (SEM); figure 13, equatorial view, aperture (LM); figure 14, aperture (LM); figure 15, surface detail (SEM). Scale bars: 1–4, 6–9, 11–14 =  $5 \mu\text{m}$ ; 2, 5, 10 =  $2 \mu\text{m}$ ; 15 =  $1 \mu\text{m}$ .





Characteristics: Understorey tree, elliptic leaves attenuate at the base, cultivated in the Reserve, distributed in Central and Western Amazon and the Guianas.

Palynological description: monad, isopolar, average size ( $P = 34.0 \pm 0.44 \mu\text{m}$ ;  $E = 37.1 \pm 0.28 \mu\text{m}$ ),  $P/E = 0.91$ , oblate-spheroidal, amb circular, tricolporate. The colpi are very long ( $26.2 \times 2.6 \mu\text{m}$ ), undifferentiated margin, acute extremities (Plate 1, figure 12), membrane ornamented, with a fastigium (Plate 1, figure 11), endoaperture circular ( $8.0 \times 7.1 \mu\text{m}$ ), exine thin ( $1.3 \mu\text{m}$  in thickness), sexine with conspicuous perforations (Plate 1, figure 15). In the medial region of the mesocolpium there is a depression with granulated ornamentation (Plate 1, figures 13, 14), best observed under SEM.

Species variations: endoaperture shape varies from lalongate, circular to lolongate.

*Forsteronia* G.F.W. Meyer

*Forsteronia acouci* (Aublet) A. DC. (Plate 2, figures 1–3)

Characteristics: woody canopy liana, DBH = 8.0 cm; 25 m in height, yellow petals, brown anthers; stylus, stigma and ovary green with white indument, collected in slope forest, clay soil, infrequent, found in northern South America.

Palynological description: monad, isopolar, average size ( $P = 24.7 \pm 0.74 \mu\text{m}$ ;  $E = 27.8 \pm 0.74 \mu\text{m}$ ),  $P/E = 0.89$ , oblate-spheroidal, amb circular, tetraporate – hexaporate (Plate 2, figures 1, 2), exine rugulate-perforated. Pores are small, circular ( $2.9 \times 3.2 \mu\text{m}$ ), annuli  $1.0 \mu\text{m}$  thick, exine thin (ca.  $1 \mu\text{m}$  in thickness), sexine rugulate,  $0.5 \mu\text{m}$ , with perforations in the regions between the rugulae (Plate 2, figure 3), best observed under SEM.

Species variations: tetraporate grains.

*Forsteronia gracilis* (Benth.) Müll. Arg. (Plate 2, figures 4–7)

Characteristics: woody liana, creeping or in the canopy, DBH = 1.5 cm; 3.0 m in height, white petals, greenish calyx, dark brown androecium and gynoecium, dark peduncle and fruits, collected in secondary forest as ‘capoeira’, infrequent, widely distributed in the Amazon and the Guianas.

Palynological description: monad, isopolar, small size ( $P = 19.5 \pm 0.29 \mu\text{m}$ ;  $E = 23.3 \pm 0.34 \mu\text{m}$ ),  $P/E = 0.84$ , suboblate, amb. circular, triporate – tetraporate (Plate 2, figures 4–6). Pores are very small, circular ( $1.9 \times 2.0 \mu\text{m}$ ), annulate (ca.  $1.0 \mu\text{m}$  in thickness), region around the annuli with grains, exine thin (ca.  $1.0 \mu\text{m}$  in thickness), exine scabrate, perforated (Plate 2, figures 5, 7).

Species variations: stephanoporate pollen grains may also be observed.

*Geissospermum* Allemão

*Geissospermum argenteum* Woodson (Plate 2, figures 8–12)

Characteristics: tree, DBH = 35 cm, dark-gray buds, pedicels and sepals, beige flowers, petals free internally at the lobes

with white pilosity, collected in plateau forest, frequent, found in Central and Eastern Amazon and in the Guianas.

Palynological description: monad, isopolar, average size ( $P = 49.3 \pm 0.70 \mu\text{m}$ ;  $E = 43.0 \pm 0.43 \mu\text{m}$ ),  $P/E = 1.15$ , prolate-spheroidal, amb circular, stephanocolporate. Colpi are long ( $24 \times 5.9 \mu\text{m}$ ), surrounded by two thick ‘cords’: the first one shorter and parallel to colpi and the second one surrounding both the aperture and the first thickening, margin with a thickness of  $2 \mu\text{m}$ . This set of margins makes it difficult to visualise and measure the aperture, giving the impression that it is only the colpus; exine thin ( $1.6 \mu\text{m}$  in thickness) or thick (ca.  $2 \mu\text{m}$  close to the aperture), scabrate, nexine  $0.8 \mu\text{m}$ , sexine  $0.8 \mu\text{m}$ . The apocolpium is formed by the connection between the two margin-forming ‘cords’.

*Himatanthus* Willd. ex Schult.

*Himatanthus bracteatus* (A. DC.) Woodson var. *bracteatus* (Plate 2, figures 13–15)

Characteristics: tree, 12 m in height, DBH = 10 cm, white flowers, infrequent, found in the Amazon-Atlantic Forest Disjunction.

Palynological description: monad, isopolar, average size ( $P = 39.6 \pm 0.52 \mu\text{m}$ ;  $E = 46.6 \pm 0.59 \mu\text{m}$ ),  $P/E = 0.85$ , suboblate, amb triangular (Plate 2, figure 13), tricolporate, exine psilate. Colpi are long ( $27.5 \times 1.9 \mu\text{m}$ ) with truncated extremities, colpus with a thick margin (ca.  $2.0 \mu\text{m}$ ), endoaperture lalongate  $7.2 \times 7.7 \mu\text{m}$ , hard to visualise and measure, exine thick ( $3.5 \mu\text{m}$  in thickness), sexine (ca.  $2.5 \mu\text{m}$ ) thicker than nexine (ca.  $1 \mu\text{m}$ ), sexine psilate throughout most of the surface; in the mesocolpium region there is a depression with rugulate ornamentation (Plate 2, figures 14, 15).

*Himatanthus stenophyllus* Plumel (Plate 3, figures 1–4)

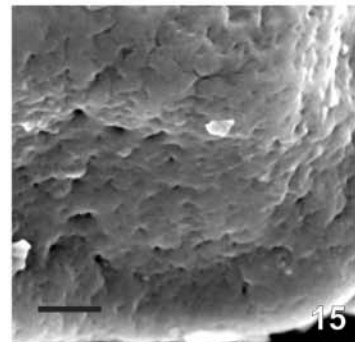
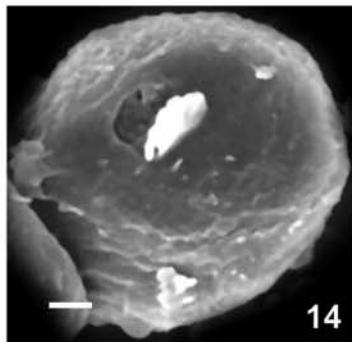
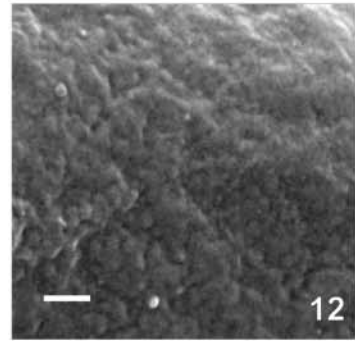
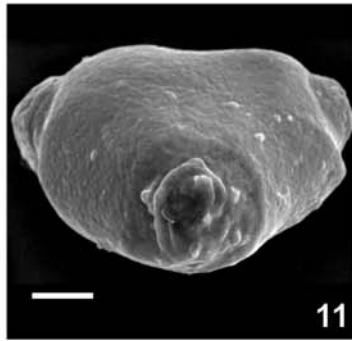
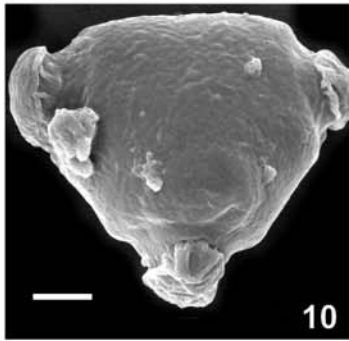
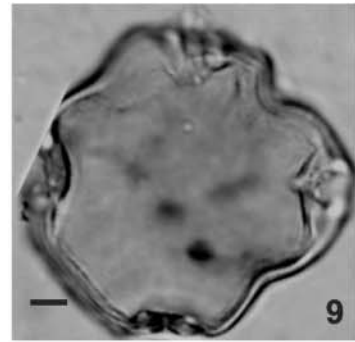
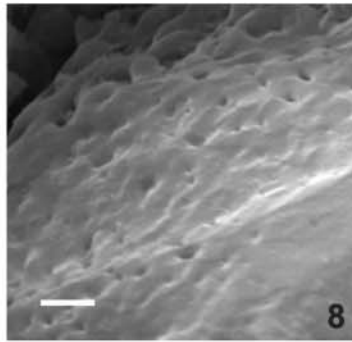
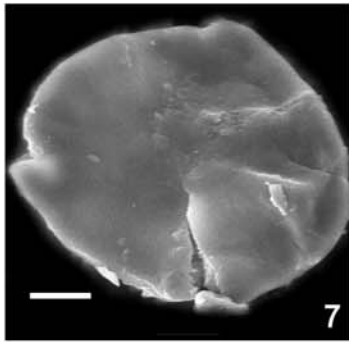
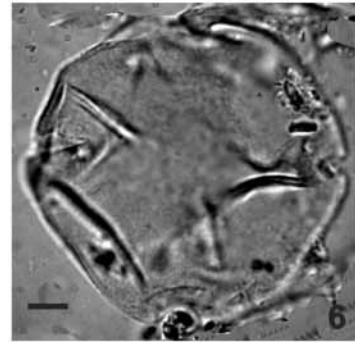
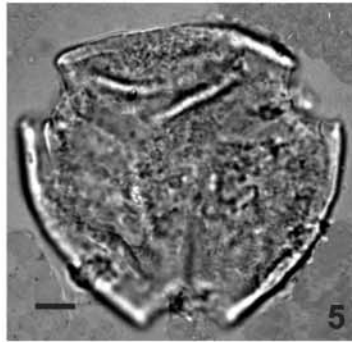
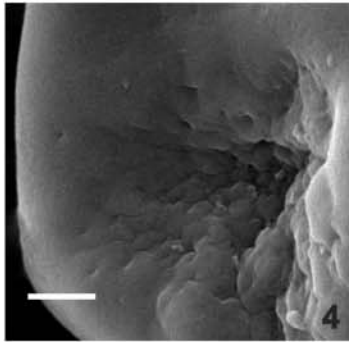
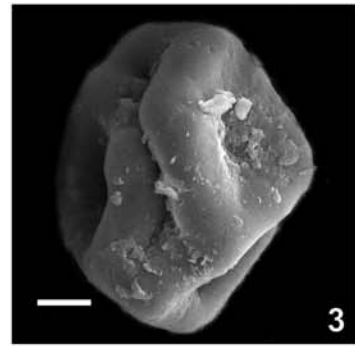
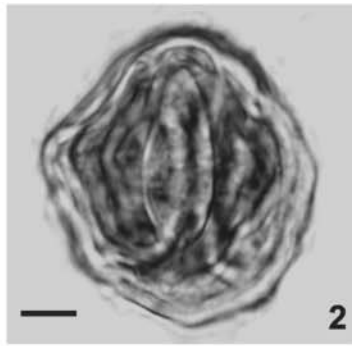
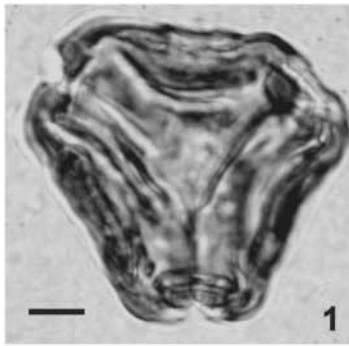
Characteristics: tree, 18 m in height, DBH = 19 cm, white flowers, collected in plateau forest, frequent, widely distributed in the Amazon.

Palynological description: monad, isopolar, average size ( $P = 37.2 \pm 0.58 \mu\text{m}$ ;  $E = 43.2 \pm 0.36 \mu\text{m}$ ),  $P/E = 0.86$ , suboblate, amb triangular (Plate 3, figure 1), tricolporate. Colpi are long ( $22.7 \times 2.1 \mu\text{m}$ ), with truncated extremities (Plate 3, figures 2, 3), colpus with a thick margin (ca.  $2–3 \mu\text{m}$ ), endoaperture lalongate ( $4.9 \times 2.1 \mu\text{m}$ ), exine thick (ca.  $3.2 \mu\text{m}$ ), sexine thicker than nexine (ca.  $2.1 \mu\text{m}$ ), nexine (ca.  $1.1 \mu\text{m}$ ), sexine psilate throughout most of the surface, ornamentation perforate (Plate 3, figures 3, 4).

*Himatanthus sucuuba* (Spruce ex Müll. Arg.) Woodson (Plate 3, figure 5)

Characteristics: tree, green sepals, white petals yellow at the base, collected in slope forest, sandy soil, frequent, found in tropical South America.

**Plate 2.** Light micrographs (LM) and scanning electron micrographs (SEM) of Apocynaceae. *Forsteronia acouci*: figure 1, polar view, general view (LM); figure 2, equatorial view, general view (SEM); figure 3, surface detail (SEM). *Forsteronia gracilis*: figure 4, polar view, general view (LM); figure 5, general view (SEM); figure 6: equatorial view, general view (LM); figure 7, aperture (SEM). *Geissospermum argenteum*: figure 8, polar view, general view (LM); figure 9, general view (SEM); figure 10, equatorial view, general view (LM); figure 11, general view (SEM); figure 12, surface detail (SEM). *Himatanthus bracteatus* var. *bracteatus*: figure 13 polar view, general view (LM); figure 14, general view (SEM); figure 15, equatorial view, surface detail (SEM). Scale bars: 1 =  $10 \mu\text{m}$ ; 2, 4–6, 8–11, 13–15 =  $5 \mu\text{m}$ ; 3 =  $1 \mu\text{m}$ ; 7, 12 =  $2 \mu\text{m}$ .



Palynological description: monad, isopolar, average size ( $P = 38.0 \pm 0.53 \mu\text{m}$ ;  $E = 42.7 \pm 0.43 \mu\text{m}$ ),  $P/E = 0.89$ , oblate-spheroidal, amb subtriangular (Plate 3, figure 5), tricolporate. Colpi ( $25.8 \times 1.5 \mu\text{m}$ ) have acute extremities; endoaperture circular ( $7.6 \times 7.5 \mu\text{m}$ ); exine thick ( $2.8 \mu\text{m}$ ), sexine psilate to finely perforated; sexine ( $1.9 \mu\text{m}$ ) as thick as nexine ( $0.9 \mu\text{m}$ ).

Species variations: tetracolporate grains were also observed.

*Lacmellea* H. Karst.

*Lacmellea arborescens* (Müll. Arg.) Markgr. (Plate 3, figures 6–8)

Characteristics: tree, leathery leaves, greenish flowers and buds, collected in plateau forest, rare, found in Central and Western Amazon.

Palynological description: monad, isopolar, average size ( $P = 42.3 \pm 0.85 \mu\text{m}$ ;  $E = 41.0 \pm 0.70 \mu\text{m}$ ),  $P/E = 1.03$ , prolate-spheroidal, amb circular (Plate 3, figures 6, 7), tetracolporate. Colpi are short ( $8.2 \times 1.9 \mu\text{m}$ ) with acute extremities, with a costa, endoaperture circular ( $2.4 \mu\text{m}$ ), exine thick ( $1.6 \mu\text{m}$ ), sexine thicker than nexine, exine scabrate with perforations (Plate 3, figure 8).

Species variation: annuli thickness varying from 2 to  $4 \mu\text{m}$ .

*Lacmellea gracilis* (Müll. Arg.) Markgr. (Plate 3, figures 9–12)

Characteristics: tree, 7.0 m in height, DBH = 10.0 cm, green-whitish flowers, collected in plateau forest, understory, clay soil, frequent, found in Central and Western Amazon.

Palynological description: monad, isopolar, average size ( $P = 32.3 \pm 0.69 \mu\text{m}$ ;  $E = 17.2 \pm 0.55 \mu\text{m}$ ),  $P/E = 1.87$ , prolate, amb circular or triangular (Plate 3, figures 9, 10), tricolporate – tetracolporate (Plate 3, figures 9, 10). Colpi are short (ca.  $10 \mu\text{m}$  in length), with fastigiate costa (Plate 3, figures 9–11), endoaperture circular (ca.  $3.6 \mu\text{m}$ ), exine thin ( $1.4 \mu\text{m}$ ), sexine scabrate with sparse perforations (Plate 3, figure 12).

*Macoubea* Aublet

*Macoubea sprucei* (Mull. Arg.) Markgr. (Plate 3, figures 13–15)

Characteristics: treelet, 7 m in height, DBH = 11.8 cm, green and yellow buds, yellow fragrant flowers, collected in campinarana forest (vegetation type that grow over pure leached white sand (Pires & Prance 1985), understory, sandy soil, frequent, found in Central Amazon to Central America.

Palynological description: monad, isopolar, average size ( $P = 40.9 \pm 0.59 \mu\text{m}$ ;  $E = 37.2 \pm 0.68 \mu\text{m}$ ),  $P/E = 1.10$ , prolate-spheroidal, amb circular, diporate. Pores ( $11.7 \times 5.9 \mu\text{m}$ ) are large, have a thick annulus (ca.  $3 \mu\text{m}$ ), exine thicker and scabrae more abundant close to the pore, exine  $1.0 \mu\text{m}$  in thickness in the other regions of the pollen grain.

*Mandevilla* Lindl.

*Mandevilla scabra* (Roem. & Schult.) K. Schum. (Plate 4, figures 1–3)

Characteristics: prostrate herb, voluble, creeping, collected in secondary vegetation (capoeira), sandy soil.

Palynological description: monad, apolar, large size ( $D1 = 139.0 \pm 3.10 \mu\text{m}$ ;  $D2 = 138.7 \pm 4.17 \mu\text{m}$ ), amb circular, pantoporate (4–6 pores) (Plate 4, figure 1), exine rugulate. Pores are small, circular ( $20.5 \times 21 \mu\text{m}$ ), with a thin annulus (Plate 4, figure 2), exine thin ( $1.5 \mu\text{m}$ ), sexine with inconspicuous rugulae, best seen under SEM (Plate 4, figure 3).

*Odontadenia* Benth.

*Odontadenia perrottetii* (A. DC.) Woodson (Plate 4, figures 4–6)

General plant characteristics: tall liana in terra-firme forest, yellow flowers, rare, found in Central and Eastern Amazon.

Palynological description: monad, isopolar, large size ( $P = 40.7 \pm 1.47 \mu\text{m}$ ;  $E = 55.8 \pm 1.59 \mu\text{m}$ ), amb circular (Plate 4, figure 4), triporate – tetraporate, exine psilate. Pores are small ( $4.4 \mu\text{m}$ ), circular, with thin annuli (ca.  $3 \mu\text{m}$ ) (Plate 4, figure 5), exine thin ( $0.5 \mu\text{m}$ ), sexine psilate to scabrate close to the pore (Plate 4, figure 6).

*Odontadenia puncticulosa* (L. C. Rich.) Pulle (Plate 4, figures 7–10)

Characteristics: woody liana, yellow flowers, collected in campinarana forest, frequent, found in southern Central America and northern South America.

Palynological description: monad, apolar, large size ( $D1 = 62.9 \pm 1.09 \mu\text{m}$ ,  $D2 = 54.8 \pm 1.04 \mu\text{m}$ ), amb circular, pantoporate (6–8 pores). Pores are large ( $6.2 \mu\text{m}$ ), circular, with thin annuli (Plate 4, figures 7–9), exine thin ( $1.4 \mu\text{m}$ ), sexine with conspicuous rugulae and sparse perforations (Plate 4, figure 10).

*Odontadenia verrucosa* (Willd. ex Roem. & Schult.) K. Schum. ex Markgr. (Plate 4, figures 11–15)

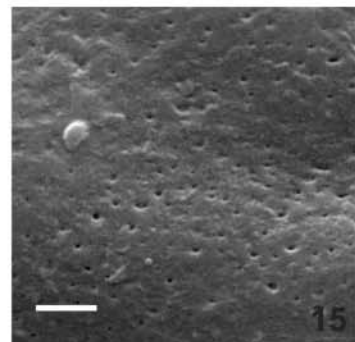
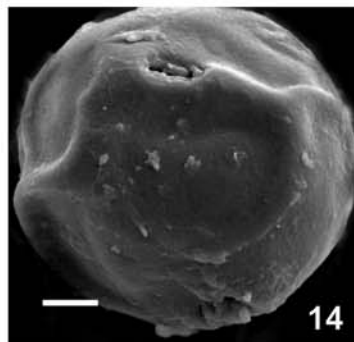
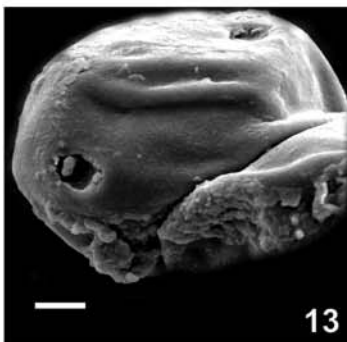
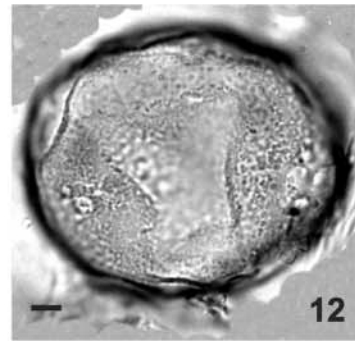
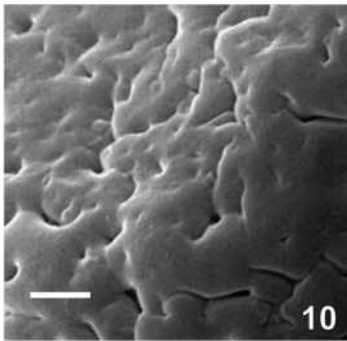
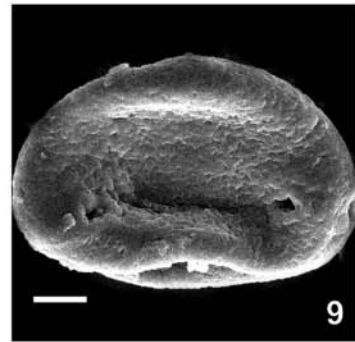
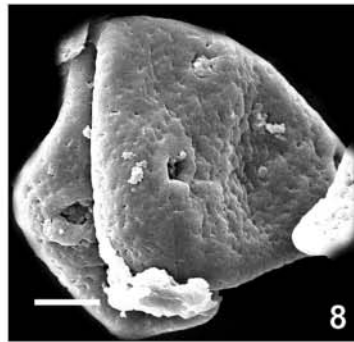
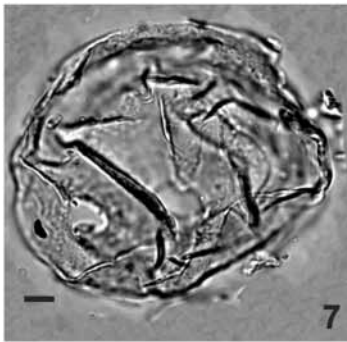
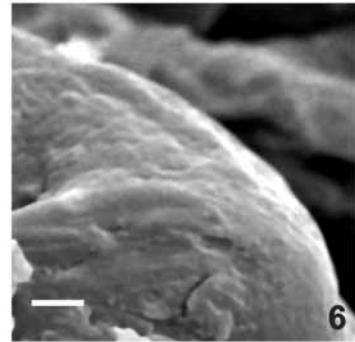
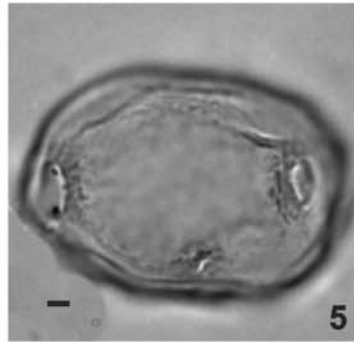
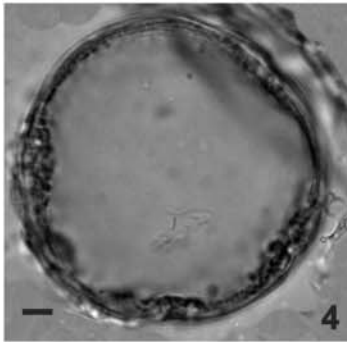
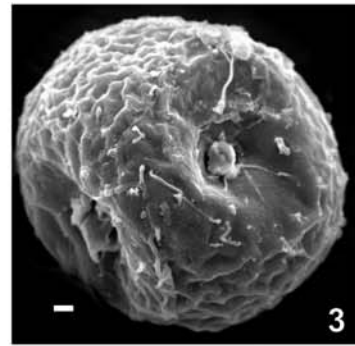
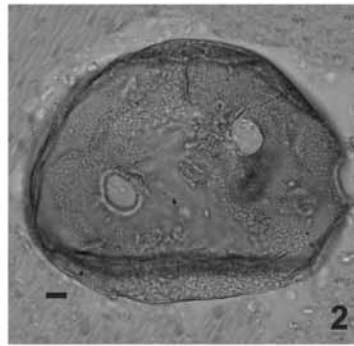
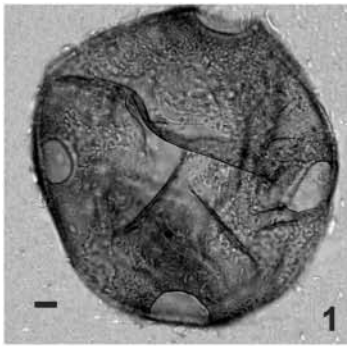
Characteristics: canopy liana, green sepals, golden-yellow petals, orange with red bands in the tube interior, very fragrant, collected in lowland forest, common, found in southern Central America and northern South America.

Palynological description: monad, apolar, large size ( $D1 = 52.3 \pm 1.26 \mu\text{m}$ ,  $D2 = 45.2 \pm 1.08 \mu\text{m}$ ), amb circular (Plate 14, figure 11), pantoporate (6–8 pores). Pores are large, circular ( $9.0 \mu\text{m}$ ), with thin annuli (ca.  $1 \mu\text{m}$  in thickness), with granules in their surroundings (Plate 4, figures 12–14), exine scabrate with perforations, thin (ca.  $2 \mu\text{m}$ ), up to  $3 \mu\text{m}$  close to the pores (Plate 4, figure 15).

*Parahancornia* Ducke

*Parahancornia fasciculata* (Poir.) Benoist (Plate 5, figures 1–3)

**Plate 3.** Light micrographs (LM) and scanning electron micrographs (SEM) of Apocynaceae. *Himatanthus stenophyllus*: figure 1, polar view, general view (LM); figure 2, equatorial view, general view (LM); figure 3, general view (SEM); figure 4, surface detail (SEM). *Himatanthus sucuuba*: figure 5, polar view, general view (LM). *Lacmellea arborescens*: figure 6, polar view, general view (LM); figure 7, general view (SEM); figure 8, surface detail (SEM). *Lacmellea gracilis*: figure 9, polar view, general view (LM); figure 10, general view (SEM); figure 11, equatorial view, general view (SEM); figure 12, surface detail (SEM). *Macoubea sprucei*: figure 13, equatorial view, general view (LM); figure 14, general view (SEM); figure 15, surface detail (SEM). Scale bars: 1–3, 5–7, 9–11, 13 =  $5 \mu\text{m}$ ; 4, 8, 14, 15 =  $2 \mu\text{m}$ , 12 =  $1 \mu\text{m}$ .



Characteristics: Canopy tree, 20.0 m in height, DBH = 25.0 cm; yellowish-green buttons, white petals, yellow sepals, collected in lowland forest, infrequent, widely distributed in the Amazon and the Guianas.

Palynological description: monad, isopolar, average size ( $P = 38.6 \pm 0.85 \mu\text{m}$ ;  $E = 36.7 \pm 0.94 \mu\text{m}$ ),  $P/E = 1.05$ , prolate-spheroidal, amb subcircular, triporate (Plate 5, figure 1). Pores are large, circular ( $7.6 \mu\text{m}$ ), with an annulus (ca.  $1 \mu\text{m}$ ), exine thin ( $1.7 \mu\text{m}$ ), sexine psilate to scabrate in the mesopore and granules surrounding the pores (Plate 5, figures 2, 3).

#### *Rauvolfia* L.

*Rauvolfia sprucei* Mull. Arg. (Plate 5, figures 4–7)

Characteristics: treelet, flowers with a greenish tube and purple lobes, DBH = 6 cm, 10 m in height, collected in plateau forest, infrequent.

Palynological description: monad, isopolar, very large size ( $P = 98.9 \pm 1.43 \mu\text{m}$ ;  $E = 106.8 \pm 0.81 \mu\text{m}$ ),  $P/E = 0.93$ , oblate-spheroidal, amb subcircular, tricolporate. Colpi are short ( $17.8 \times 6.6 \mu\text{m}$ ), with a margin (ca.  $5.0 \mu\text{m}$ ), a distinct fastigium (Plate 5, figure 4); endoaperture circular ( $8.7 \mu\text{m}$ ) (Plate 5, figures 5–7). Each aperture is located in a depression formed by two wide and thick margins, exine psilate and thin ( $1.1 \mu\text{m}$ ).

Species variation: tetracolporate grains were also observed.

#### *Rhigospira* Miers

*Rhigospira quadrangularis* (Müll. Arg.) Miers (Plate 5, figures 8–10)

Characteristics: canopy tree, DBH = 25.0 cm; terminal yellowish-green inflorescence; petals yellowish-green in the tube and internally, free lobes of the petals white, collected in campinarana forest, infrequent, found in Central and Western Amazon.

Palynological description: monad, isopolar, average size ( $P = 37.0 \pm 0.60 \mu\text{m}$ ;  $E = 36.5 \pm 0.68 \mu\text{m}$ ),  $P/E = 1.01$ , prolate-spheroidal, amb subtriangular, tricolporate. Colpi are short (ca.  $10 \times 14 \mu\text{m}$ ), endoaperture circular ( $5.6 \mu\text{m}$ ), with a distinct fastigium (Plate 5, figures 8, 9), granules in the surroundings of the aperture (Plate 5, figure 10), exine psilate and thin ( $1.4 \mu\text{m}$ ).

#### *Secondatia* A. DC.

*Secondatia duckei* Markgr. (Plate 5, figures 11, 12)

Characteristics: woody liana, leaves with a recurved margin, yellow flowers, collected in campinarana, sandy to sandy-clay soils, common, found in Central Amazon.

Palynological description: monad, isopolar, small size ( $P = 24.8 \pm 0.57 \mu\text{m}$ ;  $E = 20.6 \pm 0.48 \mu\text{m}$ ),  $P/E = 1.20$ , subprolate, amb circular, triporate – stephanoporate (Plate 5, figure 11). Pores are very small and circular ( $2.0 \mu\text{m}$ ), with an annulus (ca.  $2 \mu\text{m}$ ), exine thin ( $1.2 \mu\text{m}$ ), sexine scabrate with perforations best seen under SEM (Plate 5, figures 12, 13) and granules surrounding the pores.

#### *Tabernaemontana* L.

*Tabernaemontana angulata* Mart. ex Müll. Arg. (Plate 5, figures 13, 14)

Characteristics: shrub, 2 m in height, calyx and corolla white, with a purple base, collected in plateau forest, common, found in Central and Eastern Amazon.

Palynological description: monad, isopolar, large size ( $P = 57.7 \pm 1.65 \mu\text{m}$ ;  $E = 37.2 \pm 0.70 \mu\text{m}$ ),  $P/E = 1.55$ , prolate, amb circular, tricolporate. Colpi are short ( $20.4 \times 0.8 \mu\text{m}$ ), with a costa, endoaperture endocingulate ( $7.7 \mu\text{m}$ ) (Plate 5, figure 14), exine thin ( $2 \mu\text{m}$ ), sexine (ca.  $1.5 \mu\text{m}$ ) thicker than nexine (ca.  $0.5 \mu\text{m}$ ), sexine scabrate in the mesocolpium and rugulate with perforations on the pole (Plate 5, figure 15).

Species variation: verrucae were observed close to the endocingulum in some grains.

*Tabernaemontana flavicans* Willd. ex Roem. & Schult. (Plate 6, figures 1–4)

Characteristics: tree, DBH = 7 cm, greenish buds, clear yellow flowers with an apex of yolk-yellow petals, collected in plateau forest, common, found in tropical South America.

Palynological description: monad, isopolar, large size ( $P = 83.4 \pm 2.46 \mu\text{m}$ ;  $E = 64.0 \pm 1.76 \mu\text{m}$ ),  $P/E = 1.30$ , subprolate, amb circular (Plate 6, figure 1), tricolporate. Colpi are short ( $34.3 \times 4.5 \mu\text{m}$ ), with an ornamented membrane, with a costa, endoaperture endocingulate ( $13.4 \mu\text{m}$ ) (Plate 6, figures 2–4), with a fastigium, exine thin ( $1 \mu\text{m}$ ), sexine densely perforated.

*Tabernaemontana macrocalyx* Mull. Arg. (Plate 6, figures 5–7)

Characteristics: treelet, DBH = 5 cm, 2.5 m in height, cream buds and cream flowers with internally yellow petals, fragrant flowers, collected in lowland forest, rare, widely distributed in the Amazon.

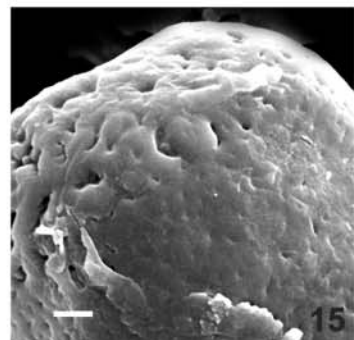
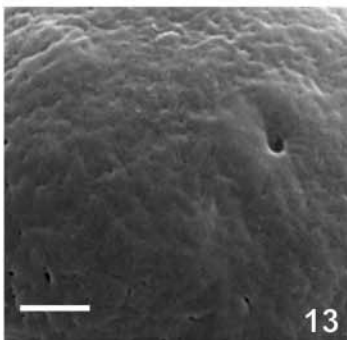
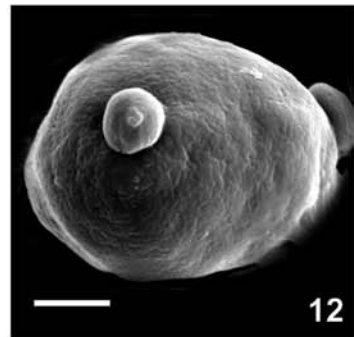
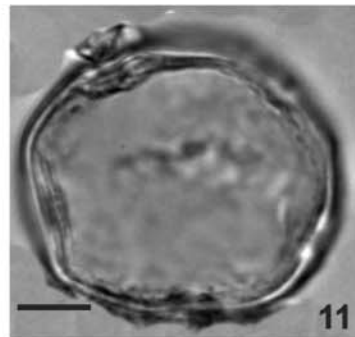
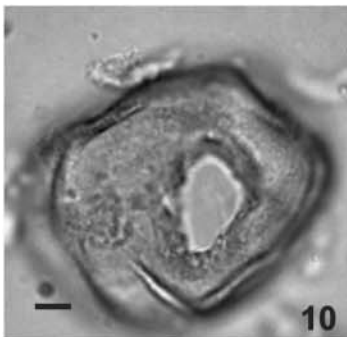
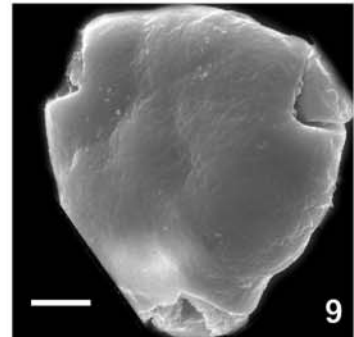
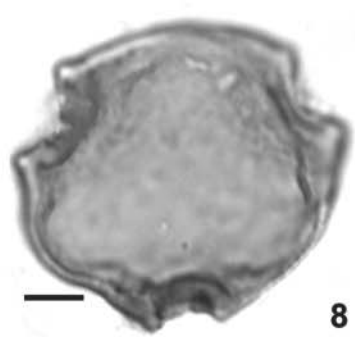
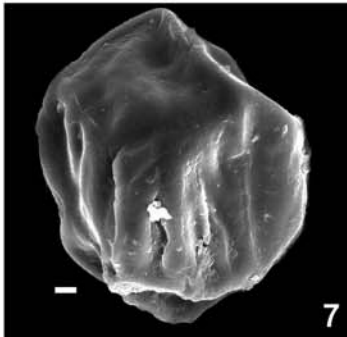
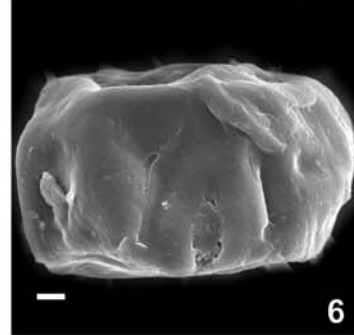
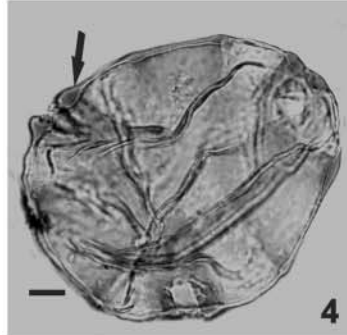
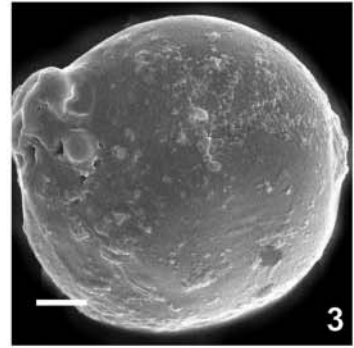
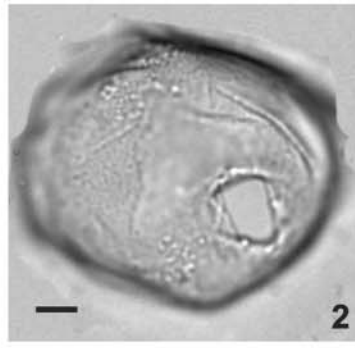
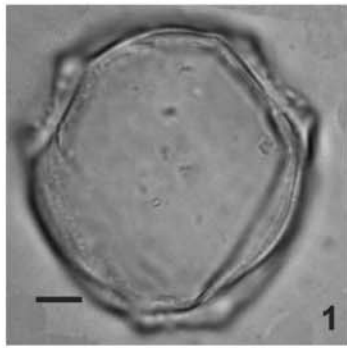
Palynological description: monad, isopolar, very large size ( $P = 91.0 \pm 1.64 \mu\text{m}$ ;  $E = 46.0 \pm 0.88 \mu\text{m}$ ),  $P/E = 1.98$ , prolate, amb circular, tricolporate. Colpi are short ( $30.3 \times 1.8 \mu\text{m}$ ), with an ornamented membrane, with a costa, endoaperture endocingulate ( $9.4 \mu\text{m}$ ) (Plate 6, figure 6), exine thick ( $3.2 \mu\text{m}$ ), sexine (ca.  $2 \mu\text{m}$ ) thicker than nexine (ca.  $1.2 \mu\text{m}$ ), sexine scabrate, with conspicuous perforations at the poles (Plate 6, figure 7).

*Tabernaemontana muricata* Spruce ex Müll. Arg. (Plate 6, figures 8–10)

Characteristics: treelet, white flowers, collected in terra-firme forest, common, found around Manaus.

Palynological description: monad, isopolar, large size ( $P = 57.6 \pm 1.08 \mu\text{m}$ ;  $E = 44.4 \pm 0.91 \mu\text{m}$ ),  $P/E = 1.30$ , subprolate, amb circular, tricolporate. Colpi are short ( $23.4 \times 2.8 \mu\text{m}$ ), with a costa, with an ornamented membrane (Plate 6, figure 9), endoaperture endocingulate ( $10.3 \mu\text{m}$ ), with a costa (Plate 6, figure 8), exine thick ( $2 \mu\text{m}$ ), sexine (ca.  $1 \mu\text{m}$ ) as thick as nexine

**Plate 4.** Light micrographs (LM) and scanning electron micrographs (SEM) of Apocynaceae. *Mandevilla scabra*: figure 1, polar view, general view (LM); figure 2, equatorial view, general view (LM); figure 3, general view (SEM). *Odontadenia perrottetii*: figure 4, general view (LM); figure 5, general view (LM); figure 6, surface detail (SEM). *Odontadenia puncticulosa*: figure 7, general view (LM); figures 8, 9, general view (SEM); figure 10, surface detail (SEM). *Odontadenia verrucosa*: figure 11, general view (LM); figure 12, aperture (LM); figures 13, 14, general view, aperture (SEM); figure 15, surface detail (SEM). Scale bars: 1–5, 7–9, 11–14 =  $5 \mu\text{m}$ ; 6 =  $2 \mu\text{m}$ , 10, 15 =  $1 \mu\text{m}$ .



(ca. 1  $\mu\text{m}$ ), sexine scabrate with perforations at the poles (Plate 6, figure 10).

*Tabernaemontana undulata* Vahl (Plate 6, figures 11–15)

Characteristics: treelet, 3 m in height, DBH = 5 cm, pink-white calyx, corolla tube purple-whitish in its lower part, pinkish in its upper part, collected in slope forest, common, found in southern Central America and northern South America.

Palynological description: monad, isopolar, large size ( $P = 61.5 \pm 1.10 \mu\text{m}$ ;  $E = 41.6 \pm 0.62 \mu\text{m}$ ),  $P = 1.48$ , prolate, amb circular, tricolporate. Colpi are short ( $26.4 \times 0.7 \mu\text{m}$ ), membrane ornamented (Plate 6, figure 11–13), with a costa (Plate 6, figure 12), endoaperture endocingulate ( $4.6 \mu\text{m}$ ) (Plate 6, figure 12, 14), exine thick ( $3 \mu\text{m}$ ), sexine (ca.  $2 \mu\text{m}$ ) thicker than nexine (ca.  $1 \mu\text{m}$ ), sexine scabrate with distinct perforations in the polar regions (Plate 6, figure 15).

### 3.1. Pollen key for species separation

1. Apolar, porate pollen grains
  2. Sexine psilate or scabrate
    3. Sexine psilate.....*Odontadenia perrottetii*
    3. Sexine scabrate.....*Odontadenia verrucosa*
  2. Sexine rugulate
    4. Sexine with inconspicuous rugulae, pores ca.  $20.5 \times 21 \mu\text{m}$ .....*Mandevilla scabra*
    4. Sexine with conspicuous rugulae and sparse perforations, pores ca.  $6.2 \mu\text{m}$ .....*Odontadenia puncticulosa*
1. Isopolar pollen grains
  5. Porate pollen grains
    6. Diporate pollen grains.....*Macoubea sprucei*
    6. triporate – hexaporate pollen grains
      7. Sexine rugulate or scabrate
      8. Sexine rugulate-perforated.....*Forsteronia acouci*
      8. Sexine scabrate-perforated.....*Forsteronia gracilis*
    7. Sexine psilate to scabrate
      9. Sexine psilate to scabrate at the mesoporum.....*Parahancornia fasciculata*
      9. Sexine scabrate with perforations.....*Secondatia duckei*
  5. Colporate pollen grains
    10. Solely stephanocolporate pollen grains, colpi surrounded by two thick 'cords'.....*Geissospermum argenteum*
    10. Tricolporate or tetracolporate pollen grains
    11. Tricolporate – tetracolporate pollen grains.....*Lacmellea arborescens* and *L. gracilis*
    11. Solely tricolporate pollen grains
      12. Pollen grains with an endocingulate endoaperture
      13. Sexine densely perforated.....*Tabernaemontana flavicans*

13. Sexine scabrate with perforations at the poles, or scabrate in the mesocolpium and rugulate at the poles
14. Sexine scabrate in the mesocolpium and rugulate at the poles.....*Tabernaemontana angulata*
14. Sexine scabrate with perforations at the poles.....*Tabernaemontana macrocalyx*, *Tabernaemontana muricata*, *Tabernaemontana undulata*
12. Pollen grains without endocingulate endoaperture
15. Sexine scabrate
  16. Endoaperture (ca.  $3\text{--}6 \mu\text{m}$ ), with granulated surroundings.....*Ambelania acida*
  16. Endoaperture ( $11.2 \times 6.2 \mu\text{m}$ ), without granulated surroundings.....*Couma guianensis*
15. Sexine perforated or psilate
  17. Sexine perforated, conspicuous perforations; in the medial mesocolpium region there is a depression with granulated ornamentation.....*Couma utilis*
  17. Sexine psilate
    18. In the mesocolpium region there is a depression with rugulate ornamentation, with perforations.....*Himatanthus bracteatus* var. *bracteatus* and *Himatanthus stenophyllus*
    18. Without a depression in the mesocolpium
      19. Colpi located in a depression formed by two wide and thick margins.....*Rauvolfia sprucei*
      19. Colpi not located in a depression
        20. Colpi with a distinct fastigium and granules in the surroundings of the aperture.....*Rhigospira quadrangularis*
        20. Colpi without a fastigium and without granules in the surroundings of the aperture.....*Himatanthus sucuuba*

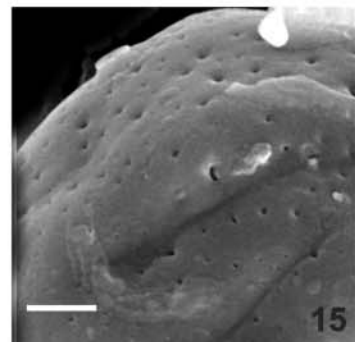
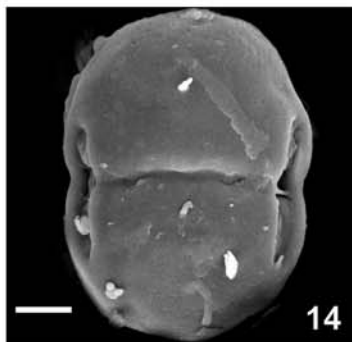
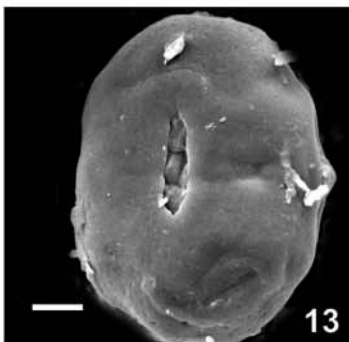
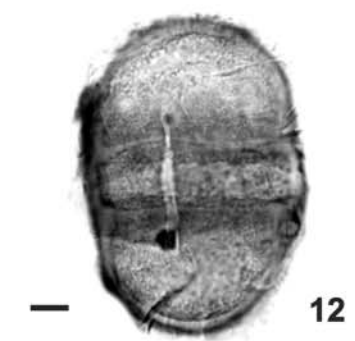
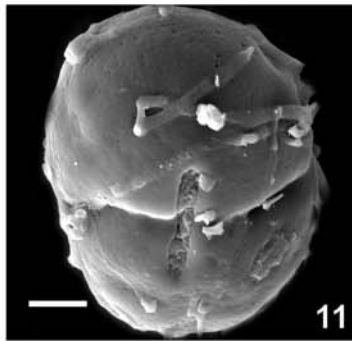
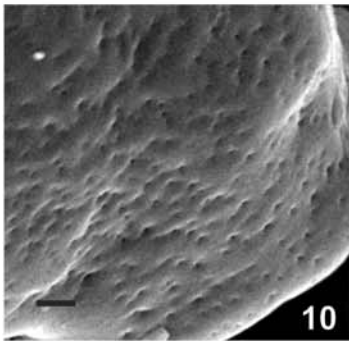
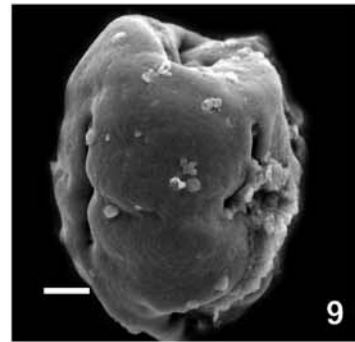
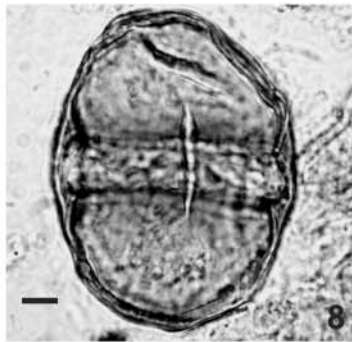
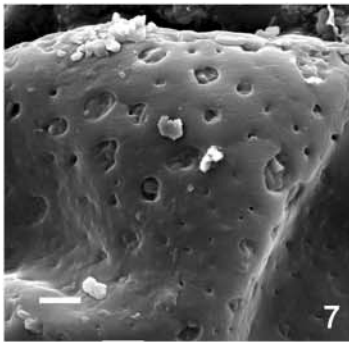
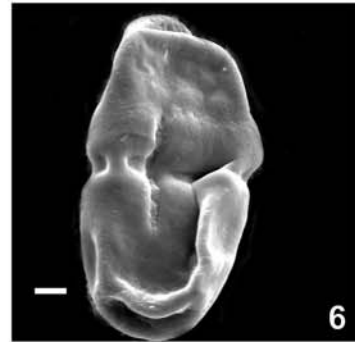
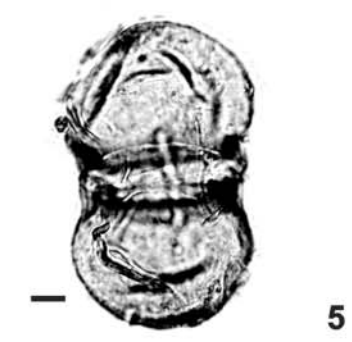
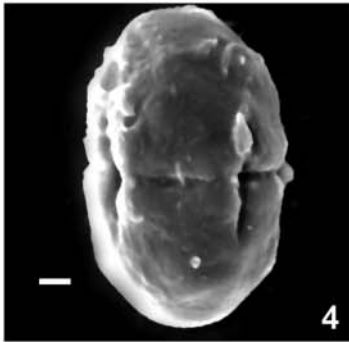
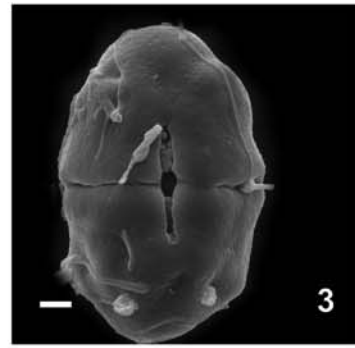
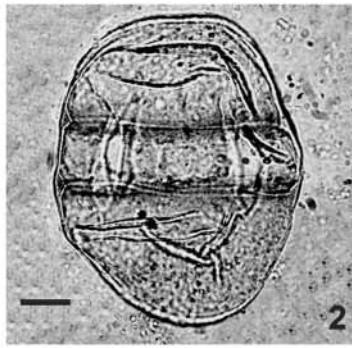
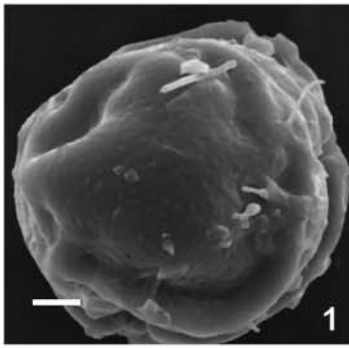
### 4. Discussion and conclusion

In general, there was a great degree of morphological variation among the pollen grains, which were apolar or isopolar, diporate to stephano (col)porate, with ornamentation ranging from psilate, scabrate to rugulate.

Endress & Bruyns (2000) proposed the tribal classification within the subfamilies of Apocynaceae. Pollen grains of Rauvolfioideae (tribes Alstonieae, Vinceae, Willughbeieae, Tabernaemontaneae, Melodineae, Hunterieae, Plumerieae, Carisseae and Alyxieae) are usually colporate, while those of Apocynoideae (tribes Wrightieae, Malouetieae, Apocynae, Mesechiteae and Echiteae) are nearly always porate. Psilate-perforate is the most common ornamentation type (Middleton 2007). In the species

**Plate 5.** Light micrographs (LM) and scanning electron micrographs (SEM) of Apocynaceae. *Parahancornia fasciculata*: figure 1, polar view, general view (LM); figure 2, equatorial view, aperture (LM); figure 3, general view (SEM). *Rauvolfia sprucei*: figure 4, polar view, general view (LM), arrow indicates the costa; figure 5, equatorial view, general view (LM); figures 6, 7, general view (SEM). *Rhigospira quadrangularis*: figure 8, polar view, general view (LM); figure 9, general view (SEM); figure 10, equatorial view, aperture (LM). *Secondatia duckei*: figure 11, polar view, general view (LM); figure 12, equatorial view, general view (SEM); figure 13, surface detail (SEM). *Tabernaemontana angulata*: figure 14, equatorial view, general view (LM); figure 15, surface detail (SEM). Scale bars: 1–3, 6–12, 14 =  $5 \mu\text{m}$ ; 4, 5 =  $10 \mu\text{m}$ ; 13, 15 =  $2 \mu\text{m}$ .





found in the RFAD, the great majority presented the same characters as the type of aperture and ornamentation in the subfamilies Rauvolfioideae: *Geissospermum argenteum* (colporate, scabrate), *Lacmellea arborescens* (colporate, scabrate with perforations), *L. gracilis* (colporate, scabrate with sparse perforations), *Tabernaemontana angulata*, *T. macrocalyx*, *T. muricata* and *T. undulata* (colporate, scabrate perforate), *T. flavicans* (colporate, perforate); and Apocynoideae: genera *Odontadenia* and *Secundaria* (porate) and *Mandevilla scabra* (pantoporate). According to phylogenetic studies of Endress & Bruyns (2000), Rauvolfioideae represents a basal group within the subfamilies Apocynaceae s. l. Particularities such as pollen grains usually porate and inaperturate, in most of Apocynoideae, Periplocoideae, Secamonoideae and Asclepiadoideae, as opposed to the brevicolporate condition in the most Rauvolfioideae, represent derived characters (Sennblad & Bremer 2002). In the RFAD, monad pollen grains of Rauvolfioideae and Apocynoideae are found. Characters such as tetrads and polynyas of the other subfamilies correspond to derived structures within Apocynaceae s. l. According to Middleton (2007), this condition correlates with the increase of floral morphological complexity within Apocynaceae s. str.; tetrads occur in only six out of the 162 genera.

According to the classification of the Apocynaceae s. l. by Endress & Bruyns (2000), the genus *Rauvolfia* is inserted into the tribe Vinceae, subfamily Rauvolfioideae. The morphology of *Rauvolfia sprucei* described in this study is not significantly different from that described by Barth & Luz (2008) with respect to polarity (isopolar), size (large;  $P = 98.9$ ;  $E = 106.8 \mu\text{m}$ ), amb (subcircular), number and type of apertures (tricolporate), as well as exine (psilate). However, the shape (oblate-spheroidal) and the presence of a thick margo between the colpi described in the present study were different from earlier descriptions, which reported suboblate grains lacking a significant margin between the colpi. Two species of the Colombian Caribbean have only one characteristic in common with *R. sprucei* of the RFAD, namely, a psilate sexine; however, they differ in various characteristics, such as the prolate spheroidal shape, triporate and amb circular in *R. littoralis* and subprolate shape, tetraporate – stephanoporate and amb circular in *R. tetraphylla* (García-M. et al. 2011).

The grain of *Odontadenia puncticulosa*, described by Roubik & Moreno (1991), is apolar and tetraperiporate; *O. macrantha* is apolar and diporate – triporate; while the grain of *O. puncticulosa* of RFAD is apolar and periporate (6–8 pores). In *Odontadenia geminata* (Colombian Amazon), described by Rangel Ch (2008), the grain is triporate, tetraporate – stephanoporate or periporate (5–7 pores), amb circular, suboblate, apolar or isopolar. The same species described by Carreira & Barth (2003) grains are triporate, amb circular and isopolar. The two species *O. perrottetii* and *O. verrucosa* in this study also provide similar descriptions to previous results, isopolar grains and triporate or

tetraporate for the first species and apolar and periporate (6–8 pores) for the second species. The *Odontadenia* genus studied by Marques & Melhem (1966) also presents variability in the number of pores. *Odontadenia*, belonging to the tribe Apocynaceae, subfamily Apocynoideae, from Malaysia, has monad grains, small- to medium-sized or medium-sized to large, mostly stephanoporate (3–4 pores), sometimes stephanoporate (2–5 pores), oblate to prolate. The ornamentation is psilate to scabrate, sparsely to densely perforate or imperforate (*Anodendron*, *Beaumontia*, *Elytropus*, *Odontadenia*, *Urceola*) (Middleton 2007). In the RFAD the genus *Odontadenia* has grains similar to those of Malesia, in the presence of monad grains, large, ornamentation scabrate (*O. perrottetii* and *O. verrucosa*) and pantoporate (*O. puncticulosa* and *O. verrucosa*).

For *Geissospermum argenteum*, belonging to the subfamily Rauvolfioideae, tribe Alstonieae, Nilsson et al. (1993) described the pollen grains as tricolporate, tectate and spheroidal to subprolate, whereas pollen grains from the same species collected in the Adolpho Ducke Forest Reserve were stephanocolporate, prolate-spheroidal and had a distinct margin forming ‘cords’ around the colpus. Middleton (2007) described *Geissospermum* and *Aspidosperma* with more or less prominent extracolpal ridges. Some species of *Aspidosperma* Juss. have been synonymised with *Geissospermum*, and analyses of the pollen grains from species of these two genera have revealed many similarities. Moreira et al. (2004) performed a palynological analysis of *Aspidosperma parvifolium* A. DC., and Barth & Luz (2008) examined four species of this genus, and their results are similar to those reported for *Geissospermum argenteum* in this study.

The pollen of *Lacmellea* was described by Colinvaux et al. (1999) and it is peroblate, with lalongate pores and amb circular, which differs from the species *Lacmellea arborescens* and *L. gracilis* from RFAD, which have prolate spheroidal and prolate grains, respectively, of amb varying circular or triangular and endoaperture circular. Rangel Ch (2008) described the grains of *L. arborescens* of Brazilian Amazonia (Rondônia) with different variations in this species, such as tricolporate, tetraporate – stephanocolporate, endoaperture lalongate, amb circular to convex triangular or quadrangular straight and peroblate. Middleton (2007) described the pollen species belonging to this subfamily Rauvolfioideae (tribe Willughbeieae) of Malaysia as monads, oblate spheroidal to three- or four-aperturate, sometimes porate (*Lacmellea*). The psilate-scabrate ornamentation in *Lacmellea* from Malaysia finds some correspondence to the genus of RFAD, which is scabrate with perforations. The morphological characterisation of *Tabernaemontana* pollen has subsidised phylogenetic studies and allowed the species classification of the New and Old World in the tribe Tabernaemontaneae.

*Tabernaemontana* belongs to the subfamily Rauvolfioideae (tribe Tabernaemontaneae) (Middleton 2007). Tabernaemontaneae

**Plate 6.** Light micrographs (LM) and scanning electron micrographs (SEM) of Apocynaceae. *Tabernaemontana flavicans*: figure 1, polar view, general view (SEM); figure 2, equatorial view, aperture (LM); figure 3–4, general view (SEM). *Tabernaemontana macrocalyx*: figure 5, equatorial view, aperture (LM); figure 6, general view (SEM); figure 7, surface detail (SEM). *Tabernaemontana muricata*: figure 8, equatorial view, aperture (LM); figure 9, general view (SEM), figure 10, surface detail (SEM). *Tabernaemontana undulata*: figure 11, polar view, general view (SEM); figure 12, aperture (LM); figure 13, general view, aperture (SEM); figure 14, general view, mesocolpi (SEM); figure 15, surface detail (SEM). Scale bars: 1, 3–6, 8, 9, 11–14 = 5  $\mu\text{m}$ ; 2 = 10  $\mu\text{m}$ ; 7, 10 = 1  $\mu\text{m}$ ; 15 = 2  $\mu\text{m}$ .

is considered monophyletic by the occurrence of distinctly lalongate endoapertures that might be fused to form an endocingulum, which occurs in species of the Old World. The clade *Tabernaemontana* of the Old World is supported by the occurrence of densely perforate pollen with long colpi (Van der Weide & Van der Ham 2012). *Tabernaemontana* is the largest genus in *Tabernaemontaneae* and contains both Old and New World species (Leeuwenberg 1991, 1994a, 1994b).

In *Tabernaemontana*, pollen grain size varied from large in most species to very large in *T. macrocalyx*. Zonorate grains characterise the *Tabernaemontanoideae* (Erdtman 1966). The equatorial zone was quite wide and continuous and consisted of endocingulum costate in all species from RFAD, as described by Van Campo et al. (1979) for *T. flavicans*.

The last mentioned authors characterised *T. flavicans* pollen grains as tetracolporate (solely tricolporate in the present study), similar to the present study. Moreira et al. (2004) described *T. flavicans* pollen grains as triporate – tetraporate, with a very large polar area, circular amb and endocingulate aperture; this latter characteristic has also been observed for all *Tabernaemontana* species described in the RFAD. The presence of a costate endocingulum was observed in all pollen grains from this genus. Characteristics such as a circular amb and an extremely short colpi, as described by these authors for *T. flavicans*, were also consistent with the pollen samples from the RFAD. *T. undulata* grains were brevicolporate, costate, amb circular and possessed an endocingulum, an exine with a thickness of 3  $\mu\text{m}$  and a sexine with a thickness of 2  $\mu\text{m}$ . Likewise, Nilsson (1990) described the same species with these characteristics, except with an exine of 2  $\mu\text{m}$ . Van Campo et al. (1979) also observed tricolporate pollen grains in *T. undulata*. Species with common characteristics such as *T. submollis*, occurring in the Serra dos Carajás (Pará Amazon), are isopolar but are tetracolporate (Carreira & Barth 2003). *T. cymosa* and *T. arborea* are also tricolporate (Garcia-M et al. 2011; Roubik & Moreno 1991). In the same way, *T. cerea* has a prolate grain and short colpi, differing from the species of the RFAD in the presence of lalongate pores and aperture (tetraporate, stephanoaperturate) (Leal et al. 2011). Middleton (2007) characterised the *Tabernaemontana* pollen grains as medium sized, prolate; with short colpi (brevicolporate) and lalongate endopores, which are fused into an endocingulum (mostly with equatorial costae), similar to *Tabernaemontana* of RFAD in the following aspects: prolate or subprolate grains, short colpi and endocingulate endoapertures, differing in the size from large to very large.

Van der Weide & Van der Ham (2012) described the *Tabernaemontana* pollen with the following characteristics: small to large and suboblate to prolate, the endoapertures are lalongate to endocingulate, and the ornamentation is psilate, and perforate to imperforate. Prolate, endocingulate pollen occurs mainly in the New World species. The pollen from the five species of *Tabernaemontana* from RFAD varied from large to very large. (*T. macrocalyx*), from subprolate to prolate, endocingulate and ornamentation scabrate. Endocingulate pollen occur in 15 of 23 New World *Tabernaemontana* species. In species of the Old World long colpi occur in most Madagascan and Asian species and in two basal African species. The *T. muricata* pollen size is 73.1  $\mu\text{m}$  (Van der Weide & Van der Ham 2012). In the

*Tabernaemontana* of RFAD the colpi are short and the size of the *T. muricata* is large (57.6  $\times$  44.4  $\mu\text{m}$ ). The endocingulum can be seen as a synapomorphy of *Neotabernaemontana* (*Stemmadenia* and the New World *Tabernaemontana* species) and might be regarded as an advanced feature. *Bonafousia* (included in present study: *T. angulata*, *T. coriacea*, *T. cuspidata*, *T. disticha*, *T. flavicans*, *T. lorifera*, *T. muricata*, *T. penduliflora*, *T. rupicola*, *T. sananho*, *T. siphilitica*, *T. undulata*) and *Woytkowski* (included in *T. cuspidata*) have endocingulate pollen (class E), while *Stenosolen* (included: *T. heterophylla*) has distinctly lalongate endoapertures (class C/D). (Van der Weide & Van der Ham 2012). The same condition is found in species of *Tabernaemontana* of RFAD, which have the endocingulum of class E (Plates 5 and 6), according to the endoapertures shape classes of Van der Weide & Van der Ham (2012).

The grain of *Macoubea sprucei* from RFAD has scabrate exine, 1  $\mu\text{m}$ , prolate spheroidal shape and diporate. It differs from the verrucate grain and exine of 2  $\mu\text{m}$  of *Macoubea* described by Colinvaux et al. (1999), as well as of *M. guianensis* from Rio Negro (Amazon), with an oblate grain, with amb elliptical circular to triangular convex and dicolporate – tricolporate (Rangel Ch 2008). Moreover, *M. sprucei* from RFAD has the same characteristics of *M. guianensis* described by Herrera & Urrego (1996), prolate spheroidal grains and scabrate, but differing in the apertures (dicolporate). Phylogenetic studies conducted by Zaruchi (1988) included *Macoubea* genus and six other genera, emphasising *Ambelania* and *Rhigospira* that were dealt with in this study, in the tribe *Tabernaemontaneae*, forming an unstable nucleus. In other studies *Macoubea* is included in *Macoubeaeae* and the other six genera in *Ambelanieae* (Pichon 1948a, 1948b; Leeuwenberg 1994a, b). On the other hand, molecular studies conducted by Simões et al. (2010) show *Macoubea* as sister to *Ambelanieae*.

The species of *Himatanthus bracteatus* var. *bracteatus*, *H. stenophyllus* and *H. sucuuba* (subfamília *Rauvolfioideae*; tribe *Plumerieae*) of RFAD have tricolporate grains, characteristic also found in this genus in the study by Marques & Melhem (1966) and for *H. articulatus* of the Colombian Amazon (Rangel Ch 2008). *H. articulatus* also has the same characteristics as in the shape (suboblate) and amb (triangular) of *H. bracteatus* var. *bracteatus* and *H. stenophyllus*. Both differ from *H. sucuuba* in the shape (oblate spheroidal) and amb (subtriangular). Middleton (2007) described the *Himatanthus* grain of Malaysia as monads, medium-sized, usually oblate spheroidal, rarely oblate or subprolate, tricolporate and ornamentation usually psilate-perforate or psilate-scabrate.

The pollen grains of *Ambelania acida*, as observed in this study, have a lalongate endoaperture (3–6  $\mu\text{m}$ ), a thin exine (1.4  $\mu\text{m}$ ) and a sexine with perforations. Variations were observed in this species, with respect to the presence of stephanocolporate grains. This species, as described by Nilsson (1990), has an exine of 3  $\mu\text{m}$ , and a lalongate endoaperture measuring 4–8  $\mu\text{m}$ , as well as densely perforated ornamentation. By means of phylogenetic studies Zarucchi (1988) included genus *Ambelania* and another six genera, highlighting *Macoubea* and *Rhigospira* that were dealt with in this study, in the tribe *Tabernaemontana*, forming an unstable nucleus; together with nine genera, emphasising *Tabernaemontana* (treated in this study) that are more or less stable.

The largest genus in the Apocynaceae is *Mandevilla* containing 150 species in America (Middleton 2007). Four *Mandevilla* species were analysed by Moreira et al. (2004), and our results for *M. scabra* are similar to theirs. It is also similar to grains described by Marques & Melhem (1966) as to the variability of the number of pores. *Mandevilla scabra* from RFAD has the apolar and pantoporate grain, similar characters to *M. subsagitata* and *M. villosa* grains, which are apolar and periporate (Roubik & Moreno 1991). Grains of *M. annulariifolia* (stephanoporate (4–5 pores)) and *M. hirsuta* (tetraporate) were described by Rangel Ch (2008) and Carreira & Barth (2003), respectively. Leal et al. (2011) described *M. scabra* (savannas of Guyana) as spherical and pantoporate and *M. bentharii*, spheroidal and stephanoporate (3–6 pores). Luz et al. (2007) also described *M. emarginata* and *M. pohliana* as periporate (5 pores) and periporate (4–7 pores), respectively. Pollen grains described by Middleton (2007), tribe Mesechites (Apocynoideae), were monads, small size (*Secondatia*) to very large (*Mandevilla*), oblate to subprolate, sometimes irregular (*Tintinnabularia*), triporate or tetraporate, rarely also stephanoporate – hexaporate (*Mandevilla*, *Mesechites*). With similar characters, *Mandevilla* of RFAD presents monads grains, very large size and periporate (4–6 pores).

The pollen grain of *Rhigospira quadrangulares* from RFAD is characterised by amb subtriangular, tricolporate and exine psilate, short colpi (ca. 10–14  $\mu\text{m}$ ), circular endoaperture, clear fastidium (Plate 5, figures 8, 9) and granules present around the apertures (Plate 5, figure 10). That same species, occurring in the savannas of Guyana, was described by Rangel Ch (2008), as tricolporate and with elliptical lalongate endoapertures and also studied by Leal et al. (2011), with samples of Colombia, as triporate, stephanoporate, and with circular pores. By means of phylogenetic studies *Rhigospira* and six more genera (*Ambelania*, *Macoubea*, *Molongum*, *Mucua*, *Neocouma* and *Spongiosperma*) are still found unstably within the tribe Tabernaemontaneae (Rauvolfioideae), together with a more or less stable nucleus, containing nine genera (*Callichilia*, *Calocrater*, *Carvalhoa*, *Crioceras*, *Schizozygia*, *Stemmadenia*, *Tabernaemontana*, *Tabernanthe* and *Voacanga*) (Zarucchi 1988).

*Parahancornia fasciculata* from RFAD has prolate spheroidal shape, amb subcircular, triporate, circular pores and thin exine; while the same species from Santarém (Pará Amazon), differs in shape (suboblate), the amb (triangular convex to straight triangular) and the aperture (tricolporate) (Rangel Ch 2008). In common, these species share only the presence of thin exine.

*Couma macrocarpa* of the Colombian Amazon presents tricolporate, tetracolporate or stephanocolporate grains, endoaperture lalongate elliptical, amb triangular convex, spheroidal oblate (Rangel Ch 2008). It differs from the species of RFAD as to the opening (tricolporate), the shape (suboblate) and amb (subcircular) (*C. guianensis*); amb circular and circular endoaperture (*C. utilis*). *C. macrocarpa* described by Herrera & Urrego (1996) is also tricolporate.

For *Forsteronia acouci*, Nilsson et al. (1993) reported that the pollen grains are triporate – tetraporate, oblate to spheroid, and of irregular size. By contrast, the pollen grains of *F. acouci* described in the present study were tetraporate – hexaporate

and oblate spheroidal. This difference may be a common variation in this species. As in this study, the grain described of the Colombian Amazonia also presents circular pores, shape spheroidal oblate and amb circular, although with apertures varying of triporate, tetraporate, pentaporate or stephanoporate and circular pore to slightly lalongate (Rangel Ch 2008). The genus *Forsteronia*, belonging to the Apocynoideae subfamily, was in the tribe Apocynaeae; however, it was transferred to Mesechiteae (Endress et al. 2007).

The genus *Secondatia* was studied by Endress et al. (2007), who transferred it to the tribe Malouetieae, subfamily Apocynoideae. Middleton (2007) described the species of the tribe Mesechiteae, subfamily Apocynoideae and, among other characters, highlighted monad grains, sometimes small (18–33  $\mu\text{m}$ ; *Secondatia*), oblate to subprolate ( $P/E = 0.67–1.26$ ), triporate or tetraporate and ornamentation psilate-perforate, sometimes slightly scabrate (*Allomarkgrafia*, *Mandevilla*). These characteristics can be shared by *Secondatia duckei* da RFAD, as monads, small size (24.8  $\times$  20.6  $\mu\text{m}$ ), subprolate ( $P/E = 1.20$ ), tetraporate – stephanoporate and ornamentation scabrate.

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## Disclosure statement

No potential conflict of interest was reported by the authors.

## Notes on contributors



**ISABELLA DESSAUNE RODRIGUES** is a biologist at the Federal University of Amazonas (UFAM) in Manaus, Brazil. She graduated in Biology from the Federal University of Espírito Santo (UFES) in 1999. Isabella also holds a masters in Botany, awarded in 2006, from the National Institute for Amazon Research (INPA), Manaus. She specialises on palynology, specifically pollen morphology, Quaternary pollen and taxonomy.



**MARIA LÚCIA ABSY** is a research palynologist at the National Institute for Amazon Research (INPA), Manaus, Brazil. She received her bachelors degree in Natural History during 1968 from the Catholic University of Parana, Curitiba, Parana. Maria Lúcia was awarded her masters in Botany from the University of São Paulo (USP), and her PhD in Mathematics and Natural Sciences in 1979 from the University of Amsterdam, The Netherlands. Her research at INPA is on Quaternary pollen. Another aspect of her research is on the study of pollen to determine the foraging resources of native stingless Amazonian bees. She also analyses pollen in honey to determine the food sources of the bees, and the different types of honey. Maria Lúcia has written several papers, chapters and books.



and pollen morphology.

**VANIA GONÇALVES LOURENÇO ESTEVES** is Titular professor in the Department of Botany of the Universidade Federal do Rio de Janeiro, Museu Nacional, Brazil. She is also a research fellow at the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). Vania graduated in Botany from the Universidade do Estado da Guanabara in 1974. She received a masters in Palynology from the Universidade Federal do Rio de Janeiro, Museu Nacional in 1981, and a PhD in Palynology from the Universidade de São Paulo in 1994. Her research is on the palynology of modern Brazilian floras.



**CLAUDIA BARBIERI FERREIRA MENDONÇA** is a Professor in the Department of Botany of the Universidade Federal do Rio de Janeiro, Museu Nacional, Brazil and also a research fellow at the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). Her masters and PhD degrees, both in Botany, are also from the Universidade Federal do Rio de Janeiro, Museu Nacional. Claudia's research is on the palynology of modern Brazilian floras.



the Central Amazon. Marcos's research interests are entomology, insect-plant interactions and palynology.

**CLEONICE DE OLIVEIRA MOURA** graduated in wood technology from the Amazon Institute for Technology (UTAM) in Brazil. She is currently a botanist at the National Institute for Amazon Research (INPA). Cleonice works on palynology, specifically researching in mellitopalynology, pollen morphology and taxonomy.

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## Studi Karakteristik Morfologi Polen Buah Naga Super Red (*Hylocereus costaricensis*) dengan Scanning Electron Microscope sebagai Sumber Belajar Biologi SMA

### The Pollen Morphological Characteristics Pollen Super Red Dragon Fruit (*Hylocereus Costaricensis*) with A Scanning Electron Microscopy as Biology Learning Source of Senior High School

Yayuk Robidah\*, Sri Wahyuni, Lud Waluyo

Universitas Muhammadiyah Malang,  
Jl. Raya Tlogomas 246 Malang 651444, Malang, Indonesia  
\*Email: robidahyayuk@gmail.com

**Abstract:** The study palinologi important to prove especially in plant taxonomy. Technological progress with the scanning electron microscopy (SEM) can support in the field of knowledge palinologi because of the world of more than a light microscope. The purpose of this research is described morphological structure pollen *Hylocereus costaricensis* (super red dragon fruit) use SEM, and use it as biology learning source of senior high school. This research is a descriptive qualitative study that describes the results of observations of pollen *Hylocereus costaricensis* based on relevant literature. The sample is pollen *Hylocereus costaricensis*. The object of study that observed is a unit of pollen, the form of pollen, size, aperture and ornamentation eksin. The result showed that *Hylocereus costaricensis* are categorized in the unit of a monad, the form of subsferodial, the size of magna, the aperture of tricolpate and the ornamentation of spinulose. This research result can be used as biology learning source of senior high school.

**Keywords:** Pollen, *Hylocereus costaricensis*, Scanning Electron Microscopy; Source of learning biology

## 1. PENDAHULUAN

*Hylocereus costaricensis* merupakan sekelompok dari tanaman buah naga yang memiliki warna buah merah pekat (super red). Secara morfologis dapat digambarkan bahwa tanaman buah ini merupakan tumbuhan tidak lengkap sebab tidak memiliki daun seperti tumbuhan yang lainnya. Meskipun demikian, tanaman buah naga pada spesies ini juga memiliki akar, batang, cabang, biji dan juga bunga (Idawati, 2013).

*Hylocereus costaricensis* memiliki sistem perakaran yang bersifat epifit, merambat dan menempel pada tanaman lainnya. Batang mengandung air dalam bentuk lendir dan berlapis lilin bila sudah dewasa dengan ukuran panjang berbentuk siku atau segitiga (Kristanto, 2009). Biji berwarna hitam, berbentuk bulat berukuran kecil dan keras (Emil, 2011). Bunga pada spesies ini berbentuk corong, dimana dalam bunga terdapat putik sekaligus benang sari sebab tanaman ini digolongkan dalam kelompok tanaman hermaphrodit (berkelamin dua) (Idawati, 2013).

Morfologi akar, batang, daun, bunga, dan alat-alat tambahan merupakan bukti taksonomi yang selama ini digunakan oleh para ahli taksonomi. Khususnya untuk morfologi bunga, serbuk sari atau pollen selain sebagai gametofit jantan, belum banyak digunakan sebagai bukti taksonomi (Sulistiyono, dkk, 2000).

Walker (1999) menyatakan bahwa serbuk sari merupakan alat penyebaran dan perbanyakan generatif dari tumbuhan bunga. Secara sitologi, serbuk sari merupakan sel dengan tiga nukleus, yang masing-masing dinamakan inti vegetatif, inti generatif I, dan generatif II. Sel dalam serbuk sari dilindungi oleh dua lapisan (disebut *intine* untuk yang didalam dan *exine* yang berada dibagian luar).

Pollen merupakan sel gamet jantan pada tumbuhan yang berbentuk di ruang sari (*theca*) yang telah dewasa. Jumlah pollen dalam ruang sari sangat banyak ukurannya kecil-kecil. Serbuk sari kadang kala terlihat seperti butir-butir tepung yang sangat halus, kering, dan ringan, sehingga mudah sekali terbang terbawa oleh angin. Akan tetapi ada pula serbuk sari yang berlemak, lengket, dan menggumpal



sehingga mudah melekat pada tubuh serangga yang mencari nektar bunga. Bentuk serbuk sari dari berbagai jenis tanaman bermacam-macam, misalnya bulat bundar, bulat telur, bersudut, permukaan berduri, kasar, halus, dan lain-lainnya (Darjanto & Satifah, 1990).

Palioologi merupakan salah satu cabang ilmu dari biologi yang mempelajari tentang spora dan pollen pada tanaman. Spora dan pollen pada suatu tumbuhan memiliki nomor pada ciri morfologi dan ultrastruktural, ciri yang dapat dijadikan dasar untuk mengetahui karakter dalam menentukan hubungan filogenetik pada tanaman. Selain itu karakteristik yang dimiliki baik spora dan pollen digunakan untuk mengidentifikasi klasifikasi dari suatu tanaman (Simpson, 2006).

Beberapa alasan yang disampaikan diatas, rumusan masalah yang dapat dibuat adalah bagaimana struktur morfologi pollen pada spesies *Hylocereus costaricensis* bila diamati dengan menggunakan SEM dan pemanfaatannya sebagai sumber belajar biologi SMA?

Morfologi pollen memiliki beberapa sifat penting yang dapat dipelajari. Sifat utama pollen yang dapat dipelajari antara lain unit pollen, polaritas dan simetri pollen, struktur dinding pollen, aperture, ukuran pollen, bentuk pollen dan ornamentasi eksin.

Penelitian ini bertujuan untuk mengetahui struktur morfologi pollen pada spesies *Hylocereus costaricensis* bila diamati dengan menggunakan SEM dan pemanfaatannya sebagai sumber belajar biologi SMA.

## 2. METODE PENELITIAN

### 2.1 Jenis Penelitian

Jenis penelitian ini merupakan penelitian deskriptif. Penelitian deskriptif adalah penelitian yang berusaha untuk memberi gambaran atau mendeskripsikan keadaan obyek atau permasalahan tanpa ada maksud membuat kesimpulan dan generalisasi (Purwanti, 1998). Penelitian deskriptif yang digunakan ini menggunakan pendekatan deskriptif kualitatif. Penelitian ini dilaksanakan pada tanggal 15 Juni 2015 di Laboratorium Biologi Universitas Muhammadiyah Malang (Kampus III) yang beralamat di JL. Raya Tlogomas No. 246 Malang.

### 2.2 Populasi dan Sampel

#### 2.2.1 Populasi

Populasi adalah objek atau subjek yang meliputi keseluruhan, kualitas, dan karakteristik yang telah ditemukan oleh peneliti untuk diteliti dan dipelajari yang kemudian ditarik kesimpulan (Sugiyono, 2010).

Populasi dalam penelitian ini adalah pollen bunga dari buah naga *Hylocereus costaricensis* yang didapatkan di Desa Ketindan Lawang Kabupaten Malang.

#### 2.2.2 Sampel

Sampel adalah bagian dari populasi baik berupa jumlah maupun karakteristik dan kualitas yang akan dipelajari, yang diambil beberapa saja tidak mungkin untuk dipelajari keseluruhan populasi, dan kesimpulan atau hasil akhir penelitian dari sampel yang diambil harus representatif (Sugiyono, 2011). Adapun sampel yang digunakan dalam penelitian adalah pollen dari *Hylocereus costaricensis*.

## 2.3 Variabel Penelitian

Variabel dalam penelitian ini yaitu karakteristik morfologi pollen yang meliputi tipe unit pollen, bentuk pollen (indek P/E), ukuran pollen, tipe/jenis pollen (apertur) dan ornamentasi eksin dari spesies *Hylocereus costaricensis*.

## 2.4 Metode Pengumpulan Data

Metode pengumpulan data dilakukan dengan cara melakukan observasi pengamatan terhadap hasil pengamatan pollen dengan menggunakan Scanning Elektron Microscope (SEM) yang selanjutnya data akan dipelajari menggunakan bantuan sumber-sumber literatur yang relevan dan studi pustaka sebelumnya mengenai morfologi pollen pada *Hylocereus costaricensis*.

## 3. HASIL DAN PEMBAHASAN

Berdasarkan penelitian identifikasi struktur morfologi pollen pada Bulan Juni di Laboratorium Biologi Universitas Muhammadiyah Malang Kampus III, peneliti ingin menyajikan hasil penelitian yaitu: 1) Hasil dari identifikasi pollen pada spesies *Hylocereus costaricensis* menggunakan Scanning Electron Microscope yang meliputi tipe unit pollen, bentuk pollen (Indek P/E), ukuran pollen, tipe/jenis pollen (aperture) dan ornamentasi eksin; 2) Pemanfaatan hasil penelitian pada spesies *Hylocereus costaricensis* sebagai sumber belajar Biologi SMA Kelas X semester 1. Hasil dari pengamatan menggunakan *Scanning Electron Microscope* sebagai berikut:



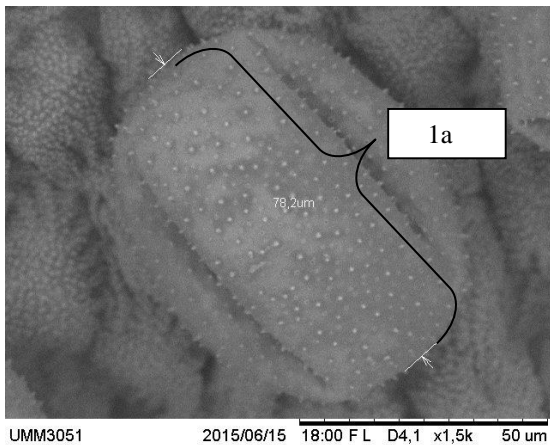
### 3.1 Hasil Penelitian

#### 3.1.1 Tipe Unit Pollen

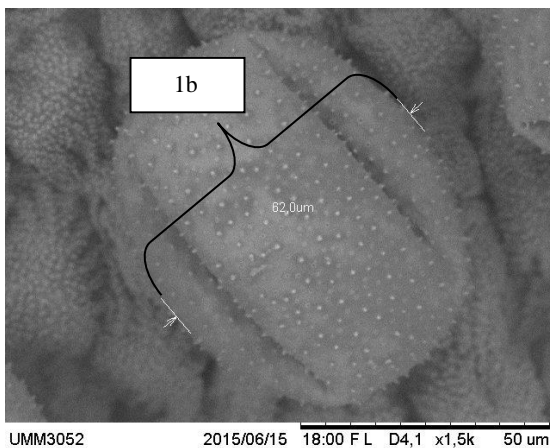
Tipe unit pollen berdasarkan hasil penelitian didapatkan hasil bertipe monad.

#### 3.1.2 Bentuk Pollen

Hasil pengamatan bentuk pollen yang didasarkan pada pengukuran panjang bidang polar (P) dan panjang bidang ekuator (E) dengan menggunakan SEM seperti gambar berikut:



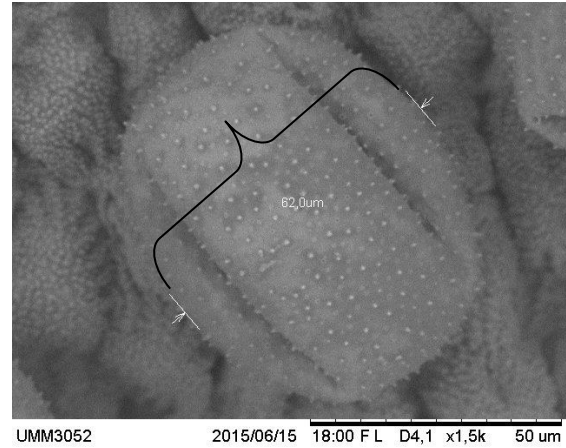
Gambar 1a. Pengukuran panjang bidang polar (dokumen pribadi)



Gambar 1b. Pengukuran panjang bidang ekuator (dokumen pribadi)

#### 3.1.3 Ukuran Pollen

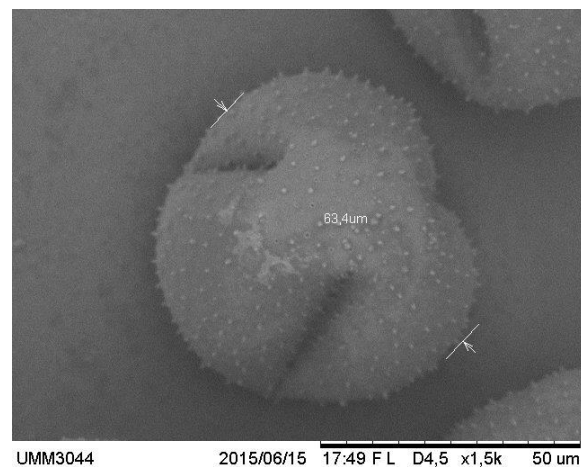
Hasil penelitian ukuran pollen didasarkan pada diameter ekuatorial dengan menggunakan SEM dapat dilihat seperti gambar berikut:



Gambar 2. Pengukuran diameter bidang Ekuatorial (dokumen pribadi)

#### 3.1.4 Tipe/Jenis Pollen (Apertur)

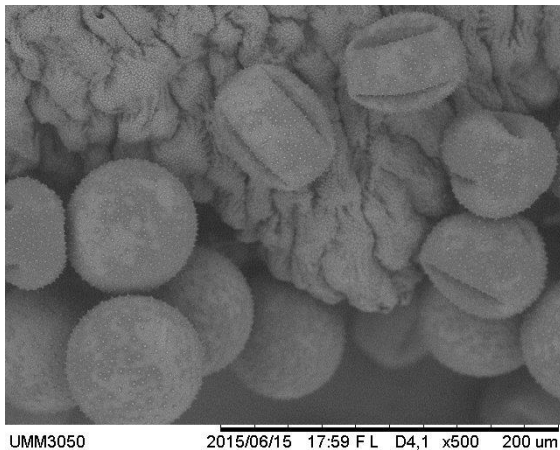
Hasil pengamatan aperture dengan menggunakan SEM dapat dilihat seperti gambar berikut:



Gambar 3. Bentuk aperture pollen (dokumen pribadi)

#### 3.1.5 Ornamentasi Eksin

Hasil penelitian ornamentasi eksin dengan menggunakan SEM dapat dilihat seperti gambar berikut:



Gambar 4. Tipe Ornamentasi Eksin (dokumen pribadi)

### 3.2 Pembahasan

Pengamatan morfologi pollen dengan menggunakan alat berupa Scanning Electron Microscope (SEM) mampu menghasilkan gambar pengamatan dalam bentuk 3 dimensi dengan revolusi yang lebih baik dibandingkan dengan mikroskop cahaya. Berdasarkan hasil pengamatan tipe unit pollen pada *Hylocereus costaricensis* adalah monad, dimana satu unit serbuk sari bebas terdiri dari satu butir serbuk sari (Sudarsono, 2005). Menurut Simpson (2006), unit pollen dengan tipe monad sangat mudah ditemukan pada angiospermae. Berdasarkan hasil penelitian dan literatur *Hylocereus costaricensis* termasuk dalam kelompok angiospermae. Karakteristik dari unit pollen yang sama dapat menjadi ciri pada *Hylocereus costaricensis*.

Bentuk pollen pada *Hylocereus costaricensis* berdasarkan panjang eksin polar (P) dari gambar 1a didapatkan hasil pengukuran dengan panjang 78.2  $\mu\text{m}$  dengan diameter ekuatorial (E) dari gambar 1b didapatkan hasil pengukuran 62,0  $\mu\text{m}$ , dengan indek P/E ( $\mu\text{m}$ ) 1,26, berdasarkan indek P/E bentuk pollen ini masuk dalam tipe subprolate karena berada diantara 1,14 dan 1,33. Menurut Kapp (1969), tipe subprolate tergolong dalam bentuk Subsferodial.

Ukuran pollen yang didasarkan pada pengukuran diameter ekuatorial dari gambar 2 didapatkan hasil pengukuran 62,0  $\mu\text{m}$ . Hal ini menunjukkan bahwa pollen *Hylocereus costaricensis* berdasarkan ukurannya berjenis magna, dimana angka tersebut berada diantara 50  $\mu\text{m}$  dan 100  $\mu\text{m}$  (Erdmant, 1952).

Berdasarkan pada gambar 3 pengamatan polar view, nampak aperture bertipe colpi dan berjumlah tiga buah. Menurut Kapp (1969) jenis aperture dengan colpi yang berjumlah tiga termasuk dalam tipe Tricolpate. Hal ini juga didukung oleh penelitian

sebelumnya oleh Ziasifa (2014) yang menggunakan *Hylocereus costaricensis* dalam penelitiannya. Hasil dari penelitian tersebut mengungkap bahwa aperture pada *Hylocereus costaricensis* adalah Tricolpate. Karakteristik dari aperture yang sama ini diperkirakan dapat menjadi ciri pada *Hylocereus costaricensis*.

Tipe ornamentasi eksin pada *Hylocereus costaricensis* adalah spinulose (Gambar 4). Menurut Simpson (2006), spinulose merupakan tipe ornamentasi yang memiliki elemennya berbentuk seperti duri dengan panjang kurang dari 1  $\mu\text{m}$ .

### 3.3 Pemanfaatan Hasil Penelitian Sebagai Sumber Belajar Biologi SMA dikembangkan dalam bentuk Buku Saku

Pada bagian dari akhir penelitian ini adalah menyusun buku struktur morfologi pollen spesies *Hylocereus costaricensis*.

Menurut Afandi (2014) dalam Susilana (2007), mengatakan buku teks merupakan buku tentang suatu bidang studi atau ilmu tertentu yang disusun untuk memudahkan para guru dan siswa dalam upaya mencapai tujuan pembelajaran. Selain itu, Menurut Departemen Pendidikan Nasional (2008) buku yang baik yaitu buku yang ditulis dengan menggunakan bahasa yang baik dan mudah dimengerti pembaca, disajikan secara menarik, dilengkapi gambar-gambar dan keterangannya, isi buku juga menggambarkan sesuatu yang sesuai dengan ide yang diinginkan.

Berdasarkan hal tersebut, maka peneliti memanfaatkan hasil penelitian dalam bentuk buku saku. Adapun komponen-komponen yang perlu dimasukkan dalam pembuatan buku saku studi karakteristik morfologi pollen pada *Hylocereus costaricensis* dengan Scanning Electron Microscope sebagai berikut:

1. Halaman Sampul yang terdiri dari:

- Judul
- Nama Penyusun
- Ilustrasi gambar

2. Kata pengantar
3. Daftar isi
4. Bab I Pendahuluan

Pada bab pendahuluan menjelaskan uraian singkat dan umum mengenai pollen. Selain itu, dijelaskan mengenai palinologi dan perannya sebagai ilmu biologi serta menjelaskan pengetahuan secara umum mengenai SEM dan alasan penggunaan SEM dalam identifikasi pollen.

5. Bab II Identifikasi Morfologi Pollen

Pada bab II, membahas mengenai parameter yang digunakan dalam identifikasi morfologi pollen. Parameter tersebut meliputi tipe unit pollen,

bentuk pollen, ukuran pollen, apertur dan ornamentasi eksin. Peneliti berharap dengan adanya parameter tersebut dapat membantu dalam mengidentifikasi morfologi pollen.

6. Bab III Scanning Electron Microscope Hitachi TM-3000  
Pada bab III, dijelaskan secara umum pengetahuan mengenai SEM.
7. BAB IV *Hylocereus costaricensis*  
Pada bab IV berisi tentang menginformasikan habitat dan persebaran *Hylocereus costaricensis* hingga perkembangbiakan.
8. Bab V Hasil Identifikasi Morfologi Pollen *Hylocereus costaricensis*  
Pada bab V berisi uraian tentang hasil studi morfologi pollen pada *Hylocereus costaricensis*. Pada bab ini juga dijelaskan bahwa studi morfologi pollen tersebut merupakan salah satu penerapan penggunaan SEM untuk mengembangkan ilmu pendidikan, khususnya di bidang biologi.
9. Bab VI Manfaat *Hylocereus costaricensis*  
Pada bab VI, membahas tentang manfaat dari *Hylocereus costaricensis* karena masih banyak masyarakat yang belum mengetahui manfaat dari *Hylocereus costaricensis* secara luas.
10. Bab VII Penutupan
11. Daftar Pustaka
12. Biodata penulis

#### 4. KESIMPULAN

Berdasarkan hasil penelitian karakteristik morfologi pollen pada *Hylocereus costaricensis* dengan Scanning Electron Microscope sebagai sumber belajar biologi SMA dapat diperoleh kesimpulan tipe unit pollen pada *Hylocereus costaricensis* berbentuk monad, bentuk pollen subsferodial, ukuran pollen magna, jenis aperture tricolpate dan tipe ornamentasi eksin yaitu spinulose.

Saran dan rekomendasi yang diberikan penulis bagi pembaca maupun calon peneliti lain yang ingin mengamati pollen pada *Hylocereus costaricensis* maupun dari tanaman lainnya antara lain, perlu dilakukan penelitian lanjutan dengan menggunakan lebih banyak lagi spesies yang difokuskan pada tingkat Genus *Hylocereus* maupun Famili Cactaceae yang dapat ditemukan di Indonesia. Perlu dilakukan dengan pengamatan SEM yang memiliki kemampuan lebih tinggi agar mendapatkan hasil yang lebih jelas dan akurat. SEM yang disarankan yaitu Hitachi SU1510 yang memiliki perbesaran hingga 300.000x.

#### 5. UCAPAN TERIMAKASIH

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**Saran:**

Maya Probosari, S.Si., M.Si  
Universitas Sebelas Maret (UNS)

Mikroskop SEM merupakan mikroskop 3 dimensi, jadi tidak cocok kalau judul penelitiannya hanya menyebutkan morfologi karena topik yang dibahas sampai ke bagian dalam tumbuhan seperti apertura, jadi lebih cocok jika judulnya struktur morfologi anatomi pollen buah naga.

**Tanggapan Presenter**

Terimakasih atas masukannya.

## Studi Morfologi Serbuk Sari pada Beberapa Varietas *Coleus scutellarioides* L.

Des M, Moralita Chatri, dan Ficil Mikaf

Jurusan Biologi Fakultas Matematika dan Ilmu Pengetahuan Alam  
Universitas Negeri Padang. [des.unp@gmail.com](mailto:des.unp@gmail.com)

**Abstrak.** *Coleus scutellarioides* termasuk familia Labiatae yang memiliki varietas yang sangat banyak, hal ini dapat dilihat dari perbedaan bentuk dan warna daunnya yang sangat beragam. Dalam kegiatan identifikasi tidak cukup hanya berdasarkan karakter morfologi organ saja, tapi dapat juga dilihat dari morfologi serbuk sari (pollen). Apakah varietas-varietas *Coleus* ini mempunyai morfologi serbuk sari yang berbeda ?. Tujuan penelitian ini untuk mengetahui morfologi serbuk sari tujuh varietas dari *Coleus scutellarioides*. Penelitian ini dilakukan di laboratorium Botani Jurusan Biologi FMIPA Universitas Negeri Padang, bulan April-Mei 2012. *Coleus* yang digunakan 7 varietas dari Padang Panjang dan Lintau Buo. Serbuk sari diambil dari bunga yang sudah mekar lalu dibuat preparat dengan metode asetolisis dan pewarnaan safranin 1%. Data dianalisis secara deskriptif meliputi unit serbuk sari, polaritas, simetri, ukuran, bentuk, apertur, dan bentuk permukaan serbuk sari. Serbuk sari ke 7 varietas mempunyai kesamaan yaitu unit serbuk sari tipe *monad*, polaritas tipe *isopolar*, radial simetri, jumlah apertur 6 dengan tipe *colpate* yang terletak secara ekuatorial (*stephano*), dan permukaan serbuk sari berbentuk *reticulate*. Bentuk *prolate spheroidal* ditemukan pada var. Eleanor, bentuk *subprolate* ditemukan pada var. Batique Fetish, var. Fack, var. Apricot, var. Burgundy Giant, var. Eleanor, dan var. Flambe. Sedangkan bentuk *prolate* ditemukan pada var. Batique Fetish, var. Fack, dan var. Va Va Boom. Morfologi serbuk sari ketujuh varietas *Coleus scutellarioides* hanya berbeda dari segi bentuk dan penulis hanya menemukan 3 bentuk yaitu *prolate spheroidal*, *subprolate* dan *prolate*.

**Key word:** pollen, serbuk sari, *Coleus scutellarioides*

### PENDAHULUAN

Ilmu yang mempelajari tentang serbuk sari disebut *palinologi* (Erdtman, 1972). Selain sebagai tempat gametofit jantan dan alat penyerbukan pada tumbuhan berbunga, serbuk sari memiliki fungsi dan penting dalam beberapa bidang meliputi morfologi serbuk sari dan kaitannya dalam taksonomi, filogeni dan palinologi fosil. Hasil dari beberapa penelitian menunjukkan bahwa serbuk sari adalah penyebab utama alergi pernafasan (aeropalnologi). Selain itu juga dapat menunjang beberapa data antara lain dalam kriminologi, medis dan *melittopalnologi* yaitu studi mengenai kandungan serbuk sari didalam madu (Bhojwani dan Bhatnagar, 1978, dalam Aprianty dan Kriwiyanti, 2007), serta

penggunaan serbuk sari dalam menganalisis efek bahan kimia ekotoksik (Shivana dan Sawhney, 1997).

Beberapa karakter dari morfologi serbuk sari adalah: simetri, ukuran dan bentuk, struktur dinding serbuk sari (pollen wall), stratifikasi eksin, ornamentasi eksin, kerutan/alur dan lubang (Agashe dan Caulton, 2009).

Selama ini para ahli taksonomi mengelompokkan tumbuhan menggunakan morfologi akar, batang, daun, bunga, dan alat-alat tambahan dalam taksonomi. Morfologi serbuk sari dapat digunakan untuk mengidentifikasi takson di tingkat *familia*, *genus*, *species*, dan di bawah *species*, penempatan taksa yang diragukan, penyusunan kembali, penggabungan dan pemisahan, serta sebagai penguat bukti



yang lain (Davis and Heywood, 1973 dalam Pudjoarinto dan Hasanudin, 1996). Hal ini ditegaskan pula oleh Rifai (1976) dalam Budi (2012) bahwa variasi yang diperlihatkan serbuk sari antara lain jumlah, letak alur, dan lubang (apertur) di permukaannya, begitu pula bentuk maupun ukuran serta bentuk dan ukuran eksinnnya, sekarang dapat menjadi sumber bukti taksonomi yang penting.

Hasil penelitian morfologi serbuk sari dapat menyokong pemisahan genus berdasarkan sifat makromorfologis (Pennington and Styles, 1975; Pannel, 1992; Mabberley *et al.*, 1995) yang memisahkan duku, kokosan dan pisitan dari *genus Aglaia* menjadi *genus* yang terpisah, yaitu *Lansium*. Kemudian Bagu (2003) melaporkan bahwa 4 *species* dari *Delphinium* (Ranunculaceae) dipisahkan menjadi 2 kelompok berdasarkan ukuran dan tebal eksin serbuk sarinya.

Setyowati (2008) melaporkan 9 *species* dari *familia* Asteraceae memiliki persamaan pada sifat unit serbuk sari, simetri, apertur, ukuran dan ornamentasinya, dan perbedaannya terletak pada bentuk dan panjang papila serbuk sari. Aprianty dan Kriwiyanti (2007) melaporkan bahwa morfologi serbuk sari Kembang sepatu (*Hibiscus rosa-sinensis* L.) dengan 10 warna mahkota yang berbeda menunjukkan variasi dari ukuran panjang aksis polar dan diameter bidang ekuatorial kemudian digolongkan menjadi kelas *prolat sferoidal* (8 tanaman) dan kelas *oblat sferoidal* (2 tanaman) berdasarkan bentuk serbuk sarinya. Des (1986) melaporkan bahwa struktur morfologi serbuk sari kelima varietas dari *Linum usitatissimum* L. berdasarkan hasil analisis statistik menunjukkan perbedaan yang nyata.

*Coleus* terdiri atas 150 *species* dan yang paling terkenal adalah *C. scutellarioides* L. (Sila, 2011). *Coleus* termasuk kedalam *familia* Labiatae, tumbuhan ini kosmopolitan dalam distribusinya dan bernilai komersial karena senyawa kimia

yang dikandungnya (Core, 1959).. *Coleus* ditanam di pekarangan sebagai tanaman hias atau tanaman obat, kadang-kadang ditemukan tumbuh liar pada tempat-tempat yang lembab dan terbuka seperti di tepian air, pematang sawah, atau di tepi jalan (Wijayakusuma dkk, 1998).

*Coleus* merupakan tanaman hias yang mempunyai warna dan bentuk daun yang bervariasi (Core, 1959). Perbedaan varietas tersebut dapat dilihat dari perbedaan warna daun yang sangat beragam yang ditentukan oleh kandungan pigmen di dalam daun (Ridwan, 2007). Kegiatan identifikasi tidak cukup hanya berdasarkan pada morfologi organ luar saja. Padahal pengamatan morfologi serbuk sari juga merupakan salah satu karakter yang penting dalam taksonomi (Erdmant, 1972). Berdasarkan uraian diatas telah dilakukan penelitian tentang “Studi Morfologi Serbuk Sari pada Beberapa Varietas *Coleus scutellarioides* L.”.

## METODA PENELITIAN

Pengambilan sampel dilakukan di Padang Panjang dan Lintau Buo. Pengamatan morfologi serbuk sari dilakukan dilaboratorium Botani, Jurusan Biologi, FMIPA Universitas Negeri Padang.

Untuk mengamati morfologi serbuk sari digunakan metode asetolisis dari Aprianty dan Kriswiyanti (2007). Bunga tanaman *Coleus* yang sudah mekar dimasukkan ke dalam botol film yang telah berisi larutan FAA. Bagian bunga dikeluarkan satu persatu menggunakan pinset dan diguncang sedikit agar serbuk sari yang menempel dapat terlepas. Lalu pindahkan larutan FAA yang berisi serbuk sari kedalam tabung reaksi, sentrifuge dengan kecepatan 1000 rpm selama 15 menit. larutan FAA dibuang perlahan-lahan agar serbuk sari yang mengendap didasar tabung tidak ikut terbawa keluar.



Selanjutnya serbuk sari difiksasi dalam larutan Asam Asetat Glasial (AAG) 45% selama 24 jam dalam suhu ruang. Setelah difiksasi disentrifugasi 15 menit, lalu larutan AAG dibuang.

Langkah selanjutnya pencucian dengan aquades dan disentrifuge 15 menit, pencucian dilakukan 2 kali. Setelah itu dicuci dengan alkohol 50% dan 70 %, dan disentrifuge 15 menit lalu larutan alkohol dibuang.

Setelah itu diwarnai dengan menggunakan safranin 1 % dalam alkohol 70%. Endapan serbuk sari diambil menggunakan kuas kecil lalu disapukan diatas gelas objek, teteskan safranin 1% dan tutup dengan gelas penutup. Pengamatan dilakukan dengan mikroskop perbesaran 40x10 dan kemudian difoto menggunakan

kamera digital. Pengukuran dilakukan pada 30 butir serbuk sari tiap varietas menggunakan mikrometer.

Analisis data dilakukan secara kualitatif yaitu dengan melihat morfologi serbuk sari meliputi unit, polaritas, simetri, ukuran, bentuk, tipe apertur, dan bentuk permukaan dari serbuk sari. Sedangkan secara kuantitatif dengan mengukur panjang aksis polar (P) dan diameter bidang ekuatorial (E) serbuk sari dengan mikrometer. Hasil nantinya akan diuraikan secara deskriptif.

### HASIL DAN PEMBAHASAN

Hasil pengamatan morfologi serbuk sari tujuh varietas *Coleus scutellarioides* dapat dilihat pada tabel 1.

Tabel 1. Hasil Pengukuran Serbuk Sari Tujuh Varietas *Coleus scutellarioides*

No	Objek	Panjang aksis polar (P) dan diameter bidang ekuatorial (E)		Indeks P/E	Bentuk	Apertur		
		P	E			Jml	Tipe	Posisi
1	Batique Fetish	30-37,5 $\mu\text{m}$	20-32,5 $\mu\text{m}$	1,15-1,50	<i>Subprolate-prolate</i>	6	<i>Colpate</i>	<i>Stephano</i>
2	Fack	30-35 $\mu\text{m}$	22,5-25 $\mu\text{m}$	1,33-1,40	<i>Subprolate-prolate</i>	6	<i>Colpate</i>	<i>Stephano</i>
3	Va Va Boom	32,5-37,5 $\mu\text{m}$	17,5-27,5 $\mu\text{m}$	1,36-1,85	<i>Prolate</i>	6	<i>Colpate</i>	<i>Stephano</i>
4	Apricot	27,5-37,5 $\mu\text{m}$	22,5-30 $\mu\text{m}$	1,22-1,25	<i>Subprolate</i>	6	<i>Colpate</i>	<i>Stephano</i>
5	Burgundy Giant	30-35 $\mu\text{m}$	22,5-27,5 $\mu\text{m}$	1,27-1,33	<i>Subprolate</i>	6	<i>Colpate</i>	<i>Stephano</i>
6	Eleanor	27,5-32,5 $\mu\text{m}$	22,5-30 $\mu\text{m}$	1,08-1,22	<i>Prolate spheroidal-subprolate</i>	6	<i>Colpate</i>	<i>Stephano</i>
7	Flambe	25-32,5 $\mu\text{m}$	20-27,5 $\mu\text{m}$	1,18-1,25	<i>Subprolate</i>	6	<i>Colpate</i>	<i>Stephano</i>

Polaritas serbuk sari dari ketujuh varietas *Coleus* adalah tipe *isopolar* karena memiliki bagian distal dan peroksimal yang sama. Polaritas merupakan gambaran dari bentuk sumbu polar dari serbuk sari. Sesuai dengan pendapat (Hesse, 2009). Bahwa polaritas *isopolar* apabila kutub polar satu dengan lainnya bentuknya sama.

Simetri ketujuh varietas *radiosymmetric* (radial). Sesuai dengan pernyataan Agashe and Caulton (2009) menyatakan bahwa sebagian besar Dicotyledoneae mempunyai simetri bentuk radial. Varietas *Coleus* memiliki simetri radial yaitu bila dibagi secara vertikal di daerah manapun akan menghasilkan dua bagian yang simetri, sesuai dengan pernyataan Erdtman (1972), simetri radial memiliki lebih dari dua bagian vertikal yang simetri.

Ukuran serbuk sari termasuk medium dengan panjang aksis polar (P) dan diameter bidang ekuatorial (E) berkisar antara 25-37,5 x 17,5-32,5  $\mu\text{m}$  (Tabel 1). P terpanjang yaitu 37,5  $\mu\text{m}$  ditemukan pada var. *Batique Fetish*, var. *Va Va Boom* dan var. *Apricot*, sedangkan P terpendek yaitu 25  $\mu\text{m}$  ditemukan pada var. *Flambe*. E terpanjang yaitu 32,5  $\mu\text{m}$  ditemukan pada var. *Batique Fetish*, sedangkan E terpendek yaitu 17,5  $\mu\text{m}$  ditemukan pada var. *Va Va Boom*. Mengacu pada pengelompokan ukuran serbuk sari berdasarkan aksis polar terpanjang oleh Erdmant (1972) ukuran tersebut termasuk dalam serbuk sari berukuran sedang (*mediae*), dengan ukuran antara 25-50  $\mu\text{m}$ .

Ukuran serbuk sari varietas *Coleus* memiliki sedikit perbedaan dengan hasil penelitian yang diungkapkan oleh Huang (1972) yang menemukan bahwa *C. Scutellarioides* (L.) Benth. var. *Crispopilus* (Merr.) Keng memiliki ukuran serbuk sari 32-49  $\mu\text{m}$  x 27-39  $\mu\text{m}$ . Perbedaan ini dapat terjadi, sebagaimana Erdmant (1952) dalam Aprianty dan Kriswiyanti (2008) menyatakan bahwa bentuk, ukuran ataupun tipe serbuk sari bisa juga bervariasi menurut tahap kematangannya.

Bentuk serbuk sari dari tujuh varietas *Coleus* adalah bentuk *prolate spheroidal*, *subprolate* dan *prolate* (Tabel 1). Bentuk serbuk sari digambarkan berdasarkan indeks P/E (Tabel 1) yang merupakan perbandingan rasio panjang aksis polar (P) dengan diameter sumbu ekuatorial (E), yang dikalikan 100 (Erdmant, 1972). Var. *Batique* memiliki bentuk serbuk sari *subprolate* sampai *prolate* dengan indeks P/E x 100 115-150  $\mu\text{m}$ . Var. *Fack* bentuk *subprolate* sampai *prolate* dengan indeks P/E x 100 133-140  $\mu\text{m}$ . Var. *Va Va Boom* bentuk *prolate* dengan P/E x 100 136-185  $\mu\text{m}$ . Var. *Apricot* bentuk *subprolate* dengan indeks P/E x 100 122-125  $\mu\text{m}$ . Var. *Burgundy Giant* memiliki bentuk *subprolate* dengan indeks P/E x 100 127-133  $\mu\text{m}$ . Var. *Eleanor* memiliki bentuk *prolate spheroidal* sampai *subprolate* dengan indeks P/E x 100 108-122  $\mu\text{m}$ . Var. *Flambe* memiliki bentuk *subprolate* dengan indeks P/E x 100 118-125  $\mu\text{m}$ . Hal ini diperkuat dengan penjelasan Erdmant (1972) dan Huang (1972) bahwa *C. scutellarioides* (L.) Benth. memiliki serbuk sari berbentuk *subprolate* sampai *prolate*. Serbuk sari varietas *Coleus* bila dilihat secara polar berbentuk *circular*. Hal ini sesuai dengan penemuan Huang (1972) bahwa bentuk sumbu polar (*polar view*) pada *C. Scutellarioides* L. Benth. Var. *Crispopilus* (Merr.) Keng adalah bentuk *circular*.

Apertur yang dimiliki oleh ketujuh varietas *Coleus* adalah sama yaitu *6-stephanocolpate*. Erdmant (1972) menjelaskan bahwa bentuk serbuk sari dari *familia* Labiatae umumnya 3-4 atau *6-colpate*. Jumlah apertur serbuk sari adalah 6 dan tipe apertur adalah *colpate* atau *colpi* karena aperturnya yang memanjang dan terletak secara ekuatorial. Posisi apertur berada didaerah ekuatorial dan sering disebut dengan awalan *stephano*.

Bentuk permukaan serbuk sari *Coleus* adalah bentuk *reticulate* (berpola seperti jala). Hal ini diperkuat dengan hasil





penelitian Huang (1972) yang menemukan bahwa *C. scutellarioides* (L.) Benth. var. *Crispopilus* (Merr.) Keng memiliki permukaan berbentuk *reticulate* (berpola seperti jala).

Berdasarkan uraian diatas, beberapa karakter morfologi serbuk sari dari tujuh varietas *Coleus* yang diamati menunjukkan variasi dari ukuran dan bentuk serbuk sari. Sehingga karakter morfologi serbuk sari ketujuh varietas *Coleus* dapat dijadikan sebagai salah satu alat identifikasi dalam taksonomi. Kemudian Faegri dan Iversen (1989) dalam Aprianty dan Kriswiyanti (2008) juga menyatakan bahwa penelitian serbuk sari dari beberapa ahli terhadap beberapa species tumbuhan di Eropa menunjukkan adanya variasi ukuran serbuk sari berdasarkan letak geografisnya.

### KESIMPULAN

Berdasarkan pengamatan karakter morfologi serbuk sari dari tujuh varietas *Coleus scutellarioides* dapat disimpulkan bahwa unit serbuk sarinya adalah tipe *monad* (tunggal), memiliki polaritas tipe *isopolar* dan simetri radial. Serbuk sari berukuran sedang (*median*) dan memiliki tiga bentuk serbuk sari yaitu bentuk *prolate spheroidal*, *subprolate* dan *prolate*. Tipe apertur *colpate* berjumlah 6 yang terletak didaerah ekuatorial (*stephano*) dan memiliki bentuk permukaan serbuk sari berbentuk *reticulate* (berpola seperti jala).

### SARAN

Setelah dilakukan penelitian, maka disarankan untuk melakukan penelitian mengenai morfologi serbuk sari pada varietas *C. scutellarioides* yang lain. Kemudian karena adanya keterbatasan alat dalam pengamatan morfologi serbuk sari, maka perlu ditambahkan karakter morfologi serbuk sari lainnya seperti bentuk membran apertur, ketebalan *eksin* dan *intin*.

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## **Keanekaragaman Tumbuhan Berdasarkan Morfologi Polen dan Spora dari Sedimen Telaga Warna Dieng, Kabupaten Wonosobo, Jawa Tengah**

**Nurrahmah Azizah<sup>1</sup>, Sri Widodo Agung Suedy<sup>1\*</sup>, Erma Prihastanti<sup>1</sup>**

<sup>1</sup>Jurusan Biologi, Fakultas Sains dan Matematika, Universitas Diponegoro.

\*Email : agung.suedy@gmail.com

### **ABSTRACT**

Pollen and spore may be used to identify the name of plants because on pollen and spore there is an outer wall, called exine, which have specific structure and sculpture. This specific morphology of pollen and spore may be easily identified, therefore the name of plant itself may be known directly. The aim of this research is to find out the various of pollen and spore morphology of Telaga Warna sediment and the name of plant itself may be known, moreover the plant diversity and the plant which is dominant around Telaga Warna may be known as well. This research had been conducted with fetched the sediment sample from the edge of Telaga Warna, Dieng, preparation of sample were using acetolysis method, and finally make microscopic preparation. Pollen and spore observed by some parameters: shape, size, polarity, symmetry, aperture, and sculpture. The information, furthermore, analyzed by making description of pollen and spore morphology and quantitative data. The result of this research reveal that there are 34 kind of plants from pollen and spore observation. The amount of Pteridophytes is 53%, Non-Arboreal Pollen (NAP) is 29%, and Arboreal Pollen (AP) is 18%. The plant which dominant around Telaga Warna is Polypodiaceae, with the value of dominance index is 5,66. Its spore morphology has trilete aperture, heteropolar, bilateral symmetry, and the sculpture is psilate. The average of plant diversity temporally in Telaga Warna is low, with the average value of diversity index is 1,56, however the alteration of vegetation temporally in Telaga Warna is stable dynamics.

*Keywords: morphology, pollen, spore, telaga warna*

### **ABSTRAK**

Polen dan spora dapat digunakan untuk mengidentifikasi tanaman karena pada polen dan spora terdapat lapisan eksin yang mempunyai struktur dan ornamentasi yang khas. Morfologi yang khas dari polen dan spora dapat diidentifikasi sehingga secara taksonomi dapat diketahui tumbuhan penghasilnya. Tujuan dari penelitian ini adalah untuk mengetahui macam-macam morfologi polen dan spora dari sedimen di Telaga Warna sehingga dapat diketahui tumbuhan penghasilnya, selanjutnya dapat diketahui keanekaragaman tumbuhan dan tumbuhan apa saja yang mendominasi di Telaga Warna. Penelitian ini dilakukan dengan pengambilan sampel sedimen di tepi Telaga Warna, Dieng, sampel kemudian dipreparasi dengan metode asetolisis, dan dibuat preparat mikroskopis. Pengamatan polen dan spora dilakukan dengan melihat beberapa parameter seperti bentuk, ukuran, polaritas, simetri, aperture, maupun ornamentasinya. Data yang diperoleh dianalisis dengan membuat deskripsi morfologi polen dan spora serta data kuantitatif. Hasil penelitian menunjukkan terdapat 34 jenis tumbuhan yang ditemukan. Persentase jumlah Pteridophyta mencapai 53%, *Non-Arboreal Pollen* (NAP) 29%, dan *Arboreal Pollen* (AP) 18%. Jenis tumbuhan yang paling mendominasi di Telaga Warna adalah Polypodiaceae dengan nilai indeks dominansinya 5,66. Ciri morfologi spora Polypodiaceae adalah memiliki tipe aperture *trilete*, polaritas heteropolar, simetri berbentuk bilateral, serta tipe ornamentasi berupa *psilate*. Rata-rata tingkat keanekaragaman tumbuhan Telaga Warna yang diamati secara temporal termasuk kedalam kategori rendah dengan nilai indeks 1,56, namun dinamika vegetasi Telaga Warna secara temporal dapat dikatakan dinamis stabil.

*Kata kunci: morfologi, polen, spora, telaga warna*

## PENDAHULUAN

Indonesia merupakan negara megabiodiversiti flora dan fauna. Kekayaan alam ini harus dilestarikan dengan cara menginventarisasi setiap jenis spesies flora dan fauna yang ada di Indonesia. Identifikasi flora di Indonesia sudah banyak dilakukan namun masih perlu dikaji informasi terkini menyangkut status jenis-jenis flora untuk mengetahui potensinya dan status terakhir masing-masing jenis di habitat alamnya. Salah satu cara untuk mengidentifikasi flora adalah dengan mengamati morfologi polen dan sporanya (Bismark dan Setyawati, 2010).

Polen dan spora itu sendiri memiliki definisi, dimana polen atau serbuk sari adalah alat perkembangbiakan jantan yang dihasilkan oleh tumbuhan Spermatophyta, baik yang berasal dari tumbuhan Gymnospermae maupun Angiospermae, sedangkan spora biasanya dihasilkan oleh tumbuhan non vaskuler seperti alga, jamur, lumut serta tumbuhan vaskuler tingkat rendah yaitu tumbuhan lumut (Bryophyta) dan paku (Pteridophyta) (Buvat, 1989). Polen dan spora dapat digunakan untuk mengidentifikasi tanaman karena pada polen dan spora terdapat lapisan eksin yang mempunyai struktur dan ornamentasi yang khas serta dapat terawetkan karena mengandung senyawa sporopolenin yang resisten terhadap kondisi lingkungan yang ekstrim. Eksin ini memberikan keistimewaan dalam studi palinologi, sehingga dapat digunakan untuk mengidentifikasi tumbuhan. Variasi morfologi polen dan spora pada eksin juga bersifat spesifik untuk kelompok tumbuhan tertentu. Morfologi yang khas ini dapat diidentifikasi, sehingga secara taksonomi diketahui tumbuhan penghasilnya (Septina, 2004).

Identifikasi tumbuhan berdasarkan morfologi polen dan spora selanjutnya juga dapat digunakan untuk merekonstruksi perubahan vegetasi yang tumbuh baik lokal maupun regional yang berada di sekeliling lingkungan pengendapannya (Morley, 1990).

Vegetasi atau komunitas tumbuhan merupakan salah satu komponen biotik yang menempati habitat tertentu seperti hutan, padang ilalang, semak belukar, dan lain lain. Struktur dan komposisi vegetasi pada suatu wilayah dipengaruhi oleh komponen ekosistem lainnya yang saling berinteraksi, sehingga vegetasi yang tumbuh secara alami pada wilayah tersebut sesungguhnya merupakan pencerminan hasil interaksi berbagai faktor lingkungan dan dapat mengalami perubahan drastis karena pengaruh antropogenik (Arrijani dkk, 2006).

Keanekaragaman tumbuhan dalam suatu vegetasi menunjukkan berbagai komposisi baik variasi dalam bentuk, struktur atau morfologi, warna, jumlah, dan sifat lain dari tumbuhan di suatu daerah. Keanekaragaman hayati, terutama tumbuhan dalam bentuk hutan yang membentuk ekosistem atau bioma, memiliki fungsi yang banyak dan sangat penting bagi penanggulangan masalah lingkungan (Arrijani dkk, 2006). Menurut Mardiyanti (2013) kelompok tumbuhan yang hidup secara bersamaan, telah menyesuaikan diri, dan menghuni suatu tempat alami disebut komunitas tumbuhan. Karakteristik dari vegetasi pada suatu lingkungan disebut keanekaragaman. Semakin beranekaragam komponen biotiknya pada suatu vegetasi, maka semakin tinggi keanekaragamannya. Sebaliknya semakin sedikit keanekaragaman komponen biotik pada suatu

vegetasi, maka dapat dikatakan keanekaragamannya rendah.

Penelitian tentang palinologi di Telaga Warna, Dieng, sebelumnya belum pernah dilakukan. Namun Pudjoarianto (1999) pernah melakukan penelitian palinologi di kawasan Telaga Balekambang yang berjarak sekitar 1 km dari Telaga Warna. Pudjoarianto (1999) menyatakan bahwa berdasarkan interpretasi palinologi dapat dibuktikan bahwa tingginya nilai persentase tipe serbuk sari non-pohon, *Trema orientalis*, *Macaranga*, *Plantago major*, dan tipe serbuk sari tanaman budidaya pada sedimen pengendapan dapat digunakan sebagai indikator adanya aktivitas manusia di sekitar kawasan tersebut.

Penelitian di Dieng selanjutnya dilakukan oleh Sajekti (2009) pada kawasan Telaga Cebong, yang berjarak sekitar 2.5 km dari Telaga Warna. Sajekti (2009) menyatakan bahwa tumbuhan yang dominan tumbuh di kawasan Telaga Cebong berasal dari 6 takson famili, yaitu *Arecaceae*, *Asteraceae*, *Poaceae*, *Myricaceae*, *Engelhardia sp.* (Fam. *Juglandaceae*), *Urticaceae*, dan spora monolet. Vegetasi dari takson *Asteraceae* sangat fleksibel dalam beradaptasi pada semua kondisi lingkungan, sehingga disebut juga sebagai kelompok tumbuhan kosmopolit karena tumbuh diberbagai tempat. Adanya *Asteraceae* merupakan indikator bahwa telah terjadi aktivitas manusia di kawasan tersebut. Takson *Gramineae* juga memberikan informasi adanya aktivitas pertanian oleh masyarakat.

Berdasarkan informasi yang telah diperoleh dari penelitian di Telaga Balekambang dan Telaga Cebong yang jaraknya cukup dekat dengan Telaga Warna, maka perlu dilakukan

penelitian di kawasan Telaga Warna sebagai penelitian lanjutan. Data yang diperoleh dapat digunakan sebagai acuan guna mengetahui keanekaragaman tumbuhan dan merekonstruksi kondisi lingkungan pada masa lampau di Telaga Warna, Dieng.

## METODE PENELITIAN

### Tempat dan Waktu Penelitian

Penelitian dilakukan dalam dua tahap yaitu penelitian lapangan yang meliputi pengambilan sampel sedimen di daerah Telaga Warna, Dieng, dan penelitian laboratorium yang meliputi preparasi sampel untuk dibuat sediaan preparat mikroskopis yang dilakukan di Laboratorium Sedimentologi dan Stratigrafi, Prodi Teknik Geologi Universitas Jenderal Soedirman. Pengamatan, identifikasi, serta analisis data dilakukan di Laboratorium Biologi Dasar, jurusan Biologi Fakultas Sains dan Matematika Universitas Diponegoro Semarang. Penelitian dilaksanakan pada Maret–Oktober 2015.

### Bahan dan Alat

Bahan - bahan yang digunakan dalam penelitian ini antara lain sampel sedimen, aquadest,  $\text{HNO}_3$ , KOH 5%, HCl 32%, HF 40%, alkohol 10%, gliserin jelly, entelan, kertas lakmus biru. Alat - alat yang digunakan adalah alat bor, paralon, timbangan analitik, gelas beker, tabung reaksi, pengaduk kayu, pinset, baki, kompor listrik, filter nilon, corong, pipet, botol vial, lemari asam, filter aquadest, mikropipet, *yellow tip*, *hotplate*, kaca preparat, kaca penutup, mikroskop.

### Pengambilan Sampel

Sampel sedimen diambil dari tepi Telaga Warna, Dieng, Kabupaten Wonosobo. Titik Lokasi pengambilan sampel pada koordinat: 7°12'50.8"S 109°54'57.8"E, dengan menggunakan alat bor tangan berdiameter 1 dm ( $\pm$  4cm) dengan kedalaman 100 cm. Sampel kemudian dipindahkan ke dalam paralon. Sedimen yang telah diambil diberi kode sampel Telaga Warna (TW). Paralon kemudian diberi tanda lapisan paling bawah yang merupakan lapisan umur tua dan lapisan paling atas yang merupakan lapisan umur muda.

### Preparasi Sampel Sedimen

Preparasi polen dan spora menggunakan metode Moore dan Webb (1978) yang telah dimodifikasi di Laboratorium Palinologi dan Paleobotani, Teknik Geologi, Fakultas Sains dan Teknik, Universitas Jenderal Soedirman:

- Sampel sedimen sebanyak 5 g dalam gelas bekkor diberi larutan HCl 32%, didiamkan selama 2 jam, dan dinetralkan dengan akuades sampai pHnya menjadi netral (pH 7).
- Sampel sedimen diberi larutan HF 40%, didiamkan selama 24 jam, dan dinetralkan dengan akuades sampai pHnya menjadi netral (pH 7).
- Sampel sedimen diberi larutan HCl 32%, dipanaskan selama 2 jam, dan dinetralkan dengan akuades sampai pHnya menjadi netral (pH 7).
- Sampel disaring menggunakan saringan bertingkat 10  $\mu$ m dan 5  $\mu$ m. Sampel diberi larutan HNO<sub>3</sub> dan dipanaskan selama 10 menit. Sampel dinetralkan dengan akuades

dan disaring dengan filter nilon berukuran 5  $\mu$ m.

- Sampel diberi larutan KOH 5% dan dipanaskan selama 5 menit. Sampel dinetralkan dengan akuades dan dimasukkan kedalam botol vial.
- Sampel sebanyak 200  $\mu$ l diteteskan pada kaca benda yang sebelumnya dioleskan gliserin jelly, sampel dikeringkan diatas *hotplate*, ditetesi dengan entelan, dan ditutup dengan kaca penutup.

### Identifikasi Polen dan Spora

Polen dan spora diamati dibawah mikroskop cahaya dengan perbesaran 400x-1000x untuk melihat bentuk, ukuran, polaritas, simetri, jumlah apertura, serta ornamentasi eksin. Identifikasi dan dokumentasi polen dan spora menggunakan fotomikrograf Olympus BX51 dengan perbesaran sampai 1000x. Identifikasi polen dan spora dilakukan berdasarkan acuan Erdtman (1952), Huang (1972), Morley (1990), Halbritter (2007), Hesse (2009), dan koleksi referensi dari Smithsonian Tropical Research Intitute (pada [www.striweb.si.edu/roubik](http://www.striweb.si.edu/roubik)).

### Analisis Data

Hasil dari pengamatan morfologi polen dan spora dapat diketahui habitus tumbuhan penghasilnya sehingga dijadikan acuan data kuantitatif dalam membahas keanekaragaman tumbuhan di Telaga Warna. Data kuantitatif ini diolah dengan menggunakan beberapa program aplikasi yaitu, PAST (Paleontological Statistics) ver. 0.99, Ms. Excel, dan Sigmaplot ver 12.0.

## HASIL DAN PEMBAHASAN

Penelitian dilakukan untuk mengetahui keanekaragaman tumbuhan berdasarkan ciri morfologi polen dan spora dari sedimen Telaga Warna. Macam-macam polen dan spora yang didapat diidentifikasi morfologinya sehingga diketahui tumbuhan penghasilnya. Hasil dari identifikasi menunjukkan bahwa terdapat 34 tipe/taksa berdasarkan polen dan spora yang ditemukan. Identifikasi polen dan spora sampai pada tingkatan famili dan genus, namun ada juga beberapa polen dan spora yang diketahui tumbuhan penghasilnya hingga tingkatan spesies. Hasil identifikasi tumbuhan penghasil sampai pada tingkat famili berjumlah 9 tipe/taksa (26%), sampai tingkat genus berjumlah 6 tipe/taksa (18%), dan 19 tipe/taksa (56%) sampai tingkat spesies.

Hasil dari perhitungan polen dan spora secara keseluruhan telah teridentifikasi sejumlah 10.170 *grain* polen dan spora (Tabel 1). Jumlah spora mendominasi dengan persentase mencapai 91,53%, sedangkan persentase jumlah polen 8,46%. Spora didominasi oleh Polypodiaceae yang persentasenya lebih dari separuh total jumlah antara polen dan spora, yaitu 59,85%. Jumlah ini melebihi dari spora yang mendominasi kedua, yaitu Davalliaceae dimana persentasenya 13,08%. Jumlah polen yang mendominasi adalah Ulmaceae dengan jumlah persentase 2,11%, kemudian diikuti oleh Gramineae yang berjumlah 2,01%.

Taksa yang telah ditemukan kemudian dikelompokkan berdasarkan habitusnya. Habitus merupakan perawakan dari tumbuhan penghasil dari polen dan spora yang dapat diklasifikasikan dalam Pteridophyta, NAP (*Non Arboreal Pollen*),

ataupun AP (*Arbooreal Pollen*). Pteridophyta sebagai kelompok tumbuhan tingkat rendah yang menghasilkan spora, NAP sebagai kelompok tumbuhan tidak berkayu seperti semak atau perdu, dan AP sebagai kelompok tumbuhan berkayu (Suedy, 2012).

Hasil dari pengelompokan taksa berdasarkan habitusnya menunjukkan bahwa taksa yang paling dominan adalah kelompok tumbuhan tingkat rendah yang menghasilkan spora, yaitu Pteridophyta. Persentase Pteridophyta (P) mencapai 53% dengan jumlah 18 taksa. Kelompok tumbuhan yang terbanyak selanjutnya adalah kelompok tumbuhan *Non-Arboreal Pollen* (NAP) yang memiliki persentase 29% dengan jumlah 10 taksa. Kelompok tumbuhan *Arboreal Pollen* (AP) memiliki persentase 18 % dan merupakan kelompok tumbuhan yang memiliki jumlah paling rendah, yaitu 6 taksa.

Dinamika tumbuhan temporal pada Telaga Warna dapat dilihat melalui grafik indeks keanekaragaman dan juga dinamika dari beberapa tumbuhan yang merepresentasikan *Arboreal Pollen* (AP), *Non-Arboreal Pollen* (NAP), serta Pteridophyta dari umur tua hingga umur yang lebih muda. Grafik pada Gambar 1 menunjukkan dinamika vegetasi Telaga Warna dari umur yang paling tua hingga paling muda (temporal). Grafik dibagi menjadi 4 zona dengan keterangan Zona I sebagai zona dengan umur yang paling tua hingga Zona IV sebagai zona paling muda.

Berdasarkan grafik dinamika keanekaragaman tumbuhan *Shannon-Wiener* secara temporal (Gambar 1), Pteridophyta merupakan kelompok tumbuhan yang paling mendominasi. Hal ini diakibatkan oleh kondisi lingkungan di kawasan Telaga Warna yang selalu

lembab dan basah. Banyaknya jumlah spora tumbuhan paku yang ditemukan dapat menunjukkan bahwa kondisi lingkungan tersebut

lembab (Tjitrosomo, 1986), karena habitat dari tumbuhan paku adalah lingkungan dengan tingkat kelembaban yang tinggi (Sastrapradja, 1979).

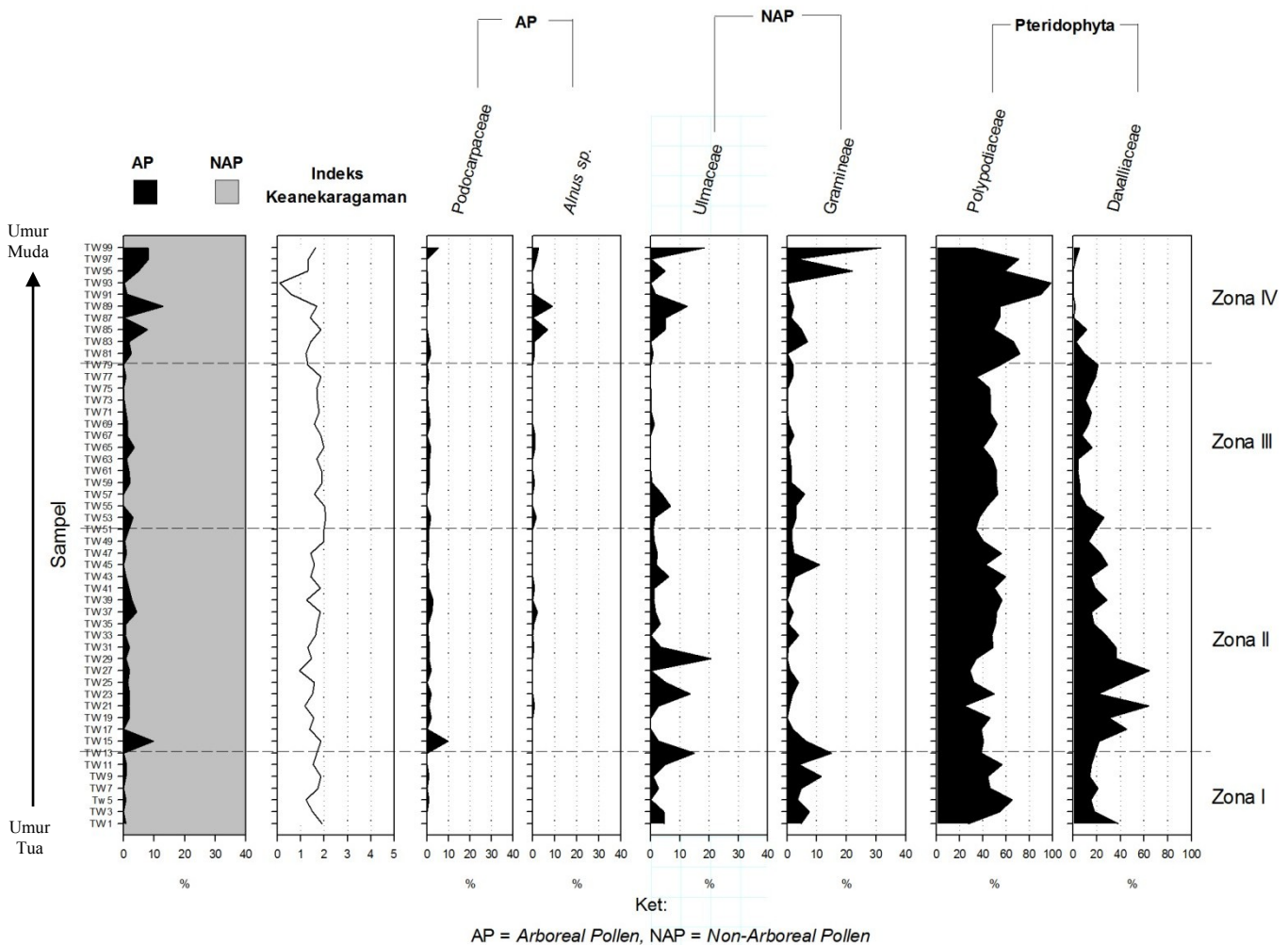
Tabel 1. Jumlah dan persentase polen dan spora yang ditemukan dalam sedimen Telaga Warna ( /200 µl).

No.	Nama	Jumlah ( /200 µl)	Persentase (%)
1	Polypodiaceae	6087	59.853
2	Davalliaceae	1331	13.088
3	Cyatheaceae	599	5.890
4	<i>Gleichenia sp.</i>	284	2.793
5	Gleicheniaceae	262	2.576
6	<i>Cyathea petiolata</i>	251	2.468
7	Ulmaceae	215	2.114
8	Gramineae	205	2.016
9	<i>Stenochlaena palustris</i>	132	1.298
10	<i>Lycopodium phlegmaria</i>	129	1.268
11	<i>Lycopodium sp.</i>	93	0.914
12	Podocarpaceae	76	0.747
13	<i>Alnus sp.</i>	64	0.629
14	<i>Vitis tiliifolia</i>	61	0.600
15	<i>Polygonum</i>	52	0.511
16	Ericaceae	47	0.462
17	<i>Acacia glomerosa</i>	37	0.364
18	<i>Podocarpus imbricatus</i>	35	0.344
19	<i>Lycopodium annotium</i>	35	0.344
20	<i>Alsophila sp.</i>	31	0.305
21	<i>Selaginella sp.</i>	29	0.285
22	<i>Lycopodium cunninghamioides</i>	21	0.206
23	Loranthaceae	17	0.167
24	<i>Glochidion sp.</i>	13	0.128
25	<i>Vaccinium sp.</i>	13	0.128
26	<i>Cissus microcarpa</i>	12	0.118
27	<i>Casuarina junghuniana</i>	10	0.098
28	<i>Macrotelyptheris laxa</i>	10	0.098
29	<i>Adiantum decoratum</i>	5	0.049
30	<i>Pteris vittata</i>	4	0.039
31	<i>Lygodium scandens</i>	4	0.039
32	<i>Lycopodium cernuum</i>	2	0.020
33	<i>Celtis sp.</i>	2	0.020
34	Polygonaceae	2	0.020
TOTAL		10.170	
TOTAL SPORA		9.309	91.534
TOTAL POLEN		861	8.466



Tumbuhan paku dapat dijumpai hidup secara kosmopolit pada sembarang tempat asalkan kondisi lingkungannya basah dan lembab tumbuhan paku dapat dengan mudah tumbuh. Beberapa kondisi lingkungan tersebut diantaranya adalah di bawah pohon, di pinggiran sungai, di lereng-lereng terjal, dan di pegunungan. Tidak

sedikit juga tumbuhan paku yang memiliki sifat epifit atau hidupnya menempel pada batang pohon dan batu. Sifat epifit (menempel) ini berbeda dengan parasit, tumbuhan epifit hanya menumpang pada tumbuhan lain sebagai tempat hidupnya dan tidak merugikan karena tidak mengambil apapun dari substratnya tempatnya menempel (Edwina, 2012).



Gambar 1. Dinamika Indeks Keanekaragaman *Shannon-Wiener* dan persentase AP, NAP serta Pteridophyta terpilih secara temporal berdasarkan polen dan spora yang ditemukan dalam sedimen Telaga Warna

Banyaknya kehadiran polen Gramineae yang ditemukan diakibatkan karena pada daerah di sekeliling tepi Telaga Warna banyak dijumpai rumput-rumputan yang tumbuh. Selain itu, titik

lokasi pengambilan sedimen juga dekat dengan lahan terbuka yang ada diantara Telaga Warna dan Telaga Pengilon dimana diantara telaga ini banyak ditumbuhi tumbuhan dari *Non-Arboreal Pollen*

(NAP) dengan jenis rumput-rumputan. Ditambah lagi, faktor antropogenik dari aktivitas pertanian yang dilakukan oleh masyarakat lokal di sekitar kawasan Telaga Warna juga turut berpengaruh. Transport polen dapat juga terjadi dari daerah pertanian ke dalam kawasan Telaga Warna.

Grafik indeks keanekaragaman *Shannon-Wiener* secara temporal (Gambar 1) dari kawasan Telaga Warna menunjukkan vegetasi yang dinamis stabil. Walaupun hasil dari nilai indeks

menunjukkan tingkat keanekaragamannya rendah, namun kisaran nilai indeks keanekaragaman Telaga Warna dari umur yang paling tua hingga umur yang paling muda tidak jauh berbeda. Rata-rata nilai indeks keanekaragamannya *Shannon-Wiener* ada dikisaran 1,56 (Tabel 2). Hal ini menunjukkan bahwa komposisi vegetasi di kawasan Telaga Warna tidak banyak berubah dari umur yang paling tua hingga umur yang paling muda.

**Tabel 2. Indeks Keanekaragaman *Shannon-Wiener***

Kode	Indeks Shannon-Wiener	Kode	Indeks Shannon-Wiener	Kode	Indeks Shannon-Wiener
TW 1	1.91	TW 35	1.715	TW 69	1.576
TW 3	1.511	TW 37	1.827	TW 71	1.781
TW 5	1.225	TW 39	1.247	TW 73	1.712
TW 7	1.737	TW 41	1.821	TW 75	1.667
TW 9	1.859	TW 43	1.42	TW 77	1.868
TW 11	1.523	TW 45	1.568	TW 79	1.289
TW 13	1.689	TW 47	1.422	TW 81	1.204
TW 15	1.859	TW 49	1.988	TW 83	1.434
TW 17	1.382	TW 51	1.988	TW 85	1.863
TW 19	1.546	TW 53	2.068	TW 87	1.402
TW 21	1.165	TW 55	2.021	TW 89	1.681
TW 23	1.5	TW 57	1.588	TW 91	0.5742
TW 25	1.568	TW 59	1.899	TW 93	0.0938
TW 27	0.9481	TW 61	1.879	TW 95	1.303
TW 29	1.439	TW 63	1.673	TW 97	1.332
TW 31	1.303	TW 65	1.987	TW 99	1.637
TW 33	1.639	TW 67	1.869	RERATA	1.564

Pada dasarnya keseimbangan lingkungan merupakan keseimbangan yang dinamis, artinya keseimbangan yang dapat mengalami perubahan, tetapi perubahan ini bersifat menjaga keseimbangan komponen lain, bukan berarti menghilangkan komponen yang lainnya. Pada lingkungan yang stabil, secara ekologi, adanya gangguan dalam lingkungan dapat dinetralisir melalui proses-proses dalam ekosistem (Winarno, 1992).

Komposisi vegetasi yang tidak banyak berubah di kawasan Telaga Warna dikarenakan telaga tersebut terdapat dalam kawasan konservasi. Telaga Warna dikelilingi oleh hutan yang cukup luas dan dijadikan sebagai area hutan konservasi oleh pemerintah dalam pengelolaan Seksi Konservasi Wilayah II BKSDA Jawa Tengah, dengan luas kawasan 39,6 ha. Kawasan hutan konservasi ini memiliki fungsi utama untuk perlindungan keanekaragaman hayati dan

ekosistemnya. Biasanya vegetasi di kawasan hutan konservasi sangat baik karena dijaga dan dipelihara oleh pemerintah maupun masyarakat. Pada tahun 2007 pemerintah bersama Balai Penelitian Teknologi Kehutanan Pengelolaan DAS (BPTKPDAS) pernah melakukan rehabilitasi untuk tetap menjaga keseimbangan ekosistem hutan konservasi yang ada di sekitar Telaga Warna dengan menanam tumbuhan *Arboreal Pollen* (AP) seperti *Schima walichii* (Puspa), *Acacia decurens*, dan *Casuarina junghuniana* (Cemara Gunung). Tahun 2015 BPTKPDAS juga melakukan kegiatan revitalisasi di Telaga Warna dan Telaga Pengilon untuk menjaga kelestariannya (Sumedi dkk, 2014).

## SIMPULAN

Hasil dari identifikasi ditemukan 34 taksa dari sedimen di Telaga Warna. Taksa yang diidentifikasi sampai tingkat famili berjumlah 9, sampai tingkat genus berjumlah 7, dan 18 sampai tingkat spesies. Jumlah kelompok Pteridophyta mencapai 53%, kelompok tumbuhan NAP (*Non Arboreal Pollen*) mencapai 29%, dan AP (*Arboreal Pollen*) mencapai 18%. Tingkat keanekaragaman tumbuhan secara temporal di Telaga Warna dikategorikan rendah dengan nilai indeks rata-rata 1,56 dan dinamika vegetasinya secara temporal dapat dikatakan dinamis stabil.

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## Review Article

# A review on *Adenium obesum*: A potential endemic medicinal plant in Oman

Associate Professor Dr. Md. Amzad Hossain

School of Pharmacy, College of Pharmacy and Nursing, University of Nizwa, P.O. Box 33, Postal Code 616 Nizwa, Oman



## ARTICLE INFO

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## ABSTRACT

Medicinal plants have played a vital role in the treatment of various human diseases and development of the society since the ancient times. Medicinal plants are the only safe sources for new drugs to treat curable and incurable diseases. About 25% of the prescription drugs available worldwide are derived from natural resources. *Adenium obesum* (AO) is one of the rare endemic medicinal plants in Oman and it belongs to family Apocynaceae. A biochemical investigation of the local AO species showed that the selected plant contained different groups of chemical compounds such as carbohydrate, cardiac glycoside, flavonoid, prenylated flavonoids, terpenoids, pregnanes etc. In addition, the pharmacological activities on the selected Omani species showed significant antimicrobial, antioxidant, anticancer, antiviral and immune modulatory activities. Only a few scientific research has been performed on the indigenous AO plant species. For this reason, it is mandatory for human, mainly the young generation to be aware of the toxicity, biochemical and pharmacological activities of the selected AO plant species. This comprehensive review report of the selected medicinal plant includes taxonomy, biological activity, phytochemicals, and potential uses. The study concludes that the plant extracts or isolated phytochemicals might be used as safe novel medicine in the near future for therapy and prevention of different diseases in the near future.

## 1. Introduction

### 1.1. Plant profile

Since the ancient times, plants and plant products have been exponentially increasing in the field of traditional systems like homeopathy, acupuncture, aromatherapy, ayurvedic medicine system etc. Many people are known to be treating different diseases by naturally obtained medicine through traditional systems due to their low costs and fewer side effects. Presently, more than 80% of the world population is using those natural medicines for therapy and prevention of different diseases (Martins, 2013). In addition, around two-thirds of commercial drugs launched in the world global market yearly is extracted or isolated from natural resources. Recent data from the US reveals that about 25% of the prescribed pharmaceutical drugs available in the global market to treat different diseases are based on plant chemicals (Orhan, 2012). In general, plants are still the best natural source of secondary metabolic compounds, which can be used for the treatment of different diseases (Hossain et al., 2013; Said et al., 2018; Akhtar et al., 2017; Raqiya and Hossain, 2017; Asma et al., 2017). The biochemical investigation of the selected plant species showed that the plant contained carbohydrate, cardiac glycoside, flavonoid, prenylated flavonoids, terpenoids, pregnanes along with several other minor chemical compounds (Akhtar et al., 2017). The groups of chemical

compounds are increasing day by day. Furthermore, the pharmacological activities of the selected plant showed significant antimicrobial, antioxidant, anticancer, antiviral and immunomodulation activities (Hossain et al., 2013; Yash et al., 2015). However, there is still a lack of animal study on the selected Omani AO species.

### 1.2. Synonyms

There are six synonyms available globally. However, only two are available in the southern part of the Sultanate of Oman.

1. *Adenium multiflorum*
2. *Adenium obesum*
3. Desert rose
4. Impala lily
5. Kudu lily
6. Mock azalea

### 1.3. Taxonomic classification

**Kingdom Plantae:** Plants; **Subkingdom Tracheobionta:** Vascular plants; **Subdivision Spermatophyta:** Seed plants; **Division Magnoliophyta:** Flowering plants; **Class Magnoliopsida:** Dicotyledons; **Subclass:** Asteridae; **Order:** Gentianales; **Family:**

E-mail address: [amzad@unizwa.edu.om](mailto:amzad@unizwa.edu.om).

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Apocynaceae; **Genus:** *Adenium*; **Species:** *obesum*.

#### 1.4. Distribution of plant

Initially, AO species originated from African countries, but, nowadays it is now found in most tropical and subtropical countries (Hossain et al., 2013; Akhtar et al., 2017). The selected plant species is widely distributed across the African region (e.g., Ethiopia, Kenya, Senegal, Somalia, Sudan and Tanzania) and also in Asian region (e.g., most of the Arabian countries, Malaysia, Pakistan, India etc.). Several species of the selected plant are available in Oman (Akhtar et al., 2017). One of which is the desert rose that can be found in the Sultanate of Oman. All parts of the specific species are used as medicine for the treatment of varied diseases. Therefore, the selected plant species are cultivated commercially all over the world due to its medicinal values (Hossain et al., 2013; Akhtar et al., 2017).

#### 1.5. Description of plant

Globally *Adenium obesum* (AO) is considered as a medicinal plant belonging to the Apocynaceae family. Locally, it is known as desert rose and the plant is considered as a slow growing long-leaved plant. It is also known as an ornamental plant and is currently cultivated most humid countries. The plant grows well in rocky and sandy soils (Hossain et al., 2017). The height of this species is about two to four meters (Fig. 1). Initially, the bark is pale yellow but later turn into shades of grey and brown. The bark is smooth with gummy, white latex; branchlets glabrescent, pubescent at apex. The shape of the leave is oval and spirally arranged, clustered at the end of branch lets (Hossain et al., 2014a,b,c). The flowers and fruits of the selected species are a special type and they depend on environmental conditions (Mouza and Hossain, 2015). Normally, the flowers are multi coloured. The fruit is follicle and at maturity, it splits along one side to release seeds (Hossain et al., 2014a,b,c). All AO species including the Omani ones are produce milky sap containing some toxic chemical compounds that can create skin irritation (Hossain et al., 2017).

#### 1.6. Traditional use

All parts of local AO species are important and are traditionally used as medicine to treat different diseases. In Omani tradition, the most important use of the paste of the whole plant is to treat venereal diseases (Mouza and Hossain, 2015; Hossain et al., 2014a,b,c). The lotion which is isolated from the root and the bark is used to treat different skin diseases and to kill lice (Mouza and Hossain, 2015; Hossain et al., 2014a,b,c). The white latex of this plant is very good medicine in the treatment of tooth decay and septic wounds (Hossain et al., 2017;

Mouza and Hossain, 2015). The isolated latex of the endemic plant species is toxic, hence it is used as a pesticide. On the other hand, the Somalian use it to treat nasal infections (Hossain et al., 2014a,b,c). Kenyans use the white latex to kill lice and the powder of the stem to kill skin parasites for camels and cattle (Hossain et al., 2014a,b,c). Also the bark is a good medicine to treat abortifacient (Hossain et al., 2014a,b,c; Codd, 2011; Dimmitt and Hanson, 2002). Nigerians also use the whole plant for antiplasmodial, anti-trypanosomal and anti-leishmanial activities (Codd, 2011; Dimmitt and Hanson, 2002). Omani people also traditionally use it to treat wounds, skin diseases, headaches, muscle pain and joint pain (Hossain et al., 2017; Mouza and Hossain, 2015).

#### 1.7. Plant collection

The selected whole plant was collected from Dhofar region in the Southern part of Oman in the year 2014. Firstly, the stem-barks were separated from the plant and sliced into small pieces for drying and processing. After the drying, it was ground and extracted with methanol. The methanol extract was fractionated through a solvent–solvent extraction process using different polarities of solvents with increasing polarity (Hossain et al., 2017; Mouza and Hossain, 2015). All polarities of crude extracts were used for the determination of biochemical analysis and different pharmacological activities.

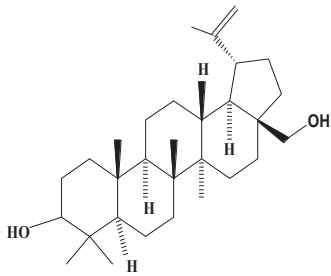
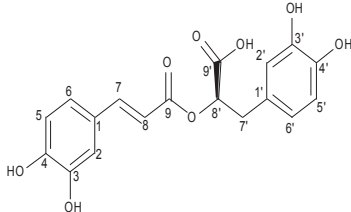
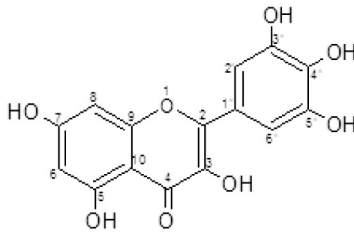
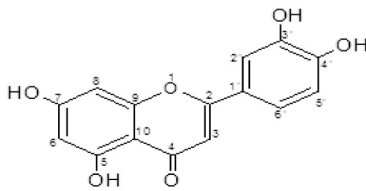
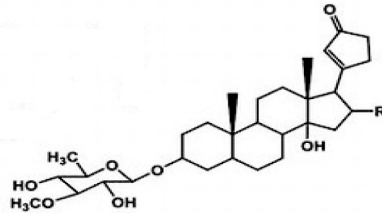
## 2. Biochemical

Different types of compounds found in the locally grown whole AO plant which is increased gradually based on the age of the plant (Malebo et al., 2009). The phytochemical study showed that the selected plant contained different groups of chemical compounds like carbohydrate, cardiac glycoside, flavonoid, prenylated flavonoids, terpenoids, and pregnanes etc. (Akhtar et al., 2017). Most of the isolated individual chemical compounds from the selected plant were biologically active (Akhtar et al., 2017; Amin et al., 2013; Harshet al., 2002). Previous studies of the selected plant by different authors showed that a total 53 compounds were isolated and identified (Amin et al., 2013; Harshet al., 2002). Some are toxic and they have different biological activities like antiviral, antitumor, and cytotoxic activities (Hossain et al., 2013). However, in the Gulf countries, only a few studies have been conducted on the selected endemic medicinal plant. In addition, only a few phytochemical studies have been done on the local AO plant (Amin et al., 2013; Harshet al., 2002). Therefore, the aim of this review is to deal with the biological and phytochemical studies on different parts of endemic AO species. The isolated chemical compounds reported so far from the various part of endemic AO species is presented in Table 1.



Fig. 1. Different part of plant picture.

**Table 1**  
Chemical Compounds of AO in Oman.

Plant part	Name of Chemical compounds	Structure	Reference
Stem-bark	1. Betulin		Amin et al. (2013), Harshet al. (2002)
	2. Rosmarinic Acid		Hossain et al. (2017)
Stems	1. 3,5,7,3',4',5'-Hexahydroxy flavone		Hossain et al. (2017)
	2. 5,7,3',4'-Tetrahydroxy flavone		
Leaves	1. Honghelin		Amin et al. (2013), Harsh et al. (2002)
	2. Obeside B		
	3. Obeside C		
		1. R = H 2. R = OH 3. R = OCOCH <sub>3</sub>	

### 3. Pharmacological activities

The selected plant species is a rare long-leaved plant and it is found in most of the Gulf countries, including the Sultanate of Oman (Hossain et al., 2017). The plant contains several groups of compounds with different biological activities. In the Gulf region, the plant is used for the treatment of different ailments. Traditionally, different parts of the selected plant are used by Omani people to treat venereal diseases, wounds, skin diseases, headaches, muscle pain, joint and pain lice (Mouza and Hossain, 2015). The plant also showed significant antimicrobial, antioxidant, anticancer, antiplasmodial, anti-trypanosomal and anti-leishmanial activities (Hossain et al., 2014a,b,c; Codd, 2011;

Dimmitt and Hanson, 2002; Malebo et al., 2009; Amin et al., 2013).

#### 3.1. Antioxidant activity

The antioxidant activity of all polarity extracts of Omani AO species was measured by a well-established DPPH method (Hossain et al., 2014b). All polarity extracts showed different antioxidant activities within the range of 44–96%. According to the published results among the different polarity extracts, the highest antioxidant activity was obtained in butanol extract and the lowest was obtained in hexane extract. The activity of the plant extract depends on the chemical compounds which were isolated by using different polarity solvents from the plant.

The experimental results showed that butanol extract of Omani AO species have the highest activity which means that the majority of the active compounds are present in the butanol extract. On the other hand, hexane extract showed minimum activity, which means that hexane extract contains less number of active chemical compounds. Almost similar results were obtained from other countries and other AO species (Hossain et al., 2014a,b,c; Codd, 2011; Dimmitt and Hanson, 2002). Besides, the antioxidant activity also varies from one part to the other parts of the plant. Previous studies on antioxidant activity indicated that the stem-bark extract showed the highest activity compared to other parts (Hossain et al., 2014b). Similar pattern results obtained from Omani AO species also revealed the same pattern comparing different parts (Hossain et al., 2014b). Extraction methods also play a vital role in the antioxidant activity of the plant extracts. Several other previous studies showed that Soxhlet extraction method is better than the maceration method. In the Soxhlet method, the solvent is evaporated by heating and the fresh solvent recycled again and again to dissolve the compounds from the plant samples. On the other hand, in the maceration method, the solvent is used at the beginning of the experiment and it can dissolve the compounds until the solvent is saturated by the compounds. After saturation, the solvent is not able to dissolve any more compounds in the plant samples. Therefore, the antioxidant activity is more comparative when the Soxhlet extract method is used for extraction (Hossain et al., 2014b).

### 3.2. Antimicrobial activity

All polarity crude extracts of the selected endemic plant species were examined for their antimicrobial activity against Gram (+ and –) bacterial strains such as *Staphylococcus aureus*, *Escherichia coli*, *Pseudomonas aeruginosa* and *Valgurais* by existing method (Harsh et al., 2002; Malebo et al., 2009; Amin et al., 2013). Antibiotics, amoxicillin and dimethyl sulphoxide solvent (DMSO) were used as positive and negative controls. All the bacterial strains were clinically isolated and collected from the local hospital. All the crude extracts showed potentially moderate activity against the Gram (+ and –) bacterial strains. Among the prepared extracts, the highest antimicrobial inhibition was obtained in butanol extract. The experimental results showed that the biological activity depended on the polarity of the solvents. It indicated that antimicrobial activity was responsible for bioactive compounds (Hossain et al., 2014a,b; Agrawal, 1989; Goad and Akihisa, 1997; Gohari et al., 2003; Dewick et al., 1992; Fairouz et al., 2004; Gordon, & David, 2001; Hakim et al., 2002; Harborne, 1986; Hodek et al., 2002). In addition, among the employed bacterial strains, only the gram-negative type strains showed moderate antimicrobial activity against all polarity crude extracts at all concentrations of the selected plant species. Similar results were reported in the literature by several authors (Hossain et al., 2014a,b; Hui et al., 2001; Naji et al., 2013; Mabry et al., 1997; Markhman, 1992; Masry et al. 2002; Neuwinger, 2011; Rowley, 1983; World Health Organisation, 2001). Recently, the biological activities of the isolated compounds were reported on the selected plant species (Akhtar et al., 2017; Hossain et al., 2017). The maximum inhibition shown by hexahydroxyflavone compared to trahydroxyflavone against *P. vulgaris*. Similar experiment results were also reported on the isolated pure flavonoids compounds against *S. aureus*, *E. coli*, *P. aeruginosa* and *P. vulgaris*. All isolated flavonoids against the Gram (+ and –) tested bacteria gave the moderate activity at all applied concentrations. The range of inhibition zones of the pure compounds was 9–14 mm. The isolated hexahydroxyflavone showed maximum inhibition against *P. vulgaris* (IZ = 14 mm) in comparison with the standard antibiotics. The experimental results indicate that the activity is increases with the increase of hydroxyl group. Similarly, the antimicrobial activity of the isolated pure compounds and crude extracts was determined by our existing disc diffusion method (Akhtar et al., 2017; Hossain et al., 2017). All prepared crude extracts and isolated plant compounds showed moderate antimicrobial potential within the

range of 0–13 mm. The different extracts and pure isolated plant compounds showed moderate antimicrobial activity against *E. coli*. This could reveal the variety of bioactive compounds and the negotiation of their bioactivity by the polarity of solvents (Harsh et al., 2002; Agrawal, 1989; Goad and Akihisa, 1997). Our experimental results completely agree with previous results presented by Tijjani et al. (2011a,b). The isolated rosmarinic acid from other plant species has earlier been shown to have maximum activity (Tijjani et al., 2011a,b).

### 4. Conclusion

The local AO is an ornamental and toxic plant widely available in Arabian Gulf including Oman. All parts of the selected plant were used as medicine to treat different ailments. Traditionally, in Oman, the plant is used mainly to treat infectious and venereal diseases. It is a long-leaved plant that grows mainly in the hilly, rocky and sandy soil. From the literature, about 53 compounds were isolated from the selected plant. All the isolated compounds and different polarity crude extracts from different parts of the selected plant showed different moderate biological activities. The literature survey showed that the plant crude extracts and isolated compounds have varied biological activities such as antitumor, antimicrobial, anti-influenza, molluscicidal, locusticidal, and antiviral activities, including potential immunomodulatory and cardiotoxic activities. Still, no study on essential oil of the plant parts has been carried out. Furthermore, no investigation has been done on the animal study of the isolated pure compounds as well as the different polarity extracts. According to previous reports, the plant could be a good source for new drugs. Therefore, this current review report of the selected plant might help other researchers to carry out further investigations into its better use in pharmaceutical, agrochemical, and cosmetics industries.

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# Allamanda violacea: Purple Allamanda<sup>1</sup>

Edward F. Gilman, Ryan W. Klein, and Gail Hansen<sup>2</sup>

## Introduction

This evergreen vine or climbing shrub has 3-inch-long, funnel-shaped blooms which are reddish-purple fading to pink, giving a two-toned effect. The light green, pubescent leaves are arranged in whorls on weak, sprawling stems. While it can be allowed to rapidly cover an arbor or other support, purple allamanda also makes an attractive free-standing specimen shrub with careful pruning. Many people use it to cover the base of a mailbox or pole. Allamanda will cascade over a wall and makes a nice hanging basket. Rapid growth creates a sprawling form with individual shoots growing alone, away from the rest of the plant. Regular pinching will keep the plant in bounds, but too much pinching removes flower buds which form on new growth.



Figure 1. Full form—*Allamanda violacea*: purple allamanda.  
Credits: Edward F. Gilman, UF/IFAS

## General Information

**Scientific name:** *Allamanda violacea*

**Pronunciation:** al-luh-MAN-duh vye-o-LAY-see-uh

**Common name(s):** purple allamanda

**Family:** *Apocynaceae*

**Plant type:** shrub; ground cover

**USDA hardiness zones:** 9B through 11 (Figure 2)

**Planting month for zone 9:** year-round

**Planting month for zone 10 and 11:** year-round

**Origin:** not native to North America

**Invasive potential:** not known to be invasive

**Uses:** container or above-ground planter; ground cover; cascading down a wall; hanging basket

**Availability:** generally available in many areas within its hardiness range



Figure 2. Shaded area represents potential planting range.

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2. Edward F. Gilman, professor, Environmental Horticulture Department; Ryan W. Klein, graduate assistant, Environmental Horticulture Department; and Gail Hansen, associate professor, Environmental Horticulture Department; UF/IFAS Extension, Gainesville, FL 32611.

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## Description

**Height:** depends upon supporting structure

**Spread:** depends upon supporting structure

**Plant habit:** spreading

**Plant density:** moderate

**Growth rate:** moderate

**Texture:** coarse

## Foliage

**Leaf arrangement:** whorled

**Leaf type:** simple

**Leaf margin:** entire

**Leaf shape:** elliptic (oval)

**Leaf venation:** brachidodrome

**Leaf type and persistence:** evergreen

**Leaf blade length:** 4 to 8 inches

**Leaf color:** green

**Fall color:** no fall color change

**Fall characteristic:** not showy

## Flower

**Flower color:** lavender; purple

**Flower characteristic:** year-round flowering

## Fruit

**Fruit shape:** unknown

**Fruit length:** unknown

**Fruit cover:** no fruit

**Fruit color:** green

**Fruit characteristic:** inconspicuous and not showy

## Trunk and Branches

**Trunk/bark/branches:** not particularly showy; typically multi-trunked or clumping stems

**Current year stem/twig color:** green

**Current year stem/twig thickness:** medium

## Culture

**Light requirement:** plant grows in full sun

**Soil tolerances:** occasionally wet; acidic; slightly alkaline; clay; sand; loam

**Drought tolerance:** moderate

**Soil salt tolerance:** unknown

**Plant spacing:** 36 to 60 inches

## Other

**Roots:** not applicable

**Winter interest:** plant has winter interest due to unusual form, nice, persistent fruits, showy winter trunk, or winter flowers

**Outstanding plant:** plant has outstanding ornamental features and could be planted more

**Pest resistance:** no serious pests are normally seen on the plant

## Use and Management

Flowering best in full-sun locations, purple allamanda should be planted in frost-free sheltered locations in nematode-free soil. Water plants generously until well-established. All parts of the plant are poisonous and should be used with caution in areas frequented by young children.

Propagation is by cuttings, but it is grown best when grafted on *A. cathartica* (yellow allamanda) cultivars 'Hendersonii' or 'Schottii.'

## Design Considerations

The purple allamanda works well as a background or massing plant when grown on a trellis or fence to block undesirable views or fill gaps along walls. It can also be used to add interest to an arbor or pole. The medium-size, light green foliage of the allamanda shows well with contrasting plant features such as large leaves, coarse texture, thick stems, and dark green or burgundy color. The loose, sprawling form of the vine contrasts with neat plants such as the clumping, arching forms of grasses and other vase-shaped, small-leaved shrubs. Low-growing groundcover with a mounding or matting form will emphasize the upright form of a trained allamanda on a trellis or arbor. To create a large plant mass along a fence select other vines with a variety of flower colors, such as white, pink, or yellow to mix with the allamanda for more interest.

## Pests and Diseases

No pests or diseases are of major concern except for nematodes. Purple allamanda is only occasionally bothered by scale and mites.

## Apocynaceae

Apocynaceae Jussieu, Gen. Pl. 143 (1789) (Apocinae), nom. cons.

Asclepiadaceae Borkh. (1797) (Asclepiadeae), nom. cons.

Periplocaceae Schltr. (1905).

M.E. ENDRESS, U. MEVE, D.J. MIDDLETON, AND S. LIEDE-SCHUMANN

Woody climbers, vines, perennial herbs, trees or shrubs, more rarely annuals, sometimes with large water-storing tubers or a xylopod, sometimes succulent, with large grappling hooks and/or tendrils in several lianoid genera of Willughbeieae; latex in non-articulated laticifers present, most commonly white, but in some genera usually translucent and in others yellowish or reddish. Leaves simple and usually entire, very rarely dentate or repand, usually isophyllous, but often anisophyllous in Tabernaemontaneae-Tabernaemontaninae, sometimes with distinctly different juvenile and adult foliage, normally petiolate, sometimes sessile, usually opposite, less frequently alternate or whorled (whorled phyllotaxis characteristic for a number of Rauvolfioid genera); stipules usually absent or small and caducous, sometimes enlarged and fused into dentate interpetiolar collars (a few Periplocoideae genera), commonly with interpetiolar lines or ridges, sometimes the petioles of a leaf pair connate at the node, forming a short ocrea, which may be expanded into small intrapetiolar flaps clasping the stem (Tabernaemontaneae), almost always with colleters in the axil of the leaf, sometimes on the petiole, in a cluster adaxially at the juncture of petiole and lamina or along the midrib above, occasionally with abaxial domatia in the axils of the secondary veins (mainly in Apocynoids). Flowers perfect, rarely functionally dioecious, often scented, sessile or more commonly pedicellate, in solitary or more commonly in axillary, extra-axillary or terminal multi-flowered

cymes, panicles or thyrses, sometimes appearing as an axillary fascicle. Perianth almost always actinomorphic, very rarely slightly zygomorphic; calyx almost always 5- (rarely 4- or 6-7)-merous, lobes normally quincuncially arranged, synsepalous or aposepalous, commonly with colleters, in Periplocoideae, Secamonoideae and Asclepiadoideae these are usually in the sinuses, but in some Rauvolfioids and several Apocynoids colleters in a continuous ring, in multiple rows in some Tabernaemontaneae and Hunterieae, or a single antesepalous colleter (especially in Echiteae), and in several genera of Rauvolfioids and Apocynoids colleters are absent; corolla sympetalous, rarely apopetalous (a few Ceropegieae), salverform, infundibuliform, tubular, urceolate or rotate, lobes almost always 5 (very rarely 4), usually contorted in bud, either dextrorse or sinistrorse, more rarely valvate; corolline or gynostegial coronas often present; stamens 5 (rarely 4), filaments mostly straight, sometimes geniculate, sometimes connate around the style (some species of *Forsteronia*, *Thoreauea*), sometimes coiled around the style (*Dewevrella*, some species of *Parsonsia* and *Thenardia*), inserted on the corolla tube, on prominent staminal feet (broadened filament base fused with corolla tube) or forming a staminal tube, included to exerted; anthers introrse, rarely latrorse, in almost all Apocynoids, Secamonoideae and Asclepiadoideae with highly elaborated and lignified guide rails (lignified guide rails absent in most Rauvolfioids and in Periplocoideae) and often with an apical connective

Rauvolfioids and Apocynoids contributed by David J. Middleton and Mary E. Endress. Periplocoideae, Secamonoideae and Asclepiadoideae contributed by Sigrid Liede-Schumann and Ulrich Meve.

Ulrich Meve and Sigrid Liede-Schumann wish to thank Prof. Dr. Focke Albers, Münster, for his input in the initial planning of the then Asclepiadaceae treatment in this series; he and his students obtained several preliminary results we built on.

appendage, thecae 4, unequal in most Apocynoids, with dorsal ones smaller through presence of guide rails, reduced to 2 in Asclepiadoideae, dehiscence longitudinal, attached to the style-head forming a gynostegium (gynostegium absent in Rauvolfoideae); nectaries in alternistaminal pockets on the staminal tube, on sides of staminal feet or 5 (rarely 2) lobes encircling the base of the ovary, these often fused to varying degrees into an (often deeply lobed) ring (in some Rauvolfoideae and early-branching Apocynoids nectaries are adnate to the outer wall of the ovary at the base or are sometimes nonfunctional or absent); gynoeceum normally of two carpels (very rarely up to five); ovary mostly apocarpous, sometimes congenitally (Rauvolfoideae only) or postgenitally syncarpous (several Apocynoids), in some genera only one carpel developing, superior to subinferior; placentation marginal when the ovary is apocarpous, parietal or axile when syncarpous, when apocarpous upper part of the carpels fusing postgenitally to form a complex style-head that produces adhesive for pollen transport, with a pollen-trapping basal collar and/or pollen-presenting upper crest present in many Rauvolfoideae and Apocynoids; stigma mostly on the underside of the style-head, often restricted to five chambers behind the guide rails, but style-head scarcely morphologically differentiated and nearly uniformly receptive in some Rauvolfoideae; adhesive a sticky foam or mucilage, or differentiated into five translators with a scoop-like pollen receptacle and sticky base, or as five hard clips (corpuscles) usually accompanied by five pairs of flexible arms (caudicles) forming a pollinarium. Fruit in Rauvolfoideae diverse: drupes, berries, follicles or capsules; seeds usually without a coma, naked, arillate, or winged or fimbriate at the margin very rarely with a coma (*Haplophyton*); in the remainder of the family, fruit almost always a pair of ventrally dehiscent follicles (often only one due to abortion or due to postgenital fusion; rarely a septicidally dehiscent capsule) with small seeds with a micropylar coma, rarely with a chalazal coma, coma at both ends (only in early-branching Apocynoids), or fringed with long trichomes circumferentially (a few Periplocoid and *Hoya* species), or without a coma.

The classification used here employs both formal and informal ranks for the main divisions

of the family. The two subfamilies comprising the traditional Apocynaceae—Rauvolfoideae and Apocynoideae—are paraphyletic and thus used here informally, as Rauvolfoideae and Apocynoids, respectively, whereas formal ranks are maintained for Periplocoideae, Secamonoideae and Asclepiadoideae, which are all nested within Apocynoids. The clade consisting of the Apocynoids along with Periplocoideae, Secamonoideae and Asclepiadoideae is here referred to as the APSA clade. The taxa in the APSA clade have many features in common that set them apart from the less derived Rauvolfoideae. The family comprises 378 genera and about 5,350 species and is predominantly pantropical, with some genera reaching temperate regions.

**VEGETATIVE MORPHOLOGY.** Apocynaceae are primarily woody plants. A large percentage of the Rauvolfoideae and several genera in the early-branching Apocynoid tribes Wrightieae, Nerieae and Malouetieae are trees or shrubs, whereas the great majority of the remainder of the family is lianas or vines. Herbs are rare in Rauvolfoideae and Apocynoids, except in some genera that are adapted to drier or colder habitats, where they are usually perennial (e.g., *Apocynum*); some have a water-storing xylopod, which produces herbaceous shoots (e.g., several species of *Mandevilla*). The majority of Periplocoideae, Secamonoideae and Asclepiadoideae are herbaceous or only basally woody; thus twiners, perennial herbs and subshrubs are the dominant growth forms. In the Periplocoideae, small trees occur only in *Decalepis*. In Secamonoideae, Lahaye et al. (2005) report the evolution of a shrub-like growth form from lianoid ancestors. No trees or large shrubs are known in Asclepiadoideae (except *Calotropis*), but secondary woodiness has been proposed for *Marsdenia erecta* (Yaman and Tumen 2012). Geophytes with root and hypocotyl tubers are frequent in African Periplocoideae (*Raphionacme*, *Schlechterella*, *Pentopetia*) and Asclepiadoideae (diverse Asclepiadeae, *Ceropegia*). Succulents are rare in Rauvolfoideae and Apocynoids; in Rauvolfoideae, *Plumeria* and *Himantanthus* are subsucculent. In Apocynoids two genera from Africa/Madagascar are stem succulent: *Adenium* and *Pachypodium*. Ceropegieae include the often bizarre-looking, stem succulent Stapeliads (e.g., *Stapelia*, *Caralluma*, *Duvalia*,

etc., and some *Ceropegia* species). *Cynanchum* (Asclepiadeae) includes ca. 50 stem succulent species from Madagascar, and the “*Sarcostemma* group”, widespread in the Paleotropics and tropical Australia. True epiphytes are unknown in Rauvolfioids and Apocynoids. There are reports of *Mandevilla boliviensis* growing in trees in Costa Rica and it is therefore sometimes said to be epiphytic (e.g., Gentry and Dodson 1987; Morales 1998). However, this species is normally terrestrial, and is probably best interpreted as merely an accidental epiphyte (Kress 1986). In Periplocoideae epiphytes are restricted to *Epistemma* and *Sarcorrhiza*, but are more frequent in Marsdenieae (Asclepiadoideae), including numerous species of *Hoya* and *Dischidia*. In addition, some species of *Dischidia* and *Hoya* have a close association with ants; the leaves of many species are modified into inflated structures (imbricate or pitcher leaves) that house ants. In turn, the waste products of the ants provide additional nutrients, which are absorbed by the plant (Peeters and Wiwatwitaya 2014).

Leaves are simple and entire (except in *Emicocarpus*), almost always with an entire smooth margin (very rarely dentate in *Alyxia* or repand in *Parsonsia*), and predominantly opposite. Alternate or whorled leaves are characteristic for certain genera in Rauvolfioids, but these become infrequent in the more derived APSA clade. The leaves of immature plants can sometimes be of a remarkably different shape and/or size from those of mature plants (e.g., in *Parsonsia* and *Micrechites*), although this has been recorded in very few genera and its prevalence is as yet unknown. Venation is typically pinnate, and mostly brochidodromous. Stipules in the usual sense are normally lacking (although stipules have been reported in some species of *Rauvolfia* and petioles of a leaf pair may be connate at the base forming a short ocrea, which may be expanded in the intrapetiolar region, forming flaps, which are characteristic for some Tabernaemontaneae and found occasionally in other Rauvolfioid genera); other outgrowths, especially stipular or interpetiolar ridges, are common throughout the family. Whereas stipular glands are the common state in Ceropegieae, spiny stipules characterize the Stapeliad *Tavaresia*. Paired, often branched, spines in the leaf axils are characteristic for *Carissa* (Carisseae), decidu-

ous, blunt, conical spines occur on the trunk in some species of *Lacmellea* and ternate spines (the middle one often very reduced or absent) are found in *Pachypodium*. Except for *Boucerosia frerei*, leaves are rudimentary in all Stapeliads, and sometimes form spines (*Hoodia*, *Edithcolea*). Tendrils are common in Willughbeieae, where they are often modified inflorescences. In most genera, young leaves show flat to curved ptyxis (Cullen 1978); only in Rauvolfioids is conduplicate ptyxis found (*Alyxia*, *Carissa*, *Cerbera*, *Plumeria*), and involute ptyxis is known from *Vinca* (Vinceae) and *Landolphia* (Willughbeieae).

Tooth-like colleters are usually present in the leaf axil throughout the family (decreasing in number and size in derived Asclepiadoideae), sometimes spreading along the adaxial side of the petiole (e.g., some species of *Rauvolfia*, and Periplocoideae); in many species of *Mandevilla* small, round, black colleters are scattered along the adaxial side of the petiole. A cluster of flat, deltoid-shaped colleters at the base of the leaf blade on the adaxial surface is found in most Mesechiteae and is widespread in Asclepiadoideae. In Baisseeae, colleters are absent in the leaf axils, but tooth-like colleters are present along the adaxial side of the petiole, and/or as a cluster at the base of the adaxial side of the leaf blade. Abaxial domatia are found in the axils of the secondary veins with the midrib of the leaf in some genera of Malouetieae (e.g., *Funtumia*, *Malouetia*), Apocyneae (e.g., *Urceola*), Odontadenieae (e.g., *Pinochia*), many Mesechiteae (e.g., *Tintinnabularia*, *Forsteronia*) and are characteristic for Baisseeae.

**VEGETATIVE ANATOMY.** The presence of non-articulated, branched or unbranched laticifers containing white (or sometimes differently colored) latex is one of the distinguishing characteristics of Apocynaceae (Mahlberg 1980). White latex is the most common state, but many Wrightieae and Echiteae (Apocynoids), all Ceropegieae, and some genera of Asclepiadeae (*Astephanus*, *Microlooma*, *Oncinema*, *Pentatropis*, and many species of *Vincetoxicum*) and some species of *Hoya* have translucent latex. Many species of *Aspidosperma* (Rauvolfioids) as well as *Cryptolepis sanguinolenta* (Periplocoideae) have red or orange latex, and some species of *Cynanchum* (Asclepiadoideae) have yellow latex. Leaves are normally

dorsiventral, but isobilateral leaves have been reported in *Nerium*. In stem succulent Ceropegieae and *Cynanchum* species, leaves are almost always reduced to scales. Stomata are ranunculaceous or rubiaceous, and sometimes both types occur in a single species (Metcalf and Chalk 1972). In Asclepiadoideae, they can be tetracytic, and in Stapeliads even hexacytic (Metcalf and Chalk 1979). Trichomes of various types occur; they may be simple, uniseriate, and several-celled (e.g., *Chonemorpha*), unicellular (e.g., *Vinca*, *Allamanda*), sometimes uniseriate, but with a series of compressed basal cells (e.g., *Echites*); in *Anechites* hooked trichomes with enlarged multicellular bases occur (Fallen 1983). The typical trichome in Asclepiadoideae is multicellular, eglandular, transparent to whitish or occasionally colored, antrorse or retrorse. Glandular trichomes are known in *Dischidia* (Solereder 1899), *Vincetoxicum hirsuta* (Trivedi and Upadhyay 1984, as *Tylophora*), *Araujia* (Metcalf and Chalk 1972), and in a wide range of Gonolobinae (e.g., *Gonolobus*, *Macrosepsis*, *Matelea*, Metcalf and Chalk 1972).

Internal phloem is nearly always present, either as a continuous ring or as separate bundles at the margin of the pith; the pericycle is generally in the form of a continuous ring or as separate strands of white cellulose fibers. Cork is present in Rauvolfioids and Apocynoids, but its origin has not been investigated. Cork, as far as is known, arises from a phellogen in the endodermis in Periplocoideae (except for *Cryptolepis*) and Marsdenieae (Asclepiadoideae), but from the epidermis in Ceropegieae and Asclepiadeae (except for succulent *Cynanchum* (former *Sarcostemma*); Treiber 1891). Wood features that are uniform throughout Apocynaceae include simple vessel perforations, sometimes with short, scalariform perforation plates, alternate vested intervessel pits, and vessel-ray pits that are similar in shape and size to intervessel pits (Lens et al. 2009), and vested perforate tracheary elements either septate with simple pits, or non-septate and with bordered pits. Wood parenchyma is often apotracheal, sometimes also with some paratracheal, in some genera predominantly paratracheal, and absent in genera with septate fibers. There are a number of general evolutionary trends evident from Rauvolfioids to the more derived Apocynaceae of the APSA clade including: shorter vessel elements (on average 700–1000

µm in Rauvolfioids versus 200–500 µm in Periplocoideae, Secamonoideae and Asclepiadoideae); a higher proportion of vessels in multiples and more vessels per multiple (solitary vessel elements or radial vessel multiples in Rauvolfioids and Wrightieae, Nerieae and Malouetieae of the Apocynoids versus large vessel clusters in more derived members of the ASPA clade). There is a close correlation between vessel grouping pattern and the type of imperforate tracheary cells in the ground tissue: tracheids coevolve with solitary vessels, whereas fibers are linked with vessel multiples and clusters (Carlquist 1984). Reduction of vessel element length and the trend toward large vessel clusters are correlated with vasicentric tracheid abundance, increase of paratracheal parenchyma, and decrease in number of cells per axial parenchyma strand (6–12 in Rauvolfioids versus 2–5 in Periplocoideae, Secamonoideae and Asclepiadoideae; Lens et al. 2009). Most of these evolutionary trends are typically correlated with habitat shift to more arid regions and/or a shift to climbing habit (Baas et al. 1983; Lens et al. 2008). Other features, such as vessel grouping, vessel element length, fiber type, frequency of uniseriate rays and fused multiseriate rays, vary and, in combination, are indicative of specific tribes in Rauvolfioids and Apocynoids and in Periplocoideae (Lens et al. 2009). Sieve-element plastids are of the derived S-type (Behnke 1981).

**INFLORESCENCE STRUCTURE.** Terminal thyrsoidal systems are regarded as the plesiomorphic condition throughout the family; the diversity of inflorescences found in the family results from different degrees of reduction (Liede and Weberling 1995). Inflorescences in Rauvolfioids and Apocynoids are mostly cymose, simple or compound in dichasia, thyrses or panicles, sometimes fasciculate (e.g., *Kibatalia*, *Malouetia*, *Pleiocarpa*) or umbelloid cymes (sciadioids, e.g., *Thernardia*). In some lianoid genera of Apocynoids, inflorescences are racemose (e.g., *Mandevilla*, *Asketanthera*). In some genera, an inflorescence may be reduced to 1–2 flowers (e.g., *Haplophyton*, *Vinca*, *Catharanthus*, *Rhabdadenia*, *Salpinctes*). Inflorescences may be axillary and/or terminal.

Synflorescences in Periplocoideae and Secamonoideae show some deviations from terminal and/or axillary branching thyrses (e.g., *Tacazzea*)

to extra-axillary branching ones with racemose, corymbose or sciadioidal inflorescences (e.g., *Raphionacme*), and/or cyme formation and reduction of the number of flowers to two or one (e.g., *Secamone*). Inflorescence types are most diverse in Asclepiadoideae, where extra-axillary inflorescences predominate, whereas the axillary inflorescences found in some American Asclepiadeae are best regarded as secondary (e.g., *Orthosia*, *Oxypetalum*, *Peplonia*; cf. Liede and Weberling 1995). In consequence, inflorescences are usually solitary (one inflorescence per node) and only rarely paired (two inflorescences per node). Compound inflorescences are rare in the subfamily, while simple, many-flowered sciadioids are typical for the horticulturally attractive groups of Marsdenieae (*Dregea*, *Hoya*) and Ceropegieae (e.g., *Boucerosia*, *Caralluma*). By reduction of paracladia in number and size, originally dichasially branching cymes become few-flowered bostrices and sciadioids, or geminiflorous helices (e.g., *Cynanchum*, *Stapelia*). In many species of *Tassadia*, the  $\alpha$ -bract supports the continuation of the inflorescence, producing sympodial shoots of very regular length, while the  $\beta$ -bract produces a few-flowered, very dense bostryx (Liede and Weberling 1995).

**FLORAL STRUCTURE AND ANATOMY.** Flowers are bisexual, very rarely functionally unisexual in a few Rauvolfioids (e.g., *Carissa*, Schroeder 1951; *Rauvolfia*, Koch et al. 2002), and andromonoecious in *Cynanchum* (*Glossonema*) *varians* (Ali and Ali 1996) and *Cynanchum hemsleyanum* (= *Metaplexis japonica*, Tanaka et al. 2006). They are actinomorphic or rarely slightly zygomorphic (monosymmetric) due to a gibbous, arcuate (some species of *Rauvolfia* and *Mandevilla*) or strongly bent corolla tube (some species of *Lacmellea*) and/or 3 + 2 organization of the corolla lobes (*Allamanda schottii*, *Adenium*). The number and arrangement of floral organs is quite uniform: flowers are almost always pentamerous (rarely 4-merous), with each type of organ arranged in a whorl, except for the gynoecium, which, with few exceptions, is of two carpels. A calyx is always present, and is almost always 5-merous, but is consistently 4-merous in *Leuconotis* and *Parahancornia*. Three species of *Aspidosperma* (*A. illustre*, *A. megalocarpon* and *A. myristicifolium*) have a 4-merous calyx; in the

first two the four lobes are decussate, with the outer two significantly larger and fused at the base, and the inner two much reduced, and the calyx is reported to be 6–7-merous in *Aspidosperma darienense*, though more thorough study may show some of these to be modified bracts. The calyx lobes are fused into a 2-lipped tube or partial tube in *Alyxia kabaenae*. Usually the calyx is green, though large, showy, unequal and overlapping white or pink calyx lobes are frequent in certain *Tabernaemontana* species from South America, and in *Rhodocalyx* the large petaloid calyx lobes are the same wine-red color as the corolla; yet, even in genera where it may be foliose or petaloid, the calyx is normally easily differentiated from the corolla. The calyx lobes are typically split nearly to the base; sometimes they may be fused in the lower part or for most of the length into a cup (e.g., *Chonemorpha*, *Voacanga*). In the majority of the genera, collectors are found at the base of the calyx on the adaxial side. Most frequently calycine collectors are few and in alternisepalous position, quincuncially arranged, but in several Apocynae collectors are more numerous and in a single ring, most Echiteae are characterized by solitary antesealous collectors, many *Tabernaemontaneae* have multiple rows of collectors, and in many Rauvolfioids calycine collectors are absent.

A corolla is always present, though it may be minute (e.g., many *Urceola* species, *Cynanchum roulinioides*, *Orthosia meridensis*), and is almost always 5-merous (4-merous in *Leuconotis* and two species of *Parsonsia*: *P. kimberleyensis* and *P. lanceolata*). It comprises a congenitally fused lower corolla-staminal tube (stapet), and a postgenitally fused upper corolla tube (Nishino 1982, 1983). Fusion of the upper tube occurs relatively late in development, and occurs from the apex to the base; in some Rauvolfioids the flower reaches maturity before the two epidermal edges are completely fused, leaving gaps just above the insertion of the stamens, which are characteristic for certain genera (e.g., *Aspidosperma*, *Stephanostegia*; Endress and Bruyns 2000). Corolla shape is extremely variable. Corollas are most commonly salverform in Rauvolfioids and Apocynoids, although lignification of the anthers in the latter protects the pollen from desiccation, making possible more open corolla types, including rotate corollas with the reproductive organs completely



exserted (e.g., *Forsteronia*, *Thenardia*, *Pottsia*, many species of *Parsonsia* and *Wrightia*). Infundibuliform corollas are also common, especially in the Apocynoids. Urceolate corollas are found in *Urceola* and *Ecua*.

Corolla lobes are normally contorted and the direction of contortion is a systematically important character (Endress et al. 1990). In Rauvolfioids, corolla lobe aestivation is almost always sinistrorse (exceptions include *Geissospermum*, *Kopsia*, *Ochrosia* and some species of *Tabernaemontana*, *Haplophyton*, *Alstonia* and *Carissa*, which all have dextrorse corolla lobe aestivation). In Apocynoids, Periplocoideae, Secamonoideae and Asclepiadoideae, in contrast, corolla lobe aestivation is typically dextrorse, with a few exceptions (e.g., all Wrightieae as well as some species of *Urceola* (Apocynoids), and all *Gentianthus* and *Pervillaea* (Secamonoideae), all of which have sinistrorse corolla lobe aestivation, and some *Urceola* and *Parsonsia* species, which have valvate corolla lobe aestivation). Valvate corolla lobe aestivation is characteristic for some derived Asclepiadoideae, especially the complex flowers of some Ceropegieae (e.g., *Ceropegia*), in which complicated structures arise through postgenital fusions of petals during ontogeny. Corolla lobes are typically not inflexed in bud, but strongly inflexed corolla lobes are characteristic for some genera of Alyxieae and rarely in Apocynoids, and weakly inflexed corolla lobes are found in *Tabernaemontana* (Leeuwenberg 1991, 1994b).

Coronas are an important feature of the flower and play a key role in the characterization of genera in the more derived APSA clade (Fishbein 2001; Wanntorp and Forster 2007). They are simple to very elaborate outgrowths, which may be grouped into two main types depending on their location: corolline and gynostegial. It should be emphasized, however, that the same location does not necessarily imply homology. In the Rauvolfioids and Apocynoids coronas are mostly corolline (Kunze 1990, 2005), and are most commonly found in the staminal (alternipetalous) sectors, either in the corolla throat or somewhat lower down, near the anthers and the region of confluence between the congenitally (stapet) and postgenitally fused parts of the corolla. There is a great variety of different forms of corolline coronas (see e.g., Endress and Bruyns

2000). They may be in the form of free lobes, or fused to varying degrees into annular structures. In *Wrightia* the corona is alternipetalous or antepetalous or both, depending on the species. In some species of *Wrightia* and in *Pleioceras* the corona consists of many fimbriate lobes. They may be petaloid (as in *Melodinus*, *Nerium* or *Strophanthus*); they may be in the form of a knob-like protuberance behind the anther (as in *Artia* or *Cycladenia*); often they are rather inconspicuous pocket-like flaps that join two petals across the sinus (e.g., *Vinca*). In *Prestonia* (Apocynoids) a thick annular corona is usually present in the corolla mouth, and in addition, in many species, knob-like free lobes are present just above the anthers. More rarely corolline coronas are in the alternistaminal (antepetalous) sectors (e.g., *Apocynum*). In addition, ledge-like outgrowths of the corolla are found in some genera (e.g., *Baissea*, *Ixonoderium*). The homology of these various types of coronas has not been determined. In Periplocoideae the corona lobes are typically initiated near the petal sinuses, in the region of confluence between the congenitally (stapet) and postgenitally fused regions of the corolla (Fig. 24).

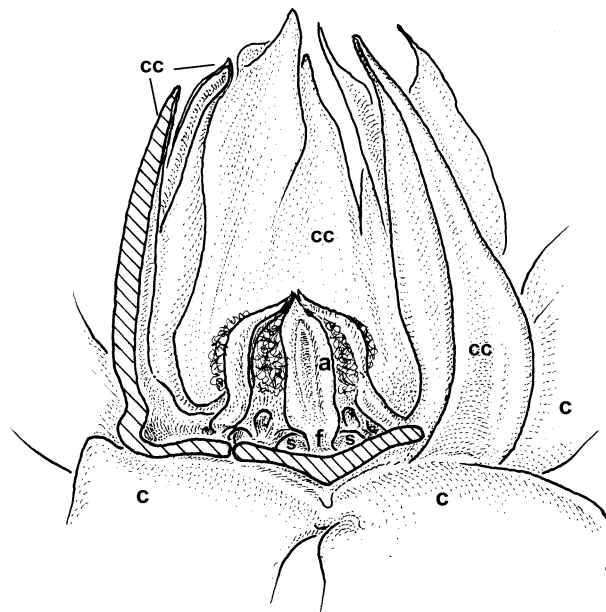


Fig. 24. Apocynaceae-Periplocoideae. *Raphionacme*. Gynostegium with corona (front corona lobe removed). (a = anther, c = corolla lobe (mostly cut away), cc = corolline corona lobe, f = filament, s = staminal foot). (Drawn by U. Meve)

Gynostegial coronas, which have their origin as outgrowths of the back of the stamens, are the rule in Asclepiadoideae (Fig. 25), but absent in Rauvolfioids and rare in Apocynoids (e.g., *Kibatalia*, *Vallaris*) and Periplocoideae (e.g., *Finlaysonia obovata*, where they occur as simple staminal corona lobes). Interstaminal elements, which are usually combined with the staminal elements, are apomorphic in Asclepiadoideae (Kunze 1990). A system of classification of the multitude of sometimes extravagant corona forms has been developed by Liede and Kunze (1993). Basic corona composition (e.g., whether just in the staminal sectors, or in both staminal and interstaminal sectors) has been used widely for recognizing larger taxonomic groups, but has been found to be misleading in several examples (e.g., *Cynanchum* (former *Sarcostemma*) and *Funastrum*, Liede and Täuber 2000, circumscription of *Cynanchum*, Liede and Täuber 2002). (Fig. 25).

Stamens are morphologically clearly differentiated into an anther and filament in the Rauvolfioids, Apocynoids and Periplocoideae, although the anthers are often sessile, and thus a distinct filament is not present in many taxa (e.g.,

*Thevetia*, *Vallaris*, *Voacanga*). In Secamonoideae and Asclepiadoideae, the anthers are  $\pm$  sessile on a tube. The tube has often been called a staminal tube or filament tube, the latter implying that it is formed of the fused filaments (Kunze 1990). Endress and Bruyns (2000), conversely, hypothesized that the filaments have been lost, and that the tube is formed by the gynostegial corona. This was based for the most part on the presence of a staminal tube in *Hemidesmus* and *Phyllanthera grayi* (Periplocoideae), both of which have distinct staminal filaments arising from atop the tube. Conclusive evidence, however, is lacking for both interpretations. The anthers are introrse (to latrorse in some Plumerieae-Thevetiinae). Each anther contains two thecae, and in all of the family except Asclepiadoideae, each theca contains two pollen sacs. In Asclepiadoideae, the dorsal pollen sac in each theca has been lost, so that in each anther only the two ventral pollen sacs develop. In most Tabernaemontaneae (Rauvolfioids), Apocynoids, Secamonoideae and Asclepiadoideae the anthers are morphologically and histologically highly specialized. Pollen production is restricted to the upper part of the anther. The lower part is enlarged and sterile; thick, lignified guide rails develop laterally. Lignified guide rails are absent in Rauvolfioids (except Tabernaemontaneae), and in Periplocoideae. Based on character optimization, this is interpreted as plesiomorphic in Rauvolfioids, and as a secondary loss in Periplocoideae. Older suggestions that the absence of lignified guide rails in Periplocoideae implies a closer relationship to Rauvolfioids (Wanntorp 1988) have been shown to be incorrect (Nilsson et al. 1993; Sennblad and Bremer 2000; Potgieter and Albert 2001; Livshultz et al. 2007). Conversely, the homology of lignified guide rails in Tabernaemontaneae and Apocynoids with those in Secamonoideae and Asclepiadoideae has not been proven. Although character optimization implies that at least those within Apocynoids are homologous, there are some differences in the detailed morphology and histology of the anthers (Kunze 1996) that suggest this interpretation may be overly simplistic. In higher Asclepiadoideae, the guide rails usually consist of two ridges with upwardly directed bristles between them (Liede 1996a).

There is a high degree of synorganization both within the androecium as well as between

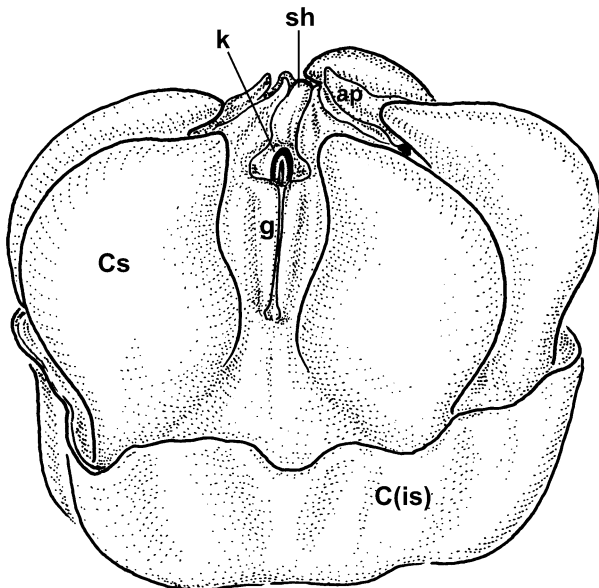


Fig. 25. Apocynaceae-Asclepiadeae. *Cynanchum*. Gynostegium with corona. (ap = anther appendage, Cs = staminal corona lobe, C(is) = ring-shaped gynostegial corona of connate staminal and interstaminal parts, g = guide rail, k = corpusculum, sh = style-head). (Drawn by U. Meve)

the androecium and the gynoecium, intensified by postgenital fusions. In Apocynoids, Secamonoideae and Asclepiadoideae, the guide rails of adjacent anthers are separated only by a narrow slit, and are synorganized to function in guiding the pollinators' proboscis or leg into the pollination unit. In addition, adjacent anthers may be laterally postgenitally united, forming a ring (e.g., *Hemidesmus*, some species of *Mandevilla*; Nilsson et al. 1993; Moré et al. 2007). The anthers are postgenitally united with the style-head, forming a gynostegium except in Rauvolfioids. This results in a pentamerous revolver flower with five separate nectar/pollination chambers. Rarely, in some basal Apocynoids and Periplocoideae, the union occurs farther down on the filament, and may then be very weak (e.g., *Holarrhena*). In most Apocynoids a special pad of hairs is present on the ventral face of the connective, by which the anthers are attached to the style-head. In some genera of Mesechiteae (e.g., *Mandevilla*, *Mesechites*; Fallen 1986; Nilsson et al. 1993) the ventral face of the anther connective is smooth, and the anthers and style-head become postgenitally united by cellular fusion, as is the case in Periplocoideae, Secamonoideae and Asclepiadoideae. The connective apex is sometimes drawn out into a long filiform appendage (e.g., *Skytanthus*, *Nerium*, *Strophanthus*, *Pentalinon*), or a narrowly triangular to deltoid appendage (most Tabernaemontaneae, many Apocynoids), or a more or less membranous flap (most Asclepiadoideae). In Rauvolfioids, although a gynostegium is absent, the anthers may become stuck to the copious style-head secretions; the anthers sometimes closely surround the style-head (in e.g., *Allamanda*, *Cerbera*, *Vinca* and many other genera) forming a cone over its top, with their thecae resting against the slopes of the sterile upper part.

The majority of genera have distinct nectaries or nectar-producing tissue. In a number of genera of Rauvolfioids a distinct nectary disc or lobes cannot be distinguished, yet studies have found nectar to be present. Microtome sectioning and appropriate staining has revealed that in some of these taxa the lower part of the outer carpel wall is thickened and comprises cytoplasm-rich cells with stomata in the epidermis that secrete nectar (e.g., several genera of Tabernaemontaneae, *Hancornia* (Willughbeieae), *Chilocarpus*, *Condylocarpon* and *Lepinia* (Alyxieae), *Picralima* (Hun-

terieae) and *Acokanthera* (Carisseae); Haber et al. 1981; Zarucchi 1987; Endress et al. 1996, 1997; Darrault and Schindwein 2005; Simões et al. 2007, 2016; Moura et al. 2011). In detailed studies of *Condylocarpon isthmicum* by Morokawa et al. (2015), nectar was found to be secreted by modified stomata with guard cells that have lost the ability to close their pores (Fahn 1979; Davis and Gunning 1992). Other genera without a discernible nectary disc, or with a much reduced one, are nectarless. This has been demonstrated in *Aspidosperma* (Aspidospermateae) and in *Plumeria* (Plumeriinae) in the Rauvolfioids as well as in some genera of the two early-branching tribes of Apocynoids (Wrightieae and Nerieae) and in *Holarrhena* and *Malouetiella* (Malouetieae). In all other tribes of the Apocynoids as well as in the Periplocoideae, Secamonoideae, and Asclepiadoideae, nectaries are characteristic. In Rauvolfioids and Apocynoids nectaries, when present, surround the base of the ovary (Endress and Bruyns 2000). Typically there are five, alternate to the staminal filaments. These may be distinct lobes (e.g., *Cleghornia*, *Trachelospermum*, *Apocynum* (Apocyneae), some species of *Forsteronia* (Mesechiteae); Nilsson et al. 1993; Middleton 2007), but often are fused to varying degrees into a disc, which may be of nearly free lobes, which are fused only near the base (e.g., many species of *Prestonia* (Echiteae) or *Mandevilla* (Mesechiteae); Simões et al. 2006; Morales et al. 2017b), or the segments may be  $\pm$  completely fused into a ring, often with a lobed or crenulate top (e.g., all Baisseeae and many Apocyneae such as *Aganosma*, *Amphineurion*, *Anodendron*, *Epigynum*; De Kruif 1983; Middleton 2007, 2014). The nectary is of two lobes that are alternate to the carpels in several genera of Vinceae (e.g., *Catharanthus*, *Kopsia*, *Vinca* (Rauvolfioids) and in a few genera of Apocynoids, such as *Spirolobium*, *Carruthersia* (Malouetieae), *Salpinctes* (Odontadenieae) and several species of *Mandevilla*; Woodson 1936; Simões et al. 2006; Middleton 2007; Endress et al. 2007a.

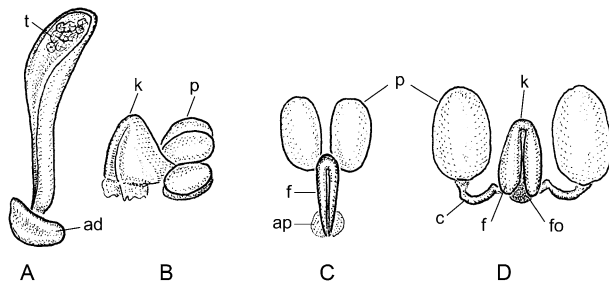
In Periplocoideae, Secamonoideae and Asclepiadoideae distinct nectary lobes or a disc, such as found in Rauvolfioids and Apocynoids, are absent. Instead, nectar is secreted by specialized patches of secretory epithelium found in five pockets (chambers) on the staminal tube beneath the guide rail base (Kunze 1997). Another region

of epithelium is often found along the anther flanks within the guide rails, or on the sides of the thickened corona lobes (or region between them) below the filaments in Periplocoideae. In Asclepiadoideae, nectar is frequently collected and presented in cups formed by the gynostegial corona; in *Asclepias* and its relatives, elaborate nectar conducting systems have evolved (Galil and Zernoni 1965; Kunze 1997).

The gynoecium is of two carpels, with a few rare exceptions in Rauvolfioids (up to five carpels in *Lepinia*, *Lepiniopsis* and *Pleiocarpa*), and in the great majority of taxa it is apocarpous. In Rauvolfioids, congenital syncarpy is characteristic for all genera of the Willughbeieae and Carisseae and the non-arillate members of the Tabernaemontanaeae. Sometimes the gynoecium is syncarpous in the lower part, but apocarpous above (e.g., many species of *Rauvolfia*). In the APSA clade congenital syncarpy is absent; rather, in genera with syncarpous gynoecia, these come about by postgenital fusion (e.g., *Amalocalyx*, *Artia*, *Beaumontia*, *Nerium*, *Parepigynum*, *Parsonsia*, *Temnadenia*, *Thenardia* and *Vallaris*). In the great majority of genera the gynoecium is differentiated into ovaries, style and style-head. However, genera of some of the derived tribes of Asclepiadoideae typically lack a style. In genera with apocarpous gynoecia, the carpel apices undergo a temporary postgenital fusion, which lasts at least through anthesis. Where the flanks of the two carpels come together, the epidermis is obliterated and a uniform tissue is formed (Walker 1975, 1978; Sage et al. 1990). The uppermost part of this postgenitally fused region develops into an enlarged style-head, the enlarged apices of which sometimes contribute to flower attraction and pollinator control (*Araujia*, *Oxypetalum*). The style-head is a complex structure, which functions not only as a stigma, but also has a secretory epithelium, which produces adhesive components that play an important role in pollination biology (Schick 1980, 1982a; Fallen 1986). The adhesive is a heterogeneous mixture of polysaccharides and free sugars, terpenes and cutin derivatives, with the different components expressed to various degrees in the different parts of the family (Schick 1982b). Except in a few genera of Rauvolfioids, in which the style-head is uniformly receptive and secretory all over (e.g., *Alyxia*), the style-head is differentiated into zones: the five

regions between the adnate anthers secrete the adhesive used in pollen transport. In the Periplocoideae, Secamonoideae and Asclepiadoideae, the secretions harden into acellular bodies that aid in the transport of pollen, and are called translators. Generally the stigmatic region is located beneath or on the lower half of the style-head. In Asclepiadoideae the receptive region is restricted to five stigmatic chambers on the underside of the style-head alternating with the stamens and behind the guide rails.

In Rauvolfioids the adhesive secreted forms a continuous ring of foamy or viscous substances around the style-head. In Apocynoids, the adhesive is interrupted in five regions due to the adnate anthers, so that it is restricted to five alternistaminal sectors. In both Rauvolfioids and Apocynoids two different components of the adhesive can often be distinguished in serial sections based on differences in staining and consistency. Sometimes both are frothy with considerable air spaces; sometimes one is frothy and the other is firm and compact. Secretion of these different components is sequential, and may be either temporally (epithelial cells producing first one, then switching to a second component) or spatially differentiated (i.e., specialized regions on the style-head secrete only one or the other component; Endress, unpubl. data). Rarely in Apocynoids the secreted substances become firm through desiccation, forming five simple band-like translators (e.g., *Apocynum*, some species of *Forsteronia*; Nilsson et al. 1993). In Periplocoideae, differentiation of the two adhesive components is both temporal and spatial: the denser adhesive component forms a firm spoon-like translator that is morphologically differentiated into three regions: (1) a broad, upper, flattened pollen-presenting scoop; (2) an inwardly rolled stalk; and (3) a broadened, flattened base (Fig. 26A). The foamy component, which is secreted over the scoop, helps pollen tetrads to adhere. At the base of the translator, the foamy component is secreted copiously, and is pushed outward forming a sticky glob (sometimes called a sticky disc or viscidium) that projects from the periphery of the style-head, and by which the translator adheres to the pollinator. In Secamonoideae and Asclepiadoideae, the translators are formed from the firmer secretory components; the foamy, sticky component has been



**Fig. 26.** Translators and pollen in Periplocoideae, Secamonoideae and Asclepiadoideae. **A** Periplocoideae. Spoon-shaped translator with pollen tetrads. **B** Secamonoideae. Pollinarium with four pollinia. **C** Asclepiadoideae-Fockeeae. Pollinarium with two pollinia and without caudicles, corpusculum with flanks and adhesive pads. **D** Asclepiadoideae-Marsdenieae. Pollinarium with two pollinia, connected via caudicles to corpusculum, corpusculum with flanks flanks and floor. (ad = adhesive disc, ap = adhesive pad, c = caudicle, f = flank of corpuscle, fo = floor of corpuscle, k = corpusculum, p = pollinium, t = pollen tetrad). (Figures not to scale; drawn by U. Meve)

interpreted to have been greatly decreased (Demeter 1922; Schick 1982b; Kunze et al. 1994). The secretions are differentiated into a hard clip-like corpuscle to which the pollinia are attached (Fig. 26B, D). In Asclepiadoideae, in addition to the corpuscle, two slender, more flexible arms (caudicles) are secreted, by which the pollinia are attached to the corpuscle (Fig. 26D; Kunze 1994). In some Secamonoideae slender thread-like caudicles are present (Civeyrel 1995; Civeyrel and Rowe 2001), but their homology to those in Asclepiadoideae is uncertain, particularly since the first branch of Asclepiadoideae, Fockeeae, with the two genera *Fockea* and *Cibirhiza*, lacks the caudicles characteristic for all other Asclepiadoideae (Fig. 26C). In these two genera the pollinia are  $\pm$  sessile on a flat plate of adhesive on the dorsal side of the corpuscle, similar to the situation in most Secamonoideae (Fig. 26B; Kunze 1993; Civeyrel 1994, 1995; Kunze et al. 1994).

**EMBRYOLOGY.** The embryology of the Apocynaceae has been summarized by Johri et al. (1992). Maheswari Devi (1964) gives an overview for Periplocoideae and Asclepiadoideae. The anther tapetum is secretory. The pollen mother cells undergo simultaneous as well as successive cytokinesis in Rauvolfioids, Apocynoids and Periplocoideae (sometimes within the same species), and successive in Asclepiadoideae. In Rauvolfioids

and Apocynoids the tetrads are tetrahedral and isobilateral. Decussate, T-shaped and linear tetrads are known from Periplocoideae (e.g., *Hemidesmus indicus*). The formation of linear tetrads is the rule in Asclepiadoideae, but T-shaped tetrads occur as well (e.g., *Pergularia*). In Rauvolfioids and Apocynoids pollen grains are triporate and three-celled at maturity. Two-celled pollen has been reported for *Catharanthus*, *Plumeria* and *Holarrhena*. In Asclepiadoideae pollen grains are three-celled at maturity and are aggregated into pollinia. The pollinium is covered by a persistent tapetal membrane of sporopollenin, which can be discontinuous in one region, which is the germination pore. The ovules are hemianatropous or anatropous, unitegmic, tenuinucellate, usually with an integumentary tapetum. Of the original one-layered nucellus, the lateral cells become crushed while the apical cells persist. Ategmic ovules have been reported in the following genera of Asclepiadoideae: *Araujia*, *Asclepias*, *Gomphocarpus*, *Cynanchum* and *Marsdenia*. But these are older studies (e.g., Maheswari Devi 1964, and references therein) that need to be reconfirmed. The archesporium is one-celled, rarely 2–3-celled. The chalazal megaspore develops into an embryo sac, and development is of the Polygonum type. A report of bisporic development in *Cynanchum* (Asclepiadoideae; Maheswari Devi 1964) should be reconfirmed. The polar nuclei fuse before fertilization; the antipodal cells are ephemeral and secondary multiplication is found in Asclepiadoideae. Starch grains accumulate in the embryo sac.

Endosperm development is of the nuclear type. Embryogenesis of the Asterad, Onagrad, Caryophyllad and Chenopodiad type has been reported in Rauvolfioids and Apocynoids, and of the Solanad type in Asclepiadoideae. Apomixis, as far as is known, occurs only in *Vincetoxicum* as integumentary polyembryony (Naumova 1992). Endosperm is ruminant in some Rauvolfioids (e.g., Tabernaemontaneae-Tabernaemontaninae and some Alyxieae such as *Alyxia*, *Lepinia*, *Lepiniopsis*, *Condyllocarpon*, some species of *Chilocarpus*; Periasamy 1963; Corner 1976). The seed is typically albuminous and exotestal.

**POLLEN MORPHOLOGY.** Palynological characters have long been the most important morphological features in distinguishing larger taxonomic

units in the family (Brown 1810; Civeyrel et al. 1998; Endress 2001). Pollen is shed as monads in Rauvolfioids and Apocynoids, with a few sporadic exceptions where it remains in tetrads. Tetrads are known from five genera of Rauvolfioids, where they occur sporadically in *Tabernaemontanaeae*, *Melodineae* and *Alyxieae*, and in Apocynoids only in *Apocynum* (Erdtman 1952; Lodder et al. 2007). Pollen is typically shed as tetrads in Periplocoideae (Nilsson et al. 1993). In seven (mostly Asian) genera of Periplocoideae (*Decalepis*, *Epistemma*, *Finlaysonia*, *Gymnanthera*, *Hemidesmus*, *Schlechterella* and *Streptocaulon*) each anther produces four pollinia (Verhoeven and Venter 1998, 2001; Ionta and Judd 2007). Likewise, in Secamonoideae each anther produces four pollinia, whereas in Asclepiadoideae each anther produces two pollinia (Civeyrel et al. 1998).

In general, Rauvolfioids have 3–5-colporate pollen grains (Nilsson 1986), but pollen of *Craspidospermum* is in 5–10-periporate tetrads, and most *Alyxieae* have distinctive, barrel-shaped (2–)3–5-porate, triangular pollen grains (sometimes 1-porate in *Chilocarpus* and *Plectaneia*, and inaperturate tetrads in *Condylocarpon*; Nilsson 1990; Van der Ham et al. 2001; Endress et al. 2007a). Pollen grains in Apocynoids are generally (2–)3(–6)-porate or 2–6-stephanoporate, but (1–)2(–4)-porate grains have been reported for *Mascarenhasia* and *Pachypodium* (Lienau et al. 1986), and 4–8(–22)-periporate grains have been reported in *Isonema*, *Carruthersia*, *Apocynum*, *Trachelospermum* and *Micrechites* (Endress et al. 1990; Lodder et al. 2007). In both Rauvolfioids and Apocynoids, the outer exine surface is usually smooth and perforate, whereas the inner surface is variously patterned. Rauvolfioids show much more variation as to the inner exine patterning than do Apocynoids, with endocracks, colp and mesocolpial plates, or granules (Nilsson 1986). In most New World species of *Tabernaemontana* (and some paleotropical species and a few species of *Voacanga*) endoapertures are fused into an endocingulum (Van der Weide and Van der Ham 2012). In Apocynoids the inner exine is always granular. Tetrads in both Rauvolfioids and Apocynoids are acalymmate. In Rauvolfioids tetrahedral, colporate tetrads are found in *Callichilia*, at least one species of *Tabernaemontana* and some species of *Melodinus*.

*Condylocarpon* has non-tetrahedral, inaperturate tetrads with a reduced exine, a suite of features considered to be neotonic, and *Craspidospermum* has non-tetrahedral, irregularly pantoporate tetrads, which are quite similar to those found in *Apocynum* (Van de Ven and Van der Ham 2006).

In Periplocoideae, in contrast, the tetrads are calymmate, and are generally rhomboidal or decussate, although other arrangements are present in some genera. The grains are 4–6-porate in most genera, although *Raphionacme*, one of the largest genera in the subfamily, has 8–16-porate grains. The pores are typically lined up pair-wise where two pollen grains abut. The inner walls of the tetrads have the same structure as the outer wall, but are interrupted by intine wall bridges. Periplocoideae pollinia (known from seven genera) are always four per anther and comprise loosely coherent tetrads that show a reduction of the number of pores in the distal wall. A pollinium wall is absent (Verhoeven and Venter 2001). Pollinia in Periplocoideae have evolved at least three times independently, and also separately from those in the other subfamilies (Ionta and Judd 2007).

Secamonoideae pollinia (four per anther) are small, globose, and comprise loosely coherent calymmate, inaperturate tetrads. The inner walls of the tetrads are reduced compared to the outer walls, and are interrupted by intine wall bridges. A pollinium wall is absent (Verhoeven and Venter 2001).

Asclepiadoideae pollinia (two per anther—the two dorsal pollen sacks are reduced; Kunze 1982) comprise single, inaperturate pollen grains, and are surrounded by a pollinium wall (Frye 1901; Verhoeven and Venter 2001). The only exception known is *Fockea*, in which the pollinia consist of coherent inaperturate calymmate tetrads not covered by a pollinium wall (Verhoeven et al. 2003). There is great variation in the size and shape of the pollinia (El-Gazzar et al. 1974; Schill and Jäkel 1978). In Secamonoideae and Asclepiadoideae, pollinia of neighboring anthers are joined in a pollinarium by an acellular translator apparatus secreted by the style-head (Fig. 26; Schnepf et al. 1979). Within the Secamonoideae, this structure normally lacks translator arms but displays considerable variation (Civeyrel 1994; Civeyrel et al. 1998). Orientation details of pollinaria morphology are the basis of

tribal delimitation in Asclepiadoideae. In Fockeeae, the two erect pollinia are attached dorsally directly to the corpusculum, which has broad outer flanks at least basally isolated and not united by a floor (Fig. 26C). These flanks continue basally into adhesive pads glued to the anther wings (Kunze et al. 1994). Marsdenieae and Ceropegieae have erect pollinia (Fig. 26D), and sterile insertion crests on the outer side in Marsdenieae, if present (Swarupanandan et al. 1996), but always present on the inner side in Ceropegieae. Asclepiadeae have pendent pollinia, except for most Gonolobinae and some *Vincetoxicum* species with horizontally oriented pollinia. Some species of *Vincetoxicum* (*Sphaerocodon* group) and *Cynanchum verrucosum* even have erect pollinia, caused by upward-curved caudicles. Sterile insertion crests on the top or the outer margin are rare, but characteristic for most Gonolobinae.

**KARYOLOGY.** Karyological information is available for about 190 genera. The most comprehensive reviews are those of Van der Laan and Arends (1985) and Albers and Meve (2001). The base chromosome number of  $x = 11$  is predominant, and is found in 60% of the genera of Rauvolfioids and Apocynoids, without exceptions in Periplocoideae and Secamonoideae, and in 96% of the genera of Asclepiadoideae. In Rauvolfioids, no deviations from the base number were found in Willughbeieae, Tabernaemontaneae, Hunterieae, and Carisseae. Most genera have only one base number, but both  $x = 11$  and  $x = 8$  have been reported for *Apocynum*. Significant deviations include  $x = 9, 10$  for all of the genera of Plumerieae counted (six out of ten), and  $x = 6, 9$  for all of the Echiteae counted (five genera out of 20). In addition, sporadic variation in base number has been found in some genera of all other tribes of Apocynoids. In Asclepiadoideae, reduction to  $x = 9, 10$  is restricted to Asclepiadeae;  $x = 10$  is characteristic for *Funastrum*, *Microloma* and *Orthosia* (and is also found in around ten more genera), whereas an increased base number occurs sporadically in all tribes.

In Rauvolfioids and Apocynoids polyploidy has been reported in nine genera (ca. 13%), and in Asclepiadoideae only about 6% of the taxa are polyploid, with tetraploidy being by far most common (Albers and Meve 2001).

Chromosome morphology is similar throughout the family, with (sub)metacentric chromosomes being predominant. Usually, each genome possesses one pair of chromosomes with secondary constrictions and satellites (Van der Laan and Arends 1985; Albers and Meve 2001).

Average chromosome length is ca. 1.5  $\mu\text{m}$  in Rauvolfioids and Apocynoids, and gradually decreases to an average of 1.3  $\mu\text{m}$  in Periplocoideae, 1.2  $\mu\text{m}$  in Secamonoideae, and somewhat less than 1  $\mu\text{m}$  in Asclepiadoideae. Within Asclepiadoideae, chromosome length on the average is greatest in Fockeeae (1.2  $\mu\text{m}$ ), and gradually diminishes from the more basal to the most derived tribes: 1.1  $\mu\text{m}$  in Marsdenieae, 1.0  $\mu\text{m}$  in Ceropegieae, and 0.9  $\mu\text{m}$  in Asclepiadeae (Albers and Meve 2001).

**REPRODUCTIVE BIOLOGY AND POLLINATION.** Flowers are bisexual. In a few genera of Rauvolfioids, gender dimorphism and associated functional dioecy have been reported (e.g., *Carissa*, Schroeder 1951, and *Rauvolfia*, Koch et al. 2002), and in *Cynanchum* (*Glossonema*) *varians* (Ali and Ali 1996) and *Cynanchum hemsleyanum* (= *Metaplexis japonica*, Tanaka et al. 2006), both Asclepiadoideae, andromonoecy has been demonstrated. The flowers are protandrous. In Rauvolfioids and Apocynoids pollen is shed as single grains, or rarely as tetrads, shortly before anthesis onto the sides of the sterile upper style-head or into a pollen chamber formed by the cone of anthers above it, where it is secondarily presented (Church 1908; Fallen 1986). In Periplocoideae the tetrads or pollinia are shed onto morphologically and histologically differentiated spoon-like translators, which are arranged radially around the style-head between adjacent anthers. The translators include an adhesive-covered scoop onto which the pollen is shed, a stalk and a sticky disc (viscidium) by which they become attached to pollinators (Nilsson et al. 1993). In Secamonoideae and Asclepiadoideae the pollinia more or less remain in the anther at anthesis, although they have already become attached to the translator. In Rauvolfioids, in which the anthers are free from the style-head, the corolla is sometimes shed after the male phase (Boiteau and Allorge 1978). In the APSA clade the antepetalous anthers are adnate to the style-head,

thus the corolla remains attached longer, until the style breaks off. Longevity of flowers has rarely been investigated in Rauvolfioids and Apocynoids. In *Aspidosperma quebracho-blanco*, the male phase lasts 1.5–2 days, followed by the female phase, which lasts 1 day (Lin and Bernardello 1999). *Nerium* flowers are said to last up to 7 days if unpollinated (Herrera 1991). In the night-flowering *Kametia chandeei*, no open flowers can be observed on plants during the day but early each morning fallen corollas carpet the ground, suggesting the corolla lasts less than 1 day and is dropped immediately after pollination, presumably by moths (Middleton et al. 2006). In Periplocoideae and Asclepiadoideae flowers last from less than 1 day (e.g., *Schlechterella abyssinica*, *Piaranthus* p.p.) to 8 or even 14 days (*Hoya*, *Marsdenia* s.l.; Meve 1994, unpubl. data).

The complex flower construction suggests that the family is predominantly out-crossing (Albers and van der Maesen 1994). However, relatively few detailed studies have been conducted on breeding systems in the family except in Asclepiadoideae. In *Aspidosperma quebracho-blanco* (Rauvolfioids), the plants were found to be self-compatible when artificially selfed; due to dichogamy, however, autogamy is unlikely (Lin and Bernardello 1999). Similarly, *Mandevilla pentlandiana* and *Wrightia arborea* (Apocynoids) were found to be self-compatible, but not autogamous (Torres and Galetto 1999; Barman et al. 2018). *Apocynum* apparently has a late-acting self-incompatibility system (Lipow and Wyatt 1999); the same is true for *Gonolobus suberosus* and *Periploca aphylla* (Lipow and Wyatt 1998). Stapeliads are usually self-incompatible when diploid, but tetraploidy is correlated with self-compatibility (Meve 1997; Meve et al. 2004). The bulk of the breeding system literature is focused on *Asclepias*. Wyatt and Broyles (1994) recognized two main types of breeding systems in *Asclepias*: species that are (almost) completely self-incompatible and species that are (almost) completely self-compatible. Most species of *Asclepias* have been shown to possess a late-acting self-incompatibility system similar to that in *Apocynum* (Wyatt 1976, 1981; Kahn and Morse 1991; Sage and Williams 1993, 1995; Wyatt et al. 1998). However, *Asclepias incarnata* (Kephart 1981; Ivey et al. 1999), *A. curassavica* and *A. fruticosa* have been shown to be self-compatible

(Wyatt and Broyles 1997), and self-compatibility is assumed to have arisen multiple times within the genus (Wyatt and Broyles 1994). Even spontaneous self-pollination was observed in *A. curassavica* (Wyatt and Broyles 1997). For *Vincetoxicum* autogamy and apomixis have been demonstrated (Chaturvedi 1988; Lumer and Yost 1995; Leimu 2004; Yamashiro et al. 2008).

Apocynaceae are entomophilous, with two possible exceptions both involving pollination by birds. The first is in *Mandevilla* (Apocynoids), in which two species, *M. hirsuta* and *M. veraguasensis*, were found to be pollinated by trap-lining hummingbirds (Feinsinger 1978; Linhart and Feinsinger 1980). Hummingbirds have been observed visiting other species of *Mandevilla* for nectar as well—e.g., *M. guanabarica*, *M. pentlandiana* and *M. scabra* (Torres and Galetto 1998; Machado 2009; Abrahamczyk and Kessler 2010; Fonseca et al. 2015)—but in these species it was not shown that they effected pollination; in the case of the small-flowered *M. pentlandiana* they are considered to be nectar thieves, not pollinators (Galetto, pers. comm.), which is supported by the small diameter of the openings between adjacent anthers (see Moré et al. 2007) and as no pollen was found in the stigmatic region after a visit (Endress, pers. obs.). The second, well-documented case is *Microlooma* (Asclepiadoideae), where sunbirds (Nectarinidae) have been shown to take up pollinia on their tongue (Pauw 1998). Visits of the sunbird *Nectarinia sovimanga* to *Pleurostelma cernuum* on Aldabra have been observed as well (Woodell 1979). Two other species of *Nectarina*, *N. cuprea* and *N. chloropygia*, frequently visit flowers of *Voacanga africana*, but they puncture the corolla tube and steal nectar, without effecting pollination; the real pollinators for this species is more likely Lepidoptera (Albers and van der Maesen 1994).

The floral reward is consistently nectar. The chemical composition of nectar in some species has been reported (Galetto 1997). In some genera flowers produce no floral reward and are considered to be pollinated by deceit (Herrera 1991); these have visual and olfactory cues that promise a reward, but offer none. They are often floral mimics, and depending on the model, they may be a specialized or generalized mimic (sometimes called non-model mimicry); in the latter plants use cues that potential pollinators innately



recognize, and which are not tied to a specific model (Haber 1984). The plants are often mass-flowering and/or may have an extended flowering period, producing a surplus of flowers in a (sometimes showy) display to compensate for the low visitation/pollination rates once pollinators realize there is no reward. Deceit pollination of this type requires naïve or inexperienced pollinators, and thus pollination events are uncommon. In Rauvolfioids deceit flowers have been reported in Plumeriaceae-Plumeriinae. *Plumeria* has flowers with general adaptations typical for sphingid pollination and it has been suggested it is a generalized mimic (Haber 1984). In addition to being mass-flowering, the large showy flowers are long-lived and have a strong sweet scent (Haber 1984). In the closely related genus *Himatanthus*, although few flowers open each day, flowering can continue for more than a year (Schlindwein et al. 2004). Both *Plumeria* and *Himatanthus* are host plants to caterpillars of the same sphingids that pollinate their flowers (Plumel 1991). *Aspidosperma pyriforme* and *A. quebracho-blanco* (Aspidospermateae) are also mass-flowering and pollinated by deceit, but in this genus the individual flowers are small and inconspicuous, and thus they are grouped into many-flowered inflorescences in order to make a greater impact; they open toward evening and have a sweet scent. The pollinators in these two species of *Aspidosperma* were shown to be moths (Lin and Bernardello 1999; Queiroz 2009). In Apocynoids deceit flowers are suspected in *Nerium* and *Strophanthus* (Nerieae). Both genera have mass flower displays and additional optical attractants, such as a showy, dissected petaloid corona and long, hairy, filiform anther appendages (*Nerium*) and/or thin, extremely elongate, dangling petal appendages (*Strophanthus*), which has made them popular in cultivation. The movements of the long, thin appendages in the breeze presumably attract pollinators. As with the deceit flowers in Plumeriinae, pollination events are very rare, and to date the pollinators in these two genera are unknown. In the Asclepiadoideae-Ceropegieae, deceit flowers are common (Meve and Liede 1994).

In Rauvolfioids and Apocynoids night-flowering occurs sporadically in many tribes, whereas in Asclepiadoideae night-flowering seems to be restricted to Marsdenieae (*Stephanotis*, *Telosma*) and Asclepiadeae (*Vincetoxicum*, *Pergularia*),

though it may occur more frequently. Bhatnagar (1986) reported Lepidoptera (Noctuidae) as pollinators. In Rauvolfioids and Apocynoids the pollen is transferred on the proboscis, and many genera have flowers with a slender, salverform corolla, in which nectar accumulates at the base. To reach the nectar, the pollinator must have a proboscis long enough to reach nearly to the bottom of the tube. The most likely pollinators are, therefore, butterflies, hawkmoths, moths or large bees. Relatively few actual observations of pollination have been made, however. *Rauvolfia grandiflora* was shown to be pollinated by one species of long-tongued bee in northeastern Brazil (Lopes and Machado 1999). Some genera of Apocynoids with more open flowers are pollinated by flies (e.g., *Apocynum androsaemifolium*, Ludwig 1880). Wasps have been identified as the pollinators of *Parsonsia alboflavescens* (Livshultz, unpubl. obs.). Night-flowering species of *Mandevilla* with white corollas with a slender tube up to 15 cm long are adapted for sphingid pollination, in which not only length, but also width of the proboscis restrict the assemblage of pollinators that can reach the nectar (Moré et al. 2007). Sphingids have been observed to pollinate *Cryptostegia grandiflora* (Periplocoideae) in Madagascar (Walther 1994) and *Oxypetalum* species (Asclepiadoideae), which are also characterized by long corolla tubes in Argentina (Liede-Schumann, unpubl. obs.). Often more than one type of insect may visit flowers of the same plant. Darvaul and Schlindwein (2005) observed 33 different insect species visiting flowers of *Hancornia speciosa*, but that fruit set was correlated with pollen load, so that some pollinators, in this case hawkmoths, are more efficient than others. Thus, even though a taxon may exhibit a particular floral syndrome associated with a specific type of pollinator, this often does not exclude visitation (and in some cases pollination) by other types as well. For example, Torres and Galetto (1998) observed flowers of *Mandevilla pentlandiana* to be visited by bumblebees and honeybees, as well as the hummingbird *Chlorostilbon aureoventris*. Waddington (1976) concluded that, although the flowers of *Apocynum sibiricum* are visited by a variety of insects, only Lepidoptera (including species from seven different families) actually pollinate it. In Periplocoideae, the majority of the genera have a nearly rotate corolla,

which suggests fly pollination, and fly pollination has been reported for some species of *Periploca* (Schick 1982b). The more open flower construction makes possible the attachment of the translator in regions other than the proboscis (e.g., on the leg, back or head of the insect). Some genera of Periplocoideae have a salverform corolla and these are presumably not fly-pollinated. In Australia, Forster (1991a) reported a possible transfer of *Gymnanthera* pollinia by mosquitos. *Cryptostegia*, with a corolla ca. 5–6 cm long, was observed to be pollinated not only by sphingids (Walther 1994), but also by large *Xylocopa* bees (S. Vogel, pers. comm.).

In Asclepiadoideae, some species tend to be specialists, being pollinated exclusively or nearly so by one pollinator, whereas others are generalists, with several types of insects visiting the same flower, which may or may not be pollinators (Fishbein and Venable 1996). The main morphological changes associated with pollination mode shifts are found in the corolla and/or corona (Yamashiro et al. 2008). In Marsdenieae (Asclepiadoideae), Hesperidae butterflies have been reported to transfer *Hoya australis* pollinia (Forster 1992a), but several visitors and possible pollinators have been observed for *Marsdenia cymulosa* (Forster 1992b). *Cynanchum hemsleyanum* (= *Metaplexis japonica*) was found to be moth-pollinated (Sugiura and Yamazaki 2005). Examples of the specialist flowers from South Africa include *Asclepias woodii* and *Sisyranthus trichostomus*, which are pollinated almost exclusively by fruit beetles (Ollerton et al. 2003), or species of *Pachycarpus* and *Miraglossum* that are pollinated exclusively or nearly so by large spider-hunting wasps (Ollerton et al. 2003; Shuttleworth and Johnson 2006). Wasps play an important but hitherto understudied role in Asclepiadoideae pollination. A species of *Pepsis* was observed on several New World Asclepiadoideae *Morrenia* and *Philibertia* (Baranzelli et al. 2014; Cocucci et al. 2014). The *Hemipepsis*-wasp-pollination-guild was found to include 17 South African species of *Asclepias*, *Aspidoglossum*, *Miraglossum*, *Pachycarpus*, *Periglossum*, *Woodia* and *Xysmalobium* (Shuttleworth and Johnson 2012). Bitter nectar only palatable to wasps can play an important role as a filter in the pollination system of some of these Asclepiadinae species (e.g., Shuttleworth and Johnson 2009). *Polybia ignobilis*

pollinates four *Oxypetalum* species in Brazil (Vieira and Shepherd 1999), and various wasps were found to carry pollinaria of Old World *Cynanchum* species (Kugler 1973). Reports of more generalist flowers have been published by Pant et al. (1982), who studied the flowers of *Calotropis procera*, *Leptadenia reticulata*, *Oxystelma secamone* and *Wattakaka volubilis* and recorded 17 species of insect visitors, several of which take nectar but do not carry pollinia. In Brazilian *Ditassa capillaris* and *D. hastata* not only Hymenoptera, Diptera and Lepidoptera were reported as pollinators but also ants of the genera *Cephalotes* and *Dorymyrmex* (Domingos-Melo et al. 2017). Flowers of *Xysmalobium gerardii* were found to be pollinated by large pompilid wasps, fruit beetles and lygaeid bugs (Ollerton et al. 2003). Pollinaria of *Calotropis procera* were found to be transported not only by large carpenter bees (*Xylocopa*), which carry them on the forelegs (Wanntorp 1974), but also by small species of *Micrapis* and *Apis*, which are small enough to creep through the stigmatic slits to reach the nectar; upon leaving the flower, pollinia become attached to the back legs. Both Ramakrishna and Arekal (1979) and Eisikowitch (1986), however, found that only species of *Xylocopa* are pollinators of *Calotropis*. Pollination requires not only removal, but also correct insertion of the pollinia into the germination slit of another flower, and it is doubtful that this can be achieved by all the insects that carry pollinia of any given generalist species. According to a study by Ollerton et al. (2003) in South Africa, the majority of flower visitors did not pick up pollinia and must therefore be considered nectar thieves, rather than pollinators. A myophilous pollination syndrome has evolved independently in the Stapeliads (Ceropegieae) and in the Gonolobinae (Asclepiadeae) (Meve and Liede 1994; Kunze 1995). Flowers in these two groups show both visual and olfactory specializations mimicking typical substrates of calyptrate flies (e.g., dung, carrion, decaying organic matter) by imitating odors and surfaces that are glossy or warty, often reddish brown and occasionally blotched (Jürgens et al. 2006). Small, kleptoparasitic flies (1–3 mm) are attracted by scent mimicking hymenopteran alarm pheromones emitted by the pitfall flowers of *Ceropegia sandersonii*—a pollination system described as kleptomyiophily

(Heiduk et al. 2016). Similar, but not yet understood selective pressures have led to striking similarities, especially in floral structure, between unrelated genera of both hemispheres (e.g., between *Funastrum* and some *Cynanchum* species (formerly *Sarcostemma*), and between *Philibertia*, *Oxystelma* and another *Cynanchum* species (formerly *Platykeleba*); Liede and Täuber 2000). A survey of pollination patterns in Periplocoideae, Secamonoideae and Asclepiadoideae is given in Ollerton and Liede (1997).

The pollination mechanism of the Apocynaceae is complex and centers around the specialized secretions produced by the style-head. In Rauvolfioids and Apocynoids, in which the secretions usually remain undifferentiated, the most common flower shape is a salverform corolla with a constricted orifice, although large infundibuliform corollas can be found in genera that have anthers with hardened guide rails (Tabernaemontaneae, several tribes of Apocynoids). The inner surface of the corolla tube often has various sorts of emergences (e.g., corona lobes, protruding ridges below the stamens, rings or ridges of downward-directed hairs, etc.) that guide the proboscis of the pollinating insect into one of the five nectar channels of the revolver flower construction. The proboscis extends, searching into the nectar channel, with relatively little resistance. When it is withdrawn, however, it is directed inward, where it first encounters the base of the enlarged style-head. In many Rauvolfioids, the style-head is broadest at the base, and is equipped with a collar (like an inverted cup) or a wreath of longer hairs, which act as a scraper to scrape off the pollen that was introduced on the proboscis, where it accumulates in the stigmatic region at the base of the style-head. As it moves upward on its way out of the flower, the proboscis next slides through the region where the pollen transport adhesive is secreted, and becomes coated with sticky adhesive. Finally, it slides up through an upper chamber into which the anthers have shed pollen; the pollen grains adhere to the sticky adhesive, coating the proboscis. When the pollinator visits the next flower, the process is repeated. In Apocynoids, the mechanism is more precise due to the adnate anthers. Upon being withdrawn, the pollinator's proboscis is threaded between the lignified guide rails of adja-

cent anthers and forced through one of the five pollination chambers. Once threaded inside the guide rails, the insect must pull its proboscis upward in order to escape (Fallen 1986).

In Periplocoideae, the floral structure is usually more open, and the secretions harden into distinctly shaped translators. Here the nectar is generally openly presented in shallow pockets, into which the insect can crawl or easily reach with its proboscis. Dangling directly above the nectar pocket is the sticky base of the translator, which becomes stuck to the pollinator. When the pollinator flies away, it pulls the translator (and its load of pollen tetrads or pollinia) free from the style-head. When it visits the next flower, some pollen will hopefully be rubbed off in the vicinity of the nectar pocket, which is also the stigmatic region (Nilsson et al. 1993). In Secamonoideae and Asclepiadoideae, the construction is reminiscent of that in Apocynoids (Safwat 1962), with the proboscis or leg of the pollinator being caught between the guide rails of adjacent anthers (Kunze 1991). In order to free itself it must proceed upward. In these two subfamilies, one part of the style-head secretions develops into a hard narrow clamp (corpuscle), into which the proboscis or leg is threaded and becomes wedged. In order to escape, the insect must pull the corpuscle (with its attached pollinia) free from the style-head. When it visits the next flower, pollination is achieved when a pollinium becomes wedged in one of the five pollination chambers, which lie just behind the narrow slit between adjacent anther wings. Usually a basal or apical part of the pollinium, rarely the entire pollinium, is inserted into the pollination chamber. A specialized protruding insertion crest has evolved independently in the Paleotropics and Australia in the Ceropogoneae and some Marsdenieae (e.g., *Hoya*), and in the New World in more derived Gonolobinae (Asclepiadeae), and only this crest is inserted into the pollination chamber. In Ceropogoneae, this crest is also the germination pore, through which the pollen tubes germinate (Kunze 1995). In Stapeliads, the size and shape of structures involved in pollination were shown to operate in a key (pollinium, germination crest) and lock (guide rail) manner causing mechanical prezygot-ic isolation in most cases (Meve et al. 2004).

**FRUIT AND SEED.** In the great majority of taxa of the APSA clade the 2-carpellate, apocarpous gynoecium results in a fruit that is apocarpous and consists of a pair of follicles, each one of which at maturity dehisces along the ventral suture, releasing the seeds. In some genera of Apocynoids, instead of the ventral margins of each individual carpel fusing, the two carpels fuse postgenitally along their ventral margins. This postgenital fusion occurs early in floral ontogeny, and thus can be seen only with a microscope and in sections of very early stages of carpel development. In these cases, instead of a pair of follicles, each flower produces a single postgenitally syncarpous “double-follicle”, which at maturity splits apart along the lines of fusion. The fusion between the united follicles in this type of fruit varies from relatively weak to a union indistinguishable from that of congenital fusion. Genera with flowers that produce a single postgenitally syncarpous fruit include *Amalocalyx*, *Beaumontia*, *Parepigynum* and *Vallaris* (Apocynae), *Artia*, *Ecuia*, *Parsonsia*, *Temnadenia*, *Thenardia* and *Thoreauea* (Echiteae), *Nerium* (Nerieae) and several species of *Wrightia* (Wrightieae; Candolle 1844; Thomas and Dave 1994; Li et al. 1995b; Middleton 2007, 2010, 2014; Simões et al. 2007), and in a few genera of Asclepiadoideae (e.g., *Heterostemma* p.p.). In certain alliances there is a tendency for only one of the carpels to develop, and thus the fruit consists of a single follicle. In the majority of genera the follicles are slenderly fusiform or linear, non-fleshy, less frequently fleshy, sometimes woody at maturity—e.g., many genera of Apocynoids, *Fischeria* (Asclepiadoideae). In some genera of Asclepiadoideae (e.g., *Gonolobus* and *Marsdenia*) the follicles are rather stout and winged. The fruit wall is most commonly smooth, but may be ornamented with irregular corky protuberances, prickles, ridges or wings. Single rheophytic species of various genera, e.g., *Cynanchum*, *Vincetoxicum* and *Oxystelma*, form an inflated pericarp capable of flotation; in these cases, dehiscence is delayed or incomplete. *Emiocarpus* is the only genus in the family with one-seeded, spiny nutlets. In all taxa with follicular fruits, these often remain fused at the apices for some time after anthesis, until the bond is ruptured by the enlarging follicles. Only rarely are the apices still fused by the time the fruit

reaches maturity (e.g., some species of *Echites*, *Prestonia*, *Jobinia*).

In contrast to this fixed uniformity in the more derived APSA clade, fruit and seed morphology are complex and homoplasious in the Rauvolfioids. Though usually 2-carpellate, fruits are up to 5-carpellate in some genera of Hunterieae and Alyxieae. Fruits are apocarpous, congenitally syncarpous or more rarely postgenitally syncarpous (*Allamanda*, *Alstonia rostrata*; Fallen 1985; Sidiyasa 1998) and include follicles, capsules, drupes and berries. There is a great evolutionary potential, and selective pressures acting on this lability have resulted in a complex array of fruit types with very similar morphology evolving independently in different lineages. For example, drupes have evolved in Vinceae, Plumerieae and Alyxieae, and berries have evolved in Willughbeieae, Tabernaemontaneae, Melodineae, Hunterieae and Carisseae (Endress et al. 2007a). In both *Petchia* (Vinceae) and *Alyxia* (Alyxieae) a distinctive type of drupaceous fruit has evolved in parallel. The fruiting carpels consist of a number of articles, each formed by an individual seed surrounded by a stony endocarp; the regions between the articles are very narrow, so that the fruiting carpels are strongly torulose, resembling beads on a string (Simões et al. 2016). In addition, in both tribes the fleshy outer fruit wall is most often bright orange or red, sometimes black, making these some of the showiest fruits in the family. In other cases, genera that are very closely related may have very different fruit types. For example, in the small tribe Aspidospermateae *Aspidosperma* with a dry follicle and *Geissospermum* with a fleshy berry are otherwise very similar morphologically and are sisters in phylogenetic analyses (Simões et al. 2007). Similarly, within Vinceae, about half of the genera have follicular fruits, but drupes have arisen independently at least three times (Simões et al. 2016). In Plumerieae, fruit types include dry, spiny capsules or follicles, drupes, nutlets or samaras (Simões et al. 2007). Also in Alyxieae genera with woody drupes occur next to ones with follicles. Some of the most unusual fruits in the family are found in this tribe. The fruit of *Chilocarpus* is syncarpous with a somewhat fleshy mesocarp and hard, dry endocarp (like a drupe), but splits apart into two halves at maturity. *Chilocarpus* also has

perhaps the most variable fruits in the family: from more or less globose to up to 40+ cm long and slenderly moniliform and everything in-between (illustrated in Markgraf 1971: 157; Middleton 2007; Endress et al. 2007a). Probably the strangest fruits of all are those of *Lepinia*, which are of 4–5 carpels that are congenitally fused into a stipe at the base, and remain firmly postgenitally fused at the apex, with the region in-between apocarpous, and bowed outward, so that the fruit resembles a Chinese lantern (Endress et al. 1997; illustrated in Lorence and Wagner 1997, and Middleton 2007).

The number of seeds per fruiting carpel is highly variable, ranging from one to a few hundred, with Rauvolfioids being the most variable. The tendency is for an increase in seed number in the genera with small seeds with a coma (i.e., the APSA clade), although in a few cases there has been an extreme reduction in the number of seeds per fruiting carpel in the more highly derived subfamilies (e.g., 2-seeded in *Stigmatorhynchus*, and a 1-seeded nutlet in *Emicocarpus*, both Asclepiadoideae).

Except in Rauvolfioids, seeds in Apocynaceae are generally small, lightweight, one end of which almost always has a coma—a (mostly easily detached) tuft of hairs. In the early-branching Apocynoids (Wrightieae, Nerieae and Malouetieae) the position of the coma is not fixed; it may be on the micropylar end (e.g., *Carruthersia*, *Holarrhena*, *Spirolobium*) or the chalazal end (Wrightieae, *Kibatalia*), on both the micropylar and chalazal ends, where the chalazal one is often smaller and quickly deciduous (e.g., *Adenium*, *Farquharia*, *Funtumia*, *Isonema*, *Strophanthus*), or it may be lacking completely (*Eucorymbia*, some *Malouetia* species). In higher Apocynoids, Periplocoideae, Secamonoideae and Asclepiadoideae the coma is always micropylar. In Apocynoids, the color of the coma varies from brown to yellow, cream or white, whereas it is often yellowish in Periplocoideae. In almost all Asclepiadoideae, the coma is silky and white. Sporadically, in various subfamilies, the coma has been lost in at least some species of a genus (e.g., *Marsdenia* p.p., *Sarcolobus* species). In some *Malouetia* species, a normal coma is lacking; rather, the whole seed testa is covered by long lanate hairs. Similarly, in *Batesanthus*, *Finlaysonia*, and some *Raphionacme* species, a coma in the normal

sense is absent. Instead, hairs occur around the whole seed margin. *Cynanchum adalinae* has hairs firmly attached along the margin of the chalazal half of the seed. *Diplolepis (Grisebachiella) hieronymi* is the only Asclepiadoideae species with heavy discoid seeds with a much reduced coma on the hilar side. Fruits and seeds of Asclepiadoideae are often parasitized by Tephritidae (Landolt 1994; Meve 1995; Solbreck 2000). The seeds of Apocynoids are variable in shape, from flat and ovoid to fusiform, often inrolled or flattened longitudinally, sometimes with a rostrum or beak, sometimes slightly curved, usually smooth and glabrous, and rarely with hairs (e.g., *Nerium*, *Urceola*). When a rostrum is present the coma may arise only at the end of the rostrum (e.g., *Chonemorpha*), along the rostrum with the hairs pointing away from the seed (e.g., *Anodendron*), or along the rostrum with the hairs pointing back toward the seed (e.g., *Kibatalia*). The testa of the cylindrical to flat seeds of Periplocoideae, Secamonoideae and Asclepiadoideae can be smooth, papillate, distinctly tuberculate or hairy, usually identical on both sides, but occasionally more pronounced on the side without the raphe (sometimes termed a seta side). In many species of Periplocoideae, Secamonoideae and Asclepiadoideae the seeds are distinctly winged (all around except the micropylar region). Anatomy of these wings is three-layered with (1) a one cell layer thick dorsal testa, (2) a thin central layer of simple parenchymatic tissue, and (3) a ventral testa layer. In Ceropegieae this ventral testa consists of voluminous, elongated and intensively pitted cells allowing quick and efficient water uptake, whereas in *Asclepias* this layer, like the dorsal layer, is simple. In *Vincetoxicum*, in contrast, the wing is reduced to a simple margin derived from collapsed testa cells (Sylla and Albers 1989). The endosperm is almost completely reduced; the chlorophyllous embryo has fairly large cotyledons. Polyembryony occurs in *Vincetoxicum*, e.g., *V. nigrum* and *V. rossicum* (Denis and Capucino 2004). In the stem succulent Stapeliads the cotyledons are more or less reduced, while the hypocotyl is succulent and oil-rich.

Seeds in Rauvolfioids are diverse, and the seed type is usually correlated with fruit type. If the fruit is a dry, dehiscent follicle or capsule, the seed is most commonly compressed and winged

or ciliate at the margin (e.g., *Alstonia*, *Aspidosperma*, *Cameraria*, *Craspidospermum*, *Plumeria*, *Tonduzia*), although in *Catharanthus* and *Vinca* (Vinceae) and *Amsonia* (Amsonieae) with thin-walled, dry follicles, seeds are not compressed and are naked. There is a great diversity of winged seeds, and at least one genus with winged seeds is found in the majority of Rauvolfioid tribes (though none occur in Carisseae, Hunterieae, Tabernaemontaneae and Willughbeieae). The wings may be concentric (e.g., *Aspidosperma*, *Dyera*), they may be only on one end (e.g., *Diplorhynchus*, *Plumeria*) or at both ends of the seed (e.g., *Gonioma*, *Kametia*, *Strempeleopsis*). Seeds with long fimbria around the margin have evolved in parallel in *Alstonia* (Alstonieae) and *Tonduzia* (Vinceae). Seeds with a coma are rare in Rauvolfioids, but seeds of *Haplophyton* have both a micropylar and a chalazal coma. In Tabernaemontaneae-Tabernaemontaninae (with fleshy follicular fruits) seeds are globular with a deep furrow on the hilar side, and lines of shallower grooves on the other side; in addition, they have an (often brightly colored) aril and strongly ruminant endosperm. In berry-fruited taxa of the same tribe (Tabernaemontaneae-Ambelaniinae), the seeds are often globular or somewhat flattened, are unadorned and have smooth endosperm. In *Chilocarpus* (Alyxieae), seeds have a corky aril (the only known occurrence of arils outside of Tabernaemontaneae), and some species have smooth endosperm whereas in others it is strongly ruminant. In the genera with drupaceous fruits, the seeds are enclosed in a lignified or stony endocarp; in most Alyxieae, seeds are cylindrical with a long hilar furrow and thick, ruminant endosperm. In Vinceae, the seeds of drupaceous taxa are somewhat flattened and the endosperm is not ruminant. In Plumerieae the seeds of drupaceous taxa may be  $\pm$  globular (e.g., *Thevetia*) or thin and flattened (*Anechites*; Alvarado-Cárdenas and Ochoterena 2007), and endosperm is not ruminant. In general, germination follows the epigeous type, but in some species of derived Asclepiadeae (*Vincetoxicum*) hypogeal germination has been observed.

**DISPERSAL.** Wind dispersal is the rule for the majority of genera of the APSA clade, with the dispersal unit being the seed, which in almost all cases has a coma. Exceptionally, the coma has

been lost (often in conjunction with a shift to water-dispersal), and this has occurred in parallel at least once in Apocynoids (*Malouetia*), Periplocoideae (*Finlaysonia*) and Asclepiadoideae (*Marsdenia rubrifusca*, *M. oblanceolata*, several *Sarcolobus* species, *Asclepias perennis*, *Matelea*). In Rauvolfioids, many genera are wind- or water-dispersed. In the former, the dispersal unit is normally the seed, which is usually winged or has long hairs around the margin; the samaras in *Cameraria* and *Cerberiopsis* (Plumerieae) are also presumably wind-dispersed. Most water-dispersed genera of Rauvolfioids have drupaceous fruits and the dispersal unit is often the whole fruit, one fruiting carpel, or, in moniliform fruits, one or more one-seeded segments. Specializations for sea water dispersal are found mainly in genera with drupaceous fruits in Plumerieae, Vinceae and Alyxieae, and include hollow flotation chambers in the endocarp or a mesocarp with a thick layer of fibers, which serve to protect the seeds, so that they remain viable over long distances in sea water (e.g., *Cerbera*, *Lepiniopsis* and *Ochrosia*; Simões et al. 2016). In Alyxieae, the hard endocarp of *Pteralyxia* forms a complex framework shaped like a boat around the seed (Endress et al. 2007a), and in *Lepinia*, each long-stipitate fruiting carpel of the 4-5-carpellate fruits has an air-filled cavity; the carpels are connate at the base and apex, so that expansion can only occur in the free middle part, causing the long slender fruiting carpels to curve strongly outward, forming a light-weight flotation dispersal unit (Endress et al. 1997). The genera of Rauvolfioids with fleshy fruits are primarily mammal- and/or bird-dispersed. In the New World, monkey and/or bird dispersal has been reported for *Couma*, *Lacmellea*, *Macoubea*, *Pacouria* and *Parahancornia*. *Geissospermum* (Aspidospermateae) is dispersed by spider monkeys and woolly monkeys (Defler and Defler 1996; Nevo et al. 2015), and *Lacmellea* by monkeys and kinkajous (Van Roosmalen 1985). Reports of animal dispersal in the Paleotropics have also mostly been for primates. In Africa *Cylindropsis*, *Dictyophleba*, *Landolphia*, *Hunteria* and *Tabernaemontana* are reported to be consumed and dispersed by cercopithecine monkeys (Gautier-Hion and Michaloud 1989; Astaras and Waltert 2010), in Africa and Madagascar *Carissa*, *Landolphia* and *Saba* are reported to be

consumed and dispersed by a number of primate species including lemurs and chimpanzees (Wrangham and Waterman 1983; Birkinshaw 2001; Britt and Iambana 2003) and at least one species of *Petchia* is dispersed by lemurs (Raza-findratsima et al. 2014); *Picralima* is dispersed by various sorts of rodents as well as elephants (Gautier-Hion et al. 1985; Beaune et al. 2013). In Asia, orangutans eat and disperse *Willughbeia* (Leighton 1993) and long-tailed macaques are reported to disperse *Leuconotis* and *Willughbeia* (Corlett and Lucas 1990). In the dehiscent-fruited *Tabernaemontaneae* with arillate seeds, aril color ranges from red to orange, through white to translucent-white (Leeuwenberg 1991, 1994b). Birds are probably the primary dispersers of the seeds with red or orange arils. This has been demonstrated in *Tabernaemontana* in Central America (McDiarmid 1977). At least in the New World both birds and monkeys often disperse the same species of *Tabernaemontana* (Cant 1979; Van Roosmalen 1985). It is also likely that birds are the primary seed dispersers of genera with brightly colored fruits on low shrubs or small twiners such as *Carissa*, *Alyxia* and *Petchia*.

**PHYTOCHEMISTRY.** Apocynaceae are well known as a family that contains poisonous and bioactive compounds; these evolved as a response to stress encountered by the plants (Sabir et al. 2016)—for example, as defense against herbivores—and diversified into a broad spectrum of different secondary metabolites (Hegnauer 1970, 1989). In Rauvolfioids, taxa in the tribes Aspidospermateae, Alstonieae, Vinceae, *Tabernaemontaneae*, Amsonieae, Melodineae and Hunterieae produce a vast array of monoterpenoid indole alkaloids (Bisset 1958, 1961; Hegnauer 1964, 1989; Taylor and Farnsworth 1975; Kisakürek et al. 1983; Van Beck and Van Gessel 1988; Zhu et al. 1990; Van der Heijden et al. 2004), a plesiomorphic feature they share with some other families of Gentianales, such as Rubiaceae, Gelsemiaceae and Loganiaceae (Kisakürek et al. 1983; Sabir et al. 2016). A single species often contains a great number of indole alkaloids; for example, more than 100 indole alkaloids have been isolated from *Amsonia stricta* (Gilani et al. 2007), and some 200 from *Rauvolfia serpentina* (Pathania et al. 2015). In *Willughbeieae*, indole alkaloids are apparently restricted to the two genera of subtribe *Leucono-*

*tidinae*, *Bousigonia* and *Leuconotis* (Goh et al. 1989; Abe and Yamauchi 1994; Fu et al. 2012, 2014). In Rauvolfioid tribes Carisseae, Plumerieae and Alyxieae indole alkaloids have been lost and the role of protection against predators has been taken over by other secondary metabolites (Endress et al. 1990, 2007a). Plumerieae contain iridoid glycosides (e.g., *Allamanda*, *Plumeria*) or cardenolides (e.g., *Cerbera*, *Cerberiopsis*, *Thevetia*; Hegnauer 1964, 1970, 1989; Coppen and Cobb 1983; Jensen 1992). *Acokanthera* (Carisseae) is rich in cardenolide glycosides (Hegnauer 1970; Kingston and Reichstein 1974). In Alyxieae no cardenolides or iridoid glycosides have been found; however, coumarins have been isolated from *Alyxia*, *Lepinia* and *Lepiniopsis* (Johns et al. 1968; Hegnauer 1970, 1989). In Apocynoids, the early-branching tribes Wrightieae and Malouetieae are characterized by steroidal alkaloids (e.g., *Funtumia*, *Holarrhena*, *Kibatalia* and *Malouetia*; Endress et al. 1990; Bisset 1992), and Nerieae are characterized by cardenolides and/or steroidal alkaloids (e.g., *Adenium*, *Nerium*, *Strophanthus*; Bisset 1987; Yamauchi and Abe 1990). In the higher Apocynoids (comprising Odontadenieae, Mesechiteae, Apocyneae, Rhabdadenieae, Echiteae and Baisseeae), characteristic secondary compounds in the first three tribes seem to be mainly cardenolides (Hegnauer 1964; Abe and Yamauchi 1985, 1989; Yamauchi et al. 1990; Burrows and Tyril 2013), though steroidal alkaloids have been reported in *Amalocalyx* and *Chonemorpha* (Apocyneae; Hegnauer 1964; Endress et al. 1990; Hu et al. 1992), but detailed analyses are still lacking for a number of genera. In Echiteae, parsonsine type pyrrolizidine alkaloids (Colegate et al. 2016) are found in *Echites*, *Parsonsia*, *Peltastes*, *Prestonia* and *Temnadenia*, suggesting that parsonsine type pyrrolizidine alkaloids may have replaced cardenolides as the characteristic secondary metabolites in the tribe (Morales et al. 2017a). A number of genera in Echiteae are an important source of pyrrolizidine alkaloids for ithomiine and danainae butterflies and arctiid moths, which have evolved a tolerance to these toxins and use them as a defense against predators (Boppré 1990). This has been best studied in *Parsonsia* and *Prestonia* (Edgar 1984; Trigo and Brown 1990). Certain lineages in both groups of these insects have evolved a dependency on pyrrolizidine alkaloids as the basis for the

production of mating pheromones (Boppré and Schneider 1985; Boppré 1995; Burzynski et al. 2015). In *Baisseeae* spermidine alkaloids have been isolated from *Oncinotis* (Hegnauer 1989).

In Periplocoideae, Secamonoideae and Asclepiadoideae cardenolides are widespread. In Asclepiadoideae, they are found predominantly in *Asclepias* and its relatives (Abisch and Reichstein 1962). Coevolutionary relationships between the monarch butterfly *Danaus* and *Asclepias* (e.g., Morse 1985) and between the milkweed beetle *Tetraopes* (Coleoptera: Cerambycidae) and *Asclepias* (Farrell and Mitter 1998) have been studied. In both Periplocoideae and Asclepiadoideae, steroidal glycosides are the most important components. Glycosides with pregnane skeletons, pregnane-12-esters and pregnane-12,20-esters are widely distributed in Marsdenieae, Ceropegieae (*Caralluma* s.l.) and Asclepiadeae. The occurrence of 14,15-seco-pregnane skeletons and 13,14:14,15-diseco-pregnane skeletons is rare and was the first hint to demonstrate the close relationship between *Tylophora* and *Vincetoxicum* (Liede 1996b). Steroidal alkaloids were found in *Cryptolepis* (Periplocoideae; Paulo et al. 2000), *Marsdenia* (Summons et al. 1972) and *Cynanchum* sect. *Rhodostegiella* (Lee et al. 2000). From *Cryptolepis*, indoloquinoline alkaloids are also reported (Sharaf et al. 1996). A furopyridine, Ceropegin, was isolated from *Ceropegia juncea* (Sukumar et al. 1995) and confirmed for *Ceropegia pusilla* (Kalimuthu and Prabakaran 2013). Hordenin, an alkaloid of the phenethylamine class, was found in *Stapelia gigantea* (Meyer et al. 1981). Phenanthroindolizidine alkaloids are found in *Telosma* and *Vincetoxicum* (Govindchari 1967). Salicylic acid is found in *Dischidia* (Chen et al. 1993) and 4-methoxy-salicylaldehyde in several Periplocoideae genera (Hegnauer 1964).

#### SUBDIVISION AND RELATIONSHIPS WITHIN THE FAMILY.

Robert Brown (1810) split the Asclepiadaceae from Jussieu's (1789) "Apocinae" based on what he called their "essential character": pollen shed in tetrads or fused into pollinia attached to a translator (Endress 2001). For most of the period since then until the mid-1990s the Apocynaceae and Asclepiadaceae have been recognized as two separate families. It has long been known, however, that in a number of morphological charac-

ters many genera of Apocynaceae sensu stricto are more similar to Asclepiadaceae than to other Apocynaceae. With a few exceptions, those Apocynaceae with dextrorse corolla lobe aestivation, presence of a gynostegium, apocarpous gynoe-cium, seeds with a coma, and secondary compounds steroidal alkaloids or cardenolides (never indole alkaloids) are more similar to Asclepiadaceae than to those Apocynaceae with sinistrorse corolla lobe aestivation, lacking a gynostegium, seeds without a coma, and secondary compounds indole alkaloids, sometimes iridoids or cardenolides (Endress and Bruyns 2000). Nevertheless, most traditional treatments recognized Apocynaceae and Asclepiadaceae as two very closely related but separate families with Apocynaceae comprising the two subfamilies Rauvolfioideae and Apocynoideae, and Asclepiadaceae comprising the three subfamilies Periplocoideae, Secamonoideae and Asclepiadoideae. Because their floral structure and pollination mechanism differ significantly from those of Secamonoideae and Asclepiadoideae, Schlechter (1905) raised Periplocoideae to family rank, and up until at least the mid-1990s Periplocoaceae were still sometimes recognized as a distinct family (e.g., Nilsson et al. 1993; Swarupanandan et al. 1996).

One of earliest proposals for a unified Apocynaceae was by Judd et al. (1994), who discussed the "family pair" Apocynaceae/Asclepiadaceae in a phylogenetic context using non-molecular characters and clearly showed that Apocynaceae s. str. are paraphyletic unless Asclepiadaceae are included. The advent of molecular phylogenetics, with its emphasis on recognizing only monophyletic groups, dramatically changed the way we do systematics. These corroborated that Asclepiadaceae are firmly embedded with strong support in Apocynoideae, rendering Apocynaceae paraphyletic; furthermore, the three major lineages recognized in the traditional Asclepiadaceae since Brown (1810) do not come out together in Apocynoideae. Rather than Periplocoideae, *Baissea* (*Baisseeae*, Apocynoideae) is supported as sister to Secamonoideae + Asclepiadoideae. In larger molecular analyses *Baisseeae* is strongly supported as sister to Secamonoideae + Asclepiadoideae, whereas Periplocoideae, which are undisputedly monophyletic (Ionta and Judd 2007), are one of five main clades in an unresolved polytomy



comprising the crown clade of Apocynaceae (together with Rhabdadenieae, Apocyneae, Mes-echiteae + Odontadenieae + Echiteae, and Baisseeae + Secamonoideae + Asclepiadoideae) (Lahaye et al. 2007; Livshultz et al. 2007; Livshultz 2010; Straub et al. 2014). The relationship of Periplocoideae to the other crown clade Apocynaceae remains one of the most enigmatic systematic puzzles in the family. There are various solutions in order to make Apocynaceae monophyletic (Civeyrel et al. 1998), but the simplest is to unite Apocynaceae and Asclepiadaceae into a single family, as was done by Endress and Bruyns (2000).

The two main groups of the traditional Apocynaceae were described as the subfamilies Plumerioideae and Echitoideae for the first time by Schumann (1895), who recognized three tribes and six subtribes in Plumerioideae, based mainly on fruit and seed characters: Arduineae (including Melodininae and Landolphiinae), Pleiocarpaeae, Plumerieae (including Alstoniinae, Tabernaemontaninae, Rauwolfiinae and Cerberinae), whereas Echitoideae were divided into two tribes (Echiteae and Parsonsieae) based on whether the anthers were included or exerted.

The next person to make significant contributions to our understanding of Apocynaceae s. str. as a whole was Pichon who, between 1948–1950, published a number of seminal papers (for a more detailed discussion, see Endress and Bruyns 2000, pp. 5–7). In addition to Plumerioideae and Echitoideae, Pichon recognized two further subfamilies: Tabernaemontanoideae (Pichon 1949), which corresponded to Schumann's subtribe Tabernaemontaninae, and Cerberioideae (Pichon 1948b), which contained half of the genera in Schumann's Cerberinae, together with *Skytanthus* and *Cameraria* (from Schumann's Alstoniinae). In addition to splitting and redefining Schumann's Cerberinae, Pichon also, for example, recognized that Schumann's Pleiocarpaeae contained taxa of two unrelated groups, which had been brought together only because they had more than two carpels. He recognized that those with drupaceous fruits were related to *Alyxia* rather than *Pleiocarpa*, and split and redefined the group accordingly. Similarly, he recognized that *Ambelania*, *Allamanda*, and *Craspidospermum* were out of place in Schumann's Arduineae, and moved them to more plausible positions in other tribes. Pichon's Plu-

merioideae contained six tribes: Allamandaeae, Alstonieae, Ambelanieae, Carisseae, Chilocarpeae and Rauvolfiieae (Pichon 1948a, 1949, 1950b). Overall, Pichon's classification was an improvement over that of Schumann's due to more careful observation of characters. But, like Schumann, Pichon also used mainly fruit and seed characters to delimit tribes in his Plumerioideae and thus overlooked more subtle convergences, with the result that most of his tribes also contained at least one or two genera placed elsewhere in recent phylogenetic studies.

Pichon's classification of the Echitoideae (Pichon 1950a) completely abandoned Schumann's two tribes and instead divided the subfamily into four tribes based on the manner in which the anthers are attached to the style-head, a feature he called the "retinacle" (Pichon 1948c).

The last classification of Apocynaceae s. str. published before the molecular revolution was that by Leeuwenberg (1994a). His Plumerioideae differed relatively little from that of Pichon; the main difference being that Pichon's Tabernaemontanoideae and Cerberioideae were again reduced to tribes of Plumerioideae and *Macoubea* was placed in its own tribe, Macoubeeae. Further, application of the principle of priority (McNeill et al. 2012) resulted in name changes for one subfamily and two tribes: Echitoideae became Apocynoideae, Alstonieae became Plumerieae, and Rauvolfiieae became Alyxieae. Leeuwenberg's Plumerioideae thus comprised the nine tribes Allamandaeae, Alyxieae, Ambelanieae, Carisseae, Cerbereae, Chilocarpeae, Macoubeeae, Plumerieae and Tabernaemontaneae. Leeuwenberg divided the genera of Apocynoideae into three tribes: Echiteae and Wrightieae (which corresponded for the most part to Pichon's Parsonsieae and Nerieae, respectively), and Apocyneae (which contained elements of Pichon's Ecdysanthereae and Ichnocarpeae).

The first system to classify all genera of the Apocynaceae into subfamilies and tribes after inclusion of Asclepiadaceae, and which incorporated molecular data, was that of Endress and Bruyns (2000). In that treatment, further name changes following the Priority Principle were made for one subfamily and one tribe: Plumerioideae became Rauvolfoideae and Rauvolfiieae became Vinceae. They also recognized nine tribes in Rauvolfoideae (Alstonieae, Alyxieae,

Carisseae, Hunterieae, Melodineae, Plumerieae, Tabernaemontaneae, Vinceae and Willughbeieae), but their compositions differed significantly from those of Leeuwenberg (1994a). They recognized five tribes in Apocynoideae: Apocynae, Echiteae, Malouetieae, Mesechiteae and Wrightieae, and again the composition differed from that of Leeuwenberg (1994a).

Since 2000, two more classifications have been published. The first was by Endress et al. (2007b) and incorporated results from publications published between 2001 and 2007, in particular larger phylogenetic analyses (e.g., Simões et al. 2004, 2006, 2007; Livshultz et al. 2007). The last update to the classification was that of Endress et al. (2014), which took into consideration larger phylogenetic studies published after 2007 (e.g., Simões et al. 2010; Middleton and Livshultz 2012). Since 2014 two further tribal level phylogenetic studies providing insights into relationships in Apocynaceae s. str. have been published: Simões et al. (2016) and Morales et al. (2017a).

The first molecular-based study of Periplocoideae was conducted by Meve and Liede (2004a), who investigated relationships among tuberous genera from Africa and Madagascar. This was followed by a large-scale molecular phylogenetic study by Ionta and Judd (2007), which supported Periplocoideae as monophyletic, but did not attempt to determine its position within the family.

The question whether or not Secamonoideae should be included in Asclepiadoideae had been raised by Robert Brown (1810), who distinguished *Secamone* as an unnamed group from the “Asclepiadeae verae”. Molecular results (Civeyrel et al. 1998; Sennblad and Bremer 2000; Livshultz et al. 2007) firmly place Secamonoideae as sister to Asclepiadoideae, but they do not answer the question about the appropriate rank for the group. Based on the current phylogeny, it could be treated as either a subfamily or as a tribe within Asclepiadoideae. Here we recognize Secamonoideae as a distinct subfamily.

Asclepiadoideae were divided by Endlicher (1838) into three tribes, depending on the orientation of the pollinia, “Cynancheae” (pendulous), “Gonolobeae” (horizontal) and “Pergularieae” (erect). “Pergularieae” were divided in two subtribes, the “Hoyeae” and the “Stapelieae”, with and without membranous connective appen-

dages, respectively. Decaisne (1844) raised Gonolobeae and Stapelieae to tribal status, and Bentham (1876) divided Asclepiadoideae and Secamonoideae into a total of six tribes. Schumann (1895) and later Wagenitz (1964) essentially followed the system of Bentham (1876). Rosatti (1989) gave a detailed overview of the classification history of Periplocoideae, Secamonoideae and Asclepiadoideae. Molecular studies have largely confirmed tribal circumscriptions based on pollinarium characters, with Marsdenieae and Ceropegieae having erect and Asclepiadeae pendulous (to horizontal) pollinia. The two genera of Fockeeae with pollinia directly attached to the corpusculum were removed from Marsdenieae with well-developed caudicles and are sister to the remainder of Asclepiadoideae (Kunze et al. 1994; Verhoeven et al. 2003). Marsdenieae and Ceropegieae are sister groups, distinguished by the presence of a pellucid germination zone on the proximal margin or the apex of the pollinia and the absence of connective appendages (except for *Caudanthera*) in the latter. Thus, Marsdenieae could also be included within an expanded Ceropegieae, as was proposed by Swarupandan et al. (1996). More recently, a fifth tribe, Eustegieae, was proposed for two small genera with a 3-seriate corona, pendent pollinia and somewhat ambiguous molecular signal, placing *Eustegia* in a sister group relationship either to Asclepiadeae (Surveswaran et al. 2014) or to Marsdenieae + Ceropegieae (Rapini et al. 2003).

Of the three larger Asclepiadoideae tribes, the further subdivision of Ceropegieae and Asclepiadeae has been confirmed by molecular methods. Four subtribes (Anisotominae, Heterostemmiinae, Leptadeniinae and Stapeliinae) have been found in Ceropegieae (Meve and Liede 2004b), and twelve in Asclepiadeae. Among the latter, Liede (1997), following Swarupandan et al. (1996), included the Gonolobeae of Endlicher in Asclepiadeae as subtribe Gonolobinae, because they share true styles and essentially pendulous pollinia.

The classification here follows that of Endress et al. (2014), which was an update of Endress et al. (2007b) and included 364 genera divided among five subfamilies, 25 tribes and 49 subtribes, with the following differences: (1) both Rauvolfioideae and Apocynoideae have repeatedly been shown to be paraphyletic; the first is a grade, and the

second has the three formal subfamilies of the traditional Asclepiadaceae nested within it (Sennblad and Bremer 1996, 2000; Sennblad et al. 1998; Potgieter and Albert 2001; Livshultz et al. 2007; Simões et al. 2007); therefore, here the two subfamilies of the traditional Apocynaceae are treated as informal ranks as proposed in Simões et al. (2016); (2) Echiteae are recircumscribed to comprise 14 genera following Morales et al. (2017a). The five major divisions of the family are thus Rauvolfioids, Apocynoids, Periplocoideae, Secamonoideae and Asclepiadoideae.

**BIOGEOGRAPHY.** The age of the family is still a matter of debate. Rapini et al. (2007) calibrated the age of crown-group Apocynaceae at ca. 54 Ma, but Bell et al. (2010) suggested an age of only ca. 21 Ma. The most recent dating (Tank et al. 2015) gave a stem age for the family of 47 (43–62) Ma.

The fossil record of Apocynaceae is poor (Martínez-Millán 2010), but supports the higher estimates for family age. The oldest pollen of the *Alyxia* type is known from the Paleocene of Borneo (Muller 1968). Further records of *Alyxia* type pollen are known from the Eocene of Europe (Muller 1981). Pollen of the *Rauvolfia* type is known from the Upper Eocene and the Lower Oligocene (Muller 1981). A seed, *Cypselites*, resembling the seeds of some modern genera of Apocynoids, was retrieved from the Middle Eocene (ca. 47 Ma) Messel biota in Germany (Collinson et al. 2010, 2012). Several apocynaceous seeds have been retrieved from the Bembridge flora of England (Reid and Chandler 1926). In contrast, the Lower Eocene fossils from the London Clay cannot be assigned to Apocynaceae with certainty (Kirchheimer 1957).

For Periplocoideae, the oldest described fossil is *Polyporotetradites laevigatus* from the Oligocene and the Lower Miocene of Cameroon.

Recently, a distinctive pollinia-bearing fossil, *Discoflorus neotropicus*, has been retrieved from Dominican amber (dated 20–15 Ma or 45–30 Ma, depending on the dating method used; Poinar 2017). A pollinarium with two or even four pollinia is attached to the head of a termite (Termitidae: Isoptera) adjacent to the flower. The flower is somewhat similar to that of *Metastelma parviflorum*, but smaller and of a different fine structure.

The origin of the family is certainly tropical, with the first-branching tribe Aspidospermateae restricted to the New World, whereas the second-branching Alstonieae is restricted to the Asia-Pacific region (Simões et al. 2007). Studies focusing on broadscale biogeographic patterns in Rauvolfioids and Apocynoids are lacking, including attempts to assess the age of various clades. Biogeographic patterns can, however, be seen in well-sampled phylogenies of particular groups. In *Tabernaemontana*, for example, Simões et al. (2010) found that the first divergence in the genus is between neotropical and paleotropical clades. Within the paleotropical clade, the Madagascan species are sister to the African + Asian species. The only endemic species from New Caledonia sampled, *Tabernaemontana cerifera*, is nested in the Asian clade. Simões et al. (2016) found a similar divergence into neotropical and paleotropical clades in *Rauvolfia* but, unlike in *Tabernaemontana*, within the paleotropical clade the first divergence was between an Asian clade and an African + Madagascan clade. The Hawaiian *Rauvolfia sandwicensis* is nested in the neotropical clade and must be assumed to be the result of long-distance dispersal. Phylogenetic studies are lacking for other large Rauvolfioid genera such as *Alyxia*, which occurs in Asia, Australasia and the Pacific Islands, although Middleton (2002) speculated that patterns of variation in *Alyxia stellata*, a species widespread across the Pacific Islands, may in part be due to human influence.

Livshultz et al. (2007: their Fig. 1A) suggest an African origin for the entire APSA clade and for the “Crown clade” and “Malouetia clade”, which comprise all taxa in the APSA clade except for Wrightieae and Nerieae. An African origin is also suggested for Wrightieae even though the highest diversity is now in Asia. Within the Crown clade, distribution patterns of Apocynoids are strongly aligned with phylogeny. Apocynaceae is a clade of Asian origin, although *Apocynum* itself is distributed from temperate Asia to southeastern Europe and North America. A large American clade comprises the taxa now placed in Mesechiteae, Odontadenieae and Echiteae, the last of which also includes *Parsonsia* and its relatives, which are most diverse in Australasia but reach into continental Southeast Asia,

suggesting Gondwanan vicariance and long-distance dispersal.

Goyder (2006) showed that southern Africa and Madagascar are key areas of diversity for the subfamilies Asclepiadoideae, Secamonoideae and Periplocoideae. This conclusion was also reached by Livshultz (2010), who showed that pollinia have evolved several times independently in Africa, in *Epistemma* and *Schlechterella* of Periplocoideae and in Secamonoideae + Asclepiadoideae. This African origin is documented by the restriction of the small relictual Fockeeae, Eustegieae, and Astephaninae to the continent. Both Ionta and Judd (2007) and Joubert et al. (2016) retrieved the Australian *Phyllanthera grayi* and the southern African *Pentopetia natalensis* as the first two branches of Periplocoid taxa, making it difficult to narrow down an area of origin for the group. For Secamonoideae, no comprehensive phylogeny that would allow a biogeographic interpretation is available. Asclepiadoideae are firmly rooted in Africa, with the first-branching Fockeeae ranging from the southern tip of the continent to the Arabian peninsula (Bruyns and Klak 2006). For the sister tribes Marsdenieae and Ceropegieae, the ancestral area lies in the Old World, but cannot be identified more precisely at present. For Ceropegieae, Meve et al. (2017) reconstructed Southeast Asia as the ancestral area, with subsequent dispersal and vicariance events via India and the Arabian peninsula to Africa, from where the most derived subtribe, Stapeliinae, radiated to Madagascar and back to India and Southeast Asia several times (Bruyns et al. 2015). The stem succulent Stapeliads expanded their area of occurrence twice across Africa, once from north to south and later again from south to north (Meve and Liede 2002a; Bruyns et al. 2014).

Asclepiadeae, again, are firmly rooted in Africa, both with their sister tribe Eustegieae and the first-branching Astephaninae, both relictual groups of southern Africa (Surveswaran et al. 2014). For Asclepiadinae, Cynanchinae, and Tylophorinae, the first-branching taxa are all African. However, beyond this fact, the biogeographic histories of the three subtribes are widely different. In Asclepiadinae, the New World taxa branch off early, as sister to a species-rich and yet poorly resolved eastern and southern African group. The role of *Asclepias* (*Trachycalymma*) *pseudofim-*

*briata* from Ethiopia either as sister of both American *Asclepias* and the African group or unresolved with both (Chuba et al. 2017) needs further study, but points in the direction of a northern East African ancestral area for the group. In Cynanchinae, an early split separates the species-rich Madagascan lineage, out of which some succulent taxa have spread from Madagascar into Africa and Asia (*Cynanchum gerrardii* and former "*Sarcostemma*" species, see Meve and Liede 2002b) from the remainder of the genus. Two clades have radiated in Asia, one of them extending into Europe, the other one into Southeast Asia. The New World species of *Cynanchum* are monophyletic and sister to the northeastern African and Arabian "thick-fruited" clade (Khanum et al. 2016). In Tylophorinae, the most recent radiations have taken place in Asia (Liede-Schumann et al. 2012) and the subtribe has reached the New World only by human introduction (e.g., Sheeley and Raynal 1996). Shifts between tropical and temperate habitats, accompanied by a change in habit from twining evergreen lianas to rhizomatous perennials, have occurred at least twice (Liede-Schumann et al. 2016). While one of these temperate radiations is restricted to the Far East, a continuous westward expansion along the Asian mountain ranges into Europe can be reconstructed for the crown clade.

Biogeography in the second-branching Asclepiadeae clade, comprising all exclusively New World genera, is not yet completely understood. The first-branching New World genus, *Pentaclyphus*, shows a probably relictual distribution along the Andes from southern Peru to Venezuela (Meve and Liede-Schumann 2015), while the second-branching genus, *Diplolepis*, is restricted to southwestern South America, reaching from northern Patagonia to northern Chile, with radiations in forest, near-desert and desert, and high elevations (Hechem et al. 2011a, b). *Monsanima*, sister to the remaining, widespread South American Orthosiinae, is relictual with two species restricted to a single Brazilian mountain top each. Ribeiro et al. (2014) date the origin of Metastelmatinae to the Late Miocene and suppose an origin most likely in open savanna-like vegetation. The biogeography of *Minaria*, the second-branching lineage in Metastelmatinae, provides an insight into the complex migrations and

adaptations of an Asclepiadoid genus during climatic oscillations of the Pleistocene. Spatial, ecological and dating analyses suggest that the distribution of *Minaria* seems to be mainly governed by an overall retraction (larger ancestral distributions resulting in smaller, disjunct distributions), in parallel with a general trend of decreasing temperatures and increasing aridity through the Quaternary. Biogeographical analysis of *Metastelma*, one of the few Asclepiadoid genera with a center of distribution in Central America and the Caribbean, revealed that the colonization of Central America most likely did not take the Panamanian isthmus route, but went from northern South America via the Caribbean to the Yucatán isthmus of Tehuantepec area. From here, radiations northward along the Sierra Madre mountain massifs and southward to southern Central America occurred (Liede-Schumann et al. 2014).

In *Tweedia*, the first-branching genus of the Oxypetalinae, two clades were retrieved, one from Argentina, the other one from Chile, west of the Andes, comprising the species from a Mediterranean climate. Because the Mediterranean climate was only established in the late Neogene, dispersal across the Andean barrier and the invasion of new habitats that provided novel opportunities for speciation is likely for *Tweedia* (Calviño et al. 2014).

**AFFINITIES.** Apocynaceae (often as two families, Apocynaceae and Asclepiadaceae) has typically been placed within the Gentianales, together with Gentianaceae, Loganiaceae and Rubiaceae. In the 1980s to 1990s Saccifoliaceae was also included in the order (Thorne 1992; Nicholas and Baijnath 1994), but is now included in Gentianaceae (Thiv et al. 2000). Sometimes Retziaceae (Cronquist 1981) was also included, a family that is currently placed in Stilbaceae (Lamiales). Based on more recent molecular evidence Gentianales comprises five families: Apocynaceae, Gelsemiaceae, Gentianaceae, Loganiaceae and Rubiaceae (Backlund et al. 2000; APG IV 2016). Within Gentianales, Rubiaceae is usually considered the most different, and is often the first-branching family, followed by Gentianaceae. The closest relatives of Apocynaceae seem to be either Loganiaceae or Gelsemiaceae, depending on which species are sampled and what type of characters are analyzed (Struwe et al. 1994;

Endress et al. 1996; Bremer et al. 1999; Backlund et al. 2000; Yang et al. 2016).

**DISTRIBUTION AND HABITAT.** Apocynaceae are a predominantly pantropical family, with relatively few genera ranging north or south into temperate regions. For Rauvolfioids and Apocynoids the main centers of diversity are tropical South America, Asia and, to a lesser extent, tropical Africa, although notable radiations of particular genera have also taken place on islands (e.g., *Parsonsia* on Australia and on New Guinea, *Alyxia* on New Caledonia and on New Guinea and *Petchia* on Madagascar). Two subfamilies, Periplocoideae and Secamonoideae, are restricted to the Paleotropics (extending to Australia).

Middleton (2007) mapped the numbers of genera, species and endemic species in each of the regions/islands of Malesia for Rauvolfioids and Apocynoids. Species diversity was, unsurprisingly, shown to be highest in the everwet regions of Peninsular Malaysia, Borneo and New Guinea and lower in the more seasonal areas of the Lesser Sunda Islands and Philippines. The relatively lower than expected diversity on Sumatra could be an artefact of lack of exploration. Generic diversity declined from West to East. Endemism was by far the highest in New Guinea but was also high in the Philippines.

Good (1947 and later editions, 1952) mapped the distributions of many taxa in the subfamilies Asclepiadoideae, Secamonoideae and Periplocoideae, and concluded that southern Africa and Madagascar are key areas of diversity for these groups. While diversity in southern Africa is made up of a large number of genera, diversity in Madagascar is largely due to a few genera with species-rich radiations, such as *Pentopetia* in Periplocoideae (Klackenberg 1999, ca. 20 species), *Secamone* in Secamonoideae (ca. 60 species, Klackenberg 1992; Lahaye et al. 2005) and *Cynanchum* in Asclepiadoideae (ca. 100 species, Liede-Schumann unpubl. data).

Asclepiadoideae, Rauvolfioids and Apocynoids are found in both the Paleotropics and Neotropics though many tribes tend to be predominantly in either one or the other. For example, in Rauvolfioids all genera of Aspidospermateae are New World, whereas Alstonieae, Melodineae, Hunterieae and Carisseae are restricted to Africa and the Asia-Pacific region, as is Alyxieae except

for *Condylocarpon*, *Rauvolfia* and *Tabernaemontana* are pantropical although clades within these two genera tend to be exclusively paleotropical or neotropical. In Apocynoids the two earliest branching tribes, Wrightieae and Nerieae, are found in Eurasia and the Paleotropics, and the next, Malouetieae, is both paleo- and neotropical. Apocyneae are also restricted to the Paleotropics (most of them in Asia) except for *Apocynum*, which has a disjunct distribution between temperate Eurasia and North America (Rosatti 1989); Baisseeae are restricted to tropical Africa and Madagascar (De Kruif 1983). Conversely, Rhabdadenieae, Mesechiteae and Odontadenieae are restricted to the New World, as are Echiteae with the exception of *Artia*, *Ecua* and *Parsonsia*.

In Asclepiadoideae, only Marsdenieae and Asclepiadeae have representatives in the New World, and only three genera are presently considered to have representatives in both hemispheres, *Cynanchum* (Liede and Täuber 2002; Khanum et al. 2016), *Asclepias* and *Marsdenia*. The species-rich (> 1050 species) clade of Pentacyphinae, Diplolepineae, Orthosiinae, Metastelmatinae, Tassadiinae, Oxypetalinae, Gonolobinae and Topeninae is restricted to the New World (Rapini et al. 2003; Liede-Schumann et al. 2005).

In Rauvolfioids and Apocynoids, the largest genera are *Mandevilla* (ca. 170 species), *Tabernaemontana* (ca. 122 species), *Alyxia* (ca. 106 species), *Parsonsia* (ca. 82 species), *Rauvolfia* (ca. 60 species), *Prestonia* (ca. 58 species), *Aspidosperma* (ca. 50 species) and *Alstonia* (ca. 45 species) (Middleton 2007, 2014; Pereira et al. 2016, 2017; Morales and Zamora 2017; Morales et al. 2017b). In Periplocoideae, *Raphionacme* is the largest genus (36 species, Venter 2009), in Secamonoideae, *Secamone* s.str. comprises ca. 90 species (Klackenberg 2001). In Asclepiadoideae, *Hoya* (ca. 350–450 species) is by far the largest genus in Marsdenieae (Rodda 2015), and *Ceropegia* (ca. 330 species) in Ceropegieae. In Asclepiadeae, *Cynanchum* (Cynanchinae, ca. 250 species, Meve and Liede-Schumann 2017), *Vincetoxicum* (Tylophorinae, ca. 140 species, Liede-Schumann et al. 2016) and *Asclepias* (ca. 100 species) are the most species-rich genera. In the New World Clade, *Gonolobus* (Gonolobinae, 120–140 species) and *Oxypetalum* (Oxypetalinae, ca. 130 species, Farinaccio and Mello-Silva 2006) are the most species-rich genera since the former

largest genus *Matelea* (Gonolobinae) has now been split into various smaller genera (Morillo 2012, 2013, 2015).

In general, Rauvolfioids and Apocynoids are most diverse in humid lowland tropical habitats, although some species are found at high elevations. In lowland evergreen forest in Asia some of the largest trees belong to *Dyera* and *Alstonia* (Middleton 2007). Other tree genera, such as *Kibatalia*, *Kopsia* and *Wrightia* are part of the forest understory (Middleton 2007). *Alstonia* is particularly diverse in habit and habitat with trees over 60 m tall in lowland forest, small understory trees in lowland and montane forest, small and large trees in swamp forest, and shrubs on karst limestone (Sidiyasa 1998). Many of the lianas, particularly in genera such as *Chilocarpus*, *Leuconotis*, *Melodinus*, *Micrechites* and *Willughbeia*, can grow to enormous heights and reach the canopy in tropical lowland rainforest. Some genera (e.g., *Adenium*, *Pachypodium* and some species of *Alyxia*, *Aspidosperma*, *Himatanthus* and *Mandevilla*) have radiated into drier habitats, others into swamp forest and then often developing pneumatophores to survive the waterlogged soils (some species of *Alstonia* and *Dyera*), and others are littoral or on the edge of mangrove (e.g., *Cerbera*, *Lepinia* and *Ochrosia*). In the case of *Mandevilla*, most of the species at the extremes of its distribution, in the deserts of Mexico and the southwestern USA to the North, and in the open cerrado vegetation of Brazil, Argentina and Paraguay to the South, have a water-storing xylopod. Of the handful of genera that are restricted to temperate climates, both *Amsonia* and *Apocynum* are perennial herbs with a disjunct distribution in temperate Eurasia and North America, *Haplophyton* is restricted to dry desert habitats in Mexico and the extreme southwestern USA, and *Cycladenia* is a dwarf, subsucculent perennial herb, restricted to a few mountain peaks in California, Arizona and Utah. In addition, in the Old World, *Vinca* and *Nerium* occur in temperate to subtropical climates, respectively. They remain evergreen in temperate climates. *Malouetia*, which has an African-Neotropical disjunct distribution, has several species in Amazonia that are adapted to the seasonally flooded forest (mostly blackwater rivers) and/or nutrient-poor white sand soils, and are able to tolerate long periods of inundation. Another white sand specialist is

the beautiful *Galactophora*, which is found in the white sand savannas of the Guiana Shield. Periplocoideae, Secamonoideae and Asclepiadoideae have also been successful in expanding and diversifying into drier or cooler habitats, and to an extent that surpasses the outer limits of the adaptability of Rauvolfioids and Apocynoids. Periplocoideae and Asclepiadoideae both have members with special adaptations to arid habitats such as tubers (e.g., *Raphionacme* (Periplocoideae), *Ceropegieae*) or succulent stems as in many *Ceropegieae* and about half of the Malagasy *Cynanchum* species. *Ceropegieae* have their highest diversity in Africa, the species-rich stem succulent *Stapeleads* and *Ceropegia* have centers of distribution in East Africa, South Africa and India. *Marsdenieae* are most diverse in Asia and include many species that are truly epiphytic, a habit unknown in the Rauvolfioids, Apocynoids, and Secamonoideae. In Asclepiadoideae, *Vincetoxicum* has radiated in Asia and Europe, reaching as far north as southern Sweden. In the New World, members of *Asclepias* reach southern Canada (Woodson 1954), and *Diplolepis* extends south to Patagonia (Hechem et al. 2011a, b).

Asclepiadeae in Africa often have storage roots, and are typically confined to grasslands. The majority of Asclepiadoideae species, however, are leafy twiners and lianas in the tropics and subtropics, where they inhabit different kinds of forests and scrub, often in slightly disturbed habitats. In lowland rainforests of Africa and the Americas, however, they are rare, whereas they are most diverse in this habitat in Southeast Asia. Abundances are usually low with single scattered plants and without forming thickets or smothering other plants.

**USES AND ECONOMIC IMPORTANCE.** Due to the vast array of bioactive compounds in the family, numerous genera of Apocynaceae figure prominently in folk medicines. One genus is often used to treat a broad spectrum of diverse ailments such as fever, malaria, jaundice, cancer, hypertension, inflammation, pain, diarrhea, skin diseases, gastrointestinal problems, as a purgative, to promote healing of wounds, etc. (e.g., *Allamanda*, *Alstonia*, *Alyxia*, *Amsonia*, *Aspidosperma*, *Catharanthus*, *Cerbera*, *Kibatalia*, *Melodinus*, *Ochrosia*, *Picalima*, *Rauvolfia*, *Strophanthus*, *Tabernaemontana*, *Thevetia*, *Vallaris*, *Vinca*, *Voacanga*;

Bisset 1958, 1961, 1989, 1991, 1992; Schultes 1979; Van Beck et al. 1984; Hutchings 1989; Neuwinger 1994a; Metzner 1998; Hendrian 2001a, b; Rahayu 2001; Rudjiman 2001; Teo 2001; Tran 2001; Chua and Horsten 2001; Sangat-Roemantyo and Middleton 2001; Van Valkenburg and Hendrian 2001; Van Valkenburg and Horsten 2001; Gilani et al. 2007; Wong et al. 2013). Indeed, the names of several species emphasize their medicinal use, such as *Wrightia antidysenterica*, *Rauvolfia vomitoria* and *Allamanda cathartica*. The toxic latex of some of the genera that contain cardenolides or steroidal alkaloids has long been used to make arrow poisons by indigenous peoples in both Africa and South America; the three most widely used are *Acokanthera* (Watt and Breyer-Brandwijk 1962), *Strophanthus* (Beentje 1982) and *Malouetia* (Schultes 1979; Bisset 1992). *Anisopus* (Neuwinger 1994b), *Marsdenia* and *Vincetoxicum* (*Tylophora*) species are used as canine and rat poisons. In southern Africa and Australia, several Asclepiadoideae species are serious toxic weeds for cattle and sheep (Watt and Breyer-Brandwijk 1962; Hall 1964; Everist 1981). The cardenolide-containing and commonly planted ornamentals *Cerbera*, *Nerium* and *Thevetia* have been involved in human poisoning (Gaillard et al. 2004; Bandara et al. 2010). Hallucinogenic drinks are made from *Tabernanthe* in Africa (Bisset 1958) and *Malouetia* in Amazonia (Schultes 1979). An important role in traditional medicine has been reported for *Mondia whitei* (Periplocoideae), including use as an antidepressant and aphrodisiac (Aremu et al. 2011). Many Periplocoideae and Asclepiadoideae species are used in folk medicine in China (e.g., Hong et al. 2015; Brand et al. 2017; Chang et al. 2017), tropical Asia (Perry 1980; Kiew 1994, 2001), Africa (Burkill 1985; Hutchings 1989), and Central America (Williams 1981). *Calotropis* is still the most important medicinal plant in Asclepiadoideae, with a variety of uses across its distribution area (Neuwinger 1994a). Several species of *Asclepias* are used medicinally because of their cardenolide glycosides (Usher 1974). Many species of *Vincetoxicum* contain phenanthroindolizidine alkaloids and are used in folk medicine (Schultes and Raffauf 1990). Members of *Cynanchum* sect. *Rhodostegiella* have anti-epileptic properties (Mu et al. 1986). *Hoodia* contains appetite-suppressing pregnane glycosides, which

were expected to become a drug of high economic value (Van Heerden 2008), but market introduction failed. Recently, also *Caralluma adscendens* s.l. has been identified as an appetite suppressant and is offered as a dietary supplement in India and online (Dutt et al. 2012). *Gymnema sylvestre* (Asclepiadoideae–Marsdenieae) contains gymnesin (triterpene glycosides, Yoshikawa et al. 1997), acting as powerful sweetness inhibitors (Suttisri et al. 1995).

Few genera of Apocynaceae are of broadscale economic importance in Western medicine. In the last century, pharmacognosists or ethnopharmacologists (often working for pharmaceutical companies) made excursions to the tropics to observe which plants were being used by indigenous peoples (often performing simple tests in the field to determine presence or absence of alkaloids or other secondary metabolites), and in this way brought the first apocynaceous drugs to the Western world. One of the first was extracted from *Strophanthus* seeds, which are used to make arrow or dart poison in various parts of Africa; strophanthin was administered as a cardiac stimulant to treat heart failure. By 1970, several tons of *Strophanthus* seeds were being imported to Europe per year (Beentje 1982). Today strophanthin is still sometimes prescribed as an alternative treatment for heart disease (Bisset 1991). Ibogaine, extracted from *Tabernanthe iboga*, is used in private clinics in Europe and North America to treat opioid withdrawal symptoms (Alper et al. 2008). Today, compounds of plant origin still provide the template for many synthetically produced drugs (De Luca et al. 2012). A number of genera show promise as anticancer or antimalarial drugs. Two genera of Vinceae (Rauvolfioids) have been the source of drugs based on indole alkaloids that have become commercially available: *Catharanthus roseus* is the source of vinblastine and vincristine, which are used to treat leukemia and other types of cancer (Taylor and Farnsworth 1975; Wong et al. 2013), and *Rauvolfia serpentina* is the source of reserpine, which has long been used in traditional and Ayurveda medicines and was earlier used in Western medicine for treating hypertension and mental illness. *Rauvolfia serpentina* has also recently shown great promise as a drug against diabetes (Pathania et al. 2013). *Hemidesmus indicus* (Indian Sarsaparilla; Periplocoideae)

is widely used in India in Ayurveda medicine and is used to treat a variety of diseases and in cosmetics. The alkaloids of *Cryptolepis sanguinolenta* (Periplocoideae) are known for their hypoglycemic properties (Bierer et al. 1998) and are being tested for tumoristatic effects (Bonjean et al. 1998); Buhner (2012) reported on their considerable activity against multi-resistant bacteria. Both *Calotropis procera* in Africa and Arabia (Neuwinger 1994a) and *Calotropis gigantea* on the Indian subcontinent (Kumar et al. 2013) are widely used as poison and in folk medicine.

Apocynaceae contain too many toxic secondary compounds to be an economically important food source, although local uses are reflected in several plant names such as *Carissa edulis* and *Willughbeia edulis*. Most genera of Willughbeieae have edible fruits, which are consumed by people in the regions where they grow and are sometimes sold in local markets (e.g., several species of *Landolphia*, *Hancornia*). Fruits of *Carissa* can be used to make jam. The latex of *Couma* makes a refreshing drink and that of *Dyera* was once an important source of latex for chewing gum. The flowers of *Echites pandurata* (Apocynoids) are popular as a condiment in cooking in parts of Central America (Morton et al. 1990), and flower buds of *Telosma cordata* are used similarly in parts of Asia. Green fruits of *Gonolobus edulis* and related species are consumed in a sugared preparation called “guayote” in Costa Rica. The young fruits, seeds and sometimes leaves of *Telectadium edule* (Periplocoideae), *Morrenia odorata* (Arenas 1999) and *Cynanchum (Glossonema) boveanum* (Asclepiadoideae–Asclepiadeae, Burkill 1985) are cooked and eaten in a variety of ways. The raw or cooked stems of *Caudanthera edulis* (Stapeliinae) are popular as a vegetable in southeastern Africa and parts of the Indian subcontinent.

A number of genera are cultivated as ornamentals, particularly in tropical and subtropical climates (e.g., *Adenium*, *Allamanda*, *Amsonia*, *Araujia*, *Asclepias*, *Beaumontia*, *Catharanthus*, *Cerbera*, *Chonemorpha*, *Cryptostegia*, *Dischidia*, *Hoya*, *Mandevilla*, *Nerium*, *Pachypodium*, *Pergularia*, *Periploca*, *Plumeria*, *Tabernaemontana*, *Telosma*, *Thevetia*, *Wrightia* and *Vinca*). Many genera of Ceropegieae are cultivated worldwide by enthusiasts of succulent plants for their beautiful and often bizarre flowers.



Some species are used in religious and other traditional ceremonies. *Wrightia religiosa* and some species of *Plumeria* are commonly planted in temple and burial grounds in Southeast Asia. *Alyxia* species are used in the making of leis in Polynesian cultures. The hard endocarps of *Thevetia peruviana* and *T. thevetioides* are strung together to make folk instruments such as rattles, which can be hand-held, collected into bracelets or worn as “ayoyotes”, the traditional leg shakers used by Aztec dancers (Alvarado-Cárdenas et al. 2017).

The wood of *Alstonia* and *Aspidosperma* is used for construction, especially for cabinetmaking, furniture, floors, tool handles and carving (Ezcurra et al. 1992; Middleton 2007). Before *Hevea* dominated the rubber industry, the latex of Apocynaceae was used, particularly various genera of Willughbeieae (certain species of *Landolphia* and *Willughbeia*). During World War II *Cryptostegia grandiflora* (Periplocoideae), a native of Madagascar, was introduced into several other countries as a source of rubber. It has since become an aggressive, invasive weed, and has greatly impacted the ecology where it has been introduced (McFadyen and Harvey 1990; Rodríguez-Estrella et al. 2010). *Araujia sericifera* and *Morrenia odorata* (Asclepiadoideae-Asclepiadeae-Oxypetalinae) are known as noxious weeds in *Citrus* groves in California, Florida, Southern Africa, Australia, New Zealand, Israel, Italy, and Spain (Spellman and Gunn 1976). For *Morrenia odorata* a mycoherbicide based on an isolate of *Phytophthora palmivora* is available (Winks and Fowler 2000), for *Araujia sericifera*, the *Araujia mosaic virus* is discussed as a potential biological control agent (Winks and Fowler 2000). Three species of *Vincetoxicum* (Asclepiadoideae-Asclepiadeae-Tylophorinae), *V. hirundinaria*, *V. nigrum* and *V. rossicum*, have been introduced into North America, and two of them are invasive in natural areas. *Hypena opulenta* (Lepidoptera: Erebidae) has been tested as an efficient biological control (Young and Weed 2014).

CONSERVATION. Apocynaceae, being predominantly tropical, are threatened mainly by the destruction of their natural habitats. Some of the more showy species, such as in *Pachypodium*, and those used in traditional medicines, such as *Rauvolfia serpentina*, are listed in CITES, but this

is only the tip of the iceberg. The majority of Apocynaceae species have not yet been assessed for the IUCN Red List of Threatened Species and large numbers of those that have been need to be updated in light of taxonomic changes and better distribution data. In both the Neotropics and the Paleotropics, many taxa are narrow ecological endemics, sometimes highly specialized and known from a single locality (e.g., the blackwater-white sand endemics of the Guianas and NW Amazonia (e.g., many species of *Malouetia*) and karst limestone endemics in Southeast Asia), where destruction of habitat equates to species extinction. It has recently been suggested that all three species of *Thevetia* endemic to Mexico be considered for protection as critically endangered, vulnerable or near threatened (IUCN categories CR, VU and NT, respectively: Alvarado-Cárdenas et al. 2017). *Dyera polyphylla*, a species restricted to peat swamp forest, is considered vulnerable due to habitat loss and over-exploitation (IUCN category VU A1cd; Middleton 2007). *Kibatalia* is particularly diverse in the Philippines, where there has been major forest loss, and many species have not been collected for decades. As forests are cleared the large timber species, such as in *Dyera* and *Alstonia*, are lost but so are the understory tree species in genera such as *Kopsia*, *Wrightia* and *Kibatalia*. Along with the loss of these large and small trees, the lianas, twiners and predominantly epiphytic species, such as in *Hoya* and *Dischidia*, are also lost to logging and clear-cutting; many species are already extinct and many more threatened with extinction (Kleijn and van Donkelaar 2001).

Islands present especially fragile ecosystems. In addition to habitat destruction due to human activity such as deforestation and fire, island taxa are often threatened by introduced species such as feral animals (e.g., goats, rats) and invasive plants. This has been well documented for Apocynaceae on various islands in French Polynesia. On Reunion Island, for example, the endangered endemic *Carissa xylopicron* has been almost completely decimated by introduced giant African land snails (*Achatina* species; Meyer and Picot 2001), while on Mauritius the last remaining individuals of the endemic *Tabernaemontana persicariifolia* are threatened by road construction and listed as endangered (IUCN category EN; Pynee et al. 2013). *Lepinia taitensis*, endemic on

Tahiti and Moorea, is losing the battle against the introduced garden plant *Miconia calvescens* (Meyer 1996) and is considered critically endangered (IUCN category CR). In the Marquesas *Ochrosia* and *Rauvolfia* are represented by two endemic species each, *O. brownii* and *O. nukuhivensis* and *R. nukuhivensis* and *R. sachetiae*, respectively. All four species are considered critically endangered (IUCN category CR). In many cases the remaining individuals of a species can be counted on one hand. *Rauvolfia sachetiae* is known from a single tree on Hiva Oa, but has not been seen at the type locality since 1977; the area is overgrazed by goats and has been invaded by *Syzygium cumini* (Meyer and Butaud 2009; Lorence and Butaud 2011). On Madagascar, several of the endemic *Pachypodium* species have a restricted distribution and are endangered, mainly due to over-exploitation by hobby gardeners and plant poachers as well as to habitat destruction. Stronger conservation measures have been urged for at least three species: *P. baronii*, *P. windsorii*, and *P. decaryi* (Burge et al. 2013).

A number of genera have diversified on karst limestone in Southeast Asia and these areas are particularly vulnerable to habitat destruction, particularly through over-exploitation for the manufacture of concrete. Other limestone sites, even in protected areas, receive unsustainable numbers of tourists. Consequently, some species in genera such as *Wrightia*, *Alstonia* and *Dischidia* are in rapid decline. As narrowly endemic species in these genera continue to be discovered as karst limestone areas are explored, there is considerable potential for species loss even before those species have ever been collected and catalogued. This problem, of course, is not confined to species of Apocynaceae. Also in temperate regions, some taxa are rare or endangered. In southwestern USA, for example, a number of species of *Amsonia* found in arid habitats, and also *Cycladenia*, which is restricted to three or four mountain peaks in California, Arizona and Utah are rare or threatened. While Africa is home to a number of extremely threatened—or maybe extinct—paleoendemics such as *Emicocarpus fisifolius*, the Americas, in particular the Andes, are home to swarms of very narrow neoendemics, e.g., species of *Orthosia* and *Scyphostelma* known from a single valley each.

Many species of all larger genera of Asclepiadoideae are known only from the type collection. In the horticulturally popular and mostly succulent Ceropegieae nearly every second species deserves conservation concern (Albers and Meve 1997). Commercial collecting activities like those in *Hoodia* (see “Uses and Economic Importance”) severely increase the risks for some of the species.

#### CLASSIFICATION OF APOCYNACEAE

##### I. Rauvolfioids

1. Tribe Aspidospermateae Miers (1878).  
Gen. 1–6
2. Tribe Alstonieae G. Don (1837).  
Gen. 7–8
3. Tribe Vinceae Duby (1828).
  - a. Subtribe Kopsiinae Leeuwenb. (1994).  
(Gen. 9).
  - b. Subtribe Ochrosiinae Pichon ex Boiteau (1981).  
(Gen. 10).
  - c. Subtribe Tonduziinae M.E. Endress (2014).  
(Gen. 11–12).
  - d. Subtribe Vincinae M.E. Endress (2014).  
(Gen. 13).
  - e. Subtribe Catharanthinae Pichon ex Boiteau (1981).  
(Gen. 14–16).
  - f. Subtribe Rauvolfiinae Benth & Hook.f. (1876).  
(Gen. 17).
4. Tribe Willughbeieae A. DC. (1844).
  - a. Subtribe Leuconotidinae Pichon ex Leeuwenb. (1994).  
(Gen. 18–20).
  - b. Subtribe Willughbeiiinae A. DC. (1844).  
(Gen. 21).
  - c. Subtribe Landolphiinae K. Schum. (1895).  
(Gen. 22–31).
  - d. Subtribe Lacmelleinae Pichon ex Leeuwenb. (1994).  
(Gen. 32–35).
5. Tribe Tabernaemontanae G. Don (1837).
  - a. Subtribe Ambelaniinae A.O. Simões & M.E. Endress (2010).  
(Gen. 36–42).
  - b. Subtribe Tabernaemontaninae A. DC. (1844).  
(Gen. 43–50).
6. Tribe Amsonieae M.E. Endress (2014).  
(Gen. 51).
7. Tribe Melodineae G. Don (1837).  
(Gen. 52–56).

8. Tribe Hunterieae Miers (1878).  
(Gen. 57–60).
  9. Tribe Alyxieae G. Don (1837).
    - a. Subtribe Condylocarpinae Pichon ex Leeuwenb. (1994).  
(Gen. 61–63).
    - b. Subtribe Alyxiinae A. DC. (1844).  
(Gen. 64–67).
  10. Tribe Plumerieae E. Mey. (1838).
    - a. Subtribe Allamandinae A. DC. (1844).  
(Gen. 68).
    - b. Subtribe Plumeriinae Pichon ex Leeuwenb. (1994).  
(Gen. 69–71).
    - c. Subtribe Thevetiinae A. DC. (1844).  
(Gen. 72–77).
  11. Tribe Carisseae Dumort (1829).  
(Gen. 78–79).
- II. Apocynoids**
1. Tribe Wrightieae G. Don (1837).  
(Gen. 80–82).
  2. Tribe Nerieae Baill. (1889).
    - a. Subtribe Neriinae Benth. & Hook.f. (1876).  
(Gen. 83–84).
    - b. Subtribe Alafiinae Pichon ex Leeuwenb. (1994).  
(Gen. 85–88).
  3. Tribe Malouetieae Müll. Arg. (1860).
    - a. Subtribe Galactophorinae Pichon ex M.E. Endress (2014).  
(Gen. 89).
    - b. Subtribe Pachypodiinae Pichon ex Leeuwenb. (1994).  
(Gen. 90–91).
    - c. Subtribe Malouetiinae Pichon (1950).  
(Gen. 92–101).
  4. Tribe Rhabdadenieae Pichon ex M.E. Endress (2014).  
(Gen. 102).
  5. Tribe Odontadenieae Miers (1878).  
(Gen. 103–111).
  6. Tribe Mesechiteae Miers (1878).  
(Gen. 112–117).
  7. Tribe Echiteae Bartl. (1830).
    - a. Subtribe Laubertiinae J.F. Morales, M.E. Endress & Liede (2017).  
(Gen. 118–119).
  - b. Subtribe Peltastinae Pichon ex M.E. Endress (2014).  
(Gen. 120–122).
  - c. Subtribe Echitinae Kitt. (1843).  
(Gen. 123–127).
  - d. Subtribe Parsonsinae Benth. & Hook.f. (1876).  
(Gen. 128–130).
  - e. Subtribe Prestoniinae Pichon ex M.E. Endress (2014).  
(Gen. 131).
8. Tribe Apocyneae Rchb. (1831).
  - a. Subtribe Papuechitinae Pichon ex M.E. Endress (2014).  
(Gen. 132–134).
  - b. Subtribe Amphineuriinae Pichon ex M.E. Endress (2014).  
(Gen. 135–137).
  - c. Subtribe Beaumontiinae Pichon ex M.E. Endress (2014).  
(Gen. 138–140).
  - d. Subtribe Apocyninae Pichon ex Leeuwenb. (1994).  
(Gen. 141–142).
  - e. Subtribe Urceolinae Pichon ex M.E. Endress (2014).  
(Gen. 143).
  - f. Subtribe Chonemorphae Pichon ex M.E. Endress (2014).  
(Gen. 144–147).
  - g. Subtribe Ichnocarpinae Benth. & Hook.f. (1876).  
(Gen. 148–152).
9. Tribe Baisseeae (Pichon ex De Kruif) M.E. Endress (2007).  
(Gen. 153–156).
- III. Subfam. Periplocoideae** Endl. (1838).  
(Gen. 157–189).
- IV. Subfam. Secamonoideae** Endl. (1838).  
(Gen. 190–197).
- V. Subfam. Asclepiadoideae** Burnett (1835).
1. Tribe Fockeeae H. Kunze, Meve & Liede (1994).  
(Gen. 198–199).
  2. Tribe Marsdenieae Benth. (1868).  
(Gen. 200–225).
  3. Tribe Ceropegieae Orb. (1843).
    - a. Subtribe Heterostemminae Meve & Liede (2004).  
(Gen. 226).

- b. Subtribe Leptadeniinae Meve & Liede (2004). (Gen. 227–230).
- c. Subtribe Anisotominae Meve & Liede (2004). (Gen. 231–235).
- d. Subtribe Stapeliinae G. Don (1837). (Gen. 236–271).
- 4. Tribe Eustegieae Rchb. ex Meve & Liede (2014). (Gen. 272–273).
- 5. Tribe Asclepiadeae Duby (1828).
  - a. Subtribe Astephaninae Endl. ex Meisn. (1840). (Gen. 274–276).
  - b. Subtribe Asclepiadinae Decne. ex Miq. (1857). (Gen. 277–302).
  - c. Subtribe Cynanchinae K. Schum. (1895). (Gen. 303–304).
  - d. Subtribe Tylophorinae K. Schum. (1895). (Gen. 305–306).
  - e. Subtribe Pentacyphinae Liede & Meve (2014). (Gen. 307).
  - f. Subtribe Diplolepinae Liede & Meve (2014). (Gen. 308).
  - g. Subtribe Orthosiinae Liede & Rapini (2005). (Gen. 309–312).
  - h. Subtribe Metastelmatinae Endl. ex Meisn. (1840). (Gen. 313–324).
  - i. Subtribe Tassadiinae Liede & Meve (2014). (Gen. 325).
  - j. Subtribe Oxypetalinae E. Fourn. (1885). (Gen. 326–331).
  - k. Subtribe Gonolobinae Liede (1997). (Gen. 332–376).
  - l. Subtribe Topeinae H.A. Keller & Liede (2017). (Gen. 377).
- Genus of uncertain subtribal placement in Asclepiadeae (Gen. 378).
  - Anthers free from style-head; corolla lobe aestivation in bud typically sinistrorse (overlapping to the left), rarely dextrorse; fruit dehiscent or indehiscent, syncarpous or apocarpous, a berry, drupe, follicle, or capsule; seeds naked, with wings, or arils, but almost never with a coma at one end
    - I. **Rauvolfioids** (p. 253)
  - 2. Nectaries, if present, encircling the base of the ovary, as five distinct lobes, or these fused to varying degrees into a lobed or crenulate ring, rarely 2 distinct lobes alternating with the carpels; anthers 4-locular; pollen almost always shed as monads; style-head secretions normally a foamy adhesive or gummy, undifferentiated translators
    - II. **Apocynoids** (p. 281)
    - Nectaries located in alternistaminal pockets on staminal feet or staminal tube; anthers 2–4-locular; pollen in tetrads or united in pollinia; style-head secretions forming differentiated translators with a sticky pad (viscidium) or consisting of a corpuscle and two caudicles 3
    - 3. Anthers 4-locular, pollen in tetrads or, when in pollinia, then these without a waxy outer wall 4
      - Anthers 2-locular, pollen in pollinia, these almost always covered by a waxy outer wall (ectexine)
      - V. **Subfam. Asclepiadoideae** (p. 324)
    - 4. Translators with a sticky end (viscidium) that adheres to pollinator for removal; pollen usually shed in tetrads, sometimes in pollinia, from anthers onto a spoon- or cornet-shaped receptacle of the translator
      - III. **Subfam. Periplocoideae** (p. 309)
      - Translators with a hardened clip-like corpusculum in which some part of pollinator body becomes caught for removal; pollen in 4 minute pollinia attached directly or indirectly to the corpusculum
      - IV. **Subfam. Secamonoideae** (p. 321)

## KEY TO THE MAJOR DIVISIONS OF APOCYNACEAE

1. Anthers adnate to the style-head; corolla lobe aestivation in bud typically dextrorse (overlapping to the right) or valvate, rarely sinistrorse; fruit dehiscent, almost always apocarpous, a pair of follicles, sometimes reduced to one by abortion or postgenitally fused; seeds small, almost always with a coma at one end 2

## KEY TO THE GENERA OF RAUVOLFOIDS AND APOCYNIDS (APOCYNACEAE S. STR.)

1. Plants erect: trees, shrubs, subshrubs or herbs 2
  - Plants twining: vines, lianas, scrambling shrubs or rarely stoloniferous perennials 113
2. Plants with paired, often branched, sharp spines in the axils; leaves opposite; fruit a berry 79. *Carissa*

- Plants without paired sharp spines in the axils or, if spines present, then leaves not opposite and fruit not a berry 3
- 3. Herbs (often with a woody base) or subshrubs usually < 2 m tall 4
  - Shrubs or trees, generally > 2 m tall but sometimes shorter 23
- 4. Leaves alternate; calycine colleters absent 5
  - Leaves opposite or verticillate; calycine colleters absent or present 7
- 5. Corolla broadly bowl-shaped; anthers exposed, firmly attached to the style-head; nectaries present 142. *Apocynum*
  - Corolla salverform; anthers hidden, free from the style-head; nectaries absent 6
- 6. Inflorescences thyriform, several-flowered; flowers blue; seeds naked 51. *Amsonia*
  - Inflorescences consisting of only 1–4 flowers in the upper leaf axils; flowers yellow; seeds with a coma at each end 3. *Haplophyton*
- 7. Ovary completely syncarpous; fruit a berry (Willughbeieae-Landolphiinae) 8
  - Ovary apocarpous (sometimes partially syncarpous at the base); fruit a pair of follicles 10
- 8. Inflorescences elongated, branched terminal panicles; fruit densely velutinous on the outer surface 26. *Ancylobothrys*
  - Inflorescences short and usually congested, terminal or axillary cymes; fruit glabrous 9
- 9. Corolla tube 9–13 mm long; anthers inserted in the lower quarter of the corolla tube 27. *Chamaecлитandra*
  - Corolla tube 4–11 mm long; anthers inserted in the upper half of the corolla tube 31. *Landolphia*
- 10. Leaf blades adaxially with colleters clustered at the base of the midrib, or scattered along its length; calycine colleters present 117. *Mandevilla*
  - Leaf blades without colleters; calycine colleters absent or present 11
- 11. Nectaries or nectary disc absent 12
  - Nectaries or nectary disc present 13
- 12. Petaloid corona present in the corolla mouth; corolla lobes often caudate; seeds with a rostrate coma at one end and a deciduous coma at the other 85. *Strophanthus*
  - Petaloid corona absent; corolla lobes not caudate; seeds with a sessile coma at each end 3. *Haplophyton*
- 13. Nectaries 2, alternating with the carpels 14
  - Nectaries in a ring surrounding the base of the ovary 16
- 14. Corolla lobe aestivation sinistrorse in bud; seeds naked 16. *Catharanthus*
  - Corolla lobe aestivation dextrorse in bud; seeds with a micropylar coma 15
- 15. Corolla infundibuliform; anthers cordate at the base, only very weakly attached to the style-head; plants of SE Asia and Borneo 92. *Spirolobium*
  - Corolla salverform; anthers sagittate at the base and firmly attached to the style-head; plants of Amazonia 109. *Salpinctes*
- 16. Leaves in whorls of 3–5 (rarely opposite at some nodes); fruit indehiscent, drupaceous, often only one carpel developing; seeds one per carpel, naked 17. *Rauvolfia*
  - Leaves opposite; fruit dehiscent, follicular, usually both carpels developing; seeds several per carpel, with a micropylar coma 17
- 17. Bracts very conspicuous, large and foliaceous to subpetaloid, often purplish red tinged; annular corona present in the corolla mouth 121. *Rhodocalyx*
  - Bracts small, inconspicuous, green or scarious; annular corona absent 18
- 18. Corolla usually showy, > 2 cm long; plants of the Neotropics 19
  - Corolla smaller, < 2 cm long; plants of temperate regions 22
- 19. Sepals foliaceous to subfoliaceous, without colleters on the inner surface; corolla usually pink, purple, red or magenta 20
  - Sepals smaller, not foliaceous, with colleters on the inner surface; corolla yellow or cream (Odontadenieae) 21
- 20. Calyx and corolla tube often with glandular hairs on the outer surface; corolla tube with five longitudinal, alternipetalous ridges on the outer surface; seed coma sessile; follicles fused from the base to about 2 cm (stipitate), free above 89. *Galactophora*
  - Calyx and corolla tube without glandular hairs; corolla tube without five longitudinal, alternipetalous ridges on the outer surface; seed coma rostrate; follicles free or fused only at the very base (not stipitate) 102. *Rhabdadenia*
- 21. Anthers with a long, slender spiraled apical appendage 111. *Pentalinon*
  - Anthers without a long apical appendage 110. *Angadenia*
- 22. Corolla white, greenish white or cream, sometimes with pink stripes, tubular, urceolate or broadly campanulate, with small v-shaped corona lobes near the base of the tube in the alternistaminal sectors 142. *Apocynum*

- Corolla reddish purple to violet, infundibuliform, with small corona lobes just above the anthers in the staminal sectors **105. *Cycladenia***
- 23. Leaves alternate 24
  - Leaves opposite or verticillate 38
- 24. Corolla lobe aestivation dextrorse in bud; plants succulent or not; seeds either naked or with a well-developed coma at one end 25
  - Corolla lobe aestivation sinistrorse in bud; plants subsucculent or not; seeds almost always without a coma; if hairs present, then these distributed over the seeds and not restricted to one end 27
- 25. Plants succulent; flowers large and showy; fruit a pair of dehiscent follicles; seeds with a coma 26
  - Plants not succulent; flowers small and inconspicuous; fruit a pair of leathery or fleshy berries; seeds without a coma **5. *Geissospermum***
- 26. Plants with spines; anther connective without a long terminal appendage **91. *Pachypodium***
  - Plants without spines; anther connective with a long, hairy apical appendage **84. *Adenium***
- 27. Ovary of 3–5 carpels (Alyxieae-Alyxiinae) 28
  - Ovary of 2 carpels 29
- 28. Carpels long-stipitate, fused at the base and the apex, but free in the middle **65. *Lepinia***
  - Carpels sessile, completely syncarpous **66. *Lepiniopsis***
- 29. Corolla with a corona lobe directly above each anther; sepals mostly large, subfoliaceous, usually spreading or reflexed, sometimes caducous; flowers relatively showy, the corolla tube (7–1)13–33(–55) mm long, white, often with red or yellow markings in the throat or rose-tinged, to cream, bright yellow or salmon-orange; fruit indehiscent (Plumerieae-Thevetiinae) 30
  - Corona absent; sepals usually smaller; flowers showy or not, usually white, rarely with yellow or red markings; fruit dehiscent or indehiscent 32
- 30. Calycine colleters present; nectary disc fleshy, distinct, surrounding the ovary; corolla mostly yellow or orangish, tubular-campanulate, rarely cream-colored and  $\pm$  salverform; fruit drupaceous, red or black **75. *Thevetia***
  - Calycine colleters absent; nectary disc absent, adnate or indistinct; corolla mostly salverform, sometimes slightly subcampanulate above, white to cream (rarely red), sometimes with yellow, red or rose markings in the throat; fruit various 31
- 31. Corolla tube 7–14 mm long; fruit a pair of samaroid drupes with two lateral wings **77. *Cerberiopsis***
  - Corolla tube (15–)20–45 mm long; fruit a fleshy, globose or ovoid drupe **76. *Cerbera***
- 32. Ovary sunken into the receptacle; stamens inserted at the base of the corolla tube; flowers mostly large and showy, often waxy in appearance; calyx lobes small, often rudimentary or caducous; fruit a pair of follicles (Plumerieae-Plumeriinae) 33
  - Ovary not sunken into the receptacle; flowers usually small; stamens inserted in the upper half of the corolla tube; calyx lobes normally developed; fruit various 35
- 33. Floral bracts large, foliaceous, with numerous colleters at the base; calyx rudimentary, persistent, with 1–5 lobes of varying sizes, these eglandular at the apex; seeds normally with a large concentric papery wing **71. *Himatanthus***
  - Floral bracts inconspicuous, scarious, caducous; calyx of 5  $\pm$  equal lobes, these glandular or eglandular at the apex; seeds with a narrow flattened rim around the margin, or if wing present, then not concentric 34
- 34. Petiole with a cluster of 2–3 colleters about midway on the adaxial side; calyx lobes caducous, eglandular at the apex; seeds unwinged, with merely a narrow, flattened rim around the margin **69. *Mortoniella***
  - Petiole without colleters on the adaxial side; calyx lobes persistent, glandular at the apex; seeds with a wing at one end **70. *Plumeria***
- 35. Nectary lobes 2, alternating with the carpels; both carpels developing normally; fruit a pair of long and slender follicles; seeds flattened and with long brown hairs at least at the margins **12. *Laxoplumeria***
  - Nectary absent, adnate or indistinct; normally only one carpel developing; fruit an indehiscent drupe, if dehiscent, then not a pair of long, slender follicles; seeds naked or winged 36
- 36. Fruit dehiscent, a usually compressed, stout follicle with thick, woody pericarp; seeds with a papery concentric or excentric wing; corolla not fused (with short slits) just above stamen insertion; shrubs to big trees up to 40 m tall **6. *Aspidosperma***
  - Fruit indehiscent, drupaceous; seeds naked; corolla tube fused (without slits) above stamen insertion; shrubs or small trees 37
- 37. Leaves coriaceous, oblong to broadly ovate,  $\geq$  4 cm wide; fruit bright red, 5–7 cm long **64. *Pteralyxia***
  - Leaves membranous to subcoriaceous; fruit opalescent, subreniform,  $<$  2 cm long **2. *Vallesia***

38. Leaves whorled, occasionally opposite at some nodes 39  
 – Leaves strictly opposite 57
39. Corolla infundibuliform, large and showy, colorful; fruit syncarpous 40  
 – Corolla salverform, smaller, usually white, cream or yellow, sometimes pinkish; fruit apocarpous (rarely syncarpous) 41
40. Anther connective with a long, filiform, hairy terminal appendage; mouth of the corolla with a dissected petaloid corona; nectary disc absent; leaves coriaceous, ternate; fruit smooth; seeds pubescent with a coma at one end, not flattened **83. Nerium**  
 – Anther without a long hairy appendage; petaloid corona absent; nectary disc present around ovary; leaves thin, usually 4 per whorl; fruit usually with spines; seeds flattened, winged **68. Allamanda**
41. Corolla lobe aestivation dextrorse in bud 42  
 – Corolla lobe aestivation sinistrorse in bud 43
42. Ovules few (up to 6 per carpel); fruit indehiscent, a pair of ovoid to globose, red, yellow or green drupes; pericarp fleshy; seeds without hairs or cilia  
**10. Ochrosia**  
 – Ovules numerous (up to 100 or more); fruit dehiscent, a pair of long, slender, dry, green to brown follicles; seeds with long hairs or cilia around the margins **7. Alstonia**
43. Ovary syncarpous; fruit many-seeded 44  
 – Ovary apocarpous (rarely hemi-syncarpous in some *Tabernaemontana* species); fruit few- to many-seeded 46
44. Petioles with interpetiolar flap of tissue in the axils; fruit indehiscent, a berry **34. Couma**  
 – Petioles without a flap of tissue in the axils; fruit dehiscent, a capsule or two follicles fused along the ventral side 45
45. Leaves with 20–60 pairs of secondary veins; branches terete; stamens inserted in the upper half of the corolla tube; fruit long and cylindrical, of fused follicles, 15–30 cm long **7. Alstonia**  
 – Leaves with 10–20 pairs of secondary veins; branches quadrangular or triangular; stamens inserted near the base of the tube; fruit small and squat, a capsule up to 6 cm long  
**55. Craspidospermum**
46. Ovary 2–5-carpellate; inflorescences ramiflorous, fasciculate, the flowers sessile in the leaf axils; fruit of 2–5 one-seeded berries **60. Pleiocarpa**  
 – Ovary 2-carpellate; inflorescences normally not ramiflorous, the flowers usually pedicillate; fruit of 2 (or sometimes 1 by abortion) follicles or drupes 47
47. Calycine colleters present, in a row at the base of each sepal 48  
 – Calycine colleters absent 49
48. Giant trees; leaves in whorls of 4–8; corolla rotate; seeds surrounded by a membranous wing **8. Dyera**  
 – Shrubs ca. 2 m. tall; leaves in whorls of three with occasional opposite pairs at some nodes; corolla salverform; seeds surrounded by an aril  
**50. Tabernaemontana**
49. Style-head with a membranous collar at the base 50  
 – Style-head without a membranous collar at the base 54
50. Nectaries well-developed, distinct from the ovary 51  
 – Nectaries indistinct, adnate or absent 52
51. Nectaries forming a fleshy ring surrounding the ovary; fruit indehiscent, one-seeded drupes, often only one developing **17. Rauvolfia**  
 – Nectary with 2 conspicuous deltoid to narrowly triangular lobes alternating with the carpels; fruit dehiscent, many-seeded follicles, usually both developing **7. Alstonia**
52. Colleter(s) in the leaf axils deltoid or triangular; leaves in whorls of (3–)4–9; fruit a pair of dehiscent follicles; seeds with long cilia, sometimes more than 1 cm long, at the ends; large trees up to 70 m tall; Africa, Asia and Pacific Islands **7. Alstonia**  
 – Colleters in the leaf axils small, ligulate to linear; leaves in whorls of 3; fruit a pair of drupes or follicles; seeds with cilia or not; shrubs or small trees up to 20 m tall; Central America, Africa, Madagascar, Indian Ocean Islands and Sri Lanka (Vinceae) 53
53. Anthers inserted at about the middle of the corolla tube; fruit a pair of thinly woody follicles; seeds ciliate at the margin; plants of Central America  
**11. Tonduzia**  
 – Anthers inserted just below the orifice of the corolla tube; fruit indehiscent, a pair of fleshy, torulose, red or orange drupes; plants of the Old World  
**15. Petchia**
54. Leaf axils lacking colleters (Aspidospermateae) 55  
 – Leaf axils with colleters 56
55. Leaves less than 5 cm long, with a spine at the tip; corolla glabrous externally; fruit usually a single (through abortion) thick, woody orbicular to broadly obovoid follicle; seeds compressed with a membranous, concentric wing **6. Aspidosperma**  
 – Leaves more than 5 cm long, without a spine at the tip; corolla densely silvery green villous externally;

- fruit a pair of slender cylindrical follicles; seeds cylindrical, unwinged
- 4. *Microplumeria***
56. Ovules attached in 2 rows, 2–6(–7) per carpel; fruit indehiscent, a pair (sometimes only 1 by abortion) of strongly torulose drupes; seeds not compressed; endosperm ruminant
- 67. *Alyxia***
- Ovules attached in more than 2 rows, ca. 20 per carpel; fruit dehiscent, a pair of non-torulose follicles; seeds compressed with a papery wing at one end; endosperm non-ruminant
- 57. *Gonioma***
57. Corolla lobe aestivation dextrorse; anthers often adnate to the style-head; seeds naked or with a coma, rarely with a brightly colored aril
- 58
- Corolla lobe aestivation sinistrorse; anthers mostly free from the style-head; seeds naked, winged, arillate (arils sometimes brightly colored) or, rarely, with a coma
- 75
58. Anthers free from the style-head; fruit apocarpous, rarely partially syncarpous, dehiscent or indehiscent
- 59
- Anthers adnate to the style-head; fruit apocarpous and dehiscent
- 65
59. Colleters absent on the inner surface of the sepals; fruit a pair of drupes (rarely solitary)
- 60
- Colleters present near the base on the inner surface of the sepals; fruit a pair of follicles
- 61
60. Sepals with a colleter just below the apex on the outer surface; disc of 2 well-developed lobes alternating with the carpels,  $\pm$  as high as the carpels or higher; drupes almost always with a hollow spur-like appendage
- 9. *Kopsia***
- Sepals without a colleter on the outer surface; disc absent or of 2 tiny rudimentary lobes alternating with the carpels and much shorter than them; drupes without a spur-like appendage
- 10. *Ochrosia***
61. Colleters centered at the base of the sepals on the inner surface; seeds arillate, without a coma
- 62
- Colleters few, in the sepal sinuses corresponding to the quincuncial pattern; seeds with a coma, aril absent
- 64
62. Inflorescences pendent; calycine colleters 5–30 per sepal in 2–4 rows; corolla infundibuliform
- 43. *Callichilia***
- Inflorescences erect; calycine colleters 1–several in a single row
- 63
63. Petiole bases of a leaf pair fused into a short ocrea around the node; corolla white, the tube 17–36 mm long; plants of SW India
- 50. *Tabernaemontana***
- Petiole bases of a leaf pair not forming an ocrea; corolla yellow to cream-yellow, the tube 4–5 mm long; plants of tropical C and E Africa and the Comoro Islands
- 48. *Schizogygia***
64. Corolla infundibuliform, the tube 17–35 cm long; nectary of 2 well-developed lobes alternating with the carpels
- 92. *Spirolobium***
- Corolla salverform, tube 9–22 mm long; nectary absent
- 96. *Holarrhena***
65. Nectaries absent or adnate or indistinct from the base of the ovary
- 66
- Nectaries present, of 2 or 5 lobes at the base of the ovary
- 68
66. Corolla infundibuliform to subcampanulate; petaloid corona present in the corolla mouth; petals often caudate; seeds with a rostrate coma
- 85. *Strophanthus***
- Corolla salverform or narrowly tubular-campanulate; petaloid corona absent; petals not caudate; seed coma sessile or absent (Malouetieae-Malouetiinae)
- 67
67. Anthers with lignified basal appendages; seeds without a coma
- 100. *Malouetiella***
- Anthers without lignified basal appendages; seeds with a sessile coma
- 96. *Holarrhena***
68. Nectaries 2, distinct, alternating with the carpels; small shrubs up to 2 m
- 92. *Spirolobium***
- Nectaries 5, separate or fused at the base into a ring surrounding the carpels; mostly trees, more rarely shrubs
- 69
69. Calycine colleters solitary, centered at the base of the sepals; anthers completely exerted from the corolla tube; Amazonia
- 119. *Hylaea***
- Calycine colleters mostly few in the sinuses or few to many in a ring at the base of the sepals or rarely absent; anthers included to exerted; tropics of the Old and New World and South Pacific (Malouetieae)
- 70
70. Inflorescences bostrychoid cymes or reduced to a solitary flower; leaves without domatia; colleters absent or much reduced, rarely few and alternisepalous; nectaries separate or connate just at the base; seeds with sessile coma at the micropylar end; plants of the West Indies
- 90. *Neobracea***
- Inflorescences usually in alternate leaf axils and  $\pm$  fasciculate, subsessile or shortly pedunculate; leaves often with abaxial domatia in the axils of the secondary veins; calycine colleters few and alternisepalous or several to many in a ring; nectaries fused into a 5-lobed ring; seeds with coma at one end, at both ends or without a coma and seed body naked or with a sparse scattering of hairs or a thick indument of long hairs; plants of the tropics in Africa, Asia,



- America and the Solomon Islands (Malouetieae-Malouetiinae) 71
71. Corolla lobes induplicate in bud, the margins often long-ciliate or crispate; seeds with a well-developed sessile micropylar coma and a small deciduous chalazal coma; domatia absent **95. Mascarenhasia**
- Corolla lobes not induplicate in bud, the margins not long-ciliate or crispate; seeds either without a coma or with a chalazal coma only; abaxial domatia often present in axils of secondary veins 72
72. Seeds with a rostrate chalazal coma with retrorse hairs; testa almost always glabrous; calycine colletes few and alternisepalous or up to 100 in a ring; plants of tropical Africa and Asia 73
- Seeds without a coma; testa glabrous to densely velutinous or villous; calycine colletes few and alternisepalous; plants of tropical Africa, America and the South Pacific 74
73. Corolla thick and fleshy, salverform, the tube constricted at the orifice; anthers completely included; plants of tropical Africa **101. Funtumia**
- Corolla mostly thinner, membranous, the tube usually with a narrow cylindrical lower part and an expanded cupular upper part (tubular-campanulate); anthers included to nearly completely exerted; plants of SE Asia and Malesia **98. Kibatalia**
74. Leaves mostly with abaxial domatia in the axils of the secondary veins; small bifid corona lobe present behind each anther; anthers included to nearly completely exerted; seed body naked, very sparsely pilose or densely velutinous to villous; plants of the American and African tropics, often growing in white sand and/or blackwater habitats and seasonally inundated forest **97. Malouetia**
- Leaves without abaxial domatia; corona lobes absent; anthers included; testa glabrous; plants endemic to the Solomon Islands, growing in well-drained forest **99. Allowoodsonia**
75. Anthers adnate to the style-head; petaloid or much dissected corona normally present in the corolla mouth; seeds with a sessile chalazal coma; plants of the Old World (Wrightieae) 76
- Anthers free from the style-head; petaloid or dissected corona usually absent; seeds without a coma; plants of the Old and New Worlds 78
76. Corona bright yellow, of two sorts of lobes, the alternipetalous ones of 3–4 filiform segments on a long, slender stalk; inflorescences multi-flowered panicles with many simultaneously open flowers, often thyrsoid **81. Pleioceras**
- Corona variously colored, entire, crenulate, or lobed in various ways, rarely on long, slender stalks; inflorescences usually few-flowered, or if multi-flowered usually with only few open flowers or, if multi-flowered and many simultaneously open flowers, then never thyrsoid and corona either absent or united into a cup 77
77. Flower resembling a miniature daffodil; corolla yellow; corona white, the lobes united for nearly their entire length into a crenulate cup much surpassing the anthers **80. Stephanostema**
- Flower not daffodil-like; corona and corolla variously colored, sometimes concolorous; corona lobes either free or united to varying degrees, if forming a cup around the anthers this only short **82. Wrightia**
78. Anthers with lignified, sagittate basal appendages; fruit an indehiscent berry with naked seeds, or a pair of follicles (these sometimes partially to nearly completely fused) and seeds mostly arillate (Tabernaemontaneae) 79
- Anthers simple, ovate or, if sagittate at base, then not lignified; fruit various; seeds not arillate (except in some species of *Tabernaemontana*) 94
79. Corolla infundibuliform to tubular-campanulate; calyx lobes often foliaceous 80
- Corolla salverform; calyx lobes foliaceous or not 84
80. Corolla small, white with red stripes, the tube up to 10 mm long **47. Carvalhoa**
- Corolla large, yellow, cream, white, or rarely orange or mauve, not striped, the tube 11–135 mm long 81
81. Bracts very large, 4–11 cm long, completely covering the calyx; inflorescences long-pedunculate, of 1–2 large, white pendulous flowers **46. Crioceras**
- Bracts smaller, never completely covering the calyx; inflorescences various 82
82. Corolla yellow, cream, white or orange, the tube almost always twisted at the level of the anthers, the lobes inflexed in bud; style-head with a basal flange **50. Tabernaemontana**
- Corolla white, the tube not twisted at the level of the anthers, lobes not (or only scarcely) inflexed in bud; style-head almost always without a basal flange 83
83. Peduncle very short, up to 2 mm long; calycine colletes few or absent; fruit 2/3 or more syncarpous **45. Calocrater**

- Peduncle longer, 5–230 mm long; calycine colleters several, multiseriate; fruit usually apocarpous (except in *C. orientalis*) **43. Callichilia**
- 84. Style-head shed with the corolla; sepals often united for up to 2/3 their length into a tubular, circumscissile calyx; petals not inflexed in bud **44. Voacanga**
  - Style-head not shed with the corolla; sepals usually free or united for less than 2/3 their length and not forming a circumscissile calyx; petals inflexed in bud or not 85
- 85. Ovary completely syncarpous; fruit a berry; seeds arillate or not 86
  - Ovary apocarpous, sometimes partially syncarpous; fruit usually a pair of follicles (rarely these partially to nearly totally fused); seeds arillate or covered in a translucent membrane 92
- 86. Nectary disc present; seeds with a white aril; plants of the tropical W and C Africa **49. Tabernanthe**
  - Nectary disc absent; plants of Amazonia (Tabernaemontanae-Ambelaniinae) 87
- 87. Calycine colleters present 88
  - Calycine colleters absent 91
- 88. Corolla tube completely glabrous within, short (3–9 mm); fruit few-seeded, with thin pericarp; seeds embedded in fluffy white pulp **37. Molongum**
  - Corolla tube pilose within in some regions, short to long (3.5–50 mm); fruit few- to many-seeded, with a thick or thin and leathery or crustaceous pericarp; seeds embedded in pulp or not 89
- 89. Calycine colleters in a single series; corolla tube 10–30 mm long; fruit unilocular; seeds not embedded in pulp, attached to the fruit wall by fleshy funicles **38. Spongiosperma**
  - Calycine colleters multiseriate; corolla tube 3.5–15 mm long; fruit bilocular; seeds embedded in stringy pulp 90
- 90. Inflorescences axillary; young stems compressed; peduncles mostly reduced; fruit many-seeded, with a thick, granular pericarp **40. Mucoa**
  - Inflorescences terminal; young stems terete; peduncles elongate; fruit few- to many-seeded, with thin crustaceous pericarp **41. Neocouma**
- 91. Inflorescences axillary; young stems ± terete; seeds not embedded in pulp, attached to fleshy funicles **36. Ambelania**
  - Inflorescences terminal; young stems sharply quadrangular; seeds embedded in reddish pulp **39. Rhigospira**
- 92. Ovary pubescent; fruit indehiscent with a thick, somewhat indurated pericarp; usually only one carpel developing, with the rudimentary second carpel present at the base, sometimes both carpels developing, these often partially syncarpous; seeds covered in a translucent membrane that liquefies when the fruit is mature; plants of Amazonia and southern Central America **42. Macoubea**
  - Ovary glabrous; fruit almost always dehiscent (sometimes only tardily so, very rarely indehiscent), with a thick or thin, non-indurated pericarp; both carpels usually developing, or, if only one, then not with the second rudimentary carpel attached at the base 93
- 93. Petals not inflexed in bud; calycine colleters single in the sepal sinuses; nectary distinct; fruit completely apocarpous to partly syncarpous; aril white **49. Tabernanthe**
  - Petals inflexed in bud; calycine colleters mostly in groups (occasionally multiseriate) in the center of the sepal; nectary indistinct, adnate or absent; fruit apocarpous; aril red, orange, white or gray **50. Tabernaemontana**
- 94. Ovary syncarpous; fruit a solitary berry 95
  - Ovary apocarpous (sometimes partially syncarpous at the base); fruit dehiscent or indehiscent, various 100
- 95. Calyx usually 4-merous **32. Parahancornia**
  - Calyx 5-merous 96
- 96. Corolline corona present in throat **56. Melodinus**
  - Corona absent in throat 97
- 97. Inflorescences terminal, few-flowered; ovules numerous; fruit up to 5 cm in diameter, pubescent or not 98
  - Inflorescences axillary, few- to many-flowered; ovules few to numerous; fruit smaller, glabrous 99
- 98. Corolla tube > 2 cm long; anthers inserted near the orifice of the corolla tube; fruit glabrous to pubescent, 1–6-seeded **33. Hancornia**
  - Corolla tube to 1 cm long; anthers inserted in the lower 1/3 of the corolla tube; fruit densely velutinous, many-seeded **26. Ancylobothrys**
- 99. Ovary with several ovules per placenta; fruit yellow to orange; plants of the Neotropics **35. Lacmellea**
  - Ovary with 1 ovule per locule; fruit black to purplish black; plants of Africa **78. Acokanthera**
- 100. Calycine colleters present, mostly in a group in the center of the sepal, sometimes in multiple series 101
  - Calycine colleters absent 103
- 101. Calycine colleters covering 1/3 or more of the adaxial surface of the sepals; ovules 1–6(–30) per carpel; fruit indehiscent, 1–9(–20)-seeded berries **58. Hunteria**

- Calycine colleters usually covering less than 1/3 of the adaxial surface of the sepals, typically in a single row at the base; ovules 70–150 per carpel; fruit dehiscent or indehiscent, 10–80 seeded 102
- 102. Fruit dehiscent, 2 follicles (these rarely partially syncarpous or indehiscent) with a fleshy, thin or thick, but not hard and fibrous, wall; seeds arillate; plants of tropical Africa, S and SE Asia and S and South West Pacific 50. *Tabernaemontana*
- Fruit indehiscent, 2 berries with a very hard and fibrous wall, sometimes only one developing; seeds without arils; plants of tropical W and C Africa 59. *Picralima*
- 103. Anthers with sublateral dehiscence and filiform apical appendages; corolla tube with small appendages below the anthers (Plumerieae-Thevetiinae) 104
- Anthers with introrse dehiscence, without filiform apical appendages; corolla tube without small appendages below the anthers 105
- 104. Flowers yellow; ovules 40–70 in several series in each carpel; fruit a pair of long, slender corkscrew-like, several-seeded follicles; plants of Brazil and Chile 74. *Skytanthus*
- Flowers white; ovules 2–6 in 2 series in each carpel; fruit a pair of strongly compressed, single-seeded samaroid drupes; plants of the Greater Antilles and Central America 72. *Cameraria*
- 105. Nodes without intrapetiolar or interpetiolar colleters; fruit normally consisting of a single, thick, woody pyriform to nearly circular follicle; seeds with a membranous, concentric wing; plants of the Neotropics 6. *Aspidosperma*
- Nodes with intrapetiolar and/or interpetiolar colleters; fruit and seeds various; plants of the Paleotropics and Oceania (except *Strempeleopsis*) 106
- 106. Colleters in the leaf axils deltoid or triangular; seeds with long cilia at least at each end, usually also around the margin 7. *Alstonia*
- Colleters in the leaf axils small, ligulate to linear; seeds without cilia 107
- 107. Inflorescences ramiflorous, the flowers in sessile fascicles in the leaf axils; ovary (2–)3–5-carpellate; fruit of (2–)3–5 separate, few-seeded, yellow to bright orange berries 60. *Pleiocarpa*
- Inflorescences normally with a distinct peduncle; ovary always 2-carpellate; fruit follicles or drupes, never berries 108
- 108. Ovules 2–4(–7) per carpel; style-head without a basal collar 109
- Ovules up to 20 per carpel; style-head with or without a basal collar 110
- 109. Corolla tube 1.5–3 mm long, shorter than the lobes; petioles usually 1–2 cm long; ovules 4 per carpel; fruit of 2 follicles less than 5 cm long; seeds compressed with a wing at one end 52. *Diplorhynchus*
- Corolla tube 1.5 mm or longer, almost always noticeably longer than the lobes; petioles often less than 1 cm long; ovules up to 7 per carpel; fruit indehiscent, of a pair of strongly torulose drupes with 1–7 articles; seeds ellipsoid (not compressed) and unwinged 67. *Alyxia*
- 110. Style-head with free apical appendages longer than the body; corolla tube with visible slits just above stamen insertion and a callous ring in the mouth; fruit dehiscent, a pair of non-compressed follicles; seeds with a thin wing around the margin 54. *Stephanostegia*
- Style-head with free apical appendages shorter than the body; corolla tube without visible slits, with or without a callous ring in the mouth; fruit and seeds various 111
- 111. Style-head with a short collar at the base; corolla tube with a callous ring in the mouth; fruit indehiscent, a pair of torulose, red or orange drupes; seeds without a wing 15. *Petchia*
- Style-head without a collar at the base; corolla tube without a callous ring in the mouth; fruit dehiscent, a pair of non-torulose follicles; seeds winged 112
- 112. Seeds with a wing at each end; leaf blades 6–16 × 2–7 cm, obovate to oblong-obovate; peduncles up to 11 cm long; plants of Jamaica and Cuba 1. *Strempeleopsis*
- Seeds with a wing at one end; leaf blade 2.5–12 × 0.5–3 cm, narrowly elliptic to oblong-elliptic; peduncles up to 1 cm long; plants of southern Africa or Madagascar 57. *Gonioma*
- 113. Plants with paired, often branched spines in the axils 79. *Carissa*
- Plants without paired spines in the axils 114
- 114. Leaf blades adaxially with colleters clustered at the base of the midrib (these sometimes caducous) or scattered along its length, or sometimes colleters scattered along the length of the petiole (colleters in the axil of the petiole absent or present), abaxial domatia often present in axils of secondary veins; anthers adnate to the style-head; seeds with a coma 115
- Leaf blades and petioles adaxially without colleters (but colleters in the axil of the petiole often present), usually without abaxial domatia, more rarely present; anthers free from the style-head or adnate to it; seeds with or without a coma 122

115. Ovary half-inferior; leaf blades adaxially with colleters scattered along the petiole, with hair-filled or cilia-rimmed abaxial domatia in the axils of the secondary veins; corolla tube 1–6 mm long, with small knob-like corona lobes in the mouth or above the anthers; plants of Africa and Madagascar (Baisseeae) 116
- Ovary superior; leaf blades adaxially with colleters clustered at the base of the midrib or with colleters scattered along the length of the midrib, but not along the length of the petiole; abaxial domatia mostly absent, if present then usually glabrous; corolla tube often longer than 6 mm and without knob-like corona lobes; plants of the Neotropics (Mesechiteae) 118
116. Anthers with an enlarged apical connective appendage covered with coarse hairs; inflorescences terminal 153. *Motandra*
- Anthers without an enlarged hairy apical connective appendage; inflorescences axillary and terminal 117
117. Corolline corona present in the mouth of the corolla tube consisting of 5 alternipetalous lobes; corolla mouth usually constricted 155. *Oncinotis*
- Corolline corona present below the mouth of the corolla tube consisting of 5 alternipetalous lobes, one just behind each anther; corolla tube mouth not constricted 154. *Baissea*
118. Inflorescences simple, unbranched (racemose); colleters scattered along the length of the midrib adaxially or clustered at its base 117. *Mandevilla*
- Inflorescences branched 2–3 times (corymbose or dichasial cymes or thyrses); colleters clustered at the base of the midrib only 119
119. Leaves mostly with abaxial domatia in at least some axils of the secondary veins; stamens almost always inserted at the base of the corolla tube, with well-developed filaments 120
- Leaves without abaxial domatia; stamens inserted higher in the corolla tube, often just at the base of the expanded upper part; stamens without a well-developed filament, anthers  $\pm$  sessile 121
120. Corolla infundibuliform to tubular-campanulate, the tube  $>$  1 cm long; anthers with pubescent, filiform apical appendages; staminal filaments 10–30 mm long (or if without filiform apical appendages and long staminal filaments, then corolla tube  $>$  2 cm long); anthers included or only apical appendages exerted 115. *Tintinnabularia*
- Corolla tubular to subcampanulate or rotate, the tube  $<$  3 mm long; anthers without filiform apical appendages; staminal filaments  $\leq$  2 mm long; anthers mostly  $\pm$  completely exerted from the corolla tube 116. *Forsteronia*
121. Corolla salverform 114. *Mesechites*
- Corolla infundibuliform 113. *Allomarkgrafia*
122. Leaves verticillate, sometimes opposite at some nodes 123
- Leaves strictly opposite 133
123. Corolla lobe aestivation dextrorse in bud; anthers united with the style-head; fruit dry; seeds with a coma 124
- Corolla lobe aestivation sinistrorse in bud; anthers free from the style-head; fruit dry or fleshy; seeds mostly without a coma 127
124. Petaloid corolline corona present in the throat; petals often with a caudate appendage at the apex; seeds with a rostrate coma 85. *Strophanthus*
- Petaloid corona absent; petals never with caudate appendages; seed coma sessile 125
125. Flowers small, the corolla tube tubular to urceolate or  $\pm$  rotate and almost always  $<$  10 mm long; knob-like corona lobes present or absent; anthers usually at least partially exerted; ovary and fruit syncarpous; filiform, stipule-like outgrowths absent 126
- Flowers larger, the corolla tube salverform, 10–15 mm long; knob-like corona lobes absent; anthers included; ovary and fruit apocarpous; long, filiform stipules present 108. *Odontadenia*
126. Knob-like corolline corona lobe present just above each anther 130. *Artia*
- Knob-like corolline corona lobes absent 129. *Parsonsia*
127. Petaloid corona present in the corolla mouth; ovary syncarpous; fruit a hard-walled solitary berry 56. *Melodinus*
- Petaloid corona absent; ovary apocarpous; fruit berries, drupes or follicles 128
128. Sepals with multiple rows of colleters at the base within; fruit a pair of berries 58. *Hunteria*
- Sepals without colleters within; fruit various 129
129. Corolla lobes with a long ligulate appendage; fruit a pair of indehiscent, torulose drupes 62. *Condylocarpon*
- Corolla lobes without a long ligulate appendage; fruit dehiscent or indehiscent, berries, drupes or follicles 130
130. Corolla campanulate, the tube up to 2 mm long, ca. 1/3 the length of the lobes; anthers with a short sterile apex and sagittate (but non-lignified) base; seeds with a concentric papery wing 53. *Pycnobotrya*

- Corolla salverform to tubular, the tube up to 22 mm long, usually longer than the lobes; anthers without sterile apex and sagittate base; seeds various 131
- 131. Carpels usually 3–5, rarely only two; fruit 1-seeded, subglobose to ovoid berries **60. *Pleiocarpa***
  - Carpels 2; fruit follicles or drupes 132
- 132. Corolla tube curved; fruit dehiscent, a pair of slender cylindrical follicles (usually both carpels developing); mesocarp dry; seeds compressed, with a wing at each end; carpels conspicuously notched at the apex **14. *Kametitia***
  - Corolla tube straight; fruit indehiscent, carpels forming torulose chains of up to 7 articles, sometimes reduced to a single article (often only 1 carpel developing); mesocarp fleshy; seeds naked, globose to ovoid, not compressed; carpels not conspicuously notched at the apex **67. *Alyxia***
- 133. Stoloniferous herbs; flowers 1 (rarely 2) in the axils; corolla usually bluish violet, occasionally white; nectary lobes 2, alternating with the carpels **13. *Vinca***
  - Woody plants without stolons; inflorescence type, number of flowers and corolla color various; nectaries absent or present 134
- 134. Leaves peltate; seeds with the coma at the end of a glabrous rostrum 135
  - Leaves not peltate; seed coma rostrate or not 136
- 135. Corolla infundibuliform, usually yellow to green; plants mostly with ferruginous pubescence; calyx lobes foliaceous to subfoliaceous, up to 3 cm long **122. *Macropharynx***
  - Corolla salverform, pinkish; plants glabrous; calyx lobes smaller, not foliaceous,  $\leq 2$  mm long **106. *Stipecoma***
- 136. Corolla lobe aestivation sinistrorse; anthers mostly free from the style-head, more rarely adnate to the style-head; fruit various, often syncarpous and indehiscent 137
  - Corolla lobe aestivation dextrorse or valvate; anthers adnate to the style-head (sometimes only weakly so); fruit usually apocarpous, of 2 follicles (these sometimes postgenitally syncarpous and weakly to firmly fused) (Apocynoids) 164
- 137. Anthers adnate to the style-head; fruit a pair of follicles; seeds with a coma **143. *Urceola***
  - Anthers free from the style-head; fruit usually berries, less frequently drupes or follicles; seeds without a coma (Rauvolfioids) 138
- 138. Corolla 4-merous; leaves punctate abaxially **19. *Leuconotis***
  - Corolla 5-merous; leaves punctate abaxially or not 139
- 139. Corolline corona present in the corolla mouth; ovary syncarpous **56. *Melodinus***
  - Corolline corona absent; ovary apocarpous or syncarpous 140
- 140. Anthers with sterile, sagittate, lignified bases and guide rails; calycine colleters present or absent (Tabernaemontaneae-Tabernaemontaninae) 141
  - Anthers without sterile sagittate bases and guide rails, or, if present, then not lignified; calycine colleters mostly absent 142
- 141. Corolla infundibuliform; stamens inserted in the upper part of the corolla tube; nectary disc present **43. *Callichilia***
  - Corolla salverform; stamens inserted near the base of the corolla tube; nectary disc adnate or indistinct **50. *Tabernaemontana***
- 142. Ovary syncarpous; fruit mostly berries, rarely capsules 143
  - Ovary apocarpous (rarely partially syncarpous at the base); fruit various 158
- 143. Corolla infundibuliform to tubular-campanulate, bright yellow or purple, the tube  $> 3.5$  cm long; nectary disc well-developed; fruit a dry (usually spiny) capsule; seeds with a concentric wing or flattened margin; pollen colporate **68. *Allamanda***
  - Corolla tube salverform, smaller; mostly cream or white, greenish white or pale yellow or orange; nectary disc absent or present; fruit dehiscent or indehiscent, but never a spiny capsule; seeds and pollen various 144
- 144. Plants with grappling tendrils often formed from modified inflorescences (Willughbeieae) 145
  - Plants without tendrils 155
- 145. Calycine colleters numerous, 3–5-seriate across the base of the sepals **24. *Vahadenia***
  - Calycine colleters absent or, more rarely, few in the sepal sinuses 146
- 146. Inflorescences terminal, laxly branched, with an elongate peduncle and flowers  $\pm$  sessile 147
  - Inflorescences axillary or terminal, often short-pedunculate and congested and appearing fasciculate, sometimes with longer peduncles 150
- 147. Ovary pubescent 148
  - Ovary glabrous 149
- 148. Anthers dorsally with 2 vertical ridges (keeled); fruit velutinous on the outer surface; plants of tropical Africa, Madagascar and the Comoro Islands **26. *Ancylobothrys***
  - Anthers dorsally without vertical ridges (unkeeled); fruit glabrous on the outer surface; plants of the

- Guianas, Amazonian Brazil and Bolivia
- 30. *Pacouria***
149. Corolla lobes with hairs 1.2–5 mm long on the margin that is covered in bud; plants of Africa
- 25. *Dictyophleba***
- Corolla lobes either completely glabrous or with only short cilia on the margin; plants of Indomalaysia
- 21. *Willughbeia***
150. Anthers with a dorsal ridge (keeled); wall of the corolla tube not thickened above the level of stamen insertion; secondary veins 16–32 pairs, closely spaced
- 29. *Orthopichonia***
- Anthers without a dorsal ridge (not keeled); wall of the corolla tube thickened above the level of stamen insertion or not; secondary veins typically 5–9(–19) pairs, more widely spaced 151
151. Corolla tube thickened above the level of stamen insertion
- 31. *Landolphia***
- Corolla tube not thickened above the level of stamen insertion 152
152. Inflorescences terminal only
- 28. *Saba***
- Inflorescences mostly axillary, sometimes also terminal 153
153. Endosperm thin (less than 1 mm); cotyledons thick (2–3 mm), cartilaginous; plants of Asia and Africa 154
- Endosperm thick (ca. 20 mm), cartilaginous; cotyledons thin (ca. 0.2 mm); plants of Africa
- 23. *Clitandra***
154. Ovary glabrous; plants of Indomalaysia
- 21. *Willughbeia***
- Ovary pubescent; plants of Nigeria and C Africa
- 22. *Cylindropsis***
155. Nectary disc present, a fleshy ring surrounding the base of the ovary; calycine colleters usually present; each placenta with 1–6 ovules; pollen colpore 156
- Nectary disc absent, adnate or indistinct; calycine colleters absent; each placenta normally with numerous ovules; pollen porate 157
156. Nectary disc up to half as high as the ovary; inflorescences axillary cymes; seeds not compressed, embedded in pulp; plants of SE Asia and southern China
- 18. *Bousigonia***
- Nectary disc higher than the ovary; inflorescences terminal thyrses; seeds compressed, not embedded in pulp; plants of W and C Africa
- 20. *Cyclocotyla***
157. Leaves usually punctate beneath; corolla lobes strongly inflexed in bud; fruit fleshy, nearly berry-like at first, becoming leathery to dry at maturity and splitting open on at least one side; seeds angular to ovoid, not compressed, with a pulpy to corky aril on the funicle
- 61. *Chilocarpus***
- Leaves not punctate beneath; corolla lobes not inflexed in bud; fruit a dry, usually winged or strongly ribbed septicidal capsule; seeds compressed, with a wing at each end
- 63. *Plectaneia***
158. Leaves with recurved hairs with multicellular bases on the adaxial surface; nectar disc present; fruit a pair of 1-seeded drupes with short recurved hairs
- 73. *Anechites***
- Leaves without recurved hairs; nectary disc absent or indistinct; fruit various, but never with recurved hairs 159
159. Calycine colleters present, covering at least 1/3 of the inner surface of the sepal; fruit a pair of berries
- 58. *Hunteria***
- Calycine colleters absent; fruit various, dehiscent or indehiscent 160
160. Carpels 3–5, with 2 ovules each; inflorescences ± sessile, mostly axillary; corolla tube 10–22 mm long; fruit of 3–5 berries
- 60. *Pleiocarpa***
- Carpels 2, with 2–16 ovules each; inflorescences various; corolla tube mostly ≤ 10 mm long; fruit dehiscent or indehiscent, a capsule or a pair of follicles or drupes 161
161. Leaves abaxially with numerous black dots; secondary veins numerous, ± straight and inconspicuous; anthers with sterile apical appendage and sagittate base; fruit a pair of obliquely ovoid, compressed follicles; seeds with a concentric wing
- 53. *Pycnobotrya***
- Leaves abaxially without black dots; secondary venation various; anthers without sterile apical appendage and sagittate base; fruit a pair of drupes or a capsule (Alyxieae) 162
162. Corolla lobes inflexed in bud, sometimes with a ligulate appendage on one margin; fruit a pair of woody indehiscent drupes (sometimes only a single carpel developing); pollen seemingly inaperturate, in tetrads at maturity
- 62. *Condylocarpon***
- Corolla lobes not inflexed in bud, without a ligulate appendage; fruit drupaceous or capsular; pollen 2–3-porate, in single grains at maturity 163
163. Ovary glabrous; ovules 10–16 per carpel; fruit a single dry, septicidal capsule; seeds compressed, with a wing at each end; endosperm not ruminant
- 63. *Plectaneia***
- Ovary glabrous or pubescent; ovules 2–7 per carpel; fruit a pair of fleshy torulose drupes with 1–7 articles each (sometimes only one carpel developing)
- 67. *Alyxia***

164. Nectary absent; latex often translucent (Nerieae-Alafiinae) 165  
 – Nectary present; latex mostly white, sometimes translucent or other colors 168
165. Petaloid corona present in the corolla mouth; seed coma rostrate with long hairs also along the rostrum **85. *Strophanthus***  
 – Petaloid corona not present in the corolla mouth; seed coma rostrate or not 166
166. Stamens inserted in the mouth of the corolla, with distinct filaments, the anthers almost completely exerted; style-head with a membranous basal collar **86. *Isonema***  
 – Stamens inserted at various levels in the corolla tube, the filaments very short, the anthers  $\pm$  sessile, completely included or just the apices exerted; style-head without a basal collar 167
167. Style filiform, tuberculate, not enlarged at the apex; corolla tube 10–21 mm long, the lobes without conspicuous cilia at the margin; follicles rust-brown puberulent on the outer surface; chalazal coma present **88. *Farquharia***  
 – Style rather thick and enlarged at the apex, not tuberculate; corolla tube mostly 4–11 mm (rarely up to 21 mm) long, the lobes often conspicuously ciliate at the margin; follicles glabrous on the outer surface; chalazal coma absent **87. *Alafia***
168. Carpels postgenitally united; fruit syncarpous, of two follicles fused (sometimes only weakly so) along their ventral margins, which split apart at or near maturity 169  
 – Carpels free; fruit apocarpous, of 2 separate follicles, each of which dehisces along its ventral margins 180
169. Anthers dorsally with a rounded hump-like swelling at the base (corona) **138. *Vallaris***  
 – Anthers dorsally without a rounded swelling 170
170. Corolla infundibuliform to tubular-campanulate, usually relatively large and showy, mostly > 2.5 cm long 171  
 – Corolla salverform, tubular, urceolate or rotate (if campanulate, then the corolla tube < 1 cm long), often small and inconspicuous, sometimes larger and showy (Echiteae) 174
171. Anthers exerted or included, filaments 1–6 cm long; corolla tube up to 13 cm long **139. *Beaumontia***  
 – Anthers included, filaments usually shorter; corolla tube less than 10 cm long 172
172. Calycine colleters solitary and centered at the base of each sepal; latex translucent  
 – Calycine colleters alternisepalous, singly or in groups, or spread  $\pm$  irregularly in a ring around the base of the calyx; latex white; corolla tube pubescent on the outer surface (Apocynae) 173
173. Corolla lobes 1/5 to 1/7 the length of the corolla tube; calycine colleters in a ring around the base of the calyx; ovary superior, glabrous; style-head with a basal collar; fruit at maturity with corky warts, velvety pubescent **147. *Amalocalyx***  
 – Corolla lobes longer than 1/5 the length of the corolla tube; calycine colleters few, alternisepalous; ovary partly inferior to inferior, pubescent; style-head without a basal collar; fruit at maturity smooth, without corky warts, not velvety pubescent **140. *Parepiginum***
174. Corolla salverform, the tube at least 9 mm long, with an uninterrupted thickened annulus in the throat **131. *Prestonia***  
 – Corolla rotate, tubular, urceolate or campanulate, the tube less than 9 mm long, without a thickened annulus in the throat, or if annulus present, then deeply divided, of a ring of linear-lanceolate lobes 175
175. Upcurved knob-like corona lobes present just above anthers **130. *Artia***  
 – Upcurved knob-like corona lobes absent 176
176. Orifice of the corolla tube with ring of linear-lanceolate corona lobes **124. *Thoreauea***  
 – Orifice of the corolla tube without a ring of corona lobes 177
177. Inflorescences umbelloid, the showy flowers clustered at the ends of long peduncles; corolla and ovary completely glabrous; plants of Mexico **123. *Thenardia***  
 – Inflorescences mostly branched several times, usually not umbelloid, or if the small flowers clustered at the end of long peduncles, then ovary pubescent or corolla pubescent either on inner or outer surface; plants of the Old World 178
178. Anthers partially to completely exerted from the corolla tube **129. *Parsonsia***  
 – Anthers included within the corolla tube 179
179. Corolla urceolate, glabrous in the throat; stamens inserted in the corolla throat, the filaments curving downward and then back up **128. *Ecua***  
 – Corolla mostly tubular, cylindrical rotate or salverform, mostly with hairs in a ring or in patches in the throat; stamens inserted at various levels in the corolla tube, the filaments straight or upcurved, sometimes strongly geniculate or twisted **129. *Parsonsia***
- 120. *Temnadenia***

180. Pedicels with more than 2 bracts; plants usually with an indument, pubescent to hirsute or strigillose; inflorescences not or scarcely branched 181  
 – Pedicels with 0–2 bracts; plants glabrous or with an indument; inflorescences various 182
181. Corolla campanulate, the tube 6–9 mm long; inflorescences 1–3-flowered; calycine colleters absent; seed coma sessile 112. *Elytropus*  
 – Corolla salverform to subinfundibuliform, the tube 10–80 mm long; inflorescences up to 20-flowered; calycine colleters solitary, centered at the base of the each sepal adaxially; seed coma rostrate 122. *Macropharynx*
182. Anthers partially to completely exerted from the corolla tube 183  
 – Anthers included within the corolla tube 191
183. Anther connective with a long filiform apical appendage; upper expanded part of the corolla much longer than the narrow cylindrical basal part; seed coma rostrate 111. *Pentalinon*  
 – Anther connective without a long filiform apical appendage; ratio of upper and lower part of the corolla tube various; seed coma sessile or rostrate 184
184. Staminal filaments distinct; calycine colleter arrangement various, sometimes obscure or absent 185  
 – Staminal filaments scarcely developed, the anthers  $\pm$  sessile; calycine colleters present, several in a row across the base of the calyx abaxially 190
185. Corolla rotate, tube  $\leq$  3 mm long; anthers conspicuously exerted on long, slender filaments 186  
 – Corolla tube salverform or tubular at the base with a slightly expanded upper cupular part, usually  $>$  3 mm long 187
186. Staminal filaments not coiled, fused around the style for at least some of their length; calycine colleters present at the margins of the sepals; abaxial domatia often present in the axils of the secondary veins of the leaves 103. *Pinochia*  
 – Staminal filaments tightly coiled around the style, but not fused; calycine colleters absent; abaxial domatia absent 156. *Dewevrella*
187. Corolla with a thickened annular corona present in the mouth and/or with a finger-like corona lobe just above each anther; style without swollen section; plants of the Neotropics 188  
 – Corolla without a thickened annular corona in the mouth or a finger-like corona lobes; section of style distinctly swollen; plants of the Paleotropics 149. *Pottsia*
188. Annular corona absent; finger- or knob-like corona lobes present on the corolla just above stamen insertion; anthers completely to partially exerted 119. *Hylaea*  
 – Annular corona present in the corolla tube mouth; finger- or knob-like free corona lobes just above anther insertion present or absent; only the apices of the anthers exerted 189
189. Sepals each with a solitary colleter in the center at the base adaxially 131. *Prestonia*  
 – Sepals without colleters 118. *Laubertia*
190. Style-head with a turbinate, upturned cup-like lower part; anthers barely exerted from corolla tube 146. *Micrechites*  
 – Style-head without an upturned cup-like lower part; anthers distinctly exerted from corolla tube 145. *Trachelospermum*
191. Nectary of 2 separate lobes alternating with the carpels; stamens inserted in the lower 1/5 of the corolla tube 93. *Carruthersia*  
 – Nectary of 5 free lobes or these fused to varying degrees into an annular nectary disc, this often crenate or lobed; stamens inserted at various levels 192
192. Corolla infundibuliform to tubular-campanulate, (1.5–)2.5–4.5(–6) cm long, large and showy; plants of the Neotropics 193  
 – Corolla salverform, subsalverform, tubular, urceolate or rotate (if campanulate or tubular-campanulate, then the corolla tube  $<$  1 cm long), sometimes small and inconspicuous, sometimes larger and showy; plants of the Neo- or Paleotropics 197
193. Calycine colleters absent; inflorescences usually with only 2 flowers; calyx lobes foliaceous to subfoliaceous; seed coma rostrate 102. *Rhabdadenia*  
 – Calycine colleters present; inflorescences normally with  $>$  2 flowers; calyx lobes foliaceous or not; seed coma rostrate or not 194
194. Calycine colleters solitary (but sometimes deeply dissected), centered at the base of each sepal; seed coma rostrate (Echiteae-Echitinae) 195  
 – Calycine colleters alternisepalous, often quincuncially arranged, sometimes spread irregularly across the base of each sepal; seed coma rostrate or sessile (Odontadenieae) 196
195. Corolla throat with conspicuous, 2–3 mm long white hairs; anther bases obtuse to broadly acute; plants of



- Mexico, Central America and the Caribbean
126. *Echites*
- Corolla throat glabrous to inconspicuously puberulent; anther bases slender and acuminate; plants of the Atlantic coast of Brazil 201
127. *Bahiella*
196. Style-head without a well-developed membranous collar at the base; seed coma sessile; calyx lobes often closely imbricate at anthesis and conspicuously unequal in size; plants of Central and South America (2 species reaching the West Indies)
108. *Odontadenia*
- Style-head with a well-developed membranous collar at the base; seed coma rostrate; calyx lobes not closely imbricate at anthesis or conspicuously unequal in size; plants of Florida and the West Indies 199
110. *Angadenia*
197. Anthers with a conspicuous tuft of soft hairs at the apex; plants of C China and SE Asia (Apocynae-Amphineuriinae) 198
- Anthers without a conspicuous tuft of soft hairs at the apex; plants of the Paleo- or Neotropics or subtropics 199
198. Ovary pubescent; nectary disc a ring, sometimes somewhat 5-lobed; calycine colleters in a continuous ring; pedicel not twisted in fruit
136. *Sindechites*
- Ovary glabrous; nectary disc irregularly 2-lobed; calycine colleters alternisepalous; pedicel twisted in fruit 200
137. *Streptoechites*
199. Leaves usually with abaxial domatia in at least some axils of the secondary veins; ovary pubescent, at least at the apex; seed coma sessile (Apocynae) 200
- Leaves without abaxial domatia; ovary pubescent or glabrous; seed coma rostrate or sessile 201
200. Calycine colleters alternisepalous or absent; seed body pubescent 143. *Urceola*
- Calycine colleters spread in a ring around the calyx; seed body glabrous 148. *Baharuia*
201. Flowers medium-sized to large and showy; corolla tube at least 1 cm long 202
- Flowers mostly small, inconspicuous or somewhat showy; corolla tube < 1 cm long 215
202. Calycine colleters solitary (sometimes deeply dissected), centered at the base inside each sepal, rarely absent; plants of the New World (Echiteae) 203
- Calycine colleters alternisepalous or spread  $\pm$  in a ring around the base inside the calyx (occasionally absent); plants of the Paleotropics (except *Odontadenia*) 206
203. Orifice of the corolla tube with a thickened annular corona in the throat and/or a knob-like corona lobe just above each anther 131. *Prestonia*
- Corolla tube without an annular corona in the throat or a knob-like corona lobe above each anther 204
204. Bracts and calyx lobes lanceolate to ovate, > 5 mm wide, markedly foliaceous; inflorescences simple bostrychoid racemes 125. *Asketanthera*
- Bracts and calyx lobes mostly trigonal, narrowly lanceolate, not foliaceous; inflorescences compound dichasial or helicoid cymes 205
205. Leaves coriaceous with revolute margins and inconspicuous secondary and tertiary venation; anther bases slender and acuminate; plants of E Brazil 127. *Bahiella*
- Leaves membranous, without revolute margins; secondary and tertiary venation conspicuous; anther bases obtuse to broadly acute; plants of S Florida, the West Indies, Mexico and Central America 126. *Echites*
206. Sepals longer than the corolla tube (very rarely same length), mostly subfoliaceous, puberulent to tomentose or strigillose on the outer surface 150. *Aganosma*
- Sepals shorter than the corolla tube, subfoliaceous or not, glabrous or with an indument 207
207. Calyx lobes deciduous; anthers only weakly attached to the style-head; seeds without a coma 94. *Eucorymbia*
- Calyx lobes persistent; anthers firmly attached to the style-head; seeds with a coma 208
208. Calyx lobes connate into a tube at the base 144. *Chonemorpha*
- Calyx lobes  $\pm$  free to the base 209
209. Corolla tube inside glabrous above the level of stamen insertion; seed coma sessile; plants of northern South America 108. *Odontadenia*
- Corolla tube inside pubescent above the level of stamen insertion; seed coma rostrate or sessile; plants of East, South, and SE Asia (Apocynae) 210
210. Nectaries  $\pm$  separate; seed coma sessile 211

- Nectaries fused into an often 5-lobed or crenulate disc; seed coma sessile or rostrate 212
- 211. Anthers inserted in the lower half of the corolla tube; inflorescences flat-topped and umbrelliform; style-head with a short basal collar **152. *Epigynum***
  - Anthers inserted above the middle of the corolla tube; inflorescences not flat-topped or umbrelliform; style-head without a basal collar **145. *Trachelospermum***
- 212. Calycine colleters few, alternisepalous; seed coma on a long, hairy rostrum **134. *Anodendron***
  - Calycine colleters either distributed in a continuous ring or absent; seed coma sessile or at the end of a glabrous rostrum 213
- 213. Leaves with a marginal vein that is as well-developed as the secondary veins; corolla lobes not or only weakly falcate and strap-shaped **135. *Amphineurion***
  - Leaves without a marginal vein that is as strongly developed as the secondary veins; corolla lobes distinctly falcate and widening from base 214
- 214. Corolla lobes distinctly shorter than corolla tube; seed coma sessile **152. *Epigynum***
  - Corolla lobes as long as or longer than corolla tube; seed coma at the end of a glabrous rostrum **144. *Chonemorpha***
- 215. Calyx lobes usually narrowly lanceolate, longer than the corolla tube **150. *Aganosma***
  - Calyx lobes shorter than the corolla tube, mostly deltoid or ovate, sometimes lanceolate 216
- 216. Calycine colleters spread in a ring; seed coma sessile or long rostrate with the coma arising only at the end 217
  - Calycine colleters restricted to the margins of the sepals (alternisepalous), usually in a quincuncial arrangement, rarely absent; seed coma sessile or shortly rostrate or long rostrate but with the coma arising along the rostrum 219
- 217. Leaves with a marginal vein that is as well-developed as the secondary veins; corolla throat without vertical ridges; seed coma sessile **135. *Amphineurion***
  - Leaves without a marginal vein that is as strong as the secondary veins; corolla throat with vertical ridges in the staminal sectors; seed coma sessile or rostrate (Apocynae-Chonemorphae) 218
- 218. Inflorescences panicles; calyx lobes fused into a short cup at the base; nectary disc an entire 5-crenate ring; seed coma rostrate **144. *Chonemorpha***
  - Inflorescences cymes; calyx lobes essentially free to the base; nectary of five distinct lobes; seed coma sessile **145. *Trachelospermum***
- 219. Ovary puberulent to tomentose or hirsute 220
  - Ovary glabrous 223
- 220. Corolla red or pink; thickened annular corona or corona of 5 lobes present in the throat; seed coma rostrate (Apocynae-Papuechitinae) 221
  - Corolla white, greenish white, yellowish, or rarely orange; corolline corona absent; seed coma sessile 222
- 221. Corona of 5 distinct lobes in corolla throat; inner surface of the corolla tube glabrous above the insertion of the stamens; plants of New Guinea and the islands of Aru and Ambon **132. *Papuechites***
  - Corona a thickened annular ring in corolla throat; inner surface of the corolla tube pubescent above the insertion of the stamens; plants endemic to Vietnam **133. *Ixonoderium***
- 222. Nectary annular; corolla urceolate or campanulate, not constricted at the throat; corolla lobe aestivation dextrorse or valvate; seed body hirsute **143. *Urceola***
  - Nectary of 5 distinct narrow lobes; corolla salverform, constricted at the throat; corolla lobe aestivation dextrorse; seed body glabrous **151. *Ichnocarpus***
- 223. Nectary disc usually annular; seeds with a rostrate coma, the rostrum also with long hairs along its length **134. *Anodendron***
  - Nectary of 5 separate lobes, or these fused only at the base; seed coma sessile or at the most with a very short beak and the hairs only at the end 224
- 224. Corolla tube ca. 2 mm long, the lobes remaining slightly inrolled at anthesis; plants of Sri Lanka, China and SE Asia **141. *Cleghornia***
  - Corolla tube 5–18 mm long, the lobes spreading at anthesis; plants of the New World (Odontadenieae) 225
- 225. Calyx lobes usually aristate and keeled, with calycine colleters in pairs or groups in the sinuses; follicles slender, ca. 4 mm diam.; plants of SE USA **104. *Thyrsanthella***
  - Calyx lobes not aristate or keeled, with calycine colleters single in the sinuses; follicles robust, 1.5–3.5 cm. diam.; widespread in South America **107. *Secondatia***

## I. RAUVOLFOIDS

- Rauvolfioideae Kostel. (1834) (subfamily rank dubious).  
 Plumerioideae Luer. (1882).  
 Cerberioideae Pichon (1948).  
 Tabernaemontanoideae Stapf ex Boiteau & Sastre (1975).

Trees, shrubs, woody lianas or vines, rarely herbs; latex typically white (this very rarely bluish tinged), rarely red, orange or yellow. Leaves opposite, whorled, or alternate. Inflorescences cymose or racemose. Flowers almost always 5-merous (4-merous in *Leuconotis*), inconspicuous to large and showy; calyx almost always 5-merous, rarely 4- (*Parahancornia*), 6- or 7-merous; calycine colleters often absent, when present usually at the base of the sepals in a single series (but often multiseriate in Tabernaemontaneae, some Hunterieae and paleotropical Willughbeieae); corolla mostly salverform, more rarely with inflated throat (tubular-campanulate or infundibuliform, mainly in some Tabernaemontaneae and Plumerieae); corolla lobe aestivation almost always sinistrorsely contorted (but dextrorsely contorted in *Kopsia*, *Ochrosia*, some species of *Haplophyton*, *Alstonia* and *Tabernaemontana*); corona when present almost always in the staminal sectors, usually of simple lobes or pouches in the petal sinuses (rarely fused into an annulus), sometimes lower down on the corolla tube as small lobes or thickenings above the stamens; stamens inserted at various levels in the corolla tube, almost always included in the corolla tube (partially exerted in some Tabernaemontaneae and Plumerieae), the filaments mostly short or anthers subsessile; anthers usually fertile to the base (fertile in the upper part only and with sterile lignified basal appendages in most Tabernaemontaneae, and with small sterile, non-lignified basal appendages and apical appendage in some Melodineae and Hunterieae, and with non-lignified basal appendages in *Allamanda*), free from the style-head; pollen mostly 3-4-colporate, but typically porate and often with only 2 apertures in Alyxieae and a few Melodineae; nectaries as free lobes surrounding the base of the ovary (these sometimes fused into a crenulate or lobed ring), or indistinct and adnate to the base of the outer ovary wall or absent; gynoeceum almost always bicarpellate (but normally with 3-5 carpels in *Pleiocarpa* (Hunterieae), and *Lepinia* and *Lepiniopsis* (Alyxieae)); ovary normally superior, but half-inferior in some genera (e.g., *Plumeria*, *Himatanthus* and *Mortoniella*); ovary congenitally syncarpous or apocarpous (postgenitally syncarpous in *Allamanda*); ovules few to many; style-head differentiated vertically, usually the tips of the carpels unfused and forming two

unreceptive free appendages at the top, sometimes with a crest of longer hairs below this and/or a collar or expanded flange at the base, beneath which the stigmatic region is normally found, more rarely the style-head is not noticeably differentiated and the entire body is more or less uniformly receptive. Nectaries free, surrounding the base of the ovary, indistinct and adnate to the base of the outer ovary wall or absent. Fruit apocarpous or syncarpous, dehiscent or indehiscent; pericarp dry or fleshy; endocarp sometimes stony. Seeds generally naked or winged, testa glabrous or hairy, smooth, or pitted, ridged or rugulose, without coma (except in *Haplophyton*); endosperm smooth, sometimes ridged or strongly ruminate. Indole alkaloids often present, cardenolides less frequently. 79 genera, most either in the Paleo- or Neotropics.

#### KEY TO THE TRIBES OF RAUVOLFOIDS

1. Anthers sagittate at the base, lignified (except in some species of *Tabernaemontana*); leaves almost always opposite; calycine colleters usually present; fruit fleshy, either a pair of follicles (these rarely hemi-syncarpous or indehiscent) with arillate seeds or a berry **5. Tabernaemontaneae** (p. 266)
  - Anthers rarely sagittate at the base, non-lignified; leaves opposite, whorled or alternate; calycine colleters usually absent, sometimes present; fruit fleshy or dry, berries, drupes, follicles or capsules; arils absent (except in *Chilocarpus*) 2
2. Ovary congenitally syncarpous; fruit a berry; phyllotaxis almost always opposite 3
  - Ovary apocarpous (syncarpous in *Chilocarpus*, *Lepiniopsis* and *Allamanda* and hemi-syncarpous in *Diplorhynchus*); fruit various, dehiscent or indehiscent; phyllotaxis various (opposite, whorled or alternate) 5
3. Placentas forming a lignified partition in fruit; spines often present in leaf axils (*Carissa*); indole alkaloids absent **11. Carisseae** (p. 280)
  - Placentas becoming pulpy in fruit; without spines in leaf axils; indole alkaloids present or absent 4
4. Corolline corona present; lianas without tendrils **7. Melodineae** (p. 271)
  - Corolline corona absent; trees, shrubs or lianas (the latter often with tendrils), rarely rhizomatous subshrubs **4. Willughbeieae** (p. 261)

5. Ovary 2–5-carpellate; fruit berries
8. **Hunterieae** (p. 273)
- Ovary 2-carpellate (except in some *Alyxieae*); fruit dehiscent or indehiscent, but not berries 6
6. Anthers with latrorse to sublaturse dehiscence and mostly with elongated cylindrical apical connective appendages; epistaminal appendages usually present on the corolla
10. **Plumerieae** (p. 277)
- Anthers with introrse dehiscence, normally lacking elongated apical appendages (but large flat apical appendages present in *Vinca*); epistaminal appendages normally absent 7
7. Forest trees of the Paleotropics, Australia and Pacific islands; leaves whorled, with up to 9 per node (opposite in some species of *Alstonia*); both carpels usually maturing; fruit a pair of several-seeded follicles; seed margin with cilia, hairs or wings
2. **Alstonieae** (p. 257)
- Shrubs, trees, lianas or herbs of the Paleotropics, Australasia, Oceania and temperate Eurasia and the New World; leaves opposite, alternate or if whorled, then usually 3–5 per node; sometimes only one carpel maturing; fruit mostly indehiscent, few-seeded drupes or several-seeded follicles, rarely berries; seed margin usually naked or winged 8
8. Flowers large, showy; corolla usually > 2 cm long, often thick, waxy in appearance; ovary partly inferior in *Plumeria*, *Himatanthus* and *Mortoniella*; leaves usually alternate, rarely opposite (whorled only in *Allamanda*); corolla tube without slits above stamen insertion; indole alkaloids absent;  $x = 9$
10. **Plumerieae** (p. 277)
- Flowers small to medium-sized; corolla usually < 2 cm long, usually thin, delicate in texture (but sometimes somewhat thick in *Ochrosia*); ovary almost always superior; leaves often whorled, sometimes alternate or opposite; corolla tube normally with slits above stamen insertion; indole alkaloids present or absent;  $x = 10, 11$  9
9. Pollen porate; style-head without membranous basal collar; seeds not compressed, usually with a hilar groove and ruminate endosperm; indole alkaloids absent
9. **Alyxieae** (p. 274)
- Pollen colporate; style-head with or without membranous basal collar; seeds compressed or not, without hilar groove or ruminate endosperm; indole alkaloids present 10
10. Style-head cylindrical, almost always with a basal collar or wreath of hairs at the base (except in *Kametia*) 11
- Style-head mostly ovoid, usually without a basal collar or wreath of hairs at the base 12
11. Leaves whorled or opposite (if alternate, then seeds covered with long lanate hairs) 3. **Vinceae** (p. 258)
- Leaves alternate; seeds naked 6. **Amsonieae** (p. 271)
12. Corolline corona often present as small lobes in throat or ridges behind anthers; anthers sometimes with short, sterile apical appendages (*Diplorhynchus*) or with short sterile appendages at apex and thecae bases (*Pycnobotrya*); leaves opposite; fruit follicular, usually both carpels developing; trees or lianas of the Paleotropics, Australasia and Oceania
7. **Melodineae** (p. 271)
- Corolline corona absent; anthers without apical or basal extensions; leaves most frequently alternate, rarely whorled or opposite; fruit and seeds very diverse, often only one carpel maturing; trees, shrubs or subshrubs of the tropics and subtropics of the New World 1. **Aspidospermateae** (p. 255)

### I.1. Tribe **Aspidospermateae** Miers (1878).

Trees or shrubs, rarely subshrubs; latex in some species of *Aspidosperma* red, orange or yellow. Leaves alternate, less frequently whorled or opposite. Inflorescences axillary and/or terminal, cymose, dichasial or thyriform, few- to many-flowered. Flowers mostly small; calyx rarely 4-, 6- or 7-merous (some species of *Aspidosperma*), calycine colleters absent; corolla salverform to tubular with slits in the tube behind the stamens (i.e., incomplete fusion of the postgenitally fused upper corolla tube); corolla lobe aestivation sinistrorse (dextrorse in *Geissospermum* and one species of *Haplophyton*); corona absent; stamens usually inserted about midway or above in the corolla tube; pollen 3-colporate; nectary disc absent, adnate or inconspicuous; ovary apocarpous; ovules few to several per carpel; style-head mostly without apical crest or basal collar (with a short basal collar in *Haplophyton*), concomitantly receptive and secretory. Fruit apocarpous; normally with dry pericarp and dehiscent, a pair of follicles, but often only one carpel reaching maturity, but fruit fleshy in *Geissospermum* and *Vallesia*; endocarp usually not stony, but somewhat woody in *Vallesia*. Seeds various: thin and compressed with papery wing in *Aspidosperma* and *Strempeleipsis*, or seeds cylindrical without wing or hairs (*Vallesia*, *Geissospermum*, *Microplumeria*). Indole alkaloids present.

$x = 10, 11$ . Six genera in the tropics and subtropics of the New World.

### 1. *Strepeliopsis* Benth.

*Strepeliopsis* Benth. in Benth. & Hook. f., Gen Pl. 2: 702 (1876).

Small trees or shrubs. Leaves opposite. Inflorescences terminal, cymose, many-flowered; corolla salverform, greenish white; tube inside with moniliform hairs above the stamens; ovules 10–14 per carpel. Follicles slender,  $\pm$  terete. Seeds several per carpel, compressed, with a papery wing at each end.

Two spp., one on Cuba, the other on Jamaica.

### 2. *Vallesia* Ruiz & Pav.

*Vallesia* Ruiz & Pav., Fl. Peruv. Prodr. 28, t. 5 (1794); Morales, Novon 8: 263–264 (1998), tax.; Morales, Anales Jardin Bot. Madrid 66: 257–258 (2009), reg. rev.

Trees or shrubs. Leaves alternate. Inflorescences axillary, congested, cymose. Corolla salverform, white or yellowish; ovules 6 per carpel. Fruit an opalescent, one-seeded drupe, usually only one carpel maturing. Seeds not compressed, slightly arcuate.  $2n = 22$ .

Nine spp. from Florida to the West Indies, Mexico, Central America, the Galapagos and Colombia, to N Argentina, usually in wooded areas, often along rivers.

### 3. *Haplophyton* A. DC.

*Haplophyton* A. DC., Prodr. 8: 412 (1844); Williams, Sida 16: 469–475 (1995), rev.

Subshrubs. Leaves alternate, occasionally opposite. Inflorescences axillary or terminal, 1–4-flowered. Sepals glandular at the apex; corolla salverform, cream flushed with pink; corolla lobe aestivation sinistrorse in one species, dextrorse in the other; ovules several. Follicles slender, thin-walled. Seeds with longitudinal grooves and a deciduous tawny to gray coma at the chalazal and the micropylar end.

Two spp. in SW USA to S Mexico, often in rocky or open areas, hillsides or canyons, at low to mid elevations.

### 4. *Microplumeria* Baill.

*Microplumeria* Baill., Bull. Mens. Soc. Linn. Paris 1: 749 (1889); Zarucchi, Fl. Venez. Guayana 2: 531 (1995), reg. rev.

Small tree or shrub. Leaves in whorls of three or opposite. Inflorescences terminal, cymose, few- to many-flowered. Corolla tubular, densely silvery green villous outside, the lobes much shorter than the tube; ovules numerous. Follicles slender, thin-walled. Seeds cylindrical, diagonal at the ends (as if broken off).

One sp., *M. anomala* (Müll. Arg.) Markgr., in NW South America, usually along seasonally flooded river banks or along streams, at low elevations.

### 5. *Geissospermum* Allemão

*Geissospermum* Allemão, Pl. Novas Brasil 707 (1846); Gentry, Ann. Missouri Bot. Gard. 71: 1075–1081 (1984), synop.; Zarucchi, Fl. Venez. Guayana 2: 503 (1995), reg. rev.

Trees. Leaves alternate, usually silvery sericeous. Inflorescences normally arising from between nodes, cymose, few- to many-flowered. Corolla tubular to salverform, white, cream to greenish or brownish; corolla lobe aestivation dextrorse; stamens subsessile; ovules many. Berries stout, leathery, containing much latex, often only one developing. Seeds few, somewhat flattened, elliptic; testa pitted, somewhat rugulose.

Five spp. in NW South America.

### 6. *Aspidosperma* Mart. & Zucc.

Fig. 27

*Aspidosperma* Mart. & Zucc., Flora 7 (Beil. 4): 135 (1824), nom. cons.; Marcondes-Ferreira, *Aspidosperma* Mart. nom. cons. (Apocynaceae): Estudios Taxonômicos, Ph. D. Thesis, University of Campinas, Brazil: 1–431 (1988), rev.; Potgieter, Phylogenetic study of Apocynaceae Juss. and *Aspidosperma* Mart. and Zucc., Ph.D. Thesis, University of Illinois-Urbana, USA: 1–530 (1999), rev.; Pereira et al., Biota Neotrop. 16: e20150080 (2016), reg. rev.; Morales & Zamora, Phytoneuron 68: 1–13 (2017), reg. rev.

Shrubs to big trees; latex white, yellow, orange or red. Leaves alternate, rarely opposite or verticillate. Inflorescences axillary and/or terminal, compound-cymose, dichasial or thyriform, usually

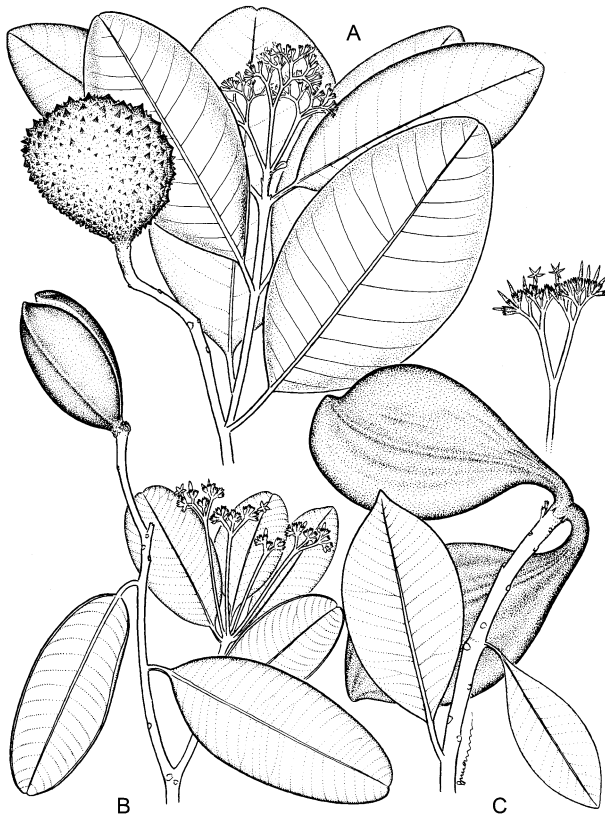


Fig. 27. Apocynaceae-Aspidospermateae. Branches, flowers and fruits. A *Aspidosperma excelsum*. B *A. pachypterum*. C *A. neblinae*. (From Zarucchi et al. 1995, p. 489, with permission from the Missouri Botanical Garden Press, St. Louis; drawn by B. Manara)

many-flowered. Calyx (4–)5(–7)-merous; corolla tubular to salverform, usually white, yellow or greenish; ovules few to many. Follicles dry, woody, usually compressed, nearly cylindrical to falciform or dolabriform, surface smooth, lenticillate, sometimes warty or spiny, frequently only one developing. Seeds 2–many, peltately attached, strongly compressed, with eccentric or concentric papery wing, this rarely thicker and rudimentary.

About 50 spp. with a center of diversity in Brazil, but ranging from Mexico and the Antilles to Argentina. The hard wood of some species is used to make as simple tools, tool handles, wheels small art objects, others for cabinetry and floors.

## I.2. Tribe Alstonieae G. Don (1837).

Trees or shrubs. Leaves whorled or opposite. Flowers mostly small; calycine colleters absent except in *Dyera*; corolla salverform to tubular (rotate in *Dyera*); corolla lobe aestivation sinistorse (dextrorse in many species of *Alstonia*); corona absent; stamens inserted midway or above in the corolla tube; filaments filiform; anthers with sterile apical and basal appendages in *Dyera*; pollen 3-colporate; nectary disc absent, adnate or inconspicuous, 2-lobed in some species of *Alstonia*; ovary apocarpous, hemi-syncarpous or rarely completely syncarpous, half inferior in *Dyera*; ovules numerous per carpel; style-head with or without a membranous basal collar. Fruit apocarpous, a pair of follicles with woody pericarp (these fused into a syncarpous “double-follicle” in *Alstonia rostrata*). Seeds thin, compressed, testa glabrous or pubescent with long hairs around the margin (*Alstonia*) or surrounded by a membranous wing (*Dyera*). Indole alkaloids present.  $x = 10, 11$ . Two genera in the Paleotropics.

### 7. *Alstonia* R. Br.

Fig. 28

*Alstonia* R. Br., *Asclepiadeae* 64 (1810), nom. cons.; Monachino, *Pacific Sci.* 3: 133–182 (1949), rev.; Sidiyasa, *Blumea Suppl.* 11: 1–230 (1998), rev.; Sidiyasa, *Fl. Males. I*, 18: 31–64 (2007), reg. rev.; Middleton, *Fl. Cambodia, Laos and Vietnam* 33: 18–29 (2014), reg. rev.

*Blaberopus* A. DC. (1844).

*Winchia* A. DC. (1844).

*Paladelpha* Pichon (1947).

Trees or shrubs; latex white. Leaves verticillate or opposite. Inflorescences terminal, cymose. Typical calycine colleters absent, but colleters often on the edges of the sepals; corolla white, yellow or red; corolla lobe aestivation sinistorse or dextrorse; nectary disc adnate, indistinct, sometimes 2-lobed; ovary apocarpous, hemi-syncarpous or syncarpous; ovules numerous; style-head with a basal collar. Follicles long and slender, free or rarely fused (*Alstonia rostrata* C.E.C. Fisch.). Seeds with hairs around the margins, longer at ends.  $2n = 22, 42, 44, 80, 84, 88$ .

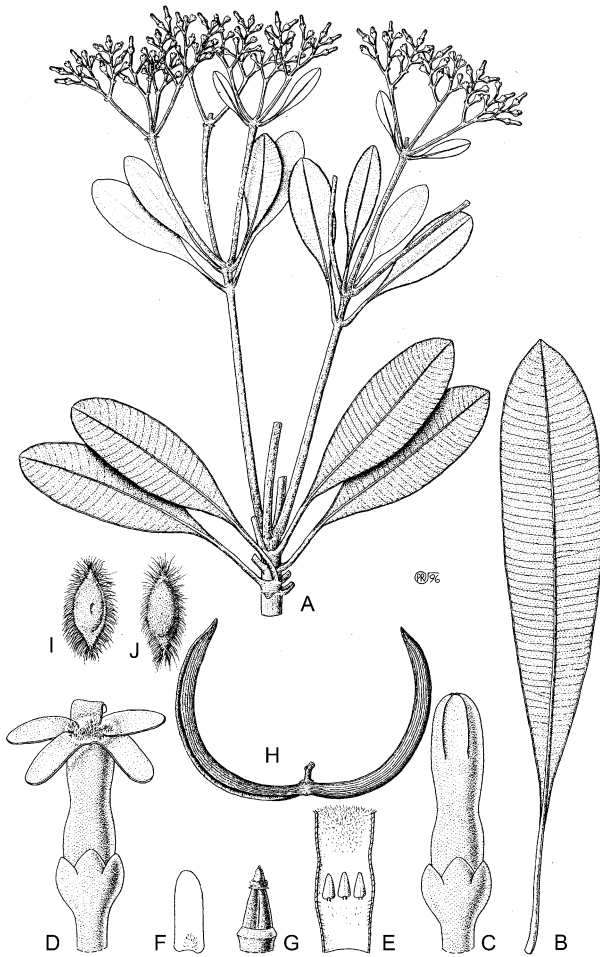


Fig. 28. Apocynaceae-Alstonieae. *Alstonia quaternata*. A Flowering branch. B Leaf. C Flower in bud. D Open flower. E Opened corolla tube, showing three anthers. F Corolla lobe. G Gynoecium. H Fruit. I Seed, raphe side. J Seed, antiraphe side. (From Sidiyasa 1998, p. 167, with permission from Naturalis, Leiden; drawn by Priyono)

About 43 spp. from Africa and China and the Himalayas to Australia and Pacific Islands, in primary and secondary forests, swamps or dry habitats, up to 2900 m.

#### 8. *Dyera* Hook. f.

*Dyera* Hook. f., J. Linn. Soc. Bot. 19: 293 (1882); Monachino, Lloydia 9: 174–202 (1946), rev.; Middleton, Gard. Bull. Sing. 55: 209–218 (2003), rev.; Middleton, Fl. Males. I, 18: 186–190 (2007), reg. rev.

Giant trees up to 80 m and 300 cm diameter; latex white. Leaves in whorls of 4–8. Inflorescences axillary, many-flowered cymes. Calycine colleters

ca. 4 per sepal; corolla small, white, greenish or pinkish yellow, lobes longer than tube, spreading; nectary disc annular, inconspicuous, adnate; ovary half inferior; ovules many; style very short; style-head scarcely enlarged, undifferentiated, without collar at base. Follicles thick, woody, up to 40 cm long, spreading. Seeds 12–24 per carpel, peltately attached, elliptic, compressed, surrounded by membranous wing.

Two spp. in the far S of Thailand and W Malesia, in lowland evergreen forest. *Dyera costulata* (Miq.) Hook. f. was once cultivated in large plantations as a source of latex (“jelutong”) for chewing gum.

#### I.3. Tribe Vinceae Duby (1828).

Trees or shrubs, more rarely lianas, vines or herbs. Leaves whorled or opposite, rarely alternate. Flowers small to medium-sized, often whitish, showy in some genera; typical calycine colleters absent, but colleters at exposed edge of calyx lobes in *Ochrosia*, *Vinca* and several species of *Rauvolfia*; corolla salverform (infundibuliform in *Vinca*), the orifice usually constricted by a thickened ring and hairs; free corona lobes absent; corolla lobe aestivation usually sinistrorse (dextrorse in *Kopsia* and *Ochrosia*); stamens usually inserted at the middle of the corolla tube or above (except in *Kamettia*); filaments normally filiform and anthers without lignified guide rails or sagittate basal appendages (in *Vinca* with spatulate apical appendage); pollen mostly 3-colporate; nectaries when present often consisting of 2 lobes alternating with the carpels (a 5-lobed nectary disc in *Rauvolfia*), sometimes adnate and indistinct or absent; ovary generally apocarpous, (hemi-syncarpous or syncarpous in some species of *Rauvolfia* and *Ochrosia*), usually glabrous, often only one carpel maturing; ovules few to numerous; style usually filiform; style-head cylindrical, almost always with a wreath of hairs around the top and a basal collar or wreath of hairs at the base (except in *Kamettia*). Fruit apocarpous, of 2 separate fruiting carpels (in *Rauvolfia* often partially or wholly syncarpous and sometimes only one carpel developing); either indehiscent and drupaceous with a thick pericarp and stony endocarp or a pair of thin-walled woody to papery follicles. Seeds 1–4(–6) per carpel, rarely more, ovoid or compressed, mostly not

winged (the flat margins forming a rudimentary ledge in *Ochrosia*); in *Tonduzia* and *Laxoplumeria* seeds numerous, elliptic-compressed with long hairs around the margin; endosperm usually fleshy and smooth (very thin, seemingly absent in *Kopsia*). Indole alkaloids present.  $x = 9, 10, 11, 23$ . Nine genera, pantropical, one in temperate regions of the Old World.

### 9. *Kopsia* Blume

*Kopsia* Blume, Catalogus 12 (1823), nom. cons.; Pichon, Mém. Mus. Natl. Hist. Nat. 27: 153–252 (1948); Markgraf, Blumea 20: 416–425 (1972), morph.; Forster, Fl. Australia 28: 134–138 (1996), reg. rev.; Middleton, Harvard Pap. Bot. 9: 89–142 (2004), rev.; Middleton, Fl. Males. I, 18: 232–260 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 116–127 (2014), reg. rev.  
*Calpicarpum* G. Don (1837).  
*Kentrochrosia* K. Schum. & Lauterb. (1900).

Trees or shrubs; latex white. Leaves opposite. Inflorescences terminal, cymose. Sepals with colletter abaxially below apex; corolla often large and showy, white, yellowish or pink, lobes usually shorter than tube; stamens inserted high in corolla tube, very rarely near base; nectaries of two free lobes; ovary apocarpous; ovules 2 per carpel. Drupes one-seeded, usually with cavity forming a hooked or sharp appendage on ventral side, this rarely absent; mesocarp stringy or pulpy. Seeds curved, slightly compressed; endosperm very thin or absent.  $2n = 36, 72$ .

23 spp. from S China and Burma to N Australia and Vanuatu.

### 10. *Ochrosia* Juss.

*Ochrosia* Juss., Gen. Pl. 144 (1789); Markgraf, Blumea 25: 233–247 (1979); Fosberg & Sachet, Adansonia II, 17: 19–22 (1977), nomen.; Wagner et al., Man. Fl. Pl. Hawai'i 1: 216–218 (1990), rev.; Li et al., Fl. China 16: 22–164 (1995), reg. rev.; Forster, Fl. Australia 28: 134–137 (1996), reg. rev.; Hendrian, Blumea 49: 101–228 (2004), reg. rev.; Hendrian, Fl. Males. I, 18: 289–302 (2007), reg. rev.; Hendrian & Kondo, Chromosome Bot. 2: 127–149 (2007), phyl.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 144–146 (2014), reg. rev.  
*Lactaria* Rumph. (1838).  
*Neisosperma* Raf. (1838).  
*Bleekeria* Hassk. (1855).  
*Excavatia* Markgr. (1927).

Small trees; latex white. Leaves in whorls of 3–6, occasionally opposite. Inflorescences axillary

cymes. Colletters at the outside edge of the sepals in most species; corolla white, cream or orange; nectary two small lobes or adnate, indistinct or absent; ovary rarely hemi-syncarpous or syncarpous; ovules 2–6 per carpel. Drupes yellow, red, purple or black; endocarp splitting into fibers or entire around two lateral cavities. Seeds 1–3 per carpel, compressed, with a wing-like structure round the margin.  $2n = 22$ .

About 40 spp. in continental SE Asia, Malesia, N Australia, the West Pacific Islands, Marquesas and Hawaiian Islands.

### 11. *Tonduzia* Pittier

*Tonduzia* Pittier, Contr. U. S. Natl. Herb. 12: 103 (1908); Morales, Darwiniana 47: 176–177 (2009), reg. rev.  
*Alstonia* section *Tonduzia* (Pittier) Pichon (1947).

Shrubs or trees. Leaves narrowly elliptic, in whorls of 3(–4). Inflorescences terminal, many-flowered, cymose. Corolla small, white to cream; lobes shorter to slightly longer than the tube; nectary disc obscure, annular, adnate to the base of the ovary; ovary apocarpous; ovules numerous. Follicles often rostrate, often stipitate. Seeds numerous, elliptic, with cilia of different shapes and sizes along the margin.

Two spp. in Mexico and Central America, in open woodlands or dense tropical forest, on slopes, hills or on rocky soil, up to 2000 m.

### 12. *Laxoplumeria* Markgr.

*Laxoplumeria* Markgr., Notizbl. Bot. Gart. Berlin-Dahlem 9: 981 (1926); Monachino, Phytologia 3: 67–70, synop.

Trees. Leaves alternate, unusually long-petiolate. Inflorescences terminal, many-flowered, cymose. Corolla small, white, the lobes linear, longer than the tube; nectary disc a low ring with two lobes alternate to the carpels; ovary apocarpous, glabrous; ovules numerous. Follicles up to 40 cm long, slender. Seeds numerous, compressed, elliptic, acute at the ends, the testa covered by long, brown hairs.

Five spp., in South America, one of them reaching Panama.

### 13. *Vinca* L.

*Vinca* L., Sp. Pl. 1: 209 (1753); Lawrence, Bailey 7: 113–119 (1959), synop.



Perennial herbs, often procumbent. Leaves opposite. Inflorescences seemingly axillary, 1-flowered. Flowers showy; colleters at outside edge of sepals in most species; corolla infundibuliform, blue, rarely violet or white, with pouch-like corona in petal sinuses, lobes mostly shorter than tube; staminal filaments thick, geniculate; anthers with hairy, spatulate apical appendage; nectary of two lobes; ovary apocarpous; ovules 6–8 per carpel; style gradually thickened toward the apex. Follicles slender, Seeds oblong with a hilar groove, testa warty.  $2n = 46, 92, 32$ .

About seven spp. in SE Europe, SW Asia and NW Africa, some cultivated and naturalized.

#### 14. *Kamettia* Kostel.

*Kamettia* Kostel., Allg. Med.-Pharm. Fl. 3: 1062 (1834); Middleton et al., Thai Forest Bull. Bot. 33: 75–80, synop. *Ellertonia* Wight (1848).

Woody lianas; latex white. Leaves verticillate, sometimes opposite at some nodes. Inflorescences terminal, lax, dichasial, few- to many-flowered. Corolla red outside, white inside, the tube usually curved; stamens inserted in the lower third of the tube; nectary disc absent, adnate or indistinct; ovary apocarpous; ovules numerous; style-head ellipsoid, without upper wreath or basal collar. Follicles fusiform, divergent, often lenticellate. Seeds compressed, with a wing at each end.

Two spp., one in the Western Ghats of India, and one in Thailand.

#### 15. *Petchia* Livera

*Petchia* Livera, Ann. Roy. Bot. Gard. (Peradeniya) 10: 140 (1926); Huber, Fl. Ceylon 1(1): 1–27 (1973), reg. rev.; Leeuwenberg, Wageningen Agric. Univ. Pap. 97-2: 53–80 (1997), rev. *Cabucala* Pichon (1948).

Shrubs or small trees. Leaves in whorls of 3–5, often opposite at branchings. Inflorescences terminal or axillary, cymose, few-flowered. Corolla sometimes slightly zygomorphic, creamy white; nectary disc adnate, indistinct or absent; ovary apocarpous; ovules up to 26 per carpel. Fruits drupaceous, stipitate, torulose, orange or red;

mesocarp fleshy. Seeds 1–several per carpel, ellipsoid, not compressed.

Eight spp. in Madagascar, the Comoro Islands, and one each in Cameroon and Sri Lanka, in the forest understory in rainforest, montane forest, or bush, up to 1700 m.

#### 16. *Catharanthus* G. Don

*Catharanthus* G. Don, Gen. Hist. 4: 95 (1837); Lawrence, Bailey 7: 113–119 (1959), synop.; Plaizier, Meded. Landbouwhogeschool Wageningen 81-9: 1–12 (1981), rev.; Allorge et al., Candollea 70: 61–66 (2015), reg. rev.

Perennial or annual herbs or subshrubs; latex white. Leaves opposite. Inflorescences axillary, sessile, on alternate sides of the nodes, usually 2-flowered. Flowers showy; corolla salverform, pink, red or white, with a ring of strigose hairs in the orifice; nectary of two lobes; ovary apocarpous, usually glabrous, rarely sparsely pilose on top; ovules numerous. Follicles slender. Seeds numerous, black, oblong, with a hilar groove; testa rugose.  $2n = 16, 32, 24$ .

Nine spp., one restricted to India and Sri Lanka, the rest endemic to Madagascar, mostly in exposed, sandy or rocky areas up to 2000 m. One sp., *C. roseus* (L.) G. Don, is a widely cultivated ornamental, and has become naturalized in many regions of the tropics. Because of its many indole alkaloids, this genus is widely used in folk medicine, and compounds from *C. roseus* have been used commercially in treating leukemia.

#### 17. *Rauvolfia* L.

Fig. 29

*Rauvolfia* L., Sp. Pl. 1: 208 (1753); Rao, Ann. Missouri Bot. Gard. 43: 253–355 (1999), reg. rev.; Leeuwenberg & van Dilst, Bull. Jard. Bot. Natl. Belg. 61: 21–69 (1991), reg. rev.; Hendrian & Middleton, Blumea 44: 449–470 (1999) reg. rev.; Koch, Estudos das espécies neotropicais do gênero *Rauvolfia* L. (Apocynaceae), Ph.D. Thesis, University of Campinas, Brazil: 1–292 (2002), reg. rev.; Hendrian & Middleton, Fl. Males. I, 18: 347–359 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 160–172 (2014), reg. rev. *Podochrosia* Baill. (1888).

Subshrubs to trees; latex white. Leaves in whorls of 3–5(–7), rarely opposite, sometimes

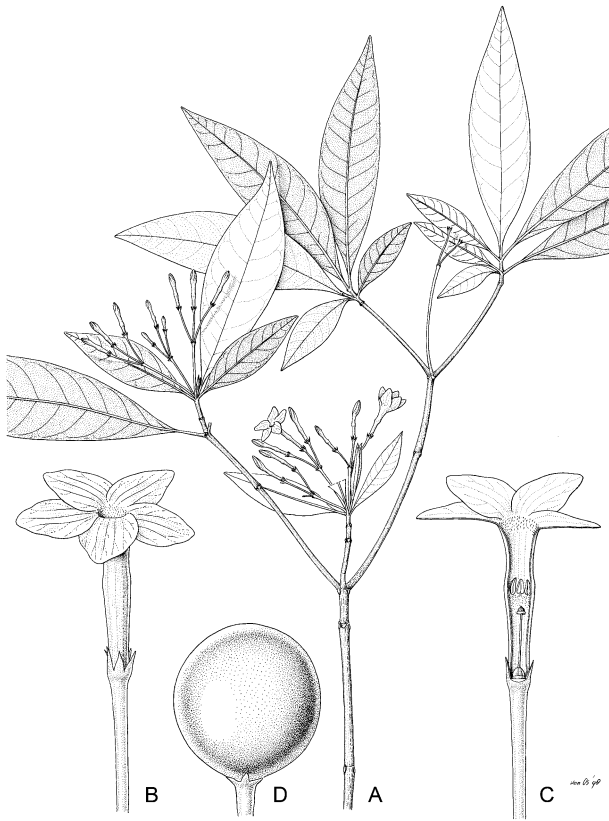


Fig. 29. Apocynaceae-Vinaceae. *Rauvolfia kamarora*. A Flowering branch. B Flower. C Opened corolla tube showing spatial relationship between anthers and style-head. D Fruit with only one carpel developed. (From Hendrian and Middleton 1999, p. 455, with permission from Naturalis, Leiden; drawn by J. van Os)

anisophyllous; petioles with colleters along adaxial side. Inflorescences usually terminal, cymose. Colleters at outside edge of sepals in several species; corolla sometimes slightly zygomorphic, mostly white, sometimes other colors, the lobes normally (much) shorter than tube; nectary disc annular; ovary apocarpous to syncarpous; ovules 1–2 per carpel. Drupes variously colored, apocarpous, hemi-syncarpous to syncarpous (often only one carpel developing). Seeds 1 per carpel, compressed.  $2n = 22, 44, 66, 88$ .

About 60 spp., pantropical in various habitats. Hundreds of different indole alkaloids have been extracted from *Rauvolfia* species, and the genus is an important plant in folk medicine throughout the regions where it occurs, and is used for treating a wide variety of ailments.

A worldwide revision for this genus is lacking.

#### I.4. Tribe Willughbeieae A. DC. (1844).

Woody lianas, often very large and climbing high into the canopy, sometimes with grappling often with tendrils, less frequently trees, shrubs or pyrophytic subshrubs; latex usually white, sometimes reddish or bluish tinged in *Hancornia*; trunk in some species of *Lacmellea* with deciduous, blunt conical spines. Leaves opposite (verticillate in *Couma*). Flowers small- to medium-sized; 4-merous in *Leuconotis*; calycine colleters mostly absent in neotropical taxa and the great majority of the paleotropical taxa (but numerous and multiseriate in *Bousigonia*, *Leuconotis* and *Cyclocotyla* (subtribe Leuconotidinae), and *Vahadenia* (subtribe Landolphiinae)), and few and alternisepalous in some species of *Ancylobothrys* and *Landolphia*; corolla salverform; corolline corona absent; corolla lobe aestivation sinistorse, not inflexed in bud except in *Cyclocotyla*; pollen (1–)3(–4)-colporate; nectary disc normally absent, adnate or indistinct from ovary (but well-developed and higher than the ovary in *Cyclocotyla*), ovary congenitally syncarpous; uni- to bilocular; placentation parietal to axile; ovules few to numerous; style usually filiform; style-head often not clearly differentiated into different morphological regions, usually ellipsoid or ovoid to ovoid-conical, without a distinct upper crest or basal collar. Fruit indehiscent, a berry, often edible, with fleshy, non-fibrous pericarp, mostly without a sclerified layer (but sclerified layer characteristic for *Landolphia*, *Clitandra*, *Orthopichonia* and *Saba* (subtribe Landolphiinae)); placentas mostly becoming pulpy in fruit; endocarp not stony. Seeds few to numerous, ovoid or often irregular in shape, not or somewhat compressed, embedded in sweet to acidic, usually edible pulp, with or without a hilar groove; endosperm smooth or superficially ruminant longitudinally, typically either scanty and associated with cartilaginous cotyledons (subtribes Leuconotidinae, Willughbeiiinae) and in *Cylindropsis* (subtribe Landolphiinae) or cartilaginous to subcorneous and associated with thin membranous cotyledons (subtribes Lacmelleinae and Landolphiinae); cotyledons usually cordate at the base, sometimes attenuate. Indole alkaloids present in subtribe Leuconotidinae.  $x = 11, 18$  genera, pantropical.

### 18. *Bousigonia* Pierre

*Bousigonia* Pierre, Bull. Mens. Soc. Linn. Paris II, 1: 35 (1898); Middleton, Fl. Cambodia, Laos and Vietnam 33: 63–66 (2014), reg. rev.

Woody lianas without tendrils. Leaf blades with scattered dots abaxially. Inflorescences axillary or terminal cymes. Calycine colleters numerous, in a row; corolla white, the lobes much shorter than the tube; stamens inserted around middle of corolla tube; ovary bilocular, glabrous; placentas axile; ovules 2 per placenta; style filiform; style-head ellipsoid. Berries few-seeded, ovoid to pyriform. Seeds not or only slightly compressed, without hilar groove, testa thin, smooth; endosperm scanty to absent, cotyledons fleshy, deeply incised at the base.

Two spp. in China, Thailand, Laos and Vietnam, in mixed forest, forest edges and montane forest up to 1600 m.

### 19. *Leuconotis* Jack

*Leuconotis* Jack, Trans. Linn. Soc. London 14: 121 (1823); Leeuwenberg, Syst. Geogr. Pl. 72: 111–126 (2002), rev.; Middleton, Fl. Males. I, 18: 264–269 (2007), reg. rev.

Woody lianas without tendrils. Leaves usually with scattered black dots abaxially. Inflorescences axillary and terminal cymes. Flowers 4-merous; calycine colleters in single row; corolla cream, yellow or orange; stamens inserted around middle of corolla tube; filaments short; ovary bilocular, glabrous or pubescent; placentation axile; ovules 2–3 per carpel; style-head globose. Berries soft, with pulp. Seeds not or only slightly compressed, without hilar groove, testa thin, smooth; endosperm scanty to absent, cotyledons fleshy, deeply incised at the base.

Four spp. recognized in the most recent revision, in western Malesia, in tropical rainforest up to 1000 m, usually lower.

### 20. *Cyclocotyla* Stapf

*Cyclocotyla* Stapf, Bull. Misc. Inform. Kew 1908: 259 (1908); Van der Ploeg, Agric. Univ. Wageningen Pap. 85-2: 57–85 (1985), rev.

Woody liana without tendrils. Leaves with closely spaced secondary veins. Inflorescences terminal

and axillary, many-flowered. Calycine colleters multiseriate; corolla white, pink or red; corolla lobes inflexed in bud; stamens inserted near base of corolla tube; nectary disc annular, higher than the ovary; ovary bilocular, without pulp, glabrous; placentation axile; ovules 4 per locule; style-head fusiform. Berries pale green, few-seeded. Seeds compressed, with a ridge on the antiraphe side; testa smooth; endosperm thin; cotyledons fleshy, spatulate.

One sp., *C. congolensis* Stapf, found in W and C Africa in primary and secondary forest, near rivers, at low altitudes.

### 21. *Willughbeia* Roxb.

*Willughbeia* Roxb., Pl. Coromandel 3: 77, t. 280 (1820), nom. cons.; Middleton, Blumea 38: 1–24 (1993), rev.; Middleton, Fl. Males. I, 18: 420–436 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 230–234 (2014), reg. rev.  
*Urnularia* Stapf (1901).

Woody lianas with branched tendrils formed from modified inflorescences. Inflorescences axillary, congested to lax, thyrsoid or cymose. Corolla white to yellowish; lobes spreading; stamens inserted at various heights; ovary glabrous, superior to partly inferior, unilocular; placentas parietal; ovules numerous; style-head ellipsoid with long apical apex. Berries large, spherical to pear-shaped; pulp edible. Seeds numerous, compressed, without a hilar groove, testa smooth; endosperm scanty to absent; cotyledons fleshy, rounded at base.

16 spp. in Asia from NE India, Sri Lanka, continental SE Asia, the Malay Peninsula, Borneo and Palawan, in primary and secondary forest, and peat swamps, up to 1600 m.

### 22. *Cylindropsis* Pierre

*Cylindropsis* Pierre, Bull. Mens. Soc. Linn. Paris II, 1: 38 (1898). Pichon, Mém. Inst. Franç. Afrique Noire 35: 329–331 (1953), rev.; Haegens, Bull. Jard. Bot. Nat. Belg. 63: 313–328 (1994), rev.

Woody liana with curled tendrils. Inflorescences axillary, sometimes also terminal, few-flowered, congested cymes. Corolla white, the tube sometimes greenish, tube about twice as long as the lobes; stamens inserted near the orifice of the

tube; filaments short, slender; ovary usually pubescent at the apex, unilocular with parietal placentation or incompletely bilocular (placentas meeting below) with seemingly axile placentation; ovules several per carpel; style-head cylindrical-pentagonal. Berries globose to ovoid, orange, edible, few- to several-seeded; pericarp smooth, spongy; pulp slimy. Seeds ellipsoid; endosperm scanty, cotyledons fleshy.

One sp., *C. parvifolia* Pierre, in Nigeria and C Africa, in rainforest and riverine forest up to 700 m.

### 23. *Clitandra* Benth.

*Clitandra* Benth. in Hook., Niger Fl. 445 (1849); Pichon, Mém. Inst. Franç. Afrique Noire 35: 205–211 (1953); Leeuwenberg & Berndsen, Bull. Jard. Bot. Nat. Belg. 58: 159–168 (1988), rev.

Large liana with curled tendrils. Leaves with secondary veins closely spaced. Inflorescences axillary, often paired in the axils. Corolla white, pinkish or yellowish, pubescent on the outer surface; stamens inserted at about the middle region of corolla tube; filaments short, slender; ovary unilocular, pubescent on top; placentation parietal (sometimes meeting at top and bottom and there placentation seemingly axile); ovules few to several. Berries with a sclerified layer; pulp fibrous, red, edible. Seeds ovate, endosperm thick, cartilaginous, cotyledons membranous.

One sp., *C. cymulosa* Benth. in tropical Africa, from Guinea to Tanzania, in forests up to 1750 m.

### 24. *Vahadenia* Stapf

*Vahadenia* Stapf, Fl. Trop. Africa 4(1): 26, 29 (1902); Pichon, Mém. Inst. Franç. Afrique Noire 35: 266–272 (1953), rev.; Haegens, Bull. Jard. Bot. Nat. Belg. 63: 313–328 (1994), rev.

Large lianas with tendrils. Inflorescences axillary or terminal, cymose. Calycine colleters numerous, irregularly 3–5-seriate; corolla white, reddish at base; lobes about as long as the tube; stamens inserted ca. midway or somewhat below in the corolla tube; ovary unilocular, pubescent at apex; placentation parietal; ovules many; style-head cylindrical. Berries glabrous, greenish, orange or

reddish; pulp edible. Seeds ellipsoid to somewhat irregularly shaped, somewhat compressed; endosperm thick, cartilaginous, cotyledons membranous.  $2n = 22$ .

Two spp. in tropical W Africa, from Guinea to the Ivory Coast, in humid forest, up to 1000 m.

### 25. *Dictyophleba* Pierre

*Dictyophleba* Pierre, Bull. Mens. Soc. Linn. Paris II, 1: 92 (1898); Pichon, Mém. Inst. Franç. Afrique Noire 35: 250–265 (1953), rev.; Hoogh, Bull. Jard. Bot. Nat. Belg. 59: 207–226 (1989), rev.

Lianas or shrubs with curled tendrils. Inflorescences terminal, cymose, several- to many-flowered, often tendriloid. Corolla white, yellow, pink or red; lobes shorter to longer than the tube, with long cilia at the margins; stamens inserted at various levels in the tube; filaments short; ovary unilocular, glabrous; placentation parietal; ovules several to many; style-head ovoid to truncate-conical. Berries red, orange or yellow; pulp yellow, edible. Seeds somewhat irregularly compressed; endosperm thick, cartilaginous, cotyledons membranous.  $2n = 22$ .

Five spp. in tropical Africa, in forests, often on periodically inundated river banks, in gallery forests and savannas, up to 1300 m.

### 26. *Ancylobothrys* Pierre

*Ancylobothrys* Pierre, Bull. Mens. Soc. Linn. Paris II, 1: 91 (1898); Vonk et al., Wageningen Agric. Univ. Pap. 94-3: 1–44 (1994), rev.

Large lianas or low shrubs with large, curled, terminal tendrils. Inflorescences terminal panicles, sometimes reduced to a single cyme. Calyx with 1–5 alternisepalous colleters or colleters absent; corolla white to yellowish, sometimes rose-tinted; stamens inserted in lower 1/3 of corolla tube; ovary hairy, unilocular; placentas parietal; ovules several to many; style-head cylindrical to ovoid. Berries velutinous, yellow, orange or reddish, many-seeded; pulp edible; endosperm thick, cartilaginous, cotyledons membranous.  $2n = 22, 44, 66$ .

Seven spp. in Africa, one reaching Madagascar and the Comores.

### 27. *Chamaecлитandra* (Stapf) Pichon

*Chamaecлитandra* (Stapf) Pichon, Mém. Inst. Franç. Afrique Noire 35: 202–205 (1953), rev.; Leeuwenberg & Berndsen, Bull. Jard. Bot. Nat. Belg. 58: 159–168 (1988), rev.  
*Clitandra* sect. *Chamaecлитandra* Stapf (1902).

Rhizomatous shrub up to 1 m tall with erect shoots, without tendrils. Leaves glaucous, secondary veins relatively closely spaced. Inflorescences axillary and terminal few-flowered cymes. Corolla white to pinkish; ovary pubescent toward the apex, unilocular; placentas parietal; ovules few. Berries globose or pyriform, edible, without a sclerified layer. Seeds 1–33; endosperm thick, cartilaginous, cotyledons membranous.

One sp., *C. henriquesiana* (Hallier f.) Pichon, in tropical Africa in SE DR Congo, Angola and Zambia, at forest edges and woodland, up to 1500 m.

### 28. *Saba* (Pichon) Pichon

*Saba* (Pichon) Pichon, Mém. Inst. Franç. Afrique Noire 35: 302–324 (1953), rev.; Leeuwenberg & van Dilst, Bull. Jard. Bot. Nat. Belg. 59: 189–206 (1989), rev.  
*Landolphia* sect. *Saba* Pichon (1948).

Lianas (sometimes shrub-like) with curled tendrils. Inflorescences terminal or in forks, rarely axillary. Calycine colleters absent; corolla white or cream with yellow or orange throat; stamens inserted in lower half of corolla tube; ovary mostly pubescent at the top; placentas parietal; ovules numerous; style-head narrowly fusiform. Berries orange to red, with a sclerified layer; placentas becoming pulpy, pulp yellowish or orange, edible. Endosperm thick, cartilaginous, cotyledons membranous.  $2n = 22$ .

Three spp. in Tropical Africa, in riverine vegetation and open woodland, up to 1650 m.

### 29. *Orthopichonia* H. Huber

*Orthopichonia* H. Huber, Kew Bull. 15: 437 (1962); Pichon, Mém. Inst. Franç. Afrique Noire 35: 202–205 (1953), rev.; Vonk, Wageningen Agric. Univ. Pap. 89-4: 27–50 (1989), rev.

Lianas with tendrils. Leaves usually with numerous,  $\pm$  parallel secondary veins. Inflorescences usually axillary, if terminal then tendril-like. Corolla usually white; stamens inserted in lower

half of corolla tube; ovary glabrous to pubescent, unilocular to imperfectly bilocular; placentation parietal; ovules several to numerous; style-head ovoid. Berries green, yellow or orange, edible, with a sclerified layer. Seeds ellipsoid to reniform, smooth; endosperm thick, cartilaginous, cotyledons membranous.  $2n = 22$ .

Six spp. in Tropical W and C Africa, in tropical rainforest or humid savanna, up to 1500 m.

### 30. *Pacouria* Aubl.

*Pacouria* Aubl., Hist. Pl. Guiane. 268, pl. 105 (1775); Pichon, Mém. Inst. Franç. Afrique Noire 35: 245–250 (1953), rev.; Monachino, Lloydia 8: 291–317 (1945), rev.

Large woody lianas. Inflorescences terminal and pseudo-axillary, cymose, the axis long and tendriliform; flowers many, subsessile, clustered at the ends of the inflorescence branches. Corolla greenish white to cream; stamens inserted in lower half of corolla tube; ovary unilocular, pubescent; placentas parietal; ovules numerous; style-head spindle-shaped. Berries many-seeded, up to 10 cm diam.; pericarp thick, leathery; placentas not becoming pulpy. Seeds plano-convex, smooth; endosperm thick, cartilaginous, cotyledons membranous.

Two spp. in the Guianas, Amazonian Brazil and Bolivia, in evergreen lowland forests, up to 100 m.

It is disputed whether *Pacouria* should be recognized as distinct from *Landolphia*. The fruits are edible, and the latex is a source of gum.

### 31. *Landolphia* P. Beauv.

Fig. 30

*Landolphia* P. Beauv., Fl. Oware 1: 54 (1806), nom. cons.; Pichon, Mém. Inst. Franç. Afrique Noire 35: 40–202 (1953), reg. rev.; Persoon et al., Wageningen Agric. Univ. Pap. 92-2: 1–232 (1992), reg. rev.; van Dilst, Syst. Geogr. Pl. 69: 91–110 (1999), reg. rev.

*Carpodinus* R. Br. ex G. Don (1837).

*Aphanostylis* Pierre (1898).

*Anthoclitandra* (Pierre) Pichon (1953).

Lianas or shrubs with tendrils, rarely rhizomatous subshrubs. Inflorescences terminal and/or axillary cymes. Corolla white, cream, or yellow, sweet-scented; ovary glabrous or pubescent, unilocular or bilocular, placentation parietal with

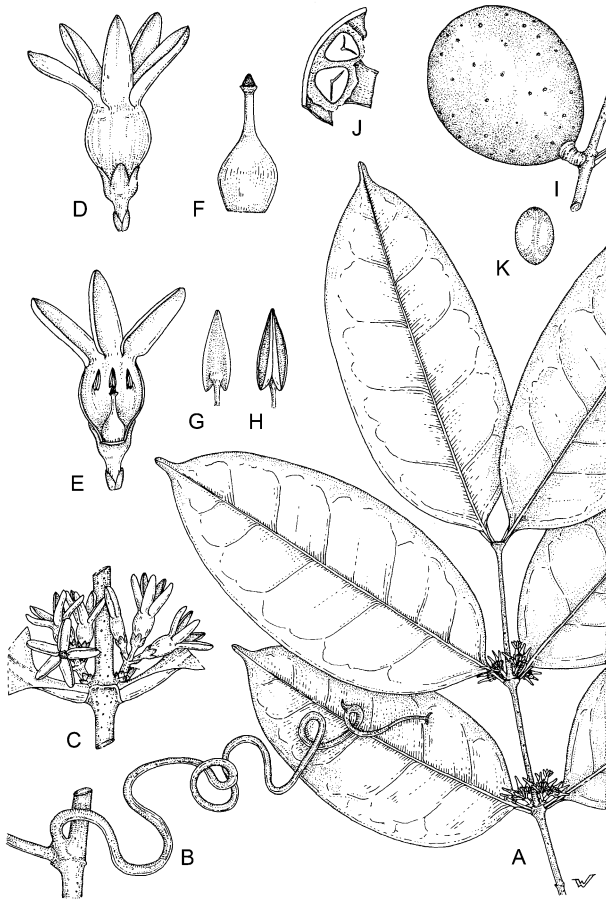


Fig. 30. Apocynaceae-Willughbeieae. *Landolphia letestui*. A Branch showing axillary inflorescences. B Tendril. C Inflorescences. D Flower. E Opened flower, showing spatial relationship of stamens and style-head. F Gynoecium. G Anther dorsal side. H Anther ventral side. I Fruit. J Fragment of fruit, showing seeds embedded in pulp. K Seed. (From Persoon et al. 1992, p. 124, with permission from the Library of Wageningen University, Wageningen; drawn by W. Wessel-Brand)

prominent placentas; ovules many. Berries mostly yellow, orange or brownish and often with lentils or rough spots, many-seeded, variously shaped, with a sclerified layer; placentas becoming pulpy, pulp sweet and acidic, edible. Seeds irregularly ellipsoid; endosperm thick, cartilaginous, cotyledons membranous.  $2n = 22$ .

A genus of about 56 spp. in Africa, Madagascar and the Mascarenes.

The delimitation of *Landolphia* has fluctuated greatly; the genus and its many segregate genera are in need of revision based on modern methods.

### 32. *Parahancornia* Ducke

*Parahancornia* Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 242 (1922); Monachino, Lloydia 6: 240–247 (1944), rev.; Zarucchi, Novon 1: 37–44 (1991), synop.; Zarucchi et al., Fl. Venez. Guayana 2: 543–545 (1995), reg. rev.

Shrubs or trees. Inflorescences terminal, cymose, usually many-flowered. Calyx normally 4-merous; corolla 5-merous, white to cream; stamens inserted in lower half of the tube; ovary unilocular, pubescent; placentation parietal; ovules numerous. Berries many-seeded; pericarp thick, leathery. Seeds not compressed, elliptic to ovate with a hilar groove, embedded in pulpy placentas; endosperm cartilaginous, superficially ruminant, with regular longitudinal furrows, cotyledons thin, tender, cordate at base.

Seven spp. in NW South America, in non-flooded evergreen lowland forests, on seasonally flooded margins of blackwater rivers or on granitic outcrops, sandstone or white sand savannas or gallery forests in these areas, up to 600 m.

### 33. *Hancornia* Gomes

*Hancornia* Gomes, Mem. Math. Phis. Acad. Real Sci. Lisboa 3: 51 (1812); Monachino, Lilloa 11: 19–48 (1945), rev.

Small tree; latex whitish, sometimes reddish or bluish tinged. Leaves with numerous  $\pm$  parallel secondary veins. Inflorescences terminal, few-flowered dichasia. Flowers relatively large; corolla white to yellowish; stamens inserted in upper quarter of corolla tube; filaments short; ovary unilocular; glabrous or pubescent at apex, placentation parietal; ovules numerous. Berries few-seeded. Seeds not compressed, elliptic to ovate with a hilar groove, embedded in pulpy placentas; endosperm cartilaginous, superficially ruminant, with regular longitudinal furrows, cotyledons thin, tender, attenuate at the base.

One extremely variable sp., *H. speciosa* Gomes, widespread in Brazil, reaching Paraguay and Argentina, often in sandy or rocky areas, up to 1500 m. The fruits are sold in markets. Extracts of the bark are used in folk medicine to treat internal disorders. The latex is used in a wide variety of folk remedies. The hard wood is used to manufacture small utility items.

### 34. *Couma* Aubl.

*Couma* Aubl., Hist. Pl. Guiane 2, supp. 39, t. 392 (1775); Monachino, Lloydia 6: 230–247 (1944), rev.

Shrubs or trees. Leaves in whorls of 3–4(5); petiole base with small interpetiolar flaps. Inflorescences axillary, cymose, few- to many-flowered. Corolla white to dark pink; stamens inserted at the middle of the tube or above; ovary unilocular, half-inferior; placentation parietal; ovules many. Glabrous, many-seeded berries with seeds embedded in pulpy placentas; pericarp thick, leathery. Seeds not compressed, elliptic to ovate with a hilar groove; endosperm cartilaginous, superficially ruminate, with regular longitudinal furrows, cotyledons thin, tender, cordate at base.

Six spp., one widespread from Guatemala to Amazonian Bolivia, the rest in Amazonia and Bahia, Brazil, in non-flooded forest, lower montane and montane forest, or on sandy soil in low forest adjacent to savannas, up to 1600 m. The latex is used as a milk substitute, as a base for chewing gum and for caulking canoes. The fruits are edible, and some species are sold in markets.

### 35. *Lacmellea* H. Karst.

*Lacmellea* H. Karst., Linnaea 28: 449 (1857); Monachino, Lloydia 275–302 (1944), rev.; Morales, Novon 8: 259–262 (1998), reg. rev.

Shrubs or trees; trunk in some species with deciduous blunt conical spines. Inflorescences axillary, cymose, few- to many-flowered. Corolla sometimes slightly zygomorphic, greenish white, white or cream; stamens inserted about the middle of the tube; ovary glabrous (rarely pubescent), unilocular; placentation parietal; ovules numerous. Berries yellow to orange, 1–3 cm diam., 1- to few-seeded; sweet, edible; pericarp thin. Seeds somewhat compressed, elliptic to ovate with or without a hilar groove, testa thick, tough; endosperm subcorneous, smooth; cotyledons thin, delicate, attenuate at the base.

Around 23 spp. in Central America and NW South America, in white sand savannas, periodically flooded white sand savannas, lower montane forests, and on granitic outcrops, often along rivers, up to 600 m. The latex of some species is

used as a milk substitute in tea and coffee; the fruits are eaten fresh and used for making juice or preserves.

The genus is in need of revision.

### I.5. Tribe *Tabernaemontaneae* G. Don (1837).

Trees or shrubs (1 species of *Callichilia* and 1–2 species of *Tabernaemontana* lianoid), almost always glabrous, with white latex; young stems often compressed or quadrangular. Leaves opposite, rarely in whorls of 3 (*Tabernaemontana ternifolia*); petioles of leaf pair often connate at the node, forming a short ocrea, this usually expanded into small intrapetiolar flaps, the blades isophyllous in Ambelaniinae, often anisophyllous in *Tabernaemontaninae*. Inflorescences axillary, terminal, or (usually paired) in the forks of branches. Flowers mostly medium-sized to very large and showy; calyx lobes mostly small, but sometimes larger and foliaceous or thick and fused into a tube in some genera of *Tabernaemontaninae*; calycine colleters mostly present and centered on the lower part of the sepal, often multiseriate, rarely absent, very rarely (*Carvalhoa*, *Tabernanthe*) alternisepalous; corolla usually salverform, but tubular-campanulate or infundibuliform in some genera of *Tabernaemontaninae*; corona absent; corolla lobes normally extended in bud, but inflexed in *Tabernaemontana*; corolla lobe aestivation almost always sinistrorse (dextrorse in *Schizozygia*, 1 species of *Callichilia* and 2 species of *Tabernaemontana*); stamens inserted at various levels in the corolla tube; anthers mostly sessile or nearly so, mostly with massive lignified guide rails (these absent in all species of *Tabernaemontana* from Asia and in some species from Australasia and one from Africa), usually included (but the tips exerted in a few species of *Tabernaemontana*); pollen 3–5-colporate, sometimes zonocolporate; in *Callichilia* in tetrads; nectary disc surrounding the base of the ovary adnate, indistinct or more rarely fleshy and free (in some genera of *Tabernaemontaninae*); ovary syncarpous or apocarpous, glabrous (except in *Macoubea*); ovules numerous in most genera; style slender or thick, sometimes twisted; style-head almost always with a strongly five-ribbed upper crest (star-shaped in cross-section) and the stigmatic region beneath an expanded basal flange

(subglobose and topped by two elongate slender appendages, without basal flange or upper crest and body uniformly receptive in all species of *Tabernaemontana* from Asia and in some species from Australasia and one from Africa). Fruit with fleshy, rarely woody, pericarp, endocarp not stony; either a berry with the non-arillate seeds embedded in pulp or projecting into the ovary on enlarged funicles (Ambelaniinae) or a pair of follicles (these sometimes hemi-syncarpous) with arillate seeds (most Tabernaemontaninae). Testa often wrinkled, pitted or with longitudinal ridges, often with a long hilar groove; endocarp not stony; endosperm often ruminant. Highly evolved indole alkaloids of the heynean type present.  $n = 11$ . 15 genera, mostly either in Africa or South America, *Tabernaemontana* pantropical.

### 36. *Ambelania* Aubl.

*Ambelania* Aubl., Hist. Pl. Guiane 1: 265, t. 104 (1775); Monachino, Lloydia 8: 109–130 (1945), rev.; Zarucchi, Agric. Univ. Wageningen Pap. 87-1: 23–40 (1988), rev.

Trees up to 25 m tall; young stems terete to subterete. Petioles of leaf pair often connate at the node, forming a short ocrea, the blades isophyllous. Inflorescences axillary. Calycine colleters absent; corolla white to orange, lobes about as long as tube; stamens inserted about middle of tube or below; ovary bilocular; ovules numerous. Berries bilocular, many-seeded, ovoid to elongate, sometimes ribbed; pericarp thick, leathery. Seeds projecting into ovary cavities on fleshy funicles; testa smooth to pitted.

Three spp., widespread in N South America in humid forest and forest edges up to 1000 m.

### 37. *Molongum* Pichon

*Molongum* Pichon, Mém. Mus. Natl. Hist. Nat. 24: 167 (1948); Zarucchi, Agric. Univ. Wageningen Pap. 87-1: 66–79 (1988), rev.

Shrubs or small trees up to 12 m tall; young stems terete to subterete. Petioles of leaf pair often connate at the node, forming a short ocrea, the blades isophyllous. Inflorescences terminal. Calycine colleters several, multiseriate; corolla lobes slightly longer than tube; stamens inserted about middle of tube; ovary bilocular; ovules numerous per carpel. Berries bilocular, few-seeded, nar-

rowly ellipsoid to narrowly ovoid; pericarp indurated, thin. Seeds embedded in fluffy, white pulp; testa muriculate and finely reticulate.

Three spp., Amazonia, in sandy soil in riparian forests along blackwater rivers, or in open sandy savannas, up to 200 m.

### 38. *Spongiosperma* Zarucchi

*Spongiosperma* Zarucchi, Agric. Univ. Wageningen Pap. 87(1): 48–66 (1988), rev.

*Molongum* sect. *Trichosiphon* Pichon (1948).

Shrubs or small trees up to 6 m tall; young stems terete to subterete. Petioles of leaf pair often connate at the node, forming a short ocrea, the blades isophyllous. Inflorescences terminal. Calycine colleters in a single row; corolla lobes about as long as tube; stamens inserted below middle of tube; ovary bilocular; ovules numerous per carpel. Berries unilocular (due to septum tearing during fruit maturation), many-seeded, globose, obovoid, narrowly ellipsoid to fusiform; pericarp thick, leathery. Seeds attached to fruit wall by fleshy funicles, not embedded in pulp; testa spongy, finely pitted, covered with irregular protuberances.

Six spp. in Amazonia, in sandy soil in seasonally flooded forests along blackwater streams or savannas over sandy soil, up to 600 m.

### 39. *Rhigospira* Miers

*Rhigospira* Miers, Apocyn. S. Amer. 67, t. 10 (1878); Pichon, Mém. Mus. Natl. Hist. Nat. 24: 169, t. IV, 18, 28, 39 (1948), synop.; Zarucchi, Agric. Univ. Wageningen Pap. 87(1): 79–86 (1988), rev.

Tree up to 30 m tall; young stems strongly quadrangular, becoming terete with age. Petioles of leaf pair often connate at the node, forming a short ocrea, the blades isophyllous. Inflorescences terminal. Calycine colleters absent; corolla lobes less than half the length of the tube; stamens inserted near base of tube; ovary bilocular; ovules numerous per carpel. Berries unilocular (due to septum tearing during fruit maturation), ellipsoid to obovoid, many-seeded; pericarp indurated, grainy. Seeds embedded in red to maroon, acidic pulp; testa irregularly reticulate.

One sp., *R. quadrangularis* (Müll. Arg.) Miers, in C and NW South America, in evergreen lowland and lower montane forests.



#### 40. *Mucoa* Zarucchi

*Mucoa* Zarucchi, Agric. Univ. Wageningen Pap. 87-1: 40-48 (1988), rev.

Trees up to 15 m tall; young stems compressed, becoming terete with age. Petioles of leaf pair often connate at the node, forming a short ocrea, the blades isophyllous. Inflorescences axillary. Calycine colleters many, multiseriate; corolla lobes about as long as tube; stamens inserted just below middle of tube; ovary bilocular; ovules numerous per carpel. Berries bilocular, globose to ellipsoid, many-seeded; pericarp indurated, grainy. Seeds embedded in stringy, aromatic pulp; testa shiny, finely reticulate.

Two spp., Amazonia, in montane forest up to 1400 m.

#### 41. *Neocouma* Pierre

*Neocouma* Pierre, Bull. Soc. Mens. Soc. Linn. Paris II, 1: 33 (1898); Zarucchi, Agric. Univ. Wageningen Pap. 87-1: 86-94 (1988), rev.

Trees up to 25 m tall; young stems terete to subterete, with large petiole scars. Petioles of leaf pair often connate at the node, forming a short ocrea, this usually expanded into small intrapetiolar flaps, the blades isophyllous. Inflorescences terminal. Calycine colleters numerous, multiseriate; corolla lobes shorter to much longer than tube; stamens inserted about middle of tube; ovary bilocular; ovules numerous per carpel. Berries uni- or bilocular, ellipsoid to globose, few- to many-seeded; pericarp crustaceous, thin. Seeds embedded in somewhat stringy pulp; testa finely pitted with irregular protuberances.

Two spp., NW Amazonia, in non-flooded and upland forests up to 900 m.

#### 42. *Macoubea* Aubl.

*Macoubea* Aubl., Hist. Pl. Guiane 2 (Suppl.): 17, t. 378 (1775); Monachino, Lloydia 8: 291-317 (1945), rev.; Morales, Novon 9: 86-88 (1999), synop.

Trees, sometimes exceeding 30 m height; young stems subterete. Petioles of leaf pair often connate at the node forming a short ocrea with interpetiolar flaps, the blades isophyllous. Inflorescences

terminal, dichasial, usually many-flowered. Calycine colleters several, 1-3-seriate; corolla rather thin, lobes longer than tube; stamens inserted near base of tube; ovary apocarpous to hemisyncarpous, puberulent to densely sericeous; placentation marginal; ovules numerous per carpel. Berries many-seeded, up to 2/3 syncarpous or only 1 carpel developing and fruit asymmetric, clog-shaped; pericarp thick, woody. Seeds with thin, translucent membrane that liquefies at maturity; testa pitted, with shallow hilar depression.

Three spp., tropical Central and South America, in humid forest at lower elevations.

#### 43. *Callichilia* Stapf

*Callichilia* Stapf, Fl. Trop. Africa 4(1): 130 (1902); Beentje, Meded. Landbouwhogeschool Wageningen 78-7: 1-32 (1978), rev.

*Ephippiocarpa* Markgr. (1923).

Mostly erect shrubs (one species said to be climbing); young stems terete. Leaves sessile or petiolate, blades of a pair isophyllous or anisophyllous. Inflorescences 1-2 in forks, cymose, 1- to several-flowered, pendulous, conspicuously bracteate at base. Calyx lobes foliaceous, often unequal, with 1-4 rows of colleters within; corolla tubular-infundibuliform, white; tube fleshy, longer than lobes; corolla lobe aestivation rarely dextrorse; nectary disc fleshy, shallowly lobed; ovary apocarpous or hemi-syncarpous (*C. orientalis* S. Moore); ovules numerous. Follicles free to nearly completely united, sometimes only tardily dehiscent, pulp juicy. Aril thin,  $\pm$  translucent.  $2n = 22$ .

Seven spp. in tropical Africa, in rainforest, secondary or riverine forest, especially in moist localities, near streams up to 1000 m.

#### 44. *Voacanga* Thouars

Fig. 31

*Voacanga* Thouars, Gen. Nov. Madagasc. 10 (1806); Leeuwenberg, Agric. Univ. Wageningen Pap. 85-3: 1-122 (1985), rev.; Middleton, Fl. Males. I, 18: 411-420 (2007), reg. rev.

Trees and shrubs; young stems terete to subterete. Petioles of leaf pair often connate at node, the blades isophyllous or anisophyllous. Inflorescences paired in branch forks. Calyx of free

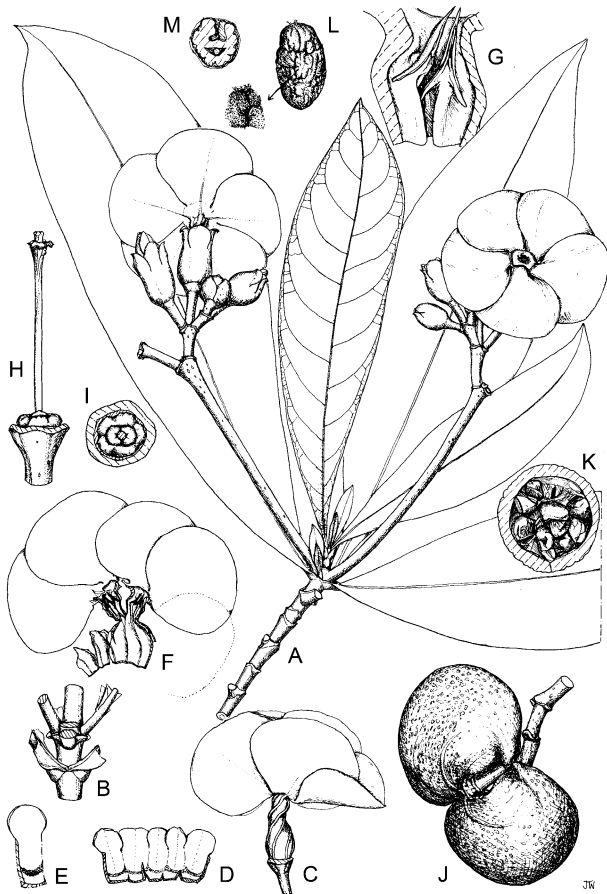


Fig. 31. Apocynaceae-Tabernaemontaneae. *Voacanga grandifolia*. A Flowering branch. B Part of branch, showing connate leaf bases at nodes. C Flower with calyx removed showing twisted corolla tube. D Opened calyx with colleters spread across the base. E One calyx lobe with colleters near the base. F Opened corolla. G Section through top of corolla tube showing exerted anther apices. H Gynoecium with fleshy lobed nectary disc at base. I Ovary surrounded by nectary disc seen from above. J Fruit. K Section through fruit, showing seeds. L Seed (arrow: detail of testa). M Transverse section through seed showing deep hilar groove and ruminant endosperm. (From Leeuwenberg 1985, p. 54, with permission from the Library of Wageningen University, Wageningen; drawn by J. Beentje-Williamson)

lobes or fused into tube; calycine colleters usually multiseriate; corolla mostly cream or yellow; tube twisted; stamens inserted in upper half of corolla tube; nectary disc annular, sometimes lobed, adnate to ovary base; ovary apocarpous, hemi-syncarpous or syncarpous; ovules numerous per carpel. Follicles free to completely united, green

spotted, white, yellow or orange. Aril yellow to orange-red, pulpy.  $2n = 22$ .

Twelve spp. in tropical Africa, Malesia and Australia (Queensland).

#### 45. *Calocrater* K. Schum.

*Calocrater* K. Schum. in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 175, t. 58, s-t. (1895); Hallé, Adansonia 5: 507-510 (1965), synop.; Leeuwenberg, Fontqueria 42: 11-16 (1995), rev.

Single-stemmed or once-branched shrub; young stems terete. Leaves sessile, large and thin; petioles of leaf pair often connate at node, the blades isophyllous. Inflorescences axillary, few-flowered; peduncle with many sepal-like bracts. Flowers large, sessile; calycine colleters in single row; corolla infundibuliform-campanulate; tube thin; lobes much shorter than tube; stamens inserted in lower 1/3 of corolla tube; ovary glabrous, 2/3 or more syncarpous; ovules several per carpel. Fruit syncarpous, subglobose to ellipsoid, yellow to orange, bicuspidate at the apex. Aril white.

One sp., *C. preussii* K. Schum., found in Cameroon, Gabon and DR Congo, in the shady forest understory, often on creek banks, up to 500 m.

#### 46. *Crioceras* Pierre

*Crioceras* Pierre, Bull. Mens. Soc. Linn. Paris 1: 1311 (1897); Hallé, Adansonia 11: 301-308 (1971), synop.; Leeuwenberg, Fontqueria 42: 11-16 (1995), rev.

Shrub or small tree up to 8 m tall; young stems terete. Leaves sessile, large and thin, those of a pair isophyllous or anisophyllous. Inflorescences axillary, long-pedunculate, with 1(-3) large pendulous flowers; pedicels with large foliaceous bracts completely covering sepals. Calycine colleters in single row; corolla tubular-campanulate; tube thin, lobes much shorter than tube; stamens inserted at base of expanded mouth; ovary  $\pm$  apocarpous or hemi-syncarpous; ovules numerous. Fruit hemi-syncarpous, ellipsoid with recurved apex. Seeds ellipsoid. Aril thin, white.

One sp., *C. dipladeniiflorus* (Stapf) K. Schum., in Cameroon, Gabon, DR Congo and Angola, in the shady forest understory, up to 600 m.

47. *Carvalhoa* K. Schum.

*Carvalhoa* K. Schum., in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 189 (1895); Leeuwenberg, Agric. Univ. Wageningen Pap. 85-2: 49–55 (1985), rev.

Shrubs or small trees; young stems terete to subterete. Petioles of leaf pair often connate at the node, forming a short ocrea, the blades isophyllous or anisophyllous. Inflorescences axillary, paired in the forks, few-flowered panicles. Calycine colleters alternisepalous, rarely in a single row; corolla campanulate, white to pale yellow; tube thin, with many red stripes distally and at base of lobes; lobes suborbicular, much shorter than tube; stamens inserted in lower part of corolla tube; nectary disc annular, fleshy, adnate to base of ovary; ovary apocarpous; ovules numerous. Follicles yellow or pale orange, soft, thin-walled. Aril dark orange, pulpy.

Two spp. in E Africa, in montane rainforest or secondary forest, up to 1900 m.

48. *Schizogygia* Baill.

*Schizogygia* Baill., Bull. Mens. Soc. Linn. Paris 1: 752 (1888); Barink, Meded. Landbouwhogeschool Wageningen 83-7: 47–53 (1983), rev.

Shrub or small tree up to 8 m tall; young stems terete to subterete. Leaves sessile, those of a pair isophyllous. Inflorescences axillary, congested, few-flowered, usually paired in the branch forks. Calyx foliaceous; calycine colleters several, in a single row; corolla yellow; tube thin; the lobes somewhat shorter than tube; corolla lobe aestivation dextrorse; stamens inserted at about middle of corolla tube; nectary disc adnate to lower part of ovary; ovary apocarpous; ovules several per carpel. Follicles dry, thinly coriaceous, laterally compressed, irregularly grooved, yellow to orange. Aril thin, yellow to orange-red, pulpy.  $2n = 22$ .

One sp., *S. coffaeoides* Baill. in C and E Africa, in rainforest understory or bush.

49. *Tabernanthe* Baill.

*Tabernanthe* Baill., Bull. Mens. Soc. Linn. Paris 1: 783 (1889); Vonk & Leeuwenberg, Wageningen Agric. Univ. Pap. 89-4: 1–26 (1989), rev.

Shrubs or small trees up to 4 m tall; young stems terete to subterete. Leaves of a pair isophyllous or anisophyllous. Inflorescences paired in the branch forks, few- to many-flowered, corymbose. Calycine colleters few, alternisepalous; corolla white to pale yellow or orange, mostly with pink to violet markings in the throat; tube thin, longer than the lobes; stamens inserted about midway in the corolla tube; ovary congenitally syncarpous to nearly completely apocarpous; ovules several to numerous per carpel. Fruiting carpels fused and smooth or separate and with soft prickles, yellow, orange or red. Aril white, pulpy.  $2n = 22$ .

Two spp. in C Africa.

50. *Tabernaemontana* L.

*Tabernaemontana* L., Sp. Pl. 1: 210 (1753); Leeuwenberg, Rev. Tabernaemontana 1 (1991), 2 (1994), reg. revs.; Morales & Méndez, Candollea 60: 345–371 (2005), reg. rev. (as *Stemmadenia*); Middleton, Fl. Males. I, 18: 371–390 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 184–202 (2014), reg. rev.

*Pandaca* Noronha ex Thouars (1806).

*Rejoua* Gaudich. (1829).

*Conopharyngia* G. Don (1837).

*Bonafousia* A. DC. (1844).

*Peschiera* A. DC. (1844).

*Stemmadenia* Benth. (1844).

*Anacampta* Miers (1878).

*Anartia* Miers (1878).

*Gabunia* K. Schum. (1896).

*Ervatamia* (A. DC.) Stapf (1902).

*Pagiantha* Markgr. (1935).

*Stenosolen* Markgr. (1937).

*Hazunta* Pichon (1948).

*Muntafara* Pichon (1948).

*Pandacastrum* Pichon (1948).

*Woytkowskia* Woodson (1960).

*Camerunia* (Pichon) Boiteau (1976).

*Leptopharyngia* (Stapf) Boiteau (1976).

*Sarcopharyngia* (Stapf) Boiteau (1976).

Shrubs or small trees, mostly between 1–15 m tall (but a few species may be much taller); young stems terete to subterete. Leaves opposite, rarely in whorls of 3; petioles of leaf pair often connate at node, forming a short ocrea, this usually expanded into small intrapetiolar flaps, the blades sometimes anisophyllous. Inflorescences usually paired in branch forks. Calycine colleters often numerous, multiseriate; corolla white, yellow or mauve; tube sometimes twisted; lobes inflexed in bud; stamens inserted at various levels in corolla

tube; anther tips sometimes exerted; ovary apocarpous, sometimes hemi-syncarpous; ovules several to many. Follicles normally free, sometimes hemi-syncarpous, slender and elongate to globose, sometimes echinate or warty; pericarp thin and delicate to thick and fleshy, spongy or woody, sometimes indehiscent. Seeds few to many; aril white, gray, orange or red, pulpy.  $2n = 22, 33$ .

Pantropical genus of some 122 spp. A few species are planted as ornamentals.

#### I.6. Tribe Amsonieae M.E. Endress (2014).

Subshrubs or perennial herbs with white latex. Leaves alternate. Calycine colleters absent; corolla salverform; corolla lobe aestivation sinistrorse; anthers free from the style-head, wholly fertile, included; nectaries absent, adnate or indistinct; ovary apocarpous; ovules numerous; style-head squat, with a collar at the base and a conspicuous wreath of hairs around the top. Fruit a pair of delicate follicles. Seeds naked, not compressed, oblong to ovoid with slanted ends; testa not smooth. Indole alkaloids present.  $x = 11$ . One genus in southern USA, Japan and Europe.

#### 51. *Amsonia* Walter

*Amsonia* Walter, Fl. Carol. 98 (1788); Woodson, Ann. Missouri Bot. Gard. 15: 379–435 (1928), rev.; Woodson, R.E., Jr., North American Fl. 29: 126–131 (1938), reg. rev.; McLaughlin, Ann. Missouri Bot. Gard. 69: 336–350 (1982), reg. rev.

*Rhazya* Decne (1835).

Subshrubs or perennial herbs. Leaves alternate. Inflorescences terminal, few- to many-flowered thyrses or corymbs. Flowers medium-sized, relatively showy; calycine colleters absent; corolla thin, white, blue or pink, the tube not strongly constricted or with thickened annulus at the orifice; filaments slender; anthers without lignified guide rails or sagittate basal appendages; nectary disc absent, adnate or indistinct; ovary apocarpous; ovules numerous. Follicles terete, thin-walled. Seeds cylindrical, oblong to ovoid (in *A. stricta* flattened at the margins into two irregular ribs); testa rugulose, pitted or corky.  $2n = 22, 32$  or 16.

Genus with a disjunct distribution: ca. 16 spp. in SE to SW USA, one in Japan and one in Europe, mainly in woods, margins of streams, prairies, fields, sand hills and barrens, rocky ravines and canyons, mountain slopes and desert.

*Rhazya* is sometimes treated as a genus distinct from *Amsonia*, but molecular evidence to support this is lacking.

#### I.7. Tribe Melodineae G. Don (1837).

Trees, shrubs or woody lianas, tendrils absent; latex white (sometimes yellow in *Diplorhynchus* and *Pycnobotrya*). Leaves opposite or whorled. Inflorescences terminal and in the upper leaf axils. Flowers mostly small- to medium-sized; calycine colleters usually absent (reported in a few species of *Melodinus*); corolla salverform, sometimes unfused (with gaps) just above the insertion of the stamens; corolla lobe aestivation sinistrorse; small corolline corona lobes often present in petal sinuses or behind the anthers (well-developed and usually annular and petaloid in *Melodinus*); stamens included, stamens inserted at various levels in the corolla tube; anther connective with an apical extension in *Diplorhynchus*, and with both apical connective extension and small sterile basal lobes in *Pycnobotrya*; pollen usually 3-colporate (in tetrads in some *Melodinus* species, and porate tetrads in *Craspidospermum*); nectary disc absent or an adnate, indistinct ring around the base of the ovary; ovary apocarpous or congenitally syncarpous (hemi-syncarpous in *Diplorhynchus*); ovules few to numerous per carpel; style slender, often short; style-head mostly without basal collar or upper wreath. Fruit mostly a pair of follicles with woody pericarp (fruit a capsule in *Craspidospermum* and a berry with sclerotic outer pericarp in *Melodinus*); endocarp not stony. Seeds usually numerous, smooth, flat and winged, often peltately attached with a long funicle (somewhat verrucose, only slightly compressed and embedded in pulpy placenta in *Melodinus*); endosperm mostly thin. Indole alkaloids present.  $x = 10, 11$ . Five genera, most restricted to Africa or Madagascar, *Melodinus* widespread in the Paleotropics.

This tribe is morphologically heterogeneous, likely non-monophyletic and sorely in need of molecular phylogenetic study.

#### 52. *Diplorhynchus* Welw. ex Ficalho & Hiern.

*Diplorhynchus* Welw. ex Ficalho & Hiern., Trans. Linn. Soc. London, Bot. II, 2: 22, t. 5 (1881); Plaizier, Meded. Landbouwhogeschool Wageningen 80-12: 28–40 (1980).

Shrub or small many-stemmed tree with many raised lenticels (occasionally reported as scrambling). Leaves opposite. Inflorescences thyrses. Corolla white to cream, with a strong jasmine-like scent; stamens inserted about midway in corolla tube; filaments flattened toward the apex; anthers with sterile apical and basal appendages; ovary hemi-syncarpous; placentation parietal; ovules four per carpel. Fruit apocarpous; follicles widely divergent, stout, woody, with much latex. Seeds obliquely oblong, peltately attached, with a large, elongate wing on one end.  $2n = 22$ .

One sp., *D. condylocarpon* (Müll. Arg.) Pichon in tropical and S Africa, usually found in wetter spots in savannas and open forests, up to 1700 m.

### 53. *Pycnobotrya* Benth.

*Pycnobotrya* Benth. in Benth. & Hook. f., Gen. Pl. 2: 688, 715 (1876); Van der Ploeg, Meded. Landbouwhogeschool Wageningen 83-4: 13–20 (1983), rev.

Large woody liana. Leaves opposite or ternate. Inflorescences many-flowered panicles. Corolla pink, sometimes with pale yellow throat, rotate, fragrant; stamens inserted below the middle of corolla tube; anthers sessile, with sterile basal appendages and an elongate, apical connective appendage; ovary apocarpous; ovules four per carpel; style very short. Fruit apocarpous; follicles broadly and obliquely elliptic, laterally compressed, warty. Seeds 1–4 per carpel, obliquely oblong, peltately attached, surrounded by a papery wing that is thickened at the margins.

One poorly known sp., *P. nitida* Benth., in W and C Africa, in forest, often on river banks.

### 54. *Stephanostegia* Baill.

*Stephanostegia* Baill., Bull. Mens. Soc. Linn. Paris 1: 748 (1888); Leeuwenberg, Wageningen Agric. Univ. Pap. 97-2: 95–102 (1997), rev.

Trees. Leaves opposite, coriaceous. Inflorescences lax cymes. Corolla white or lilac, the tube incompletely fused behind the stamens, with a thickened ring constricting the orifice; stamens inserted in upper half of corolla tube, filaments very short; ovary apocarpous; ovules ca. 10 per carpel. Follicles ellipsoid, woody. Seeds few to several per carpel, elliptic to ovate, peltately attached, surrounded by an elliptic papery wing.

Two spp. endemic to Madagascar, in wet or lowland forest, up to 400 m.

### 55. *Craspidospermum* Bojer ex A. DC. Fig. 32

*Craspidospermum* Bojer ex A. DC., Prodr. 8: 323 (1844); Leeuwenberg, Wageningen Agric. Univ. Pap. 97-2: 11–16 (1997), rev.

Tree; branches angled near apex. Leaves in whorls of 3–4(–6), coriaceous. Inflorescences many-flowered thyrses. Corolla white to rose, often with dark pink or red tube; tube incompletely

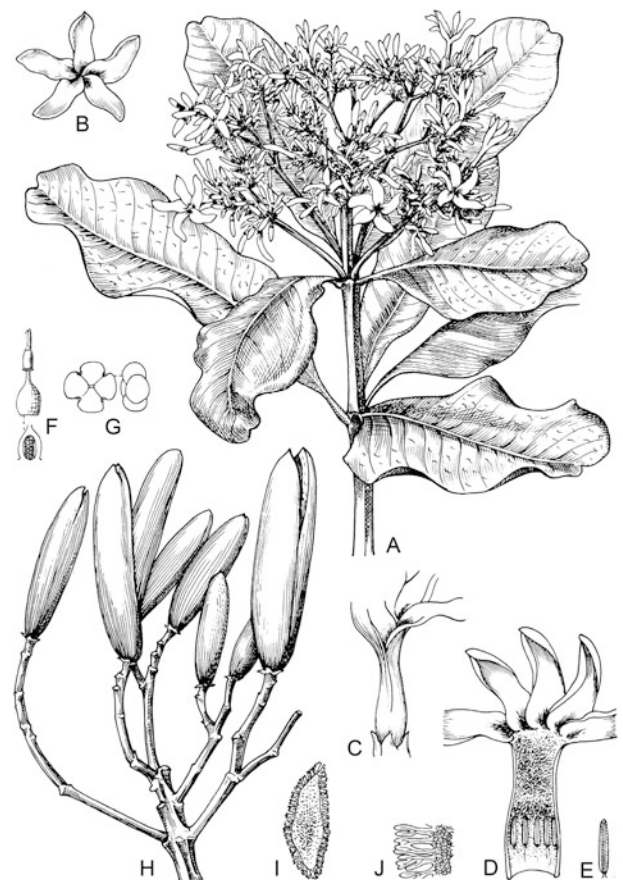


Fig. 32. Apocynaceae-Melodineae. *Craspidospermum verticillatum*. A Flowering branch. B Flower viewed from above. C Corolla, detail of tube and base of lobes. D Opened corolla. E Stamen ventral side. F Gynoecium and longitudinal section through ovary showing median cylindrical placenta with many ovules. G Non-tetrahedral, porate pollen tetrad, top and side view. H Fruiting branch, showing dehiscence into two halves. I Seed. J Detail of seed margin showing flattened, fringed emergences. (From Markgraf 1976, p. 99; drawn by M. Rabarijaona)

fused behind the stamens, inside with moniliform hairs above the stamens; stamens inserted near the base of the tube; pollen porate, in tetrads; ovary congenitally syncarpous; placentation parietal; style-head apical appendages long, slender. Fruit syncarpous, a 2-valved woody capsule. Seeds compressed, elliptic, with flattened, fringed emergences around the margin.

One sp., *C. verticillatum* Bojer ex A. DC., endemic to Madagascar, in rainforest up to 1800 m.

#### 56. *Melodinus* J.R. Forst. & G. Forst.

*Melodinus* J.R. Forst. & G. Forst., Char. Gen. Pl. 37, t. 19 (1776); Pichon, Mém. Mus. Natl. Hist. Nat. II, 24: 125–130 (1948), synop.; Markgraf, Blumea 19: 149–166 (1971), reg. rev.; Leeuwenberg, Syst. Geogr. Pl. 73: 3–62 (2003), rev.; Middleton, Fl. Males. I, 18: 270–281 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 127–139 (2014), reg. rev.

*Clitandropsis* S. Moore (1923).

Woody lianas. Leaves opposite, rarely ternate. Inflorescences cymose, axillary and/or terminal. Calycine colleters almost always absent; corolla white to orange; petaloid corolline corona in mouth; stamens inserted at about the middle of corolla tube or below; filaments short; ovary congenitally syncarpous, unilocular, placentation parietal; ovules numerous. Fruit a subglobose to pear-shaped berry; pericarp with a sclerotic outer layer. Seeds not compressed, without a hilar groove, embedded in pulpy placentas; endosperm fleshy, superficially irregularly wrinkled, cotyledons thin, cordate at the base.  $2n = 22$ .

About 25 spp. currently recognized, widespread in the Paleotropics, Australasia and Oceania.

The genus is in need of a new revision.

#### I.8. Tribe Hunterieae Miers (1878).

Glabrous trees or shrubs, rarely lianas, with white latex (latex sometimes translucent in *Gonioma*). Leaves opposite, rarely in whorls of 3. Inflorescences cymose. Flowers mostly small to medium-sized, with a strong sweet scent; calycine colleters absent or, when present, several and multiseriate; corolla salverform; corolla lobe aestivation sinistorse; corona absent; stamens inserted midway or above in the corolla tube; anthers ovate, without lignified guide rails, sometimes shortly sagit-

tate at the base, included; pollen 3-colporate; nectary disc an adnate or indistinct ring around the base of the ovary; ovary apocarpous, 2–5-carpellate, glabrous; ovules few to numerous; style-head ovoid to narrowly clavate, without basal collar or upper crest, but often with slender, elongate non-receptive apices. Fruit apocarpous, indehiscent, of 2–5 broadly divergent berries with fleshy, fibrous pericarp (fruit dehiscent, a pair of woody follicles in *Gonioma*); endocarp not stony. Seeds ovoid, without a longitudinal groove, embedded in pulp (seeds compressed with a papery wing at one end in *Gonioma*); endosperm smooth, mostly thick and rather hard. Indole alkaloids present.  $n = 11$ . Four genera in Africa, one in Madagascar and one reaching south and continental South-East Asia.

#### 57. *Gonioma* E. Mey.

*Gonioma* E. Mey., Comm. Pl. Afr. Austr. 188 (1837); Leeuwenberg, Wageningen Agric. Univ. Pap. 97-2: 16–21 (1997), rev.

Shrubs or small slender trees. Leaves in whorls of 3–4, the upper leaves often opposite. Inflorescences terminal, congested. Calycine colleters absent; corolla yellow; staminal filaments short; ovary 2-carpellate; ovules numerous. Fruit a pair of oblong, woody, longitudinally finely ribbed follicles. Seeds numerous, compressed, subrectangular, with a papery wing at one end.  $2n = 20$ .

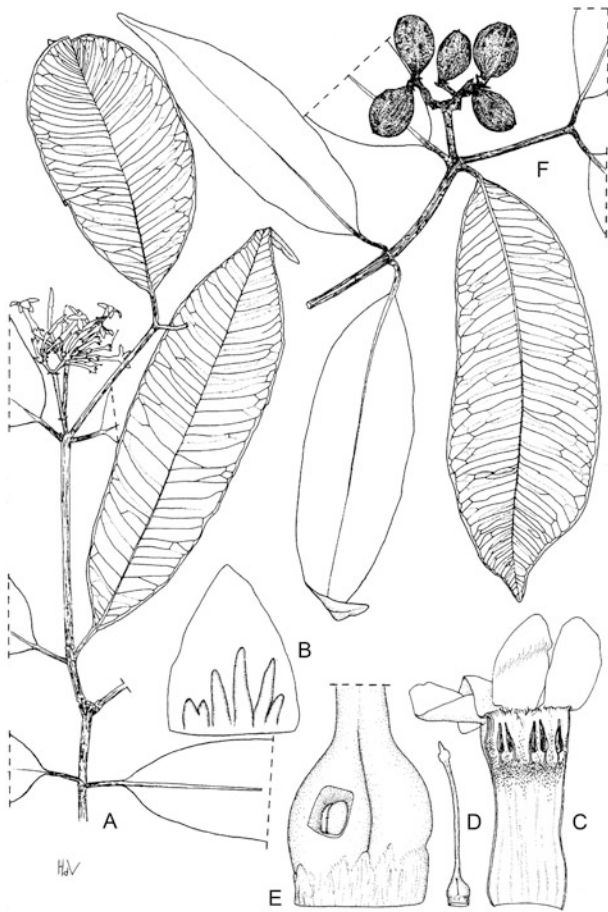
Two spp., one endemic to the Cape Province of South Africa, the other to Madagascar, in forest understory and dry forest up to 900 m. The hard wood is used to make small objects such as tool handles, shuttles, etc.

#### 58. *Hunteria* Roxb.

Fig. 33

*Hunteria* Roxb., Fl. Ind., ed. 1832, 1: 695 (1832); Omino, Wageningen Agric. Univ. Pap. 96-1: 88–128 (1996), rev.; Middleton, Fl. Males. I, 18: 200–203 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 102–105 (2014), reg. rev.

Trees, shrubs or rarely lianas. Leaves opposite, with numerous straight secondary veins. Inflorescences terminal, rarely axillary, few- to many-flowered dichasial cymes. Calycine colleters several, multiseriate; corolla white, yellow or red; staminal filaments short; ovary glabrous; style-



**Fig. 33.** Apocynaceae-Hunterieae. *Hunteria zeylanica*. **A** Flowering branch. **B** Inner surface of calyx lobe showing colleters at base. **C** Opened corolla showing position of stamens. **D** Gynoecium. **E** Ovary with section cut from wall showing the position of the two ovules. **F** Fruiting branch. (From Omino 1996, p. 122, with permission from the Library of Wageningen University, Wageningen; drawn by H. de Vries)

head ovoid with slender apex; ovary 2-carpellate; ovules 2–30 per carpel. Berries stipitate, subglobose to obovoid, yellow to orange, smooth or warty, often only one developing. Seeds few, smooth or slightly verrucose.  $2n = 22$ .

12 spp. in Africa, one of them, *H. zeylanica* (Retz.) Gardner ex Thwaites, also widespread in S and continental SE Asia; most species are found in primary or secondary forest often along streams or forest edges, usually at low elevations.

### 59. *Picalima* Pierre

*Picalima* Pierre, Bull. Mens. Soc. Linn. Paris 2: 1278 (1896); Omino, Wageningen Agric. Univ. Pap. 96-1: 81–177 (1996), rev.

Tree or shrub. Leaves opposite. Inflorescences terminal, sometimes axillary, compound umbellate cymes. Calycine colleters numerous, multi-seriate; corolla white to yellow, the tube often greenish, more or less the same length as the lobes; anthers with slightly developed basal appendages; ovary 2-carpellate; ovules numerous per carpel. Berries obovoid to ellipsoid or pear-shaped, somewhat compressed, yellow to orange. Seeds somewhat angular and irregularly shaped, embedded in soft pulp.  $2n = 22$ .

One sp., *P. nitida* (Stapf) T. Durand & H. Durand, in tropical Africa.

### 60. *Pleiocarpa* Benth.

*Pleiocarpa* Benth. in Benth. & Hook. f., Gen. Pl. 2: 699 (1876); Omino, Wageningen Agric. Univ. Pap. 96-1: 134–178 (1996), rev.

*Carpodinopsis* Pichon (1953).

Trees, shrubs or rarely lianas. Leaves opposite or in whorls of 3–5, glabrous. Inflorescences axillary, rarely terminal, fascicles. Flowers sessile; calycine colleters absent; corolla white to yellow; ovary 2–5-carpellate; ovules 1–6 per carpel. Berries subglobose to obovoid, or elliptic, yellow to orange, 1–6-seeded. Seeds angular, rather irregularly shaped.  $2n = 22$ .

Five spp. in Africa, in secondary or primary forest, montane forest, low bush, swampy areas, or along river banks up to 2000 m.

### I.9. Tribe Alyxieae G. Don (1837).

Trees, shrubs or woody lianas; latex white. Leaves often whorled, sometimes opposite or alternate. Inflorescences cymose, terminal and/or axillary, often congested. Flowers mostly small to medium-sized and inconspicuous; calycine colleters absent; corolla salverform (sometimes throat somewhat expanded in *Condylocarpon*); corolla lobes inflexed in bud or not; corolla lobe aestivation sinistrorse;

corona absent (rudimentary corona lobes reported in *Plectaneia*); stamens inserted in the upper half of corolla tube (usually lower in *Chilocarpus*, sometimes lower in *Alyxia*), included; filaments short; anthers ovate, without lignified basal appendages; nectary disc absent, indistinct or adnate; pollen 2–3-porate (sometimes barrel-shaped with two large pores, in tetrads in *Condylorpon*); ovary apocarpous or syncarpous, normally bicarpellate with axile or marginal placentation (up to 5-carpellate in *Lepinia* and *Lepiniopsis*, and in *Chilocarpus* unilocular with parietal placentation), sometimes stipitate; ovules 2 to several per carpel; style slender; style-head globose, ovoid or fusiform, without basal collar or upper wreath, body uniformly receptive. Fruit usually indehiscent (dehiscent in *Chilocarpus* and *Plectaneia*), with fleshy pericarp and stony endocarp (pericarp dry in *Condylorpon*, *Chilocarpus* and *Plectaneia*). Seeds usually globular or ovoid (not compressed), with deep hilar groove or depression and thick, strongly ruminant endosperm (in *Chilocarpus* seeds with an aril on the funicle and endosperm reported to be non-ruminant in some spp; in *Plectaneia* seeds compressed with wings and with non-ruminant endosperm). No alkaloids or cardenolides are known to occur in the tribe.  $x = 9$  (known only for *Alyxia*). Seven genera, six in the Paleotropics, one in Central and South America.

#### 61. *Chilocarpus* Blume

*Chilocarpus* Blume, Catalogus 22 (1823); Markgraf, Blumea 19: 161–166 (1971), reg. rev.; Middleton, Fl. Males. I, 18: 164–178 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 75–78 (2014), reg. rev. *Neokeithia* Steenis (1948).

Woody lianas. Leaves opposite, usually with numerous black dots beneath. Inflorescences terminal and/or axillary; pedicels sometimes with numerous bracteoles. Corolla variously colored, lobes strongly inflexed, forming a globose head in bud; stamens sometimes inserted below the middle of corolla tube; ovary syncarpous, unilocular; placentas parietal; ovules numerous. Fruit syncarpous, variously colored, leathery to woody, ellipsoid to globular or long, narrow and torulose, dehiscent. Seeds globular-ovoid, with a corky aril on the funicle; endosperm ruminant or smooth.

14 spp. in continental SE Asia and Malesia, mainly in evergreen forest or swamp forest up to 650 m.

#### 62. *Condylorpon* Desf.

*Condylorpon* Desf., Mém. Mus. Hist. Nat. 8: 119 (1822); Fallen, Ann. Missouri Bot. Gard. 70: 149–169 (1983), rev.

Woody lianas. Leaves opposite or in whorls of 3 (–4). Inflorescences terminal and axillary. Corolla salverform or narrowly infundibuliform (throat not constricted), white, yellow or orange, lobes often with a ligulate appendage, strongly inflexed and forming conspicuously globose head in bud; ovary apocarpous; ovules 4–6(–16) per carpel. Fruit apocarpous; drupes thinly woody, indehiscent, usually torulose, rarely only one uniovulate carpel developing; endocarp thick, leathery. Seeds fusiform, longitudinally folded with a deep groove from end to end.

Seven spp. in Brazil and the Guianas, one in Central America; found in coastal and lowland forest, usually near water.

#### 63. *Plectaneia* Thouars

*Plectaneia* Thouars, Gen. Nov. Madagasc. 11 (1806); Leeuwenberg, Wageningen Agric. Univ. Pap. 97-2: 81–95 (1997), rev.

Woody lianas, often shrubby. Leaves opposite. Inflorescences terminal and axillary. Corolla yellowish white, greenish yellow to yellow-brown, with five small corona lobes in the throat in the staminal sectors, the lobes not inflexed in bud; ovary seemingly apocarpous viewed externally, but carpels partially united ventrally; ovules many. Fruit of two fused follicles forming a septical capsule with four ribs or wings. Seeds compressed, subrectangular, peltately attached, with a papery wing at each end; endosperm not ruminant.

Three spp. currently recognized, endemic to Madagascar, in coastal forest, dry open forest or brush, up to 1500 m.

#### 64. *Pteralyxia* K. Schum.

*Pteralyxia* K. Schum. in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 151 (1895); Degener, Fl. Hawaiiensis, fam. 305 (1933), synop.; Wagner et al., Man. Fl. Pl. Hawai'i 1: 219–220 (1990), rev.

Trees; branches thick with prominent lenticels and leaf scars. Leaves alternate. Inflorescences terminal, congested. Corolla waxy, yellow-green,



lobes not inflexed in bud; ovary apocarpous; ovules 2 per carpel. Fruit with usually only one carpel maturing, drupaceous, fleshy, bright red; endocarp woody, with a network of crests and wings. Seeds 1 per carpel, not compressed; endosperm ruminant.

Two spp., one each endemic to Kauai and Oahu, Hawaii, on slopes and ridges in mesic to wet forest below 800 m.

#### 65. *Lepinia* Decne.

*Lepinia* Decne., Ann. Sci. Nat. Bot. 3, 12: 194, t. 9 (1849); Lorence & Wagner, Allertonia 7(4): 254–266 (1996), rev.; Endress et al., Allertonia 7(4): 267–272 (1997), fl. morph.; Middleton, Fl. Males. I, 18: 260–262 (2007), reg. rev.

Small trees or shrubs. Leaves alternate. Inflorescences apparently terminal but appearing axillary due to lateral prolongation of the axis, few-flowered. Corolla thick, white to cream, lobes shorter than the tube, strongly inflexed in bud; ovary stipitate, of 3–5 2-ovulate carpels, apocarpous but the apices remaining firmly postgenitally fused. Fruit basket-like, of 3–5 stipitate, indehiscent, woody, uniovulate carpels bowed outward in the middle and fused at the apex. Seeds elongate, with a long hilar groove; endosperm ruminant.

Four spp. disjunct across the Pacific Basin from New Guinea to the Marquesas Islands.

#### 66. *Lepiniopsis* Valetton

*Lepiniopsis* Valetton, Ann. Jard. Bot. Buitenzorg 12: 251, t. 28 (1895); Merrill, Bull. Bur. For. Philip. 1: 48 (1903), reg. rev.; Markgraf, Blumea 30: 169–172 (1984), reg. rev.; Middleton, Fl. Males. I, 18: 262–264 (2007), reg. rev.

Shrubs or small trees. Leaves alternate. Inflorescences axillary, long-pedunculate. Flowers  $\pm$  sessile. Corolla thick, white, lobes strongly inflexed in bud; ovary syncarpous, 3–5-locular; ovules two per locule. Fruit red to purple-black, plum-like, syncarpous, indehiscent, by abortion 1–3-locular, each locule uniovulate; mesocarp fibrous; endocarp lignified. Seeds elongate, with a long hilar groove; endosperm ruminant.

Two spp., one in the Philippines and E Malasia, the other on the Palau Islands, on sandy beaches or other open areas, lowland rainforest, sago swamps, up to 900 m.

#### 67. *Alyxia* Banks ex R. Br.

Fig. 34

*Alyxia* Banks ex R. Br., Prodr. 469 (1810), nom. cons.; Middleton, Blumea 45: 1–146 (2000), Blumea 47: 1–93 (2002), rev.; Middleton, Fl. Males. I, 18: 64–128 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 30–44 (2014), reg. rev.  
*Discalyxia* Markgr. (1927).

Woody lianas, shrubs, rarely small trees. Leaves in whorls of 3–4 or opposite. Inflorescences axillary, 1- to many-flowered; bracts with colleters immediately below the calyx in some species. Corolla usually white, cream or yellow, the tube sometimes orange or purple, lobes not inflexed in bud; ovary apocarpous; ovules 2–6 per carpel. Fruit apocarpous, a pair of stipitate, torulose drupes with 1–6 articles each, red, orange, black or yellow when ripe; mesocarp fleshy. Endosperm ruminant.  $2n = 36$ .

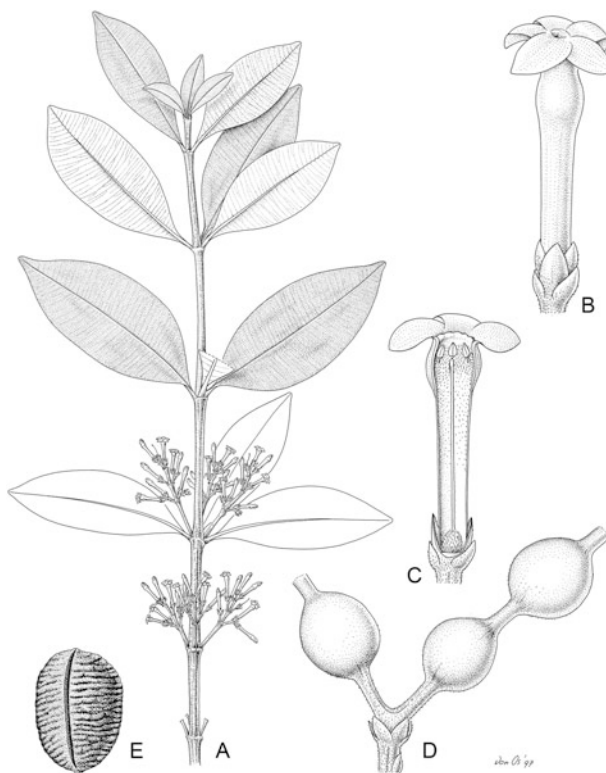


Fig. 34. Apocynaceae-Alyxieae. *Alyxia concatenata*. A Flowering branch. B Flower. C Open flower. D Fruit. E Seed showing ruminant surface with deep hilar groove. (From Middleton 2000, p. 42, with permission from Naturalis, Leiden; drawn by J. van Os)

Currently 106 spp. are recognized, from NE India, continental SE Asia, Malesia, Australia, and the Pacific Islands in various habitats and elevations.

#### I.10. Tribe *Plumerieae* E. Mey. (1838).

Trees or shrubs, rarely lianas; latex white. Leaves usually alternate, sometimes opposite (whorled in *Allamanda*). Inflorescences usually terminal in erect species and axillary in those that are lianoid. Flowers mostly large to medium-large and showy (smaller in *Cameraria* and *Anechites*); calycine colleters mostly absent (present in *Anechites*, *Thevetia* and some species of *Allamanda*); corolla salverform, infundibuliform or tubular-campanulate, the lobes not inflexed in bud; corolline corona often present below the petal sinuses behind stamens (usually much dissected in *Allamanda*) and infrastaminal appendages generally present; corolla lobe aestivation sinistrorse; stamens inserted at various levels in the corolla tube; anther connective often broadened resulting in sublateral dehiscence and with an elongate filiform apical appendage, these often exerted, anthers otherwise included, without lignified guide rails; pollen 3-colporate; nectary disc mostly absent (but well-developed in *Allamanda*, *Anechites* and *Thevetia*); ovary normally apocarpous (hemi-syncarpous in some species of *Thevetia* and *Cerbera* and postgenitally syncarpous in *Allamanda*), partly inferior in *Plumeria*, *Himatanthus* and *Mortoniella*; placentation normally marginal (axile at the base in hemi-syncarpous taxa, in *Allamanda* unilocular with parietal placentation); ovules many in the genera with woody dehiscent fruits, and 2–6 in genera with indehiscent fruits; style slender or thick; style-head with free apices conspicuously enlarged, mostly with basal collar or lobes (no distinct basal collar in *Plumeria*, *Himatanthus*, and *Mortoniella*), mostly without upper wreath (well-developed upper wreath present in *Allamanda*). Fruit usually apocarpous, sometimes hemi-syncarpous or syncarpous (in *Allamanda* postgenitally syncarpous), either indehiscent, and a pair of drupes or samaroids with fleshy or dry pericarp and stony endocarp, or dehiscent and a pair of dry, woody follicles (in *Allamanda* fruit a capsule, usually with spines). Seeds typically many in the genera with dehiscent fruits and 1–4 in those

with indehiscent fruits, usually compressed with a narrow wing-like margin or distinct papery wing. Cardenolides or iridoid glycosides present.  $x = 9, 10$ . Ten genera, eight in the Neotropics, one endemic on New Caledonia and one widespread in the Paleotropics.

#### 68. *Allamanda* L.

*Allamanda* L., Mant. Pl. 2: 146, 214 (1771); Sakane & Shepherd, Revista Bras. Bot. 9: 125–149. (1986), rev.; Morales, Phytotaxa 162: 51–56 (2014), reg. rev.

Shrubs, sometimes scandent. Leaves in whorls of (3–)4–5. Inflorescences terminal, sometimes also axillary, cymose, few- to several-flowered; sepals foliaceous, some species with colleters; corolla tubular-campanulate, yellow or violet; stamens inserted just below expanded upper part of the tube; anthers with sagittate, but non-lignified basal appendages; ovary superior; ovules many; style-head spool-shaped with a well-developed wreath at the top and collar at the base. Fruit a septicidal capsule, usually subglobose and spiny, rarely compressed and without spines; seed wing circular.  $2n = 18, 36$ .

14 spp. in tropical America, often at forest margins or river banks, sometimes in cerrado, caatinga or rocky areas, up to 1000 m. Two species, *A. cathartica* L. and *A. schottii* Pohl, widely cultivated and naturalized throughout the tropics.

#### 69. *Mortoniella* Woodson

*Mortoniella* Woodson, Ann. Missouri Bot. Gard. 26: 257 (1939); Morales, Darwiniana, n.s. 43: 138–139 (2005), reg. rev.

Tree up to 30 m. Leaves alternate; petioles at about mid-length with an adaxial cluster of long, tooth-like colleters. Inflorescences terminal, cymose, thyriform, several-flowered; bracts small, scarious, caducous, without colleters at the base. Calyx lobes thin, caducous, eglandular at the apex; corolla salverform, white; stamens inserted near the base of the tube; ovary partly inferior; ovules numerous. Follicles long-stipitate, thinly woody. Seeds slightly thickened and angular, naked or with a narrow rudimentary wing.  $2n = 32$ .

One sp., *M. pittieri* Woodson, in Belize, Nicaragua and Costa Rica.

### 70. *Plumeria* L.

*Plumeria* L., Sp. Pl. 1: 209 (1753); Woodson, Ann. Missouri Bot. Gard. 25: 189–224 (1938), rev.

Small trees or shrubs, stems thick, with corky periderm and conspicuous leaf scars. Leaves alternate, usually clustered near ends of branches. Inflorescences terminal, cymose and thyriform, usually many-flowered bracts small scarious, caducous, without colleters at base. Calyx lobes small, ± equal, glandular at apex; corolla salverform, thick, waxy, white, pink or red, often with yellow in throat; stamens inserted near base of tube; ovary partly inferior; ovules numerous. Follicles large, stout. Seeds with thin, papery wing at one end.  $2n = 36, 54, 45$ .

About 7 spp., native to the Caribbean and Central America, but cultivated in tropical and subtropical regions worldwide for their showy flowers.

Despite its wide cultivation, this genus has never been treated in a modern revision.

### 71. *Himatanthus* Willd.

*Himatanthus* Willd. in Roem. & Schult., Syst. Veg. 5: 221 (1819); Woodson, Ann. Missouri Bot. Gard. 25: 189–224 (1938), rev.; Plumel, Bradea 5, suppl. 1: 1–120 (1991), rev.; Spina et al., Taxon 62: 1304–1307 (2013), synop.

Trees or shrubs; stems thick, with corky periderm and conspicuous leaf scars. Leaves alternate. Inflorescences terminal, cymose to thyriform, few- to many-flowered; bracts large and showy, caducous, with many colleters at the base. Calyx of thick, irregular sepal rudiments; corolla salverform, thick, waxy, white, often with a yellow eye; stamens inserted near the base of the tube; ovary partly inferior; ovules numerous. Follicles large, stout, leathery to thinly woody. Seed wing concentric, papery.  $2n = 18$ .

About nine spp. in tropical South America.

This genus has a complex taxonomic history, and the generic limits between it, *Plumeria* and *Mortoniella* need to be tested using modern methods.

### 72. *Cameraria* L.

*Cameraria* L., Sp. Pl. 1: 210 (1753).

Shrubs. Leaves opposite, usually with numerous parallel veins. Inflorescences terminal, cymose. Corolla relatively small, salverform, white, expanded near orifice, with epistaminal appendages, the lobes large; stamens inserted in upper part of corolla tube; anther connective broad with long filiform apical appendage, included except for apical appendages; dehiscence sublatrorse; ovary superior; ovules 1–2 per carpel; style-head broad, lenticular, with membranous collar and two large apical lobes. Fruit a pair of one-seeded samaroid drupes. Seed margin narrow, wing-like.

Two spp. in the Greater Antilles and Central America.

### 73. *Anechites* Griseb.

*Anechites* Griseb., Fl. Brit. W. I. 410 (1861); Fallen, Brittonia 35: 222–231 (1983), rev.; Morales, Anales Jard. Bot. Madrid 66: 224 (2009), reg. rev.

Liana. Leaves opposite; blades with recurved hairs with multicellular bases. Inflorescences alternate-axillary, several-flowered dichasia. Calycine colleters present; corolla white, salverform, lobes large, broadly ovate; stamens inserted about midway in the corolla tube, included; anthers with broadened connective and elongate apical appendage; dehiscence sublatrorse; nectary disc annular, adnate, lobed; ovary superior; ovules 2–6 per carpel; style-head lenticular with basal collar and two large lobes at apex. Drupes indehiscent, slender, one-seeded, with recurved hairs and sterile beak at distal end. Seed margin compressed.

One sp., *A. nerium* (Aubl.) Urban, found in the Greater Antilles, Caribbean coast of Central and South America and Pacific coast of N South America, in lowland tropical moist to wet forest usually below 600 m.

### 74. *Skytanthus* Meyen

*Skytanthus* Meyen, Reise I: 376 (1834).

Shrubs, sometimes prostrate. Leaves alternate and/or opposite, small, coriaceous. Inflorescences terminal and axillary, few-flowered, cymose. Corolla yellow, tubular-campanulate, with small corona lobe above stamens and epistaminal appendages below; stamens inserted at base of expanded part of corolla; anthers with

broadened connective and long filiform apical appendage, included except for apical appendages; ovary superior; ovules numerous per carpel; style-head lenticular with collar, and two large apical lobes. Follicles long, slender, terete, woody, corkscrew-like; placentas forming hard articles between the seeds. Seeds with wing at each end.

Three spp. in Brazil and Chile in drier habitats and often higher elevations.

### 75. *Thevetia* L.

*Thevetia* L., Opera Var. 212 (1758), nom. cons.; Alvarado-Cárdenas & Ochoterena, Ann. Missouri Bot. Gard. 94: 298–323 (2007), rev.  
*Cascabela* Raf. (1838).

Shrubs or small trees. Leaves alternate. Inflorescences terminal and axillary, few- to several-flowered, cymose. Calycine colleters present; corolla infundibuliform, rarely salverform, yellow to orange, rarely white; tube with infrastaminal appendages and corona lobes behind anthers; stamens inserted near orifice of tube; anthers with broad connective and relatively short apical appendage; dehiscence sublateral; nectary disc annular, fleshy; ovary sometimes hemi-syncarpous; ovules 2–4 per carpel. Fruit hemi-syncarpous to syncarpous, red or black, drupaceous, indehiscent; mesocarp fleshy. Seeds broadly ovate, moderately compressed, with a narrow, denticulate margin and apical wing.  $2n = 20$ .

Nine spp. in tropical America, one, *T. peruviana* (Pers.) K. Schum., widely cultivated and naturalized in tropical regions.

*Cascabela* is sometimes recognized as a distinct genus (Alvarado-Cárdenas et al. 2017) based mainly on fruit structure; but the chromosome number combined with the specialized floral morphology that it shares with *Thevetia* outweigh the differences in fruit structure (Williams and Stutzman 2008).

### 76. *Cerbera* L.

Fig. 35

*Cerbera* L., Sp. Pl. 1: 208 (1753); Forster, Austrobaileya 3: 569–579 (1992), reg. rev.; Leeuwenberg, Wageningen Agric. Univ. Pap. 98-3: 1–64 (1999), rev.; Middleton, Fl. Males. I, 18: 157–163 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 72–75 (2014), reg. rev.

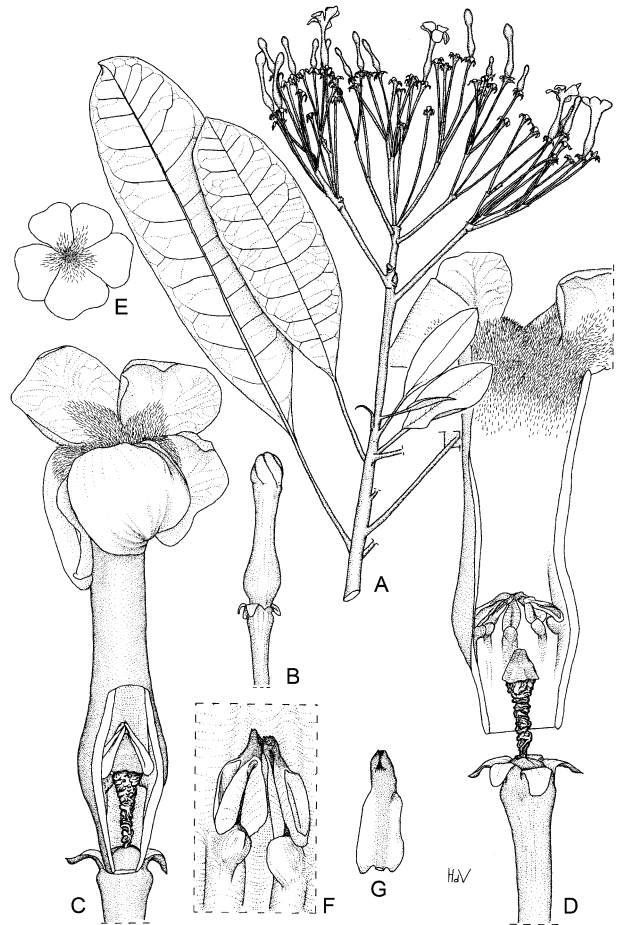


Fig. 35. Apocynaceae-Plumerieae. *Cerbera laeta*. A Flowering branch. B Bud. C Flower, with section removed at base showing position of reproductive organs. D Flower with opened, detached corolla and intact gynoecium. E Flower from above. F Two stamens showing lateral dehiscence and infrastaminal appendages. G Anther dorsal side. (From Leeuwenberg 1999, p. 19, with permission from the Library of Wageningen University, Wageningen; drawn by H. de Vries)

Small trees, sometimes shrubs. Leaves alternate. Inflorescences terminal, several-flowered compound corymbs; bracts and sepals large, foliaceous; calycine colleters absent; corolla salverform, sometimes weakly infundibuliform at top of tube, usually white; tube with infrastaminal appendages and corona lobes behind anthers; stamens inserted near base to near orifice of tube; anthers with broad connective and elongate apical appendage; ovary superior; ovules usually 4 per carpel; style-head with conical

upper part and basal collar. Drupes, adapted for water dispersal; mesocarp fibrous. Seeds usually somewhat compressed with narrow flattened rim around margin.  $2n = 40, 44$ .

Six spp. in Madagascar and the Seychelles and from Japan (Ryukus) to Australia (Queensland) and Pitcairn, in rainforest, open forest, woodland, coastal forest or thickets, mostly at low elevations. *Cerbera odollam* Gaertn. is widely cultivated in SE Asia.

#### 77. *Cerberiopsis* Vieill. ex Pancher & Sébert

*Cerberiopsis* Vieill. ex Pancher & Sébert in Sébert, Not. Bois. Nov. Caledonia 187 (1874); Boiteau, Fl. Nouvelle-Cal. 10: 222–232 (1981), rev.

Trees or shrubs; branching monopodial, branches in pseudo-whorls at regular intervals along main stem, often fistulose. Leaves alternate. Inflorescences terminal, few- to many-flowered cymes or panicles. Sepals caducous; corolla tubular-campanulate, white, usually with yellow or reddish markings; stamens inserted about midway in the tube; anthers with broad connective and apical appendage; dehiscence sublatrorse; ovary superior; ovules 2 per carpel. Fruit apocarpous; a pair of one-seeded, flat, dry samaroid drupes, each with two lateral wings. Seeds flat with thin wing-like margin.

Three spp., endemic to New Caledonia.

#### I.11. Tribe Carisseae Dumort. (1829).

Shrubs or small trees, rarely scandent, with or without (often branched) spines in leaf axils; latex white. Leaves opposite (verticillate in some species of *Carissa*). Inflorescences usually axillary, cymose, mostly much contracted,  $\pm$  umbelliform. Calycine colleters almost always absent; corolla salverform, usually white or cream, sometimes flushed with pink, the lobes not inflexed in bud; corolla lobe aestivation sinistrorse (dextrorse in some species of *Carissa*); corona absent; stamens inserted at the middle of the corolla tube or above; anthers ovate, without lignified guide rails or basal appendages, subsessile, included, or tips exerted; pollen 3-colporate; style-head ovoid to ovoid-cylindrical, body scarcely differentiated, uniformly receptive, without basal collar; nectary disc absent or an indistinct ring adnate to the base of the ovary; ovary congenitally syncarpous,

bilocular, usually glabrous or with just a few hairs at the apex; placentation axile; ovules 1–5 per locule, rarely more. Fruit syncarpous, indehiscent, a berry with fleshy, non-fibrous, non-sclerotic pericarp; endocarp not stony, but placentas becoming indurated in fruit forming a pseudo-stone. Seeds 2–6(–12), rarely more, compressed, without a hilar groove; testa thin, smooth; endosperm smooth, mealy; cotyledons thin, delicate. Cardenolides often present.  $x = 11$ . Two genera in the Paleotropics.

#### 78. *Acokanthera* G. Don

*Acokanthera* G. Don, Gen. Hist. 4: 485 (1837); Kupicha, Kew Bull. 37(1): 40–67. 1982, reg. rev.

Trees or shrubs without spines; latex poisonous. Inflorescences dense axillary fascicles. Corolla lobes much shorter than the tube; anthers subsessile, usually with some hairs at the apex, the tips sometimes exerted; ovule one per locule. Fruit a globose, 1–2-seeded, purplish black to black berry. Seeds compressed with a glabrous testa.  $2n = 22$ .

Five spp. in Africa. The toxic latex of *Acokanthera* has long been used by native peoples in Africa as arrow and spear poison.

Pichon (1948a) considered *Acokanthera* to be congeneric with *Carissa*, though they have mostly been treated as distinct genera, especially due to the presence of cardenolide glycosides in *Acokanthera* and their absence in *Carissa*. Phylogenetic analyses place the two genera as sisters, but expanded sampling may show that they are better treated as congeneric.

#### 79. *Carissa* L.

Fig. 36

*Carissa* L., Syst. Nat., ed. 12. 2: 135, 189 (1767), nom. cons.; Markgraf, Fl. Madagascar et Comores, Fam. 169: 13–33 (1976), reg. rev.; Forster, Fl. Australia 28: 107–110 (1996), reg. rev.; Leeuwenberg & van Dilst, Wageningen Univ. Pap. 2001-1: 3–109 (2001), rev.; Middleton, Fl. Males. I, 18: 151–154 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 66–70 (2014), reg. rev.

Shrubs or small trees, sometimes scandent, with paired straight, often branched spines; latex non-poisonous. Leaves sometimes in whorls of 3–4, mostly coriaceous. Inflorescences axillary, sometimes also terminal, few-flowered cymes. Corolla lobe aestivation dextrorse in some species; ovules

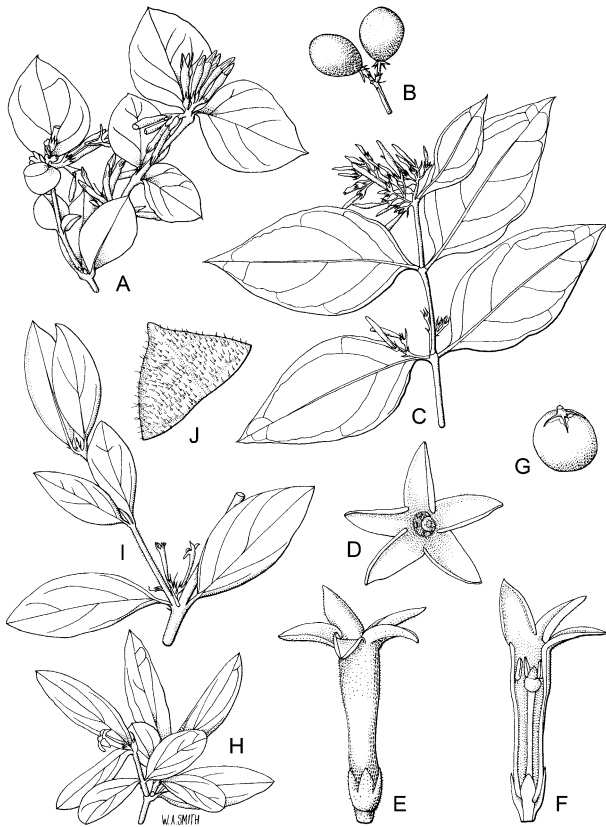


Fig. 36. Apocynaceae-Carisseae, *Carissa*. A, B *Carissa ovata*. A Flowering branch. B Fruit. C–G *C. laxiflora*. C Flowering branch. D Flower from the top. E Flower from the side. F Longitudinal section through flower showing spatial relationship of anthers and style-head. G Fruit. H *C. lanceolata*, flowering branch. I, J *C. scabra*. I Flowering branchlet. J Leaf apex showing scabrid indumentum. (From Forster 1992c, p. 584, with permission from the CSIRO Publishing, Clayton; drawn by W.A. Smith)

1–4, rarely more per locule. Fruit globose or oblong, red, purple, bluish black or black. Seeds mostly 1–4, rarely more; seed compressed-discoid, testa rough to velutinous.  $2n = 22$ .

Estimates of species number ranges from seven, in the most recent revision, to about 20 spp. in Asia, Australia, Madagascar, the Mascarenes and Africa. A modern phylogenetic study of the genus is lacking. The fruits of several species are edible, and some are used to make jam. Some species are widely cultivated as ornamentals.

## II. APOCYNIDS

Apocynoideae Burnett (1835).  
Echitoideae Luer. (1882).

Woody lianas, vines, less frequently trees, shrubs or subshrubs, rarely perennial herbs; latex usually white (translucent in many Echiteae and Nerieae, and in some Malouetieae). Leaves almost always opposite, sometimes with cluster of colletes at juncture of petiole and blade adaxially (some Mesechiteae and Baisseeae), less frequently colletes spread along the length of midrib of the leaf blade adaxially (some Mesechiteae), sometimes abaxial domatia in axils of secondary veins (some Apocyneae, Malouetieae, Mesechiteae and Baisseeae). Flowers small, whitish and inconspicuous to large, colorful and showy; calycine colletes normally present; corolla infundibuliform, tubular-campanulate, salverform, urceolate, tubular or rotate; corolla lobe aestivation almost always dextrorsely contorted (sinistrorsely contorted in Wrightieae and in *Urceola* p.p.), rarely valvate (*Parsonsia* p.p., *Urceola* p.p.); corolline corona often present, sometimes annular, often petaloid or dissected (Wrightieae, Nerieae), sometimes lower down in corolla tube behind stamens (Baisseeae, Echiteae), sometimes more than one kind of corona present (mainly Echiteae); rarely corona lobes on dorsal side of anther (some Apocyneae); stamens inserted at various levels; anthers included or exserted, almost always fertile only in upper part, lower part enlarged and sterile, and sides elaborated into lignified guide rails (guide rails poorly developed in some Malouetieae), united with the style-head by a pad of specialized hairs on the enlarged connective via agglutination in most cases (only very weakly so in some Nerieae and Malouetieae), more rarely via postgenital fusion, sometimes also attached at the base of the thecae; pollen porate, most commonly with 3–4 apertures; occasionally grains 2–5-aperturate or polyaperturate; nectaries usually present around base of ovary, sometimes fused into ring (absent in Wrightieae, Nerieae and some Malouetieae); ovary bicarpellate, usually apocarpous, more rarely postgenitally syncarpous (especially

in some *Echiteae* and *Wrightieae*), normally superior, more rarely partly inferior; ovules mostly numerous per carpel; style mostly slender, sometimes thick; style-head variously shaped, differentiated longitudinally, sometimes with collar at base and crest at the apex, normally with two small free appendages at the apex; epidermis of the body usually radially interrupted by the adnate anthers into 5 secretory and non-secretory zones; stigmatic region on the lower part of the style-head below the adnate anthers or beneath flange or collar, when present. Fruit dehiscent, usually apocarpous, a pair of slender to stout, thinly to thickly woody, ventrally dehiscent follicles with dry pericarp, less frequently the 2 follicles postgenitally fused along their ventral margins, forming a syncarpous "double-follicle", which splits apart at maturity; pericarp dry; endocarp thin, not stony. Seeds usually numerous, compressed, with coma usually on micropylar end, sometimes with a coma at the chalazal end (*Wrightieae*) or at both micropylar and chalazal ends (some *Nerieae* and *Malouetieae*) rarely without a coma (some *Malouetieae* and *Apocynaeae*); endosperm thin, not ruminant. Steroidal alkaloids or cardenolides often present, pyrrolizidine alkaloids reported from a number of genera of *Echiteae*, indole alkaloids absent. 77 Genera, most restricted to either the Paleo- or Neotropics.

#### KEY TO THE TRIBES OF APOCYNIDS

1. Corolla lobe aestivation sinistrorse; seeds with a chalazal coma (on the end of the seed directed toward the base of the fruit); nectary absent
  1. **Wrightieae** (p. 283)
    - Corolla lobe aestivation dextrorse, very rarely valvate or sinistrorse; seeds with a micropylar coma (on the end of the seed directed toward the apex of the fruit); nectary present (except in some *Nerieae* and *Malouetieae*) 2
2. Leaf blades adaxially with colleters clustered at the base of the midrib or scattered along its length, or sometimes colleters scattered along the length of the petiole, (colleters in the axil of the petiole absent or present), abaxial domatia often present in axils of secondary veins 3
  - Leaf blades and petioles adaxially without colleters (but colleters in the axil of the petiole often present), abaxial domatia usually absent in axils of secondary veins, rarely present in some taxa from Asia 4
3. Corolla tube mostly with a small knob-like corona lobe above each anther; style-head 5-angled, but without strongly projecting ribs; plants of Africa and Madagascar 9. **Baisseeae** (p. 307)
  - Corolla tube lacking knob-like corona lobes above the anthers; style-head with 5 strongly projecting ribs, at least at the base; plants of the New World 6. **Mesechiteae** (p. 294)
4. Calycine colleters absent; style-head with a large membranous basal collar; seeds rostrate; suberect to scandent perennial herbs or lianas usually growing in mangroves or swampy areas 4. **Rhabdadenieae** (p. 291)
  - Calycine colleters normally present, if absent seeds either not rostrate or plant not growing in mangroves or swamps; style-head with or without basal collar; habit various 5
5. Calycine colleters five, solitary (though sometimes deeply dissected and rarely appearing as a continuous ring), and centered at the base of the sepals (antepetalous position), sometimes absent; nectary disc always present; style-head almost always with a membranous basal collar, the main body typically spool-shaped or clavate; latex often translucent; lianas or vines, rarely erect subshrubs or perennial herbs 7. **Echiteae** (p. 297)
  - Calycine colleters most commonly few (5-10) and quincuncially arranged on the margins at the base of the sepals (alternisepalous position) or several and more or less in a continuous ring, occasionally absent; nectary disc present or absent; style-head variously shaped, with or without a basal collar; latex white or translucent; habit various 6
  - Nectary disc absent; style-head with a basal collar, rarely absent, never 5-lobed at base; latex often translucent; seeds mostly with a deciduous chalazal coma in addition to the micropylar coma 2. **Nerieae** (p. 284)
  - Nectary disc present or absent; style-head mostly without a basal collar, more rarely basal collar present, very rarely style-head 5-lobed at the base; latex mostly white, rarely translucent; seeds usually with only a micropylar coma, rarely also with a chalazal coma, rarely without a coma 7
7. Anthers attached to the style-head at one level: the thecae usually not agglutinated to the style-head, the

connective attached at about the middle of the style-head (sometimes only very weakly so) by a circular to ovate pad of hairs; style-head globose with a slender, elongate, conical apex; latex translucent or white; shrubs, trees or perennial herbs, very rarely climbers

3. *Malouetieae* (p. 287)

- Anthers attached to the style-head at two levels: the bases of the thecae mostly agglutinated to the upper style-head, and the connective firmly attached to the style-head at about the middle or near the base; style-head of various shapes; latex white; plants mostly lianas and scrambling shrubs, sometimes perennial herbs

8

8. Style-head globose to ovoid and often with a collar around the base, or spool-shaped or broadly fusiform, the last sometimes weakly pentagonal; plants restricted to the New World

5. *Odontadenieae* (p. 291)

- Style-head broadly ovoid to very broadly fusiform, sometimes pentagonal, almost never with a collar at the base, very rarely present; plants of the Paleotropics and, rarely, temperate Eurasia and North America

8. *Apocyneae* (p. 301)

## II.1. Tribe *Wrightieae* G. Don (1837).

Shrubs, trees or woody climbers; latex white. Leaves opposite. Inflorescences mostly terminal, sometimes axillary, few- to many-flowered panicles or aggregate dichasia. Calycine colleters few, alternisepalous; corolla salverform to infundibuliform or rarely tubular-campanulate; corolla lobe aestivation sinistrorse; showy corona of flat petaloid to fimbriate segments at mouth (these fused into a cup in *Stephanostema*), rarely absent or very small; stamens inserted near the top of the corolla tube, mostly exserted (rarely inserted lower in the tube and included in some species of *Wrightia*); filaments slender; anthers with relatively short lignified guide rails, expanded sterile part of connective attached to base of style-head (thecae not attached); pollen 3–4-porate, shed onto upper hair wreath; nectary disc absent, adnate or indistinct; ovary apocarpous (syncarpous in some species of *Wrightia*); style-head usually  $\pm$  spool-shaped and with a basal collar and upper wreath of longer hairs; stigma located beneath basal collar. Fruit usually apocarpous and consisting of a pair of follicles, these rather stout or long and slender, rarely the follicles post-genitally fused along their ventral margins (some

species of *Wrightia*). Seeds with a chalazal coma. Cardenolides present.  $x = 10, 11$ . Three genera, two restricted to Africa, one widespread in the Paleotropics.

The generic limits between the genera of *Wrightieae* need to be tested using modern methods.

### 80. *Stephanostema* K. Schum.

*Stephanostema* K. Schum., Bot. Jahrb. 34: 325 (1904); Barink, Meded. Landbouwhogeschool Wageningen 83-7: 42–53 (1983), rev.

Small shrub. Inflorescences few-flowered, terminal and axillary panicles. Flowers conspicuously globose in bud, with the appearance of miniature daffodils when open, the tube salverform, white, lobes yellow, about the same length as the tube; corona white, cupular, crenulate; anthers yellow, exposed at the base of the corona; ovules ca. 18 per carpel. Follicles pendent, slender, thinly coriaceous.  $2n = 22$ .

One sp., *S. stenocarpum* K. Schum., known only from a single locality in Tanzania, in forest and bush.

This genus is very closely related to *Wrightia* and especially to *Pleioceras*. The main difference between *Stephanostema* and *Pleioceras* is that the corona lobes are fused into a cupular structure in the former, and free in the latter. Whether this is worthy of recognition at the generic level needs to be investigated.

### 81. *Pleioceras* Baill.

Fig. 37

*Pleioceras* Baill., Bull. Mens. Soc. Linn. Paris 1: 759 (1888); Barink, Meded. Landbouwhogeschool Wageningen 83-7: 21–53 (1983), rev.

Small trees, shrubs or lianas. Inflorescences terminal, lax, several- to many-flowered panicles. Flowers small; corolla yellow, red or violet, the lobes usually longer than the tube; corona bright yellow, consisting of two types of segments, one type shorter, broader, and irregularly lobed, the other long, filiform and split into 3–4 finger-like lobes; ovules numerous. Follicles pendent, slender, thinly coriaceous.  $2n = 22$ .

Five spp. in tropical Africa in forest, bush and open places, up to 400 m.





Fig. 37. Apocynaceae-Wrightieae. *Pleioceras zenkeri*. A Flowering branch. B Flower. C Flower opened lengthwise showing exserted gynostegium and fimbriate corona lobes at corolla mouth. D Part of corolla showing a stamen and two types of corolline corona lobes. E One follicle of the fruit. F Base of fruit. G Seed showing sessile chalazal coma. (From Barink 1983, p. 40, with permission from the Library of Wageningen University, Wageningen; drawn by Y.F. Tan)

## 82. *Wrightia* R. Br.

*Wrightia* R. Br., *Asclepiadeae* 62 (1810); Brown, *Prodr. Fl. Nov. Holland.* 467 (1810); Ngan, *Ann. Missouri Bot. Gard.* 52: 114–175 (1965), rev.; Forster, *Fl. Australia* 28: 190–194 (1996), reg. rev.; Middleton, *Fl. Thailand* 7(1): 79–90 (1999), reg. rev.; Middleton, *Harvard Pap. Bot.* 10: 161–182 (2005), reg. rev.; Middleton, *Fl. Males. I*, 18: 436–447 (2007), reg. rev.; Middleton, *Fl. Cambodia, Laos and Vietnam* 33: 234–252 (2014), reg. rev.

*Scleranthera* Pichon (1951).

*Wallida* (A. DC.) Pichon (1951).

Shrubs or trees. Inflorescences terminal, few- to many-flowered aggregate dichasia. Corolla salverform (rarely infundibuliform), white, rose, mauve or yellowish; corona of entire or variously dissected petaloid to filiform appendages in the mouth, very rarely absent or very small; anthers usually exserted (rarely inserted lower in the tube and anthers included); ovary apocarpous or syncarpous; ovules numerous. Follicles usually thinly woody, free or fused along the ventral sides, forming a “double-follicle”, which splits apart into 2 follicle-like halves at maturity.  $2n = 20, 22$ .

About 25 spp. from E Africa to the Solomon Islands and India and S China to NE Australia, in evergreen, deciduous and eucalypt forests, thickets and clearings, up to 1650 m. Some species are cultivated for their attractive flowers.

## II.2. Tribe Nerieae Baill. (1889).

Shrubs, trees or woody climbers; latex typically translucent, sometimes white. Leaves usually opposite (alternate in *Adenium*, ternate in *Nerium*, and exceptionally ternate or quaternate in *Strophanthus*). Inflorescences terminal or in the branch forks (in lianoid taxa sometimes axillary as well), few- to several-flowered dichasial cymes or thyrses. Calycine colleters few, alternisepalous or more numerous, rarely absent (*Adenium*); corolla infundibuliform to tubular-campanulate or rarely salverform (*Isonema*); corolla lobes in *Strophanthus* often with elongate apical appendages; corolline corona almost always present in the petal sinuses of genera with an expanded corolla mouth, sometimes small bifid lobes but often larger, petaloid segments in *Strophanthus*, and these much dissected and fused into a more or less continuous, showy, variously lobed ring in *Nerium*; corolla lobe aestivation dextrorse; stamens inserted at the base of the expanded part of the corolla in species with infundibuliform to tubular-campanulate corollas and from about the middle or above in species with salverform corollas, included to partly or completely exserted; anthers specialized, with short filaments or more commonly more or less sessile on thick ridges, lignified guide rails often relatively short, in *Strophanthus*, *Nerium* and *Adenium* with long, filiform, hairy, interspiraling apical appendages much longer than the anther, connective often only weakly attached to base of style-head at

one level (thecae not attached); pollen 3–4-porate; nectary disc absent, adnate or indistinct; ovary apocarpous (in *Strophanthus* congenitally syncarpous at the base up to ca. halfway, apocarpous above and in *Nerium* and one species of *Alafia* a completely syncarpous), usually partly inferior in *Strophanthus*; ovules numerous per carpel; style in most genera gradually thickening toward the apex, thickest just below the style-head, sometimes tuberculate; style-head usually  $\pm$  spool-shaped and with a basal collar and upper wreath of longer hairs (but these poorly developed to absent in *Alafia* and *Farquharia*); stigma located beneath basal collar; ovary apocarpous or more rarely partially to nearly completely syncarpous. Fruit almost always apocarpous and consisting of a pair of follicles, these often rather stout, sometimes long and slender (follicles postgenitally fused along their ventral margins in *Nerium* forming a “double-follicle”). Seeds usually oblong, elliptic, to narrowly fusiform and somewhat compressed, mostly with a smaller deciduous chalazal coma (this sometimes discernible only in undehisced follicles), and larger persistent micropylar coma, the latter sometimes beaked to long-rostrate (seeds with only a micropylar coma in *Nerium* and *Alafia*). Cardenolides present.  $x = 10, 11$ . Six genera, most in tropical Africa, some also in Madagascar, one reaching Asia, two in more arid habitats extending to the Arabian Peninsula or the Mediterranean.

The poisonous properties of plants in this tribe are well known. *Nerium*, *Adenium*, *Strophanthus* and *Alafia* have long been used as arrow poison, or, in smaller doses, as treatment for a diverse array of external and internal ailments by the native peoples where they occur. The responsible compounds are cardiac glycosides. Extracts from the seeds of certain species have been found to have powerful cardiotoxic, and more recently, cytotoxic properties that can be utilized in modern medicine. Little is known about the secondary chemistry of *Isonema* or *Farquharia*.

### 83. *Nerium* L.

*Nerium* L., Sp. Pl. 1: 209 (1753); Pagen, Agric. Univ. Wageningen Pap. 87-2: 1–113 (1987), rev.

Shrub or small tree. Leaves ternate, coriaceous. Inflorescence terminal or in the forks, thyrsoïd, lax. Corolla showy, infundibuliform, white, pink, red, yellow or salmon, often with darker markings in the throat, double forms in cultivation; showy petaloid corona present in the mouth; anthers with a conspicuous, ca. 8 mm long hairy apical connective appendage; ovary postgenitally syncarpous, pubescent; ovules numerous; style thick, tuberculate in the upper part. Fruit a woody, glabrous “double-follicle”. Seeds covered with short, brown, tomentellous hairs grading into a short micropylar coma.  $2n = 22$ .

One sp., *Nerium oleander* L., native to the Mediterranean region and the Middle East but widely cultivated as well as naturalized in many warmer regions, in exposed sites, usually in wet spots such as along stream banks or in the beds of streams or periodically flooded wadis, up to 2500 m. A number of showy cultivars of *Nerium* make it a popular ornamental.

### 84. *Adenium* Roem. & Schult.

*Adenium* Roem. & Schult., Syst. Veg. 4: 35, 411 (1819); Plaizier, Meded. Landbouwhogeschool Wageningen 80-12: 1–40 (1980), rev.

Succulent shrubs or trees; latex sometimes recorded as being white. Leaves alternate, congested at the ends of the branches. Inflorescence terminal, thyrsoïd, few-flowered. Corolla showy, tubular-campanulate, red, pink or white, sometimes striped, slightly zygomorphic; corona lobes small, bifid; stamens included to exerted; anthers with a long, hairy apical connective appendage; ovary glabrous or pubescent; ovules numerous; style enlarged at apex. Follicles stout, spreading or recurved, pubescent. Testa glabrous, rarely minutely puberulent; micropylar and chalazal comas sessile and about equally developed.  $2n = 22$ .

Five spp. in S Arabia, Africa and Socotra, in savannas or open forests with sandy or rocky soil. A genus with showy flowers, often cultivated in succulent collections, and an important source of arrow poison used by indigenous peoples in Africa.

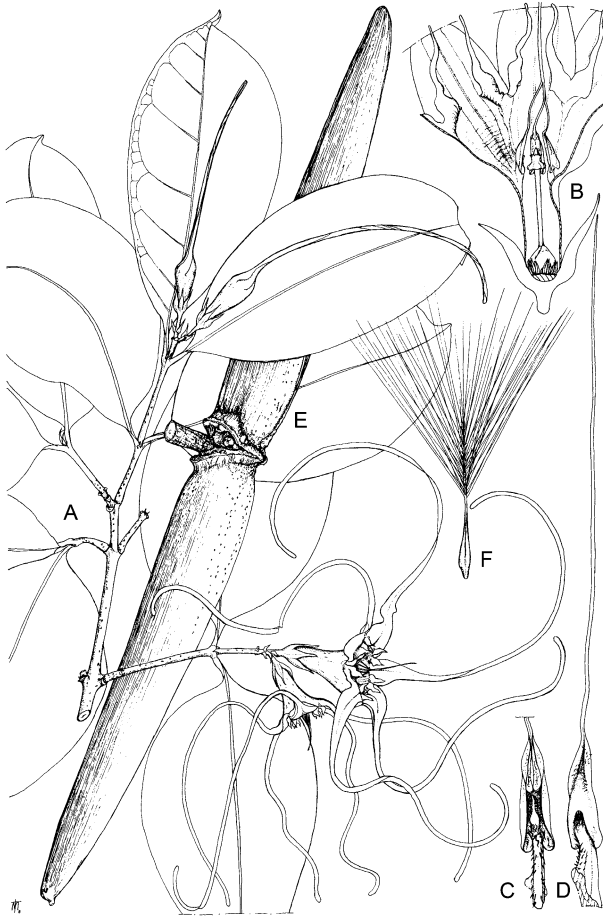


Fig. 38. Apocynaceae-Nerieae. *Strophanthus caudatus*. A Flowering branch. B Longitudinal section through flower showing position of gynostegium and paired corolline corona lobes in the staminal sectors. C Stamen ventral side, most of apical appendage not shown. D Stamen dorsal side showing entire apical appendage. E Fruit. F Seed showing rostrate micropylar coma. (From Beentje 1982, p. 56, with permission from the Library of Wageningen University, Wageningen; drawn by Y.F. Tan)

### 85. *Strophanthus* DC.

*Strophanthus* DC., Bull. Sci. Soc. Philom. Paris 3: 122 (1802); Beentje, Meded. Landbouwhogeschool Wageningen 82-4: 1–191 (1982), rev.; Beentje, Fl. Zambesiaca 7: 468–480 (1985), reg. rev.; Middleton, Fl. Males. I, 18: 361–371 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 176–184 (2014), reg. rev. *Christya* Ward & Harv. (1841). *Roupellia* Wall. & Hook. (1849).

Shrubs, lianas, or rarely trees. Leaves opposite, occasionally whorled. Inflorescences terminal,

less often axillary or in forks of branches. Calycine colleters rarely absent; corolla showy, tubular-campanulate, variously colored, the lobes often undulate and/or with long, slender apical appendages; corona of five well-developed strongly bifid lobes; ovary partly inferior, rarely superior, hemi-syncarpous, glabrous to densely pubescent; ovules numerous; style thick. Follicles thickly to thinly woody, very broadly divergent. Testa mostly pubescent; chalazal coma poorly developed, micropylar coma well-developed, conspicuously long-rostrate.  $2n = 18, 20$ .

38 spp. widely distributed in tropical Africa, Madagascar and Asia, mostly in forest or at forest margins, some species in dry woodlands or more open habitats, at lowland to montane elevations. *Strophanthus* is rich in cardiac glycosides, and is the main ingredient in arrow poison used by several African tribes. It is also the source of the drug ouabain, a cardiac stimulant used to treat heart failure. Several species are cultivated in tropical conditions for their showy flowers with long, dangling petal appendages.

### 86. *Isonema* R. Br.

*Isonema* R. Br., Asclepiadeae 52 (1810); Van der Ploeg, Meded. Landbouwhogeschool Wageningen 83-4: 1–20 (1983), rev.

Scrambling shrubs or lianas. Petioles with colleters spread along the adaxial side. Inflorescences terminal, more rarely axillary, few- to many-flowered dichasia. Corolla salverform, variously colored, the lobes with a subapical, crisped appendage; stamens inserted at the orifice of corolla tube; anthers completely exerted; ovary pubescent; ovules numerous; style slender, sometimes tuberculate just below the style-head. Follicles broadly divergent, velvety brown pubescent, narrowly fusiform. Chalazal coma scanty, micropylar coma well-developed, ca. 3–4 cm long.  $2n = 22$ .

Three spp. in W and C Africa, in rainforest, secondary vegetation, often near rivers, or in coastal brush.

### 87. *Alafia* Thouars

*Alafia* Thouars, Gen. Nov. Madagasc. 11 (1806); Leeuwenberg, Kew Bull. 52: 769–840 (1997), rev.

Fig. 38

Lianas or climbing shrubs; latex sometimes white in some parts and translucent in others. Inflorescences sometimes axillary, usually dense, few- to many-flowered cymes. Corolla salverform, white, pink, mauve, red or yellowish; lobes mostly with long hairs at margins; orifice constricted by a callous ring; stamens inserted in upper part of corolla tube; anthers included or the tips exerted; ovary pubescent; ovules numerous; style gradually enlarged to the apex; style-head poorly developed, without basal collar. Follicles long, slender, cylindrical, glabrous to pubescent. Testa glabrous; coma sessile.

About 23 spp. in tropical Africa and Madagascar, in rainforest, secondary forest, gallery forest, seasonally flooded or riverine forest and bush, up to 1500 m.

### 88. *Farquharia* Stapf

*Farquharia* Stapf, Bull. Misc. Inform. Kew 1912: 278 (1912); Zwetsloot, Meded. Landbouwhogeschool Wageningen 81-16: 1-46 (1981), rev.

Large woody liana. Petioles with colleters spread along the adaxial side. Inflorescences several- to many-flowered terminal dichasia. Corolla infundibuliform, white to pale yellow; anthers included; ovary rusty brown villous; ovules numerous; style slender, tuberculate for almost the whole length; style-head scarcely developed, without upper wreath or basal collar. Follicles broadly divergent, woody, puberulent rusty brown. Seeds with a deciduous chalazal coma of shorter hairs and a firm, shortly rostrate micropylar coma of longer hairs.  $2n = 22$ .

One sp., *F. elliptica* Stapf, in tropical Africa.

### II.3. Tribe Malouetieae Müll. Arg. (1860).

Shrubs, trees, subshrubs, rarely woody lianas or perennial herbs, the latter sometimes with a xylopod; latex usually white (translucent in *Pachypodium* and sometimes so in *Galactophora*). Leaves opposite (rarely verticillate in *Galactophora*) but alternate in *Pachypodium*, often with abaxial domatia in the axils of the secondary veins. Inflorescences terminal or axillary, mostly cymose, few- to several-flowered. Calycine colleters mostly present (absent in *Galactophora* and *Pachypodium* and sometimes absent in *Neobra-*

*cea*), mostly few, alternisepalous (several and more or less in a ring in *Mascarenhasia* and apparently in *Eucorymbia* and some species of *Carruthersia*); corolla usually infundibuliform to tubular-campanulate, often large, showy and colorful (large and salverform in *Carruthersia* and *Holarrhena*) and smaller, salverform and white or cream in *Allowoodsonia* and *Funtumia*; corolla lobe aestivation dextrorse; corona usually absent, but present as a ring of 5 small bifid protuberances at the orifice of the corolla tube in *Malouetia*; stamens inserted at the base of the expanded part of the corolla in species with infundibuliform to tubular-campanulate corollas in which there is an abrupt division between the expanded upper part and the tubular lower part, and from about the middle or above in species with salverform corollas, included or exerted; anthers sessile or with short filaments, normally clearly morphologically specialized with well-developed lignified guide rails sagittate at the base and firmly attached at about the middle of the style-head (anther base cordate or shortly sagittate and only very weakly attached to the style-head in *Holarrhena*, *Spirolobium*, *Carruthersia* and *Eucorymbia* and additionally non-lignified in *Holarrhena*); pollen quite variable: mostly 3-4-porate, but (1-)2(-4)-porate in *Mascarenhasia* and *Pachypodium*, 2-4-porate in *Malouetia*, and polyantoporate in *Spirolobium*; 5 nectaries usually present around the base of the gynoeceium, these often fused into a 5-lobed disc (in *Spirolobium* and *Carruthersia*, 2 separate lobes alternating with the carpels, and nectaries absent in *Holarrhena* and *Malouetiella*); ovary apocarpous; ovules usually numerous per carpel (except in *Malouetiella* and *Allowoodsonia* where only 4-8 per carpel); style-head usually globose with narrowly conical upper part or broadly fusiform, usually without basal collar or upper wreath (in *Eucorymbia* cylindrical and ribbed with a basal collar); stigmatic region on sides of lower cylindrical part below adnation of anthers. Fruit apocarpous, of a pair of follicles mostly long and slender, sometimes stouter, clavate. Seeds flat, linear to fusiform, ellipsoid or ovate, often sometimes elongated at the coma end; seed coma usually micropylar, sessile, of hairs 1-5 cm long (but *Kibatalia* and *Funtumia* with a long-rostrate chalazal coma with retrorse hairs, *Mascarenhasia* with both normally developed micropylar coma

and small deciduous chalazal coma (discernible only in undehisced follicles), in *Eucorymbia*, *Allowoodsonia* and *Malouetiella* seeds without a coma, and in *Malouetia* either entire testa glabrous with a few scattered hairs or with an dense indument of long hairs). Steroidal alkaloids.  $x = 11$  (9 in *Pachypodium*). 13 genera, 11 in the Paleotropics, two in the Neotropics.

Most genera have been used for treatment of a broad array of external and internal ailments by the native peoples where they occur; *Pachypodium* and *Malouetia* have long been used as arrow poison.

### 89. *Galactophora* Woodson

*Galactophora* Woodson, Ann. Missouri Bot. Gard. 19: 49 (1932); Woodson, Ann. Missouri Bot. Gard. 23: 174–178 (1936), rev.; Morales, Sida 21: 2053–2079 (2005), rev.

Subshrubs or perennial herbs, rarely scrambling, with glandular-setose hairs; latex translucent or white. Leaves coriaceous to subcoriaceous, usually revolute at margin. Inflorescences terminal or subterminal, few-flowered. Calyx lobes foliaceous; calycine colleters absent; corolla large, infundibuliform, with 5 longitudinal ridges outside, variously colored; stamens included, weakly attached to style-head; ovary syncarpous at base; style-head conical in upper part, with 5 strongly projecting ribs at base. Follicles slender, terete, united at base into ca. 2 cm stipe. Seed testa glabrous; coma micropylar, tawny, sessile.

Six spp. in NW South America, in sandy savannas and low open forest, from 50–2000 m.

### 90. *Neobraccia* Britton

*Neobraccia* Britton in Britton & Millsp., Bahama Fl. 335 (1920); Woodson, Ann. Missouri Bot. Gard. 23: 169–174 (1936), rev.

Shrubs or small, willowy trees. Leaves clustered near the tips of the branches, subcoriaceous, margin revolute. Inflorescences terminal, less frequently subterminal or lateral, few- to several-flowered. Calycine colleters absent or much reduced, rarely few and alternisepalous; corolla infundibuliform, white, pink, rose or purplish; stamens included; nectaries separate or connate at the base; style-head cylindrical with a wreath at the apex. Follicles terete, slender. Seed testa gla-

brous; coma micropylar, pale yellowish to tawny, sessile.

Four spp. on Cuba, one of them reaching the Bahamas.

### 91. *Pachypodium* Lindl.

*Pachypodium* Lindl., Edward's Bot. Reg. 16: t. 1321 (1830); Rapanarivo et al., *Pachypodium*, Balkema Publ. (1999), rev.; Burge et al., Peer J. 1: 1–20 (2013), phyl.

Succulent trees, shrubs or perennial herbs with spines at nodes, stems usually swollen at base, often with xylopod; latex translucent. Leaves alternate, crowded at tips of the branches. Inflorescences axillary, cymose, few- to several-flowered. Calycine colleters absent; corolla large, showy, variously colored, tubular-campanulate, infundibuliform or subsalverform; stamens included or exserted; style-head with a basal rim; nectaries free or fused at the base. Follicles stout, glabrous to pubescent. Seeds broad with flattened margin, testa glabrous; coma micropylar white to gray-white, sessile.  $2n = 18$ .

About 21 spp., 12 endemic to Madagascar, the others in Africa. The succulent growth form of *Pachypodium* and its large showy flowers make it a favorite of succulent plant enthusiasts. A number of species are in cultivation, and species are endangered, mainly due to the over-exploitation by hobby gardeners and plant poachers as well as to habitat destruction.

### 92. *Spirolobium* Baill.

*Spirolobium* Baill., Bull. Mens. Soc. Linn. Paris 1: 773 (1889), nom. cons.; Middleton, Fl. Males. I, 18: 359–361 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 172–173 (2014), reg. rev.

Small shrub. Leaves narrowly lanceolate, coriaceous. Inflorescences terminal. Flowers large, showy, solitary or in 2–3-flowered cymes; calyx lobes long-lanceolate; calycine colleters few, alternisepalous; corolla infundibuliform, slightly zygomorphic, with long tube curved and gradually widening to the mouth, white with pale yellow markings; stamens inserted in lower part of corolla tube, included; anther bases weakly cordate; nectaries 2, alternate with the carpels; ovary sparsely pubescent on top; style long, slender; style-head cylindrical. Follicles long, erect, slender, glabrous.

Seed testa glabrous to puberulent; coma micropylar, sessile.

One sp., *S. cambodianum* Baill., found in SE Asia, in open grassy areas, scrub, open forests and mangrove thickets, up to 300 m.

### 93. *Carruthersia* Seem.

*Carruthersia* Seem., Fl. Vit. 155 (1866); Middleton, Blumea 41: 489–498 (1997), rev.; Middleton, Fl. Males. I, 18: 154–157 (2007), reg. rev.

Woody lianas. Leaves long-petiolate, cordate to round at the base. Inflorescences axillary and/or terminal cymes or panicles. Calycine colleters alternisepalous or in a ring; corolla salverform, white to cream, sometimes reddish tinged; stamens inserted near the base of the tube, included, weakly attached to the style-head at the base of the filaments, anther bases short; nectaries 2, alternate with the carpels; ovary glabrous; style slender; style-head fusiform. Follicles terete to fusiform, glabrous. Seed testa glabrous; coma micropylar, sessile.

Four spp. in the Philippines, Solomon Islands, Fiji and Tonga.

### 94. *Eucorymbia* Stapf

*Eucorymbia* Stapf, Hooker's Icon. Pl. 28: t. 2764 (1903); Pichon, Bull. Mus. Natl. Hist. Nat. II, 21: 270–271 (1949), synop.; Middleton, Fl. Males. I, 18: 196 (2007), reg. rev.; Middleton, Fl. Penins. Mal. II, 2: 144–146 (2011), reg. rev.

Glabrous liana. Inflorescences lax terminal corymbs. Flowers large, showy; sepals subfoliaceous, caducous, with a row of colleters at the base within; corolla tubular, white; lobes broadly obovate; stamens included; filaments short; anthers pubescent dorsally, only weakly attached to the style-head; nectary disc 5-lobed, much shorter than the ovary; ovary glabrous; style filiform; style-head cylindrical with a basal collar. Follicles stout. Seeds elliptic, compressed, testa glabrous; coma absent.

Very little is known about this genus, which contains only one sp., *E. alba* Stapf, known from Sumatra, Peninsular Malaysia and Borneo.

### 95. *Mascarenhasia* A. DC.

*Mascarenhasia* A. DC., Prodr. 8: 487 (1844); Pichon, Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 2: 68–93 (1949),

synop.; Markgraf, Fl. Madagascar, Fam. 169: 248–276 (1976), rev.; Leeuwenberg, Wageningen Agric. Univ. Pap. 97-2: 21–52 (1997), rev.

Trees or shrubs. Inflorescences axillary or terminal, cymose, sometimes reduced to a single flower. Calyx lobes often foliaceous; calycine colleters many and more or less in a ring, or fewer and alternisepalous; corolla infundibuliform to tubular-campanulate, white flushed with rose, tube sometimes yellow, the lobes induplicate in bud, margins often long-ciliate and/or crispate; nectary disc 5-lobed. Follicles long and slender or stouter. Seeds with sessile, micropylar coma and small deciduous chalazal coma; testa glabrous.  $2n = 22$ .

Eight spp. in Madagascar, one of them reaching tropical Africa, in gallery forest, dry forest, brush or woodland, often on river banks, up to 1250 m.

### 96. *Holarrhena* R. Br.

*Holarrhena* R. Br., Asclepiadeae 52 (1810); De Kruif, Meded. Landbouwhogeschool Wageningen 81-2: 1–40 (1981), rev.; De Kruif, Fl. Zambesiaca 7: 456–458 (1985), reg. rev.; Middleton, Fl. Males. I, 18: 197–200 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 96–102 (2014), reg. rev.

Shrubs or trees. Inflorescences terminal or seemingly axillary due to overtopping. Calycine colleters few, alternisepalous; corolla salverform, white to greenish white; stamens inserted in lower third of corolla tube; filaments short; anthers with only rudimentary basal appendages, not lignified, weakly attached to the style-head via hair pads at the base of the filaments; nectary disc absent; ovary superior to partly inferior. Follicles long and slender, thinly coriaceous. Seed testa glabrous; coma micropylar, sessile.  $2n = 22$ .

Four spp. in S and SE Asia and tropical Africa.

### 97. *Malouetia* A. DC.

Fig. 39

*Malouetia* A. DC., Prodr. 8: 378 (1844); Woodson, Ann. Missouri Bot. Gard. 22: 238–270 (1935), rev. Amer. spp.; Van der Ploeg, Agric. Univ. Pap. 85-2: 70–83 (1985), reg. rev.; Endress, Fl. Venez. Guayana 2: 513–517 (1995), reg. rev.

Shrubs or trees. Leaves mostly with abaxial domatia in the axils of the secondary veins.

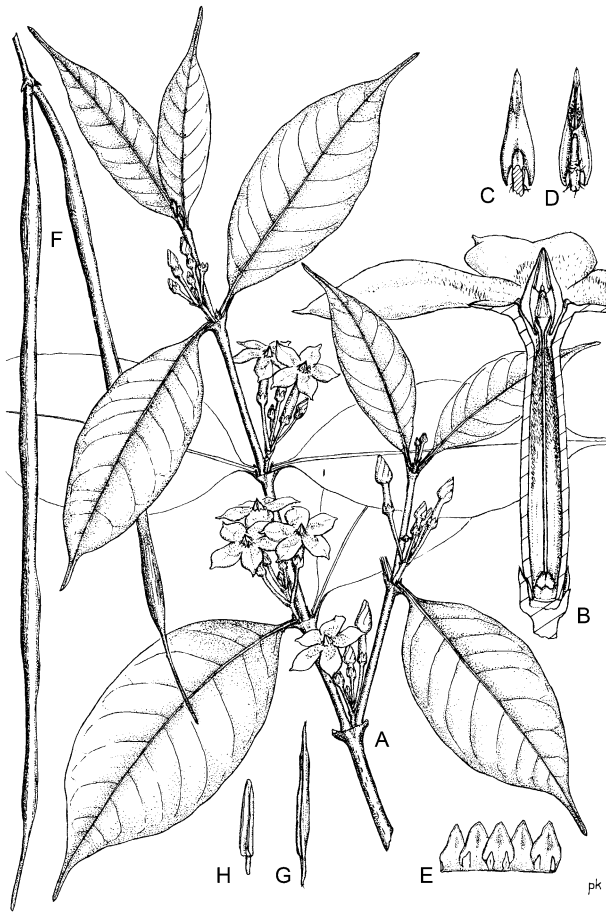


Fig. 39. Apocynaceae-Malouetieae. *Malouetia heudelotii*. A Flowering branch. B Longitudinal section through flower, showing partially exerted gynostegium. C Stamen dorsal side. D Stamen ventral side. E Opened calyx showing quincuncial arrangement of adaxial colleters. F Fruit. G Ecomose seed. H Embryo. (From Van der Ploeg 1985, p. 78, with permission from the Library of Wageningen University, Wageningen; drawn by P.J. Kostense)

Inflorescences axillary or terminal, fasciculate, few- to many-flowered. Calycine colleters few, alternisepalous; corolla tubular-campanulate, variously colored; corolline corona of five notched lobes behind the anthers often present; anthers exerted to included; nectary disc five-lobed. Follicles thinly to thickly woody, usually slender or stouter, green. Seeds without a coma; testa glabrous or with a few scattered hairs or densely covered with long hairs.

About 27 spp. with a disjunct distribution in the tropics of the New World and tropical W and C Africa, mostly in seasonally inundated forest, riverine forest, swamp forest or mangroves at low

altitudes, rarely montane forest. *Malouetia* has long been used as an arrow poison by indigenous peoples in Amazonia.

#### 98. *Kibatalia* G. Don

*Kibatalia* G. Don, Gen. Hist. 4: 86 (1837); Woodson, Philip. J. Sci. 60: 205–229 (1936), rev.; Rudjiman, Agric. Univ. Wageningen Pap. 86-5: 35–89 (1986), rev.; Middleton, Fl. Males. I, 18: 207–232 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 112–116 (2014), reg. rev.

*Paravallaris* Pierre (1898).

Trees or shrubs. Leaves often with abaxial domatia in the axils of the secondary veins. Inflorescences terminal or alternating in the upper leaf axils, fasciculate, few- to many-flowered. Calycine colleters few, alternisepalous, more rarely numerous and spread across the base of the sepals; corolla tubular-campanulate, white or off-white; anthers exerted to included; nectary disc annular, 5-lobed. Follicles thinly to thickly woody, narrowly fusiform to clavate. Seeds with rostrate chalazal coma of long retrorse hairs; testa glabrous.

15 spp. in continental SE Asia and Malesia, particularly in the Philippines, in tropical lowland or montane forest, swamp forest, thickets, savanna, mountain slopes, often on stream banks, road sides, up to 1200 m. Several species from now deforested areas have not been collected for decades and may be extinct.

#### 99. *Allowoodsonia* Markgr.

*Allowoodsonia* Markgr., Gard. Bull. Singapore 22: 23 (1967).

Tree; latex translucent to white. Inflorescences axillary, few-flowered. Calycine colleters few, alternisepalous; corolla salverform, white; corona absent; stamens inserted ca. midway in the tube; anthers subsessile, just reaching the tube orifice; nectary disc annular, 5-lobed; ovules ca. 8 per carpel. Follicles woody, broadly divergent, long, cylindrical, slightly inflated. Seeds obliquely oblong-lanceolate, without a coma; testa glabrous.

A poorly known genus of one sp., *A. whitmorei* Markgr., from the Solomon Islands, found in primary forest in valley bottoms and in coastal swamp forest.

100. *Malouetiella* Pichon

*Malouetiella* Pichon, Bull. Jard. Bot. État. 22: 131 (1952).

Tree or shrub. Leaves usually with abaxial domatia in at least some of the axils of the secondary veins. Inflorescences axillary or terminal lax dichasia. Calycine colleters few, alternisepalous; corolla tubular-campanulate, white, somewhat thickened in the throat; stamens inserted about midway in the corolla tube, included; nectary disc absent; ovules 4–6. Follicles slender. Seeds obliquely fusiform, longitudinally folded, without a coma; testa very sparsely pilose at ends.

One sp., *M. mildbraedii* Gilg & Stapf, from Nigeria to DR Congo, in montane forest up to 1400 m.

101. *Funtumia* Stapf

*Funtumia* Stapf, Hooker's Icon. Pl. 27: pl. 2694 (1901); Zwetsloot, Meded. Landbouwhogeschool Wageningen 81-16: 1–46 (1981), rev.

Trees or shrubs; latex white. Petioles of leaf pair often connate at the node, forming a short ocrea; abaxial domatia often present in axils of secondary veins. Inflorescences terminal and axillary, congested, cymose, several- to many-flowered. Calycine colleters few to several, alternisepalous; corolla thick, salverform, orifice constricted by a callous ring, white to cream, the tube greenish; stamens inserted at about the middle of corolla tube; anthers subsessile, included; nectary disc 5-lobed; style thick, obconical. Follicles woody, fusiform to clavate, 8–32 cm long. Seed coma chalazal, rostrate, the rostrum also with long retrorse hairs; testa glabrous.  $2n = 22$ .

Two spp. in tropical Africa.

II.4. Tribe *Rhabdadenieae* Pichon ex M.E. Endress (2014).

Slender woody lianas or perennial herbs with white latex. Leaves opposite. Flowers large and showy; calycine colleters absent; corolla infundibuliform; corolla lobe aestivation dextrorse; anthers with truncate, lignified guide rails fused to filaments, firmly attached to style-head, included; nectaries five separate lobes or fused basally; ovary apocarpous; style filiform; style-head cylindrical, conspicuously pilose apically, with a large

membranous basal collar. Fruit a pair of narrowly fusiform follicles. Seeds numerous, narrowly boat-shaped, glabrous; coma micropylar, long-rostrate. One neotropical genus in mangroves or swampy areas.

102. *Rhabdadenia* Müll. Arg.

Fig. 40

*Rhabdadenia* Müll. Arg. in Mart., Fl. Bras. 6(1): 173, t. 52 (1860); Woodson, Ann. Missouri Bot. Gard. 23: 205–211 (1936), rev.; Morales, J. Bot. Res. Inst. Texas 3: 541–564 (2009), rev.

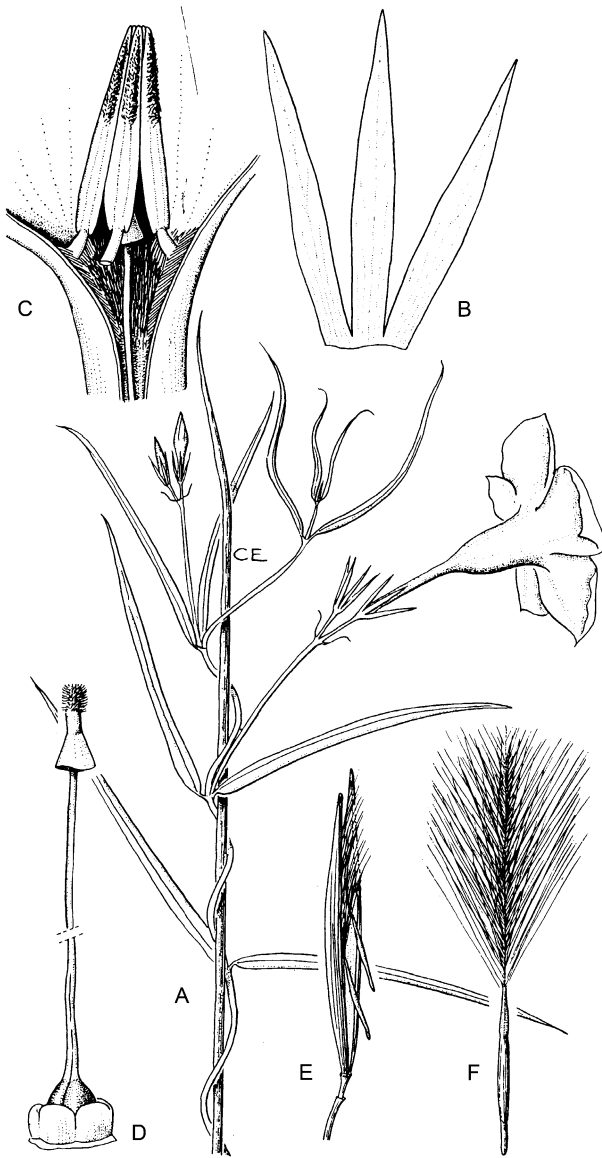
Lianas; latex white. Leaves opposite. Inflorescences axillary or subterminal cymes, typically of 2 flowers. Calyx lobes usually foliaceous; corolla large, showy, infundibuliform, white, white with yellow throat, rose, red or purple; stamens sessile to subsessile, inserted at the base of the throat, included; anthers truncate, non-auriculate at the base; ovary apocarpous; ovules many; style-head cylindrical, conspicuously pilose at the apex. Fruit a pair of narrowly fusiform follicles. Seeds narrowly boat-shaped; coma white to cream, up to 4 cm long.

Three spp., two restricted to South America in wet or swampy areas at low elevations; one, *R. biflora* (Jacq.) Müll. Arg., with exceptionally light-weight wood, is frequently found in mangroves, and reaches the Caribbean and Florida.

II.5. Tribe *Odontadenieae* Miers (1878).

Woody climbers or scrambling shrubs; latex white. Leaves opposite, rarely whorled or alternate (some species of *Odontadenia*), the blades lacking colleters adaxially. Inflorescences axillary, sometimes terminal, cymose. Calycine colleters few and alternisepalous or numerous and spread across base of sepals inside (rarely absent); corolla salverform to infundibuliform; corolla lobe aestivation dextrorse; corona absent; stamens inserted in the lower half of the corolla tube; anthers with well-developed lignified guide rails, the bases slender, acuminate; main attachment of the anthers at about the middle of style-head; base of thecae normally agglutinated to upper style-head as well; pollen (2–)3(–4)-porate; nectaries usually 5, these usually fused into a lobed or crenulate ring around the base of the ovary; ovary apocarpous; ovules many; style-head fusiform to ovoid (subcapitate in *Cycladenia*),





**Fig. 40.** Apocynaceae-Rhabdadenieae. *Rhabdadenia ragonesei*. A Flowering branch. B Three sepals showing lack of adaxial colleters. C Gynostegium showing nearly truncate basal appendages. D Gynoecium and nectary. E Dehiscent follicle showing seeds with micropylar coma. F Seed showing rostrate coma. (From Ezcurra et al. 1992, p. 102, © Conservatoire et Jardin botaniques de la Ville de Genève and with their permission; drawn by Cecilia Ezcurra)

broadest and often with equatorial flange at about the middle, normally without basal collar or upper wreath; stigmatic region usually on lower cylindrical region below adnation of anthers. Fruit apocarpous, of 2 separate follicles; follicles

generally thin-walled. Seeds flat, linear to ellipsoid or ovate, the testa glabrous or hairy, with micropylar (sometimes rostrate) coma. Cardenolides.  $x = 10, 11$  (more rarely 8, 12). Nine genera in the Americas, eight tropical, one restricted to mountain peaks in W and SE USA.

103. *Pinochia* M.E. Endress & B.F. Hansen

*Pinochia* M.E. Endress & B.F. Hansen, *Edinb. J. Bot.* 64: 269–274 (2007), nom. cons., synop.

Woody lianas or scrambling shrubs. Leaf blades usually with abaxial domatia in axils of secondary veins. Inflorescences terminal, less often axillary, thyrsiform, many-flowered. Flowers very small; calycine colleters alternisepalous, evenly distributed or rarely absent; corolla tubular to subcampanulate; tube short, usually with hairs in throat; stamens inserted near base of tube, barely included to completely exerted; nectary a 5-lobed disc; style-head ovoid, without ribs. Follicles free. Seeds slender, fusiform, without longitudinal ribs; coma yellowish brown, sessile.

Four spp. in Mexico, Central America and the Greater Antilles, usually in forest, often in coastal thickets or riparian forest up to 1000 m.

104. *Thyrsanthella* (Baill.) Pichon

*Thyrsanthella* (Baill.) Pichon, *Bull. Mus. Nat. Hist. Natl.* II, 20: 192 (1948); Livshultz et al., *Ann. Missouri Bot. Gard.* 94: 324–359 (2007), phyl.  
*Forsteronia* sect. *Thyrsanthella* Baill. (1889).

Woody liana. Leaf blades lacking abaxial domatia. Inflorescences terminal or axillary, many-flowered dichasia. Flowers small; calycine colleters alternisepalous; corolla inconspicuous, whitish, narrowly infundibuliform, with a ring of hairs in the throat; stamens inserted about midway in the corolla tube; filaments short, free; anthers barely included or the tips exerted; nectary of 5 lobes, nearly as high as the ovary; style-head ovoid, without ribs. Follicles free, narrowly terete to subtorulose. Seeds slender, fusiform; coma pale yellowish gray, sessile.

One sp., *T. difforme* (Walt.) Pichon, in the SE USA in a variety of wet to dry habitats, usually at low elevations.

105. *Cycladenia* Benth.

*Cycladenia* Benth., Pl. Hartw. 322. (1849); Woodson, Ann. Missouri Bot. Gard. 23: 214–217 (1936), rev.; Livshultz et al., Ann. Missouri Bot. Gard. 94: 324–359 (2007), phyl.

Low, subsucculent perennial herb; petioles winged and concrescent at the nodes. Inflorescences lateral, few- to several-flowered cymes. Calycine colleters absent; corolla infundibuliform, with lower cylindrical tube and upper expanded throat, reddish violet to cream; stamens inserted at base of throat, included; filaments short; nectary disc annular; style-head subcapitate. Fruit apocarpous; follicles small, relatively stout, sometimes remaining united at their apices. Seeds somewhat flattened and asymmetrical, brown-papillose with a pale tawny, sessile coma.

One sp., *C. humilis* Benth., with four described varieties, one each restricted to high elevations on disjunct mountain peaks in California, and one to high mesas in Utah and Arizona, respectively.

106. *Stipecoma* Müll. Arg.

*Stipecoma* Müll. Arg. in Mart., Fl. Bras. 6(1): 175 (1860); Woodson, Ann. Missouri Bot. Gard. 23: 189–191 (1936), rev.; Morales, Candollea 60: 307–311 (2005), synop.

Glabrous liana, woody at base but shoots delicate; latex white. Leaf blades peltate, glaucous, coriaceous, with well-developed colleters in axils of petioles. Inflorescences axillary, alternate, bostrychoid racemose. Calycine colleters few to several in alternisepalous groups; corolla salverform, pink; stamens inserted about midway in corolla tube; anthers with slender basal appendages; filaments short; nectaries connate at very base; style-head fusiform. Fruit apocarpous; follicles slender, terete, broadly divergent. Seeds slender; coma rostrate, cream to tan-cream colored.

One sp., *S. peltigera* (Stadelm.) Müll. Arg., in NE and C Brazil (rare in Bolivia) in open cerrado, campo rupestre and disturbed vegetation from 700–1600 m.

107. *Secondatia* A. DC.

*Secondatia* A. DC., Prodr. 8: 445 (1844); Woodson, Ann. Missouri Bot. Gard. 22: 224–232 (1935), rev.; Morales, Candollea 58: 305–319 (2003), rev.

Woody lianas; branches usually conspicuously lenticellate. Leaf blades with conspicuously reticulate tertiary venation. Inflorescences terminal or less frequently axillary, few- to many-flowered thyrses. Calycine colleters few, alternisepalous; corolla salverform, usually small, white or greenish yellow; stamens inserted in lower half of corolla tube; anthers with narrowly acuminate sagittate bases; nectary disc thin, 5-lobed; style-head elongate-fusiform without basal collar, sessile or with a very short style. Follicles ovoid-fusiform, stout. Seeds narrowly fusiform; coma cream, sessile to very shortly rostrate.

Four spp., in tropical South America from Colombia and Venezuela to Bolivia and Paraguay, in forest or more open, drier habitats such as savannas, cerrados or granitic outcrops.

108. *Odontadenia* Benth.

Fig. 41

*Odontadenia* Benth., J. Bot. (Hooker) 3: 242 (1841); Woodson, Ann. Missouri Bot. Gard. 22: 270–306 (1935), rev.; Morales, Bull. Jard. Bot. Belg. 67: 381–477 (1999), rev.

Woody lianas; branches often conspicuously lenticellate. Inflorescences axillary or axillary and terminal, thyriform to scorpioid, several-flowered. Calycine colleters few and alternisepalous to many and unevenly distributed; corolla infundibuliform or more rarely salverform, cream to yellow, often with red lines, rarely orange to red; stamens inserted at the base of the throat, included; anthers with sagittate bases; nectary disc usually 5-lobed; style-head fusiform. Follicles apocarpous, usually robust. Seeds narrowly fusiform; coma yellowish to pale tawny, sessile.  $2n = 24$ .

About 20 spp. in Central and South America and the Caribbean.

109. *Salpinctes* Woodson

*Salpinctes* Woodson, Bull. Torrey Bot. Club 58: 453 (1931); Morales, Novon 8: 429 (1998), synop.; Morales et al., Taxon 66: 623–644 (2017), phyl.

Perennial herb or woody subshrub, all parts glabrous; latex white. Leaves opposite, subsessile, thick-coriaceous. Inflorescences terminal, usually 1-flowered. Calycine colleters numerous, irregularly distributed; corolla salverform, large and showy, bright pink; stamens inserted near the



Fig. 41. Apocynaceae-Odontadenieae. Flowering and/or fruiting branches. A *Odontadenia funigera*. B *O. macrantha*. (From Zarucchi et al. 1995, p. 541, with permission from the Missouri Botanical Garden Press, St. Louis; drawn by B. Manara)

apex of corolla tube, included; nectaries 2, alternating with the carpels; style-head fusiform with a membranous collar at the base. Follicles terete, relatively stout. Seeds unknown.

One scarcely collected and poorly known sp., *S. kalmiaefolius* Woodson, endemic in savannas in Guyana and Amazonas State, Venezuela.

#### 110. *Angadenia* Miers

*Angadenia* Miers, Apocyn. S. Amer. 173 (1878), pro parte; Woodson, Ann. Missouri Bot. Gard. 23: 191–198 (1936), rev.; Morales et al., Taxon 66: 623–644 (2017), phyl.

Woody subshrubs; stems erect or sometimes twining; branches alternate; latex white. Inflorescences lateral, infrequently terminal, scorpioid. Calycine colleters few, alternisepalous; corolla infundibuliform, with a lower cylindrical tube and an upper expanded cup, white to pale yellow; stamens inserted somewhat below midway in the

corolla tube, included; nectary disc deeply 5-lobed; style-head fusiform with a basal collar. Fruit apocarpous; follicles terete, slender. Seeds narrowly fusiform; coma rostrate, pale yellowish.

Two to three spp. in the Caribbean, usually in sandy areas or in pine or palm barrens near the sea.

This genus has a complex taxonomic history, and has included up to 22 species, all but three of which are now included in genera of diverse tribes of neotropical Apocynoids.

#### 111. *Pentalinon* Voigt

*Pentalinon* Voigt, Hort. Suburb. Calcutt. 523 (1845); Woodson, Ann. Missouri Bot. Gard. 23: 198–205 (1936), rev. (as *Urechites*); Morales et al., Taxon 66: 623–644 (2017), phyl. *Urechites* Müll. Arg. (1860).

Woody lianas or subshrubs with twining stems; latex white. Inflorescences axillary to terminal, simply scorpioid, few- to many-flowered. Calycine colleters few and alternisepalous or more numerous and irregularly distributed; corolla infundibuliform, yellowish or cream, often marked with red; stamens inserted at base of throat, with conspicuous long, spirally coiled, filamentous connective appendages; nectaries separate or connate at base; style-head fusiform with membranous collar at base. Follicles terete, slender. Seeds pubescent with long-rostrate, pale brown coma.  $2n = 12$ .

Two species, one in Florida and the Caribbean, the other in Mexico and Central America. A popular ornamental in tropical countries.

#### II.6. Tribe *Mesechiteae* Miers (1878).

Vines, woody lianas or perennial herbs or subshrubs, the latter often with a xylopod; latex usually white. Leaves opposite, rarely whorled in some *Mandevilla* species, mostly with a cluster of sometimes deciduous colleters adaxially at base of the leaf blade (distributed along the length of midrib in some species of *Mandevilla*), sometimes with abaxial domatia in the axils of the secondary veins. Inflorescences axillary and/or terminal. Calycine colleters mostly in alternisepalous groups or in continuous ring, more rarely solitary and centered at the base of the sepals;

corolla usually divided into narrow lower tube and expanded upper throat, mostly infundibuliform or tubular-campanulate, more rarely tubular or salverform; corolla lobe aestivation dextrorse; distinct corona usually absent; stamens mostly inserted at base of the expanded upper part; anthers with long, well-developed lignified guide rails, sometimes  $\pm$  the entire anther (except for the thecae) strongly lignified and the thecae extending nearly to the base; pollen (2–)5 (–6)-porate; nectaries present, usually 5 fleshy lobes (2 lobes in some species of *Mandevilla*),  $\pm$  separate or fused at the base, forming a ring around the base of the ovary; ovary apocarpous (postgenitally syncarpous in a few species of *Forsteronia*); ovules many; style-head with five arms, which usually project from lower part (arms forming long ridges for most of the length of the style-head in *Mandevilla*) to which the anthers are attached; upper wreath and membranous basal collar absent; stigmatic zone confined to the underside or lower region of the style-head. Fruit apocarpous, of 2 separate follicles (these postgenitally syncarpous in a few species of *Forsteronia* and forming a “double-follicle”), usually slender. Seeds narrowly fusiform to oblong, testa glabrous or minutely puberulent, with a sessile micropylar coma.  $x = 10, 11$ . Cardenolide glycosides have been reported from some species of *Mandevilla*. Six neotropical genera.

#### 112. *Elytropus* Müll. Arg.

*Elytropus* Müll. Arg., Bot. Zeitung (Berlin) 18: 21 (1860); Woodson, Ann. Missouri Bot. Gard. 23: 383–214 (1936), rev.; Ezcurra, Darwiniana 24: 390–391, t. 5 (1981), reg. rev.; Morales, Darwiniana n.s. 1: 40–42, t. 1 (2013), reg. rev.

Woody scrambler with ferruginous pubescence; stems twining to erect; branches alternate above, mostly opposite below. Leaf blades without colleters at base adaxially. Inflorescences opposite lateral cymes of 1 (sometimes 2) pendent flowers; bracts subfoliaceous, pilose. Calycine colleters absent; corolla campanulate, white with rose to lilac markings at base; stamens inserted near base of tube; anthers with pilose apex and slender, acuminate basal appendages; nectaries 5, connate at base; style-head spool-shaped. Follicles relatively stout, ferruginous-hirtellous. Seeds oblong, chalazal end narrowed; testa glabrous.

One sp., *E. chilensis* (A. DC.) Müll. Arg., in Chile and Argentina, shaded rainforest floor on the sides of the coastal mountains near Valdivia up to ca. 2000 m.

*Elytropus* is an isolated genus and its inclusion in Mesechiteae is tentative (Livshultz et al. 2007).

#### 113. *Allomarkgrafia* Woodson

*Allomarkgrafia* Woodson, Ann. Missouri Bot. Gard. 19: 45 (1932); Woodson, Ann. Missouri Bot. Gard. 20: 625–628 (1933), rev.; Morales, Brittonia 49: 337–345 (1997), rev.

Glabrous woody lianas. Leaf blades with several colleters clustered at base adaxially. Inflorescences axillary, dichasial cymes. Calycine colleters numerous, uniformly distributed; corolla infundibuliform, with a lower cylindrical tube and an expanded campanulate throat, white to rose-white, cream to greenish white; stamens inserted at base of throat, included; anthers with uniformly fertile thecae; nectaries separate or connate at base; style-head fusiform above, five-ribbed below. Follicles slender, terete. Seeds narrowly oblong, chalazal end narrowed, micropylar end truncate.

Nine spp. in Central America and N South America, in humid forest, montane cloud forests, sometimes in disturbed areas, up to 1500 m.

There is evidence suggesting that *Allomarkgrafia* may be congeneric with *Mesechites* (Simões et al. 2004; Livshultz et al. 2007), but results are inconclusive at present.

#### 114. *Mesechites* Müll. Arg.

*Mesechites* Müll. Arg. in Mart., Fl. Bras. 6(1): 150 (1860); Woodson, Ann. Missouri Bot. Gard. 20: 625–645 (1933), rev.; Simões et al., Amer. J. Bot. 91: 1409–1418 (2004), phyl.; Morales, Candollea 61: 215–277 (2006), rev.

Woody lianas. Leaf blades with 1–several colleters clustered at base adaxially. Inflorescences axillary, compound cymose. Calycine colleters alternisepalous or numerous and irregularly distributed; corolla salverform to tubular-campanulate or infundibuliform, white to greenish white or rose, often flushed with pink and green; stamens inserted about midway in tube or at base of expanded throat, included; anthers with uniformly fertile thecae; nectaries separate or

connate at base; style-head fusiform to pentagonal above, strongly 5-ribbed in lower part. Follicles slender, terete. Seeds slender, fusiform, micropylar end truncate.

Eight spp. in Central and South America, and the Caribbean, in thickets, humid forest, montane cloud forests or cerrado and other more arid vegetation types, sometimes in disturbed areas at low elevations.

### 115. *Tintinnabularia* Woodson

*Tintinnabularia* Woodson, Ann. Missouri Bot. Gard. 23: 387 (1936); Morales, Novon 6: 392–394 (1996); Williams, Lundellia 2: 136–141 (1999), rev.

Woody lianas. Leaf blades with a few colleters clustered at base of midrib adaxially; abaxial domatia present in axils of secondary veins. Inflorescences axillary, corymbose, several-flowered; bracts and calyx sometimes foliaceous. Calycine colleters in alternisepalous groups; corolla showy, cream, infundibuliform; stamens inserted at base of throat, included except for filiform appendages; anthers with uniformly fertile thecae and obtuse bases; apical connective appendage filiform or absent; nectaries separate or connate at base; style-head fusiform above, strongly five-ribbed at base. Follicles long, slender, torulose. Seeds narrowly fusiform, longitudinally ridged, micropylar end truncate.

Three spp. in Mexico, Guatemala and Honduras; in humid montane forests, usually above 1000 m.

### 116. *Forsteronia* G. Mey.

*Forsteronia* G. Mey., Prim. Fl. Esseq. 133 (1818), nom. cons.; Woodson, Ann. Missouri Bot. Gard. 22: 153–224 (1935), rev.; Hansen, A monographic revision of *Forsteronia* (Apocynaceae), Ph.D. Thesis, University of South Florida, USA: 1–382 (1985), rev.

Woody lianas or scrambling shrubs. Leaf blades with colleters clustered at base of midrib adaxially; abaxial domatia usually present in secondary vein axils. Inflorescences terminal, less often axillary, thyriform, many-flowered. Flowers very small; calycine colleters alternisepalous, evenly distributed or rarely absent; corolla tubular to subcampanulate; stamens inserted near base of tube, barely included to completely exerted; anther bases cordate to truncate, more rarely

attenuate; nectary a 5-lobed disc; ovary usually apocarpous, sometimes postgenitally syncarpous; style-head 5-ribbed. Follicles usually free, sometimes postgenitally fused. Seeds narrowly elliptic, longitudinally ridged, micropylar end truncate; testa commonly minutely puberulent.

About 42 spp. in the Neotropics, usually in forest at lower elevations.

### 117. *Mandevilla* Lindl.

Fig. 42

*Mandevilla* Lindl., Edward's Bot. Reg. 26: t. 7 (1840), nom. cons. prop.; Woodson, Ann. Missouri Bot. Gard. 20: 645–790 (1933), rev.; Henrickson, Aliso 14: 179–195 (1996), part. rev. (as *Macrosiphonia* and *Telosiphonia*); Morales, Brittonia 50: 214–232 (1998), synop.; Simões et al., Amer. J. Bot. 91: 1409–1418 (2004), phyl.; Morales, Darwiniana 43: 131–137 (2005), reg. rev.; Morales, Darwiniana 44: 472–474 (2006), reg. rev.

*Exothostemon* G. Don (1837).

*Dipladenia* A. DC. (1844).

*Macrosiphonia* Müll. Arg. (1860).

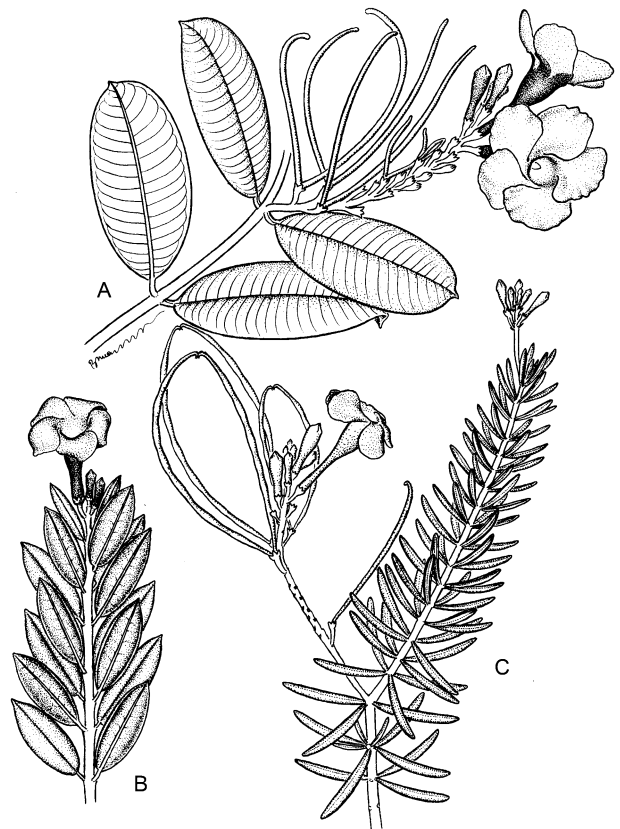


Fig. 42. Apocynaceae-Mesechiteae. Flowering and/or fruiting branches. A *Mandevilla subcarnosa*. B *M. turgida*. C *M. benthamii*. (From Zarucchi et al. 1995, p. 527, with permission from the Missouri Botanical Garden Press, St. Louis; drawn by B. Manara)

*Quiotania* Zarucchi (1991).  
*Telosiphonia* (Woodson) Henrickson (1996).

Woody lianas, perennial herbs, or rarely subshrubs; stems occasionally winged; sometimes with xylopod. Leaves opposite, more rarely verticillate, blades adaxially with colleters at base of midvein or along length (rarely absent). Inflorescences mostly axillary, occasionally terminal, usually racemose (unbranched). Calycine colleters usually present, variously distributed; corolla infundibuliform, sometimes salverform or tubular-campanulate, corolla often with curved tube, variously colored; stamens usually inserted at base of expanded throat, usually included; anthers strongly fused to style-head ribs; filaments very short; nectaries 2–5, separate or connate at base; style-head 5-ribbed. Follicles slender, terete to somewhat torulose. Seeds narrowly fusiform; testa usually minutely puberulent.  $2n = 16, 20$ .

About 170 spp. widely distributed from SW USA and northern Mexico, Central America and the Antilles to Paraguay and Uruguay and found in a variety of habitats, from rainforest to dry cerrado, dry rocky areas, desert scrub-grasslands and pine or oak forests, from lowland to montane elevations. A few species are cultivated and in recent years a number of showy cultivars of these are widely available for home gardens.

Although progress has been made, many species are rarely collected and poorly known, and the genus is in need of more in-depth study to better understand species-level relationships.

## II.7. Tribe Echiteae Bartl. (1830).

Vines or woody lianas, rarely erect shrubs or perennial herbs; latex often translucent, sometimes white. Leaves opposite (verticillate in most *Artia* and some species of *Parsonsia*). Inflorescences mostly axillary, less commonly terminal. Calycine colleters often solitary and antesealous, in the center of the sepal at the base, or several and spread across base of sepal, rarely absent; corolla salverform, infundibuliform, tubular-campanulate, campanulate (rotate in *Artia* and *Thenardia*, urceolate in *Ecua* and *Thoreauea*); corolla lobe aestivation dextrorse or valvate; stamens mostly inserted in upper part of corolla tube (near base in some *Parsonsia* and *Thenardia*); anthers often partially to almost completely exerted, with large lignified guide rails, attached

near base of style-head; pollen 3–5(–8)-porate; nectary present, encircling the base of the ovary, usually of  $5 \pm$  free lobes, these sometimes fused at the base, less frequently nectary an (often lobed or crenulate) ring; ovary apocarpous (postgenitally syncarpous in *Parsonsia*, *Artia*, *Ecua*, *Thenardia*, *Thoreauea*, *Temnadenia*, and some species of *Prestonia*); ovules many; style-head cylindrical to narrowly fusiform, broadest and with (usually well-developed, often membranous) collar at base and sometimes upper wreath as well; stigmatic zone located on underside of style-head beneath collar. Follicles typically slender (torulose in *Thenardia*), and postgenitally fused and forming a “double-follicle” in *Parsonsia*, *Artia*, *Thenardia*, *Thoreauea*, *Temnadenia*, probably in *Ecua* (fruit not known) and in some species of *Prestonia*, but splitting apart along suture into 2 follicle-like halves at maturity. Seeds mostly narrowly fusiform but broadly ovate in *Parsonsia* and *Artia* (and probably *Ecua*), the testa glabrous, with a micropylar (often rostrate) coma, the rostrum always glabrous. Pyrrolizidine alkaloids.  $x = 6, 7, 8, 9, 11$ . 14 genera, 11 in the Neotropics, three mainly in Australasia, of which one reaching continental Asia.

## 118. *Laubertia* A. DC.

*Laubertia* A. DC., Prodr. 8: 486 (1844); Woodson, Ann. Missouri Bot. Gard. 23: 370–375 (1936), rev.; Morales, Rhodora 104: 170–185 (2002), rev.; Morales et al., Taxon 66: 623–644 (2017), phyl.; Morales, Anales Jardin Bot. Madrid 74(2): e063 (2017), tax.

Woody lianas. Leaves usually opposite, rarely ternate. Inflorescences axillary, rarely terminal, few- to several-flowered scorpioid cymes. Calycine colleters absent; corolla salverform, variously pink, red, purple or white; tube straight or twisted, with thickened annular corona at orifice; stamens inserted midway or above in the corolla tube, usually partly exerted; anthers sessile, narrowly sagittate at the base; nectaries separate or fused at the base; ovary apocarpous; style-head fusiform. Fruit apocarpous, the follicles slender, weakly torulose. Seeds fusiform; coma sessile.

Four spp. with a disjunct distribution: two in Mexico and N. Central America, one in NW South America and one in the Amazon basin, up to 1600 m.

119. *Hylaea* J. F. Morales

*Hylaea* J. F. Morales, Novon 9: 83–85 (1999); Morales et al., Taxon 66: 623–644 (2017), phyl. Fig. 43

Woody lianas or small trees; latex usually translucent. Leaves glabrous. Inflorescences axillary, many-flowered, often umbelloid. Calycine collectors solitary, antesepalous; corolla salverform to subinfundibuliform, white and pink- to purple-tinged, glabrous, with a corona lobe inserted above each anther; lobes longer to about same length as tube; stamens inserted near orifice of corolla tube, almost completely exerted; filaments short, puberulent; anther bases acute to acuminate; nectaries distinct, as high as or surpassing the ovary; ovary apocarpous, glabrous; style-head fusiform. Fruit unknown.

A rarely collected and poorly known genus of two spp. restricted to Brazilian-Venezuelan Ama-

zonias, often on white sand soils and/or associated with blackwater rivers, below 400 m.

120. *Temnadenia* Miers

*Temnadenia* Miers, Apocyn. S. Amer. 207 (1878); Woodson, Ann. Missouri Bot. Gard. 23: 253–260 (1936), rev.; Morales, Candollea 60: 207–231 (2005), rev.; Morales et al., Taxon 66: 623–644 (2017), phyl.

Woody or suffruticose lianas; latex usually translucent. Inflorescences axillary, rarely subterminal, compound, alternate, many-flowered. Calycine collectors solitary, antesepalous, dissected; corolla salverform or infundibuliform, showy rose or purple, rarely greenish or yellowish; stamens with short filaments; anthers with slender basal appendages; nectaries separate or connate at very base; ovary postgenitally syncarpous; style-head fusiform. Fruit syncarpous, of 2 slender, terete follicles postgenitally fused into a “double-follicle”, which splits into 2 halves at maturity. Seeds with a tawny rostrate coma.  $2n = 18$ .

Three spp. in tropical South America, often at forest edges.

121. *Rhodocalyx* Müll. Arg.

*Rhodocalyx* Müll. Arg. in Martius, Fl. Brasil. 6(1): 172 (1860); Woodson, Ann. Missouri Bot. Gard. 23: 367–370 (1936), rev.; Stranghetti & Kinoshita, Rev. Bras. Bot. São Paulo 19: 133–144 (1996), morph.; Morales, Novon 9: 89–91 (1999), synop.; Morales et al., Taxon 66: 623–644 (2017), phyl.

Small erect subshrubs with xylopod or suffruticose liana; latex translucent. Leaves sessile to petiolate. Inflorescences terminal or lateral, simple racemes of few to several flowers. Calyx petaloid; calycine collectors antesepalous, several or solitary and deeply dissected; corolla salverform, orifice constricted by annular corona; stamens inserted in upper corolla tube; filaments bent inward; anthers with acute basal appendages; nectaries  $\pm$  separate but fused at base into 5-lobed ring; ovary apocarpous; style-head spool-shaped with membranous basal collar. Fruit apocarpous, follicles falcate, pubescent. Seeds numerous; coma sessile.

Two spp. found from NE Brazil to SE Bolivia and NE Paraguay in savannas, cerrados and campo rupestre vegetation.

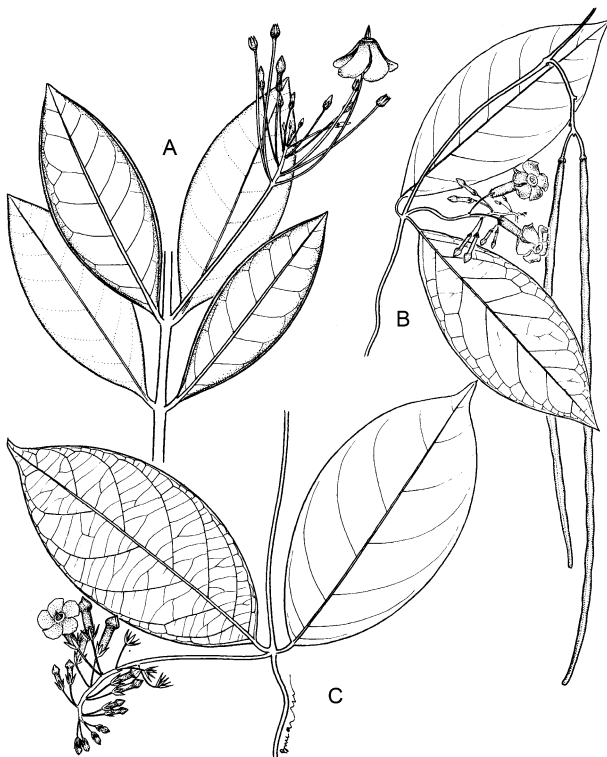


Fig. 43. Apocynaceae-Echiteae. Flowering and/or fruiting branches. A *Hylaea arborescens*. B *Prestonia acutifolia*. C *P. vaupesiana*. (From Zarucchi et al. 1995, p. 551, with permission from the Missouri Botanical Garden Press, St. Louis; drawn by B. Manara)

122. *Macropharynx* Rusby

*Macropharynx* Rusby, Memo. N.Y. Bot. Gard. 7: 327, t. 6 (1927); Woodson, Ann. Missouri Bot. Gard. 23: 268–271 (1936), rev.; Morales, Rhodora 99: 252–262 (1997), rev.; Morales, Candollea 60: 29–334 (2005), rev.; Morales et al., Taxon 66: 623–644 (2017), phyl.  
*Peltastes* Woodson (1932).

Woody lianas; branches often with rusty brown indument, at least in younger stages; latex translucent, rarely white. Leaves sometimes peltate. Inflorescences axillary, rarely terminal, few- to many-flowered; bracts foliaceous in some species. Calycine colleters solitary and antesealous or many, irregularly distributed; corolla salverform to infundibuliform, greenish white to pale yellow; tube twisted in some species; stamens inserted in mid-tube or higher, included; anthers with slender basal appendages; filaments short; nectaries 5,  $\pm$  separate; ovary apocarpous; style-head fusiform. Fruit of two stout, falcate follicles, often with rusty brown indument. Seeds glabrous; coma rostrate.

15 spp. in tropical Central and South America in wet, moist or seasonally dry forest, often at forest margins, some species in cerrados, savannas or disturbed habitats, from low elevations up to 2000+ m.

*Macropharynx meyeri* (Ezcurra) Xifreda does not fit well with the rest of the genus morphologically and probably would be better placed elsewhere. Until additional material of this species can be obtained for investigation, however, its placement remains speculative.

123. *Thenardia* Kunth

*Thenardia* Kunth in Humboldt et al., Nov. Gen. Sp. (quarto ed.) 3: 209, t. 240 (1818); Woodson, Ann. Missouri Bot. Gard. 23: 271–276 (1936), rev.; Williams, Lundellia 1: 78–94 (1998), rev.; Morales et al., Taxon 66: 623–644 (2017), phyl.

Glabrous woody or suffruticose lianas; latex translucent. Inflorescences axillary, condensed umbeloid cymes. Calycine colleters solitary, antesealous; corolla rotate or shortly salverform, white to pink; stamens inserted in mouth of corolla, completely exserted, filaments slender, sometimes coiled; anthers narrowly sagittate at base; nectaries separate, as long as or shorter than ovary; ovary postgenitally syncarpous; style-

head fusiform. Fruit syncarpous, of two slender, torulose follicles postgenitally fused into a “double-follicle”, which splits into halves at maturity. Seeds narrowly fusiform, tapering at coma end; coma white, sessile.

Three spp., endemic to Mexico, in semi-deciduous, montane, and cloud forest, sometimes near water, from 1100–2200 m.

124. *Thoreauea* J.K. Williams

*Thoreauea* J.K. Williams, Lundellia 5: 47–58 (2002); Morales, Brittonia 57: 258–263, synop.; Morales et al., Taxon 66: 623–644 (2017), phyl.

Lianas; latex white. Leaves glabrous. Inflorescences axillary, umbeloid cymes. Calycine colleters solitary, antesealous; corolla urceolate, whitish to greenish, 5–10-lobed annular corona at mouth; stamens inserted near base of corolla tube, included or tips exserted; anthers with slender auricles; filaments connate in a ring around style; nectaries 5, free or some of them fused at the base; ovary postgenitally syncarpous; style slender; style-head spool-shaped with basal collar. Fruit syncarpous, of two follicles postgenitally fused into a “double-follicle”, which splits apart at maturity. Seeds slender, navicular; coma sessile.

Three spp., all from southern Mexico, above 2600 m in montane pine-oak forest.

125. *Asketanthera* Woodson

*Asketanthera* Woodson, Ann. Missouri Bot. Gard. 19: 46 (1932); Woodson, Ann. Missouri Bot. Gard. 23: 263–268 (1936), rev.; Morales et al., Taxon 66: 623–644 (2017), phyl.

Woody or suffruticose lianas. Inflorescences axillary, simply scorpioid, several-flowered; pedicels subtended by single markedly foliaceous bract. Calyx markedly foliaceous; calycine colleters solitary, antesealous; corolla salverform, greenish white, yellowish, pinkish or cream; stamens inserted near base to midway in corolla tube, anthers included; filaments short; anthers with slender basal appendages; nectaries separate or connate at the base; ovary apocarpous; style-head fusiform. Fruit of two slender, terete follicles. Seeds with a tawny rostrate coma.



Four spp. in the Antilles, often on rocky (limestone) hillsides or cliffs, up to  $\pm$  500 m.

126. *Echites* P. Browne

*Echites* P. Browne, Civ. Nat. Hist. Jamaica 182 (1756); Woodson, Ann. Missouri Bot. Gard. 23: 217–252 (1936), rev.; Morales, Brittonia 49: 328–336 (1997), synop.; Williams, Sida 21: 117–131 (2004), part. synop. (as *Allotoonia*); Morales, Darwiniana 44: 467–469 (2006), reg. rev.; Morales, Darwiniana 47: 149–152 (2009), reg. rev.; Morales et al., Taxon 66: 623–644 (2017), phyl. *Fernaldia* Woodson (1932). *Allotoonia* J.F. Morales & J.K. Williams (2004).

Woody lianas or vines; latex white or translucent. Inflorescences axillary, rarely terminal, alternate, 1- to many-flowered. Calycine colleters solitary, antesealous, often deeply dissected; corolla salverform to infundibuliform, whitish or orangish; annulus at mouth and corona absent; stamens inserted at base of upper expanded part of corolla tube, included; nectaries separate or connate into a lobed disc; ovary apocarpous; style-head fusiform. Fruit of two slender, terete follicles, which sometimes remain united at apices. Seeds fusiform to broadly ovoid; coma rostrate.  $2n = 12$ .

13 spp. in tropical Mexico, Central America and the Caribbean. At one time several hundred species of Apocynoids were either described or combined in *Echites* from both the Old and New Worlds. Over time these were removed to many and varied other genera leaving a relatively small number of species.

127. *Bahiella* J.F. Morales

*Bahiella* J.F. Morales, Sida 22: 333–353, t. 2, 3 (2006).

Woody lianas; latex white. Leaves coriaceous with revolute margins. Inflorescences many-flowered axillary cymes. Calycine colleters solitary, antesealous, but usually deeply dissected; corolla large, mostly red to purple, salverform or infundibuliform; stamens inserted about midway in the corolla tube; anthers included, the sagittate bases slender, acuminate; nectaries fused into an irregularly 5-lobed ring; ovary apocarpous; style-head fusiform with basal collar. Fruit of two free follicles. Seeds fusiform; coma rostrate.

Two spp., known at present only from Bahia, Brazil, in humid forest, coastal vegetation, and *restinga*, at low elevations.

*Bahiella* is only rarely collected and poorly known.

128. *Ecua* D.J. Middleton

*Ecua* D.J. Middleton, Blumea 41: 33–35 (1996); Middleton, Fl. Males. I, 18: 190–191 (2007), reg. rev.

Liana or scrambling shrub. Inflorescences axillary elongated cymes. Calyx lobes small; calycine colleters solitary, antesealous; corolla urceolate, with inflated tube; lobes ca. a quarter as long as the tube, erect; stamens inserted near orifice of corolla tube, included; filaments curving downward and then up again; anther bases curved strongly outward; nectary lobes cupped, fused at the base; ovary postgenitally syncarpous, pubescent on top; style slender; style-head fusiform with a short collar. Fruit unknown.

One sp., *E. moluccensis* D.J. Middleton, collected only on Morotai and Halmahera in the Moluccas (Indonesia), in thickets below 100 m.

A rarely collected and poorly known genus, which shares most features with *Parsonsia*.

129. *Parsonsia* R. Br.

*Parsonsia* R. Br., Asclepiadeae 53 (1810), nom. cons.; Boiteau, Fl. Nouvelle-Cal. 10: 245–285 (1981); Williams, Fl. Australia 28: 154–189 (1996), reg. rev.; Middleton, Blumea 42: 191–248 (1997), reg. rev.; Middleton, Fl. Thailand 7(1): 135–138 (1999), reg. rev.; Middleton, Fl. Males. I, 18: 310–344 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 152–156 (2014), reg. rev.

*Lyonsia* R. Br. (1810).

*Delphyodon* K. Schum. (1898).

*Grisseea* Bakh. f. (1948).

Woody lianas or scrambling shrubs; latex often translucent, sometimes white. Leaves rarely verticillate; juvenile leaves often much smaller/narrower. Inflorescences axillary, sometimes terminal, cymose to paniculate. Calycine colleters usually solitary, antesealous, sometimes absent; corolla usually 5-merous, rarely 4-merous, tubular, variously colored; corolla lobe aestivation dextrorse or valvate; stamen insertion variable; anthers almost always partially to nearly completely exerted; filaments usually long, sometimes interspiraled; nectaries usually free; ovary postgenitally syncarpous, usually glabrous; style filiform; style-head fusiform, with short collar at base. Fruit syncarpous, glabrous, of two follicles

postgenitally fused into a “double-follicle”, which splits into two follicle-like halves at maturity. Seeds broadly ovate; coma sessile.  $2n = 18$ .

About 82 spp., in S Asia, continental SE Asia, Malesia to the western Pacific Islands, Australia and New Zealand, mostly in forest.

### 130. *Artia* Guillaumin

*Artia* Guillaumin, Bull. Soc. Bot. France 88: 380 (1941); Boiteau, Flore Nouvelle-Cal. 10: 285–298 (1981), rev.

Lianas; latex translucent to yellowish. Leaves usually in whorls of 3–4, sometimes opposite. Inflorescences axillary or terminal, cymose. Calycine colleters solitary, antesealous; corolla campanulate to urceolate or subrotate, usually whitish externally, with red-brown, orange, yellow or violet nectar guides at base of lobes internally, corona lobe just behind each anther; corolla lobe aestivation dextrorse; stamens inserted in upper half of corolla tube; filaments relatively long, geniculate; nectary disc annular; ovary postgenitally syncarpous, glabrous; style-head fusiform, with short collar at base. Fruit syncarpous, of two follicles postgenitally fused into a “double-follicle”, which splits into two follicle-like halves at maturity. Seeds flat, broadly ovate; coma sessile.

Four spp., endemic to New Caledonia.

This genus is sister to *Parsonsia*.

### 131. *Prestonia* R. Br.

Fig. 43

*Prestonia* R. Br., Asclepiadeae 58 (1810), nom. cons.; Woodson, Ann. Missouri Bot. Gard. 23: 276–367 (1936), rev.; Morales, Novon 7: 59–63 (1997), reg. rev.; Rio & Kinoshita, Hoehnea 32: 233–258 (2005), reg. rev.; Morales & Liede-Schumann, Phytotaxa 265: 204–224 (2016), reg. rev.; Morales et al., Ann. Missouri Bot. Gard. 102: 520–541 (2017), phyl.

Woody lianas; latex translucent to white. Inflorescences axillary, rarely subterminal, simple or compound. Calycine colleters solitary, antesealous; corolla salverform, rarely infundibuliform; thickened annular corona usually present at orifice of tube, corona of five appendages behind the anthers often present, sometimes reduced to ridges, corolla salverform, rarely infundibuliform, variously colored; stamens included to almost completely exerted; anthers narrowly sagittate at the base; nectaries separate to

completely fused; ovary usually apocarpous, more rarely postgenitally syncarpous; style-head fusiform with collar at base. Follicles apocarpous, or of two follicles postgenitally fused into a “double-follicle”, which splits into two halves at maturity. Seeds narrowly oblong; coma sessile or scarcely rostrate.  $2n = 18$ .

About 58 spp. ranging from the West Indies through Mexico, Central and South America as far as N Argentina, in a variety of habitats, from rainforest to dry forest, cerrado, open areas, from lowland to montane elevations.

## II.8. Tribe Apocyneae Rchb. (1831).

Woody climbers or scrambling shrubs (*Apocynum* perennial herbs); latex white. Leaves opposite, rarely whorled (alternate in some species of *Apocynum*), with abaxial domatia often present in the axils of secondary veins in *Urceola* and *Baharuia*. Inflorescences terminal and/or axillary, most commonly cymes, dichasia, thyrses or panicles. Calycine colleters few and alternisealous or numerous and spread across base of sepals inside (rarely absent); corolla salverform, campanulate or urceolate; corolla lobe aestivation dextrorse (sinistrorse in *Urceola* p.p.), rarely valvate; corona, if present, mostly as small pouches in petal sinuses, sometimes lower down on corolla tube behind stamens (*Apocynum* with alternistaminal appendages near base of corolla tube); stamen insertion variable, commonly near base, included except partly exerted in some spp. of *Trachelospermum* and *Micrechites* and appearing exerted in *Vallaris* and *Beaumontia* but then mostly due to the wide open upper tube rather than because the stamens protrude beyond length of entire tube; anthers with long, well-developed lignified guide rails, bases sagittate; main attachment of the anthers at about the middle of style-head; base of thecae normally agglutinated to upper style-head as well; pollen (2–)3(–4)-porate (polyantoporate in some *Micrechites*, *Trachelospermum* and *Apocynum*); nectaries 5, separate, or these fused into a (usually lobed or crenulate) ring around the base of the ovary; ovary apocarpous (postgenitally syncarpous in *Beaumontia*, *Parepigynum* and *Vallaris*), sometimes partly inferior; ovules almost always numerous; style-head broadly fusiform, broadest and often with equatorial flange at about middle, with or without basal collar (basal collar present in *Streptocheites*,

*Sindechites* and *Epigynum*); stigmatic region usually on lower cylindrical region below adnation of anthers. Fruit apocarpous, of 2 separate follicles; in *Beaumontia*, *Parepigynum* and *Vallaris* the follicles are postgenitally united along their ventral margins, forming a stout “double-follicle” that splits apart into 2 follicle-like halves at maturity (though sometimes only one carpel matures); follicles generally thin-walled but thick in *Beaumontia*. Seeds flat or not, linear to ellipsoid or ovate, the testa glabrous or hairy with micropylar (sometimes rostrate) coma. Cardenolides.  $x = 10, 11$  (more rarely 8, 12). 21 genera, almost all in tropical Asia and/or Oceania, one in temperate regions of the Old and New World.

### 132. *Papuechites* Markgr.

*Papuechites* Markgr., Nova Guinea 14, 2: 287 (1925); Middleton, Blumea 40: 439–442 (1995), rev.; Middleton, Fl. Males. I, 18: 303–305 (2007), reg. rev.

Liana. Inflorescences terminal and/or axillary thyrses. Colleters few, alternisepalous; corolla small, salverform to tubular-campanulate, pink or red; small corona lobes in mouth in the alternistaminal sectors and with ridges above the anthers, lobes about as long as tube, inflexed in bud; stamens inserted near the middle of corolla tube, included; filaments short; nectaries separate; ovary pubescent on top. Follicles broad at the base, abruptly tapering to a slender apex. Seeds elliptic, flattened, testa glabrous; coma on a long, glabrous rostrum.

One sp., *P. aambe* (Warb.) Markgr., in New Guinea and the Moluccas, in humid forest up to 1300 m.

### 133. *Ixodonerium* Pit.

*Ixodonerium* Pit. in Lecomte & Humbert, Fl. Indo-Chine 3: 1228 (1933); Lý, Feddes Repert 97: 669–670 (1986), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 110–111 (2014), reg. rev.

Liana. Inflorescences terminal, thyrses with short lateral axes, spike-like, pubescent. Calycine colleters few, alternisepalous; corolla red, tube cylindrical, swollen in the middle, thickened at the orifice, with ridges above the anthers; stamens inserted in lower third of corolla tube, included; anther bases divergent; filaments short; nectary

disc fleshy, annular, 5-dentate, higher than ovary; ovary densely pubescent on top; style short; style-head fusiform, pentagonal. Follicles broad at the base, abruptly tapering to a slender apex. Seeds elliptic, flattened, testa glabrous; coma rostrate.

One sp., *I. annamense* Pit., known only from C Vietnam in mountain forest.

### 134. *Anodendron* A. DC.

*Anodendron* A. DC., Prodr. 8: 443 (1844); Middleton, Blumea 41: 37–68 (1996), rev.; Middleton, Fl. Males. I, 18: 132–145 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 52–59 (2014), reg. rev. *Formosia* Pichon (1948).

Lianas. Inflorescences terminal or axillary cymes, often forming panicles. Calycine colleters few, alternisepalous; corolla salverform, whitish or yellowish; tube with ridges above the anthers; stamens inserted near base of corolla tube, included; filaments short; nectary disc annular; style short, thick, conical; style-head ovoid. Follicles glabrous, stout, ovoid, narrowed at the apex. Seeds flattened, ovoid, with a long rostrum with long hairs both along the rostrum and at its apex.

17 spp., India and China to Japan through SE Asia to Australia and the Solomon Islands, in forest up to 1600 m.

### 135. *Amphineurion* (A. DC.) Pichon

*Amphineurion* (A. DC.) Pichon, Bull. Soc. Bot. France 95: 215 (1948); Middleton, Fl. Males. I, 18: 129–131 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 48–51 (2014), reg. rev. *Aganosma* (Blume) G. Don sect. *Amphineurion* A. DC. (1844).

Liana or scrambling shrub; stems densely lenticellate. Leaves with strong marginal vein. Inflorescences lax, terminal or axillary panicles. Calycine colleters forming continuous ring; corolla salverform, white, lobes narrowly lanceolate, much longer than tube; stamens inserted about midway in the corolla tube, included; anthers sessile; nectary disc of 5 lobes or these fused into an ring, shorter than the ovary; ovary minutely puberulent to glabrous; style filiform. Follicles long, terete, rather stout, lenticellate. Seeds narrowly elliptic with sessile micropylar coma.

One sp., *A. marginata* (Roxb.) D.J. Middleton, widely distributed in NE India, SE Asia and

Malesia, in a variety of habitats, especially drier evergreen or deciduous forest or scrubland, up to 850 m.

136. *Sindechites* Oliv.

*Sindechites* Oliv. in Hooker's *Icones Pl.* 18: t. 1772 (1888); Xu, *Agric. Univ. Wag. Pap.* 88-6: 25-35 (1988), rev.; Li et al., *Flora of China* 16: 188 (1995), reg. rev.

Liana. Inflorescences terminal and/or axillary corymbs. Flowers small; calyx lobes small; calycine colleters few, alternisepalous; corolla salverform, white, tube much longer than lobes; lobes broadly ovate; stamens inserted about midway in corolla tube, included; filaments short; anthers with a tuft of hairs at the apex; nectary disc fleshy, entire or 5-lobed, shorter than or as high as the ovary; ovary glabrous or pubescent at the top; style filiform; style-head with basal collar. FollICLES slender, cylindrical, glabrous. Seeds linear; coma sessile.

One sp., *S. henryi* Oliv., widespread in C China, in montane forest, brush, roadsides, often near streams, up to 1500 m.

137. *Streptoechites* D.J. Middleton & Livsh.

*Streptoechites* D.J. Middleton & Livsh., *Adansonia* III, 34: 370 (2012); Middleton, *Fl. Cambodia, Laos and Vietnam* 33: 173-175 (2014), reg. rev.

Woody climber. Inflorescences terminal or axillary, cymose. Calyx without colleters within; calycine colleters few, alternisepalous; corolla salverform, white, tube much longer than lobes; stamens inserted about midway in the corolla tube, included; anthers with a tuft of hairs at the apex; nectary disc shallowly bilobate, shorter than or as high as the ovary; ovary glabrous; style filiform; style-head with basal collar. FollICLES slender, weakly torulose, glabrous; pedicels twisted in fruit. Seeds fusiform, testa glabrous; coma sessile, white.

One sp., *S. chinensis* (Merr.) D.J. Middleton & Livsh., from China and SE Asia.

138. *Vallis* Burm. f.

Fig. 44

*Vallis* Burm. f., *Fl. Indica* 51 (1768); Rudjiman, *Meded. Landbouwhogeschool Wageningen* 81-11: 1-17 (1981), rev.; Li et al., *Fl. China* 16: 177 (1995), reg. rev.; Middleton,

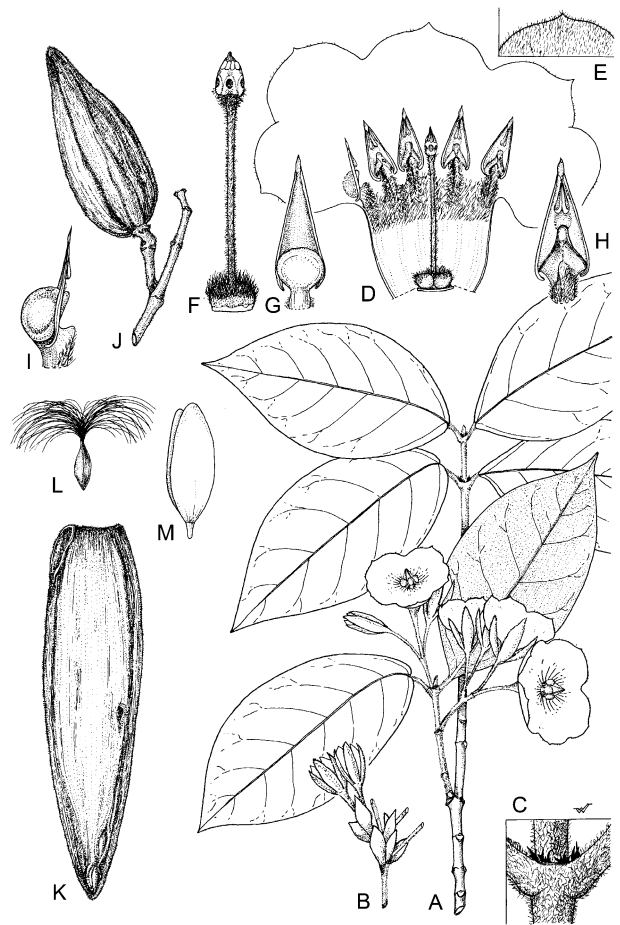


Fig. 44. Apocynaceae-Apocynaeae. *Vallis indecora*. A Flowering branch. B Inflorescence with flower buds. C Node showing colleters at petiole base. D Opened flower showing exerted reproductive organs. E Corolla lobe apex showing abaxial pubescence. F Gynoecium. G Anther dorsal side. H Anther ventral side. I Anther from side showing dorsal swelling. J Postgenitally connate immature fruit. K One half of dehiscent mature fruit. L Seed. M Embryo. (From Rudjiman 1982, p. 8, with permission from the Library of Wageningen University, Wageningen; drawn by W. Wessel-Brand)

*Fl. Males. I*, 18: 409-410 (2007), reg. rev.; Middleton, *Fl. Cambodia, Laos and Vietnam* 33: 229-230 (2014), reg. rev. *Parabeaumontia* Pichon (1948).

Woody climbers. Inflorescences axillary, rarely terminal, cymose; bracts large, foliaceous. Calycine colleters few, alternisepalous, or absent; corolla of lower cylindrical tube and much-expanded upper cup, white or off-white; stamens inserted at base of upper cup; filaments short; anthers with conspicuous dorsal hump, exerted from lower tube; nectary disc annular, lobed; ovary pubescent; style filiform, pubescent; style-

head without upper wreath or basal collar. Fruit of two follicles postgenitally fused into an ovoid “double-follicle”, which splits into two halves at maturity (though sometimes only one maturing). Seeds flat, broadly ovate; testa puberulent; coma sessile.  $2n = 20, 22$ .

Three spp. from Kashmir to S China, SE Asia and western Malesia.

### 139. *Beaumontia* Wall.

*Beaumontia* Wall., Tent. Fl. Nepal. 14, pl. 7 (1824); Rudjiman, Agric. Univ. Wageningen Pap. 86-5: 3–35 (1986), rev.; Middleton, Fl. Males. I, 18: 147–151 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 59–63 (2014), reg. rev.  
*Muantum* Pichon (1948).

Lianas. Inflorescences axillary or terminal, cymose, few-flowered. Calyx lobes usually large, foliaceous; calycine colleters usually many, rarely few and alternisepalous; corolla mostly very large, of cylindrical lower tube and much-expanded upper cup, usually white; stamens inserted at base of upper cup; anthers on long, slender filaments, sometimes projecting beyond corolla tube; nectary disc annular, 5-lobed; carpels postgenitally fused; style slender; style-head fusiform, without upper wreath or basal collar. Fruit of two follicles postgenitally fused into a woody, stoutly fusiform “double-follicle”, which splits into two halves at maturity. Seeds broadly ovate; coma sessile.  $2n = 24$ .

Ten spp. in tropical Asia from India to Bali, in thickets and humid lowland, montane, or monsoon forest, often on river banks or coasts, up to 1700 m. One species, *B. grandiflora* Wall., reaching temperate regions in Nepal, Bhutan and Sikkim, and also widely cultivated in Europe, America, and Africa.

### 140. *Parepigynum* Tsiang & P.T. Li

*Parepigynum* Tsiang & P.T. Li, Acta Phytotax. Sin. 11: 394, t. 54 (1973); Middleton, Fl. Cambodia, Laos and Vietnam 33: 150–152 (2014), reg. rev.

Liana. Inflorescences terminal and axillary, corymbose, long-pedunculate. Calyx pubescent, alternisepalous colleters few; corolla salverform, yellow, the tube densely pubescent, the lobes about as long as the tube; stamens inserted about midway in the corolla tube, included; fila-

ments short; nectary disc fleshy, of  $5 \pm$  fused lobes; carpels postgenitally syncarpous, ovary partly inferior to inferior, pubescent; style cylindrical; style-head conical, without upper wreath or basal collar. Fruit of two follicles postgenitally fused into a woody, stoutly fusiform “double-follicle”, which splits into two halves at maturity. Seeds narrowly elliptic; coma shortly rostrate.

A rare genus of one sp., *P. funingense* Tsiang & Li, from southern China and northern Vietnam, in dense montane forests, up to 1800 m.

### 141. *Cleghornia* Wight

*Cleghornia* Wight, Icon. Pl. Ind. Orient. 4(2): 5, t. 1310, 1312 (1848); Xu, Agric. Univ. Wageningen Pap. 88-6: 1–29 (1988), rev.; Middleton, Fl. Males. I, 18: 184–186 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 88–89 (2014), reg. rev.  
*Giadotrum* Pichon (1948).

Woody climbers. Inflorescences terminal and/or axillary, paniculate-corymbose. Flowers small; calyx lobes small; calycine colleters few, alternisepalous; corolla salverform, variously colored; lobes much shorter to about as long as tube; stamens inserted near base of corolla tube, included; filaments short; anthers pubescent dorsally near apex; nectary a disc or 5 separate fleshy lobes, as long as or shorter than the ovary; ovary glabrous; style short, slender. Follicles slender. Seeds narrowly elliptic, testa glabrous; coma shortly rostrate.

Two spp. in Sri Lanka, China and SE Asia, in montane forest or brush, often along river banks or near streams, up to 1600 m.

### 142. *Apocynum* L.

*Apocynum* L., Sp. Pl. 1: 213 (1753); Woodson, Ann. Missouri Bot. Gard. 17: 1–213 (1930), rev.; Li et al., Fl. China 16: 181 (1995), reg. rev.  
*Poacynum* Baill. (1888).  
*Trachomitum* Woodson (1930).

Perennial herbs. Leaves opposite, alternate or rarely verticillate. Inflorescences terminal and axillary, few- to many-flowered aggregate dichasia. Calycine colleters absent; corolla greenish to white, sometimes with pink veins, campanulate to urceolate or tubular; lower tube with five appendages opposite the lobes; stamens inserted at base of tube, included; filaments thick, curved inward; pollen in persistent tetrads; nectaries five, fused at

the base; ovary partly inferior to superior; style-head thick, fleshy, ovoid-fusiform, sessile. Follicles slender; coma sessile.  $2n = 16$  or  $22$ .

About nine spp., temperate to subtropical North America, Europe and Asia, in disturbed areas, pastures, cultivated fields, saline regions, dry stream beds, etc.

#### 143. *Urceola* Roxb.

*Urceola* Roxb., *Asiat. Res.* 5: 169 (1798), nom. cons.; Middleton, *Blumea* 41: 82–114 (1996), rev.; Middleton, *Fl. Males. I*, 18: 394–408 (2007), reg. rev.; Middleton, *Fl. Cambodia, Laos and Vietnam* 33: 212–228 (2014), reg. rev. *Ecdysanthera* Hook. & Arn. (1837). *Chavannesia* A. DC. (1844). *Parameria* Benth. (1876). *Xylinabaria* Pierre (1898). *Aganonerion* Pierre ex Spire (1905). *Parabarium* Pierre ex Spire (1905). *Xylinabariopsis* Pit. (1933). *Chunechites* Tsiang (1937). *Parameriopsis* Pichon (1948).

Woody climbers. Leaves often with abaxial domatia in axils of the secondary veins. Inflorescences axillary and/or terminal, cymose, often forming panicles or spike-like. Flowers small; calycine colleters few to numerous, alternisepalous or continuous; corolla urceolate, salverform or campanulate, variously colored; corolla lobe aestivation sinistrorse, dextrorse or valvate; stamens inserted near base of corolla tube, included; filaments short; nectary disc annular, 5-dentate or 5-lobed; ovary densely puberulent; style short; style-head fusiform. Follicles torulose or not. Seeds narrowly elliptic, testa hirsute; coma sessile, with a crown of shorter hairs at base.  $2n = 20$ .

20 spp. from S Asia, S China, SE Asia and Malesia, in humid evergreen, deciduous or swamp forest (more rarely in open thickets and on dry, sandy soil), up to 1500 m.

#### 144. *Chonemorpha* G. Don

*Chonemorpha* G. Don, *Gen. Hist.* 4: 76 (1837), nom. cons.; Chatterjee, *Kew Bull.* 1947: 47–52 (1947), synop.; Li et al., *Fl. China* 16: 170–171 (1995), reg. rev.; Middleton, *Fl. Males. I*, 18: 178–184 (2007), reg. rev.; Middleton, *Fl. Cambodia, Laos and Vietnam* 33: 78–878 (2014), reg. rev. *Rhynchodia* Benth (1876).

Woody lianas; plants usually with most parts pubescent. Inflorescences terminal or axillary,

few- to several-flowered cymes. Calyx usually cupular; colleters numerous, in continuous ring; corolla usually large, salverform, white or pinkish; stamens inserted in lower half of corolla tube, included; filaments short; nectary annular; style slender; style-head fusiform-pentagonal, with an upturned cup-like structure at the base, to which the anthers are firmly attached. Follicles ovoid, attenuate, rather stout. Seeds compressed ovate; coma rostrate; rostrum glabrous.  $2n = 20$ .

About ten spp. in India, China and SE Asia to western Malesia, mostly in forest at low to mid elevations.

The genus is in need of revision.

#### 145. *Trachelospermum* Lem.

*Trachelospermum* Lem., *Jard. Fleur.* 1, t. 61 (1851), nom. cons.; Woodson, *Sunyatsenia* 3: 65–105 (1936), rev.; Li et al., *Fl. China* 16: 166–168 (1995), reg. rev.; Middleton, *Fl. Males. I*, 18: 390–394 (2007), reg. rev.; Middleton, *Fl. Cambodia, Laos and Vietnam* 33: 202–211 (2014), reg. rev.

Woody climbers. Inflorescences terminal or axillary lax or congested cymes. Calycine colleters  $\pm$  in a continuous ring or few and alternisepalous; corolla salverform, white to yellowish or purplish, the tube 5-angled; stamens inserted in lower or upper half of tube, included or partly exerted; nectary of 5 free lobes or fused in a ring; style short; style-head conical. Follicles linear or fusiform. Seeds linear-oblong; testa glabrous; coma sessile.  $2n = 20$ .

Six to ten spp. from China and Japan through SE Asia and W Malesia, in deciduous, evergreen or gallery forest, often in open areas, climbing in trees or over rocks, sometimes near streams.

This genus is in need of a comprehensive, modern revision.

#### 146. *Micrechites* Miq.

*Micrechites* Miq. *Fl. Ned. Ind.* 2: 457 (1857); Middleton, *Blumea* 39: 73–94 (1994), rev.; Middleton, *Fl. Males. I*, 18: 281–289 (2007), reg. rev.; Middleton, *Fl. Cambodia, Laos and Vietnam* 33: 139–144 (2014), reg. rev. *Lamechites* Markgr. (1926). *Vallariopsis* Woodson (1936).

Woody lianas or scrambling shrubs; latex white. Leaves opposite. Inflorescences terminal and/or axillary, often thyrsoid. Calycine colleters in continuous ring or alternisepalous, sometimes

absent; corolla salverform, whitish to reddish; lobes strongly inflexed in bud; stamens inserted in lower half to middle of corolla tube, included or slightly exerted; nectary of five lobes or fused in a ring; ovary apocarpous; style slender; style-head with a turbinate lower and cylindrical upper part. Follicles slender and terete to fusiform. Seeds narrowly elliptic; testa glabrous; coma sessile.

Ten spp. in NE India, S China, SE Asia and Malesia, in rainforest, mostly in moist to dry evergreen or deciduous forest up to 1000 m.

#### 147. *Amalocalyx* Pierre

*Amalocalyx* Pierre, Bull. Mens. Soc. Linn. Paris II, 1: 28 (1898); Middleton, Fl. Cambodia, Laos and Vietnam 33: 45–47 (2014), reg. rev.

Woody liana, most parts pubescent. Inflorescences axillary and terminal, dichasial. Flowers showy; calycine colleters in continuous ring; corolla infundibuliform, white to pink, darker inside; lobes much shorter than tube; stamens inserted around middle of corolla tube, at base of expanded part, included; nectary annular, higher than the ovary; ovary postgenitally syncarpous; style slender; style-head cylindrical with a membranous collar at base. Fruit of two follicles weakly postgenitally fused into an ovoid, densely pubescent and unevenly corky “double-follicle”, which splits into two halves at maturity. Seeds compressed, broadly ovate; coma sessile.

One sp., *Amalocalyx microlobus* Pierre ex Spire, in S China and SE Asia, in deciduous or dry evergreen forest.

#### 148. *Baharuia* D.J. Middleton

*Baharuia* D.J. Middleton, Blumea 40: 443–447 (1995); Middleton, Fl. Males. I, 18: 145–147 (2007), reg. rev.

Woody climber. Leaves with hair-filled, abaxial domatia in the axils of the secondary veins. Inflorescences terminal and/or axillary cymes. Flowers small; calycine colleters in a continuous ring; corolla urceolate to salverform, yellow or orange, puberulent outside, lobes slightly shorter than tube; stamens inserted near base of corolla tube; filaments short; nectary disc 5-dentate or 5-crenulate; ovary pubescent. Follicles narrow and

somewhat torulose. Seeds linear, testa glabrous, coma sessile.

One sp., *B. gracilis* D.J. Middleton, in Borneo and Sumatra, in evergreen forest or forest margins up to 900 m.

#### 149. *Pottsia* Hook. & Arn.

*Pottsia* Hook. & Arn., Bot. Beechey Voy. 198, t. 43 (1837); Middleton, Fl. Males. I, 18: 344–347 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 156–160 (2014), reg. rev.

Woody climbers; latex white. Inflorescences terminal, large, many-flowered panicles. Calycine colleters in a continuous row; corolla salverform, without corona, pinkish; stamens inserted near mouth of corolla, almost completely exerted; filaments short, slender; nectary of free lobes or in ring; ovary apocarpous, pubescent; style inflated in the middle or near the base; style-head fusiform. Follicles long, slender, terete, glabrous, often somewhat spirally twisted. Seeds narrowly elliptic; testa glabrous; coma sessile.

Three spp. in India, S China, continental SE Asia and W Malesia, in montane forest, open forest, forest borders, thickets, up to 1100 m.

#### 150. *Aganosma* (Blume) G. Don

*Aganosma* (Blume) G. Don, Gen. Hist. 4: 77 (1837); Middleton, Kew Bull. 51: 455–482 (1996), rev.; Middleton, Fl. Thailand 7(1): 104–110 (1999), reg. rev.; Middleton, Fl. Males. I, 18: 30–31 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 12–18 (2014), reg. rev. *Echites* P. Browne sect. *Aganosma* Blume (1826).

Woody climbers. Inflorescences terminal or axillary few- to many-flowered cymes. Calyx lobes mostly large and foliose; colleters alternisepalous; corolla cylindrical or infundibuliform; tube often conspicuously 5-ribbed; stamens inserted in lower part of corolla tube, included; filaments short; nectary tubular, usually higher than the ovary; style slender; style-head fusiform-pentagonal, without a basal collar. Follicles long, cylindrical. Seeds compressed, lanceolate, testa glabrous; coma sessile or scarcely rostrate.  $2n = 22$ .

Seven spp., from India, S China, continental SE Asia and W Malesia, in forest at low to mid elevations.

151. *Ichnocarpus* R. Br.

*Ichnocarpus* R. Br., Asclepiadeae 50 (1810), nom. cons.; Middleton, Blumea 39: 73–94 (1994), rev.; Middleton, Fl. Males. I, 18: 203–207 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 105–110 (2014), reg. rev.

Woody climbers. Inflorescences terminal or axillary cymes, thyrsoïd, often puberulent to villous. Flowers small; calycine colleters few, alternisepalous (rarely absent); corolla salverform, sometimes with a thickened ring in the throat, lobes much longer than tube, white or yellowish; stamens inserted in lower half of corolla tube, included; filaments short; nectaries five, separate; ovary usually pubescent on top. Follicles long and slender, pubescent or glabrous. Seeds linear, compressed; testa glabrous; coma sessile, fawn, cream or white.  $2n = 20$ .

Three spp. from India, S China, continental SE Asia, Malesia and Australasia, in primary or secondary forest, sometimes more open drier habitats.

152. *Epigynum* Wight

*Epigynum* Wight, Icon. Pl. Ind. Orient. 4(2): 4, t. 1308 (1848); Middleton, Harvard Pap. Bot. 10: 67–81 (2005), rev.; Middleton, Fl. Males. I, 18: 192–195 (2007), reg. rev.; Middleton, Fl. Cambodia, Laos and Vietnam 33: 89–96 (2014), reg. rev.

*Nouettea* Pierre (1898).

*Argyronerium* Pit. (1933).

Woody climbers; latex white. Inflorescences congested, flat-topped, terminal and/or axillary corymbs. Calycine colleters in a row at base inside, alternisepalous, or absent; corolla salverform, white to pinkish, lobes obovate, shorter than tube; stamens inserted about middle of corolla tube or below, included; filaments short; nectary 5 separate lobes or crenate ring; ovary apocarpous, pubescent or glabrous; style filiform, style-head long, cylindrical, 5-angled with a (sometimes small) basal collar. Follicles slender. Seeds compressed-ovate; testa glabrous; coma sessile.

Five spp. from S China to W Malesia, in evergreen or deciduous forest below 1000 m.

II.9. **Tribe Baisseeae** (Pichon ex De Kruif) M.E. Endress (2007).

Woody lianas or climbing shrubs (rarely rhizomatous creepers); latex white. Leaves opposite, with colleters adaxially along the petiole and sometimes extending onto the base of the blade, abaxial domatia usually present in the axils of the secondary veins. Inflorescences axillary or terminal, usually many-flowered thyrses. Calycine colleters few, alternisepalous and quincuncially arranged (absent in *Dewevrella*); corolla tube with 5 small knob-like corona lobes in the alternipetalous sectors, one above each anther, and with tufts of stiff hairs alternating with the anthers (in *Dewevrella* corolla tube less than 0.5 mm long, the lobes long and strap-like); corolla lobe aestivation dextrorse; stamens mostly inserted on a thickened ring near the base of the corolla tube; anthers usually sessile, fertile only in the upper part, the enlarged, sterile basal part with well-developed lignified guide rails, the bases usually spreading outward and ending in a conspicuous subglobose thickening (in *Dewevrella*, stamens completely exerted with long, filiform filaments interspiraled around the style); pollen 3(–4)-porate; nectaries fused into a 5-lobed ring around the ovary; ovary apocarpous, usually partly inferior; ovules many; style usually short, thick, but filiform in *Dewevrella*; style-head usually more or less fusiform, greatest in diameter and 5-angled in the middle (where the anthers are attached) with an elongate tapering apex; membranous basal collar and upper wreath absent. Fruit apocarpous, of 2 woody follicles, spreading and joined at the very base; follicles squat and fusiform to narrowly cylindrical. Seeds narrowly ellipsoid, somewhat compressed laterally and navicular, testa glabrous with a sessile micropylar coma. Spermidine alkaloids (but only *Oncinotis* investigated). Four genera in tropical Africa, one also on Madagascar.

153. *Motandra* A. DC.

*Motandra* A. DC., Prodr. 8: 423 (1844); De Kruif, Meded. Landbouwhogeschool Wageningen 83-7: 1–20 (1983), rev.

Climbing shrubs or lianas. Leaves with abaxial domatia in axils of secondary veins. Inflorescences terminal, many-flowered thyrses. Calycine colleters few, alternisepalous; corolla tubular to infundibuliform; corona below petal sinuses, a



bulge just behind each anther; stamens included; anthers with tufts of coarse hairs at the apex; nectary disc 5-lobed, adnate to the ovary; ovary partly inferior, syncarpous at base, apocarpous above; style-head thick, sessile or almost so. Follicles thinly to thickly woody, connate at very base, divergent at ca. 180°.  $2n = 22$ .

Three spp. in W and C Africa, in rainforest, secondary deciduous forest, gallery forest, also in open areas, up to 1200 m.

#### 154. *Baissea* A. DC.

*Baissea* A. DC., Prodr. 8: 424 (1844); van Dilst, Bull. Jard. Bot. Nat. Belg. 64: 89–178 (1995), rev.

Climbing shrubs, lianas or, rarely, rhizomatous creepers. Leaves with abaxial domatia usually present in abaxial axils of secondary veins. Inflorescences axillary and terminal, cymose, paniculate sometimes corymbose. Calycine colleters few, alternisepalous; corolla infundibuliform, campanulate or cylindrical, usually with ridges or a distinct corona behind the anthers; stamens inserted near base of corolla tube; filaments stout; anthers exposed; nectary disc crenate to 5-lobed; ovary partly inferior; ovules many; style-head thick, sessile. Follicles narrowly cylindrical.  $2n = 22$ .

18 spp. in tropical Africa, in primary and secondary rainforest, riverine and swamp forest, coastal forests and montane forest, rarely open woodland, up to 2000 m.

#### 155. *Oncinotis* Benth.

Fig. 45

*Oncinotis* Benth. in Hook., Niger Fl. 451 (1849); De Kruif, Agric. Univ. Wageningen 85-2: 5–45 (1985), rev.

Climbing shrubs or lianas. Leaves usually with abaxial domatia in axils of secondary veins; petioles mostly with colleters along adaxial side. Inflorescences terminal or axillary, many-flowered thyrses. Calycine colleters few, alternisepalous; corolla urceolate to salverform; corolline corona of five simple lobes in petal sinuses; stamens included; anthers with basal appendages curved backward and globose at base; nectary disc a 5-lobed ring; ovary partly inferior; style-head thick, sessile. Follicles pendulous, woody, connate at very base, broadly divergent.  $2n = 22$ .

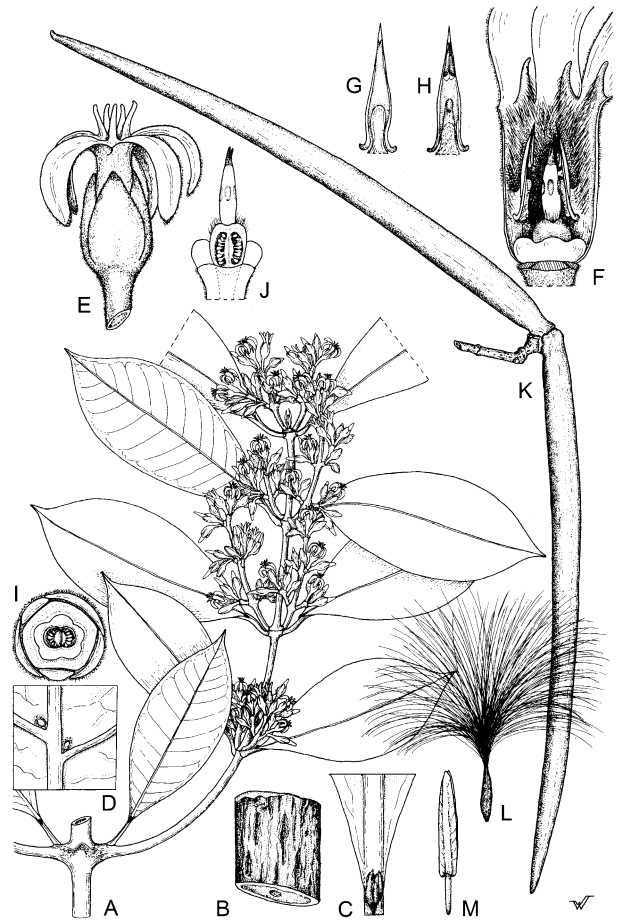


Fig. 45. Apocynaceae-Baisseeae. *Oncinotis nitida*. A Flowering branch. B Section of branch longitudinally fissured by elongate lenticels. C Leaf blade base showing cluster of colleters at juncture of petiole. D Close-up of leaf showing abaxial domatia. E Flower. F Longitudinal section through flower showing gynoecium at base and corolline corona at mouth. G Stamen dorsal side. H Stamen ventral side. I Transverse section through flower at level of ovary. J Gynoecium. K Fruit. L Seed. M Embryo. (From De Kruif 1985, p. 26, with permission from the Library of Wageningen University, Wageningen; drawn by W. Wessel-Brand)

Seven spp. in tropical Africa and Madagascar, primary and secondary rainforest, swamp forest and gallery forest, from 0–2200 m.

#### 156. *Dewevrella* De Wild.

*Dewevrella* De Wild., Miss. Em. Laurent 1: 548 (1907); Van der Ploeg, Agric. Univ. Wageningen 85-2: 57–85 (1985), rev.

Liana. Leaves without abaxial domatia in axils of secondary veins. Inflorescences terminal or

axillary, many-flowered thyrses. Calyx without colleters within; corolla rotate, white; lobes strap-like; stamens inserted at the base of corolla tube, conspicuously exerted and twisted around the style; anthers white with a yellow apical connective appendage; nectary disc irregularly 5-lobed; ovary partly inferior; ovules 8–15 per carpel; style filiform; style-head fusiform. Follicles slender with a thin wall.

One sp., *D. cochliostema* De Wild., endemic to DR Congo, usually found growing near waterways.

### III. SUBFAM. PERIPLOCOIDEAE Endl. (1838).

Woody perennials; lianas, shrubs to small trees, erect, scrambling or twining herbs or geophytes with underground tuber; latex white (orange in *Cryptolepis sanguinolenta*, translucent in *Raphionacme namibiana*). Leaves opposite, decussate, petiolate, with interpetiolar lines or collars (stipules) and sometimes with cluster of colleters adaxially at juncture of petiole and blade; venation brochidodromous or camptodromous. Inflorescences usually axillary, often paired. Calyx lobes free or basally fused, lanceolate to ovate, acute, usually with few adaxial alternisepalous colleters. Corolla ovoid or conical in bud, rotate to rarely tube longer than lobes; lobes usually spreading, with valvate to dextrorsely imbricate, often contorted aestivation, usually glabrous; corolline corona usually present, usually glabrous (except for *Chlorocyathus* and some species of *Pentopetia*); gynostegial corona absent; gynostegium exposed just above base of corolla; stamens inserted between base of corolla lobes and base of tube on apex of thickened, ridge-like staminal foot running down corolla tube and mostly fusing at base into solid ring around narrow neck in style above carpels, apex of staminal foot also sometimes with corona lobe behind point of insertion of filament, this corona lobe sometimes confluent with corolline corona lobes and more or less in series with them; filaments usually inclined toward style-head, usually more or less cylindrical; anthers usually exposed, four-locular, much broader than filament, usually more or less deltoid, nearly horizontal to ascending with membranous margins not lignified or fashioned into guide rails, often laterally adherent or postgenitally fused into more or less umbrella-

like structure over style-head, adaxially fused to style-head usually above its thickest portion (rarely below: *Hemidesmus*); connective appendages usually shorter than anthers; nectaries on sides of staminal foot or in five troughs between staminal feet bearing stamens; pollen usually shed as T-shaped to rhomboidal tetrads, sometimes united into more or less horizontally oriented pollinia (two per locule) not surrounded by waxy outer wall; grains porate, with few to many pores, these scattered or pairwise at the juncture of the four monads; styles glabrous, style-head broad and flat-topped to tapering from broad base into narrow, often bifid apex, with thick and short to long and slender neck joining it to carpels and five stigmatic zones near lower edge between anthers, with five vertically oriented grooves between anthers in which translator is secreted; translator consisting of spoon- to cornet-shaped receptacle above (into which pollen / pollinia is deposited), with small sticky viscidium at lower end projecting vertically over edge of style-head or horizontally beneath it; gynoecium apocarpous, semi-inferior, rarely superior (*Gymnanthera*). Fruit a pair of slender to sometimes very swollen, fusiform, ventrally dehiscent follicles (sometimes one by abortion) with dry, usually thin pericarp. Seeds numerous, compressed, usually narrowly elliptical in outline and without wing-like margin, with micropylar coma (extended around entire margin in *Finlaysonia* and *Raphionacme namibiana*), endosperm thin. 33 genera in the Paleotropics and Australia.

#### KEY TO THE GENERA OF PERIPLOCOIDEAE

1. Gynostegium enclosed and concealed within the corolla tube 2
  - Gynostegium exposed from short-tubed corolla (corolla usually rotate), or gynostegium in mouth of or exerted from corolla with distinct tube 9
2. Flowers large, 3–6 cm long and 5–9 cm in diameter (Madagascar, widely naturalized elsewhere in the tropics) 165. *Cryptostegia*
  - Flowers small, less than 2 cm long and less than 3 cm in diameter 3
3. Corolla subhemispherical to urceolate with five deep vertical cavities (E Asia) 188. *Telectadium*

- Corolla rotate, campanulate or cylindrical, without any cavities 4
- 4. Corona in mouth of corolla tube or in sinuses of petals 5
  - Corona arising lower down in corolla tube, mostly around the middle of the tube 8
- 5. Erect shrubs with pale green to yellow, 8–12 mm long, salverform corolla (SW Africa)
  - 167. Ectadium**
  - Climbers or lianas; corolla usually shorter, when 8–12 mm long, then not salverform 6
- 6. Corolla less than 3 mm long, dark red; corolline corona lobes corniculate and bifurcate (West Tropical Africa)
  - 173. Maclaudia**
  - Corolla at least 3 mm long, white, cream or pink to mauve; corolline corona lobes of different shapes, but not corniculate or bifurcate 7
- 7. Corolline corona lobes subulate, of various colors, but not green; calyx lobes eciliate (Madagascar)
  - 177. Pentopetia**
  - Corolline corona lobes club- or matchstick-like, glossy green; calyx lobes ciliate (southern Africa)
    - 185. Stomatostemma**
- 8. Inside of corolla tube and adaxial side of petals papillate; corona lobes adnate to the corolla for most of their length forming vertical ridges with hooded apices, radiating into the corolla tube cavity, without a spongy swelling between corona lobe base and stamen base (tropical Africa)
  - 176. Parquetina**
  - Inside of corolla tube and adaxial side of petals glabrous; corona lobes free from the corolla for most of their length, clavate, filiform or acicular, almost always with a spongy pad between corona lobe base and stamen base (Africa, Arabia and E Asia)
    - 164. Cryptolepis**
- 9. Pollen in pollinia 10
  - Pollen in tetrads 16
- 10. Corona lobes fused into a ring outside the stamens (E Africa)
  - 184. Schlechterella**
  - Corona lobes not fused into a ring outside the stamens 11
- 11. Corolla salverform, tube conspicuous (E Asia to Australia)
  - 170. Gymnanthera**
  - Corolla rotate, tube bowl-shaped to indistinct 12
- 12. Inflorescence thyrsoid with a total of more than 10 flowers (E Asia)
  - 186. Streptocaulon**
  - Inflorescence cymoid, occasionally with one or two basal dichasial branches, total number of flowers less than 10 13
- 13. Petals valvate in bud; interstaminal nectary lobes fused into a tube around the style, creating five pockets between the style and stamens (southern Asia)
  - 171. Hemidesmus**
  - Petals contorted in bud; interstaminal nectaries not fused around the style, not forming any pockets between the style and stamens 14
- 14. Style-head with a flat or concave apex on which five hemispherical depressions contain include the receptacles of the pollen translators (southern Asia)
  - 166. Decalepis**
  - Style-head apex convex, umbonate or rounded, without any hemispherical translator depressions 15
- 15. Epiphytic climbers; corolla tube with five radial ridges; corona lobes with dilated hairy apex (tropical Africa)
  - 168. Epistemma**
  - Terrestrial climbers; corolla without radial ridges; corona lobes not dilated at apex, glabrous (Asia to Australia)
    - 169. Finlaysonia**
- 16. Epiphytic shrubs with aerial tubers (tropical Africa)
  - 183. Sarcorrhiza**
  - Terrestrial climbers, shrubs or herbs; when tuberous, then tubers subterranean or on ground surface 17
- 17. Corolline corona lobes laterally connate 18
  - Corolline corona lobes free 21
- 18. Corolla tube inside with a ring of horizontally projecting outgrowths (Madagascar)
  - 162. Camptocarpus**
  - Corolla tube inside without such outgrowths 19
- 19. Gynostegium raised high above corolla base (Asia, Australia)
  - 180. Phyllanthera**
  - Gynostegium sessile or inconspicuously raised above corolla base (Africa, Madagascar) 20
- 20. Corolline corona 10-partite, fused to an uneven ring-like structure, interpetiolar stipules absent (Madagascar)
  - 158. Baroniella**
  - Corolline corona 5-partite, fused with staminal feet to a collar-like structure; interpetiolar stipules present (tropical Africa)
    - 160. Batesanthus**
- 21. Stamens abaxially hairy 22
  - Stamens glabrous 23
- 22. Corolla lobes adaxially basally glandular (Africa, Arabia, Europe and Asia)
  - 178. Periploca**
  - Corolla lobes adaxially not glandular (Madagascar)
    - 177. Pentopetia**
- 23. Filaments united with style-head (Asia)
  - 180. Phyllanthera**
  - Anthers, but not filaments, united with style-head 24
- 24. Subterranean organs tuberous 25
  - Subterranean organs not tuberous 32
- 25. Erect shrubs, more than 50 cm tall 26
  - Twiners or lianas, when erect herbs, then less than 50 cm tall 27

26. Corolla more than 8 mm long; leaves in whorls of three (Madagascar) **172. *Ischnolepis***  
 – Corolla less than 8 mm long; leaves opposite (East Africa) **182. *Sacleuxia***
27. Shoots reddish (South Africa) **179. *Petopentia***  
 – Shoots green or brown 28
28. Twiners with distinct short shoots (East Africa) **161. *Buckollia***  
 – Twiners or erect herbs without short shoots 29
29. Strong lianas without tuber from primary root but with tuberous secondary roots, with distinct and dentate interpetiolar collar; leaf bases subcordate **174. *Mondia***  
 – Woody or herbaceous twiners or erect herbs with one (rarely more) conspicuous root tubers, when interpetiolar stipules present, then not collar-like; leaf bases obtuse or rounded 30
30. Corona inconspicuous, of very small carnose projections underneath stamens; corolla completely reflexed (East Africa) **159. *Baseonema***  
 – Corona conspicuous, at least as long as the gynostegium; corolla not reflexed 31
31. Plants with numerous tubers, stipules interpetiolar, carnose; corolla semi-succulent **163. *Chlorocyathus***  
 – Plants with single root tuber, stipules rarely interpetiolar, not carnose; corolla not semi-succulent **181. *Raphionacme***
32. Apical appendages of anther connectives at least as long as the anthers and combined into a long lance-like cone above the style-head (Asia) **157. *Atherandra***  
 – Apical appendages of anther connectives not longer than the anthers, erect or connivent above style-head 33
33. Interpetiolar collar present, formed of green frills or reddish colleters 34  
 – Interpetiolar lines present 35
34. Interpetiolar collar green, dentate; flowers large, 15–25 mm in diameter; follicles smooth (tropical and subtropical Africa) **174. *Mondia***  
 – Interpetiolar collar with reddish colleters; flowers small, up to 10 mm in diameter; follicles winged (E Asia) **175. *Myriopteron***
35. Corona lobes bifid 36  
 – Corona lobes simple 37
36. Corona lobes apically reflexed (Asia) **189. *Zygostelma***  
 – Corona lobes erect, often apically curled (Africa) **187. *Tacazzea***
37. Corona only of antesealous lobes, not longer than the corolla (Madagascar) **177. *Pentopetia***

- Corona with longer antesealous and shorter antepetalous lobes, when only antesealous lobes present, then much longer than the corolla (Africa) **187. *Tacazzea***

**157. *Atherandra* Decne.**

*Atherandra* Decne., Prodr. 8: 497 (1844); Ionta & Judd, Ann. Missouri Bot. Gard. 94: 360–375 (2007), phyl. *Atherostemon* Blume (1850).

Liana or herbaceous twiner; glabrous or shortly puberulous. Leaves 4–5 cm long, elliptic to ovate, apically acute to acuminate, glabrous. Inflorescences paired, few-flowered, long-pedunculate. Corolla yellow, lobes lanceolate, carnose, often reflexed, twisted; corolline corona shorter than corolla, equaling to longer than the gynostegium, lobes free, filiform, erect to reflexed; filaments with basal bristly appendage; nectaries lobular, fused to staminal feet; anthers sagittate, adnate to connate to each other; connective appendages forming a lance-like cone above the style-head; spathe spoon-like, apically bifid, viscidium orbicular, stalk present; style-head (elongated-)conical. Follicles 8.5–15 cm long, narrowly oblong. Seeds winged.

One sp., *A. acuminata* Decne., in continental SE Asia and Malesia.

**158. *Baroniella* Costantin & Gallaud**

*Baroniella* Costantin & Gallaud, Ann. Sci. Nat., Bot., IX, 6: 354 (1907); Klackenberg, Candollea 52: 383–407 (1997), rev.

Suffrutescent twiners to 4 m; entirely glabrous. Leaves occasionally succulent, waxy, 2–6 cm long, linear to ovate. Inflorescences usually paired, 1- to many-flowered, longer than subtending leaves. Corolla small, purplish, lobes ovate; corolline corona very short, 10-partite, laterally connate to an uneven ring-like structure; nectaries lobular, free; anthers free from each other; connective appendages conspicuously long; spathe folded, obovate or rounded, viscidium orbicular, stalk usually absent; style-head umbonate, neck discoid to conical, with five interstaminal lobes protruding between anthers, and occasionally with five additional lobes

opposite anthers. Follicles 20–28 cm long, narrowly oblong, moniliform.

Nine spp. in Madagascar, forests along the E coast, ericoid scrub in the central highland, from 400–1700 m.

159. *Baseonema* Schltr. & Rendle

*Baseonema* Schltr. & Rendle, J. Bot. 34: 97 (1896); Venter & Verhoeven, S. Afr. J. Bot. 75: 445–455 (2009), rev.

Suffrutescent twiner with root tubers, glabrous to pubescent. Leaves 4.5–5 cm long, circular; with interpetiolar collar inflated and dentate, or with frills. Inflorescences paired, many-flowered, lax. Corolla ca. 10 mm long, yellow-green, abaxially with trichomes; lobes ovate-oblong, strongly reflexed; corolline corona of very small carnosely projections underneath stamens; filaments basally flattened, apically narrow; nectaries lobular, fused to staminal feet; anthers sagittate, connate to each other, fused to upper side of style-head; connective appendages triangular; spathe folded, obovate, viscidium orbicular, stalk short; style-head umbonate. Follicles occasionally solitary, ca. 9 cm long, oblong, obtuse, pubescent.  $2n = 22$ .

One sp., *B. gregorii* Schltr. & Rendle, in Kenya and Tanzania.

160. *Batesanthus* N.E. Br.

*Batesanthus* N.E. Br. in Hooker's Icon. Pl.: ad t. 2500 (1896); Venter & Verhoeven, S. Afr. J. Bot. 75: 445–455 (2009), rev.

Suffrutescent twiners, entirely glabrous; shoots lenticellate. Leaves 7–16 cm long, oblong; interpetiolar collar inflated, dentate. Inflorescences paired, 10–25-flowered, longer than subtending leaves. Corolla to 18 mm long, purple; lobes oblong, reflexed; corolline corona inserted in corolla tube, very short, annular, apically indistinctly five-partite; stamens inserted at base of corolla tube; nectaries lobular, fused to staminal feet; anthers adnate to each other; connective appendages triangular; spathe folded, rhombic and bifid, viscidium cylindrical, stalk present; style-head conical. Follicles basally fused, 11–12 cm long, moniliform. Seeds with coma attached along entire seed margin.

Two spp. in W and C Africa.

161. *Buckollia* Venter & R.L. Verh.

*Buckollia* Venter & R.L. Verh., S. Afr. J. Bot. 60: 97 (1994); Venter, Fl. Ethiopia and Eritrea 4.1: 102–103 (2003), reg. rev.; Venter, Fl. Somalia 3: 135–136 (2006), reg. rev.

Suffrutescent twiners to 4 m, tuberous, with distinct long and short shoots; lenticellate, densely white or rusty puberulous or tomentose. Leaves opposite or fascicled, 2.6–6 cm long, ovate, occasionally undulate. Inflorescences usually solitary, 5–10-flowered, dichasial at base, monochasial in higher order branching. Corolla 5–8 mm long, creamish green, occasionally puberulous; corolline corona ivory to pink, glabrous to puberulous, exceeding gynostegium; lobes free, filiform; filaments filiform; nectaries lobular, fused to staminal feet; anthers ovoid; spathe folded, broadly obovate, viscidium hemispherical or bifid, stalk short; style-head umbonate or bifid, neck ovoid. Follicles 13–19 cm long, tuberculate.

Two spp. in Ethiopia, Kenya, Somalia and Uganda in semi-arid *Combretum–Acacia–Commiphora* scrub, from 1400–1800 m.

162. *Camptocarpus* Decne.

*Camptocarpus* Decne., Prodr. 8: 493 (1844), nom. cons.; Klackenberg, Bot. Jahrb. Syst. 120: 45–85 (1998), rev. *Harpanema* Decne. (1844). *Tanulepis* Balf. (1877). *Symphytonema* Schltr. (1895).

Suffrutescent twiners, glabrous. Leaves occasionally waxy, 1.5–7 cm long, linear to orbicular. Inflorescences solitary or paired, 1- to many-flowered, simple, (sub-)sessile; floral bracts conspicuous, occasionally caducous. Corolla 2–5 mm long, rose or greenish yellow, adaxially with purple center; lobes ovate or triangular, occasionally twisted; corolline corona exceeding gynostegium, five-partite; lobes partially connate to corolla, slender; nectar pockets at base of corolla tube; nectaries lobular, fused to staminal feet; anthers free from each other; spathe folded, (sub-)circular, viscidium (sub-)orbicular; styles distinct; style-head conical. Follicles occasionally solitary, 8–25 cm long, moniliform.  $2n = 22$ .

Nine spp. in two sections (Klackenberg 1998), Madagascar and Mascarene Islands, in forests and forest remnants, some species in xerophytic scrub and dunes; 0–1800 m.

163. *Chlorocyathus* Oliv.

*Chlorocyathus* Oliv. in Hooker's Icon. Pl. 16: t. 1557 (1887); Venter, S. Afr. J. Bot. 74: 288–294 (2008), rev. *Kappia* Venter, A.P. Dold & R.L. Verh. (2006).

Lianas to 12 m, with root tubers. Leaves discolorous, 1–6 cm long, lanceolate to ovate with undulate margins, glabrous or sparsely pubescent; interpetiolar collar carnosely, dentate. Inflorescences usually solitary, 2–10-flowered, dichasial at base, monochasial in higher order branching. Corolla 6–12 mm long, funnel-shaped, semi-succulent, (light) green, occasionally abaxially pubescent, lobes ovate, occasionally adaxially hirsute; corolline corona yellowish or pinkish, apically minutely sculptured, lobes free, obcordate, occasionally trifid with filiform median segment; gynostegium exerted from corolla; filaments filiform, nectar pockets at base of corolla tube, anthers free from each other; spathe spoon-like, ovate, viscidium (ob)ovate, stalk short; style-head broadly ovoid. Follicles 6.5–11 cm long, ellipsoid.

Two spp., one widespread in S tropical Africa, the other restricted to South African riverine forest.

164. *Cryptolepis* R. Br.

Fig. 46

*Cryptolepis* R. Br., Asclepiadeae 58 (1810); Forster, *Austrobaileya* 4: 67–73 (1993), reg. rev.; Venter & Verhoeven, *Ann. Missouri Bot. Gard.* 88: 550–568 (2001), phyl.; Ionta & Judd, *Ann. Missouri Bot. Gard.* 94: 360–375 (2005), phyl.; Venter et al., *S. Afr. J. Bot.* 72: 139–143 (2006), new taxa; Ionta, *Phylogeny reconstruction of Periplocoideae (Apocynaceae) based on morphological characters and a taxonomic revision of Decalepis*, Ph.D. Thesis, Univ. Florida (2009), phyl.; Joubert et al., *Taxon* 65: 487–501 (2016), phyl.

*Curroria* Planch. ex Benth. (1849).

*Ectadiopsis* Benth. (1876).

*Mitolepis* Balf. f. (1883).

*Socotranthus* Kuntze (1903), nom. illegit.

*Mangenotia* Pichon (1954).

Suffrutescent twiners or lianas, 3–6 m tall, rarely shrubs, glabrous; Leaves 1.5–18 cm long, oblong, often apiculate, glaucous. Inflorescences occasionally extra-axillary, solitary, 9–15-flowered, thyrsoidal. Corolla 9–20 mm long, campanulate or salverform, creamish yellow; lobes oblong to lanceolate, twisted; corolline corona inserted in corolla tube; lobes free, ovate or clavate, bifid; gynostegium concealed in corolla tube; nectar

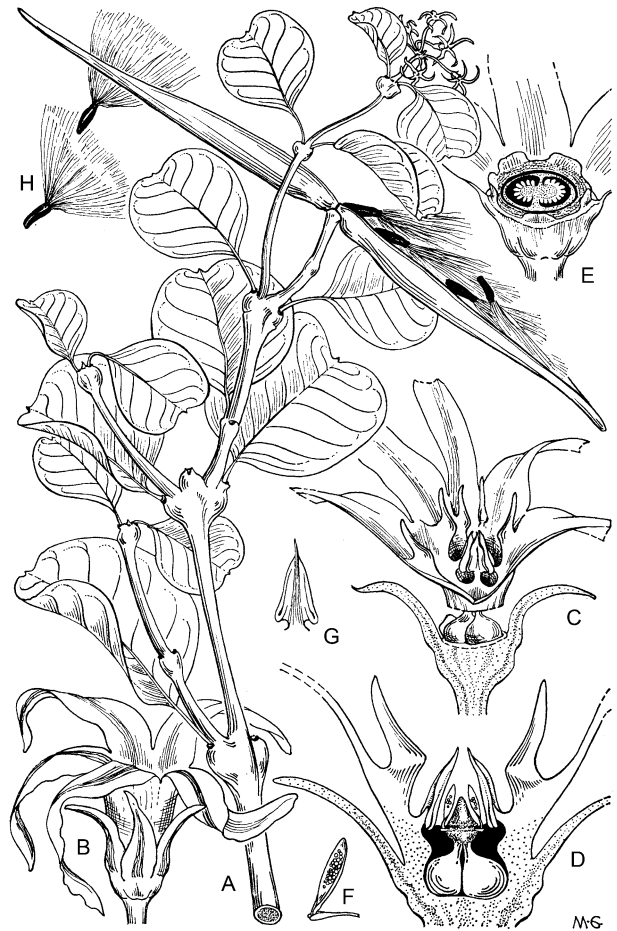


Fig. 46. Apocynaceae-Periplocoideae. *Cryptolepis macrophylla*. A Shoot with flowers and fruit. B Flower. C Flower with corolla cut open and raised to show carpels. D Flower, showing gynostegium and carpels. E Carpel, with intercalary scales. F Translator. G Stamen. H Seeds. (From Smith 1971, pl. 3685, with permission from Hooker's Icones Plantarum © Board of Trustees of the Royal Bot. Gard., Kew; drawn by Mary Grierson)

pockets and the flattened filaments arising in the middle of the corolla tube; nectaries five transversal ridges; anthers sagittate, dorsally occasionally with trichomes; connective appendages occasionally twisted; spathe oblong, acuminate, viscidium cylindrical, stalk absent; style-head umbonate. Follicles (4.5–)7–20 cm long.  $2n = 22$ .

10–15 spp. in Africa, Asia and Australia.

The circumscription of *Cryptolepis* is much disputed; the inclusion of *Phyllanthera* (Forster 1993) is not supported by molecular results (Ionta and Judd 2007; Joubert et al. 2016). The inclusion of *Parquetina*, suggested by Joubert

et al. (2016), seems premature and is not followed here.

165. *Cryptostegia* R. Br.

*Cryptostegia* R. Br., Bot. Reg., ad t. 435 (1820); Marohasy & Forster, Aust. Syst. Bot. 4: 571–577 (1991), rev.; Klackenberg, Adansonia III, 23: 205–218 (2001), rev.

Shrubs, suffrutescent twiners or lianas; shoots lenticellate, glabrous or pubescent. Leaves 7–12 cm long, elliptic. Inflorescences terminal, 1–4(–9)-flowered, thyrsoidal; floral bracts conspicuous. Corolla 3–6 cm long, salverform, pale rose or white, occasionally adaxially with trichomes; lobes lanceolate, twisted; corolline corona inserted in corolla tube, reaching the sinus of corolla lobes; lobes free, filiform, deeply bifid; gynostegium concealed in corolla tube; nectar pockets at base of corolla tube; nectaries five transversal ridges, fused to staminal feet; basally connate to each other, connective appendages distinct, lanceolate; spathe flat, stalk absent. Follicles 6–15.5 cm long, obclavate, winged.  $2n = 22$ .

Two spp. in Madagascar, in riverine and seasonally flooded forests, introduced throughout the tropics, noxious weeds in disturbed vegetation and plantations. Plants highly toxic (cardenolides); used as arrow poison in parts of Africa. *C. madagascariensis* Bojer pollinated by Sphingidae.

166. *Decalepis* Wight & Arn.

*Decalepis* Wight & Arn. in Wight, Contr. Bot. India 64 (1834); Venter & Verhoeven, Ann. Missouri Bot. Gard. 88: 550–568 (2001), tax.; Ionta, Phylogeny reconstruction of Periplocoideae (Apocynaceae) based on morphological characters and a taxonomic revision of *Decalepis*, Ph.D. Thesis, Univ. Florida (2009), phyl.; Sharma & Shahzad, J. Pl. Sci. Res. 1: 1–13 (2014), morph., pharm.; Joubert et al., Taxon 65: 487–501 (2016), phyl.; Kambale et al., Taxon 64: 475–477 (2016), tax.

*Brachylepis* Wight & Arn. (1834), non C.A. Mey. (1829).

*Cornacchinia* Endl. (1841), non Savi (1837).

*Baeolepis* Decne. ex Moq. (1849).

*Utleria* Bedd. ex Benth. (1876).

*Janakia* J. Joseph & V. Chandras (1978).

Small trees, shrubs or lianas, glabrous; roots often fleshy and fascicled, nodulous. Leaves occasionally alternate to fascicled, 1–15 cm long, linear to ovate, undulate. Inflorescences frequently termi-

nal, 8–10-flowered, thyrsoidal, long-pedunculate. Corolla 2–3 mm long, greenish white; lobes ovate; corolline corona inserted in corolla tube, basally connate to the filaments, fused to lower half of corolla, very short; lobes free, ovate; filaments short; nectaries lobular, fused to staminal feet; anthers fused to underside of style-head; pollen in ovoid pollinia; spathe spoon-like, viscidium orbicular, stalk present; style-head umbonate with hemispherical depressions. Follicles 4.5–5.5 cm long, obclavate. Seeds occasionally winged.

Five spp. in India; the roots of *D. hamiltonii* Wight & Arn. are used medicinally (Sharma and Shahzad 2014).

While the inclusion of *Janakia* and *Utleria* in *Decalepis*, suggested by Venter and Verhoeven (2001) without explanation, was confirmed by molecular analysis (Joubert et al. 2016), the inclusion of *Brachylepis* is not supported by their results.

167. *Ectadium* E. Mey.

*Ectadium* E. Mey., Comm. Pl. Afr. Austr. 188 (1838); Venter et al., S. Afr. J. Bot. 56: 113–124 (1990), rev.

Shrubs, 1–3 m tall, with tap roots, glabrescent or puberulous. Leaves coriaceous to subsucculent, 2–8 cm long, narrowly elliptic, puberulous to tomentose. Inflorescences solitary or paired, 5–20-flowered, simple, subsessile. Corolla salverform, (greenish) yellow; lobes oblong, slightly twisted; corolline corona exceeding gynostegium; lobes free, subulate, basally dilated, fused to corolla lobes; gynostegium concealed in corolla tube; stamens inserted at base of corolla tube; nectaries lobular, fused to staminal feet; anthers free from each other, connective appendages subulate, hirsute, exceeding anthers; spathe flat, oblong, viscidium ellipsoid, stalk short; style-head conical, bifid. Follicles 3.5–9 cm long, obclavate. Seeds small, winged.  $2n = 22$ .

Three spp. in Namibia, very dry and sandy river beds, stony or rocky sandplains.

168. *Epistemma* D.V. Field & J.B. Hall

*Epistemma* D.V. Field & J.B. Hall, Kew Bull. 37: 117 (1982); Huber, Adansonia IV, 11: 447–452 (1989), new taxa; Fischer et al., S. Afr. J. Bot. 77: 680–684 (2011), key, tax.

Twining subsucculent epiphytes; mature shoots with smooth, gray, papery bark. Leaves 8.5–12.5 cm long, broadly elliptic. Inflorescences terminal on lateral branches, few-flowered, simple; peduncles very short and thick. Corolla 5–7 mm long, corolla yellowish green or purple, adaxially with trichomes on the tube and with five pubescent ridges radiating from the center; lobes broadly ovate; corolline corona short; lobes free, clavate; filaments filiform; nectaries lobular, fused to staminal foot; anthers apically adnate to each other; connective appendages triangular, thickened, strongly inflexed; spathe folded, obcordate, viscidium hemispherical, stalk short; styles short; style-head umbonate. Follicles 9–13 cm long. Seeds folded along seta; raphe winged.  $2n = 22$ .

Four spp. in lowland forests of W Africa (Gabon, Ghana, Ivory Coast, Rwanda).

#### 169. *Finlaysonia* Wall.

*Finlaysonia* Wall., Pl. Asiat. Rar. 2: 48, t. 162 (1831); Venter & Verhoeven, Ann. Missouri Bot. Gard. 88: 550–568 (2001); Ionta & Judd, Ann. Missouri Bot. Gard. 94: 360–375 (2007), phyl.; Sidney, M.Sc. Thesis, University of Free State, Bloemfontein (2012), morph.  
*Atherolepis* Hook. f. (1883).  
*Stelmacrypton* Baill. (1889).  
*Hanghomia* Gagnep. & Thérin (1936).  
*Meladerma* Kerr (1938).

Lianas. Leaves 5–10 cm long, linear to ovate. Inflorescences usually solitary, few-flowered, thyrsoidal or dichasial at base, monochasial in higher order branching; flowers malodorous. Calyx urceolate; ciliate; corolla 3–6 mm long, greenish or purplish, adaxially occasionally with trichomes, or five pubescent ridges radiating from the center; lobes ovate; corolline corona inserted in corolla tube, basally connate to the filaments; lobes free; nectaries lobular, fused to staminal feet; anthers ovoid, connective appendages with some trichomes; pollen in pyriform pollinia; spathe hollow, spoon-like, viscidium orbicular, stalk present. Follicles 2.5–9 cm long, occasionally ellipsoid, ribbed. Seeds with coma occasionally along entire seed margin, reflexed.

Eight spp. in India, China, continental SE Asia, Malesia and Australia, often on limestone as well as along tidal rivers and in wetlands at low altitudes.

The inclusion of *Atherolepis*, *Hanghomia*, *Meladerma* and *Stelmacrypton* in *Finlaysonia* was suggested by Venter and Verhoeven (2001), repeated by Sidney (2012), on the basis of morphological characters without established synapomorphic value, and remains questionable until the type species of *Finlaysonia*, *F. obovata* Wall., has been sequenced.

#### 170. *Gymnanthera* R. Br.

*Gymnanthera* R. Br., Asclepiadeae 47 (1810); Forster, Aust. Syst. Bot. 4: 563–569 (1991), rev.; Forster, Austral. Entomol. Mag. 18: 61–64 (1991), ecol.  
*Dicerolepis* Blume (1850).  
*Cylixylon* Llanos (1851).

Shrubs or lianas; shoots often lenticellate. Leaves to 12 cm long, elliptic or ovate; stipules small. Inflorescences solitary, 3–10-flowered, simple. Corolla 9–17 mm long, salverform, yellowish to green; lobes ovate; corolline corona inserted in corolla tube behind the stamens, short; lobes free, often bifid; gynostegium exerted from corolla tube mouth; nectar pockets at base of corolla tube; nectaries five transversal ridges, free; anthers free from each other, fused to underside of style-head; pollen in clavate pollinia; spathe hollow, cup-like, viscidium orbicular, stalk long, thin; style-head (depressed-)conical. Follicles 6–14 cm long.

Two spp. in Indonesia, the Philippines, Australia and Papua New Guinea on banks surrounding areas of permanent or semi-permanent water, mangrove fringes. Food source for larvae of the Common Crow butterfly (*Euploea core corinna*, fide Forster 1991b).

#### 171. *Hemidesmus* R. Br.

*Hemidesmus* R. Br., Asclepiadeae 45 (1810); Ali, Fl. Pakistan 150: 56–57 (1983), reg. rev.; Watson, Fl. Bhutan 2.2: 694 (1999), reg. rev.; Jagtap & Singh, Fasc. Fl. India 24: 301–303 (1999), reg. rev.

Suffrutescent twiner; shoots lenticellate; root-stock woody, occasionally tuberous. Leaves 1.4–17 cm long, linear to (ob-)ovate, ciliate. Inflorescences paired, few-flowered, simple, (sub-)sessile; floral bracts conspicuous, persistent. Corolla 5 mm long, adaxially purplish brown; lobes sub-orbicular; corolline corona dorsally adnate to



anthers, short; lobes free, almost orbicular; gynostegium raised high above corolla; stamens inserted at base of corolla tube, filaments long; nectar pockets on a tube of fused staminal feet; nectaries tubular around style without slits; filaments fused to style-head; pollen in ovoid pollinia; spathe hollow, cup-like, viscidium cylindrical, stalk flattened. Follicles 10–15 cm long.

One sp., *H. indicus* (Willd.) R. Br., in India and Peninsular Malaysia, lowlands. Roots widely used medicinally.

#### 172. *Ischnolepis* Jum. & H. Perrier

*Ischnolepis* Jum. & H. Perrier, Rev. Gén. Bot. 21: 53 (1909); Klackenberg, Candollea 54: 257–339 (1999), rev.; Venter & Verhoeven, Ann. Missouri Bot. Gard. 88: 550–568 (2001), phyl.; Meve & Liede, Ann. Bot. 93: 407–414 (2004), phyl.

Shrub to 2 m; glabrous; shoots red, glossy; bark flaky; roots forming many big tubers. Leaves 3-whorled, 10–25 cm long, linear, often falciform. Inflorescences solitary, 1–7-flowered, simple. Corolla 8–14 mm long, yellowish; lobes slightly twisted; corolline corona inserted in corolla, yellow; lobes free, filiform; filaments filiform; nectaries lobular, fused to stamens; anthers free from each other; spathe folded, elliptic, channeled; viscidium of two broad wings, beaked, stalk indistinct; style-head conical, neck conical with five grooves supporting anthers and five broad knobs at the base. Follicles 12 cm long.  $2n = 22$ .

One sp., *I. graminifolia* (Costantin & Gallaud) Klack., in Madagascar, savanna, grassland or on almost bare granitic, gneissic or sandstone rocks; 0–2000 m.

Venter and Verhoeven (2001) include *Petropentia* in *Ischnolepis*, but a molecular study (Meve and Liede 2004a) has shown that the two genera are not closely allied.

#### 173. *Maclaudia* Venter & R.L. Verh.

*Maclaudia* Venter & R.L. Verh., Bot. J. Linn. Soc. 115: 57–63 (1994).

Suffrutescent twiner or liana; shoots lenticellate, scabrous. Leaves 3–4 cm long, ovate, glabrous, scabrous on the nerves. Inflorescences occasionally paired, many-flowered, thyrsoïdal, longer than subtending leaves, condensed; inflorescence

bracts two, larger than the persistent subulate floral bracts forming decussate rows along the rachis. Corolla 2.5–3 mm long, campanulate, dark red; lobes broadly elliptic; corolline corona short; lobes corniculate and bifurcate, reflexed; gynostegium concealed in corolla tube; stamens inserted at base of corolla tube; nectaries lobular; anthers ovoid; spathe flat, narrowly ovate and bifid, viscidium hemispherical; style-head ovoid.

One sp., *M. felixii* Venter & R. L. Verh., in Guinea, dry forest; ca. 1000 m.

#### 174. *Mondia* Skeels

*Mondia* Skeels, U.S.D.A. Bur. Pl. Industr. Bull. 223: 45 (1911); Bullock, Fl. W. Trop. Afr. 2: 82 (1963), reg. rev.; Venter et al., S. Afr. J. Bot. 75: 456–465 (2009), rev.; Aremu et al., S. Afr. J. Bot. 77: 960–971 (2011), econ. *Chlorocodon* Hook. f. (1871) non (DC.) Fourr. (1869).

Lianas; shoots lenticellate; rootstock woody; secondary roots often tuberous. Leaves 10–20 cm long, (ob)ovate; interpetiolar collar inflated, dentate. Inflorescences usually paired, 3–10-flowered, thyrsoïdal, lax, long-pedunculate. Corolla 10–15 mm long, adaxially yellow or purple; lobes valvate, oblong, unilaterally ciliate; corolline corona white, short; lobes free, triangular, occasionally with slender appendage; filaments absent or short, broadened; nectaries lobular, fused to staminal feet; anthers triangular, adnate to each other, fused to upper side of style-head; spathe flat, ovate with revolute margins, stalk absent. Follicles 9–10 cm long, elongate-ellipsoid; pericarp thick, woody. Seeds winged.  $2n = 22$ .

Two spp. in tropical Africa, forest gaps. Roots used medicinally and for ginger beer.

#### 175. *Myriopteron* Griff.

*Myriopteron* Griff., Calcutta J. Nat. Hist. 4: 385 (1844); Jagtap & Singh, Fasc. Fl. India 24: 313 (1999, under *Streptocaulon*), reg. rev.; Li et al., Fl. China 16: 194–195 (1995), reg. rev.; Venter & Verhoeven, Ann. Missouri Bot. Gard. 88: 550–568 (2001), phyl.; Ionta & Judd, Ann. Missouri Bot. Gard. 94: 360–375 (2007), phyl.

Herbaceous twiner, to 10 m, glabrous; shoots lenticellate. Leaves papery, 8–20(–30) cm long, elliptic to ovate; with interpetiolar line, reddish, stipules prominently lobed. Inflorescences paired, 20–30-flowered, thyrsoïdal, lax, long-

pedunculate. Calyx very short; corolla ca. 3 mm long, lobes oblong, acute; corolline corona short; lobes free, filiform; filaments flattened; nectaries lobular, fused to staminal feet, connate to each other at tips; spathe folded, oblong, viscidium rounded, stalk short; style-head conical. Follicles ca. 6.5 cm long, obclavate, with many membranous wings 3–6 mm wide.

One sp., *M. extensum* (Wight & Arn.) K. Schum., in Asia, thickets, open woods; 600–1600 m. Roots used medicinally in China.

Jagtap and Singh (1999) treat *Myriopteron* as a synonym of *Streptocaulon*, but Li et al. (1995a) and Venter and Verhoeven (2001) consider it a different genus, a view supported by Ionta and Judd (2007).

#### 176. *Parquetina* Baill.

*Parquetina* Baill., Bull. Mens. Soc. Linn. Paris 2: 806 (1889); Venter & Verhoeven, S. Afr. J. Bot. 62: 23–30 (1996), rev.; Ionta & Judd, Ann. Missouri Bot. Gard. 94: 360–375 (2007), phyl.; Venter, S. Afr. J. Bot. 75: 557–559 (2009), tax.; Joubert et al., Taxon 65: 487–501 (2016), phyl. *Omphalonus* Baill. (1890).

Lianas to 20 m; shoots lenticellate, glabrous. Leaves discolorous, 9–11.5 cm long, broadly ovate. Inflorescences solitary, 10–30-flowered, dichasial at base, monochasial in higher order branching, long-pedunculate. Flowers malodorous; corolla 11–16 mm long, cyathiform, carnose, adaxially papillate or velvety, rose to purple-black; lobes elliptic; corolline corona inserted in corolla tube, purplish, basally fused to corolla or fused for half of its length and radiating into the tube's cavity, short; lobes free, rounded; filaments filiform; nectaries five transversal ridges, fused to staminal foot; anthers dorsally with trichomes; spathe folded, oblong, viscidium ellipsoid or triangular, stalk present. Follicles 9–25 cm long, obclavate, black; pericarp woody.  $2n = 22$ .

Two spp. in tropical Africa; at least *P. nigrescens* (Afzel.) Bullock is widely used in traditional medicine. Flowers are visited by flies.

A molecular analysis (Ionta and Judd 2007) has shown that these two Periplocoideae species are nested in *Cryptolepis* unless *C. stefaninii* Chiov. is removed from the latter (Joubert et al. 2016).

#### 177. *Pentopetia* Decne.

*Pentopetia* Decne., Prodr. 8: 500 (1844); Klackenberg, Candollea 54: 257–339 (1999), rev.

*Acustelma* Baill. (1889).

*Gonocrypta* Baill. (1899).

*Kompitsia* Costantin & Gall. (1906).

*Pentopetiopsis* Costantin & Gall. (1906).

Suffrutescent twiners; shoots lenticellate, occasionally with reddish trichomes. Leaves occasionally fascicled on brachyblasts, 0.5–8 cm long, linear to obovate, occasionally pubescent. Inflorescences solitary, 1–15-flowered, dichasial at base, monochasial in higher order branching. Corolla 3–12 mm long, yellowish or reddish, usually with trichomes; lobes triangular to ovate, occasionally twisted; corolline corona short, rarely absent, occasionally with trichomes; lobes free, subulate; filaments occasionally distinctly arched; nectaries lobular, free; basal part of thecae without pollen; connective appendages absent or short, hirsute; spathe folded; viscidium cylindrical, stalk broad; styles occasionally with trichomes; style-head usually flat. Follicles 5–20 cm long, obclavate or narrowly oblong, occasionally 3–5 ribbed or winged.  $2n = 22$ .

23 spp. in Madagascar, the Comores, Seychelles and Aldabra, dry forest, savanna and scrub vegetation, 0–2000 m.

#### 178. *Periploca* L.

*Periploca* L., Sp. Pl. 211. (1753); Li et al., Fl. China 16: 195–196 (1995), reg. rev.; Venter, S. Afr. J. Bot. 63: 123–128 (1997), rev.; Chaudhari, Fl. Kingd. Saudi Arabia 2.2: 32–33 (2001), reg. rev.; Venter, Fl. Somalia 3: 138–139 (2006), reg. rev.; Heneidak & Naidoo, Turk. J. Bot. 39: 353–363 (2015), flow. morph.

*Campelepis* Falc. (1842).

*Socotora* Balf. f. (1883).

*Cyprinia* Browicz (1966).

Shrubs, suffrutescent twiners or lianas, glabrous. Leaves occasionally caducous or scale-like, 1.5–10 cm long, elliptic or ovate, occasionally with dentate interpetiolar line. Inflorescences occasionally terminal, solitary, (1)3–15(–30)-flowered, thyrsoïdal or simple. Corolla 5–12 mm long, adaxially brown or purple, occasionally with dark center, and/or with papillose white spots; lobes oblong or

ovate, basally with glandular zone, with trichomes; corolline corona yellow or purplish, as long as corolla; filiform, often segmented; nectaries lobular, fused to staminal feet; anthers apically with trichomes, often bearded; spathe flat, oblong, stalk present; style-head ovoid. Follicles occasionally apically fused, 7–21(–45) cm long, occasionally moniliform.  $2n = 22, 44$ .

13 spp. in two sections, S Europe, Asia, Africa, Arabia and the Canary Islands, humid forests to semi-deserts.

### 179. *Petopentia* Bullock

*Petopentia* Bullock, Kew Bull. 1954: 362 (1954); Venter et al., African J. Bot. 56: 393–398 (1990), tax.; Venter & Verhoeven, Ann. Missouri Bot. Gard. 88: 550–568 (2001), phyl.; Meve & Liede, Ann. Bot. 93: 407–414 (2004), phyl.; Venter & Venter, S. Afr. J. Bot. 88: 425–431 (2013), rev.

Lianas, 10–15 m tall; shoots reddish with suberose bark, glabrous; root tubers large, occasionally nodulous, semi-subterranean. Leaves 7–11 cm long, broadly oblong. Inflorescences occasionally paired, 5–8-flowered, dichasial at base, monochasial in higher order branching. Corolla 13–15 mm long, greenish yellow; lobes triangular, occasionally twisted; corolline corona exceeding gynostegium; lobes free, filiform, basally broadened; filaments filiform with dilated bases; nectaries lobular, fused to staminal feet; anthers broadly oblong, fused to upper side of style-head; spathe flat, obovate, viscidium orbicular, stalk short and narrow; style-head conical. Follicles (6)9–12 cm long, obclavate.  $2n = 22$ .

Two spp. in South Africa, rocky river bank forests to forested sandstone cliff faces in humid subtropical areas.

### 180. *Phyllanthera* Blume

*Phyllanthera* Blume, Bijdr. 1048 (1827); Venter & Verhoeven, Ann. Missouri Bot. Gard. 88: 550–568 (2001), phyl.; Ionta & Judd, Ann. Missouri Bot. Gard. 94: 360–375 (2007), phyl.; Takeuchi, Phytotaxa 163: 173–179 (2014), consp., reg. tax.  
*Pentanura* Blume (1850).  
*Streptomanes* K. Schum. ex Schltr. (1905).

Lianas, glabrous. Leaves linear to ovate, discolorous, adaxially occasionally purple-veined. Inflorescences occasionally paired, 1–10-flowered,

thyrsoidal, lax. Corolla 8–12 mm long, rotate, basally fused, yellowish brown or purple, occasionally papillate; lobes lanceolate or triangular, twisted; corolline corona inserted in corolla tube, basally connate to filaments, short, annular and/or lobes free, bifid; gynostegium raised high above corolla; stamens inserted at base of corona; nectaries tubular around style with slits, fused to staminal feet; anthers rectangular to trullate, free; filaments fused to style-head; connective appendages exceeding anthers; spathe spoon-like; viscidium rounded; stalk present; style-head conical or semi-globose. Follicles ca. 9 cm long, linear to ovoid-fusiform, woody.

Nine spp., seven of them in New Guinea, the remainder elsewhere in Malesia and Australia, forests and river banks. In recent phylogenies, *Phyllanthera* is retrieved as sister to the remainder of Periplocoideae.

### 181. *Raphionacme* Harv.

*Raphionacme* Harv., London J. Bot. 1: 22 (1842); Venter, Fl. Ethiopia and Eritrea 4.1: 108–110 (2003), reg. rev.; Venter, Fl. Somalia 3: 139–140 (2006), reg. rev.; Venter, S. Afr. J. Bot. 75: 292–350 (2009), rev.; Pienaar, Phylogeny of the genus *Raphionacme* (Apocynaceae), M.Sc. Thesis, Univ. of Free State, Bloemfontein (2013), phyl.  
*Apoxyanthera* Hochst. (1843).  
*Zucchellia* Decne. (1844).  
*Zaczatea* Baill. (1889).  
*Mafekingia* Baill. (1890).  
*Pentagonanthus* Bullock (1962).

Erect herbs, herbaceous or suffrutescent twiners, puberulous; roots tuberous, single. Leaves (sub-) sessile, linear to (ob-)ovate. Inflorescences often terminal, solitary, few-to many-flowered, simple. Corolla ca. 10 mm long, white, (yellowish) green, purplish or bluish, occasionally papillose, ridged; lobes ovate, occasionally twisted; corolline corona inserted in corolla tube, exceeding gynostegium; lobes free, filiform, bifid or trifid; gynostegium exerted from, stamens inserted in corolla tube; filaments short; nectar pockets at base of corolla tube; nectaries lobular, free; spathe folded, ovate; viscidium hemispherical; stalk present; style-head conical to rostrate. Follicles usually 3.5–8 cm long, ellipsoid to obclavate. Seeds occasionally with copper-colored coma, occasionally attached along entire margin.  $2n = 22, 44$ .

About 35 spp. in Africa, one sp. in Arabia, arid and semi-arid habitats.

182. *Sacleuxia* Baill.

*Sacleuxia* Baill., Hist. Pl. 10: 265 (1890).  
*Gymnolaema* Benth. & Hook. f. (1876) non *Gymnoleima* Decne. (1844).  
*Macropelma* K. Schum. (1895).

Erect shrubs, 0.5–1.5 m tall; rootstock woody or tuberous. Leaves subsessile; ca. 9 cm long, linear to ovate, glabrous; with interpetiolar collar dentate and/or inflated. Inflorescences solitary, many-flowered, simple, long-pedunculate. Corolla 3–8 mm long, campanulate, carinose, yellow or reddish; lobes ovate; corolline corona short; lobes free, oblong, apically bifid or emarginate; filaments absent; nectaries lobular, free; spathe folded, oblong, stalk present; style-head depressed-conical. Follicles 3–6 cm long. Seeds winged.  $2n = 22$ .

Two spp. in Kenya and Tanzania.

183. *Sarcorrhiza* Bullock

*Sarcorrhiza* Bullock in Hooker's Icon. Pl. 36: ad t. 3585 (1962).

Epiphytic shrub, glabrous; root tubers ovoid, reddish brown. Leaves subsessile, to 8 cm long, oblong. Inflorescences solitary, 2–4-flowered, simple, sessile; floral bracts conspicuous, triangular to ovate. Corolla ca. 6 mm long, greenish yellow, with purplish center; lobes ovate; corolline corona white, exceeding gynostegium; lobes free, filiform, basally thickened, inflexed, twisted; filaments filiform; nectaries lobular, fused to staminal feet; anthers adnate to each other, fused to upper side of style-head; spathe folded, oblong, abaxially with trichomes, stalk present; styles short; style-head conical. Follicles ca. 15 cm long.

One sp., *S. epiphytica* Bullock, in DR Congo and Tanzania.

184. *Schlechterella* K. Schum.

*Schlechterella* K. Schum. in Engler & Prantl, Nat. Pflanzenfam. Index 2–4: 462 (1899); Nachtr. 2: 60. (1900); Venter & Verhoeven, S. Afr. J. Bot. 64: 350–355 (1998), rev.; Venter, Fl. Ethiopia and Eritrea 4.1: 110–112 (2003), reg. rev.; Pienaar, Phylogeny of the genus *Raphionacme*

(Apocynaceae), M.Sc. Thesis, Univ. of Free State, Bloemfontein (2013), phyl.

Suffrutescent twining geophytes; root tuber cylindrical, napiform-oblongoid. Leaves (sub-)sessile, 3–10 cm long, linear or obovate, occasionally undulate or revolute, discolorous. Inflorescences paired, 9–15-flowered, simple, lax, long-pedunculate; floral bracts conspicuous. Corolla 4–12 mm long, cream or purplish, occasionally with greenish pattern; lobes linear to (ob-)ovate, twisted; corolline corona whitish, exceeding gynostegium; basally connate into a ring; lobes filiform, bipentafid, occasionally connivent; gynostegium much exerted; filaments filiform; nectar pockets at base of corolla tube; nectaries five transversal ridges, free; pollen in small ellipsoid pollinia; spathe folded, oblong, viscidium orbicular; stalk present; style-head umbonate. Follicles ca. 4–7 cm long.  $2n = 22$ .

Two spp. in East Africa, *Acacia-Commiphora* woodland, *Terminalia* grassland with scattered trees, desert scrub.

*Schlechterella abyssinica* (Schltr.) K. Schum. is nested in *Raphionacme* in the ITS phylogeny of Pienaar (2013), suggesting that *Raphionacme* is paraphyletic without *Schlechterella*.

185. *Stomatostemma* N.E. Br.

*Stomatostemma* N.E. Br. in Thiselton-Dyer, Fl. Trop. Afr. 4(1): 252 (1902); Venter & Verhoeven, S. Afr. J. Bot. 59: 50–56 (1993), rev.

Shrubs or suffrutescent twiners; shoots lenticellate, glabrous; roots tuberous. Leaves 4–11 cm long, linear to (ob-)ovate. Inflorescences paired, 5–25-flowered, thyrsoidal. Flowers fragrant; corolla 9–22 mm long, campanulate; whitish with reddish center, glabrous; lobes ovate, acute, slightly twisted; corolline corona glossy green, exceeding gynostegium; lobes free, basally terete, apically clavate; gynostegium concealed in corolla; stamens inserted at base of corolla tube; filaments short; nectar pockets at base of corolla tube; nectaries five transversal ridges, fused to staminal feet; anthers free; spathe folded, ovate and deeply bifid; viscidium bifid; stalk absent; style-head ovoid. Follicles 6–9 cm long, obclavate.  $2n = 22$ .

Two spp. in SE Africa; dry (Mopane) woodland.

186. *Streptocaulon* Wight & Arn.

*Streptocaulon* Wight & Arn. in Wight, Contr. Bot. India 64 (1834); Li et al., Fl. China 16: 194 (1995), reg. rev.; Jagtap & Singh, Fasc. Fl. India 24: 312–316 (1999), reg. rev.; Sidney, M.Sc. Thesis, University of Free State, Bloemfontein (2012), morph., tax.

*Triplolepis* Turcz. (1848).

*Gongylosperma* King & Gamble (1908).

Shrubs or lianas to 8 m, tawny pilose or tomentose; rootstock woody. Leaves 3–20 cm long, ovate or obovate, pubescent. Inflorescences paired, many-flowered, thyrsoïdal, lax, shortly pedunculate. Corolla 3–5 mm long, yellowish-greenish to purplish; lobes ovate; corolline corona basally connate to filaments, exceeding gynostegium; filiform, inflexed; filaments (almost) absent; nectaries lobular, fused to staminal feet; pollen in ovoid or ellipsoid pollinia; spathe spoon-like, oblong; stalk present; style-head depressed-conical and bifid. Follicles 7–13 cm long, obclavate, densely pubescent. Seeds occasionally with copper-colored coma.

Widely distributed in India, S China, SE Asia, montane forests and thickets; 0–1000 m.

Seven spp. if the two spp. originally published in *Gongylosperma* are moved to *Streptocaulon* as suggested by Sidney (2012).

187. *Tacazzea* Decne.

*Tacazzea* Decne., Prodr. 8: 492 (1844); Venter et al., S. Afr. J. Bot. 56: 93–112 (1990); Venter, Fl. Ethiopia and Eritrea 4.1: 106–108 (2003), reg. rev.; Venter, Fl. Somalia 3: 140–142 (2006), reg. rev.

Shrubs or lianas to 20 m, hirsute; shoots lenticellate. Leaves occasionally whorled, 6–13 cm long, elliptic to ovate. Inflorescences occasionally paired, many-flowered, thyrsoïdal, lax; inflorescence bracts large, ovate. Corolla 5–10 mm long, green or yellowish red; lobes ovate to oblong, occasionally ciliate; corolline corona yellowish, five- or ten-partite; lobes free, antese-palous lobes exceeding gynostegium, filiform or ovate; antepetalous lobes short, subquadrate or bifid, emarginate; nectaries lobular, fused to staminal feet; anthers 2-thecous, ovoid, fused to margin of style-head; spathe flat, apically bifid; viscidium orbicular, ellipsoid or bifid, stalk

absent; style-head conical. Follicles 5–14(–20) cm long, obclavate, occasionally keeled; woody.  $2n = 22$ .

Six spp. in Sub-Saharan Africa, lianas in lowland swamp forests along fresh water to mountain forests; shrubby species in more arid areas, but near water.

188. *Telectadium* Baill.

*Telectadium* Baill., Bull. Mens. Soc. Linn. Paris 2: 801 (1889).

Low shrubs, occasionally pubescent. Leaves occasionally whorled; 5–10 cm long, lanceolate. Inflorescences terminal, 4- to many-flowered, dichasial at base, monochasial in higher order branching, long-pedunculate; floral bracts conspicuous. Corolla 14–20 mm long, urceolate, white; lobes oblong, obtuse, twisted; corolline corona inserted in corolla tube, exceeding gynostegium; lobes free, irregularly triangular, erect; gynostegium concealed; stamens inserted at base of corolla tube, filaments flattened; nectar pockets at base of corolla tube; nectaries five transversal ridges, free; anthers sagittate, with two pouches at the base, fused to upper side of style-head; spathe ocreate, oblong when flattened, viscidium orbicular, stalk present; style-head conical. Follicles occasionally ellipsoid, occasionally moniliform. Seeds with winged raphe.

Three spp. in Laos and Vietnam, lowland forests. Flowers of *T. edule* Baill. eaten in SE Asia.

189. *Zygotelma* Benth.

*Zygotelma* Benth. in Benth. & Hook. f., Gen. Pl. 2: 740 (1876).

Suffrutescent twiner; shoots lenticellate, glabrous. Leaves 6–15 cm long, oblong to ovate. Inflorescences solitary, 2–4-flowered, simple, subsessile; floral bracts persistent, conspicuously imbricate, ciliate. Calyx ciliate; corolla 6–8 mm long, glabrous; lobes elliptic, ciliate; corolline corona inserted in corolla tube, short; lobes basally connate, rectangular and deeply bifid, reflexed; stamens inserted at base of corolla tube, filaments very short; nectaries lobular, fused to staminal feet; anthers oblong; connective appendages

lanceolate; spathe spoon-like, elliptic, viscidium orbicular, stalk present; style-head umbonate. Follicles 10–11 cm long, obclavate. Seeds slightly winged.

A single species, *Z. benthamii* Baill., in Cambodia, Laos and Thailand.

#### IV. SUBFAM. SECAMONOIDEAE Endl. (1838).

Large lianas to twining perennial herbs or small erect shrubs; latex white. Leaves paired, usually with colleters at the base. Corolla rotate to campanulate; lobes mostly with dextrorsely, more rarely sinistrorsely contorted or valvate aestivation; corolline corona present only in *Genianthus*, *Goniostemma*, and *Secamone*; gynostegial corona often present, usually of free staminal lobes; gynostegium sessile; stamens inserted on staminal tube around carpels and adaxially fused to sides of style-head (usually in its lower cylindrical portion); anthers 4-locular, sessile on apex of staminal tube, with well-developed, lignified anther wings below fertile part; staminal tube with simple to complex corona attached dorsally (rarely absent) and without clear vascularization; nectaries consisting of 5 vertical alternistaminal troughs behind guide rails on staminal tube; pollen inaperturate, united into minute pollinia, two per locule, not surrounded by waxy outer wall; pollinia more or less erect, formed above guide rails, more or less ellipsoid, without insertion crest, sometimes adjacent pairs adhering to form a single body; style-head very variably shaped, usually with discoid or cylindrical lower part (neck) just above carpels, with the 5 stigmatic zones located on the sides, upper part usually bifid; translator secreted by style-head just above each guide rail, consisting of small, porous, clip-like cream or yellowish corpusculum with flanks and sometimes with floor, sometimes with one or two caudicles (when two, each attaching a pair of pollinia to corpusculum; *Genianthus*, *Secamonopsis*, and some *Secamone* species); gynoecium apocarpous, semi-inferior. Fruit a pair of slender to stout, fusiform follicles (sometimes one by abortion) with dry, thin pericarp. Seeds numerous, compressed, more or less elliptical in outline, usually without wing-like margin, with micropylar coma, endosperm thin. Eight genera in the Palearctic and Australia.

#### KEY TO THE GENERA OF SECAMONOIDEAE

1. Staminal corona absent or reduced to five small triangular depressions **197. *Trichosandra***
  - Staminal corona more or less well-developed 2
2. Staminal corona lobes fused into a tube for more than half of their length **192. *Goniostemma***
  - Staminal corona lobes free or, at the most, basally fused 3
3. Connective appendages completely enclosing style-head 4
  - Connective appendages not enclosing style-head 5
4. Connective appendages with a very long filiform extension forming a cone above the style-head or sometimes much broadened and adhering to each other forming a calyptra above the thecae crowned by five distinct clubs on long strings; plants and follicles without conspicuous indumentum **190. *Calyptanthera***
  - Connective appendages lacking a very long, filiform prolongation, plants and follicles with a conspicuous, long and soft indumentum **193. *Pervillaea***
5. Abaxial leaf epidermis tuberculate-papillate (observable at ca.  $\times 50$ ) 6
  - Abaxial leaf epidermis not tuberculate-papillate 7
6. Pollinia attached in pairs to two long, recurved caudicles **195. *Secamonopsis***
  - Pollinia attached directly to the corpusculum, or, when caudicles present, these not long or convexly recurved **194. *Secamone***
7. Staminal corona lobes subulate or falcate; inflorescences frequently axillary, when with an indumentum, then trichomes white or yellowish; upper part of style-head capitate or shortly bifurcate **194. *Secamone***
  - Staminal corona lobes dorsiventrally flattened, with or without adaxial appendage, inflorescences normally extra-axillary, when with an indumentum, then trichomes reddish or brown, upper part of style-head cylindrical or ovoid 8
8. Corolla bearded adaxially (except in *G. valvatus* and *G. rectinervis* with five patches of trichomes at the corolla tube mouth), corolla lobe aestivation valvate or only slightly contorted (margins only slightly overlapping), the lobes symmetrical, buds truncate **191. *Genianthus***
  - Corolla normally with evenly distributed trichomes adaxially, corolla lobe aestivation distinctly contorted, the lobes asymmetrical, buds acute **196. *Toxocarpus***

190. *Calyptranthera* Klack.

*Calyptranthera* Klack., Novon 6: 27 (1996); Klackenberg, Bull. Mus. Natl. Hist. Nat., B, Adansonia IV, 19: 21–37 (1997), rev.; Klackenberg, Adansonia III, 29: 113–121 (2007), new taxa.

Suffrutescent twiners, 2–5 m tall; younger branches densely tomentose with stiff, occasionally uncinuate reddish trichomes. Leaves 6–14 cm long, discolorous, oblong, abaxially pubescent; stipules filiform; petioles often twisted. Inflorescences extra-axillary, solitary, 2–8-flowered, simple. Corolla 5–50 mm long, greenish or purplish, usually with long straight trichomes; lobes sinistrorsely contorted, elliptic to oblong; staminal corona lobes papillose, carnose, filiform or spatulate; filament tube forming cup-like projections underneath the short anther wings; connective appendages triangular, forming a cone or a calyptra above the style-head; pollinia occasionally horizontal, directly attached to the U-folded, soft corpusculum; style-head discoid, slightly depressed. Follicles solitary, ca. 16 cm long.

11 spp. in Madagascar, forests.

191. *Genianthus* Hook. f.

*Genianthus* Hook. f., Fl. Brit. Ind. 4: 15 (1883); Klackenberg, Bot. Jahrb. Syst. 117: 401–467 (1995), rev.; Watson, Fl. Bhutan 2.2: 697 (1999), reg. rev.

Suffrutescent twiners, several meters tall; occasionally densely pubescent. Leaves 7–19 cm long, ovate or oblong. Inflorescences extra-axillary, solitary, many-flowered, indeterminate, thyrsoidal, lax. Corolla 1.5–6 mm long, yellowish, usually with long trichomes; lobes valvate to slightly sinistrorsely contorted, oblong to triangular; gynostegial corona of free staminal lobes; lobes short, narrowly triangular to ovate, basally broadened, with adaxial appendage; connective appendages absent; pollinia usually free, occasionally paired; caudicles cylindrical or flattened; corpusculum soft, ovoid; style-head prominent, discoid, elongate-peltate or ovoid, neck obconical. Follicles occasionally solitary, 9–14 cm long, obclavate to narrowly oblong, occasionally sculptured or with indumentum. Seeds oblong.

16 to 18 spp. in two sections (Klackenberg 1995) distinguished by inflorescence structure; India, Bhutan, China, continental SE Asia, W Malesia, forests.

192. *Goniostemma* Wight

*Goniostemma* Wight, Contr. Bot. India 62 (1834); Li et al., Fl. China 16: 1999 (1995), reg. rev.

Suffrutescent twiners; glabrescent. Leaves discolorous, 6–9 cm long, elliptic to oblong, acute. Inflorescences axillary, paired, many-flowered, thyrsoidal, lax, longer than subtending leaves; peduncles with reddish trichomes. Corolla 5 mm long, yellow, with trichomes; lobes sinistrorsely contorted, oblong, occasionally emarginate; corolline corona of scales; gynostegial corona of connate staminal parts equaling the gynostegium, tubular to campanulate; lobes carnose, lingulate, apically reflexed; connective appendages absent; pollinia directly attached to the minute corpusculum or caudicles very short; style-head fusiform. Follicles occasionally solitary, 10–15 cm long, woody. Seeds pyriform, winged.

Two spp. in China and India, forests.

193. *Pervillaea* Decne.

*Pervillaea* Decne., Prodr. 8: 613. (1844); Klackenberg, Adansonia IV, 19: 21–37 (1997), rev. *Menabea* Baill. (1889).

Shrubs or suffrutescent twiners; shoots densely villous with long, curled to wavy trichomes. Leaves linear to broadly ovate, occasionally undulate; stipules filiform. Inflorescences extra-axillary, solitary, many-flowered, simple, condensed. Corolla 5–10 mm long, yellowish, finely pubescent; lobes sinistrorsely contorted, oblong, twisted; staminal corona lobes glabrous, longer than gynostegium, erect, lanceolate to narrowly ovate; connective appendages lanceolate, sometimes long-papillose, forming a cone over the gynostegium; pollinia directly attached to the U-folded, soft corpusculum; style-head discoid. Follicles 7–14 cm long, ellipsoid to obclavate, woolly. Seeds ovate.

Five spp. in S and W Madagascar and Mauritius, dry forests and thickets.

194. *Secamone* R. Br.

*Secamone* R. Br., Prodr. 464 (1810); Goyder, Kew Bull. 47: 437–474 (1992), reg. rev.; Klackenberg, Kew Bull. 47: 595–612 (1992), reg. rev.; Klackenberg, Opera Botanica 112: 127 pp. (1992), reg. rev.; Klackenberg, Blumea 55: 231–241 (2010), reg. rev.

*Rhynchosigma* Benth. (1876).

Shrubs, suffrutescent or herbaceous twiners to 6 m, occasionally puberulous. Leaves 0.6–7.5 cm long, narrowly elliptic to ovate; stipules minute. Inflorescences axillary, few- to many-flowered, thyrsoïdal or simple. Corolla 2–4.5 mm long, yellowish or greenish, occasionally with trichomes; lobes occasionally sinistrorsely contorted, oblong to ovate to triangular; corolline corona of five paired carnosé ridges; staminal corona lobes falcate; connective appendages ovate, occasionally with fimbriate margins; pollinia directly attached to the ovoid, porous corpusculum or caudicles extremely short; style-head capitate or shortly bifurcate. Follicles 4.5–10(–20) cm long. Seeds occasionally winged.  $2n = 22$ .

About 90 spp. (Klackenberg 2001) mainly in Africa and Madagascar, Asia and Australia, dry to humid, lowland to montane forests and bushland.

If the Asian *Toxocarpus* is included in *Secamone*, as suggested by Klackenberg (2010), the species number is ca. 120.

195. *Secamonopsis* Jum.

*Secamonopsis* Jum., Compt. Rend. Hebd. Séances Acad. Sci. 147: 689 (1908); Civeyrel & Klackenberg, Novon 6: 144 (1996).

Shrubs or herbaceous twiners, with distinct long and short shoots. Leaves occasionally fascicled on opposite brachyblasts, oblong to obovate, occasionally revolute, densely tomentose, abaxial epidermis papillose. Inflorescences extra-axillary on brachyblast, solitary, 1- to few-flowered, simple. Corolla 1.5–2 mm long, urceolate, yellow, with long retrorse trichomes in the tube and bunches of erect trichomes in the sinuses; lobes imbricate, oblong; staminal corona lobes short, carnosé, lingulate; anthers basally projecting; thecae apically glandular-papillose; pollinia attached in pairs to two long, recurved caudicles, corpusculum ellipsoid, soft; style-head capitate,

slightly bifurcate. Follicles ca. 45 mm long, obclavate. Seeds ovate.

Two spp. in Madagascar, arid scrub.

196. *Toxocarpus* Wight & Arn.

Fig. 47

*Toxocarpus* Wight & Arn. in Wight, Contr. Bot. India 61 (1834); Li et al., Fl. China 16: 198–199 (1995), reg. rev.; Watson, Fl. Bhutan 2.2: 695–696 (1999), reg. rev.; Klackenberg, Blumea 55: 231–241 (2010), reg. rev.

Shrubs, suffrutescent twiners or lianas, 5–10 m tall; shoots rusty tomentose or villous. Leaves 2.5–15 cm long, discolorous, ovate, abaxially occasionally rusty puberulous. Inflorescences axillary or extra-axillary, 3–10-many-flowered, thyrsoïdal, lax; floral bracts occasionally persistent. Corolla 4–15 mm long, yellowish, occasionally papillose and with long trichomes; lobes

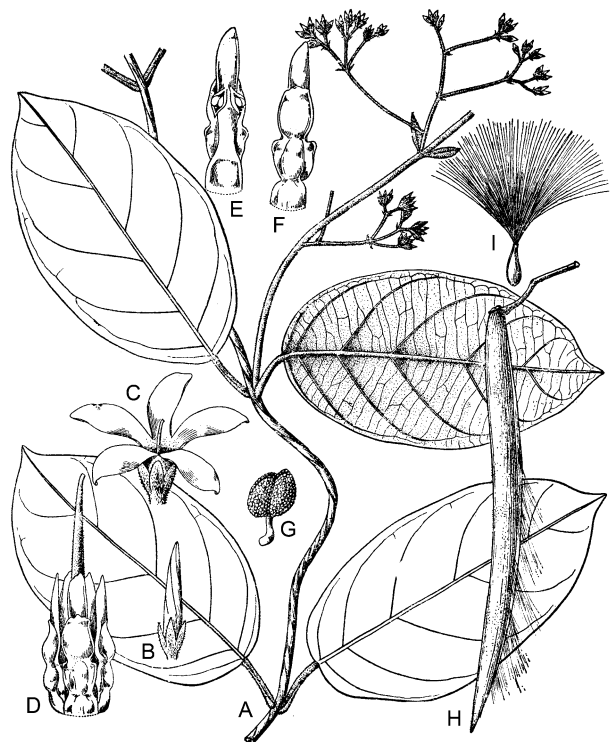


Fig. 47. Apocynaceae-Secamonoideae. *Toxocarpus villosus*. A Flowering branch. B Flower bud. C Flower. D Gynostegium with corona. E Anther, adaxial view. F Anther abaxial view and corona. G Pollinarium. H Follicle. I Seed. (From Flora of China Editorial Committee 1999, Fig. 165, with permission from the Missouri Botanical Garden Press, St. Louis, and Science Press, Beijing; drawn by Chen Guoze)



occasionally sinistrorsely contorted, usually lanceolate, asymmetrical; staminal corona lobes linguulate or lobed, occasionally with adaxial appendage; connective appendages fimbriate or ciliate; pollinia directly attached to the rhomboid soft corpusculum or caudicles very short; style-head ob-infundibuliform, capitate or bifurcate. Follicles 8–15 cm long, obclavate, with dense indumentum; pericarp thick. Seeds ovate.

About 30 spp. in Africa, Madagascar, Asia, Australia and Pacific Islands, forests, scrub, roadsides.

Floral size, style-head shape and flat corona lobes separate *Toxocarpus* well from *Secamone* in Asia and Australia, but not in Madagascar. *Toxocarpus* will, therefore, probably be merged with *Secamone* when more data are available.

#### 197. *Trichosandra* Decne.

*Trichosandra* Decne., Prodr. 8: 625 (1844); Friedmann, Bull. Mus. Natl. Hist. Nat. Paris IV, 12, sect. B, Adansonia 2: 131–138 (1990), rev.

Liana, glabrous. Leaves ovate. Inflorescences extra-axillary, solitary, to 10-flowered, simple. Corolla ca. 5 mm long, subcampanulate, fused for ca. two thirds of their length, with trichomes on the tube and along two V-shaped ridges toward the center of lobes; lobes valvate, ovate, carnosae; staminal corona reduced to triangular depressions; connective appendages ovate, fimbriate; pollinia directly attached to the U-folded corpusculum; style-head papillose, clavate or capitate. Follicles 65–85 mm long, obclavate. Seeds ovate, winged.

One sp., *T. borbonica* Decne., endemic to Mauritius.

#### V. SUBFAM. ASCLEPIADOIDEAE Burnett (1835).

Trees to shrubs or herbs, succulents, or small geophytes (rarely annual or even ephemeral), with white, yellow or translucent latex. Leaves opposite (rarely whorled), sometimes reduced to small rudiment or occasionally a spine, often with a cluster of colleters adaxially at base of midrib. Inflorescences usually extra-axillary, solitary, simple. Calyx usually with few to many adaxial, more or less alternisepalous colleters; corolla rotate to tubular; lobes valvate to imbricate; corolline corona rare in sinuses of lobes (except in some Ceropegieae and

*Gonolobus* relatives, where present as ring); stamens inserted on staminal tube around carpels and adaxially fused to style-head below its thickest portion near its base; anthers 2-locular, sessile on apex of staminal tube, spreading, erect, or horizontal, rarely descending, deltoid, subquadrate, with or without sterile, membranous, apical appendage, lateral margins sometimes becoming membranous after dehiscence, with well-developed, lignified guide rails alongside or below fertile part; staminal tube with simple to complex corona attached dorsally (rarely absent) and without clear vascularization: outer corona frequently present at or near base, of 5 free lobes to fused into tube; inner corona usually present at or just below bases of anthers at apex of staminal tube, usually of 5 free lobes; nectaries consisting of 5 vertical alternistaminal troughs behind or below guide rails on staminal tube; pollen united into pollinia, one per locule, with waxy outer wall, often with hyaline insertion crest; style-head broad, often with flat or concave apex (rarely conical to slenderly conical), sessile on top of carpels to tapering with narrow neck into them, with 5 stigmatic zones located on sides of lower cylindrical part behind guide rails, secreting translator just above each guide rail; translator consisting of hard, clip-like, brown to black corpusculum, mostly with flanks and floor, with two flexible, translucent caudicles (rarely absent in same Marsdenieae), each of which attaches one pollinium to corpusculum; gynoeceium apocarpous, mostly superior. Fruit a pair (often one by abortion) of slender to stout fusiform, more or less obclavate (rarely very stout to more or less spherical), ventrally dehiscent follicles with dry pericarp. Seeds usually numerous, compressed, more or less elliptical in outline, often with wing-like margin, usually with micropylar coma (rarely absent or present around seed margin), endosperm thin.  $x = 11$  (rarely 10, 9). 181 genera worldwide.

#### KEY TO THE TRIBES OF ASCLEPIADOIDEAE

1. Pollinia without well-developed caudicles
  1. *Fockeeae* (p. 325)
  - Pollinia with well-developed caudicles 2
2. Pollinia pendulous in each pollen sac (where the apex of the pollen sac is defined as the upper end of the pollen sac when it is vertical on the stamen, or the outer end when horizontal on the stamen) 3

- Pollinia erect in each pollen sac (where the base of the pollen sac is defined as the lower end of the pollen sac when vertical on the stamen, or the inner end when horizontal) 4
- 3. Leaves palmately lobed or (at least some) with one or two spreading lateral teeth a little above the base; corona gynostegial, consisting of a ring of very basally fused staminal and deeply tripartite interstaminal parts with an additional inner ring of smaller staminal parts 4. **Eustegieae** (p. 353)
- Leaves always entire; corona corolline or gynostegial; when gynostegial, then not consisting of a ring of very basally fused staminal and deeply tripartite interstaminal parts with an additional inner ring of smaller staminal parts 5. **Asclepiadeae** (p. 354)
- 4. Pollinia without pellucid germination zone; or, when present, then on distal margin only; connective appendages present 2. **Marsdenieae** (p. 326)
- Pollinia with pellucid germination zone on proximal margin or apex; connective appendages absent (except *Caudanthera*) 3. **Ceropegieae** (p. 336)

#### V.1. Tribe **Fockeeae** H. Kunze, Meve & Liede (1994).

Suffrutescent twiners with large root tubers; latex white. Corolla dextrorsely contorted in bud, rotate to campanulate; corolline corona absent; gynostegial corona of a ring of fused staminal and interstaminal parts, and free inner staminal lobes; gynostegium sessile; anthers with large apical appendages; pollinium consisting of two pollinia without sterile hyaline regions or germination pores, attached dorsally to the corpusculum, caudicles absent; corpusculum with broad outer flanks at least basally isolated and not united by a floor; flanks continuing basally into adhesive pads glued to the anther wings; style-head umbonate. Follicles solitary, obclavate to fusiform. Seeds ovate, winged.

A molecular study (Verhoveen et al. 2003) has shown that Fockeeae are sister to all remaining Asclepiadoideae. Two genera in Africa and the Arabian Peninsula.

#### KEY TO THE GENERA OF FOCKEEAE

1. Corona with free staminal lobes; corolla rotate, adaxially with trichomes; inflorescences many-flowered (> 5 flowers per inflorescence) 198. ***Cibirhiza***

- Corona without free staminal lobes; corolla campanulate, adaxially glabrous; inflorescences few-flowered (< 6 flowers per inflorescence) 199. ***Fockea***

#### 198. ***Cibirhiza*** Bruyns

*Cibirhiza* Bruyns, Notes Roy. Bot. Gard. Edinb. 45: 51–54 (1988); Kunze et al., Taxon 43: 367–376 (1994); Verhoveen et al., Grana 42: 70–81 (2003), phyl.; Thulin et al., Kew Bull. 63: 617–624 (2008), new taxon.

Twining geophytes; sparsely pilose; shoots lenticellate. Leaves 4–15 cm long, ovate. Inflorescences 5–25-flowered, sessile. Corolla fused to half of its length, greenish with purple blotches, papillose; lobes triangular-ovate; gynostegial corona ring short, fused for almost half of its length, staminal parts lingulate; inner free staminal lobes brownish, surpassing the gynostegium, subulate; occasionally with lingulate proximal lobe; connective appendages large, membranous, inflexed; pollinia ovoid to rectangular, directly attached to the U-folded corpusculum with a high apical dome and broad flanks; pollen grains single; style-head bifurcate. Follicles 7–10 cm long,  $2n = 22$ .

Three spp.: one in Oman, the other two in E Africa (Ethiopia, Tanzania) and Zambia, respectively, in woodland, bushland or riparian thicket.

#### 199. ***Fockea*** Endl.

Fig. 48

*Fockea* Endl. in Endlicher & Fenzl, Nov. Stirp. Dec. 17 (1839); Court, Asklepios 40: 69–74 (1987), rev.; Bruyns & Klak, Ann. Missouri Bot. Gard. 93: 535–564 (2006), phyl., rev.

*Chymocormus* Harv. (1842).

Twining geophytes, glabrescent, occasionally succulent. Leaves (sub-)sessile, 1.3–15 cm long, linear-elliptic or ovate. Inflorescences 2–6(–many)-flowered, (sub-)sessile. Corolla 5–15 mm long, creamish yellow, occasionally papillose; lobes linear-lanceolate or ovate, with revolute margins; gynostegial corona ring white, tubular to half of its length, staminal parts trifid; inner staminal lobes white, surpassing the gynostegium, subulate, basally fused to outer ring; connective appendages large and inflated, erect, exceeding the anthers; pollinia directly attached to the ovoid corpusculum with large adhesive pads; pollen in tetrads. Follicles 6–7(–20) cm long, woody.

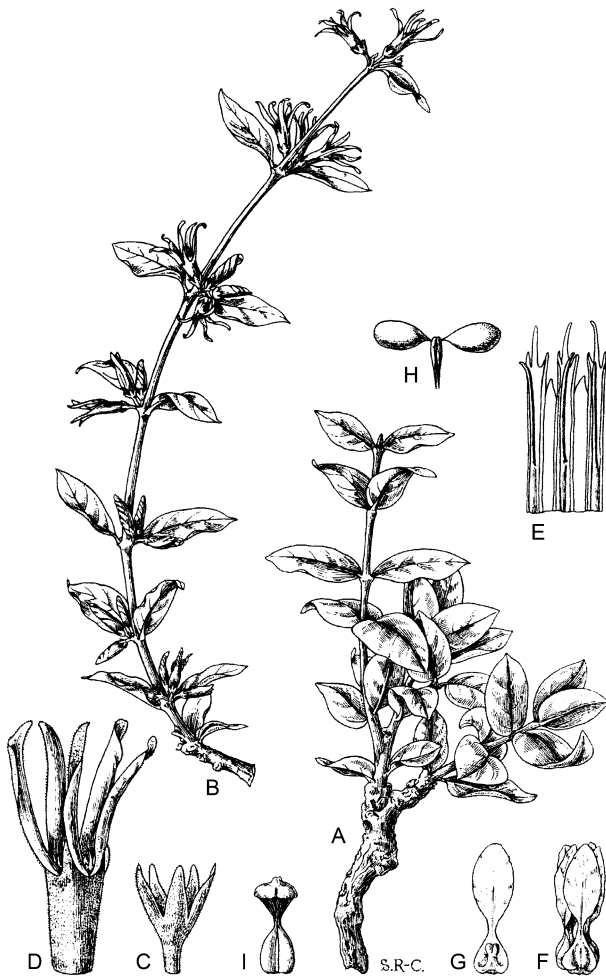


Fig. 48. Apocynaceae-Fockeeae. *Fockea edulis*. A Habit, above ground. B Flowering branch. C Calyx. D Corolla. E Corona portion in adaxial view. F Androecium. G Anther adaxial, with pollinarium and terminal anther appendage. H Pollinarium. I Gynostegium with ovaries and style-head. (From Dyer 1933, pl. 3221, with permission from Hooker's Icones Plantarum © Board of Trustees of the Royal Bot. Gard., Kew; drawn by Stella Ross-Craig)

Seeds with coma occasionally attached along entire margin.  $2n = 22$ .

Six spp. in southern and E Africa, Mopane and *Acacia-Commiphora* woodland, Karoo; *F. edulis* K. Schum. with coastal distribution.

## V.2. Tribe Marsdenieae Benth. (1868).

Omlor, Generische Revision der Marsdenieae (Asclepiadaceae). Ph.D. Thesis, Univ. Kaiserslautern (1998), rev.

Herbs, vines, lithophytes or epiphytes (these usually leaf succulents), rarely stem succulents, with

white, yellow or translucent latex. Leaves herbaceous or coriaceous, with brochidodromous venation, usually apically acute or acuminate. Calyx with one or two colleters in the sinuses, occasionally lacking; corolla rotate to urceolate; lobes with valvate to dextrorsely imbricate aestivation; corolline corona rare, consisting of ridges near sinuses of petals running down corolla tube to near base; gynostegial corona normally of five staminal lobes, attached below or along the back of the anthers; gynostegium usually sessile, exposed just above base of corolla; anthers erect to more or less horizontal, normally with apical appendage, but this never constricted at base, with guide rails below fertile part; pollen in single grains in two pollinia per anther; pollinia erect to horizontal, mostly more or less ellipsoid, occasionally with hyaline insertion crest along inner or lower ledge through which the pollen tubes emerge, pollinia normally basally attached to the caudicles; caudicles (sub-)basally inserted at the corpusculum, horizontal to ascending, usually cylindrical; style-head broad, with thick convex to conical apex, sessile on top of the usually glabrous carpels. Follicles two (often only one by abortion) slender to fusiform or obclavate, rarely nearly spherical, occasionally ornamented with longitudinal ridges on exterior. Seeds ovate to oblong, usually with apically attached coma.  $x = 11$ . 26 genera in the Paletropics and Australia, one in the Neotropics, one extending to southern Europe.

## KEY TO THE GENERA OF MARSDENIEAE

1. Plants epiphytic 2
  - Plants terrestrial 7
2. Adventitious roots conspicuous 3
  - Adventitious roots inconspicuous or lacking 5
3. Pollinia without pellucid margin; leaves generally carnose or coriaceous, sometimes concave, a few species additionally with pitcher leaves; corolla urceolate or salver-shaped (rotate in *Dischidia hoyella*), lobes with valvate aestivation; staminal corona lobes anchor-shaped, sagittate, or largely reduced; India to Fiji 207. *Dischidia*
  - Pollinia with pellucid margin; plants never with pitcher leaves; corolla of various shapes, staminal corona not anchor-shaped or sagittate 4

4. Inflorescences long-pedunculate, pendent umbels with strongly recurved pedicels; plants with long, narrowly linear, carnose leaves; Borneo  
**200. *Anatropanthus***
- Inflorescences umbels of various shapes, but pedicels not recurved, leaves, when present (absent in *Hoya spartioides*), much broader **214. *Hoya***
5. Non-twining epiphytic shrub with terminal inflorescences; corolla salverform; tube with prominent folds and dilated between the calyx lobes, adaxially with long trichomes; Java **213. *Heynella***
- Plants twining or non-twining, with extra-axillary inflorescences; corolla of various shapes, but not as above 6
6. Corona with two apical teeth and revolute lateral keels; gynostegium atop a densely villous column; Timor **218. *Oreosparte***
- Corona of various shapes, without two apical teeth; gynostegium mostly sessile, when atop a stipe or column, these not densely villous **214. *Hoya***
7. Pollinia with pellucid germination zone along the outer margin (except *Hoya mitrata* and *H. sect. Eriostemma*); corona staminal, lobes generally with a short inner tip that is appressed to the anthers and a prominent outer part that is mostly spreading and has revolute lower margins **214. *Hoya***
- Pollinia without pellucid margin (except *Telosma* with a small curved margin at the base of the outer side); with or without a staminal corona, but corona lobes never with revolute lower margins 8
8. Stems with two opposite longitudinal wings; corolla lobes inside with very long, soft trichomes; follicles always paired, 20–25 cm long, connected at their tips; Laos and Vietnam (apparently very rare)  
**203. *Campestigma***
- Stems smooth, with lenticels or with a layer of corky ridges, but never with two longitudinal wing-like ridges; follicles not connected at their tips 9
9. Hirsute twiners with thickened or carnose, racemiform inflorescences; flowers small, with a short tube and narrowly elongated corolla lobes extended into a long tip 10
- Plants different; flowers different with corolla lobes not extended into a long tip 11
10. Twiners with yellowish hirsute stems and ovate leaves; inflorescence a long-pedunculate, slightly thickened, unbranched spike, about 9 cm long; flowers small, rotate, corolla lobes reddish purple, ovate; staminal corona lobes bilobed; connective appendages extended into a very long tip; China  
**208. *Dolichopetalum***
- Hirsute twiners with narrowly obovate leaves (13 × 5 cm); flowers purplish black, in pairs along a spirally elongated, few-branched, carnose, racemiform inflorescence; staminal corona lobes with an apical tooth; connective appendages not extended into a very long tip; Malacca (apparently very rare or extinct)  
**219. *Pycnorhachis***
11. Corolla lobes inflexed in bud **216. *Lygisma***
- Corolla lobes not inflexed in bud 12
12. Corolla flattened globose, with a very small opening and very short, triangular lobes; gynostegium enclosed by a cuff-like annular corona; Australia  
**211. *Gunnessia***
- Corolla rotate, campanulate, urceolate or salverform, gynostegium not enclosed by a cuff-like annular corona 13
13. Staminal corona differentiated into distal and proximal lobule (ligule); distal lobules erect, ovate to oblong or triangular; proximal lobules inflexed, ligules longer than distal lobules, oblong to linear; pollinia with distal-basal sterile hyaline region; SE Asia to Malaya **224. *Telosma***
- Staminal corona simple or lacking; pollinia without hyaline region 14
14. Corolla more than 15 mm long, salverform, rarely urceolate 15
- Corolla less than 15 mm long, rotate or campanulate, rarely salverform or urceolate 18
15. Corolla tube inside, opposite to the stamens, with five corolline ridges, which are covered with two lines of upwardly directed trichomes; staminal corona lobes largely or completely reduced; China to Borneo  
**215. *Jasminanthes***
- Corolla tube without hairy ridges behind the stamens; staminal corona lobes not completely absent 16
16. Staminal corona lobes elongate-triangular; Madagascar **222. *Stephanotis***
- Staminal corona lobes not elongate-triangular 17
17. Staminal corona lobes hook-shaped and carnose, inserted at the base of the gynostegium; inflorescences long-pedunculate; leaves herbaceous, narrowly ovate, about 10 × 5 cm; Thailand  
**210. *Gongronema* (*G. filipes*)**
- Staminal corona of different shapes, attached along the filament tube; inflorescences sessile or shortly pedunculate; leaves coriaceous and elliptic

- (*Marsdenia speciosa*, *M. praestans*), or herbaceous and cordate (*M. stenantha*) **217. *Marsdenia***
18. Corolline corona of five scale-like lobes in the sinuses of the corolla lobes or as longitudinal ridges inside the corolla tube 19  
 – Corolline corona completely absent 22
19. Corolline corona of five longitudinal ridges opposite the stamens, each with two lines of upwardly directed, stiff hairs; in some species these ridges project apically into carnose lobes; style-head massive, cylindrical with blunt apex, always protruding beyond the anthers; staminal corona largely or completely reduced; inflorescences often paired **212. *Gymnema***  
 – Corolline corona usually in the sinuses of the corolla; when ridges below the sinuses, then style-head flattened, or with well-developed staminal corona 20
20. Corpusculum very narrowly ellipsoid (at least five times longer than wide), caudicles strongly geniculate, ribbon-shaped, at least twice as long as pollinia, style-head flattened, with a papillate hump in the center; guide rails very short; corolline corona glabrous, either as ridges or as bulge-like thickenings in the sinuses of the mostly rotate corolla; mostly mangrove or littoral plants; India to New Caledonia **221. *Sarclobus***  
 – Corpusculum less narrow (less than five times longer than wide), caudicles shorter, not ribbon-shaped or strongly geniculate, style-head without a papillate hump in the center, guide rails longer, corolline corona glabrous or with trichomes, between adjacent corolla lobes 21
21. Corolline corona pubescent, domed swellings at the mouth of the corolla tube; Africa **201. *Anisopus* (*A. mannii*)**  
 – Corolline corona hairy or glabrous small scales between adjacent corolla lobes, carnose obtuse lobes perpendicular to the corolla lobes (*Marsdenia longiloba*), or triangular longitudinal ridges (*M. harmandiella*) **217. *Marsdenia***
22. Gynostegial corona absent **220. *Rhysolobium***  
 – Gynostegial corona present 23
23. Style-head rostrate, protruding well beyond the anthers 24  
 – Style-head short-conical, hemispherical or flattened, not or only slightly protruding beyond the anthers 27
24. Follicles with only 1 or 2 seeds; erect, rigid shrubs; Africa **223. *Stigmatorhynchus***  
 – Follicles with numerous seeds; lianas or twiners, when erect, then usually apically twining 25
25. Pollinia with warty anticlinal walls in the apical half, corolla lobes narrowly elongate, up to 8 mm long, fused only at the base; SE Mediterranean to Iran **205. *Cionura***  
 – Pollinia smooth; corolla lobes broader, or when narrowly elongate then with well-developed corolla tube 26
26. Inflorescences axillary and paired, one larger than the other **201. *Anisopus* (*A. mannii*)**  
 – Inflorescences extra-axillary, alternate (rarely paired) **217. *Marsdenia***
27. Gynostegial corona cupular; staminal lobes obtuse, apically bi- or trifid, laterally fused in lower half; corolla rotate, yellow or pink with a dark red eye; Java **202. *Asterostemma***  
 – Gynostegial corona not cupular, staminal lobes of various shapes, but not apically bi- or trifid; corolla of various shapes, when rotate, then not yellow or pink with dark red eye 28
28. Corolla rotate or bowl-shaped, lobes at least as long as tube, usually longer 29  
 – Corolla campanulate or urceolate; lobes generally shorter than tube 37
29. Top of gynostegium truncate, with very short guide rails 30  
 – Top of gynostegium not truncate, guide rails longer 32
30. Style-head flattened with a small papillate hump in the center; corpusculum very narrowly ellipsoid (at least five times longer than wide); mostly mangrove or littoral plants; India to New Caledonia **221. *Sarclobus***  
 – Style-head blunt conical, rounded or flattened, not papillate; corpusculum less narrow 31
31. Corolla and staminal corona lobes carnose, protruding well beyond the short gynostegium, with a very broad basal part and an incurved, finger-like apical part; inflorescences solitary; Sumatra, Philippines **214. *Hoya*** (former *Clemensiella* species)  
 – Corolla and staminal corona lobes usually not carnose, not protruding beyond the gynostegium and not incurved; inflorescences often paired **217. *Marsdenia* (*M. secamonoides* group)**
32. Inflorescences axillary, paired; C and W Africa **201. *Anisopus* (*A. efulenis*)**  
 – Inflorescences extra-axillary, solitary; Asia and Australia 33
33. Inflorescences long-pedunculate 34  
 – Inflorescences short-pedunculate or sessile 36
34. Corolla lobes marginally glabrous, latex translucent **206. *Cosmostigma***

- Corolla lobes marginally ciliate, latex white 35
- 35. Staminal corona lobes carnose, subglobose, with short inner tips appressed to the anthers; corolla lobes fused only at the base, light-colored; carpels completely or partly hairy; leaves herbaceous; India to China **209. *Dregea***
- Staminal corona lobes laminar, oblong; corolla fused for ca. half of its length, dark purple; carpels glabrous; leaves thick-coriaceous; E Himalayas **225. *Treutlera***
- 36. Leaves coriaceous, broadly elliptic to obovate; inflorescences sciadioidal, pedicels thread-like, 2–4 cm long; corolla deeply lobed; Java, Philippines **204. *Cathetostemma***
- Leaves herbaceous, elliptic; inflorescences at first sciadioidal, later becoming racemiform with a thickened, contracted rachis; corolla not deeply lobed; New Guinea, Australia **217. *Marsdenia* (*M. hemiptera* group)**
- 37. Staminal corona of carnose, scale-like or hook-shaped lobes, inserted at the base of the gynostegium; lower surface of corona lobes often bulged **210. *Gongronema***
- Staminal corona of mostly erect lobes with a free apical tip, attached to the filament tube and appressed to the anthers (except *Marsdenia thyrsoflora*, *M. cavalierei* and *M. urceolata* with hook-shaped corona lobes); lower surface of corona lobes not bulged **217. *Marsdenia***

#### 200. *Anatropanthus* Schltr.

*Anatropanthus* Schltr., Bot. Jahrb. Syst. 40. Beibl. 92: 18 (1908).

Epiphyte with pendent branches and adventitious roots, glabrous. Leaves succulent, linear, mucronate, marginally revolute. Inflorescences 10–20-flowered, sciadioidal, long-pedunculate. Flowers with 180° inwardly bent pedicels; corolla tubular to urceolate; lobes apically abruptly inflexed; free staminal corona lobes differentiated into an erect distal lobule and a slenderly oblong, inflexed, proximal lobule; gynostegium shortly stipitate, concealed in corolla tube; anthers oblong; connective appendages subulate, inflated, erect; pollinia with distal hyaline germination pore;

caudicles very short, flattened; corpusculum ellipsoid; style-head elongate-conical.

One sp., *A. borneensis* Schltr., Borneo, forest. Insufficiently known genus with the type specimen destroyed in Berlin (B); possibly related to *Hoya*.

#### 201. *Anisopus* N. E. Br.

*Anisopus* N. E. Br., Bull. Misc. Inform. 1895: 259 (1895); Goyder, Kew Bull. 49: 737–747 (1994), rev.

Suffrutescent twiners or lianas, glabrous. Leaves 4–15 cm long, obovate(-oblong), basally cordate, truncate or rounded. Inflorescences axillary, paired, 5–20-flowered. Corolla 2.5–8 mm long, rotate, carnose, yellowish or reddish purple, densely covered with trichomes; lobes ovate to oblong; corolline corona, when present, of free, oblongoid lobes, with trichomes; free staminal corona lobes attached along filament tube, almost equaling the gynostegium, obovate, pointed, winged, with a tooth projecting from the top of the inner face; connective appendages broadly ovate; pollinia ovoid; caudicles convexly recurved; style-head conical to semi-globose or rostrate. Foliolles 8–16 cm long. Seeds with undulate wing.

Two spp. in W Africa, evergreen tropical rainforest, 0–1800 m.

#### 202. *Asterostemma* Decne.

*Asterostemma* Decne., Ann. Sci. Nat. Bot. II, 9: 371, t. 10, f. D (1838); Omlor, Gener. Rev. Marsdenieae: 107 (1998), consp.

Suffrutescent twiner; shoots sparsely pubescent. Leaves ovate to oblong, marginally crenulate, hirsute. Inflorescences 4–8-flowered, condensed bostrychoid. Corolla rotate, yellow to rose, center purple; staminal corona lobes connate for about half of their length, slightly carnose, bi- or trifold; pollinia oblongoid to obovoid; caudicles long-geniculate, first horizontal, then erect, articulated; corpusculum ellipsoid-oblongoid, larger than pollinia; style-head umbonate.

One sp., *A. repandum* Decne., in Indonesia (Java).

203. *Campestigma* Pierre ex Costantin

*Campestigma* Pierre ex Costantin in Lecomte, Fl. Indo-Chine 4: 117 (1912); Omlor, Gener. Rev. Marsdenieae: 103–104 (1998), consp.

Suffrutescent twiner, glabrous; shoots twisted, with two opposite wings. Leaves long-petiolate, broadly ovate, cordate. Inflorescences 5–10-flowered, thyrsoidal, condensed; flowers long-pedicellate. Corolla ca. 6.5 mm long, rotate, lobes densely covered with trichomes to 5 mm long, elongate-ovate; corolline corona annular, with trichomes; free staminal corona lobes dolabriform; pollinia pyriform; caudicles S-shaped; corpusculum elongatedly clavate; style-head rostrate. Follicles paired, apically fused when mature, 20–25 cm long, narrowly oblong. Seeds winged.

One sp., *C. purpureum* Pierre ex Costantin, in continental SE Asia.

204. *Cathetostemma* Blume

*Cathetostemma* Blume, Rumphia 4: 30 (1849); Omlor, Gener. Rev. Marsdenieae 129–130 (1998), consp.

Suffrutescent twiner, sparsely pubescent. Leaves 9–15 cm long, elliptic to obovate. Inflorescences short, sciadioidal, pedicels 2–4 cm long, filiform. Corolla ca. 7.5 mm long, rotate, greenish white; lobes ovate; free staminal corona lobes attached along the filament tube, almost equaling the gynostegium, erect, slightly carnose; gynostegium sessile; anther wings extending beyond the anther; pollinia ovoid; caudicles horizontal; style-head umbonate.

A single species, *C. laurifolium* (Blume) Decne., island of Timor and Philippines.

205. *Cionura* Griseb.

*Cionura* Griseb., Spicil. Fl. Rumel. 2: 69 (1844); Field, Fl. Iraq 4.1: 561–563 (1980), reg. rev.; Omlor, Gener. Rev. Marsdenieae: 107–108 (1998), consp.

Shrub to 1 m tall, occasionally apically twining, glabrous. Leaves 4–10 cm long, broadly ovate, cordate. Inflorescences 15–20-flowered, lax. Corolla rotate, whitish; lobes oblong; free staminal corona lobes shorter than the gynostegium, erect to reflexed, lanceolate; connective appendages oblong, about twice as long as the anthers;

pollinia clavate, with warty anticlinal walls; caudicles S-shaped, cylindrical; corpusculum elongate- bone-shaped; style-head rostrate, apically bifurcate. Follicles solitary, 6.5–8 cm long, obclavate. Seeds winged.  $2n = 22$ .

One sp., *C. erecta* (L.) Griseb., southern Europe and Asia Minor, oak forests, rocky slopes, sandy beaches and dry ravines on limestone.

206. *Cosmostigma* Wight

*Cosmostigma* Wight, Contr. Bot. India 41 (1834); Omlor, Gener. Rev. Marsdenieae 107–108 (1998), consp.; Jagtap & Singh, Fasc. Fl. India 24: 71–72 (1999), reg. rev.

Suffrutescent twiners or lianas, occasionally yellowish pubescent; latex translucent. Leaves occasionally papery, 5–11 cm long, ovate, cordate. Inflorescences 6–15-flowered; long-pedunculate. Corolla 4–6 mm long, rotate to campanulate, yellowish green, occasionally with trichomes in the throat; lobes valvate or contorted, ovate to oblong; free staminal corona lobes shorter than the gynostegium, erect, ovate or rectangular, deeply bilobed or irregularly dentate; gynostegium sessile, exserted from corolla tube; pollinia clavate; caudicles horizontal or declinate, cylindrical; corpusculum ovoid to oblongoid, larger than pollinia; style-head umbonate. Follicles 12–20 cm long, obclavate; pericarp thick. Seeds broadly winged.

Three spp. in India, Sri Lanka, China and the Philippines, humid forests.

207. *Dischidia* R. Br.

*Dischidia* R. Br., Prodr. 461 (1810); Rintz, Blumea 26: 81–126 (1980), reg. rev.; Weir & Kiew, Biol. J. Linn. Soc. 27: 113–132 (1986), ecol.; Livshultz et al., Blumea 50: 113–134 (2005), reg. rev.; Peeters & Wiwatwitaya, Asian Myrmecol. 6: 49–61 (2014), ecol.

*Dischidiopsis* Schltr. (1904).

*Oistonema* Schltr. (1908).

*Dolichostegia* Schltr. (1915).

*Hoyella* Ridl. (1917).

Twining, pendent or creeping herbaceous or succulent epiphytes, usually glabrous, leaves occasionally 3–4-whorled, occasionally reduced, elliptic or ovate; often with modified, hollow leaves invaded by adventitious roots, or shell-shaped leaves appressed to substrate. Inflorescences with persistent, straight, thickened rachis.

Corolla urceolate or tubular, carnose, tube barbate; lobes valvate, ovate, occasionally cucullate; occasionally with corolline corona inserted in tube, annular or 5-lobate, glabrous; free staminal corona lobes, when present, bilobed or sagittate; gynostegium atop a bulge, concealed in corolla; connective appendages conspicuous; pollinia oblongoid; corpusculum very small; style-head conical or ovoid. Follicles 4–8 cm long; pericarp papery. Seeds apically winged.  $2n = 22$ .

About 80 spp. in India, China, continental SE Asia, Malesia and Australia, dry to humid lowland to montane forests, littoral scrub. Many species associated with ants, e.g., housing them under imbricate leaves or in pitchers (Peeters and Wiwatwitaya 2014).

### 208. *Dolichopetalum* Tsiang

*Dolichopetalum* Tsiang, Acta Bot. Sin. 15: 137 (1973); Li et al., Fl. China 16: 237–238 (1995), reg. rev.; Omlor, Gener. Rev. Marsdenieae: 104 (1998).

Suffrutescent twiner, to 4 m tall; densely yellowish brown villous. Leaves papery, 8–12 cm long, ovate, strongly cordate, basally with 10 colleter. Inflorescences long-pedunculate raceme-like thyrses. Corolla ca. 14 mm long, cyathiform, purple, abaxially villous; lobes valvate, ovate, caudate, ciliate; free staminal corona lobes shorter than gynostegium, erect, rectangular, slightly bifid; gynostegium sessile, concealed in corolla tube; anthers nearly square; connective appendages triangular, extended in a long tip, erect; pollinia oblongoid; caudicles horizontal; corpusculum clavate; style-head conical. Follicles solitary, 6.5–11 cm long, obclavate. Seeds winged.

One sp., *D. kwangsiense* Tsiang, in southern China, mountain forests.

### 209. *Dregea* E. Mey.

*Dregea* E. Mey. Comment. Pl. Africae Austr. 199 (1838), nom. cons., non *Dregea* Eckl. & Zeyher (1837), Apiaceae, nom. rej.; Omlor, Gener. Rev. Marsdenieae 109–110 (1998), consp.; Jagtap & Singh, Fasc. Fl. India 24: 172–177 (1999), reg. rev. *Wattakaka* Hassk. (1857).

Suffrutescent twiners or lianas, 4–8 m tall, pubescent; latex translucent; shoots lenticellate, leaves long-petiolate; 2–20 cm long, broadly ovate, occasionally shallowly cordate. Inflorescences 10–30-flowered, pendulous, long-pedunculate. Flowers long-pedicellate, sweetly fragrant; corolla 5–12 mm long, whitish, yellow or purplish, occasionally veined, occasionally pilose; lobes ovate, ciliate; free staminal corona lobes white or greenish, subglobose and pointed, almost equaling the (sub-)sessile gynostegium; pollinia slenderly ellipsoid; caudicles geniculate, rectangular; corpusculum very elongate-oblongoid; carpels at least partially with trichomes; style-head yellow, conical. Follicles paired, 7–9 cm long, obclavate, with thick pericarp and dense indumentum. Seeds ovate, broadly winged.  $2n = 22$ .

About 12 spp. in China, S Asia, continental SE Asia and Malesia, forests. *Dregea volubilis* (L.f.) Benth. is known for its medicinal properties, much used in Ayurveda and traditional Chinese medicine.

### 210. *Gongronema* (Endl.) Decne.

*Gongronema* (Endl.) Decne., Prodr. 8: 624 (1844); Li et al., Fl. China 16: 240–241 (1995), reg. rev.; Omlor, Gener. Rev. Marsdenieae 131–132 (1998), consp.; Jagtap & Singh, Fasc. Fl. India 24: 78–82 (1999), reg. rev.; Watson, Fl. Bhutan 2.2: 706–708 (1999), reg. rev. *Gymnema* subg. *Gongronema* Endl., Gen. Pl.: 595 (1838).

Suffrutescent twiners or lianas, 5–8 m tall, glabrous. Leaves occasionally papery, 5–14 cm long, elliptic to oblong. Inflorescences condensed, usually long-pedunculate, rachis straight, occasionally thickened (then floral bracts conspicuous), with spirally arranged flowers. Corolla 4–8 mm long, urceolate or campanulate, fused for about half of its length, creamish yellow, occasionally with trichomes, lobes ovate, occasionally ciliate; free staminal corona lobes attached below filament tube, shorter than gynostegium, ovate, linguulate or unguiculate, erect; gynostegium concealed in corolla tube; connective appendages very small; pollinia ovoid; style-head conical. Follicles 4.5–8 cm long.  $2n = 22$ .

At least 12 spp. in Africa, S and SE Asia, China.



211. *Gunnessia* P.I. Forst.

*Gunnessia* P.I. Forst., *Austrobaileya* 3: 273–289 (1990).

Liana; shoots densely pubescent. Leaves to 15 cm long, ovate, (almost) glabrous, basally with 6 colleters. Inflorescences 1–8-flowered, sciadioidal. Corolla 3–4 mm long, 16 mm diam., broadly urceolate, yellowish green, tips triangular; gynostegial corona yellowish, of a short, completely fused outer ring of connate staminal and interstaminal parts, and of an inner ring of almost completely fused, toothed staminal parts, attached below the filament tube, overtopping the gynostegium; carnose, adaxially papillose; free tips triangular, strongly reflexed; gynostegium sessile, concealed in corolla; pollinia globose; caudicles geniculate, flattened; style-head papillose, semi-globose. Follicles to 8 cm long, ovoid, keeled along suture. Seeds ovate.

One sp., *G. pepo* P.I. Forst., in Australia, endemic to Cape York Peninsula, deciduous vine thickets.

212. *Gymnema* R. Br.

Fig. 49

*Gymnema* R. Br., *Prodr.* 461 (1810); Forster, *Austral. Syst. Bot.* 8: 703–933 (1995), reg. rev. (under *Marsdenia*); Li et al., *Fl. China* 16: 238–240 (1995), reg. rev.; Meve & Alejandro, *Willdenowia* 43: 81–86 (2013), morph., tax. *Bidaria* (Endl.) Decne. (1844).

Suffrutescent twiners or lianas, 1–10 m tall; shoots lenticellate. Leaves 1–13 cm long, oblong, occasionally cordate. Inflorescences occasionally paired. Corolla 5–8 mm long, campanulate, fused for about half of its length, yellowish; lobes valvate or slightly contorted; oblong or ovate; corolline corona of five longitudinal ridges below corolla lobe sinuses, sometimes forming carnose appendages, usually with (dense) trichomes along two lines; gynostegial corona absent; gynostegium concealed in corolla; pollinia oblongoid; style-head conical, rostrate or semi-globose. Follicles 3.5–9(–16) cm long, occasionally ellipsoid. Seeds winged.  $2n = 22$ .

About 30 spp., often very similar in flower structure; Africa [only *G. sylvestre* (Retz.) R. Br.] and most Asian-Pacific countries, littoral scrub, bushland, forests.

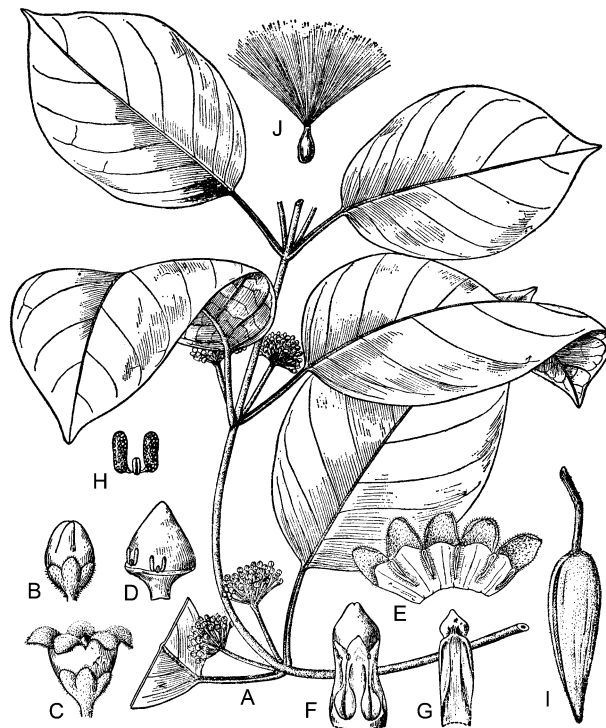


Fig. 49. Apocynaceae-Marsdenieae. *Gymnema latifolium*. A Flowering branch. B Flower bud. C Flower. D Style-head with two pollinaria attached. E Opened corolla showing corolline corona. F Gynostegium. G Anther adaxial view. H Pollinarium. I Follicle. J Seed. (From *Flora of China* Editorial Committee 1999, Fig. 231, with permission from the Missouri Botanical Garden Press, St. Louis, and Science Press, Beijing; drawn by Chen Guoze)

The inclusion of *Gymnema* in *Marsdenia* (Forster 1995) would make the latter genus too heterogeneous and is therefore not accepted here.

213. *Heynella* Backer

*Heynella* Backer, *Blumea* 6: 381 (1950); Omlor, *Gener. Rev. Marsdenieae* 152 (1998), consp.

Epiphytic shrub, 25–30 cm tall. Leaves ovate to oblong. Inflorescences terminal, sciadioidal. Corolla 10–12 mm long, tubular to salverform, fused for about three quarters of length, slightly carnose, cream; tube dilated at base and grooved apically, with long trichomes; lobes valvate, ovate to oblong, erect to patent; free staminal corona lobes laterally compressed, basally widened, with a groove on the back.

One sp., *H. lactea* Backer, in Indonesia (Java). Insufficiently known genus.

214. *Hoya* R. Br.

*Hoya* R. Br., Prodr. 459 (1810); Rintz, Malayan Nat. J. 30: 467–522 (1978), reg. rev.; Wanntorp, Taxon 56: 465–478 (2007), morph.; Wanntorp et al., Mol. Phyl. Evol. 33: 722–733 (2006), phyl.; Wanntorp & Forster, Ann. Missouri Bot. Gard. 94: 36–55 (2007), phyl.; Wanntorp et al., Taxon 60: 4–14 (2011), phyl.; Wanntorp & Meve, Willdenowia 41: 97–99 (2011), tax.; Simonsson Juhonewe & Rodda, Gard. Bull. Singapore 96: 97–147 (2017).

*Otostemma* Blume (1849).

*Absolmsia* Kuntze (1891).

*Micholitzia* N.E. Br., Bull. Misc. Inform. 1909: 358 (1909).

*Clemensiella* Schltr. (1915), nom. nov. pro *Clemensia* Schltr. (1915), non *Clemensia* Merr. (1908), Meliaceae.

*Antiostelma* (Tsiang & P.T. Li) P.T. Li (1992); *Hoya* sect.

*Antiostelma* Tsiang & P.T. Li (1974).

*Madangia* P.I. Forst., D.J. Liddle & I.M. Liddle (1997).

(Hemi-)epiphytes, herbaceous or suffrutescent twiners, rarely shrubs; latex occasionally translucent; adventitious roots often conspicuous. Leaves coriaceous, succulent or waxy, occasionally caducous. Inflorescences many-flowered, occasionally long-pedunculate (to 25 cm). Corolla rotate, campanulate, subglobose, rarely tubular, carnos, often pilose or pubescent; lobes valvate, broadly triangular; staminal corona at least equaling the gynostegium, lobes horizontally spreading, solid, often differentiated into a distal lobule with apical tooth and revolute lateral keels forming a deep nectar groove and a dentiform proximal lobule, basally occasionally spurred; gynostegium usually sessile, occasionally concealed; pollinia usually elongate-ellipsoid, mostly with distal germination crest; corpusculum occasionally with basal projections. Follicles usually solitary, 4–10(–30) cm long, occasionally ellipsoid. Seeds (apically) winged, occasionally with coma attached along entire margin.  $2n = 22, 44$ .

Probably more than 350–450 spp., number constantly increasing due to new discoveries. Tropical Asia and Oceania, littoral areas, various forest types, frequently associated with water courses; on rocks, tree trunks.

215. *Jasminanthes* Blume

*Jasminanthes* Blume, Ann. Mus. Bot. Lugduno-Batavum 1: 148 (1850); Li et al., Fl. China 16: 242–243 (1995), reg. rev.; Omlor, Gener. Rev. Marsdenieae 126–128 (1997), consp.; Tran et al., PhytoKeys 69: 17–22 (2016), key, morph., reg. tax.

Lianas, to 12 m tall; latex occasionally translucent; shoots pubescent. Leaves 7–19 cm long, oblong, long-acuminate, glabrous or glabrescent. Inflorescences to 12-flowered. Flowers sweetly fragrant; corolla 2–10 cm long, urceolate or salverform; tube dilated at base and with five grooves, creamish to green, occasionally with trichomes; lobes oblong to falcate, twisted; corolline corona of two lines with trichomes, fused to corolla tube, occasionally with free tips, opposite the stamens; gynostegial corona absent; gynostegium sessile, concealed in corolla; pollinia ovoid; caudicles horizontal, short; lower part of style-head obconical, upper part conical or capitate. Follicles solitary, 12–21 cm long.

Seven spp. in China, Japan, continental SE Asia and W Malesia, little disturbed tropical forests.

216. *Lygisma* Hook. f.

*Lygisma* Hook. f., Hooker's Icon. Pl. 15: ad t. 1423 (1883); Li et al., Fl. China 16: 262 (1995), reg. rev.; Omlor, Gener. Rev. Marsdenieae 106 (1998), consp.

*Costantina* Bullock (1965), nom. nov. pro *Pilostigma* Costantin (1912), non *Pilostigma* Tiegh. (1894), Loranthaceae.

Herbaceous or suffrutescent twiners, to 3 m long, pubescent. Leaves papery, 3–6.5 cm long, ovate. Inflorescences occasionally axillary or terminal, occasionally paired, short, to 8-flowered, lax, distinctly pedunculate. Corolla 3–4 mm long, campanulate, white; tube pilose; lobes inflexed in bud, oblong; free staminal corona lobes equaling the gynostegium, erect, slightly carnos, ovate; gynostegium concealed in corolla; anther wings shorter than anthers; pollinia oblongoid; caudicles short, S-shaped; style-head papillose, flat. Follicles solitary, 5–7 cm long, obclavate. Seeds winged.

At least five spp. in China, continental SE Asia and W Malesia, thickets, open woods; 100–300 m.

217. *Marsdenia* R. Br.

*Marsdenia* R. Br., Prodr.: 460 (1810), nom. cons.; Rothe, Bot. Jahrb. Syst. 52: 354–434 (1915); Forster, Austral. Syst. Bot. 8: 703–933 (1995); Li et al., Fl. China 16: 243–249 (1995), reg. rev.; Omlor, Gener. Rev. Marsdenieae (1998), consp.; Jagtap & Singh, Fasc. Fl. India 24: 122–135 (1999), reg. rev.; Watson, Fl. Bhutan 2.2: 708–712 (1999), reg. rev.

*Leichardtia* R. Br. (1849).  
*Thozetia* F. Muell. ex Benth. (1868).  
*Stephanotella* E. Fourn. (1885).  
*Verlotia* E. Fourn. (1885).  
*Traunia* K. Schum. (1895).  
*Harmandiella* Costantin (1912).  
*Pseudosarcolobus* Costantin (1912).  
*Dalzielia* Turrill (1916).  
*Dischidanthus* Tsiang (1936).  
*Loniceroides* Bullock (1964), nom. nov. pro *Harrisonia* Hook. (1826), non *Harrisonia* R. Br. ex A. Juss. (1825), (Simaroubaceae).  
*Papuastelma* Bullock (1965), nom. nov. pro *Astelma* Schltr. (1913), non *Astelma* R. Br. ex Ker-Gawl. (1821), Asteraceae.  
*Sinomarsdenia* P.T. Li & J.J. Chen (1997).

Lianas, twiners or shrubs, occasionally tuberous; glabrous, or with white, yellow, or rusty indument; latex white, yellow, brown, or translucent. Leaves oblong or linear. Corolla 6–35 mm long, rotate, campanulate, urceolate or salverform, occasionally with trichomes; lobes valvate, imbricate or contorted; corolline corona, when present, of five ridges opposite the stamens, with or without free tips and trichomes; free staminal corona lobes attached along filament tube, scaly or carnosose, short; pollinia oblongoid or clavate; caudicles straight; corpusculum smaller than pollinia; carpels occasionally with trichomes; style-head occasionally semi-globose or rostrate. Follicles occasionally winged, occasionally with woody or thick pericarp. Seeds winged; coma rarely absent.  $2n = 22$ .

About 150 spp. in Africa, Asia, Australia, Central and South America and Oceania. *M. tinctoria* R. Br. yields an indigo dye, and *M. cundurango* Reichenb.f. yields the medicinal drug condurango.

The limits of *Marsdenia* are still unclear; while Forster (1995) advocated a very wide concept for Australia and Papuasia, the concept of Omlor (1998), which is adopted here, is much narrower. Omlor (1998) recognized three sections in Africa; the species of the Americas and Australasia, however, are too little known for a sub-generic concept.

#### 218. *Oreosparte* Schltr.

*Oreosparte* Schltr., Beih. Bot. Centralbl., Abt. 2, 34: 16 (1916); Omlor, Gener. Rev. Marsdenieae: 151–152 (1998), consp.; Rodda & Omlor, Webbia 68: 91–95 (2013), morph.

Large scandent twiner, pubescent. Leaves slightly carnosose, 5.5–9 cm long, ovate-oblong, glabrous. Inflorescences long-pedunculate, 1 or 2 flowers open synchronously. Corolla ca. 13 mm long, campanulate, white, glabrous; lobes adaxially thickened opposite the stamens, lanceolate, spreading; free staminal corona lobes surpassing the gynostegium, horizontally spreading, solid, apically bifid, with revolute lateral keels, forming a deep groove containing nectar, basally truncate; gynostegium atop a column, raised high above corolla; pollinia oblongoid, caudicles short; corpusculum thickly rhomboid; style-head depressed-conical, papillate. Follicles ca. 10 cm long. Seeds small, wingless, with long coma.

Only one species, *O. celebica* Schltr., in Indonesia (Sulawesi), mountain forest; 1200 m.

Rodda and Omlor (2013) keep the genus separate from *Hoya*.

#### 219. *Pycnorhachis* Benth.

*Pycnorhachis* Benth. in Benth. & Hook. f., Gen. Pl. 2: 737, 776 (1876); Omlor, Gener. Rev. Marsdenieae: 153 (1998), consp.

Suffrutescent twiner, hirsute. Leaves ca. 13 cm long, ovate, cordate. Inflorescences shortly pedunculate, flowers pairwise along a very long, thickened, occasionally bifurcate rachis. Corolla rotate, blackish purple, lobes valvate, subulate, apically extended into a long tip, with trichomes; tube inflated; free staminal corona lobes obliquely oblongoid with an apical tooth, horizontally spreading; pollinia oblongoid.

One sp., *P. maingayi* Hook.f., peninsular Malaysia only.

#### 220. *Rhysolobium* E. Mey.

*Rhysolobium* E. Mey., Comm. Pl. Afr. Austr. 217 (1838); Huber, Prodr. Fl. Südwestafr. 114: 50 (1967), reg. rev.; Omlor, Gener. Rev. Marsdenieae: 85 (1998), consp.

Rigid, strongly branched dwarf shrub, to 40 cm tall; young shoots densely pubescent. Leaves subsessile, leathery-coriaceous, to 1 cm long, elliptic, obtuse, strongly revolute, adaxially glabrescent, abaxially densely pubescent. Inflorescences 1–3-flowered, (sub-)sessile. Corolla 4–5 mm long, campanulate, with long, erect trichomes on

lobes and sinuses; lobes oblong; corona absent; anther wings surpassing anther; connective appendages long; pollinia oblongoid to obovoid; caudicles straight, horizontal, short; corpusculum narrowly ellipsoid; style-head conical. Follicles 4–5 cm long, ellipsoid, with thick pericarp. Seeds 1–2 per follicle, almost circular, broadly winged.

One sp., *R. dumosum* E. Mey., in Namibia and South Africa, rocky, arid coastal winter-rainfall areas.

### 221. *Sarcolobus* R. Br.

*Sarcolobus* R. Br., *Asclepiadeae* 23 (1810); Rintz, *Blumea* 26: 65–79 (1980); Forster, *Austrobaileya* 3: 335–360 (1991), reg. rev.; Omlor, *Gener. Rev. Marsdenieae*: 132–136 (1998), consp.; McHone et al., *Phytotaxa* 197: 45–53 (2013), morph., reg. tax.

*Dorystephania* Warb. (1904).

*Quisumbingia* Merr. (1936), nom. nov. pro *Petalonema* Schltr. (1915), non *Petalonema* Berk. ex Correns (1898), (Cyanophyceae–Scytonemataceae).

Lianas or rheophytic shrubs, 0.5–5 m tall; shoots hollow, glabrescent; bark papery. Leaves 7–13 cm long, oblong, occasionally cordate, acute or retuse. Inflorescences 1–6-flowered, (sub-)sessile. Corolla 4–8 mm long, cream, green, brown or reddish, often patterned; lobes contorted, ovate, occasionally papillose or pilose; corolline corona, when present, of glabrous or hairy patches or ridges fused to corolla; free staminal corona lobes, when present, ovate to rectangular; pollinia ovoid or oblongoid; caudicles usually ribbon-shaped; corpusculum slenderly ellipsoid, equaling pollinia; style-head papillose, umbonate or semi-globose. Follicles solitary, 4–10 cm long, thick, occasionally inflated. Seeds broadly winged; coma short or missing.

About 12 spp. in India, continental SE Asia, Malesia and Australia, littoral and in mangroves.

Omlor (1998) disputed the inclusion of *Papuastelma* Bullock (*Astelma* Schltr.) in *Sarcolobus* as suggested by Forster (1991c) and transferred it to *Marsdenia*. Rintz (1980) recognized four species of *Sarcolobus*, Forster (1991c) found 11 for Australia and Papuaia alone.

### 222. *Stephanotis* Thouars

*Stephanotis* Thouars, *Gen. Nov. Madagasc.* 11 (1806); Omlor, *Gener. Rev. Marsdenieae*: 89–90 (1998), consp. *Isaura* Comm. ex Poir. (1913), nom. illegit.

Lianas, glabrous; latex translucent. Leaves car-nose, elliptic to ovate, cordate. Inflorescences few-flowered, short-pedunculate. Flowers intensely sweetly fragrant; corolla 3–4 cm long, sal-verform, car-nose; tube rose, with trichomes; lobes white, contorted, ovate, obtuse or emarginate; free staminal corona lobes shorter than gynostegium, elongate-triangular; gynostegium concealed in corolla tube; anther wings following the basal margin of the anther; pollinia ellipsoid to rectangular, caudicles straight, horizontal, shortly trapezoidal; style-head white, conical. Follicles solitary, ellipsoid, with thick pericarp, occasionally inflated. Seeds winged.  $2n = 22$ .

About five spp. in Madagascar. *Stephanotis floribunda* Brongn. (Madagascar jasmine) is a popular and economically important ornamental.

### 223. *Stigmatorhynchus* Schltr.

*Stigmatorhynchus* Schltr., *Bot. Jahrb. Syst.* 51: 141 (1913); Bruyns, *Bothalia* 25: 170–172 (1995); Omlor, *Gener. Rev. Marsdenieae*: 72 & 84–85 (1998), consp.

Rigid shrubs, 0.5–2 m tall, glabrescent or shortly pubescent; shoots lenticellate with age. Leaves subsessile; blades 1–3 cm long, ovate, obtuse. Inflorescences few-flowered, subsessile. Corolla ca. 5 mm long, slenderly campanulate, white, bearded in the tube opposite anthers; lobes contorted, oblong, obtuse; staminal corona lobes basally fused, attached along the filament tube, exceeding gynostegium (except for style-head), erect, lanceolate, basally broadened; gynostegium concealed in corolla; pollinia ovoid; caudicles geniculate, broadened at insertion of pollinium; style-head rostrate. Follicles 3.5–5 cm long, obclavate. One seed per follicle, 10–12 mm long, ovate.

Two or three spp. in Namibia, Somalia, Tanzania, savanna and semi-deserts.

### 224. *Telosma* Coville

*Telosma* Coville, *Contr. U.S. Natl. Herb.* 9: 384 (1905); Li et al., *Fl. China* 16: 237–238 (1995), reg. rev.; Omlor, *Gener. Rev. Marsdenieae*: 136–137 (1998), consp. *Prageluria* N.E. Br. (1907), nom. superfl.

Suffrutescent twiners or lianas, to 8 m tall; latex occasionally translucent. Leaves long-petiolate, 4–13 cm long, ovate, cordate. Inflorescences

15–30-flowered, pendulous. Flowers fragrant; corolla 10–20 mm long, salverform with basally urceolate tube, yellowish; throat bearded; lobes twisted, lanceolate or ovate, occasionally ciliate; free staminal corona lobes attached along the filament tube, differentiated into an erect, oblong or triangular distal lobule and a longer, inflexed, oblong to linear proximal lobule; gynostegium sessile, concealed in corolla tube; pollinia obovoid, with distal-basal sterile hyaline region; caudicles shortly rectangular; style-head conical to semi-globose. Follicles 4.5–16 cm long, occasionally winged, with thick pericarp. Seeds winged; coma yellowish.  $2n = 22$ .

Six spp. in Africa and Madagascar, widely distributed in India, S China, continental SE Asia and Malesia, open wood- and bushland.

#### 225. *Treutlera* Hook. f.

*Treutlera* Hook. f., Hooker's Icon. Pl. 15: ad t.1425 (1883); Omlor, Gener. Rev. Marsdenieae: 130–131 (1998), consp.; Watson, Fl. Bhutan 2.2: 712–713 (1999), reg. rev.

Suffrutescent twiner, glabrescent. Leaves coriaceous, 7–13 cm long, elliptic, apiculate. Inflorescences 5–7-flowered, pendulous, long-pedunculate. Corolla ca. 4 mm long, purple; lobes triangular-ovate, spreading, ciliate; free staminal corona lobes brownish, slightly shorter than gynostegium, erect, oblong; anthers rectangular; pollinia oblongoid to reniform; caudicles straight, horizontal; corpusculum oblongoid, much smaller than pollinia; style-head conical.

One sp., *T. insignis* Hook.f., in India (Sikkim), Nepal; 2000–3000 m.

#### V.3. Tribe *Ceropegieae* Orb. (1843).

Herbs, vines, stem succulents or tuberous geophytes; latex translucent, occasionally white-cloudy; roots fibrous, rarely woody; often primary roots (occasionally incl. the hypocotyl) producing tubers or carnosose secondary roots, fusiform. Leaves opposite or rarely whorled, herbaceous, but often reduced to minute caducous scales or persistent spines, occasionally absent (*Duvaliandra*, *Socotrella*, *White-sloanea*), sometimes with colleters at base of lamina (e.g., *Het-*

*erostemma*); stipules membranous or glandular, rarely reduced to few trichomes or absent. Inflorescences usually cymose. Calyx usually basally fused, rotate; flowers with fetid, carrion, dull-fruity or sweetish fragrances; corolla rotate, campanulate, cylindrical (e.g., *Ceropegia*) or urceolate (e.g., *Stapeliopsis*), occasionally with carnosose ring around mouth of tube, glabrous or sculptured with emergences and/or papillae, and/or unicellular, mostly verrucose (occasionally vibratile) trichomes; corolla usually fused between a quarter and half of its length; lobes usually valvate, sometimes remaining fused at apices; corolline corona occasionally present in sinuses of corolla lobes (e.g., *Leptadenia*); anthers erect to horizontal, rarely with connective appendage (*Caudanthera*, *Heterostemma*, *Sisyranthus*), anthers inversely T-shaped, anther wings of adjacent anthers parallel to each other forming guide rails. Interstaminal (“outer”) corona from 5 free, spreading lobes to partially or entirely fused into cup around column; staminal (“inner”) corona usually of 5 free, ascending to erect lobes, occasionally divided in distal and proximal lobules, basally often fused with adjacent interstaminal corona, rarely with a third subtending corona series (coronal skirt, *Neoschumannia*); secondary nectaries sometimes on corona lobes; pollinia erect to horizontal, nearly spherical, ellipsoid to D-shaped in outline, dorsiventrally flattened, with hyaline germination crest along proximal (mostly) to apical margin through which pollen tubes emerge, baseo-laterally attached to the caudicles; corpusculum with flanks and floor and (usually) two spreading lateral projections with caudicles attached to the lower side; style-head broad, with flattened to concave apex, white or greenish white. Follicles paired, sometimes solitary by abortion, narrowly oblong to stoutly fusiform. Seeds ovate to pyriform, usually with wing-like margin and apically attached coma.  $x = 11$ . *Ceropegieae* and *Marsdenieae* are sister groups according to molecular analyses (e.g., Meve and Liede 2004b; Rapini et al. 2007). Characteristic secondary compounds are “Asclepiadaceae bitter principles” (glycosides). 46 genera in the Paleotropics, one extending to Australia, arid temperate and tropical climates.

## KEY TO THE SUBTRIBES OF CEROPEGIEAE

1. Stems (sub-)succulent (if wiry, then at least peduncles, pedicels and roots fleshy) V.3.d. Stapeliinae
  - Stems wiry or suffrutescent to woody (roots fibrous, occasionally secondary roots slightly fleshy in Anisotominae) 2
2. Leafy twiners (Asia only: India to Papua-New Guinea); gynostegial corona of five free or connate staminal corona lobes usually divided into an inner and a spreading outer part; anthers with membranous, reniform sterile apical appendages; two follicles reaching maturity per flower V.3.a. Heterostemminae
  - Shrubs, herbs or twiners (Africa, Arabia, Asia); gynostegial corona absent or one-, two or tri-partite; staminal corona solid (rarely bilobed) anther appendage, if present, not reniform; one or two follicles reaching maturity per flower 3
3. Corolline corona lobes often present; gynostegial corona absent or a ring of fused staminal and interstaminal parts; one follicle per flower V.3.b. Leptadeniinae
  - Corolline corona lobes absent (corolla sometimes with annulus); gynostegial corona of basally fused or not staminal lobes, with or without distinct interstaminal corona lobes; two follicles reaching maturity per flower (Africa) V.3.c. Anisotominae
- Perennial herbs, twiners or shrubs, corolline corona, when present, usually not subulate, gynostegial corona present or absent 4
4. Erect shrubs or creeping subshrubs, shoots hollow; whole plant frequently densely whitish pubescent **229. *Orthanthera***
  - Herbs, shrubs or twiners, shoots not hollow; plants not densely whitish pubescent; often pitfall flowers 5
5. Inflorescences lax, paniculate; rachis filiform, tough **234. *Riocreuxia***
  - Inflorescences not lax or paniculate; rachis soft, when wiry then soft and not tough **243. *Ceropegia***
  - Plants without tubers or fleshy roots (occasionally with slightly thickened, but rather tenacious secondary roots) 6
6. Staminal corona lobes differentiated into proximal and distal parts **226. *Heterostemma***
  - Staminal corona lobes absent or simple 7
7. Corona, when present, formed of free staminal lobes; erect or prostrate herbs 8
  - Corona, when present, formed of fused staminal and interstaminal parts; shrubs, twiners or herbs 9
8. Corolla fused only at the base, white; lobes lanceolate **230. *Pentasachme***
  - Corolla fused for ca. half of its length, cream; lobes oblong or ovate **235. *Sisyranthus***
9. Gynostegial corona absent or of poorly differentiated fused staminal and interstaminal parts; shrubs or suffrutescent twiners **228. *Leptadenia***
  - Gynostegial corona of fused staminal and interstaminal parts with clearly differentiated staminal lobes; delicate herbs or twiners, shoots wiry 10

## KEY TO THE GENERA OF CEROPEGIEAE

1. Stems woody, suffrutescent or herbaceous, terete, erect to decumbent, scrambling or twining (occasionally stems carnose or (sub-)succulent, but then always with pitfall flowers); leaves usually well-developed 2
  - Stems succulent, distinctly (3-)4- to many-angled; leaves reduced to scales or spines (except for the Indian *Boucerosia frerei*), caducous or spiny 11 (*Stapeliads*)
2. Large liana; gynostegial corona in three series **233. *Neoschumannia***
  - Shrubs, herbs or twiners; gynostegial corona in one or two series, or absent 3
3. Ephemeral, erect annual herbs; corolline corona present, subulate; gynostegial corona absent **227. *Conomitra***
  - Stems with well-developed succulent leaves **240. *Boucerosia* (*B. frerei*)**
    - Stems with rudimentary leaves transformed into scales or spines, or leaves absent 12
10. Anthers apically glabrous; pollinia with proximal germination crest **232. *Emplectanthus***
  - Anthers apically with trichomes; pollinia with apical germination crest **231. *Anisotoma***
11. Stems with well-developed succulent leaves **240. *Boucerosia* (*B. frerei*)**
  - Stems with rudimentary leaves transformed into scales or spines, or leaves absent 12
12. Interstaminal corona with large, free and erect lobes 13
  - Interstaminal corona different (when lobes large and erect then fused below to form basal pouches) 14
13. Staminal corona lobes long, subulate, erect; Namibia and South Africa **270. *Tromotriche***
  - Staminal corona lobes short, triangular, inflexed; Madagascar **266. *Stapelianthus***
14. Scale-like leaves persistent, tough, becoming spiny 15

- Leaf rudiments inconspicuous, caducous or absent 18
- 15. Stems cereoid with many parallel angles, with sharp spines 16
  - Stems 4- to 5-angled, with short, rigid (occasionally sharp) spines or with inconspicuous scale-like leaves 17
- 16. Spines 3-partite (a complex of leaf scale and stipules); stems soft, 5–14-angled, 1.5–2.5 cm diam.
  - 268. *Tavaresia***
  - Spines simple; stems rather firm, at least 10-angled, 2.5–6.0(–10.0) cm diam. **249. *Hoodia***
- 17. Plants decumbent to erect; flowers small, less than 2.5 cm in diameter; inflorescences lateral **261. *Quaqua***
  - Plants prostrate-creeping; flowers very large, at least 7 cm in diameter; inflorescences basal **248. *Edithcolea***
- 18. Corolla with small projecting lobes in the sinuses of lobes (occasionally also present in *Tavaresia* and *Stapelianthus*); filament tube with humps in front of guide rail entrance **250. *Huernia***
  - Corolla lobe sinuses not tipped; filament tube without humps at entrance of guide rails 19
- 19. Stems distinctly tessellate (with transverse furrow between the leaf bases) 20
  - Stems not tessellate 26
- 20. Leaf bases irregularly arranged, polygonal, thus stems not angular; staminal corona lobes linear-spathulate 21
  - Leaf bases regularly arranged, ovate-rectangular; stems 4- to 6-angled, staminal corona lobes triangular to linear 22
- 21. Scale-like leaves orbicular; peduncle caducous; top of style-head convex, thickish **236. *Anomalluma***
  - Scale-like leaves absent or nearly so; peduncle long-lived; top of style-head flat **260. *Pseudolithos***
- 22. Scale-like leaves triangular to subulate, stems slender (to 1 cm diam.), prostrate-creeping; E Africa to Arabia **247. *Echidnopsis***
  - Scale-like leaves absent or indistinct, stems > 1 cm diam., usually erect or ascending; southern Africa 23
- 23. Corolla with simple trichomes regularly distributed over surface 24
  - Corolla glabrous or papillose or with emergences tipped with a short simple or clavate trichome 25
- 24. Stems creeping, green, 9–13 mm wide, 6–8-angled; scale-like leaves persistent, minute or absent **254. *Notechidnopsis***
  - Stems erect, blue-green, 20–25 mm wide, 8-angled; scale-like leaves forming spines to 4 mm long **263. *Richtersveldia***
- 25. Stems 10–12-angled; leaf bases flat; scale-like leaves firm, acute **252. *Lavrania***
  - Stems 12–20-angled; leaf bases conical; scale-like leaves thickish, sunken in a groove **251. *Larryleachia***
- 26. Gynostegial corona only in staminal position, interstaminal part reduced to fringe or minute flap 27
  - Gynostegial corona biseriate, interstaminal corona well-developed 30
- 27. Stems 4-angled, without scale-like leaves and stipules 28
  - Stems 4–5- (to 6-)angled, with scale-like leaves and stipular glands 29
- 28. Stems thick (10–15 mm diam.); flowers rotate; gynostegium sessile **246. *Duvaliandra***
  - Stems thin (4–7 mm diam.); flowers campanulate; gynostegium and corona atop a column **264. *Socotrella***
- 29. Stems blue-green, 3–10 mm wide; interstaminal corona conspicuous, spreading, bifid **238. *Australluma***
  - Stems green (occasionally brownish green), 8–20 mm wide; interstaminal corona inconspicuous **259. *Piaranthus***
- 30. Stems rugose and papillose 31
  - Stems not rugose or papillose 32
- 31. Scale-like leaves erect, papillate; inflorescences sunken into dented stem surface **262. *Rhytidocaulon***
  - Scale-like leaves spreading to slightly ascending, smooth; inflorescences not sunken **239. *Baynesia***
- 32. Corolla urceolate, corolla lobes at the most as long as corolla tube 33
  - Corolla usually not urceolate, corolla lobes at least as long as corolla tube 34
- 33. Stems 4-angled; translator not winged **267. *Stapeliopsis***
  - Stems 5- to many-angled; translator with wing-like projections **250. *Huernia***
- 34. Stems 4–9 mm diam., indistinctly 4-angled, creeping 35
  - Stems > 8 mm diam. (when less, then ascending to erect), 4- to 6-angled 36
- 35. Gynostegial corona glabrous, staminal corona abaxially with spreading, pectinate or warty hump **255. *Ophionella***
  - Gynostegial corona with trichomes, staminal corona lobes simple, solid, erect **257. *Orbeanthus***

36. Stems 4-, 5- or 6-angled, leaf bases bulging considerably 37  
 – Stems strictly 4-angled, leaf bases bulging only weakly 42
37. Stems 6-angled; translator without basal projections **258. *Pectinaria***  
 – Stems 4–5-angled; translator with wing-like basal projections 38
38. Stipules reduced to few multicellular trichomes **269. *Tridentea***  
 – Stipules glandular or absent 39
39. Stems 4-angled, cylindrical; scale-like leaves deltoid (occasionally absent) **270. *Tromotriche***  
 – Stems 4–5-angled, cylindrical or clavate; scale-like leaves triangular to subulate 40
40. Filament tube with a little hump in front of entrance of nectarial orifices **250. *Huernia***  
 – Filament tube without a hump 41
41. Guide rails oblique, embedded in gynostegial tissue **245. *Duvalia***  
 – Guide rails vertical, not embedded in gynostegial tissue **256. *Orbea***
42. Stems unbranched, leafless, short and clumpy, cuboid to ovoid; inflorescences along (basal) angles of stem **271. *White-sloanea***  
 – Stems branched, usually with scale-like leaves, less clumpy; inflorescences terminal or on upper half of stem 43
43. Inflorescences pedunculate, mostly arising basally; flowers large, rotate to campanulate; pollinaria large, translator with wing-like basal projections 44  
 – Inflorescences sessile, arising from apical regions of the stems, lateral or terminal, often many-flowered clusters (sciadioids); flowers rather small, of various shapes; pollinaria small, translator without basal projections 45
44. Stems with pungent scent; scale-like leaves ciliate, with tufts of (stipular) glandular trichomes, or when stems not pungent leaf bases grooved on upper side and without stipular trichomes **253. *Monolluma***  
 – Stems not with pungent scent; leaf bases not grooved; scale-like leaves ascending-erect, not ciliate but occasionally pubescent, stipules glandular, globose **265. *Stapelia***
45. Inflorescences in terminal sciadioids 46  
 – Inflorescences not in terminal sciadioids 47
46. Scale-like leaves (broadly) lanceolate, ciliate, stipules absent **240. *Boucerosia***  
 – Scale-like leaves absent or minute, suborbicular, cordate to lanceolate, rarely ciliate (rarely acute and persistently spiny as in *Desmidorchis foetida* and *D. speciosa*), with scattered (stipular) glandular trichomes **244. *Desmidorchis***
47. Stipular glands present 48  
 – Stipular glands absent, usually with (tufts of) stipular trichomes instead 49
48. Scale-like leaves 0.5–2 mm long; stems not tapering **238. *Australluma***  
 – Scale-like leaves 4–12 mm long; stems tapering **242. *Caudanthera***
49. Scale-like leaves subsessile to petiolate, with isolated stipular trichomes only **237. *Apteranthes***  
 – Scale-like leaves sessile, stipules reduced to tufts of stipular trichomes **241. *Caralluma***
- V.3.a. **Subtribe Heterostemminae** Meve & Liede (2004).
- Leafy twiners, stems wiry or suffrutescent to woody, latex white or translucent, roots fibrous, gynostegial corona of five free or basally connate staminal corona lobes usually differentiated into a proximal and a spreading to erect distal lobule; anthers with membranous, reniform sterile apical appendages; corpusculum without basal projections; two follicles reaching maturity per flower. Meve and Liede (2004b) and Meve et al. (2017) retrieved Heterostemminae as sister to the remaining Ceropegieae. One genus, India to Australasia.
226. ***Heterostemma*** Wight & Arn.
- Heterostemma* Wight & Arn. in Wight, Contr. Bot. India 42 (1834); Forster, Austral. Syst. Bot. 5: 71–80 (1992), reg. rev.; Swarupanandan et al., Bot. J. Linn. Soc. 191: 249–259 (1989), rev.; Jagtap & Singh, Fasc. Fl. India 24: 244–258 (1999), reg. rev.; Rodda, Phytotaxa 263: 1–17 (2016), nom. *Symphysocarpus* Hassk. (1857).  
*Oianthus* Benth. (1876).  
*Dittoceras* Hook. f. (1883).
- Herbaceous to suffrutescent twiners, 1–5 m long; shoots occasionally with trichomes in two lines. Leaves ovate, indistinctly cordate, basally with colleters. Inflorescences pedunculate. Corolla 8–10 mm long, rotate, campanulate or urceolate, yellowish or purple, occasionally maculate, occasionally with carnose ring; lobes triangular; gynostegial corona yellow to green, distal lobules of staminal parts oblongoid, basally often spurred or winged; proximal lobules inflexed, lingulate or dentiform; pollinia ellipsoid, germination crest subapical; caudicles straight or geniculate,



cylindrical to spatulate. Follicles rarely fused, 5–15 cm long, fusiform to narrowly oblong. Seeds broadly winged.  $2n = 22$ .

About 30 spp. in Asia and Australia, one in New Caledonia, wet and evergreen forests.

V.3.b. **Subtribe Leptadeniinae** Meve & Liede (2004); Meve et al., *Syst. Biodivers.* 15: 143–155 (2017).

Shrubs, herbs or twiners, stems wiry or suffrutescent to woody, roots fibrous; corolline corona lobes often present; gynostegial corona absent or a ring of fused staminal and interstaminal parts; pollinia basally or laterally attached to the caudicles; germination crest (sub-)apical. Follicles usually solitary, fusiform or narrowly oblong. Seeds ovate or oblong.

Four genera in Africa, Arabia and Asia.

## 227. *Conomitra* Fenzl

*Conomitra* Fenzl in Endlicher & Fenzl, *Nov. Stirp. Dec.* 65 (1839); Field, *Kew Bull.* 37: 341–347 (1982); Goyder, *Fl. Ethiopia and Eritrea* 4.1: 156–157 (2003), reg. rev.; Goyder, *Fl. Somalia* 3: 168 (2006), reg. rev.

Ephemeral, erect herb, 6–35 cm tall, unbranched; shoots papillose. Leaves 1–7 cm long, linear, papillose on midrib and toward margins. Inflorescences 1-flowered, subsessile. Calyx reaching about half of corolla length, campanulate, ciliate; corolla 2–3 mm long, campanulate, green; lobes triangular, extended into a long tip; corolline corona shorter than corolla; lobes antesealous, basally connate, subulate; gynostegial corona absent; gynostegium sessile; connective appendages minute, subulate, erect; pollinia ovoid; caudicles trapezoidal; style-head elongate-conical. Follicles occasionally paired, 5–6 cm long.

One sp., *C. linearis* Fenzl, widespread across the Sahel (Ethiopia, Kenya, Niger, Somalia, Sudan), but rarely collected, ephemeral in *Acacia-Commiphora* bushland; 200–900 m.

## 228. *Leptadenia* R. Br.

*Leptadenia* R. Br., *Asclepiadeae* 23 (1810); Jagtap & Singh, *Fasc. Fl. India* 24: 258–262 (1999), reg. rev.; Chaudhary, *Fl. Kingd. Saudi Arabia* 2.2: 41–42 (2001), reg. rev.; Goyder, *Fl. Ethiopia and Eritrea* 4.1: 155–156 (2003), reg. rev.; Goyder, *Fl. Somalia* 3: 166–168 (2006), reg. rev.; Masrahi, *Saudi J. Biol. Sci.* 22: 31–36 (2015), new taxon; Meve et al., *Syst. Biodivers.* 15: 143–155 (2017), phyl.

Shrubs or suffrutescent twiners, 0.3–2(–5) m tall, glabrous to pubescent; shoots often suberose or finely striate. Leaves occasionally caducous and scale-like, 0.5–10 cm long, elliptic, lanceolate, ovate or hastiform; stipules filiform. Inflorescences 10–20-flowered; flowers sweetly fragrant. Corolla 3–4 mm long, rotate, creamish, with erect, verrucose trichomes, with ridges or five hairy pouches; lobes lanceolate, spreading, ciliate; corolline corona five free, short, creamish, deltoid lobes, dorsally adnate to anthers; gynostegial corona absent or annular, ivory; gynostegium sessile; connective appendages absent; pollinia ovoid; caudicles curved, trapezoidal. Follicles pendulous, 5–11 cm long.  $2n = 22$ .

Six spp. in Africa, Arabia and Asia, (semi-) arid areas, *Acacia-Commiphora* bushland, dry forests.

## 229. *Orphanthera* Wight

*Orphanthera* Wight, *Contr. Bot. India* 48 (1834); Huber, *Prodr. Fl. Südwestaf.* 114: 46–47 (1967), reg. rev.; Jagtap & Singh, *Fasc. Fl. India* 24: 263–265 (1999), reg. rev. *Barrowia* Decne. (1844).

Erect shrubs or creeping subshrubs, 20–150 cm tall, whitish pubescent to tomentose; shoots hollow, greenish. Leaves occasionally caducous, scale-like or absent, 0.1–2 cm long, linear, oblong or ovate, acute; stipules filiform. Inflorescences 3–10-flowered. Corolla 5–15 mm long, tubular, whitish or greenish, glabrous; lobes lanceolate, spreading to erect; corolline corona, when present, short, five-partite, adnate to corolla; lobes free, antepetalous, oblongoid, erect; gynostegial corona a ring of deltoid, erect to spreading staminal and fringe-like interstaminal parts, carnose; gynostegium concealed in corolla; connective appendages, when present, short; pollinia ellipsoid; caudicles horizontal and S-shaped. Follicles 5–12 cm long.  $2n = 22$ .

Five spp. in Africa and Asia. *O. albida* Schinz is moth-pollinated (Nel 1995).

## 230. *Pentasachme* Wall. ex Wight

*Pentasachme* Wall. ex Wight, *Contr. Bot. India* 60 (1834); Rahman & Wilcock, *Blumea* 36: 109–121 (1991), reg. rev.; Jagtap & Singh, *Fasc. Fl. India* 24: 265–268 (1999), reg. rev. *Spiladocorys* Ridl. (1893). *Vietnamia* P.T. Li (1994).

Erect or prostrate rheophytic herbs, occasionally pendent, 10–70 cm tall. Leaves 6–13 cm long, linear to ovate, acuminate, occasionally ciliate. Inflorescences 1–5-flowered. Corolla 5–30 mm long, campanulate, white, forming bulges at sinuses; lobes contorted, lanceolate; corolline corona, when present, inserted in the tube; lobes free, short, antesealous, subulate, corniculate or knobby, erect; gynostegial corona, when present, of short, lanceolate free staminal lobes; gynostegium subsessile or atop a column; anthers occasionally gibbous, erect; connective appendages lanceolate or deltate, strongly inflexed; pollinia ellipsoid, obovoid or pyriform; caudicles S-shaped, trapezoidal. Follicles 5–6 cm long.

Five spp. in S Asia, continental SE Asia and W Malesia. Reminiscent of non-twining *Vincetoxicum* Wolf in habit.

V.3.c. **Subtribe Anisotominae** Meve & Liede (2004); Meve et al., Syst. Biodivers. 15: 143–155 (2017).

Shrubs, herbs or twiners, stems wiry or suffrutescent to woody, roots fibrous or secondary roots slightly carnos; corolline corona lobes absent (corolla sometimes with ring); gynostegial corona of staminal lobes, basally fused or free, with or without distinct interstaminal corona lobes; connective appendages usually absent; pollinia usually ovoid; corpusculum usually without basal projections. Follicles usually paired, fusiform or narrowly oblong. Seeds ovate or oblong. Five genera in Africa.

### 231. *Anisotoma* Fenzl

*Anisotoma* Fenzl, Linnaea 17: 330 (1844); Meve et al., Syst. Biodivers. 15: 143–155 (2017), phyl., new taxon.  
*Anisotomaria* C. Presl (1844), nom. illegit.  
*Lophostephus* Harv. (1863), nom. illegit.  
*Aulostephanus* Schltr. (1896).

Creeping or erect herbs; with fleshy lateral roots; shoots wiry, pilose in single line. Leaves 1–5 cm long, ovate to circular, cordate, pilose. Inflorescences 2–10-flowered; floral bracts conspicuous. Corolla 3–5 mm long, rotate, yellow, cream with brown center or vice versa, glabrous or pilose; lobes sinistrorsely contorted, triangular; gynostegial corona ivory, campanulate, of inconspicuous ovoid-rectangular, erect staminal parts or of long,

erect, filiform adaxial appendages and interstaminal parts basally fused into a ring; gynostegium subsessile, anthers thickish, apically with trichomes; pollinium germination crest apical; caudicles cylindrical. Follicles 8–10 cm long.

Three spp. in South Africa.

### 232. *Emplectanthus* N.E. Br.

*Emplectanthus* N.E. Br. in Thiselton-Dyer, Fl. Cap. 4(1): 771 (1908); Meve, Bot. Jahrb. Syst. 120: 123–130 (1998), rev.; Styles, Plantlife 39&40: 24–32 (2010), new taxon; Meve et al., Syst. Biodivers. 15: 143–155 (2017), phyl.

Delicate, suffrutescent twiners to 1–2(–4) m tall, sparsely branched, with fleshy lateral roots; shoots wiry, with stiff trichomes in a single line. Leaves horizontally spreading, 5–9 cm long, ovate, cordate; stipules filiform. Inflorescences 3–10-flowered, lax. Corolla 2.5–3.5 mm long, shallowly campanulate, membranous, purple or creamish, spotted pinkish; mouth of tube with ring of trichomes; lobes contorted, triangular, acuminate; gynostegial corona brownish, shallowly cyathiform, of deltate, spatulate or strap-like, erect, long staminal parts and saccate, rarely bilobed, spreading to reflexed interstaminal parts basally fused into a ring; pollinia occasionally D-shaped; caudicles cylindrical. Follicles solitary, 4–7 cm long.  $2n = 22$ .

Three spp. in South Africa, gorges, riverine woodlands.

### 233. *Neoschumannia* Schltr.

*Neoschumannia* Schltr., Bot. Jahrb. Syst. 38: 38 (1905); Meve, Pl. Syst. Evol. 197: 233–242 (1995), rev.; Meve & Liede, Taxon 53: 61–72 (2004), phyl.; Fischer et al., Phytotaxa 77 (2): 19–26 (2013), new taxon.  
*Swynnertonia* S. Moore (1908).

Lianas, 2–10 m long, roots fibrous. Leaves discolorous, 5–15 cm long, (oblong-)elliptic, acuminate; stipules glandular, ovoid. Inflorescences 3–5-flowered, lax, pedunculate; rachis persistent, thick; flowers nodding from long filiform pedicels, not nectariferous. Corolla 15–20 mm long, apopetalous, membranous, cream with purplish tips or green; tube with clavate, purple trichomes; lobes lanceolate, spreading, occasionally ciliate; gynostegial corona ivory or green, in three series: a basally fused ring of staminal and interstaminal parts extended into a 5-lobed, glabrous skirt; free

staminal lobes oblong(-obovate), occasionally bifid, erect, with trichomes; interstaminal lobes unguiculate, spreading-ascending, canaliculate, apically bidentate, with trichomes; gynostegium atop a column; caudicles rectangular. Follicles pendulous, 25–35 cm long.  $2n = 22$ .

Three spp., one each in W, C and E Africa, evergreen forests.

#### 234. *Riocreuxia* Decne.

*Riocreuxia* Decne., Prodr. 8: 640 (1844); Dyer, Fl. Southern Afr. 27.4: 83–88 (1980), reg. rev.; Masinde, Kew Bull. 60: 401–434 (2005), rev.; Meve et al., Syst. Biodivers. 15: 143–155 (2017), phyl.

Erect or twining herbs, 1–3 m tall; rootstock woody or roots slightly fusiform; shoots puberulous. Leaves 1.5–10 cm long, elliptic or ovate, cordate; stipules as pilose interpetiolar line. Inflorescences 10–40-flowered, lax, pedunculate. Corolla 10–30 mm long, elongate-conical (pitfall flower), rarely campanulate, (whitish) green or (orange-)yellow, occasionally streaked white; lobes linear or lanceolate, usually remaining connate at apices, smooth; gynostegial corona of free or basally fused staminal lobes, ivory, erect, ovate, basally with wings fused to interstaminal projections; gynostegium subsessile, concealed in corolla; anther wings basally forming a distinct mouth; pollinia rarely D-shaped. Follicles pendulous, 8–17(–35) cm long, occasionally moniliform.  $2n = 22$ .

Eight spp. in E and SE Africa.

#### 235. *Sisyranthus* E. Mey.

*Sisyranthus* E. Mey., Comm. Pl. Afr. Austr. 197 (1838); Ollerton et al., Ann. Bot. 92: 807–834 (2003), ecol.

Erect, perennial herbs to 25 cm tall, sparsely branched, occasionally densely pubescent; roots thinly fusiform. Leaves linear. Inflorescences terminal or extra-axillary, 2–20-flowered, lax. Corolla 4–10 mm long, campanulate or urceolate, cream, occasionally barbate, occasionally with five adaxial ridges; lobes valvate or imbricate, oblong or ovate, spreading; gynostegial corona of free staminal lobes, adnate to both corolla and gynostegium, carnosely, ovoid, occasionally emarginate, basally broadened; gynostegium ses-

sile, concealed in corolla; anthers apically occasionally bearded or with a few trichomes; connective appendages, when present, oblong, erect, occasionally with a few hairs. Follicles horizontal, 7–9 cm long. Seeds occasionally elliptical.  $2n = 22$ .

13 spp. in South Africa. *S. trichostomus* K. Schum. pollinated by Coleoptera (Ollerton et al. 2003).

#### V.3.d. Subtribe Stapeliinae G. Don (1837).

Stems (sub-)succulent (when wiry, then at least peduncles, pedicels and roots carnosely), mostly glabrous. Leaves often reduced to sessile, caducous scales; often supported by expanded leaf bases (podaria). Inflorescences usually (sub-)sessile. Corolla usually rotate to campanulate, often carnosely, rugose or papillose. Corolla lobes usually spreading to reflexed; gynostegial corona usually carnosely, rotate or cyathiform; pollinia ovoid-ellipsoid or D-shaped, corpusculum usually with two basal projections. Follicles usually paired, narrowly oblong. Seeds ovate or pyriform. Fly pollinated. In a molecular analysis (Meve and Liede 2004b), Stapeliinae were sister to Anisotominae. 36 genera in arid areas of Africa, Arabia and Asia.

#### 236. *Anomalluma* Plowes

*Anomalluma* Plowes, Cact. Succ. J. (Los Angeles) 65: 167 (1993); Meve & Liede, Pl. Syst. Evol. 234: 172–209 (2002), rev.

Clump-forming stem succulents to 5 cm tall, often with subterranean shoots, pale green, 10–60 cm long, 4–10 mm wide, sharply 4-angled, irregularly tuberculate or tessellate. Scale-like leaves suborbicular, stipules absent. Inflorescences one to several, apical, 3-flowered, peduncles and pedicels deciduous; flowers with sourish odor. Corolla 3–4 mm long, maroon; lobes triangular; gynostegial corona purplish, of lingulate, inflexed staminal parts and reflexed, bilobed interstaminal parts basally fused into a ring; pollinia D-shaped; caudicles medifixed to the corpusculum. Follicles occasionally solitary, 2–4 cm long, seeds with thick, puffed wing.  $2n = 22$ .

Two spp. in Somalia and Oman.

237. *Apteranthes* J.C. Mikan

*Apteranthes* J.C. Mikan, Nova Acta Acad. Caes. Leop.-Carol. Nat. 17: 594, t. 41. (1835); Plowes, Haseltonia 3: 63 (1995), rev.; Meve & Liede, Pl. Syst. Evol. 234: 172–209 (2002), phyl.; Meve & Heneidak, Bot. J. Linn. Soc. 149: 419–432 (2005), chem.; Formisano et al., Molecules 14: 4597–4613 (2009), chem. ecol., poll.  
*Borealluma* Plowes (1995).

Clump-forming or creeping stem succulents to 40 cm tall; usually rhizomatous; shoots (blue)-green, 5–70 cm long, 10–25 mm wide, 4-angled. Scale-like leaves reflexed or slightly ascending, basally cordate, apically obtuse; stipules absent. Inflorescences apical, 3–15-flowered; flowers usually fetid. Corolla 6–16 mm long, creamish or purple, often patterned, glabrous, papillose or hirsute; lobes lanceolate or triangular; gynostegial corona yellow or purplish red, of inflexed, subulate or triangular staminal parts and subulate or bilobed interstaminal parts shortly fused into a ring; gynostegium sessile; pollinia D-shaped; caudicles spatulate. Follicles 50–130 mm long.  $2n = 22$ .

Six spp. in Africa, Arabia (incl. Sinai), Europe and Asia.

238. *Australluma* Plowes

*Australluma* Plowes, Haseltonia 3: 54 (1995); Bruyns, Excelsa 10: 107–111 (1982), morph.; Bruyns, Stapeliads of S. Afr. Madag. 1: 61–65 (2005), rev.

Erect stem succulents to 30 cm tall, rhizomatous; shoots often annual, blue-green, 20–30 cm long, 3–5 mm wide, with 4 rounded angles. Scale-like leaves ascending, ovate; stipules glandular, ovate. Inflorescences several along stems, 1–2-flowered; flowers unscented. Corolla 4–6 mm long, adaxially greenish, purple-maculate, with verrucose trichomes; lobes triangular; gynostegial corona brownish, of trianguloid, spreading, apically reflexed, emarginate staminal parts with inflexed subulate-triangular tooth-like projection and interstaminal parts basally fused into a ring; gynostegium sessile; pollinia broadly ellipsoid, germination crest apical; caudicles rectangular. Follicles obtuse-angled.  $2n = 22$ .

Two spp., one in Namibia (summer rainfall areas), and one in South Africa.

239. *Baynesia* Bruyns

*Baynesia* Bruyns, Novon 10: 354–358 (2000); Bruyns, Stapeliads of S. Afr. Madag. 1: 66–67 (2005), consp.; Bruyns et al., Mol. Phyl. Evol. 77: 251–263 (2014), phyl.

Creeping stem succulent, 5 cm tall; shoots blue-green, 3–8 cm long, 6–12 mm wide, with 4 rounded angles, papillose. Scale-like leaves persistent, slightly ascending, succulent, ovate; occasionally with stipules. Inflorescences along stems, 1–3(–5)-flowered, corolla 3–4 mm long, reddish(-maroon) with cream center; lobes ovate, acute, keeled; gynostegial corona cream, of ovoid, basally winged, apically inflexed staminal parts longer and thicker than the deltoid-triangular, spreading, purplish interstaminal parts, basally fused into a ring; pollinia ellipsoid; caudicles flattened. Follicles 2.5–3.5 cm long.  $2n = 22$ .

One sp., *B. lophophora* Bruyns, in N Namibia (Baynes Mountains). *Baynesia* was retrieved as sister to the similarly small-stemmed Cape Stapeliad *Ophionella* (Bruyns et al. 2014).

240. *Boucerosia* Wight & Arn.

*Boucerosia* Wight & Arn. in Wight, Contr. Bot. India 34 (1834); Meve & Liede, Pl. Syst. Evol. 234(3&4): 172–209 (2002), phyl. & tax.

*Hutchinia* Wight & Arn. (1834).

*Frerea* Dalz. (1864).

Clump-forming or creeping stem succulents, 2–12 cm tall; shoots green, 3–20 cm long, 3–20 mm wide, 4-angled, smooth. Leaves as succulent scales to 0.3 cm long or with well-developed blades, 2–3 cm long, oblong, ciliate; stipules absent or glandular-ovoid. Inflorescences terminal, (1–)3–60-flowered; flowers fetid, not nectariferous. Corolla 5–15 mm long, whitish to yellowish, often banded brownish, glabrous, papillose or with trichomes; lobes triangular, occasionally ciliate; gynostegial corona purplish red, occasionally campanulate, of triangular or rectangular, inflexed staminal parts and ascending, bilobulate interstaminal parts fused into a ring for more than half of total length; gynostegium sessile; pollinia D-shaped; caudicles spatulate. Follicles 6.5–10(15) cm long.  $2n = 22$ , 44.

Seven spp. in India, Sri Lanka, Nepal and Myanmar.

The inclusion of the sole Stapeliad bearing true leaves, *Boucerosia frerei* (G.D. Rowley) Meve & Liede (= *Frerea indica* Dalzell), is not always accepted.

#### 241. *Caralluma* R. Br.

*Caralluma* R. Br., Asclepiadeae 14 (1810); Gilbert, *Bradleya* 8: 1–32 (1990), rev.; Plowes, *Haseltonia* 3: 49–70 (1995); Meve & Liede, *Pl. Syst. Evol.* 234: 171–209 (2002), phyl.; Lavranos, *Fl. Somalia* 3: 174–178 (2006), reg. rev.; Bruyns et al., *Taxon* 59: 2031–1043 (2010), phyl. *Spathulopetalum* Chiov. (1912). *Saurolluma* Plowes (1995). *Somalluma* Plowes (1995).

Erect stem succulents, 10–70 cm tall; shoots (light) green, blue-green or light brown, 10–70 cm long, 5–25 mm wide, 4-angled. Scale-like leaves ovate; stipules reduced to a few trichomes. Inflorescences along tapering stems, 1–4-flowered. Corolla 5–15 mm long, occasionally apetalous, white, green, brown or purple, occasionally patterned; lobes linear, lanceolate or obovate (often replicate along midrib), rarely apically connate, often ciliate; gynostegial corona membranous, brownish or purplish red, of ovoid or trianguloid, erect or inflexed staminal parts and subulate to deltoid, often bilobed interstaminal parts fused into a ring; gynostegium often atop a column. Follicles 8–15 cm long.  $2n = 22$ .

23 spp. in Africa, Arabia and Asia.

#### 242. *Caudanthera* Plowes

*Caudanthera* Plowes, *Haseltonia* 3: 58 (1995); Meve & Liede, *Pl. Syst. Evol.* 234: 171–209 (2002), phyl.; Meve & Heneidak, *Bot. J. Linn. Soc.* 149: 419–432 (2005), chem. *Cryptolluma* Plowes (1995). *Spiralluma* Plowes (1995).

Erect stem succulents, 10–60 cm tall; occasionally rhizomatous; shoots blue-green, 5–30 cm long, 5–10 mm wide, with 4 rounded angles. Scale-like leaves slightly ascending, ovate, acute; stipules glandular, ovate. Inflorescences along tapering stems, 1–5-flowered. Corolla 4–8 mm long, creamish, occasionally with red spots and trichomes; lobes lanceolate, acute; gynostegial corona yellowish, of subulate or triangular staminal parts and saccate, deltoid or bilobed

interstaminal parts fused into a ring; gynostegium occasionally atop a column; occasionally with lanceolate, long, erect connective appendages; pollinia with proximal to apical germination crest; caudicles ribbon-shaped; corpusculum without basal projections. Follicles 5–6 cm long.  $2n = 22$ .

Three spp. in Africa, Arabia (incl. Sinai) and Asia.

#### 243. *Ceropegia* L.

Fig. 50

*Ceropegia* L., *Sp. Pl.* 211 (1753); Huber, *Mem. Soc. Brot.* 12: 1–203 (1957); Dyer, *Fl. South. Afr.* 27.4: 1–82 (1980), reg. rev.; Ansari, *Fasc. Fl. India* 16 (1984), reg. rev.; Jagtap & Singh, *Fasc. Fl. India* 24: 178–190 (1999), reg. rev.; Meve, *Fl. Kingd. Saudi Arabia* 2.2: 42–48 (2001), reg. rev.; Meve & Liede, *Pl. Syst. Evol.* 228: 89–105 (2001), phyl.; Meve, *III. Handb. Succ. Pl.*: 20–46, 63–107 (2002), rev.; Gilbert, *Fl. Ethiopia and Eritrea* 4.1: 158–169 (2003), reg. rev.; Gilbert, *Fl. Somalia* 3: 168–173 (2006), reg. rev.; de Kock, *Checklist Brachystelma, Ceropegia & Stapeliads*: 83–113 (2007), checkl.; Meve & Liede-Schumann, *Ann. Missouri Bot. Gard.* 94: 392–406 (2007), phyl.; Masinde, *Kew Bull.* 62: 37–84 (2007), reg. rev., phyl.; Surveswaran et al., *Pl. Syst. Evol.* 281: 51–63 (2009), phyl.; Bruyns et al., *Mol. Phyl. Evol.* 90: 49–66 (2015), phyl.

*Niota* Adans. (1763), nom. illegit.

*Apegia* Necker (1790), nom. inval.

*Microstemma* R. Br. (1810), nom. rej. vs. *Brachystelma* Sims (1822).

*Brachystelma* Sims (1822).

*Tenaris* E. Mey. (1838).

*Eriopetalum* Wight (1843).

*Macropetalum* Burch. ex Decne. (1844).

*Dichaelia* Harv. (1868).

*Micraster* Harv. (1868).

*Lasiostelma* Benth. (1876).

*Tapeinostelma* Schltr. (1893).

*Brachystelmaria* Schltr. (1895).

*Blepharlanthera* Schltr. (1913).

*Kinepetalum* Schltr. (1913).

*Siphonostelma* Schltr. (1913).

Herbs, lianas or stem succulents, up to 10 m tall; roots often tuberous or fleshy fusiform; shoots 1.5–12 mm wide, terete or 4–(rarely 6)-angled. Leaves occasionally scale-like, linear to ovate, with stipules; inflorescences to 25-flowered, occasionally pedunculate; flowers often with dull-fruity odor or malodorous. Corolla 3–100 mm long, elongate-conical, with basal inflation (ostium), tube usually bent and constricted in the middle, highly fused, lobes usually remaining connate at apices, often keeled and with trichomes (lantern-shaped pitfall flower), or radiate

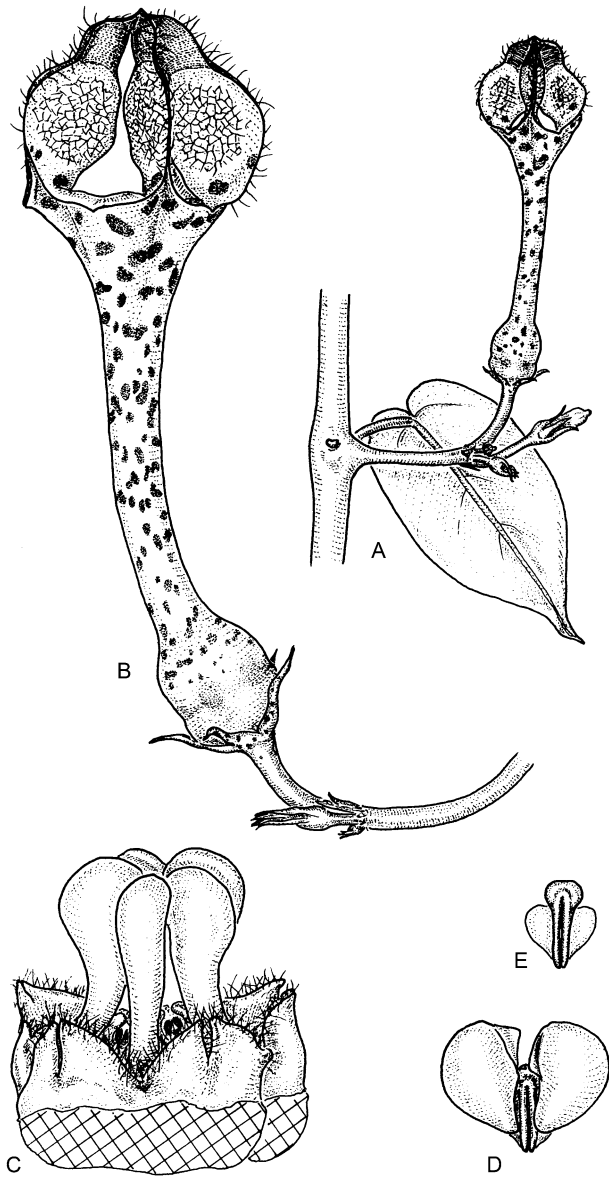


Fig. 50. Apocynaceae-Ceropegieae. *Ceropogia zambesiaca*. A Flowering branch (one leaf removed). B Flower in lateral view. C Corona in lateral view. D Pollinarium. E Corpuscle with lateral projections. (From Masinde and Meve 2002, p. 207, with permission from Kew Bulletin © Board of Trustees of the Royal Bot. Gard., Kew; drawn by U. Meve)

with lobes reflexed, spreading or connate at apices (*Brachystelma* flower type), occasionally urceolate; variably colored and patterned; gynostegial corona of lingulate, ovoid, deltoid, subulate to filiform staminal parts and occasionally reduced deltoid to subulate, often bilobed, spreading interstaminal parts fused into a ring; gynoste-

gium occasionally atop a column; pollinia subquadrate, globose, ovoid or pyriform. Follicles 3–40 cm long, occasionally obclavate.  $2n = 22, 44$ .

About 330 spp. in Africa, Arabia, Asia and Australia. Horticulturally one of the most popular Asclepiad genera. Tubers occasionally and locally eaten.

*Ceropogia* has been found to be paraphyletic without *Brachystelma* and without the Stapeliads (Meve and Liede-Schumann 2007; Surveswaran et al. 2009; Bruyns et al. 2015). While the inclusion of *Brachystelma* seems to be justified, considering growth form/habit and the multiple switches between pitfall and open flowers, the suggestion by Bruyns et al. (2017) to include all Stapeliinae in *Ceropogia* is not followed here.

#### 244. *Desmidorchis* Ehrenb.

*Desmidorchis* Ehrenb., Abh. Königl. Akad. Wiss. Berlin 1829: 31, 39 (1832); Lavranos, Fl. Kingd. Saudi Arabia 2.2: 50–53 (2001), reg. rev.; Meve & Liede, Pl. Syst. Evol. 234: 171–209 (2002), phyl.  
*Sarcocodon* N.E. Br. (1878).  
*Crenulluma* Plowes (1995).

Erect or clump-forming stem succulents to 1.2 m tall; shoots light (blue-)green or brown, 20–80 cm long, 10–50 mm wide, sharply 4-angled, smooth. Scale-like leaves spreading, carnosely or forming spines, ovate; stipules reduced to a few trichomes. Inflorescences terminal, 10–80(–200)-flowered; flowers with dung-like odor, not nectariferous. Calyx aposepalous; corolla 1.5–3 cm long, yellowish or purplish, often maculate, often sculptured or with trichomes; lobes triangular, occasionally ciliate; gynostegial corona a ring of triangular to subulate, inflexed staminal parts and subulate, bifid, spreading, interstaminal parts, occasionally with trichomes; gynostegium (sub-)sessile, concealed in corolla; caudicles rectangular. Follicles 10–15 cm long.  $2n = 22$ .

15 spp. in N and E Africa and Arabia.

The genus as circumscribed by Meve and Liede (2002a) is not generally accepted, leading Bruyns (2010) to describe a new species under *Caralluma*.

#### 245. *Duvalia* Haw.

*Duvalia* Haw., Syn. Pl. Succ. 44 (1812); Meve, Pl. Syst. Evol. Suppl. 10: 1–133 (1997), rev.; Bruyns, Stapeliads of S.

Afr. Madag. 1: 68–91 (2005), reg. rev.; Lavranos, Fl. Somalia 3: 191–193 (2006), reg. rev.  
*Ballyanthus* Bruyns (2001).

Creeping stem succulents, 2–4 cm tall; shoots (blue-)green, occasionally spotted, conical or club-shaped, 1–10 cm long, 10–25 mm wide, with 4–6 rounded angles. Scale-like leaves succulent, deltoid to subulate; stipules glandular, globose. Inflorescences usually basal, 1–20-flowered, occasionally pedunculate; flowers often fetid, not nectariferous. Corolla 5–25 mm long, cream, yellow or reddish brown, occasionally patterned, occasionally papillose, with central, often trichome-bearing ring; lobes triangular, replicate along midrib; gynostegial corona a flattened ring of staminal and interstaminal parts covering the ring, and free oblongoid, cucullate or subulate staminal lobes with tooth-like projection incumbent on anther; gynostegium atop a column; caudicles spathulate; basal projections of corpusculum wing-like. Follicles 6–18 cm long.  $2n = 22$ , 44 or 66.

17 spp. in two sections; S and NE Africa and SW Arabia.

#### 246. *Duvaliandra* M.G. Gilbert

*Duvaliandra* M.G. Gilbert, Cact. Succ. J. Gr. Brit. 42: 101 (1980); Meve & Liede, Pl. Syst. Evol. 234: 171–209 (2002), phyl.

Clump-forming stem succulent, to 6 cm tall; shoots light greenish brown, 2–10 cm long, 10–15 mm wide, roundly 4-angled. Leaves absent. Inflorescences on flanks of lower half of stems, 1–5-flowered, sessile; flowers with carrion odor. Corolla 9–28 mm long, pale yellow-green or light brown, adaxially rose or reddish, with purple-brown trichomes; lobes ovate, spreading; gynostegial corona of basally fused staminal lobes, rose, very fleshy, lingulate, inflexed; pollinia ovoid, caudicles spathulate; corpusculum nearly the same size as pollinia, with elongated-triangular basal projections; style-head greenish white, cylindrical. Follicles 3–6 cm long.  $2n = 22$ .

One sp., *D. dioscorides* (Lavranos) M.G. Gilbert, endemic to Socotra (Yemen).

#### 247. *Echidnopsis* Hook. f.

Fig. 51

*Echidnopsis* Hook. f., Bot. Mag.: ad t. 5930 (1871); Bruyns, Bradleya 6: 1–48 (1988), rev.; Thiv & Meve, Pl. Syst. Evol. 265: 71–88 (2007), phyl., tax.  
*Virchowia* Vatke ex K. Schum. (1893), non *Virchowia* A. Schenk 1852, Scrophulariaceae.  
*Pseudopectinaria* Lavranos (1971).

Creeping stem succulents, to 10 cm tall, rarely rhizomatous; shoots green, 1–10 cm long, 8–25 mm wide, roundly 5–20-angled, papillose or tessellate. Scale-like leaves lanceolate to trianguloid; stipules globose. Inflorescences apical, 1–6-flowered. Corolla 2–10 mm long, occasionally subglobose or tubular, highly fused, creamish to purplish, occasionally maculate, occasionally with trichomes; lobes lanceolate or triangular; gynostegial corona occasionally with trichomes, occasionally subglobose, of triangular to subulate staminal parts and spur-shaped or saccate

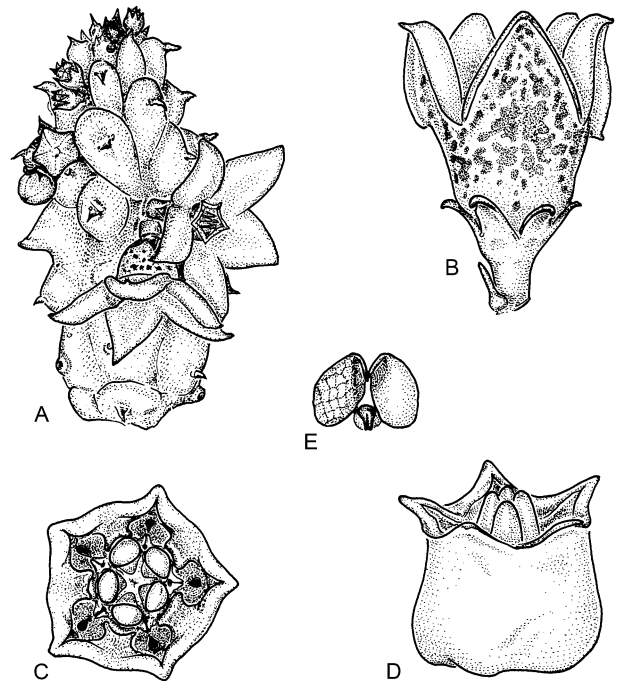


Fig. 51. Apocynaceae-Ceropegieae. *Echidnopsis bentii*. A Flowering branch. B Flower in lateral view. C Corona in top view. D Corona in lateral view. E Pollinarium. (From Meve and Wolf 2001, p. 117, with permission from Kakteen und andere Sukkulentent; drawn by U. Meve)

interstaminal parts almost completely fused into a ring; gynostegium sessile; caudicles trapezoidal. Follicles 6–10 cm long.  $2n = 22, 44$ .

About 30 spp. in Africa and Arabia.

248. *Edithcolea* N.E. Br.

*Edithcolea* N.E. Br., Bull. Misc. Inform. Kew 1895: 220 (1895); Gilbert, Fl. Ethiopia and Eritrea 4.1: 184–185 (2003), reg. rev.; Lavranos, Fl. Somalia 3: 184–185 (2006), reg. rev.; Bruyns et al., Taxon 59: 2031–2043 (2010), phyl.

Creeping stem succulent, to 15 cm tall; shoots green with darker markings around spines, 2–30 cm long, 10–18 mm wide, roundly 4-angled. Scale-like leaves spiny, spreading; stipules reduced to a few trichomes. Inflorescences usually basal, 1(-2)-flowered. Corolla 4–5 cm long, creamish yellow, maroon-maculate, fused for about half of total length, tube with a small central depression, lobes adaxially with emergences tipped by a brownish trichome; lobes triangular, ciliate; gynostegial corona ivory or brownish, of clavate, connivent-erect, apically warty staminal parts and rectangular interstaminal parts basally fused into a ring; gynostegium sessile. Follicles 9–20 cm long, winged.  $2n = 22$ .

One variable species, *E. grandis* N.E. Br., in E Africa and Arabia.

249. *Hoodia* Sweet ex Decne.

*Hoodia* Sweet ex Decne., Prodr. 8: 664 (1844); Bruyns, Bot. Jahrb. Syst. 115: 145–270 (1993), rev.; Bruyns, Stapeliads of S. Afr. Madag. 1: 92–129 (2005), rev.; Liede-Schumann & Meve, Taxon 67: 446 (2018), nom.

*Monothylaceum* G. Don (1837), nom. rej. prop. *Scytanthus* Hook. (1844), non *Skytanthus* Meyen (1834), (Apocynaceae: Plumerieae).

*Trichocaulon* N.E. Br. (1878).

*Hoodiopsis* C.A. Lückh. (1933).

Robust, *Cereus*-like stem succulents, 25–220 cm tall; shoots (light) greenish to brownish, 20–150 cm long, 25–100 mm wide, sharply 11–31-angled. Scale-like leaves spreading acute spines, 0.3–1.2 cm long. Inflorescences 1–5-flowered; flowers occasionally with carrion-odor. Corolla 4–80 mm long, yellowish to reddish, occasionally with emergences tipped by trichomes; lobes broadly triangular; gynostegial corona yellowish or reddish, of ovoid or trianguloid, inflexed staminal

parts and rectangular to bilobed interstaminal parts fused into a ring for about half of total length; gynostegium (sub-)sessile; caudicles spatulate. Follicles 4–18(-22) cm.  $2n = 22$ .

13 spp., arid and semi-arid regions of S Africa. *Hoodia* has been listed under CITES (Appendix II) since 2005, the sole genus of Asclepiadoideae. The reputed activity of *Hoodia* ingredients as an appetite suppressant (see Introduction) causes specific threats to wild populations due to uncontrolled collecting.

250. *Huernia* R. Br.

*Huernia* R. Br., Asclepiadeae 11 (1810); Leach, Excelsa Tax. Ser. 4: 1–196 (1988), rev.; Gilbert, Fl. Ethiopia and Eritrea 4.1: 190–193 (2003), reg. rev.; Lavranos, Fl. Somalia 3: 195–196 (2006), reg. rev.; Bruyns, Stapeliads of S. Afr. Madag. 1: 130–211 (2005), rev. *Decodontia* Haw. (1812), nom. illegit.

Clump-forming or creeping stem succulents, 1–15 cm tall; shoots (blue) green, 1–40(-1500) cm long, 5–25 mm wide, 4–6(-25)-angled. Scale-like leaves occasionally as spines, 0.1–0.5 cm long; stipules absent. Inflorescences basal, 1–7-flowered, pedunculate; flowers occasionally fetid. Corolla 1–4 cm long, occasionally with central ring, creamish to purplish, often patterned, often sculptured, emergences tipped by trichomes; lobes triangular; gynostegial corona creamish or purplish red, an often emarginate disc of staminal and interstaminal parts connate to free, oblongoid, erect or inflexed staminal lobes; gynostegium sessile, with humps below anther wings; caudicles medifixed, triangular or trapezoidal. Follicles 8–12 cm long, stout.  $2n = 22, 44, 66$ .

About 70 spp. in Africa and Arabia.

251. *Larryleachia* Plowes

*Larryleachia* Plowes, Excelsa 17: 5 (1996); Bruyns, Bot. Jahrb. Syst. 115: 145–270 (1993); Meve & Liede, S. Afr. J. Bot. 67: 161–168 (2001), phyl.; Bruyns, Stapeliads of S. Afr. Madag. 1: 212–228 (2005), rev.

*Leachia* Plowes (1992), non *Leachia* Cass. (1822), Asteraceae.

*Leachiella* Plowes (1992), non *Leachiella* Kugrens (1982), Rhodophyceae.

Erect stem succulents, 5–30 cm tall, usually unbranched; shoots (blue-)green 5–30 cm long,



20–60 mm wide, roundly 12–20-angled, tessellate. Scale-like leaves in spirals or whorled, persistent, slightly sunken into the stem-surface, thickish. Inflorescences mostly apical, 1–6-flowered. Flowers occasionally with dung-like odor; corolla 3–8 mm long, creamish to purplish, often patterned, with papillae or emergences tipped by short trichomes; lobes triangular; gynostegial corona occasionally campanulate, ivory or yellow, usually patterned red, of linear (triangular), usually inflexed staminal parts, with long inflexed, adaxial appendage and spreading, bilobed interstaminal parts fused into a ring; gynostegium sessile; caudicles medifixed, trapezoidal. Follicles 5–10 cm long.  $2n = 22$ .

Five spp. in Namibia and South Africa.

### 252. *Lavrania* Plowes

*Lavrania* Plowes, Cact. Succ. J. (Los Angeles) 58: 122 (1986); Bruyns, Bot. Jahrb. Syst. 115: 145–270 (1993), rev.; Meve & Liede, S. Afr. J. Bot. 67: 161–168 (2001), phyl.; Bruyns, Stapeliads of S. Afr. Madag. 1: 229–231 (2005), morph.

Clump-forming stem succulent, 10–20 cm tall; shoots (blue-)green; 5–30 cm long, 20–30 mm wide, roundly 10–12-angled, tessellate. Scale-like leaves minute, broadly conical. Inflorescences basal, 5–15-flowered. Flowers with urine odor; corolla 6–8 mm long, very fleshy, yellowish, purple-maculate, warty; lobes triangular, with emergences tipped by papillae; gynostegial corona purplish, of lingulate, inflexed staminal parts and spreading, bilobed interstaminal parts fused into a ring for about half of total length; gynostegium sessile; caudicles spatulate. Follicles ca. 7 cm long.  $2n = 22$ .

One sp., *L. haagnerae* Plowes, in N Namibia only, on cliffs.

### 253. *Monolluma* Plowes

*Monolluma* Plowes, Haseltonia 3: 64 (1995); Meve & Liede, Pl. Syst. Evol. 234: 172–209 (2002), phyl. *Cylindrillum* Plowes (1995). *Sanguillum* Plowes (1995). *Sulcolluma* Plowes (1995).

Erect or clump-forming stem succulents, 3–50 cm tall; shoots occasionally pungent, (light) green, 2–

40 cm long, 1–30 mm wide, sharply 4-angled. Scale-like leaves minute, persistent, ciliate; stipules reduced to a few trichomes. Inflorescences terminal, 1–15-flowered. Corolla 5–10 mm long, green, white, yellow or reddish, occasionally dark-maculate, occasionally sculptured; lobes triangular; gynostegial corona yellow or purplish red, occasionally with trichomes, occasionally tubular, of lingulate or triangular, inflexed staminal parts and erect or reflexed, bilobed, occasionally ciliate interstaminal parts fused into a ring; caudicles trapezoidal. Follicles 7–10 cm long, occasionally winged.  $2n = 22$ .

Five spp. in Africa and Arabia.

### 254. *Notechidnopsis* Lavranos & Bleck

*Notechidnopsis* Lavranos & Bleck, Cact. Succ. J. (Los Angeles) 57: 255 (1985); Bruyns, Kew Bull. 54: 327–345 (1999), rev.; Meve & Liede, S. Afr. J. Bot. 67: 161–168 (2001), phyl.; Bruyns, Stapeliads of S. Afr. Madag. 1: 232–233 (2005), morph.

Creeping stem succulent, 2–6 cm tall, rhizomatous; shoots green, 3–10 cm long, 9–13 mm wide, roundly 6–8-angled, tessellate, glabrous. Scale-like leaves minute or absent. Inflorescences 2–5-flowered, slightly sunken into the stem surface; flowers honey-scented. Corolla 3–4 mm long, yellowish, reddish maculate, with verrucose trichomes; lobes triangular, spreading to slightly reflexed; gynostegial corona yellow, of trianguloid, erect staminal parts and reflexed, bilobed interstaminal parts fused into a ring; gynostegium sessile; caudicles trapezoidal. Follicles 4–6 cm long.  $2n = 22$ .

One sp., *N. tessellata* (Pillans) Lavranos & Bleck, in South Africa.

### 255. *Ophionella* Bruyns

*Ophionella* Bruyns, Cact. Succ. J. Gr. Brit. 43: 70 (1981); Bruyns, Bot. J. Linn. Soc. 131: 383–398 (1999), rev.; Bruyns, Stapeliads of S. Afr. Madag. 1: 234–235 (2005), rev.

Creeping stem succulents, rhizomatous; shoots brownish green, 4–10 cm long, 3–6 mm wide, with 4 rounded angles. Scale-like leaves persistent, minute, sessile, triangular; stipules absent. Inflorescences 1–2(–5)-flowered. Flowers

inodorous; corolla 4–14 mm long, campanulate or subglobose, white or cream, with purplish pattern; lobes lanceolate or triangular, usually remaining connate at apices; gynostegial corona yellow, of trianguloid, inflexed, occasionally denticulate staminal parts abaxially with a pronounced spreading pectinate or warty hump and small, spreading, spur-shaped interstaminal parts basally fused into a ring; gynostegium sessile; pollinia oblongoid; corpusculum without basal projections. Follicles 2.5–4.5 cm long.  $2n = 22$ .

Two spp. in South Africa.

#### 256. *Orbea* Haw.

*Orbea* Haw., Syn. Pl. Succ. 37 (1812); Leach, Excelsa Tax. Ser. 1: 1–75 (1978), rev.; Bruyns, Aloe 37: 72–76 (2000, publ. 2001), tax.; Bruyns, Syst. Bot. Monogr. 63: 1–196 (2002), rev.; Bruyns, Stapeliads of S. Afr. Madag. 1: 240–329 (2005), rev.; Lavranos, Fl. Somalia 3: 193–195 (2006), reg. rev.

*Podanthes* Haw. (1812), nom. rej., non *Podanthes* Lag. (1816), Asteraceae.

*Diplocyatha* N.E. Br. (1878).

*Stultitia* E. Phillips nom. nov. pro *Stapeliopsis* E. Phillips (1932), non *Stapeliopsis* Pillans (1928).

*Orbeopsis* L.C. Leach (1978).

*Pachycymbium* L.C. Leach (1978).

*Angolluma* R. Munster (1990).

Clump-forming stem succulents, 5–15 cm tall; latex rarely yellowish; occasionally rhizomatous; shoots (light) green or blue-green, often maculate, conical or club-shaped, 1–25 cm long, 10–30 mm wide, 4(–5)-angled. Scale-like leaves spreading, triangular; stipules glandular, (sub-)globose. Inflorescences lateral, 1–30-flowered. Flowers fetid; corolla 5–35 mm long, creamish, frequently patterned purplish, usually sculptured, occasionally with verrucose, erect trichomes, occasionally with ring; lobes lanceolate to ovate, often ciliate; gynostegial corona yellow to purplish, of long, occasionally adaxially humped staminal parts and shorter, often bilobed interstaminal parts fused into a ring; gynostegium occasionally atop a column; caudicles trapezoidal to spatulate. Follicles 4–18 cm long.  $2n = 22, 44$ .

About 55 spp., Africa and Arabia.

#### 257. *Orbeanthus* L.C. Leach

*Orbeanthus* L.C. Leach, Excelsa Tax. Ser. 1: 71 (1978); Meve & Liede, Pl. Syst. Evol. 234: 172–209 (2002), phyl.

Creeping stem succulents, 2 cm tall, sparsely branched; shoots blue-green, mottled purple, 5–30 cm long, 8–9 mm wide, with 4 rounded angles. Scale-like leaves triangular, without stipules. Inflorescences usually basal, 1–2-flowered. Flowers slightly fetid, not nectariferous; corolla 15–20 mm long, rotate or urceolate, cream and reddish, unsculptured, with vesicle-like trichomes, rarely with a broad ring; lobes triangular; gynostegial corona creamish, tinged or mottled reddish, of triangular or clavate, apically pilose staminal parts and spreading, bilobed, apically pilose interstaminal parts shortly fused into a ring; gynostegium sessile; pollinia D-shaped; caudicles broadly spatulate.  $2n = 22$ .

Two spp. in South Africa.

Bruyns (2002, 2005) proposed that *Orbeanthus* be included in *Orbea* Haw., a concept rejected by Meve and Liede (2002a).

#### 258. *Pectinaria* Haw.

*Pectinaria* Haw., Suppl. Pl. Succ. 14 (1819), nom. cons., non *Pectinaria* Bernh. (1800), Apiaceae, nom. rej.; Bruyns, Cact. Succ. J. (Gr. Brit.) 43: 61–83 (1981), rev.; Bruyns, Stapeliads of S. Afr. Madag. 2: 331–344 (2005), rev.

*Vadulia* Plowes (2003).

Clump- to mat-forming stem succulents, 1–5 cm tall; shoots (blue-)green, 1.5–8 cm long, 10–25 mm wide, with 6 rounded angles. Scale-like leaves persistent, triangular; stipules absent. Inflorescences 1–2-flowered. Flowers nodding, inodorous; corolla 3–7 mm long, occasionally subglobose, yellowish to maroon (patterned), occasionally warty by spiculate emergences; lobes lanceolate or ovate, occasionally remaining connate at apices; gynostegial corona yellow, of triangular, occasionally denticulate staminal parts with a pectinate hump and bilobed interstaminal parts highly fused into a ring; gynostegium subsessile or atop a column; caudicles rectangular; corpusculum without basal projections. Follicles 6.5–9 cm long.  $2n = 22$ .

At least three spp. in two sections, South Africa.

#### 259. *Piaranthus* R. Br.

*Piaranthus* R. Br., Asclepiadeae 12 (1810); Meve, Bradleya 12: 57–12 (1994), rev.; Bruyns, Syst. Bot. 24: 379–398

(1999), rev.; Bruyns, *Stapeliads of S. Afr. Madag.* 2: 345–368 (2005), reg. rev.  
*Obesia* Haw. (1812).  
*Huerniopsis* N.E. Br. (1878).

Clump- to mat-forming stem succulents, 2–10 cm tall; shoots green, usually club-shaped, 1–6 cm long, 8–20 mm wide, with 4–5 rounded angles. Scale-like leaves succulent, deltate; stipules glandular, (sub-)globose. Inflorescences lateral, 1–10-flowered. Flowers with fruity or fetid odor; corolla 8–21 mm long, uniform or patterned, papillate or with trichomes; lobes lanceolate or triangular, occasionally with vibratile trichomes; gynostegial corona ivory or yellow, of subulate to triangular staminal parts abaxially with a pronounced, grooved, rugose, pectinate hump and indistinct interstaminal parts basally fused into a ring; gynostegium sessile or atop a column; caudicles cylindrical. Follicles 6–14 cm long.  $2n = 22$ .

Nine spp., South Africa, Namibia, Botswana.

Inclusion of *Huerniopsis* (sister to *Piaranthus* s.str.) is a matter of taste.

#### 260. *Pseudolithos* P.R.O. Bally

*Pseudolithos* P.R.O. Bally, *Candollea* 20: 41 (1965); Bruyns, *Bradleya* 8: 33–38 (1990), rev.; Lavranos, *Fl. Somalia* 3: 180–182 (2006), reg. rev.

Clump-forming stem succulents, 2–7 cm tall, unbranched or sparsely branched; shoots blue-green or light brown, cube-like to globose, 1.5–6 cm long, 0.8–6 mm wide, obtusely 4-angled, tessellate. Scale-like leaves (almost) absent; stipules absent. Inflorescences terminal or lateral, often on short shoots, 4–30-flowered. Flowers fetid; corolla 2.5–6 mm long, campanulate or urceolate, creamish to purplish, occasionally maculate, with spiculate papillae or trichomes, adaxially with five ridges; lobes (sub-)triangular; gynostegial corona yellow(-green) or purplish red, occasionally with trichomes, occasionally urceolate, of lingulate or trianguloid, inflexed staminal parts and deltoid or saccate, bilobed interstaminal parts almost completely fused into a ring; caudicles trapezoidal or spatulate. Follicles 5–6 cm long.  $2n = 22$ .

Five to six spp. in Ethiopia and Somalia.

#### 261. *Quaqua* N.E. Br.

*Quaqua* N.E. Br., *Gard. Chron.*, II, 12: 8 (1879); Bruyns, *Bot. Jahrb. Syst.* 121: 311–402 (1999), rev.; Bruyns, *Stapeliads S. Afr. Madag.* 2: 369–415 (2005), rev.  
*Sarcophagophilus* Dinter (1923).

Erect stem succulents, 15–60 cm tall; shoots (blue-)green, 5–50 cm long, 15–40 mm wide, 4-angled (rarely 5–6-angled). Scale-like leaves persistent, forming spines (occasionally nearly absent); stipules glandular, ovate (occasionally absent). Inflorescences apical, 1–30-flowered. Flowers with fetid or sweetish odor; corolla 5–15 mm long, uniform, tinged or patterned, occasionally warty, papillose or with verrucose trichomes; lobes oblong, lanceolate or triangular, occasionally ciliate; gynostegial corona yellow or purplish red, of (small) trianguloid staminal parts occasionally with a spreading dorsal appendage and saccate, subulate, deltoid or bilobed interstaminal parts fused into a ring; gynostegium (sub-)sessile; caudicles trapezoidal and spatulate. Follicles 2–13 cm long.  $2n = 22$ .

19 spp. in Namibia and South Africa.

#### 262. *Rhytidocaulon* P.R.O. Bally

*Rhytidocaulon* P.R.O. Bally, *Candollea* 18: 335 (1962); Bruyns, *Edinb. J. Bot.* 56: 211–228 (1999), rev.; Gilbert, *Fl. Ethiopia and Eritrea* 4.1: 176–178 (2003), reg. rev.; Lavranos, *Fl. Somalia* 3: 183–184 (2006), reg. rev.; de Kock, *Asklepios* 101: 5–15 (2008), morph.

Creeping or erect stem succulents, 5–30 cm tall, sparsely branched from a distinct main stem; shoots dark brownish green, 2–50 cm long, 0.7–2.5 mm wide, with 4 rounded angles, papillose or tessellate. Scale-like leaves strongly ascending; stipules glandular, globose. Inflorescences lateral, 1–3-flowered, slightly sunken into stem surface. Flowers often with dull fruity odor; corolla 2.5–20 mm long, rotate or elongate-conical, cream, green or purple, often patterned, glabrous, papillose or with often vibratile trichomes; lobes linear to ovate, occasionally caudate, or tips remaining connate; gynostegial corona yellow, or purplish red, of lingulate, trianguloid or rectangular staminal parts and subulate, deltoid (to fringe-like) or bilobulate interstaminal parts fused into a ring;

gynostegium sessile; corpusculum without basal projections; follicles ca. 4 cm long; seeds with thick, puffed margin.  $2n = 22$ .

About 14 spp. in E Africa and Arabia.

263. *Richtersveldia* Meve & Liede

*Richtersveldia* Meve & Liede, Pl. Syst. Evol. 234: 204 (2002); Bruyns, Stapeliads of S. Afr. Madag. 2: 416–417 (2005), morph.

Erect stem succulent, 10–20 cm tall; rhizomatous; shoots blue-green, 5–20 cm long, 20–25 mm wide, sharply 8-angled, tessellate. Scale-like leaves persistent, forming spines. Inflorescences apical, 1–5 (–20)-flowered, subsessile. Flowers with dull fruity odor; corolla 5–8 mm long, depressed-rotate, greenish yellow to ochre, reddish maculate, unsculptured, papillose or with trichomes, lobes triangular, spreading; gynostegial corona yellowish, spotted red, of broadly linear, inflexed staminal parts and deltoid-rectangular, occasionally bilobed, spreading interstaminal parts basally fused into a ring; gynostegium sessile; caudicles trapezoidal. Follicles 6–8 cm long.  $2n = 22$ .

One sp., *R. columnaris* (Nel) Meve & Liede, in South Africa, in the Richtersveld only.

264. *Socotrella* Bruyns & A.G. Miller

*Socotrella* Bruyns & A.G. Miller, Novon 12: 330 (2002); Řičánek & Hanáček, Cact. Succ. J. (Los Angeles) 78: 6–9 (2006), ecol.; Bruyns et al., Mol. Phyl. Evol. 77: 251–263 (2014), phyl.

Stem succulent forming scattered clumps, 10 cm tall, rhizomatous; shoots green, 5–15 cm long, 4–7 mm wide, with 4 rounded angles. Leaves and stipules absent. Inflorescences lateral, 1–5-flowered. Flowers long-pedicellate, erect, with vanilla scent; corolla 9–12 mm long, campanulate, yellow, tube streaked reddish to maroon, glabrous; lobes ovate to deltate, spreading, marginally slightly revolute; gynostegial corona yellow, of long, rectangular, basally bulged free staminal lobes and tiny interstaminal flaps; gynostegium atop a column; pollinia ellipsoid; caudicles spatulate; corpusculum rhomboid, the same size as the pollinia.

One sp., *S. dolichocnema* Bruyns, in Yemen (Socotra); sister to the also monotypic Socotran endemic *Duvaliandra*.

265. *Stapelia* L.

*Stapelia* L., Sp. Pl. 217 (1753), nom. cons.; Leach, Excelsa Taxon. Ser. 3: 1–157 (1985), rev.; Bruyns, Stapeliads of S. Afr. Madag. 2: 418–489 (2005), rev. *Stisseria* Heister ex Fabr. (1759), nom. illeg. *Gonostemon* Haw. (1812).

Clump-forming stem succulents, 10–20 cm tall; occasionally rhizomatous; shoots green, cylindrical, 6–30 cm long, 5–30 mm wide, 4-angled, occasionally pubescent. Scale-like leaves ascending to erect, oblong or lanceolate; stipules glandular, globose. Inflorescences basal, 1–10-flowered, pedunculate. Flowers fetid; corolla 5–200 mm long, globose, rarely campanulate, uniform or banded, mostly rugose, occasionally with flat ring; lobes ovate or triangular, often ciliate; gynostegial corona of subulate staminal parts, occasionally with adaxial appendage, and often apiculate interstaminal parts basally fused into a ring; gynostegium (sub-)sessile or atop a column; pollinia ovoid or reniform; caudicles spatulate; corpusculum with linear to deltoid basal projections. Follicles 9–13 cm long.  $2n = 22, 44$ .

43 spp. in southern Africa.

266. *Stapelianthus* Choux ex White & Sloane

*Stapelianthus* Choux ex White & Sloane, Stapelieae 71 (1933); Bruyns & Klak, Ann. Missouri Bot. Gard. 91: 410–437 (2004), rev. *Stapeliopsis* Choux (1931), non *Stapeliopsis* Pillans (1928).

Clump-forming stem succulents, 5–10 cm tall; shoots greenish to brownish, streaked or mottled, 2–30 cm long, 5–12 mm wide, 4–6(–8)-angled, tuberculate or tessellate. Scale-like leaves succulent or spiny. Inflorescences usually basal, 1–5-flowered. Flowers fetid; corolla 6–18 mm long, occasionally cyathiform or urceolate, very car-nose, cream or purple, occasionally maculate, occasionally sculptured or with trichome-tipped emergences, occasionally with ring; lobes broadly ovate; gynostegial corona purplish red, cyathiform, of ovoid or trianguloid, inflexed staminal parts and erect, rectangular or bifid interstaminal parts basally fused into a ring; gynostegium occasionally atop a column; caudicles spatulate; corpusculum with small basal projections. Follicles 6–10 cm long.  $2n = 22$ .

Seven spp. in Madagascar.

### 267. *Stapeliopsis* Pillans

*Stapeliopsis* Pillans, S. African Gard. 18: 32 (1928); Bruyns, Cact. Succ. J. (Gr. Brit.) 43: 61–83 (1981), rev.; Bruyns et al., Bot. J. Linn. Soc. 148: 125–155 (2005), rev. & phyl.; Bruyns, Stapeliads of S. Afr. Madag. 2: 507–525 (2005), morph.

*Hermanschwartzia* Plowes (2003).

*Neoplectinaria* Plowes (2003).

Clump-forming stem succulents, 2–8 cm tall; rhizomatous; shoots blue-green, often mottled, 3–15 cm long, 5–20 mm wide, 4-angled, papillose. Scale-like leaves succulent or spiny. Inflorescences basal, 1–3-flowered, pedunculate. Flowers usually fetid; corolla 10–30 mm long, urceolate, subglobose or tubular, white to purple, occasionally sculptured or with trichome-tipped emergences; lobes triangular, occasionally connate at apices; gynostegial corona purplish, of subulate to clavate staminal parts and spreading, deltoid, rectangular or triangular interstaminal parts, occasionally fused into a ring; gynostegium occasionally atop a column, concealed in corolla; caudicles rectangular; corpusculum without basal projections. Follicles 7–11 cm long.  $2n = 22$ .

Eight spp. in Namibia and South Africa.

### 268. *Tavaresia* Welw.

*Tavaresia* Welw., Ann. Cons. Ultramarino, Ser. 1: 79 (1854); White & Sloane, Stapelieae 3: 1099–1108 (1937) rev.; Bruyns, Stapeliads of S. Afr. Madag. 2: 526–530 (2005), rev.

*Decabelone* Decne. (1871).

Clump-forming stem succulents, 8–12 cm tall; green, 2–25 cm long, 15–25 mm wide, sharply 5–14-angled. Scale-like leaves and stipules persistent, forming three spines to 1 cm long, very acute. Inflorescences basal, 1–5-flowered. Flowers with dull pungent or carrion odor; corolla 3–14 cm long, tubular, cream, maculate with (ob-)conical, sometimes trichome-tipped emergences; lobes triangular; gynostegial corona ivory, maculate, cyathiform, forming a ring of sublanceolate staminal parts and saccate, bilobed, subulate, interstaminal parts topped by a red, globose, vibratile trichome; gynostegium atop a short column; pollinia large, obovoid, caudicles spatulate; corpusculum with linear basal projections. Follicles 5–19 cm long. Seeds suborbicular.  $2n = 22$ .

Two spp. in Angola, Botswana, Namibia and South Africa.

### 269. *Tridentea* Haw.

*Tridentea* Haw., Syn. Pl. Succ. 34 (1812); Leach, Excelsa Tax. Ser. 2: 1–69 (1980); Bruyns, S. Afr. J. Bot. 61: 180–208 (1995), rev.; Bruyns, Stapeliads of S. Afr. Madag. 2: 531–550 (2005), reg. rev.

Clump-forming stem succulents, 5–10 cm tall; occasionally rhizomatous; shoots blue-green, (2–)5–15(–20) cm long, 10–20(–25) mm wide, 4-angled. Scale-like leaves basally constricted, (sub-)lanceolate; stipules reduced to a few glandular hairs. Inflorescences basal, 1–5-flowered. Flowers fetid; corolla 10–50 mm long, cream or yellow, occasionally patterned purplish, sculptured or with erect conical or spine-like trichome-tipped emergences; lobes triangular; free staminal corona lobes yellow or purplish, subulate(-deltoid), occasionally with basal spreading dorsal spur; interstaminal lobes rectangular, ovate, apiculate, bifid or trifid, spreading; gynostegium (sub-)sessile; caudicles trapezoidal to spatulate. Follicles 11–16 cm long.  $2n = 22$ .

Eight spp. in Namibia and South Africa.

### 270. *Tromotriche* Haw.

*Tromotriche* Haw., Syn. Pl. Succ. 36 (1812); Leach, Excelsa Tax. Ser. 2: 1–69 (1980), rev.; Bruyns, S. Afr. J. Bot. 61: 180–208 (1995), rev.; Bruyns, Stapeliads of S. Afr. Madag. 2: 551–574 (2005), morph.

*Caruncularia* Haw. (1812).

Clump-forming or creeping stem succulents, 3–10 cm tall, rhizomatous; shoots blue-green, 5–50 (–300) cm long, 6–25 mm wide, 4-angled. Scale-like leaves minute, triangular; stipules glandular, globose. Inflorescences 1–5-flowered, pedunculate. Flowers fetid; corolla 7–32 mm long, occasionally cyathiform, cream, yellow, or purplish, occasionally patterned, often rugose and papillate; lobes ovate or triangular, reflexed or spreading, often ciliate; gynostegial corona (black) purplish, cyathiform, of subulate or clavate, staminal lobes with adaxial appendage and rectangular, triangular or bifid interstaminal lobes occasionally basally fused into a ring; gynostegium atop a column with 5-angled foot; caudicles

trapezoidal or spatulate. Follicles ca. 8 cm long.  $2n = 22$ .

Nine spp. in Namibia and South Africa.

271. *White-sloanea* Chiov.

*White-sloanea* Chiov., *Malpighia* 34: 541 (1937); Bruyns, *J. Bot.* 55: 27–37 (1998), morph.; Lavranos, *Fl. Somalia* 3: 196–197 (2006), reg. rev. *Drakebrockmania* White & Sloane (1937), non *Drake-Brockmania* Stapf (1912), Poaceae.

Erect, mostly single-stemmed stem succulent, 3–13 cm tall; shoots light green to brown, 3–13 cm long, 4–5.5 mm wide, 4-angled. Leaves absent. Inflorescences lateral, 5–20-flowered, shortly pedunculate. Flowers fetid; corolla 3 cm long, campanulate, cream, red-maculate, with hemispherical emergences and flexuous trichomes; lobes triangular, with vibratile clavate trichomes near base of lobes; gynostegial corona creamish, striped red, rotate, of oblong-trapezoidal, apically denticulate staminal parts and rectangular, bifid interstaminal parts basally fused into a ring; gynostegium atop a short column; anthers with short, deltoid connective appendages; pollinia rectangular-ellipsoid, caudicles spatulate. Follicles 5–6 cm long, thick fusiform.  $2n = 22$ .

One sp., *W. crassa* (N.E. Br.) Chiov., in Somalia.

V.4. Tribe *Eustegieae* Rchb. ex Meve & Liede (2014).

Leaves palmately lobed or (at least some) with one or two spreading lateral teeth a little above the base. Inflorescences extra-axillary and terminal. Corolla rotate, glabrous; corona gynostegial, consisting of a very basally fused ring of simple staminal and deeply tripartite interstaminal parts with an additional inner ring of smaller staminal lobes; gynostegium (sub-)sessile. Recent molecular study (Surveswaran et al. 2014) has shown that *Eustegieae* are sister to *Asclepiadeae*. Two genera in southern Africa.

KEY TO THE GENERA OF EUSTEGIEAE

1. Leaves palmately 5–7-lobed; follicles triangular, indehiscent, seeds single, wingless 272. *Emicarpus*

- Leaves linear, often with one or two lateral teeth a little above the base; follicles a single, fusiform follicle, seeds several, winged 273. *Eustegia*

272. *Emicarpus* K. Schum. & Schltr. Fig. 52

*Emicarpus* K. Schum. & Schltr., *Bot. Jahrb. Syst.* 29. *Beibl.* 66: 21 (1900).

*Lobostephanus* N.E. Br. (1901).



Fig. 52. Apocynaceae-Eustegieae. *Emicarpus fissifolius*. A Flowering branch. B Flower. C Portion of the outer ring-shaped gynostegial corona of staminal and interstaminal parts. D Staminal corona lobes and style-head. E, F Pollinaria. G Follicle. H Follicle in longitudinal section, showing the seed in natural position. (From Brown 1901, pl. 2692, with permission from Hooker's *Icones Plantarum* © Board of Trustees of the Royal Bot. Gard., Kew; drawn by Matilda Smith)

Prostrate herb, 0.6–1 m tall, almost glabrous. Leaves 1–5 cm long, palmately 5–7-lobed. Inflorescences 5–8-flowered, sciadioidal, long-pedunculate. Corolla 2–3 mm long; lobes oblong to lanceolate; gynostegial corona exceeding gynostegium (except for style-head), forming a ring of connate filamentous to spatulate, erect staminal and shorter tripartite interstaminal parts, with additional inner erect, oblong, free staminal lobes; pollinia oblongoid; caudicles declinate, ribbon-shaped; corpusculum ovoid, minute; style-head rostrate. Follicles 10 mm long, triangular, with woody pericarp, not opening at maturity. Seeds one per fruiting carpel, U-shaped, wingless.

A single species, *E. fissifolius* K. Schum. & Schltr., in Mozambique, sandy areas, sea level; possibly extinct. Closely related to *Eustegia*.

### 273. *Eustegia* R. Br.

*Eustegia* R. Br., *Asclepiadeae* 40 (1810); Bruyns, *Bot. Jahrb. Syst.* 121: 19–44 (1999), rev.; Surveswaran et al., *Bot. J. Linn. Soc.* 174: 601–619 (2014), phyl.

Erect or prostrate herbs, 20–30 cm tall; sparsely pubescent; latex translucent; rhizomatous, with tap roots; shoots annual. Leaves sessile, 0.5–3 cm long, linear to hastiform. Inflorescences 2–8-flowered, sciadioidal. Corolla 3–4 mm long, grayish green; lobes oblong, revolute; gynostegial corona whitish, equaling gynostegium, forming a ring of basally connate filamentous staminal and deeply tripartite interstaminal parts, with additional inner ring of five small, basally connate staminal lobes; pollinia reniform; caudicles geniculate, articulated, triangular at pollinium end; corpusculum deltoid, frail; style-head cylindrical to rostrate. Follicles 8–10 cm long, fusiform-obclavate. Seeds winged.

Three spp. (only one accepted by Bruyns 1999), in South Africa, winter rainfall area, ephemeral in fynbos and renosterveld; to 2000 m.

### V.5. Tribe *Asclepiadeae* Duby (1828).

Herbs, trees (up to 6 m, *Calotropis*), vines, geophytes with subterranean tubers, occasionally succulents, with white (rarely translucent or yellow) latex. Leaves opposite, rarely whorled, herbaceous, often with cluster of colleters adaxially at juncture of petiole and leaf blade. Corolla rotate to occasionally tubular; lobes with valvate

to imbricate aestivation; corolline corona rare; anthers generally erect to spreading, with deltoid apical appendage, distinctly constricted at base, with guide rails alongside fertile part (rarely below: some species of *Cynanchum*, *Vincetoxicum*, most *Gonolobus* relatives); gynostegial corona rarely absent (*Astephanus*, *Microloma*, single species in various genera); usually either an outer ring of connate staminal and interstaminal parts, annular (*Gonolobus* relatives) or differentiated in staminal and/or interstaminal position or an inner corona of 5 massive, free, often channeled lobes, often with additional lobules on adaxial surface (rarely partially fused with corolla, *Parapodium*, *Oxypetalum*); occasionally both a ring and an inner corona present (*Cynanchum*, former *Sarcostemma* species); pollinia pendulous or rarely erect (some *Cynanchum* species, former *Karimbolea* species), or more or less horizontal (some *Vincetoxicum* species, *Gonolobus* relatives), small and more or less ellipsoid to long, narrow and dorsiventrally flattened, rarely with hyaline insertion crest along inner edge (*Pergularia*), on upper margin near attachment of caudicles (*Gonolobus* relatives), upper edge (some *Schizoglossum* species) or with caudicles attenuate into small apical spike (*Oncinema*); pollinia usually (sub-)apically, more rarely laterally attached to the straight or S-shaped caudicles; pollen tubes emerging through inner, upper edge or through the concave face of the pollinium (*Gonolobus* relatives); style-head broad, with flat to concave (sometimes conical to slenderly conical) apex, tapering below into narrow neck above carpels; caudicles frequently with projecting hooks and ridges supporting insertion into guide rail; gynoecium apocarpous, mostly superior. Follicles usually one by abortion, occasionally extremely inflated (*Araujia*, *Calotropis*), rarely spherical, more usually fusiform obclavate, occasionally ornamented with spine-like processes or protuberances or longitudinal ridges. Seeds more or less elliptical in outline, with or without wing-like margin, with coma.  $x = 11$  (rarely 10, 9); some extra-tropical *Vincetoxicum* species with hypogeal germination. Secondary compounds “Asclepiadaceae bitter principles” (glycosides), more rarely cardenolides; alkaloids only in *Vincetoxicum* and relatives. 105 genera worldwide, mainly tropical and subtropical climates, but several genera extending into the temperate zones.

## KEY TO THE SUBTRIBES OF ASCLEPIADEAE

1. Plants of Africa, Eurasia, Australia 2
  - Plants of the Americas 5
2. Small twiners or rigid shrubs; latex translucent; gynostegial corona usually absent, if present, then leaves linear; plants of southern Africa
  - V.5.a. *Astephaninae*
    - Plants of various habits; latex usually white, if translucent, then plants larger and with gynostegial corona, but without linear leaves 3
3. Gynostegial corona of five staminal lobes, at the most basally fused 4
  - Gynostegial corona with a well-developed annular part, rarely with additional free staminal lobes
    - V.5.c. *Cynanchinae*
4. Plants often erect; inflorescences always sciadioidal; staminal corona lobes three-dimensional, often intricately folded, with or without inner teeth and ornamentations
  - V.5.b. *Asclepiadinae*
    - Plants rarely erect; inflorescences complex or sciadioidal; staminal corona lobes usually laminar, if three-dimensional, then of simple shape and at least partially fused to the anthers V.5.d. *Tylophorinae*
5. Corolla lobes with vibratile trichomes on the adaxial side; plants of southern South America
  - V.5.l. *Topeinae*
    - Corolla lobes without vibratile trichomes on the adaxial side 6
6. Plants erect; staminal corona lobes three-dimensional, often intricately folded, with or without inner teeth and ornamentations
  - V.5.b. *Asclepiadinae*
    - Plants usually twining, rarely erect; corona structure different 7
7. Anthers usually broader than long, frequently horizontal, with transversally dehiscent membrane; pollinia usually with apical to distal sterile hyaline region
  - V.5.k. *Gonolobinae*
    - Anthers usually longer than broad, never horizontal and without transversally dehiscent membrane; pollinia never with sterile hyaline region 8
8. Inflorescences usually axillary, paired, with one inflorescence shorter, often multi-flowered, thyrsoidal, partial inflorescences often condensed; follicles paired, narrowly oblong, often with a basal thickening; follicles forming an acute angle
  - V.5.i. *Tassadiinae*
    - Inflorescences usually extra-axillary, rarely axillary, never thyrsoidal; follicles solitary or paired, usually fusiform, if narrowly oblong, then without basal thickening; follicles at various angles 9
9. Corolla campanulate, adnate to gynostegium, forming five hairy pouches; gynostegial corona of free staminal lobes with additional peg-shaped parts along filament tube; plants of the northern Andes
  - V.5.e. *Pentacyphinae*
    - Corolla of various shapes, but not adnate to gynostegium and not forming five hairy pouches; gynostegial corona of different construction and without additional peg-shaped parts 10
10. Leaves cordiform, basally deeply cordate
  - V.5.c. *Cynanchinae*
    - Leaves of various shapes, but basally never deeply cordate 11
11. Flowers usually large (> 1 cm diam.), often brightly colored; follicles usually one per flower, with thick pericarp; if two, then plants often erect, and caudicles with conspicuous appendage
  - V.5.j. *Oxypetalinae*
    - Flowers usually smaller (< 1 cm diam.), usually white, cream, yellowish or greenish; follicles one or two per flower, with thin pericarp 12
12. Corolla lobes adaxially usually with trichomes, often barbate; gynostegial corona of five staminal lobes, at the most basally fused; follicles solitary
  - V.5.h. *Metastelmatinae*
    - Corolla lobes adaxially usually glabrous, if with trichomes, then these of equal length; gynostegial corona usually with conspicuous annular part; follicles usually paired, if solitary, then plants of southern South America 13
13. Plants without conspicuous long shoot–short shoot architecture; follicles usually solitary, fusiform; plants of southern South America
  - V.5.f. *Diplolepiniae*
    - Plants usually with conspicuous long shoot–short shoot architecture; follicles usually paired, narrowly oblong
      - V.5.g. *Orthosiinae*

## KEY TO THE GENERA OF ASCLEPIADEAE

(by Sigrid Liede-Schumann and G.N. Morillo)

1. Erect shrubs or small trees, to 3 m tall, branches woody, never twining even apically; corona with a conspicuous basal spur on the prominent staminal lobes; native to tropical Africa and Asia, but widely introduced and naturalized in New World tropics

**282. *Calotropis***



- Plants erect or twining, when 3 m or more then not erect or woody only toward the base; corona always lacking a conspicuous coiled basal spur, otherwise variable 2
- 2. Plants of Africa, Europe, Asia or Australia 3
  - Plants of the New World 57
- 3. Corona of any kind completely absent or at the most forming a small projection on the adaxial side of the corolla 4
  - Distinct corona of various composition present 7
- 4. Leaves cordiform, basally broadly cordate; inflorescences bostrychoid; latex white; plants of Asia
  - 303. *Cynanchum*** (former *Adelostemma*)
    - Leaves of various shapes, but basally not broadly cordate; inflorescences sciadioidal; latex translucent; plants of Africa 5
  - 5. Corolla fused only at the base, lobes strongly twisted; style-head rostrate, much longer than connective appendages
    - 306. *Vincetoxicum*** (former *Pleurostelma* species)
      - Corolla fused for at least half of its length, lobes usually not strongly twisted; style-head longer or about as long as connective appendages 6
    - 6. Corolla tubular, partly or almost entirely obscuring the gynostegium, corolla occasionally with small projections or trichomes; style-head not longer than connective appendages **275. *Microlooma***
      - Corolla campanulate, not obscuring the gynostegium; style-head longer than connective appendages **274. *Astephanus***
  - 7. Plants with succulent stems, with or without well-developed leaves 8
    - Plants without succulent stems, with well-developed leaves 9
  - 8. Plants with cordate leaves; latex translucent; (outer) corona fused into bowl-shaped tube with 10 lobules around mouth leaving gynostegium well visible from the top; caudicles extended along distal side of pollinia; plants of Africa **304. *Schizostephanus***
    - Plants with or without well-developed leaves; latex usually white, white or yellow, when almost translucent, then plants always leafless; corona gynostegial, but not forming a bowl-shaped tube with 10 lobules around mouth; plants of Madagascar, when African, then with scale-like leaves **303. *Cynanchum***
  - 9. Plants erect, not even apically twining 10
    - Plants twining, at least apically 45
  - 10. Plants strongly branched, herbaceous or shrubby 11
    - Plants unbranched or sparsely branched, erect herbs 20
  - 11. Latex translucent 12
    - Latex white 13
- 12. Small shrublets (< 40 cm); leaves carnose, tiny (to 3 mm long); plants of Somalia
  - 281. *Calciophila*** (*C. gillettii*)
    - Plants basitonically branched perennial herbs, leaves herbaceous, ovate to linear, often basally cordate; widespread in Europe and Asia, introduced to N America; occasionally in Africa
  - 306. *Vincetoxicum***
- 13. Prostrate annual herbs; leaves often with undulate margins, soft, broadly ovoid; follicles thick-walled, with a few soft spines
  - 303. *Cynanchum*** (former *Glossonema* species)
    - Plants perennial, leaves normally not with undulate margins and not soft; follicles of various shapes, but not with a few soft spines 14
  - 14. Corona present, but not of free staminal lobes 15
    - Corona of free staminal lobes 16
  - 15. Corona of five basally fused lobes adnate to the corolla, forming a cup from which the long-stipitate gynostegium emerges; plants strongly basitonically branched shrubs; leaves slenderly elliptic, strongly ascending; follicles broadly ovoid, thick-walled, smooth; plants of northern Africa and Arabia
    - 297. *Solenostemma***
      - Corona gynostegial, not adnate to the corolla, cup-shaped or otherwise, but not with a long-stipitate gynostegium emerging; leaves of various shapes, usually not strongly ascending; follicles thin-walled, narrowly obclavate or fusiform, usually slightly grooved, rarely winged or with slender emergences **303. *Cynanchum***
  - 16. Leaves petiolate and cordate; staminal corona lobes fusiform, small free interstaminal lobules present; plants of northern Africa and Arabia
    - 294. *Pergularia*** (*P. tomentosa*)
      - Leaves (sub-)sessile, linear to obovate, at the most indistinctly cordate; staminal corona lobes not fusiform; interstaminal lobules absent 17
    - 17. Leaves broadly obovate; staminal corona lobes with a coiled basal spur **282. *Calotropis***
      - Leaves linear to slenderly elliptic; staminal corona lobes without a coiled basal spur 18
  - 18. Inflorescences mostly terminal; rootstock a tuberous caudex **278. *Asclepias***
    - Inflorescences extra-axillary; rootstock usually fibrous, occasionally woody and tuberous 19
  - 19. Inflorescences bostrychoid; follicles fusiform to narrowly ovoid, smooth; rheophytes along seasonal water courses **287. *Kanahia***

- Inflorescences sciadioidal; follicles often inflated and covered with soft spines; occurring in various habitats, but not in riverbeds **286. *Gomphocarpus***
- 20. Gynostegial corona a ring of connate staminal and interstaminal parts 21
  - Gynostegial corona of free (or almost free) staminal lobes 22
- 21. Gynostegial corona adnate to gynostegium only, laminar; interstaminal parts undifferentiated, corolla lobes oblong, ovate, lanceolate or cucullate; plants of Madagascar **303. *Cynanchum***
  - Gynostegial corona adnate to both corolla and gynostegium, carnose, interstaminal parts rectangular and bifid; corolla lobes spatulate; plants of southern tropical Africa **290. *Odontostelma***
- 22. Leaves obovate to oblong, sessile, carnose; corolla lobes to 15 mm long; plants of the Himalayas **282. *Calotropis (C. acia)***
  - Leaves of various shapes, but broadest always below the middle, not carnose; corolla lobes mostly smaller 23
- 23. Staminal corona lobes petaloid, red or pale bluish lilac; as long as to longer than corolla lobes, occasionally apically broadened and emarginate, with a basal tooth projecting into the center of the flower; plants of east tropical Africa **288. *Margaretta***
  - Staminal corona lobes not petaloid; not exceeding the corolla lobes; never apically broadened 24
- 24. Staminal corona lobes laminar or somewhat carnose, flat, never folded (laterally or ventrally) to form a central cavity, lacking conspicuous ventral or apical projections 25
  - Staminal corona lobes not laminar, three-dimensional, solid or folded (laterally or ventrally) to form a central cavity, often with apical or ventral teeth or other projections 30
- 25. Pollinia with a pellucid germination zone on the circumference, but not at the point of attachment to the caudicle **296. *Schizoglossum***
  - Pollinia without a pellucid germination zone on the circumference 26
- 26. Leaves linear; inflorescences long-pedunculate, almost as long as or longer than subtending leaves, inflorescences forming dense, globose heads; marsh and grassland plants 27
  - Leaves of various shapes, but not linear; inflorescences sessile or pedunculate, but peduncles distinctly shorter than subtending leaves; inflorescences of various shapes, but not forming dense, globose heads 28
- 27. Gynostegium cylindrical, connective appendages resting on style-head, caudicles shorter than pollinia, style-head fully exposed, clavate or ovoid **283. *Cordylogyne***
  - Gynostegium barrel-shaped, connective appendages connivent over style-head, caudicles at least twice as long as pollinia, style-head fully hidden by connective appendages, flat or umbonate **295. *Periglossum***
- 28. Corolla lobes adaxially apically densely villous **284. *Fanninia***
  - Corolla lobes not densely villous 29
- 29. Gynostegium sessile; free staminal corona lobes equaling gynostegium, erect, trifold with central lobe pronouncedly keeled; plants of E South Africa **301. *Woodia***
  - Gynostegium elevated, free staminal corona lobes overtopping gynostegium, incurved, subrectangular; plants of African woodlands **285. *Glossostelma (G. carsonii)***
- 30. Style-head distinctly conical, occasionally bifid 31
  - Style-head flat, with a central depression or umbonate 35
- 31. Inflorescences sessile, fasciculate; occasionally with dark brown glandular hairs on the vegetative parts; pollinia often with sterile hyaline regions at the point of caudicle attachment **279. *Aspidoglossum***
  - Inflorescences not sessile, or fasciculate; never with dark brown glandular hairs; pollinia always without sterile hyaline regions 32
- 32. Corolla fused for more than a quarter of its length, broadly campanulate, lobes reflexed; corona adnate to both corolla and gynostegium; follicles with protuberances; plants of South Africa **293. *Parapodium***
  - Corolla only basally fused, of various shapes, but lobes normally not reflexed; corona not adnate to corolla; follicles with or without protuberances 33
- 33. Corolla lobes at least 9 mm long, usually brightly colored, horizontally spreading or reflexed; staminal corona lobes concave-cucullate over at least part of their length, inner apical margins forming a pair of teeth, occasionally with tooth in cavity; pollinaria with conspicuously winged and contorted caudicles; follicles smooth or longitudinally grooved **298. *Stathmostelma***
  - Corolla lobes not more than 8 mm long, usually dull colored, not conspicuously spreading nor reflexed; staminal corona lobes not intricately folded; pollinaria without winged and contorted caudicles; follicles smooth or with protuberances 34

34. Staminal corona lobes exceeding gynostegium, usually subulate, S-shaped; plants delicate; leaves always linear, with revolute margins; inflorescences mostly terminal, surrounded by much longer leaves  
**299. *Stenostelma***  
 – Staminal corona lobes not exceeding gynostegium, solid, carnose; plants usually stout; leaves ovate, occasionally undulate, or linear; inflorescences often also along the stem **302. *Xysmalobium***
35. Pollinia with sterile hyaline regions 36  
 – Pollinia without sterile hyaline regions 37
36. Inflorescences pedunculate (rarely sessile), sciadioidal; pollinia dorsiventrally compressed, usually laterally attached to the caudicles, sterile hyaline regions apical, but never at the point of caudicle attachment; plants without glandular hairs on vegetative parts **296. *Schizoglossum***  
 – Inflorescences sessile, fasciculate; pollinia oblongoid, subapically attached to the caudicles, sterile hyaline regions at the point of caudicle attachment; plants occasionally with dark brown glandular hairs on vegetative parts **279. *Aspidoglossum***
37. Flowers nodding in the sciadioidal, extra-axillary inflorescences, very rarely in subglobose heads along the stem; leaves often non-linear; follicles often with soft spines 38  
 – Flowers erect, terminal inflorescence usually present; leaves often linear; follicles without soft spines 40
38. Corona lobes at least twice as long as gynostegium **279. *Aspidoglossum***  
 – Corona at the most slightly exceeding gynostegium 39
39. Staminal corona lobes attached to the back of the anthers, strongly laterally compressed and with a central cavity; rootstock fibrous, occasionally woody, or with a stout woody rhizomatous rootstock but never forming a tuberous caudex; corolla lobes usually ciliate; follicles often inflated  
**286. *Gomphocarpus***  
 – Staminal corona lobes always arising from the base of the staminal column and adnate to it over the whole length, highly diverse in shape; rootstock tuberous; corolla lobes usually not ciliate; follicles never inflated **300. *Trachycalymma***
40. Gynostegium elevated 41  
 – Gynostegium sessile 44
41. Stems usually unbranched; with a stout vertical rhizome from which fusiform lateral tuberous roots arise; leaves semi-succulent, venation obscure; inflorescences terminal and lateral; flowers broadly campanulate; staminal corona lobes carnose, united at the base, when longer than gynostegium then connivent above it **285. *Glossostelma***  
 – Stems branched or unbranched; without a stout vertical rhizome; leaves linear or herbaceous with apparent venation; inflorescences terminal; flowers not broadly campanulate; staminal corona lobes intricately folded, not united at the base, when longer than gynostegium then laterally expanding 42
42. Staminal corona lobes with conspicuous teeth in the cavities; single-stemmed plants of montane areas in southern Africa **280. *Aspidonepsis***  
 – Staminal corona lobes without conspicuous teeth in the cavities 43
43. Staminal corona lobes conspicuously laterally extended **277. *Aidomene***  
 – Staminal corona lobes not laterally extended **278. *Asclepias***
44. Leaves with stiff hairs, scabrid to touch, usually not linear; plants stout; flowers often broadly campanulate; corolla lobes at least 10 mm long; staminal corona lobes usually forming long apical or subapical appendages; follicles often winged  
**292. *Pachycarpus***  
 – Leaves glabrous or with soft indumentum, almost always linear; plants delicate; flowers rotate; corolla lobes mostly shorter than 10 mm; staminal corona lobes usually forming long apical or subapical appendages; follicles never winged **289. *Miraglossum***
45. Staminal corona lobes separate, with or without additional annular corolline corona 46  
 – Staminal corona lobes fused, at least basally, always without additional annular corolline corona 51
46. Staminal corona lobes exceeding gynostegium and connivent above it; corolla ciliate 47  
 – Staminal corona lobes not connivent above gynostegium, corolla not ciliate 48
47. Leaves narrowly elliptic or ovate; corolla broadly campanulate, almost entirely fused, white with dark red center; follicles ovoid, shortly beaked or inflated, solitary or paired, smooth; plants of riverine vegetation **291. *Oxystelma***  
 – Leaves broadly ovate, deeply cordate to reniform; corolla salverform, fused to less than half of total length, cream, yellowish or reddish; follicles always paired, narrowly clavate, with soft spines **294. *Pergularia***
48. Free corona lobes alternating with the anthers; latex white; plants of China (Sichuan)  
**303. *Cynanchum*** (former *Sichuania* species)

- Free corona lobes opposite the anthers; latex white, translucent or yellow 49
- 49. Flowers large, to 4 cm long, narrowly campanulate, adaxially glabrous; leaves deeply cordate to reniform; latex white; plants of Asia
  - 303. *Cynanchum*** (former *Raphistemma* species)
  - Corolla of various shapes, but at the most 2 cm long, adaxially usually with slender trichomes; lobes often conspicuously twisted; leaves basally cuneate, rounded or indistinctly cordate; latex usually translucent, but occasionally white or yellow 50
- 50. Guide rails conspicuously extended along the carinate corona lobes; corolla lobes almost free, apically often strongly twisted; leaves carnosae; latex translucent; plants predominantly of seaside habitats
  - 305. *Pentatropis***
  - Guide rails not conspicuously extended along corona lobes; corolla lobes free or fused to various degrees, apically twisted or not, latex usually translucent, but occasionally white or yellow
- 306. *Vincetoxicum***
- 51. Inflorescences dichasially branched cymes 52
  - Inflorescences simple 53
- 52. Corolla 2.5–6 mm long, adaxially with trichomes; staminal corona parts connate to the filament for not more than one third of gynostegium length; leaves not ciliate; calyx lobes acute or obtuse
  - 306. *Vincetoxicum***
  - Corolla 7–8 mm long, connate to the filament for more than one third of gynostegium length; leaves ciliate; calyx lobes apiculate; insufficiently known plants from Indonesia (Sulawesi) **378. *Mahawoa***
- 53. Latex translucent, plants without prophylls 54
  - Latex white, plants often with prophylls 56
- 54. Style-head extending well beyond connective appendages, rostrate; plants of South Africa
  - 276. *Oncinema***
  - Style-head not extending well beyond connective appendages, flat, umbonate or conical 55
- 55. Leaves at the most 1.5 cm long, caducous; inflorescences bostrychoid, with conspicuously long rachis; plants of Somalia **281. *Calciphila*** (*C. galgalensis*)
  - Leaves usually larger, persistent (but plants often geophytic); inflorescences without conspicuous rachis; plants of Eurasia **306. *Vincetoxicum***
- 56. Plants often with prophylls; corolla adaxially glabrous, corona usually ring-shaped, with staminal and interstaminal parts of the same thickness (but occasionally staminal parts with ligule)
  - 303. *Cynanchum***
  - Plants never with prophylls; corolla adaxially at least with a few trichomes; corona either only of staminal parts, or, when ring-shaped, then staminal parts thicker than interstaminal parts **306. *Vincetoxicum***
- 57. Plants entirely devoid of a corona 58
  - Corona of various origin and composition present 64
- 58. Leaves linear 59
  - Leaves ovate, cordiform or triangular 61
- 59. Plants strongly branched from a woody rootstock; corolla adaxially glabrous; plants of North America **327. *Funastrum*** (*F. utahense*)
  - Plants sparsely branched, grass-like; corolla adaxially papillose or with trichomes; plants of South America 60
- 60. Leaves whorled or alternate; inflorescences subsessile; follicles obclavate **316. *Hemipogon***
  - Leaves opposite; inflorescences long-pedunculate; follicles narrowly fusiform **320. *Morilloa***
- 61. Leaves less than 5 mm long, strongly recurved, plants erect, sparsely branched; plants of Brazil
  - 319. *Minaria*** (*M. graziellae*)
  - Leaves more than 5 mm long, not strongly recurved, when sparsely branched, then not erect 62
- 62. Plants apically twining subshrubs, leaves coriaceous; seeds almost orbicular, ca. 10 mm wide and to 5 mm thick, with a few short (to 5 mm long) yellowish trichomes; plants of southern Argentina
  - 308. *Diplolepis*** (*D. hieronymi*)
  - Plants of various growth forms, leaves herbaceous; seeds ovate, oblong or pyriform, not more than 5 mm wide and 1 mm thick; when coma present, then white, at least 10 mm long 63
- 63. Plants prostrate, hirsute all over, leaves ovate, basally rounded, sessile; inflorescences few-flowered, sessile; corolla lobes only basally fused; plants of Argentina and southern Brazil **321. *Nautonia***
  - Plants erect or twining, but not prostrate, softly puberulous, pubescent or tomentose, leaves pronouncedly cordiform; inflorescences few- or many-flowered, distinctly pedunculate; corolla lobes fused for at least one third of their length, often more **330. *Philibertia***
- 64. Pollinia without sterile hyaline region 65
  - Pollinia with sterile hyaline region 109

65. Inflorescences distinctly compound 66  
 – Inflorescences simple, occasionally a single basal dichasium bearing two monochasia 69
66. Inflorescences forming elongate thyrses with strongly condensed, sessile partial inflorescences; rachis often conspicuously zigzag-shaped; gynostegial corona variable, but not cyathiform or tubular 67  
 – Inflorescences many-flowered dichasia; gynostegial corona cyathiform or tubular 68
67. Plants hirsute to tomentose; flowers pedicellate; staminal corona lobes distinctly shorter than gynostegium; follicles unknown; endemics of central Brazil 317. *Hypolobus*  
 – Plants with indumentum, but not distinctly hirsute; flowers sessile; staminal corona lobes equaling gynostegium; follicles usually cylindrical, paired 325. *Tassadia*
68. Plants medium-sized twiners; leaves (narrowly) ovate, often long-acuminate, basally rounded or indistinctly cordate, soft; inflorescences lax; corona equaling or exceeding gynostegium, style-head occasionally rostrate or capitate; follicles usually paired, slender, less than 15 cm long, with thin pericarp 309. *Jobinia*  
 – Plants large twiners (to 12 m); leaves roundly ovate, basally strongly cordate; inflorescences conspicuously storied, with condensed partial inflorescences in elongate dichasia; corona shorter than gynostegium; style-head flat; follicles solitary, ovoid, large (to 30 cm), with thick pericarp 303. *Cynanchum* (former *Metalepis* species)
69. Style-head with five to seven pronounced appendages 329. *Oxypetalum* (former *Schistogyne* species)  
 – Style-head of various shapes, but not with five to seven pronounced appendages 70
70. Translators with pronounced hyaline teeth (very rarely inconspicuous); style-head rostrate, bifid; corolla lobes often strongly twisted; corona of five free carnose lobes often adnate to corolla and gynostegium 329. *Oxypetalum*  
 – Translators without pronounced hyaline teeth; style-head variable, but when rostrate then usually not deeply bifid; corolla lobes rarely strongly twisted; corona usually not adnate to both corolla and gynostegium 71
71. Corona of three-dimensional staminal lobes adnate to the back of the anthers, well separated from each other 72  
 – Corona otherwise, when of staminal origin then laminar and not adnate to the back of the anthers 77
72. Leaves usually glabrous on both sides, occasionally ciliate, linear or narrowly ovate, basally obtuse or cuneate, usually discolorous, lateral veins conspicuously dense and parallel; flowers often nodding; corolla lobes often long-ciliate; staminal corona lobes often bicornous 314. *Blepharodon*  
 – Leaves with or without indumentum, elliptic, oblong, (ob-)ovate or triangular-deltate, basally often deeply cordate, rarely discolorous, lateral veins not conspicuously dense and parallel; flowers nodding or erect; corolla lobes finely ciliate or glabrous; staminal corona lobes never bicornous 73
73. Flowers nodding; corolla broadly campanulate to salverform 74  
 – Flowers usually erect; corolla rotate 75
74. Leaves elliptic, oblong or obovate; corolla large (at least 1.5 cm diam.); rare endemics of Andean high altitudes 307. *Pentacyphus*  
 – Leaves usually cordate, corolla usually smaller (less than 1.5 cm diam.) 330. *Philibertia*
75. Plants erect; staminal corona lobes differentiated into an outer hood and an inner horn 278. *Asclepias*  
 – Plants twining; staminal corona lobes not differentiated into hood and horn 76
76. Latex with a disagreeable scent; leaves often ovate-elliptical, rarely linear, basally distinctly cordate unless leaves very slender; corolla lobes ciliate, but adaxially glabrous 327. *Funastrum*  
 – Latex unscented; leaves usually elliptical, never cordate; corolla lobes not ciliate, but adaxially densely pubescent; plants of central South America 324. *Petalostelma*
77. Plants single-stemmed, occasionally very sparsely branched, erect perennials, not more than 1 m tall 78  
 – Plants usually twiners of variable size when erect then multi-stemmed 81
78. Flowers erect in a terminal bostryx; style-head rostrate, bifid; corolla lobes twisted; follicles solitary, erect, fusiform; swamp plants of Argentina, Bolivia, southern Brazil and Paraguay 329. *Oxypetalum* (former *Widgrenia*)  
 – Flowers on long pedicels and peduncles, nodding, arising between the upper, occasionally reduced leaves; corolla lobes straight; follicles pendulous when solitary 79
79. Leaves linear, occasionally subwhorled; staminal corona lobes without a proximal lobule; follicles usually paired 322. *Nephradenia*

- Leaves sessile, broadly to very narrowly cordate; staminal corona lobes often with a proximal lobule; follicles usually single 80
- 80. Leaves stem-clasping, glabrous, often glaucous, margins straight, with conspicuously crowded and parallel lateral veins; peduncles and pedicels well-developed; plants of central Brazil and Bolivia  
**313. *Barjonia***
- Leaves not stem-clasping, often with dense indumentum, not glaucous, lateral veins not conspicuously crowded or parallel; flowers almost sessile  
**319. *Minaria***
- 81. Leaves distinctly elongate-triangular with truncate base or hastate, often margins slightly undulate; follicles ovoid, to 15 cm long, with thick pericarp, smooth, keeled, or strongly rugose, containing > 100 seeds; large (> 1 m), very lactiferous twiners; plants of southern South America, worldwide weeds, mainly in *Citrus* plantations 82
- Leaves not distinctly elongate-triangular and not pronouncedly truncate or hastate, not undulate; when so, then plants not exceeding 1 m; follicles always smaller, club-shaped or fusiform, containing < 100 seeds 83
- 82. Style-head usually conspicuously clavate, massive; corolla campanulate to widely salverform, fused for at least one third of its length; gynostegium usually concealed in corolla; corona of free, short, erect, carnose lobes  
**326. *Araujia***
- Style-head umbonate or rostrate but slender; corolla rotate, only basally fused; gynostegium usually concealed in tubular corona  
**328. *Morrenia***
- 83. Style-head distinctly rostrate; mostly plants of southern South America 84
- Style-head of various forms, but not distinctly rostrate 89
- 84. Plants decumbent; corolla and corona chocolate brown; plants of Argentina and Uruguay  
**329. *Oxypetalum*** (former *Rhysostelma*)
- Plants usually twining, more rarely erect; at least corona not chocolate brown 85
- 85. Leaves linear or narrowly triangular to cordate-sagittate; plants not exceeding 1 m, at the most weakly twining; plants of Argentina and Chile 86
- Leaves ovate, elliptic or cordate; plants usually larger, twining 87
- 86. Leaves linear; corona gynostegial, annular, much shorter than gynostegium  
**308. *Diplolepis*** (*D. australis*)
- Leaves mostly narrowly cordate-sagittate, occasionally narrowly triangular-truncate; corona corolline, usually 5-lobed, equaling to exceeding gynostegium (except for style-head)  
**331. *Tweedia***
- 87. Leaves pronouncedly cordate, often discolorous, soft; corona of five separate, carnose staminal lobes  
**330. *Philibertia***
- Leaves ovate or elliptic, but not distinctly cordate, usually concolorous; corona lobes at least basally fused 88
- 88. Flowers bright yellow, leaves elliptic; follicles single; plants of Chile  
**308. *Diplolepis*** (*D. menziesii*)
- Flowers of various colors, but not bright yellow; leaves ovate, often long-acuminate; follicles paired; plants of the Andes and Brazil  
**309. *Jobinia***
- 89. Inflorescences two per node 90
- Inflorescences one per node 96
- 90. Inflorescences clearly axillary (both inflorescences of a pair equally developed) 91
- Inflorescences subaxillary to extra-axillary (usually one inflorescence of a pair with a longer peduncle) 94
- 91. Inflorescences distinctly pedunculate 92
- Inflorescences sessile 93
- 92. Corona simple  
**309. *Jobinia***
- Corona double; plants of Brazil  
**323. *Peplonia***
- 93. Leaves glabrous, often discolorous; corona either simple, of five free or basally fused lobes, or double, with the outer corona enclosing the gynostegium; plants of Brazil  
**323. *Peplonia***
- Leaves often softly pilose; corona simple, fused over at least half of its length  
**311. *Orthosia***
- 94. Plants large twiners, leaves pronouncedly cordiform; inflorescences long-pedunculate, occasionally a basal dichasium with two bostrychoid partial inflorescences  
**303. *Cynanchum*** (subgen. *Mellichampia*)
- Plants small twiners, often with distinct long shoot-short shoot architecture, leaves linear, ovate or elliptic, but not pronouncedly cordiform; inflorescences sessile or short-pedunculate 95
- 95. Leaves not conspicuously distichous; inflorescences often seemingly axillary; corolla lobes adaxially without trichomes, but often papillose; gynostegium usually sessile  
**311. *Orthosia***
- Leaves conspicuously distichous esp. on short shoots; inflorescences always extra-axillary; corolla lobes adaxially glabrous or with trichomes; gynostegium stipitate or sessile  
**312. *Scyphostelma***
- 96. Corolla lobes apically with long vibratile, claviform or capitate trichomes  
**377. *Topea***
- Corolla lobes glabrous or with an indumentum, but without claviform or capitate trichomes 97

97. Corolla lobes adaxially papillose to barbate; corona of five separate, very rarely basally fused staminal lobes; follicles solitary 98  
 – Corolla lobes occasionally papillose or pilose, but not barbate; corona lobes at least basally fused to form a ring-, bowl-, or tube-shaped structure; follicles solitary or paired 101
98. Corona lobes without a proximal appendage 99  
 – Corona lobes with a proximal appendage 100
99. Plants twining, leaves petiolate, herbaceous  
 318. *Metastelma*  
 – Plants erect, leaves (sub-)sessile, often coriaceous  
 319. *Minaria*
100. Plants twining; leaves usually petiolate 315. *Ditassa*  
 – Plants erect; leaves often sessile; plants of Brazil  
 319. *Minaria*
101. Prophylls often present at nodes; leaf bases deeply cordate to almost lobate; leaves triangular; free corona parts often intricately folded or extended into long apices; follicles one, clavate  
 303. *Cynanchum* (subgen. *Mellichampia*)  
 – Prophylls always absent; leaf bases indistinctly cordate, rounded or, truncate; corona either without free parts or, when with free parts forming long apices, then follicles always paired 102
102. Leaf blades ovate, often with an extended tip, usually longer than 5 cm 103  
 – Leaf blades linear to lanceolate, when of other shapes, then distinctly shorter than 5 cm 105
103. Leaves hirsute; corona connivent above gynostegium 310. *Monsanima* (*M. tinguensis*)  
 – Leaves usually glabrous, if with trichomes, then not hirsute; corona not connivent above gynostegium 104
104. Leaves carnose to subsucculent; corona cyathiform, weakly lobed; follicles usually one, fusiform or subclavate with long beak; plants of Argentina and Chile 308. *Diplolepis*  
 – Leaves soft; free corona parts occasionally extended into long apices; follicles always paired, usually 5 cm or longer, at acute angles, occasionally remaining fused at the tips 309. *Jobinia*
105. Leaves conspicuously whorled; corolla lobes densely pilose, plants of southern South America 324. *Petalostelma* (*P. robertii*)  
 – Leaves opposite; corolla lobes glabrous or with trichomes, but not densely pilose 106
106. Corona united into a tube obscuring the gynostegium; tube folded inward apically; anther wings not extending along the entire length of the anther, basally strongly centrifugal; plants of central Brazil 310. *Monsanima* (*M. morrenioides*)  
 – Corona either not united into a tube obscuring the gynostegium, or, when so, then the tube not folded inward apically; anther wings usually extending along the entire length of the anther, never strongly centrifugal basally 107
107. Small herbs, prostrate or somewhat twining, or shrublets; leaves usually ovate to orbicular, more rarely lanceolate or ovate-lanceolate; follicles one, fusiform, solitary; plants of Argentina and Chile 308. *Diplolepis*  
 – Plants profusely branched ramblers with a pronounced long shoot–short shoot architecture; leaves linear to ovate, never orbicular; follicles one or two, fusiform or cylindrical 108
108. Stems usually soon turning brown, leaves on short shoots often smaller and more crowded than on long shoots, when indistinct then long shoots not green; follicles single or paired, at various angles, distinctly fusiform or spindle-shaped and often beaked 312. *Scyphostelma*  
 – Stems green, leaves on long and short shoots similar in size and spacing, often leafless at flowering time; follicles always in pairs at obtuse angles, more or less cylindrical without distinct beak 311. *Orthosia*
109. Plants of South America 110  
 – Plants of Central America or the Caribbean 135
110. Mature branches and leaves inconspicuously short-pubescent to almost glabrous 111  
 – Mature branches and leaves moderate to densely pubescent 117
111. Base of mature leaf blades acute or obtuse to shallowly and broadly subcordate 112  
 – Base of mature leaf blades cordate 115
112. Abaxial leaf blade all over with dense or sparse short (0.2–0.35 mm long) spreading eglandular trichomes; style-head concave; anthers somewhat bent toward flower axis; pollinia subpendent from the caudicles 333. *Atrostemma*  
 – Abaxial leaf blade usually glabrous or with few eglandular and sometimes glandular trichomes on midvein or on surface at apex; style-head plane or convex, rarely rostrate; anthers and pollinia horizontal or almost so 113
113. Inflorescences long-pedunculate, peduncles 5–7.5 cm long; corolla campanulate, throat with 5 pubescent interlobular pads; corona gynostegial, staminal corona segments 3-dentate, adnate to the base of stipe; plants of SE Brazil 354. *Malinvaudia*

- Inflorescences short-pedunculate, sometimes subsessile, peduncles up to 1.7 cm long; corolla usually rotate or rotate-campanulate, limb or throat glabrous or pubescent, but then without pubescent pads; corona gynostegial, staminal corona segments of apically ligulate ascending ridges, adnate to the stipe for most of its length, or truncate and adnate to the base of stipe 114
- 114. Stems and leaves glabrous throughout; leaf colleters 2, in the distal quarter of the petiole; staminal corona of 5 truncate segments -adnate to base of stipe; plants of SE Brazil 339. *Coelostelma*
- Stems and leaves usually short pubescent, with at least some trichomes on nodes and on leaf blades along midvein and/or apex; leaf colleters 2-7 at the adaxial leaf base; staminal corona of apically ligulate ascending ridges adnate to the stipe for most of its length; plants of Central and South America 355. *Matelea*
- 115. Stem pubescence in two lines, of retrorse eglandular trichomes and spreading glandular trichomes; corolla lobes oblong, tightly contorted in bud; staminal corona segments of 5 fleshy, distinctly bilobed elements, interstaminal segments not differentiated; follicles pentagonal and 5-costate; plants of southern Brazil 352. *Lhotzkiella*
- Stem pubescence generally on entire surface, of spreading or retrorse eglandular trichomes and spreading glandular trichomes; corolla lobes ovate or oblong, moderate or loosely contorted in bud; staminal and interstaminal corona of flat, not distinctly bilobed, laterally connate segments, forming an annular or cup-shaped structure; follicles muricate 116
- 116. Basal stem internodes thinly suberized, not sulcate; stem nodes without axillary colleters; calyx with 4-5 colleters in each sinus; corolla lobes dull dark purplish, with several long flat and long white trichomes at adaxial apex; pollinia horizontal from the caudicles; follicles muricate, with blunt-tipped non-suberized tubercles; seeds without a coma; plants of riparian wet or rain forests of Amazonia 369. *Riparoampelos*
- Basal internodes with thick sulcate cork layer; stem nodes with several small axillary colleters; calyx usually with 1-2 colleters in each sinus; corolla lobes white, green, brown or purple, adaxially glabrous or pubescent, when pubescent, then trichomes short, on entire surface or on one side; pollinia pendent from the caudicles; follicles muricate, tubercles acute or with a thick irregular corky apex; seeds with a coma; plants of neotropical dry scrub, seasonally dry forests and savannas 349. *Ibatia*
- 117. Herbs or shrubs with erect, prostrate, decumbent or short twining stems, usually much less than 4 m long when mature; plants mostly from dry savannas (cerrados), deserts, dry scrub or seasonally dry forests 118
- Subshrubs or shrubs with twining stems, 5-30 m long when mature; plants from seasonally dry, wet or rain tropical forests, or from temperate austral savannas or forests 123
- 118. Leaves distichous; stems and inflorescences generally prostrate; plants of the savannas of southern Brazil, E Paraguay and NE Argentina 119
- Leaves decussate; stems erect, sprawling or vining; inflorescences spreading or nodding 120
- 119. Inflorescences one per node, usually prostrate; corolla lobes adaxially verrucose at least at apex; corona gynostegial, of fused staminal and interstaminal segments, cup-shaped, with 10 internal rays; follicles muricate 334. *Austrochthamalia*
- Inflorescences 2-3 per node, erect or spreading; corolla lobes not verrucose; corona of basally connate segments forming a short tube surrounding gynostegium, with 5 erect laminar apical lobes; follicles almost smooth 335. *Brargentina*
- 120. Leaves early caducous, blades with conspicuously undulate margins; corolla salverform, with 5 fascicles of long white trichomes at the throat; corona gynostegial, annular, adnate to the corolla tube; pollinia horizontal or slightly ascendent; deserts of NW Peru 358. *Peruviasclepias*
- Leaves usually persistent, blades with entire or slightly undulate margins; corolla rotate to broadly campanulate, without fascicles of long white trichomes; corona gynostegial, of 5 free staminal segments, annular and 5-lobed, or cup-shaped, adnate to base of corolla and to the stipe; pollinia pendent 121
- 121. Stems with dense grayish tomentose pubescence, eglandular trichomes up to 0.45 mm long; corolla lobes erect and apically recurved, glabrous; corona of 5 free, bifid, conspicuously fimbriate segments; style-head truncate or slightly concave, with 5 bluntish scales at top; plants of dry vegetation in Gran Chaco, northern Argentina, SE Bolivia, southern Paraguay, southern Brazil 370. *Rojasia*
- Stems with dense yellowish or white-translucent pubescence, eglandular trichomes 0.25-3 mm long; corolla lobes usually spreading or slightly recurved,



- glabrous or pubescent; corona of 5 partly or completely connate staminal and interstaminal segments, entire or lobed, glabrous or puberulous; style-head concave, convex or rostrate, without scales; plants of dry scrub, seasonally dry forests and savannas 122
122. Adaxial petiole base with several small digitate colleters; leaf blades usually ovate or elliptic, subcordate or cordate and with several colleters at base 122
- 349. *Ibatia***
- Adaxial petiole base without colleters; leaf blades oblong or oblong-lanceolate, obtuse to cuneate and without colleters at base 347. ***Gyrostelma***
123. Corolla campanulate, urceolate, tubular or salverform; pollinia pendent from the caudicles 124
- Corolla rotate; pollinia horizontal or pendent from the caudicles 127
124. Gynostegial corona dark to blackish purple, adnate to the stipe, mostly exerted from the corolla; follicles muricate and hirsute; plants of southern and SE Brazil, Bolivia and northern to NE Argentina 124
- 340. *Cristobalia***
- Gynostegial corona usually white, pink or yellow, adnate to the corolla tube and the stipe, included in the corolla or exerted in the upper quarter; follicles winged or with wings and projections, glabrous or pubescent 125
125. Corolla urceolate or tubular, lobes usually not reticulate; corolline corona present; gynostegial corona lobes apically truncate or crenulate; follicles (5–)7-winged, or with 7–9 lines of short conic projections; plants widespread in the Neotropics 125
- 353. *Macroscepis***
- Corolla campanulate or salverform, lobes usually conspicuously reticulate; corolline corona absent; gynostegial corona lobes apically bifid-digitate; follicles with 5 wings and several blunt projections 126
126. Nodes usually with 1–2 subaxillary colleters; corolla campanulate; pedicels 2–6.2 times longer than peduncle plus rachis; plants of tropical wet or rain forests of E South America, below 800 m, one species on a sandstone mountain of the Venezuelan Guayana above 1500 m 359. ***Phaeostemma***
- Nodes without subaxillary colleters; corolla generally salverform, narrow-campanulate in one species; pedicels 0.5 to 1.5 times longer than peduncle plus rachis; plants mainly of mountain wet forests above 1000 m in western and northern South America, from Peru to northern Venezuela 351. ***Lachnostoma***
127. Corolla and calyx lobes strongly reflexed; corona gynostegial, shortly tubular or salverform and as long as or a bit shorter than gynostegium; pollinia pendent from the caudicles; follicles 5-winged, long-attenuate at apex; plants of wet and rain lowland and submontane forests, Central and South America 127
- 366. *Pseudolachnostoma***
- Calyx lobes usually ascendent, not reflexed, corolla lobes ascendent, spreading or slightly recurved; corona gynostegial, annular, shallowly cup-shaped, flabellate or of five distinct staminal segments, adnate to the stipe or to the corolla tube, shorter than gynostegium; pollinia horizontal from the caudicles; follicles smooth, with small conical or irregular projections, or winged; when winged, then annular corona present 128
128. Eglandular trichomes on stems, leaves and inflorescences usually translucent or light yellow, sparse to dense, 0.3–2.5(–3.5) mm long; gynostegial and corolline corona present; follicles 3–5-winged, rarely smooth 129
- Eglandular trichomes on stems, leaves and inflorescences usually light brown, yellowish brown or golden-yellow, 1.9–7 mm long; gynostegial corona present; corolline corona absent; follicles smooth or with short inconspicuous projections, unknown for *Orinoquia* 131
129. Lower internodes of mature stems conspicuously lenticellate; anthers with radial laminar dorsal appendages; widespread from northern America to Argentina 345. ***Gonolobus***
- Lower internodes of mature stems usually thinly suberized, not lenticellate; anthers without dorsal appendages 130
130. Corolla lobes narrowly ovate to ovate-oblong, adaxial side basally densely covered with erect trichomes; style-head exerted 337. ***Chloropetalum***
- Corolla lobes narrowly triangular, adaxial side basally lanose; style-head included in the corolla tube 373. ***Tressensia***
131. Inflorescences 7–30-flowered, long-pedunculate; corolla lobes usually apically undulate and crenate, adaxially papillate along a medial line; gynostegium stipitate; anthers convex, sometimes dorsally inflated and vesicular; corona gynostegial, annular or 5-lobed, smooth, striate, sometimes rugose, mainly adnate to the stipe 132
- Inflorescences 2–6-flowered, subsessile or long-pedunculate; corolla lobes usually obtuse or emarginate at apex, not undulate and crenate nor

- papillate; gynostegium sessile or subsessile; anthers slightly convex or emarginate, not vesicular; gynostegial corona shallowly cup-shaped, flabellate or of five almost distinct staminal segments, not striate or rugose nor verrucose, adnate to base of corolla tube and to gynostegium 133
132. Anthers inflated, thick and vesicular dorsally, hiding most of style-head; staminal corona annular, sometimes slightly 5-lobed, smooth or somewhat striate, without radial projections 344. *Fischeria*
- Anthers convex, not inflated, with a thin translucent apical membrane, not hiding style-head; staminal corona of five almost distinct, conspicuously rugose or verrucose lobes, frequently with five laterally flat or conic projections that arise radially from the stipe 368. *Rhytidostemma*
133. Inflorescences subsessile; calyx lobes oblong-elliptic, usually with 1–2 axillary colleters; gynostegial corona purple to black, forming a deeply 5-lobed disc; pollinia oblongoid or narrowly calceolate; follicles somewhat tuberculate, with small conic protuberances; plants of tropical rain forests and lower montane wet or rain forests from Colombia to Bolivia 365. *Pruskortizia*
- Inflorescences long-pedunculate; calyx lobes ovate, usually without colleters; gynostegial corona shallowly cup-shaped or of five almost distinct staminal lobes, yellowish as far as known; pollinia obovoid or obovoid-reniform; follicles smooth or slightly striate when dried (unknown for *Orinoquia*) 134
134. Stems, leaves and inflorescences with sparse to moderate pubescence of dark brown, long (1.9–3 mm) eglandular trichomes, and dense pubescence of dark brown to black glandular trichomes (0.3–0.4 mm long); corolla 17–18 mm diam., with deltoid lobes; pollinia 0.6–0.7 mm long; plants of non-flooded wet forests of French Guiana 346. *Graciemoriana*
- Stems, leaves and inflorescences with moderate pubescence of golden-yellow, eglandular, very long (5–7 mm long) trichomes, and scarce pubescence of translucent glandular trichomes (0.1–0.15 mm long); corolla 50–55 mm diam., with narrowly ovate lobes; pollinia 0.9–1 mm long; plants of wet or rain forest, at headwaters of the Orinoco river, Venezuela 357. *Orinoquia*
135. Plants of Central or North America 136
- Plants of the Caribbean 159
136. Mature branches and leaves inconspicuously short-pubescent or almost glabrous 137
- Mature branches and leaves moderately or densely puberulous to hirsute 141
137. Gynostegial corona and corolline corona (annular or cup-like, entire or discontinuous) present 138
- Only gynostegial corona present 139
138. Lower internodes of mature stems conspicuously lenticellate; anthers with radial laminar dorsal appendages 345. *Gonolobus*
- Lower internodes of mature stems usually thinly suberized, not lenticellate; anthers without dorsal appendages 337. *Chloropetalum*
139. Plants with a thick, erect, conspicuously corky caudex; pubescence of stems, leaves and inflorescence of appressed ferruginous more or less vermiform eglandular trichomes, these trichomes with thin non-sculptured walls, glandular-capitate trichomes few or absent; leaves early caducous, blades suborbicular; follicles narrowly fusiform, with short, obtuse, suberized projections 372. *Suberogerens*
- Plants without a caudex; pubescence of stems, leaves and inflorescence of spreading or retrorse eglandular trichomes and sparse glandular-capitate trichomes, eglandular trichomes with sculptured walls; leaf blades ovate, elliptic or oblong-lanceolate, usually persistent; follicles fusiform or fusiform-attenuate, winged, ridged or smooth, and sometimes with conic or uncinata, non-suberized projections 140
140. Leaf blade abaxial surface frequently with sparse, equally distributed pubescence of short, spreading, eglandular trichomes; style-head concave; anthers somewhat bent toward flower axis; pollinia subpendent; corona of partly connate staminal and interstaminal segments, staminal segments thickly laminar or fleshy, adnate to the stipe only at base, interstaminal segments deeply concave, usually puberulous abaxially; follicles with 5 wings and several conical or conical-uncinate projections 333. *Astrostemma*
- Leaf blade abaxial surface glabrous or with few eglandular trichomes, sometimes short eglandular and glandular trichomes on midvein and/or margins; style-head plane or convex, rarely rostrate; anthers and pollinia horizontal or almost so; corona of partly connate staminal and interstaminal segments, staminal segments fleshy, elevated, ligulate ridges adnate to stipe for most of its length, interstaminal segments plane or slightly concave, glabrous throughout; follicles 5-winged, 5-ridged or almost smooth 355. *Matelea*
141. Stems, leaves, inflorescences and follicles with dense white-silvery woolly indumentum, of intermixed

- ribbon-like multicellular eglandular trichomes; corolla lobes with long, plumose, caudate, purple appendages; pollinia pendent, with a slender sterile horn-like basal process connected to the caudicles
- 374. *Trichosacme***
- Stems, leaves, inflorescences and follicles pubescent to glabrescent, pubescence generally hirsute, hirtelous or puberulous, usually with a mixture of short and long acicular or uncinat e glandular trichomes, or of glandular-capitate and eglandular acicular or uncinat e trichomes; corolla lobes without plumose appendages; pollinia horizontal or pendent, without a horn-like basal process 142
142. Stems, leaves and inflorescences with glandular capitate trichomes with white crystalline inclusions; corona of 5 diversely digitat e appendag ed lobes; follicles long fusiform-cylindrical, smooth, glabrous and mottled **363. *Polystemma***
- Stems, leaves and inflorescences with translucent, glandular, capitate trichomes, yellowish brown or reddish, without white crystalline inclusions, remaining translucent or turning brown to black when dried; corona lobes diverse, not digitat e appendag ed (except in *Dictyanthus*, but then glandular trichomes translucent and follicles muricate); follicles ovate or fusiform, muricate or winged, or almost smooth and with few sparse conic projections, usually puberulent to hirsute, sometimes glabrous, not mottled 143
143. Corolla lobes undulate and crenate at apex; anthers inflated dorsally, vesicular, frequently pear-shaped; follicles usually obtuse at apex, smooth or with some small conic projections, not muricate or winged **344. *Fischeria***
- Corolla lobes marginally entire or undulate, sometimes marginally revolute but not undulate and crenate; anthers not inflated dorsally; follicles generally acute, acuminate or attenuate at apex, with smooth, muricate or winged surface 144
144. E glandular long trichomes (5–6 celled) on conic or column-like multicellular bases present on stems, leaves, inflorescences and follicles; style-head long-rostrate, appendage narrowly clavate, apically obtuse; whole plant turning blackish when dried **364. *Prosthecidiscus***
- E glandular long trichomes usually surrounded by a narrow ring of small modified epidermal cells present on stems, leaves, inflorescence and sometimes on follicles; style-head not rostrate, or short-rostrate and apically rugose or bifid; plants usually not turning blackish when dried 145
145. Corolla urceolate or tubular; follicles 7-winged or with 7–9 lines of conic projections; petioles with several (ca. 3–5) digitate axillary colleters **353. *Macroscepis***
- Corolla rotate to campanulate; follicles muricate or 3–5 winged, rarely smooth; petioles without axillary colleters except for small axillary colleters on petioles of *Ibatia*, but then follicles muricate 146
146. Herbs or subshrubs with erect, prostrate, decumbent or short twining stems, usually less than 3 m long when mature; plants mostly from dry savannas, deserts, dry scrub or seasonally dry forests 147
- Subshrubs or shrubs with twining stems, 5 to 40 m long when mature; plants from seasonally dry, wet or rain tropical forests, or from temperate forests or savannas 153
147. Erect herbs or subshrubs, up to 0.7 m tall; leaf blades attenuate, obtuse, acute, rounded or indistinctly cordate at base; follicles smooth, hirsute, with conspicuous mixed pubescence **360. *Pherotrichis***
- Prostrate, decumbent, sometimes erect herbs or short vining (sub-)shrubs, stems 0.2–3 m long; leaf blades hastate or cordate at base; follicles with obtuse, acute or uncinat e projections, glabrous or with homogeneous or mixed pubescence 148
148. Corona digitat e 5-lobed, with lobes partly adnate to the corolla tube; pubescence of stems, leaves and inflorescences mixed, consisting of eglandular, uncinat e or spreading, long and short trichomes, and spreading glandular, short translucent trichomes; corolla tube internally convoluted with raised parts opposite corona lobes and sacs formed between them; corolla lobes often sharply revolute **342. *Dictyanthus***
- Corona diverse, lobes entire, dentate, fimbriate or ligulate-spathulate, not digitate, adnate to the corolla tube only at the base; pubescence of stems, leaves and inflorescences usually mixed, of eglandular and glandular capitate trichomes, without uncinat e trichomes; corolla tube not internally convoluted; corolla lobes plane to somewhat revolute 149
149. Thick erect conspicuously corky caudex present; pubescence of stems, leaves, and inflorescences of appressed ferruginous, more or less vermiform eglandular trichomes, with thin non-sculptured walls; glandular-capitate trichomes few or absent; follicles narrowly fusiform, with short, obtuse, suberized projections **372. *Suberogerens***
- Caudex small or absent; pubescence on stems, leaves and inflorescences of spreading or retrorse translucent eglandular trichomes with sculptured walls,

- glandular capitate trichomes usually dense; follicles fusiform or ovate-fusiform, with short or long projections, with or without cork 150
150. Corolla tube adaxially with long, linear-spathulate whitish or purplish spreading trichomes 2.5–3.5 mm long; corona gynostegial, conical-truncate, adnate to stipe of gynostegium, marginally differentiated into 10 ligulate-spathulate erect lobes in pairs in interstaminal position, and 5 short, subulate lobes in staminal position; anthers with dorsal-apical dehiscence and without hyaline membranes 348. *Himantostemma*
- Corolla tube adaxially glabrous or pubescent, when pubescent then trichomes acicular or papillate white-translucent, less than 1 mm long; corona gynostegial, of 5 lobes at least basally connate, cyathiform, lobate, crenulate, dentate or fimbriate; anthers with lateral or dorso-lateral dehiscence and with hyaline margins 151
151. Stems usually twining, rarely trailing, not prostrate, usually single, with thick fissured cork on lower internodes; pollinia pendent, with a narrow hyaline sterile margin close to or along the proximal end (close to the caudicles); plants widespread in the Neotropics 349. *Ibatia*
- Stems prostrate or trailing, usually several or many, slightly or not suberized in lower internodes; pollinia horizontal or somewhat bent toward flower axis, with a hyaline furrow or margin along distal half 152
152. Leaf axils with 3–4 small digitate colleters, blades usually with 5 colleters at the base; corolla lobes spreading, adaxially barbate, with a small tooth-like projection at base; gynostegial corona tubular-urceolate, apically with 5 short involute ligulate lobes; plants endemic to sandhills and dry scrub in SE United States 343. *Edisonia*
- Leaf axils without colleters, blades without colleters or these early-caducous; corolla lobes usually ascending to erect, adaxially glabrous or sparsely pubescent, without a basal tooth; gynostegial corona 5-lobed, connate to 3/4 of its length, usually adnate to gynostegium; plants endemic to deserts of Northern Mexico (and probably to SW United States) 338. *Chthamalia*
153. Pubescence of eglandular short and long trichomes present on vegetative structures and inflorescences; corolline corona present 154
- Pubescence of glandular and eglandular trichomes present on vegetative structures and inflorescences; corolline corona present or absent 156
154. Stem and leaf pubescence of long eglandular trichomes 1.5–5.3 mm; corolla rotate, 36–48 mm diam., lobes spreading, ovate-orbicular or broadly deltoid; gynostegium sessile; corolline corona a shallow fleshy cup, roughly pentagonal with prominent radial angles; pollinia horizontal from the caudicles 371. *Rotundanthus*
- Stem and leaf pubescence of short (0.25–0.75 mm) and long (1–2.5 mm) eglandular trichomes; corolla campanulate or rotate-campanulate, 7–28 mm diam., lobes spreading to reflexed, ovate or oblong; gynostegium stipitate; corolline corona cupuliform-urceolate, shortly urceolate or tubular; pollinia pendent from the caudicle 155
155. Corolla lobes ovate, spreading; corolline corona tubular-cupuliform, apically fimbriate; follicles hispid, densely prickled, with long, curved, conspicuous projections; plants from upper mountain cloud forest; plants of northern Guatemala and southern Mexico 376. *Vulcanoa*
- Corolla lobes narrowly ovate to oblong, reflexed; corolline corona tubular or shortly funnel-shaped, apically entire or dentate, not fimbriate; follicles sparsely puberulous, 5-winged or 5-costate; plants from tropical or premontane rain forest; plants of Peru, SW Brazil, extending to Nicaragua 366. *Pseudolachnostomma*
156. Anthers with radial laminar dorsal appendages; gynostegial and corolline corona (annular, entire or discontinuous) present; follicles 3–5-winged, rarely smooth 345. *Gonolobus*
- Anthers without laminar dorsal appendages; only gynostegial corona present; follicles strongly muricate 157
157. Leaf blade adaxial base and interpetiolar line with fascicles of 30–50 colleters; corollas shallowly campanulate, 38–44 mm in diam., with broadly elliptic or ovate-elliptic lobes; pollinia pendent, oblong-spathulate, ca. 1.3 mm long; follicles dark-brown, densely pubescent, 22–27 cm long, with long, strongly curved projections 2.5–3.5 cm long; plants of Central America 336. *Bruceholstia*
- Leaf blade adaxial base with ca. 4 digitate colleters, interpetiolar line with 3–4 colleters; corollas rotate to shallowly campanulate-rotate, 7.5–25 mm in diam., with elliptic, narrowly deltoid to oblong-obovate lobes; pollinia horizontal or almost so, narrowly subquadrate to rounded-rectangular or almost reniform, 0.15–0.2 mm long; follicles green, 6–10 cm long, inconspicuously pubescent or

- glabrescent, with antrorse or spreading projections 0.1–0.3 cm long; plants of the United States 158
158. Stout vines; inflorescences umbelliform cymes, 3–6-flowered; corolla rotate, lobes elliptic, reticulate; corona of 5 completely fused staminal and interstaminal elements, forming a marginally undulate low ring adnate to base of corolla, and 5 elevated ridges adnate to the gynostegial stipe; dorsal-external anther margin mostly covered by style-head
- 341. *Cyclodon***
- Herbaceous vines; inflorescences dichasial or racemiform cymes, usually 8–20-flowered; corollas shallowly campanulate-rotate, lobes usually oblong or spatulate, reticulate or not; corona cup-shaped, arising near the junction of the gynostegial stipe and the corolla, of 5 staminal elements partly united in a ring that reaches or surpasses style-head, each segment usually with two triangular teeth on abaxial side; anthers radially protruding from below style-head
- 356. *Odontostephana***
159. Stems, leaves and inflorescences sparsely to more or less densely covered with whitish multicellular eglandular trichomes, glandular capitate trichomes absent, or few and inconspicuous 160
- Stems, leaves and/or inflorescences sparsely to more or less densely covered with whitish, yellowish or light brown multicellular eglandular and glandular capitate trichomes 161
160. Leaf blades oblong-lanceolate, basally sagittate; staminal corona segments prominent-convex and cucullate (hooded), not ligulate; plants of Cuba
- 361. *Poicilla***
- Leaf blades ovate, oblong-ovate to narrowly elliptic, basally cuneate, rounded, obtuse, truncate or indistinctly cordate; staminal corona segments not cucullate, ligulate or not 164
161. Corolla campanulate, lobes glabrous, basally incurved with an eyespot-like concavity and large, white eyespot at apex; staminal corona a costate ridge adnate to stipe along most of its length, apically ligulate; follicles ovoid, 5-ridged; plants of Jamaica
- 350. *Jacaima***
- Corolla rotate-subcampanulate or urceolate, lobes pubescent at least on the adaxial face, spreading or somewhat curved, without a basal concavity and without ocelli; staminal corona laminate or thick-laminate, adnate to the stipe only at base, not ligulate; follicles fusiform, 10-ridged, smooth or with some isolated protuberances, strongly beaked in some species 162
162. Corolla rotate, lobes reticulate, pubescent on both surfaces; staminal corona lobes oblong, extending ca. 0.5 mm beyond style-head; corolline corona a protuberance at the base of the staminal corona; follicles oblong-fusiform, longitudinally 10-ridged; plants endemic to Hispaniola
- 332. *Anemotrochus* (*A. viridivenius*)**
- Corolla urceolate, lobes not reticulate, abaxially glabrous; staminal corona lobes well differentiated, or part of a highly complex system of fused staminal-interstaminal coronas, which are folded into the corolline corona, shorter or as long as gynostegium, sometimes apparently absent; corolline corona absent or forming a complicated system of ridges and bulges mostly in the fused part of the corolla; follicles smooth or with some isolated protuberances 163
163. Leaf blades tapering and without colleters at base; corolla lobes twisted, adaxially on left side pubescent with needle-like or short and blunt trichomes; corolline corona absent or a protuberance at base of staminal corona parts; follicles with protuberances; plants of the West Indies
- 332. *Anemotrochus***
- Leaf blades basally rounded or indistinctly cordate, with 2–4 colleters at base; corolla lobes carnose, not twisted, adaxially without needle-like or short and blunt trichomes; corolline corona part of a complicated system of ridges and bulges mostly in the fused part of the corolla, or apparently absent or reduced; follicles (as far as known) smooth and glabrous; plants of Cuba
- 375. *Tyodontia***
164. Mature leaf blades 2 × 1 cm to ca. 6 × 3 cm, basally rounded, obtuse or truncate, with glabrous or nearly glabrous surface, pubescent on veins 165
- Mature leaf blades usually from 6 × 4 cm to 20 × 15 cm or larger, basally cordate or subcordate (truncate to cuneate in few *Gonolobus* species, where dorsal laminar anther appendages and corolline coronas occur), usually with whole surface pubescent 166
165. Corolla lobes ovate, adaxially pubescent; staminal corona lobes obovate to suborbicular, rounded to emarginate at apex, with a small internal ligule, as long as the gynostegium; anther wings thick, slightly incurved; style-head flat; follicles subcylindrical-fusiform, not winged; plants of Cuba
- 362. *Poicillopsis***
- Corolla lobes linear-lanceolate, glabrous; staminal corona lobes swollen at base, subtriangular in front view, ridged, rising vertically and then connecting to the stipe below the anthers, without internal ligule, shorter than gynostegium; anther wings thin, with divergent apices; style-head conical or convex with a

- slightly raised protuberance; follicles fusiform, with 5 undulating wings (follicles unknown for one species); plants of Hispaniola **367. *Ptycanthera***
166. Mature stems with thick fissured cork on lower internodes; latex with unpleasant smell; pollinia pendent from the caudicles 167  
 – Mature stems lenticellate or with thin layer of cork on lower internodes; latex with or without an unpleasant smell; pollinia horizontal or slightly bent down from the caudicles 168
167. Inflorescence an umbelliform cyme; corolla urceolate or tubular; gynostegium generally included; staminal corona segments fleshy, basally adnate to the corolla tube over at least half of its length, free at apex and frequently concealing corolla throat; corolline corona present; follicles (5–)7-winged, 2 of the wings incomplete (Neotropics) **353. *Macrosepiis***  
 – Inflorescence a racemiform cyme; corolla subcampanulate or campanulate, gynostegium generally exserted; staminal corona segments usually laminar, adnate to the base of the corolla tube, not concealing corolla throat; corolline corona absent; follicles muricate (Neotropics) **349. *Ibatia***
168. Mature stems 5–10 mm thick or thicker, with light brown pubescence of eglandular, spreading long trichomes (1.5–6 mm), and glandular capitate trichomes (0.15–0.4 mm), these turning black when dried; corolla lobes conspicuously undulate and crenate on one or both margins; gynostegial corona usually forming an annular structure adnate to the stipe, apically 5-lobed in some species; anthers inflated dorsally, vesicular, frequently pear-shaped; corolline corona absent; follicles broadly ovoid to fusiform, smooth or with some small protuberances, not muricate or winged (Neotropics) **344. *Fischeria***  
 – Mature stems generally 1.5–4 (–5) mm thick, usually with whitish or yellowish pubescence, eglandular trichomes spreading or retrorse (0.4–2 (–2.5) mm), glandular capitate trichomes (0.1–0.4 mm) translucent to light brown when dried; corolla lobes plane, sometimes somewhat concave or marginally undulate, but not undulate and crenate; gynostegial corona of staminal and interstaminal segments; gynostegial corona of staminal lobes adnate to base of corolla tube, usually ridge-like and raised, not ligulate, interstaminal segments flabellate, oblong-sulcate or cup-like; corolline corona present, annular but sometimes interrupted or discontinuous, or of pubescent mounts of tissue subopposite to the anthers; laminar dorsal anther appendages present or absent; follicles 3–5-winged, wings sometimes discontinuous or reduced, absent in one species 169
169. Laminar dorsal anther appendages present; mature stems conspicuously lenticellate (Neotropics and temperate North America) **345. *Gonolobus***  
 – Laminar dorsal anther appendages absent; mature stems with a thinly suberized layer, not lenticellate (Neotropics) **337. *Chloropetalum***
- V.5.a. Subtribe *Astephaninae* Endl. ex Meisn. (1840).**
- Usually small twiners; latex translucent, leaves small, subcoriaceous. Inflorescences mostly sessile to shortly pedunculate, sciadioid; pollinia ovate to clavate; caudicles flattened with conspicuous hyaline margin. Follicles fusiform. In molecular analysis, *Astephaninae* are sister to the remaining *Asclepiadeae* (Liede 2001). Three genera in southern Africa.
- 274. *Astephanus* R. Br.**
- Astephanus* R. Br., *Asclepiadeae* 43 (1810); Bruyns, *Kew Bull.* 58: 867–887 (2003), rev.  
*Haemax* E. Mey. (1838).
- Suffrutescent twiners, glabrous or sparsely puberulous, 0.15–3 m tall, roots fibrous. Leaves 5–20 (–36) cm long, ovate to oblong. Inflorescences 6–8-flowered. Corolla 3–5 mm long, tubular, highly fused; adaxially apically papillose and with a ring of stiff reflexed trichomes in the tube opposite the anthers; lobes oblong, spreading at anthesis; corona absent; gynostegium sessile; anther wings minute; style-head rostrate. Follicles 5–6 cm long. Seeds pyriform, wingless.  $2n = 20$ .
- Two spp. in South Africa's winter rainfall area, Table Mountain sandstone and limestone; at low altitudes.
- Hitherto all species of *Astephanus* reported from the New World have been found to belong to other genera, so that the genus, which is closely related to *Microloma*, is restricted to the two African species.
- 275. *Microloma* R. Br.**
- Microloma* R. Br., *Asclepiadeae* 42 (1810); Wanntorp, *Opera Botanica* 98: 1–69 (1988), rev.; Bruyns & Linder, *Bot. Jahrb. Syst.* 112: 453–527 (1991), rev.; Bruyns, *Asklepios* 52: 71–74 (1991).

Suffrutescent twiners or rigid, spinescent shrubs, to 1 m tall, pubescent or tomentose; rootstock woody. Leaves occasionally caducous, occasionally alternate, subsessile, 0.4–7 cm long, linear to triangular. Inflorescences 1–15-flowered. Calyx lobes occasionally showy; corolla 2–9 mm long, urceolate to tubular, occasionally carnose, green and white, yellow or red, tube with stiff reflexed trichomes, occasionally with antesealous ridges; lobes orbicular or triangular, twisted, keeled, usually ciliate, usually connivent into mouth of tube, closing it completely; occasionally with corolline corona knobs; gynostegium stipitate, connective appendages lanceolate with intertwined trichomes; style-head (depressed-) conical. Follicles 2–10 cm long. Seeds pyriform, wingless.  $2n = 20$ .

12 spp. in four sections in South Africa and Namibia, winter rainfall area; to 2000 m. Bird-pollinated according to Pauw (1998).

#### 276. *Oncinema* Arn.

*Oncinema* Arn., Edinb. New Philos. J. 17: 261 (1834); Liede, Ann. Missouri Bot. Gard. 88: 657–668 (2001), phyl. *Glossostephanus* E. Mey. (1838).

Suffrutescent twiner, 50–75 cm tall, glabrous; rhizomatous. Leaves 4–8 cm long, linear to oblong. Inflorescences 6–12-flowered, pedunculate, botrychoid. Flowers sweetly fragrant; corolla 6–7 mm long, rotate, greenish yellow, adaxially apically papillose, basally with trichomes; lobes linear, acute, twisted; gynostegial corona equaling gynostegium (except for style-head), of basally fused, subulate, erect staminal lobes; gynostegium sessile, style-head rostrate, neck obconical. Follicles 5.5–7.5 cm long. Seeds ovate, winged.

One sp., *O. lineare* (L. f.) Bullock, in South Africa (Cape Province), winter rainfall area; river banks, valleys; 30–1000 m.

#### V.5.b. Subtribe Asclepiadinae Decne. ex Miq. (1857).

Usually erect herbs, often with root tubers. Leaves usually sessile, linear or narrowly elliptic. Inflorescences usually terminal and subterminal, extra-axillary, sciadioid. Corolla usually rotate, basally fused; corona gynostegial, of free staminal lobes; gynostegium usually sessile; style-head flat

to conical. Follicles fusiform or obclavate, often paired. Seeds ovate, winged, usually with white apical coma.

Generic circumscriptions in Asclepiadinae are still in a state of flux; following molecular analysis, Goyder (2009) proposed that all genera except for *Calotropis*, *Kanahia* and *Pergularia* be united under a wide concept of *Asclepias*. Here, *Asclepias* is restricted to the monophyletic New World species and the traditional concept for the African species is adopted, even though some of the genera are known to be polyphyletic. 26 genera in Africa, Asia and the Americas.

#### 277. *Aidomene* Stopp

*Aidomene* Stopp, Bot. Jahrb. Syst. 87: 21 (1967).

Usually unbranched herb, ca. 50 cm tall, with root tubers; shoots annual. Leaves slightly ascending; 3–5 cm long, adaxially patchily puberulous, abaxially glabrous. Inflorescences 2–5-flowered, long-pedunculate. Corolla ca. 8 mm long, brown, glabrous; lobes ovate, marginally membranous; staminal corona lobes surpassing gynostegium, horizontally spreading, transversely lingulate, adaxially basally with wings forming a cup-like structure; pollinia clavate; caudicles horizontal, cylindrical. Follicles 4–5 cm long.

A single species, *A. parvula* Stopp, in Angola, moist grassland.

#### 278. *Asclepias* L.

*Asclepias* L., Sp. Pl. 214. (1753); Woodson, Ann. Missouri Bot. Gard. 41: 1–211 (1954); Goyder et al., Ann. Missouri Bot. Gard. 94: 423–434 (2007), phyl.; Fishbein et al., Syst. Bot. 36: 1008–1023 (2011), phyl.

*Acerates* Elliott (1817).

*Anthanotis* Raf. (1817).

*Podostigma* Elliott (1817).

*Otaria* Kunth (1818).

*Podostemma* Greene (1897).

*Asclepiodella* Small (1933).

Herbs or shrubs, usually perennial, to 1 m tall, with fibrous, often carnose, roots. Leaves occasionally alternate or whorled, 2–17 cm long, 0.1–3 cm wide, occasionally triangular-deltate, elliptic or oblong. Inflorescences extra-axillary and terminal, (1–)7–30-flowered. Corolla 5–15 mm long, uniformly white, green, yellow, brownish, reddish

or orange-red, glabrous or evenly covered with trichomes, lobes ovate to oblong, usually strongly reflexed; staminal corona lobes light colored, mostly surpassing gynostegium, differentiated into erect, cucullate distal lobules (“hood”), and inflexed, solid, spur-shaped proximal lobules (“horn”); gynostegium highly elevated by column, or, rarely, stipe; pollinia clavate; caudicles S-shaped, cylindrical or ribbon-shaped. Follicles occasionally with soft spines, occasionally inflated. Seeds rarely lacking a coma.  $2n = 22$ .

About 100 spp. in the Americas, with a center of distribution in N America.

The results of Goyder et al. (2007) and Fishbein et al. (2011) suggest that *Asclepias* s. str. is a purely American genus; thus, the inclusion of several African species by Goyder (2009) is not followed here.

279. *Aspidoglossum* E. Mey.

*Aspidoglossum* E. Mey., Comm. Pl. Afr. Austr. 200 (1838); Kupicha, Kew Bull. 38: 599–672 (1984), rev.  
*Rhinolobium* Arn. (1838).

Sparsely branched, apically pendulous, tuberous geophytes, 0.3–1.1 m tall, with dark brown glandular trichomes. Leaves occasionally alternate or whorled, 1–7.5 cm long, occasionally (ob-)ovate. Inflorescences 1–13-flowered, occasionally thyrsoidal, (sub-)sessile; flowers usually nodding. Corolla 2–8 mm long, creamish yellow or green, streaked reddish, occasionally with trichomes; lobes elliptic, occasionally remaining connate at apices, occasionally right-hand margin ciliate; staminal corona lobes usually surpassing gynostegium, erect, basally dorsally compressed, truncate or caudate, with erect or inflexed, triangular or ovate, often caudate proximal lobules; pollinia occasionally with apical germination pore. Follicles 2.5–9 cm long, occasionally with protuberances, with dense indumentum. Seeds pyriform.

35 spp. in four sections across tropical Africa, usually (moist) grassland and open woodland, occasionally in rock outcrops or coastal sandflats; 0–2800 m.

280. *Aspidonepsis* Nicholas & Goyder

*Aspidonepsis* Nicholas & Goyder, Bothalia 22: 24 (1992); Müller et al., III. Handb. Succ. Pl.: 18–20 (2002), part. rev.

Herbs, 17–65 cm tall, sparsely branched, (almost) glabrous, root tubers fusiform to globose. Leaves 0.5–13.5 cm long, occasionally lanceolate or falciform. Inflorescences 2–17-flowered. Corolla 4–10.5 mm long, greenish yellow or reddish brown, lobes elliptic or ovate, occasionally reflexed, occasionally revolute; staminal corona mostly surpassing gynostegium, lobes horizontally spreading, cucullate or unguiculate, occasionally basally or apically elongated, occasionally with shorter, erect to inflexed, subulate or liguliform proximal lobules; gynostegium atop a column, pollinia oblongoid or clavate; caudicles articulated; carpels occasionally with trichomes; style-head white or green. Follicles ca. 3.5 cm long, with dense indumentum.

Five spp. in two subgenera, E South Africa, high altitude mountain grasslands; (450–)1000–2100 m.

Closely related to *Aspidoglossum*.

281. *Calciphila* Liede & Meve

*Calciphila* Liede & Meve, Novon 16: 369–370 (2006); Liede-Schumann, Fl. Somalia 3: 138–139 (2006), as “*Calcareophilum*”, reg. rev.

Small shrubs or herbaceous twiners, to 40 cm tall, densely pubescent; latex translucent. Leaves caducous, sessile, carnosely, 0.15–1.4 cm long, elliptic or obovate. Inflorescences 3–40-flowered. Corolla 1.5–1.7 mm long, creamish, occasionally with red tinge, occasionally with verrucose trichomes; lobes ovate; gynostegial corona ring cyathiform or urceolate, exceeding gynostegium, creamish, of connate, ovate or bifid, sulcate to slightly cucullate staminal and shorter, rectangular or oblong interstaminal parts; pollinia oblongoid, caudicles flattened; style-head white, umbonate or tabular. Follicles 13–30 mm long, fusiform. Seeds oblong, winged, tuberculate.

Two spp. in Somalia, calcareous areas; 800–2000 m.

The genus is weakly associated with Asclepiadinae in molecular analysis (Surveswaran et al. 2014).

282. *Calotropis* R. Br.

*Calotropis* R. Br., Asclepiadeae 28 (1810); Rahman & Wilcock, Nord. J. Bot. 11: 301–308 (1991), rev.  
*Madorius* Kuntze (1891), nom. illegit.



Shrubs to small trees or erect herbs (*C. acia* Buch.-Ham.), to 6 m tall; occasionally densely tomentose when young. Leaves coriaceous or car-nose, 9–28 cm long, (ob-)ovate or elliptic, occa-sionally undulate. Inflorescences 3–17-flowered, occasionally thyrsoïdal. Corolla 10–15 mm long, white, green or lilac; lobes valvate, ovate to lance-olate, occasionally undulate; free staminal corona lobes whitish or lilac, maximally equaling gynos-tegium, erect, solid, laterally compressed, basally with a coiled spur; gynostegium stipitate; pollinia clavate; caudicles declinate, cylindrical; style-head creamish yellow. Follicles 6.5–12.5 cm long, ellipsoid, with thick pericarp, inflated.  $2n = 22$ .

Three spp., Africa, Asia; naturalized in the arid tropics all over the world, roadsides, savan-nas, open places at low to medium altitudes.

### 283. *Cordylogyne* E. Mey.

*Cordylogyne* E. Mey., Comm. Pl. Afr. Austr. 218 (1838); Bester et al., Phytotaxa 321: 114–124 (2017).

Grass-like geophytes, 30–80 cm tall, puberulous; root tubers narrowly cylindrical. Leaves (sub-) sessile, linear, ascending to spreading, 5–12 cm long. Inflorescences 4–15-flowered, long-pedun-culate. Corolla 2.5–8 mm long, campanulate, greenish-white to brown; lobes oblong, suberect, revolute; gynostegial corona of basally fused, erect, car-nose, oblong staminal corona lobes with a transverse ridge or flap, shorter than gynostegium, with or without interstaminal teeth; gynostegium cylindrical; anther wings short; connective appendages ovate, appressed to style-head; pollinia linear-oblong; caudicles short, ribbon-shaped; corpusculum ovoid, small; style-head ovoid or clavate, protruding. Follicles erect, 9–10 cm long.

Two spp. in Namibia and South Africa, wet-lands. Closely related to *Periglossum* (Bester and Nicholas 2016).

### 284. *Fanninia* Harv.

*Fanninia* Harv., Gen. S. Afr. Pl., ed. 2: 235 (1868); Meve, III. Handb. Succ. Pl. Asclepiadaceae: 137 (2002).

Densely villous herb. Leaves 3–5 cm long, lanceo-late or elliptic. Inflorescences occasionally paired,

4–8-flowered, long-pedunculate. Corolla 10–15 mm long, white; lobes oblong to elliptic, spread-ing, with long, soft trichomes on apical parts; staminal corona lobes purplish red, surpassing gynostegium, erect, oblong, emarginate, with conspicuous midrib, with shorter, erect proximal lobules of two basally fused lingulate parts; gynostegium atop a column; connective appen-dages apically with fimbriate margins. Follicles paired, felty.

One sp., *F. caloglossa* Harv., in South Africa, montane grasslands; 750–2000 m

### 285. *Glossostelma* Schltr.

*Glossostelma* Schltr., J. Bot. 33: 321 (1895); Goyder, Kew Bull. 50: 527–555 (1995), rev.

Usually unbranched herbs, 0.2–1 m tall, (sub-) glabrous; with stout vertical rhizomes and several fusiform root tubers. Leaves 3–8(–10) cm long, occasionally (ob-)ovate. Inflorescences 2–7-flow-ered. Corolla 15–20 mm long, campanulate, cream, green or maroon, occasionally maculate, rarely apically papillose; lobes (ob-)ovate; stam-inal corona lobes occasionally basally fused, white, green, orange, or reddish, mostly surpass-ing gynostegium, erect, dolabriform or clavate, sometimes dorsally flattened, apically with 1–3 inflexed teeth; rarely with free shorter, rounded interstaminal lobes; gynostegium occasionally atop a column; pollinia occasionally falcate; cau-dicles occasionally geniculate, or articulated. Fol-licles paired, 7–13 cm long.

12 spp. in S and E Africa, deciduous wood-land (miombo) or montane grasslands; (500–) 1200–2500 m.

### 286. *Gomphocarpus* R. Br.

*Gomphocarpus* R. Br., Asclepiadeae 26 (1810); Goyder & Nicholas, Kew Bull. 56: 769–836 (2001), rev.

Perennial herbs or shrubs 0.5–1.5(–3) m tall, often with indumentum, with woody rootstock or tap roots. Leaves occasionally whorled, occa-sionally car-nose or coriaceous, 3–12(–18) cm long, linear to ovate. Inflorescences 4–15(–30)-flowered; flowers nodding. Corolla 8–10 mm long, whitish, yellowish, or reddish; lobes ovate, occasionally reflexed, ciliate to barbate on right

margin; staminal corona lobes equaling gynostegium, erect, cucullate, occasionally with additional teeth; free interstaminal lobes minute; gynostegium occasionally atop a short column; pollinia obovoid; caudicles occasionally geniculate or articulated. Follicles 2–8 cm long, frequently ellipsoid, often with soft spines, occasionally inflated.  $2n = 22$ .

20 spp. in Africa, naturalized in Madagascar, Australia, Asia, Central and South America, pioneers of open disturbed habitats; (150–)600–2700 m.

Probably a polyphyletic genus.

### 287. *Kanahia* R. Br.

*Kanahia* R. Br., *Asclepiadeae* 28 (1810); Field et al., *Nord. J. Bot.* 6: 787–792 (1986), consp.; Chaudhary, *Fl. Kingd. Saudi Arabia* 2.2: 35–36 (2001), reg. rev.; Goyder, *Fl. Ethiopia and Eritrea* 4.1: 121 (2003), reg. rev.

Herbs or shrubs, 1.2–1.5 m tall, strongly basally branched, glabrous; shoots with wide pith. Leaves to 20 cm long, with yellow interpetiolar line and glandular fringes. Inflorescences 20–25-flowered. Flowers occasionally sweetly fragrant; corolla 9–22 mm long, occasionally cyathiform or campanulate, white or greenish; lobes ovate, ciliate to barbate; staminal corona lobes white, maximally equaling gynostegium, erect to inflexed, dolabriliform, grooved on upper surface; gynostegium atop a column; pollinia oblongoid or falcate; caudicles convexly recurved or straight, cylindrical. Follicles occasionally paired, 5–6 cm long, occasionally ellipsoid. Seeds pyriform, convex, margin strongly revolute.  $2n = 22$ .

At least two spp. in tropical Africa and Arabia, rheophytic; to 2200 m.

Flowers (corona) very variable.

### 288. *Margaretta* Oliv.

*Margaretta* Oliv., *Trans. Linn. Soc. London* 29: 111 (1875); Mwanyambo, *Kew Bull.* 51: 717–728 (1996), tax.

Sparsely branched herb, 50–70 cm tall, sparsely hirsute; root tuber carrot-shaped. Leaves 2.5–19.5 cm long, lanceolate. Inflorescences 3–10-flowered, pedunculate. Corolla 3.5–10.5 mm long, whitish, orange-red or lilac; lobes lanceolate, reflexed and revolute; free staminal corona lobes

orange-red or lilac, obovate, erect, surpassing gynostegium, lower part claw-like, occasionally with two lateral teeth, or with tooth on midrib; upper part petaloid, with entire or lacerate margins; gynostegium concealed between corona lobes; pollinia clavate or oblongoid; caudicles S-shaped, rectangular; style-head occasionally capitate or semi-globose. Follicles 6–9 cm long. Seeds with revolute margin.

One sp., *M. rosea* Oliv., with six subspecies, in tropical Africa.

Closely allied to *Stathmostelma*.

### 289. *Miraglossum* Kupicha

*Miraglossum* Kupicha, *Kew Bull.* 38: 625 (1984); Kupicha, *Kew Bull.* 38: 599–672 (1984), rev.

Unbranched tuberous geophytes, 10–60 cm tall, long-pilose. Leaves occasionally alternate or whorled, 2–5 cm long, occasionally triangular-deltate, revolute. Inflorescences 2–9-flowered, sessile; calyx almost equaling corolla. Corolla 5–15 mm long, (brownish) green, occasionally streaked with purple; lobes elliptic, densely puberulent except for ciliate left-hand margin; free staminal corona lobes surpassing gynostegium, carnosose, rectangular, apiculate or cruciform, occasionally with longer, filiform proximal lobules; pollinia oblongoid to falcate; caudicles ribbon-shaped, occasionally with hyaline margin. Follicles 3.5–7 cm long, occasionally with knobby protuberances, with dense indumentum.

Seven spp. in South Africa, grassland, stony slopes; 600–2400 m.

### 290. *Odontostelma* Rendle

*Odontostelma* Rendle, *J. Bot.* 32: 161, t. 344 (1894); Meve, *III. Handb. Succ. Pl. Asclepiadaceae* 186 (2002).

Sparsely branched herbs, 15–30 cm tall, glabrous; with carnosose fusiform roots or a spindle-shaped root tuber. Leaves slightly ascending, 5–7.5 cm long. Inflorescences 3–6-flowered, pedunculate. Corolla 8–10 mm long, campanulate; lobes spatulate; gynostegial corona carnosose, short, adnate to both corolla and gynostegium, of ovate, erect, long staminal parts and short, rectangular, bifid interstaminal parts basally fused into a ring;

pollinia oblongoid; caudicles horizontal, cylindrical. Follicles ca. 9 cm long.

Two spp. in Angola and Zimbabwe.

291. *Oxystelma* R. Br.

*Oxystelma* R. Br., Prodr. 462 (1810); Jagtap & Singh, Fasc. Fl. India 24: 33–35 (1999).

Suffrutescent twiners to 4 m, glabrous; rhizomatous; shoots green, basally often suberose. Leaves papery, 6–11 cm long, linear to ovate. Inflorescences (1–)2–4-flowered. Corolla 8–12.5 mm long, broadly campanulate, glabrous, white, reticulate with purple-red; lobes triangular, densely ciliate; corolline corona inserted near base of corolla, densely covered with trichomes, short, annular; staminal corona lobes ovoid, inflated, extended into a long tip connivent above gynostegium; caudicles declinate, triangular; style-head rostrate. Follicles ca. 5 cm long, narrowly obclavate or broadly ovoid, occasionally inflated. Seeds ovate, winged.  $2n = 22$ .

Two spp. in E and W Africa, tropical Asia, riverine vegetation.

Molecular analyses indicate an association to Asclepiadinae (Liede and Täuber 2000; Surveswaran et al. 2014), and the structure of the staminal corona corroborates this placement.

292. *Pachycarpus* E. Mey.

*Pachycarpus* E. Mey., Comm. Pl. Afr. Austr. 209 (1838); Smith, S. Afr. J. Bot. 54: 399–439 (1988), reg. rev.; Goyder, Kew Bull. 53: 335–374 (1998), rev.

Sparsely branched herbs, 50–70 cm tall, densely pubescent, with slender, vertical root tubers. Leaves spreading, occasionally coriaceous, often discolorous, 7–12(–15) cm long, lanceolate, elliptic (-ovate), scabrous. Inflorescences 5–18-flowered. Corolla 10–20 mm long, occasionally campanulate or cyathiform, green, creamish or purple, often dark-patterned, occasionally papillose; lobes oblong to (ob-)ovate, occasionally with trichomes; free staminal corona lobes equaling gynostegium, spreading, cucullate, consisting of a dorsiventrally flattened plate with 1–2 erect keels; occasionally upper part papillose; pollinia (ob-)ovoid or falcate, occasionally attached to caudicles through a clasping overlap. Follicles

4–12 cm long, ellipsoid or obclavate, occasionally keeled or winged, occasionally inflated. Seeds wingless.  $2n = 22$ .

38 spp. in tropical Africa, montane grassland, open woodland; (100–)700–2500(–2700) m.

Probably polyphyletic (Goyder et al. 2007; Fishbein et al. 2011). Wasp-pollinated (Shuttleworth and Johnson 2009).

293. *Parapodium* E. Mey.

*Parapodium* E. Mey., Comm. Pl. Afr. Austr. 221 (1838). *Rhombonema* Schltr. (1895).

Sparsely branched herbs, 20–40 cm tall, sparsely puberulous in two lines. Leaves 4–9 cm long, oblong. Corolla ca. 10 mm long, campanulate; lobes ovate, reflexed; gynostegial corona adnate to both corolla and gynostegium; staminal corona lobes shorter than gynostegium, erect, rhomboid; with minute, free interstaminal lobes; gynostegium concealed in corolla; pollinia oblongoid; caudicles declinate, cylindrical; style-head apically bifid. Follicles paired, ca. 11 cm long, ellipsoid, with soft spines. Seeds with revolute and strongly folded wing.

Three spp. in South Africa, grasslands.

294. *Pergularia* L.

*Pergularia* L., Syst. Nat., ed. 12: 135, 191 & Mant. Pl. 8, 53 (1767); Goyder, Kew Bull. 61: 245–256 (2006).

Suffrutescent twiners or erect herbs, to 4 m tall, pubescent or tomentose. Leaves softly herbaceous, 3–8 cm long, ovate, deeply cordate. Inflorescences 10–25-flowered, peduncles and pedicels long, thin. Flowers nodding, often sweetly fragrant; corolla 10–12 mm long, salverform, whitish to yellowish, occasionally with trichomes in the tube; lobes ovate to oblong, ciliate or barbate; staminal corona lobes surpassing gynostegium, obliquely erect, slenderly fusiform; free interstaminal corona lobes much shorter, bifid; pollinia clavate, with distal germination pore; caudicles horizontal, cylindrical, with pronounced hyaline margin; carpels with trichomes. Follicles paired, 4–9 cm long, with soft spines.  $2n = 22$ .

Two spp., one with three subspecies, Africa, Arabia and Asia, savanna, arid areas. Moth-pollinated (Bhatnagar 1986).

Sister to the remaining Asclepiadinae s. str. (Goyder et al. 2007).

295. *Periglossum* Decne.

*Periglossum* Decne., Prodr. 8: 520 (1844); Bester & Nicholas, Phytotaxa 282: 28–36 (2016).

Grass-like geophytes, 30–80 cm tall, puberulous; root tubers shortly napiform. Leaves (sub-)sessile, linear, ascending to spreading, 2.5–14 cm long. Inflorescences 4–20-flowered, long-pedunculate. Corolla 4–9 mm long, campanulate, white, green or maroon; lobes oblong to lanceolate, erect, apically reflexed, revolute; gynostegial corona of basally fused, erect, fleshy, oblong to ovate staminal lobes, ventrally occasionally with keels or flaps, surpassing gynostegium, with tiny interstaminal teeth; gynostegium barrel-shaped; anther wings short; connective appendages cordiform, connivent over style-head; pollinia falcate, with apical sterile hyaline region; caudicles attached through a clasping overlap, ribbon-shaped; corpusculum ellipsoid, small. Follicles erect, ca. 7 cm long.

Five spp. in Mozambique, South Africa, Swaziland and Zimbabwe; wetlands to grasslands. Closely related to *Cordylogyne* (Bester and Nicholas 2016).

296. *Schizoglossum* E. Mey.

*Schizoglossum* E. Mey., Comm. Pl. Afr. Austr. 218 (1838); Kupicha, Kew Bull. 38: 599–672 (1984), rev.

*Lagarinthus* E. Mey. (1838).

*Mackenia* Harv. (1868).

Sparsely branched, tuberous geophytes, 7–130 cm tall. Leaves occasionally whorled or alternate, 2–8.5 cm long, occasionally triangular or oblong, sagittate. Inflorescences 3–15-flowered. Corolla 5–10 mm long, white, greenish brown, or purplish, occasionally streaked darker, occasionally with trichomes; lobes elliptic or cucullate, marginally revolute, occasionally ciliate; free staminal corona lobes whitish, yellow or green, surpassing gynostegium, subulate to subglobose, occasionally deeply bifid, occasionally emarginate; occasionally with deeply bifid proximal lobules exceeding distal lobules; gynostegium often stipte-

tate; pollinia with apical germination pore. Follicles 4.5–8 cm long.

About 15 spp. in E and S Africa, grasslands, often near streams; 10–2700 m.

297. *Solenostemma* Hayne

*Solenostemma* Hayne, Getreue Darstell. Gew. 9: ad t. 38 (1825); Chaudhary, Fl. Kingd. Saudi Arabia 2.2: 39 (2001), reg. rev.

*Argelia* Decne. (1838), nom. superfl.

Erect herb, 50–75 cm tall, (sub-)glabrous; rootstock woody. Leaves coriaceous, elliptic. Inflorescences many-flowered, thyrsoïdal. Corolla ca. 7 mm long, rotate, white, glabrous; lobes lanceolate; corolline corona shorter than both corolla and gynostegium, five-partite; lobes laterally connate, antepetalous, ovate, erect; gynostegium stipitate, raised high above corolla; pollinia oblongoid; caudicles horizontal, cylindrical; style-head flat. Follicles 3–4 cm long, obclavate, with thick pericarp. Seeds marginally with crenulate, revolute margin.  $2n = 22$ .

One sp., *S. oleifolium* (Nect.) Bullock & E.A. Bruce ex Bullock, in N Africa and Arabia, rocky valleys.

298. *Stathmostelma* K. Schum.

*Stathmostelma* K. Schum., Bot. Jahrb. Syst. 17: 129 (1893); Goyder, Kew Bull. 53: 577–616 (1998), rev.

Sparsely branched, (sub-)glabrous geophytes, with stout, vertical tubers, 10–150 cm tall. Leaves 10–24 cm long, occasionally ovate. Inflorescences 3–8-flowered. Corolla 9–20 mm long, white, green, yellow or orange-red, (sub-)glabrous; lobes ovate or lanceolate, often reflexed, occasionally revolute; staminal corona lobes yellow, orange or green, glabrous except along midline of cavity, equaling gynostegium, cucullate, inner apical margins forming a pair of teeth, occasionally with tooth in cavity; gynostegium often atop a column; anther wings occasionally forming a contorted basal tail; caudicles articulated with filiform distal portion broadening abruptly into clasping overlap; corpusculum black. Follicles 8–16 cm long. Seeds with inflated wing thicker than body.  $2n = 22$ .

13 spp. in tropical Africa, grasslands, often seasonally waterlogged, *Brachystegia* woodland; 0–2300 m.

Closely allied to *Margaretta*.

299. *Stenostelma* Schltr.

*Stenostelma* Schltr., Bot. Jahrb. Syst. 18, Beibl. 45: 6 (1894); Müller et al., III. Handb. Succ. Pl., Asclepiadaceae 263–264 (2001), consp.  
*Krebsia* Harv. (1868), non *Krebsia* Eckl. & Zeyh. (1836), Fabaceae.

Sparsely branched herbs, 10–50 cm tall, pilose; roots a single tuber. Leaves slightly ascending; linear to filiform, revolute. Inflorescences 8–12-flowered. Corolla 3–5 mm long, campanulate to urceolate; lobes lanceolate or obovate, apically reflexed; free staminal corona lobes far exceeding gynostegium, carnose, usually subulate, S-shaped; with free, tiny interstaminal teeth; gynostegium concealed in corolla; pollinia ovoid to falcate; caudicles articulated, twisted; style-head (elongate-) conical, apically bifid. Follicles obclavate.  $2n = 22$ .

About four spp. in southern Africa.

300. *Trachycalymma* (K. Schum.) Bullock

*Trachycalymma* (K. Schum.) Bullock, Kew. Bull. 1953: 348 (1953); Goyder, Kew Bull. 56: 129–161 (2001), rev.; Goyder et al., Ann. Missouri Bot. Garden 94: 423–434 (2007), phyl.; Fishbein et al., Syst. Bot. 36: 1008–1023 (2011), phyl.  
*Gomphocarpus* subsect. *Trachycalymma* K. Schum. (1895).

Sparsely branched tuberous geophytes, 10–60 cm tall, densely spreading-pubescent. Leaves 3–16 cm long, linear-lanceolate or oblong-ovate, ciliate. Inflorescences 5–40-flowered; flowers usually nodding. Corolla 3–10 mm long, white, greenish, or purplish, occasionally dark-veined, occasionally papillose; lobes ovate; free staminal corona lobes equaling gynostegium, erect, cucullate, occasionally with fringed margins, papillose and occasionally with tooth in cavity; gynostegium often atop a column; pollinia obovoid or clavate, caudicles articulated; attached through a clasping overlap. Follicles 5–15 cm long, occasionally obclavate, occasionally with soft spines.

Ten spp. in tropical Africa, montane and plateau grasslands or deciduous woodlands; 900–2600 m.

Goyder et al. (2007) and Fishbein et al. (2011) retrieved *T. pseudofimbriatum* Goyder from Ethiopia as sister to all Asclepiadinae except for *Calotropis*, *Kanahia* and *Pergularia*, while the remaining species seem to form a polyphyletic group.

301. *Woodia* Schltr.

*Woodia* Schltr., Bot. Jahrb. Syst. 18, Beibl. 45: 30 (1894).

Sparsely branched herbs, 15–25 cm tall, sparsely puberulous. Leaves 4–7 cm long, oblong to lanceolate, sharply apiculate, marginally thickened, undulate and minutely scabrous, glabrous. Inflorescences 4–8-flowered; calyx equaling or exceeding corolla, campanulate. Corolla 5–7 mm long, greenish brown; lobes ovate, inflexed; free staminal corona lobes equaling gynostegium, erect, trifid with central lobe pronouncedly keeled, the two lateral ones much shorter; connective appendages transversely lunate, strongly inflexed; pollinia obovoid. Follicles 7.5–12 cm long, with soft spines. Seeds wingless.

Three spp. in South Africa.

302. *Xysmalobium* R. Br.

*Xysmalobium* R. Br., Asclepiadeae 27 (1810); Goyder, Fl. Ethiopia and Eritrea 4.1: 131–133 (2003), reg. rev.

Sparsely branched herbs, 30–80 cm tall, (sub-) glabrous; roots cylindrical, to 1 m long tubers. Leaves 3–15 cm long, frequently undulate. Inflorescences 4–20-flowered. Corolla 4–8 mm long, white, green or brownish purple, occasionally reticulate with brown, occasionally with erect trichomes; lobes triangular, spreading or reflexed, often revolute, rarely barbate; staminal corona lobes basally fused, not exceeding gynostegium, erect, oblongoid, subglobose or dolabriform; pollinia ovoid or clavate. Follicles solitary, 10–20 cm long, ellipsoid, with soft spines and thick pericarp. Seeds with undulate wing.  $2n = 22$ .

46 spp. in southern and E Africa, grasslands.

*X. undulatum* (L.) W.T. Aiton shows a bimodal pollination system with a chafer beetle and a pompilid wasp acting as pollinators (Shuttleworth and Johnson 2008).

### V.5.c. Subtribe *Cynanchinae* K. Schum. (1895).

Usually suffrutescent twiners, often with stipule-like small leaves, constituting prophylls of an extremely reduced short shoot. Leaves ovate, or cordiform, basally usually distinctly cordate. Inflorescences extra-axillary, condensed-bostrychoid or sciadioidal. Corolla rotate to campanulate; lobes ovate, oblong or triangular, glabrous or with equally distributed verrucose trichomes; gynostegial corona usually a ring of fused staminal and interstaminal parts, usually glabrous, white; pollinia ovoid, subapically to laterally attached to the caudicles; caudicles usually declinate, cylindrical. Follicles usually solitary, fusiform to obclavate, usually with thin pericarp. Seeds ovate, often papillose or tuberculate, winged. Two genera in the tropics and subtropics worldwide.

### 303. *Cynanchum* L.

*Cynanchum* L., Sp. Pl. 212 (1753); Sundell, Evol. Monogr. 5: 1–63 (1981), reg. rev.; Liede, Ann. Missouri Bot. Gard. 83: 283–345 (1996), reg. rev.; Liede & Kunze, Org. Divers. Evol. 2: 239–269 (2002), phyl.; Khanum et al. Taxon 65: 467–486 (2016), phyl., tax.  
*Holostemma* R. Br. (1810).  
*Metaplexis* R. Br. (1810).  
*Sarcostemma* R. Br. (1810).  
*Ampelamus* Raf. (1819).  
*Raphistemma* Wall. (1831).  
*Decanema* Decne. (1838).  
*Glossonema* Decne. (1838).  
*Odontanthera* Wight (1838).  
*Pentarrhinum* E. Mey. (1838).  
*Pycnoneurum* Decne. (1838).  
*Steinheilila* Decne (1838).  
*Metalepis* Griseb. (1866).  
*Graphistemma* (Champ. ex Benth.)  
 Champ. ex Benth. (1876).  
*Adelostemma* Hook. f. (1883).  
*Telminostelma* E. Fourn. (1885).  
*Mellichampia* A. Gray ex S. Watson (1887).  
*Vohemaria* Buchenau (1889).  
*Flanaganiana* Schltr. (1894).  
*Platykeleba* N.E. Br. (1895).  
*Decanemopsis* Costantin & Gall. (1906).  
*Folotsia* Costantin & Bois (1908).  
*Mahafalia* Jum. & H. Perrier (1911).  
*Nematostemma* Choux (1921).  
*Karimbolea* Desc. (1960).  
*Seshagiria* Ansari & Hemadri (1971).  
*Rhodostegiella* (Pobed.) C.Y. Wu & D.Z. Li (1990).  
*Sichuania* M.G. Gilbert & P.T. Li (1995).

Suffrutescent twiners, lianas, erect or prostrate herbs, stem succulent twiners or erect stem succulents, 0.3–4(–20) m tall, latex white; occasionally rhizomatous; occasionally with root tubers. Leaves often cordate; scale-like in most stem succulents; often with ovate prophylls. Inflorescences (3–)5–15(–50)-flowered. Corolla 3–10(–40) mm long, rarely tubular, elongate-conical, or urceolate, white, cream, green, yellow, brown or rose, occasionally with verrucose trichomes; lobes usually straight; gynostegial corona highly variable, rarely absent, usually with a ring of fused staminal and interstaminal parts, staminal parts occasionally with adaxial appendage; occasionally with additional free staminal lobes connate to ring (former *Sarcostemma* species); gynostegium sessile or stipitate, style-head umbonate to rostrate. Follicles thin-walled, club-shaped, often keeled or winged, or thick-walled, then sometimes with soft spines.  $2n = 22$ .

About 250 spp., cosmopolitan, with centers of distribution in Africa and Asia, very variable, often in slightly disturbed habitats.

The concept of *Cynanchum* has been changed considerably over the last ten years; for circumscription see Liede and Täuber (2002). Recent molecular phylogenetic work (Khanum et al. 2016) has shown that several small genera with atypical morphology have to be included in *Cynanchum*.

### 304. *Schizostephanus* Hochst. ex K.Schum. (1893).

*Schizostephanus* Hochst. ex K.Schum., Bot. Jahrb. Syst. 17: 139 (1893); Liede, Bot. Jahrb. Syst. 114: 503–550 (1993), rev.; Liede, Fl. Ethiopia and Eritrea 3: 136–137 (2003), reg. rev.; Bruyns & Klak, S. Afr. J. Bot. 75: 532–536 (2009), phyl.

Stem succulent shrubs or twiners, 0.5–4 m tall, glabrous; shoots lenticellate, 5–25 mm diam.; latex translucent. Leaves 3.5–8 cm long, ovate-cordate. Inflorescences 15–30-flowered. Flowers sweetly fragrant; corolla 5–6 mm long, yellow, basally maroon, lobes oblong, occasionally basally with long, slender trichomes; gynostegial corona ring tubular, exceeding gynostegium, staminal and interstaminal parts ovate to triangular, erect, marginally occasionally emarginate; occasionally

with additional short inner rectangular staminal lobes; gynostegium stipitate; pollinia clavate, with apical-distal pellucid margin; caudicles declinate, triangular; style-head flat to umbonate, neck conical. Follicles 4.5–5 cm long. Seeds pyriform, winged.  $2n = 22$ .

Two spp. in S and E Africa, steep slopes, rocky sites in open scrub.

Phylogenetic analyses have retrieved *Schizostephanus* as sister to the speciose genus *Cynanchum* (Bruyans and Klak 2009; Khanum et al. 2016).

#### V.5.d. Subtribe Tylophorinae K. Schum. (1895).

Usually suffrutescent twiners; latex usually translucent. Leaves ovate or elliptic, basally occasionally indistinctly cordate. Inflorescences extra-axillary, lax, often dichasial at base, bostrychoid monochasial in higher order branching, often many-flowered. Corolla rotate to campanulate, occasionally with evenly distributed verrucose trichomes, usually with long slender trichomes; gynostegial corona usually of free staminal lobes; gynostegium (sub-)sessile; pollinia ovoid, subapically to laterally attached to cylindrical caudicles; style-head flat to umbonate. Follicles usually fusiform to obclavate, usually with thin pericarp. Seeds ovate, often papillose or tuberculate, winged. Two genera in the Paleotropics and Oceania, also in temperate Eurasia.

#### 305. *Pentatropis* R. Br. ex Wight & Arn.

*Pentatropis* R. Br. ex Wight & Arn. in Wight, Contr. Bot. India 52 (1834); Liede-Schumann et al., Taxon 61: 803–825 (2012), phyl.

*Eutropis* Falc. (1839), nom. illegit.

*Strobopetalum* N.E. Br. (1894).

*Pseudopentatropis* (1912).

Herbaceous or suffrutescent twiners to 4 m. Leaves usually carnose, 1–6.5 cm long, ovate. Inflorescences 1–5-flowered, sciadioidal, (sub-)sessile. Corolla 6–8 mm long, yellowish green or purple, occasionally with yellow apices, with trichomes; lobes contorted, lanceolate, occasionally extended into a long, twisted tip, occasionally revolute; free staminal corona lobes ivory or greenish yellow, at least equaling gynostegium, erect, basally horizontally spreading, oblongoid, carinate; anther wings usually following the basal

margin of the anther; pollinia ovoid; caudicles declinate; style-head green. Follicles 5–7 cm long.  $2n = 22$ .

About four spp. in Africa, Madagascar, Arabia, India and Indochina, coastal habitats, sand, rocks, rocky places in dry forests; 0–200 m.

Phylogenetic analyses have retrieved *Pentatropis* as sister to the speciose genus *Vincetoxicum* (Liede-Schumann et al. 2016).

#### 306. *Vincetoxicum* Wolf

*Vincetoxicum* Wolf, Gen. Pl. 130 (1776); Liede, Taxon 45: 193–211 (1996), phyl.; Yamashiro et al., Mol. Phyl. Evol. 31: 689–700 (2004), phylog.; Liede-Schumann et al., Taxon 61: 803–825 (2012), phyl.; Liede-Schumann et al., Mol. Phyl. Evol. 94: 436–446 (2016); Liede-Schumann & Meve, Phytotaxa 369(3): 129–184 (2018), tax.

*Tylophora* R. Br. (1810).

*Blyttia* Arn. (1838).

*Rhyncharrhena* F. Muell. (1859).

*Sphaerocodon* Benth. (1876).

*Pleurostelma* Baill. (1890).

*Podostelma* K. Schum. (1893).

*Diplostigma* K. Schum. (1895).

*Biondia* Schltr. (1905).

*Ischnostemma* King & Gamble (1908).

*Merrillanthus* Chun & Tsiang (1941).

*Pentastelma* Tsiang & P.T. Li (1974).

*Goydera* Liede (1993).

Shrubs, erect herbs or herbaceous twiners, 0.4–4 m tall; latex usually translucent; roots usually wiry, fascicled, rarely forming a woody rootstock. Leaves occasionally carnose, 0.5–10 cm long, linear to ovate. Inflorescences occasionally paired, 1–25-flowered. Corolla 1.5–10 mm long, rarely campanulate, urceolate or elongate-conical, yellowish cream or purplish brown, with long flexuous trichomes on the tube, occasionally additionally with verrucose trichomes; lobes oblong, lanceolate or ovate; gynostegial corona of carnose free staminal lobes or of a ring of connate staminal and laminar interstaminal parts, very rarely (former *Diplostigma canescens*) with both, maximally equaling gynostegium; caudicles erect, horizontal or ascending; style-head rarely rostrate (former *Pleurostelma* species). Follicles 2–12 cm long, rarely ellipsoid.  $2n = 22, 44$ .

At least 150 spp. throughout the tropics, subtropics of Africa, Asia, and Oceania, extending into temperate Eurasia as far north as Sweden, forest margins, steppes, rocky slopes in arid

areas. Contains phenanthroindolizidine alkaloids, seco- and discopregnanes. Some species aggressively invasive in the USA and Canada (e.g., Sheeley and Raynal 1996), capable of selfing (e.g., Lumer and Yost 1995).

Molecular analyses (Liede-Schumann et al. 2012, 2016) have shown that *Tylophora* is inseparable from *Vincetoxicum* and needs to be included in the latter.

V.5.e. **Subtribe Pentacyphinae** Liede & Meve (2014).

Weakly twining subshrubs. Inflorescences sciadoid, flowers nodding. Corolla campanulate, adnate to gynostegium, forming five hairy pouches; gynostegial corona of free staminal lobes with additional peg-shaped parts along filament tube; pollinia medifixed or (sub-)basally inserted on corpusculum. Follicles solitary, fusiform. One genus in the northern Andes of South America.

307. ***Pentacyphus*** Schltr.

*Pentacyphus* Schltr., Bot. Jahrb. Syst. 37: 605, f. 3 (1906); Holm, Ann. Missouri Bot. Gard. 37: 477–560 (1950), rev. (under *Sarcostemma*); Liede & Täuber, Pl. Syst. Evol. 225: 133–140 (2000), phyl.; Meve & Liede-Schumann, Pl. Syst. Evol. 301: 997–1004 (2015), rev. *Tetraphysa* Schltr. (1906).

Plants glabrous or sparsely finely pilose. Leaves 1.5–9.5 cm long, elliptic, oblong or obovate. Inflorescences 1–several-flowered; flowers nodding. Corolla 18–22 mm long, creamish green to yellow, occasionally with reddish maculation, with trichomes on the entire surface; lobes ovate, obtuse; staminal corona lobes equaling gynostegium, erect, saccate or dolabriform with long apical extension; pollinia oblongoid; caudicles declinate or geniculate, cylindrical; style-head conical and bifid. Follicles ca. 8 cm long.  $2n = 22$ .

Three spp. in Columbia, Ecuador, Peru and Venezuela, mountain rain forest; 1800–3100 m.

All molecular analyses (e.g., Liede-Schumann et al. 2005; Surveswaran et al. 2014) retrieve *Pentacyphus* as sister to all other New World Asclepiadeae except for *Asclepias* and *Cynanchum*.

V.5.f. **Subtribe Diplolepinae** Liede & Meve (2014).

Suffrutescent twiners, shrublets or shrubs. Inflorescences sciadoid. Corolla rotate, campanulate or urceolate; corona gynostegial, occasionally vestigial or absent; gynostegium sessile, pollinia ovoid to oblongoid, laterally attached to horizontal, flattened caudicles; style-head often rostrate. Follicles solitary, usually slenderly obclavate. Seeds usually ovate, winged. One genus in southern South America.

308. ***Diplolepis*** R.Br.

*Diplolepis* R. Br., Asclepiadeae 30 (1810); Liede et al., Syst. Bot. 30: 183–194 (2005), phyl.; Hechem et al., Taxon 60: 638–648 (2011), phyl. *Sonninia* Reichenb., nom. illegit. (1828). *Grisebachiella* Lorentz (1880).

Plants with coriaceous, marginally revolute leaves, 1–2.5 cm long, ovate to linear. Inflorescences 1–10-flowered. Corolla 6–9 mm long, yellow, pink or whitish, often with purple tinge, usually with trichomes; lobes obovate or oblong; gynostegial corona an urceolate to cyathiform ring of connate oblong staminal parts, often with adaxial appendage, and interstaminal parts; pollinia ovoid to oblongoid, style-head white. Follicles 3–8.5 cm long. Seeds rarely thick and with reduced yellowish coma.  $2n = 20, 22$ .

14 spp. in Argentina, southern Brazil and Chile.

Following molecular studies (Liede-Schumann et al. 2005; Hechem et al. 2011b), the formerly monotypic *Diplolepis* was recently enlarged to comprise all southern South American former “*Cynanchum*” species, one former *Tweedia* species, and two species without a corona, one previously listed as “*Astephanus*” and one constituting the monotypic *Grisebachiella*.

V.5.g. **Subtribe Orthosiinae** Liede & Rapini (2005).

Suffrutescent or herbaceous twiners. Leaves herbaceous. Inflorescences often (sub-)axillary, occasionally paired. Corolla rotate to cyathiform; corona gynostegial, of free or basally to entirely fused staminal lobes; gynostegium usually sessile;



style-head flat to umbonate. Follicles often paired, fusiform. A molecular analysis retrieved Orthosiinae in an unresolved position with the other New World subtribes. Four genera in South and Central America.

### 309. *Jobinia* E. Fourn.

*Jobinia* E. Fourn. in Mart., Fl. Bras. 6(4): 327, t. 97 (1885); Araujo Schwarz & Fontella Pereira, Acta Biol. Paran. 24: 49–157 (1995), rev.; Fontella Pereira et al., Fl. Ilustr. Catarinense, Apocináceas-Asclepiadóideas: 165–178 (2004), reg. rev.; Pereira & Capello de Sales, Fl. Fan. Estad. São Paulo 4: 180–190 (2005), reg. rev.; Stevens, Fl. Nicaragua 1: 252–253. (2001), reg. rev.; Liede-Schumann & Meve, Ann. Missouri Bot. Gard. 99: 44–81 (2013), tax. *Cyathostelma* E. Fourn. (1885). *Kerbera* E. Fourn. (1885). *Dicarpophora* Speg. (1926). *Cynanchum* L. sect. *Formosum* Liede (1997).

Suffrutescent twiners, glabrous. Leaves 3–10 cm long, ovate to oblong. Inflorescences axillary, occasionally paired, 8–30-flowered, lax. Corolla 1.5–3 mm long, yellowish green; lobes oblong or lanceolate, occasionally extended in a long, twisted tip, with flexuous trichomes; gynostegial corona of basally to highly fused oblanceolate or oblong staminal lobes, tubular or cyathiform, occasionally obscuring the gynostegium; occasionally with short interstaminal lobules or teeth; anthers dorsally rarely with trichomes; pollinia oblongoid, occasionally with warty anticlinal walls, equaling corpusculum in size; style-head umbonate, rostrate or capitate. Follicles 5–15 cm long, seeds ovate, winged.

About 25 spp., one in Central America, the others in Argentina, Bolivia, Brazil, Ecuador and Venezuela, forests, thickets.

### 310. *Monsanima* Liede & Meve

*Monsanima* Liede & Meve, Ann. Missouri Bot. Gard. 99: 66 (2013); Silva et al., Phytotaxa 173: 11 (2014), new taxon.

Slender twiners, pubescent. Leaves 2–4 cm long, linear. Inflorescences 2–4-flowered. Corolla 5 mm long, brown, glabrous; lobes ovate; gynostegial corona of highly fused staminal lobes folded inward apically over the gynostegium, completely obscuring it; anthers with short, strongly centrifugal anther wings, pollinaria with short, broad, horizontal caudicles; connec-

tive appendages strongly inflexed. Follicles solitary, ca. 8 cm long.

Two spp. in Brazil (Bahia), endemic to high altitude cerrado and campo rupestre.

Recent molecular studies consistently retrieved *Monsanima* as sister to the remaining Orthosiinae (Silva et al. 2014; Liede-Schumann and Meve 2015).

### 311. *Orthosia* Decne.

*Orthosia* Decne., Prodr. 8: 526 (1844); Fontella Pereira et al., Fl. Ilustrada Catarinense, Apocináceas-Asclepiadóideas: 165–178 (2004), reg. rev.; Liede-Schumann et al., Syst. Bot. 30: 184–195 (2005), phyl.; Liede-Schumann & Meve, Novon 18: 202–210 (2008), new taxa. *Amphistelma* Griseb. (1862). *Tainionema* Schltr. (1899).

Suffrutescent or rarely herbaceous twiners, 0.5–8 m tall, with distinct long and short shoots, often creeping when young, rhizomatous; shoots green, often with suberose bark. Leaves often caducous, 1–9 cm long, linear or oblong. Inflorescences occasionally paired, 1–20-flowered. Corolla 1–2.5 mm long, rarely urceolate, creamish or purple; lobes oblong or lanceolate, usually papillose; gynostegial corona of free or fused staminal lobes, occasionally reduced, white to yellowish, lobes frequently trifid with median tooth prominent; gynostegium rarely stipitate; corpusculum occasionally with hastate basal projections. Follicles 4–7 cm long, narrowly oblong to obclavate. Seeds oblong, wingless.  $2n = 20$ .

About 25 spp. from SW and SE USA and Mexico through Central America, the Caribbean and South America, forests, often in clearings, thickets, roadsides; to 2000 m.

### 312. *Scyphostelma* Baill.

*Scyphostelma* Baill., Hist. Pl. 10: 252 (1890), Liede-Schumann & Meve, Ann. Missouri Bot. Gard. 99: 44–81 (2013), tax. *Cynanchum* L. sect. *Microphyllum* Liede (1997). *Liedea* W.D. Stevens (2005).

Herbaceous or suffrutescent twiners, often densely white, yellow or brown pilose, velvety or villous; often with distinct long and short shoots and adventitious buds forming shoots. Leaves frequently distichous, 0.8–1.5 cm long, linear to circular. Inflorescences occasionally paired, 2–8-flowered. Corolla 1–4 mm long, rarely entirely

fused, creamish or reddish; lobes ovate to oblong; gynostegial corona ring tubular or cyathiform, exceeding gynostegium; staminal parts rectangular, ovate, triangular or oblong, erect; gynostegium rarely stipitate. Follicles 35–40 mm long, narrowly oblong to obclavate. Seeds oblong, wingless.  $2n = 22$ .

More than 50 spp. in Costa Rica, Bolivia, Colombia, Ecuador, Peru and Venezuela, mountain forests; 1500–3800 m.

Genus under revision.

V.5.h. **Subtribe Metastelmatinae** Endl. ex Meisn. (1840).

Inflorescences usually extra-axillary, sciadioidal. Corolla rotate to campanulate, small; lobes frequently with trichomes; gynostegial corona of free or fused staminal lobes; gynostegium usually sessile, style-head flat or umbonate. Follicles fusiform, usually solitary. Seeds ovate. Twelve genera in the tropics and subtropics of the New World.

313. **Barjonia** Decne.

*Barjonia* Decne., Prodr. 8: 512 (1844); Marquete, Rodriguésia 31: 7–70 (1979), rev.; Farinaccio, Syst. Bot. 38: 764–768 (2013), key, new taxon.

Subshrubs to erect herbs, 0.4–1 m tall, glabrous, glaucous. Leaves (sub-)sessile, 1.5–5 cm long, oblong triangular-deltate to ovate, with interpetiolar colleters. Inflorescences 3–8-flowered, condensed, occasionally in racemiform, leafless terminal aggregates. Corolla 4–6 mm long, rotate to campanulate, greenish cream or maroon; lobes ovate, with unicellular trichomes and papillae; with multicellular trichomes in sinuses; free staminal corona lobes erect, oblong, rectangular or apiculate, adnate to both corolla and gynostegium, exceeding gynostegium, occasionally with shorter oblongoid or dentiform proximal lobules; pollinia laterally attached to triangular or trapezoidal caudicles. Follicles 4–7.5 cm long. Seeds often with revolute wing.

Seven spp. in C Brazil, Suriname and Bolivia.

314. **Blepharodon** Decne.

*Blepharodon* Decne., Prodr. 8: 603 (1844); Morillo, M.Sc. Thesis, St. Louis University, St. Louis, MO, pp. 1–163

(1976), rev.; Ferreira & Pereira, Fl. Fan. Est. São Paulo 4: 101–104 (2005), reg. rev.

*Anomotassa* Schltr. (1898).

*Vailia* Rusby (1898).

Herbaceous or suffrutescent twiners, rarely shrubs or herbs, to 10 m long, usually glabrous. Leaves discolorous, 0.8–21 cm long, ovate to linear, occasionally revolute, occasionally ciliate; with interpetiolar line or colleters. Inflorescences 6–14-flowered. Corolla 4–20 mm long, rotate or campanulate, greenish or yellowish; lobes ovate or triangular, occasionally revolute, occasionally ciliate, occasionally with trichomes; free staminal corona lobes attached along anther backs, exceeding gynostegium, erect, cucullate, bicornate or bucket-shaped; pollinia (sub-)horizontal, laterally attached to cylindrical caudicles with pronounced hyaline margin. Follicles obclavate. Seeds wingless.  $2n = 22$ .

About 15 spp. in Central and South America, forest margins, road sides, dry sandy or rocky savanna; 0–2000 m.

A recent molecular study indicated that the genus in its present circumscription is polyphyletic (Liede-Schumann et al. 2005).

315. **Ditassa** R. Br.

*Ditassa* R. Br., Asclepiadeae 38 (1810); Morillo, Fl. Venez. Guayana 3: 145–152 (1997), reg. rev.; Konno & Pereira, Fl. Fan. Est. São Paulo 4: 107–111 (2005), reg. rev.; Silva et al., Syst. Bot. 37: 795–806 (2012), phyl.

*Nematuris* Turcz. (1848).

*Calathostelma* E. Fourn. (1885).

*Husnotia* E. Fourn. (1885).

Herbaceous or suffrutescent twiners, rarely (sub-)shrubs, occasionally yellow or brown tomentose. Leaves rarely alternate or whorled, occasionally strongly ascending or reflexed, 0.5–5 cm long, linear to obovate or obdeltate, often strongly revolute. Inflorescences 1–10-flowered. Corolla 1–5 mm long, occasionally urceolate, whitish cream, with verrucose or barbate trichomes; lobes oblong, ovate or triangular; staminal corona lobes free, rarely basally fused, erect, filiform, oblong, triangular or apiculate, always with shorter proximal lobes, very rarely absent; gynostegium occasionally stipitate; style-head occasionally capitate. Follicles occasionally paired, occasionally narrowly oblong. Seeds

oblong to ovate, usually wingless; coma rarely absent.  $2n = 22$ .

About 140 spp., South America, forest margins, thickets; 100–3000 m.

A recent molecular study indicated that the genus in its present circumscription is polyphyletic (Silva et al. 2012).

### 316. *Hemipogon* Decne.

*Hemipogon* Decne., Prodr. 8: 509 (1844); Rapini, Bol. Bot. Univ. São Paulo 19: 140–147 (2001), reg. rev.; Pereira & Capello de Sales, Fl. Fan. Estad. São Paulo 4: 116–118 (2005), reg. rev.; Fontella et al., Bonplandia (Corrientes) 23: 25–31 (2014), tax.

Erect herbs or subshrubs, 30–50 cm tall, (sub-)glabrous. Leaves usually alternate or whorled, (sub-)sessile, 15–40 cm long, linear. Inflorescences subsessile, 1–3-flowered. Corolla 3–7 mm long, urceolate, highly fused, creamish or maroon; lobes ovate to triangular, papillose or with erect trichomes, often barbate in sinuses; free staminal corona lobes adnate to both corolla and gynostegium, short, erect, oblong, often absent; gynostegium concealed in corolla tube; caudicles occasionally with pronounced hyaline margin. Follicles obclavate, seeds ovate to pyriform, wingless.

Eight spp. in Bolivia, Brazil and Paraguay, open rocky spaces.

A recent molecular study indicated that the genus in its present circumscription is polyphyletic (Liede-Schumann et al. 2005).

### 317. *Hypolobus* E. Fourn.

*Hypolobus* E. Fourn. in Mart., Fl. Bras. 6(4): 311 (1885); Fontella Pereira & Konno, Bradea 7: 139–143 (1999), rev.

Suffrutescent twiner, hirsute to tomentose. Leaves 2.5–3 cm long, ovate. Inflorescences occasionally paired, 15–30-flowered, thyrsoïdal, condensed, shortly pedunculate. Corolla 1.5–2 mm long, abaxially with trichomes, adaxially glabrous; lobes imbricate, ovate; free staminal corona lobes adnate to both corolla and gynostegium, shorter than gynostegium, erect, laminar, triangular; pollinia broadly ovoid; caudicles geniculate, cylindrical.

One sp., *H. infracta* E. Fourn., in Brazil (Bahia), but possibly extinct.

### 318. *Metastelma* R. Br.

*Metastelma* R. Br., Asclepiadeae 41 (1810); Liede & Meve, Ann. Missouri Bot. Gard. 91: 31–86 (2004), reg. rev.; Liede-Schumann et al., Syst. Bot. 39: 594–612 (2014), phyl. *Acrocoryne* Turcz. (1852).

*Stelmation* E. Fourn. (1885).

*Meresaldia* Bullock (1965), nom. nov. pro *Esmeraldia* E. Fourn. (1882), non *Esmeralda* Rchb. (1862), Orchidaceae.

Herbaceous or suffrutescent twiners to 4 m, usually pubescent. Leaves 1.5–6 cm long, linear to ovate. Inflorescences 2–12-flowered, flowers occasionally sweetly fragrant. Corolla 1.5–4.5 mm long, whitish; lobes imbricate, oblong or ovate, with smooth and/or verrucose trichomes, often barbate; free staminal corona lobes attached below the anthers, along the stipe or shifted to corolla base, exceeding gynostegium, white, triangular, oblong or subulate; gynostegium often stipitate or atop a column. Follicles 2–7 cm long. Seeds (almost) wingless.  $2n = 22$ .

About 75 spp., from SW and SE USA and Mexico through Central America, the Caribbean and South America, forest margins, disturbed areas, coastal shrub and riverine vegetation, to 3000 m.

### 319. *Minaria* T.U.P. Konno & Rapini

*Minaria* T.U.P. Konno & Rapini, Taxon 55: 424 (2006); Ribeiro et al., Mol. Phyl. Evol. 65: 915–925 (2012), phyl.; Ribeiro et al., Taxon 63: 1253–1264 (2014), biogeogr.

(Sub-)shrubs, 10–60(–100) cm tall; usually hirsute or scabrous. Leaves often sessile, often strongly reflexed, coriaceous, 0.5–2 cm long, linear to ovate or triangular-deltate, often revolute to conduplicate. Inflorescences 1–5-flowered, subsessile; flowers usually nodding. Corolla 2–5 mm long, campanulate to urceolate; white to yellowish, rarely rose, usually barbate; lobes ovate; free staminal corona lobes filiform, lanceolate or ovate, usually with shorter proximal lobules, rarely absent; gynostegium stipitate when corona simple or absent; corpusculum smaller than pollinia. Follicles often densely puberulous or velutinous.  $2n = 22$ .

19 spp. in Brazil, extending to Argentina and Bolivia, in open vegetation, on well drained sandy soil; 600–1900 m.

320. *Morilloa* Fontella, Goes & S.A. Cáceres

*Morilloa* Fontella, Goes & S.A. Cáceres, Bonplandia (Corrientes) 23: 28 (2014).

Twiningers, glabrous or glabrescent all over. Leaves subsessile, linear. Inflorescences long-pedunculate, 3–9-flowered; flowers white or (greenish) yellow. Corolla urceolate or bottle-shaped, adaxially barbate or whitish puberulent; corona absent or vestigial; gynostegium sessile or shortly stipitate; style-head mamillate. Follicles narrowly linear-lanceolate, seeds verrucose.

Four spp. endemic to C Brazil, campos rupestres, cerrados, forest margins, on stony or sandy soils 1000–1600 m.

321. *Nautonia* Decne.

*Nautonia* Decne., Prodr. 8: 509 (1844); Meyer, Lilloa 7: 379–394 (1942), reg. rev.

Prostrate herb, densely rusty tomentose. Leaves distichous, sessile, ca. 1.5 cm long, ovate. Inflorescences 2–5-flowered, subsessile. Corolla 4–5 mm long, yellowish cream; lobes lanceolate, erect, with trichomes on central parts; corona absent; gynostegium stipitate, but concealed in corolla; pollinia ovoid to oblongoid, laterally attached to the horizontal, rectangular caudicles. Follicles 3.5–4 cm long, obclavate. Seeds winged, tuberculate with long, several-celled fringes.

A single species, *N. nummularia* Decne., in Argentina, Brazil and Paraguay, sandy areas.

Probably a *Ditassa* lacking a corona.

322. *Nephradenia* Decne.

*Nephradenia* Decne., Prodr. 8: 604 (1844); Rapini, Bol. Bot. Univ. São Paulo 19: 149–150 (2001), reg. rev.

Erect herbs, 30–50 cm tall, almost glabrous. Leaves occasionally whorled, (sub-)sessile, 2–4 cm long, linear, with interpetiolar colleters. Inflorescences 2-flowered, thinly pedunculate and pedicellate. Corolla 8–12 mm long, broadly campanulate, reddish to purple; lobes triangular, papillose or with trichomes; free staminal corona lobes adnate to both corolla and filament tube, shorter than gynostegium, erect, subulate or oblongoid; pollinia laterally attached to cylindrical

cal, ascending caudicles with very broad hyaline margin (therefore seemingly horizontal). Follicles occasionally paired, 5–6 cm long. Seeds wingless.

About five spp., centered in C Brazil, extending to Bolivia, Colombia, Venezuela and Suriname; cerrado, open rocky areas; 70–1500 m.

323. *Peplonia* Decne.

*Peplonia* Decne., Prodr. 8: 545 (1844); Rapini et al., Kew Bull. 59: 531–539. (2004), rev.; Silva et al., Syst. Bot. 37: 795–806 (2012), phyl.

*Gonioanthela* Malme (1927).

*Macroditassa* Malme (1927).

Suffrutescent twiningers, glabrous, with interpetiolar colleters. Leaves 4–10 cm long, elliptic or (ob-)ovate. Inflorescences axillary, paired, 3–10-flowered. Corolla 4–5 mm long, cream or yellowish green, occasionally papillose; lobes ovate to lanceolate, occasionally with erect trichomes or barbate; staminal corona lobes ivory, rectangular or oblong, free or basally fused, very rarely fused in a tube, exceeding gynostegium, occasionally with proximal appendage; style-head occasionally papillose, conical. Follicles 5–12 cm long. Seeds with dentate wing.

Eight spp. in C Brazil, seaside scrub, restinga, riverine vegetation.

Following a molecular study (Liede et al. 2005), the morphologically unique *P. asteria* (Vell.) Fontella & E.A. Schwarz, formerly the only species of *Peplonia*, is sister to *Gonioanthela*. According to Silva et al. (2012), *Macroditassa* is a synonym of *Peplonia*.

324. *Petalostelma* E. Fourn.

Fig. 53

*Petalostelma* E. Fourn. in Mart., Fl. Bras. 6(4): 328, t. 98. (1885).

Suffrutescent twiningers to 1 m, (sub-)glabrous. Leaves rarely whorled, 3–5 cm long, linear or ovate. Inflorescences 4–8-flowered; peduncles and pedicels filiform. Corolla 2.5–3.5 mm long, green or maroon; lobes ovate, spreading, papillose or with long, soft trichomes; corolline corona, when present, short, five-partite with free antepalous lobes or annular, occasionally with trichomes; free staminal corona lobes, when present, brownish, erect or spreading, lingulate or cross-shaped, shorter than gynostegium, basally with straight spur,

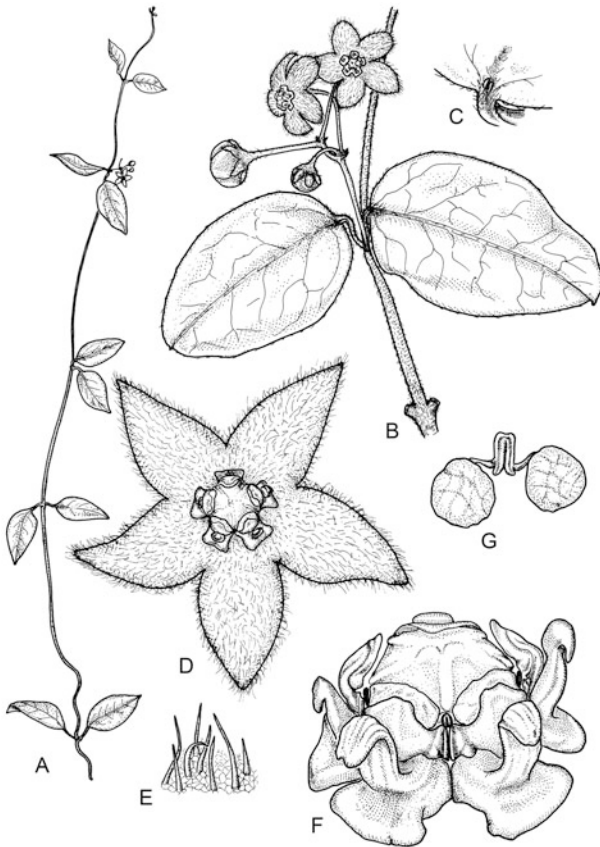


Fig. 53. Apocynaceae-Asclepiadeae. *Vincetoxicum coriaceum*. A Flowering plant. B Inflorescence. C Base of lamina with two colleters on rachis. D Flower in top view. E Microscopic details of adaxial corolla lobe epidermis with trichomes. F Gynostegium with corona. G Pollinarium. (From Liede and Meve 1994, p. 753, with permission from Kew Bulletin © Board of Trustees of the Royal Bot. Gard., Kew; drawn by U. Meve)

occasionally with shorter, dentiform, inflexed proximal lobules; gynostegium rarely stipitate; pollinia small, ovoid. Follicles 6–9 cm long, narrowly oblong. Seeds oblong, winged.

Seven spp. in Argentina, Bolivia, Brazil and Paraguay.

#### V.5.i. Subtribe Tassadiinae Liede & Meve (2014).

Suffrutescent twiners. Inflorescences usually axillary, paired, with one inflorescence shorter, often multi-flowered, thyrsoïdal, partial inflorescences often condensed. Corolla with trichomes in the tube; lobes frequently with trichomes; gynostegial corona a ring of connate staminal and interstaminal parts; gynostegium usually (sub-)sessile; caudicles cylindrical. Follicles paired, narrowly

oblong. Seeds oblong. One genus in South America, extending to the Caribbean and to Central America.

#### 325. *Tassadia* Decne.

*Tassadia* Decne., Prodr. 8: 579 (1844); Fontella Pereira, Arq. Jard. Bot. Rio de Janeiro 21: 235–392 (1977), rev.; Liede-Schumann & Meve, Phytotaxa 202: 35–44 (2015), new taxa.

*Stenomeria* Turcz. (1852).

Plants often with distinct long and short shoots, occasionally rusty tomentose. Leaves distichous or decussate, 2–9.5 cm long, oblong or ovate. Inflorescences occasionally single, 20–50-flowered; rachis often conspicuously zigzagging. Corolla 3–5 mm long, creamish green; lobes imbricate or contorted, occasionally strongly twisted, ovate to oblong; gynostegial corona ring cyathiform, staminal parts ovate, trifold or apiculate, erect, occasionally with adaxial appendage; pollinia occasionally with apical sterile hyaline region; style-head occasionally papillose, rarely rostrate. Follicles 2–5 cm long, often with basal thickening, rarely inflated. Seeds occasionally without coma.

Probably more than 35 spp. in South America, extending to Central America and the Caribbean, mountain forests, disturbed places, river shores, flood plains; to 1900 m.

#### V.5.j. Subtribe Oxypetalinae E. Fourn. (1885).

Erect herbs or suffrutescent twiners. Gynostegial corona of free or basally fused staminal lobes; gynostegium usually sessile. Follicles usually obclavate or fusiform. Seeds ovate or pyriform, often with distally denticulate wing. Six genera centered in South America, only a few species in the Caribbean and Central America.

#### 326. *Araujia* Brot.

*Araujia* Brot., Trans. Linn. Soc. London 12: 62, t. 4–5 (1817); Malme, Ark. Bot. 8: 1–30, t. 31 (1908), rev.

Suffrutescent twiners, 5–6 m tall, densely hirsute. Leaves discolorous, 5–11 cm long, ovate to hastiform, abaxially felty or tomentose. Inflorescences 1–5-flowered. Corolla 5–20 mm long, urceolate or campanulate, highly fused, white to rose; tube occasionally papillose or with trichomes; lobes

triangular, often twisted; staminal corona lobes adnate to corolla and gynostegium, short, erect, carnos, rectangular or triangular, occasionally apically with trichomes; gynostegium concealed in corolla tube, connective appendages rarely fimbriate; corpusculum larger than pollinia, with hyaline margin; style-head rostrate, or capitate and bifid. Follicles 7.5–15 cm long, ovoid, occasionally vaguely tuberculate, with thick woody pericarp. Seeds wingless, denticulate.  $2n = 20, 22$ .

Nine spp. in three sections in Argentina, Bolivia, Brazil, Paraguay and Uruguay, Chaco, dry to moist forest, often in disturbed situations. *A. sericifera* Brot. is invasive in many dry subtropical areas, and a noxious weed particularly in *Citrus* plantations.

### 327. *Funastrum* E. Fourn.

Fig. 54

*Funastrum* E. Fourn., Ann. Sci. Nat. Bot., VI, 14: 388 (1882); Liede & Meve, Nord. J. Bot. 22: 579–591 (2002, publ. 2004), phyl.

*Macbridea* Raf. (1818), nom. rej., non *Macbridea* Elliott (1818), Lamiaceae, nom. nov. pro *Lyonia* Elliott (1817), non *Lyonia* Raf. (1808), Polygalaceae, nec *Lyonia* Nutt. (1818), Ericaceae.

*Seutera* Rchb. (1828), nom. illegit. nom. superfl. pro *Macbridea* Raf.

*Pattalias* S. Watson (1889).

*Philibertella* Vail (1897).

*Ceramanthus* (Kunze) Malme (1905), non *Ceramanthus* Hassk. (1844), Phyllanthaceae.

Herbaceous or suffrutescent twiners; frequently rhizomatous; latex with disagreeable garlic scent. Leaves occasionally caducous, often soft, 2–9 cm long, ovate, linear, elliptic, or hastiform. Inflorescences 6–18-flowered. Corolla 6–12 mm long, rotate, whitish, green or reddish; lobes oblong, or ovate(-lanceolate), usually revolute and ciliate; gynostegial corona whitish, usually a completely fused, short ring of connate staminal and interstaminal parts, and, connate to this ring, erect, dolabriform free staminal lobes equaling the gynostegium; pollinia oblongoid to clavate; caudicles horizontal, cylindrical; style-head umbonate or conical. Follicles 5–8.5 cm long. Seeds ovate, winged.  $2n = 20, 40, 44$ .

About 15 spp., from SW and SE USA and Mexico through Central America, the Caribbean and South America, rheophytes, arid and semi-arid areas, plains, pampa, stony slopes, to 1500 m.

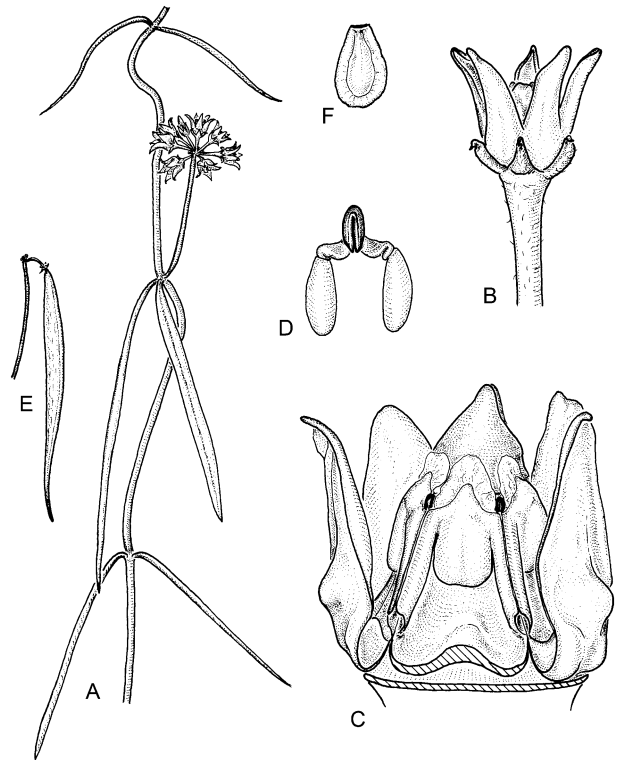


Fig. 54. Apocynaceae-Asclepiadeae. *Funastrum angustifolium*. A Flowering branch. B Flower. C Gynostegium surrounded by staminal corona lobes, front corona lobe removed. D Pollinarium. E Follicle. F Seed. (From Liede and Meve 2002, p. 588, with permission from Nordic Journal of Botany; drawn by U. Meve)

Although the molecular, chemical and karyological results of Liede and Meve (2002, publ. 2004) placed *Seutera* within *Funastrum*, Fishbein and Stevens (2005) continue to recognize it as an independent genus.

### 328. *Morrenia* Lindl.

*Morrenia* Lindl., Edwards's Bot. Reg. 24, Misc. 71 (1838); Malme, Ark. Bot. 8: 1–30, t. 31 (1908), rev.; Goyder, Kew Bull. 58: 713–721 (2003), rev.; Wiemer et al., Ann. Bot. 109: 77–93 (2012), ecol.

*Stuckertia* Kuntze (1903), nom. nov. pro *Choristigma* Kurtz ex H. Heger (1897), nom. illegit., non *Choristigma* (Baill.) Baill. (1892), Olacaceae.

*Hickenia* (1919).

Suffrutescent twiners to 5 m, usually pubescent. Leaves 4–7(–11) cm long, triangular, undulate, abaxially tomentose. Inflorescences 4–10-flowered, subsessile; flowers sweetly fragrant,

nectariferous. Corolla 10–15 mm long, rotate, white, brown or greenish yellow; lobes lanceolate, occasionally revolute; gynostegial corona whitish, tubular, extending into ovate, often bifid, staminal parts folding in to obscure gynostegium, occasionally with trichomes; anther wings extending beyond anther, forming an outward curve; pollinia ovoid or oblongoid; caudicles ribbon-shaped; style-head umbonate or rostrate, bifid. Follicles 5–9 cm long, ellipsoid to obclavate, with more than 6 wings, pericarp thick, woody. Seeds pyriform, wingless, denticulate.  $2n = 22$ .

Eight spp. S South America, Chaco, dry to moist forest, often in disturbed situations. *M. odorata* Lindl. is a noxious weed in *Citrus* groves in Florida and Australia; the young fruits are eaten, the latex is used to produce cheese; the plant is said to enhance milk flow in cows and women.

The suggestion of Rapini et al. (2011) to include *Morrenia* in *Araujia* is not followed here.

### 329. *Oxypetalum* R. Br.

*Oxypetalum* R. Br., Asclepiadeae 30 (1810); Hoehne, Monographia das Asclepiadaceas brasileiras, Fasc. I e II. Relat. Comm. Lin. Telegr., Bot. 38 (1, Suppl.): 1–131, t. 1–59 (1916); Meyer, Lilloa 9: 5–72 (1943); Farinaccio, Fl. Fan. Estad. São Paulo 4: 130–150 (2005), reg. rev.

*Schistogyne* Hook. & Arn. (1834).

*Schizostemma* Decne. (1838).

*Rhysostelma* Decne. (1844).

*Dactylostelma* Schltr. (1895).

*Widgrenia* Malme (1900).

*Schistonema* Schltr. (1906).

*Corollonema* Schltr. (1914).

*Amblyopetalum* (Griseb.) Malme (1927).

*Metoxypetalum* Morillo (1994).

Often erect herbs, usually with uniform indumentum. Leaves 3–12 cm long, linear, ovate or triangular-deltate. Inflorescences 10–20-flowered. Corolla 5–15 mm long, campanulate or urceolate; lobes linear, lanceolate, or (ob-)ovate, occasionally twisted, with verrucose or barbate trichomes; free staminal corona lobes often adnate to corolla and gynostegium, erect, occasionally carnose, lanceolate, oblong, often bifid, rarely with proximal lobule; rarely with interstaminal rim or teeth; gynostegium occasionally shortly stipitate; caudicles with conspicuous appendage; style-head

white, often apically purple, rostrate and bifid or 5-fid (former *Schistogyne* species). Follicles normally two, rarely muricate.  $2n = 18, 20, \text{ or } 22$ .

About 125 spp. in three subgenera, South America, mostly Argentina and Brazil; one sp. in Mexico and the Caribbean, in forest and open, often slightly disturbed areas.

The genus is in urgent need of revision.

### 330. *Philibertia* Kunth

*Philibertia* Kunth in Humboldt et al., Nov. Gen. Sp. (4th ed.) 3: 195 & pl. 230 (1819); Holm, Ann. Missouri Bot. Gard. 37: 477–560 (1950), rev. (under *Sarcostemma*); Liede & Täuber, Pl. Syst. Evol. 225: 133–140 (2000), phyl.; Liede et al., Syst. Bot. 30: 183–194 (2005), phyl.; Goyder, Kew Bull. 59: 415–451 (2004), rev.

*Melinia* Decne. (1844).

*Mitostigma* Decne. (1844).

*Amblystigma* Benth. (1876).

*Podandra* Baill. (1890).

*Stigmamblys* Kuntze, nom. illegit. (1903).

*Steleostemma* Schltr. (1906).

*Aphanostelma* Malme (1933), nom. illegit., non *Aphanostelma* Schltr. (1914).

*Fontellaea* Morillo (1994).

Suffrutescent twiners, prostrate or erect herbs, frequently white or yellow tomentose; latex with garlic scent, rarely translucent. Leaves usually long-petiolate, blades softly herbaceous, often discolorous, 0.4–16 cm long, ovate or triangular, cordate. Inflorescences 2–10-flowered, often long-pedunculate; flowers nodding. Corolla 5–15 (–45) mm long, (broadly) campanulate or salverform; lobes triangular, or ovate, usually hirsute; often with short corolline corona ring; usually with free, white, ovoid or dolabriform staminal corona lobes equaling gynostegium, occasionally with proximal lobule; gynostegium occasionally stipitate; pollinia oblongoid or clavate; style-head occasionally rostrate and bifid. Follicles 3–10 cm long, rarely ellipsoid, occasionally rugose or spiny, often tomentose, with thick pericarp.  $2n = 18, 20, \text{ or } 22$ .

43 spp. in South America.

The inclusion of *Amblystigma*, *Melinia*, and *Mitostigma* by Goyder (2004) has rendered the genus morphologically rather heterogeneous, but this clade is supported by DNA sequence data (Liede et al. 2005).

331. *Tweedia* Hook. & Arn.

*Tweedia* Hook. & Arn., J. Bot. (Hooker) 1: 291 (1834); Malme, Ark. Bot. 2: 1–18 (1904), rev.; Rua, Parodiana 5: 375–410 (1989), rev.; Calviño et al., Taxon 63: 1265–1274 (2014), phyl.

Erect herbs or suffrutescent twiners, to 1 m tall. Leaves occasionally whorled, 0.8–7 cm long, linear, obtriangular, or hastiform, revolute. Inflorescences 2–40-flowered. Corolla 3.5–9 mm long, campanulate, white or yellow, veined green; lobes oblong, twisted; corolline corona inserted and fused to tube, occasionally with trichomes in adaxial sinus, short, five-partite; lobes free or laterally connate, rectangular or rounded, bifid, erect; gynostegium (sub-)sessile; pollinia ellipsoid to oblongoid; caudicles trapezoidal; style-head rostrate and bifid. Follicles occasionally paired, 40–95 mm long, fusiform. Seeds pyriform, wingless.  $2n = 40$ .

Seven spp. in Argentina, Bolivia, Chile and Uruguay, open bushland.

V.5.k. **Subtribe Gonolobinae** Liede (1997).  
by S. Liede-Schumann and G.N. Morillo

Usually suffrutescent twiners, densely puberulous to hispid or hirsute, often with short spreading glandular capitate and long or short eglandular sculptured antrorse to retrorse trichomes. Corolla rotate, campanulate, urceolate or tubular; gynostegium sessile or stipitate; anthers usually broader than long, frequently horizontal, with transversally dehiscent membrane; pollinia horizontal or pendent, with apical to distal sterile hyaline region; laterally attached to caudicles; style-head flat or convex, rarely rostrate. Follicles solitary, ovoid or fusiform, usually with thick pericarp. Seeds ovate, winged, mostly with a coma.

Following results of a molecular analysis, Gonolobinae are sister to Oxypetalinae (Rapini et al. 2003). 45 genera in the tropics and subtropics of the New World.

332. *Anemotrochus* Mangelsdorff, Meve & Liede

*Anemotrochus* Mangelsdorff, Meve & Liede, Willdenowia 46: 452 (2016).

Prostrate to ascending vines with eglandular trichomes. Leaves subsessile, to  $1.5 \times 0.5$  cm, ovate. Inflorescences subsessile, to 6-flowered; flowers to 4.5 mm long. Corolla urceolate or subcampanulate with expanded lobes, uniformly whitish or with greenish reticulation; lobes ovate to linear, often twisted, adaxially pubescent on the left side; corolline corona a protuberance or absent; staminal corona shorter than gynostegium; interstaminal corona inconspicuous; anther wings separated in basal and apical part; pollinaria with pendulous, slightly furrowed pollinia. Follicles one or two per flower, fusiform, occasionally 10-costate, with protuberances.

Three spp., Caribbean, one endemic to Cuba, one to Hispaniola, coastal and in xerophytic thickets, occasionally on ultramafic soils; 0–150 m.

333. *Atrostemma* Morillo

*Atrostemma* Morillo, Pittieria 39: 198 (2015).

Twining shrubs; branches shortly pubescent. Leaves 6–18 cm long, broadly ovate to oblong-elliptic, basally cuneate to broadly cordate, apically apiculate to long-acuminate, both surfaces sparsely puberulous. Inflorescences 3–7-flowered. Corolla rotate, 10–34 mm diam., (yellowish) green and dark-reticulate, lobes oblong-lanceolate to obovate-elliptic; gynostegial corona (annular-)cyathiform, staminal segments incurved, thickly laminar or fleshy, basally adnate to stipe, interstaminal segments concave, usually puberulous abaxially; anthers suberect, subtriangular, pollinia subpendent; style-head concave. Follicles asymmetrically oblong or boat-shaped, obtusely muricate, glabrous.

Ten spp. in Central and South America, forests and thickets; 100–1700 m.

334. *Austrochthamalia* Morillo & Fontella

*Austrochthamalia* Morillo & Fontella, Rev. Biol. Neotrop. 10: 3 (2013).

Subshrubs, with xylopodium ca. 1.5 cm diam.; stems trailing, less than 1.5 m long; hirsute all over, with eglandular trichomes. Leaves distichous, blades to 5 cm long, deltoid or (oblong-)



ovate, basally cordate, apically acute. Inflorescences 2–4-flowered, shortly pedunculate, usually prostrate. Corolla 16–38 mm diam. (sub-)campanulate, green to purple; lobes deltoid, narrowly ovate to broadly oblong, adaxially verrucose and pilose; gynostegial corona a cup of fused staminal and interstaminal segments, with 10 internal rays, purple; gynostegium shortly stipitate; pollinia subhorizontal or pendent; style-head concave. Follicles ovoid, muricate.

Five or six spp. in Brazil, Paraguay and Argentina, savanna, below 600 m.

### 335. *Brargentina* Morillo & H.A. Keller

*Brargentina* Morillo & H.A. Keller, *Bonplandia* 25(2): 131 (2016).

Subshrub; stems trailing or vining, 0.15–0.75 m long, corky at base, densely pubescent mainly with eglandular trichomes. Leaves distichous or 3-whorled, blades membranous, up to 3.5 × 2.1 cm, narrow-ovate to oblong, narrowly obtuse to subcordate at base, pubescent throughout. Inflorescences 2–3 per node, 2–4-flowered. Calyx lobes oblong, acute, longer than corolla tube, abaxially pubescent; corolla white, rotate-campanulate, 20–21 mm diam.; lobes strongly contorted, asymmetrically oblong-lanceolate, glabrous except puberulent at adaxial base; corona gynostegial; staminal lobes laminar, oblong-subrectangular, incurved and partly covering the convex style-head; pollinia pendent. Follicles ovoid, 5.5–8 cm long, glabrous and almost smooth. Seeds thick, with a coma.

One sp., *B. bornmuelleri* (Malme) Morillo & H.A. Keller in SE Brazil, NE Argentina and SE Paraguay, cerrados and prairies; 100–500 m.

### 336. *Bruceholstia* Morillo

*Bruceholstia* Morillo, *Pittieria* 39: 207 (2015).

Woody vine to 40 m long; with dense (yellowish) brown mixed pubescence all over; with fascicles of 30–50 colleters at the base of petioles and blades; blades to 30 cm long, basally broadly cordate. Inflorescences 4–6-flowered. Corolla ca. 40 mm diam., fleshy, pale orange or yellowish green, reticulate; lobes broadly elliptic; gynostegial corona

annular-cyathiform, fleshy, dark brown to purple; staminal segments ligulate, adnate to the base of the anthers; gynostegium sessile; pollinia pendent. Follicles fusiform, with long curved processes and dark-brown pubescence.

A single species, *B. magnifolia* (Pittier) Morillo, in Central America, tropical wet forests; 70–1600 m.

### 337. *Chloropetalum* Morillo

*Chloropetalum* Morillo, *Pittieria* 39: 213 (2015).

Suffrutescent twiners or trailers, stems, pedicels and inflorescences hirtellous to hirsute, leaves (oblong-)ovate, basally cordate, apically acuminate, shortly pubescent to almost glabrous. Inflorescences 2–14-flowered. Corolla subcampanulate, 17–40 mm diam., (yellowish) green, reticulate; lobes ovate(-oblong); corolline corona usually present as clusters of short trichomes on corolla tube; gynostegial corona disciform or deeply 5-lobed, adnate to base of corolla and gynostegium; gynostegium (sub-)sessile; pollinia subtriangular or pyriform, horizontal or slightly pendent; style-head flat or slightly concave. Follicles 5-costate or 5-winged.

About seven spp. in Central and South America, and the Antilles, seasonally dry and riparian forests and thickets; 0–1000 m.

### 338. *Chthamalia* Decne.

*Chthamalia* Decne. *Prodr.* 8: 605 (1844).

*Tetracustelma* Baill. (1890).

*Amphorella* Brandegee (1910).

Prostrate to procumbent suffrutices or herbs, usually with a corky xylopodium or caudex with several short, hirtellous to hirsute stems. Leaves usually distichous; blades to 4 cm long, subsessile, ovate to suborbicular, basally truncate to cordate, pubescent on at least one surface. Inflorescences 2–6-flowered. Corolla 4–13 mm diam., tubular to suburceolate, cream, green, or purple; lobes oblong or lanceolate, veined lengthwise; gynostegial corona 5-lobed, connate to 3/4 of its length, usually adnate to gynostegium; style-head concave to shortly rostrate. Follicles 5–10 cm long, muricate.

Two to ten spp. in Mexico and SW USA, deserts and scrub. Delimitation and number of species presently under study, deserts and scrub.

339. *Coelostelma* E. Fourn.

*Coelostelma* E. Fourn. in Mart., Fl. Bras. 6(4): 320 (1885).

Erect suffrutex, 30–60 cm high, glabrous all over. Leaves shortly petiolate, to 9.5 cm long, oblong-lanceolate, basally rounded to truncate, apically acuminate. Inflorescences shortly pedunculate, 2-flowered. Corolla rotate-campanulate, throat and adaxial basal lobes puberulent, lobes 13–18 mm long, acuminate, conspicuously veined; gynostegial corona of 5 distinct fleshy staminal lobes, these truncate, entire, with inconspicuous external central flap; gynostegium sessile, anthers obtriangular, dorsally without appendages; pollinia horizontal, narrowly obovoid; style-head broadly pentagonal, flat or slightly concave.

One sp., *C. refractum* E. Fourn., endemic to E Brazil.

340. *Cristobalia* Morillo, S.A. Cáceres & H.A. Keller

*Cristobalia* Morillo, S.A. Cáceres & H.A. Keller, Pittieria 40: 132 (2016).

Twining shrubs; stems hirsute, not corky at base. Leaves petiolate, blades to 15 cm long; obovate-elliptic to deltoid-ovate, basally cordate. Inflorescences subsessile, 3–15-flowered. Corolla 14–21 mm diam., rotate to campanulate; lobes ovate, adaxially green or dark pink to purple, reticulate; gynostegial corona cyathiform, 5-lobed, radially sinuate-lobulate, with five broad cavities in interstaminal position, (blackish) purple; gynostegium exerted, shortly stipitate; anthers with prominent, curved, laminar wings; pollinia reniform or asymmetric and shortly calceolate. Follicles fusiform-ellipsoid, muricate, with many conic to unciform projections, hirsute.

Two spp. in Argentina, Bolivia and Brazil, temperate forests; 200–2670 m.

341. *Cyclodon* Small

*Cyclodon* Small, Man. S.E. Fl. 1075 (1933).

Twining shrub; stems with mixed pubescence. Leaves petiolate; blades 6–15 cm long, ovate,

basally cordate, apically acuminate, sparingly pilose. Inflorescences 3–6-flowered, pedunculate. Corolla rotate, light-green, reticulate; lobes 6–8 mm long, spreading, narrowly elliptic, abaxially puberulent or sparsely hirtellous; gynostegial corona thinly fleshy, consisting of an outer ring attached to the corolla tube with 5 erect, crest-like apically ligulate staminal lobes adnate to the stipe; gynostegium stipitate; anthers horizontal, with lateral dehiscence; pollinia narrowly obovoid, horizontal; style-head flat. Follicles fusiform, strongly short-muricate and puberulous.

One sp., *C. alabamensis* (Vail.) Small, endemic to SE USA, low elevations.

342. *Dictyanthus* Decne.

*Dictyanthus* Decne., Prodr.8: 604 (1844); Stevens, Ann. Missouri Bot. Gard. 75: 1533–1564 (1988), rev.

*Tympananthe* Hassk. (1847).

*Pachystelma* (1920).

Erect, trailing or vining small herbs or subshrubs; usually woody at base, pubescent all over; trichomes eglandular, uncinata or spreading, and glandular, spreading. Leaves petiolate; blades 1.3–13 cm long, ovate, basally cordate, apically acuminate, inflorescences 1- to few-flowered. Corolla campanulate, tubular or urceolate; tube internally convoluted with raised parts opposite corona lobes and sacs formed between them; lobes 2.5–25 mm long, marginally often sharply revolute; gynostegial corona adnate to corolla tube, and partly, by a thin septum, to gynostegium; gynostegium stipitate; pollinia subhorizontal; style-head flat or apiculate. Follicles fusiform, muricate.

About 16 spp. in Mexico to Costa Rica, mainly seasonally dry forests and savanna; 0–1500(–2250) m.

343. *Edisonia* Small

*Edisonia* Small, Man. S.E. Fl. 1078 (1933).

Trailing herb or subshrub; stems to 1.1 m long, hispid with eglandular and glandular translucent trichomes. Leaves petiolate, blades to 5 cm long, broadly ovate to deltoid-reniform, basally cordate, apically acute or acuminate, hispid. Inflorescences (sub-)sessile, 2–6-flowered. Corolla ca. 10 mm diam., campanulate, olive-green or

reddish brown; lobes ca. 2 mm long, spreading, deltoid-ovate, with a basal small tooth-like projection, adaxially conspicuously barbate; gynostegial corona tubular-urceolate, apically with 5 short involute ligulate lobes; pollinia horizontal, with longitudinal hyaline sterile lateral margin. Follicles prostrate, ovoid-fusiform, muricate.

One sp., *E. pubiflora* (Decne.) Small, in SE USA, sandhills and dry scrub in coastal plains, 15–100 m.

#### 344. *Fischeria* DC.

*Fischeria* DC., Cat. Horti Pl. Monsp. 112 (1813); Spellman, Ph.D. Thesis, St. Louis Univ. (1975), rev.; Murphy, Syst. Bot. 11: 229–241 (1986), rev.

Suffrutescent twiners, 3–20 m tall, densely puberulous to hispid, trichomes yellow to light brown. Leaves long-petiolate; blades 5–18 cm long, elliptic to ovate, basally cordate. Inflorescences pedunculate, to 25-flowered. Corolla 5–15 mm long; lobes lanceolate, ovate or triangular, papillose, right margin undulate and crenate; gynostegial corona short, carnose, annular, adnate to corolla and gynostegium; abaxially warty or with trichomes, adaxially fimbriate; anthers without transversally dehiscent membrane, dorsally with inflated appendage, free; connective appendages pyriform, inflated; pollinia reniform, horizontal. Follicles 11–15 cm long, obliquely ellipsoid or ovoid, almost smooth.

Eight spp. in Central and South America, forests and thickets; 0–1700 m.

#### 345. *Gonolobus* Michx.

*Gonolobus* Michx., Fl. Bor.-Amer. 1: 119 (1803); Stevens, Fl. Fan. Valle México 2: 236 (1985), reg. rev.; Stevens, Fl. Nicaragua 1: 247–252 (2001), reg. rev.; Stevens, Novon 15: 222–244 (2005); Krings, Harvard Pap. Bot. 13: 209–218 (2007), reg. rev.; Krings et al., Syst. Bot. 33: 403–415 (2008), phyl.

*Gonolobium* R. Hedw. (1806), nom. illegit.

*Fimbristemma* Turcz. (1852).

*Exolobus* E. Fourn. (1885).

*Trichostelma* Baill. (1890).

Mostly suffrutescent twiners, lenticellate on older internodes, usually pubescent with long, yellow or translucent trichomes, frequently with glandu-

lar trichomes. Leaves long-petiolate, to 16 cm long, broadly ovate to linear. Inflorescences 1–15-flowered. Corolla 10–35 mm long, often reticulate, frequently pubescent; lobes linear to ovate-elliptic, tightly twisted; corolline corona inserted in corolla tube, usually annular, ciliate or fimbriate; gynostegial corona annular or cup-shaped, basally adnate to corolla and gynostegium; gynostegium occasionally stipitate, anthers with dorsal appendage; pollinia horizontal, oblong-ovoid to reniform. Follicles 3–5-winged, rarely smooth, basally asymmetric.  $2n = 22$ .

About 120–140 spp. from SW and SE USA and Mexico through Central America, the Caribbean and South America, dry or wet forests and thickets; 0–2500 m.

#### 346. *Gracemoriana* Morillo

*Gracemoriana* Morillo, Pittieria 39: 223–224 (2015).

Twining vine, ca. 10 m long; with mixed dense brownish pubescence of spreading, glandular and eglandular trichomes all over. Leaves petiolate; blades 18–26 cm long, broadly (obovate-)elliptic, basally narrowly cordate, apically obtuse and acuminate. Inflorescences pedunculate, 3–4-flowered. Corolla ca. 18 mm diam., rotate-campanulate, green; lobes broadly deltoid, obtuse, emarginate and reticulate; gynostegial corona of 5 staminal irregularly trapezoidal segments, marginally rugose-carunculate, fleshy; gynostegium shortly stipitate; pollinia subhorizontal, asymmetrically obovoid-reniform; style-head slightly convex. Follicles broadly ovoid, brown-puberulent.

One sp., *G. graciae* (Morillo) Morillo, French Guiana, non-flooded moist forest, 200–400 m.

#### 347. *Gyrostelma* E. Fourn.

*Gyrostelma* E. Fourn. in Mart., Fl. Bras. 6(4): 302 (1885); Rapini, Bol. Bot. Univ. São Paulo 19: 71–72 (2001), reg. rev.

Erect or creeping subshrub, hirsute all over with stiff trichomes. Leaves ca. 3 cm long, elliptic. Inflorescences ca. 6-flowered, subsessile. Corolla 4–5 mm long, campanulate, glabrous; lobes oblong; gynostegial corona of free, erect, oblong, apically bifid, staminal lobes exceeding

gynostegium; anthers rectangular or truncated obtriangular, erect; pollinia ovoid, caudicles cylindrical with pronounced hyaline margin; corpusculum rhomboid, smaller than pollinia; style-head flat to broadly conical.

One sp., *G. oxypetaloides* E. Fourn., Brazil.

348. *Himantostemma* A. Gray

*Himantostemma* A. Gray, Proc. Amer. Acad. Arts 20: 294 (1885).

Spreading herb or suffrutex; branches to 30 cm long, pubescent all over. Leaves to 4.5 cm long, sagittate-cordate to deltate-hastate, apically acute or acuminate. Inflorescences 2-flowered. Corolla 11–13 mm diam., rotate, lobes whitish or green, purple with age, broadly oblong to narrow-lanceolate, reflexed, adaxial tube with long, white, linear-spathulate trichomes; gynostegial corona of basally fused staminal and interstaminal segments; staminal segments dentate, short; interstaminal segments prolonged into 10 erect, strap-shaped lobes; anthers erect, apically dehiscent; pollinia pendent. Follicles fusiform, muricate.

One sp., *H. pringlei* A. Gray, Sonora Desert, NW Mexico and SW USA, 0–250 m.

349. *Ibatia* Decne.

*Ibatia* Decne., Prodr. 8: 599 (1844); Krings & Saville, Syst. Bot. 32: 862–871 (2007), phyl.; Morillo, Pittieria 36: 13–57 (2012).

*Callaeolepium* H. Karst. (1866).

*Omphalophthalma* H. Karst. (1866).

*Amphidetes* E. Fourn. (1885).

*Pycnobregma* Baill. (1890).

*Pseudibatia* Malme (1900).

Twining or sometimes erect (sub-)shrubs, usually densely mixed-pubescent all over. Leaves 2.5–15 cm long, ovate to suborbicular, basally usually (sub-)cordate. Inflorescences shortly pedunculate, few to many-flowered. Corolla rotate to campanulate, white or green to purple; lobes 3–6.5 mm long, ovate to oblong; gynostegial corona of connate staminal and interstaminal segments, annular, cup-shaped or 5-lobed; gynostegium stipitate; anthers radially protruding, with dorso-apical dehiscence; pollinia pendent, usually

obovate, proximally hyaline; style-head concave to rostrate. Follicles muricate.  $2n = 22$ .

About 25 spp., South and Central America, Caribbean, seasonally dry forests and scrub, 0–2200 m.

Of the genera formerly included in *Matelea*, *Ibatia* is monophyletic with high support by molecular data (Krings and Saville 2007).

350. *Jacaima* Rendle

*Jacaima* Rendle, J. Bot. 74: 340. (1936).

Twining vine; stems with eglandular pubescence, on entire surface or in 2 lines. Leaves 3–9 cm long, ovate, basally rounded to subtruncate, glabrous or sparsely pubescent on midvein. Inflorescences 4–7-flowered, pedunculate. Corolla campanulate, white; lobes 1.5–2.7 mm long, narrowly ovate, basally incurved, with an eyespot-like concavity and large, white eyespot at apex, glabrous; staminal corona a costate ridge adnate to stipe over most of its length, apically ligulate; gynostegium stipitate; pollinia horizontal; style-head umbonate. Follicles ovoid, 5-ridged, glabrous.

A single species, *J. costata* (Rendle) Morillo, endemic to Jamaica, dry rocky thickets and mesophytic forests, 15–200 m.

351. *Lachnostoma* Kunth

*Lachnostoma* Kunth in Humboldt et al., Nov. Gen. Sp. (4. ed.) 3: 198 (1818, publ. 1819); Morillo, Pittieria 36: 24–27 (2012).

Twining, densely pubescent mainly with eglandular trichomes all over. Leaves to 15 cm long, (oblong-)ovate, basally (sub-)cordate, apically acuminate. Inflorescences 5–15-flowered, pedunculate; pedicels 0.5–1.5 times as long as peduncle plus rachis. Corolla 10–30 mm diam., usually salverform, narrow-campanulate in one species; lobes (yellowish) green or purple, frequently reticulate; gynostegial corona adnate to stipe and to corolla tube over at least half of its length, apically bilobed-digitate; pollinia pendent, oblongoid-pyriform. Follicles narrowly ovoid to fusiform, with 5 obtuse ridges and blunt intercostate projections.

About 12 spp., W and N South America, Peru to Venezuela, montane wet forests, above 1000 m.

### 352. *Lhotzkyella* Rauschert

*Lhotzkyella* Rauschert, Taxon 31: 557 (1982); nom. nov. pro *Pulvinaria* E. Fourn. (1885), non *Pulvinaria* Bonorden (1851), Fungi-Sphaeriales.

Twiner with short mixed-pubescence in 2 lines; eglandular trichomes retrorse. Leaves 5–7.5 cm long, narrowly ovate or oblong-ovate, basally shortly cordate, sparsely puberulous. Inflorescences short-pedunculate, 4–6-flowered. Corolla ca. 16 mm long, campanulate, dark purple; lobes 12–13 mm long, tightly contorted in bud, oblong, puberulous only at adaxial base; staminal corona segments of 5 distinct fleshy bidentate elements, shorter than gynostegium; gynostegium stipitate, anthers ventricose, with dorso-lateral dehiscence; pollinia subpendent, narrowly obovoid; style-head disciform, slightly convex. Follicles narrowly ovoid, acute, pentagonal and 5-costate.

One sp., *L. lhotzkyana* (E. Fourn.) Rauschert, Mato Grosso, Brazil, savanna (cerrados), below 500 m.

### 353. *Macroscepis* Kunth

*Macroscepis* Kunth in Humboldt et al., Nov. Gen. Sp. (4. ed.) 3: 201 & ed. fol.: 156 (1819); Stevens, Fl. Nicaragua 1: 254–255 (2001), reg. rev.; Fontella Pereira & Konno, Fl. Fan. Estad. São Paulo 4: 121–122 (2005), reg. rev. *Schubertia* Mart. (1824).

Suffrutescent twiners, 5–20 m long, frequently suberized at base; usually hirsute with eglandular trichomes all over. Leaves 6–30 cm long, obovate-oblong to suborbicular, basally narrowly cordate. Inflorescences pedunculate, 2–20-flowered, bracts foliaceous. Corolla 18–25 mm diam., urceolate, tubular or infundibuliform, white, green to brown, fleshy; corolline corona present; gynostegial corona fleshy, partly adnate to gynostegium and corolla, staminal lobes apically truncate or crenulate, occasionally included; pollinia pendent, with thin hyaline margin; style-head convex or concave. Follicles usually (5–)7-winged.  $2n = 22$ .

About 20 spp., the Americas, from Mexico to Argentina, dry or wet forests and thickets, 0–1600 m.

### 354. *Malinvaudia* E. Fourn.

*Malinvaudia* E. Fourn. in Martius Fl. Bras. 6(4): 312, t. 92 (1885).

Twiner, stems glabrous. Leaves shortly petiolate, blades to  $13 \times 4.5$  cm, oblong-lanceolate, basally subcordate, apically long-acuminate, almost glabrous. Inflorescences 6–9-flowered; peduncles to 7.5 cm long. Corolla campanulate, throat with 5 interlobular pubescent pads; lobes ca. 10 mm long, acuminate, conspicuously veined, adaxially proximally puberulent; gynostegial corona shorter than gynostegium, of 5 distinct, fleshy, 3-dentate staminal segments; gynostegium sessile, anthers obtriangular, dorsally without appendages; pollinia horizontal, narrowly obovoid; style-head broadly pentagonal, almost flat. Follicles unknown.

One sp., *M. capillacea* E. Fourn., E Brazil and NE Argentina, below 600 m.

### 355. *Matelea* Aubl.

*Matelea* Aubl., Hist. Pl. Guiane 277, t. 109, f. 1 (1775); Stevens, Flora Fan. Valle México 2: 228–241 (1985), reg. rev.; Stevens, Fl. Nicaragua 1: 236–239 (2001), reg. rev.; Rapini, Bol. Bot. Univ. São Paulo 19: 69–71 (2001), reg. rev.; Konno & Fontella Pereira, Fl. Fan. Estad. São Paulo 4: 118–120 (2005), reg. rev.

*Hostea* Willd. (1798), nom. illegit.

*Peckoltia* E. Fourn. (1885).

*Acomosperma* K. Schum. ex Ule (1908).

Erect or twining (sub-)shrubs; pubescent all over with mixed indumentum of short glandular and eglandular trichomes. Leaves ovate to oblong-lanceolate, basally obtuse to subcordate, apically acute to acuminate. Inflorescences shortly pedunculate, 3–12-flowered. Corolla to 16 mm diam., rotate or shortly campanulate; lobes green, reticulate; gynostegial corona marginally annular; staminal segments apically ligulate ascending ridges, interstaminal segments usually concave; gynostegium stipitate or sessile; anthers narrowly triangular; pollinia usually horizontal, obovoid or obpyriform; style-head frequently flat or convex. Follicles fusiform to ovoid, 5-costate, 5-winged or almost smooth.  $2n = 22$ .

About 75 spp., Central and South America, wet and riparian transitional forests; 0–2200 m.

356. *Odontostephana* Alexander

*Odontostephana* Alexander in Small, Man. S.E. Fl. 1076 (1933).

Herbaceous vines; hirtellous or hirsute all over. Leaves ovate to almost orbicular, basally cordate, apically acuminate. Inflorescences dichasial or racemiform cymes, (4–)8–20-flowered. Corolla shallowly campanulate-rotate; lobes 7–18 mm long, oblong or spatulate, occasionally reticulate, adaxially glabrous, abaxially pubescent; gynostegial corona a cup-shaped ring of 5 staminal segments reaching or surpassing style-head, each segment abaxially usually with two triangular teeth; anthers radially protruding from below style-head; pollinia horizontal. Follicles narrowly fusiform or narrowly ovoid, muricate.

About seven spp., USA, mainly in prairies and deciduous temperate forests.

357. *Orinoquia* Morillo

*Orinoquia* Morillo, Pittieria 39: 229 (2015).

Twining subshrub; with moderate pubescence of golden-yellow, very long (to 7 mm), eglandular trichomes all over, and scarce pubescence of short translucent glandular trichomes. Leaves 10–13 cm long, broadly ovate(-elliptic), basally cordate, apically abruptly acuminate. Inflorescences very long-pedunculate, 3–5-flowered. Corolla 50–55 mm diam., rotate; lobes 18–19 mm long, narrowly ovate; gynostegial corona shallowly cup-shaped, staminal lobes 10, radially disposed, bifid and marginally expanded; inter-staminal lobes narrow-ligulate, reflexed; pollinia horizontal, obovoid. Follicles unknown.

One sp., *O. yanomamica* (Morillo) Morillo, endemic to Venezuela, rain forest, headwaters of the Orinoco river, 150–400 m.

358. *Peruviasclepias* Morillo

*Peruviasclepias* Morillo, Pittieria 39: 232 (2015).

Erect, prostrate or short twining herb or subshrub, 0.4–1.5 m long; stems frequently scarred, densely glauco-villous when young. Leaves 2–4.5 cm long, basally cordate, somewhat fleshy, pubescent on both surfaces. Inflorescences 6–12(–24)-

flowered. Corolla 6–7 mm diam., yellowish green, salverform or short-campanulate, with 5 fascicles of white trichomes in throat opposite the anthers; gynostegial corona annular, adnate to corolla tube; gynostegium long-stipitate; anthers protruding from style-head, with white-translucent deltoid apical membrane; pollinia subhorizontal to erect, oblongoid-pyriform. Follicles fusiform, muricate, with short curved projections.

One sp., *P. aliciae* (Morillo) Morillo, NW Peru, deserts, 100–500 m.

359. *Phaeostemma* E. Fourn.

*Phaeostemma* E. Fourn. in Mart., Fl. Bras. 6(4): 311, t. 91 (1885).

Shrubby vines up to 10 m long; densely pubescent all over with eglandular long and short trichomes, and scarce glandular short trichomes. Leaves 8–20 cm long, broadly (oblong-)ovate or elliptic, basally indistinctly cordate, apically acuminate. Inflorescences shortly pedunculate, 2–12-flowered; pedicels 2–6.2 times longer than peduncle plus rachis. Corolla 23–38 mm diam., broadly campanulate, (yellowish) green; lobes narrowly ovate to deltoid, reticulate; gynostegial corona of 5 apically bifid-digitate staminal segments partly adnate to corolla tube and stipe; pollinia pendent, narrowly pyriform. Follicles with 5 wings and blunt projections.

Six or seven spp., E South America, from Venezuela, Guayana to Argentina, tropical wet, rain or montane forests, 100–700 m; one species on a sandstone mountain of the Venezuelan Guayana above 1500 m.

360. *Pherotrichis* Decne.

*Pherotrichis* Decne., Ann. Sci. Nat. Bot. 2, 9: 322 (1838); Juárez-Jaimes & Lozada, Fl. Valle Tehuacán-Cuicatlán 37: 53–55 (2003), reg. rev.

Erect herbs, 30–40 cm tall, densely hirsute with erect eglandular and glandular trichomes; with spindle-shaped root tubers. Leaves sessile, 3.5–8 cm long, elliptic, or obovate. Inflorescences seemingly axillary, sessile, (3–)5–10(–14)-flowered; bracts linear, conspicuous. Corolla 5–7 mm long, campanulate, creamish green with dense, flexuous or barbate trichomes; lobes

ovate, occasionally long-acuminate; gynostegial corona of free, erect, rectangular, emarginate, slightly bifid staminal lobes, adnate to corolla and gynostegium; gynostegium atop a bulge; anthers truncated, obtriangular; pollinia pendent, caudicles with pronounced hyaline margin; style-head elongate-conical to rostrate. Follicles obclavate.

About five spp., Guatemala, Mexico, USA, open grassy slopes, pine forests.

### 361. *Poicilla* Griseb.

*Poicilla* Griseb., Cat. Pl. Cub. 176 (1866).

Slender woody vine; stems densely pubescent all over with mixed trichomes; eglandular trichomes retrorse or spreading. Leaves oblong-lanceolate, basally sagittate, apically obtuse to acute. Inflorescences few-flowered, subsessile. Corolla subcampanulate, greenish purple to maroon, lobes 1.9–3.5 mm long, reticulate, ovate to deltoid, obtuse to rounded, abaxially pubescent; staminal corona segments prominent-convex and cucullate, adnate to stipe for most of its length; gynostegium stipitate; pollinia obovoid. Follicles fusiform, 4–5-angled or ridged, (almost) glabrous.

One sp., *P. tamnifolia* Griseb., Cuba; thickets, semi-deciduous forests and woodland pastures.

### 362. *Poicillopsis* Schltr. ex Rendle

*Poicillopsis* Schltr. ex Rendle, J. Bot. 74: 343 (1936).

Slender vine; stems pubescent in two lines with mixed retrorse trichomes. Leaves 1–2.7 cm long, ovate to oblong, basally rounded, apically obtuse and apiculate, nearly glabrous. Inflorescences shortly pedunculate, few-flowered. Corolla ca. 7 mm diam., subcampanulate, white to green; lobes 1.8–3.3 mm long, ovate, obtuse to acute, adaxially densely pubescent except along left margin; gynostegial corona of basally fused obovate to suborbicular staminal and interstaminal segments, equaling gynostegium; pollinia lanceolate-oblong to falcate. Follicles subcylindrical-fusiform, pubescent or glabrous.

One sp., *P. ovatifolia* (Griseb.) Rendle, Cuba, Sierra Maestra, 1000 m.

### 363. *Polystemma* Decne.

*Polystemma* Decne., Prodr. 8: 602 (1844).  
*Rothrockia* A. Gray (1885).  
*Urostephanus* B.L. Rob. & Greenm. (1895).  
*Labidostelma* Schltr. (1906).  
*Microdactylon* Brandegee (1908).  
*Heliostemma* Woodson (1935).

Shrubby vines, sometimes erect, stems from a thickened taproot; with dense mixed pubescence all over; glandular trichomes with crystalline-white inclusions. Leaves ca. 4–10 cm long, ovate to deltoid, basally cordate, apically acuminate. Inflorescences pedunculate, 2–6-flowered. Corolla broadly to narrowly tubular campanulate; lobes (triangular-)ovate, obtuse, reticulate; gynostegial corona of 5 connate staminal segments, each with filiform or digitate appendages usually in 2 series; gynostegium sessile or stipitate; pollinia subhorizontal or pendent, reniform or obovoid. Follicles fusiform-subcylindrical, long-attenuate, smooth, mottled.

About 20 spp. in northern Mexico to Costa Rica, dry deciduous forests and scrub, 200–1300 m.

### 364. *Prosthecidiscus* Donn. Sm.

*Prosthecidiscus* Donn. Sm., Bot. Gaz. 25: 149 (1898).

Woody coarse vine; 8–10 m long, branches densely pubescent with short glandular and eglandular spreading trichomes, and long bristly trichomes. Leaves 8–22 cm long, elliptic, basally cordate, apically abruptly acuminate, adaxially sparsely setulose to glabrous, abaxially moderately to densely puberulent. Inflorescences pedunculate, 3–6-flowered. Corolla green and red or purple; lobes 12–19 mm long, oblong-spathulate, adaxially glabrous, abaxially glandular-puberulous; corolline corona present; gynostegial corona 5-lobed and ligulate, adnate to stipe; style-head long-rostrate; pollinia subpendent, obpyriform. Follicles strongly and densely muricate.

One sp., *P. guatemalensis* Donn. Sm., Central America and Mexico, mainly in dry deciduous forests, 30–1800 m.

### 365. *Pruskortizia* Morillo

*Pruskortizia* Morillo, Pittieria 40: 97 (2016); Morillo, Pittieria 39: 236 (2015).

Woody vines; stem pubescence of brown or yellowish long eglandular and short glandular trichomes. Leaves more than 15 cm long, obovate to oblong-elliptic, shortly and narrowly cordate, acuminate. Inflorescences subsessile, 3–6-flowered. Corolla 33–65 mm diam., rotate; lobes spreading to reflexed; gynostegial corona dark purple; staminal corona segments hemidiscoid, with a short central ridge at base of the anthers; gynostegium sessile; pollinia horizontal, oblongoid or narrowly calceolate; anthers with triangular or deltoid apical membrane; style-head flat. Follicles broadly ovoid, thick-walled, pubescent, somewhat tuberculate, with small conic protuberances.

Two spp. in Colombia to Bolivia, wet, rain or montane forests, 100–2550 m.

### 366. *Pseudolachnostoma* Morillo

*Pseudolachnostoma* Morillo, Pittieria 36: 44 (2012).

Suffrutescent twiners, densely pubescent with yellow trichomes, glandular trichomes absent. Leaves 7–14 cm long, ovate-elliptic, apically acuminate. Inflorescences few-flowered, sciadioidal. Corolla 3.5–7 mm long, yellowish, green or maroon, occasionally veined with green, diminutively hispid; lobes strongly reflexed; gynostegial corona tubular to cyathiform, adnate to corolla and stipe with five laminar lobules forming deep nectaries, subcarinose; gynostegium stipitate; anthers fused to upper side of style-head; connective appendages absent; pollinia pendent, pyriform, larger than corpusculum. Follicles narrowly fusiform, conspicuously 5-costate, attenuate.

About 12 spp., tropical Americas, rain and premontane forests, 200–1350 m.

### 367. *Ptycanthera* Decne.

*Ptycanthera* Decne., Prodr. 8: 606 (1844).

Slender vines; stem pubescent in two lines. Leaves oblong to ovate, 0.9–5.7 cm long, basally obtuse to truncate, apically obtuse to rounded and apiculate, glabrous. Inflorescences subsessile or pedunculate, 2–3-flowered. Corolla (sub-)rotate; lobes 4.7–7.5 mm long, linear-lanceolate, obtuse; gynostegial corona of basally swollen staminal segments, subtriangular in front view, rising ver-

tically and connecting to the stipe below the anthers; gynostegium stipitate; anther wings with divergent apices; pollinia horizontal, obovate or oblong-obovate; style-head conical or slightly rostrate. Follicles fusiform, with 5 undulating wings.

About five spp. in the Caribbean.

### 368. *Rhytidostemma* Morillo

*Rhytidostemma* Morillo, Pittieria 37: 127 (2013).

Twiners with a mixed indumentum of short glandular trichomes and long or short non-glandular trichomes all over. Leaves elliptic, basally rounded, apically acute. Inflorescences long-pedunculate, 4–18-flowered. Corolla campanulate; lobes narrowly ovate to oblong, conspicuously undulate and crenate along both margins in the upper third; gynostegial corona of 5 distinct, conspicuously verrucose lobes surrounding base of gynostegium, frequently with 5 laminar laterally flat segments arising radially from upper part of stipe; gynostegium shortly stipitate; carpels densely pubescent. Follicles fusiform, with thick walls, with dense, short, brown glandular pubescence.

About ten spp., Panama to Guianas, Peru and Brazil.

### 369. *Riparoampelos* Morillo

*Riparoampelos* Morillo, Pittieria 39: 241 (2015).

Suffrutescent twiner; stems shortly pubescent. Leaves 8–13 cm long, lanceolate to obovate-elliptic, basally shortly and narrowly cordate, apically acuminate, abaxially with short erect trichomes. Inflorescences subsessile, 2–3-flowered. Corolla 20–24 mm diam., rotate(–campanulate); lobes dark purplish, spreading, apically with long, flat and white trichomes; gynostegial corona fleshy, dark purple to black, staminal segments incurved, interstaminal segments broadly concave; gynostegium subsessile; pollinia horizontal, asymmetrically pear-shaped. Follicles narrowly ovoid or fusiform, muricate, with irregular blunt-tipped projections.

A single species, *R. amazonica* (Morillo) Morillo, Amazon basin and Guianas, wet or rain forests, mainly in riparian vegetation, 100–300 m.



370. *Rojasia* Malme

*Rojasia* Malme, Ark. Bot. 4(14): 10, t. 2, f. 4 (1905); Goyder, Kew Bull. 61: 31–33 (2006), rev.

Suffrutescent twiner, 3–4 m long; densely grayish tomentose. Leaves 3–6 cm long, ovate to triangular-deltate, basally cordate. Inflorescences 4–6-flowered. Corolla ca. 10 mm long, white; lobes spatulate, glabrous, erect; gynostegial corona of free staminal lobes attached below the filament tube, laminar, erect, branched, fimbriate, exceeding gynostegium; gynostegium stipitate; pollinia ovoid, pendent, laterally attached to the articulated caudicles. Follicles ca. 10 mm long, obclavate, finely pubescent, muricate, projections long and slender.

One sp., *R. gracilis* (Morong) Malme, in Argentina, low Chaco forest, 50–450 m.

371. *Rotundanthus* Morillo

*Rotundanthus* Morillo, Pittieria 39: 245 (2015).

Woody vine to 9 m long, densely pubescent with eglandular, long, yellowish, spreading trichomes. Leaves 8–17 cm long, oblong-lanceolate or narrowly elliptic, basally shortly cordate, apically acuminate. Inflorescences subsessile, 2–5-flowered. Corolla 36–48 mm diam., rotate-campanulate, bright yellow; lobes spreading, ovate-orbicular or broadly deltate; gynostegial corona a shallow fleshy cup, roughly pentagonal with rounded angles, marginally crenulate; staminal lobes shortly ligulate; gynostegium sessile; anthers horizontal, with acicular wings; pollinia horizontal, auriculate; style-head peltate. Follicles fusiform, densely muricate, pubescent.

One sp., *R. fulvidus* (Ballard) Morillo, S Mexico to Costa Rica, wet or rain forests, below 600 m.

372. *Suberogerens* Morillo

*Suberogerens* Morillo, Pittieria 39: 249 (2015).

Suffrutex with woody and corky caudex; stems to 2 m long, appressed-puberulent when young. Leaves 9–17 cm long, broadly ovate to roundly reniform, basally cordate, apically acuminate, adaxially sparsely puberulent or glabrous, abaxially appressed-puberulent. Inflorescences sessile, 2–3-flowered. Calyx as long as corolla; corolla

rotate, 18–25 mm diam., green to dark-purple; lobes abaxially appressed-puberulent to glabrous, adaxially white pilose; gynostegial corona purple, disciform, with five small erect ligulate lobes; gynostegium sessile; anthers with white apical membranes; pollinia horizontal; style-head flat. Follicles narrowly fusiform, minutely muricate.

One sp., *S. cyclophylla* (Standl.) Morillo, in Mexico, thorn scrub and dry deciduous forests, 200–1350 m.

373. *Tressensia* H.A. Keller

*Tressensia* H.A. Keller, Lilloa 54: 196 (2017).

Herbaceous twiner, pubescent with eglandular and glandular trichomes. Leaves 2.5–12 cm long, (oblong-)ovate, basally auriculate, apically acute. Inflorescences long-pedunculate, 3–6-flowered; flowers long-pedicellate. Corolla ca. 3 cm diam., shallowly campanulate, green-reticulate; tube and throat lanose; lobes narrowly triangular, reflexed; gynostegial corona annular, yellow; staminal parts fleshy; gynostegium sessile; pollinia ovate, laterally compressed, horizontal; style-head decagonal, umbonate. Follicles obclavate, 5-winged. Seeds verrucose, with dentate wing.

One sp., *T. viridis* H.A. Keller & S.A. Cáceres, in Argentina, riverine forest fragments.

374. *Trichosacme* Zucc.

*Trichosacme* Zucc., Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 4(2): 11 (1846).

Twining or erect herb, to 1 m long, with dense white-silvery woolly indumentum all over. Leaves 3.5–9 cm long, (oblong-)ovate, basally subcordate to rounded, apically obtuse or shortly acute. Inflorescences pedunculate, 6–10-flowered; flowers subsessile. Corolla 9–10 mm diam., subrotate, dark purple; lobes ovate, adaxially glabrous or puberulous at base, apically with long, plumose, caudate, purple appendages; gynostegial corona annular, bright orange, adnate to corolla tube, shortly 5-dentate; gynostegium subsessile, pollinia pendent, narrowly clavate, with a slender, sterile, horn-like basal process; style-head convex. Follicles cylindrical-fusiform.

One sp., *T. lanata* Zucc., in Mexico, thorny scrub; 1300–1800 m.

375. *Tylo dontia* Griseb.

*Tylo dontia* Griseb., Cat. Pl. Cub. 175 (1866); Mangelsdorff et al., Willdenowia 46: 443–474 (2016), rev.

Sparsely branched herbaceous twiners, pubescent with eglandular recurved trichomes. Leaves 1.5–4.5 cm long, lanceolate to ovate, inflorescences few to 70-flowered, thyrsoidal. Corolla 1.8–6 mm long, urceolate, white, carnosae, adaxially usually densely pubescent; corolline corona of antepetalous lobules in tube; gynostegial corona of staminal and interstaminal segments, carnosae, short; gynostegium occasionally stipitate, concealed in corolla, anther wings separated in a basal, mostly longer, vertically oriented part and an upper, almost horizontal (basally centrifugal) part; connective appendages often strongly inflexed; style-head green, with central depression. Follicles 60–70 mm long, fusiform or narrowly oblong. Seeds pyriform, winged.

Four spp. endemic to Cuba, mountainous regions.

376. *Vulcano a* Morillo

*Vulcano a* Morillo, Pittieria 39: 253 (2015).

Woody vine, densely ferruginous-pilose; trichomes eglandular, retrorse or spreading. Leaves narrowly ovate to ovate-elliptic, basally cordate, apically acuminate to cuspidate. Inflorescences shortly pedunculate, few-flowered. Corolla ca. 28 mm diam., campanulate, white, reticulate with green; lobes spreading, narrowly ovate, adaxially hispidulous; corolline corona tubular-cupuliform, apically fimbriate; gynostegial corona adnate to stipe, with 5 horn-like staminal lobes; gynostegium stipitate; anthers suberect, with short membranes; pollinia pendent, narrowly pyriform; style-head convex. Follicles fusiform, densely muricate, with long, curved projections.

One sp., *V. steyermarkii* (Woodson) Morillo, in Guatemala and Mexico, upper montane cloud forests, on volcanos, 1700–3300(–3900) m.

V.5.l. *Subtribe Topeinae* H.A. Keller & Liede (2017).

Twining plants with leaves oblong-lanceolate to lanceolate, basis deeply cordate to auriculate. Inflorescences sciadioidal, pendulous, present all

the year. Corolla lobes with vibratile trichomes on the adaxial side. Corona with flattened lobes opposite the anthers. Caudicles sigmoidal, corpusculum with basal hyaline appendix. Follicles solitary, pendulous, narrowly fusiform, with long pointed apex. One genus in South America.

377. *Tope a* H.A. Keller

*Tope a* H.A. Keller, Bonplandia 26: 134 (2017), nom. nov. pro *Aenigma* H.A. Keller, Lilloa 54: 59 (2017), nom. illeg., non *Enigma* Weber-van Bosse (1932), Rhodophyceae.

Twiners, glabrous or pilose. Leaves 5–12 cm long, oblong-lanceolate, auriculate. Inflorescences long-pedunculate, 3–12-flowered, sciadioidal. Corolla rotate, 3–15 mm diam., lobes lanceolate, patent or reflexed, adaxially with long trichomes, apically with clavate vibratile trichomes; staminal corona lobes lanceolate, basally fused, exceeding the gynostegium; gynostegium sessile, pollinia reniform, caudicles with hyaline projections; style-head flat; follicles solitary, fusiform, to 15 cm long. Seeds obovate, with apically dentate wing.

Two spp. in Argentina and Paraguay, moist forest, lowlands.

**Genus of uncertain subtribal placement in Asclepiadeae**378. *Mahawoa* Schltr.

*Mahawoa* Schltr., Beih. Bot. Centralbl. 34(2): 2 (1916).

Suffrutescent twiner; shoots and leaves hirsute with retrorse trichomes. Leaves 4.5–7 cm long, ovate to elliptic. Inflorescences longer than subtending leaves, few-flowered, dichasial at base, bostrychoid monochasial in higher order branching, lax. Corolla 7–8 mm long, rotate, glabrous; lobes ovate; gynostegial corona ring exceeding the gynostegium, fused for about a quarter of its length; staminal parts connate to filaments for more than a third of gynostegium length, linguulate, inflexed; gynostegium sessile, pollinia ovoid, caudicles horizontal, short; style-head flat.

One sp., *M. montana* Schltr., in Indonesia (Sulawesi), forests, at 1200 m.

With an inflorescence reminiscent of Tylophorinae and a corona pointing to Cynanchinae, the position of *Mahawoa* remains uncertain

because the type was destroyed in Berlin and no other specimen has ever been encountered.

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# Plumeria rubra

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## Scientific Name

*Plumeria rubra* L.

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## Synonyms

*Plumeria acuminata* W.T.Aiton, *Plumeria acutifolia* Poir., *Plumeria acutifolia* var. *gasparrini* A.DC., *Plumeria angustifolia* A.DC., *Plumeria arborea* Noronha, *Plumeria arborescens* G.Don, *Plumeria aurantia* Endl., *Plumeria aurantia* Lodd. ex G.Don, *Plumeria aurantiaca* Steud., *Plumeria bicolor* Ruiz & Pav., *Plumeria blandfordiana* Lodd. ex G.Don, *Plumeria carinata* Ruiz & Pav., *Plumeria conspicua* G.Don, *Plumeria gouanii* D.Don ex G.Don., *Plumeria incarnata* Mill., *Plumeria incarnata* var. *milleri* (G.Don) A.DC., *Plumeria jamesonii* Hook., *Plumeria kerrii* G.Don, *Plumeria kunthiana* Kostel., *Plumeria lambertiana* Lindl., *Plumeria loranthifolia* Müll.Arg., *Plumeria lutea* Ruiz & Pav., *Plumeria macrophylla* Lodd. ex G.Don, *Plumeria megaphylla* A.DC., *Plumeria mexicana* Lodd., *Plumeria milleri* G.Don, *Plumeria mollis* Kunth, *Plumeria northiana* Lodd. ex G.Don, *Plumeria purpurea* Ruiz & Pav., *Plumeria rubra* f. *acuminata* (W.T.Aiton) Woodson, *Plumeria rubra* f. *acutifolia* (Poir.) Woodson, *Plumeria rubra* f. *lutea* (Ruiz & Pav.) Woodson, *Plumeria rubra* f. *tricolor* (Ruiz & Pav.) Woodson, *Plumeria rubra* f. *typica* Woodson, nom. inval., *Plumeria rubra* var. *acuminata* (W.T.Aiton) R.S.Rao & Balamani, *Plumeria tenuifolia* Lodd. ex G.Don, *Plumeria tricolor* Ruiz & Pav.

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## Family

Apocynaceae

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## Common/English Names

Common Frangipani, Frangipani, Graveyard Tree, Hawaiian Lei Flower, Nose Gay, Pagoda Tree, Red Frangipani, Red Jasmine, Red Jasmine Of Jamaica, Red Paucipan, Temple Flower, Temple Tree, Tree of Life, West Indian Jasmine

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## Vernacular Names

**Aztec:** Cacalloxochitl

**Brazil:** Jasmim-De-Caiena, Jasmim-Do-Pará, Jasmin-Do-Pará, Jasmin-Manga

**Burmese:** Mawk-Sam-Ka, Mawk-Sam-Pailong, Sonpabataing, Tayok-Saga, Tayoksaga-Ani

**Canary Islands:** Flor De Cebo

**Chinese:** Hong Ji Dan Hua, Ji Dan Hua, Kang Nai Xin

**Chuukese:** Seewurun, Seur

**Cuba:** Lirio Colorado

**Czech:** Plumérie Červená, Plumérie Ostrolistá

**Danish:** Mexican Frangipani, Pagodetræ

**El Salvador:** Flor De Mayo

**French:** Frangipanier

**German:** Frangipani, Roter Frangipani

**Guatemala:** Flor De La Cruz

**Hawaii:** Pumeli, Melia

**India:** Deva Ganneru (Andhra Pradesh), Frangipani, Goburchampa, Kath Champa, Kath Golap (Bengali), Dolochampo, Rhada Champo (Gujarati), Chameli, Gulachin, Gulechin, Lal Gulachin (Hindi), Chaempae (Konkani), Vellachampakam (Malayalam), Khageleihao Angouba, Khera Chappha, Pandhra Chappha, Sonchampa (Marathi), Kishirachampa (Sanskrit), Arali, Kallimandarai, Perungalli, Sampangi (Tamil), Vadaganneru (Telugu), Achin (Urdu)

**Indonesia:** Kamboja, Sambija, Semboja (Java), Kamoja, Samoja (Sundanese)

**Italian:** Fragipane, Pomelia

**Khmer:** Champei

**Kosraen:** For

**Laos:** Champa, Dok Champa

**Malaysia:** Kemboja, Bunga Kemboja, Chempaka, Cempaka muliya, Chempa Raya, Chempaka Biru, Pokok Kubur, Bunga Kubur

**Mexico:** Caxtaxanat, Flor De Mayo, Tenech Coahuil

**Nicaragua:** Flor De Leche, Sacuanjoche

**Pakistan:** Champa

**Palauan:** Chelilai

**Panama:** Caracucho Colorado

**Persian:** Gulacin

**Peru:** Caracucho, Suche

**Philippines:** Kalachucho (Bikol), Kachuchi (Cebu Bisaya), Kalanucho, Kalonocho (Iloko), Kalachucho, Kalasusi, Kalatsutsi, Karachucha Karatucho (Tagalog)

**Pohnpeian:** Pwohmaria

**Portuguese:** Flor-De-Santo-Antônio

**Puerto Rico:** Alhelí

**Sicily:** Pomelia

**Spanish:** Alhelí Cimarrón, Suche

**Sri Lanka:** Araliya, Pansal Mal

**Tahiti:** Tipanier

**Thailand:** Champa Lao, Champa Khawm, Rantom, Lantom, Leelawadee

**Venezuela:** Amapola

**Vietnam:** Sú Cúi, Đai

**Yapese:** Suwur

world, especially Hawaii, where it flourishes abundantly.

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## Agroecology

It thrives in tropical to subtropical areas with warm temperature of 20–32 °C and evenly distributed annual rainfall of 1,000–2,000 mm. It is rather drought hardy but will lose its leaves under prolonged drought. In subtropical areas, it needs to be frequently watered in summer but sparingly so in winter. Frangipani does best in well-drained, fertile soils in full sun or partial shade.

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## Edible Plant Parts and Uses

The fruits and flowers are edible (Burkill 1966; Kunkel 1984; Facciola 1990; Hu 2005). The fruits are reported eaten in the West Indies. The flowers are eaten in sweetmeats and together with betel nut for ague. The flowers are dried and used for herbal teas. It is one of five floral components in the popular Chinese cooling herbal beverage ‘Five Flower Tea.’

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## Botany

Small, deciduous tree to 8 m high with pale greenish-brown, smooth, thin bark becoming rough with age. Branches swollen and leafy at the tips. Latex copious and milky white. Leaves alternate, glossy dark green on long stout petioles. Lamina simple, elliptic to narrowly elliptic, large, 15–30 cm by 6–8 cm, base acute, apex acute to acuminate, margin entire, glabrous, unicostate with 30–40 pairs of lateral veins (Plates 1, 2, 3 and 4). Inflorescences terminal, 2–3-branched cymes, 2–4-flowered with deciduous bracts. Flowers large and showy, sweetly fragrant, bracteolate, pedicellate, bisexual, actinomorphic, pentamerous, perigynous, 5–7 cm diameter. Calyx synsepalous, five obtuse lobes. Corolla sympetalous, salverform, tube cylindrical, five obovate lobes, contorted, overlapping to the left; lobes pink, red, yellow, or white, with a yellow base (Plates 1, 2, 3, 4 and 5). Stamens 5,

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## Origin/Distribution

*Plumeria rubra* is native to Mexico, Central America and Venezuela. From its native range, it has been distributed to all tropical areas of the



**Plate 1** Red-flowered cultivar



**Plate 4** Acute-tipped leaves and flowers of white-yellow flowered cultivar



**Plate 2** Acute tip leaves and red-yellow flowers of a bicoloured cultivar



**Plate 5** Close view of white-yellow flowers



**Plate 3** Close view of the red-yellow flowers

epipetalous alternate the lobes, inserted in corolla tube; the anthers ditheous and linear-oblong. Ovaries 2, distinct, half inferior, each ovary 1-carpelled, 1-loculed with parietal placentation, the ovules numerous in each, the style

1, the stigma single and massive. Fruit follicles linear-oblong, 11–25 × 2–3 cm. Seeds oblong, plano-convex, winged, with thin fleshy endosperm.

### Nutritive/Medicinal Properties

Flowers, leaves and bark of *Plumeria rubra* contain many bioactive compound with anti-cancerous, antiinflammatory and antimicrobial activities.

### Phytochemicals from Flowers

*P. rubra* flowers were found to contain tannins, flavonoids, terpenoids, reducing sugars and alkaloids (Egwaikhide et al. 2009). Two iridoid

diastereoisomers were isolated from the flowers of *Plumeria rubra* cv. *acutifolia* (Ye et al. 2008). A new iridoid alkaloid containing a spironolactone unit, plumericidine, was isolated from the flowers of *Plumeria rubra* L. cv. *acutifolia* (Ye et al. 2009). Two anthocyanins cyanidin 3-*O*-β-(2"-glucopyranosyl-*O*-β-galactopyranoside) (75 %) and cyanidin-3-*O*-β-galactopyranoside (20 %) were isolated from ornamental reddish flowers of *Plumeria rubra* (Byamukama et al. 2011).

Norsita et al. (2006a) reported *P. rubra* pink flowers to have the following main volatile constituents: lauric acid (30.8 %), myristic acid (17.4 %), palmitic acid (9.8 %), nonadecane (8.2 %), methyl stearate (5.6 %), linalool (4.8 %), docosane (2.8 %) and tricosane (2.8 %); *P. rubra* orange flowers to have linalool (3.3 %), α-fenchyl alcohol (2.1 %), geraniol (4.1 %), (*E*)-nerolidol (14.4 %), caryophyllene oxide (3.1 %), (*E,E*)-farnesol (4.4 %), benzyl benzoate (8.6 %), myristic acid (2.9 %), 2-phenyl benzoate (3.9 %), benzyl salicylate (20.9 %), 2,6,10,14-teyramethylheptadecane (2.8 %), neryl phenylacetate (4.1 %), palmitic acid (4.4 %) and ethyl palmitate (3.1 %); reddish-orange flowers to have *n*-nonadecane (3.6 %), *n*-heneicosane (4.1 %), tricosane (3.6 %), docosane (2.7 %), pentyl benzoate (4 %), benzyl benzoate (4 %), phenylethyl benzoate (12.3 %), benzyl salicylate (4.1 %), methyl stearate (3.4 %), phenylethyl cinnamate (2 %), lauric acid (11.8 %), myristic acid (3.9 %), palmitic acid (9.3 %) and linalool (5.3 %); *P. rubra* red flowers to have *n*-nonadecane (2 %), methyl stearate (3.3 %), lauric acid (10.6 %), myristic acid (18.9 %), palmitic acid (27.2 %), linoleic acid (20.7 %), linalool (2.1 %) and terpinene-4-ol (3.7 %). Norsita et al (2006b) also reported *P. acuminata* yellowish-white flowers to have the following main volatile components: benzyl salicylate (39 %), benzyl benzoate (17.2 %), (*E*)-nerolidol (10.6 %), neryl phenylacetate (10.5 %), linalool (8.9 %), cinnamyl cinnamate (2.9 %), geraniol (2.6 %) and camphor (1.9 %) and *P. acuminata* yellow flowers to have palmitic acid (36.2 %), linoleic acid (16.8 %), lauric acid (10.4 %), myristic acid (10.3 %), pentacosane (8.1 %), tricosane (0.1 %) methyl stearate

(4.4 %). Earlier Pino et al. (1994) reported the following main volatiles from *P. rubra* var. *acutifolia* flowers: *n*-butyl oleate (13.8 %), *n*-butyl palmitate (11.5 %), methyl palmitate (9.7 %), methyl oleate (9.3 %), linalool (8.2 %), α-terpineol (7.63 %), cinnamyl alcohol (6.3 %), *n*-butyl stearate (5.3 %), benzoic acid (4.3 %), *trans*, *trans*-farnesol (3.2 %) and methyl stearate (2.8 %).

The major volatile constituents of *Plumeria rubra* white-yellow flowers (L2) were L-linalool, benzaldehyde 22.07 %, methyl salicylate 8.1 %, nerolidol 4.65 %, *trans*-β-ocimene 3.28 % and geraniol 3.08 % (Chitsamphandhvej 2010). The major volatile constituents of *Plumeria* sp. pink flowers (L1) were L-linalool 37.61 %, benzene ethanol 20.71 %, *trans*-geraniol 12.66 %, methyl benzoate 8.86 %, benzene acetonitrile 3.73 %, linalool oxide 3.37 % and nerolidol 0.95 %. The major volatile constituents of *Plumeria rubra*, Leung Anghong (L3) flowers, were *trans*-β-ocimene 48.73 %, benzene methanol 12.1 %, benzene ethanol 8.98 %, methyl salicylate 7.18 %, methyl benzoate 6.21 %, L-linalool 4.68 %, *trans*-geraniol 3.06 %, benzene acetonitrile 2.9 %, benzaldehyde 1.46 % and linalool oxide 1.03 %. The major volatile constituents of *Plumeria rubra* red flowers (L5) were isoamyl alcohol 17.96 %, *trans*-geraniol 11.86 %, benzene ethanol 8.51 %, 2-methyl-1-butanol 6.01 %, 2-methyl-2-butanal 4.47 %, benzene acetonitrile 2.34 %, methyl benzoate 1.16 % and L-linalool 1.15 %.

A total of 74 compounds were identified in the essential oil of *Plumeria rubra* forma *acutifolia* (Poir.) Woodson cv. 'Common Yellow' flowers (Omata et al. 1991). Linalool (14.1 %), phenylacetaldehyde (16.1 %), *trans*, *trans*-farnesol (11 %), β-phenylethyl alcohol (8.8 %), geraniol (5.4 %), α-terpineol (2.8 %), neral and geraniol were found to make a major contribution to the floral scent of the flower, the last two comprised 0.9 %. A total of 67 compounds were identified in the essential oil of *Plumeria rubra* 'Irma Bryan' flowers (Omata et al. 1992). β-phenylethyl alcohol (31.6 %), phenylacetaldehyde (12.1 %) and methyl cinnamate (1 %) were found to make a major contribution to the floral spicy scent of the flower, while 2-methylbutan-1-ol (10.5 %) did

not contribute to its scent. Forty-three components were identified from the flower essential oil of *Plumeria rubra* var. *acutifolia* (Li et al 2006). The main components were fatty acid such as hexadecanoic acid, dodecanoic acid and linoleic acid; other components included terpenoids such as *trans*-nerolidol,  $\beta$ -linalool and *trans*-geraniol. Sixteen compounds were identified from the flower essential oil of *Plumeria rubra* cv. *acutifolia* (Han 2007). The major components in essential oil were nerolidol (20.25 %) and geranyl linalool isomer (10.1 %). Other main content components were heptacosane (7.65 %), tetradecanoic acid (6.73 %), hexadecanoic acid, 2,3-dihydroxypropyl ester (2.98 %) and 1,2-benzenedicarboxylic acid, bis(2-methylpropyl) ester (2.68 %). The main components of the essential oil of *Plumeria rubra* var. *acutifolia* extracted by supercritical carbon dioxide fluid extraction comprised 1, 6, 10-dodecatrien-3-ol; 3,7,11-trimethyl; benzoic acid; 2-hydroxy-, phenylmethyl ester; 1,2-benzenedicarboxylic acid; and bis(2-methylpropyl) ester (Xiao et al. 2011). The last components comprised 66.11 % of the total.

Seven compounds, namely, 2-methylbutan-1-ol,  $\beta$ -phenylethyl alcohol, nonadecane, heneicosane, benzyl salicylate, tetradecanoic acid and phenylacetaldehyde were found in the essential oil of *P. rubra* red flower variety; 19 compounds, namely,  $\alpha$ -terpineol, geraniol,  $\beta$ -phenylethyl alcohol, nonadecane, heneicosane, *trans*-farnesol, benzyl benzoate, geraniol, dodecanoic acid, benzyl salicylate, phenylethyl benzoate, tetradecanoic acid, tetracosane, octadecanoic acid, tricosane, docosane, eicosane and phenylacetaldehyde in the yellow flower variety; and 14 compounds in *P. obtusa* (Sulaiman et al. 2008). The major components found in all three species were 2-hydroxybenzoic acid phenylmethyl ester. All three also shared two alkane hydrocarbons, nonadecane and heneicosane.

### Phytochemicals from Plant

Albers-Schönberg and Schmid (1961) isolated isoplumericin,  $\beta$ -dihydroplumericin and  $\beta$ -dihydroplumericin along with plumericin from *Plumeria*

*rubra* var. *alba*. They also isolated  $\beta$ -dihydroplumericin acid from the same source and also fulvoplumericin (Albers-Schönberg et al. 1962). Stearic acid was isolated from leaf and stem of *P. rubra*, and flavonoids quercetin, quercitrin found in the leaf, flower and stem of *Plumeria rubra* and *Plumeria rubra* var. *alba* (Mahran et al. 1974b).

Taraxasteryl acetate, lupeol, stigmasterol, oleanolic acid, cycloart-22-ene-3  $\alpha$ ,25-diol and rubrinol, a new triterpene of the ursane series, were isolated from whole plants of *P. rubra* (Akhtar et al. 1994). The structure of rubrinol was elucidated as 3  $\beta$ ,30-dihydroxy-12-ursene. Two new oleanene-type triterpenes 6 $\alpha$ -hydroxy-3-epi-oleanolic acid and 3 $\alpha$ ,27-dihydroxy-olean-12-ene were isolated from *Plumeria rubra* (Akhtar and Malik 1993).

Acidic proteins with molecular masses between 12.5 and 74.5 kDa predominated in laticifers of *P. rubra* (de Freitas et al. 2010). Strong antioxidative activity of superoxide dismutase was detected in *P. rubra* latices, and to a lesser extent ascorbate peroxidase and isoforms of peroxidase were observed. In laticifer cells of *P. rubra*, four proteinases were detected, including cysteine and serine types. A protease with molecular weight of approximately 81.85 kDa was purified from the latex of *Plumeria rubra* plant and given the trivial name, plumerin-R (Chanda et al. 2011). It remained active over a broad range of temperature but had optimum activity at 55 °C and pH 7.0 when casein was used as substrate. Activation of the protease by a thiol-activating agent indicated the presence of sulfhydryl as an essential group for its activity.

### Phytochemicals from Leaves

L-(+)-bornesitol was isolated from the leaves of *Plumeria acutifolia* (Nishibe et al. 1971). A new monoterpene alkaloid, (R)-4'-((S)-1-hydroxyethyl)-5,6-dihydro-5' H-spiro[cyclopenta[C]pyridine-7,2'-furan]-5'-one, designated as plumerianine; the iridoid 15-demethylplumeride; and three known triterpenes, namely lupeol, uvaol and ursolic acid, were isolated from the methanol extract of *Plumeria acutifolia* leaves (Hassan et al. 2008). *P. rubra* leaves were found to contain tannins, phlobatannins,

saponins, flavonoids, steroids, terpenoids, reducing sugars, carbonyl and alkaloids (Egwaikhide et al. 2009).

## Phytochemicals from Stem/Roots

The stem bark was found to contain highest content of plumerid, and *Plumeria rubra* plant contains a higher percentage of plumerid than those of *Plumeria rubra* var. *alba* (Mahran et al. 1974a). Plumerinine, a novel bicyclic lupin alkaloid, was isolated from *Plumeria rubra* stem (Kazmi et al. 1989). The following compounds were isolated from *P. rubra* bark: iridoids, fulvoplumerin, allamcin, allamandin, plumeride,  $\alpha$ -allamcidin, 15-demethylplumeride,  $\beta$ -allamcidin and 13-*O-trans-p*-coumaroylplumeride; the lignan, liriodendrin, and 2,5-dimethoxy-*p*-benzoquinone (Kardono et al. 1990b). A novel flavan-3-olglycoside, plumerubroside, was isolated from a water-soluble extract of the stem bark of *Plumeria rubra*, and its structure was elucidated as (2*R*,3*S*)-3,4'-dihydroxy-7,3',5'-trimethoxyflavan-5-*O*- $\beta$ -D-glucopyranoside (Kardono et al. 1990a). Two new ferulic acid derivatives, 34-hydroxy tetratriacontanyl ferulate and 34-*O*-acetyl tetratriacontanyl ferulate, were isolated, along with plumericin and isoplumericin, from *Plumeria bicolor* stem bark (Dobhal et al. 1999). A new iridoid, 15-demethylisoplumeride acid, was isolated from the bark of *Plumeria rubra* var. *acutifolia* (Barreto et al. 2007).

Four new iridoids, namely, plumeridoids A, B and C and epiplumeridoid C, were isolated from the stem bark of *Plumeria rubra* together with 24 known compounds, namely, 1-(*p*-hydroxyphenyl)propan-1-one; isoplumericin; plumericin; dihydroplumericin; allamcin; fulvoplumerin; allamandin; plumeride; *p-E*-coumaric acid; 2,6-dimethoxy-*p*-benzoquinone; scopoletin; cycloart-25-en-3 $\beta$ ,24-diol; 2,4,6-trimethoxyaniline; arjunolic acid; ursolic acid; oleanolic acid;  $\beta$ -amyrin acetate; betulinic acid; lupeol and its acetate; 2,3-dihydroxypropyl octacosanoate, glucoside of  $\beta$ -sitosterol, and a mixture of common sterols (stigmasterol and  $\beta$ -sitosterol) (Kuigoua et al. 2010).

Hamburger et al. (1991) isolated six compounds from the heartwood: plumericin, isoplumericin, protoplumericine A, plumeride, 13-*O-trans-p*-

coumaroylplumeride and 4-hydroxyacetophenone 3 and several additional iridoids: 15-demethylplumeride,  $\alpha$ -allamcidin and  $\beta$ -allamcidin.

## Antioxidant Activity

Methanol leaf extract of *Plumeria acuminata* was found to possess antioxidant and free radical scavenging activity (Gupta et al. 2007a). The extract inhibited peroxidation of linoleic acid emulsion in a dose-dependent manner. Likewise the effect of the extract on reducing power increased in a dose-dependent manner. In DPPH radical and nitric oxide radical scavenging assays, the extract exhibited maximum activity of 60.42 and 56.38 % inhibition at the concentration of 125  $\mu$ g/ml. Further, the extract was found to scavenge the superoxide generated by PMS/NADH-NBT system. The extract also inhibited the hydroxyl radical generated by Fenton's reaction, where the IC<sub>50</sub> value of the extract was found to be 74.39  $\mu$ g/ml and for catechin the IC<sub>50</sub> value was found to be 5.27  $\mu$ g/ml.

## Anticancer Activity

Six cytotoxic constituents characterized from the bark of *Plumeria rubra*, namely, three iridoids fulvoplumerin, allamcin and allamandin and 2,5-dimethoxy-*p*-benzoquinone from petroleum-ether- and CHCl<sub>3</sub>-soluble extracts and iridoid plumericin, and the lignan liriodendrin from the water-soluble extract demonstrated general cytotoxic activity when evaluated against a panel of cell lines composed of murine lymphocytic leukemia (P-388) and a number of human cancer cell-types (breast, colon, fibrosarcoma, lung, melanoma, KB) (Kardono et al. 1990a, b). Five additional iridoids: 15-demethylplumeride, plumeride,  $\alpha$ -allamcidin,  $\beta$ -allamcidin and 13-*O-trans-p*-coumaroylplumeride, were obtained as inactive constituents. Of the six compounds isolated from the heartwood, plumericin and isoplumericin exhibited cytotoxic and antibacterial activities, whereas 4-hydroxyacetophenone 3 was weakly cytotoxic (Hamburger et al. 1991). Ethanol leaf extract of *Plumeria rubra* administered orally at

the dose of 200 mg/kg body and 400 mg/kg body weight was found to increase the life span of Ehrlich ascites carcinoma-treated mice and restored the hematological parameters as compared with the untreated Ehrlich ascites carcinoma-bearing mice (Rekha and Jayakar 2011).

Plumericin from *Plumeria rubra* was listed as one of the ten most cytotoxic compounds isolated from 148 medicinal plants listed in Cameroon National Cancer Institute (NCI) database (Kuethe and Efferth 2011). The  $IC_{50}$  value for plumericin of 60 NCI cell lines were associated with the microarray-based transcriptome-wide mRNA expression. Gene products identified for plumericin activity were mainly involved in enzymatic activity and transcriptional processes or were structural constituents of ribosomes.

### Antimutagenic Activity

The ethanol extract of *Plumeria rubra* leaves contains several bioactive compounds that exhibited antimutagenic activities (Guevara et al. 1996). At a dosage of 2 mg isolate/25 g mouse, unidentified compound A1 reduced the number of micronucleated polychromatic erythrocytes induced by the mutagen, mitomycin C, by 75 %; stigmast-7-enol by 80 %; lupeol carboxylic acid by 57 %; and ursolic acid by 76 %.

### Antiinflammatory Activity

The methanol leaf extract also possessed potent antiinflammatory activity (Gupta et al. 2006). It exhibited significant antiinflammatory activity in both acute and chronic experimental animal models. The extract (500 mg/kg/bw) exhibited maximum antiinflammatory effect, that is, 30.51, 47.06, 34.48 and 32.50 % at the end of 3 hours using carrageenan, dextran, histamine and serotonin assays, respectively. Administration of the extract (500 mg/kg/bw) and indomethacin (10 mg/kg/bw) significantly reduced the formation of granuloma tissue induced by cotton pellet method at a rate of 45.06 and 51.57 %, respectively. The effect produced by the extract

was comparable to that of indomethacin, a prototype of a nonsteroidal antiinflammatory agent. The crude methanol extract of *Plumeria rubra* leaves was found to possess antiinflammatory (Rastogi et al. 2009). The antiinflammatory activity was dose dependent and found to be statistically significant at the concentration 100 and 200 mg/kg.

In the passive cutaneous anaphylaxis model, plumerianine isolated from the root bark of *Plumeria acutifolia* elicited a significant dose-dependent decrease in the leakage of Evans blue dye leaked at the site when compared with control (Vijayalakshmi et al. 2011). In the passive paw anaphylaxis model, plumerianine produced as significant dose-dependent decrease in paw volume induced by antiserum. Plumerianine also exhibited significant inhibition of rat paw oedema and granuloma tissue formation, including significant protection of red blood cells against the haemolytic effect of hypotonic solution, an indication of membrane-stabilizing activity. The authors postulated that anti-anaphylactic activity of plumerianine may be possibly due to inhibition of the release of various inflammatory mediators. Antiinflammatory activity of plumerianine may be related to the inhibition of the early phase and late phase of inflammatory events.

### Antimicrobial Activity

Rubrinol isolated from the whole plant was found to be active against *Bacillus anthracis*, *Pseudomonas aeruginosa*, *Pseudomonas pseudomallei* and *Corynebacterium pseudodiphthericum* (Akhtar et al. 1994). Ethanol extract of the stem bark exhibited in vitro antimicrobial activity against Gram-positive bacteria (*Bacillus subtilis*, *Enterococcus faecalis*, *Staphylococcus aureus*), Gram-negative bacteria (*Escherichia coli*, *Klebsiella pneumoniae*, *Pseudomonas aeruginosa*, *Salmonella typhimurium*) and fungi (*Aspergillus niger* and *Candida albicans*) (Rasool et al. 2008). The ethanol extract showed the strong in-vitro antimicrobial activity against *E. faecalis*, *B. subtilis*, *S. aureus*, *P. aeruginosa*, *S. typhimurium*, *A. niger* and *C. albicans*.

The crude methanol leaf extract of *P. acuminata* inhibited the growth of both Gram-positive bacteria (*Bacillus subtilis*, *Staphylococcus aureus* and *Micrococcus luteus*) and Gram-negative bacteria (*Escherichia coli*, *Pseudomonas aeruginosa* and *Salmonella typhimurium*) (Gupta et al. 2008). Gram-positive bacteria tested appeared to be more susceptible to the extract than the Gram-negative bacteria. The extracts also showed significant antifungal activity against *Aspergillus niger* and *Candida albicans*. All tested microorganisms showed dose-dependent susceptibility towards the methanol extracts. Ethanol and chloroform leaf extracts of *P. rubra* exhibited partial antibacterial activity in vitro against *Staphylococcus epidermidis* at 750 and 1,000 µg/ml but at 1,500 µg/ml was completely inhibitory to *S. epidermidis* and *Escherichia coli* (Baghel et al. 2010). The ethyl acetate and aqueous leaf extract was partially inhibitory to *S. epidermidis* at 1,000 µg/ml but at 1,500 µg/ml was completely inhibitory to *S. epidermidis* and *Escherichia coli*. The standard drug ciprofloxacin is showing complete antibacterial activity against *S. epidermidis* and *Escherichia coli* at 500 and 750 µg/ml, respectively.

The methanol extract of *P. rubra* flowers inhibited significantly in-vitro growth of *Corynebacterium pyogenes*, *Staphylococcus aureus*, *Streptococcus faecalis*, *Bacillus stearothermophilus*, *Staphylococcus epidermidis*, *Bacillus cereus*, *Bacillus polymyxa*, *Klebsiella pneumoniae*, *Pseudomonas aeruginosa*, *Bacillus anthracis*, *Bacillus subtilis*, *Escherichia coli*, *Pseudomonas fluorescens* and *Clostridium sporogenes* (Egwaikhide et al. 2009). The methanol leaf extract was also inhibitory but comparatively less to all the bacteria tested and was not inhibitory to *Corynebacterium pyogenes* and *Klebsiella pneumoniae*.

The essential oil of *P. rubra* red flower variety inhibited growth of *Bacillus cereus*, *Candida albicans*, *Candida humicola* and *Trichophyton rubrum*, while the essential oil from the yellow flower variety inhibited growth of *Bacillus cereus* and *Candida humicola* (Sulaiman et al. 2008). *Plumeria rubra* was one of four Latin American plant extracts that exhibited inhibitory activity against the subcutaneous fungus *Fonsecaea pedrosoi* with MIC of 12.5 µg/ml (Gaitán et al. 2011)

## Antiviral Activity

*Plumeria rubra* yielded the iridoid, fulvoplumerin—an active, inhibitory compound with an IC<sub>50</sub> 45 µg/ml against the human immunodeficiency virus type 1 reverse transcriptase (HIV-1 RT) (Tan et al. 1991).

## Larvicidal Activity

Silver nanoparticles (AgNPs) synthesized using *Plumeria rubra* plant latex were found to be toxic to second and fourth larval instars of *Aedes aegypti* and *Anopheles stephensi* (Patil et al. 2012). AgNPs were more toxic to the larval stages than the crude latex extract. Toxicity studies carried out against nontarget fish species *Poecilia reticulata*; the most common organism in the habitats of *A. aegypti* and *A. stephensi* showed no toxicity at LC<sub>50</sub> and LC<sub>90</sub> doses of the AgNPs.

## Hypoglycemic Activity

*P. rubra* was reported as one of several Mexican medicinal plants used in folkloric medicine to control diabetes mellitus (Hernandez-Galicia et al. 2002). Treatment of alloxan-induced hyperglycaemic rats with the flavone glycoside from *P. rubra* significantly reduced the level of serum triglycerides but did not alter blood glucose and serum total cholesterol (Merina et al. 2010). Administration of the glycoside significantly reduced the elevated levels of blood urea and creatinine and the activities of aspartate aminotransferase (SGOT) and alanine aminotransferase (SGPT) when compared with the hyperglycaemic control animals. Antioxidant activity of the flavone glycoside was also confirmed through in-vitro studies wherein the rate of malondialdehyde formation was markedly inhibited. The authors concluded that the beneficial effect of the flavone glycoside treatment on triglycerides observed assumes greater significance as a useful drug to decrease hyperlipidemic risks in diabetes.



### Antipyretic and Antinociceptive Activity

Gupta et al. (2007b) showed that a single oral administration of different doses (100, 250 and 500 mg/kg) of the methanol leaf extract of *P. acuminata* significantly reduced brewer's yeast-induced hyperthermia in rats. The extract also elicited pronounced inhibitory effect on acetic acid-induced writhing, hot plate, tail-flick and tail immersion responses in mice in the antinociceptive tests.

Intraperitoneal administration of boiled milk at a dose 0.5 ml/kg body weight in albino rabbit led to pyrexia; this pyrexia was reverted by intraperitoneal administration of ethanol leaf extract of *P. rubra* at a dose 200 mg/kg body weight (Misra et al. 2012). The extract significantly reduces the elevated body temperature of rabbit which was compared with aspirin (standard drug) and solvent used.

### Anxiolytic Activity

Subchronic oral administration of *Plumeria rubra* flower ethanol extract at 100 mg/kg p.o. to male Swiss mice increased the time spent in the open arms of the elevated plus-maze test (Chatterjee et al. 2013). The extract was further fractionated into hexane, chloroform, butane soluble and *n*-butane-insoluble fractions, out of which the butanol-insoluble fraction (BIF) showed significant anxiolytic activity comparable to standard anxiolytic drug, diazepam. Both the flower ethanol extract and BIF did not show any significant alterations in the horizontal activity, total distance and stereotypy count in the activity monitor. No motor incoordination side effects were observed after the extract and BIF pretreatment in the rotarod test in mice.

### Antifertility Activity

Studies in female Sprague–Dawley rats showed that the aqueous (2 g/kg), ethanol (0.75 g, 1.3 and 1.5 g/kg), methanol and dichloromethane

(1.3 g and 1.5 g/kg) extracts of stem bark of *Plumeria rubra* exhibited antifertility activity (Gunawardana et al. 1998). The extracts were embryotoxic causing foetal death and subsequent resorption. Toxic symptoms observed in these experiments included reduced food intake, loss of body weight, and diarrhoea. Two deaths were recorded in the dichloromethane-treated group. The weight loss observed with some extracts, which showed significant antifertility activity, varied from slight to moderate to large.

The aqueous, alcohol, ethyl acetate and chloroform extract of *P. rubra* pods exhibited abortifacient activity (8–10 %) when administered to pregnant rats from day 11 to 15 of pregnancy (Dabhadkar and Zade 2012). The extracts significantly reduced the number of live foetuses, and the resorption index and post-implantation losses increased significantly. The percent of abortion was found to be highest (100 %) with 200 mg/kg dose of alcohol extract of *P. rubra* pods. In another paper, they reported that the ethanol extracts of *P. rubra* pods exhibited abortifacient activity (13.46–100 %) (Dabhadkar et al. 2012). The extract significantly reduced the number of live foetuses, whereas the resorption index and post-implantation losses increased significantly. The rate of abortion was found to be highest (100 %) at 200 mg/kg dose of alcoholic extract of *P. rubra* pods. In ovariectomized immature young rats, the extract showed significant estrogenic effect (vaginal opening, vaginal cornification and increased uterine weight) at the dose 200 mg/kg body weight. The phytochemical screening revealed the presence of alkaloids, flavonoids, simple phenolics, steroids, tannins and saponins in the extract.

### Anthelmintic Activity

The crude methanol extract of *Plumeria rubra* leaves was found to possess anthelmintic activity (Rastogi et al. 2009). The anthelmintic effect of at 25 mg/ml concentration was comparable to the reference standard piperazine citrate.

## Molluscicidal Activity

Of the six compounds isolated from the heartwood, plumericin and isoplumericin exhibited molluscicidal activity (Hamburger et al. 1991).

## Toxic Immunoreactive Activity

Radford et al. (1986) found significant amounts of immunoreactive cardiac glycoside in *Plumeria rubra*. Awareness of the existence of such compound in *Plumeria* and their dangers allows them to be avoided and poisoning prevented.

## Traditional Medicinal Uses

In traditional medicinal system, different parts of the plant have been mentioned to be useful in a variety of diseases. In India, the plant material is widely used as a purgative, remedy for diarrhoea and cure for itch. The milky juice is employed for the treatment of inflammation and rheumatism. The bark has been reported to be useful in hard tumours, diarrhoea, fever and gonorrhoea. The flowers are eaten with betel nut to cure ague.

In Mexico, the natives used it for skin complaints, for intermittent fevers and for dispersing dropsies by purging when applied to the stomach. In the West Indies, the bark is diuretic and the latex is used for purging. In the Philippines, the bark is used as a purgative, emmenagogue and febrifuge; the latex has the same effects. In Java and Madura, the bark is given for gonorrhoea, dropsy and dysuria due to venereal disease. The milky latex is used as a counterirritant for toothache and for sores. A decoction of the leaves is applied as lotion for cracks and eruptions on the sole of the feet and the paste of the leaves for poulticing swellings. In Thailand, a flower infusion is used as cosmetic applied after bathing but is slightly rubefacient. In Myanmar, the shoot, bark and flowers are employed for leprosy, for pruritis and for healing boils, carbuncles, and ascites. They are analgesic and employed as febrifuge for persistent fever. The bark and leaves are used for rheumatism, abdominal tumours and

inflammation. The flower and shoots are used also for Malaria. In Mexico, decoction of flowers is used in diabetes.

Flowers of *Plumeria rubra*, *Chrysanthemum morifolium*, *Lonicera japonica*, *Bombax morifolium*, and *Sophora japonica* are the five primary constituents of the popular cooling herbal beverage 'Five Flower Tea' (Hu 2005; Kong et al. 2006). This Five Flower Tea is one of the top five remedies for 'Hot Qi' (Kong et al. 2006). 'Hot Qi' is often used by Chinese parents to describe listless symptoms in their children in Hong Kong. Eye discharge (37.2 %), sore throat (33.9 %), halitosis (32.8 %), constipation (31.0 %), and irritability (21.2 %) were the top five symptoms of 'Hot Qi' in children in Hong Kong.

*P. rubra* is one of several plants reported to be used for permanent sterilization for birth control in different parts of Assam, India (Tiwari et al. 1982). The Irula tribe of the Chittoor district of Andhra Pradesh use the flowers to treat itch (Vedavathy et al. 1997).

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## Other Uses

*P. rubra* has become a popular ornamental landscape tree in many tropical and subtropical countries. Flowers are popularly used in garlands or leis in Hawaii and also for wreaths elsewhere. In 2005 over 14 million blooms were sold for lei in Hawaii (Criley 2009). Collectors have descended upon Hawaii to find different colour forms, fragrances and flower shapes, and the fever to own a new plant has brought prices as high as \$75 per cutting for rare and unusual forms. The blooms are often used for decorating bath in aroma therapy. *P. rubra* is Laos national flower.

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## Comments

It can be differentiated from *Plumeria obtusa* using salient leaf characteristics; in *Plumeria rubra*, the leaf blade is acute or acuminate at apex, matte adaxially and glaucous. In *Plumeria obtusa*, the leaf blade is rounded at apex, shiny adaxially and dark green.

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