

ERICACEAE

James L. Luteyn and Paola Pedraza-Peñalosa

A family of ~110 genera and 4,000 species from boreal to warm temperate regions and the highlands of the tropics. Represented in the Neotropics by 46 genera and 850–900 species, a keystone family of vascular plants in the montane cloud forest. Neotropical Ericaceae are mostly terrestrial or epiphytic shrubs in a variety of habitats between 900 and 3,500 m, and normally are not thought of as climbers although their climbing habit may be overstated on collection labels, because “epiphytes are often mistaken for climbers” (Argent 2018). Relatively few species of neotropical Ericaceae are recognized by us as climbers, all of which are members of the inferior ovary tribe Vaccinieae (the blueberries or “arándanos”). A total of 15 genera and ~121 species are sometimes reported as climbers.

Diagnosics: Leaves alternate (rarely subopposite or verticillate), simple, coriaceous, and entire, newly unfolding leaves usually with reddish pigmentation. Flowers (4)5(6)-merous, actinomorphic, usually elongate-tubular, odorless; anthers terminating in tubules that dehisce by pores or slits; fruits berries, usually juicy.

General Characters

1. **STEMS.** Woody, cylindrical, the bark thin, often exfoliating; cross sections with regular anatomy, i.e., xylem forming a continuous large cylinder traversed by narrow rays (Figure 105A), the medulla in some species consisting of cells with thick cellulose walls (Metcalf & Chalk 1957).
2. **CLIMBING MECHANISM.** Climbing Ericaceae are terrestrial or more frequently epiphytic shrubs that generally reach (0.5–)1–2.5(–3) m long while some species of *Psammisia*, *Satyria*, *Thibaudia* and *Vaccinium* are robust lianas that may reach 10 or more

m in length. Commonly they are scramblers that lean on other plants, unable to support their own extended growth (Sperotto et al. 2020). Root climbers are observed in the more wiry and smaller genera, and often found in very humid, high-precipitation areas, where there is always a heavy moss covering (Groff & Kaplan 1988). Under favorable light conditions, terrestrial plants may produce large shrubs but in shaded, low-light, or closed canopy situations (and whether terrestrial or epiphytic) in their search for light they become “passive climbers” *sensu* Sperotto et al. (2020). However, climbing mechanisms is an area that has seldom been studied or judiciously recorded in the Ericaceae, where field notes are not always equivalent or accurately recorded.

3. LEAVES. Newly unfolding leaves usually flush with intense red pigmentation (Figure 105C); mature leaves small to large, simple, spirally arranged (rarely subopposite or verticillate), sclerophyllous, thick- to thin-coriaceous, xeromorphic, with margins entire and usually minutely revolute, very few strongly recurved, rarely remotely crenate; venation pinnate to plinerved; petiolate; stipules absent. Usually both surfaces of young leaves with multicellular, multiseriate, reddish brown, slightly sunken, glandular fimbriae, and when caducous, the leaf surface may appear punctate.
4. INFLORESCENCES. Axillary, rarely cauliflorous (*Satyria*, *Thibaudia*); flowers solitary to several-fasciculate, more commonly racemose; floral bracts (one per pedicel) small, inconspicuous, and caducous, or sometimes large, showy, and persistent in *Cavendishia* and some *Orthaea*.
5. PEDICELS. Bibracteolate, usually long and stout to inconspicuous in the sessile flowers of *Disterigma*.

6. FLOWERS. Pendent or erect, (4)5(6)-merous, bisexual, actinomorphic, showy, odorless; aestivation valvate, rarely imbricate; calyx continuous or articulate with pedicel, terete to angular to winged; corollas urceolate to (long-)tubular, often fleshy, mostly in shades of red to orange, rarely bicolorous and then usually white to green at apex, the lobes triangular, subacute to long-acuminate; stamens obdiplostemonous, equal to unequal in length, the filaments distinct or connate, their connectives rarely spurred, the anthers dorsifixed or basifixed, membranous, thecae smooth to coarsely papillate, extended apically into long to short tubules, dehiscing by terminal pores or oblique and short longitudinal slits; ovary inferior, 5-locular, the nectariferous disk on top of ovary; style about as long as corolla, filiform, fluted, the stigma simple, truncate; ovules numerous, with axile placentation; pollination primarily by hummingbirds in red to orange, long-tubular flowers, whereas primarily by bees in white to pinkish small (< 10 mm) flowers.
7. FRUITS. Berries, erect at maturity as the pedicel rotates upwards during maturation, many-seeded, spherical, fleshy, usually dark blue-black, sometimes translucent white and with thin exocarp. Mature *Psammisia* fruits are dry, mealy, green and have a leathery exocarp. All fruits are usually bird-dispersed.
8. SEEDS. Seeds numerous, small, 0.5–1 mm long, the testa ruminant; sometimes covered with a mucilaginous sheath; embryos white to green.

USES

Several neotropical Vaccinieae are used locally as medicines or as part of traditional beverages, sometimes as forage for cattle or as superstitious charms. Four species are cultivated locally in the Andes as small-fruit crops for their edible, juicy berries, i.e., *Vaccinium*

floribundum Kunth and *V. meridionale* Sw., *Macleania rupestris* (Kunth) A.C. Sm., and *Cavendishia bracteata* (Ruiz & Pav. ex J.St.-Hil.) Hoer., many of which show high antioxidant potential (Dastmalchi et al. 2011). A couple species of *Cavendishia* (*C. adenophora* Mansf., *C. bracteata*) and *Anthopterus wardii* Ball are occasionally cultivated in the Neotropics as ornamentals (Cornejo 2014). Several species of Vaccinieae, however, have horticultural potential as florist crops, with several species of *Macleania*, for example, having been under cultivation since the mid-1800s, although currently only a few species are found at botanical gardens.

Key to the genera of climbing Ericaceae

1. Stamens alternately strongly unequal.2
1. Stamens equal4
2. Filaments unequal, connate into a tube; anther tubules widening distally (V-shaped)*Satyria*
2. Filaments equal, free or partially connate; anther tubules not widening distally (the sides parallel or only slightly broader) 3
3. Floral bracts minute to sometimes large and showy, but usually caducous; anthers equal, the tubules dehiscent by terminal or slightly oblique pores *Orthaea*
3. Floral bracts usually large, showy and persistent; anthers alternately unequal, the tubules dehiscent by introrse, elongate slits *Cavendishia*
4. Anthers dehiscent extrorsely.....*Notopora*
4. Anthers dehiscent introrsely or latrorsely5
5. Most distal pair of bracteoles inserted directly at apex of short pedicel and enveloping calyx to various degrees, differentiated in size and shape from other bracts *Disterigma*

5. Bracteoles undifferentiated, not clasping the calyx or inserted at apex of the pedicel, but usually located at base or medial 6
6. Calyx and corolla both conspicuously 5-winged *Anthopterus*
6. Calyx and corolla terete or angulate, rarely winged, very rarely the calyx winged but then the corolla terete or angulate 7
7. Leaves alternate, margin entire; anther tubules thin, about as half as wide (or less) as thecae..... 8
7. Leaves alternate or subopposite, margin entire, crenulate or serrate; anther tubules about as wide as thecae 11
8. Calyx continuous with pedicel..... *Semiramisia*
8. Calyx articulate with pedicel 9
9. Corolla usually very thick and with the base ventricose, the lobes proportionally long, sometimes to half the overall length of the corolla *Ceratostema*
9. Corolla usually coriaceous to thin, not ventricose at base, the lobes proportionally short and one third or less the overall length of the corolla..... 10
10. Filaments connate over entire length; anther dehiscing by perfectly terminal pores *Siphonandra*
10. Filaments distinct; anther dehiscing by oblique pores *Gonocalyx*
11. Anther thecae conspicuously papillate, the tubules rigid..... 12
11. Anther thecae smooth to minutely papillate, the tubules flexible..... 13
12. Staminal connectives never spurred; anther tubules often laterally connate or sometimes fused into one, rarely free *Macleania*
12. Staminal connectives alternately spurred, rarely all spurred, if not then the connective thickened; anther tubules distinct *Psammisia*

13. Flowers 4- or 5-merous; aestivation imbricate to valvate; stamens 8 or 10; anthers with or without spurs *Vaccinium*
13. Flowers 5-merous; aestivation valvate; stamens 10; anthers always without spurs14
14. Leaves alternate; staminal filaments distinct or connate; anther tubules as long or twice as long as the thecae, dehiscing by elongate, introrse slits *Thibaudia*
14. Leaves alternate or opposite; staminal filaments distinct; anther tubules 2–6 times longer than the thecae, dehiscing by elongate slits or oblique flaring pores *Demosthenesia*

ANTHOPTERUS W.J. Hooker, Icon. Pl. 3: pl. 243. 1839.

Low shrubs or small trees, sometimes epiphytes and climbers up to 3 (10) m long. Leaves



Anthopterus cuneatus, photo by A. Zuluaga.

alternately, subopposite, or verticillate; venation pinnate or plinerved. Inflorescence racemose; aestivation valvate; floral bract to 20 mm long but usually small and inconspicuous. Flowers 5-merous, with calyx continuous with pedicel, the hypanthium broadening distally and winged; corolla subcylindrical, cylindrical-urceolate or subglobose,

narrowly to broadly 5-winged; stamens 10, essentially equal, nearly as long as the corolla, the filaments distinct or basally slightly connate, shorter than anthers, lacking spurs; anthers with thecae smooth, the tubules 2, longer than the thecae, dehiscing by short to elongate slits; nectariferous disc annular or cupuliform. Fruit a juicy, blue-black berry.

Distinctive features: Calyx continuous with the pedicels and conspicuously 5-winged (strongly angled in 1 species); corollas conspicuously to narrowly 5-winged (or sharply angled in 1 species); a tendency towards opposite or verticillate leaves; more or less geniculate stamens.

Distribution: Twelve species ranging from southeastern Panama to northeastern Peru, five of which are sometimes reported as climbers; tropical rainforest to montane cloud forest and mangroves; 0–2,460 m.

CAVENDISHIA Lindley, Bot. Reg. 21: pl. 1791. 1835 (nom. cons).

Erect, epiphytic or terrestrial shrubs, rarely scrambling or root-climbing vines, 4–5 (9) m long. Leaves alternate; venation plinerved or pinnate. Inflorescence racemose or subfasciculate;



Cavendishia tarapotana, photo by P. Pedraza.

floral bract usually large, showy and persistent. Flowers 5-merous, with valvate aestivation; calyx articulate with the pedicel, the hypanthium basally apophysate (flaring) or not; corolla tubular; stamens 10, subequal or rarely unequal, about equal to the corolla, the filaments usually distinct, rarely slightly

coherent at base, alternately unequal, lacking spurs, anthers alternately unequal, with thecae smooth or slightly papillate, the tubules 2, about the same width as the thecae and about twice as long, dehiscing by introrse, elongate slits; ovary with style straight or sigmoid, the stigma minutely 5-lobed, truncate but slightly flaring at anthesis. Fruit a juicy, dark blue-black berry; embryo white.

Distinctive features: Inflorescence and floral bracts large, imbricate, usually showy and persistent; filaments and anthers alternately unequal.

Distribution: A genus with ~180 species distributed from Mexico to Bolivia. Twelve species are sometimes reported as climbing shrubs from Mexico to Bolivia, most of which are found in Colombia; mangroves, caatinga forest, and tropical rainforest to subparamo; 0–3,200 m.

CERATOSTEMA Jussieu, Gen. Pl. 163. 1789.

Terrestrial or epiphytic shrubs, sometimes scrambling and reaching 3–6 m long, often



Ceratostema campii, photo by J. Luteyn.

arising from lignotubers. Leaves alternate; venation plinerved or pinnate. Inflorescences axillary, solitary, fasciculate, or racemose; floral bract small to large and showy. Flowers (4–)5(–6)-merous; aestivation valvate; calyx articulate with the pedicel (obscurely so in *C. loranthiflorum* Benth.), the hypanthium obconical or campanulate, terete, angled to costate, or winged, the lobes elongate-triangular or triangular, often distinctly veined; corolla thick-fleshy, often large, subcylindrical but often ventricose at base, terete or more commonly bluntly angled, usually deeply lobed, the lobes usually narrowly-elongate; stamens (8–)10, equal or alternately slightly unequal, nearly as long as corolla, slightly exserted or appearing exserted when corolla lobes become reflexed, the filaments distinct or connate, equal or alternately slightly unequal, nearly dorsifixed, lacking spurs, the thecae often alternately slightly unequal, usually strongly papillate, the tubules often

alternately slightly unequal, much thinner and often 2–5 times longer, rarely equal to or shorter than the thecae, flexible, distinct to base to connate nearly to apex, dehiscing by short, oblique slits or nearly terminal pores, these sometimes flaring; style as long as corolla or slightly exerted. Fruit a juicy berry, usually dark blue-black but rarely translucent, greenish white.

Distinctive features: Characterized by a calyx that is articulate with the pedicel (obscure in one species); corolla large and usually conspicuously ventricose basally, with lobes deep, long and narrow; and stamens with the filaments distinct or connate, the thecae strongly papillate, and the tubules very long and thin, dehiscing by short, oblique slits.

Distribution: A genus of ~33 species, distributed in NW South America (Guyana to Peru) with most species (26) endemic to eastern Ecuador, seven of which are sometimes reported as climbing shrubs; premontane wet forest to subparamo; 800–3,500 m.

DEMOSTHENESIA A.C. Smith, Bull. Torrey Bot. Cl. 63: 310. 1936.

Terrestrial or usually epiphytic shrubs, sometimes climbing, often with lignotubers; stems



Demosthenesia spectabilis, photo by P. Pedraza.

often with swollen nodes. Leaves alternate, opposite or subopposite, blades entire or remotely crenate, venation pinnate or plinerved. Inflorescences axillary, solitary to fasciculate, racemose. Flowers 5-merous with valvate aestivation; calyx continuous with pedicel, the hypanthium obconic, terete or angled to slightly winged, the

lobes often elongate; corolla actinomorphic to (slightly) zygomorphic, cylindrical or rarely

urceolate, to 5 cm long; stamens 10, about equaling the corolla, often slightly alternately unequal, the filaments distinct, equal or alternately unequal, shorter than anthers, lacking spurs, the thecae slightly papillate, the tubules 2, broad, flexible, 2–6 times longer than the thecae, dehiscing introrsely by elongate slits or obliquely subterminal flaring pores; nectariferous disc annular. Fruit a blue-black berry.

Distinctive features: Leaves often opposite to subopposite; continuous calyx with elongate lobes; often large corollas; usually slightly dimorphic stamens with elongate anther tubules.

Distribution: A genus with ~11 species, ranging from central Peru to northern Bolivia, the following two Peruvian species are reported as climbers: *Demosthenesia cordifolia* Luteyn and *D. vilcabambensis* Luteyn; wet montane forest; 2,400–3,400 m.

DISTERIGMA (Klotzsch) Niedenzu, Bot. Jahrb. Syst. 11: 160, 209. 1889.

Bushy to straggly, terrestrial or epiphytic shrubs, sometimes scramblers. Leaves alternate,



Disterigma campii, photo by P. Pedraza.

< 3 cm long, venation plinerved but usually obscure. Inflorescence axillary, 2–4(–11)-flowered fascicles or flowers solitary, subsessile flowers subtended by a few, minute bracts; bracteoles persistent, the most distal pair inserted directly at apex of pedicel and enveloping calyx to various degrees or rarely exceeding it by several

millimeters, differentiated in size and shape from other bracts. Flowers 4(5)-merous with valvate or imbricate aestivation; calyx articulate with the pedicel; corolla subcylindrical, campanulate or

cylindrical, usually white or pink, usually < 1 cm long; stamens usually twice as many as the corolla lobes, equal, about as long as corolla, the filaments mostly distinct, lacking spurs, the anthers equal, with thecae slightly papillate, the tubules (1)2, dehiscent by elongate, elliptical, introrse clefts; ovary with style about as long as the corolla. Fruit a red, purple, violet, wine-red or white berry; embryo white or green.

Distinctive features: Small leaved shrubs with inconspicuous flowers that are usually < 1 cm long, often white or pink, and are arranged in fascicles of a few flowers; pedicel inconspicuous and articulate with the calyx; bracteoles persistent, the most distal pair inserted directly at apex of pedicel and enveloping calyx and differentiated from other bracts.

Distribution: A genus of ~32 species, ranging from southern Mexico to Bolivia, and east to Guyana and Brazil, with four species referred to as climbers; premontane to montane cloud forests, less often in paramo; 800–3,700 m.

GONOCALYX Planchon & Linden, *Établ. Linden, prix-courant* 10: 5. 1855.

Small, compact terrestrial or usually epiphytic shrubs, less often scrambling and



Gonocalyx concolor, photo by R. Bello.

sometimes reaching 3–5 m long. Leaves alternate, sessile or petiolate; blades with margin entire or crenate, venation obscurely plinerved. Inflorescence axillary, flowers solitary, in pairs, or in loose few-flowered racemes; bract small, persistent. Flowers (4–)5-merous, with aestivation valvate; calyx articulate with pedicel, somewhat obprismatic, the hypanthium terete, bluntly angled or narrowly winged; corolla tubular, subcylindrical, cylindrical-campanulate, or globose-urceolate; stamens 10, equal, nearly as long as corolla, the filaments distinct or

connate, the anthers basifixed, the thecae papillate, the tubules 2, longer and thinner than thecae, dehiscent by minute, subterminal, introrse, oblique pores or short slits; style filiform about as long as corolla, or slightly exserted. Fruit a juicy, blue-black berry.

Distinctive features: Calyx articulate with the pedicel; corollas tubular-cylindrical with short lobes; stamens isomorphic, filaments distinct or connate, anthers with long and thin tubules and short thecae, dehiscent by oblique pores or short slits.

Distribution: Eleven species, ranging from Costa Rica and Panama to Colombia, and the West Indies (Dominican Republic, Puerto Rico, Dominica, Guadeloupe), with the following four species reported as climbers: *G. amplexicaulis* Luteyn from Panama, *G. tetrapterus* Alain from

Dominican Republic, and *G. concolor* Nevling and *G. portoricensis* (Urb.) A.C. Sm. from Puerto Rico; tropical rainforest to montane forest; 500–1,400 m.

MACLEANIA W.J. Hooker, Icon. Pl. 2: tab. 109. 1837.

Terrestrial or epiphytic, erect, compact shrubs, sometimes scrambling or root-climbing



Macleania benthamiana, photo by P. Pedraza.

scrubs or lianas, reaching to 6 m in length,

rarely arborescent (to 8 m), often arising

from lignotubers. Leaves alternate, lower

surface with or without 1–2 dark, circular,

concave glands, 0.1–0.2 mm diam. on either

side of midrib base, venation plinerved or

pinnate. Inflorescences racemose to

fasciculate, usually axillary, rarely appearing

from defoliate axils or ramiflorous in *M. peduliflora* Luteyn, rarely flowers solitary; bracteoles

sometimes provided with extra-floral nectaries dorsally at base. Flowers 5-merous with valvate

aestivation; calyx articulate with the pedicel (this sometimes obscure) or continuous, the

hypanthium terete to conspicuously winged alternate with the lobes, the wings sometimes

distally protruding beyond the calyx limb as a spur; corolla long-tubular, subcylindrical or

elongate-urceolate, terete to bluntly pentagonal or sharply 5-angled opposite the lobes,

concolorous or bicolorous, the lobes very rarely spurred; stamens 10, essentially equal, about

one-quarter to nearly equaling the corolla in overall length, the filaments distinct to connate,

equal, lacking spurs, the connectives often thickened and shouldered distally, the anthers conical,

rigid, equal, with thecae strongly papillate, the tubules 2 or 1 (by fusion), dehiscing introrsely by

2 distinct or 1 fused slits; style about as long as the corolla or slightly exerted, usually glabrous; nectariferous disc annular or cupuliform. Fruit a fleshy, juicy, dark blue-black or translucent-white berry; seeds often enclosed in a mucilaginous sheath.

Distinctive features: Calyx hypanthium terete or winged; stamens equal, rigid, forming a conical tube, the filaments distinct or connate, the anther thecae coarsely papillate, the anther tubules 1 or 2, the anther connectives lacking spurs; berries juicy, blue-black or translucent white; nearly all species produce lignotubers.

Distribution: A genus of 30 species, ranging from southern Mexico to northern Bolivia, with 10 species reported as climbers; mangroves, tropical rainforest to paramo; 50–4,200 m.

NOTOPORA J.D. Hooker, *Icon. Pl.* 12: 53, pl. 1159. 1873.

Terrestrial shrubs, sometimes scrambling. Leaves congested, margins often strongly



Notopora schomburgkii, photo by J. Luteyn.

recurved, venation pinnate. Inflorescence axillary, racemose (2–5-flowered) or the flowers solitary or in pairs. Flowers 5-merous, with valvate aestivation; calyx articulate with pedicel; corolla cylindrical to urceolate-subcylindrical; stamens 10, equal, nearly as long as corolla, the filaments equal, longer than the anthers,

lacking spurs, at first weakly adherent to the corolla but soon free, the anthers equal, the thecae papillate, the tubules 2, slightly shorter than thecae, dehiscent by wide, extrorse slits; style about as long as corolla. Fruit a berry.

Distinctive features: Leaves pinnately nerved; filaments noticeably longer than anthers, anther tubules shorter than thecae, and anther dehiscence by wide, extrorse slits.

Distribution: A genus of five species endemic to the Guiana Shield, centered in southern Venezuela and adjacent Guyana. *Notopora schomburgkii* Hook. f. has been reported as a scrambler in Venezuela (Edo. Bolívar) and Guyana; upland forest, shrubland and savannas; 400–1,300 m.

ORTHAEA Klotzsch, *Linnaea* 24: 23. 1851.

Low shrubs, frequently epiphytic, sometimes scrambling, epiphytic vines up to 6 m long.



Orthaea secundiflora, photo by J. Luteyn.

Leaves alternate, venation pinnate or plinerved. Inflorescence axillary, racemose, subfasciculate, or 1- or 2-flowered; floral bracts minute to sometimes large and showy, but usually caducous. Flowers 5-merous, with valvate aestivation; calyx articulate with pedicel, the hypanthium terete; corolla tubular to subcylindrical; stamens 10,

alternately unequal, usually about $\frac{1}{3}$ the length of the corolla, the filaments distinct or slightly coherent at base, alternately unequal, lacking spurs, the anthers equal, thecae smooth, tubules 2, about the same width as the thecae but shorter, dehiscing by terminal or slightly oblique pores; ovary with style about as long as corolla. Fruit a juicy berry; embryo white.

Distinctive features: Characterized by flowers 5-merous, calyx without eglandular hairs, corolla tubular to subcylindrical, stamens of two different lengths in which the anthers are of similar

length, but the filaments are unequal, connate or distinct, dehiscence by terminal pores or short lateral slits; anthers from the long cycle laterally dehiscent, with the pores facing the pore of the adjacent long stamen.

Distribution: *Orthaea s.l.* is a polyphyletic group of 37 accepted species (Salinas 2015), mostly found in Andean forests from Colombia to Bolivia, with a few species found in the Guiana Shield (Venezuela, Guyana), S Mexico and Central America. Eleven species are sometimes reported as climbers; premontane to montane cloud forest; 900–3,400 m.

PSAMMISIA Klotzsch, Linnaea 24: 42. 1851.

Epiphytic or terrestrial shrubs, sometimes scrambling, 3-7 m long. Leaves alternate, very



Psammisia ferruginea, photo by J. Luteyn.

rarely pseudoverticillate, venation pinnate or plinerved.

Inflorescence axillary, racemose or subfasciculate.

Flowers 5-merous, with valvate aestivation; calyx articulate with the pedicel; corolla subcylindrical, elongate-urceolate or subglobose; stamens (8–)10(–12),

equal, from about $\frac{1}{3}$ to often nearly as long as the corolla, the filaments equal, distinct or connate,

connectives either all laterally or distally 2-spurred, or alternately spurred, or rarely spurs obscure or lacking,

when present the spurs either acute and conspicuous or rounded and not very apparent, the anthers equal, stout

with strongly papillate thecae, the tubules 2, distinct,

1/4 to about as long as the thecae, dehiscent by elongate introrse slits; style often exerted. Fruit a leathery, dry, mealy, berry, green when mature; embryo white.

Distinctive features: Characterized by stamens equal, rigid, forming a conical tube, the filaments distinct or connate, anther connectives usually spurred, thecae coarsely papillate, tubules 2, distinct to base; and the fruit a leathery, dry, mealy, green berry.

Distribution: A genus of 70 species, ranging from Costa Rica to Bolivia, and eastwards into the Guianas, Brazil, and Trinidad, 23 of which are sometimes reported as climbers; mangrove, tropical rainforest to montane forest, 0–3,700 m.

SATYRIA Klotzsch, *Linnaea* 24: 14, 21. 1851.

Epiphytic or terrestrial shrubs, often scrambling lianas reaching 5-15 m in length. Leaves



Satyria grandifolia, photo by P. Pedraza.

alternate; venation plinerved, rarely pinnate. Inflorescence axillary, glomerulate, racemose, or subfasciculate, often ramiflorous, with few to many pendent flowers. Flowers 5-merous, with valvate aestivation; calyx articulate with the pedicel; corolla cylindrical to narrowly

urceolate, terete to angled; stamens 10, alternately unequal, usually about $\frac{1}{3}$ as long as the corolla, the filaments equal and firmly connate into a tube for more than half their length, lacking spurs, the anthers basifixed, firm, alternately unequal, slightly dimorphic, the longer ones spreading distally with the tips often incurved and the tubules twisted to present latrorse

dehiscence, the shorter ones laterally coherent distally with the tips straight and the tubules straight to present introrse dehiscence; anther thecae subcoriaceous, slightly to not papillate, the tubules 2, not sharply differentiated from the thecae, dehiscing by subapical pores; style as long as corolla or slightly exserted; nectariferous disc usually conspicuous, annular-pulvinate. Fruit a dark blue-black or rarely translucent white juicy berry.

Distinctive features: Scrambling lianas, with abundant and often ramiflorous inflorescences; stamens alternately unequal, about $\frac{1}{3}$ as long as the corolla, the filaments equal and firmly connate into a tube, the connectives lacking spurs; anthers basifixed, firm, alternately unequal, slightly dimorphic, the thecae hardly differentiated from the tubules, the tubules 2, not sharply differentiated from the thecae, often distally ornate.

Distribution: A genus of ~25 species, ranging from southern Mexico to Bolivia, and eastwards into the Guianas and Brazil. Sixteen species are reported as climbers, these are found from Honduras to Peru and the Guianas, with most species found in Colombia; tropical rainforests to montane cloud forests; 0–2,000 m.

SEMIRAMISIA Klotzsch, *Linnaea* 24: 15, 25. 1851.

Terrestrial or epiphytic shrubs, rarely scrambling lianas. Leaves alternate, venation



Semiramisia speciosa, photo by P. Pedraza.

plinnerved. Inflorescence axillary, short-racemose or flowers solitary. Flowers 5-merous with valvate aestivation; calyx continuous with pedicel, the hypanthium obconical, terete to angled or winged, the lobes apiculate; corolla terete, broadening distally, fleshy when fresh but drying membranous, shallowly lobed, the lobes short and broad; stamens 10, equal, slightly shorter than the corolla, the filaments connate or distinct, shorter than anthers, lacking spurs, the anthers equal, the thecae

strongly papillate, the tubules 2, elongate, about one-half as broad as thecae, dehiscing by terminal or subterminal oblique, sometimes flaring pores; style nearly equaling corolla. Fruit a juicy berry.

Distinctive features: Calyx continuous with pedicel; large corollas broadening distally, shallowly lobed; staminal tubules about half as broad as and usually much longer than the thecae, conspicuously papillate thecae, and dehiscence usually by short oblique clefts.

Distribution: A genus of four species, ranging from Venezuela to Peru. Only *Semiramisia speciosa* (Benth.) Klotzsch is sometimes a scrambler with branches to 5 m long (Colombia, Ecuador, Peru); premontane to montane forests; 850–3,810 m.

SIPHONANDRA Klotzsch, *Linnaea* 24: 24. 1851.

Terrestrial or epiphytic shrubs. Leaves alternate; blade marginally recurved and entire or



Siphonandra elliptica, photo by P. Pedraza.

faintly crenulate; venation pinnate.

Inflorescences axillary, solitary, racemose.

Flowers 5-merous, with valvate aestivation;

calyx articulate with pedicel, the

hypanthium terete to narrowly winged;

corolla cylindrical; stamens 10, equal, often

slightly longer than corolla, the filaments

equal, distinct to connate, shorter than

anthers, lacking spurs; anthers basifixed, the thecae papillate, the tubules 2, distinct, elongate, slender, flexible, about half as wide (or less) as thecae, 4–5 times longer than thecae, dehiscing by strictly terminal, slightly flaring pores; ovary with style slightly exserted; nectariferous disc annular. Fruit a juicy berry; embryo unknown.

Distinctive features: Narrow anther tubules dehiscing by strictly terminal, slightly flaring pores.

Distribution: A distinctive high-elevation genus of five species, ranging from northern Peru to northern Bolivia. The only climber is *S. nervosa* Luteyn & E.M. Ortiz; Peru; montane forest; 2,600 m.

THIBAUDIA Ruiz & Pavón ex J. Saint-Hilaire, Expos. Fam. 1: 362. 1805.

Epiphytic or terrestrial shrubs, sometimes scrambling lianas reaching 3-5 (-20) m long.



Thibaudia inflata, photo by J. Luteyn.

Leaves alternate, margins entire or crenulate, venation pinnate or plinerved. Inflorescence axillary, subfasciculate, racemose or paniculate, sometimes ramiflorous.

Flowers 5-merous with valvate aestivation; calyx articulated with the pedicel or rarely

continuous, the hypanthium short-cylindrical or campanulate, terete, occasionally narrowly 5-angled, or rarely conspicuously 5-winged; corolla subcylindrical, terete, occasionally 5-angled, rarely weakly to strongly winged, usually red or red with white apices, rarely white; stamens 10, equal, often nearly as long as the corolla, the filaments equal, distinct or connate, the anthers equal, basifixed, the thecae smooth or slightly papillate, the tubules 2, as long as the thecae or rarely twice as long, dehiscent by elongate, introrse slits; style as long as the corolla or slightly exserted. Fruit a juicy berry, dark purple to blackish.

Distinctive features: Lacks truly unique features, in general leaf blades with entire or crenate margins; inflorescences often with abundant flowers arranged in subfascicles, racemes or panicles, sometimes ramiflorous; calyx articulated with the pedicel or rarely continuous, terete, occasionally narrowly 5-angled, or rarely conspicuously 5-winged; corolla terete, occasionally 5-angled, rarely weakly to strongly winged; stamens 10, equal, with distinct or connate filaments.

Distribution: *Thibaudia* is polymorphic and a highly polyphyletic genus of ~70 species, ranging from Costa Rica to Bolivia, with 19 species reported as sometimes climbing plants; scrub-forests, tropical rainforests to paramo; 250–3,600 m.

VACCINIUM Linnaeus, Sp. Pl. 349. 1753.

Terrestrial shrubs, rarely trees to 15 m tall, or scrambling lianas to 5 m long, sometimes creeping, often rhizomatous, sometimes arising from lignotubers. Leaves alternate, rarely subopposite, evergreen or deciduous, coriaceous to membranous, sometimes bullate, the bases sometimes clasping to amplexicaulous, the margins entire or serrate, venation pinnate or rarely plinerved. Inflorescence axillary, racemose (sometimes appearing corymbose), rarely only 1- or 2-flowered, or paniculate. Flowers 4- or 5-merous with imbricate or valvate aestivation; calyx articulate or continuous with the pedicel, often glaucous, the hypanthium sometimes 5-10-ribbed; corolla cylindrical, urceolate, or campanulate, fleshy to membranous, sometimes

densely pilose internally at the throat, white, pink, red, or green; stamens 8 or 10, equal, about

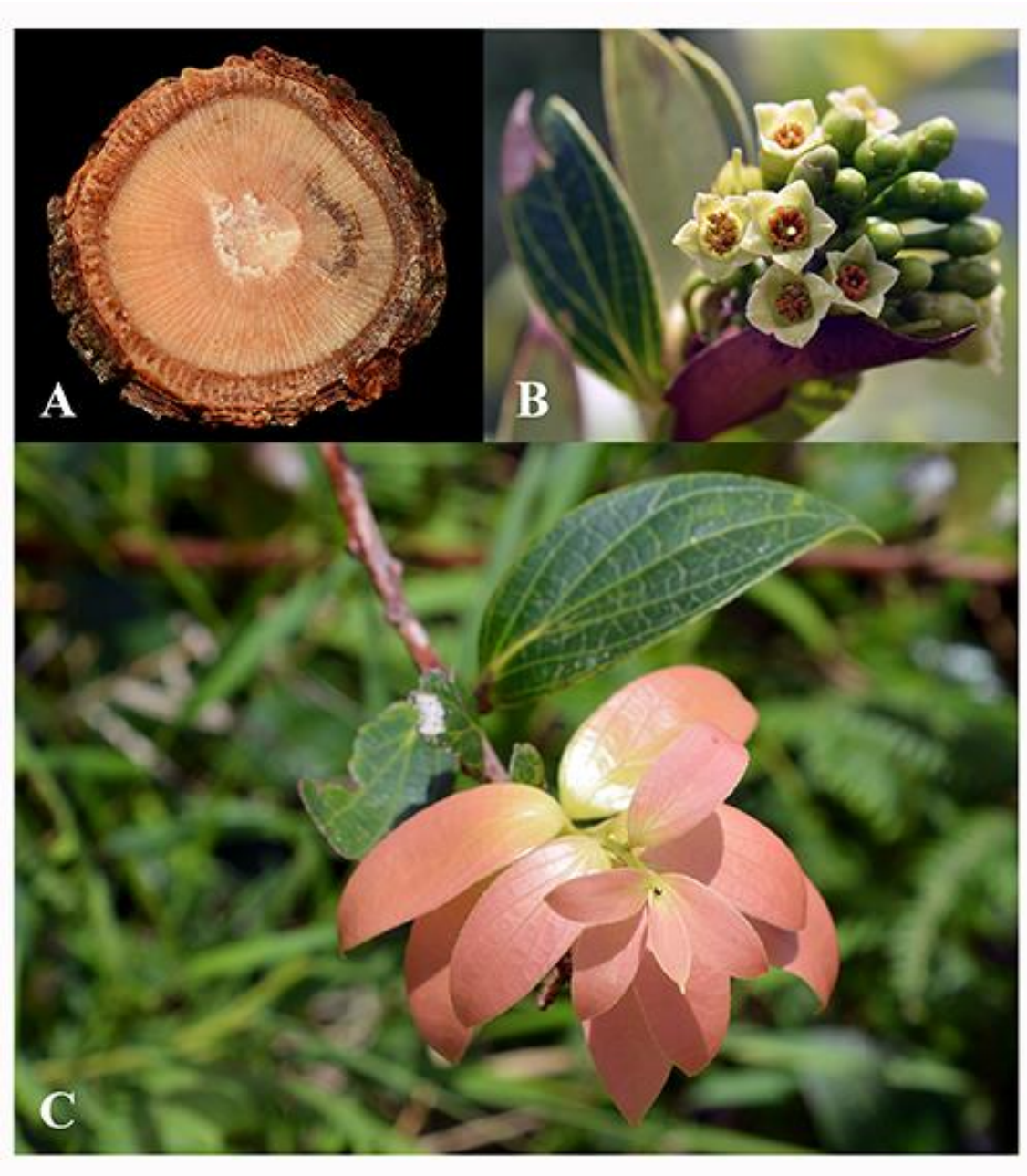


Figure 105. *Vaccinium racemosum*. **A.** Stem cross section showing regular anatomy with conspicuous rays. **B.** Inflorescence. **C.** Newly unfolding leaves flush with reddish pigmentation. Photos by P. Acevedo.

as long as the corolla or longer, the filaments equal, lacking dorsal spurs to sometimes long-spurred, the anthers equal, with tubules 2, long to sometimes very short, dehiscing by a terminal pore, rarely oblique slits, or rarely latrorse slits; ovary completely or partly inferior, 4- or 5(– falsely 10)-locular, stigma small, simple or somewhat capitate. Fruit a juicy, blue-black berry, sometimes glaucous; embryo white.

Distinctive features: *Vaccinium* is a highly polymorphic, polyphyletic genus that lacks truly unique morphological characters. *Vaccinium s.l.* has blades with the margins entire or serrate; inflorescence axillary, racemose (sometimes appearing corymbose), rarely only 1- or 2-flowered, rarely paniculate. Flowers 4- or 5-merous; aestivation imbricate to valvate; calyx articulate or continuous with the pedicel, often glaucous, the hypanthium sometimes 5-10-ribbed; stamens 8 or 10, equal; fruits often glaucous

Distribution: A cosmopolitan genus with ~450 species in the Paleotropics and ~66 species in the Neotropics, six of which are reported as scrambling or climbing shrubs that sometimes reach 2 or more m in length; savannah, scrub-forest, premontane forest to paramo; 400–2,700 m.

Note. The “green-flowered” species of Central America and the Caribbean have been placed in *Symphysia* (see especially Vander Kloet et al. 2004) but as the molecular analyses for this complex and widespread genus are too preliminary, we have retained *Vaccinium*.