SAPINDACEAE

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A predominantly tropical family of trees, shrubs, lianas and vines, with few species extending to temperate zones. Lianas and vines in the Sapindaceae are restricted to six genera all belonging to the predominantly neotropical tribe Paullinieae. About 488 out of a total 800 species of Sapindaceae in the Neotropics are either lianas or vines which are ubiquitous in lowland moist forests, savannas, gallery forests, and in open disturbed biomes. Neotropical Sapindaceae is most diverse between 300 and 800 m of elevation, becoming less diverse between 1,500 and 3,000 m.

Diagnostics: In the absence of fertile material, climbing Sapindaceae are easily distinguished from vines in other families by the presence of compound, alternate leaves with stipules; a pair of circinate tendrils at the end of short axillary branches, or at the base of axillary inflorescences rachis.

General Characters

1. STEMS. Woody or less often herbaceous (e.g., some *Cardiospermum* and *Urvillea*). Woody, mature stems are usually 1–4 cm in diam., although in species of *Paullinia, Serjania, and Thinouia* they may reach 15 cm or more in diam., and up to 30 m in length. Stems are cylindrical (Figure 221 E, F), trigonous (Figure 221B), trilobed (Figure 221C), or pentagonal in cross section, and usually deeply furrowed (Figures 221A; 222A). Barks are smooth, lenticellate, rough and sometimes with scattered prickles (a few species of *Serjania*). Stem cross sections have been traditionally used as an important character for the differentiation of species or even genera within tribe Paullinieae. It has been used
as an ancillary character in species descriptions as well as in taxonomical keys. The characterization of these features has slowly improved as better field data and collections (of stems) have become available (Refer to Bastos et al 2016 and Pace et al 2020 for a review). Following the guidelines stated in the introduction, stem cross sections in Sapindaceae contain the following macroanatomical types (refer to the introduction for definitions).

a. Regular configuration. Rays are either uniseriate (inconspicuous) or multiseriate. Present in all six genera (at least during early secondary growth stages) but more common within *Paullinia* (Figure 220F). As discussed by Chery et al. (2020), species showing this pattern are either cylindrical or lobed in early stages.

b. Non-cylindrical Stems (lobed). Present in *Paullinia, Serjania* and *Urvillea*. Stems presenting this configuration are commonly deeply trilobed (Figure 220C), less often bilobed or shallowly 5-lobed.

c. Compound stems. A feature unique to *Paullinia* and *Serjania* within the plant kingdom. Characterized by the presence of multiple vascular cylinders, where a central vascular cylinder is accompanied by 3–10, (often) smaller peripheral vascular cylinders.

i. 3(5) peripheral cylinders. These are roughly arranged in a triangular disposition around the central vascular cylinder. This configuration is present in ~21 species of *Paullinia* (Figure 220B) and in ~86 species of *Serjania*. 
ii. 5 or 6 peripheral cylinders. Like the previous subcategory, the peripheral cylinders are in a triangular disposition around the central vascular cylinder. This arrangement is present in ~8 species of *Serjania* (Figure 220A).

iii. 8–10 peripheral cylinders. In this subcategory the peripheral cylinders are in a more or less circular position around the central cylinder. This arrangement is unique to ~25 species of *Serjania* (Figures 220E; 221C).

d. Fissure stems. This arrangement is unique within Sapindaceae to *Urvillea laevis* Radlk. (Figure 221E).

e. Divided xylem. An arrangement unique within the plant kingdom to a group of 8 species of *Serjania* related to *Serjania paradoxa* Radlk (Figure 221D).

f. Axial Vascular Elements in Radial Segments. This arrangement is currently known from *Serjania dura* Radlk. and *S. gracilis* Radlk.

g. Successive cambia. Production of successive bands of vascular tissue, found in *Serjania grandifolia* Radlk. (Figure 221F), *S. inscripta* Radlk., *S. meridionalis* Cambess., *S. multiflora* Radlk., *S. pernambusensis* Radlk., *Paullinia pseudota* Radlk., *Paullinia* sp. nov. and *Urvillea filipes* Radlk.

h. Neoformed vascular cylinders. found in many species of *Thinouia* (Figure 221A, B), and in a few species of *Serjania* (e.g., *S. caracasana* (Jacq.) Willd. (Figure 221C), *S. neei* Acev.-Rodr., *S. polyphylla* (L.)
Radlk., and *S. pyramidata* Radlk.). Stems with neo-formed vascular cylinders are superficially similar to compound stems but in the former the peripheral vascular cylinders are initiated during primary growth, while in the latter the neoformed cylinders are formed during late secondary growth.

i. Phloem wedges. In this arrangement the cambium is continuous (e.g., *S. lethalis* St. Hill.) or interrupted as in many species of *Paullinia, Serjania* (Figure 220D) and *Urvillea stipularis* Radlk.
Figure 221. Cross sections of mature stems. A. *Thinouia mucronata*, late secondary growth with a central vascular cylinder and neo-formed cylinders of different sizes at the periphery. B. *Thinouia mucronata*, early secondary growth with incipient neoformed vascular cylinders external to the main vascular cylinder. C. *Serjania caracasana*, late secondary growth of compound stem with neoformed cylinders (smaller cylinders near the periphery of stem). D. *Serjania paleata* stem with divided xylem. E. *Urvillea laevis* fissure stem. F. *Serjania grandifolia*, stem with successive cambia. Photos by P. Acevedo.
EXUDATES. For the most part exudates are odorless and colorless in all genera, with the exception of *Paullinia* and *Serjania* where many species are known to have milky white exudates (Figure 220A, D, E).

CLIMBING MECHANISM. All climbing Sapindaceae have circinate or less often spiral tendrils that are produced in pairs at the base of the floriferous rachis of an axillary inflorescences or distally on short axillary shoots (homologous to an inflorescence, Figure 222A, B).

STIPULES. Usually minute or small (0.5–10 mm long), subulate, lanceolate or triangular and persistent. Less often, stipules are large (1.5–3 cm long), falcate, cordate, rounded or dissected (Figure 222C–E), and usually deciduous. Minute and small stipules are found in all genera, while large stipules are restricted to *Paullinia, Serjania,* and a few species of *Urvillea.* Large stipules, however, are more common in *Paullinia,* some of which have dissected margins or cordate bases.

LEAVES. Alternate, imparipinnate; these include 5–9-pinnate (Figure 223A, E), partially bipinnate-tripinnate (Figure 223D), trifoliolate (Figure 223C), biternate (Figure 223B), triternate or a combination of these. Palmate leaves and unifoliolate leaves are found in few species of *Paullinia* (e.g., *Paullinia echinata* Huber; *Paullinia unifoliolata* Perdiz & Ferrucci). Petioles and rachis are nearly cylindrical (Figure 223A, C), slightly flattened adaxially (Figure 223B, D) or winged (Figure 224E).
INFLORESCENCES. Ascending or hanging, axillary, distal, or cauliflorous thyrses with flowers in lateral cincinni. Axillary inflorescences are solitary, racemose (Figure 224E), spicate (Figure 224F), or umbelliform (Figure 224B), and less often grouped in fascicles (Figure 224C). Distal inflorescences form a
paniculate synflorescence at the end of branches and are common to all genera.

Cauliflorous and fasciculate inflorescences are known only from Paullinia (Figure 224A), while umbelliform inflorescences are exclusive to species of Thinouia (Figure 224B), Cardiospermum and Urvillea. Axillary, solitary inflorescences are usually subtended by a pair of tendrils, but tendrils are mostly lacking in cauliflorous, fasciculate, and distal inflorescences.

7. PEDICELS. Articulate, with an abscission zone above the base.

8. FLOWERS. Zygomatic in Cardiospermum, Lophostigma, Paullinia, Serjania, and Urvillea (Figure 224A, C–E) actinomorphic in Thinouia (Figure 224B), seemingly bisexual but functionally unisexual where plants are dichogamous, monoecious, or dioecious. Sepals distinct or two of them partly connate in zygomatic flowers; petals distinct, usually white or cream; in zygomatic flowers 4, with an adaxial hood-shaped appendage that has a fleshy crest; in actinomorphic flowers, petals auriculate with bifurcate appendages; nectary disc extrastaminal, unilateral, entire or lobed in zygomatic flowers; annular in actinomorphic flowers; stamens 8; ovary superior and tricarpellate, with same number of locules as carpels, the style more or less elongated, the stigmas elongated or capitate; placentation axial, ovules 1 per locule. flowers 4, with an adaxial hood-shaped appendage that has a fleshy crest; in actinomorphic flowers, petals auriculate with bifurcate appendages; nectary disc extrastaminal, unilateral, entire or lobed in zygomatic flowers; annular in actinomorphic flowers; stamens 8; ovary superior and tricarpellate, with same number of locules as carpels, the style
Figure 223. Leaves. A. 5-pinnately compound in *Paullinia allenii*. B. Biteminate in *Serjania cornigera*. C. Trifoliolate in *Paullinia turbacensis*. D. Partially bipinnate-tripinnate in *Serjania trachygona*. E. Partially bipinnate (7-pinnate, with compound basal pair of leaflets) *Paullinia* sp. Photos by P. Acevedo.
more or less elongated, the stigmas elongated or capitate; placentation axial, ovules 1 per locule.

2. **FRUITS.** Fruit type is the most important character in recognizing the genera of climbing Sapindaceae. These are either capsules or schizocarps. *Thinouia*, *Serjania*, and *Lophostigma* have schizocarps that split into 3 winged mericarps. Wings in *Thinouia* (Figure 225A) are in distal position while those of *Serjania*
and *Lophostigma* (Figure 225B, C) are basal. *Paullinia, Cardiospermum*, and *Urvillea* have septicidal marginicidal capsules. Those of *Paullinia* (Figures 225F; 227) are coriaceous to woody, while those of *Cardiospermum* (Figure 225E) and *Urvillea* (Figure 225D) are papery. Capsules in *Cardiospermum* have locules that are completely inflated while those of *Urvillea* flattened to various degrees.

3. **SEEDS.** Seeds in *Paullinia* are globose, sub-globose or ellipsoid and partially to entirely covered with a fleshy tissue which is usually derived from the outer coat of the testa (Figure 227A–C). Those of *Cardiospermum* and *Urvillea* are globose or nearly so, lacking a fleshy tissue, and usually have a with heart-shape arillode surrounding the hilum (Figure 226D). Seeds in *Serjania, Lophostigma* and *Thinouia* are usually lenticular and lack any fleshy tissue.
USES

In general, most species of Sapindaceae including the climbers are used for fish poisoning in the Neotropics (Radlkofer 1886; Acevedo-Rodríguez 1990). Numerous species of Paullinia have been reported to be useful in the preparation of medicines, caffeine-rich beverages, binding and weaving material, and for fish, human and arrow poisoning (Beck 1990). The seeds of Paullinia cupana are the source of the important Brazilian crop guaraná, a source of caffeine and flavoring of soft drinks. Macerated stems of Paullinia yoco Schultes are used in the preparation of a caffeine-rich drink. Three species of Cardiospermum are used as an ornamental
worldwide. Some species of *Serjania* (e.g., *S. lethalis* A. St.-Hil.) have been reported as toxic to grazing animals.

**Key to the genera of climbing Sapindaceae**

1. Flowers actinomorphic, with an annular nectary disc; fruit a schizocarp; mericarps with a distal wing; leaves always trifoliolate (Mexico to South America) .................. *Thinouia*

1. Flowers zygomorphic with a unilateral nectary disc that is semi-annular or represented by 2 or 4 lobes; fruit a capsule or if a schizocarp the mericarps with a basal or peripheral wing; leaves of many kinds .................................................................2

2. Petals short, with a pair of minute, basal appendage, concealed by the sepals; stamen filaments of equal length and as long as the anthers; nectary semi-annular, 4-lobed; pollen grains cylindrical-ellipsoid, 4-syncolporate; cross section of stem simple (Ecuador, Peru, Bolivia) .................................................................*Lophostigma*

2. Petals much longer than the sepals, with a hood-shaped petaloid appendage almost as long as the petal; filaments of anterior stamens shorter than those of posterior ones; anthers much shorter than the filaments, appressed against petal appendages; nectary reduced to 4 or 2 lobes; pollen grains trigonous, triporate or tricolporate; cross section of stem simple or compound.................................................................................................................3

3. Fruit a schizocarp, mericarps with a basal or less often a peripheral wing; cross section of stem simple or compound; inflorescence never cauliflorous (southwestern North America to South America, West Indies) .............................................. *Serjania*

3. Fruit a capsule; cross section of stem simple or compound; inflorescence sometimes cauliflorous (*Paullinia*) ...........................................................................................................................................4
4. Fruit wall thick, coriaceous cross section of stem simple or compound (Mexico to South America, West Indies) ....................................................... \textit{Paullinia}

4. Fruit wall papery; cross section of stem simple..................................................................................................................5

5. Fruit lobes inflated (North America to South America, West Indies) .......... \textit{Cardiospermum}

5. Fruits lobes more or less flattened lengthwise (Mexico to South America, Lesser Antilles)
........................................................................................................................................................................\textit{Urvillea}

\textbf{Identification of genera based on vegetative characters}

The genera of climbing Sapindaceae are characterized by the type of fruit they bear, and to a certain degree by the symmetry of the flower; vegetatively the genera are very similar and difficult to tell apart. However, the following generalities can be useful in distinguishing the genera with a certain degree of confidence.

Biternate leaves (Figure 223B) are found in \textit{Serjania}, \textit{Paullinia}, and \textit{Cardiospermum} with a total of 169 species showing this leaf type. There is a higher probability for an individual having this type of leaf to be a \textit{Serjania} since nearly 60\% of its species (145 species) are known to have biternate leaves. In contrast, 15 species of \textit{Paullinia}, ~5 species of \textit{Cardiospermum}, and 1 species of \textit{Urvillea} are known to have biternate leaves.

Multijugate leaves (Figure 223E) are more prevalent in \textit{Paullinia} with 33 species exhibiting this character. In contrast, only 8 species of \textit{Serjania} have multijugate leaves.

Compound stems with a central vascular cylinder surrounded by (6)8–10 smaller peripheral vascular cylinders (Figures 220E; 221C) is a feature only present in ~30 species of \textit{Serjania}. The widely distributed \textit{Serjania caracasana} (Jacq.) Willd. is an example of a species with this kind of stem anatomy.
Co-occurrence of biternate leaves and compound stems. This combination of characters is unique to *Serjania* and is present in ~56% of its species. Conversely, all species of *Paullinia*, *Cardiospermum* and *Urvillea* with biternate leaves have simple stems.

*White or milky exudate.* A character restricted to a few species of *Paullinia*, *Serjania* and *Thinouia* (Figure 220A, D, E).

*Prickly stems.* A character found only in 4 species of *Serjania* (e.g., *S. mexicana*).

*Cauliflorous inflorescences.* A character found only in ~20 species of *Paullinia* (Figure 224A) and in one or two species of *Thinouia*. The widely distributed *Paullinia alata* (Ruiz & Pav.) D. Don is an example of a species that has this character.

**CARDIOSPERMUM** Linnaeus, Sp. Pl. 366. 1753.

Herbaceous tendrilled vines, or less often erect subshrubs, with woody base and watery sap; stems furrowed, cylindrical or slightly angled; cross section with regular anatomy. Leaves trifoliolate or biternate, membranous or chartaceous; leaflets deeply serrate or lobed; petioles and rachis unwinged; stipules minute, early deciduous. Flowers zygomorphic, functionally staminate or pistillate, produced in axillary thyrses; thyrses bearing a

*Cardiospermum corindum* capsules, photo by P. Acevedo.
pair of tendrils at base of rachis; calyx of 4 or 5 unequal sepals; petals 4, distinct, white, with a hood-shaped appendage; nectary unilateral reduced to 4 lobes or 2 corniform projections; stamens 8, the filaments unequal, connate at base, the anthers dorsifixed; ovary 3-carpellate, each locule with a single ovule, the style slender, the stigmas 3, recurved. Fruit an inflated, membranous, capsule, with a persistent septa. Seeds spherical, black, with a small, white, cordate, dry arillode (Figure 226D), seeds are persistent on the septa after the fruit has dehisced.

**Distinctive features:** Fruit inflated, membranous capsules; seeds with a white, heart-shaped dry arillode; leaves trifoliolate or biternate.

**Distribution:** A tropical genus with six or seven species, native to the Neotropics, but a few species with pantropical distribution. Also cultivated as an ornamental in North America and Europe, some species becoming weedy; disturbed sites, scrubs, secondary forests; 0–800 (∼1,800) m.


Woody vines, reaching few m in length; stems nearly cylindrical; cross section of stem with regular anatomy, xylem with conspicuous rays. Leaves alternate, trifoliolate; stipules minute. Inflorescences axillary thyrses with a pair of tendrils at base of rachis. Flowers zygomorphic, functionally unisexual;
sepals 5, unequal, imbricate; petals 4, much shorter than the sepals, with 2 basally adnate digitate appendages; disk unilateral, 4-lobed; stamens 8, with short filaments; pollen cylindrical-ellipsoid, 4-aperturate; ovary 3-carpellate, with a single ovule per carpel; style with 3 stigmatic branches. Fruit a schizocarp splitting into 3 mericarps with an elongated proximal wing. Seeds lenticular, exarillate.

**Distinctive features**: Petals much shorter than the sepals; pollen cylindrical-ellipsoid, 4-aperturate; mericarps with a proximal wing similar to *Serjania*.

**Distribution**: Two species, *L. schunkei* (Acev.-Rodr.) Acev.-Rodr. from lowland (250–400 m), moist forests in Ecuador, Peru and Bolivia, and *L. plumosum* Radlk. from Bolivia in scrub vegetation (2,000–2,400 m.).

**PAULLINIA** Linnaeus. Sp. Pl. 365. 1753.
Figure 227. Capsules in *Paullinia*. A. Echinate capsules of *P. hystrix*. B. Smooth capsules of *P. obovata*. C. Ridged capsules of *P. verrucosa*. D. Winged capsules of *P. caloptera*. Photos by P. Acevedo.
Lianas, vines or less often understory shrubs; stems cylindrical, deeply 3-lobed, or 3–5-angled; cross section quite variable: regular (Figure 220F), compound [3(5) peripheral vascular cylinders (Figure 220B)], phloem wedges, and successive cambia in two species; often producing milky sap. Stipules minute to foliaceous, persistent or deciduous (Figure 222C–E). Leaves alternate, trifoliolate, 5-pinnately foliolate, biternate, triterinate, or partially bipinnate (Figure 223A, C, E). Thyrses solitary or fascicled, axillary, terminal, or cauliflorous, racemiform, spicate, or paniculate (Figure 224A, C, F), with flowers in lateral cincinni. Flowers zygomorphic; calyx 4–5-merous, the sepals distinct, or the two anterior ones connate to different degrees into a larger sepal; petals 4, distinct, clawed, bearing a hood-shaped appendage, these with a fleshy, yellowish apex, smaller in anterior petals; disc unilateral, 2- or 4-lobed; stamens 8, the filaments of unequal length, usually pubescent; ovary 3-carpellate, the carpels with a single ovule. Fruit a septifragal (marginicidal) capsule, rugose, or echinate, membranous, crustose, leathery or woody (Figure 227). Seeds usually globose, with a sarcotesta at base, but sometimes covering almost the whole seed. A few species of Paullinia are known to be shrubby in early stages but can grow into lianas as they mature.

**Distinctive features:** Seed mostly sarcotestal; some species with cauliflorous inflorescences; pollen grains triporate.

**Distribution:** A neotropical genus with ~200 species, most of which are climbers; Mexico to northern Argentina, including the West Indies, with its center of distribution in western Amazonia. The widespread neotropical *P. pinnata* L. is also found (apparently naturally) in tropical Africa and Madagascar; mostly in non-flooded moist forests or rainforests, some species in riparian and seasonally flooded forests or even along the margins of disturbed forests; 0–900 (–2500) m.

SERJANIA Miller, Gard. Dict. Abr. Ed. 4. 1754.
Lianas or vines of forest canopy, open disturbed areas, or savannas; stems 3–5 angled or lobed, less often cylindrical; cross section with the following arrangements: compound stems with 3–10 peripheral cylinders (Figures 220A, E; 221C), regular, divided xylem (Figure 221D), phloem wedges (Figure 220D) or rarely with successive cambia (Figure 221F); often producing milky sap. Stipules minute to small, early deciduous or persistent. Leaves alternate, trifoliolate, 5-pinnately foliolate, biternate, or tr ternate, or seldom bipinnate. Thyrses axillary or terminal, racemose or paniculate, with flowers on lateral cincinni. Flowers zygomorphic; sepals 4 or 5, distinct, or two of them connate; petals 4, distinct with a hood-shaped appendage; disc unilateral, 2-to 4-lobed; stamens 8, the filaments of unequal length, the anthers dorsifixed; ovary 3-locular, the locules with a single ovule. Fruit a schizocarp splitting into three samaroid mericarps, with a proximal wing, or less often, the wing marginal or exceptionally fruits late dehiscent. Seeds lenticular to globose, not arillate.

**Distinctive features:** Co-occurrence of biternate leaves and stems with multiple vascular cylinders; stem (cross section) with a central vascular cylinder surrounded by 8–10 smaller vascular cylinders.
**Distribution:** A neotropical genus currently with ~250 species but perhaps as many as 300, mostly distributed below 1,500 m in savannas, dry forest, or open, disturbed habitats from Mexico to northern Argentina, including the West Indies, with a main center of distribution in the Brazilian plateau and the Mexican savannas; mostly in savannas, scrubs and disturbed vegetation, a few species in moist forests; 0 –1,400 (–3,280) m.


Tendrilled lianas or erect shrubs. Stems terete or trilobed, lenticellate, becoming warty with age; cross section cylindrical, regular, some species developing vascular cylinders within the cortex in older stems; exudate watery or whitish in a few species. Stipules minute, early deciduous. Leaves alternate, trifoliolate; petioles and petiolules unwinged; leaflets coriaceous. Inflorescences axillary, umbel-like or racemiform thyrses, with lateral cincinni, sometimes bearing tendrils, cauliflorous in a few species. Flowers actinomorphic; calyx cup-shaped with 5 distinct sepals; petals 5, distinct, spatulate, auriculate or with a petaloid appendage; disc annular; stamens 6–8, the filaments of equal length, free; ovary 3-locular, each locule with a single ovule. Fruit a schizocarp, splitting into 3, samaroid mericarps with a distal wing (Figure 225A). Seeds subglobose, not arillate.
**Distinctive features:** Actinomorphic flowers; mature stems with cortical vascular cylinders of different diameters.

**Distribution:** About 13 species from southern Mexico, Central America and South America, with its center of distribution in southern tropical South America; moist forest, riparian seasonally flooded forests, or in seasonal dry forests; 150–550 (–1,800) m.


Herbaceous or slightly woody tendrilled vines, or decumbent subshrubs. Stems terete and lenticellate, in some species becoming 3-lobed with age; cross section: deeply 2- or 3-lobed, *U. stipularis* with phloem wedges, *U. laevis* with fissured stems, and *U. filipes* with successive cambia (Ferrucci 2020, Neto et al. 2023); exudates clear or whitish. Stipules minute, deciduous or persistent.

Leaves trifoliolate, exceptionally simple; petioles unwinged. Inflorescence a thyrse with closely spaced cincinni. Flowers zygomorphic, bisexual. Calyx of 5 unequal sepals; petals 4, distinct, usually < 4 mm long, spatulate, with an adnate, hood-shaped appendage on adaxial surface; disk unilateral, 4-lobed, receptacle enlarged into a short androgynophore. Stamens 8; filaments unequal; anthers usually with an apical expansion of the connective. Ovary of 3 uniovular carpels; style terminal with 3 stigmatic branches. Fruits thin, papery, semi-inflated capsules, with
narrow marginal wing. Seeds subglobose, black, with a heart-shaped or reniform white arillode around the hilum; embryo with the abaxial cotyledon bent over the biplicate adaxial cotyledon.

**Distinctive features**: Capsules thin, papery, carpels with a narrow marginal wing; seeds subglobose, black, with a heart-shaped or reniform white pseudo-hilum.

**Distribution**: A genus of ~20 species, 18 of which are climbers and 17 of which occur in the Neotropics; Central America, South America (except Chile), and some of the Lesser Antilles, with its center of distribution in the Brazilian plateau; scrubs, savannas, secondary forests and forest edges; 0–1,800 m.