

THE VASCULAR FLORA OF LA SELVA BIOLOGICAL STATION,
COSTA RICA*
CYCLANTHACEAE

BARRY E. HAMMEL†

Department of Botany, Duke University,
Durham, North Carolina 27706

HARLING, G. 1958. Monograph of the Cyclanthaceae. Acta Horti Berg. 18: 1-428.

Monoecious, perennial, often palmlike herbs either terrestrial, rooted in the ground and climbing or wholly epiphytic; stems either stout, often tough and liana-like or more or less acaulescent. *Leaves* distichous or spirally arranged; blades mostly bifid, 1-, 2-, or 3-costate, rarely palmately divided or entire; petioles flattened above, with or without a narrow groove, or rarely terete, basally sheathing. *Inflorescence* an unbranched pedunculate spadix enclosed by 2-11 usually deciduous spathes. *Flowers* densely congested with either each floral group consisting of a central pistillate flower surrounded by four staminate flowers or fused in alternate staminate and pistillate whorls and the individual flowers not discernible; the staminate with an inconspicuous perianth of several resinous knobs or finger-like projections arising from the margin of the flat-

topped or funnel-shaped receptacle, the stamens numerous, longitudinally dehiscent; the pistillate 4-parted; tepals coriaceous, basally each bearing adaxially a conspicuous filamentous staminode, the stigmas forming a cross diagonal to, and sometimes projecting between, the corners of the square formed by the tepals. *Fruits* partially or completely fused, together forming a cylindrical or sometimes globose syncarp (often circumcissilely dehiscent); seeds small, narrowly elliptic to ovoid, flattened or terete, mucilaginous, numerous.

A neotropical family of ten genera and approximately 200 species found almost exclusively in mid to low elevation, wet primary forest from southern Mexico to southeastern Brazil. Presumably most are pollinated by beetles and small weevils attracted to strong, sweet floral fragrances.

KEY TO THE GENERA

1. Leaf blades deeply bifid nearly to the base, each segment with a conspicuous major central costa running its entire length; spadix a cylinder of rings each formed by alternating staminate and pistillate whorls, the individual flowers not evident; plants terrestrial, usually acaulescent. 3. *CYCLANTHUS*.
1. Leaf blades entire to deeply lobed, lateral costae absent or disappearing well below the tip of the segment; spadix a cylinder or sphere of tightly packed but distinct staminate and pistillate flowers; plants usually epiphytic and caulescent or occasionally terrestrial and acaulescent.
 2. Petioles mostly 1.5 to 2.5 m long, terete; leaf blades palmately divided into 4 segments, the segments deeply (5-10 cm) and regularly lobed; surface of the mature spadix irregularly splitting and recurving to reveal the bright orange seed pulp. 2. *CARLUDOVICA*.
 2. Petioles less than 1 m long, flattened above; leaf blades entire or bifid, not lobed; surface of mature spadix neither splitting nor recurving.
 3. Leaf blades always entire; fruiting spadix nearly smooth, the pistillate flowers embedded in the rachis. 6. *LUDOVIA*.
 3. Leaf blades of mature individuals bifid; fruiting spadix not smooth, the pistillate flowers protruding.
 4. Leaves distichous, 1-costate; anthers with apical secretion globules; canopy epiphytes. 7. *SPHAERADENIA*.
 4. Leaves spirally arranged, 1- or 3-costate; anthers without secretion globules; climbing or terrestrial plants.
 5. Spathes attached irregularly to about the middle of the peduncle or somewhat clustered but not immediately subtending the spadix; leaves 1- or 3-costate. 1. *ASPLUNDIA*.
 5. Spathes all attached immediately below the spadix; leaf blades 1-costate.

* ROBERT L. WILBUR, Flora Editor, Department of Botany, Duke University, Durham, North Carolina 27706.

† Present address: Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299.

6. Tepals truncate, not incurved, about the same height as or shorter than the stigmas, the pistillate flowers distant; leaves not scabrous; plants terrestrial, often epipetric, nearly acaulescent or rarely climbing for a short distance up tree trunks. . . . 4. *DICRANOPYGIUM*.
6. Tepals of pistillate flowers acute, exceeding the stigmas and curving inward above them; pistillate flowers congested, leaves scabrous when dry; plants climbing, viny and never epipetric. . . . 5. *EVODIANTHUS*.

1. *ASPLUNDIA* Harling

Root-climbing or terrestrial, somewhat palm-like plants. *Leaf* blades usually longer than broad, always bifid, 1- to 3-costate; petiole usually about the same length as the blade, flattened and usually narrowly grooved above. Spathes 3-6(8), dispersed along the rachis; *spadix* usually cylindrical, most often bright yellowish orange at maturity. *Staminate flowers* symmetrical and funnel-shaped or more typically asymmetrical with the pedicel to one side of the receptacle, the sta-

minate perianth reduced to glandular protuberances along the edge of the receptacle, the stamens numerous; *pistillate flowers* with stigmas linear to ovoid as seen from above, their styles either distinct and fused or lacking. Separate *fruits* of the mature spadix partially embedded in the rachis, the free portion regularly dehiscent circumscissilely with the "caps" falling away to reveal seeds still attached to the placentas; seeds ovate-elliptic, flattened, lustrous.

Approximately 90 species from southern Mexico to southeastern Brazil.

KEY TO THE SPECIES

1. Leaf blades 1-costate, the divisions much longer than broad; stems loosely climbing; staminate flowers symmetrical.
 2. Spadix cylindrical; tepals of pistillate flowers entire, dorsally subtended by accrescent appendages; spathes scattered along the rachis; petioles and lower surface of leaves (especially along the nerves) spotted with rusty scales. . . . 8. *A. vagans*.
 2. Spadix ovoid-globose; tepals 3-lobed, dorsal appendages lacking; spathes clustered above the middle of the peduncle; leaves lacking scales. . . . 5. *A. multistaminata*.
1. Leaf blades 3-costate (lateral costae sometimes on the leaf margin), the divisions nearly as broad as long; stems usually appressed throughout if climbing; staminate flowers asymmetrical.
 3. Plants terrestrial.
 4. Leaf blades bifidly divided for less than 1/2 their length; spathes cream; fruiting spadix cylindrical, erect or horizontal; plants caulescent, very common. . . . 7. *A. uncinata*.
 4. Leaf blades bifidly divided for about 3/4 their length; spathes pink; fruiting spadix globose, pendent and often touching the ground; plants acaulescent, occasional. . . . 6. *A. sleeperae*.
 3. Plants climbing.
 5. Epidermis at base of petiole shiny and cracking in dried material, bright yellow or yellowish tan.
 6. Lateral costae borne on the leaf margin for most of their length; petiole grooved, often longer than the blade; tepals of pistillate flowers fused for 2/3 their length. . . . 2. *A. costaricensis*.
 6. Lateral costae borne well inside the leaf margin; petiole not grooved, equal to or shorter than the blade; tepals free. . . . 1. *A. antioquiæ*.
 5. Epidermis at base of petiole dull, not shiny and brittle in dried material, the surface scurfy, brownish or pink.
 7. Lateral costae borne on the leaf margin for short distance at the base; stigmas not laterally compressed, ovoid; leaf blades divided for about 3/4 their length. . . . 4. *A. ferruginea*.
 7. Lateral costae always well inside the leaf margin; stigmas laterally compressed; leaf blades bifidly divided for no more than 2/3 their length.
 8. Leaf blades bifidly divided for less than 1/2 their length; stigmas linear, uncinata and protruding between the tepals; base of staminode inconspicuous. . . . 7. *A. uncinata*.
 8. Leaf blades bifidly divided for 2/3 their length; stigmas elliptic, facing inward; base of staminode conspicuous and persistent in fruit. . . . 3. *A. euryspatha*.

1. *Asplundia antioquiæ* Harling

Stout-stemmed climbers. *Leaf* blades 3-costate, 65-80 cm long, narrowed and decurrent at the base for about 5 cm, bifid to 2/3 their length, the divisions 15-20 cm wide; petiole to 70 cm long. Young *fruiting spadix* 4-8 cm long, 2-3 cm

thick; tepals much longer than the stigmas; stigmas ovoid. Flowering (3-4 m above ground) and fruiting in the rainy season, July through December. Costa Rica, Panama and Colombia.

Locally uncommon species and apparently restricted to the northern portion of the property. Several individuals, probably of this species, grow

as wholly terrestrial plants on the "cloud forest" ridge just west of the far southwest corner.

2. *Asplundia costaricensis* Harling

Stout-stemmed climbers. *Leaf* blades 3-costate, 60–70 cm long, acute at the base, bifid between $\frac{2}{3}$ and $\frac{3}{4}$ their length, the divisions 10–20 cm wide; petiole 60–70 cm long. *Flowering spadix* 5–6 cm long, 1.5–2 cm thick; tepals longer than the stigmas; stigmas ovoid; facing inward. Flowering 4–10 m above ground, mostly near the end of the wet season and early in the dry season, September through February. Honduras south into Panama.

The most common and highest growing epiphytic *Asplundia* at La Selva, where it can be found in primary forest throughout the property. Its rather widely divergent leaf divisions, dark green leaves and relatively long petioles make *A. costaricensis* distinctive even from a distance. Except for the shiny yellow or tan and cracking epidermis of the petiole base, *A. costaricensis* is very similar to *A. ferruginea*. Although the two can be found in the same habitat and even sometimes on closely adjacent trees, they do not appear to hybridize perhaps because *A. costaricensis* usually flowers a few months earlier than *A. ferruginea*.

3. *Asplundia euryspatha* Harling

Stout-stemmed climbers. *Leaf* blades 3-costate, 60–85 cm long, narrowed and decurrent at the base for about 10 cm, bifid for $\frac{1}{2}$ to $\frac{2}{3}$ their length, the divisions 12–17 cm wide; petiole 50–65 cm long, narrowly grooved at summit. Spathes often purple tinged, the lower most persistent into early fruiting stage; young *fruiting spadix* 5–7 cm long, 1.5–2 cm thick. Tepals same height as stigmas at anthesis but in later stages the stigmas extending well above the tepals; base of staminode persistent and conspicuous in fruit, equal in length to the subtending tepal. Flowering 3–4 m above ground, late in the rainy season, August through November. Costa Rica and western Panama.

Occasional throughout the forest but most often found along streams and in low, somewhat swampy forested areas. It is always a very robust plant and because of its size and leaf venation might be mistaken for *Asplundia antioquiiae*. Even vegetatively, however, *A. euryspatha* differs quite markedly from that species in having a dull, somewhat scurfy rather than shiny and cracking petiole base. In fact, the dull purplish tinge of the petiole base in this species makes it unique among all La Selva epiphytic cyclanths.

4. *Asplundia ferruginea* Grayum & Hammel

Stout-stemmed climbers. *Leaf* blades 3-costate, 40–60 cm long, acute at the base, bifid for $\frac{2}{3}$ to $\frac{3}{4}$ their length, the divisions 8–10 cm wide; petiole 20–30 cm long, narrowly grooved at the summit, dull and brownish scurfy at the base. Spathes white internally, brownish scurfy externally; *flowering spadix* about 5 cm long, 2 cm thick. Tepals about the same height as the stigmas; stigmas ovoid, facing inward. Flowering 3–5 m above ground, in middle of dry season, February to April. Costa Rica and Panama.

Common and widespread in primary forest usually on slopes and ridges. Vegetatively it is quite similar to *Asplundia uncinata*, which also bears brownish scurf on the petioles. The latter, however, is only rarely epiphytic at La Selva and the lateral costae of its leaves are never on the margin. Apparently *A. ferruginea* is closely related to *A. costaricensis* from which it differs primarily in having a dull rather than shiny and cracking petiole base.

5. *Asplundia multistaminata* Harling

Viny-stemmed climbers. *Leaf* blades 1-costate, to 30 cm long, bifid for $\frac{3}{6}$ their length, the divisions 3–4 cm wide; petioles to about 20 cm long, shallowly grooved at the summit. Spathes persisting into the fruiting stage, clustered near the spadix; *fruiting spadix* ovoid, 4–5 cm long, 3 cm thick. Tepals 3-lobed. Flowering in the dry season, 2–6 m above ground, fruiting specimens seen from May and June. Costa Rican endemic.

Known at La Selva from only three collections along the Río Puerto Viejo. The plants become quite large; their many, intertwined stems and outstretched leaves festooning the lower tree trunks. Vegetatively *Asplundia multistaminata* might be confused with *A. vagans* or *Evodianthus funifer*. From both it differs in having narrower leaf divisions and lacking brownish scales along the veins of the lower leaf surface. The only other *Asplundia* at La Selva with 3-lobed tepals, *A. sleeperae*, is otherwise very different; in Harling's classification the two belong to different subgenera.

6. *Asplundia sleeperae* Grayum & Hammel

Terrestrial, acaulescent plants to 1.5 m tall. *Leaf* blades 3-costate, 65–90 cm long, not or only slightly decurrent at the base, the lateral costae running well inside the margin of the blade or rarely on the margin at the base, blades bifid for $\frac{2}{3}$ to $\frac{3}{4}$ their length, the divisions 15–25 cm wide; petiole about as long as the blade, narrowly grooved at the summit, dull olive green at base.

Spathes thin, pink; *fruiting spadix* ovoid. Tepals 3–4, 3-lobed, shorter than the stigmas; staminode base persistent, bulbous, conspicuous; stigmas ovoid, distant. Costa Rica. Flowering at the end of the dry season and during the rainy season, May through August. Costa Rica and Panama.

At La Selva nowhere abundant but found throughout most of the primary forest, especially in low areas and slopes along streams. The broad dark green leaves are more rounded and appear somewhat jagged or wavy along the margin distinguishing *Asplundia sleeperae* from the more abundant *A. uncinata*. Although *A. sleeperae* shares the unusual feature of 3-lobed tepals with the sympatric *A. multistaminata*, its 3-costate leaves and asymmetrical staminate flowers place it in a different subgenus.

7. *Asplundia uncinata* Harling

Stout-stemmed terrestrial plants to 1.25 m tall. *Leaf* blades 3-costate, 60–70 cm long, narrowed and slightly decurrent at the base, bifid for less than ½ their length, the divisions 12–15 cm wide; petiole about 45 cm long, narrowly grooved towards the summit, dull brownish scurfy at the base. Spathes scurfy with brownish scales; *fruiting spadix* 8 cm long, 2.5 cm thick. Tepals lower than the stigmas; stigmas laterally flattened, their tips protruding between the tepals and pointing downwards; stamens drying with a bluish or gray green tinge. Flowering in the rainy season, from May through December. Caribbean lowlands of Costa Rica and Panama.

Only the palm *Asterogyne martiana* approximates the abundance and ubiquity of *Asplundia uncinata* as a conspicuous understory plant at La Selva. The two are similar in habit and appear to replace each other ecologically with *Asterogyne* growing in lower areas and *Asplundia* growing on better-drained slopes and ridges. In such areas *A. uncinata* often forms breast-high thickets. Plants rarely climb a few meters up trunks but can be distinguished from other 3-costate climbers at La Selva by the leaf blades being bifid for less than one-half their length.

8. *Asplundia vagans* Harling

Viny-stemmed climbers. *Leaf* blades 1-costate, 45–60 cm long, bifid for ⅔ to ¾ their length, the divisions 4–8 cm wide; petiole 20–30 cm long, narrowly grooved above; lower surface of leaves and petioles lightly spotted with loose brown scales. *Fruiting spadix* 4–6 cm long, 1.5–2 cm thick. *Pistillate flowers* surrounded by a whorl of tissue; stigmas elliptic, sulcate (at least in age), somewhat uncinata and projecting be-

tween the tepals. Flowering 2–4 m above ground, March through August. Guatemala to Peru.

Occasional throughout the forest. It is the only frequently encountered, narrow leaved (1-costate) *Asplundia*. *Asplundia vagans* belongs to an apparently natural subgroup within the genus, characterized, in part, by the radially symmetrical staminate flowers and by the unusual whorl of tissue surrounding the pistillate flowers.

2. CARLUDOVICA Ruiz & Pavon

Terrestrial, usually acaulescent, palmlike plants to 2.5 m tall. *Leaf* blades 3-costate, as wide as long or wider, palmately divided into 4, wedge-shaped segments, the tips of the segments coarsely dentate; petioles terete, much longer than the blade. Spathes 3–4, densely clustered just below the spadix; *spadix* long cylindrical. *Staminate flowers* symmetrical, the pedicel about as broad as the receptacle. *Pistillate flowers* somewhat connate; tepals distinct and of varying lengths, stigmas laterally compressed or ovoid, styles raised or the stigmas sessile. Mature *fruiting spadix* irregularly splitting from the rachis to reveal the bright orange fleshy interior; seeds ovoid to globose, angled, not flattened.

Four species of *Carludovica* are known ranging from Mexico to Bolivia with all four species occurring in Costa Rica. The manner in which the inflorescences of *Carludovica* dehisce is unique in the family.

KEY TO THE SPECIES

1. Stigmas not sulcate, even in fruiting stages; linear and uncinata curved, borne on laterally flattened styles; stamens 20–30; leaf blades deeply 4-parted only in mature leaves. 1. *C. rotundifolia*.
1. Stigmas deeply sulcate, especially in fruiting stages, linear but horizontal and each borne on an ovate or rectangular style; stamens 50–90; leaf blade deeply 4-parted even in immature leaves. 2. *C. sulcata*.

1. *Carludovica rotundifolia* Wendl. ex Hook. f.

Terrestrial, acaulescent plants to 2.5 m tall. Segments of *leaf* blades about 75 cm long, 25 cm wide, dividing the blade to within 5 cm of the base, light green; teeth of the segments to 14 cm long, 2–3 cm wide; petiole to 2.5 m long. Spathes 3; *spadix* to 12 cm long. *Staminate flowers* with about 15 tepals each and 20–30(60) stamens, the anthers 1.2 mm long. *Pistillate flowers* with the tepals about 3 mm long; stigmas convex, curved laterally, flattened and somewhat uncinata at least in early stages. Flowering middle rainy season, July. Honduras south into Panama.

At La Selva known only from steep wooded banks along the Sarapiquí River on the Western Annex. *Carludovica rotundifolia* was originally confused with the locally more abundant species but can be distinguished even vegetatively by its lighter green leaves that are four parted only in mature leaves. In Costa Rica *C. rotundifolia* appears to be more common at higher elevation.

2. *Carludovica sulcata* Hammel

Terrestrial, acaulescent plants to 2.5 m tall. Segments of the *leaf* blades about 75 cm long and 25 cm wide, dividing the blade to within 5 cm of the base, dark green; teeth of the segments to 10 cm long, 2–3 cm wide. Spathes 3; *spadix* to 12 cm long. *Staminate flowers* with 20–25 tepals, stamens 50–90, anthers 1.2 mm long. *Pistillate flowers* with the tepals about 4 mm long; stigmas more or less linear but deeply sulcate, spreading wide in fruit, mounted on the ovate or rectangular-inflated style, not uncinat. Flowering in mid rainy season, July and August. Nicaragua and Costa Rica.

Locally common in the shade of old secondary woods and somewhat disturbed habitats such as steep banks along streams in the forest; it has not yet been found with *Carludovica rotundifolia*.

3. *CYCLANTHUS* Poit.

Terrestrial usually acaulescent plants to 3 m tall. Mature *leaf* blades deeply bifid nearly to the base (rarely undivided), each segment with a strong central costa running to the tip of the segment; petiole about as long as the blade, terete, with scant to copious milky sap. Spathes 4, attached near the base of *spadix*, thick and leathery; *spadix* cylindrical with staminate and pistillate flowers in alternate horizontal whorls (sometimes spirals), the individual flowers not discernible. Mature *fruiting spadix* greenish yellow, the pistillate cycles swelling and splitting to expose the seeds, the *spadix* finally breaking up into disks; seeds ovoid to globose, long stalked and longitudinally ribbed.

Although most authors consider *Cyclanthus* to be a monotypic genus, the genus is quite variable in vegetative characters and some of the variation is geographically restricted.

1. *Cyclanthus bipartitus* Poit.

Terrestrial acaulescent plants to 3 m tall. Mature *leaves* bifid nearly to the base, the juvenile leaves undivided. Plants flowering even when only 1 m tall. Flowering at the end of the dry season, April to May. Mexico south to Peru.

Characteristic of the wet lowland tropics. The large beetle, *Cyclocephala atripes* Bates, may be a specialist pollinator of this plant (BEACH, J. H. 1982. Amer. J. Bot. 69: 1074–1081). Unlike most other species in the family, the fruits do not appear to develop any visual display suggestive of animal dispersal. Harling (1958) considered ants the most likely agents of dispersal.

4. *DICRANOPYGIUM* Harling

Terrestrial or occasionally root-climbing a short distance, mostly acaulescent plants less than 1 m tall. *Leaf* blades 1-costate (rarely 3-costate elsewhere), bifid; petiole about the same length as the blade, flattened above. Spathes 2–4, all crowded just below the *spadix*; *spadix* cylindrical, rarely ovoid, few-flowered. *Staminate flowers* asymmetrical, the pedicel attached to one side of the receptacle; *pistillate flowers* connate; tepals reduced to low fleshy ridges; stigmas ovoid or slightly compressed laterally, styles short or lacking. *Fruiting spadix* gray green at maturity, eventually rupturing irregularly along the thin walled tissue at the base of the tepals; seeds elliptic, terete, mucilaginous, containing starch.

Dicranopygium, a genus of about 50 species, ranges from southern Mexico to central Peru.

Species in this genus are often abundant on rocks in small streams and seem to have especially tough leaves; they withstand frequent torrential flooding. The seeds may be either torrent- or perhaps fish-dispersed. Pressure appears to build up in the *spadix* at maturity and a puncture at the base of the tepals causes the seeds to spurt out.

KEY TO THE SPECIES

1. Leaves mostly 5–7.5 cm wide, divided for $\frac{1}{2}$ to $\frac{3}{5}$ their length, dark green; peduncles purplish, scurfy; stigmas narrowly oblong; plants growing in the forest. 1. *D. umbrophila*.
1. Leaves mostly 3.5–4.5 cm wide, divided for $\frac{2}{3}$ to $\frac{3}{4}$ their length, light green; peduncles green, glabrous; stigmas ovate; plants growing on steep banks along river, on rocks in and along fast moving streams. 2. *D. wedelii*.

1. *Dicranopygium umbrophila* Hammel

Terrestrial or sometimes climbing, caulescent plants usually about 50 cm tall. *Leaf* blades 30–45(47) cm long, 1-costate, bifid for $\frac{1}{2}$ to $\frac{3}{5}$ their length, the divisions (4)5–7.5(10) cm wide; petiole 30–50 cm long, purple brown, scurfy below. Peduncle 3–7 cm long at anthesis, (7)17–19(30) cm long in fruit, purple and covered with brownish scurf below. Spathes 2, 3.5–4.5 cm long,

purplish within. Receptacle of the *staminate flowers* flat, the perianth lobes (4)6–7(9), the stamens (20)24–32(35), the anthers 0.9–1.1(1.3) mm long, 0.5–0.6 mm wide, filaments no more than 0.1 mm long; basal bulbs large, globose; tepals of the *pistillate flowers* truncate, connate at least in later stages, shorter than the stigmas, 5–8 mm wide in fruit; stigmas narrowly oblong, sometimes slightly projecting through the tepals, about 3 mm long in fruit, the actual stigmatic crest linear. *Fruiting spadix* 3–4.5 cm long, 1–1.5 cm thick. Flowering throughout the year. Costa Rica.

Most species of *Dicranopygium* grow in close proximity to streams (fide Harling, 1958) but *D. umbrophila* is common in the forest understory. It is met with most frequently in swamp forest where it is often seen to climb on fallen logs or a short distance up tree trunks.

2. *Dicranopygium wedelii* Harling

Terrestrial or epipetric, nearly acaulescent plants about 20–60 cm tall. *Leaf* blades (15)20–30(45) cm long, 1-costate, bifid for $\frac{2}{3}$ to $\frac{3}{4}$ their length, the divisions (2)3.5–4.5(6.5) cm wide; petiole (10)20–30(64) cm long, green at base. Peduncle 5–6(11) cm long at anthesis, (7)13–20 cm in fruiting stages; spathes 2, 3–5 cm long, pink or white. Stamens 25–35, the anthers oblong to ovoid, 0.7–1 mm long, 0.5–0.6 mm wide, basal bulbs large, globose; tepals of the *pistillate flowers* shorter than the stigmas, 6–8 mm long in fruit. Young *fruiting spadix* 1.5–3 cm long, 1 cm wide. Flowering throughout the year. Costa Rica and Panama.

This species is common and often abundant along streams and rivers, sometimes forming dense, knee-high growth on the rocks in streams. Unlike La Selva's other species, which occurs in low areas in the forest, it is restricted to the stream-side habitats.

5. *EVODIANTHUS* Oersted

Viny, root-climbing plants. *Leaf* blades 1-costate, bifid, the segments much longer than broad, scabrous when dry; immature leaves often undivided. Spathes 3, clustered just below the ovoid or globose spadix. *Staminate flowers* symmetrical, funnel-shaped, pedicellate; *pistillate flowers* not connate; tepals triangular, pointed, surpassing and curving inward over the stigmas, the stigmas laterally compressed when young, ovoid later in fruiting state. Mature *fruits* pale orange, the wall of the fleshy capsule falling away leaving the fleshy mass of seeds exposed but embedded in the rachis; seeds oblong-elliptic, flattened.

Harling considered the genus to be monotypic

but with four subspecies differentiated mostly vegetatively and ranging from Costa Rica to Peru.

1. *Evodianthus funifer* (Poit.) Lindman

Viny, root-climbing plants. *Leaf* blades bifid for $\frac{2}{3}$ their length, the segments 4–5 cm wide, dark glossy green above, paler and dull below as a result of the embedded crystals that also make the leaves scabrous when dry, the petiole 30–40 dm long, flattened but not grooved above. *Spadix* ovoid-globose, 2.5–3 cm long, 0.5–2 cm thick. Flowering near the end of the dry season, March to April. Nicaragua south into Brazil.

Frequent and widespread throughout the forest especially on ridges and slopes. It might be confused, when sterile, with *Asplundia vagans*, La Selva's only other common viny, unicostate cyclanth. The ungrooved petiole and lack of brownish scales, however, are sufficient to distinguish it from that species. The leaves become scabrous when dry through the exposure of large embedded crystals. These reflect light in fresh material giving the leaves a bluish cast. Specimens from La Selva fit well within subspecies *funifer*.

6. *LUDOVIA* Brongn.

Viny, root-climbing plants reaching to mid-canopy and dangling in masses. *Leaves* distichous but distant, the blades undivided and 1-costate, the petiole shorter than the blade, wing-margined toward the summit. Spathes 3–5, irregularly dispersed along the upper half of the peduncle; *spadix* narrowly cylindrical to fusiform. *Staminate flowers* symmetrical, short pedicellate or sessile; *pistillate flowers* connate; the tepals barely visible at anthesis, later reduced to low indistinct ridges, the stigmas laterally compressed and uncinatate, the styles lacking. *Fruiting spadix* bright yellowish orange, an apparently indehiscent syncarp; seeds ovoid, provided with a caruncle.

Ludovia, a genus of three species, was previously known only from northwestern South America and eastern Panama. According to Harling, the distichous-leaved cyclanths, including *Ludovia*, *Sphaeradenia* and *Stelestylis*, form a natural group within the family.

1. *Ludovia integrifolia* (Woodson) Harling

Liana-like climbers, often dangling and thus in habit very much like certain aroids. *Leaf* blades about 20 cm long and 6 cm wide. *Fruiting spadix* about 6 cm long, 1 cm thick. Fertile branches borne as high as 25 m above ground

level. Flowering mostly during the rainy season. Nicaragua south into Ecuador.

Known from throughout the forest but not often found except in treefalls. It also occurs however, in secondary or remnant habitats, and occasionally is seen dangling close to the ground from old trees left standing in pastures. Because of its habit and leaf shape this plant is often mistaken for a species of Araceae. However, *Ludovia's* multiple spathes and strictly parallel venation arising from the base of the blade are unknown in the Araceae.

7. SPHAERADENIA Harling

Epiphytic or more typically terrestrial plants; stems short and stout or lacking. *Leaves* distichous, much longer than broad, the blades bifid and 1-costate, usually coriaceous; petiole shorter than the blade. Spathes 3–5, dispersed along the peduncle; *spadix* ovoid to cylindrical, at maturity often brightly colored, orange, red, or white. *Staminate flowers* mostly asymmetrical, the pedicel attached to one side of the receptacle, the anthers usually tipped with a small, dark bead-like secretion globule; *pistillate flowers* connate at least basally, the tepals distinct and of various lengths, the stigmas usually laterally compressed, the styles connate for most of their length, rarely lacking, the ovary more or less embedded in the rachis with a single or 4-parted placenta, with the top of the fruit dehiscing as a cap with the mucilaginous seed mass remaining on the rachis; seeds ovoid or elliptic, terete, often brightly colored, reddish orange to purple.

This, the third largest genus in the family, has about 40 species ranging from Nicaragua to southeastern Peru with the majority montane and occurring in northwestern South America. Since Harling's monograph (1958) which recognized a total of eight species north of South America at least nine additional species have been collected there.

KEY TO THE SPECIES

1. Leaf blades divided for about ¼ their length, gradually tapering to the winged petiole, divisions triangular, 5–7 cm wide. 1. *S. carrilloana*.
1. Leaf blades divided nearly to the base, abruptly attached at an acute angle to the unwinged petiole, divisions strap-shaped, 2 cm wide. 2. *S. pendula*.

1. *Sphaeradenia carrilloana* Grayum & Hammel

Nearly acaulescent epiphytes. *Leaves* to about 175 cm long, 10–20 cm wide, bifid for about 30 cm, the divisions 5–7 cm wide; blades gradually tapering to the base of the petiole, the distinction between blade and petiole thus more or less arbitrary. Spathes apparently 3, *fruiting spadix* to 9 cm long, 2.5 cm thick, bright orange at maturity, the stigmas laterally compressed, uncinate, slightly surpassed by the tepals, the placenta single and the ovary partially immersed in the rachis; seed mass remaining on the rachis at maturity after loss of fruit wall. Flowering towards the end of the rainy season about 10–25 m above the forest floor. Nicaragua south into Panama.

Occasional in trees along streams at La Selva where it is found mostly in the southeastern portion of the property.

2. *Sphaeradenia pendula* Hammel

More or less acaulescent pendent epiphytes. *Leaf* blades very thick, coriaceous, divided nearly to the base, the divisions 65–95 cm long, 1.5–2.5 cm wide; petiole 40–70 cm long. Spathes 3–4, the lowermost one to 14 cm long, 1 cm wide, acuminate; *flowering spadix* 3 cm long, 1 cm thick, in fruit to 8 cm long, 2.5 cm thick, green. *Staminate flowers* asymmetrical, 2.5 mm tall by 1.6 mm wide, stamens 20–25, the anthers 0.6–1.0 mm long, 0.4 mm wide, provided with a small secretion globule, the basal bulbs same diameter as the anthers; *pistillate flowers* separate to the base, the tepals connate at base in fruit; style about the same height as the tepals, the ovary distinctly protruding from the spadix at maturity, the separate *fruits* indehiscent; placentae four. Seeds elliptic, the funicular end blunt and mucilaginous and the chalazal with an acuminate appendage. Fertile as midcanopy epiphyte; flowering in the wet season, August. Caribbean lowlands of Costa Rica and Panama.

One of the most common and distinctive, high growing epiphytes at La Selva. The grayish green, very long, inverted Y-shaped leaves make these plants distinguishable even from great distances. The species is also unusual in being one of the few *sphaeradenia* species common at low elevations.